Capinera *Ed.*

Encyclopedia of Entomology

2nd Ed.

SPRINGER REFERENCE

John L. Capinera
Editor

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2nd Edition

Springer

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Edited by
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University of Florida

Second Edition

Volume 4
S–Z

Springer

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Library of Congress Control Number: 2008930112

ISBN: 978-1-4020-6242-1
This publication is available also as:
Electronic publication under ISBN 978-1-4020-6359-6 and
Print and electronic bundle under ISBN 978-1-4020-6360-2

springer.com

Editor: Zuzana Bernhart, Dordrecht/ Sandra Fabiani, Heidelberg
Development Editor: Sylvia Blago, Heidelberg
Production Editor: le-tex publishing services oHG, Leipzig
Cover Design: Frido Steinen-Broo, Spanien

Printed on acid-free paper SPIN: 11757993 2109 — 5 4 3 2 1 0

Editorial Board

Acknowledgments

This project is the labor of many people, including some who labored diligently behind the scenes. Among those to whom I am greatly indebted for their 'behind-the-scenes' assistance are Pam Howell and Carole Girimont (first edition) and Pam Howell (second edition) for document processing and editing assistance; Mike Sanford, Pat Hope, and Jane Medley (first edition) and Hope Johnson (second edition) for assistance with the images, and Marsha Capinera for compiling the list of contributors. Ron Cave, Andrei Sourakov, and Lyle Buss helped greatly by supplying numerous photographs for the second edition.

Howard Frank deserves special mention for his editing acumen and assistance. Drion Boucias contributed the lengthy unattributed sections on insect pathology. The unattributed biographic sketches with last names beginning with A to J were contributed by Howard Frank. All other unattributed sections were contributed by John Capinera.

Preface

Some biologists have called this the 'Age of Insects.' Among animals, certainly the diversity of insects is unrivaled. Nearly one million species have been described to date, and some entomologists estimate that as the tropics are fully explored, we will find that there are actually more than three million insect species. The large number of insects is often attributed to the divergence of plants (angiosperms), which provide numerous hosts and places to feed, but if plant feeders are excluded from the tabulation the biodiversity of insects remains unrivaled. Virtually every environment has been exploited by these resilient organisms. Even if one dislikes insects, they are impossible to ignore, and a little knowledge about them could be indispensable should one have a 'close encounter' of an unpleasant kind.

Insects are remarkable biological organisms. They are small enough to escape the detailed scrutiny of most people, but I have yet to meet anyone whom, once provided the opportunity to examine insects closely (through a microscope) is not completely amazed by the detail and complexity of these exquisitely designed (by natural selection) beasties. They are fascinating in function as well as form. Insects are the only invertebrates to fly, they are disproportionately strong, and their ecological adaptability defies belief. For example, some insects produce their own version of anti-freeze, which allows them to be frozen solid yet to regain normal function upon thawing. Their sensory abilities are beyond human comprehension; a male insect can sometimes locate a female by her 'perfume' (pheromone) from several kilometers distance. Although not normally considered intelligent, insects display surprisingly complex behaviors, and altruistic social systems that could well serve as models for human societies.

Insects and their close relatives are important for many reasons besides their sheer diversity. Their effect on humans is profound. Insects are our chief competitor for food and fiber resources throughout the world. Annual crop losses of 10 to 15% are attributed to insects, with both pre-harvest and post-harvest losses considerably more at times. Insects also are the principal vector of many human, animal, and plant diseases, including viruses, mollicutes, bacteria, fungi, and nematodes. The ability to transmit diseases magnifies their effect, and makes it more difficult to manage injury. Over the course of human history, insect-transmitted disease has caused untold human suffering. For example, introduction of flea-transmitted bubonic plague to Europe centuries ago killed millions of people and caused severe disruption to western civilization. Though less dramatic, mosquito-transmitted malaria kills thousands annually throughout the world, and unlike plague, which is now mostly a historical footnote, the toll continues to mount.

Advances in technology, particularly the introduction of chemical insecticides, have done much to remove the threat of insect-related damage from the consciousness of most humans. Insecticides are applied preventatively to avoid pre- and post-harvest damage to crops, to our dwellings, and to our landscape. This is an oft-overlooked but remarkable achievement that has increased stability in the supply and price of resources, and in the lives of resource producers. No longer are people faced with starvation or economic ruin due to the ravages of insects; in almost all parts of the world, the ready availability of insecticides can be used to prevent massive insect population outbreaks. However, we realize increasingly that this approach is not without its own set of health, environmental and economic costs, and alleviating dependency on insecticides, or making alternatives to insecticides more readily available, has assumed greater priority.

We are faced with an interesting dichotomy. There is a wealth of information about insects, but it is known mostly to 'insect scientists' (entomologists). The public (non-entomologists or 99.99% of all people) has little knowledge about insects, and poor access to vital information about these important organisms. So this encyclopedia is presented to bridge the gap – to better enable those with a need to know to find fundamental information provided by more than 450 experts in the field of entomology. We provide a broad overview of insects and their close relatives, including taxonomy, behavior, ecology, physiology, history, and management. Importantly, we provide critical links to the entomological literature, much of which presently is unavailable for search electronically. The contributors are distinguished entomologists from around the world. They hope that the availability of this encyclopedia will help others to reap the benefits of centuries of discovery, and to discover the wonders that make the study of insects so compelling. It was constructed with college and university students in mind, but others may find it a handy reference.

John L. Capinera, Gainesville (Florida) April, 2008

Highlights of the Encyclopedia of Entomology

Major Taxa of Insects and Their Near Relatives

Alderflies and Dobsonflies (Megaloptera)
Angel Insects (Zoraptera)
Bark-Lice, Book-Lice, or Psocids (Psocoptera)
Beetles (Coleoptera)
Bristletails (Archeognatha)
Bugs (Hemiptera)
Butterflies and Moths (Lepidoptera)
Caddisflies (Trichoptera)
Centipedes (Chilopoda)
Chewing and Sucking Lice (Phthiraptera)
Cockroaches (Blattodea)
Diplurans (Diplura)
Dragonflies and Damselflies (Odonata)
Earwigs (Dermaptera)
Fleas (Siphonaptera)
Flies (Diptera)
Gladiators (Mantophasmatodea)
Grasshoppers, Katydids, and Crickets (Orthoptera)
Lacewings, Antlions, and Mantispids (Neuroptera)
Mayflies (Ephemeroptera)
Millipedes (Diplopoda)
Mites (Acari)
Pillbugs and Sowbugs, or Woodlice (Isopoda)
Praying Mantids (Mantodea)
Proturans (Protura)
Rock Crawlers (Grylloblattodea)
Scorpionflies (Mecoptera)
Scorpions (Scorpiones)
Sea Spiders (Pycnogonida)
Silverfish (Zygentoma)
Snakeflies (Raphidioptera)
Spiders (Araneae)
Springtails (Collembola)
Stick and Leaf Insects (Phasmida)
Stoneflies (Plecoptera)
Stylopids (Strepsiptera)
Symphylans (Symphyla)
Termites (Isoptera)
Thrips (Thysanoptera)
Ticks (Ixodida)
Wasps, Ants, Bees, and Sawflies (Hymenoptera)
Webspinners (Embiidina)

Other Groups

Anagrus Fairyflies (Hymenoptera: Mymaridae)
Ants (Hymenoptera: Formicidae)
Aphids (Hemiptera: Aphididae)
Apoid Wasps (Hymenoptera: Apoidea: Spheciformes)
Argasid (Soft) Ticks (Acari: Ixodida: Argasidae)
Assassin Bugs, Kissing Bugs and Others (Hemiptera: Reduviidae)
Bark Beetles, *Dendroctonus* spp. (Coleoptera: Curculionidae: Scolytinae)
Bees (Hymenoptera: Apoidea: Apiformes)
Bess Beetles (Coleoptera: Passalidae)
Biting Midges, *Culicoides* (Diptera: Ceratopogonidae)
Black Flies (Diptera: Simuliidae)
Blister Beetles (Coleoptera: Meloidae)
Bulb Mites, *Rhizoglyphus* (Acari: Acaridae)
Burnet Moth Biology (Lepidoptera: Zygaenidae)
Brush-Footed Butterflies (Lepidoptera: Nymphalidae)
Butterflies (Lepidoptera: Rhopalocera)
Carpenter Bees (Hymenoptera: Apidae: Xylocopinae)
Carrion Beetles (Coleoptera: Silphidae)
Cicadas (Hemiptera: Cicadoidea)
Clearwing Moths (Lepidoptera: Sesiidae)

Stink Bugs (Hemiptera: Pentatomidae), Emphasizing Economic Importance
Tachinid Flies (Diptera: Tachinidae)
Tent Caterpillars, *Malacosoma* spp. (Lepidoptera: Lasiocampidae)
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Tiphiid Wasps (Hymenoptera: Tiphiidae)
Treehoppers (Hemiptera: Membracidae)
Underwing Moths –*Catocala* (Lepidoptera: Noctuidae)
Velvet Ants (Hymenoptera: Mutillidae)
Water Penny Beetles (Coleoptera: Psephenidae)
Weevils, Billbugs, Bark Beetles, and Others (Coleoptera: Curculionoidea)
Weta (Orthoptera: Anostostomatidae, Rhaphidophoridae)
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Abdomen of Hexapods
Antennae of Hexapods
Head of Hexapods
Internal Anatomy of Insects
Alimentary Canal and Digestion
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Mouthparts of Hexapods
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Nervous System
Eyes and Vision
Integument: Structure and Function
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Wing Coupling

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Reselin

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Baculoviruses
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Nosema locustae (Protozoa: Microsporidia)
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Notable and Pioneer Entomologists

Abafi-Aigner, Lajos (Ludwig Aigner)
Abbott, John
Agassiz, Jean Louis Rodolphe
Aldrovandi, Ulisse (Ulysse, Ulysses)
Alexander, Charles Paul
Amerasinghe, Felix P.
Andrewartha, Herbert George
Arnett, Jr., Ross Harold
Audinet-Serville, Jean-Guillaume
Audouin, Jean-Victor
Barber, Herbert Spencer
Bates, Henry Walter
Bates, Marston
Beck, Stanley Dwight
Beklemishev, Vladimir NikolayevicH
Bell, William J.
Becquaert, Joseph Charles
Berlese, Antonio
Bernhauer, Max
Bertram, Douglas Somerville
Bíró, Lajos
Blackburn, Thomas
Blackwelder, Richard Elliot
Blaisdell, Frank Ellsworth
Blatchley, Willis Stanley
Bodenheimer, Friedrich (Frederick) Simon
Bohart, Richard M.
Boheman, Carl Heinrich
Boisduval, Jean-Baptiste Alphonse Dechauffour
Bokor, Elemér
Bonnet, Charles
Borgmeier, Thomas
Bøving, Adam Giede
Brauer, Friedrich Moritz
Broun, Thomas
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Brues, II, Charles Thomas
Brullé, Gaspard Auguste
Brunner von Wattenwyl, Carl
Buffon, Georges Louis Leclerc (Comte de)
Burgess, Albert Franklin
Burmeister, Carl Hermann Conrad
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Cameron, Malcolm
Candèze, Ernest Charles Auguste
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Carter, Herbert James
Casey, Thomas Lincoln
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Chaudoir, Maximilien Stanislavovitch de
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Chapman, Reginald Frederick
Chevrolat, Louis Alexandre Auguste
Chiang, Huai C.
China, William Edward
Chittenden, Frank Hurlbut
Christophers, (Sir) Samuel Rickard
Cockerell, Theodor Dru Alison
Comstock, John Henry
Coquillett, Daniel William
Craw, Alexander
Cresson, Ezra Townsend
Criddle, Norman
Crotch, George Robert
Crowson, Roy Albert
Csiki, Erno (Ernst Dietl)
Curran, Charles Howard
Curtis, John
Cushman, Robert Asa
Cuvier, (Baron) Georges Léopold Chretien Frédéric Dagobert
Dahlbom, Anders Gustav

Darlington, Jr., Philip J.
Darwin, Charles
Davis, William Thompson
Debach, Paul
Degeer, Carl (Carolus, Karl, Charles)
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Emerson, Alfred Edwards
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Endrödy-Younga, Sebastian (Sebestyén Endrödy-Younga, Sebestyén Endrödy)
Erichson, Wilhelm Ferdinand
Esaki, Teiso
Evans, Howard Ensign
Fabre, Jean-Henri Casimir
Fabricius, Johann Christian
Fairchild, Alexander Graham Bell
Fairmaire, Léon
Fall, Henry Clinton
Fauvel, Charles Adolphe Albert
Felt, Ephraim Porter
Fenichel, Sámuel
Fennah, Ronald Gordon
Fernald, Charles Henry
Ferris, Gordon Floyd
Fischer Von Waldheim, Gotthelf
Fitch, Asa
Fletcher, James
Foote, Richard H.
Forbes, Stephen Alfred
Ford, Edmund Brisco
Forel, Auguste Henri
Fourcroy, Antoine-François (Comte de)
Frisch, K. von
Frivaldszky, Imre
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Froggatt, Walter Wilson
Gahan, Arthur Burton
Ganglbauer, Ludwig
Germar, Ernst Friedrich
Ghilarov, Mercury Sergeevich
Girault, Alexandre Arsène
Glover, Townend
Gmelin, Johann Friedrich
Goeldi, Emil (Emilio) August
Gorgas, William Crawford
Graham, Marcus William Robert de Vere
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Gravenhorst, Johan Ludwig Christian
Gressitt, Judson Linsley
Grote, Augustus Radcliffe
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Kellogg, Vernon Lyman
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Kevan, Douglas Keith McEwan
Kiesenwetter, Ernst August Hellmuth von
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Knipling, Edward Fred
Koebele, Albert
Kraatz, Ernst Gustav
Kring, James Burton
Lamarck, Jean-Baptiste
Latreille, Pierre André
Lea, Arthur Mills
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LeConte, John Lawrence
Leech, Hugh Bosdin
Lefroy, Harold Maxwell
Leng, Charles William
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Lindroth, Carl H.
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Linsley, Earle Gorton
Loew, Hermann
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Lugger, Otto
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Macquart, Pierre Justin Marie
Mallis, Arnold
Mann, William M.
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Metcalf, Clell Lee
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Meyrick, Edward
Miller, David
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Morgan, Thomas Hunt
Morrison, Herbert Knowles
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Müller, Johann Friedrich Theodor
Müller, Josef
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Needham, James George
Newell, Wilmon
Newman, Edward.
Newsom, Leo Dale
Olivier, Guillaume Antoine
Ormerod, Eleanor Anne
Osborn, Herbert
Osten Sacken, C.R.
Packard, Alpheus Spring
Painter, Reginald Henry
Palm, Thure
Pass, Bobby Clifton
Patch, Edith Marion
Paykull, Gustaf
Peairs, Leonard Marion
Peck, William Dandridge
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Pickett, Allison Deforest
Pomerantsev, Boris Ivanovich
Potter, Charles
Prokopy, Ronald J.
Provancher, (l'abbé) Léon

Putzeys, Jules Antoine Adolphe Henri
Rabb, Robert Lamar
Radoshkowsky, Octavius John
de Réaumur, René Antoine Ferchault
Redi, Francesco
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Reed, Walter.
Rehn, James Abram Garfield
Reitter, Edmund
Remington, Charles Lee
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Richards, Owain Westmacott
Riley, Charles Valentine
Robineau-Desvoidy, Jean Baptiste
Rondani, Camillo
Rosen, David
Ross, Herbert Holdsworth
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Roubal, Jan
Sabrosky, Curtis
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Sailer, Reece I.
Sanderson, Dwight
Saunders, William
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Say, Thomas
Scheerpeltz, Otto
Schneiderman, Howard Allen
Schwarz, Eugene Amandus
Scudder, Samuel Hubbard
Selys-Longchamps, Michel Edmond de
Sharp, David
Shelford, Victor Ernest
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Smith, John Bernhardt
Smith, Harry Scott
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Snodgrass, Robert Evans
Snow, Francis Huntington
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Stern, Vernon M.
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Szent-Ivány, József Gyula Hubertus
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Thomson, Carl Gustav
Thunberg, Carl Peter
Tillyard, Robin John
Torre-Bueno, José Rollin De La
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Treherne, John E
Uhler, Philip Reese
Usinger, Robert Leslie
Uvarov, (Sir) Boris Petrovich
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Varley, George C
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Walsh, Benjamin Dann
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Wasmann, Erich
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Westwood, John Obadiah
Wheeler, William Morton
Wiedemann, Christian Rudolph Wilhelm
Wigglesworth, (Sir) Vincent Brian
Williams, Carroll Milton
Williston, Samuel Wendell
Wirth, Willis Wagner
Wolcott, George N.
Wollaston, Thomas Vernon
Young, Jr., David A
Zeller, Philipp Christoph
Zetterstedt, Johann Wilhelm
Zachvatkin (Jasykov), Aleksei Alekseevich

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Filth Fly Parasitoids (Hymenoptera: Pteromalidae) in North America
Carabid Beetles (Coleoptera: Carabidae) as Parasitoids
History of Biological Control of Wheat Stem Sawflies (Hymenoptera: Cephidae)
Parasitism of Lepidoptera Defoliators in Sunflower and Legume Crops, and Adjacent Vegetation in the Pampas of Argentina
Transmission of Plant Diseases by Insects
Plant Viruses and Insects
Management of Insect-Vectored Pathogens of Plants
Transmission of *Xylella fastidiosa* Bacteria by Xylem-Feeding Insects
Vectors of Phytoplasmas

Pesticides and Pesticide Application

Acaricides or Miticides
Boric Acid
DDT
Insecticides
Insecticide Application: The Dose Transfer Process
Food-Based Poisoned Baits for Insect Control
Soil Fumigation
Structural Fumigation
Insecticide Bioassay
Insecticide Formulation
Insecticide Resistance
Insecticide Toxicity

Pesticide Hormoligosis
Synergism
Chronotoxicology
Detoxification Mechanisms in Insects
Enhanced Biodegradation of Soil-Applied Pesticides
Pesticide Resistance Management
Natural Products Used for Insect Control
Botanical Insecticides
Chinaberry, *Melia azedarach*, a Biopesticidal Tree
Pyrethrum and Persian Insect Powder
Neem
Horticultural Oils
Soaps as Insecticides
Diatomaceous Earth
Photodynamic Action in Pest Control and Medicine
Neurological Effects of Insecticides and the Insect Nervous System
Regulations Affecting Use of Pesticides

Pests Groups and Their Management

Agricultural Crop Pests in Southeast Asia Including South China
Alfalfa (Lucerne) Pests and Their Management
Apple Pests and Their Management
Banana Pests and Their Management
Bark Beetles in The Genus *Dendroctonus*
Cassava Pests and Their Management
Citrus Pests and Their Management
Coffee Pests and Their Management
Crucifer Pests and Their Management
Desert Locust, *Schistocerca gregaria* Forskål (Orthoptera: Acrididae) Plagues
Grasshoppers and Locusts as Agricultural Pests
Grasshoppers of the Argentine Pampas
Grasshopper and Locust Pests in Africa
Grasshopper and Locust Pests in Australia
Grasshopper Pests in North America
Gramineous Lepidopteran Stem Borders in Africa
Mahogany Pests and Their Management
Maize (Corn) Pests and Their Management
Mite Pests of Crops in Asia
Musk Thistle Suppression Using Weevils For Biological Control
Palm Insects
Pests and Their Natural Enemies (Parasitoids and/or Predators) in The Middle East
Potato Pests and Their Management
School IPM, or Pest Management on School Grounds
Shade Tree Arthropods and Their Management
Small Fruit Pests and Their Management
Stored Grain and Flour Insects and Their Management
Sugarcane Pests and Their Management
Sweetpotato Weevils and Their Eradication Programs in Japan
Tropical Fruit Pests and Their Management
Turfgrass Insects of the United States and Their Management
Urban Entomology
Vegetable Pests and Their Management
Veterinary Pests and Their Management
Wheat Pests and Their Management
Whitefly Bioecology and Management in Latin America
Wood-Attacking Insects

Medical and Veterinary Entomology

African Horse Sickness Viruses
Argasid (Soft) Ticks (Acari: Ixodida: Argasidae)
Avian (Bird) Malaria
Bed Bugs (Hemiptera: Cimicidae: *Cimex* spp.)
Biting Midges, *Culicoides* spp. (Diptera: Ceratopogonidae)
Black Flies Attacking Livestock: *Simulium arcticum* Malloch and *Simulium luggeri* Nicholson & Mickel (Diptera: Simuliidae)
Bluetongue Disease
Bovine Hypodermosis: Phenology in Europe
Brown Dog Tick, *Rhipicephalus sanguineus* (Latreille) (Acari: Ixodida: Ixodidae)

Arthropods of Economic Importance

American Grasshopper, *Schistocerca americana* (Drury) (Orthoptera: Acrididae)
Almond Seed Wasp, *Eurytoma amygdali* Enderlein (Hymenoptera: Eurytomidae)
American Serpentine Leafminer, *Liriomyza trifolii* (Burgess) (Diptera: Agromyzidae)
Argentine Ant, *Linepithema humile* (Mayr), (Hymenoptera: Formicidae: Dolichoderinae)
Army Cutworm, *Euxoa auxiliaris* (Grote) (Lepidoptera: Noctuidae)
Armyworm, *Pseudaletia unipuncta* (Haworth) (Lepidoptera: Noctuidae)
Asian Citrus Psyllid, *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae)
Asparagus Aphid, *Brachycorynella asparagi* (Mordvilko) (Hemiptera: Aphididae)
Aster Leafhopper, *Macrosteles quadrilineatus* Forbes (Hemiptera: Cicadellidae)
Australian Sheep Blowfly, *Lucilia cuprina* Wiedemann (Diptera: Calliphoridae)
Banana Weevil, *Cosmopolites sordidus* (Germar) (Coleoptera: Curculionidae)
Bed Bugs (Hemiptera: Cimicidae: *Cimex* spp.)
Bee Louse, Bee Fly, or Braulid, *Braula coeca* Nitzsch (Diptera: Braulidae)
Beet Armyworm, *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae)
Bertha Armyworm, *Mamestra configurata* Walker (Lepidoptera: Noctuidae)
Black Cutworm, *Agrotis ipsilon* (Hufnagel) (Lepidoptera: Noctuidae)
Black Fig Fly, *Silba adipata* McAlpine (Diptera: Lonchaeidae)
Bogong moth, *Agrotis infusa* (Boisduval) (Lepidoptera: Noctuidae)
Boll Weevil, *Anthonomus grandis* Boheman (Coleoptera: Curculionidae)
Brown Citrus Aphid, *Toxoptera citricida* (Kirkaldy) (Hemiptera: Aphididae)
Cabbage Aphid, *Brevicoryne brassicae* (L.) (Hemiptera: Aphididae)
Cabbage Maggot or Cabbage Root Fly, *Delia radicum* (Linnaeus) (Diptera: Anthomyiidae)
Cabbage Looper, *Trichoplusia ni* (Hübner) (Lepidoptera Noctuidae)
Cabbageworm, *Pieris rapae* (Linnaeus) (Lepidoptera: Pieridae)
Cactus Moth, *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae)
Cape Honey Bees, *Apis mellifera capensis* Escholtz
Cassava Mealybug, *Phenacoccus manihoti* Matile-Ferrero (Hemiptera: Pseudococcidae)
Chilli Thrips, *Scirtothrips dorsalis* Hood (Thysanoptera: Thripidae)
Chinch Bug, *Blissus leucopterus* (Say) (Hemiptera: Blissidae)
Cluster Fly, *Pollenia rudis* (Fabricius) and *P. pseudorudis* Rognes (Diptera: Calliphoridae)
Coconut Mite, *Aceria guerreronis* (Acari: Eriophyidae)
Coffee Berry Borer, *Hypthenemus hampei* (Ferrari) (Coleoptera: Curculionidae: Scolytinae)
Colorado Potato Beetle, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae)
Corn Delphacid, *Peregrinus maidis* (Ashmead) (Hemiptera: Delphacidae)
Corn Earworm, *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae)
Corn Leaf Aphid, *Rhopalosiphum maidis* (Fitch) (Hemiptera: Aphididae)
Corn Leafhopper, *Dalbulus maidis* (Delong And Wolcott) (Hemiptera: Cicadellidae)
Cotton Leafworm, *Spodoptera littoralis* (Boisduval)
Crapemyrtle Aphid *Sarucallis kahawaluokalani* (Kirkaldy) (Hemiptera: Aphididae)
Date Palm Stem Borer, *Pseudophilus testaceus* Gah. (= *Jebusea hammershmidti* Reiche) (Coleoptera: Cerambycidae)
Diamondback Moth, *Plutella xylostella* (Linnaeus) (Lepidoptera: Plutellidae)
Diaprepes Root Weevil, *Diaprepes abbreviatus* (L.) (Coleoptera: Curculionidae)

Differential Grasshopper, *Melanoplus differentialis* (Thomas) (Orthoptera: Acrididae)
Douglas-Fir Beetle, *Dendroctonus pseudotsugae pseudotsugae* Hopkins (Coleoptera: Curculionidae, Scolytinae)
Driver Ants (*Dorylus* Subgenus *Anomma*) (Hymenoptera: Formicidae)
Dubas Bug (Old World Date Bug), *Ommatissus binotatus* (Hemiptera: Tropiduchidae)
Eastern Lubber Grasshopper, *Romalea microptera* (Beauvois) (Orthoptera: Acrididae)
Elm Leaf Beetle, *Xanthogaleruca* (= *Pyrrhalta*) *luteola* (Müller) (Coleoptera: Chrysomelidae)
Eri Silkworm, *Philosamia ricini* (Lepidoptera: Saturniidae)
Eurasian Spruce Bark Beetle, *Ips typographus* Linnaeus (Coleoptera: Curculionidae, Scolytinae)
European Cherry Fruit Fly *Rhagoletis cerasi* (Linnaeus) (Diptera: Tephritidae)
European Corn Borer, *Ostrinia nubilalis* (Hübner) (Lepidoptera: Pyralidae)
European Earwig, *Forficula auricularia* Linnaeus (Dermaptera: Forficulidae)
Face Fly, *Musca autumnalis* De Geer (Diptera: Muscidae)
Fall Armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae)
Formosan Subterranean Termite, *Coptotermes formosanus* Shiraki (Isoptera: Rhinotermitidae)
Fruit Stalk Borer, *Oryectes elegans* Prell (Coleoptera: Scarabaeidae)
Gamagrass Leafhopper *Dalbulus quinquenotatus* Delong & Nault (Hemiptera: Cicadellidae)
Glassy-Winged Sharpshooter, *Homalodisca vitripennis* (Hemiptera: Cicadellidae)
Grape Phylloxera, *Daktulosphaira vitifoliae* (Fitch) (Hemiptera: Aphidoidea: Phylloxeridae)
Grapevine Leafhopper Complex (Hemiptera: Cicadellidae) in Cyprus
Greater Date Moth, *Arenipses sabella* Hmps (Lepidoptera: Pyralidae)
Greenhouse Whitefly, *Trialeurodes vaporariorum* (Westwood) (Hemiptera: Aleyrodidae)
Green Peach Aphid, *Myzus persicae* (Sulzer) (Hemiptera: Aphididae)
Gypsy Moth, *Lymantria dispar* Linnaeus (Lepidoptera: Lymantriidae)
Harlequin Bug, *Murgantia histrionica* (Hahn) (Hemiptera: Pentatomidae)
Hazelnut and Walnut Twig Borer, *Oberea linearis* Linnaeus (Coleoptera: Cerambycidae)
Hessian Fly, *Mayetiola destructor* (Say) (Diptera: Cecidomyiidae)
Honey Bee, *Apis mellifera* Linnaeus (Hymenoptera: Apidae)
Horn Fly, *Haematobia irritans* (L.) (Diptera: Muscidae)
House Fly, *Musca domestica* L. (Diptera: Muscidae)
Human Botfly, *Dermatobia hominis* (Linneaus, Jr.) (Diptera: Oestridae)
Japanese Beetle, *Popillia japonica* Newman (Coleoptera: Scarabaeidae)
Jewel Wasp, *Nasonia vitripennis* (Walker) (Hymenoptera: Pteromalidae)
Khapra Beetle, *Trogoderma granarium* Everts (Coleoptera: Dermestidae)
Large Milkweed Bug, *Oncopeltus fasciatus* (Dallas) (Hemiptera: Lygaeidae)
Large Cabbage White Butterfly, *Pieris brassicae* (Linnaeus) (Lepidoptera: Pieridae)
Larger Grain Borer, *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae)
Leaf-Cutting Ants (Formicidae: Myrmicinae: Attini)
Lesser Date Moth, *Batrachedra amydraula* Meyrick (Lepidoptera: Cosmopterygidae)
Lettuce Root Aphid, *Pemphigus bursarius* (Linnaeus) (Hemiptera: Aphididae)
Locust Borer, *Megacyllene robiniae* (Forster) (Coleoptera: Cerambycidae)

Roundheaded Pine Beetle, *Dendroctonus adjunctus* Blandford (Coleoptera: Curculionidae, Scolytinae)
Seedcorn Maggot or Bean Seed Fly, *Delia platura* (Meigen) (Diptera: Anthomyiidae)
Silkworm, *Bombyx mori* (Linnaeus) (Lepidoptera: Saturniidae)
Silverleaf Whitefly, *Bemisia argentifolii* Bellows and Perring (Hemiptera: Aleyrodidae)
Small Green Stink Bug, *Piezodorus guildinii* (Westwood) (Hemiptera: Heteroptera: Pentatomidae)
Small Hive Beetle, *Aethina tumida* Murray (Nitidulidae: Coleoptera)
Small Honey Ant, *Prenolepis imparis* (Say) (Hymenoptera: Formicidae)
Small Rice Stink Bug, *Oebalus poecilus* (Dallas) (Hemiptera: Heteroptera: Pentatomidae)
Southern Green Stink Bug, *Nezara viridula* (L.) (Hemiptera: Heteroptera: Pentatomidae)
Soybean Aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae)
Spined Soldier Bug, *Podisus maculiventris* (Say) (Hemiptera: Pentatomidae)
Spotted Cucumber Beetle or Southern Corn Rootworm, *Diabrotica undecimpunctata* Mannerheim (Coleoptera: Chrysomelidae)
Spruce Budworms, *Choristoneura* Lederer (Lepidoptera: Tortricidae)
Squash Bug, *Anasa tristis* (DeGeer) (Hemiptera: Coreidae)
Squash Vine Borer, *Melittia cucurbitae* (Harris) (Lepidoptera: Sesiidaae)
Stable Fly, *Stomoxys calcitrans* (Linnaeus) (Diptera: Muscidae)
Sweetpotato and Silverleaf Whiteflies, *Bemisia* spp. (Hemiptera: Aleyrodidae)
Sweetpotato Flea Beetle, *Chaetocnema confinis* Crotch (Coleoptera: Chrysomelidae Alticinae)
Sweetpotato Weevil, *Cylas formicarius* (Fabricius) (Coleoptera: Brentidae)
Taiga Tick, *Ixodes persulcatus* Schulze (Acari: Ixodida: Ixodidae)
Tarnished Plant Bug, *Lygus lineolaris* Palisot de Beauvois (Hemiptera: Miridae)
Taro Caterpillar or Rice Cutworm, *Spodoptera litura* (Fabricius)
Tent Caterpillars, *Malacosoma* spp. (Lepidoptera: Lasiocampidae)
Termites (Isoptera) in South America
Timarcha Latreille (Coleoptera: Chrysomelidae, Chrysomelinae)
Tomato Hornworm, *Manduca quinquemaculata* (Haworth) and Tobacco Hornworm, *Manduca sexta* (Linnaeus) (Lepidoptera: Sphingidae)
Tracheal Mite, *Acarapis woodi* Rennie (Acarina: Tarsonemidae)
Tsetse Flies, *Glossina* spp. (Diptera: Glossinidae)
Turnip Aphid, *Lipaphis erysimi* (Kaltenbach) (Hemiptera: Aphididae)
Turnip Root Maggot, *Delia floralis* (Fallen) (Diptera: Anthomyiidae)
Twospotted Spider Mite, *Tetranychus urticae* Koch (Acari: Tetranychidae)
Two-Spotted Stink Bug, *Perillus bioculatus* (Fabricius) (Hemiptera: Pentatomidae)
Twostriped Grasshopper, *Melanoplus bivittatus* (Say) (Orthoptera: Acrididae)
Varroa Mite, *Varroa destructor* Anderson & Truemann (Acari: Varroidae)
Variegated Cutworm, *Peridroma saucia* (Hübner) (Lepidoptera: Noctuidae)
Vegetable Leafminer, *Liriomyza sativae* Blanchard (Diptera: Agromyzidae)
Viburnum Leaf Beetle, *Pyrrhalta viburni* (Paykull) (Coleoptera: Chrysomelidae)
Vine Mealybug, *Planococcus ficus* Signoret (Hemiptera: Pseudococcidae)
Western Balsam Bark Beetle, *Dryocoetes confusus* Swain (Coleoptera: Curculionidae, Scolytinae)
Western Corn Rootworm, *Diabrotica virgifera virgifera* Leconte (Coleoptera: Chrysomelidae)
Western Grapeleaf Skeletonizer, *Harrisina brillians* Barnes & McDunnough (Lepidoptera: Zyganeidae)

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Ludwig Aigner was born on the 11 February 1840 at Nagyjécsa, Torontál Shire, Transylvania, Hungary, now Romania. His family moved to Temesvár, a large town in Transylvania, where he received a formal education in commerce and begun his career as a book merchant. His family was of ethnic German stock and young Ludwig only learned Hungarian when, in 1858, they moved to Pozsony (now Bratislava and in the Slovak Republic), a large town with predominantly Hungarian inhabitants. From here he soon moved on to Pest (now Budapest) and in 1863, as it was the custom in those years, he wandered all over Austria and Germany. He completed his studies in Köln and Stuttgart before returning to Pest. He always had an interest in entomology and he became a keen amateur lepidopterologist. However, besides entomology, he had a great variety of other interests too, especially in the field of publishing, writing, historical research as well as aspirations in business. He found success in publishing and in establishing a popular bookshop. In 1870 he was initiated as a Freemason and eventually he rose to the highest positions in the Order. For 12 years he has worked on an extensive monograph of the history of Freemasonry. He used his Hungarian pen name "Abafi" in a hyphenated form with his original family name: Abafi-Aigner and changed his German Christian name "Ludwig" to the Hungarian equivalent "Lajos." However, despite his successes in publication and writing his business begun to decline in the 1880s and within a few years he faced financial difficulties, which ultimately led to the closure of his famous bookshop. Disillusioned, he discontinued most of his business activities, and from 1890 he devoted all his time and energy to lepidopterology. In 1895, he published the results of his studies in the *Természetrajzi Füzetek* (Notebooks of Natural History), the journal of the National Museum's Natural History Department and he was one of the authors of *Fauna Regni Hungariae* (Catalogue of Hungary's Fauna). He resurrected *Rovartani Lapok* (Entomological Papers), which was established in 1884 but ceased to exist in 1886. His treatment of the butterfly fauna of Hungary won the coveted Bugát Prize. Based on this work he published *Butterflies of Hungary* in 1907. The book was (and probably still is) one of the most popular entomological publications in Hungary. It has inspired countless young entomologists and made the name of Abafi-Aigner well known to every naturalist in the country. He passed away on the 19 June 1909.

Reference

Horváth C (1990) A rovartan tudósa. E' let és Tudomány 45:290, 312

Abaxial Surface

The lower surface of a leaf (contrast with adaxial surface).

Abbott, John

John Abbott was born in London in 1751. In England, he was given drawing lessons and, through his drawing instructor, was introduced to Dru Drury, a collector of insects who had been president of the Linnean Society. These two encounters encouraged him to collect insects and draw them, but his father was training him to be an attorney. Finding legal paperwork not to his liking, he emigrated to Virginia in 1773. After 2 years in Virginia, he relocated to Georgia, where he served as a private in the Third Georgia Continental Battalion during the Revolutionary War. For his military service he received several hundred acres of land, and worked as a planter and schoolmaster. In Virginia he had collected American insects and bird skins, and drew and painted insects and birds. Some of the specimens and paintings were shipped to England for sale. Some of the paintings, after sale, adorned books on birds, insects, and spiders written by various authors, not necessarily with acknowledgment to Abbott. In all, Abbott produced over 3,000 drawings of a quality that was very high for that time. Some of the insect illustrations included not only adults, but also larvae and the plants on which they fed, and even observational notes. He died about 1840.

Reference

Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Abbott' s Formula

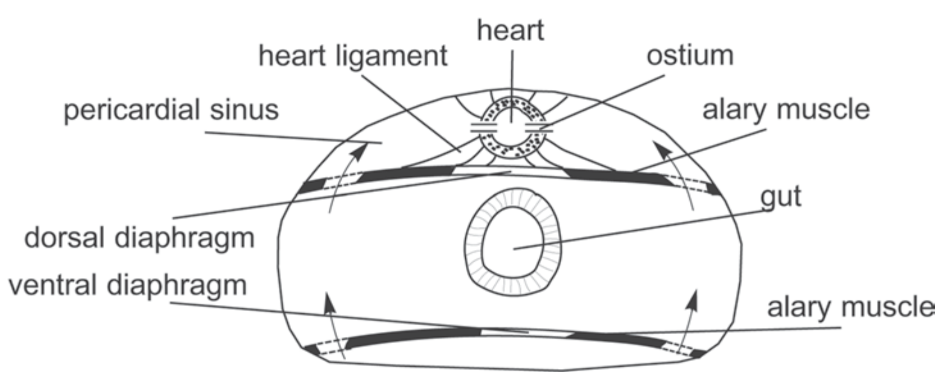
A mathematical technique commonly used to assess mortality in insecticide trials when there is need to correct for a change (decrease) in the background population density (i.e., in the check or control plots). The formula is:

% corrected control = 100 × (% alive in the check % alive in the treatment)/(% alive in the treatment)

Abdomen

The posterior of the three main body divisions of an insect (Fig. 1).

► Abdomen of Hexapods



Abdomen, Figure 1 **Cross section of an insect abdomen, showing components of the insect circulatory system and direction of hemolymph flow (adapted from Evans, Insect biology).**

Abdomen of Hexapods

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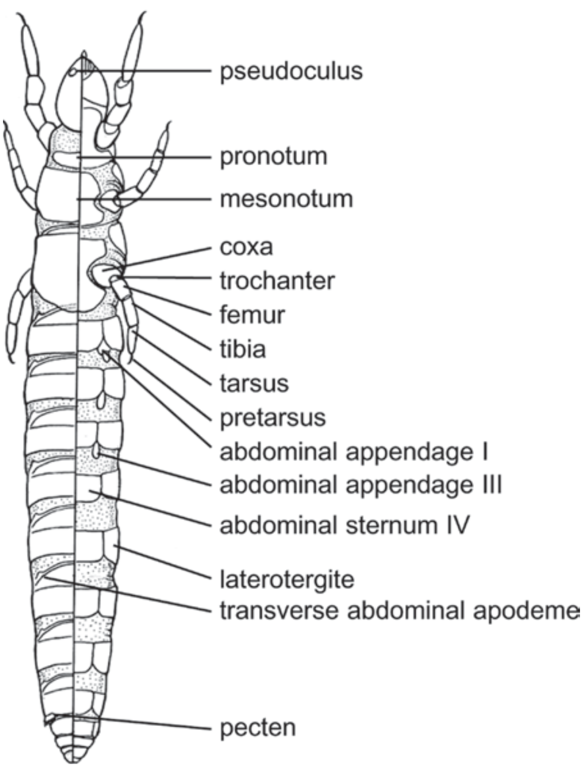
The abdomen constitutes the caudal tagma in the hexapods and is usually larger than the other two, the head and the thorax. This region is also referred to as a visceral area because it houses the visceral organs. Its form can vary depending on the group, and even on the species. The maximum number of observed segments is 11, although certain authorities consider a twelfth segment that in fact corresponds to a telsonic caudal region. In general, the number of segments decreases from the preimaginal phases to the adult stage, especially in those holometabolous insects in which the last segments of the adults are formed from imaginal discs during pupation. In the groups considered most primitive, the number of abdominal segments is usually greater, as occurs in the Protura with 11 segments (Figs. 2–5). An exception is the Collembola, which only possess six. In addition, it is necessary to keep in mind that, in certain cases, the total number of visible segments does not coincide with what a particular individual actually possesses, since some segments remain "invisible" upon being telescoped, particularly those of the posterior region of the abdomen.



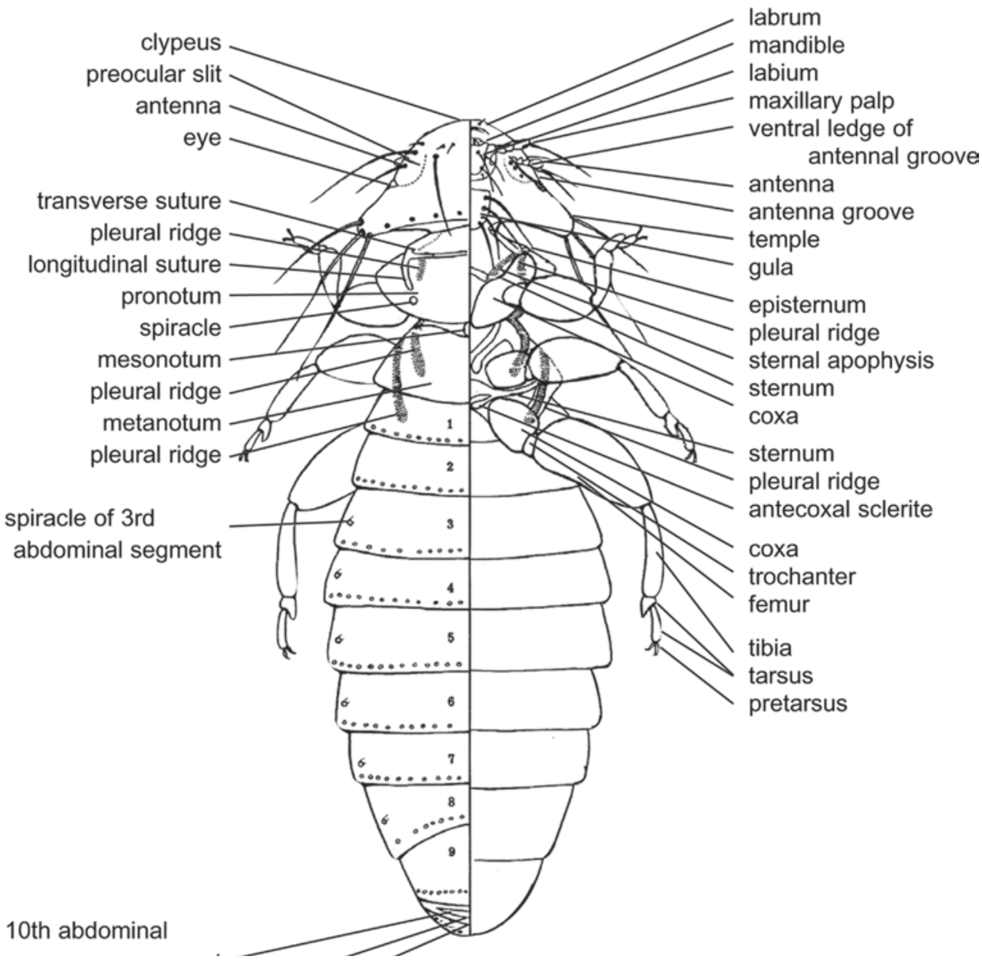
Abdomen of Hexapods, Figure 2 Diagram of a proturan (Protura) showing abdominal segments and appendages: dorsal view (left), ventral view (right).

According to Bitsch, a generalized abdominal segment would be limited anteriorly by a presegmentary domain, separated from the segmentary domain proper (of greater size) by a suture that begins an internal crest named the costa or antecosta. This crest anteriorly delimits an acrotergite or precosta in the tergal part and a presternite in the sternal part. In this idealized model, the muscles would be inserted in successive antecostas. No known structure is homologous to the thoracic furca.

The presence of the gonopore (double in Ephemeroptera) in segments VIII and IX (in VII in the case of Ephemeroptera), and fundamentally of the external structures related to reproduction (the genitalia), produce important modifications in those segments. Considering the presence of these genitalia, three regions of the abdomen are recognized: an anterior (pregenital or visceral region that includes the first eight segments), median (genital region, eighth and ninth segments), and caudal regions (postgenital region, tenth and eleventh segments plus the telsonic region).

The Pregenital Region

In the most generalized condition, the first abdominal segments conserve their basic structure, being easily distinguished from the thoracic segments. Nevertheless, the most frequent condition is that which produces morphological modifications that affect the thoracic-abdominal union. These modifications usually consist of reductions that affect the sternal region and involve a greater or lesser desclerotization of different structures and their

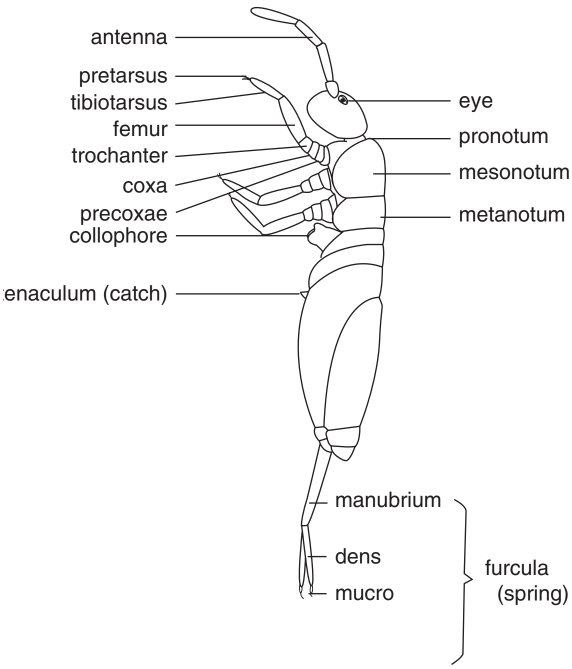


Abdomen of Hexapods, Figure 3 **Diagram of chewing louse (Mallophaga) showing abdominal segments, including numbering of segments: dorsal view (left), ventral view (right).**

incorporation to the metathorax. In this sense, the case of the Hymenoptera, Apocrita stands out, in which a narrowing is produced between the second and the third abdominal segments, which incorporate the thorax and is named the propodeum. The rest of the abdominal segments are called the gaster or metasoma. The region formed by the propodeum and the thorax constitutes the mesosoma. The narrowing allows a great amplitude of movements of the metasoma, which permits stinging in the capture of prey in aculeates. In some groups, like Formicidae and Sphecidae (Aculeata), one or two segments of the metasoma form a narrower zone called the petiole.

In the pregenital region, several appendicular structures can be found. Thus, three pairs of highly modified appendages exist in Collembola. In Archaeognatha, very developed coxites are differentiated, above which are inserted styli in a median position and the exsertile vesicles in the most internal position.

The styli are elongated pieces, articulated in their base above the external face of the coxite. They are unisegmentary and lack muscles inserted in their base, often presenting an apical spine. Taking into account their position and their embryonic development, the styli are considered by the majority of authorities as vestigial appendages, and more concretely as reduced telepodites. The exsertile vesicles are considered internal coxal formations (internal coxalia of some authorities).



Abdomen of Hexapods, Figure 4 Diagram of springtail (Collembola) showing furcular appendage at tip of abdomen.

In Pterygota the abdominal appendages remain restricted to the larval forms (Lepidoptera and Hymenoptera, Tenthredinoidea), although rough appendicular pairs already exist in the polypodous type of embryos. These abdominal appendages are named "false legs" or "prolegs" and are retractile, conical and membranous projections, with a circular planta that bears a crown, usually with hooks, to adhere to the substrate.

The Genital Region

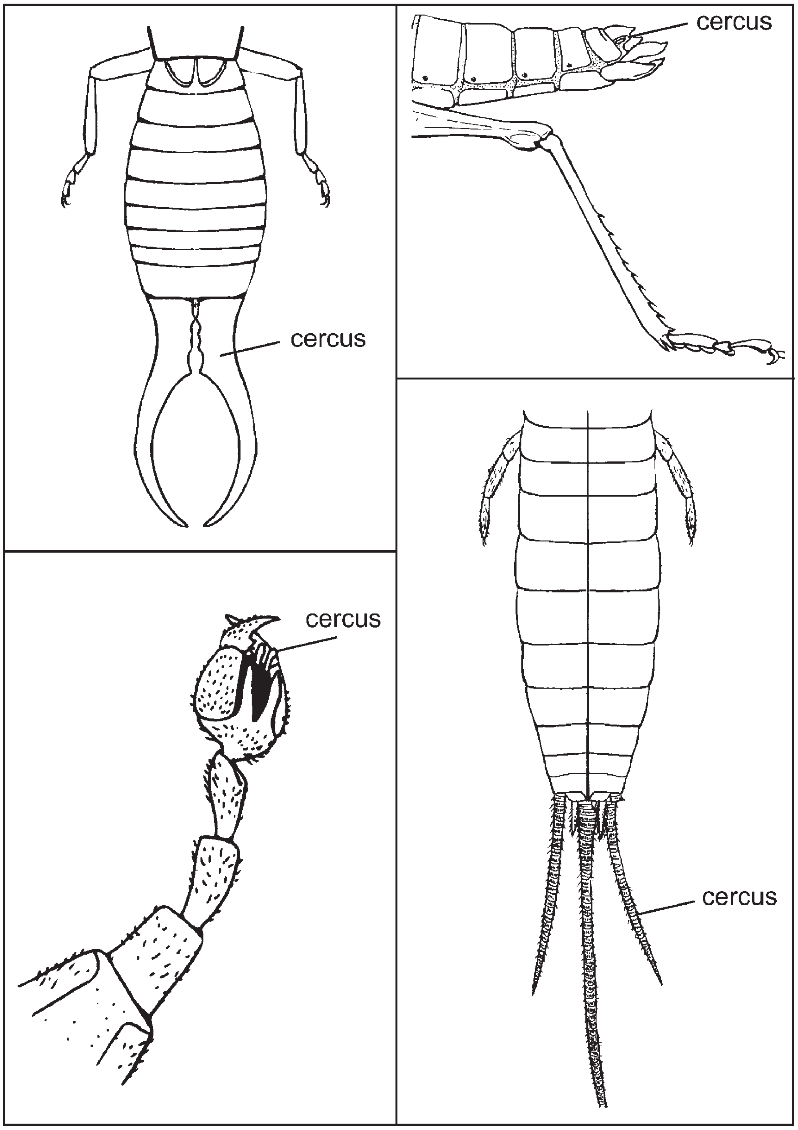
The transformations that affect the eighth and ninth abdominal segments are a consequence of the development of special external structures that in the case of the male serve in the transfer of sperm, and in the case of the female allow for oviposition. These structures together are known by the name genitalia.

The origin of the genitalia is controversial, although the majority of authorities accept that, at least in part, it is of appendicular origin. In this sense, it is clear that in the Archaeognatha the eighth and ninth segments are basically similar in males and females and their structures are homologous to those already indicated for the pregenital segments. Taking into account this relationship, the genitalia of Archaeognatha are considered primitive, and therefore fundamental to interpret the genitalia of Pterygota.

In the eighth segment of the Archaeognatha, the basal part of the appendicular structure is named first gonocoxa or gonocoxite and bears the first gonostylus; in the ninth is found the second gonocoxa with its corresponding stylus. In both segments (at times in the eighth, always in the ninth) formations homologous to the exsertile vesicles appear, which are called gonapophyses (parameters in the males and gonapophysis proper in the females). The fundamental difference between both sexes lies in the presence in the males of a phallic structure.

The female genitalia in the Pterygota constitute the ovipositor. The gonocoxites are incorporated into the lateral wall of the genital segments in a complete manner in the eighth segment, forming the first valvifer. In the ninth segment the basal part is incorporated into the lateral wall, originating the second valvifer, while the rest is extended, forming the third pair of valves (dorsal or lateral valves of some authorities), which are not homologous in Archaeognatha. The other two pairs of valves are the ventral valves, corresponding to the eighth segment, and the internal valves, corresponding to the ninth segment. These two pairs of valves are homologous to the gonapophysis of Archaeognatha. In the case of the generalized type of ovipositor like that of Orthoptera, these three pairs of valves are linked through the length of their course, forming in their interior a canal for oviposition.

Among the sclerites that are situated in the base of the valves (in addition to the valvifers already mentioned) are found the intervalves (intervalvulae of the authorities) by way of elongated transverse formations, one in the base of the valves of the eighth segment and another in the base of the valves of the ninth segment. The typical ovipositor



Abdomen of Hexapods, Figure 5 **Comparative development of cerci on earwig (Dermaptera, top left); grasshopper (Orthoptera, top right); scorpion fly (Mecoptera, lower left); silverfish (Zygentoma).**

that was just described can experience modifications according to the functions that it carries out; one of the most drastic is found in Hymenoptera, Aculeata, where it is transformed into a sting that serves the females as an attacking organ, either to capture prey or as a defense. On the other hand, the process of oviposition can be carried out through other, different structures, as occurs in the females of certain Diptera. In that case, the last segments are retractile and the intersegmental zones are highly developed, in such a way that they can become telescoped, forming oviposition tubes; this type of "ovipositor" is named the ovicauda. Not being homologous to the genitalia, many authorities call it terminalia.

The masculine genitalia present great morphological variability, which together with their taxonomic importance, have been the object of an infinity of descriptions, many of them without truly anatomical criteria. This has originated the use of very varied terminologies that have done nothing but complicate its study and impede the establishment of homologies even in the same group, creating in this way a great nomenclatorial chaos.

In the males, in addition to the genitalia proper, other structures (processes, lobes, etc). exist that intervene in functions other than those strictly related to the transfer of sperm; among the most common is the grasping of the female during mating. It has already been mentioned that the majority of authorities consider that the interpretation of the genitalia of Pterygota should be made by homology with the basic condition that is found in Archaeognatha. In this group, the phallic complex is formed by a median organ, the phallus or penis, and a pair of segmented pieces named parameres, that in the case of maximum development can exist in the eighth and ninth segments. The parameres correspond to the gonapophysis of the females (although the term gonapophysis is utilized indistinctly for both sexes by some authorities).

Many morphological models have been proposed to describe the male genitalia of Pterygota. The most complete, since it gathers and discusses early data, is that proposed by Bitsch. According to this author, what together forms the copulatory organ (phallus or penis) and the structures associated with the parameres (considered in the sense expressed by the Archaeognatha) is named the phallic complex.

The aedeagus is a sclerotized tube, situated above a largely membranous phallobase, although in more complex cases the phallobase presents an internal fold that remains membranous (endotheca) while the external part is sclerotized (phallotheca or theca). The aedeagus presents an invagination that forms a more or less developed internal chamber (the endophallus), which communicates with the gonopore at its base and in the other extreme communicates with the exterior through the phallotreme. In counter-proposition to the endophallus, the part formed by the external walls of the phallobase and the aedeagus forms the ectophallus. The phallic complex can present variable development, even being able to cause the aedeagus to disappear, or on the contrary, increase in complexity, developing spines and other types of processes named flagellum, virga or pseudovirga over the internal walls of the endophallus. When the endotheca and the endophallus are evaginated, the genitalia are converted into authentic intromittent organs.

The primitive position of the male genitalia can be displaced through different types of turns; one of the most showy cases is that which occurs in some Hymenoptera, Symphyta that present the condition called strophandric, which is characterized by a 180° rotation of the genitalia. Rotations have also been observed in males of Diptera.

The postgenital region, as was mentioned in the beginning of this section, comprises the tenth and eleventh segments plus the telsonic region. The tenth segment has been detected in Protura, Diplura, Archaoegnatha, Thysanura (Zygentoma), Ephemeroptera, Plecoptera, and some Orthoptera. The morphology of this segment is basically similar to the pregenital segments, although with certain frequency it can form a ring when the tergum and sternum unite, or the sternal region can be membranous. In embryonic forms, a pair of appendicular outlines is seen above this segment. In certain holometabolous insects, structures of uncertain meaning appear, such as the socii of some Hymenoptera.

The eleventh segment is recognized in the majority of embryonic phases of hexapods. In Archaeognatha and Thysanura it forms an annular structure from whose dorsal part is differentiated a long and narrow process called filum terminale, while from the lateroventral position are differentiated the cerci that in the adults possess numerous divisions. In the Pterygotes, the eleventh segment is formed by the epiproct (tergal region) and the paraprocts (in the lateroventral position); in the more primitive groups exist cerci (whose length and number of divisions are variable) situated in the membranous zones that exist between the epiproct and the paraprocts. The telsonic, asegmentary region constitutes the perianal membrane or periproct.

► Alimentary Canal and Digestion

References

Bitsch J (1979) Morphologie abdominal des insects. In: Grassé, P-P (ed) Traité de Zologie, VIII (II): 291–600

Bitsch J (1994) The morphological groundplan of Hexapoda: critical review of recent concepts. Annales de la Société Entomologique de France 30:103–129

Deuve T (2001) The epipleural field in hexapods. Annales de la Société Entomologique de France 37:195–231

Matsuda R (1970) Morphology and evolution of the insect abdomen. Pergamon Press, New York, NY

Snodgrass RE (1935) Principles of insect morphology. MacGraw Hill, New York, NY

Abdominal Pumping

Contraction of the muscles associated with the abdomen can result in collapse and expansion of the air sacs. This forces relatively large volumes of air in and out of the insect through the spiracles, promoting ventilation. This is called active ventilation, in contrast with the more normal gas exchange mechanism of insects, diffusion or passive ventilation. To a small degree, abdominal pumping also promotes gas exchange through the trachea, but the trachea is quite resistant to change in shape. Abdominal pumping is more important for larger insects such as locusts, which display abdominal pumping almost continuously, but especially when active. In these insects air is sucked in through some spiracles and pumped out through others.

► Active Ventilation

Abiotic Disease

A disease caused by factors other than pathogens (e.g., weather or nutrition).

Abiotic Factors

Factors, usually expressed as factors affecting mortality, characterized by the absence of life. Abiotic factors include temperature, humidity, pH, and other physical and chemical influences.

Abnormality

In insect pathology, deviation from the normal; a malformation or teratology; a state of disease.

Abrocomophagidae

A family of chewing lice (order Phthiraptera).

► Chewing and Sucking Lice

Absolute Methods of Sampling

Techniques used to sample insect populations that provide an estimate per unit of area (e.g., per square meter, per leaf or per plant). Types of absolute methods include unit of habitat, recapture, and removal trapping. (contrast with relative methods of sampling).

► Sampling Arthropods

Acanaloniidae

A family of insects in the superfamily Fulgoroidae (order Hemiptera). They sometimes are called planthoppers.

► Bugs

Acanthmetropodidae

A family of mayflies (order Ephemeroptera).

► Mayflies

Acanthopteroctetidae

A family of moths (order Lepidoptera). They commonly are known as archaic sun moths.

► Archaic Sun Moths
► Butterflies and Moths

Acanthosomatidae

A family of bugs (order Hemiptera).
► Bugs

Acaricide

A pesticide applied to manage mite populations. An acaricide is also called a miticide.
► Acaricides or Miticides

Acaricides or Miticides

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An acaricide or miticide is a pesticide that provides economic control of pest mites and ticks. Mites and ticks are collectively called either acari or acarina. Some products can act as insecticides or fungicides as well as acaricides.

An acaricide is a pesticide used to kill mites and ticks (Table 1). Always check with state and federal authorities to be sure products containing these active ingredients are registered for use. Always read labels carefully and follow the directions completely.

The toxicity of an acaricide is determined by a dose-response curve or a concentration-response curve. Such curves are obtained by exposing test mites or insects to increasing concentrations or doses of the pesticide and recording the resulting mortality after a given time interval. One estimate of toxicity used is the term LD_{50} (which is the dose required to kill 50% of the test population). The LC_{50} is the concentration required to kill 50% of the test population. If the dose is introduced through the insect's mouth it is an oral LD_{50}, if it is introduced through the skin or integument it is a dermal LD_{50}, and if it is introduced through the respiratory system it is the inhalation LD_{50}. A measured dose is applied to an arthropod by inserting a measured amount of toxicant into the gut or by applying a measured amount to the integument. The lower the LD_{50} or LC_{50}, the more toxic the poison.

An LC_{50} is obtained when a mite is exposed to a particular *concentration* of toxicant but the actual amount of toxicant the individual experiences is not determined. For example, if the pesticide is applied to foliage and the mite walks about on the foliage, the actual amount of toxicant the mite is exposed to depends on the activity of the mite, the amount taken up through the integument or by feeding.

Figure 6 shows a concentration-response curve in parts per million (ppm) for the acaricide Omite (propargite) exhibited by adult females from colonies of the Pacific spider mite *Tetranychus pacificus*. The concentration required to kill 50% of the individuals is the LC_{50}. The two types of F1 females (produced by crossing Chapla males and Bidart females, and vise versa) respond similarly and their concentration-response curves are about midway between those of the resistant (Bidart) and susceptible (Chapla) colonies, which indicates that resistance may involve a semidominant mode of inheritance. The term mode of inheritance describes how the trait is inherited; for example, the resistance can be determined by a single major dominant (only one copy of the gene is required for the mite to express the resistance) or recessive (two copies of the gene are required) gene. Or, the resistance can be a quantitative trait determined by multiple genes of equal and additive effect. In this example, the propargite resistance may be determined a single semidominant gene with modifying genes, but additional tests are required to resolve whether more than one gene actually contributes to this resistance.

Acaricide Classification

Pesticides are classified in several ways, including: (i) their mode of entry into the target pest, (ii) chemical structure, or (iii) source.

Acaricides or Miticides, Table 1 Acaricides (miticides) currently or recently available for general and restricted use to control mites and ticks*

Name** (chemical type) Some trade names	General Use (GU)*** Restricted Use (RU)	Potential use
Abamectin (avermectin B1a; produced from the bacterium Streptomyces avermitilis) Affirm, Agri-Mek, Avid, vertimec, Zephyr	GU, Class IV (practically nontoxic)	Also an insecticide; affects nervous system and paralyzes insects or mites; used in citrus, pears, nut tree crops
Amitraz (triazapentadiene) Acarac, Mitac, Ovidrex,Triatox,Topline	GU, Class III (slightly toxic)	Used in pears, cotton, and on cattle, and hogs to control insects, ticks and mites
Azadirachtin (tetranortriterpenoid extracted from the Neem tree) Align, Azatin, Turplex	GU, Class IV	Azadirachtin is similar to insect hormones called ecdysones, which control metamorphosis; also may serve as a feeding deterrent; used to control insects and mites on food, greenhouse crops, ornamentals and turf
Bifenazate (carbazate) **Floramite**	Class IV	Mites on greenhouse, shadehouse, nursery, field, field, landscape and interiorscape ornamentals, not registered in USA for use on food
Bifenthrin (pyrethroid) Talstar, Brigade, Capture	RU, Class II (moderately toxic)	Insecticide and acaricide that affects the nervous system and causes paralysis; used on greenhouse ornamentals and cotton
Carbaryl (carbamate) Adios, Bugmaser, Crunch, Dicarbam on formulation Hexavin, Karbaspray, Septene Sevin, Tornadao, Thinsec	GU, Class I, II or III, depending	General use pesticide to control insects on citrus, fruits, cotton, forests, lawns, nuts, ornamentals, shade trees, poultry, livestock and pets. Also works as a mollusccide and acaricide
Chlorobenzilate (chlorinated hydrocarbon) Acaraben, Akar, Benzilan, Folbex	RU, Class III, may cause tumors in mice	Used for mite control on citrus and in beehives; also kills ticks; use cancelled in USA
Chlorfenapyr (pyrrole) Pylon, Pyramite, Pirate	Class I	Used to control spider mites, broad ites, budmites, cyclamen mite, rust mites and some insects.
Cinnamon oil (cinnamaldehyde) Cinnamite	Exempt from registration under FIFRA	Broad spectrum miticide/ insecticide/fungicide controls or repels pests; could be phytotoxic in some cases; used in ornamentals, shade or nursery trees, vegetables, herbs and spices
Citronella oil	Exempt from FIFRA	Repels insects and ticks
Demeton-S-Methyl (organophosphate) Meta-Systox, Azotox, Duratox, Mifatox	No longer registered for use in USA; Class I, highly toxic	Systemic and contact insecticide and acaricide, widely used against diverse pests

Acaricides or Miticides, Table 1 **(Continued)**

Name** (chemical type) Some trade names	General Use (GU)*** Restricted Use (RU)	Potential use
Dicofol (organochlorine) Acarin, Difol, Kelthane, Mitigan	GU, Class II or III, depending on formulation	Miticide used on fruits, vegetables, ornamentals and field crops
Dicrotophos (organophosphate) Bidrin, Carbicron, Dicron, Ektafos	RU	Contact systemic pesticide and acaricide used to control sucking, boring and chewing pests on coffee, cotton, rice, pecans; used to control ticks on cattle
Dienochlor (organochlorine) Pentac, often formulated with other pesticides	GU, Class III	Contact material used for plant-feeding mites on ornamental shrubs and trees outdoors and in greenhouses; disrupts egg laying of female mites; use cancelled in USA
Dinocap (dinitrophenyl) Arathane, Caprane, Dicap, Dikar Karathane, Mildane	GU, Class III	Used as a fungicide and as an acaricide for ticks and mites; use cancelled in USA
Disulfoton (organophosphate) Disyston, Disystox, Dithiodemeton, Dithiosystox, Solvigram, Solvirex	RU, Class I, highly toxic	Systemic insecticide and acaricide used to control sucking insects/mites on cotton, tobacco, sugar beets, cole crops, corn, peanuts, wheat, grains, ornamentals, potatoes
Endosulfan (chlorinated hydrocarbon) Afidan, Cyclodan, Endocide, Hexasulfan, Phaser, Thiodan, Thionex	RU, Class I	Contact insecticide and acaricide used to control many pests on tea, coffee, fruits, vegetables, grains
Ethion (organophosphate) Acithion, Ethanox, Ethiol, Nialate, Tafethion, Vegfru Foxmite	GU, Class II	Insecticide and acaricide used on wide variety of food, fiber and ornamentals, including greenhouse crops, citrus, lawns and turf
Eucalyptus oil	Exempt from FIFRA	Repels mites; repels fleas and mosquitoes
Fenamiphos (organophosphate) Nemacur, Phenamiphos, Bay 68138	RU, Class I	A nematicide that has some activity against sucking insects and spider mites
Fenbutatin oxide (organotin) Vendex	RU	Miticide used on perennial fruits, eggplant and ornamentals
Fenitrothion (organophosphate) Accothion, Cyfen, Dicofen, Fenstan, Folithion, Mep, Metathion, Micromite Pestroy, Sumithion, Verthion	GU	Acaricide and insecticide effective gainst a wide array of pests

Acaricides or Miticides, Table 1 (Continued)

Name** (chemical type) Some trade names	General Use (GU)*** Restricted Use (RU)	Potential use
Formothion (organophosphate) Aflix, Anthio, Sandoz S-6900	RU, Class II	Systemic and contact insecticide and acaricide, used against spider mites on tree fruits, vines, olives, hops, cereals, sugar cane, rice
Hexythiazox (ovicide, growth regulator) Savey	Class III	Ovicide/miticide effective against spider mites on tree fruits, christmas trees, strawberries, hops, peppermint, caneberries
Lambda cyhalothrin (pyrethroid) Charge, Excaliber, Granade, Hallmark, Icon, Karate, Matador, Saber, Sentinel	RU, Class II	Insecticide and acaricide used to control a variety of pests in cotton, cereals, hops, ornamentals, potatoes, vegetables; controls ticks
Lindane (organochlorine) Agrocide, Benesan, Benexane, BHC, Gammex, Gexane, HCH, Isotox, Kwell, Lindafor, Lintox, Lorexane, Steward	RU, Class II Most uses cancelled in USA because of potential to cause cancer	Insecticide and fumigant; used in lotions, creams and shampoos for control of lice and mites (scabies) in humans
Methamidophos (organophosphate) Monitor, Nitofol, Tamaron, Swipe Patrole, Tamanox	RU, Class I	Systemic, residual insecticide/acaricide/avicide with contact and stomach action, used to control chewing and sucking insects and mites in many crops outside the USA
Methidathion (organosphosphate) Somonic, Supracide, Suprathion	RU, Class I	Insecticide and acaricide with stomach and contact action used to control a variety of insects and mites in many crops
Methomyl (carbamate) Acinate, Agrinate, Lannate, Lanox, Nudrin, NuBait	RU, Class I	Broad spectrum insecticide and an acaricide to control ticks, acts as a contact and systemic pesticide
Mevinphos (organophosphate) Fosdrin, Gesfid, Meniphos, Menite, Mevinox, Mevinphos, Phosdrin, Phosfene	RU, Class I	Insecticide and acaricide effective against a broad spectrum of pests, including mites and ticks; use cancelled in greenhouses
Monocrotophos (organophosphate) Azodrin, Bilobran, Monocil 40, Monocron, Nuvacron, Plantdrin	RU, registration in USA withdrawn in 1988	Systemic and contact insecticide and acaricide
Naled (organophosphate) Bromex, Dibrom, Lucanal	GU, Class I	Contact and somach insecticide and acaricide, used against mites in greenhouses
Oxamyl (carbamate)	RU, Class I granular form is banned in USA	Insecticide/acaricide/nematacide that controls a broad spectrum of mites, ticks and roundworms on field crops, vegetables, fruits, ornamentals

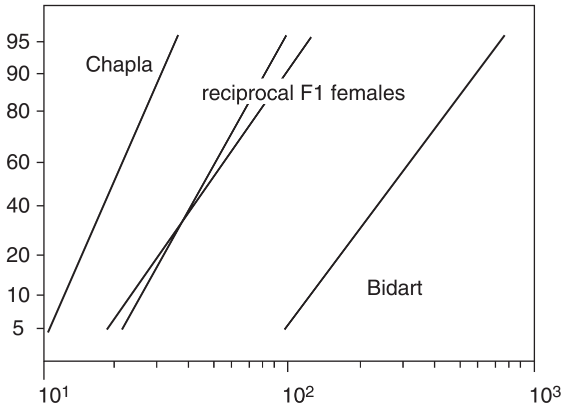
Acaricides or Miticides, Table 1 **(Continued)**

Name** (chemical type) Some trade names	General Use (GU)*** Restricted Use (RU)	Potential use
Neem oil Trilogy		Broad spectrum fungicide and acaricide in citrus, deciduous fruits and nuts, vegetables, grains
Permethrin (pyrethroid) Ambush, Cellutec, Dragnet, Ectiban, Indothrin, Kafil, Kestrel, Pounce, Pramex, Zamlin, Torpedo	Class II or III, depending on formulation RU in agriculture because of adverse effects on aquatic organisms	Broad spectrum used on nut, fruit, vegetable, cotton, ornamentals, mushrooms, potatoes, cereals, in greenhouses, home gardens, on domestic animals
Petroleum oils (refined petroleum distillate) Sunspray and others	Class IV	Kills by contact a wide range of mite and insects; complete coverage is essential; may act as a feeding or oviposition deterrent. Phytotoxicity can occur if plants are stressed, especially by lack of water; some plant cultivars are more susceptible than others. Used as dormant and as foliar sprays.
Phorate (organophosphate) Agrimet, Geomet, Granutox, Phorate Rampart, Thimenox, Thimet, Vegfru	RU, Class I	Insecticide and acaricide used on pests, including mites, in forests, root and field crops, ornamentals and bulbs
Phosalone (organophosphate)	GU, No longer for sale in USA due to carcinogenic effects	Broad spectrum insecticide/ acaricide used on deciduous trees, vegetables, cotton.
Phosmet (organophosphate)	GU, Class II, some tolerances in foods changed in 1994 by EPA	Broad spectrum insecticide, used to control insect and mites on apples, ornamentals, vines; is used in some dog collars.
Propargite (organosulfide) Comite, Omite	GU	Acaricide used in many crops but not USA
Rosemary oil (rosemary essential oil) Hexacide	Meets requirements of USDA National Organic Program Exempt from FIFRA	Broad spectrum contact insecticide/miticide used in fruits, nuts, vegetables. Could be phytotoxic on some cultivars.
Soybean oil (essential oil)	Low acute toxicity to humans, generally recognized as safe	
Spinosad (macrocyclic lactone) Conserve		Broad spectrum insecticide and miticide used on ornamentals and in greenhouses.
Sulfur (sulfur) Cosan, Hexasul, Sulflox, Thiolux	GU, Check label for restrictions	Fungicide and acaricide; used to control plant diseases, gall mites, spider mites, used widely in food and feed crops, ornamentals, turf and residential sites; a fertilizer or soil amendment, mixing with oil can cause phytotoxicity

Acaricides or Miticides, Table 1 (Continued)

Name** (chemical type) Some trade names	General Use (GU)*** Restricted Use (RU)	Potential use
Triforine (piperazine derivative)	RU, Class I	Fungicide used on almonds, apples, asparagus, berries, cheeries, hops, ornamentals, peaches, rose; also controls spider mites
Wintergreen oil (contains methyl salicylate)	Exempt from FIFRA	Used to control mites (Varroa) in honey bees; causes contact mortality and reduced fecundity when mites feed on syrup

* The list is based on chemicals currently registered in the USA, which can change as new information regarding environmental impact and human health effects become available. Inclusion in this list does not necessarily indicate that the products are effective acaricides; application methods and resistance levels in individual mite populations can affect efficacy.
**Most have a variety of trade or other names, as well as different formulations, which can affect their toxicity.
***Restricted Use (RU) means that pesticides may be purchased and used only by certified applicators. Check with specific state regulations for local restrictions.



Acaricides or Miticides, Figure 6 **This is a concentration-response curve showing the responses of a colony of *Tetranychus pacificus* resistant (Bidart) and susceptible (Chapla) to propargite (Omite). The mortality of adult females at different concentrations has been transformed into a straight line. The concentration-responses of the reciprocal F1 females in crosses between the susceptible and resistant populations are intermediate and similar.**

Mode of Entry

A pesticide can enter and kill mites as stomach poisons, contact poisons, and or as fumigants. A systemic acaricide is absorbed into a plant or animal and protects that plant or animal from pests after the pesticide is translocated throughout the plant or animal.

Chemical Structure

Pesticides are classified as organic or inorganic. Inorganic pesticides do not contain the element carbon (but include arsenic, mercury, zinc, sulfur, boron, or fluorine). Most inorganic pesticides have been replaced by organic pesticides.

Source

Organic pesticides include botanicals (natural organic pesticides) produced by plants (such as natural pyrethrums, nicotine, rotenone, essential oils such as those from the neem tree, soybean oil). Essential oils are any volatile oil that gives distinctive odor or flavor to a plant, flower or fruit, such as lavender oil, rosemary oil, or citrus oil. Essential oils have been registered as pesticides since 1947 and at least 24 different ones are available in registered products. These are used as repellants, feeding depressants, insecticides, and miticides. Botanicals have relatively high LD50 values to mammals, so usually are considered safe to humans. Some newer pesticides are derived from microbes, such as avermectin or spinosad.

Synthetic organic pesticides are commonly used in pest management programs and can be separated into groups based on their chemistry. The main groups are: chlorinated hydrocarbons (such as DDT and chlordane, which are banned from use in most parts of the world), organophosphates (such as malathion, parathion, azinphosmethyl), carbamates (carbaryl, propoxur), pyrethroids (permethrin, fenvalerate),and a variety of newer products with very different chemistries including nicitinoids, pyrroles, carbazates, and pyridazinones.

Insecticides as Acaricides

Many insecticides have acaricidal properties. Sometimes an insecticide is more effective as an insecticide than as an acaricide (lower concentrations are required to kill the insect than are required to kill the mite species). Some products are more toxic (often for unknown reasons) to mites than to insects. We think that mites have the same fundamental physiological responses to toxic chemicals as insects, although mite physiology and responses to pesticides have been studied less often. Different mite species appear to respond differently to different products, which could be due to behavioral differences (feeding behavior, location on plant, activity levels), differences in cuticle thickness, differences in detoxification rates, or other biochemical, morphological or behavioral factors. Different formulations also can influence toxicity to different species of both insects and mites.

Many insecticides are effective acaricides (or at least they were before resistance to them developed). For example, many OPs (such as azinphosmethyl, parathion, ethion, dimethoate) were toxic to spider mites until resistance to these products developed. Likewise, carbamates, formamides, and many pyrethroids have both insecticidal and acaricidal properties. Other products have both fungicidal and acaricidal properties. The reasons as to why these products are effective on particular taxonomic groups are generally unknown.

Acaricide Types

Pesticide registrations change frequently so some of the materials listed here may be obsolete. Always check with state and federal authorities to be sure products containing these active ingredients are registered for use. Always read labels carefully and follow the directions completely.

Chlorinated Hydrocarbons

Dienochlor (Trade name = Pentac) is a chlorinated hydrocarbon acaricide with long residual activity. It has been used in greenhouses and on outdoor ornamentals. Pentac cannot be used on food crops and has short residual activity when used outdoors. It has a rapid effect on mites, stopping their feeding within hours. Endosulfan and DDT have also been used as acaricides (as well as insecticides).

Essential Oils

Soybean oil was first registered in 1959 for use as an insecticide and miticide. Three products currently are registered to control mites on fruit trees, vegetables and a variety of ornamentals. Soybean oil is not phytotoxic under most conditions. Many of these oils are approved for organic farming.

Inorganics

Sulfur is a good acaricide and fungicide, although it can be phytotoxic (cause plant injury), especially if plants are not well watered during hot weather. Sulfur is probably the oldest known acaricide. Sulfur (dusts, wettable p owders and flowable formulations) are usually highly effective acaricides for spider mites and rust mites, with two known exceptions.

Spider mites in California vineyards (*Tetranychus pacificus* and *Eotetranychus willamettei*) developed resistance to sulfur, probably because sulfur was applied up to 20 times a season over many years to control powdery mildew. After a number of years, these spider mites became pests because they were no longer controlled by the sulfur which had been applied to control powdery mildew. A number of years later, a predatory mite called *Metaseiulus occidentalis* was demonstrated to have developed a resistance to sulfur. The resistance to sulfur in this natural enemy of spider mites is based on a single major dominant gene; once the predator became resistant to sulfur it became an effective predator of spider mites in San Joaquin Valley vineyards in California.

The resistance to sulfur in *M. occidentalis* is unusual; even very high rates of sulfur are non-toxic to the resistant populations. Interestingly, populations of this predator collected from nearby almond orchards in California are susceptible to sulfur, indicating that populations are subjected to local selection and evolution. No genetic analyses have been conducted on the resistance to sulfur in the spider mites, so their mode of inheritance to sulfur resistance remains unknown. The biochemical mechanism of resistance is unknown for both spider mites and their predators.

Petroleum Oils

Petroleum oils are excellent insecticides/acaricides/fungicides for integrated mite management programs and have been used in pest management programs for over 100 years.

Different types of petroleum oils are used with different molecular weights. Most oils used are distillations of petroleum, although some oils derived from plants (sesame, almond, citrus) are used.

Crude petroleum oil is a complex mixture of hydrocarbons with both straight chain and ring molecules. Crude oil is separated into a range of products by distillation and refining. The lightest fractions include gasoline, kerosene, diesel and jet fuel. As these lighter fractions distill or boil, they are separated into different fractions. Spray oils are derived from the lighter lubricating oil fraction and distill at a temperature range of 600 to 900°C.

Currently used petroleum oils in the USA are narrow-range oils and have had the waxes, sulfur, and nitrogen compounds removed. Labels on sprays usually describe the degree to which the sulfur compounds have been removed and the percentage of active oil. The sulfur compounds are likely to cause phytotoxic effects, so the degree of removal of these compounds (called the UR rating) is an important piece of information on the label and commonly is greater than 92%. The composition of oil should be greater than 60%.

Since the mid-1960s, narrow-range horticultural oils have been used both as dormant or summer oil sprays. These highly refined and narrow range petroleum oils rarely cause phytotoxicity and increasingly are used for controlling both insect and mite pests on deciduous trees, citrus, and ornamental trees and shrubs. Oils have a wide range of activity against scales, mites, psyllids, mealybugs, whiteflies, leafhoppers, and eggs of mites, aphids and some Lepidoptera. Heavier dormant sprays are used to control overwintering pests in deciduous trees and vines. Summer oils are used to control pests during the growing season.

Oil kills mites and their eggs by contact. The toxicity appears to be due to suffocation of the pest, although it may also be due to chemical effects. Oils block spiracles, reducing the availability of oxygen and suffocation occurs within 24 h. Penetration and corrosion of tracheae, damage to muscles and nerves may also contribute to the toxicity of oils. Oils are sometimes a repellent to pests. Once the oil dries it is no longer toxic to most natural enemies; thus the very short residual activity of oil makes it a useful material for integrated mite management programs, although it also means that there is no residual toxicity to the pests.

No resistance to oils has been reported in pest arthropods, including mites, perhaps because oils have a relatively short residual activity. Oils are easy to apply, relatively inexpensive, and safe to handle. They are relatively harmless to vertebrates, dissipate quickly after spraying, and leave little or no residue on crops. Oils man be used by organic farmers.

A disadvantage to petroleum oils is that they have little residual activity and kill only upon contact, so thorough and precise coverage is necessary to achieve effective control. Phytotoxicity can occur even with these narrow-range oils, especially if plants are weakened or under moisture stress. Thus, applications should not be made during droughts, or periods of very high temperatures. Some varieties of plants are more susceptible to phytotoxicity than others, so caution should be taken when using oils for the first time on a particular crop or cultivar. Oils are not compatible with sulfur or some other pesticides, causing serious phytotoxicity problems.

Organosulfurs

Tetradifon (Tedion) and propargite (Omite, Komite) are organosulfurs. These products contain sulfur as a central atom with two phenyl rings. Tedion is particularly toxic to mites, but has very low toxicity to insects. Organosulfurs are often ovicidal as well as toxic to active stages. Propargite was used for many years (more than 20) and appeared to some to be immune to the development of resistance in spider mite populations. However, propargite resistance has now developed in many populations of spider mites around the world. Propargite is less toxic to beneficial phytoseiid predators than to pest spider mites, and thus could be used in integrated mite management programs, although at high concentrations it also is toxic to phytoseiid predators.

Organotins

Cyhexatin (Plictran) and fenbutatin-oxide (Vendex) are examples of tin compounds that are primarily acaricides and fungicides. Plictran (cyhexatin) was introduced in 1967 and was widely used for many years before resistance developed in spider mites. Some people had assumed that the organotins were immune to resistance problems. The organotins were useful products because they were more toxic to spider mites than to phytoseiids and thus were very useful in integrated mite management programs. Fenbutatin-oxide (Vendex) is another organotin. These products were taken off the market in the USA due to concerns about safety.

Insecticides with Acaricidal Activity

Organophosphorus Pesticides

The organophosphates (pesticides that include phosphorus) are derived from phosphoric acid and are the most toxic of all pesticides to vertebrates. They are, in fact, related to nerve gases by structure and mode of action. Organophosphorus pesticides (OPs) are less persistent in the environment than the organochlorines such as DDT.

Organophosphorus pesticides (such as azinphosmethyl, parathion, ethion, demeton, dimethoate) function by inhibiting important enzymes (cholinesterases) in the nervous system. Acetylcholine is the chemical signal that is carried across synapses (where the electrical signal is transmitted across a gap to a muscle or another neuron. After the electrical signal (nerve impulse) has been conducted across the gap by acetylcholine, the cholinesterase enzyme removes the acetylcholine so the circuit won't be kept on. When OPs poison an organism, the OP attaches to the cholinesterase so it cannot remove the acetylcholine. The circuits then remain on because acetylcholine accumulates. This gives rise to rapid twitching of the voluntary muscles and to paralysis, which is can be lethal if it persists in the vertebrate respiratory system.

Not all OPs are highly toxic to vertebrates; if the phosphorus is modified by esterification (adding oxygen, carbon, sulfur and nitrogen), six different classes of OPs can be produced. Some of these are relatively safe to vertebrates, such as malathion. The use of most OPs is being eliminated in the USA due to the Food Quality Protection Act.

Carbamates

Carbamates (aldicarb, carbofuran, methomyl, propoxur) are derivatives of carbamic acid. The mode of action of carbamates is to inhibit cholinesterase. The carbamates were introduced in the 1950s. Carbaryl (Sevin) is one of the most popular products available to home gardeners for controlling a variety of insect pests and has low mammalian oral and dermal toxicity. Methomyl (Lannate) and aldicarb (Temik) are examples of other carbamates.

Sevin is well known to induce outbreaks of spider mites after applications are made to control other pests. The outbreaks are due to two factors; (i) Sevin kills phytoseiid predators and other natural enemies of spider mites, and (ii) it stimulates reproduction of spider mites, a process called hormoligosis. Even very low doses of Sevin appears to act like a hormone to stimulate reproduction of the two-spotted spider mite *Tetranychus urticae*. It is likely that the use of carbamates also will be eliminated or greatly reduced in the USA due to the Food Quality Protection Act.

Formamides

Formamides include chlorodimeform (Galecron or Fundal), amitraz, and formetanate (Carzol). These products are effective against the eggs of Lepidoptera and also against most stages of mites and ticks. The mode of action of these products is unclear, but thought to be due to the inhibition of monoamine oxidase, which results in the accumulation of compounds called biogenic amines.

Pyrethroids

Many of the pyrethroids have acaricidal activity. Some (such as bioresmethrin, fenpropathrin and bifenthrin) are considered effective acaricides. Unfortunately, pyrethroids usually are very toxic to beneficial arthropods, including phytoseiid predators. These detrimental effects can be very long lasting because the residues persist a long time. Few have been found useful for integrated mite management programs for this reason. Laboratory selection of phytoseiids (*Amblyseius fallacis, Metaseiulus occidentalis, Typhlodromus pyri*) for resistance to two pyrethroid insecticides has been successful. The pyrethroid-resistant strains were developed for use in apple pest management programs using both laboratory and field selection methods.

Pyrroles

Pyridaben is a novel pyrrole pesticide that works as a mitochondrial electron transport inhibitor to block cellular respiration, causing pests to become uncoordinated and die. Can be used on both insects and mites.

Other Acaricides

Azadirachtin

This is a triterpenoid extracted from the seeds of the neem tree *Azadirachta indica*. Extracts include a combination of compounds, the proportion of which vary from tree to tree. Such variability in this natural product makes it difficult to predict the precise effect of the product when extracted by local people. Commercial products may be more consistent in their effect because they have been tested to confirm their quality and are blended to achieve a consistent product. Azadirachtin blocks the action of the molting hormone ecdysone.

Avermectin

Avermectin is a natural product containing a macrocyclic lactone glycoside that is a fermentation product of *Streptomyces avermitilus*, which was isolated from soil. Avermectin is actually a mixture of two homologs, both of which have biological activity. Avermectin has insecticidal and acaricidal properties and is closely related to ivermectin, which kills nematodes.

At appropriate rates, abamectin is less toxic to beneficial phytoseiids than to spider mites; it paralyzes active spider mite stages, but is not toxic to eggs. Avermectin has translaminar activity (meaning it is taken up by the plant tissue and subsequently by spider mites feeding on the plant tissues), but has a short residual toxicity to phytoseiids.

Resistance to this product has been reported in some populations of spider mites. A resistant strain of *M. occidentalis* was obtained after laboratory selection, suggesting that resistance mechanisms may be present in field populations.

The mode of action of avermectin involves blocking the neurotransmitter gamma-aminobutyric acid (GABA) at the neuromuscular junction. Mites that are exposed to abamectin become paralyzed and, although they do not die immediately, the paralyzed mites do stop feeding.

Clofentezine and Hexythiazox

These are very interesting growth regulators of mites; they kill eggs (ovicides) of spider mites, but not the active stages of spider mites. The products have different chemistries, but both are nontoxic to phytoseiid mite eggs or active stages! In fact, the phytoseiid mite *Metaseiulus occidentalis* can be fed a diet consisting solely of spider mite eggs that have been killed with these products and the predator females reproduce and their progeny develop normally. This selectivity makes the products particularly useful for integrated mite management programs because predators can be maintained while suppressing spider mite populations. Unfortunately, resistance to these products has developed in spider mite populations in several locations around the world, including Europe and Australia.

Tebufenpyrad

This is a phenoxypyrazole and has been evaluated under the trade name Pyranica in Australia, where it was shown to be useful in integrated mite management programs in apples because it is selective (relatively nontoxic) to phytoseiid predators.

Acaricides and Fungicides

Benomyl is a carbamate that has been used primarily as a fungicide, but also has acaricidal properties. Benomyl is interesting because it acts as a sterilant of phytoseiid predators. Adult phytoseiid females treated with benomyl survive, but they do not deposit eggs. This product apparently disrupts spindle fiber formation in cells and interferes in the synthesis of DNA, resulting in females that are unable to reproduce.

Resistance in Mites

Resistance to pesticides is an increasingly serious problem around the world. Resistance to one or more pesticides has been documented in more than 440 species of insects and mites. Spider mite and tick species have readily developed resistance to all classes of pesticides.

Resistance is a decreased response of a population of animal to a pesticide or control agent as a result of their application. It is an evolutionary or genetic response to selection. Tolerance is an innate ability to survive a given toxicant dose without prior exposure and evolutionary change. Cross resistance is a genetic response to selection with compound A that generates resistance to both compound A and other compounds (B and C). Multiple resistance is resistance to different compounds due to the coexistence of different resistance mechanisms in the same individuals. Multiple resistances usually are generated by sequential or simultaneous selection by more than one type of pesticide.

Methods for Evaluating Resistance

There are a variety of methods available for assessing resistance to pesticides in mites. The test method chosen will depend upon the goals of the researcher. Each method has strengths and weaknesses.

Resistance is a genetically-determined change in the ability to tolerate a pesticide. Therefore, one must have at least two different populations to test – one that is putatively resistant and one that exhibits the normal, wild type response. Unless these two populations can be compared under identical laboratory conditions, it is difficult to document resistance because historical data are of questionable value in assessing whether a population is resistant. This is because it is very difficult to conduct identical bioassays in two different laboratories, even when attempts are made to use the same methods. Small differences in techniques can result in very large differences in toxicity data. For example, spider mites tested on smooth leaves may respond very differently than spider mites tested on the same plant species but on a variety with hairy leaves. Small differences in formulations and temperature also influence responses of mites to pesticides. Small differences in age or feeding status also influence toxicity responses. Most conclusions about resistance should be based on comparative data obtained by the same researcher under identical conditions.

The apparent failure of a product to control a mite population under field conditions is NOT adequate evidence for resistance. Field failure is a reason to investigate further, but field failures can occur for a variety of reasons that have nothing to do with resistance. Failures could occur because the pesticide applicator may have mixed the product improperly, coverage may have been inadequate, the pH of the water used to mix the pesticide could have altered the toxicity of the product, and the product could have been old or degraded due to improper storage.

Slide Dip Bioassays

Slide dip bioassays of adult female spider mites and phytoseiids have been proposed as a standard method for assessing resistance or tolerance. This method involves placing adult female on their backs on to double-sided sticky tape applied to glass microscope slides and dipping the slides into a specific pesticide concentration. This method has the virtue of being relatively rapid and easy to conduct. However, measuring toxicity to adult females after 24 or 48 h is not an appropriate assay for many pesticide types (for example ovicides, growth regulators). Also, the results probably bear little relation to the field toxicity of the product. It is very likely that many products are much more toxic to the mites using this assay than they would be under field conditions, where mites can feed and move around and coverage is rarely complete, so this method may give no information about whether the resistance level induced is relevant to field concentrations used.

Leaf Dip or Leaf Spray Bioassays

Leaf dip or leaf spray bioassays involve placing mites on leaf disks, which are then sprayed or dipped into a specific concentration of pesticide. This type of bioassay provides an exposure that is more similar that the mites would experience under field conditions and it is possible to measure survival, fecundity, and ability to successfully develop on pesticide residues.

Whole Plant Bioassays

This approach, which involves spraying the entire plant, is very realistic, unless the plants (and pesticide residues) are not exposed to sunlight or rain.

Field Tests

Field trials are the most realistic method for assessing resistance, but it can be difficult to determine why the predators or spider mites died (did other tolerant predators fly in and eliminate the pest?). If adequately replicated over time and space, field trials provide very relevant information. The relevance of application method (high or low volume), coverage, and droplet size can be assessed. Unfortunately, field trials are the most expensive to carry out so the methods described above are often used to save time and funds.

► Insecticides
► Insecticide Toxicity
► Insecticide Formulation
► Detoxification Mechanisms in Insects
► Pesticide Resistance Management
► Pesticide Application

References

Cranham JE, Helle W (1985) Pesticide resistance in Tetranychidae. In: Helle W, Sabelis MW (eds) Spider mites: Their biology, natural enemies and control, vol. 1B. Elsevier, Dordrecht, The Netherlands, pp. 405–421

Croft BA (1990) Arthropod biological control agents and pesticides. Wiley-Interscience, New York, NY

Davidson NA, Dibble JE, Flint ML, Marer PJ, Guye A (1991) Managing insects and mites with spray oils. IPM Education and Publications, Statewide IPM Project, Publication 3347. University of California, Division of Agricultural Natural Resources, Oakland, California.

EXTOXNET: extoxnet@ace.orst.edu This site provides information about pesticides, including concepts in toxicology and environmental chemistry. It is a cooperative effort of the University of California-Davis, Oregon State, Michigan State, Cornell and the University of Idaho.

Roush RT, Tabashnik BE (1990) Pesticide resistance in arthropods. Chapman and Hall, New York, NY

Accessory Cell

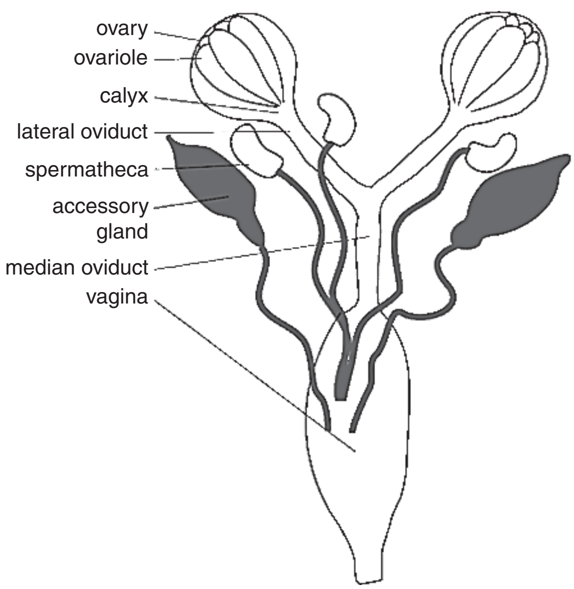
A wing cell not normally present in the taxon.

Accessory Circulatory Organ

Although the dorsal vessel (heart) is normally considered to be the organ responsible for blood circulation in insects, sometimes small sac-like structures are located at the base of appendages (antennae, legs, wings). These structures are capable of contractions independent of the dorsal vessel, and assist in circulation. This is also called "accessory pulsatile organ."

Accessory Gland

A gland associated with the male or female reproductive system, and producing substances associated with the sperm or eggs, respectively (Fig. 7). Male accessory glands produce such substances to



Accessory Gland, Figure 7 **Diagram of the female reproductive system, as found in *Rhagoletis* (Diptera) (adapted from Chapman, The insects: structure and function).**

facilitate sperm transfer, as a barrier to further insemination, as a means of altering female behavior, and as a means of providing nutrition to the female. Females produce substances for packaging their eggs, adhering them to a substrate, and providing a protective coating over the eggs.

Accessory Vein

An extra branch of a longitudinal vein. Such veins normally are designated by a subscript of "a."

► Wings of Insects

Accessory Hearts

Pulsatile, sac-like organs that assist in circulation of the hemolymph into appendages such as the antennae, wings, and legs.

Accidental Host

A host in which the pathogenic microorganism (or parasite) is not commonly found.

Accidental Species

Species that occur with a low degree of consistency in a community type. Such species are not useful for community definition.

Acclimation

The adaptation of an organism' s physiological responses to existing environmental conditions. A nearly equivalent term is "acclimatization," though acclimation may be a more rapid or laboratory-based phenomenon, whereas acclimatization is a long term, field-based phenomenon.

Accuracy

A measure of the closeness of an estimate to the true mean or variance of a population.

► Sampling Arthropods

Acephalous

The condition of lacking an apparent head. This term is usually applied to certain flies and wasps that lack a well-defined head.

Acerentomidae

A family of proturans (order Protura).

► Proturans

Acetylcholine

The synaptic transmitter substance found in the insect central nervous system. When released into the synaptic cleft, it is bound to a receptor, depolarizing the postsynaptic membrane and stimulating nervous excitation.

Acetylcholine Esterase

An enzyme that breaks down acetylcholine after it is released into the synaptic cleft of insect neurons. Interference with acetyl choline esterase, as by exposure to some insecticides, results in prolonged stimulation of the nerves.

Achilidae

A family of insects in the superfamily Fulgoroidae (order Hemiptera). They sometimes are called planthoppers.

► Bugs

Aclerididae

A family of insects in the superfamily Coccoidae (order Hemiptera).

► Bugs

Acoustical Communication in Heteroptera (Hemiptera: Heteroptera)

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Acoustic signaling is found in many hemipteran families. It serves a variety of purposes, particularly defensive behavior such as repelling potential predators and signaling alarm or distress, but also for species spacing within a particular habitat, reproduction, and coordination of group actions. Vibratory signals for reproductive purposes may be produced by males and/or females, leading to aggregation to mate attraction, courtship and copulation. Non-receptive females may sing to reject copulation (male-deterring stridulation), as in the subfamily Triatominae (Reduviidae) and in Pentatomidae (e.g., *Nezara viridula*).

The vibratory signals produced by many insect species cannot be heard by the human ear because the sounds are low frequency and generally transmitted by mechanical vibrations through the substrate, and not by the air. The study of acoustical communication has greatly progressed in accordance with improvement of recording and analyzing equipment, including the necessary computer software.

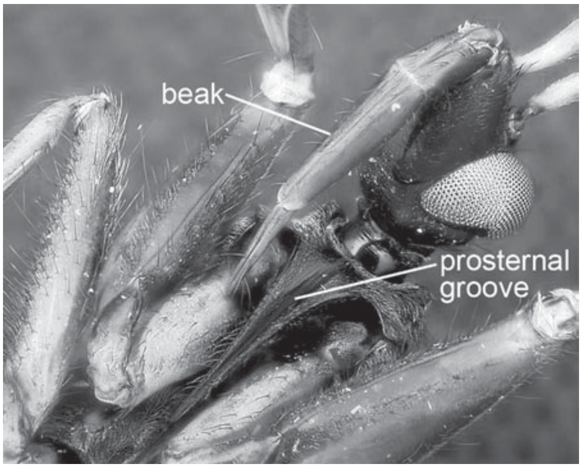
Production of Vibrational Signals and Songs

Vibrational signals and songs are produced by stridulation (stridulatory device, stridulatory organs), by body vibration, or by a simple tymbal mechanism. Stridulation occurs widely in Heteroptera, and is the act of producing sound or vibration by rubbing together certain body parts. The first systematic survey of sound-producing devices in the Heteroptera was that of Handlirsh in 1900. To stridulate, usually both a movable and a stationary portion are needed. The movable part is called the plectrum or scraper. The stationary portion may be called the stridulitrum, file, strigil (strigile, strigilis) or lima (pl., limae). The stridulitrum is typically striated or finely tuberculated, and the plectrum is a structure with a well-defined lip or ridge, tubercles, or provided with spines.

Different parts of the body may be involved to function as the stridulatory device. The forewing edge is most commonly used as a stridulitrum (file), while the hind femur is the most usual structure used as a plectrum (scraper). Other stridulitrum may be located in the head, associated with the mouth (labium, maxillary plate), the thorax (propleurum, metapleuron, prosternal groove), the wings (metathoracic wing vein, hypocostal lamina or articulatory sclerite, underside of clavus), the legs (forecoxa, mesotrochanter, tibia, femora), and the abdomen (sternum, the connexival margin, posterior margin of the pygophore). There are also a variety of locations for the plectrum or scraper: the rostrum, the legs (forecoxal cavity, coxal peg, hind tibia, and fore-, middle or hind femur) or the abdomen. Some stridulatory devices are present in several families, whereas others are only known from a few genera or even a single species.

Examples of stridulation devices are that of the Corixidae (spinose area inside the front femur against the clypeus, genitalia against abdomen segments), Scutelleridae (wart-like, toothed tubercles in the hind tibia against the femur), Reduviidae (tip of the labium against a cross-striated furrow (Fig. 8) in the prosternal groove), some Pentatomoidea and Lygaeiodea (dorsal abdominal files against teeth on the under-sides of the hindwings), some Miridae, Lygaeidae, Largidae and Alydidae (hind femur against forewing edge) and some other Pentatomoidea (tubercles on the hind femora against strigose regions on abdominal sterna).

Morphological differences in the stridulatory device may, in some cases, be related to differences in the songs emitted by either males or females, as



Acoustical Communication in Heteroptera (Hemiptera: Heteroptera), Figure 8 The stridulatory apparatus in Reduviidae: the tip of the labium is rubbed against a cross-striated furrow in the prosternal groove.

occurs in the burrower bugs (Fig. 9) *Scaptocoris castanea* and *S. carvalhoi*. In *S. castanea*, males have a longer stridulitrum than females. However, in *S. carvalhoi* the stridulitrum length does not differ between sexes. Instead, in *S. carvalhoi* the male stridulitrum has more teeth than in the female stridulitrum. There are no intersexual differences for this latter morphological trait in *S. castanea*.

Differences in the stridulatory apparatus may be related to interspecific differences, with a specific diagnostic value. In the genus *Triatoma* (Reduviidae), it is possible to distinguish between *T. guazy* and *T. jurbergi* at any nymph stage or in the adults by studying the stridulatory sulcus (stridulitrum). As *T. jurbergi* is naturally infected with *Trypanosoma cruzi*, the causal protozoan of Chagas disease (American trypanosomiasis), identification of specimens along their whole life cycle is of great medical importance.

In other instances, morphological differences in the stridulatory device do not cause differences in their song patterns. For example, in Reduviidae of the subfamily Triatominae, individuals of the same species have stridulatory grooves with different inter-ridge distances, though the frequency spectra and repetition rates are similar.

A tymbal is formed by abdominal tergal plates fused together and which vibrate over a hollow chamber within the abdomen. The tymbal is activated by muscular contractions and produces body vibrations that are low frequency. Tymbals have been found in Piesmatidae, Pentatomidae, Acanthosomatidae, Cydnidae, Lygaeidae, Coreidae and possibly Reduviidae, and similar vibration-producing mechanisms have been found in Plataspidae and Rhopalidae. Differences exist about precise abdominal parts and muscle contraction mechanisms among the tymbals of different families. For example, the description of the *N. viridula* tymbal follows: The first and second abdominal tergites are fused into a forward-backward movable tymbal-like plate that is loosely fixed, anterior and posterior, to the thorax and to the third abdominal tergum, by a chitinous membrane, and more firmly, laterally, to the pleurites. Longitudinal and lateral compressor muscles contract synchronously and in phase with these vibratory waves.

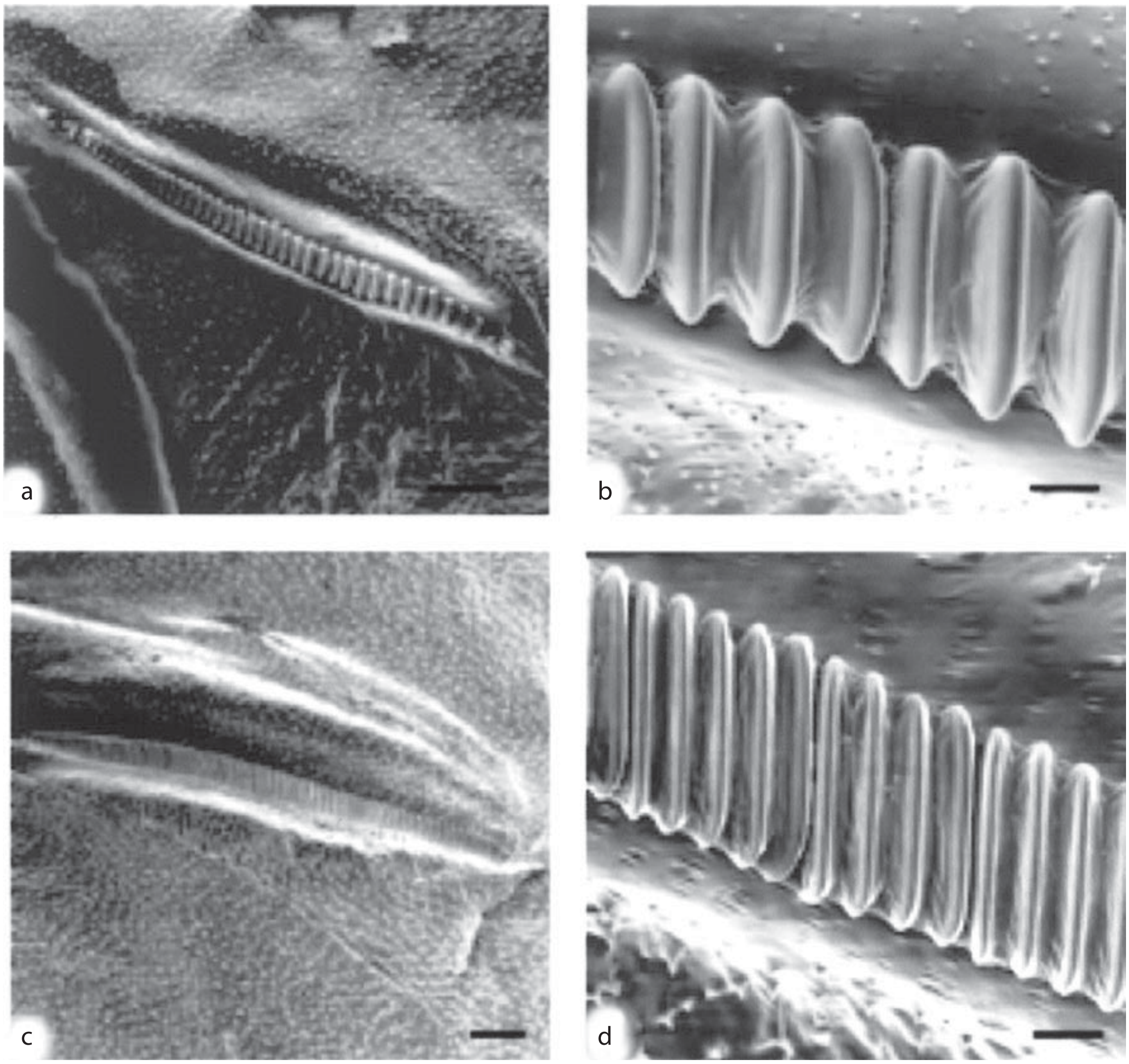
All Heteroptera species investigated so far emit low frequency narrow-band signals by body vibration, and/or broadband signals produced by stridulation. For example, in Cydnidae and Pentatomidae, vibratory mechanisms produce a low frequency vibration (around 100 Hz), and the stridulatory vibration extends up to 10 kHz.

Reception of Vibrational Signals and Songs

Although sound production is found quite widely in Heteroptera, it is not common to find structures specialized for sound reception. Sound reception in Heteroptera is possible due to the presence of either scolopophorous organs or tympanal organs.

Scolopophorous organs are mechanoceptors, and they occur widely in insects. They are composed of sensory sensilla (scolopodia), which may be arranged in groups, and are distally attached to a membrane in the body wall or to the body wall itself. Scolopophorous organs may be located in antennae (Johnston's organ), legs (subgenual organ, joint chordotonal organ), thoracic pleura, or abdominal terga.

Legs are the site of sensory organs that detect vibratory signals with highest sensitivity. For example, at the dorsal side of each leg of *N. viridula* there are four scolopodial organs: femoral, tibial, tarsopretarsal and subgenual organs. The receptor neurons may be low frequency (most sensitive between 50 and 100 Hz) or high frequency sensitive (there are two types: middle frequency neurons being sensitive around 200 Hz, and higher frequency



Acoustical Communication in Heteroptera (Hemiptera: Heteroptera), Figure 9 Interspecific differences in the stridulatory devices found in females of the burrower bugs *Scaptocoris castanea* and *S. carvalhoi* (Hemiptera: Cydnidae). Images a and b are *S. castanea*; images c and d are *S. carvalhoi*. Images a and c show the stridulitrum in the postcubital vein of the hind wings (scale bar = 100 μ); images b and d show the central section of the stridulitrum, showing details of the teeth (scale bar = 10 μ) (adapted from Čokl et al (2006) Physiol Entomol 31:371–381).

neurons sensitive around 700–1000 Hz). Also, the Johnston's organ of *N. viridula* has several vibratory sensitive organs which respond in the frequency range between 30 and 100 Hz. When standing on its host plant, the male of *N. viridula*, by different combinations of legs and antennae, may compare the vibratory signals on two branches of the host plant, and choose the best one in order to locate the singing female. The most probable mechanism underlying resolution of direction by vibratory cues (vibratory directionality) may be time-of-arrival differences (perception of vibratory signals by two different receptors in the insect). For example, when legs of the receptor bug are separated by 2 cm, a time-of-arrival difference between 0.125 and 0.250 ms is created, very close to that found in scorpions, where vibrational directionality is well known. Reduviidae also receive vibratory signals via legs and antennae. Fewer data are available on leg vibratory receptor organs in other land bug species. Among land bugs, no sensory organs for airborne sound have been found.

Tympanal organs have been found in the mesothorax of the Corixidae, and are in contact with the physical gill air bubble. They are able to catch airborne sounds, and to respond to stridulation frequencies produced by conspecific bugs.

Transmission of Vibratory Signals and Songs

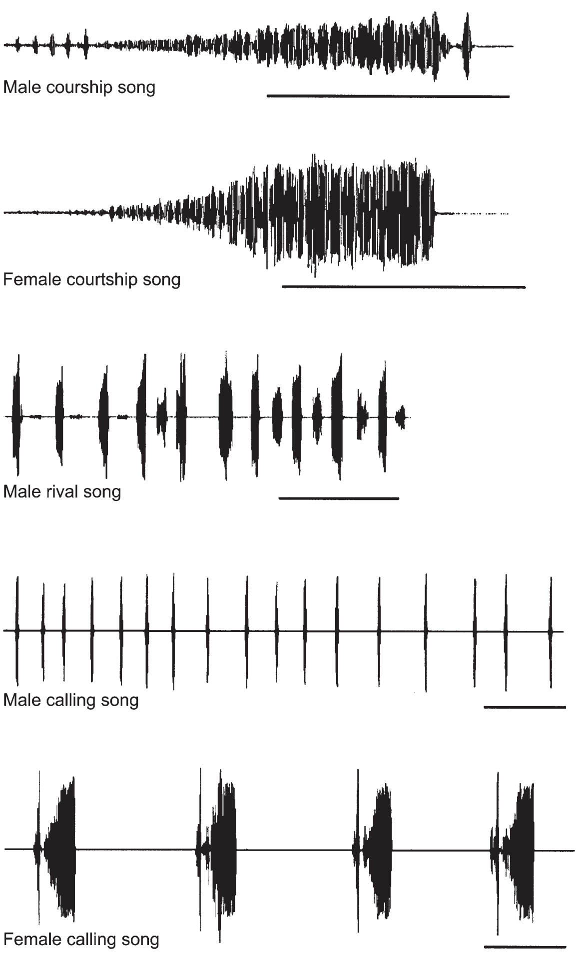
Independent of their mode of production, vibrational signals may be transmitted by the substrate (substrate-borne vibrations) or by the air (airborne vibrations). The signals may travel a short or long distance, or travel at a low or high speed. Low-frequency components are more suitable for longer-range communication through plants. Low frequency signals travel longer distances, but slowly; high frequency signals travel shorter distances, but quickly. Long-range vibratory songs are associated with pre-mating calling and vibrational orientation, and close-range vibratory songs are associated with courting rivalry and repelling.

Substrate-borne vibrations are less costly to the emitter. Also, substrate-borne vibrations are more far-reaching signals for intraspecific communication and not easily perceived by a potential predator or parasitoid. Usual substrates to transmit vibrational signals are plants or soil.

The characteristics of plants as transmission media for insect-produced vibrations have been described, and in many respects they determine signal production and the mode of reception. Depending on the physical properties of the host plant, the vibratory signals are transmitted effectively or not. Vibrations can be transmitted all along the stem, but the physical properties of a plant (e.g., elasticity, water content) affect resonance of insect vibrations. For transmission through plants, insects commonly emit broadbanded-mixed stridulatory and vibratory signals. Higher-frequency signals produced by stridulation are less relevant for long-distance communication through plants. However, narrow-band and low frequency songs are efficient in long-distance communication when well tuned to the resonant spectra of their host plants. The vibrational pulse reflects when attaining both the root area and top of the plant, and reflected waves travel up and down the stem several times. Reflections change the patterns of the input signal. Abiotic factors (temperature, rain, wind) may significantly modify plant resonance, masking insect vibratory signals and thus the effectiveness of the signal. Plant-borne vibrations seem to be important in the success of group-living, herbivorous insects for locating and remaining in a group of conspecifics, for locating food resources, and to avoid predation. Also, small insects that are not able to emit airborne sounds efficiently at low frequencies in many cases communicate with vibratory signals transmitted through plants.

In the stink bug *Nezara viridula* (Pentatomidae) (Figs. 10 and 11), a species which has become a model for all Pentatomorpha in relationship to acoustical communication, its vibratory signals were recorded and described first as airborne sound. However, further investigations showed that their most important mode of transmission is as substrate-borne vibrations. In *N. viridula*, a male could perceive a female calling in a *Cyperus* stem 2 m away from him, mechanically coupled only by roots and the surrounding earth. Below the leg of the singing bug, the intensity of signals was about 4 mm s^{-1}. On the bottom of the same stem (a distance of 80 cm) it decreased to around 3 mm s^{-1}, and at the place of the receiving bug, 200 cm away, it was approximately 0.5 mm s^{-1}.

When transmitted through the soil, signals travel a shorter distance and are more attenuated than when transmitted through a plant stem. For example, in *Scaptocoris* species (Cydnidae) the velocity of soil transmitted signals varied between 1.5 and 12.9 ms^{-1} at a distance of 0.5 cm.



Acoustical Communication in Heteroptera (Hemiptera: Heteroptera), Figure 10 Oscillograms of songs emitted by males and females of the southern green stink bug, *Nezara viridula* (Pentatomidae) (adapted from Čokl, Virant-Doberlet (2003) Annu Rev Entomol 48: 29–50).

Acoustic Characteristics of Vibrational Signals

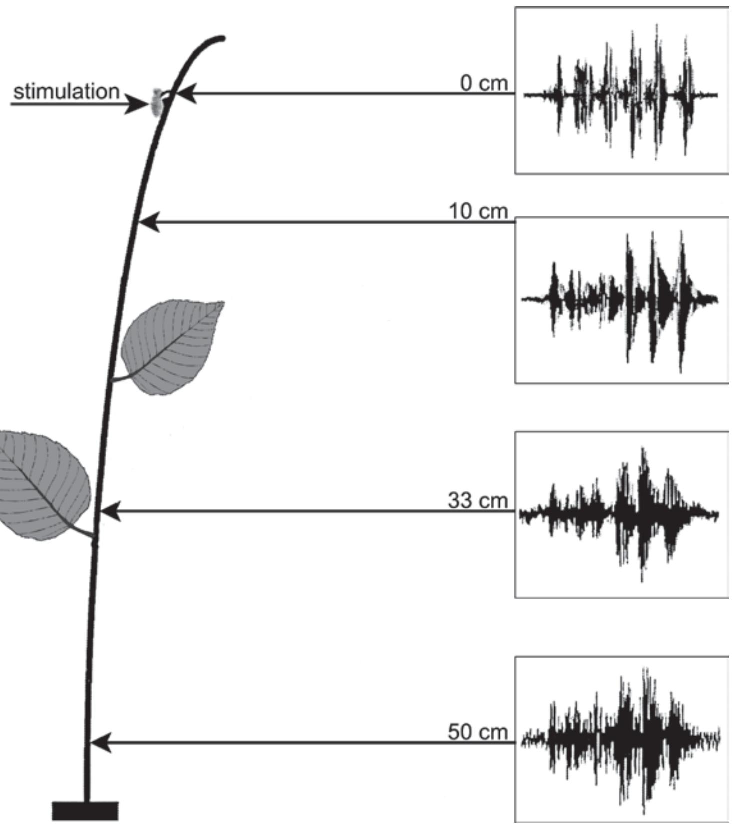
A vibrational signal may be characterized by its temporal (pulse train duration, repetition times, inter-pulse intervals) (Fig. 12) and spectral characteristics (dominant frequency). All of these characteristics may be measured by the receptor insect, who may modify its behavior in response to the message. The dominant frequency of signals produced by the vibratory mechanism lies between 50 and 200 Hz in most Heteroptera. Between species, songs differ in their time structure and amplitude modulation of their units. On the other hand, spectrally and temporally different pulse trains trigger the same male behavior in *N. viridula*.

In *Rhodnius prolixus* (Reduviidae), the male-deterring call has a main carrier frequency of about 1500 Hz, and the disturbance stridulation has a main carrier frequency of about 2200 Hz. In *Rhinocoris iracundus* (Reduviidae), low-frequency components of carrier frequency below 200 Hz are exchanged with frequency-modulated stridulatory components whose dominant frequency lies between 1 and 2 kHz. In *Triatoma infestans* (Reduviidae), distress songs have a peak of frequency between 700 and 800 Hz, although in other reduviids the carrier frequency may reach about 2000 Hz.

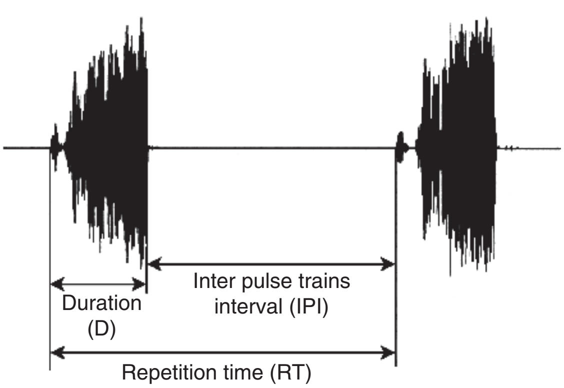
In *N. viridula*, dominant frequencies between 80 and 150 Hz were found in songs either as airborne sounds, or substrate or body vibrations. Body vibrations are around 100 Hz, and lie close to the range of best frequency sensitivity of low frequency receptor cells.

Specificity and Variability of Vibratory Signals

Sounds, especially those involved in the reproductive process (attraction, courtship, copulation),



Acoustical Communication in Heteroptera (Hemiptera: Heteroptera), Figure 11 **Laser vibrometer recordings taken from a plant fed upon by *Nezara viridula* showing the pattern of recordings at various distances (in cm) from the point of stimulation (adapted from Miklas et al (2001) J Insect Behav 14: 313–332).**



Acoustical Communication in Heteroptera (Hemiptera: Heteroptera), Figure 12 **Temporal parameters of a vibratory signal (adapted from Miklas et al (2003) Behav Process 61: 131–142).**

can be very complex and highly species-specific, and may be used as taxonomic characters of land bugs. In contrast, signals are much less specific when they provide information about enemies, rival mates, or serve as distress (disturbance or alarm) signals.

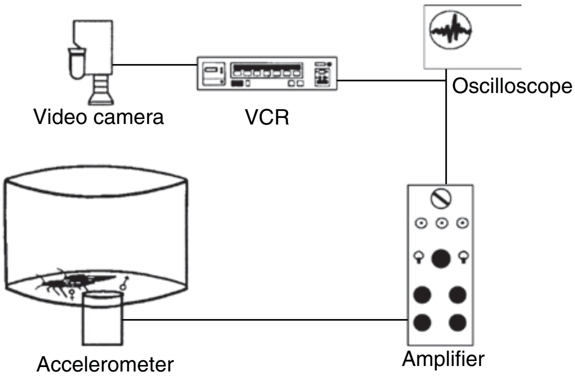
Females of *N. viridula* sing to trigger the male approach, and to evoke emission of the male courtship song. Females coming from populations of different geographic origin emit different calling songs, which can be differentiated by males. Females of *N. viridula* may emit a song that rejects copulatory attempts of males and stops their courting, and this is also known in the reduviid *Rhodnius prolixus*. The courtship songs of both males and females in different populations are not markedly different, but the calling songs may differ in some features and may be the source of reproductive isolation among populations. *Nezara viridula* produces four different species and sex-specific songs, and two of them play a vital role in mate location. There is song variability within populations (inter-individual variability). To assess those differences, the temporal song (pulse train duration, repetition times, inter-pulse intervals) and spectral song characteristics (dominant frequency) may be measured. Males usually show a preference for the females of their own population, although they may recognize females from other populations as potential partners.

In *Tritoma infestans*, stridulation songs differ in their syllable durations, repetition rate and main carrier frequency, depending on the song function. Differences come from rubbing their rostrum (scraper) at different speeds on the prosternal file. Also in *Rhodnius prolixus*, the different frequency between deterrent and disturbing signals can be explained on the basis of a different rubbing velocity by the proboscis against the prosternal stridulatory organ (Fig. 13).

In *Scaptocoris carvalhoi* and *S. castanea* (Cydnidae), two sympatric burrower bugs, high individual variation of the dominant frequency was observed in both male and female emissions (Fig. 14).

Vibratory Signaling in the Families of Heteroptera

Vibratory signaling has been reported in several Dipsocoromorpha and Leptodomorpha, but has been better studied in the following families: Veliidae (Gerromorpha), Nepidae, Corixidae, Notonectidae (Nepomorpha), Reduviidae, Miridae, Tingidae, Nabidae (Cimicomorpha), Aradidae, Acanthosomatidae, Cydnidae, Pentatomidae, Scutelleridae, Tessaratomidae, Thaumastellidae, Colobathristidae, Lygaeidae, Piesmatidae, Largidae, Alydidae, Coreidae, Rhopalidae (Pentatomorpha) (Figs. 15 and 16). Selected examples follow:



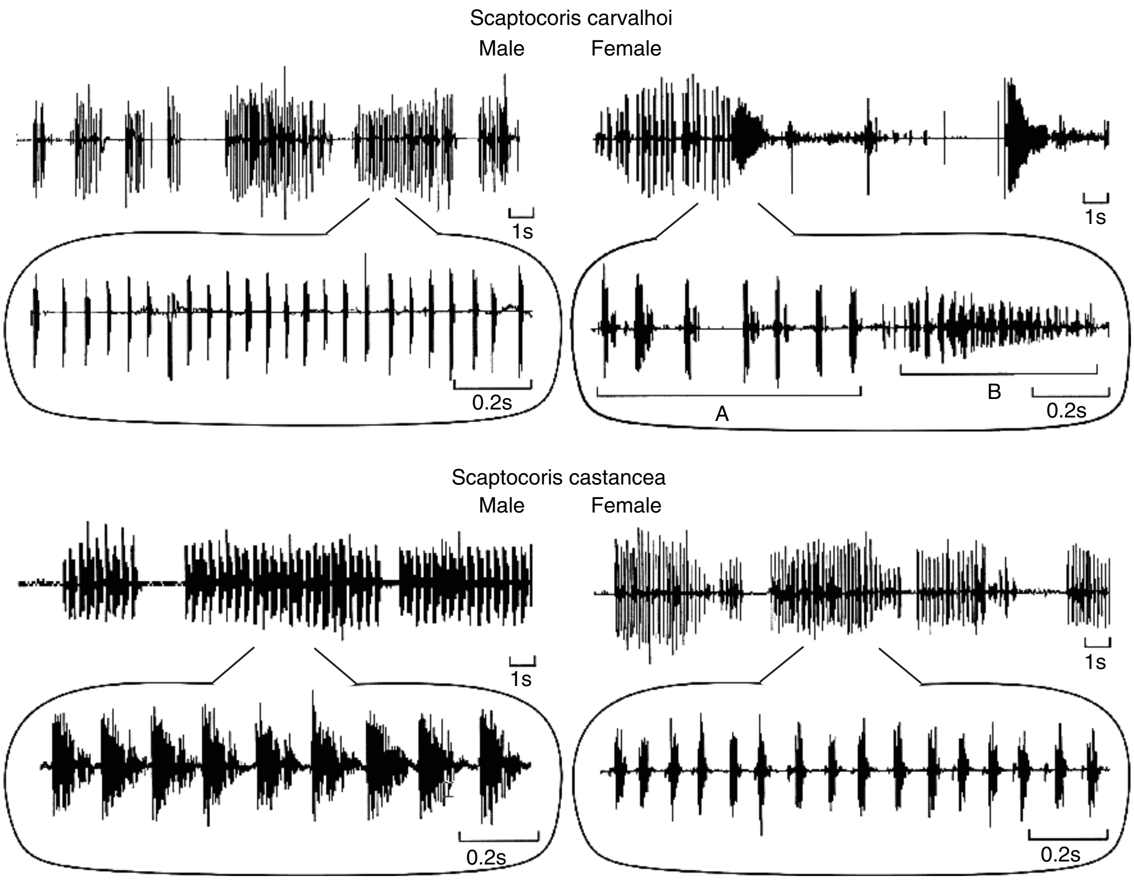
Acoustical Communication in Heteroptera (Hemiptera: Heteroptera), Figure 13 **Experimental setup used to study substrate-borne signals produced by stridulation in *Rhodnius prolixus* (Hemiptera: Reduviidae). The accelerometer generated a signal with voltage proportional to the instantaneous acceleration of the moving object, electrical signals were amplified and monitored by an oscilloscope, then this information was stored in the sound track of a videotape. Also, the behavior of the bugs was simultaneously videotaped (adapted from Manrique, Schilman (2000) Acta Trop 77:271–278).**

Corixidae

In Corixidae, males or both sexes use species-specific sound for mate attraction and in courtship. The sounds are produced by stridulation, i.e., rubbing together specially modified parts of the body, or the partner's body.

Notonectidae

In Notonectidae, males produce species-specific courtship sounds by rubbing roughened parts of their front tibiae and femora against a special stridulatory region at the base of the rostrum (Fig. 17). In genus *Buenoa*, the sound can be heard at a distance of several meters. While next to the female, but before clasping her, the sound pattern can change.

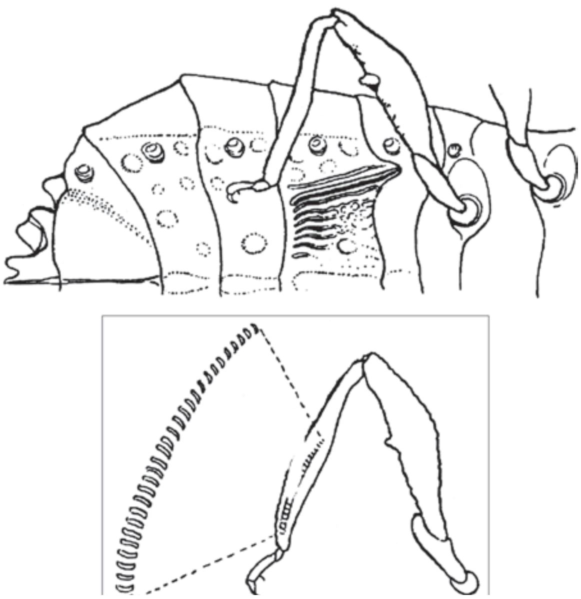


Acoustical Communication in Heteroptera (Hemiptera: Heteroptera), Figure 14 Vibratory emissions of male and female burrower bugs *Scaptocoris carvalhoi* (above) and *S. castanea* (below) (Hemiptera: Cydnidae). A and B designate the two types of female song found in *S. carvalhoi*. Time scales are marked below oscillograms (adapted from Čokl et al. (2006) Physiol Entomol 31:371–381).

Reduviidae

Distress (disturbance or alarm) signals in Reduviidae may be produced either as nymphs or adults (males and/or females). In *Panstrongylus rufotuberculatus* (Reduviidae), stridulation occurs only under conditions of extreme provocation. Its sound is audible by the human ear, which is unusual among stridulating Triatominae, and is similar to the sound of sandpaper scraping wood. The tip of the rostrum is rubbed along the transversely ridged prosternal groove with an anterior-posterior movement; the return stroke (posterior-anterior) is silent. Stridulation lasts for about 5 min, although the insect remains immobile when held for a longer time. In a silent environment, the sound is audible at about 1 m away. A disturbance call has been described in the following triatomine species: *Dipetalogaster maxima*, *Triatoma infestans*, *T. guasayana*, *T. sordida*, *Panstrongylus megistus* and *Rhodnius prolixus*.

In the spined assassin bug, *Sinea diadema*, agonistic interactions between adult females may be resolved by stridulation in 33% of the cases. Stridulating individuals retreated more often than their non-stridulating opponents, indicating that stridulation may be a startle mechanism employed by temporarily disadvantaged individuals to escape from encounters. Together with other signs, stridulations provide information on the identity and relative fitness of the opponent.

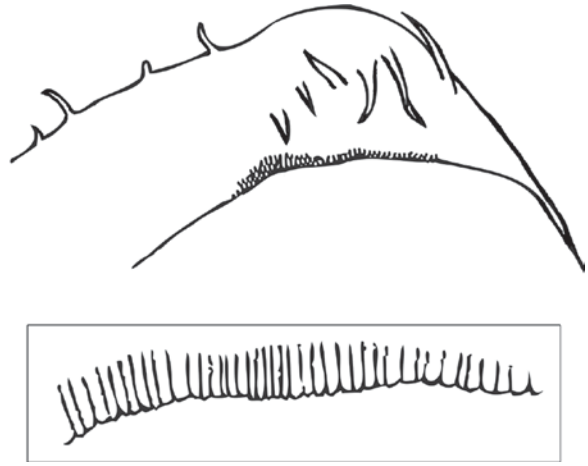


Acoustical Communication in Heteroptera (Hemiptera: Heteroptera), Figure 15 ***Artabanus lativentris*** **(Hemiptera: Aradidae): (above) ventral view of abdomen, with file (stridulitrum), (below) hind leg with detail of scraper (plectrum) in the interior surface of the hind tibia (adapted from Schuh and Slater 1995 True bugs of the world (Hemiptera-Heteroptera): classification and natural history. Cornell University Press, Ithaca, NY, 335 pp).**

The acoustic repertoire of the ambush bug, *Phymata crassipes*, is quite large and may be displayed by females, males or nymphs. Its vibrational songs may be emitted in response to, and alternating with, calls from conspecifics, or even human speech or whistle. Sound emission is related to disturbance, interaction with other males and females, or courtship. Signals are produced by locomotory, stridulatory and/or vibratory mechanisms. Airborne signals directly or indirectly stimulate vibrational receptors. Bugs within a group respond to each other only via substrate, even in close proximity.

Miridae

Although a stridulatory device has been described in several tribes and subfamilies, the functions of acoustical communication in Miridae are still unknown.



Acoustical Communication in Heteroptera (Hemiptera: Heteroptera), Figure 16 ***Phyllomorpha laciniata*** **(Hemiptera: Coreidae): (above) dorsal view of pronotum with scraper (plectrum) at its margin, (below) detail of spines of scraper (adapted from Moulet 1995 Faune de France 81).**

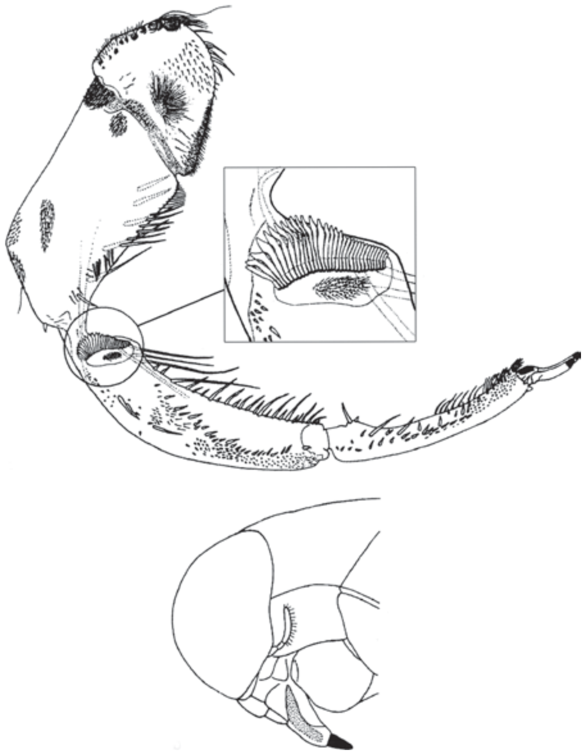
Tingidae

In the tingid *Corythuca hewitti*, vibrational signaling during group movements may occur as groups of nymphs are attended by a female. It has been reported that a disturbance of the leaf where *C. hewitti* aggregated caused feeding to stop and dispersal by the bugs, with occasional stopping of the bugs to vibrate the abdomen in a vertical plane, a behavior followed by conspecifics.

Cydnidae

In cydnids, the low species and sex specificity of pure stridulatory signals indicates that these vibratory emissions may play a role in disturbance (defensive) behavior, as in *Tritomegas bicolor*. Stridulatory signals are also related to aggregation or some other unspecific behavioral context. Cydnid bugs engage in rival singing and also distress (disturbance or alarm) signals, either as nymphs or adults (males and/or females).

Courtship, acceptance and rivalry songs show higher specificity and in most cases are



Acoustical Communication in Heteroptera (Hemiptera: Heteroptera), Figure 17 **Male *Anisops megalops* (Hemiptera: Notonectidae): (above) foreleg with detail of scraper (plectrum) in the interior surface of the fore-tibia, (below) lateral view of the head with file (stridulitrum) on the labium (adapted from Schuh and Slater 1995 True bugs of the world (Hemiptera-Heteroptera): classification and natural history. Cornell University Press, Ithaca, NY, 335 pp).**

produced by low frequency body vibration and/or by stridulation. *Tritomegas bicolor* produces courtship, mating, and male rivalry calls by stridulation and body vibration. In *Sehirus luctuosus*, the male's courtship call is produced by body vibration, giving a drumming song. Two types of species-specific male courtship songs, produced by stridulatory and vibratory mechanisms, have been described. The first type triggers female response, a species-specific agreement song. The second type stimulates pair formation.

In the group-living species of genus *Scaptocoris*, the absence of low frequency components of the emitted signals and the uniformity of songs indicate that calling and courtship may be mediated by signals of other modalities. The lack of low frequency signals may be explained by the direct contact of the bug with soil, which mechanically prevents free vibration of the abdomen.

Pentatomidae

Pentatomid bugs engage in rival singing. For example, *Nezara viridula* and *Rhapigaster nebulosa* may alternate rival songs until one or both stop singing, and in *P. lituratus*, males perform rival singing. Vibrational directionality has been demonstrated in host or prey searching in the predatory stink bug *Podisus maculiventris*.

The general pattern of singing during pre-mating behavior is similar for all Pentatomoidea. Calling starts with the emission of the female calling song, which triggers males to respond with calling and courtship songs, activates them to walk on the plant, and enables directional movement toward the female. Alternation of male and female songs may result in more or less complex duets, as is the case in *N. viridula*. *Nezara viridula* vibrates its body as part of intersex communications (courtship, directional cue for locating the mate, mate recognition), which implies that substrate-borne signals are highly species-specific. The female song causes the male to walk, to respond with the calling and courtship songs, and to approach the source of the song with characteristic search behavior. In contrast, females show no reaction to vibratory stimulation and no vibrational directionality.

► Insect Acoustics
► Cicada Acoustics
► Vibrational Communication

References

Čokl A, Virant-Doberlet M (2003) Communication with substrate-borne signals in small plant-dwelling insects. Annu Rev Entomol 48:29–50

Čokl A, Nardi C, Bento JMS, Hirose E, Panizzi AR (2006) Transmission of stridulatory signals of the burrower bugs *Scaptocoris castanea* and *Scaptocoris carvalhoi* (Heteroptera: Cydnidae) through the soil and soybean. Physiol Entomol 31:371–381

McGavin GC (1993) Bugs of the world. Blandford, London, UK, 192 pp

Miklas N, Čokl A, Renou M, Virant-Doberlet M (2003) Variability of vibratory signals and mate choice selectivity in the southern green stink bug. Behav Process 61:131–142

Reyes-Lugo M, Díaz-Bello Z, Abate T, Avilán A (2006) Stridulatory sound emission of *Panstrongylus rufotuberculatus* Champion, 1899 (Hemiptera: Reduviidae: Triatominae). Braz J Biol 66(2A):443–446

Schuh RT, Slater JA (1995) True bugs of the world *(Hemiptera – Heteroptera):* classification and natural history. Cornell University Press, Ithaca, NY, 335 pp

Wheeler AG Jr (2001) Biology of the plant bugs. Cornell University Press, Ithaca, NY, 507 pp

Acoustic Aposematism (Clicking) by Caterpillars

Adult Lepidoptera are well known to perceive sound, such as the ultrasonic cries of insectivorous bats. Some even produce sounds that are used for social communication. Less well known is the sound production and reception of larvae. Some caterpillars employ vibrational signals with ants (e.g., Lycaenidae and Riodinidae), communicate about space with conspecifics (e.g., Gracillariidae), or detect insect predators or parasitoids (e.g., Noctuoidea and Gracillariidae). However, "clicking" sounds are an audible sound produced by caterpillars of silk moth (Saturniidae) and hawk moth (Sphingidae). This noise has also been described as "squeaking" or "crackling," and originates with the mandibles. Defensive sounds are usually categorized as startle or warning behaviors; startle sounds warn a potential predator, causing momentary hesitation and escape of the potential prey, whereas warning sounds alert a potential predator that it is inadvisable to attack. Associated with the clicking sound is regurgitation behavior, and both actions follow disturbance of the larva. Regurgitant usually is adverse to predators, and is a widespread defensive behavior among insects. Thus, clicking is thought to warn potential predators of an unpleasant experience if predation is attempted, but it is also possible that clicks function as startle sounds, allowing escape. This latter explanation seems unlikely, however, as caterpillars usually move very slowly, so escape is not very likely.

► Acoustic Communication in Insects
► Vibrational Communication

Reference

Brown SG, Beottner GH, Yack JE (2007) Clicking caterpillars: acoustic aposematism in *Antheraea polyphemus* and other Bombycoidea. J Exp Biol 210:993–1005

Acoustic Communication in Insects

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Sound is used by a wide variety of insects for diverse purposes. It is difficult to evolve an acoustic communication system. There must be modifications to produce sound, transmit the sound in the environment and modify the sound to specific biological purposes, as well as the evolution of structures that will receive and decipher the signals. Arthropods are one of only two major groups of animals (along with the vertebrates) that have evolved acoustic communication and insects are the primary group of arthropods to exhibit acoustic behavior. At least ten orders of insects possess species that produce acoustic signals.

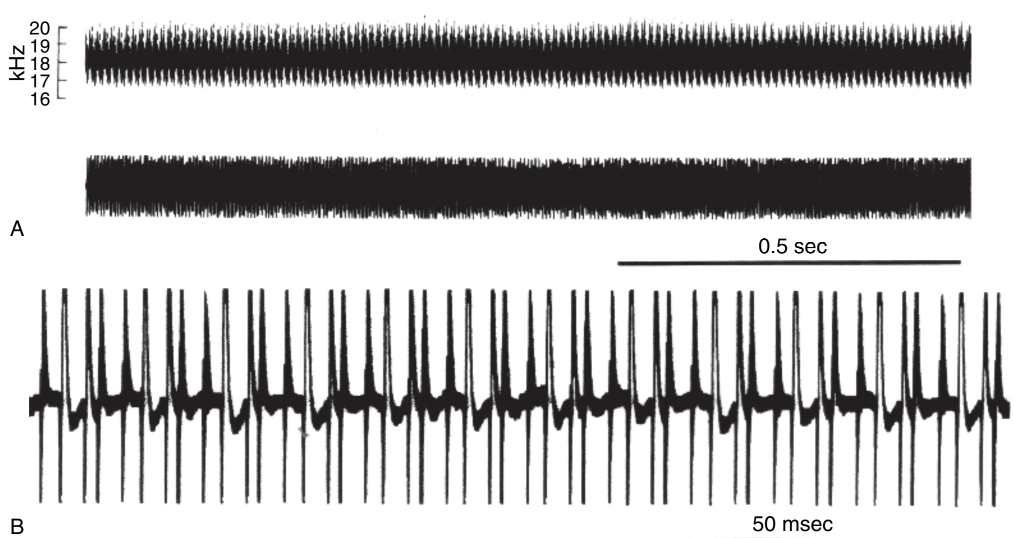
Sound

Sound is generated by causing the repeated compression and rarefaction of an elastic medium. The waves of compression produced will then travel through the medium to the receptor or target. The medium can be air, water or a substrate – so sound also encompasses vibrations. As the sound energy travels through the environment, it is modified by various interactions with the components of that environment. In addition, sound waves are reflected as they move through any environment. This bending of sound waves can initiate interactions among the waves. The signal begins to deteriorate as a result of these wave interactions and with the variations in the signal initiated due to temperature and humidity. Acoustic energy is also lost as it is absorbed by structures in the environment and as a result of spherical spreading from the sound source. The loss of signal integrity due to these environmental interactions is termed the excess attenuation of the signal. The amount of excess attenuation varies with the habitat and the original signal properties.

To complicate matters, the small size of insects requires that they use high frequencies (Fig. 18) to transfer energy efficiently to the signal. This will limit the range of a given signal because higher frequencies attenuate more rapidly in the environment. To use lower frequencies, insects must modify their bodies or behaviors to increase the efficiency of sound production. For example, tree crickets (Gryllidae) create a baffle by inserting their body in a leaf to decrease the acoustic short circuiting of a small dipole sound source, mole crickets (Gryllotalpidae) dig burrows which act as loudspeakers that amplify and direct their calls skyward, and the hollow abdomen of male cicadas (Cicadidae) acts as a resonating structure to amplify the acoustic signals produced by the tymbals.

The sound producing systems of insects are generally vibrating structures. These structures are necessary because muscles cannot contract rapidly enough to produce high frequency sounds. The sound generating structures vibrate multiple times for each muscle contraction, so the sound producing systems act as frequency multipliers. Once the vibrations are initiated, the sound can be modified by attached resonant structures.

There are many different schemes that can be employed to describe insect calls. The variety of sound production mechanisms has led to a variety of terminologies. No one terminology has been successful in describing the different sound production mechanisms or phylogenetic relationships of insects. When sounds are recorded and analyzed in any acoustic work, each analysis of acoustic signals in



Acoustic Communication in Insects, Figure 18 **Acoustic signal produced by the cicada *Beameria venosa* (Uhler). (a) Sonogram of calling song illustrating energy distribution of the call. Middle trace is an oscillogram illustrating the temporal pattern of the call. (b) Expanded oscillogram to show individual sound pulses within the call.**

insects should provide a detailed description of the terminology used to describe the signals, and illustration of the terminology on any oscillogram or sonogram in the work.

Sound Production

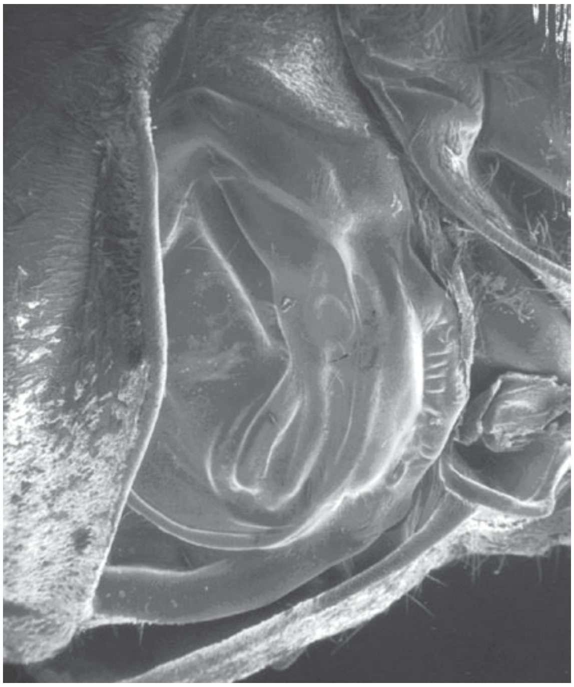
There are several different types of sound production mechanisms that have evolved in insects. The relatively low muscle contraction frequency means that additional structures had to evolve in order to produce the high frequency sounds that small body size will require to generate acoustic signals efficiently.

The primary mechanism used by insects to produce sound is a stridulatory apparatus. The chitinous exoskeleton and jointed appendages of insects are preadapted for modification into stridulatory apparati. Each stridulatory apparatus is composed of a file and plectrum or scraper. The file is generally a row of small cuticular teeth that is rubbed against a ridge or blade (the plectrum) on some other body part (Fig. 19). The teeth are bent as they catch on the plectrum and pop forward as they release from the plectrum. The release causes the teeth to vibrate alternately compressing and expanding air molecules producing sound. In general, these vibrations will occur in a single plane, resulting in a dipole being formed that produces an asymmetrical sound field at close range. The joints and exoskeleton of insects have permitted stridulatory apparati to evolve in many locations on the body. There are file and scrapers found between antennal segments (Phasmatodea), separate mouthparts (Orthoptera), head and thorax (Coleoptera), abdominal segments (Hymenoptera), wings and thorax (Lepidoptera, Hemiptera), body parts and legs (Hemiptera, Orthoptera), legs and wings (Orthoptera, Lepidoptera, Coleoptera), legs and legs (Thysanoptera, Hemiptera), between wings (Orthoptera), and between segments on the genitalia (Lepidoptera, Hemiptera). A tymbal organ is a specialized sound production organ. It is a ribbed, chitinous membrane attached to a tymbal

Acoustic Communication in Insects, Figure 19 **Stridulatory apparatus of the cicada *Tettigades undata* Torres. The file (illustrated) is located on the mesothorax in this group of cicadas. The plectrum is located on the tegmina. Sound pulses are produced as the tegmina is rubbed over the series of mesothoracic ridges.**

muscle (Fig. 20). The tymbal buckles as the tymbal muscle contracts. Sound pulses are produced when the tymbal buckles, when individual ribs buckle and potentially when the tymbal returns to its relaxed position. The unbuckling of the tymbal is assisted by the resilin within the tymbal. The resonant frequency of the tymbal determines the frequency of the sound pulses produced. Additional structures such as the opercula, tymbal covers, various muscles and the abdominal air sacs can modify the sound produced. The abdominal air sacs can become rather large as in the bladder cicada *Cystosoma saundersii* Westwood whose abdomen is so large, to resonate at a low frequency, that the male has difficulty flying. The tymbal is a common organ in the Hemiptera and acts as the ultrasonic pulse generator in the Lepidoptera.

Percussion is another mechanism of sound production used by insects. Crepitation, a clicking sound produced by the wings, is another percussion mechanism in insects. The wings are clapped together or banged on the substrate to produce a sound pulse in some Hemiptera. It is relatively rare for airborne signals which are generally produced as a by-product of flight. The wings may strike each other or the legs



Acoustic Communication in Insects, Figure 20
Tymbal organ of the cicada *Beameria venosa* (Uhler). The internally attached tymbal muscle buckles the tymbal to produce a sound pulse.

during flight-producing sound pulses as in the acridid grasshoppers (Orthoptera). However, specialized percussive sound production systems have evolved. A castanet is found on the costal margin of the tegmina in some moths (Lepidoptera) which produces a pure tone when struck. The acridid grasshopper *Paratylotropidia brunneri* Scudder can snap their mandibles together to generate sound. Percussion has been observed in Hemiptera, Isoptera, Plecoptera, Lepidoptera, and Orthoptera.

Tremulation is the vibration of unspecialized body parts to generate sound. The abdomen is often moved dorso-ventrally or laterally to send vibrations through the legs to the substrate. This mechanism has been well studied in the lacewings (Neuroptera). Wing vibrations can also be used to send information over short distances. This type of signal is produced by members of the Diptera (flies and mosquitoes) and Hymenoptera.

The expulsion of tracheal air is the final and relatively rare mechanism of insect sound production in insects. This method of sound production has been described in a number of insects, most notably the Madagascan hissing cockroach (*Gromphadorhina portentosa* [Schaum]), the Death's Head hawk moth (*Acherontia atropos* [L.]) and some African Sphingids (Lepidoptera).

In addition to the airborne signals produced by acoustic insects, it has now been shown that vibrational signals are also produced by sending information through the substrate. These vibrational signals are primarily produced by tremulation but also can be important in deciphering an airborne signal, particularly at close range to the sound source. Vibrational signals have been identified in members of the Neuroptera, Diptera, Hemiptera, Plecoptera, Coleoptera, Orthoptera, Mecoptera, Raphidioptera, Lepidoptera and Hymenoptera.

Sound Reception

A receptor for acoustic signals is necessary for a communication channel to exist. Because sound is produced by changing air pressure, a modified mechanoreceptor is needed to sense the acoustic information. The receptors can be classified as either a pressure detector or a particle detector. Pressure detectors are membranes that bend when pressure is unequal on the two sides of the detector. Particle detectors are long structures that move when impacted by many particles moving in the same direction. The movement of the particle detector alternately stretches and compresses sensory cells at the base of the organ.

The primary type of pressure receptor organ is a tympanum, which has evolved independently in at least eight orders of insects. Tympana are generally a thin membrane system stretched over a closed cavity. The tympanum bends away from the side of higher pressure setting up oscillations as the sound waves strike the membrane. Each tympanum has a resonant frequency based on its thickness, size and shape. The resonant frequency is generally tuned to the carrier frequencies of the communication channel to increase the efficiency of information transfer.

The tympana are associated with other mechanoreceptor organs to transduce the signal for the nervous system. As the tympana oscillate, vibrations are sent to various types of receptors, generally a specialized chordotonal organ called a scolopidial organ, which act as the input site to the central nervous system. There can be elaborate structures associated with the tympana to transduce energy into the central nervous systems such as the crista acoustica of the crickets and katydids (Orthoptera) and Müller's organ of locusts (Orthoptera), which provides frequency discriminating abilities. These pressure receptors are generally found in pairs, one on each side of the body. This provides an animal with a means to determine the direction from which the sound originated.

The sensory structures for vibrational signals are trichoid sensilla generally found on the feet or cerci or through specialized subgenual and metatarsal organs located in the legs. The subgenual organs are located just distal to the femoral-tibial joint in all six legs to promote detection and directional hearing. They are similar to tympana in that they are chordotonal organs but lack the tympanal membranes and tracheal air sacs of the tympanal system.

Particle receptors are generally specialized structures found in specific groups of insects. For example, female fruit flies (Diptera) sense the courtship signals produced by the male with a special antennal segment called an arista. Male mosquitoes and midges (Diptera) have plumose antennae which detect the species-specific wing beat frequencies produced by females. Johnston's organ is a more complex chordotonal organ found in the antennal pedicel of some Diptera and Hymenoptera which is stimulated by the vibration of the antennal flagella. The long bristles and antennae provide a mechanical advantage to the sensory cells increasing the sensitivity of the receptor.

Functions of Acoustic Signals

Sound has many potential benefits in that the signals can be used day or night, can be modified quickly, and can travel a significant distance even if conditions are not optimal for other signal pathways. However, sound is energetically costly to produce and advertises your position to potential predators as well as potential mates. Even with these potential problems, insects have evolved diverse functions for acoustic signals. Acoustic signals are used for a variety of purposes in insects including sexual signaling, courtship signals, aggression, social recruitment and defense.

A primary function of acoustic signals is as an intraspecific communication channel. Sounds are used to attract mates and to isolate species reproductively. Each species has a characteristic call that can prevent related species from cross mating. The calls produced by individual signalers can be compared by receivers providing the opportunity to select a mate who is producing a call that exhibits specific characteristics. This is particularly true when callers have congregated into localized areas, which is another function of acoustic signaling. Mates may be selected based on the number of calls, the temporal patterns, loudness, etc. The specific characteristics used by a given species are usually chosen based on their ability to demonstrate the viability of the caller. Duets between individuals (either intrasexual or intersexual) can also act as mechanisms to determine mate choice. The signals often change as potential mates approach. These courtship sounds are modified advertisement calls which provide further opportunities for mate assessment. Acoustic signals can also be used intraspecifically to space individuals in the environment, as aggression signals, or as competitive signals to jam the signal of a neighbor. Eusocial insects use acoustic signals as warnings, to recruit a defensive response within the colony, and to recruit foragers to specific food sources.

Predator deterrence is another significant function of acoustic signals. The loud sounds produced by many insects (e.g., cicadas [Hemiptera]), can startle a potential predator giving the insect a chance to escape. The percussion sounds produced by acridid grasshoppers (Orthoptera) are thought to be defensive displays. Sound production has evolved specifically for this anti-predator function in click beetles (Coleoptera). The acoustic systems that use air movement in the Death's Head moth (Lepidoptera), cockroaches (Blattodea) and grasshoppers (Orthoptera) also have anti-predator functions. Moths (Lepidoptera) have evolved a sound production system that is used to jam the ultrasonic signals of the bats that prey upon them. The arctiid moths emit ultrasonic pulses as bats approach which act to confuse the bat as to the exact location of its target. This gives the moth a chance to escape while the bat circles around for another attempt at capturing the insect. These pulses may also have an aposomatic function warning bats of a potentially distasteful meal.

Insects have also evolved specialized acoustic receptors as a means of avoiding predation. Bat-detectors have evolved independently in geometrid, noctuid and hawk moths (Lepidoptera), lacewings, (Neuroptera), praying mantises (Mantodea), beetles (Coleoptera), crickets, locusts and katydids (Orthoptera). These bat-detectors provide an early warning system for the insects that a bat is nearby giving the insect a chance to escape before the bat can sense an insect in the vicinity.

► Sound Production in the Cicadoidea
► Acoustic Aposematism
► Drumming Communication and Intersexual Searching Behavior of Stoneflies (Plecoptera)

References

Bailey WJ (1991) Acoustic behavior of insects, an evolutionary perspective. Chapman and Hall, London, UK, 225pp

Drosopoulos S, Claridge MF (eds) (2006) Insect sounds and communication: physiology, behavior, ecology and evolution. CRC Press, Boca Raton, FL, 532 pp

Elliot L, Hersberger W (2007) The songs of insects. Houghton-Mifflin Company, Boston, MA, 228 pp

Ewing AW (1989) Arthropod bioacoustics: neurobiology and behavior. Comstock Publishing Associates, Ithaca, NY, 260 pp

Gerhardt HC, Huber F (2002) Acoustic communication in insects and anurans: common problems and diverse solutions. University of Chicago Press, Chicago, IL, 531 pp

Greenfield MD (2002) Signalers and receivers: mechanisms and evolution of arthropod communication. Oxford University Press, New York, NY, 414 pp

Acrididae

A family of grasshoppers (order Orthoptera). They commonly are known as shorthorned grasshoppers.

► Grasshoppers, Katydids and Crickets

Acriology

The study of grasshoppers, katydids, crickets and their relatives (Orthoptera). This is sometimes expanded to include the orders of insects related to Orthoptera (the Orthopteroids) such as cockroaches (Blattodea), mantids (Mantodea), stick insects (Phasmatodea), earwigs (Dermaptera), and gladiators (Mantophasmatodea).

► Classification
► Grasshoppers, Katydids and Crickets

Acrobat Ants (Hymenoptera: Formicidae)

A term applied to ants of the genus *Crematogaster*. Typically they are small, shiny brown or black, and possess a pedicel with two nodes. They elevate the gaster (tip of the abdomen) over the thorax or head when alarmed. Acrobat ants usually are found in association with wood or trees, including the tunnels of termites and wood boring beetles. They are omnivorous and tend aphids. Their bite can be painful.

► Ants (Hymenoptera: Formicidae)
► Ant-Plant Interactions

Acroceridae

A family of flies (order Diptera). They commonly are known as small-headed flies.

► Flies

Acrolepiidae

A family of moths (order Lepidoptera). They commonly are known as false diamondback moths.
► False Diamondback Moths
► Butterflies and Moths

Acrolophidae

A family of moths (order Lepidoptera). They commonly are known as tube moths.
► Tube Moths
► Butterflies and Moths

Acron

A preoral, unsegmented portion of the body, anterior to the first true body segment. This is also known as the prostomium.

Acrosternite

The narrow marginal region at the anterior edge of a sternite. It appears to be the posterior edge of the preceding sternite, and includes the intersegmental fold. It is found on the abdominal sterna, but absent from the thoracic sterna.

Action Threshold

A level of pest abundance that stimulates action to protect plants from serious damage.
► Economic Injury Level (EIL) and Economic Threshold (ET) Concepts in Pest Management

Active Dispersal

The redistribution of animals caused by their own actions such as flying or walking. The wings of insects allow active dispersal frequently (contrast with passive dispersal).

Active Ingredient (A.I.)

The toxic component of an formulated pesticide. It also is known as the toxicant.

Active Space

The area or space in which the concentration of pheromone (or other behavioral chemical) is at or above threshold concentration necessary to elicit a response from the receiver.

Active Ventilation

Although most gas exchange in insects occurs through diffusion (passive ventilation), in some cases it is inadequate to meet the oxygen needs of insects, particularly large or flying insects. Thus, muscular contractions acting via hydrostatic pressure (pressure on the hemolymph) compress the trachea and air sacs to force carbon dioxide out and allow more rapid intake of air. The exact mechanism varies among taxa, but usually involves contraction of the abdomen, and synchronization of opening and closing of the spiracles.
► Abdominal Pumping

Aculae

Small spines on the wing membrane of Lepidoptera.

Aculeus

This term has several meanings depending on the taxon of insects under consideration. In Hymenoptera, it is synonymous with the sting, an eversible hollow cylindrical structure at the tip of the abdomen used to deliver venom. Though derived from the ovipositor, it is not used to deliver eggs. Among Diptera, this term is sometimes used to refer to a pointed, sclerotized structure associated with the reproductive system in males. Among Lepidoptera, this term refers to hair-like structures on the body and wings of primitive moths; these also are known as microtrichia.

Acute

Of short duration, characterized by sharpness or severity.

Acute Bee Paralysis

A disease of honey bees caused by a picornavirus. Symptoms include trembling, sprawled appendages, and sometimes hairlessness (contrast with chronic bee paralysis).

Aculeate

Pertaining to the stinging Hymenoptera (suborder Aculeata), a group including the bees, ants, and many wasps.

► Wasps, Ants, Bees and Sawflies (Hymenoptera)

Acute Toxicity

The toxicity of a pesticide determined after 24 h. The toxicity resulting from a single dose or exposure.

► Insecticide Toxicity
► Insecticides

Adaptation

This term has at least two meanings: changes in the form or behavior of an organism during its life, and natural selection of organisms in evolutionary time. In entomology, usually the latter definition is intended.

Adaptation of Indigenous Insects to Introduced Crops

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Host range expansion, or adaptation of insects to new crops, is a world-wide phenomenon that has been observed repeatedly and extensively. It is particularly well documented in North America, where forests and prairies consisting of indigenous plants were planted extensively to introduced cultivated crops only after European emigrants arrived in the eighteenth century. Although many new insect pests were also accidentally introduced from Europe into Canada and the United States, many species of native insects adapted to the new crops and became economically important pests (Table 2).

Prior to widespread introduction of cultivated crops, some species of native insects fed on a wide range of plants and therefore might be expected to accept the new crops readily. Although polyphagous insects such as grasshoppers (Orthoptera: Acrididae), wireworms (Coleoptera: Elateridae), and cutworms (Lepidoptera: Noctuidae) readily accepted corn, wheat and other crops, not all of the species within these groups became agricultural pests. For example, several hundred species of cutworms and grasshoppers are present, but only about a dozen species in each group have achieved regular pest status.

Other native insect species had a narrower host range, and therefore adapted to a more narrow range of crops, or perhaps only a single crop. In the south the boll weevil, *Anthonomus grandis grandis* Boheman (Coleoptera: Curcullionidae), originally fed on native plants in Mexico related to cultivated cotton, and dispersed northward into the new cotton belt of the southeastern United States as cotton was planted extensively. In the north, the wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae), fed on hollow-stemmed wild grasses, and within 10 years after tillage began in Alberta, wheat was damaged from

Adaptation of Indegenous Insects to introduced Crops, Table 2 **Examples of American insect pests that have adapted to introduced crops**

Insects with wide host ranges	Old host plant	New host plant
Apple maggot, *Rhagoletis pomonella* (Walsh) Diptera: Tephritidae	Hawthorne	Apple
Chinch bug, *Blissus leucopterus leucopterus* Heteroptera: Lygaeidae	Grasses	Corn
Western corn rootworm, *Diabrotica virgifera virgifera* LeConte Coleoptera: Chrysomelidae	Grasses	Corn
Western bean cutworm, *Loxagrotis albicosta* (Smith) Coleoptera: Chrysomelidae	Solanaceous weeds	Corn, beans
Colorado potato beetle, *Leptinotarsa decemlineata* (Say) Coleoptera: Chrysomeliodae	Buffalo burr	Potato
Carrot weevil, *Listronotus oregonensis* (LeConte) Coleoptera: Curculionidae	Umbelliferous weeds	Carrots, etc.
California red scale, *Aonidiella aurantii* (Maskell) Hemiptera: Diaspididae	Shrubs and trees	Citrus
Boll weevil, *Anthonomus grandis* Boheman Coleoptera: Curculionidae	Malvaceous weeds	Cotton
Insects with wide host ranges	**Old host plant**	**New host plant**
Sugar beet wireworm, *Limonius californicus* Coleoptera: Elateridae	Weeds, grasses	Field and vegetable crops
White grubs, *Phyllophaga* spp. Coleoptera: Scarabidae	Weeds, grasses	Field and vegetable crops
False chinch bug, *Nysius raphanus* Howard Hemiptera: Lygaeidae	Weeds, grasses	Field and vegetable crops
Tarnished plant bug, *Lygus lineolaris* (Palisot de Beauvois) Hemiptera: Miridae	Weeds, grasses	Field and vegetable crops
Army cutworm, *Euxoa auxiliaris* (Grote) Lepidoptera: Noctuidae	Weeds, grasses	Field and vegetable crops
Yellow striped armyworm, *Spodoptera ornithogalli* (Guenée) Lepidoptera: Noctuidae	Weeds, grasses	Field and vegetable crops
Redlegged grasshopper, *Melanoplus femurrubrum* (de Geer) Orthoptera: Acrididae	Weeds, grasses	Field and vegetable crops

Adaptation of Indegenous Insects to introduced Crops, Table 2 (Continued)

Insects with wide host ranges	Old host plant	New host plant
Migratory grasshopper, *Melanoplus sanguinipes* (Fabricius) Orthoptera: Acrididae	Weeds, grasses	Field and vegetable crops

the Canadian prairie provinces south into Montana and North Dakota. In the eastern United States the apple maggot, *Rhagoletis pomonella* (Walsh) (Diptera: Tep hritidae), expanded its host range to included newly introduced cultivated fruits, especially apples. The Colorado potato beetle, *Leptinotarsa decemlineata* Say (Coleoptera: Chrysomelidae) originally fed on solanaceous weeds in Mexico or the southwestern United States, and quickly spread across the United States on potatoes once it gained access to potato acreage. These are just a few examples of insects accepting new hosts, and the same phenomenon is well documented for important tropical crops such as sugarcane and cacao, and other crops, as they were introduced and cultivated in various locations around the world.

Some of the native insect populations originally occurred at low levels because their host plants were relatively sparse. Large acreage of new monocrop habitats therefore resulted in an abundant food supply, excellent survival, and eventually in pest population outbreaks. Also, the native environments were relatively stable, and supported a wide range of beneficial insects suppressed herbivorous insects. However, soil tillage within the agricultural environments produced highly disturbed systems, and pests with high fecundity were not effectively suppressed by predators and parasitoids.

America's native insects displayed considerable plasticity in acquiring new hosts. This trend has been noted everywhere agriculture is practiced, and we can expect the number of pests to increase with time, and especially with the area planted to each particular crop, as indigenous species adapt to imported host plants or crops are exposed to additional potential pests in new geographic areas. However, species accrual occurs most rapidly soon after plant introduction, and the number of species feeding on a plant (species richness) does not increase indefinitely, leveling off after less than 300 years if there is not an increase in crop acreage.

We can observe insects with both broad and narrow host selection behavior expanding their host range to include introduced crop plants. This is not surprising for generalist species, which feed broadly on many plants, but it is quite interesting when insects with a narrow host range adopt new hosts. In such cases the species with a narrow host range usually are pre-adapted to accept the foreign crops because they feed on plants in the same family as the introduced crop. North America possesses close relatives to nearly all the introduced crops among its indigenous flora, so it is not surprising that insects associated with the native plants would adapt to the introduced crops. The presence of secondary plant metabolites (allelochemicals) such as alkaloids, terpenoids, and cyanogenic glycosides often serves to keep non-adapted insects from feeding extensively on plants, but may serve as chemical cues or stimulants for insects that are adapted. Thus, insects that specialize on cruciferous weeds and crops are attracted to allylisothiocyanate, and insects that feed on cucurbitaceous weeds and crops are attracted to cucurbitacin.

Host selection behavior by insects is not a static situation, nor is it as simple as the single-chemical scenario presented above. It is constantly evolving in response to various biotic characteristics such as herbivory, and even to crop cultural practices. Some natural selection of insect strains may have occurred during the adaptation from native to introduced plants. In the northern Great Plains, wheat matures earlier in the season than wild grasses. Therefore, after a century, adult wheat stem sawflies are now active nearly a month earlier than previously, and now are more effective in utilizing wheat.

Changes in farming practices that have also impacted populations of native insect pests in croplands. Originally, horses were used for farming, and oats were needed for their feed. Later, the horses were replaced by tractors, and the need for oats was reduced. Oats are resistant to wheat stem sawflies, and when oats was eliminated from the cropping system, the vast acreages of wheat resulted in a population explosion of the sawflies. More recently, canola has been included in the Canadian Prairie Provinces, and populations of grass-feeding insects are somewhat disrupted by the presence of a non-host, cruciferous crop. Other water and soil conservation practices such as alternate-year summer fallow, strip cropping, and chemical fallow have affected the prevalence of both pest and beneficial insects.

Beneficial insect populations were also impacted by tillage and cultural practices, and changes in the chemical constituency of crop plants. Parasitoids have complex host searching behavior that begins with finding plant environments in which their hosts could occur. Therefore, it was necessary for the parasitoids to learn that the new crops could be sources of hosts. In the case of the wheat stem sawfly, only two of the known parasitoid species have currently adapted from wild grasses to wheat. Parasitoids may be more favored by one plant cultivar than another, or less favored by a crop than a similar weed. The availability of food for the adult parasitoid or predator, either nectar from blossoms or extra floral nectaries or pollen from blossoms, is often implicated in differential survival of beneficial insects among different plants.

Overall, adaption by herbivorous insects to new host plants is a dynamic and widespread phenomenon. Though sometimes it is difficult to determine whether it is the change in the constituency of the host plant that accounts for insect acceptance, or it is some other factor such as widespread host plant availability that accounts for insect abundance, it is clear that the relationship between insects and plants is not static, resulting in a continuing stream of new pest problems for crop plants.

► Host Plant Selection by Insects
► Allelochemicals
► Plant Resistance to Insects

References

Bernays EA, Chapman RF (1994) Host-plant selection by phytophagous insects. Chapman and Hall, New York, NY

Connor EF, McCoy ED (1979) The statistics and biology of the species-area relationship. Am Nat 113:791–833

Kim KC (1993) Insect pests and evolution. In: Kim KC, McPheron BA (eds) Evolution of insect pests; patterns of variation. Wiley, New York, NY, pp 3–25

Morrill WL, Kushnak GD (1996) Wheat stem sawfly (Hymenoptera: Cephidae) adaptation to winter wheat. Environ Entomol 25:1128–1132

Strong DR (1979) Biogeographic dynamics of insect-host plant communities. Annu Rev Entomol 24:89–119

Adaxial Surface

The upper surface of a leaf (contrast with abaxial surface).

Adeheterothripidae

A family of thrips (order Thysanoptera).

► Thrips

Adelgidae

A family of insects in the order Hemiptera. They sometimes are called pine and spruce aphids.

► Aphids
► Bugs

Adelidae

A family of moths (order Lepidoptera). They commonly are known as long horned fairy moths.

► Long horned Fairy Moths
► Butterflies and Moths

Adephaga

One of four suborders of beetles (Coleoptera), and one of two suborders that contain numerous and important beetles (the other is suborder Polyphaga). It is comprised of about nine families, the principal ones being Carabidae, Gyrinidae, and Dytiscidae. Nearly all groups are predatory, and many are aquatic.
► Beetles (Coleoptera)

Aderidae

A family of beetles (order Coleoptera). They commonly are known as antlike leaf beetles.
► Beetles

Adfrontal Areas

A pair of narrow oblique sclerites on the head of a caterpillar. The adfrontal areas border the front, which normally is triangular, so the adfrontal areas take on the shape of an inverted "V."
► Head of Hexapods

Adelphoparasitism

A type of hyperparasitism occurring in Hymenoptera: Aphelinidae in which the males are parasitoids of females of their own species (the females parasitize Hemiptera).

Adherence

The ability of a material such as a pesticide to stick to a surface.

Adipohemocyte

A type of hemocyte, ovoid in shape and likely secretory in function.
► Hemocytes of Insects: Their Morphology and Function

Adipokinetic Hormone (AKH)

A decapeptide hormone synthesized in neurosecretory cells of the corpora cardiaca and important in the regulation of lipid metabolism, and sometimes carbohydrate or proline metabolism and other physiological functions.
► Adipokinetic and Hypertrehalosemic Neurohormones

Adipokinetic and Hypertrehalosemic Neurohormones

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The adipokinetic hormones and hypertrehalosemic hormones of insects comprise a family of peptide hormones that primarily regulate the levels of energy metabolites, such as trehalose, diacylglycerol and proline that circulate in the hemolymph. These peptide hormones are products of neurosecretory neurons located in the corpora cardiaca, neuroendocrine glands attached to the brain. The structural organization of the insect corpora cardiaca is similar to the hypothalamus-neurohypophysis of the vertebrate endocrine system.

Historical Perspective

The existence of hypertrehalosemic hormones was discovered with the observation that injections of extracts of corpora cardiaca elevated the concentration of trehalose in the hemolymph of cockroaches (hypertrehalosemia). Unlike vertebrates that use glucose as the major blood carbohydrate, the hemolymph of insects generally contains the disaccharide trehalose, an α-1-1-gluco-glucoside, as its major circulating carbohydrate. In addition, the enzyme glycogen phosphorylase in the fat body of cockroaches was demonstrated to be activated when these insects were injected with an extract from the corpora cardiaca. Subsequently, studies in locusts showed that injections of corpora cardiaca extracts elevated hemolymph diacylglycerols, instead of trehalose, and this action was referred to as an adipokinetic or hyperlipemic effect. Injections of locust corpora cardiaca extracts into cockroaches produced the hypertrehalosemic response, and vice versa. Hence, it was likely that the adipokinetic hormone (AKH) of locusts and the hypertrehalosemic hormone (HrTH) of cockroaches were related, or identical, peptides.

The locust adipokinetic hormone was isolated and characterized first. It was obtained from the migratory locust, *Locusta migratoria*, and its primary structure consisted of ten amino acids. It was designated Locmi-AKH-I according to the newest nomenclature for naming insect neurohormones. The amino acid composition and sequence of Locmi-AKH-I had a remarkable similarity to a previously reported red pigment-concentrating hormone (Panbo-RPCH) obtained from the shrimp *Pandalus borealis* and later found in various crustaceans. It was shown that Locmi-AKH-I was also present in the desert locust, *Schistocerca gregaria*.

Subsequently, both *L. migratoria* and *S. gregaria* were shown to contain a second adipokinetic hormone (Locmi-AKH-II and Schgr-AKH-II, respectively) that differed from each other by the amino acids in position 6. The two locust AKH-IIs were octapeptides with sequences similar to those of Locmi-AKH-I and Panbo-RPCH. A third octapeptide AKH (Locmi-AKH-III) was also found in *L. migratoria* and a similar octapeptide (designated Phymo-AKH-III) occurs in pyrgomorphid and pamphagid grasshoppers, but an AKH-III is missing in *S. gregaria*. Subsequently, three research groups ultimately reported, in the same year, the presence of two octapeptides from the corpora cardiaca of the American cockroach, *Periplaneta americana*, that were structurally related to the locust AKHs and the crustacean RPCH. These two peptides were isolated on the basis of myotropic or heartbeat acceleration bioassays and are referred to as cardio acceleratory hormones (Peram-CAH-I and Peram-CAH-II), but they also produced hypertrehalosemia in the cockroach and represent the hypertrehalosemic hormones. These pioneering studies, along with numerous subsequent studies, demonstrated that there are, so far, about forty structurally related, but distinct, peptides with adipokinetic and hypertrehalosemic effects in the insects and one in crustacean (Table 3). The name adipokinetic hormone/red pigment-concentrating hormone (AKH/RPCH) family was coined for this general family of peptides, which likely encompasses the arthropods.

Chemistry of the AKH/RPCH Family

The members of the adipokinetic hormone/red pigment-concentrating hormone family share numerous structural features. They consist either of eight, nine or ten amino acids, depending on the insect species from which they are isolated. They are blocked by pyro-glutamate at the N-terminus and by an amide moiety at the C-terminus. Presumably, blocked termini prevent degradation of the neuropeptides by amino- and carboxypeptidase enzymes while circulating in the hemolymph. Aromatic amino acids, usually phenylalanine and tryptophan, always occupy positions 4 and 8, respectively, but aromatic amino acids can also occupy other positions. The peptides are usually neutral under physiological conditions, but a few have a negatively charged aspartate at position 7. Glycine is always present at position 9 as deduced from cDNA analysis of the precursor. The terminal glycine is converted to the amide moiety on the tryptophan in the octapeptides.

Adipokinetic and Hypertrehalosemic Neurohormones, Table 3 **Representative sequences of adipokinetic/hypertrehalosemic peptides from various insect orders**

Order	Peptide name	Genus	Structure										
			1	2	3	4	5	6	7	8	9	10	
Odonata	Libau-AKH	*Libellula, Pantala, Orthetrum*	pGlu	Val	Asn	Phe	Thr	Pro	Ser	Trp	NH_2		
	Anaim-AKH	*Anax, Aeshna*	pGlu	Val	Asn	Phe	Ser	Pro	Ser	Trp	NH_2		
	Psein-AKH	*Pseudagrion, Ischnura*	pGlu	Val	Asn	Phe	Thr	Pro	Gly	Trp	NH_2		
Blattodea Blattidae Blaberidae Blattellidae	Peram-CAH-I[a]	*Periplaneta, Blatta*	pGlu	Val	Asn	Phe	Ser	Pro	Asn	Trp	NH_2		
	Peram-CAH-II[a]	*Periplaneta, Blatta*	pGlu	Leu	Thr	Phe	Thr	Pro	Asn	Trp	NH_2		
	Bladi-HrTH	*Blaberus, Nauphoeta*	pGlu	Val	Asn	Phe	Ser	Pro	Gly	Trp	Gly	Thr	NH_2
		Leucophaea, Blattella											
		Gromphadorhina											
Mantodea	Emppe-AKH	*Empusa, Sphodromantis*	pGlu	Val	Asn	Phe	Thr	Pro	Asn	Trp	NH_2		
Phasmatodea	Carmo-HrTH	*Carausius, Sipyloidea, Extatosoma*	pGlu	Leu	Thr	Phe	Thr	Pro	Asn	Trp	Gly	Thr	NH_2
Mantophasmatodea	Manto-AKH	Not known	pGlu	Val	Asn	Phe	Ser	Pro	Gly	Trp	NH_2		
Orthoptera, Caelifera	Locmi-AKH-I	*Locusta, Schistocerca*	pGlu	Leu	Asn	Phe	Thr	Pro	Asn	Trp	Gly	Thr	NH_2
	Locmi-AKH-II	*Locusta*	pGlu	Leu	Asn	Phe	Ser	Ala	Gly	Trp	NH_2		
	Schgr-AKH-II[a]	*Schistocerca, Phymateus*	pGlu	Leu	Asn	Phe	Ser	Thr	Gly	Trp	NH_2		
	Locmi-AKH-III	*Locusta*	pGlu	Leu	Asn	Phe	Thr	Pro	Trp	Trp	NH_2		
	Phymo-AKH-III	*Phymateus*	pGlu	Ile	Asn	Phe	Thr	Pro	Trp	Trp	NH_2		
Orthoptera, Ensifera	Grybi-AKH[a]	*Gryllus, Acheta, Gryllodes*	pGlu	Val	Asn	Phe	Ser	Thr	Gly	Trp	NH_2		
	=Schgr-AKH-II	*Tettigonia, Decticus*	pGlu	Leu	Asn	Phe	Ser	Thr	Gly	Trp	NH_2		

Isoptera	Micvi-CC	*Microhodotermes*	pGlu	Ile	Asn	Phe	Thr	Pro	Asn	Trp	NH_2		
Dermaptera	=Grybi-AKH	*Labidura, Forficula*	pGlu	Val	Asn	Phe	Ser	Thr	Gly	Trp	NH_2		
Hemiptera/Homoptera	Placa-HrTH	*Platypleura, Munza, Cacama, Magici-cada, Diceroprocta*	pGlu	Val	Asn	Phe	Ser	Pro	Ser	Trp	Gly	Asn	NH_2
Hemiptera, Heteroptera	Pyrap-AKH	*Pyrrhocoris, Disdercus*	pGlu	Leu	Asn	Phe	Thr	Pro	Asn	Trp	NH_2		
	=Peram-CAH-II	*Pyrrhocoris, Disdercus*	pGlu	Leu	Thr	Phe	Thr	Pro	Asn	Trp	NH_2		
	Corpu-AKH	*Corixa*	pGlu	Leu	Asn	Phe	Ser	Pro	Ser	Trp	NH_2		
	Letin-AKH	*Lethocerus*	pGlu	Val	Asn	Phe	Ser	Pro	Tyr	Trp	NH_2		
	Nepci-AKH	*Nepa*	pGlu	Leu	Asn	Phe	Ser	Ser	Gly	Trp	NH_2		
Neuroptera	=Grybi-AKH	*Palpares*	pGlu	Val	Asn	Phe	Ser	Thr	Gly	Trp	NH_2		
Coleoptera	Scade-CC-I	*Scarabaeus, Gareta, Onitis*	pGlu	Phe	Asn	Tyr	Ser	Pro	Asp	Trp	NH_2		
	Scade-CC-II	*Scarabaeus, Gareta*	pGlu	Phe	Asn	Tyr	Ser	Pro	Val	Trp	NH_2		
	Oniay-CC	*Onitis*	pGlu	Tyr	Asn	Phe	Ser	Thr	Gly	Trp	NH_2		
	=Peram-CAH-I	*Leptinotarsa*	pGlu	Val	Asn	Phe	Ser	Pro	Asn	Trp	NH_2		
	=Peram-CAH-II	*Leptinotarsa*	pGlu	Leu	Thr	Phe	Thr	Pro	Asn	Trp	NH_2		
Lepidoptera	Manse-AKH[a]	*Manduca, Vanessa, Bombyx, Heliothis*[b]	pGlu	Leu	Thr	Phe	Thr	Ser	Ser	Trp	Gly	NH2	
	Helze-HrTH	*Heliothis*[b]	pGlu	Leu	Thr	Phe	Ser	Ser	Gly	Trp	Gly	Asn	NH_2
Hymenoptera	Tenar-HrTH	*Tenthredo*	pGlu	Leu	Asn	Phe	Ser	Thr	Gly	Trp	Gly	Gly	NH_2
	=Schgr-AKH-II	*Xylocopa, Bombus*	pGlu	Leu	Asn	Phe	Ser	Thr	Gly	Trp	NH_2		
	=Grybi-AKH	*Vespula, Vespa*	pGlu	Val	Asn	Phe	Ser	Thr	Gly	Trp	NH_2		
	=Manse-AKH	*Apis*	pGlu	Leu	Thr	Phe	Thr	Ser	Ser	Trp	Gly	NH_2	

Adipokinetic and Hypertrehalosemic Neurohormones, Table 3 Representative sequences of adipokinetic/hypertrehalosemic peptides from various insect orders (Continued)

Order	Peptide name	Genus	Structure										
			1	2	3	4	5	6	7	8	9	10	
Diptera	Phote-HrTH	*Phormia, Drosophila*	pGlu	Leu	Thr	Phe	Ser	Pro	Asp	Trp	NH_2		
	Anoga-AKH	*Anopheles*	pGlu	Leu	Thr	Phe	Thr	Pro	Ala	Trp	NH_2		
	Tabat-AKH	*Tabanus*	pGlu	Leu	Thr	Phe	Thr	Pro	Gly	Trp	NH_2		
Crustacea	Panbo-RPCH	*Pandalus*	pGlu	Leu	Asn	Phe	Ser	Pro	Gly	Trp	NH_2		

[a]Note that the peptide in certain orders is identical. For example: Peram-CAH-I and -II of the Blattodea, Blattidae is also present in Coleoptera (Leptinotarsa); Schgr-AKH-II of Orthoptera, Caelifera is present in Orthoptera, Ensifera and in Hymenoptera (***Xylocopa***, ***Bombus***); Grybi-AKH of Orthoptera, Ensifera is also present in Dermaptera, Neuroptera and Hymenoptera, etc.

[b]***Heliothis*** is revised to ***Helicoverpa.***

Some of the members of this peptide family have additional post-translational modifications besides the blocked termini. For example, two HrTH decapeptides are present in the corpora cardiaca of the stick insect, *Carausius morosus*; one of these decapeptides is glycosylated and has a unique C-glycosylation where the sugar is linked to the C-2 atom of the indole ring of tryptophan. Another unusual modification has been found in an AKH of the protea beetle, *Trichostetha fascicularis*: the corpora cardiaca contain two AKHs, one of which is an octapeptide with a phosphothreonine at position 6.

The relationships between individual AKH and HrTH peptides and insect species are complex. There are no clear rules concerning which peptide occurs in which order of insects. Several species within an order may share the same peptide and have other species-specific sequences, and the same peptide may be present in species of different orders. As described above, the two locust species, *S. gregaria* and *L. migratoria*, share an identical decapeptide (Locmi-AKH-I); each species possesses a second, unique octapeptide (Locmi-AKH-II; Schgr-AKH-II); and *L. migratoria* contains a third octapeptide (Locmi-AKH-III) that does not have a complement in *S. gregaria*. Cockroach species of the families Blattellidae and Blaberidae share a single hypertrehalosemic decapeptide hormone (Bladi-HrTH), whereas cockroaches of the family Blattidae contain two octapeptide hormones (Peram-CAH-I and -II). In addition, there is overlap between orders. Grybi-AKH is present in certain crickets and in species of Neuroptera, Dermaptera and Heteroptera. Peram-CAH-I and -II of the blattid cockroaches are also found in the Colorado potato beetle, *Leptinotarsa decemlineata*, and Peram-CAH-II is shared with the heteropteran bug, *Pyrrhocoris apterus*. Whereas Peram-CAH-I and -II mobilize glycogen from the fat body of the cockroach to increase hemolymph trehalose, the same or similar peptides increase hemolymph proline in beetles to serve as the major flight substrate.

Unlike the complex situation in insects, the crustaceans apparently possess only the single Panbo-RPCH peptide which has a chromatophorotropic effect. Panbo-RPCH has also been found in an insect species, the heteropteran stinkbug, *Nezara viridula*, where it has an adipokinetic effect.

Phylogenetic relationships of the HrTHs have been proposed for the cockroaches based on morphological, behavioral and physiological characters congruent with the distribution of the various structures of the HrTHs within the order.

Physiological Actions

The general physiological action of the adipokinetic and hypertrehalosemic hormones in insects is to elevate the hemolymph metabolites that are used by the muscles and other tissues as a source of energy, regardless of the nature of the metabolites. This is accomplished by stimulating the fat body, which is the hormone's target tissue, to convert its stores of triacylglycerides or glycogen to diacylglycerides or trehalose, respectively, or to synthesize proline. The diacylglycerides, trehalose or proline are released from the fat body to increase their respective levels in the hemolymph. The same peptides that elevate diacylglycerides in locusts elevate trehalose when administered to cockroaches, and vice versa, and the hormones of locusts and cockroaches elevate proline in the Colorado potato beetle. The decision as to whether lipid-, carbohydrate-, or proline-mobilizing pathways are activated is a species-related function of the enzyme composition in the fat body.

Muscular activity for animal locomotion can involve either long-term or short-term events. Long-term activities might entail sustained, non-emergency actions such as migration or persistent searching for food, mates or shelter. Short-term activities might consist of local searching activities but may also require immediate, brief, emergency responses such as evading attack by a predator or defending a breeding territory. Long-term events require a steady supply of energy metabolites, whereas short-term events may be brief but intense, and, if successful, they can be followed by a period of recovery to replenish exhausted metabolites.

The adipokinetic hormones are often involved in prolonged, constant muscular activity such as migration. This is characteristically true for the locusts whose migratory behavior has been described since biblical times. Migration is a sustained flight activity that uses muscular oxidation of fatty acids to produce energy, since fatty acids deliver more energy per mole than carbohydrates. However, carbohydrate serves as the major source of muscular energy during initial flight, and lipid becomes the major source for energy as flight persists and becomes sustained. Based on differing physiological effects, it is speculated that the three AKHs may exert different regulatory actions on metabolite mobilization and use during the different stages of migration. Locmi-AKH-II is likely to be the major carbohydrate-mobilizing hormone that provides trehalose for initial flight; Locmi-AKH-I is the major hormone responsible for fat mobilization during sustained flight and Locmi-AKH-III may be responsible for regulating energy metabolism during rest. Furthermore, during lipid mobilization, AKH performs several distinct but related actions. In the fat body, AKH activates lipase for triacylglyceride degradation; this is achieved by binding of the AKH to a G-protein coupled receptor at the cell membrane, activation of adenylate cyclase resulting in the second messenger cAMP which, in conjunction with Ca^{2+}, is responsible for lipase activation. In the hemolymph, AKH increases the lipid-carrying capacity of lipophorins (proteins) resulting in increased amounts of low-density lipophorin for shuttling lipids from the fat body to the muscles. At the flight muscle level, AKH increases the rate of lipid oxidation. Recent research on a number of terrestrial and aqueous heteropteran bugs that have various feeding patterns (plant sap sucking, predators, obligatory hematophagous), also established a lipid-based activity (flight and/or swimming) metabolism that is regulated by the respective AKHs of these insects.

By contrast, insects such as cockroaches, bees and flies use only carbohydrate (trehalose) as the primary source of energy for muscular activity and locomotion. These species do not migrate and lack the adipokinetic response, but they are faced with emergency situations of predator evasion, and in such cases, the hypertrehalosemic hormone mobilizes trehalose in response to the emergency. However, injections of hypertrehalosemic hormone show that significant elevation of the hemolymph trehalose may take as long as 10–30 min. This delay in elevating hemolymph carbohydrate is too long to significantly assist the insect in evading capture. Furthermore, the open circulatory system of insects does not efficiently direct circulating metabolites to the muscles in the manner of the closed circulatory system of vertebrate animals. Energy metabolites, such as trehalose, must constantly be maintained at high levels in the hemolymph to meet urgent, immediate demands. Hence, the role of the hypertrehalosemic hormone appears to be to replace depleted hemolymph trehalose and maintain it at high levels. Maintenance of high trehalose levels allows the insect to make quick responses to elude capture that may require only seconds, or at most, several minutes to conclude. If the insect is successful at escape, the hormone stimulates the degradation of fat body glycogen to restore the high trehalose levels by activating specifically the enzyme glycogen phosphorylase after the hormone has bound to a G-protein coupled receptor on the membrane of a fat cell and had activated a phospholipase C, resulting in the production of inositol trisphosphate and the release of Ca^{2+} from internal stores (influx of external Ca^{2+} is also activated by HrTH) which sets in motion a cascade of activation of kinases and, finally, glycogen phosphorylase. Removal of the hypertrehalosemic hormone does not affect the ability of such insects to be active for the short term (several minutes), but after exhaustion, lengthens their recovery time.

Tsetse flies and various beetle species fuel their flight metabolism by the partial oxidation of proline and the production of alanine. For continuous flight or replenishment of proline reserves in the fat body a unique system exists in these insects to synthesis proline: the respective AKHs activate a lipase in the fat body and the fatty acids that are liberated from triacylglyerols undergo β-oxidation, and the resulting acetyl CoA units are used in conjunction with alanine to synthesize proline. Alanine, which is derived from the partial oxidation of proline, is re-used for proline synthesis and can be viewed as a shuttle system for the transport of acetyl units.

Although the mobilization of energy for flight and other metabolically intense situations is likely the major function for the adipokinetic and hypertrehalosemic hormones, the hormones exhibit pleiotropic actions. The hypertrehalosemic hormones were isolated originally based on their cardioacceleratory action on the heart. This is a logical action for the hormone since elevated heartbeat rate would facilitate distribution of the energy metabolites throughout the body and assure their ready access to the muscles. In keeping with the stimulatory action of AKH on lipid degradation in locusts, lipid synthesis is inhibited by AKH. Other, less well characterized actions include: inhibition of RNA and protein synthesis related to vitellogenesis in locusts and crickets, and the stimulation in cockroaches of the oxidative capacity of mitochondria during fat body maturation, and of gene expression for a fat body cytochrome P450 related to lipid oxidation. These latter actions by the hormones may be equally important as their effects on mobilization of energy metabolites, but they are poorly elucidated because of insufficient research, and they cannot yet be placed into perspective as to their physiological significance. Other actions in which AKHs seem to be involved are an enhanced activation of the locust immune system and, possibly, in the activation of an antioxidant protection mechanism in potato beetles.

In summary, the adipokinetic-hypertrehalosemic-hyperprolinemic hormones constitute a family of peptides that are adapted to the individual biology of the insect species in which they are found. They display a unique relationship with their target tissue in that the hormone carries the endocrine message to the target tissue (fat body) to mobilize energy stores, but the target tissue determines which metabolic pathways are activated depending on the biology of the species. It is this biology that determines the nature of the muscular activity (prolonged–migration; brief–predator evasion) and its metabolic need for consuming carbohydrates, lipids or proline as a source of energy.

References

Beenakkers AMT (1969) The influence of corpus allatum and cardiacum on lipid metabolism in *Locusta*. Gen Comp Endocr 13:492

Fernlund P, Josefsson L (1972) Crustacean color-change hormone: amino acid sequence and chemical synthesis. Science 177:173–175

Gäde G (1989) The hypertrehalosaemic peptides of cockroaches: a phylogenetic study. Gen Comp Endocr 75:287–300

Gäde G (2004) Regulation of intermediary metabolism and water balance of insects by neuropeptides. Annu Rev Entomol 49:93–113

Mayer RJ, Candy DJ (1969) Control of haemolymph lipid concentration during locust flight: an adipokinetic hormone from the corpora cardiaca. J Insect Physiol 15:611–620

Steele JE (1961) Occurrence of a hyperglycemic factor in the corpus cardiacum of an insect. Nature 192:680–681

Stone JV, Mordue W, Batley KE, Morris HR (1976) Structure of locust adipokinetic hormone, a neurohormone that regulates lipid utilization during flight. Nature 263:207–221

Vroemen SF, van der Horst DJ, van Marrewijk WJA (1998) New insights into adipokinetic hormone signalling. Mol Cell Endocrinol 141:7–12

Adjuvants

Chemicals added to insecticides to improve their effectiveness. Examples of adjuvants include toxicity, stability, and adhesion.

► Insecticide Formulations

► Insecticides

Adoption Substance

A secretion presented by a social parasite that induces the host insects to accept the parasites as members of their colony.

► Social Insect Pheromones

Adult

The sexually mature stage of an animal. The adult is usually the winged stage in insects. With rare exceptions, the adult does not molt again.

► Metamorphosis

Adulticide

A pesticide used to kill adult insects. This term often is used to describe products used to kill adult mosquitoes. (contrast with larvicide)

► Insecticides

Adultoid Reproductive

In higher termites, a supplementary reproductive that in indistinguishable morphologically from the reproductive.

Adult Transport

A behavior in which social insects (usually ants) drag or carry their nestmates to a new location. This normally occurs during colony emigration.

Adventitious Veins

In some insects, additional wing veins are present which are neither secondary nor intercalary veins. They usually are the result of the lining up of cross veins.

► Wings of Insects

Adventive

An organism that has arrived in an area from elsewhere. It is not native, and likely arrived as an invader or accidental introduction. It is also known as nonindigenous.

► Invasive Species

Aedeagus

The intromittent (copulatory) organ of the male; the distal portion of the phallus. Sometimes referred to as the penis.

► Abdomen of Hexapods

Aenictopecheidae

A family of bugs (order Hemiptera).

► Bugs

Aeolothripidae

A family of thrips (order Thysanoptera). They commonly are known as broad-winged thrips or banded thrips.

► Thrips

Aepophilidae

A family of bugs (order Hemiptera). The sometimes are called marine bugs.

► Bugs

Aeshnidae

A family of dragonflies (order Odonata). They commonly are known as darners.

► Dragonflies and Damselflies

Aetalionid Treehoppers

Members of the family Aetalionidae (order Hemiptera).

► Bugs

Aerial Photography

In pest management, photographs taken by an airplane or satellite that are used to identify variations within fields/crops to help make management decisions.

Aeropile

The opening in the egg surface (chorion) through which air enters.

Aerosol

The air suspension of liquid or solid particles of small diameter. This is a common formulation for flying insects or for household use where no additional formulation or preparation is desired.

► Insecticides

► Insecticide Formulations

Aesthetic Injury Level

The level of pest abundance above which aesthetic, emotional, or sociological considerations require pest control actions. Economic considerations are not relevant.

► Economic Injury Level (EIL) and Economic Threshold (ET) Concepts in Pest Management

Aesthetic Pest

A pest which, through its presence or actions, is deemed objectionable and in need of elimination even though it causes no economic loss. The presence of some insects in homes or on ornamental plants are examples of aesthetic pests, though in the latter case if they inhibit the ability to market plants then the same insect can be come an economic pest.

► Economic Injury Level (EIL) and Economic Threshold (ET) Concepts in Pest Management

Aestivation

A state of inactivity or curtailment of normal activity during the summer months. Diapause

Aetalionidae

A family of insects in the order Hemiptera. They sometimes are called aetalionid treehoppers.

► Bugs

► Treehoppers

African Armyworm, *Spodoptera exempta* (Walker) (Lepidoptera: Noctuidae)

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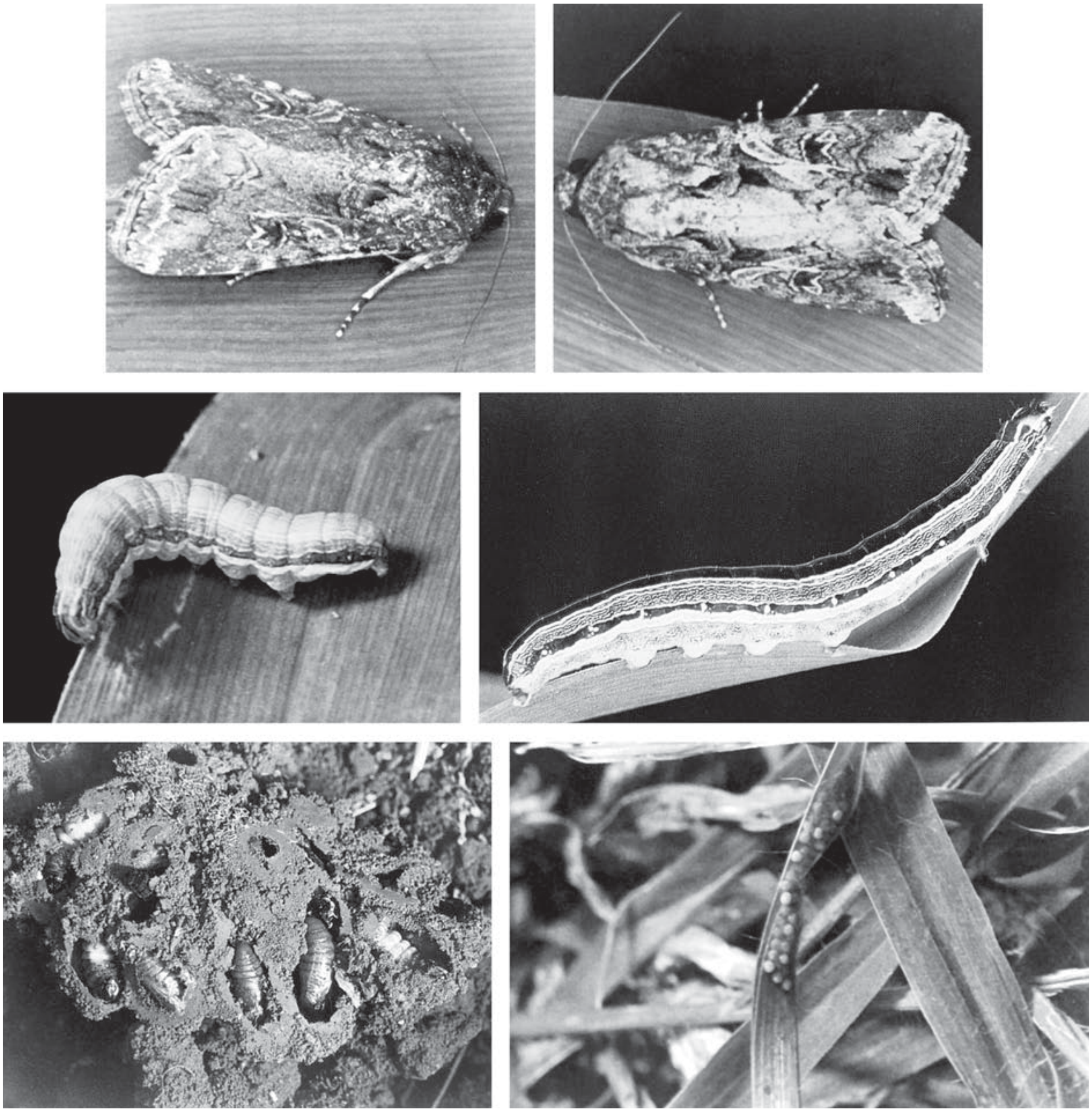
The African armyworm (Fig. 21) is a larva of a nocturnal moth, *Spodoptera exempta* (Walker). This species, although commonly referred to as the African armyworm, occurs rather widely in the grasslands of tropical and subtropical Africa and Asia. In Africa, where *S. exempta* is of major economic importance, its occurrence is confined to countries south of the Sahara: Tanzania, Kenya, Uganda, Ethiopia, Somalia, Malawi, Zimbabwe, Zambia and South Africa. Outside Africa, *S. exempta* has been reported from southwest Saudi Arabia in the republic of Yemen, southeast Asia, Australia, New Zealand and Hawaii.



African Armyworm, *Spodoptera exempta* (Walker) (Lepidoptera: Noctuidae), Figure 21 **African armyworm: top left, adult female, top right, adult male; middle left, solitary form of larva; middle right, gregarious form of larva; lower left, pupae in soil; lower right, eggs on foliage.**

During an armyworm outbreak, larvae of *S. exempta* march together in long columns, akin to army columns, in search of susceptible plant material. This is the basis for the name "armyworm." When susceptible plant material is found, it is often voraciously devoured to ground level. In typical armyworm outbreaks, larval density may exceed 1,000 per m^2 over areas covering tens or even hundreds of square km.

In Africa, *S. exempta* is adapted for survival on seasonal grasslands by combining a high intrinsic rate of increase with "migration" to places of rainfall where grasses are suitable for survival of its caterpillars. Because of its capability to move over long distances, hundreds and sometimes thousands of km across national boundaries freely, *S. exempta* is truly an international pest. Often times it appears sporadically and suddenly in dense outbreaks capable of causing extensive and enormous damage to susceptible rangeland grasses, cereal crops and sugarcane. Because of its ability to appear suddenly and then disappear equally suddenly, the African armyworm has sometimes been referred to by farmers as the "mystery worm." The scale of devastation to crops and pastures by armyworm is comparable only to that caused by locusts. Thus, the armyworm is greatly feared wherever it occurs.

Biology and Ecology

Adult moths of *S. exempta* have a wing span in the range of 20–37 mm. The forewings are characterized by an overall dull gray-brown appearance. The hind wings are whitish with dark veins. The two sexes can be distinguished by examining the number of bristles on the frenulum (the mechanism that couples the fore and hind wings during flight), which are single in the males and multiple in the females. A characteristic feature of the African armyworm is the presence of racquet-shaped scales at the tip of the abdomen of the males and black scales on the tip of the body of the females.

Females of *S. exempta* lay between 100 and 400 eggs per night in a mass covered by black scales from the tip of their abdomen. Eggs are small, 0.5 mm in diameter, whitish in color, but then turn black prior to hatching. Eggs are often laid on the lower side of leaves and hatch in about 2–4 days after oviposition. There are six larval instars extending over a larval period of between 14 and 22 days depending on the temperature and the host plant on which the larvae have been reared. Fully grown sixth instar larvae are often 25–35 mm long. Pupation occurs 2–3 cm below the soil surface. This process is often preceded by a sudden and synchronized disappearance of larvae that quickly burrow into the ground, particularly if soil conditions are moist enough.

Adults emerge within 7–12 days after pupation and can live up to 14 days if appropriately fed. In their lifetime, females can lay up to 1,000 eggs. *Spodoptera exempta* is not known to enter into any type of diapause. This probably explains why this species has to migrate soon after emergence.

Spodoptera exempta exhibits a phenomenon called polyphenism, or phase polymorphism (i.e., the occurrence in a population of two or more phenotypes due to exposure to different environmental conditions). For example, up until the third molt, all larvae of *S. exempta* remain green in body color. However, at this stage, depending on whether there are many larvae or just a few, they will turn black or remain in various shades of green or brown. If there are large numbers of larvae present as in a typical outbreak situation, larvae tend to be characteristically velvety black on top with pale lines on each side and greenish-yellow underside; this phenotype is called the gregarious phase. It is during this phase that *S. exempta* is most devastating to crops. Larvae in the gregarious phase tend to be very active and often march on the soil in one direction only looking for fresh food. They also feed high on the plant during the day.

However, if not crowded, the developing larvae remain one of the many shades of green, pink or brown color until they pupate. In contrast to black gregarious larvae, they are sluggish, living mostly at the bases of plants and are not as destructive to crops. Although their appearance is so different, they are the same insect and one may easily be converted into the other. Nevertheless, because moths derived from gregarious and solitary larvae exhibit the same level of readiness to fly, phase change in *S. exempta* is construed as being merely a stress phenomenon associated with crowding. It is unknown whether this aspect of phase polymorphism is of any evolutionary significance to *S. exempta*. In the case of locusts, it is thought that the solitary form is the one that enables the populations to persist at a low level during the dry season when there are no outbreaks occurring. It is worth speculating, in the case of *S. exempta*, that at such low densities, its populations continue to breed during the dry season in areas where grasses remain green, such as in the cool highland areas and, more especially, the coastal areas where it is hot and there are periodic showers during the dry season. This form may, therefore, be of some critical survival value for this pest.

Seasonal Movements and Armyworm Outbreaks

Upon emergence, adult moths of *S. exempta* are fully capable of movement from their breeding sites to new areas. Such flights can be very short, or very long, depending on whether they are carried in a downwind direction or not. Nevertheless, because they are one-way journeys, they cannot, therefore, be regarded as migration in its strict ethological sense – where there is invariably a return flight to breeding sites.

The question of how armyworm outbreaks start has baffled scientists and farmers alike for a long time. Because moths emerge over a period of up to 12 days, and can also fly off on "migration" at different times, they become widely dispersed and do not form swarms as occurs with locusts. Moreover, the moths are weak fliers and are often carried in a downwind direction. Thus, moths disperse in space and time downwind. For purposes of this narrative, an armyworm outbreak is simply described as the sudden appearance of larval infestations, often simultaneously on many farms in one region.

Two hypotheses, the continuity and the concentration hypotheses, have been put forward in order to explain how outbreaks begin during an armyworm season. The continuity hypothesis, which is based on biogeographical analyses of past outbreaks, proposes that much of the armyworm population is always at crowded, outbreak densities, and that the seasonal absence of reports represents not a real absence of outbreaks, but a temporary loss of contact with the main population in remote and perhaps uninhabited areas. This continuity implies that the first outbreaks to appear in East Africa are due to the migration of parent moths from the north at the end of the season. Although there is ample evidence of adult dispersal on the wind over distances up to several hundred km in a few successive nights, there is little evidence in support of a southward dispersal at the start of an armyworm outbreak in East Africa.

The concentration hypothesis, on the other hand, postulates that because of occasional capture of moths in traps during the off-season, as well as the finding of rare caterpillars after concerted searches, *S. exempta* persists during such times of year as uncrowded populations (the solitary phase, in which caterpillars remain green and unreported), and that the first outbreaks of the season are due to concentration of moths before the synchronized mating and egg laying.

Thus, there seem to be two types of armyworm outbreaks: primary and secondary outbreaks. During primary outbreaks, sources of outbreaks are the low density populations that survive and breed during dry seasons in green areas of the coast and the highlands. Secondary outbreaks occur downwind from the coast near the first highlands. During years of serious armyworm outbreaks, the first outbreaks often start in Tanzania, Zimbabwe and Malawi at about the beginning of the wet season in December, and are followed by a progression of outbreaks at about one generation time-intervals from Tanzania through Kenya, Uganda, Ethiopia, Somalia to the Yemen and from Zimbabwe to South Africa. Wind convergence plus localized weather and moth behavior provide the mechanism for transporting and concentrating moths emerging from primary outbreaks.

Flight mechanisms of *S. exempta* prior to outbreaks have been the subject of extensive studies. After drying and hardening their wings, moths first move up into the trees. Then, when they are ready, they fly up several hundreds of meters into the air, where if caught up by prevailing wind, are carried away downwind. When dawn arrives, the moths descend and hide on the ground in the grass, but at dusk they take off again. They will continue to do this for several days, either until they die, or until they come to an area where rain is falling. Rain causes the moth to descend to the ground. The winds coming out of the rainstorm have the effect of concentrating the moths, rather as though they were being swept together with a brush. This is the reason why armyworms occurring during outbreaks are not evenly distributed. Upon descent to the ground, moths tend to drink water if this is available, mate and then lay their eggs. At this stage dispersal will have come to an end.

In Africa, seasonal rains are brought by the meeting of large scale winds from the northeast and the southwest at the Inter-Tropical Convergence Zone (ITCZ). The position of the ITCZ moves with the sun across the tropical zone twice each year, from north to south between July and December and from south to north between January and June. The first outbreaks, designated as primary outbreaks in East Africa, usually occur in central Tanzania in November or December. Occasionally they occur further south, in Mbeya, Mtwara and Lindi regions of Tanzania. More rarely, they occur in southeastern Kenya.

Moths produced by these primary outbreaks are then carried by the wind towards the ITCZ, which has meanwhile moved north. The moths are thus concentrated in areas where the rains are just beginning, and so they breed and multiply yet again. If conditions are suitable, they will increase at an enormous rate. Although the first outbreaks are only a few hectares in extent, by February and March there may be outbreaks of hundreds of square km.

Thus, as the ITCZ takes the rains northwards, so the moths, carried by the prevailing wind, move with it, bringing new armyworm outbreaks, designated secondary outbreaks, to northern Tanzania, Kenya, Somalia, Ethiopia, Sudan and eventually Yemen. Armyworm outbreak seasons vary greatly in severity, extent and timing in each of these countries.

From September to November, there are seldom armyworm outbreaks in any part of eastern Africa. The armyworm seems to disappear during the dry season. But since they have no diapause, they must be living and breeding somewhere. It has now been established that they survive in quite low numbers along the coastal area, where some rain falls in every month of the year. When the rains begin again in central Tanzania, small numbers of moths migrate inland from the coast and it is these that cause the first outbreaks.

Economic Importance of Outbreaks of *S. exempta*

During armyworm outbreaks, feeding damage by *S. exempta* to cultivated and wild host plants is almost entirely restricted to the leaves, although when food is scarce, the young stems or flowers, particularly of wild grasses, may also be eaten up. The young larvae at first eat the upper and lower surface tissue of the leaves, which results in the skeletonization, or windowing, of the leaves. As a rule, armyworm larvae tend to prefer young plants and recently germinated crops, often defoliating them to ground level. It is estimated that two larvae can completely destroy a 10-day-old maize plant with 6–7 leaves and a single larva can consume 200 mg of dry mass of maize leaves in the course of the sixth instar.

Destruction of cereal crops such as maize, rice, wheat or sorghum often necessitates replanting of the entire affected crop. *S. exempta* larvae are most damaging to cultivated and wild host plants during outbreaks when gregarious bands of larvae travel together on the ground. Such armyworm outbreaks are often capable of causing total crop loss within hours at the local level. Thus, crop losses as a result of armyworm outbreaks can be potentially devastating to local and national economies as they occur in some of Africa's most impoverished economies. Losses are sometimes difficult to assess quantitatively because of hidden costs such as effects of forage destruction, damage to subsistence farms, the expense of additional seed and, most importantly, food aid from international donors.

Survey and Control

Circumstantial evidence from light and pheromone traps shows that long distance migrations occur between moth emergence and the next breeding areas which are in the vicinity of seasonal passages of low-level wind convergence such as Inter-tropical Convergence Zone or African Rift Convergence Zones. Furthermore, increasing levels of moth catches in light and pheromone traps have been found to be followed by increased probability of infestations of larvae occurring 2–4 weeks later at up to 200 km from the trap.

Because primary outbreaks of *S. exempta* originate from moths taken downwind from sources nearest the coasts of eastern Africa, and concentrate where heavy rains are falling, control of this pest involves accurately detecting primary outbreaks and eliminating them before the subsequent moths emerge and move downwind causing secondary outbreaks in another region or country. The major objective is to kill as many armyworms as possible on pasture or crops before subsequent moths emerge and move downwind. Normally, the largest and densest outbreaks are attacked first. This approach is referred to as "strategic control." However, because primary outbreaks often remain unnoticed until after secondary outbreaks have occurred, direct elimination of the latter becomes the main objective in multiple outbreak situations.

Monitoring possible sources of the moths that cause primary outbreaks has involved deployment of a network of light and pheromone traps, as well as ground searches for low-density larvae in the off-season in areas historically known to be sites of primary outbreaks. In addition, for all primary outbreak areas, rainfall stations must report on a weekly or daily basis the amount of rainfall during the first month of the rainy season. Recently, there have been attempts to introduce predictive models that integrate African Real Time Environmental Monitoring and Information System (ARTEMIS) and satellite imagery and synoptic weather data that has been applicable for detection and elimination of gregarious locusts. The major challenge associated with armyworm monitoring, forecasting and control in countries most ravaged by this pest is the inadequacy of funding for these operations.

Because elimination of all primary outbreaks is almost impossible to achieve, management strategies for *S. exempta* tend to focus more on suppression of secondary outbreaks. This approach has invariably been dependent on the application of pesticide sprays. To date, a series of low toxicity pesticides are often used (e.g., synthetic pyrethroids, carbamates and organophosphates). Previously, highly toxic, persistent and broad spectrum pesticides such as DDT, BHC, dieldrin and a series of others were used due to lack of alternative, safer products. However, due to the need for rapid intervention and coverage of fairly extensive areas during outbreaks, newer oil-based pesticides are being applied as ultra-low volume (ulv) formulations using hand held, battery driven applicators. Nevertheless, suppression tactics are only cost-effective when applied in a timely manner on farmland. Outbreaks occurring on uncultivated land often remain unchecked.

Unfortunately, control of armyworms by less toxic means has received far less attention than in the case of other international migratory pests such as locusts, which have been the targets for tests involving fungi, protozoa and even viruses.

Extensive studies in eastern Africa have confirmed that all life stages of the armyworm are subject to attack by a diversity of natural enemies. For example, up to 90% of armyworm caterpillars in the last instar can be killed by a nuclear polyhedrosis virus (NPV). Similarly, pupal and prepupal stages can be killed by a cytoplasmic virus. The only fungus known to attack armyworms during conditions of high humidity and temperature is *Normuraea rileyi*. Armyworms infected by this fungi typically climb to the top of grass blades where they die amidst masses of mycelia.

Armyworm larvae are also subject to parasitism by some 28 species of tachnid flies (Diptera: Tachinidae). In cases of parasitism from wasps (Hymenoptera), some 25 parasitoids have been isolated from eggs, larvae and pupae of *S. exempta*. Apart from attack by parasitoids, there are several arthropod predators that prey on armyworms, including ants (Hymenoptera: Formicidae) and beetles (Coleoptera), which often prey on eggs and early larval stages of *S. exempta*. To date, there has been no effort to study the potential of some of these natural enemies for commercialization. Armyworm outbreaks also attract flocks of avian predators, notably storks such as Marabou storks, white (European) storks and Abdim's storks. Occasionally, such assemblages of predators help to eliminate small primary or secondary outbreaks of *S. exempta*.

For the more foreseeable future, it is evident that preventive control of armyworms will continue to rely on diligent surveillance during recessions and, as outbreaks occur, intensified scouting will be necessary to locate and then eliminate pockets of solitary morphs before outbreaks.

References

Regional Armyworm Programme of Desert Locust Control Organization for Eastern Africa (1992) The African armyworm DLCO-EA, Addis Ababa, Ethiopia, 19 pp

Meinzingen WF (ed) (1993) African armyworm. In: A guide to migrant pest management in Africa. FAO AGP, Rome, Italy, pp 71–85

Rose DJW (1979) The significance of low-density populations of the African armyworm, *Spodoptera exempta*. (Walker). Philos Trans R Entomol Soc London B 287:393–402

Odiyo PO (1979) Forecasting infestation of a migrant pest: the African armyworm, *Spodoptera exempta*. (Walker). Philos Trans R Entomol Soc London B 287:403–413

African Honey Bee, Africanized Honey Bee, or Killer Bee, *Apis mellifera scutellata* Lepeletier (Hymenoptera: Apidae)

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The African honey bee (*Apis mellifera scutellata* Lepeletier) is a subspecies (or race) of western honey bee (*A. mellifera* L.) that occurs naturally in sub-Saharan Africa but has been introduced into the Americas. More than 10 subspecies of western honey bees exist in Africa and all justifiably are called "African" honey bees. However, the term "African (Africanized) honey bee" refers exclusively to *A.m. scutellata* in the bee's introduced range (Fig. 22).

Subspecies of western honey bees are native to Europe and Africa but have been spread widely outside their native range due to their economic importance as pollinators and producers of honey. Initially, only European subspecies of honey bees (hereafter referred to as European bees) were introduced into the Americas, where they were found to be productive in temperate North America but less so in Central and South America where tropical/subtropical climates dominate. In response to the poor performance of European bees in Brazil, Warwick Kerr, a Brazilian scientist, traveled to southern Africa to screen African honey bee subspecies for productivity and viability. His visit resulted in the importation of *A.m. scutellata* into Brazil in the late 1950s.

Dr. Kerr hoped that through experimentation and selective breeding, the African bee could be made manageable and available for use by Brazilian beekeepers. As such, he initiated efforts to breed gentleness into the African stock while amplifying its many positive traits. The breeding effort was not carried to completion because the African bees swarmed accidentally, ending their initial quarantine. Following this, the bees began to spread throughout Brazil and into other parts of South America.

All subspecies of *Apis mellifera* can interbreed or hybridize. Consequently, African bee hybridization with European bees became frequent as African bees moved into areas previously occupied by European bees. It is this hybridization with

African Honey Bee, Africanized Honey Bee, or Killer Bee, *Apis mellifera scutellata* Lepeletier (Hymenoptera: Apidae), Figure 22 The natural distribution of *Apis mellifera scutellata* in Africa (modified from Hepburn HR, Radloff SE (1998) Honeybees of Africa. Springer-Verlag, Berlin, 370 pp), and its distribution in the Americas.

European honey bees that earned them the name "Africanized" honey bees. Traditionally, "African" and "Africanized" have been used interchangeably although the former really refers to the pure race and the latter to the hybrid.

The spread of African bees throughout South and Central America, fueled by rapid hybridization with European subspecies and the dominance of African alleles over European ones, occurred at a rate of 200–300 miles per year. Because their movement through South and Central America was rapid and largely unassisted by humans, African bees earned the reputation of being the most successful biologically invasive species of all time. In 1990, populations of African honey bees had saturated South and Central America and begun to move into the USA. As of 2006, African honey bees were established in the southernmost USA: Texas, California, New Mexico, Arizona, Oklahoma, Louisiana, Arkansas, Alabama, and Florida.

The spread of African bees in the U.S. continues, albeit at a much slower rate than what occurred throughout South and Central America. This slowed rate of territory expansion appears due to climatic limitations. African bees do not survive in temperate climates as well as European bees do. Therefore, they have failed to establish populations below about 32° latitude in the southern hemisphere. Although they have expanded beyond this parallel in the northern hemisphere, African bee expansion northward also appears limited climatically, being found only below about 34° latitude currently.

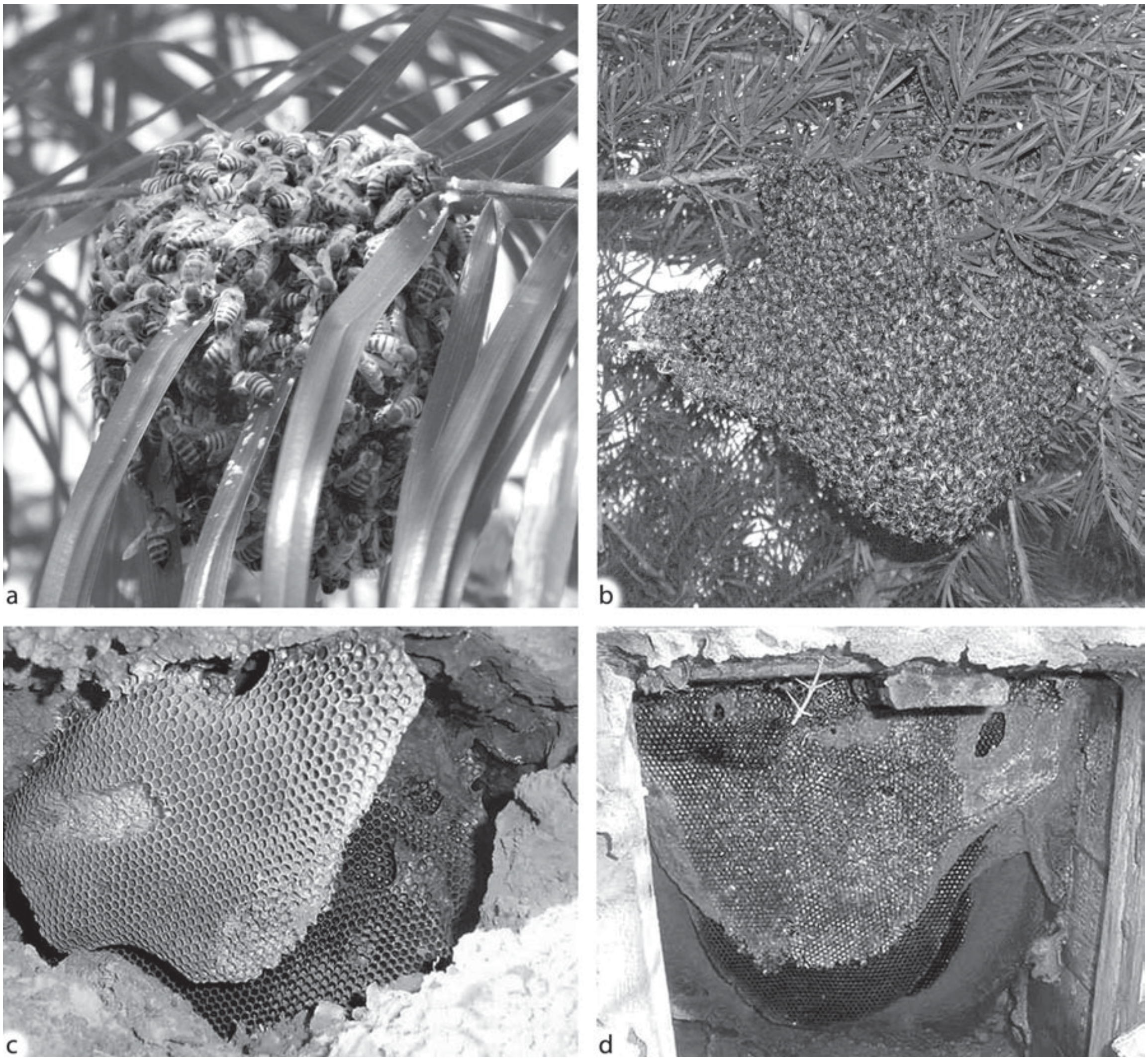
Description and Behavior

African honey bees cannot be distinguished from European honey bees easily, although they are slightly smaller than the various European races. Laboratory personnel use morphometric analyses to determine the likelihood that a given colony is Africanized or fully African. With honey bees, the measurement of wing venation patterns and the size and coloration of various body parts (morphometry) are important determinants of identification at the subspecific level. Morphometry has been used to differentiate honey bee races since the 1960s and remains the first round of identification when suspect colonies are discovered. Morphometric analyses were first used to differentiate Africanized and European honey bees in South America in 1978. A more rigorous identification is achieved by genetic analysis and often is necessary when the suspect bees are a hybrid between African bees and the European subspecies.

Other differences between African and European bees manifest themselves behaviorally. To the casual bystander, the primary identifying behavioral characteristic of Africanized bees is their heightened defensiveness compared to that of European subspecies. Selection pressures induced by man are, in part, responsible for this increased defensiveness. "Beekeeping" (management of honey bee colonies by humans) is more common in Europe, where the native honey bees have been bred for gentleness and ease of management. In contrast, "honey hunting" (near-complete destruction of hive to harvest contents) is more common in Africa, resulting in a bee that is more defensive of its nest. Other selection pressures that led to a heightened defensiveness in African bees include climatic stresses, resource availability, and predation by birds, mammals, and various reptiles. These selection pressures resulted in an African race of bee that can be 10 + times more defensive than any of the various European races of bee.

All honey bees readily defend their nests, and an attack usually means that the victim is too close to the nest. While European races of bees may attack a nest intruder with >10 bees, African bees may attack the same intruder with >1,000 bees. Further, African bees defend a larger radius around their nest and require lower levels of stimuli to initiate an attack. Because of these characteristics, African bees are capable of killing large mammals, including man. This defensiveness has earned them the nickname "killer" bee. It is important to note that their ability to kill humans has nothing to do with their size or the potency of their venom. African bees are smaller than European bees and probably deliver a comparatively smaller dose of venom to their victim than do European bees. Because both bees use the same type of venom, human deaths are a result of the number of stings they receive rather than an increased potency of African bee venom.

Another behavioral difference between African and European bees concerns colony level reproduction and nest abandonment. African honey bees swarm and abscond in greater frequencies than their European counterparts. Swarming, bee reproduction at the colony level, occurs when a single colony splits into two colonies, thus ensuring survival of the species. European colonies commonly swarm 1–3 times per year. African colonies may swarm >10 times per year. African swarms tend to be smaller than European ones, but the



African Honey Bee, Africanized Honey Bee, or Killer Bee, *Apis mellifera scutellata* Lepeletier (Hymenoptera: Apidae), Figure 23 (a) African bees swarm readily and nest in unusual locations, including (b) exposed on tree limbs, (c) within cavities in the soil, (d) within discarded furniture.

swarming bees are docile in both races. Regardless, African colonies reproduce in greater numbers than European colonies, quickly saturating an area with African bees. Further, African bees abscond frequently (completely abandon the nest) during times of dearth or repeated nest disturbance, while this behavior is atypical in European bees.

Another common difference between African and European honey bees is their choice of nest locations. African honey bees are less selective when considering a potential nesting site than are European bees. They will nest in a much smaller volume than European honey bees and have been found in water meter boxes, cement blocks, old tires, house eaves, barbecue grills, cavities in the ground, and hanging exposed from tree limbs, just to name a few places. One rarely finds European colonies in any of these locations because they prefer to nest in larger cavities like those provided by tree hollows, chimneys, etc. As one can imagine, humans inadvertently provide multiple nesting sites for African bees. Therein lies the primary reason African bees are encountered frequently by humans (Fig. 23).

A final behavioral curiosity of African bees concerns nest usurpation (or colony takeover) of European colonies. Small African swarms containing a queen often land on the outside infrastructure of a European colony (a wall, beekeeper-managed hive, etc.). As time passes, the worker bees in the African swarm begin to exchange food/pheromones with the European workers from the colony. This gradually ensures the adoption of the African bees into the European colony. Somewhere during this process, the European queen is lost (perhaps killed by the African bees – her fate remains uncertain at this point) and the African queen is introduced into the colony, thus becoming the reigning matriarch. European bees do not display this behavior but often fall victim to it, thus creating an African colony from a preexisting European one.

Other behavioral differences between African and European races exist and are worth discussing briefly. For example, African bees are more “flighty” than European bees, meaning that when a colony is disturbed, more of the bees leave the nest rather than remain in the hive. African bees use more propolis (a derivative of saps and resins collected from various trees/plants) than do European bees. Propolis is used to weather-proof the nest and has various antibiotic properties. African colonies produce proportionally more drones (male bees) than European bees. Their colonies grow faster and tend to be smaller than European colonies. Finally, they tend to store proportionately less food (honey) than European bees, likely a remnant of being native to an environment where food resources are available throughout the year.

Life Cycle and Genetic Dominance

Mating biology and developmental time play an important role in the success of African bee colonies in replacing European colonies in an area. For the most part, mating and developmental biology are similar for African and European bees, but key differences confer adaptive benefits to the former.

Virgin queens of all western honey bees emerge from peanut hull-shaped waxen cells. After a short time of further maturation, a virgin queen will leave the colony to mate with drones. All mating occurs in the air, with the fastest drones being the most successful suitors. Queens will mate multiple times over the course of 7–10 days and during this time they will mate with an average of 12–20 drones. Queen bees store semen in an organ called a spermatheca. African colonies produce more drones/colony so drone populations in an area tend to favor African bees. As such, virgin European queens are more likely to mate with African drones rather than European ones. Further, flight time and distances of mating flight from the colony tend to result in European queens encountering African drones more often than European drones, thus setting the stage for hybridization.

All honey bees undergo complete metamorphosis but the time from egg to adult varies by subspecies. The newly-mated queen bee oviposits in wax cells constructed by worker bees. Fertilized eggs result in female offspring, either workers or queens. If fed a diet rich in royal jelly, the female larva will develop into a queen, with the reciprocal true for the development of workers. Drones result from unfertilized eggs and consequently only inherit genetic material from their mother (they have no father).

Developmental time varies by caste member (see Table 4) and favor African honey bees because they generally develop faster than European bees. When bee colonies decide to make a new queen, newly emerged female larvae are fed royal jelly constantly. Because Africanized offspring, including queens, develop faster than European offspring, a queen having an African genotype is more likely to emerge earlier than a queen with a European genotype. The first queen to emerge kills all of her queen sisters that have not yet emerged from their cells. The Africanized virgin proceeds to mate in an area having higher densities of African drones. Over time, this results in the colony becoming more African with the European phenotype being replaced almost altogether. This process is exacerbated further due to the dominance of African genetic traits over European ones.

Finally, African bees are more resistant to many honey bee pests/pathogens than are European bees. Western honey bees face a myriad of pests and diseases, the most severe of which include varroa mites (*Varroa destructor*), tracheal mites (*Acarapis woodi*), small hive beetles (*Aethina tumida*), and American foulbrood (*Paenabacilis larvae*). These bee pests almost eliminated all wild colonies of European honey bees in North America. Because African bees are resistant to many of these pests/diseases, their survivorship in the wild is favored over that of European bees.

Public Risks

Due to their heightened defensive behavior, African honey bees can be a risk to humans. Children, the elderly, and handicapped individuals are at the highest risk of a deadly attack due to their inability or hampered ability to escape an attack. African honey bees are agitated by vibrations like those caused by power equipment, tractors, lawn mowers, etc. Further, their nesting habits often put them in close proximity to humans. Because of this, precautions should be taken in an area where Africanized honey bees have been established. These precautions are not suggested to make people fearful of honey bees but only to encourage caution and respect of honey bees. The precautions include remaining alert for honey bees flying into or out of an area (suggesting they are nesting nearby), staying away from a swarm or nest, and having wild colonies removed from places that humans frequent. The latter is perhaps the most important advice one can heed when dealing with African bees. In the USA, a large percentage of African bee attacks occur on people who know a nest is present but elect not to have it removed (or try to do it themselves).

If an attack occurs, remembering a few simple recommendations will increase one's chances of minimizing the effects and severity of the attack. If attacked, a victim should run away from the area using his shirt to cover his head and especially airways. Running through tall grass or small trees will help to disrupt the attacking bees. The victim should not stand and swat at the bees. The bees are defending their nest, and the victim needs to get away from that nest as quickly as possible. It is important that the victim get cover in a bee-proof vehicle or structure if either is available. One should not jump into the water or hide in bushes. The bees can remain defensive and in the area for some period of time, thus increasing the risk to the victim. If stung, the victim should remove the stinger quickly by scraping it rather than by pulling it. One should see a doctor immediately if breathing is affected.

Many African bee attacks can be prevented by limiting the number of nesting sites that are available to the bees. A homeowner, school worker, etc. can "bee proof" his or her property by eliminating possible nesting sites. This can be accomplished by removing any unnecessary debris from an area and closing off wall, chimney, electrical and plumbing-related gaps that are >30 mm using a small-mesh hardware cloth or caulking. This will limit bee access to potential nesting sites. Finally, one should check walls and eaves of structures regularly, looking for bee activity.

African Honey Bee, Africanized Honey Bee, or Killer Bee, *Apis mellifera scutellata* Lepeletier (Hymenoptera: Apidae), Table 4 The developmental time in days (from egg to adult) of European and African honey bees

	European honey bees	African honey bees
Queen	16	14
Worker	21	19–20
Drone	24	24

Managing African Bee Colonies

It is important to remember that African honey bees pollinate crops and produce honey just like other races of honey bees. Beekeepers in South Africa use African honey bees as the bee of choice in their operations. So, African bees can be managed efficiently and safely but the skills required to manage African bee colonies differ from those required to manage European bee colonies.

In general, the management of African bee colonies has been discouraged in the US while accepted in Central and South America. This may have to do with the public perception of honey bees, particularly African bees, in the USA and the robust legal system in place in the USA. On the other hand, beekeepers in Central and South America routinely use African bees in their operations with slight management modifications. In fact, some South American countries are among the leading honey producers in the world, due largely to the presence of African bees in the country.

Beekeepers in South and Central America utilize a number of management practices in order to keep African bees. First, they keep single bee colonies on individual hive stands rather than using one hive stand for multiple colonies. This limits the management activity to one colony at a time rather than aggravating other colonies while working only one.

Secondly, beekeepers in South and Central America use ample amounts of smoke when working African bee colonies. It is believed that smoke masks the alarm pheromone of the bees, thus lessening the defensive response of the colony. Most South and Central American beekeepers agree that copious amounts of smoke should be used when working African bee colonies. It is important to smoke the colonies well before any work is done, for once bees from a colony are agitated, smoke may fail to calm them down.

Beekeepers managing African bees wear appropriate protective gear. A typical beekeeper working an African colony would wear a full bee suit, boots, gloves, and a bee veil. Bee veils (protective headgear) are worn by almost all beekeepers worldwide. Traditionally, the veil mesh protecting the face is colored black to keep down the sun's glare. African bees (and most honey bees) attack dark colors so black-faced veils often get covered with bees. Consequently, beekeepers can use white-faced veils to keep the bees off of their veils. Beekeepers managing African colonies often tape their bee suits to their boots and gloves to limit the possibility of bee access.

Finally, some beekeepers in areas with African bees try to requeen African bee colonies with European queens. This is not a common practice in sub-Saharan Africa. Most African beekeepers in areas having African bees gladly use the bee in their operations, paying little attention to the bees' defensiveness.

Conclusion

The economic impact of African bees in an area can be substantial. Keepers of European bees often notice a decrease in resource availability for their bees because of the density of African bee colonies in an area, and thus the demand on the available resources is high. Furthermore, cities, municipalities, etc., often initiate eradication programs, with much futility. Finally, the loss of animal and human lives is a tragic occurrence, being beyond measurable cost.

African bees also may affect the environment negatively. Colony densities as high as 300 African bee colonies per square mile have been suggested. If true, African bees may have a substantial impact on the native flora and fauna in an area. While this impact often is not reported and largely is not understood, it could be significant considering the potential number of colonies and their need for resources. Thus, the world's most infamous honey bee is among nature's most enigmatic creatures.

► Apiculture (Beekeeping)
► Honey Bee

References

Caron DM (2001) Africanized honey bees in the Americas. The A.I. Root Co., Medina, OH, 228 pp

Hepburn HR, Radloff SE (1998) Honeybees of Africa. Springer-Verlag, Berlin, 370 pp

Winston ML (1992) Killer bees: the Africanized honey bee in the Americas. Harvard University Press, Cambridge, MA, 176 pp

African Horse Sickness Viruses

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African horse sickness is a highly fatal, noncontagious disease of equines, particularly horses. The African horse sickness virus group consists of nine serotypes, in the genus *Orbivirus*, family Reoviridae. It is closely related to the bluetongue viruses, which cause disease in cattle and sheep. Infection with any of the serotypes of African horse sickness virus usually results in severe disease and high mortality in horses. Donkeys and mules generally exhibit less severe disease and lower mortality, while wild equids such as zebra generally show no signs of disease or mortality after infection. The serotypes are differentiated based on the host immune response, and there is some cross reaction between serotypes.

All nine serotypes are endemic to sub-Saharan Africa, and have caused serious epidemics when introduced outside this area. African horse sickness has had a significant impact on the history of some parts of Africa, as horses could not be used in exploration and farming. Outbreaks of African horse sickness have a significant economic impact, resulting from the direct loss of animals, the costs of control programs, and trade regulations and quarantines restricting movement of equines from infected areas.

The virus is transmitted by biting midges in the genus *Culicoides*. *Culicoides imicola* has been implicated in most outbreaks, while in endemic areas there may be several species of *Culicoides* midge involved in the transmission cycle. Most species of equines can develop viremias sufficiently high to infect midges. Some tick species have been shown to be able to become infected and transmit the virus in the laboratory, but the importance of this transmission route in nature is unknown.

In endemic areas, African horse sickness viruses circulate primarily between midges and zebra, and frequently multiple serotypes are present. Transmission rates can be very high. For example, in the Kruger National Park, South Africa, zebra foals typically are exposed to all nine serotypes by the time they are 1 year old.

The first outbreak outside the sub-Saharan zone began in 1959 in Saudi Arabia and Iran, spreading to involve Afghanistan, Pakistan, Syria, Lebanon, Jordan, Iraq, Turkey, Cyprus and parts of India before being controlled by vaccination campaigns and the loss of most susceptible horses by the end of 1961. Another outbreak occurred in North Africa in 1965, crossing into Spain in 1966. An outbreak of African horse sickness serotype 4 virus began in central Spain in 1987 and ultimately encompassed a large part of Spain, along with parts of Portugal and Morocco. This outbreak was the first recorded instance of an African horse sickness virus overwintering outside of Africa. African horse sickness cases occurred for four subsequent years in Spain, and it was not eradicated until 1990. The most likely route of introduction was via zebra imported from Namibia. Control and eradication of the virus was achieved only by extensive vaccination campaigns and slaughter of infected or exposed equines. It is estimated that 2,000 horses died and over 350,000 were vaccinated during this outbreak. In 1989, an outbreak of serotype 9 occurred in Saudi Arabia.

Spain was divided into African horse sickness-free and infected regions, in order to allow movement of horses for the 1992 Olympics held in Barcelona. No vaccination was allowed in the African horse sickness-free region, so that any transmission activity would be observed. Equine movement out of the infected region was prohibited.

A similar strategy is used in South Africa, with an African horse sickness-free zone in the Western Cape Province, based on historically low incidence of African horse sickness, and that *C. imicola* is rare. Surrounding this zone is a surveillance zone and a protection zone. No vaccination is allowed in the free and surveillance zones, and strict movement controls are in place for equines moving from other areas of the country. The zoning creates an area where animals can be held prior to exportation. In 1999, there was an outbreak of African horse sickness in the surveillance zone, opening debate about the effectiveness of the movement restrictions and the vector species involved. Currently, the zoning is still in place and there have not been further outbreaks in the African horse sickness-free zone.

Clinical signs of African horse sickness in horses generally begin with fever. There are three forms of African horse sickness disease in horses: pulmonary, cardiac, and febrile. The febrile form, often referred to as horse sickness fever, does not progress beyond fever and generally resolves. The pulmonary form begins with fever and progresses to respiratory difficulty, coughing and nasal discharge. Death is due to pulmonary edema and cardiac failure. The cardiac form also begins with fever, and subsequently edemas develop around the head, neck and chest. Death results from cardiac insufficiency and progressive pulmonary edema. Mortality rates can be as high as 95% in horses, although donkeys and mules are much less susceptible and mortality rates are much lower. Movement of donkeys may be important in the spread of these viruses outside the endemic area, as they are rarely clinically ill and so infected animals are not noticed. There is variation in virulence between the nine African horse sickness serotypes, along with differences between breeds of horse and individual immune responses to the virus.

Vaccines have been developed against these viruses, but due to the immunological differentiation between the serotypes, cross protection is not complete and full protection requires vaccination against each serotype. Routine vaccination of horses, against all serotypes, is practiced in endemic areas. Elsewhere, vaccination generally is not used routinely or is not allowed. In outbreak situations, the virus is first typed to determine the serotype involved, then vaccination is targeted against that serotype only.

Most countries restrict importation of equids from endemic countries. An extended quarantine period usually is imposed, thus restricting the movement of horses for competition. Because it is difficult to differentiate between vaccinated and infected animals, generally there are restrictions on importing vaccinated animals.

Antibodies to African horse sickness viruses have been found in other animals such as elephants, camels, and bovines, but there is no apparent illness and their impact on the transmission cycle is not known. Dogs can become infected and die by eating meat from the carcass of an infected animal. Antibodies to African horse sickness have been found in wild canids and other carnivores, most likely also via feeding on infected carcasses. Humans have been infected only rarely, generally through laboratory accidents with vaccine strains.

African horse sickness has never been found in the New World. However, there are species of *Culicoides*, particularly the *C. variipennis* complex, present throughout the U.S. Some members of this complex are competent vectors of African horse sickness viruses in the laboratory, and will be competent vectors in the field should an African horse sickness virus be introduced. Vector competence for the *C. variipennis* complex varies considerably for the closely related bluetongue viruses, but we lack information on similar variation for African horse sickness viruses. The implications of this for an introduction of any of the African horse sickness viruses is unknown, but requires further study.

References

Bram RA, George JE, Reichard R, Tabachnick WJ (2002) Threat of foreign arthropod-borne pathogens to livestock in the United States. J Med Entomol 39:405–416

Holbrook FR, Tabachnick WJ, Schmidtmann ET, McKinnon C, Bobian RJ, Grogan WL (2000) Sympatry in the *Culicoides variipennis* complex (Diptera: Ceratopogonidae): a taxonomic reassessment. J Med Entomol 37:65–76
House JA (1993) Recommendations for African horse sickness vaccines for use in nonendemic areas. Rev élev Méd Vét Pays Trop 46:77–81
Mellor PS, Boorman J (1995) The transmission and geographical spread of African horse sickness and bluetongue viruses. Ann Trop Med Parasitol 89:1–15
Mellor PS, Boorman J, Baylis M (2000) biting midges: their role as arbovirus vectors. Annu Rev Entomol 45:307–340

Africanized Bees

Honeybees in the Western Hemisphere that are derived from hybridization of African and European subspecies of *Apis mellifera*. The degree of hybridization is unresolved.

► Bees
► Honeybee
► African Honey Bee

African Mahogany-Feeding Caterpillar, Heteronygmia dissimilis aurivillius (Lepidoptera: Lymantriidae)

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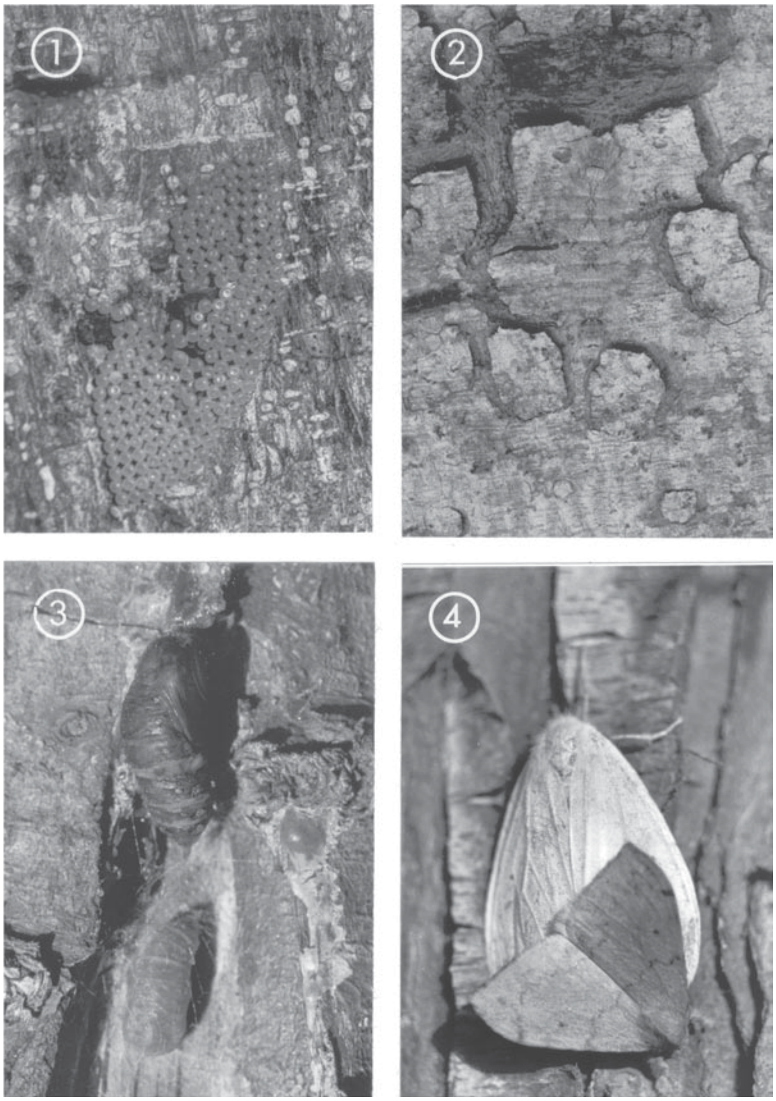
Several genera and species of mahoganies in various parts of the tropics are highly valuable timber species, among them African mahogany (*Khaya* spp.). Relatively few defoliators are known to target this genus, among them caterpillars of several silkmoths, the nymphalid Charaxes and the lymantriid *Heteronygmia*. Only the latter, presumably monophagous on *Khaya*, appears to have pest potential as indicated by small-scale outbreaks observed in Morogoro, Tanzania, in the 1980s.

A succession of four generations per year allow *Heteronygmia dissimilis* to be active most of the year, except for a period of estivation during the hottest season, i.e., from November to February. Eggs are found from early March to late October with peaks from May to August, i.e., during the cool, dry season. Egg clusters are located mostly on the lower trunks of trees and consist of 24–130 glossy, globular or dimpled spheres, each about 1 mm in diameter. They hatch 6–10 days after oviposition, depending on the season (Fig. 24).

Caterpillars of various instars are found anytime between early March to the end of November, with periods of greatest abundance from June to September. All larval instars are hairy and last instars occur in two color phases. One of them is milky-green; the other, more common one, a highly camouflaged, brown to greyish-white mottled bark pattern including up to three, more or less distinct dorsal saddles. Caterpillars feed solitarily, and move with great speed and agility when disturbed, including a hopping and ballooning response during the first four instars. Early instars skeletonize *Khaya* leaflets at night and spend the day motionless on or underneath leaflets. Older instars are free feeders and rest on the lower trunk during the day. All instars shun the foliage of just-expanding shoots. There are five instars in males and six in females, each of them lasting from 5–6 days.

Pupae are found from late February to early December, abundantly so from June to September. They often are cradled in loose leaf shelters tied together by sparse strands of silk or in other hiding places, such as under bark scales.

The moths are present from February to mid-November, most abundantly so from May to September. They rest during the day and are attracted to lights at night. Slender male moths are light to dark or reddish brown with substantial plumose antennae, whereas the white to cream-colored females are bigger and more robust with smaller antennae. Males have wingspans of about 40 mm and are able fliers, while females with wingspans of about 50 mm, are reluctant to take to the air and then only as poor fliers. Both sexes have faint to more pronounced grey line markings and a small black dot on each front wing. Before oviposition, the greatly distended abdomen of the female is greenish. Male moths reach adulthood after an average of 41 days (September/October), females after about 45



African Mahogany-Feeding Caterpillar, Heteronygmia Dissimilis aurivillius (Lepidoptera: Lymantriidae), Figure 24 **Egg (top left) (2x), last instar larva (top right) (1x), pupa (bottom left) (1.7x) and (mating) adult stages (bottom right) (2x) of *Heteronygmia dissimilis*, respectively. Both sexes are represented in the bottom figures, the larger females being above in each picture. (Photo: H. Schabel et al. 1988; reprinted with permission from ICIPE, the International Centre of Insect Physiology and Ecology.)**

days of development. On the average, each female produces about 200 eggs, laid in several batches.

While no field control of *Heteronygmia* has been undertaken to date, a laboratory study documented full protection of *Khaya* leaves from defoliation by *H. dissimilis*, following application of 1% crude, aqueous seed extracts of the neem tree (*Azadirachta indica*).

Numerous arthropod predators of the caterpillars and pupae are believed to be generalists with little impact. On the other hand, four hymenopterous and two dipterous parasites affecting various stages of *H. dissimilis* seem more specific. Seasonally, egg parasites in particular had significant impacts on this insect and in conjunction with the fungus *Paecilomyces farinosus*, which severely decimated pupae during the rainy season, were responsible for serious setbacks in the annual buildup of *H. dissimilis*. As a result, natural controls seem to be quite effective with this insect.

References

Ballard E (1914) Two pests of mahogany in Nyasaland. Bull Entomol Res 5:61–62

Rwamputa AK, Schabel HG (1989) Effects of crude aqueous neem extracts on defoliation of *Khaya nyasica* by *Heteronygmia dissimilis* (Lepidoptera: Lymantriidae) in East Africa. In: Alfaro RI, Glover SG (eds), Proceedings, IUFRO Working Group on Insects Affecting Afforestation, XVIII International Congress of Entomology. Vancouver, British Columbia, Canada, pp 245–250

Schabel HG, Schabel A, Msanga HP (1988) Bioecological aspects of the mahogany defoliator *Heteronygmia dissimilis* in Morogoro, Tanzania. Insect Sci Appl 9:179–184

African Maiden Moths (Lepidoptera: Thyretidae)

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African maiden moths, family Thyretidae, include 212 species, all African. The classification remains controversial and various specialists also place the group within Arctiidae. The family is in the superfamily Noctuoidea, in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults medium-size (23–57 mm wingspan). Haustellum usually reduced or vestigial; antennae pectinate; wings very elongated, with reduced hindwings (some with greatly reduced hindwings). Maculation typically dark with white or hyaline patches, or more colorful. Adults perhaps mostly diurnal; often wasp mimics. Larvae are thought to be leaf feeders, but most species remain unknown biologically. Host plant records include Thymelaeaceae and Ulmaceae, for the few species known biologically.

References

Janse AJT (1945) On the South African species of Metarctia, with the description of a new species. J Entomol Soc South Africa 8:91–98

Kiriakoff SG (1949) Over de phylogenie van de Thyretidae fam. nov. (Lepidoptera). Natuurwetenschappen Tijdschrift 30:3–10

Kiriakoff SG (1953) Les Thyretidae du Musée Royal du Congo Belge (Lepidoptera Notodontidae). Annales du Musée Royal du Congo Belge, Sciences Zoologiques (8) 26:1–91

Kiriakoff SG (1957) Notes sur les Thyretidae (Lepidoptera: Notodontidae). Bulletin et Annales de la Société Royale Entomologique de Belgique 93:121–160

Kiriakoff SG (1960) Lepidoptera. Fam. Thyretidae. In: Genera Insectorum. Brussels, 214:1–66

African Pine-Feeding Grasshoppers, *Plagiotriptus pinivorus* (Descamps) and P. Hippiscus (Gerst.) (Orthoptera: Eumastacidae)

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These grasshoppers are excellent examples of indigenous insects that developed a preference for an exotic plantation-grown crop, in this case pines. *Plagiotriptus pinivorus* attained some prominence after causing persistently severe defoliation of exotic pines, especially *Pinus patula*, in Malawi in the 1960s, resulting in significant tree mortality. A smaller scale defoliation of *P. patula* was observed at Morogoro in Tanzania in the mid-1980s, which was attributable to another, very closely related species, *Plagiotriptus hippiscus*. Both of these grasshoppers are highly polyphagous, including herbaceous hosts, shrubs and both angiosperm and gymnosperm trees. The prime requirement for *P. pinivorus* seems to be access to evergreen or semi-evergreen vegetation in areas of moderate to heavy rainfall, i.e., mostly at altitudes between 1,525–2,135 m, but occasionally as low as 490 m.

Plagiotriptus pinivorus in Malawi exhibits three generations every 2 years, and the complete life cycle takes about 1 year. Nymphs and adults have been observed on pines throughout the year, except from December to late January. Copulation occurs anytime, but peaks from October to January and May to June. During copulation, the small male assumes a characteristic dorso-lateral position by clinging to one of the hind femurs of the female. Both males and females are promiscuous. About 7–20 days after the last mating, females seek bare soil and dig a shallow pit to lay a batch of up to six eggs. They then resume voracious feeding in the trees, before laying other batches of eggs at 17–35 day intervals.

Eggs incubate from 49–248 days, with an average of 115 days. The winter population hatches from April to May, maturing in November, while the summer population hatches from December to January and matures from May to July. Within the same batch, an average of 34 days and a maximum of 88 days may elapse between first and last hatch.

Nymphal peak emergence and rainfall are strongly correlated in February, allowing prediction of emergence two weeks in advance. Another smaller peak in emergence in August, however, cannot be explained by rainfall. The first instar nymph is ephemeral (about 12 h), and will molt immediately when reaching the soil surface, before feeding on ground vegetation for the next 2–3 weeks. Advanced instars complete their life cycle on trees, each instar lasting about one and a half to over two months. Young instars are wasteful feeders. There are generally six instars for males and seven for females. Despite the extra instar, females develop more rapidly and reach adulthood at about the same time as do males.

Adult males (Fig. 25) are about 1.5–2 cm long, moderately robust grasshoppers. Their abdomen, shield-like pronotum and greatly enlarged hind femora are strongly compressed. A minute set of non-functional wings, not found on nymphs, is hidden under the pronotum. The thread-like antennae are about one third the length of the head. The abdomen is strongly reflexed over the back in the male. The insect is largely leaf-green, but sports inconspicuous, small areas of blue, pink, red and white on various parts of the legs, wings, antennae and the pronotal

African Pine-Feeding Grasshoppers, *Plagiotriptus pinivorus* (Descamps) and *P. hippiscus* (Gest.) (Orhthoptera: Eumastacidae), Figure 25 ***Plagiotriptus hippiscus*** **female (above) and male (below) with size comparison (shaded) (drawing, Paul Schroud).**

ridge. Eyes are golden yellow. Females are about twice the size of males, more robust and generally less compressed. They are uniformly leaf-green, except for the golden yellow eyes and valves of the ovipositor. Their wings are also minute and hidden under the pronotal shield.

Numerous invertebrate and vertebrate predators, including skinks, birds and blue monkeys, as well as parasites were documented, but ultimately they were deemed insufficient by themselves to reduce populations of the grasshopper to non-damaging levels. As a result, sticky bands and chemical controls were relied on for monitoring and control purposes, respectively. In the 1960s in Malawi, gamma-BHC at 0.5% proved the most effective insecticide for ground and aerial applications at ultra-low volume formulations. Spraying of road banks was particularly recommended, as insects clustered there for oviposition in the bare ground.

References

Lee RF (1972) A preliminary account of the biology and ecology of *Plagiotriptus* spp. (Orthoptera: Eumastacidae). Malawi Forest Research Institute Research Record 48, Forestry Research Institute of Malawi, Zomba, 100 pp

Schabel HG, Hilje L, Nair KSS (1999) Economic entomology in tropical forest plantations: an update. J Trop For Sci Xth Anniversary Issue: 303–315.

African Primitive Ghost Moths (Lepidoptera: Prototheoridae)

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African primitive ghost moths, family Prototheoridae, comprise 12 species of small moths from South Africa. The family is in the superfamily Hepialoidea, in the infraorder Exoporia. Adults small (18–mm wingspan), with head rough-scaled; haustellum reduced and vestigial mandibles present; labial palpi long and porrect, 3-segmented; maxillary palpi short and 3-segmented; antennae short. Maculation is brown or gray, with various darker spots. Biologies and larvae remain unknown.

References

Davis DR (1996) A revision of the southern African family Prototheoridae (Lepidoptera: Hepialoidea). Entomol Scand 27:393–439

Davis DR (2001) A new species of *Prototheora* from Malawi, with additional notes on the distribution and morphology of the genus (Lepidoptera: Prototheoridae). Proc Entomol Soc Wash 103:452–456

Davis DR (2003) Prototheoridae. In: Lepidopterorum Catalogus, (n.s.). Fasc. 11. Assoc Trop Lepid Gainesville, 8 pp

Janse AJT (1942) Prototheoridae. In: Janse AJT (ed) The moths of South Africa, Pretoria, 4(1): 65–74

African Red Tick, *Rhipicephalus evertsi*, (Acarina: Ixodidae)

This important tick, known as African red tick, affects ungulates in Africa.

► Ticks

African Skipper Moths (Lepidoptera: Apoprogonidae)

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African skipper moths, family Apoprogonidae, includes only a single species from South Africa. The family is in the superfamily Uranioidea, in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults medium size (46–56 mm wingspan), with head rough scaled and eyes large; haustellum naked; labial palpi porrect; maxillary palpi minute, 1-segmented; antennae clubbed (hooked at tip). Wings triangular and

African Skipper Moths (Lepidoptera: Apoprogonidae), Figure 26 Example of African skipper moths (Apoprogonidae), *Apoprogones hesperidis* Hampson from South Africa.

short; body robust. Maculation dark gray with some pale markings, plus pale discal spot on fore- and hindwings. Adults presumed diurnal, but nothing is known of the biology or larvae (Fig. 26).

References

Janse AJT (1932) Family Sematuridae. In: The moths of South Africa, 1:87–89. Pretoria [Apoprogones]

Seitz A (1926) Subfamilie: Apoprogeninae [sic]. In: Seitz A (ed) Die Gross-Schmetterlinge der Erde. Teil 14. Die afrikanischen Spinner und Schwärmer, pl. 1. A. Kernen, Stuttgart, pp 16–17

African Sleeping Sickness

A disease of humans caused by protozoans in the genus *Trypanosoma*. It is also known as human sleeping sickness or human trypanosomiasis. The same disease, when infecting other vertebrate animals, is called nagana. It is transmitted by tsetse flies in Africa.

► Sleeping Sickness or African Trypanosomiasis
► Trypanosomes
► Tsetse Flies
► Nagana

African Slug Caterpillar Moths (Lepidoptera: Chrysopolomidae)

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African slug caterpillar moths, family Chrysopolomidae, are a small African family of about 30 known species. Two subfamilies are known: Ectropinae and Chrysopolominae. The family is in the superfamily Cossoidea (series Limacodiformes) in the section Cossina, subsection Cossina, of the division Ditrysia. Adults medium size (24–52 mm wingspan), with head scaling smooth; haustellum and maxillary palpi absent; antennae short and bipectinate in males. Body robust. Wings rounded and broad (some with irregular distal margins). Maculation mostly pale brown, often with subapical wing line and light discal spot; hindwing with forewing line and coloration continued (Fig. 27). Adults nocturnal as far as is known. Larvae leaf-feeding and slug-like, with small spines; often colorful. Host plants include Celastraceae. No economic species are known.

References

Aurivillius C (1911) Chrysopolomidae. In Lepidopterorum catalogus, 1:1–4. W. Junk, Berlin.

Hering EM (1928) Familie: Chrysopolomidae. In: Seitz A. (ed) Die Gross-Schmetterlinge der Erde. Teil 14. Die afrikanischen Spinner und Schwärmer, pl. 76. A. Kernen, Stuttgart, pp. 477–479

Herring EM (1937) Revision der Chrysopolomidae (Lep.). Ann Transvaal Mus 17:233–257, pl. 9

African Swine Fever

A viral disease of hogs, this tick-transmitted disease is found on several continents.

► Ticks

African Slug Caterpillar Moths (Lepidoptera: Chrysopolomidae), Figure 27 **Example of African slug caterpillar moths (Chrysopolomidae), *Chrysopoloma similis* Aurivillius from South Africa.**

Agaonidae (Hymenoptera)

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A tropical family of about 750 species of miniscule wasps (order Hymenoptera) that are mutualistically associated with fig plants (*Ficus* spp.). The associations are usually between a unique pair of fig and wasp species and are crucial for the reproduction of both. The winged female wasp enters a young floral receptacle, the flask-like syconium, and lays single eggs in many of the tiny female flowers lining its inner surface. Carrying pollen from her natal fig, she deposits it onto the stigmas during oviposition, ensuring seed production for the fig and food for her own offspring. The syconium will generally not ripen without pollination. The female is trapped inside the syconium and dies there. After the larvae develop and pupate in seed-galls, the wingless adult males emerge first and chew holes into galls to mate with the quiescent females inside, and then cooperatively chew an opening through the syconial wall. The changed atmosphere inside the syconium wakes the females, which chew out of their galls, actively or passively pick up pollen, and leave through the opening. The females of some species actively gather and carry pollen in thoracic pockets or specialized leg structures. The cultivated fig, *Ficus carica*, has many varieties that no longer rely on pollination to produce edible ripe syconia. However, a few varieties still require the pollination service provided by the agaonid partner, *Blastophaga psenes*.

► Wasps, Ants, Bees and Sawflies
► Fig Wasps

References

Bronstein JL (1988) Mutualism, antagonism, and the fig-pollinator interaction. Ecology 69:1298–1302
Galil J, Eisikowitch D (1968) On the pollination ecology of *Ficus sycomorus* in East Africa. Ecology 49:259–269
Galil J, Zeroni M, Bar Shalom D (Bogoslavski) (1973) Carbon dioxide and ethylene effects in the co-ordination between the pollinator *Blastophaga quadriceps* and the syconium in *Ficus religiosa*. New Phytol 72:1113–1127
Machado CA, Jousselin E, Kjellberg F, Compton SG, Herre EA (2001) Phylogenetic relationships, historical biogeography and character evolution of fig-pollinating wasps. Proc R Soc London B 268:685–694
Ramirez BW (1969) Fig wasps: mechanisms of pollen transfer. Science 163:580–581
Weiblen GD (2002) How to be a fig wasp. Annu Rev Entomol 47:299–330
Wiebes JT (1966). Co-evolution of figs and their insect pollinators. Annu Rev Ecol Syst 10:1–12

Agathiphagidae

A family of moths (order Lepidoptera). They commonly are known as Kauri moths.

► Kauri Moths
► Butterflies and Moths

Agassiz, Jean Louis Rodolphe

Louis Agassiz was born at Môtier-en-Vuly, Switzerland, on May 28, 1807. He displayed an early interest in natural history. In 1824 he entered Universität Zürich for medical training, then moved to Universität Heidelberg in Germany. In Heidelberg his interest in natural history increased. His next move was to Universität München and, while there in 1829 and still only 21 years old, he published a work on Brazilian fishes, using the collected materials of von Martius and von Spix. His next zoological endeavor was to begin research on fossil fishes. In 1831, he moved to Paris still with the ambition of completing his medical training. However, he spent part of each day studying fossil fishes and he came under the influence of Cuvier and adopted the latter's views of creation. Thus, according to Agassiz, each species was the result of separate creation, not of evolution. In 1832–1846 he was a professor at Université de Neuchâtel, Switzerland. In 1836, Louis began to study glaciers and their effects, on which he published works in 1840, 1846 and 1847. In Switzerland, he also published a large catalog "Nomenclator zoologici" of the names of animals, of which some fascicles were on insects. In 1846 he moved to the USA, was welcomed as a famous scientist, and in 1848 was appointed professor of zoology and geology at Harvard University. At Harvard, he clashed with Asa Gray, professor of botany, about evolution, because Gray supported Darwin's theory. However, it was Louis' efforts and influence that led to the foundation of the Museum of Comparative Zoology at Harvard University, an institution that became very influential in research on insect systematics. He also was a co-founder of the U.S. National Science Foundation. He died in Cambridge, Massachusetts, on December 14, 1873. His son Alexander and two daughters of his first marriage accompanied him to the USA (his first wife having died in Switzerland). Alexander Agassiz (1835–1910) likewise became a zoologist. Louis Agassiz remarried in 1850 in the USA.

References

Anon (1998) Jean Louis Rodolphe Agassiz. Encyclopedia of world biography, 2nd ed. Gale, Detroit, MI

Nordenskiöld E (1935) The history of biology: a survey. Tudor, New York, 629 pp.

Age Polythism

This refers to the division of labor within a colony of social insects wherein the responsibilities of the individuals change as they mature.

Aggregation

A group of individuals consisting of more than just family members; a coming together of individuals to form a group. (contrast with colony)

► Cycloalexy
► Allelochemicals

Aggregation Pheromone

A pheromone that causes insects to aggregate. This type of pheromone is used by insects for mating, feeding, or oviposition.

► Pheromones

Aggregative Response

The response of predators in which they increase their time spent in areas with more prey, leading to higher predator density, and fewer prey.

► Learning in Insects
► Predation: The Role of Generalist Predators in Biodiversity and Biological Control

Agnathous

This term is used to refer to insects that lack mandibles, which essentially means that they lack mouth structures.

► Mouthparts of Hexapods

Aggressive Mimicry

This is a type of mimicry in which a predator mimics their prey, allowing ready capture and consumption of the victim.

► Mimicry
► Myrmecomorphy
► Myrmecophiles

Agonoxenidae

A family of moths (order Lepidoptera). They commonly are known as palm moths.

► Palm Moths
► Butterflies and Moths

Agricolous

This refers to species that dwell in agricultural habitats.

Agricultural Chemicals

Pesticides, adjuvants, and other chemicals, other than fertilizers, that are used to enhance crop production.

► Insecticides
► Acaricides or Miticides

Agricultural Consultant

Someone trained in the agricultural and management sciences who provides plant and animal production and protection services for a fee. Independent crop consultants sell the advising service only, deriving no income from sale of products, whereas other crop consultants usually derive some income from product sales such as pesticides or fertilizer.

► Careers in Entomology

Agricultural Crop Pests in Southeast Asia Including Southern China

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Southeast Asia is often called the Oriental faunal region and includes the provinces of southern China south of the Yangtse river (Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hainan, Hubei, Hunan, Jiangshu, Jiangxi, Sichuan, Yunnan and Zhejiang) as well as the island of Taiwan, islands and peninsular area of Hong Kong, Macao and those countries to the south including Vietnam, Malaysia, Singapore, Myanmar (Burma), Cambodia and Laos, as well as portions of Pakistan and India. The northern provinces of India share similar faunal elements as southern China as both are at a similar latitude. The insect fauna of northern China is more Palearctic in nature and many of the northern species will differ from those in the southern provinces or elsewhere in Southeast Asia.

Insects of Rice

What are believed to be key pests, or those of major importance as opposed to minor can vary from country to country. In Vietnam and southern China, the rice stemborer complex of lepidopterous insects includes the yellow or small rice borer, *Scirpophaga incertulas* (Wlk), the striped rice-stalk borer, *Chilo suppressalis* (Wlk), the dark-headed rice borer, *C. polychrysus* (Meyr) (all Pyralidae) and the noctuid pink borer, *Sesamia inferens* (Wlk). Although they are considered minor pests in some regions, because the rice plants are able to tolerate some damage and can compensate for light infestations, these insects have been ranked as major pests in the countries of Malaysia and Thailand. The yellow or small rice borer, *Sc. incertulas*, has a wide distribution in Southeast Asia and is found in India, Pakistan, Sri Lanka, Bangladesh, Myanmar (Burma), Vietnam, Singapore, Taiwan and Hong Kong.

The common names of these insects generally refer to the color of the larval stage such as the pink borer, *S. inferens*, with pinkish-colored larvae, or the yellow larvae of the small rice borer. The head capsule in larvae of *C. suppressalis* is brown in color while larvae of *Sc. incertulas* are yellow with brown heads and the pink borer caterpillar, *Sc. inferens*, is pink in color and larger when mature than the other species. The larvae tunnel as caterpillars into the stems of the rice plants. There they feed on the plant tissues and destroy the growing points of the plant causing wilting of new shoots, eventually producing a condition known as "dead heart." In mature plants, empty panicles appear white in color, and the condition is known as "white-head." Masses of eggs are generally laid on the leaves in the case of the female dark-headed borer or striped rice borer. Pupation generally occurs in the stem with these species. The female pyralid moths in the genus *Scirpophaga* have a scale tuft at the tip of their abdomens, while female moths in the genus *Chilo* have no scale tuft at the end of the abdomen. The female *Sc. incertulas* has a yellow forewing, which is whitish in *Sc. nivella*.

The eggs of stemborers are often attacked by the parasitoid wasps *Trichogramma* sp. (Trichogrammatidae) and *Telenomus rowani* (Scelionidae). In Malaysia, granular insecticides have been used to control rice stem borers when the incidence in stems (tillers) exceeds 10%, but this practice is not recommended in southern China or in northern Vietnam where the plants are able to tolerate some damage and compensate for injury.

Rice Leafhopper and Planthopper Complex

The rice leafhopper and planthopper complex includes *Nephotettix virescens* (Dist) and *N. nigropictus* (Stål), the green rice leafhoppers (Hemiptera: Cicadellidae) and *Nilaparvata lugens* (Stål) and the brown plant-hopper (Hemiptera: Delphacidae). These leafhoppers are important in Thailand and Malaysia as well as in India and Pakistan, while the planthopper is more widely distributed and is found in southern China, India, Taiwan, Japan and some of the Pacific Islands. The planthopper is unusual in that it is able to migrate between land masses and migrates from East China to Japan annually. This insect also has migrated to Macao (where rice is no longer grown due to urbanization) from mainland China.

Nephotettix virescens is an important vector of two viral diseases in Malaysia. The first disease is similar to yellow dwarf disease and the second is called Tungro disease. Both cause a stunting of plant growth, the first disease a general yellowing and profusion of tillers, while the second causes a reddening of the leaves. Both diseases decrease crop yield.

The eggs of the rice leafhoppers are laid in rows within leaf-sheaths. The five nymphal stages are completed in 17 days in Malaysia. Leafhoppers generally feed on the upper parts of the plant, while the planthopper, *Nilaparvata*, feeds at the base of the plants near the water line. The brown planthopper is sometimes considered the most serious pest of rice in Asia. They cause a "scorching" of the plants, or a condition known locally as "hopperburn," when the number of nymphs and adults per clump of rice exceeds 900 or more. The eggs are generally laid in plant tissue. The young resemble the parents except for their smaller size and absence of wings. Five nymphal stages generally require two weeks to develop. Predators can include the staphylinid beetle *Paederus fuscipes* and the coccinellid beetle *Harmonia octomaculata*.

In Thailand and Malaysia, another important pest of rice is the rice gall midge, *Orseolia oryzae* (W.-M.) (Diptera: Cecidomyiidae), which is also found in Pakistan, India, Bangladesh, Sri Lanka and parts of Indonesia as well as in southern China, where it is considered of minor importance. The larvae of the fly feed between the leaf sheaths and, when reaching the apical buds, can lacerate tissue and can cause the formation of a gall known locally as a "silver" or onion shoot. The adults are delicate looking midges, long and brown in color with long legs. Upon hatching, the pale, 1 mm long larva grows to 3 mm and becomes reddish in color. The pupa, when formed, is pinkish and turns red with age. Grassy vegetation near the rice fields is often associated with the presence of the midge.

The rice leaf folder, *Cnaphalocrocis medinalis* (Gn), (Lepidoptera: Pyralidae), is considered one of the more important pests of rice in southern China as well as in Malaysia and Thailand. It is also found in India, Pakistan, Sri Lanka and Bangladesh. The larvae fold the leaf while feeding and transparent patches form so that the rice plant appears ragged. The adult moths lay eggs on young, 4 to 6-week-old plants or in nursery stock in Malaysia. Early instar caterpillars feed by scraping the epidermis from rice leaves, while later instar caterpillars fold them. The opposite edges of the leaf, or one edge of the leaf, is attached to the midrib by silken threads produced by the larvae. Pupation occurs inside a silken cocoon within the folded leaf. Parasitoid wasps, such as *Apanteles opacus* (Braconidae) or *Temelucha philippinensis* (Ichneumonidae), often keep populations in check in Malaysia.

The lepidopterous armyworm and cutworm complex, including the rice armyworm, *Mythimna loreyi* (Duponchel), and the rice ear-cutting caterpillar or paddy armyworm, *Mythimna separata* (Wlk), are important pests in Thailand and southern China. The paddy armyworm affects rice in Pakistan, Sri Lanka, India and Bangladesh. The larvae feed on leaves and stems and can defoliate the plants.

The rice skipper, *Parnara guttata* (Bremer & Grey) (Lepidoptera: Hesperiidae), was formerly considered a major pest in southern China, but recent mass production and release of parasitic wasps has probably lowered its status to a minor pest. The larvae roll the apical portion of the leaves, web the sides and cut off the apex, forming long, conspicuous tubes.

Sugar Cane Insects

The lepidopterous sugar cane borer complex in Thailand includes several pyralids including the yellow top or early shoot borer, *Chilo infuscatellus* (Snellen), the sugar cane stem borer, *Chilo sacchariphagus* (Bojer), the white top borer, *Scirpophaga excerptalis* (Walker) and the noctuid sugar cane stalk borer, *Sesamia inferens* (Wlk).

The larvae of these insects bore into the shoots of sugarcane. As the common name suggests, the larvae of the yellow top or early shoot borer tunnel into the growing shoots of the plant, while the larvae of *C. sacchariphagus* bore into the stems. The noctuid moth larvae of purple stalk borer, *Sesamia inferens*, previously discussed as a pest of rice, also affects sugar cane, but sugar cane is not preferred for oviposition as are rice and grasses. The larvae are colored purple to pink dorsally and white ventrally and have a reddish-orange head capsule. The adult moth is fawn-colored with dark brown streaks on its forewings and whitish hindwings.

In Malaysia, the white sugar cane aphid, *Ceratovacuna lanigera* Zehntner, a mealybug-like insect (Hemiptera), causes injury. The non-winged females and nymphs are covered by a waxy layer, while the winged adults are bluish-green in color and are not covered with a layer of wax.

Fruit Tree Insects: Mango-Citrus-Banana-Litchi

One of the most important fruit tree insects is considered to be the Oriental fruit fly, *Batrocera dorsalis* Hendel (Tephritidae). It is found in Hawaii as well as in other Pacific islands and the southeast Asian countries of Thailand and Malaysia where it is a serious mango pest. In southern China, where there are fewer mangoes grown, it is considered a minor pest. In addition to mangoes, the guava and carambola are affected in Malaysia. The larvae or fly maggots feeding inside the skin of the fruit cause it to decay. Female flies puncture the skin of the fruit with their ovipositors, laying several eggs inside. The larvae can hatch in one day and develop through three instars in about a week. When mature, they are able to leave the fruit by "flipping" themselves in the air and dispersing to enter the ground to pupate. Fruits can be protected from these flies by bagging them using paper bags. The use of traps treated with methyl eugenol as an attractant has met with some success, but as only the males are attracted, it is not totally effective as a control.

In Malaysia, a longhorn beetle known as the mango shoot borer, *Rhytidodera stimulans* (White), tunnels into the young growing shoots of the tree. Eventually it kills the outer branches, which often break off during subsequent wind storms. In southern China, the citrus long-horn beetle, *Anoplophora chinensis* (Forst.) (Cerambycidae), is considered one of the most important pests of citrus trees. The larvae of these beetles tunnel under the bark of young trees and sometimes into the heartwood, which can cause the death of the plants. The adult beetles have striking black and white body coloration. Parasitoid wasps have difficulty reaching the larvae that bore into young healthy trees.

Butterflies (Lepidoptera) are not considered to be serious pests of agricultural crops in the northern hemisphere with the exception of the small white, *Pieris rapae*. However, in the semi and tropical regions of the world, cold climatic conditions are not as severe and the insects often do not have to enter diapause (hibernation), so there can be continuous generations in some regions almost throughout the year. Papilionid butterflies, as well as several species of skippers (Hesperiidae), cause injury to plants because they are able to oviposit in both the spring and the fall.

In Southeast Asia, the lemon or lime butterfly, *Papilio demoleus* (L.), and another species known by the common names of the common Mormon swallowtail or the white-banded swallowtail, *Papilio polytes* L., lay their eggs on the undersides of leaves of citrus plants and are considered important in southern China as pests of citrus. Another species, *Papilio xuthus* L., is also becoming increasingly important, particularly in the Pacific island area. The first instar in these Papilionid butterflies are colored differently than older larvae, which may be an adaptation that protects them from predators such as birds or lizards. The early stage larva resembles a bird or lizard dropping as it is dark brown in color with white markings that may appear to be unappetizing to the predator. When the caterpillar is older, its color changes to green with grey and white markings. Hand picking the larvae is probably an adequate control in young plants.

The orange spiny whitefly, *Aleurocanthus spinifera* (Quaintance) (Hemiptera: Aleyrodidae), is an important insect in southern China as well as India, Sri Lanka, Bangladesh, Malaysia and Thailand. The adults are l mm in length and lay eggs on the undersides of leaves. There are three nymphal stages and the third-stage nymph appears blackish in color with waxy secretions on the outer edge of the body so it looks superficially like an insect pupa. Both the nymphs and the adults remove plant nutrients when feeding, and the honeydew produced by the nymphs encourages a sooty mold to grow on the upper surfaces of the leaves and the fruits. Heavy infestations of this insect cause fruit production to fall off. A parasitic wasp, *Eretmocerus serius* (Aphelinidae), has been effective in regulating the orange spiny whitefly in Malaysia.

Aphids, such as the black citrus aphid, *Toxoptera aurantii* (Bayer de Fonscolombe), and the brown citrus aphid, *Toxoptera citricida* (Kirkaldy), are important in southern China and also range into India, Sri Lanka and Bangladesh.

Fruit-piercing moths, such as *Othreis fullonia* (Cl.) (Noctuidae), pierce the ripening fruits of citrus, mango, papaya and guava or banana in order to obtain sap. A short, stout proboscis with a barbed tip enables the moth to puncture the skin of the fruit and can permit the entry of plant pathogens such as viruses or secondary rots that can cause premature fruit drop. Fruit-piercing moths are considered of major importance today in southern China. Management of their populations is difficult as the immature of *O. fullonia* do not feed on citrus trees. Instead, the caterpillars feed on the foliage of the *Erythrina* species of shade trees. On the Pacific island of Guam, the eggs can be laid on the foliage all year round and the insects are considered to be major pests as they feed on ripe banana, mango, papaya, pomegranate and guava as well as tough-skinned citrus fruits.

On banana plants, there are two species of leaf rollers or banana skippers in Southeast Asia, one of which is *Erionota thrax* (Hesperiidae), which rolls the banana leaves in Malaysia, Thailand and in southern China. The caterpillars cut and roll strips of banana leaf, then hide in the roll that is held together by silken threads. They emerge at night to feed and are often covered with a white powdery secretion.

Litchi and Longan Fruit Insects

The litchie stink bug, *Tessaratoma papillosa* (Drury) (Hemiptera: Tessaratomidae), has been considered the most important pest of litchi (*Litchi chinensis*) and longan (*Euphoria longan*) fruit trees in the Guangdong region of southern China, including Hong Kong and Macao as well as Vietnam and Thailand. The adults are mostly brown dorsally and whitish underneath. Immature bugs, more brightly colored than the adults, have red markings dorsally often with a white waxy secretion underneath. Plant sap is taken from the stems of fruit trees. The saliva of the bug can stain the clothing of fruit tree workers. Also, the fluid is extremely irritable if it gets in the eyes. An effective biological control of the litchie stink bug has been developed in southern China by the Guangdong Entomological Institute in which the egg parasitic wasp, *Anastatus japonicus* (Eupelmidae), has been mass-reared and released to achieve control in the Fujian, Guangdong and Guangzi provinces. Biological control of the litchie stink bug has also been reported from the northern highlands of Thailand.

Vegetable Insects

The diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), is currently considered among the top 25 most important arthropod pests in southern China. It was the first agricultural pest in Malaysia to be reported resistant to pesticides, and it is also an important pest in Thailand as well as in India. Its distribution has been considered cosmopolitan. Cruciferous plants, such as the cabbages, are affected. The caterpillars penetrate the epidermis of leaves, mining the tissue and making windows or holes in it. The adult is recognized by the pale triangular or diamond-shaped marks seen on the midline of the back when the wings are closed.

The caterpillar is pale green in color, and it wriggles violently when disturbed, sometimes falling off the edge of the leaf. A microbial insecticide, *Bacillus thuringiensis*, is effective in the control of the diamondback moth, but farmers in some areas of Malaysia have not accepted it because this method takes longer to kill the caterpillars than other insecticides.

The green stink bug, *Nezara viridula* (L.) (Hemiptera: Pentatomidae), is a cosmopolitan insect in Southeast Asia that damages developing vegetables, such as potato, sweet potato, tomato and cotton, by their feeding punctures. Three color varieties or subspecies of this insect are recognized in southern China. An all-green form, known as *N. viridula smaragdula*, is the most common, accounting for 75–80% of vegetable bugs observed in Macao in l996. A second form with yellow on the head and pronotum, *N. viridula torquata*, makes up about 10% of the stink bug population, while the least common form is mostly all yellow with green spotting on the hemelytra and abdomen, and is called *N. viridula aurantiaca* (1.0%).

The small white butterfly, *Pieris rapae* (L.) (Lepidoptera: Pieridae), along with two other species, is still considered important in southern China and Southeast Asia. The small cabbage butterfly, *Pieris canidia* (Sparrman), also damages nasturtium. In both species, larvae feed singly in the cabbage heart, make holes in the leaves and cause frass accumulation. The insects are also found in India, Taiwan and the

Philippines, and breeding can be continuous with up to eight generations annually, which is not the case in northerly regions, where overwintering occurs in the pupal stage.

The Asian corn borer, *Ostrinia furnacalis* (Guenee) (Lepidoptera: Pyralidae, Pyraustinae), is more important in the northern countries of Southeast Asia including southern China where corn is grown. The Guangdong Entomological Institute rates it as a highly important pest there. The larvae bore into the stalks and the ears of corn, and can also survive on foxtail millet, *Setaria italica*, and on *Panicum* grasses. The eggs are laid in clusters of 10–40 underneath leaves about a week before the plant forms its inflorescence. The young larvae can scarify the leaves and later, bore into the stem. Pupation generally occurs within the stalk, but can occur within the ear. The Asian corn borer's range includes India, Sri Lanka, Korea, China, Hong Kong, Taiwan, Vietnam, Japan, Malaysia, Thailand, Singapore and Indonesia.

► Tropical Fruit Pests and Their Management
► Sugarcane Pests and Their Management
► Vegetable Pests and Their Management

References

Denton GWR, Muniappan R, Austin L, Diambra OH (1999) Fruit-piercing moths of Micronesia. Agricultural Experiment Station, University of Guam. Tech Report #217, 26 pp
Hirose Y (ed) (1992) Biological control in South and East Asia. Kyushu University Press, Fukuoka, Japan, 68 pp
Ooi PAC (1999) Insects in Malaysian agriculture. Tropical Press, Kuala Lumpur, Malaysia, 106 pp
Robinson GS, Tuck KR, Shaffer M (1994) Field guide to smaller moths of Southeast Asia. Malaysian Nature Society, Kuala Lumpur & Natural History Museum, London, 308 pp
Waterhouse DF (1998) Prospects for the classical biological control of major insect pests and weeds in Southern China. Entomologia Sinica 5:320–341

Agroecology

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Agroecology is the application of ecological principles to agricultural production systems and the resources needed to sustain them. A convenient unit of study is the agroecosystem, often a single agricultural field. A major difference between an agroecosystem and a natural ecosystem is in the level of human intervention and management involved. Like natural ecosystems, agroecosystems consist of living (biological) and nonliving (chemical, physical) portions. The science of agroecology examines the living organisms (collectively called the community) in the system, their interactions with one another, and the environmental factors that influence them.

Nutrient Cycling

The organisms within an ecological community depend on one another for energy and materials. Green plants are referred to as producers since they are at the base of the food chain in ecosystems. Initially, carbon and energy are stored in plant tissues through the process of photosynthesis. Consumers must obtain their carbon and energy by eating plants or other organisms. Therefore carbon and other materials move from green plants to herbivores to carnivores, including predators and parasites. The different levels of energy production and consumption (producers, herbivores, predators) are called trophic levels, although in reality many organisms do not restrict their feeding to one level. For instance, some Hymenoptera that are parasitoids as larvae may feed on pollen or nectar as adults. As a result, the paths along which materials move through the organisms in the community can be quite complicated, and collectively they make up the food web within the community.

Many nutrients, including nitrogen, phosphorus, potassium, and other elements, are essential components of plant and animal tissues. These nutrients have distinct cycles in ecosystems, and they cycle in food webs along with carbon and other materials. Nutrients are released into the soil during decomposition of organic molecules, where they are converted into forms that can be taken up by plant roots, completing the nutrient cycle. Microarthropods such as mites and springtails are particularly important in the decomposition process.

Cropping Systems

Crop performance depends on a range of key resources including nutrients, water, soils, and other environmental factors, and many agricultural management practices are aimed at optimizing and conserving these resources. Various types of cropping systems may be selected to address specific goals or conservation issues. Conservation tillage and other reduced tillage practices are important for soil conservation and reduction of erosion. The crop residues that remain on the soil surface in uncultivated sites can also aid in conservation of water and organic matter, and may provide some nutrients when they decompose (Fig. 28). Monoculture allows a grower to specialize by growing only one crop, while polyculture permits a grower to diversify by growing multiple crops on the same land. Multiple cropping on the same site may occur at the same time or over time. In the United States, the most common form of multiple cropping is crop rotation, in which different crops are grown on the same site in different seasons or years. Cover crops are crops with limited market value that are grown on the site during seasons that are unfavorable for growing the main economic crops for the region. In the southeastern United States for example, a winter cover crop of rye (*Secale cereale*) or crimson clover (*Trifolium incarnatum*) may be grown in a field reserved for cotton or peanut production during the summer. Cover crops can provide various advantages, including erosion reduction, increased supply of nitrogen, competition with weeds, or hay for animals. Green manures, which are usually legume cover crops, are grown specifically for their nitrogen-rich residues and soil fertility benefits. Intercropping, or mixed cropping (Fig. 29), refers to the growing of two or more crops at the same time on the same land. The practice is quite common in some regions, and many variations exist. Some tropical subsistence intercropping systems are especially diverse and complicated.

Pest Management

The cropping system used has a direct effect on pest management, which is an important aspect of agroecology. For example, monoculture may encourage buildup of some pests, such as corn rootworms (*Diabrotica* spp.) or wireworms (Elateridae), that can be managed by appropriate crop rotation. In many cases, the use of intercropping has resulted in less severe pest outbreaks and increased diversity of natural enemies compared to monocultured systems.

Tritrophic (plant-herbivore-predator) interactions and the structure of the food web may be affected by changes in the cropping system, such as use of an intercrop, or changes in crop variety or fertility level. The development and use of biologically based pest management tactics such as use of natural enemies or resistant varieties require a detailed knowledge of pest biology and ecology, including life cycle, population dynamics, and interactions with the physical and biological environment, including potential competitors, predators, and parasites. Such tactics may be directed toward preventing pest buildup rather than reacting to high pest numbers already present in crisis situations. However, the design of a system in which pest numbers are less likely to reach crisis levels, due to the presence of effective natural enemies for example, requires advanced planning based on sound ecological data.

Landscape Ecology

An individual agroecosystem does not stand alone, since organisms, materials, and energy move freely in and out of the system. Landscape ecology examines the agroecosystem in the context of the surrounding region or landscape, an essential

Agroecology, Figure 28 Residues from a previous rye crop cover the soil surface between plant rows in this conservation tillage system.

approach in dealing with migrating insects or regulated pests. The condition of field borders, hedgerows, and adjacent fields critically affects pest management within a specific field. Movement of pesticides, fertilizers, and other potential pollutants from the agroecosystem to natural ecosystems is a major environmental concern.

Many natural ecosystems are highly dependent on recycling, since cycles of nutrients, water, and other materials tend to be relatively closed. In contrast, an agroecosystem is not a closed system, because its purpose is to produce harvest for export to other ecosystems. This process depletes essential resources from the agroecosystem

Agroecology, Figure 29 One of the simplest forms of intercropping is to use one crop as a windbreak, like the sugarcane planted along with the eggplant crop shown here.

which must be restored if the system is to remain productive. The movement of essential resources into the agroecosystem and the recycling of existing resources are therefore critical concerns, to anticipate and ensure that supplies of critical resources for agricultural production will be conserved over time to sustain future agricultural production.

► Organic Agriculture
► Integrated Pest Management (IPM)
► Conservation Biological Control
► Flower Strips as Conservation Areas for Pest Management
► Plant Resistance to Insects
► Cultural Control of Insect Pests

References

Altieri MA (1994) Biodiversity and pest management in agroecosystems. Food Products Press, New York, NY
Cavigelli MA, Deming SR, Probyn KL, Harwood RR (eds) (1998) Michigan field crop ecology. Extension Bulletin E-2646. Michigan State University, East Lansing, MI
Coleman DC, Crossley DA Jr (1996) Fundamentals of soil ecology. Academic Press, San Diego, CA
Collins WW, Qualset CO (eds) (1991) Biodiversity in agroecosystems. CRC Press, Boca Raton, FL
Gliessman SR (1998) Agroecology: ecological processes in sustainable agriculture. Sleeping Bear Press, Chelsea, MI
Jackson LE (ed) (1997) Ecology in agriculture. Academic Press, San Diego, CA
Powers LE, McSorley R (2000) Ecological principles of agriculture. Delmar Thomson Learning, Albany, NY

Agromyzidae

A family of flies (order Diptera). They commonly are known as leaf-miner flies.

► Flies
► Leaf-miner Flies (Agromyzidae)

Agyrtidae

A family of beetles (order Coleoptera). They commonly are known as primitive carrion beetles.

► Beetles

A.I.

An abbreviation for "active ingredient," the active component of an insecticide, or the toxicant.

► Insecticides
► Insecticide Formulation
► Insecticide Toxicity

Alarm-Defense System

Defensive behavior that also serves as an alarm signaling mechanism.

Air Sacs

The trachea of insects are sometimes dilated or expanded to form pouch-like structures called air sacs. Their occurrence varies among taxa, but their presence lowers specific gravity and enhances air exchange, thus enhancing flight.

► Active Ventilation
► Abdominal Pumping

Alarm Pheromone

A pheromone released to trigger alertness, dispersion or group defense by insects.

► Alarm Pheromones of Insects
► Chemical Ecology

Alarm Pheromones of Insects

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Alarm pheromones are defined as chemical substances, produced and released by an organism, that warn or alert another of the same species of impending danger. This is exemplified by many species of aphids (Hemiptera: Aphididae) in which the pheromone is caused to be released by attack, for example, by predators, with ensuing dispersal by which individual aphids may avoid a subsequent attack. However, the term alarm pheromone also is employed when the responding individuals are stimulated to show aggression towards the attacking agent. This is common in the social Hymenoptera; for example, the honeybee, *Apis mellifera* (Hymenoptera: Apidae), and many ant species respond aggressively to their alarm pheromones.

As alarm pheromones can benefit the survival of members of the species involved, it is common for insects that employ alarm pheromones to live in congregations for some or all of their life cycle. In the case of social Hymenoptera, the colony is genetically related, and in asexually reproducing aphids, the colony is clonal. Although the survival of siblings or clones by alarm pheromone response at the cost of the attacked individual appears altruistic, in genetically related colonies, genes from the individual will predominate in the survivors and be passed on to their kin.

Hemipteran Alarm Pheromones

Alarm Pheromones of Aphids (Hemiptera: Aphididae)

When disturbed or attacked, many aphid species release alarm pheromone from droplets secreted from tube-like structures called cornicles on their dorsal posterior. This phenomenon has been studied exclusively in the asexual forms and most often in asexually reproducing wingless females. Aphids nearby exhibit a variety of behaviors ranging from stopping feeding and moving away, to running or dropping off the plant and even attacking the predator. However, not all aphids in a group respond. The relative risks of predation and costs of escape, for example, cessation of feeding and risk of desiccation, affect the likelihood of any particular response. In studies of the peach-potato aphid, *Myzus persicae*, the pea aphid, *Acyrthosiphon pisum*, and the rose-grain aphid, *Metopolophium dirhodum*, early stages were found to be less sensitive to alarm pheromone than later ones.

However, older wingless *M. persicae* require the greatest stimulation of alarm pheromone before responding, while winged *M. persicae*, particularly those not feeding, are extremely sensitive to alarm pheromone. The lack of response from the early stages suggests that the risk of predation to these nymphs is lower than the risk involved in ceasing to feed and dropping from the plant. When young *M. dirhodum* respond to alarm pheromone, they do so by moving to another part of the plant rather than by dropping. Winged adults, on the other hand, are more responsive to alarm pheromone, perhaps because they can more readily move off the host. The sugarcane woolly aphid, *Ceratovacuna lanigera*, also shows different reactions to alarm pheromones at different life stages; it shows attack behavior until adult, when the normal aphid dispersal response takes over.

Considerable variation is seen between aphid species in their sensitivity to alarm pheromones and in both the speed and the form of the response. This variation often can be explained by differences in the ecology of the species. Some aphids, particularly those tended by ants, stay on the plant and respond by walking or "waggling" their abdomens rather than falling off the plant. These aphids appear to depend more on the protection afforded by their ant attendants than their own defensive mechanisms. Aphids that walk away from a source of alarm pheromone tend to form new clusters a short distance from the original site, thus ensuring continued ant attendance.

Susceptibility to insecticide also has been found to correlate with responses to alarm pheromone. Susceptible strains produce more pheromone and respond more quickly and in higher numbers than insecticide-resistant strains. In addition, clones collected from around the world showing knockdown resistance to pyrethroid insecticides, and esterase-based insecticide resistance, showed lower levels of disturbance to the synthetic alarm pheromone. These aphids may therefore suffer increased predation or parasitism in the absence of insecticides, affecting the evolutionary fitness of insecticide resistant clones. This may be due to physiological effects associated with resistance, which could affect mobility or sensitivity of the nervous system to stimuli.

Aphids that have dropped from a plant may re-colonize or may move to another host plant further away. The turnip aphid, *Lipaphis erysimi*, and *M. persicae* dislodged by alarm pheromone are less likely to return to the original host plant than when mechanically dislodged. Similar patterns of behavior are found in *A. pisum*. Aphids dislodged by a predator or experimentally with synthetic alarm pheromone spend longer "running" before the "search" for a host plant began, whereas aphids dislodged mechanically are more likely to begin to search for a host plant immediately.

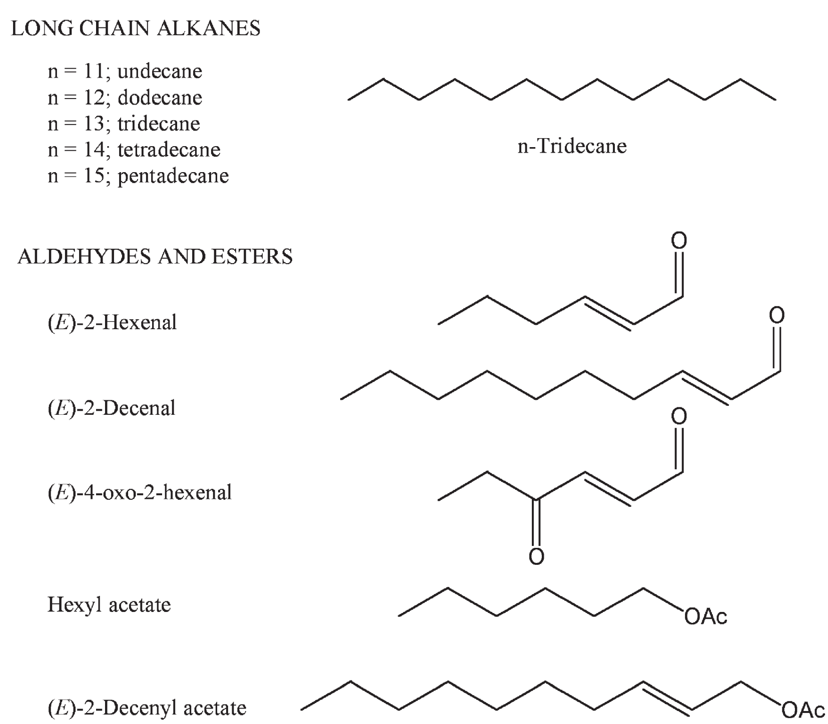
Droplets secreted from the cornicles comprise two types of material: a volatile, rapidly vaporizing fraction which is the alarm pheromone, and a waxy fraction, consisting mainly of triglycerides, that crystallizes on contact with foreign particles outside of the aphid's body. The waxy component appears to function as a sticky or quick-setting irritant to predators and parasitoids and a releasing substrate for the alarm pheromone component.

The main component of the alarm pheromone (Fig. 30) of many aphids is the sesquiterpene hydrocarbon (E)-β -farnesene (**1**). Other components may also be present as found in the alarm pheromone blend of the vetch aphid, *Megoura viciae*, which contains the monoterpenes (-)-α -pinene, (-)-β -pinene, (Z,E)-α -farnesene and (E,E)-α -farnesene, in addition to (E)-β -farnesene. There is a high degree of cross-activity of both natural alarm pheromone and (E)-β -farnesene among species within the aphid subfamilies, Aphidinae and Chaitophorinae. This is typical of insect alarm pheromones in general, since such cross-activity does not reduce their evolutionary value. However, the main component of the alarm pheromone of the spotted alfalfa aphid, *Therioaphis maculata*, and the sweet clover aphid, *T. riehmi*, in the Drepanosiphinae, is the cyclic sesquiterpene (-)-germacrene-A (**2**).

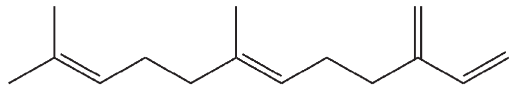
In the turnip aphid, *L. erysimi*, it has been demonstrated that isothiocyanates, acquired from chemicals in the host plants, synergize the effect of the alarm pheromone. These isothiocyanates are likely to be released from aphid honeydew so that, when there is a high number of other aphids in the immediate vicinity, the percentage of aphids responding to alarm pheromone increases.

Alarm Pheromones of True Bugs (Hemiptera, Heteroptera)

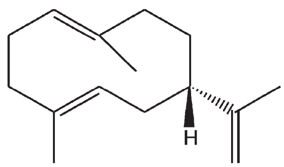
The Pentatomidae is the dominant family of stinkbugs, or shield bugs. The family comprises many species that are pests of economic importance, especially in warmer climates. These insects secrete a complex mixture of chemicals when strongly molested. The energetic cost of the defense response, especially production of defense chemicals, is significant and considerable provocation usually is required to cause release. In adults, the source of the defense compounds is the metathoracic gland, while in nymphs it is the dorsal abdominal glands. These are precursors to the metathoracic gland in adults and perform the same defense function. The chemical content of these secretions is similar throughout the order; for example, the components of the secretion of the stinkbug *Cosmopepla bimaculata* are a complex mixture of hydrocarbons, aldehydes and esters. The secretion, which can be ejected from either or both metathoracic glands in controlled amounts or even resorbed, displays a defensive function as a predator repellent. In one case, researchers have shown uncommon dedication in describing the repellency by squeezing adults in their mouths and chewing nymphs. The effects were a burning sensation and numbness of the tongue for up to two hours. In addition to repelling predators, the secretions possess alarm pheromone activity and cause adults to drop off plants. In the field, *C. bimaculata* are found highly clumped and the occurrence of large



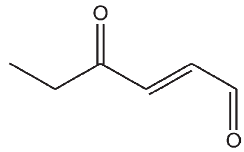
Alarm Pheromones of Insects , Figure 30 **Defense secretion of *Cosmopepla bimaculata* showing a typical range of compounds produced by stinkbugs. Chemical structures of alarm pheromones are referenced in the text by bold numbers.**



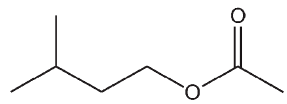
(*E*)-β-Farnesene **1**



(-)-Germacrene-A **2**

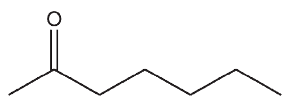


(*E*)-4-Oxo-2-hexenal **3**

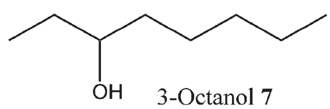


Isopentyl acetate **4**

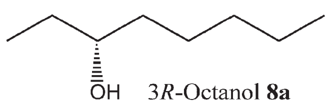
(*Z*)-11-Eicosan-1-ol **5**



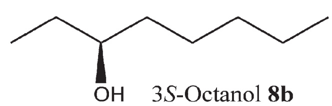
2-Heptanone **6**



3-Octanol **7**



3*R*-Octanol **8a**

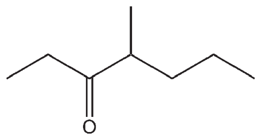


3*S*-Octanol **8b**

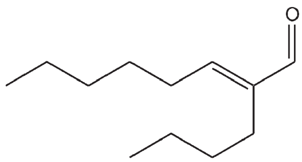
Alarm Pheromones of Insects, Figure 30 (Continued)

numbers living together gives an evolutionary advantage to possessing an alarm pheromone.

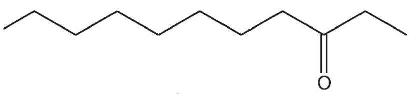
Six-carbon-long aldehydes, in particular (E)-2-hexenal, are common components of defensive secretions and are found in many families of heteropterous insects, including the Pentatomidae, Coreidae, Pyrrhocoridae, Cimicidae, Cynidae and Alydidae. it is thought that the general irritant properties of aldehydes provide a repellent effect to predators with hydrocarbons such as n-tridecane, another ubiquitous component, acting to spread the oily secretion so that the aldehydic components can exert full irritant effect. (E)-2-Hexenal has been reported to have the added dual functions of both alarm and aggregation pheromone, depending on the stimulus concentration, as well as use as a defense chemical. In the case of the bed bug, *Cimex lectularius*, and *Eurydema rugosa*, low concentration of (E)-2-hexenal acts as an aggregation pheromone while high concentration produces an alarm response. Alternatively, it has been reported that n-tridecane, the other



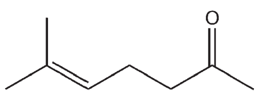
4-Methyl-3-heptanone **9**



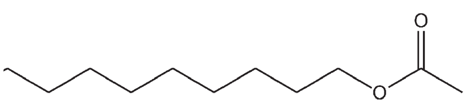
(*E*)-2-Butyl-2-octenal **10**



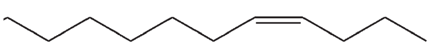
3-Undecanone **11**



6-Methyl-5-heptene-2-one **12**



Dodecyl acetate **13**



(*Z*)-4-Tridecene **14**

Alarm Pheromones of Insects, Figure 30 (Continued)

ubiquitous component of defense secretions, is a bifunctional pheromone for the southern green stinkbug, *Nezara viridula* (Heteroptera: Pentatomidae), which causes dispersal at high concentration (one individual equivalent) and aggregation at low concentrations. The multifunctional aspect of these compounds has important repercussions for their practical use as dispersal agents for pest species in the field, as the low concentration response of aggregation may dominate once the applied high concentration of compounds has diminished.

The pentatomid bug *Erthesina fullo* is a major pest of pine and hardwood trees. Both sexes produce a secretion from the metathoracic gland causing conspecific adults to drop from plants, fly or move away. The secretion comprises nine identified compounds, esters and aldehydes (about 35%) including (E)-2-hexenal and (E)-4-oxo-2-hexenal (**3**) and long chain alkanes, including 50% n-tridecane. Likewise, adult and nymph secretions from *Dysdercus cingulatus* (Heteroptera: Pyrrhocoridae) revealed 55 identified compounds, although the major components are again aldehydes and n-tridecane, features common with several more species of pentatomids from the genus *Chlorochroa* and *Piezodorus guildinii*.

The leaf-footed bug, *Leptoglossus zonatus* (Heteroptera: Coreidae), is an economically important pest of Brazilian corn. An extract obtained from the metathoracic gland by immersion in hexane showed that the major compounds were all of six-carbon length: hexanal, hexanol, hexyl acetate, hexanoic acid, and (E)-**4**-oxo-2-hexenal (**3**). (E)-2-Hexenal was found in the nymph extracts but not in the adult, an example of the general rule that exocrine chemistry of heteropterous nymphs is distinct from that of the adult. In this case, different life-stages possess different alarm pheromone systems. When tested individually, all components produced varying degrees of alarm response in adults and nymphs and even mating insects would stop and disperse, over-riding the sex pheromone response. These compounds are not species specific and are, for instance, found in *L. oppositus* and *L. clypealis*, a situation that mirrors the cross-activity of (E)-β-farnesene in many aphid species (see above), providing more evidence that this non-specific activity does not reduce alarm pheromone value in evolutionary terms.

Adults of the bean bug, *Riptortus clavatus* (Heteroptera: Alydidae), a pest of Japanese soybean, secrete (*E*)-2-hexenyl acetate in its defensive response. This causes an alarm response in adults and nymphs. Interestingly, adults also produce (E)-2-hexenal, and although some response was found when tested at high concentration, there was no response at physiological concentration, suggesting that this compound is not an alarm pheromone.

The examples shown above demonstrate that alarm pheromones of heteropteran families are based on a chemical selection general to insects of a wide taxonomy and show little species specificity. The alarm behavior caused by high concentrations of n-tridecane or (E)-2-hexenal is rationalized easily but the aggregation due to low concentrations is more difficult to explain. Perhaps these substances are constantly emitted in very small quantities due to their volatility and act so as to direct individuals to a region where conspecifics can be found and therefore where food most probably is located, as well as the defensive advantage in being part of a large group.

Triatomine bugs (Heteroptera: Reduviidae) are blood-sucking insects that live throughout the Americas and cause public health problems by transmitting the protozoa *Trypanosoma cruzi*, the causative agent of Chagas disease, to humans. Secretions from Brindley's gland (a simple sac, metathoracic in origin) of several species all revealed isobutyric acid as the major component. Subsequently, other short-chain and branched-chain fatty acids have been identified, and together with isobutyric acid, they act as a powerful defensive secretion. Pure isobutyric acid vapor, however, also caused an alarm response in *Rhodnius prolixus* while another report revealed that low concentrations of isobutyric acid attracted *R. prolixus* adults. This defense compound therefore shows the same multifunctional alarm and aggregation properties as described for components of the stinkbug secretions (see above). Triatomine bugs are inactive and hide during the day, congregating in protective sites. This aspect of group living can help explain the evolutionary advantage in possessing aggregation and alarm responses.

Alarm Pheromones of Social Insects (Hymenoptera)

The Honeybee (Hymenoptera: Apidae)

When the honeybee (*Apis mellifera*) is attacked, alarm pheromones released serve to muster help and to direct the attack. Specialized guard bees present at the nest entrance carry out attacks. Although these guards are relatively few compared to the colony population, release of alarm pheromone can result in synchronized attacks by more than 100 workers against an intruder. Guard bees initiate attacks by raising their abdomens, protruding their stings and releasing alarm pheromone from the sting chamber. The workers then alert the rest of the hive by wing beating, aiding dispersal of the pheromone, and by running into the hive. After a few seconds, many excited bees may rush out of the hive entrance and search, or stop and assume a characteristic tense and aggressive posture with a slightly raised body, wings extended, mandibles agape and antennae waving. In this highly activated state, they will fly to attack at the slightest further provocation. These two stages of alarm response are called alerting and activation and are characteristic of alarm pheromones.

Alerted workers need to search for and discover the enemy to prevent any further threat. To do this, they rely on other cues to direct the attack such as odor, jerky movement and hairy body covering. Once the threat is located, it is stung, injecting a dose of venom. However, the shaft of a sting is barbed and a bee is unable to withdraw it from the skin of vertebrates, so the sting, together with associated motor apparatus and glands, are severed from the bee as it attempts to fly away and are left attached to the enemy. The severed sting apparatus continues to pump venom into the victim and alarm pheromone is dispersed from the exposed under-surface of the sting shaft membrane to mark an enemy and make it a more obvious target.

The main alarm pheromone component of the sting gland was identified in 1962 as isopentyl acetate (**4**). Although a number of other compounds are known to be present, isopentyl acetate and (Z)-11-eicosen-1-ol (**5**) account fully for the activity of the sting pheromone. The roles of the two compounds in the pheromone appear to differ, with (Z)-11-eicosen-1-ol responsible for prolonging the activity of isopentyl acetate. Other compounds such as 1-hexanol and 1-butanol increase the number of bees responding.

Stinging bees often grip an enemy with their mandibles and deposit an alarm substance. At the hive entrance, more bees examine mandibular gland extracts of worker honeybees applied to filter paper than examined unscented filter paper. 2-Heptanone (**6**) has been identified from the mandibular gland secretion, and when filter papers or small corks carrying 2-heptanone were placed at the hive entrance, the guard bees were alerted and attacked them. As the mandibles are used for grasping an intruder, it seems likely that the main function of 2-heptanone is to label the intruder to be attacked.

Under certain circumstances, honeybee alarm pheromones are repellent. The presence of alarm pheromone deters honeybees from foraging at dishes of sugar syrup and from exposing their Nasonov glands and fanning which normally attracts other bees. Furthermore, a high concentration of alarm pheromone repelled foraging bees from crops including oilseed rape, normally highly attractive to bees, in an area that had many honeybee colonies.

Alarm Pheromones of Ants (Hymenoptera: Formicidae)

The Formicidae is a huge family comprising thousands of ant species, all of which are social insects, living in colonies that vary hugely in size. Members of an ant colony may be differentiated into castes that specialize in carrying out particular tasks and vary in their response to alarm pheromone. Soldiers show a more aggressive response, are more likely to respond when the threat is closer to the nest and may be specialized to deal with vertebrate predators. Also, workers of the Texas leaf-cutting ant, *Atta texana* (Formicidae: Myrmicinae), have a lower threshold for alarm pheromone response than the queen and males. Other factors governing the type and intensity of alarm response are the age and size of ant colony. When alarm pheromone is present in sufficient concentration to excite the workers, other stimuli are needed to direct an attack. Workers often will touch everything they encounter and the full-scale alarm response may rely on additional cues, such as the presence of an alien object. Alarm pheromones also may function with acoustic alarm signals. Ant species in the sub-family Dolichoderinae produce vibration signals using their mandibles to scratch the ground or the abdomen to hit the ground, increasing alarm behavior in other workers. Vibrations are produced also by leaf-cutting ants which act as warning signals. Alarm pheromones also are used by ants to attract attention if they are trapped, and may be released by reproductive ants just before mating flights to ensure that aggressive workers protect them from potential predators.

The context in which a worker encounters an alarm pheromone also influences the response. Workers of the grass-cutting ant *Atta capiguara* (Formicidae: Myrmicinae) are less likely to show alarm behavior if already engaged in a task. Foragers carrying leaves do not respond to alarm pheromone, whereas minor workers and foragers that are not carrying leaves do respond.

Ant alarm pheromones may be produced from one or several sources. The army ants or Eciton ants (Formicidae: Ecitoninae) and the rare *Leptanilla* sp. (Formicidae: Leptanillinae) of Indonesia have large mandibular glands, which are believed to be the sole source of the alarm pheromone. However, other species rely on a combination of secretions from several glands. *Formica* and *Myrmica* species use products from the poison and Dufour's gland (both opening near the base of the sting), as well as the mandibular gland. Ponerine ants (Formicidae: Ponerinae) use secretions from the pygidial gland as alarm components, whereas the poison gland is the most important gland of several other species, including the harvester ant, *Messor barbarus* (Formicidae: Myrmicinae).

Ants are able to detect and respond to specific isomers of their alarm pheromone. *Myrmica rubra* and *M. scabrinodis* use 3-octanol (**7**) as the alarm pheromone produced from mandibular glands. Experiments carried out using the two optical isomers (**8a, b**) of this compound showed that *M. rubra* workers only responded to one of the isomers, (*R*)-3-octanol (**8a**), while *M. scabrinodis* workers reacted more strongly to the natural 9:1 mixture of R and S isomers. This work suggests that there may not only be specific chemicals but also species-specific mixtures of isomers. Many other *Myrmica* species have 3-octanol and 3-octanone as alarm pheromones but may have species-specific ratios of the two, which allow ant species to only show a full alarm reaction to their specific alarm pheromone blend.

Myrmica species of grass-cutting ants share the main component of alarm pheromone, 4-methyl-3-heptanone (**9**), but they have species-specific modifying components. The response to 4-methyl-3- heptanone was compared to that elicited by the bodies of workers that had their heads crushed to release the natural alarm pheromone. 4-Methyl-3-heptanone and bodies caused the same level of attraction but the full range of alarm behavior was seen only with the bodies. In contrast, workers of the giant tropical ant, *Paraponara clavata* (Formicidae: Paraponera), produce two components, 4-methyl-3-heptanone and 4-methyl-3-heptanol.

Atta capiguara is a grass-cutting ant species that lives in colonies with hundreds of thousands of workers. Workers are polymorphic, varying in size from small minors and medias to the larger foragers and soldiers. Minors and medias do most of the nest tasks whereas foragers collect the grass; however, minors often are found on foraging trails despite the fact they do not carry grass. They are believed to be patrollers as they have a stronger response to alarm pheromone than foragers and soldiers. Minors of other *Atta* species are also more efficient at recognizing intruding ants than other castes.

As is the case with honeybees described above, the complete alarm response can be described by a number of behaviors. These behaviors and their elicitors have been dissected in an elegant piece of research on the African weaver ant, *Oecophylla longinoda*. The major workers produce a secretion from the mandibular gland comprising four active components: hexanal, hexanol, (*E*)-2-butyl-2-octenal (**10**), a dimer of hexanal produced chemically by self-condensation, and 3-undecanone (**11**). Hexanal, a highly volatile component with an active space of 5–10 cm (the area around an emission where the concentration is at or above that required for a behavioral response), causes the ants to be alerted, making quick runs in random and changing direction with mandibles open and antennae waving. Hexanol attracts directly to the source at a range of 1–5 cm; it is repellent at very close range and also causes further excitement. As the hexanol disperses, 3-undecanone is attractive over this close range and, along with (*E*)-2-butyl-2-octenal, acts as a marker for attack and biting to hold the source occurs. This process is called a local attack. In addition, *O. longinoda* also has a mass attack alarm response. The poison gland of the major and minor workers contains venom that is ejected by raising the gasters above vertical when an attacked object is held in the jaws. The venom contains a blend of straight chain hydrocarbons and formic acid. Formic acid initiates approach and attack while n-undecane causes mandible opening, gaster raising and also short-range approach to the source. The combination of these behaviors allows location and initial attack of still and moving objects followed by recruitment of workers to continue attack.

The properties that make alarm pheromone cues for conspecifics also enable them to act as cues for parasites and predators of ants to find their prey. *Apocephalus paraponerae* is a parasitic fly that attacks the ant *Paraponera clavata*. Females and males of *A. paraponerae* are attracted to injured, fighting or freshly killed workers. After finding a worker, the female lays a few eggs, which will hatch and then feed on the victim for 3–7 days. Both male and female *A. paraponerae* also feed on the wounds of the injured workers and gather near their victims to mate. The heads of *P. clavata* workers contain two chemicals, 4-methyl-3-heptanone and 4-methyl-3-heptanol, which are particularly attractive to *A. paraponerae*. These compounds are common alarm pheromone components of ants and are released when the workers are stressed. However, it has been suggested that because these parasites use alarm pheromone for finding their host, *P. clavata* may be under pressure to reduce the amount of alarm pheromone released and that this ant may even have lost alarm behavior response as a result of this pressure. Similarly, the zodariid spider, *Habronestes bradleyi* (Zodariidae), a predator of the meat ant, *Iridomyrmex purpureus*, detects the alarm pheromone, in this case 6-methyl-5-hepten-2-one (**12**), given out by fighting workers and uses it to locate its prey.

Alarm Pheromones of Thrips (Thysanoptera: Thripidae)

Thrips are small, economically important pest insects, often known as thunderflies. The defensive behavior of thrips includes raising and lowering the abdomen and secretion of a droplet of anal fluid highly repellent to predatory ants. Western flower thrips, *Frankliniella occidentalis* (Thysanoptera: Thripidae), are not social but tend to be found in clumped distributions. Adults and nymphs of western flower thrips produce an anal droplet containing decyl acetate and dodecyl acetate (**13**) in a molar ratio of 1.5:1. Each component, at levels of 1 ng, produces the alarm response of walking away from the source or dropping from leaves. The response, however, is only over short distances and limits the potential for pheromone use in pest management.

Cockroach Alarm Pheromones (Blattodea: Blattidae)

Defensive secretions are well known in cockroaches. They are produced from ventral inter-segmental glands and comprise an organic and an aqueous phase. In the case of the Florida woods cockroach, *Eurycotis floridana* (Dictyoptera: Blattidae), 90% of the organic phase (which comprises 85% of the total secretion) is (E)-2-hexenal, a compound found in many heteropteran bugs and discussed above. The rest of the organic secretion comprises approximately 40 other components, including mainly aldehydes, alcohols and carboxylic acids, while the aqueous phase contains gluconic acid, glucose and gluconolactone. The secretion acts as a conspecific alarm pheromone in these gregarious insects with nymphs responding at lower concentrations than adults do. Ethanolic extracts of the American cockroach, *Periplaneta americana*, also repel conspecifics from aggregations in daytime shelters. However, there was no evidence that this repellent is released by living insects as an alarm pheromone but is instead endogenously produced from dead insects and is effective against other cockroaches with diverse phylogenetic relationships. The effect, therefore, is not pheromonal, as the authors explain the activity in terms of unsaturated fatty acids (oleic, linoleic and linolenic acids) which emerge as signals of death and injury among organisms from a wide phylogenetic background. Both of the reports described above provide evidence that the use of alarm pheromones to increase dispersal for pest management purposes will be of limited value. Due to the aggregation effect at low concentration, treated areas could become attractive. Also, if low concentrations were used as attractants in a lure and kill approach, dead insects would repel others before they become ensnared.

Alarm Pheromones of Beetles (Coleoptera)

Despite the vast numbers of species in the order Coleoptera, inhabiting a wide range of ecological niches, little is known of the existence of behavioral responses to alarm pheromones they may possess. Species of beetles that are group-living are most likely to demonstrate alarm responses. Gyrinid beetles (Coleoptera: Gyrinidae), known as whirligig beetles, live in open habitats on fresh water surfaces and typically aggregate in groups containing hundreds of individuals, dispersing in the evening to forage. Although easy to detect by fish, they are seldom preyed upon due to a repellent secretion released as a last resort to physical attack. The secretion also acts as an alarm pheromone over short distances, increasing locomotory activity and defensive movement, such as diving and active underwater swimming. Although alarm dispersal after attack can occur, the aggregations of beetles themselves indicate to experienced predators to avoid the group and confer an aposematic effect acting at the group level rather than the individual level.

Lacewing Alarm Pheromones (Neuroptera: Chrysopidae)

The green lacewing, *Chrysoperla carnea* (Neuroptera: Chrysopidae), is an important predator of pest aphids and, as such, is a beneficial insect. It discharges a malodorous secretion from glands at the anterior of the prothorax. The major component of this secretion has been identified by gas chromatography, mass spectroscopy and chemical synthesis as (Z)-4-tridecene (**14**) and gas chromatography coupled electroantennagrams revealed that it is detected by the lacewing antennae. Predatory ants displayed avoidance behavior in response to it, suggesting a defensive function, and in laboratory experiments, adult lacewings avoid entering areas where it is present. In the field, it acts as an antagonist to trap catches using known attractants and, as such, could be described as an alarm pheromone. Another species of lacewing, *Peyerimhoffina gracilis*, also produces the identical compound. As lacewings are not known to be gregarious, the exact ecological purpose of this compound is being investigated.

Conclusions

It can be seen that alarm pheromones are used widely by a broad taxonomic diversity of insects and elicit equally varied behavioral responses, including escape or aggressive behavior. Alarm pheromones are generally low molecular weight, organic compounds and so are volatile, dispersing quickly, and do not persist in the environment. In addition, the chemical nature of the alarm pheromone often is unstable, increasing the lack of persistence. This allows conspecifics to be alerted very quickly over a fairly large area and yet not cause false alarm after the danger has passed. Alarm pheromones are often produced in glands responsible for biosynthesis, storage or release of defense secretions. This association between alarm pheromones and defense glands, including those near the sting or mandibles, has led to the hypothesis that alarm pheromones have evolved from chemicals that originally had a defensive role, or are themselves defense compounds that have taken on an additional alarm pheromonal role. The fact that known defense components have additional multifunctional pheromonal roles of alarm (high concentration) and aggregation (low concentration) also points to the possibility that these pheromonal roles have evolved from compounds originally used for defense. Of particular interest is the common lack of species specificity found in alarm pheromones, which is in contrast to that of other pheromones. Sex pheromones, for example, are so specific that they can be the sole identifiable trait in defining morphologically identical populations, such as within the species complex of the sandfly, *Lutzomyia longipalpis* (Diptera: Psychodidae). However, the alarm pheromone of different aphid species is (E)-β-farnesene and different species of *Atta* grass-cutting ant use 4-methyl-3-heptanone. In addition, production of (E)-2-hexenal and n-tridecane is ubiquitous as multifunctional pheromone components in terrestrial true bugs, and it is possible that (E)-4-tridecene may reveal itself to be common in green lacewings. Discrimination between these behavioral signal compounds, therefore, is not essential to their function as alarm pheromones, and there may even be evolutionary benefits in being able to respond to alarm pheromones of related species of insects.

References

Aldrich JR, Blum MS, Lloyd HA, Fales HM (1978) Pentatomid natural products. Chemistry and morphology of the III-IV dorsal abdominal glands of adults. J Chem Ecol 4:161–172

Bowers WS, Nault LR, Webb RE, Dutky SR (1972) Aphid alarm pheromone: isolation, identification, synthesis. Science 177:1121–1122

Bradshaw JWS, Baker R, Howse PE (1979) Multicomponent alarm pheromones in the mandibular glands of major workers of the African weaver ant. Physiol Entomol 4:15–25

Dawson GW, Griffiths DC, Pickett JA, Woodcock CM (1983) Decreased response to alarm pheromone by insect-resistant aphids. Naturwissenschaften 70:254–255

Free JB, Pickett JA, Ferguson AW, Simpkins JR, Smith MC (1985) Repelling foraging honeybees with alarm pheromones. J Agric Sci 105:255–260

Hölldobler B, Wilson EO (1990) The ants, 1st ed. The Belknap Press of Harvard University Press, Cambridge, MA

Nault LR, Phelan PL (1984) Alarm pheromones and sociality in pre-social insects. In: Chemical ecology of insects. Chapman and Hall, London, UK, pp 237–256

Pickett JA, Griffiths DC (1980) Composition of aphid alarm pheromones. J Chem Ecol 6:349–360

Alarm-Recruitment System

Recruitment of nest members to a particular location to aid in colony defense.

► Sociality of Insects

Alary Muscles

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The alary muscles, so named because of their general wing or delta shape in many insects, lie immediately on top of the dorsal diaphragm. The muscles probably aid the dorsal diaphragm in providing support for the heart, the part of the dorsal vessel in the abdomen. The muscle fibers fan out from a small point of origin on the lateral wall of the dorsum to a broad insertion on the heart in many insects, presenting the typical delta appearance. In some insects, however, the delta shape is not so evident. Some alary muscle fibers pass beneath the heart and extend laterally from side to side, and thus help to support the heart. In places, the fibers may also run parallel to the long axis of the heart for a short distance. The pairs of alary muscles tend to agree with the number of pairs of ostia, the (usually) lateral openings in the dorsal vessel that allow hemolymph to flow into the heart in the abdomen. Alary muscles generally do not occur in the thorax, but in some insects, a few ostia open outward in the thorax, allowing hemolymph to flow outward.

In addition to support, the alary muscle may assist in the expansion (diastole) of the heart after each contractile wave passes a given point, and thus aid in pulling hemolymph into the incurrent ostia. They are not necessary for diastole, however, as evidenced by severing them with little or no apparent effect on the heart beat.

Alate (pl., Alatae or Alates)

The winged forms of insects, particularly aphids.

Alderflies

Members of the family Sialidae (order Megaloptera).

► Alderflies and Dobsonflies

Alderflies and Dobsonflies (Megaloptera)

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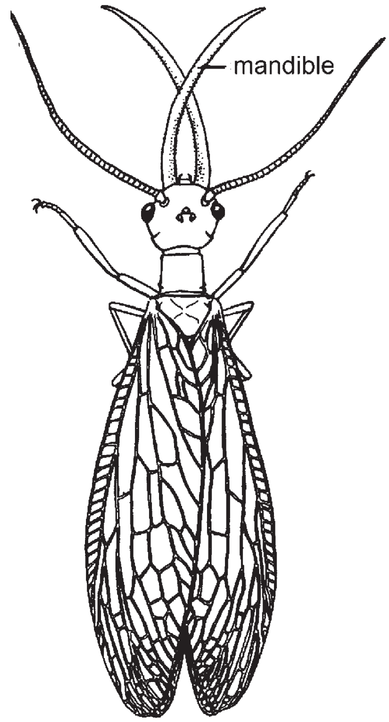
The order Megaloptera comprises about 190 species in 60 genera in two families. All the larvae are aquatic. The larvae, especially of Corydalinae, are among the most primitive of the Holometabola. The metamorphosis from larva to adult is relatively simple.

The family Sialidae, commonly called alderflies, is a small group of about 70 species in about eight genera. They are worldwide. Most of the adults have a similar appearance and are usually dark brown to black in coloration. They lack ocelli and have the fourth tarsomere bilobed. They are an ancient group known from the Permian, about 200 million years ago, and evidently have not evolved much since then. In fact, the wing venation has many features in common with the Protoperlaria, a fossil order considered by some as ancestral to the Plecoptera. The adult life span is probably short since the reduced mouthparts do not seem adapted for extensive feeding. The eggs are laid in rows, forming large masses situated on branches, bridges, and other objects overhanging the water. The larvae hatch and fall into the water where they are predacious on other aquatic insects, especially caddisflies. There are as many as 10 larval instars which may last up to two or more years until pupation. The larva crawls out of the water and digs into the bank to form an earthen cell several feet from the edge of the water. The genera are restricted geographically. The genus *Sialis* Latreille is Holarctic, *Protosialis* Van der Weele is South American, *Austrosialis* Tillyard and *Stenostialis* are Australian, *Haplosialis* Navas is from Madagascar, *Leptosialis* is African, *Indosialis* Lestage is Oriental and *Nipponsialis* Kuwayama is Japanese. The larva has seven lateral processes and the abdomen terminates in an elongate process. The only world compilation is by Van der Weele (1910) but is greatly out of date.

The family Corydalidae, or dobsonflies, is characterized by having three ocelli and the anal region of the hindwing is very wide, folded fanlike at rest (Fig. 31). The fourth tarsomere is not modified. There are several hundred species in about 20 genera and two subfamilies.



Alderflies and Dobsonflies (Megaloptera), Figure 31 **Adult dobsonfly (Corydalidae).**

The Corydalinae with about 60 species, is distributed in the New World (three genera), South Africa (one genus) and Asia (five genera). This subfamily does not have pectinate antennae and the head is usually quadrate, often with a postocular spine. Often there are more than four crossveins between the radius and radial sector. The male terminalia are distinctive with a well developed ninth gonostylus. Many of the species are very large. *Corydalis* Latreille is the largest genus in the New World with about 30 species. The males of this genus often have the mandibles greatly extended which is similar to *Acanthacorydalis* Van der Weele from Asia. *Platyneuromus christil* (Navás) from Central America, has a tremendously expanded postocular flange. The larva has eight lateral processes and the abdomen ends in a pair of claw-like structures. In America, the larvae are called hellgrammites and are used for fishing. In one case, a larva was found inside a fish stomach many hours after ingestion. Glorioso (1982) has provided a good reference.

The Chauliodini was reviewed by Kimmins (1954) who recognized 12 genera. The genera are restricted in distribution similar to the Corydalinae and are found in the Cape region of South Africa (two genera), North America (four genera), Chile (three genera), Australia (one genus), Madagascar (one genus), and Asia (four genera). Males and rarely females have pectinate antennae in some genera.

References

Glorioso MJ (1981) Systematics of the dobsonfly subfamily Corydalinae (Megaloptera: Corydalidae). Sys Entomol 6:253–290

Kimmins DE (1954) A new genus and some new species of the Chauliodini (Megaloptera), with notes on certain previously described species. Bull Br Mus Nat Hist Entomol 3:417–444

Van der Weele (1910) Megaloptera. Collections Zoologiques du Baron Edm. de Selys Longchamps, fasc 5, 93 pp

Aldrovandi, Ulisse (Ulysse, Ulysses)

Ulisse Aldrovandi was born in Bologna, Italy, in 1522. He studied law in Bologna, and then philosophy and medicine in Padua and Rome, earning a doctorate in medicine in 1552. In 1560, he was appointed professor in Bologna, a position that he held for 40 years. He lectured mainly on pharmacology, but he collected natural history objects and employed artists to draw them. He published four large volumes during his lifetime, but his friends and pupils used his voluminous manuscripts to publish 10 more volumes after his death. His (1602) "De animalibus insectis libri VII" was the first book to be published on insects, although the "insects" included various other kinds of invertebrates. A chapter was devoted to the structure of the insect body. Insect reproduction and metamorphosis were described; respiration and the senses of touch, taste, and smell are discussed, and the life of honey bees is described. He died in 1605.

References

Beier M (1973) The early naturalists and anatomists during the renaissance and seventeenth century. In: Smith RF, Mittler TE, Smith CN (eds) History of entomology. Annual Reviews, Inc., Palo Alto, CA, pp 81–94

Nordenskiöld E (1935) The history of biology: a survey. Tudor, New York, NY, 629 pp

Aldyidae

A family of bugs (order Hemiptera). They sometimes are called broad-headed bugs.

► Bugs

Aleyrodidae

A family of insects in the order Hemiptera. They sometimes are called whiteflies.

► Whiteflies
► Bugs

Alexander, Charles Paul

Charles Alexander was born in New York state on September 25, 1889. He entered Cornell University in 1909, receiving B.Sc. and Ph.D. degrees in 1913 and 1918, respectively. He was employed as systematic entomologist in the Snow Entomological Museum at the University of Kansas in 1917–1919 and then by Illinois Natural History Survey in 1919–1922. Next he moved to Massachusetts Agricultural College and was placed in charge of teaching entomology. He served as chairman of the Department of Entomology and Zoology for 10 years, for the last three of which he was dean of the School of Science (of what had by then become the University of Massachusetts). He was president of the Entomological Society of America in 1941–1943 (two terms). His almost exclusive subject of research was the family Tipulidae (crane flies) about which he published over 1,000 papers and described over 10,000 species, an enormous production. After retirement from teaching, he moved his insect collection to his house and continued working on it until the death of his wife, Mabel, in 1979. Two years later he transferred his collection to the National Museum of Natural History in Washington, DC. He died at home in Massachusetts on December 12, 1981.

Reference

Byers GW (1982) In memoriam Charles P. Alexander 1889–1981. Journal of the Kansas Entomological Society 55:409–417

Alfalfa Leafcutting Bee, *Megachile rotundata* (Hymenoptera: Megachilidae)

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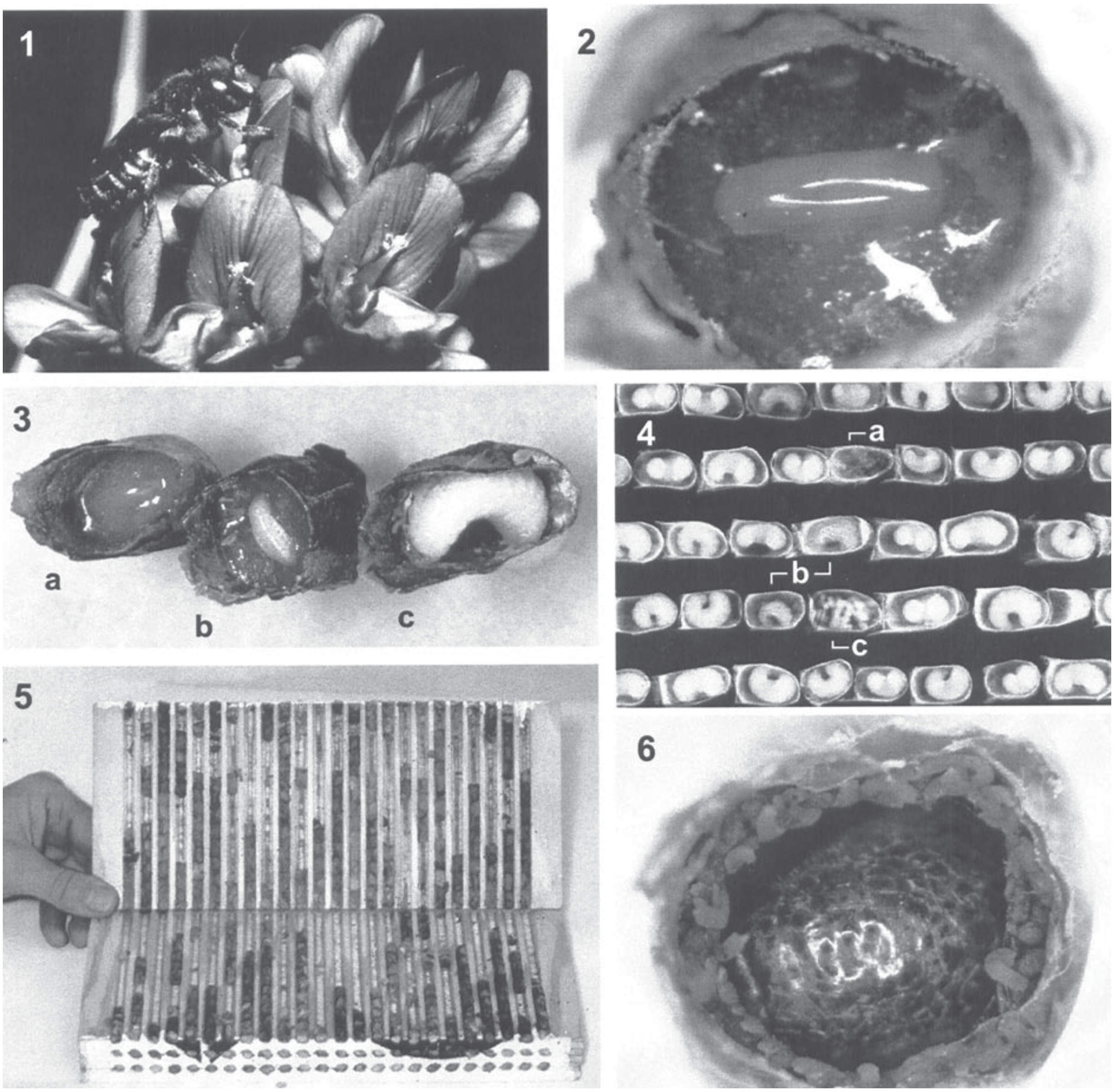
The alfalfa leafcutting bee, *Megachile rotundata* Fabricius (Hymenoptera: Megachilidae), has been successfully semi-domesticated within the last 50 years to pollinate alfalfa for seed production in North America. Honey bees are inefficient pollinators of alfalfa and, although bumbles bees and some other wild bees are efficient pollinators, they have proved difficult to manage. The use of the alfalfa leafcutting bee has succeeded in greatly increasing the seed yield of alfalfa. In western Canada, the average alfalfa seed yield using this bee exceeds 300 kg/ha, whereas without it is usually less than 50 kg/ha. The genus *Megachile* contains many species that nest in tunnels in dead trees or fallen logs. Most are solitary, but *M. rotundata* is gregarious and, although each female constructs and provisions her own tunnel, she will tolerate close neighbors. This behavioral characteristic is one of the main reasons why this species has been amenable to management on a commercial scale. *M. rotundata* is of eastern Mediterranean origin and was first found in North America in the 1940s near seaports. It probably gained entry as diapausing pre-pupae within tunnels in the wood used to make shipping crates or pallets.

Life History

Once a suitable tunnel has been found, the female uses her mandibles to neatly cut oblong pieces of leaves or flower petals which she uses to build cells end to end in the tunnel, starting at the far end and finishing near the entrance (Fig. 32). About 15 leaf pieces are arranged in overlapping layers and cemented together to form a thimble-shaped cell with a concave bottom. The cell is then provisioned with nectar and pollen. During this process, the female enters the tunnel head first, regurgitates the nectar, then turns around to remove the pollen from the scopa (the pollen-collecting hairs on the underside of her abdomen) and tamps the pollen into the nectar with the tip of her abdomen. The provisions for each cell consist of about two-thirds nectar and one-third pollen, requiring 15–25 provisioning trips. It is while collecting the nectar and pollen that the bees pollinate the flowers that they visit. When the cell has been adequately provisioned, the female lays a single egg directly on the surface of the provisions and then caps the cell with several circular leaf pieces. She then proceeds to construct the next cell, repeating this process until the tunnel is filled. She then plugs the end of the tunnel with 10–15 leaf pieces cemented together to form a plug. Females continue filling tunnels with cells until pollen and nectar sources are no longer available. Upon hatching, the larva immediately begins feeding on the provisions within its cell, undergoing four instars before reaching maturity. It then deposits a ring of fecal pellets within the cell and spins a tough silken cocoon within which it overwinters as a diapausing pre-pupa. During the feeding period, the waste



Alfalfa Leafcutting Bee, *Megachile Rotundata* (Hymenoptera: Megachilidae), Figure 32 **Alfalfa leafcutting bee, *Megachile rotundata*. (1) Adult on alfalfa flower. Flowers are pollinated while the bees visit the flowers to collect nectar and pollen for provisioning their cells. (2) A single egg is deposited on the surface of pollen/ nectar provisions within a cell which the female constructs within tunnels using oblong pieces of leaves or flower petals. (3) The egg placed into the cell hatches within 2 to 3 days and the larva immediately begins to consume the provisions. The larva pupates after undergoing 4 instars. (a) single egg, (b) 3rd instar, and (c) 4th instar larvae within the cell. Cell caps have been removed. (4) X-ray of leafcutting bee cells used to determine quality of commercial bees. (a) empty cell, (b) chalkbrood cadavers, (c) *Pteromalus venustus* parasitoid cocoons. (5) Nesting boards separated to show arrangement of bee cells constructed within the tunnels. In the fall, the boards are removed from the field and the cells are stripped from the boards using specialized automated equipment. (6) Chalkbrood cadaver within the cell. Note the ring of frass deposited on the outside edge of the cell. Normally, the larva would spin a tough silken cocoon within which it overwinters as a diapausing pre-pupa. Larvae infected with chalkbrood usually succumb just after defecating and just prior to cocoon spinning.**

products of digestion are accumulated internally until the larva defecates just before forming the cocoon. In the spring, the pre-pupa pupates. After a pupal period of 3–4 weeks, the adult emerges and chews its way out of the cocoon. Mating takes place soon after emergence of the adults. Females store enough sperm from a single mating to fertilize all of their eggs. Soon after mating, the females seek out suitable sites in which to excavate tunnels or select suitable preexisting ones, either natural or man-made.

Domestication

The gregarious nature of *M. rotundata* and its willingness to accept artificial domiciles has permitted the commercial scale management of this species for crop pollination. Initially, observant alfalfa seed producers in the northwestern U.S.A. noticed that this species, which had undergone a population increase following natural establishment, would nest in man-made structures such as shingled roofs and they started to provide artificial tunnels by drilling holes in logs positioned around the edges of the seed fields. The next step was to provide nests consisting of wooden blocks drilled with closely spaced tunnels. Although reasonably successful on a small scale, this method was not suitable for the management of the large numbers of bees (50,000–75,000/ha) required for commercial alfalfa seed production. Consequently a "loose-cell" system was developed. This system uses 10 mm thick boards of wood or polystyrene which are grooved on both sides and stacked together to form hives of closely packed tunnels about 7 mm in diameter and 150 mm in length. At the end of the season, the boards are separated and the cells removed using specialized automated equipment. After being stripped from the boards the cells are tumbled and screened to remove loose leaf pieces, molds and some parasites and predators. The clean cells are then placed in containers for overwintering storage at about 50% R.H. and 5°C. In the spring, the cells are placed in trays for incubation at 70% R.H. and 30°C. A few days before the bees are due to emerge, the trays are moved to especially designed shelters spaced throughout the alfalfa seed fields. By selecting the date when incubation begins, and if necessary manipulating the incubation temperature, the emergence of the bees can be adjusted to coincide with the start of alfalfa bloom.

An advantage of the loose cell system of management is that it facilitates the control of parasitoids, predators and disease, and assessment of the quality of the progeny. Leafcutting beekeepers routinely send samples of cells to specialized leafcutting bee "cocoon" testing centers, where they are x-rayed and incubated to provide estimates of numbers of intact cells, incidence of parasites and pathogens, and sex ratio. These data are used to determine stocking rates and to set a price if bees are to be marketed. The proportion of females, which is usually only about a third, is of particular interest because they are the primary pollinators.

Natural Enemies

About 20 species of insects are known to parasitize or prey on the immature stages of the alfalfa leafcutting bee. The most important of these are several species of chalcid wasps, including *Pteromalus venustus* Walker, *Monodontomerus obscurus* Westwood, *Melittobia chalbii* Ashmead and *Diachys confusus* (Girault). The most widespread and damaging is *P. venustus*, which probably arrived in North America with its host. The female parasitoid pierces the host cocoon with her ovipositor, stings the larva or pupa to paralyze it, and then lays some eggs on its surface. The parasitoid larvae then feed upon the bee larva eventually killing it. Normally 15–20 adult *P. venustus* emerge from each host cocoon.

Two other enemies, which are more of biological interest than economic significance, are several species of cuckoo bees, *Coelioxys* (Megachilidae) and the brown blister beetle, *Nemognatha lutea* LeConte. Cuckoo bees are very similar to leafcutting bees, but lack the structures required for collecting pollen. The female cuckoo bee lays her egg in the partially provisioned cell of the leafcutting bee while the rightful owner is out foraging. When partly grown, the cuckoo bee larva kills the leafcutting bee larva and usurps the provisions. Brown blister beetle females lay their eggs on flowers and the first instar larvae (triungulins) attach themselves to any bee that visits the flower. When the bee returns to its nest, the triungulin detaches and begins feeding on the cell contents, destroying 2 or 3 cells before reaching maturity.

Several stored-product insects including the driedfruit moth, *Vitula edmandsae serratilinnella* Ragonot, and stored-product beetles such as the sawtoothed grain beetle, *Oryzaephilus surinamensis* (Linnaeus), the red flour beetle, *Tribolium castaneum* (Herbst) and the confused flour beetle, *Tribolium confusum* (Jacquelin du Val) can cause serious damage during overwintering storage, especially if sanitation practices are lax.

Most of the parasitoids and predators can be largely controlled by proper construction of hives and nesting materials, physical removal during the loose-cell processing and strict hygiene during storage. However, successful control of the major pest, the chalcid *P. venustus*, often requires carefully controlled fumigation using dichlorvos (2, 2-dichloro-vinyl dimethyl phosphate) resin strips.

The only disease causing significant losses to the leafcutting bee industry is chalkbrood, caused by the fungus *Ascosphaera aggregata* Skou. The disease was first reported in leafcutting bees in 1973, and remains most severe in the western U.S. states, where losses of more than 65% of bees are not uncommon. Bee larvae become infected after consuming pollen provisions contaminated with the fungal spores which germinate within the midgut and penetrate into the hemocoel. Larvae soon die and turn a chalk white color as the mycelium fills the body. Sporogenesis occurs beneath the host cuticle resulting in the formation of ascospores which are bound in "spore balls" within ascomata. At this stage, the cadaver turns black. Spores are spread by adults that must chew their way through infected cadavers in order to exit their nesting tunnels. Chalkbrood can be adequately managed through strict hygiene and decontamination of the bee cells, nest materials and shelters. Initially, decontamination was performed by dipping in household bleach. However, fumigation with paraformaldehyde has become the method of choice, and is highly effective for the control of both *A. aggregata* and foliar molds, which can sometimes pose a health risk to the beekeeper.

► Bees

References

Goerzen DW, Watts TC (1991) Efficacy of the fumigant paraformaldehyde for control of microflora associated with the alfalfa leafcutting bee, *Megachile rotundata* (Fabricius) (Hymenoptera: Megachilidae). BeeScience 1:212–218

Goettel MS, Richards KW, Goerzen DW (1993) Decontamination of *Ascosphaera aggregata* spores from alfalfa leafcutting bee (*Megachile rotundata*) nesting materials by fumigation with paraformaldehyde. BeeScience 3:22–25

Hill BD, Richards KW, Schaaljie GB (1984) Use of dichlorvos resin strips to reduce parasitism of alfalfa leafcutter bee (Hymenoptera: Megachilidae) cocoons during incubation. J Econ Entomol 77:1307–1312

Richards KW (1984) Alfalfa leafcutter bee management in Western Canada. Publication #1495E. Agriculture Canada, Ottawa, Canada, 53 pp

Richards KW (1987) Alfalfa leafcutter bee management in Canada. Bee World 68:168–178

Vandenberg, JD, Stephen WP (1982) Etiology and symptomatology of chalkbrood in the alfalfa leafcutting bee, *Megachile rotundata*. J Invertebr Pathol 39:133–137

Alfalfa (Lucerne) Pests and their Management

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Alfalfa (lucerne), *Medicago sativae*, is one of the most important legumes used in agriculture. It is the principal roughage for ruminants, as well as being an important source of protein in animal diets. It is surpassed only by grass, corn, and soybean as an animal feed, and is especially important to the dairy industry. The USA is the world's largest producer of alfalfa, but it also is an important crop in Australia, Europe, Argentina, China, South Africa, and the Middle East.

There are other uses for alfalfa, though they are minor. Alfalfa sprouts are a salad ingredient, alfalfa shoots are sometimes consumed as a leafy vegetable, and dehydrated alfalfa is sometimes formulated as a tablet to be consumed as a dietary supplement. Alfalfa is a cross-pollinated species. It relies on insects, often domesticated leafcutting bees, honey bees, alkali bees, and various wild bees, for pollination. Wind pollination does not occur because the blossom is structured in a way that physical "tripping" to expose the stigma to the anthers is required. Bees manipulate the blossom when foraging for nectar and pollen and thereby "trip" the blossom, an action that results in the bee being struck in the head. An interesting aspect of pollination is that some bees learn to avoid the tripping process to avoid being struck, thereby robbing the flower without pollination occurring. Older honey bees are good at avoiding tripping, but naïve young honey bees trip the blossom and provide pollination.

Alfalfa is normally harvested before, or at, the initiation of flowering, which maximizes protein content of the harvested hay. Because pollinators are often present in alfalfa fields during the bloom period, care must be taken when using insecticides for pest suppression to avoid products that are highly toxic to pollinators, at least if seed production is a concern. However, most alfalfa is grown only for forage, and without regard for seed production. Thus, insecticide use may include the bloom period, though if pollinator populations are reduced, other crops that require pollination may be inadvertently affected.

Alfalfa is unusual as a field crop in that it is a short-lived perennial, living 3–12 years. It may be harvested from once to 12 times per year, depending on climate and growing conditions. It has deep roots, and is resistant to drought, though in arid climates it is irrigated. It is tolerant of cold, growing well in cool and cold climates. It does not tolerate hot, humid climates, however.

Alfalfa often is cut and dried before it is baled and stored. To speed up the process of drying, alfalfa is commonly flailed or passed through a set of rollers to break or crush the stems, facilitating the drying process. The crushing process is called crimping and sometimes can cause problems for horses because blister beetles (Coleoptera: Meloidae) are incorporated into the hay (see below, blister beetles). Dried alfalfa is tied into bales of various sizes, including large cylindrical bales, and stored under shelter, or packaged in plastic, to avoid moisture. If the alfalfa is to be fed to cattle, however, it is not dried, and instead it is finely chopped and stored in trenches, silos, or bags where it can ferment and maintain high nutrient levels. Cattle are not very susceptible to poisoning by blister beetles.

Alfalfa has undergone considerable breeding to produce strains that have not only suitable agronomic conditions, but also are disease and pest resistant. Nevertheless, insects can damage alfalfa nearly everywhere it is grown. Some of the important pests are listed in the table, and the most important are discussed below.

Alfalfa Weevil, *Hypera postica* (Gyllenhal) (Coleoptera: Curculionidae)

In many regions, this is the most important pest of alfalfa. It is found in Europe, the Middle East, Central Asia, and North America. Alfalfa weevils overwinter as adults in the soil of weedy, brushy areas near alfalfa fields. They disperse to alfalfa in the spring and oviposit within the stems. The eggs are oval and yellow. Early instars developing from these eggs are slate colored, but develop a bright green color and a white stripe down the middle of the back as they mature. Larvae have a black head capsule. They display four instars and will grow to about 8–10 mm in length. After feeding for 3–4 weeks, larvae spin loosely constructed cocoons on

Alfalfa (Lucerne) Pests and their Management, Table 5 **Some pests of alfalfa (lucerne), and locations where they are considered to be damaging**

Feeding behavior	Primary taxon	Common name	Scientific name	Location
Above-ground, chewing	Coleoptera	Sitona weevil	*Sitona discoides*	Australia
		Small lucerne weevil	*Atrichonotus taeniatulus*	Australia
		Vegetable weevil	*Listroderes obliquus*	Australia
		Alfalfa weevil	*Hypera postica*	Europe, Asia, N. America
		Clover leaf weevil	*Hypera punctata*	Europe, Asia, N. America
		Clover head weevil	*Hypera meles*	Europe, N. America
		Blister beetles	*Epicauta* spp.	N. America
		Flea beetles	*Epitrix, Systena, Disonycha* spp.	N. America
	Orthoptera	Grasshoppers	*Melanoplus* spp.	N. America
		Wingless grasshopper	*Phaulacridium* spp.	Australia
	Lepidoptera	Armyworm	*Mythimna* spp.,	Australia
		Armyworm	*Persectania* spp.	Australia
		Armyworm	*Pseudaletia unipuncta*	N. America
		Variegated cutworm	*Peridroma saucia*	Europe, Asia, Africa, N. America
		Army cutworm	*Euxoa auxiliaris*	N. America
		Granulate cutworm	*Agrotis subterranean*	N. America, S. America
		Black cutworm	*Agrotis ipsilon*	N. America, Europe, Africa
		Beet armyworm	*Spodoptera exigua*	Asia, N. America
		Fall armyworm	*Spodoptera frugiperda*	N. America, S. America
		Budworm	*Helicoverpa punctigera*	Australia
		Corn earworm	*Helicoverpa zea*	N. America, S. America
		Alfalfa looper	*Autographa californica*	N. America

Alfalfa (Lucerne) Pests and their Management, Table 5 Some pests of alfalfa (lucerne), and locations where they are considered to be damaging (Continued)

Feeding behavior	Primary taxon	Common name	Scientific name	Location
		Lucerne leafroller	*Merophyas divulsana*	Australia
		Alfalfa caterpillar	*Colias eurytheme*	N. America
		Webworms	*Loxostege* spp.	N. America, Europe, Asia
	Collembola	Lucerne flea	*Sminthurus viridis*	Australia, Europe, Africa
	Diptera	Alfalfa blotch leafminer	*Agromyza frontella*	Europe, N. America
Above-ground, sucking	Acari	Redlegged earth mite	*Halotydeus destructor*	Australia
		Clover mite	*Bryobia* spp.	Australia
		Twospotted spider mite	*Tetranychus urticae*	No. America
	Collembola	Lucerne flea	*Sminthurus viridis*	Europe, N. Africa, Australia
	Hemiptera	Pea aphid	*Acythosiphum pisum*	Europe, Asia, Australia, N. & S. America
		Blue alfalfa aphid	*Acythosiphum kondoi*	Mediterranean, Australia, N. & S. America
		Spotted alfalfa aphid	*Therioaphis maculata*	Mediterranean, Australia, N. America, Asia
		Potato leafhopper	*Empoasca fabae*	N. America
		Lucerne leafhopper	*Austroasca alfalfae*	Australia
		3-cornered alfalfa hopper	*Spissistilus festinus*	N. America
		Meadow spittlebug	*Philaneus spumarius*	N. America
		Tarnished plant bugs	*Lygus* spp.	Europe, N. America
		Alfalfa plant bug	*Adelphocoris* spp.	Europe, N. America
	Thysanoptera	Flower thrips	*Frankliniella* spp.	Europe, Asia, N. America
Below-ground	Coleoptera	Clover root curculio	*Sitona hispidula*	Europe, N. & C. America

Alfalfa (Lucerne) Pests and their Management, Table 5 Some pests of alfalfa (lucerne), and locations where they are considered to be damaging (Continued)

Feeding behavior	Primary taxon	Common name	Scientific name	Location
		Alfalfa snout beetle	*Otiorhynchus ligustici*	N. America
		African black beetle	*Heteronychus arator*	Africa, Australia
		Whitefringed beetle	*Naupactus leucoloma*	Australia, S. America
		Small lucerne weevil	*Atrichonotus taeniatulus*	Australia

plants or in litter on the soil, pupate, and emerge as adults in 1–2 weeks. Adults are 5–6 mm long, have a long snout, and have a dark stripe down the back. They are light brown at emergence and darken in several days. The number of generations varies according to climate, but eventually they leave fields for grassy, brushy, weedy areas where they become inactive until the onset of winter.

Damage is caused by the larval stage which feeds on leaves; damage ranges from pinholes to skeletonization of leaves. Adults generally cause minor damage. Peak damage is usually just prior to the first cutting or after the first cutting, as both larvae and adults feed on new growth; this can seriously affect regrowth of the stand. Also, cool, cloudy weather exacerbates damage done by the alfalfa weevil. Cool and cloudy weather conditions slow the regrowth rate of alfalfa, and also increase the daily feeding period of the weevil because both larvae and adults tend to hide under crop residue during bright sunlight and will not actively feed during such periods.

Weevil larvae can be found early in the Spring. It is important to scout for live larvae and injured terminals on the first crop, but also subsequent crops. Sweep net sampling can be used to detect weevil presence. Several species of wasps can be effective in maintaining weevil populations below economic threshold levels. Among the effective parasitoids are *Bathyplectes curculionis* (Thomson), *B. anurus* (Thomson) and *B. stenostigma* (Thomson) (Hymenoptera: Ichneumonidae); *Microctonus aethiopoides* Loan and *M. colesi* Drea (Hymenoptera: Braconidae) *Oomyzus incertus* (Ratzenberg) (Hymenoptera: Eulophidae); *Dibrachoides dynastes* (Forester) and *Peridesmia discus* (Walker) (Hymenoptera: Pteromalidae); and *Anaphes luna* (Girault) (Hymenoptera: Mymaridae). A fungal pathogen, *Zoophthora phytonomi* Arthur (Phycomycetes: Entomophthoraceae), attacks weevil larvae and can control populations in several days, though it is most effective under moist conditions. These biological control agents are extremely effective control measures in all but major outbreak periods. However, when fields show damage on 35–40% of plant tips more than 7–10 days prior to harvest, chemical suppression is often initiated.

Early harvest (first crop) is very effective in killing larvae, and is preferred to chemical control if the planned harvest is less than 7–10 days away. If harvesting is used to control alfalfa weevil, the stubble and debris should be examined closely for adults and larvae, and stems should be examined for feeding signs. It may be necessary to spray stubble, though in many areas producers can avoid insecticide use consistently through timing of harvest.

Root Weevils, *Sitona* spp., *Atrichonotus taeniatulus* (Berg), Others (Coleoptera: Curculionidae)

Root weevils such as clover root curculio, *Sitona hispidula* (Fabricius), in North America; and sitona weevil, *Sitona discoideus* Gyllenhal, small lucerne weevil, *Atrichonotus taeniatulus* (Berg), in Australia, and whitefringed beetle, *Naupactus leucoloma* Boheman in Australia and South America, can be significant pests of alfalfa. Although the adults commonly feed on the foliage, the principal damage is due to larval feeding on the roots of the alfalfa plant.

Eggs are laid in fall or spring, on the soil surface or lower parts of plants. Eggs hatch in the winter or spring. White, legless larvae move into the soil and feed on roots until they pupate. Pupae are found just below the soil surface. Adults emerge in the summer months and live up to a year. The adults are brown or black, blunt-snouted weevils up to about 10 mm long. There is one generation per year. Adults migrate by crawling, and thus infest new areas rather slowly.

The adults feed on alfalfa leaf margins, leaving crescent-shaped notches, and chew on stems and leaf buds of seedlings, but this tends to cause minor loss. Most damage is caused by the larvae. First larval instars feed on root nodules and lateral roots; later instars feed on the taproot. Feeding on the taproot can girdle the plant, resulting in plant death. Such damage also weakens the overall vigor of a stand, perhaps contributing to winter-kill and increased susceptibility to disease.

It is difficult to control larvae because they are in the soil and largely protected from insecticide. Suppression aimed at adults usually requires multiple applications. It is inadvisable to plant alfalfa into a field which has previous ly been infested, to plant into fields previously supporting legume crops, or to seed alfalfa next to established stands.

Blister Beetles (*Epicauta* spp.) (Coleoptera: Meloidae)

There are several species of North American blister beetles that can be of concern in alfalfa. They are a problem not because of their food habits (they tend to feed mostly on blossoms) but because they contain the toxin cantharidin within their bodies. When alfalfa is harvested, if the hay is crimped it may contain crushed blister beetles that may prove toxic to horses that ingest the hay. The most abundant blister beetle in alfalfa fields generally is the black blister beetle, *E. pensylvanica* (De Geer). However, the species that is most toxic is *E. vittata* (Fabricius).

Most blister beetles are recognized by the shape of their body. They are narrow, cylindrical, and soft. The region between the head and wings is distinctly narrower than the wings, and is usually narrower than the head. Most species have one generation per year, although some have two. Blister beetles overwinter as larvae. The adults begin to emerge in the Spring and adults deposit their eggs where grasshopper egg pods may occur, as larvae feed on the grasshopper eggs.

If grasshoppers are not abundant, then blister beetles are unlikely to be abundant. When both are numerous, it is advisable to harvest alfalfa early, before bloom, as this is the only time that beetles are attracted to the crop. There is some yield loss associated with this approach, of course, and an alternative it to treat the crop with insecticides. If insecticide is used, alfalfa should be harvested as soon as possible after the pre-harvest interval expires, to get hay out of the field before it is re-infested. A principal problem with blister beetle management is that the beetles tend to aggregate. Thus, there may be relatively few beetles in field, but a large number in one location, and these may be crushed together and concentrated into one or a few bales of hay. Thus, they are hard to detect by standard sampling methods. When alfalfa hay is purchased for horses, it is advisable to acquire early-crop hay, or hay from areas free of high grasshopper populations. Alternatively, inspection of the hay as it is fed to horses can reveal the presence or absence of beetles.

Potato Leafhopper, *Empoasca fabae* (Harris) (Hemiptera: Cicadellidae)

Potato leafhopper is indigenous to eastern North America. Adults are about 3.5 mm long, wedge-shaped, winged, and green. Nymphs are similar in appearance, but are smaller, yellowish-green to fluorescent green, and wingless. Each Spring, potato leafhoppers migrate north from southern states where they overwinter. Timing of the first and subsequent arrivals in the north is heavily dependent on weather patterns. Adults lay eggs in stems and leaf veins; eggs hatch in 6–9 days in mid-summer. Each generation takes approximately 30–35 days to mature, resulting in several generations.

Adults and nymphs both feed on alfalfa with piercing-sucking mouthparts, sucking plant sap and injecting a toxin into the plant. Damage is called "hopperburn," and is a yellow wedge-shape area beginning at the tips of leaves. The leaves may eventually turn entirely yellow or reddish. Plants may become stunted. Leafhoppers cause yield loss, reduced nutritional quality of alfalfa, and reduced plant vigor that results in increased winter-kill and slower regrowth of the crop the next spring.

In some regions of the USA, the potato leafhopper is the worst insect pest of alfalfa, and can cause losses of 80% or more if not controlled. Leafhoppers are not generally a problem in the first crop in an established stand, but as the population increases, all subsequent crops will need to be monitored for infestation. The characteristic hopperburn will not appear until some yield and quality loss has occurred, so it is important to scout for leafhoppers weekly on the second and subsequent crops. Scouting may be concluded 7–10 days prior to harvest.

Potato leafhopper economic thresholds are based on plant height. Scouting is accomplished by sweep net sampling. As an example, following are treatment thresholds recommended for Minnesota, USA.

Average plant height	# adult leafhoppers/ sweep
< 3 inches	0.3
3–7 inches	0.5
8–12 inches	1.0
> 12 inches	2.0

Although the potato leafhopper has natural enemies, they often get left behind when the adults disperse. Thus, a combination of crop monitoring and insecticide suppression is often the principal management strategy. Chemical control of potato leafhopper is effective, but should not be used if harvest is within seven days of harvest. Cutting will kill a large percentage of nymphs, and will force adults out of the field. Cutting is the control of choice if thresholds are reached within seven days of harvest. Additionally, early harvest may be an alternative to insecticides when thresholds are reached late in the year.

Aphids (Hemiptera: Aphididae)

Several aphids are pests of alfalfa, including pea aphid, *Acyrthosiphon pisum* (Harris); blue alfalfa aphid or bluegreen aphid, *Acyrthosiphon kondoi* Shinji, cowpea aphid, *Aphis craccivora* Koch; green peach aphid, *Myzus persicae* Sulzer; and spotted alfalfa aphid, *Therioaphis maculata* Buckton.

All these aphids are small, measuring 3 mm or less. Their color varies, depending on species. They may or may not be winged. In most climates, in early Spring nymphs hatch from eggs that were laid in the fall; these aphids are all female. Females can reproduce without mating when conditions are favorable, and they do so in Spring and Summer. In the Summer, the entire life cycle takes only a few days. Males appear in late Summer, and mate with females to produce eggs capable of overwintering.

Aphids use piercing-sucking mouthparts to remove plant sap, and prefer to feed on young growth. Aphid feeding can result in stunted or wilted plants. The plants may also turn yellow.

Aphids commonly attain high densities in alfalfa, but in most years natural enemies keep aphid populations at levels that are not economically important. Many natural enemies of pea aphids exist, including green lacewing larvae (Neuroptera: Chrysopidae), damsel bugs (Hemiptera: Nabidae), and parasitic wasps

(Hymenoptera, various families), lady beetles (Coleoptera: Coccinellidae), and disease (fungi).

Plant Bugs (Hemiptera: Miridae)

Several species of plant bugs affect alfalfa, but the most common are tarnished plant bug, *Lygus lineolaris* (Palisot de Beauvois), and alfalfa plant bug, *Adelphocoris lineolatus* (Goeze). Adult tarnished plant bugs are brown, winged, and 4–6 mm long; nymphs are green, wingless, and the third and subsequent instars have black spots. Adult alfalfa plant bugs are light green, winged, and 7.5–10 mm long; nymphs are green, wingless, and have red eyes. Tarnished plant bugs overwinter as adults; alfalfa plant bugs overwinter as eggs in plant tissue. During the growing season, the entire life cycle takes 20–50 days, depending on temperature. There are two to five generations per year.

Plant bugs suck sap from plants and inject toxic saliva into the plant. They cause leaves to crinkle, plants to be stunted, and flower buds to abort. They are abundant in all but the earliest portions of the season. Although traditionally considered mostly a seed pest, plant bugs also contribute to forage yield reductions. If bugs are abundant more than seven days prior harvest, chemical control may be warranted.

Grasshoppers (*Melanoplus* spp. and *Phaulacridium* spp.) (Orthoptera: Acrididae)

Everywhere alfalfa is grown, grasshoppers and locusts will feed on the crop. However, they are only casually associated with alfalfa, attacking the crop only when abundant. None feed preferentially on alfalfa. In North America, the principal pests are *Melanoplus* spp., and in Australia *Phaulacridium* spp. is the major grasshopper pest. These economically important grasshoppers overwinter as eggs. Populations disperse into cultivated fields or pastures as their populations build through the season. Most egg laying occurs in late summer and fall in production areas; most species prefer uncultivated, grassy or weedy areas, and lay eggs 1–3 cm below the soil surface.

Grasshoppers are generally considered a minor pest except during periods of great abundance, and then they can do great damage. An exception is Australia, where wingless grasshopper has become an increasingly severe pest of alfalfa. Damage has increased in Australia due to widespread cultivation of alfalfa, which is more suitable than grasses for nymphal growth and survival. Grasshopper nymphs and adults damage alfalfa by chewing on leaves from the margin inward in an irregular pattern. Attacks are often on new growth, but will occur on any stage. The margins of fields are most likely to be damaged.

In North America, grasshopper infestations are more severe in warm and dry years. Warm, dry weather immediately following egg hatch favors survival of nymphs, because nymphal growth rates and survival are lower in cool, wet weather. Long, warm autumns prolong the egg-laying season, and result in larger populations in the next growing season. It can take 3–5 years for populations to build to economically important levels. In Australia, drought also is implicated, but mermithid nematodes are a critical element in grasshopper biology. Absence of rainfall, and clearing of drier, higher elevation pasture impedes the ability of the nematodes to parasitize the grasshoppers.

Grasshoppers are naturally suppressed by numerous natural enemies, but when weather conditions favor the grasshoppers their populations increase quickly. The natural enemy population increases as their food supply becomes more available, but the lag in natural enemy abundance can result in crop damage by the grasshoppers. Weedy fence rows, irrigation ditches, and fallow fields are important sources of grasshoppers. Weed populations should be managed, which may require tillage or burning to make these habitats less productive for grasshoppers.

Cutworms, Armyworms and Budworms (Lepidoptera: Noctuidae)

The caterpillars of several moths can become abundant enough to cause significant loss to alfalfa. Among these are the armyworms *Mythimna* spp., *Persectania* spp., and *Pseudaletia unipuncta* Haworth; variegated cutworm, *Peridroma saucia* (Hübner); army cutworm, *Euxoa auxiliaris* (Grote); granulate cutworm, *Agrotis subterranea* (Fabricius); beet armyworm, *Spodoptera exigua* (Hübner); budworm, *Helicoverpa punctigera* (Wallengren), and many others. The important species vary among regions, though they are similar ecologically.

The larvae of cutworms, armyworms, and budworms range in color from greenish-yellow to brownish-black. Larvae are 2–5 cm long at maturity. The wings of the adults vary from tan to dark brown with mottling or stripes. Pupae are 1–3 cm long and are reddish-brown to black in color. There are one to six generations per year. Larvae overwinter in the larval or pupal stage, depending on species.

Larvae feed on stems and leaves of plants, and can limit regrowth after harvest. Larvae will also cut the stems of seedlings. Their occurrence as economic pests is sporadic. Although these insects have many natural enemies, when they are abundant insecticides are the preferred approach to population reduction.

Lucerne Flea, *Sminthurus viridis* (Collembola)

Sminthurus viridis, the lucerne flea or clover springtail, is an insect relative (hexapod) belonging to the order Collembola (the springtails). It is bright green with a roughly spherical body and may swarms in large numbers on living plants, including alfalfa or lucerne, thus the first part of the common name. The second part of the common name was given for its jumping ability and its minute size, not because it is a flea or related to fleas. This species has a patchy distribution in Europe and North Africa, and has been accidentally introduced to Australia, where it is most injurious. It also affects lupine flowers, lentils, beans, and field peas. Immature lucerne fleas consume small patches of foliage, whereas adults consume the entire leaf except for the veins. Early season spraying of insecticide is the most common recommendation to curb their damage.

Mites (Acari)

Mites generally are not major pests of alfalfa, but under arid conditions or along the margins of fields they can be quite damaging. The most important are clover mites, *Bryobia* spp. (Acari: Tetranychidae), and redlegged earth mite, *Halotydeus destructor* Tucker (Acari: Penthaleidae), in Australia, and twospotted spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae) in North America. They rupture the cells of leaf tissue, imparting a silver or yellow appearance, and reducing yield.

Pest Management in Alfalfa

Alfalfa is an excellent crop for the practice of modern pest management tactics because (i) it is quite tolerant of damage; cosmetic injury is not important; (ii) it is a perennial crop, providing harborage throughout the year for an immense assemblage of insects, including predators and parasitoids; (iii) it is an important crop, so extensive research on the pests have been conducted; (iv) it is amenable to various cultural manipulations, and produces multiple crops over a large portion of the year; and (v) it is a favorite crop for rotations, so there is ample opportunity to integrate its culture with the culture of other crops.

The principal tactics used for alfalfa production include scouting and use of an economic threshold for decision making, natural and classical biological control, cultural control, and chemical control. The economic threshold varies among insect species, geographic locations, crop management practices and economic conditions, but most locations have established such benchmarks for initiating chemical control. A large number of insecticides are registered for this crop, so growers have ample opportunity to select products according to their need and budget. A modest level of host plant resistance apparently exists in alfalfa, and although resistance is effective mostly against aphids, there is also some success with alfalfa weevil and leaf hoppers.

A large number of beneficial arthropods have been moved around the world in an effort to attain biological suppression of invading alfalfa-feeding insects. In some cases this has met with success. For example, alfalfa blotch leafminer, *Agromyza frontella* (Diptera: Agromyzidae), was considered a serious pest when it first invaded the eastern USA, but following release of wasp parasitoids it fell to minor pest status. Similarly, the status of spotted alfalfa aphid, pea aphid and blue alfalfa aphid was affected by importation of beneficial insects. A native entomopathogenic fungus, *Zoophthora phytonomi*, has adapted to the invasive alfalfa weevil and sometimes provides good suppression. Pea aphid is affected by the fungus *Erynia neoaphidis* under favorable weather conditions. Generalist predators such as lacewings, lady bird beetles, nabids, soft-winged flower beetles, big-eyed bugs, and minute pirate bugs are often active in alfalfa, and provide good suppression of aphids, thrips, and also consume eggs and young larvae of caterpillars.

Cultural manipulations are the most important tactics for management of alfalfa pests. In particular, early harvesting can provide acceptable or even nearly complete control of alfalfa weevil, alfalfa blotch leafminer, several caterpillars, aphids, and leaf hoppers because when the crop is cut the insects are exposed to lethal levels of heat and dryness, or the environment becomes so unsuitable that the insects move elsewhere. Crop rotation is most important for root feeding pests, many of which take several years to develop damaging populations. Strip cropping is commonly recommended because the uncut areas retain populations of natural enemies, allowing the beneficial insect to move into newly harvested alfalfa as it regrows and becomes infested with pests. Farmers rarely embrace this approach, however, opting for operational efficiency over economic pest control.

References

University of California (1981) Integrated pest management for alfalfa hay. Publication #3312, 98 pages

Summers CG (1998) Integrated pest management in forage alfalfa. Integr Pest Manage Rev 3:127–154

Alfalfa Weevil, *Hypera postica* (Gyllenhal) (Coleoptera: Curculionidae)

An important defoliator of alfalfa (lucerne).

► Alfalfa (Lucerne) Pests and their Management

Alga (pl., Algae)

An aquatic non vascular plant, often very small in size. Algae can reach pest status when weather and nutrient levels favor its growth, and pesticides may be needed to suppress it.

Alien

An organism that is native elsewhere. These are also referred to as exotic or foreign.

► Invasive Species

Alienicolae

In heteroecious aphids, viviparous parthenogenetic females developing on herbaceous (secondary) host plants.

► Aphids

Alimentary Canal and Digestion

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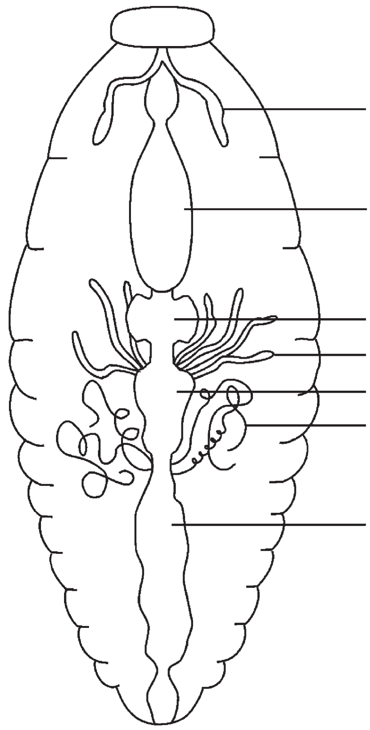
Insects feed upon many different kinds of food, including paper, wood, plant phloem and xylem sap, plant leaves, roots and stems, animal tissues, hair, wool, and vertebrate blood. The alimentary canal (often simply called the gut in much of the literature) evolved to accommodate such diverse foods in a variety of morphological and physiological ways. Thus, there is no "typical" insect alimentary canal just as there is no typical insect. Nevertheless, there are similarities in the structure of the alimentary canal in all insects and nearly all must digest some of the same complex molecules, such as proteins, lipids, and carbohydrates.

In every insect alimentary canal three regions can be identified morphologically and physiologically: the foregut or stomadeum, the midgut or mesenteron, and the hindgut or proctodeum (Fig. 33). One or more of these regions may be greatly reduced in size, or expanded in size, depending upon the feeding behavior of the insect. A cuticular layer, the intima, attached to the epithelial cells, lines the fore- and hindgut regions. The old intima is partially digested and the residue sloughed off into the gut and excreted at each molt, and a new intima is secreted. The midgut does not have an attached cuticular lining, but may have a non-attached peritrophic membrane that separates the food enclosed within from the delicate surface of the midgut cells. If a peritrophic membrane is present, it is often secreted several times each day.



Alimentary Canal and Digestion, Figure 33 A generalized drawing of the alimentary canal in a cockroach to show the major divisions of the canal. Many variations occur in the overall structure of the alimentary canal in insects, and this is not intended to suggest that the cockroach alimentary canal is typical of insects.

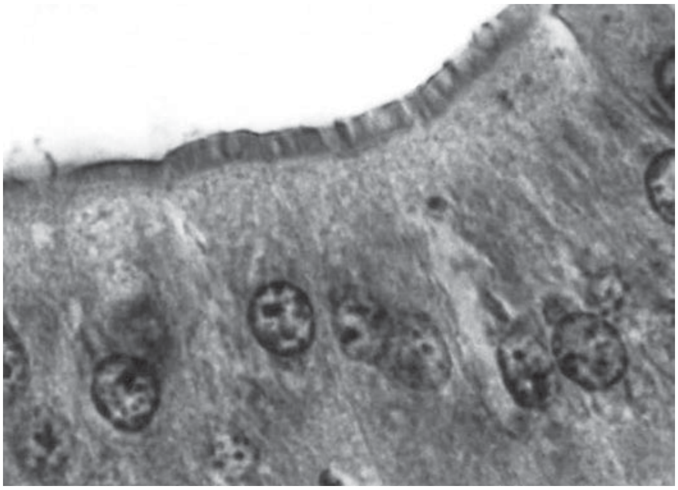
The Foregut

The buccal cavity (mouth), pharynx, esophagus, crop, proventriculus and attached salivary glands comprise the foregut. Secretions from the salivary glands attached near the mouth are swallowed with the food, lubricate the food, and may begin some carbohydrate digestion. In some insects the crop is not a noticeably modified part of the foregut, but often the crop comes off the foregut as a diverticulum. In other insects it is an enlarged portion of the foregut. In opportunistic and possibly irregular feeders such as praying mantids, the crop composes more than half of the alimentary canal, apparently an evolutionary development to store a large amount of food when available and tide the mantid over periods when prey is scarce. Some insects (for example, many orthopterans) regurgitate enzymes from the midgut into the crop, and these enzymes, along with salivary secretions, digest food in the crop. The digested food components still enter the midgut to be absorbed, and there is no evidence that the crop ever secretes enzymes itself. The cuticular intima creates a barrier even against the absorption of water from the crop. The proventriculus controls the entry of food into the midgut in liquid feeders, but in many insects it is modified into a grinding apparatus with hard, sclerotized ridges and spines, and heavy musculature for breaking and tearing the food into smaller particles.

The Midgut

The midgut in most, but not all, insects is the main site for digestion, absorption, and secretion of digestive enzymes. The epithelium is a single layer of cells, but several types of cells occur in some insects. The most common cells are tall, relatively narrow ones called columnar or primary cells by various authors. They have extensive microscopic microvilli on the apical or lumen surface (Fig. 34) and extensive invaginations of the basal cell membrane, features that greatly increase the surface area on both sides of the cell over which secretion and absorption occur. The columnar cells are the primary cells that secrete digestive enzymes and absorb digested products. In all insects that feed as adults and live for days or weeks, there are small regenerative cells distributed at the base of the columnar cells, or sometimes clustered together in nidi (nests). The regenerative cells grow into mature epithelial cells to replace cells worn out or those that disintegrate to release digestive enzymes. Midgut cells may be completely replaced every few days in insects that live longer lives. Gastric caeca, small finger or sac-like diverticula from the midgut, often arise at or near the origin of the midgut, but may be located at various points along the midgut. The caeca appear to secrete digestive enzymes and may be important in absorption of digested products.

The midgut does not have an attached cuticular lining on the surface of the cells, but midgut cells in the majority of insects secrete a thin membrane composed of chitin and protein, the peritrophic membrane, that surrounds the food and shields the delicate microvilli of the midgut cells from contact with potentially rough and abrasive food particles. Although the peritrophic membrane is thin, varying from 0.13 μm to about 0.4 μm thick, it also is thought to make it more difficult for viruses, fungi, bacteria, and protozoans to get to the surface of the midgut cells where they might be able to enter the cells and create an infection. Some insects produce several peritrophic membranes per day, each encasing the one before it, perhaps increasing protection from random breaks or punctures by larger food particles, and thus affording more protection for the midgut



Alimentary Canal and Digestion, Figure 34 **A brush border of microvilli on the lumen surface of midgut cells in a mole cricket.**

cells from possible fungi, parasites, viruses, and bacteria ingested with the food. A peritrophic membrane occurs in living representatives of some of the earliest insects to evolve, and it is believed to have evolved very early in a generalist scavenger feeder in which protection of midgut microvillar surfaces from food particles, sand, or other hard substances coincidentally ingested was likely to be important. A peritrophic membrane is present in many insects that do not feed upon rough or solid food, such as some blood feeders (but not all blood feeders), and in adult lepidopterans that take flower and plant nectars. Although the peritrophic membrane is not present in all groups of insects, like other gut features, it has been conserved over long evolutionary time, lending support to views that it has multiple functions, especially protection from disease invaders and may even have properties that could bind toxicants and limit their access to cells.

Absorption of digested food substances has not been studied in most insects, but one mechanism has been partially elucidated for absorption of amino acids derived from protein digestion in larvae of Lepidoptera. Interspersed among the tall columnar cells lining the midgut in larvae of Lepidoptera (and some other groups of insects as well) are cells shaped much like a goblet and called, appropriately enough, goblet cells. The apical cell membrane of the goblet cavity has metabolic machinery that uses energy derived from splitting ATP to push or pump protons (H^+) into the goblet cavity. A different set of machinery in the goblet cell membrane, an antiporter mechanism, reabsorbs the protons and simultaneously secretes potassium ions into the goblet cavity. The net result of the secretion of potassium ions is that a strongly alkaline midgut (a midgut pH as high as pH 8 to about 11) is produced, and a high voltage (up to 240 mV in some reports) is created between the gut lumen (positive) and the interior of cells lining the gut. The voltage created by the pump enables an absorptive mechanism in membranes of columnar cells to reabsorb K^+ and amino acids from protein digestion. Thus, potassium ions are recycled between the epithelium cells and the gut lumen and seem to play a major role in amino acid absorption. The high midgut pH may provide plant feeding insects some protection against tannins that are common in the food plants of phytophagous insects. Tannins can complex with an insect's own enzymes and proteins in the food, and may result in reduced digestion and absorption. Many details and the precise metabolic components in the cell membrane that support and enable these secretory and absorptive mechanisms remain to be elucidated, but what is already known emphasizes the complexity of insect digestive functions.

The Hindgut

The hindgut is not only a posterior extension of the alimentary canal, but it also plays a major role in excretion through secretion of some substance into the lumen, and reabsorption of useful substances such as ions, water and some nutrients from the Malpighian tubule effluent. The Malpighian tubules typically arise at the origin of the hindgut (but exceptions do occur) and pass relatively large volumes of an ultrafiltrate of hemolymph components minus proteins into the beginning of the hindgut. The cuticular lining on hindgut cells is thinner and has larger pores than the lining in the foregut, permitting reabsorption of water, some ions, and useful metabolites that are returned to the hemolymph. In most terrestrial insects, water conservation is vital to life, and the hindgut must conserve the water that the Malpighian tubules flush into the hindgut. Waste products such as undigested food material (cellulose, for example, which most plant-feeding insects cannot digest and use), uric acid, and other allelochemicals picked up from the food are concentrated in the rectum and eventually excreted. The hindgut secretes some molecules into the lumen for excretion. Experimental evidence indicates that secretion and selective reabsorption helps regulate pH of the hemolymph in some insects. Specialized cells, the rectal papillae and rectal pad cells, in the rectum of many insects have characteristic ultrastructure and physiological mechanisms typical of highly reabsorptive cells. Water conservation by the rectum results in the relatively dry frass or fecal pellets characteristic of many terrestrial insects.

The highest degree of specialization in the hindgut occurs in those insects that digest cellulose, such as termites. In termites, the hindgut is usually divided into several chambers harboring either bacteria or protozoa that secrete all or part of the cocktail of enzymes needed to digest cellulose. Glucose, liberated from cellulose digestion, may be fermented by the resident microorganisms, with the end products being short chain fatty acids (principally acetic acid) that can be absorbed by the termite and used as an energy source. Some termites release methane, a greenhouse gas, from the metabolic activities of their microorganisms, but whether this is a significant natural source of methane is a topic of debate by various scientists.

Digestive Enzyme Secretion

Midgut cells secrete and release digestive enzymes in several ways. They may enclose digestive enzymes in small vesicles surrounded by a membrane and then release the enzymes into the alimentary canal by fusing the vesicle membrane with the cell membrane. In some insects, parts of the cell (some of the microvilli) or the entire midgut cell may disintegrate and release enzymes into the gut lumen. Of course, when the entire cell breaks down, the cell must be repaired or replaced. Replacement occurs through the growth of the regenerative cells.

Extraoral digestion (digestion outside the insect body) occurs in some insects, including seed feeders and some predatory insects. By injecting enzymes from the salivary glands and midgut into the food source (animal or plant material) and then sucking back the liquefied digestion products, insects can utilize very high percentages of the nutrient value of the food source. Some insects reflux enzyme secretions and partially digested products by repeatedly sucking up and reinjecting the liquefied juices into the food. Refluxing mixes the secretions and fluids and extends the effective life of the digestive enzymes, and is particularly effective when the food contains a limiting boundary, such as the shell of a seed or the cuticle of an insect that acts as a container for the liquefying body contents.

Carbohydrate Digestion

Starch and sucrose are the typical carbohydrates that insects digest from plant food, and glycogen and various sugars are present in animal tissue eaten by carnivorous insects. Cellulose, the major complex polysaccharide present in plant tissue, cannot be digested by most insects. Carbohydrate digestion begins with the action of α-amylase, an enzyme present in the salivary gland secretions of many insects. Amylase works best at slightly acid pH, and hydrolyzes interior glucosidic linkages of starch and glycogen, resulting in a mixture of shorter dextrins. In the midgut *α* -glucosidase and oligo-1, 6-glucosidase (isomaltase) digest smaller dextrins, releasing glucose. Many insects also have one or more *α*- or *β*-glycosidases that digest a broad range of small carbohydrates, such as maltose, sucrose, trehalose, melezitose, raffinose, stachyose, melibiose, raffinose, and stachyose. Some insects can secrete trehalase in the gut to digest trehalose, the principal blood sugar typically in high concentration in insects. *β*-glucosidase, *β*-galactosidase, and *β*-fructofuranosidase act upon various substrates to release simple sugars in the gut. An insect usually has only a few of these carbohydrate digesting enzymes, depending upon the food it eats. For example, *Apis mellifera* honeybees have several *α* -glucosidases or sucrases that act rapidly upon sucrose, usually the principal carbohydrate in the nectar taken by honeybees. They utilize the resulting glucose and fructose for an immediate energy source and for making honey. Termites, some beetles, a few cockroaches, and woodwasps in the family Siricidae digest cellulose with aid (usually) from fungi, bacteria, or protozoa, which produce some or all of the complement of three enzymes necessary for cellulose digestion.

Lipid Digestion

The major storage forms of lipids (fats) in both plants and insects are triacylglycerols, esters of fatty acids with glycerol. Midgut cells, and in some cases symbionts, secrete lipases, which are enzymes that hydrolyze triacylglycerols and release fatty acids and glycerol. Amino acids, proteins, and fatty acylamino complexes act as emulsifiers in the midgut of some insects facilitating the digestion of fats. The glycocalyx layer, a viscous protein and carbohydrate complex that often lies on the surface of the microvilli, probably aid in emulsifying fats and in promoting contact between lipases and triacylglycerols. Fatty acids released from triacylglycerols are resynthesized into the insect's own triacylglycerols and stored in fat body cells. Immature insects typically store relatively large amounts of triacylglycerols, and use some of the released fatty acids during pupation and for egg development. Some insects, for example Orthoptera, Lepidoptera, and some aphids, mobilized fatty acids rapidly enough to use fatty acid metabolism to support flight, but other groups such as Diptera and Hymenoptera cannot release fatty acids from the fat body and transport them to the flight muscles rapidly, and so they only use carbohydrates for flight energy. They still can use lipids during pupation, and for other metabolic processes that occur more slowly.

Protein Digestion

All animals must have a pool of amino acids available for synthesis into proteins, and for repair of tissues and organs. Most animals, including insects, get their amino acids from digestion of dietary proteins. Within insects as a group, there are several different types of protein digesting enzymes, some of which act at acid pH, others at slightly alkaline pH, and some at highly alkaline pH. Usually a particular species will have several different proteinases, but no insect is known to have both an acid-effective proteinase and an alkaline-effective proteinase. The pH of the alimentary canal is important to the action of any digestive enzyme, and no insect is known to have an alimentary canal that is strongly acid in one part and strongly alkaline in another part.

Proteinases are classified broadly as serine, cysteine, aspartic acid, and metallo-proteinases depending upon the amino acid or metal at the active site of the enzyme. Trypsin and chymotrypsin are two endoproteinases with alkaline pH optima (about pH 8) that are common in many insects and which attack large proteins internally at the linkage between certain amino acid, thus breaking the protein into smaller polypeptides. Most insects appear to have several types of exopeptidases that remove the terminal amino acid from a protein or peptide chain. Thus, through the concerted action of both types of digestive enzymes, a protein can be completely digested with release of its component amino acids. Cysteine- and aspartic acid-proteinases have mildly acid pH optima, and are called cathepsins by some authors. All members of a taxonomic group may not have the same type of proteinases. Many beetles have cysteine proteinases most active at slightly acid pH, while some scarabeid beetles secrete serine-proteinases that act at the high midgut pH typical of these insects, and they have no detectable cysteine-proteinases. Lepidoptera typically secrete trypsin-like enzymes active at alkaline pH.

One defense mechanism that has evolved against herbivory in many plants is the presence of proteinase inhibitors, some of which inhibit serine proteinases while others act upon cysteine proteinases. Experimentally, it has been shown that some insects secrete multiple trypsin enzymes (isozymes of trypsin) and others just secrete larger amounts of the same few isozymes after consuming a trypsin inhibitor. This counter action by the insect probably allows some protein digestion to escape ingested inhibitors, but transgenic plants designed to have proteinase inhibitors have been tested and proven to have adverse effects upon the growth of some insects.

Absorption of Digested Products

Few details are known about the absorption of digested products by insects. In many vertebrates, glucose absorption from the alimentary canal requires an active mechanism involving ATP to supply the energy. In those insect that have been studied, glucose from digestion of carbohydrates is rapidly absorbed passively by a process known as facilitated diffusion, and involvement of ATP is not necessary. Fat body cells on the hemolymph side of the gut rapidly synthesize absorbed glucose into the disaccharide trehalose, keeping the hemolymph concentration of glucose low in most insects. Consequently, even low concentrations of glucose in the gut have a favorable diffusion pathway to the hemolymph and continue to be absorbed passively. In larvae of a few lepidopterans that have been carefully studied (*Manduca sexta*, *Philosamia cynthia*, *Bombyx mori*), amino acids are actively absorbed by transport proteins in the apical membranes of midgut columnar cells. Energy for absorption comes from the high K^+ concentration in the gut lumen and high transepithelial potential created by the proton-ATPase pump active in midgut goblet cells. The transport proteins in these membranes show strong specificity for particular amino acids, and transport systems for at least six different amino acids are known, and transport systems for other amino acids probably will be discovered. In the Colorado potato beetle, *Leptinotarsa decemlineata*, transport proteins for leucine and tyrosine have been demonstrated in midgut tissue.

Gut pH

The pH of the alimentary canal is highly variable in different species of insects. The pH of a gut segment influences the action of enzymes secreted into or carried with the food into the gut, influences solubility and toxicity of toxins and plant allelochemicals, and may alter the population of gut microorganisms. In most insects, the crop has little or no presence of buffering agents and tends to be slightly acidic, a factor favoring carbohydrate digesting enzymes. Larvae of Lepidoptera and Trichoptera tend to have a very high midgut pH, varying from about 8 to 10, promoted by goblet cells that secrete potassium and bicarbonate into the lumen of the midgut. They have protein digesting enzymes that are favored by the high pH, and the high pH may afford some protection from tannins and other allelochemicals that they ingest with their plant food.

Illustrative Examples of Diversity in Food, Form and Function of the Alimentary Canal

The following examples are not intended to be a comprehensive review of foods, and alimentary canal structure and physiology, but will merely highlight interesting diversity.

Opportunistic feeders may have evolved modifications to capture and store food when available, and thus survive lean periods when food is not available. For example, the foregut of the praying mantis, *Tenodora sinensis*, is long and wide, and occupies nearly the entire length of the body, apparently an adaptation for storage of prey when it can be captured. The midgut, eight gastric caeca, and hindgut are compressed into the last three abdominal segments. Probably much of the digestion occurs in the posterior part of the crop with enzymes passed forward from the small midgut.

Considering the universal presence of cellulose in plant tissues, relatively few insects evolved the ability to use cellulose as a source of nutrients.

Termites, some beetles, a few hymenopterans, and a few cockroaches do use cellulose as a carbohydrate source. The hindgut of termites is highly specialized for housing gut microbiota that provide the cellulase enzymes needed to digest cellulose, although there is some evidence that certain termites may be able to produce some or all of the several enzymes necessary to completely digest cellulose. Gut variation exists among the castes in a colony; for example, soldiers in the family Rhinotermitidae are fed liquid food by the worker caste, and do not have to digest cellulose so they have reduced gut structure. The workers are responsible for colony construction and nutrition, and they have highly evolved hindgut chambers to hold various types of microbiota. Termites hatch without their gut microbiota, and lose most of their gut symbionts at each molt, but they become reinfested by feeding upon fluid and excreta from older nymphs. Termites in the family Termitidae have symbiotic bacteria in the hindgut, while termites in some other families have flagellate protozoans as well as bacteria in a multi-compartmented hindgut, and they get some or all of their cellulase(s) from their symbionts. Some termites, the Macrotermitinae, cultivate fungus gardens in their underground nests and get their cellulases from the conidiophores of the fungus. Symbionts in the hindgut of some termites can capture atmospheric nitrogen in an organic form, which is probably quite important to many termites because their diet of wood is relatively low in proteins. Some fungus-growing termites convert some of the protons (H^+) and carbon dioxide from the initial fermentation of glucose into methane (CH_4), and some investigators have suggested that termites are a significant environmental source of methane, a greenhouse gas.

Larvae of the woodwasp (Hymenoptera, Symphyta, Siricidae, genus *Sirex*) acquire cellulase and xylanase from fungi ingested with the wood on which they feed. Larvae of cerambycid beetles and of some other beetles feed upon wood in down or dying trees; they generally have long life cycles because wood is so nutrient poor, especially protein poor. Fungi growing in the dead wood and ingested by the larvae may provide additional nutrients and/or enzymes for digesting the wood.

Hemiptera take xylem or phloem sap, both of which are poor in amino acids and protein, but usually rich in sucrose (150 to more than 700 mM). They typically excrete a copious, dilute fluid, and in some, such as aphids, the fluid contains so much sugar that it is called honeydew. They have to ingest large volumes of fluid to get the amino acids, and then they have to get rid of the excess water and sucrose. A characteristic evolutionary feature of the gut in Hemiptera is the filter chamber in which a loop of the hindgut is in direct contact with part of the foregut and a great deal of the ingested fluid diffuses directly into the hindgut from the foregut without passing through the midgut. This, of course, causes loss of some amino acids and other components that may be needed, but water and sucrose, both of which are in excess of needs, are the major components lost. The filter chamber is able to concentrate gut fluid up to 10-fold in some xylem feeders (Cicadoidea and Cercopoidea), but only about 2.5-fold in members of the Cicadelloidea, which are phloem feeders. Xylem feeders probably need to concentrate xylem fluids more because of the lower amino acid content (3–10 mM amino acids per liter in xylem fluid) than do phloem feeders (15–65 mM amino acids per liter in phloem fluid).

Pre-oral digestion with enzymes secreted into the prey occurs in many of the predacious beetles. Seed feeders also employ pre-oral digestion by injecting salivary secretions and possibly regurgitated midgut enzymes into the seed, allowing these to liquefy part of the seed, and then sucking the nutrients and enzymes back. Pre-oral digesters often reflux the liquefied contents by repeatedly imbibing and then reinjecting the mixture of enzymes and digested nutrients into the seed. Refluxing likely conserves enzymes longer, gives them more opportunity to function, and allows the insects to use more of their potential food.

In honeybees and some other related hymenopterans, the midgut is closed off from the hindgut by a plug of cellular tissue during larval development, and any food that cannot be digested and absorbed into the body must remain in the midgut. Just before pupation the connection between midgut and hindgut is opened, and accumulated undigested residue, such as the shells of pollen grains, is excreted into the cell. Adult honeybees clean the cell and the larva pupates inside the cell.

Nectar taken by male and female mosquitoes is stored in a large, sac-like crop that is a diverticulum from the foregut, but blood meals taken by the females are passed directly into the midgut for the beginning of digestion. The midgut is differentiated functionally into an anterior and a posterior region. The anterior part secretes carbohydrate digesting enzymes, and nectar components are digested as fluid from the crop and is passed into the anterior midgut. This arrangement keeps possible trypsin inhibitors that may be present in nectar away from the site of protein digestion, which occurs in the posterior midgut. Simple sugars resulting from digestion, or those already in the nectar, are absorbed in the anterior midgut. The posterior midgut cells secrete trypsin-like enzymes and protein (blood) digestion and absorption occur in the posterior midgut. The posterior midgut cells, more so than anterior midgut cells, have extensive microvilli and basal infoldings characteristic of secretion and absorptive processes. The midgut cells in this region get stretched by the large volume of blood that a mosquito takes if it is allowed to feed to repletion. Consequently, the cells have several types of connecting structures (desmosomes) between cells to help hold them together and prevent excessive leaking of materials in or out between cells while they are stretched.

Larvae of Lepidoptera have a very short foregut, a large, long, relatively straight midgut, and a short hindgut. There is no storage or digestion in the short, nearly vestigial foregut. Nearly all lepidopterous larvae are phytophagous feeders, and the gut modifications appear to be an adaptation to pass food quickly into the long midgut so that digestion can begin. Feeding is nearly continuous when plenty of food is available, and larvae may ingest more than their body weight in food daily. Food moves rapidly through the relatively straight gut and frass droppings are frequent in phytophagous caterpillars. Because the larval and adult forms of Lepidoptera have very different life histories and food habits, the adult gut is quite different from that of the larva. Many adult Lepidoptera feed only upon nectar, which is stored in the crop and slowly released into the midgut for digestion to simple sugars. Some adult Lepidoptera have vestigial mouthparts and do not feed at all; they survive and (females) produce eggs at the expense of body substance, and they generally live only a few days. An unusual food utilized by *Tineola bisselliella* larvae (clothes moth) is wool, and larvae have a very strong reducing action in the midgut that breaks disulfide bonds between adjacent loops of the proteins, causing the wool proteins to lose their three-dimensional shape and unfold. This allows more access for protein digesting enzymes.

References

Chapman RF (1998) The insects: structure and function. Cambridge University Press, Cambridge, UK, 770 pp

Klowden MJ (2002) Physiological systems in insects. Academic Press, New York, NY, 415 pp

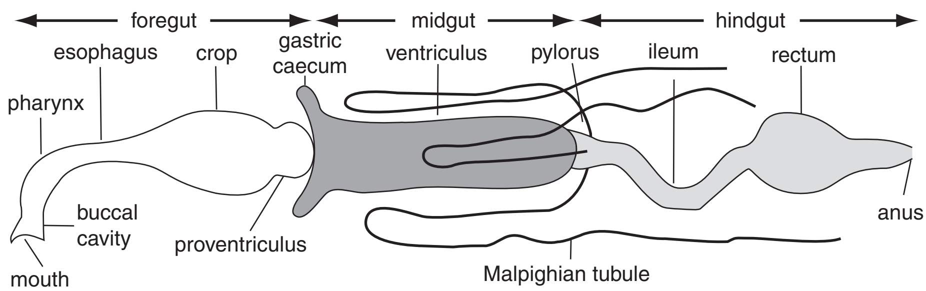
Nation JL (2002) Insect physiology and biochemistry. CRC Press, Boca Raton, FL, 485 pp

Alimentary System

The alimentary system (canal) is a system of tubular structures that takes in food at the mouth, stores the food, fosters digestion and absorption of nutrients, and allows excretion of waste materials from the rectum. It is conveniently divided into the foregut, midgut, and hindgut (Fig. 35).

► Alimentary Canal and Digestion

► Foregut



Alimentary System , Figure 35 Generalized insect alimentary system (adapted from Chapman, The insects: structure and function).

► Midgut
► Hindgut

Alinotum

The notal plate of the meso- or metathorax in a pterygote insect.
► Thorax of Hexapods

Alitrunk

The portion of the thorax to which the wings are attached.
► Thorax of Hexapods

Allatostatins

These are neuropeptides from neural and non-neural tissues that affect the corpora allata, inhibiting production of juvenile hormone. They likely have other effects as well, but they are still relatively unknown (contrast with allatotropins).
► Juvenile Hormone

Allatotropins

These are neuropeptides from neural and non-neural tissues that stimulate the corpora allata, resulting in synthesis of juvenile hormone. They likely have other effects as well, but they are still relatively unknown (contrast with allatostatins).
► Juvenile Hormone

Alleculidae

A family of beetles (order Coleoptera). They commonly are known as comb-clawed beetles.
► Beetles

Allegheny Mound Ant, *Formica exsectoides* (Hymenoptera: Formicidae)

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The Allegheny mound ant, *Formica exsectoides* Forel, is a common mound-building ant of the northeastern and central United States. Workers are approximately 3/8 inch long (1 cm) with a reddish-tan head and thorax, and a dark brown abdomen. In suitable habitat, *F. exsectoides* will form dense populations, their presence easily discernible due to conspicuous mound-type nests which can be as large as 15 feet (4.6 m) in diameter and 4 feet (1.2 m) high. At one site near Altoona, Pennsylvania, researchers counted more than 30 large mounds per acre. Despite the conspicuous nature of *F. exsectoides* nests and its wide geographic range, relatively few papers concerning this species have been published since H.C. McCook's first paper in 1877.

Nests tend to be clustered in the habitat (Fig. 36). Nests in each cluster often will share foraging trails and resources. Although there is little aggression between workers from different nests or nest clusters, the workers still show fidelity to a home nest. Nests of *F. exsectoides* have multiple queens (polygynous) although there is tremendous variation in the number of queens per mound. Over 1,400 queens were reported in one mound, but that is probably an anomaly. Most mounds probably contain fewer than 20 queens. Due to the large number of queens, the reproductive output of a nest can be prodigious resulting in large numbers of workers in a colony. More than 250,000 workers have been found in some nests. Reproductive forms (alates) are present in the nests from mid-summer until early fall. Activity of the ants is related to ambient conditions but, in general, workers are active from late March until November. *Formica exsectoides* are generalist predators, scavengers and collect honeydew from symbiotic hemipterans.

Habitat has a significant effect on physical characteristics of *F. exsectoides* nests. Forest nests tend to be significantly larger in height, width, length, nest footprint and volume than nests in meadows. In general, the nests are round, but it is not uncommon to find elongated nests that are orientated to the sun. The shape of a nest and its orientation may help the ants to maintain a relatively constant internal temperature and relative humidity.

References

Andrews EA (1925) Growth of ant mounds. Psyche 32:75–87

Andrews EA (1927) Ant mounds as to temperature and sunshine. J Morphol Physiol 44:1–20

Bristow CM, Cappaert D, Campbell NJ, Heise A (1992) Nest structure and colony cycle of the Allegheny mound ant, *Formica exsectoides*. Forel (Hymenoptera: Formicidae) Insectes Sociaux 39:385–402

Bristow CM, Yanity E (1999) Seasonal response of workers of the Allegheny mound ant, *Formica exsectoides*. (Hymenoptera: Formicidae) to artificial honeydews of varying nutritional content. Great Lakes Entomol 32:15–27

Allegheny Mound Ant, *Formica Exsectoides* (Hymenoptera: Formicidae), Figure 36 Three large nest mounds of *Formica exsectoides* in a Pennsylvania forest clearing.

McCook HC (1877) Mound-making ants of the Alleghenies, their architecture and habits. Trans Entomol Soc Am 6:253–296
Rowe HC, Bristow CM (1999) Sex ratio and sexual dimorphism in *Formica exsectoides,* the Allegheny mound ant (Hymenoptera: Formicidae). Great Lakes Entomol 32:207–218

Allele

One of two or more alternative forms of a gene at a particular locus. If more than two alleles exist, the locus is said to exhibit multiple allelism.

Allelochemic

A non-nutritional chemical produced by one species (often a plant) that affects the growth, health, or behavior of another species (often an herbivore).

► Allelochemicals

Allelochemicals

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For thousands of years insects and plants have been locked in a battle for which survival is the ultimate prize. For insects, plants constitute food sources for growth and development, and in some cases, sites for reproduction. On the other hand, plants attempt to counter insects feeding on their tissues (herbivory) so that their own vigorous growth and development will occur and lead to reproductive success. The consequences of this warfare are great and for humankind the outcomes of these battles may be of major economic significance in terms of the production of various foods. The welfare of various human populations can be threatened if hordes of ravenous insects consume specific crops that are the mainstays of these populations. But plants do not take this "lying down." Over thousands of years, plants have done everything possible to make life miserable for insects. On the other hand, insects have returned the favor many times over. In recent geological time, plants and insects have changed their "spots" (plant-feeding strategies), resulting in an incredible point-counterpoint relationship of these organisms that is characterized by some remarkable developments.

As far as nutrients are concerned, different kinds of plants (species) are fairly similar and can provide an insect herbivore with the basic nutrients required for growth and development. These compounds (chemicals) are called primary compounds because they are required for the insect's growth, development, and reproduction. All insects require these compounds and in theory they should be readily available from a wide variety of plant species. But most species of insects, rather than feeding on many different kinds of plants, limit their plant menu to a relatively small number of plant species (monophagy), most of which are related. Significantly, the limited preferences that insects have for their food plant species are due to non-nutritive compounds that usually vary from one plant group to another. These compounds are not related to the primary compounds identified with growth and development, and it is apparent that these plant-derived compounds (allelochemicals) generally have functions related to other species of organisms. These compounds are obviously not primary compounds but rather secondary compounds (non-nutritive) whose manufacture has been described as secondary metabolism. Indeed, these allelochemicals appear to be responsible for both the associations and non-associations that insects have with specific groups of plant species. In essence, it would be no exaggeration to state that the host-plant preferences of insects really reflect the ability of an insect species to either tolerate, or be repelled by, an allelochemical. Allelochemicals are not mysterious compounds but rather are a very important part of the everyday world, especially in terms of human food preferences. In a sense, the strong food preferences exhibited by insects are not so different from those of humans, with one striking exception. Many insect species are "locked in" to specific food plants, and these insects will reject a foreign plant species and die in the absence of their normal food plant. On the other hand, there is little evidence that human beings will subject themselves to starvation if their favorite foods are not readily available.

A World of Allelochemicals

Fruits and vegetables possess characteristic odors and tastes that create desire (preference) for these foods. Significantly, these tastes and smells are not identified with the primary compounds responsible for plant growth and development, such as sugars, fats, and proteins. Therefore, the plant has invested in producing a variety of chemicals that will not help it grow or reproduce. While an onion may possess a distinctive odor and taste for both insects and humans (not necessarily the same odor and taste for both), this fact hardly justifies the onion spending its energy and resources to produce an onion fragrance. On the other hand, if the taste and odor of onions combine to make this vegetable distasteful and repellent to most plant-feeding insects, then these allelochemicals perform a very vital function. In essence, it is generally believed that these secondary compounds are responsible for protecting plants from herbivores and possibly pathogens as well. A brief examination of some well-characterized allelochemicals offers a means of examining these compounds as agents of defense both as toxins and as repellents.

Oleander, which has a very limited number of herbivores, is extremely toxic because of the presence of allelochemicals that are somewhat related to cholesterol. The odor of the plant probably constitutes an early-warning system that makes potential herbivores aware of the danger of feeding on this plant. The same can be said for the tobacco plant which, like oleander, does not have too many insect herbivores. Leaves of the tobacco plant are quite toxic, but in some South American populations young children become addicted to the nicotine in the leaves before they are ten years old. Nitrogen-containing compounds (alkaloids) produced by opium poppies are powerful repellents for a wide range of insect species, and there is no doubt that compounds such as morphine and heroin, which are powerful human narcotics, were evolved to deter herbivores rather than to function as narcotics for humans.

Alkaloids such as nicotine have been adapted to function as insecticides, and a variety of plant products such as derris, rotenone, ryania, and sabadilla are also used as insecticides in different cultures. In some cases, allelochemicals such as prunasin in cherry leaves cause poisoning in livestock. Not to be outdone, humans have frequently utilized the alkaloid strychnine to murder people. However, it would be a mistake to lose track of the fact that, human abuses notwithstanding, these allelochemicals were evolved as plant protectants long before humans appeared. Obviously, allelochemicals do not provide plants with absolute protection against herbivores. Indeed, probably all plants containing allelochemicals are fed upon by insects, and in many cases these herbivores are only found on a limited number of host plant species. For example, monarch butterfly caterpillars are limited to the milkweed species. Bark beetles limit their attacks to pines and related conifers, developing in environments that are rich in toxic turpentines. These insects have breached the chemical defenses of their hosts, and in so doing, they have "captured" specific kinds of food plants that are either repellent or highly toxic to most other species of insects. Guaranteed these "forbidden fruits," these herbivores should have to share their food resources with very limited numbers of competitors. Barring an ecological disaster does not devastate the populations of their host plant species, this specialization should have much to recommend it. On the other hand, many insect species choose a lifestyle which is characterized by feeding on a variety of unrelated plant species.

Insects like the monarch butterfly and bark beetles that are restricted to a limited number of related plant species are referred to as specialists.

These herbivores have become resistant to the toxic effects of their host plant allelochemicals, and in many cases they appear to be completely immune to the plant toxins they ingest. In the case of monarch caterpillars feeding on milkweeds, it has been demonstrated that these larvae actually grow more rapidly on milkweed plants containing the highest concentration of toxins.

Indeed, allelochemical concentrations may be generally quite high, often averaging 5–10% of the dry weight of the plant. By contrast, plant-feeding generalists feed on a wide range of plant species, often unrelated. However, in general, these herbivores select plant species in which the concentrations of allelochemicals are not too high, enabling them to process low levels of a wide variety of plant toxins.

The immunity of specialists to the toxic effects of the allelochemicals in their diets demonstrates that for these insects these compounds can no longer be considered poisons. Surprisingly, the basis for this important allelochemical resistance, which has great economic significance, was only understood about thirty years ago.

Sequestration and its Consequences

Insects such as the monarch butterfly store compounds in their tissues that render them unpalatable to predators. These compounds, the cardenolides, were ingested by the larvae from their milkweed food plants, and retained in their bodies into the adult stage. The storage of these milkweed compounds is called sequestration, and constitutes a widespread phenomenon among specialists feeding on allelochemical-rich plants. In a sense, sequestration represents the insect's success in utilizing the plant's chemical defenses for its own purposes. Indeed, sequestration can be regarded as a form of detoxication since potentially toxic compounds are removed from the circulation and stored in the tissues.

Sequestration has been detected in at least seven orders of insects including species of toxic grasshoppers, aphids, lacewings, beetles, wasps, butterflies and moths. In general, these insects are brightly (= warningly) colored, a characteristic described as aposematic. Armed with the toxins from their food plants, large insects such as brilliantly colored grasshoppers move very slowly, as if to advertise their poisonous qualities to the world. Obviously the term toxic is relative, since these insects routinely sequester these allelochemicals during normal feeding. However, since these specialists are physiologically adapted for ingesting these compounds, their ability to tolerate these allelochemicals is really not surprising. On the other hand, non-adapted species (e.g., predators) would certainly encounter toxic reactions if they ingested these toxic plant products.

The fates of allelochemicals, which are usually present in mixtures, are not at all predictable after ingestion by an adapted herbivore. Although many compounds are sequestered immediately after ingestion, others may be metabolized before being stored, or even eliminated after being metabolized. In other cases selected allelochemicals in a mixture may be absorbed and sequestered whereas other compounds in the mixture may be eliminated immediately. An examination of the options for initially processing ingested allelochemicals emphasizes the versatility of specialists in treating the toxic compounds produced by their food plants.

Sequestration of Insect Toxins by Vertebrates: A Significant "Allelochemical" Phenomenon

It has become evident that the allelochemical relationship of insects and plants is paralleled by a similar relationship of amphibians and insects. It is now recognized that the sequestration of ingested toxic insect compounds by vertebrates differs little from this phenomenon in insect herbivores and plants. In essence, a variety of insect toxins is sequestered by amphibians and these compounds have similar protective functions for frogs and insects (see *Allelochemicals as phagostimulants*). Frogs exploit insect allomones (defensive compounds) as if they were animal "allelochemicals," and it seems worthwhile to emphasize this congruency in examining the scope of allelochemistry.

Frogs in the genus *Dendrobates* contain mono-, di-, and tricyclic alkaloids which are clearly of ant origin. The alkaloids, termed pumiliotoxins, appear to be products of ant species in the genera *Brachymyrmex* and *Paretrechina* and constitute the only known dietary source of alkaloids of these frogs, not unlike the specialist insects feeding on narrow plant diets enriched with allelochemicals. The same phenomenon has been described for the myrmicine ant *Myrmicaria melanogaster* which synthesizes ten alkaloids. Some of these alkaloids have previously been identified in a dendrobatid frog and a toad.

Neurotoxic steroidal alkaloids, the batrachotoxins, have been isolated from New Guinea birds in the genera *Pitohui* and *Ifrita*. These compounds are among the most toxic natural substances known, and they are not produced by captive birds, suggesting a dietary source. Recently, the batrachotoxins were identified in beetles in the genus *Chloresine* (Melyridae) which are normally fed on by the bird species. Since the genus *Chloresine* is cosmopolitan, it is the possible source of some of the avian alkaloids found in birds in different areas.

Vertebrate sequestration of alkaloids from insects has only recently been explored. Clearly this chemical storage has a common denominator with sequestration of alkaloids by insects (see *Allelochemicals as pheromonal precursors*) and should be examined as a paradigm of comparative physiology. Clearly, insects are pivotal to both systems, either as food for vertebrates or food for insects, with sequestration the major common feature.

Initial Processing of Allelochemicals by Specialists

Once an adapted insect has ingested an allelochemical, a menu of options is available for processing it. An insect species may utilize a variety of adaptive strategies for processing a single compound that is characteristic of the host plant defense.

Immediate Allelochemical Excretion

Some insects essentially fail to absorb ingested allelochemicals from the gut. These compounds are excreted directly and are concentrated in the feces. A lymantriid moth larva that is a specialist on the coca plant, which is the source of the alkaloid cocaine, rapidly excretes this compound with only traces being found in the blood. However, cocaine may still have defensive value for the larva as part of an oral regurgitate that is externalized when the larva is disturbed.

Three different species of moth larvae that feed on tobacco plants rapidly excrete nicotine, a very toxic and reactive alkaloid. There is no evidence that nicotine is absorbed from the gut of any tobacco feeder, but as is the case for the moth larva excreting cocaine, nicotine in oral or anal exudates constitutes an excellent defensive compound.

Allelochemical Metabolism

Many insect specialists rapidly metabolize ingested allelochemicals which are then sequestered, or in some cases excreted. Nicotine, which is both highly reactive and very toxic, is converted to a non-toxic metabolite called cotinine by both tobacco-feeding insects and those that are not tobacco feeders. Since cotinine has virtually no toxicity to insects, it is probable that its production from nicotine constitutes true detoxication.

Cabbage-feeding insects feed on plants that are rich in sinigrin, a compound that yields a highly toxic mustard oil when metabolized.

Although sinigrin can be sequestered without generating the reactive mustard oil in a variety of cabbage-feeding species, cabbage butterflies (whites) actually break down sinigrin and sequester the highly reactive mustard oil. For these butterflies, the mustard oil is more suitable for storage than sinigrin.

Larvae of the tiger moth *Seirarctia* have evolved a novel strategy for coping with the toxic effects of MAM, a compound derived from cycasin which is a constituent in the cycad leaves upon which they feed. When larvae encounter MAM, they convert it to cycasin which is absorbed through the gut wall before being sequestered. Since the enzyme that produces cycasin or MAM is only found in the gut, once cycasin crosses the gut wall into the blood prior to sequestration there is no chance of MAM being generated from cycasin.

Many species of moths, butterflies, and grasshoppers feed on plant species that produce extremely toxic compounds known as pyrrolizidine alkaloids. These alkaloids, present as mixtures, are frequently sequestered by these specialist insects and, in some cases, metabolized plant compounds are the preferred storage forms. For example, larvae of the tiger moth (*Tyria* species) feed on ragwort and primarily sequester the alkaloid seneciphylline, although this compound is present in the plant as the N-oxide. Conversely, the grasshoppers of the *Zonocerus* species convert the ingested alkaloid monocrotaline to its N-oxide before sequestering the compound.

Insects feeding on milkweed metabolize the toxic cardenolides (steroids) produced by these plants, converting them into compounds that can be readily sequestered. The milkweed bug (*Oncopeltus* species) oxidizes cardenolides as a mechanism for converting these steroids into compounds that can be efficiently sequestered. Similarly, larvae of the monarch butterfly store metabolized cardenolides in tissues after oxidizing these compounds into suitable chemical forms for sequestration.

Selective Biomagnification of Allelochemicals in Tissues

There is little indication that the profiles of insect-stored allelochemicals in any way mirror those of their host plant. In a sense, each insect species treats ingested allelochemicals distinctively, so that a compound totally excreted by one species may constitute the main sequestration product of another.

The very toxic grasshopper *Poekilocerus bufonius* sequesters only two of the cardenolides that it ingests from its milkweed food plant. Similar selectivity is shown by moth larvae (*Syntomeida* species) which sequester oleandrin, the main steroid found in the leaves of oleander. On the other hand, a variety of other insects feeding on oleander leaves do not sequester oleandrin.

Similar unpredictability characterizes the sequestration of pyrrolizidine alkaloids by moth larvae. Tiger moths (*Amphicallia* species) sequester the alkaloids crispatine and trichodesmine, whereas the main alkaloid present is crosemperine. Another tiger moth (*Tyria* species) concentrates senecionine in its tissues in spite of the fact that this compound is a trace constituent in the leaves. *Tyria* is no less curious as a sequestrator because it stores jacobine, jacozine, and jacoline as minor constituents in adults, yet these three compounds are major alkaloids in the leaves.

The Diverse Functions of “Captured” Allelochemicals

While highly concentrated allelochemicals may constitute a major deterrent to non-adapted insects, these compounds can represent a real treasure trove for species for which these plant products are non-toxic. Indeed, in the course of exploiting for their own protection compounds that are repellent or toxic to most insect species, specialists have gone beyond the point of simply being resistant to allelochemicals. In many cases, a variety of specialist species have utilized the rich allelochemical pool that is available in order to develop a menu of remarkable functions.

Insect Sequestration of Bacterial Compounds and their Glandular Secretion

Prokaryotes (bacterial types) are almost everywhere and their widespread association with insects is certainly well established. But the bases for these diverse bacteria-insect relationships are, for the most part, *terra incognita*. However, very recent research suggests one very surprising function for bacteria in insect glands.

All major types of metabolism evolved in prokaryotes and the success of these organisms was both cause and effect of changing environments on earth. If these bacteria are sequestered in insect secretory glands, their great metabolic abilities could be utilized to biosynthesize bacterial allelochemicals which could be used as potent defensive compounds. This possibility appears to have been realized as a product of the virtual ubiquity of both insects and their biosynthetically versatile prokaryotes.

Predaceous diving beetles (*Dytiscus* species) are distinguished by their ability to produce defensive steroids, some of which are novel animal products that are limited to species of diving beetles. Furthermore, insects do not synthesize cholesterol which in insects must be obtained from exogenous sterols. However, it now appears that the surprising steroidal versatility of dytiscids may reflect the biosynthetic elegance of bacteria rather than insects.

Adult diving beetles may contain concentrations of at least 10 bacterial species, mostly detected in a variety of organs. Culturing individual bacterial species resulted in the identification of diverse steroids that had previously been characterized in the prothoracic defensive glands of the adults. The steroid-rich secretions of these glands function as vertebrate deterrents that can cause emesis of fish that swallow these beetles. If the dytiscid-bacterial association is typical of a variety of insect species and their bacterial symbiotes, then a multitude of insect-bacterial relationships may require re-evaluation of possible examples of insect sequestration of bacterial allelochemists.

Non-pathogenic bacteria are commonly housed in insects and, in a sense, these prokaryotes are sequestered by their insect hosts. Furthermore, if the bacteria synthesize toxic compounds which may be externalized from a defensive gland (prothoracic glands of dytiscids), then the bacterial products may be regarded as bacterial allelochemicals that have been sequestered. Indeed, bacterial compounds of symbiotic bacteria of insects clearly constitute an unrecognized group of allelochemicals.

Additives in Defensive Glands

Milkweed bugs (*Oncopeltus* species) add cardenolides, derived from their milkweed host plants, to their thoracic defensive gland secretion which considerably enhances the deterrency of their secretion. Similarly, a warningly colored generalist, the lubber grasshopper (*Romalea guttata*) incorporates a large number of allelochemicals derived from a variety of plant species into its thoracic gland secretion. This grasshopper generally feeds on plants with low concentrations of allelochemicals, but if it is fed high concentrations of plants with known repellents (e.g., onion), the odorous secretion can be highly deterrent.

Another toxic grasshopper, *Poekilocerus bufonius*, utilizes allelochemicals as the mainstay of its defensive secretion. This aposematic (very warningly colored) insect sequesters two of six cardenolides from its milkweed diet which are the major irritants in the secretion when it is sprayed at adversaries. Utilization of allelochemicals as defensive gland constituents is particularly pronounced in the swallowtail larvae of *Atrophaneura alcinous*, which feed on leaves that are rich in toxic aristolochic acids. Seven aristolochic acids are sequestered by the larvae and all are transferred to the defensive gland in the head. The acids are concentrated in the gland and are the major deterrents for birds.

Regurgitation and Defecation of Allelochemicals

The intestines of stimulated grasshoppers can discharge ingested plant products which may serve as repellents for predators. Regurgitated allelochemicals can effectively repel ants, as is the case for anal discharges from the hind gut. When tactually stimulated, the milkweed bug, *Oncopeltus fasciatus*, also defecates a solution containing repellent allelochemicals. In this case, they are cardenolides ingested from their milkweed food plant.

Allelochemicals as Tissue Colorants

The cuticular (skin) coloration of many insects is diet-dependent and is highly adaptive since it enables the insect to respond in a positive way to its background color. Diet-induced changes may result in the insect being cryptic (background matching), whereas aposematic species can be background contrasting. Background quality, which is of great survival value, appears to be controlled by allelochemicals that are widespread in the diets of moths, butterflies and true bugs. These insects are particularly sensitive to the carotenoids (e.g., tomato red) that fortify their host plants.

If the large white butterfly, *Pieris brassicae*, is reared on its normal diet of cabbage leaves, the pupae are green and contrast with their background. This toxic insect contains high concentrations of carotenoids, and the carotenoid lutein is concentrated in the cuticle. On the other hand, if these insects are reared on an artificial diet lacking carotenoids, they possess a turquoise-blue coloration and exhibit no response to background. In the absence of carotenoids, these insects are quite conspicuous on their background and could be readily detected by predators.

Allelochemicals as Inhibitors of Toxin Production

Some plant toxins are present in plants in an inactive form only to be converted to toxic compounds after ingestion by herbivores. This is particularly true for many cyanogens (cyanide-containing toxins) that generate cyanide when the leaf surface is broken as would occur with a plant feeder. It now appears that cyanogenesis (producing cyanide) in damaged leaves may be inhibited by allelochemicals that are compartmentally isolated from the cyanogens in the intact leaves.

Leaves of papaya, *Carica papaya*, contain two cyanogens that yield hydrogen cyanide after enzymatic attack. However, tannins, which are widely distributed in plants, inhibit the release of cyanide caused by the action of enzymes that attack the cyanogens. Insects attacking plants containing cyanogens may have adapted tannins to prevent cyanide release, a strategy that may be suitable for other plant groups that yield toxic products after leaf damage.

Allelochemicals as Pheromonal Precursors

Bark beetles (Scolytidae) in the genera *Dendroctonus* and *Ips* convert the hydrocarbons produced by their pine hosts into alcohols that are utilized as either aggregation or sex pheromones (communication compounds) by the attacking beetles. Similarly, butterflies in the family Nymphalidae and moths in the family Arctiidae convert pyrrolizidine alkaloids (PAs) into sex pheromones that are especially critical during courtship. The PAs may be collected from damaged plants by males to be transformed into sexual pheromones that constitute the key to reproductive success. For these males, the allelochemicals (PAs) are identified with reproductive fitness.

Allelochemicals as Structural Paint

Some insects actually "paint" structures with ingested compounds possessing considerable biological activity. Larvae of the parsnip webworm, *Depressaria pastinacella*, apply ingested allelochemicals to silk-webbed flowers that serve as housing units. The applied compounds are derived from wild parsnip, a food plant that is rich in highly toxic furanocoumarins. These compounds are sequestered in the silk glands before being applied to the flowers in which the larvae reside. Since the larvae are quite sensitive to ultraviolet light, the presence of UV-absorbing furanocoumarins on their silken housing is highly adaptive. In addition, because these allelochemicals possess pronounced antimicrobial activity against bacteria and fungi, their presence on the silk can act as a major barrier to pathogens.

Allelochemicals as Metabolites in Primary Metabolic Pathways

Some specialist herbivores metabolize the characteristic allelochemicals in their host plants into compounds that are of major significance in growth and development. In essence, these specialists exploit their food plants by utilizing not only their primary nutrients for growth and development, but their allelochemicals as well.

Larvae of the bruchid beetle, *Carydes brasiliensis*, develop exclusively on seeds of a legume (pea family) that contains canavanine, a foreign amino acid related to arginine. Canavanine is highly toxic when incorporated into proteins by non-adapted herbivores. On the other hand, larvae of *C. brasiliensis* metabolize canavanine into products of great metabolic significance. Large amounts of ammonia are generated for fixation into organic compounds, and an amino acid is produced from canavanine for ready metabolism. Thus, the very toxic allelochemical of the legume has been thoroughly exploited by the beetle larvae as a source for key nutrients.

Beetle larvae in the genus *Chrysomela* also convert a toxic allelochemical into a metabolite with considerable importance in growth and development. These larvae feed on leaves of willow (*Salix*), a rich source of salicin, a toxic metabolite. Metabolism of salicin yields a very effective defensive compound that is sequestered by the larvae in defensive glands. In addition, this metabolism generates enough glucose to account for about one-third of the daily caloric requirements of the larvae. Salicin should be regarded as an allelochemical nutrient.

Allelochemicals as Agents of Sexual Development

Tiger moths in the genus *Creatonotus* feed on plant species that produce high concentrations of pyrrolizidine alkaloids (PAs). These compounds are converted to sex pheromones by the males. Additionally, these allelochemicals control the development of important secondary sexual characters called coremata. The coremata are eversible andraconial (male) organs that are the source of the volatile sex pheromones of the males, and their degree of development is controlled by the amount of PAs ingested by the developing larvae. In effect, PAs are functioning as male hormones that regulate both sex pheromone production and development of the coremata.

Allelochemical Discharge from Non-glandular Reservoirs

Some insects sequester ingested allelochemicals in non-glandular reservoirs that can be evacuated upon demand. Gregarious larvae of the European pine sawfly, *Neodiprion sertifer*, sequester toxic turpentine terpenes in foregut pouches. These pine-derived compounds can be discharged upon demand to function as highly effective predator deterrents. Similarly, lygaeids such as the milkweed bug, *Oncopeltus fasciatus*, sequester cardenolides from their milkweed hosts in dorsolateral spaces on the thorax and abdomen. Significantly, high concentrations of cardenolides are stored in these spaces, resulting in a concentrated deterrent discharge which repels potential predators.

Allelochemicals as Defensive Agents of Eggs

Insects ingesting allelochemicals often utilize these compounds as protectants for the next generation of insects. These plant compounds may be sequestered in the eggs in order to provide a formidable defense against predators and pathogens. The insect embryo must be resistant to the toxic effects of the allelochemicals that have been sequestered in the reproductive system. For example, chrysomelid beetle adults feeding on willow and poplar sequester the toxic allelochemical salicin which is used to fortify the eggs. Salicin has different functions in the embryo and the larvae. For the embryo, salicin is a deterrent toxin which can kill ants. For the young larvae, salicin is converted to salicylaldehyde, a powerful repellent that is not frequently encountered in insects. A wide variety of allelochemicals are sequestered in insect eggs which includes pyrrolizidine alkaloids, aristolochic acids, cannabinoids, quinones, cardenolides and mustard oils. It is evident that the females of a large number of species have appropriated their host-plant defenses (allelochemicals) for protection of their eggs.

Allelochemicals as a Copulatory Bonus

Females may obtain allelochemicals suitable for their own protection and that of their eggs from the seminal ejaculate. For example, males of ithomiine butterflies gather pyrrolizidine alkaloids (PAs) from flowers and decomposing foliage and about half of the PAs are channeled to the spermatophore (sperm packet) that is transferred to the female during copulation. Since the females are rarely found feeding on alkaloid sources, the copulatory bonus ensures that these toxic allelochemicals will be available to protect both the female and her eggs. It is also very significant that the resistance of the spermatozoa to the known toxic effects of the pyrrolizine alkaloids enables the copulatory bonus strategy to be highly adaptive.

Allelochemicals as Synergists for Pheromones

The intimate relationship of specialist insects and their food plants is exemplified by the turnip aphid, *Lipaphis erysimi*, and its alarm pheromone. This aphid is typical of many aphid species. Paired glands near the tip of the abdomen secrete an alarm pheromone that causes both adults and larvae to disperse and drop off of the food plant. The alarm pheromones synthesized by the aphids are key communications chemicals that enable these insects to "abandon ship" when threatened by a predator. Surprisingly, (*E*)-*B*-farnesene, the major alarm agent for a large variety of aphid species, is only weakly active when secreted by the turnip aphid. However, the activity of this pheromonal secretion is increased appreciably by allelochemicals that act as powerful synergists for the major alarm pheromone. These synergists are derived from typical food plant compounds that have been modified by the aphids.

Allelochemicals as Phagostimulants

The close relationship of insect specialists and their allelochemicals is further demonstrated by some species of sawflies and chrysomelid beetles which feed on very bitter food plants. Adults of the turnip sawfly, *Athalia rosae*, feed on the surface of a plant that is not a larval food plant. Compounds in the leaf surface that are responsible for their bitter taste are powerful phagostimulants for *A. rosae*. In addition, these bitter compounds are incorporated into the cuticle, thus providing these sawflies with a cuticular set of "armor" to protect against aggressive predators.

Similarly, species in three genera of chrysomelid beetles utilize cucurbitacins, compounds found in their squash and pumpkin hosts, as phagostimulants that are biomagnified in their bodies. The beetles are rendered distasteful and, as is the case for the sawflies, the allelochemicals possess dual roles that both induce ingestion and promote sequestration of highly distasteful compounds.

Allelochemicals as Inducers of Detoxifying Enzymes

Both generalist and specialist insects can encounter a diversity of allelochemicals with varying degrees of toxicity. For generalists this is particularly true since a generalist diet can sample a wide variety of plant species containing a large diversity of allelochemicals. On the other hand, specialists may encounter fewer allelochemicals but it is likely that these compounds will be at high concentrations. In the case of both feeding modes, it is obviously necessary to possess mechanisms for blunting the toxic properties of the ingested allelochemicals. Detoxication would appear to constitute the key process for neutralizing the toxicities of ingested allelochemicals. The enzymes chiefly identified with converting allelochemicals into less toxic compounds are the mixed-function oxidases, particularly cytochrome P-450.

Mixed-function oxidases metabolize fat-soluble toxins into water-soluble ones that can be excreted. The level of these enzymes may determine the tolerance of an insect for a particular allelochemical. For a generalist ingesting a large diversity of allelochemicals derived from many plant species, the induction of a variety of these oxidases would promote the possibility of detoxifying many kinds of plant compounds. For a specialist, fewer oxidases at very high levels would enable the herbivore to detoxify the very high concentrations of allelochemicals in its restricted food plants.

Mixed-function oxidases play a key role in protecting the southern armyworm, *Spodoptera eridania*, from a host of allelochemicals. Unrelated plant compounds rapidly induce enzymatic increases of 2 to 3-fold in larvae. Significantly, the rise in P-450 activity is immediate and proceeds rapidly over much of its course during the first few hours. These results strongly suggest that P-450 induction is critical to allelochemical tolerance.

Allelochemicals as Allomonal Precursors

In some cases, insects have produced powerful repellents from allelochemicals in their food plants and have thus exploited the plant's defensive chemistry in a very efficient way. Such a strategy is particularly adaptive because the insect has benefited both nutritionally and defensively from feeding on its host.

Host plant exploitation is particularly pronounced in some chrysomelid beetle larvae in the genera *Chrysomela* and *Phratora*. The larvae feed on willow and poplar leaves, both of which contain salicin, a well known feeding deterrent for non-adapted species. The beetle larvae convert salicin to salicylaldehyde and glucose, utilizing the former for defense and the latter for growth. For these chrysomelid larvae, the conversion of salicin to salicylaldehyde is doubly beneficial. Very little energy is used to synthesize salicylaldehyde, compared to what is required to produce other defensive compounds that must be totally synthesized. Because salicylaldehyde is a far more effective repellent than salicin, the beetle larvae receive a very important double bonus by converting the allelochemical into a compound that can be readily stored and secreted from the defensive glands.

Allelochemicals as Communicative "Jamming" Agents

In theory, plant species could reduce or eliminate herbivory if the plants generated volatile compounds identical to or similar to the pheromones utilized by herbivores as signals. If these signals were behaviorally disruptive, feeding could be appreciably diminished, to say the least.

The wild potato, *Solanum berthaultii*, has effectively "jammed" the pheromonal alarm signal of its potential aphid herbivore. (*E*)-*B*-farnesene, an alarm pheromone of the aphid *Myzus persicae*, is also produced by wild potatoes, resulting in repellency and dispersion of the aphids. In effect, the potato has exploited the aphid's herbivory by utilizing a highly disruptive compound that has been evolved by aphids as a warning signal.

Quenchers of Phototoxic Allelochemicals

Diverse plant species produce photo-activated compounds that are highly toxic to insects after digestion. In essence, these compounds generate highly toxic species of oxygen that attack key biochemicals such as nucleic acids. On the other hand, if the herbivore simultaneously ingests allelochemicals that are effective quenchers of toxic oxygen species along with the phototoxins, then survival and prosperity are possible. The availability of these allelochemical antioxidants has enabled some insect species to utilize food plants that are "forbidden fruits" for most herbivores.

Larvae of the tobacco hornworm feed on a variety of plant species that contain the phototoxin α-terthienyl, a constituent of many species of asters (Asteraceae). However, the additional ingestion of β-carotene reduces mortality from 55% (controls) to 3% (+carotene) during 48 h. β-carotene, an effective quencher of toxic oxygen species, is concentrated in the tissues of the larvae where it can serve as a potent antioxidant for photoactivated toxins found in its food plant.

Antibiotic Functions of Allelochemicals

The demonstrated range of allelochemicals against insect-associated viruses, fungi and bacteria makes it probable that these arthropods have commonly exploited plant compounds as key elements in their phytochemical defenses.

A compound commonly produced by conifers is *a*-pinene, which inhibits diverse microorganisms including the insect pathogen *Bacillus thuringiensis*. Along with several related compounds, α-pinene reduces the infectivity of *B. thuringiensis* for larvae of the Douglas fir tussock moth, *Orgyia pseudotsugata*. At concentrations approximating those found in fir needles, *a*-pinene increases the 50% lethal dose for *B. thuringiensis* by 700-fold.

A pathogenic fungus, *Nomuraea rileyi*, frequently attacks lepidopterous (moth) larvae such as the corn earworm, *Helicoverpa zea*. However, the pathogenicity to this larva can be reduced if the moth ingests a tomato alkaloid, α-tomatine. If the larvae ingest α-tomatine prior to exposure to fungal conidia, it increases larval survivorship considerably. The alkaloid is a further asset to *H. zea* because it is quite toxic to larval parasites of the corn earworm.

The pathogenicity of viral pathogens of *H. zea* can also be compromised by host plant allelochemicals. Chlorogenic acid, a common plant compound, is oxidized to chlorogenoquinone by plant enzymes, and this oxidation product binds to a nuclear polyhedrosis virus. Binding to this baculovirus results in a reduction in digestibility and a decrease in infectivity. Furthermore, it appears that the liberation of infective virons in the midgut, which is a requirement for successful infection, is impaired by the binding of chlorogenoquinone to the baculovirus.

Specialists and Generalists: Two Selected Case Studies

Although specialists and generalists may be highly efficient sequestrators, the storage characteristics of both groups differ considerably. Some insights into how these insects manipulate the allelochemicals in their diets have been provided by recent studies of the fates of a variety of ingested plant chemicals. An analysis of these studies demonstrates that the particulars of sequestration are, if nothing else, very unpredictable.

The Monarch Butterfly, *Danaus plexippus*

The monarch is a specialist that feeds exclusively on different species of milkweeds. Milkweeds contain steroids called cardenolides, which are somewhat related to vertebrate hormones such as testosterone. These compounds are toxic and highly emetic, vomiting often following their ingestion by non-adapted species.

Polar (water soluble) cardenolides are sequestered in the large volume of gut fluid possessed by the larvae. Sequestration is much more efficient from plants with low level cardenolide concentrations than with high concentrations. Significantly for the monarch, and not necessarily for other milkweed feeders, it is the large volume of gut fluid that makes it possible to feed and develop on these plants.

The cardenolide-rich gut fluid, which may exceed one-third of the larva's total liquid volume, is withdrawn at pupation to become part of the hemolymph (blood) pool, stored primarily under the wings. Subsequently, the wing scales (bird predators beware), along with the hemolymph, become the richest sources of cardenolides in the body after being withdrawn from the gut fluid. The volume of gut fluid decreases before pupation only to increase again before pupal molting. Again, gut fluid diminishes during pupal development only to increase again in the new adult. The cardenolide-rich gut fluid is again converted to hemolymph during adult development so that very little remains to be lost when the newly developed adult evacuates accumulated waste products from its gut.

The polar cardenolides in the gut fluid clearly are the source of the defensive compounds manipulated by the monarch at all stages. The larval and pupal exuviate (cast skins) eliminated after molting are an excretory form for the cardenolides, as is the case for these compounds in the wing scales. Excretion notwithstanding, the ability of all life stages to manipulate the cardenolide pool is quite pronounced. This is evident in 2-day-old pupae that contain low concentrations of cardenolides in the gut fluid but high concentrations in the hemolymph. However, before wing expansion in the newly developed adult, the cardenolide level in the hemolymph is at its lowest, only to increase to the highest level in any life stage.

The presence of high levels of cardenolides in the blood of the adult demonstrates that these compounds are not locked in tissues but rather are circulating freely, possibly to be utilized upon demand. The warningly colored (aposematic) adult monarch utilizes a defensive system based on compounds that it did not ingest as an adult. Although the complexities of cardenolide sequestration in this species are evident, it is highly significant to understand these ingested steroids are an extraordinarily dynamic state.

The Lubber Grasshopper, *Romalea microptera* (also known as *R. guttata*)

This large grasshopper found in the southeastern United States is quite conspicuous because of it red, black and yellow coloration. It is one of the most aposematic (warningly colored) species in its habitat. This brightly colored grasshopper is especially distinctive because it is a generalist that feeds on a very wide range of plants belonging to a variety of species. Lubber grasshopper is known to feed on 104 plant species belonging to 38 families, many of which produce toxic allelochemicals. Both immature and mature grasshoppers are capable of causing emesis in predators such as lizards, demonstrating that all stages of these insects are protected from at least some predatory vertebrates.

Immature individuals of *R. microptera* produce defensive compounds that cause emesis in both lizard and bird predators. Additionally, mature and adult grasshoppers secrete defensive compounds from paired tracheal (respiratory) glands in the metathorax. These glands only become active near the adult period and their secretion can be extremely repellent to small predatory insects such as ants. At least 50 compounds are produced by the defensive glands, the secretions varying intraspecifically, so that components of females of the same age and population sometimes differ by 70-fold, with some compounds being absent in certain individuals. However, in addition to the compounds synthesized in the metathoracic glands, a number of allelochemicals are sequestered in these glands as a reflection of an individual grasshopper's diet. Indeed, the composition of the metathoracic gland secretion of each grasshopper appears to be unlike that of any other grasshopper, since no two of these generalist grasshoppers have identical diets from which to sequester allelochemicals. For a predator, each lubber secretion may be sufficiently distinctive to make it impossible to learn an olfactory pattern that clearly identifies the prey as lubber grasshopper.

Lubber grasshopper is unusual in being a polyphagous (eating many plant species) insect species that sequesters allelochemicals. In general, monophagous (feeding on one group of plant species) and stenophagous (feeding on a limited range of plant species) insect herbivores characteristically sequester plant compounds, but not generalist feeders. Furthermore, if *R. microptera* is presented with a restricted diet (specialist feeding mode), the number of compounds in the secretions and their concentrations are reduced, and the relative composition of the secretion is markedly different from that of field-collected grasshoppers. Significantly, if grasshoppers are presented with only a single-host plant as a food source, they frequently feed readily, sequestering host-plant volatiles, and exhibit no immediate ill effects. Lubbers feeding only on wild onion sequester a large number of onion volatiles which impart a strong onion odor to the secretion. The secretion is a powerful repellent to hungry ants and is considerably more active than the secretions of field-collected grasshoppers. Compounds in other single-plant diets (e.g., catnip) produce secretions that are similarly active.

The secretion of lubber grasshopper clearly has both a dietary and an individual origin that correlates with great variations in secretory components. The possibility that these grasshoppers can temporarily switch to a monophagous feeding mode in the presence of a preferred host plant is not unreasonable, and can result in a secretion with a high a concentration of sequestered allelochemicals as is characteristic of some specialist insects.

Lubber grasshopper is quite unpalatable and emetic to a variety of vertebrates, especially birds. Diverse bird species have been demonstrated to vomit after ingestion of these grasshoppers, presumably as a consequence of *Romalea*-synthesized toxins that fortify their bodies. While *Romalea* would appear to be completely defended against birds, as is often the case, the best defense has been overcome by a better offense. Shrikes, predatory birds that impale their insect prey on spines or even barbed wire, capture lubber grasshoppers and impale them. However, the birds wait for about 48 h before they remove and eat the grasshoppers. Though shrikes "store" all their food in this manner, in all likelihood the emetic toxin(s) produced by *Romalea* decomposes during the time the grasshopper is impaled.

References

Blum MS (1981) Chemical defenses of arthropods. Academic Press, New York, NY

Blum MS (1983) Detoxication, deactivation, and utilization of plant compounds by insects. In: Hedin P (ed), Plant resistance to insects. American Chemical Society, Washington, DC, pp 265–275

Bowers MD (1990) Recycling plant natural products for insect defense. In: Evans DL, Schmidt JO (eds), Insect defenses. Adaptive mechanisms and strategies of prey and predators. State University of New York, Albany, NY, pp 353–386

Evans DL, Schmidt JO (eds) Insect defenses. Adaptive mechanisms and strategies of prey and predators. State University of New York, Albany, NY, 482 pp

Gibson RW, Pickett JA (1983) Wild potato repels aphids by release of aphid alarm pheromone. Nature 302:608–609

Pasteels JM, Gregoire JC, Rowell-Rahier M (1983) The chemical ecology of defense in arthropods. Annu Rev Entomol 28:263–289

Whitman DW (1988) Allelochemical interactions among plants, herbivores, and their predators. In: Barbosa P, Letourneau D (eds), Novel aspects of insect-plant interactions. Wiley, New York, NY, pp 11–64

Allelopathy

The ability of a plant species to produce substances that are toxic to certain other plants. Allelopathic chemicals may affect germination, growth or reproduction of plants.

Allen's Rule

Among mammals and birds, individuals of a species occurring in colder climates tend to have shorter appendages, and a correspondingly lower surface to volume ratio, than members of the same species living in warmer climates. This trend results from the need to conserve heat in cold climates but to eliminate excess heat in hot climates. A variant of this is Bergmann's rule. These rules do not apply to ectothermic animals such as insects.

► Bergmann's Rule
► Thermoregulation

Allochronic Speciation

A mechanism of speciation wherein new species develop in the same place but are separated due to their tendency to occur at different times.

► Speciation Processes Among Insects

Allogenic Succession

A temporal succession of species that is driven by processes from outside the community (contrast with autogenic succession).

Allometric Growth

A growth pattern in which different parts of an organism grow at defined rates. In some cases, the body parts remain proportional (isometric growth), in other cases they do not. Departure from isometric growth is used to explain castes of social insects, which may have disproportionately large heads, mandibles, etc.

Allomone

A chemical that is released by one species that influences the behavior or physiology of a different species. The organism releasing the substance usually benefits. Allomones are a type of semiochemical used in warning.

► Chemical Ecology

Allopatric

Having separate and mutually exclusive areas of distribution (contrast with sympatric).

Allopatric Speciation

A mechanism of speciation resulting from geographic separation of populations, particularly physical barriers such as mountains and oceans.

► Speciation Processes Among Insects

Allophagic Speciation

A mechanism of speciation wherein new species develop in the same place, but are separated by their preference for different food.

► Speciation Processes Among Insects

Allozyme

Allozymes are a subset of isozymes. Allozymes are variants of enzymes representing different allelic alternatives of the same locus.

Almond Seed Wasp, *Eurytoma amygdali* Enderlein (Hymenoptera: Eurytomidae)

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The almond seed wasp is a serious pest of almonds, *Prunus amygdalus* Batch, in several countries of southeastern Europe and the Middle East, and also in Armenia, Azerbaijan, and Georgia. The adult female is 6–8 mm long and has a black head with dark brown eyes. The thorax and the spindle-shaped abdomen are shiny black. The tibiae and tarsi are light brown while the remaining parts of the leg are black. The male is usually smaller than the female (4–6 mm long). The larva is whitish, legless, tapering in both ends, curved and clearly segmented. Its head is light brown and very small. Its length when fully grown is about 6 mm.

Almond seed wasp is a univoltine species, with a small part of the population completing its life cycle in two or more years because of prolonged diapause. The diapause terminates during the winter. Pupation takes place inside the fruit in late winter to early spring. Adults emerge after boring a circular exit hole through the hard pericarp with their mandibles. Shortly after adult emergence, virgin females release a volatile sex pheromone to attract males for mating. Within a few days they mate and the females start ovipositing (Fig. 37) into unripe, green almonds. Using her long ovipositor, the female drills through the pericarp of unripe, green almonds and the integument of the seed, and deposits a stalked egg within the translucent nucellar tissue. After oviposition, the female deposits onto the fruit surface a host-marking pheromone. This pheromone enables females to discriminate between the infested and uninfested fruit, and to select the latter for oviposition. Thus, a uniform distribution of eggs among available fruits is achieved, and an optimal use of the available fruit for larval development. The newly hatched larva bores through the nucellus and the embryo sac to feed on the developing seed embryo. The larva attains full size in midsummer, and enters diapause within the seed integument of the destroyed almond, which usually remains on the tree in a mummified condition.

Owing to oviposition by the wasp certain varieties suffer a heavy premature drop. In most varieties though, the main damage consists in the consumption of the seed by the larvae. This damage varies depending on the variety. Certain soft-shelled varieties may lose up to 90% of their crop. Others are nearly immune because by the time females emerge in spring their pericarp has become too thick and endocarp too hard for the ovipositor to penetrate. Though not a common practice, planting of resistant varieties might be an effective strategy against this pest.

The pest can be controlled by collection and destruction of mummified fruits before adult

Almond Seed Wasp, *Eurytoma Amygdali Enderlein* (Hymenoptera: Eurytomidae), Figure 37 Female *Eurytoma amygdali* ovipositing into an almond.

emergence in spring, which is an effective measure if applied in large areas by multiple growers. However, the method most commonly used is the application of systemic insecticides against the neonate larvae within the oviposited almonds. This strategy is meant for varieties that do not suffer fruit drop because of oviposition. Recent studies have indicated that a single spraying can be effective if applied when 10–50% of the eggs have hatched. This percentage can be determined by dissecting sampled almonds under a binocular microscope. Estimates of egg hatch can be obtained by knowing the time the first adults emerge from infested almonds in spring. This can be determined by following the exit of adult wasps from infested almonds kept in cages in the orchard, or by following the population of males with the use of sex pheromone traps containing live virgin females as lures.

References

Katsoyannos BI, Kouloussis NA, Bassiliou A (1992) Monitoring populations of the almond seed wasp, *Eurytoma amygdali*, with sex pheromone traps and other means, and optimal time of chemical control. Entomologia Experimentalis et Applicata 62:9–16

Kouloussis NA, Katsoyannos BI (1991) Host discrimination and evidence for a host marking pheromone in *Eurytoma amygdali*. Entomologia Experimentalis et Applicata 58:165–174

Plaut HN (1971) On the biology of the adult of the almond seed wasp, *Eurytoma amygdali* End. (Hym., Eurytomidae) in Israel. Bull Entomol Res 61:275–281

Plaut HN (1972) On the biology of the immature stages of the almond wasp, *Eurytoma amygdali* End. (Hym., Eurytomidae) in Israel. Bull Entomol Res 61:681–687

Tzanakakis ME, Papadopoulos NT, Katsoyannos BI, Drakos GN, Manolakis E. Premature fruit drop caused by *Eurytoma amygdali* (Hymenoptera: Eurytomidae) on three almond varieties. J Econ Entomol 90:1635–1640

Alpha Taxonomy

The identification of organisms, and particularly the description and naming of organisms (species) new to science.

► Beta Taxonomy
► Gamma Taxonomy

Alternate Host

One of the hosts of a pathogen or insect where a portion of the life cycle occurs. Often this term is used to refer to a weed host of a crop pest or disease.

Alternation of Generations

Some insects undergo reproduction that involves alternation of sexual and asexual generations. Typically, females produce both males and females but at some point females cease producing males and produce only females parthenogenetically. Later generations then commence production of males again, allowing sexual reproduction to occur before the parthenogenetic cycle begins again. This occurs most often in Hymenoptera and Hemiptera.

► Aphids (Hemiptera: Aphididae)
► Gall Wasps (Hymenoptera: Cynipidae)

Altruism

Self destructive behavior that is performed for the benefit of others; sacrifice.

Alucitidae

A family of moths (order Lepidoptera). They commonly are known as many-plumed moths.

► Many-Plumed Moths
► Butterflies and Moths

Alula

The expanded membrane at the base of the trailing edge of the front wing.

► Wings Of Insects

Amazonian Primitive Ghost Moths (Lepidoptera: Neotheoridae)

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Amazonian primitive ghost moths, family Neotheoridae, are defined on the basis of a single species from the Amazonian area of southern Brazil, although two additional species have been discovered for the family recently. The family is part of the superfamily Hepialoidea, in the infraorder Exoporia. Adults medium size (38 mm wingspan), with head roughened; haustellum short and vestigial mandibles present; labial palpi long, porrect and 3-segmented; maxillary palpi very small and 2-segmented. Wing maculation is dark and unicolorous. Biologies and larvae remain unknown.

References

Kristensen NP (1978) A new familia of Hepialoidea from South America, with remarks on the phylogeny of the subordo Exoporia (Lepidoptera). Entomologia Germanica 4:272–294

Kristensen NP (1999) The homoneurons Glossata. In: Kristensen NP (ed), Lepidoptera, moths and butterflies, vol 1: evolution, systematics, and biogeography. Handbuch der Zoologie. Band IV. Arthropoda: Insecta. Teilband 35:51–63. W. de Gruyten, Berlin

Amber Insects: DNA Preserved?

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Amber is a polymerized form of tree resin that was produced by trees as a protection against disease agents and insect pests. The resin hardened and, sometimes, captured insects, seeds, feathers, microorganisms, plants, spiders, and even small vertebrates that got stuck in the sticky exudate. The hardened resin was preserved in the earth for millions of years, especially in regions where it was deposited in dense, wet sediments such as clay or sand that formed in the bottom of an ancient lagoon or river delta. For thousands of years, people have collected amber. Many people use amber as a gem, but scientists find amber a magnificent way to identify ancient organisms.

Amber can be found in a variety of sites around the world. The composition, color, clarity, and other properties of amber vary according to age, conditions of burial and type of tree that produced the resin. The oldest amber is from the Carboniferous (360–285 million years ago, mya) and can be found in the United Kingdom and in Montana in the USA. Permian amber is 185–145 million years old and found most often in Russia. Triassic amber (245–215 mya) can be found in Austria, and Jurassic amber (215–145 mya) is found in Denmark. Cretaceous amber (65–140 mya) is found in many locations around the world and represents the time when dinosaurs reigned and flowering plants evolved along with a variety of insects. For example, the rich amber deposits in central New Jersey in the USA are from the Turonion period of the Upper Cretaceous, about 92 mya. Other Cretaceous-period amber is found in North Russia and Japan. Baltic amber is found in the Baltic sea where amber has been collected and made into decorative objects for at least 13,000 years. In the Dominican Republic, amber deposits 23–30 million years old are found in rock layers. Dominican amber is particularly rich in insect inclusions. This amber was formed from the resin of an extinct tree in the legume family. Tertiary amber deposits are found in several locations around the world and are from 1.6 to 65 million years old. Tertiary deposits in the USA are found in Arkansas. Some websites with photographs showing amber inclusions can be viewed at:

- Amber Inclusions at: http://www-user.uni-bremen.de/~18m/amber.html;

– Amber on-line at: www.ambericawest.com/amberpics.html;
– American Museum of Natural History at: www.amnh.org/exhibitions/amber/; or
– The Amber Room at: http://home.earthlink.net/-skurth/AMBER.HTM.

Insect DNA in Amber?

The ability to amplify dinosaur DNA from insects preserved in amber in the film *Jurassic Park* captured the imagination of the public. Subsequently, the PCR was used to amplify DNA fragments from insects preserved in ancient amber, but these results have been controversial, as have been the results from amplifying dinosaur DNA.

Why the controversy? Is amber a special form of preservative that allows DNA to persist for unusually long periods of time (millions of years)? Amber entombs insect specimens completely, after which they completely dehydrate so the tissue is effectively mummified. Terpenoids, which are major constituents of amber, could inhibit microbial decay. Certainly, preservation of amber-embedded insects seems to be exceptional and insect tissues in amber appear comparable in quality to the tissues of the frozen wooly mammoth (which is "only" 50,000 years old). But is the DNA in these tissues preserved?

DNA has been extracted from a variety of insects in amber, including a fossil termite *Mastotermes electrodominicus* estimated to be 25–30 million years old, a 120- to 130-million year old conifer-feeding weevil (Coleoptera: Nemonychidae) and a 25- to 40-million year old bee. These are extraordinary ages for DNA!

The DNA sequences obtained from all amber-preserved insects meet several, but not all, criteria of authenticity; the fossil DNA sequences "make phylogenetic sense" and DNA has been isolated from a number of specimens in several cases (although the weevil example was derived from a single specimen). However, the extraction and amplification of fossil DNA sequences from amber-preserved insects has yet to be reproduced in independent laboratories, despite multiple attempts to do so, which has cast doubt on the authenticity of the reports.

One of the most controversial claims involved the isolation of a "living" bacterium from the abdomen of amber-entombed bee. Bacterial DNA from a 25-million-year-old bee was obtained and sequenced and a bacterial spore was reported to be revived, cultured, and identified. The classification of the bacterium is controversial because the bacterium could have come from a currently undescribed species of the *Bacillus sphaericus* complex. The modern *B. sphaericus* complex is incompletely known, so the "new" sequence obtained could be that of a modern, but previously unidentified, bacterium because this group of bacteria often is isolated from the soil.

Other claims of amplifying ancient DNA have been disproved. For example, the mitochondrial cytochrome b sequence of an 80-million-year-old dinosaur from the Upper Cretaceous in Utah was later discovered to be, most probably, of human origin. Likewise, a 20-million-year-old magnolia leaf produced sequences that were similar to those of modern magnolias. The authenticity of the magnolia sequences were cast into doubt because they were exposed to water and oxygen during preservation and DNA is especially vulnerable to degradation under such conditions.

The most common ancient DNA analyzed is usually mitochondrial DNA because it is so abundant; however, this abundance makes it easy to contaminate the ancient sample with modern mtDNA. The amplification of ancient DNA remains highly controversial because the technical difficulties are great.

DNA is a chemically unstable molecule that decays spontaneously, mainly through hydrolysis and oxidation. Hydrolysis causes deamination of the nucleotide bases and cleavage of base-sugar bonds, creating baseless sites. Deamination of cytosine to uracil and depurination (loss of purines adenine and guanine) are two types of hydrolytic damage. Baseless sites weaken the DNA, causing breaks that fragment the DNA into smaller and smaller pieces. Oxidation leads to chemical modification of bases and destruction of the ring structure of base and sugar residues. As a result, it is almost always impossible to obtain long amplification products from ancient DNA.

PCR products from ancient DNA often are "scrambled." This is due to the phenomenon called "jumping PCR," which occurs when the DNA polymerase reaches a template position which carries either a lesion or a strand break that stops the polymerase. The partially extended primer can anneal to another template fragment in the next cycle and be extended up to another damaged site. Thus, in vitro recombination can take place until the whole stretch encompassed by the two primers is synthesized and the amplification enters the exponential part of the PCR. This phenomenon makes it essential that cloning and sequencing of multiple clones be carried out to eliminate this form of error in interpretation.

Most archeological and paleontological specimens contain DNA from exogenous sources such as bacteria and fungi, as well as contaminating DNA from contemporary humans. Aspects of burial conditions seem to be important in DNA preservation, especially low temperature during burial. The oldest DNA sequences reported, and confirmed in other laboratories, come from the remains of a wooly mammoth found in the Siberian permafrost; these sequences are "only" 50,000 years old rather than millions of years old.

Theoretical calculations and empirical observations suggest DNA should only be able to survive, in a highly fragmented and chemically modified form, for 50,000–100,000 years. Because only tiny amounts of DNA usually can be extracted from an archeological specimen, stringent precautions and multiple controls are required to avoid accidental contamination with modern DNA.

A methodology to deal with ancient specimens has been proposed that includes careful selection of well-preserved specimens, choice of tissue samples that are likely to have best DNA preservation, and surface sterilization to eliminate surface contamination. The operations should be carried out in a laboratory dedicated to work on ancient specimens and work on ancient DNA should be separated from that on modern DNA. Most importantly, multiple negative controls should be performed during DNA extraction and PCR set up, although a lack of positives in the negative controls is not definitive proof of authentic ancient DNA. Another crucial step is the authentication of the results. Putatively ancient DNA sequences should be obtained from different extractions of the same sample and from different tissue samples from different specimens. The ultimate test of authenticity should be independent replication in two separate laboratories. So far, this type of replication has not been achieved for DNA from amber-preserved arthropod specimens.

References

Austin JJ, Ross AJ, Smith AB, Fortey RA, Thomas RH (1997) Problems of reproducibility— does geologically ancient DNA survive in amber-preserved insects? Proc R Entomol Soc London B 264:467–474

Hofreiter M, Serre D, Poinar HN, Kuch M, Paabo S (2001) Ancient DNA. Nat Rev Genet 2:353–359

Poinar G Jr, Poinar R (2001) The amber forest: a reconstruction of a vanished world. Princeton University Press, Princeton, NJ

Poinar HN, Stankiewicz BA (1999) Protein preservation and DNA retrieval from ancient tissues. Proc Natl Acad Sci USA 96:8426–8431

Yousten AA, Rippere KE (1997) DNA similarity analysis of a putative ancient bacterial isolate obtained from amber. FEMS Microbiol Lett 152:345–347

Ambrosia Beetles

Some members of the subfamily Scolytinae (order Coleoptera, family Curculionidae).

► Beetles

Ambush Bugs

Members of the family Reduviidae (order Hemiptera).

► Bugs

Ameletopsidae

A family of mayflies (order Ephemeroptera).

► Mayflies

Amelitidae

A family of mayflies (order Ephemeroptera).

► Mayflies

Amerasinghe, Felix P

Felix Amerasinghe was a noted Sri Lankan medical entomologist. He was known for his work on the taxonomy and ecology of disease-transmitting arthropods. Amerasinghe graduated from the University of Peradeniya, Sri Lanka, and received his Ph.D. from the University of Bristol, United Kingdom, in 1977. He made important long-term studies in the effects of irrigation on mosquito populations and malaria transmission, and became an authority on Japanese encephalitis. The development of keys for the identification of South Asian mosquitoes was one of his important contributions, greatly enhancing disease surveillance programs.

Amerasinghe worked principally at the University of Peradeniya, but also at the University of Sri Lanka, and in later years joined the International Water Management Institute as research leader, initiating studies on the socioeconomic impact of malaria, malaria parasitology, and molecular biology. He died in Colombo, Sri Lanka, on June 7, 2005.

Reference

Konradsen F, de Silva A, van der Hoek W (2005) Felix P. Amerasinghe. American Entomologist 51:191

American Butterfly Moths (Lepidoptera: Hedylidae)

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American butterfly moths, family Hedylidae, total only 40 known species, all Neotropical. The family is in the superfamily Geometroidea, in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults medium size (35–65 mm wingspan), with head scaling normal; haustellum naked; labial palpi upcurved; maxillary palpi 1 to 2-segmented; antennae filiform. Wings triangular, with forewings somewhat elongated and often with apex emarginated (Fig. 38); hindwings usually more rounded. Body usually narrow. Maculation somber hues of brown and gray, often with apical dark patch and some speckling, plus pale or hyaline patches (rarely mostly pale or hyaline). Adults nocturnal. Larvae are leaf feeders. Host plants are recorded in Euphorbiaceae, Malvaceae, Sterculiaceae, and Tiliaceae.

American Butterfly Moths (Lepidoptera: Hedylidae), Figure 38 **Example of American butterfly moths (Hedylidae), *Macrosoma lucivittata* (Walker), from Ecuador.**

References

Aiello A (1992) Nocturnal butterflies in Panama, Hedylidea (Lepidoptera: Rhopalocere). Quintero D, Aiello A (eds), Insects of Panama and Mesoamerica. Oxford University Press, Oxford, pp 549–553

Scoble MJ (1986) The structures and affinitxies of the Hedyloidea: a new concept of the butterflies. Bull Br Mus Nat Hist Entomol 53:251–286

Scoble MJ (1990) An identification guide to the Hedylidae (Lepidoptera: Hedyloidea). Entomologica Scandinavica 21:121–158

Scoble MJ (1998) Hedylidae. In Lepidopterorum Catalogus, (n.s.). Fasc. 93. Association for Tropical Lepidoptera, Gainesville, FL, 9 pp

Scoble MJ, Aiello A (1990) Moth-like butterflies (Hedylidae: Lepidoptera): a summary, with comments on the egg. J Nat Hist 24:159–164

American Dog Tick

► Ticks

American False Tiger Moths (Lepidoptera: Dioptidae)

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American false tiger moths, family Dioptidae, total 507 species, primarily Neotropical (505 sp.); actual fauna likely exceeds 800 species. Two subfamilies are known: Dioptinae and Doinae. Some specialists place the family within the Notodontidae. The family is in the superfamily Noctuoidea, in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults medium size (22–58 mm wingspan) (Fig. 39). Maculation mostly very colorful, with various patterns of large spotting, and some lustrous. Larvae and pupae often also colorful Adults are mostly nocturnal, but some are diurnal or crepuscular. Larvae are leaf feeders, particularly toxic plants in families like Aristolochiaceae, Euphorbiaceae, Passifloraceae, and Violaceae, but also on various others like Fagaceae. Very few are economic.

American False Tiger Moths (Lepidoptera: Dioptidae), Figure 39 Example of American false tiger moths (Dioptidae), *Josia gigantea* Druce, from Mexico.

References

Bryk F (1930) Dioptidae. Lepidopterorum catalogus, 42:1–65. W. Junk, Berlin, Germany

Miller JS (1987) A revision of the genus *Phryganidia* Packard, with description of a new species (Lepidoptera: Dioptidae). Proc Entomol Soc Wash 89:303–321

Prout LB (1918) A provisional arrangement of the Dioptidae. Novitates Zoologicae 25:395–429

Seitz A (ed) (1925–1927) Familie: Dioptidae. In: Die Gross-Schmetterlinge der Erde. 6. Die amerikanischen Spinner und Schwärmer, pl. 67–71. A. Kernen, Stuttgart, Germany, pp 499–534

Todd EL (1981) The noctuoid moths of the Antilles – Part I (Lepidoptera: Dioptidae). Proc Entomol Soc Wash 83:324–325

American Grasshopper, *Schistocerca americana* (Drury) (Orthoptera: Acrididae)

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This grasshopper is found widely in eastern North America, from southern Canada (where it is an occasional invader) south through Mexico to northern South America. In the midwestern states, where it is common, the resident population receives a regular infusion of dispersants from southern locations. In the southeast it is quite common, and one of the few species to reach epidemic densities. It is native to North America.

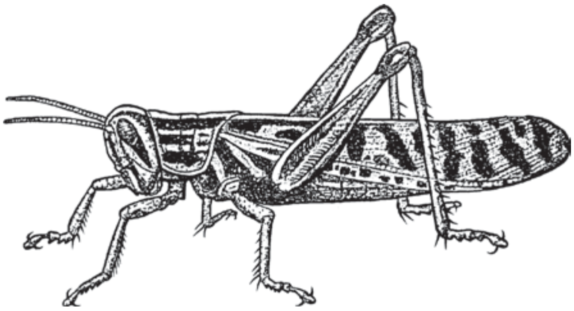
Life History

In warm climates, American grasshopper has two generations per year and overwinters in the adult stage. In Florida, eggs produced by overwintered adults begin to hatch in April-May, producing spring generation adults by May-June. This spring generation produces eggs that hatch in August-September. The adults from this autumn generation survive the winter.

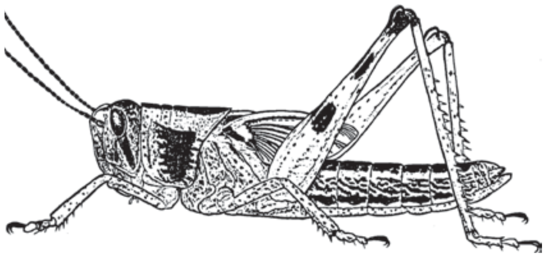
The eggs of *S. americana* initially are light orange in color, turning tan with maturity. They are elongate-spherical in shape, widest near the middle, and measure about 7.5 mm in length and 2.0 mm in width. The eggs are clustered together in a whorled arrangement, and number 75–100 eggs per pod, averaging 85 eggs. The eggs are inserted into the soil to a depth of about 4 cm and the upper portion of the oviposition hole is filled by the female with a frothy plug. Duration of the egg stage is about 14 days. The nymphs, upon hatching, dig through the froth to attain the soil surface.

Normally there are six instars in this grasshopper though sometimes only five. The young grasshoppers are light green in color. They are extremely gregarious during the early instars. At low densities the nymphs remain green throughout their development, but normally gain increasing amounts of black, yellow, and orange coloration commencing with the third instar. Instars can be distinguished by their antennal, pronotal, and wing development. The first and second instars display little wing development but have 13 and 17 antennal segments, respectively. In the third instar, the number of antennal segments increases to 20–22, the wings begin to display weak evidence of veins, and the dorsal length of the ventral lobe of the pronotum is about 1.5 times the length of the ventral surface. Instar four is quite similar to instar three, with 22–25 antennal segments, though the ratio of the length of the dorsal to ventral surfaces of the pronotal lateral lobe is 2:1. In instar five there are 24–25 antennal segments, and the wing tips assume a dorsal rather than ventral orientation but the wing tip does not exceed the first abdominal segment. In the sixth instar (Fig. 41) there are 24–26 antennal segments and the wing tips extend beyond the second abdominal segment. The overall body length is about 6–7, 12–13, 16–18, 22–25, 27–30, and 35–45 mm for instars 1–6, respectively. Development time is about 4–6, 4–6, 4–6, 4–8, 6–8, and 9–13 days for the corresponding instars when reared at about 32°C.

The adult (Fig. 40) is rather large, but slender bodied, measuring 39–52 and 48–68 mm in length in the male and female, respectively. A creamy white stripe normally occurs dorsally from the front of the head to the tips of the forewings. The forewings bear dark brown spots, the pronotum



American Grasshopper, *Schistocerca Americana* (Drury) (Orthoptera: Acrididae), Figure 40 **Adult of American grasshopper, *Schistocerca americana* (Drury).**



American Grasshopper, *Schistocerca Americana* (Drury) (Orthoptera: Acrididae), Figure 41 **Sixth instar of American grasshopper, *Schistocerca americana* (Drury).**

dark stripes. The hind wings are nearly colorless. The hind tibiae normally are reddish. Overall, the body color is yellowish brown or brownish with irregular lighter and darker areas, though for a week or so after assuming the adult stage a pinkish or reddish tint is evident.

Adults are active, flying freely and sometimes in swarms. They normally are found in sunny areas, but during the warmest portions of the day will move to shade. Adults are long lived, persisting for months in the laboratory and apparently in the field as well. This can lead to early-season situations where overwintered adults, all instars of nymphs, and new adults are present simultaneously. Mild winters favor survival of overwintering adults and apparently lead to population increase if summer weather and food supplies also are favorable.

Adults of American grasshopper tend to be arboreal in habit, and a great deal of the feeding by adults occurs on forest, shade, and fruit trees. The nymphs, however, feed on a large number of grasses and broadleaf plants, both wild and cultivated. During periods of abundance, almost no plants are immune to attack, and vegetables, grain crops, and ornamental plants are injured. American grasshopper consumes bean, corn, okra, and yellow squash over some other vegetables when provided with choices, but free-flying adults normally avoid low-growing crops such as vegetables, corn (maize) being a notable exception.

The natural enemies of *S. americana* are not well known. Birds such as mockingbirds, *Mimus polyglottos polyglottos* (Linnaeus), and crows, *Corvus brachyrhynchos brachyrhynchos* Brehm have been observed to feed on these grasshoppers. Fly larvae, *Sarcophaga* sp. (Diptera: Sarcophagidae) are sometimes parasitic on overwintering adults. Fungi have also been investigated for grasshopper suppression and *Metarhizium anisopliae* var. *acridum* kills American grasshopper quickly under laboratory conditions. This fungus is effective under adverse field conditions in Africa, so it may prove to be a useful suppression tool.

Damage

Grasshoppers are defoliators, eating irregular holes in leaf tissue. Under high density conditions they can strip vegetation of leaves, but more commonly leave plants with a ragged appearance. American grasshopper displays a tendency to swarm, and the high densities of grasshoppers can cause severe defoliation.

Because American grasshopper is a strong flier, it also sometimes becomes a contaminant of crops. When the late-season crop of collards in the Southeast is harvested mechanically, for example, American grasshopper may become incorporated into the processed vegetables. Although most grasshoppers can be kept from dispersing into crops near harvest by treating the periphery of the crop field, it is much more difficult to prevent invasion by American grasshopper because it may fly over any such barrier treatments.

Populations normally originate in weedy areas such as fence rows and abandoned fields. Thus, margins of fields are first affected and this is where monitoring should be concentrated. It is highly advisable to survey weedy areas in addition to crop margins if grasshoppers are found, as this gives an estimate of the potential impact if the grasshoppers disperse into the crop. Also, it is important to recognize that this species is highly dispersive in the adult stage, and will fly hundreds of meters or more to feed.

Management

Foliar applications of insecticides will suppress grasshoppers, but they are difficult to kill, particularly as they mature. Bait formulations are not usually recommended because these grasshoppers spend little time on the soil surface, preferring to climb high in vegetation.

Land management is an important element of *S. americana* population regulation. Grasshopper densities tend to increase in large patches of weedy vegetation that follow the cessation of agriculture or the initiation of pine tree plantations. In both cases, the mixture of annual and perennial forbs and grasses growing in fields that are untilled seems to favor grasshopper survival, with the grasshoppers then dispersing to adjacent fields as the most suitable plants are depleted. However, as abandoned fields convert to dense woods or the canopy of pine plantations shades the ground and suppresses weeds, the suitability of the habitat declines for grasshoppers.

Disturbance or maturation of crops may cause American grasshopper to disperse, sometimes over long distances, into crop fields. Therefore, care should be taken not to cut vegetation or till the soil of fields harboring grasshoppers if a susceptible crop is nearby. Planting crops in large blocks reduces the relative amount of crop edge, and the probability that a crop plant within the field will be attacked.

► Grasshopper Pests in North America
► Grasshoppers and Locusts as Agricultural Pests
► Grasshoppers, Katydids and Crickets (Orthoptera)

References

Capinera JL (1993) Differentiation of nymphal instars in *Schistocerca americana* (Orthoptera: Acrididae). Fla Entomol 76:175–179

Capinera JL (1993) Host-plant selection by *Schistocerca americana* (Orthoptera: Acrididae). Environ Entomol 22:127–133

Capinera JL, Scott RD, Walker TJ (2004) Field guide to the grasshoppers, katydids, and crickets of the United States. Cornell University Press, Ithaca, NY, 249 pp

Kuitert LC, Connin RV (1952) Biology of the American grasshopper in the southeastern United States. Fla Entomol 35:22–33

American Foulbrood

Historically, this is the most virulent disease of honey bees throughout the world. The bacterium responsible for the disease, *Paenibacillus* (= *Bacillus*) *larvae*, form heat- and drought-resistant spores that persist for years and germinate under favorable conditions. It is expressed in older larvae and young pupae, though infection occurs earlier, and young larvae are more susceptible than older larvae. Infected individuals turn darker in color, then black, and eventually collapse into a hardened mass in the cell. Signs of infection include a sour odor, perforated or sunken caps on the cells, and the presence of black deposits in the cells. If foulbrood is present, insertion of a twig or probe into a suspect cell will result in a gummy, stretchy substance being drawn out of the cell, often forming a thread or rope and called "ropy." Field diagnosis is possible by experienced inspectors, but is best confirmed microscopically or by molecular techniques. There are several subspecies of *P. larvae*, and *P. larvae* ssp. *larvae* is considered responsible for American foulbrood, with other subspecies also affecting honey bees.

Transmission occurs by feeding infected honey or pollen, by using infected equipment, and sometimes by installing infected package bees or queens. Feeding bees sugar syrup therefore is preferable to feeding them honey, and disinfection of hive tools is always recommended. Natural transmission from hive to hive can occur through robbing behavior. Queens and workers can carry the disease. Bee colonies that are infected normally are eliminated by burning them. Antibiotics can be fed to colonies to prevent infection.

► Honey Bees
► Apiculture
► *Paenibacillus*

References

Alippi AM, López AC, Aguilar OM (2002) Differentiation of *Paenibacillus larvae* subsp. *larvae*, the cause of American foulbrood of honeybees, by using PCR and restriction fragment analysis of genes encoding 16S rRNA. Appl Environ Microbiol 68:3655–3660

Morse RA, Nowogrodzki R (1990) Honey bee pests, predators and diseases, 2nd ed. Cornell University Press, Ithaca, NY, 474 pp

American Serpentine Leafminer, *Liriomyza trifolii* (Burgess) (Diptera: Agromyzidae)

This leafminer has long been found in eastern North America, northern South America, and the Caribbean. However, in recent years it has been introduced into California, Europe, and elsewhere. Expanded traffic in flower crops appears to be the basis for the expanding range of this species. *Liriomyza trifolii* (Burgess), sometimes known as the American serpentine leafminer, readily infests greenhouses. As a vegetable pest, however, its occurrence is limited principally to tropical and subtropical regions.

Life Cycle and Description

Leafminers have a relatively short life cycle. The time required for a complete life cycle in warm environments is often 21–28 days, so numerous generations can occur annually in tropical climates. Growth at a constant 25°C requires about 19 days from egg deposition to emergence of the adult. Development rates increase with temperature up to about 30°C; temperatures above 30°C are usually unfavorable and larvae experience high mortality. At 25°C, the egg stage requires 2.7 days for development; the three active larval instars require an average of 1.4, 1.4, and 1.8 days, respectively; and the time spent in the puparium is 9.3 days. Also, there is an adult preovipostion period that averages 1.3 days. The temperature threshold for development of the various stages is 6–10°C, except that egg laying requires about 12 C.

Egg

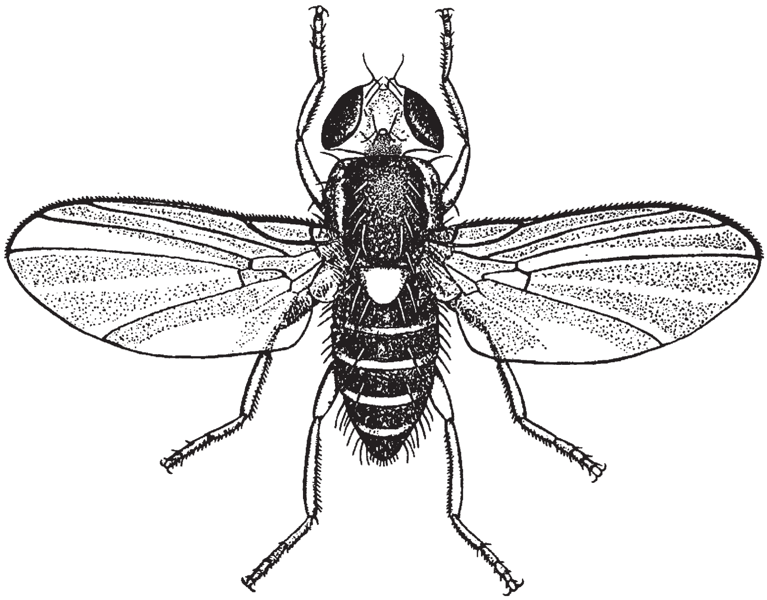
Eggs tend to be deposited in the middle of the plant; the adult seems to avoid immature leaves. The female deposits the eggs on the lower surface of the leaf, but they are inserted just below the epidermis. Eggs are oval in shape and small in size, measuring about 1.0 mm long and 0.2 mm wide. Initially they are clear, but soon become creamy white in color.

Larva

Body and mouth part size can be used to differentiate instars; the latter is particularly useful. For the first instar, the mean and range of body and mouth parts (cephalopharyngeal skeleton) lengths are 0.39 (0.33–0.53) mm and 0.10 (0.08–0.11) mm, respectively. For the second instar, the body and mouth parts measurements are 1.00 (0.55–1.21) mm and 0.17 (0.15–0.18) mm, respectively. For the third instar, the body and mouth parts measurements are 1.99 (1.26–2.62) mm and 0.25 (0.22–0.31) mm, respectively. A fourth instar occurs between puparium formation and pupation, but this is a nonfeeding stage and is usually ignored by authors. The puparium is initially golden brown in color, but turns darker brown with time.

Adult

Adults (Fig. 42) are small, measuring less than 2 mm in length, with a wing length of 1.25–1.9 mm. The head is yellow with red eyes. The thorax and abdomen are mostly gray and black although the ventral surface and legs are yellow. The wings are transparent. Key characters that serve to differentiate this species from the vegetable leafminer, *Liriomyza sativae* Blanchard, are the matte, grayish black mesonotum and the yellow hind margins of the eyes. In vegetable leafminer the mesonotum is shining black and the hind margin of the eyes is black. The small size of this species serves to distinguish it from pea leafminer, *Liriomyza huidobrensis* (Blanchard), which has a wing length of 1.7–2.25 mm. Also, the yellow femora of American serpentine leafminer help to separate it from pea leafminer, which has darker femora. Oviposition occurs at a rate of 35–39 eggs per day, for a total fecundity of 200–400 eggs. The female makes



American Serpentine Leafminer, *Liriomyza Trifolii* (Burgess) (Diptera: Agromyzidae), Figure 42 **Adult of American serpentine leafminer, *Liriomyza trifolii*.**

numerous punctures of the leaf mesophyll with her ovipositor, and uses these punctures for feeding and egg laying. The proportion of punctures receiving an egg is about 25% in chrysanthemum and celery, both favored hosts, but only about 10% in tomato, which is less suitable for larval survival and adult longevity. Although the female apparently feeds on the exuding sap at all wounds, she spends less time feeding on unfavorable hosts. The males live only two to three days, possibly because they cannot puncture foliage and therefore feed less than females, whereas females usually survive for about a week. Typically they feed and oviposit during much of the daylight hours, but especially near mid-day.

Host Plants

Liriomyza trifolii is perhaps best known as a pest of chrysanthemums and celery, but it has a wide host range. For example, at least 55 hosts are known from Florida, including bean, beet, carrot, celery, cucumber, eggplant, lettuce, melon, onion, pea, pepper, potato, squash, and tomato. Flower crops that are readily infested and which are known to facilitate spread of this pest include chrysanthemum, gerbera, gypsophila, and marigold, but there are likely many other hosts, especially among the Compositae. Numerous broad-leaved weed species support larval growth. The nightshade *Solanum americanum*, Spanish needles, *Bidens alba*, and pilewort, *Erechtites hieracifolia*, were suitable weed hosts in Florida.

Damage

Punctures caused by females during the feeding and oviposition processes can result in a stippled appearance on foliage, especially at the leaf tip and along the leaf margins. However, the major form of damage is the mining of leaves by larvae, which results in destruction of leaf mesophyll. The mine becomes noticeable about three to four days after oviposition, and becomes larger in size as the larva matures. The pattern of mining is irregular. Both leaf mining and stippling can greatly depress the level of photosynthesis in the plant. Extensive mining also causes premature leaf drop, which can result in lack of shading and sun scalding of fruit. Wounding of the foliage also allows entry of bacterial and fungal diseases. Although leaf mining can reduce plant growth, crops such as tomato are quite resilient, and capable of withstanding considerable leaf damage. It is often necessary to have an average of one to three mines per tomato leaf before yield reductions occur. Leafminers are most damaging when they affect floricultural crops due to the low tolerance of such crops for any insect damage.

Natural Enemies

Parasitic wasps (parasitoids) of the families Braconidae, Eulophidae, and Pteromalidae are important in natural control, and in the absence of insecticides usually keep this insect at low levels of abundance. At least 14 parasitoid species are known from Florida alone. Species of Eulophidae such as *Diglyphus begina* (Ashmead), *D. intermedius* (Girault), *D. pulchripes*, and *Chrysocharis parksi* Crawford are generally found to be most important in studies conducted in North America, although their relative importance varies geographically and temporally. Predators and diseases are not considered to be important, relative to parasitoids. However, both larvae and adults are susceptible to predation by a wide variety of general predators, particularly ants.

Management

Sampling

There are many methods to assess leafminer abundance. Counting mines in leaves is a good index of past activity, but many mines may be vacant. Counting live larvae in mines is time consuming, but more indicative of future damage. Puparia can be collected by placing trays beneath foliage to capture larvae as they evacuate mines, and the captures are highly correlated with the number of active miners. Adults can be captured by using adhesive applied to yellow cards or stakes.

Insecticides

Chemical insecticides are commonly used to protect foliage from injury, but insecticide resistance is a major problem. Insecticide susceptibility varies widely among populations, and level of susceptibility is directly related to frequency of insecticide application. In Florida, longevity of insecticide effectiveness is often only two to four years, and then is usually followed by severe resistance among the treated populations. Rotation among classes of insecticides is recommended to delay development of resistance. Reduction in dose level and frequency of insecticide application, as well as preservation of susceptible populations through nontreatment of some areas, are suggested as means to preserve insecticide susceptibility among leafminer populations. Insect growth regulators have been more stable, but are not immune from the resistance problem. Insecticides also are highly disruptive to naturally occurring biological control agents, particularly parasitoids. Use of many chemical insecticides exacerbates leafminer problems by killing parasitoids of leafminers. This usually results when insecticides are applied for lepidopterous insects, and use of more selective pest control materials such as *Bacillus thuringiensis* is recommended as it allows survival of the leafminer parasitoids. Because parasitoids often provide effective suppression of leafminers in the field when disruptive insecticides are not used, there has been interest in release of parasitoids into crops. This occurs principally in greenhouse-grown crops, but is also applicable to field conditions. *Steinernema* nematodes have also been evaluated for suppression of leaf mining activity. High levels of relative humidity (at least 92%) are needed to attain even moderately high (greater than 65%) levels of parasitism. Adjuvants that enhance nematode survival increase levels of leafminer mortality, but thus far nematodes are not considered to be a practical solution to leafminer infestations.

Cultural Practices

Because broadleaf weeds and senescent crops may serve as sources of inoculum, destruction of weeds and deep plowing of crop residues are recommended. Adults experience difficulty in emerging if they are buried deeply in soil.

► Vegetable Pests and Their Management
► Flies

References

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, CA, 729 pp

Leibee GL (1984) Influence of temperature on development and fecundity of *Liriomyza trifolii* (Burgess) (Diptera: Agromyzidae) on celery. Environ Entomol 13:497–501

Minkenberg OPJM (1988) Life history of the agromyzid fly *Liriomyza trifolii* on tomato at different temperatures. Entomologia Expimentalis et Applicata 48:73–84

Minkenberg OPJM, van Lenteren JC (1986) The leafminers *Liriomyza bryoniae* and *L. trifolii* (Diptera: Agromyzidae), their parasites and host plants: a review. Wageningen Agric Univ Pap 86–2. 50 pp

Parrella MP, Robb KL, Bethke J (1983) Influence of selected host plants on the biology of *Liriomyza trifolii* (Diptera: Agromyzidae). Ann Entomol Soc Am 76:112–115

Schuster DJ, Gilreath JP, Wharton RA, Seymour PR (1991) Agromyzidae (Diptera) leafminers and their parasitoids in weeds associated with tomato in Florida. Environ Entomol 20:720–723

Zehnder GW, Trumble JT (1984) Spatial and diel activity of *Liriomyza* species (Diptera: Agromyzidae) in fresh market tomatoes. Environ Entomol 13:1411–1416

American Silkworm Moths (Lepidoptera: Apatelodidae)

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American silkworm moths, family Apatelodidae, are exclusively New World, and total 252 species, mostly Neotropical (247 sp.). Three subfamilies are known: Apatelodinae, Epiinae, and Phiditiinae.

American Silkworm Moths (Lepidoptera: Apatelodidae), Figure 43 Example of American silkworm moths (Apatelodidae), *Apatelodes palma* Druce, from Ecuador.

Some researchers consider the family part of Bombycidae. The family is in the superfamily Bombycoidea (series Bombyciformes), in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults (Fig. 43) small to medium size (20–74 mm wingspan), with head scaling roughened; haustellum absent (rarely vestigial); labial palpi small; maxillary palpi absent; antennae bipectinate; body robust. Wings broadly triangular; hindwings rounded. Maculation varied but mostly shades of brown or gray, rarely more colorful, with various markings. Adults are nocturnal. Larvae are leaf feeders. Host plants include various records in Aquifoliaceae, Betulaceae, Bignoniaceae, Lauraceae, Oleaceae, Rosaceae, among others.

References

Franclemont JG (1973) Apatelodidae. In: Dominick RB, et al (eds), The moths of America north of Mexico including Greenland. Fasc. 20.1, Bombycoidea, 16–23. Classey EW, London

Seitz A (ed) (1929) Familie: Bombycidae. Die Gross-Schmetterlinge der Erde, 6:675–711, pl. 89, 140–142. A. Kernen. [Apatelodidae], Stuttgart, Germany

American Swallowtail Moths (Lepidoptera: Sematuridae)

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American swallowtail moths (Fig. 44), family Sematuridae, total 36 Neotropical species, one of which just reaches into the United States, in southern Arizona. The family is in the superfamily Uranioidea, in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults medium to large (42–100 mm wingspan), with head roughened and eyes large; haustellum naked; labial palpi upcurved, with long second segment and correctly angled short, smooth apical segment; maxillary palpi minute, 1-segmented; antennae thickened, with elongated club (slightly hooked at tip). Wings triangular, with hindwings tailed (usually hindwings with some emarginations); body sometimes robust. Maculation various shades of darker brown, with vertical lines and bands, often brightly colored in the hindwings; often with eyespots on the tails. Adults are nocturnal but some may be crepuscular.

American Swallowtail Moths (Lepidoptera: Sematuridae), Figure 44 Example of American swallowtail moths Sematuridae), *Sematura lunus* (Linnaeus), from Costa Rica.

Larvae are leaf feeders, but few known biologically. Host plants are unrecorded.

References

Seitz A (ed) (1930) Familie: Uraniidae [part]. Die Gross-Schmetterlinge der Erde, 6:829–837, pl. 139. A. Kernen, Stuttgart, Germany
Fassl AH (1910) Die Raupe einer Uranide. Zeitschrift für Wissenschaftliches Insektenbiologie 6:355
Strand E (1911) Zur Kenntnis der Uraniidengattung Coronidia Westw. and Homidia Strand n. g. (=Coronidia auct. p.p.) (Lep.). Deutsche Entomologische Zeitschrift 1911:635–649
Westwood JO (1879) Observations on the Uraniidae, a family of lepidopterous insects, with a synopsis of the family and a monograph of Coronidia, one of the genera of which it is composed. Trans Zool Soc London 10:507–542, 4 pl

American Tropical Silkworm Moths (Lepidoptera: Oxytenidae)

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American tropical silkworm moths, family Oxytenidae, include 60 species, all Neotropical. Some specialists consider this family a subfamily of Saturniidae. The family is in the superfamily Bombycoidea (series Saturniiformes), in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults medium size to large (45–98 mm wingspan), with head vertex somewhat roughened; haustellum developed; labial palpi very large; maxillary palpi absent; antennae bipectinate; body somewhat slender or robust but with hair-like scales. Wings triangular with with falcate apex but sometimes rounded; hindwings somewhat angled and with short tails or sometimes rounded. Maculation mostly white with paired dark gray vertical striae and hindwings similar, but some species are dark brown with indistinct markings. Adults nocturnal. Larvae are leaf feeders; some mimic snakes. Host plants recorded in Rubiaceae.

References

Heppner JB (2003) Oxytenidae. Lepidopterorum catalogus, (n.s.). Fasc. 115. Association for Tropical Lepidoptera, Gainesville, FL, 12 pp

Jordan K (1924) On the Saturnoidean families Oxytenidae and Cercophanidae. Novitates Zoologicae 31:135–193

Schüssler H (1936) Oxytenidae. Lepidopterorum catalogus, W. Junk, The Hague, 75:1–20

Ametabolous

Organisms that do not display the process of metamorphosis. In ametabolous organisms there is little change in body form during growth and molting.

► Metamorphosis

Ametropodidae

A family of mayflies (order Ephemeroptera).

► Mayflies

Amino Acid

Chemical compounds that may occur free, or linked by peptide bonds into proteins.

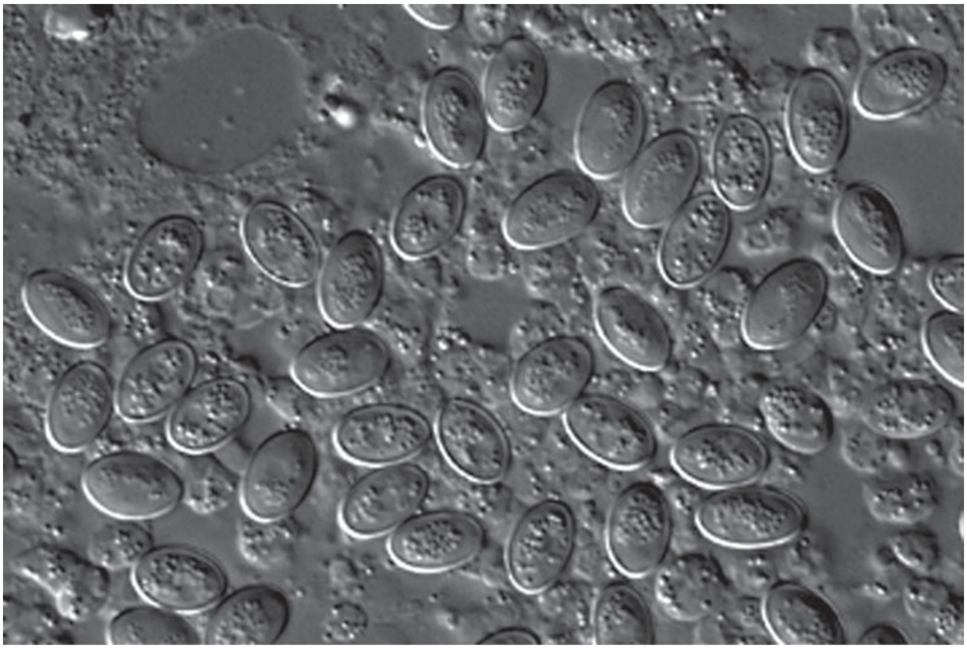
Ammophilous

Sand loving. Organisms inhabiting or preferring sandy habitats are called ammophilous (adjective) or ammophiles (noun).

Amoebae

The two best-studied insect amoebae are *Malpighamoeba mellificae* and *Malamoeba locustae*, which are associated with the honeybee, *Apis mellifera*, and the *Melanoplus* grasshoppers, respectively. The cysts of the honeybee amoeba are ingested and excyst, releasing slender primary trophozoites that penetrate and multiply in the midgut epithelium. Secondary trophozoites emerge from these cells and migrate to the lumen of the Malpighian tubules. These trophozoites, having pseudopodia, feed in the lumen and cause a flattening of the epithelial layer and a distension of the tubules. The brush border in contact with the amoeba swells in size and loses the associated secretory transport vesicles. Infected tubules contain a mix of secondary trophozoites, precysts, and cysts. The primary damage to the host bee is the malfunction of the Malpighian tubules. Both numbers of amoeba and the presence of other disease agents determine the severity of the amoebiasis in the bee. In general, this disease either induces stress or under appropriate conditions in the springtime can be debilitative, resulting in hive dwindling.

Malamoeba locustae, also known as *Malamoeba locusta*, has been detected in a wide range of grasshopper species and in a single *Thysanuran* species. Its life cycle is very similar to that observed with *M. mellificae*. The host grasshoppers ingest the resistant uninucleate cysts, and excysted primary trophozoites invade the midgut and caecal tissues. Within these tissues the trophozoites grow and divide, and within about 10 days release progeny secondary trophozoites into the lumen. These cells migrate to the lumen of the Malpighian tubules and undergo additional cell divisions (Fig. 45). The vegetative development of this amoeba damages the serosal membrane of the tubules, inhibiting their response to insect diuretic hormone. The infected tubules become packed with trophozoites and cysts. At high levels, *M. locustae* may inhibit the excretory function of the tubules and cause the grasshoppers to become lethargic prior to death. The distended, amoeba-infected tubules may rupture, releasing both trophozoites and cysts into the hemocoel. These amoebas are quickly recognized as non-self and are encapsulated by circulating phagocytic



Amoebae, Figure 45 **Light micrograph of the cysts of *Malamoeba locusta* released from infected Malpighian tubules.**

hemocytes. This disease, although a problem in laboratory cultured grasshoppers, is rarely detected in natural populations.

References

Brooks WM (1988) Entomogenous Protozoa. In: Ignoffo C (ed), Handbook of natural pesticides, vol 5. Microbial insecticides. Part A. Entomogenous protozoa and fungi. CRC Press, Boca Raton, FL, pp 1–149

Liu TP (1985) Scanning electron microscopy of developmental stages of *Malpighamoeba mellificae* Prell in the honeybee. J Protozool 32:139–144

Amoebiasis

Infection of an insect by amoebae.

Amorphoscelididae

A family of praying mantids (Mantodea).

► Praying Mantids

Amphienotomidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice, or Psocids

Amphiposocidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice, or Psocids

Amphipterygidae

A family of damselflies (order Odonata).

► Dragonflies and Damselflies

Amphitheridae

A family of moths (order Lepidoptera) also known as double-eye moths.

► Double-Eye Moths
► Butterflies and Moths

Amphitoky

A type of parthenogenesis in which both females and males are produced.

Amphizoidae

A family of beetles (order Coleoptera). They commonly are known as trout stream beetles.

► Beetles
► Wasps, Ants, Bees and Sawflies

Amplification

In molecular biology, the production of additional copies of a chromosomal sequence, found as either intrachromosomal or extrachromosomal DNA. In medical entomology, the production of increased numbers of virus in a host. This is often a prerequisite to acquisition and transmission of the virus by a blood-feeding insect.

Amplification Hosts

Hosts of viruses that allow amplification of the virus, usually used in the context of arboviruses. Some hosts do not allow amplification, and so serve as an end-point in the virus cycle.

► Dead-end Hosts

Ampulicidae

A family of wasps (order Hymenoptera).

Anagrus Fairyflies (Hymenoptera: Mymaridae)

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Anagrus species (Mymaridae), among the smallest insects known, are endoparasitoids of eggs of Odonata and Hemiptera. The genus is worldwide and about 60 species is now recognized.

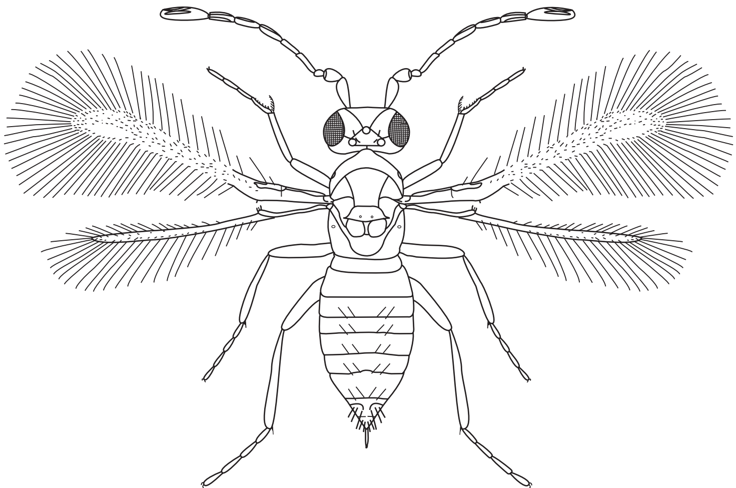
Taxonomy and Adult Morphology

The metasoma of *Anagrus* is not constricted basally, so it appears broadly sessile, the hypochaeta in front of the marginal vein is basal to the first macrochaeta, the tarsi are 4-segmented, the posterior scutellum is longitudinally divided, and the foretibia has a comb-like spur. Adult males and females are similar, differing mainly in their antennae, with nine segments and clubbed in females (Fig. 46) and 13 segments and filiform in males. Body color is often darker in males. The genitalia, both in males (the aedeagus) and in females (the ovipositor), have features of taxonomic importance.

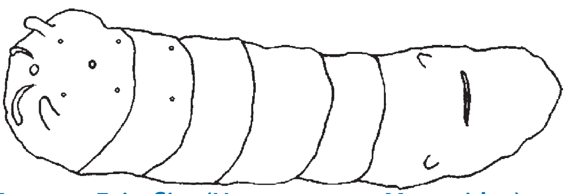
The genus is subdivided into three subgenera – *Anagrella*, *Anagrus*, and *Paranagrus*.

Biology

Like all holometabolous insects, *Anagrus* species have three distinct immature stages, egg, larva and pupa. The egg is stalked, with an ovoid body that swells during embryogenesis. There are two, apodous, larval instars (Fig. 47), which appear completely different from one another. The first instar is sacciform and usually attached to the egg chorion. It does not show any cuticular structure that could serve to feed, breathe or feel. It is completely immobile and probably obtains nourishment and breathes through its cuticle. The second instar is divided weakly into six body segments, has a mouth and a salivary gland opening, two mandibles and an anus, and various other, probably sensory, structures. No spiracle is present. Second instar larvae are very active and fight each other when in the same host egg. The mature larva (prepupa) develops inside the egg into an exarate pupa and does not spin a cocoon. When development is complete, adults are



Anagrus Fairyflies (Hymenoptera: Mymaridae), Figure 46 **Adult female of *Anagrus* sp.**



Anagrus Fairyflies (Hymenoptera: Mymaridae), Figure 47 **Larva of *Anagrus* sp.**

recognizable through the host egg chorion, through which they chew a hole to exit. After emergence the adults shed their waste products (meconium). Males are usually protandrous.

Behavior and Ecology

Reproduction is bisexual or parthenogenetic. The latter reproduction is usually arrhenotokous but, rarely, thelytokous parthenogenesis has been recorded. Females are ready to oviposit as soon as they emerge. Copulation, if it occurs, is usually very quick (some tens of seconds) and inseminated females generally do not copulate again. When fed with sugar water, honey or nectar, adults may live for up to 10 days. It is thought that adult host feeding may occur as in other parasitoids.

Anagrus species mainly parasitize leafhoppers (Cicadellidae), planthoppers, (Delphacidae) and damsel- or dragonfly (Odonata) eggs, all of which are embedded in plant tissue. To reach the eggs, females insert their ovipositor into the slit made by the host or through the plant tissue itself, depending on the species. Adults occur in various habitats, both natural and cultivated, depending on where their hosts occur. This includes dry habitats such as vineyards and beet fields to damp or aquatic ones (ponds) where host eggs are found in plants such as *Cyperus* or *Nuphar*.

Certain *Anagrus* species can develop both as solitary or gregarious parasitoids in eggs of different size, whereas others appear to be much more specialized on eggs of the same size, in which they always develop as solitary parasitoids.

Many *Anagrus* are extremely important because they provide control of potentially serious pests on many agricultural crops. The most important examples are against leafhoppers such as *Empoasca vitis* Goethe and *Zygina rhamni* (Ferrari) in vineyards in Europe and *Erythroneura* spp. in North America, against leaf- and planthoppers such as *Nilaparvata* spp. and *Sogatella* spp. on rice in eastern Asia, and against *Perkinsiella sacharicida* Kirkaldy on sugarcane in Hawaii.

Some biological supply companies mass produce and sell *Anagrus atomus* L. for biological control. Care must be taken to ensure the sanitary conditions of the product as the parasitoid is bred on the natural host eggs inserted into plant tissue, which could be a potential vehicle for other pests or diseases.

References

Chiappini E, Lin NQ (1998) *Anagrus* (Hymenoptera: Mymaridae) of China, with descriptions of nine new species. Ann Entomol Soc Am 91:549–571

Chiappini E, Triapitsyn SV, Donev A (1996) Key to the Holarctic species of *Anagrus* Haliday (Hymenoptera: Mymaridae) with a review of the Nearctic and Palaearctic (other than European) species and descriptions of new taxa. J Nat Hist 30:551–595

Moratorio MS (1990) Host finding and oviposition behavior of *Anagrus mutans* and *Anagrus silwoodensis* Walker (Hymenoptera: Mymaridae). Environ Entomol 19:142–147

Moratorio MS, Chiappini E (1995) Biology of *Anagrus incarnatosimilis* and *Anagrus breviphragma*. Bollettino di Zoologia Agraria e di Bachicoltura, Serie II, 27:143–162

Triapitsyn SV (1997) The genus *Anagrus* (Hymenoptera: Mymaridae) in America south of the United States: a review. Ceiba 38:1–12

Triapitsyn SV (1998) *Anagrus* (Hymenoptera: Mymaridae) egg parasitoids of *Erythroneura* spp. and other leafhoppers (Hemiptera: Cicadellidae) in North America vineyards and orchards: a taxonomic review. Trans Am Entomol Soc 124:77–112

Anajapygidae

A family of diplurans (order Diplura).

► Diplurans

Anal Angle

The hind angle of the forewings.

► Wings of Insects

Anal Cell

A cell in the anal area (anal lobe) of a wing.

► Wings of Insects

Anal Comb

This term is applied to a variety of structures that differ depending on the taxon. In flea (Siphonaptera) larvae, it refers to several rows of setae on the tenth abdominal segment; in caterpillars (Lepidoptera) it refers to a ventral projection at the tip of the abdomen that is used to eject frass; in some beetle (Coleoptera) larvae it refers to cerci-like projections near the tip of the abdomen.

Anal Gills

Gills found at the tip of the abdomen and usually consisting of three to five small clusters.

► Abdomen of Hexapods

Anal Hooks

In Lepidoptera, small hook or club-shaped structures at the tip of the abdomen that serve to anchor the pupa to the cocoon or silk pad.

Anal Furrow

The suture-like groove in the membrane of the wing.

► Wings of Insects

Anal Legs (Prolegs)

In holometabolous larvae, especially Lepidoptera larvae, the appendages of the tenth abdominal segment (the terminal prolegs).

Anal Lobe

The posterior region of the wing, occupied by the anal veins.

► Wings of Insects

Anal Loop

A cluster of cells between the anal wing veins, or between the cubitus and anal vein, in Odonata.

► Wings of Insects

Anal Plate

The shield-like plate or dorsal covering on the terminal segment in caterpillars, and some other larvae. It usually is dark in color, and is also called the anal shield.

Anal Tube

Eversible, tubular organs in the anal region of larval Coleoptera. These organs are armed with microspines and assist in attachment to the substrate.

Anal Vein

Longitudinal unbranched vein, or veins, extending from the base of the wing to the outer margin of the wing, below the cubitus vein.
► Wings of Insects

Anamorphosis

Postembryonic development in which additional abdominal body segments are added at the time of molting (the opposite of epimorphosis).

Anaxyelidae

A family of wood wasps (order Hymenoptera, suborder Symphyta). They commonly are known as incense-cedar wood wasps.
► Wasps, Ants, Bees and Sawflies

Ancistrosyllidae

A family of fleas (order Siphonaptera).
► Fleas

Andean Moon Moths (Lepidoptera: Cercophanidae)

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Andean moon moths, family Cercophanidae, include 30 species of mostly austral South American moths. There are two subfamilies: Cercophaninae (four sp.) and Janiodinae (26 sp.). Some specialists consider this family a subfamily of Saturniidae. The family is in the superfamily Bombycoidea (series Saturniiformes), in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults (Fig. 48) medium size to large (24–105 mm wingspan), with head vertex roughened; haustellum absent; labial palpi very large; maxillary palpi absent; antennae bipectinate; body robust, with long hair-like scales. Wings broadly triangular, often with apex falcate, or more rounded; hindwings rounded or emarginated but sometimes with tails. Maculation various, but mostly shades of brown with diagonal line and fainter markings, but some with long tails and lighter tan, and with eyespots. Adults are nocturnal. Larvae are leaf feeders.

Andean Moon Moths (Lepidoptera: Cercophanidae), Figure 48 Example of Andean moon moths (Cercophanidae), *Cercophana venusta* (Walker) from Chile.

Host plants recorded in Celastraceae, Lauraceae, Saxifragaceae, and Tiliaceae.

References

Angulo AO, Heppner JB (2004) Cercophanidae. Lepidopterorum catalogus, (n.s.). Fasc. 116. Association for Tropical Lepidoptera, Gainesville, FL, 8 pp

Jordan K (1924) On the Saturnoidean families Oxytenidae and Cercophanidae. Novitates Zoologicae 31:135–193, pl. 6–21

Schüssler H (1936) Cercophanidae. Lepidopterorum catalogus, W. Junk, The Hague, 76:1–12

Ureta RE (1943) Revisión del género Polythysana Wlk. (Saturniidae). Boletin del Museo Nacional de Historia Natural de Chile 21:55–70, 4 pl

Wolfe KL, Balcázar LMA (1994). Chile's *Cercophana venusta* and its immature stages (Lepidoptera: Cercophanidae) Trop Lepidoptera 5:35–42

Andesianidae

A family of moths (order Lepidoptera) also known as valdivian forest moths.

► Butterflies and Moths
► Valdivian Forest Moths

Andrenidae

A family of bees (order Hymenoptera, superfamily Apoidae).

► Bees
► Wasps, Ants, Bees and Sawflies

Andrewartha, Herbert George

Herbert Andrewartha was born in Perth, Australia, on December 21, 1907. In 1924, he entered the University of Western Australia from which he obtained a bachelor's degree in agriculture. He was then appointed as assistant entomologist by the Western Australia Department of Agriculture. He began a study of a weevil pest of fruit trees, *Otiorhynchus cribricollis*, that required detailed autecological studies. In 1933, he moved to Melbourne, appointed by the CSIR as assistant research officer, to work on the autecology of *Thrips imaginis*, a pest of apple trees. He worked in the School of Agriculture and Forestry at the University of Melbourne. While working, he was able to complete a thesis for which he was awarded the degree of Master of Agricultural Sciences. He married, and in 1935 moved to the Waite Agricultural Research Institute in Adelaide. His main duties now turned to a study of *Austroicetes cruciata*, a plague grasshopper, and diapause of its eggs. However, his supervisor, who had been working on *Thrips imaginis*, died suddenly, leaving copious unanalyzed data, whose completion and publication fell to Herbert. The published work was criticized because it concluded that climatic factors were all-important in the population dynamics of the pest, without room for action of biotic factors. But it led to collaboration with L.C. Birch on a book (1954) "The distribution and abundance of animals." Then, after Herbert moved to the Zoology Department of the University of Adelaide, it led to a book designed as a textbook for students: (1961) "Introduction to the study of animal populations." In 1962, Herbert was appointed chairman of the Zoology Department. In the 1960s, with collaborators, he developed a program for control of *Dacus tryoni*, Queensland fruit fly, by release of sterile males. His next book, also co-authored with L.C. Birch was (1984) "The ecological web." He died on January 27, 1992, following his wife by some years, but survived by his son and daughter.

Reference

Birch LC, Browning TO (1993) Herbert George Andrewartha 1907–1992. Historical Records of Australian Science 9(3), Available at www.asap.unimelb. edu.au/bsparcs/aasmemoirs/andrewar.htm Accessed August 2002

Androconia

In Lepidoptera, glandular wing and body scales. Scent scales.

Androparae

In aphids, viviparous females that are produced on the secondary host in the autumn, and then fly to the primary host to produce males.

► Aphids

Anemometer

An instrument used for measuring wind speed, an important tool when considering use of pesticides because high wind speeds can result in pesticide drift.

Anemotaxis

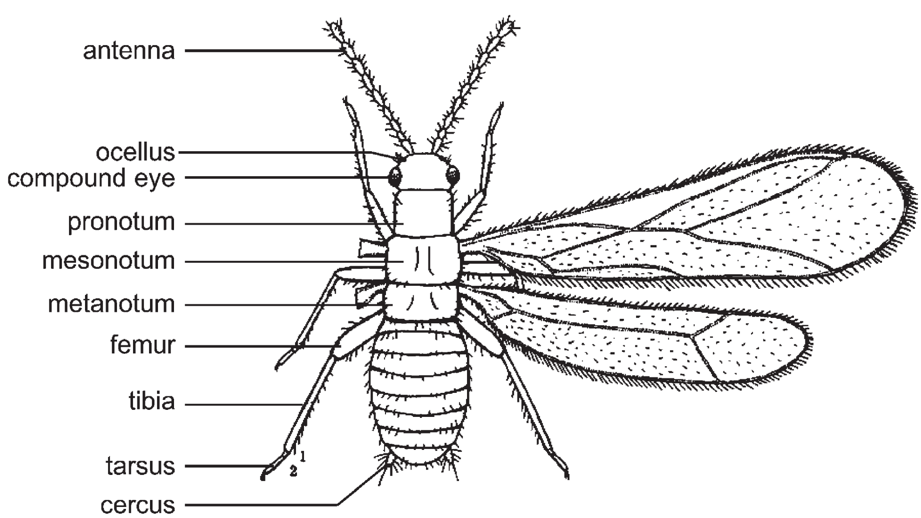
A movement in response to air movement or air currents.

Angel Insects (Zoraptera)

This is a small group of minute insects. They are infrequently encountered, and poorly known. The order name is based on the Greek words *zoros* (pure), *a* (without), and *pteron* (wing). There are only about 30 species described, all in the family Zorotypidae.

Characteristics

Angel insects are only about 3 mm long, with a wing span of 7 mm. They are dimorphic: a wingless form that lacks eyes, ocelli, and is only slightly pigmented, and a winged form (Fig. 49) that bears eyes, ocelli, and is darker in color. They have chewing mouthparts. The antennae are filiform, and consist of nine segments. The legs are unspecialized, the tarsi 2-segmented. The wings have simplified venation, and the wings can be shed, as is the case with termites. The abdomen is cylindrical and consists of 11 segments. Very short, 1-segmented cerci occur near the tip of the abdomen. Metamorphosis is not pronounced.



Angel Insects (Zoraptera), Figure 49 **A diagram of an angel insect showing a dorsal view. The wings are removed from the left side of the body.**

Biology

Angel insects are found beneath bark, in humus, decaying wood, and sometimes in association with termites. They are believed to feed on fungi. Apparently they swarm, and drop wings after swarming. They are gregarious, but there is no evidence of social organization.

References

Arnett RH Jr (2000) American insects, 2nd edn. CRC Press, Boca Raton, FL, 1003 pp

Riegel GT (1987) Order Zoraptera. In: Stehr FW (ed) Immature insects, vol 1. Kendall/Hunt Publishing, Dubuque, Iowa, pp 184–185

Gurney AB (1938) A synopsis of the order Zoraptera with notes on the biology of *Zorotypus hubbardi* Caudell. Proc Entomol Soc Wash 40:57–87

Angoumois Grain Moth, *Sitotroga cerealella* (Lepidoptera: Gelechiidae)

This is an important primary pest of stored grain.

► Stored Grain and Flour Insects

Angulate

Forming an angle.

Anholocyclic Life Cycle

A life cycle in which there is a complete lack of male insects (generally aphids). In this type of life cycle only viviparous parthenogenetic females are present throughout the year. (contrast with holocyclic life cycle)

► Aphids

Animal Sleeping Sickness

Also known as nagana, this is a disease of animals caused by protozoans in the genus *Trypanosoma*. In humans the same disease is known as African sleeping sickness or human trypanosomiasis. It is transmitted by tsetse flies in Africa.

► Trypanosomes
► Tsetse Flies
► Sleeping Sickness or African Trypanosomiasis

Anisembiidae

A family of web-spinners (order Embiidina).

► Web-spinners

Anisopodidae

A family of flies (order Diptera). They commonly are known as wood gnats.

► Flies

Anneal

The process by which the complementary base pairs in the strands of DNA combine.

Annual

A plant that normally completes its life cycle of seed germination, vegetative growth, reproduction, and death in a single growing season or year.

Anobiidae

A family of beetles (order Coleoptera). They commonly are known as death-watch beetles.

► Beetles

Anomosetidae

A family of moths (order Lepidoptera). They also are known as Australian primitive ghost moths.

► Australian Primitive Ghost Moths
► Butterflies and Moths

Anoplura

A suborder of wingless ectoparasitic insects commonly known as sucking lice (order Phthiraptera). It is sometimes treated as an order.

► Chewing and Sucking Lice

Anostostomatidae

A family of crickets (order Orthoptera). They commonly are known as wetas and king crickets.

► Grasshoppers, Katydids and Crickets

Anteclypeus

The lower of the two divisions of the clypeus.

► Mouthparts of Hexapods

Antagonist

An antagonist usually is an organism (usually a pathogen) that does no significant damage to the host, but its colonization of the host protects the host from significant subsequent damage by a pest.

Antecosta (pl., antecostae)

An internal ridge on the anterior portion of a tergum or sternum. It serves as a point of attachment for the longitudinal muscles.

Antenna (pl., antennae)

The paired segmented sensory organs, borne one on each side of the head. The antennae commonly protrude forward. Each antenna (Figs. 50 and 51) consists of three segments: the basal scape, a small pedicel, and an elongate flagellum. The flagellum is usually subdivided into many sections.

► Antennae of Hexapods

Antennae of Hexapods

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According to the known data on anatomy and embryology, the antennae are postoral structures of an appendicular nature that have been displaced, and now situated secondarily above the anterolateral regions of the cranium, in front of the mouth.

Taking into account their intrinsic musculature, two fundamental types of antennae can be distinguished:

Segmented Type

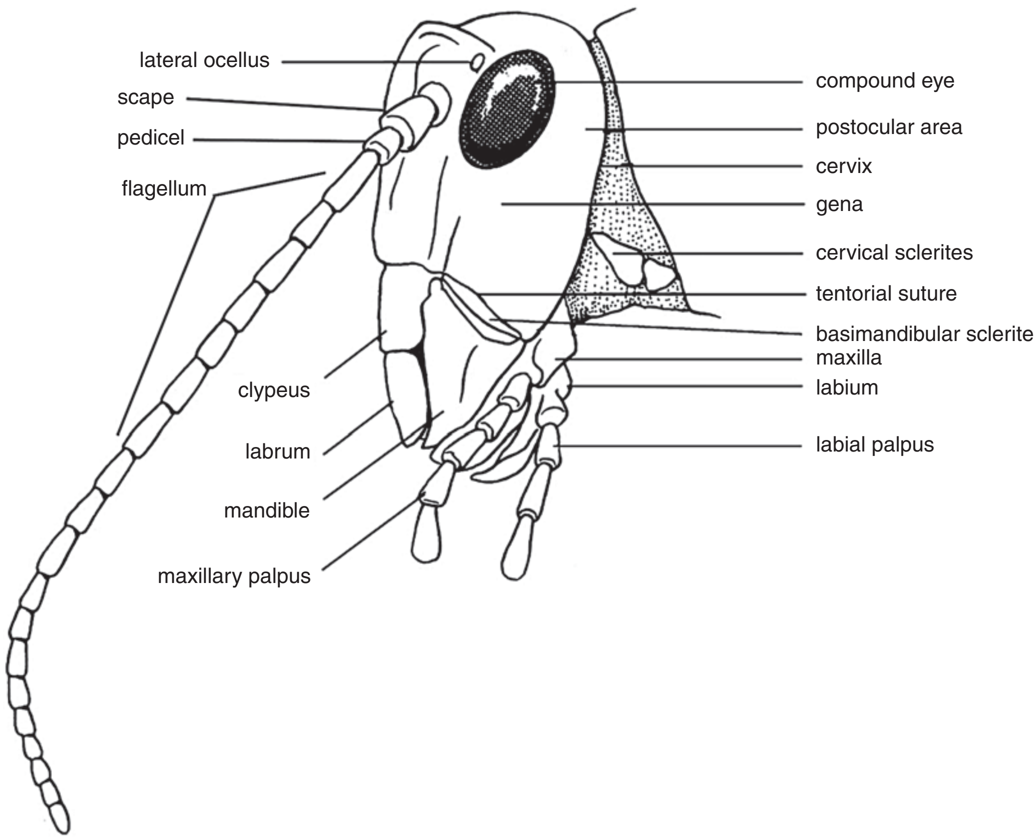
Each antennal division (antennomere) possesses intrinsic musculature (although the last segment generally lacks it). This type is found in Diplura and Collembola.

Annulated Type

Three segments are recognized that, from the basal to the apical zone of the antenna, are called scape, pedicel and antennal flagellum (Fig. 50).

The scape is a robust segment that unites the head capsule with a cuticular reinforcement (Fig. 51), the antennal socket (also called the torulus). In the antennal socket one or two condyles are distinguished, which serve to articulate the scape. The second segment is called the pedicel, and it usually varies in form and development, although it is generally small. Lastly, the flagellum is usually divided into several divisions called flagellomeres.

The movement of the antennae is carried out through extrinsic or motor muscles of the scape, generally forming three or four functional groups. Depending on the insect group, these muscles are inserted in the head capsule or in the tentorium.



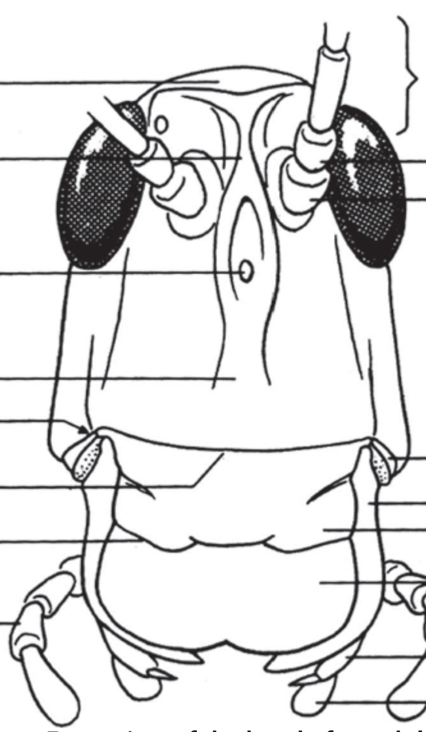
Antennae of Hexapods, Figure 50 **Side view of the head of an adult grasshopper, showing some major elements.**

The antennae usually have bristles and sensilla of different types that act as chemoreceptor-, thermoreceptor- or hygroreceptor-type sensory organs. In addition, the antennae of males display modifications tending to increase their surface area, which permits harboring a great number of sensilla and acting as "detectors" that detect pheromones emitted by the females, and enable (usually) the males to locate the females for reproductive functions. Certain modifications in the antennae of the males can also be related to particular courtship behavior prior to mating.

In relation to the functions carried out by the antennae, it is necessary to highlight the presence, in the pedicel, of Johnston's organ, which is formed by cordotonal sensilla. It is fundamentally a proprioreceptor organ that provides information about the position of the antennae with respect to the head, the direction and force of the wind, or of the water currents in aquatic insects. In addition, it can act as an auditory organ in male mosquitoes and chirinomids, which perceive the sound produced by the females in flight.

The number of flagellomeres is a character that, in certain cases, is related to the sex, as occurs in some Aculeate Hymenoptera in which the males display 11 flagellomeres and the females 10. In others, it represents an important taxonomic character, emphasized in this sense the family Argidae (Hymenoptera: Symphyta) whose individuals display the flagellomere undivided.

Various types of antennae exist (Fig. 52), the appearance of which is owed fundamentally to the variation in form and development of the flagellomeres. The most important are:



Antennae of Hexapods, Figure 51 Front view of the head of an adult grasshopper, showing some major elements.

Filiform

The flagellomeres, normally numerous, are narrow, cylindrical, and of similar size. It is the most common type in the insects.

Moniliform

There exists a narrowing in the union of each flagellomere, which are more or less spherical, with the antenna acquiring a "rosaried" appearance (like the beads of a rosary). There are examples in various families of beetles.

Setaceous

The flagellomeres are extremely fine and diminish in diameter gradually toward the tip; the antenna thus acquires an appearance of seta or hair. The antennae of Odonata constitute a typical example.

Aristate

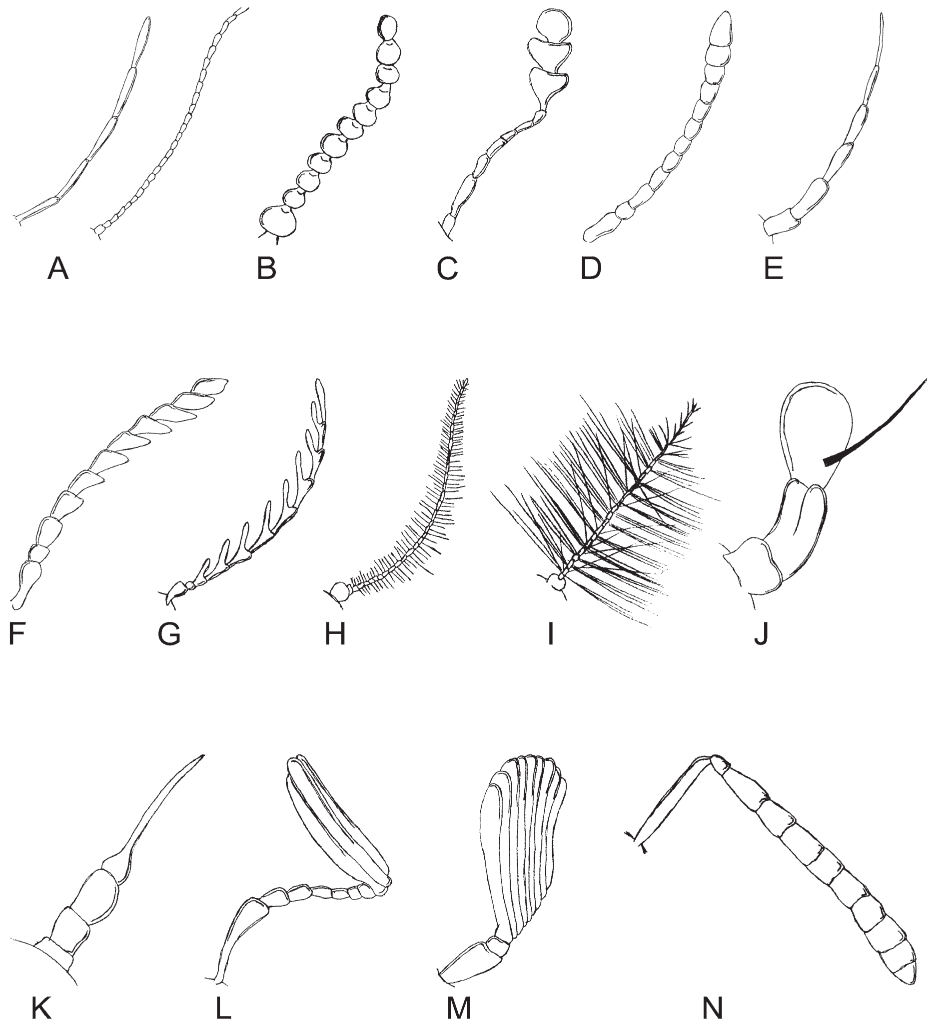
The last flagellomere is normally very wide and bears a conspicuous bristle named the arista. Examples are found in Diptera (Syrphidae and Muscidae).

Stylate

The last flagellomere is prolonged apically in a fine and elongated process named the style. Examples are found in Diptera (Rhagionidae and Asilidae).

Clavate

The flagellomeres increase in diameter gradually toward the apex. Examples are found in Coleoptera (Coccinellidae and Tenebrionidae).



Antennae of Hexapods, Figure 52 **Some common types of antennal forms: A, filiform; B, moniliform; C, capitate; D, clavate; E, setaceous; F, serrate; G, pectinate; H, bipectinate; I, plumose; J, aristate; K, stylate; L, lamellate; M, flabellate; N, geniculate.**

Capitate

In this case the last flagellomeres are of greater diameter, in contrast with the preceding, forming a "club" or "mace." Examples are found in Coleoptera (Nitidulidae and Silphidae).

Serrate

The flagellomeres display pointed, lateral prolongations, on one side or on both. Examples are found in Coleoptera (Elateridae).

Pectinate

The flagellomeres project laterally, forming a fine and more or less elongated projection. When it is produced over two sides of each flagellum, the antennae are called bipectinate. Examples are found in Coleoptera (Pyrochroidae).

Flabellate

The flagellum displays long, flattened or more or less cylindrical expansions. Examples are found in some species of Coleoptera (Scarabeidae).

Lamellate

Only the last flagellomeres display long, lateral expansions. Examples are found in Coleoptera (Scarabeidae, subfamily Melolonthinae).

Plumose

Flagellomeres with numerous long hairs are arranged in a feather-like or whorled form. Examples are found in male mosquitoes (Diptera).

Geniculate

The scape is relatively long, forming a clear angle with the rest of the antenna (pedicel plus flagellum). Examples are found in Hymenoptera (Formicidae and Chalcidoidea), and in Coleoptera (Lucanidae). Within this type of antenna, particular variations can exist, as in the case of the Ormyridae (Hymenoptera: Chalcidoidea), in which the first divisions of the flagellum are of a lenticular type (lens shaped, or double convex).

References

Denis JR, Bitsch J (1973) Morphologie de la tête des insects. In: Grassé PP (Dir) Traité de Zoologie, VIII (I):1–593

Gillot C (1995) Entomology, 2nd edn. Plenum Press, New York, NY

Manton SM (1977) The Arthropoda. Habits, functional morphology and evolution. Clarendon Press, Oxford, UK

Quéinnec E (2001) Insights into arthropod head evolution. Two heads in one: the end of the “endless dispute”? Annales de la Société Entomologique de France 37:51–70

Snodgrass RE (1951) Comparative studies on the head of mandibulate Arthropods. Comstock, Ithaca, NY

Antennal Club

On a clubbed antenna, the enlarged distal segments.

► Antennae of Hexapods

Antennal Fossa

A groove or cavity in which the antennae are located or concealed. This is also called the antennal insertion.

► Antennae of Hexapods

Antennal Sclerite

A ring into which the basal joint of each antenna is inserted.

► Antennae of Hexapods

Antennation

Sensory or tactile movements with the antennae that result in contact of the antennae with an object.

Antennule

A small antennal or feeler-like process.

Anterior

This term usually is used to refer to the end of the body containing the head, or the direction of the head, or the front of the insect.

Anthelidae

A family of moths (order Lepidoptera) also known as Australian lappet moths.

► Australian Lappet Moths
► Butterflies and Moths

Anther Smut of Carnations

This is a fungal disease of carnations that is transmitted by insects.

► Transmission of Plant Diseases by Insects

Anthicidae

A family of beetles (order Coleoptera). They commonly are known as antlike flower beetles.

► Beetles

Anthocoridae

A family of bugs (order Hemiptera). They sometimes are called minute pirate bugs.

► Bugs

Anthomyiid Flies

Members of the family Anthomyiidae (order Diptera).

► Flies

Anthomyiidae

A family of flies (order Diptera). They commonly are known as anthomyiid flies or root maggots.

► Flies

Anthomyzid Flies

Members of the family Anthomyzidae (order Diptera).

► Flies

Anthomyzidae

A family of flies (order Diptera). They commonly are known as anthomyzid flies.

► Flies

Anthophilous

Flower loving. Most insects that feed on nectar or pollen are anthophilous, including many butterflies and moths (Lepidoptera), wasps, ants and bees (Hymenoptera), but also numerous flies (Diptera), beetles (Coleoptera) and thrips (Thysanoptera).

► Pollination and Flower Visitation
► Butterfly Gardening
► Night Blooming Plants and their Insect Pollinators
► Pollination by Yucca Moths
► Apiculture
► Plant Extrafloral Nectaries

Anthribidae

A family of beetles (order Coleoptera). They commonly are known as fungus beetles.

► Beetles

Anthrophagy

Feeding on humans by other organisms. The most common anthrophagous organisms are insects, particularly biting flies, followed by lice, fleas, and ticks.

► Mosquitoes
► Lice
► Fleas
► Ticks
► Pathogen Transmission by Arthropods

Anthrophoridae

A family of bees (order Hymenoptera, superfamily Apoidae). They commonly are called cuckoo bees, digger bees, and carpenter bees.

► Bees, Wasps, Ants and Sawflies

Anthropocentric

An interpretation based on the belief that humans are the central fact or element of the universe, and interpreting everything in relation to human values of interests.

Anthropomorphism

The attribution of human qualities or forms to animals or their behaviors.

Anthropophilic

An insect that prefers humans as a source of food. A blood-sucking insect that feeds on humans.

Antibiosis

A characteristic, often a chemical within a plant, that inhibits survival or reproduction when an insect feeds upon it.

► Plant Resistance to Insects

Antibiotic

A chemical produced by a microorganism that affects the ability of another microorganism to survive or grow.

Anticodon

The triplet of nucleotides in a transfer RNA molecule that is complementary to and base pairs with a codon in a messenger RNA.

Antidote

A treatment used to treat the effects of chemical (e.g., insecticidal) poisoning.

Antidiuretic Hormones

Hormones acting on the hindgut to promote water reabsorption and conservation.

Anti-Drift Agent

A compound that is added to pesticides to reduce the number of droplets produced at the spray nozzle, and therefore to reduce the possibility of the product drifting away from the target.

Antixenosis

An effect due to a characteristic, often a physical or chemical attribute of a plant, that deters feeding or oviposition. This is also called nonpreference.

► Plant Resistance to Insects

Antlike Flower Beetles

Members of the family Anthicidae (order Coleoptera).

► Beetles

Antlike Leaf Beetles

Members of the family Aderidae (order Coleoptera).

► Beetles

Antlike Stone Beetles

Members of the family Scydmaenidae (order Coleoptera).

► Beetles

Antlions

Members of the family Myrmeleontidae (order Neuroptera).

► Lacewings, Antlions and Mantidflies

Ant-plant Interactions

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Drop a spoon at a picnic and the ubiquity of ants (family Formicidae) is soon apparent. Ants are everywhere, lurking in leaf litter or brazenly scouring terrestrial and arboreal habitats for food in any form. Except in extreme climates that are inhospitable to insects, most terrestrial organisms have necessarily evolved ways to reduce the damage ants can cause, and many have managed even to extract benefits from them. Relationships between ants and humans provide examples: not only have we devised means of protecting our food stores from ants, but we have utilized ants to protect our food. Centuries ago, nests of Old World weaver ants (*Oecophylla smaragdina*) were cultivated in Asian orchards to control plant pests. Workers of this highly predatory species captured and devoured both the juvenile and adult stages of herbivorous (plant-eating) insects.

In some ways, early ants were better suited to serve plants than to injure them. Descended from predatory wasps, they were poorly adapted for herbivory (consumption of plant tissues), and no ant is truly folivorous (leaf-eating). Unable to digest cellulose themselves, ants also differ from termites in lacking gut microbes that can do this for them. Although much of the plant world is therefore not available to ants, plant sap, seeds, and fruit pulp are relatively easy to digest, and many (mostly arboreal) taxa feed on those resources. Such foods tend to be rich in carbohydrate (CHO) but poor in nitrogen (N) (amino acids, peptides and proteins), and dietary excesses of energy-rich CHOs may have subsidized colonization of the arboreal zone, where foragers must commute around a three-dimensional and poorly connected environment. Most ants also scavenge N-rich arthropod carrion, and many are active predators that can potentially benefit plants by attacking their herbivores. In some taxa, associations with intracellular and extracellular gut microbes contribute to the colony's N economy through N-recycling and possibly upgrading (conversion of non-essential to essential amino acids).

When disturbed by ants, many active insects and other animals can simply fly or walk to safety, but for plants and their seeds, as well as for comparatively immobile nesting animals and juvenile insects, there are no ready escape routes. It is in these organisms that we find some of the most unique or unusual adaptations for both defending against ants and exploiting their behaviors to advantage. Here, several categories of interactions between ants and plants are explored, together with some of the myriad ways in which plants have evolved to reduce or promote association with these ubiquitous insects. Included also are the influence of plant resources on ant ecology and evolution, and the effects of ants on the evolution of plant defenses.

Ants as Seed Predators

In warm deserts and other arid regions, ants are often both abundant and diverse, and annual and perennial plants are present more often as seeds than as adults. Here, seed-eating ants abound and may exert strong selection pressures on plant. Selection is mediated mainly by seed consumption, but also by ant effects on soil disturbance and nutrient availability. Seed-eating "harvester ants" typically return seeds individually to a central nest site where they husk and then cache them in underground granaries, often for long time periods. By storing foods that degrade slowly over time, ant colonies can persist in habitats where the production of seeds and other resources is sporadic and unpredictable. During periods of low food availability, many of these ants simply remain underground and forego the risks and poor rewards of external activity.

The small individual sizes and ectothermy of ants are correlated with low foraging costs, enabling these insects to forage economically even for tiny seeds with dispersed distributions. Ants can

Ant-plant Interactions, Figure 53 An extensive nest of leaf-cutter ants in the genus *Atta* (above) and high rates of leaf removal from an unlucky tree (below).

therefore reduce soil seed banks to lower levels than can large, endothermic ("warm-blooded") vertebrate seed-eaters like rodents and birds. Those taxa have higher foraging costs and tend to specialize in feeding on seeds in high density "hotspots," either in soils or on the plants themselves. Though reduced seed densities can potentially affect both plant densities and community composition, ants may commonly have less impact on plant communities than do vertebrate seed predators. This is so because seed predation by ants tends to fall most heavily on offspring of small-seeded plant species, whereas that by vertebrates often targets large seeds. Seedlings germinating from large seeds begin life with more resources than do those from small seeds and are therefore superior competitors within plant communities. Consequently, the removal of small seeds by ants has comparatively little effect on the densities of large-seeded species, while the removal of large seeds by rodents may lead to increases in the densities of small-seeded species.

In at least some localities, differences in seed size specialization by ants and rodents account for disparities in the short-term and long-term effects of these granivores on one another's populations. When seed-eating rodents were removed experimentally in one study, densities of harvester ants first increased and then declined. The short-term increase was likely due to competition between the two types of granivores, as there was some overlap in the sizes and species of seeds used by the two groups. However, rodent removal eventually led to increases in the densities of large-seeded plants, which subsequently out-competed small-seeded species, to the long-term detriment of ants.

Coexisting species of harvester ants often differ in worker body sizes, and small ants cannot carry the largest seeds. To a degree, therefore, worker size differences may remove small and large ants from resource competition with one another, and also determine disparate effects on plant communities. When ant communities are disturbed, either directly or by the introduction of non-native ants, there can be consequences for plant communities. Pathways of interaction can be indirect and complex. For example, if an introduced ant species produces a decline in populations of a native harvester ant, plant species on which the native ants specialize may increase at the expense of other components of the plant community. Such changes in community composition are hard to predict, and often become apparent only over long time periods, especially in arid lands with variable climates.

On an evolutionary time scale, some plants have acquired adaptation that reduce depredation of their progeny by ants. An example of such an adaptation is the use of hygroscopic awns (e.g., that of *Erodium cicutarium*) that alternately extend and coil when wet and dry, respectively, pushing the attached seeds beneath the soil surface. Unlike seed-eating rodents, harvester ants have little access to individually buried seeds, so such awns do appear to proffer a refuge from predation by granivorous ants. Whether mechanical, chemical, or phenological (e.g., timing of seed production), mechanisms of seed escape from granivorous ants remain poorly explored.

Early "Farmers" (Attines)

To the uninitiated, the cutting and transport of leaf, flower and fruit fragments by New World ants in the tribe Attini looks a great deal like herbivory (Fig. 53). However, as was originally proposed by Thomas Belt, a nineteenth century British mining engineer and amateur naturalist, the ants themselves do not digest cut leaves. Rather, they cultivate fungi that degrade cellulose and other plant products otherwise inaccessible to the ants. In more recent members of this group (species of *Atta* and *Acromyrmex*), the workers themselves feed on plant sap released from cut leaves, whereas larvae are fed gonglydia, or swollen tips of fungal hyphae (arms). Together, fungal mycelia and gongylidia supply CHOs (simple sugars, as well as glycogen in *Acromyrmex*), lipids and N (amino acids and protein). On her nuptial flight, the queen carries fragments of fungal gardens in her infrabuccal chamber, adjacent to the anterior digestive tract in the head. After mating, she removes her wings, excavates a terrestrial nest, begins to cultivate her fungal garden, and feeds her first worker brood on trophic eggs composed of resources from her degraded wing muscles.

Workers eventually take over cultivation and maintenance of the fungal gardens. Larger castes cut, drop, and carry the leaf fragments, while their smaller nestmates "hitch-hike" rides on leaf fragments to defend larger workers against parasitic phorid flies, and care for brood inside the nest. There, they lick and shred leaf fragments into finer pieces, and then chew their edges, depositing fecal droppings with digestive enzymes to aid in decomposition. Protein-degrading enzymes are recycled from the fungi themselves through the ant's digestive system, which lacks enzymes to degrade them. New leaf fragments are then inoculated with mycelia of older parts of the garden and fertilized with plant material (recent attines) and/or feces and animal matter (early attines). Through application of growth hormones, enzymes, nutrients, and antibiotics, higher attines maintain their fungi almost in monocultures. Nevertheless, recent studies by M. Poulsen, C.R. Currie, and colleagues have identified a virulent fungal pathogen of the gardens, as well as a bacterium living in fovea (small depressions) in worker exoskeleton. These filamentous bacteria, or actinomycetes, produce antibiotics directed mainly toward the common pathogen.

Although most folivorous insects are limited to eating a narrow spectrum of plant species, use of fungi as agents of digestion may explain leafcutter tolerance of more varied diets. Nevertheless, different taxa of higher attines specialize on grasses or dicots, and specialization exists even within those categories. Like other herbivores, leafcutters are especially likely to harvest tender young leaves, which lack the fiber and lignin to make them tough. For *Atta cephalotes*, J.J. Howard and colleagues showed that, the diet is apparently not chosen in response to energy, nitrogen, or moisture content, but rather to avoid various terpenoids that could poison fungi.

According to U.G. Mueller and colleagues, all attines appear to have descended from a common ancestor that forged relationships with fungi either growing on walls of leaf-litter nests or using ants to disperse their spores. Together, with gene sequence data, the fossil record, and confinement of this group to the New World, suggests that this ant-fungal partnership first formed between 45 and 65 million years ago. Direct transmission of fungi from queens to reproductive daughters provided opportunities for greater specialization and dependency to evolve in both partners. Nevertheless, new fungal species have also been domesticated by older, less specialized ant taxa in recent times.

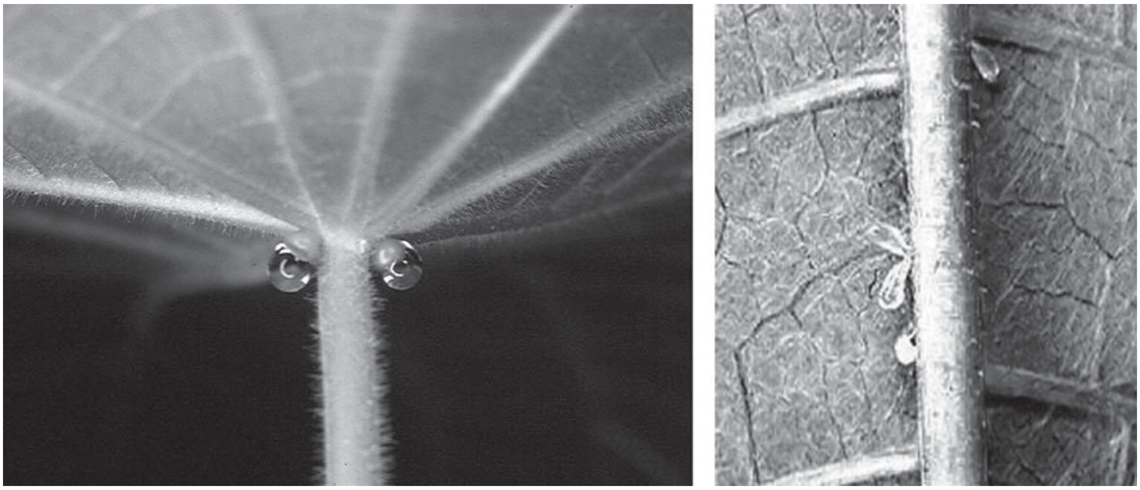
The success of the attine-fungal partnership is measurable in its impact on the forest. Mature *Atta* nests can range over several hundreds of square meters, and worker columns can reach trees more than 100 m from the colony along trails cleared of vegetation. In tropical areas not regularly flooded, attines can be very abundant and exact a considerable toll on plants. Some accounts in the literature judge them to be responsible for 12–17% of all herbivory, but these figures may be too high because they fail to include the mostly invisible losses of plant resources to sap-feeding insects. Throughout much of the Neotropics, higher attines also thrive in disturbed areas dominated by poorly defended pioneer (weedy) plant species. They are similarly destructive to agriculture, and cause millions of dollars in losses annually to crop plants that have been selected by humans for low toxicity.

Ant-plant Interactions, Figure 54 Ants tending Hemiptera outside and inside plant stems: (above) *Azteca* tending mealy bugs (Pseudococcidae) in the New World tropics, and (below) *Podomyrma* sp. tending scale insects (Coccidae, arrows) inside branches of *Chisocheton* (Meliaceae) near Madang, Papua New Guinea.

Pastoralists

Ants may also affect plants indirectly through the farming (or "tending") of insects in the order Hemiptera. With mouthparts highly modified as stylets, or "soda straws," these insects are phloem- or xylem-sucking consumers of plant sap (Fig. 54) and include aphids, leafhoppers, treehoppers, scale insects, and the like. Because plant sap is N-poor, sap-feeding hemipterans must process large quantities of these liquids to concentrate sufficient nitrogen for growth and reproduction. Moreover, while they feed, their relatively immobile immature or nymphal stages are exposed for long time periods to the risks of predation and parasitism. As a by-product of processing large quantities of sap for N, many Hemiptera release excess sugars as "honeydew" from their abdomens. When compensated by this attractive resource, ants forego predation of these insects and even protect them from other natural enemies. Relatively N-rich tissues like young leaves, and the pedicels of flowers and fruits, are particularly good sites for sap-feeders and the ants which herd them there. In Asian rain forests, where plant reproduction is highly sporadic, ants in the genus *Dolichoderus* have evolved as "migratory herdsmen," carrying their sap-feeding mealy bugs over long distances in search of optimal feeding sites.

Hemipteran tending, often compared to human tending of domestic livestock, is a mainstay for many arboreal ants. Still, to balance their diets, ants occasionally harvest some of the tender hemipteran nymphs and consume N-containing hemolymph of these and other arthropods. The relative strengths of positive and negative effects of the ants (herbivore reduction vs. hemipteran tending) determine the net effect of ants on a plant's well-being and reproduction (i.e., its fitness). This net outcome can be positive if herbivores are abundant and tending ants are effective in driving them away. However, as hemipteran populations thrive and grow under ant protection, removal of large quantities of sap can threaten the host plant's health. Living in intimate contact with hosts, Hemiptera also transmit viral and other plant pathogens. Not surprisingly then, plants appear to have fought back over evolutionary time. For example, hairs (trichomes) on leaves or stems prevent hemipteran stylets from reaching the plant surface. Other evolved responses are best understood in the context of the old adage that "the enemy of my enemy is my friend." Thus, many plants may have short-circuited the Hemiptera out of these tripartite interactions by paying the ants directly, i.e., by provisioning them with carbohydrate rewards in the form of sugar-rich extrafloral nectars (EFNs, Fig. 55) or lipid-rich pearl bodies (PBs). J.X. Beccera and D.L. Venable hypothesize that by increasing the CHO:protein ratio in the ants' own diets, plants induce ants to consume more of their Hemiptera. Arguing against this hypothesis for the origin of EFNs are observations of ants tending both sap-feeders and EFNs. Despite such observations, D.W. Davidson and colleagues have proposed that the hypothesis might help to



Ant-plant Interactions, Figure 55 **Myrmecophyte-produced food rewards for ants: (left) Extrafloral nectaries (EFNs) at the junction of leaf blade and petiole of *Endospermum medullosum* (Euphorbiaceae) near Madang, Papua New Guinea; (right) pearl bodies (PBs) on lower leaf surface of *Cecropia engleriana* (Cecropiaceae) at Cocha Cashu, Peru. Both EFNs and PBs also occur in myrmecophilic plants.**

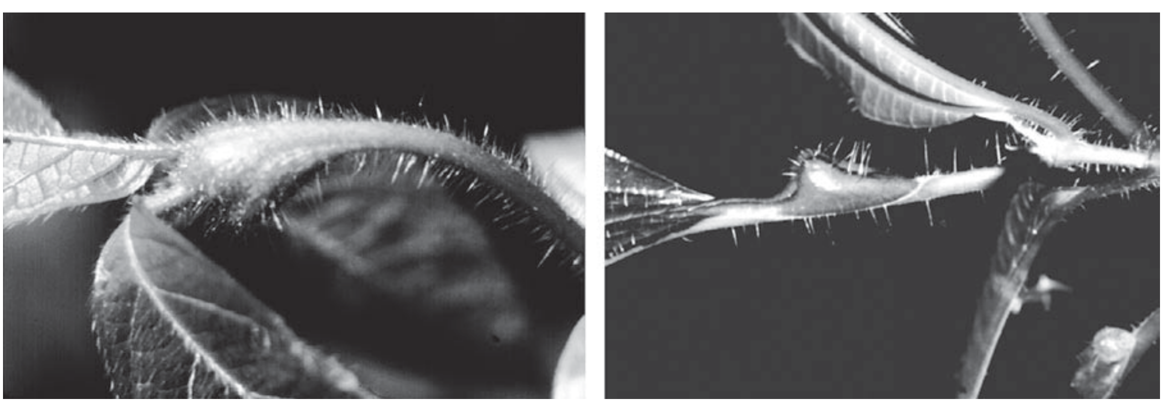
explain early divergence in foraging habits of major ant taxa that differ in their propensity to tend hemiptera versus EFNs.

Biotic Defenses of Plants

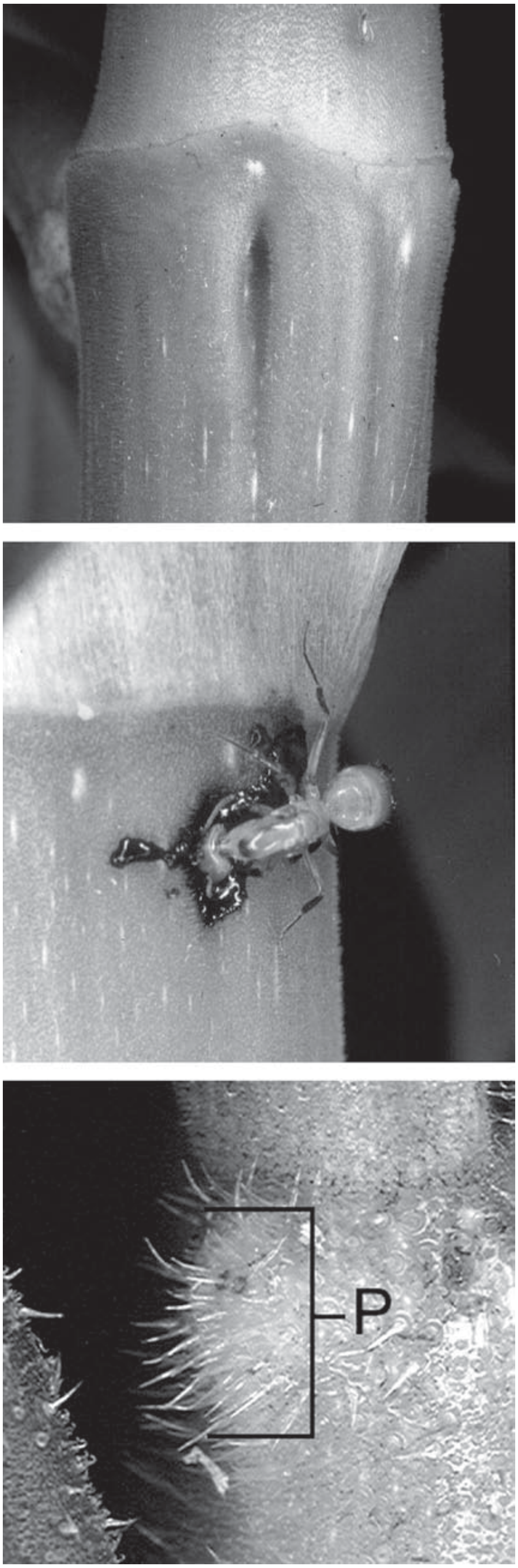
Even in relationships not (or no longer) involving Hemiptera, production of ant attractant foods should increase the presence of ants on vegetative and reproductive plant tissues and help to deter a variety of insect and other herbivores. Plant adaptations for defense by ants, wasps and other potential predators of insect herbivores are referred to as "biotic defenses," since they require the collaboration of other living things.

Some Definitions and Constructs

Whether the anti-herbivore protection of plants by ants is afforded through consumption of Hemiptera or deterrence of other herbivores, such protection completes the requirement for what are termed "mutualistic" interactions. Both parties in these relationships benefit, the ants directly from plant provisioning of resources, and the plants indirectly, usually through deterrence of damaging herbivores. Mostly, these interactions are opportunistic and unspecialized, depending on which ants, herbivores, and plants co-occur within a community. Plants with opportunistic ant associations based on production of food rewards alone are said to be "myrmecophilic" or "ant-loving." In contrast, at tropical latitudes, many ant-plant relationships have become more highly specialized and obligatory. That is, in the context of their natural communities, partners cannot survive and reproduce in the absence of their associates. In this case, resident "phytoecious" ants protect their host plants, (Fig. 56) and "myrmecophytes" (true "ant-plants") provide not only food but housing in stem or leaf structures termed "domatia." Individual ant colonies and myrmecophytes may live together over substantial portions of their life histories in relationships therefore termed "symbiotic mutualisms." (Although often used incorrectly in place of "mutualism," the term "symbiosis" - literally "living together" - is value neutral, including negative interactions like parasitism, as well as mutually beneficial interactions.) "Cheater" ants, which benefit plants less than the evolved partner, or otherwise negatively



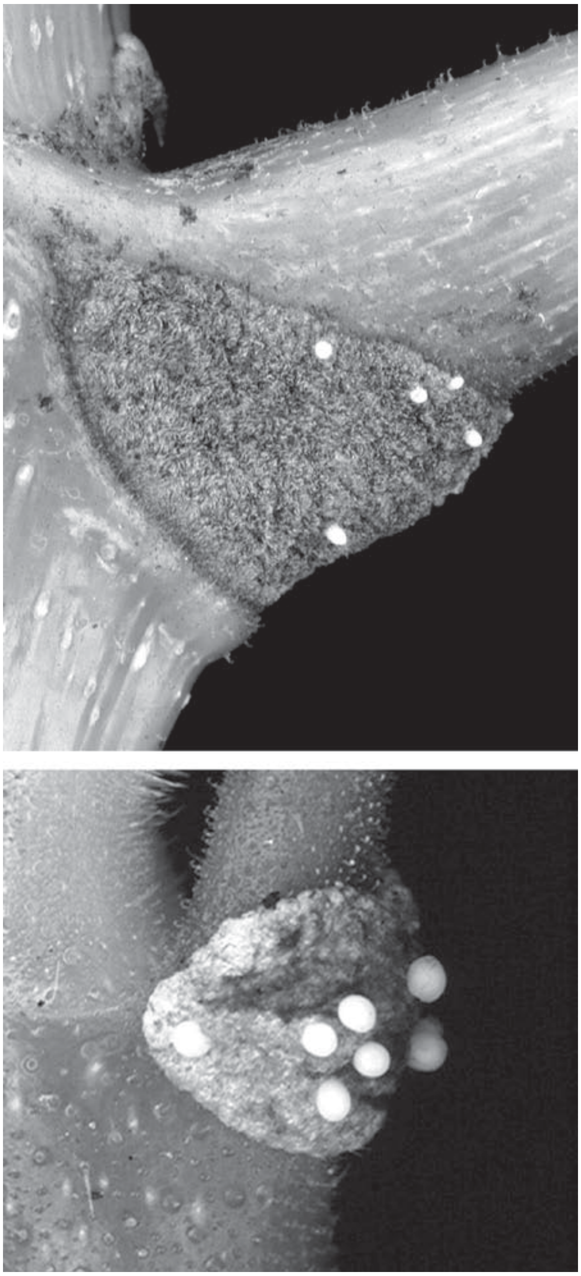
Ant-plant Interactions, Figure 56 **Caulinary (left) and foliar (right) domatia of ant-plants. Forming the domatia of many myrmecophytes are swollen stems or support structures, either naturally hollow or with weak pith, removed by ants. Shown here (left) is a branch of *Duroia hirsuta* (Rubiaceae, vic. Iquitos, Peru), swollen at attachment of large opposite leaves. Tiny ants in genus *Myrmelachista* inhabit these naturally hollow caulinary domatia. Foliar domatia, like that shown here for *Tococa* sp. (Melastomataceae, from Cocha Cashu, Peru) (right) are highly modified and more obviously evolved to accommodate ants.**



impact hosts, may occasionally prevail in symbioses because they are better colonists or competitors.

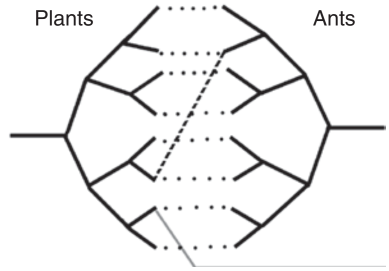
In symbiotic ant-plant relationships, partners are more likely to have undergone coevolution, i.e., reciprocal genetic (evolutionary) responses to selection pressures exerted by each partner on the other. Coevolution has two aspects: coadaptation and cospeciation, and only the former occurs frequently in symbiotic ant-plant partnerships. Illustrating coadaptation (reciprocal adaptation), many plants have evolved restrictive (Fig. 57) entrances to their domatia as a means of favoring colonization by certain ant taxa over others, while queens of phytoecious ants have responded by evolving traits enabling them to recognize and colonize such entrances expeditiously. Similarly, plants and ants may have coadapted with respect to the types or sizes of food rewards offered (Fig. 58) and their utilization or accessibility. In contrast, cospeciation (the co-radiation of ant and plant lineages to give congruent phylogenies) appears to be quite rare even in tropical symbiotic ant-plant relationships. Rarity likely results from the fact that ant and plant propagules (i.e., new queens and seeds) disperse independently, leaving much opportunity for new partnerships to form over evolutionary time. Seeds must germinate and produce seedlings of a threshold size before the next generation of hosts can support ant colonies. Environmental variation or randomness in the abundances of, and proximities

Ant-plant Interactions, Figure 57 The prostomata (stem entrances) of *Cecropia* species come in various sizes and forms correlated with host use by different ant taxa: *Cecropia engleriana* (above) produces a narrow inverted prostoma, recognized and colonized by comparatively small queens of *Azteca australis* (Dolichoderinae) (center); in contrast (below), those of *Cecropia* sp. nov ("pungara") are convex and covered in urticating hairs; this host species attracts much larger queens of a ponerine ant, *Pachycondyla luteola*. Both photos are from Cocha Cashu, Peru.



Ant-plant Interactions, Figure 58 **Food bodies of myrmecophytic *Cecropia* also come in different sizes, as shown here for *Cecropia membranacea* (above), usually associated with tiny *Azteca* ants, and closely related *Cecropia* sp. nov. ("pungara") (below), housing the much larger *Pachycondyla luteola*. Both are from at Cocha Cashu, Peru.**

to, sources of colonizing queens, provide ample opportunity for host-switching or *de novo* colonization by previously uninvolved ant taxa. This



Ant-plant Interactions, Figure 59 **A hypothetical case of cospeciation, illustrated by the congruent or mirror-image phylogenies (= genealogies, solid dark lines) of associated (dotted lines) ant and plant taxa. On each occasion when a plant species splits into two distinct taxa, the associated ant lineage also undergoes a speciation event. For cospeciation to have occurred, splits in plant and ant lineages must have occurred contemporaneously and be attributable to selection imposed by the partner. Otherwise, an ant lineage may have just radiated secondarily over a pre-existing plant lineage. The dotted and grey lines depict two kinds of evolutionary colonization events: respectively, host switching and *de novo* colonization by a previously unassociated ant lineage.**

picture contrasts sharply with that for, e.g., higher attines and their fungi; there, I.H. Chapela and colleagues have shown that queens transmit fungi between generations of colonies, and phylogenies of the two lineages are largely congruent (Fig. 59).

Despite little evidence for cospeciation in symbiotic ant-plant associations, contemporaneous diversification within partner lineages may occur through diffuse coevolution, defined by D.H. Janzen as reciprocal evolutionary responses to a suite of potential partners. Additionally, if host availability were often limiting, phytoecious ants may frequently have colonized non-myrmecophytic relatives of those plants, exerting new selection on these species to evolve ant-attractive traits. Based on multiple independent origins of myrmecophytism in older and more recent Asian *Macaranga*, S.-P. Quek and colleagues have proposed just such a scenario. A parallel argument is that, lacking their typical associates, habitat-switching hosts could have provided evolutionary opportunity for the origin of new phytoecious ant taxa.

These examples are relevant in the context of the different selection pressures driving diversification in myrmecophytes versus phytoecious ants. As noted by D.W. Davidson and D. McKey, proliferation of plant species has been driven principally by colonization of new habitats, accompanied by evolution of new defensive strategies and (correlated) growth rates, etc. In contrast, ants have diversified mainly in response to biogeographic factors and (especially) plant traits favoring certain associates over others (below). Why this asymmetry? Plants grow through seedling stages without their ants, and their success during this most vulnerable period depends on factors such as light and nutrient regimes, i.e., on habitat. Additionally, any of several ant taxa may provide acceptable protection against herbivores. In contrast, phytoecious ants are typically restricted to their hosts throughout the life history, and disparities in host characteristics (e.g., habitat-correlated growth rates and investment in biotic defense) should be highly consequential. This asymmetry in selection pressures is reflected in both the specificity of partnerships and evidence for coadaptation. Individual *Cecropia* species can house ants in different genera or even sub-families, while associated ants do not inhabit plants outside this genus. Similarly, phytoecious ants of bamboos have adapted to these hosts by evolving means of water evacuation from nest culms (active bailing or passive engineering), and they do not live elsewhere. In contrast, no bamboo has been determined to have evolved ant attractants.

Factors Driving Evolutionary Specialization

Factors driving evolutionary specialization in phytoecious ants are apparent from assessing both the taxonomic affiliations of these ants and traits of coadapted partners. Despite the frequent impression that such ants are ferociously aggressive against vertebrates (including many an unfortunate investigator), they appear often to include comparatively weakly competitive ant taxa that persist only in association with myrmecophytes. Several plant traits, separately or in combination, contribute to the capacity of these plants to serve as refugia from natural enemies. First, many myrmecophytes produce nutritionally complete food rewards that eliminate the need for resident ants to forage in more competitive environments off their hosts. *Acacia* and *Macaranga* are examples. Second, derived from taxa in which stem hairs are common, a number of myrmecophytes possess stems and domatia covered with long, dense hairs (trichomes, Fig. 55) that exclude larger-bodied enemy ants, competitors and perhaps predatory army ants, while permitting tiny resident taxa to commute among them. Such hosts include *Cordia nodosa*, *Duroia hirsuta*, and *Hirtella* spp., with tiny *Allomerus* and *Azteca* ants, as well as a variety of myrmecophytic Melastomataceae. Third, many myrmecophytes, e.g., *Macaranga* and *Cecropia*, grow as little-branched, pole-like plants with few points of contact over which enemy ants might invade from neighboring vegetation. Fourth, the mutualism between ants and *Macaranga* has been shown by S.-P. Quek, S.J. Davies, and colleagues to have originated on hosts with irregular “wax blooms” on stems. Many insects, including most ants, have difficulty walking on epicuticular waxes, but as W. Federle and colleagues have demonstrated, “wax-running” ants in at least two genera (*Crematogaster* and *Camponotus*) evolved to utilize the slippery hosts. During the co-radiation of plant and *Crematogaster* lineages, stem types (waxy or smooth) continued to constrain host shifts.

All of the previously described traits are attributes that likely preadapted plants to associate with competitively inferior ants searching for sanctuary. In addition, phytoecious ants themselves have often evolved to reduce interaction with enemies by pruning vines and other vegetation contacting their hosts. (This behavior may coincidentally enhance the host’s light environment.) At least one such ant species (*Pseudomyrmex dendroicus* on

Triplaris americana) even prunes leaves of its own host when they bear invasions of enemy ants. In the Neotropics, a majority of pruning ants defend themselves using proteinaceous stings, which tend to be very effective against vertebrate enemies, but less effective than chemical sprays against social insect enemies, including many other arboreal ant taxa. Also suggesting that pruning evolved to limit invasions of competitors, Federle and colleagues find that ant taxa living on waxy-stemmed *Macaranga* hosts do not prune as intensively as do those inhabiting more recent non-waxy species. The latter ants are also more recent, and the evolution of pruning in ants may have benefited host plants by reducing the cost of epicuticular waxes. The advent of pruning coincides with a switch to more generalized host associations, as ant taxa from waxy stem hosts expanded their host ranges to non-waxy hosts. Finally, M. Frederickson has shown that phytoecious ants best at pruning are not always those that are best at protecting plants from herbivores. Therefore, a myrmecophyte's failure to filter out supposed "cheaters" that didn't prune may be due to alternative benefits provided by the ant species in question.

Conflicts of Interest between Partners

As for partners in virtually all interspecific interactions, the evolutionary interests of paired ants and plants are often in conflict. For example, although selection may favor ant colonies that extract the maximum resource possible from their hosts (e.g., by tending sap-feeders, as well as consuming plant-produced ant rewards), selection on plants should magnify cost-efficiency by producing the greatest protection for the least investment in resources devoted to housing and feeding of ants. The most striking examples of evolutionary conflicts of interest come from cases where ants modify plant architecture in ways that are beneficial to them but harmful to their hosts. Working in African savannahs, M.L. Stanton and colleagues have shown that *Crematogaster nigriceps* attacks the axillary buds of its host (*Acacia drepanolobium*), killing apical meristems (growing tips) and greatly curtailing host reproduction in the process. However, by reducing lateral spread, destruction of meristems may also diminish potential contacts between branches of hosts and those of neighboring acacias, some with competitively superior ants that threaten resident colonies. *Tetraponera penzigi*, a second, competitively subordinate occupant destroys EFNs of its host, perhaps making it less attractive to more dominant ants on neighboring hosts.

Similar conflicts of interest are apparent in neotropical ant-plant relationships. The most common inhabitant of *Cordia nodosa* in southeastern Peru is an *Allomerus* that destroys flowers and fruits of its host. D.W. Yu and N.E. Pierce have shown that ant fecundity is greater on plants with curtailed reproduction, because hosts produce more domatia and associated leaves, sites of food body production. *Cordia* populations might be expected to decline to local extinction under such "cheating" by *Allomerus*, but Yu and colleagues have also demonstrated that alternative and beneficial *Azteca* ants are better long-distance colonists, and that the frequency of association with these ants increases as plant density declines. Finally, T.J. Izzo and H.L. Vasconcelos report that selection on plants to fight back under similar circumstances is apparent in relationships between *Allomerus* and another Amazonian ant plant, *Hirtella myrmecophila*. Reproductive structures of this understory treelet are produced only on older branches from which leaf domatia have been aborted, and where worker ants are therefore few or absent.

Long-Term Evolutionary Histories of Ant-Plant Associations

Over long-term evolutionary history, one can expect "ownership" of host taxa to have changed hands in concert with changes in the fortunes of one-time ant partners and their competitors for the benefits of mutualistic association. Are there regularities in the trajectories that these relationships take over time? One might speculate that competition among ants for plants, together with filtering of ants by plants, could produce even greater specialization by the associated taxa, and that this might be a one-way and largely irreversible process. For ants, possible examples involve several closely related genera of tropical arboreal, stem-nesting ants in the formicine tribe Plagiolepidini. (Together, these genera are set apart from others in the tribe by workers possessing just 9 or 10 antennal segments.) Two Old World tropical genera, *Petalomyrmex* and *Aphomomyrmex*, are each represented by just a single West African species and are specialized to one and two host plant species, respectively. Because the probable closest relatives of these taxa (*Myrmelachista* and *Brachymyrmex*) occur as free-living species in the New World, it seems likely that ancestors of the African species were once free-living and more widely distributed, and that competition could have driven *Petalomyrmex* and *Aphomomyrmex* to extreme specialization. The genus *Myrmelachista* includes both free-living and plant-associated species. On average, the former (mainly with 10-segmented worker antennae) have generalized foraging and stem-nesting habits and reside mainly in high elevation cloud forests along the Andean and Central American mountain chains, normally above the elevational ranges of dominant free-living competitors in ant genera *Crematogaster* and *Azteca*. At intermediate and low elevations, and within the ranges of these dominants, J.T. Longino has found that congeneric species are mostly phytoecious ants, principally inhabiting hosts in plant families Lauraceae and Meliaceae. *Myrmelachista* hosts generally lack domatia and food rewards (i.e., are not true myrmecophytes), and associated ants tend sap-feeders inside stem nests. At least some phytoecious *Myrmelachista* occurring at intermediate elevations apparently do not attack encircling vines, though a congeneric species at lower elevations (likely *M. flavocotea* in a more competitive environment) does prune vegetation contacting its host.

Finally, in Central Amazonia, at least two different *Myrmelachista* species occupy and maintain "supay chacras," or "devil gardens." These are orchard-like stands where all but one or two myrmecophytes (and sometimes small, herbaceous resource plants) are killed by the tiny workers that cut major leaf veins and deposit formic acid in the wounds. Leaves necrose and die, and none but favored host and resource plants are able to recruit new individuals inside these bizarre areas. In summary, it is possible that basal *Myrmelachista* species persist only in the absence of strong competitors, or where competitively dominant ant taxa have driven lowland lineages toward increasing specialization that permits coexistence with strong competitors. However, this hypothesis will remain conjecture until tested rigorously after reconstructing phylogenetic histories of associated lineages.

Natural selection to magnify the colonizing and competitive abilities of particular ant associates, coupled with that to filter cheaters, may eventually reduce partnerships to relationships between single, highly specialized ant and plant species, whose persistence is balanced precariously on the premise that each partner will thrive despite changes in the abiotic (physical) and biotic environment. However, natural selection is short-sighted, capable only of enhancing short-term fitness. Over the long term, it can neither anticipate nor respond to the threat of loss of the sole partner. Therefore, it is reasonable to speculate that fewer than all of the ant-plant associations that have ever existed still exist today. Nevertheless, the most thoroughly studied evolutionary trajectories of phytoecious ants are those described by S.-P. Quek and colleagues for *Crematogaster* of *Macaranga*, and show wax runners breaking away from hosts with waxy stems to occupy plants that should constitute a more competitive environment.

Implications of Exudate-Feeding for the Evolutionary Ecology of Ants

The most conspicuous effects of plants on ant ecology and evolution involve phytoecious ants whose colonies are specialized to live their entire life histories on myrmecophytic plants. However, more generally, plants appear to have markedly influenced the biology of ant taxa feeding substantially as "herbivores," either directly on plant wound secretions and EFN, and/or indirectly, on insect honeydew. Such foods, collectively termed "exudates," consist principally of sugars (EFN) and water and are notoriously poor sources of essential amino acids and proteins. Though a certain amount of carbohydrate might be paired with available nitrogen sources as the "nutritionally complete food" needed to subsidize growth and reproduction, exudate-feeders should be left with an "excess" of CHOs. Natural selection may then favor colonies that are able to deploy excess CHO for acquisition of more limiting nutrient, N.

Across the spectrum of exudate-feeding ants, species appear to accomplish this in one or more of several ways. First, they may use excess CHOs to subsidize rapid locomotion, leading to what have been termed higher "dynamic densities." Faster locomotion enables workers to cover more area per unit time, and potentially, to encounter protein resources at a faster rate. Second, defense of true spatial territories is rare among ants generally, but appears to be commonest in species most apt to have excess CHOs to fund this costly behavior. Third, N-starved ants may also reduce percent body weight N, though there are competing explanations for this pattern. Thus, evolutionary transitions from predation and scavenging to substantial dependence on plant and insect exudates correlate with transitions in chemical weaponry. N-rich proteinaceous compounds, or N-containing alkaloidal compounds (both mediated by stings) are replaced by N-free compounds released as volatile sprays or sticky glues from the same or different glands. Whether such transitions are due to N-limitation, or the ineffective nature of C-based weaponry in killing or paralyzing prey, is currently unsettled.

By "paying" ants mainly in CHO-rich food rewards, myrmecophilic and myrmecophytic plants may encourage predatory behavior by attending ants seeking to balance their diets (above). Recently, D.W. Davidson and S.C. Cook found that rainforest plants supply EFN at sugar concentrations far exceeding those acceptable to most arboreal ants. They therefore suggest that high sugar concentrations may serve to manipulate communities of attending ants by favoring the most protein-limited taxa that would not forage for sugar at lower concentration.

Finally, widespread availability of CHO-rich plant foods in the arboreal zone undoubtedly selected for domination of these foods by placing nests near the food source. For ants already nesting in leaf-litter twigs, this transition may not have been difficult, but appropriate cavity space would not always have been available. Many arboreal ant taxa have therefore evolved the capacity to construct their own nests from carton, silk, or leaves cemented to one another to create cavity space.

Some Parallels Between Ants and Plants

A central theme running through this article has been that the balance of resources accessible to animals (Hemiptera and ants) affects the evolutionary ecology of these organisms by determining the types of resources available for various organismal functions. This argument is no less true for myrmecophytic plants and, in fact, was adopted by ant biologists based on its explanatory power in plants. In rainforest plants, for example, E.W. Schupp and D.H. Feener have shown that N-free but carbon-rich food rewards for ants (EFNs and PBs) are more typical of taxa growing in disturbed habitats under high light, than of groups typical of the dark forest understory. Apparently, high rates of carbon-gain in open habitats enable plants to divert some of that carbon to defense.

A second reason why biotic defenses may occur at high frequency in fast-growing, "pioneer" species of disturbed sites may relate to the shorter average leaf life spans of those species. D. McKey has argued persuasively that shorter leaf life spans should favor foliar defenses that are "reclaimable," i.e., can be diverted from aging leaves to more valuable young leaves as time passes. In contrast, much higher, but one-time, investment in non-reclaimable defenses (e.g., the lignin and fiber contributing to leaf toughness) are warranted only when the life expectancy of leaves is relatively long. One can speculate that the pattern in plants might also be applied to predict aspects of ant biology. For example, a substantial, one-time investment in producing thicker (N-rich) exoskeleton might only be warranted in ant species with long-lived workers. This interesting hypothesis has yet to be tested.

Two final patterns in defensive investment are apparent in at least some myrmecophytic plants, and may extend as well to ants and other social insects. Comparing closely-related pairs of *Cecropia* species from different microhabitats at the same rainforest site, it appears that relatively slow-growing taxa from shaded habitats invest in biotic defenses both earlier and more heavily than do their faster-growing relatives from sunny habitats. The latter pattern is understandable in the context of a cost-benefit analysis of defense. For species growing regularly at low light, leaf replacement is very slow due to resource limitation, so plants ought to defend existing leaves well. Moreover, any opportunity cost of defense (calculated in lost growth, survivorship, and reproduction) would be low in comparison to that for species capable of growing rapidly in high light. The combination of high replacement costs and low opportunity costs is thought to select for high defensive investment. (Applied to ants, this pattern suggests the currently untested hypothesis that mean colony growth rates are inversely related to defensive investment in individual workers.) C. Brouat and D. McKey have argued that, in myrmecophyte lineages with interspecific variation in developmental onset of biotic defense, precocious (early) onset should be the derived state; however, few data are available to test this prediction. Others have suggested that costly chemical defenses produced early in development should be abandoned after onset of biotic defense, but recent tests in genera *Acacia* and *Inga* contradict this theory, and suggest that chemical and biotic defenses may be targeted at different types of herbivores.

With respect to ants and other social insects, parallel reasoning might predict an inverse relationship between colony growth rate and investment in defense of incipient (young) colonies. One form of protection for young colonies is production of "nanitic" workers, scaled-down in size. This strategy enables young colonies to make more workers from a given resource base, and to spread the risks of foraging over more individuals. Are young workers smaller relative to normal workers in otherwise comparable species with intrinsically slow growth rates? Again, relevant data are lacking.

In summary, ant colonies and plants share some intriguing features that make models developed in one taxon potentially useful to investigators of the other taxon. Both types of organisms live anchored to a central place (not perfectly true for ants), grow to indeterminate size set by local resource availability, and add vegetative and reproductive parts in a modular way. These commonalities suggest that we might eventually discover additional models that are useful in explaining life history traits and other characters shared by the two groups.

Nutritional Benefits to Plants (Myrmecotrophy)

Among plants evolving associations with benevolent ants are certain epiphytic higher plants. Depending on trunks and branches of other plant species for structural support, epiphytes grow without directly parasitizing their hosts and obtain water and nutrients from rainfall and aerial deposition. Because high humidity and warm temperatures are conducive to this lifestyle, epiphytic higher plants are exceptionally diverse and abundant in tropical lowland wet forests, and (especially) in misty montane forests. (Tropical Africa is exceptional in this regard, due to frequent and severe droughts during the evolutionary histories of its plant life, and small expanses of montane forests in contemporary times.) By virtue of small size, these unrooted plants stand to benefit significantly from even small quantities of nutrients amassed as workers retrieve prey, discard refuse, and defecate within a confined area. From a mix of vegetable fiber, glandular secretions, refuse, and feces, many ants build "carton" shelters (for themselves and tended Hemiptera), and carton can potentially contribute to plant nutrition.

Two categories of plants, New World "ant-garden" epiphytes and Australasian "ant-house" epiphytes, have evolved a variety of traits that increase frequency and intimacy of relationships with beneficial ants. To encourage seed dispersal to nutrient hotspots in ant nests and carton, both sets of species produce seeds with attractive chemicals and/or food bodies. The common occurrence of methyl-6-methyl-salicylate on seeds of 11 unrelated ant-garden epiphytes, combined with the use of these same compounds as pheromones (within-species communication chemicals), suggests that this chemical could function as an ant attractant. Generations of seed dispersal by ants appears to have allowed ants to "capture" the evolution of their epiphytes, just as humans have captured and diverted the evolutionary histories of their crop species. (Alternatively, in both of these systems, plants may have captured and diverted the evolutionary histories of their gardeners!) The successes of ant-epiphyte partnerships are evident from their often remarkable abundances. Ant gardens can account for the majority of epiphytic higher plants in forests with a distinct dry season, and ant-house plants dominate the epiphytic floras of open kerangas forests in Asia. Whereas other epiphytes cannot survive extended periods of drought, ant-garden taxa benefit from moisture absorbed from the air and stored in the rich, organic ant cartons.

Ant-house epiphytes have evolved even more elaborate adaptations to procure benefits from their ant inhabitants. Those in the sub-family Hydnophytinae (Family, Rubiaceae) are descended from tuberous ancestors whose storage tissues were devoted principally to water storage. Ant-associated species in several different genera have reduced their investments in storage and allocated space within their tubers to two types of cavities used by the ants. Colonies of *Anonychomyrma* and *Philidris* nest in smooth- and dry-walled cavities, while placing feces and refuse in wet-walled cavities with "warts," actually modified roots. The epiphytes satisfy a significant fraction of their nitrogen requirements by tapping into these wastes. Epiphytic *Dischidia* species (Asclepiadaceae) frequently grow adjacent to the Hydnophytinae on the same hosts and are inhabited by the same ant colonies. In addition to their "normal" leaves, which grow appressed to tree trunks, these species produce highly modified leaves, involuted to form the cavities in which ants live. Stomata are concentrated on internal cavity walls formed by abaxial (lower) leaf surfaces. Through their stomata, plants take up the carbon dioxide (CO_2) needed for photosynthesis. When stomata (Fig. 60) open to perform this chore, they lose precious water, an especially limiting commodity for unrooted epiphytes of the hot, dry canopy. However, stomata of ant-house *Dischidia* open into a relatively moist, enclosed space where the partial pressure of CO_2 is enhanced by ant respiration, and this alleviates transpirational water losses. Using stable isotope technologies, K.K. Treseder and colleagues showed that *Dischidia major* from Bako National Park in Sabah, Malaysia, obtains about 39% of its carbon from ant-respired CO_2. Isotopic studies of N revealed that about 29% of the plant's N comes from ant feces, refuse and carton, into which plants insert adventitious roots from the bases of both normal leaves and leaf domatia.

Often growing with the Hydnophytinae and *Dischidia* are ant-occupied ferns in the genus *Lecanopteris*, and any of several ant taxa can occupy each of these epiphytes. Although associations between ants and epiphytes are not obligate for either party, it is rare to find one partner in the absence of the other. This is likely due to the combination of frequent nest site limitation in ants, and water and nutrient limitation in epiphytes.

Ant-plant Interactions, Figure 60 **Myrmecotrophic epiphytes: (upper left) At Cocha Cashu, Peru, 11 different epiphyte species from seven plant families can occur in carton "ant-gardens." This garden contains mainly seedling *Peperomia macrostachya*; (upper right) *Myrmecodia tuberosa* (Rubiaceae, Hydnophytinae) growing on a stunted tree in open "kerangas" forest at Bako National Park, Sarawak; (lower left) cross section of *Anthocephalus* sp., vic. Wau, Papua New Guinea, showing dry-walled cavities inhabited by ants, and wet-walled cavities with warts (modified roots) that extract nutrients deposited as ant refuse and feces; (lower right) Bornean *Dischidia major* (Asclepiadaceae, also from Bako): small, circular, flat leaves are typical of non-myrmecotrophic members of the genus, whereas much larger, involuted leaves have evolved in myrmecotrophic species and house associated ants.**

Myrmecotrophy is commonest in epiphytes, but as P. J. Solano and A. Dejean have shown, it can also occur where ants leave waste in abandoned domatia as colonies move to new growth. Thus, in *Maieta guianensis*, protrubances on domatia walls appear to take up N from waste of *Pheidole minutula*. By an as yet poorly defined mechanism, some rattan palms also benefit nutritionally from ants that build carton nests among spines on external stems. Another monocot (*Guadua* bamboo), apparently cannot take advantage of ant waste inside stems and actually loses N to scale insects tending by resident carpenter ants.

Ants as Seed Dispersers, Pollinators and Partners of Insectivorous Plants

Seed Dispersal

Tropical epiphytes are not the only group of plants to take advantage of the willingness of ants to transport seeds. In general, plants are thought to be selected for both "distance dispersal" and "directional dispersal," and the balance of selection for the two objectives almost certainly varies from species to species. Distance dispersal, or seed dispersal away from the maternal parent, is important for avoiding both asymmetrically strong competition from the mature plant against its seedlings, and transfer of pathogens and seed predators to these offspring. Because ants generally forage over relatively short distances from a central place, they are probably more important in directional dispersal, i.e., directing seeds to "safe sites" or favorable microhabitats. The importance of both forms of dispersal may explain why some "diplochorous" species accomplish both objectives, e.g., by first explosively propelling seeds away from the parent and then using ants to target seeds to a preferred location. The majority of ant-dispersed seeds are taken to or near the nest site, if not into the nest itself, and evolutionary advantages of "myrmecochory" (dispersal by ants) are usually discussed in relation to these sites.

Ant-plant Interactions, Figure 61 **Seeds of *Acacia cana* (northwestern New South Wales, Australia) have white arils contrasting with black seeds and are "displayed" at the soil surface, where ants are most likely to find them.**

Ant-dispersed plants, bearing small food rewards for ants, are common in habitats ranging from rain forests (e.g., herbs in the Marantaceae) to temperate deciduous forests (e.g., violets) and arid lands (North American jimson weed and some Australian acacias and saltbushes, Fig. 61), but the greatest diversity of myrmecochores may occur in areas with infertile soils, Mediterranean climates, and high fire frequency, e.g., especially African fynbos and Australian heath. Depending upon habitat characteristics, hypotheses for the adaptive value of myrmecochory have included giving seeds refuge from fire (chaparral), from competing plants (temperate deciduous forests, where ant nests may be the only vacant sites), or from seed predators (diverse habitats), as well as dispersal to nutrient hotspots on ant mounds (e.g., the nutrient-poor soils of arid Australia). While controversies continue about particular plants and sites, it is likely that each of these hypotheses holds for a subset of plant species.

The rewards that plants offer for seed dispersal fall mainly into the category of "elaiosomes," a kind of aril (= dry fruit) that is rich in oils. Both birds and mammals also feed on arillate fruits. When ant-dispersed species were compared with bird-dispersed (ornithochorous) species in the same sub-genus of Australian *Acacia*, fruits and seeds of the two types of species differed in size, aril composition, color, and presentation. Myrmecochorous seeds were somewhat smaller on average, with arils poorer in lipids (an energy source) and water, but marginally richer in N (amino acids or proteins). In contrast to the colorful arils that ornithochores display prominently on the host, arils targeting ants were white (contrasting readily with black seeds) and presented on the ground after dehiscing. A study by L. Hughes and colleagues compared the elemental composition of myrmecochore arils with that of fleshy fruits from diverse vertebrate-dispersed plant plants. A difference in potassium (K) levels suggested that vertebrate frugivores may require comparatively high levels of K in their fruits. Species growing in poor soils may simply have too little K to produce K-rich fruits, and so may be relegated to myrmecochory. Hughes and colleagues have also identified fatty acids (especially 1,2-diolein) as important components of elaiosomes, which may mimic the composition of insect prey (especially haemolymph) and therefore induce a variety of carnivorous and omnivorous ant species to transport seeds to the nest. Given the ubiquity of ants in most habitats, plants may have evolved to attract ant species that consume only the appendage and not the seed itself. Together, these studies point to syndromes of traits characterizing species with different dispersal agents.

Inconstancy in availability of elaiosomes probably prevents ants from specializing on fruits of a particular plant species. Moreover, aside from making a dispersal unit smaller or larger, it is difficult logistically to direct seeds to particular ant species. Not surprisingly then, relationships between ants and myrmecochorous plants tend to be diffuse rather than species-specific, with a variety of ants carrying seeds of a given plant, and often more than one type of elaiosome in an ant diet. Nevertheless, all ant species are not equal in their effects on plant reproductive success. Interspecific differences among carriers affect transport distances, frequency of dropping without retrieval, and rates of seed burial and escape from seed predators. Despite the opportunistic nature of interactions between myrmecochorous plants and ants, one or more ant species may often have a disproportionate effect on plant reproductive success. For example, at increasing frequency, disruption of ant communities by non-native species (e.g., Argentine ants, *Linepithema humile*) threatens populations of native plants, including rare and endemic (geographically restricted) species.

Ants as Pollinators

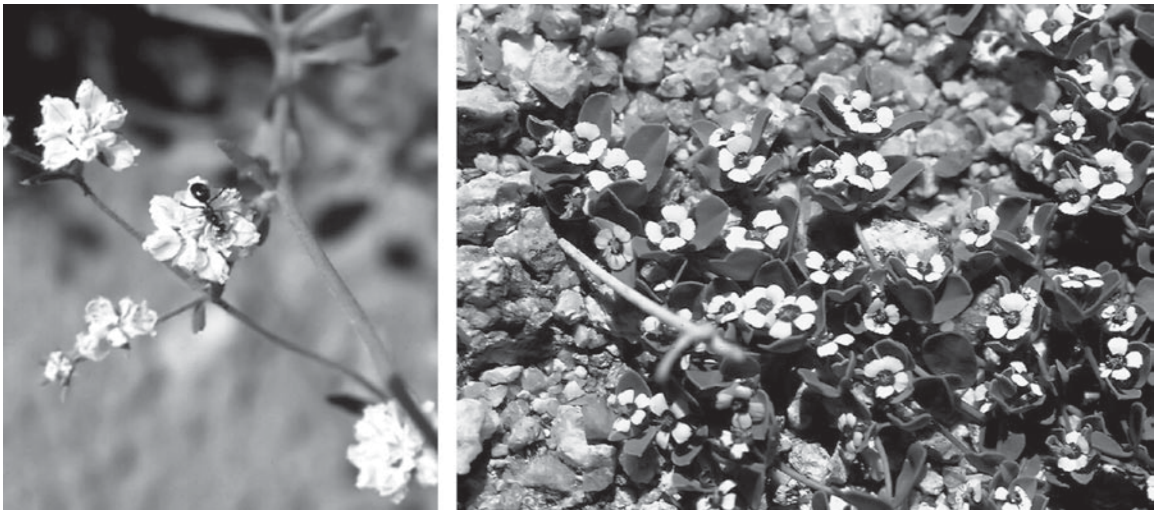
While we think most often of bees, flies and hummingbirds as agents of plant pollination, ants can also be effective pollinators under a restrictive set of circumstances. This is apparent despite observations by A.J. Beattie and colleagues that antibiotic compounds produced by the ants' metapleural and poison glands can suppress pollen germination and pollen-tube growth. (Unlike their wasp ancestors, ants often inhabit nests for multiple generations, and metapleural glands with hygienic function appeared early in ant evolution.) Nevertheless, M. Ramsey suggests that if ubiquitous ants were otherwise effective pollinators, some or even many plant species might be expected to have evolved pollen insensitive to metapleural secretions. The apparent rarity of such immunity suggests that ants may be inadequate as pollinators for some other reason(s). A signal attribute of ants is their tendency to revist food sources such as extrafloral nectaries and Hemiptera. Very likely, conservatism in ant movements detracts from their ability to transmit pollen effectively among individual plants, a requisite for reproduction by self-sterile taxa. Nonetheless, ants may play a role in pollination where smaller plants (e.g., epiphytes or annual herbs) occur at high densities, or by enhancing rates of self pollination when more effective pollinators are scarce.

Among the few plant taxa pollinated by ants, a suite of traits, or an "ant-pollination syndrome" (a term coined by J.C. Hickman) points to the circumstances under which ants can be induced to move among individual plants. Ant-pollinated plants (Fig. 62) tend to be small in stature and mostly prostrate in growth form, so as to preclude the need to compensate ants energetically for walking vertically rather than horizontally. As a consequence of paying little reward, plants encourage workers to keep moving in search of additional nectar or fuel. Other aspects of the ant-pollination syndrome are white color, and open structure, granting ants access to floral nectars, but just small amounts of pollen, and thereby diminishing the need for ants to groom pollen from their bodies. Ant-pollinated flowers also have relatively few ovules, which may all be pollinated even by small pollen deliveries.

Given their general ineffectiveness as pollinators, and their almost universal taste for sweet solutions, ants mostly interact with flowers as parasites of the relationships between plants and their real pollinators. Almost certainly for this reason, numerous plants have evolved barriers to exclude ants from floral rewards, e.g., with dense fields of hairs or sticky bands inside the corolla. It has even been suggested that nectars are made toxic or disagreeable to ants, though the taxonomic and geographic distributions of such nectars remain poorly known. J. Ghazoul presents some of the strongest evidence for floral ant repellents, demonstrating that a diversity of ants are repelled by something in floral tissues themselves. Still unresolved is the extent to which protection of nectar versus pollen has been the principal stimulus for the evolution of ant repellents. At least some pseudomyrmecine and myrmicine (*Cephalotes*) ants feed on pollen, but nectar feeding is more widespread in ants, probably because less specialization of the digestive system was required to use that resource. Nevertheless, early in their evolution, flowering plants must have found ways of protecting nutritious pollen from the ubiquitous and often protein-limited ants.

Relationships Between Ants and Insectivorous Plants

Carnivorous plants of diverse forms occur on infertile soils in various locations throughout the



Ant-plant Interactions, Figure 62 ***Mymecocystus* species pollinate flowers of at least two desert annuals: *Eriogonum abertianum* (Polygonaceae) (left) at Portal, AZ, and *Euphorbia* sp. (Euphorbiaceae) (right) from southern California. The latter is more typical of ant-pollinated plants because of its prostrate growth form. Individual flowers of both species produce minute quantities of nectar, so ants must walk back and forth among individual plants to fill their crops. However, on both species, workers can commute among individuals without energetically costly vertical movement. *E. abertianum* is rare except in years when winter rains continue through the spring; then it grows in almost monospecific stands with branches of adjacent individuals overlapping at the same level.**

world, and are united by their use of trapped insects as N sources. Pitcher plants are a particularly fascinating life form. They lure insects to the slippery edges of steep-walled pitchers into which fluids with digestive enzymes are secreted and protected from dilution by rainfall by a sort of "roof." Ants are among the most abundant prey of pitcher plants, being attracted to the pitcher edges by a form of extrafloral nectar. However, C.M. Clarke and R.L. Kitching show that one *Camponotus* species has evolved a more complicated relationship, perhaps a mutualism, with a carnivorous pitcher plant in Borneo. Thus, the hollow tendrils of *Nepenthes bicalcarata* house ants that feed on both large insects trapped by its pitchers and mosquito larvae therein. Unlike smaller prey, large insects apparently overwhelm the plant's digestive capacity and lead to accumulation of ammonia in the pitcher fluids. Removal of excess prey by *Camponotus* prevents putrefaction of the fluids. Therefore, although the ants do rob some prey from their host plants, the net effect of their presence may be positive.

Effects of Ant-Plant Interactions on the Diversification of Ants

Given the extraordinary diversity and widespread abundance of interactions between plants and ants, the two groups would be expected to have influenced one another's evolutionary histories. This conjecture is supported by recent molecular phylogenetic studies by C. Moreau and colleagues, who show that the diversification of ant "crown groups" (contemporary major taxa) occurred coincidentally with that of flowering plants (angiosperms) in the Late Cretaceous and early Eocene, and involved major taxa of litter ants, as well as the arboreal ants reviewed in the present article.

With respect to plants, relationships with ants likely contributed to recent and rapid diversification of species in the genus *Inga* (Fabaceae), defined in part by EFNs on leaf rhachis, and containing an estimated 300–450 species. Major radiations of ant inhabited plant taxa have also occurred in genera *Cecropia* (Cecropiaceae), *Macaranga* (Euphorbiaceae), Ocotea (Lauraceae), *Tachigali* (Fabaceae), *Triplaris* (Polygonaceae) *Tococa* and *Clidemia* (Melastomataceae), as well as in various genera of ant-house epiphytes in sub-family Hydnophytinae (Rubiaceae).

► Ants
► Leaf-Cutting Ants
► Pollination
► Insectivorous Plants
► Carnivorous Plants

References

Davidson DW (1997) The role of resource imbalances in the evolutionary ecology of tropical arboreal ants. Biol J Linn Soc 61:153–181

Davidson DW, Epstein WW (1989) Epiphytic associations with ants. In: Lüttge U (ed), Vascular plants as epiphytes. Springer-Verlag, New York, NY, pp 200–233

Davidson DW, Inouye RS, Brown JH (1984) Granivory in a desert ecosystem: experimental evidence for indirect facilitation of ants by rodents. Ecology 65:1780–1786

Davidson DW, McKey D (1993) Ant-plant symbioses: stalking the Chuyachaqui. Trends Ecol Evol 8:326–332

Federle W, Maschwitz U, Bert Hölldobler (2002) Pruning of host plant neighbours as defense against enemy ant invasions: Crematogaster ant partners of Macaranga protected by "wax barriers" prune less than their congeners. Oecologia 132:264–270

Ghazoul J (2001) Can floral repellents pre-empt potential ant-plant conflicts? Ecol Lett 4:1–5

Hickman JC (1974) Pollination by ants: a low-energy system. Science 184:1290–1292

Hölldobler B, Wilson EO (1990) The ants. Belknap Press of Harvard University, Cambridge, MA

Izzo TJ, Vasconcelos HL (2002) Cheating the cheater: stability of a mutualism between an ant-plant and its associated ants. Oecologia 133:200–205

Mueller UG, Schultz TR, Currie CR, Adams RM, Malloch D (2001) The origin of the attine ant-fungus mutualism. Q Rev Biol 76:169–197

Palmer TM, Stanton ML, Young TP (2003) Competition and coexistence: exploring mechanisms that restrict and maintain diversity within mutualist guilds. Am Nat 162:S63–S79

Quek SP, Davies SJ, Itino T, Pierce NE (2004) Codiversification in an ant-plant mutualism: stem texture and the evolution of host use in *Crematogaster* (Formicidae: Myrmicinae) inhabitants of Macaranga (Euphorbiaceae). Evolution 58:554–570

Yu DW, Pierce NE (1998) A castration parasite of an ant-plant mutualism. Proc R Entomol Soc London 265:375–382

Ants

Certain members of an order of insects (order Hymenoptera)

► Ants (Hymenoptera: Formicidae)
► Wasps, Ants, Bees and Sawflies

Ants (Hymenoptera: Formicidae)

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Ants are one of the most highly evolved and dominant insect groups. They are the largest family of insects in terms of the diversity of species and certainly sheer numbers of individuals. Currently there are well over 12,000 described species of ants, and some suggest that a similar number is yet to be discovered. Individual colonies of some species can contain over 20 million members. Ants belong to the family Formicidae, which consists of 23 subfamilies and 287 genera that are not extinct.

Order Hymeoptera
  Suborder Apocrita
    Superfamily Vespoidea
      Family Formicidae

They are found in all terrestrial regions of the world, including the cold subarctic tundra and dry deserts. About half of the world's precinctive genera are from the Neotropics and a third from the Afrotropical [sub-Saharan Africa] region. The subfamily with the greatest number of species is the Myrmicinae, and is followed by the Formicinae.

Ants are true social (eusocial) insects, which is defined by the following characteristics: (i) cooperative brood care, where immature ants are tended by groups of adults that are not their parents; (ii) overlapping generations, where at least two different generations of adults occur simultaneously in the same colony; and (iii) reproductive and non-reproductive castes, where only the reproductives are capable of producing fertile offspring. The non-reproductives, or workers, perform tasks necessary for colony survival, such as foraging for food, caring for immature ants and reproductives, and nest building. Eusocial insects have a competitive advantage over nonsocial insects because there is a better probability that groups of sterile workers will be able to complete a task necessary for the survival of the reproductive queen, and also complete a series of tasks simultaneously. If a task is not completed by one worker, another worker can finish the job. This is opposed to a solitary insect where the entire burden of completing tasks from start to finish rests with the individual.

Caste determination, or what causes an ant to develop into a reproductive or a worker, is thought to be due to differential genetic expression stimulated by environmental factors. Based on a limited number of species, at least six factors have been identified as being influential in reproductive and worker caste determination: (i) Egg size, where eggs with more yolk and hence larger in size will more likely become queens. (ii) Chilling, eggs and larvae that have been exposed to sufficiently cold winter temperatures tend develop into reproductives in the spring. (iii) Larval nutrition, where food quality and quantity affect larval size. Larvae that reach a threshold size by a critical developmental time become the reproductives. (iv) Temperature, larvae that grow in optimal developmental temperatures tend to become queens. (v) Caste inhibition, production of new queens is inhibited by the presence of a mother queen. (vi) Queen age, where younger queens generally produce more workers. Regulating the occurrence of some of these factors are titers of juvenile hormone. Depending on species and colony conditions, all or just some of these factors may be involved and the degree of the factors' influence also varies. A sequence of criteria may need to be met for an egg to more likely develop into a queen, otherwise it will be a worker. To illustrate, for an egg to develop into a queen the following criteria may need to be met more or less sequentially: (i) is the egg of sufficient size, (ii) did it receive enough winter chilling, (iii) was food sufficient and (iv) temperatures optimal for the larva to reach a critical size by the right time, (v) are mother queens young and preventing new queen development? Meeting criteria will bias or increase the probability of the development of a queen. Determination of major (soldiers) and minor workers in some species is under both environmental and genetic regulation, thus maintaining a characteristic major: minor ratio within a colony. Recently, genetic regulation of workers and queens was found to be absolute in a hybridization zone between two species, where workers were heterozygous and reproductives were homozygous at marker loci for caste determination.

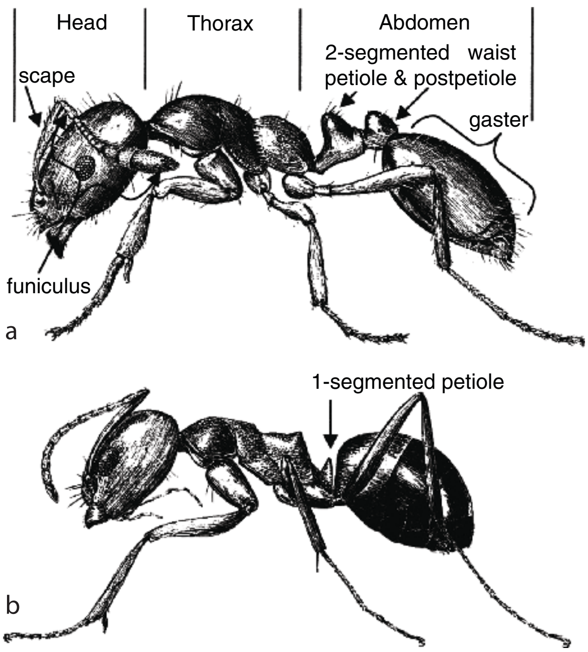
Communication needed to coordinate the activities within a colony is mediated by chemical signals called pheromones. Some of the pheromones that have been isolated include a queen pheromone that allows worker ants to recognize a queen, trail-following pheromone which workers use to mark paths between the nest and food, and alarm pheromones which cause ants to disperse and/or attack. Chemical cues also are used in the recognition of colony nest mates, and play a role in aggression and establishing territorial boundaries between colonies.

Ants are omnivorous and mobile, allowing them to exploit a wide range of habitats. This is in contrast to termites, another abundant eusocial insect, which are restricted to feeding on wood or other vegetation. Moist environments are conducive to microbial contamination. Secretions from the ant's metapleural gland contain antibiotics that disinfect moist environs. Having a portable means of sanitation allows ants to exploit areas that other organisms may not be able to live in. These attributes permitted ants to become a dominant terrestrial organism, especially in the tropics. With their large populations and adaptation to a plethora of ecological niches, ants play an important role in natural ecosystems. They are tremendous earth-movers because of their underground nest building, and thus contribute greatly to the cycling of nutrients. They disperse seeds, scavenge dead organisms, and are a major predator of other arthropods and small invertebrates. In some instances they are directly beneficial to man by being major predators of pests such as crop feeding caterpillars, and ticks of livestock.

Morphology

Ants are easy to distinguish from other insects mainly because of the combination of a thin-waist and the presence of elbowed antennae. The waist refers to a segmented constriction called the petiole, located between the thorax and the gaster. The gaster is composed of the broad 4 or 5 posterior segments of the abdomen. Morphologically ants are distinguishable by having a one or two-segmented waist (Fig. 63); always consisting of a petiole if one-segmented, and both a petiole and a postpetiole if two-segmented. The petiole and postpetiole are actually the second and third segments of the abdomen that are reduced or constricted in size. They often have a distinctive node-like form, however in some species it is scale-like or just a small cylindrical segment. Following (Table 6) is a list of four terms that describe sections of the ant abdomen and the corresponding abdominal segments for ants with one- and two-segmented waists.

The adult workers and queens have antennae that are geniculate, meaning bent or elbowed. The elbowed appearance arises from having a long first, or basal, antennal segment called the scape, followed by 3–11 short segments (collectively called the funiculus). The basal segments in male antennae are usually not long, and thus, the antennae will not appear to be elbowed. Another unique feature of ants is the small opening or orifice of the metapleural gland. This is located just above the basal segment of the third leg, but often requires magnification to be visible.



Ants (Hymenoptera: Formicidae) , Figure 63
Distinguishing morphological structures of ants: (a) two-segmented petiole or (b) one-segmented petiole. Elbowed antenna consisting of a long basal segment (scape) and 3–11 short segments (funiculus); posterior portion of abdomen beyond petiole (gaster) [drawings modified from M.R. Smith 1965, (a) *Monomorium minimum*, (b) *Dorymyrmex pyramicus*].

Ants (Hymenoptera: Formicidae), Table 6
Abdominal segments that compose sections of the abdomen for ants with one- and two-segmented waists

Abdominal Sections	One-segmented waist	Two-segmented waist
Propodeum	abdominal segment 1 fused to posterior of thorax	
Petiole	abdominal segment 2	abdominal segment 2
Postpetiole	None	abdominal segment 3
Gaster	abdominal segments 3–7	abdominal segments 4–7

Life/Colony Cycle

Ants are holometabolous, having a complete life cycle consisting of eggs, larvae, pupae, and adults. Thus, little adult ants do not grow into big adult ants. The eggs, larvae, and pupae are collectively called brood. In general, colony development is as follows: ant colonies originate after a mating flight when winged virgin queens mate with winged males. After mating, the males die, while the newly mated queen sheds her wings and finds a protected location or excavates a chamber in soil. Within this chamber she will lay a batch of eggs and care for the subsequent larvae and pupae until they become adults. These adults are usually sterile females, which are the worker caste, and they will assist the queen by caring for additional brood, foraging for food, and expanding the nest. An important aspect to the survivorship and growth of ant colonies is trophallaxis, or the exchange of regurgitated food among nestmates. Trophallaxis ensures that food is distributed to all members of the colony including the queen and brood. Once the colony is well established, winged virgin females and males (reproductives) will be produced and will proceed to have a mating flight when environmental conditions are suitable. The original colony will continue to be maintained and produce new reproductives as long as the queen is able to produce viable eggs. Depending on the species, queens have been reported to live from less than a year to as long as 29 years. A major variation to this cycle is the absence of a mating flight by the virgin queens in some species. Mating takes place within the nest with either their brothers or males that fly in from other colonies. New colonies are formed by budding, where a portion of the colony, containing adults, brood, and either or both mated or virgin queen(s), separate from the original colony and move to a new location.

In addition to the tremendous number of ant species, there is a broad range of interesting behaviors or life styles among species. Many species have mutualistic relationships with honeydew-producing insects such as aphids and mealybugs

(Hemipteran). Ants will transport and protect these insects in order to harvest the honeydew they produce. In essence, these ants tend and herd the honeydew producers as if they were cows. Some hemipterans carry plant pathogens, and disease spread is facilitated by ants moving the infected hemipterans to other plants.

Another agrarian life-style is that of the leaf-cutting ants that raise their food in fungal gardens within their nest. These ants use leaves and other fresh vegetation to provide a substrate on which to grow the fungus, and these ants can defoliate trees overnight. Leaf-cutting ants cut pieces of leaves or flowers with their jaws and then carry them back to their nest. Once in their nest, they further chew the vegetation and add feces to form a suitable medium for fungal growth. Finally, they plant and maintain a specific fungus species on the substrate. In Central and South America, leaf-cutting species in the genus *Atta* and *Acromyrmex* (subfamily Myrmicinae) can have colonies with an estimated 1–8 million individuals. They build nests consisting of an extensive network of subterranean galleries, and are the most significant pests of agriculture in South America, feeding on citrus, forage grasses, and other crops.

Symbiotic relationships with plants been reported for several ant species. One well-studied mutualistic relationship is that between *Acacia cornigera* trees and the ant *Pseudomyrmex ferruginea* (subfamily Pseudomyrmecinae). The acacia tree produces thorns, which serve as nesting sites for the ants and it produces structures, called Beltian bodies, that are eaten by the ants. The ants protect the plant from herbivorous arthropods and vertebrates, and destroy competing plants that sprout nearby.

Besides their symbiotic interactions with plants and other insects, ant species also have parasitic relationships among each other of which slavery, or dulosis, is one of the more interesting forms. The genus *Polyergus* (subfamily Formicinae) consists entirely of slave-making species. Workers of *Polyergus* colonies dash into the nests of ants in the genus *Formica* (subfamily Formicinae) and steal their larvae and pupae. The stolen immatures are allowed to develop into adult workers and carry out colony maintenance tasks for their abductors. In fact, the *Polyergus* workers are so specialized for raiding and killing other ants that their jaws are like sharp curved sabers, morphologically ill-suited for nest building, tending immatures, and food gathering.

More extreme extensions of this parasitism are species without a worker caste. These species contain only males and queens that are cared for by the workers of a host colony, which they have infiltrated. They are either fed by the workers or steal food from the host queen, which they often mount and hold onto. The eggs of the parasite are reared to adulthood by the host workers. Parasitized host colonies can be smaller in size, presumably because of the partial diversion of resources to the parasites. Examples of these parasitic ants include *Solenopsis daguerrei*, a parasite of imported fire ants (*Solenopsis invicta, S. richteri*), and *Teleutomyrmex schneideri*, a parasite of *Tetramorium caespitum* and *T. impurum* (all in the subfamily Myrmicinae).

In contrast to the symbiotic life-styles, many species of ants are extremely predatory and have gained the reputation of being an unrelenting scourge of the jungle. The subfamily Dorylinae consists of a single genus, *Dorylus*, which contains the African driver ants, also referred to as army ants or legionary ants. Most species are found in the Afrotropical region (sub-Saharan Africa), but a few species are also found in the southern Palearctic, Oriental, and Indo-Australian regions. The various species of African driver ants have colonies with millions of individuals, which regularly move nesting sites and forage for food in large swarming columns or groups. The columns can fan out to produce a large moving front that preys on anything that remains in its path, especially arthropods. At night the colony forms a bivouac, protecting their queens and brood within a mass of worker ants. Thus, there is no permanent nest structure for these nomadic ants. Besides the army ants in the Dorylinae, the subfamily Ecitoninae contain many species of army ants found in the Neotropics, and a few species in the Nearctic. These armies are smaller than the African species, with colonies of hundreds of thousands rather than millions.

The pillaging, nomadic life of the army ants requires a high level of organization and cooperation. Extraordinary cooperative behavior is further exhibited during nest construction by the weaver ants in the genus *Oecophylla* (subfamily Formicinae). These ants are dominant arboreal ants of the Afrotropical region. They link their bodies together to form chains by grasping the petiole of an adjacent worker with their jaws. The living chains are used to pull the edges of leaves together. Once leaves are held in a desired position, other workers bring forth silk-producing larvae and individually press larval heads to one leaf surface then another, resulting in thousands of sticky silk threads being drawn between the leaves to hold them together. Eventually leaves and stems are bound together to form a tent within which a nest of silken galleries is constructed. This communal nest construction is unique in that it involves the use of immature stages that secrete silk on command. It has allowed these ants to build expansive networks of nests across several trees, which can house a colony of over 500,000 individuals.

The adaptability and high reproductive output of many species of ants allow them to thrive in many environments, including that of humans. As such, ants that live in buildings or have high populations in areas used by man are often considered pests. Many pest ants have characteristics that typify the "tramp species". These ants generally (i) spread around the world via human commerce; (ii) can thrive in man-made environments; (iii) have colonies that are not territorial and thus can result in interconnected nest sites; (iv) have many queens per colony; and (v) have limited or no mating flights resulting in colony reproduction by budding. Ants that sting, such as red imported fire ants (*Solenopsis invicta*, subfamily: Myrmicinae), are of veterinary and medical importance. Newborn livestock can be blinded or killed by stings at birth. People who are stung usually develop itching pustules that last for several days, but some can have hypersensitive reactions, resulting in anaphylaxis and even death in rare instances. Non-stinging ants, such as the Pharoah ant (*Monomorium pharaonis*, subfamily: Myrmicinae) may be a nuisance to building occupants and are also known to contaminate sterile surgical units, supplies, and food items in hospitals. Invasive ant species, such as the red imported fire ant and the Argentine ant (*Linepithema humile* subfamily: Dolichoderinae), establish and thrive in non-native locations, invade surrounding areas, and eventually become the dominant faunal species. Invasive ants are a major concern in many areas, ranging from nature preserves to suburbia, because they displace native ants as well as other native organisms.

Control

Controlling pest ants can be a difficult task given their broad habitat range, large populations, and a social organization that protects the queen(s) from external influences such as insecticides. Because traditional control approaches of excluding ants from buildings by sealing cracks and crevices or applying insecticides directly to ants or nests generally do not target the queen, significant population reductions, if any, are temporary. Ant baits, however, were developed to use the foraging and nest mate feeding behaviors of ants to distribute a toxicant throughout a colony, including the queen(s). Ant baits typically contain a toxicant dissolved into a liquid food preferred by the pest ant species. This poisoned food can be mixed with an absorbent carrier such as corn grit or formulated into a gel to facilitate handling and application. Some baits are left in liquid form and must be dispensed in a container that serves as a feeding station.

Key to effective ant bait is a toxicant with the following three characteristics. First, the concentration of toxicant used should not deter feeding on the bait, because ideally enough bait should be readily foraged upon to be shared with adults and immature stages of all castes within a colony. Second, the toxicant should not immediately kill the ants foraging upon the bait. In general, a delay in death or sickness of a minimum of 8 hours from the time of ingestion is required to allow sufficient toxicant to be collected and fed to a significant portion of the colony. If the toxicant causes sickness or death too quickly, distribution of the bait to the rest of the colony stops before enough of the colony is affected, and control will not be obtained. Third, the toxicant should provide a delay in mortality over a wide range of concentrations (typically at least a 10 fold range) because the toxicant is diluted as it is shared among nest mates. Depending on the type of toxicant and colony size, ant baits may take from three days to several months to eliminate a colony. Some bait toxicants do not kill adults but instead disrupt reproduction by the queen, whereby worker caste ants are no longer produced. As the original adult worker population dies naturally, the lack of replacement workers dooms the colony to a slow death as functions that sustain a colony such as food gathering, defense, nest repair, and queen care cannot be carried out.

While ant bait development has been a major focus for ant control, other strategies have been developed for specific species. For example, planting forage grasses that are a non-conducive substrate for the growth of fungus needed by leaf-cutting ants can significantly reduce their populations. Natural enemies of ants are also used to suppress ant populations. In particular, tiny parasitic flies, in the genus *Pseudacteon*, that develop in the heads of ants, and a pathogen, *Thelohania solenopsae*, that debilitates queens are being used to suppress populations of imported fire ants. These natural enemies require development within fire ants and unlike chemical control measures, are self-sustaining and can spread naturally among fire ant populations. Effective control of pest ants, as with most insect pests, generally requires the use of several control tactics adapted for a particular species and circumstance.

► Myrmecophiles
► Myrmecomorphy
► Ant-plant Interactions
► Driver Ants
► Leaf-cutting Ants
► Carpenter Ants
► Castes

References

Agosti D, Johnson NF (eds) (2005) Antbase World Wide Web electronic publication. antbase.org version (05/2005). Accessed September 2007

Bolton B (1994) Identification guide to the ant genera of the world. Harvard University Press, Cambridge, MA, 222 pp

Bolton B, Alpert G, Ward PS, Naskrecki P (2006) Bolton's catalogue of ants of the world: 1758–2005. Harvard University Press, Cambridge, MA

Julian GE, Fewell JH, Gadau J, Johnson RA, Larrabee D (2002) Genetic determination of the queen caste in an ant hybrid zone. Proc Natl Acad Sci USA 99:8157–8160

Hölldobler B, Wilson EO (1990) The ants. Harvard University Press, Cambridge, MA, 732 pp

Smith MR (1965) House-infesting ants of the eastern United States: their recognition, biology and economic importance. United States Department of Agriculture, Agricultural Research Service Technical Bulletin No. 1326. 105 pp

Williams DF (Ed) (1994) Exotic ants: biology, impact, and control of introduced species. Westview Press, Boulder, CO, 332 pp

Williams DF, Oi DH, Porter SD, Pereira RM, Briano JA (2003) Biological control of imported fire ants (Hymenoptera: Formicidae). Am Entomol 49:150–163

Anus

The external opening of the digestive tract, through which the food remnants and metabolic waste products are passed.

► Alimentary Canal and Digestion
► Internal Anatomy of Insects

Aorta

A tube located dorsally in the insect's body that conducts blood from the heart forward to the head region.

Apatelodidae

A family of moths (order Lepidoptera). They commonly are known as American silkworm moths.

► American Silkworm Moths
► Butterflies and Moths

Aphelinidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Aphelocheiridae

A family of bugs (order Hemiptera).

► Bugs

Aphicide

An insecticide that is especially effective against aphids.

Aphididae

A family of insects in the order Hemiptera. They sometimes are called aphids, green flies, and plant lice.

► Aphids
► Bugs

Aphidivorous

Aphid loving. Many insects are associated with aphids because the feed on the honeydew produced by the aphids (e.g., many ants, some flies including mosquitoes) or on the aphids (e.g., many lady beetles and flower flies). Those that feed on the aphids are said to be "aphidophagous."

► Aphids
► Sugar Feeding in Blood-Sucking Flies
► Aphidophagous

Aphidophagous

Aphid feeding.

► Aphidivorous
► Predation: The Role of Generalist Predatory in Biodiversity and Biological Control
► Natural Enemies Important in Biological Control

Aphids (Hemiptera: Aphididae)

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Aphids are among the most interesting, unusual, and thoroughly studied of all insect groups. They are worldwide in distribution, and are also called plant lice, antcows, green flies, die Blattläuse, les aphides, los áfidos, etc. They have economic importance because many aphid species are pests of agricultural crops, forest and shade trees. Although small in size (1–10 mm) compared to many other insects, professional as well as amateur entomologists have always been intrigued by their specialized life cycles that are influenced by their host plant relationships. This results in both sexual and asexual reproduction, with a highly dependent, almost parasitic mode of sessile existence that can be parthenogenetic during lengthy periods with a telescoping of generations. Yet, when the photoperiod shortens and the temperature cools, offspring are produced that reproduce sexually. In addition, aphids have life cycles with a polymorphism in adults that have wingless (apterous) and winged (alate) forms or morphs, as well as polyphenism or different morphs even within clones. As alates, migration is enhanced, and this can be involved with overwintering behaviors because of host plant alternation. Hence, aphids are excellent animals for the study of multitrophic ecology, behavior, physiology, genetics, evolution, biological control, molecular biology, etc. Besides using field studies of aphids for population sampling and damage assessment, many species can be reared rather easily in the laboratory and greenhouse, thus making them ideal subjects for precise observation and experimentation.

Classification

Aphids are usually classified in the order Hemiptera, series Sternorryncha or sometimes suborder Homoptera along with the psyllids, whiteflies, scale insects, and mealybugs. Another approach is to put aphids in the order Homoptera and suborder Sternorryncha. Some taxonomists have increased the number of aphid families to as many as 20 with a corresponding realignment of the subfamilies. Further phylogenetic studies with molecular techniques are in progress, but in this overview summary the following composite scheme of the major taxa in aphid classification is given below such that there are 8 subfamilies in the family Aphididae:

Order Hemiptera
- Series Stemorrhyncha (= Suborder Homoptera)
  - Superfamily Aphidoidea
    - Family Aphididae (aphids)
      - Subfamily Aphidinae
        - Tribe Aphidini
        - Tribe Macrosiphini
      - Subfamily Calaphidinae (= Drepanosiphinae)
      - Subfamily Lachninae
      - Subfamily Chaitophorinae
      - Subfamily Greenideinae
      - Subfamily Eriosomatinae
      - Subfamily Hormaphidinae
      - Subfamily Anoeciinae
    - Family Adelgidae (adelgids)
    - Family Phylloxeridae (phylloxerans)

Although the number and organization of the subfamilies can vary, there is general agreement that within the family aphididae, the largest subfamily is the aphidinae, followed by the calaphidinae (=Drepanosiphinae), and the Lachninae. There are over 4,000 species of aphids which is a relatively small number compared to many other insect taxa. However, adult polymorphism as winged (alate) and wingless (apterous) morphs, as well as polyphenism within clones increases their overall diversity.

Distribution

Although aphids are found worldwide, their species are most abundant in the temperate latitudes, and less so in the tropics. This preferential distribution may have evolved in response to the selective pressures of the temperate regions having constantly changing, yet rather predictable, environmental conditions. As a result, unlike most other phytophagous (herbivorous) insects, aphids show an inverse relationship between the number of aphid species and the number of plant species in different parts of the world. Hence, there are many more aphid species in the temperate latitudes than in the tropics, although there are more plant species in the tropics than in the temperate regions, but with fewer species of aphids. Most aphids (70%) are in the subfamilies Aphidinae and Calaphidinae (=Drepanosiphinae), and many are pests of crops in these temperate zones. However, when some of these species are introduced (accidentally) into tropical and subtropical regions, they are still able to adapt and become pests in these new environments. In addition, although the tropics and subtropics are fairly constant in temperature and photoperiod, it is surprising that there are some endemic species in these regions that are holocyclic in their life cycles (female cyclical parthenogenesis, alternating with sexual reproduction by males and females) which is more common in the temperate zones. This is in addition to the expected anholocyclic life cycle (absence of males, only parthenogenesis by females) which would be normal in the tropics and subtropics. Aphids find their host plants by random search, and ecologists emphasize the importance of the concept of "plant apparency." Of the more numerous species of aphids in the temperate regions, many are monophagous (feed on one or only a few species of related host plants). However, in the tropics where there are more species of plants and relatively fewer aphid species, these aphids are more polyphagous (feeding on a variety of host plants). Hence, some suggest that aphids originated in the northern hemisphere, and that the tropics presented a barrier to a similar multiplication of species in the southern hemisphere.

Origin and Evolution

Based on the classification given above, in the hemipteran superfamily Aphidoidea are the families Aphididae (aphids), Adelgidae (adelgids), and Phylloxeridae (phylloxerans). Paleontology and phylogeny are two sources of information used by systematists to study the evolutionary history of this group. According to these experts, although paleontology should provide a time scale for their ages, unfortunately the fossil evidence is very limited. Only about 125 fossil species have been described, while the number of extant aphid species is over 4,000. Two kinds of fossils exist: (i) imprints from carbonized remnants in clay, limestone or other sediments, which provide only minimal information because aphids are soft-bodied and are not well preserved; and (ii) amber inclusions which have entire specimens that are often caught in a natural position, and so are much more important as fossils.

Probably aphids, along with the closely related adelgids and phylloxerans, evolved from a common ancestor about 280 million years ago in the late Carboniferous or early Permian Periods when there were seasonal climatic changes associated with the glacial period. They are now classified together in the superfamily Aphidoidea, and their host plants were primitive gymnosperms (Cordaitales, Cycadophyta). By utilizing their specialized piercing – sucking stylets on the phloem and parenchyma tissues of the gymnosperms, polyphagy was most likely the primitive feeding behavior of the superfamily Aphidoidea. As a result of their parasitic mode of life, individual size in these three families (Aphididae, Adelgidae, Phylloxeridae) was similar and rather small. Although their wings were delicate, their light body weight could take advantage of air currents for dispersal. Some consider monophagy as a recent development in aphid evolution, although others speculate that like parthenogenesis, it could have evolved early in the evolutionary history of the Aphidoidea. Another characteristic which aphids share with the adelgids and phylloxerids is the simple nymphal eye of three lenses (triommatidium).

From the Triassic Period (240–205 million years ago), only the front wing of one species of aphid (*Triassoaphis cubitus*) from Australia is known, and it is not easily placed in any superfamily of later periods. Cytogenetic evidence indicates that parthenogenetic reproduction by means of unfertilized eggs may have evolved over 200 million years ago, before these three families (Aphididae, Adelgidae, Phylloxeridae) became independent. This view is supported because a holocyclic life cycle (cyclical parthenogenesis by females, alternating with sexual reproduction by males and females) is now common to all three groups. However, viviparity (live birth) is a special characteristic of aphids, and must have evolved later because the modern adelgids and phylloxerans are only oviparous (lay eggs). By the Jurassic Period (205–138 million years ago), there had developed the recognizable shape of the body, wing venation, proboscis, and legs, while the siphunculi or cornicles and cauda evolved in the Cretaceous Period (138–65 million years ago).

A major botanical event also occurred during the Cretaceous with the evolution of angiosperms (flowering plants), which coincided with the radiation and species diversification of aphids. Within the family Aphididae, the Aphidinae (the largest subfamily of modern aphids) is not represented in the fossil record until the late Tertiary Period (65–1.65 million years ago). Tribes of the second largest subfamily, the Calaphidinae (=Drepanosiphinae), developed much earlier in the Upper Cretaceous and early Tertiary Periods. Concerning the third largest subfamily, the Lachninae, there is limited palaeontological evidence of its evolution. Hence, there is some debate as to the relative age of the lachnids. Because 80% of them live on conifers (which are older than the angiosperms), the lachnids have generally been regarded as ancient, although some genera may have a recent origin.

Metamorphosis

Regardless of whether aphids are born from an egg of oviparous sexual females or live from viviparous parthenogenetic females, their type of metamorphosis is called simple or incomplete: the developmental sequence is egg, to nymph(s), to adult. A nymph resembles the adult, and usually develops in four molts (four nymphal instars or stages) growing larger each time until the adult stage of sexual maturity is reached. This type of metamorphosis is to be distinguished from complex or complete metamorphosis wherein the developmental sequence is from egg, to larva (several molts and instars), to pupa, to adult.

External Morphology

Aphids are mostly soft-bodied insects and relatively small (only 1–10 mm in length), usually being plump and ovoid in shape. Because they are plant-sucking insects, they feed by inserting their slender mouthparts into the plant. These needle-like stylets consist of an outer pair of mandibles and an inner pair of maxillae. The inner faces of the maxillary stylets lock together to form two canals: a large central food-canal for the uptake of plant sap, and a fine duct down which saliva is injected into the plant. The tips of these mouthparts also have a chemosensory function. When the stylets penetrate the plant, they often go between the cells instead of passing through the cells, and in this way they reach the phloem sieve tubes within the veins of the host plant.

Most aphids have well-developed compound eyes (larger in the alates than in the apterous morphs) with a great many individual round lenses called facets or ommatidia. In addition, at the posterior margin of the eye protrudes an ocular tubercle or triommatidium composed of three lenses. Aphids without wings are called apterous, while alate aphids have wings with the hind wings being much smaller than the front wings. Alate aphids (but not apterous) bear three ocelli on the front of the head. The antennae are usually long and thin with five or six segments, and bear placoid sensilla called rhinaria which are the olfactory organs. Legs of aphids do not show much interspecific variation, although more active species tend to have longer legs. Both sets of wings are membranous with the fore wing having two longitudinal veins, one being prominent and the other a weak vein. Both veins run apically into the pterostigma which is a dark, thickened area near the leading edge of the fore wing. When flying, the two pairs of wings work as one, being held together by small hooklets or hamuli on the leading edge of the hind wings that fit into a groove on the trailing edge of the fore wings.

On the dorsal surface of both the thorax and the abdomen, many species have cuticular glands that secrete copious quantities of waxy exudates that are powdery or filamentous or rod-like. As a result, when these species are gregarious, the entire colony appears as a white, powdery or cottony mass. At the end and dorsal surface of the abdomen, there are usually a pair of tubular structures called siphunculi or cornicles. By contraction of a muscle, a droplet of a waxy exudate is discharged through the cornicles which rapidly solidifies in the air. When an aphid is touched or attacked by a predator, one or both cornicles may be raised and the sticky fluid released in a defensive role to gum-up the mouth parts and/or antennae of an attacking predator. This may also function as a pheromone either as an alarm to warn other aphids of a predator or for maintaining distance between aphids on a leaf. Above the anal opening, adult aphids usually have a distinct tail or cauda which varies in shape among species from being short and stubby or long and tapering. In the latter case, aphids can flick off a droplet of honeydew that emerges from the anus. Concerning the external genital organs in the adults, the female genital opening or vulva is only a small slit because there is no ovipositor. On the other hand, the male genitalia have prominent sclerotized claspers and an aedeagus or penis that can be retracted.

Internal Anatomy

Digestive System

Aphids have the usual regions: pharynx, foregut, midgut, hindgut, etc. with subdivisions and associated parts. However, some species have a filter chamber which is a special structure. With some variations, it consists of a concentric filter system in which the tubular anterior region of the midgut is enveloped by the anterior region of the ectodermal hindgut forming a filter chamber. Perhaps this permits selective filtering of the required nitrogen compounds while rejecting the sugars and conveying excessive amounts of water to the hindgut. The precise function is not clear, and since most aphids do not have a filter chamber, it is probably not essential to their method of feeding.

Bacteriocytes

Most aphids have specialized groups of cells called bacteriocytes (or mycetocytes) that usually contain the bacterium *Buchnera aphidicola*. This symbiotic association seems to be mutualistic, and it is not surprising because many insects that live on specialized and often unbalanced diets such as plant sap do indeed possess symbionts. Although their role in aphid biology is still not completely known, they may help the aphid with its nitrogen utilization, synthesis of vitamins, sterols, etc. Although numerous at birth, the bacteriocytes decrease in number during growth. By the end of the aphid's reproductive period, practically none remain, suggesting a contribution to embryonic development. These bacterial symbionts are transmitted transovarially to the embryos so that nymphs are born with them.

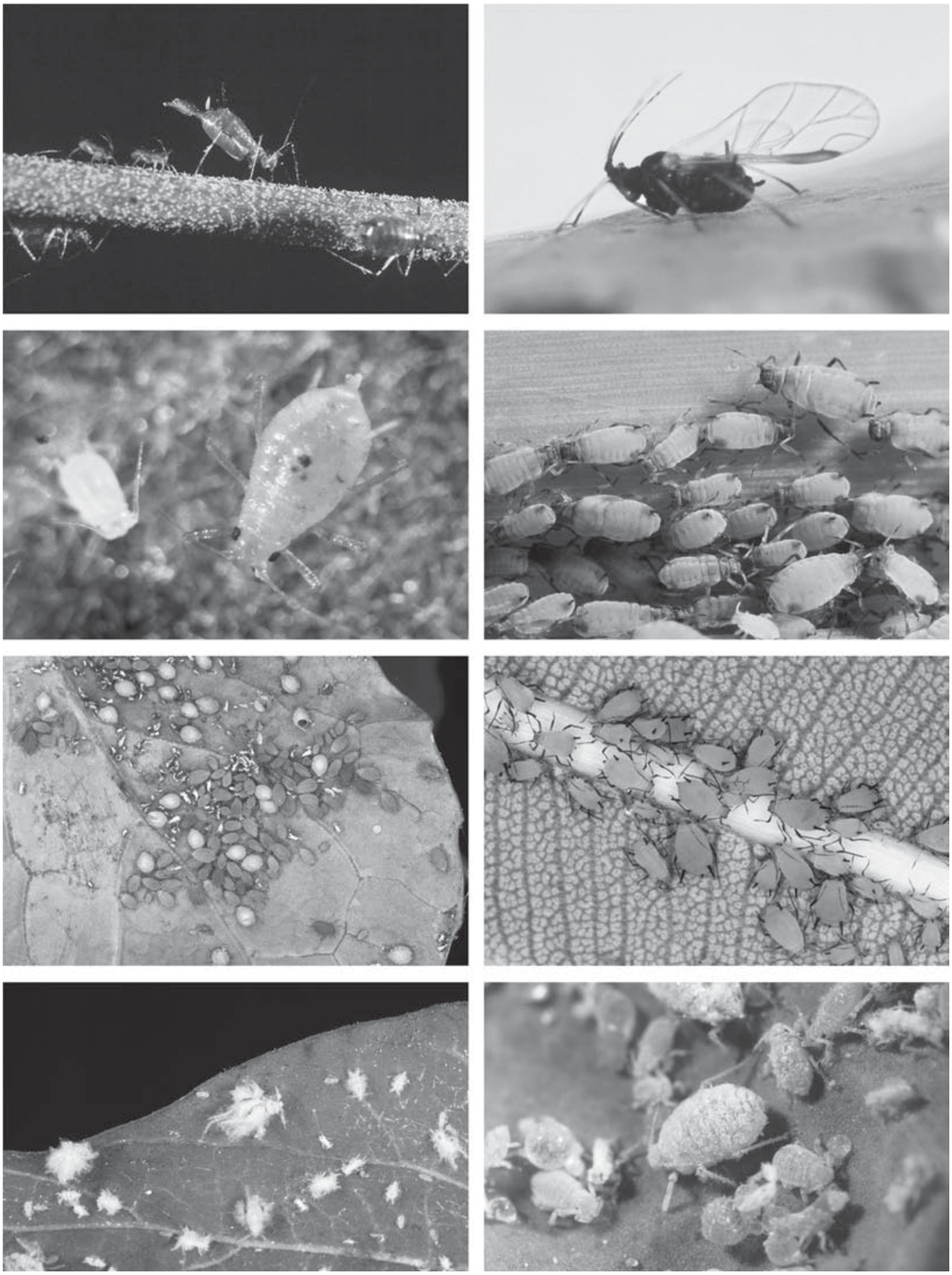
Nervous System

The nervous system comprises four structural parts: brain or supraoesophageal ganglion in the head, suboesophageal ganglion under the brain, thoracic ganglionic mass terminating in the ventral nerve cord, and ganglia plus nerves of the stomatogastric system.

Reproductive System

Female aphids have two ovaries composed of 4–6 ovarioles. They are remarkable because different female morphs can reproduce parthenogenetically (Fig. 64) and be virginopara/vivipara (give birth to live young by larviposition) without mating because males do not exist at this time. At other times, females can reproduce sexually and be ovipara (deposition of eggs that have been fertilized by males). Development of the female embryo depends on whether it is destined to become a vivipara (live birth) or an ovipara (lays eggs). Influences on the adult female can be genetic as well as environmental. Realizing exceptions depending on the aphid species and geographical location, in general when the environment is favorable (long photoperiod, moderate temperature), the viviparous mother will reproduce parthenogenetically. The embryonic female within her will be born alive as a female nymph, and in turn will give live birth to other viviparae also being all females (see below about anholocyclic life cycle). On the other hand, with less favorable conditions (shorter photoperiod, cooler temperature), the oviparous mother will reproduce sexually after mating with a male, and she will lay fertilized eggs (see holocyclic life cycle).

The viviparous parthenogenetic female does not require fertilization, and eggs begin development as soon as they are ovulated from the ovary. Even ovarioles of newly born parthenogenetic females contain developing embryos rather than just eggs. Hence, "telescoping of generations" refers to the fact that a mother can have in her ovarioles developing embryos which in turn also contain embryos or future granddaughters. In the modern family Aphididae, therefore, development may commence even before the mother is born, resulting in a consequent "telescoping of generations." As a result,



Aphids (Hemiptera: Aphididae), Figure 64 **Aphid diversity. Top left, aphid giving birth to a nymph (photo J.L. Capinera); top right, winged brown citrus aphid, *Toxoptera citricida* (photo Paul Choate); second row left, green peach aphid, *Myzus persicae* (photo Jim Castner); second row right, corn leaf aphid, *Rhopalosiphum maidis* (photo Paul Choate); third row left, turnip aphid, *Lipaphis erysimi* (photo Jim Castner); third row right, oleander aphid, *Aphis nereii* (photo Jim Castner); bottom row left, Asian woolly hackberry aphid, *Shivaphis celti* (photo Lyle Buss); bottom row right, cabbage aphid, *Brevicoryne brassicae* (photo Paul Choate). Note copious and moderate amounts of waxy exudate on woolly hackberry and cabbage aphids, respectively.**

postnatal development periods and generation times are short, and reproductive rates are potentially very high. Because aphids are born on the very host plant where they can feed, in many species it requires only 7–14 days for an immature aphid or nymph to metamorphose by several molts into a sexually mature adult when it can begin reproducing. When this is combined with a high fecundity (30 or more nymphs born to each aphid) in a short period of time, the rate of increase is very rapid not only for the individual, but even more so for the entire colony.

The offspring of viviparous parthenogenetic females are born rear first, and are fully active. A nymph is similar in shape to the adult, only much smaller. If destined to be a winged (alate) adult it is either born with wing buds or in some species during the early postnatal period the nymph itself will develop them. This can be triggered by unfavorable conditions due to aphid crowding and/or plant deterioration as well as by seasonal changes such as shorter photoperiod and cooler temperatures. However, colonies founded by alates usually produce only apterous offspring, and only later on might alates develop. Hence, there seems to be a "biological clock" mechanism so that there is a gradual switch to alates that depends on an interval of time.

In the superfamily Aphidoidea, this viviparity (live birth) characterizes the entire family Aphididae. But only females in this family do this, and not females in the families Adelgidae and Phylloxeridae. However, in all three of these families there are sexual females (oviparae) that mate and deposit eggs (see Life Cycles).

Male aphids usually have two to four follicles per testis, although the number, size, and shape varies between species. The vasa deferentia lead to the ejaculatory duct, and in some species there are paired accessory glands.

Excretion

Unlike most insects, aphids have no Malpighian tubules, and excrete nitrogenous waste in the form of ammonia instead of uric acid. The large amounts of water in the diet may dilute the ammonia, and in addition, symbionts in the mycetomes may detoxify it as well.

Ingestion and Digestion

Both as nymphs and as adults, aphids feed by sucking up the sap from the host plant. When the stylets penetrate the plant between the cells, they reach the phloem sieve tubes. In a healthy plant, the sap is under turgor pressure which forces the sap up the food canal between the stylets which reduces the energy needed by the aphid to suck the sap. Nevertheless, there is also a muscular cibarial food pump at the entrance to the pharynx which can be used when the plant wilts and the sap ceases to be under pressure.

Although this plant sap is rich in sugars, it is poor in amino acids that are essential for the growth of the aphid. Hence, aphids ingest large amounts of sap in order to acquire sufficient protein. Although there are less nitrogenous compounds in plant sap compared to leaf tissue (such as would be eaten by other phytophagous insects such as the larvae or caterpillars of lepidopterans), aphids make up for this deficiency by imbibing sap at a very fast rate. The unneeded portion of the sap is mainly sugars which can be stored temporarily in a dilated rectum. This sugary material can be eliminated by ejection from the anus in the form of a sugary droplet called honeydew (see section on Ant-Aphid Mutualism). When aphids are numerous, the leaves of their host plant can become coated with sticky honeydew on which sooty mold fungus can develop causing an economic problem on fruit, vegetables, and even cars parked under a tree.

Sex Determination

As expected, the number of chromosomes varies with aphid species, but all aphids have sex chromosomes for females designated as XX and males as XO. This system of sex determination is called the XX:XO type wherein females have the full diploid complement of autosomes plus one pair of sex chromosomes: XX.

Males also have a diploid set of autosomes, but they have only one sex chromosome (XO) rather than two (not the XY as in some other insects and even humans). As discussed below, in holocyclic life cycles (female cyclical parthenogenesis, alternating with sexual reproduction), sexual females and males are produced in response to cues/stimuli that could be external or internal. On the other hand, anholocyclic life cycles (absence of males, only parthenogenesis by unfertilized females) usually exists when the environment (photoperiod and temperature) is relatively constant.

Parthenogenesis

This is reproduction without mating, and therefore without a female's egg being fertilized. As mentioned above, all aphids have the normal diploid autosomes, but the sex chromosomes for females are XX and males are XO (lacking an X). Among insects in general (not just aphids), when a female's egg is not fertilized, there can be two types of parthenogenetic reproduction:

Arrhenotokous parthenogenesis by females produces only male offspring that are all haploid (n) from her unfertilized eggs (common in the order Hymenoptera – ants, bees, wasps). In aphids, some authors hold that the male's XO sex chromosome determination is only a "type of arrhenotoky" probably resulting from a mini-meiosis in the unfertilized female by which her two X-chromosomes pair and then separate. Males are then XO with the result that they could produce two types of sperm (X and O). However, during meiosis in the male, those sperm without an X-chromosome (designated O) degenerate. This leaves the X-chromosome as the only viable sperm which can fertilize an adult female's haploid egg (X) resulting in all of her offspring being female (XX). Hence, males are produced by the loss of an X chromosome during a meiotic division resulting in the sex determination of XO. Adult male aphids then produce haploid sperm all of which contain one X chromosome. However, this is not really "arrhenotoky" as traditionally used with other insects because although male aphids have the sex determination of XO, they do have two sets of autosomes, but only one X chromosome.

Thelytokous parthenogenesis by females produces only adult diploid (2n) females from unfertilized eggs, but no males. Female aphids seem to have "diploid parthenogenesis" because there is no reduction division, and development starts from a cell with a complete set of chromosomes including the XX sex chromosomes. Both the adult parthenogenetic females and the sexual females are diploid (2n) with XX sex chromosomes. In anholocyclic life cycles (absence of males, only parthenogenesis by unfertilized females), this reproductive method could continue almost indefinitely, if the environmental conditions permitted. However, in holocyclic life cycles (female cyclical parthenogenesis, alternating with sexual reproduction), sexual females and males are produced. The sexual female produces only haploid eggs (X), and requires mating and fertilization by a male (X) resulting in a diploid zygote with two XX sex chromosomes, such that all aphids hatching from these fertilized eggs are females.

Life Cycles

Life cycles in aphids are varied and complicated, but the essential terms are given below:

Holocyclic life cycle: A viviparous parthenogenetic female produces live nymphs without mating. But, this is cyclical because it is interrupted during the year with the production of males and females that mate, and this oviparous sexual female deposits eggs.

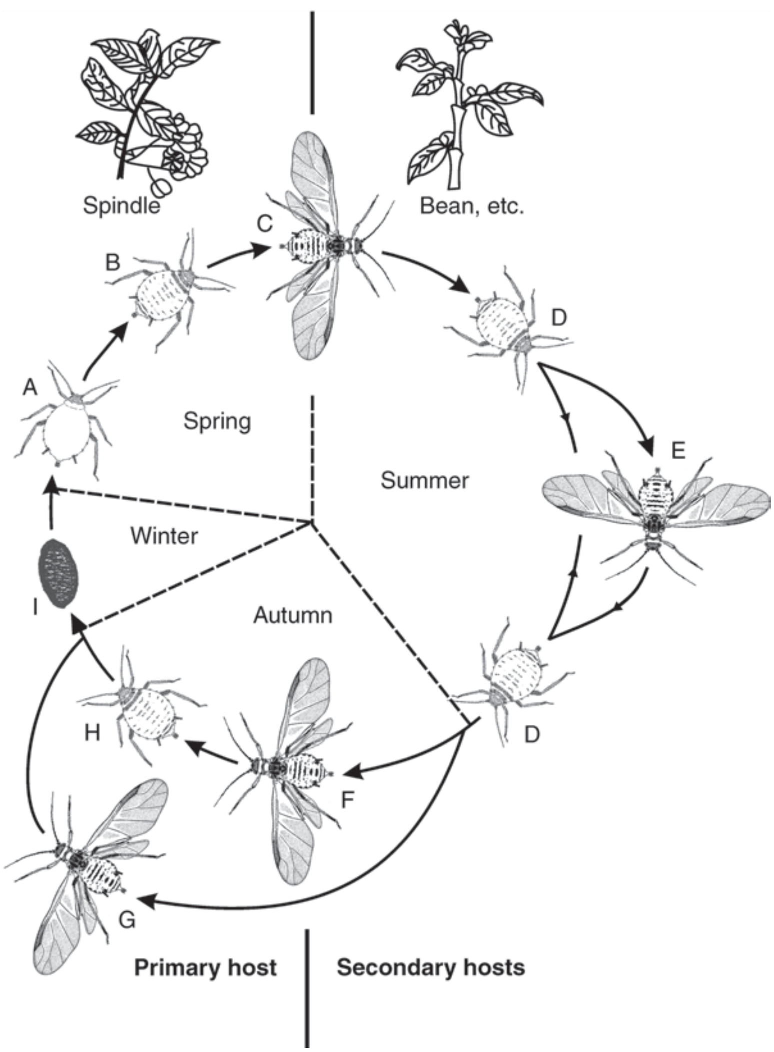
Anholocyclic life cycle: This is the complete absence of males, so that only viviparous parthenogenetic females exist with parthenogenetic reproduction continuing throughout the entire year with all the progeny being female.

Host Plant Alternation

Host plant alternation in aphids involves the two types of life cycles:

Autoecious (monoecious) in which aphids are host plant specific, and live on one or only a few species of closely related plants even within a particular genus during the entire year. Most aphid species (over 90%) are of this type, and as a result, there is usually no need for an annual alternation between primary and secondary hosts, so that the anholocyclic life cycle is common.

Heteroecious or host plant alternation life cycle (Fig. 65) by which about 10% of aphid species spend autumn, winter, and spring on a primary woody host, and the summer usually on secondary herbaceous plants. The primary and secondary host plants usually are unrelated and belong to different families of plants. Although such aphids may be classified as polyphagous, many species are really sequentially monophagous if they live on only one host plant species at a time. This alternation of host plants during the year is accomplished by the holocyclic life cycle described above. These aphids



Aphids (Hemiptera: Aphididae), Figure 65 **Life cycle of the heteroecious holocyclic black bean aphid, *Aphis fabae*. (a) Fundatrix or apterous stem mother, (b) her apterous viviparous parthenogenetic female progeny or fundatri-genia, (c) alate emigrant or spring migrant, (d) apterous virginopara, (e) alate virginopara or summer migrant, (f) alate autumn remigrant or gynopara, (g) alate male, (h) apterous ovipara or mating female, (i) egg (after Dixon 1998; Kluwer Academic Publishers).**

use a specialized reproductive strategy by which the sexual generation produces eggs on the primary (woody) host plant on which they overwinter. This is done because eggs are better able to survive the rigors of a cold winter, snow, etc. The cold period of winter is required before the embryo in the egg can complete its development, and this suspended physiological state is called diapause. The embryo will not hatch until the warmth of spring arrives, and when it does, all of the offspring will be female. This female fundatrix or stem mother on the primary (woody) plant is the first individual to begin the new parthenogenetic line which results in only female offspring all of which are genetic clones of herself. Spring not only provides nutrient availability, but also at this time natural enemies probably have not arrived in dangerous numbers. Again there is a trade-off such that all fundatrices are apterous, thus avoiding unnecessary expenditure of energy on developing wings that are not needed because they do not migrate. Instead, energy can be concentrated on embryological development resulting in very high fecundity of more and more females by viviparous parthenogenesis.

When the colonies of female progeny on the primary (woody) plant become crowded, morphs appear and become alate spring migrants that fly (often with the help of wind currents) to the secondary host plant. The summer secondary host plant is usually herbaceous, and since these alate migrants are all viviparous females, they will produce only females parthenogenetically for as long as this favorable summer weather continues. By dispensing with mating and egg-laying, their numbers can increase at an astonishing rate. These aphids are usually apterous and sessile, remaining on the host plant for long periods in a parasitic "plant lice" mode. But if there is crowding and/or the plant deteriorates, alates will develop in the next generation, thus permitting movement to a new location and even to a new herbaceous host plant. However, such relocation need not be far away if the agroecosystem consists of many acres planted to monoculture. In the autumn, environmental cues (shorter photoperiod and cooler temperature) will trigger the seasonal alternation back to a primary (woody) host plant, and a behavioral change into an alate autumn migrant or gynopara. This parthenogenetic female produces sexual females that will mate with males. Overwintering fertilized eggs are deposited, and the cycle is repeated.

Polymorphism and Polyphenism

Polymorphism means that there are two or more phenotypes or morphs in a population of the same species. Polyphenism means that there are two or more phenotypes or morphs in the same clone. In other words, genetically identical individuals derived from the same mother by parthenogenesis can differ even though they are all clones. This phenomenon is more common in aphids than in any other insect group, especially in aphids that have host plant alternation. In such a parthenogenetic system of genetic clones, females may have as many as eight different phenotypes that differ in such characteristics as morphology, color, physiology, timing of reproduction, developmental time, numbers and sizes of offspring, longevity, host plant preferences, and alternative host plant species. It is probable that some of this variation is not caused only by genetic differences, but also by variations in the host plant and/or the environment.

When environments are regularly cyclical, then seasonal changes and predictable weather patterns can influence the availability and quality of phloem sap that is the basis of aphid feeding. Because of this predictability and reliability, the evolution of aphid species occurred mainly in temperate zone habitats. With this in mind, it is understandable that there has been an environmentally induced morphological and behavioral trade-off so that because alate morphs have energy-costly wings, their developmental time should be slower/longer with a reduced lifetime fecundity compared to the apterous morphs that do not have to expend their energy on wings but rather on offspring production. Hence, there has evolved in aphids both polymorphism and polyphenism that is adapted to changing yet predictable environmental conditions, and resulting in the types of sexual and migrant morphs already mentioned above in earlier sections. No other group of insects can match this diversity.

Soldiers

In addition to the sexual and migrant morphs, there is still another of interest: soldiers. These are female nymphs in only a few (1%) of the more than 4,000 species of aphids, and are found in some but not all gall-forming aphids (see section on Galling). They exhibit a behavior of defending the colony against predators, but they do not molt into reproductive adult females and will never produce offspring. These soldiers aggressively attack invaders, sometimes being suicidal. In some, the fore legs and middle legs are thickened which they use to hold and even crush the intruder. If they have frontal horns, they will use these as well as their stylets as weapons in combat. Both soldiers and normal nymphs can be produced by the same mother aphid. In some species, soldiers (like males) do not have symbionts. Animal behaviorists note the evolutionary convergence of "altruism" in these aphid soldiers with the sterile soldier castes of ants, termites, and thrips.

Color Morphs

Coloration in aphids may be caused by: (i) brown or black pigmentation of the integument (mainly the tergum) or by sclerotization of the cuticle which can give a metallic shine; (ii) body contents show through the cuticle revealing pigments in internal organs, tissues, hemolymph (types of glycosides not found in any other group of animals or plants), bacteriocytes, etc. Colors can vary between and even within species, but the color is usually green, yellow, reddish, creamy, or almost black; (iii) waxy exudates that form a pattern from glands on the body and appear powdery white or grey.

Intraclonal color variation is usually induced by environmental factors, especially temperature, crowding, and poor nutrition. Therefore, it is reversible if these factors revert to the previous state. On the other hand, interclonal color variation is genetically fixed between different color morphs of males and females in some species or between the green and red-pink morphs in the pea aphid (*Acyrthosiphon pisum*), green peach aphid (*Myzus persicae*), and potato aphid (*Macrosiphum euphorbiae*). In the first two aphid species, the red-pink allele is dominant to the green allele, so there may be some biological differences influencing fecundity, reproductive rate, host plant preferences, selection of feeding sites, activity, high or low temperature tolerance, etc. For instance, it seems that thermal conditions may influence the pea aphid when the red-pink morph appears in the summer with the green morph doing better in cooler weather. Also crowding and/or reduced plant nutritional value may cause the red-pink morph of the pea aphid to become green. Any ecological significance such as defensive behavior using camouflage or cryptic coloration has not been demonstrated. However, colonies of some species may use color as aposematic warning behavior against birds or other predators as with the oleander or milkweed aphid, *Aphis nerii*, with its bright yellow color contrasted with black cornicles and cauda, and dark antennae and legs. In other species, some color or pigmented bands may absorb solar radiation that would be advantageous in cool weather.

Aphid Influence on Host Plants

Negative Effect

Aphids like many sucking insects can have a negative effect on the host plant in one or more of the following ways as will be discussed below: nutrient drain, pathogen transmission, salivary toxins, and honeydew excretion.

Nutrient Drain

When aphids are in sufficient numbers, they can drain the plant of its nutrient sap and cause a breakdown in its tissues. Ironically, it could be this less-healthy situation for the plant that satisfies the nutrient needs of this "parasite." As a result, the plant may have its leaf area reduced, growth slowed, early leaf fall, become stunted and/or die before its time.

Pathogen Transmission

The major danger to plants is probably the damage done only indirectly by aphids sucking sap. The greater harm is done when they are inadvertently the vectors of plant pathogens that cause disease. Most important of such plant pathogens are the viruses**.** There is a parallel here between aphids transmitting viruses to plants, and mosquitoes transmitting such pathogens as protozoa and viruses to humans resulting in malaria, yellow fever, etc. Like the mosquito, the aphid's mouthparts are ideally suited for such transmission because the stylets act like a hypodermic needle injecting the virus into the plant as it probes and then sucks the sap. Also, even if the aphid did not have the virus, it would pick it up when it feeds on an already virus-infected plant. A winged aphid (alate) is especially like the mosquito because by flying it can disperse the pathogen to many other host plants.

There are two ways in which an aphid vector can transmit a virus from one plant to another: (i) stylet-borne transmission, where the virus contaminates the mouthparts just by the aphid's probing the host plant. However, this virus is non-persistent on the stylets, lasting only an hour or so, and therefore will eventually disappear on the aphid vector. (ii) circulative transmission, when the aphid actually feeds on an infective plant already having the virus. As a result, the virus invades the body of the aphid. After a latent period, the virus multiplies in the aphid's tissues and enters the salivary glands, from where it can be injected into the next plant when it goes to feed. What is especially dangerous about this mode of transmission is that once infected, the aphid maintains the virus for life, and so continues as a vector being able to infect many other plants in succession.

In either case, more plant viruses are transmitted by aphids than by any other group of animals, and they probably do more damage this way than by merely sucking the sap from plants. Vegetatively propagated plants such as potatoes are especially susceptible because the disease is transferred with the seed tubers to the progeny causing further yield losses. Weeds sometimes act as host reservoirs for such viruses.

Salivary Toxins

Some aphids have toxins in their saliva that cause plant tissues to yellow around the feeding site, and sometimes develop deformities such as leaf-curl, galls, etc. This can negatively influence plant growth and reduce a productive yield of the crop.

Honeydew Excretion

This very natural aspect of aphid biology and behavior is discussed later in the section on "Ant–Aphid Mutualism." In the present context, however, the honeydew that is deposited not only becomes sticky to the touch, but can attract saprophytic sooty-mold fungi to the plant. This may cover the leaf surface and accelerate aging of the plant. It is economically damaging if the fruit or vegetable is blemished and rendered unattractive for sale in a market. Also, car owners are unhappy with this sticky goo on their automobiles if they unknowingly parked under a tree infested with aphids.

Beneficial Effect

Some researchers suggest that aphids may be beneficial to plants in a kind of symbiotic mutualism.

In this unproven scenario, plants benefit by having the aphids remove surplus sugars (especially trisaccharide melezitose) which can be utilized by nitrogen fixing bacteria in the soil. As a result, these bacteria increase in the soil beneath aphid-infested plants and make more nitrogen available for the plant's growth, and hence are beneficial to the plant.

Galling

Some species are called gall aphids because they cause the plant to develop swollen tissues called "galls" that are usually on the leaf or petiole. This involves a combination of both inhibition and stimulation of the plant tissue at the feeding site that results from stylet probing and injection of saliva. Galls are hollow outgrowths on the plant and can appear as abnormalities or deformities. This cecidogenesis or gall-forming behavior is not limited to aphids, but is also produced by hymenopteran gall wasps and dipteran gall flies or midges. Although relatively few species of aphids induce galls, the shape of the galls is often characteristic for each species of aphid, so that the aphid seems to have the major role in forming the shape of the gall. Galls not only give protection to the aphid, but may also provide a better food source in the following way. A gall provides sheltered protection for the aphid from insect predators and parasitoids, and the aphid's feeding may influence the metabolism of the plant and cause physiological changes that could improve the aphid's food supply. Often, there can be intense competition and aggressive behavior among gall aphids for the best feeding sites on a leaf or petiole where a gall can be formed.

The formation of a gall by the plant probably is due to the plant tissue's reaction to aphid feeding when it probes with its stylets and injects large amounts of saliva into the host plant. It is known that a plant growth hormone called indole acetic acid (IAA) is present in aphid saliva, and so it may be that this chemical induces gall formation. However, this growth hormone normally is found in the plant itself which may account for its presence in the sap-feeding aphid. Gall aphids synchronize their development with their host plant, and may even modify the development of the host plant itself. Finally, some galling aphids are unusual in having soldiers (see section above on Soldiers), and these species tend to produce completely closed galls on their primary hosts. However, not all aphid galls are completely closed, but in those that are, a monoclonal colony of aphids can exist within the gall that was started by a fundatrix. Hence, there is probably a long evolutionary history between the plant as host and the aphid as parasite in this galling behavior. As is often true in similar host-parasite relationships among animals, the host plant may not suffer unduly in this parasitic type of symbiosis when both organisms have been in contact with each other over millions of years.

Ant-Aphid Mutualism

There is a symbiotic mutualism between these two major groups of insects by which the ants obtain a sugar-rich food (honeydew) from the aphids, while the ants protect aphids from predators and parasitoids (see section on Natural Enemies). This is the result of a long-term evolutionary history. An ant that imbibes this sugary honeydew can transport it to nestmates in its crop, and then transfer it to another ant by means called trophallaxis. However, not all species of aphids are ant-attended, nor do all species of ants attend aphids, and even myrmecophilous (ant-loving) aphids differ in their dependence on ants. Most myrmecophilous aphids live above-ground and are gregarious, rather large in size, and often conspicuously colored. But as a result of this mutualism with ants, these aphids do not have well-developed defensive structures on their bodies, and do not display escape behavior to avoid an approaching ant nor even a predator or parasitoid, perhaps because they feel "safe" in the company of their ant protectors.

This mutualistic behavior is all the more amazing when it is realized that most ant species are aggressive predators that would normally attack any available prey, especially rather helpless aphids. Yet, the ants that associate with aphids do so in an almost tender way, and "milk" them for their sugary honeydew which comes from the anus. The ant may antennate or stroke the rear of the aphid's abdomen to stimulate this release of honeydew droplets which the aphid does in an accommodating way without any interruption in its normal feeding behavior.

Aphids that are not attended by ants behave differently by raising and contracting the abdomen/rectum, thus ejecting the droplet of honeydew some distance from themselves. Some species even use their hind legs to flick the honeydew away, perhaps to avoid contaminating the colony with this sugary material that might develop sooty-mold fungus. As a general rule, aphids that are not ant attended have a long cauda and long siphunculi or cornicles, perhaps used for defensive purposes against predators and parasitoids, since there are no ants to protect them.

Studies have shown that ants can have a positive effect on the number of aphids, and even on the efficiency of feeding by increasing the ingestion of phloem sap with a resulting increase in the production of honeydew as a reward for the ants. Ant attended aphid colonies are usually larger, feed more heavily, and produce fewer winged (alate) offspring. There can also be a stabilizing effect on aphids, so that the size of the aphid colony may be dependent on the presence of ants. However, when an aphid colony becomes too large, the host plant will deteriorate more quickly and the aphids may move off it leaving the ants behind. To avoid this loss of honeydew source, it may be that ants control the aphid population size and keep it stable so that the host plant will not be excessively harmed. On the other hand, if the aphids become too few to produce an adequate supply of nutritious honeydew, the ants may switch to another and larger myrmecophilous aphid colony or even to a different aphid species that might be nearby.

Ants search plants for aphids, and when they are discovered, the ant returns to the nest laying down a recruitment chemical pheromone trail which worker ants from the nest follow to the aphids. Since many species of ants tend a variety of species of aphids, it has been suggested that at least some elements of the ants'behavior are learned rather than innate. Both ants and aphids make great use of intra-specific and perhaps even inter-specific pheromonal communication. Most ant colonies tend a number of aphid species simultaneously, and it seems likely that there is competition between the aphids for the ants'attention. Seasonal changes in ant availability and their demand for honeydew might be factors in this competition. In temperate regions, host plant availability for aphids and therefore honeydew production vary seasonally, as does the ants'ability to collect these sugars.

It is unclear to what extent there may be predation of aphids by their ant "protectors," but it seems that a significant amount of predation does indeed occur. Perhaps the ants need some protein as well as carbohydrates from honeydew, and in a coevolutionary way the aphids may find limited predation (especially in large colonies) a necessary price to pay for protection from natural enemies, and even for the removal of potentially contaminating sugary honeydew.

Natural Enemies of Aphids

This discussion will be limited to the natural enemies of aphids that are themselves insects, and not other animals such as birds, nor even pathogenic fungi, etc., that also can kill aphids. In entomology, insects that attack, feed on, and kill other insects are called entomophagous insects. However, in the present context, insects that kill aphids are more precisely called aphidophagous insects. As a general introduction, some definitions must be given. Insects that attack, feed on, and kill other insects (not just aphids) are divided into two major categories:

Predators

Predators are insects that attack, feed on, and kill the prey directly. Depending on the species of predator, both males and females as well as the immature stage and/or the adult can do this. Usually, more than one prey is required for the predator to reach adult sexual maturity.

Predators of aphids expend energy and time searching for prey, and so maximum efficiency is achieved when the predator finds an entire colony of aphids and not just an individual. Once in a colony, many predators proceed slowly and stealthily so as not to raise an alarm. An extreme example of such a predator would be the blind, legless larva of a syrphid hoverfly (mentioned below). Examples of major predators of aphids are given next:

Ladybird Beetles (Order Coleoptera, Family Coccinellidae)

These are the best known of aphid predators, and they feed both as immature larvae and also as adults. These are very familiar beneficial insects, but often incorrectly called "ladybugs" because "bug" should be limited to the true bugs in the order Hemiptera that have piercing-sucking mouthparts. They have a convex shape and usually colorful markings. Because they are very common wherever aphids are found around the world, they have been intensely studied for their use in biological control programs. The coccinellids that are brightly colored are demonstrating warning or aposematic behavior, i.e., they are distasteful to their own predators, such as birds. Even their eggs are often orange or yellow. The larvae that hatch from these eggs are notorious for their cannibalism on coccinellid eggs and other smaller sibling larvae because they have to feed almost immediately on some prey or die. As the larva molts and increases in size, it can sometimes consume more than 100 aphids per day. The larva has pointed jaws which it uses to pierce the aphid cuticle. Saliva is then injected into the aphid which digests the body contents into a semi-liquid which can be sucked up. Solid remains of the aphid may be eaten later if the larva is large enough. However, coccinellids have their own natural enemies especially in the orders Diptera and Hymenoptera.

Lacewings (Order Neuroptera, Families Chrysopidae, Hemerobiidae)

These are delicate "nerve-winged" insects with large transparent wings that are often colored light green or brown as is the body. Depending on the species, they feed both as larvae and adults, and are considered important predators of aphids (perhaps second only to coccinellids) and have therefore been used in biological control programs. The larvae have hook-like piercing jaws that are used to suck up the body contents. The aphid prey is held up in the air while it is being eaten. In some species, the adult lacewing lays eggs with each one attached to the end of a vertical stalk which is quite visible when many eggs are laid together on a leaf.

Hoverflies (Order Diptera, Family Syrphidae)

As the name indicates, the adult flies hover in the air over one spot, and then dart to another location. The adults can be seen visiting flowers where they feed on nectar and pollen, and so are also called flower flies. The abdomen is often brightly colored with bands of white or yellow contrasting with a black background, perhaps as mimicry of wasps. It is not the adults that eat aphids, but rather the female lays her eggs close to or within an aphid colony. From each egg hatches a dipteran larva or maggot that is blind and legless, dorso-ventrally flattened and tapered at the anterior end. Like lacewings, the syrphid larva feeds on the aphid by piercing and sucking out the body contents, while holding the prey aloft.

Cecid Flies (Order Diptera, Family Cecidomyiidae)

These tiny flies are often called gall midges although the species that attacks aphids do not form galls on plants. Hence, these cecid flies are also called aphid midges, but the adult does not feed on aphids. Each female can lay about 100 eggs on leaves and stems of plants infested with aphids. It is the maggot-like larva that feeds by piercing the aphid with its long serrated mandibles, sucking out the body contents.

Anthocorid Bugs (Order Hemiptera, Family Anthocoridae)

These are called minute pirate bugs or flower bugs because they are often found on flowers where they may feed on plant juices. Most species are general predators on thrips, mites, and other small arthropods besides aphids. However, the two genera *Anthocoris* and *Orius* are predominantly aphid predators. Being hemipterans, they have simple or incomplete metamorphosis, and the adults as well as the nymphs feed on aphids by sucking out the insides through their styliform mouthparts.

Parasitoids

Parasitoids are insects (orders Hymenoptera and Diptera) in which the adult female attacks what is called the host, but she only indirectly kills the host because the female merely lays her egg in, on or near it. It is the larval offspring from the egg that actually feeds on and kills the host. In older literature, these parasitoids were called parasites, but this terminology was misleading because a true parasite (flea on a dog) usually does not kill the host (dog).

Parasitoids of aphids are micro-wasps (4 to 5 mm in length or smaller) in the order Hymenoptera, and are usually classified both taxonomically and behaviorally in only two families, Aphelinidae (superfamily Chalcidoidea) and Aphidiidae (or Family Braconidae and Subfamily Aphidiinae) (superfamily Ichneumonoidea). These parasitoids are quite host specific in using only aphids as hosts (and no other group of insects). But, even among the thousands of aphid species as possible hosts, different parasitoid species display a feeding behavior that ranges from a continuum of polyphagy to a certain host specificity of oligophagy to monophagy, so that many species of parasitoids limit their attacks to only one or a few species of aphids.

Using as an example a typical species in the genus Aphidius in the family Aphidiidae, the female micro-wasp is quite host-specific, and is called endophagous because she lays an egg inside the live aphid. Her ovipositional behavior is to attack the aphid with a quick thrust of her ovipositor which is usually brought forward between her legs, and is positioned in front of and beneath her head. After the egg has been successfully deposited inside the live aphid, the female departs to attack another aphid, and her involvement with the first aphid is ended. Her offspring, however, is the parasitoid larva that hatches from the egg inside the live aphid that will ultimately kill the aphid. Oddly enough, the aphid host usually continues to feed on the host plant as if nothing had happened and without changing its normal behavior. Over a period of approximately 8–10 days that varies with the species of aphid and parasitoid, the larva molts several times while gradually devouring the aphid internally, finally killing it. Then the fourth and last larval instar spins a cocoon inside the dead aphid, whose exoskeleton becomes hard and changes from its original color to brown (which is now referred to as a "mummy"). The parasitoid larva may fasten the ventral side of the mummy to the leaf. It pupates inside the mummy, and approximately 4–5 days later (or about 12–15 days after the original oviposition) the new adult wasp parasitoid cuts a circular emergence or exit hole in the mummy (usually in the dorsum of the abdomen) and pulls itself out. The adult wasp will find a mate within a short time after emerging from the dead aphid mummy. When fertilized, this new generation of adult female will start the cycle again by attacking and depositing her egg inside another aphid. Note that it is the parasitoid larva that feeds on and kills the host aphid, not the adult female that only oviposits inside the aphid and then departs. Remember that during the moderate summer months, there are long periods in the life cycle of an aphid colony when it is sessile and does not move very far away as long as the host plant provides sufficient nourishment. Perhaps for this reason, micro-wasp parasitoids of aphids have been used quite successfully in biological control programs around the world.

Hyperparasitoids

The micro-wasp parasitoid described above is technically called a primary parasitoid, and it is considered beneficial because it kills the aphid which may be a pest insect. However, there are other species of micro-wasps also in the order Hymenoptera, but not in the same families as the primary parasitoids of aphids just discussed. These micro-wasps have evolved to a higher trophic level so that we have an example of multitrophic ecology and behavior. At the 1st trophic level is the host plant, then at the second trophic level is the herbivorous or phytophagous aphid, and at the third trophic level is the carnivorous or entomophagous primary parasitoid. Finally, at the fourth trophic level is a different species of micro-wasp called a secondary parasitoid or hyperparasitoid that attacks the primary parasitoid while it is still inside the aphid. This food web involving four trophic levels of plant, to aphid, to primary parasitoid, to hyperparasitoid has been used as a model system in community ecology.

Since many aphid species are such worldwide pests, hyperparasitoids of aphids have been especially well-studied, and can be categorized as follows depending on their adult ovipositional and larval feeding behaviors: (i) The female wasp of endophagous hyperparasitoid species deposits her egg inside the primary parasitoid larva while it is still developing inside the live aphid, before the aphid is mummified. But, the egg does not hatch until after the mummy is formed, and then the hyperparasitoid larva feeds internally on the primary larval host still inside the mummy. (ii) The female wasp of ectophagous hyperparasitoid species waits until the primary parasitoid larva has killed the aphid and formed the mummy. Then she drills a hole through the mummy, and deposits her egg externally on the surface of the primary parasitoid larva inside. After hatching, the hyperparasitoid larva feeds externally on the primary larval host while both are still inside the mummy. In both cases, the hyperparasitoid larva then pupates inside the mummy, and as with the primary parasitoid described above, the new adult wasp hyperparasitoid cuts an emergence or exit hole in the mummy (usually in the dorsum of the abdomen) and pulls itself out. The adult wasp hyperparasitoid will find a mate within a short time after emerging from the dead aphid mummy. When fertilized, this new generation of adult female hyperparasitoid will start the cycle again by attacking and depositing her egg in or on a primary parasitoid larva inside another aphid.

There is an economic interest in hyperparasitism because if primary parasitoids are considered beneficial insects (especially when used in biological control programs) then it would seem that hyperparasitoids that attack primary parasitoids might be detrimental. On the other hand, some ecologists suggest that perhaps hyperparasitoids play a positive role in the ecosystem by preventing an excessive increase in the numbers of the primary parasitoids that might so reduce the phytophagous host as to result in the local elimination not only of the insect pest, but also the beneficial primary species as well. If more phytophagous insects of the same species (such as aphids for example) were to move into this local area without sufficient primary parasitoids to attack them, then there might be a resurgence of the insect pest.

Aphid Defenses

As mentioned earlier in the section on polymorphism, there are aphid soldiers in a few species that perform an altruistic role. These are female nymphs that have morphological adaptations to defend a colony against predators. Even if they are not killed in this action, they do not reproduce. Usually, species that have soldiers tend to form closed galls on their primary hosts (see section on Galling). However, the majority of aphid species do not have soldiers, yet many species are still capable of defending themselves by various means such as the following: aggressive kicking, thick defensive cuticles and/or spines, waxing predators and parasitoids, using stylets to attack and kill eggs of predators and even other species of aphids, or suddenly falling off the leaf onto the substrate as a tactic that permits their escape from an impending attack by an aphidophagous natural enemy. Some aphids also emit chemical alarm pheromones that warn other aphids nearby of imminent danger. In this regard, it is interesting that some aphid alarm pheromones may also act as kairomones (communication chemicals between different species) so that predator coccinellid beetles are actually attracted to the aphids.

Control of Aphids

Prevention of damage to plants is especially important when a major agricultural crop could be destroyed by aphids at great financial loss to the farmer. Even forest and shade trees have economic as well as esthetic significance when they are used for logging or as parks. Control involves using methods to protect the crop from aphid attack by various means such as chemicals, natural enemies (biological control), host plant resistance (HPR), modifying aphid behavior, and finally integration of these methods (IPM).

Chemical Control and Resistance

Prior to World War II, chemical control of aphids was limited to nicotine and arsenical products. These aphicides were sprayed on the crop, and at the time seemed to have little negative residual or systemic effects. After the war, however, DDT and other chlorinated hydrocarbons were developed and widely used as broad-spectrum insecticides that were considered to be a panacea not only for control of aphids, but for many other insect pests as well. Although not systemic, they did have residual effects that in the beginning seemed to be a benefit because they were long-lasting. But eventually, evidence from field studies demonstrated that these residues persisted in the ecosystem, and accumulated in the food chain causing unexpected dangers to non-target organisms, especially to fish, birds, and even mammals. In addition, the unintended killing of beneficial insects that were the natural enemies of the insect pest resulted in pest resurgence, traded-pests, etc. The excessive use of these chemicals with these dangerous side-effects was eventually banned in many countries around the world.

New generations of chemical insecticides were developed such as the organophosphates, carbamates, and pyrethroids. To control aphids, special aphicidal properties were emphasized:

1. Selective toxicity: predators and parasitoids not killed, nor any other non-target organisms.
2. Systemic activity: chemical is applied not only to foliage and seeds, but especially to the soil where the roots take it up via the vascular system where aphids feed on the phloem sieve tubes.
3. Residues: Some residual activity may be needed to prevent aphids from reinfesting the crop. In the case of food and fodder crops, however, chemical persistence can be dangerous. Aphicides on such

plants should decompose into harmless compounds before harvest.

4. Rapid action: to prevent transmission of non-persistent viruses, quick mortality of aphids is necessary. Some synthetic pyrethroids show repellent action that deters aphids from settling.
5. Low phytotoxicity: the aphicide should not harm the crop itself because the purpose of the chemical is to protect the plant from aphids without having a toxic effect on the plant.

Application of Aphicides

No general rule can be given because so much depends on local conditions, type of chemical, length of growing season, aphid population size, time of day, weather, etc. Sometimes soil or seed application is sufficient instead of dusting or spraying, and of these two, if the crop is dense, then perhaps dusting is better than spraying. Farm advisors should be contacted because they know the local situation for making recommendations.

Resistance

It is well-documented that chemical insecticides are powerful agents of natural selection so that over time some mutated insects such as aphids develop resistance. This renders the chemical inefficient, resulting in attempts to restore success by repeating applications, then increasing the dosage, etc. In addition, as mentioned above, the beneficial natural enemies are also negatively affected. There are reports of 20 or more aphid species that have developed resistance to various chemical insecticides. The green peach aphid, *Myzus persicae* (Sulzer), is an excellent example. It is a notorious aphid pest that not only has secondary hosts in over 40 different plant families, but it is one of the most important vectors of over 100 plant viruses. Although *M. persicae* is probably of Asian origin, it is now found worldwide.

As a result of many years of subjection to chemical insecticides, natural selection has developed resistance in large populations of many aphid species not only in the field, but especially in greenhouses. The biochemical cause of resistance in aphids is still being studied, and there seems to be a positive correlation between resistance and the activity of enzymes (esterases). It has also been suggested that symbionts are involved in resistance. In any case, although some chemical aphicides may still need to be used, they should be applied judiciously to avoid the typical insecticide treadmill cycle of excessive dependence on chemicals with unintended results such as pest resurgence, traded-pests, etc.

Biological Control

Biological control is the intentional use by humans of an insect pest's natural enemies such as beneficial insect predators and parasitoids as well as pathogens (bacteria, viruses, protozoa, fungi, nematodes, etc.) in order to lower the population level of the insect pest below the economic threshold so that crop loss is reduced and the farmer can have a successful harvest. In the field, the aphids'sessile feeding behavior for long periods of the year makes them especially attractive to natural enemies. In addition, aphids are amenable to studies in the laboratory where many species can be rather easily reared along with their natural enemies for research and experimentation in insect cages, growth chambers, and environmentally controlled walk-in rooms. As a result, and because of their worldwide pest status (especially in the temperate zones), aphids have been the target of many successful biological control programs.

There is an aspect of this method called classical biological control wherein the natural enemy is introduced as an exotic parasitoid or predator from another country or even more frequently from another continent. Also, the insect pest is often an exotic invader into a new habitat or the insect pest could be indigenous. In either case, it seems that the indigenous natural enemies are incapable of keeping the new or old insect under control so that it has now reached pest status. To obtain the exotic natural enemy involves foreign exploration and importation, mass rearing, colonization, establishment, etc. Three examples of this type of classical biological control of aphid pests are given here because they are so well documented, and can be easily referenced in the entomological literature:

1. The first case of successful aphid biological control was against the wooly apple aphid, *Eriosoma lanigerum* (Hausmann), a serious pest of apple in North America and now worldwide in distribution. Beginning in 1920, an aphelinid wasp parasitoid, *Aphelinus mali*, was imported from the United States and became established in 42 countries with generally satisfactory results.
2. Another success was with the spotted alfalfa aphid, *Therioaphis trifolii* (=*maculata*) (Buckton), which invaded the southwestern United States in 1953. Two aphidiid wasp parasitoids, *Trioxys complanatus* and *Praon exsoletum*, as well as the aphelinid *Aphelinus exsoletum* were imported from the Middle East, and resulted in excellent control of this exotic aphid. This case was also important historically because the concept of integrated pest management (IPM) was pioneered during this period by entomologists at the University of California.
3. Finally, although the pea aphid, *Acyrthosiphon pisum* (Harris), was a Palearctic species, it had existed as an exotic invader in North America since the end of the 1800s where it was a pest on alfalfa and peas. Indigenous predators and parasitoids seemed ineffective, so in 1958 the specialized aphidiid parasitoid, *Aphidius smithi*, was imported from India into the western United States. Later in 1963, the polyphagous aphidiid parasitoid, *Aphidius ervi*, was introduced from Europe into the eastern U.S. Both parasitoids have been successfully established resulting in good control. Of ecological interest here is that over time, it seems that *A. smithi* is being replaced in the west by *A. ervi* that was first introduced in the east. However, good control of the pea aphid continues across the continent.

Unlike these three examples of classical biological control involving exotic aphids, it can happen that for various ecological and behavioral reasons the aphid pest is indigenous and the native natural enemies do not control it. In this case, at least the conservation of the existing, indigenous natural enemies is of primary importance. This can even be assisted by augmentation and inundative releases of these indigenous natural enemies from mass-rearing insectaries. Sometimes, exotic but taxonomically closely related species to the indigenous species of natural enemy might be imported from abroad and used to complement the native species, thus improving the possibility of controlling an indigenous pest.

In comparison with chemical control, biological control is non-polluting, non-toxic, and self-perpetuating, and makes no claim about completely eradicating the insect pest. Instead, the population level of the pest is lowered to an economic threshold acceptable to the farmer. Since this involves a living ecosystem, biological control tends to be permanent, and therefore less expensive. Needless to say, whether the pest is an aphid or some other insect, proper scientific procedures demand that extensive research be done on the biological aspects of both the insect pest as well as the natural enemies (indigenous and exotic) in relation to the ecosystem.

Finally, pathogens such as bacteria, viruses, protozoa, fungi, nematodes, etc., can be used as microbial insecticides against insect pests. Aphid diseases have been recognized for over 150 years, but only entomogenic fungi in the order Entomophthorales have been considered as the main pathogen against aphids. Usually warm and humid weather can spread the fungus very quickly into an epizootic, especially when the aphid colony is crowded. The infected aphid becomes brown and inflated with liquid when it dies of mycosis. This can happen in the tropics and greenhouse, but in field conditions in temperate regions humidity is not that predictable. Much can still be done to use the potential of fungi in biological control programs against aphids. The other pathogens such as bacteria and protozoa do not seem to have been demonstrated to cause infections in aphids. Although baculoviruses and picornaviruses can be transmitted transovarially and reduce the longevity of an aphid, no viral epizootics of aphids have been reported.

Host Plant Resistance (HPR)

Many plant species have defenses against herbivores including insects that is genetically heritable, and hence controlled by one or more genes. Resistance of plants to insect attack is related to the heritable qualities of the plant that may reduce the damage. The main task of agronomists is to increase the yield and quality of a crop by standard breeding methods. However, this can also include trying to breed genotypes into crops that make them resistant to insect attack by using one or more of the following mechanisms:

1. Antibiosis: physico-chemical characteristics of the plant that kill the insect;
2. Antixenosis: pest insect is repelled by the plant or at least has no preference for it;
3. Tolerance: the plant can recover even after some feeding damage by the insect.

Plant characteristics vary depending on the species, but host plant resistance can be morphological (leaf size, shape, color, pubescence, thickness, texture), biochemical (lack of nutrients, allomones [feeding repellents, ovipositional and feeding deterrents, toxins], kairomones [attractants for natural enemies]). Entomologists work closely with the agronomists to test or screen the supposedly resistant crops (but still as high-yielding as possible) to see if indeed these genotypes are also resistant to a particular insect pest that is being studied. To do this, hundreds of insect pests are constantly being mass-reared in the insectary. These are used not only for laboratory studies of insect-plant interactions, but especially for the purpose of bringing them into the field for artificial infestation. In the field, these insect pests are placed on the cultivar to be infested and eventually evaluated as to the amount of damage caused to the plant as it grows. It must be stated, however, that HPR to one insect pest does not mean that a cultivar is resistant to other taxa or even to related species. Furthermore, the genotype may not be resistant to other biotypes or races of the same insect pest species that initially showed host plant resistance.

Concerning HPR for aphids, the same general principles and procedures are used as just mentioned above. Hundreds of cultivars have been developed for resistance to aphids for more than fifty important crop plants in the families Leguminosae, Gramineae, Compositae, Cruciferae, Cucurbitaceae, Rosaceae, Solanaceae, etc. The problem of biotypes or races also occurs among aphids because of their parthenogenesis, telescoping of generations, host plant alternation, etc.

Modifying Aphid Behavior

Aphid behavior can be modified by both prevention of landing by aphids in flight, and by repelling aphids that have already landed.

Flying aphids are attracted or repelled from plants by light of a particular wavelength. When winged aphids first fly, they are attracted to the blue-ultraviolet light from the sky. However, after a period of flight this is reversed, and instead of flying upwards, the sky may repel them and they are attracted to the orange-yellow-green light reflected from the leaves below. This behavior might be exploited by using yellow traps to lure them away from crops in a field (though as yet this has not been demonstrated). The yellow trap can be filled with some liquid that kills the aphids that have landed in them. Yellow traps are used extensively to monitor flights of aphids.

Plant odors are volatile substances produced by plants that attract aphids in their host selection. Aphids on agricultural crops tend to be polyphagous, so perhaps specific volatile cues are not too important. However, aphids on perennial crops and wild plants are more oligophagous and even monophagous for which plant odors are needed. Hence, attractant baits have been tried as well as repellent chemicals that may also have a role in aphid control.

Alarm pheromones are released by some species of aphids when they are attacked by natural enemies. It would be advantageous for flying aphids to avoid landing on a plant where aphid colonies are being attacked and have released an alarm pheromone. Synthetic alarm pheromones have been used successfully, but because some are highly volatile, a formulation with a slow release would enhance this control method.

Synthetic chemical repellents would be a non-toxic alternative to insecticides, and are safer to the applicator and to the environment. However, there is a problem with aphids that are vectors of a non-persistently transmitted virus. It would have to have its repellent effect act very quickly before the aphid makes its first probe. Even chemical aphicides have this difficulty in not acting fast enough to prevent that first probe by which an uninfected aphid picks up the virus, or if already infected, then before the aphid probes into a healthy plant. There is a continuing need to study the chemoreception of aphids and their resulting behavioral responses.

Cultural Control

This method involves the use of normal agricultural practices to reduce pest damage not only by aphids but also by other insects. Such cultural techniques can include the following: timing of planting and/or harvesting to disrupt the normal cycle of aphid landing and feeding; crop rotation varies the crop during the season or annually with another plant that would be unattractive to the aphid and/ or less important to the farmer; intercropping uses the same principle but alternates field rows or sections of the crop with another plant; tillage (mechanical manipulation of soil to reduce weeds, improve drainage by plowing, hoeing, etc.); sanitation is the removal of weeds or crop residues that might provide the aphid an alternate host; water management depends on the needs of the host plant and the biology of the aphid species.

Integrated Pest Management (IPM)

In their evolution, aphids have taken advantage of favorable agricultural habitats especially through monoculture, thus making the agroecosystem an attractive food source. Although different species of aphids vary in their host range from polyphagy to monophagy, they are often able to survive on herbs in the vicinity of the crop or simply to fly to another area where a more suitable host plant is more available. Realistically therefore, eradication is all but impossible. Because of various side effects mentioned earlier, reliance only on chemical insecticides should not be the main option. Instead, it is sensible to integrate as many of these control methods just discussed. This concept of integrated pest management (IPM) was first developed at the University of California during the late 1950s. An acceptable definition of integrated pest management (IPM) should include the following entomological and ecological aspects: a pest management system that utilizes all suitable control methods to reduce and maintain the pest population level below that causing economic injury, with special concern for the environment including the insect's natural enemies. This sound ecological philosophy should be applied to aphids and to other insect pests whenever possible.

Important Aphid Species

Although there are over 4,000 aphid species, only a small percentage of these are pests. Nevertheless, it is not surprising that general interest and most of the funded research at universities and institutes should be concentrated on aphid species that indeed are pests of agricultural crops, forest and shade trees because of their commercial and economic importance. With this bias in mind, listed in alphabetical order (English names) is a sampling of some important aphid species: black bean aphid, *Aphis fabae* Scopoli; black citrus aphid, *Toxoptera aurantii* (Fonscolombe); blue alfalfa aphid, *Acyrthosiphon kondoi* Shinji; brown citrus aphid, *Toxoptera citricidus* (Kirkaldy); cabbage aphid, *Brevicoryne brassicae* (Linnaeus); corn leaf aphid, *Rhopalosiphum maidis* (Fitch); corn root aphid, *Aphis* (*Protaphis*) *maidiradicis* Forbes; cotton or melon aphid, *Aphis gossypii* Glover; cowpea or black legume aphid, *Aphis craccivora* Koch; grain aphid, *Sitobion avenae* (Fabricius); green apple aphid, *Aphis pomi* De Geer; green peach aphid, *Myzus persicae* (Sulzer); greenbug, *Schizaphis graminum* (Rondani); oleander or milkweed aphid, *Aphis nerii* Fonscolombe; poplar petiole gall aphid, *Pemphigus populitransversus* Riley; pea aphid, *Acyrthosiphon pisum* (Harris); potato aphid, *Macrosiphum euphorbiae* (Thomas); rose aphid, *Macrosiphum rosae* (Linnaeus); spotted alfalfa aphid, *Therioaphis trifolii* forma *maculata* (Buckton); tulip-tree aphid, *Illinoia liriodendri* (Monell); walnut aphid, *Chromaphis juglandicola* (Kaltenbach); woolly apple aphid, *Eriosoma lanigerum* (Hausmann).

Several of these important aphid species are worth special mention:

Green Peach Aphid

Myzus persicae (Sulzer) is probably the most polyphagous of all aphids. As a result, it is the most important insect vector of plant diseases including transmission of over 100 plant viruses such as curly top of sugar beets, peach yellows, cranberry false blossom, aster yellows, and various potato viruses, etc. It is pr obably of Asian origin on its principal primary host *Prunus persica* (peach), and then followed this host wherever it was planted which is now worldwide in distribution. Its secondary hosts are in over 40 different plant families, including many that are also economically important. In temperate regions it is usually heteroecious holocyclic, but can be anholocyclic where peach is absent and the climate permits winter survival. Because it is relatively easy to rear in laboratories and greenhouses, this aphid's biology, anatomy, physiology, etc., has been intensely researched. In addition, because of its economic importance, the ecology of *M. persicae* has been studied, especially for use with biological control.

Black Bean Aphid

Aphis fabae Scopoli is also heteroecious holocyclic, and in Europe it alternates between *Euronymus* (strawberry bush) and various secondary hosts where it feeds on many agricultural crops including *Vicia faba* (broad bean) and other legumes. Besides this polyphagous behavior, it is a vector of more than 30 plant viruses. It is widespread in temperate regions of the Northern Hemisphere, as well as South America and Africa, except for the hotter parts of the tropics and the Middle East. *A. fabae* may be a complex of species, and outside of Europe where it seems to have originated, its taxonomic status is unclear. However, because of its importance, it too has been intensely studied in both field and laboratory research projects.

Cotton or Melon Aphid

Aphis gossypii Glover is very polyphagous not just on cotton and cucurbits, but also on such diverse crops as citrus, eggplant, okra, peppers, coffee, potato, cocoa, and many ornamentals such as *Hibiscus*. In addition, it can transmit over 50 plant viruses to important crops such as beans, peas, soybeans, crucifers, celery, cowpea, sweet potato, tobacco, tulips, strawberry. Its distribution is now worldwide including the tropics and many Pacific islands. In the temperate latitudes with cold temperatures where crops are raised in greenhouses, *A. gossypii* is a major pest. Perhaps it is of palaearctic origin because it is anholocyclic in Europe. However, it seems to be holocyclic in North America, China, and Japan.

Oleander or Milkweed Aphid

Aphis nerii Fonscolombe is an especially interesting aphid because of its attractive bright yellow color contrasted with black cornicles and cauda, and dark antennae and legs. Such aposematic behavior advertises and warns potential predators that it is unpalatable and even harmful. This is because while feeding, it has sequestered poisonous chemicals (cardiac glycosides) from its host plants mainly in the families Apocynaceae and Asclepiadaceae such as oleander and milkweed. It has thus coevolved by transferring for its own protection the "poisonous" defense of these host plants. Instead of using cryptic or camouflage defense as many other insects do, *A. nerii* demonstrates behavioral convergent evolution with the similarly bright warning coloration (orange and black) of the monarch butterfly that also feeds on milkweed. *A. nerii* then reinforces this aposematic behavior by forming dense colonies that are frequently concentrated on young stems. Also unusual is its life cycle that seems to be only anholocyclic with no sexual morphs. It is widely distributed in the warmer regions of the Old and New World, plus the tropics and subtropics.

Pea Aphid

Acyrthosiphon pisum (Harris) is a large aphid with slender appendages and long cornicles. There are both green and red-pink morphs, similar to the potato aphid, *Macrosiphum euphorbiae* (Thomas), that also has green and red-pink morphs with both aphid species being in the same aphidine tribe Macrosiphini. The pea aphid seems to be a complex of races and subspecies on different host plants, but mostly important legumes such as alfalfa, clover, peas, broad beans, etc. *A. pisum* is a vector of more than 30 virus diseases, and although probably palaearctic in its origin, it is now worldwide in its distribution where it is holocyclic in the temperate regions, and perhaps anholocyclic in warmer climates. Because it can be reared easily in the laboratory with its micro-wasp parasitoids, as mentioned earlier, it was an example of a classical biological control program that was successful.

Summary

Aphids fascinate the non-entomologist as well as amateur and professional entomologists because of their sometimes unique and always unusual biologies. Although small in size, their external morphology and internal anatomy as well as their polymorphism and polyphenism make aphids interesting. One marvels at their reproductive behavior (parthenogenesis, telescoping of generations, sex determination), life cycles (host plant alternation), ant–aphid mutualism, etc. Finally, of course, aphids have had an enormous economic impact as pests on the world's agricultural crops, forest and shade trees, not only by their feeding, but as vectors of plant viruses. This is a great challenge to humankind to control them by using ecologically safe as well as effective methods. Hence, aphids are a rewarding subject for observation and research.

► Bugs
► Transmission of Plant Diseases by Insects
► Plant Viruses and Insects

References

Blackman RL (1974) Aphids. Ginn and Company, London, UK, 175 pp

Blackman RL, Eastop VF (2000) Aphids on the world's crops: an identification and information guide, 2nd edn. Wiley, Chichester, UK, 466 pp

Dixon AFG (1998) Aphid ecology - an optimization approach, 2nd edn. Chapman and Hall, London, UK, 300 pp

Minks AK, Harrewijn P (eds) (1989) Aphids: their biology, natural enemies and control, vol 2A (450 pp), vol 2B (364 pp), vol 2C (312 pp). Elsevier, Amsterdam, The Netherlands
van Emden HF (ed) (1972) Aphid technology: special reference to aphids in the field. Academic Press, New York, NY, 344 pp

Aphid Flies

Members of the family Chamaemyiidae (order Diptera).

► Flies

Aphodius Grubs (Coleoptera: Scarabaeidae)

At least two species of *Aphodius* are important pests of turfgrass.

► Turfgrass Insects and their Management

Aphrophoridae

A family of bugs (order Hemiptera, suborder Cicadomorpha).

► Bugs

Aphylidae

A family of bugs (order Hemiptera, suborder Pentamorpha).

► Bugs

Apiary

A location where honey bees and bee hives are kept.

► Apiculture (Beekeeping)

Apical

A term pertaining to the apex (tip) or outer end.

Apiculture (Beekeeping)

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The science and art of managing honey bees called apiculture or beekeeping is a centuries-old tradition. The first beekeepers were hunters, seeking out wild nests of honey bees, which often were destroyed to obtain the sweet reward, called honey, for which these insects are named. As interest in honey bees grew, so too did the entomological and biological knowledge needed to better manage colonies of *Apis mellifera*. The innovations that allowed modern beekeeping to arise were primarily developed in the 19th century. The most important include the moveable-frame hive, smoker and centrifugal extractor. It is remarkable that these continue to be the hallmark of the beekeeper a century and a half later.

Honey bees are native to the Old World, but were quickly introduced into the Americas and Australia as part of European settlement. This social, perennial insect is now found on all continents and in most environments. Although honey continues to be an important product of honey bees, their most valuable service is pollination. A large commercial pollination effort exists in many countries to ensure maximum quality and quantity of crops pollinated by honey bees. The major crops involved are nuts, berries, fruits and vegetables.

Although the technology employed in beekeeping is traditional, the problems facing present day apiculture are modern and formidable. This is due primarily to worldwide distribution of exotic diseases and pests that have devastated beekeeping industries and honey bees alike. The major problems affecting U.S. beekeeping over the last thirty years come from introduction of the tracheal mite (*Acarapis woodi*), Varroa mite (*Varroa destructor*) and small hive beetle (*Aethina tumida*). These have produced a new kind of beekeeping that is much more aligned with production agriculture because it has become associated with and/or reliant on chemicals. It is an irony that honey bees, heretofore considered wild animals needing minimal human intervention, have become more domesticated, requiring human help to survive human-induced introduction of exotic species.

In spite of the increase in time and effort needed to keep bees in the modern setting, the fascination presented by the honey bee and its products continues. Thus, a small but enthusiastic cadre of novice beekeepers appears each season to take up the challenge of managing one of nature's most complex creatures. This infectious "joy of beekeeping" continues to proliferate across the generations, afflicting both beginners and commercial beekeepers generations removed from the first person in their family to be smitten by the beekeeping bug.

The purpose of this article is to describe aspects of beekeeping that will be important for a basic understanding of the craft by both novice beekeepers and the general public. It includes information on the honey bee colony and its management, as well as that with reference to nectar and floral resources and the use of these important insects in commercial pollination.

Products of the Hive

Many people keep bees because they are fascinated by these social insects. The vast majority, however, are also interested in collecting the useful products of the hive, which include:

Honey: Modified nectar collected by honey bees that is mostly carbohydrate.

Pollen: The male floral part collected by honey bees that is mostly protein.

Propolis: A mixture of resins and oils collected by bees from plants used to "glue" hive parts together and patch holes.

Beeswax: The material that makes up the bee nest.

Royal Jelly: A high-protein food that is used to feed developing queens.

Venom: A mixture of compounds injected by bees for defensive purposes.

The Honey Bee Colony

Honey bee biology is described elsewhere in this document. The colony of *Apis mellifera* is composed of one queen (fertilized female), up to several thousand males (drones) and tens of thousands of workers (unfertilized females). For the purposes of the beekeeper, worker bees are the most important; they are often divided into two classes, young nurse bees (feed the young) and older forager bees (collect pollen and nectar).

Major Developments in Beekeeping

Most new ideas in beekeeping are not novel. A scan of the literature usually will show that they have been developed, sometimes on several separate occasions, by enterprising apiculturists in the past. Three eras have been identified in the development of the craft.

Beekeeping prior to 1500 was primitive (rustic), and consisted of little more than honey hunting, robbing the sweet from established nests. A famous rock painting at Cueva de las Arañas, Spain, depicts this activity as early as 5000 B.C. The Philistines dabbled in beekeeping as did the ancient Egyptians, Greeks, Sumerians, and others. Even before the honey bee was introduced to the Americas, other kinds of bees were kept for honey and wax. The Inca and Maya of the New World cultured the stingless bees (meliponidae). There is a renaissance in this activity in the American tropics, but the term "beekeeping" has always been reserved for those managing the Old World western honey bee (*Apis mellifera*).

From 1500 to 1851 (pre-modern beekeeping), great strides occurred in knowledge about honey bees. The queen was discovered to be female in 1586. Drones were first identified to be males in

1609. Pollen was determined to be the male part of plants in 1750. Drones were shown to mate with the queen in 1792 and recognized as parthenogenic in 1845.

Concurrently with biological knowledge, management technique evolved. For example, the concept of supering (adding boxes on top of colonies for honey storage) was developed in 1665. A wide variety of so-called "patent" hives were marketed in the 1800s, an era known for huge controversy over size and style of box, none of which were really suitable to launch a new kind of beekeeping.

The modern beekeeping era began in 1851 when the Reverend L.L. Langstroth discovered the significance of the "bee space," which led to the invention of the movable-frame hive. Other advances followed: Johannes Mehring developed the first foundation in 1857. Major Hruschka produced an extractor in 1865. Moses Quinby invented the smoker in 1875 and published his first bee book in 1853. Comb honey production began with W.C. Harbison of California in 1857.

The years 1859 to 1890 encompassed the era of comb honey, known as the "golden age of beekeeping." Samuel Wagner published the first issue of *American Bee Journal* in 1861. *Gleanings in Bee Culture* was first published in 1873; it became simply *Bee Culture* in the 1990s. Migratory beekeeping up and down the Mississippi River began in 1878 (it occurred much earlier in ancient Egypt on the Nile). Package bees were first used in 1879. J. George Doolittle developed the concept of commercial queen rearing in 1888, using the grafting (larval transfer) technique.

Lloyd Watson first used instrumental insemination of the queen bee in 1926. This technology spawned studies in controlled genetics, which led to selection of commercial lines such as "Starline" and "Midnite" honey bees. This continues to be of importance and increasingly is responsible for advances in selecting for hygienic behavior (disease resistance) and tolerance to pests.

With recognition that apiculture was a legitimate vocation, the honey bee has been spread worldwide by beekeepers. This continues even today. The Irish and Norwegians may have brought honey bees to the Americas as early as 900 A.D. They came to the colony of Massachusetts in 1665, where the aborigines called them "white man's flies". These insects may have been introduced sooner into the New World by the Spanish conquistadors via Mexico, Florida, or Cuba.

Italian bees (*Apis mellifera ligustica*) were first introduced into the United States in the 1860s, and Frank Benton imported Cyprian and Tunisic stock in the 1870s. Many more introductions succeeded these first attempts. African honey bees (*Apis mellifera scutellata*) were brought to Brazil in 1957. Semen from these so-called "killer bees" was introduced into the United States in the 1960s, but natural migration through Latin America allowed a population to become established in the United States only when it crossed the Texas border in 1990. *Varroa jacobsoni* (now known as *Varroa destructor*) was introduced to *Apis mellifera* in the 1950s via its original Asiatic host *Apis cerana*. This parasitic mite had spread to all continents except Australia by the 1990s. New bee foods, including high fructose corn syrup and the Beltsville Bee Diet® were introduced in the 1970s. Honey became a world commodity in the 1980s. The small hive beetle (*Aethina tumida*) was introduced from South Africa into the United States in 1998.

Sources of Information

Beekeeping information can be found many places. Traditional print resources include:

Bee Culture, A.I. Root Co., P.O. Box 706, Medina, Ohio 44258, phone 1-800-289-7668 extension 3220, fax 330-725-5624

American Bee Journal, 51 South 2nd Street, Hamilton, Illinois 62341, phone 217-847-3324, fax 217-847-3660

The Speedy Bee, P.O. Box 998, Jesup, Georgia 31598-0998, phone 912-427-4018, fax 912-427-8447

The Internet is now a prime source on information. However, it is suggested beginners find the bee inspector and state university extension educator in their state and address questions directly to them. Each year, the magazine Bee Culture publishes a comprehensive list in the April edition.

Equipment

Of all things in beekeeping that are affected by the modern world, perhaps beekeeping equipment is the best candidate to look at within the context of newly evolving technology. Plans for standard, traditional wooden beehives can be found in many publications. Some parts of a beehive are easily made at home, especially brood chambers, supers, tops and bottoms. However, others may not be; frame construction, for example, is best left to commercial manufacturers.

A major equipment consideration is use of beeswax, recycled from the bees themselves. Traditionally bees have been guided to make their nest (comb) through use of embossed beeswax "foundation." This material not only guides the bees in making worker cells, but also saves much time and energy in the bargain. Plastic (wax-coated or not) is being increasingly used for foundation.

Beekeeping equipment is available from many places across the nation. Several concepts are important when considering equipment. These are: (i) standardization, usually based on conserving the bee space; (ii) changes in nominal lumber size, contributing to availability and wastage problems in cutting wooden ware; and (iii) constant development and evaluation of new materials. Although plastics come to mind, there have even been hives made from concrete to withstand tropical conditions. Nevertheless, wood continues to be the material of choice by most beekeepers.

Because individual suppliers or equipment and prices are constantly changing, only an overview of beekeeping implements and paraphernalia is possible here. For up-to-date prices, it's best to consult the bee journals, which actively cater to the trade and bee supply outlets.

Protective equipment for the beekeeper has also followed the same route. New materials such as plastic netting, Velcro® and others have meant that beekeepers can work with more peace of mind during manipulation of colonies.

As already noted, traditional beekeeping equipment is made from wood. However, plastic equipment also is in use for the traditional bee box. Plastic is also widely used as a wax foundation base and in single component plastic frames. Plastic frames resist damage, do not require painting, and do not require assembly. However, it often takes more resources by the bees to "draw out" plastic or beeswax-coated plastic foundation. Some disadvantages of plastic are its tendency to warp and become brittle when exposed to sunlight and difficulty in being sterilized by heat. Various companies use plastic to make containers for bee products. Such containers eliminate the extracting phase of beekeeping and provide a container for honey in its natural comb.

There are all manner of gadgets used in the art and business of keeping bees that do not generally get mentioned in standard references. The following are some of these gems:

1. The slatted (or slotted) rack was used initially to take up the space of a deep bottom board. It assists in ventilation and reduces brace and ladder comb. Some beekeepers swear by it, some at it.
2. A division board feeder is a hollow insert filled with syrup that takes the place of a frame in a super when a population is small. Easily homemade from a board and nails, they quickly feed a small colony.
3. A robber screen can be used to protect small colonies from being foraged by larger colonies, especially during nectar dearth.
4. Top feeders come in various styles. These avert the necessity to open the colony and/or to fill a frame-style division board feeder. Top feeders hold more and are more accessible.
5. A screened ventilated bottom board provides air circulation during both summer and winter. Newer information also suggests these are useful in controlling exotic mite populations.

6. Various painted patterns on the front of colonies can help bees identify their own home, thus reducing drifting (bees losing their way and entering foreign colonies).
7. Drip boards serve several purposes. They collect errant honey leaks from supers stored on them, provide air space between the floor and honey stored in frames, and a space for two-wheeled hand trucks to grip the stack.
8. A screened division board placed between two alien colonies enables them to access each other's odors, while keeping them physically separate. The end result is two queens working together to produce a large population. Eventually they can be joined after this close but separate association, however, one of the queens is eliminated in the bargain.

Building Equipment

Although it can rarely be built more cheaply than it can be purchased, only basic woodworking skills and tools are needed to build wooden beekeeping equipment. Box joints are currently the most common, and according to some, the strongest kind to use in beekeeping applications. Producing them requires a jig, usually home made, to neatly and precisely cut the slots to line up with the fingers. Butt joints are more forgiving; two boards are butted together and simply nailed. The TIM joint is fast but weak. If a colony is not going to be moved, it will probably work okay. The dado joint, used by some manufacturers, is becoming more popular, and is strong enough to withstand the rigors of moving and manipulation. When building equipment, in all instances, respect bee space requirements and be sure to build your equipment to fit standard measurements.

Protecting Wooden Equipment

Some wood may last longer while some may last much less time, depending on the climate, but hives are definitely helped by some type of protective coating. The average life of a bee box is about seven years. Scraped and routinely painted, equipment can go much longer. Since the inside surfaces of bee hives should not be painted, the paint film on the outer surface is often stressed by water migrating to the film from the inside of the hive rather than from the outside. Oil-based paints will readily peel within just a couple of years. Due to ease of application and lower cost, latex paints are better. The rubber-based latex paints will flex and resist chalking and peeling much more than oil paints, but they, too, will finally succumb to mildew and peeling.

Some commercial beekeepers and beekeepers in other countries routinely dip equipment in paraffin or beeswax. This is a good finish that protects the wood from all sides and ends, but requires working around hot, flammable paraffin. Once the equipment has begun to show signs of wear, simply dip it again in hot paraffin to recoat the finish and to remove wax and propolis residue. In recent years, polyurethane exterior stains have become popular and have been consistently improved. As with paraffin impregnation, many of these stains are water repellent, resist mildew and fading, and clean up with water and soap.

A final warning concerns pressure-treated wood. The materials used to preserve the wood are usually toxic to honey bees. Thus, treated wood is not recommended for bee colonies. Even the sawdust is considered a health hazard and dust masks are recommended when working so-called Wolmanized® treated wood.

Wearing Protective Equipment

The most important protective equipment is the veil, which protects the face, the most sought-after target for guard bees. Veils can be used without a helmet, or attached to a pith-type helmet, made of plastic or other material. Almost any hat that keeps the veil material off the face and neck will work. Veils usually have a mesh bottom that is snugged down over the collar onto the shoulders with a variety of ties and/or strings. Veils that attach to the bee suit with a zipper are popular, mostly because they are convenient, easily maintained, and virtually bee proof. They are also more expensive.

Bee suits usually are light in color, but many wear what's available, simply to keep their clothes clean. The white coverall suit is most popular, with a variety of pockets, cuffs and attachments. White is also the most difficult to keep clean. They are made from a variety of materials – cotton, cotton blends and synthetics – each with its own peculiar attributes. Suits should be "roomy," to allow bending and stretching and lifting room, and for other clothes underneath. This also keeps the suit from stretching tautly over the skin underneath, which bees can then easily sting through.

Seasoned beekeepers seldom wear gloves because they feel they lose that "delicate" touch when manipulating colonies. However, many beginners start with them. Most gloves have cloth gauntlets of some type to seal the sleeves of the bee suit. Glove materials range from full leather to plastic to split leather to rubber. Some are ventilated, while others have no fingers. Wearing gloves can help build confidence in manipulating bees. As one gains experience, the finger tips can be cut off, which still protects most of the hand, while ensuring a more sensitive manipulation.

Boots and pants-cuff clasps range from high top rubber boots to baling twine. The goal is to keep bees on the ground from crawling up pants legs – an unnerving experience. Comfort, durability, safety and cost are all important. All equipment should fit the job. A hobbyist with a few colonies will use, and need, different equipment than a commercial pollinator.

Management

The "meat and potatoes" of beekeeping is management. It is often the best manager who makes the most honey from his/her bee colonies. Experience is extremely important if one is to manage bees successfully. There is no better piece of advice for the novice beekeeper than to begin small and only expand as experience is gained. A vital ingredient of this experience is permanent, detailed record keeping and knowing intimately the characteristics of the honey bee ecotype one is working with. One must also master the basics of opening and inspecting a colony with the aid of smoke, yet not destroying its cohesiveness.

Beekeeping knowledge comes about slowly and being able to implement it effectively often takes far longer than expected. In order to appreciate the techniques of beekeeping, one must first gain an understanding of the dynamics of the colony during the year. A recommended exercise for the beginning beekeeper is to construct a beekeeping calendar. Regional characteristics of beekeeping are easily identified through the use of the calendar, which shows average dates of bloom, colony population characteristics and bee manipulations. Such a timetable also can be broken down into a number of beekeeping activities, each requiring certain decisions. These include inspecting a colony in spring, feeding pollen and sugar, monitoring population buildup, controlling swarming, supering, monitoring and removing the honey crop, requeening, preparing for winter and migrating in search of better nectar resources or to move bees into commercial plantings for pollination.

No year is ever the same, so the beekeeper must learn to "think like a bee colony," closely watching environmental changes and anticipating the potential effects on colonies. Major management problems in beekeeping are controlling swarming (the reproductive process of a colony), requeening and managing diseases and pests. Swarming has befuddled even experienced beekeepers. Requeening and queen introduction techniques have been written about for many years, but still confound beekeepers on occasion. Several options often need to be considered for successful introduction of new queens, the life blood of any beekeeping operation. Finally, the challenges of diseases (American and European foulbrood) and exotic pests (mites, beetles) are complex, requiring an understanding of many possible treatment regimes under the rubric of Integrated Pest Management (IPM).

Although controversial, most beginners are advised to begin by managing two colonies. The reasons for this are several. If a hive begins to fail, there are resources in the other the beekeeper can use to help the weaker one along. If one colony is lost entirely, the novice beekeeper may easily lose interest if another colony is not present to take its place.

A Model Bee Yard

Somewhere the perfect bee yard exists, but if so, it is not the general rule. Most are the result of a beekeeper's style that fits both location and management philosophy. Bee yards should be right-up-next-to-the-hives easy to get to all year long. Newly plowed fields, suddenly erected fences, rising creeks, muddy roads, locked gates and the like should be anticipated, and avoided.

The most accessible location is worthless without something for the bees to forage on. There should be enough blooms to produce surplus honey for every colony in the apiary. Field crops, hay crops, tree canopies, weed species, horticultural or oil crops all can work. But there needs to be large areas of blossoms blooming a relatively long time. Water is required all season long, too. A lake, stream or pond is best. Swimming pools, cattle troughs or leaky faucets cause potential neighbor problems and should be avoided as bee watering possibilities.

A wind break, especially during the colder months in temperate latitudes, is recommended. A tree line, fence or hill works best. Air drainage is important. Cold air drains downhill; colonies at the bottom of a hill get "dumped on" in cold weather. Hill tops, too, suffer winds and wind chill problems. Avoid both. Exposure seems important to some. Colonies receiving morning sun start to forage earlier than those in the shade (at least with some races of bees). Southeast is the most common, and probably works best.

Bee colonies must be protected from all manner of pests and predators, including humans. Bear (electric fencing), skunks and possum (fencing), cattle and horses (regular fences, though stout), and neighbor prying eyes (screening, hedges) must all be considered. For large bee yards, an out-building that works as a storage shed, work area, extracting room (sometimes) and lunch room is needed. Most of all, a bee yard should be a pleasant place to visit. Scenic, quiet, distant and, most importantly, not a challenge to use.

Inspecting Honey Bees

The productivity of honey bee colonies should be actively monitored by the beekeeper, whose job it is to recognize certain conditions and help a colony overcome those causing adversity. Generally, inspection will determine the state of the colony in terms of reproductive ability (queen condition; population of worker bees), nutritional resources (honey and pollen stored in the comb) and whether diseases or pests are present.

The latter is increasingly important as exotic organisms continue to proliferate around the globe. Of special significance at the present are two introduced mites, the internal *Acarapis woodi* and external *Varroa destructor*. These mites have caused beekeepers to take a closer look at and often use chemical controls inside the living beehive with the concomitant risks that these substances may harm the colony and/or contaminate its products. As a consequence, honey bees have become much more domesticated, as they are increasingly reliant on beekeepers in many areas of the world to help control exotic bee mites. Other diseases that affect colonies are caused by bacteria, fungi, viruses and protozoans. Of particular significance are two bacterial conditions, American foulbrood (*Paenibacillus larvae* subspecies *larvae*) and European foulbrood (*Melissococcus pluton*).

American foulbrood, in particular, is caused by a spore-forming organism that can resist harsh ecological conditions. Epidemics of this disease are the reason state bee inspection services exist, although many of these have been discontinued recently due to budgetary constraints and lack of support. Discovery of sulfa drugs and later antibiotics has caused a shift in beekeepers' perceptions concerning the disease, which they have actively kept at bay for decades. Unfortunately, the recent appearance of antibiotic-resistant strains of *Paenibacillus larvae* subspecies *larvae* is causing second thoughts by many beekeepers concerning official inspection backed up by apiary legislation.

An important adult disease is known as nosema and is caused by the protozoan *Nosem apis*. This is probably present in every colony of honey bees, but only becomes epidemic when bees are put under stress. It may be far more important in determining bee colony health than is generally given credit.

There continue to be numerous so-called "exotic" organisms that impact colonies of honey bees around the world. Ironically, two of these are ecotypes of honey bees themselves: the Africanized honey bee (*Apis mellifera scutellata*) and the thelytokus Cape of Good Hope bee (*Apis mellifera capensis*). In addition, various mites are found on Asian honey bees (*Apis cerana*, *Apis dorsata*, *Apis laboriosa*) that conceivably could transfer to *Apis mellifera* as *Varroa destructor* did previously. No better example of this constant threat is the surprise introduction of the South African small hive beetle (*Aethina tumida*) into the United States in the late 1990s.

Honey Bee Ecotypes

All honey bees are not the same. This statement, it seems, cannot be said too often around beekeepers and/or the general public. There are those who manage bees exactly the same whether or not their stocks have been selected for overwintering, swarming, rapid brood rearing, pollen collecting and/or stinging. The belief that all honey bees must behave or act similarly no matter the conditions is the root of many beekeeping controversies over the last two centuries, and the reason many lay persons fail to understand the complexities of these stinging insects. Usually, beekeeping "arguments" pertain to whether or not a certain management technique or a special kind of beekeeping apparatus is practical or efficient. The kind of bee a beekeeper has in his apiaries often will determine whether some concept or idea works or doesn't work. All too often, however, the bees' genetics are ignored when contemplating solutions to many of the mysteries of beekeeping.

Unfortunately, most beekeepers really do not know what kind of bee they are using. That's because present bee stock is literally a melting pot of honey bee genes. The predominant races (subspecies or ecotypes) of bees which make up the honey bee genetic mix found in the United States are: Italian (*Apis mellifera ligustica*), Caucasian (*Apis mellifera caucasica*), Carniolan (*Apis mellifera carnica*) and German (*Apis mellifera mellifera*), the dark bee. Each population evolved under certain ecological conditions and natural selection over a long period of time that have provided them with their own particular survival techniques. These ecotypes are thoroughly intermixed and are extremely difficult to separate in novel environments. In addition, other genes of other ecotypes also are present in small quantities.

Because there is such great variability, however, the possibility of quantum leaps in honey bee selection programs is possible. With the coming of the mite *Varroa destructor*, however, the honey bees' genetic base has narrowed in many parts of the world. But fortunately there remain pockets of bees that appear to be resistant (tolerant) and these may provide the foundation for rebuilding a honey bee stock devastated by this parasite.

Africanized Bees

One of the biggest biological stories of the Americas concerns honey bees. Introduction of the African honey bee ecotype (*Apis mellifera scutellata*) has been responsible for raising the public consciousness about these insects. This bee is nothing more than an ecotype adapted to tropical conditions, generally characterized by higher rates of defensive behavior and reproduction. Unfortunately, its fearsome reputation is an outgrowth of sensationalized press coverage of stinging incidents by these so-called "killer bees," which caused deaths of animals and people in Latin America. As a result many people now view honey bees as aggressive rather than defensive, and think them responsible for a good many human fatalities. The reality is that the number of verified deaths by honey bees is much smaller than reported (almost all stinging insects are routinely called bees). This over-sensationalized topic has affected beekeepers in several ways, most notably by loss of access to beekeeping locations. North America is the last frontier for the Africanized (or African) honey bee and its final distribution is still unknown. Nevertheless, the challenge for many beekeepers in the future will be to strike a balance in their communication with the public about the risks/benefits of their bees. Beekeepers also will have to adapt to this ecotype's different behavior, which often can be a radical departure from the European ecotypes previously present.

A special ecotype inhabits Africa known as *Apis mellifera capensis*. This bee is characterized by a high degree of thelytoky, which means workers can become laying queens, producing diploid females, in spite of laying unfertilized eggs. This ecotype has created a crisis of sorts in African beekeeping. It is hoped that this honey bee will not be moved out of its homeland by beekeepers and introduced to the rest of the world. The history of honey bee introductions around the world over the last two centuries, however, is not a good omen in this regard.

Smoking Bees

Within and outside the dark hive, bees communicate extensively by smell. Nectar, pollen, diseases, other insects, brood, the queen, drones – everything in the hive has an odor cue. As complicated as the bees' odor communication system appears to be, the manner that beekeepers have developed to overcome the bees' ability to perceive odors, both inside and outside the hive, is relatively simple, and that is to puff cool, white smoke in and around the hive. For reasons not clearly understood, smoke stimulates bees to move to honey stores and engorge, which reduces their propensity to sting.

Early smokers were little more than a smoldering fire beneath or near a hive. Later, tobacco pipes were modified to direct smoke into hives as were other devices. After evolving through many different designs and styles, beekeepers in North America have a small, but adequate range of smoker designs from which to choose.

Smoker fuels are as numerous as are the beekeepers who use them. Common types include grass clippings, pine straw, sumac pods, cloth rags, rotted wood, wood shavings, and burlap. Essentially, anything can be used that produces cool, white billowing smoke and has not been treated with pesticides, fire retardants or other noxious chemicals. Under normal conditions, smoke is effective for about 2 to 4 minutes before needing to be reapplied.

Moving Bees

Bees can be moved almost any way imaginable. Some, of course, are easier and safer than others. Commercial operations need the economy of size and efficiency. A large, flatbed truck serves that purpose. Some come with a flatbed trailer that attaches to the truck to increase efficiency. These trucks usually have customized tie-downs, tool boxes and equipment storage areas. Getting the bees on and off the truck can be done by hand (muscle) or machine.

Regular two-wheeled carts, sized to hold hives, often are used for moving. Motorized carts are common, as are booms and Tommy-lifts. Fastest are fork-lifts. There are several models available, from the standard, to large, specially designed models for specific bee pallets. Some have cabs, most have protective cages and large tires to navigate easily in muddy conditions. Some can swivel or pivot in the center.

Once loaded on the truck bed (many are built to hold an exact number of pallets), tie-downs can be regular rope, self-tightening straps, or wide canvas belts affixed to wooden frames that are used for extra security. A secure net is required at all times to avoid escaped bees on the road. Anytime bees are moved, the boxes should be fastened, entrances closed, the load netted and tied down to prevent shifting.

An important consideration in moving bees is temperature. Traditionally this has been managed by periodically spraying the load of bees with fresh water when signs of overheating are evident.

Package Bees

The most common way to start a colony, or start beekeeping, is to install a package of bees into an empty home-to-be by removing them from the shipping cage. Packages generally come in three- to five-pound sizes (3,500 bees equal a pound). And there are nearly as many ways to get bees from the shipping cage to the functioning unit as there are people doing the task. But basic biology dictates certain principles be obeyed. A starter box with some or all drawn comb is better than just frames with foundation, as it gives the bees some place to be, and store food immediately, and reduces the amount of gathered food required for wax production, freeing it for brood food.

Bees can be "moved in" by dumping them (they are often sprayed with water first to inhibit flying) inside the box (with three frames removed, then replaced, to accommodate the resultant mass); they also can be dumped directly in front, to march right in; or a combination of the above two techniques, where some are placed inside, the remainder outside. The empty package is removed in a day or so. Once installed, several precautions are recommended. The first rule is: feed, feed, feed. Then feed more, until they don't take any more. Feeding well into the summer may be required if adequate forage is not available.

Checking for queen acceptance, and then queen production is a must, but there is a fine line between too-often and too-seldom observations. It is safer to edge toward the too-often, but just barely. Once established, remove feeders, add supers and prepare for the honey flow and harvest.

Dividing Colonies

Splitting a colony is the easiest and least expensive way to increase the number of hives managed. But there are other reasons to split a colony, and there are nearly as many ways to split one as there are colonies to split.

The overall principle in making a split is to start with a large, healthy, populous colony (or colonies). The goal is to remove some uncapped brood, some honey and pollen resources to a new box, or two, to start a new colony. A new queen may, or may not be, added. Usually the parent colony should not be reduced to less than half its resources so it can continue to keep pace with the season. Bees, brood or food may be taken from more than one parent to successfully build a new split. Splits must have enough nurse bees to care for the brood, some foragers to gather resources, sealed brood for immediate colony expansion, younger brood for continued expansion and some resources for immediate consumption.

Splits are used to "make increase," or for other reasons. Popular swarm control/prevention measures include splitting a large colony to allow room for expansion, and to relieve brood-nest congestion. Often the "new" colony is rejoined to the parent when the swarming urge is over so the actual number of colonies does not increase. One technique used to reduce mite infestation is to divide a colony later in the season, eliminating the older, infested bees, and overwintering the younger, less infested bees.

Feeding Colonies

Providing food to colonies is one of the most time-consuming and tedious tasks facing any beekeeper. Two types of food are required: carbohydrate and protein. Generally, carbohydrates are provided by nectar in nature and the best analogy to this is sugar syrup, made up by dissolving cane sugar in water. This is then provided through various hive modifications or feeders, some of which are mentioned elsewhere in this article.

A relatively new bee food is high fructose corn syrup (HFCS) that is manufactured in huge amounts to service the soft drink and candy trade. Two types exist: 42 and 55. The 55 is generally considered more acceptable to bees because it has more sugar solids. Many beekeepers consider feeding both sugar syrup and HFCS, depending on hive condition. Sugar syrup high in sucrose is considered superior for colony population build up, while HFCS is used strictly to maintain populations.

Most suggested feeding regimens concentrate on providing carbohydrate. However, it must be complemented with protein for a balanced diet. This is provided by pollen to the honey bee in nature. The beekeeper, too, can trap and give back pollen or combine it with soy flour and/or yeast (supplement). Protein supplement often is sold ready-made in patties by beekeeping supply outlets.

Producing the Honey Crop

The beekeeper seeks to have as large a population of worker honey bees as possible coincidentally when the most nectar-producing flowers are blooming. This nectar is stored above a bee colony in the wild. Thus, beekeepers emulate this by adding extra boxes on top of hives (supers) into which bees place the nectar. Nectar is modified by the bees into honey. The insects add enzymes, changing the material chemically, and reducing the moisture content from 80% (nectar) to about 18.6% (honey). The bees determine when the moisture is correct and then cap over the honey with wax. When the supers are filled, they are removed and the honey is extracted from the comb using centrifugal force in special machinery (extractors). Sometimes honey is sold in the comb (known as section or comb and cut-comb).

Extracting the Honey Crop

A large honey crop is clearly a mixed blessing. The more supers that go on, the more honey to be processed. More honey means more work, but it also means more money. For years, clever people have tried to develop equipment to make the uncapping, extracting, pumping, filtering, and bottling procedure more convenient, even easy. Though "easy" extracting has not yet been achieved, the process has become much more streamlined. Old processing equipment was made from galvanized tin with lead solder joints. It was solid equipment that was built to stand years of heavy use. The clutch-drive mechanism was simple, heavy-duty, and a bit dangerous. Belts, drives, shafts, and pulleys were all exposed. In fact, a few early extractors were powered by low compression gasoline engines. Extracting was done outside on occasion, a practice that generally has been abandoned.

Stainless steel with welded joints is now used on extractors. Other metals may impart an objectionable odor. Smaller hobby-type extractors may use plastic barrels. In many instances, variable-speed direct-current (DC) drive motors are used that allow for the gentle extraction of full combs of honey. The equipment is mechanically simpler, but technologically more complicated. It's lighter and more maintenance free. Most commercial honey processing lines would be ordered as follows:

1. uncapper
2. extractor(s)
3. heated sump
4. honey pump
5. filter
6. settling tank
7. bottler

Other equipment in honey processing can include a barrel melter, a flash heater, wax spinner and other equipment-moving devices. A second line would drain honey from wax cappings to the sump. Dried cappings would be melted into beeswax, which could be returned to the bees as foundation.

Managing Swarming

Swarms can be both reproductive and migratory. Little can be done about swarming once the "impulse" is generated in a colony. The best ways to control swarming are providing room in the colony and/or regularly requeening with younger individuals. This is a "preventive" strategy that is much more effective. As stated earlier, once the impulse to swarm gets going, it is almost impossible to stop. Generally swarms are reproductive in nature, especially with European honey bees, and can be both a blessing and a curse. The blessing part is that one can be harvested and put to work in an apiary. A secondary blessing, obviously, is that a swarm happens. That means a colony is healthy enough to swarm, something all too rare in these days of increasing stress on managed honey bees.

The first thing to do with a swarm is collect it. At times this is easy, sometimes impossible. Swarms high in the air can be collected with vacuum devices, long ladders, or heroic gymnastics. Most can be collected into bags, boxes, supers or whatever and transported to permanent housing. The key is to provide ventilation; putting a strong swarm into an air-tight container is a recipe for disaster! Swarms are generally the gentlest of bees, but if left exposed for several days, they can become hungry and much more defensive. Always have a lighted smoker at the ready when working swarms.

The public relations aspect of swarm gathering should not be overlooked. But the macho image many beekeepers display while on the job communicate a mixed message. Once collected and transported, a beekeeper can do many things with this bunch of bees. The deciding factor is often the size of a swarm. Large swarms, about four or five pounds of bees (3,500 bees equal one pound), can easily survive by themselves. Smaller swarms of one to three pounds can be combined with other swarms to start a large colony; or added to another colony to boost its nectar- and pollen-gathering capability during a major flow.

To be safe, all swarms should be considered infested with mites and treated accordingly. As the queen heading the swarm is from essentially unknown heritage, replacing her with a young one of known parentage should be considered.

With the advent of the tropically adapted Africanized (*Apis mellifera scutellata*) honey bee, another kind of swarming is increasingly seen. This is the migratory swarm, thought to be brought on by stress such as lack of forage or water. This kind of swarm often behaves differently than the reproductive one and may be much more defensive, though not always so.

Managing and Rearing Queens

The queen is the key to managing the genetic component of a colony. She contributes one half of all the genes found in a colony, whereas a single drone provides for less than half (queens mate with 17 to 20 drones during a short period in their life just after emerging from the cell). The colony's characteristics, therefore, have a good chance of being perpetuated in the queen and research has shown that queen selection followed by open mating will ensure a good deal of progress in breeding bees with specific traits.

Queen rearing is one of the most demanding beekeeping activities, and more often than not is a true art form. Anybody can produce a queen, but rearing a quality queen with the correct genetic complement for a beekeeping operation is far more difficult. Queen rearing also is directly tied to a timetable, which must be rigidly followed. Often the question is raised whether or not one should produce queens him/herself, let the bees do it, or purchase a queen. There is no easy answer. The only reply may be to ask the question, "Whose quality control is the best under the circumstances, that of nature or of human beings?"

Again, the queen honey bee usually mates with many drones. This ensures large genetic variability, but also means a lack of controlled breeding. It is possible to instrumentally inseminate queen honey bees in an attempt to control genetics in a population. This is not easy, however, and can only be accomplished by trained workers. Most queen rearing facilities produce daughter queens from selected stock that are open mated (uncontrolled) in a natural setting.

Managing Wintering

The honey bee can live in almost any climatic environment, but is most stressed by winter in continental climates. Honey bees can produce a warm brood nest even in the coldest winters if supplied with the proper nutrition and number of workers. This leads to the adage that "honey bees never freeze to death, they starve to death." Beekeepers in cold climates, therefore, have a significant challenge to help their colonies overcome severe conditions of wind and cold. Many pack their hives wintered outdoors in various kinds of materials to conserve warmth. Others move their colonies indoors to protect them. The latter activity was employed by old timers who put their colonies into cellars. This was risky as too much warmth would stimulate a colony to begin to build population, a prescription for disaster. With development of refrigeration, however, it now is routine in some areas to bring smaller-than-normal hives (nuclei) into climate-controlled buildings and keep them in a kind of human-induced diapause, which reduces nutritional requirements to a minimum and conserves worker bee energy and vitality so they can begin to rear brood quickly and efficiently in spring.

An alternative to wintering is to simply collect all the stores and kill colonies off in winter, establishing new hives the following spring with package bees from more tropical areas. This was routinely practiced by Canadian beekeepers who simply purchased bees from the southern US until the border was closed in the early 1980s due to introduction of tracheal and then Varroa mites. To many beekeepers this was a repugnant practice and they were not sorry to see it abandoned. Effective wintering continues to be an important part of bee management as more colonies are lost during this trying time than other seasons of the year.

Nectar and Pollen Sources

Nectar and pollen are the only natural foods of honey bees, strictly vegetarian insects, and each geographic area has different sources of these important foods. Every good beekeeper, therefore, must be somewhat of a botanist in order to make sure the bees are located so they have an adequate food supply. Bee plants may also differ from each other in several ways, such as the kinds of nectaries (nectar glands) each supports and/or the time of day they may secrete nectar and/or produce pollen.

Nectar and pollen production by flowers is dependent on a great variety of environmental conditions such as soil moisture, pH, profile and fertility, as well as rainfall distribution, temperature and humidity. Over the last four decades, there has been an overall decrease in honey bee forage in the United States due to many factors, especially changing agricultural patterns and increasing urban development. Improving nectar production by genetically selecting for varieties of certain crops that produce large amounts of nectar, or purposely planting nectar-producing varieties in so-called "waste" land, along roadways or on lands reclaimed for mining, are some ways suggested to reverse this systematic reduction of bee forage.

Few plants produce the vast quantities of nectar the honey bee needs to make a large honey crop. In the state of Florida, for example, less than ten plants are responsible for sizeable honey crops on a consistent basis. Fortunately, in most areas a number of minor nectar crops usually are found which help support honey bees throughout the year, although they often contribute little to the beekeeper's honey crop. It is of more than passing interest to know that many introduced plants assist honey bees in a number of ways, and the insects may contribute to their proliferation.

Though not as readily available as honey, another type of sweet is collected and processed by honey bees. Aphids and other sucking insects often take more than they need from the plants. The excess is extruded and may be collected by ants or honey bees. The resultant product is honeydew. Some think this might have been the "manna" that descended from heaven as noted in the Bible (Exodus 16:1–36).

Commercial Pollination

Honey bees are cosmopolitan pollinators, transferring pollen both within and between flowers. Although important to many crops (fruits and vegetables), honey bees are not the most effective pollinators in many situations. This has led to some proclaiming that other bees should be used in preference, such as bumblebees (*Bombus* sp.) and/or blue orchard bees (*Osmia* sp.). However, honey bees have significant advantages including very large populations that are easily moved, and a well-known rearing technology.

There is no stable pollination service in the United States of the kind described by S.E. MacGregor in his classic volume on insect pollination. This means that pollination is carried out by a number of independent contractors. More recently, pollination brokers in the western United States have become more common. The vast majority of commercial pollination takes place in California on the almond crop. Literally hundreds of thousands of colonies are needed.

Commercial pollination is a service, a much different business than producing a product like honey or pollen. As such, it is not suited to all beekeepers and each should look carefully at the characteristics of this enterprise before dedicating many resources to it.

Recently, pollination has received more respect from the general public due to a scarcity of feral or wild honey bees caused by devastating effects of exotic bee mites. This represents a teachable moment for beekeepers, who can now describe with pride the value of their insect charges to the public at large.

Honey Contrasted to Pollination

Honey is a world commodity, and is labor intensive to produce. As such, the price of the product can always be expected to be influenced by societies with low labor costs. Indeed, beekeeping is being promoted aggressively as a development tool in many countries because it is relatively environmentally friendly and not capital intensive.

Although honey can be imported cheaply in many instances, a process exacerbated by globalization of world commerce, pollination services cannot. In addition, because no food product is involved, chemical treatment for exotic pests (mites) can be applied in a more forgiving way to colonies used strictly for pollination. This means that in the future there will always be a demand for pollination no matter the price of honey. Because commercial pollination seems more assured in the future, beekeepers should continually carefully consider this activity in their enterprise mix.

Conclusion

The future of beekeeping or apiculture continues to be mixed. On one hand, the honey bee will be more and more important as growers and the general public continue to realize how necessary this insect is for producing a quality food supply through pollination. Because honey is a world commodity, it also is continually under price pressures in developed countries, as it represents a good source of income for countries with a labor-intensive work force. Its reputation is also at risk, however, given the chemicals needed to keep (treated) bee colonies alive and the potential they have to damage the sweet's reputation through contamination. Whether or not honey and/or pollination are primary, there also are other reasons to keep bees, including using their products, both manufactured (royal jelly, honey, beeswax, venom) and collected (pollen, propolis), for the benefit of humanity, as well as for the general joy of communing with nature and one of its fascinating social organisms.

The history of beekeeping activities is long, and it takes time and experience to become a proficient manager of honey bee colonies. This article can provide only some of the basic information on the craft. The authors hope that it will serve as a catalyst for those thinking of taking up the activity, and also a source of basic information for anyone interested in one of humankind's most fascinating activities.

► Honey Bee
► Bees
► African Bee
► Cape Honey Bee
► Varroa Mite
► Small Hive Beetle
► Bee Louse
► Pollination by *Osmia* Bees
► Polination and FlowerVisitation

References

Bee Culture, A. I. Root Co., Medina, Ohio, accessed June 7, 2002; http://bee.airoot.com/beeculture/*Electronic*

American Bee Journal, Dadant and Sons, Hamilton, Illinois, accessed June 7, 2002; http://www.dadant.com/.

Sanford MT. Beekeeping in the Digital Age, Bee Culture, accessed June 7, 2002; http://bee.airoot.com/beeculture/digital/

Who's Who in Apiculture, Bee Culture, accessed June 7, 2002; http://bee.airoot.com/beeculture/who/who_2002.htm

Online Source Book for Beekeeping, accessed June 7, 2002: http://www.beesource.com/suppliers/index.htm

McGregor SE (1976) Insect pollination of cultivated crop plants. Agriculture Handbook 496, published by the Agricultural Research Service. Online version accessed June 17, 2002; http://bee.airoot.com/beeculture/book/index.html

Caron D (1999) Honey bee biology and beekeeping. Wicwas Press, Cheshire, CT 363 pp

Caron D (2001) The Africanized honey bee in the Americas. A.I. Root Co., Medina, OH

Graham JM (ed) (1992) The hive and the honey bee. Dadant and Sons, Hamilton, IL

Hooper T (ed) (1976) Guide to bees and honey. Rodale Press, Emmaus, Pennsylvania

Morse, Roger A (1972) The complete guide to beekeeping. E.P. Dutton, Inc., New York, NY

Morse, Roger A, Flottum K (eds) (1990) ABC and XYZ of bee culture. A.I. Root Co., Medina, OH

Morse, Roger A, Nowogrodzki R (1990) Honey bee pests, predators, and diseases. Cornell University Press, Ithaca, NY

Sammataro D, Avitable A (1998) The beekeeper's handbook. Cornell University Press, Ithaca, NY

Taylor R (1984) The how-to-do-it book of beekeeping. Linden Books, Interlaken, NY

Webster TC, Delaplane K (2001) Mites of the honey bee. Dadant and Sons, Hamilton, Illinois

Apidae

A family of bees (order Hymenoptera, superfamily Apoidae). They commonly are called bumble bees, honey bees, and orchid bees.

► Bees
► Honey Bee
► Wasps, Ants, Bees and Sawflies

Apioceridae

A family of flies (order Diptera). They commonly are known as flower-loving flies.

► Flies

Apivorous

Bee eating. Birds, and some predatory insects such as robber flies (Diptera: Asilidae) kill and consume honey bees or, in the case of blister beetles (Coleoptera: Meloidae), ground nesting bees.

Apneumone

A chemical released by a nonliving substance that is beneficial to the receiver. An apneumone is a type of semiochemical.

► Chemical Ecology
► Semiochemicals

Apodal

The condition of lacking "feet" (tarsi). Fly larvae and some beetle larvae, for example, have simple tubercles that aid in movement, but lack legs, including tarsi.

Apodeme

A thickened section of the exoskeleton that serves as a point for muscle attachment. On the external surface, it usually is marked as a suture or fold, but internally there may be a significant invagination.

Apodous Larva

A larval body form that is legless, robust, and C-shaped or spindle-shaped. The head may be well developed, or not. Apodous larval types include curculionoid, muscoid, and apoid.

Apoidae

A superfamily in the order Hymenoptera known as bees. It consists of several families.

► Bees
► Wasps, Ants, Bees and Sawflies

Apoid Larva

A larval body form that is robust, with a well-developed head, and cared for by nestmates or provisioned by the parent. It occurs in ants, bees, and wasps (Hymenoptera).

Apoid Wasps (Hymenoptera: Apoidea: Spheciformes)

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Apoid wasps are a morphologically, behaviorally, and ecologically diverse group of insects that are common in many habitats. Apoid wasps are most closely related to bees, and are placed with them in the superfamily Apoidea, one of three superfamilies of the so-called "stinging Hymenoptera" or Aculeata; the other two subfamilies are Chrysidoidea and Vespoidea (Table 7).

The subfamily Apoidea is subdivided into the series Apiformes and Spheciformes, the latter of which are the apoid wasps. Thus, the term "apoid wasps" refers to all members of the superfamily Apoidea that are not bees. Of the four families making up the Spheciformes (Heterogynaeidae, Ampulicidae, Sphecidae, Crabronidae), all but the Heterogynaeidae were formerly placed in the single family Sphecidae (*sensu lato*) in the superfamily Sphecoidea. But recent consensus splits the old Sphecidae into the Ampulicidae, Sphecidae (*sensu stricto*), and Crabronidae. The correspondence in taxonomic names between this recent family-level classification and what we might call the "classical" system represented in *Sphecid Wasps of the World* by Richard Bohart and Arnold Menke is given in the following table. The reason for the recent taxonomic reworking is sound. The "old" Sphecidae and Sphecoidea were artificial groupings evolutionarily, because the wasps in what we now call the Crabronidae are actually more closely related to bees than they are to the Ampulicidae or the "new" Sphecidae.

The Apoidea, as a whole, likely has its origins in the early Cretaceous, and it is the wasps that predate the bees. Species of over two dozen extinct apoid wasp genera, including members of the

Apoid Wasps (Hymenoptera: Apoidea: Spheciformes), Table 7 Superfamilies of aculeate wasps (classification of the Apoidea is after *The bees of the world* by Charles Michener)

Superfamily	Series	Families	Included groups
Chrysidoidea		multiple families	cuckoo wasps, bethylid wasps, and others
Vespoidea		multiple families	ants, social wasps, spider wasps, velvet ants, and others
Apoidea	Apiformes	seven families	bees
	Spheciformes	Heterogynaeidae	apoid wasps
		Ampulicidae	
		Sphecidae	
		Crabronidae	

Ampulicidae, Sphecidae, Crabronidae, and the extinct family Angarosphecidae, have been found in Cretaceous deposits. Over 9,500 described extant species of apoid wasps are unequally distributed among the four families and over 250 genera. Bees, in contrast, are divided among seven families, 425 genera, over 16,000 described species, and perhaps 30,000 species overall (Table 8).

As a group, apoid wasps share a number of traits that unite them with bees in a discrete evolutionary lineage: (i) a gap present between tegula (at the base of the wings) and the apex of the posterior edge of the pronotum; (ii) a broadly U-shaped pronotum when viewed dorsally; and (iii) the "propodeal triangle" on the dorsal posterior of the abdomen. A dozen or so shared traits link bees in a single clade within the Apoidea. For example, bees feed pollen and nectar to their young, and continue to eat both pollen and nectar as adults. In contrast, with perhaps one exception, all apoid wasps either feed their young arthropod prey or are brood parasites in the nests of other carnivorous wasps; the single exception is the genus *Krombeinictus* (Crabronidae) from India whose females provision with pollen and nectar. Adult wasps feed on nectar, sap, or honeydew, and some consume body fluids of prey. Another marked difference between apoid wasps and many bees is that body hairs are simple in the former, but often branched or even plumose in the latter, where they function to trap and carry pollen (though this may not have been their original function).

As a group, apoid wasps vary widely in habits and body size, form, and color. Most species are sexually dimorphic to a greater or lesser extent, females having almost universally larger body sizes and stouter mandibles. Also, only females have stings. Females of ground-nesting species also commonly bear two features not found in either males or in females of species that nest in other locations. The first feature is conspicuous rows of "rake spines" on their foretibia that aid in digging in soil. The second feature is flattened pygidial plates that aid in tamping soil in place during nest construction. Males of some species exhibit peculiar anatomical structures used in courtship and mate competition. Examples include the clypeal and abdominal hair brushes that male beewolves (*Philanthus*) use to disseminate sex pheromones, and the expanded translucent foretarsal plates of male *Crabro* that sport species-specific color patterns and which are apparently placed over female's eyes during courtship.

Heterogynaeidae

While the Heterogynaeidae are clearly apoid wasps, their exact relationship to the other three families is somewhat controversial. Heterogynaeids are small wasps, 1.5–5.0 mm in length, that are restricted in

Apoid Wasps (Hymenoptera: Apoidea: Spheciformes), Table 8 Correspondence of taxa names under the "classical" (Bohart and Menke 1976) and revised (Pulawski 2007) systems of classification of the apoid wasps. Note a few minor taxa have been left out of the table

"Classical" taxonomy	Revised taxonomy	Number of extant genera/species[a]	Some important genera (number of described species[a])	Nest type[b]	Host/prey orders[c]
not included	Heterogynaeidae	1/8	*Heterogyna* (8)	–	Unknown
Sphecidae: Ampulicinae	Ampulicidae	6/198	*Ampulex* (131)	C	Bla
			Dolichurus (48)	C	Bla
Sphecidae: Sphecinae	Sphecidae	19/731	*Ammophila* (201)	S	Lep
			Chalybion (45)	C	Ara
			Chlorion (20)	S, Pa	Ort
			Isodontia (61)	C	Ort
			Palmodes (20)	S	Ort
			Podalonia (66)	S	Lep
			Podium (23)	C	Blat
			Prionyx (59)	S	Ort
			Sceliphron (35)	M	Ara
			Sphex (118)	S	Ort
Sphecidae: Pemphredoninae	Crabronidae: Pemphredoninae	37/1021	*Arpactophilus* (43)	C	Hom
			Diodontus (73)	C	Hom
			Microstigmus (29)	Ps	Clm, Thy
			Mimesa (71)	S	Hom
			Passaloecus (35)	C, P	Hom
			Pemphredon (43)	C, P	Hom
			Pluto (58)	S	Hom
			Polemistus (36)	C	Hom
			Psen (92)	R	Hom
			Psenulus (159)	C	Hom
			Spilomena (86)	C, P, R	Hom, Thy
Sphecidae: Astatinae (part)	Crabronidae: Astatinae	4/151	*Astata* (80)	S	Hem
			Diplopectron (20)	S	Hem
			Dryudella (52)	S	Hem
Sphecidae: Astatinae (part)	Crabronidae: Dinetinae	1/12	*Dinetus* (12)	S	Hem
Sphecidae: Larrinae	Crabronidae: Larrinae	38/2686	*Gastrosericeus* (61)	S	Ort
			Larra (63)	Pa	Ort

Apoid Wasps (Hymenoptera: Apoidea: Spheciformes), Table 8 **Correspondence of taxa names under the "classical" (Bohart and Menke 1976) and revised (Pulawski 2007) systems of classification of the apoid wasps. Note a few minor taxa have been left out of the table (Continued)**

"Classical" taxonomy	Revised taxonomy	Number of extant genera/species[a]	Some important genera (number of described species[a])	Nest type[b]	Host/prey orders[c]
			Liris (350)	C, S	Ort
			Miscophus (183)	S	Ara
			Nitela (60)	C	Pso, Hom
			Palarus (34)	S	Hym
			Pison (196)	C, M	Ara
			Plenoculus (20)	S	Hem, Lep
			Sericophorus (69)	S	Dip
			Solierella (111)	C	Ort, Pso, Hem
			Tachysphex (391)	S	Ort
			Tachytes (294)	S	Ort, Lep
			Trypoxylon (629)	M	Ara
Sphecidae: Crabroninae	Crabronidae: Crabroninae	56/1886	*Belomicrus* (109)	S	Hem
			Crabro (88)	S	Dip
			Crossocerus (236)	C, P, S	Eph, Pso, Hom, Mec, Tri, Lep, Dip
			Ectemnius (184)	P, R, S	Dip
			Entomognathus (63)	S	Col
			Lindenius (60)	S	Dip
			Oxybelus (262)	S	Dip
			Podagritus (116)	S	Col
			Rhopalum (277)	P, S	Hom
Sphecidae: Nyssoninae	Crabronidae: Bembicinae[b]	84/1708	*Alysson* (42)	S	Hom
			Argogorytes (31)	S	Hom
			Bembecinus (187)	S	Hom
			Bembix (346)	S	Odo, Neu, Lep, Dip, Hym
			Bicyrtes (27)	S	Hem
			Clitemnestra (67)	S	Hom
			Gorytes (46)	S	Hom
			Harpactus (73)	S	Hom
			Hoplisoides (79)	S	Hom
			Microbembex (34)	S	Art[d]
			Nysson (102)	Bp	Apo[e]
			Stictia (28)	S	Dip
			Stizus (120)	S	Ort, Man
			Stizoides (29)	Bp	Apo[e]

Apoid Wasps (Hymenoptera: Apoidea: Spheciformes), Table 8 Correspondence of taxa names under the "classical" (Bohart and Menke 1976) and revised (Pulawski 2007) systems of classification of the apoid wasps. Note a few minor taxa have been left out of the table (Continued)

"Classical" taxonomy	Revised taxonomy	Number of extant genera/species[a]	Some important genera (number of described species[a])	Nest type[b]	Host/prey orders[c]
Sphecidae: Philanthinae	Crabronidae: Philanthinae	8/1141	*Aphilanthops* (4)	S	Hym
			Cerceris (868)	S	Col, Hym
			Clypeadon (9)	S	Hym
			Eucerceris (41)	S	Col
			Philanthus (137)	S	Hym
			Trachypus (31)	S	Hym

[a]number described species worldwide (see Pulawski 2007); genera included based on genus size and biological interest (but certain larger genera for which no biological data are available are left off the list).
[b]Bp = brood parasite in nests of other wasps; C = cavity nests; M = mud nests; P = nest excavated in plant stems; Ps = free-standing nest made of plant material bound with silk; R = nest excavated in rotten wood; S = nest excavated in soil.
[c]Apo = apoid wasps; Art = Arthropoda; Ara = Araneae; Bla = Blattodea; Col = Coleoptera; Clm = Collembola; Dip = Diptera; Eph = Ephemeroptera; Hem = Hemiptera; Hom = Homoptera; Hym = Hymenoptera; Lep = Lepidoptera; Man = Mantodea; Mec = Mecoptera; Neu = Neuroptera; Odo = Odonata; Ort = Orthoptera; Pso = Psocoptera; Thy = Thysanoptera; note that each species may prey upon a narrow range of families within each order.
[d]females are scavengers of dead arthropods.
[e]*Nysson* and *Stizoides* are brood parasites whose larvae feed on prey provisioned by other wasp species.

distribution to the eastern Mediterranean region, southern Africa, and Madagascar. Nothing is known about their biology, but there are hints that it may be unique among apoid wasps: females have such short wings as to make them flightless and they have been observed active at night; based on morphological evidence, it has been inferred that heterogynaeids are parasitoids, though they probably do not dig in soil.

Ampulicidae

The Ampulicidae have rather elongate bodies and legs that make them proficient runners; they range up to 3 cm or so in body size, and may be metallic blue or green in color. Though geographically widespread, ampulicids appear to be relatively consistent in their habits. Females of all species prey on cockroaches that are stung into temporary paralysis, placed singly in existing cavities, and quickly covered with debris after a single egg is laid on each prey. Venoms of certain species are known to have specific pharmacological effects on cockroaches, which are somewhat subdued following stinging, but remain active enough that the female wasp can lead them to the nest cavity, as if walking a tethered cow to pasture. Nests of ampulicids may have multiple cells separated by partitions made of plant debris, but are relatively simple compared to nests constructed by many Sphecidae and Crabronidae.

Sphecidae

The wasps in what is now called the Sphecidae are sometimes referred to as "thread-wasted wasps" in reference to their narrow cylindrical petioles. Sphecids often have quite striking body colors, including the metallic blue (*Chlorion aerarium*), black and yellow (*Sceliphron caementarium*), and black and orange with either silver (some *Ammophila*) or golden hairs (*Sphex ichneumoneus*). The family includes some of the largest apoid wasps, including members of the genera *Dynatus*, *Parasammophila*, and *Sphex* that can reach as long as 4–5 cm; sphecids are rarely less than 1 cm long, though this is the case for some *Ammophila* and *Prionyx*. Sphecids are more diverse in their nesting habits than are ampulicids. Some dig nest burrows in soil, others nest in existing cavities in wood or construct mud nests *de novo*. Certain species of *Chlorion*, on the other hand, are parasitoids that construct no nests at all, but simply sting their cricket prey and then place it back in its own burrow. Prey of sphecids include three orders of insects, along with spiders; some take prey that are large relative to their own body size. *Palmodes laeviventris* (which preys upon Mormon crickets, *Anabrus simplex*), *Sphex ichneumoneus* (which takes crickets and katydids), and certain *Ammophila* (that take large caterpillars) may provision with prey that approach or even exceed the adult female in body mass.

Crabronidae

The Crabronidae, the largest and most diverse of apoid wasp families, contains 90% of the apoid wasps. Crabronids range in size from 1.5 mm long *Spilomena* that prey on psyllids and thrips, to 35 mm long *Sphecius speciosus* that prey on cicadas, and 45 mm long *Editha magnifica* that take butterflies. Even individual genera can exhibit wide size variation; *Philanthus* in North America, for example, range from the 5 mm long *Philanthus parkeri*, predators of tiny andrenid bees, to 25 mm long *Philanthus bicinctus*, predators of worker bumble bees. As a group, crabronids prey on insects of at least 17 orders, along with spiders. The reproductive biology of the Ampulicidae, Sphecidae, and Crabronidae are covered in more detail below.

Reproductive Biology of Females

The reproductive strategies of female apoid wasps fall into three broad categories: parasitoidism, brood parasitism, and nest-provisioning. The nest provisioners include solitary, communal, and eusocial species, the latter two of which will be discussed in the following section. Unlike some apoid wasps, no vespid wasps or bees are parasitoids, and only the bees include brood parasites. However, apoid wasps have just barely crossed the threshold into eusociality, whereas bees and vespid wasps contain some of the most highly eusocial Hymenoptera.

Among apoid wasps, parasitoids lay their eggs singly on a host insect that has been stung by the adult female wasp; no nest is constructed by the female parasitoid, though she may return the host to its own burrow and cover it with debris. Parasitoids are found in the Ampulicidae, a few genera of Crabronidae (*Chlorion*, *Larra*), and perhaps the family Heterogynaeidae, though this has yet to be confirmed. Brood parasitic apoid wasps occur in the crabronid tribe Nyssonini (226 species) and genus *Stizoides* of the Gorytini (29 species). Brood parasites enter provisioned nest cells of other apoid wasps and deposit their own eggs (one per nest cell); the brood parasite larva then feeds on the host's stored prey, the host egg having been already killed either by the adult female parasite at the time of oviposition (*Stizoides*) or the parasite larva itself (Nyssonini).

The vast majority of female apoid wasps are solitary nest-provisioners that work without assistance from conspecifics to construct a nest and provision each of its brood cells with one or more paralyzed prey. The prey placed in a cell must provide all of the nourishment required by the maggot-like larva (one per nest cell in almost all species) that remains restricted to its own nest cell throughout development. Apoid wasp nest types can be grouped in five categories: cavity nests; nests excavated in plant material; nests excavated in soil; free-standing mud nests; and free-standing nests made of various materials bound with silk. In some genera, different species may construct nests in different categories.

Cavity nests, those built within existing cavities, are often constructed in old beetle tunnels in wood, but have also been found in such locations as empty snail shells, old plant galls, pitcher plants, rolled leaves, and gaps between stones or between boards on the siding of houses. Such nests usually contain multiple cells separated by a species-specific choice of materials; for example, *Chalybion* uses mud; *Isodontia*, chopped grass fragments and plant fibers; *Passaloecus*, conifer resins; *Nitela*, wood chips; and *Podium*, an eclectic mix of detritus, mud, and resin. Wasps that excavate their own nest tunnels in plant materials may tunnel through the pith of plant stems (e.g., in raspberry or sumac) or rotten wood in logs. Cells may be arranged in a linear sequence, and tunnels in the same nest may diverge into separate branches. Nests excavated in soil are, by far, the most common type of nest among apoid wasps. They may be simple, unbranched shallow tunnels terminating in the single brood cell, as is the case for some or all species of *Ammophila*, *Bembecinus*, *Bembix*, *Podalonia*, and *Prionyx*. Other species dig branched nests with side tunnels leading to as many as 1–2 two dozen brood cells provisioned in succession over a period of several weeks. Single and multi-celled nests can be found not only among different species of the same genus, but among different females in one species. Free-standing nests constructed *de novo* by females may be built of mud sculpted into species-specific shapes, as is the case for species of *Pison*, *Sceliphron*, and *Trypoxylon*. Mud nests may be attached to vines, trees, cliff faces, or nowadays, buildings; they may also have multiple cells.

In most cases, each nest cell is completely provisioned and closed off by the adult before the next cell is begun, but there is some variation in the duration and timing of provisioning relative to the developmental schedule of offspring. Most species are *mass provisioners* that completely provision cells with one or more prey before the egg hatches. More rarely, females are *progressive provisioners* that continue to bring in prey after the egg hatches, sometimes until the larva is ready, or nearly so, to spin its cocoon. Among solitary apoid wasps, only certain *Ammophila* provision two cells simultaneously. During provisioning, females of those species that hunt relatively small prey carry the prey in flight from hunting grounds to the nest. Prey are usually carried in the wasp's legs, sometimes with the aid of the mandibles, but some *Oxybelus* tote prey impaled on their stings, whereas *Clypeadon* females carry their ant prey grasped by the thorax using structures on the terminal abdominal segments aptly referred to as "ant clamps."

When they leave nests to forage, females of nest-provisioning apoid wasps face two problems in particular, other than the obvious need to find, sting, and transport their prey: the necessity to protect the unguarded nest from natural enemies and the need to find their way home again. Before departing to hunt, wasps often plug the entrance temporarily as a means of excluding intruders. And when a nest is completed, the female may construct an even more elaborate closure and take steps to conceal the entrance; in ground nesting species, this involves often elaborate and prolonged leveling of the mound of excavated soil adjacent to the nest entrance. Nevertheless, although these actions are likely successful in many cases, apoid wasp larvae are plagued by a variety of natural enemies that commence their attacks at varying times in the life cycle of the wasp. Brood parasites, which include not only other apoid wasps, but mites, flies (Phoridae, Sarcophagidae), and non-apoid wasps (Chrysididae) that feed on the wasps' own prey, may kill the wasps' young either directly or indirectly (through starvation). Parasitoids that feed directly on wasp larvae or pre-pupae include, among other insects, flies (Bombyliidae), beetles (Rhipiphoridae), and other aculeate wasps (Chrysididae and Mutillidae).

Several detailed studies attest to the fact that female wasps often have excellent homing abilities that lead them back to their nest, even when that nest is one of many hundreds or thousands densely packed into the apparently featureless soil surface of a nesting area. As far back as 1930, Niko Tinbergen's research showed that a *Philanthus triangulum* female can relocate her nest by learning the image of the landscape surrounding the nest and matching the memorized image to the configuration of local landmarks when she later returns with prey. The initial task of learning the image is apparently accomplished during an orientation flight, which in the case of *P. triangulum*, begins when the female circles the nest in flight, then gradually expands the diameter and height of her loops before departing for her hunting grounds. The form of the orientation flights varies among species, but females of all species share an uncanny ability to find their way home, even after being transported several hundred meters away by researchers.

When we examine the ovaries of female apoid wasps, we find several features that vary among species and correlate with overall reproductive strategies. First, although the paired ovaries of nest provisioning species each have three ovarioles (except for *Oxybelus* which have two), each ovary of brood parasitic species is comprised of four ovarioles (and sometimes five in *Stizoides renicinctus*). Second, although it is common for females of nest provisioners (especially progressive provisioners) to carry a maximum just one or two mature oocytes in their ovaries at a any time, brood parasites commonly carry 4–6 mature oocytes; and the parasitoid species *Larra amplipennis* can carry as many as 21. Third, the eggs produced by nest provisioners tend to be larger (relative to overall body size) than those of brood parasites or of *Larra*. All in all, this meshes with the fact that nest provisioning apoid wasps, because they invest so highly in individual offspring, have relatively low lifetime fecundities compared to parasitoids and brood parasites in their same families. Thus, it is likely common that even the most successful females of some nest provisioners can expect to have fewer than ten offspring during their lives. This contrasts markedly with the high potential fecundities of non-aculeate parasitoid Hymenoptera (e.g., Braconidae, Ichneumonidae).

Communal and Social Species

The vast majority of apoid wasps are solitary species, each of whose females occupies a nest alone and provisions it without assistance from conspecifics. Nests of both ground- and mud-nesters do sometimes occur in dense aggregations, but true communal and eusocial behavior is relatively rare among apoid wasps. Communal nests, in which small groups of females share a main nest burrow, but in which each provisions her own brood cells, have been reported in several genera (e.g., *Cerceris*, *Moniaecera*, *Spilomena*). In the Neotropics, *Microstigmus comes* is eusocial, inhabiting nests in which (i) two generations of adult females are present (likely a mother and her daughters), (ii) each nest cell is provisioned cooperatively, and (iii) one female is the primary egg layer. The nests, which are founded by one or more females, have as many as 18 brood cells and 10 adult females (as well as a smaller number of adult males). The nests of *Microstigmus* are unique among apoid wasps, that of *M. comes* consisting of a 1–3 cm deep bag of plant fibers embedded in a matrix of silk and suspended from the underside of a leaf by a short, coiled petiole. Other *Microstigmus* create similar nests, but embedding small pieces of bark, wood, leaf hairs, lichens, sand, or stone in the silk mesh. The use of silk produced by adults in nest construction is limited among apoid wasps to *Microstigmus* and other Pemphredoninae (e.g., *Arpactophilus*, *Psenulus*); however, larval apoid wasps commonly incorporate silk into their cocoons. Finally, whereas other social insects build nests gradually, expanding their size over time, *Microstigmus* construct their silken abodes all at once and so are limited to their confines until all cells in the nest are completed.

Mating Strategies

In 1960, a comprehensive review of the diversity of male apoid wasp behavior would have occupied a brief paragraph, but we now have a much better understanding of male behavior. Perhaps the best-known male behaviors are the so-called “sun dances” of sand wasps (Bembicinae) in which hundreds or thousands of males swarm over the surface of nesting areas seeking newly emerged virgin females (as in many species of *Bembix*). A variation on this theme sees males attempting to rendezvous with females at the point at which they emerge from the ground when they leave their natal nests (e.g., *Bembecinus quinquespinosus*, *Bembix rostrata*, and *Glenostictia satan*).

In other species, males defend discrete territories that are often plots of ground in emergence or nesting areas, as is the case for *Sphecius* (cicada-killers) and many *Philanthus* (beewolves). Or males may defend individual nests that are in the process of being provisioned by females (as in some *Trypoxylon* and *Oxybelus*, for example). Less commonly, males establish territories at hunting sites frequented by females (e.g., *Aphilanthops subfrigidus* which defend territories in mating swarms of prey, and *Mellinus rufinodus* which defend feces that attract flies hunted by females). In yet other species, territories are situated in locations that have no other apparent attractiveness to females other than the presence of the males themselves (e.g., *Eucerceris flavocincta*, *Philanthus basilaris*). While defending their territories, male wasps may engage in rowdy battles that involve, depending on the species, wrestling, biting, head butting, abdomen slapping, or mutual flights in which the contestants swirl about one another at dizzying speeds. One should not be left with the impression, however, that males of any given species have just one way to find a mate, as alternative mating tactics are common. Male *Stictia heros*, for example, may patrol the nesting area in the morning, but shift to defending territories later in the day. And some males of *Philanthus zebratus* patrol the air space above the nesting area, while others simultaneously defend scent-marked territories nearby.

Ultimately, it appears that in most cases it is the females that control which males are successful. Females, after all, are usually the larger sex, so are physically dominant to males (and in the case of *Philanthus basilaris*, may even prey upon them). So mating is sometimes, though not always, preceded by obvious courtship activities during which the male induces the female to copulate. This, however, is one of the least-studied aspects of apoid wasp reproductive biology.

Economic Significance of Apoid Wasps

A least one genus of apoid wasps, *Larra*, whose females prey on mole crickets, includes species that have found some success as biological control agents. Other genera contain species that may provide some natural control of pests such as aphids (*Passaloecus*), biting flies (*Bembix*, *Stictia*), cutworms (*Podalonia*), grasshoppers (*Prionyx*, *Tachysphex*), Mormon crickets (*Palmodes*), and leafhoppers (many genera). On the negative side of the ledger, apoid wasps can be a nuisance to those people that cannot abide the presence of a wasp, no matter what its activities. In North America, large territorial males of the cicada-killer wasp, *Sphecius speciosus*, sometimes bother homeowners and park visitors who mistake male investigatory flights for something more hostile. The large nest mounds of female cicada-killers that appear in otherwise immaculate lawns are considered unsightly by some. In Africa, *Palarus latifrons* and *Philanthus triangulum* can be outright pests when large numbers of females invade apiaries and decimate worker honey bee populations. And we know very little about the potential effect of apoid wasp predators on the biology of other beneficial insects such as native pollinators and biological control agents.

► Wasps, Ants, Bees and Sawflies
► Bees

References

Bohart RM, Menke AS (1976) Sphecid wasps of the world: a generic revision. University of California Press, Berkeley, CA, pp 695

Evans HE (1966) The comparative ethology and evolution of the sand wasps. Harvard University Press, Cambridge, MA, pp 526

Evans HE, O'Neill KM (1988) The natural history and behavior of North American beewolves. Cornell University Press, Ithaca, NY, pp 278
Evans HE, O'Neill KM (2007) The sand wasps: behavior and natural history. Harvard University Press, Cambridge, MA, pp 340
Goulet H, Huber JT (1993) Hymenoptera of the world: an identification guide to families. Research Branch, Agriculture Canada, Publication 1894/E. Centre for Land and Biological Resources Research, Ottawa, Canada, pp 668
Grimaldi D, Engel MS (2005) Evolution of the insects. Cambridge University Press, New York, NY, pp 772
Krombein KV (1967) Trap-nesting wasps and bees: life histories, nests, and associates. Smithsonian Press, Washington, DC, pp 570.
Matthews RW (1991) Evolution of social behavior in the sphecid wasp. In Ross KG, Matthews RW (eds) The social biology of wasps. Cornell University Press, Ithaca, NY, pp 570–602
Michener CD (2000) The bees of the world. The Johns Hopkins University Press, Baltimore, MD, 913 pp
Melo GAR (1999) Phylogenetic relationships and classification of the major lineages of Apoidea (Hymenoptera), with emphasis on the crabronid wasps. Natural History Museum, University of Kansas, Scientific Papers 12:1–55
Melo GAR, Gonçalves RB (2005) Higher-level bee classifications (Hymenoptera, Apoidea, Apidae sensu lato). Revista Brasileira de Zoologia 22:153–159
Ohl M, Bleidorn C (2006) The phylogenetic position of the enigmatic family Heterogynaidae based on molecular data, with description of a new, nocturnal species (Hymenoptera: Apoidea). Syst Entomol 31:321–337.
O'Neill KM (2001) Solitary wasps: natural history and behavior. Cornell University Press, Ithaca, NY, pp 406
Pulawski WJ (2007) Catalog of the Sphecidae sensu lato (=Apoidea excluding Apidae). California Academy of Sciences. Available at http://www.calacademy.org/research/entomology/Entomology_Resources/Hymenoptera/sphecidae/Genera_and_species_PDF/introduction.htm
Tree of Life Web Project (1995) Apoidea. Bees, digger wasps. Version 01 January 1995 (temporary). http://tolweb.org/Apoidea/11190/1995.01.01 *in* The Tree of Life Web Project. Available at http://tolweb.org/

Apolysal Space

During molting, a very small space is created by the separation of the epidermis from the old cuticle. This space, called the apolysal space, contains molting fluid during the process of cuticle digestion.

Apolysis

Separation of the epidermal cells from the inner surface of the endocuticle. This is the first step in the process of molting.

Apomorphic

A character that is derived and not ancestral.

Apomorphy

When considering classification and phylogeny, a derived character state.

Apophysis

An internal or external elongate projection of the body wall.

Apoprogonidae

A family of moths (order Lepidoptera). They also are known as African skipper moths.

► African Skipper Moths
► Butterflies and Moths

Aposematism

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Aposematism is a strategy used by many organisms that increases their conspicuousness, and alerts or warns potential predators of their toxicity, their ability to inflict pain or, more simply, their unpredictability. Insects have evolved this strategy to a high degree, although it is found occasionally in other terrestrial organisms such as snakes, lizards, and frogs, and in aquatic organisms such as nudibranches. Aposematic signals usually are visual in nature and involve bright and contrasting coloration, usually black and red, yellow or orange or black and white. Visual signals may be enhanced by certain odors, sounds or behaviors, presenting a multimodal signal that predators may recognize and learn more easily.

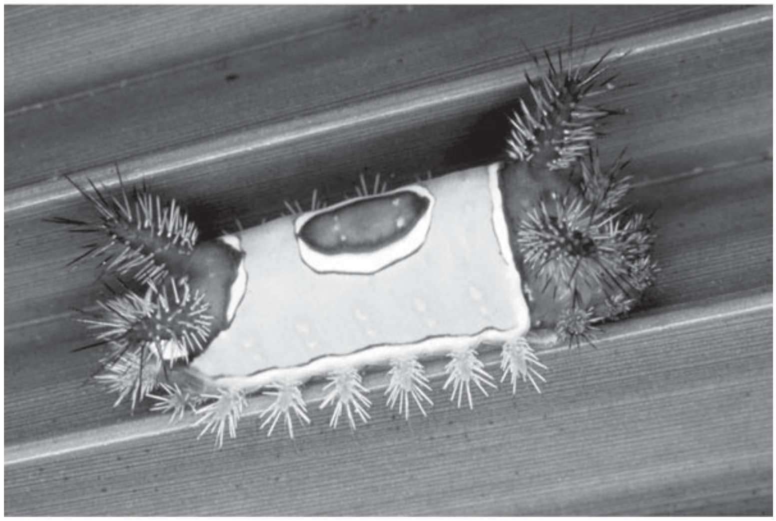
Visual aposematism as an antipredator strategy only works well against predators with color vision and good learning ability. Birds, and to a lesser extent lizards and amphibians, are the most common predators for which aposematic coloration (Figs. 66 and 67) is an effective deterrent. The naïve predator associates the particular color pattern of an aposematic organism with the unpleasant after effects of eating or attempting to eat it. Aposematic insects usually back up their warning signal with chemical defenses (unless they are harmless mimics of another toxic organism). These chemical defenses may be toxins that are stored inside the insect's body that could cause death if ingested and absorbed by the predator. However, the toxins themselves often are emetic (for example, cardiac glycosides in the Monarch butterfly, *Danaus plexippus*, and lucibufagins in *Photinus* fireflies), meaning that they cause the predator to regurgitate the prey item before a lethal dose of the toxin has been absorbed. The toxins also are often bitter so that the predator is less likely to pursue the attack once the bitter compounds have been contacted. In other insects, toxins are not stored within the body but are injected into predators through sharp urticating hairs or spines (for example, larvae of the saddleback moth, (Fig. 68) *Sibine stimulea*). In these insects, the predator is warned of the prey item's distastefulness without having to breach the cuticle of the aposematic organism.

The naïve predator may need only one trial to associate the color pattern of the aposematic insect with emesis or a bitter taste but more often, learning takes several trials. The speed of learning can be enhanced in several ways. If the predator encounters several toxic insects with the same aposematic pattern within a short period of time, it appears to learn the warning

Aposematism, Figure 66 **Aposematic insects are often aggregated, perhaps increasing the rate at which predators associate aposematic coloration with toxicity. The orange and black larvae of the oleander caterpillar, *Syntomeida epilais* (Ctenuchidae), aggregate in the early instars on oleander, *Nerium oleander*, a plant containing heart poisons (cardiac glycosides) (photo by James Castner).**

Aposematism, Figure 67 **The black and white larvae of the Giant African Skipper (Hesperiidae) also aggregate on their host plant (photo by Andrei Sourakov).**

coloration faster. This may explain why aposematic insects are often gregarious, living in small, usually related, groups. For example, oleander caterpillars, *Syntomeida epilais* and oleander aphids, *Aphis nerii* live gregariously on oleander which contains heart poisons. Other factors that can increase the rate of learning are the pairing of the visual pattern with acoustic signals or olfactory signals. Many aposematic insects hiss, stridulate or make some other noise when predators attack them. Arctiic moths and lubber grasshoppers, *Romalea guttata*, commonly do this. The association of sound with the color pattern and bitter chemical toxins in the aposematic



Aposematism, Figure 68 **Larvae of the saddleback moth, *Sibine stimulea* (Limacodidae), advertise their urticating hairs with a pronounced brown and white "saddle" on the lime-green bodies (photo by James Castner).**

insects help the predator better remember the color pattern. We are becoming increasingly aware that many insects release volatile pyrazine compounds when under attack. These nitrogen-containing compounds are extremely odorous at low concentrations and are thought to produce a universal warning odor in plants and animals.

Insects that are aposematic often exhibit what we might call bold behavior, at least for an insect. They are usually active during the day and are not cryptic, rather feeding in an exposed position. Aposematic adults may have an exaggerated slow flight, as do *Heliconius* butterflies and many arctiid moths. Larvae may wave tentacles and other long protuberances from their body to warn predators. Larvae of the Monarch butterfly (Fig. 69) integrate aposematic behaviors into their multimodal signal to warn of their toxicity. In addition to being conspicuously striped white, yellow and black, they release pyrazine from the head collar region when roughly handled and nod their heads up and down every 2 s while simultaneously twitching their anterior filiform tentacles.

► Allelochemicals
► Mimicry
► Chemical Ecology

References

Guilford T, Nicol C, Rothschild M, Moore BP (1987) The biological roles of pyrazines: evidence for a warning odour function. Biol J Linn Soc 31:113–128

Guildford T (1990) The evolution of aposematism. In: Evans DL, Schmidt JO (eds) Insect defenses: adaptive mechanisms and strategies of prey and predators. State University of New York Press, New York, NY, pp 23–61

Huheey JE Bell WJ, Cardé RT (eds) (1984) Chemical ecology of insects. Sinauer Associates, Inc., Sunderland, MA, pp 257–297

Rothschild M, Bergström G (1997) The monarch butterfly caterpillar (*Danaus plexippus*) waves at passing Hymenoptera and jet aircraft-are repellent volatiles released simultaneously? Phytochemistry 45:1139–1144

Rowe C (2002) Sound improves visual discrimination learning in avian predators. Proc R Soc Biol Sci B 269:1353–1357

Aposymbiotic

Separated from its symbiotes, or symbiote-free; this usually refers to mutualistic symbiotes.

(a)

Aposematism, Figure 69 **Larvae of the Monarch butterfly, *Danaus plexippus* (Danaidae), use a multimodal signal to warn potential predators. Their aposematic coloration of black, white, and yellow stripes is enhanced with the release of pungent pyrazine and the behavioral display involving rhythmic nodding of the head and twitching of the filiform tentacles (photo by Lyle Buss).**

Apotome

A narrow anterior portion of each abdominal sternum, separated by a fold from the rest of the plate. They are present in Apterygota, but indistinct in Pterygota.

► Abdomen of Hexapods

Apparent Resources

Food resources (either insect or plant) that are "easy to locate" or apparent to potential predators or herbivores. Apparent resources often are protected against consumption by generalist and specialist predators, and generalist or specialist herbivores, by possessing broadly effective (though metabolically expensive) chemical defenses such as digestibility reducing substance (contrast with unapparent resources).

Appeasement Substance

A secretion presented by a social parasite that reduces aggression by the host insects, and aids parasites in being accepted as members of the colony.

Apple Maggot

► Apple Pests and their Management

Apple Pests and their Management

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Insects with chewing mouthparts inflict great damage on foliage, causing leaves to be skeletonized, riddled with holes, eaten around the edges, or entirely consumed (e.g., larvae of moths, sawflies, and beetles). Other insects suck sap from leaves, stems, or other plant parts, producing a characteristic spotting or browning, curling, or wilting. Feeding on stems or twigs results in dwarfing or wilting. Damage is caused both by removal of the sap and by injury to the plant tissue (e.g., scale insects, aphids, and true bugs). Also included in this category (Fig. 70) are mites, such as the European red mite and the two-spotted spider mite, which damage the leaves by piercing the cell walls with bristle-like mouthparts and ingesting their contents, including the chlorophyll. The injury results in off-color foliage that, in severe cases, becomes bronzed.

Scale insects are usually minute, but if they are abundant enough to encrust bark, twigs, or stems they can kill orchard and shade trees. Aphids produce a curling of the leaves and, when feeding on fruit, may cause it to be stunted or misshapen and may change the sugar content, greatly impairing the flavor.

Many insects feed as miners in leaves or as borers in stems, roots, or fruits. Feeding between the upper and lower surfaces of the leaf may cause as much defoliation as external feeding. There are about 500 leafmining species in the United States (e.g., spotted tentiform and apple blotch leafminers).

Tunneling causes serious damage. Insects that tunnel into fruit include codling moth, oriental fruit moth, apple maggot, and plum curculio. Damage with more serious consequences can be done by insects that tunnel into the tree trunk, bark, or foliar shoots, such as apple-boring beetles (roundheaded, flatheaded), dogwood borer, American plum borer, European corn borer, and oriental fruit moth.

Injection of a chemical into plant tissues while the insect feeds causes abnormal growth (e.g., rosy apple aphid) or produces a gall (woolly apple aphid). Each species of gall insect produces a characteristic gall on a certain part of a particular plant.

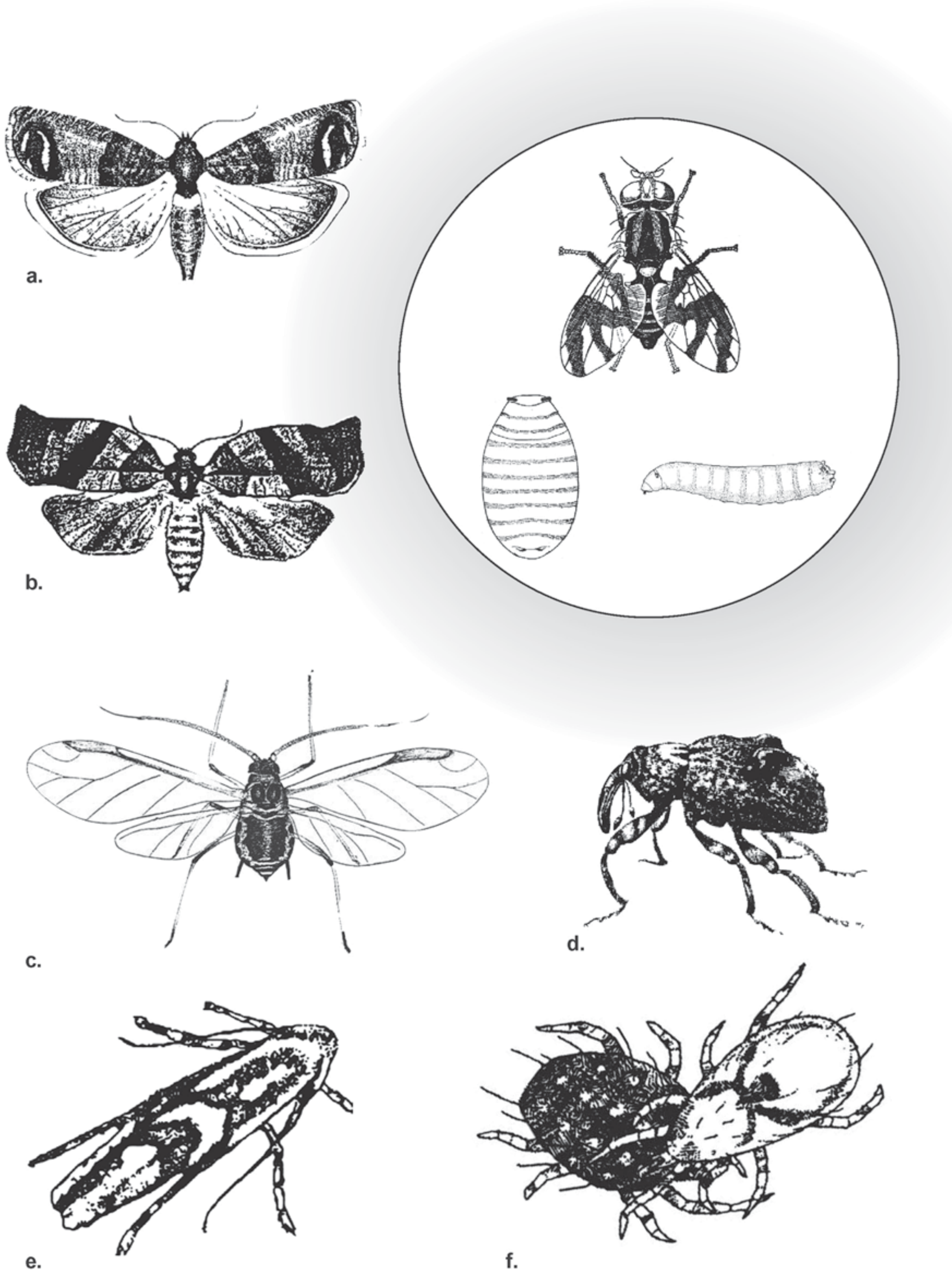
Insects at the larval and nymphal stages (e.g., woolly apple aphid) that live in the soil and attack the underground plant parts cause extensive damage.

Shelters in plants are built by leafrollers and leaf folders, which roll or fold the leaves and tie them with silk, feeding in the shelter so formed. Leaf tiers and webworms tie several leaves or even entire branches together, producing large silken webs or tents.

A few insects injure plants when they lay their eggs, particularly in stems or fruits (e.g., plum curculio, apple maggot, periodical cicadas, tree crickets, leafhoppers).

Major Economic Pests

Early researchers in New York estimated nearly 500 species of insects known to feed on apple. Fortunately, only a relatively small number of these ever reach economic pest status. A survey conducted in the northeastern U.S. identified a



Apple Pests and their Management, Figure 70 **Some North American apple pests: (a) codling moth; (b) obliquebanded leafroller; (c) rosy apple aphid; (d) plum curculio; (e) spotted tentiform leafminer; (f) European red mite attacked by predatory mite; within circle, apple maggot adult, larva and pupa.**

total of 191 phytophagous (plant-feeding) insect species in managed and abandoned apple orchards. Most numerous were species of Lepidoptera (mostly moths and their caterpillars, 43%) and Hemiptera (leafhoppers, plant bugs, aphids and scale insects, 32%). Current tabulations of actual economic pests list just over 60 species in New York, approximately half of which are considered important enough to warrant specific control recommendations. This compares with 17 pest species for pear, 12 for peach, and seven for tart cherry and plum. A similar accounting in other production regions reveals certain species with a worldwide distribution, and others, largely representing the above major orders, that are prevalent only in specific areas (Table 9). The following are some of the key pests in the northeastern U.S. growing regions.

Rosy Apple Aphid, *Dysaphis plantaginea* (Passerini)

Biology and Impact

The rosy apple aphid is the most damaging of the aphids that attack apple. Its saliva, injected while feeding, is translocated to nearby fruit, causing leaf curling and small, deformed apples. The rosy apple aphid can be distinguished from other aphids by its long cornicles and purple-rose color. It overwinters as an egg on twigs, in bud axils, and in bark crevices. The overwintering eggs of the rosy apple aphid are oblong and pale green at first, then turn shiny black. Rosy apple aphid nymphs are visible beginning around the tight cluster bud stage but are most easily observed at the pink bud stage. The first adults appear around bloom. Second-generation adults appear two to three weeks after petal fall. Some of these move to alternate hosts (such as narrowleaf plantain) and the rest remain in the orchard. The third generation develops by mid-July and moves to alternate hosts. In later summer, adult rosy apple aphids return to the trees to lay eggs.

Decision Making

Because rosy apple aphid populations are highly variable, it is important to assess their densities before making a treatment. Sampling can begin at the tight cluster bud stage but is better done at the pink stage when rosy apple aphid nymphs are more easily seen. Rosy apple aphid densities are estimated by sampling 10 fruit clusters from the interior canopy area of 10 trees. Treatment is generally recommended if one infested cluster is found, but for experienced samplers of rosy apple aphids, this is probably too conservative and a threshold of three to five infested clusters would be more appropriate.

Control

It is not known how important natural enemies (such as larvae of the fungus gnats, Cecidomyiidae) are in regulating rosy apple aphid populations. Several pesticides can effectively control this pest when applied at the pink bud stage. A material should be used that will conserve natural enemy populations, such as *Typhlodromus pyri*, an important mite predator.

Spotted Tentiform Leafminer, *Phyllonorycter blancardella* (Fabricius)

Biology and Impact

The spotted tentiform leafminer was introduced from Europe in the 1880s. Its host plants include apple, wild cherry, hawthorn, quince, plum, and crabapple. Spotted tentiform leafminer overwinters as a pupa in leaf litter on the ground. Adults emerge at the green tip apple bud stage and lay small, flattened eggs that are deposited singly on leaf undersides. Egg laying begins when leaves unfold after the half-inch green bud stage, and deposition is nearly complete by the end of the pink bud stage. Its five larval stages are divided

Apple Pests and their Management, Table 9 **Major insect and mite pests of apple**

Taxon scientific and common name	Geographical distribution	Plant parts affected
Acari: Eriophyidae		
Aculus schlechtendali (Nalepa), apple rust mite	North America, South America, Europe, Australia/New Zealand	Foliage
Eriophyes pyri (Pagenstecher), pearleaf blister mite	North America, South Africa	Foliage
Acari: Tetranychidae		
Bryobia praetiosa Koch, clover mite	North America	Foliage
Bryobia rubrioculus (Scheuten), brown mite	Worldwide	Foliage
Panonychus ulmi (Koch), European red mite	Worldwide	Foliage
Tetranychus canadensis (McGregor), fourspotted spider mite	North America	Foliage
Tetranychus kanzawai Kishida, kanzawa mite	Asia	Foliage
Tetranychus mcdanieli McGregor, McDaniel spider mite	North America	Foliage
Tetranychus urticae Koch, two spotted spider mite	Worldwide	Foliage
Tetranychus viennensis Zacher, hawthorn spider mite	Asia	Foliage
Coleoptera: Bostrichidae		
Amphicerus bicaudatus (Say), apple twig borer	North America	Twigs, Wood
Coleoptera: Buprestidae		
Chrysobothris femorata (Olivier), flatheaded appletree borer	North America	Cambium, Wood
Coleoptera: Cerambycidae		
Prionus imbricornis (Linnaeus), tilehorned prionus	North America	Cambium, Roots
Prionus laticollis (Drury), broad necked root borer	North America	Cambium, Roots
Saperda candida Fabricius, roundheaded appletree borer	North America	Cambium, Wood
Coleoptera: Chrysomelidae		
Nodonota puncticollis (Say), rose leaf beetle	North America	Fruit
Coleoptera: Curculionidae		
Anthonomus pomorum (Linnaeus), apple blossom weevil	Europe, Asia	Buds
Anthonomus quadrigibbus Say, apple curculio	North America	Foliage, Fruit
Conotrachelus nenuphar (Herbst), plum curculio	North America	Fruit

Apple Pests and their Management, Table 9 **Major insect and mite pests of apple (Continued)**

Taxon scientific and common name	Geographical distribution	Plant parts affected
Naupactus xanthographus (Germar), grape snout beetle	South America	Buds, Foliage
Phlyctinus callosus Boheman, banded fruit weevil	South Africa	Fruit
Scolytus rugulosus (Müller), shothole borer	North America	Cambium, Wood
Coleoptera: Scarabaeidae		
Macrodactylus subspinosus (Fabricius), rose chafer	North America	Foliage, Fruit
Popillia japonica Newman, Japanese beetle	North America	Foliage, Fruit
Dermaptera: Forficulidae		
Forficula auricularia Linnaeus, European earwig	Europe	Fruit
Diptera: Agromyzida		
Liriomyza brassicae (Riley), serpentine leafminer	North America	Foliage
Diptera: Cecidomyiidae		
Dasineura mali (Kieffer), apple leafcurling midge	North America, Europe, Australia/New Zealand	Foliage
Diptera: Tephritidae		
Anastrepha fraterculus (Weidemann), S. American fruit fly	South America	Fruit
Bactrocera tryoni (Froggatt), Queensland fruit fly	South America, Australia/New Zealand	Fruit
Ceratitis capitata (Wiedemann), Mediterranean fruit fly	South Africa	Fruit
Ceratitis rosa Karsch	South Africa	Fruit
Rhagoletis pomonella (Walsh), apple maggot	North America	Fruit
Hemiptera: Miridae		
Atractotomus mali (Meyer), apple brown bug	North America	Fruit
Campylomma liebknechti (Girault), apple dimpling bug	Australia/New Zealand	Fruit
Campylomma verbasci (Meyer), mullein plant bug	North America, Europe	Fruit
Lygidea mendax Reuter, apple red bug	North America	Foliage, Fruit
Lygocoris pabulinus (Linnaeus)	Europe	Fruit
Lygus lineolaris Palisot de Beauvois, tarnished plant bug	North America	Fruit
Plesiocoris rugicollis Fallén	Europe	Fruit
Hemiptera: Pentatomidae		

Apple Pests and their Management, Table 9 Major insect and mite pests of apple (Continued)

Taxon scientific and common name	Geographical distribution	Plant parts affected
Antestiopsis orbitalis Ghesquierei Car., antestia bug	South Africa	Fruit
Heteroptera: Tingidae		
Stephanitis pyri Fabricius	Europe	Foliage
Hemiptera: Aphididae		
Aphis pomi DeGeer, apple aphid	North America, South America, Europe	Foliage, Fruit
Aphis spiraecola Patch, spirea aphid	North America, South America, South Africa, Asia	Foliage
Dysaphis plantaginea (Passerini), rosy apple aphid	North America, Europe	Foliage, Fruit
Eriosoma lanigerum (Hausmann), woolly apple aphid	Worldwide	Roots, Twigs
Myzus malisuctus Matsumura, apple leafcurling aphid	Asia	Foliage
Rhopalosiphum fitchii (Sanderson), apple grain aphid	North America, South America	Buds, Foliage
Schizaphis piricola Matsumura	Asia	Foliage
Hemiptera: Cicadellidae		
Edwardsiana crataegi (Dg.), apple leafhopper	South America	Foliage
Edwardsiana frogatti Baker	Europe	Foliage
Edwardsiana rosae (Linnaeus), rose leafhopper	North America	Foliage
Empoasca fabae (Harris), potato leafhopper	North America	Foliage
Empoasca maligna (Walsh), apple leafhopper	North America	Foliage
Typhlocyba pomaria McAtee, white apple leafhopper	North America	Foliage, Fruit
Hemiptera: Cicadidae		
Magicicada septendecim (Linnaeus), periodical cicada	North America	Twigs, Wood
Hemiptera: Coccidae		
Parthenolecanium corni (Bouché), European fruit lecanium	North America	Wood, Fruit
Hemiptera: Diaspididae		
Aonidiella aurantii (Maskell), California red scale	North America, South Africa	Twigs, Wood
Chionaspis furfura (Fitch), scurfy scale	North America	Cambium, Fruit

Apple Pests and their Management, Table 9 **Major insect and mite pests of apple (Continued)**

Taxon scientific and common name	Geographical distribution	Plant parts affected
Epidiaspis leperii (Signoret), Italian pear scale	South America, Europe	Cambium
Hemiberlesia lataniae (Signoret), latania scale	South America	Cambium
Lepidosaphes ulmi (Linnaeus), oystershell scale	North America, South America, Europe	Cambium
Quadraspidiotus forbesi (Johnson), Forbes scale	North America	Cambium
Quadraspidiotus perniciosus (Comstock), San Jose scale	Worldwide	Cambium, Fruit
Hemiptera: Flatidae		
Metcalfa pruinosa (Say)	Europe	Fruit
Hemiptera: Margarodidae		
Icerya purchasi Maskell, cottony cushion scale	South Africa	Wood, Twigs, Fruit
Hemiptera: Membracidae		
Stictocephala bisonia Kopp & Yonke, buffalo treehopper	North America, Europe	Twigs, Wood
Hemiptera: Pseudococcidae		
Pseudococcus calceolariae (Maskell), citrophilus mealybug	Europe, Australia/New Zealand, South Africa	Fruit
Pseudococcus comstocki (Kuwana), Comstock mealybug	North America	Foliage, Fruit
Hemiptera: Psyllidae		
Cacopsylla mali (Schmidberger), apple sucker	North America, Europe	Foliage
Hymenoptera: Tenthredinidae		
Hoplocampa testudinea (Klug), European apple sawfly	North America, Europe	Fruit
Lepidoptera: Arctiidae		
Hyphantria cunea (Drury), fall webworm	North America, Europe, Asia	Foliage
Lophocampa caryae Harris, hickory tussock moth	North America	Foliage
Lepidoptera: Carposinidae		
Carposina niponensis Walshingham, peach fruit moth	Asia	Fruit
Carposina sasakii Matsumura, peach fruit moth	Asia	Fruit
Lepidoptera: Choreutidae		
Choreutis pariana (Clerck), apple-and-thorn skeletonizer	North America, Europe, Asia	Foliage

Apple Pests and their Management, Table 9 **Major insect and mite pests of apple (Continued)**

Taxon scientific and common name	Geographical distribution	Plant parts affected
Lepidoptera: Coleophoridae		
Coleophora multipulvella (Chambers), pistol casebearer	North America, Asia	Foliage, Fruit
Coleophora serratella (Linnaeus), cigar/birch casebearer	North America, Europe, Asia	Foliage
Lepidoptera: Cossidae		
Cossus cossus Linnaeus, European goat moth	North America, Europe, Asia	Cambium, Wood
Zeuzera pyrina Linnaeus, leopard moth	North America, Europe, Asia	Wood, Twigs
Lepidoptera: Geometridae		
Alsophila pometaria (Harris), fall cankerworm	North America	Foliage
Operophtera brumata Linnaeus, winter moth	North America, Europe, Asia	Buds, Foliage, Fruit
Paleacrita vernata (Peck), spring cankerworm	North America	Foliage
Lepidoptera: Gracillariidae		
Marmara elotella (Busck), apple barkminer	North America	Cambium
Marmara pomonella Busck, apple fruitminer	North America	Fruit
Phyllonorycter blancardella (Fabricius), spotted tentiform leafminer	North America, Europe, Asia	Foliage
Phyllonorycter crataegella (Clemens), apple blotch leafminer	North America	Foliage
Phyllonorycter elmaella Doganlar & Mutuura, western tentiform leafminer	North America	Foliage
Phyllonorycter ringoniella (Matsumura), apple leafminer	Asia	Foliage
Lepidoptera: Lasiocampidae		
Malacosoma americanum (Fabricius), eastern tent caterpillar	North America	Foliage
Lepidoptera: Lymantriidae		
Euproctis chrysorrhoea (Linnaeus), browntail moth	North America, Europe, Asia	Foliage
Lymantria dispar (Linnaeus), gypsy moth	North America, Europe, Asia	Foliage
Orgyia antiqua (Linnaeus), rusty tussock moth	North America, South America, Europe, Asia	Buds, Foliage
Orgyia leucostigma (J.E. Smith), whitemarked tussock moth	North America	Foliage, Fruit
Lepidoptera: Lyonetiidae		
Bucculatrix pomifoliella (Clemens), apple bucculatrix	North America	Foliage

Apple Pests and their Management, Table 9 **Major insect and mite pests of apple (Continued)**

Taxon scientific and common name	Geographical distribution	Plant parts affected
Leucoptera malifoliella (Costa), pearleaf blister moth	Europe, Asia	Foliage
Lyonetia prunifoliella (Hübner), apple lyonetid	North America, Europe, Asia	Foliage
Lyonetia speculella Clemens, apple leafminer	North America	Foliage
Lepidoptera: Noctuidae		
Amphipyra pyramidoides Guenée, humped green fruitworm	North America	Foliage, Fruit
Helicoverpa armigera (Hübner), cotton bollworm	Europe, Asia, South Africa	Fruit
Lacanobia subjuncta (Grote & Robinson), Lacanobia fruitworm	North America	Foliage, Fruit
Lithophane antennata (Walker), green fruitworm	North America	Fruit
Orthosia hibisci (Guenée), speckled green fruitworm	North America	Foliage, Fruit
Xestia c-nigrum (Linnaeus), spotted cutworm	North America, Europe, Asia	Foliage
Lepidoptera: Notodontidae		
Datana ministra (Drury), yellownecked caterpillar	North America	Foliage
Schizura concinna (J. E. Smith), redhumped caterpillar	North America	Foliage
Lepidoptera: Pyralidae		
Conogethes punctiferalis (Guenée), yellow peach moth	Asia, Australia/New Zealand	Fruit
Euzophera semifuneralis (Walker), American plum borer	North America	Cambium, Wood
Ostrinia nubilalis (Hübner), European corn borer	North America, South America, Europe, Asia	Foliage, Fruit
Lepidoptera: Sesiidae		
Podosesia syringae (Harris), lilac/ash borer	North America	Cambium, Wood
Synanthedon myopaeformis Borkhausen, apple clearwing moth	Europe, Asia	Cambium, Wood
Synanthedon pyri (Harris), apple bark borer	North America	Cambium, Wood
Synanthedon scitula (Harris), dogwood borer	North America	Cambium, Wood
Lepidoptera: Tisheriidae		
Tischeria malifoliella Clemens, apple trumpet leafminer	North America	Foliage
Lepidoptera: Tortricidae		

Apple Pests and their Management, Table 9 Major insect and mite pests of apple (Continued)

Taxon scientific and common name	Geographical distribution	Plant parts affected
Adoxophyes orana Fischer Von Röslerstamm, summer fruit tortrix	South America, Europe, Asia	Fruit
Archips argyrospila (Walker), fruittree leafroller	North America	Foliage, Fruit
Archips podana Scopoli, fruittree tortrix	North America, Europe, Asia	Foliage, Fruit
Archips rosana (Linnaeus), rose tortrix	North America, Europe, Asia	Fruit
Argyrotaenia citrana (Fernald), orange tortrix	North America	Fruit
Argyrotaenia pulchellana Haworth	Europe	Foliage, Fruit
Argyrotaenia velutinana (Walker), redbanded leafroller	North America	Foliage, Fruit
Choristoneura rosaceana (Harris), obliquebanded leafroller	North America, South America	Foliage, Fruit
Cydia lobarzewskii Nowicki	Europe	Fruit
Cydia pomonella (Linnaeus), codling moth	Worldwide	Fruit
Epiphyas postvittana (Walker), light brown apple moth	Europe, Australia/New Zealand	Foliage, Fruit
Grapholita molesta (Busck), oriental fruit moth	Worldwide	Fruit, Foliage, Twigs
Grapholita prunivora (Walsh), lesser appleworm	North America	Fruit
Hedya dimidioalba (Retzius), marbled orchard tortrix	North America, Europe, Asia	Buds, Foliage
Pandemis heparana Denis & Schiffermüller, fruittree tortrix	North America, Europe, Asia	Foliage, Fruit
Pandemis limitata (Robinson), threelined leafroller	North America	Foliage, Fruit
Platynota flavedana Clemens, variegated leafroller	North America	Foliage, Fruit
Platynota idaeusalis (Walker), tufted apple budmoth	North America	Foliage, Fruit
Proeulia auraria (Clarke), fruit leaf folder	South America	Foliage, Fruit
Pseudexentera mali Freeman, pale apple leafroller	North America	Foliage, Fruit
Sparganothis sulfureana Clemens, Sparganothis fruitworm	North America	Foliage, Fruit
Spilonota ocellana (Denis & Schiffermüller), eyespotted bud moth	North America, Europe, Asia	Foliage, Fruit
Tortrix capensana (Walker)	South Africa	Foliage, Fruit
Orthoptera: Gryllidae		

Apple Pests and their Management, Table 9 **Major insect and mite pests of apple (Continued)**

Taxon scientific and common name	Geographical distribution	Plant parts affected
Oecanthus fultoni Walker, snowy tree cricket	North America	Cambium, Wood, Twigs
Thysanoptera: Thripidae		
Frankliniella occidentalis (Pergande), western flower thrips	North America, Europe	Foliage, Fruit
Taeniothrips inconsequens (Uzel), pear thrips	North America, South America, Europe	Buds

into sap-feeders (instars 1–3) and tissue-feeders (instars 4–5). The second-generation adults begin emerging in early June in the northeastern states (average date is June 13 ± 8 days), and larvae are usually present in early July. Third-generation larvae are usually present in late August.

The spotted tentiform leafminer damages only foliage, which the larvae eat and mine. This causes reduced photosynthesis and possibly sequestered nutrients. Foliar damage can cause smaller fruit size, premature drop, and poor color. Damage caused by the second generation is usually of the greatest concern. Third-generation leafminers usually are not a problem if the second generation was controlled properly.

Decision Making

A sequential sampling plan can be used to classify spotted tentiform leafminer egg density at the pink stage or the density of sap-feeding mines immediately after petal fall. Treatment is recommended if eggs average 2 or more per leaf on leaves 2, 3, and 4 of a fruit cluster at the pink stage, or if sap-feeding mines average 1 or more per leaf on these leaves at petal fall. Sampling can be completed in approximately 10 min.

Proper timing is essential for both the assessment of second-generation leafminer densities and control, if required. If done too early, sampling will underestimate the population. If control is applied too late, it will not be effective. Sampling for "sap-feeding mines" should be done at approximately 690 degree-days (base 43°F) after the start of the flight of the second generation. On average, second-generation spotted tentiform leafminer moths begin flying in early to mid-June. A decision regarding the third generation is generally not required unless the density of the second brood exceeds two mines per leaf.

Control

Many parasitoids effectively limit spotted tentiform leafminer populations in some orchards. Most important are the wasps *Apanteles ornigis*, *Sympiesis marylandensis*, and *Pnigalio maculipes*. Insecticide sprays applied in July and August probably do the most harm to these natural enemies. Some leafminer pesticides are effective without being toxic to natural enemies such as mite predators. Depending on the product chosen, application can be made any time from initial egg deposition until the larvae enter the tissue-feeding stages.

Obliquebanded Leafroller, *Choristoneura Rosaceana* (Harris)

Biology and Impact

The oblique banded leafroller prefers plants in the Rosaceae family but will feed on many unrelated deciduous trees. This leafroller overwinters as a second-or third-instar larva on the tree within closely spun cocoons or hibernacula. Larvae become active in the spring when buds begin to open. As foliage pushes from the buds, larvae often tie leaves together and conceal themselves in the resulting chamber. Spring-generation moths emerge in early June in the northeast, with peak activity in mid-June. First-generation larvae complete their development in late July or early August. Summer-generation moths begin flying in early August. Second-generation larvae feed primarily on foliage, but may cause surface injury to fruit if they are very abundant. After feeding briefly, second-generation larvae enter their winter hibernacula.

Spring-generation larvae may eat away large portions of developing fruit. If the fruit survive, they are misshapen with large, deep cavities of healed-over injuries. Fruit damaged by first-brood larvae generally falls off the tree. If not controlled, this spring generation of obliquebanded leafroller may cause only small fruit losses (2–4%).

The principal impact of summer-generation obliquebanded leafroller is its feeding damage to the fruit. This generally occurs if a leaf is webbed to an apple or clustered apples touch each other. Feeding areas on the fruit are shallow, irregular, and may range from small punctures to large excavations. This injury is more serious than that caused by the overwintering generation because most injured fruits remain on the tree.

Decision Making

During bloom or immediately after petal fall, spring-generation larval densities can be classified as above or below a treatment threshold using a sequential sampling procedure. Treatment is recommended if more than 3% of fruit spurs contain live obliquebanded leafroller larvae. Sampling can usually be completed in approximately 10–15 min.

Sampling for the summer-generation larvae should take place approximately 600 DD (base 43°F) after the start of the first summer flight. On average, summer-generation obliquebanded leafroller moths start flying the first or second week of June. The value of knowing the precise date of this event on a local basis cannot be overemphasized. If information on adult moth flight is not available, July 5 to 10 is a rough approximation of the appropriate sampling period in the northeast. At 600 DD after the start of the adult flight, populations can be classified according to whether the average percentage of terminals infested with live larvae is greater than 3%.

Control

Several parasitoids attack the obliquebanded leafroller, but their effectiveness in regulating leafroller populations in commercial orchards is largely unknown. Most growers favor chemical sprays to reduce damage caused by this insect. A contact insecticide is sometimes applied at bloom to petal fall. Most orchards with a history of leafroller infestation require 1–2 pesticide applications against the second-generation larvae. Selective pesticides, including insect growth regulators and those that are based on the bacterium *Bacillus thuringiensis* are compatible with IPM because they are not toxic to natural enemies (especially mite predators).

European Red Mite, *Panonychus ulmi* (Koch)

Biology and Impact

The European red mite overwinters as an egg on the tree. Egg hatch is usually closely correlated with tree phenology, ordinarily beginning at the early pink bud stage and continuing into bloom. If egg hatch does not coincide with the pink stage, it is usually delayed and starts during early bloom. European red mite adults normally appear by petal fall, but few eggs are laid by the first generation of adults on leaves until the first week after petal fall. Early hatching European red mite nymphs feed on older fruit cluster leaves and may cause bronzing by petal fall if populations are high. Early season damage before petal fall is usually insignificant, but some studies have shown that heavy damage in early to mid-June can reduce yields during the next season.

In the summer months, the European red mite damages apple leaves by inserting its mouthparts to feed on plant juices. This injury reduces the capacity of the leaf to use sunlight as an energy source (photosynthesis), which may lead to reduced yield and fruit quality. Recent studies of European red mite impact have found that the only effect of moderate European red mite injury during the mid- to late season was a reduction in the color of some red varieties of apples. These results have identified the densities of mites that can be tolerated at various times of the growing season.

Decision Making

The natural mortality of overwintering eggs can be substantial but is highly variable (10–to 60%). Therefore, sampling or rating schemes are generally not used for predicting the potential early season severity of the European red mite in commercial orchards by assessing the density of overwintering eggs. During late bloom and petal fall, the European red mite is concentrated on older fruit cluster leaves, and therefore the overall density of the first generation will be overestimated by counting mites on the oldest leaves at that time.

Early control of the European red mite is essential to prevent early season damage during the postbloom period. One method used to quantify mite presence is the "mite-day" concept, which measures the number of mites and the period of time they are present on the leaves. One mite-day is equivalent to an average of one mite feeding on a leaf for one day. Thus 10 mite-days can be accrued by one mite feeding on a leaf for 10 days or 10 mites feeding for one day. The current economic threshold of approximately 550 total mite-days (for the growing season) assumes that no significant accumulations of mite-days occur before mid- to late June. Therefore, a protective prebloom oil treatment is currently recommended for control of early season European red mites.

During the summer, the need for a miticide to control the European red mite can be determined from a sample of the mite population in an orchard. A sampling procedure is available that determines mite presence based on examination of leaves of intermediate age. This procedure divides mite populations into three categories: greater than threshold, below threshold, and much below threshold. The last two categories provide an indication of when the population must be sampled again. If the density is much below threshold, the population should be sampled in 11–16 days. If it is minimally below threshold, it should be sampled again in 6–10 days. If mite predators are present, these intervals can be lengthened by approximately 50%.

Sampling involves recording on a chart the presence or absence of mites in distinct samples of leaves and continues until a decision on whether to treat them can be reached. From petal fall until June 30, a threshold of 2.5 mites per leaf is used. From July 1 to 31, the threshold is 5 mites per leaf. From August 1 to 15, a threshold of 7.5 mites per leaf is used. Treatment for mites is not currently recommended after mid-August. Adherence to these thresholds will prevent serious injury.

Control

The European red mite is an induced pest in commercial apple orchards. This means that pesticides used against other arthropods usually destroy naturally occurring mite predators, allowing European red mite numbers to increase to damaging levels. Several major predators of the

European red mite may be found in commercial orchards, depending on the part of the country where they are located:

Typhlodromus pyri (Scheuten)

Adults of *T. pyri*, a major predacious mite species, are present in the tree at about the time of the European red mite hatch. These predators control low to moderate densities of European red mites but do not regulate high populations. This mite predator is very effective against the European red mite and when present in substantial numbers it will eliminate the need for chemical mite control. *T. pyri* spends its entire life in the tree, overwinters as an adult female, and is active by bloom. It prefers to feed on the European red mite but will sustain itself on other food sources. Once established in an orchard, if it is not disrupted by pesticides, *T. pyri* will keep European red mite populations to densities of less than one mite per leaf year after year. It may take two to three years for *T. pyri* to become abundant in an orchard once a selective pesticide regimen is adopted.

Amblyseius fallacis (Garman)

A. fallacis is also an effective predator of the European red mite, but its continued presence in the tree from year to year is not reliable. It overwinters both in apple trees and in the ground cover beneath them. Ground cover, however, appears to have little influence on number and movement of *A. fallacis* in the tree. *A. fallacis* was previously believed to a poor biological control agent because it did not move into the trees until late in the growing season after the European red mite had reached problem levels. More likely, *A. fallacis* numbers often remain low until late in the season because pesticides toxic to them are used early in the season. If a site has a history of *A. fallacis*, pesticides should be managed to conserve it. Because *A. fallacis* remains in the tree year-round, even early season applications of pyrethroids are damaging to it.

Metaseiulus occidentalis (Nesbitt)

Predominantly found in drier climates such as the northwestern states, this predator can also provide biological control of the European red mite in commercial apple orchards. It has high reproductive and prey consumption rates, and disperses readily into orchards. However, it requires the presence of an alternative prey population in the orchard, such as apple rust mites, to preserve its population numbers when red mites are at low levels.

Zetzellia mali (Ewing)

This minute yellow mite is present in nearly all orchards, overwintering as a gravid female in concealed parts of the tree. Although it prefers older rust mites and the eggs and immature stages of European red mites and two spotted spider mites, it feeds on all stages of these species. It undoubtedly helps to control European red mites but is of little benefit if it is the sole predator species present.

Stethorus punctum (Leconte)

This small, black ladybird beetle feeds on several small arthropods, including European red mites. It is more common in orchards in the middle Atlantic states. Success in controlling European red mites depends on keeping a relatively high population of European red mites in the tree (3–5 mites per leaf).

For chemical control during the early season, petroleum oil is often recommended (a 2% solution at the half-inch green bud stage or 1% at the tight cluster stage) as an early season IPM program. Oil is relatively safe to predators, relatively economical, and European red mite populations have never shown resistance to it. Furthermore, a thorough application of oil applied before foliage is fully developed can kill nearly all the eggs present. Other early season treatment options include contact miticides or ovicides applied at the pink bud stage or at petal fall. Miticides will likely cover less of the foliage present by this time, and most are able to be overcome by the development of resistance in local mite populations, so this is a less desirable alternative.

Relatively few miticides can control European red mite during the summer. The available contact miticides must be chosen by their individual performance traits, including their activity against specific mite stages and beneficial arthropods, rate of action and length of residual effectiveness, optimal application conditions for each, and any possible resistance that may be exhibited by local mite populations. Because of the limitations of all contact miticides, good spray coverage is essential.

Some research has been done on the use of highly refined petroleum oils to control summer mite populations. Acceptable season-long control has been achieved by using a multiple-spray program starting at petal fall, followed by periodic monitoring throughout the summer. Potential difficulties with this approach include leaf damage and incompatibility with some of the fungicides used to control summer diseases.

Plum Curculio, *Conotrachelus nenuphar* (Herbst)

Biology and Impact

Plum curculio adults move into orchards from overwintering sites in hedgerows or the edges of woods and are present in the trees from the late pink stage to early bloom before the fruit is susceptible to damage. Adults are active in the spring when temperatures exceed 60°F. Adult females oviposit in fruit during both day and night but feed mostly at night. Depending on temperature, overwintering adults remain active for two to six weeks after petal fall.

Although adults may feed on blossoms, apples are not susceptible to damage until petal fall, at which time adults damage fruit by both feeding and ovipositing. Unlike fruit injured by other pests, many apples damaged by plum curculio will remain on the tree until harvest. Because adults are not highly mobile, orchards near overwintering sites, woodlands, and hedgerows are most susceptible to attack. Fruit damage is usually most common in border rows next to sites where adults overwinter.

Decision Making

Monitoring for the plum curculio is not often recommended because of the amount of time and labor involved and because it is generally assumed to be present in every orchard where populations are endemic. Nonetheless, various techniques have been used to monitor plum curculio damage and the presence of adults:

- Clubs or shakers can be used to jar adults from limbs into catching frames or cloths for counting.
- Polyethylene funnels hung under branches can be used to capture adult PC.
- Immature "scout apples" hung in trees near the edges of orchards serve to measure oviposition scars before petal fall so potential damage can be estimated before control sprays are applied.
- Oviposition scars on immature fruit can be counted in orchards starting at petal fall to estimate damage. Because substantial oviposition and damage can occur even after a single warm day and night, frequent scouting for damaged fruit is necessary after petal fall.

Control

Several species of wasps parasitize the eggs and larvae of the plum curculio. Ants, lacewings, and ground beetles prey on larvae in the soil, and some fungi kill larvae. These organisms are not usually sufficient to regulate populations of plum curculio in commercial orchards.

The plum curculio is difficult to control completely with insecticides. Relatively high rates and persistent applications are important because adults may be active for two to six weeks after petal fall depending on temperatures. Several commercial products are available to control this insect. In normal orchards that are not near woodlots or hedgerows and have not suffered previous damage, a single application at petal fall will provide seasonal control. In problem orchards, a petal fall application followed by a second spray 10–14 days later will provide adequate control. In orchards with chronic problems, or in seasons when adult activity is prolonged by unusually cool and wet weather, two cover sprays applied 10–14 days apart after petal fall may be necessary to prevent late damage. Research on heat unit accumulation and plum curculio oviposition has proposed that control sprays are no longer necessary whenever the last spray has been applied within 10–14 days after the accumulation of 340 DD (base 50°F) from petal fall.

Codling Moth, *Cydia pomonella* (Linnaeus)

Biology and Impact

The codling moth overwinters as a larva in a cocoon under loose bark on the tree trunk. Adults emerge during bloom, and the first flight continues until about 30 days past petal fall. Eggs, laid singly on the upper surface of leaves or fruit, start to hatch at petal fall and continue for two to three weeks. Larvae feed only on fruit. Surface bites, referred to as stings, cause blemishes, and deeper injuries are caused by feeding inside the fruit. Fruits injured by extensive internal feeding usually drop in the middle of June at which time early season damage becomes noticeable.

Adults from the second or summer generation of codling moth start to fly about mid-July, and the peak flight occurs around the first week in August. Larvae from this generation are active in fruit throughout August. Fruit damage by second generation larvae is generally more serious than that of the first.

Decision Making

Adult males can be captured in pheromone traps, but numbers of males captured in these traps cannot be related to potential fruit damage. Thus, pheromone traps are used only to monitor the seasonal activity patterns of adults within an area. It is not practical to monitor commercial apple orchards for CM eggs or larval fruit entries because of the theoretical zero tolerance for internal fruit damage. Developmental models, based on temperature accumulations after the first catch of males, can be used to predict the first egg hatch of codling moths. This approach is used to time initial control sprays for the codling moth at 250–360 DD (base 50°F) after first adult catch for the first generation, and 1260–1370 DD after this same biofix date for the second generation.

Control

The codling moth is attacked by both parasites and predators, but these natural enemies cannot effectively control this pest in commercial orchards. To kill the larvae before they enter the fruit, chemical sprays for the codling moth must be initiated before the eggs hatch. The codling moth is most effectively controlled by the same conventional insecticides used against the plum curculio, but it can also be controlled by more selective pesticides such as bacteria (*Bacillus thuringiensis*), insect growth regulators, viruses, and botanicals, although many of these products are less effective than standard insecticides.

Apple Maggot, *Rhagoletis pomonella* (Walsh)

Biology and Impact

The apple maggot overwinters as a pupa in the soil. Adults from the single annual generation of flies emerge in late June to early July. Females cannot lay eggs until they become reproductively mature, 7–10 days after emergence. Females lay eggs in fruit and the larvae develop there, emerging in the autumn after the fruit has fallen and entering the soil to pupate. Flies are active from July to mid-September, but commercial orchards require protection only from about mid-July through August. Flies do not reach orchards in large numbers until mid-July, and before this date, fruit remaining on the tree is unfavorable for larval development so early infestations do not cause sustainable populations in the orchard. In addition, for unknown reasons, fly activity between late August and mid-September generally does not result in serious damage in most commercial orchards.

Larval tunneling inside fruit causes it to become rotten and unmarketable. Early stings caused by punctures from female ovipositors may severely deform the fruit of some varieties, even though no larvae survive.

Decision Making

Monitoring to determine whether control sprays are necessary is recommended only in orchards that are not near large sources of outside infestation, such as abandoned orchards or those with no indigenous infestations of flies. In early to mid-July, red sphere traps baited with apple volatile lures are hung in trees along the edge of the block closest to an abandoned orchard or a stand of woods. These traps are checked one to two times per week. A spray of a suitable insecticide is applied if a cumulative average of 3–5 apple maggot flies per trap is captured. After spraying, trap catches are not checked again until after a 10 to 14-day period, during which spray residues would kill any immigrating flies.

Theoretically, there is absolutely no tolerance for apple maggot damage in fruit. In practice, apple maggot damage is not usually detected in normal fruit inspections unless there is approximately 3% fruit damage.

Control

Small wasps parasitize apple maggot larvae in fruit, and predators such as birds and crickets may eat larvae or pupae in or near the soil. In natural, unsprayed apple and hawthorn trees, apple maggot populations are not regulated by natural enemies. Parasites and predators are also ineffective at controlling apple maggot in commercial orchards.

Apple maggot flies have a limited migratory capability, so all apple and hawthorn trees within 1/4 to 1/2 mile of commercial orchards should be removed if possible. Dropped fruit should not be allowed to remain beneath the tree for more than one or two days. Eliminating fruit drops will break the life cycle of flies in an orchard by preventing larvae from exiting the fruit and entering the soil.

Apple maggot flies can be trapped in small, well-pruned trees that are not near large sources of outside infestations. A relatively high density of sticky red spheres (plain or volatile-baited) is required, approximately 1 trap per 100 apples. Mass trapping is usually less effective than chemical control, and apple maggot may still damage 1–5% of fruit from mass-trapped orchards.

Most commercial orchards have no indigenous populations of flies. Therefore, chemical control sprays are usually directed against flies immigrating into orchards from outside, unsprayed hosts, including both apples and hawthorns. Most broad-spectrum insecticides are remarkably effective in controlling adults. Insecticides must kill females before they oviposit in the fruit. Residual effectiveness of insecticides is particularly important in controlling apple maggot in commercial orchards when flies are continuously immigrating.

References

Helle W, Sabelis MW (1985) World crop pests, vol 1: spider mites: their biology, natural enemies and control. Elsevier, Amsterdam, The Netherlands

Metcalf RL, Metcalf RA (1993) Destructive and useful insects: their habits and control, 5th edn. McGraw-Hill, New York, NY, pp 1073

Minks AK, Harrewijn P (1987) World crop pests, vol 2: aphids: their biology, natural enemies and control. Elsevier, Amsterdam, The Netherlands

Pimentel D (1991) CRC handbook of pest management in agriculture, vol 3. CRC Press, Boca Raton, FL

Robinson AS, Hooper G (1989) World crop pests, vol 3: fruit flies: their biology, natural enemies and control. Elsevier, Amsterdam, The Netherlands

Van der Geest LPS, Evenhuis HH (1991) World crop pests, vol 5: Tortricid pests: their biology, natural enemies and control. Elsevier, Amsterdam, The Netherlands

Apple Proliferation

This is an important insect-transmitted mollicute (bacterial) disease of apples in Europe.

► Transmission of Plant Diseases by Insects

Apple Rust Mite, *Aculus Schlechtendali* (Acarnia: Eriophyidae)

This is an important apple pest in some areas.

► Four-Legged Mites
► Mites
► Apple Pests and their Management

Apposition Eye

A type of compound eye found in diurnal insects in which the ommatidium is shielded by pigment. This type of eye is also called a phototopic eye.

Appressorium

The swollen tip of a fungal hypha that facilitates attachment to the host, and penetration by the fungus.

Apterae

Wingless forms, usually used in reference to wingless parthenogenetic female aphids.

► Aphids

Apteropanorpidae

A family of insects in the order Mecoptera.

► Scorpionflies

Apterous

A term used to denote that the insect is lacking wings.

Apterygote

Insect taxa that do not possess and never possessed (in evolutionary time) wings. A member of the class Insecta, subclass Apterygota.

Apystomyiidae

A family of flies (order Diptera).

► Flies

Aquatic Entomology and Flyfishing

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The use of aquatic insects as lures for fish dates back to the second century A.D. In the seventeen volume treatise, *De Animalum Natura*, the Roman Aelianus discussed his observations of fish consuming insects at the water surface and how Macedonian fishermen used dry flies or spinners to catch what were thought to be trout from the Astraeus River. Not until fifteen centuries later did Charles Cotton propose the utility of aquatic insects in fishing. In 1836, Alfred Ronald's *Fly Fisher's Entomology* was published. This publication elaborated on fly tying methods and fishing techniques from an entomological perspective. Most recently, fly anglers are attempting to increase their knowledge about insects, specifically aquatic insects, in terms of imitating fish food items or "matching the hatch." This quest for entomological knowledge by anglers, in addition to aquatic scientists and fish managers, has prompted the need for better taxonomic and ecological treatments friendly to both the scientist and the angler. In order to create a functional artificial imitation of an insect to improve one's chances of catching a trophy fish, the angler requires basic identification, ecological and behavioral information of both insects (prey) and fish (quarry).

Terminology: Entomology Versus Flyfishing

As with many fields of scientific study, understanding the complexities of both entomology and fly fishing requires an understanding of both languages. While the term "fly fishing" technically refers to only one insect order, Diptera, in reality it encompasses all insect and non-insect invertebrates used as food by fish. Representatives from several orders of terrestrial insects (e.g., Hymenoptera, Orthoptera, Diptera, and Lepidoptera) are common food items of fish and are mimicked with artificial flies. However, aquatic insects are the primary interest of anglers and are the majority of fly patterns mimicked. For example, there are thirteen orders of insects that are classified as aquatic. Only 3% of all insects have a life stage in an aqueous environment. Some of these orders are entirely aquatic whereas others have a few semi-aquatic representatives. Truly aquatic orders are those in which all of their members exhibit some portion of their life cycle in an aquatic habitat. The orders, Ephemeroptera (mayflies), Plecoptera (stoneflies), and Trichoptera (caddisflies) are examples of truly aquatic orders. Semi-aquatic orders are largely terrestrial with a number of families exhibiting life stages in or near water. Coleoptera (beetles), Diptera (flies), and Lepidoptera (butterflies) represent semi-aquatic orders.

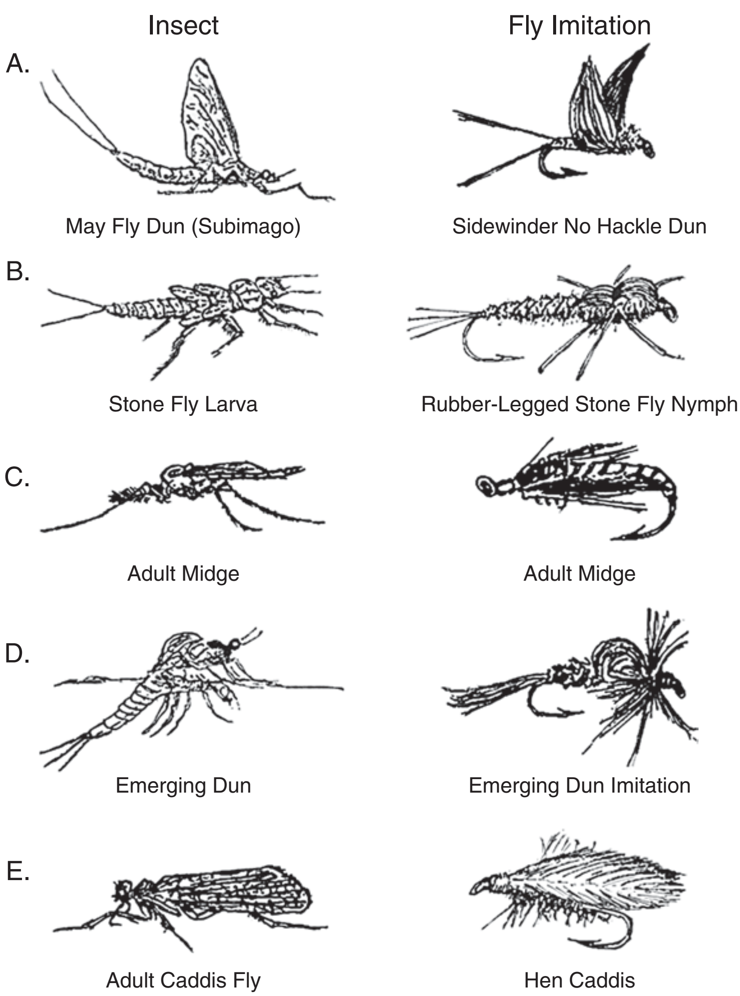
Typically, anglers refer to an emergence of insects (but more specifically to those with aquatic larval stages) as a "hatch." What the angler will call a nymph, the entomologist would refer to as the larval stage of an insect. Mayflies are the only group of insects that have a non-reproductive adult stage (the subimago); anglers refer to this stage as "duns." Post-ovipositing mayflies typically die with their wings spread on the water surface, and anglers term these "spinners," referring to the spinning action they exhibit while floating on the water surface. In addition, anglers refer to reproductively mature insects that end their life cycle on the water surface either by nature or that accidentally hop, fly or are blown onto the water surface as "dry flies." Fly patterns will mimic the larval and adult stages of both terrestrial and aquatic insects.

The sports angler often refers to insects by a number of colloquialisms. Educated fishermen often use the term caddis or caddisfly in reference to the order Trichoptera, fishflies for Megaloptera, and sandflies for some Diptera. Mayflies are known by a variety of names such as drakes or upwings.

Morphological Importance

Although the standard "mantra" of the dedicated fly angler is that the three most important aspects to catch fish are presentation, size and pattern, anglers must be familiar with many aspects of insect morphology. Most often, hand-tied flies incorporate the obvious features of the insect they are imitating. For many mayfly presentations, large characteristics such as wing size, caudal filaments, and body color are considered when tying flies. Small traits such as specific setation, paraglossae, and tarsal segments are often ignored largely due to their size relative to the insect and the investment of time that would be spent including these features in a fly. A fish will not recognize these small features because, at times, they may see the lure for only a few seconds.

Flies fit into two general classes based on their presentation. Dry flies are presented on the surface and signify the adult stage. Wet flies are fished below the surface and represent larvae. Success of the presentation is largely dependent on the time of the year. Presentation should mimic the natural life cycle of the native insects. A sample taken with a kick seine or observation of emergences will indicate what type of fly to use. An emergence of mayflies in the summer is the reason why an adult mayfly mimic presented on the surface may outfish a wetfly of a caddisfly. Several aquatic insect orders are often used as models for fly tying and as live bait. There are many fly imitations of caddisflies, mayflies and stonefly larvae (Fig. 71), as well as aquatic Diptera larvae and adults, due to their ecological importance of providing food for fish.



Aquatic Entomology and Flyfishing, Figure 71 A collection of common aquatic insects used as mimics for wet and dry artificial fly patterns. (A, C, D, and E = represent dry flies; B represents a wet fly or nymph). Illustrations by Mike Gouse (published in Swisher D, Richards C (1991) Emergers. Lyons & Burford Publishers, New York, NY).

Ecological and Behavioral Importance

Though fly fishing strategists argue over imitation vs. presentation, fly fishing tactics that employ ecological and behavioral aspects are as important as using a fly pattern based on the appearance of natural insects. Although insect abundance is important, fish will not eat the most abundant insect if it is not available to them. Three ecological aspects important in the availability of a particular insect include: stage of development, habitat use and activity (either associated with drift or foraging for food).

Although aquatic insect larvae are most abundant after hatching, they are not as available as fish food due to their small size and ability to avoid predators. In terms of energetics, a small insect is equivalent to small energetic payoffs. However, as aquatic insects grow and develop from one stage to the next they become more obvious to fish predators through their feeding activities. Thus, availability increases as insects grow and develop. Emergence for aquatic insects is a risky task. It is these emergers that are most available as they struggle to reach the water surface, plant stem or emergent rock from which they attempt to emerge as adults. Fish will concentrate feeding efforts on emerging insects if the adult stage escapes quickly. Those adult insects, both terrestrial and aquatic, that expire on the water surface are readily fed upon by fish.

Aquatic insects inhabit a wide variety of microhabitats within a given stream or pond, including rock or log surfaces, on plant stems or other submerged vegetation, as well as swimming openly in the water column. Habitat use by aquatic insects is relative to their needs. For example, foraging for food may put an insect in a different microhabitat other than used during non-feeding periods. Some mayflies may exhibit this behavior switch. Diel feeding activities among Phantom midges (Chaoboridae) also is an example of this type of behavior. Finally, phenological aspects of aquatic insect activity related to emergence, drift and oviposition increase insect availability. Some of these ecological/behavioral phenomena are tied to weather changes, lunar activity, water temperature and current regime.

References

Hafele R, Roederer S (1995) An angler's guide to aquatic insects and their imitations for all North America. Johnson Books Publisher, Boulder, Colorado, 182 pp

McCafferty PW (1983) Aquatic entomology. Jones and Bartlett Publishers, Boston, MA, 448 pp

Merritt RW, Cummins KW (1996) An introduction to the aquatic insects of North America. Kendall/Hunt Publishing, Dubuque, IA, 862 pp

Swisher D, Richards C (1991) Emergers. Lyons & Burford Publishers, New York, NY, 120 pp

Aquifer

An underground formation of sand gravel or porous rock that contains water. Aquifers are an important source of water is some areas, and must be protected from pesticide contamination, affecting the type of pesticides and pesticide application technologies that are used.

Aradidae

A family of bugs (order Hemiptera). They sometimes are called flat bugs.

► Bugs

Arbovirus

Viruses transmitted by arthropods. This is an acronym for ARthropod-BOrne VIRUSes.

Archaic Bell Moths (Lepidoptera: Neopseustidae)

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Archaic bell moths, family Neopseustidae, include nine known species (six from Southeast Asia and three from Chile). The family forms a monobasic superfamily, Neopseustoidea, and the only member of the infraorder Neopseustina, of the suborder Glossata and subcohort Myoglossata. Adults small (14–27 mm wingspan), with head roughened; haustellum short, with vestigial mandibles; labial palpi 3-segmented and somewhat upcurved; maxillary palpi 5-segmented; antennae are mostly rather long and somewhat thickened. Maculation is pale, usually translucent with gray spots, and wing shapes rather broad and quadrate. When resting the wings are held in a rounded shape that resembles a bell. Adults are crepuscular or diurnal. Biologies and larvae remain unknown, but species in Chile are thought to possibly feed on native bamboos.

References

Davis DR (1975) Systematics and zoogeography of the family Neopseustidae with a proposal of a new superfamily (Lepidoptera: Neopseustoidea). Smithsonian Contributions to Zoology 210:1–45

Davis DR (1997) Neopseustidae. In Lepidopterorum Catalogus, (n.s.). Fasc. 7. Association for Tropical Lepidoptera, Gainesville, p 8

Davis DR, Nielsen ES (1980) Description of a new genus and two new species of Neopseustidae from South America, with discussion of phylogeny and biological observations (Lepidoptera: Neopseustoidea). Steenstrupia 6:253–289

Archaic Sun Moths (Lepidoptera: Acanthopteroctetidae)

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Archaic sun moths, family Acanthopteroctetidae, are very similar to Eriocraniidae, and include only four species, all North American except for one in the Palearctic (originally described in a separate family Catapterigidae). The family, plus the related Eriocraniiidae, are the only members of the superfamily Eriocranioidea, which form the infraorder Dacnonypha of the suborder Glossata. There are two subfamilies: Acanthopteroctetinae and Catapteriginae. Adults small (11–16 mm wingspan, with roughened head scaling and only short 2-segmented labial palpi; maxillary palpi are 5-segmented and folded; haustellum is reduced and vestigial mandibles are present. Maculation is more somber than in Eriocraniidae and adults are thought to all be diurnal. Larvae are blotch leafminers on *Ceanothus* (Rhamnaceae) in the single known biology.

References

Davis DR (1969) A review of the genus *Acanthopteroctetes* with description of a new species (Eriocraniidae). J Lepid Soc 23:137–147

Davis DR, Frack DC (1987) Acanthopteroctetidae (Eriocranioidea). In: Stehr FW Jr (ed) Immature insects, vol 1. Kendall/Hunt Publishing, Dubuque, IA, pp 345–347

Zagulajev AK, Sinev SY (1988) Catapterigidae, a new family of lower Lepidoptera (Dacnonypha). Entomol Obozrenie 68:593–601 [in Russian] (English translation 1989: Entomol Rev 68:35–43)

Archeognatha

An apterygote order of insects, also called Microcoryphia. They commonly are known as bristletails.

► Bristletails

Archipsocidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice or Psocids

Arctics

Some members of the family Nymphalidae, subfamily Satyrinae (order Lepidoptera).

► Butterflies and Moths

Arctiidae

A family of moths (order Lepidoptera). They commonly are known as tiger moths, footman moths, or wasp moths.

► Tiger Moths

► Butterflies and Moths

Arculus

A small cross vein of the wing. The position of the cross vein (Fig. 72) varies among orders, but is associated with the cubitus vein.

► Wings of Insects

Area-Wide Insect Pest Management

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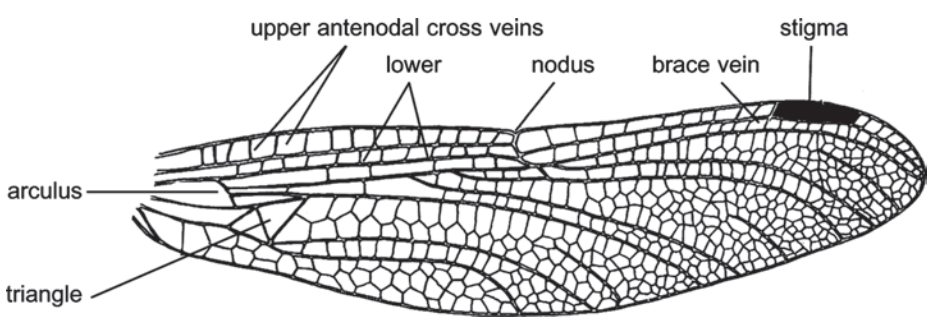
Area-wide pest management is one of several major plans or strategies for coping with pest problems. Management of localized populations is the conventional or most widely used strategy, wherein individual producers, other operators and households practice independent pest control. However, since individual producers or households are not capable of adequately meeting the challenge of certain very mobile and dangerous pests, the area-wide pest management strategy was developed.

The area-wide pest management strategy includes several substrategies including (i) management of the total pest population in all of an ecosystem, (ii) management of the total pest population in a significant part of an ecosystem, (iii) prevention, which includes containment of an invading population and quarantine, and (iv) eradication of an entire pest population from an area surrounded by naturally occurring or man-made barriers sufficiently effective to prevent reinvasion of the area except through the intervention of man.

Characteristics of Area-Wide Pest Management

Immigration of pests into a managed ecosystem prevents their eradication. However, it is easy to underestimate the tremendous impact of the immigration of pests from small untreated foci into a managed area. For example, very few codling moths, *Cydia pomonella* (L.) develop in the well managed commercial apple orchards, but researchers found that the number of codling moths that overwintered in the in Wenas Valley of Washington State dropped by 96% when a few abandoned orchards and neglected noncommercial apple trees were either removed or sprayed with insecticide. This study indicated that most of the codling moths in commercial orchards originated on untreated host trees that in aggregate were <5% of the host resources of the codling moth. Similarly, experience in coping with the pink bollworm, *Pectinophora gossypiella* Saunders,

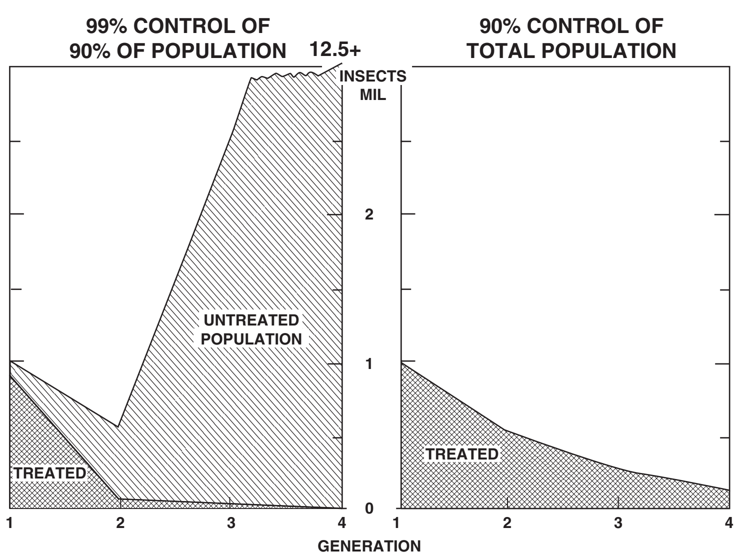


Arculus, Figure 72 **Front wing of a dragonfly (Odonata).**

and cotton boll weevil, *Anthonomus grandis* Boheman, have shown that a few growers who do not destroy crop residues immediately after harvest provide the food required by these pests to reproduce and to enter diapause. This lapse in field sanitation can directly cause the occurrence of devastating levels of these pests in the following season on neighboring farms.

The implications of allowing a small fraction of a population of a major pest species to reproduce without control can be seen graphically (Fig. 73). E. F. Knipling calculated that over a period of a few generations more pest individuals would be produced if 1% of the total population were allowed to reproduce without control, while 100% control was applied to 99% of the population, than if only 90% control was imposed uniformly on the total population. Thus, Knipling elaborated the basic principle of total population suppression: "Uniform suppressive pressure applied against the total population of the pest over a period of generations will achieve greater suppression than a higher level of control on most, but not all, of the population, each generation." Therefore, it is very important to eliminate any places of refuge or foci of infestation from which recruits could come to re-establish damaging densities of the pest population in areas of concern.

For the most part, the control of many highly mobile and very destructive pests is carried out by individual producers who rely heavily on the use of insecticides. Although other control technologies are often incorporated into the producer's integrated pest management (IPM) system, these technologies, too, are usually applied by producers independently of other producers. Such an uncoordinated farm-by-farm IPM strategy provides opportunities for the pest population to build up and to establish damaging infestations in well-managed fields. Consequently, on most farms insect pest populations increase to damaging levels each year, and the farmer is forced to apply



Area-Wide Insect Pest Management, Figure 73 **Results of a model that show that outcome of neglecting to suppress a small fraction of a pest population in an agroecosystem versus the effects of uniformly suppressing the entire pest population. On the left, 10% of the population is untreated and it produces a large number of individuals in four generations, while the 90% of the population that is treated declines. On the right, the entire pest population in the agroecosystem is suppressed uniformly and its numbers decline from generation to generation. (After Knipling, 1972. Reproduced with permission of the Australian Journal of Entomology.)**

broad-spectrum fast-acting insecticides as a rescue treatment (Table 10). This defeats the primary goal of the IPM system, which is to take maximum advantage of naturally occurring biological control agents.

Moreover, application of insecticides when an insect pest population reaches the economic threshold does not prevent the losses that occur before the threshold has been reached. For commodities that are planted on vast areas, such losses in aggregate are immense. For example, the world production of corn (maize) is roughly 600 million metric tons. Avoidance of a loss of 3% would make available 18 million metric tons, which could be a major factor in alleviating hunger. Some examples of crop losses caused by insects.

Area-wide pest management differs from the conventional pest management of local pest populations in several important ways. The area-wide strategy focuses on managing the insect populations in all of the niches in which they occur, while the conventional strategy focuses narrowly on protecting the crop, livestock, people, buildings, etc., from direct attack by pests. The area-wide strategy requires detailed multiyear planning and an organization dedicated exclusively to implementing the strategy. The conventional strategy involves less planning, tends to be reactive, and is implemented independently by individual operators or households. The area-wide strategy tends to utilize advanced technologies, whereas the conventional strategy tends to rely on traditional tactics and tools that can be reliably implemented by non-specialists.

The use of separate organizations to conduct area-wide programs provides opportunities to utilize sophisticated technologies and professional management. Computer-based models are utilized in planning and management. Satellite imagery is used in area-wide programs to identify localities of alternate hosts that can be treated to reduce pest populations that produce migrants that cause the damage in commercial production areas. Area-wide programs acquire or develop highly sensitive detection systems, and employ geographic information systems software to help manage data. They may implement approaches to prevent or retard the development of insecticide resistance or loss of host plant resistance. Computer programs and real-time environmental data to predict insect populations can be effectively used in an area-wide program but usually not on an individual farm basis. Thus, pest immigration patterns, analysis

Area-Wide Insect Pest Management, Table 10 Percent crop losses in the USA caused by various insect pests without and with control measures

		Percent loss	
Commodity	**Pest**	**Without control**	**With control**
Bean	*Helicoverpa zea*	37.0	6.0
Bean (snap)	*Epilachna varivestis*	20.0	9.9
Beet (sugar)	*Tetanops myopaeformis*	22.7	8.2
Corn (field)	*Diabrotica* spp.	15.7	5.0
Corn (field)	*Ostrinia nubilalis*	–	2.0
Corn (field)	*Helicoverpa zea*	–	2.5
Cotton	*Helicoverpa zea*	–	4.0
Cotton	*Pectinophora gossypiella*	35.5	10.0
Peanut	*Helicoverpa zea*	–	3.0
Soybean	*Pseudoplusia includens*	15.7	4.8
Sugar cane	*Diatraea saccharalis*	28.6	8.0

of weather to predict increase or decreases of populations, genetic analysis to determine resistance levels, etc., are utilized in area-wide programs.

Finally, area-wide programs are able to take advantage of the power and selectivity of specialized methods of insect control that for the most part are not effective when used on a farm-by-farm basis. These include the sterile insect technique (SIT), certain programs of inundative releases of parasites, semiochemicals, mating inhibitors, large scale trap cropping, treatment of hosts on public lands and in private gardens, etc.

Benefits of Area-Wide Pest Management

Experience has shown that pest suppression on an area-wide basis can be more effective than on a farm-by-farm basis for reducing losses caused by highly mobile pests and for capturing the benefits of highly mobile natural enemies. Area-wide programs enable many producers to pool resources in order to utilize technologies and expertise that are too expensive for individual producers. These may include mass rearing facilities, aircraft, information technologies and highly trained specialists. In addition, a coordinated area-wide program can achieve the avoidance or internalization of external costs. External costs (externalities) are the harmful effects arising from pest control operations that affect parties other than the pest control ker, but for which no compensation is paid to the persons harmed. For example, spray drift onto neighboring properties frequently provokes disputes. Also, pesticide use to protect agricultural crops has caused insecticide resistance to develop in insect vectors of disease.

Finally, economies of scale can be captured in area-wide programs, although complex trade-offs may be involved. The more mobile the pest and the more uniform the damage caused by the pest, the larger can be the area under coordinated management. The total costs of pest detection and monitoring and suppression per hectare of crop usually decline as the size of the managed area increases. However, the per hectare organizational costs usually increase as the project size increases because of the increased need for meetings and other communication costs. For these reasons, in very large programs such as the effort to eradicate the cotton boll weevil from the USA, the vast area was subdivided into a number of zones. Also, considerable organizational cost savings may be realized in instances where towns, municipalities or cooperatives already have structures in place for communication, decision-making, collection of fees, etc.

Contingencies Often Dictate Changes in Strategy

Contingencies often arise that require replacement of one strategy with another. For example, at various times during the 43-year campaign to remove the screwworm from the United States, Mexico and Central America, different pest management strategies had to be selected. This program began when an unusual series of frosts beginning early in December 1957 killed all screwworms in the southeastern USA north of a line in southern Florida from Tampa to Vero Beach. Sexually sterile flies from a culture in a research laboratory were released in a broad band north of this line to contain the pest population while a high capacity rearing facility was being readied. This containment strategy was replaced by the strategy of eradication in the summer of 1958 when the mass rearing facility was able to produce 50 million sterile flies per week, and eradication was accomplished in 1959.

A similar change of strategies was employed in eradicating the screwworm from west of the Mississippi River. Beginning in 1962, the parasite population was strongly suppressed north of the U.S. border with Mexico, and the influx of flies from Mexico was retarded by the release of sexually sterile flies in a 130 km-wide zone along the entire USA-Mexico border. (For political reasons in 1966, the U.S. Secretary of Agriculture declared the screwworm to be eradicated from the United States, even though it was obvious to entomologists that unless the parasite was removed from northern Mexico, it would continuously reinvade the United States.) However, the eradication strategy could be implemented soon after the governments of the USA and Mexico reached an agreement in 1972 to eradicate the parasite as far south as the Isthmus of Tehuantepec. Operations against the screwworm in Mexico began in 1974, and the last screwworm case occurred in the United States in 1982.

In the next phase, these containment and eradication strategies were employed to eradicate the parasite from all of Central America to Panama, where a sterile fly barrier was established in 2001.

Legal Authority for Area-Wide Pest Management

The legal authority needed for area-wide and other regulatory programs is still evolving. In about 1860, the grape phylloxera, *Phylloxera vitifoliae* (Fitch), was transported from the United States to France. Within 25 years of its arrival, this insect had destroyed 1 million hectares of vineyards or fully one-third of the capacity of France to produce grapes. In order to protect the German wine industry, the government of Germany in 1873 passed the first law that provided for quarantines and regulatory control of agricultural pests. Other governments quickly followed the example set by Germany. In 1881 representatives of many European countries met and developed a set of regulations governing the movement of grape propagating material.

In about 1880 the San Jose scale, *Aspidiotus perniciosus* Comstock, was established in California. Its rapid spread throughout the country on nursery stock, and the failure of a program to eradicate it, caused Canada, Germany and Austria-Hungary to prohibit the admission of American fruit and living plants beginning in 1898. This crisis led to the passage, by the U.S. Congress, of a series of eleven federal acts beginning in 1905 on quarantine and the regulation of interstate shipments in the USA. In 1999, most of these acts were consolidated into the Agriculture Risk Protection Act of 2000. Indeed, most countries adopted legislation on: (i) prevention of the introduction of new pests from foreign countries, (ii) prevention of spread of established pests within the country or state, (iii) enforcement of the application of control measures to prevent damage by exotic pests, to retard their spread or to eradicate them. In many countries, the law allows people who wish to organize a program against a pest to hold a referendum. If the referendum passes by a certain margin (usually 67%) then all parties at interest must cooperate in the venture.

Currently, in Florida, the program to eradicate citrus canker has been delayed for several years. This pathogen is carried considerable distances on driving rains, and to achieve eradication, the Division of Plant Industry has found it necessary to destroy all citrus trees within a radius of 578 m from an infected tree. Homeowners in urban areas, who do not understand the need for such drastic action, feel that workers who enter residential yards and destroy citrus trees as part of the eradication program violate their rights. Thus, the Broward County Circuit Court has ruled that program employees must have a separate court-issued warrant to enter each privately owned property. The need to apply for tens of thousands of warrants has prompted the Florida Department of Agriculture and Consumer Services to appeal this ruling. The outcomes of this and other judicial proceedings are likely to more clearly define procedures that must be followed in conducting eradication programs, and the levels of reimbursement owed to affected homeowners. Unfortunately, the tensions between urban and rural populations caused by the adversarial nature of this process are likely to persist for many years.

Apathy, Outrage and Area-Wide Pest Management

Some of the programs conducted on an area-wide basis, especially those aimed at eradication, have aroused opposition. The strategy of eradication emerged just over one century ago as the brainchild of Charles Henry Fernald of the University of Massachusetts. Under Fernald's leadership, Massachusetts attempted to eradicate an introduced pest, the gypsy moth, *Lymantria dispar* L., in an 11-year campaign from 1890 to 1901. Initially, the primary eradicant was Paris green spray. The use of Paris green, which suffered from modest efficacy and phytotoxicity, had to be abandoned because of adverse public reaction including threats of violence and mass protests.

Those stakeholders who are not primarily concerned with the economic dimension of the pest problem tend to be highly concerned with ecological, environmental, social and human health implications of area-wide programs. Therefore, leaders of area-wide pest management programs need to be highly sensitive to the perceptions and attitudes of the public toward certain program operations. Often, eradication efforts must be conducted by the ground rules of the urban rather than the rural setting. In programs to eradicate the Mediterranean fruit fly in California and Florida, members of the public strongly protested the aerial pesticide applications even if the same insecticide was used without dissent for mosquito abatement. On the other hand, the same public generally has applauded the release of Mediterranean fruit fly sterile males.

Normally the public is apathetic towards technological programs. However, certain factors inherent in programs and in the manner in which they are managed can precipitate an almost irreversible shift of the public's attitude from apathy to outrage. A sense of outrage can be evoked by involuntary exposure to pesticide residues, imposed levies or fees, quarantines, right of trespass, unfair and inequitable sharing of risks, costs and benefits, temporary loss of control of one's property or field operations, the perception that endangered species may be harmed, etc.

Acceptance of risk by the public is more dependent on the public's confidence in the risk manager than on the quantitative estimates of risk consequences, probabilities and magnitudes. The public' confidence in the managers of an area-wide program is of paramount importance.

In each area-wide program, a special effort must be made to anticipate and identify those factors that may be emotionally upsetting to various people and to take preemptive actions to avoid or mitigate adverse reactions. Public officials must be kept apprised, effective two way communication with the public must occur, surrogates of the public must be included in oversight and decision-making processes, and referenda may have to be conducted to secure support and funding for the program.

Invasive Pests, Global Trade and Area-Wide Pest Management

The rapid globalization of trade in agricultural products, and increasing tourism, have dramatically increased the spread of invasive harmful organisms. We have entered an era of an unprecedented level of travel by exotic invasive organisms. The greatest harm being done by non-indigenous invasive organisms is occurring on islands, and major pests are becoming established with increasing frequencies on all continents except, perhaps, Antarctica. For about one century many countries have relied on inspection of arriving cargo and passengers at the port of entry as a primary exclusionary strategy. However, volumes of arriving cargo are doubling every 5–6 years, and it is not possible to increase similarly the human and other resources devoted to inspection at ports of entry. Clearly exclusion at the port of entry is no longer sufficient to protect against exotic pests, even though a number of emerging technologies are likely to facilitate safeguarding activities. Thus, in order to stem the influx of exotic pests, it is important to shift primary reliance from exclusion at the port of entry to off-shore actions, namely on pest risk mitigation in the areas of production and elsewhere, certification at the point of origin, and preclearance at the port of export.

An important approach to offshore mitigation is the creation of pest-free areas. Indeed, countries that export raw agricultural commodities can effectively remove the threat of exotic pests to the importing country by creating and maintaining pest-free areas. A pest-free area is one that lacks a quarantine-significant pest species, and is separated from infested areas by natural or artificial barriers. There are two types of pest-free areas: (i) pest-free zones are large geographic areas, such as the entire country of Chile, that is certified free of tropical fruit flies of economic importance, and (ii) pest-free production fields, that require the demonstrated suppression of quarantine pests to non-detectable levels. Area-wide pest management is an important tool for promoting safe trade and contributing as much as possible to the complementary goals of food security and economic security for all countries.

Requirements to establish pest-free fields of crop production include a sensitive detection program, suppression of the quarantine-significant pest to non-detectable levels, strict control of the fields, and safeguards to prevent infestation during packing and transit to the port of export. For example, Florida is able to export grapefruit to Japan by creating pest-free grapefruit groves in about 22 counties. Regulatory experts from Japan inspect the entire process of production, packing and transit. Similarly fruit groves free of the South American cucurbit fruit fly, *Anastrepha grandis* (Macquart), have been created in Mossoro, Brazil and Guayaquil, Ecuador.

The concept of pest-free fields based on bait sprays and the sterile insect technique was pioneered during the early 1960s against the Mexican fruit fly along the Mexico-USA border Mexico. Also in the early 1960s, the Citrus Marketing Board in Israel developed a concerted area-wide program against the Mediterranean fruit fly that has been able to meet the certified quarantine security requirements of fruit importing countries. Chile used the sterile insect technique to rid the entire country of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann). By 1980 the entire country of Chile had become a medfly-free zone, and since then Chilean fruits in huge volumes have entered the U.S. market without the need for any quarantine treatments. This has dramatically strengthened the economy of Chile. Now Argentina, Peru and other countries have sterile insect technique programs that they hope will enable them to become fly-free zones with free access to markets in southern Europe, Japan and the United States. Also Mexico has used the sterile insect technique to get rid of the Mediterranean fruit fly. Indeed Mexico is ridding large sections of its territory of all fruit fly species of economic importance. The Mexican states of Baja California, Chihuahua and Sonora have been freed of all economically important species of fruit flies, so that citrus, stone fruits, apples and vegetables are being exported from these states without any postharvest treatment.

A more recent, highly significant development has been the continuous area-wide release of sexually sterile male medflies over the Los Angeles Basin and around high-risk ports in southern Florida. This further reduces the risk of pest establishment in these port areas.

Selected Episodes in the History of Area-Wide Pest Management

Migratory Locusts

Migratory locusts probably were one of the plagues that caused prehistoric man to attempt forms of group or area-wide control. Because migratory locust swarms can be seen approaching from a distance and descending onto crops, it seems likely that people banded together and used whatever means at hand to stamp out as many as possible. No doubt invasions of armyworms, leafcutter ants and other insects caused people to cooperate in combating them. In China, since 707 B.C., more than 800 outbreaks of *Locusta migratoria manilensis* L. have been recorded along the floodplains of the Hwang, Huai and Chang Jiang rivers. In 1929, an outbreak devastated 4.5 million hectares of cropland. Consequently, about 120 million people were mobilized to modify the floodplains by damming, terracing and reforestation. Over almost 30 centuries, the Chinese slowly developed an area-wide pest management program that now folds together knowledge of biology, ecology, forecasting cultural practices, and water management.

During the late 1920s, catastrophic locust plagues were widespread in Africa and southwest Asia. Boris Uvarov and Zena Waloff of the British Ministry of Overseas Development responded by establishing the International Unit of Locust Research. This Unit became the Antilocust Research Centre and it provided the focal point for international cooperation in coping with plagues of the desert locust, the red locust and the African migratory locust. The Centre created databases and provided a sustained regular flow of information on the status of locust populations throughout their ranges. The Centre developed a system of monthly forecasting. Uvarov was able to interest the FAO in creating the International Desert Locust Information Service to coordinate forecasting and the planning of campaigns. Leadership in these vitally important functions has been assigned to the FAO's Locust Group.

In recent decades locust experts have attempted to shift the prevailing strategy from reactive to proactive, and eventually to outbreak prevention. The reactive strategy initiates interventions after plague status has been reached in order to contain the magnitude of the damage. The proactive strategy seeks to prevent the occurrence of plague status by intervening against localized outbreaks. Proaction requires early detection of bands and swarms, preferably still in breeding areas, and prepositioning of locust campaign supplies. The outbreak prevention strategy seeks to intervene before the phase shift from solitary to gregarious. Possibly the outbreak prevention strategy would rely substantially on inducing epizootics by inoculating breeding populations with selective pathogens. A difficulty in implementing the proactive strategy and moving toward the outbreak prevention strategy is that donor support tends to wane in the absence of full-blown plagues.

Insect Vectors of Human Diseases

Doubtless the scientific pioneers of area-wide approaches were influenced strongly by concepts from the field of public health and hygiene. About 2,500 years ago the Greek spirit and the Roman capacity for organization had produced a highly developed system of hygiene in what is now southern Europe. The Romans procured safe supplies of water by means of aqueducts, practiced daily bathing and removed garbage from cities. The rationale for these measures was explained by Varro (116–27 B.C.), who served Pompey and Julius Caesar. Varro asserted that minute living creatures cause malaria. He wrote: "In damp places there grow tiny creatures, too small for us to see, which make their way into our bodies…and give rise to grave illness." However, with the collapse of the Roman Empire and the storms of folk-migrations, classical hygiene eroded. Nevertheless, raging outbreaks of malaria, typhoid, typhus and bubonic plague during the latter Middle Ages reawakened concepts of hygiene and public health. Doctors and public authorities joined forces to erect walls against these plagues. Dr. Johann Peter Frank (1745–1821) had considerable success in persuading the rulers of Europe during the late 1700s and early 1800s to establish public hygiene policies and to enforce them vigorously. While only a 21-year old student at the University of Strasbourg, Frank called for "systematic action by the authorities" to intervene in the lives of all citizens in order to forestall or halt epidemics. The discoveries of Pasteur, Koch and others on the nature of diseases were foundation stones for rational policies of public health.

Mosquito-Borne Diseases

Through collective action within communities, even without an overall national plan and central coordination, malaria in southern Europe and North America largely disappeared in consequence of education, the universal adoption of window screens, destruction of habitats of *Anopheles* larvae and the treatment of all cases with quinine.

Investigations conducted in the late 1800s and in early years of the 1900s on the transmission by mosquitoes of deadly diseases led to widespread use of area-wide programs. Yellow fever, dengue, filariasis and malaria were shown to be transmitted by various species of mosquito. In 1892 Howard, and in 1900 Ross, began to recommend that the habitat of mosquito larvae over extensive areas be either treated with kerosene or drained. These practices were first implemented in west Africa to combat malaria, and soon adopted by communities in many countries. Mosquito abatement districts were pioneered by John B. Smith in New Jersey. The New Jersey Mosquito Extermination Association, founded in 1912, provided the model for the organization and operation of area-wide mosquito abatement districts of which there are about 260 in the United States and a thousand or more worldwide.

Yellow fever was wiped out in Havana, Cuba, under the leadership of Dr. W. C. Gorgas, who in 1898 implemented a strict sanitation program to prevent breeding of the disease vector, *Aedes aegypti* L. Subsequently, Gorgas implemented a program in the Panama Canal Zone against *Aedes aegypti* and *Anopheles* spp. vectors of yellow fever and malaria, respectively. This highly effective program was key to the successful construction of the Panama Canal.

Because the *Plasmodium* pathogen requires 12 days to develop in the mosquito vector before it can be transmitted to man, residual sprays can sufficiently reduce the proportion of mosquitoes that survive 12 days, and so interrupt malaria transmission. Therefore, in 1955 the World Health Assembly urged WHO to lead and organize worldwide eradication of malaria. By 1959, almost 65% of the people at risk were protected and this percentage rose to 74 by 1970. Malaria eradication was claimed in 37 countries, and the incidence of malaria had dropped dramatically in many countries. In Sri Lanka, the number of cases dropped from more than 2.8 million per year to just 17 in 1963, but then the effort floundered as WHO was unable to deal with the widespread hue and cry for local control. In 1969, the Global Program disintegrated. Soon DDT was banned in the United States and WHO's resources for malaria were reallocated. Malaria resurged to more than half a million cases per year in Sri Lanka and to more than 100 million cases worldwide.

In 1969 and 1970, the Indian Council for Medical Research and the WHO initiated several projects relevant to area-wide control. Unfortunately, in 1974 these projects became the target of a press campaign by writers who feared that these projects were actually a USA-funded effort to develop methods of biological warfare. Because the government of India was unable to restore confidence, the projects were terminated.

Many authorities maintain that the area-wide use of insecticide impregnated bednets is superior to house spraying for suppressing malaria, that a considerable pool of effective technology relevant to the application of the SIT against mosquito vectors was developed three decades ago, and that area-wide programs against malaria vectors can move ahead as soon as the international community develops the political will to do so.

Onchocerciasis Control Program in West Africa

River blindness is caused by the microflilariae of the *Nematode Onchocerca volvulus*, and is transmitted by the *Simulium damnosum* species complex of black flies. People and blackflies are alternate hosts of this parasite, and it has no other hosts. The female parasite lives in the human skin and gives birth to the microfilariae for most of her lifespan of 12 years. Microfilariae may invade the human eye, and blindness typically sets in between the ages of 30 and 39 years. A number of small-scale larviciding operations against the vectors were mounted beginning in 1950, and beginning in 1960 the European Development Fund financed a major campaign in a 60,000-km^2 zone at the intersection of Mali, Burkina Faso and Cote d'Ivoire (Fig. 74).

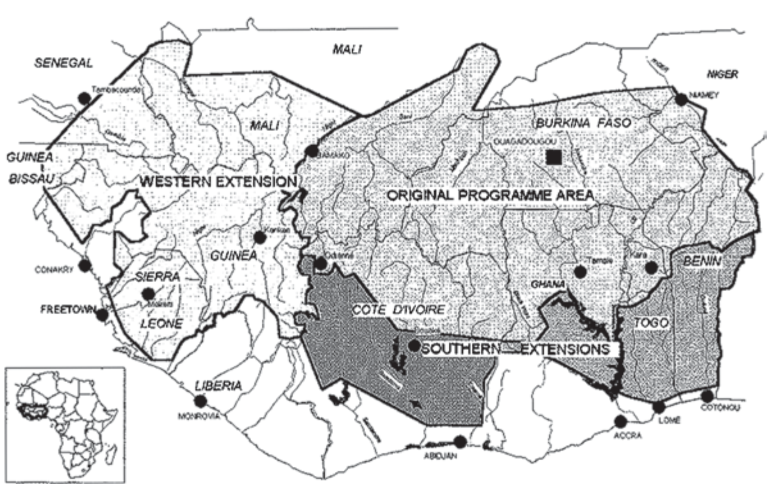
In 1974 the international community approved the Onchocerciasis Control Program and the World Health Organization was designated as Executing Agency. In order to manage the Program, National Onchocerciasis Committees were established in the seven participating countries (Benin, Burkina Faso, Cote d'Ivoire, Mali, Niger and Togo). A Joint Programme Committee has served as the supreme governing body and receives guidance from an Expert Advisory Committee. A Committee of Sponsoring Agencies coordinates the activities of the World Bank, FAO, WHO and UNDP. The Onchocerciasis Fund was created to accept donations, and the World Bank oversees it.

The Programme Director is assisted by seven units: Office of Director, Administrative Management, Epidemiological Evaluation, Vector Control, Applied Research, Biostatistics and Information Systems and Devolution. The latter conducts training and coordinates devolution activities with participating countries.

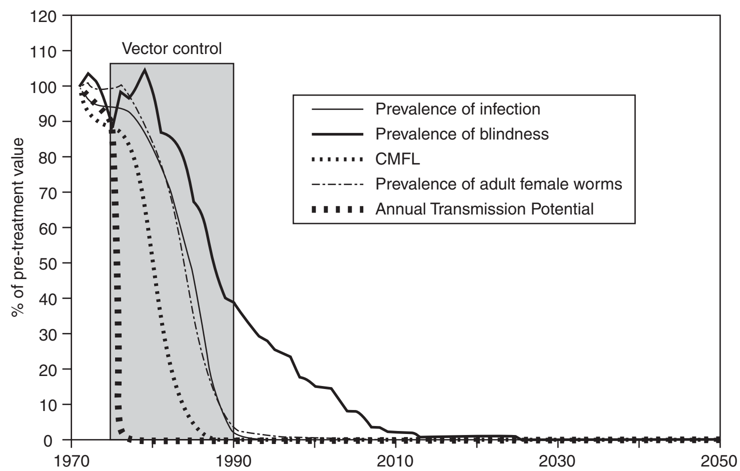
The limits of the program area were extended several times because of invasions of infective black flies over greater distances than initially foreseen. Thus the program area expanded from 654,000 km^2 in 1974 to 1,066,000 km^2 by 1990.

Two intervention tactics have been employed area-wide: larviciding largely by helicopter but also manually where streams are overgrown with vegetation, and treatment of humans with the microfilaricide, ivermectin. Because the period of development from egg to pupa rarely exceeds 1 week, larviciding must be carried out on a weekly basis. Seven insecticides are employed on a rotational basis to prevent the development of resistance. In order to achieve the proper concentration of insecticide in the flowing water, an automated hydrological surveillance network was created and real-time data are fed to an on-board computer to enable the pilot to properly manage spray operations.

The results of the program have been dramatic (Fig. 75). As a result of this program, 25 million hectares of land suitable for cultivation have become available, and rapid resettlement is underway. Because vector control operations were phased out in 2002, ivermectin remains as the only means of control.



Area-Wide Insect Pest Management, Figure 74 **The original area of the Onchocerciasis Programme established in 1974 and the subsequent western and southern extensions required to exclude migration of the black fly vectors. (After World Health Organization, 1994.)**



Area-Wide Insect Pest Management, Figure 75 Actual and projected impact of 15 years of suppressing black fly vectors of Onchocerciasis in the West Africa Programme. Reproduced from World Health Organization, 1994. CMFL is the community microfilarial load (geometric mean of microfilarial levels in all people in a given community).

Chagas Disease Vectors

Chagas disease, first recognized in 1909, has been ranked as the most important parasitic disease in the Americas. Although the infection is still largely incurable, transmission can be halted by (i) eliminating the domestic vectors, blood-sucking reduviids of the subfamily Triatominae, and (ii) screening blood donors to avoid risk of transmission through transfusions. Small-scale vector control programs began during the 1940s based on spraying the interior of homes with benzene hexachloride or dieldrin to control the primary vectors, *Triatoma infestans* (King) and *Rhodnius prolixus* (Stahl), as well as several other species of Triatoma. However, these programs suffered from under-funding and interruptions of funding, so that reinfestation occurred.

In 1983 a national program was launched in Brazil to eliminate the primary vector, *Triatoma infestans*, based initially on use of benzene hexachloride and later on pyrethroids. Although not without difficulties, this Brazilian program proved to be highly successful, and it inspired an area-wide program encompassing the Southern Cone countries (Argentina, Bolivia, Brazil, Chile, Paraguay, and Uruguay) plus Peru. This 10-year program was launched in 1991 under the leadership of the Pan American Health Organization with funding, in part, from the European Union. Total program costs were estimated at US $190 million to $350 million. The program's tremendous technical and economic success (internal rate of return of 30–60% largely based on savings in health costs) spurred a similar Central America Initiative (El Salvador, Guatemala, Honduras and Nicaragua) and an Andean Pact Initiative (Colombia and Venezuela).

Each program began with a centrally managed attack phase of about 3 years in which all homes are sprayed by trained professionals, followed by a more community-based phase, which relies substantially on the efforts of homeowners and local authorities. Adventitious transmission may be accomplished by sylvatic vector species, which can enter houses to form domestic colonies. In addition, migrant workers and other travelers can carry vectors. Currently, vector populations in Mexico and the Amazon Basin remain as major challenges. Elsewhere, the focus is shifting to epidemiological surveillance and care of people already infected.

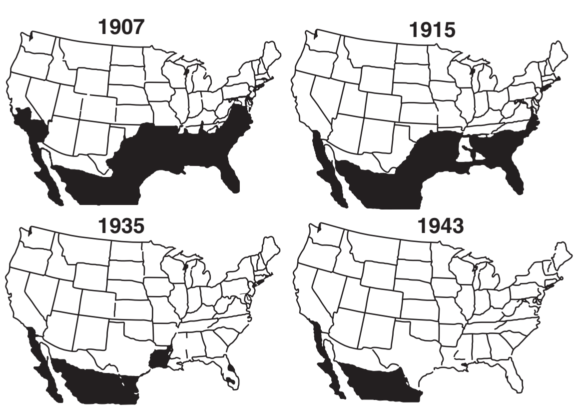
Cattle Ticks

The discovery in 1889 by Theobald Smith and colleagues that cattle fever is caused by a tick-transmitted parasite of red blood cells led to the initiation in 1906 of a county-by-county effort to eliminate the two *Boophilus* tick vectors (Fig. 76) from the United States. Many pastures were rendered tick-free by excluding all host animals until all ticks had starved to death. Livestock were dipped in an arsenical solution at 2-week intervals. Quarantines were used to prevent the movement of infested cattle into areas that had been cleared. By 1943, after 37 years of grueling effort, the ticks had been eliminated entirely from the United States for a total cost of about $40 million dollars, or the equivalent of the annual losses suffered before the program was initiated. Quarantines have been effective in preventing these ticks from becoming re-established from their populations in Mexico. A broadly shared vision sustained this program in spite of war and the great economic depression.

Contributions of Natural Enemies

Area-wide pest management began to be practiced widely during the nineteenth century using natural enemies. During the eighteenth and nineteenth centuries, people began to understand the roles of natural enemies in preventing insect outbreaks. Further, the powerful synthetic insecticides were not available to allow small holders independently to protect their crops and livestock. The beneficial work of coccinellids and other predators had been common knowledge for centuries, and they were collected and distributed for insect control. Insect parasitism was discovered only around 1700 by Leuwenhoeck in the Netherlands and in 1706 by Valisnieri in Italy. Emperor Francis 1 of Austria ordered Vincent Kollar to publish his work on the role of natural enemies in suppressing pests. Kollar's great work appeared in 1837 and the English translation appeared in London's Gardner's Magazine in 1840.

E. F. Knipling has analyzed the potential contributions of parasitoids to area-wide pest suppression. Parasite augmentation could be an especially desirable preventive measure because the release of host specific parasites poses no danger to humans, beneficial organisms, or the environment. Highly misleading conclusions have been drawn from past augmentation experiments, because the experiments were done in small non-isolated areas. Most pest arthropods and parasites or predators are highly mobile. Therefore, meaningful results can be obtained only if augmentation experiments are conducted over large areas. Even though many species of natural enemies have developed efficient host finding by following odor plumes of



Area-Wide Insect Pest Management, Figure 76 Progress in eradicating *Boophilus* ticks in the United States, 1906–1943.

kairomones emanating from the host, under natural conditions the level of parasitization does not threaten the host with extinction. Augmentation utilizes the host resources in nature to produce large numbers of parasite progeny. If done properly, parasite augmentation for several generations can become a self-perpetuating suppression measure. Augmentation causes progressive increases in the rate of parasitism with each succeeding parasite generation, provided that the initial rate of parasitism is above 50%. In addition, a host-dependent species will tend to distribute itself proportionally to the distribution of its host. No other method of insect control has the characteristic of concentrating its suppressive action where it is most needed.

Lasting Suppression of Cottony Cushion Scale by Vedalia Beetle

That classical biological control can provide area-wide solutions was dramatically illustrated against an exotic pest in California in 1888 and 1889. At that time an introduced pest, the cottony cushion scale, *Icerya purchasi*, was killing hundreds of thousands of citrus trees. However Albert Koebele was able to introduce a scale predator, the vedalia beetle, *Rodolia cardinalis* (Mulsant), from Australia and New Zealand. Less than 11,000 vedalias were distributed, but they spread throughout the entire citrus growing area of southern California and saved the industry. The vedalia beetle continues to effectively protect citrus in California, and nothing needs to be done other than to avoid the use of certain insecticides, which would decimate this invaluable natural enemy.

Lasting Suppression of Cassava Mealybug by *Epidinocarsis lopezi*

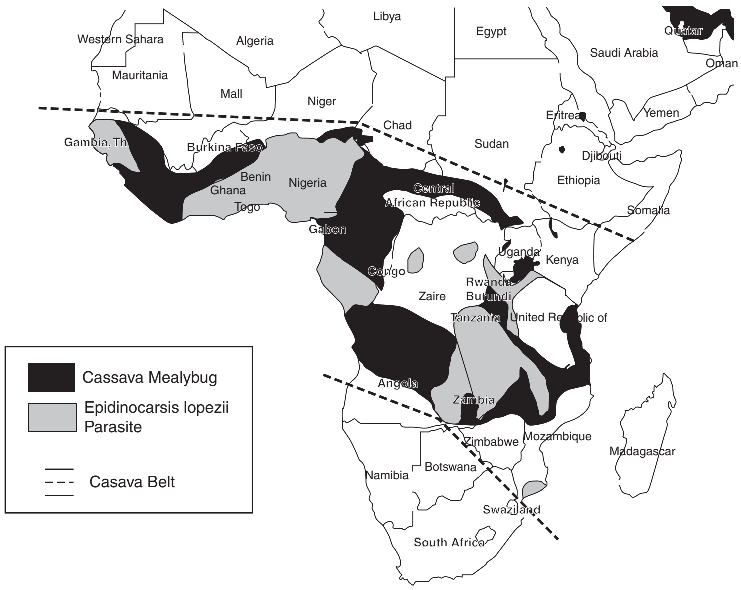
Almost exactly 100 years after the great vedalia success, a team led by Dr. Hans Herren of the International Institute for Tropical Agriculture (IITA) successfully implemented the largest classical biological control program in history. In 1973, cassava near Brazzaville and Kinshasa was found to be attacked by the cassava mealybug, *Phenacoccus manihoti* (Matile-Ferrero). In a few short years immature crawlers were dispersed by wind throughout sub-Saharan Africa.

The cassava mealybug created starvation and hardship for many of the 200 million people for whom cassava had become a staple crop. In 1981, an excellent parasitoid, *Epidinocarsis lopezi* (DeSantis), found in Paraguay by A.C. Bellotti, proved capable of bringing the cassava mealybug under control. The parasite was mass-reared and released by aircraft over 38 countries (Fig. 77) of sub-Saharan Africa (an area much larger than the combined area of the United States, Mexico and India) with excellent results. This singular accomplishment required strong and imaginative leadership and action by IITA, generous funding by donors, and brilliant scientific and technical work by Herren's team and their cooperators in Africa, Europe, and the Americas.

Area-Wide Conservation of Predators of the Brown Planthopper

In many cases, natural enemies are effective only if most smallholders in an area work to conserve them. Because both pests and natural enemies are mobile, their populations distribute themselves throughout the region in which their food sources are available. Even smallholders who do not participate in the conservation program receive some of its benefits. They get a free ride, and for them this is a positive externality of the program. On the other hand, the movement of natural enemies off the property of the participating farmer to that of the free rider is a negative externality.

The brown planthopper, *Nilaparvata lugens* (Stål), has been the scourge of rice production in southeast Asia for many years. However, during the 1980s, Indonesia (with technical assistance from FAO and Germany's GTZ) simultaneously



Area-Wide Insect Pest Management, Figure 77 **Biological control of the cassava mealybug in sub-Saharan Africa by mass rearing a parasite from Paraguay and distributing it by air over 38 countries.**

achieved substantial increases in rice production and major reductions in insecticide use. Generally, brown planthoppers are effectively controlled by indigenous spiders and other predators. Moreover, since insecticides have a greater impact on the predators than on the pest, the brown planthopper populations are able to resurge after being sprayed. In the past, farmers induced resurgence by beginning to spray at 40 days after transplanting the rice. However, cage studies showed that the smallholder who delays spraying until 65 days after transplanting saves two insecticide applications, and realizes a yield increase of about two tonnes, for a total benefit of US $588 per hectare.

It is possible to model what happens when some smallholders delay spraying to conserve natural enemies but others do not. If about 10% of smallholders conserve natural enemies, they gain only one-fifth of the potential benefit. If 30% of smallholders conserve natural enemies, they gain only one-quarter of the potential benefit, and the free riders gain about 7%. When 50% of small holders conserve natural enemies they gain one-third of the potential benefit, and the free riders gain about 18%.

When 70% of smallholders participate, they gain almost 60% and the free riders gain about 40%, and when 90% participate, they gain about 83% of the potential benefit, while the free riders gain 66%. Clearly, a conservation program is almost futile until about one-half of the smallholders participate, and the program becomes progressively more beneficial as the percent participation increases toward 100.

Bark Beetles

Dendroctonus pine bark beetles are dangerous pests in forestry because of their mass attacks on healthy trees. During the first decades in the twentieth century, foresters focused on destroying the developing broods of potentially destructive beetles before they could emerge and attack valuable trees. This was implemented by felling dead trees, peeling and burning the bark or by storing the infested logs in millponds until they could be sawed into lumber. The futility of such attempts by focusing directly on killing beetles became apparent when, in 1932, an extremely cold winter occurred and destroyed at least 80% of the beetles in western North America. The destruction of the beetle broods by frost was more complete, extensive and uniform than could be accomplished by forest managers. Yet, within 2 years the beetle populations had resurged and were again killing ponderosa pine on a vast scale.

However, forest entomologists recognized that the most vulnerable trees were those that lacked vigor or were in decline. Thus, in 1937 control of bark beetles based on susceptibility of trees to attack was pilot tested in California by a program called sanitation-salvage logging. In this approach, up to 20% of trees at highest risk of beetle attack were removed and sawed into lumber. During the first year following the removal of the most vulnerable trees, losses to bark beetles were reduced by 90%, and losses remained low for at least 10 years after the selective logging.

Boll Weevil Eradication in the USA

E. F. Knipling, with the support of the National Cotton Council, was determined to eradicate the boll weevil from the United States because the weevil necessitated the use on cotton of one-third of the insecticides used in U.S. agriculture. Also, highly insecticide-resistant boll weevil populations had emerged. Newsom and Brazzel, at Louisiana State University, had discovered that in the fall of the year the boll weevil enters a reproductive diapause and hibernates in trash along the edges of cotton fields. Brazzel showed that the number of weevils surviving the winter is reduced 90% if insecticides are applied just before diapausing weevils leave the fields. Moreover, Knipling's analysis showed that if insecticide sprays were targeted also to kill the generation producing individuals going into diapause, then the number overwintering would be reduced by more than 99%. Knipling's model was verified, and this ignited great interest in actually eradicating the boll weevil. An effective pheromone-baited trap was developed for detection. Weevils were sexually sterilized with the anti-leukemia drug, busulfan.

In 1971–1973, a large pilot field experiment to assess the feasibility of eradication was centered in southern Mississippi. The eradication zone was surrounded by three buffer zones. Very intensive suppression was implemented in the two inner zones, and farmers were expected to practice diligent control in the outer zones, although some grew cotton simply to qualify for government payments and with no intention to harvest a crop. Only one application of the suppressive system was made, because of a shortfall in appropriations. Nevertheless, the boll weevil was suppressed below detectable levels in 203 of 236 fields in the eradication zone. All of the 33 lightly infested fields were located in the northern one-third of the eradication zone and less than 40 km from substantial populations farther north. In the southern two-thirds of the eradication zone, no reproduction could be detected in any of the 170 fields. Knipling and some others concluded that the available technology was sufficiently effective to achieve eradication. Their experience with the screwworm indicated that eradication could be accomplished iteratively, following an application of the suppressive system that clears the pest from most of the target zone. Next, surviving populations are delimited and similar suppressive measures are applied to them. In this iterative fashion, the aggregate range occupied by the pest is progressively reduced toward zero. However, some felt that the technology was not adequate to mount an eradication campaign, unless a single application of the system of suppression eliminated all weevils in the target zone.

A Cotton Study Team appointed by the National Academy of Sciences drafted a very negative interpretation of the results. Because Knipling was a member of the Academy, he had access to this draft, and he wrote a strong rebuttal. Therefore, the Cotton Study Team wrote a "toned down statement" that continued to express strong reservations about the feasibility of eradicating the boll weevil, but concurred to conduct a new trial eradication program in North Carolina.

Grudgingly the Academy team legitimized the concept of continuing large-scale eradication experiments, but with the caveat that they would probably fail.

The new trial program, started in 1978 in Virginia and North Carolina, was highly successful. Subsequently, piece-meal programs, each run by a separate foundation, have removed the boll weevil from about 5 million acres in Virginia and the Carolinas, Georgia, Florida, south Alabama, California, and Arizona. These programs have caused significant reductions in pesticide usage, and the eradication efforts are continuing. Thus, the job is about half done. However, the corrosive effect of the Academy's report persists. The US Congress reduced the share of federal funds from the traditional 50 to <30% of the cost. However, such cost sharing is no longer guaranteed, and in 1997 the US Department of Agriculture initiated a program of making loans to officially recognized boll weevil eradication foundations. Moreover, the process of eradication is being conducted piece-meal with a minimum of technology. Pheromone traps are used to delimit infestations, and the attack begins with insecticides applied late in the growing season against weevil still reproducing and those entering diapause. As many as 15 insecticide applications per year are made against dense persistent populations. Planting by all growers is synchronized and delayed, short season varieties are grown, harvested as soon as possible, and stalks are destroyed immediately after harvest. Eradication is usually accomplished by the end of the third growing season.

Attempts to Sharply Define the Area-Wide Pest Management Strategy

A few scientists have attempted to sharply define the area-wide pest management strategy. Knipling stated: "Area-wide pest management is the systematic reduction of a target key pest(s) to predetermined population levels through the use of uniformly applied control measures over large geographical areas clearly defined by biologically based criteria." D. A. Lindquist wrote: "An area-wide insect control program is a long-term planned campaign against a pest insect population in a relatively large predefined area with the objective of reducing the insect population to a non-economic status".

Both of these definitions have considerable merit and they fit the majority of area-wide programs. However, slightly different definitions may be needed to describe programs on the conservation of natural enemies (which can tolerate some free-riders) and on classical biological control where the adaptation of the introduced biological agent to all new environments cannot be known in advance of making releases. Also, in programs to contain an invasive pest population, it may not be possible to clearly define the boundary of the pest population. In the similar vein, A. T. Showler stated: "Locust swarms can be highly variable, influenced by many factors, including geography, vegetative conditions, land-use patterns, environmental sensitivity, availability of resources and tactics, prevailing winds, insecure areas, and rainfall patterns. Reliance on a single control strategy is therefore unrealistic. A more appropriate approach would be to develop specific strategies that will fit with projected scenarios, mostly by harmonizing them with national contingency plans." The common thread that runs through all area-wide pest management programs is the strong emphasis on preventing the existence of any places of refuge or foci of infestation from which recruits can come to re-establish damaging densities of the pest population in areas of concern.

Benefit-Cost Assessment and Discounting Net Returns

Usually, investments in area-wide programs are made with the expectation that program benefits will accrue over a multi-year time horizon. Therefore, we must discount future benefits to balance them against present or near term expenditures. The stream of discounted annual benefits and costs for many years of an undertaking can be summed up and expressed as a single value, known as the present value net benefits (PVNB). The formula for calculating the PVNB for a 15-year project is as follows:

$$PNVB = NB_1 + w_2NB_2 + w_3NB_3 + w_4NB_4 + w_5NB_5 + w_6NB_6 + wtNB_t + w_{15}NB_{15}$$

where NB_t represents the net benefits in year t, and w_t represents the weighting factor for year t. The weighting factors are a function of a discount rate (r):

$$w_t = \frac{1}{(1+r)^t}$$

The discount rate is the opportunity cost of the money, or the interest value that money could earn if allocated to the best alternative use. This rate may be established by subtracting the national inflation rate from the bank interest rate for savings. In normal times, this procedure will generally produce a figure around 4 or 5% in developed countries. This represents the reasonable person's discount on the future, because people put their money in the bank to gain this premium, and otherwise they would spend it now. So, the benefit of eradication next year is worth 5% less if it is brought back to the present. Benefits in 20 years are only worth 37% of their face value when brought back to the present. In riskier economic environments, discount rates will be much greater, so the calculated net present value of future benefits may be insignificant. However, for programs involving vectors of human diseases, the futures of groups of people are at stake, and it does not seem appropriate to discount benefits in the manner appropriate for private investments. The health of the human population 30 years in the future seems just as important as the health of the population at present. Nevertheless, investments in vector control programs must be subjected to critical analysis in the interest of efficient and sound management. However, if high discount rates (e.g., 25%) are selected commensurate with economic risk in many developing countries, then it seem unlikely that vector control programs in these countries would ever be launched.

Knipling's Imperative

When the World Food prize was awarded to Knipling and Bushland, Knipling stated: "If major advances are to be made in coping with most of the major arthropod pest problems, then the tactics and strategies for managing such insects, ticks and mites must change. They must change from the current, limited scale, reactive, broad-spectrum measures to preventive measures that are target-pest specific and rigidly applied on an area-wide basis." Great and enduring strides can be made by adopting the strategy of area-wide pest management to help meet world food, health and environmental challenges.

References

Klassen W (1989) Eradication of introduced arthropod pests: theory and historical practice. Miscellaneous Publications of the Entomological Society of America 73:1–29

Klassen W (2000) Area-wide approaches to insect pest interventions: history and lessons. In: Teng-Hong Tan (ed) Joint Proceedings of the FAO/IAEA International Conference on Area-Wide Control of Insect Pests, May 28–June 2, 1998, and the Fifth International Symposium on Fruit Flies of Economic Importance, June 1–5, 1998. I.A.E.A, Penerbit Universiti Sains Malaysia, Pulau, Pinang, Malaysia, pp 21–38

Klassen W, Lindquist DA, Buyckx EJ (1994) Overview of the Joint FAO/IAEA Division's involvement in fruit fly sterile insect technique programs. In Calkins CO, Klassen W, Liedo P (eds) Fruit flies and the sterile insect technique. CRC Press, Boca Raton, FL, pp 21–38

Knipling EF (1979) The basic principles of insect population suppression and management. USDA agriculture handbook 512. Washington, DC, 659 pp

Knipling EF (1992) Principles of insect parasitism analyzed from new perspectives: practical implications for regulating insect populations.USDA agricultural handbook 693. Washington, DC, 337 pp

Reichelderfer KH, Carlson GA, Norton GA (1984) Economic guidelines for crop pest control. FAO plant production and protection paper 58. FAO, Rome, Italy, 93 pp

Argasid (Soft) Ticks (Acari: Ixodida: Argasidae)

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The family Argasidae is second to the family Ixodidae with regard to its medical and veterinary significance and the number of species. According to the novel classification based on a phylogenetic analysis of relationships at the generic to subgeneric level, the argasid ticks comprise four genera and about 185 species, among which three genera are represented by a large number of species: *Carios* (87 species), *Argas* (57 species) and *Ornithodoros* (36 species, one of which consists of three subspecies). The fourth genus (*Otobius*) is represented by three species. Not all researchers fully agree with the currently proposed systematic groupings of the family. This classification has its weaknesses but is considered superior to traditional classifications. In any case, further molecular taxonomic study is necessary.

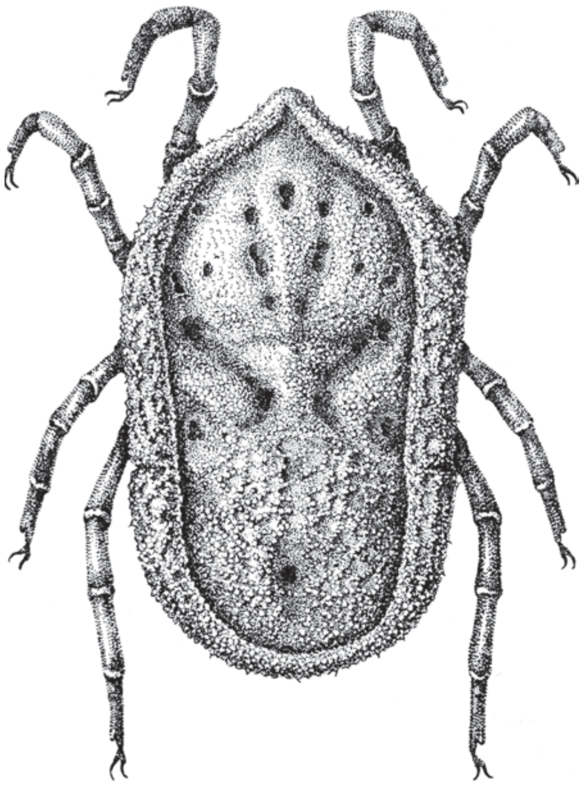
The main morphological difference between argasid and ixodid ticks is the lack of the scutum in argasids; thus, they are called "soft ticks." The lack of the scutum leads to the absence of such a clear sexual dimorphism in the adult stage of this family compared with ixodid ("hard") ticks. The integument of the Argasidae looks wrinkled and leathery. The mouthparts are located on the ventral side of the body, covered by the frontal margin of the body, and are invisible from above.

There are a number of significant biological differences between soft and hard ticks. Firstly, argasid ticks have several nymphal stages (instars), varying from 2 to 8, usually from 3 to 6. The number of instars is not constant, and is controlled by exogenous factors such as the size of the blood meal and the ambient temperature during development. Secondly, nymphs and adults of argasid ticks cannot engorge as much blood as ixodid ticks. The integument of adult argasids is strongly folded and capable of stretching during feeding, but does not grow at that time. Females of most argasid ticks increase their body mass after feeding by only 3–6-fold. The blood feeding time of argasid ticks is much shorter than that of ixodids, taking from several minutes to 1–2 h, and male gorging taking 1.5–2 times less than that of females. In contrast, nymphal argasids feed in much the same manner as ixodids; this is explained by their capacity to create new cuticle during feeding. Thirdly, adult ticks can gorge blood several times during their life, and can oviposit after each feeding. The maximal number of possible feedings is unclear, though as many as nine feedings have been documented.

Ecology

Argasid ticks are spread over all continents (with the exception of Antarctica) but have been studied very unevenly; in particular, there is insufficient information on this group in South America and Australia. Both in the Palaearctic and the Nearctic, soft ticks inhabit regions with a hot climate, mainly deserts, semi-deserts and southern savannas (steppes, veldts, prairies), but some species penetrate as far north as 50–55°N. The maximum number of species and their greatest abundance are known in foothill areas (300–900 m above sea level), but some ticks can be found at higher elevations (a maximum of 2,900 m above sea level for the cave tick *Ornithodoros tholozani* (Fig. 78) in the Pamirs).

Almost all species of argasid ticks are nidicolous, i.e., they live in or near shelters of various kinds. *Ornithodoros transversus* is an exceptional species that spends its entire life on the giant tortoises of the Galapagos Islands. Endophilous nidicoles inhabit bird and rodent nests, mammal burrows, and caves as well as stalls, poultry houses and farms. Harborage-infesting parasites live near nests or burrows, very often in rock or stone ledges as well as in human dwellings and temporary human-made cabins in places of resting, hunting or fishing. In such shelters, ticks inhabit all kinds of cover: cracks and crevices on walls, sandy or



Argasid (Soft) Ticks (Acari: Ixodida: Argasidae), Figure 78 **The cave tick, *Ornithodoros tholozani*.**

dusty soil surface of burrows and caves, spaces between nest fibers, etc. Ambient conditions, such as air temperature, relative humidity and light intensity, are more uniform and suitable for ticks in shelters than in the surroundings; this enables tick survival in extremely unfavorable areas. Being dependent on the hosts living in the shelters, the ticks have developed different patterns of adaptation, the main one being their unusual ability to persist without feeding. This is especially characteristic of nest and burrow inhabitants because death of the host or migration to another habitation are common phenomena, whereas active migration between shelters is not typical for most argasid ticks except in several species parasitizing ungulates and hares. Under laboratory conditions, unfed adult *O. tholozani* survived without feeding for more than 10 years and unfed adult *Argas lahorensis* for as long as 18 years.

As a rule, females of argasid ticks are characterized by gonotrophic harmony, though the number of eggs in each batch may fluctuate widely. After each complete blood feeding, they lay off-host from 50 to 200 eggs. If blood feeding is not complete, the number of eggs laid diminishes proportionally. During its entire life, a female can lay up to 1,200 eggs. Female oviposition depends on their insemination, which occurs off-host, and can take place either before or after feeding. Some cases of female insemination several months after feeding, followed by oviposition, have been described. One mating is sufficient for several ovipositions. Multiple gonotrophic cycles have been recorded among the Argasidae. There are some exceptions from gonotrophic harmony when a female lays eggs without feeding, using nutritional reserves remaining after nymphal feeding.

Feeding Behavior

Several feeding nymphal instars and repeated feedings in adult females allow us to describe the Argasidae (with a few exceptions) as multi-host ticks, though consecutive feedings may take place on the same host. Most argasid species feed on specific groups of hosts and, in a broad sense, can be considered specialists. Ticks of some subgenera of *Argas* parasitize birds available to them during nesting or resting. The genus *Carios* contains nearly all bat-associated argasids. When the ticks are offered unusual hosts, they either do not feed at all or have some abnormalities in their metamorphosis after such feeding. An extreme specialization was observed in Cuban *Carios natalinus* and *C. tadaridae*, which parasitize only bats of the genera *Natalus* and *Tadarida*, respectively. In contrast, such ticks as *Ornithodoros erraticus*, *O. tartakovskyi*, or *O. tholozani* must be considered generalists. They can feed on any mammals, birds and reptiles available to them. Among exceptions are the one-host *Ornithodoros transversus* and the two-host *Otobius megnini* and *A. lahorensis*. The latter species demonstrates some characteristics of exophilic ticks which are followed by adaptations to hot xeric environments. This tick has an extremely high critical temperature of the epicuticle (61°C in contrast to 42 to 54°C in other species studied) and minimal water loss under low RH. Among other adaptations are the development on the host from larval attachment until engorgement of nymphs of the last instar with a constant number of nymphal instars (3) and nymphal feeding at each instar for several days which increases the blood meal size and, hence, the number of eggs laid (300–500).

A capacity of unfed argasid ticks to parasitize and feed on engorged specimens of the same species presents an interesting phenomenon called homoparasitism (homovampirism, in Russian literature). Usually, unfed nymphs and males parasitize engorged nymphs of late instars and females. Unfed ticks prick the integument and gut walls of engorged specimens, and suck the gut contents. As a rule, such an operation is not followed by the death of the victim, so that this phenomenon cannot be called cannibalism. This phenomenon has been documented many times for a number of species of both *Argas* and *Ornithodoros* under laboratory conditions, but there are also a few observations from the field. Apart from this, feeding of unfed ticks on engorged specimens of other species has also been recorded.

Depending on the conditions of tick habitats, ticks have different forms of seasonal activity. The seasonality is absent or weakly pronounced in ticks inhabiting shelters with a relatively stable microclimate. In the tropical zone, ticks attack hosts, feed and oviposit all year round according to observations on the African tampan *Ornithodoros moubata*. A similar pattern of activity was recorded on *O. erraticus* inhabiting the Nile grass rat burrows in Egypt. In the subtropical and especially temperate zones, the seasonality in tick activity is much better defined. Ticks feed and oviposit during the summer and have one or two gonotrophic cycles during this period. In the winter months, a morphogenetic diapause in the form of ovipositional delay takes place in argasid species that parasitize migratory birds. Such diapause also occurs in ticks parasitizing bats, which hibernate in cool caves. Photoperiod seems to be the main but not the only factor regulating the induction and termination of diapause. A prolonged hunger is not considered diapause even when it continues for several years.

The abundance of argasid ticks in their shelters can be extremely high. A single cave inhabited by bats may contain hundreds of thousands of bat-parasitizing argasids. Cases have been documented when seabirds abandoned their nests in the middle of the breeding season because of enormous tick density. Especially high tick density has been noted in abandoned habitations of Central Asia. Such constructions are even more dangerous than dwellings; the longer ticks are without hosts and the hungrier they become, the more aggressively they attack occasional visitors. In past centuries special "bug traps" full of hungry argasids were used by Central Asian rulers for the torture of prisoners who died from exsanguination by thousands of ticks. The capability of argasid ticks to migrate varies depending on the habitation of a particular species. Endophilous nidicoles inhabiting nests, burrows and caves are usually considered non-migratory species because the distance to the host is very short. Harborage-infesting species can migrate over larger distances measured in many meters. As in the hard ticks, the migration toward a host is influenced by a spectrum of factors, such as CO_2, host body heat, various odors, etc. However, the effect of a single stimulus is weaker than for hard ticks, and the maximal effect has been observed when all stimuli worked together.

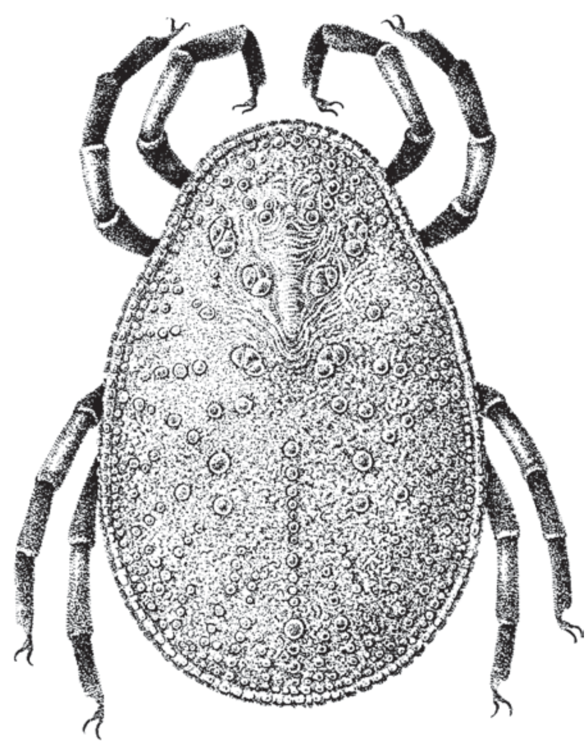
Evolutionarily, the Argasidae are more primitive than the Ixodidae. This primitivism is exemplified by a number of characteristics, such as rather narrow ecological patterns, low capacity for active migrations, existence of many nymphal instars, and slight morphological difference between the last nymphal instar and the adult stage. These characteristics are considered typical for more primitive forms among different groups of the Arachnida.

Medical Importance

The medical significance of argasid ticks is mainly determined by their participation in transmission of many species of *Borrelia* pathogenic to humans. These closely related bacteria are causative agents of tick-borne relapsing fevers. Each species of *Borrelia* is transmitted by its specific tick vector. *Borrelia duttoni* and its vector *Ornithodoros moubata* were the first combination of such kind recognized in Africa in the very beginning of the twentieth century. The disease occurs in the central, eastern and southern parts of the continent and humans are the primary reservoir host, which is unusual because in other combinations, mammals, especially rodents, are the main reservoir hosts. More than 15 combinations of *Borrelia* with particular species of argasid ticks are recently known worldwide. They occur in North, Central and South America, Africa, and the Mediterranean area, including some European countries, the Caucasus, Asia from the Near East to western China. In the western and southwestern United States the following combinations have been identified: *B. hermsi*-*Ornithodoros hermsi*, *B. parkeri* -*O. parkeri*, *B. turicatae*-*O. turicata*, *B. mazzottii*-*Carios talaje*. The ticks are capable of transovarial and transstadial passage of *Borrelia* for many generations, as well as of prolonged preservation of pathogens, even during prolonged hunger. The passage of pathogens from hungry to engorged specimens as a result of homoparasitism has been proved experimentally. Because tick vectors are nidicolous, the human infection depends on human closeness to tick habitation. Tick species inhabiting human dwellings, such as *Ornithodoros moubata* and *O. tholozani*, are especially dangerous vectors. In other cases the infection takes place only when humans intrude into tick shelters or settle themselves nearby.

Veterinary Importance

Some argasid ticks are also of veterinary importance. *Ornithodoros porcinus porcinus* and *O. erraticus* are the main vectors of the African swine fever virus, an acute contagious disease affecting domestic pigs and several wild representatives of the family Suidae. Epidemics of this disease have occurred in many African countries, as well as in some southern European-Mediterranean countries, but also in Brazil and Central America (Cuba, Dominican Republic, Haiti). *Ornithodoros coriaceus* transmits *Borrelia coriaceae*, the causative agent of epizootic bovine abortion in the western United States. Cattle, and especially sheep, densely parasitized by *Argas lahorensis*, may suffer from large losses of blood and often die. Some representatives of the genus *Argas* that are closely connected with poultry transmit destructive diseases of domestic birds. Fowl (or avian) spirochetosis caused by *Borrelia anserina* affects chickens, geese, ducks, turkeys, pheasants and some other fowl and decorative birds. The fowl tick, *A. persicus* (Fig. 79), the most important cosmopolitan poultry parasite, is the main vector of the pathogen. The pigeon tick *A. reflexus* (and,



Argasid (Soft) Ticks (Acari: Ixodida: Argasidae), Figure 79 **The fowl tick, *Argas persicus*.**

perhaps, other species from the *A. reflexus* group) also participates in transmission of the disease. The mode of transmission is unique for tick-borne borrelioses, by contamination from infectious tick feces. Transovarial passage of the pathogen has been proved. Fowl spirochetosis is spread worldwide: in North, Central and South America, Europe, Australia and many regions of Asia and Africa. *Argas persicus* is also responsible for transmission of a rickettsia, *Aegyptianella pullorum*, infecting some fowl. The disease is especially destructive for young chickens. *Argas walkerae*, whose adults transmit this disease in South Africa, also causes paralysis in chickens when its larvae feed on them.

A number of other human and animal pathogens have been isolated in nature from some species of argasid ticks, but there is not enough data to consider such ticks as competent vectors. On the other hand, some argasid ticks have been successfully infected by different pathogens in the laboratory, and maintained the pathogens for some time, but this also does not constitute proof of the tick importance in transmission of the disease. Nevertheless, the involvement of argasid ticks in the transmission of other diseases is very possible.

Human Response to Tick Feeding

Human skin reacts to argasid bites, sometimes rather severely. People are often insensitive at the time of the tick bite but later a strong itch appears followed by scratching and the appearance of ulcers. The strength of the human reaction depends on the tick species. Evidence of *Ornithodoros tholozani* bites may be in evidence for many months. *Argas* ticks living in towns and parasitizing pigeons often inhabit human dwellings, even some apartments in many-story buildings, and may cause allergic responses and toxicoses in humans. Many cases of anaphylactic reactions (sometimes even with fatal results) caused by bites of *A. reflexus* have been reported in European towns where pigeon populations increased dramatically during past decades. Such reactions are typical for other members of *Argas reflexus* group (e.g., for *A. latus* in Israel).

The most severe form of tick toxicosis is tick paralysis, which only occurs after prolonged feeding. In argasid ticks, the known cases of tick paralysis were described only for larvae characterized by prolonged feeding. Larvae of several *Argas* species cause paralysis of fowl with total recovery after all larvae drop off the host. Paralysis and death of sheep and cattle caused by *Argas lahorensis* has been reported from some European countries, Caucasus and Central Asia after attachment of 100–200 nymphal ticks of the slow-feeding third instar.

Management of Tick Populations

Personal prophylaxis is the basis of human protection from argasid ticks. It is necessary to avoid resting and overnighting in sites where tick attacks are possible. The most efficient method of tick eradication in human dwellings is the improvement of dwellings so that ticks are deprived of possible shelter. The maintenance of good sanitary conditions in poultry houses and farms with limited use of acaricides should maintain the abundance of fowl ticks at a low level. The acaricidal treatment of domestic animals infested by argasids is an effective mode of tick control. Some animal diseases, such as African swine fever, can be eradicated either by very severe quarantining of the infected herds or by destroying the infected herds together with the ticks infesting the animals. Only a small number of pathogens, parasites and predators of argasid ticks are known, thus it is impossible to estimate the prospects of their use for argasid tick control.

References

Balashov YS (1972) Bloodsucking ticks (Ixodoidea) – vectors of diseases of man and animals. Miscellaneous Publications of the Entomological Society of America 8:163–376

Filippova NA (1966) Argasid ticks (Argasidae). Fauna S.S.S.R. Paukoobraznye, 4(3). "Nauka," Moskva-Leningrad, p 256. (in russian)
Hoogstraal H (1985) Argasid and Nuttalliellid ticks as parasites and vectors. Adv Parasitol 24:135–238
Horak IG, Camicas J-L, Keirans JE (2002) The Argasidae, Ixodidae and Nuttalliellidae (Acari: Ixodida): a world list of valid tick names. Exp Appl Acarol 28:27–54
Klompen JSH, Oliver JH Jr (1993) Systematic relationships in the soft ticks (Acari: Ixodida: Argasidae). Syst Entomol 18:313–331
Mans BJ, GotheR, Neitz AWH (2004) Biochemical perspectives on paralysis and other forms of toxicoses caused by ticks. Parasitology 129:S95–S111
Obenchain FD, Galun R (eds) (1982) Physiology of ticks. Pergamon Press, Oxford, UK, 509 pp
Sonenshine DE (1991) Biology of ticks, vol 1. Oxford University Press, New York, NY, 447 pp
Sonenshine DE (1993) Biology of ticks, vol 2. Oxford University Press, New York, NY, 465 pp

Argentine Ant, *Linepithema humile* (Mayr) (Hymenoptera: Formicidae: Dolichoderinae)

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Identification and Taxonomy

Argentine ants belong to the subfamily Dolichoderinae, or odorous ants, characterized in the worker caste by the presence of a single constricted petiolar segment, the lack of a sting, and a transverse slit-like anal orifice. Worker ants (Fig. 80) of the genus *Linepithema* can be further recognized by the combination of the anterior clypeal margin bearing a medial concavity and a distinct mandibular dentition bearing a series of larger teeth interspersed with two to three small denticles.

The Argentine ant is distinguished from all other *Linepithema* species in the worker caste by a lack of erect setae on the mesosomal dorsum, the presence of dense pubescence on the mesopleuron, large compound eyes comprised of 80–110 ommatidia, and the long antennal scapes that are as long or slightly longer than head length. Worker ants are uniformly reddish brown to dark brown and are between two and three millimeters in length. *Linepithema humile* males are unmistakable as they have an unusually robust mesosoma, longer than the gaster, that bears a distinctly concave posterior propodeal face.

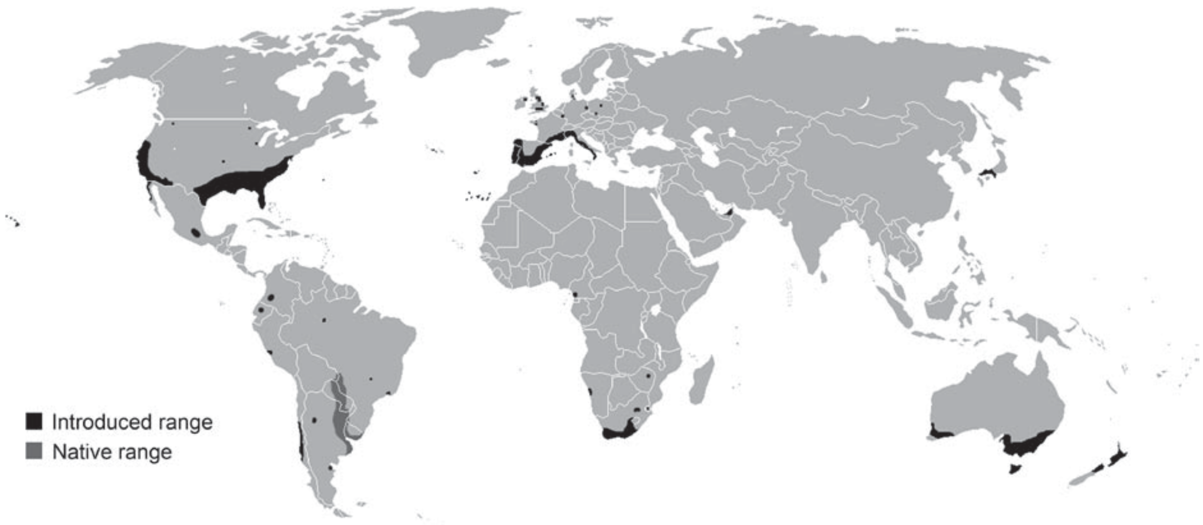
Argentine Ant, *Linepithema humile* (Mayr), (Hymenoptera: Formicidae: Dolichoderinae), Figure 80 A foraging Argentine ant, ***Linepithema humile*.**

Much of the early literature about this species is found under the name *Iridomyrmex humilis*. The change to current nomenclature occurred when recent phylogenetic research revealed a number of new world dolichoderine species, including the Argentine ant, to be unrelated to true *Iridomyrmex*, a strictly Indo-Australian group.

Distribution

The natural distribution of *Linepithema humile* (Fig. 81) extends in the south from the Buenos Aires province across Paraguay to the Pantanal in the north, and is closely associated with major waterways in subtropical South America's Paraná River drainage. This species typically inhabits lowland forests and grasslands in the Paraná and Paraguay floodplains.

In the eighteenth century, *L. humile* began to appear elsewhere in the world, arriving on the Atlantic island of Madeira in the 1850s and in the southern United States and in Portugal in the 1890s. In spite of its humid subtropical provenance, this insect has been most successful invading Mediterranean climates. Thriving introduced populations are now found in California, Mexico, Hawaii,



Argentine Ant, *Linepithema humile* (Mayr), (Hymenoptera: Formicidae: Dolichoderinae), Figure 81 **Current distribution of Argentine ant, *Linepithema humile*.**

Ecuador, Colombia, Chile, Peru, South Africa, Japan, temperate Australia, New Zealand, numerous Pacific islands, and throughout the Mediterranean region. Occasional populations persist indoors in northern Europe and North America. Microsatellite evidence suggests that at least some of these introduced populations originated in Argentina near the port city of Rosario.

Biology

Like most ant species, Argentine ants are haplodiploid and eusocial. They live in colonies composed largely of sterile female workers and a smaller number of fertile queens and males. Unlike most ants, queens of *L. humile* do not fly, mating instead in the nest. Genetic evidence suggests that queens are singly mated. For reasons that remain obscure, up to 90% of queens in a colony are periodically executed by the workers. Males are present in early summer and disperse by wing at dusk. As for all Holometabola, metamorphosis is complete. Development time is dependent on temperature and has been estimated at 445 degree-days above a 16°C threshold for workers. Under field conditions, the process from egg to adult can take several weeks to several months.

Argentine ants possess a number of life history traits that facilitate colonization and possibly pre-adapt this species as a globally successful invader. First, Argentine ant colonies have a large number of fertile queens, in some colonies running into the thousands. This polygyny increases the chance that an isolated nest fragment will contain a queen and be able to grow into a successful colony. Second, colony reproduction occurs by budding. Argentine ants do not have to pass through the high mortality bottleneck at colony founding endured by haplometrotic species that found new colonies with single queens drawing on body reserves. Indeed, *L. humile* queens without workers are incapable of founding new colonies, but propagules as small as 10 workers with a queen or even female brood can mature into populous colonies. Finally, Argentine ants cope with frequent disturbance of nesting sites. Nests tend to be superficial and transitory, occupying the top level of soil or litter. The ants move among existing nests and establish new nests frequently in response to changes in moisture and temperature. In their native range colonies will climb trees to escape rising flood waters.

Argentine ant colonies can reach extraordinary sizes, inhabiting a diffuse system of interconnected nests spanning a few meters to several hundred kilometers or more. While colony networks in the native range are restricted to at most a few thousand square meters, introduced populations normally comprise unicolonial "supercolonies" on the scale of landscapes or even continents. Supercolonies are thought to arise following population bottlenecks at introduction that produce genetic homogeneity among descendents. Such colonies are normally diagnosed using aggression assays and have been documented to cover coastal Chile, California, most of Southern Europe, and parts of Australia.

Argentine ants, like all *Linepithema* species, are trophic generalists. They predate and scavenge a wide variety of protein sources, often arthropods, and display a high affinity for honeydew. Argentine ants recruit quickly to food sources using chemical communication and are often seen running in active foraging trails. The trail pheromone is (Z)-9-Hexadecenal, produced by the Pavan's gland at the tip of the abdomen.

Effects

Introduced populations of *L. humile* penetrate both human-disturbed and natural habitats. They disrupt ecosystem processes both through active predation and exploitative competition. Community diversity is often reduced following invasion, and Argentine ants have been documented displacing native arthropods in California, Hawaii, Japan, South Africa, and Spain. Long term effects of Argentine ant invasions have included changes in South African fynbos plant community structure via displacement of native seed-dispersing ants, and local extinction of *Phrynosoma* lizards in California following the decline of their native ant prey.

Damage to agriculture stems largely from the ants' association with honeydew-producing pests. The ants protect their insect symbionts from attack by predators and transport them to uninfested plants, leading to outbreaks in populations of aphids, scale insects and mealybugs. Argentine ants are especially problematic in orchards and greenhouses where they confound biological control efforts.

The extent of Argentine ant invasion is likely limited by a combination of abiotic conditions and interactions with other ant species. Invasions are facilitated in arid regions by development-related increases in moisture from irrigation and run-off. Highly competitive local ant communities may limit the spread of the Argentine ant. In the southeastern United States, for example, Argentine ant numbers declined following the introduction of the fire ant *Solenopsis invicta*.

Management

The diffuse network structure of Argentine ant colonies renders control more difficult than for many other ant pests, as extirpated nests are readily replenished from neighboring areas. Effective control is unlikely to be gained with any single strategy, and pest managers may have to experiment with different approaches to treat an infestation. Treatment of Argentine ants around homes should include cleaning indoor ant trails when they appear, removal of potential water and food sources, and sealing the ants' entry points into the house. Control using toxic baits is often effective, and boric acid-based liquid baits are generally more palatable to the ants than most commercially available ant baits. As a last resort, appropriate perimeter insecticides or repellents may be applied. For agricultural infestations, chemical or physical barriers applied to individual plants have reduced ant damage.

No specialized natural enemies are known for the Argentine ant, but this insect has received relatively little research in its native range and some may yet be discovered. Recent work suggests that native populations may be held in check by intraspecific competition among colonies and interspecific competition with species such as *Solenopsis invicta*, also native in the Paraná drainage. If this is the case, long-term strategies for limiting the effects of Argentine ants may include the maintenance of robust native ant communities.

References

Human KG, Gordon DM (1996) Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile* and native ant species. Oecologia 105:405–412

Soeprono M, Rust MK (2004) Strategies for controlling Argentine ants (Hymenoptera: Formicidae). Sociobiology 44:669–682

Suarez AV, Holway DA, Case TJ (2001) Patterns of spread in biological invasions dominated by long-distance jump dispersal: insights from Argentine ants. Proc Natl Acad Sci USA 98:1095–1100

Tsutsui ND, Case TJ (2001) Population genetics and colony structure of the Argentine ant (*Linepithema humile*) in its native and introduced ranges. Evolution 55:976–985

Wild AL (2004) Taxonomy and distribution of the Argentine ant *Linepithema humile* (Hymenoptera: Formicidae). Ann Entomol Soc Am 97:1204–1215

Argidae

A family of sawflies (order Hymenoptera, suborder Symphyta).

► Wasps, Ants, Bees and Sawflies

Argyresthiidae

A family of moths (order Lepidoptera). They commonly are known as shiny head-standing moths.

► Shiny Head-Standing Moths
► Butterflies and Moths

Arista

A large hair or bristle on the antennae of flies.

► Antennae of Hexapods

Armored Scales

Members of the family Diaspididae, superfamily Coccoidae (order Hemiptera).

► Bugs
► Scale Insects and Mealybugs

Army Ants

Ants that display group predatory and nomadic behaviors. The nest site is changed at regular intervals, and workers forage in groups.

► Ants

Army Cutworm, *Euxoa auxiliaris* (Grote) (Lepidoptera: Noctuidae)

This insect is found in the Great Plains and Rocky Mountain regions of the United States and Canada. It has been recorded from all states west of the Mississippi River, and as far east in Canada as Ontario, but attains high densities only in semiarid areas, especially along the western edge of the Great Plains.

Host Plants

Army cutworm has been reported to feed on a large number of plants. It is known principally as a pest of small grains, perhaps because these crops dominate the landscape where army cutworm occurs. It damages such field crops as alfalfa, barley, clover, flax, rye, sanfoin, sunflower, sweet clover, timothy, vetch, and wheat. Among vegetable crops, it has been reported to damage beet, cabbage, celery, corn, onion, pea, potato, radish, rhubarb, tomato, and turnip. Other crops injured include such fruit crops as apple, apricot, blackberry, cherry, currant, gooseberry, peach, plum, prune, raspberry, and strawberry. Army cutworm also feeds on noncultivated plants such as bluegrass, *Poa* spp.; bromegrass, *Bromus* spp.; buffalograss, *Buchloe dactyloides*; grama grasses, *Bouteloua* spp.; field pennycress, *Thlaspi arvense*; dandelion, *Taraxacum officinale*; lambsquarters, *Chenopodium album;* and lupine, *Lupinus* spp.

Natural Enemies

Many natural enemies have been found associated with army cutworm, and both hymenopterous parasitoids and disease have been documented to cause considerable mortality. In the central Great Plains, mortality studies over a 20-year period demonstrated parasitism levels of up to 33% and disease incidence of up to 57%. Not surprisingly, incidence of disease was greatest at high armyworm population densities. In a 3-year study in Oklahoma, researchers found that <12% of larvae were parasitized, with most parasitism due to two species, *Meteorus leviventris* (Wesmael) and *Apanteles griffini* Viereck (both Hymenoptera: Braconidae). A polyembryonic wasp, *Copidosoma bakeri* (Howard) (Hymenoptera: Encyrtidae), causes larvae to consume more food, to become larger, and live longer; this can result in the appearance of artificially high rates of parasitism, which sometimes exceeds 50%.

Among the other parasitoids known from army cutworm are such wasps as *Apanteles marginiventris* (Cresson), *A. militaris* Walsh, *Chelonus insularis* Cresson, *Macrocentrus incompletus* Muesebeck, *Microplitis feltiae* Muesebeck, *M. melianae* Viereck, *Rogas* sp., *Zele melea* (Cresson) (all Hymenoptera: Braconidae); *Campoletis flavicincta* (Ashmead), *C. sonorensis* (Cameron), *Diphyus nuncius* (Cresson), *Exetastes lasius* Cushman, and *Spilichneumon superbus* (Provancher) (all Hymenoptera: Ichneummonidae). Flies known to parasitize this species include *Bonnetia comta* (Fallen), *Euphorocera claripennis* (Macquart), *Mericia* spp., *Peleteria* sp., *Periscepsia cinerosa* (Coquillett), *P. helymus* (Walker), and *P. laevigata* (Wulp) (all Diptera: Tachinidae).

Several viruses are known to infect army cutworm, including entomopox, granulosis, and nonoccluded viruses. The relative importance of each is uncertain, but the granulosis virus is unusually pathogenic.

Life Cycle and Description

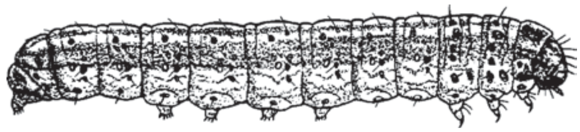
There is a single generation per year throughout the range of this insect. Eggs are deposited on soil in August-October. Eggs hatch in autumn or early winter, and larvae overwinter, feeding actively in the spring. Pupation occurs about a month before adults appear. Adults first become active in April-May in southern locations such as Kansas and Texas, whereas in more northern locations such as Alberta and Montana they may not appear until June-July. The moths migrate from the plains, where the larvae develop, to higher elevations in the Rocky Mountains, where the adults feed on nectar from flowers. The adults return to the plains in August-September.

Egg

Eggs are deposited singly or in small clusters just beneath the soil surface on a solid substrate. The eggs are a slightly flattened sphere, measuring about 0.6 mm in diameter and 0.5 mm in height. The egg is white to yellow initially, becoming gray to brown as the embryo matures. The egg is marked with about 18 very narrow ridges that radiate from the apex. Survival of eggs is reported to be affected by moisture, and above-average rainfall in late summer and autumn tends to assure good insect survival and damaging populations the subsequent year. Field-collected females were reported to produce 200–300 eggs, with the potential to produce about 500 eggs.

Larva

The eggs hatch in the autumn or early winter but the larvae are usually not noticed until spring when they increase in size and begin to consume considerable foliage. There are 6–7 instars, with head capsule widths of 0.26–0.30, 0.40–0.45, 0.65–0.72, 1.04–1.21, 1.70–2.10, and 2.90–3.40 mm, respectively, for instars 1–6 among larvae with only 6 instars. Additional instars apparently occur when larvae feed on less suitable host plants. The body color of the larvae is (Fig. 82) grayish brown, but bears numerous white and dark brown spots. There usually is evidence of 3 weak light-colored dorsal stripes. Laterally there tends to be a broad dark band, and the area beneath the spiracles is whitish. The head is light brown with



Army Cutworm, *Euxoa auxiliaris* (Grote) (Lepidoptera: Noctuidae), Figure 82 Larva of army cutworm *Euxoa auxiliaris*.

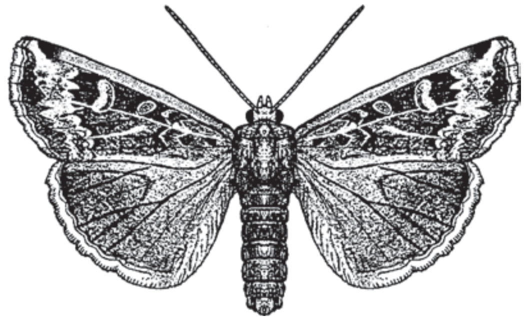
dark spots. Larvae attain a length of about 40 mm. They usually are found beneath the surface of the soil, emerging in late afternoon or early evening to feed. On cloudy days, however, they may be active during the daylight hours. Larvae will assume a migratory habit when faced with food shortage, and large numbers will proceed in the same direction, consuming virtually all vegetation in their path. It is this dispersive behavior that is the basis for their common name, and larvae have been observed to disperse over 4 km.

Pupa

Pupation occurs in the soil, in a cell prepared by the larva. The walls of the cell are formed with salivary secretion, which hardens and provide a degree of rigidity. The depth of pupation varies according to soil and moisture conditions, but may be any depth up to 7.5 cm. The larva spends about 10 days in the cell prior to pupation. Duration of pupation is 25–60 days. The pupa is dark brown in color, and measures about 17–22 mm in length and 6 mm in width.

Adult

The adults measure 35–50 mm in wingspan. They are quite variable in appearance, with five named subspecies, but moths generally assume two basic forms. One common form has the leading edge of the forewing marked with a broad (Fig. 83) yellowish stripe, and the remainder of the wing blackish but marked with white-rimmed bean-shaped and round spots, and a light transverse line. In another common color form the forewing is mottled brown,



Army Cutworm, *Euxoa auxiliaris* (Grote) (Lepidoptera: Noetuidae), Figure 83 Army cutworm adult, light form.

bearing bean-shaped and round spots but lacking bands and stripes. In all cases, the hind wings are brownish with dark veins, and darker distally. The brown body of the moth is quite hairy.

As previously noted, the adults are migratory, dispersing from the plains to the mountains annually. In transit and in the mountains they feed on nectar from flowering plants. They are nocturnal, and seek shelter during the daylight hours. They have the habit of aggregating in houses, automobiles, and other sheltered locations where they become a nuisance, soil walls, and induce allergic reactions among some individuals. They also may aggregate in natural shelters in mountainous regions, where they become prey for bears. In the Rocky Mountain region they are commonly called "miller moths".

Damage

These insects principally are pests of small grain crops grown in arid regions, although a number of irrigated crops also are at risk. Larvae readily climb plants to consume foliage, eating holes in vegetation initially, and eventually destroying the entire plant. Although they burrow into the soil during the daylight hours they do not normally feed below-ground. However, when succulent food is in short supply they will follow the plant stem down into the soil. When food supplies are exhausted large numbers of larvae may disperse in search of additional food.

Management

Adults can be captured in light traps and pheromone traps. However, males are attracted to the sex pheromone only during the autumn flight. Pheromone traps positioned at a height of 1 m or lower are more effective than those place higher. Larvae can be recovered from soil by raking through the top 5–7 cm.

Persistent insecticides can be applied to vegetation to kill army cutworm larvae when they emerge from the soil to feed; *Bacillus thuringiensis* is not effective. Larvae also will accept bran bait containing insecticide.

Cultural manipulations are not generally effective to prevent oviposition because moths will deposit eggs on barren soil. Delayed planting of crops can be effective, however, as larvae complete their development on weeds or starve before crops are planted. If larvae are dispersing, creation of deep ditches with steep sides, or filled with running irrigation water, may prevent invasion of fields.

To protect plants grown in the home garden, barriers are sometimes used to reduce access by cutworms to seedlings. Metal or waxed paper containers with both the top and bottom removed can be placed around the plant stem to deter consumption. Aluminum foil can be wrapped around the stem to achieve a similar effect. Because larvae will burrow and feed below the soil line, the barrier should be extended below the soil surface.

► Wheat Pests and their Management

References

Burton RL, Starks KJ, Peters DC (1980) The army cutworm. Oklahoma Agricultural Experiment Station Bulletin 739:1–35

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, 729 pp

Kendall DM, Kevan PG, LaFontaine JD (1981) Nocturnal flight activity of moths (Lepidoptera: Noctuidae) in alpine tundra. Can Entomol 113:607–614

Armyworm, *Pseudaletia unipuncta* (Haworth) (Lepidoptera: Noctuidae)

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Armyworm also occurs in many areas of the world, including North, Central and South America, southern Europe, central Africa, and western Asia. It is known principally as a grain pest. It does not overwinter in northern latitudes, but disperses northward each spring, and then southward during the autumn. Because it is found widely, it has acquired several common names, including true armyworm, rice armyworm, and American armyworm.

Life History

Although not surviving year-round in cold winter areas, larvae apparently overwinter at intermediate levels, and in warm weather areas all stages may be found during the winter. The number of generations varies among locations, but in North America two generations occur annually in Ontario, Canada, whereas in the USA there are 2–3 generations in Minnesota and New York, 4–5 are reported in Tennessee, and 5–6 in southern states. A complete generation requires 30–50 days.

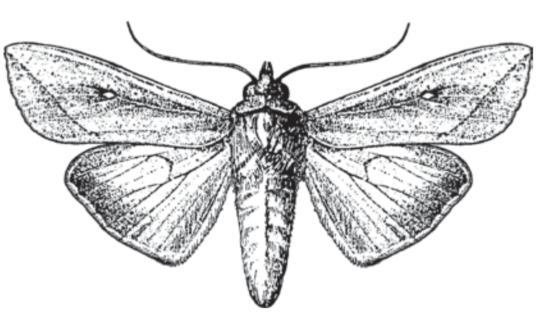
Females deposit eggs in clusters consisting of two to five rows, in sheltered places on foliage, often between the leaf sheath and blade, especially on dry grass. Often females seem to deposit large numbers in the same vicinity, resulting in very high densities of larvae in relatively small areas of a field. Nevertheless, the eggs are very difficult to locate in the field. The eggs are white or yellowish, but turn gray immediately before hatching. Eggs are spherical, and measure about 0.54 mm (range 0.4–0.7 mm) in diameter. The egg surface appears to be shiny and smooth, but under high magnification fine ridges can be observed. The egg clutches are covered with an adhesive secretion that is opaque when wet but transparent when dry. As the adhesive material dries it tends to draw together the foliage, almost completely hiding the eggs. Mean duration of the egg stage is about 3.5 days at 23°C, and 6.5 days at 18°C, but the range is 3–24 days over the course of a season. Hatching rates are affected by temperature, with cool weather more favorable for embryonic survival. In Tennessee, about 98% egg hatch occurs in early spring and autumn, with hatching rates dropping to less than 30% during the summer; this probably accounts for the evolution of the dispersal behavior in this species.

Larvae normally display 6 instars, though up to 9 instars have been observed. Mean head capsule widths (range) are 0.34 (0.30–0.37), 0.55 (0.49–0.63), 0.94 (0.83–1.12), 1.5 (1.29–1.70), 2.3 (2.08–2.56), and 3.3 (3.04–3.68) mm, respectively, for instars 1–6. Head capsule widths increase slightly with increased temperature up to about 30°C. Larvae attain a body length of 4, 6, 10, 15, 20, and 35 mm, respectively, during instars 1–6. Except for the first instar, which is pale with a dark head, the larvae of armyworm are marked with longitudinal stripes throughout their development. The head capsule is yellowish or yellow-brown with dark net-like markings. The body color is normally grayish green, but a broad dark stripe occurs dorsally and along each side (Fig. 85). A light subspiracular stripe often is found laterally beneath the dark stripe. Development time varies with temperature. During summer larvae complete their development in about 20 days, but this is extended to about 30 days during the spring and autumn, and greatly prolonged during winter. Instar-specific development times recorded during early summer in Tennessee are 2–3, 2–3, 2–4, 2–3, 4–5, and 7–10 days for instars 1–6, respectively. The larvae tend to disperse upward following hatching, where they feed on tender leaf tissue. If disturbed, they readily extrude silk and spin down to the soil. Larvae in instars 3–6 are active at night, seeking shelter during the day on the soil beneath debris or clods of soil.

Larvae pupate in the soil, often under debris, at depths of 2–5 cm. Pupation occurs in an oval cell that contains a thin silken case. The pupa is moderate in size and robust, measuring 13–17 mm long and 5–6 mm wide. The pupa is yellowish brown initially, but soon assumes a mahogany brown color. The tip of the abdomen bears a pair of hooks. Duration of the pupal stage is 7–14 days during summer but longer early and late in the season, sometimes lasting 40 days.

The adult is a light reddish brown moth with a wing span measuring about 4 cm. The forewing is fairly pointed (Fig. 84), appearing more so because a transverse line of small black spots terminates in a black line at the anterior wing tip. The forewing is also marked with a diffuse dark area centrally containing one or two small white spots. The hind wings are grayish, and lighter basally. Adults are nocturnal. Mating commences 1–3 days after moths emerge from the soil, and usually 4–7 h after sunset. Eggs are normally deposited within a 4–5 day period (range 1–10). Females produce an average of 4.9 egg masses (range 1–16). Reproductive capacity varies, with authors reporting mean egg production anywhere from 500 to 1500 per female. Feeding is necessary for normal oviposition. Mean longevity at warm temperatures is about 9 days in males and 10 days in females (range 3–25) whereas at cool temperatures mean longevity of males is 19 days and females 17 days.

Armyworm generally prefers to oviposit and feed upon plants in the family Gramineae, including weedy grasses. Thus, such grain and grass crops as barley, corn, millet, oats, rice, rye, sorghum, sugarcane, timothy, and wheat may be consumed, as well as wild or weed grasses. During periods of abundance larvae feed more generally, damaging such crops as alfalfa, artichoke, bean, cabbage, carrot, corn, celery, cucumber, lettuce, onion, parsley,



Armyworm, *Pseudaletia unipuncta* (Haworth) (Lepidoptera: Noctuidae) Figure 84 Adult of armyworm, *Pseudaletia unipuncta* (Haworth).

parsnip, pea, pepper, radish, sugarbeet, sweet potato, watermelon, and others. Adults feed on nectar of various flowers and sometimes feed on other sweet foods such as ripe and decaying fruit.

The importance of natural enemies, especially parasitoids, has been studied, though nearly all data are derived from periods of high armyworm density, which is not typical for this insect. Over 60 species of wasp and fly parasitoids are known, and vary considerably from time to time and place to place in importance.

Predators readily consume armyworm larvae. Ground beetles (Coleoptera: Carabidae) are especially effective because larvae spend a great deal of time in association with soil, but various predatory bugs (Hemiptera: various families), ants (Hymenoptera: Formicidae), and spiders (Araneae: Lycosidae and Phalangiidae) also feed on armyworm. Avian predators are often credited with destruction of armyworms. The bobolink, *Dolichonyx oryzivorus* (Linnaeus), prospers during outbreak years and has sometimes been called the "armyworm bird" in North America. Other birds of note include the crow, *Corvus brachyrhynchos* Brehm, and starling, *Sturnus vulgaris* Linnaeus.

Diseases commonly infect armyworms, especially during periods of high density. Bacteria and fungi, particularly the fungus *Metarhizium anisopliae*, are reported in the literature. Nematodes are sometimes considered to be important mortality factors. However, undoubtedly the most important diseases are viruses; several granulosis, cytoplasmic polyhedrosis, and nuclear polyhedrosis viruses often kill virtually all armyworms during periods of outbreak, especially when larvae are also stressed by lack of food or inclement weather.

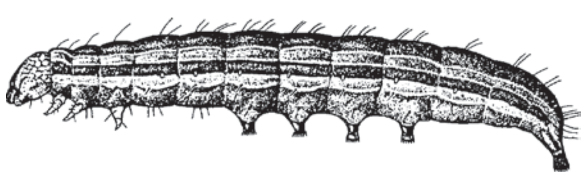
Armyworm attains high densities irregularly, often at 5–20 year intervals. The exact cause is unknown, but outbreaks often occur during unusually wet years and are preceded by unusually dry years. Armyworm is not well adapted for hot temperature; survival decreases markedly when temperatures exceed about 30°C. Consequently, at southern latitudes populations are higher early and late in the year, but at northern latitudes it is a mid season pest.

Damage

Larvae initially skeletonize foliage, but by the third instar they eat holes in leaves, and soon afterwards consume entire leaves. Larvae of armyworm (Fig. 85) are notorious for appearing out of nowhere to inflict a high level of defoliation. This occurs for several reasons: a highly clumped distribution of young larvae, with most of the crop uninfested until larvae are nearly mature and highly mobile; a tendency by larvae to feed on grass weeds preferentially, only moving to crops after the grass is exhausted; occurrence of a preponderance of feeding, about 80%, in the last instar; the nocturnal behavior of larvae, which makes them difficult to observe during the day; and the gregarious and mobile behavior of mature larvae, which form large aggregations or bands (hence the common name "army" worm). As previously noted, grasses and grains are preferred, but as these plants are consumed larvae disperse, often in large groups, to other plants. During outbreaks, few plants escape damage.

Management

Adults can be captured with blacklight traps, and a sex pheromone has been identified and can be used for population monitoring. It is advisable to examine crop fields for larvae, especially if moths have been captured in light or pheromone traps. Fields should be examined at dawn or dusk, because larvae are active at this time. If it is necessary to check fields during the day, it is important to sift through the upper surface of the soil and under debris for resting larvae.



Armyworm, *Pseudaletia unipuncta* (Haworth) (Lepidoptera: Noctuidae), Figure 85 Larva of armyworm, *Pseudaletia unipuncta* (Haworth).

Larvae will consume wheat bran or apple pomace baits treated with insecticide, but foliar and soil-applied insecticides are also effective, and used frequently.

Cultural practices have limited effect on armyworm abundance due to their highly dispersive behavior. However, grass weeds are a focal point of infestation, and should be eliminated, if possible. Not surprisingly, no-till and minimum tillage fields experience greater problems with armyworm, relative to conventional tillage fields. Proximity to small grain crops is considered to be a hazard due to the preference of moths for such crops, and the suitability of grains for larval development. In Virginia, destruction of winter cover crops by herbicide application is more favorable to armyworm survival than is mowing of cover crops, apparently because predators are more disrupted by herbicide treatment. Prior to the availability of effective insecticides, deep furrows with steep sides were sometimes plowed around fields to prevent invasion by dispersing armyworm larvae. Although this approach remains somewhat useful, it is rarely practiced.

► Turfgrass Insects and their Management
► Wheat Pests and their Management

References

Breeland SG (1958) Biological studies on the armyworm, *Pseudaletia unipuncta* (Haworth), in Tennessee (Lepidoptera: Noctuidae). J Tennessee Acad Sci 33:263–347

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, 729 pp

Guppy JC (1961) Life history and behaviour of the armyworm, *Pseudaletia unipuncta* (Haw.) (Lepidoptera: Noctuidae), in eastern Ontario. Can Entomol 93:1141–1153

Guppy JC (1969) Some effects of temperature on the immature stages of the armyworm, *Pseudaletia unipuncta* (Lepidoptera: Noctuidae), under controlled conditions. Can Entomol 101:1320–1327

Arnett, Jr., Ross Harold

Ross Arnett was born on April 13, 1919, in the state of New York. He attended Cornell University and earned a B.S. degree in 1942. That same year, he married Mary Ennis, spent a short time working for the New York Conservation Department, then joined the U.S. army. His army duties had him controlling mosquitoes in Florida, and then teaching mosquito taxonomy in Panama. In October 1945, he was discharged by the army, and returned to Cornell University as a graduate student. He received his master's degree in 1946, having studied medical and aquatic entomology. For his doctoral research, he returned to his early interest in beetles, beginning a taxonomic revision of the North American Oedemeridae, and he received his Ph.D. in 1948. He was employed (1948–1954) by the U.S. Department of Agriculture as a taxonomist at the U.S. National Museum, 1954–1958 as professor of biology at Saint John Fisher College in New York state, 1958–1963 as professor of biology at the Catholic University of America (in Washington, DC), 1966–1973 at Purdue University (Indiana), and 1973–1979 at Siena College (New York state). Thereafter, he left academic life and derived his income from publishing. His research interests were in the family Oedemeridae. ("false blister beetles"), on which he published several scientific papers. However, it is as a teacher (he guided several graduate students in taxonomy of Coleoptera) and author of books and journals and publishing projects that entomologists knew him best. His "Beetles of the United States. A manual for identification" was the standard identification reference from its publication in 1962 until its replacement by the two-volume "American Beetles" (volume 1: 2000, volume 2: 2002) that he began. In 1947 he founded The Coleopterists' Bulletin and was for years its editor (it was later and ungrammatically renamed by others The Coleopterists Bulletin). In 1985 he founded the journal Insecta Mundi, which is now published by the Center for Systematic Entomology, of Gainesville, Florida, as a low-cost outlet for taxonomic publications on insects. He published a book on Coleoptera collections of North America, which later was greatly expanded to become "The insect and spider collections of the world" (1986) and still later (1993) was revised, and another (Entomological Information

Storage and Retrieval, 1970) on documentation, both of which were ahead of their time. He was author or coauthor of books on botany, on "How to know the beetles," of "Simon and Schuster's Guide to Insects," and of two volumes on "The Beetles of northeastern North America." His "American Insects" (1985) won the R.R. Hawkins award from the American Association of Publishers, but coleopterists would argue that his works on Coleoptera were far greater. He was the founder of a short-lived journal featuring colored photographs (hitherto rarely seen in entomology because of cost, yet common in everyday advertisements for commercial products) called Insect World Digest, and of two publishing companies (Flora and Fauna publications, and Sandhill Crane Press), which helped entomologists and other biologists to publish their works. He was the instigator in the 1970s of the "North American Beetle Fauna Project," whose ambition was to catalog and document all of the North American Coleoptera. He was the greatest proponent of North American coleopterology for over 50 years. He died on July 16, 1999, in Gainesville, Florida, survived by his devoted wife, Mary Ennis Arnett, who died on January 3, 2002, and eight children.

References

Gerberg EJ (1999) Ross Harold Arnett, Jr. Am Entomol 45:191–192

Thomas MC (1999) Ross H. Arnett, Jr. Coleopterists Bull 53:300

Arolium

A pad or pads found between the tarsal claws or at the base of the tarsi.

► Legs of Hexapods

Arrestant

A factor that causes an insect to aggregate at the site of the factor, but not a factor facilitating long-distance orientation (i.e., not an attractant).

Arrhenogenic

A sex determining system, in which females produce male progeny only. Found in the blow fly *Chrysomya rufifacies* (Calliphoridae).

Arrhenophanidae

A family of moths (order Lepidoptera). They also are known as tropical lattice moths.

► Tropical Lattice Moths
► Butterflies and Moths

Arrhenotoky

A form of parthenogenesis in which an unfertilized egg develops into a male by parthenogenesis and a fertilized egg develops into the female. Arrhenotoky is found in many Hymenoptera.

Artematopididae

A family of beetles (order Coleoptera). They commonly are known as soft-bodied plant beetles.

► Beetles

Artheneidae

A family of bugs (order Hemiptera, suborder Pentamorpha).

► Bugs

Arthropleidae

A family of mayflies (order Ephemeroptera).

► Mayflies

Arthropod-Associated Plant Effectors (AAPEs): Elicitors and Suppressors of Crop Defense

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Interactions between plants and insects have played a significant role in the evolution of both groups of organisms. In response to herbivory, plants have evolved the ability to perceive and defensively respond to insect herbivores (or potential herbivores), either directly, by inducing biochemical changes that impede pest growth or indirectly, by promoting advantageous interactions with beneficial organisms, often through the release of volatile signals. These volatile signals indicate to parasitic and predaceous insects the location of potential prey. Insects may also partly inhibit these induced plant responses by limiting the accumulation of defense-related biochemicals at the feeding site. We collectively refer to substances that either negatively or positively alter plant responses to attack as arthropod-associated plant effectors (AAPEs). Those effectors that increase a plant's defense against an arthropod pest are termed elicitors while those that reduce a plant's defense are suppressors.

Research on arthropod-associated elicitors and suppressors of plant responses traces its roots to the 1972 discovery by Clarence Ryan and colleagues that feeding by Colorado potato beetle (*Leptinotarsa decemlineata*), as well as mechanical damage to tomato plants, rapidly increases the concentration of leaf protease inhibitors. This ultimately led to the discovery of systemin, an 18 amino acid peptide, and established the existence of peptide signals in plants. In 1988, Marcel Dicke and colleagues demonstrated that herbivory by spider mites (*Tetranychus urticae*) induced plant volatiles in lima bean (*Phaseolus lunatus*) leaves, which in turn served as attractants for predatory mites (*Phytoseiulus persimilis*). Shortly thereafter, Jim Tumlinson and colleagues demonstrated similar volatile-mediated tritrophic interactions among the beet armyworm (*Spodoptera exigua*) herbivore, corn (*Zea mays*), and host-seeking parasitic wasps (*Cotesia marginiventris*). In corn, this rapidly induced increase in volatile emission could not be stimulated by mechanical damage alone yet was readily mimicked by the application of beet armyworm oral secretions to wounded leaves. In 1997 the fatty acid-amino acid conjugate *N*-17-hydroxylinolenoyl-L-glutamine, termed volicitin, was discovered in the oral secretions of beet armyworm. This elicitor of corn leaf volatiles marked the first AAPE isolated and identified from insects.

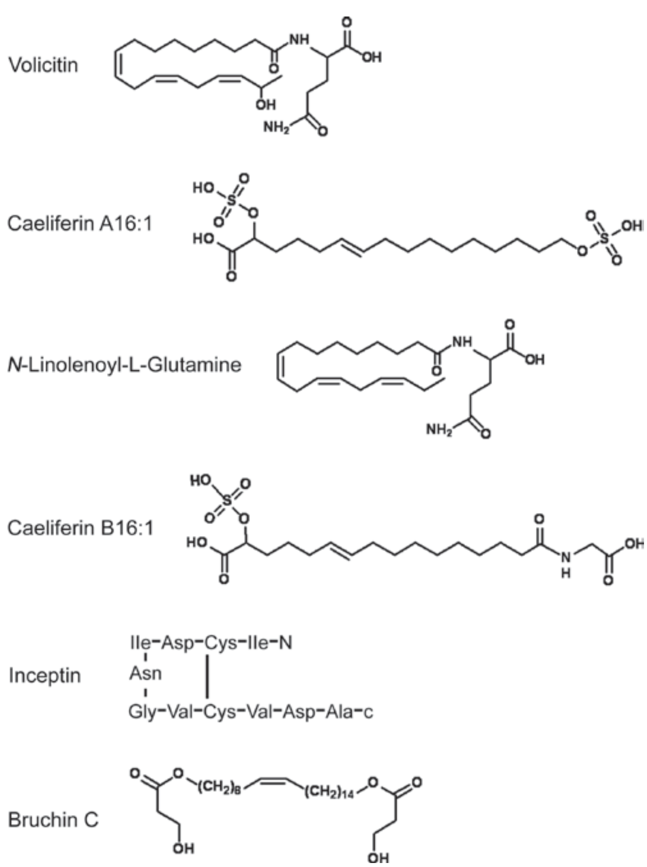
During arthropod feeding or oviposition, mechanical wound responses in the plant can be greatly amplified by the presence of elicitors. Elicitors are specific bioactive chemicals present at the plant wound-site that may be derived from the insect, the plant, or from the interactions between organisms. The mode of action of elicitors may vary, but increasingly some classes are predicted to act as ligands that bind plant receptors (likely membrane-bound extracellular leucine-rich repeat receptor kinases) initiating a complex cascade of signal transduction leading to induced plant responses. Typically, over the course of a few hours, elicitors will cause a rapid induction of defense-related phytohormones, including jasmonic acid, ethylene, and salicylic acid which serve as both markers and signals for subsequent plant defense responses. In contrast to elicitors, suppressors of plant defense may act through direct insect-derived protein/enzyme interactions within the plant. The majority of recently identified AAPEs described below act as elicitors of plant defense; however, glucose oxidase acts as a suppressor of plant defense.

Volicitin

In 1997, Hans Alborn and colleagues isolated and identified volicitin from the larval oral secretions of the beet armyworm (BAW), *Spodoptera* *exigua*. Subsequently, other analogous fatty acid amide elicitors have been identified in the oral secretions of several other species of Lepidoptera. This class of elicitors consists of plant fatty acids, typically linolenic, linoleic, and oleic acid, or their 17-hydroxy analogs, conjugated with glutamine or glutamic acid. They were initially thought to be specific for Lepidoptera but recently they have also been found in katydids, crickets and fruit flies. Thus far, three herbivore-produced fatty acid-amino acid elicitors, volicitin, *N*-linolenoyl-L-glutamine and *N*-linolenoyl-L-glutamate (Fig. 86), have been demonstrated to have significant activity in inducing plants to produce and release volatile organic compounds that are synthesized by several different biosynthetic pathways, including the lipoxygenase, shikimate and isoprenoid pathways. Fatty acid amides seem to have activity on a broad range of plants, although some clear exceptions exist (see inceptin below). A significant release of volatiles can typically be detected a few hours after an application of about 10 pmol volicitin/corn seedling.

Caeliferins

In the early 1990s, when working on the isolation of volicitin, the Tumlinson group observed that not only feeding by lepidopteran larvae but also feeding by the American grasshopper (*Schistocerca americana)* induced corn seedlings to release volatile organic compounds. This led to the recent discovery of a new type of elicitor named caeliferins. These



Arthropod-Associated Plant Effectors (AAPEs): Elicitors and Suppressors of Crop Defense, Figure 86 Structures of some elicitors.

compounds are comprised of saturated and monounsaturated, sulfated alpha-hydroxy fatty acids (with fatty acid chains of 15–20 carbons) in which the omega carbon is functionalized with either a sulfated hydroxyl or a carboxyl conjugated to glycine via an amide bond. In the oral secretions of the American grasshopper, the 16-carbon analogs are predominant and also most active in inducing release of volatile organic compounds when applied to damaged leaves of corn seedlings. It appears that caeliferins, which are the first non-lepidopteran elicitors of volatiles identified in insect herbivores, might be present in most, if not all, grasshoppers (members of the suborder Caelifera), but not in crickets or katydids (suborder Ensifera). Interestingly, oral secretions of at least some crickets and katydids contain some of the same glutamine and glutamic acid-based fatty acid amides that are found in Lepidoptera larvae. Preliminary results indicate that the activity of caeliferins might be restricted to monocotyledons where the response mimics that of volicitin. The typical lowest active dose is about 100 pmol/corn seedling.

Inceptin and Related Peptides

In cowpea (*Vigna unguiculata*) and beans (*Phaseolus vulgaris*), herbivory by fall armyworm (*Spodoptera frugiperda*) larvae and applications of oral secretions elicit phytohormone changes and induce volatile emission due to the presence of a disulfide-bridged peptide termed inceptin. Inceptin and related fragments are derived from the γ-subunit of chloroplastic ATP synthase (cATPC) present in leaf tissue. As a result of insect gut proteolysis, the oral secretion of larval fall armyworm contains a mixture of related peptides derived from cATPC, including additional amino acids at the N terminus and also C-terminal truncations. Inceptin is the one of the most potent AAPEs known to date, and has measurable elicitor activity starting at 1 fmol/leaf. Inceptin elicits a rapid and sequential induction of defense-related phytohormones, such as jasmonic acid, ethylene and salicylic acid, and also stimulates the emission of large amounts of volatile organic compounds. However, inceptin has additional roles in direct plant defense including upregulation of protease inhibitor transcripts and reduced growth of larvae on induced tissues. Similar to established peptide signals with known plant receptors, such as systemin and flg22 (derived from bacterial flagellin), inceptin is also believed to act as a ligand that specifically binds a plant receptor initiating these responses. In cowpea and beans, insect gut proteolysis following herbivory generates inappropriate fragments of an essential metabolic enzyme that enables plant non-self recognition.

Bruchins

The first beetle-derived elicitor of physical plant defense was described from the cowpea weevil (*Callosobruchus maculatus* F.). Oviposition of pea weevil (*Bruchus pisorum* L.) on pods of specific varieties of pea (*Pisum sativum* L.) promotes neoplastic cellular growths that impede entry of neonate weevil larvae into the pod and increase the probability of predation, parasitism and dehydration. This class of elicitors, collectively named bruchins, represents long-chain α,ϖ-diols, partly or entirely esterified with 3-hydroxypropanoic acid. Like the inceptin peptide, bruchins exhibit potent biological activity with as little as 1 fmol (0.5 pg) inducing neoplastic growth on pea pods. Supportive of a role for specific plant receptors, only pea plants harboring the yet uncloned Np allele exhibit these responses.

Glucose Oxidase

The first demonstration of a suppressive effect of AAPEs came from studies of the corn earworm (*Helicoverpa zea*) feeding on leaves of tobacco (*Nicotiana tabacum*). During herbivory larvae secrete the salivary enzyme glucose oxidase (GOX) from the spinneret which reacts with glucose to form hydrogen peroxide and gluconic acid. GOX levels in labial glands vary considerably dependent upon larval diet and host plants. Insect secretion of glucose oxidase limits the wound-induced accumulation of the toxic alkaloid nicotine following herbivory. As a product of GOX, hydrogen peroxide may either directly or indirectly inhibit wound-induced nicotine accumulation but this hypothesis awaits confirmation.

Other Systems for Consideration

Enzymatic activity consistent with β-glucosidase has been found in larvae of the cabbage white butterfly (*Pieris brassicae*). Applications of β-glucosidase preparations from almonds have been reported to promote volatile emission in excised leaves of Brussels sprouts (*Brassica oleracea* L. var *gemmifera*) that have been additionally wounded. Curiously, the role of β-glucosidase as an elicitor of plant volatile emission has not been followed up on in over a decade nor demonstrated outside of the aforementioned experimental system. Many lytic enzymes have the potential to influence plant physiological responses; however, clear and careful experimentation is required prior to demonstrating a substance to be a relevant effector.

Alkaline phosphatase activity has been demonstrated to exist in the salivary glands of adult whiteflies (*Bemisia tabaci* B biotype, syn. *B. argentifolii*) and is also secreted into artificial diets. This enzyme exists as a candidate AAPE but at this time no specific action on plant physiology has been shown. Alternatively, the pore-forming peptide alamethicin and larger polypeptides from preparations of cellulysin, originating from the fungus *Trichoderma viride*, are potent inducers of plant defense responses. These bioactive substances have been demonstrated to have activities similar to known AAPEs yet they are not known to exist in the secretions of arthropods at meaningful levels. Many additional plant-insect systems, such as the plant response to oviposition of insect eggs, have been clearly demonstrated to involve putative AAPEs, yet the majority of these await detailed characterization.

Significance of AAPEs

Many insect herbivores are vulnerable to predators and other natural enemies only during narrow developmental windows. For example, the parasitoid wasp *Cotesia marginiventris* must locate hosts before the end of the caterpillar's second instar. Long range attraction to the hosts is mediated by herbivore-induced plant volatiles, yet the amount of mechanical damage caused by first instar larvae is low. Elicitors, whether plant-or arthropod-produced, serve an important ecological function in amplifying plant signal transduction cascades such that a significant response (i.e., release of volatile organic compounds) is generated from a very modest initial injury.

Photosynthetic organisms have had to cope with biotic stress in the form of microbes long before the existence of insects. A significant component of plant pathology research focuses on the molecular aspects of how plants recognize pathogens and the mechanisms by which pathogens avoid recognition. Emphasis on this area of inquiry arose from necessity and the microscopic nature of the interactions. Entomologists have additional levels of complexity to confront including insect behavior, multiple instars of development and complex multitrophic interactions. Studies involving these visible markers have historically been more numerous than molecular level investigations. Plant breeders strive to maintain insect resistance in new crop cultivars, ideally one step ahead of emerging insect biotypes that overcome these defenses. Currently, numerous examples of genes responsible for plant resistance to insects are being identified as receptor kinases. These receptors are not directly toxic and by themselves do not result in plant resistance. Instead, ligand (i.e., elicitor) binding to receptors triggers induced plant responses that result in resistance. In plant pathology research, some virulent pathogens lack key biochemicals or possess slightly modified protein sequences enabling evasion of receptor-mediated plant recognition. We can fully expect the same interactions to be occurring in insect pests that are specialized on specific crops.

Once basic insect recognition systems are understood in plants at molecular and mechanistic level, strategies will be tractable to transgenically modify and promote a plant's ability to induce rapid defense responses. Some examples of future research on insect biotypes that overcome plant resistance will likely demonstrate mechanisms involving the alterations of receptor-ligand binding interactions. Currently not a single plant-insect interaction involving AAPEs is understood at this level. This research direction is essential for further progress. Understanding the chemistry of the AAPEs that mediate these interactions is more than just a research curiosity. AAPEs represent literal and figurative keys to induced plant defense and resistance to insect pests.

► Allelochemicals
► Tritrophic Interactions
► Plant Resistance to Insects

References

Alborn HT, TurlingsTCJ, Jones TH, Stenhagen G, Loughrin JH, Tumlinson JH (1997) An elicitor of plant volatiles from beet armyworm oral secretion. Science 276: 945–949

Alborn HT, Hansen TV, Jones TH, Bennett DC, Tumlinson JH, Schmelz EA, Teal PE (2007) Disulfooxy fatty acids from the American grasshopper, *Schistocerca americana*, elicitors of plant volatiles. Proc Natl Acad Sci USA 104:12976–12981

Dicke M, Sabelis MW (1988) How plants obtain predatory mites as bodyguards. Netherlands J Zool 38:148–165

Doss RP, Oliver JE, Proebsting WM, Potter SW, Kuy SR, Clement SL, Williamson RT, Carney JR, DeVilbiss ED (2000) Bruchins: insect-derived plant regulators that stimulate neoplasm formation. Proc Natl Acad Sci USA 97:6218–6223

Green TR, Ryan CA (1972) Wound-induced proteinase inhibitor in plant leaves – possible defense mechanism against insects. Science 175:776–777

Halitschke R, Schittko U, Pohnert G, Boland W, Baldwin IT (2001) Molecular interactions between the specialist herbivore *Manduca sexta* (Lepidoptera, Sphingidae) and its natural host *Nicotiana attenuata*. III. Fatty acid–amino acid conjugates in herbivore oral secretions are necessary and sufficient for herbivore-specific plant responses. Plant Physiol 125:711–717

Mattiacci L, Dicke M, Posthumus MA (1995) Beta-Glucosidase – an elicitor of herbivore-induced plant odor that attracts host-searching parasitic wasps. Proc Natl Acad Sci USA 92:2036–2040

Musser RO, Hum-Musser SM, Eichenseer H, Peiffer M, Ervin G, Murphy JB, Felton GW (2002) Herbivory: caterpillar saliva beats plant defences – A new weapon emerges in the evolutionary arms race between plants and herbivores. Nature 416:599–600

Schmelz EA, Carroll MJ, LeClere S, Phipps SM, Meredith J, Chourey PS, Alborn HT, Teal PEA (2006) Fragments of ATP synthase mediate plant perception of insect attack. Proc Natl Acad Sci USA 103:8894–8899

Turlings TCJ, Tumlinson JH, Lewis WJ (1990) Exploitation of herbivore-induced plant odors by host-seeking parasitic wasps. Science 250:1251–1253

Arthropods

Those members of the phylum Arthropoda. Animals with jointed legs. The principal arthropod taxa of interest to entomologists are:

Phylum Arthropoda
- Subphylum Trilobita – Trilobites (these are extinct)
- Subphylum Chelicerata
  - Class Merostomata – Horseshoe crabs
  - Class Arachnida – Arachnids (scorpions, spiders, ticks, mites, etc.)
  - Class Pycnogonida – Sea spiders
- Subphylum Crustacea – Crustaceans (amphipods, isopods, shrimp, etc.)
- Subphylum Atelocerata
  - Class Diplopoda – Millipedes
  - Class Chilopoda – Centipedes
  - Class Pauropoda – Pauropods
  - Class Symphyla – Symphylans
  - Class Entognatha – Collembolans, proturans, diplurans
  - Class Insecta – Insects

In addition, the Phylum Onychophora is sometimes considered to be arthropods, but it is best considered to be a separate phylum, evolutionarily intermediate between arthropods and annelids.

► Centipedes
► Diplurans
► Entognatha

- ► Millipedes
- ► Mites
- ► Pillbugs and Sowbugs
- ► Proturans
- ► Scorpions
- ► Spiders
- ► Springtails
- ► Ticks

Articulation

A connection or joint between two sections of the cuticle, or structures. Articulations take many forms, ranging from membranous or lightly sclerotized area between two plates, to a ball and socket joint.

Ascalaphidae

A family of insects in the order Neuroptera. They commonly are known as green owlflies.

► Lacewings, Antlions and Mantidflies

Ascosphaera apis

One of the best-known ascomycetous insect pathogens is *Ascosphaera* (Plectomycetes). *Ascosphaera apis* causes chalk-brood disease mainly in honey bees, a condition that may not necessarily be serious depending upon the hygienic behavior of the insects; colonies from which diseased brood is removed by worker bees appear to be resistant to the disease. The fungus is usually heterothallic, and during sexual reproduction the trichogyne (receptive female hypha) fuses with a nutriocyte, an inflated part of the ascogonium. The nutriocytes develop asci and ascospores that form into tightly packed spheres called spore balls. The chambers that encase the spore balls are termed the sporocysts, and these appear as dark specks on mummified larvae. Enzyme analysis has been used to identify strains of *Ascosphaera*, whereas certain morphological characteristics can facilitate separation of species. These characteristics include ascospore shape, size, color and arrangement, as well as the size, color, etc., of sporocysts. The location (i.e., subcuticular, external) of the cysts also can be relevant in identification, although it has been reported that cysts of *A. apis* can occur beneath the integument in carpenter bee larvae.

Ascosphaera spores can initiate infection in healthy bee larvae either by breaching the external cuticle or through the digestive tract. Chilling appears to facilitate the infection process, and the peripheral brood, where the temperature may be lower, is therefore more easily infected. Some species of the fungus can infect solitary insects; for example, *A. aggregata* commonly occurs in alfalfa leafcutting bees. The infection is initiated only by ingestion of the spores. The hyphae invade the midgut wall and hemocoel, and eventually replace most of the larval tissues. This species of Ascosphaera does not readily digest chitin, so that sporulation is subcuticular, in contrast to *A. apis* in which the mummified surfaces usually are covered with white mycelia and darkened cysts. When sexual reproduction in *A. aggregata* is complete, and the mature ascospores are formed, the fungal mat becomes dark brown and is hard and dry. This species requires a complex medium for *in vitro* growth and thus appears to be a true obligate parasite. Other species are considered to be opportunistic since they can grow saprophytically, or only infect stressed insects.

References

Gilliam M, Lorenz BJ, Buchmann SL (1994) *Ascosphaera apis*, the chalkbrood pathogen of the honey bee, *Apis mellifera*, from larvae of a carpenter bee, *Xylocopa californica arizonensis*. J Invertebr Pathology 63:307–309

Gilliam M, Taber III S, Lorenz BJ, Prest DB (1988) Factors affecting development of chalkbrood disease in colonies of honey bees, *Apis mellifera*, fed pollen contaminated with *Ascosphaera apis*. J Invertebr Pathol 52:314–325

McManus WR, Youssef NN (1984) Life cycle of the chalk brood fungus, *Ascosphaera aggregata*, in the alfalfa leafcutting bee, *Megachile rotundata*, and its associated symptomatology. Mycologia 76:830–842

Vandenberg JD, Stephen WP (1983) Pathogenicity of *Ascosphaera* species for larvae of *Megachile rotundata*. J Apic Res 22:57–63

Ascoviruses

The members within the proposed Ascoviridae family are characterized by the accumulation of virion-containing vesicles (asco = sac, or bladder) in the hemolymph of host noctuid larvae. The membrane-bound vesicles (1–10 μm) contain hundreds of enveloped allantoid shaped virus particles that are 300–400 nm in length and 130 nm in diameter. The outer surface of the bilayer viral envelope possesses a characteristic reticulate pattern. Purified ascoviruses contain a complex of 12 structural proteins ranging from 11 to 200 kDa. Ascoviruses encapsidate a circular dsDNA (140–180 kbp) having a G + C ratio of 60%. Comparative sequence analysis of the DNA polymerase genes suggests that ascoviruses and iridoviruses shared a common ancestor. Presently, ascoviruses have been detected in several noctuids including *Autographa californica*, *Trichoplusia ni* (TAV), *Spodoptera frugiperda* (SAV), *Heliothis virescens* (HAV), *Heliocoverpa zea* (HZV), and *Scotogramma trifolii* (STV). Southern blot hybridization studies have demonstrated that the SAV genome (140 kbp) differed from the closely related TAV and HAV genomes (180 kbp). Histological examinations revealed that TAV and HAV both replicated in the nuclei of epidermal and mesodermal insect tissues, whereas SAV replication was restricted to fat body tissue.

Ascovirus infections normally retard growth and development of diseased larvae. This virus, originally identified as a Rickettsial-like organism, is slow acting, causing larval death after a prolonged period (20–30 days) of arrested larval growth. These viruses infect a limited number of cells within a particular tissue. Examination of the milky infected hemolymph under light microscopy revealed the presence of numerous virion-containing vesicles. These vesicles are produced by infected cells that undergo an apoptotic-like cleavage. *In vivo*, infected larvae have been observed to discharge infectious virus from the eversible gland. The vesicles, when fed to neonate larvae, resulted in erratic infection patterns (2–85%). However, challenge with a minutin pin dipped in virus suspensions resulted in 100% infection rates. As few as ten vesicles are infectious when delivered into the insect hemocoel. Research has demonstrated that ascoviruses can be mechanically transmitted from infected larvae to healthy larvae during oviposition by parasitoids. The ascoviruses are able to outcompete the developing parasitoid and successfully infect host larvae. It has been suggested that the incidence of ascovirus in noctuid populations, ranging from 1 to 25%, may be associated with the presence of larval parasitoids.

References

Federici BA (1983) Enveloped double-stranded DNA insect virus with a novel structure and cytopathology. Proc Natl Sci Foundation 80:7664–7668

Federici BA, Vlak JM, Hamm JJ (1990) Comparative study of virion structure, protein composition and genomic DNA of three ascovirus isolates. J Gen Virology 71:1661–1668

Bigot Y, Stasiak K, Rouleux-Bonnin F, Federici BA (2000) Characterization of repetitive DNA regions and methylated DNA in ascovirus genomes. J Gen Virol 81: 3073–3082

Asexual

Lacking separate sexes, and reproducing by parthenogenesis.

Ash-Gray Leaf Bugs

Members of the family Piesmatidae (order Hemiptera).

► Bugs

Ash Whitefly, *Siphoninus phillyreae* (Hemiptera: Aleyrodidae)

This species affects citrus and other shrubs and trees. See also, Citrus Pests and their Management, Hemiptera.

► Citrus Pests and their Management

Asian Citrus Psyllid, *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae)

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The Asian citrus psyllid *Diaphorina citri*, is of Far Eastern origin and is also called the oriental citrus psyllid. Its known range of distribution covers tropical and subtropical Asia including India, Burma, Thailand, Nepal, Sikkim, Hong Kong, Ryukyn Islands, the Philippines, Malaysia, Indonesia, Ceylon, Pakistan, Afghanistan, Reunion, and Mauritius. It is also found in Saudi Arabia in the Near East, and Brazil in South America. This insect was first discovered in the United States in 1998, and is now widespread in southern Florida.

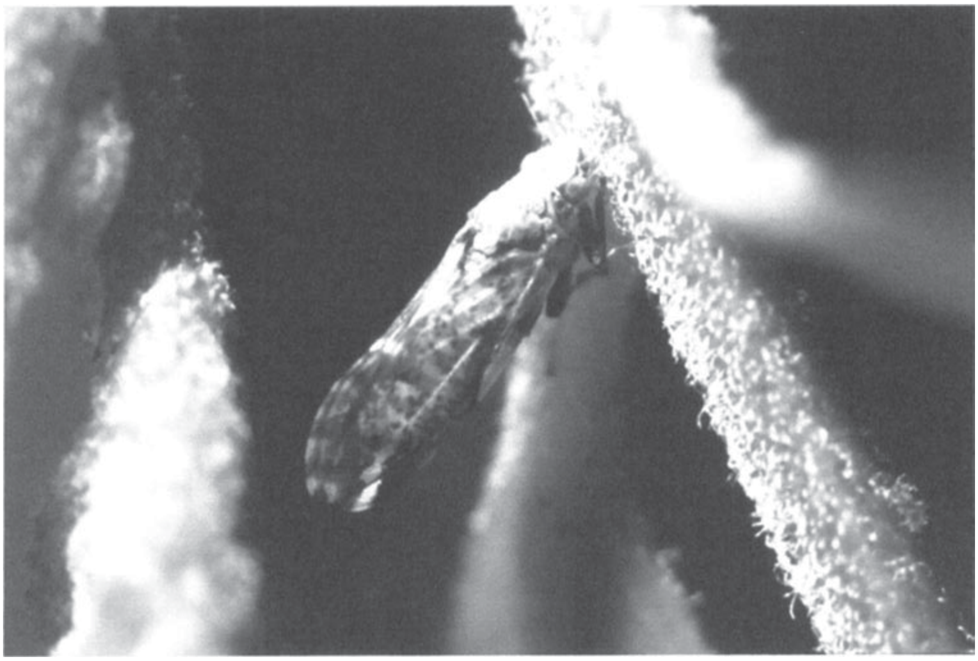
Diaphorina citri causes severe damage to citrus by: (i) withdrawal of a large quantity of sap from the foliage, affecting the overall growth of citrus, and promotion of sooty mold on honeydew secreted onto leaves, which results in reduction of photosynthesis; and (ii) efficient transmission of greening bacterium (*Liberobacter asiaticum*) by *D. citri*. The greening disease (Huanglungbin) is a limiting factor in citrus production in the Far East, though it does not occur in Florida. Citrus infected by the greening agent initially shows leaf mottling and chlorosis symptoms, followed by stunted growth, unseasonable bloom and leaf and fruit drops. Eventually, branch dieback and a general decline will result. Fruits from infected trees are small, uneven in size, off color, and having objectionable flavor. In Southeast Asia, mandarins and oranges are the main citrus trees planted in commercial groves, and they are the most susceptible cultivars. *Liberobactor asiaticum* is a phloem-limited, gram-negative bacterium which also can be readily transmitted by grafting and propagating with infected plant material. Both the nymph and adult can transmit the greening agent in 15 min acquisition feeding time. The incubation period in the vector is about 3 weeks. The infectious vector can retain the pathogen for life.

The length of the life cycle of Asian citrus psyllid varies from 27 to 117 days, depending on rearing temperature and host plants. The average developmental time for the immature stages is from 14 to 49 days within 15–28°C. *D. citri* nymphs undergo five instars. The adult longevity averages from 34 to 88 days within the temperature range of 15–30°C. The maximal longevity of individual females is 117 and 51 days at 15 and 30°C, respectively. The individual female may lay more than 748 eggs at 28°C. A total of 1,378 eggs have been reported to be deposited by a single female on grapefruit. Asian citrus psyllid can feed and breed on most citrus spp., two species of *Murraya* and three genera of Rutaceae. The developmental time of immature stages on various host plants varies significantly, ranging from 69 days on sour orange to 85 days on grapefruit. The average adult longevity on rough lemon is significantly longer than those on orange jassamine, grapefruit and sour orange. However, the females preferentially lay more eggs (averaging 858 eggs/female) on grapefruit than the other hosts mentioned above. The egg incubation period is about 4 days regardless of host plants. Eggs are deposited within 2 cm lengths of terminal tissue, including leaf folds, petioles, axillary buds, upper and lower surfaces of young leaves and tender stem. The egg is anchored on a slender stock-like process arising from the plant tissue. The egg is elongate, with a broad basal end and tapering towards its distal and curved end. The average size of egg measures 0.31 mm long and 0.14 mm wide. Freshly deposited eggs are light yellow, turning bright orange with 2 distinct red eye spots at maturity.

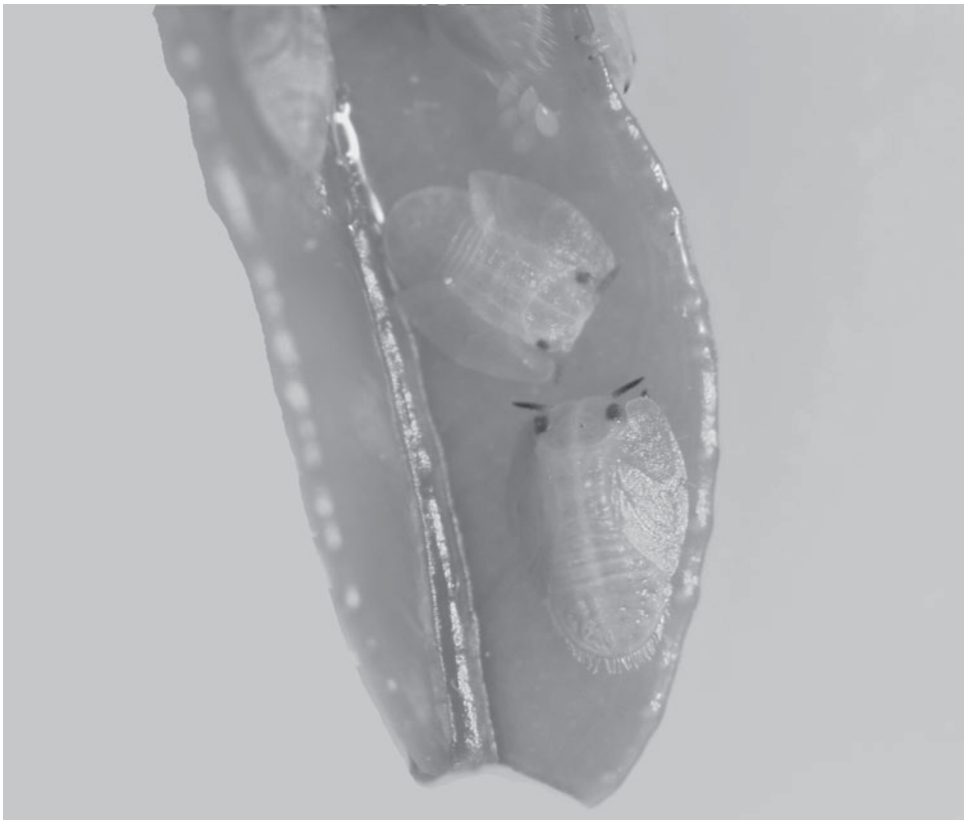
First and 2nd instar nymphs mostly aggregate and feed on the inside of folded leaves, the terminal stem and between the axillary bud and the stem of tender shoots. Young nymphs are quite docile and they only move when disturbed or overcrowded. The nymphs continuously secrete a copious amount of honeydew from the anus, and thread-like waxy substance from the circumanal glands, resulting in the growth of black sooty mold on the lower leaves. The average size of 1st instars measures 0.30 mm in length and 0.17 mm in width with light pink body and a pair of red compound eyes. The measurement of 2nd instars averages 0.45 mm long and 0.25 mm wide. The rudimentary wing pads are visible on thoracic dorsum. The average size of 3rd instars is 0.74 mm long and 0.43 mm wide. The wing pads are well developed and the segmentation of antenna is evident. The 4th instar averages 1.01 mm long and 0.70 mm wide. The wing pads are well developed; the mesothoracic wing pads extend towards 1/3 of compound eyes and the metathoracic wing pads extend to 3rd abdominal segment. The 5th instar averages 1.60 mm long and 1.02 mm wide. The mesothoracic wing pads extend towards the front of compound eyes; the metathoracic wing pads extend to 4th abdominal segment. In some mature nymphs, the abdominal color turned bluish green instead of pale orange.

Adults of *D. citri* (Fig. 87) are often found to rest on the terminal portion of plants, especially on the lower side of the leaves, with their heads pointing to the leaf surface at a 30° angle. When disturbed, they readily take flight to a short distance. The females only oviposit on the tender shoots. In the absence of suitable tissue, oviposition ceases temporarily. The average size of the adult female is 3.3 mm in length and 1.0 mm in width; the mean size of the adult male is 2.7 mm long and 0.8 mm wide.

Control of Asian citrus psyllid can be achieved by insecticide application. It is advisable to target the nymphs, (Fig. 88) as they are less mobile and concentrated on terminal tissue. However, other non-chemical control methods have been widely accepted; they include the use of such natural enemies as syrphids, chrysopids, coccinellids and parasitic wasps. The success in Reunion of using the eulophid (*Tamarixia radiata* Waterston) to control Asian citrus psyllid is a good example of biological



Asian Citrus Psyllid, *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae), Figure 87 Adult Asian citrus psyllid, *Diaphorina citri* (photo J. Tsai).



Asian Citrus Psyllid, *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae), Figure 88 Nymphs of Asian citrus psyllid (photo Lucy Skelley, University of Florida).

control. Other control measures, such as injecting infected trees with tetracyline antibiotics, establishing disease free nursery and monitoring and removing diseased trees from the grove are also known to be effective.

References

Liu YH, Tşai JH (2000) Effects of temperature on biology and life table parameters of the Asian citrus psyllid *Diaphorina citri* Kuwayama (Homoptera: Psyllidae). Ann Appl Biol 137:201–206

Mead FW (1977) The Asiatic citrus psyllid, *Diaphorina citri* Kuwayama (Homoptera: Psyllidae). Florida Department of Agriculture and Consumer Services, Division Plant Industry, July 1977

Pande YD (1971) Biology of citrus psyllid, *Diaphorina citri* Kum (Hemiptera: Psyllidae). Israel J Entomol 5: 307–311

Tsai JH, Chen ZY, Shen CY, Jin KX (1988) Mycoplasmas and fastidious vascular prokaryotes associated with tree diseases in China. In: Hiruki C (ed) Tree mycoplasmas and mycoplasma disease. The University of Alberta Press, AB, Canada, pp 69–240

Tsai JH, Liu YH (2000) Biology of *Diaphorina citri* (Homoptera: Psyllidae) on four host plants. J Econ Entomol 93:1721–1725

Tsai JH, Wang JJ, Liu YH (2000) Sampling of *Diaphorina citri* (Homoptera: Psyllidae) on orange jassamine in south Florida. Fla Entomol 83:446–459

Asiatic Garden Beetle, *Maladera castanea* (Coleoptera: Scarabeidae)

A native of Asia, this insect was accidentally introduced to northeastern North America where it became a turf pest. See also, Turfgrass Insects and their Management.

► Turfgrass Insects and their Management

Asilidae

A family of flies (order Diptera). They commonly are known as robber flies.

► Flies
► Robber Flies

Asiopsocidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice or Psocids

Asiopsocidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice or Psocids

Asparagus Aphid, *Brachycorynella asparagi* (Mordvilko) (Hemiptera: Aphididae)

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Asparagus aphid is found widely in eastern Europe and along the Mediterranean Sea. It invaded North America about 1969, where it was first detected in New York. It dispersed (or was dispersed) quickly, attaining North Carolina in 1973, British Columbia in 1975, Missouri and Washington in 1979, Alabama, Georgia, Oklahoma and Idaho in 1981, and California in 1984. Although it is abundant across the northern portions of North America, and very abundant along the west coast including southern California, it is uncommon in the humid southeastern states.

Life History

Oviparous aphids deposit overwintering eggs on asparagus ferns in September or later. Beginning in about March, eggs hatch into aphids that develop into stem mothers (fundatrices). Fundatrices move to asparagus spears and give birth to about 18 nymphs. Subsequent generations may be apterous (wingless) or alate (winged). Sexual forms are produced in the autumn, mate, and the females deposit eggs on the asparagus plant. Duration of a complete generation is about 15–19 days at 25°C.

The eggs initially are green in color, but turn shiny black within 1–2 days. Females produce, on average, 10.5 overwintering eggs during their life span. The elliptical eggs are deposited in the lower one-third of the asparagus canopy.

The grayish green nymphs exhibit four instars, the durations of which are about 2 days each, regardless of the morph or sex. Thus, nymphal development time averages about 8–9.5 days. Each female produces about 55 nymphs at 23°C, but only 27 and 9 at 14 and 32.5°C, respectively.

Both the alate and apterous adult viviparous aphids are present throughout the summer months, and reproduce parthenogenetically. The adults are relatively small, measuring 1.2–1.7 mm in length, and with short antennae. They are elongate oval in shape, and green or gray-green in color, often covered with a whitish waxy secretion. They blend in well with asparagus foliage, but impart a slightly bluish gray tint when the infestation is heavy. The most important character for distinguishing viviparous asparagus aphid from other asparagus-infesting species is the inconspicuous cornicles and long cauda of *B. asparagi*. Egg-producing females survive up to about 20 days.

This aphid feeds only on species of *Asparagus*. In addition to garden asparagus, *Asparagus officinalis*, it is known to feed on ornamental *Asparagus* spp.

A large number of native predators, parasitoids, and insect diseases affect asparagus aphid. Among the most important are ladybirds (Coleoptera: Coccinellidae), green lacewings (Neuroptera: Chrysopidae), and a parasitoid of many aphid species, *Diaeretiella rapae* (M'Intosh) (Hymenoptera: Braconidae). Other species of some importance are brown lacewings (Neuroptera: Hemerobiidae), the predatory midge *Aphidoletes aphidimyza* Rondani (Diptera:

Cecidomyiidae), flower flies (Diptera: Syrphidae), and other wasps (Hymenoptera: Braconidae and Aphelinidae). Natural enemies are reported to keep the population in check in eastern North America, but once attaining the arid western regions of North America asparagus aphid developed into a severe pest, and was seemingly little influenced by natural enemies. This suggests that climate plays a significant role, perhaps in conjunction with weather-sensitive natural enemies such as fungi.

Damage

Aphids feed on the new growth, causing shortening of the internodes, rosetting, dwarfing, and reduced root growth. Asparagus aphids deplete the sugars, particularly in the roots, and to a greater degree than some other aphids. Heavily infested plants have a bushy or bonsai-like appearance. Aphid infestation can kill seedlings or small plants in a relatively short time. Older, well established plantings may show damage and even death in the year following infestation by aphids, especially following a particularly cold winter. Freezing and aphid infestation are synergistic; together they reduce survival and vigor of dormant asparagus crowns greater than either aphid feeding or freezing alone. The threat of damage is much greater in western areas than in eastern North America, and it remains an infrequent pest in Europe.

Management

Egg hatch can be predicted from temperature models. Eggs can be separated from foliage by washing with petroleum cleaning solvent. Nymphs can be extracted from plants by heat or methyl isobutyl ketone. Aphid distribution tends to be clumped, with most aphids in basal regions of the plants. A sample of about 140 branches per field is optimal for making management decisions.

Foliar insecticides can suppress aphids, but multiple applications may be necessary, especially under high density conditions. Granular systemic insecticides may provide long term control. Some research has also been done to demonstrate the possibility of delivering insecticides to asparagus through the irrigation system.

Several cultural practices for suppression of asparagus aphid were investigated. Autumn and spring tillage reduce aphid overwintering but also reduce subsequent spear production. Mowing and herbiciding within asparagus fields can destroy early season aphids and delay the buildup of damaging populations. However, destruction of wild (volunteer) asparagus is the most important cultural practice available because it eliminates overwintering sites and limits invasion of aphids into commercial, aphid-free fields. Herbiciding, burning and removal of asparagus crowns by digging are all viable options to eliminate volunteer asparagus.

References

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, CA, 729 pp

Hayakawa DL, Grafius E, Stehr FW (1990) Effects of temperature on longevity, reproduction, and development of the asparagus aphid (Homoptera: Aphididae) and the parasitoid, *Diaeretiella rapae* (Hymenoptera: Braconidae). Environ Entomol 19:890–897

Tamaki G, Gefre JA, Halfhill JE (1983) Biology of morphs of *Brachycolus asparagi* Mordvilko (Homoptera: Aphididae). Environ Entomol 12:1120–1124

Wright LC., Cone WW (1986) Sampling plan for *Brachycorynella asparagi* (Homoptera: Aphididae) in mature asparagus fields. J Econ Entomol 79:817–821

Wright LC, Cone WW (1988) Population dynamics of *Brachycorynella asparagi* (Homoptera: Aphididae) on undisturbed asparagus in Washington state. Environ Entomol 17:878–886

Wright LC, Cone WW (1988) Population statistics for the asparagus aphid, *Brachycorynella asparagi* (Homoptera: Aphididae), on different ages of asparagus foliage. Environ Entomol 17:699–703

Aspergillus spp. Fungi

Aspergillus spp. fungi cause a disease in honeybees called stonebrood. Several species may be involved, although *A. flavus* and *A. fumigatus* are most commonly implicated.

► Stonebrood

Aspirator

A device used to collect small terrestrial arthropods. Although there are many variations in design, the principle behind the designs is the same – air current causes the insect to be sucked (aspirated) into a tube or tubing that leads to a container/receptacle area. The key feature of the aspirator is that although the arthropod can be sucking into the container, it cannot be sucked further (inhaled in the case of mouth aspiration) because a fine screen blocks its egress, so it is retained/captured. The principal variables associated with aspirators are the form of suction (mouth or mechanical), length and shape of the tube/intake, and the size of the container/receptacle. This apparatus works well for small and/or weakly flying insects.

Assassin Bugs, Kissing Bugs and Others (Hemiptera: Reduviidae)

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The Reduviidae are a large, cosmopolitan, and morphologically diverse family of predatory true bugs. They include assassin bugs (genera include *Melanolestes*, *Psellipus*, *Rasahus*, *Reduvius*, *Rhiginia*, *Sinea*, and *Zelus*), wheel bugs (*Arilus cristatus*), kissing bugs (species of *Triatoma*, *Rhodnius* and *Panstrongylus*), ambush bugs (genera *Apiomerus* and *Phymata*), and thread-legged bugs (the subfamily Emesinae, including the genus *Emesaya*).

Taxonomy

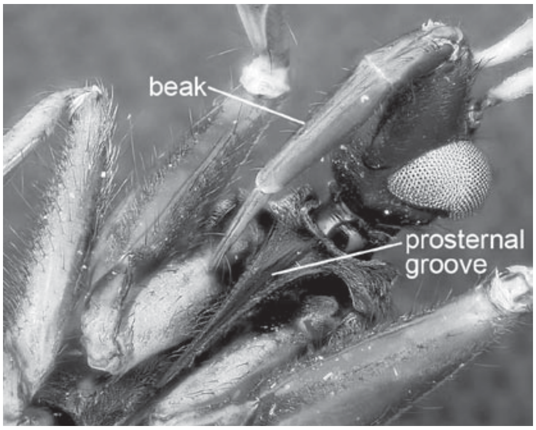
In 1843, Amyot and Serville recognized the reduvids as a discrete group. In its present systematic organization, the large family Reduviidae contains around 25 subfamilies, about 930 genera and 6800 species. Composition of subfamilies and relationships between them remain unsettled. Subfamilies Harpactocorinae (about 2,000 species), Reduviinae (about 1,000 species), Emesinae (about 900 species), Stenopodinae (more than 700 species) and Ectenodeminae (more than 600 species) together total more than 80% of known reduviid species. An additional five minor subfamilies contain only 3 or 4 species. Ten genera contain between a hundred and two hundred species each.

Morphology

Adult bugs vary greatly in body size, ranging from 3.5 mm in such reduviids as the genus *Empicoris* (Emesinae) to 40 mm in the genus *Arilus* (Harpactorinae). The body shape is also extremely variable. Reduviidae may be robust and oval, as occurs in the genus *Reduvius,* to elongate and thread-like, as in the genus *Empicoris*. Body coloration may be cryptic or aposematic. Most species are dark in color, with hues of brown, black, red, or orange. Others are masters of disguise and camouflage, colored to blend with their substrate or to resemble their prey. Many species are very hairy or spiny, with varied body expansions.

Reduviidae can be distinguished from other bug families by their elongated head, with a transverse groove behind the compound eyes, and the short, prominent, apparently three-segmented rostrum curved (Figs. 89 and 90) outwards from the head. A characteristic of the family is that the tip of the rostrum, in repose, fits into that groove.

The head has a pair of large compound eyes, usually two ocelli, and a pair of four-segmented antennae about the same length as the body. However, subdivision of antenna segments gives an appearance of antennae with a larger number of segments. The forewings (hemelytra) lack the costal feature, and the membrane usually has two elongated cells and a few veins emanating posteriorly. Legs are usually long, normally with 3-segmented tarsi, although the tarsal formula is variable.



Assassin Bugs, Kissing Bugs and Others (Hemiptera: Reduviidae), Figure 89 **A ventral view of the reduviid head, showing the curved rostrum and a groove located ventrally. A characteristic of the family is that the tip of the rostrum, in repose, fits into that groove.**

The male genitalia are usually symmetric and the ovipositor of females is usually plate-like. Eggs have three or more micropyles.

Biology

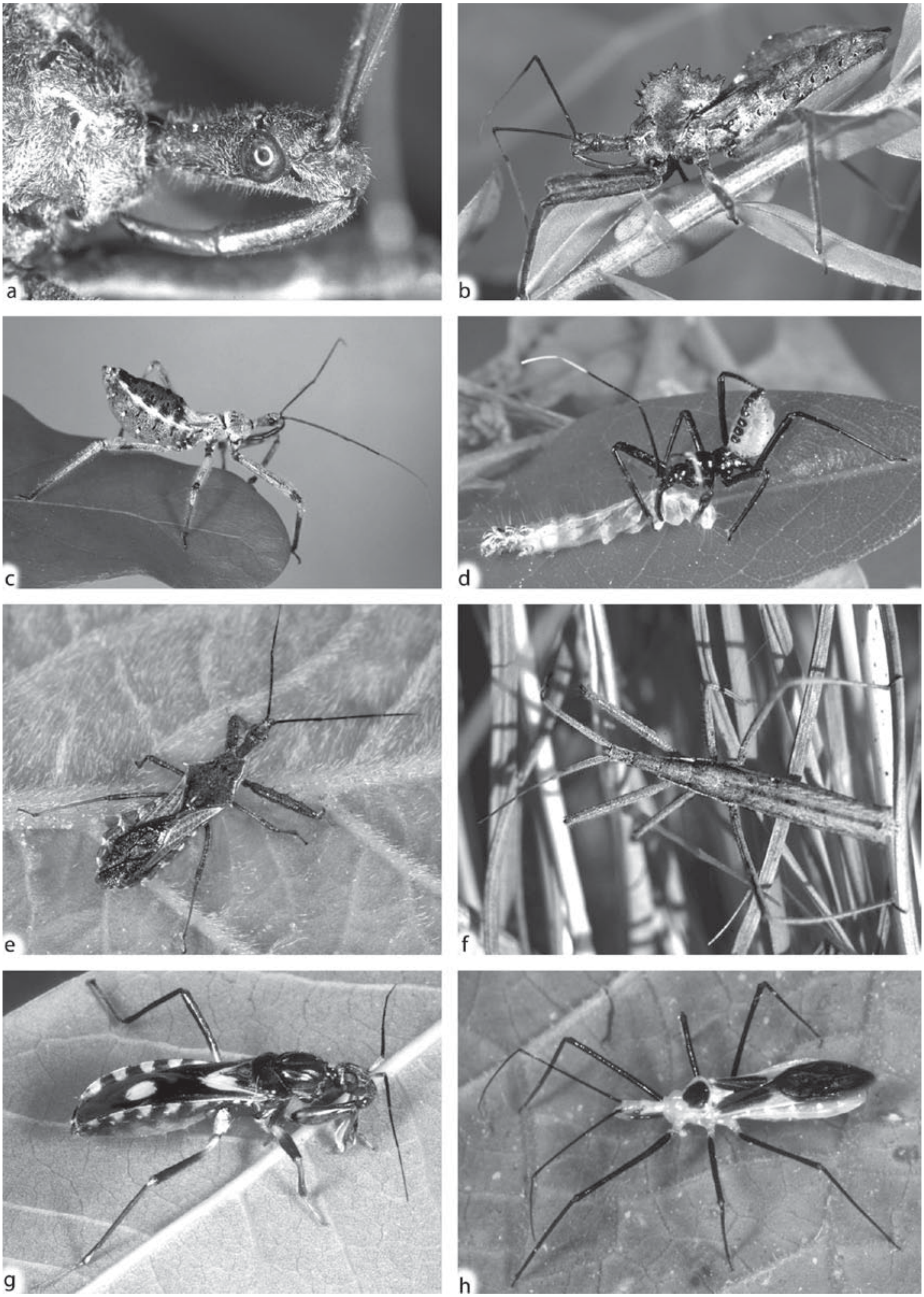
Despite their abundance and interest, reduviids have been largely ignored, and we do not know much on their biology. Triatominae are the exception, as their relationship with human diseases has stimulated their study under laboratory conditions.

Reduviidae may live in a variety of habitats in the wild, and tend to occupy warm environments. Sylvatic triatominae are found in burrows and nests of wild vertebrates, among rocks, fallen timber, hollow trees, roots, palms and bromeliads. In the subfamily Emesinae, some species are cavernicolous, but lack the characteristics common to many cave dwellers such as eyelessness or depigmentation. Among Emesinae and Triatominae, some species are domestic or peridomestic, which increase the medical importance of Triatominae as vectors of the protozoan *Trypanosoma cruzi*. The attraction of Triatominae to light also enhances the likelihood that they will enter inhabited structures and contact humans.

Reduviidae are well adapted for their physical environment. They may pass through inclement periods in the egg, nymphal or adult stage. Number of generations per year ranges from one to several, but in other cases the completion of life cycle may take more than 1 year. Longevity is also very variable among species. Some Salyavatinae live <2 weeks, whilst some Reduviinae live for about 7 months.

Except for Triatominae, which are hematophagous and feed on vertebrate blood, all reduviids prey on other insects. First step of attack is with the legs, whose length allow a longer attack distance. Also, the legs of some of these bugs are covered in tiny hairs that serve to make them sticky to grip prey while they feed in the manner of flypaper. Other assassin bugs (subfamily Apiomerinae) go one step further and collect certain plant resins which they spread over their front legs; these resins are very attractive to insects, and to bees in particular. Once the prey is grasped, the reduviid feeds by puncturing it with sharp stylets in their rostrum, injecting saliva which will paralyze the prey and liquify its tissues, to then finally sucking up the body fluids. The saliva is commonly effective at killing prey substantially larger than the predatory bug itself. In contrast, the genus of the small reduviid *Ptilocerus* uses chemical lures located in a special ventral abdominal gland to trap and prey on ants. The ants are very attracted by this secretion, which paralyses them. Also, reduviids that tackle large and dangerous prey like wasps or bees tend to make the first stab near the victim's head or neck, thus ensuring that their toxic saliva has maximum effect in the shortest possible time.

In Triatominae, ingestion of blood is possible thanks to different enzymes present in the bug saliva that counterbalances the hemostatic response on the part of the vertebrate host. Bug saliva is provided with anticoagulants (preventing the coagulation of host blood in the insect's suction apparatus), apyrases, platelet antiaggregation factors, antiserotonin, antihistamine, tryalisine (lytic protein which



Assassin Bugs, Kissing Bugs and Others (Hemiptera: Reduviidae), Figure 90 Some reduviids: (a) Anterior view of a reduviid, showing their elongated head and the short, prominent, apparently 3-segmented rostrum curved outwards from the head; (b) adult wheel bug, *Arilus cristatus.* This is one

permeabilizes mammalian cells), emollient factors, antithromboxane and a vasodilator. Blood is stored in the crop and stomach of triatomine. Several days later, erythrocytes are lysed, and the accessible hemoglobin is then digested. Blood ingestion is needed by nymphs to complete development, and by adults to perform reproduction, as cyclical egg laying is related to blood meals.

Reduviids are generally polyphagous, but there are also cases of prey specialization. For example, the subfamily Emesinae contains a number of genera (*Eugubinus*, *Ploiaria*, *Emesa*, *Stenolemus* and *Empicoris*) in which elongate, thread-legged member species feed on insects caught in spiders' webs, or on the spiders themselves. These slender, slow-moving bugs never get trapped in the spider silk, as they avoid the sticky spirals and walk very carefully so that they are not trapped in the spider silk. An extraordinary case of coprophagy is found in the Indian harpactorine *Lophocephala guerini*, which feeds on fermenting cow dung. Its microhabitat is underneath stones, in association with the formicine ant *Anoplolepis longipes,* and it is always attended and guided by these ants. However, the trophic habits of most reduviid species are still unknown.

Courtship behavior is much like in other insects, although it has some characteristic features. The sequential acts of mating behavior can be categorized into arousal, approach, riding over (precopulatory riding of Harpactorinae), nuptial clasp, extension of genitalia and connection, copulation, and postcopulatory acts. The fecundity varies between 50 eggs of the Stenopodainae to the 670 eggs of Harpactorinae. Eclosion and ecdysis occur usually in daytime.

Many species glue their eggs to the plants, often in a group, sometimes covering the eggs with a gelatinous material. Ground-dwelling species may bury their eggs in the soil, and some species of the subfamily Reduviinae have more well-developed ovipositors, suitable for the insertion of eggs into cracks.

A few species are known to guard their eggs, and in this case, the males perform the guarding. In the genus *Rhinocoris*, the female lays a batch of eggs on the plant leaf immediately after copulating. The male stands by and, when the female finishes laying, takes up his position aside the egg mass. Over the course of the next days the female lays additional egg batches. While the male is guarding he generally does not feed, unless an easily catchable prey comes his way. However, when the eggs have all hatched, he loses interest and moves away. Exceptionally, the guarding male may be relieved by a female that had copulated with him.

In the majority of nymphs and adults, the rostrum can be used to produce sounds (stridulation) by being scraped along a medially located, ridged groove on the underside of the thoracic segments. The aim of this acoustical communication may be mate attraction, courtship and copulation. In other cases, the aim is intimidation, and thus, some reduviids stridulate defensively. Non-receptive females may emit male-deterring vibrations.

Reduviids have an array of defensive and offensive behaviors, accompanied by morphological adaptations. These behaviors threaten other

of the largest and most easily recognized reduviids. It is found in North America and Central America, where it feeds on numerous insects, but also inflicts a nasty bite when handled by humans; (c) nymphal wheel bug, *Arilus cristatus*; (d) nymphal wheel bug, *Arilus cristatus*, feeding on a leaftier larva; (e) adult *Sinea diadema*. This species is found through most of North America including Mexico, where it inhabits meadows and crop fields. It often is reported to be an important predator of crop pests; (f) nymphal *Vibertiola cinerea*, an African savanna-inhabiting species that is now found in the Iberian Peninsula. Its host plant is the grass *Hyparrhenia hirta*, where it blends in well due to its elongated body; (g) *Rasahus* sp. bugs are found predominantly in the neotropics; (h) *Zelus longipes* is found throughout the western hemisphere where its often found feeding on caterpillars (photo credits: f, Eva Ribes, University of Barcelona; others Lyle Buss, University of Florida).

insects, aid escape from enemies and larger prey, and give protection from cannibalism. Some nymphs and adults of different subfamilies (Reduviinae, Cetherinae, Salyavatinae, Triatominae) will cover and camouflage themselves with debris, including soil particles or the remains of dead preyed insects, which are affixed by sticking objects to the viscid secretions of specialized setae located on the dorsum. The elongated slender bodies of *Rhaphiodosoma* and *Vibertiola* species (Harpactorinae) and stenopodaeines provide camouflage among the elongated grasses where they live, imparting protection from vertebrate predators. In other cases defense is active, as in harpactorine nymphs, which often fight to the death.

Some Aspects of Distribution

The distribution of Reduviidae is nearly cosmopolitan, though most taxa inhabit the tropical and subtropical regions, where they are particularly varied and abundant. Of the 6,800 species, 16% occur in Oceania, 37% in sub-Saharan Africa and 21% in the neotropics. Certain taxa with a wide distribution suggest transport by humans and their goods, or by migratory animals.

Ecological and Economic Significance

As predators, Reduviidae play a role in biological control. Their worldwide distribution, abundance, diversity, large pest prey record, amenability for mass culturing, ready synchronization and freedom from hyperparasites and predators are the merits of reduviids as potential biological control agents.

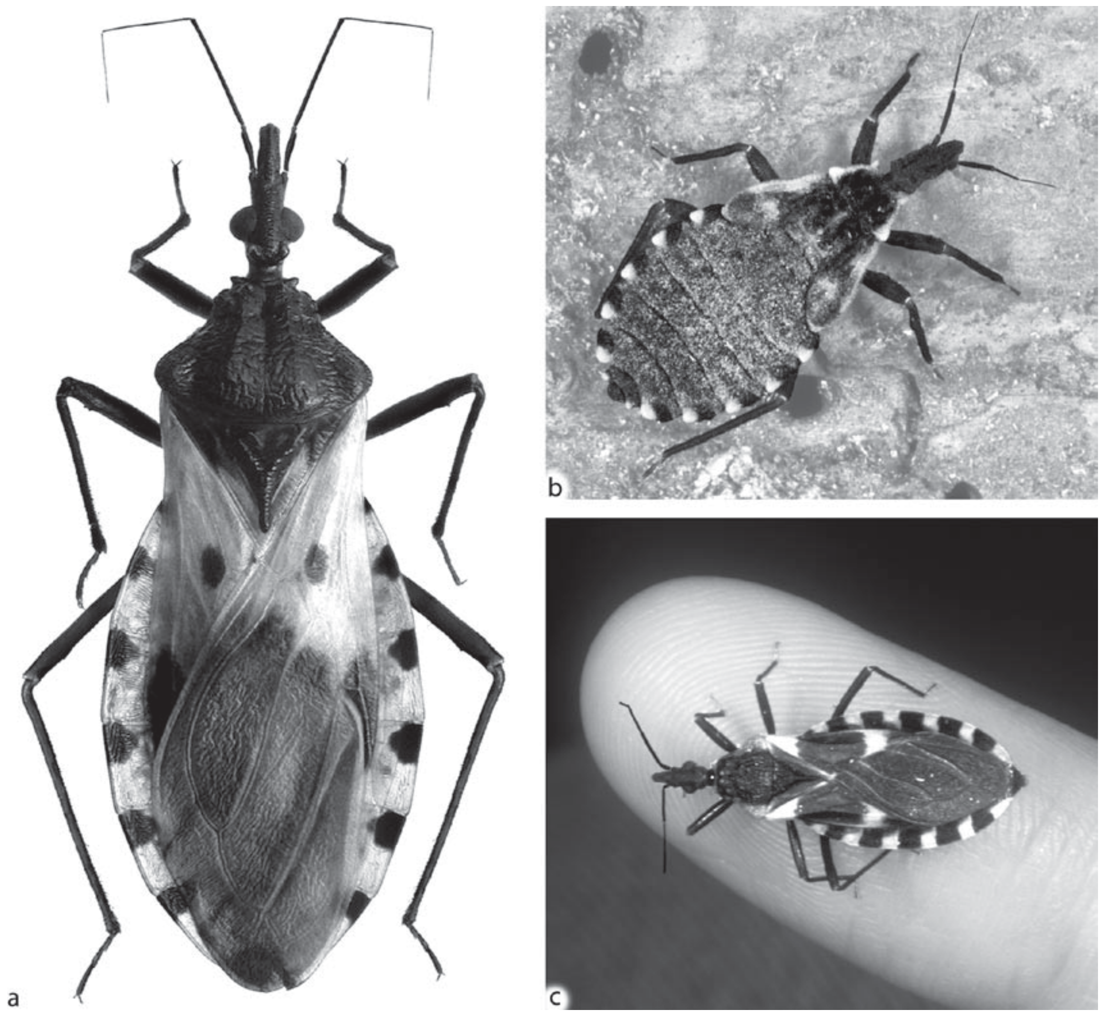
More than 150 reduviids predators belonging to 53 genera and seven subfamilies have been found preying upon a wide array of insect pests. Some species have been known to feed on cockroaches or bedbugs (in the case of the masked hunter *Reduvius personatus*) and are regarded in many locations as beneficial. They kill more prey than they need to satiate themselves. Reduviids exhibit a positive numerical response by killing more prey in terms of available prey population per predator at a given time, and by increasing their population through higher fecundity and survival.

In spite of their merits as beneficials, their potential as biocontrol agents of pests has been little studied. The better studied species in this area focus on *Rhinocoris fuscipes*, *R. kumarii*, *R. marginatus*, *Ectomocoris tibialis* and *Acanthapsis pedestris*. Other promising groups of predatory reduviids are species of *Sinea* and *Zelus*, which may help regulate insect pests on cotton. Recently, *Amphibolus venator* has been reported as a useful predator on last-instar larvae, pupae and adults of the stored-product insect pest *Trobolium confusum* (red flour beetle [Coleoptera: Tenebrionidae]). *Amphibolus venator* is commonly found in stored product facilities, shipments of groundnuts, warehouses or in rice milling facilities, and preys on other stored-product insect pests.

Because of their polyphagy, reduviids may not be useful as predators on specific pests, but they are a valuable help when a variety of insect pests occur. The counterpart of that polyphagy is that from time to time they may attack beneficial arthropods. A few of them appear to specialize on insects of some value; for example, several apiomerine reduviids feed on bees of the genus *Trigona*, that are useful pollinators.

Unfortunately, assassin bugs interact with human health negatively. They may become a nuisance, as many assassin bugs have been known to bite humans when not handled carefully. For some species the bite is known to be very painful, sometimes causing allergic reactions, and bites can become infected, as with any wound. Some of them are known to produce toxic saliva containing powerful enzymes similar to those in snake venom. As with any severe allergic reaction in humans, side effects of repeated bites may include shock and possible death. The fecal material of some reduviids can cause irritation of the eyes and nose and temporary blindness in humans.

Most important to human health are some blood-feeding triatominae species, also known as kissing bugs due to their habit of biting humans in their sleep on the soft tissue of the lips and eyes. A number of these hematophagous species are able to transmit a potentially fatal trypanosome disease known as human Chagas disease (HCD), also named American trypanosomiasis, caused by the protozoan *Trypanosoma cruzi*. These reduviids belong to genera *Triatoma*, *Rhodnius* and *Panstrongylus*, and the three most important species in this regard are *Triatoma infestans*, *T. dimidiata* and *Rhodnius prolixus* (Fig. 91). About 50 additional species belonging to the three genera mentioned above can also act as disease vectors, but they are more local in distribution so they are not as important, or as well known. Other genera involved locally in transmission of HCD are *Meccus* (Mexico), and *Microtiatomba* and *Parabelminus* (Brazil). Infestation rates of triatominae by *Trypanosoma cruzi* vary greatly from one area to another. As examples, in Brazil, 41% of 2412 triatominae bugs were infested whereas in Panama, 68.8% of 740 *Rhodnius pallescens* were infested, but only 17.7% of 94 *Triatoma dimidiata* were. In Yucatan (Mexico), infection rates of



Assassin Bugs, Kissing Bugs and Others (Hemiptera: Reduviidae), Figure 91 Kissing bugs or bloodsucking conenoses, *Triatoma* spp.: (a) adult *T. dimidiata*; (b) immature of *T. sanguisuga*; (c) adult of *T. sanguisuga* (photo credits: a, Ron Cave; others Lyle Buss, both University of Florida).

Triatoma dimidiata by *T. cruzi* ranged from 0% (in Tipoco) to 25% (in Tella). In Santander (Colombia), 48% of *T. dimidiata* contained the protozoan, while in Guayaquil (Ecuador), 50% were infested. Once infested, a bug may be infective for about 2 years. In contrast with other arthropod vectors (i.e., ticks), the protozoan cannot be transmitted to the offspring transovarially.

In 1909, the Brazilian doctor Carlos Chagas discovered the disease, and reported both the vector and the causative flagellate protozoan *Trypanosoma cruzi*. He recognized and described the disease in humans but also investigated the life cycle and other aspects of the protozoan and its insect vector. This disease is mostly found in rural areas, where the Triatominae can breed and feed on the natural reservoirs, such as opossums, raccoons, and armadillos. In fact, wild animals reported as infected with *T. cruzi* belong to the Orders Marsupialia (opposums), Edenteta (armadillos, etc.), Chiroptera (bats), Carnivora (cats, foxes, etc.), Lagomorpha (rabbits), Rodentia (mice and rats, squirrels) and Primates (monkeys). But, depending on the special local interactions of the vectors and their hosts, other infected humans and domestic animals may act as reservoirs too. Among domiciliary and peridomiciliary reservoirs are *Canis familiaris* (dog), *Capra hyrcus* (goat), *Cavia porcellus* (Guinea pig), *Felis domesticus* (cat), *Mus musculus* (mice), *Oryctolagus cuniculus* (rabbit), *Rattus novervegicus* and *Rattus rattus* (rats) and *Sus scrofa* (pig).

Trypanosoma cruzi may have both sylvatic and domestic cycles. The sylvatic cycle involves its circulation among wild small mammals and the Triatominae. The sylvatic cycle usually does not affect humans unless they enter in the wild and disturb the natural balance of wild fauna and flora. The domestic cycle, which has evolved more recently, involves humans, domestic mammals and a small number of Triatominae species that are able to live in domestic or peridomestic habitats. Although some reports on Chagas disease date back to precolumbian times, the real dispersion of the American trypanosomiases occured as a result of European conquest and the resulting disturbance of the natural balance and habitats of *T. cruzi*, its triatomine vectors, and its mammalian reservoirs.

Kissing bugs are strictly nocturnal, taking blood meal for 20–30 min and inflicting no pain to the host. When they feed, the bugs leave (infected) excrement behind on the skin. Transmission of the protozoan occurs when people scratch their bites and allow protozoa in bug defecations to infect their blood. Other forms of transmission are possible, though, such as ingestion of raw food contaminated with parasites, blood transfusion, organ transplantation and placental transmission (from infected mother to fetus).

The human disease occurs in three stages or phases: (i) the primary or acute phase, shortly after the infection, with an incubation of 15 (direct bite)-40 days (blood transfusion infection); symptoms are an inflammatory reaction, with necrosis around the bug bite site; meningoencephalitis and myocarditis are very severe consequences of this stage in children under 10 years old; (ii) indeterminate phase, 8–10 weeks after the acute stage and which may last for years without any symptom; the main danger is that the individual is unaware of being infested, acting as reservoir of *T. cruzi*; (iii) chronic stage that may develop up to 10 years after infection; the main signs are liver and heart dysfunctions, as well as, hypertrophy of the heart and certain parts of the digestive and/or excretory systems. The parasite circulates in the bloodstream, and infects, multiplies and ultimately destroys muscle and nerve cells all around the body, particularly in the heart and digestive system. The negative effects of the disease are reflected in a progressive deterioration of health, associated to increasing apathy, a decreasing capacity to perform work and a general reduction in the quality of life. If no action is taken, disease is lethal.

The disease is distributed in the Americas, ranging from the southern United States to southern Argentina, mostly in poor, rural areas of Central and South America. Domestic infestation in very poor rural zones may be of 1,000 insects per house. Human Chagas disease (HCD) has been spread into nonendemic urban areas by people migrating to cities from rural areas. In most countries where Chagas disease is endemic, testing of blood donors is already mandatory, since this can be an important route of transmission. Up to 18 million humans were affected by this disease in 1990, but recently data suggests nine million people affected, after coordinated initiatives throughout the endemic HCD area. Of some 100 million at risk of acquiring the disease in 1990, now about 60 million people are out of risk. About 200,000 new cases, and about 70,000 deaths are reported annually. Rates of human infection in endemic areas are very different, relating to different vector species or populations. In Zacapa (Guatemala), where *R. prolixus* is the principal vector, 38.8% of 373 people were infected. In contrast, in Santa Rosa (Guatemala), where *T. dimidiata* is the only vector found, only 8.9% of the 428 people studied had the protozoan. The same trends were reported in Honduras, in relationship to HCD vectors. Outside of the Americas, one genus and several bug species occur in India, where theoretically they may transmit Chagas disease.

Once infected, there are some pharmaceuticals useful to fight infections, but they are very toxic and have a lot of undesirable secondary effects. The best way to reduce HCD incidence is prevention, either by fighting the vector (*Triatoma*) or improving housing and sanitary conditions in the rural area. Vector insects may be eliminated by using sprays and paints containing insecticides (synthetic pyrethroids). Although resistance development is much lower than in mosquitos (due to long life-cycle and use of different insecticides), significant levels of resistance to deltamethrin and other pyrethroids have been reported in *Rhodnius proxilus* (Venezuela) and *Triatoma infestans* (Brazil and Argentina). Recently, oil-formulated *Beauveria bassiana* has been used against *T. sordida* and has proven to be useful in peridomestic areas of central Brazil. This could lead to implementation of integrated control by alternating application of fungi in the rainy season with synthetic insecticides in the dry season, or a combined application of fungi and insecticides in the rainy season. Those strategies could promote an efficient and permanent reduction of triatomine vectors in peridomestic areas. Also, several plant extracts showed insecticidal activity against triatomines. As examples, plants belonging to genera *Salvia*, *Annona*, *Neurolaena*, *Tagetes*, *Erythroxylon*, *Cassia*, *Senna* and *Cabralea* elicited an increase in the mortality rate (16–52%) of *Rhodnius neglectus*. Topical treatment of *T. infestans* with *Achryrocline* extracts resulted in a 45% mortality of triatomine bug. Five plant species (*Aspidosperma macrocarpon*, *Talauma ovata*, *Guarea guidonia*, *Guarea kunthiana* and *Simarouba versicolor*) from the Brazilian biome Cerrado, selected according to ethnobotanical information, have been tested in the form of 24 plant crude extracts on *Rhodnius milesi*. Most promising results were obtained from ethanolic extract of the root bark of *S. versicolor* (probably due to its antifeedant growth regulating activity) and the hexane extract of the root of *G. guidonia* (by a not yet clear activity). In addition to investigating new methods to kill triatomine bugs, considerable success has been made preventing bugs taking up residence in human domiciles.

However, the peridomicilium (considered to be the area within 100 m proximity of human dwellings) has been shown to be crucial in management of HCD. Henhouses, pigpens, corrals, perches, piles of tiles, bricks, wood and straw have to be taken into account. In research conducted in 121 peridomiciliary environments in rural areas of the state of Ceará (Brazil), triatominae (2670 specimens collected) were present in 30% of the environments, with 68.7% being shelters for domestic animals (mainly goat/sheep corrals, perches, henhouses and pigpens), and 32.3% were piles of bricks, roofing tiles or wood. Also, palm trees growing near human habitations are of great importance in HCD, as *Rhodnius* species breed in the crowns of many genera of palm trees. Specificity among insect and palm tree species may be very strict, as is the case of *R. brethesi* on *Leopoldinia piassaba*, or *R. colombiensis* on *Attalea butyracea*, but this is not always the case, as in *R. pallescens* or *R. pictipes*, which dwell in association with five host palm species each, or *R. prolixus*, with 13 host palm species. Peridomestic palm trees, especially in the presence of bird nests, may be regarded as high-risk habitats. In Ecuador, the palm seed endosperm (vegetable ivory or "tagua") and leaves of *Phytelephas aequatorialis* are used for handicraft manufacturing and roof thatching; as a result, those palms, which are the primary habitat of *Rhodnius ecuadoriensis* (a major vector of Chagas disease in Ecuador and Peru), are often found around dwellings.

For urban dwellers who spend vacations outdoors or camp in the wilderness, or who sleep at hostels or primitive houses in HCD-endemic areas, a mosquito net is recommended to reduce the risk of infection. If the traveler intends to travel to an area of HCD prevalence, he/she should get information on the incidence of Chagas disease from traveler advisories, such as the USA's Communicable Disease Center (CDC).

The Southern Cone Initiative against HCD was launched in 1991, following a resolution of the Ministers of Health of Argentina, Bolivia, Brazil, Chile, Paraguay and Uruguay. It focused on interruption of *T. cruzi* transmission by eliminating domestic vectors (particularly *T. infestans*), extending screening of blood donors, and promoting maternal screening and specific treatment of infected newborns. Similar initiatives were launched in 1997 for Central America and the Andean Pact countries. Those multinational initiatives, coordinated by the Pan American Health Organization (PAHO) allowed that on June 9, 2006, at the 15th annual meeting, the Intergovernment Commission of the Southern Cone Initiative against Chagas disease declared Brazil to be free of Chagas disease transmission due to *Triatoma infestans*. Also in Uruguay, Chile, most of Argentina, Bolivia, Paraguay and parts of Central America, transmission has been effectively eliminated. In 2004, a surveillance initiative was announced for the nine countries of the Amazon basin. To assure and increase the success obtained in this 15-year initiative, surveillance and control of the disease and its vector are currently on the agenda of all endemic countries. It is essential to keep in mind the perennial need of surveillance, data assimilation and selective interventions, as triatomines will always be present in the wild, as well as *T. cruzi* and its wild reservoirs. Schools and hospitals (obstetrics, blood donors, organ transplantation) are essential surveillance hot-spots where infestations may be detected and controlled.

► Bugs (Hemiptera)
► Trypanosomes
► Chagas Disease: Biochemistry of the Vector
► Area-Wide Pest Managment
► Chagas Disease or American Trypanosomiasis
► Parental care
► Acoustical Communication

References

Ambrose DP (1999) Assassin Bugs. Science Publishers, Enfield, New Hampshire, 337 pp

Ambrose DP (2000) Assassin bugs (Reduviidae excluding Triatominae). In: Schaefer CW, Panizzi AR (eds) Heteroptera of economic importance. CRC Press, Boca Raton, FL, pp 695–712

Aukema B, Rieger C (eds) (1996) Catalogue of the Heteroptera of the Palaearctic Region, vol 2: Cimicomorpha I. Netherlands Entomological Society, Amsterdam, The Netherlands, 361 pp

Coll M (1998) Living and feeding on plants in predatory Heteroptera. In: Coll M, Ruberson JR (eds) Predatory Heteroptera in agroecosystems: their ecology and use in biological control. Thomas Say Publications in Entomology, Entomological Society of America, Lanham, MD, pp 89–129

Garcia ES, Azambuja P, Dias JCP (2000) Triatominae (Reduviidae). In: Schaefer CW, Panizzi AR (eds) Heteroptera of economic importance. CRC Press, Boca Raton, FL, pp 539–552

Maldonado CG (1990) Systematic Catalogue of the Reduviidae of the World. Special Publication, Caribbean Journal of Science, Mayaguez, Puerto Rico, 694 pp

Putshkov PV, Putshkov VG (1996) Family Reduviidae Latreille, 1807 – assassin bugs. In: Aukema B, Rieger C (eds) Catalogue of the Heteroptera of the Palaearctic Region. Netherlands Entomological Society, Amsterdam, The Netherlands, pp 148–265

Schofield CJ, Jannin J, Salvatella R (2006) The future of Chagas disease control. Trends Parasitol 22:583–588

Schuh RT, Slater JA (1995) True bugs of the world (Hemiptera – Heteroptera): classification and natural history. Cornell University Press, Ithaca, NY, 335 pp

Assemblage

The species within a particular taxon at a location.

Associative Learning

The capacity to associate a stimulus, which itself has no positive or negative effects, with positive or negative effects. For example, bees can learn to associate color with food sources. Insects commonly display this ability.

► Learning in Insects
► Habituation
► Latent Learning
► Insight Learning

Assimilation Efficiency

The proportion of energy ingested by an animal that is absorbed into the body.

Astatidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Asteiid Flies

Members of the family Asteiidae (order Diptera).

► Flies

Asteiidae

A family of flies (order Diptera). They commonly are known as asteiid flies.

► Flies

Aster Leafhopper, *Macrosteles quadrilineatus* Forbes (Hemiptera: Cicadellidae)

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Aster leafhopper is native to North America, where it is nearly everywhere. It is most common, however, in the central region of the continent. Also, it overwinters poorly in cold areas. Most areas with aster leafhopper problems are invaded annually by leafhoppers originating in the southern Great Plains. In the mild-climate northwest, however, leafhoppers are able to overwinter successfully, and long-distance dispersal is not an important factor.

Life History

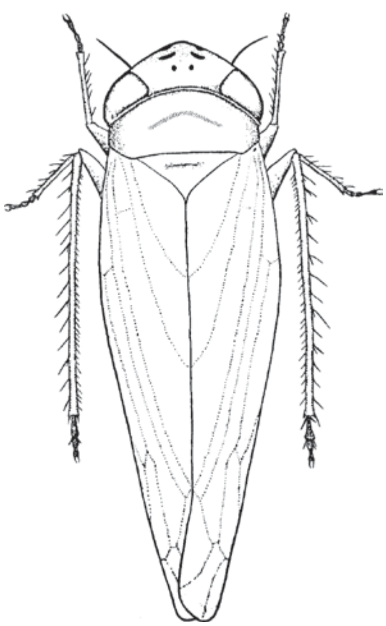
This insect overwinters in the egg stage in northern locations, and in the adult stage in warmer climates. In northern areas, there are three generations per year, whereas up to five generations may occur in more favorable midwestern locations. Because the generations overlap, and are initiated by both overwintering eggs and migrating leafhoppers, it is difficult to discern the generations. Total generation time requires about 27–34 days.

Eggs are deposited in leaf, petiole, or stem tissue, often near the juncture of the leaf blade and stem. They are deposited singly, but often in short rows of up to five eggs. They require a moist environment, and perish if the foliar tissue desiccates. The eggs are translucent when first produced, soon turning white. They average 0.80 mm in length (range 0.73–0.87 mm) and 0.23 mm in width. They are slightly curved, with one side concave and the opposite side convex, and taper to a blunt point at each end. The incubation period of the egg is about 7–8 days.

Newly hatched nymphs are nearly white, but soon become yellow and gain brownish markings, including dark markings on the head. There are five instars, the duration of which are about 3–4, 4–5, 3–4, 4–6, and 5–7 days, respectively, when reared at 21–25°C. The body length measures about 0.6–1.0, 1.2, 2.0, 2.5, and 3.0 mm in instars 1–5, respectively. As the nymphs mature, they gain spines on the hind tibiae, the number increasing from about 6–7 to 8–9. The tip of the abdomen also bears spines. The wing pads are indistinct through the third instar, but are apparent in the fourth instar, and overlap the abdominal segments in the fifth instar.

The adults (Fig. 92) are small, the males about 3.2–3.4 mm long, and the female 3.5–3.8 mm. These insects are light green in color, with the forewings tending toward grayish green and the abdomen yellowish green. There are six pairs of black spots, some of which are elongated almost into horizontal bands, starting at the top of the head and extending along the front of the head almost to the base of the mouthparts. The six pairs of spots are the basis for the other common name of this insect, "six-spotted leafhopper." Strong winds moving north in the spring transport adults into midwestern and northern crop production areas annually. Adults usually arrive in advance of egg hatch by overwintering populations, and populations of long-distance dispersants greatly exceed resident leafhoppers. Arrival time in the north varies, but May arrival dates are common.

When dispersal was studied in the western Great Plains of North America, the western edge of the principal migration path, overwintering of the adult leafhoppers was found only in Texas, USA, although north of Texas eggs may overwinter. By May, northward movement was evident, with adults present in Kansas, Nebraska, and South Dakota, where no nymphs had been found previously. By June the leafhoppers had progressed northward into Montana and North Dakota, and westward into Colorado and Wyoming. Thus, northward migration occurs rather rapidly, and the leafhoppers are present during most of the growing season in these areas.



Aster Leafhopper, *Macrosteles quadrilineatus* Forbes (Hemiptera: Cicadellidae), Figure 92 **Adult of aster leafhopper, *Macrosteles quadrilineatus* Forbes.**

Aster leafhopper has a wide host range. It tends to overwinter on grains such as wheat and barley, and on grasses, clover, and weeds, then dispersing to other crops in the summer months. Several vegetable crops are damaged by aster leafhopper, including carrot, celeriac, celery, corn, lettuce, parsley, potato, and radish, but among vegetables only lettuce is consistently suitable for leafhopper reproduction. Other crops fed upon are barley, clover, dill, field corn, flax, oat, rice, rye, sugarbeet, and wheat.

In Washington, USA, studies indicated that the most important breeding areas were mixtures of clover and pasture grasses, followed by clover, sweet corn, oats, carrots, lawn grasses, rye, field corn, and various weeds. Among the weeds favored were fleabane, *Erigeron* spp.; ragweed, *Ambrosia* spp.; dandelion, *Taraxacum officinale*; wild lettuce, *Lactuca canadensis*; tumble mustard, *Sisymbrium altissimum*; and lambsquarters, *Chenopodium album*. Low, sparse, and young vegetation provided the best habitat. In Minnesota, large crabgrass, *Digitaria sanguinalis*; horseweed, *Conyza canadensis*; barnyardgrass, *Echinochloa crusgalli*; fowl-meadow grass, *Poa palustris*; and barley, wheat, and oats were especially suitable for reproduction. Carrot, dill, potato, and radish were important adult food plants, but not good breeding hosts.

Natural enemies are not well known, or very important in the population ecology of aster leafhopper. The most important enemies are the parasitoids *Pachygonatopus minimus* Fenton, *Neogonatopus ombrodes* Perkins, and *Epigonatopus plesius* Fenton (all Hymenoptera: Dryinidae). The best known among these is *P. minimus*, which has caused up to 37% parasitism.

Damage

Leafhoppers pierce leaf tissue of plants and remove the sap. The feeding punctures cause death and discoloration of individual plant cells, resulting in a yellow, speckled appearance in affected plants. This feeding damage, while unsightly, is minor in comparison to the damage caused to a great number of vegetable crops by transmission of aster yellows by leafhoppers.

Aster yellows is a plant disease caused by a mycoplasma-like organism (MLO), and is transmitted almost exclusively by aster leafhopper. Such crops as carrot, celery, cucumber, lettuce, potato, pumpkin, and squash are affected. Losses of 50–100% are reported due to this disease. MLO-infected plants are discolored, stunted, and deformed. On carrots, for example, the symptoms are red or yellow foliage and excessively hairy, bitter-tasting roots. On lettuce, symptoms are chlorosis, stunting, and lack of head formation.

Management

Leafhoppers are sampled with sweep nets, especially from grasses and grain fields. Yellow sticky traps are also useful and easy to use, and light traps equipped with fans for suction also have been used effectively to capture leafhoppers.

In addition to sampling for leafhopper abundance, it is also desirable to determine the proportion of leafhoppers that harbor the MLO. Formulas based on both insect number and disease incidence, called the "aster yellows index," have been developed to trigger control measures before the pathogen is widely transmitted to susceptible crops. Leafhoppers are collected before they enter an area, fed on aster plants, and the plants read for disease. This works effectively to alert large areas, such as entire states, but is not useful for local prediction.

Insecticides commonly are used to kill leafhoppers, and thereby minimize disease transmission. Because there are protracted acquisition and incubation times associated with this disease, chemical-based disease suppression is feasible. Insecticides are especially effective in the absence of long-distance dispersal by leafhoppers. Systemic insecticides are often favored due to their persistence, but contact insecticides can also be effective. Insecticides are often applied at 5–7 day intervals. Because it takes 10–15 days for infected plants to show signs of infection, it is not necessary to treat plants just prior to harvest.

Crop varieties differ in their susceptibility to infection with aster yellows; this is well studied both for carrots and lettuce, two of the more susceptible crops. Cultural manipulations can also enhance resistance. In studies conducted in Minnesota, very significant reductions in disease incidence were shown where aluminum foil mulch was used. Straw mulch was equally effective. Row covers, where economically feasible, should provide good protection against leafhoppers and disease transmission. Destruction of weed species known to harbor aster yellows is desirable.

Aster leafhopper acquires the MLO by feeding on infected perennial or biennial weeds or crop plants. Acquisition requires a prolonged period of feeding, usually at least 2 h, before the leafhopper is infected. Usually <2% of dispersant leafhoppers become infected. There is evidence that the MLO multiplies in the body of the leafhopper, and there is an incubation period of about 2 weeks in nymphs, and 6–10 days in adults, before the insects are capable of transmitting aster yellows. Leafhoppers remain infective for the duration of their life, but the MLO is not transmitted between generations through the egg stage. Thus, there is ample time for insecticides to interrupt disease transmission.

References

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, CA, 729 pp

Hagel GT, Landis BJ (1967) Biology of the aster leafhopper, *Macrosteles fascifrons* (Homoptera: Cicadellidae), in eastern Washington, and some overwintering sources of aster yellows. Ann Entomol Soc Am 60:591–595

Hoy CW, Heady SE, Koch TA (1992) Species composition, phenology, and possible origins of leafhoppers (Cicadellidae) in Ohio vegetable crops. J Econ Entomol 85:2336–2343
Nielson MW (1968) The leafhopper vectors of phytopathogenic viruses (Homoptera: Cicadellidae). Taxonomy, biology, and virus transmission. USDA Technical Bulletin 1382, p 386

Asterolecaniidae

A family of insects in the superfamily Coccoidae (order Hemiptera). They sometimes are called pit scales.

► Bugs

Aster Yellows

This is an important insect-vectored disease that affects many plants. See also, Transmission of Plant Disease by Insects.

► Transmission of Plant Diseases by Insects

Ateluridae

A family of silverfish (order Zygentoma).

► Silverfish

Athericid Flies

Members of the family Athericidae (order Diptera).

► Flies

Athericidae

A family of flies (order Diptera). They commonly are known as anthericid flies.

► Flies

Astrotaxis

Taxis response with respect to the sun, moon, stars or polarization of light.

Asymmetric Competition

Competition between two individuals or species in which one is more severely affected than the other.

Asymmetric PCR

Single-stranded DNA produced by providing an excess of primer for one of the two DNA strands. Asymmetric primer ratios are typically 50:1–100:1. Single-stranded DNA produced can be sequenced directly without cloning.

Asynchronous Muscle

Muscle in which the frequency of contraction is not controlled directly by nervous impulses, with the contraction frequency a property of the muscle. Asynchronous muscle produces several to many contractions in response to a single nervous stimulation. (contrast with synchronous muscle)

ATP

Adenosine triphosphate is the primary molecule for storing chemical energy in a cell.

Atrophy

Decrease in size of a tissue, organ, or part after full development has been obtained. In pathology, a condition in which the affected cells undergo degenerative and autolytic changes, become smaller, and have a lessened functional capacity.

Attelabidae

A family of beetles (order Coleoptera). They commonly are known as leaf-rolling weevils.

► Beetles

Attenuation

The process of decreasing the virulence of a microorganism.

Attractant

An odor, or the material producing an odor, that attracts insects.

Attraction of Insects to Organic Sulfur Compounds in Plants

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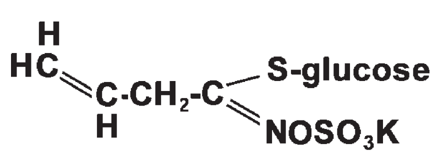
Among the secondary plant metabolites, two types of organic sulfur compounds are of considerable importance: glucosinolates and cystein derivative amino-acids, and their respective breakdown products. These compounds, in various ways, influence the diversity of organisms associated with plants bearing these compounds.

Glucosinolates

Glucosinolates (=mustard oil glycosides) occur predominantly throughout the order Capparales, consisting of Brassicaceae (=Cruciferae), Capparaceae, Moringaceae, Resedaceae, Tovariaceae, and sporadically in some other families (e.g., Caricaceae, Limnanthaceae, and Tropaeolaceae). About 50 different glucosinolates are found in Brassicaceae, and over 100 glucosinolates throughout the plant kingdom. Several to about twenty glucosinolates occur in each cruciferous species. For example, in leaves there are 14 glucosinolates in cabbage, 12 in cauliflower, 11 in Brussels sprouts, 7 in broccoli and Chinese cabbage. In roots, there are 18 glucosinolates in turnip and 8 in kohlrabi. In oilseeds, there are 9 glucosinolates in rapeseed and turnip rape, and 5 in mustard. Glucosinolates having a bitter taste are broken down to mustard oils (isothiocyanates) and other substances by enzymes which are known as myrosinases.

Isothiocynates, in general, have hot and pungent odors. However, those which have a bigger molecule lose pungent odor and have more sweet and mild odors. For example, 2-propenyl isothiocyanate (allyl isothiocyanate, C_3H_5NCS), which is (Fig. 93) split from sinigrin, has a very pungent odor; however, 2-phenylethyl isothiocynate ($C_6H_5CH_2CH_2NCS$), which is derived from gluconastrutiin, has a sweet odor.

E. Verschaffelt, a botanist from the Netherlands, first noticed the relationships between insects and glucosinolates early in the twentieth century. He found that the host plants of the large and small white butterfly larvae, *Pieris brassicae* and *P. rapae*, were limited to the plants containing glucosinolates. By smearing sinigrin on leaves which had been rejected before, the larvae came to readily attack and feed on some of these. Half a century later, this result was verified and developed by Thorsteinson and his group in Canada with the diamondback moth, *Plutella xylostella*, using artificial agar diet containing a known quantity of glucosinolate. Sinigrin, sinalbin, glucocheirolin, and progoitrin stimulated larval feeding in the presence of glucose. After these important works, the stimulation of feeding by glucosinolates, mainly sinigrin, was shown in a variety of specialist herbivores feeding on cruciferous plants: the cabbage aphid, *Brevicoryne brassicae*, the cabbage fly, *Delia brassicae*, the cabbage beetle, *Phaedon cochlearia*, and *P. brassicae*. The gravid female white butterflies tap the leaf surface with their forelegs (called "drumming") when they attempt to oviposit on leaves. They receive chemical



Attraction of Insects to Organic Sulfur Compounds in Plants, Figure 93 Chemical structure of sinigrin.

stimulation from glucosinolates in leaves via the sensilla on their tarsal undersurface. Glucobrassicin (3-indolylmethyl glucosinolate) is effective at 10^{-6} M, 1,000-fold more effective than sinigrin (2-propenyl glucosinolate), in initiating oviposition by *P. brassicae*. Each crucifer plant has a few or many glucosinolates so that they seem to work together.

In Japan during the 1950s, the olfactory stimulation of insect by isothiocynates was first proven by Sugiyama and Matsumoto with both of adults and larvae of the vegetable weevil, *Listroderes costirostris*. This species is a typical generalist, feeding on over 120 species in 28 plant families, in which Brassicaceae are among the important host plants. Each allyl-, 1-butyl-, 2-butyl-, phenyl-, benzyl-, 2-phenylethyl isothiocynate evoked every step of the chain reaction of host selection behavior in adults, consisting of the orientation (=attraction), antennae tapping and final continuous biting (=feeding) against the odor-material in the absence of any taste substances or nutrients. For newly hatched larvae, nine isothiocynates, methyl-, ethyl- to 2-phenylethyl, 1-naphtyl isothiocynates indicated a significant attractiveness, increasing with an increasing number of CH_2 groups. These results clearly show that not only the specialist herbivores, but also the generalist herbivores, use plant odors as the token stimuli for their host selection behavior. In Germany, the attraction of the flea beetles, *Phyllotreta crucifera* and *P. striolata*, by allyl isothiocynate was first shown in field trapping. Thereafter, allyl-isothiocynate was proven to be effective in attraction to the cabbage root fly, *Delia radicum*, the turnip root fly, *D. floralis*, *D. brassicae* adults, and also in stimulation of oviposition by *P. rapae* and *P. xylostella* females. The cabbage seed weevil, *Ceutorhynchus assimilis*, is attracted by isothiocynate mixtures similar to the composition of odor chemicals in oilseed rape plants. However, omission of two isothiocynate, 3-butenyl isothiocynate and 4-pentenyl isothiocynate from the mixture significantly reduces the attractiveness.

In general, favorable effects such as feeding and oviposition stimulation by glucosinolates and attraction by isothiocynates are observed in specialist herbivores on Brassicaceae. Contrarily, unfavorable effects such as feeding and oviposition inhibition and repulsion are observed in non-adapted herbivores, such as the bertha armyworm, *Mamestra configurata*, Colorado potato beetle, *Leptinotarsa decemlineata* and the desert locust, *Schistocerca gregaria*.

Plant breeding strategies have concentrated on reducing the glucosinolate content of rape seeds because of reducing the risk of causing goiter and organ abnormalities in livestock animals. However, the response of insects to the glucosinolate and/or isothiocynate content is not so simple. A worker reported that *Phyllotreta cruciferae* and *P. xylostella* larvae fed at equal rates on *Brassica juncea* and its low-glucosinolate lines, indicating that these species are insensitive to sinigrin. Another group of workers reported that the feeding activity, such as the proportion of time feeding and area damaged, by *P. xylostella* larvae is higher on the lines with low myrosinase activity than on the lines with high mirosinase activity. In contrast, the feeding activity of the southern armyworm, *Spodoptera eridania*, a generalist, is not related to myrosinase activity. Relative growth rates of both insect species are lower on cotyledons of lines with high glucosinolate content, but are not related to myrosinase activity in the lines. Thus, glucosinolate reduction is not always promising for protecting crops against the insects.

Organic Sulfur Compounds in *Allium* Plants

V. G. Dethier first proposed investigation of behavioral reactions of typical allium-feeders to organic sulfur compounds, which seemed to be characteristic of odor in allium plants. During the late 1950s to early 1960s, the fast progress of instrumental analysis brought forth the component data of onion volatiles. Allium plants produce very specific sulfur compounds. Cysteine derivative amino acids are converted by enzymatic splitting into sulfenic acids and thiosulfinates, which evolve into numerous substances. This results in production of odorous substances consisting mostly of mono-, di-, tri-sulfides, and n-dipropyldisulfide (n-DPDS, n-$C_3H_7SSC_3H_7$) and 1-propanethiol (1PTH, n-C_3H_7SH), which are reported to be the main components of onion odor. The attraction and oviposition stimulation of female onion fly, *Delia antiqua*, by these two compounds was first demonstrated by Matsumoto and Thorsteinson in laboratory experiments and field trapping in Manitoba, Canada in 1963–1964. However, no attraction nor oviposition stimulation was observed to di-methyldisulfide (DMDS). Newly hatched larvae also were shown to be attracted to over 20 compounds of various mono-, di-sulfides and alkyl-thiols, including DMDS. The larvae are likely to be less strict in the selection of odor chemicals.

Over 10 years later, the analysis of green onion-seedling odor was conducted in Canada and Japan independently, so that nine alkyl di- and trisulfides including n-DPDS and 1PTH were found. A propylthio (n-C_3H_7S) moiety was shown to be essential for a compound to induce attraction and oviposition stimulation activities. The compounds having butylthio (n-C_4H_9S) or amylthio (n-$C_5H_{11}S$) moiety also were reported to be attractive, although these compounds were not found in volatiles from onion. The green onion seedlings of susceptible cultivars give a larger quantity of propylthio compounds than those of resistant cultivars, because the allinase activity is higher than in the resistant cultivars.

Host finding by the leek moth, *Acrolepiopsis assectella*, an allium specialist, is also controlled by sulfur compounds, with propylpropanethiosulfinate (n-$C_3H_7SOSC_3H_7$) the most attractive. The adults of Diadromus pulchellus, an endoparasitoid of the young larvae of *A. assectella* and *P. xyllostera*, use the volatiles from the frass excreted by their hosts, and from the plant leaves fed by their hosts. In the volatiles from the frass of both moths, the same three disulfides (dimethyl, dipropyl, and methyl propyl) are the most abundant substances. Thus, volatile sulfur compounds in allium plants have been found to favor the host finding by an allium specialist, but to deter the approach and attack to the plant by generalists. This is similar as in glucosinolates.

References

Dethier VG (1947) Chemical insect attractants and repellents. Blakiston, Philadelphia, Pennsylvania, and Toronto, Canada

Fenwick GR, Heaney RK, Mullin WJ (1983) Glucosinolates and their breakdown products in food and food plants. CRC Critical Rev 18:123–201

Finch S (1981) Chemical attraction of plant feeding insects to plants. Appl Biol 5:67–143

Matsumoto Y (1970) Volatile organic sulfur compounds as insect attractants with special reference to host selection. In: Wood DL, Silverstein RM, Nakajima M (eds) Control of insect behavior by natural products. Academic Press, New York, NY, UK

Miller JA, Stricker KL (1984) Finding and accepting host plants. In: Bell WJ, Cardé RT (eds) Chemical ecology of insects. Chapman and Hall, New York, NY, pp 128–157

Städler E (2000) Secondary sulfur metabolites influencing herbivorous insects. In: Rennenberg H, Brunold C, Stulen I, Dekok L (eds) C et al (eds) Sulfur nutrition and sulfur assimilation in higher plants. Paul Haupt, Bern, Switzerland, pp 187–202

Thorsteinson AJ (1960) Host selection in phytophagous insects to plants. Ann Rev Entomol 5:67–143

Verschaffelt E (1910) The cause determining the selection of food in some herbivorous insects. Proc Royal Acad Science, Amsterdam 13:536–542

Audinet-Serville, Jean-Guillaume

Jean-Guillaume Audinet-Serville was born in Paris on November 11, 1775. The family wealth was lost during the French revolution, and Jean-Guillaume was sent to work in a coal store. The wife of the director of the store, Mme. de Tigny, author and correspondent of several notable entomologists, influenced him to collect and study insects. He married, and had three children before losing his wife. Latreille asked him to continue a work that Palisot de Beauvois had left incomplete due to the death of that entomologist. Thus, the 15th (last) part of "Insectes recueillis en Afrique et en Amérique…" was written by Audinet-Serville and published in 1819. Another famous work, Olivier's "Encyclopédie méthodique," was likewise incomplete, and here again Latreille persuaded Audinet-Serville, with help from Lepelletier de St. Fargeau and Latreille, to write volume 8, published in 1825. A third work, "Faune française" was also completed by Audinet-Serville in 1830, when he wrote the natural history of Coleoptera. Then, in 1831, he began publishing his own studies, first on the genus *Pirates*, and then "Revue méthodique de l' ordre des orthoptères," both in the pages of Annales des Sciences Naturelles. Other works followed, of which a notable one in 1839 was on "Orthoptères" and formed a supplement to Buffon's series of volumes "Histoire naturelle…." He died on March 27, 1858. His collections were broken up and sold to various collectors.

Reference

Amyot CJB (1858) Notice necrologique sur Audinet-Serville. Ann Soc Entomol France 6:343–351

Audouin, Jean-Victor

Jean-Victor Audouin was born in Paris on April 2, 1797. He began to study law, but turned instead to medicine. His (1826) thesis was on the chemistry, pharmaceutical uses, and medical effects of "cantharides" (cantharidin), and on the beetles that produce it. He was made assistant to Latreille, and then succeeded Latreille as chairman of entomology at the Muséum National d' Histoire Naturelle, and reorganized and enriched the collections. In 1829, he coauthored a book with Milne Edwards on natural history of Crustacea. His (1834) book "Histoire naturelle des insectes" was of several volumes. He contributed some of his work to Cuvier's "Règne animal…" In 1838, he was elected a member of the Academie des Sciences. He did not build a personal collection of insects. He also published on applied entomology with a book (1842) "Insectes nuisibles à la vigne." With Brongniart and Dumas he founded the journal Annales des Sciences Naturelles. He died in Paris on November 9, 1841.

Reference

Fauvel A (1868) Biographie et bibliographie. In: Faune gallo-rhénane…Coléoptères. vol 1, pp 59–130

Augmentation

The practice of rearing and releasing biological control agents to effect pest suppression. This is also called augmentative biological control.

► Augmentative Biological Control

Augmentative Biological Control

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Augmentation involves efforts to increase populations or beneficial effects of natural enemies (parasitoids, predators, pathogens, entomopathogenic nematodes) of pest insects, mites and weeds. Various techniques can be employed in augmentation, but augmentation typically involves releases of natural enemies or environmental manipulation to enhance effectiveness of naturally occurring natural enemies. Environmental manipulation may involve providing alternative hosts or prey, food or nesting sites or modifying cropping practices to favor natural enemies.

Periodic releases may be labeled inundative or inoculative, depending upon the numbers of natural enemies released and the time interval during which they are expected to provide control. The distinction between inundative and inoculative augmentative releases may become blurred. Inundative releases involve releasing large numbers of natural enemies with the goal of achieving an immediate effect on pest populations. In essence, the natural enemies are "living pesticides." Pathogens and nematodes are commonly released inundatively. Parasitoids or predators are less often released in this manner because it is more difficult to mass produce high quality natural enemies inexpensively. For inoculative releases, relatively small numbers of natural enemies are released early in the cropping season and it is assumed that they will multiply and provide control of the target pest later in the season.

Examples of Augmentative Releases

Augmentation is an appropriate tactic to consider if indigenous natural enemies cannot suppress pest populations to an adequate level because the natural enemy population lags behind that of the pest, or if the natural enemies cannot persist over winter. Releasing natural enemies into crops that are sprayed with pesticides that are toxic to the natural enemies is unlikely to be effective unless the sprays are applied in a selective manner.

Examples of augmentative releases include releases of *Cryptolaemus montrouzieri*, a coccinellid predator of mealybugs into California citrus groves. This ladybird beetle has established permanently only in a narrow coastal area of California and does not overwinter elsewhere, so releases of 10–20 *Cryptolaemus* beetles per tree at the beginning of the summer can result in control of the mealybugs during the growing season. Periodic releases of the parasitoid *Aphytis melinus* are made to control California red scale on citrus grown in the coastal citrus region of California; approximately 200,000–400,000 wasps per acre are released. Several species of phytoseiid predatory mites have been released to control the two-spotted spider mite, *Tetranychus urticae*, in strawberries in California. Releases became essential and cost effective after this spider mite developed resistance to the pesticides used previously to control it. Releases of the parasitoid *Muscidifurax raptor* to control house flies, *Musca domestica*, on dairy farms can be effective if conducted as part of an integrated pest management program.

Augmentative releases are extensively employed in European glasshouses (or greenhouses). Releases of parasitoids or predators are made to control spider mites, whiteflies, leafminers, aphids and other pests on cucumbers, tomatoes and sweet peppers. For example, greenhouse whiteflies, *Trialeurodes vaporariorum*, are controlled by releases of a pathogenic fungus, *Aschersonia* sp. or a parasitoid wasp, *Encarsia formosa*. Several aphids can be controlled with releases of the cecidomyiid predator *Aphidoletes aphidimyza*, and the aphid *Myzus persicae* can be controlled by releases of the parasitoid *Diaeretiella rapae*. Leafminers, *Liromyza* sp., can be controlled by releases of several commercially available parasitoids. The two-spotted spider mite, *Tetranychus urticae*, a major pest of both ornamental and vegetable plants, is controlled by releases of the phytoseiid mite *Phytoseiulus persimilis*. Much of the information developed for releasing natural enemies in European glasshouses can be adapted to control glasshouse pests elsewhere because these pests are widely distributed.

Controversies about Augmentative Releases

Some augmentative release programs are controversial. For example, egg parasitoids of the genus *Trichogramma* attack eggs of many Lepidoptera. These tiny wasps have been mass reared and released against moth pests on millions of hectares of crops around the world. However, their efficacy rarely has been documented. It is suspected that efficacy may be less than expected because the wasps usually are reared, for economic reasons, on host eggs other than those of the target pest. Parasitoids produced on alternative host eggs may be of lower quality (small in size or with crumpled wings). Effective *Trichogramma* releases may require releasing as many as 150,000–500,000 wasps per hectare every 2 weeks during the growing season. Other elements of effective *Trichogramma* releases include collecting the species or biotype (specific strain) that attacks the target pest in the target crop for mass rearing. Reestablishing colonies on an annual basis using field-collected material has been recommended in order to maintain high quality.

Some augmentative releases of natural enemies have appeared to be effective because they induced the farmer to stop pesticide applications. However, the released natural enemy may not have provided control, which was actually provided by naturally occurring parasitoids, predators and pathogens. Knowingly using augmentative releases as a "placebo effect," in which the pest control is achieved by native natural enemies which are no longer disrupted by pesticide applications, is considered unethical because the consumer pays for unnecessary natural enemies.

Other releases of natural enemies may be of little direct benefit to the consumer purchasing them. For example, releases of some predators (such as some species of lady beetles or lacewing adults) may provide limited benefit at the release site because these predator species may be genetically programmed to fly long distances prior to settling down to feed and reproduce.

Another, more recent, issue that has been raised is whether some natural enemy species released in augmentative biological control programs could become permanently established in the environment. If the natural enemy is not native, some have questioned whether the natural enemies could have unintended effects on nontarget species in natural environments, perhaps reducing biodiversity. In the USA, importation of nonnative natural enemies, whether for classical biological control or for augmentative releases, must be approved by the U.S. Department of Agriculture after undergoing risk analysis.

When and Where are Releases Made?

Augmentative releases are most likely to offer practical alternatives to pesticides in situations where the crops are of high value, the natural enemies are reliably available at competitive prices, and guidelines on release methods, rates and timing are available. However, relatively few predators and parasitoids (probably <50) have been evaluated for efficacy, reliability and economic feasibility.

Augmentative releases can be hampered if high quality parasitoids and predators are not be available at the right time. Mass rearing of parasitoids and predators is restrained by high costs, lack of effective artificial diets, ineffective or limited quality controls and an inability to stockpile or store natural enemies during periods when they are not needed. Typically, parasitoids or predators are reared on insect hosts or prey, which are themselves reared on plants, making the rearing system complex and expensive. Maintaining pure and vigorous colonies of both hosts and natural enemies, as well as disease-free plants, requires skill and resources. If effective artificial diets could be developed for additional natural enemies, costs could decline and availability could increase. Although artificial diets for some arthropods are available, many diets are less effective than natural foods in producing high quality natural enemies. Concerns have been raised as to whether parasitoids or predators reared in insectaries are less fit than desired. For example, sex ratios in parasitoid populations reared in the laboratory often change due to inbreeding. Optimal methods for maintaining quality and genetic variability need to be developed to increase the effectiveness of natural enemies reared for augmentative releases in biological control programs.

Relatively few microbial products are available for pest management programs despite the fact that it may be easier and less expensive to produce viruses, bacteria or fungi than to rear parasitoids or predators. The commercial production of microbial pesticides involve a series of steps, including: isolating a suitable pathogen by screening a large number of isolates to identify those which show activity against the target pests; conducting laboratory and greenhouse tests to evaluate the efficacy of potential agents and to determine what environmental issues could affect their effectiveness;

producing commercial scale quantities of the product, which usually involves fermentation; developing the correct formulation of the microbe so the product can be stored, handled and applied effectively in the field; conducting efficacy trials of the agent under field conditions using commercial types of formulations. Microbial pest control products are expected to increase in popularity, but are not expected to replace synthetic organic pesticides. These microorganisms often are not pathogenic to predators and parasitoids, which can allow these agents to be compatible.

Several problems limit the use of microbial pesticides. Microbial products are not always reliable under field conditions due to limitations in both formulation and the microorganism itself. The activity of the microorganism may be too specific, which can be a disadvantage when there are multiple pests in the cropping system. Most microbial products have a short residual activity in the field (especially in comparison to synthetic organic pesticides), which makes it necessary to make multiple applications which increases labor and product costs. Microbial products may act slowly, making them appear ineffective or allowing excessive damage to occur in the crop.

Some Logistical and Ethical Issues

Augmentative biological control with releases of natural enemies requires that the user (grower, farmer, home owner) have considerable information. Consumers need to be informed before using augmentative biological control or consult with a knowledgeable pest control advisor. Some augmentative releases should be considered experiments because necessary information is lacking. It is possible that the release rates and timing may not have been evaluated under the specific climatic conditions and crop production conditions at the release site.

Detailed information about the pest species you wish to control is usually required for effective augmentative releases of natural enemies. Some natural enemies, such as some lady beetles, are generalists and will eat many species of aphids. However, even generalist lady beetles may not eat all species of aphids because the aphids are repellent or contain toxic chemicals. Many pests require specific natural enemies to achieve control. For example, a predatory mite that is known to feed on spider mites may not consume other plant-feeding mite species such as rust mites or tarsonemid mites. Many parasitoids have a very limited host range, sometimes limited to one or a few species. Thus, a taxonomic identification of the pest to species or strain may be required.

Next, the best natural enemy(ies) for that target pest need to be identified. Companies provide lists of pests against which their products may be applied, but these may be less than reliable. Consult your land grant university extension service, the U.S. Department of Agriculture or licensed pest control advisors for additional information as to which natural enemies are appropriate for your target pest.

One of the most difficult questions to answer is "how many do I have to purchase for release"? This question should be answered after careful consideration; if too few natural enemies are released, the releases will be ineffective and the funds used to purchase the natural enemies will be wasted. Furthermore, the additional damage to the crop caused by the pest could reduce yield or quality.

There are some common "rules of thumb" in release rates: for example, releasing 1 predatory mite for each 10 or 20 spider mites will provide relatively rapid pest population suppression. However, even this release rate is inadequate if the 10 or 20 spider mites have caused economic damage to the plant prior to the release; an average of ten mites per leaf results in different levels of damage than an average of ten mites per plant. Thus, information about the damage the plant can tolerate is needed. Different cultivars of a crop may vary in sensitivity to feeding by pests, so release rates and timing may have to be tailored to the specific crop cultivar.

To calculate the number of natural enemies required in an augmentative release program, the number of pests should be estimated by an effective sampling scheme. For example, it may be useful to estimate the mean number of spider mites per leaf, the mean number of leaves per plant and the mean number of plants per acre or hectare to calculate the total number of mites present and, thus, the number of predators to order. Do not forget to allow for a continued population increase between the time you calculate the pest population density and the time you receive the natural enemies (typically several days to a week later). The sooner the releases occur the less damage will accrue to the crop plant.

Once the natural enemies arrive, follow the directions on how to store them before releasing them, monitor the containers to be sure the natural enemies are healthy, and follow the directions on how to release them. Once the releases have occurred, know how to monitor the release site to be sure the natural enemies are performing as expected.

Time is of the Essence

Because natural enemies are relatively expensive, it is desirable to release them as early as possible in a pest population outbreak so that fewer natural enemies are required to perform the job. Waiting until the pest population is abundant increases costs and reduces the likelihood that the natural enemies will perform effectively.

Many natural enemies arrive from commercial producers as adults, and they may have been stressed during shipment. As a result, they may require a "lag time" before they feed or reproduce on the target pest. Furthermore, many natural enemies, such as predatory mites, typically live as adults less than a week; if we assume that the adults were collected immediately after emerging for shipping and the shipping process takes 1 day, such individuals will still have "lost" approximately 2 days in their potential effectiveness.

Ideally, augmentative releases will be planned prior to the start of the growing season and a monitoring program will be implemented so that releases can be scheduled as soon as the target pest population appears.

Costs of Releasing Natural Enemies

Costs of releasing natural enemies depend on the number that must be released. It is often the case that too few natural enemies are released and, as a result, in inadequate control occurs. In California strawberries, it was estimated to cost approximately US $600 per acre to release predatory mites to control two-spotted spider mites in strawberries. This cost was accepted because the spider mites were resistant to the currently registered pesticides and no other effective control method was available. Furthermore, the high value of strawberries (approximately $30,000 per acre) made this control cost feasible. In lower value crops, augmentative releases might not be economically justifiable.

- What is the specific pest you need to control?
- Which natural enemies are known to perform well on that specific pest species under similar climatic and geographic conditions?
- How many pests do you have? Per leaf? Per plant? How many plants per row or acre? How many acres?
- What is the effective release rate for that natural enemy? For example, should the natural enemy be released in a ratio of one natural enemy to each 10 pest individuals? If so, the earlier the releases can be conducted, the less expensive such releases will be. For example, If hundreds of spider mites are present on each plant, then it is expensive and difficult to release sufficient predators to suppress them; it would be better to make releases when less than one spider mite per leaf is present.
- Calculate the number of natural enemies needed based on release rate, area to be covered and abundance of the pest per plant, row, acre.

- Are multiple releases needed over days or weeks to achieve the necessary level of pest suppression?
- How should the natural enemies be stored and handled after your receive them from the commercial producer to reduce mortality and enhance effectiveness after release?
- When should releases be conducted (time of day, temperature conditions) and in what manner? For example, do natural enemies disperse readily or should they be released on each plant or each leaf.
- How can you monitor the results of the releases to know if the natural enemies are performing as expected?
- Does the commercial producer provide information on release rates, timing, methods, and guarantee quality of the natural enemies during shipping?

Key Research Needs

Additional resources committed to improving augmentative releases of natural enemies could increase the use of this pest management tactic. These include research to develop adequate quality control tests so that only high quality natural enemies are shipped from the commercial producers. Appropriate tests should be conducted to confirm that the correct natural enemy species is shipped, that it is disease free, vigorous and viable. Research should also be devoted to developing improved methods for producing natural enemies at peak demand times, or for storing natural enemies without a loss in quality, so that adequate numbers are available when needed. High quality, but inexpensive, artificial diets could reduce production costs. Shipping and storage methods could be improved; many natural enemies arrive stressed or, even, dead. Finally, accurate information on release rates and timing could be improved and developed for additional geographic regions and climates.

Because data are not available for all situations, many augmentative releases of natural enemies should be considered experiments and conducted on a relatively small scale initially until it is clear that the necessary information is available and appropriate for the new situation.

Future of Augmentation

Pests in greenhouses in Europe, in which eggplants, cucumbers and tomatoes are grown, are often under complete biological control due to augmentative releases of natural enemies. There are several moderately large companies that produce natural enemies for this market, provide information on release rates and timing, and provide other information. Control of pests of ornamental plants in Europe is less often achieved by augmentative biological control because damage to foliage or flowers reduces quality. Greenhouse-grown crops in other geographic areas may be limited due to difficulties in obtaining natural enemies in a timely fashion, differences in pest and disease complexes, and differences in climatic conditions.

Citrus growers in California have developed grower-owned cooperatives to produce natural enemies. This approach has proven successful for over 50 years, suggesting that grower-owned cooperatives might be a useful model for increasing the use of augmentative releases in other crops in other geographic areas.

Augmentative releases can be an effective pest management tool for many pests in a diverse array of crops. However, augmentative biological control requires that the pest manager have considerable information on pest and natural enemy biology, an understanding of pest-natural enemy dynamics, and the availability of adequate numbers of high quality natural enemies for release at the right time. Thus, it is an information-intensive and logistically critical management approach.

Augmentation has the potential to become a more dominant component of pest management programs if sufficient resources are devoted to

Some natural enemies considered suitable for augmentative biological control

Natural enemy	Pest
Predators	
Amblyseius barkeri	*Thrips tabaci, Frankliniella occidentalis*
Amblyseius cucumeris and A. degenerans	*Thrips tabaci, Frankliniella occidentalis*
Anthocorus nemorum	Thrips
Aphidoletes aphidimyza	Aphids
Cryptolaemus montrouzieri	Mealybugs and some scalaes
Chrysoperla carnea	Aphids
Hippodamia convergens	Aphids
Metaseiulus occidentalis	*Tetranychus urticae, T. pacificus*
Orius sp.	*Frankliniella occidentalis*
Phytoseiulus persimilis	*Tetranychus urticae*
Parasitoids	
Aphelinus abdominalis	*Macrosiphum euphorbiae*
Aphidius colemani	*Aphis gossypii*
Dacnusa sibirica	*Liriomyza bryoniae, L. trifolii, L. huidobrensis*
Diglyphus isaea	*L. bryoniae, L. trifolii, L. huidobrensis*
Encarsia formosa	*Trialeurodes vaporariorum, Bemisia tabaci*
Eretmocerus californicus	*Bemisia tabaci*
Leptomastix dactylopii	*Planococcus citri*
Metaphycus helvolus	Scales
Opius pallipes	*Liriomyza bryoniae*
Trichogramma spp.	Lepidopteran eggs
Pathogens	
Bacillus thuringiensis	Lepidopteran larvae
NPV-virus	*Spodoptera exigua*
Trichoderma harzianum	*Fusarium* spp.
Verticillium lecanii	Aphids
Entomopathogenic nematodes	
Heterorhabditis spp.	*Otiorrhynchus sulcatus*
Steinernema spp.	Sciaridae

obtaining the necessary information and improvements in rearing and deployment.

► Natural Enemies important in Biological Control
► Culture of Natural Enemies on Factitious Foods and Artificial Diets
► Rearing of Insects

An Important Website: http://www.cdpr.ca.gov/docs/ipminov/bensuppl.htm, which provides a list of commercial suppliers of natural enemies in North America. A variety of natural enemies are produced commerc ially for the control of greenhouse and other pests.

References

Flint ML, Dreistadt SH (1998) Natural enemies handbook. The illustrated guide to biological pest control. Publication 3386. University of California, Division of Agriculture and Natural Resources, Oakland, CA
Hoy MA, Nowierski RM, Johnson MW, Flexner JL (1991) Issues and ethics in commercial releases of arthropod natural enemies. Am Entomol 37:74–75
Parrella MP, Heintz KM, Nunney L (1992) Biological control through augmentative releases of natural enemies: a strategy whose time has come. Am Entomol 38: 172–179
Ridgway RL, Vinson SB (eds) (1977) Biological control by augmentation of natural enemies. Plenum Press, New York, NY
Sullivan DJ (1987) Efficacy of inundative releases. Ann Rev Entomol 22:515–531
van Lenteren JC, Woets J (1988) Biological and integrated pest control in greenhouses. Ann Rev Entomol 33:239–269

Auricular Openings

Lateral, slit-like openings to the insect heart by which blood is admitted into the dorsal vessel. These are also known as ostia or incurrent ostia.

Australian Archaic Sun Moths (Lepidoptera: Lophocoronidae)

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Australian archaic sun moths, family Lophocoronidae, have six known species in Australia. The family comprises its own superfamily, Lophocoronoidea, and is the only member of the infraorder Lophocoronina, of the suborder Glossata. Adults small (10–15 mm wingspan), with head roughened; labial palpi 3-segmented; haustellum short and vestigial mandibles are present; maxillary palpi are long and 4-segmented. Maculation is pale monotone with some darker spotting. Biologies and larvae remain unknown, but adults are crepuscular in eucalyptus sclerophyll woodlands.

References

Common IFB (1973) A new family of Dacnonypha (Lepidoptera) based on three new species from southern Australia, with notes on the Agathiphagidae. J Aust Entomol Soc 12:11–23
Nielsen ES, Kristensen NP (1996) The Australian moth family Lophocoronidae and the basal phylogeny of the Lepidoptera-Glossata. Invertebr Taxonomy 10: 1199–1302

Australian Lappet Moths (Lepidoptera: Anthelidae)

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Australian lappet moths, family Anthelidae, total 100 species, all from Australia. There are two subfamilies: Munychryiinae and Anthelinae. The family is in the superfamily Bombycoidea (series Bombyciformes), in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults medium size to very large (22–166 mm wingspan), with head vertex scaling (Fig. 94) rough; haustellum absent (sometimes short or more rarely long); labial short and mostly upcurved but some more porrect; maxillary palpi vestigial; antennae bipectinate (serrate to filiform in some females); body robust. Wings broadly triangular

Australian Lappet Moths (Lepidoptera: Anthelidae), Figure 94 **Example of Australian lappet moths (Anthelidae), *Munychryia senicula* Walker from Australia.**

and rounded (rarely somewhat acute or even falcate); hindwings rounded (rarely somewhat acute); rarely with micropterous females. Maculation mostly shades of brown with few markings, but some more marked or lighter. Adults nocturnal, but at least one species with diurnal males. Larvae are leaf feeders and generally colorful. Host plants recorded in several plant families, including Casuarinaceae, Gramineae, Leguminosae, and Myrtaceae, among others. Some species have urticating larval setae.

References

Common IFB, McFarland N (1970) A new subfamily for *Munychryia* Walker and *Gephyroneura* Turner (Lepidoptera: Anthelidae) and the description of a new species from Western Australia. J Aust Entomol Soc 9:11–22

Hulstaert PG (1928) Lepidoptera Heterocera. Fam. Anthelidae. In: Genera Insectorum, vol 191, P. Wystman, Brussels, pp 1–13, 1 pl

Mills MB (1954) Observations on the life history of the moth *Anthela xantharcha* (Meyrick) (Anthelidae). Western Aust Nat 4:86–90

Seitz A (ed) (1925) Subfamilie: Anthelinae. In: Die Gross-Schmetterlinge der Erde, vol 10. A. Kernen, Stuttgart, 364–375, pl 46, 56–58

Turner AJ (1921) Revision of Australian Lepidoptera – Hypsidae, Anthelidae. Proc Linn Soc New South Wales 46:159–191

Australian Primitive Ghost Moths (Lepidoptera: Anomosetidae)

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Australian primitive ghost moths, family Anomosetidae, comprise a single genus with 1 known species from Australia. The family is in the superfamily Hepialoidea, of the infraorder Exoporia. Adults small (18 mm wingspan), with head rough-scaled; haustellum short and vestigial mandibles present; labial palpi short, 3-segmented; maxillary palpi minute, 2-segmented; antennae short. Maculation is darkened with some darker forewing spots. Biologies and larvae remain unknown.

Reference

Kristensen NP (1978) Observations on *Anomoses hylecoetes* (Anomosetidae), with a key to the hepialoid families (Insecta: Lepidoptera). Steenstrupia 5:1–19

Australian Realm

The zoogeographic region of Australia and nearby islands. It is characterized by a preponderance of marsupials, large flightless birds, and parrots, as well as an absence of mammals.

► Zoogeographic Realms

Australian Sheep Blowfly, *Lucilia cuprina* Wiedemann (Diptera: Calliphoridae)

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Sheep in many areas of the world are plagued by fly problems, but Australia, with 103,000,000 sheep, has the most severe fly problems. The problem starts when wool becomes excessively wet. Continually wet wool is irritating to the sheep's skin, and a condition called "fleece rot" develops. Fleece rot results in skin inflammation and the secretion of serum from the irritated skin. Such a site is soon teeming with bacteria. The wet, serum-containing wool is attractive to ovipositing flies, and soon the maggots hatching from those eggs feed not only on the fleece, serum, and bacteria, but the underlying skin. The problem is exacerbated by the presence of urine, feces, sweat or other animal secretions, all of which are attractive to flies. The attack of flies on sheep in this manner is called "flystrike," and this condition can result in the death of animals or the expense of treatments to prevent or cure this fly-based problem. The problem is greatest in environments where warmth and moisture occur frequently, and the cost for fly treatments and loss of sheep due to flies is estimated at $100–150 million annually in Australia. The principal problem fly is *Lucilia cuprina*, known in Australia as Australian sheep blowfly or primary green blowfly. It is responsible for over 90% of the flystrike in Australia, but other flies can be involved.

Beginning in about 1988, *L. cuprina* first appeared in New Zealand, greatly exacerbating the flystrike problem with sheep there, and extending flystrike attacks into a nearly season-long problem. In recent years, about half of the flystrike incidents in New Zealand were caused by *L. cuprina*, but the proportion attributable to this fly seems likely to grow as it continues to spread.

Sheep producers can take several actions to reduce or prevent flystrike. The mechanical removal of the wool around the tail, anus and vulva (in ewes) is called "crutching," and helps prevent flystrike because these sites are most likely to stay wet and soiled, and thus attractive to ovipositing females. However, the wool grows continuously, so repeated removal of wool is necessary for this process to be effective, and is not cost-effective for large producers of sheep. A more permanent treatment is the surgical removal of skin around the anus and vulva, resulting in wrinkle-free and wool-free tissue in these areas, which tend to remain clean and free of flies. This surgery is called "mulesing," and is normally conducted on lambs a few weeks after birth. It takes about 4 weeks for the wounds to heal, and should be conducted before flies are active, or they will be attracted to the wounds, making the problem worse. Mulesing is quite controversial because it is painful for the sheep, and is being phased out in Australia. The tails of lambs also can be docked to reduce the tendency of the anal region to remain soiled and wet, and this practice evokes less opposition. A common alternative to crutching and mulesing is chemical protection, though this also requires repeated treatment. Other alternatives include limiting sheep raising to regions that are too dry or cool for optimal fly population growth. Some breeds of sheep, such as Merino sheep, are particularly prone to problems because the are very wrinkled and have a very dense wool. Historically, Merino is the preferred sheep in Australia.

Over 90% of the flystrikes in Australia are initiated by *Lucilia cuprina*, an introduced species. As is generally the case with blowflies, the primary hosts are carrion, but when sheep are afflicted with fleece rot or have thick mats of wet wool, female flies will deposit eggs on live sheep. The presence of even a few flies (7–10 per hectare) is enough to cause severe problems if susceptible sheep are present. The adults are metallic blue or green in color, and about 9 mm long. Flies initiate oviposition only after completing a protein meal, which enables egg production, and then up to 250 eggs can be deposited in a single batch on soiled wool. Each female typically produces two to three egg clusters during her life span of 2–3 weeks. The eggs hatch within 8–24 h, and the maggots feed and grow to a length of 10–15 mm in about 3 days. They then drop to the soil, usually during the night or early morning, and pupate. About a week after pupation, the adults emerge and start the cycle again. Thus an entire life cycle is completed in about 2 weeks. They reproduce best under warm (at least 18°C), wet conditions, but cannot tolerate high (over 38°C) temperatures, so fly populations may decrease during the middle of the summer in hot areas. Thus, peak blowfly populations tend to occur in spring, and late summer or autumn, in Australia.

Sheep producers have several options when it comes to control of sheep blowfly. Producers can apply organophosphate insecticides for rapid fly control, but these products tend not to be very persistent (2–4 weeks), and resistance to some organophosphates is known. Insect growth regulators take longer to take effect, but persist longer (up to 14 weeks). Other products are available, of course, and confer different advantages. Resistance to pyrethroid insecticides is widespread in Australia. The insecticides are sometimes applied by hand, which is advantageous because they can be directed to the areas of the animal most susceptible to flystrike. To reduce labor costs, automated (walk-through) sprayers are sometimes used, but such applications are less directed and commonly less effective in their coverage of sheep. Applications are most common soon after shearing, and if applications are delayed, unacceptable insecticide residues on the sheep may result.

In addition to chemical treatment, growers have recently adopted the practice of trapping flies. Traps consist of buckets with special lids containing entrance cones that allow the blowfly to enter but not leave the trap. Each bucket contains a number of chemical lures that mimic the odors of fleece rot, urine, feces, and animal carcasses. Once trapped inside the bucket, the flies die from dehydration. Traps are distributed at a rate of one trap per 100 sheep, and they are recommended to be used early in the season when the fly population in naturally at its lowest. In addition to removing flies from the population, and thereby reducing the rate of flystrike, the traps are useful for monitoring population densities.

Optimal management of sheep blowfly is accomplished with implementation of an integrated or multi-faceted approach. This involves reducing the attractiveness of sheep to flies by docking lamb's tails, and by shearing, crutching or mulesing all sheep. Keeping the flocks separated helps reduce the movement of flies from flock to flock. Regular inspection of the flock is desirable, and catching and shearing of sheep, and spot treatment of sheep with fly infestations is desirable. Trapping and monitoring of adult fly populations with fly traps are helpful. Treatment of the entire flock may be necessary if the fly population becomes high, but timing needs to be optimized to avoid contamination with pesticide residues. Avoidance of pesticides with a history of fly resistance is important.

Some of the other calliphorid species associated with sheep in Australia, and their local common names, include:

- *Lucilia sericata* Meigen, the European green blowfly. This invader is the principal sheep blowfly in the United Kingdom, but only a minor pest in Australia. It is virtually identical to *Lucilia cuprina* in appearance.
- *Calliphora stygia* (Fabricius), the eastern goldenhaired blowfly. This fly is native to Australia. It is brown and about 13 mm long. It prefers cooler weather, disappearing in the summer months.
- *Calliphora augur* (Fabricius), the lesser brown or bluebodied blowfly. This native fly is a secondary species, not usually attacking sheep until other species have attacked. It is mostly brown, but has a metallic blue patch on its abdomen. It is about 11 mm long. It is found commonly in the summer. It differs from most other blowflies in depositing larvae rather than eggs.
- *Chrysomya rufifacies* (Macquart), the green hairy maggot blowfly. This is another native, secondary species. It is metallic green, and can be distinguished from *Lucilia* by the broad bands on its abdomen and its black forelegs. The adult is about 9 mm long. The larvae are distinctive, bearing sharp spines (the "hairs") over its dark body. It also is known to feed on other maggots.

References

Armstrong R, Knights G, Urech R, Green P, Ward M. Undated. Sheep parasites. The LuciTrap sheep blowfly trapping system. Queensland Government, Department of Primary Industries and Fisheries, DPI&F note, 4 pp

Heath ACG, Bishop DM (2006) Flystrike in New Zealand: an overview based on a 16-year study, following the introduction and dispersal of the Australian sheep blowfly, *Lucilia cuprina* Wiedemann (Diptera: Calliphoridae). Vet Parasitol 137:333–344

Joshua E, Evans I (1999) Sheep blowflies. New South Wales Agriculture, Agnote DAI-70, 3 pp

Levot G (2000) Common blowflies that strike sheep in NSW, Australia. New South Wales Agriculture, Agnote DAI-152, 4 pp

Wilson K, Armstrong R (2005) Sheep parasites. Management of blowflies. Queensland Government, Department of Primary Industries and Fisheries, DPI&F note. 5 pp

Australian Silkworm Moths (Lepidoptera: Carthaeidae)

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Australian silkworm moths, family Carthaeidae, are a monobasic relict family in Bombycoidea with a single species from western Australia. The family is in the superfamily Bombycoidea (series Bombyciformes), in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults large (75–100 mm wingspan), with head scaling roughened; haustellum developed; maxillary palpi small, 3-segmented; antennae bipectinate, or apparently tripectinate (serrate in females); body robust. Wings broad and triangular but termen rounded; forewing with somewhat acute apex (Fig. 95). Maculation gray with large dark eyespot medially on all wings and band of gray-brown at base and along termen; hindwing reddish at apex with blue in eyespot. Adults are nocturnal (usually after midnight).

Australian Silkworm Moths (Lepidoptera: Carthaeidae), Figure 95 **Example of Australian silkworm moths (Carthaeidae), *Carthaea saturnioides* Walker from Australia.**

Larvae are leaf feeders, with numerous clubbed setae. Host plants are only in Proteaceae.

References

Common IFB (1966) A new family of Bombycoidea (Lepidoptera) based on *Carthaea saturnioides* Walker from Western Australia. J Entomol Soc Queensland 5:29–36

Common IFB (1990) Family Carthaeidae. In: Moths of Australia. Melbourne University Press, Melbourne, pp 401–403

Heppner JB (2003) Carthaeidae. In Lepidopterorum Catalogus, (n.s.). Fasc. 105. Association for Tropical Lepidoptera, Gainesville, p 8

Austrophasmatidae

A family of gladiators (order Mantophasmatodea)

► Gladiators (Mantophasmatodea)

Autecology

The ecology of individuals, or the effects of the physical and chemical environment on individual organisms (rather than on populations or communities).

► Synecology

Autocidal Control

The use of insects for self destruction, normally through release of sterile or genetically altered insects into a natural population.

Autoecious Life Cycle

A life cycle in which the insects (generally aphids) are host plant specific, living on a single host or some closely related hosts throughout the year. This is also called monoecious (contrast with heteroecious life cycle).

► Aphids

Attevidae

A family of moths (order Lepidoptera). They are commonly known as tropical ermine moths.

► Tropical Ermine Moths

► Butterflies and Moths

Aulacidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Aulacigastrid Flies

Members of the family Aulacigastridae (order Diptera).

► Flies

Aulacigastridae

A family of flies (order Diptera). They commonly are known as aulacigastrid flies.

► Flies

Australembiidae

A family of web-spinners (order Embiidina).

► Web-Spinners

Australian Parasite Moths (Lepidoptera: Cyclotornidae)

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Australian parasite moths, family Cyclotornidae, include only five known species from Australia. The family is in the superfamily Cossoidea (series Limacodiformes) in the section Cossina, subsection Cossina, of the division Ditrysia. Adults small (10–30 mm wingspan), with head scaling average; haustellum absent; labial palpi short; maxillary palpi absent; antennae filiform (thicker in males). Body robust. Wings elongated and rounded. Maculation somber hues of gray, with mainly a single forewing marking (one species is yellow and black). Adult activity uncertain but may be crepuscular. Larvae flattened, with lateral protrusions; highly evolved as parasites of leafhoppers, scale insects, or psyllids (Hemiptera) in early instars, and then as predators of ant larvae. The ants tolerate the predatory larvae, keep them in their nests and care for them, since they give the ants desirable exudates. Eggs are laid on plants frequented by likely hemipteran hosts and young larvae then search for a suitable host to parasitize upon hatching; eggs are tended by protective ants.

References

Common IFB (1990) Family Cyclotornidae. In: Moths of Australia. Melbourne University Press, Carlton, pp 306–309

Epstein ME (1996) Epipyropidae Dyar, 1903 and Cyclotornidae Meyrick, 1912. In: Revision and phylogeny of the limacodid-group families, with evolution ary studies on slug caterpillars (Lepidoptera: Zygaenoidea). Smithsonian Contributions to Zoology 582:1–102

Hinton HE (1951) Cyclotornidae. In Myrmecophilous Lycaenidae and other Lepidoptera – a summary, 167–168. Proceedings of the South London Entomological and Natural History Society 1949–50:111–175

Nielsen ES, Common IFB (1991) Cyclotornidae. In: Lepidoptera (moths and butterflies), Insects of Australia. Melbourne University Press, Carlton, pp 879–880

Australimyzidae

A family of flies (order Diptera).

► Flies

Austremerellidae

A family of mayflies (order Ephemeroptera).

► Mayflies

Austroniidae

A family of wasps (order Hymenoptera).
► Wasps, Ants, Bees and Sawflies

Austroperlidae

A family of stoneflies (order Plecoptera).
► Stoneflies

Austropetaliidae

A family of dragonflies (order Odonata).
► Dragonflies and Damselflies

Autogenic Succession

A temporal succession of species that is driven by processes within the community (contrast with allogenic succession).

Autogenous

Among blood-feeding insects, the ability to produce eggs without a prior blood meal.

Autoradiography

A method for detecting radioactively labeled molecules through exposure of an x-ray sensitive photographic film.

Autoregulatory Control

Regulation of the synthesis of a gene product by the product itself. In some systems, excess gene product behaves as a repressor and binds to the operator of its own structural gene.

Autosomes

All chromosomes except the sex chromosomes. Each diploid cell has two copies of each autosome.

Autotomy

Self-amputation which functions as an escape mechanism. Under some circumstances, body parts are deliberately shed to avoid capture by predators. Arthropod legs are shed readily, and when this occurs early in life they can be regenerated, in whole or in part.

Autotroph

Organisms that obtain energy from the sun and other materials from inorganic sources (contrast with heterotroph).

Auxiliary Vein

A supplementary vein. The subcosta is often considered to be auxiliary.
► Wings of Insects

Auxiliae

Small plates beneath the base of the pretarsal claws, bearing the pulvilli (if present). These are sometimes known as auxilliary sclerites.
► Legs of Hexapods

Avermectins

Macrocyclic lactones derived from a soil-dwelling microbe, the actinomycete *Streptomyces avermitilis*. They are chloride channel agonists. These materials are considered to be broad spectrum, slow acting, natural pesticides, and display activity against helminths, insects, mites, and nematodes. They are used widely to treat animals for parasitic organisms, but also for insect and mite pests in agriculture. They degrade readily and lack persistence and mobility, so are valued in integrated pest management programs and even in some organic agriculture situations. Common commercial products include Abamectin, Agrimek, Avert, Avid, and Vertimec.

► Insecticides

Avian Malaria, Bird Malaria

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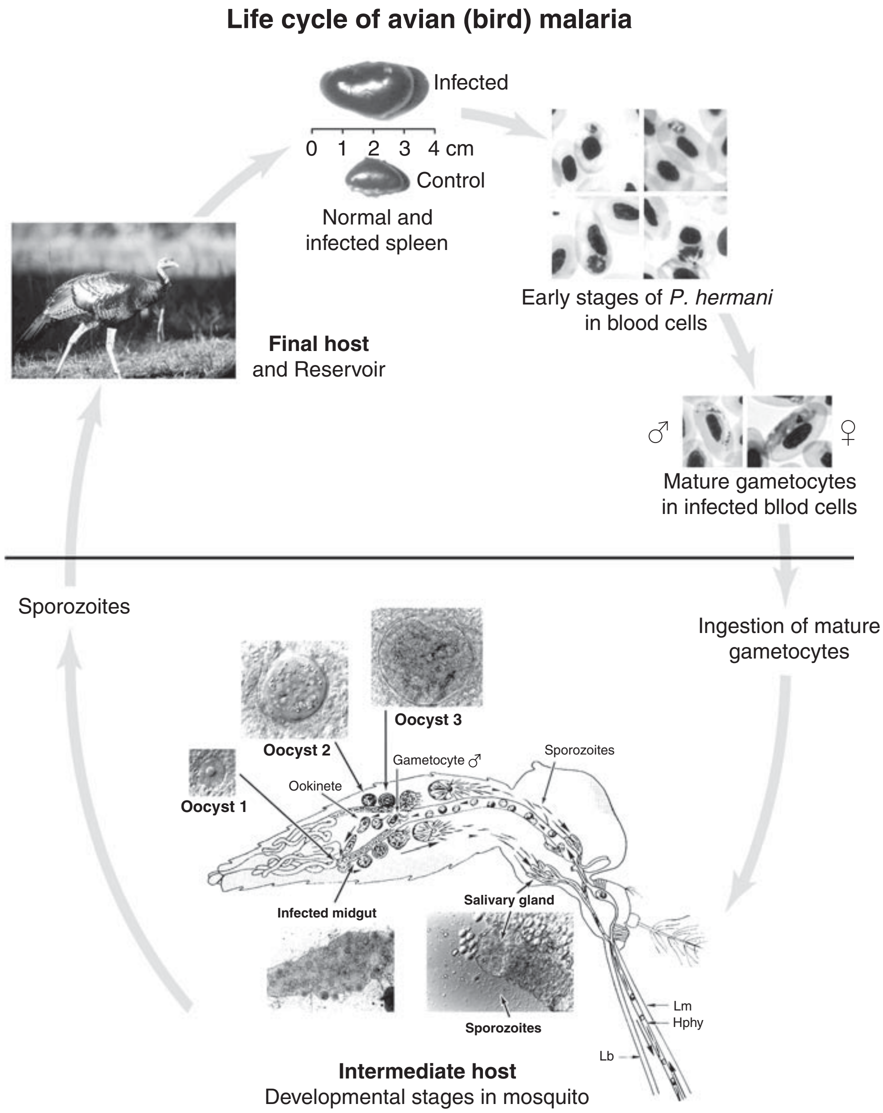
Avian malaria is an infectious disease and it is found all over the world, especially in tropical and temperate areas. It produces a wide range of effects in avian hosts, from no apparent clinical signs to severe anemia and death. It has served as an experimental model for human malaria during the early history of malaria research. Avian malaria is not one disease, but many and is caused by distinct species of a protozoan blood parasite, *Plasmodium*, that is transmitted by mosquitoes. It belongs to Class Sporozoa, Subclass Telosporidia, Order Coccidiomorphida and Suborder Haemosporidina, and Genus *Plasmodium*. There are about 30 species of *Plasmodium* parasites recognized that infect birds world-wide and they are grouped into four subgenera depending on the shape and size of the parasite in erythrocytes and presence or absence of schizogony: *Haemamoeba* species have round gametocytes; *Huffia* species have elongate gametocytes and schizogony in primitive red cells; *Giovannolaia* species have relatively large asexual stages and no schizogony; and *Novyella* species have small asexual stages and no schizogony.

Plasmodium parasites in birds are primarily blood parasites, but in the acute phase they do infect a variety of other tissues, the lungs, endothelial cells of capillaries in the brain, and the reticular cells of the splenic Malpighian body. The parasites multiply in all of these tissues. Later generations of the parasites are less selective in host cell preference and the parasites may be found in various other tissues. In the chronic phase the parasite causes little harm. Several species of mosquitoes belonging to genera *Anopheles*, *Culiseta*, *Mansonia*, *Aedes*, *Armigeres* and *Culex* are found to be experimentally susceptible to different *Plasmodium* species that infect birds, but the natural vectors are mostly *Culex* and rarely *Aedes* species.

The life cycle of *Plasmodium* (*Huffia*) *hermani*, a parasite of wild turkeys (*Meleagris gallopavo* L.) that was described (Fig. 96) from Florida in 1975, will serve as an example. This parasite was discovered after specialized subinoculation technique of blood (heparinized or citrated) from chronically infected wild older turkeys into young poults of broad-breasted-white domestic turkeys. In turkeys (both wild and domestic) the malaria parasite infection causes anemia, splenomegaly, and reduced weight gains in poults. Natural infection of the young turkey poults begins with the bite of an infected culicine mosquito. Sporozoites introduced with the salivary gland secretions are carried to the reticular cells of the splenic Malpighian body. After a minimum of three generations of exoerythrocytic development in these cells that takes about 10–14 days, the stage of parasite called merozoites may spill over in the blood circulation and invade basophilic cells of the erythrocyte series, or may continue asexual reproduction. These merozoites after invasion of basophilic cells of the erythrocyte series transform into trophozoites (uninucleated, either elongate or round), schizonts (rounded with 6–14 nuclei arranged peripherally as a rosette) and finally elongate slender gametocytes (male and female) with irregular margins in mature erythrocytes. Time required may vary from 2 to 4 days. In general erythrocytic avian merozoites appear to be able to choose among four possible fates. Most may continue schiozgony in erythrocytes, but some may become micro- and macro-gametocytes (male or female gametocytes, respectively) or they may re-initiate asexual reproduction in the tissues as phanerozoites. Northern bobwhites



Avian (Bird) Malaria, Figure 96 **Life cycle of *Plasmodium hermani*. Stages of avian malarial parasite in mosquitoes: oocyst 1 = young oocyst about 4 days old, oocyst 2 = about 7 days old, oocyst 3 = about 10 days old. Lm = labium, Lb = labrum, and Hphy = hypopharynx.**

(*Colinus virginianus*) in Florida is also a natural and experimental host of *P. hermani*.

Natural and experimental vector for *P. hermani* in wild turkeys and northern bobwhites in Florida is *Culex nigripalpus*, but experimental studies indicate that other culicines (*Cx. salinarius* and *Cx. restuans*) may be involved to a lesser degree. *Plasmodium hermani* is not transmitted by *Cx. quinquefasciatus* in Florida and it does not infect young chicks (*Gallus domesticus*). Three additional species of turkey malaria have been reported from other parts of the U.S.A. These are *P. hexamerium-like* from Texas, *P. lophurae* from Wisconsin, and *P. kempi* from Missouri, Wisconsin, Minnesota and North Dakota. Natural vectors of these species of avian malaria are presumably also culicines although they have not been determined. Experimental studies have shown that *Cx. tarsalis* and *Cx. pipiens pipiens* can be infected with *P. kempi*. Other species of *Aedes*, *Culiseta* and *Wyeomyia* can be experimentally infected with avian malarias, but their contribu tion in natural transmission of the parasite is unknown. In some of the experimental mosquitoes that are not natural vectors, a defense reaction occurs and development of oocysts in the mosquitoes is compromised by intracellular melanization of the developing oocysts.

The developmental cycle of the avian malarial parasite within the susceptible mosquito is similar in all vector species and begins with the ingestion of erythrocytes (blood cells) containing male and female gametocytes from the infected bird. As the blood meal passes into the gut, the change in the environmental factors induces gametocytes to emerge from the erythrocytes (within 4–6 h). The microgametes (male gametocytes) begin the prefertilization process by undergoing exflagellation. Soon thereafter individual microgametes are released, which swim actively to the macrogametes (female gametes) and penetrate them culminating in fertilization. This results in the formation of a zygote, which elongates and undergoes cytoplasmic changes and forms motile ookinetes (within 24 h). The mature ookinetes migrate intracellularly through the midgut cells and move into the outer wall of the midgut facing the hemocoel, where the ookinetes form a tumor like body, or oocyst. Within 8–12 days, the timing depending on temperature and species of the parasite, schizogony within the oocyst produces hundreds, or even thousands of sporozoites. Sporozites are spindle-shaped organisms measuring about 8–9 μm in length and about 1 μm wide. These are liberated into the body cavity by rupture of the oocyst wall, and some find their way into the salivary glands, where they mature in 1–2 days. A bite of an infected mosquito causes infection in young turkey poults and starts the life cycle all over again.

Recently, *Cx. nigripalpus*, *Cx. restuans* and *Cx. salinarius* were shown be experimental vectors of *P. elongatum* from 3 raptors species (red-tailed hawk, bald eagle and eastern screech owl) in Florida and *Cx. restuans* was shown to be the experimental vector of *P. forresteri* n. sp., from several species of raptors from Florida and Georgia.

Normally epizootics of avian malaria are rare. Several species of avian malaria, e.g., *P. gallinaceum*, *P. juxtanucleare* and *P. durae* are the most dangerous for poultry, producing up to 90% mortality. In addition, there are a few documented cases where avian malaria has been shown to either eliminate or reduce bird populations. Until 1826, birds were plentiful in Hawaii and mosquitoes were absent from the region. Introduction of *Culex pipiens* from ships traveling to Hawaiian Islands introduced a lethal form of avian malaria, which eliminated indigenous bird populations. In another case, it is suggested that an abnormally early rainy season over a 2-year period in southern Florida in the 1960s resulted in a widespread malaria epizootic in wild turkey populations, which caused a significant decline in the wild turkey population. In recent years, avian malaria has caused severe mortality in exotic bird populations, especially penguins, in zoos across the U.S.A.

References

Atkinson CT, Drake BM, Shema NP (2001) Pathogenicity, serological responses, and diagnosis of experimental and natural malarial infection in native Hawaiian thrushes. Condor 103:209–218

Forrester DJ (1991) The ecology and epizootiology of avian pox and malaria in wild turkeys. Bull Soc Vector Ecol 16:127–148

Garnham PCC (1966) Introduction to the avian subgenera, *Haemamoeba, Giovannolaia, Novyella* and *Huffia*. Chapter XVII. In: Malarial parasites and other Haemosporidia. Blackwell Scientific Publications, Oxford, UK, pp 514–741

Huff CG (1965) Susceptibility of mosquitoes to avian malaria. Exp Parasitol 16:107–132

Nayar JK, Knight JW, Telford SR Jr (1998) Vector ability of mosquitoes form isolates of *Plasmodium elongatum* from raptors in Florida. J Parasitol 84:542–546

Seed TM, Manwell RD (1977) Plasmodia of birds. In Parasitic protozoa. vol III. Gregarines, Haemogregarines, Coccidia, Plasmodia, and Haemoproteids. Academic Press, New York, NY

Telford SR, Jr Forrester DJ (1975) *Plasmodium (Huffia) hermani* sp. n. from wild turkeys (*Meleagris gallopavo*) in Florida. J Protozool 22:324–328
Telford SR, Jr Nayar JK, Foster GW, Knight JW (1997) *Plasmodium forresteri* n. sp., from raptors in Florida and southern Georgia: its distinction from *Plasmodium elongatum* morphology within and among host species and by vector susceptibility. J Parasitol 83:932–937

Axenic

Free from associated organisms. Including internal symbionts.

Axenic Culture

Culture of insects in the complete absence of other species (usually of microorganisms), including internal symbionts.

Axiidae

A family of moths (order Lepidoptera) also known as gold moths.

► Gold Moths
► Butterflies and Moths

Axillary

This refers to the point of origin of a structure, often a junction or angle. Thus, the axillary region of the wing is the wing base, and the axillary lobe in Diptera is the sclerite covering the base of the wing.

Axon

A portion of the nerve cell that transmits nerve impulses away from the cell body to a synapse. This also is called nerve fiber.

► Nervous System

Azadirachtin

This is a triterpenoid derived from the neem tree, *Azadirachta indica*. It is found in many parts of the tree, but is particularly concentrated in the seeds, from which it is extracted as used as an insecticide. It also has other properties, including medicinal. Although azadirachtin is a principal factor in insecticidal products, it is not the only active property, and is not especially useful as a feeding deterrent, though crude extractions of the tree contain feeding deterrents.

► Neem

B

Babesia

A genus of Protozoa that is transmitted to animals by ticks.

► Babesiosis
► Piroplasmosis

Babesiosis

Several related diseases caused by infection with *Babesia* protozoans, and transmitted by ticks.

► Piroplasmosis

Bacillary Paralysis

A disease of silkworm larvae caused by ingestion of spores and parasporal crystals of *Bacillus thuringiensis*.

Bacillus larvae (=Paenibacillus larvae; Bacteria)

The bacterium responsible for causing American foulbrood in honey bees; it is now known as *Paenibacillus larvae*.

► American Foulbrood
► Paenibacillus

Bacillus sphaericus

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The bacterium *Bacillus sphaericus* is best-known to entomologists because of the toxicity of some strains to the larval stages of mosquitoes. This toxicity will be examined below but first, some consideration of the taxonomic group that is known as "*Bacillus sphaericus*" is necessary.

Taxonomy

Identification of a bacterium as a *B. sphaericus* isolate is based on relatively few morphological features (e.g., the possession of a spherical terminal spore) and a limited number of biochemical tests (e.g., inability to ferment sugars). As a result, the classification contains a heterogeneous collection of strains and it has been shown that, at the DNA level, these can be divided into five major homology groups (groups I-V), each of which could be considered as a separate species. All of the insecticidal strains of *B. sphaericus* are found within a subdivision of one of these groups – Group IIA; however, not all strains that fall within this group are insecticidal. It is the insecticidal strains of *B. sphaericus* and their properties that will be considered further below.

Target Range

Bacillus sphaericus is toxic to a small range of dipteran target insects, principally mosquitoes (with some possible activity against *Chironomus* species). Within the mosquitoes, *B. sphaericus* is often seen as most active against *Culex* species with lower activity against *Anopheles*, *Mansonia* and *Psorophora* and lowest activity against *Aedes* species. However, these generalizations should be treated with caution as some *Aedes* species are as sensitive as *Culex* species so that susceptibility must be judged at the species level and not by genus. In addition, activity of a *B. sphaericus* toxin has been reported against the German cockroach, *Blattela germanica*.

Field Use

Bacillus sphaericus strains have been used in control programs worldwide to suppress mosquito populations that are of nuisance or public health importance. For this purpose, only strains showing high-level, spore-associated toxicity are used (e.g., VectoLex® and Spherimos® from Valent BioSciences, or Sphaerus® from Bthek Ltda). For production of maximum toxicity, as well as for ease of production and storage, such formulations are produced from fully sporulated *B. sphaericus* cultures that can be sprayed or applied as blocks or granules that disperse in the aqueous habitats.

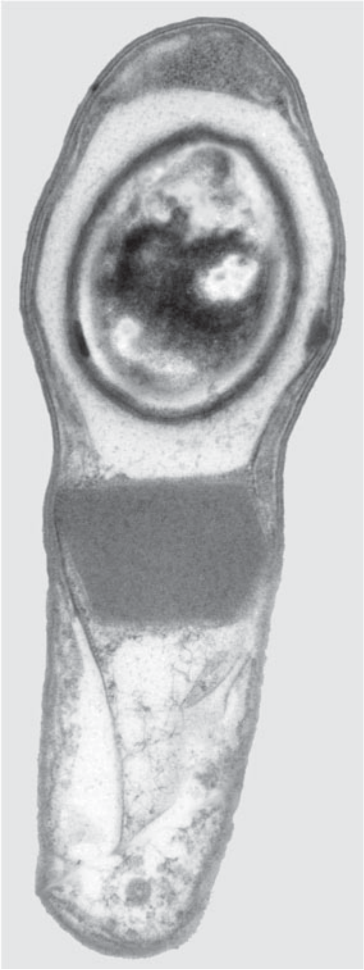
The Insecticidal Toxins

Insecticidal strains of *B. sphaericus* owe this property to the fact that they produce protein toxins. To date, several different types of toxins have been identified. The names of these toxins, along with notes on their mechanisms of action, are given in the table below.

All the toxins except sphaericolysin exert their effects on the gut of the aquatic larval form of the mosquito after ingestion of the bacterium. The binary toxin (Bin) is produced on sporulation whereupon it is deposited in spore-associated crystal As shown in the figure of *B. sphaericus*, (Fig. 1) the spore is the round body at the top, the crystal is the grey, rhomboid body in the center, and both are contained within the elongated exosporium. Once eaten by a mosquito larva, the crystal dissolves and its two component proteins (BinA -42 kDa and BinB -51 kDa) are able to bind to specific receptors in the gut before lysing the cell by pore formation. Note: although the Bin proteins form a spore associated toxin crystal, they are not related to the majority of the crystal-associated Cry and Cyt toxins of *Bacillus thuringiensis*. Most highly toxic *B. sphaericus* strains produce only the Bin toxin in association with spores (Mtx toxins are produced only in vegetative cells and in very low quantities). The existence of only one toxin in spores applied in mosquito control programs in the field can lead to resistance in target populations. A few strains of *B. sphaericus* can overcome this resistance in *Culex* mosquitoes. These

Bacillus sphaericus*, Table 1** **Toxins of *Bacillus sphaericus

Toxin (molecular wt.)	Mechanism of action	Reference
Bin (51 and 42 kDa)	Pore formation	Oei et al. (1992), Schwartz et al. (2001)
Mtx1 (100 kDa)	ADP-ribosylation	Thanabalu et al. (1993)
Mtx2 (31.8 kDa)	Pore formation	Thanabalu and Porter (1996)
Mtx3 (35.8 kDa)	Pore formation	Liu et al. (1996)
Cry48/Cry49 (136 and 53 kDa)	Pore formation	Jones et al. (2007)
Sphaericolysin (53 kDa)	Pore formation	Nishwaki et al. (2007)



***Bacillus sphaericus*, Figure 1** *Bacillus sphaericus*. **(Photo courtesy of Dr. J.F. Charles.)**

strains produce a novel toxin pair, Cry48/Cry49, which are deposited as crystals outside the exosporium. The Cry48 protein is related to 3-domain Cry toxins of *B. thuringiensis* while Cry49 is related to the Bin proteins. Both components are required for toxicity to *Culex* larvae and do not appear to kill other insects (including *Anopheles* and *Aedes* mosquitoes).

Despite reports of resistance developing in mosquito populations, careful use of this bacterium is likely to enable the continued favorable use of this product for integrated control programs in the field.

References

Ahmed I, Yokota A, Yamozoe A, Fujiwara T (2007) Proposal of *Lysinibacillus boronitolerans* gen. nov. sp. nov., and transfer of *Bacillus fusiformis* to *Lysinibacillus fusiformis* comb. nov. and *Bacillus sphaericus* to *Lysinibacillus sphaericus* com. nov. Int J Syst Evol Microbiol 57:1117–1125

Jones GW, Nielsen-Leroux C, Yang Y, Yuan Z, Dumas VF, Monnerat RG, Berry C (2007) A new Cry toxin with a unique two-component dependency from *Bacillus sphaeriucs*. FASEB J 21:4112–4120

Krych VK, Johnson JL, Yousten AA (1980) Deoxyribonucleic acid homologies among strains of *Bacillus sphaericus*. Int J Syst Bacteriol 30:476–484

Liu J-W, Porter AG, Wee BY, Thanabalu T (1996) New gene from nine *Bacillus sphaericus* strains encoding highly conserved 35.8-kilodalton mosquitocidal toxins. Appl Environ Microbiol 62:2174–2176

Nielsen-LeRoux C, Rao DR, Murphy JR, Carron A, Mani TR, Hamon S, Mulla MS (2001) Various levels of cross-resistance to *Bacillus sphaericus* strains in *Culex pipiens* (Diptera: Culicidae) colonies resistant to *B. sphaericus* strain 2362. Appl Environ Microbiol 67:5049–5054

Nishiwaki H, Nakashima K, Ishida C, Kawamura T, Matsuda K (2007) Cloning, functional characterization, and mode of action of a novel insecticidal pore-forming toxin, sphaericolysin, produced by *Bacillus sphaericus*. Appl Environ Microbiol 73:3404–3411

Oei C, Hindley J, Berry C (1992) Binding of purified *Bacillus sphaericus* binary toxin and its deletion derivatives to *Culex quinquefasciatus* gut: elucidation of functional binding domains. J Gen Microbiol 138:1515–1526

Schwartz J-L, Potvin L, Coux F, Charles J-F, Berry C, Humphreys MJ, Jones AF, Bernhart I, Dalla Serra M, Menestrina G (2001) Permeabilization of model lipid membranes by *Bacillus sphaericus* mosquitocidal binary toxin and its individual components. J Membr Biol 184:171–183

Silva-Filha MH, Nielsen-LeRoux C, Charles J-F (1999) Identification of the receptor for *Bacillus sphaericus* crystal toxin in the brush border membrane of the mosquito *Culex pipiens* (Diptera: Culicidae). Insect Biochem Mol Biol 29:711–721

Silva-Filha M-H, Regis L, Nielsen-LeRoux C, Charles JF (1995) Low-level resistance to *Bacillus sphaericus* in a field-treated population of *Culex quinquefasciatus* (Diptera: Culicidae). J Econ Entomol 88:525–530

Thanabalu T, Berry C, Hindley J (1993) Cytotoxicity and ADP-ribosylating activity of the mosquitocidal toxin from *Bacillus sphaericus* SSII-1: Possible roles of the 27- and 70-kilodalton peptides. J Bacteriol 175:2314–2320

Thanabalu T, Porter AG (1996) A *Bacillus sphaericus* gene encoding a novel type of mosquitocidal toxin of 31.8 kDa. Gene 170:85–89

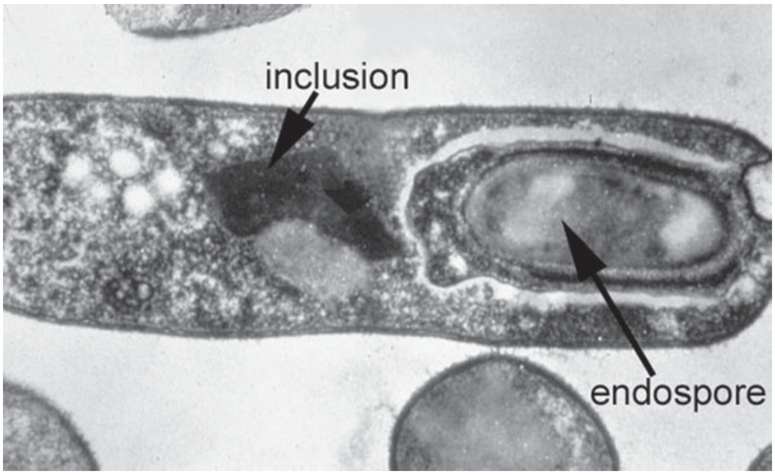
Yuan Z, Zhang YM, Cai QX, Liu EY (2000) High-level field resistance to *Bacillus sphaericus* C3–41 in *Culex quinquefasciatus* from Southern China. Biocontrol Sci Technol 10:41–49

Bacillus thuringiensis

Bacillus thuringiensis was initially described early in the 1800s as the causal agent of the "sotto bacillus disease" of the silkworm *Bombyx mori*. Later studies by Aoki in 1915 demonstrated that this bacterial agent produced a crystalline toxic material at sporulation. In 1911, Berliner isolated the type species *Bacillus thuringiensis var. thuringiensis* from the flour moth in the province of Thuringia, Germany. Following this report, a series of papers demonstrated that *B. thuringiensis* could infect and kill a variety of lepidopteran host insects. Until the 1970s, all *B. thuringiensis* isolates were characterized as being toxic to immature insects within the order Lepidoptera. However, today various *B. thuringiensis* subspecies have been identified which are lethal to lepidopterans, dipterans, coleopterans, and/or nematodes.

Historically, *Bacillus thuringiensis* has been isolated from environments associated with insect populations and/or plant material. For example, *B. thuringiensis* was discovered initially in silkworm farms. Additional *B. thuringiensis* isolates have been detected in various insectaries, stored product environments, and grain processing facilities. Studies have suggested that *B. thuringiensis* is a normal inhabitant of the foliage of plants. However, the soil habitat has been the primary source for isolating novel *B. thuringiensis* isolates. Whether or not *B. thuringiensis* undergoes saprophytic development in soil is unclear. Many bacilli considered to be close relatives of *B. thuringiensis* are known to inhabit hypogean environments. Presently, it has been estimated that over 60,000 isolates of *B. thuringiensis* are being maintained in culture collections worldwide.

Members of *B. thuringiensis* are rod-shaped (1.0–1.2 by 3–5 microns), gram positive, facultative anaerobes which utilize carbohydrates as preferred energy sources. Classification based on 16S rRNA sequence data clusters *B. thuringiensis* with *B. cereus*, *B. mycoides*, and *B. anthraxis* within the *B. subtilus* group. Bacteriological tests define *B. thuringiensis* isolates as being closely related to *B. cereus*. In fact, the ability of *B. thuringiensis* to produce the crystalline inclusion is the major feature that separates it from *B. cereus*. Acrystalliferous strains of *B. thuringiensis* generated by plasmid curing are nearly identical to *B. cereus*. The growth of *B. thuringiensis* on relatively simple media (0.1% glucose, 0.2% NH_2SO_4, 0.2% yeast extract) is biphasic and involves both a



***Bacillus thuringiensis*, Figure 2** **Electron micrograph of thin section of sporulating cell of *Bacillus thuringiensis*. Note the thick-walled endospore and endotoxin-containing crystalline inclusion.**

vegetative cell division phase and a sporulation phase. During sporulation, *B. thuringiensis* produces both the (Fig. 2) endospore and crystalline inclusions. The endospore, highly resistant to environmental stress, provides a mechanism for long-term survival of *B. thuringiensis*. This mesophilic bacterium can be produced easily on solid media or under submerged fermentation conditions. The rapid growth and sporulation of *B. thuringiensis* in relatively inexpensive media under submerged fermentation conditions have been key factors in its successful development as a biopesticide. Many of the advances made in the fermentation industry over the past three decades have improved the quality of *B. thuringiensis* products.

Initially, it was presumed that the *B. thuringiensis* was an infectious agent and much effort was spent on maximizing the delivery of bacterial spores to host insects. Early field experiments in the 1960s involving applications of spore-based formulations against pest insect populations produced erratic results. By the 1970s, it was demonstrated that the primary insecticidal activity of *B. thuringiensis* against lepidopteran hosts was due to the δ-endotoxins comprising the crystalline inclusions. These endotoxins are extremely potent and are toxic to target insects at picomole concentrations. However, with certain insects such as the larvae of the Indian meal moth *Plodia interpunctella*, the addition of spores synergizes the activity of the δ-endotoxins. Potentially, this synergism is due either to additional toxins in the spore coat or to the outgrowth of vegetative cells from ingested spores. Many commercial formulations containing high levels of δ-endotoxin have proven to be as effective as chemical insecticides yet exhibit high specificity to target pests without detrimental effects on beneficial insects and animals. By the 1990s, *B. thuringiensis*-based products represented more than 90% of the biopesticides used worldwide. Until the 1980s, it was proposed that microbial-based products such as *B. thuringiensis*, unlike their chemical pesticide counterparts, did not select for resistance in treated insect populations. The critical element required for the selection of *B. thuringiensis* resistance is the same as that required for resistance to the neurotoxic insectides: a multigenerational (continuous) exposure of the host to the mortality agent. With *B. thuringiensis*, this may be achieved either by a conventional spray program or by a contiguous planting of B.t.-transgenic plants.

Early work on the mode of action of the δ-endotoxin addressed the effect of extracted inclusions on lepidopteran larvae. Initial symptoms, occurring within one hour of ingestion of inclusions, include a cessation of larval feeding and gut paralysis. The endotoxin-induced gut paralysis retards passage of ingested plant material and spores, allowing spores to germinate and undergo vegetative development. At later stages, intoxicated larvae display a general paralysis followed by death within one to two days post-challenge. Histological studies demonstrated that the toxins released from inclusions and proteolytically activated in the gut lumen specifically target the midgut columnar cells. Examination of midgut tissue dissected from treated larvae initially revealed that columnar cells are slightly swollen but over time goblet and columnar cells become heavily vacuolated. At the late stages, midgut cells dislodge from the basement membrane and are sloughed off. At subcellular levels, the δ-endotoxins produce pores in the membrane. The activated toxin recognizes specific cell membrane receptors and then generates small pores in the cell membrane. The subsequent depolarization of the columnar cell stimulates the closure of the gap junctions, causing an increase in intracellular pH and cell hypertrophy. Without a functional columnar cell, the K^+ pump in goblet cells ceases to function. Intoxicated cells, due to increases in internal pH and loss of ion transport, become osmotically sensitive and lyse.

Importantly, the δ-endotoxins are primary translation products of bacterial genes and are amenable to genetic engineering techniques. By the early 1980s, U.S. and European laboratories had successfully isolated, cloned, and characterized genes coding for δ-endotoxins. During the past two decades over 90 different protoxin genes containing representatives of both Cry and *cyt* classes have been cloned and sequenced. The technology developed to study the structure and function of the δ-endotoxin has provided the foundation for the genetic engineering of this class of biopesticides. In several respects, the δ-endotoxin gene has played a pivotal role in agricultural biotechnology. The δ-endotoxins derived from recombinant bacteria represent the first group of genetically engineered products released into agricultural systems. To date, recombinant microbes expressing δ-endotoxin genes have been field tested worldwide in numerous agricultural systems. Secondly, the δ-endotoxin genes have been used as models for optimizing the gene expression in transgenic plants. Over the past decade, researchers have manipulated the δ-endotoxin gene and have altered the protoxin profile as well as the toxicity and specificity of individual Cry toxins. Significantly, Cry gene expression in transgenic plants has provided protection against insect herbivory

References

Aronson A (2002) Sporulation and δ-endotoxin synthesis by *Bacillus thuringiensis*. Cell Mol Life Sci 59:417–425

Fieltelson JS, Payne J, Kim L (1992) *Bacillus thuringiensis* and beyond. Bio/Technology 10:271–276

Knowles BH, Dow JA (1993) The crystal δ endotoxin of *Bacillus thuringiensis*: models for their mechanism of action on the insect gut. Bioassays 15:469–476

Maagt RA, Bravo A, Crickmore N (2001) How *Bacillus thuringiensis* has evolved specific toxins to colonize the insect world. Trends Genet 17:193–199

Whiteley HR, Schnepf HE (1986) The molecular biology of parasporal crystal body formation in *Bacillus thuringiensis*. Annu Rev Microbiol 40:549–576

Backswimmers

Members of the family Notonectidae (order Hemiptera).

► Bugs

Bacterial Conjugation

A temporary union between two bacteria, during which genetic material is exchanged. All or some of the chromosomes are transferred from the donor to the recipient

Bacterial Wilt of Corn

This is an important insect-transmitted disease of corn (maize).

► Transmission of Plant Diseases by Insects

Bacterial Wilt of Cucumbers

This is an important insect-transmitted disease of cucurbit crops.

► Transmission of Plant Diseases by Insects

Bacteremia

The presence of bacteria in the hemolymph or blood of invertebrates and other animals without production of harmful toxins or other deleterious effects

Bacteriophage

A virus whose host is a bacterium

Bacteriophage Wo

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Bacteriophages are obligate intracellular viruses that infect and kill bacteria. These viruses are ubiquitous and shape aspects of bacterial population ecology in almost every environment on earth. Bacteriophage WO infects the alpha-proteobacterium

Wolbachia, which is commonly associated with insects, mites, nematodes, and terrestrial isopods. *Wolbachia* is notorious for causing reproductive alterations in its hosts such as feminization, male killing, cytoplasmic incompatibility, and parthenogenesis. The diversity of *Wolbachia* strains and their influence on host biology has stimulated research encompassing broad topics including genetics, ecology and evolution. In addition, removing obligate *Wolbachia* infections from filarial nematodes has provided a novel treatment for human disease. The significance of both basic and applied research involving *Wolbachia* has made it one of the most well understood endosymbiont-host associations.

Virus-like particles (bacteriophage WO) were discovered inside *Wolbachia* cells in the reproductive tract of the mosquito *Culex pipiens* using electron microscopy in 1978. Bacteriophage WO particles are approximately 40 nm in diameter with short tails, contain linear double-stranded DNA, and are found near the *Wolbachia* cell membrane. Since its discovery, researchers have focused on characterizing the basic biology, distribution, and evolution of bacteriophage WO.

Bacteriophage WO has both a lysogenic phase, where its genetic information is integrated into the *Wolbachia* chromosome as a prophage, and a lytic phase, where the virion resides in the cytoplasm and can lyse *Wolbachia* cells. Little is currently known about what triggers the virus to kill *Wolbachia*. Bacteriophage WO may prevent excessive proliferation of *Wolbachia*, and this may have evolutionary implications for long-term maintenance of the association with the host.

Bacteriophage WO is transmitted transovarially inside arthropod eggs along with its host *Wolbachia* cells. This transmission mechanism provides an efficient and stable means for *Wolbachia* and its associated bacteriophage WO to infect arthropod populations at a high frequency. This notion is substantiated by the similarity of the G + C content and codon usage of phage and *Wolbachia* genes, indicating a long-term evolutionary tie between bacteriophage WO and *Wolbachia*. However, it also appears that both *Wolbachia* and bacteriophage WO are horizontally transmitted between different arthropod species by unknown mechanisms. This is supported by evolutionary studies showing incongruence between phylogenetic trees constructed using DNA sequences from *Wolbachia* and bacteriophage WO. Interestingly, some insects host multiple strains of *Wolbachia* that are infected with different types of bacteriophage WO, and even individual strains of *Wolbachia* can harbor multiple phage types. *Wolbachia* has a broad and dynamic host range that may be facilitated by the horizontal transfer of virulence factors it acquires from bacteriophage WO.

In 2000, the first bacteriophage WO was completely sequenced using DNA isolated from the Mediterranean flour moth *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) infected with *Wolbachia*. A total of 33 open reading frames were detected among a genome of approximately 25,000 base pairs of DNA. The open reading frames represent the DNA coding information that dictates the construction and assembly of proteins. Some of the putative proteins identified were related to proteins known from a diverse group of other bacteriophages, while others showed no significant similarities to known phage proteins. Additional bacteriophage WO types have since been sequenced using DNA isolated from *Wolbachia* infecting the almond moth, *Cadra cautella* Walker (Lepidoptera: Pyralidae), and from *Wolbachia* infecting *Drosophila melanogaster* Meigen (Diptera: Drosophilidae).

Using the polymerase chain reaction (PCR), the putative minor capsid protein gene, *orf7*, is commonly used to detect bacteriophage WO in *Wolbachia* strains infecting arthropods. More than 100 *orf 7* sequences of bacteriophage WO have been deposited in GenBank as of May 2007. The *orf 7* gene has been detected in many, but not all, *Wolbachia*-infected arthropods. Using species representing multiple orders of arthropod hosts, between 70 and 100% of the *Wolbachia* strains tested are PCR-positive for bacteriophage WO. However, multiple *Wolbachia*-infected species of parasitoids in the genus *Trichogramma*

(Hymenoptera: Trichogrammatidae) and the parasitoid *Diaphorencyrtus aligarhensis* Shafee, Alam and Agarwal (Hymenoptera: Encyrtidae) lack bacteriophage WO. In addition, the nematodes *Dirofilaria immitis*, *Litosomoides sigmodontis*, *Setaria equine* and *Brugia malayi*, and a population of the predatory mite *Metaseiulus occidentalis* (Nesbitt) all had *Wolbachia* infections but lacked bacteriophage WO, based on PCR analysis of the *orf7* gene.

In vitro cultures of *Wolbachia* must be maintained using insect cell cultures because the endosymbiont is intracellular. Currently, no methods have been developed to transform (genetically modify) *Wolbachia* that would provide a tool to study its interactions with arthropods in detail. Bacteriophage WO has the potential to be developed as a vector to genetically modify *Wolbachia* because it integrates into the *Wolbachia* genome and its genes are actively expressed.

► Sex Ratio Modification by Cytoplasmic Agents
► Symbionts of Insects

References

Braquart-Varnier C, Grève P, Fèlix C, Martin G (2005) Bacteriophage WO in *Wolbachia* infecting terrestrial isopods. Biochem Biophys Res Commun 337:580–585

Fujii Y, Kubo T, Ishikawa H, Sasaki T (2004) Isolation and characterization of the bacteriophage WO from *Wolbachia*, an arthropod endosymbiont. Biochem Biophys Res Commun 317:1183–1188

Masui S, Kamoda S, Sasaki T, Ishikawa H (2000) Distribution and evolution of bacteriophage WO in *Wolbachia*, the endosymbiont causing sexual alterations in arthropods. J Mol Evol 51:491–497

Masui S, Kuroiwa H, Sasaki T, Inui M, Kuroiwa T, Ishikawa H (2001) Bacteriophage WO and virus-like particles in *Wolbachia*, an endosymbiont of arthropods. Biochem Biophys Res Commun 283:1099-1104

Gavotte L, Henri H, Stouthamer R, Charif D, Charlat S, Boulétreau M, Vavre F (2007) A survey of the bacteriophage WO in the endosymbiotic bacteria *Wolbachia*. Mol Biol Evol 24:427–435

Hoy MA, Jeyaprakash A (2005) Microbial diversity in the predatory mite *Metaseiulus occidentalis* (Acari: Phytoseiidae) and its prey, *Tetranychus urticae* (Acari: Tetranychidae). Biol Control 32:427–441

Baculoviridae

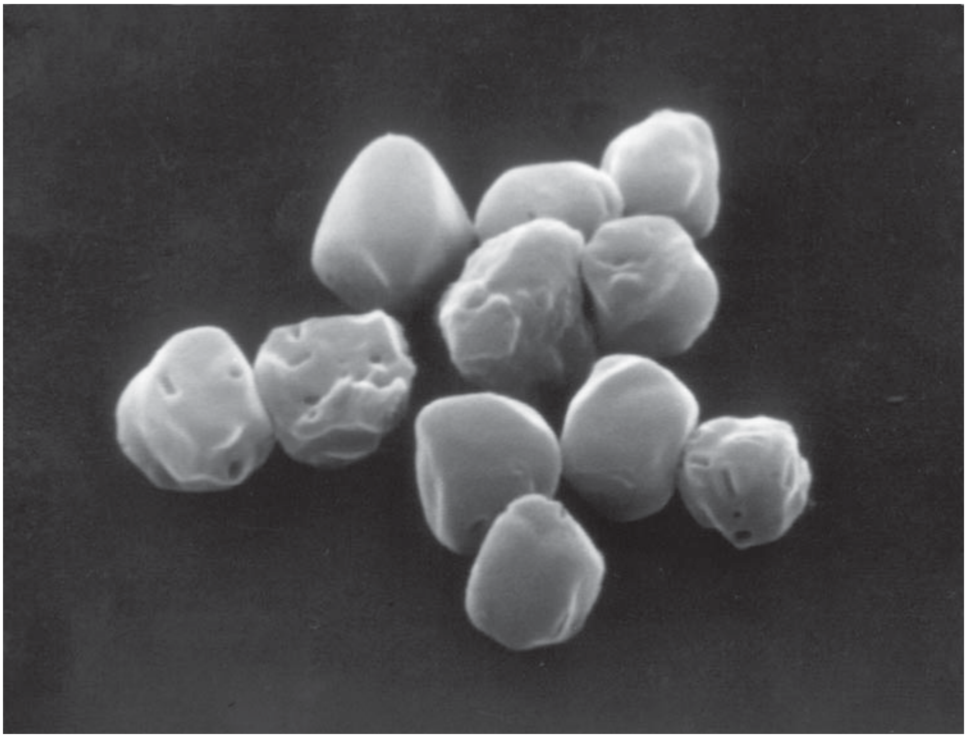
A family of insect pathogenic viruses known as baculoviruses.

► Baculoviruses

Baculoviruses

The insect baculoviruses, the nucleopolyhedroviruses (NPVs) and the granuloviruses (GVs), are the most intensely studied insect viruses. Historically, the first reports of a baculovirus-induced viremia were associated with the silkworm *Bombyx mori*. The spread of sericulture from Asia to Europe led to the introduction of the affiliated diseases grasserie or jaundice disease (NPV), as well as flacherie (non-occluded virus, bacteria), into the silk-producing regions. In the sixteenth century poem titled "De bombyce," Marco Vida describes the rupture of tissues and the release of fluid from diseased silkworm larvae. It is presumed he is describing the last stages of *B. mori* NPV-induced jaundice. In 1856, the Italian scientist Maestri made the first scientific observation of the causal agent of jaundice. With the aid of the compound microscope, he described the presence of polyhedral bodies (Fig. 3) or occlusions in the fluid and tissues of diseased silkworm larvae

By the late 1890s, J. Bolle reported that the polyhedral bodies were proteinaceous crystals resistant to various solvents but sensitive to alkaline solutions. Bolle reported that healthy silkworms that fed on the polyhedral bodies contracted jaundice. The intracellular inclusions described initially by Bolle as *Microsporidium polydricum* were named later by Prell as *Crystalloplasma polyhedricum*. Glaser and Chapman, who in 1916 reported that the infectious agent was a filterable agent of dimensions much smaller than the micron-sized polyhedral bodies, questioned the infectious nature of the polyhedral bodies. They and others proposed that the polyhedral bodies were metabolic by-products and not causal agents of the disease. The nature of the polyhedral



Baculoviruses, Figure 3 **Scanning electron micrograph of occlusion bodies of the nucleopolyhedrovirus depicting their three dimensional shape.**

bodies and capsules finally was resolved in the 1940s by the German scientist G. Bergold. He and co-workers examined alkali-treated baculovirus inclusions under the newly developed electron microscope and described the occluded, rod-shaped virus particles.

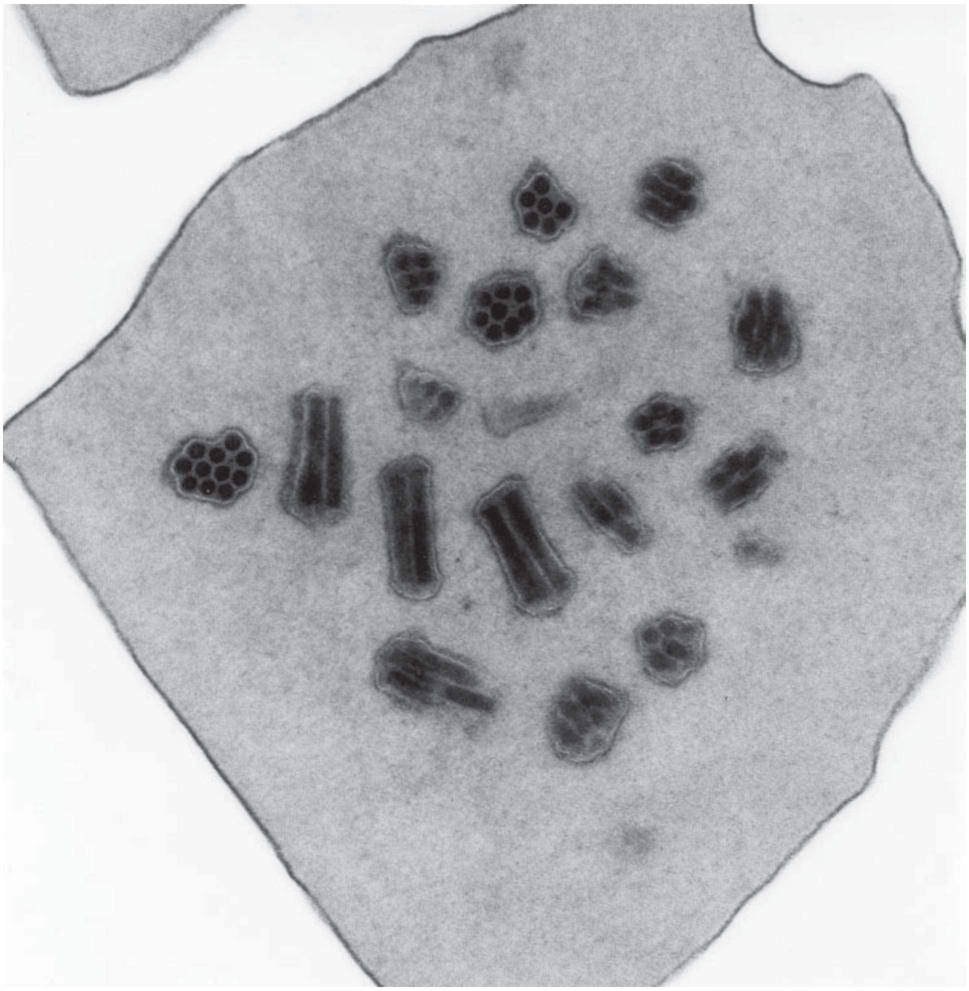
In the late 1930s, the French scientist A. Paillot described a new type of viral disease in the cabbage butterfly, *Pieris brassicae*, that, unlike the NPVs, produced numerous minute capsules (granules). Using high-speed centrifugation, Paillot and co-workers determined that the infectious entities were associated with the granules in the high-speed pellets. Paillot observed that this viral disease, termed pseudo-grasserie, multiplied in the fat body and caused infected larvae to exhibit a whitish coloration. In the early 1930s, he described a similar disease in the cutworm *Euxoa segetum* that caused nuclear hypertrophy of infected fat body cells followed by the formation of the granules. In 1947, Steinhaus discovered a similar disease in the larvae of the variegated cutworm, *Peridroma margaritosa*, the first report of this disease outside of France. To date, granulosis viruses have been found to infect only lepidopteran hosts. These viruses are considered to be among the most specific insect viruses, capable of infecting a single species or species within the same genus

Prior to their identification, baculoviruses were recognized as important natural regulators of various lepidopteran defoliators. At the end of the nineteenth century in central Europe, nun moth (*Lymantria monacha*) populations were decimated periodically by a wilt disease. Prior to death, infected insects migrated to the tops (Wipfeln) of the trees, attached by their prolegs, and died. Upon death, the body disintegrated and released infectious fluid. Initially, the causal agent of the disease, known as Wipfelkrankheit, was described as a bacterium, then later as a protozoan within the genus *Crystalloplasma*. Although it was not properly named, a great deal was learned from these early studies of this disease agent. Experiments showed that the infectious material resisted putrification and was stable for 3 years when stored in a dry state. Furthermore, the disease agent persisted in the soil and could be extracted from washings using differential centrifugation. This agent was transmitted per os; the fluid released from the cadavers was highly infectious to healthy larvae. Finally, it was reported that the infectious agent displayed specificity to certain insect species. For example, the fluid released from diseased nun moth larvae was infectious to the related gypsy moth, *Lymantria dispar*, but was harmless to silkworm larvae. Throughout the 1920s, a program in Europe promoted the spread and distribution of the causal agent into disease-free areas. This involved a variety of tactics, including the use of mortars to deliver infectious material into the tree canopy. The field studies on the nun moth NPV suggested that this disease operated as a density-dependent disease agent

In the United States, a similar scenario was observed in populations of the gypsy moth, an imported defoliator of deciduous hardwoods. This insect, originally imported as an alternative silk producer, escaped into the oak forests and spread throughout southern New England. In the early 1900s, collapses of gypsy moth populations were attributed to the natural occurrence of wilt or flacherie disease. At this time, Glaser and Chapman initiated a series of key studies on this disease. Microscopic examination revealed that this virus replicated initially in the tracheae then spread to virtually all the insect tissues. Infected cells were recognized by the large number (Fig. 4) of intranuclear occlusion bodies. In 1913, Glaser and Chapman reported that the filterable agent, the causal agent of gypsy moth wilt disease, was sensitive to sunlight and to heat treatment. In 1916, it was determined that the occlusions could be disrupted readily when placed in alkaline solutions and could be re-formed by neutralization of the alkaline solution.

One of the classic examples of biological control of insects has involved the introduction of a baculovirus. In Canada, the European pine sawfly, *Neodiprion sertifer*, was introduced and became established as a major forest defoliator. In the early 1950s, T. Bird (Canadian Forest Service) reported that a sawfly virus imported from Sweden was highly virulent to *N. sertifer* larvae. The introduction of this virus resulted in widespread epizootics that spread through the sawfly population and provided a natural control of this defoliator. This virus, unlike the lepidopteran baculoviruses, was transmitted easily from infected adults to the egg stage. The combination of its high virulence and ability to be vertically transmitted were responsible for its ability to provide effective long-term control of this pest insect. The natural occurrence of baculovirus epizootics and their potential to be manipulated as biological control agents against key pest insect defoliators served as the catalysts for baculovirus research during the past 30 years. During this period more than 4,000 research papers have been published on baculoviruses, of which more than 3,000 have focused on the nucleopolyhedrovirus group. In the 1970s and early 1980s, the major focus was studying the effects of wild-type baculovirus strains on insect population. From the mid-1980s to the present, the emphasis has been directed at the biochemistry and molecular biology of these viruses. This work, in addition to providing detailed insight into the workings of this complex virus, has provided the scientific community with a highly efficient eukaryotic expression vector system that is being used commercially to produce various protein products. Lastly, the basic research has provided a means to engineer the baculovirus, which in future years may provide highly efficacious recombinant strains for managing insect pest populations (Table 2).

Nucleopolyhedroviruses are horizontally transmitted to susceptible insects per os; larvae become infected by ingesting foliage contaminated with occlusions. In limited cases, chronically infected adults may disseminate baculovirus onto the chorion surface during oviposition,



Baculoviruses, Figure 4 **Transmission electron micrograph of a thin section of the multiply embedded nucleopolyhedrovirus, not the crystalline protein matrix within which are embedded membrane bound rod shaped virus particles. Ingestion of these occlusions by host insects results in the digestion of the matrix protein and release of occluded virus.**

resulting in a vertical transfer of the pathogen to progeny caterpillars. Not all baculoviruses cause lethal infections; latent infections can persistently infect insect colonies in which the virus is transmitted within the egg stage. At present, very little is known about the frequency and impact of such persistent baculovirus infections on natural insect populations. The initiation of baculovirus epizootics has been attributed mainly to insects contacting and ingesting overwintering virus inocula that are associated with plant and/or soil substrates. It is likely that latent infections play a role in both the initiation and maintenance of natural virus epizootics. During the epizootic phase the primary route of baculovirus transmission is per os. Ingested viral occlusions are disrupted by the action of alkaline proteases in the midgut lumen. The types and amounts of gut proteases produced by an insect influence the processing of ingested occlusions. Increased feeding rates, as displayed by mature larvae, may result in the rapid passage of ingested food containing intact or only partially digested occlusions, thereby preventing contact with the midgut

Baculoviruses, Table 2 Examples of baculoviruses isolated from different insect hosts

Baculovirus	Host
Nucleopolyhedrovirus	
AcNPV	Lepidoptera: *Autographa californica*
AgMNPV	Lepidoptera: *Anticarsia gemmatalis*
LdMNPV	Lepidoptera: *Lymantria dispar*
SeMNPV	Lepidoptera: *Spodoptera exigua*
CfMNPV	Lepidoptera: *Choristonuera fumiferana*
TnSNPV	Lepidoptera: *Trichoplusia ni*
BmSNPV	Lepidoptera: *Bombyx mori*
TpSNPV	Diptera: *Tipula paludosa*
CnSNPV	Diptera: *Culex nigripalpus*
NsSNPV	Hymenoptera: *Neodiprion sertifer*
Granulovirus	
TnGV	Lepidoptera: *Trichoplusia ni*
PiGV	Lepidoptera: *Plodia interpunctella*
CpGV	Lepidoptera: *Cydia pomonella*

tissue. Alternatively, the ingestion of plant material that either buffers gut alkaline conditions or contains endogenous protease inhibitors or antiviral allelochemicals may reduce the susceptibility of an insect to baculovirus infection.

The released occlusion derived virus (ODVs) must bypass the peritrophic membrane in order to access the initial target midgut cells. The peritrophic membrane is a dynamic structure that varies among different species and between the different developmental stages. As insects mature they often display a developmental resistance to infection that is related in part to the production of a well-defined peritrophic membrane. The ODVs do not orientate to the microvilli in any particular fashion, suggesting that the anti- receptors, if present, are distributed throughout the ODV envelope. The viral membrane fuses to the microvillar membrane and the nucleocapsids are released into the cytoplasm. Nucleocapsids are transported to the nucleus and attach to the nuclear pores of the columnar epithelial cells. In addition to directly infecting the columnar cells, investigators have reported that parental nucleocapsids can traverse the columnar cells and infect underlying regenerative cells. Viral development in the columnar epithelial cells may be aborted by the preferential sloughing off of infected cells and by the removal of the midgut layer at larval molt. Therefore, the ability of a baculovirus to infect the regenerative cells may play a key role in maintaining a systemic infection.

The naming of the different viruses includes the initial letter of the host species followed by mnv (multiply embedded nucleopolyhedrovirus), Snpv (singly embedded nucleopolyhedrovirus) or Gv (granulovirus).

In the midgut cells, viral particles either attach to the nuclear pore and uncoat, or enter the nucleus and uncoat. The release of the viral genome into the nuclear region marks the initiation of the primary replication phase. In various lepidopteran hosts the majority of baculoviruses produce only the non-occluded virus; occlusions are not normally synthesized in either virus-infected columnar or regenerative cells. Unlike other enteric viruses (e.g., Cypoviruses), the virus released from the infected columnar cells do not horizontally spread to adjacent midgut cells but can infect adjacent tracheal cells or migrate to the basal face of the midgut. However, the basement membrane, comprised of exocellular matrix proteins, surrounds the basal face of the midgut and is believed to act as a barrier to prevent the large-scale release of baculoviruses into the hemocoel. The virus that has penetrated the tracheal cells can undergo a complete replication cycle and may then infect neighboring tracheal cells. Utilizing the host tracheal system as a conduit, the virus can access and infect other susceptible insect tissues. In addition to being disseminated via the tracheal conduit, NPV-infected hemocytes also can spread the virus to healthy tissues

During baculovirus replication, various viral proteins are produced which modulate the host at the cellular as well as organism level. Baculoviruses may contain genes that code for proteins with anti-apoptotic activities that block the internal cell suicide program. Premature cell death would abort the production of viral progeny particles. Baculovirus replication also has been observed to disrupt the developmental program of host insects. For many years it has been known that baculovirus infection retards larval development and prevents the larval-to-pupal molt. In the late 1980s baculoviruses were found to contain a gene (egt) which codes for a ecdysteroid UDP-glucosyl transferase (egt). The egt gene encodes for a 57 kDa polypeptide with 506 aa. The egt holoenzyme, an oligomer of 3–5 subunits, catalyzes the transfer of glucose or galactose from UDP-glucose or UDP-galactose, respectively, to ecdysteroids producing inactive sugar conjugates of this steroidal hormone. Expression of the egt gene inhibits the molting process and maintains the host in the larval stage. This gene is non-essential, deletion mutants retain their ability to infect and to replicate both in cell culture and in host insects. However, egt expression alters host ecdysone titers, results in a massive reprogramming of host tissues, and disrupts larval molting and pupation. The prolongation of the larval stage results in increased viral yields. Alternatively, the disruption of pupation due to viral infection reduces the likelihood of viral-infected adult insects. Since the initial report in AcMNPV, homologous genes have been detected in various NPVs.

In non-midgut tissues, NPVs, in addition to producing the baculovirus phenotype, produce massive numbers of the ODV phenotype and associated occlusion bodies. The very late stage of NPV development is characterized by the presence of hypertrophied, infected nuclei becoming filled with highly refractile occlusions. Virtually all host tissues become infected and larvae are extremely fragile. Frequently, NPV infected larvae will disintegrate into a puddle of occlusion bodies. This “wilting” symptom is believed to result in part from the production of virally encoded hydrolases having either proteolytic or chitinolytic activities. The production of this enzyme, detected in culture supernates at 12 h post-infection, is under the regulation of a late gene promoter. This enzyme, stable between pH 3 and 10, is believed to be partially responsible for the liquefication of baculovirus-infected insects. The disintegration of infected insects also is aided by the production of various viral proteases. A variety of viral, host, and environmental factors determine the rate and level of occlusion formation in a baculovirus-infected insect. Regardless, the biomagnification of baculoviruses in their respective lepidopteran hosts is phenomenal. Neonate larvae may be infected by ingesting as few as 1–10 occlusions, succumb to viremia within 4–12 days, and then release 10^7 occlusions into the environment.

References

Clem RJ, Fechheimer M, Miller LK (1991) Prevention of apoptosis by a baculovirus gene during infection on insect cells. Science 254:1388–1390

Granados RR, Federici BA (eds) (1986) Biology of the baculoviruses. CRC Press, Boca Raton, Florida

Maramorosch K, Sherman KE (1985) Viral insecticides for biological control. Academic Press, Orlando, FL, 809 pp

Miller LK (1996) Insect Viruses. In: Fields BN, Knipe DM, Howley PM (eds) Fundamentals of virology. Lippincott-Raven Publishers, Philadelphia, PA, pp 401–424

Miller LK (1984) Exploring the gene organization of baculoviruses. Methods Virol 7:227–258

Rohrmann GF (1992) Baculovirus structural proteins. J Gen Virol 73:749–761

Baetidae

A family of mayflies (order Ephemeroptera).

► Mayflies

Baetiscidae

A family of mayflies (order Ephemeroptera).

► Mayflies

Bagworm Moths (Lepidoptera: Psychidae)

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Bagworm moths, family Psychidae, total 1,001 known species, mostly Palearctic and African, with only 88 known for the New World; actual fauna likely (Fig. 5) exceeds 1,200 species. The family is now divided into six subfamilies, although various tribes are sometimes elevated as additional subfamilies: Lypusinae, Naryciinae, Taleporiinae, Penestoglossinae, Psychinae, and Oiketicinae (most of the subfamilies have also been treated as separate families in the past). The family is part of the superfamily Tineoidea, in the section Tineina, subsection Tineina, of the division Ditrysia. Adults minute to medium size (4–60 mm wingspan), with very rough head scaling; haustellum vestigial and naked; labial palpi reduced, 1 to 2-segmented but fused together (rarely 3-segmented); maxillary palpi; antennae usually bipectinate. Maculation mostly dull colored, but sometimes with clear wings or translucent wing spots; some are spotted; rarely colorful. Adults are mostly diurnal or crepuscular. Larvae are mostly leaf feeders or feed on lichens, all making distinctive types of larval cases, or bags. Pupation is within the larval case and females often remain there in a wingless or larviform shape, using pheromones to attract the winged males. A number of species are economic and many are general plant feeders.

Bagworm Moths (Lepidoptera: Psychidae), Figure 5 **Example of bagworm moths (Psychidae), *Eumeta pryeri* (Leech) from Taiwan.**

References

Betrem JG (1952) The genotypes of the Indo-Australian Psychidae (Lepidoptera). Tijdschrift voor Entomol 95:331–340

Dalla Torre KW, von Strand E (1929) Psychidae In: Bryk F (ed) Lepidopterorum catalogus, vol 34. W. Junk, Berlin, 211 pp

Davis DR (1964) Bagworm moths of the Western Hemisphere (Lepidoptera: Psychidae). Bull US Natl Mus 244:1233

Hättenschwiler P (1997) Psychidae – Sachträger. In: Schmetterlinge und ihre Lebensräume: Arten – Gefährdung – Schutz. Schweiz und angrenzenden Gebiete, 2:165–308, pp4–7. Pro Natura-Schweizerische Bund fuer Naturschutz., Basel

Kozhanchikov IV (1956) Nasekomye Chechuekrulye. Chechlonosye Meschechnitsky (sem. Psychidae). In Fauna USSR. Insects. Lepidoptera 3(3):15–16. Moscow [Engl transl: 1969. 525 pp, Smithsonian Institution, Washington]

Bait

A food or food-like substance that is used to attract pests. It often is combined with an insecticide to poison insects, slugs, snails and rodents.

► Food-Based Baits

Balanced Mortality Hypothesis

The belief that the level of reproduction is scaled to the probability of survival, with insects living in hostile environments having higher levels of reproduction than those occurring in more benign environments

Balance of Nature

This is the idea that in nature there exists an inherent equilibrium founded on the interactions of plants and animals, resulting in a stable, continuing system of life on Earth. This belief is fundamental to many cultures, though Carl Linnaeus is often credited with popularizing it ("oeconomia naturae") in his writings of 1749. Sometimes this natural order was attributed to divine providence, but at other times maintained by nature. Once a popular notion, it no longer is popular with ecologists.

Some elements of "balance" exist, such as the adaptations of different elements in a natural ecosystem such that resource production and use are commonly balanced and optimized. However, the so-called "balance" is continually upset by natural events and by the activities of humans. Outbreaks of insects are an example of the disequilibrium that calls into question the notion of "balance." However, the resistance of systems to perturbation, the resiliency (rapidity of return to equilibrium after perturbation) of both producer and consumer organisms, and the persistence (tendency of organisms to persist even when faced with catastrophic changes in abundance), can be construed as supportive of the balance hypothesis, or at least supportive of the idea of continuance or constancy.

Much of the disagreement about the "balance of nature" is due to differences in scale. Ecosystems are mosaics of patches, and environmental stochasticities or biological feedbacks that appear to be destabilizing or catastrophic on a local scale may be much less so when viewed on a larger scale. Clearly, ecological stability is scale-dependent, and broad-scale stability (metastability) usually exists only at the meta-scale.

References

Egerton FN (1973) Changing concepts of the balance of nature. Q Rev Biol 48:322–350

Wu J, Loucks OL (1995) From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. Q Rev Biol 70:439–466

Banana Pests and Their Management

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Bananas are among the most important food crops in the world. Despite their importance, banana yields are continuously declining due to attack by insect pests. Insects attack the banana rhizome, pseudostem, leaf and fruit. The most serious insect pest on a global basis is the banana weevil. Other pests include the sugarcane weevil, pseudostem weevil, banana scab moths, banana skipper, banana thrips and banana aphids. Pests of minor or localized importance include the spiraling whitefly, mealybugs, big-headed ant, chinese rose beetle and coconut scale. Thrips cause cosmetic damage directly to the fruit, reducing marketability. Most pests do not attack the bunch and cause indirect damage. For example, banana weevils attack the rhizome and pseudostem causing yield reductions through plant loss, delayed maturation and bunch weight reduction. Some pests, such as *Pentalonia nigronervosa*, are vectors of serious diseases. In this article, the pest status, distribution, biology and control options of major pests of banana are discussed.

Banana Weevil, *Cosmopolites sordidus* (Germar) (Coleoptera: Curculionidae)

The banana weevil is the most important insect pest of banana and plantain. Its host range is restricted to wild and cultivated clones of *Musa* (banana, plantain, abaca) and *Ensete*. The insect originated in southeast Asia and has spread to all important banana and plantain growing areas. It is not normally a pest in its area of origin.

Because of its importance, detailed treatment of this insect is provided elsewhere in the *Encyclopedia*.

► Banana Weevil, *Cosmopolites sordidus*

Sugarcane Weevil, *Metamasius hemipterus sericeus* (Coleoptera: Curculionidae)

The sugarcane weevil *Metamasius hemipterus sericeus* (Olivier) (Coleoptera: Curculionidae: Dryophthorinae) primarily infests banana, plantain, sugarcane and, less commonly, ornamental palms. The insect is endemic to the America tropics. It has been found on plantain in West Africa but has not been reported from East Africa.

The importance of *M. hemipterus* as a pest of banana is disputed but it is considered more serious than the banana weevil, *Cosmopolites sordidus*, in the banana growing areas of western Colombia. In this region, *M. hemipterus* is known to transmit *Erwinia chrysanthemi* pv *paradisiaca* causing rotting of the banana pseudostem. Some authors argue that *M. hemipterus* is unimportant or only a secondary pest of banana.

There are three recognized subspecies, all of which attack banana: *M. h. hemipterus* (L.) is distributed from Puerto Rico through the Lesser Antilles and into most of South America; *M. h. sericeus* (Olivier) is found in the Greater Antilles, southern Florida (USA) and from Nicaragua to Ecuador; while *M. h. carbonarius* (Chevrolat) occurs from Mexico to El Salvador and Honduras. The three subspecies have similar external morphological features and all show extreme variation in color. The adults are 9–14 mm long black adults with red or yellow markings. The base of the elytra is one-half to one-third red or yellow on a black background. The pronotum and venter are black to red and black. This species can be confused with *Metamasius calligsona* which infests bromeliads. *M. hemipterus* adults are active fliers (unlike *C. sordidus*).

Biology

The three subspecies of *M. hemipterus* have similar biology. The adults are most often found in moist, dark places. They are attracted to, and oviposit in, healthy banana pseudostems, rotting banana plants, banana residues, damaged or stressed sugarcane stalks, ripe fruit (i.e., pineapple, mango, papaya), or palm sheaths or stems. More is known about the oviposition habits of *M. hemipterus* on sugarcane than on banana. The weevil is attracted to stalks damaged by either mechanical cultivation, harvesting equipment, rats, borers, disease or natural growth cracks. In some cases, *Metamasius* females prefer to deposit eggs on sugarcane that has been damaged by *Diatraea* (Lepidoptera: Pyralidae). In Colombia, this type of damage is known as the *Diatraea-Metamasius* complex. *Metamasius hemipterus* has also been observed infesting canes used as seed pieces.

The females lay their eggs in cracks and damaged areas of bananas and sugarcane, or in petioles and crown shafts of certain species of healthy palms. The adult can live up to 60 days during which time the female can deposit 400–500 eggs. This contrasts with the biology of *C. sordidus*, which is longer lived but produces far fewer eggs. As with *C. sordidus*, *M. hemipterus* places single eggs in holes made in the host by the insect's rostrum.

The oval egg is 1.2–1.5 mm in length and creamy-white. The egg stage is 3–7 days. The cream-color, yellowish larvae are typical legless weevil grubs and similar in most aspects to other members of the Rhynchophorinae. Fully developed larvae are 1.3–2.0 cm. The larval stage lasts 50–60 days.

Metamasius hemipterus larvae can be differentiated from those of *Cosmopolites* by color (creamier coloration), behavior (more active), and morphological features (stigmata, cranial sutures, and structures on the labium and clypeum). Mature *M. hemipterus* larvae construct a fibrous pupal case (similar to that of the giant palm weevil, *Rhynchophorus palmarum*) and pupation takes place mostly within the banana pseudostem. The pupal stage is 10–20 days. Thus, depending on temperature, the life cycle is completed in 63–86 days.

Pest Status

Damage in banana is caused by the larvae, which feed in the upper part of the pseudostem. The larvae bore into the stem causing extensive physical damage and, in heavy infestations, can kill the plant. The first symptoms of *M. hemipterus* attack are yellowing of the lower leaves and consequent rotting of the pseudostem. In cases of extensive damage to the pseudostem, the plants cannot resist the weight of fruit, increasing the likelihood that the plants may double and eventually die. The pest has also been reported to attack the banana rhizome and cause damage similar to that of *C. sordidus*. Moreover, there are reports that *M. hemipterus* did not show any preferences between rhizome and pseudostem tissue of the cultivars Gross Michel (AAA) and Bout Rond. Unfortunately, there are no yield loss data for *M. hemipterus* in banana.

Larvae of *M. hemipterus* can seriously affect the ornamental palms *Phoenix canariensis*, *Ptychosperma macarthurii*, *Ravenia rivularis*, and *Roystonia*. Larval tunneling in palms starts in the petioles, wounds in petioles, crown, stem and then extends into healthy leaf or stem tissue. Affected palms are often characterized by the production of an amber-colored, gummy exudate in the stem, crown shaft or petioles, and galleries in the leaves, petioles and stems.

Trapping and Monitoring

Trapping of adults is often used to monitor weevil numbers, although interpretation of trap captures is difficult. The use of a “sandwich trap” using banana pseudostem as an attractant has been suggested. A maximum of ten weevils per trap per week have been captured using banana pseudostem disc traps, although the number of weevils collected at these traps was consistently too low to accurately assess weevil density. Fermenting sugarcane has also been used to attract *M. hemipterus*. An average of 30 weevils per trap using pieces of bamboo filled with pieces of fermenting cane have been captured. Tests conducted on different trap designs and the response of adults to semiochemicals demonstrated that weevil counts increased with combinations of ethyl acetate, sugarcane and/or the aggregation pheromone metalure, compared with the use of any compound alone. The major male-produced aggregation pheromones and host kairomone compounds have identified the trap designs and protocols that can be used for enhanced monitoring of weevil populations in the field. In addition, it has been demonstrated that pheromone and host-baited traps can be used to mass trap *M. hemipterus* infesting banana and sugarcane in Costa Rica.

► Control Measures

Chemical Control

Labeled rates of acephate, carbofuran, chlorpyrifos, cyfluthrin, disulfoton, imidachloprid, isofenphos, lindane and vydate have been demonstrated to kill adults of *M. hemiperus*. The data suggest that poisoned sugarcane traps may be adequate for control of *M. hemipterus*, although inadequate control with chemical insecticides has also been reported. Moreover, chemically based pest controls represent short term and questionable strategies for resource-poor farmers in developing countries, along with accompanying health and environmental concerns.

Cultural Control

Sanitation of residues harboring the weevil has been recommended. This procedure is done by cutting up pseudostems and allowing them to dry up. No data are available on efficacy.

Biological Control

Both entomopathogens and naturally occurring biological control agents affect sugarcane weevil.

Entomopathogens

The use of entomopathogens provides a promising, yet still expensive means of control of *M. h. sericeus*. The entomogenous fungi *Beauveria bassiana* (Balsamo) Vuillemin and *Metarhizium anisopliae* (Metchnikoff) Sorokin have gained considerable attention as potential control for weevils. For example, studies have demonstrated that naturally occurring *B. bassiana* was an important mortality factor to adults of *M. hemipterus* in Florida. *Beauveria bassiana* infection increased up to 70% between March and April 1991 when more than ten weevils were captured per trap. In Brazil, *B. bassiana* and *M. anisopliae* caused high death rates of adults applied under laboratory conditions.

Applying fungal formulations to traps made from banana pseudostems was considered the most effective delivery system, while applications outside traps were deemed impractical. It was observed that *M. hemipterus* adults were more susceptible to infection by both fungi than *C. sordidus* adults. In Cuba, a strain of *B. bassiana* from the sweet potato weevil, *Cylas formicarius elegantulus*, which is reported to be highly pathogenic to *M. hemipterus* and *C. sordidus* was isolated. More information is needed on the effect of these fungi before pest management decisions can be made.

The nematode *Steinernema carpocapsae* has been demonstrated to be effective against *M. hemipterus* larvae, but not adults. However, the authors concluded that chemical insecticides and entomopathogenic nematodes would need to be applied frequently and over a long period of time for effective management because of the weevil's high reproductive potential and the cryptic habitat of the immature stages.

Natural Enemies

Reported predators of *M. hemipterus* include labidurids, histerids, staphylinids, carabids, cicindelids, formicids and reduviids. Little is known on the control potential of predators. In Florida, Colombia and Ecuador, surveys for predators and parasitoids of *M. hemipterus sericeus* have been unsuccessful. There are reports that trials with the tachinid *Microseromasia sphenophori* failed. However, the tachinid *Admontia* spp, observed parasitizing *Metamasius quadrilineatus* in Honduras, could be tested as a possible parasitoid of *M. hemipterus*. Thus, to date, very little research has been done on parasitoids of *M. hemipterus* in the neotropics, so it is unclear whether or not effective biological control will be possible.

Banana Pseudostem Weevil, *Odoiporous longicollis* (Coleoptera: Curculionidae)

The banana pseudostem weevil, *Odoiporous longicollis* (Olivier) (Coleoptera: Curculionidae) is considered a minor to important pest of banana and Manila hemp in parts of India, Nepal, Burma, Sri Lanka, Thailand, Indonesia, China and elsewhere in Asia. The weevil bears a superficial resemblance to the banana weevil, *Cosmopolites sordidus* (Germar), but is slightly larger and its elytra do not completely cover the abdomen. The color of the adult weevil varies with age from reddish-brown to black. Sexing of adults is based on punctuation of the rostrum. Males also tend to be smaller than females. The sex ratio ranges from as 1:1.2 (male:female) to 1:1.5.

Biology

The weevil is characterized by long life span, negative phototropism, thigmotropism, gregariousness, hydrotropism and death mimicry. Most adults live 6–10 months, although some can survive for more than 2 years. In contrast to the banana weevil, the adult readily flies, although it has been described as a poor flyer. Still, it has sufficient capability to move between proximal banana stands. In spite of being negatively phototrophic, diurnal flight occurs.

Oviposition is in the leaf sheaths of living plants or residues. The weevils are especially attracted to, and readily oviposit in, cuts in banana material. Some authors have suggested that ovipositing females prefer stressed plants, while others observed greater oviposition in residues than in living plants. The greatest oviposition has been found in pseudostems with a girth of 25–50 cm, with little oviposition in plants less than 25 cm or more than 75 cm in girth. The eggs are placed singly in chambers made with the female's rostrum. The egg stage has been reported as 3–4 days and 5–12 days.

The larvae pass through four instars. The first instar remains near eclosion sites in the same leaf sheath. Subsequent instars bore into the inner leaf sheaths or pseudostem. The mature larvae may be twice the size of those of banana weevil. The larval stage has been reported by several authors to be 14 days, 3–6 weeks and 26–68 days.

The prepupa forms a pupal chamber within the host plant. Pupation is within a cocoon formed out of plant fibers. The prepupal stage lasts 3–9 days, while the pupal period has been reported as 3–20 days. Following emergence, the adults may pass extended periods and even mate within the host plant. The pre-oviposition period lasts 1 month.

Pest Status

The adult weevils feed on living and decomposing banana leaf tissues, but eat little and are not considered pests. Damage is done by the larval stage. The larvae attack the pseudostem and stem of banana plants, although they will occasionally feed within the rhizome. This contrasts with the banana weevil, which attacks the rhizome and uncommonly enters the pseudostem. As such, pseudostem borer damage may be clearly visible, while banana weevil damage can only be observed by dissection of the rhizome. The pseudostem borer will attack both living plants and harvested stumps.

Larval damage can lead to the rotting of pseudostem tissues and breakage in the wind. Breakage of damaged plants is potentially a serious problem, although such losses are rarely quantified. Thus although the weevil has been described as an important pest, there are no available data on plant loss and/or yield reductions. Further work in this area is required for the development of any integrated pest management program.

Control Measures

Cultural Control

There is limited information available on control of banana pseudostem weevil. Selecting new and clean sites, use of clean planting material, crop sanitation (e.g., burying infested residues), rogueing of infested plants, crop rotation (to rid fields of weevils), and trapping by placement of residue slices on the ground has been recommended. Because the weevil flies and its dispersal capacity has not been determined, it is unclear how effective the use of these cultural methods might be. One scientist reportedly collected more than 2 million weevils in traps over a 4-month period, but did not provide information on the effect of this trapping program on weevil populations.

Chemical Control

Swabbing of the pseudostem and weevil holes with insecticides has also been recommended. No data are available on efficacy.

Host Plant Resistance

Host plant resistance has been suggested to be effective in reducing weevil infestations. In India, one variety was found to be completely free of the weevil, while two others appeared resistant. In screened banana germplasm studies, six varieties were found to be severely infested, three heavily infested, four moderately infested, and 27 lightly infested.

Banana Scab Moth, *Nacoleia octasema* (Lepidoptera: Pyralidae)

Banana scab moth, *Nacoleia octasema* (Meyrick) (Lepidoptera: Pyralidae), is a serious pest of bananas in the Samoan Islands and elsewhere in the southwestern Pacific. The pest also attacks *Heliconia* spp. and *Pandanu*s spp. Other moths that attack banana but are considered of minor importance include *Opogona sacchari* and *Othreis fullonia*.

Biology

Banana scab moth females lay eggs on banana flower bracts or leaves as the inflorescence emerges. Larvae hatch, enter the flower, and feed on the developing fruits within. The feeding results in rough and irregular scars (brownish-black) on fruit skin. Large infestations can scar the entire fruit and cause deformed fingers.

Eggs are laid singly or in small, flattened, almost transparent clusters of a few to over 20 eggs. The eggs hatch in 3–4 days and the larvae enter the banana lower, where they feed. The larval period is 11–19 days. Pupation is inside a loose silken cocoon, often placed between banana fingers, in folds of the dead leaves still attached to the pseudostem, or in litter near the base of the plant. Adult moths emerge in 8–10 days and are short-lived, dying after about 3–10 days. Females lay approximately 80–120 eggs during their lifetime. The moths are rarely seen, because they hide among dead leaves and vegetation during the day and are active only during the early night.

Pest Status

Banana scab moth females lay eggs on the outside of the banana flower bracts or on nearby leaves as the flower first emerges. Upon hatching, the larvae enter the flower and feed on the developing fruits within. Feeding results in irregular dark brown to black corky blotches on the fruit skin. Light damage may be superficial and confined to the upper end and outer side of the curved fingers. Heavier infestations can scar the entire fruit, cause deformed fingers, or penetrate into the flesh of the fruit.

Control Measures

Uses of biological control, resistant varieties, or cultural controls have not proven effective for managing banana scab moth.

Chemical Control

Chemical control works well when used properly. Because the larvae begin damaging the developing fruits when they are still enclosed inside the flower, the best control can be achieved by injecting an insecticide into the flower after it first becomes visible, but before it starts bending over from the vertical position. A single injection at this stage, applied about 1/3 of the way down from the flower tip, will percolate down to protect all the hands inside. This protection will last until the bracts begin to fall away and no more egg laying occurs.

Some growers prefer to lift or remove the flower bracts and dust or spray insecticide onto the fruits after the flower has bent over. This method can stop some of the damage, but not all of it, because by this stage feeding has already begun.

Flowering is more or less continuous in banana plantations in American Samoa, and the stage at which insecticide must be applied lasts only a few days for each plant. Therefore, it is important to check the plantation frequently to ensure that all emerging inflorescences are treated.

Biological Control

Several kinds of natural enemies attack the banana scab moth, but in general they do not provide sufficient control to reduce damage to acceptable levels. Spiders and ants may prey on the immature stages of banana scab moth. Parasitic wasps may also help reduce banana scab moth numbers. In the Samoan Islands, the most common parasitoid is *Chelonus* sp. (Hymenoptera: Braconidae), which lays its egg inside the egg of the scab moth. The *Chelonus* larva then develops inside the scab moth egg and larva. It finally emerges from the nearly full grown scab moth larva to spin a cocoon nearby in which it pupates.

Host Plant Resistance

Some banana varieties appear to be less susceptible to scab moth damage. Left untreated, these varieties may produce a satisfactory product for markets that can tolerate some damage.

The Banana Skipper, *Erionota thrax* (Lepidoptera: Hesperiidae)

The banana skipper, *Erionota thrax* (Linnaeus) (Lepidoptera: Hesperiidae) is a minor to severe pest of bananas and *Musa textilis* in Southeast Asia and Papua New Guinea. Damage has also been reported from bamboo, coconut and other plants although it has been suggested that other species may be responsible for the records on palms and bamboo. Banana clumps in isolated villages in Java had a very patchy damage distribution, ranging from severe defoliation to nil on clumps growing within close proximity. Heavy rainfall and strong winds are unsuitable for banana skipper. Entry of water into the leaf rolls drowns the larva (particularly the first instar) and wind-torn leaf laminae are unsuitable for the production of leaf roll shelters. For these reasons, outbreaks in Malaysia and Indonesia are more common after a drought and in wind protected areas.

The banana skipper is a large brown *Hesperiid* with large yellow spots on the forewings above. Adults are less often seen although the caterpillars can be quite common on the host plants. This may be due to the fact that the butterfly is only active during the early morning hours and just before dusk. It is sometimes attracted to the lights of dwellings and flies towards the lights in the evenings.

The caterpillars can be found where the banana plants (*Musa* spp.) are cultivated. Occasionally, an infestation is severe enough for the species to be considered one of the banana farmer's pests. The characteristic rolled up portions of the banana leaves are a dead giveaway to the presence of the caterpillars. Pupation takes place in a rolled up leaf as well, and the adult butterfly emerges after about 7 days. The caterpillar swings from side to side when disturbed, and exudes a greenish fluid. The pupa also wriggles violently when disturbed.

Biology

The adult butterfly lays bright yellow eggs singly or in groups of up to 25. Oviposition is mostly on the lower leaf lamina midway between the midrib and the outer edge. Eggs turn bright red and the pale green larvae hatch after about 5–8 days. The larvae move to the outer leaf lamina where they commence feeding and then produce loose rolls by cutting the leaf and rolling the lamina towards the midrib. Larvae feed and grow within the rolls, commencing a new roll once the midrib is reached. The second and subsequent three instars are covered in a white waxy powder that provides protection from drowning during high rainfall. The larval stage lasts 20–30 days, depending on temperature. Pupation occurs within the leaf roll and lasts 8–12 days. Adults emerge in the afternoon and are most active in the evening and early morning when they actively fly around banana plants to mate and oviposit.

Pest Status

Direct fruit production losses is only significant following heavy defoliation since banana plants can withstand at least 20% leaf lamina loss before production is affected. Nonetheless, bananas in Southeast Asia are grown for aesthetic value and for culinary purposes where even minor infestations would be detrimental.

Control Measures

The banana skipper is adequately controlled by a range of beneficial insects such that other control measures are seldom required. In Indonesia, egg parasitoids, including *Ooencyrtus erionotae*, *Agiommatus* sp. and *Anastatus* sp., can parasitize 50–70% of the eggs. Young larvae are attacked by *Apanteles erionotae* while older third instar larvae are preferred by *Scenocharops* sp. The pupal parasitoids *Brachymeria* sp., *Xanthopimpla* sp. and *Pediobius* sp. also contribute to biological suppression of *E. thrax*. If unusually heavy outbreaks occur, the collection and destruction of leaf rolls may reduce subsequent damage.

Banana Thrips (Thysanoptera: Thripidae)

Species of thrips that attack and damage banana include Chaetanaphothrips orchidii (Moulton), C. signipennis, Caliothrips bicinctus, Frankliniella parvula, Heliothrips haemorrhoidalis (Bouché), Hercinothrips bicinctus (Bagnall), Thrips hawaiiensis (Morgan), and Tryphactothrips lineatus. The banana thrips H. bicinctus (Bagnall), C. bicinctus, C. orchidii, C. signipennis, T. hawaiiensis and T. lineatuss are the most important peel-blemishing insects, producing a range of damage symptoms on immature fruit.

Thrips cause superficial skin blemishes on immature and developing banana fruit. Damage is primarily cosmetic although severe attacks may result in splitting of the peel with subsequent development of secondary rots. Usually only fruit grown commercially requires treatment with prophylactic pesticides. In Australia, chemical treatments are routinely applied to prevent the rusty brown discoloration caused by the pantropical banana rust thrips *C. signipennis*. The closely related *C. orchidii* (Moulton) causes similar damage in Central and South America. The banana flower thrips *T. hawaiiensis*, a widespread and polyphagous flower feeder in Oriental and Pacific regions, damages fruit at flowering as it oviposits and feeds on fruit during and immediately after emergence of the inflorescence. The slightly raised, silvery grey lesions caused by these thrips are locally referred to as "corky scab."

In Mexico, *Frankliniella parvula* prefers to oviposit in the epidermis of young banawna fruits and less frequently in the flower parts. In Yemen, *Scirtothrips aurantii* and *Thrips pusillus* cause fruit spotting on bananas. Small circular spots first appear on the surface of the fruit, gradually enlarge, blacken, and develop into oily, water soaked lesions.

In Australia, *T. hawaiiensis* causes a superficial skin injury locally referred to as corky scab. Adults are attracted to the emerging inflorescence. Female oviposition and subsequent nymphal and adult feeding cause damage on the developing fruit while the bunch is wrapped closely in the bracts. Oviposition punctures result in localized raised "pimples" which disappear as the fruit develops, while the superficial grazing by the thrips develops into the slightly raised silvery-grey areas of corky scab. This damage is more prevalent during dry periods and is more commonly associated with fruit fingers on the lower bunch hands, the rachis and attacked cushion.

Biology

Eggs are inserted into the plant tissues including fruit, pseudostem and leaf petioles, depending on species. Surfaces that are in close contact are preferred for oviposition and development. The eggs hatch in 1–2 weeks. Nymphs are clear to straw-colored and, like the adults, shun sunlight, quickly dispersing when disturbed from their cryptic hiding places between adjacent fruit or from under leaf bracts on the pseudostem. Pupation takes place on the plant or in the soil near the base of the plants, depending on species. Banana rust thrips (*C. signipennis*) may spend part of their life cycle in the soil, while banana flower thrips stages all occur on the host plant. For example, in Australia, the entire life cycle of *T. hawaiiensis* is spent on the fruit or other parts of the plant. During summer months, the period from egg to adult for this species is 3 weeks.

Pest Status

Thrips can scar, stain, or deform banana fruits by feeding on the fruit skin. Thrips are small, winged insects that feed on banana flowers and/or the tender green skin of developing fruits. The two factors of feeding site and species determine the type and extent of fruit damage. Thrips outbreak can occur during periods of dry weather. Thrips cause superficial skin blemishes on immature and developing banana fruit. Damage is primarily cosmetic although severe attacks may result in splitting of the peel with subsequent development of secondary rots. Usually only fruit grown commercially requires treatment with prophylactic pesticides.

Most of the species are found in the inflorescences or between fruits. The skin of severely infested fruit may crack, allowing secondary invasion of pathogens. In Brazil, injury by *T. lineatus* is regularly observed on 30-day old fruits, or fruits larger than 32 mm in diameter.

Control Measures

Cultural control methods, such as clean cultivation and removal of trash, promote the exposure of pupae to desiccation, but do not provide effective control. In Brazil, use of chemical control as soon as the flowers are formed, elimination of flowers after the fruits are formed, removal of alternate host plants, and covering banana bunches with a bag impregnated with insecticides have been recommended. There are no known useful natural enemies of banana thrips. Reportedly there is a lack of effective predators for *C. signipennis* in north Queensland, Australia, although a number of generalist predatory bugs, coccinellids and chrysopids feed on flower thrips and can reduce their numbers.

Chemical control methods consist of enclosing the bunch inside an insecticide-treated bag. This practice, once widespread, is still recommended in South America. A single pesticide injection into the emerging inflorescence, a treatment specifically aimed at the banana scab moth, is also efficacious against *T. hawaiiensis* and helps protect from early *C. signipennis* infestation. Attaching a piece of chlorpyrifos impregnated ribbon to the upper bunch stalk also provides extended protection against *C. signipennis*. Untreated polythene bunch covers significantly reduced damage compared to uncovered fruit, while bunch covers impregnated with 1% chlorpyrifos provided almost total protection.

The Banana Aphid, *Pentalonia nigronervosa* (Hemiptera: Aphididae)

The banana aphid, *Pentalonia nigronervosa* Coquerel, (Hemiptera: Aphididae) is present worldwide where banana (*Musa* spp.) is grown. The aphid is a serious problem on banana because it is a vector of Banana Bunchy Top Virus (BBTV), the most damaging virus disease of bananas. The preferred host of this aphid is banana but also may infest many tropical and subtropical food and ornamental plants, including *Alpinia purpurata* (floral red and pink ginger), *Xanthosoma* ("ape or elephant ear), cardamom, *Heliconia*, tomatoes, taro, *Calla*, *Costus*, kahili ginger, torch ginger, and *Zingiber*.

The banana aphid is present just about everywhere banana is grown. It has been reported throughout tropical Africa, Atlantic Islands, Australia, California, Florida and Hawaii (USA), Central America, Cook Islands, Egypt, Fiji, Kiribati, India, Indonesia, Malaysia, Madagascar, Marshall Islands, Mauritius, Mexico, Micronesia, the Middle East, Mozambique, New South Wales, Papua New Guinea, the Philippines, Réunion, Samoa, northern South America, Taiwan, Tokelau, Tonga, Tuvalu, Vanuatu, Wallis Island, and much of the West Indies.

Biology

Reproduction in the banana aphid is entirely parthenogenetic (without mating). Females give birth to live female young. Males are not known for this species. The life cycle (nymph to adult) is completed in 9–16 days. The adult life span ranges from 8 to 26 days; there could be as many as 30 generations produced per year in Hawaii.

There is no egg stage. Young are born live. Like most other aphid species, the banana aphid has four nymphal stages. Newborn nymphs are oval at first and become slightly elongated. They are reddish brown, with four segmented antennae, and measure 0.1 mm in length. The second stage nymphs are similar in appearance and measure approximately 0.7 mm long. The third nymphal stage individuals are light brown, measuring about 0.9 mm in length; the compound eyes are more noticeable beginning with this stage, and the nymphs have five-segmented antennae. The fourth stage nymphs have six-segmented antennae, are light brown in color, and are 1 mm long. The first, second, third, and fourth nymphal stages last 2–4, 3–4, 2–4, and 2–4 days, respectively.

Adult banana aphids are small to medium sized aphids (1–2 mm), shiny, reddish to dark brown or almost black. They have six-segmented antennae that are as long as the body. Alates have prominent, dark (brown or black) wing veins. Adults start producing young one day after reaching maturity. They can give birth to four aphids per day with an average production of 14 offspring per female.

Colonies of the banana aphid are commonly found in the upper leaf sheaths and lower flower bracts of the ginger stem. The entire inflorescence may be infested. Small colonies occasionally occur on the leaf blade. Ants are associated with the banana aphid. The ants feed on the honeydew secreted by the aphid and, in turn, establish new aphid colonies and ward off natural enemies. Winged adults often develop after 7–10 generations of wingless individuals. Dispersing winged adults establish new colonies on other new host plants. Although they are not strong fliers, they may be carried considerable distances by light winds. Flight activity peaks between 9:00–11:00 A.M. and 5:00 P.M. to dusk.

Pest Status

The banana aphid is a phloem feeder that uses its long stylets to pierce plant tissues to suck the sap directly from the vessels. This can cause plants to become deformed; the leaves become curled and shriveled, and in some cases galls are formed on the leaves. Young plants may be killed or their growth checked if there is sufficient feeding by the banana aphid. However, direct damage by this aphid is generally negligible.

The insects do far more harm as vectors of numerous viruses, including bunchy top. The aphid picks up the virus while feeding on a sick plant, then spreads it to healthy banana plants in subsequent feedings. Both wingless (apterous) and winged (alate) aphids are able to transmit viruses. Transmission is usually in a non-persistent manner where the virus is taken up into the aphids' mouthparts while feeding on an infected plant and transferred to a healthy plant during subsequent feedings. In non-persistent transmission, the virus reproduces in the plant, and aphids simply aid in transporting the virus. With these types of virus-vector associations, the aphid acquires the virus and is only able to transmit the virus temporarily. Once all the infective charge is reduced by feeding or the passing of time, the aphid is unable to transmit the virus until it feeds on infected tissue again.

Symptoms of banana bunchy top disease include bunched, yellow leaves at the top of the plant, dark green streaks on the leaves and midribs, progressively smaller leaves, leaf curling, and small, distorted fruits. Since the aphid harbors the virus only temporarily, it needs a regular diet of infected plant tissue to remain infective.

Control Measures

Farmers typically manage banana bunchy top disease by destroying infected plants, which serve as a reservoir for the virus, and controlling aphids with insecticides. A wasp that is a known parasitoid of the aphids and ladybird beetles that prey on them was introduced in Hawaii as biological control agents. However, none will control banana aphid adequately enough to prevent the transmission of BBTV.

Chemical Control

Chlorpyrifos and acephate foliar sprays have been effective in reducing aphid populations and the attending ants. Immersing flowers and foliage in hot water at 49°C for 10 min kills banana aphids. This treatment is safe for many commodities, but preconditioning may be required.

Biological Control

Introductions of the braconid *Lysiphlebius testaceipes* were made in 1923, 1953, and 1965 by the Hawaii Department of Agriculture to combat aphids. The sources of the introduced wasps include Japan, Cuba, California, and Mexico. This parasitoid is established on all populated Hawaiian Islands and is a known parasitoid of the banana aphid.

Biological control experts from the Hawaii Department of Agriculture have introduced ladybird beetles to the islands to control insects. *Coccinella 7-punctata* var. *brucki* was brought in from Okinawa in 1958 and is established on the major islands, and is listed as a banana aphid predator. Other predators that have been successfully introduced to combat aphids are *Coelophora inaequalis*, *C. pupillata*, *Hippodamia convergens*, *Scymnodes lividigaster*, *Diomus notescens* (Coleoptera: Coccinelidae), and *Nesomicromus navigatorum* (Neuroptera: Hemerobiidae). The larvae, as well as the adults, of ladybird beetles and lacewings are very active aphid feeders, and have been found, along with syrphid fly larvae, in floral red ginger in Hawaii.

An entomopathogenic fungus, *Acremonium* sp., was also observed on banana aphids. The fungus observed to reduce reproduction, development and population of banana aphid, *Pentalonia nigronervosa*, a vector of bunchy top virus diseases of banana.

► Banana Weevil, *Cosmopolites Sordidus*
► Tropical Fruit Pests and Their Management

References

Botha J, Hardie D, Power G (2000) Banana scab moth (*Nacoleia octasema*): exotic threat to Western Australia. Fact sheet No. 45/2000. Hortguard TM Initiative AGWEST, Department of Agriculture, Australia

Giblin-Davis RM, Peña JE, Oehlschlager AC, Perez AL (1996) Optimization of semiochemical-based trapping of *Metamasius hemipterus sericeus* (Olivier) (Coleoptera: Curculionidae). J Chem Ecol 22:1389–1410

Gold CS, Pinese B, Peña JE (2002) Pests of banana, pp 13–56 In: Peña JE, Sharp JL, Wysoki M (eds) Tropical fruit pests and pollinators. CABI, Oxford, UK, 448 pp

Scot C, Nelson R, Ploetz C, Kepler A (2006) *Musa* species (banana and plantain). Species profiles for Pacific Island agroforestry. Traditional tree initiative, Version 2.2. (www.traditionaltree.org)

Sosa O, Shine J, Tai P (1997) West Indian cane weevil (Coleoptera: Curculionidae): a new pest of sugarcane in Florida. J Econ Entomol 90:634–640

Banana Weevil, *Cosmopolites sordidus* (Germar) (Coleoptera: Curculionidae)

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The banana weevil is the most important insect pest of banana and plantain. Its host range is restricted to wild and cultivated clones of *Musa* (banana, plantain, abaca) and *Ensete*. The insect originated in Southeast Asia and has spread to all important banana and plantain growing areas. It is not normally a pest in its area of origin.

Banana weevil larvae bore in the corm, damaging the root and vascular system, reducing nutrient and water uptake, and weakening the stability of the plant. Attack in newly planted banana stands can lead to crop failure. In established fields, weevil damage can result in plant loss (death of suckers, toppling, snapping), reduced bunch weights, mat disappearance (following failure to produce suckers), and shortened stand life. Damage and yield losses increase over time. Yield losses may exceed 50% in ratoon crops. Stand life can be reduced from more than 30 years to less than five.

Banana weevil pest status is affected by clone selection, ecological conditions, and management system. Highland bananas (AAA-East Africa) and plantains (AAB) are most susceptible. Other clonal groups, including export dessert bananas (e.g., Cavendish, AAA), tend to be moderately to highly resistant. *Ensete* is susceptible, but usually grown above the pest's upper elevation threshold and therefore escapes attack.

The Host Crop

Banana is an herbaceous perennial that is propagated through lateral buds giving rise to new plants (suckers). The plant consists of an underground corm and a pseudostem composed of overlapping leaf sheaths. The true stem emerges from the corm, grows through the pseudostem, and bears the inflorescence. The plant dies after the bunch matures. A group of plants sharing a common corm comprise a mat. Suckers may be detached from the mat and planted elsewhere.

Edible bananas are ultimately derived from two wild progenitors, *Musa acuminata* and *M. balbisiana*. Banana clones (or cultivars) are assigned to genome groups (e.g., AB, AAA, AAB, ABB, AAAA) based on ploidy and the relative genetic contribution of *M. acuminata* and *M. balbisiana*. Cooking, roasting, dessert and brewing types are grown. Production systems range from kitchen gardens and small, low input stands to large-scale export plantations.

Biology and Life Cycle

Adult Stage

Adults are uniform black or dark brown and average 12.5–13 mm in length. The sex ratio is 1:1. Males can be distinguished from females on the basis of small pits on the rostrum extending beyond the point of insertion of the antennae and by greater curvature of the last abdominal sternite. Males are on average 20% smaller than females in size and weight.

The banana weevil displays a classical "K" selected life cycle with long life span and low fecundity. Adults may live 4 years though most live less than 1 year. They are free living but closely associated with banana mats and cut residues. They are usually hidden during daylight hours and most often observed at traps. The adults feed on rotting banana tissues and can survive months without food. They require moist environments and die within days if maintained on dry substrates. Banana weevils are attracted to their hosts by volatiles, especially those released from damaged corms. Males produce an aggregation pheromone attractive to both sexes.

Banana weevils are negatively phototrophic and most active between 2100 and 0400 h Temperature thresholds for activity are 15–18°C. Flight is uncommon. Dispersal by crawling is limited; fewer than half move 50 m in a year. The banana weevil's narrow host range and limited dispersal capability preclude immigration of adults into isolated stands. Dissemination is primarily through movement of infested planting material (suckers).

Ovipositing weevils prefer flowered plants and crop residues but accept all plant stages. Females are attracted to freshly cut corms, making suckers detached from banana mats especially vulnerable; a single larva can kill a young plant if it damages the growing point. Oviposition rates are usually 0.5–4 eggs per week, although averages of 14 eggs per week have been observed. Low fecundity contributes to the slow build-up of weevil populations over time.

Immature Stages

Eggs (0.5 × 2 mm) are cylindrical and laid in the corm and base of the leaf sheaths. Eggs are deposited singly in holes (1–2 mm deep) excavated by the female with her rostrum. Eclosion rates are 80–100%. Larvae emerging in leaf sheaths usually move to the corm, although feeding in the true stem and, rarely, the pseudostem also occurs. In the corm, the larvae prefer cortical tissue to the central cylinder. The larvae pass through 5–8 instars. Pupation is in a bare chamber near the plant surface.

In West Africa, developmental thresholds and thermal requirements were 12°C and 89 degree-days for eggs, 8.8°C and 538 degree-days for larvae, and 10.1°C and 121 degree-days for pupae. Under ambient tropical conditions, stage duration is 6–8 days for eggs, 21–55 days for larvae, and 6–8 days for pupae. In addition to temperature, larval stage duration is affected by clone, plant stage, size of corm, and weevil density. The data suggest extended periods of low night-time temperatures (e.g., at higher elevations) are bottlenecks for immature development and/or adult survival. The banana weevil is rarely important at elevations above 1,600 m.

Semiochemicals

Both males and females are attracted to hosts by kairomones containing mono- and sesquiterpenes. Attraction to corm material is greater than to pseudostems. Field observations suggest that banana weevils are attracted to both susceptible and resistant clones and will accept any clone for oviposition. A male aggregation pheromone (sordidin) is attractive to both sexes. This has been synthesized and is commercially available as lures. The attraction range of semiochemicals is unlikely to exceed 10 m and may be much less.

Monitoring

Accurate assessment of banana weevil population levels and damage are necessary for understanding pest status, screening germplasm and evaluating the impact of intervention strategies. The insect's biology makes assessment and control difficult.

Damage Assessment

The reclusive behavior of the adults and the difficulties in measuring larval damage in the interior of the corm has resulted in a multitude of scoring and evaluation systems. These include monitoring adult numbers through trapping; measuring damage to the corm periphery; and measuring internal corm damage through cross and longitudinal sections. Some of these methods are subjective, making results hard to interpret or compare. Moreover, sites of banana weevil attack may differ among clones. In Uganda, for example, the dessert banana Ndiizi (AAB) had similar levels of damage to the corm surface as that of highland cooking banana (AAA-EA), but only 16% as much internal damage within the corm.

Damage to the corm interior is better related to yield loss than damage to the corm periphery, while damage to the central cylinder is more important than damage to the corm cortex. Measuring larval damage in cross sections at the collar (corm-pseudostem junction) and 10 cm below the collar in recently harvested plants is recommended. A common method is to visually estimate percentage cross section surface area consumed by weevil larvae in the central cylinder and cortex, respectively.

Yield losses tend to increase over time. In one trial, yield losses increased from 9% in the plant crop to 48% in the third ratoon. In Ghana, weevil damage in plantain stands was often low in spite of susceptible germplasm, favorable temperatures and low management levels. Shifting agricultural systems predominated with most plantain abandoned after two crop cycles. As such, short plantation life precluded adequate time for weevil populations to build up to damaging levels. Weevil problems became evident in the few plantations maintained beyond two cycles.

Population Densities

Adult populations may be monitored using traps made from corm or pseudostem residues. However, interpretation of trap data is difficult as a multitude of factors (e.g., materials, size, number, location, weather) influence trap catches. Therefore mark and recapture studies (using pseudostem traps) are recommended for estimating population densities. Weevils are marked by scratching the elytra. In Uganda, densities among proximal farms ranged from 850 adults/ha (1.5 per mat) to 149,000 adults/ha (240/mat), while in Cameroon density estimates for subplots ranged from 10 to 337 adults/mat.

This within-site variability suggests that management plays an important role in regulating weevil populations. Weevil pressure is widely believed to be associated with clonal susceptibility, management levels, bad drainage, acid or low fertility soils, weedy fields, inadequate sanitation, extended droughts and nematode infestations. However, on-farm and on-station studies have failed to find strong relationships between weevil damage and management factors or plant stress. Moreover, only a modest relationship ($r = 0.22$) existed between weevil adult density and damage across 50 farms within one watershed. Population estimates may be a poor indicator of economic status if a high population reflects build-up on residues rather than maturing plants. Also, adult populations may be as much as 2.5 times higher in mulched than in unmulched plots because of more favorable soil moisture conditions.

Pest Status

The pest status of banana weevil was once controversial as many clones are resistant and attack in some (e.g., Cavendish, AAA) is often realized on crop residues where damage has no effect on yield. Meaningful yield losses have now been demonstrated in highland banana (AAA-EA) and plantain (AAB) systems. The banana weevil has also been shown to be an important component of yield decline leading to the disappearance of highland bananas in its traditional growing areas in East Africa.

Crop establishment may be impeded if planting is in an already infested field or if planting material carries eggs and larvae. Plant loss of up to 40% has been recorded in newly planted highland banana and plantain stands. In fields with minor initial infestations of banana weevils, population build-up is slow and problems may not appear for several years. In a highland banana trial in Uganda, damage to the central cylinder increased from 4% in the plant crop to 17% in the third ratoon. Similarly, in surveys of plantain systems in Ghana, damage increased from 2% in the plant crop to 7% in the second ratoon. Damage will have a greater effect on yield if the same mat has sustained heavy attack in preceding crop cycles. Thus, single cycle yield loss trials may underestimate weevil importance. For example, yield losses in several highland banana trials went from negligible in the plant crop to 48–60% within a few years.

Yield loss is reflected in plant loss, reduced bunch weights and dying out of mats. Plant loss attributable to banana weevil attack in two highland banana trials increased from 4% in the plant crop to 29% in the third ratoon, while heavily damaged plants suffered reductions in bunch weights of 20–45%. In another trial, 35% of banana mats died out in 5 years in plots infested with weevils, compared to 2% mat loss in controls. This suggests that the weevil can severely reduce stand life. Farmers in central Uganda reported that banana weevil had contributed to reductions in highland banana stand life from >30 years to 4 years, while in Colombia the weevil reportedly reduced plantain stand life to two to three crop cycles.

Integrated Pest Management

Current research results suggest that no single control strategy will provide complete control for banana weevil. Therefore, a broad integrated pest management (IPM) approach, combining a range of methods, might offer the best chance for success in controlling this pest. The components of such a program include cultural control (habitat management), biological control, host plant resistance, botanicals and (in some cases) chemical control.

Cultural Control (Habitat Management)

Cultural controls for banana weevil include clean planting material, selected cropping systems, improved agronomic practices to promote plant vigor, crop sanitation (destruction of crop residues) and trapping with crop residues.

Clean planting material: Infested suckers provide the principal entry point of banana weevils into newly planted fields. Thus, clean planting material eliminates the most important source of infestation in new plantations. The insect's low fecundity and slow population growth suggest that a reduction in initial infestation level can retard pest build-up and damage for at least several cycles. The use of clean planting has been widely recognized and promoted.

Recommended methods include the use of tissue culture plantlets, paring and selection of weevil-free suckers, pesticides, and entomopathogens. Tissue culture plants are insect-free at the time of planting. Once established in the field, it is unclear whether tissue culture plants are more or less susceptible to banana weevils than plants grown from suckers. Paring (removal of the outer corm surface) eliminates most eggs and first instar larvae, and exposes weevil galleries, allowing farmers to reject heavily damaged suckers. Paring cannot remove larvae that have penetrated below the corm surface. Suckers may be dipped in pesticide solutions or pesticides may be applied to the planting hole. Alternatively, *Beavueria bassiana* formulations can be applied to planting holes to reduce weevil attack of suckers. None of these methods assure elimination of weevils. Adults may already be in the field from a previous planting or may invade from nearby plantations. As a result, the benefits of clean planting material may be limited to a few crop cycles.

Selected cropping systems: Mixed cropping systems often result in lower insect pressure by reducing immigration rates, interfering with host plant location and increasing emigration rates. However, banana weevils are sedentary insects that live in perennial systems with an abundant supply of hosts. Coffee intercrops and residues (e.g., husks) may repel banana weevils but this requires further study. Otherwise there is little evidence that intercrops or insect-repellent green manures (*Canavalia*, *Mucuna*, *Tephrosia*) have meaningful effects on banana weevil populations.

Crop Sanitation

Banana residues serve as adult refuges and oviposition sites and contribute to population growth. In Uganda, 25–32% of adult weevils were associated with prostrate (cut or fallen) residues, while another 10–12% was found in standing stumps. In Australia, 60% of adults emerged from residues. For some clones, banana weevil damage is much higher on residues than on growing banana plants. It is widely believed that destruction of crop residues (splitting of harvested pseudostems and/or removal of corms) lowers overall weevil populations and reduces damage on standing plants in susceptible clones. In Ugandan field surveys, sanitation level had more impact on weevil pest status than any other management practice. In on-farm trials, increasing sanitation level from low to high for 3 years reduced adult population density from 52,000 to 13,000 ha^{-1}, lowered corm damage by 41% and increased yield by 70%.

Trapping

Traps exploit banana weevil attraction to crop residues. The most common are split pseudostem traps (30–60 cm lengths split longitudinally and placed flush on the soil surface at the base of banana mats) and disk-on-stump traps (a piece of cut corm placed on top of a banana stump). Inclusion of corm material in a trap increases its attractivity to weevils. Thus disk-on-stump traps tend to have higher weevil catches than pseudostem traps. However, pseudostem trapping is more often recommended for systematic trapping studies because a single harvested plant can only support one disk-on-stump trap (fixed in space), while the same plant can provide material for many pseudostem traps (placed where the farmer deems most useful). The effect of trapping on weevil populations will, in part, reflect trap density and trapping frequency. Intensive trapping in established fields results in a gradual decline in weevil numbers with a lag time required before effects are manifested in reduced damage. In a 1-year study in farmer's fields in Uganda, weevil numbers declined by 61% in farms with intensive trapping (1 trap/mat/month), 53% with moderate trapping (0.3–0.6 traps/mat/month) and 38% in farms without trapping. Trapping success was affected by management level and weevil immigration from neighboring farms. Although farmers were convinced that trapping was beneficial, adoption was low due to resource and labor requirements.

Biological Control

Biological control efforts against banana weevil have included the use of exotic natural enemies (classical biological control), endemic natural enemies and microbial control (e.g., entomopathogens, entomophagous nematodes). Microbial control agents may require repeated applications as biopesticides and entail application costs on the part of the farmer.

Classical Biological Control

Introduced pests, unimportant in their areas of origin, often reach damaging levels when released from the control of co-evolved natural enemies. The banana weevil appears to fit this pattern. Searches in southeast Asia identified histerids (*Plaesius javanus* Erichson and *Hololepta* spp.), staphylinids (*Belonuchius ferrugatus* Erichson and *Leptochirus unicolor* Lepeletier), a hydrophilid (*Dactylosternum hydrophiloides* MacLeay), a cucujid (*Canthartus* sp.), and a leptid (rhagionid) fly (*Chrysophila ferruginosa* (Wied.)) as predators of banana weevil. Of these, *P. javanus* appeared most important. Between 1913 and 1959, 45 attempts were made to introduce eight natural enemies from Asia to other banana growing regions in the world. *P. javanus*, for example, was released in Australia, Oceania, Latin America and Africa. In most cases, the predators did not establish and in no case did they provide control. Recent searches for egg and larval parasitoids in Indonesia came up empty handed. Classical biological control of banana weevil, therefore, remains an elusive objective.

Indigenous Natural Enemies

Reported arthropod predators of banana weevil immatures include nabids, cydnids, capsids, reduviids, mirids, thrips, rhagionids, sarcophagids, histerids, carabids, hydrophilids, staphylinids, tenebrionids, labiids, carcinophorids, and formicids. Ants appear to be the most promising while other predators seem of little importance. In Cuba, the myrmecine ants *Pheidole megacephala* and *Tetramorium guineense* (Mayr) reduced banana weevil populations and damage by 54–69% following artificial establishment of ant colonies in plantain stands. In Uganda, *Pheidole* sp. and *Odontomachus troglodytes* were most effective in reducing weevil egg and larval populations in pot experiments. Both species readily entered and removed larvae from galleries in crop residues.

Microbial Control

Microbial agents tested against the banana weevil include entomopathogenic fungi (e.g., *Beauveria bassiana* and *Metarhizium anisopliae*) and entomopathogenic nematodes (e.g., *Steinernema* spp. and *Heterorhabditis* spp.). Entomopathogenic fungi and nematodes are most often used to kill adult weevils. *Beauveria bassiana* has been established as an endophyte, although its potential against banana weevil immatures is not yet clear.

Although a number of strains of entomopathogenic fungi and entomopathogenic nematodes have shown promise in the laboratory and in preliminary field studies, efficient and economically viable mass production and delivery systems still need to be developed, while the performance of microbial control agents against banana weevil under different agro-ecological conditions is not well understood. Only in a few sites have entomopathogens been reported to establish following applications in banana fields. Without adequate establishment, entomopathogens will require repeated applications as a biopesticide. This will entail continued production, distribution and storage costs that will be passed on to the farmer.

The conidia of *Beauveria* and *Metarhizium* enter the insect through its spiracles or digestive system or by producing extracellular proteolytic, chitinolytic and lipolytic enzymes which facilitate penetration through the insect's cuticle. The fungi can kill the insect through direct attack on the insect's nutrients or through toxic metabolites. Dead insects kept in moist environment quickly developed surface growth of mycelia. *Beauveria bassiana* can invade the haemocoel where it produces a toxin, beauvericin, that reduces competition with bacteria and weakens the immune system. Strain virulence is often related to toxin production.

Natural rates of infestation are normally low (i.e., <5%). Nevertheless, numerous strains of *B. bassiana* and *M. anisopliae* have been demonstrated to kill >90% of banana weevils when applied topically in the laboratory or in pot trials. In Ghana, *B. bassiana* applications to planting holes reduced damage to suckers, while in Brazil, Colombia, Costa Rica, Cuba and Uganda, applications *B. bassiana* at the base of established mats in banana or plantain stands reduced weevil populations and/or increased yields. In Uganda, transmission from infected to uninfected weevils under field conditions was 13%. While these studies demonstrate field potential, cost-effective production and delivery systems still need to be developed. However, field establishment of *B. bassiana* tends to be low, so repeated applications are usually necessary.

Entomopathogenic nematodes in the genera *Steinernema* and *Heterorhabditis* have been tested against banana weevil, most notably in Australia. Infective juvenile nematodes enter through natural orifices (*Steinernema*) or interskeletal membrane (*Heterorhabditis*). After entering the host, the nematodes penetrate mechanically into the haemocoel and release *Xenorhabdus* bacteria which cause septicemia and death within 1–2 days. In Brazil, entomopathogenic nematodes were widespread in plantain stands, but naturally occurring mortality of banana weevils was low and, as with entomopathogenic fungi, viable delivery systems are an important consideration. The cryptic habitat of weevil larvae within living plants makes delivery against these stages difficult; therefore, applications of entomopathogenic nematodes should target adult weevils.

The most effective entomopathogenic nematode delivery system, developed in Australia, capitalizes on the weevil's attraction to cut corms and damaged plants. This system employs conical shaped cuts in residual corms, i.e., a cone is cut and removed, and then loosely replaced into the corm. These cuts attracted adult weevils and provided thigmotactic stimuli that encouraged them to remain at the infection sites. The holes also buffered the delivery site against temperature extremes and provided excellent conditions (high humidity, moderate temperatures, protection against ultraviolet light) for nematode persistence. The nematodes were released at a density of 250,000 per hole in a formulation including a polyacrylic gel (to reduce water build-up and incidence of nematode drowning) with an adjuvant of 1% paraffin oil (to encourage the weevils to raise their elytra, exposing the first spiracle for nematode entry). However, controls based on entomopathogenic nematodes are more costly than pesticides in Australian commercial banana systems.

Host Plant Resistance

Highland bananas (AAA-EA) and plantains (AAB) are most susceptible to banana weevil attack. Some variability exists among clones within these genome groups. Among highland bananas, for example, Atwalira and Kisansa displayed weevil damage scores two to three times higher than those for Mbwazirume and Nakyetengu, while the degree of penetration into the central cylinder was greatest for Nakitembe, Namwezi and Musakala.

In screening trials, *Ensete* appeared to be highly susceptible. However, in Ethiopia where the crop is most widely grown, *Ensete* escapes attack because most production is above the weevil's upper elevational threshold. Export Cavendish dessert bananas (AAA) are generally considered resistant, although serious banana weevil problems may occur in some areas (e.g., southeastern coast of South Africa). A wide range of other banana dessert and brewing types (AB, AAA, AAB, ABB) are moderately to highly resistant to banana weevil.

Antixenosis (nonpreference) is of little importance. Laboratory and field studies suggest that banana weevils (i) appear to be attracted equally to susceptible and resistant clones, and (ii) will accept all clones for oviposition. Clonal attraction and acceptance (i.e., number of eggs) were not related to damage. In one field trial, oviposition was similar on resistant Pisang awak (ABB) and susceptible five highland bananas (AAA-EA), while subsequent damage was 5–25 times higher on the highland clones. Thus, antibiosis appears to be the most important in conferring host plant resistance to banana weevil.

Antibiotic factors are those which negatively influence larval performance (i.e., poorer survivorship, slower development rates, reduced fitness). These factors may be physical (e.g., sticky sap and latex, corm hardness), antifeedants, toxic secondary plant substances and nutritional deficiencies. To test these factors, banana weevil larvae are commonly reared on potted plants or excised corm material. One difficulty in this system is that resistant factors may quickly break down after harvest or *ex situ*. For example, Pisang awak (ABB) is highly resistant to banana weevil in Indonesia; larvae freely feed without problems in its residues. Similarly, Yangambi- Km5 is highly resistant to banana weevil, often showing no damage in screening trials, yet larvae may be successfully reared on excised corm material taken from this clone.

Nevertheless, screenhouse and laboratory studies have shown that immature banana weevils may have higher mortality, extended developmental periods and lower pupal weights on resistant clones. Corm extracts from resistant Pisang awak placed on corm material of susceptible highland banana clones severely inhibited larval feeding while extracts from other clones did not. A bioassay-guided separation process of the Pisang awak extract was then undertaken using chromatographic techniques. Two of the 16 fractions obtained were found to be very active against weevil larvae. However, the compounds responsible for activity against banana weevil have not been identified.

To date, there have been no attempts to breed bananas or plantains for resistance to banana weevil. Conventional breeding of banana is a difficult and complicated procedure as the most widely used clones are triploids and sterile. This entails crossing wild diploid and highly fertile males to female triploid clones followed by extensive hybrid selection. Nevertheless, there does appear to be useful sources of resistance within the available germplasm. The wild diploid Calcutta-4 (AA), Yangambi-Km5 (AAA) and the hybrid FHIA-03, for example, show high levels of resistance and might be exploited in breeding programs. Corm hardness has been shown to be a key resistance mechanism and screening for this trait may assist in weevil improvement. Secondary metabolites found in resistant clones also appear to be important.

Transgenic approaches (i.e., biotechnology) are also being used to develop resistant clones by transforming banana through insertion of foreign genes, in particular cysteine proteinase inhibitors (cystatins) from rice and papaya and toxins derived from the bacterium *Bacillus thuringensis* (Bt). Cysteine proteinases are mid-gut enzymes that many beetles, including banana weevil larvae, use in the digestion of dietary proteins. Cysteine proteinase inhibitors are defensive compounds produced by some plants in response to insect attack or wounding. These inhibitors impede digestion resulting in protein deficiency and stunted development. Bt has been used as a biopesticide in the control of several insect pests. More recently, Bt toxin genes have been inserted into crop plants to improve resistance.

Successful incorporation of cysteine proteinase inhibitors from rice and papaya into banana tissue reduced banana weevil larval body weights by 60% in 10 d. Current efforts are to insert the genes into banana plants. In preliminary bioassays, incorporation of the Cry3A Bt toxin into artificial diets resulted in 30% mortality of banana weevil larvae. It is believed that high rates of mortality can ultimately be achieved by pyramiding cysteine proteinase inhibitors and Bt toxins. Research in this area is on-going.

Botanical Control

In Kenya, varying formulations of neem (*Azadirachta indica*) seed derivatives (neem seed powder, neem kernel powder, neem cake and neem oil) applied to banana material greatly (i) reduced adult settling on corm pieces, (ii) reduced oviposition rates, (iii) reduced eclosion success, (iv) increased larval penetration time, (v) extended larval development, (vi) increased larval mortality, (vii) reduced larval weights, (viii) impeded population build-up in field trials, and (ix) reduced damage in pot and field experiments. Neem kernel powder and neem oil appeared toxic to the banana plants and may have interfered with nutrient and water uptake, whereas neem seed powder and neem cake displayed phytotoxic effects only at very high application rates. Neem applications in farmers' fields in Tanzania also resulted in reduced damage. In spite of these encouraging results, neem has not been widely adapted by farmers due to availability and costs.

Chemical Control

Chemical pesticides for control of banana weevil may be applied to protect planting material (through dipping of suckers or applications in planting holes), periodically applied at the base of the mat after crop establishment, and/or applied to pseudostem traps to increase trap catches. There have been numerous studies on the relative efficacy of different insecticides under different formulations and application rates, persistence and the appearance of insecticide resistance in banana weevils. At least 45 pesticides have been used at one time or another against banana weevil. Insecticide resistance in banana weevil has been documented in Australia, Latin America and Africa for a range of chemicals including cyclodienes, organophosphates, and carbamates. Cross-resistance has also been demonstrated. Nevertheless, chemicals remain an important part of banana weevil control although costs often make them prohibitive for subsistence farmers. Pesticides remain the fastest action method that can be used to bring a weevil outbreak under control.

► Tropical Fruit Pests and Their Management

References

Collins PJ, Treverrow NL, Lambkin TM (1991) Organophosphorous insecticide resistance and its management in the banana weevil borer, *Cosmopolites sordidus* (Germar) (Coleoptera:Curculionidae), in Australia. Crop Protect 10:215–221

Gold CS, Peña JE, Karamura EB (2001) Biology and integrated pest management for the banana weevil, *Cosmopolites sordidus* (Germar) (Coleoptera:Curculionidae). Integr Pest Manag Rev 6:79–155

Gold CS, Ragama PE, Coe R, Rukazambuga NDTM (2005) Selection of assessment methods for evaluating banana weevil *Cosmopolites sordidus* (Germar) (Coleoptera: Curculionidae) damage on highland cooking banana (*Musa* spp., genome group AAA-EA). Bull Entomol Res 95:115–123

Kiggundu A, Gold CS, Labauschagne MT, Vuylsteke D, Louw S (2003) Levels of host plant resistance to banana weevil, *Cosmopolites sordidus* (Germar) (Coleoptera: Curculionidae), in Ugandan *Musa* germplasm. Euphytica 133:267–277

Kiggundu A, Pillay M, Viljoen A, Gold C, Tushemereirwe W, Kunert K (2003) Enhancing banana weevil (*Cosmopolites sordidus*) resistance by genetic modification: a perspective. Afri J Biotechnol 2:563–569

Nankinga CM, Moore D (2000) Reduction of banana weevil populations using different formulations of the entomopathogenic fungus *Beauveria bassiana.* Biocontr Sci Technol 10:645–657

Pavis C, Lemaire L (1997) Resistance of *Musa* germplasm to the banana weevil borer, *Cosmopolites sordidus* Germar (Coleoptera: Curculionidae): a review. Infomusa 6:3–9

Tinzaara W (2005) Chemical ecology and integrated management of the banana weevil *Cosmopolites sordidus* in Uganda. Ph.D. Thesis, Wageningen University, Wageningen, UR, 184 pp

Treverrow NL (1994) Control of the banana weevil borer, *Cosmopolites sordidus* (Germar), with entomopathogenic nematodes, pp 124–138. In: Valmayor RV, Davide RG, Stanton JM, Treverrow NL, Roa VN (eds) Proceedings of Banana Nematode/Borer Weevil Conference, Kuala Lumpur, 18–22 April 1994INIBAP, Los Banos, Philippines

Band

A transverse line, usually wide, crossing the body. This term often is confused with "stripe," a term used to designate a longitudinal line running the length of the body. The term band is also used to describe an aggregation of insects, usually immature grasshoppers or caterpillars, dispersing in the same direction.

Band Application

An application in which an insecticide (or other chemical) is applied in strips, usually to the planting bed or seed row.

Banded Thrips

Members of the family Aeolothripidae (order Thysanoptera).

► Thrips

Bandwinged Grasshoppers

A subfamily (Oedipodinae) of grasshoppers in the order Orthoptera: Acrididae.

► Grasshoppers

► Katydids and Crickets

Banks Grass Mite, *Oligonychus pratensis* (Banks)

A mite (Acarina: Tetranychidae) pest of grasses, including wheat.

► Wheat Pests and Their Management

Barb

Any of a number of sharp projections armed with teeth or hooks. Insects sometimes have spines or setae equipped with projections pointed backward (to the base, or away from the point) that cause them to remain imbedded once contact with them is made. Presumably they function in defense, especially against vertebrate predators. Structures bearing such projections are said to be barbed, and the occurrence of numerous setae is sometimes described as barbate. A small barb is called a barbule.

Barber, Herbert Spencer

Herbert Barber was born in South Dakota on April 12, 1882. His father, an engineer, encouraged his son's interest in natural history. At the age of 16 he was given employment as an insect preparator at the U.S. National Museum. He worked at such tasks as arranging the Hubbard and Schwarz collection of Coleoptera, but including a collecting trip with Schwarz to Arizona and New Mexico. Although he was employed continuously at the museum until retirement, his pay was, after some years, and until his retirement, provided by the U.S. Department of Agriculture. In time, by association with entomologists and through experience, he began to publish results of his own studies. His publications eventually amounted to some 90 papers. One of the most intriguing was on his discovery of the strange life history of *Micromalthus* (Coleoptera: Micromalthidae) in which there are several forms of larvae, and that some larvae may produce eggs and larvae. He died in Washington, DC, on June 1, 1950.

Reference

Mallis A (1971) Herbert Spencer Barber, pp 281–283. In: American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Barberry Whitefly, *Parabemisia myricae* (Kuwana)

A whitefly (Hemiptera: Aleyrodidae) pest of citrus.

► Citrus Pests and Their Management

Bark Beetles

Some members of the subfamily Scolytinae (order Coleoptera, family Curculionidae).

► Beetles
► Bark Beetles in the Genus *Dendroctonus*

Bark Beetles in the Genus *Dendroctonus*

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The genus *Dendroctonus* (Coleoptera: Curculionidae, Scolytinae), originally described by Erichson in 1836, currently includes 19 species that are widely distributed. Seventeen species occur between Arctic North America and northwestern Nicaragua, and an additional two species are in northern Europe and Asia. *Dendroctonus* species attack and infest conifer hosts (Pinaceae) in the genera *Larix*, *Picea*, *Pinus*, and *Pseudotsuga*. Species within the genus can be identified by the host species they attack, egg gallery patterns, population behavior, and morphological distinctions. The smallest species is *D. frontalis* (male length 2.0–3.2 mm) and the largest is *D. valens* (male length 5.3–8.3 mm). Members of the *Dendroctonus genus*, which means "tree killers," are noted as the most economically and ecologically significant species affecting forest ecosystems in western North America. Tree mortality resulting from *Dendroctonus* outbreaks can adversely affect timber management, forest planning, and recreational opportunities. In contrast, disturbance events caused by native bark beetle species are important drivers of forest succession, foster heterogeneity and biodiversity, promote biomass recycling, and play a critical role in the fire ecology and overall health of many ecosystems.

Dendroctonus beetles are monogamous, and spend the majority of their lifecycle in a cryptic habitat beneath the bark of host trees where larvae feed within the inner bark or phloem. Relative to the length of their life cycle, only a short time is spent as an adult moving from tree to tree. The majority of the species in this genus is capable of killing the host tree in one generation. In fact, death of the host is often a requirement for successful brood production. Although most of the species are capable of attacking and killing standing, vigorous trees, recently fallen trees are favored by some species. The female is the colonizing sex in the majority of *Dendroctonus* species. After attack of a new host, mating typically occurs in a nuptial chamber beneath the bark and an egg gallery is initiated. Adults of a few species, however, mate before emerging from the brood host. Eggs are laid either singly along the sides of the gallery, or in clumps. Egg galleries may be either vertical or sinuous, and larvae mine and feed horizontally in the phloem, either singly or en mass, depending on the species. Pupation takes place in individual niches within the phloem or in the outer bark of the host tree. Upon adult emergence, which is usually temperature dependent, beetle dispersal to a new host occurs and the process begins again.

Aggregation, which facilitates host selection and mating, is an important life history strategy of most, although not all, *Dendroctonus* species. Aggregation is often a response to chemicals produced by the host tree, adults from the same or a different species attacking the host tree, microbes, or a combination of these factors. Aggregation on a single host tree allows for a mass attack by conspecific beetles, thereby overcoming the resin defensives of the conifer hosts. To overcome the defenses of healthy, vigorous hosts, many beetles must attack within a short time (1–3 days). Conversely, trees of poor health may be overcome by fewer beetles (e.g., endemic population levels). Because a single tree is a limited resource, some *Dendroctonus* species have evolved a response to a series of chemicals that interrupt aggregation. These chemicals act to space beetle attacks along a single tree and signal incoming beetles to begin attack on another, nearby tree. Synthetic forms of both attractive and interruptive aggregation chemicals have been developed for many *Dendroctonus* species. The attractive aggregant chemical(s) are commonly used, often with traps, for monitoring and control of many economically important species in the genus. The complexity of the signal for interruption of aggregation has made it difficult to identify the chemical makeup of compounds, as well as, the specific biological action of the compounds within the population ecology of many *Dendroctonus* species. Consequently, the current use of synthetic interruptive aggregation chemicals is limited.

As with most poikilothermic organisms, temperature is a strong driving force of *Dendroctonus* population dynamics and an important controller of seasonality. Diapause, which is often temperature related, is typically considered the universal adaptation of insects for maintaining seasonality. However, with the exception of an adult reproductive diapause in *D. rufipennis* and *D. pseudotsugae*, and a prepupal diapause in *D. rufipennis*, this physiological timing mechanism appears to be absent in the *Dendroctonus* genus. Instead, *Dendroctonus* seasonality appears to be under direct temperature control. Life cycle duration in the genus is variable depending on the species, latitude, elevation, and microclimate of the population. Species in the south can have as many as seven generations per year, whereas in the north, or at high elevation some species require up to 3 years to complete a single generation. Intraspecific latitudinal differences in many temperature-associated life history traits exist as well. Global climate warming will undoubtedly have significant impacts on the distribution and seasonality of the *Dendroctonus* species.

Many *Dendroctonus* species carry spores of symbiotic fungi either passively on the exoskeleton or in specialized structures of the integument called mycangia. The fungi are disseminated among host trees via adult *Dendroctonus* beetles. Although little research has been conducted on fungal associations of the majority of *Dendroctonus* species, the work that has been done shows both a benefit and a detriment to the beetle, depending on the particular fungal associate. Benefits gained include protecting the beetle brood from other antagonistic associates, aiding beetles in overcoming host tree defenses through pathogenic action of the fungi, altering the moisture composition of the phloem, and providing or concentrating nutrients essential for reproduction or development.

Native *Dendroctonus* bark beetles play significant roles in long term forest ecosystem function and structure. However, forest conditions in many parts of the *Dendroctunus* range in North America have changed from conditions that existed prior to pre-European colonization. The result is large landscapes vulnerable to *Dendroctonus* outbreaks which are often in conflict with current land use objectives. The formulation of effective management strategies for *Dendroctonus* populations requires careful consideration of all aspects of land use including timber production, the urban/wildland interface, wilderness, watershed, recreation and wildlife. Synthetic attractive and interruptive aggregation chemicals and silvicultural options are available for some species to aid in the prevention and suppression of large scale outbreaks. Any action, including no action, should be tightly tied to the management objectives for the landscape under consideration. Restoration of the landscape to reestablish ecological integrity after an outbreak is also important for maintaining long-term ecosystem health.

► Mountain Pine Beetle
► Douglas-Fir Beetle
► Roundheaded Pine Beetle

References

Coulson RN, Witter JA (1984) Forest entomology, ecology and management. Wiley, New York, NY, 669 pp

Mitton JB, Sturgeon KB (1982) Bark beetles in North American conifers, a system for the study of evolutionary biology. University of Texas Press, Austin, TX

Schowalter TD, Filip GM (1993) Beetle-pathogen interactions in conifer forests. Academic Press, London, UK. 252 pp

Samman S, Logan J (2000) Assessment and response to bark beetle outbreaks in the rocky mountain area. Report to Congress from Forest Health Protection Washington Office, Forest Service, U.S. Department of Agriculture. USDA Forest Service, Rocky Mountain Research Station, General Technical Report RMRS-GTR-62

Seybold SJ, Bohlmann J, Raffa KF (2000) Biosynthesis of coniferophagous bark beetle pheromones and conifer isoprenoids: evolutionary perspective and synthesis. Can Entomol 132:697–753

Wood SL (1982) The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. Great Basin Naturalist Memoirs, Number 6 Brigham Young University Provo, UT, 1359 pp

Bark-Gnawing Beetles

Members of the family Togossitidae (order Coleoptera).

► Beetles

Bark-Lice, Book-Lice or Psocids (Psocoptera)

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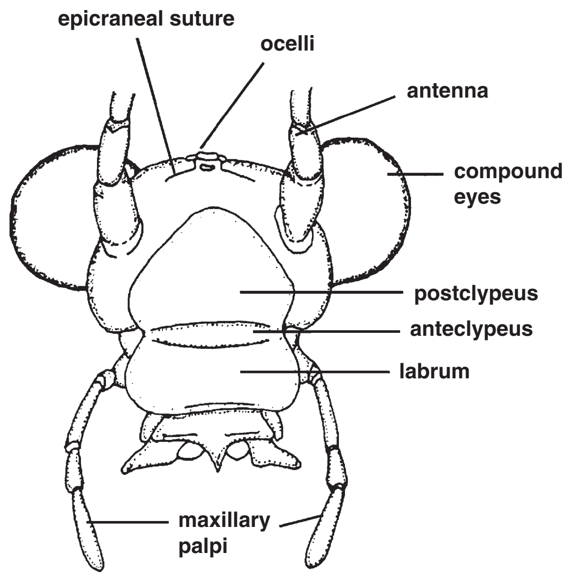
The insects of the order Psocoptera (=Copeognatha, Corrodentia) are commonly called psocids, although outdoor species living on tree trunks and branches have been called bark-lice, whereas indoor species, sometimes found in old books, have been called book-lice. The Psocoptera are a small order of paraneopteran insects (near 4,000 species have been described around the world) which are found in a wide range of terrestrial ecosystems throughout the world. Most psocids inhabit trees and shrubs, some others occur in ground litter, others are found on rocks and in the nests of birds and mammals. Some live on herbs and grasses, and a few in moss, whereas others are found in caves. Lastly, several species are found in domestic habitats. The Psocoptera share certain morphological features with the lice (orders Mallophaga and Siphunculata; Phthiraptera of some authors), and these taxa are grouped together in the superorder Psocodea by some authors. Fossil insects identified as psocids have been reported from as far back as the Permian period in Kansas, Russia and Australia. These, together with Jurassic material from Germany and Russia, differ in many ways from more recent forms. So, although these fossils are quite psocid-like, some doubts exist about their ordinal placement. The earliest unquestionable fossil psocids are those from Cretaceous amber. These Cretaceous forms are essentially modern and do not show any clear connections with the older fossils of doubtful assignment.

Morphology

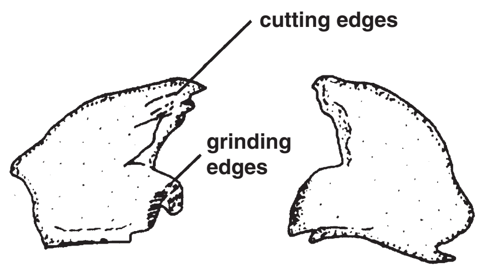
Psocoptera are free-living exopterygote insects ranging in body length from 0.6 to 25 mm, although rarely exceeding 10 mm.

Head

The head capsule is large compared to the rest of the body, with a large bulbous postclypeus. The antennae are long and filiform with 11–50 flagellomeres. The eyes commonly are large and globose, varying from multi-faceted structures down to the complete reduction in a cavernicolous species. Three ocelli are usually present in winged forms, but absent in apterous species. The Y-shaped epicraneal suture is prominent. The mouthparts (Figs. 6–10), although retaining a chewing function, are specialized. The mandibles are asymmetrical, and each has both grinding and cutting edges. In the maxillae the cardo is not differentiated; the galea is a large, fleshy lobe, whereas the lacinia is a narrow, sclerotized rod (the pick). The lacinia is perhaps the most specialized and characteristic psocid structure. The lacinia may be used to scrape food from the substrate, but such has not been directly observed. Some authors inferred that the lacinae may be used as "picks," because psocids move laciniae vertically in a manner which suggests this may be so. Also, they appear to be used to support the head whilst feeding and may act to regulate the depth of feeding on the substrate. The maxillary palpi are 4-segmented.

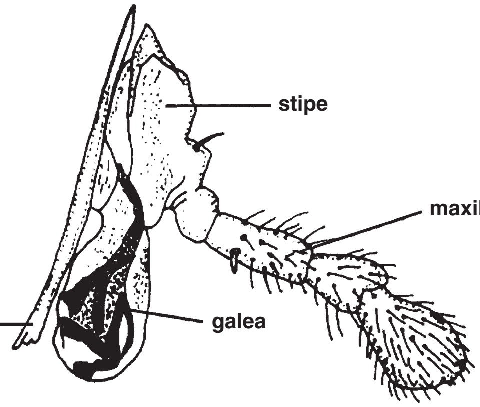


Bark-Lice, Book-Lice or Psocids (Psocoptera), Figure 6 Head of ***Stenopsocus stigmaticus*** in frontal view.

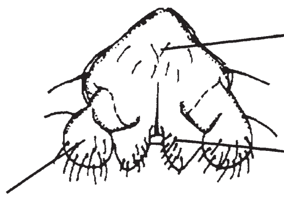


Bark-Lice, Book-Lice or Psocids (Psocoptera), Figure 7 Mandibles of ***Cerobasis guestfalica.***

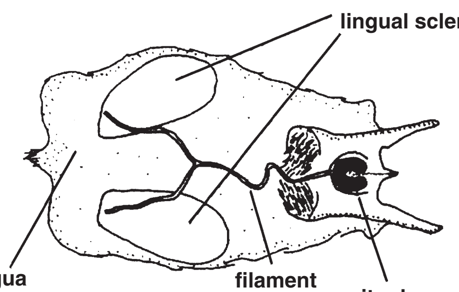
The labium has reduced one- or 2-segmented palpi, and the chitinous mentum is divided apically into lateral halves (paraglossae) by a small protuberance (glossa) representing the opening of the salivary glands to the exterior. The labrum is simple, with the distal margin bearing two groups of setae: an anterior group of 4–10 sensilla, and a posterior group which has some taxonomic value. The palatal lining of the labrum and the anteclypeus is the hypopharynx, which has a characteristic structure. The lingua bears a pair of ventral sclerites (lingual sclerites) which are connected to the median sitophore sclerite by ligaments; these lingual sclerites when protruding are capable of taking up water from the atmosphere (Fig. 11). The sitophore sclerite is situated on the ventral surface of the base of the cibarium. On



Bark-Lice, Book-Lice or Psocids (Psocoptera), Figure 8 Left maxilla of ***Cerobasis guestfalica.***



Bark-Lice, Book-Lice or Psocids (Psocoptera), Figure 9 Labium of ***Cerobasis guestfalica***.

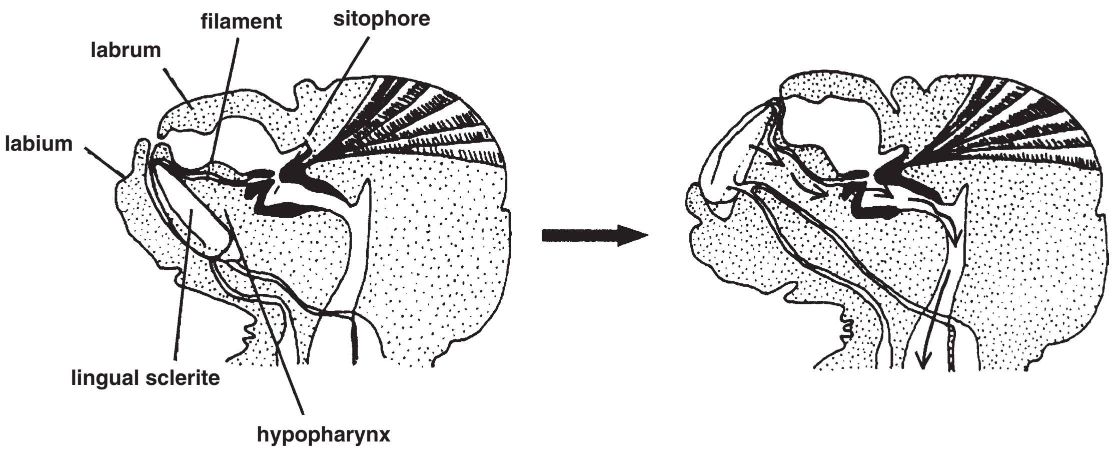


Bark-Lice, Book-Lice or Psocids (Psocoptera), Figure 10 **Hypopharynx.**

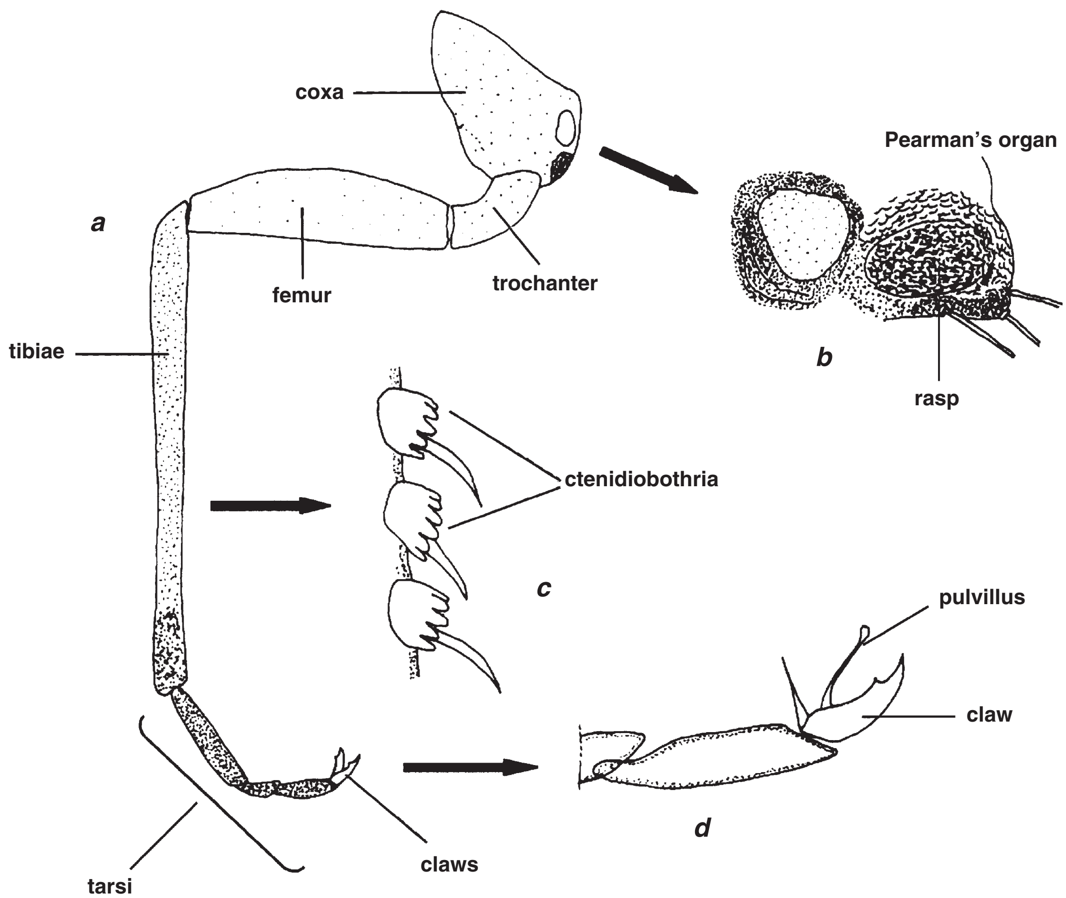
the dorsal surface of the cibarium wall (opposite the sitophore) is a knoblike process that is believed to move against the sclerite in the manner of a mortar and pestle and facilitate the grinding up food.

Thorax

The thorax unites to the head with a membranous and flexible neck. In a general way, the prothorax of both winged and apterous psocids is clearly separated from the other thoracic segments. Legs are slender, and hind legs are longer, which allows them to carry out small jumps. The coxae of hind legs are modified in many species by having cuticular projections of various kinds. The most usual are a small blister-like projection on the inner surface, an ovoid "rasp" bearing rows of small denticles; in some cases near the "rasp," a rounded area of similar size can be found. These structures are called "coxal organs" or "Pearman's organs" (Fig. 12) and the function is unknown, although it has been suggested that they are stridulatory. The small trochanters are articulated with the coxae but their junction with the femora is usually immovable. The femora are simple, but sometimes markedly convex on their outer surface. Tibiae may have a row of characteristic ctenidiobothria (setal sockets, having four to ten conspicuous teeth, with each bearing a simple spine) along the ventral surface. The tarsi are of either two or three segments (all the immatures possess two segments and this character remains in some adults); all except the apical segment have apical spines, and ctenidiobothria may be present on the basal or all segments. The tarsus terminates in a pair of claws; the base of each claw usually has two ventral projections: the proximal one is setiform and the distal (the pulvillus) is of various forms. Some pulvilli are greatly expanded, whereas others are slender or narrow. Expanded pulvilli can act as a



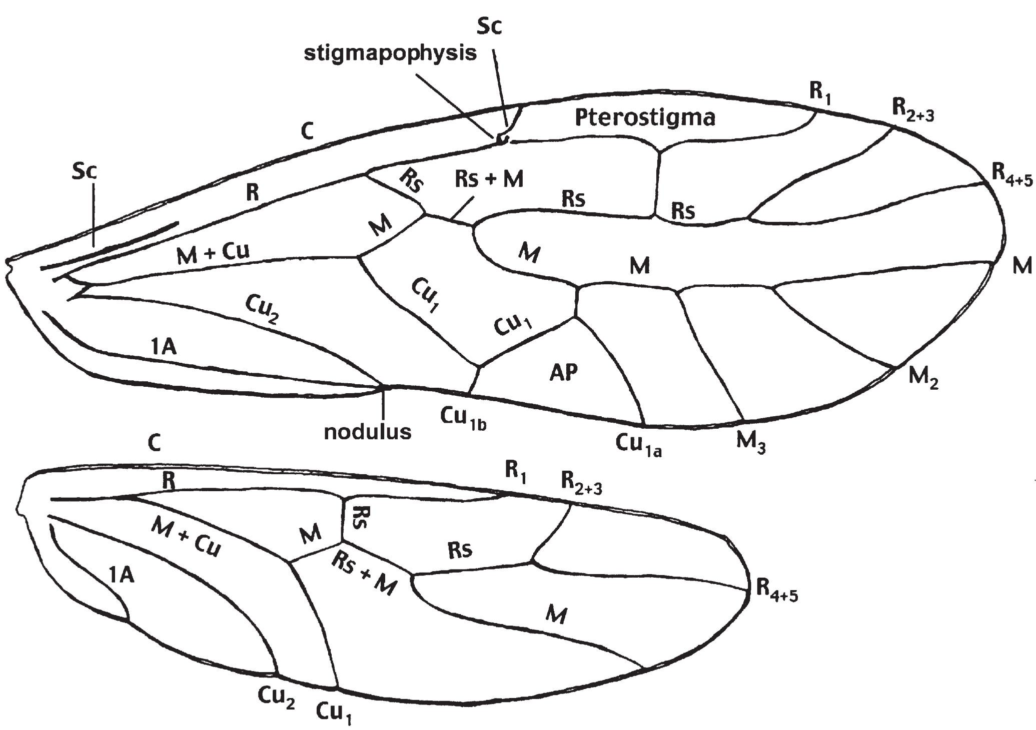
Bark-Lice, Book-Lice or Psocids (Psocoptera), Figure 11 Mechanism of absorption of atmospheric water.



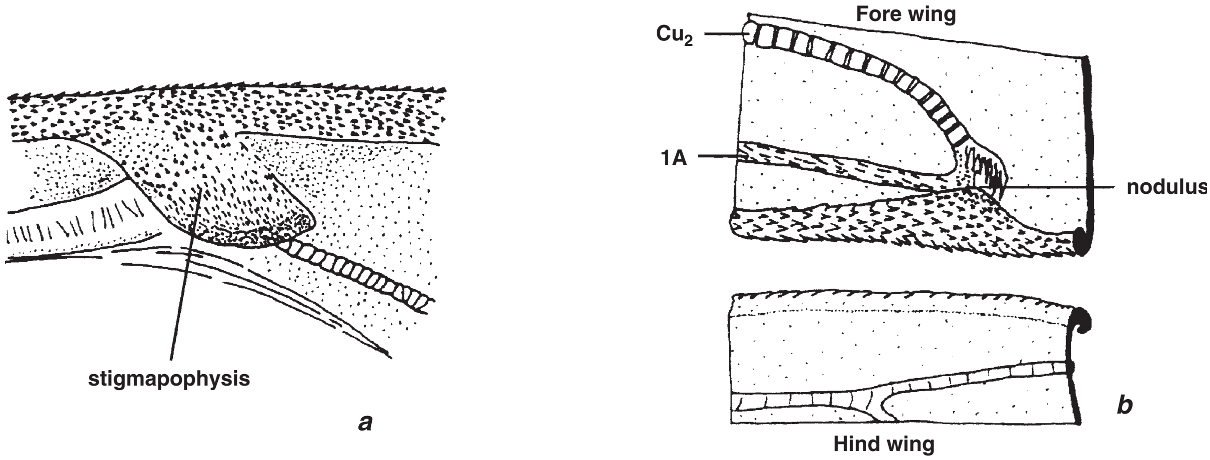
Bark-Lice, Book-Lice or Psocids (Psocoptera), Figure 12 Metathoracic leg (**a**); Pearman's organ of ***Psococerastis gibbosa*** (**b**); ctenidiobothria from a metathoracic tibia (**c**); detail of a metathoracic tarsus (**d**).

sucker, enabling the insect to walk on smooth surfaces. Most foliage-frequenting psocids have a pulvillus of this type, whereas most bark-frequenters have a narrow pulvillus. Two pairs of wings (Fig. 13) are found in many psocids, although one or both pairs may be reduced in size, showing various states of reduction (brachyptery, micropterty) and sometimes absent (aptery). Some species are dimorphic, with macropterous individuals of one sex (usually males) and apterous or micropterous individuals of opposite sex (usually females). The anterior wings are larger than the hind pair. At rest they are held rooflike over the body. The fore and hind wings are coupled during flight and at rest. Most psocids have simple venation, with few crossveins.

In the forewing, the costa (*C*) forms the wing margin. The subcosta (*Sc*) is often greatly reduced to a small vein at the base of the wing (the basal sector) and a short vein closing basally the pterostigma (the distal sector). The radius (*R*) runs more or less parallel to the costa and forms the posterior border of pterostigma. The radial sector (*Rs*) terminates in an apical fork, named the radial fork, which is composed of R_{2+3} and R_{4+5}, and contacts the median (*M*) in the middle of the wing. At this junction, the two veins (*Rs* and *M*) may meet in a point, be linked by a short crossvein or be fused for a short length. M usually has three branches (M_1, M_2, M_3). The first cubital vein (CU_1) reaches the posterior border of the wing, sometimes simply, but in many psocids it is two-branched, forming a cell known as "areola postica" (*AP*), which is bordered by CU_{1a} and CU_{1b}. The presence and shape of the "areola postica" vary considerably in different groups of psocids, and it may be joined to the median, or fused with it or completely free. The second cubital vein (CU_2) is morphologically distinct from the more anterior veins. It is simple and unbranched. Behind this is one anal vein (*1A*), which reaches the wing margin near the same point as CU_2. When the vein *1A* reaches the margin at the same point as CU_2 it forms the "nodulus." In a few groups a small second anal vein (*2A*) is



Bark-Lice, Book-Lice or Psocids (Psocoptera), Figure 13 Wings of ***Stenopsocus stigmaticus.***



Bark-Lice, Book-Lice or Psocids (Psocoptera), Figure 14 Stigmapophysis from the ventral surface of the forewing in *Cerastipsocus* sp (a); joining system of the wings of *Lachesilla* sp. (b).

present. The cells take the name of the vein immediately anterior to them. The one exception is the large "discoidal cell" bordered by *M* and *Cu1*, and present in the forewing of the family Psocidae and others forms in which *AP* is joined to *M*. In the hind wing the venation is more reduced. *Sc* is often vestigial, R_1 reduced and simple, *Rs* forked in two branches as in the forewing, *M* usually simple but sometimes having two branches, both cubital veins are simple, and one small anal vein is usually present. As in the forewing, the form of the *R-M* junction can be variable. Of particular interest is the fact that in the families Lepidopsocidae and Amphientomidae the forewings are typically covered by scales, and give the insect the appearance of a small moth. In this case, the shapes of scales are sometimes of specific value. Psocids possess two independent methods of wing coupling. At rest, some species have a protrusion at the base of the pterostigma on the underside of the forewing, formed from modified trichia and tracheolar rings of R_1; this projection (known as "stigmapophysis") engages the costal vein of the hind wing in repose (Fig. 14). Similar structures for coupling wings in repose can be found in the family Lepidopsocidae, where it is composed of a row of comb-like teeth on *Sc* or R_1. When they fly, many psocids have another mechanism for coupling wings. Underside the forewing the distal end of Cu_2 possess a hook which engages the hind costa in flight.

Abdomen

The abdomen consists of ten segments and the terminal region (telson) formed by three lobes: the epiproct which is dorsal and the paraprocts which are lateral. In many psocids the last tergite (tg 9 + 10) and the distal half of tergite eight are strongly sclerotized, forming a structure called the clunium. The epiproct is, normally, a very simple structure, of rounded, trapezoidal or triangular shape in both sexes. In some species, the male epiproct bears rows or fields of hooks or denticles. The paraprocts are variable in shape. On the dorsal basal region there is often a well-defined area (sensorial field) containing long setae each rising from a sunken rosette-like socket. These setae are called "trichobothria" and are, presumably, involved in the orientation in flight or air currents. Near the apex of the paraprocts of the Trogiomorpha is a long, thickened spine (anal spur).

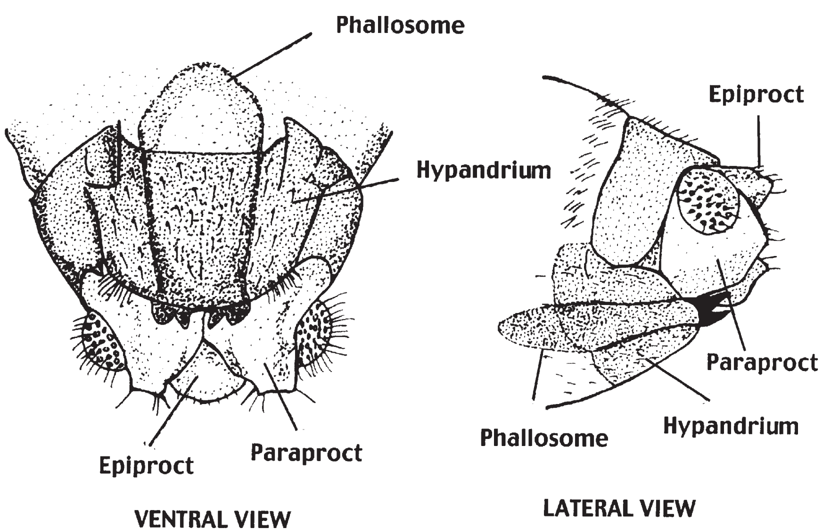
Male genitalia comprise a hypandrium (male subgenital plate) and a phallosome (copulatory apparatus). The hypandrium is an expansion of the 9th sternite, defining a cavity in which lodges the phallosome. The hypandrium varies from a broad shield, varying from slightly convex and weakly sclerotized to a strongly convex and heavily sclerotized, and bearing apophyses of different kinds. The phallosome (Figs. 15 and 16) comprises the endophallus, the parameres and the aedeagus. The endophallus is a membranous structure which is everted during copula. Its surface is adorned with small sclerites (radulae). The parameres are symmetrical, sclerotized structures with small pores sensilla on the distal end. From each paramere an inner branch often protrudes; these branches are fused apically, forming a sclerotized arch (the aedeagus).

Female genitalia comprise, in the majority of species, a subgenital plate, one pair of gonapophyses from the 8th segment (ventral valvulae), two pairs of gonapophyses from the 9th segment (dorsal valvulae and external valvulae), the modifications of the 9th sternite around the spermapore, and the spermatheca or "receptaculum seminis" (Fig. 17). The subgenital plate is a extension of the 8th sternite; commonly it is a large broad plate having the apical margin rounded. However, in many groups a pronounced median posterior lobe is present which has (Fig. 17) been termed the "egg guide." The ventral valvulae are shorter than the others, glabrous, and apically pointed. The dorsal valvulae run parallel to the ventral valvulae, and sometimes resembles it in appearance. The external valvulae are attached to the surface of the base of the dorsal valvulae, and commonly are broad and setose. The spermapore (female gonopore) opens between the gonapophyses in the 9th sternite. Sometimes the cuticle around the spermapore is heavily sclerotized to form a distinct plate (spermapore plate).

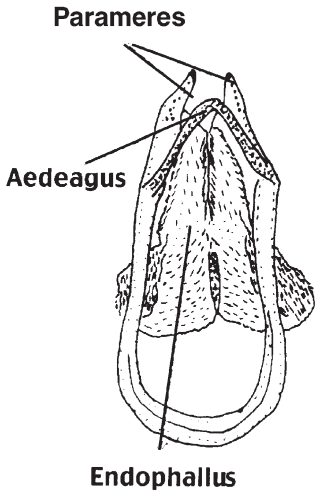
The internal structure of psocids resembles that of other insects. The tracheal system usually opens to the exterior by means of two pairs of thoracic and eight pairs of abdominal spiracles. Four Malpighian tubules are attached at the posterior end of the midgut. The nervous system is very simple and comprises the following ganglionar centers: brain, subesophageal ganglion, prothoracic ganglion, pterothoracic ganglion and the abdominal ganglion. The reproductive system in females comprises two ovaries, each with three to five polytrophic ovarioles, lateral oviducts which open into a larger median duct, and a spermatheca. In the males the testes are round or three-lobed.

Systematics

Living Psocoptera are divisible into three well-defined suborders: Trogiomorpha, Troctomorpha and Psocomorpha. The earliest fossils from the



Bark-Lice, Book-Lice or Psocids (Psocoptera), Figure 15 **Male terminalia of *Mesopsocus unipunctatus.***

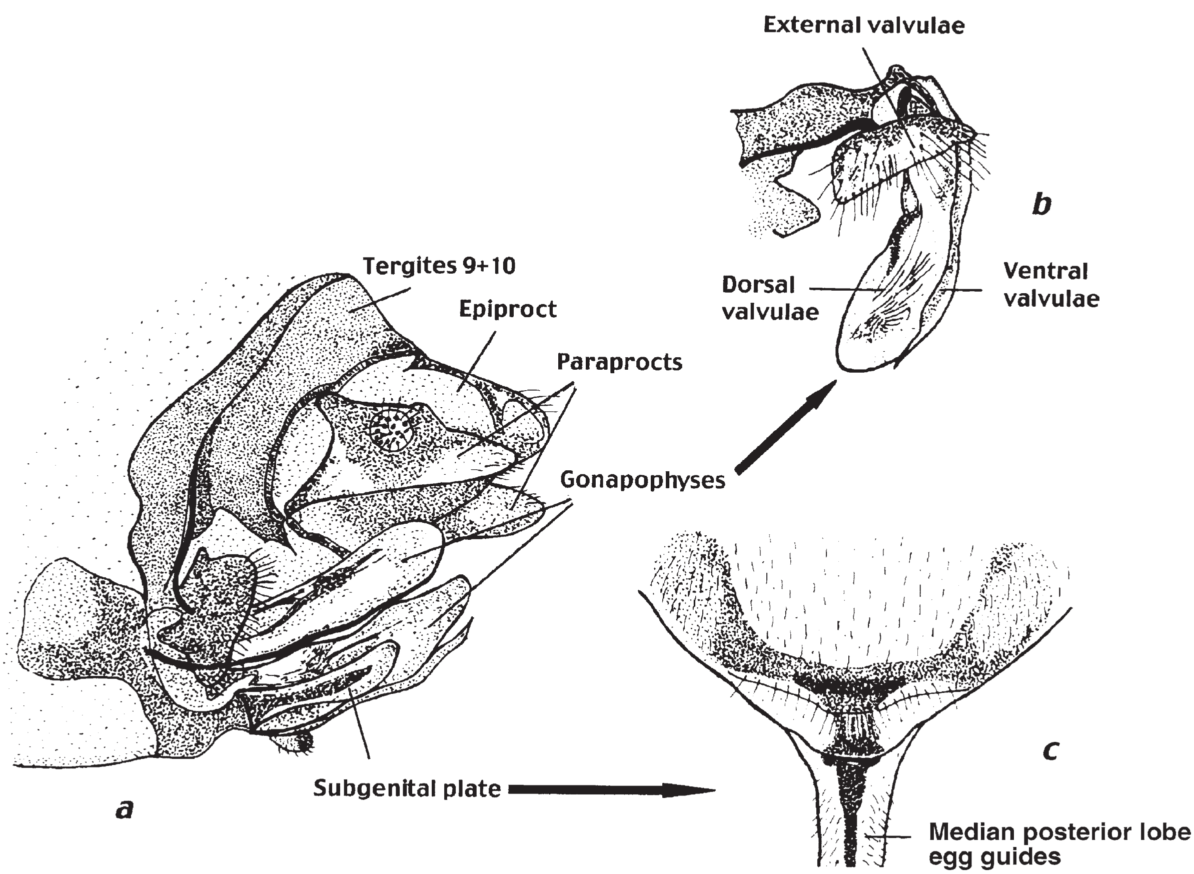


Bark-Lice, Book-Lice or Psocids (Psocoptera), Figure 16 Phallosome of ***Elipsocus*** **sp.**

Lower Permian of Kansas, regarded as Psocoptera by some authors, differ from modern species in wing venation and mouthpart characters. Thus, they have been placed in a distinct suborder, Permopsocina. The Trogiomorpha contain the most primitive forms, and the Psocomorpha the most advanced.

Suborder: Trogiomorpha

Diagnostic characters of Trogiomorpha are as follows: antennae with more than 20 segments; hypopharyngeal filaments separate, never fused on midline; tarsi of the adults 3-segmented; labial palps 2-segmented; pterostigma not thickened



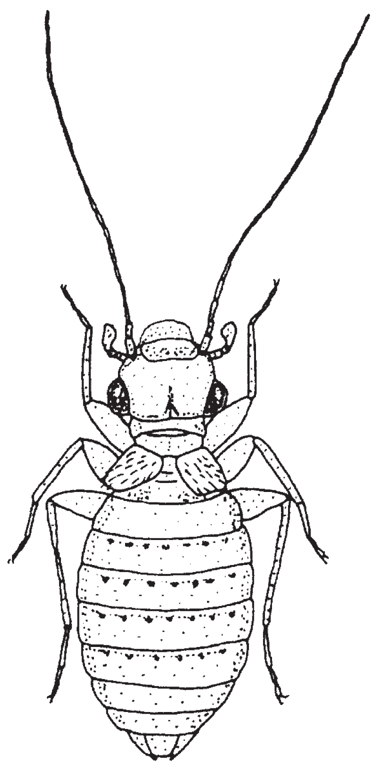
Bark-Lice, Book-Lice or Psocids (Psocoptera), Figure 17 **Female terminalia of *Metylophorus nebulosus* in lateral view (a); detail of the gonaphyses of *Metylophorus nebulosus* (b); detail of the subgenital plate of *Metylophorus nebulosus* (c).**

or absent; and paraprocts with strong posterior spine.

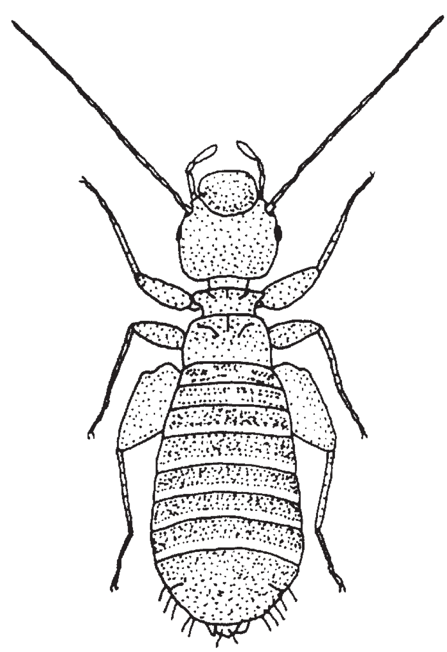
This suborder (Fig. 18) contains five families into two family groups: Atropetae (Lepidopsocidae, Trogiidae and Psoquillidae) and Psocatropetae (Psyllipsocidae and Prionoglarididae). Lepidopsocidae (the major family of the suborder) form a primarily tropical group of bark- and leaf-litter inhabiting forms recognized by their moth-like appearance caused by the scales that cover their body and wings. Trogiidae comprise species with reduced wings (apterous or brachypterous); this cosmopolitan family includes several domestic species, in particular *Lepinotus* sp., which causes great infestations in granaries and warehouses. Psoquillidae and Psyllipsocidae are both small and widely distributed families. Psoquillids are commonly found on bark whereas Psyllipsocids occur in caves or leaf-litter. Both families include some domestic species; for instance, some species of the genus *Dorypteryx* (Psyllipsocidae) are exclusively found in domestic situations. Lastly, the Prionoglarididae are a small family containing three genera (*Prionoglaris* from the Palaearctic, *Speleketor* from the United States and *Sensitibilla* from Namibia) and seven species. The members of these families live almost exclusively in caves or under stones.

Suborder: Troctomorpha

Characters of Troctomorpha (Fig. 19) are: antennae with 14–15 segments, rarely with fewer segments (the only exception is the Palaearctic genus *Nephax* which possess antennae of 13 segments), the flagellar segments beyond the fifth usually with secondary annulations; hypopharynx with filaments separated only in distal region; tarsi 3-segmented; labial palps 2-segmented; forewing, when present, lacking sclerotized pterostigma.

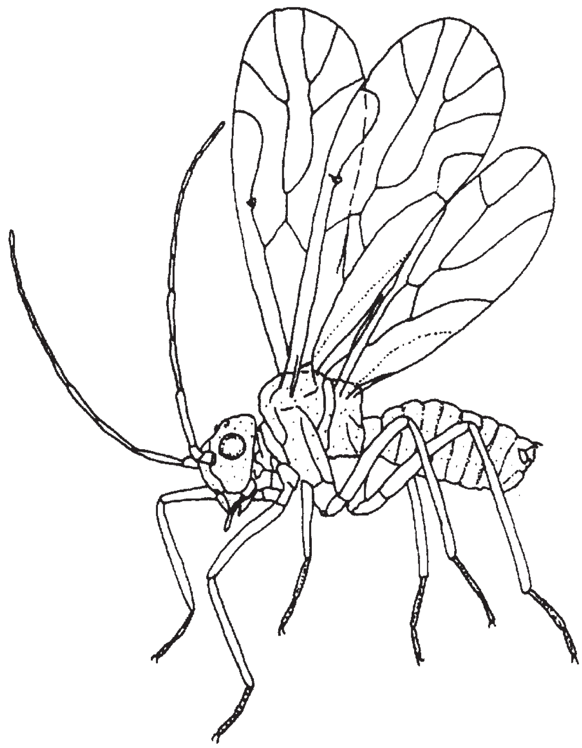


Bark-Lice, Book-Lice or Psocids (Psocoptera), Figure 18 ***Trogium pulsatorium*** **(Trogiomorpha).**



Bark-Lice, Book-Lice or Psocids (Psocoptera), Figure 19 ***Liposcelis bostrychophila*** **(Troctomorpha).**

This suborder contains eight families in two family groups: Amphientometae (Musapsocidae, Troctopsocidae, Manicapsocidae, Compsocidae and Amphientomidae) and Nanopsocetae (Liposcelididae, Pachytroctidae and Sphaeropsocidae). The largest families in this suborder are the Liposcelididae (near 150 species), Amphientomidae and Pachytroctidae. The Liposcelididae are a cosmo-politan group of apterous psocids (although a few species possess reduced wings) whose members are recognized by their small size (1–2 mm) and their greatly enlarged hind femora. The family includes a number of common booklice (*Liposcelis* spp.) found in houses, warehouses and ships holds where they may cause measurable weight loss and quality deterioration in stored grain. Some authors concluded that *Liposcelis* spp are secondary pests of grain whose diet is supplemented by mold. Outdoor species occur in leaf-litter and under bark. The other families are mainly tropical, occurring in both the Old and the New World.



Bark-Lice, Book-Lice or Psocids (Psocoptera), Figure 20 ***Lachesilla pedicularia*** **(Psocomorpha).**

Suborder: Psocomorpha

This suborder is characterized by possessing antennae with 13 or fewer segments, never with secondary annulations. The labial palpus is 1-segmented, lacking-basal segment. The hypopharynx has chitinous filaments separated in posterior region. The forewings usually are present, with sclerotized pterostigma. Adults have 2- or 3-segmented tarsi.

This very large suborder contains nearly 80% of all known species of Psocoptera. It consists of 23 families, in four family groups: Epipsocetae (Epipsocidae, Dolabellopsocidae, Ptiloneuridae and Cladiopsocidae). Epipsocidae are the largest family of this group with 133 described species, mostly tropical and subtropical in distribution. In some species, females are apterous or brachypterous. Most species live in particularly damp situations: under stones, in caves, on dead branches in humid forests, or in damp leaf litter. The family group Caeciliusetae comprises the following families: Asiopsocidae, Caeciliusidae, Stenopsocidae and Amphipsocidae. The Caeciliusidae are one of the largest families of Psocoptera, with nearly 400 known species. It is a family of worldwide distribution, in which most species are foliage dwellers. Amphipsocidae (150 species) are a large family widely distributed in the Old World (a few species can be found in the Americas); these psocids are generally found on broad-leaved foliage. The group Homilopsocidea was erected to hold those families which could not easily be associated with families in the other family groups. The result is a heterogeneous assemblage of 11 families (Lachesillidae, Ectopsocidae, Peripsocidae, Calopsocidae, Pseu-docaeciliidae, Bryopsocidae, Trichopsocidae, Elipsocidae, Philotarsidae, Mesopsocidae and Archipsocidae). Most of these families are of cosmopolitan distribution and can be found forming part of the psocid faunas around the world. Lachesillidae consist of more than 250 species (most of them living in the Americas), primarily found in dry foliage. Some species (e.g., *Lachesilla pedicularia*) are widely distributed, occurring in granaries, warehouses and human habitations, occasionally in great numbers. Ectopsocidae and Peripsocidae are two closely related families, and are cosmopolitan in distribution (although Peripsocidae are more diverse in the Oriental region). Some species of Ectopsocidae (*Ectopsocus briggsi*) and Trichopsocidae (*Trichopsocus clarus*) are commonly found on fruit-bearing trees, and possibly are involved in the transmission of pathogenic fungi. Pseudocaeciliidae and Archipsocidae are mainly tropical groups. Some species of Archipsocidae live in massive aggregations under sheets of webbing that may cover an entire tree. Philotarsidae live on bark or low vegetation. Members of this family can be found around the world but are especially common in the Oriental region. Elipsocidae and Mesopsocidae are bark inhabitants, and also may be found in many types of bushes. Both families are abundant in temperate regions.

Lastly, the family group Psocetae consists of four families (Psocidae, Psilopsocidae, Myopsocidae and Hemipsocidae). Psocidae are the largest family in the order with near 600 known species. It is a cosmopolitan group of psocids which are, in a general way, darkly colored and live on bark or, occasionally, on the ground or under stones. Myopsocidae (near 150 species) are large, tropical Psocoptera living on bark. The members of this family usually have densely spotted brown wings.

Reproductive Biology

Courtship and Mating

Many observations of courtship in various species of psocids show that elaborate behavior patterns may be involved, and that behavioral differences may constitute effective isolating mechanisms for closely related species. In a general way, mating it is preceded by the male nuptial dance, in which the male describes circles around the females. Simultaneously, males vibrate the wings or, in apterous species, vibrate the antennae. Courtship requires a variable time (2–20 min) and is followed by mating. The male approaches the female from the side or from behind, passes over her in a forward direction, then backs underneath, and copulation ensues. The copulation has a variable duration, ranging from the 5–10 s (as observed in *Stenopsocus stigmaticus*) to 2–4 h in the Trogiidae. Copulation length depends on the degree of complexity of the genitalia, and the sperm transmission mode. In the species with extremely short copulation, the terminalia are very simple and little sclerotized in both sexes. Also, the spermatophore is directly deposited on the atrium from which the sperm is transferred to the spermatheca. In other species the coadaptation of the genital apparatus is more intense, which explains the long duration of copulation. In the Atropetae and the Amphientometae, sperm are transferred in a liquid medium into the spermatheca within a structure called a "sperm packet." This structure apparently is formed by glandular secretions of males and females, a process that lengthens the duration of the copulation.

Eggs, Oviposition, Hatching, Viviparity, Parthenogenesis

Eggs of Psocoptera are often simple, elongate ovoids or cylinders without a micropyle, and usually are smooth, lacking any conspicuous sculpture. In the more primitive psocids, however, eggs have pronounced areolate folds or a crest on the upper surface. Observations on psocid eggs allow us to recognize four categories of egg deposition:

1. Eggs laid bare: (a) webbed, (b) not webbed.
2. Eggs encrusted with material from the digestive tract: (a) webbed, (b) not webbed.

There is a systematic and an ecological basis for the pattern of egg deposition. Thus, species which are open bark inhabitants (as Psocidae) lay unwebbed encrusted eggs, whereas leaf inhabiting species (Caeciliusidae, Pseudocaeciliidae) usually lay bare, webbed eggs.

Batch size varies considerably, but egg number is constrained by the fact that two follicles mature in each ovariole at once, thus imposing a maximum batch size (for example, 12 eggs in *Graphopsocus*; 16 in *Caecilius* and *Stenopsocus*, and 20 in *Ectopsocus briggsi*). However, larger batches are occasionally laid by such species (32 eggs in the first batch of an individual of *Graphopsocus cruciatus*). This is a rare phenomenon, but occurs because the presence of two eggs in an ovariole does not inhibit maturation of further follicles.

Hatching is accomplished with the aid of a specialized egg burster on the frontal region of the pronymph. This egg burster has the form of a blade or tooth, or a row of several spines. By pushing this structure against the egg cuticle, the pronymph creates a hatching orifice, and the nymph is partially extruded through this orifice. The first instar then emerges from the pronymphal cuticle attached to the hatching orifice.

Viviparity is an unusual habit in the psocids. Only a few species are known as viviparous. In the best-known viviparous genus of psocids (*Archipsocopsis*), females lack gonapophyses and the abdomen may contain more than a dozen embryos in different stages of development. Eggs remain in the ovarian tubules and pass down the common oviduct to the exterior.

Parthenogenesis in psocids is widespread. The usual form of parthenogenesis is obligatory thelytoky, although a few examples of facultative thelytoky are known. This mode of reproduction is known in at least 12 families, representing all three suborders. However, the situation actually is more complex, as demonstrated by *Caecilius flavidus* and *Psocus bipunctatus* (two European species). These species consist of two races, one bisexual and other parthenogenetic. Females of the parthenogenetic race in the presence of males of the bisexual race provoke no reaction from the males, whereas the introduction of a female of the bisexual race is immediately followed by a nuptial dance by the males, which eventually results in copulation. Meanwhile, the parthenogenetic females remain indifferent. This incompatibility of the races within the same species could be the rule in all Psocoptera possessing such biologic races, driving reproductive isolation of the races. This ultimately can be responsible for speciation. More recently, in the common domestic psocid pest *Liposcelis bostrychophila* dense concentrations of small bacterial inclusions have been found. These bacteria are tentatively identified as *Wolbachia*, a genus implicated in changes in reproductive function (in which parthenogenetic reproduction is included) in many other insect groups.

Postembryonic Development

The juvenile instars of psocids (nymphs) generally resemble adults in body form and markings. They lack functional ocelli, never have more than two tarsomeres, and early instars have fewer flagellomeres than adults of their species. Nymphs of some genera of the families Troctopsocidae, Psocidae and Myopsocidae have gland hairs, which in some cases retain bits of debris, thus forming a camouflaging coat over the body surface. The usual number of nymphal instars in psocids is six for the two sexes, but this can be reduced to five (micropterous form of *Psyllipsocus ramburii*), four (apterous females of *Embidopsocus enderleini*) or, more rarely, three (apterous males of *Embidopsocus enderleini*). The reduction of instars number is frequently associated with alary polymorphism, in which some species with sexual alary dimorphism differ in instar number between sexes: the apterous sex having one less instar than the macropterous one. Also, the reduction of the number of larval stages is generally regarded as a case of neoteny, and associated with the reduction of other characters (lack of ocelli, only two tarsomeres and reduction in numbers of ctenidiobothria and paraproct trichobothria).

Feeding

Psocids are herbivores or detritivores, feeding on microflora and organic debris on the surface of vegetation and other substrates. They are among a relatively small number of insects that actively exploit these food resources (according to some authors, the psocids together with the Collembolans constitute the guild of epiphyte grazers). The primary components of their diet are green algae of the genus *Pleurococcus*, lichens (especially corticicoles and lapidicoles) and fungal spores and hyphae. Although it is common to find pollen grains in their alimentary tract (mainly of coniferous trees), detritus of all types and even remains of dead arthropods (probably already in decomposition) are consumed. A few psocids are partial predators, taking insect eggs and possibly scale insects. The differences in the diet depend on the habitat occupied by the species. For example, the bark-inhabiting psocids feed on pleurococcine algae and lichens. Leaf-inhabiting psocids feed primarily on small leaf fungi, and often ingest small amounts of leaf tissue with the fungal hyphae. Domestic psocids feed on mold that develops on the organic matter found on furniture in dwellings, and on the rotted wood and the old papers found in basements. Psocids that live in the kitchens of houses become consumers of stored food (flour, cereals, rice, bags of tea, etc.).

Natural Enemies

Parasites

The intestine of most species contains gregarines (Protozoa) fixed to the intestinal wall. These gregarines are also found in the feces, and can infect other individuals.

Psocids have been mentioned occasionally as intermediary hosts of tapeworms (Cestoda). Cestode larvae of the genera *Thysanosoma*, *Thysaniezia* and *Avitellina*, have been found in various psocid species of the genera *Lachesilla*, *Lepinotus*, *Liposcelis*, *Ectopsocus* or *Rhyopsocus*.

Other organisms parasitizing psocids are nematodes that live in the abdominal cavity, and fungi of the order Entomophtorales (species of the genus *Erynia*).

Parasitoids

The parasitoids of psocids are Hymenoptera attacking both eggs and nymphs.

Parasitic Hymenoptera that attack the eggs belong to the genus *Alaptus* (Mymaridae), and include several species. In general, only a few eggs of each batch are parasitized, and each egg contains only a single individual of *Alaptus*. Some studies reveal that the proportion of parasitized eggs varies between 6–10% although in some species of *Mesopsocus*, proportions of 20–70% have been observed. Parasitic Hymenoptera attacking the nymphs belong to the genus *Leiophron* (Braconidae: Euphorinae). The proportion of parasitized nymphs is sometimes 50–60%, as has been reported in some populations of *Caecilius flavidus* studied in England.

Ectoparasites

The presence of larvae of Acari (genus *Hauptmannia*) living as ectoparasites on psocids has been mentioned. Some phoretic Acari (Phytoseiidae) attached to larvae of psocids have also been described.

Predators

The main predators of psocids are arthropods and vertebrates. Among the arthropods, numerous species that feed on eggs, nymphs or adult psocids have been reported. For example, several arachnids (Acari, spiders, Opiliones, pseudoscorpions) and numerous representatives of various orders of insects (Dermaptera, Heteroptera, Neuroptera, Hymenoptera [ants], Diptera and Coleoptera) are known. The main vertebrate predators on psocids are birds. Many bird species include psocids in their diet, although they represent only a small fraction of the total insect captures: 1.5% in the diet of swifts (*Apus pallidus*) that hunt flying insects, or 3.6% in the diet of treecreepers (*Certhia*) and nuthatches (*Sitta*) that hunt on the trunks of trees.

Occasionally, predation by reptiles has been mentioned, as in the case of an arboricolous lizard in Chile.

Defense Mechanisms

Most psocids possesses features or develop behaviors to avoid parasites and predators. These defense mechanisms can be included in several categories:

First, defense by hiding is called crypsis. Among psocids, many examples can be recognized: eggs covered with silk and detritus helps reduce detection, nymphs with glandular hairs covering the body surface to which detritus adheres, and both adults and nymphs with color patterns matching the substrate where they live. Protective coloration has been well studied in British populations of the species *Mesopsocus unipunctatus*, providing a case of industrial melanism for this species (the darker individuals are more frequent on trees near industrial areas as a consequence of differential predation by birds).

On the other hand, some cases of mechanical defenses are known: the ability of the Liposcelidiidae to run backward swiftly, the surprising jumping abilities of some species (*Dorypteryx*, *Psocathropos*, and the females of *Cyrtopsochus*), or the partial autotomy of the antennal flagellum as have been observed among some species, such as *Prionoglaris stygia*. Some species combine two defense methods. For example, *Hemineura bigoti* blend in well with dried Genista bushes, but *H. bigoti* also shows a hiding behavior that consists of revolving around the *Genista* shoots, thereby keeping out of sight of possible predators.

Some authors suggest the existence of mimicry in some species. The best example is the case of *Chelyopsocus garganicus*, which resembles a beetle, a less consumable species.

Dispersal

Interchange of psocids between different habitats, and extension of habitat or geographical range, occurs frequently and may result from one or more of three interrelated forms of dispersal. These are:

1. Aerial dispersal by flight, as revealed by the abundance and frequency of catches in aerial traps (suction traps or Malaise traps).
2. Passive dispersal. Psocids, like many other small insects, frequently become incorporated in the aerial plankton after active take-off, and may be transported over considerable distances. On the other hand, phoresy of psocids on vertebrates has been observed. Psocids have been recovered from the plumage of several species of birds, and from rats, chinchillas, puppies and humans.
3. Hitchhiking in vehicles or cargoes. This method is probably responsible for the broad occurrence of many domestic species. In fact, most of them are cosmopolitan despite being flightless.

Ecology

Habitats

Psocids occupy a wide range of habitats, although the various habitat categories of psocids intergrade substantially. The following ecological categories hold for a great majority of psocids:

Trees and Shrubs (*Foliage-Frequenting and Bark-Frequenting Psocids*)

Most psocids live on trees and bushes, but not all occupy the same parts of the plant. So, in a general way, we can consider two categories of psocids: foliage-frequenting and bark frequenting.

The foliage-frequenting habitat has been adopted by relatively few species, but some groups use this habitat. Some of them contains species that live on live leaves. The claws of most of these species lack a preapical tooth, and the pulvillus is broad. With the aid of this pulvillus, psocids moves without problems onto flat leaf surfaces. Also, the presence of abdominal vesicles in some species guarantees adherence that is particularly effective against the action of the wind. Other psocids that can also be considered foliage inhabitants are those that live on dead leaves, including those that remain attached to the trees, as well as those that fall to the ground. This habitat (the dead leaves) harbors an epiphytic microflora that is attractive to some psocids (members of the families Lachesillidae and Ectopsocidae). For example, several Brazilian *Lachesilla* species appear to be closely associated with palm foliage, and their numbers are considerably greater on dead foliage than on living fronds. In general, psocid abundance tends to be greater on dead foliage than on living foliage if the two types are available together.

Most of the psocids living on trees are bark-frequenters. In fact, in some areas, psocids are the most abundant animals found feeding on bark surface microfloral communities. Some families are almost exclusively found on this habitat (Psocidae, Myopsocidae, Mesopsocidae, Peripsocidae and Philotarsidae). In these species, the shape of the claws is different: the claws possess a preapical tooth and the pulvillus is, in general, setiform and with the apex pointed, which favors the attachment to a surface more or less rough. Among the psocids living in barks and trunks, an important group is the subcortical psocids, which live under the bark, where they find food and protection. They show morphological adaptations for subcortical existence: extreme dorsoventral flattening with legs inserted laterally, apterism or somewhat thickened forewing held flat on the abdomen (rather than in a more vertical position of other arboreal psocid) and a strong tendency towards alary polymorphism. The principal psocid group of this category is the family Liposcelididae.

Low Vegetation

Some species have a clear preference for low vegetation (herbaceous or woody). This fauna is typically found in those ecosystems where low vegetation predominates (heathers, brooms, gorses, thyme, grasses and herbs). Some examples of true grass-frequenting psocids are *Asiopsocus meridionalis* in semi-arid regions of Spain, *Peripsocus alboguttatus* on heaths in southern Britain, or *Caecilius antillanus* in Brazil.

Litter

Psocoptera are a small portion of the active mesofauna of litter and are encountered in litter habitats in many parts of the world. However, distribution of litter Psocoptera is extremely variable. For example, in northern temperate regions only a small part of the total psocid fauna is found in this habitat, whereas in the southern temperate zone of South America (Chile), edaphic Psocoptera may be more diverse than arboreal species. Traditionally, the litter psocid fauna has been included in three ecological categories:

1. Primary litter dwellers. These species spend their entire life in the litter, and do not frequent other habitats. Species typical of this category are Lepinotus reticulatus and many species of Liposcelis.
2. Secondary litter dwellers. These species have generations in two distinct habitats each year, with at least one being in the litter. Some species that could be included in this category carry out seasonal local migrations from the litter onto trees and vice versa. For example, in a Mediterranean species (*Hemineura sclerophallina*) the edaphic populations are composed only of nymphs, with a peak during July, while the nymphal populations on trees have a

peak during October (adults are found exclusively on plants). The edaphic populations are restricted to the dry season when the humidity conditions are, presumably, more suitable for psocids in leaf litter than in trees.

3. Casual litter dwellers. These species do not normally breed in litter, but are present intermittently as a result of falling from trees.

Generally, the bulk of primary litter dwellers belong to the more primitive suborders, while Psocomorpha are relatively rare in this role.

Rock Surfaces

A few psocids appear to have become specialized for dwelling on the surface of rocks. This category includes species that are located under the stones on soil, as well as species living on the stones of walls (for example, on the walls of old houses). In Europe, members of the families Psocidae, Myopsocidae, and Peripsocidae such as *Psocus bipunctatus*, *Neopsocus rhenanus*, *Myopsocus eatoni* and *Peripsocus subfasciatus* are habitually found in this habitat type, although most of such species have broader habitats, either in the litter or on bark with similar lichen or algal associations.

Caves

Nymphs and adults of psocids are regularly found in caves. Psyllipsocidae (in Europe the most common psocid in caves is *Psyllipsocus ramburii*) and Prionoglarididae are perhaps particularly characteristic of caves. Some authors hypothesize that the hypogean fauna (from caves and similar habitats) had a remote origin in Cretaceous tropical forests. These forests disappeared during the early Tertiary, as a consequence of climatic change, and the fauna moved to colonizing some subterranean habitats. In the case of psocids, it has been suggested that the Psyllipsocidae (an ancient group) may have survived by avoiding competition with more recent forms by inhabiting caves or similar habitats.

Bird and Mammal Nests

Psocids frequently have been reported from mammal and bird nests. For ground-nesting mammals, the psocids are primarily leaf-litter species, while for tree-nesting species the psocids usually are those occurring on bark. Psocids are common inhabitants of bird nests, because psocids find favorable conditions in the bird nests. The association between psocids and the birds in the nest is not parasitic because the psocids feed on the microflorae that grow on the nest material. Most species of psocids living in bird nests are apterous or micropterous and are members of the families Trogiidae, Liposcelididae and Ectopsocidae. Less frequently, some psocids species live inside the nests of other insects. For example, *Liposcelis formicaria* and *Liposcelis myrmecophila* occur in ant nests, *Lachesilla pedicularia* is found in nests of wasps of the genus *Polistes*, and numerous species of psocids have been reported in the hives of honey bees.

Domestic Habitats

Among the Psocoptera, a considerable number of species (predominantly Trogiomorpha and Troctomorpha) occur in houses and other buildings, feeding mainly on fungal hyphae, spores of molds, and on green algae. Psocids are common inhabitants of domestic environments such as humid rooms, basements, damp walls and room partitions. Psocids are commonly associated with products in food stores, granaries, warehouses, railway boxcars and ships' holds. Many species seem to be exclusively domestic, including some species of the genus *Dorypteryx*, *Ectopsocus* and *Liposcelis* (*Liposcelis mendax* is frequently encountered in rice). Psocids are usually not seriously unhygienic, causing only minor problems of contamination and allergies. Their principal damage to buildings is their effect on property values: lawsuits resulting from the presence of psocids often prove costly. For example, in a Spanish coastal town, three species of psocids were involved in spreading infestation of the alga *Pleurococcus* on recently constructed buildings, and were the basis of a legal conflict.

Ecological Distribution

Altitudinal Distribution

Although some psocid habitats are distributed over a wide altitudinal range, many of the psocids present are usually limited to a part of this range. In the most comprehensive work concerning altitudinal distribution of psocids, only two of 53 species of psocids found on mango (*Mangifera indica*) in Jamaica were found throughout the plant's altitudinal range of 150–1,200 m. An altitudinal zonation of psocids has also been observed in central Spain between a range of 900–1,700 m. In this case, of the 15 species studied, three showed preferences for the low altitude, four were distributed mostly at high altitudinal levels, while the remainder were distributed throughout the altitudinal range. The same has been observed in Swiss National Park; only 14 of 55 species were taken in the upper alpine zone (above 1,900 m) and 24 were not found above the montane level (to 1,500 m). So, from the available data, psocids can be classified into three altitudinal groups:

1. eurytopic species, found over most of the range.
2. low altitude stenotopes, restricted to lower elevations.
3. high altitude stenotopes, found at higher elevations only.

Although data are not available from most parts of the world, it seems that individuals at the upper end of an altitudinal gradient may be larger than those lower down. In Jamaica, there was a linear increase in the size of females of *Pseudocaecilius citricola* and *Hemipsocus roseus* with increasing altitude. This tendency is probably due to temperature gradients.

Substrates and Plant "Preferences"

Psocids are not strictly phytophagous because they feed on the microflora that grows on the plants. However, occasionally they show a certain specificity toward their substrate plant. In a general way, this specificity refers to groups of plants. For example, among the foliage-frequenting psocids, a marked division exists among those that live on conifers and those that live on broad-leaved trees. Also, they are more frequent on plants with rough leaves (*Ulmus* spp.), or with small leaves that are easily moved by the wind (*Betula* spp.). However, among the bark-frequenting species this specificity is less marked. The ecological conditions of a site that favors a type of vegetation can be more important for psocids than the presence or absence of certain substrate plants. In central Spain, some well defined psocid communities have been found, in particular those that live in the Spanish juniper forests (*Juniperus thurifera*) and in the Scots pine forests (*Pinus sylvestris*), suggesting that changes in structure and composition of psocid communities can be determined by both climate and vegetation types. Psocid faunas inhabiting different plant species are affected by taxonomic relatedness and by architectural similarities among the substrate plant species. For example, there are discrete faunal communities on shrublands (*Cistus* sp., *Rosmarinus* sp., and *Genista* sp.), junipers (*Juniperus thurifera*, *J. sabina*, *J. comunis* is *J. oxycedrus*), pines (*Pinus pinaster*, *P. nigra*, *P. halepensis*, *P. sylvestris*) and oaks (*Quercus faginea*, *Q. pyrenaica*, *Q. rotundifolia*).

Humidity

The thinness of the integument of psocids (particularly in the nymphs) is responsible for the fact that most psocids are very susceptible to desiccation. This means that relative humidity is a limiting factor to psocids and that, therefore, high humidity is desirable. Psocids can ingest water with the food or, exceptionally, as liquid, but it is generally insufficient to prevent desiccation. However, psocids are able to actively take up water from the atmosphere. This process (this is not exclusive of psocids because it is also found in some Mallophaga) is carried out with the mouthparts. The lingua bears a pair of ventral sclerites) which are connected to the median sitophore sclerite by ligaments; these lingual sclerites are capable of taking up water from the atmosphere and driving it by means of the tubular filaments into the alimentary tract.

Psocids and Humans

In general, psocids are of little economic and health importance to man. Occasionally they may cause human health problems such as skin diseases or scalp infestations. The dead bodies of some domestic psocids in household dust are responsible for allergies and asthmatic attacks. Also, several species of psocids serve as intermediate hosts of some cestodes, particularly of the fringed tapeworm of sheep. Psocids also have been revealed to be disease vectors on plants. For example, *Ectopsocus briggsi* may occasionally disseminate fungal pathogens on fruit-bearing trees by leaving viable spores in feces deposited on uninfected sites. As mentioned previously, three species of psocids were involved in spreading infestation of the alga *Pleurococcus* on recently constructed buildings.

Some species of psocids can be considered to be pests. Among the psocids occurring out-of-doors, the large webs of Archipsocidae have occasionally required removal due to their unsightliness. Those of *Archipsocus nomas* in Florida, for example, are sometimes removed by scrubbing larger branches and trunks of trees with oil emulsions. In Europe, the species *Lachesilla pedicularia* can form dense clouds that are a temporary nuisance. However, most of the psocid species that become pests are domestic species. Most of the domestic psocids occur in large numbers in houses or stored products when the environmental conditions are particularly favorable (namely *Lepinotus* and *Liposcelis*). In general, they have been assumed to cause little damage, but the observations on some species of *Liposcelis* that cause primary damage to stored grain indicate that some species may cause direct economic loss. On the other hand, although domestic psocids are generally only contaminants, the appearance of some species in large numbers can cause a direct damage to insect collections, herbaria, older books and animal products. Most of these species (genus *Liposcelis*) are difficult to eliminate because they can survive without food and tolerate unfavorable conditions of temperature and relative humidity, recovering their normal activity once the environmental conditions become favorable. Also, as a consequence of the parthenogenetic mode of reproduction in many of these species, they are able to multiply in an explosive way and to expand their population very quickly. Some authors suggest maintenance of relative humidity of less than 50% with temperatures of 15°C or less, in order to retard development and slow the increase in populations. However, though such measures may be feasible in temperate regions, they are likely to prove extremely difficult in many tropical areas. Other control measures include the use of insecticides in varied forms; one of the most widely used is pyrethrin dust.

References

Lienhard C (1998) Psocoptères Euro-méditerranéens. Faune de France, 83. Federation Française des Sociétés de Sciences Naturelles (ed) Paris, France, 517 pp, 11 plates

Mockford EL (1993) North American Psocoptera (Insecta). Flora and fauna handbook 10. Sandhill Crane Press, Gainesville, FL, 455 pp

New TR (1987) Biology of the Psocoptera. Oriental Insects 21:1–109

Smithers CN (1972) The classification and phylogeny of the Psocoptera. Aust Mus Memoir 14:1–351

Smithers CN (1990) Keys to the families and genera of Psocoptera (Arthropoda: Insecta). Tech Rep Aust Mus 2:1–82

Smithers CN, Lienhard C (1992) A revised bibliography of the Psocoptera (Arthropoda; Insecta). Tech Rep Aust Mus 6:1–86

Thornton IWB (1985) The geographical and ecological distribution of arboreal Psocoptera. Ann Rev Entomol 30:175–196

Barley Thrips, *Limothrips cerealium* (Haliday)

A thrips (Thysanoptera) pest of some grasses, including wheat.

► Wheat Pests and Their Management
► Thrips

Basal

A term used to refer to the base or point of attachment, or the portion of the appendage nearest the main body.

Basalare

A small section above the principal pleuron, anterior to the wing, to which flight muscles are inserted.

Base Pair (bp)

Two nucleotides that are in different strands of nucleic acid and whose bases pair by hydrogen bonding. In DNA, adenine pairs with thymine and guanine pairs with cytosine.

Basement Membrane

A noncellular layer that separates the epidermal cells from the hemolymph. This membrane is the innermost layer of the integument.

► Epidermis
► Cuticle

Basic Reproductive Rate

(R_0) The average number of offspring produced by a population of individuals over the entire course of their life.

Bat Bugs

Members of the family Polyctenidae (order Hemiptera).

► Bugs

Bates, Henry Walter

Henry Bates was born in Leicester, England, on February 8, 1825, and developed an early interest in entomology. At the age of only 17 or 18 he published notes on Coleoptera in the Zoologist. At about the age of 20, he met Alfred Russel Wallace, who was then teaching English in a school in Leicester and had an interest in botany. Through the influence of Bates, Wallace began to collect beetles. In 1847, Wallace proposed a trip to Pará, Brazil, to collect insects and other natural history objects, having read W.H. Edwards' "Voyage up the Amazon". These two explorers, together with Bates' brother, sailed from Liverpool for Pará in April 1848. They intended to support themselves by the sale in Europe of natural history objects that they expected to collect in Brazil. Many hardships followed. These included his affliction with yellow fever, the death of Bates' brother, and the loss at sea of Wallace's first collection of natural history objects. Nevertheless, he persevered (Wallace traveled separately after the first 2 years, and departed from Brazil years sooner than Bates), and assembled large collections, including over 14,500 species of insects, of which 8,000 were new to science during the 11 years that he spent in Brazil. He returned to England, worked on the specimens he had collected, and published. In 1861 his paper "Contributions to an insect fauna of the Amazon Valley"; was read before the Linnean Society. It explained mimicry (see Batesian mimicry). In 1863, his two-volume book "A naturalist on the river Amazons"; was published by John Murray with an introduction by Charles Darwin, to great acclaim. These works resulted in his being offered the job of assistant secretary to the Royal Geographical Society in 1864. This at last freed him from financial worry, but reduced the time available for him to work on his Amazonian insects. He later contributed (1881–1889) volumes to the series "Biologia Centrali-Americana";, published numerous other works, and was twice president of the Entomological Society of London. He died on February 16, 1892.

References

Sharp D (1892) Henry Walter Bates, F.R.S. Entomologist 25:7–780

Woodcock G (1969) Henry Walter Bates. Naturalist of the Amazons. Fader and Fader, London, 269 pp

Batesian Mimicry

Resemblance of a palatable insect to a less palatable one, a process that benefits the palatable mimic by reducing predation.

► Mimicry

Bates, Marston

Marston Bates was born in the state of Michigan, USA, on July 23, 1906. He graduated from the University of Florida with a B.S. degree in 1927. He worked for the United Fruit Company in 1928–1931. He entered Harvard University and was awarded an A.M. degree in 1933 and Ph.D. in 1934. In 1935–1937 he worked as a research assistant at Harvard. In 1937–1952, he worked at various laboratories of the Rockefeller Foundation, and his studies of mosquitoes in northern South America contributed to an understanding of epidemics of yellow fever. In 1952–1971 he was a faculty member of the University of Michigan. He contributed much to ecology of mosquitoes and to environmentalism. His books include (1949) "The natural history of mosquitoes", (1950) "The nature of natural history", and (1955) "The prevalence of people". He died on April 3, 1974.

References

Anon (2002) Marston Bates. Available at http://www.netwalk.com/~vireo/bates.html. Accessed Aug 2002

AN Marquis Company (1968) World who's who in science. AN Marquis Company, Chicago, IL

Today in Science History (2002) Marston Bates. Available at http://www.todayinsci.com/7/7_23.htm. Accessed Aug 2002

Bat Fleas

Members of the family Ischnopsyllidae (order Siphonaptera).

► Fleas

Bat Flies

Members of the families Streblidae and Nycteribiidae (order Diptera).

► Flies

B Chromosomes

B chromosomes are non-vital supernumerary chromosomes found in many organisms. They are thought to be derived from normal chromosomes, and often transmitted at higher rates than expected, thus exhibiting "drive."

Beach Flies

Members of the family Canacidae (order Diptera).

► Flies

Beaded Lacewings

Members of the family Berothidae (order Neuroptera).

► Lacewings, Antlions and Mantidflies

Beak

A prolongation of the head, usually referring to the snout of weevils. This term also is used to describe the jointed piercing-sucking, or sucking, mouthparts of Hemiptera.

Beauveria

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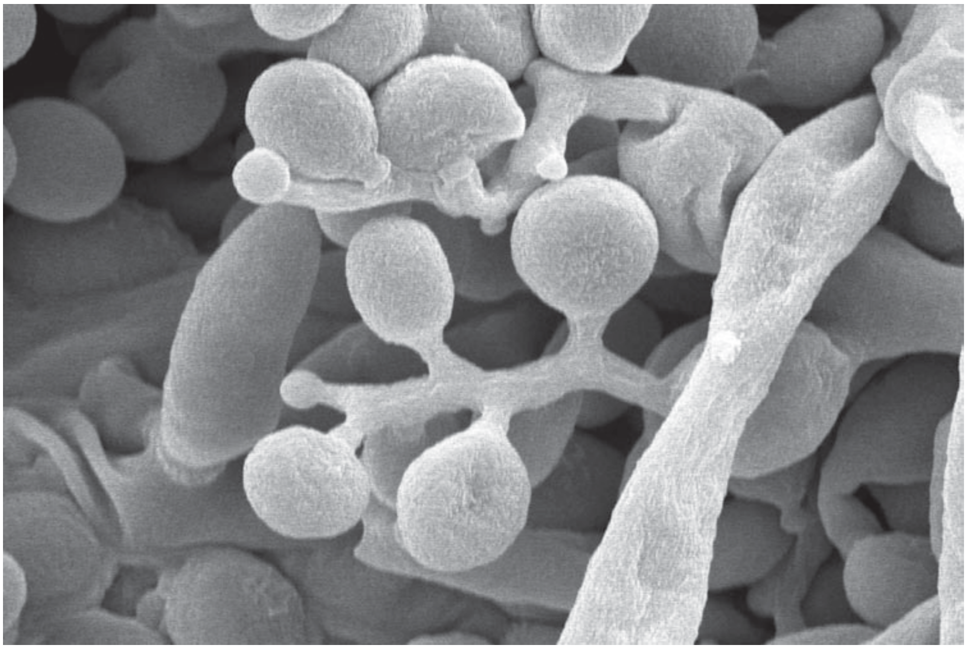
The genus *Beauveria* (Deuteromycota) includes several entomopathogenic species, the most notable being *B. bassiana*. *Beauveria* has a worldwide distribution and has a wider host range than the other Deuteromycetes infecting insects from most orders. In addition to *B. bassiana*, three other species, including *B. brongniartii* (=*tenella*), *B. relata*, and *B. amorpha* have been identified. The latter two species are South American isolates from Lepidopteran larvae and Coleoptera, respectively. *Beauveria brongniartii* (*B. tenella*), found predominantly in soil-inhabiting insects, has been described as a naturally occurring pathogen of mosquito larvae. *Beauveria bassiana*, the white muscardine fungus, was observed around 900 A.D. in silkworms in Japan. Insects mummified by *B. bassiana* also were used for medicinal purposes, e.g., as an antiseptic for wounds and sore throats. Importantly, it was through a study of this fungus that the germ theory of disease (i.e., the idea that microorganisms could cause infectious disease in animals) was postulated by A. Bassi in 1834. Also of historical significance is the discovery that a 25 million-year-old worker ant embedded in amber was covered with a fungus similar to present day *B. bassiana* isolates.

The infective propagules, the conidia of *Beauveria*, are dry, hyaline (colorless), and globose to oval in shape (Figs. 21 and 22). The conidiophores can occur singly or can be grouped in irregular clusters or in whorls; the base of the conidiophore is inflated or flask-shaped, with conidia borne on a distinctive apical zigzag extension (rachis). Like other entomopathogenic hyphomycetes, *B. bassiana* conidia initiates infection of host insects at the outer integument, although invasion through the alimentary tract has been reported in certain ants and termite hosts. Successful infection by *B. bassiana* by cuticular penetration depends upon a number of factors. For example, younger insects are usually more easily infected than older larvae. Specific *Beauveria* strains are infectious to adult insects such as grasshoppers, as well as to insects undergoing a molt. The type of plants that the target insects consume is also important since some plants produce compounds inhibitory to fungal growth. Conidial germination on a susceptible host requires optimal temperature and humidity (>75%). Conidia, for example, will not infect overwintering adult Colorado potato beetles because the soil is too dry and cool; however, post-emergent beetles can become infected later in the spring when conditions are more favorable. Even if conditions are optimal for the germination and penetration processes, *B. bassiana* conidia must first bind to the host cuticle after contact has been made. Attachment, as in the case of other fungi that produce dry conidia, is likely due to the hydrophobicity of both the conidial and cuticular surfaces. In *B. bassiana*, conidial hydrophobicity can be attributed, at least in part, to the presence of a hydrophobin-type protein in the outermost rodlet layer. In addition to attachment, conidial surface hydrophobicity may prevent desiccation of the propagules and aid in their dispersal. Fungal enzymes may help to consolidate attachment of *B. bassiana* conidia to host cuticle.

Beauveria, **Figure 21 Adult mole cricket, *Scapteriscus vicinus*, infected with *Beauveria bassiana*. Note the external conidiospores emerging from the head, thorax, and leg regions.**



Beauveria, **Figure 22 Scanning electron micrograph of the conidiophore of *Beauveria bassiana*.**

Under the proper conditions, germination of *B. bassiana* conidia occurs within hours. Studies have shown that different strains of *B. bassiana* produce different amounts of cuticle-degrading enzymes. There are several classes of enzymes produced by *B. bassiana* during germination, including proteases, chitinases, and lipases that function in the breakdown of host cuticle.

Penetration of insect cuticle (e.g., *Helicoverpa zea*) by *B. bassiana* germ tubes usually does not involve the formation of appressoria. Once the germ tubes penetrate the cuticular and epidermal regions, the fungus grows towards the hemocoel, where blastospores become evident at about 48 h post-infection. *In vivo* produced blastospores, unlike *in vitro* cells, lack a formal cell wall and contain a thin fibrillar layer on the plasma membrane. In *Heliocoverpa zea*, there is very little tissue damage until 60–70 h post-infection, when the fat body may show some signs of deterioration. The gut and Malphigian tubules can become affected at 6–7 days, when death and mummification also occur. However, the gut, muscle, silk glands, and tracheae can remain intact during the entire infection process. Death is likely due to nutrient depletion, dehydration, and/or toxin production by the fungus.

Host response to *Beauveria* invasion varies, of course, depending upon the insect and its susceptibility to the particular isolate used. Melanized patches (dark spots) can occur on the cuticle at the penetration site, thus indicating the induction of phenoloxidase activity in the insect. In grasshoppers injected with *B. bassiana* conidia, levels of phenoloxidase in the hemolymph were found to increase by 24 h post-treatment. After topical application with conidia and penetration of the cuticle, as the fungus reaches the hemocoel, host immunoreactive hemocytes may surround the hyphal tip and further melanization reactions can occur. If *B. bassiana* cells become surrounded by hemocytes either via phagocytic and/or nodulation or granuloma-type mechanisms, the fungus can still remain viable as an intracellular parasite, and later emerge from the insect blood cells to continue growth and replication in the hemocoel and tissues. Thus, *B. bassiana* can overcome host cellular defense response even if it has already been initiated, and as mentioned earlier, some toxins produced by the fungus appear able to suppress such responses (phagocytosis, nodulation) entirely. *Spodoptera exigua* larvae injected with *B. bassiana* blastospores show both a reduction in the overall number of immunocompetent granular hemocytes and a suppression in their abilities to spread and form filopodia.

In addition to being a ubiquitous soil entomopathogen, certain strains of *B. bassiana* have been reported to be endophytic and colonize plant tissue. Unlike most insect mycopathogens, *B. bassiana* has been associated with fatal respiratory infections in some cold-blooded animals, including tortoises, crocodiles and American alligators. One strain causes the rupture and/or death of fish embryos due to attachment of the conidia to the chorion with subsequent germination and penetration of the fungus. A second strain tested also caused teratogenic responses, including abnormalities in embryos. As a result of these tests, there is some concern that large-scale applications of *B. bassiana* conidia could be harmful to aquatic ecosystems. Infections in the lungs and nasal passages of mammals have been reported but are rare since the fungus probably does not grow well at 37°C; however, *B. bassiana* can cause allergic reactions in some people.

Beauveria conidia from field-collected cadavers can be inoculated onto mycological media such as SMY agar or broth and maintained in culture by transfer at regular intervals to fresh media. *Beauveria*, less fastidious than *Nomurea rileyi*, can be grown on oatmeal agar or potato dextrose media, and stored at ultra-low temperatures (-70°C). Isolation of *Beauveria* from a soil environment may require the selective media containing antibiotics such as streptomycin, tetracycline, gentamycin and cycloheximide to eliminate bacterial growth and N-dodecylguanidine acetate (dodine) to inhibit growth of other soil fungi.

Due to its broad host range, including members within the orders Lepidoptera, Coleoptera and Hemiptera, and to the fact it is cultured easily on inexpensive media, *B. bassiana* has long been targeted as a potential biocontrol agent. Insect pests such as the Colorado potato beetle, *Leptinotarsa decemlineata*; European corn borer, *Ostrinia nubilalis*; codling moth, *Laspeyresia pomonella*; Japanese beetle, *Popillia japonica*; European cockchafer, *Polyphylla fullo*; chinch bug, *Blissus leucopterus*; and the European cabbageworm, *Pieris brassicae*, are susceptible to *B. bassiana*. However, the inability to produce and formulate fungal propagules that are stable and provide consistent mortality rates in constantly changing biotic and abiotic conditions has restrained large-scale development of this mycopathogen. For example, over the years both *B. bassiana* and *B. brongniartii* have been targeted to control some soil-inhabiting insects, but due to this hypogean environment, *Beauveria* is placed in direct contact with the antagonistic soil microfauna that can be lethal or can inhibit its growth.

References

Bing LA, Lewis LC (1992) Endophytic *Beauveria bassiana* (Balsamo) Vuillemin in corn: the influence of the plant growth stage and *Ostrinia nubilalis* (Hübner). Biocontr Sci Technol 2:39–47

Boucias DG, Pendland JC (1991) Attachment of mycopathogens to cuticle. In: Cole GT, Hoch MC (eds) The fungal spore and disease initiation in plants and animals. Plenum Press, NY, pp 101–127

Hung S-Y, Boucias DG (1992) Influence of *Beauveria bassiana* on the cellular defense response of the beet armyworm, *Spodoptera exigua*. J Invert Pathol 60:152–158

Middaugh DP, Genthner FJ (1994) Infectivity and teratogenicity of *Beauveria bassiana* in *Menidia beryllina* embryos. Arch Environ Contamin Toxicol 27:95–102

Pendland JC, Hung S-Y, Boucias DG (1993) Evasion of hose defense by *in-vivo* produced protoplast-like cells of the insect mycopathogen *Beauveria bassiana*. J Bacteriol 175:5962–5969

Beck, Stanley Dwight

Stanley Beck was born in the state of Oregon on October 17, 1919, but grew up in the adjoining state of Washington. As a young man he worked in a lumber mill for a year to save money to pay for a university education. With those funds, he entered Washington State University to study biology, and earned a B.S. degree in 1942. He then served 3 years in the U.S. navy. From 1945 to 1950 he was a graduate student at the University of Wisconsin at Madison, earning an M.S. degree in 1947 and a Ph.D. in zoology in 1950. At the same university, he was appointed assistant professor in 1950, a full professor in 1964, and a distinguished professor in 1969. He taught a course on insect physiology. His research interests were in host-plant resistance to pests, and insect nutrition and metabolism. His publications were 138 scientific papers and several books including (1963) "Animal photoperiodism" and (1968) "Insect photoperiodism". He received several awards, was elected to the U.S. National Academy of Sciences in 1988, and served as president of the Entomological Society of America. His accomplishments were the more remarkable because by 1952 he was essentially paralyzed by poliomyelitis and was confined to a wheelchair for the rest of his life. He died on July 8, 1997, in Madison, Wisconsin, survived by his wife, Isabel, and three of his four daughters.

Reference

Wedberg J (1998) Stanley D. Beck. Am Entomol 44:127

Bed

In modern agriculture, a raised area of soil into which crops are planted (planting bed). Beds are bounded by furrows which sometimes are used to deliver irrigation water to the beds. In traditional agriculture, a bed (seed bed) is also an area used to grow seedlings for later transplant into fields.

Bed Bugs (Hemiptera: Cimicidae: *Cimex* spp.)

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The Cimicidae are obligate blood feeding ecto-parasites of humans and other animals. There are 74 species of cimicids, including the human bed bugs, bat bugs, chicken bugs, swallow bugs, and pigeon bugs. Cimicids are organized into 22 genera and 6 subfamilies. Of the 22 genera, 12 have evolved to feed exclusively on bats while another 9 genera feed exclusively on birds. There is only one genus, *Cimex*, which contains species that feed on multiple hosts, typically specializing on birds, bats, or humans. Of all the cimicid species only three feed on humans. These include *Leptocimex boueti* Brumpt, a West African species that feeds on humans and bats; *Cimex hemipterus* F. (tropical bed bug), found in both the new and old world tropics feeding on humans and chickens; and *Cimex lectularius* L. (common bed bug), which is found all over the world and feeds on humans, chickens and bats.

Cimicids that feed on humans get their common name "bed bugs" from their long history of harboring in human dwellings, particularly in those locations where the host would come to rest at night (bed or bedding). By harboring in the "bed," the bugs could feed undisturbed while the host was asleep.

While the origin of the bed bug is unknown, it is thought that human bed bugs were originally ecto-parasites of bats. When humans moved into caves and either lived with the bats or removed them, the bat parasites adapted to the presence of the new host. Those bat bugs that survived and proliferated on human blood continued to inhabit human environments.

The exact geographic origin of human bed bugs is also unknown, but both Neanderthal man (100,000 years ago) and, later, Cro-Magnon man (12,000 B.C.) populated caves in the Middle East. It is most likely in these Middle Eastern caves where humans began their cohabitation with the ancestral bed bug. As humans began to practice agriculture (8000–5000 B.C.) within the "fertile crescent" (present day Iraq), people moved from their cave dwellings into villages near their agricultural fields. It has been speculated that bed bugs were transported into these newly civilized environments, thus becoming permanently associated with humans and human dwellings.

Morphology

Adult bed bugs are easily identified by their brownish red color and their lack of wings. The body is broadly flattened and ovoid, typically 5–8 mm in length and about 4 mm wide. Because the adults only have wing pads, the first 11 dorsal abdominal segments are usually easy to see when the body is not engorged.

The morphology of the bed bug head is very similar to that of other cimicids. The multifaceted eyes of the bed bug look like small knobs protruding from the sides of the head. The antennae of the bed bug are 4-segmented and project forward from a small protuberance between the eye and clypeus. The third and forth segments of the antennae are thinner than either the basal or second segment.

The most prominent feature on the head is the labrum. The labrum extends out from the clypeus at the extreme anterior of the head and is marked with a labral suture. The labium arises just below the labrum, at the anterior margin of the head, and has three segments. When the labium is held at rest (under the bed bug head), the ventral side of the labium contains a longitudinal groove which holds a fascicle of mandibular and maxillary stylets. Between the maxillary stylets are a large food canal and a smaller salivary canal. The food canal and the stylet fascicle are connected with the cibarial pump inside the head of the bed bug. The 3-segmented labium, including the maxillary and mandibular stylets and the food and salivary canals, are collectively referred to as the rostrum (Fig. 23). The rostrum pierces the host's skin and the cibarial pump is used to pump the blood from the host into the head of the bed bug.

The pronotum of the bed bug is very distinct and the shape or hairiness of the dorsal side is often used for species identification. In general the pronotum is broad, surrounding the base of the head within the concave anterior margin. The sides of the pronotum extend up around the base of the head in a wing-like fashion.

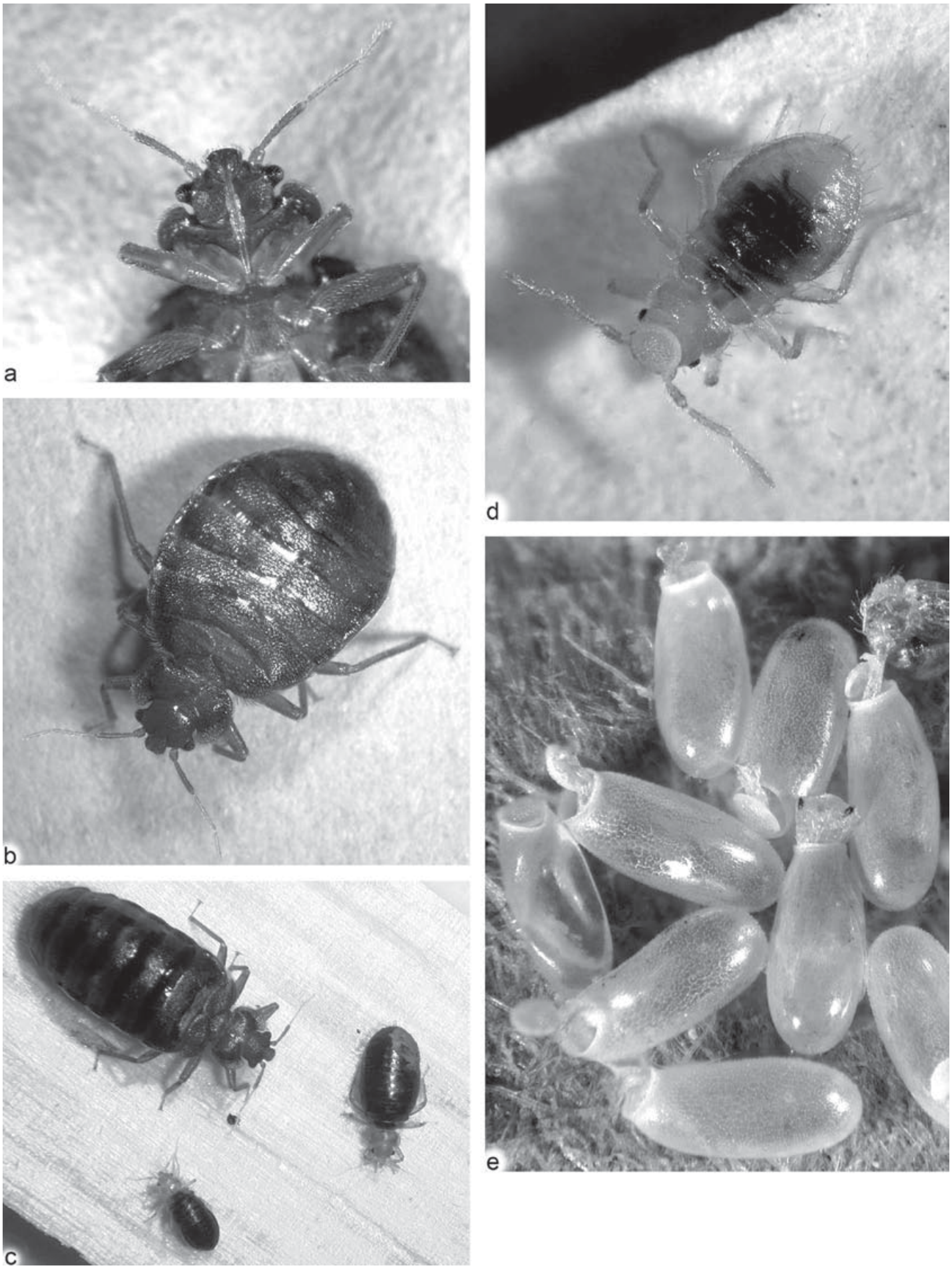
The abdomen of the adult bed bug consists of 11 segments and is completely sclerotized. However, the sclerotized abdomen is capable of enormous expansion due to the wide intersegmental membranes and the "hunger folds" (ventral membranous sections) located within the second and fifth abdominal segments. The female reproductive organs (gonapophyses) are homologous to the ovipositor found in other species and are located on the ventral side of the 8th and 9th abdominal segments. The female spermalege or paragenital sinus appears as a notch located on the ventral side of the abdomen between the 5th and 6th segments. The genitalia of the male bed bug also originate on the ventral side of the abdomen near the apex. The male abdomen is narrower at the apex than that of the female and the 9th segment is longer and asymmetrical. The male paramere is strongly curved to the left and lies in a groove within the 9th segment.

Immature bed bugs differ from adults in their morphology in several ways. First, they lack the characteristic reddish color of the adults. Nymphs are typically translucent white, making their internal structures visible after a blood meal. Nymphs also differ from adults in that not all of their abdominal segments are sclerotized, particularly on the ventral surface of the abdomen. Nymphs also have a 2-segmented tarsus while the adult tarsus is 3-segmented. Finally, immature bed bugs lack any structures associated with reproduction.

Life Cycle

The bed bug life cycle is unique in that it begins with an unusual form of copulation known as traumatic insemination. Unlike other hemipterans, *Cimex* males never insert their copulatory organs into those of the female. Instead the male awkwardly mounts the female's back and wraps his abdomen around the right side of her body. He then punctures her body wall, wounding the female as he inserts his copulatory organ into her paragenital sinus or "Organ of Berlese" to inject his sperm. Mating usually lasts for several minutes but can last up to half an hour in some cases. Within 2 h of mating the male spermatozoa pass from the female Organ of Berlese into her abdominal cavity. Once in the hemocoel, the spermatozoa accumulate at the base of the oviducts, moving into the seminal conceptacles within 12 h.

After mating, a female held at 23°C will begin to produce eggs within 3 days. Several sources have indicated that female bed bugs, when fed regularly, are able to produce viable eggs for 5–7 weeks after a single mating. However, mated females will usually cease oviposition after about 11 days without an additional blood meal. Under laboratory conditions (23°C and 75% RH) a typical female that has been fed and mated regularly can produce 3–4 eggs every day averaging more than 200 eggs total over her entire lifespan. Under natural conditions fecundity can be quite variable, depending not only on the availability of mates but also temperature and nutrition. Egg production is closely correlated to ambient temperature, the weight of the unfed female, and size of the female blood meal. An increase in temperature from 17 to 23°C has been shown to produce as much as a ten-fold increase in weekly egg production among well fed, mated females. The mean weight of unfed females also influences egg production. As expected, larger females produce more eggs. Also, because larger females tend to take larger blood meals, the size of the blood meal has also been shown to result in increased egg production.



Bed Bugs (Hemiptera: Cimicidae: *Cimex* spp.), Figure 23 **The common bed bug, *Cimex lectularius*: (a) ventral morphology of adult bed bug head showing the rostrum, pronotum, and antennae; (b) adult female bed bug; (c) engorged adult and early instar bed bugs; (d) partially fed first instar bed bug with egg cap on head; (e) first instar bed bug emerging from egg.**

Oviposition occurs 3–6 days after mating. The bed bug eggs are about 1 mm in length, white, elongate, and slightly bow shaped. Upon oviposition, eggs are coated with sticky cement that dries quickly causing them to adhere to the substrate on which they were deposited. The eggs are typically laid in cracks and crevices near a harborage site and take 6–10 days to hatch, although temperature variation may alter hatch time. As a first instar bed bug emerges from the egg, anti-peristaltic movements of the gut drive fluid into the head, deploying hatching spines to dislodge the egg cap. After hatching, most first instars will stay near the egg capsule until they leave in search of their first blood meal. Several studies have indicated that bed bug survivorship is closely linked to the amount of energy they have to expend searching for a host. This is particularly true for first instars. While quite ambulatory for their size, first instars are at great risk of dehydration compared to the older life stages. Therefore, we can assume that many first instars are lost before they ever consume their first blood meal simply because they hatched too far from a host.

Bed bugs have five nymphal instars, each requiring a blood meal to complete development. Each nymphal stage can feed within 24 h after molting and all bed bugs are typically stimulated to feed at slightly less than weekly intervals. At higher temperatures (27°C), the feeding interval can be reduced to every 3 days, and all nymphal instars molt more quickly when exposed to warmer temperatures. In studies conducted on nymphal stages 1–5, it was found that the mean number of days between the blood meal and molting ranged between 2.1 days at 35°C and 26 days at 15°C. Ordinarily, nymphal bed bugs will feed once per instar, with each instar lasting 3–5 days at optimal temperatures (23°C). If insufficient blood meals are taken, secondary blood meals will be necessary before molting can occur. So although the average time from egg to adult is often reported as about 1 month, that time period can be extended to 4 months or more depending on the ambient temperature and the availability of regular blood meals.

Behavior

Bed bugs are thigmotrophic and seek out harborages where their bodies can be in direct contact with surrounding surfaces. They are often found aggregating in cracks and crevices of homes and other structures, or wedged into mattress tufts or staple holes where they can remain undisturbed. In hotel rooms they are often found behind removable headboards or picture frames hanging on the wall. They can also be found hiding in the wood frames of the box springs or the stuffing. In some heavy infestations, the best harborages are already filled so many bed bugs will take up residence along baseboards, behind posters on the wall, or under the carpet tacking. Bed bugs will typically avoid locations exposed to air movement but may be seen aggregating in the open on the ceiling or at the ceiling/wall junction if no other space is available. The stimulus that prompts bed bugs to leave their harborages is not well understood but obviously they have to leave in order to feed. After feeding, bed bugs will return to these same harborages after their meal and remain there while digesting. The digestion period after feeding results in the accumulation of fecal material (black spots of dried blood) in preferred harborage locations.

Bed bugs are nocturnal, usually avoiding the light. Studies have indicated that bed bugs are most active after 3:00 A.M., a time when the host would most likely be in a deep sleep. However, bed bugs will feed during the daylight hours if they are hungry and a host is available. The question regarding how these nocturnal insects are able to navigate between the host and their harborage is quite controversial. Little is known about bed bug vision, but it is suspected that they do not see well because of their nocturnal and parasitic lifestyle. Bed bugs are thought to use pheromone and odor cues for navigation. However, bed bugs have been tested repeatedly and have never been observed to detect heat sources or host odors over distances >12 cm. Several researchers have suggested that bed bug searching behavior in the natural environment must be completely random. However, others claim that random searching would be too costly for bed bugs to have achieved their obvious reproductive success. Regardless of how bed bugs detect their food source, there is no question that they have evolved to take advantage of the diurnal nature of the human host. They feed at night when the host is unconscious, thereby increasing their chances of feeding to repletion. After feeding they quickly abandon the host and return to their harborage where they remain during the daylight hours, thus decreasing their chances of being detected.

Bed Bug History

References to the bed bug as the bane of human existence appear in some of the earliest recorded history. Aristotle made reference to bed bugs in his *Historia Animalia* (384–322 B.C.), and many other historical texts document the presence of bed bugs in Greece in 499 B.C., Italy in 77 A.D., and in China by 600 A.D. Because bed bugs have co-existed with humans for centuries, many common names and folk remedies have been created regarding them. Bed bugs are known by over fifty common names in a number of different languages. The English language names include wall-louse, red coat, pursuer, crimson rambler, wall flounder, and the mahogany-flat. In addition to the various common names, there are several folk sayings that are related to bed bugs, including "crazy as a bed bug" or "snug as a bug in a rug."

Bed bugs have long been a target of folk remedies. Some remedies may have been somewhat effective while others, though creative, were probably useless. The plant *Actaea cimicifuga* or bugbane has long been regarded as viable bed bug treatment, and may have had some potential for repelling bed bugs away from the sleeping host. However, the snap bean (*Phaseolus vulgarius*) has demonstrated true potential for bed bug control. In the Balkans, the leaves of this bean plant were placed under the beds in infested rooms. Foraging bed bugs would become entangled in the hairs on the bean leaves during the night. In the morning, the leaves were simply swept up and burned to destroy the bed bugs. While the practice of sleeping over bean leaves most likely provided at least some bed bug relief, the ancient remedy of hanging the feet of a dead stag or rabbit at the foot of the bed (as host decoy), probably had little effect. Another folk method of bed bug prevention that is still used today is to place the legs of the bed frame in pans of water or kerosene. Although this method is thought to work, there have been many anecdotal references to bed bugs circumnavigating these barriers by crawling up the wall and dropping onto the sleeping host from the ceiling.

In spite of all of the recorded history of cohabitation with humans, bed bugs are still "the bug that nobody knows." The reason for this "bed bug denial" is that there is a social stigma associated with bed bug infestations. Many people believe that bed bugs only infest overcrowded or unsanitary housing. Therefore, you can only get bed bugs if you visit or live in these poor conditions. This has never been true. Bed bugs do not discriminate between human hosts and infest every social class and nation across the globe. The bed bug's ability to infest any human environment has been confirmed by the resurgence of bed bug infestations in industrialized nations over the past decade. During the 1990s, new bug infestations appeared first in five star hotels and other expensive tourist locations within the United States, Australia, Singapore, and Europe.

Geography of the Bed Bug

Today, *Cimex hemipterus* F. (tropical bed bug) and *Cimex lectularius* L. (common bed bug) are by far the two most important and widespread cimicid parasites of humans. Both are thought to have originated from the Old World but are now found all over the globe. Colonies of *C. hemipterus* have been cultured from such diverse locations as Vietnam, Taiwan, Panama, Uganda, Venezuela, Cuba, India, and Florida in the United States. Although *C. hemipterus* has a worldwide distribution, its range rarely extends beyond the tropics, therefore it has been described as strictly a tropico-politan species.

C. lectularius is a truly cosmopolitan bed bug and has expanded its range with humans throughout Europe and into the Americas. Records of *C. lectularius* have been collected from all over the world with the exception of Antarctica. However, Antarctica will no doubt have *C. lectularius* by the end of the decade due to the eco-tourist industry that has recently developed on that continent. In many tropical locations, the distribution of *C. hemipterus* and *C. lectularius* overlap. Yet, unlike *C. hemipterus*, *C. lectularius* is able to survive in both tropical and temperate climates. Interestingly, *C. lectularius* does not typically occur where populations of *C. hemipterus* are well established. Some authors have speculated that the reason for this absence is that *C. lectularius* is susceptible to fungal infection in tropical locations of high humidity while *C. hemipterus* is not. A more interesting suggestion is that the distribution of *C. lectularius* is limited by the fact that interspecific copulation is common between the two species and yet has a deleterious effect on *C. lectularius*. For example, one older study suggested that sperm fluid of *C. hemipterus* males was toxic to *C. lectularius* females. Later research indicated that the deleterious effects of interspecific copulation were due to the fact that attempts of *C. hemipterus* males to mate with *C. lectularius* females resulted in female mortality. The reason suggested for this mortality was that the paragenital sinus of the *C. lectularius* female was not suited to accommodate the *C. hemipterus* paramere. The most recent study regarding the viability of mixed bed bug populations determined that the fecundity of *C. lectularius* was compromised in the presence of *C. hemipterus*. Specifically, it was found that in mixed populations, *C. lectularius* females laid only sterile eggs when *C. hemipterus* accounted for >75% of the individuals. However, the potential negative impacts (if any) of *C. hemipterus* males on *C. lectularius* females living in mixed populations have yet to be fully determined.

Public Health Importance

Because bed bugs are blood feeders and have typically been associated with poor living conditions, they have long been suspected of being potential vectors of human disease. In fact, studies prior to the 1960s identified many diverse disease organisms that were collected from the bed bug gut, body and feces. These pathogens included those responsible for plague, murine typhus, smallpox, poliomyelitis, yellow fever and at least 20 other diseases. However, there has been no conclusive evidence that bed bugs transmit any of these diseases to humans. More recently, bed bugs have been evaluated for their ability to become infected with and transmit Human Immunodeficiency Virus (HIV) and Hepatitis B. HIV has been found to survive in bed bugs for several days after ingestion, but there has been no epidemiological evidence indicating that HIV could be transmitted from an infected bed bug to a host during the feeding process. While Hepatitis B cannot be transmitted from bed bugs to humans via the taking of a blood meal, there is evidence to suggest that the Hepatitis B virus may be mechanically transmitted to humans in bed bug feces or when bed bugs are crushed during the feeding process. However, as of this writing there is no medical record of such a transmission ever taking place.

Disease transmission is not the only health issue associated with bed bugs. In many cases, the number of bed bug bites or reactions to the bites has been cause for concern. When a bed bug bites, the mandibles and maxillae form a compact bundle (fascicle) that is rapidly injected into the host's skin. During the act of piercing, the toothed mandibles move in a rapid alternating motion slicing their way through the skin tissues slightly ahead of the maxillae. After the tissues are breached, the fascicle probes in all directions, backwards and forwards, often cutting across or entering small capillaries and larger vessels. The probing can result in numerous small hemorrhages throughout the tissues. The bed bug fascicle probes for a vessel of suitable size from which to begin feeding. Blood vessels that are too large or too small are ignored. Once the fascicle finds a suitable vessel, the maxillae enter the blood vessel and inject the saliva (anticoagulant). The pressure in the vessel causes the host's blood to rush up the food canal into the bed bug head, allowing for feeding to be completed in a matter of minutes. However, the destructive nature of the probing coupled with the injection of the bed bug saliva can produce a wide variety of reactions within the host.

It has been well documented that many people do not react to bed bug bites; however, some people can suffer severe skin reactions that last for several days. There have been many reports of married couples staying in infested hotel rooms where the wife or husband was made miserable by hundreds of itching bed bug bites while their spouse experienced nothing at all. It has also been suspected that hypersensitive individuals living with large populations of bed bugs may actually suffer asthma attacks after being bitten repeatedly by bed bugs. The reactions of people who are sensitive to bed bug bites vary widely in severity and may be immediate, delayed or both.

Bed bug saliva contains many proteins that trigger the body's immune response. The immediate immune response usually involves the development of an inflamed reddish weal that will start to itch within a couple of hours and may continue to itch for 1–2 days. People who experience the delayed response are typically unaware that they have been bitten for several days. They then begin to experience localized itching and swelling (sometimes very severe) around the bite site and the delayed response may last for longer than a week. Perhaps the worst scenario for sensitive people who experience the delayed reaction is to inadvertently spend several nights sleeping in an infested location. Only with the onset of the delayed immune response, do they realize that they have been subjected to hundreds of bed bug bites.

Fortunately, the suffering caused by receiving hundreds of bed bug bites typically has no long term physiological effects, provided the person is able to leave the infested area or have the bed bugs eliminated. Today, the most common medical consequences of bed bug bites are secondary bacterial infections that can occur from vigorous scratching and excoriation. Yet historical records indicate that excessive bed bug feeding has been known to cause iron deficiencies among infants in India.

Although bed bug bites do not produce any long-term physiological problems, the psychological aftermath of dealing with a bed bug infestation may be significant. Many people suffer from stress and anxiety after an encounter with bed bugs and are fearful that bed bugs may be infesting their homes or living on their bodies. Most people who suffer from bed bug anxiety have had an infestation in their home or have been bitten severely while traveling. Still other sufferers have never had an encounter with bed bugs, but have been told about bed bugs or have had it suggested that their itching skin may be the result of bed bug bites. Regardless of whether they have encountered real bed bugs or not, people who suffer from bed bug anxiety have great difficulty sleeping for fear that bed bugs are crawling on them. They often get up several times a night to check themselves or their children for bed bugs. Some people have moved several times and discarded most of their furniture and other belongings. Many have also paid thousands of dollars for repeated bed bug exterminations that have not worked to their satisfaction. Another characteristic of these sufferers is that they often withdraw from family and friends and spend hundreds of hours on the computer researching bed bug cures and participating in internet-based bed bug support groups.

Although not everyone who suffers from bed bug anxiety has experienced a real infestation, the potential for bed bug infestation is very real. Bed bugs have enjoyed a long history of infesting human environments and it was only within the last century that certain developed nations have enjoyed a brief respite from these noxious pests.

Control History

At the turn of the twentieth century the bed bug was a common household pest in the United States and the world. Bed bugs were frequently encountered in quality hotels and motels, laundromats, movie theaters, city buses, and taxis. Bed bugs were easily transported home via a traveler's clothing, vehicle, or luggage. Once inside the home, bed bugs could find harborage in furniture, cracks and crevices in the floor or walls, behind wallpaper, or under carpeting. The easy transportability of the bed bug coupled with the war-time movement of people in the United States and Europe (1914–1945) led to millions of homes and other structures becoming infested. However, the importance of the bed bug as a household pest began to diminish in the 1940s and 1950s with the use of pyrethrum insecticides and DDT. These insecticides were applied liberally to all walls, floors, mattresses, bed frames, curtains, cupboards, and any other surface that could be occupied by bed bugs. Complete control was usually obtained within a matter of days, and with the use of DDT, the residual activity was so long that the sprayed areas remained toxic and bed bug free for months. Therefore, in the latter half of the twentieth century the bed bug was almost eradicated in the United States and Europe, with only a few persistent populations surviving in locations where living conditions were exceptionally poor.

Current Pest Status

In the early 1990s pest management professionals began to receive complaints about new bed bug infestations within the United States. By 2001, many pest control firms were reporting tenfold increases in bed bug calls every year. While new infestations were found to be particularly common in hotels, bed bugs were increasingly being reported in homes, apartments, retirement communities, health care facilities, college dormitories, youth camps and used furniture outlets. The resurgence of the bed bug after its supposed eradication has presented a number of unique challenges to a variety of commercial industries which in their own way have contributed to the bed bug problem.

First, within the pest management industry, most pest management professionals are too young to have had any personal experience with bed bug control. This lack of experience has resulted in many incomplete and ineffective bed bug treatments since the bed bug resurgence began. Second, the medical profession has had very little experience with bed bugs, so many bite complaints were misdiagnosed, allowing bed bug infestations to continue in homes where they might have been treated had they been correctly identified. Leaders in the hospitality industry were also slow to admit that bed bugs were a problem in hotels. Therefore, the hoteliers did not readily develop bed bug prevention or treatment plans because they failed to recognize the potential damage that bed bugs could cause their industry. For example, when bed bugs were first (re)discovered in the United States, it was in five-star hotels in cosmopolitan locations like Los Angeles and New York City. The hotel industry was immediately faced with million dollar lawsuits initiated by clients who had been bitten while staying in their facilities. These lawsuits received extensive press coverage and immediately associated the hotel brand name with bed bug infestations. It was only after a number of these bed bug cases were reported that the hospitality industry began to address the expanding bed bug problem. Finally, an unanticipated source of bed bug proliferation has been the rapidly growing organic foods industry in the United States. Organic poultry farms house thousand of chickens that are being raised for either meat or eggs. There have been several documented infestations within these organic facilities where bed bugs have been found cohabitating with and feeding on the chickens. Because these facilities are pesticide-free, the bed bugs in these facilities number in the millions, causing stress to both the chickens and migrant workers. While the transport of these bed bugs to other locations has not been documented, there is the potential for these bed bugs to be shipped all across the nation via the thousands of delivery trucks that bring eggs and other poultry products to food distribution centers every day.

While the exact cause of this recent, worldwide increase in bed bug activity is not known, there are several factors that may have contributed to the resurgence of bed bugs in the USA. It has been suggested that international travel from developing nations has increased the distribution of bed bugs throughout the world. However, international travel has been common for many decades and bed bugs have only recently (1990s) become recognized as a widespread problem. Another possibility for the bed bug increase has been the reduction in residual insecticide use indoors. Because of concerns about human exposure risk, routine interior applications of spray insecticide have been greatly reduced in favor of integrated pest management (IPM), where pesticides are applied only on an "as needed" basis. IPM also uses insecticide baits as the primary method for controlling crawling insects. However, pesticide baits have no effect on blood sucking parasites. Thus, it is thought that in the absence of the residual sprays, bed bug populations have been able to establish unchecked. One final possibility that deserves consideration is that bed bug populations across the world have become resistant to insecticide products used in developing nations and the USA. If this is the case, it is reasonable to suggest that the increasing population pressure has led to the widespread dissemination of bed bugs throughout the world.

Historical records indicate that bed bugs developed resistance to a number of the insecticides used for their control. These chemicals included DDT, methoxychlor, dieldrin, aldrin, carbaryl, Malathion and other organophosphates. Many of these older chemistries have been banned by the US Environmental Protection Agency and are no longer available for bed bug treatment. However, because bed bugs have not been a problem in the USA for over 40 years, few of the existing pesticide products are labeled for bed bug control and many of these products have the same type of active ingredients. The majority of insecticide products that are labeled for the treatment of bed bugs are either natural pyrethrins, or pyrethroids. Because these active ingredients have been used for decades all over the world, and because they are from the same chemical class, it has been suspected that the newly emerging bed bug populations might already be resistant to pyrethroids.

As of 2007, bed bug resistance to a number of pyrethroids has been documented. Field populations of bed bugs have been found to have variable levels of resistance to permethrin, deltamethrin, beta-cyfluthrin, and lambda-cyhalothrin. In some cases, the resistance of field collected bed bugs exposed to specific active ingredients was found to be 1,000 times that of susceptible laboratory strain bed bugs. Likewise, the time to mortality for bed bugs confined on dried pyrethroid product residues was found to be significantly greater than that of the laboratory strain bed bugs. For example, the time it took to kill 50% of the laboratory strain bed bugs (LT_{50}) confined on panels treated with a formulation of deltamethrin (0.06%) was 61 min. However, when testing bed bugs collected from an infested apartment in Arlington, Virginia, the LT_{50} for deltamethrin was 19 days and 2 h.

Interestingly, in tests evaluating the potential repellency of pyrethroids to bed bugs, it was documented that neither the field nor the laboratory strain bed bugs found pyrethroids repellent. In choice tests where bed bugs could aggregate on either a panel treated with a pyrethroid product or a panel treated with water, there was no significant difference as to where the bed bugs chose to aggregate. In fact, many bed bugs remained in contact with the pyrethroid treated panels until they died, even though they could leave the panel to aggregate somewhere else at any time during the test.

In addition to pyrethroid resistance, these resurgent bed bug populations are not readily susceptible to the non-pyrethroid products labeled for their control. For example, pyrethroid dusts usually take several days to kill resistant bed bugs. Desiccant dusts like silica aerogel, diatomaceous earth or limestone and corn bran dusts can also take days or even weeks to kill bed bugs confined on the material. Because bed bugs do not groom, stomach toxicants like boric acid have no effect on bed bugs. Even crack and crevice sprays containing pro-insecticides like chlorfenapyr may take longer than a week to kill bed bugs, thus allowing them to reproduce prior to suffering any toxic effects. The insect growth regulator hydroprene, which has been a widely used juvenile hormone analogue for cockroach control, has been found to function as a chitin synthesis inhibitor in bed bugs, disrupting the final molt. Yet, although hydroprene kills close to 50% of exposed bed bugs during the final molt, the surviving adults are not sterilized and produce a greater number of viable offspring than unexposed bed bugs after taking their first adult blood meal. Finally, "non-toxic" mattress treatments containing isopropyl alcohol, sodium laurel sulfate or protein degrading enzymes typically kill over 80% of bed bugs that are directly sprayed with these products. However, these treatments have no residual activity once the product is dry, and like most insecticides, these non-toxic mattress treatments have no effect on bed bug eggs.

Current Management Practices

Because of their cryptic lifestyle, bed bug management begins with a thorough inspection of the infested site by a qualified professional. In many cases, infested rooms will be taken completely apart and all personal belongings inspected for live bed bugs, bed bug eggs and fecal spots. Personal belongings are then bagged for treatment, laundering, or disposal. Because clutter provides numerous harborages for bed bugs and makes insecticide applications very difficult, a "bare walls" approach is generally required to provide adequate control. After all clutter and personal belongings have been removed, the infested room and furniture can then be treated.

A back-pack vacuum cleaner with HEPA filter is recommended for the removal of live bed bugs and their cast skins. The removal of live bed bugs and their debris will not only reduce the bed bug numbers but will aid the pest management professional in identifying incipient infestations in future inspections. Once vacuuming is completed, the vacuum cleaner bag must be sealed in a plastic bag and removed from the structure immediately. It should be noted that although the vacuum cleaner will be able to remove the majority of live bed bugs it will not be able to remove the bed bugs eggs which are typically cemented to the surfaces on which they are laid. Therefore, additional treatment(s) will be necessary.

A frequently used method of reducing bed bug harborage sites is the use of sealants and caulk. Because early instar bed bugs are capable of occupying extremely small cracks it is important to inspect the walls and ceilings very carefully for bed bug harborages around switch plates, wallpaper seams, electrical outlets, inside nail holes and screw heads, around window frames, and in staples holes. Caulking and sealing these harborages will force bed bugs to wander in search of new harborage space, causing them physical stress and increasing their chances of exposure to insecticide residues.

Steam cleaning is rapidly becoming a widely used method of bed bug control. Professional steam cleaners can be used to kill bed bugs hiding in baseboards, under carpeting, in mattress seams and in the wooden components of box springs. Professional cleaners that produce dry steam at temperatures >60°C (140°F) are preferred because they produce enough heat to compensate for the insulating properties of mattresses and other upholstered furniture which might otherwise prevent bed bugs from reaching their thermal death point. When purchasing a steamer for bed bug control, it is important to select a machine with a steam head large enough to disperse the steam at a low velocity. The small steam head of some machines will disperse the steam with such force that the bed bugs and eggs are blown off the treatment areas into other parts of the room. Although steaming bed bugs is a slow and laborious task, steam cleaning is one of the most effective methods for killing both bed bugs and their eggs.

After steaming, the treated mattress and box springs should both be placed inside a bite proof, escape proof mattress cover. A variety of products are available for covering mattresses, however, most were not designed to function as a bed bug prevention tool. Many tear easily or have zipper casings that are large enough for bed bugs to crawl through. However, there are mattress covers that have been tested to ensure that bed bugs cannot get inside the cover and any bed bugs already trapped inside the cover cannot escape or bite through the fabric. Although mattress covers cannot prevent a future bed bug infestation, they do keep the client from having to throw the mattress away.

All bedding and any clothing articles that are suspected of being infested with bed bugs must be laundered. Both clothing and bedding should be bagged and marked so that they are not mixed with uninfested articles during the cleaning process. All items should be laundered at a temperature >49°C (120°F) for more than 10 min with laundry detergent. Bed bugs, like all insects, are very susceptible to drowning when exposed to soap, so the addition of laundry detergent will ensure a quick kill. Placing bed clothes in a dryer at 60°C (140°F) for 20 min or longer is also recommended to make sure that no bed bug eggs survive.

Because bed bugs are susceptible to high temperatures, heat fumigation is being used to eradicate bed bugs from large commercial facilities. Using the heat fumigation technology developed for the treatment of grain silos, fans are used to blow air in from the outside to raise the atmospheric pressure inside the facility. The air is then heated and monitored to make sure that all locations inside the building reach the appropriate temperature (bed bug thermal death point) and pressure. The heat treatment is then maintained for a period of hours to ensure that all bed bugs and bed bug eggs are killed. Although heat fumigation is an effective bed bug treatment, the cost, like that of chemical fumigation, is often prohibitively expensive for the average consumer.

Exposing bed bugs to cold temperatures will kill bed bugs but the duration of exposure is often too long to be practical. For example, the thermal death point for adult bed bugs exposed to cold temperatures for 1 h is −18°C (−1°F). Yet, most conventional freezers have a minimum temperature of 0°C (32°F), thus requiring that the bed bugs be frozen long enough to achieve 100% kill. Attempting to kill bed bugs at 0°C will take several days at least, and if the bed bugs are insulated in clothes or bedding it may take several weeks of exposure to ensure that all bed bugs are killed and bed bug eggs are no longer viable.

Although increased sanitation and exclusion techniques are necessary to remove bed bug harborages, these techniques alone will not control an established infestation. Therefore, chemical methods must also be employed as part of a comprehensive bed bug management program. As stated earlier, most modern pesticides will not control bed bug infestations when used individually. However, combinations of products with different formulations and modes of action have been evaluated in the field and have been found to produce satisfactory control. These products must be applied according to the product label and the treatment area must be regularly monitored to make sure that the products are working. Field evaluations have determined that microencapsulated products containing pyrethroids are an effective residual spray because the micro capsules stick to the bed bug body allowing for enough exposure time to kill resistant bed bugs. These products can be used for application into cracks and crevices where bed bugs hide and also along baseboards or ceiling/wall junctions where bed bugs will often harbor when the infestation levels are high. In addition to the crack and crevice applications, products labeled for upholstery treatment can be applied to infested furniture as well as to the mattress and box springs. Some mattress products have residual activity (pyrethroids) while other "non-toxic" products do not. The non-toxic products that contain isopropyl alcohol or sodium laurel sulfate as the primary killing agent will kill bed bugs on contact. Yet, these products evaporate almost immediately after application and bed bugs that survive the treatment will continue to bite and reproduce. Residual dusts are particularly useful in the frame of the box springs and wood components of the other furniture because they stay within the application site and have a very long residual. Residual dusts containing pyrethroids also adhere to the bed bug's body allowing for the long exposure period (possibly days) necessary to kill resistant bed bugs. "Non-toxic" desiccant dusts will also kill bed bugs but they too may take several days to work. Baseboard, and crack and crevice treatments with insect growth regulators are useful in that they will kill many immature bed bugs during the final molt. However, there is no evidence that insect growth regulators will kill or sterilize adult bed bugs. Although aerosols and foggers are frequently used for bed bug elimination, they are not effective control products because they do not penetrate into bed bug harborages.

Overall, a complete bed bug treatment should include the removal of infested items for either treatment or disposal, the laundering of infested clothes and bedding, the elimination of clutter, the sealing of all small cracks and holes that might provide bed bug harborage, a complete vacuuming of all carpeting and furniture, steam cleaning of upholstered furniture and mattresses to kill bed bugs and their eggs, and treatment of the mattresses and box springs with a non-toxic mattress treatment (preferred) or a labeled residual insecticide. After treating the mattress, both the mattress and box springs should be encased in bite proof, escape proof mattress covers. The infested room should be treated with a combination of residual insecticide spray and an insect growth regulator. These products should be applied according to the label to cracks and crevices, baseboards, and any other bed bug harborage locations. The infested room and all adjoining rooms should then be inspected (and/or treated) weekly to determine the efficacy of the treatment products and to make sure that the bed bug population is being eliminated.

Summary

Most entomologists and pest management professionals believe that the resurgence of human bed bugs (both *Cimex lectularius* and *Cimex hemipterus*) presents the single greatest indoor pest management challenge in decades. Since the bed bugs' widespread reappearance in the 1990s, the common bed bug has become a full blown epidemic with new infestations reported in most European countries and in all 50 states in the United States. Likewise, the tropical bed bug has spread throughout the tropics in the last 10 years increasing its range to infest Australia and reestablishing populations in Singapore and other tropical nations where they had been previously eradicated. Because these insects have never completely disappeared from developing nations they have been continuously treated with many insecticide products over the last 50 years. This continuous pesticide pressure has selected for bed bug resistance, particularly to pyrethroids. These pyrethroid resistant populations present a unique problem in developed nations where public opinion and federal legislation has eliminated entire classes of insecticides from indoor use due to their perceived toxicity. Pyrethroids have been one of the few chemical classes that remain available for indoor use due to their low mammalian toxicity. As a result, pyrethroids are the most frequently used class of chemistry for bed bug control in the United States today. However, with increasing bed bug resistance these products will gradually become less effective at controlling new infestations. Because of the prevalence of bed bug resistance many researchers believe that the bed bug epidemic will become much more severe in the future.

The key to bed bug control in developed nations will ultimately be education. People will have to accept that bed bugs exist and learn how to avoid transporting bed bugs to their homes (from hotels, taxis, air planes, camp cabins, movie theaters, laundromats, day care centers, multiple unit housing, etc.) during the course of their daily activities. The ability of the average citizen to identify bed bugs and bed bug evidence will be critical for them to successfully protect themselves and their home from bed bug infestations.

References

Cooper R, Harlan H (2004) Bed bugs and kissing bugs. In: Hedges S (ed) Mallis handbook of pest control, 9th edn. GIE Publications, Cleveland, OH, pp 494–529

Doggett S, Geary M, Russell R (2004) The resurgence of bed bugs in Australia: with notes on their ecology and control. Environ Health 4:30–38

Harlan H (2006) Bed bugs – importance, biology, and control strategies. Armed Forces Management Board Technical Guide No. 44. http//:www.afpmb.org/pubs/tims/TG44/TG44.htm

Johnson CG (1942) The ecology of the bed-bug, *Cimex lectularius L* in Britain. J Hyg 41:345–361

Moore DJ (2006) Evaluation of multiple insecticidal products for control of the common bed bug (*Cimex lectularius,* (L.)). Unpublished M.S. thesis, Virginia Tech University, Blacksburg, VA, 118 pp

Newberry K (1989) The effects on domestic infestations of *Cimex lectularius* bed bugs of interspecific mating with *Cimex hemipterus.* Med Vet Entomol 3:407–414

Potter M (2006) The perfect storm: an extension view on bed bugs. Am Entomol 2:102–104

Usinger S (1966) Monograph of Cimicidae. Thomas Say Foundation Vol. VII. Entomological Society of America, Lanham, MD, 585 pp

Vall Meyers M, Hall A, Inskip H, Lindsay S, Chotard J (1994) Do bed bugs transmit hepatitis B? Lancet 343:761–763

Webb P, Happ C, Maupin G, Johnson B, Ou C (1989) Potential for insect transmission of HIV: experimental exposure of *Cimex hemipterus* and *Toxorhynchites amboinensis* to Human Immunodeficiency Virus. J Infect Dis 160:970–977

Bee Bread

A pollen and honey mixture fed to bee larvae by worker bees

Bee Flies

Members of the family Bombyliidae (order Diptera).

► Flies

Bee Lice

Members of the family Braulidae (order Diptera).

► Flies
► Bee louse

Bee Louse, Bee Fly, or Braulid, *Braula coeca* Nitzsch (Diptera: Braulidae)

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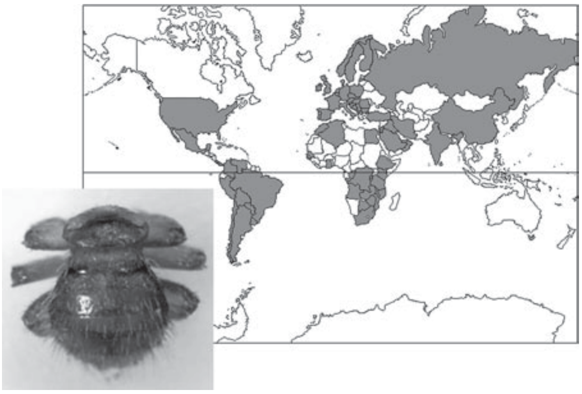
The bee louse, *Braula coeca* Nitzsch (Diptera: Braulidae), is a wingless fly that lives as a commensalist in western honey bee (*Apis mellifera* L.) colonies. Not much is known about the bee louse as its biology has been studied only irregularly since the 1920s. The fly is presumed to be harmless to its host, although this point is debatable. It is found in many countries, and because no true economic damage can be attributed to the fly, it probably poses a minimal threat to bees.



Bee Louse, Bee Fly, or Braulid, *Braula coeca* Nitzsch (Diptera: Braulidae), Figure 24 An adult *Braula coeca* (photo by James Ellis, University of Florida), and its worldwide distribution (from Ellis, Munn (2005) The worldwide health status of honey bees. *Bee World* 86(4):88–101).

Bee Louse Life Cycle and Behavior

Adult bee lice (Fig. 24) are small (<1.5 mm long) and are covered in spine-like hairs. They are round in shape and unlike most flies, have neither wings nor halteres. They are reddish-brown in color, which often leads to their misdiagnosis as varroa mites, *Varroa destructor*. Structurally, physically, and their location on the adult bee all are similar or the same for varroa. One noticeable difference between the bee louse and varroa is the presence of six legs on the bee louse while varroa has eight. Further, the adult bee louse has a raised appearance while varroa are flatter and more oval than the bee louse. Despite this, both are very small and difficult for most people to distinguish with the naked eye.

The eyes of adult bee lice are located just above the antennae. They occur as pale spots on the surface of the cuticle and are surrounded by pigmented chitinous rings. The terminal joint of a bee louse's 5-segmented tarsi is divided and modified with comb-like teeth, an adaptation that allows the fly to cling to bees. The thorax is very short. When viewed dorsally, it is less than half as long as the head, resembling an abdominal segment. The scutellum is absent.

Presumably, bee louse adults feed on nectar and pollen, as well as food and other excretions passed between adult bees trophallactically. Regarding the latter, bee louse adults often are found on the heads of workers, drones, and especially queens. More than 180 bee louse adults have been found on a single queen.

While on the head of its host, the fly will steal food from the mouth of its host as the host is fed, or is feeding another bee. There is some evidence that bee louse adults can induce regurgitation from the bees. They accomplish this by scratching the upper edge of the bee's labrum until the bee extends its tongue, at which time they will feed on food or other secretions that the bee offers.

Bee louse eggs are white, oval shaped, and have two lateral flanges. The flanges are flat and extend parallel to each other toward the long axis of the egg. The eggs range from 0.78–0.81 mm long and 0.28–0.33 mm wide without the flanges. Including flanges, the eggs average 0.84 × 0.42 mm (l x w). Female bee lice can oviposit a number of places in the bee nest (empty cells, brood cappings, debris on the floor) but only eggs oviposited on honey cappings hatch. The incubation period of the egg can range from 2–7.4 days, depending on the season.

After the incubation period, larvae emerge from the eggs oviposited on the waxy cappings of honey comb. Upon emergence, the larvae construct a tunnel under the cell cappings. This is the most noticeable damage attributed to the bee louse. Larvae tunneling under the cell cappings can visually taint the waxy cappings. Although some consider this damage, it is of minor economic importance. Regardless, the intersecting tunnels are a common sign of bee louse presence. Many beekeepers have seen this damage but few recognize it for what it is. It is believed that bee lice larvae feed on honey and pollen residues encountered while tunneling under the cell cappings. There is a modicum of control suggestions for the bee louse, largely because it is not considered a major pest. However, many of the synthetic pesticides used against varroa also demonstrate activity against the bee louse.

Larvae of the bee louse have three larval instars, ranging from 7.1–10.8 days. Following this time, the larvae become prepupae, a stage that can last from 1–2.7 days. During this time, the prepupa has a creamy-white appearance. The developing pupa is enclosed in the larval skin. The white/yellowish pupae are 1.4–1.7 mm long × 0.5–0.75 mm wide. The life cycle begins again as the adult fly emerges.

Reference

Morse RA, Flottum K (eds) (1998) Honey bee pests, predators, and diseases, 3rd edn. A.I. Root Company, Medina, OH, 718 pp

Bee Milk

Also called royal jelly, this is a substance that is secreted by *Apis* nurse bees from a gland on their head (the hypopharangeal gland), mixed with crop contents, and fed to bee larvae. All bees are fed bee milk for the first 3 days, but larvae destined to become queens are fed this material throughout their larval development whereas future workers are switched to nectar and pollen.

Bee Mites

Some species of mites (Acarina) can be serious pests of honey bees.

► Varroa Mites, Tracheal Mite, Mites

Bees (Hymenoptera: Apoidea: Apiformes)

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Bees essentially are wasps that turned to pollen for dietary protein. A combination of distinctive features, taken together, make bees unique among insects. (i) Sociality, characterized by overlapping generations, cooperative brood care and a reproductive division of labor between fertile queens and sterile female workers, has evolved multiple times within the bee lineage. Presumptive intermediate stages of sociality are represented by at least several living species, and thus are available for observation, evolutionary study, and experimental manipulation. (ii) Bees, unlike most other herbivorous insects, dine solely on pollen and nectar or floral oils. This dietary transition from their carnivorous ancestors was accompanied by the evolution of branched body hairs which aid bees in picking up pollen, plus modification of the hind legs or ventral abdominal surface for carrying large loads of pollen. These features typically distinguish bees from wasps. (iii) Unlike most insects, each adult female of every non-parasitic bee species, whether social or not, rears her young in a nest. Thus, all food and shelter needs of bee larvae are provided by their mother, or one or more sisters if the species is social, or the host female if the species is parasitic. (iv) From the central nest, females daily venture forth repeatedly on spatially extensive foraging trips to acquire floral resources for their brood. These trips require remarkable navigational skills equaled by few other insect taxa. (v) As a consequence of their extensive foraging at flowers, bees have become the primary biotic agents of pollination for continental floras worldwide. No other animal group so dominates this, or the other great plant-animal mutualism, seed dispersal.

Evolutionary History

Bees (Hymenoptera: Apoidea: Apiformes) likely arose in the Cretaceous, perhaps 120 million years ago, when they diverged from the carnivorous habits of their closest relatives, the sand wasps (Hymenoptera: Apoidea: Spheciformes). Flowering plants (angiosperms) had made their debut by this time. Most paleontological material consists of bees entombed in amber (polymerized tree resins) millennia later. Specimens from the Eocene (40 million years ago) are common. They are typically workers of the stingless bees (Meliponini) that probably became mired while gathering resin to seal their nest cavities. These represent highly evolved social genera that remain extant today, suggesting a much earlier origin for bees. Tantalizing casts of much earlier fossil nest cells are also reported, but their identity remains controversial.

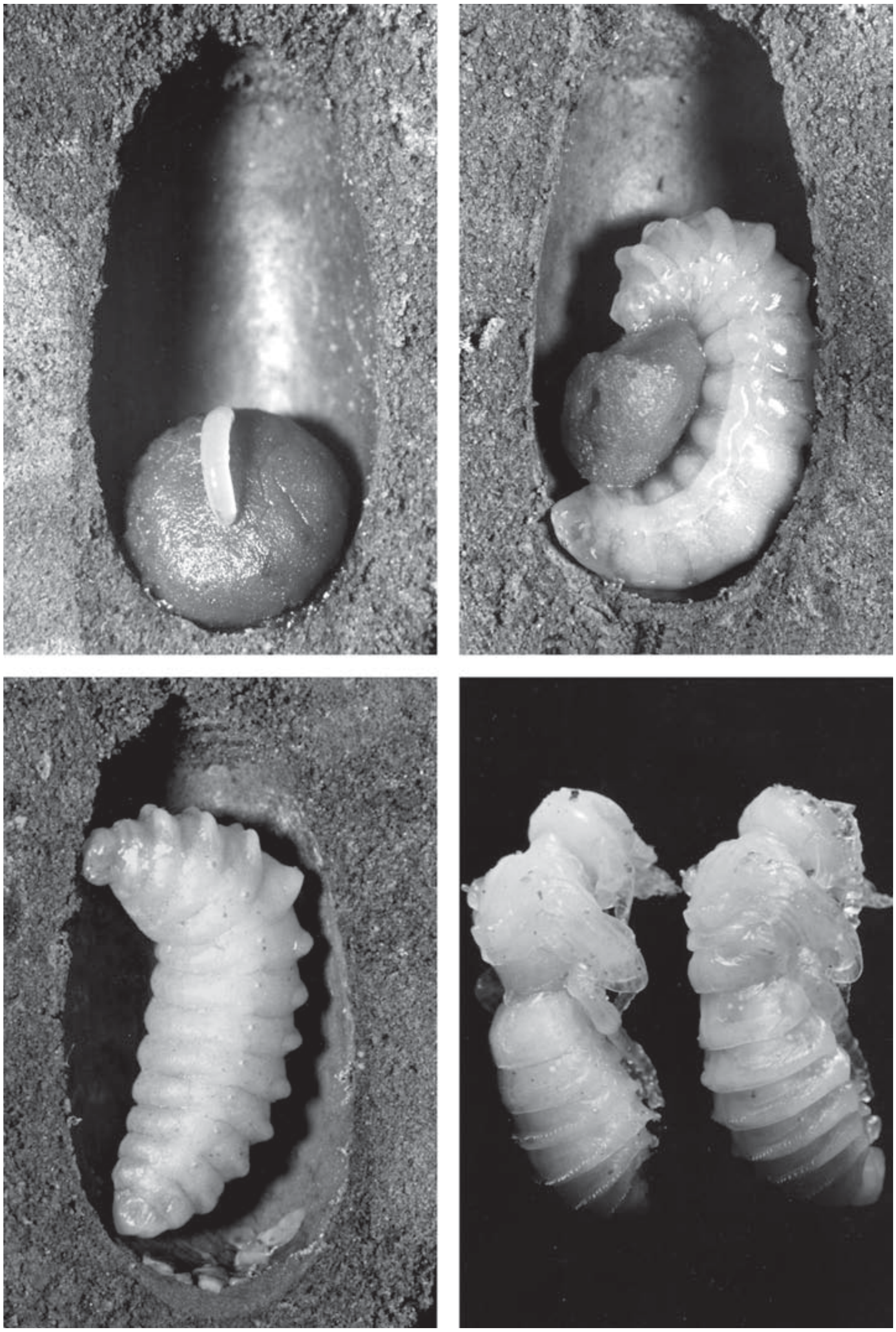
Diversity and Distribution

There are more species of bees today than the sum total of mammals, reptiles, amphibians and birds; 17,000 species of bees have been described, perhaps another 10,000 await discovery. They are distributed among only seven families. The largest genus (*Andrena*) has 1,400 described species; many have more than 100. Bees are native to all continents but Antarctica. Few species are found on isolated oceanic islands, but ranges of some hardy species extend well north of the Arctic Circle. Only social bees achieve maximum diversity in lowland tropical rainforests. Non-social (or solitary) species are most diverse in drier, more seasonal biomes of the world' s temperate zones. These include the Mediterranean Basin and areas of similar climate around the world (e.g., western South Africa, southern California, central Chile and Argentina, much of Australia) and the more vegetated, warm deserts (e.g., Sonoran, Chihuahuan and Colorado deserts of the southwestern U.S. and adjacent Mexico). Warmer grasslands also can be productive, such as the Great Plains of the U.S. In these regions, several hundred bee species can be easily expected in any given locality.

Development and Life Cycle

Like other insects with complete metamorphosis, bees pass through four discrete life stages (Fig. 25). Bee eggs are sausage-shaped. Those of the solitary, non-parasitic species can be proportionally huge for an insect; eggs of some large carpenter bees (*Xylocopa*) are 16 mm long. Non-social bee species are much less fecund than most insects, laying only 10–25 eggs in their lifetimes, averaging one to two per day. As with other Hymenoptera, progeny sex is determined by egg fertilization: male eggs remain unfertilized and are thus, haploid. Bee larvae are gently curved, soft, white, blind, largely immobile and defenseless grubs. Only specialized instars of some cleptoparasitic species are mobile and armed with powerful mandibles, adaptations that they use to assassinate host larvae before consuming the host' s provision masses.

Larvae of nearly all solitary species and most eusocial species receive an individual cache, or mass provision, of pollen moistened with nectar, or occasionally, floral oils. Provision shape and consistency varies from firm, spherical pellets to a soupy gruel on which the larva actually floats. Larvae pass through four molts (so five instars) to



Bees (Hymenoptera: Apoidea: Apiformes), Figure 25 **Bee life cycle, illustrated using the alkali bee, *Nomia melanderi* (Halictidae): (top left) egg atop a completed provision mass. Note the polished waterproof cell lining applied to the soil matrix; (top right) third instar larva feeding on remaining provision; (lower left) prepupa, the post-feeding larval resting stage; (lower right) two pupae (removed from their nest cells) (photos by William Nye).**

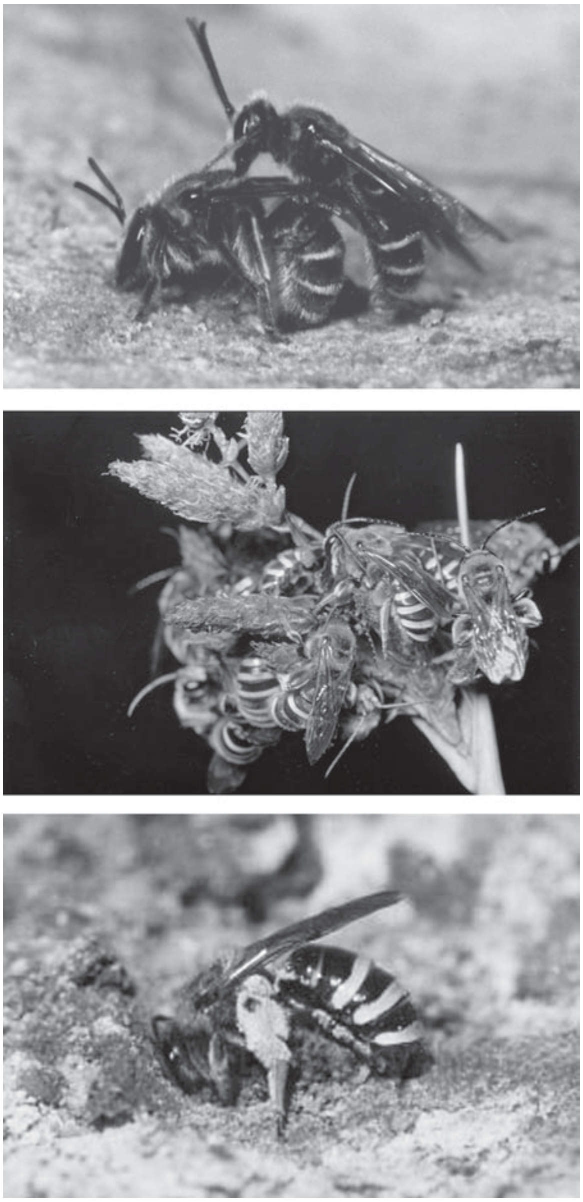
accommodate their rapid growth, consuming their provision mass in a few weeks. Larvae do not defecate until they are mature. Once the provision mass is consumed, larvae of many (but not all) species then spin a cocoon. The final larval stage is the prepupa, which is more robust and resistant to desiccation than the earlier instars, but still grub-like. This is the typical resting, or diapause, stage for those temperate-zone species whose single adult generation flies later in spring or summer. Unlike most other insects, bees do not weather inhospitable seasons as pupae. Rather, bee pupae are quite delicate, resembling waxen versions of the adult. If a bee species is one that flies in the early spring (allowing little warmth for further development), then the pupal stage lasts only a few weeks, yielding an adult that will remain in the cocoon (or nest cell) to overwinter. Some halictids (sweat bees), as well as bumble bees, emerge as adults, mate, and then disperse before overwintering.

Nesting

All larval bees live in a nest selected, constructed, maintained, defended and provisioned by their mother, sisters (social species) or host (parasitic bee). A genus of bee often can be recognized by its nesting substrate and nest architecture. Most bee species nest underground, typically excavating a central, cylindrical tunnel that is either partitioned into nest cells, or from which lateral tunnels branch that terminate in nest cells. Soil cliffs as well as more horizontal surfaces are used. Excavated soil on horizontal surfaces is often heaped in a small cone or delta of irregularly sized pellets, the "tumulus." Nest depths differ among species, ranging from a few centimeters to several meters if in sandier soils. Cells are often egg- or barrel-shaped, just large enough for a mother bee to fit with her assembled provision mass. Cell walls are commonly smoothed, even polished, usually with the addition of a secreted waxy or membranous waterproof lining, or alternatively, plant resin. Other bee species nest above ground, excavating pithy stems of plants or adopting abandoned tunnels chewed by wood-boring larvae of beetles and some other insects. Some carpenter bees (*Xylocopa*) can chew tunnels directly into sound wood. The highly social honey bees and stingless bees often build their nests in hollow tree cavities. Free-standing nests are made by a few paleotropical honey bees (pendant wax combs) and a few other bees (mostly orchid bees and some megachilids that use clay or resin).

Mating Biology

Male bees do not contribute to nesting (excavation, foraging, defense) (Fig. 26). With few exceptions, males are not welcome in the nest. They spend their days patrolling for receptive conspecific females, and their nights sleeping on flowers or vegetation, or in shallow burrows underground. Males of various species enhance their encounter rates with females using one or more search and/or advertisement strategies employing scent and vision. Among non-social species, males are often protandrous, emerging some days before females of the year. Males of floral specialists may patrol preferred floral hosts, especially if females of their species mate repeatedly during their lifetimes. Males also may patrol nesting sites; among species whose females mate but once and whose nests are aggregated, males may compete intensively to find freshly emerged virgin females, guided by the virgin female's scent. Conversely, males may apply scent-marks to attract females to a sort of trapline that males patrol. These can sometimes extend for hundreds of meters. Honey bees, some bumble bees and large carpenter bees maintain aerial territories. Some orchid bees reportedly form "leks" perfumed with scents synthesized from floral oils of orchids. A few recent cases report flightless males that linger in their natal nests to mate with their sisters. In general, courting and mating are brief affairs for bees. Most species are monandrous, each female mating but once in her lifetime. All



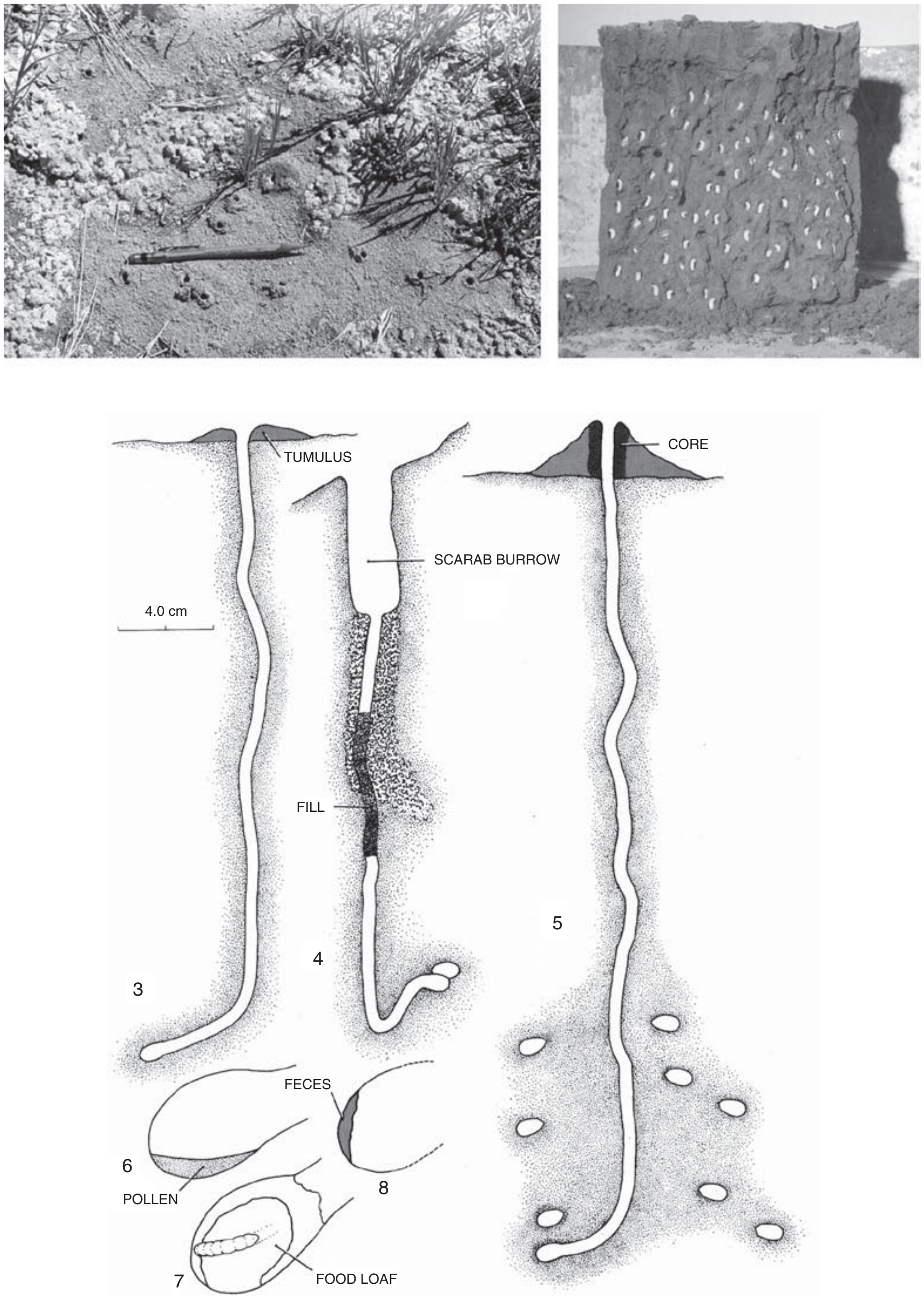
Bees (Hymenoptera: Apoidea: Apiformes), Figure 26
Mating adults (above), male atop female (photo by William Nye); aggregation of males (center) sleeping together atop plant stem (photo by William Nye); female at nest entrance (below). (photo by James Cane).

female bees are able to store live sperm to varying degrees; at the extreme, queens of social species store live male sperm for months or even years. Hence, sperm often outlive the male bees that produce them.

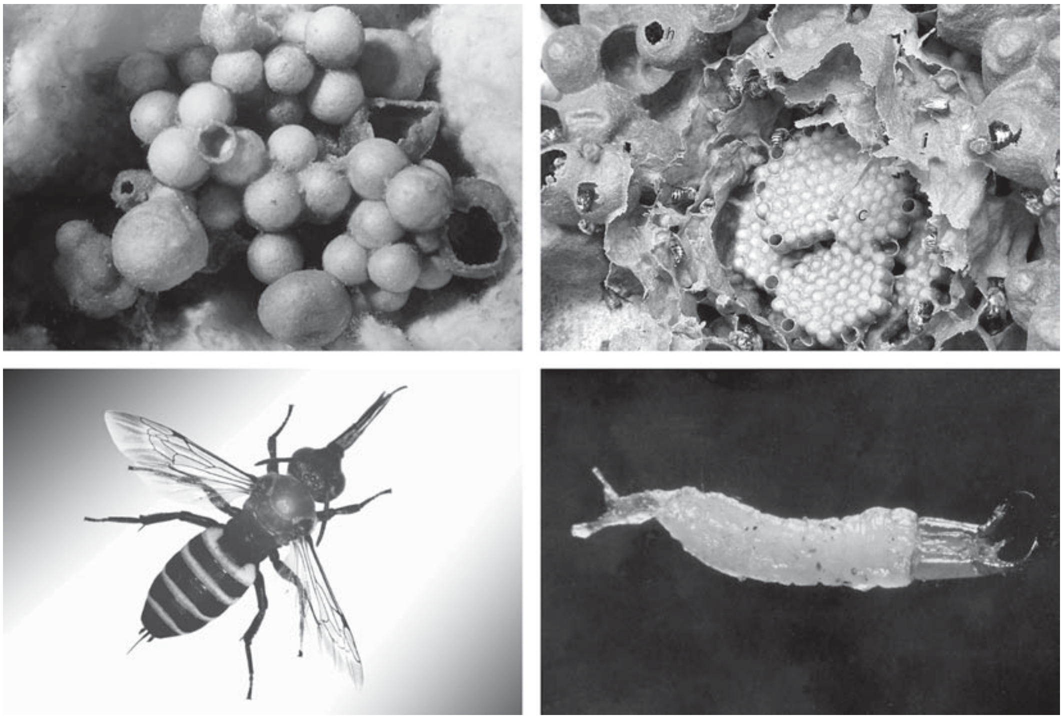
Sociality

Bees have lineages representing all degrees and hypothesized evolutionary steps of sociality, including reversion to solitary habits. Populations of a few species range from solitary to social depending on ecological circumstance. Less social arrangements include: communal species, wherein reproductive females sometimes share in a single nest's construction and defense but otherwise act solitarily; semisocial colonies founded by a group of (likely) sisters; subsocial species in which mothers actively care for growing daughters, that in turn may linger as adults to aid their mother; and several other much rarer arrangements. Many non-social species, especially ground-nesters, will nest gregariously (Fig. 27) in populous aggregations of hundreds to many thousands of individuals. During adult activity, these bee "cities" can be dramatic, with a dense traffic of foragers and patrolling males producing a loud, daylong hum.

The hallmarks of higher sociality ("eusociality") are an overlap of generations (mothers and daughters), cooperative brood care by workers, and reproductive division of labor (queens and workers). Workers are rarely, if ever, mated, and so, if they lay eggs, these are male. For primitively eusocial species (some sweat bees and carpenter bees, nearly all bumble bees), nests are founded in the spring by a single, mated female (gyne), as with solitary species. In rare cases, there are several foundresses. This mother bee builds a nest and prepares cells. Each cell receives a ball (Figs. 28 and 29) of pollen moistened with nectar and a single egg. The cell is then sealed. Emerging daughters remain with the nest rather than dispersing, helping their mother construct, provision and defend her nest. The original foundress, mother to the nest, then becomes the colony's primary egg-layer (queen). The more eusocial species have morphologically distinct queens and workers. Primitively eusocial colonies grow to, at most, a few hundred workers. Late in the summer or early autumn, reproductives are produced, and mate; only the future queens pass the winter in diapause.



Bees (Hymenoptera: Apoidea: Apiformes), Figure 27 **Gregarious nesting (above left) showing dark soil tumuli atop a square meter of soil surface (photo by James Cane); core (1 cu. ft.) of nesting soil (above right) from alkali bee nesting aggregation, showing numerous white prepupae in their individual nest cells (photo by William Nye); schematic (below) of an excavated subterranean nest of the neotropical bee *Tapinotaspis tucumana* (Apidae). Nests and enlarged views of three nest cells (Reproduced with permission from the American Museum of Natural History. Artwork by Jerome Rozen, Jr.).**

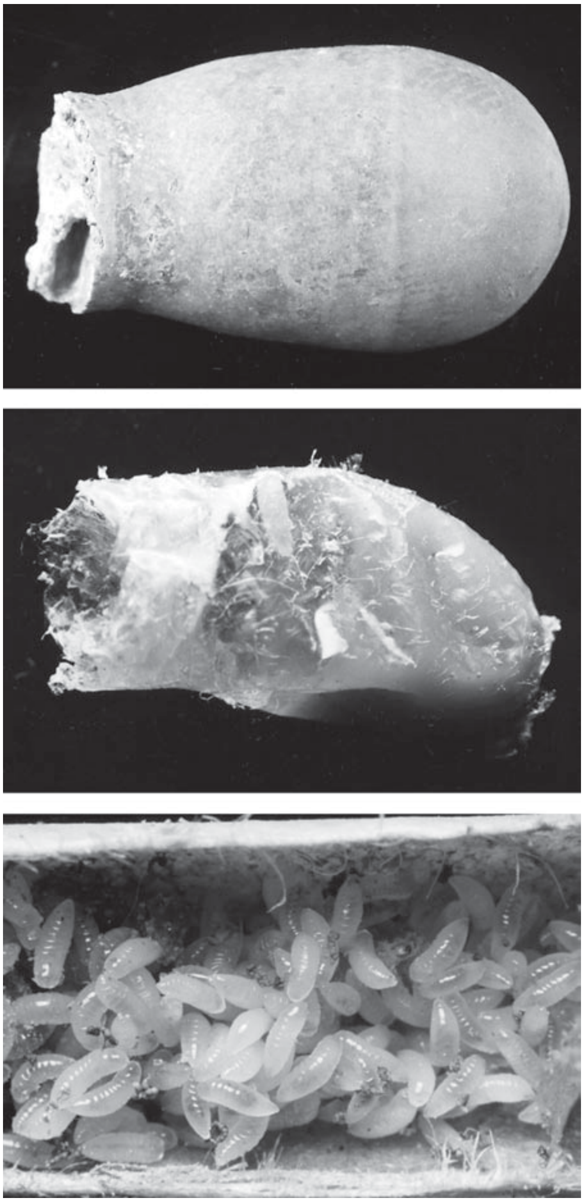


Bees (Hymenoptera: Apoidea: Apiformes), Figure 28 **Laboratory nest of the bumble bee *Bombus morrisoni* (Apidae) (above left) showing nest cells and honey pots clustered amid insulative cotton batting; Nest of a Brazilian *Melipona* sp. (Apidae)(above right). The thin pliable sheets of the involucrum (i) have been peeled back to reveal the topmost tier of horizontal combs (c). Between the involucrum and the wall of the cavity are the large pollen pots and honey pots (h). Honey is visible in those pots that remain open (Photo by James Cane); adult female of the cleptoparasitic bee, *Triepeolus dacotensis* (Nomadinae) (lower left). Note paucity of hairs, lack of pollen-transporting structures, and the exserted sting; first instar "assassin" larva of *Triepeolus dacotensis* (Nomadinae) (lower right). Note its long recurved mandibles, which are used to grip and kill the host egg or young larva. Subsequent instars resemble normal bee larvae (photos by William Nye).**

Only the stingless bees (Meliponini) and honey bees (*Apis*) are highly eusocial. Most reside in the humid tropics. Their colonies are tightly integrated and perennial, populated by thousands of workers headed by long-lived queens that are dependent on worker care. Their colonies reproduce by "fissioning," when swarms of workers accompany a queen to found a new colony.

Foraging

Except for queens and drones of highly eusocial species, all bees visit flowers. For males and individuals of cleptoparasitic species, it is only for self-maintenance and sometimes mates. All other females seek, gather and transport nutritious substances (typically pollen and nectar) and sometimes, nesting materials for their progeny. Species of honey bee size will regularly fly a kilometer or more to desirable bloom. Using the sun and local landmarks for navigation, they can then fly directly home at 15–25 kilometers per hour to find a nest entrance that is often no bigger than the bee, and, in the case of gregarious species, that is imbedded in an aggregation of hundreds or thousands of like-looking entrances of their conspecifics.



Bees (Hymenoptera: Apoidea: Apiformes), Figure 29 **Cast of nest cell of *Anthophora* (Apidae) (above); provisioned nest cell of ground-nesting *Colletes* (Colletidae), showing the thin, translucent membrane made of secreted polyesters (center); larvae of parasitic *Melittobia* wasps (Hymenoptera: Eulophidae) in nest cell of an *Osmia* bee (below) (photos by William Nye).**

Bees always take nectar at flowers. Nectar powers bees' flight and contributes carbohydrates and water to larval diets. Typical nectar sugars are glucose, fructose and sucrose. Few nectars are toxic. A retractable, complex proboscis allows bees to sip or lap nectar. A bee's access to nectar is constrained by body size, tongue length, and the flower's dimensions. Some carpenter bees, stingless bees and bumble bees regularly rob deep, tubular flowers of their nectar by perforating the corolla near its basal nectaries. Perhaps because bees can readily assess nectar volume, sugar constitution and its concentration, individuals and species can and will compare nectar yields of various flowering species, optimally choosing the most rewarding species at any given time. Some flowers, mostly tropical, secrete calorically rich oils rather than nectar. These are mopped or wiped up by bee species that have pads and "squeegees" of hairs specialized for the task, to be incorporated into larval provisions and sometimes, nest cell linings. Some ground-nesting species and many eusocial species synthesize and secrete their own calorically rich substances that they blend into progeny provisions.

Bees also seek pollen at flowers, which is their key dietary source of proteins, fats, minerals and sometimes starches, for themselves and their offspring. Pollen, of course, also contains the male gametes of flowering plants, so it really serves two reproductive purposes, plant ovule fertilization and bee reproduction. No effective dietary substitute for pollen has yet been devised for bees. Few animals match the nitrogen assimilation efficiency of bees, despite the indigestibility of the external shell, "exine," of pollen grains.

Pollen, in most cases, dusts the foraging bee as a powder that lodges in the vesture of branched hairs that envelop its body. Harvest may be enhanced by buzzing, biting, scraping and scrabbling. Many specialized structures, hairs and behaviors of foraging females then work in concert to efficiently groom and accumulate pollen from the body for transport. Pollen is transported in a brush of hairs called a "scopa," often on the hind legs (or under the abdomen of megachilids). A few taxa carry pollen internally in their crop (e.g., Hylaeus). Bumble bees, honey bees, orchid bees and stingless bees carry pollen in a pollen basket, or "corbicula," on the hind leg, a smooth, slightly concave surface surrounded by guard hairs that holds a damp pollen pellet.

Anthers of some flowers (e.g., tomato and blueberry) shed their pollen through apical pores or slits like a salt shaker. These require vibration to dispense their content of pollen. Some bees shake this pollen free by battering or stroking the anthers with their legs, while others bite the anthers to squeeze out pollen. Species of many genera can shiver their flight muscles while on the flower, sonicating these anthers to eject their content of pollen. This buzzing is audible. The effect can be duplicated with a vibrating tuning fork. Bumble bees frequently use this method of pollen extraction, even for flowers with anthers of normal morphology.

Many bee species are floral generalists ("polylectic"), taking pollen from many taxa of flowers, a necessity for the long-lived colonies of social bees. Foraging individuals often will display floral constancy, selectively visiting sequences of conspecific flowers on a given foraging trip, despite the availability of alternatives. Such preferences are labile, perhaps reflecting learning or memory constraints. In contrast, a third or more of the non-social species in a community may be "oligolectic." This is a fixed species-specific predilection to collect pollen from the same small subset of available flowering species, commonly one or several related genera within a plant family. Such unwavering fidelity is particularly common among desert bee faunas and vernal bees of the temperate zone. The reason(s) for oligolecty are not fully understood. In some cases, oligoleges seem to accumulate at reliable pollen hosts that produce generous quantities of pollen (e.g., willow, sunflowers, creosote bush, and blueberries). For other species, the association seems to reflect phenological specializations (e.g., crepuscular flowers, early spring blooms) or more or less private floral resources eschewed by other species (e.g., oil flowers of *Lysimachia* and their associated *Macropis* bees). Unlike insect herbivory, host chemical defenses rarely, if ever, dictate floral specialization by bees.

Pollination

Bees are the most important and cosmopolitan biotic pollination agents in most continental habitats, and for most prevalent plant families, such as the Asteraceae, Fabaceae, Lamiaceae, Orchidaceae, Rosaceae and Solanaceae. Few nocturnal flowers are pollinated by bees. Reciprocal co-evolution between bees and their flowers seems, at best, diffuse in nearly all cases, although adaptations that enhance attraction, resource extraction and pollination are evident everywhere. Most collected pollen ends up in a larval provision, not on a flower's stigma, but bees are still vastly more efficient than wind in moving pollen to receptive flowers. Bees are essential pollinators of some vegetable crops (or their seeds), many prominent fruit and seed-oil crops, forage legumes and a few nut or fiber crops. Crops that contribute the starches and refined sugars to the human diet are typically wind-pollinated or vegetatively propagated. Home and market gardeners benefit from pollination services of wild bees. In large mechanized agriculture, however, only hived honey bees can generally supply the millions of inexpensive foragers needed for pollination. In the past half-century, though, a growing minority of tree fruit, forage seed and greenhouse crops are benefiting from pollination services of managed solitary bees and bumble bees (rather than honey bees), a trend that seems likely to continue, given their often superior pollination efficiencies and the devastating effects of new pest problems suffered by honey bees.

Diseases, Parasites and Predators

Among insects, the superior life expectancies of bees result largely from superior maternal care of offspring. Females actively deter predators and parasites by biting, stinging and by use of chemical repellents. Nest cells are waterproofed and possibly fumigated with applied glandular secretions or plant resins. Despite such extensive maternal care and defenses, bees are nonetheless plagued by diseases, parasites and predators. Feeding larvae, in particular, succumb to various viral, bacterial and fungal diseases. Microorganisms commonly spoil provision masses, too. Nematodes and mites (mostly external) are ubiquitous bee parasites. Many larval insects devour the contents of bee nests, including clerid and meloid beetles. Others are internal or external parasitoids, including chalcidoid wasps, bombyliid flies and strepsipterans. The elaborate structural defenses of stingless bee nests attest to the intense predation pressures of ants and social parasites of the tropics. Adult bees are subject to the myriad predators of other mobile insects.

Cleptoparasitic, or cuckoo bees, are analogous to cowbirds and European cuckoos, surreptitiously inserting their eggs into the provisioned nest cells of their bee hosts. There are thousands of cleptoparasitic species, most associated with specific genera of host bees. They directly or indirectly exterminate the host larva, ultimately consuming its provision. Adult females spend much of the day searching for and evaluating host nests. They display numerous subtle adaptations to conceal their eggs from the host female and repair damage incurred to nest cells during oviposition. Odor concealment and mimicry may be practiced as well. Social bee species (other than *Apis*) host their own parasitic bees, often evolving from within their host's genus. Psithyrus queens usurp bumble bee nests, enslaving unwitting host workers to produce parasite progeny. Robber genera among the stingless bees (e.g., *Lestrimelitta*) raid host nests for honey and pollen.

Conservation

Human activities also can harm bees. Bees tend to be sensitive to broad-spectrum insecticides, which if used indiscriminately or carelessly by farmers or homeowners during bloom, can poison adults, or later, their progeny. No genetic resistance has been shown. Herbicides, when used to kill wildflowers, remove available forage for bees. Habitats and constructs that are extensive, monotonous and inhospitable (e.g., lawns, parking lots, wheat fields) fail to fulfill bees nesting and/or foraging needs, although bees can readily fly through a finer patchwork mosaic of these features if interspersed with favorable nesting and foraging habitats. Unlike accidental or misguided introductions of plants, vertebrates and shellfish, exotic bees have generally been of little ecological consequence, although ill-guided international trade (or smuggling) of honey bees and bumble bees has been disastrous in some recent cases. The greatest risk attending intercontinental transport of live bees is likely to be the inadvertent transport of diseases and pests, such as those that are currently devastating apiculture, especially *Varroa* and tracheal mites.

The Families of Bees

Seven families of bees are currently recognized. The Colletidae, Halictidae, Andrenidae, Melittidae and Stenotritidae are grouped as short-tongued bees, while the Megachilidae and Apidae are long-tongued bees. The five more common families are considered here.

Family Colletidae: Yellow-Faced, Masked and Plasterer Bees

Distribution: Worldwide, but Greatest Diversity is in the Southern Hemisphere, Including Australia. This is probably the oldest extant bee family. No studied species nests socially. Pollen is transported dry in hair brushes of the hind leg (e.g., *Colletes*) or mixed with nectar and carried internally in the crop (e.g., *Hylaeus*). Their tongue tips are distinctively bilobed. They nest underground, or rarely, in mortar and even sandstone (e.g., *Colletes*), in pithy stems (e.g., *Hylaeus*), or adopt holes in wood. The plasterer bees are so named for the peculiar, secreted, transparent, polyester membranes used to waterproof their nest cells; those of *Hylaeus* contain silk strands. *Hylaeus* (=*Prosopis*) (570 species) and *Colletes* (330 species) are the commonly encountered genera in the U.S. and Europe; *Leioproctus* has 300+ species in Australia and temperate South America; *Nesoprosopis* has radiated in the Hawaiian Islands, where many of its species appear to be endangered. This subgenus contains the only cleptoparasites in the family. *Hylaeus* may be the most cosmopolitan of all bee genera, found on all continents but Antarctica as well as many oceanic islands, their dispersal facilitated by their stem-nesting habits.

Family: Andrenidae

Distribution: Worldwide, Except Australia, Rare in the Moist Tropics. Species of this family nest underground. The family includes two enormous genera: *Andrena* (1,400 species, ubiquitous in north temperate regions) and *Perdita* (600 or more species, mostly of the American Southwest and northern Mexico). *Perdita* are small-bodied, including the tiniest bee, *Perdita minima* (slender, 2 mm long, 1/3 mg). A few species of *Perdita*, *Andrena* and *Panurgus* nest communally; no studied andrenid is social. There are no cleptoparasitic species in this family. Pollen is carried on the hind legs, and in some species, is moistened with nectar. Probably all *Perdita* are oligolectic, as are the majority of *Andrena* and species of other genera.

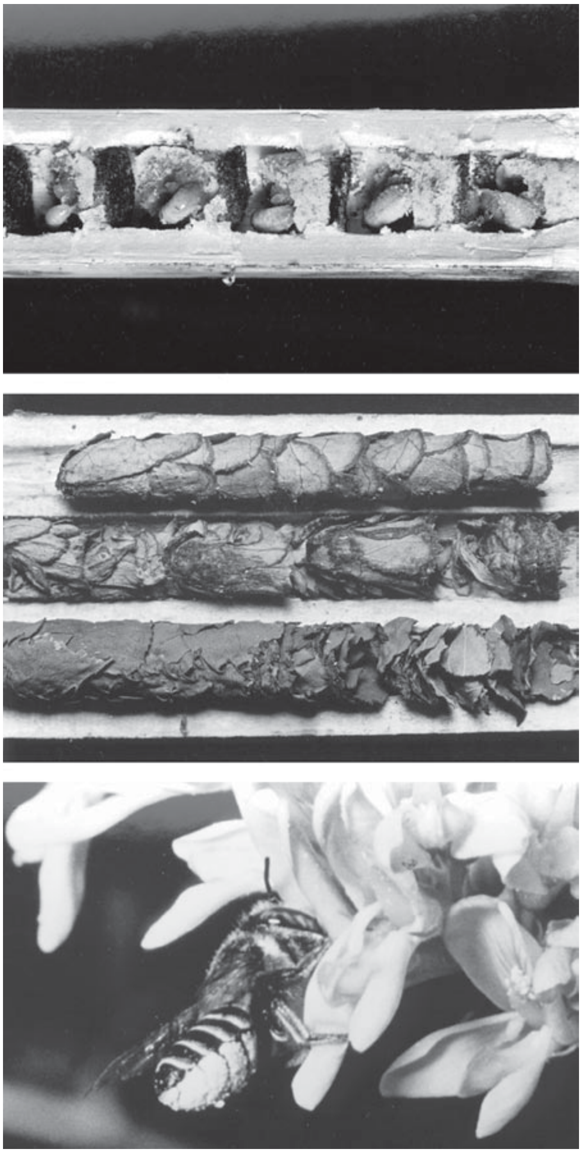
Family Halictidae: Sweat Bees, Alkali Bee, etc

Distribution: Worldwide. Most halictids are small or medium sized. Some taxa are commonly known as sweat bees because they alight on people's skin to lap up sweat for the salts that it contains. Many halictids are darkly colored, others are a brassy or brilliant emerald green. Some *Nomia* have striking pearly green or orange abdominal bands. Pollen is carried on the hind legs, typically dry. Their nests are burrows in soil, or occasionally, rotting wood, sometimes in dense aggregations. The common, cosmopolitan cleptoparasite genus in the family is *Sphecodes* (250 species). Halictids illustrate an unprecedented diversity of social organization, particularly among the 1,000+ species of *Lasioglossum*.

The alkali bee, *Nomia melanderi*, is the world's only intensively managed ground-nesting bee. In regions of the western U.S., alfalfa (=lucerne) seed growers construct large subirrigated nest sites with salt-crusted surfaces. Densities of 400 nests/m^2 over a hectare or more can be obtained with this gregarious bee. Nest sites can remain populous for more than 50 years. Another effective alfalfa pollinator, *Rhophitoides canus*, is less intensively managed in regions of eastern Europe for alfalfa seed production.

Family Megachilidae: Leaf-Cutting Bees, Mason Bees, Carder Bees and Others

Distribution: Worldwide. The common names for groups in this large family refer to the remarkable diversity of exogenous materials that they typically use to line or construct their nest cells. Many nest above ground in twigs, stems and wood, and will readily adopt drilled holes in these substrates (termed "trap nests"). A few even nest in abandoned snail shells. *Megachile* and others line their nest cells, and partition and cap their nest tunnels, with strips and disks neatly cut from leaves or petals; other species build with leaf pulp, resin, nectar, mud, plant hairs, or pebbles. Foraging females of non-parasitic species can be easily recognized, as they are unique in (Fig. 30) carrying pollen in a scopa solely beneath the abdomen. Nearly all species are solitary. There are several cleptoparasitic genera (notably *Coelioxys*, 300 species). *Megachile* is a cosmopolitan genus (900+ species); *Osmia* (300 species) are common in the Northern Hemisphere. The world's longest bee is *Megachile pluto* at 39 mm. Many megachilids are important pollinators, especially for plants in the



Bees (Hymenoptera: Apoidea: Apiformes), Figure 30 **Nest of *Osmia* (Megachilidae) in reed, split open to reveal partitioned nest cells each occupied by a single larva with its mass provision of pollen moistened with nectar (above); three nests of a leaf-cutting bee (*Megachile*: Megachilidae), consisting of a linear series of cells each wrapped with cut leaf pieces (center); female of the alfalfa leaf cutting bee, *Megachile rotundata*, visiting alfalfa flowers (below). Note the pollen load carried dry in a scopa of hairs beneath her abdomen. To the right is a "tripped" flower, the staminal column pressed against the banner petal. Good alfalfa pollinators trip the flowers frequently (photos by William Nye).**

pea and clover family (Fabaceae). The cavity-nesting species are the most successful stowaways in transoceanic travel.

The alfalfa leaf-cutting bee, *Megachile rotundata*, came to the U.S. from the Near East as a stowaway before 1937. Burgeoning feral populations of this bee prospered in the semi-arid western U.S. The species' value as an alfalfa pollinator soon became apparent. A multimillion-dollar industry developed in North America for cheaply mass rearing of this species for sale to alfalfa seed growers. Wooden or foam boards, each with several thousand nesting holes, are placed in shelters in alfalfa fields. Each shelter receives 50,000 or more females. This bee is versatile, pollinating other crops too, such as hybrid canola and various vegetable seeds.

Several species of mason bees in the genus *Osmia* are more recently being managed in Japan, the U.S. and Europe to pollinate tree crops in the rose family, such as apples, plums, sweet cherries and almonds. One of these species has been dubbed "the blue orchard mason bee." Only 250–300 blue orchard bees are needed to pollinate as many apple or cherry flowers as two to three hives of honey bees.

Family Apidae: Carpenter Bees, Orchid Bees, Bumble Bees, Stingless Bees, Honey Bees

Distribution: Worldwide. This family is large, ecologically diverse and continues to be taxonomically perplexing. One or more tribes of this family is most closely related to the lineage that evolved into today's highly eusocial Apinae. Many cleptoparasitic species are included (1,600 species). This unwieldy group is best recognized by its constituent tribes, of which there are many. Select ones are treated here.

Subfamily Nomadinae: Cuckoo Bees

Distribution: Worldwide. This is the largest group of cleptoparasitic bees (Nomada alone has 800 species). Most species are glossy, quite hairless and wasp-like with a rugged exoskeleton. They can commonly be seen patrolling low over the ground for host nests.

Subfamily Xylocopinae: Carpenter Bees

Distribution: Worldwide. Carpenter bees typically excavate nests above ground in pithy stems or even bore into sound wood. Cells are unlined. Most species are solitary, but some are subsocial or even primitively eusocial. Females overwinter as mated adults; they can be very long-lived. The large carpenter bees (*Xylocopa*) are primarily tropical. They can resemble bumble bees, but have a smooth, glossy dorsal abdomen and transport their pollen dry. *Xylocopa* pollinate commercial passion fruit; they are also adept nectar robbers. Males of some *Xylocopa* hover for hours in aerial territories, pursuing any and all small airborne objects. The small carpenter bees (*Ceratina*) nest in dead stems of roses, sumac, elderberry and some grasses.

The Corbiculate Apinae: Orchid Bees, Bumble Bees, Stingless Bees, Honey Bees

Distribution: Worldwide. This quartet of tribes contains all of the highly eusocial bees, as well as the primitively eusocial bumble bees and the mostly solitary orchid bees. All secrete wax, which they incorporate into their nest structures. They carry pollen on a specially adapted, smooth region of the hind leg referred to as the pollen basket or "corbicula." Taxonomists formerly grouped these four tribes as a separate family.

Tribe Euglossini: Orchid Bees

Distribution: New World Tropics, from Central Mexico into Argentina. The orchid bees are so named because the males collect scents from orchid flowers and, in the process, pollinate the orchids. The orchids provide no food, but rather produce scents which male euglossines collect and place in a glandular pocket of their enlarged hind legs. These perfumes attract mates. Several species have intricate male displays. These large bees are flying jewels, sporting metallic emerald, cobalt, violet and bronze colors as well as red, orange and yellow. They are important pollinators of many endangered tropical orchids and probably the Brazil nut, too.

Tribe Bombini: Bumble Bees

Distribution: The Americas, Europe, Asia, North Africa. Bumble bees (*Bombus*) are large, furry, often black and yellow, orange or red bees. They are common in the world's cooler climates, following mountain ranges into the tropics. Few species live in deserts or rainforests. They nest shallowly underground, often in abandoned rodent nests, or sometimes above ground, either in tree cavities or, less commonly, beneath a leaf heap on the forest floor. They actively brood larvae to warm them, and fan their wings at the colony entrance to cool its contents. Few other bees can fly in cooler weather. *Bombus* consists of primitively eusocial species and a lesser number of social parasites. They are important pollinators in alpine, boreal and subarctic habitats. Queens of species such as *B. nevadensis* and *B. dahlbomi* are the world's most massive bees, weighing a gram or more (the weight of a raw almond).

Bumble bees are important pollinators of several crops, especially red and crimson clover. The honey bee proboscis is too short to probe such deeply tubular flowers. Bumble bees, having longer tongues, work these flowers efficiently. Bumble bees have been imported into New Zealand and Chile for clover pollination. They aid in the pollination of several other crops like alfalfa, and several fruits, especially blueberries, cranberries and kiwi. A multimillion-dollar global business has emerged from Europe for year-round propagation of disposable bumble bee colonies to pollinate greenhouse vegetables like tomatoes, peppers, eggplants and squashes. Introduction of these few managed species outside of their native ranges can lead to feral populations that pose problems for native *Bombus* and perhaps other bees.

Tribe Meliponini: Stingless Bees

Distribution: Old and New World Tropics. The stingless bees are highly eusocial, and as a group, exhibit a sweeping diversity of adaptations and natural history traits. Their permanent colonies can be populous, containing between 300 and 80,000 workers. Although stingless, many can defend their nests with irritating bites sometimes accompanied by caustic secretions. Queens are morphologically distinct from workers, their status sometimes determined genetically, in other cases as an individual larva's reproductive gamble. Of the 260 known species, 70% are found in Central and South America. They are the most common insects in Dominican and Baltic amber.

Stingless bees usually build nests in tree hollows, although some species nest on exposed surfaces, in underground cavities, or in termite or ant nests. Workers fashion a hard shell of "batumen" for the nest, consisting of wax blended with resin, mud or vegetation. Intricate nest entrance platforms and tubes are fashioned from wax, resin, or even plant latex. Within this shell, honey and pollen are stored in large irregular waxen pots. These rim the brood chamber, whose exterior is delineated by layers of pliable, delicate sheets of the "involucrum," made of insulative wax imbued with resin. Within this chamber are the waxen combs dedicated to brood rearing, grouped in horizontal tiers supported by thin pillars, reminiscent of nests of hornets or yellow-jacket wasps. Cells are typically mass provisioned with pollen, honey, and in some genera, glandular secretions (in a few cases, consisting of digested carrion). Some genera (e.g., *Lestrimellita*) rob nests of other stingless bees for their honey and pollen stores.

Colony fission is unlike *Apis*, because for meliponines, the new home is selected and furnished before the swarm issues from the parent colony. Workers assemble a complete new nest using materials transported from the parent colony. Only then does a group of workers and new queen fly to the new nest. The old queen is too large to fly and remains with the parent colony and its workers.

Workers of some stingless bees recruit nestmates to food sources, but in ways different from *Apis*. Scouts of some species scentmark trails from productive flowers to the nest, depositing mandibular gland secretions on surfaces every few meters. Returning to the nest, this scout buzzes loudly; the longer the buzz, the greater the distance of the food from the colony. The scout's behavior excites others which follow the odor trail to the resource. This method of recruitment communicates not only the direction and distance of food from the nest, but can lead other foragers directly to the food at any height by means of the odor trail. This three-dimensional road map is especially adaptive in towering tropical forests where flowers are frequently found high in the leafy canopy.

Stingless bees benefit people in several ways. In the Neotropics, *Melipona* colonies are cultured for honey in special wooden hives, although yields are meager (2–5 pounds per year). Stingless bees pollinate numerous tropical crops, but their economic impact has not been widely estimated. Stingless bees are promising pollinators for greenhouse crops.

Tribe Apini: True Honey Bees

Distribution: Europe, Asia, Africa, Now Introduced to all Continents Except Antarctica. There are 11 currently accepted species of true honey bees, all of the genus *Apis*. These are very different from all other bees, such that their evolutionary origins and ancestry remain unresolved. The genus is largely restricted to tropical Asia. Taxonomic diversity is centered in Indonesia, Malaysia and the Philippines, where new species continue to be discovered. Only the familiar western honey bee or "hive" bee, *A. mellifera*, is also native to Europe, northern Asia, and most of Africa. Its colonization of cooler regions was facilitated by its honey storage habits that fuels the workers' warming of their brood. Because we value this species for honey, wax and pollination, and can manage it in transportable hives, it has been further introduced throughout most of the world.

The western honey bee is among the most studied animals on the planet. Certainly their hallmark behavior is the remarkable abstract dance language performed by foragers and scouts for precisely communicating distance, direction and quality for resources, translating the direction of gravity into celestial bearings. Once thought unique to *Apis mellifera*, this and other behaviors now have been observed and studied for some of the lesser-known species of *Apis*, too.

Colony activities of *Apis* require sophisticated coordination. Much of the information is communicated olfactorily using pheromones. Like the Meliponini, all *Apis* are highly eusocial, maintaining populous perennial colonies. Queens, drones and workers are morphologically distinct. Among bees, only worker *Apis* have a barbed sting that lodges in the skin and continues to pump venom even after the worker bee has been killed and swept away. Colonies reproduce by fissioning, again like stingless bees, but in *Apis*, it is the old queen that departs with the swarm, whose workers then scout out a suitable nesting site at which they must construct their combs unassisted by the parent colony. This seems a riskier strategy, but it does allow swarms to disperse more widely. Honey bees thermoregulate their colonies using evaporative as well as convective cooling. Some tropical species undertake mass defecation flights to further nest cooling. Only *Apis* produce the familiar waxen vertical combs of uniform hexagonal cells that are reused over and over to house pollen, nectar (as honey) or progeny, although the wax itself cannot be recycled. Very unusual for bees, larval honey bees are fed progressively rather than with a cache of food, which together with the uniform comb dimensions, yields adults of very consistent size.

Species of *Apis* can be assigned to one of three groups, based on body size and nesting habits. Two dwarf honey bees, exemplified by *A. florea*, have small colonies of a few thousand small workers that construct beneath a branch a single exposed comb the size of a waffle. The top of this comb is broadened horizontally; recruitment dances performed on this surface are oriented simply in the direction of the food source. Several giant honey bees (e.g., *A. dorsata*) also build a single exposed vertical comb, often in conspicuous groups, but beneath a stout branch or cliff. Living curtains of the huge workers envelop the massive comb; when disturbed, they pour off *en masse* to assail any intruder. They are nonetheless robbed for honey. The remaining species of *Apis* build nests that consist of multiple wax combs housed in a hollow tree or rock cavity. Cavities enhance defense and insulation, but present problems with ventilation for temperature, humidity and atmospheric control. The most familiar representatives of this group are *A. cerana* and *A. mellifera*, which share many similarities, including their management in hives.

► Honey Bees
► Alfalfa Leafcutting Bee
► Apiculture
► Orchid Bees
► Hymenoptera
► Carpenter Bees
► Pollination by *Osmia* Bees
► Pollination and Flower Visitation
► African Honey Bees
► Cape Honey Bees

References

Free JB (1993) Insect pollination of crops (2nd ed) Academic Press, New York, NY

Michener CD (2000) The bees of the world. Johns Hopkins University Press, New York, NY

Michener CD, McGinley RJ, Danforth BN (1994) The bee genera of North and Central America (Hymenoptera: Apoidea). Smithsonian Institution Press, Washington, DC

Müller A, Krebs A, Amiet F (1997) Bienen: Mitteleuropäische Gattungen, Lebensweise, Beobachtung. Weltbild Verlag, Augsburg, Germany

O' Toole C, Raw A (1991) Bees of the world. Facts on file, New York, NY

Prys-Jones OE, Corbet SA (1991) Bumblebees, Revised edition. Cambridge University Press, Cambridge, UK

Roubik DW (1989) Ecology and natural history of tropical bees. Cambridge University Press, Cambridge, UK

Strickler K, Cane J (eds) (2003) Thomas Say publications in entomology: proceedings: for non-native crops, whence pollinators of the future? Entomological Society of America, Lanham, MD, 204 pp

Westrich P (1989) Die Wildbienen Baden-Württembergs. Allgemeiner Teil: Lebensräume, Verhalten, ökologie und Schutz. Verlag Eugen Ulmer, Stuttgart, Germany

Beesoniidae

A family of insects in the superfamily Coccoidae (order Hemiptera).

► Bugs

Beeswax

Beeswax is produced by *Apis* bees. It is produced only by young worker bees. Beeswax consists of fatty acids, esters, and hydrocarbons, and is secreted from glands on the ventral surface of the abdomen. The beeswax is used by the bees to construct honeycomb cells, in which their young are raised. After removal of honey from the honeycomb, the wax is purified and used for many products, particularly candles, wood furniture polish, shoe polish, lubricants, and skin treatments.

Beet Armyworm, *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae)

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Beet armyworm is a tropical insect, native to Southeast Asia. It is now found around the world, except for South America. Because it is a tropical insect, and lacks a diapause mechanism, it can overwinter successfully only in warm areas or in greenhouses. Daytime temperatures below 10°C are deleterious, and it rarely overwinters in areas where frost kills its host plants. Despite its inability to overwinter in cold areas, beet armyworm nevertheless invades temperate areas annually. Despite this invasive potential, however, it is not normally considered a threat in temperate areas, except sometimes in greenhouses.

Life History

Seasonal activity varies considerably according to climate. In warm locations, all stages can be found throughout the year, although development rate and overall abundance are reduced during the winter months. The life cycle can be completed in as few as 24 days, and six generations have been reared during 5 months of summer weather in Florida. However, generation times of 50–126 days have been observed, with a total of five generations annually, in southern California.

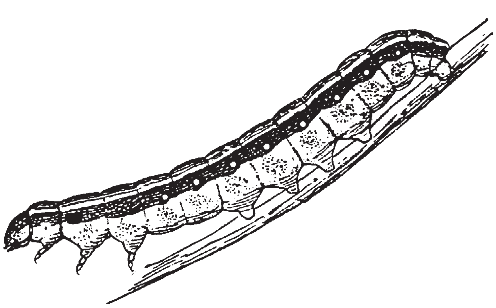
Eggs are laid in clusters of 50–150 eggs per mass. Females may deposit over 1,200 eggs during their lifetime, but normal egg production is about 300–600. Eggs are usually deposited on the lower surface of the leaf, and often near blossoms and the tip of the branch. The individual eggs are circular when viewed from above, but when examined from the side the egg is slightly peaked, tapering to a point. The eggs are greenish to white in color, and covered with a layer of whitish scales that gives the egg mass a fuzzy or cottony appearance. Eggs hatch in 2–3 days during warm weather, but the incubation period is extended to about 4 days when it is cool. The developmental threshold for eggs is estimated at 12.4°C.

Normally there are five instars, although additional instars are sometimes reported. Duration of the instars under warm (summer) conditions is reported to be 2.3, 2.2, 1.8, 1.0, and 3.1 days, respectively, and at constant 30°C, instar development time was reported to be 2.5, 1.5, 1.2, 1.5, and 3.0 days, respectively. Total larval development time is also influenced by diet quality. The developmental threshold for larvae is estimated at 13.6°C. Only 1 mm long at hatching, the larvae attain a mean length of 2.5, 5.8, 8.9, 13.8, and 22.3 mm during instars 1–5, respectively. Head capsule widths average 0.25, 0.45, 0.70, 1.12, and 1.80 mm, respectively.

The larvae are pale green or yellow in color during the first two instars, but acquire pale stripes during instar 3. During instar 4, larvae are darker dorsally, and possess a dark lateral stripe. Larvae during instar 5 are quite variable in appearance, tending to be green dorsally with pink or yellow color ventrally and a white stripe laterally. A series of dark spots, dashes or triangles (Fig. 31) is often present dorsally and dorsolaterally. Sometimes larvae are very dark in color. The spiracles are white with a narrow black border. The body is practically devoid of hairs and spines. It is easily confused with other caterpillar pests.

Initially the larvae of beet armyworm are gregarious, feeding as a group and skeletonizing plant foliage. As they mature they become solitary and quite mobile, often traveling from plant to plant. Cannibalism may occur when larvae are at high densities or feeding on food low in nitrogen.

Pupation occurs in the soil. The larva generally constructs a pupal chamber near the soil surface, digging only about one cm beneath the surface. The chamber is constructed from sand



Beet Armyworm, *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae), Figure 31 Mature larva of beet armyworm, *Spodoptera exigua* (Hübner).

and soil particles held together with an oral secretion that hardens when it dries. The pupa is light brown in color and measures about 15–20 mm in length. Duration of the pupal stage is 5–7 days during warm weather.

The moths are moderately sized, the wing span measuring 25–30 mm. The forewings are mottled gray and brown, and normally with an irregular banding pattern and a light colored bean-shaped spot. The hind wings are a more uniform gray or white color, and trimmed with a dark line at the margin. Mating occurs soon after emergence of the moths, and oviposition begins within 2–3 days. Oviposition extends over a 3–7 day period, and the moths usually perish within 9–10 days of emergence.

This insect has a wide host range, occurring as a serious pest of vegetable, field, and flower crops; even trees are sometimes attacked. Among susceptible vegetable crops are asparagus, bean, beet, broccoli, cabbage, cauliflower, celery, chickpea, corn, cowpea, eggplant, lettuce, onion, pea, pepper, potato, radish, spinach, sweet potato, tomato, and turnip. Field crops damaged include alfalfa, corn, cotton, peanut, safflower, sorghum, soybean, sugarbeet, and tobacco. Weeds also are suitable for larval development, including such common plants as lamb's-quarters, *Chenopodium album*.; mullein, *Verbascum* sp.; pigweed, *Amaranthus* spp.; purslane, *Portulaca* spp.; Russian thistle, *Salsola kali*; parthenium, *Parthenium* sp.; and tidestromia, *Tidestromia* sp. Although the host range is wide, there are significant differences in suitability even among hosts considered to be suitable.

Numerous natural enemies have adapted to this pest. Among the most common parasitoids are braconid wasps, and the tachinid *Lespsia archippivora* (Riley) (Diptera: Tachinidae). Predators frequently attack the eggs and small larvae; among the most important are minute pirate bugs, *Orius* spp. (Hemiptera: Anthocoridae); bigeye bugs, *Geocoris* spp. (Hemiptera: Lygaeidae); damsel bugs, *Nabis* spp. (Hemiptera: Nabidae); and a predatory shield bug, *Podisus maculiventris* (Say).

Pupae are subject to attack, especially by ants. Fungal diseases, *Erynia* sp. and *Nomurea rileyi*, and a nuclear polyhedrosis virus also inflict some mortality. The important mortality factors vary among crops, and among geographic regions. None except the nuclear polyhedrosis virus are highly specific to beet armyworm, which may explain why they are not especially effective. Virus is considered to be the most important mortality factor in Mexico.

Damage

Larvae feed on both foliage and fruit. Young larvae feed gregariously and skeletonize foliage. As they mature, larvae become solitary and eat large irregular holes in foliage. They also burrow into the crown or center of the head on lettuce, or on the buds of cole crops. As a leaf feeder, beet armyworm consumes much more cabbage tissue than diamondback moth, *Plutella xylostella* (Linnaeus), but is less damaging than cabbage looper, *Trichoplusia ni* (Hübner). This insect is also regarded as a serious pest of celery in California, and damage is directly correlated with abundance of late instar larvae late in the season. However, damage to foliage and petioles (stalks) during the first half of the growing season is of little consequence because these plant parts are removed at harvest. Tomato fruit is most susceptible to injury, especially near fruit maturity, but beet armyworm is not considered to be as threatening to tomato as is corn earworm, *Helicoverpa zea* (Boddie). Larvae not only damage tomato fruit, but may appear as contaminants in processed tomato.

Management

Pheromone traps can be used to detect the presence of adult beet armyworm. Visual sampling for damage and larvae, combined with an action threshold of 0.3 larvae per plant, was used successfully on cabbage in south Texas to determine the need for crop treatment with insecticides. Regular monitoring of crops, probably about twice per week, is recommended because adults frequently invade from surrounding crops or weeds.

The relatively high abundance of beet armyworm has stimulated frequent application of insecticides. Chemical insecticides and *Bacillus thuringiensis* are commonly applied to foliage to protect against defoliation. Insecticide resistance is a major problem in management of this insect, possibly because it attacks crops such as flowers, cotton, and vegetables – crops that are treated frequently with insecticides. Beet armyworm abundance is favored by frequent insecticide use, and it is considered to be a secondary or induced pest in some crops. Also, intensive use of insecticides for beet armyworm control in vegetables such as celery has stimulated outbreaks of other pests, principally American serpentine leafminer, *Liriomyza trifolii* (Burgess).

Host plant resistance in several crops has been studied for its contribution to beet armyworm pest management. In tomato, for example, resistance is correlated with total glycoalkaloid concentration in the fruit tissue. However, leaf tissue does not have any effective antibiotic chemistry, so larvae are able to develop on plants even if they have unsuitable tomato fruit.

Several insect pathogens may prove to be useful for suppression of beet armyworm. A nuclear polyhedrosis virus isolated from beet armyworm is fairly effective as a bioinsecticide under greenhouse conditions, where inactivation by ultraviolet light in sunlight is not a severe problem. It is as effective as commonly used insecticides, but presently is not commercially available. Entomopathogenic nematodes (Rhabditida: Steinernematidae and Heterorhabditidae) successfully infect both larvae and adults of beet armyworm, and infected adults can fly short distances, helping to spread the pathogens. Use of nematodes is similarly constrained by environmental conditions, but these biological control agents are available commercially.

References

Ali A, Gaylor MJ (1992) Effects of temperature and larval diet on development of the beet armyworm (Lepidoptera: Noctuidae). Environ Entomol 21:780–786

Brown ES, Dewhurst CF (1975) The genus *Spodoptera* (Lepidoptera, Noctuidae) in Africa and the Near East. Bull Entomol Res 65:221–262

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, CA, 729 pp

Wilson JW (1932) Notes on the biology of *Laphygma exigua* Huebner. Fla Entomologist 16:33–39

Wilson, JW 1933. The biology of parasites and predators of *Laphygma exigua* Huebner reared during the season of 1932. Fla Entomol 17:1–15

Beetles (Coleoptera)

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The present era could with some justification be called the "Age of the Beetles." Members of the order Coleoptera comprise the largest order of life. One out of every five species of living things on Earth is a beetle. No one knows precisely how many beetle species have been described, but estimates start at 250,000. Beetles live in almost every habitat where insects are found but do not come to the attention of the layperson as often as members of some other orders which are more conspicuous by virtue of their size or habits. The majority of beetles are capable of flight and some fly quite well, but none has adopted the truly aerial lifestyle of butterflies and dragonflies. Most spend the greater part of their lives in cryptic habitats – under bark and in dead wood, in soil and leaf litter, in the water of ponds, lakes, and streams. Although some beetles are among the largest insects, most are quite small; indeed, some are among the smallest of insects.

Nevertheless, beetles are unrivaled in their diversity of form and color and in the nearly endless ways they have found to live, feed, and reproduce.

Beetles are holometabolous insects which have the front wings hardened and serving as protection for the hind wings which are used exclusively for flying. The front wings, or elytra, are usually raised during flight; at rest, they meet in a straight line along the back. When not in use, the hind wings are folded longitudinally and transversely and hidden under the elytra. Beetles also possess chewing mouthparts, usually 11-segmented antennae, and the abdominal sternites are usually more heavily sclerotized than the tergites.

Anatomy

The body of an adult beetle is composed, like all insects, of three regions: head, thorax, and abdomen. What is visible in dorsal view in beetles, though, is the head, prothorax, and elytra (singular, elytron), which cover the meso- and metathorax, and usually all of the abdomen.

The head bears the eyes, chewing mouthparts, and usually 11-segmented antennae. The size and placement of the compound eyes varies widely within the order, and eyelessness is fairly frequent, especially in soil and litter inhabiting beetles, and those which dwell in caves. The presence of ocelli occurs in only a very few small groups. Mouthparts may be borne on the end of a rostrum (most notably in weevils, Curculionidae). Beetles exhibit almost endless modifications of the mouthparts, especially of the mandibles, which may be the most striking feature of the individual, as in Lucanidae and some Cerambycidae. The antennae in beetles range from simply threadlike (filiform) or beadlike (moniliform), to gradually (clavate) or abruptly (capitate) clubbed, or saw-like (serrate), or with the club segments asymmetrically developed and capable of opening and closing like a fan (lamellate), or elbowed like an ant's antennae (geniculate), or feathery (pectinate or flabellate). Although most beetles have 11-segmented antennae, reduction in the number of segments (to only one or two segments in extreme examples) is common, while an increase in the number of segments is quite uncommon.

The thorax is composed of three parts: the prothorax bears the forelegs; the mesothorax gives rise to the forewings, or elytra, and the middle legs; the metathorax bears the hind wings and hindlegs. The legs are 5-segmented, composed of (from closest to the body) the coxa, trochanter, femur, tibia, and tarsus. The tarsus is composed primitively of five tarsomeres, but this is often reduced and the tarsal formula (the number of tarsomeres on the front, middle, and hind legs) is important in beetle identification. The elytra generally completely cover the dorsal part of the metathoraz and abdomen, but are secondarily short in many groups (Staphylinidae, Silphidae, Cerambycidae, etc.). They almost always meet in a straight line, one of the very few exceptions being the genus *Meloe* in the Meloidae.

The dorsal part of the abdomen is usually soft, except in those groups with abbreviated elytra; the ventral surface of the abdomen is almost always heavily sclerotized.

Life Cycle

Beetles undergo complete metamorphosis. The life cycle of the typical beetle includes egg, three to five larval instars, pupa, and adult. A few beetle families have more complicated life histories: Micromalthidae have multiple larval forms and paedogenesis (reproduction by larvae); several families, e.g., Meloidae, Ripiphoridae, Passandridae, undergo hypermetamorphosis, with the first instar larva being considerably different from succeeding instars. The length of the life cycle varies widely within the order, but generation length of most beetles falls within a few weeks to 1 or 2 years. A few beetles, notably some Cerambycidae, under extraordinary conditions can spend decades as larvae.

Evolution

It is generally agreed the beetles are most closely related to the neuropteroid orders. The first fossils of true Coleoptera date back to the Triassic. They were preceded by a group of beetle-like insects called the Protocoleoptera that arose in the Lower Permian. By the Jurassic, many modern families had arisen, and most of the rest appeared during the Cretaceous, coincident with the rise of the flowering plants. Interestingly, many of the Cenozoic amber fossils can be attributed to modern genera.

Classification

Beetles were recognized as a distinct group of insects as far back as the ancient Greeks, but the classification within the group has been in a state of flux up to the present day. The limits of the order are well understood, with the only issue being whether to include or exclude the twisted-wing parasites (Strepsiptera). Most now treat them as a separate order near Coleoptera, but some have argued that their true affinities lie with the Diptera. Within the Coleoptera, the general classification is fairly well accepted but disagreement persists on the ranking or placement of some family-level groups. The classification presented here is that used in the two-volume American Beetles (Arnett and Thomas 2000, Arnett et al. 2002), the most recently published, major general work on beetles.

There are 166 families of beetles in the world; 131 of those occur in America north of Mexico. The order is divided very unequally into four suborders: Archostemata, Myxophaga, Adephaga, and Polyphaga.

Archostemata

Only four families comprise this primitive suborder. Beetles very similar to present-day Cupedidae are known from the Lower Triassic. Two families, Cupedidae and Micromalthidae, are known from the Nearctic. Most are found in decaying wood. The sole member of Micromalthidae, *Micromalthus debilis* LeConte, has an unusual and complex life history, including paedogenesis.

Myxophaga

Another four families have been assigned to this, the most recently recognized suborder. Two families, Microsporidae and Hydroscaphidae, occur in the Nearctic. The few minute species are associated with algae.

Adephaga

Nine families comprise this suborder, the only one that is composed exclusively (except for one small family of wood-inhabiting beetles, the Rhysodidae) of predacious beetles. Eight families occur in the Nearctic, the Carabidae or ground beetles, being by far the largest family in the suborder, with 2,635 species and subspecies being recorded from the Nearctic and about 40,000 for the world. Carabids often are found on the ground under stones or logs, or in leaf litter, but many, especially in the tropics, are arboreal. They are usually small to moderate in size. Most are darkly colored, but many exhibit brilliant metallic colors. Most ground beetles are predacious, feeding on soft-bodied insects, but some are specialized predators of snails and millipeds. A few are seed feeders. Beetles in most of the other families spend most of their lives in fresh water.

Polyphaga

All the rest of the beetle families are assigned to this suborder. It has been subdivided into several series and numerous superfamilies.

Series: Staphyliniformia

This series is composed of two superfamilies.

Superfamily: Hydrophiloidea
Three families, two moderately sized and one small, comprise this superfamily. The Hydrophilidae are predominantly predacious and aquatic. The Histeridae and Sphaeritidae are terrestrial and predacious. Superfamily: StaphylinoideaThis family contains six small or moderate-sized families and one huge one, the Staphylinidae, which has more than 4,100 species in the Nearctic and more than 46,000 worldwide. All the families occur in the Nearctic. Staphylinids, or rove beetles, often are found around decaying vegetable material and dead animals, where they feed on fly larvae and other insects. Many staphylinids live in the nests of social insects, ants and termites primarily, and show many physical and behavioral adaptations to that way of life. Most staphylinids have very short elytra and flexible abdomens.

Series: Scarabaeiformia

This series contains only the single superfamily

Superfamily: Scarabaeoidea
This superfamily contains 11 small or moderate-sized families and one very large one, the Scarabaeidae. There are more than 27,800 species of scarab beetles in the world; about 1,700 occur in the Nearctic. This superfamily includes the relatively small but well-known Lucanidae (stag beetles) and Passalidae (bess beetles). The Scarabaeidae include some of the largest known beetles, such as the members of the genera *Dynastes* and *Megasoma* in the New World, and *Goliathus* in tropical Africa. Males of many scarabs bear spectacular horns on the head and/or pronotum with which they battle each other for females. Scarab beetles have extremely diverse feeding habits. Many feed on dung of mammals, some being extremely specific on the kind of dung they will accept. Dung beetles provision burrows with dung for their larvae, some rolling balls of dung away for burying and sculpting the dung ball into special shapes. Some even tend the dung to prevent the growth of mold on it. Many others feed in soil, humus, and decaying wood. Some, like the Japanese beetle *Popilia japonica* Newman, feed on living plants and are economic pests of extreme

importance. Many others are found in nests of social insects, primarily ants and termites.

Series: Elateriformia

This series contains five mostly small superfamilies.

Superfamily: Scirtoidea

Four families, three of which are found in the Nearctic, comprise this superfamily. Two families, Eucinetidae and Clambidae, contain small to minute beetles that are found in leaf litter and apparently feed on fungus. Scirtidae are aquatic as larvae and adults generally are found in wet habitats.

Superfamily: Dascilloidea

Only two small families, Dascillidae and Rhipiceridae (Figs. 32 and 33) comprise this superfamily. Larvae of Rhipiceridae are hypermetamorphic and parasitic on immature annual cicadas (Heteroptera).

Superfamily: Buprestoidea

Two families, Schizopodidae and Buprestidae, are included in this superfamily. The Schizopodidae are a small family, confined to the western Nearctic. The Buprestidae are one of the larger families of Coleoptera, with 788 species and subspecies recorded from the Nearctic and more than 14,000 in the world. These often brilliantly colored beetles are mostly wood borers as larvae, although some are leaf miners. A few are of economic importance.

Superfamily: Byrrhoidea

There are 12 mainly small families assigned here; most of the species are aquatic or subaquatic. All but one of the families are found in the Nearctic. The water penny beetles, Psephenidae, with their remarkably flattened larvae, are found on rocks in streams.

Superfamily: Elateroidea

Fifteen rather diverse families comprise this superfamily, all but three of which are found in the Nearctic. The largest family is the Elateridae, or click beetles. There are about 10,000 species of click beetles in the world, with 965 recorded from the Nearctic. Click beetles (and a few of the other families) bear a “click” mechanism on the pro- and mesosternum that allows them to fling themselves into the air with some force if they are placed on their backs. Members of one mostly tropical group of click beetles are luminescent. Other large or widely distributed families include the Lampyridae, Lycidae, Cantharidae, and Eucnemidae.

Series: Bostrichiformia

The series includes two small superfamilies, plus the Jacobsoniidae, which have not been placed in a superfamily.

Superfamily: Derodontoidea

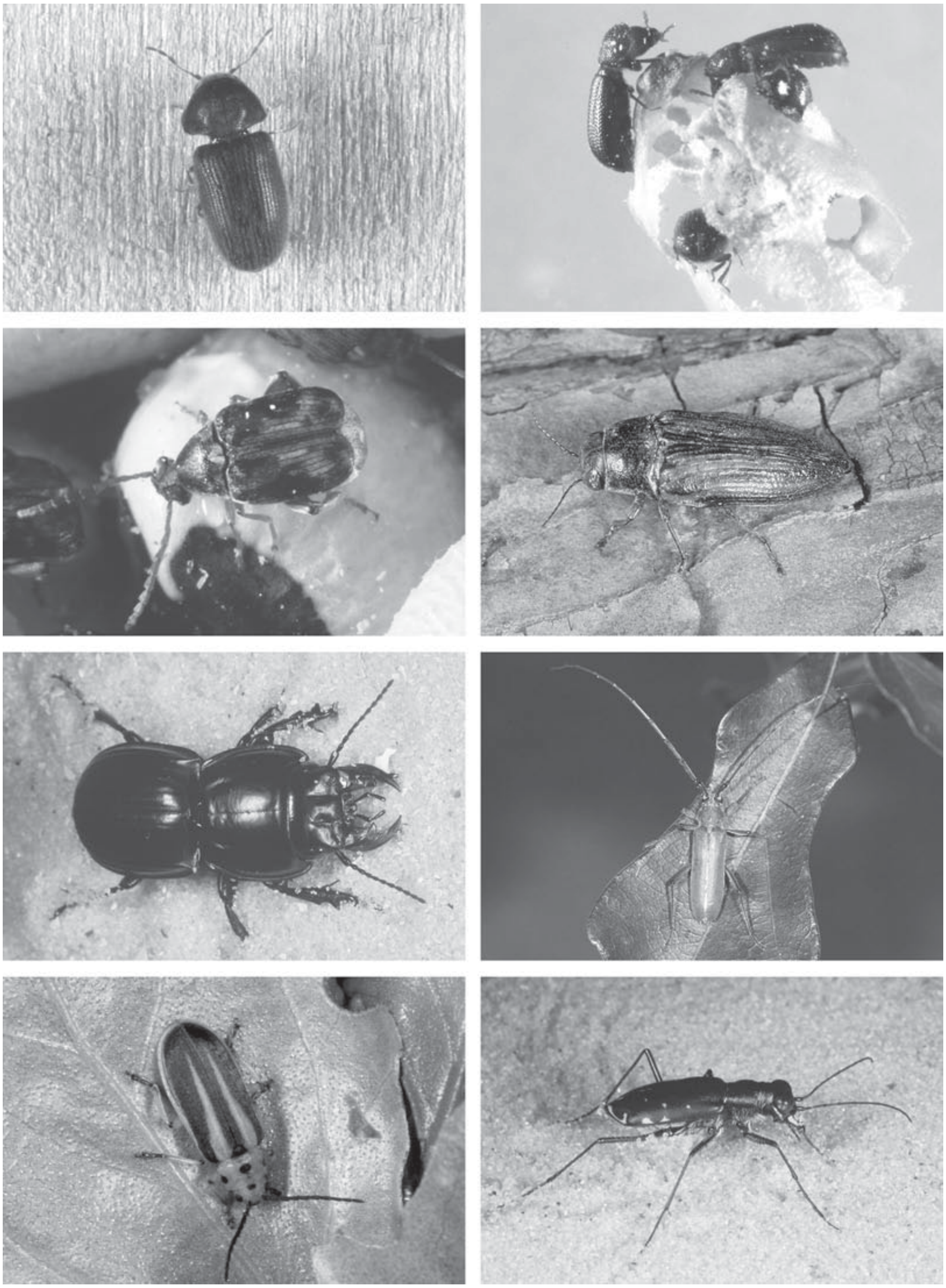
Only the Derodontidae are included in this superfamily. They are found on slime molds.

Superfamily: Bostrichoidea

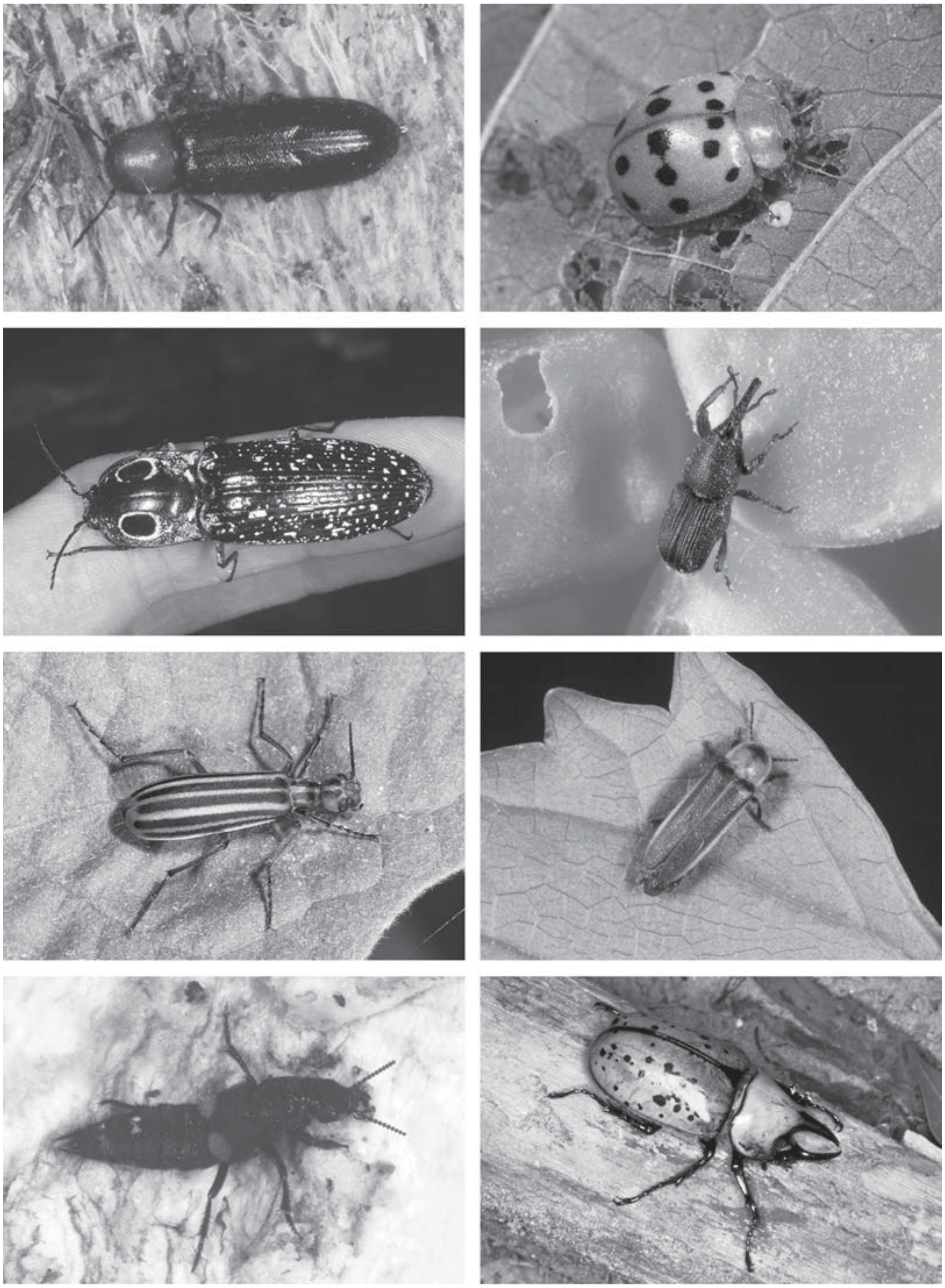
Four families are included here, Nosodendridae, Dermestidae, Bostrichidae, and Anobiidae. The last three including many economically important pests of animal products such as wool, leather, feathers, and silk (Dermestidae) and stored products and wood or wood products (Bostrichidae and Anobiidae).

Series: Cucujiformia

This huge series contains the rest of the Coleoptera, arranged in six superfamilies.



Beetles (Coleoptera), Figure 32 **Some representative beetles: top left, drugstore beetle, *Stegobium paniceum* (Anobiidae); top right, lesser grain borer, *Rhyzopertha dominica* (Bostrichidae); second row left, cowpea weevil, *Callosobruchus maculatus* (Bruchidae); second row right, *Buprestis lineatus* (Buprestidae); third row left, *Pasimachus sublaevis* (Carabidae); third row right, banded hickory borer, *Knulliana cincta* (Cerambycidae); bottom left, *Trirhabda bacharidis* (Chrysomelidae); bottom right, *Cicindela punctulata* (Carabidae) (photos by Lyle Buss).**



Beetles (Coleoptera), Figure 33 **Some additional representative beetles: top left, *Neorthopleura thoracica* (Cleridae); top right, Mexican bean beetle, *Epilachna varivestis* (Coccinellidae); second row left, eyed click beetle, *Alaus oculatus* (Elateridae); second row right, maize weevil, *Sitophilus zeamais* (Curculionidae); third row left, striped blister beetle, *Epicauta vittata* (Meloidae); third row right, a firefly, *Photinus tanytoxus* (Lampyridae); bottom left, a rove beetle, *Platydracus fossator* (Staphylinidae); bottom right, Hercules beetle, *Dynastes titus* (Scarabaeidae) (*Dynastes* and *Epilachna* by Jim Castner; other photos by Lyle Buss).**

Superfamily: Lymexyloidea

This superfamily contains only the ship-timber beetles, Lymexylidae, a small group of soft-bodied, wood-boring beetles.

Superfamily: Cleroidea

Three moderate-sized families of predominantly predacious beetles comprise this superfamily.

Superfamily: Cucujoidea

This is a large superfamily composed of 31 mostly small to moderate-sized families, ten of which do not occur in the Nearctic. Members of most of the families are associated with fungus, but some are predominantly predacious, such as the largest and best-known family, Coccinellidae, and a few (Bothrideridae and Passandridae) even contain species which have parasitic larvae.

Superfamily: Tenebrionoidea

This is the second largest superfamily with 30 families, six of which do not occur in the Nearctic. Most of the families are small to moderate in size, but the Tenebrionidae are one of the largest families of Coleoptera, with about 19,000 species worldwide and about 1,100 in the Nearctic. Although the Tenebrionidae are found in all kinds of habitats, the family is especially well represented in deserts. They are usually sombre in coloration, hence their common name of darkling beetles, and often are found on the ground under rocks and logs.

Superfamily: Chrysomeloidea

The superfamily contains five families, two of which are very large. The longhorn beetles, Cerambycidae, contains more than 20,000 species worldwide and more than 900 in the Nearctic. They are generally elongate, handsome beetles with long to very long antennae. Most are associated with dead or dying woody plants, although some attack living trees. Many are of economic importance. Some very large forms occur in the tropics and are among the largest beetles. The leaf beetles, Chrysomelidae, include about 35,000 species worldwide and about 1,720 in the Nearctic. Chrysomelids differ from cerambycids in usually being smaller, less elongate, and with shorter antennae. Often they are brightly colored. Leaf beetles are associated predominantly with living plants, feeding on the foliage and roots. Many are economically important pests of agriculturally important crops. The seed beetles, Bruchidae, often are combined with the leaf beetles. Several are important pests of stored legume seeds.

Superfamily: Curculionoidea

The largest family of living organisms is included among the eight families in this superfamily. The weevils, Curculionidae, contain more than 60,000 species worldwide and about 2,400 in the Nearctic. As presently defined, the Curculionidae are restr-icted to curculionoids with geniculate antennae. They are almost entirely herbivorous, attacking all parts of all kinds of plants. Many of the worst agricultural pests are weevils. The Brentidae, or primitive weevils, are mostly tropical but one oak pest occurs in the eastern Nearctic. The Anthribidae, or fungus weevils, are associated with fungi of various kinds.

Classification of the Order Coleoptera Linnaeus 1758.

Suborder: ARCHOSTEMATA Kolbe 1908
- Cupedidae Laporte 1836, The reticulated beetles
- Ommatidae Sharp and Muir 1912
- Crowsonellidae Iablokoff-Khnzorian 1983
- Micromalthidae Barber 1913, The telephone-pole beetles

Suborder: MYXOPHAGA Crowson 1955

Lepiceridae Hinton 1936

Microsporidae Crotch 1873, The minute bog beetles

Hydroscaphidae LeConte 1874, The skiff beetles

Torridincolidae Steffan 1964

Suborder: ADEPHAGA Schellenberg 1806

Rhysodidae Laporte 1840, The wrinkled bark beetles

Carabidae Latreille 1802, The ground beetles

Gyrinidae Latreille 1810, The whirligig beetles

Haliplidae Aubé 1836, The crawling water beetles

Trachypachidae C. G. Thomson 1857, The false ground beetles

Noteridae C. G. Thomson 1860, The burrowing water beetles

Amphizoidae LeConte 1853, The trout-stream beetles

Hygrobiidae Régimbart 1878

Dytiscidae Leach 1815, The predacious diving beetles

Suborder: POLYPHAGA Emery 1886

Series: STAPHYLINIFORMIA Lameere 1900

Superfamily: HYDROPHILOIDEA Latreille 1802

Hydrophilidae Latreille 1802, The water scavenger beetles

Sphaeritidae Shuckard 1839, The false clown beetles

Synteliidae Lewis 1882

Histeridae Gyllenhal, The clown beetles

Superfamily STAPHYLINOIDEA Latreille 1802

Hydraenidae Mulsant 1844, The minute moss beetles

Ptiliidae Erichson 1845, The feather-winged beetles

Agyrtidae C. G. Thomson 1859, The primitive carrion beetles

Leiodidae Fleming 1821, The round fungus beetles

Scydmaenidae Leach 1815, The antlike stone beetles

Silphidae Latreille 1807, The carrion beetles

Staphylinidae Latreille 1802, The rove beetles

Series: SCARABAEIFORMIA Crowson 1960

Superfamily: SCARABAEOIDEA Latreille 1802

Lucanidae Latreille 1804, The stag beetles

Diphyllostomatidae Holloway 1972, The diphyllostomatid beetles

Passalidae Leach 1815, The bess beetles

Glaresidae Semenovrlan-Shanskii and Medvedev 1932, The glaresid beetles

Trogidae MacLeay 1819, The skin beetles

Pleocomidae LeConte 1861, The rain beetles

Geotrupidae Latreille 1802, The earth-boring dung beetles

Belohinidae Paulian 1959

Ochodaeidae Mulsant and Rey 1871, The ochodaeid scarab beetles

Hybosoridae Erichson 1847, The hybosorid scarab beetles

Ceratocanthidae Cartwright and Gordon 1971, The ceratocanthid scarab beetles

Glaphyridae MacLeay 1819, The glaphyrid scarab beetles

Scarabaeidae Latreille 1802, The scarab beetles

Series: ELATERIFORMIA Crowson 1960

Podabrocephalidae Pic 1930

Rhinorhipidae Lawrence 1988

Superfamily: SCIRTOIDEA Fleming 1821

Decliniidae Nikitsky et al. 1994

Eucinetidae Lacordaire 1857, The plate-thigh beetles

Clambidae Fischer 1821, The minute beetles

Scirtidae Fleming 1821, The marsh beetles

Superfamily: DASCILLOIDEA Guérin-Méneville 1843

Dascillidae Guérin-Méneville 1843

Rhipiceridae Latreille 1834, The cicada parasite beetles

Superfamily: BUPRESTOIDEA Leach 1815

Schizopodidae LeConte 1861, The schizopodid beetles

Buprestidae Leach 1815, The metallic wood-boring beetles

Superfamily: BYRRHOIDEA Latreille 1804

Byrrhidae Latreille 1804, The pill beetles

Elmidae Curtis 1830, The riffle beetles

Dryopidae Billberg 1820, The long-toes beetles

Lutrochidae Kasap and Crowson 1975, The robust marsh-loving beetles

Limnichidae Erichson 1846, The minute marsh-loving beetles

Heteroceridae MacLeay 1825, The variegated mod-loving beetles

Psephenidae Lacordaire 1854, The water penny beetles

Cneoglossidae Champion 1897

Ptilodactylidae Laporte 1836, The toe-winged beetles

Chelonariidae Blanchard 1845, The turtle beetles

Eulichadidae Crowson 1973, The eulichadid beetles

Callirhipidae Emden 1924, The cedar beetles

Superfamily: ELATEROIDEA Leach 1815

Artematopodidae Lacordaire 1857, The soft-bodied plant beetles

Brachypsectridae Leconte and Horn 1883, The Texas beetles

Cerophytidae Latreille 1834, The rare click beetles

Eucnemidae Eschscholtz 1829, The false click beetles

Throscidae Laporte 1840, The false metallic wood-boring beetles

Elateridae Leach 1815, The click beetles

Plastoceridae Crowson 1972

Drilidae Blanchard 1845

Omalisidae Lacordaire 1857

Lycidae Laporte 1836, The net-winged beetles

Telegeusidae Leng 1920, The long-lipped beetles

Phengodidae LeConte 1861, The glowworm beetles

Lampyridae Latreille 1817, The firefly beetles

Omethidae LeConte 1861, The false firefly beetles

Cantharidae Imhoff 1856, The soldier beetles

Series: BOSTRICHIFORMIA Forbes 1926

Jacobsoniidae Heller 1926, The Jacobson's beetles

Superfamily: DERODONTOIDEA LeConte 1861

Derodontidae LeConte 1861, The tooth-necked fungus beetles

Superfamily BOSTRICHOIDEA Latreille 1802

Nosodendridae Erichson 1846, The wounded-tree beetles

Dermestidae Latreille 1804, The skin and larder beetles

Bostrichidae Latreille 1802, The horned powder-post beetles

Anobiidae Fleming 1821, The death-watch beetles

Series: CUCUJIFORMIA Lameere 1938

Superfamily: LYMEXYLOIDEA Fleming 1821

Lymexylidae Fleming 1821, The ship-timber beetles

Superfamily: CLEROIDEA Latreille 1802

Phloiophilidae Kiesenwetter 1863

Trogossitidae Latreille 1802, The bark-gnawing beetles

Chaetosomatidae Crowson 1952

Cleridae Latreille 1802, The checkered beetles

Acanthocnemidae Crowson 1964

Phycosecidae Crowson 1952

Prionoceridae Lacordaire 1857

Melyridae Leach 1815, The soft-winged flower beetles

Superfamily: CUCUJOIDEA Latreille 1802

Protocucujidae Crowson 1954

Sphindidae Jacquelin du Val 1860, The dry-fungus beetles

Brachypteridae Erichson 1845, The short-winged flower beetles

Nitidulidae Latreille 1802, The sap-feeding beetles

Smicripidae Horn 1879, The palmetto beetles

Monotomidae Laporte 1840, The root-eating beetles

Boganiidae Sen Gupta and Crowson 1966

Helotidae Reitter 1876

Phloeostichidae Reitter 1911

Silvanidae Kirby 1837, The silvanid flat bark beetles

Passandridae Erichson 1845, The parasitic flat bark beetles

Cucujidae Latreille 1802, The flat bark beetles

Laemophloeidae Ganglbauer 1899, The lined flat bark beetles

Propalticidae Crowson 1952

Phalacridae Leach 1815, The shining flower beetles

Hobartiidae Sen Gupta and Crowson 1966

Cavognathidae Sen Gupta and Crowson 1966

Cryptophagidae Kirby 1837, The silken fungus beetles

Lamingtoniidae Sen Gupta and Crowson 1969

Languriidae Crotch 1873, The lizard beetles

Erotylidae Latreille 1802, The pleasing fungus beetles

Byturidae Jacquelin du Val 1858, The fruitworm beetles

Biphyllidae LeConte 1861, The false skin beetles

Bothrideridae Erichson 1845, The dry bark beetles

Cerylonidae Billberg 1820, The minute bark beetles

Alexiidae Imhoff 1856

Discolomatidae Horn 1878

Endomychidae Leach 1815, The handsome fungus beetles

Coccinellidae Latreille 1807, The ladybird beetles

Corylophidae LeConte 1852, The minute fungus beetles

Latridiidae Erichson 1842, The minute brown scavenger beetles

Superfamily: TENEBRIONOIDEA Latreille 1802

Mycetophagidae Leach 1815, The hairy fungus beetles

Archeocrypticidae Kaszab 1964, The archeocryptic beetles

Pterogeniidae Crowson 1953

Ciidae Leach 1819, The minute tree-fungus beetles

Tetratomidae Billberg 1820, The polypore fungus beetles

Melandryidae Leach 1815, The false darkling beetles

Mordellidae Latreille 1802, The tumbling flower beetles

Rhipiphoridae Gemminger and Harold 1870, The wedge-shaped beetles

Colydiidae Erichson 1842, The cylindrical bark beetles

Monommatidae Blanchard 1845, The opossum beetles

Zopheridae Solier 1834, The ironclad beetles

Ulodidae Pascoe 1869

Perimylopidae St. George 1939

Chalcodryidae Watt 1974

Trachelostenidae Lacordaire 1859

Tenebrionidae Latreille 1802, The darkling beetles

Prostomidae C. G. Thomson 1859, The jugular-horned beetles

Synchroidae Lacordaire 1859, The synchroa beetles

Oedemeridae Latreille 1810, The pollen-feeding beetles

Stenotrachelidae C. G. Thomson 1859, The false long-horned beetles

Meloidae Gyllenhal 1810, The blister beetles

Mycteridae Blanchard 1845, The palm and flower beetles

Boridae C. G. Thomson 1859, The conifer bark beetles

Trictenotomidae Blanchard 1845

Pythidae Solier 1834, The dead log bark beetles

Pyrochroidae Latreille 1807, The fire-colored beetles

Salpingidae Leach 1815, The narrow-waisted bark beetles

Anthicidae Latreille 1819, The antlike flower beetles

Aderidae Winkler 1927, The antlike leaf beetles

Scraptiidae Mulsant 1856, The false flower beetles

Superfamily: CHRYOMELOIDEA Latreille 1802

Cerambycidae Latreille 1802, The long-horned beetles

Bruchidae Latreille 1802, the pea and bean weevils

Megalopodidae Latreille 1802, The megalopodid leaf beetles

Orsodacnidae C. G. Thomson 1859, The orsodacnid leaf beetles

Chrysomelidae Latreille 1802, The leaf beetles

Superfamily: CURCULIONOIDEA Latreille 1802

Nemonychidae Bedel 1882, The pine-flower snout beetles

Anthribidae Billberg 1820, The fungus weevils

Belidae Schönherr 1826, The primitive weevils

Attelabidae Billberg 1820, The tooth-nosed snout beetles

Brentidae Billberg 1820, The straight-snouted weevils

Caridae Thompson 1992

Ithyceridae Schönherr 1823, The New York weevils

Curculionidae Latreille 1802, The snout beetles and true weevils

► Bark Beetles
► Bess Beetles
► Blister Beetles
► Darkling Beetles
► Fireflies
► Ground Beetles
► June Beetles
► Leaf Beetles
► Longicorn Beetles
► Powderpost Beetles
► Riffle Beetles
► Rove Beetles
► Sap Beetles
► Water Penny Beetles

References

Arnett RH Jr, Thomas MC (eds) (2000)American beetles, vol 1: Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia. CRC Press, Boca Raton, FL, 443 pp

Arnett RH Jr, Thomas MC, Skelley PE, Frank JH (eds) (2002) American beetles, vol 2: Polyphaga: Scarabaeoidea through Curculionoidea. CRC Press Boca Raton, FL, 861 pp

Crowson RA (1981) The biology of the Coleoptera. Academic Press, New York, NY, 802 pp

Lawrence JF (1982) Coleoptera. In: Parker SB (ed) Synopsis and classification of living organisms, vol 2. McGraw-Hill Publishers, New York, NY, pp 482–553

Lawrence JF (Co-ordinator). Chapter 34. Coleoptera. In: Stehr F (ed) Immature insects, vol 2. Kendall/Hunt Publishing, Dubuque, IA, pp 144–658

Lawrence JF, Britton EB (1994) Australian beetles. Melbourne University Press, Carlton, Victoria, Australia, 192 pp

Lawrence JF, Hastings AM, Dallwitz M, Paine TA, Zurcher EJ (1999) Beetle larvae of the world: descriptions, illustrations, and information retrieval for families and subfamilies. CD-ROM, Version 1.1 for MS-Windows. CSIRO Publishing, Melbourne, Australia

Lawrence JF, Newton AF Jr (1995) Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). In: Pakaluk J, Slipinski SA (eds) Biology, phylogeny, and classification of Coleoptera: papers celebrating the 80th birthday of Roy A. Crowson. Muzeum i Institut Zoologii, Polska Academia Nauk, Warsaw, Poland, pp 779–1006

Behavior of Insects: Genetic Analysis by Crossing and Selection

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Sometimes, as will be demonstrated in examples below, mutations in a single gene or a few major genes will alter the behavior of insects. The genetic basis of this behavior can be assessed by traditional techniques. Traditional behavior-genetic analysis primarily employs one of two experimental appro-aches: crossing and selection. A third traditional approach, which is limited to *D. melanogaster*, involves analysis of fate maps in genetic mosaics. This method allows the researcher to locate the anatomical site of abnormalities that affect behavior in *D. melanogaster*. In addition, molecular genetic methods are becoming important in the analysis of insect behavior, but are discussed in a separate entry.

Although a specific behavior sometimes can be altered by the mutation of a single gene in a pathway leading to the behavior, an insect's behavior often is influenced by many genes. In such situations, analyses of behavior have traditionally required the use of a statistically based approach called quantitative genetics.

Crossing Experiments

Crossing experiments are used to assess the mode of inheritance of a particular behavior. The behavior (phenotype) of the F_1 and backcross progeny indicates whether the behavior under study is determined by a single gene or more than one gene. The phenotype indicates whether there is dominance (a single copy of the gene is sufficient to determine the behavior under study), sex linkage (the gene is located on a sex-determining chromosome) or maternal influences (the behavior is determined by the behavior of the mother, which suggests that the trait may be determined by factors in the cytoplasm rather than in the chromosomes located in the nucleus). If the trait is determined by many genes, it is difficult to determine the number of genes, their relationship to each other, or their location on specific chromosomes because most insect species lack sufficient genetic markers.

A crossing experiment involves mating individual insects that differ in a particular kind of behavior. The behavior of their progeny (the F_1 generation) and the progeny produced by crosses between the F_1 progeny and one of the original parental types (backcross progeny) is also evaluated. Ideally, the environment experienced by the parental, F_1 and backcross generations is controlled so that all individuals experience the same conditions. It is easiest to interpret the results of crossing experiments if the individual insects that are crossed differ only with regard to a single behavioral attribute.

Selection Experiments

Selection experiments provide a second traditional method to determine the degree to which a given behavior is determined genetically. Selection experiments do not usually allow the researcher to resolve the mode of inheritance. In a selection experiment, individuals with a specific behavioral attribute are allowed to reproduce and this process is repeated over succeeding generations until a plateau in the selection response is obtained. The behavior of the selected population is altered *if* genetic variation for the attribute is present in the initial colony *and* the selection procedures have been appropriate. The response of the population to selection can be analyzed to estimate whether the trait is heritable. An example of a selection experiment is provided by the analysis of migratory behavior in the milkweed bug *Oncopeltus fasciatus*.

Migratory and nonmigratory behaviors of *Oncopeltus fasciatus* were shown to be under genetic control. Strains of *O. fasciatus* were selected for two attributes: wing length and propensity to fly. Bidirectional selection (selection for increased or decreased wing length) on wing length was performed for 13 generations and the flight behavior of the selected individuals was monitored. Individuals also were selected for flight duration; those whose flight times totaled 30 min were considered "fliers," while those with the shortest flight times were labeled "nonfliers."

Response to selection on wing length was rapid, and flight tests of the long- and short-winged insects indicated there was a positive correlation between wing length and flight duration. Selection after two generations for flight or noflight likewise resulted in divergent responses, indicating a large genetic component to flight behavior.

Behavior Determined by One or a Few Genes

How often are insect behaviors determined by one or a few genes? How often are behaviors determined by many genes? The following examples provide some examples of behaviors determined by one or a very few genes.

Susceptibility to American Foulbrood in the Honeybee

The genetic basis of susceptibility to foulbrood disease caused by the bacterium *Bacillus larvae* in honeybees (*Apis mellifera*) originally was analyzed by Walter Rothenbuhler. Differences in resistance in different bee strains were attributed to differences in "hygienic behavior" in worker (sterile female) bees. To understand the genetic basis of the hygienic behavior, two inbred honeybee strains with differing levels of resistance were crossed and the behavior of the F_1 and backcross progeny was characterized. This research was one of the first to show that a specific behavior was determined by a few genes.

"Hygienic" workers consistently remove dead larvae and pupae from the brood nest at a high rate, thus slowing the spread of the bacteria through the colony by reducing contamination. The hygienic behavior has two components: (i) the uncapping of infected cells, and (ii) removal of the dead bee larvae. Crosses between "hygienic" and "nonhygienic" bees yield F_1 worker bees that are nonhygienic, indicating that the gene, or genes, conferring the hygienic behavior are recessive.

Progeny produced by backcrosses to the pure hygienic strain yielded approximately 25% hygienic worker progeny, which is consistent with the hypothesis that hygienic behavior is determined by two recessive genes. Under this two-gene model, hygienic worker bees have two copies of each of two genes, called *u* and *r*. Hygienic bees (*uurr*) both uncap the cells (*uu*) containing dead brood and remove them (*rr*).

As expected, worker bees that contain two copies of u but only one copy of the gene for removal (*r*) will uncap the cells, but not remove dead brood. The workers that contain only one copy of the uncapping gene (*u*) but two copies of the removal gene (*rr*) do not uncap brood, but will remove them if the cells are uncapped for them. Workers that contain only one copy each of *u* and *r* (u^+u, r^+r) are unhygienic, and will neither uncap nor remove brood. Rothenbuhler' s research on hygienic behavior became a classic in textbooks of behavior genetics because it was one of the first examples to demonstrate that behavior was inherited. The model has been confirmed, although one analysis of the data suggest that three genes might be involved in this behavior.

Research on hygienic behavior indicates it may be a general response to remove pathogens and parasites from the nest. It is clear that the expression of hygienic behavior also depends on colony strength and composition of worker types within the colony. Analyses of the olfactory responses of hygienic and non-hygienic bees to diseased brood indicates that hygienic bees have a higher sensitivity to low concentrations of the odor of diseased bee pupae. Such differences are due to a lower stimulus threshold and not a direct result of age or experience of the bee, suggesting that non-hygienic bees may be unable to detect diseased brood readily.

Understanding hygienic behavior in *A. mellifera* has great practical importance in maintaining effective colonies of pollinators and honey producers. Studies on hygienic behavior has resulted in practical recommendations to bee keepers for selecting colonies resistant to chalk brood (a fungal disease) and the pest bee mite *Varroa*. So far, no negative effects have been associated with hygienic behavior and such colonies produce as much honey as nonhygienic ones.

House-Entering Behavior in *Aedes aegypti*

The mosquito *Aedes aegypti* is an important vector of human disease and understanding its behavior could result in better management of this pest. House-entering behavior by *A. aegypti* from East Africa has been analyzed by crossing different populations that exhibited different behaviors, which were controlled by genes with additive effects. One population of *A. aegypti* commonly enters houses (domesticated or D), while others rarely do so (one is called peridomestic [P]; and the other is a wild or feral [F]; population).

Three populations of *A. aegypti* were collected either inside houses (D), near a village (P), or from tree holes in a forest (F). The populations then were bred in insectaries and crossed to produce hybrid (DP, PD, DF, FD, PF, FP) populations. The original and hybrid populations were then marked with different colored fluorescent powders and released near houses. Marked mosquitoes were captured inside houses and in the village area. Of the mosquitoes entering houses, 45% were from the domestic (D) population, 14% from hybrids between the domestic and peridomestic population (DP and PD), 10% from the peridomestic population (P), and 6% were hybrids between the domestic and feral populations (DF and FD). Only 1.5 and 0.6% of the PF and FP hybrids were collected in the house, and the feral population (F) entered the house with a frequency of only 0.6%. The recapture rates in the village area were in the reverse order. These results clearly indicate that the behavior is genetically determined.

Domesticity in *A. aegypti* is a complex phenomenon that includes a variety of behaviors, including a preference for ovipositing in man-made containers, ability of larvae to develop in drinking water stored in clay pots with a low nutritional content, and preferences for feeding on man (rather than birds) inside houses, as well as resting and mating indoors. No doubt *A. aegypti* speciated long before man began to build houses, but *A. aegypti* has adapted rapidly to human habitats, and the domestic form of *A. aegypti* is the only one known that is entirely dependent on man.

Foraging in *Drosophila*

Drosophila melanogaster larvae feed on yeast growing on fruit. Naturally occurring populations contain individuals that vary in the distance the larvae travel while foraging for food, a difference attributed to a single gene called *foraging*. Natural populations comprise approximately 70% "rovers" (who forage long distances) and 30% "sitters" (short distance foragers). The rover behavior is dominant to sitter, indicating a single-gene mode of inheritance. Sitter larvae grow at a normal rate and are of normal size. Both sitters and rovers are maintained in the field by natural selection. It appears that density-dependent selection can shift gene frequencies so that rovers are selected for in crowded larval environments and sitters in less crowded ones.

The *foraging* gene codes for a cyclic guanosine monophosphate (cGMP)-dependent protein kinase, and rovers have higher kinase activity than sitters. Thus, subtle differences in this kinase can lead to naturally occurring variation in behavior. Another gene, *Chaser*, also may affect larval foraging by increasing foraging path length.

Other Behaviors Influenced by One or a Few Genes

Crossing experiments have shown that a specific behavior is influenced by one or a few genes in the flour moth *Ephestia kuhniella* (silk mat spinning by larvae prior to pupation), the mosquito *Aedes atropalpus* (egg maturation without an exogenous source of protein such as blood), and the parasitoid wasp *Habrobracon juglandis* (flightlessness). In the silkworm *Bombyx mori*, females with the *piled egg* gene deposit eggs in a peculiar manner. *B. mori* larvae with the *Non-preference* gene are unable to discriminate mulberry leaves from others. When two tephritid fly species (*Procecidochares*) were crossed that differ in their host preference (each having only one host plant), the behavior of their progeny segregated in a manner consistent with hypothesis that the control of host preference is determined by a single gene.

A variety of mutants determined by major genes have been identified in *D. melanogaster* that affect behavior, including *Shaker*, *Hyperkinetic* and *eag*, which are expressed when the flies are anesthetized with ether. *Hyperkinetic* (Hk) causes a vigorous steady leg shaking, and mutations of *Shaker* cause vigorous and erratic shaking and a strong scissoring of wings and twitching of the abdomen. The *eag* mutant flies (*ether a-go-go*) are less vigorous in their shaking. The *easily shocked gene* of *D. melanogaster* is one of the class of "bang-sensitive" paralytic genes. Flies with this mutated gene exhibit a transient paralysis following a brief mechanical shock. A temperature-sensitive recessive mutant gene (*parats*) causes *D. melanogaster* to become immobile above 29°C. The *couch potato* locus causes flies to be less active and exhibit abnormal responses to gravity and light, resulting in altered flight behavior. The *couch potato* gene is unusually complex, spanning more than 100 kb and encoding three different messenger RNAs.

Many "single gene" mutants that affect the morphology of *D. melanogaster* also affect behavior. Some mutant flies exhibit abnormal behavior because they are unable to perform the reaction to a stimulus due to altered morphology. Other mutants exhibit altered behavior because perception of cues is impaired. For example, flies with *white* eyes may exhibit abnormal courtship behaviors.

Alterations in the brain affect behavior and genes involved in the behavior can be analyzed by mutagenesis and mosaic analysis. For example, eight different genes affecting walking behavior in *Drosophila melanogaster* strains were analyzed by chemical mutagenesis, histological analysis, and analysis of genetically mosaic flies. These eight genes caused structural defects in the central complex of the brain and affected walking motivation, fast response to light, and response to gravity. Because the aberrant behaviors were associated with changes in a portion of the insect brain called the central complex, the mutant flies confirmed that the central complex controls behavior. The central complex also regulates other behaviors (flight, singing, preening, escape).

Pheromone communication in the European corn borer *Ostrinia nubilalis* is genetically determined. Females of the E- and Z-strains of *O. nubilalis* produce different ratios of enantiomeric (molecules that are chemically the same but mirror images of each other) molecules of their sex pheromone (a substance released by an organism that causes a reaction by another individual of the same species, in this case it serves as a sexual attractant). Hybrids between these two strains produce an intermediate pheromone blend. Analysis of the F_2 and backcross progeny indicated the types of pheromones produced are controlled by a single gene, although one or more modifier genes controls the precise ratio of the isomers in hybrid females.

Males of the two *O. nubilalis* strains are attracted to the appropriate pheromone blends in the field, but hybrid males respond preferentially to the pheromone produced by hybrid females rather than to the pheromones produced by the two parental female types. The response of males to the pheromone is determined by a single sex-linked gene. The olfactory sensillae of the two types of males are different, which is controlled by an autosomal gene. Hybrid males give intermediate results when their antennae tested for their electrophysiological responses, with E- and Z- olfactory cells yielding approximately equal responses, suggesting that multiple genes are involved. The genes determining variation in pheromone production and organization of male olfactory sensillae are not closely linked and are probably on different chromosome.

Behaviors Determined by Multiple Genes

Behavior is often controlled by multiple genes with small additive effects. With such behaviors, the task of teasing apart the respective roles of genes and environment requires statistical methods of analysis. *Drosophila* behaviors determined by multiple genes include locomotor activity, chemotaxis (response to chemicals), duration of copulation, geotaxis (orientation to gravity), host plant preference, mating speed, phototaxis (response to light), preening, and the level of sexual isolation within and between species. Multiple genes may influence host plant adaptation and host preference in insects. Learning may affect host preference. Host plant choice usually is a hierarchy of several components.

A particularly interesting example of genetic analysis of host preference in insects is that of *Drosophila sechellia*, which is endemic to the Seychelles archipelago in the Indian Ocean and is morphologically almost identical to its cosmopolitan sister species *D. simulans* and to the endemic island species *D. mauritiana*. When crossed to either of these species, *D. sechellia* produces fertile hybrid females and sterile hybrid males. *D. sechellia* uses the fruit of *Morinda citrifolia* as its host, which may have allowed it to escape competition with other species of *Drosophila* there.

Host Plant Specialization in *Drosophila sechellia*

Drosophila sechellia breeds only in *Morinda citrifolia*, which is toxic to other *Drosophila* species. *D. simulans* breeds on a variety of plants in the same geographic area but cannot survive on *Morinda*. The two species can be crossed and F1 hybrids are produced. The number of genes involved in resistance was estimated to be three to five based on a biometric approach. An analysis using marker genes suggests that all chromosomes, except the Y and the small fourth, carry genes affecting resistance. Thus, resistance appears to be neither very simple nor highly polygenic.

D. sechellia is stimulated by *Morinda* to produce eggs, but oviposition in *D. simulans* is inhibited by this plant. In hybrid progeny, the inhibition observed in *D. simulans* is dominant. F_1 hybrids and backcross progeny exhibit intermediate, approximately additive, behavior. These differences result in isolation of the two species in nature, although they overlap geographically. Thus, their ecological niches are determined by tolerance to toxic products (including octanoic and hexanoic acids) in the ripe *Morinda* fruit, with *D. sechellia* exhibiting a strong preference for *Morinda* fruits, an ability to detect fragrant volatiles from *Morinda* over a long distance, and a stimulation of egg production by *Morinda*. By contrast, egg production in *D. simulans* is inhibited by *Morinda* and octanoic acid in the fruit is toxic to *D. simulans.*

Other Behaviors Determined by Multiple Genes

Other insects in which specific behavioral attributes have been shown to be complex include: *Musca domestica* (number of attempts to mate by males); *Phormia regina* (high and low ability to learn to extend the proboscis to a stimulus applied to the forelegs); hybrid crickets (call rhythm of males; female response to calling songs); *Anopheles albimanus* (ability to avoid pesticides); *Apis mellifera* (high and low collection of alfalfa pollen, and stinging behavior). The propensity for cannibalism by larvae of *Heliothis virescens* is determined by multiple genes. Most of these behaviors were analyzed by selection experiments.

► Behavior of Insects: Molecular Methods

References

Arathi HS, Burns I, Spivak M (2000) Ethology of hygienic behavior in the honey bee *Apis mellifera* L. (Hymenoptera: Apidae): behavioral repertoire of hygienic bees. Ethology 106:365–379

de Belle JS, Sokolowski MB (1987) Heredity of rover/sitter: alternative foraging strategies of *Drosophila melanogaster* larvae. Heredity 59:73–83

Osborne KA, Robichon A, Burgess E, Butland S, Shaw RA, Coulthard A, Pereira HS, Greenspan RJ, Sokolowski MB (1997) Natural behavior polymorphism due to a cGMP-dependent protein kinase of *Drosophila*. Science 277:834–836

Palmer JO, Dingle H (1989) Responses to selection on flight behavior in a migratory population of milkweed bug (*Oncopeltus fasciatus*). Evolution 43:1805–1808

Kha R, Capy SP, David JR (1991) Host-plant specialization in the *Drosophila melanogaster* species complex: a physiological, behavioral, and genetical analysis. Proc Natl Acad Sci USA 88:1835–1839

Rothenbuhler WC (1964) Behavior genetics of nest cleaning in honey bees. IV. Responses of F_1 and backcross generations to disease-killed brood. Amer Zool 4:111–123

Trpis M, Hausermann W (1978) Genetics of house-entering behavior in East African populations of *Aedes aegypti* (L.) (Diptera: Culicidae) and its relevance to speciation. Bull Entomol Res 68:521–532.

Behavior: Molecular Genetic Analyses

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Molecular genetic techniques are beginning to provide powerful new methods to analyze insect behaviors such as olfaction (response to odors), learning, circadian rhythms (daily periodicity), and mating behavior. Prior to the use of molecular methods, genetic analyses of behavior primarily involved crossing and selection experiments to resolve whether the behavior was genetically determined and the mode of inheritance of the gene(s) involved (e.g., the genes were dominant or recessive, sex-linked or autosomal, determined by single genes or more than one).

Now that the complete sequence of the genome of the fruitfly *Drosophila melanogaster* is available, it is easier to isolate specific genes that could be involved in behavior. In addition, the genetic modification of *D. melanogaster* by *P*-element mediated transformation makes it possible to insert genes from one species of *Drosophila* into the genome of another, and their effect(s) on behavior can be determined. Transgenic *D. melanogaster* carrying markers such as green fluorescent protein (GFP) also allow scientists to determine when and where specific genes are active.

Molecular genetic analyses of learning and memory in *Drosophila* may provide a means to study one of the most challenging frontiers in neurobiology. Molecular genetic methods may identify some of the individual genes among the "many" involved in determining the interesting and complex behaviors exhibited by insects.

Analyses of insect behavior employ techniques from several disciplines, including anatomy, biochemistry, ecology, ethology (study of animal behavior in the natural environment), genetics, psychology, physiology and statistics. These disciplines are required because an insect perceives the environment through its sensory systems. The external sensory stimuli are transduced into electrical information, which is then processed and decoded, leading to a behavioral response. Behavior can be divided into several sequential steps: stimulus recognition, signal transduction, integration, and response or motor outputs.

The Insect Nervous System

Behavior is based on the structure and function of the insect central and peripheral nervous systems. The insect brain contains around 10^5–10^6 neurons. It consists of three main divisions, the protocerebrum, deutocerebrum and tritocerebrum. In each of these divisions, different neuropil regions are located; a neuropil is a dense network of interwoven axons and dendrites of neurons and neuroglial cells in the central nervous system and parts of the peripheral nervous system.

In the protocerebrum, higher sensory centers are present that are associated with vision and other sensory receptors (the mushroom bodies and central complex). The superior protocerebrum, with the pars intercerebralis, contains different sets of neurosecretory cells that supply neurohemal organs in the corpora cardiaca and corpora allata, which are located in the head or prothorax in insects. The optic lobes flanking the protocerebrum consist of the most well-organized neuropils in the brain.

Mushroom bodies in the brain are associated with olfactory pathways, including olfactory learning. Among the insects, mushroom bodies differ greatly in size and shape, with the number of cells ranging from 2,500 in *Drosophila* to 50,000 in the cricket *Acheta*, 170,000 in the honey bee and 200,000 in the cockroach *Periplaneta*

The antennal centers are found in the deutocerebrum; in the tritocerebrum, neurosecretory neurons and neurons associated with the control of feeding and foregut activity are found. The brain is connected to the subesophageal ganglion via connectives and to the thoracic and abdominal ganglia, or ventral nerve cord.

Information is transmitted in the insect via nerves and by neuropeptides that coordinate the development and behavior of insects. Both neurosecretory cells and neurons use neuropeptides as messengers. Many different types of neuropeptides have been identified, including proctolin and adipokinetic hormone, that serve as both hormones and neurotransmitters or neuromodulators. Neuropeptides range in size from three amino acid residues (thyrotropin-releasing hormone) to more than 50 (insulin). They are generated from larger precursor proteins, ranging from 90 to 250 amino acids in length. A number of genes have been identified that code for neuropeptides, including bombyxin or prothoracicotropic hormone (PTTH), eclosion hormone (EH), FMRFamide- related peptides, diapause hormone and pheromone iosynthesis-activating neuropeptide (PBAN). The genes for many of these neuropeptides have been identified, cloned and sequenced.

Neuropeptides are released as cotransmitters and modulate fast transmission at neuromuscular junctions. A given neuropeptide may occur at several different sites, including central nervous system circuits and peripheral synapses, and at peripheral targets (muscles and glands). Neuropeptides regulate behavior by coordinating temporal and spatial activity of many neuronal circuits. Each of the circuits controlling behavior employs sets of sensory neurons, interneurons and motor neurons. Thus, multiple neural networks share neural elements. Molecular genetic analysis is providing rapid progress in understanding neuropeptide receptors and second messenger pathways. Research on neuropeptides and their receptors indicates that they have roles during embryonic development and as cytokines in the immune systems of insects.

Molecular genetic analyses are providing significant advances in our knowledge of behavior. "Behavior" is a complex phenotype to study because it involves the functioning of the whole organism, is dynamic, and changes in response to the environment. Molecular genetic methods are unlikely to replace traditional methods of behavior analysis, but the ability to identify, clone, and sequence specific genes in *D. melanogaster* makes it possible to understand several behaviors (including the periodicity of biological rhythms, mating behavior, locomotion, and learning) that are influenced by single genes.

It is now possible to clone a gene from one *Drosophila* species, insert it into a P-element vector, and introduce the exogenous gene into mutant strains of *D. melanogaster* to confirm that the putative gene does, in fact, code for the behavior of interest. Cloned genes from *Drosophila* can, in some cases, be used as probes to identify genes from other arthropods, which then can be sequenced and compared. The availability of the complete genome of *D. melanogaster* allows analyses of behavior that could not be conducted previously, as will be described in the discussion of olfaction in *D. melanogaster* (see below).

The Photoperiodic Clock

The potential that molecular genetics offers is exemplified by the analyses conducted using the period, and other clock genes, of *D. melanogaster*. Most insects exhibit particular behaviors at a specific time of the day, which due to the action of a circadian (approximately 24 h) clock that allows the insect to measure time. Circadian rhythms have a number of characteristics: (i) The clocks that regulate such behavior usually are free running in constant environments and are not simple responses to changes in light or temperature. (ii) Although the rhythms are free running, an initial environmental signal is required to start the clock. Among the cues that set the clock are alternating light and dark cycles, high and low temperature cycles, or short pulses of light. (iii) The circadian rhythm is relatively insensitive to changes in temperature (temperature compensated). (iv) The clock can be reset by altering the cues that entrain the clock.

Drosophila melanogaster reared in constant darkness exhibit circadian locomotor activity rhythms as adults. However, the rhythms of the individual flies composing these populations are not synchronized with one another. Rhythms can by synchronized if dark-reared flies are exposed to light treatments as first-instar larvae (or as later instars). Light treatments occurring prior to hatching of the first-instar larvae fail to synchronize adult locomotor activity rhythms, indicating the clock functions continuously from the time larvae hatch until adulthood. The rhythm can be advanced, delayed, or unchanged, depending on the phase of the cycle at which the cue is given.

Molecular genetic analyses of *Drosophila* clock mutants is providing a fundamental understanding of the mechanisms of the circadian clock. Rapid advances have been made in the past few years in understanding the molecular aspects of circadian clocks in a variety of organisms. Circadian rhythms are found in all organisms, probably evolved early, and common genetic elements are present in *Drosophila*, the fungus *Neurospora*, mammals, and cyanobacteria. In *Drosophila*, the genes called *period, timeless, Clock, cycle, doubletime* and *cryptochrome* are now known to be involved in the circadian clock.

The Period (Per) Gene of Drosophila

The *period* gene of *Drosophila* is located on the X chromosome. When the wild type gene (called per^+) is mutated, eclosion (emergence of adults from the pupa), locomotor activity and the length of the interpulse interval of the courtship song are affected. Eclosion of wild type flies typically occurs around dawn, when the presence of dew and high relative humidity increase their survival rate. Locomotor activity then decreases during midday and is followed by increased activity in the evening.

Three classes of *per* mutants exist; they either shorten (*per* mutants have 19-h eclosion rhythms instead of 24-h patterns), lengthen (per^L mutants have 29-h eclosion rhythms), or completely abolish circadian eclosion and locomotor activity rhythms (per^0 mutants). Flies with the per^0 mutation eclose arrhythmically, but periodicity in eclosion can be restored by *P* element-mediated transformation of arrhythmic flies using the wild type per^+ allele.

The *per* gene is approximately 7 kb long and the protein produced has a series of threonine-glycine (Thr-Gly) repeats in the middle of the gene. The region encoding the Thr-Gly repeat is polymorphic in length within and between *Drosophila* species and plays a role in the thermal stability of the circadian phenotype. For example, either 17, 20 or 23 repeats are found in *D. melanogaster* populations. A clinal pattern occurs along a north-south axis in Europe and North Africa, with the shorter sequences in southern Europe, suggesting that the length polymorphism cline is maintained by natural selection under different temperature conditions.

A large number of tissues express the normal (per^+) product, including embryonic, pupal and adult nervous systems, as well as the esophagus, gut and ovaries. The per^+ gene product (the PER protein) is predominantly found in cell nuclei in adult *Drosophila*, and per^+ messenger RNA levels undergo daily fluctuations, producing a feedback loop in which PER affects the oscillations of its own messenger RNA. The fluctuations in per^+ messenger RNA are due to fluctuations in gene transcription because the per^+ messenger RNA has a relatively short half-life, which is consistent with the hypothesis that PER acts to regulate its own gene activity.

The per^+ genes from *Drosophila simulans, D. virilis, D. pseudoobscura* and *D. yakuba* have been cloned and sequenced. Parts of the gene are conserved among them and parts are highly diverged, which suggests that conserved regions may encode basic functions common to all (clock-type functions), while the variable regions may affect species-specific differences influencing love songs, locomotor activity and eclosion.

Two X-linked loci, *Clock* and *Andante,* are components of the circadian clock, causing slightly shortened and lengthened cycles, respectively. In addition, other mutations on the autosomal chromosomes induce flies to emerge as adults from the pupal stage early in a light-dark cycle; *phase-angle* flies emerge in the pre-dawn part of the cycle instead of just after dawn while *gate* flies to fail to eclose during this narrow time window. The *cryptochrome* (*cry*) gene is an important clock component because it encodes a circadian photoreceptor in *Drosophila*. The gene product, CRY, belongs to a family of blue light-sensitive proteins, which includes photolyases and plant blue light photoreceptors. Flies over expressing CRY are hypersensitive to light. The CRY protein is probably the only dedicated circadian photoreceptor in *Drosophila.*

Song Cycle Behavior in *Drosophila*

The courtship song is produced when males vibrate their wings and consists of two components: (i) courtship hums, and (ii) a series of pulses with interpulse intervals, which can fluctuate between 15 and 85 ms. The variation in interpulse intervals ranges from a period of 56 ms in *D. melanogaster* and 35–40 ms in *D. simulans*. *D. melanogaster* males with the per^S mutation sing with 40-ms periods, per^L males sing with 76-ms periods, and per^0 males are arrhythmic.

The genetic basis of species-specific song instructions was confirmed by the transfer of the per^+ gene from *D. simulans* into *D. melanogaster* via P element-mediated transformation. The *D. simulans* per^+ gene restored a rhythm in these transgenic *D. melanogaster* and the transgenic *D. melanogaster* males had mean period lengths in their song cycles of approximately 35 ms, which is characteristic of *D. simulans* males. Thus, substitutions in four or fewer amino acids in the per^+ locus was shown to be responsible for this species-specific courtship behavior.

Other Effects of *Per*

The *per* alleles affect locomotion, cellular rhythms and development time. Flies with per^S develop faster than wild type flies and per^L flies develop more slowly than the wild type.

It has long been thought that circadian oscillations provided the clock for photoperiodically induced diapause in insects. Diapause is a genetically determined state of arrested development that is induced prior to the onset of detrimental conditions. Hibernal diapause, which allows insects to survive over winter, is often induced in insects when insects develop during a period of cool temperatures under a short daylength, which means they must be able to measure light and dark cycles. However, per^+ appears to have no influence on the photoperiodic clock in *D. melanogaster.*

Females of a wild-type strain of *D. melanogaster* (Canton-S) and strains with *per* mutations were able to discriminate between diapause-inducing short days and non-inductive daylengths. *D. melanogaster* adult females exhibit an ovarian diapause when reared and held under short days and low temperature (12°C). Females exposed to long days at the same temperature reproduce.

The critical daylength (the photoperiod at which 50% of the individuals enter diapause) for Canton-S females at 12°C is approximately 14 h of light per 24 h. Photoperiodic response curves for the *per*^{S}, *per*^{L} and Canton-S strains were almost identical, although *per*^{0} flies showed shortened critical daylengths. However, *per*^{0} females are able to discriminate between a long day and a short day.

Many behaviors, including learning, involve temporally patterned events. The interval between presentation of the conditioned stimulus and reinforcement is important in associative learning. The conditioned stimulus must be presented before the unconditioned stimulus and the unconditioned stimulus must follow the conditioned within a relatively brief interval. It was thought that the *per*$^{+}$ gene could be involved in learning, based on the observation that *per*^{L} males in one experiment did not exhibit normal experience-dependent courtship behavior. However, males with the wild type or *per*^{S} and *per*^{0} alleles could be conditioned normally.

Learning in *Drosophila*

It is difficult to produce a single definition of learning. Learning can be defined as a change in behavior with experience, but this definition would not exclude responses such as growth and maturation, or other processes that are triggered by events such as mating or feeding. Another definition is a reversible change in behavior with experience, but this excludes phenomena in which the modification caused by some experience is fixed and resistant to further change. Another definition is that learning is a more or less permanent change in behavior that occurs as a result of practice, but this definition is ambiguous.

The following properties are characteristic of learning in insects: (i) The individual's behavior changes in a repeatable way as a consequence of experience. (ii) Behavior changes gradually with continued experience, often following a "learning curve" to an asymptote. (iii) The change in behavior accompanying experience declines in the absence of continued experience of the same type or as a consequence of a novel experience or trauma.

Insect populations vary in their ability to learn. Genetic variability within strains has been used to analyze learning in *Drosophila*, *Phormia* flies and the honeybee *Apis mellifera*. *Drosophila melanogaster* can be sensitized and habituated, learn associations with positive or negative reinforcement, and be classically conditioned. *Drosophila melanogaster* can learn to run away from specific odors that they previously experienced with electric shock and hungry flies can learn to run toward odors previously associated with a sugar reward. Flies can learn visual, tactile, spatial and proprioceptive cues. Analyses of memory mutants in *Drosophila*, including the genes *dunce*, *rutabaga*, *amnesiac*, *radish*, *zucchini*, *cabbage*, *tetanic*, *turnip*, *linotte* and *latheo*, indicate that memory consists of distinct phases: short-term, intermediate, long-term and anesthesia-resistant memory.

Genetic analyses of learning in *Drosophila melanogaster* began in the mid-1970s in Seymour Benzer's laboratory when *D. melanogaster* was trained to avoid an odor associated with an electric shock. The learned avoidance lasted only a few hours, but the odor avoidance test was used to screen mutagenized flies for strains that had normal olfaction and aversion to shock, but an abnormally-low ability to associate odors with shocks. The mutants obtained were poor learners but each had different phenotypes. One mutant strain, *amnesiac*, had a nearly normal learning ability but forgot rapidly. The *dunce* flies had a shortened memory for several different conditioned behaviors due to a defective gene for cAMP-specific phosphodiesterase, an enzyme that regulates levels of cyclic AMP (cAMP). The *dunce* flies have elevated cAMP levels; cAMP is part of a second messenger signaling pathway in nerve cells that help form associative memories. *dunce* flies have impaired synaptic transmission because the excess of cAMP leads to hyper polarization of the synaptic terminals, resulting in a chronically lowered availability of neurotransmitter.

The *dunce* gene is one of the largest and most complex identified in *Drosophila*, extending over 140 kb. It produces, by the use of multiple transcription start sites and alternative splicing of exons and differential processing of 3′ sequences, at least eight to ten messenger RNAs ranging in size from 4.2 to 9.5 kb. One unusually large intron (noncoding sequence inside the coding region) is 79 kb in length and contains at least two other genes (*Sgs-4* and *Pig-1*) within it. This genes within an intron arrangement is uncommon. One of the contained genes, *Sgs-4*, is expressed in larval salivary glands and provides the glue used by larvae to attach themselves to the surface for pupation. *Sgs-4* is transcribed in the same direction as *dunce*. The second gene, *pre-intermolt gene*, also is expressed in larval salivary glands but is transcribed in the opposite direction. Genes homologous to *dunce* have been identified in mice, rats and humans. The mammalian counterparts of *dunce* function in regulating mood. The *dunce* gene is expressed in the mushroom bodies in the brain of *D. melanogaster.*

Mushroom bodies are important for olfactory learning and memory. In *D. melanogaster* these structures are paired and consist of about 2,500 neurons that send dendrites into a neuropil just ventral to the perikarya where inputs arrive from the antennal lobes and other centers of the brain. Mushroom bodies receive olfactory information from the antennal lobes through their dendrites located in the calyx, a region of the brain just ventral to the mushroom body. Mushroom bodies house part of the short-term memory for odors, are required for courtship conditioning memory and are necessary for context generalization in visual learning, as well as regulating the transition from walking to rest. By analyzing a *Drosophila* strain with *alpha-lobes-absent*, a mutation which causes flies to lack either the two vertical lobes of the mushroom body or two of the three median lobes which contain branches of the vertical lobe neurons, it was found that long-term memory requires the vertical lobes. Short-term memory was normal in flies lacking either vertical lobes or the two median lobes.

Learning probably requires other brain centers, including the antennal lobes, the central complex and the lateral protocerebrum in insects. During metamorphosis, the nervous system of holometabolous insects such as *Drosophila* changes significantly. A controversy has existed as to whether flies retain learned behavior after metamorphosis from larvae to adults, but there is no evidence that larval conditioning induces a change in adult olfactory responses. This is not surprising because larval sense organs undergo histolysis during the pupal stage and adult sense organs are formed *de novo* from imaginal discs. The mushroom bodies of the fly brain are extensively rewired during metamorphosis.

Drosophila carrying the mutant *turnip* have difficulty in olfactory discrimination, conditioning of leg position, larval, visual and reward learning. The *turnip* gene is located on the X chromosome and is associated with reduced protein kinase C activity. Specifically, the *turnip* mutant is defective in phosphorylation of pp76, a membrane protein in head tissues. Protein phosphorylations have been implicated repeatedly in changes underlying learning and short term memory.

Additional genes, including *radish*, *amnesiac*, *cabbage*, *latheo* and *linotte*, are involved in abnormal learning or memory of *D. melanogaster*. For example, flies with the X-linked *radish* mutation initially learn in olfactory tests, but their subsequent memory decays rapidly at both early and late times after learning. The *radish* flies show normal locomotor activity and sensitivity to odor cues and electric-shock reinforcements used in the learning tests. Anesthesia-resistant memory, or consolidated memory, is strongly reduced in *D. melanogaster* with the *radish* phenotype.

The *rutabaga* gene codes for an adenylyl cyclase, is expressed in *Drosophila* mushroom bodies, and is involved in olfactory short-term memory. *Volado*, which codes for an α -integrin that mediates cell adhesion and signal transduction, is expressed in mushroom body cells of *Drosophila* and mediates short-term memory in olfactory learning. Integrins have diverse biological roles, including cell-cycle regulation, cell migration and cell death (apoptosis), functioning as mediators of interactions between cells with the extra cellular matrix or with counter receptors displayed by their cells. They can also transduce information across cell membranes bi-directionally

The enlightenment obtained from the study of these *Drosophila* learning mutants is providing an understanding of learning in higher organisms.

Functional Genomics of Odor Behavior in *Drosophila*

The ability to respond to odors is essential for survival and reproduction, allowing insects to select mates, find and choose food, and locate appropriate oviposition sites. A beginning has been made in understanding the complex genetic basis of odor behavior in insects using *D. melanogaster* as a model system.

Odors are received by olfactory receptors located on the third antennal segments and the maxillary palps, which send their axons to the antennal lobes in insect brains. Each third antennal segment in *D. melanogaster* contains about 1,300 olfactory receptor cells and each maxillary palp carries 120 chemosensory neurons. These neurons project to 43 glomeruli in the antennal lobe of the brain. From there, processed olfactory information is relayed to higher-order brain centers (the mushroom body and the lateral horn of the protocerebrum).

D. melanogaster has approximately 1,300 olfactory receptor neurons and *D. melanogaster* is able to recognize and discriminate between a large number of odorants. Each olfactory sensory neuron responds to several odorants, but respond maximally to only one. While the average olfactory receptor gene is expressed in 20 olfactory neurons, some receptor genes are expressed in only two to three neurons. Seven olfactory receptor genes are expressed solely in the maxillary palp.

It is thought that there are fewer than 100 types of odor receptors in insects, and perhaps as few as 50 or 60. By contrast, mammals have more than 10,000 different receptor types. The approximately 50–60 odorant receptor genes in insects encode a novel family of proteins with seven predicted membrane-spanning domains; these genes are unrelated to vertebrate or nematode chemosensory receptors, suggesting the genes evolved in an independent manner throughout evolution. Furthermore, the *Drosophila* genes are poorly grouped into subfamilies of similar sequences because they are only 17–30% similar to each other.

Learning in *Apis mellifera*

Mushroom bodies in the Hymenoptera are much larger than those in *Drosophila*, which may reflect the importance of the mushroom bodies for functions underlying social behavior, learning and memory in the honey bee. Many Hymenoptera (ants, bees, wasps) have complex behaviors that include caring for their brood either as individual females or as a social group of females. Bee species such as *Apis mellifera* feed, protect and nurse larvae, store food and respond to adverse environmental factors. They search for nectar and pollen at unpredictable sites, learn the celestial and terrestrial cues that guide their foraging trips over long distances and allow them to find their nest sites once again. They learn how to respond to the changing position of the sun, to a pattern of polarized light during the day, and to landmarks. Associative learning is an essential component to foraging behavior and dance communication. Hive mates attending a dance performance learn the odor the dancing bee carries and seek out that same odor when they forage for food.

The complexity of bee behavior makes it an ideal organism to analyze to better understand learning, especially in response to odors. Associative olfactory learning in honey bees has several features similar to higher forms of learning in vertebrates.

Pheromones in Insects

Insects use chemical cues as signals to find mates, food, oviposition and hibernation sites. Molecular genetic methods are now being used to study various aspects of pheromone response behavior. For example, genes that code for proteins involved in the synthesis of pheromones, the perception of semiochemicals, and the processing of the signals are being cloned and characterized.

Pheromone biosynthesis appears to use one or a few enzymes that convert the products of normal primary metabolism into compounds that act as pheromones. For example, pheromones arise from isoprenoid biosynthesis, or by the transformation of amino acids or fatty acids. A number of the genes encoding the enzymes involved in transforming metabolites into pheromones have been cloned and sequenced. The production of pheromones by insects is regulated by three hormonal messengers: juvenile hormone III, ecdysteroids, and a neuropeptide called PBAN (pheromone biosynthesis activating neuropeptide).

Perception of the volatile pheromone is mediated by olfactory organs (sensillae) located primarily on the antennae. Receptor neurons on the antennae appear to respond to one particular chemical (specialist neurons) while others appear to respond to a number of compounds (generalist neurons). Pheromones are often perceived in combination with other chemicals, including plant volatiles.

The detection of pheromones and other chemicals by insects involves proteins (odorant binding proteins, OBPs) that carry the compounds from the surface of the antennal sensilla through the sensillum lymph to the G-protein-coupled receptors and the olfactory neurons. The odorant binding proteins (which includes pheromone binding proteins) are small, soluble proteins that are concentrated in the sensillum lymph.

Genes and complementary DNAs encoding odorant binding proteins of many insects have been cloned. Analysis indicates that the binding proteins of unrelated species have low levels of amino acid sequence similarity, although they do have a conserved region with cysteines that may be important for function. It appears that there has been gene duplication and divergence of odorant binding protein genes, with moth proteins belonging to one branch and the proteins of other insects not closely related.

The molecular receptors in an olfactory system involve G-protein-coupled seven transmembrane proteins. Such proteins also are found in the mouse and rat, where the number of such genes number approximately 1,000 or nearly 1% of the genome, indicating that odor reception is an important component of the mammalian genome. Sequencing the *Drosophila* genome has allowed receptor similar proteins to be identified in an insect. The receptors are in large multigene families and expressed at different times during antennal development. The receptor genes were found by searching the *Drosophila* genome to identify sequences that might encode transmembrane domains.

Once an odor or pheromone has activated the olfactory receptors, it needs to be deactivated. Several enzymes have been found that appear to degrade odor stimulants, including esterases, oxidases, and glutathion transferases. Multielectrode recording of the *Manduca sexta* antennal lobe indicates that the relative timing of action potentials may convey information about odor concentration and mixture. A large and diverse family of genes coding for taste receptors have been identified in *Drosophila* that are expressed in the proboscis.

Rapid advances in understanding olfaction and gustation in insects, especially based on molecular genetic analyses of *D. melanogaster*, promise to advance our understanding of how insects perceive chemical cues in their environment.

Unfortunately, early evidence suggests an extreme divergence of receptors within *D. melanogaster* that make it difficult to use homology to isolate odor receptor genes from other insects.

Divergent Functions of *Est-6* and *Est-5* in *Drosophila* Species

Evolutionary changes in gene regulation can be a prerequisite for macro evolutionary change and species divergence. One case study involves an analysis of the esterase 6 enzyme in *Drosophila melanogaster* and its homologue (esterase 5) in *D. pseudoobscura.* This gene influences behavior in *D. melanogaster* but has a very different function in *D. pseudoobscura.*

Esterase-6 (*Est-6*) in *D. melanogaster* influences male mating speed and rate of remating by females. Fast and slow variants of esterase 6 protein, as detected by electrophoresis, are produced in natural populations of *D. melanogaster*. More esterase 6 protein is produced in adult males than in females. The enzyme is highly concentrated in the anterior ejaculatory duct of males and is transferred to females during the first 2–3 min of the 20min copulation. Enzyme activity in females can be detected up to 2 h after mating and influences the timing of remating by females. Males transfer a substance in the seminal fluid which is converted in the females' reproductive tract by esterase 6 into a pheromone that serves as an antiaphrodiasiac. The antiaphrodiasiac reduces the sexual attractiveness and receptivity of females, reducing the likelihood she will remate. Because the sperm from the most recent male takes precedence in fertilizing a female's eggs, this behavior appears to encourage monogamy in *D. melanogaster* females. *Est-6* also influences the rate of mating of males in *D. melanogaster*. Males with the slow variant of the protein require 10.2 min to achieve copulation with females, while males with the faster-moving protein require only 5.7 min.

Once the *Est-6* gene was cloned, it was used as a probe to identify homologous genes in related species, which can provide clues to the evolution of behavior. *Est-6* was used to isolate a homologous gene (*Est-5*) from *D. pseudoobscura*. Surprisingly, *Est-5* has a different function in *D. pseudoobscura*. Approximately 40% of *Est-5* is expressed in the eyes of *D. pseudoobscura*, with the remainder expressed in the hemolymph of both sexes. Despite these different patterns of expression, *Est-6* and *Est-5* have similar protein products, messenger RNA transcripts, and DNA sequences.

When *Est-5* from *D. pseudoobscura* was cloned into a P element and introduced into *D. melanogaster*, its activity and pattern of expression in *D. melanogaster* matched those of *D. pseudoobscura*. These results imply that regulatory sequences in *Est-5* have been conserved since the divergence of the two species 20–46 million years ago, suggesting that the enzyme in the common ancestor of these two species had a more extensive expression pattern. After the species diverged, regulatory mutations may have occurred that enhanced *Est-5* expression in the eyes of *D. pseudoobscura*, while mutations in *Est-6* led to increased expression in the male ejaculatory duct of *D. melanogaster*. Thus, the use of homology to identify behavioral (and other) genes can lead to surprises.

Courtship Behavior in *Drosophila*

Mating behavior of *D. melanogaster* is stereotypical, with a fixed sequence of actions that are under genetic control. Courtship involves visual stimuli, acoustic signals, and pheromones. Male courtship behavior involves six elements in the following fixed order: orienting → following → wing vibration → licking → attempting to copulate → copulation.

Sexual differentiation in *Drosophila* is controlled by a short cascade of regulatory genes, the expression of which determines all aspects of maleness and femaleness in the body and the central nervous system, including complex behaviors. Such sexual behavior is irreversibly programmed during a critical period as a result of the activity or inactivity of the major control gene *tra*$^{+}$. Male behavior is replaced by female behavior when *tra*$^{+}$ is expressed around the time of puparium formation.

Other genes indirectly affect courtship behavior in *Drosophila*, including genes that involve: general behavior (*yellow*, *inactive*, *couch potato*, *cuckold*, *minibrain*, *nerd*); visual behavior (*white, optomotor-blind, no-receptor-potential-A*); olfaction (smellblind); learning/memory genes (*dunce*, *rutabaga*, *amnesiac*, *Shaker*, *ether-a-go-go*); regulating periodicity of behavior (*period*), courtship song mutants (*cacophony, dissonance, croaker, fruitless*); female receptivity (*spinster*).

The *fruitless* mutation is involved in both sex determination and courtship behavior and is active in the central nervous system. Males with the *fruitless* mutation may court both females and males without copulating. Male flies expressing this gene are unable to bend their abdomens in the presence of females they are courting because they lack a male-specific Muscle of Lawrence. Some *fruitless* mutations cause males to be homosexual (they do not court females), while others cause males to be bisexual (they court both males and females). The *fruitless*$^{+}$ gene is the first gene in a branch of the sex-determination hierarchy functioning specifically in the central nervous system, with mutants of this gene affecting nearly all aspects of male sexual behavior. It is at least 140 kb long and produces a complex array of transcripts by using four promoters and alternative splicing; the male-specific transcripts are only expressed in a small fraction of the central nervous system.

Another mutation, *dissatisfaction*, is necessary for some aspects of sex-specific courtship behavior and neural differentiation in flies of both sexes. Mutant males are bisexual but, unlike *fruitless* males, attempt to copulate. Males with the *dissatisfaction* phenotype take longer to copulate with females while females are unreceptive to male advances during courtship and do not lay mature eggs.

Mating behavior of females involves the following sequence: stopping moving → offering the courting male a chance to lick the female's genitalia → allowing males to attempt copulation. Nonreceptive females leave the courting male, and if the male pursues her, she may kick him. Nonreceptive virgin females persistently repel male approaches by lifting their abdomens up to block physically any contacts with males. Nonreceptive fertilized females lower their abdomen, extrude their ovipositors and eggs to repel males. Thus, female receptivity varies with age, diet, hormonal condition and mating experience. The *spinster* mutation affects female sexual receptivity throughout their lives, and *spinster* females continuously leave, kick, or fend off courting males.

Both *D. melanogaster* and *D. simulans* females produce contact pheromones, which consist of cuticular hydrocarbons that elicit wing displays by males. These chemical signals have a low volatility, and thus act at a very short distance (a few mm) and thus are perceived by contact rather than smell. Flies from a given strain, sex, and age produce a reproducible pattern of cuticular hydrocarbons, the biochemical pathway of which is under genetic control. The most important hydrocarbons involved in mate recognition or stimulation are 7-tricosene and 7-pentacosene. One mutation, *Ngbo*, influences the ratios of 7-tricosene and 7-pentacosene in *D. simulans*. Another, *kete*, reduces the amount of 7-tricosene and all other linear hydrocarbons but does not affect the ratio. Flies homozygous for both *kete* and *Ngbo* have reduced viability and fertility, perhaps because they have very little 7-tricosene.

Experiments were conducted to eliminate all known cuticular hydrocarbons in *D. melanogaster* in order to determine how mating behavior would be modified. The results were surprising; contrary to expectation that *D. melanogaster* females lacking cuticular pheromones would induce no courtship by males, such females remained attractive. Additional analysis indicated that undetermined pheromone(s), probably also cuticular hydrocarbons, were present on both control and transgenic flies. These newly discovered pheromones could represent ancestral attractive substances in *D. melanogaster* and its sibling species. An absence of inhibitory pheromones leads to high levels of interspecific mating among *Drosophila* species, suggesting that cuticular hydrocarbons are important in maintaining reproductive isolation.

Studies of Human Neurodegenerative Diseases and Addictions in *Drosophila*

Drosophila is perhaps unique among eukaryotes in the variety and level of sophistication that can be applied to understand its neurobiology. *Drosophila* is being studied, as well, to gain knowledge about various neurodegenerative diseases in humans.

Modeling diseases in simple invertebrate systems is attractive because genetic interactions can be used to define cellular cascades mediating, for example, death of neurons in Parkinson disease, the second most common neurodegenerative disorder in humans. Transgenic *Drosophila* containing a mutant form of the human α -synuclein gene exhibit the essential features of the Parkinson's disease in humans, making it possible to study the function of α -synuclein and determine the underlying pathogenic mechanisms in a genetically tractable animal.

The *spongecake* mutant of *Drosophila* shows degenerative changes similar to that seen in humans with Creutzfeld-Jakob disease, while the *eggroll* mutant produces changes similar to those seen in humans with Tay-Sachs disease. The *beta-amyloid protein precursor-like (Appl)* gene of *Drosophila* encodes a homolog of the human α -amyloid precursor protein which gives rise to α -amyloid, a major component of the plaques in the patients suffering from Alzheimer's disease. Another protein associated with human Alzheimer's disease, presenilin, has been found in *Drosophila* and studies suggest it may also be involved in the development of the pathology. *A Drosophila* homolog was identified for the human gene for copper/zinc superoxide dismutase; mutants of this gene are implicated in Lou Gehrig's disease.

A recessive mutant (*bubblegum*) in *D. melanogaster* exhibits adult neurodegeneration similar to that seen in the human disease adrenoleukodystrophy (ALD), otherwise known as the disease cured in the movie "Lorenzo's Oil";. In ALD, high levels of very long chain fatty acids are produced that can be lowered by dietary treatment with a mixture of unsaturated fatty acids; feeding the ALD flies one of the components, glyceryl trioleate oil, blocked the accumulation of excess very long chain fatty acids and eliminated the development of pathology. Thus, *bubblegum* flies provide a model system for studying mechanisms of disease and screening drugs for treatment.

Drosophila also has been proposed as a model organism for studying the genetics of alcohol abuse and drug addiction in humans. Alcohol addiction and many types of drug addictions appear to share common mechanisms. For example, the "dopamine hypothesis" suggests that addictive drugs may activate certain areas of the human brain leading to an increase in dopamine neurotransmitter release. Elevation of dopamine probably provides a sense of well being, pleasure, or elation (positive reinforcement). Dopamine is not the only neurotransmitter acting in alcohol abuse; glutamate, serotonin, and GABA also are may be involved. Furthermore, four of the five circadian genes (*period, clock, cycle, doubletime*) identified in *D. melanogaster* influence the fly's responsiveness to cocaine and suggest a biochemical regulator of cocaine sensitization.

Selection of *D. melanogaster* for resistance to ethanol was shown to be determined by multiple genetic components. Mutant strains with different responses to ethanol and different responses to the effects of acute ethanol exposure on locomotor behaviors are remarkably similar to those described for mammals. Thus, study of *Drosophila* could pave the way for an in-depth study of the genes involved in acute and chronic effects of ethanol. In *Drosophila*, as in mammals, dopaminergic pathways play a role in modulating specific behavioral responses to cocaine, nicotine or ethanol.

Sleep even occurs in *Drosophila* and may be a model for understanding sleep in other animals. Flies that are "resting" are sleeping, which involves the flies choosing a preferred location, becoming immobile for periods of up to 157 min at a particular time in the circadian day, and becoming relatively unresponsive to sensory stimuli. When rest is prevented, the flies tend to rest despite stimulation and then exhibit a rest "rebound." Drugs that affect sleep in mammals alter "rest" in flies, suggesting conserved neural mechanisms. During sleep, an animal cannot forage for food, take care of its young, procreate or avoid the dangers of predation, indicating that sleep must serve an important function. Sleep disorders in humans are common, but the genes underlying these disorders are unknown.

Molecular Analyses of Complex Behaviors

The genetic basis of many behavioral attributes in insects is probably determined by many genes. Furthermore, behavior is determined, not only by genetic composition, but also by the environment and can be influenced by learning. The effects of the environment may mask those of the genotype, making genetic analysis imprecise. While elaborate statistical techniques have been developed for quantitative genetic analyses, a thorough understanding of behaviors that are quantitatively determined has been slow to develop.

Understanding the mechanisms of behavior determined by single genes is hard work, but relatively straight forward. Understanding the mechanisms of behavior determined by many genes requires ingenuity and extensive effort. However, such research offers many rewards. For example, advances in understanding the molecular genetic basis of social behavior in bees and ants could allow us to understand the evolution of female choice, kin recognition, reciprocal altruism, and the organization of insect societies.

Analysis of insect behavior using insect molecular genetic approaches is still in its infancy, but the disciplines of ethology, genetics, physiology, and molecular biology promise to revolutionize the field.

References

Bellen HJ (1998) The fruit fly: a model organism to study the genetics of alcohol abuse and addiction? Cell 93:909–912

Brady JP, Richmond RC (1990) Molecular analysis of evolutionary changes in the expression of *Drosophila* esterases. Proc Natl Acad Sc USA 87:8217–8221

Costa RA, Peixoto A, Barbujani G, Kyriacou CP (1992) A latitudinal cline in a *Drosophila* clock gene. Proc R Soc London B 250:43–49

Field LM, Pickett JA, Wadhams LJ (2000) Molecular studies in insect olfaction. Insect Mol Biol 9:545–551

Fortini ME, Bonini NM (2000) Modeling human neurodegenerative diseases in *Drosophila*. On a wing and a prayer. Trends Genet 16:161–167

Greenspan RJ, Ferveur JF (2000) Courtship in *Drosophila*. Annu Rev Genet 34:205–232

Greenspan RJ, Tononi G, Cirelli C, Shaw PJ (2001) Sleep and the fruit fly. Trends Neurosci 24:142–145

Vosshall LB (2000) Olfaction in *Drosophila*. Curr Opin Neurobiol 10:498–503

Waddell S, Quinn WG (2001) Flies, genes and learning. Annu Rev Neurosci 24:1283–1309

Yamamoto D, Jallon JM, Komatsu A (1997) Genetic dissection of sexual behavior in *Drosophila melanogaster*. Annu Rev Entomol 42:551–585

Behningiidae

A family of mayflies (order Ephemeroptera).

► Mayflies

Beklemishev, Vladimir Nikolayevich

Inna Ioffe-Uspensky, Igor Uspensky
The Hebrew University of Jerusalem, Jerusalem, Israel

V.N. Beklemishev was born on October 5, 1890, in Hrodna, then a portion of Poland incorporated into the Russian Empire. He grew up in a large harmonious family with a high level of culture and education. From the family he received a good intellectual and moral education that strongly influenced him. He studied in the local grammar school which he left as the top pupil. He was interested in natural history and he collected insects and read books by Braem, Fabre and other naturalists. In 1908, he entered the University of St.-Petersburg specializing in zoology. After graduating from the University (1913) he was kept there "to prepare for the title of Professor." In 1918 he received his Master's degree in zoology and comparative anatomy with the right to lecture. However, because of terrible famine and collapse after the October Revolution of 1917 he left St.-Petersburg (Petrograd) for Perm' (in the Ural Mountains) where he received the position of an associate professor in the University of Perm'. By 1920 he was approved as a full professor in the faculty of medicine. He lectured in many general and special courses and carried out intensive research on the morphology of invertebrates, biocenology and hydrobiology. The wide range of his interests and his excellent erudition in various fields of biology were of great importance when in 1924 he headed an entomological study at the Malarial Station of the Medical and Biological Institute of Perm'. Working on the ecology of *Anopheles* larvae, he studied hydrobiological characteristics of larval biotopes and the habitat distribution of mosquito larvae. He evaluated the significance of water bodies in different landscapes not only from an entomological but also from an epidemiological point of view. As a result, he formulated the doctrine of landscape malariology which allowed the planning of control measures based on the characteristics of a particular landscape. In 1932 he was invited to Moscow to head the Department of Medical Entomology in the Tropical Institute (later the Martsinovsky Institute of Medical Parasitology and Tropical Medicine). The biology of adult mosquitoes was the main aspect of his interest at that time. Together with his followers he studied the population biology of different species of *Anopheles*. These fundamental works included the detailed study of mosquito morphology, mosquito behavior, gonotrophic cycles, physiological age, etc. He wrote that any finding illuminating unknown features in *Anopheles* biology would be important for the success of malaria control. From mosquitoes he moved to the study of other groups of arthropods which allowed him to develop a concept of the "life scheme" of species, which is considered as the total amount of species adaptations to the environment. His concept is rather close to Hutchinson's concept of a fundamental ecological niche, developed later. He liked and estimated the comparative analysis as the mostly fruitful approach in biological study. He was the founder of the comparative parasitology of bloodsucking arthropods. Comparing the life schemes of bloodsucking arthropods, he distinguished main types of their parasitism. He considered the origins and development of arthropod parasitism on terrestrial vertebrates. He developed well-balanced systems of relationships between parasitic arthropods and their hosts and showed the role of such systems in biocenoses. During the 1950s he worked intensively on the problem of tick-borne encephalitis in the USSR and significantly contributed to the understanding of the structure of natural foci and epidemiology and epizootiology of this infection. All his ideas were not only theoretical constructions but the result of laboratory studies and field expeditions to different areas of the USSR in which he participated together with his younger fellows. His main publications include: "Ecology of the malarial mosquito (*Anopheles maculipennis* Mgn)" (1944); "The planning of settlements and the problem of malaria" (1949); "Manual of medical entomology" in two volumes (editor and the author of many chapters) (1949); "Key to arthropods injuring human health" (editor and the author of some chapters) (1958). He was also the editor of many proceedings and books. Unfortunately, most of his papers were published only in Russian. He was well known among world zoologists as the author of his greatest work "Principles of comparative anatomy of invertebrates" which had three editions in the USSR (1944, 1952, 1964) and was also published in Romania, Poland and the German Democratic Republic. In 1969 this monograph was published in English (Edinburgh). In recognition of his works he was elected to the Academy of Medical Sciences of the USSR, and twice he was awarded the USSR State Prize. He was elected to the Polish Academy of Sciences. He was also much revered by his numerous pupils many of whom became well-known specialists. His interests were not limited by biology only. He knew history, liked and knew Chinese art and philosophy, and he liked poetry, fine art and architecture. He wrote verses himself. He died on September 4, 1962. In 1970 his pupils published a collection of his most important papers under the title "Biocenological principles of comparative parasitology."

References

Balashov YS (1991) The significance of V.N. Beklemishev's concepts of parasitic systems and life schemes of the species for the development of parasitology. Parazitologiya 25:185–195 (in Russian)

Smirnov ES (1962) Scientific activity of V.N. Beklemishev. In: Problems of general zoology and medical parasitology. Medgiz, Moscow, USSR, pp 7–38 (in Russian)

Belidae

A family of beetles (order Coleoptera). They commonly are known as primitive weevils.

► Beetles

Bell, William J

Bill Bell was born in Boston, Massachusetts, on January 10, 1943. His B.S. degree in biology and education was earned in 1964 from Bridgewater State College, M.A. in zoology in 1966 from the University of Massachusetts, and Ph.D. in 1969 from the University of Pennsylvania. The subject of his Ph.D. research was the role of juvenile hormone in vitellogenesis. Then followed a 1-year postdoctoral fellowship at the University of Texas before he was appointed assistant professor of entomology at the University of Kansas. His career was spent in Kansas, and he was promoted to full professor at the age of 33. He taught undergraduate and graduate classes and, between 1970 and 1996 had trained 18 Ph.D. and eight M.A. students in his laboratory. His research interests, begun with developmental biology, expanded to reproductive physiology, chemoperception, and related behaviors, and began to include field work. He served as editor of Journal of the Kansas Entomological Society (1982–1984), co-editor of Environmental Entomology (1984–1987), and as editorial board member of Journal of Insect Physiology. He served as editor of Journal of Insect Behavior, which he and Tom Payne founded, from 1988 until his death. He published over 100 research papers and reviews, edited three books, and wrote two: (1981) "The laboratory cockroach," and (1991) "Searching behavior: the behavioral ecology of finding resources." He died on October 17, 1998, after a long illness, survived by his one son and former wife.

References

Greenfield MD (1998) William J Bell 1943–1998. J Kans Entomol Soc 71:1–2

Greenfield MD (1999) William J Bell. Am Entomol 45:59

Belostomatidae

A family of bugs (order Hemiptera). They sometimes are called giant water bugs and toe biters.

► Bugs

Beneficials

Organisms that provide a benefit to crop production, especially natural enemies of pests and plant pollinators such as bees.

Benthic Community

The community of organisms inhabiting the bottom of a body of water.

Bertha Armyworm, *Mamestra configurata* Walker (Lepidoptera: Noctuidae)

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The bertha armyworm, *Mamestra configurata*, atta- cks canola (*Brassica napus L.* and *Brassica rapa* L.) in the northern great plains of North America. Other crops subject to damage by bertha armyworm include flax, *Linum usitatissimum* L., sweet clover, *Meliotus officinalis* L., and alfalfa, *Medigaco sativa* L., although development is not completed or progeny are undersized. Bertha armyworm is a Nearctic species, apparently restricted to dry grassland-type habitats in western North America. It prefers the native weed *Chenopodium album* (lamb's-quarters) but successfully develops on B. napus and B. rapa varieties with low isothiocyanate and glucosinolate levels (canola). *Mamestra configurata* has one North American relative, *Mamestra curialis* (Smith). The larvae of the two species are difficult to separate but adults are distinguished by the wing markings and by characters of the male genitalia. The two species also occupy different habitats, *M. curialis* occurs primarily in forested areas while *M. configurata* is found in grassland areas.

Importance

The economic impact of bertha armyworm is attributed to its importance as a major pest of canola crops. Young larvae consume the leaf foliage of canola and the plant generally compensates for this damage. The fifth and sixth instars cause the greatest damage because they feed on the developing nutrient rich seedpods, adversely affecting seed quality and lowering seed grade. Since 1922, bertha armyworm outbreaks have occurred at intervals of varying length and persist from one to three years. Since 1970, the increase in the incidence of bertha armyworm outbreaks has been associated with the extraordinary increase in the number of hectares planted to canola. Most outbreaks are local and not synchronized with those of other areas. Widespread outbreaks cost producers $10s of millions in yield losses and control costs.

Biology

Bertha armyworm has a univoltine life cycle requiring 6–8 weeks from egg to pupa, which overwinters. Adults emerge from the soil from early June to early August and are attracted to canola fields that are in bloom. The moths are nocturnal, and females copulate during the 2nd or 3rd night after emergence, remaining in copula for about 17 h. Females lay single-layered masses of 20–200 eggs on the underside of leaves of host plants, depositing 75% of their egg complement during the first week after emergence and up to 3,500 eggs during their lifetime.

Eggs are spherical, slightly flattened on the ventral surface, about 0.45 mm in diameter and with a series of longitudinal ridges and depressions (sculpting) radiating from the upper mitotic pole. The white eggs develop for approximately one week. As development takes place the eggs become almost black. Just before they hatch, the black headed first instar larvae are visible through the chorion.

First-instar larvae hatch and immediately disperse from the egg mass to feed on foliage. The larvae feed at night and when disturbed they may drop off the leaves using a fine silk thread which they use to climb back onto the plant. Large larvae may drop off the plants and curl up when disturbed, behavior typical of cutworms and armyworms. The first four instars feed on foliage and, although they prefer foliage, the final two instars feed on the developing pods, the most nutrient-rich plant part during this time of the growing season. The final instar larva consumes 70–80% of the total food consumed by the six larval stages. The dark color of the last two larval instars makes them noticeable in the crop. At summer's end the mature larvae drop to the ground and seek shelter in cracks 5–16 cm below the soil surface where they pupate. Larvae vary greatly in color, particularly the older individuals.

Newly hatched first instar larvae have a distinct black head and are about 0.3 cm long and are covered with sparse but distinct setae. The next five instars have light brown head capsules and the body setae are less evident. The first four instars are green, usually with distinct, narrow, whitish, stripes on their back, and a wider but indistinct band on the side of the body. Most fifth instar larvae are green, others brownish green, or brown with darker markings. The sixth instar, about 4 cm long, is commonly velvety black or brown with conspicuous yellowish-orange stripes along each side and a green underside which contrasts with the dark dorsum. Individuals of the velvety black form have three narrow, interrupted white stripes along their backs. In nature, many variants are found, singly or in homogenous groups, and appear to represent different species, increasing the difficulty of accurate identification. Larvae may exhibit limited local migration, typical of armyworms, when their preferred food source is consumed.

Pupae are reddish, slender, 5.5 mm wide and 18.5 mm long, gradually tapering caudally with flexible abdominal segments. The terminal spines are stout, about 0.7 mm long, close set but slightly divergent, and slightly out-curved at the tip. Males and females are distinguished by the structure of the terminal abdominal segments. Bertha armyworm pupae are not easily distinguished from other cutworm pupae. The pupae undergo a facultative diapause, induced by temperature and photoperiod cues experienced by 4–6 instar larvae. If fall conditions are unusually warm some pupae continue development and will emerge. Over-wintering mortality of pupae is important and is influenced by duration of exposure to temperatures near or below freezing.

The adult is large with a wingspan of about 4 cm. The forewing is mostly grey with patches of black, brown, olive and white scales. The distinguishing feature of the bertha armyworm moth is the broad olive band adjacent to the subterminal line, defined by white markings on the inner side of the forewing.

Outbreaks of bertha armyworm are sporadic, yet consist of huge numbers of larvae infesting canola crops. Population monitoring is important for determining the potential for damage. Adult bertha armyworm can be detected by close inspection of lamb's-quarters and canola plants where they roost during the day on the underside of leaves. Egg masses and early instar larvae are found by inspecting the underside of leaves. The dark late instar larvae are readily visible when feeding on developing seedpods on the tops of canola plants, even at a distance. Area-wide pest management programs use traps baited with a species-specific sex pheromone to monitor bertha armyworm adult numbers. The data are refined and mapped using geographical information systems (GIS) to provide an early warning of outbreak potential. Producers in areas of high risk are advised to regularly inspect their crops to assess larval densities.

Management

Chemical insecticides are registered for use against bertha armyworm. The decision to apply insecticides is based on the larval densities associated with the value of the crop and the cost of spraying.

However, insecticides harm natural enemies, particularly parasitoids of the bertha armyworm.

Cultural control methods for reducing the impact of bertha armyworm include crop rotation and tillage. Crop rotation has limited effectiveness because adult bertha armyworm are strong fliers and readily invade neighboring crops. Fall tillage may increase the overwintering mortality of pupae and spring cultivation may injure the pupae but these methods are not used where minimum tillage is practiced.

Naturally occurring diseases, such as the fungus *Entomophthorales* sp., a "nuclear polyhedrosis virus" (NPV), and the microsporidian *Nosema* sp., are important larval mortality factors at high population densities and NPV infections in up to 95% of local populations have been recorded. Of the native parasitoids, only *Banchus flavescens* Cresson (Ichneumonidae) and *Athrycia cinerea* (Coquillett) (Tachinidae) cause significant mortality in bertha armyworm populations. During outbreaks, *B. flavescens*, which attacks early instar larvae, is usually the most abundant parasitoid, although *A. cinerea* occasionally is more abundant. Parasitism significantly reduces food consumption by bertha armyworm larvae. The effect of arthropod predators on bertha armyworm populations is unknown. Vertebrates, particularly birds, may be important when population densities are high. How natural enemies regulate bertha armyworm populations between outbreaks is not known.

References

Bracken GK (1984) Within plant preferences of larvae of *Mamestra configurata* (Lepidoptera: Noctuidae) feeding on oilseed rape. Can Entomol 116:45–49

Bracken GK (1987) Relation between pod damage caused by larvae of bertha armyworm, *Mamestra configurata* Walker (Lepidoptera: Noctuidae), and yield loss, shelling, and seed quality in canola. Can Entomol 119:365–369

Mason PG, Arthur AP, Olfert OO, Erlandson MA (1998) The bertha armyworm (*Mamestra configurata*) (Lepidoptera: Noctuidae) in western Canada. Can Entomol 130:321–336

Mason PG, Erlandson MA, Youngs BJ (2001) Effects of parasitism by *Banchus flavescens* (Hymenoptera: Ichneumonidae) and *Microplitis meditor* (Hymenoptera: Braconidae) on the bertha armyworm, *Mamestra configurata* (Lepidoptera: Noctuidae). J Hymenopt Res 10:81–90

Mason PG, Turnock WJ, Erlandson MA, Kuhlmann U, Braun L (2001) *Mamestra configurata* Walker, bertha armyworm (Lepidoptera: Noctuidae). In: Mason PG, Huber JT (eds) Biological control programmes in Canada 1981–2000. CABI Publishers, Wallingford, UK pp 169–176

Rempel JG (1951) A study of the embryology of *Mamestra configurata* (Walker) (Lepidoptera, Phalaenidae). Can Entomol 83:1–19

Berytidae

A family of bugs (order Hemiptera). They sometimes are called stilt bugs.

► Bugs

Bequaert, Joseph Charles

Joseph Bequaert was born in Thourout, Belgium, on May 24, 1886. He earned a Ph.D. from Universiteit Gent in natural sciences in 1908. In 1910–1912, he worked for the Belgian sleeping sickness commission, and in 1913–1915 in what was then the Belgian Congo. He emigrated to the USA and became (1917–1922) an associate of the American Museum of Natural History as entomologist, malacologist, and botanist. He became a U.S. citizen in 1921. In 1923–1925 he worked as an instructor in entomology at Harvard Medical School (Massachusetts, USA), in 1925–1945 as assistant professor, and in 1929–1956 as curator of insects in the Museum of Comparative Zoology at Harvard University and in 1951–1956 as Agassiz Professor of Zoology at the same institution. Then he moved to the University of Houston (Texas, USA) as professor of biology, moving to the University of Arizona in 1960. His final move was to the University of Massachusetts. He married Frances A. Brown in 1927 and they had two children. His interests were in entomology (especially medical entomology) and malacology (especially medical malacology); he published major works in both areas and was president of the American Malacologists' Union in 1954. He died in Amherst, Massachusetts, USA, on May 24, 1982.

References

Abbott RT, Young ME (eds) (1973) American malacologists: a national register of professional and amateur malacologists and private shell collectors and biographies of early American mollusk workers born between 1618 and 1900. Falls Church, Virginia, USA, American Malacologists/ Philadelphia, USA: Consolidated/ Drake Press, 494 pp

Clench WJ (1982) Joseph Charles Bequaert 1886–1982. Nautilus 96:35

Beraeidae

A family of caddisflies (order Trichoptera).

► Caddisflies

Bergmann's Rule

Among mammals and birds, individuals of a species occurring in colder climates tend to have a larger body mass, and a correspondingly lower surface to volume ratio, than members of the same species living in warmer climates. This trend results from the need to conserve heat in cold climates but to eliminate excess heat in hot climates. A variant of this is Allen's rule. These rules do not apply to ectothermic animals such as insects.

► Allen's Rule

► Thermoregulation

Berlese, Antonio

Antonio Berlese (Fig. 34) was born in Padua on June 26, 1863. As a boy, he was interested in natural history and collected insects and mites. His studies at Università di Padova (the University of Padua) resulted in a degree in 1884 in natural sciences. He worked for a few months in a school of human anatomy, but then accepted a post at Stazione di Entomologia Agraria in Florence, which Adolfo Targione Tozzetti had founded and then directed. Finishing a professional course in 1887, he worked as Targioni's assistant until 1890 when he was nominated for a position as professor of general and agrarian zoology at R. Scuola Superiore di Agricoltura di Portici, where he worked until 1903. Then, he was nominated director of the R. Stazione di Entomologia Agraria in Florence, succeeding Targioni. He built up this station little by little until it became one of the best-equipped in Italy. From his first publication in 1880, he worked 47 years without interruption, producing a total of 275 publications. A large part of his work was devoted to the study of mites, in which he built a collection of 12,750 slide-mounted specimens. Another major endeavor was his work on olive fruit fly, and yet another on the scale *Diaspis pentagona*. His two-volume book "Gl'insetti, loro organizzazione, sviluppo, abitudini e rapporti coll'uomo" with 2,187 figures, was published in parts, from 1904 to 1923. His awards included a prize of 10,000 lire from the R. Accademia di Agricoltura di Torino, a gold medal from the province of Venezia in 1913, an award of 75,000 lire from the

Berlese, Antonio, Figure 34 **Antonio Berlese.**

council of the province of Udine in 1924, and honorary membership in the Société Entomologique de France. He died in Florence on October 24, 1927.

References

Paoli G (1928) Antonio Berlese. Memorie della Società Entomologica Italiana 6:55–84

Berlese Funnel

An extraction devise used to separate and extract small arthropods from leaf litter or similar material. A Berlese funnel normally consists of a funnel with a wire mesh insert that support the plant material above a reservoir containing alcohol or another preservative. As the arthropods move about, particularly as they move deeper into the funnel to escape drying of the plant material, they slip down the funnel into the reservoir containing liquid where they are retained for identification. This technique is useful for many arthropods, but not for those that may fly to escape, or those that are very fragile and perish from desiccation before they can escape the plant material. A modern variant of the Berlese funnel is the Tullgren Funnel, which is simply a Berlese funnel with an incandescent light suspended above the funnel to provide a source of heat and to extract the arthropods faster. Another variant uses a cover to eliminate escape by insects capable of flight, and to more efficiently direct the heat generated by the light bulb. Most "Berlese" funnels now used are actually Tullgren funnels, but the distinction is not generally appreciated.

Bernhauer, Max

Max Bernhauer was born in Müglitz, Austria (otherwise known as Mohelnice, and now in the Czech Republic) on September 24, 1866. His education was in Olomonic (now in the Czech Republic) and then at Universität Wien ("the University of Vienna," Austria), but the final degree he obtained in 1899 was as *doctor juris* ("doctor of law"), not as a biologist. He worked as a notary in Austria. It was Ludwig Ganglbauer, in particular, who instructed Max on Coleoptera. His first two papers were published in 1898. Because of the dearth of people willing to study and identify Staphylinidae, Max was soon presented with an endless flow of specimens collected from around the world, and asked to identify them (cost free, of course). For Max, this was a seemingly endless opportunity to classify and describe the species of the huge family Staphylinidae, and to build his collection. He collaborated with Karl Schubert and Otto Scheerpeltz in producing a world catalog (published by Junk-Schenkling as part of "Coleopterorum Catalogus";), completed in 1926 and listing 12,740 species, but expanded to 19,900 species by 1932 by Otto Scheepeltz and continuing to grow. The world total of Staphylinidae as of the year 2000 exceeded 45,000 species, and Max Bernhauer had described 5,251 of them, including 342 new genera, in his 285 publications, a spectacular achievement for an "amateur" coleopterist. Names of the vast majority of the species that he described are still considered valid, even though he was not in the habit of providing illustrations or keys for identification, so that confirmation of identity of the species he described is often very difficult. He died on March 13, 1946, in Horn, Austria. His collection was sold, soon after his death, a negotiation achieved by Rupert Wenzel, to the Field Museum of Natural History, Chicago, USA. There seems to have been a teacher-student train Erichson-Ganglbauer- Bernhauer-Scheerpeltz among the German-speaking students of Staphylinidae, which, unfortunately, ended with Otto Scheerpeltz.

References

Herman LH (2001) Bernhauer, Max. Bull Am Mus Nat History 265:43–44

Puthz V (1980) Bibliographie der Publikationen Max Bernhauers (1866–1946) [a bibliography, not a biography]. Philippia 4:248–261

Rambousek G (1916) Ein Lebensbild Dr. Max Bernhauer's. *Coleopterologische Rundschau* 5:73–82

Berothidae

A family of insects in the order Neuroptera. They commonly are known as beaded lacewings.

► Lacewings, antlions, and mantidflies

Bertram, Douglas Somerville

Douglas Bertram was born in Glasgow in 1913. His Bachelor's degree was from Glasgow University, after which he did graduate research and was employed as a demonstrator in the Zoology Department of that university. In 1938 he moved as Lecturer in Entomology to Liverpool School of Tropical Medicine, began insect cultures, and performed research on fowl malaria. In 1940, he enlisted in the British army and served in Egypt and Greece, but was captured in Crete and remained a prisoner in Germany for the duration of the war. In 1946, he returned to Liverpool for two years and worked on cotton rat filariasis and on control of warble fly. In 1948, he was appointed as Reader in the Department of Medical Entomology in the London School of Hygiene and Tropical Medicine, later becoming head of the department. His research was directed to mosquitoes, especially their age-grading, and their transmission of viruses and fowl malaria, but extended to other biting families of biting flies, and to biological control of triatomine bugs. He traveled extensively to tropical countries to further his research. He was consultant in entomology to the British army, fellow of the Royal Entomological Society, of the Institute of Biology, and of the Royal Society of Tropical Medicine and Hygiene. He died in 1988.

References

Busvine JR (1989) Obituary. Douglas Somerville Bertram. Antenna 13:8–9

Bess Beetles (Coleoptera: Passalidae)

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Bess, patent-leather, or passalid beetles are common, primarily tropical insects. A few of the approximately 600 species occur in temperate regions (China, Japan, Korea, Canada, U.S., and Tasmania, but not Europe, though the largest collection in the world may be that of the Paris Museum of Natural History). Five species have been collected in the U.S. (Compare to Guatemala, the size of North Carolina, with 84 species!) The most common, *Odontotaenius disjunctus* (Illiger), is known from the East Coast to the riparian forests of the eastern Great Plains north to Manitoba and Ontario, and south to Texas and Florida. Another species, *O. floridanus* Schuster is known only from sand hills of Florida scrub habitat which used to be islands during previous interglacial times. Two other species, *Passalus punctiger* Lepeletier & Serville and *P. punctatostriatus* Percheron, were collected at the beginning of the twentieth century in eastern Arizona; they may have been brought from Mexico in wood shipped by train. They haven't been collected in the U.S. since that time. A fifth species, *Ptichopus angulatus* (Percheron), was recently collected in Arizona. This has been expected; it occurs in leaf-cutter ant nests just south of the Rio Grande in Texas.

Flightless beetles tend to originate on islands or (in passalids especially) on isolated mountains, resulting in high levels of endemism (an endemic organism is one found only in a given area, e.g., endemic to Guatemala, or endemic to Pike's Peak). The distribution of endemic passalids correlates with the distribution of other endemic organisms. Because passalids are relatively easy to find, they can be used as indicator organisms for areas of endemism, especially for cloud forests on tropical mountains. For example, eight areas of endemism have been identified for Guatemala and adjacent Chiapas, Mexico, on the basis of passalid distributions. This is important for prioritizing areas for conservation.

Only one fossil passalid is known, similar, if not identical, to a species known from the lowland neotropical forests, today reaching only to northern Mexico. This fossil, from Oregon, implies the presence of such forests there in the Oligocene, more than 25 million years ago.

The classification of the Passalidae is:

Order: Coleoptera
 Superfamily: Scarabaeioidea
  Family: Passalidae
   Subfamily: Passalinae
   Subfamily: Aulacocyclinae

The Aulacocyclinae are restricted to the area from India to Oceania and Australia. The Passalinae are mostly pan-tropical. This subfamily is divided into two tribes: Proculini, restricted to the Americas, and Passalini, which is mostly pan-tropical.

Most passalids live in rotting wood; a few live in other habitats, such as leaf-cutter ant detritus chambers, termite nests or under the roots of epiphytic bromeliads – all sites of decaying organic matter. Those in wood prefer broadleaf trees; oak is a favorite. Some occur in palms and a few in pines, but few in other conifers. They are most common and diverse in tropical lowland and montane wet forests; up to ten species may be found in a single log (in Brazil). Some, flatter species, are specialized for living under the bark; others bore deep into the logs. They appear to be quite important as wood decomposers in forest ecosystems.

An unusual number of species of other organisms are associated with passalids, especially mites and certain fungi, perhaps due to their boring in wood (other groups with high mite diversity include scolytid beetles, also wood borers). At least ten species of mites are associated with *O. disjunctus* in the eastern U.S. Various animals attack passalids, including vertebrates (birds and mammals, and probably some reptiles and amphibians), nematode worms, tachinid flies, and reduviid assassin bugs.

Passalids are in the superfamily Scarabaeioidea together with the more famous scarab beetles. They are large beetles (length 11 to more than 80 mm) and are orange or reddish when they hatch from the pupal case; most change to a shiny black color as they mature. Most have grooves (striae) in the elytra (wing covers). Many have a horn of some sort in the center of the head. In the Americas, most have three lamellae in the antenna, some four or five; some Old World species have more lamellae. Certain Old World passalids have an asymmetrical "face"; such asymmetry is rare among animals.

Beetles of some other families look remarkably like passalids; indeed, one tenebrionid from Africa has the epithet *passalioides*. Tenebrionids and lucanids which resemble passalids also live in rotting wood; however, certain carabids (e.g., *Scarites*) are superficially similar to passalids, but live underground. Some scarabs resemble passalids, but live in dung or underground as well.

Eggs are placed in a specially constructed nest of masticated wood pieces and feces (frass) and are red. As they mature they change to brown, then green when ready to hatch. The larvae are easy to recognize; they look like white grubs though not as curved and they have only four easily visible legs. Actually, they do have 6; the hind pair is reduced to a scraping organ that is rasped against the base of the second pair of legs. This produces a sound, the function of which is unknown.

The larvae (and adults) require frass for feeding; even adults will die if no feces are included in their diet. They apparently have an "external rumen," as do rabbits; they feed on the fungi and bacteria and the products of microorganism digestion that are in the feces.

The larvae pupate in a specially constructed cocoon of frass that the adults and larvae build together. The fact that young adult siblings of a larva will repair a damaged pupal case implies a high level of subsocial behavior for these beetles. Adults live at least two years in nature and to at least 5 years in the laboratory. Some species have large "colonies" with many individuals; others seem restricted to a pair and perhaps their offspring. Generally, only mature individuals migrate. Though adults may be found flying or walking at many times of the year, they appear to be most commonly migrating at the beginning of the rainy season in the tropics.

Adults stridulate as well, producing sounds by rubbing the dorsal surface of the abdomen against the hind wings. In species that don't fly, the wings are reduced to thin straps, but with the stridulatory area preserved. Passalids are known to produce up to 14 different acoustical signals in one species, more than many vertebrates. Pheromones, chemical communication, is also apparently used. Sounds are used when fighting other individuals, usually of the same species. Also, sounds are important in courtship, which involves a "dance" that can last as long as 12 h in the laboratory. At least in some species, copulation occurs in the tunnels of a log; however, *O. disjunctus* has been observed copulating during flight! At least in the laboratory, copulation begins venter to venter, a rare position for insects.

References

Reyes-Castillo P (1970) Coleoptera, Passalidae: morfologia y division en grandes grupos; generos americanos. Folia Entomologica Mexicana 20–22:1–240

Schuster J (1983) Acoustical signals of passalid beetles: complex repertoires. Fla Entomol 66:486–496

Schuster J (2002) Passalidae. In: Arnett R Jr, Thomas M (eds) American beetles vol 2. CRC Press, London, UK

Schuster J, Schuster L (1997) The evolution of social behavior in Passalidae (Coleoptera). In: Choe J, Crespi B (eds) The evolution of social behavior in insects and arachnids. Cambridge University Press, Cambridge, UK, pp 260–269

Schuster J, Cano E, Cardona C (2000) Un metodo sencillo para priorizar la conservacion de los bosques nubosos de Guatemala, usando Passalidae (Coleoptera) como organismos indicadores. Acta Zoologica Mexicana (n.s.) 80:197–209

Beta Taxonomy

The arrangement of species into higher categories of classification.

► Alpha Taxonomy
► Gamma Taxonomy

Bet-Hedging

Variable life history strategies within an insect population resulting from genetic or phenetic polymorphism. Bet-hedging is manifested by variation in diapause, wing development, rate of development, rate of reproduction and other critical life history traits. Bet-hedging equips a population to survive variable and unpredictable environments that may favor certain traits in one season and certain traits in others.

Bethylidae

A family of wasps (order Hymenoptera).

► Wasps, ants, bees, and sawflies

Bias

In sampling, an unidirectional deviation of an estimate from the true mean or variance of a population.

► Sampling Arthropods

Bibionidae

A family of flies (order Diptera). They commonly are known as March flies.

► Flies

Bicaudate

Having two cauda, or filamentous tail-like processes, at the posterior end of the body.

Biddies

A family of dragonflies in the order Odonata: Cordulegastridae.

► Dragonflies and Damselflies

Biennial

A plant that completes its life cycle in two years and usually does not flower until the second growing season.

Bifid

This refers to a structure that is forked, or divided into two parts or lobes. More commonly it is described as bifurcate.

Bifurcate

This refers to the division of a structure into two parts, as when it is forked; it is also called bifid. The point where the division occurs is called the bifurcation.

Big-Headed Flies

Members of the family Pipunculidae (order Diptera).

► Flies

Bilateral Symmetry

This refers to symmetry of the body in which one side is a mirror image of the other side. When divided along the main axis, insects are almost always bilaterally symmetrical, with the left and right halves being mirror images.

Binomial Nomenclature

A system of naming organisms with two names, the genus and species. This binomial is also known as the scientific name, and is in Latin. The first of the two names is the genus, and is capitalized. The second is the species, and is not capitalized. Both words are italicized. The author's name (the person who first provided a technical description of the species) often follows the scientific name. If the genus name has been changed since the organism was named by the author, then the author's name is placed in parentheses to indicate that a change has been made. When several species in the same species are discussed together, then "species" may be abbreviated spp. For example, in discussing the genus *Spodoptera*, we might refer the members as *Spodoptera* spp. On the other hand, a single species is indicated as "sp."

Binomial Sampling

A sampling method that involves recording only the presence or absence of members of the population being sampled (such as an insect pest) in a sample unit (such as a leaf), rather than counting the numbers of individuals. This is a type of presence-absence sampling. (contrast with enumeration sampling).

► Sampling Arthropods

Biphyllidae

A family of beetles (order Coleoptera). They commonly are known as false skin beetles.

► Beetles

Bioassay

The use of a living organism to determine the effect of any chemical (or biological agent), such as a semiochemical, upon the organism.

Biocenology (Biocoenology)

Study of the organization and functioning of communities, particularly a descriptive analysis of assemblages of interacting populations within a particular area. This term is most popular in Europe; elsewhere it is referred to as synecology or community ecology. In some respects, it is the "opposite" of autecology.

► Biocenosis

Biocenosis (Biocoenosis)

An association of interacting, living creatures in an area. The environment or habitat is usually uniform, and the community self-sufficient. This term is most popular in Europe; elsewhere it is referred to as an "ecological community."

► Biocenology

Biocides

Chemicals that kill a wide range of living organisms.

► Insecticides
► Acaricides

Bioclimatic Models in Entomology

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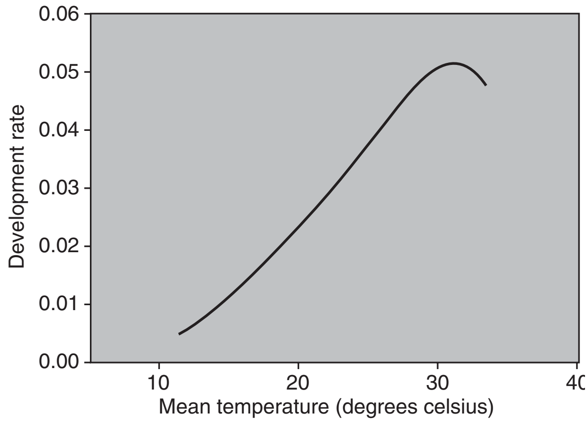
Because climate has such a profound effect on the distribution and abundance of invertebrates, quantification of climatic influences on insects has been of considerable interest to entomologists for well over a century. While simple predictive models were developed early on, easier access to computers in the 1970s resulted in the development of computer based models to predict the biotic potential of insects in relation to climate. Simple bioclimatic models are often used to predict population events so that control methods can be more precisely applied, reducing costs to the grower as well as insecticide use. Decreased insecticide use helps preserve natural enemies, reduces insecticide residues in crops, and delays the development of insecticide resistance. Other benefits are the conservation of petroleum products, increased safety to farm workers, local residents and the environment. Additionally, models of insect biotic potential and life cycle timing can increase the precision of sampling and monitoring programs, and application of biological control procedures. More complex bioclimatic assessment models have been designed to predict the potential establishment and distribution of insect species, often to assess the risk of invasion into areas where they are not normally found.

Temperature Models

Of all the climate variables that directly affect insects, temperature has the greatest influence. The influence of temperature on insect development rate, growth and fecundity has been quantified for many species. The relationship often observed in laboratory conditions between insect development rate and temperature (see development rate figure, Fig. 35) is well used by applied entomologists to predict timing and phenology of insect life cycle events. The relationship is usually nonlinear throughout the range of temperatures in which a species can survive; however, a number of mathematical functions, both linear and non-linear, have been used to describe it. Such functions comprise simple models for prediction of timing or phenology of life cycles, or can form the basis of more complex bioclimatic models.

There are three basic approaches to modeling insect development in relation to temperature. The oldest and most widely used model is a simple linear description of insect development in relation to temperature (see development rate figure). The linear model forms the basis to the well known thermal summation or degree day (DD) approach to timing prediction. Degree days



Bioclimatic Models in Entomology, Figure 35
Generalized nonlinear (solid line) and linear development rate curves.

are also called thermal units, heat units, or growing degree days. Degree days are simply the number of degrees above a threshold temperature required for growth. If temperatures are held constant in the laboratory, for example at 20°C, and if the lower threshold, T_0, for growth or development of the insect life stage of interest, is 5°C, then degree days per day or the amount of influential heat to which the insect is exposed is 20–5°C = 15 DD. Degree days per day are accumulated over the time it takes the particular life stage to complete development. For example, if that life stage takes 10 days to complete development, that time is converted to physiological time by 15 DD ×10 days = 150 DD required for development. To predict events in the field, some meaningful point or biofix from which to start degree day accumulation and some method to calculate degree days from the daily diurnal temperature curve are required. There is a large amount of literature on application of this method in applied entomology and plant growth studies.

Of special interest is how the relationship between insect development and temperature is used in forensic entomology. As gruesome as it might be, species of blowflies are often the first to find a dead body, on, or near which, they lay their eggs. By judging the age of the life stages of the fly larvae or pupae, and by applying the particular relationship between temperature and development for the fly species, the forensic entomologist can often determine the time of death of the unfortunate person. Of course, when investigating a suspicious death, things are not usually that easy and many factors that influence the temperature experienced by the flies need to be taken into account. For example, whether the body is found inside a building, a vehicle, shallow grave or other enclosed space, or whether it is found outdoors exposed to the elements is of importance. Even the heat generated by the maggots could influence the rate of development of the flies.

Notice that the linear model is confined to the more linear portion of the development rate curve (see development rate figure). Intrinsic to the use of the linear model is the assumption that development is proportional to temperature. This means that the reciprocal of the slope (1/slope) of a regression line fitted to the developmental data obtained at constant temperatures gives the DD required for development. The linear regression equation can also be used to calculate the lower threshold (T_0) for development which is defined as – a/b, where a, is the intercept and b is the slope of the regression line. The thermal optimum (if required) is often estimated by visual inspection of the development rate curve.

The linear or degree day model is easy to develop and use. While the linear model is clearly wrong in the sense that the lower and upper curvilinear portions of the development rate curve are ignored, this may not matter when field temperatures lie within the developmental extremes, but inaccurate predictions will result when temperatures stray too often beyond these points.

The second approach to predicting insect phenology in relation to temperature encompasses the many non-linear mathematical descriptions or functions used to describe nonlinear development of insects. These functions can range from a simple sine-curve fitted to the nonlinear data to more complex biophysical models or equations. Non-linear models require rate summation for timing prediction. Rate summation can be described as:

$$D = \Sigma r(T(t))dt$$

where development D is a function of temperature T which in turn is a function of time t, r is the development rate and dt is the time increment. For good precision the time increment should be hourly. While these models provide a more accurate description of the developmental relationship they are more difficult to develop and complicated to apply in practice.

Distributional Models

The third approach to life stage development in relation to temperature is represented by distribution models of insect phenology that include temperature dependant development as well as variation in development rates within the population at any particular temperature. Such models require considerable research investment but can give important information about the uncertainty of prediction and good estimates of limits to development in regions where the species is not normally found. In general, however, complexity does not ensure more accuracy, and a comparative approach is often required. Additionally, there are also differences in the performance of phenological models under variable temperature conditions that need to be taken into account.

The biological realism or practicality of each approach to phenological prediction has been widely debated. Unfortunately, that debate is not helped by the fact that the appropriateness of a model is often judged on how well it fits the observed data rather than on rigorous validation using independent data. Rigorous validation requires that a model is validated against an adequate sample of the real world. One or two sites or seasons are clearly not enough.

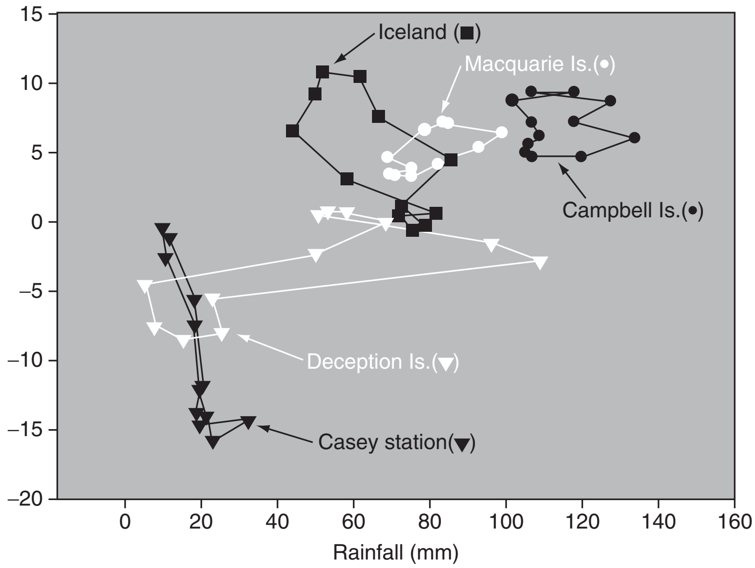
Currently, no model provides an accurate description of development in all circumstances, especially under fluctuating conditions. Clearly, we are limited by the accuracy of the temperature data that is available and that may dictate the level of accuracy that is achievable. In many cases when great accuracy is not necessary (or achievable) the simple degree day approach may be all that is required.

Obviously, other climate variables have potential to influence insect population processes, and therefore the distribution and abundance of insect species in any locality. Models that incorporate other climate variables to predict insect distribution and abundance range from simple graphical approaches called climatographs or climographs to more complex models that are process orientated. The graphs use a combination of climatic factors to predict areas that are suitable for establishment of a particular species and allow quick comparisons between sites. The simplest climatograph is a plot of the profiles of mean monthly temperatures and rainfall totals for a locality. A much more useful climate diagram or climatograph, however, can be a plot of mean monthly temperatures against mean monthly rainfall totals or humidity such that the points for the 12 months of the year are joined to create a polygon. At a glance one can see different shaped climate diagrams may or may not overlap indicating times of the year where different regions may or may not have similar climatic conditions (see climatograph figure, Fig. 36).

Multivariate Models

Other bioclimatic approaches include the use of multivariate statistical models to predict insect distribution and abundance in relation to climatic variables. Multivariate approaches such as principal components analysis (PCA) and discriminant analysis can overcome the limited dimensions that constrain graphical models. Alternatively, multivariate methods can help reduce large amounts of environmental data to a few important variables, and are often used to pre-process data to reduce the number of input variables to improve subsequent analysis by other statistical methods or models.

Because the relationship between insects and their environment can be complex there have



Bioclimatic Models in Entomology, Figure 36 Climatographs for sites in the Antarctic region compared with Iceland. Graphs were compiled to determine how likely insect species that have invaded and established in some areas of the Arctic could survive the climatic conditions in representative sites of the Antarctic and sub-Antarctic regions.

been many other attempts to characterize their response to a range of abiotic and biotic factors. Such models are called bioclimatic "envelope" models and are a type of species distribution model wherein the current geographical distribution of the species is related to local climatic variables to enable prediction of survival or establishment in new areas or climates. The most well known and well used model that combines insect species' response to a number of climate variables into meaningful, manageable indices, is called CLIMEX. CLIMEX is a computer based system that provides two levels of analysis. First is a simple match function that can be used to find climates elsewhere in the world that are analogous to, or match, within a specified level of similarity, the area of interest. Given further information on insect biological parameters, CLIMEX can give estimates in the form of simple indices of the favorability of particular geographic region for insect population growth and development. CLIMEX includes detailed long term weather data, comprising maximum and minimum temperatures, evaporation or relative humidity and rainfall for several thousand sites throughout the world.

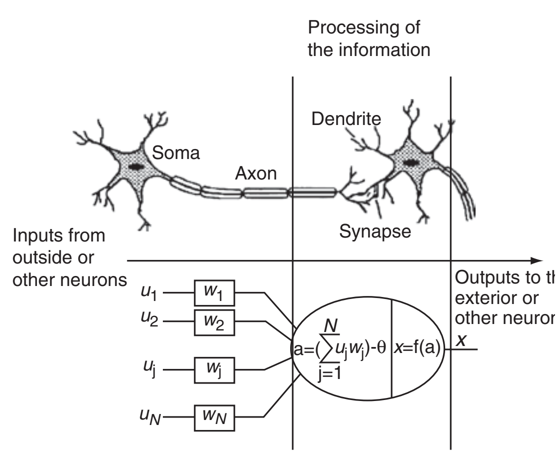
At the second level of complexity the CLIMEX program is designed to predict the potential distribution of the species by calibrating its biological responses to the climate of its current distribution. The species responses are modeled by a series of stress indices that include cold, hot, dry and wet parameters that define particular environmental limits to the sustained growth and development of the population. These indices are then combined in an "Ecoclimatic index" that describes the overall favorability of geographic locations for that particular organism. There are many examples of bioclimatic assessments of insect species using CLIMEX particularly for quarantine or risk assessment purposes. Despite being relatively easy to use, CLIMEX, like many models, should not be used as a black box, it requires a level of expertise or training to optimize its use and to ensure correct interpretation of results.

There are now many examples of bioclimatic models that have been applied to a range of taxa. Some of the most well known are STASH, BIOCLIM, CLIMATE, HABITAT, GARP and DOMAIN. In fact, the number of computer-based models, statistical approaches and machine learning techniques applied to bioclimatic prediction continue to increase, apparently driven by research interest in the distributional changes of species in response to climate change.

Computational Intelligence

More recently, applied computational intelligence models such as artificial neural networks (ANN) and other machine learning techniques have been successful for bioclimatic assessment of insects as well as other species. Such models have the advantage that they can model complex nonlinear data and they are not constrained by the distributional characteristics of data as more conventional parametric statistical models may be. In some comparative studies, ANN have been shown to be better than other methods for modeling species distribution in response to climate. The most common ANN used for prediction is the multi-layer perceptron or MLP.

ANN were first designed to mimic the vertebrate brain and consist of a network of processing elements called neurons in usually three layers; the input layer, the hidden layer and the output layer. All neurons of each layer are connected to all the neurons of the adjacent layer. As in the animal nervous system, each processing element in the network receives input from many others in the network. Each of the inputs or independent variables (U) is multiplied by its associated weight or coefficient and this dictates the strength or size of each input. The modified inputs are summed and the result is further modified by what is called a transfer function, which is usually a sigmoid function, but can be Gaussian or even a simple linear function. The result is either fed forward to other neurons in the network or becomes the network's output. The complex network algorithm adjusts the weights of the network connections over many hundreds or thousands of iterations to minimize, by least squares, the difference between the observed values and its own output values. The unique algorithm and structure means an ANN can learn to fit extremely complex functions and therefore is very useful for predicting species presence or absence based on a number of climate variables. Another advantage of machine learning approaches is that correct procedure involves training (fitting) but also testing and validation of the models. This procedure assesses how well the model can generalize to new data and as a result, over-fitting, the scourge of more conventional approaches, is avoided.Of all the modeling and statistical methods described above, none can answer all the questions concerning insect species biotic processes in relation to climate. The seemingly broad range of approaches can complicate the choice of model. Interestingly, when different models are compared over many re-organizations of the data used to create them (Fig. 37), some models can perform better than others on a particular data set, but can perform worse than the others when using a different data set. That means it is important to compare the efficacy of new methods with more standard approaches. While the bioclimatic models described here cannot replace more detailed modeling of individual species



Bioclimatic Models in Entomology, Figure 37
Comparison of a biological and artificial neuron.

responses to climate, they can provide important information to guide and inform decisions when more detailed data are lacking. Additionally, many approaches, if correctly applied, have potential for knowledge discovery that will increase our scientific understanding of how a range of abiotic variables can influence the distribution and abundance of insects.

References

Worner SP (1998) Some problems and approaches to modelling insect phenology. In: Baumgärtner J, Brandmayr P, Manly BFJ (eds) Important aspects in population ecology. Proc 20th Int Congr Entomol, Florence, Italy, August 25–31, 1997, A. A. Balkema, The Netherlands, pp 89–98

Heikkinen RK, Luoto M, Araújo MB, Virkkala R, Thuiller W, Sykes MT (2006) Methods and uncertainties in bioclimatic envelope modelling under climate change. Prog Phys Geog 30:1–27

Biocontrol

An abbreviation for "biological control."

Biogeographic Realms

Dissimilar distributions of animals (and therefore best called zoogeographic realms). The animals are usually isolated geographically and defined by continents, but sometimes separated by mountain ranges or other physiographic features.

► Zoogeographic Realms

Biogeography

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Biogeography is the study of spatial patterns of biological diversity. Biogeography is often organized into two sub-disciplines, historical biogeography and ecological biogeography, although there is overlap between the two. Historical biogeography is "big picture" biogeography. It is concerned with explaining patterns in the distributions of organisms (usually at higher taxonomic levels) using the geological history of the Earth. Historical biogeography often involves large, even global, areas, and frequently deals with extinct taxa. Ecological biogeography, on the other hand, examines interactions among organisms and their environment to explain spatial distribution patterns, usually at species and sub-specific levels. The spatial and temporal scales are generally smaller in scope than is the case with historical biogeography. As the above definitions suggest, biogeography is a highly interdisciplinary science, drawing on evolutionary biology and systematics, ecology, and the earth sciences. Biogeography is a young discipline, first beginning to coalesce into a distinct science in the mid-1900s. The first scientific periodical devoted to the discipline, the Journal of Biogeography, first appeared in 1973. The number of books and journal articles devoted to some aspect of biogeography has increased dramatically in the last few decades. But while it only recently emerged as a distinct science, biogeography as a field of endeavor has been practiced for centuries, and many of the greatest scientists of their time were biogeographers, though they may not have referred to themselves as such.

Questions about the diversity of life and its distribution across the world have been asked since the time of the ancient Greek philosophers, and probably before. But the flowering of eighteenth century exploration greatly expanded knowledge of biological diversity and led to a corresponding increase in attempts to explain the patterns seen in this diversity. At that time, explanations were hindered by the prevailing literal acceptance of the Bible, and Carolus Linnaeus (1707–1778) himself wrestled with the contradictions between present-day patterns of global biodiversity and biblical literalism.

For instance, Linnaeus hypothesized a "paradisiacal mountain" to explain the spread of species from Noah's point of landing. This mountain would have all the different environments of the Earth at different latitudes, which were colonized by the different animals as they left the Ark. These animals would then be well-suited to colonize their respective habitats as they migrated throughout the world. While these ideas may seem naive in hindsight, Linnaeus' logic was astute, and his efforts in recording the type of environment in which each species was found can be considered a precursor of the subdiscipline of ecological biogeography.

The French naturalist Georges Buffon (1707–1788) was among the earliest to seriously consider that the earth's climate, species, and even the position of the continents were not fixed, but mutable. He observed that environmentally similar but separated regions have distinct faunas, an insight that became known as Buffon's Law. Attempts to explain Buffon's Law would occupy the attention of naturalists for decades, and would require an acceptance of the dynamic nature of the Earth and its species. The German botanists Johann Reinhold Forster (1729–1798), Karl Willdenow (1765–1812), and Alexander von Humboldt (1769–1859) collected innumerable plant specimens from around the globe, and found that Buffon's Law applied to plants as well as animals. Von Humboldt is generally recognized as the "father of phytogeography." The Swiss botanist Augustin de Candolle (1778–1841) recognized distinct phytogeographic regions, and was the first to coin the word "endemic."

New discoveries in geology and paleontology would provide a framework for further advances in biogeography. The eminent geologist Charles Lyell (1797–1875) and others used the fossil record as evidence of the mutability of the Earth's climate and sea levels, and asserted the antiquity of the Earth. The biblically based time frame of a few-thousand-years-old Earth was difficult to reconcile with observed biogeographic patterns. The revolutionary theory of evolution by natural selection developed by Charles Darwin (1809–1882) and Alfred Russel Wallace (1823–1913) was critical in providing an explanation for the adaptation and diversification of organisms across time and space. Wallace would devote his life to the study of biogeography, and would become known as the "father of zoogeography." He wrote three seminal books, and developed detailed maps of the Earth's biogeographic regions. He was also the first to note the sharp division between Southeast Asian and Australasian faunas in the East Indies, a division that is now known as Wallace's line. Many of the principles proposed by Wallace are still active areas of current research among today's biogeographers. It is difficult to overestimate the contributions of Alfred Russel Wallace to the science of biogeography. British zoologist Philip Lutley Sclater (1829–1913) was also an important figure in early efforts to define the Earth's biogeographic realms. Earlier attempts to define biogeographic regions were based to a great extent on artificial boundaries, and Sclater felt that these maps were too arbitrary. His goal was to develop a system reflecting "the most natural primary ontological divisions of the Earth's surface," based on biotic similarity and dissimilarity. Being an ornithologist, he based his system on passerine birds. His system of biogeographic regions, with some revisions, is still in use today (Fig. 38).

Despite the efforts of these and other early biogeographers, explanations of the disjunct distributions of many plant and animal groups, particularly in the southern hemisphere, remained elusive. This was due in large part to the fact that biogeographers were preoccupied with mechanisms by which the organisms themselves might have dispersed across the continents. But the idea that continents might move, or drift, relative to one another over geological time was even more difficult for the scientific community to accept. This was despite the fact that much geological, paleontological, and biogeographical evidence supported a dynamic Earth with moving continents. For instance, the disjunct southern distributions of groups such as the temperate ground beetle tribe Migadopini were difficult to explain using dispersal models or short-lived land bridges, but fit well with a Gondwanaland scenario. Based on evidence from a variety of fields, the German meteorologist Alfred Wegener (1880–1930) developed the theory of continental drift in the early 1900s. However, his ideas were largely rejected by scientists initially. There were a variety of reasons for this, the most important being the lack of a known mechanism by which continents could move. But the overwhelming evidence for seafloor spreading and plate tectonics amassed by the 1960s vindicated Wegener by providing just such a mechanism.

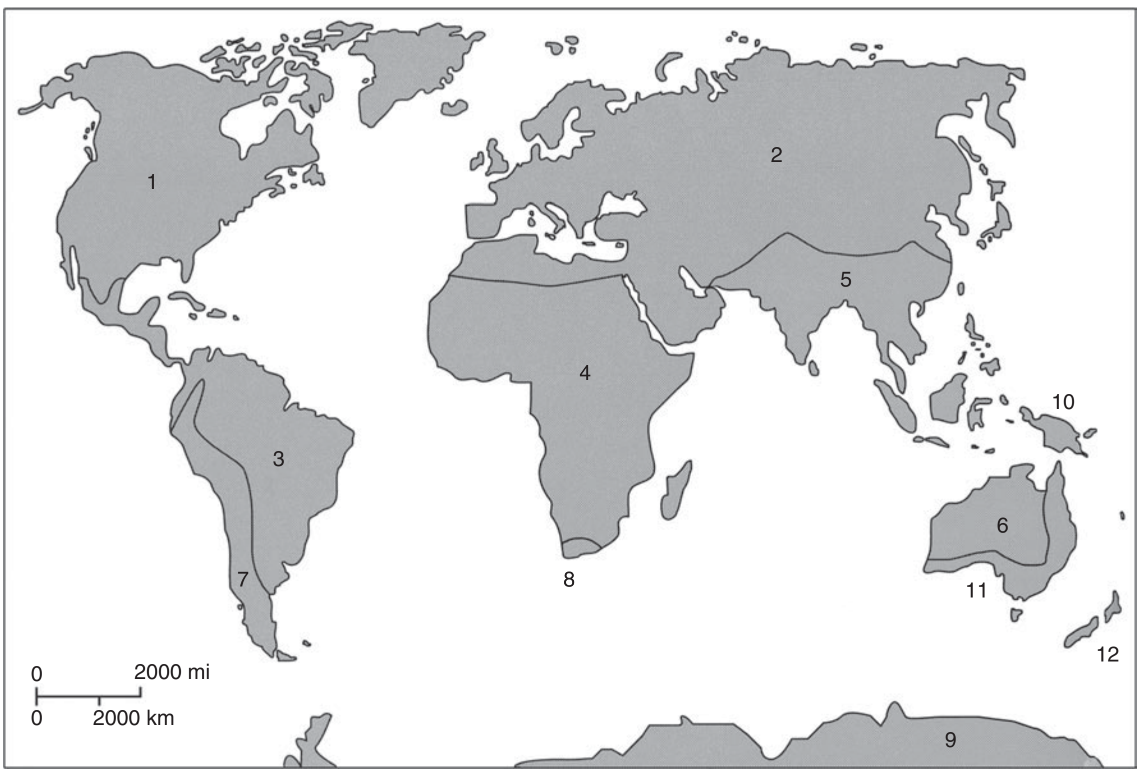
During the last half-century, the study of historical biogeography has been bolstered by increased methodological rigor in biogeographical analysis. Botanist Leon Croizat (1894–1982) developed the method of "panbiogeography" largely in response to what he believed was an over-reliance on difficult-to-test dispersal models of geographic distributions. Croizat connected the known distributions of taxa with lines, or "tracks" and then combined corresponding tracks into "generalized tracks." Croizat asserted that it would be unlikely that several taxa, with different dispersal capabilities and ecological requirements, would exhibit the same dispersal patterns. He reasoned that these distributions were established before being interrupted by geographic barriers such as oceans. These explanations required hypothetical land bridges and drifting of islands, which most biogeographers considered unrealistic. Furthermore, Croizat never really accepted Wegener's theory of plate tectonics, even though it would have provided reasonable explanations for many of the patterns Croizat observed. Although Croizat's panbiogeography never gained a wide following among biogeographers, he was a pioneer in emphasizing the importance of geographic isolation, or "vicariance," in speciation. General acceptance of the theory of plate tectonics by the biogeographical community gave a further boost to the importance of vicariant events in explaining geographic distributions, at the expense of dispersalist models, which were considered less testable than the vicariance models.

Famed evolutionary biologist Ernst Mayr's (1904–2005) studies of geographic distributions and speciation were instrumental in fostering a synthesis between evolutionary biology and biogeography, as was the work of German entomologist Willi Hennig (1913–1976). Hennig developed the methods of phylogenetic systematics, or cladistics, which provided a rigorous framework for testing hypotheses of evolutionary relatedness. Cladistics adheres strictly to classifications reflecting natural phylogeny, based on the sequence of branching as reflected by shared derived character states. This approach fits well with vicariance-based biogeographical methods. Development of molecular-based approaches and their application to biogeographical problems has also led to significant advances. The 1980s saw the development of the field of phylogeography, which has revolutionized biogeographical analysis. This approach seeks to explain recently occurring evolutionary relationships and geographical patterns at the level of species and species complexes, using molecular approaches to produce "gene trees" that reflect the spread of lineages.

Probably the most influential work in ecological biogeography in the last half-century was Robert H. MacArthur (1930–1972) and Edward O. Wilson's theory of island biogeography, unveiled in the 1960s. Interestingly (and sadly), an earlier form of this seminal theory was independently developed by lepidopterist Eugene G. Munroe in the 1940s but, for a variety of reasons, Munroe's work in this area has remained virtually unnoticed. The theory of island biogeography questioned the long-held view that species diversity and distributions on islands necessarily changed slowly, over evolutionary time. MacArthur and Wilson asserted that the number of species found on islands was a result of more proximal factors – rates of immigration and extinction, which in turn are affected by island size and distance from the mainland. These ideas provided a much needed theoretical framework for the study of biota not only on oceanic islands, but on isolated terrestrial habitat islands as well. The theory of island biogeography has also had a profound effect on the field of conservation biology. David Quammen's excellent book, Song of the Dodo: Island Biogeography in an Age of Extinctions, provides insight into the development of the theory and its implications for conservation biology, as well as criticisms of the theory. For some fascinating ideas in the area of human biogeography and the geographical patterns of wealth and power, see Jared Diamond's Guns, Germs, and Steel: The Fates of Human Societies and Collapse: How Societies Choose to Fail or Succeed.

Insect Biogeography

Many important contributions to our biogeographical knowledge base have been made by entomologists. Many of these contributions revolve around applications in pest insect control, such as studies of the migration patterns of the African migratory locust and range expansions of the gypsy moth, Africanized "killer" bees, and fire ants in the United States. In addition, many dramatic range contractions and extinctions, involving a variety of plant and animal groups, have been caused by introduced insect vectors of plant and animal diseases, or introductions of the causative agents themselves. The introduction of

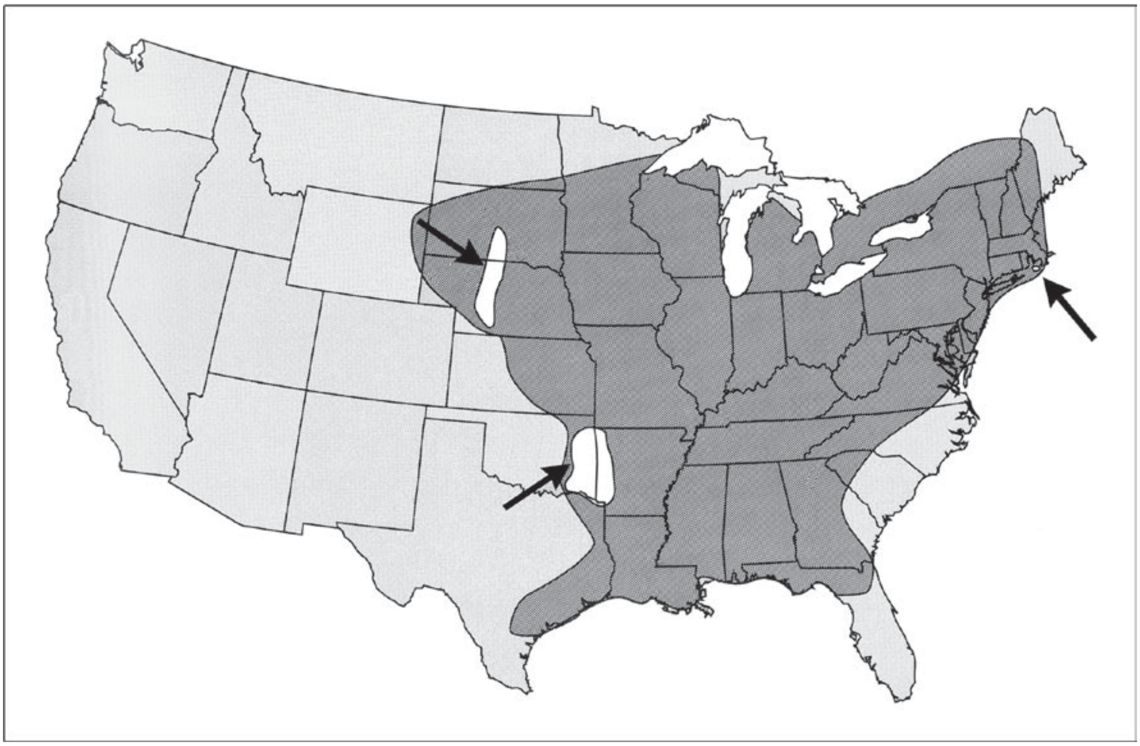


Biogeography, Figure 38 **Global biogeographic kingdoms and regions based on modern biogeographic analyses. This is more detailed than the original Sclater-Wallace portrayals and is not yet widely used. Numerical designations: 1–2, Holarctic kingdom (= Laurasia); 1, Nearctic region; 2, Palearctic region; 3–6, Holotropical kingdom (= eastern Gondwana); 3, Neotropical region; 4, Afrotropical region; 5, Oriental region; 6, Australotropical region; 7–12, Austral kingdom (= western Gondwana); 7, Andean region; 8, Cape or Afrotemperate region; 9, Antarctic region; 10, Neoguinean region; 11, Australotemperate region; 12, Neozelandic region (after Morrone 2002, J Biogegr 29:149–152).**

mosquito-borne avian malaria in Hawaii has devastated many species of lower-elevation birds there. The American elm, once a prominent part of North American landscapes, has been virtually extirpated by Dutch elm disease. The introduced smaller European elm bark beetle is a primary vector of the Dutch elm fungus.

Other studies have a strong insect conservation slant, such as analyses of the range collapse of the American burying beetle. This insect was distributed over most of the eastern United States until the mid-1900s, but is now restricted to a few widely separated locations in Nebraska and South Dakota, Oklahoma and Arkansas, and the northeast (Fig. 39). Evidence for impacts of global climate change on biotic distributions has been provided through analyses of insect distributions, such as that of Edith's checkerspot butterfly, a species that ranges along the coast of western North America from Canada to Mexico. Declines of this species do not appear to correlate with obvious human impacts such as habitat alteration. However, surveys of this species have shown that local extinctions have taken place primarily at low-altitude and low-latitude locations, as would be expected if increased temperatures were an important cause.

As mentioned earlier, some of the most important theoretical advances in biogeography have involved entomologists and the study of insects. Willi Hennig, the founder of phylogenetic systematics or cladistics, was a dipterist who produced many important works in the area of fly systematics. Hennig was drafted into the German army during World War II, and did some of his systematics work while held as a prisoner of war. Another entomologist, Lars Brundin (1907–1993), studied southern hemisphere chironomid midges. He was a pioneer in the use of cladistics in biogeographical analysis. Brundin produced a cladogram reflecting the evolutionary relationships of his chironomid



Biogeography, Figure 39 **Range decline of the American burying beetle, *Nicrophorus americanus* (Coleoptera: Silphidae). The original range is indicated by dark shading, the existing range by the small unshaded areas designated by arrows.**

species. He then inserted the name of the continent on which each species is found. This resulted in a "taxon-area cladogram." The sequence of divergence of the chironomid species corresponded well with the sequence of the separation of Gondwana into the southern continents (Africa was the first continent to break away, and the African species were the first to diverge, etc.). Thus, systematic and biogeographical evidence reinforced each other. Among other things, this work showed that geological information could be used to suggest which of several plausible cladograms is likely correct.

Ecological biogeography has also benefited greatly from entomological research. Ecologist Robert MacArthur and entomologist Edward O. Wilson developed the groundbreaking theory of island biogeography. The major tenets of the theory, in highly simplified form, are: (i) an island will contain an equilibrium number of species, (ii) this equilibrium number is a function of the balance of two processes, immigration and extinction, and (iii) immigration and extinction rates are in turn a function of the size of the island, and the distance of the island from the mainland. MacArthur and Wilson reasoned that small islands will have higher extinction rates than large islands, because populations of species on smaller islands will be smaller and thus more likely to become extinct. Likewise, islands far from the mainland will have lower immigration rates than islands near the mainland. Therefore, small, far islands will have low equilibrium numbers of species, and large, near islands will have larger equilibrium numbers of species.

Wilson, with his student Daniel Simberloff, also provided an early rigorous test of the theory through experimental defaunation studies on small mangrove islands in the Florida Keys. In this study, methyl bromide was used to kill all insects and other terrestrial arthropods on the islands. Follow-up surveys were then done to monitor recolonization of the islands. Several aspects of the theory were supported. After defaunation, the islands did eventually return to roughly their original numbers of arthropod species. In addition, the most isolated island had the fewest species, and the lowest recolonization rate. However, other studies have not supported the theory, and the theory has been criticized for a variety of reasons, such as lack of consideration for the biology of the organisms and their ecological and evolutionary interactions. For instance, it has been suggested that very small organisms, such as many insects, would be unlikely to reach saturation population levels on any but the smallest of islands. So, for most islands within the size range that humans consider important, the theory may only apply to organisms of larger size, such as vertebrates.

As is the case in other sciences, biogeographers are constantly searching for patterns in nature. Many have been discovered, and, often, insects play important roles in providing data in support of, or as exceptions to, these patterns. It has been observed in many groups of plants and animals that species diversity increases as one progresses from the higher latitudes to the tropical regions. Several theoretical explanations for this pattern have been proposed. Many insect groups fit this pattern. However, some do not. These exceptions include two huge families of parasitic wasps, the Ichneumonidae and Braconidae, as well as the sawflies and aphids. There are many possible reasons for these exceptions. It has been suggested that aphids are more diverse in temperate regions because many aphid species are specialist feeders that have difficulty locating suitable host plants from long distances. Therefore, they should fare better in regions where plant species are clumped, such as the agricultural lands of temperate regions, than in tropical regions where plant assemblages consist of many species that are each present at low densities. As is often the case, it is the exceptions to the rule that provide the most interesting research questions.

Another interesting biogeographical pattern has been termed "geographic parthenogenesis." Parthenogenesis is the production of offspring from unfertilized eggs, usually with the asexually produced offspring being female. "Geographic parthenogenesis" refers to a pattern in which parthenogenetic organisms occupy different geographic ranges than their closely related, sexually reproducing relatives. The parthenogens are often associated with what could be considered "marginal" habitats. These include more northerly latitudes, higher altitudes, disturbed habitats, islands or island-like patches of habitat, or dry environments. Such patterns have been observed in many insect groups. One interesting example is *Pelecinus polyturator*, a parasitic wasp with a huge latitudinal geographic range that extends from eastern and central North America, through the southwestern U.S. and Central America, down through South America to Argentina. *Pelecinus polyturator* exhibits patterns consistent with geographic parthenogenesis. In the northern part of its range males are extremely rare, but in tropical regions males are abundant and sexual reproduction is apparently common. Insect species in other groups, including mayflies, aphids, and stick insects, have also been found to exhibit geographic parthenogenesis.

For centuries now, biogeographers have provided fascinating insights into the patterns and processes of the natural world. As human-caused changes continue to affect global biodiversity, it will be critical that we increase our knowledge of the factors determining the geographic distributions of organisms. The science of biogeography will continue to be at the forefront of these efforts.

► Zoogeographic Realms
► Pelecinid Wasps

References

Avise JC (2000) Phylogeography: The history and formation of species. Harvard University Press, Cambridge, MA, 447 pp

Cox CB, Moore PD (2005) Biogeography: an ecological and evolutionary approach, 7th edn. Blackwell, Malden, MA, 428 pp

Diamond JM (2005) Collapse: how societies choose to fail or succeed. Viking, New York, 575 pp

Diamond JM (1997) Guns, germs, and steel: the fates of human societies. W. W. Norton, New York, 512 pp

Lomolino MV, Heaney LR (2004) Frontiers of biogeography: new directions in the geography of nature. Sinauer Associates, Sunderland, MA, 436 pp

Lomolino MV, Riddle BR, Brown JH (2006) Biogeography, 3rd edn. Sinauer Associates, Sunderland, MA, 845 pp

Lomolino MV, Sax DF, Brown JH (eds) (2004) Foundations of biogeography: classic papers with commentaries. University of Chicago Press, Chicago, IL, 1291 pp

Quammen D (1996) The song of the dodo: island biogeography in an age of extinctions. Scribner, New York, 702 pp

Bioinformatics

Researchers in bioinformatics develop computer software applications that can store, compare and analyze the very large quantities of DNA sequence data generated by the new genome technologies. New bioinformatics tools can sift through a mass of raw data, finding and extracting relevant information and their relationships.

► Genomics
► Functional Genomics
► Structural Genomics

Biointensive Pest Management

Biologically based pest management. Pest management that depends on an understanding of pest biology to prevent pests from causing damage, or uses biological agents to suppress pests.

► Integrated Pest Management

Biological Amplification

The accumulation and increase in concentration of chemicals, usually insecticides or their metabolites, in organisms at higher trophic levels.

► Biomagnification

Biological Clock

The biological/physiological timing device inside an organism that allows it to establish regular biological rhythms. It is self-sustained, but synchronized by natural biological patterns such as light and dark cycles.

► Biological Clock of the German Cockroach

Biological Clock of the German Cockroach, *Blattella Germanica (L.)*

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Have you had a terrifying experience of seeing an oily flat creature running for cover when you open a cupboard to look for a midnight snack? Even worse, while you are watching TV a cockroach runs swiftly under your feet to reach the other end of sofa! This tiny crawler is no stranger to us. It is our unwanted and unavoidable housemate, the German cockroach.

The German cockroach, *Blattella germanica* (L.) is a cosmopolitan species and well-adapted to human shelters such as houses, buildings, and factories, and sometimes it is even found on public transportation. They feed on almost any organic matter. Although no life threatening disease is transmitted by them, the existence of the German cockroach poses a health threat to humans (allergy, diarrhea) and represents deteriorating hygiene.

Since we live with the German cockroach under the same roof, our daily life coincides with its activities. We rarely see them during daytime, but we encounter them frequently at night. Do they avoid their only natural enemy, humans, during the day, or is their activity schedule controlled by a biological clock? The scientific evidence shows that timing of its activity is scheduled according to its endogenous biological clock.

What Is a Biological Clock?

A biological clock is a timing device inside an organism to give time signals so that an organism can perform proper behaviors at the right time. This self-sustained, endogenous clock is easily entrained (synchronized) by environmental signals such as light-dark cycles, temperature cycles, and other environmental changes, and allows an organism to adapt to its environment properly in time. Such an environmental time signal has been called a "Zeitgeber" (from the German for "time-giver").

There are several lengths of rhythmic period on earth, such as half-day tidal cycles, day-night cycles, semilunar and lunar cycles, annual cycles, and seasonal cycles that are caused by the movements of sun, earth and moon. Since these predictable environmental changes are consistent events, organisms depend on their endogenous clocks to synchronize with the rhythmic changes of environment. Among various lengthened environmental cycles, the daily cycle is the most prominent and universal environmental condition to influence the survival of organisms. From primitive prokaryotic single-cell cyanobateria to highly evolved eukaryotic mammals, virtually all organisms possess an endogenous circadian clock (the term "circadian" is derived from the Latin for "about a day"). Therefore, many scientists focus their research interests on circadian clocks.

Characters of Circadian Clocks

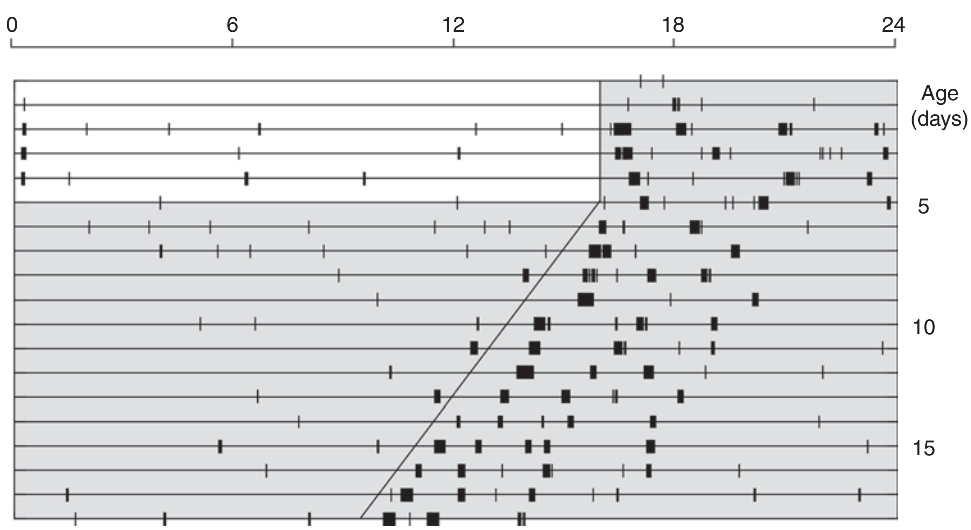
The most important characteristics of a circadian clock are: (i) a self-sustained oscillator with a period close to 24 h, (ii) a free-running rhythm under constant environmental conditions (such as constant temperature and continuous light or dark condition), and (iii) temperature-compensation. The first two characters are the essential ones that should be used as the definition of the circadian clock. When we remove all the environmental time signals from an organism, it should follow its own endogenous circadian clock and express an approximate, but not exact 24 h rhythm. Only when this free-running rhythm is expressed under an artificial, constant condition, can we definitely infer a circadian clock in this organism. The third character is the key feature to allow the clock to run as accurately as possible in different seasons or temperature conditions. Since the speed of all biochemical processes within an organism depends on the temperature, the property of temperature compensation can keep the molecular biological clock running in a constant pace regardless of environmental temperature fluctuation. This character is especially essential in ectothermal animals, those which depend on external conditions to maintain their body temperature (Fig. 40).

Molecular Clock Mechanisms

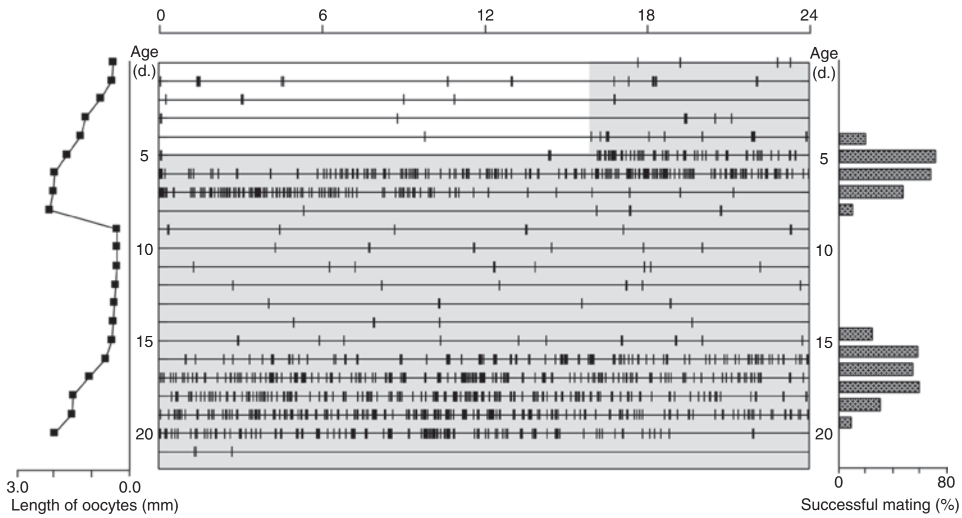
The biological clock operates in a negative feed back loop composed of various molecules. Although no universal scheme of molecular clock exists in all organisms, the molecular clock mechanisms in the fruitfly *Drosophila melanogaster* underlie the clockwork of the German cockroach. The simplified molecular clock scheme includes two clock genes, *period* and *timeless*, which are activated and transcribed-translated to PERIOD and TIMELESS proteins in the cytoplasm of cells. The phosphorylation of PERIOD enables it to bind with TIMELESS to form a heterodimer, which in turn translocates into the nucleus to inhibit further transcription of *period* and *timeless* genes. When the diminishing concentration of PER-TIM heterodimer reaches a certain low level, the *period* and *timeless* genes will be reactivated and cause another cycle. This process takes about 24 h lag time. Light can degrade the TIMELESS protein. If there is reduced TIMELESS available to bind PERIOD, then there is more delay of inhibition on the two clock genes, which prolongs the cycle and changes the clock phase. This molecular mechanism explains the synchronization of circadian clock phases with the light-dark cycles of the environment(Fig. 41).

Ecological Significance

The ecological function of biological clocks is the main reason these clocks occur in various



Biological Clock of the German Cockroach, *Blattella Germanica (L.)*, Figure 40 The locomotor activities of a male adult German cockroach at 28°C, 12L:12D cycles for 5 days then switched to constant darkness conditions. Each horizontal line shows 24 h, with each day attached below the previous day. A vertical line indicates the onset of locomotion. The shaded areas of the actogram represent darkness. The superimposed line across the actogram represents the predicted onset time of the locomotion according to its circadian period (τDD = 23.5 h) (modified from Lin and Lee, 1996).



Biological Clock of the German Cockroach, *Blattella Germanica (L.),* Figure 41 The locomotor activities of a virgin female adult German cockroach at 28°C, 12L:12D cycles for 5 days then switched to constant darkness conditions. Daily development of ovaries represented by the length of oocytes is shown on the left side of the actogram. The mating window for a virgin female is displayed on the right side of the actogram. Other symbols as above (modified from Lee and Wu, 1994; Lin and Lee, 1996).

organisms across five kingdoms. We can identify the three most important ecological functions of a circadian clock: (i) the timing of each behavior is so important that every organism within a species should time each movement very accurately. This is the key function an endogenous circadian clock can provide. (ii) Although most environmental changes are fairly rhythmic and predictable, some conditions (such as continual raining, sudden cold or heat) might cause long lasting interruption on environmental rhythmicity. These unpredictable environmental changes may last a few days and cause organisms to perform behaviors solely depending on their circadian clock for good timing. (iii) Every day is a new challenge for an organism. The active tasks ahead require good preparation in physiological conditions to overcome challenges. In order to be well-prepared for the challenge, organisms depend on their circadian clock to trigger the whole cascade of reactions. The physiological preparation in organisms occurs in the rest phase of the daily cycles. A circadian clock can provide good timing to start preparation and achieve survival in danger-ridden environments.

Natural selection has shaped the proper behaviors of organisms to act in the right place at the right time. Good timing is certainly involved in life and death decision-making processes. An endogenous circadian clock is definitely a key asset to survive and prosper for the species.

Biological Clock of the German Cockroach

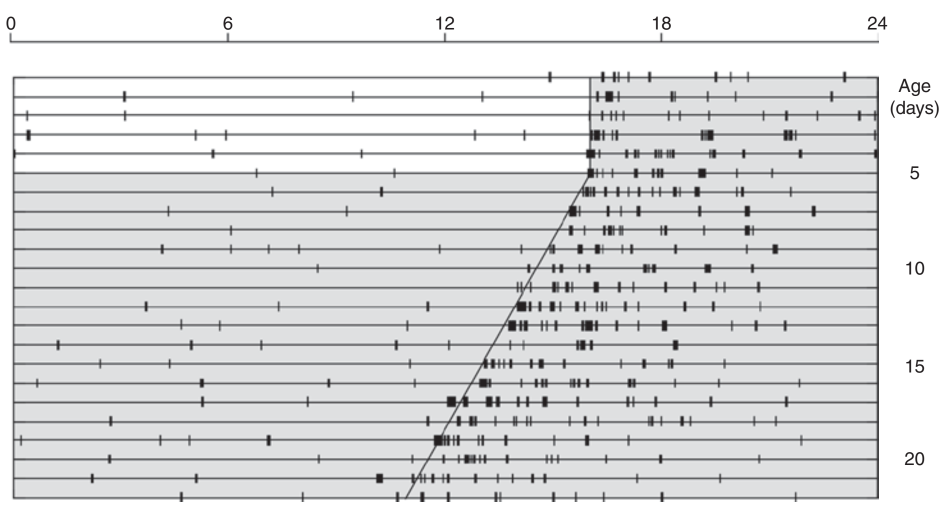
With some background information about biological clocks, we can turn our attention to the circadian clock of the German cockroach. Since it would be difficult to actually see the working clock in a multi-cellular animal, a circadian rhythmic behavior or physiological parameter can be selected and monitored as the overt expression of the endogenous clock. The locomotor circadian rhythm is chosen as the focal point of this article.

The German cockroach is a nocturnal insect, and its locomotor activities mainly occur during the scotophase (dark phase) of the daily photoperiod condition. Once the light-dark cycles are artificially changed to constant darkness condition, a male adult's free-running rhythm continues to regulate locomotion for greater activity during the time that would represent scotophase in light-dark cycles. The circadian period of the male adult is approximately 23.5 h. From this activity pattern, we know there is an endogenous clock driving its locomotion in circadian rhythmicity.

When female adults are put into the same condition, their locomotion does not show a circadian rhythm. Their locomotion is concentrated to the few days before the formation of ootheca (egg case), and activity is distributed relatively evenly across the 24 h period. This locomotor pattern coincides with the developmental cycles of ovaries. When the ovaries reach at certain developmental stage, female adults become active. Their locomotion even occurs during the day, clearly counter to the nocturnal nature of the species. In addition, this locomotor pattern coincides with the narrow mating-window of the females. When the females become sexually receptive, their daily locomotion increases significantly. Once the females mate, their locomotion decreases immediately. We conclude that locomotion represents mate-finding activities and that the locomotor pattern of female adults does not display a circadian rhythmicity.

Since possessing a circadian clock is a genetic trait for the species, female adults should also have a circadian clock underlying their arrhythmic locomotion. When the ovaries are surgically removed during the last instar, they express a locomotor circadian rhythm of 23.6 h, the same as found in male adults (Fig. 42). This circadian rhythmicity also can be seen in starving female adults whose ovaries do not develop. The locomotor circadian rhythm of females is masked by the endogenous development of ovaries. This masking effect is a unique characteristic of the biological clock in the German cockroach.

A critical function of the circadian clock in reproductive behavior is to provide good timing for bringing potential mates together. However, why does the timing of mate-finding behavior not synchronize between the sexes of the German cockroach? This question certainly implies that the masked circadian rhythm of female adults does not impair the chances of meeting males. It requires a detailed analysis of the reproductive strategies of the German cockroach to unveil the



Biological Clock of the German Cockroach, *Blattella Germanica (L.),* Figure 42 The locomotor activities of an ovariectomized female adult German cockroach at 28°C, 12L:12D cycles for 5 days then switched to constant darkness conditions. The circadian period is calculated as 23.6 h. Other symbols as above (modified from Lin and Lee, 1996).

mystery of endogenous masking effects on the locomotor circadian rhythm.

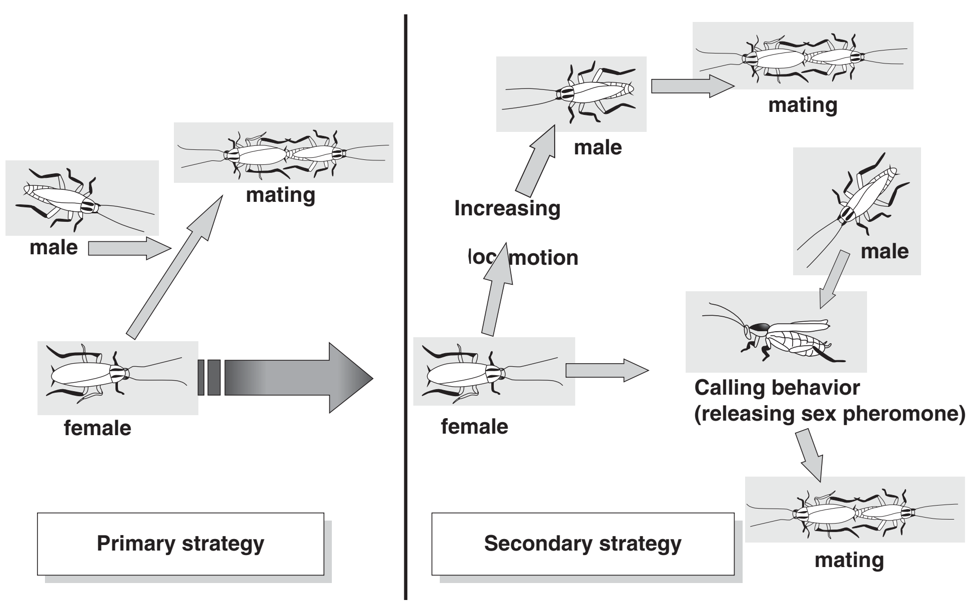
Although German cockroaches are not social insects, they do live in groups. The groups are composed of immature and adult cockroaches of both sexes, and are maintained by an aggregation pheromone secreted by every individual. This style of living provides easy opportunity for both sexes to meet when they are sexually mature. Thus, the timing of mate-finding locomotion becomes less critical in comparison with solitary cockroach species. The masked locomotor circadian rhythm does not handicap the chances of mating pair-formation. Random (Fig. 43) mate-finding is largely dependant upon group living and is the primary strategy of the species.

Since female adults produce an ootheca regardless of their mating status, the nutrient-rich oothecae is wasted when the females do not mate during the narrow mating-window. The penalty for losing the mating opportunity is severe enough to drive female adults into locomotion to find mates regardless the time of the day. The masked locomotor circadian rhythm, therefore, reflects the high importance of mate-finding. In addition, sexually mature females release sex pheromone to attract males. Combining these two mechanisms, the female adults try to mate in time.

These complicated reproductive strategies guarantee the survival and propagation of the species. In fact, the high priority of reproduction causes a unique masking effect on the mate-finding locomotion of the female. This arrhythmic locomotion is the result of high demand on mate-finding locomotion during the sexually receptive period of female adults. Underneath this arrhythmic locomotion, however, an endogenous circadian clock paces daily locomotion.

Conclusion

The biological clock of the German cockroach runs continuously in both sexes. It drives locomotion to express circadian rhythm in male adults, but adult females fail to show circadian rhythmicity. An endogenous masking factor caused by the developing ovaries obscures the overt rhythm of locomotion in females. Although this desynchronizing locomotion does not fit into the mode of



Biological Clock of the German Cockroach, *Blattella Germanica (L.)*, Figure 43 Mating scheme for the German cockroach (modified from Tsai and Lee, 1997).

function for a circadian clock, the masked arrhythmic locomotion becomes part of reproductive strategy that ensures a mating opportunity for sexually mature females.

References

Enright JT (1970) Ecological aspects of endogenous rhythmicity. Ann Rev Ecol Syst 1:221–238

Lee HJ (1994) Are pregnant females of the German cockroach too heavy to run? Zool Stud 33:200–204

Lee HJ, Wu YL (1994) Mating effects on the feeding and locomotion of the German cockroach, *Blattella germanica*. Physiol Entomol 19:39–45

Lin TM, Lee HJ (1996) The expression of locomotor circadian rhythm in female German cockroach, *Blattella germanica* (L.). Chronobiol Int 13:81–91

Lin TM, Lee HJ (1998) The parallel control mechanisms underlying locomotor activity and sexual receptivity of female German cockroach *Blattella germanica* (L). J Insect Physiol 44:1039–1051

Scully AL, Kay SA (2000) *Time flies for Drosophila*. Cell 100:297–300

Tsai CW, Lee HJ (1997) Volatile pheromone detection and calling behavior exhibition: secondary mate-finding strategy of the German cockroach, *Blattella germanica* (L.). Zool Stud 36:325–332

Tsai CW, Lee HJ (2000) Circadian locomotor rhythm masked by the female reproduction cycle in cockroaches. Physiol Entomol 25:63–73

Tsai CW, Lee HJ (2001) Analysis of specific adaptation to a domicile habitat: a comparative study of two closely related cockroach species. J Med Entomol 38:245–252

Wen HW, Lee HJ (2000) Unequal coupling between locomotor pacemakers of the German cockroach, *Blattella germanica* (L.). J Insect Physiol 46:89–97

Biological Control

The action of parasites, predators, or pathogens in maintaining another organism's population density at a lower average level than would occur in their absence. Biological control may occur naturally in the field or result from manipulation or introduction of biological control agents.

► Augmentative Biological Control
► Classical Biological Control
► Conservation Biological Control

Biological Control by *Neoseiulus californicus* (McGregor) (Acari: Phytoseiidae)

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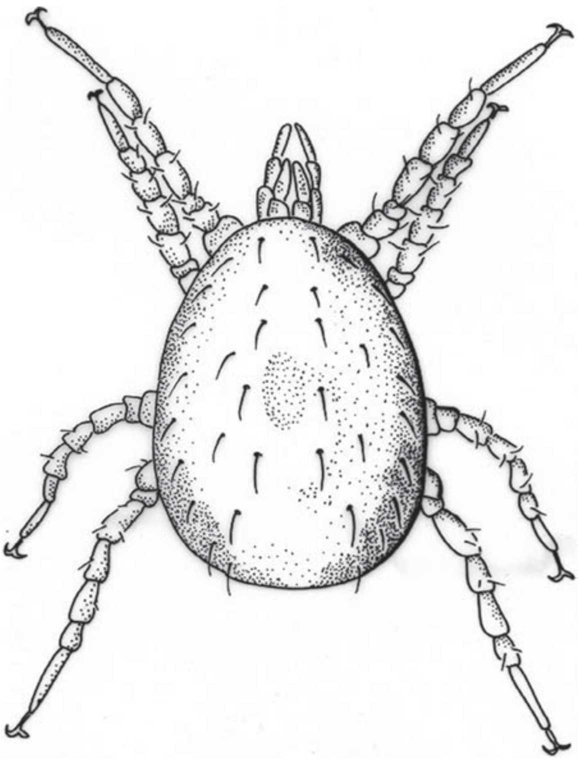
Neoseiulus californicus is a predator mite that provides an effective biological control of *Tetranychus* spp. spider mites in strawberries, corn, grapes, roses, fruit trees and ornamentals. It has a worldwide distribution in arid and humid areas, including semi-tropical and temperate South America, and arid areas of southern California and southern Europe.

This predator is very small in size. The adult measures 0.25–0.5 mm in length and is pear shaped and slightly orange in color. It passes through four developmental stages (egg, larvae, nymph and adult). Eggs are oval and translucent. At 25°C, the eggs hatch after two days. Larval and nymphal (proto- and deutonymph) stages require about three days to complete development. Then, it takes approximately five days to reach the adult stage. Adult longevity is approximately 20 days, and the oviposition period is 13.5 days. A female can lay three eggs a day (Fig. 44).

Neoseiulus californicus, as well as other predatory mites (e.g., *N. fallacis* (Garman), *Phytoseiulus persimilis* Athias-Henriot and *Mesoseiulus longipes* (Evans)) is commercially produced and used to control the two-spotted spider mite, *T. urticae* Koch, in North American and European greenhouse horticulture.

A related species in the same genus, *N. fallacis*, coexists with *N. californicus* in the Northern Hemisphere. Both species are morphologically similar and have been rated as specialized predators of spider mites, but *N. californicus* seems to be more generalist than *N. fallacis*. Pollen of different plants such as maize, almond, castor bean, avocado, and some grasses, as well as thrips are alternative food.

In South America, releases of predatory mites are not commonly used, and regular applications



Biological Control by *Neoseiulus Californicus* (McGregor) (Acari: Phytoseiidae), Figure 44
***Neoseiulus californicus* (McGregor).**

of acaricides are made to control pest mites. However, in commercial strawberry greenhouses in Argentina, *N. californicus* is the main established enemy of the two-spotted spider mite. Although this predator consumes fewer prey than other phytoseiid species, it has longer survival under starvation conditions. Moreover, the ability to feed on other food sources may contribute to its persistence in the absence of spider mites. This trait may be of critical importance for the success of conservation biological control.

Conservation biological control means the environmental manipulation to protect and enhance natural enemies. This is an ecologically, environmentally, and economically sound solution to pest problems for growers of developing countries.

Recent studies in La Plata (Buenos Aires, Argentina) showed that *T. urticae* and *N. californicus* populations exhibit a high spatial coincidence and the predator is very efficient in locating the prey. This predator seems to be a promising natural enemy for controlling *T. urticae* through the implementation of conservation techniques. Taking into account that the ability to tolerate acaricides is a serious constraint on successful conservation of phytoseiid predators, the reduction of unnecessary acaricide treatments may enhance persistence of predator mite populations.

At present, efforts are being made to reduce the number of chemical applications through monitoring of the prey/predator ratio and pest population trend to avoid both unnecessary pesticide applications and economic damage. However, more field studies are needed to help elucidate other factors that contribute to increase, and to effectively preserve the natural populations of this predator in annual as well as perennial systems. Among these factors, plant diversity may be a critical feature to increase natural enemy persistence through: (i) provision of alternative prey/host at times when the pest is scarce, (ii) provision of supplementary food, and (iii) provision of refuge (for mating or overwintering).

It is also known that physical and chemical characteristics of the food plants of prey can affect natural enemy potential effectiveness. A good example of this is the negative way in which persistence of *N. californicus,* plant colonization, and consumption of *T. urticae* are affected by tomato leaf glandular hairs. This finding reveals the risk of generalizing the effectiveness of *N. californicus* from one crop to another.

The implementation of conservation biological control is still receiving inadequate consideration in developing countries. The potential and utility of *N. californicus* as a biological control agent is worth further investigation.

References

Greco NM, Liljesthröm GG, Sánchez NE (1999) Spatial distribution and coincidence of *Neoseiulus californicus* and *Tetranychus urticae* (Acari: Phytoseiidae, Tetranychidae) on strawberry. Exp Appl Acarol 23:567–580

Ma W, Laing JE (1973) Biology, potential for increase and prey consumption of *Amblyseiulus chilenensis* (Dosse) (Acarina: Phytoseiidae). Entomophaga 18:47–60

McMurtry JA, Croft BA (1997) Life styles of phytoseiidae mites and their roles as biological control agents. Annu Rev Entomol 42:291–321

Monetti LM, Croft BA (1997) *Neoseiulus californicus* (McGregor) and *Neoseiulus fallacis* (Garman): larval responses to prey and humidity, nymphal feeding drive and nymphal predation on phytoseiid eggs. ExpAppl Acarol 21:225–234

Biological Control of Invasive Plants in Latin America

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An invasive plant is an exotic that has been introduced, intentionally or by accident, into a new region where it successfully establishes, reproduces, and spreads, eventually replacing the native vegetation. Invasive plants or weeds, also called "biological pollutants," threaten natural ecosystems and human-modified habitats by reducing biological diversity and by causing significant reductions in crop yields and other harmful effects on property, humans, and domesticated animals. The success of the exotic plant to become invasive in a new geographical region can be partially attributed to the fact that the exotic has been introduced without the arthropod natural enemies and disease-producing pathogens that limit its reproduction in the area of origin.

Manual removal and herbicides are the major invasive plant management practices currently used in cultivated crops in Latin America. Biological control, or the use of natural enemies such as arthropods, pathogens, and fish to reduce the population and reproduction of the exotic invasive, has been traditionally practiced in developed countries such as the United States, Australia, Canada, South Africa, and New Zealand, primarily in rangeland situations, conservations areas, and aquatic systems.

A frequently cited example of a successful biological control project is the control of prickly pear cactus, *Opuntia stricta* Haworth (Cactaceae) in Australia by the pyralid moth *Cactoblastis cactorum* Bergroth (Lepidoptera: Pyralidae) introduced from Argentina in the 1920s. However, this is also a good example of conflicting interests, as the invasive plant (cactus) is harmful in Australia and biological control was needed. On the other hand, it is useful as human and animal food, and as an ornamental plant for people in other regions (Mexico, Caribbean, southern regions of the USA). Here, the successful biological control agent in Australia, *C. cactorum*, threatens the native endemic cactus, so it is not regarded as a "hero" but as a "pest," and control measures including the use of natural enemies and the sterile insect technique are being undertaken.

Other well-known examples of classical biological weed control include the effective control of Klamath weed and alligator weed. Klamath weed or St. Johnswort, *Hypericum perforatum* L. (Clusiaceae) was controlled in the western USA by two European leaf-feeding beetles, *Chrysolina quadrigemina* (Suffrian) and *Chrysolina hyperaci* (Forster) (Coleoptera: Chrysomelidae), imported from Australia in the mid 1940s. In Florida, USA, complete biological control of alligator weed, *Alternanthera philoxeroides* (Martius) Grisebach (Amaranthaceae) in aquatic environments was achieved by the introduction of the flea beetle *Agasicles hygrophila* Selman and Vogt (Coleoptera: Chrysomelidae) from Argentina.

Interest in biological control of invasive plants using host-specific insects and pathogens has increased in the last decade due to the public's concern about the negative effects of pesticides in the environment, a greater demand for pesticide-free agricultural products, the reduction in the number of pesticide registrations, the development of plant resistance to commonly used herbicides, and the intensified oil crisis which increases the cost of using herbicides. A recent catalogue of biological control agents and their weeds listed 949 releases involving at least 350 organisms against

133 target weeds as of 1996. Forty-one (31%) of these weeds are considered under complete or substantial biological control.

Biological control is not a panacea and is not without an element of risk. The advantages of classical biological control over other invasive plant control methods are that it is highly specific to the target plant, it has little or no impact on non-target organisms, it does not pollute the environment, it is relatively inexpensive, and it provides self-sustaining and permanent control of the invasive plant when it works. Among the disadvantages of biological control of invasive plants with introduced insects are that it is unpredictable, and even if the insects establish, biological control may not suppress the invasive plant population enough to achieve the desired level of control.

Several factors make biological control with insects especially difficult in field crops. First, disturbance from planting, cultivation, and pesticide applications is not conducive to the establishment of the biological control agent. Second, because several species of invasive plants usually require control simultaneously, multiple biological control agents are needed. Finally, rapid control (usually within one month of planting) is necessary in order to prevent crop damage. Once invasive plant-feeding insects establish, they are unlikely to build up damaging populations in a single field season. Highly specific plant pathogens may be better suited to control invasive plants in field crop situations. Native plant pathogens can be formulated and applied as bioherbicides, or exotic pathogens can provide effective control of the invasive plants following inoculative releases. Lastly is the conflicting interest issue mentioned previously. A plant that is perceived as a nuisance by one group of people can be considered a beneficial plant by another group. Beekeepers are a good example of a special interest group that may object strongly to biological control because they may value the invasive plant as a source of nectar and pollen.

Biological Control Activities Against Invasive Plants in Latin America

The use of insects and pathogens as biological control agents of invasive plants in South America has been quite limited. Compared with the advances achieved in biological control of arthropod pests for the same region, the use of insects for control of invasive plants is in its infancy or initial stages of development. Chile can be considered a pioneer in this field, with biological control activities of invasive plants initiated in 1952 against the non-native invasive *Hypericum perforatum* L. (Clusiaceae). This project has been a great success, providing highly effective control of this weed. Other biological control projects initiated in Chile in the 1970s that had only moderate successes or have been ineffective include *Galega oficinalis* L., *Ulex europaeus* L. (Rosaceae), *Rubus constictus* Lepeure & Mueller, and *Rubus uifolius* (Rosaceae). Research efforts using insects or pathogens for biological control of invasive plants in Chile continue, with more intensity in the last decade due to enhanced funding provided by national institutions. In Argentina, there is only one case known of biological control, that of the invasive aquatic plant waterhyacinth, *Eichhornia crassipes* (Mart.) Solms (Pontederiaceae) in the province of La Rioja located in the west-central part of the country. The waterhyacinth-feeding weevil *Neochetina bruchi* Hustache (Coleoptera: Curculionidae) was introduced from the province of Buenos Aires and it was able to reduce the aquatic plant infestation from 50% to 8%.

Biological control of aquatic invasive plants in Mexico has been implemented with more intensity during the last decade using a combination of insects and pathogens against waterhyacinth. Most of the current aquatic plants have been introduced by humans from their native habitats, and are free from their natural enemies and diseases. Invasiveness is a response to the high level of nutrients in the urban, industrial and municipal wastewater. Aquatic invasive plants causes water loss through plant evapotranspiration, displacement of native species, public health risks, obstruction of channels and drains in irrigation systems, intakes to hydroelectric plants, restriction to tourist, recreational and fishing activities, and increasing sedimentation with subsequent shortening of the useful life of the body of water. In Mexico, more than 62,000 ha have been infested by aquatic invasive plants. The most important species are waterhyacinth, followed by water fern (*Salvinia* spp.), pondweed (*Potamogeton* sp.), cattail (*Typha* sp.), hydrilla (*Hydrilla verticillata* L. Royle), waterlettuce (*Pistia stratiotes* L.), and duckweed (*Lemma* spp.).

In 1993, the Aquatic Weed Control Program was initiated in Mexico by presidential mandate in response to the increasing need to control the overwhelming presence of invasive plants in the water sources. As part of this program, a biological control project was included. In Mexico, waterhyacinth is the most prolific invasive aquatic plant, infesting an estimated 40,000 ha of water. This plant was probably introduced in Mexico in the early 1900s. Chemical and mechanical control methods have been used to manage waterhyacinth, but these methods are expensive and several annual applications are needed. The difficulties in controlling this aquatic invasive are related to the plant's rapid growth rate and its ability to reinfest via the seed bank or by flood-borne plants. For these reasons, the only long-term and sustainable solution is the application of an integrated approach to waterhyacinth management in which biological agents play a key role.

The host-specific Brazilian weevils *Neochetina eichhorniae* Warner and *Neochetina bruchi* Hustache have been used in many countries worldwide to control waterhyacinth with relative success. *Neochetina eichhorniae* was introduced to Mexico from the US in the late 1970s. However, other reports indicated its presence in some Mexican water bodies as early as 1967. Another three waterhyacinth insects that have been observed occurring naturally in Mexican water bodies are *Sameodes albigutalis* (Warren) (Lepidopera: Pyralidae), *Cornops aquaticum* (Bruner) (Orthoptera: Acrididae), and *Orthogalumna terebrantis* (Wallwork) (Acari: Galumnidae). There is no evidence of them being native to Mexico, and they could have arrived with waterhyacinth plants introduced in the past. The Brazilian weevil *N. bruchi* was introduced into Mexican quarantine from the USDA Aquatic Plant Management Laboratory in Fort Lauderdale, Florida, USA. Although the *Neochetina* species are well established in Mexico, the effectiveness of biological control requires the use of additional agents to complement existing ones.

Several highly virulent waterhyacinth pathogens have been collected, identified, screened for plant host range, mass-produced, and field evaluated in Mexico. After selecting two specific and highly virulent fungal pathogens, *Cercospora piaropi* Tharp., and *Acremonium zonatum* (Saw) W. Games, the combined effects of the plant pathogens and the *Neochetina* weevils were evaluated in a seven ha water reservoir in the central part of Mexico in the state of Morelos. A total of 9,800 weevils were released and two applications of a mixture of the fungal pathogens were carried out. After three months of the combined application of the fungi and weevils, the reservoir was free of waterhyacinth. The dramatic reduction in waterhyacinth coverage was due to the increasing amount of a natural pathogen (*C. piaropi*) already present in the water reservoir, the introduction at the same time of another highly virulent pathogen (*A. zonatum*) combined with the leaf feeding scars made by the *Neochetina* adult weevils and stem damage by the *Neochetina* larvae. Weevil feeding allows the transmission of the pathogens, which results in increased disease incidence. This approach of combining insects and pathogens to get a better control of an invasive aquatic plant is currently implemented by the Instituto Mexicano de Tecnología del Agua in different regions of Mexico.

In Honduras, a limited number of biological control activities against waterhyacinth were initiated in the 1990s. The *Neochetina* weevils were introduced and released in a body of water at the Pan-American Agricultural University

"El Zamorano" located 20 miles east of Tegucigalpa. Control of waterhyacinth has been a complete success in this body of water through the combined effect of the *Neochetina* and manual removal of the fewer and smaller plants damaged by the feeding of the adult/larvae stages of the weevil.

In 2005, some biological control activities against aquatic invasive plants were initiated in Nicaragua. Aquatic systems have been sampled to determine the arthropods fauna associated with waterhyacinth and waterlettuce, which invades several lakes and rivers in Nicaragua, preventing fishing, navigation, and running of the hydroelectric plants that provide electricity to a large part of the country. A new species of *Cornops sp*. (Orthoptera: Acrididae) was found feeding heavily on waterhyacinth, and host-specificity range studies are being undertaken.

The first biological control activity in Brazil against a non-native invasive plant, *Tecoma stans* (Bignoniaceae) was initiated in 2000. This medium-size tree is originally from the southern USA, Mexico and Central America, and it is invasive in uplands and pasture areas in southern Brazil (the states of Paraná and Rio Grande do Sul) where it replaces native vegetation. The rust fungus *Prospodium appendiculatum* (G. Winter) Arthur was found attacking this plant in southern Brazil, and no other potential specific agents has been found in field explorations conducted in recent years. Initial foreign exploration in the area of origin (Nicaragua, Costa Rica) of *T. stans* was conducted for several days in June 2006 and several potential natural enemies were collected on the plant. Additional field explorations are planned once funds become available.

Exportation of Latin American Biological Control Agents

Contrary to the limited importation of biological control agents into Central and South American countries, as of the late 1900s, 127 insect species had been exported and used in other regions of the world, mainly Australia, Canada, the continental United States and Hawaii, New Zealand, India, and several African counties, principally South Africa. The three countries from which most of the biological control agents have been exported are Mexico (42 species or 33.1% of the total exported), Brazil (30 species or 23.6% of the total), and Argentina (20 species or 15.8% of the total). This trend has continued into this century and is supported by local personnel and institutions (e.g., USDA-ARS Biological Control Laboratory in Hurlingham, Argentina) established by foreign countries that have invasive plants native to South America.

Limitations on the Implementation of Biological Control of Invasive Plants in Latin America

Among the main limitations to carrying out biological control projects against invasive plants in South America is the limited number of technical personnel with training in this discipline. Some efforts of training in this field were initiated by the University of Florida in cooperation with the Universidad Nacional Agraria of Nicaragua, the Instituto de Investigaciones Agropecuarias of Temuco, Chile, and the USDA-ARS South American Biological Control Laboratory of Hurlingham, Argentina. Three intensive weed biological control courses were given in Nicaragua during June 2002, 2004, and 2006 with 78, 51, and 46 participants, respectively. This kind of training is necessary to prepare the personnel required for the implementation of biological control programs in the region.

Another important factor that limits the implementation of invasive plant biological control projects is the limited availability quarantine facilities that exist in the region. However, most of the South American countries already have quarantine facilities for the introduction of parasites/predators for biological control of arthropod pests. These installations could be modified and adapted for the introduction of biological control agents of invasive plants. Countries that have quarantines to handle natural enemies of invasive plants include Brazil, Argentina, and Chile.

A third and very important limiting factor is the lack of funds. Economic resources for any type of agricultural research are scarce and competition for grants is highly competitive. The funding required to initiate a new project for biological control of invasive plants is relatively high. Nevertheless, the ecological and/or economic benefits that will be obtained if agents become established and successful are quite substantial.

Potential for Biological Control of Invasive Plants in Latin America

The successes with biological control of invasive plants in conservation areas, agricultural situations, and aquatic systems obtained in other countries could be duplicated in Central and South America. The diversity and complexity of the agricultural practices by South American farmers suggest that management of invasive plants should be biologically based (biological control using native or introduced insects and/or pathogens) and integrated with conventional control methods. For example, cultural practices (plant density, non-tillage, intercropping, crop rotation, organic agriculture) that contribute to preservation of natural enemies of the invasive plants should be encouraged. Invasive plant pathogens can be integrated with the more disruptive chemical and mechanical methods most commonly used for high-cash crops, or in situations where the availability of manual labor is limited.

The twenty most important invasive plants in Central and South America are shown in the accompanying table: *Amaranthus spinosus* L. (Amaranthaceae; common name "spiny amaranth" in the USA, "bledo" in Central America); *Ambrosia artemisiifolia* L. (Asteraceae; common name "Amargosa," distribution North and South America); *Bidens pilosa* L. (Compositae; common name "mozote"); *Coniza bonariensis* (L.) Cronq., (Asteraceae; common name "varilla," distribution tropical America); *Cyperus rotundus* L. (Cyperaceae; known as "coyolillo" in Central America, "coquito" in Colombia); *Desmodium tortosum* (Swarts) Dc., (Fabaceae; known in Central America as "pega-pega"); *Echinocloa colona* (L.) Link (Poaceae; known as "arroz de monte" or "arrocillo," plant originally from Eurasia and very common in South American rice fields); *Eichhornia crassipes* (Pontederiaceae; common name "jacinto de agua," "lirio de agua," or "lirio acuático"); *Eragrostis plana* Nees (Poaceae; common name in Brazil "capim annoni"); *Pistia stratiotes* (Araceae; known as "lechuga de agua" in Central America and "alfaça de agua" in Brazil); *Portulaca oleraceae* L. (Portulacaceae; known as "verdolaga" in Central America), *Richardia scabra* L. (Rubiaceae; common name "botoncillo"); *Ricinus communis* L. (Euphorbiaceae; highly toxic plant known in South America as "castor" or "higuerilla"); *Rottboellia cochinchinensis* (Lour) Chyton (Poaceae; known in Central America and in the Caribbean as "la caminadora"); *Sida acuta* Burn. f. (Malvaceae; known as "escobilla negra"); *Solanum torvum* Swarts (Solanaceae, a spiny bush common in South America known as "lava platos" or "huevo de gato," a name also applied to various species of *Solanum*); *Sorghum halepense* (L.) Pers. (Poaceae; known as "grama Johnson"); *Taraxacum officinale* Weber (Asteraceae; originally from Europe and known in South America as "lechuguilla"); *Tecoma stans* (L.) Kunth ex HBK. (Bignoniaceae, known as "guabillo" in Central America, it is invasive in southern Brazil); and *Ulex europaeus* L. (Fabaceae; known in South America by the common name "tojo"). These invasive plants cause significant economic or ecological damage in Central and South America and justify the research and implementation costs of biological control. In some cases, the costs for implementing biological control programs in Central and South America can be reduced by making use of the existing technology that has been successful in other regions of the world, thus, biological control with insects and/or pathogens could provide

Biological Control of Invasive Plants in Latin America, Table 3 The twenty most important invasive plants in Central and South America

Scientific name	Common name	Family	Origin
Amaranthus spinosus	Bledo	Amaranthaceae	Tropical America
Ambrosia artemisiifolia	Amargosa	Asteraceae	America
Bidens pilosa	Mozote	Compositae	America
Conyza bonariensis	Varilla	Asteraceae	Tropical America
Cyperus rotundus	Coyolillo	Cyperaceae	India
Desmodium tortuosum	Pega-pega	Fabaceae	Tropical America
Echinocloa colona	Arroz de monte	Poaceae	Eurasia
Eichhornia crassipes	Lirio acuático	Pontederiaceae	South America
Eragrostis plana	Capim annoni	Poaceae	South Africa
Pistia stratiotes	Lechuga de agua	Araceae	South America
Portulaca oleraceae	Verdolaga	Portulacaceae	India
Richardia scabra	Botoncillo	Rubiaceae	South America
Ricinus communis	Higuerilla	Euphorbiaceae	Tropical Africa
Rottboellia cochinchinensis	La caminadora	Poaceae	India
Sida acuta	Escobilla negra	Malvaceae	Tropical America
Solanum torvum	Lava platos	Solanaceae	Africa
Sorghum halepense	Grama Johnson	Poaceae	Mediterranian
Taraxacum officinale	Lechuguilla	Asteraceae	Europe
Tecoma stans	Guabillo	Bignoniaceae	Mexico
Ulex europaeus	Tojo	Fabaceae	Europe

effective, safe, and low-cost solutions to many of Central and South America's most important invasive plant problems. Table 3.

► Biological Control of Weeds
► Classical Biological Control
► Invasive Species

Reference

Charudattan R (1996) Pathogens for biological control of waterhyacinth. In: Charudattan R, Labrada R, Center TD, Kelly-Begazo C (eds) Strategies for water hyacinth control. A report of a panel of experts meeting, Fort Lauderdale, Florida. Food and Agricultural Organization of the United Nations, FAO, Rome, pp 90–97

Gutiérrez LE, Arreguín CF, Huerto DR, Saldaña FP (1994) Control de Malezas Acuáticas en México. Ingeniería Hidráulica en México 9:15–34

Gutiérrez LE, Huerto R, Martínez M (1996) Waterhyacinth problems in Mexico and practiced methods for control. In: Charudattan R, Labrada R, Center TD, Nelly-Begazo C (eds) Strategies for water hyacinth control. A report of a panel of experts meeting, Fort Lauderdale, Florida. Food and Agricultural Organization of the United Nations, FAO, Rome, pp 125–135

Holm LG, Plucknnett DL, Pancho JV, Herberger JP (1997) The world's worst weeds. University Press of Hawaii, Honolulu

Julien MH, Griffiths MW (1998) Biological control of weeds. A world catalogue of agents and their target weeds, 4th edn. CAB International, Queensland, Australia, 223 pp

Martínez M, Charudattan R (1998) Survey and evaluation of Mexican native fungi for potential biocontrol of waterhyacinth. J Aquat Plant Manage 36:145–148

Martínez M, Gutiérrez E, Huerto R, Ruíz E (2001) Importation, rearing, release and establishment of *Neochetina bruchi* (Coleoptera: Curculionidae) for the biological control of waterhyacinth in Mexico. J Aquat Plant Manage 39:140–143

Martínez M, Gómez M (2007) Integrated control of *Eichhornia crassipes* by using insects and plant pathogens in Mexico. Crop Protection (in press)

Medal J (2004) Perspectives on biological control of invasive plants in Latin-America. In: Cullen JM et al (eds) Proc XI Int Symp Biol ContWeed. Canberra, Australia, pp 425–427

Medal J (2007) El control biológico de malezas en Latinoamérica: situación actual y Perspectivas futuras. Vedalia (in press)

Norambuena H, Ormeño J (1991) Control biológico de malezas: fundamentos y perspectivas en Chile. Agricultura Técnica (Chile) 51:210–219

Norambuena H, Escobar S, Rodriguez F (2000) The biocontrol of gorsse, *Ulex europaeus* in Chile: a progress report. In: Spencer NR (ed) Proc X Int Symp Biol Cont Weed. Montana State University, Bozeman, MT pp 955–961

Norambuena H (2004) Exploraciones en el Extranjero, Transporte, y Procedimientos de Cuarentena de los Agentes de Control Biológico. In: Medal J, Norambuena H, Gandolfo D (eds) Memorias del Segundo Curso Latinoamericano de Control Biológico de Malezas. Montelimar, Nicaragua. University of Florida-IFAS, Gainesville, FL, pp 16–21

Biological Control of Weeds

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Weeds are universally recognized as significant pests worldwide because they interfere with food and fiber production, and are considered the most important threat to biodiversity after habitat destruction. Weeds cause 90% of agricultural losses, and herbicides account for approximately half (47%) of the world's agrochemical sales. The economic effect of weeds on the U.S. economy is staggering. Weed-associated losses and costs in the mid 1990s were estimated to be in excess of $20 billion annually, with non-native or invasive weed species accounting for $13 billion, or 65%.

An invasive weed is a non-native plant that exhibits rapid population growth following its arrival in a new environment where it did not evolve. The success of the weed in its new habitat is due in part to the absence of the natural enemies that normally limit its reproduction and spread in its native range. Classical biological control seeks to reunite an invasive weed with one or more of its coevolved natural enemies to provide permanent control of the weed. Thus, classical biological control can be defined as the planned introduction and release of undomesticated target-specific organisms (usually arthropods, nematodes or plant pathogens) from the weed's native range to reduce the vigor, reproductive capacity, or density of the target weed in its adventive range. The term "adventive" in this definition acknowledges the fact that the arrival of a weed in a new geographical area can occur by any means (e.g., immigration), and is preferable to the term "introduced," which is restricted to actions taken by people. Biological weed control as it is defined here specifically excludes natural regulation (the action of organisms without human intervention), cultural control practices (grazing management, crop rotation, etc.), and plant competition (the deliberate use of one plant species to competitively exclude another). Although plant competition is not included in the definition of biological weed control, it is an essential component of the overall process that can affect the outcome of a biological control project.

Plant predation (or herbivory in the case of weed biological control) and plant competition are entirely different ecological processes. An introduced natural enemy (arthropod, nematode, or pathogen) damages or consumes portions of the weed, which rarely leads to plant death but results in a loss of biomass or nutrients that weaken and stress the plant. In plant competition, the weed and its competitors are interfering with each other for use of a common resource (e.g., light, water, nutrients or germination sites). It is the subtle interaction between these two distinct ecological processes that can lead to the permanent decline of a weed population. An invasive weed is less likely to recover from the effects of selective herbivory from biological control agents if competition from desirable native plant species is strong.

Classical biological control offers several advantages over other weed control methods: (i) it provides selective, permanent control of the target weed; (ii) it is relatively inexpensive to develop and implement compared to other methods of weed control; (iii) introduced biological control agents are self-replicating and will spread on their own throughout the infested area; and (iv) because they are living organisms, biological control agents are biodegradable.

Some of the strengths of classical biological control also contribute to its shortcomings: (i) once biological control agents are established, they cannot be recalled if desirable species are attacked; (ii) control is not immediate and may require 5–10 years for agents to attain damaging levels; (iii) natural enemies for controlling every weed may not exist; and (iv) agent establishment and suppression of the target weed are not guaranteed.

Recent examples of successful biological control of adventive weeds with introduced invertebrate organisms in the last 20 years are shown above.

Procedures in a Classical Weed Biological Control Project

From the beginning, weed biological control scientists have continued to develop and refine procedures for locating, screening, releasing and evaluating biological control agents (Summary of steps, Table 5). All countries currently

Biological Control of Weeds, Table 4 Recent successes in classical biological control of weeds with invertebrate organisms worldwide since 1980

Weed species	Country
Aquatic and Wetland Weeds	
Alligatorweed, *Alternanthera philoxeroides* (Martius) Grisebach	China, New Zealand, Thailand
Azolla, *Azolla filiculoides* (Lamarck)	South Africa
Purple Loosestrife, *Lythrum salicaria* L	Canada, USA
Water Fern, *Salvinia molesta* (D. S. Mitchell)	Australia, Fiji, Ghana, India, Kenya, Malaysia, Namibia, Papua New Guinea (PNG), South Africa, Sri Lanka, Zambia
Water Hyacinth, *Eichhornia crassipes* (Martius) Solms-Laubach	Australia, Benin, India, Indonesia, Nigeria, PNG, South Africa, Thailand, Uganda, Zimbabwe
Water Lettuce, *Pistia stratiotes* L	Australia, Botswana, Ghana, PNG, South Africa, Sri Lanka, Zambia, Zimbabwe
Terrestrial Weeds	
Annual Ragweed, *Ambrosia artemisiifolia* L	Russia
Giant Sensitive Plant, *Mimosa invisa* (Martius)	Australia, PNG
Leafy Spurge, *Euphorbia esula* L	USA
Nodding Thistle, *Carduus nutans* L	Canada, USA
Purple Sesban, *Sesbania punicea* (Cavanille) Bentham	South Africa
Spinyhead Sida, *Sida acuta* (Burman) f	Australia
Tansy Ragwort, *Senecio jacobaea* L	USA, Australia

Sources: Julien MH, Griffiths MW (1998) Biological control of weeds. A world catalogue of agents and their target weeds, 4th edn. CAB International, Queensland, Australia, 223 pp; McFadyen REC (1998) Biological control of weeds. Annu Rev Entomol 43:369–393; Spencer NR (ed) (2000) Proc X Int Symp Biol Cont Weed, Bozeman, Montana, USA, 4–14 July 1999. United States Department of Agriculture, Agricultural Research Service, Sidney, Montana, and Montana State University, Bozeman, MT conducting weed biological control projects follow this protocol in one form or another to ensure that candidate organisms are safe to introduce.

Importance of Host Specificity

Host specificity is fundamental to biological weed control because it ensures that an introduced agent will not become a plant pest. Host specific, coevolved natural enemies are considered good candidates as they are incapable of reproducing on plants other than their weedy hosts, and have proven to be the safest to introduce because they are least likely to damage nontarget species. Because these host-specific natural enemies reproduce only in the presence of their host plants, they are able to regulate weed abundance by operating in a self-sustaining, density dependent manner.

Selecting organisms as candidates for classical weed biological control can be a complicated and lengthy process because scientists must identify those natural enemies that have developed a high degree of specificity with their host plants. Scientists conduct various types of host range tests in the field and laboratory (oviposition, adult feeding, and larval development) depending on the biology of the agent. Several screening tests usually are required to demonstrate with confidence the estimated host range of the agent. Candidate

Biological Control of Weeds, Table 5 Summary of steps involved in a classical weed biological control project

Step	Description
Target selection	Review literature about target weed, related plants and known natural enemies; identify and resolve conflicts of interest; conduct cost-benefit analyses; seek approval and funding
Overseas and domestic surveys	Locate native range of target weed and survey for natural enemies; assess biocontrol potential of each organism in country of origin; conduct faunal surveys in adventive range
Host specificity studies	Examine host range of organisms in native range; compile list of test plants and import promising candidates into quarantine of country of introduction for further testing
Approval of agents	Submit screening report to appropriate regulatory agencies to obtain approval for release; respond to requests for additional host testing or other concerns
Rearing and release	Obtain release permit; mass rear biocontrol agent; identify and implement most effective release strategy; release biocontrol agent at various sites to increase likelihood of establishment
Evaluation	Conduct field studies to confirm establishment and spread of biocontrol agent on target and nontarget species; use replicated manipulative experiments to determine effect of biocontrol agent on target weed populations
Technology transfer	Provide training to land managers and extension agents about using biocontrol agents; collaborate with user groups to determine best strategies for integrating biocontrol with other control methods

Sources: Julien M, White G (eds) (1997) Biological control of weeds: theory and practical application, ACIAR Monograph No. 49. ACIAR, Camberra, Australia; Luken JO, Thieret JW (eds) (1997) Assessment and management of plant invasions organisms that fail the host specificity requirement are dropped from further consideration. According to established guidelines, no organism can be introduced into a new environment before its host range is determined.

Taxa Used in Classical Biological Control of Weeds

Through 1996, there have been at least 1,150 deliberate releases of invertebrate organisms against invasive weed species in 75 countries. Five of the countries shown here – the United States, Australia, South Africa, Canada and New Zealand – account for most of the activity, based on the number of weed species targeted and agents released.

A large number of families and species are represented in these releases, and they are listed by the taxonomic groupings shown on p. 307. The taxa used in biological control projects worldwide are predominantly insects, but mites, nematodes, and fungi also have played an important role in controlling adventive weeds in some cases. Overall, 25% of all releases made before 1985 contributed to the control of the target weed.

Classical Biological Control of Weeds in Aquatic Habitats

Compared to terrestrial weeds, biological control of aquatic weeds with insects has been remarkably successful since it was first attempted in the United States against alligatorweed (*Alternanthera philoxeroides* (Martius) Grisebach) in 1964. Complete or substantial biological control of several other aquatic weed species has been achieved in most countries where it has been attempted. Although a higher proportion of failures than successes has occurred in the field of weed biological control, the overall success rate for the aquatic weeds is extraordinary. A close examination of the various projects suggests this high success rate may be correlated with the growth form of the weeds, the taxa used as biological control agents, susceptibility to disease-causing pathogens, fluid nature of the aquatic environment, or some combination of these factors.

Biological Control of Weeds, Table 6 Number of weed species targeted and agent species released in the five most active countries through 1990

Country	Weed species	Agent species
United States	54	130
Australia	45	123
South Africa	28	61
Canada	18	53
New Zealand	15	15
TOTAL	160	391

Source: Julien M, White G (eds) (1997) Biological control of weeds: theory and practical application, ACIAR Monograph No. 49. ACIAR, Canberra, Australia

Biological Control of Weeds, Table 7 Invertebrate taxa deliberately introduced between countries for classical biological control of adventive weeds

Group	No. of families	No. of species
INSECTA		
Coleoptera	8	147
Lepidoptera	25	106
Hemiptera	10	28
Diptera	6	44
Thysanoptera	2	4
Hymenoptera	3	5
Orthoptera	1	1
ACARINA	3	5
FUNGI	4	17
NEMATODA	2	2
Total	64	359

Sources: Bellows TS, Fisher TW (eds) 1999 Handbook of biological control. Academic Press, San Diego, CA ;Julien MH, Griffiths (eds) (1998) Biological control of weeds: a world catalogue of agents and their target weeds (4th ed) CABI Publishing, New York, NY

The aquatic form of alligatorweed, water hyacinth (*Eichhornia crassipes* (Maritius) Solms-Laubach), water lettuce (*Pistia stratiotes* L.), salvinia (*Salvinia molesta* D. S. Mitchell), and water fern (*Azolla filiculoides* Lamarck) have been predictably controlled using classical biological control. An interesting pattern emerges when the weed and insect attributes associated with these successes are considered. (i) All of the aforementioned aquatic weeds are either free-floating, or produce floating mats in the case of alligatorweed. This plant growth form is susceptible to wave action and currents that are unique to aquatic environments. (ii) Reproduction in these weeds is primarily by rapid vegetative growth. High genetic uniformity usually associated with vegetative reproduction was thought to be a necessary prerequisite for successful biological control. (iii) These floating weeds are highly susceptible to secondary infection. Aquatic plants that have sustained damage by insects or disease will rot and disintegrate very rapidly. (iv) Beetles (Insecta: Coleoptera) have been responsible for most of the control, especially weevils. Coincidentally, most invertebrate organisms released for classical biological control of weeds worldwide have been beetles.

Classical Biological Control of Weeds in Stable and Ephemeral Habitats

Historically, only perennial weeds of relatively stable environments (e.g., pastures, rangelands, and aquatic systems) were regarded as appropriate targets for classical biological control with host specific introduced natural enemies. Habitat stability coupled with minimal disturbance were thought to be necessary prerequisites for successful biological control. Conversely, crop weeds were deemed inappropriate targets for classical biological control with most of these organisms because of their vulnerability to conventional cultivation practices (e.g., soil tillage, mowing) and the same pesticides used against crop pests. Also, there was the belief that invertebrate biological control agents cannot develop damaging populations quickly enough to be effective against crop weeds because rapid control is needed to prevent the weed from overwhelming the crop. Finally, most crop weeds are multi-species assemblages of short-lived annuals that traditionally were not considered amenable to biological control by introduced host-specific organisms with the exception of fungi.

Several recent examples, however, have shown that classical biological control is feasible in some intensively managed agricultural environments where most of the problems are caused by one or two species of adventive crop weeds. Field bindweed (*Convolvulus arvensis* L.), which is native to Eastern Europe, is a serious pest of corn, cotton, sorghum, turf and wheat in much of the United States and Canada. An eriophyid mite (*Aceria malherbae* Nuzzaci), imported from Greece in 1989, has proven to be effective in controlling field bindweed infestations in some parts of Texas and Oklahoma, and can survive repeated mowing. The mite attacks the plants by producing galls on the leaves, petioles, and stems that stunt new growth, deform the leaves, and limit seed production.

Puncturevines (*Tribulus terrestris* L. and *T. cistoides* L.) are annual and perennial herbaceous plants, respectively, native to the Mediterranean region and Africa. In the 1960s, these two adventive weeds were serious pests of croplands and pastures primarily in arid regions of the southwestern United States and Hawaii. Puncturevines were not only invasive but produced spiny burs, capable of penetrating tires, that were injurious to livestock. Two weevils imported from Italy, a stem borer [*Microlarinus lypriformis* (Wollaston)]; and a seed feeder [*M. lareynii* (Jacquelin du Val)]; gave complete control of both puncturevines in Hawaii, and provided substantial control of the annual species in many areas of the Southwest.

Three ragweeds that are native to North America are adventive species in the former Soviet Union where they have become invasive. One of these ragweeds (*Ambrosia artemisiifolia* L.) caused serious problems because it was infesting croplands and was difficult to control using conventional herbicides and cultural methods. A defoliating leaf beetle [*Zygogramma suturalis* (Fab.)]; obtained from Canada and the United States, was released in the former Soviet Union in 1978. This leaf beetle built up enormous populations and provided complete control of this ragweed under certain conditions. On one farm, yields of alfalfa, sainfoin and corn increased dramatically as the beetles completely destroyed all the ragweeds in the infested fields.

More recently, the invasion of natural and conservation areas by immigrant plant species or introduced ornamental plants that have escaped cultivation has generated considerable interest in classical biological control as a weed management tool. Invasive weeds of natural areas have been called "biological pollutants." Unlike other forms of environmental pollution whose effects are reversible once the source of the pollution is removed, invasive weeds pollute the environment after they become established by continuing to proliferate and spread causing potentially irreversible ecosystem damage. Incipient populations of adventive weeds often are indistinguishable from the native flora, and they usually avoid detection until severe ecological harm already has occurred. Eventually, these invasive natural area weeds change the landscape by displacing more desirable native plant species, altering fire regimes, increasing soil erosion, contributing to the loss of wildlife habitat, causing some plants and animals to become rare or endangered, and diminishing the aesthetic value of recreational areas. In some cases, invasive natural area weeds even cause human health problems.

Biological control offers an attractive alternative to conventional chemical and mechanical control methods that are too costly and damaging to the environment, especially on large tracts of public lands set aside for nature preserves as well as state and national parks. Some recent examples of successful biological control programs against invasive weeds of agricultural as well as natural areas are listed on p. 305. Although it has not been confirmed, there is every indication that insects introduced into Florida from Australia for biological control of melaleuca (*Melaleuca quinquenervia* (Cav.) S. T. Blake) are contributing to the successful integrated management of this invasive wetland tree weed that is threatening the ecology of the Florida Everglades

► Foreign Exploration for Insects That Feed on Weeds
► Host Specificity of Weed-Feeding Insects
► Classical Biological Control

References

Bellows TS, Fisher TW (eds) (1999) Handbook of biological control. Academic Press, San Diego, CA

Julien M, White G (eds) (1997) Biological control of weeds: theory and practical application, ACIAR Monograph No. 49. ACIAR, Canberra, Australia

Julien MH, Griffiths (eds) (1998) Biological control of weeds: a world catalogue of agents and their target weeds (4th ed). CABI Publishing, New York, NY

Luken JO, Thieret JW (eds) (1997) Assessment and management of plant invasions. Springer, New York, NY

McFadyen REC (1998) Biological control of weeds. Annu Rev Entomol 43:369–393

Spencer NR (ed) (2000) Proc X Int Symp Biol Cont Weed, Bozeman, Montana, USA, 4–14 July 1999. United States Department of Agriculture, Agricultural Research Service, Sidney, Montana, and Montana State University, Bozeman, MT

Biological Insecticides

Insecticides made with insect pathogens that are formulated to be applied like conventional chemical insecticides.

► Insecticides
► Microbial Control of Insects

Biology

The study of life. This is an "umbrella" term that includes all aspects of the study of life, including biochemistry, genetics, and taxonomy. Some taxonomic texts include a section with heading "Biology" under which the authors assemble information about behavior and natural history, as if taxonomy were somehow not part of biology.

Bioluminescence

Light produced by living organisms from a chemical reaction, usually involving the protein luciferin and the enzyme luciferase.

► Fireflies
► Fireflies: Control of Flashing
► Glowworms

Biomagnification

Increase in the concentration of a persistent chemical along a food chain, with the top-level predators accruing the highest concentration. Biomagnification is of special concern with long-lived pesticides, which can be retained in fat tissues rather than being excreted. Biomagnification is also known as biological concentration and food chain concentration.

► Biological Amplification

Biomass

The mass of a living organism of a defined type and from a defined area. Biomass, often expressed as dry weight, is used to estimate abundance and to ameliorate the differences between a few large individuals and many small ones.

Biome

A large ecological unit or ecosystem defined by vegetation, climate, and geography, though a biome can be found in more than one place. Examples of biomes are salt marshes and steppe regions.

Biopesticide

A product that consists of biological organisms, usually microbial agents or their products, for pest suppression. Biopesticides usually are applied as inundative or augmentative biological control agents.

►Microbial Control of Insects

Biorational Pesticides

Pesticides that are considered to be safe to humans or the environment, and based on microbial agents or naturally occurring chemicals (e.g., pheromones, hormones). Because these are based on chemical products rather than on living organisms, they are classified as chemical control rather than biological control.

►Pheromones
►Microbial Control of Insects
►Botanical Insecticides

Biosphere

The ecosystem that includes the entire earth.

Biosystematics

The branch of systematics (classification) in which the genetic and evolutionary relationships between taxa are investigated.

Biota

The species of plants and animals occurring within a defined area.

Biotechnology

The manipulation of organisms to provide desirable products. It has broader meanings, as well, including all parts of an industry that creates, develops and markets a variety of products through the molecular manipulation of organisms or using knowledge pertaining to the molecular biology of organisms. In pest management, it is the use of genetically modified organisms in the production of crops or animals, including in the production of insect-suppressive agents.

Biotic Disease

Disease caused by a pathogen, such as a bacterium, fungus, or virus.

Biotic Potential

The rate at which a species will increase in the absence of limits.

Biotic Release

The escape of a population from the regulatory effects of its natural enemies, resulting in a population increase or outbreak.

Biotope

An area of uniform environmental conditions occupied by a similar community. This term is most popular in Europe. It is essentially equivalent to "habitat," but although habitat is often used in conjunction with populations, biotope is used to describe a community.

Biotype

A race or strain of an organism that differs in some way from the principal population, often in susceptibility to a pesticide or in association with a food plant. In the case of host plant associations, such biotypes are sometimes called "host races."

Bipectinate

The presence of comb-like structures on opposing sides, usually used to refer to a form of antennae.

► Antennae of Hexapods

Bird and Rodent Fleas

Members of the family Ceratopsyllidae (order Siphonaptera).

► Fleas

Bird Cherry-Oat Aphid

► Wheat Pests and Their Management

Bird Lice

Members of the family Philopteridae (order Phthiraptera).

► Chewing and Sucking Lice

Bird Malaria

► Avian (Bird) Malaria

Birnaviruses

The family Birnaviridae contains three genera, the *Avibirnavirus* (infectious bursal disease of chickens), the *Aquabirnavirus* (infectious pancreatic necrosis virus of fish), and the *Entomobirnavirus* (*Drosophila X* virus). Birnaviruses are icosahedral viruses and lack a viral membrane. Characterized as medium-sized viruses (60 nm diameter), they encapsidate two segments (A, B) of linear dsRNA (total size 6–7 kbp). Unlike other dsRNA viruses (reoviruses), Birnavirus dsRNAs extracted from the viral capsid can serve as m-RNA; under in vitro conditions, the dsRNA molecules can bind to ribosomes and undergo translation. Segment A is polycistronic and codes for three gene products, whereas segment B is monocistronic and codes for one gene product.

The *Drosophila X* virus (DXV), the type species of the *Entomobirnavirus*, was discovered initially as a contaminant in insect cell lines. Sequence analysis of DXV has revealed that segment A contains two open reading frames (ORFs) consisting of a 3096 bp and 711 bp sequence. The 3096 bp ORF codes for the 114 kDa polyprotein which is processed post-translationally by virus-encoded protease to generate VP-2, VP-3, and VP-4. In most birnaviruses, the second ORF codes for a small, arginine-rich peptide. Segment B encodes for VP-1 putative viron associate RNA polymerase. DXV is polytropic and can replicate in the cytoplasm of both the mesodermal and epidermal cells of *D. melanogaster*. DXV replication results in extensive lysis of *Drosophila* cells within 26 h. Surviving cells maintain DXV in a repressed form (they are persistently infected) and are immune to a second challenge with DXV. Laboratory colonies of *D. melanogaster* infected with DXV exhibit anoxia sensitivity and do not recover after being anesthetized with CO_2 or N_2.

References

Chung HK, Kordyban S, Cameron L, Dobos P (1996) Sequence analysis of the bicistronic *Drosophila X* virus genome segment A and its encoded polypeptides. Virology 225:359–368

Nagy E, Dobos P (1984) Synthesis of *Drosophila X* virus proteins in cultured Drosophila cells. Virology 134:358–367

Bíró, Lajos

George Hangay
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Lajos Bíró was born on the 29th of August 1856 in Tasnád, Szilágy Shire, in Transylvania, (which was then part of Hungary). He was the sixth child of a poor cabinetmaker. His father wanted him to become a woodworker also, but young Lajos had a keen interest in natural history. Thanks to his teacher, Ferenc Török, he became quite an expert in insect collecting and various other zoological preparation techniques. From an early age he longed for the tropics but coming from a poor family and living in land-locked Hungary, he could only dream about exotic countries and the exploration of their zoological wonders. To satisfy his ambitions in discovery and research, he built an extensive insect collection of Hungary and adjacent lands. To become a university student was out of the question because of the family's financial circumstances. The only way for him to obtain some sort of a tertiary education was to become a priest. He attended Protestant Theology – but only for two years, as he couldn't develop a deep religious belief and became a teacher. From his meager earnings he tried to save up for a tropical journey. At the same time his reputation as an entomologist grew and eventually he gained government employment as grape phylloxera inspector/consultant at the Entomological Institute in Budapest. The tragic death of Samuel Fenichel prompted Bíró to take important steps towards the realization of his childhood dreams: to grasp the emerging opportunity and embark on a journey to New Guinea. To obtain the necessary financial support, he sold his collection of over 20,000 specimens to the Hungarian National Museum and secured an agreement with its management for the purchase of the material he was to collect during the expedition. He left Hungary on the 7th of November 1895 and arrived to Friedrich-Wilhelmshafen (today Madang) in Kaiser Wilhelm Land or German New Guinea (today Papua New Guinea) on the 1st of January 1896. During the following 6 years, Bíró relentlessly worked towards his goal to explore as much as possible of New Guinea's insect fauna. He was a very ambitious and prolific collector. His activities were not restricted to insects alone as he also collected other zoological and ethnographical specimens as well. The total number of his New Guinean zoological collections exceeded 200,000 specimens, while the ethnographical objects numbered over 6,000. These collections are still not fully processed yet, although its study by many researchers, including Bíró himself, generated over 100 papers, describing 2,000 species new to science. After his New Guinean years, Bíró continued his work as an entomologist, mainly focusing on Hymenoptera and Coleoptera. His greatest strength was evident in the field, where his acute sense of observation and excellent collecting methods yielded valuable information and great numbers of specimens. He has conducted fieldwork in many European locations, including Turkey, Bulgaria, Crete, etc., and he was commissioned by the British Royal Geographical Society to train young zoologists in India and Burma. In recognition of his achievements, in 1926 he was awarded an honorary doctorate by the Ferenc József University of Science in Szeged (Hungary). Fellow workers named about 150 newly described species after him. He passed away in 1931 at the age of 75. Bíró is considered today as one of the most outstanding Hungarian field entomologists, who unselfishly served his nation and his science.

Reference

Balogh J, Allodiatoris I (1972) In Memoriam Lajos Bíró and Sámuel Fenichel. Acta Zool 42:1–2, Budapest, Hungary

Bisexual

The occurrence of males and females in different members of the species.

Biting Midges, *Culicoides* spp. (Diptera: Ceratopogonidae)

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Culicoides is the most important of four genera of the family Ceratopogonidae which feed on the blood of vertebrate animals. *Culicoides* includes more than 1,400 named species, and at least 50 are thought to be vectors of disease, spreading pathogens to man and animals.

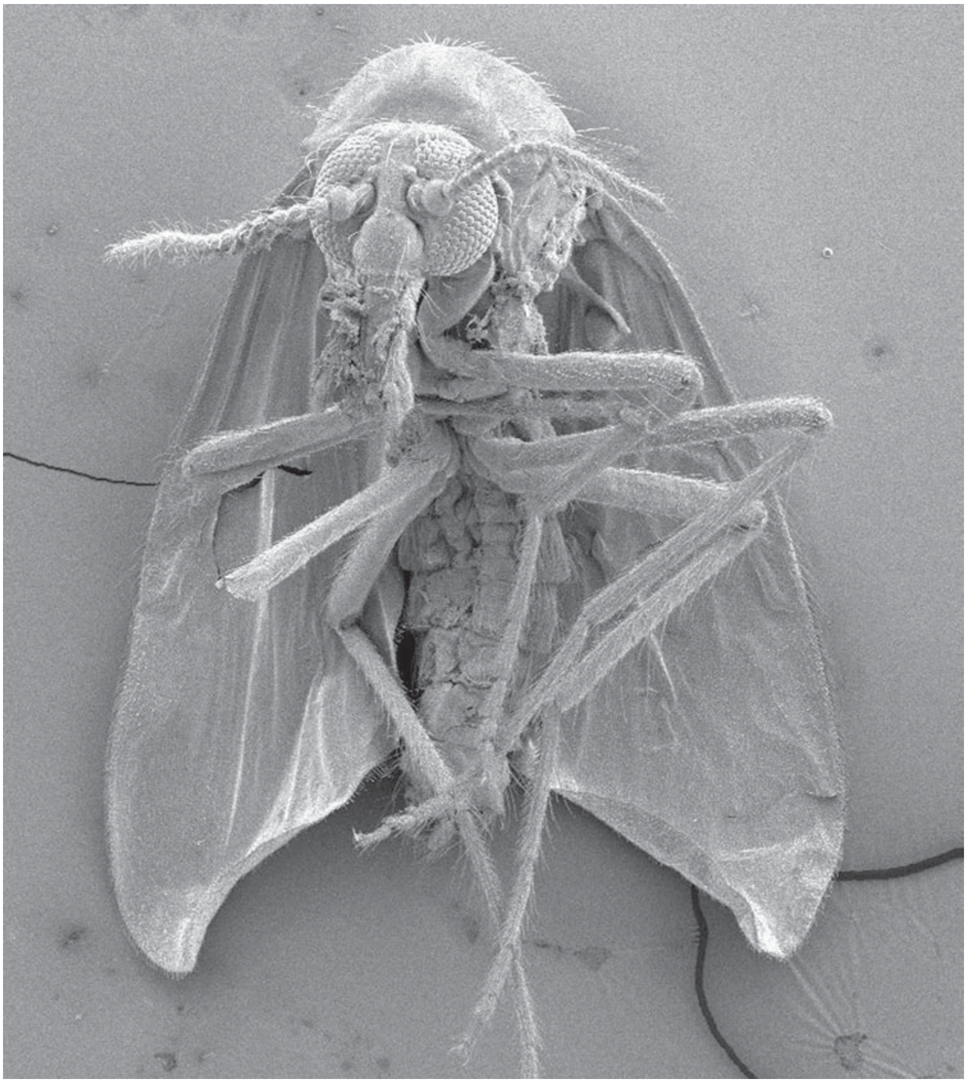
Classification and Recognition

Order: Diptera
Suborder: Nematocera
Infraorder: Culicomorpha
Superfamily: Chironomoidea
Family: Ceratopogonidae
Subfamily: Ceratopogoninae
Tribe: Culicoidini
Genus: Culicoides

The Ceratopogonidae as a whole is a family of small nematocerous flies, 2–4 mm in length with a wingspan of usually less than 2 mm. Although closely related to the non-biting midges, or Chironomidae, they are easily distinguished by the female's biting mouthparts, their short fore legs and characteristic venation on their membranous wings. They are most commonly known as "biting midges" but there are numerous geographical variations, including "sandflies," "punkies," "no-see-ums," "no-nos," "moose-flies" and "biting gnats." Some names are particularly expressive, for example, the Gaelic name for the Scottish Highland midge is *Meanbh-chuileag* (tiny fly) emphasizing its diminutive, 1.4 mm wingspan.

Culicoides are some of the smallest ceratopogonids, 1–2 mm in length, partly distinguishing them from the other blood-feeding genera (*Leptoconops*, *Austroconops* and the subgenus *Lasiohelea* within the genus *Forcipomyia*). The small head has a large pair of compound eyes in addition to five-segmented maxillary palps, which are outside of the short set of sucking and piercing mouthparts (in the female), held perpendicular to the body axis. There is also a prominent pair of segmented antennae, with long mechanoreceptors on the male antenna, giving it a feathery appearance. The dorsal thorax (mesonotum) is frequently covered in a distinctive pattern of dark spots or other markings, accompanied at the proximal end by a pair of small, elongate "humeral pits," distinguishing *Culicoides* from other genera. The body is generally a variation of brown or black, but some species are yellowish-brown/orange (Fig. 45).

The wings of *Culicoides* are often an immediate identification feature for the amateur, with the majority (but not all) having a series of dark and pale spots covering the wings, which are folded, scissor-like at rest or when feeding. Other genera, such as *Austroconops*, lack any pattern on their wings. The wings have been a major taxonomic feature of the Ceratopogonidae, with a number of admirable works detailing the degree and pattern of venation, wing color and markings, and the degree of coverage by macrotrichia, which are fine, short hairs that often cover the wing surface (Fig. 46).



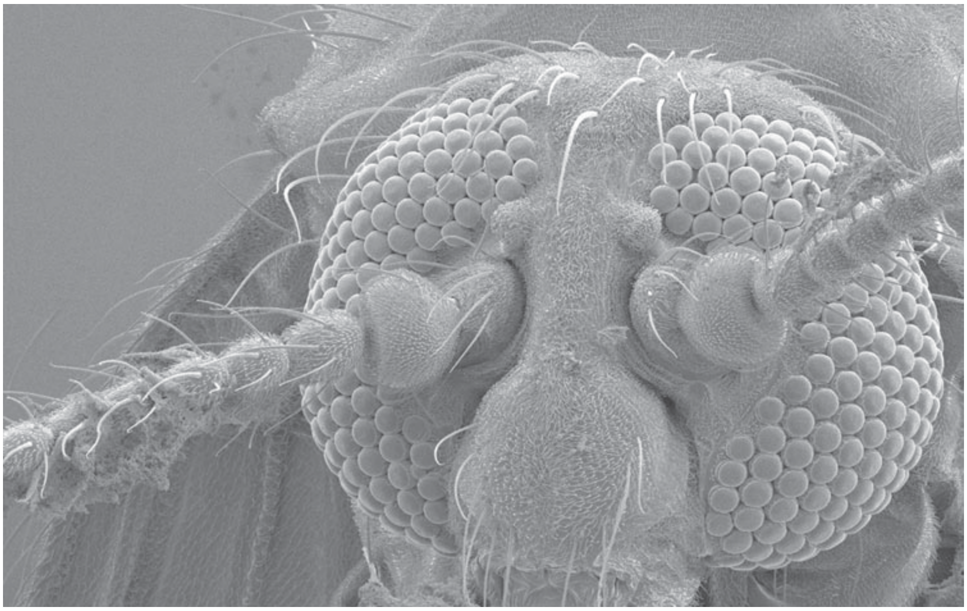
Biting Midges, *Culicoides* Spp. (Diptera: Ceratopogonidae), Figure 45 **Female *Culicoides nubeculosus*.**

In addition to the wing characteristics, further identification to species is best carried out from slide-mounted specimens. For example, the third segment of the maxillary palp contains a large pit containing palpal sensilla. Some species have small pits, each bearing individual sensilla. These sensilla are generally considered to be concerned with carbon dioxide (and hence host) detection in the female midge, with smaller numbers found in the non-blood-feeding male. The shape and size of the palpal pit, and the numbers of sensilla are often used as taxonomic tools. Likewise, the antennal sensilla are pivotal to species identification. The antenna consists of a small, flattened ring with a triangular apex (the "scape"), a globular, cup-shaped pedicel, which is enlarged in the male antenna to accommodate a well-developed Johnston's organ and the antennal flagellum, having 13 sub-segments. *Culicoides* antennae bear approximately 300–350 (male) and 200–250 (female) sensilla. Of greatest importance to the taxonomist is the number and positions of the sensilla coeloconica and sensilla trichodea. Further taxonomic detail can also be gained from both the male and female genitalia. More recently, species differentiation has been carried out by molecular techniques, particularly species complexes, such as the *C. imicola* complex, where subspecies differentiation can be difficult using morphological features alone (Figs. 46 and 47).

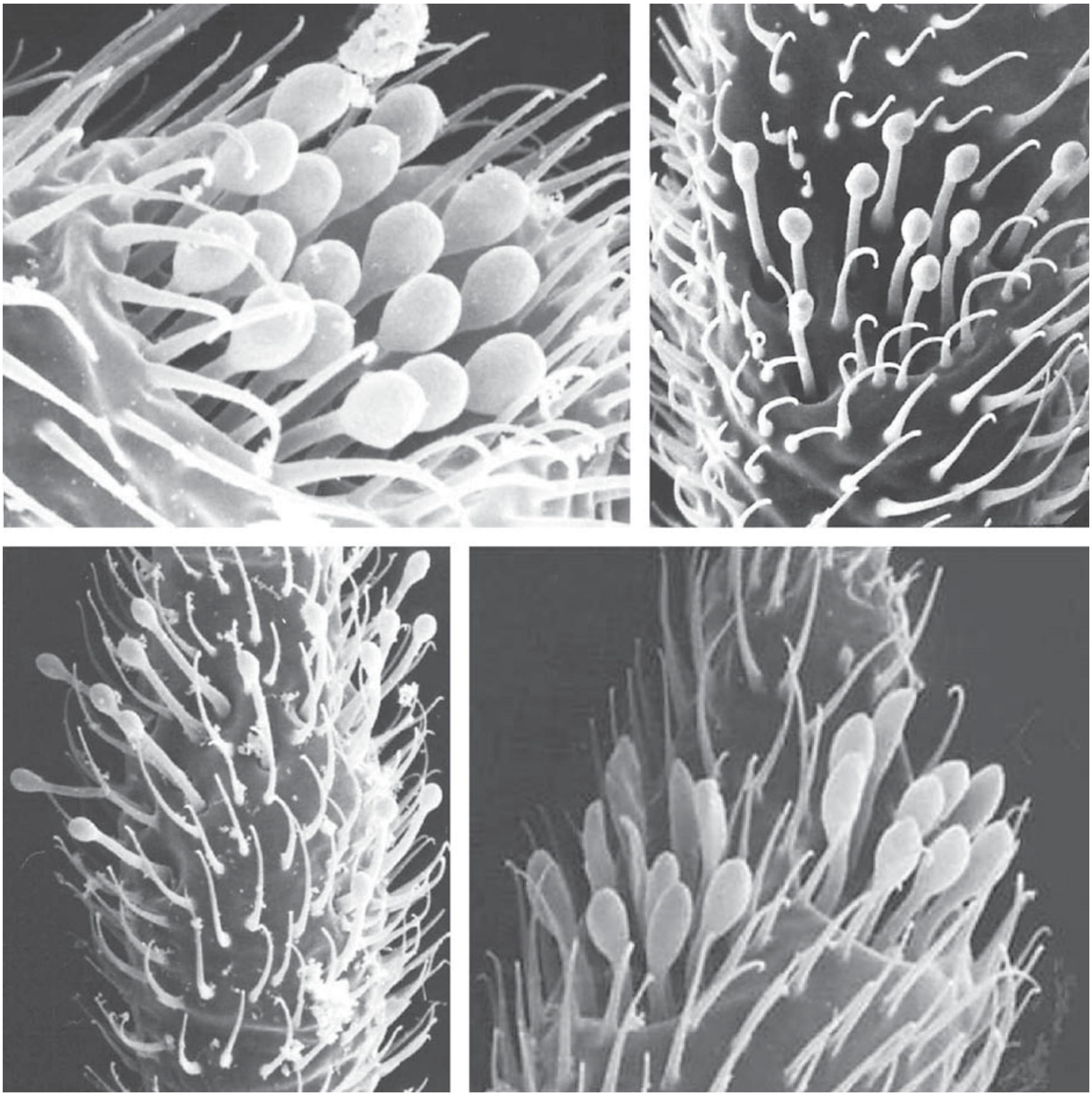
Culicoides larvae are aquatic/semi-aquatic and swim with a distinctive eel-like motion. They are found in a variety of environments, such as mud, salt-marsh, compost and leaf litter. Some of the most important veterinary species breed in damp ground contaminated to a degree with animal excreta and other organic matter. The slender larvae are primarily pale, sometimes with thoracic markings. The pharyngeal skeleton of the sclerotized head capsule is a key taxonomic feature.

Distribution

Culicoides are the most widespread of the Ceratopogonidae, occurring throughout the world, with the exception of the polar regions. The only large inhabited land masses from which they are known to be absent are New Zealand and the southern most areas of South America.



Biting Midges, *Culicoides* Spp. (Diptera: Ceratopogonidae), Figure 46 **Female *Culicoides nubeculosus* showing separated compound eyes.**



Biting Midges, *Culicoides* Spp. (Diptera: Ceratopogonidae), Figure 47 ***Culicoides*** **spp. maxillary palp, 3rd segment, showing different arrangements of the palpal sensilla: upper left, *C. insinuatus*; upper right, *C. nubeculosus*; lower left, *C. impunctatus*; lower right *C. pseudodiabolicus*.**

Ecology and Behavior

Life Cycle and Population Dynamics

The cylindrical or cigar-shaped *Culicoides* eggs (30–200 per batch) are laid on the chosen substrate surface, where they hatch (2–10 days depending on temperature) and the larvae move down into the substrate, where they live as omnivores/detritivores. The larvae commonly remain close to the substrate surface. In Scotland, more than 50% *Culicoides impunctatus* larvae have been recovered from the top two cm of the soil surface. *C. impunctatus* appears to show a weak photonegative response, with a greater proportion in deeper samples during the day than at night. This daily migration is far more marked in *Culicoides furens* larvae, which live in the muddy banks of mangrove channels. With vegetation often sparse, predation by birds is a serious threat during the daylight hours, perhaps explaining the fact that larvae feed on algae at the mud surface during the night and on nematodes deeper down in the mud during the day. In addition to a vertical component, the spatial distribution of *Culicoides* larvae also appears to have a horizontal component. Even in apparently homogeneous environments such as the Scottish Highlands, *Culicoides* larval distribution can be directly correlated with soil conditions (water and organic content) and key indicator plant species. A similar situation is seen with the salt-marsh species *Culicoides melleus*, with larval distribution related to soil pH and areas of *Distichlis spicata* (Gramineae).

There are four larval instars, and the time required for larval development varies with temperature. Development may be completed in 14 days in warmer areas, with up to seven generations produced each year. In more temperate regions, this is reduced to one or two generations with the final larval instar often acting as the over-wintering stage, although some species will aestivate as eggs. In Scotland, the over-wintering period for *Culicoides* lasts for up to 9 months, followed by two adult generations during the summer. The pupal period lasts between 2 and 10 days.

Nightly trapping program can reveal significant information on the structure of *Culicoides* populations, including autogeny (e.g., females laying their first egg batch without taking a bloodmeal), protandry (e.g., males emerging before females), in addition to reproductive and survival rates, themselves allowing the calculation of a species' vector competency (e.g., the likelihood of it being able to transmit a disease pathogen). In association with climate data, it is possible to construct models of the influence of a range of climatic conditions on midge flight and biting activity.

Records of midge dispersal rates vary enormously. Whereas male midges appear to remain close to emergence sites, host-seeking females may move several kilometers from a breeding site. One report suggests that *Culicoides mississippiensis* travels more than 3 km in 24 h, without wind assistance. When wind carriage does become important, midges can travel considerable distances and increasing evidence suggests that disease outbreaks in areas where particular *Culicoides*-transmitted diseases are not endemic may start in this way. For example, the outbreaks of bluetongue virus in Sardinia in 2000 and 2001 may have been caused by infected midges carried on the wind from Northern Africa.

Mating Behavior

Mating in *Culicoides* spp. has been studied for only a small number of species, and despite the general hypothesis that mating is initiated in male swarms (as in many other nematocerans), there are only a few records of *Culicoides* spp. swarms (including *Culicoides nubeculosus* and *C. impunctatus*). Since the conditions required for male swarming (still, warm and humid) can be rare in some temperate regions, it has been suggested that for species living in these areas (e.g., *C. impunctatus* in Scotland), at peak emergence periods it may be energetically more profitable for males to wait in the vegetation for emerging females, i.e., some species may be facultative swarming species. Male swarming can be stenogamic (swarming adjacent to hosts on which females are feeding) or eurygamic (no host involved), depending on the species. Distance and contact sex pheromones have been implicated in the mating of *C. nubeculosus* and *C. melleus*, respectively. Both of these species have been the subject of detailed studies of the mating process, including mate "selection" by the female, spermatophore formation and sperm transfer.

Host Finding and Feeding Behavior

In addition to a bloodmeal, which is necessary for female *Culicoides* to develop their eggs (including all egg batches laid after the first batch by autogenous species), a carbohydrate source is also important for most species. Direct evidence of sugar feeding in the field, however, is rare. The small number of published records include *C. mississippiensis* feeding from flowers of yaupon holly plants (*Ilex vomitoria*) in Florida.

The majority of *Culicoides* show some degree of host preference and this has been investigated by a number of different techniques, including precipitin tests, fluorescent antibody tests, latex agglutination tests, ELISA tests and most recently, DNA analysis by PCR. These tests help to refine the definition of a particular species such as, for example, ornithophilic (bird-feeding) or mammalophilic (mammal-feeding). Many species show further specialization within these broad classes. For example, using an ELISA assay, single, blood-fed *C. impunctatus* were screened against nine different potential bloodmeal hosts. The results showed that cattle, deer and sheep were the primary hosts for this species.

Culicoides spp. biting midges have a highly sensitive olfactory system, which is used in combination with other senses to locate their bloodmeal hosts accurately. The olfactory system is based around the antennae and maxillary palps, the morphology and ultrastructure of which has been fully documented for a number of species. Recent studies have used antennal responses as a screening tool to identify behaviorally active compounds. This has involved the development of electrophysiological techniques, in particular the recording of electroantennograms (EAGs) which, combined with behavioral studies and field trapping programs with active compounds, has led to the identification of several semiochemicals involved in the host location behavior of *Culicoides* spp. For mammalophilic species, one ubiquitous host-derived attractant is 1-octen-3-ol, with others including acetone, butanone and L(+) lactic acid. Responses to each of these can be either enhanced or synergized by the addition of carbon dioxide. For one species, *C. impunctatus*, there is evidence of pheromone involvement in host-seeking, with the production of a volatile "recruitment" pheromone by parous, host-seeking females, possibly analogous to the invitation pheromone of some mosquito species. Variations in these chemical cues between individuals may account for some degree of intra-species selection by *Culicoides*.

Visual cues are also important in bloodmeal host location by a range of blood-feeding insects including both diurnal and crepuscular species. *Culicoides* spp. appear to be no exception. Field populations of *C. impunctatus* in Scotland were attracted to solid-outlined, black, rectangular targets and this response was enhanced in the presence of CO_2.

Culicoides are "pool-feeders," using their finely toothed mandibles and maxillae to pierce the skin, working in a scissor-like fashion to create a pool of blood from which the insect feeds. Prior to this behavior, however, some midges display a degree of choice concerning the area to feed from. This appears to be particularly the case with large hosts, including cattle and horses. The size of the *Culicoides* bloodmeal has been estimated at 4×10^{-2} ml, with a process of rapid diuresis acting to concentrate the blood.

Biting Behavior: Implications for Man and Animals

Disease Transmission

Culicoides spp. biting midges are most important as vectors of a number of serious livestock pathogens, including African horse sickness virus and bluetongue virus (which cause OIE list "A" diseases in their equine or ruminant hosts), bovine ephemeral fever virus (which significantly reduces milk yields in cows and causes sterility in bulls), Akabane virus (which causes abortions and congenital deformities in ruminants), Palyam viruses (which cause abortion storms in cattle) and epizootic hemorrhagic disease of deer virus (which kills many species of deer and also causes disease in cattle). Each of these diseases has an established distribution, intricately linked with that of its vector. There are, however, increasing examples of disease incursions into areas previously unaffected, perhaps as a result of relaxations in international trade barriers, and a trend toward more favorable climatic conditions in these areas. For example, bluetongue virus (BTV) occurs as a clinical disease in Africa, the Middle East, the Indian subcontinent, China, the USA, and Mexico where *Culicoides* are active throughout the year. In December 1999, and January 2000, a BTV serotype 2 epidemic occurred in Tunisia, close to the Algerian border. This was the first time the disease had been reported from North Africa. Further outbreaks followed in June 2000, matched by outbreaks in contiguous coastal areas of neighboring Algeria. From there it appears that infected vectors carried bluetongue to Europe, with outbreaks reported by Italy (August: Sardinia, November: Calabria and Sicily), France (October: Corsica, for the first time) and Spain (October and November: Balearic Islands, last infected in 1960). Although there are only a small number of confirmed vectors for BTV (*Culicoides variipennis* and possibly *Culicoides insignis* in the New World, *Culicoides imicola* and possibly *Culicoides obsoletus* in the Mediterranean and Middle East and *C. imicola* and members of the *Culicoides milnei* and *Culicoides schultzei* groups in Africa), laboratory infections have demonstrated that a number of endemic species in officially unaffected countries will support virus multiplication following infection.

Culicoides spp. also transmit a number of protozoans, most of which are avian parasites (*Haemoproteus*, *Hepatocystis* and trypanosomes). In addition, they transmit a variety of filarial worms (including *Onchocerca* spp.), infecting a range of animals, including birds, cattle and horses.

Overall, pathogen transmission to man by biting midges appears to be minimal, although they do transmit several species of filarial worms in tropical and sub-tropical regions (e.g., *Mansonella ozzardie*, transmitted by *Culicoides phlebotomus* in coastal North Trinidad) and a small number of viruses, including Oropouche, which is strongly pathogenic to man in parts of South America and the West Indies.

Animal Welfare

The general irritation caused by midge bites can occasionally also lead to serious health and welfare conditions in both animals and man. Deer herds are often forced off low-lying pastures onto higher, poorer slopes by midge attacks, which has been suggested as the reason why Scottish red deer are weaker than their European counterparts. The distress caused by midges to cattle is also held to be responsible for reductions in milk yields. Horses can also suffer from a number of allergic reactions to midge bites, including "sweet itch" (also known as "Queensland itch" in Australia and "kasen" in Japan), which is an acutely irritating dermatitis, primarily confined to the mane and tail, although it may spread to the rest of the body. The horse's skin becomes thickened, weals and pustules form, and much of the hair of the mane and tail breaks off or is rubbed off, resulting in extensive damage and large sores in addition to financial loss. Causal agents have been identified as *Culicoides pulicaris* (UK), *C. obsoletus* (Canada), *Culicoides robertsi* (Australia), *C. imicola* (Israel) and *Culicoides insignis*, *Culicoides stellifer* and *Culicoides venustus* (USA). Present methods of prevention include judicious stabling during the summer months and a range of antihistamine, cortisone injections and soothing ointments.

Human Annoyance

It is the biting attacks on humans, however, for which midges are most noted in a number of areas, including the Caribbean, California, Florida and Scotland. The annoyance and discomfort they cause can influence outdoor activities significantly and directly affect the local economies, particularly when they rely heavily on tourism. When bitten, the skin reaction of humans is usually mild, including temporary burning and slight swelling. More sensitive individuals, however, can develop weals, blisters and extreme inflammation of the skin. In a very few cases, extreme allergies can lead to hospitalization. Scarring and secondary infection may occur if bites are scratched.

Control

Culicoides control programs have often been met with difficulties, due to a number of factors. These include the fact that their breeding grounds are often widely scattered, difficult to recognize and often within environmentally sensitive areas, thereby limiting the application of control products. The vast populations of adult midges and their extreme mobility and potential for wind-carriage also places limits on the use of chemical control of adults.

Chemical Control

Culicoides spp. are susceptible to the majority of the major insecticide classes and most have been used at some stage against both adults and larvae, with varying degrees of success. Due to the difficulty of targeting adult midges, chemical control programs have concentrated primarily on the larval stages. Early studies (from the 1950s to the 1970s) involved the broadcast application of a number of persistent and broad-spectrum insecticides, including members of the organochlorines (e.g., DDT) and organophosphates (e.g., chlorpyrifos). Although partly successful, today's knowledge of the significant environmental and health risks associated with these products, as well as the potential for the development of resistant strains from such wide applications of broad-spectrum insecticides, precludes their use. Similar concerns are also associated with the use of pyrethroids, investigated for *Culicoides* larval control in the 1980s with populations of *C. varipennis* and *C. mississippiensis* in the USA. For these reasons, alternative larvicides based on naturally occurring products, for example, neem-based products, are being investigated following the growing trend toward integrating botanical products into insect pest-control programs.

Insecticide treatments of adult *Culicoides* have met with less success than larvicidal programs. A number of programs in the 1950s and 60s were based on thermal insecticide fogging, but the results were disappointing, most probably because the insects avoided contact with the insecticide by hiding beneath vegetation. In addition, there is the likelihood that a sprayed area would be reinvaded as soon as the insecticidal mist had cleared, requiring regular (and expensive) re-treatment.

Where *Culicoides* are responsible for outbreaks of livestock disease, direct treatments of the animals with insecticides (e.g., pyrethroids and ivermectin) have been partially successful. Under serious virus challenge conditions, however, permethrin failed to protect cattle from bluetongue virus infection in a Californian dairy.

Habitat Manipulation

Biting midge problems world-wide have been partly alleviated through a variety of measures aimed at altering the suitability of areas for both adult and larval midges. An example is the impounding or flooding of areas in Florida and the Caribbean to eliminate breeding sites of midge larvae which cannot survive in free-water. Alternative strategies have included draining or land-filling breeding sites in salt marshes in Florida to make them too dry for midges to breed. There are various other environmental manipulations, such as stream flushing and shade removal, which are in widespread use in the tropics to control mosquitoes. Such measures have never been used in more temperate regions. In fact, it has been suggested that it is doubtful that any attempt to alter the landscape of localized areas would, in the long term, be successful against biting midges in Scotland. Considering the relatively high mobility of these insects and the vast areas of potential breeding grounds, this is probably true. Additionally, these methods are often extremely expensive, laborious and although they may make the environment less suitable for *Culicoides*, they frequently destroy the habitats of other, non-target organisms.

Repellents

The use of personal repellents can give a degree of protection against biting midges and indeed, this is generally assumed to be the best line of defense. In addition, repellents can be used to treat windows and door screens and even clothing. A range of chemical repellents, in various formulations sold under a number of different trade names, are currently available. The most widely used chemical in insect repellents is DEET (N,N-diethyl-m-toluamide), forming the main active constituent in the majority of over-the-counter preparations, with concentrations varying from 10% to 90%. Since it was first marketed in 1956, DEET has remained the most effective repellent against midges, mosquitoes and other biting pests, although there have been a number of concerns voiced regarding its safety, including a suggested contribution of DEET usage to the psychological effects associated with a number of combat situations. Although DEET toxicity from casual use is thought to be low and there are no definite reports that these products are not safe if used correctly and sensibly, for those people preferring "natural" products, there is no limit to the number of herbal concoctions marketed as insect repellents. These include oils distilled from a range of plants, including lemon-grass, eucalyptus, cypress, lavender, pennyroyal and thyme. A common factor for most of these is that they contain a number of terpenoid compounds, such as citronellal and limonene. There are a number of regional "favorites." For example, in Scotland, the oil derived from the leaves of *Myrica gale* (bog myrtle, sweet gale – Myricaceae), a deciduous shrub that grows widely in the Highlands of Scotland, has repellent properties equivalent to DEET against *Culicoides* spp. In North America, even the US military consider the use of 'Avon Skin-So-Soft'®, as an alternative to DEET to protect them from biting insects.

Traps

Traps are used mainly as population monitoring devices for *Culicoides* spp., although over limited areas, they can offer a degree of control. Traps vary from basic light-suction traps (with blacklights attracting more than whitelights), to more specialized, odor-baited traps. The latter resulted in increased and more specific *Culicoides* spp. catches. Carbon dioxide (often released from a dry ice source) provides the most impressive increase in catch size, although its attractiveness can be enhanced in combination with some of the host-related kairomones that are gradually being identified for *Culicoides* spp. For example, some commercial traps use a combination of carbon dioxide and 1-octen-3-ol.

Biological Control

The possibility of employing biological control techniques for the control of *Culicoides* spp. has been little studied. Predators, parasites and pathogenic microbes suspected of being natural control agents of *Culicoides* spp. were recorded by Bacon in 1970, including viruses, rickettsiae, bacteria, fungi, protozoa and nematodes. Few, however, have been identified and studied in relation to potentially reducing biting midge populations. Nematodes of the family Mermithidae are known to be fatal parasites of Ceratopogonidae larvae, but have been found in only a few species, including *C. variipennis* in dairy wastewater ponds in California. The only report of a fungal pathogen of *Culicoides* spp. is for *Culicoides molestus* larvae in New South Wales, Australia, in which infection rates with the Oomycete Lagenidium giganteum of 1–62% were recorded. Concerning microbial insecticides, *Culicoides* spp. are virtually unaffected by commercial applications used frequently against mosquito larvae, including *Bacillus thuringiensis var israelensis* and *Bacillus sphearicus*.

Ceratopogonid midge species are regularly infested with a variety of ectoparasitic mite species. In particular, adult *Culicoides* have been found carrying phoretic instars of several families of mesostigmatid mites and ectoparasitic larvae of the prostigmatid superfamily Trombidioidea. The trombidioids are of additional interest because, in their free-living adult stage, some species have been seen feeding on larval ceratopogonids. The precise impacts of these mites on their hosts, however, is unknown. Information is lacking on the basic biology of these mites, their precise trophic relationships and perhaps their potential as vehicles and vectors of candidate insect pathogens.

References

Blackwell A (2001) The Scottish biting midge, *Culicoides impunctatus.* Goetghebuer: current research status and prospects for future control. Vet Bull 71:2R–8R

Boorman J (1993) Biting midges (Ceratopogonidae). In: Lane P, Crosskey RW (eds) Medical insects and arachnids, 723 pp. Chapman & Hall, New York, NY, pp 288–309

Sebastiani F, Meiswinkel R, Gomulski LM, Guglielmino CR, Mellor PS, Malacrida AR, Gasperi G (2001) Molecular differentiation of the old world *Culicoides imicola.* species complex (Diptera, Ceratopogonidae), inferred using random amplified polymorphic DNA markers. Mol Ecol 10:1773–1786

Biting Rate

This is a measure of abundance of biting insects, and is expressed as number of bites per person per period of time. It is usually used in the assessment of mosquito abundance, and rather than have the insects actually bite before they are tabulated, the insects are typically captured pre-feeding, thereby alleviating stress to the census taker, and alleviating the risk of disease transmission. Under these conditions, then, it is actually the insect landing rate that is being measured, and used as an index of the potential biting rate. Biting rate is also used as a component of insect repellent assessment.

Bittacidae

A family of insects in the order Mecoptera. They commonly are known as hangingflies. Scorpionflies.

Bivoltine

The occurrence of two generation within a year.

Bivouac

Among army ants, the cluster of workers within which the queen and brood are sheltered.

Blaberidae

A family of cockroaches (order Blattodea).

► Cockroaches

Black Bean Aphid, *Aphis fabae* Scopoli (Hemiptera: Aphididae)

This is an important insect pest of several crops.

► Aphids

Blackburn, Thomas

Thomas Blackburn was born at Islington near Liverpool, England, on March 16, 1844. Ordained a deacon of the Anglican church in 1869, he was transferred to Hawaii in 1870. There, he collected insects of all orders. Next, he was transferred to Australia and became rector of a church at Port Lincoln in 1882, then one at Woodville near Adelaide, in 1886, which position he held for the rest of his life. In England, he and his brother J. B. Blackburn founded "The Weekly Entomologist" which, after two years, was renamed "Entomologist's Monthly Magazine" and is published to this day. In Australia, he collected beetles intensively, but specialized in Scarabaeidae. He became the foremost Australian coleopterist, and published descriptions of 3,069 Australian species. He died on May 28, 1912, at Woodville.

Reference

Herman LH (2001) Blackburn, Thomas. Bull Am Mus Nat Hist 265:45–46

Black Carpet Beetle, *Atagenus megatoma* (Fabricius) (Coleoptera: Dermestidae)

This is an important pest of stored products, including stored grain.

► Stored Grain and Flour Insects
► Stored Grain and Flour Insects and Their Management

Black Citrus Aphid, *Toxoptera aurantii* (Boyer De Fonscolombe) (Hemiptera: Aphididae)

This is an important pest of citrus crops.

► Citrus Pests and Their Management

Black Cutworm, *Agrotis ipsilon* (Hufnagel) (Lepidoptera: Noctuidae)

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The origin of black cutworm is uncertain, though it is now found in many regions of the world, being absent principally from some tropical regions and cold areas. It is more widespread, and damaging, in the northern hemisphere than the southern hemisphere. It annually reinvades temperate areas, overwintering in warmer or subtropical regions. It has acquired several other common names, including greasy cutworm and dark sword grass cutworm.

Long distance dispersal of adults has long been suspected in Europe, China, and North America. The basic pattern is to move north in the spring, and south in the autumn. Studies in the United States demonstrated northward displacement of moths during the spring in the range of 1,000 km in 2–4 days when assisted by northward flowing wind. Similar displacement to the south and southwest has been documented in the autumn.

Life History

The number of generations occurring annually varies with weather conditions. In North America, there are 1–2 generations in Canada but 2–4 in the United States. In Tennessee, USA, moths are present in March-May, June-July, July-August, and September-December. Based on light trap collections, moths are reported to be abundant in Arkansas, USA (a warm climate) during May-June and September-October, and in New York, USA (a cool climate), they occur mostly in June-July. However, light traps are not very effective during the spring flight, and underestimate early season. Thus, the phenology of black cutworm remains uncertain, or perhaps is inherently variable due to the vagaries associated with long range dispersal.

Overwintering has been reported to occur in the pupal stage in most areas where overwintering occurs, but larvae persist throughout the winter in Florida, USA, a subtropical environment. Pupae have been known to overwinter as far north as Tennessee, but apparently are incapable of surviving farther north. Thus, moths collected in the central region of USA in March and April are principally dispersing individuals that are past their peak egg production period. Nonetheless, they inoculate the area and allow production of additional generations, including moths that disperse north into Canada. Duration of the life cycle is normally 35–60 days.

The egg is white in color initially, but turns brown with age. It measures 0.43–0.50 mm high and 0.51–0.58 mm wide and is nearly spherical in shape, with a slightly flattened base. The egg bears 35–40 ribs that radiate from the apex; the ribs are alternately long and short. The eggs normally are deposited in clusters on foliage. Females may deposit 1200–1900 eggs. Duration of the egg stage is 3–6 days.

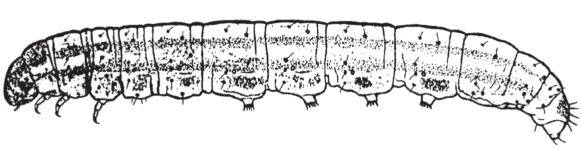
There are 5–9 instars, with a total of 6–7 instars most common. Head capsule widths are about 0.26–0.35, 0.45–0.53, 0.61–0.72, 0.90–1.60, 2.1–2.8, 3.2–3.5, 3.6–4.3, and 3.7–4.1 mm for instars 1–8, respectively. Head capsule widths are very similar for instars 1–4, but thereafter those individuals that display 8–9 instars show only small increments in width at each molt and eventually attain head capsule sizes no larger than those displaying only 6–7 instars. Larval body length is reported to be 3.5, 5.3–6.2, 7, 10, 20–30, 30–45, 50, and 50 mm for instars 1–8, respectively. Duration of the larval stage is normally 20–40 days. Mean duration of instars 1–6 was reported to be 6.0, 5.0, 4.6, 4.3, 5.6, 4.0 days, respectively, at 22°C. Larval development is strongly influenced by temperature, with the optimal temperature about 27°C. Humidity is less important, but instars 1–5 thrive best at higher humidities.

In appearance, the larva is rather uniformly colored on the dorsal and lateral surfaces, ranging from light gray or gray-brown to nearly black (Fig. 49). On some individuals, the dorsal region is slightly lighter or brownish in color, but the larva lacks a distinct dorsal band. Ventrally, the larva tends to be lighter in color. Close examination of the larval epidermis reveals that this species bears numerous dark, coarse granules over most of its body. The head is brownish with numerous dark spots. Larvae usually remain on the plant until the fourth instar, when they become photonegative and hide in the soil during the daylight hours. In these latter instars they also tend to sever plants at the soil surface, pulling the plant tissue belowground. Larvae tend to be cannibalistic.

Pupation occurs belowground at a depth of 3–12 cm. The pupa is 17–22 mm long and 5–6 mm wide, and dark brown. Duration of the pupal stage is normally 12–20 days.

The adult is fairly large in size, with a wingspan of 40–55 mm. The forewing, especially the proximal two-thirds, is uniformly dark brown (Fig. 48). The distal area is marked with a lighter irregular band, and a small but distinct black dash extends distally from the bean-shaped wing spot. The hind wings are whitish to gray, and the veins marked with

Black Cutworm, *Agrotis ipsilon* (Hufnagel) (Lepidoptera: Noctuidae), Figure 48 Adult of black cutworm, ***Agrotis ipsilon*** (Hufnagel).



Black Cutworm, *Agrotis ipsilon* (Hufnagel) (Lepidoptera: Noctuidae), Figure 49 Mature larva of black cutworm, ***Agrotis ipsilon*** (Hufnagel).

darker scales. The adult preoviposition period is about 7–10 days. Moths select low-growing broadleaf plants preferentially for oviposition, but lacking these will deposit eggs on dead plant material. Soil is an unsuitable oviposition site.

Black cutworm has a wide host range. Nearly all vegetables can be consumed, and this species also feeds on alfalfa, clover, cotton, rice, sorghum, strawberry, sugarbeet, tobacco, and sometimes grains and grasses. In the midwestern USA it is considered to be a serious corn pest. Among the weeds suitable for larval development are bluegrass, *Poa pratensis*; curled dock, *Rumex crispus*; lamb's-quarters, *Chenopodium album*; yellow rocket, *Barbarea vulgaris*; and redroot pigweed, *Amaranthus retroflexus*. The preference by black cutworm for weeds is sometimes quite pronounced, and crops will be attacked only after the weeds are consumed. Adults feed on nectar from flowers. Deciduous trees and shrub such as linden, wild plum, crabapple, and lilac are especially attractive to moths.

Numerous species of natural enemies have been associated with black cutworm, but data on their relative importance are scarce. However, in Missouri, USA, there are reports of 69% parasitism, so natural enemies probably exact a significant toll on cutworm populations. Among the wasps known to attack this cutworm are *Apanteles marginiventris* (Cresson), *Microplitis feltiae* Muesebeck, *Microplitis kewleyi* Muesebeck, *Meteorus autographae* Muesebeck, *Meterorus leviventris* (Wesmael) (all Hymenoptera: Braconidae); *Campoletis argentifrons* (Cresson), *Campoletis flavicincta* (Ashmead), *Hyposoter annulipes* (Cresson), and *Ophion flavidus* Brulle (all Hymenoptera: Ichneumonidae). Larvae parasitized by *Meteorus leviventris* (Wesmael) consume about 24% less foliage and cut about 36% fewer seedlings, so considerable benefit is derived from parasitism in addition to the eventual death of the host larva. Other parasitoids known from black cutworm include flies often associated with other ground-dwelling noctuids, including *Archytas cirphis* Curran, *Bonnetia comta* (Fallen), *Carcelia formosa* (Aldrich and Webber), *Chaetogaedia monticola* (Bigot), *Eucelatoria armigera* (Coquillett), *Euphorocera claripennis* (Macquart), *Gonia longipulvilli* Tothill, *G. sequax* Williston, *Lespesia archippivora* (Riley), *Madremyia saundersii* (Williston), *Sisyropa eudryae* (Townsend), and *Tachinomyia panaetius* (Walker) (all Diptera: Tachinidae). Predatory ground-dwelling insects such as ground beetles (Coleoptera: Carabidae) apparently consume numerous larvae. Although studies in Florida, USA, indicated that 75–80% of cutworms could be killed by a granulosis virus, there is surprisingly little information on epidemiology and of natural pathogens. Rather, such pathogens as viruses, fungi, bacteria, and protozoa from other insects have been evaluated for black cutworm susceptibility; in most cases only relatively weak pathogens have been identified. An entomopathogenic nematode, *Hexamermis arvalis* (Nematoda: Mermithidae), is known to parasitize up to 60% of larvae in the central USA.

Damage

This species occurs frequently in many crops, and is one of the best-known cutworms. Despite the frequency of occurrence, however, it tends not to appear in great abundance, as is known in some other cutworms and armyworms. Black cutworm is not considered to be a climbing cutworm, most of the feeding occurring at soil level. However, larvae will feed aboveground until about the fourth instar. Larvae can consume over 400 sq cm of foliage during their development, but over 80% occurs during the terminal instar, and about 10% in the instar immediately preceding the last. Thus, little foliage loss occurs during the early stages of development. Once the fourth instar is attained, larvae can do considerable damage by severing young plants, and a larva may cut several plants in a single night. Plants tend to outgrow their susceptibility to injury. Corn at the one-leaf stage is very susceptible to damage, but by the 4- or 5-leaf stage plant yield was not reduced by larval feeding. Leaf feeding and cutting above the soil line are less damaging to corn than cutting at the soil surface. Subterranean damage is very injurious.

Management

Adult populations can be monitored with both blacklight and sex pheromone traps. However, light traps are not consistently efficient. Light traps are most effective in the summer and autumn, but the late season generations generally pose little threat to crops. Pheromone traps are more effective during the spring flight, when larvae present the greatest threat to young plants. Trap color affects moth capture rate, with white and yellow traps capturing more than green traps.

Large larvae burrow in the soil, and are difficult to observe. However, larvae can be sampled with bait traps, and this is most effective prior to emergence or planting of seedlings. Various trap designs have been studied, but many employ a container sunk into the soil with the upper lip at the soil surface. The container is baited with fresh plant material and/or bran, and with vermiculite so the larvae can attain shelter. Larvae are effectively captured in baited containers if the vermiculite is not too near the surface, and catches are enhanced if a screen cylinder, which provides a visual stimulus to the cutworms, is suspended above the baited container. If plants are present in the field they compete with the bait in the traps, and trap efficiency declines markedly. The distribution of larvae in the spring is random.

Persistent insecticides are commonly applied to plants and soil for black cutworm suppression, but surface rather than subsurface soil applications are desirable. Larvae readily accept insecticide-treated bran and other baits. Application of systemic insecticides to seeds also provides some protection against larval injury. *Bacillus thuringiensis* is not usually recommended for cutworm control.

Black cutworm larvae feed readily on weeds, and destruction of weeds can force larvae to feed exclusively on crop plants, exacerbating damage. Thus, it is often recommended that weeds not be tilled or treated with herbicide until larvae have matured. Timing is important, however, because prolonged competition between crop and weed plants can reduce crop yield. Presence of flowering weeds also can be beneficial by supporting prolonged survival of parasitoids. In contrast, reduced tillage cropping practices, which often produce higher weed populations, seem to result in increased abundance of black cutworm and higher levels of cutting in corn. This may be due, in part, to the tendency of moths to oviposit on weeds; weedy fields tend to have higher cutworm populations.

Black cutworm populations also tend to be higher in wet areas of fields, and in fields that have been flooded. Black cutworm has been known, at times, as “overflow worm,” due to its tendency to be abundant and damaging in fields that have been flooded by overflowing rivers.

In the home garden, barriers are sometimes useful to prevent damage to seedlings by cutworms. Metal or waxed paper containers with both the top and bottom removed can be placed around the plant stem to deter consumption. Aluminum foil can be wrapped around the stem to achieve a similar effect. Because larvae will burrow and feed below the soil line it is necessary to extend to barrier below the soil surface. Because black cutworm moths, which easily circumvent such barriers, are active during the growing season, this procedure alone may have little value. Use of netting or row covers, in addition to larval barriers, should prove more effective.

Entomopathogenic nematodes (Nematoda: Steinernematidae and Heterorhabditidae) will infect and kill black cutworm larvae, but their populations normally need to be supplemented to realize high levels of parasitism. Their effectiveness is related to soil moisture conditions.

► Turfgrass Insects and Their Management
► Vegetable Pests and Their Management

References

Abdel-Gawaad AA, El-Shazli AY (1971) Studies on the common cutworm *Agrotis ypsilon* Rott. I. Life cycle and habits. Zeitschrift fur Angewandte Entomologie 68:409–412

Archer TL, Musick GL, Murray RL (1980) Influence of temperature and moisture on black cutworm (Lepidoptera: Noctuidae) development and reproduction. Can Entomol 112:665–673
Busching MK, Turpin FT (1976) Oviposition preferences of black cutworm moths among various crop plants, weeds, and plant debris. J Econ Entomol 69:587–590
Busching MK, Turpin FT (1977) Survival and development of black cutworm (*Agrotis ipsilon*) larvae on various species of crop plants and weeds, Environ Entomol 6:63–65
Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, 729 pp
Harris CR, Mazurek JH, White GV (1962) The life history of the black cutworm, *Agrotis ipsilon* (Hufnagel), under controlled conditions. Can Entomol 94:1183–1187
McCorcle, Robinson JF, Way MO, Wallendorf MJ, Goodenough JL (1993) Mechanism of southward migration of a noctuid moth [*Agrotis ipsilon* (Hufnagel)]: a complete migrant. Ecology 74:2303–2314
Schoenbohm RB, Turpin FT (1977) Effect of parasitism by *Meteorus leviventris* on corn foliage consumption and corn seedling cutting by the black cutworm. J Econ Entomol 70:457–459
Story RN, Keaster AJ (1982) Temporal and spatial distribution of black cutworms in midwest field crops. Environ Entomol 11:1019–1022

Black Earwigs

Members of the earwig family Chelisochidae (order Dermaptera).

► Earwigs

Black Fig Fly (Diptera: Lonchaeidae)

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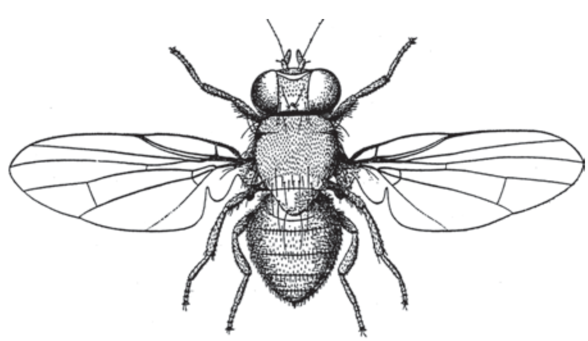
The black fig fly, *Silba adipata* McAlpine, is a pest of wild and cultivated figs, *Ficus carica* L. (Moraceae), occurring in the Mediterranean countries and Iraq. This insect was studied extensively by Silvestri in Italy at the beginning of the twentieth century, although he misidentified it as *Lonchaea aristella* Becker. The adult is glossy black, 3.5–4.5 mm in length, with reddish eyes and brown legs (Fig. 50). The female possesses a long ovipositor with which it deposits its eggs in small groups, beneath the scales protecting the ostiole (eye) of the syconium (fig "fruit"). Oviposition takes place preferably in unripe figs, but ripening ones are also attacked. The larvae feed on the tissues of the syconium, destroying the fruit. Infestation of unripe figs usually results in premature fruit drop, which is frequently mistaken by the growers as due to physiological problems of the trees. The fly completes 4–5 generations per year and overwinters in the pupal stage in the soil.

Observations conducted in Chios island, Greece showed that the flies are attracted and feed mostly on sweet exudates of ripe figs, and on fresh or dry milky fig-tree sap exuded from injured plant parts. As many as 63 pupae were obtained from a single infested, unripe fig, indicating multiple oviposition. The parasitoid *Pachycrepoideus vindemmiae* Rondani (Hymenoptera: Pteromalidae) emerged from *S. adipata* pupae. Males were observed swarming in the afternoon hours, an indication that the mating behavior is related to swarm formations. Hexanol, a generally-occurring plant volatile chemical, is very attractive for the fly and selective, especially for females. Use of McPhail traps baited with hexanol is very effective for monitoring and possibly for control of this fly. Addition of 2% ammonium sulphate in the trap water enhances trap effectiveness. Proteinaceous bait sprays are recommended when better control is needed.



Black Fig Fly (Diptera: Lonchaeidae), Figure 50 **Adult black fig fly (after Silvestri, 1917).**

References

Katsoyannos BI (1983) Field observations on the biology and behavior of the black fig fly *Silba adipata* McAlpine (Diptera: Lonchaeidae), and trapping experiments. J Appl Entomol 95:471–476

Katsoyannos BI, Guerin PM (1984) Hexanol: a potent attractant for the black fig fly, *Silba adipata*. Entomol Exp Appl 35:71–74

Silvestri F (1917) *Sulla Lonchaea aristella* Beck. (Lonchaeidae) dannosa alle infiorescenze e fruttescenze del caprifico e del fico. Bollettino del Laboratorio di Zoologia Agraria in Portici 12:123–146

Talhouk AMS (1969) Insects and mites injurious to crops in middle eastern countries. Monographien zur angewandte Entomologie 21:1–239, Paul Parey Verlag, Hamburg und Berlin, Germany

Black Flies (Diptera: Simuliidae)

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Black flies are small, morphologically homogeneous insects in the order Diptera, suborder Nematocera, best known for their economic impact as biting and nuisance pests of humans and domestic animals. Adults are readily recognized by their arched thorax, cigar-shaped antennae and strong venation at the anterior margin of each wing. Black flies breed abundantly in flowing freshwater – rivers and streams – throughout the world, from 965 km north of the Arctic Circle to the southernmost tip of South America. Within this vast realm, they are absent only from deserts and islands without flowing water. The immature stages often attain large populations and play an important role in the food web of streams and rivers.

Worldwide, more than 1,700 species have been formally named and described, with the expectation that this number will increase significantly as study of the family continues. The world's species are arranged in two subfamilies and about 24 genera. The largest genus by far is *Simulium*, which occurs worldwide. The greatest number of species, more than one third of the known fauna, inhabits the Palearctic Region, especially Russia. Approximately 260 species are known from North America north of Mexico.

The taxonomy of the family is based primarily on features of the genitalia, legs, and wings of the adults; the cocoons and gills of the pupae; and the head capsule and pigmentation patterns of the larvae. Many species, however, are structurally similar, if not identical, and are known as sibling species. They are typically revealed by studies of the banding patterns in the giant polytene chromosomes of their larval salivary glands. Nearly a quarter of the North American species, for example, were first discovered chromosomally.

The first three stages (egg, larva, pupa) of the life cycle are completed in running water. All types of flowing freshwater are exploited by black flies, from the smallest trickles to the largest rivers. Only a few species can tolerate polluted waters. The female black fly typically deposits its eggs either by dipping to the water's surface during flight to release a few eggs at a time, or by crawling about on wetted vegetation and stones while releasing masses or strings of eggs. The eggs are bluntly triangular, and a female can carry from about 20–800, depending on the species. Larvae hatch from the eggs within a few days to more than half a year. They hold onto objects in the stream, such as rocks and leaves, by means of tiny hooks at the end of the abdomen, which enmesh with a silken pad spun from the salivary glands and applied to the substrate. The larval stage, including six or seven instars, lasts from about a week to six months, depending on the species and water temperature. Mature larvae are 3–15 mm in length. Pupation occurs in flowing water, with a silken cocoon anchoring the pupa to the substrate. Some species burrow slightly into the sand and silt of the streambed to pupate. The pupal stage generally lasts no more than a few weeks. Some species are univoltine, completing only one generation per year. Other species are multivoltine, producing from two to about 15 generations in a year, depending on the latitude and species.

The majority of larval life is spent feeding. Most species feed primarily by filtering particulate matter from the water column, using a pair of head fans, with one fan projecting from each anterior corner of the head. Food particles of an appropriate size, those less than 350 µm in diameter, often include diatoms, bacteria, protozoa, pollen, and organic debris. Most species also can obtain food by scraping it from the surface of stones and other objects in the stream. About 1.5% of the world's species do not have head fans and must obtain all of their food by scraping. These species live in habitats, such as springs and glacial melt waters, where little organic matter is present in the water column. Some species, in addition to filter feeding and scraping, also prey on small arthropods in the stream.

Larvae often space themselves in characteristic patterns depending on the species and water currents. The larvae of some species space themselves closely in moss-like clumps, others space themselves rather widely, and still others pack so densely that they can exceed one million per square meter. For most of their lives, larvae remain attached to objects in the stream. When disturbed or relocating they loop short distances, inchworm fashion, or release their hold of the silk pad and drift downstream either freely or moored to a silk strand, eventually reattaching to a suitable substrate. Drift is particularly frequent at sunset and during the night, and is an important means of avoiding predation by fish and predacious arthropods.

Larvae are susceptible to parasites and pathogens, including mermithid nematodes, protozoa, microsporidia, fungi, and viruses. Only a small percentage, perhaps about 1%, of a population is usually infected, although parasitized larvae often live longer than uninfected individuals and become more apparent as the population ages and the healthy larvae pupate. Most parasites kill the larvae, but some pass through the pupae and into the adults, typically sterilizing the adult.

Larvae of most species pupate singly, but those of some species form large clusters of pupae. The adult that has developed within the pupa forcibly splits the pupal cuticle and emerges in a bubble of air, buoyed to the surface with enough force to break free of the water. The freshly emerged adult then flies to a resting spot where it tans and hardens its exoskeleton.

Adults (Fig. 51) are active during the day. They typically live less than a month, during which time they must mate and acquire food; females also must return to a stream or river to oviposit. The adults of most species probably do not disperse more than 10 km, although some species regularly travel more than 50 km in search of hosts. At least one species in Africa has been reported to disperse more than 500 km from the natal watercourses.

Mating usually takes place shortly after emergence. In many species, the males form aerial swarms over or beside landmarks such as trees, rocks, and waterfalls. Females fly into these swarms and are intercepted by males. The coupled pair quickly leaves the swarm. A small percentage of species, about 2% in North America, mate on the ground at their emergence sites. A similarly small percentage of females do not mate. These non-mating species consist of all-female, parthenogenetic populations, and they occur at northern latitudes.

Both male and female black flies feed on water and a source of carbohydrate, such as floral nectar and honeydew, that fuel their flight activities. Only females feed on blood. The mouthparts of males are

Black Flies (Diptera: Simuliidae), Figure 51
Female black fly (from Cameron 1922; Canadian Department of Agriculture Bulletin).

incapable of cutting skin. Females use their mandibles to snip the skin of warm-blooded animals, while injecting various anesthetics and anti-clotting factors. As the capillaries are severed, a pool of blood forms, which is then imbibed. Not all species have females that feed on blood. In less than 10% of the world's species, the females have mouthparts much like those of the males, too feeble to cut vertebrate flesh. These non-biting females typically occur in northern environments such as the arctic and are facultatively autogenous, meaning that by necessity, they mature their eggs without the benefit of blood. The nutrient reserves for egg production are carried over from the larval stage.

Black flies use a wide range of hosts to acquire a blood meal although many species are quite host- specific. For example, one species of black fly feeds only on loons. Other species feed only on raptors, or only on small or large mammals. Still other species appear to be true generalists. To locate their hosts, females use a series of cues such as color, shape, size, and odor. Carbon dioxide is especially attractive. Species tend either to feed on birds (ornithophily) or mammals (mammalophily). The bird feeders have a thumb-like lobe on their claws, whereas most mammal feeders have simple or slightly toothed talons.

By virtue of their requirement for blood, black flies frequently become pests of humans and domestic animals. Only a fraction of the species, about 15% in North America, actually causes economic problems. The majority of species are not attracted to humans and domestic animals but, instead, feed only on wildlife. Some of the pest species are primarily a nuisance, swarming about the head and entering the facial orifices. Those that take blood represent a more serious threat, either through exsanguination, injection of toxic saliva (simuliotoxicosis), or the transmission of disease agents. Some of the major cattle and poultry pests can cause weight loss, reduced egg and milk production, malnutrition, stampedes, stress-related afflictions, and even death. Humans may develop fever, swollen eyes and glands, headaches, nausea, or even more severe allergic reactions. More typical reactions include itching welts at the site where the person was bitten. Outdoor industries and recreational activities often are severely curtailed by both nuisance and biting species.

Black flies transmit numerous blood protozoans, filarial worms, and perhaps a few viruses to mammals and birds. Human-borne pathogens are transmitted by black flies only in Africa and parts of Central and South America. The most common and serious human disease is onchocerciasis, or river blindness, caused by a filarial worm. Filarial worms also are transmitted to cattle, deer, moose, black bears, and ducks, but apparently cause little economic impact. The major avian pathogens transmitted by black flies are malaria-like blood protozoans that cause a disease called leucocytozoonosis. In North America, turkeys, ducks, and wild birds are affected. The consequences among domestic birds can be grievous and include depressed immune systems, weight loss, decreased reproduction, and even death.

Since the 1980s, the primary means of controlling pest populations of black flies has been with the bacterium *Bacillus thuringiensis* variety *israelensis* (*Bti*), which produces a toxin highly specific to black flies and mosquitoes. When applied to streams and rivers, Bti is an environmentally safe means of management, killing only larval black flies. Management programs are operating in many parts of the world, including Pennsylvania, Quebec, sub-Saharan Africa, and Brazil. Some of these programs cost millions of dollars to conduct every year.

References

Adler PH, Currie DC, Wood DM (2004) The black flies (Diptera: Simuliidae) of North America. Cornell University Press, Ithaca, NY, 941 pp

Crosskey RW (1990) The natural history of blackflies. Wiley, Chichester, England, 711 pp

Kim KC, Merritt RW (eds) (1988) Black flies: ecology, population management, and annotated world list. Pennsylvania State University Press, University Park, PA, 528 pp

Laird M (ed) (1981) Blackflies: the future for biological methods in integrated control. Academic Press, New York, NY, 399 pp

Black Flies Attacking Livestock: *Simulium arcticum* Malloch and *Simulium luggeri* Nicholson & Mickel (Diptera: Simuliidae)

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The livestock-attacking black flies, *Simulium arcticum* Malloch and *Simulium luggeri* Nicholson & Mickel, are important pests of cattle and wild ungulates in the northern great plains of Canada. Other black fly species are pests of vertebrates including humans in other parts of the world. Females of *S. arcticum* and *S. luggeri* are greyish or brownish with the dorsum of the thorax uniformly colored. They differ in appearance (the coloration of the tibia of the hind leg is entirely dark in *S. luggeri*, but the basal half is white in *S. arcticum*), and features of the genitalia.

Damage

Economic losses occur due to the massive attacks by female black flies seeking a bloodmeal needed for production of eggs. Dispersal in search of hosts may be 150 km from the rivers where emergence and oviposition take place. In parts of Saskatchewan and Alberta, black flies are limiting to cattle production. Cattle harassed by attacking black flies become frightened and bunch together to escape the blood-seeking swarms. The cattle do not feed normally, resulting in reduced weight gain and milk production. The saliva of *S. arcticum* is toxic to cattle and allergic reaction can cause death. While *S. luggeri* do not have toxic saliva, they swarm in huge numbers around the head, causing livestock to panic, often running into fences and being injured. Bacteria that cause "pinkeye" may be transmitted as black flies land to feed near the eyes of several hosts.

Biology

Simulium arcticum has one or two generations per year, and attacks only cattle and related animals. This species prefers clean rocky locations in large, fast-flowing, silt-laden rivers such as the Athabasca River in northern Alberta. *Simulium arcticum* formerly was the dominant species in the Saskatchewan River but because of hydrological changes caused by hydroelectric developments it ceased to be abundant

Simulium luggeri has up to five generations per year and will attack humans as well as cattle. This species prefers somewhat clear, flowing water near the mouth of middle-sized rivers. The human-induced hydrological changes to the Saskatchewan River drastically reduced summertime river volumes, effectively modifying it from a fast-flowing, silt-laden system to a slower-flowing, clear system. The once deep and turbid river became shallow, clear and slow flowing. This encouraged the growth of massive vegetation beds on previously barren sand bars. This plant substrate served as suitable attachment sites allowing *S. luggeri* to replace *S. arcticum* as the dominant species. Both black fly species have four developmental stage, egg, larva, pupa, and adult. The eggs, larvae, and pupae are restricted to rivers and streams.

Eggs are tiny and trapezoid-shaped. They are "bombed" on the water surface by gravid females flying over the river. The eggs sink to the substrate where they become buried and pass the winter. In spring hatching commences about two weeks after ice breakup.

Newly hatched larvae drift downriver and attach to substrates such as clean rocks or vegetation in the swiftest flowing water. Larvae go through seven instars or growth stages during about three weeks. Larvae of *S. arcticum* are larger (0.9–mm) than those of *S. luggeri* (0.7–4.3 mm). The brown or greenish-grey larvae feed by filtering nutrients from the water using head (cephalic) fans or by scraping algae from the surface of rocks using their mouthparts. When mature, the larva spins a cocoon and pupates within it.

Pupae of *S. arcticum* have paired respiratory filaments and pupation occurs within a boot-shaped cocoon. Respiratory filaments of *S. luggeri* pupae are grouped in threes and pupation occurs within a slipper-shaped cocoon. After a few days the adult escapes from the pupa and floats to the surface in an air bubble.

Adult male and female black flies feed on nectar and other plant juices to sustain their energy requirements. Mating occurs soon after emergence, and females of biting species then seek blood, which is required to produce eggs. After locating a host, settling on its skin, and inserting their blade-like piercing mouthparts, the females suck blood until they become fully engorged. After taking the blood meal they have expanded to twice their normal size. Engorged females seek suitable flowing water habitats in which they lay eggs on particular substrates. Black flies are active during daylight hours but their rate of attack is highest during morning and afternoon. On cloudy days or when storms are imminent black flies may attack viciously at any time of day. Winds can disperse large numbers of adults from breeding areas to surrounding regions, especially open farmland, and shifting winds may disperse black flies to other districts. Cold or rainy weather temporarily ends an outbreak.

Management

Control of black flies attacking livestock is achieved most effectively through use of insecticides. Larvicides are more effective than adulticides because larvae are concentrated in a relatively definable location in rivers or streams and less insecticide is required to kill a substantial number of pest individuals. Larvicide is only applied when and where pest populations are detected. Exclusive use of adulticide is ineffective because of the extreme difficulty in implementing it; it requires repeated (about every 10 days) applications of insecticide spray or fog over large areas of ground in affected communities. In addition, applying insecticide directly to cattle via backrubbers, sprays, etc. has to be safe to the animals and consumers of animal products. Control of adults, however, can be useful as an additional emergency measure, especially on cattle during severe outbreaks. *Bacillus thuringiensis israelensis* is an effective biological insecticide, with little environmental effect.

Disease agents are commonly associated with black flies but the life cycles are almost completely unknown, so knowledge of agent transmission between hosts is lacking. Mermithid nematodes are one of the most promising biological control agents for black flies but their commercial development is hindered by a lack of basic ecological information.

References

Crosskey RW (1990) Natural history of black flies. British Museum of Natural History, London, UK, 722 pp

Kim KC, Merritt RW (eds) (1987) Black flies: Ecology, population management and annotated world list. The Pennsylvania State University Press, University Park, PA, 528 pp

Laird M (ed) (1981) Blackflies: The future for biological methods in integrated control. Academic Press, London, UK, 399 pp

Mason PG, Shemanchuk JA (1990) Black flies. Agriculture Canada Publication 1499/E, Minister of Supply and Service Canada, Ottawa, Ontario, Canada, 8 pp

Mason PG, Boisvert M, Boisvert J, Colbo MH (2001) *Simulium* spp., black flies (Diptera: Simuliidae). In: Mason PG, Huber JT (eds) Biological control programmes in Canada 1981–2000. CABI Publishers, Wallingford, UK, pp 230–237

Blackheaded Fireworm, *Rhopobota naevena* (Hübner) (Lepidoptera; Tortricidae)

A caterpillar pest of cranberries in North America.

► Small Fruit Pests and Their Management

Black Grain Stem Sawfly, *Trachelus tabidus* (Fabricius) (Hymenoptera: Cephidae)

This is a pest of wheat in the northern hemisphere.

► Wheat Pests and Their Management

Blacklegged Tick, *Ixodes scapularis* Say (Acari: Ixodidae)

This is a common pest of mammals in North America, and an important vector of Lyme disease.

► Ticks

Blacklight Trap

An insect trap used for monitoring flying insects, particularly moths, that come to the ultraviolet wavelengths produced by the "black" light source associated with the trap.

► Traps for Capturing Insects

Black Parlatoria Scale, *Parlatoria ziziphi* (Lucas) (Hemiptera: Diaspididae)

This is an important pest of citrus crops.

► Citrus Pests and Their Management

Black Pod of Cacao

This is an important insect-vectored disease of cacao.

► Transmission of Plant Diseases by Insects

Black Scale, *Saissetia* spp. (Hemiptera: Coccidae)

Several species of soft scale in the genus *Saissetia*, known as black scales, are pests of citrus crops.

► Citrus Pests and Their Management

Black Scavenger Flies

Members of the family Sepsidae (order Diptera).

► Flies

Black Turfgrass Ataenius

► Turfgrass Insects and Their Management

Blackwelder, Richard Elliot

Richard Blackwelder was born on January 29, 1909. His doctoral research was performed at Stanford University, California. That research produced a (1936) monograph "Morphology of the coleopterous family Staphylinidae" in which he acknowledges the help of his advisor, G.F. Ferris, and of R.E. Snodgrass. This work still is the foremost on its subject. Then he published short works on the systematics of North American Tachyporinae (1936, 1938) and Paederini (1939). After graduation he became a Bacon Traveling Scholar for the Smithsonian Institution (1935–1938) during which time he completed a 21-month collecting trip to many West Indian islands (June 1935 through March 1937), returning with 50,000 specimens mostly collected by hand or with a net. This culminated in his (1943) publication of a "Monograph on the West Indian species of the family Staphylinidae," this work, which dealt with the 91 genera and 468 species known to him, has not been bettered. In 1938–1940 he was Assistant Curator of the American Museum of Natural History, and in 1940–1954 Assistant and Associate Curator of the Smithsonian Institution. During these years he published short works on Lispinini and Osoriinae (1942) and the staphylinid beetles of the Cayman Islands (1947), and sundry other papers including, with the help of his wife three supplements to the Leng catalog of North American Coleoptera. His monumental works were (1944–1947, 1957) "A checklist of the coleopterous insects of Mexico, Central America, the West Indies, and South America" and (1952) "The generic names of the beetle family Staphylinidae." The first of these has been cited in just about every subsequent biogeographic study including neotropical Coleoptera and was of enormous importance. In the mid-1960s he explained to this writer the reason for the much-delayed final part (1957), the bibliography, of the first work: that his card index of bibliographic materials had disappeared during one of his absences from the Smithsonian Institution, and he had to rebuild it from his notes and reconsultation of the literature. The second undertaking, generic names, attempted to apply the rules of the International Code of Zoological Nomenclature systematically across the mishmash of usage; although it shook up the established usage, it was largely correct and inevitable. Then he retired from life as a coleopterist and researcher and became a teacher, employed first at St. John Fisher College in New York state (1956–1958) and then at Southern Illinois University (1958–1977). His tremendous energy as a researcher on Staphylinidae in his early years was directed elsewhere by the late 1950s, although he remained an active member of the Society of Systematic Zoologists, published works on systematics in Systematic Zoology and a book "Classification of the animal kingdom" in 1963 and another "Taxonomy" in 1967. He died on January 20, 2001.

Reference

Herman LH (2001) Blackwelder, Richard Elliot. Bull Am Mus Nat Hist 265:46–47

Blaisdell, Frank Ellsworth

Frank Blaisdell was born in New Hampshire on March 13, 1862, and moved with his parents and siblings to California in 1870. Despite lack of a high school education, in 1887 he entered Cooper Medical College in San Francisco, and graduated two years later with the degree of Doctor of Medicine. He worked in California at first as a medical practitioner, and from 1900 as an academic at Cooper College and then at Stanford University (into which Cooper College was absorbed). Ultimately he became Professor of Surgery, from which post he retired in 1927. His hobby for decades had been the collection and study of Coleoptera, especially the families Tenebrionidae and Melyridae. After retirement from medicine he worked from the Department of Entomology at the California Academy of Sciences, to which he deeded his collection of almost 200,000 specimens. He published 95 papers in entomology. He died on July 6, 1946.

Reference

Mallis A (1971) Frank Ellsworth Blaisdell. In American entomologists. Rutgers University Press, New Brunswick, NJ, pp 278–279

Blasticotomidae

A family of sawflies (order Hymenoptera, suborder Symphyta).

► Wasps, Ants, Bees and Sawflies

Blastobasidae

A family of moths (order Lepidoptera). They commonly are known as scavenger moths.

► Scavenger Moths
► Butterflies
► Moths

Blastoderm

The layer of cells in an insect embryo that surrounds an internal yolk mass. The cellular blastoderm develops from a syncytium by surrounding the cleavage nuclei with membranes derived from the enfolding of the surrounding membrane.

Blatchley, Willis Stanley

Willis Blatchley was born on October 6, 1859, in Connecticut, but he grew up on a farm in Indiana that his parents bought in 1860. In 1879, after taking a six-week training course, he became a country school teacher, and it was not until 1883 that he entered Indiana University, majoring in natural science and graduating four years later. From 1887 to 1894 he worked as head of a high school science department. In the first four years of that period he conducted thesis research (a thesis entitled "The Butterflies of Indiana") toward an M.A. degree, awarded in 1891, again from Indiana University. His third degree was an honorary LL.D., awarded in 1921 by the same institution. Schools have long summer vacations, and Willis Blatchley found summer employment with the Indiana State Geological Survey or with the U.S. Fish Commission. The first employment experience may have helped when in 1894 he won the elected position of Indiana State Geologist, and held it for 16 years. His duties were not just as geologist, but also to work on natural resources and natural history. The years 1906–1910 found him working on "Coleoptera of Indiana" as Bulletin 1 of the Indiana Department of Geology and Natural Resources. When another candidate was elected in 1910 as State Geologist, Blatchley retired, and spent the rest of his life working on subjects that appealed to him. He traveled abroad, within the USA, and frequently to Florida where in 1913 he bought a "winter residence" that later he occupied for months each year. With Charles Leng, he published in 1916 "Rhynchophora or weevils of northeastern America"; as sole author he published in 1920 "The Orthoptera of northeastern America," and in 1926 "Heteroptera or true bugs of eastern North America." His books included several of a less technical nature but including observations on insects: (1899) "Gleanings from nature," (1902) "A nature wooing at Ormond by the sea," (1906) "Gleanings from nature," (1912) "Woodland idylls," (1931) "My nature nook," (1932) "In days agone," and (1934) "South America as I saw it." He died in Indianapolis on May 28, 1940, surviving his wife, Clara, by 12 years. His collection of insects, including 470 holotypes, was given to Purdue University.

Reference

A Mallis (1971) Willis Stanley Blatchley. In: American entomologists. Rutgers University Press, New Brunswick, NJ, pp 272–278

Blattaria

An order of insects, also known as Blattodea. They commonly are known as cockroaches.

► Cockroaches

Blattellidae

A family of cockroaches (order Blattodea).

► Cockroaches

Blattidae

A family of cockroaches (order Blattodea).

► Cockroaches

Blattodea

An order of insects, also known as Blattaria. They commonly are known as cockroaches. Cockroaches

Blephariceridae

A family of flies (order Diptera). They commonly are known as net-winged midges.

► Flies

Blind Springtails

A family of springtails (Onychiuridae) in the order Collembola.

► Springtails

Blister Beetles (Coleoptera: Meloidae)

Blister beetles are an interesting group of insects, both because of their unusual larval development and because of their toxic effects on humans and livestock. They are widely distributed, but are absent from New Zealand and Antarctica. They are most abundant in warm, dry climates. They number about 3,000 species. Their classification is as follows:

Order: Coleoptera
  Suborder: Polyphaga
    Superfamily: Tenebrionoidae
      Family: Meloidae
        Subfamily: Eleticinae
        Subfamily: Meloinae
        Subfamily: Nemognathinae
        Subfamily: Tetraonycinae

Characteristics

These are medium-sized beetles (usually 3–30 mm, but some up to 70 mm) with 7–11 antennal segments. There are five, five and four segments on the pro-, meso-, and metathoracic tarsi, respectively. The color is variable; though often somber, some are metallic. Body hairs often are absent but sometimes dense. The pronotum of blister beetles is narrower than the head and thorax. The legs are long, and the body is unusually soft for a beetle. The body is often elongate, with the elytra flared at the tips. However, body form varies considerably and though wings usually are normal, some species have short wings and elytra, and are flightless. The immature display hypermetamorphosis. Oviposition takes place on the soil, and young larvae (triungulins) disperse to feed on grasshoppers eggs, or the eggs, larvae and provisions (usually pollen) of ground-nesting Hymenoptera. Once attaining a food supply, the larvae lose their mobility. When disturbed, the adults display reflex bleeding, wherein cantharidin-containing blood is released, principally from the femoral-tibial joints. Cantharidin is a toxic terpenoid that likely imparts some protection from predation, though it also seems to have a role in communication. The beetles also may display death feigning. Cantharidin is produced by larvae, but in the adult stage only by the males. It is transferred to females at mating, and occurs in the eggs.

Life Cycle

Following is an account of black blister beetle development, which is typical of many species. In black blister beetle is a single generation per year, with overwintering occurring in one of the larval instars. The eggs are deposited within a cavity in the soil, in clusters of 100–200 eggs. Because the likelihood of surviving is so small, blister beetles produce very large numbers of eggs, sometimes up to 10,000.

The larval instars of black blister beetle are quite varied in appearance, reflecting the unusual biology of the insect, called hypermetamorphosis. Unlike most insects, the ovipositing female does not locate a food source for her offspring, apparently depositing her eggs randomly. Thus, when young larvae hatch they must dig to the surface and disperse to find a host insect on which to feed. The first instar is thus quite mobile, and equipped with long legs with which to disperse. First instars explore cracks, crevices, and depressions in the soil as they search to find a host. Usually a single egg is adequate for complete development of the first instar. The number of instars is normally 6–7. The larvae are creamy white or yellowish white in color, with brown head capsules. After the first instar the larva moves little, and the legs become relatively shorter and shorter. The sixth instar does not feed, instead digging 2–3 cm into the soil and preparing a cell. The sixth instar may be followed by another nonfeeding instar, or by the pupal stage. The sixth and seventh instars bear only minute legs, and the head capsule is reduced in size and retracted into the body. Black blister beetle larvae consume 21–27 eggs of *Melanoplus differentialis* Thomas during its larval development. This grasshopper, and some other *Melanoplus* spp., produces 100 or more eggs, allowing more than one blister beetle to develop. If blister beetle larvae encounter one another, however, they fight and only one survives. Many grasshoppers produce small egg pods, with less than 25 eggs, thereby limiting the ability of blister beetles to develop. The pupa resembles the adult beetle in form, though the legs and wings are folded against the underside of the body, and there appears to be no tendency for diapause in this stage. The adult digs to the soil surface after pupation.

Other blister beetles sometimes require more than one year to complete a generation, or are multivoltine, depending on the favorability of the environment. The species feeding on bees differ in that the eggs may also be deposited on foliage, where the young larvae are phoretic, attaching to adult bees and are transported back to the nest of the bee.

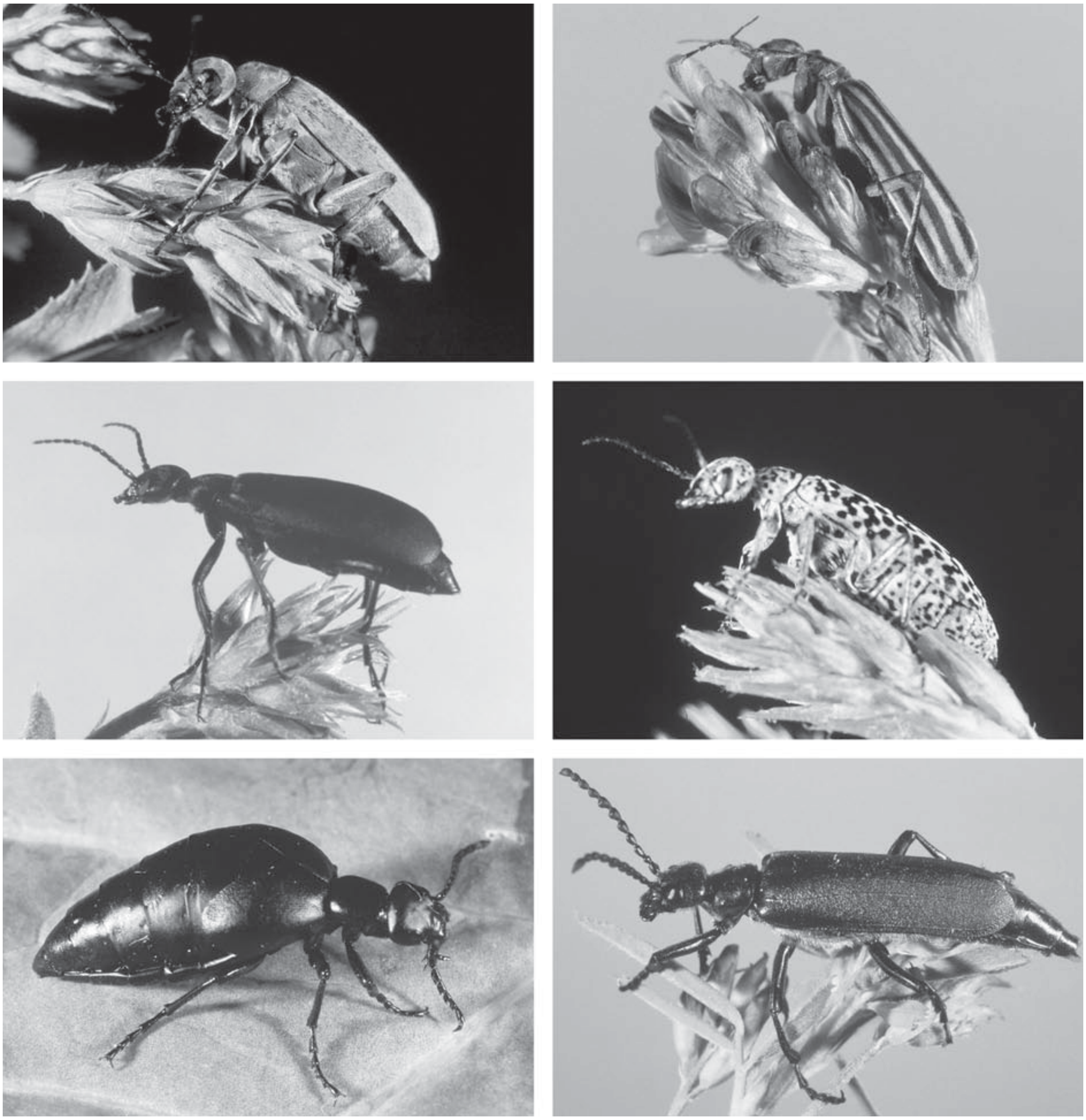
Natural Enemies

Surprisingly little is known concerning the natural enemies of blister beetles, reflecting their minor status as crop pests and the subterranean habits of larvae. Undoubtedly starvation of first instars is a very important factor during most seasons, and cannibalism is prevalent among larvae. Antlike flower beetles (Coleoptera: Anthicidae), false antlike flower beetles (Coleoptera: Pedilidae), and some plant bugs (Hemiptera: Miridae) have been implicated as mortality agents of blister beetles. The larva of the blister beetle *Epicauta atrata* (Fabricius) has also been shown to be predatory on eggs of *E. pensylvanica*, and it is possible that other species within the genus are predatory (Fig. 52).

Damage Caused by Blister Beetles

Epicauta spp. and other blister beetles sometimes feed on crops, though few are commonly destructive. In North America, black blister beetle, *Epicauta pensylvanica* DeGeer, is usually the most common species, and occurs everywhere in the eastern United States and southern Canada west to the Rocky Mountains. Immaculate blister beetle, *Epicauta immaculata* (Say); spotted blister beetle, *Epicauta maculata* (Say); and striped blister beetle, *Epicauta vittata* (Fabricius), are examples of other common crop-feeding blister beetles Other genera of Meloidae occasionally affect crops, but incidents of damage are isolated. Among such occasional pests are *Linsleya sphaericollis* (Say) in the Rocky Mountain region and west to the Pacific Ocean; Nuttall blister beetle, *Lytta nuttalli* Say, throughout the west and east to Nebraska; and *Meloe niger* Kirby, which occurs throughout the United States and southern Canada except for the southeastern states.

Blister beetle adults are found on alfalfa, clover, soybean, and sugarbeet, as well as numerous vegetable and flower crops, fruit trees, and broadleaf weeds. Adults often collect on goldenrod flowers, *Solidago* spp., in the autumn. Indeed, flowers are often a preferred food of many species. Beetles tend to aggregate, apparently in mating swarms, so damage can be severe in relatively small areas of a crop and absent or trivial elsewhere. consumption of foliage, in some instances they prefer blossoms.



Blister Beetles (Coleoptera: Meloidae), Figure 52 **Representative blister beetles: upper left, *Epicauta immaculata*; upper right, *Epicauta lemniscata*; center left, *Epicauta pensylvanica*; center right, *Epicauta andersoni*; lower left, *Meloe laevis*; lower right, *Lytta* sp.**

Preference of blister beetles for blossoms is most noticeable and potentially damaging in alfalfa, where beetles congregate mostly during periods of bloom. Aggregations of beetles can be incorporated into alfalfa hay when it is baled, particularly if the stems are crushed as part of the harvesting process. Crushing, or crimping, aids in the drying and preservation of hay, but also can result in death of aggregations of blister beetles, and incorporation of their bodies into the hay. Blister beetles, even dead individuals, contain a vesicating substance called cantharidin which, when ingested, damages the digestive tract of animals. Cantharidin also causes blisters to form on the skin of sensitive humans who come into contact with crushed beetles, and in formation of blisters in the mouths of livestock, particularly horses. This blistering action is the basis for the common name of the beetles. Cantharidin content varies among species, ranging from 5% cantharadin in *Epicauta immaculata* to about 1% cantharidin in *E. pensylvanica*. Despite the relatively low toxin content in each beetle, large numbers can be incorporated into hay, and horses can ingest enough beetles to cause death. Cantharidin likely serves as a feeding deterrent to most predators, thereby protecting blister beetles and their eggs from consumption. However, some insects are attracted to cantharidin, and this compound is involved in the chemical communication among blister beetles.

In times past in Europe the so-called "Spanish fly," *Lytta vesicatoria*, acquired the undeserved reputation as an aphrodisiac for horses. Likely ingestion of this insect irritated the animals, making them seem more restless and "spirited." Thus, the beetle was sometimes administered to horses, and even sometimes to humans, but the effects can be quite deleterious.

Beneficial Effects of Blister Beetles

The damage caused by *Epicauta* spp. blister beetles is offset, at least during periods of relatively low beetle density, by the predatory behavior of blister beetle larvae. *Epicauta* spp. larvae feed on the eggs of grasshoppers, including many crop-damaging *Melanoplus* spp. During periods of grasshopper abundance the number of blister beetles tends to increase substantially. Studies of egg pod destruction in western areas of the United States during a period of grasshopper abundance, for example, documented that 8.8% of pods were damaged by blister beetles. Although the blister beetles eventually contribute materially to the suppression of grasshopper population outbreaks, the higher numbers of blister beetles often cause greater crop injury during, and immediately after, periods of grasshopper abundance. The larvae of many blister beetles, however, seem to feed principally on ground nesting bees and the bee's nest provisions. Their abundance fluctuates less, and they provide no known agricultural benefits. There is even one instance in Canada where bee-feeding blister beetles interfered with alkali bees being managed for alfalfa pollination.

Management

Blister beetles are not usually pests, though they may become quite abundant during and following long-term grasshopper population increases. Suppression of grasshoppers indirectly suppresses blister beetles by eliminating the food supply of the blister beetle larvae. Direct suppression of blister beetles usually may not occur in conjunction with chemical treatment of grasshopper populations because the grasshoppers can occur earlier in the season, when blister beetles are still in the soil. Blister beetles are easily controlled by application of common insecticides to crop foliage, and small plantings can be protected with row covers or screening. Because some blister beetle is highly attracted to alfalfa, especially during periods of bloom, large numbers of blister beetles may disperse to nearby crops following alfalfa harvest.

► Potato Pests and Their Management
► Beetles

References

Bologna MA, Pinto JD (2001) Phylogenetic studies of Meloidae (Coleoptera), with emphasis on the evolution of phoresy. Syst Entomol 26:33–72

Pinto JD, Bologna MA (2002) In: Arnett RH Jr, Thomas MC, Skelly PE, Frank JH (eds) The American beetles, vol 2. CRC Press, Boca Raton, pp 522–529

Pinto JD, Bologna MA (1999) The new world genera of Meloidae (Coleoptera): a key and synopsis. J Nat Hist 33:569–620

Selander RB (1991) On the nomenclature and classification of the Meloidae (Coleoptera). Insecta Mundi 5:65–94

Blister Beetle Antennal Twisting Behavior

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The blister beetle, *Epicauta hirticornis*, has an interesting pre-copulating behavior. When a male dorsally mounts a female, the male continuously waves its antennae toward the female's antennae. Eventually, the male's right or left antenna, or sometimes both, grasps the corresponding female antennae and wraps around the female antennae (Fig. 53).

In northern Taiwan, blister beetles usually are found aggregating on the leaves of blooming glorybower tree, *Clerodendrum cyrtophyllum* Turcz, and a novel sexual behavior was observed. During their courtship, a male beetle mounts a female from behind and the male's antenna winds around the female's antennae. The sexual behavior of Meloidae has been studied in detail. However, entwining of male and female antennae has not been reported before. The observed frequencies of right-handed and left-handed antennal pairs were 46.7 ± 13.9% and 44.8 ± 12.5%, respectively.

► Blister Beetles

References

Selander R (1964) Sexual behavior in blister beetles (Coleoptera: Meloidae). I. The genus Pyrota. Can Entomol 96:1037–1082

Pinto JD (1975) Intra-and interspecific courtship behavior in blister beetles of the genus *Tegrodera* (Meloidae). Ann Entomol Soc Am 68:275–285

Blood Gill

A gill that lacks tracheae. In such gills, oxygen passes directly into the blood instead of entering

Blister Beetle Antennal Twisting Behavior, Figure 53 **Pre-copulating behavior of the blister beetle *Epicauta hirticornis*. (a) A male mounts a female on the leaves of *Clerodendrum cyrtophyllum*. Their antennae are twisted to the right. (b) Both male antennae are entwined with the female's antennae; right-handed and left-handed structures are seen pointing backwards.**

tracheae. Blood gills are found in some aquatic insects.

► Tracheal System and Respiratory Gas Exchange

Blow Flies

Members of the family Calliphoridae (order Diptera).

► Flies
► Myiasis

Blueberry Maggot, *Rhagoletis mendax* (Curran) (Diptera: Tephritidae)

This is an important pest of blueberry in North America.

► Small Fruit Pests and Their Management

Bluebottle Flies

Members of the family Calliphoridae (order Diptera).

► Flies
► Myiasis

Bluegrass Billbug, *Sphenophorus parvulus* Gyllenhall (Coleoptera: Curculionidae)

This is an important pest of turfgrass in North America.

► Turfgrass Insects of the United States: Biology and Management

Blues

Some members of the family Lycaenidae (order Lepidoptera).

► Gossamer-Winged Butterflies
► Butterflies
► Moths

Bluetongue Disease

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Bluetongue disease is an insect transmitted disease that occurs primarily in sheep and wild ruminants. The bluetongue viruses that cause the disease are members of a family of viruses called orbiviruses. Although cattle in many regions of the world are often infected with bluetongue virus, cattle rarely show clinical signs of this disease.

Insect Vectors

Bluetongue viruses can be found in the tropics and subtropics throughout the world. The viruses are transmitted by insect species within the genus *Culicoides*, Family Ceratopogonidae. Various species of *Culicoides* transmit bluetongue virus. Different regions of the world contain different species of *Culicoides* involved in bluetongue virus transmission. In South America, *Culicoides* insignis is the primary vector of bluetongue virus. In Africa, the primary bluetongue vector is *Culicoides imicola*, while in Australia the primary vectors are *Culicoides brevitarsis* and *Culicoides wadai*. The *Culicoides* vectors of the bluetongue viruses in parts of Asia include *Culicoides imicola*. However, the *Culicoides* vectors in large parts of Asia have yet to be identified. Bluetongue virus transmission does not occur anywhere in the world in the absence of bluetongue-competent *Culicoides* vector species. The primary North American vector of the bluetongue viruses is a member of the *Culicoides variipennis* complex, *Culicoides sonorensis*.

The Disease

The most severe clinical signs of bluetongue disease occur in sheep. Sheep with bluetongue disease show a rise in temperature lasting 5–days. There can be swelling of the buccal and nasal mucosa, swollen tongue, profuse salivation, hemorrhages in the membranes of the mouth, and hemorrhages in the bands of the hoof, which often leads to lameness. Sheep may vomit because of lesions in the esophagus and pharynx. This sign can lead to their aspirating the contents of their rumen, in pneumonia and frequently in death. Sheep mortality to bluetongue infection may range from 5 to 50% of animals infected with virus.

Although clinical signs in cattle are rare, early prenatal infection with bluetongue in cattle may lead to embryonic death. Cattle develop a very prolonged viremia lasting several weeks where bluetongue virus can be detected in blood and is available to infected susceptible *Culicoides*. As a result cattle are considered important reservoirs for the virus and play an important role in infecting susceptible *Culicoides* vectors and therefore in the disease transmission cycle in more susceptible ruminants. In the western and southern regions of the United States where *Culicoides sonorensis* is present, there are regions where it is not uncommon to find 50% or more of the cattle to have once been infected with bluetongue virus. These animals are known to have once been infected because they contain antibody to one of the United States bluetongue viruses in their blood. The presence of antibody to a virus is evidence of a previous infection.

The Viruses

There are 24 different serotypes of bluetongue virus distributed throughout the world. The viral serotypes are numbered 1–24 and, as with the different species of *Culicoides* vectors, the serotypes also are found in specific regions of the world. There appears to be an association with the particular *Culicoides* vector species in a region and the specific bluetongue virus serotypes found in the geographic region. North America has five bluetongue serotypes (2, 10, 11, 13, 17), Australia has eight serotypes (1, 3, 9, 15, 16, 20, 21, 23), Africa has 21 (1–19, 22, 24) Central America and the Caribbean region has eight (1, 3, 4, 6, 8, 12, 14, 17). Europe has been essentially free of bluetongue virus although there have been a few periodic outbreaks in Spain and Portugal due to *Culicoides imicola*. Bluetongue outbreaks in sheep in Europe occurred for the first time in 2001–2002 in Bulgaria, France (Corsica), Italy (Sardinia) and Greece. The vectors of these outbreaks were not identified, although some appear to have involved *Culicoides imicola*.

Impact and Problems

The presence of severe bluetongue disease can have disastrous consequences on sheep populations. Consequently, in an effort to reduce the potential importation of a bluetongue-infected animal and the possibility of a bluetongue outbreak, many countries impose restrictions on the movement of livestock to their country from any country where bluetongue is prevalent. The Office of International Epizootics is the international agency responsible for developing regulations to protect animals around the world. This agency develops regulations for animal trade between countries. In the case of bluetongue, the regulations in place provide for the safe movement of livestock from bluetongue areas to bluetongue free areas. For example, the United States, where one of five bluetongue serotypes may be found in cattle, has restrictions imposed on its animal export to countries in the European Union that do not have bluetongue virus. United States animal exports must be tested and certified as being free of bluetongue before they can be approved for shipment. This results in lost trade opportunities for United States animal exports. The worldwide result is that bluetongue is the cause of non-tariff trade barriers costing millions of dollars in testing and lost trade opportunities on the international livestock market.

The northeastern region of the United States does not contain the bluetongue vector species, *Culicoides sonorensis*. There is no evidence of bluetongue virus transmission to livestock in this region. Such information is essential to declare a bluetongue free region within a country that could result in improving the livestock trade opportunities for the specific region despite restrictions on bluetongue transmission regions within the same country. The economic costs due to bluetongue are considerable due to its impact on the international livestock market and may approach billions of dollars.

Several different types of bluetongue virus vaccines are available for use in domestic livestock. Unfortunately, each bluetongue serotype requires a specific vaccine for protection. These vaccines have met with varying degrees of success. Some bluetongue vaccines are attenuated forms of the virus that were manufactured using techniques to reduce their virulence in animals. Their advantage is that they can provide protection after a single or booster injection, but unfortunately some have become virulent in the animals or after they have been picked up by blood feeding *Culicoides*. Killed virus as vaccines has been used and these do not become virulent, but often require more boosters to be effective. Bluetongue vaccines have been perfected using molecular biology technology. Unfortunately, the commercial prospects for many bluetongue vaccines have not been realized so that there has been little commercial interest in their development and use. In the United States, lack of interest in the commercial use of bluetongue vaccines is due to several factors. Use of bluetongue virus vaccines must face the challenge that naturally infected animals must be readily distinguishable from vaccinated animals. Undistinguished vaccinates would not be acceptable for international movement, and vaccinated animals should not inhibit or mask naturally occurring infection that would prevent the early detection of an outbreak. Since only cattle used for export are impacted by bluetongue, there is little economic incentive for using the vaccine on the large numbers of United States cattle used for domestic purposes. This reduces the need and commercial value for any vaccine.

Although *Culicoides* control is an option to prevent or interrupt a bluetongue virus outbreak in domestic animals, the biology of these small and very numerous insects is a daunting control challenge. Outbreaks and problems with bluetongue subside due to weather and climatic conditions that naturally reduce *Culicoides* populations. *Culicoides* control has not been shown to interrupt bluetongue transmission.

References

Gibbs EPJ, Greiner EC (1989) Bluetongue and epizootic hemorrhagic disease. In Monath TP (ed) The arboviruses: epidemiology and ecology. CRC Press, Boca Raton, FL, pp 39–70

Tabachnick WJ (1996) *Culicoides variipennis* and bluetongue-virus epidemiology in the United States. Ann Rev Entomol 41:23–43

Walton TE, Osburn BI (eds) (1992) Bluetongue, African horse sickness and related orbiviruses. CRC Press, Boca Raton, Florida, 1042 pp

Boat Flies

Members of the family Notonectidae (order Hemiptera).

► Bugs

Bodenheimer, Friedrich (Frederick) Simon

Friedrich Bodenheimer was born in Cologne on June 6, 1897. He was accepted into medical school in 1914 in Munich, but soon volunteered for service in World War I in the German army. He served on the eastern front, realized the level of anti-semitism that existed, resolved eventually to emigrate to Palestine (now Israel), and decided to study entomology as a profession that would be useful in Palestine. He completed his studies at Universität Bonn by 1922, and with a doctorate in philosophy (and specialty in entomology). Before he left for Palestine, he visited the natural history museum in Hamburg, and chose to spend time studying Coccoidea. His viewpoint was that every entomologist should have a thorough taxonomic understanding of one group of insects. His choice of Coccoidea proved appropriate for his future work in Israel. Next, and still before leaving Europe, he spent six months at the R. Scuola Superiore di Agricoltura di Portici in Italy. There, he was able to study with Grandi and Silvestri, in an environment similar to that of Palestine. He moved to Palestine in 1922 and took up his appointment as head of the Division of Entomology (in fact the only entomologist) of an Agricultural Experiment station (in fact the yard of a high school) in Tel Aviv. His first task in Palestine was to inventory the pest species. He did this as a book (1931) "Die Schädlingsfauna Palästinas." In 1923 he married Rachel Ussishkin, and enlisted her help in reviewing pre-Linnean entomological works to produce his (1928–1029) "Materialen zur Geschichte der Entomologie bis Linné," a history of entomology. In 1928, he moved to the Hebrew University in Jerusalem as professor of zoology and was required to lecture to students. A difficulty was that he was required to lecture in Hebrew, that he did not speak Hebrew, and there were no Hebrew texts for the subjects in which he was required to lecture; eventually, he compiled the necessary textbooks, publishing nine of them (and later four in Turkish and one in French). He continued his interests in agricultural pests and published (1951) "Citrus entomology in the middle east," and (1957, with E. Swirski) "The Aphidoidea of the middle east." His professorship in zoology and acquired knowledge over 25 years in entomology and broader aspects of zoology induced him to write (1958) "Animal ecology to-day," in which he emphasized the importance of climate. He published more than 420 works. In 1948, although deemed too old for military service, he nevertheless served in the Israeli army, and was twice wounded. He died on October 4, 1959. He was a legendary figure, the founder of entomology in Palestine (Israel).

Reference

Harpaz I (1984) Frederick Simon Bodenheimer (1897–1959): idealist, scholar, scientist. Ann Rev Entomol 29:1–23

Body Lice

Members of the family Pediculidae (order Phthiraptera).

► Chewing and Sucking Lice
► Human Lice

Bogong Moth, *Agrotis diffusa* (Boisduval) (Lepidoptera: Noctuidae)

In most respects, Bogong moth is a typical cutworm, and is one of the more important and widespread cutworms in Australia. However, it is distinguished by its migratory tendencies: dispersal into the Australian mountains for a period of aestivation during the summer, followed by dispersal back to the plains in the cooler months. In this respect (as well as morphology) it is quite similar to an American species, *Euxoa auxiliaris* (Grote), also known as army cutworm. However, bogong moth is an interesting and well-known element in the culture of the aboriginal people of Australia, where historically the moths were collected for human consumption, so there is an unusual element of cultural anthropology associated with this moth.

Bogong moth inhabits principally the pasture-land west of the Great Dividing Range of eastern Australia (Victoria, New South Wales, Queensland), but during the summer months the moths migrate to higher country. In particular, they aggregate near Mount Bogong in the Alpine National Park, which serves as the basis of their common name. During the summer, they congregate in caves and rock crevices until autumn, when they return to the plains to deposit their eggs. They can accumulate in tremendous numbers on the floors and sides of the caves. The moths are highly nutritious, and the Aborigines traditionally have taken advantage of this resource and collected them by knocking them into bark, kangaroo skin containers or nets, and then roasting them in the hot ashes of a fire to remove the wings and legs. The moth carcasses were mashed together into "moth meat," which is said to have a nutty flavor resembling almonds or walnuts. They were formed into cakes, and if smoked, preserved well for a week or longer. The fat content is 50–60%, and harvest of moths by aborigines early in the twentieth century is estimated at several tons annually. Some tribes harvested the moths for 2–3 months annually, so the moths were a staple of the aboriginal diet, not just a minor component.

Life Cycle and Description

Eggs are deposited at the base of plants near the soil in the autumn after moths have descended from the mountains. The eggs soon hatch and the winter months are passed in the larval stage. Larvae initially are cream-colored, but later become green with pale and dark stripes, and dark spots. Overall, they are dark dorsally and pale ventrally, with a dark head and prothoracic plate. They attain a length of about 5 cm. They hide in the soil during the day, emerging at night to ascend plants and to feed. The larvae mature in spring, pupate in the soil, and after about a month the adults emerge to feed on nectar at flowers. The adults are variable in color, ranging from brown to almost black. However, they typically bear a dark streak on each forewing that is interrupted by a light circular spot and a light bean-shaped light-colored spot. The hind wing is light brown with a darker border. The wingspan is about 5 cm. The adults migrate to the mountains for the summer months, returning to the lower pasturelands in the autumn. In the mountains, the moths are reported to fly but not to feed. Interestingly, the American equivalent of bogong moth, army cutworm moth, was until recently thought to aestivate during the summer months in the Rocky Mountains, where aggregations are fed upon by grizzly bears, but not by the indigenous people of the region. Army cutworm has since been shown to feed at night on flowers at high altitudes of the Rocky Mountains. Perhaps the bogong moth also sustains itself during the summer by nocturnal feeding.

Economic Importance

Although bogong moth is an important food source for wild vertebrate animals and of the indigenous people of Australia, it is also considered to be damaging to some crops. Larvae feed on a variety of wild broad-leaf herbaceous plants such as cape weed, *Cryptostemma calendula* (Asteraceae), but do not thrive on grasses. Among cultivated plants damaged are alfalfa, linseed, cereal grains, cabbage, cauliflower, and English peas.

These moths also can be a nuisance. Sometimes strong wings carry the moths over the mountains to the cities of the eastern seaboard of Australia, and great numbers invade cities such as Canberra, Melbourne and Sydney.

► Army Cutworm
► Native American Culture and Insects
► Entomophagy: Human Consumption of Insects

References

Common IFB (1952) Migration and gregarious aestivation in the bogong moth *Agrotis infusa*. Nature 170:981–982

Common IFB (1954) A study of the ecology of the adult bogong moth *Agrotis infusa* (Boisd): (Lepidoptera: Noctuidae). Aust J Zool 2:223–263

Flood J (1980) The moth hunters. Aboriginal prehistory of the Australian Alps. Australian Institute of Aboriginal Studies, Canberra, Australia

Bohart, Richard M

Born on 28 September 1913 in Palo Alto, California, USA, Bohart became interested in insects as a young child, and went on to earn three degrees in entomology at the University of California at Berkeley. He taught at the University of California at Los Angeles (UCLA) from 1938 to 1941 before enlisting in the

U.S. Navy. He joined the faculty of the University of California at Davis in 1946 and retired in 1980.

Bohart is known for his contributions on the systematics of wasps and mosquitoes. He authored over 200 publications, including six books. Foremost are "Sphecid Wasps of the World" (with A.S. Menke) and "The Chrysidid Wasps of the World" (with L.S. Kimsey). Over the years, he acquired an outstanding collection of Nearctic Hymentoptera. He also acquired a number of successful graduate students who went on the populate museums, state departments of agriculture, and universities. Indeed, his love of students was said to be surpassed only by his affection for wasps. He died on 1 February 2007, but will long be remembered as one of the world's most important hymenopterists.

Reference

Garvey KK (2007) Richard M. Bohart. Am Entomol 53:58–59.

Bohartillidae

A family of insects in the order Strepsiptera.

► Stylopids

Boheman, Carl Heinrich

Carl Boheman was born in Jönköping, Sweden, on July 10, 1796. From the age of eight, he showed an interest in entomology. He asked permission of his father to study Latin, because Latin was necessary to read publications on natural history, although his father expected him to become a businessman. In 1812, he became a student at the university of Lund, and began to study law, but abandoned this in 1813 to enter the Swedish army. His army career gave him spare time for his favorite occupation, entomology, but he retired from the army in 1844 with the rank of captain. His army career allowed him to travel and collect insects. In 1841, he was appointed head of the entomological section of the natural history museum of Stockholm. He gave his collection to the museum, and during the following 26 years he built the museum's collections considerably. His greatest published works were his descriptions of new species in eight volumes of Schönherr's "Genera et species curculionidum" (1833–1845), his "Insecta Cafrariae" (1838–1857) and "Monographia cassididarum" (1854–1862). He published about 50 important papers, and was the describer of the boll weevil, *Anthomonus grandis*. In 1867 he resigned from his position, but continued to work at the museum until just a few days before his death in Stockholm on November 2, 1868.

References

Stål C (1869) Notice nécrologique sur C.-H. Boheman. Annales de la Société Entomologique de France 9:105–106

Boisduval, Jean-Baptiste Alphonse Dechauffour De

Jean-Baptiste Boisduval (Fig. 54) was born in Normandy, France, on June 17, 1799. He was employed by Dejean as curator of the latter's insect collection. With Lacordaire as co-author, he published (1835) "Faune entomologique des environs de Paris…" which follows the same theme as Fourcroy's (1785) work. He became one of the most famous lepidopterists of France, was one of the original members of the Société Entomologique de France, and an honorary member in 1866. In 1860 he was awarded honorary membership in the Société Entomologique de Belgique. He collected not only Lepidoptera (acquired not only from Europe but from North America too) but also Coleoptera and Hemiptera, and published about 50 works. He died in Normandy on December 30, 1879.

Boisduval, Jean-Baptiste Alphonse Dechauffour De, Figure 54 **Jean-Baptiste Boisduval.**

His collection of Lepidoptera was sold in France, his Elateridae are in the Natural History Museum (London), and the type specimens of his Curculionidae in Brussels.

References

Anon (1880) Jean-Baptiste Alphonse Dechauffour de Boisduval. Entomologist 13:1–19

Anon (1880) Dr. Boisduval. Entomologist's Monthly Magazine 16:235–236

Essig EO (1931) In A history of entomology. The Macmillan Company, New York, NY, pp 559–562

Bokor, Elemér

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Elemér Bokor was born on the 19th of January 1887, at Sátoraljaújhely, in the North- Eastern corner of Hungary. As a young man he was already interested in entomology and in the beetles which lived in caves. Although he received a military education, he carried on with his nature studies, and in 1913 he published some important works on the blind cave-dwelling beetles (új vakbogarak Magyarország faunájából. *Annales Musei Nat*. Hung. XI., 1913, and Három új vakbogár Magyarország faunájából. *Annales Musei Nat. Hung*. XI., 1913). He fought on the Russian Front in World War I as a professional officer of the Austro-Hungarian army. He suffered the life of a prisoner of war in Russia for some years. On his return to Hungary in 1921 he researched the arthropod fauna of 102 caves. In 1923 he surveyed the Abaligeti Cave and the result of this work formed the basis for his doctoral dissertation. He received his doctorate in 1924. Elemér Bokor devoted his life to the research of the Hungarian caves. He has described several new species of cave dwelling coleoptera. He was the president of the Hungarian Speleological Society as well as the Entomological Society, providing great impetus to the work of his colleagues.

References

Balázs D (1993) Magyar utazók lexikona. Panoráma, Budapest, Hungary

Székely K (1987) 100 éve történt. Karszt és Barlang. Budapest, Hungary

Bolitophilidae

A family of flies (order Diptera).

► Flies

Boll Rot of Cotton

This is an insect-transmitted disease of cotton.

► Transmission of Plant Diseases by Insects

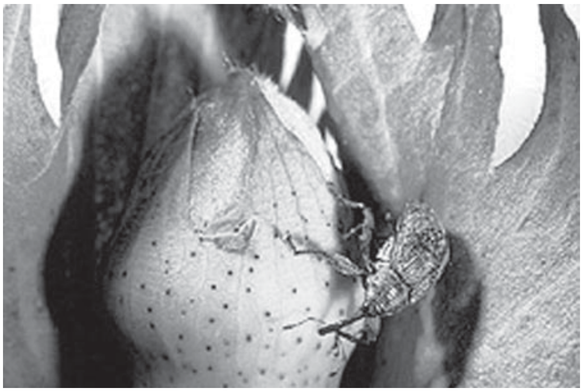
Boll Weevil, *Anthonomous grandis* Boheman (Coleoptera: Curculionidae)

This insect, known also as the cotton boll weevil, is a very serious pest of cotton in the western hemisphere, and has had a significant effect on the history of the United States. Little was known about it until about 1892 when it appeared in Texas, having moved northward from Central America or Mexico. Once it reached the United States, it spread rapidly to the north and east, and slowly to the west, eventually reaching California in 1982. In the early part of the twentieth century, little could be done to prevent damage by this insect, and the agricultural economy of the southeastern United States was seriously disrupted by this insect. Numerous farms, cotton gins and related interests such as stores and banks ceased business because the cotton crop was destroyed. On the other hand, the appearance of boll weevil in the southeast stimulated the diversification of the economy because the residents could no longer depend exclusively on cotton for their livelihood. Thus, the community of Enterprise, Alabama erected a statue in recognition of the beneficial side effects of this devastating pest (Fig. 55). Much later in the century boll weevil gained entry to South America. It now infests cotton growing regions of Argentina, Brazil, and Paraguay.

Boll Weevil, *Anthonomous Grandis* Boheman (Coleoptera: Curculionidae), Figure 55 **Boll weevil statue in Enterprise, Alabama (photo USDA, Agricultural Research Service).**

Description and Life History

Boll weevil is capable of completing its life cycle in 25 days, so 8–10 generations are possible annually. The adult stage overwinters, emerging from beneath leaf debris, bark, trash and other protected places from March to June. It begins to feed immediately and as squares become available they begin production of eggs. Females can produce from 100 to 300 eggs. The white eggs are about 0.5 mm long. The eggs hatch in 3–4 days, and the larva feeds within the square or boll. The larva is white and legless, with a brown head. It matures in about 9 days and measures about 13 mm in length. There are three larval instars, which can be distinguished by head capsule width measurements (0.4, 0.6, and 09 mm, respectively for instars one to three). At maturity, it forms a pupa within the feeding cavity, and then the adult emerges in about 5 days. The adult is gray or brown to black in color, measures about 4 mm in length, and bears a long snout. In the autumn the weevils leave the crop for sheltered (Fig. 56) areas and enter diapause. Diapause is a critical period for boll weevils, and survival is enhanced when weather is moister and above average in temperature.).



Boll Weevil, *Anthonomous Grandis* Boheman (Coleoptera: Curculionidae), Figure 56 **Adult boll weevil feeding on a cotton boll (photo USDA, Agricultural Research Service).**

Host Plants

Boll weevil feeds exclusively on malvaceous host plants, principally cotton but also okra, hollyhock, and hibiscus.

Damage

Boll weevils cause injury when the adults chew into the square (blossom) and boll (fruit) where they feed and deposit eggs. The larvae also feed within these structures, and little or no fiber is formed.

Management

Boll weevils are most effectively managed by a combination of approaches. Some of the approaches include:

1. Early destruction of plants in the field. Early harvest and destruction of crop residue kills many weevils and deprives them of shelter.
2. Use of an early maturing cultivar. Early maturing varieties produce blossoms before many weevils are present, whereas late maturing varieties are attacked by higher numbers of insects, thereby experiencing more damage. Proper agronomic practices also encourage rapid growth and maturity of the crop, hastening development before the end of the season when weevils are most abundant.
3. Insecticide. Application of insecticide can alleviate weevil injury. Applications are made early to control weevils during blossom set and maturity. Applications may also be made late in the year to reduce the number of weevils entering diapause, and thereby reducing the number emerging in the spring of the following year.
4. Eradication. An eradication program is currently under way in the United States. A combination of host destruction, insecticide application, trapping with pheromone-based traps, and release of sterile insects has eliminated boll weevil over much of its former range. Though initially costly, elimination of this key pest brings substantial savings to growers in the long run.

► Area-Wide Insect Pest Management

References

Hunter WD, Hinds WE (1905) The Mexican cotton boll weevil. USDA Bur Ent Bull 51:45–46

Hunter WD (1917) The boll weevil problem with special reference to means of reducing damage. USDA Farmers' Bull 48:1–40

Hunter WD (1922) The boll-weevil problem: methods of reducing damage. USDA Farmers' Bull 1262:1–31

Gaines RC (1959) Ecological investigations of the boll weevil, Tallulah, Louisiana, 1915–1958. USDA Tech Bull 1208:1–20

Palmer JO, Cate JR (1992) Overwintering survival of pre reproductive and post reproductive boll weevils (Coleoptera: Curculionidae) in central Texas. Environ Entomol 21:117–120

Bombycidae

A family of moths (order Lepidoptera). They commonly are known as silkworm moths.

► Silkworm Moths
► Butterflies and Moths

Bombyliidae

A family of flies (order Diptera). They commonly are known as bee flies.

► Flies

Bonnet, Charles

Charles Bonnet was born in Geneva in 1720 and remained in Switzerland all his life. He received training in law, and practiced it while deeply committed to biological studies. His sight was said to have been so damaged by the age of 25 by his constant use of microscopes that he could barely read or write thereafter. He was an observer and experimenter rather than a taxonomist. In 1745 he published "Traité d' insectologie," in which his "insectes" were all the invertebrate animals except molluscs, and the work contains results of his observations on subjects such as parthenogenesis in aphids, and respiration in caterpillars. His later books included "Contemplation de la nature" (two volumes, 1764–1765) and "Oeuvres d' histoire naturelle et de philosophie" (8 volumes, 1779–1783). He died in 1793.

Reference

Tuxen SL (1973) Entomology systematizes and describes: 1700–1815. Smith RF, Mittler TE, Smith CN (ed) History of Entomology. Annual Reviews Inc., Palo Alto, CA, pp 95–117

Book-Lice

Members of the insect order Psocoptera.

► Bark-Lice, Book-Lice and Psocids

Boopidae

A family of chewing lice (order Phthiraptera). They sometimes are called marsupial chewing lice.

► Chewing and Sucking Lice

Boreal

A term used to indicate northern faunal regions, though boreal regions can extend southward at higher altitudes.

Bootstrapping

A statistical method based on repeated random sampling with replacement from an original sample to provide a collection of new estimates of a parameter, from which confidence limits can be calculated.

Bootstrap Values

A measure of the reliability of phylogenetic trees generated using cladistic methods.

Boreidae

A family of scorpionflies (order Mecoptera). They commonly are known as snow scorpionflies.

► Scorpionflies

Borgmeier, Thomas

Thomas Borgmeier was born in Bielefeld, Germany, on October 31, 1892. After graduation from the Gymnasium ["high school"] of Bielefeld, he emigrated to Brazil and became a Franciscan monk. From 1912–1914 he studied philosophy in Curitiba, and from 1915–1918 theology in Petropolis. While he was a student, he became interested in entomology, in 1917 befriending Hermann von Ihering. A wealthy industrialist in Rio de Janeiro donated money that allowed Thomas to buy von Ihering's reprint library and a microscope. He was permitted by the Franciscans to pursue an entomological career. In 1924 he moved to the Museu Nacional in Rio de Janeiro, and then transferred to the new Instituto Biologico in São Paulo in 1928 as assistant in entomology. In 1933 he retuned to Rio de Janeiro as head of the entomological section of the Instituto de Biologia Vegetal in the botanical garden. He founded the journal Revista de Entomologia, and edited and published it until 1951 when financial difficulties ended it. Later he founded the journal Studia Entomologica. About 1973 he retired from entomological activities to a monastery in Rio de Janeiro. During his life, Thomas published 243 papers on ants and on insects associated with ant nests, especially the dipterous family Phoridae. He died on May 11, 1975.

Reference

Herman LH (2001) Borgmeier, Thomas. Bull Am Mus Nat Hist 265:48–49

Boric Acid

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This inorganic compound contains boron and many other non-volatile elements, and has many useful properties. The chemical formula is $H_3 BO_3$ and its sodium salt, or borax, is $Na_2 B_4 O_2 \cdot 10 H_2O$. A more water soluble formulation is $Na_2 B_8 O_{13} 4 H_2O$, known as disodium octaborate tetrahydrate. Formulations of borax and disodium octoborate tetrahydrate usually are known simply as "borates." Boric acid is used as a fungicide, bactericide, antiseptic, and as an insecticide, but has several other useful properties such as a flame retardant. Normally it is produced from borate minerals by reaction with sulfuric acid.

From a toxicological perspective, boric acid is a relatively nontoxic (to people and pets) insecticide. Its oral toxicity is reported to be 2,660 mg/kg in rats. Borax is even less toxic, with oral toxicity to rats estimated at 5,600 mg/kg. These chemicals are not readily absorbed by skin. However, there is some risk associated with chronic exposure to aerosols, so respiratory protection is advised when working around high concentrations. Also, accidental ingestion of large quantities can be lethal. Use of goggles and gloves are recommended for those applying these chemicals.

Normally, boric acid products are active only when insects ingest the material (as a stomach poison), though this can occur during grooming (cleaning the antennae and legs) as well as feeding. It is used in structures to control such urban pests as cockroaches, ants, fleas, termites and silverfish. It may be mixed into bait, particularly for cockroach and ant control, and is quite effective. It also is sprayed onto, or impregnated into, wood for control of termites and wood boring beetles. Application as a dust into wall voids, attics, and cracks and crevices harboring insects also is popular. Because cockroaches spend most of their time in cracks and crevices, application of boric acid into such harborages is advisable. The product is normally blown in with a bulb duster, but must be finely divided to achieve deep penetration. Research has shown that crack and crevice treatment is superior to broadcast treatment for cockroaches. Boric acid is superior to borax for cockroach control. Although it commonly takes several days for cockroaches to die from boric acid poisoning, boric acid is especially useful for sensitive areas like schools, pet shops and zoos. The slow action can be an advantage for cockroach suppression because nymphs will feed on the feces of adults, so boric acid can be transported back to harborages. Similarly, cannibalism of boric acid-killed roaches can kill the scavengers.

Boric acid is often formulated with diatomaceous earth or silica gel (as desiccants) or tricalcium phosphate (to reduce caking). Sometimes other toxicants are included, including pyrethrins or sodium fluoride. Dusts can be repellents, and although boric acid dusts tend to have low repellency, inclusion of additives in boric acid formulations increases the likelihood of the product being repellent. Thus, additives should be kept at low levels. Similarly, when incorporated into bait, boric acid concentrations should be kept low (usually 1%) so insects will not avoid ingestion. Boric acid is sometimes mixed into cleaning solutions when floor mopping in cafeterias.

Though very persistent and water soluble, boric acid is not readily impregnated deep into wood, so although the outside of structural timbers may be protected, termites may burrow through incompletely impregnated lumber. Formulations of borates and penetrating agents such as ethylene glycol are used to improve wood penetration. The formulation can be sprayed or painted onto untreated wood surfaces, or applied as a foam. Penetration is affected by a number of factors, including moisture content, and wood protection is best achieved when the wood is freshly harvested, or re-wetted to take advantage of the solubility of the damp wood to borates. Other factors affecting protection include thickness of the wood and thoroughness of application. For deep penetration, injection may be necessary. Existing fence posts, mailbox supports, and other wood in contact with soil can be protected by drilling a hole and inserting borate gel or rods, then sealing the hole. Boric acid products have herbicidal activity, however, so vegetation adjacent to treated wood can be affected. Overall, boric acid products are very useful for urban pest control, but should be used as a component of a broader management plan, not as the sole component.

References

Quarles W (1998) Borates for wood protection. The IPM Practitioner 20(3):1–12

Quarles W (2001) Boric acid, borates and household pests. The IPM Practitioner 23(3):1–12

Boridae

A family of beetles (order Coleoptera). They commonly are known as conifer bark beetles.

► Beetles

Bostrichidae

A family of beetles (order Coleoptera). They commonly are known as horned powder-post beetles.

► Beetles

Botanical

A product derived from plants or plant parts. This term often is used to describe insecticides derived from plants.

► Botanical Insecticides

Botanical Insecticides

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Botanical insecticides are those products used to kill or repel insects that consist of dried, ground plant material, crude plant extracts, or chemicals isolated from plants. The recorded use of plant material or plant extracts for insect control dates back at least 200 years. Botanical insecticides were important tools for crop protection prior to the discovery of the insecticidal action of DDT; the subsequent development of inexpensive and highly effective synthetic insecticides rendered botanicals all but obsolete. However, botanicals are enjoying renewed interest as the popularity of organically-grown food increases because botanicals are among only a handful of “natural” insect control products that can be used in organic agriculture.

Although botanicals are products of nature, they should not be considered absolutely safe or non-toxic unless so demonstrated. The active ingredients in certain botanical preparations used as insecticides are relatively toxic to animals and humans and several are toxic to fish. However, most are used at very low concentrations of active ingredients, minimizing the risk to humans and wildlife from exposure. On the other hand, the active principles in virtually all botanicals are rapidly degraded in the environment, often by exposure to sunlight, and thus are considered non-persistent. Apart from this generalization, the few botanical insecticides in commercial use vary greatly in their sources, chemistry, toxicity and other properties.

Pyrethrum

Pyrethrum is the most widely used botanical insecticide. It is the oleoresin obtained by solvent extraction of the fresh-picked flowers of the daisy *Tanacetum cinerariaefolium* (Asteraceae), native to the Balkan region of eastern Europe. Most of the world supply of pyrethrum in recent times has come from Kenya, but large scale production is under way in Tasmania (Australia). The oleoresin contains six esters with insecticidal properties. The most potent, pyrethrins I and II, typically make up 20% of the resin by weight. The pyrethrins are axonic poisons in insects and are characterized by a fast knockdown time in flying insects. They degrade rapidly in the presence of sunlight. In purity, the pyrethins have appreciable toxicity to mammals, but given their concentration in the resin and the dosages normally used, pyrethrum has minimal toxicity to mammals. Pyrethrum is a broad spectrum insecticide and has more registered uses (in the U.S.A.) than any other insecticide. Most products containing pyrethrum or pyrethrins as active ingredients are formulated with a synergist, piperonyl butoxide, that prevents the metabolic degradation of the insecticide within the insect's body, thus increasing potency. The rapid environmental breakdown of pyrethrum created the impetus for the industrial development of the synthetic pyrethroids, now the dominant class of agricultural insecticides.

Rotenone

Rotenone is the ground roots or rhizomes of the tropical legumes *Derris* (southeast Asia) and *Lonchocarpus* (South America, also known as cube root), or resins extracted from them. The name is also applied to the major insecticidal constituent, although each plant contains a number of related isoflavonoids, most of which are insecticidal. Rotenone is a mitochondrial poison in insects and vertebrates. In purity it is quite toxic to mammals, but most home and garden preparations contain 1% rotenone at most. Owing to its moderate persistence on foliage (3–5 days) and chronic effects on laboratory animals, there are some concerns about it potential health impacts on humans. It is especially toxic to fish, and in fact, more rotenone is used as a commercial fish poison (piscicide) than for insect control. As a fish poison, rotenone has been used for at least 300 years, and at least 150 years as an insecticide. In insects, rotenone is a slow-acting stomach poison particularly effective against plant-feeding beetles (e.g., the Colorado potato beetle), but much less effective against caterpillars.

Neem

Neem is an extract of the seeds of the Indian neem tree, *Azadirachta indica* (Meliaceae). Native to the Indian subcontinent, it has been widely planted throughout tropical and subtropical regions of the world. Dried neem leaves have traditionally been used in protection against stored product pests. Neem has a diverse array of behavioral and physiological actions against insects, most of which are attributable to the complex triterpenoid azadirachtin. This chemical is reputed to be the most potent antifeedant to insects (it deters insect feeding in nanogram quantities), but is also a potent disruptor of the insect neuroendocrine system. The most obvious manifestation of this latter action is that azadirachtin inhibits the molting process in insects. As such, azadirachtin is a slow-acting insecticide and requires ingestion to be effective. Another interesting property of azadirachtin is its systemic action in some plants. Of primary importance, neem and azadirachtin are non-toxic to most non-target organisms, including humans. Like pyrethrum, neem is rapidly degraded in the environment by sunlight. Neem became commercially available in the U.S.A. in 1990, and is beginning to gain acceptance for insect control in some agricultural commodities and especially in organic food production.

Tobacco

Water extracts of tobacco have been used to kill insects for over 300 years. Nicotine (from *Nicotiana tabacum*, Solanaceae), nornicotine (from *N. sylvestris*) and anabasine (from *Anabasis aphylla*, Chenopodiaceae) are alkaloids that are highly insecticidal. They poison both insects and mammals through a common mode-of-action, by mimicking the neurotransmitter acetylcholine and causing over stimulation of nerve synapses. Unlike some other botanical insecticides, nicotine is very toxic to humans, and poisoning can result not only from ingestion but from dermal exposure as well. As a consequence, nicotine is rarely used for insect control at present, although it is still used as a fogging insecticide in some greenhouses.

Other Botanicals

Other botanicals have seen some commercial use in North America. These include ryania, the ground stem wood of the Caribbean tree *Ryania speciosa* (Flacourtiaceae), containing alkaloids that poison neuromuscular junctions, and sabadilla, the ground seeds of the South American lily *Schoenocaulon officinale*, containing alkaloids that are axonic poisons. Both are examples of plants whose active principles, in purity, are relatively toxic to mammals, but for which the actual plant preparations used have a wide margin of safety to humans.

Essential oils from certain plants have been used traditionally in some regions as insect repellents. The best known among these is oil of citronella, obtained from lemongrass (*Cymbopogon nardus*, Poaceae), used as an alternative to DEET for repelling mosquitoes and biting flies. In addition, monoterpenes and phenols in clove oil, thyme oil, and various mint species have been recently shown to be insecticidal in a wide range of insects. As a result, several home and garden insect control products based on plant essential oils have been developed and these materials may have uses in agriculture (e.g., organic farming) as well.

Numerous other plant extracts have seen regional traditional use, especially in developing countries. Insecticides can be made from the seeds of chinaberry (*Melia azedarach*, Meliaceae), a relative of the neem tree, although in some countries the seeds contain substances that are toxic to animals. In the Peoples Republic of China, an insecticide is made from the bark of *M. toosendan*, considered by

Botanical Insecticides, Table 8 Properties of some important botanical insecticides

Property	Pyrethrum	Rotenone	Neem	Essential oils	Nicotine
Country of origin	Kenya, Australia	SE Asia, Venezuela	India	Worldwide	Worldwide
Active ingredients	Pyrethrins (esters)	Rotenoids (isoflavonoids)	Azadirachtin (limonoids)	Monoterpenes, simple phenols	Nicotine (alkaloids)
Formulations	Numerous	Dusts, WPs	ECs	Numerous	ECs, Dusts
% actives in formulation	6% EC	1% Dust 5% WP	1–4.5% EC	35% EC 6% Aerosol	40% EC
Action on pests	Contact/knock-down toxin	Stomach poison/ cytotoxin	Stomach poison/IGR/ antifeedant	Contact/ knockdown toxin	Contact/ knockdown toxin
Persistence	Very limited	Limited	Very limited	Very limited	Limited
Mammalian toxicity	Minimal	Moderate; very toxic to fish	Non-toxic	Non-toxic	Very toxic

some authorities to be taxonomically synonymous with *M. azedarach*. The product, Toosendanin, is reported to be effective against fruit and vegetable pests. The tropical trees *Quassia amara* and *Ailanthus altissima* (Simarubaceae) contain insecticidal terpenoids that can be extracted from the wood and used for insect control. Dried leaves of *Haplophyton cimicidum* (Apocynaceae) have been used for centuries in Mexico and Guatemala to prepare "cockroach powder" owing to a series of alkaloids in the foliage of the plant. Seeds of the custard apple (*Annona reticulata*, Annonaceae), sweetsop (*A. squamosa*) and soursop (*A. muricata*) contain potent insecticidal acetogenins and have been used for insect control in many tropical countries in the Old and New World. The dried, powdered flowers of *Rhododendron molle* (Ericaceae) have a long history of use as an insecticide in China.

Botanical insecticides are unlikely to displace conventional synthetic insecticides in many pest management contexts, but they should gain increasing favor in situations where human exposure is unavoidable and safety is of primary concern. Botanicals will also see continued use in developing countries where many of the plants from which they are obtained can be readily grown and the insecticidal preparations are a safer and less expensive alternative to imported synthetic pesticides.

► Alleochemicals
► Chinaberry
► Pyrethrum
► Persian Insect Powder
► Neem

References

Arnason JT, Philogene BJR, Morand P (eds) (1989) Insecticides of plant origin. American Chemical Society, Washington, DC, 213 pp

Isman MB (2000) Plant essential oils for pest and disease management. Crop Prot 19:603–608

Isman MB (1995) Leads and prospects for the development of new botanical insecticides. Rev Pestic Toxicol 3:1–20

Koul O, Dhaliwal GS (eds) (2001) Phytochemical biopesticides. Harwood Academic Publishers, Amsterdam, The Netherlands, 223 pp

Bot Flies

Members of the family Oestridae (order Diptera).

► Flies
► Myiasis

Bothrideridae

A family of beetles (order Coleoptera). They commonly are known as dry bark beetles.

► Beetles

Boutonneuse Fever

This is a bacterial disease transmitted by ticks.

► Ticks

Bovine Babesiosis

This is a protozoon disease of cattle transmitted by ticks.

► Piroplasmosis

Bovine Hypodermosis: Phenology in Europe

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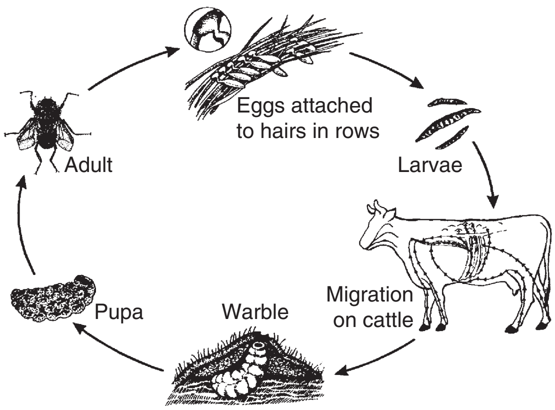
The life cycle and biology of the warble fly, *Hypoderma bovis*, and of *Hypoderma lineatum*, exhibit regional and local variation attributable to climatic and weather conditions (Fig. 57).

In Andalusia (southern Spain), it is possible to find *H. lineatum* adults from the middle of February to the beginning of May, first instar larvae (L1) in the esophagus from April to November, third instar larvae (L3) in the back from the middle of



Bovine Hypodermosis: Phenology in Europe, Figure 57 **Life cycle of *Hypoderma* spp. on cattle: eggs (a) are deposited on the legs of the host; larvae (b) burrow into the animal and migrate through the animal, eventually reaching the back where a swelling (warble) is formed (d); the mature larva drops to the soil to pupate (e) and an adult emerges from the pupa.**

November to the end of March, and the mature larva ready to commence pupation from the middle of January to the end of March. Adults of *H. bovis* occur between May and June, L1 from November to January, the period of warbles from mid-December to May, and the dropping of L3 from mid-March to May. It is possible to find third instar larvae of *H. lineatum* in the back of bovines from October to early May. Adults are found during April or May, although in some years some of them can be seen in March. First instar *H. lineatum* appear in the gullet of bovines between September and December. *Hypoderma bovis* is scarcer in western and southwestern Spain, but display the same phenology. In some areas of Portugal, such as the "Alentejo" and "Centro" areas, phenology clearly is similar to that of western Spain, which is logical due to the geographic proximity of these regions.

The phenology (Table 9) is very similar in northern Africa. In Morocco, it is possible to find adults from February to the middle of May, and L3 in the back of the hosts from December to April. In Algeria, adults are found between the end of March and July. The L1 stage can be found in the host's esophagus between August and December, while it is found in the rachis from the beginning of October until the middle of February. Warbles are found during much of the year, from October to March. In other studies, adults occur between March and August (the latter ones probably are *H. bovis*), L1 is observed in the rachis and gullet between July and December, and warbles occur between September and February.

On the other hand, there are significant differences in phenology between northern and southern Spain. In northwestern Spain (Galicia), it is not possible to observe the first flies until the middle of May, but after that they can be seen until the middle of September. First instar larvae are found from the middle of September to the end of January, or from August to December. Warbles are found from February until May. The phenology of *Hypoderma* in the north of Spain is more similar to the countries of central Europe than to the southern areas of the same country.

In the central and eastern regions of France, *Hypoderma* adults and eggs are found between the end of May and the middle of August. First instars (the period of greatest risk due to local and systemic adverse reactions) occur from the middle of August to the end of February. Warbles are found in the backs of hosts during March to May, or possibly from March to July. It is likely that the phenology is intermediate between the countries of central Europe and the southern Iberian peninsula. In Switzerland, the phenology is similar to that in France.

In Ireland, there is a delay in the presence of warbles. Warbles appear in July and August rather than in February and March. Ireland, together with the rest of United Kingdom, and also Holland, are examples of locations where *Hypoderma* are practically eradicated, at least from cattle.

In eastern Europe, specifically Czechoslovakia, extensive investigations have been conducted on *H. bovis* (throughout the country) and *H. lineatum* (in Slovakia). Warbles of *H. bovis* appear in heifers from the end of March to June, and in cows in May to June. Dropping of larvae and pupation were observed from early April to early July, while flies

Bovine Hypodermosis: Phenology in Europe, Figure 58 Warble being removed from beneath the skin of host.

are present from early June to the beginning of September. For *H. lineatum*, the period of warbles was earlier and shorter, from the second half of February to the end of April. Pupation was observed from the end of March to the end of April, and flies from May until the first days of July.

In countries such as Poland, warbles (Fig. 58) have been detected in February, though normally the warbles do not occur until April. When occurring early, warbles are found in April, but when found normally, the warbles do not occur until May and June. It is possible to observe warbles until the end of July. In Romania, the period of activity of adults is May to September for *H. lineatum*, and between August and September for *H. bovis*. The first warbles produced by the second instar larvae appear in the southern part of the country at the end of January or early February. In the north, they occur from March to April. The third stage larvae leave the host's body from late April until the end of July (until August in the northern part of Romania). Thus, the phenology in Romania is similar to central Europe. Sometimes warbles are found in the back and lumbar regions of the host in September and as late as December; in these cases the larvae are dead.

As a general rule, *H. lineatum* occurs earlier than *H. bovis*. The occurrence varies from year to year, however, due to variation in environmental conditions. They occur earlier when it is warmer in the spring, summer or winter. In southwestern Spain, the mean annual maximum temperatures are 20–21°C, with maximum summer temperatures averaging 29–30°C, and mean annual minimum temperatures of 8–9°C. The cooler temperatures of eastern and central Europe slow the biology of these pests.

To avoid damage caused by larvae, knowledge of phenology is important. Before beginning a management or eradication effort, climatic variation in *Hypodermas* must be considered.

References

Boulard C, Argenté G, Hillion E (1988) Hypodermis bovine: description et incidence économique. Le Point Véterinaire 20 (111):17–30

Martínez-Moreno FJ (1992) Estudio inmunológico de la hipodermosis bovina. Doctoral thesis. Córdoba, Spain

Minar J (1993) Cattle hypodermosis, its investigations and suppression in Czechoslovakia. Academia, Praha, 207 pp

Bovine Hypodermosis: Phenology in Europe, Table 9 **Comparative phenology (chronobiology) of *Hypoderma* species in some European ecological regions**

Species	Hypoderma lineatum				Hypoderma bovis	
Region	Southwest	Central	East	Southwest	Central	East
L1	April–December	September–March	September–April	November–January	January–May	October–May
L3	October–April	February–May	February–April	December–May	May–July	March–June
Mature larvae	January–April	April–June	March–April	March–May	May–August	April–July
Adults	February–May	May–June	May–July	May–June	May–September	June–September

Morrondo P, López C, Panadero R (1995) Ciclo biológico y epidemiología de Hypoderma. Bovis 65:27–38

Reina D, Martínez-Moreno FJ, Martínez-Moreno A, Molina JM, Hernández-Rodríguez S (1994) Present ststus of warble fly in Extremadura (South-West of Spain). In: Improvement in the control methods for warble fly in cattle and goats. Commission of the European Communities, Brussels, Belgium, pp. 59–64

Bøving, Adam Giede

Born at Saby, Denmark, on July 31, 1869, Adam Bøving graduated from the University of Copenhagen in 1888. His interests included insect larvae, and those of *Donacia* (Coleoptera: Chrysomelidae) were the subject of his Ph.D. research. Then he was appointed Assistant Curator of Entomology at the Royal Zoological Museum in Copenhagen, and he continued to study beetle larvae. Two years after the death of his first wife, he moved to the United States in 1913 and found employment with the U.S. Department of Agriculture. His work still revolved around beetle larvae, but concentrated on those of economic importance. He took an American wife and citizenship. With F. C. Craighead as coauthor, he published in 1930–1931 in Entomologica Americana, the work "An illustrated synopsis of the principal larval forms of the order Coleoptera." This major work has been much-cited by later authors for the wealth of its informational content; no such comprehensive study appeared in print until the second volume of F. C. Stehr's (1991) Immature Insects. Bøving died in Washington on March 16, 1957.

Reference

Mallis A (1971) Adam Giede Böving. In: American entomologists. Rutgers University Press, New Brunswick, NJ, pp 431–433

Brachelytry

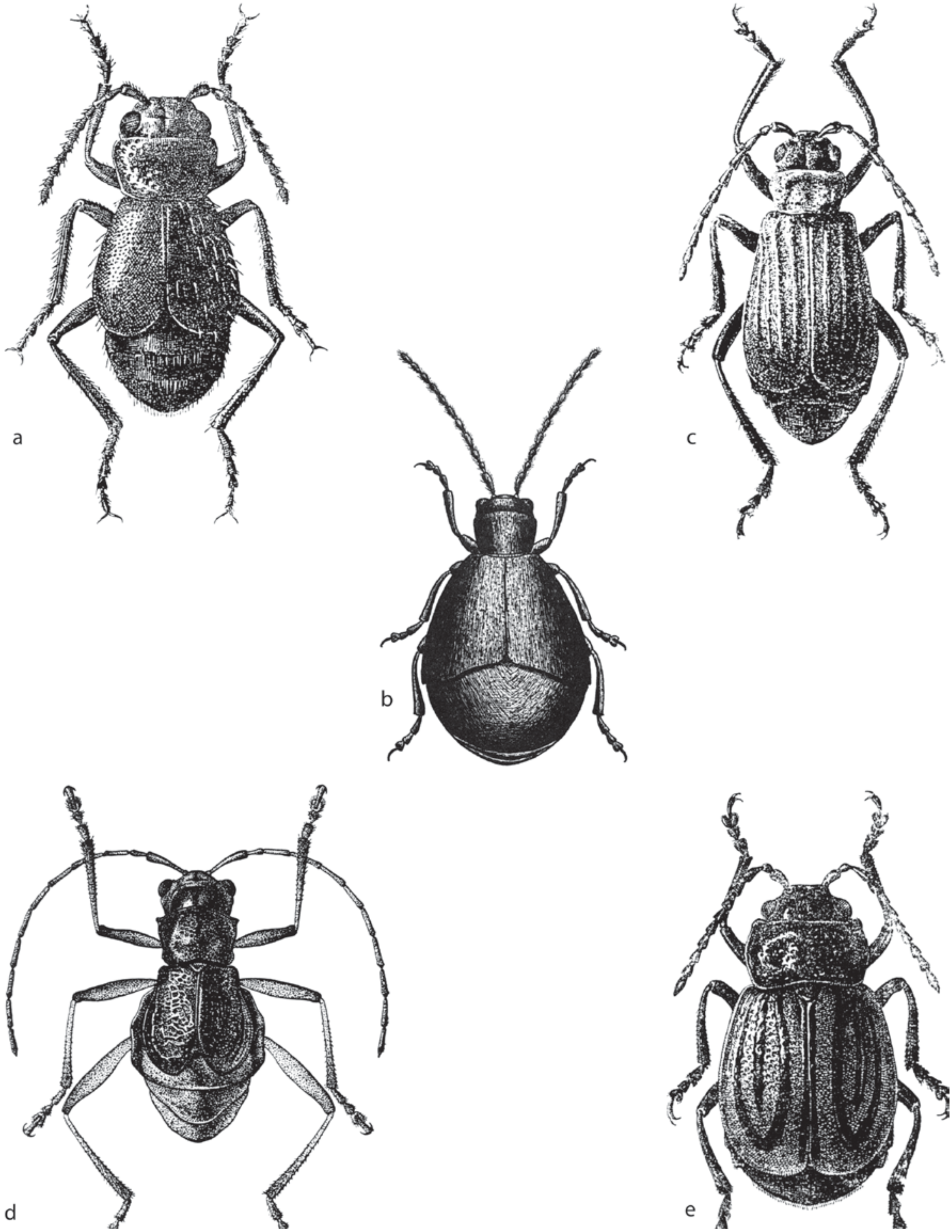
PIERRE JOLIVET
Paris, France

Elytra are characteristic of Coleoptera, and substantial thickening of the first pair of wings (elytra) is uncommon among other orders of insects. The elytra are modified mesothoracic wings, normally rigid and fitting over the abdomen. Brachelytry is the possession of abbreviated wing covers or elytra. Brachelytrous insects are commonly found among the Coleoptera, including the Carabidae, Staphylinidae, Cerambycidae, Histeridae, Meloidae and Chrysomelidae. It seems most common among Galerucinae and is unusual among Alticinae. Both subfamilies are closely related, as part of the Trichostomata. Alticinae, Galerucinae (both Chrysomelidae) and Bruchidae sometimes show only an exposed pygidium, with only a small shortening of the elytra. Some beetle families are exclusively brachelytral, as is the Lymexylidae, but they fly very well, as do most of the myrmecomorphic Cerambycidae. Brachelytry should not be confused with physogastry (the swelling of the abdomen to an unusual degree due to the hypertrophy of fat bodies, ovaries or both), which can result in a similar appearance. In that case, the abdomen is so big that it is protruding over the end of the elytra. Physogastry is common among certain Chrysomelinae (*Gastrophysa*) and Galerucinae (*Agelastica*) (both Chrysomelidae). Brachelytry occurs also in Dermaptera and Gryllidae.

Pseudophysogastry (artificial swelling of the abdomen) is also common among cavernicolous or termitophilous beetles. In many Meloidae (*Meloe*), the elytra appear to fit badly, as among physogastric beetles. The elytra overlap but the beetle is apterous already as a pupa, as in *Timarcha*. This means a long history of apterism. In certain cases, brachelytry can be seen as a consequence of apterism, but many macroelytrous (normal) beetles are alternatively brachypterous or apterous (*Chrysolina banksi*), or totally and permanently apterous (*Timarcha*). Often, in that case, the elytra are fused. They are never fused among brachelytrous beetles.

A set of mutations is surely at the origin of brachelytry, but macroelytrous and brachelytrous individuals do not occur in the same species. Brachyeletry is found mostly among mountainous or desert frequenting species or genera, but also among parasitic species. It seems absent from *arctic* species, which would seem to benefit from protection on the abdomen, though apterism or brachypterism there remains frequent. Brachelytry is also frequently linked with brachy-or apterism, though some brachelytrous beetles maintain complete wings and fly very well. Brachelytry is a very old, derived character (Fig. 59). There are a number of beetle families where the elytra become truncated, with the apical part of the abdomen uncovered, including Hydroscaphidae, Histeroidea, Staphylinidae, Nitidulidae, Inopeplidae, etc. In all these groups, the elytra completely cover the folded wings. In some others, such as the myrmecomorph Cerambycidae and the Lymexylidae, the wings are left free without any protection. The adaptive significance of this feature is not well understood. Among the Staphylinidae, the main adaptive advantage of abbreviated elytra seems to be a greater flexibility in the abdominal region, but that does not explain the truncated elytra of Histeridae. Many beetles with truncate elytra and with wings completely covered live on the ground, and are saprophagous. But there are always exceptions; among the Histeridae, for instance, some genera have the elytra entirely covering the abdomen. In the Staphylinidae, usually there are at least four abdominal segments exposed, sometimes six. There are, however, some Staphylinidae with the elytra not truncate.

There are also cases where the elytra are abbreviated and do not completely cover the folded wings. In *Atractocerus* (Lymexylonidae), the elytra are very reduced and don't cover the wings. There are also some myrmecomorphic Cerambycidae, some Cantharidae (*Malthinus* and *Malthodes*), the male of Stylopidae, and several Rhipiphoridae, which are more-or-less brachelytrous, with exposed wings. In male Stylopidae, the elytra are peculiarly modified to form balancing organs, like the halters of Diptera. Often those beetles are free-living and floricolous. This elytral reduction is increased among some endogeous Staphylinidae (Leptotyphlinae and Osoriinae), where the elytra are reduced to two contiguous scales, covering only the posterior thoracic segments and the first abdominal segment. A similar situation is found among a Moroccan *Staphylotroglops* (Cantharidae). The reduction of the elytra can also be done laterally, revealing the sides of the abdomen (some Cetonidae) or be disjunct on the back (Oedemeridae). There are also cases where only the females are



Brachelytry, Figure 59 Somes cases of brachelytry (**a**) ***Nyctiphantus nocturnus*** (Semenov). Russia. Transcaspia; (**b**) ***Marseulia dilativentris*** (Reiche). Israel; (**c**) ***Theone octocostata*** (Weise). Tibet; (**d**) ***Parageina andrewesi*** (Jacoby). India; (**e**) ***Galeruca barovsky**i* Jacobson. Tibet (after Jolivet P (2005) Brachelytry among Chrysomelidae. Lambilionea 105(3):371–384).

apterous and brachelytrous, as with *Metacycla* in Central America (Chrysomelidae: Galerucinae). Also, the elytra are completely absent in the females of glow-worms (Lampyridae), Drilidae and some Scarabeidae (*Pachypus candidae*) (Fig. 60).

Among the parasites, apterism can be linked with shortening of the elytra among the females (*Silphopsyllus*), or even among both sexes (*Platypsyllus*) (both Leiodidae). We find also a total disappearance of elytra among females of *Pachypus* (Dynastidae), *Thylodrias*, and *Rhipidius* (Rhipiphoridae).

Some Examples Among Chrysomelidae

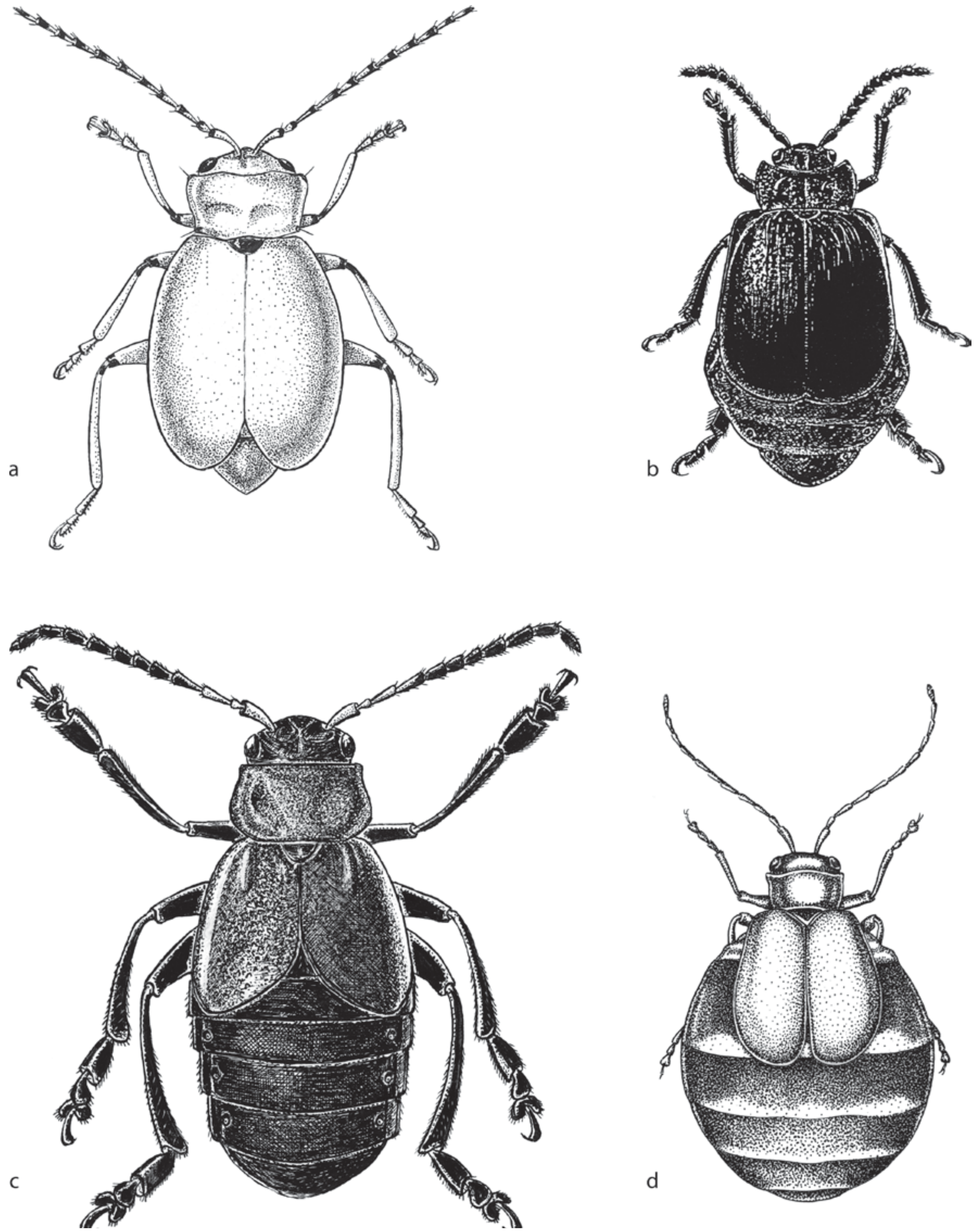
Brachypterism or apterism is common among Chrysomelidae, whereas brachelytry seems limited to Galerucinae and a very few Alticinae. As far as we know, macro-brachypterism seems to be transmitted in Mendelian fashion, when both morphologies are present. Brachelytrism is a derived character, but mixed forms do not exist.

Brachelytrous leaf beetles, which are generally apterous, are evidently devoid of a subelytral cavity, which exists among many apterous Chrysomelinae and Tenebrionidae. Probably, this lack of isolation against cold in mountains or heat and UV in deserts is compensated by other means, such as stronger sclerotizaton of the upper abdomen (tergites).

Brachelytry among Galerucinae is distributed in the Mediterranean region (*Arima marginata*, *Galeruca monticola*, *Marseulia dilativentris*); in mountains or steppe areas of Siberian, Indian and Chinese mountains (*Theone octocostata*, *Galeruca barovskyi*, *Paregeina andrewesi*, *Geinula antennata*); in Australian desert areas, where apterous beetles are common (*Rupilia ruficollis*); in the Ethiopian and East African mountainous areas (*Mahutia alluaudi*); in the Mexican and Central America dry tropics (*Metacycla caeruleipennis*); and in the highlands of South America (*Metalepta tuberculata*). Between 60 and 100 galerucine species in the whole world display brachelytry. Strangely, brachelytrous forms are extremely rare in South Africa and probably absent from Madagascar. Some live in India and Malaysia, but generally are linked with mountains. The genus *Galeruca*, which is essentially palaearctic, has numerous species (nearly 70 taxa) from Western Europe to Siberia, China, and Japan, and normally is macroelytrous and macropterous. However, it displays brachelytrism, joined with brachypterism or apterism, at higher altitudes. It can occur, as *Chrysolina*, above 5300 m in China, Himalayas and Tibet and many of those highland frequenting species are brachelytrous and all apterous. Very few real brachelytrous Alticinae can be quoted: *Hespera brachelytra* from the Yunnan mountains, *Sjoestedtina fordi*, *S. montivaga* from mountains in eastern African, though there may be more.

Flightlessness and brachelytry generally occur in both sexes. *Metacycla* is an exception, with only the female brachelytrous and apterous. Flightlessness is favored in females because it allows greater allocation of resources to egg production (physogastry); however, flight seems retained in males because it increases the probability of finding a mate. Many brachelytrous species walk on the ground and are relatively polyphagous, like *Arima* in Europe, *Galeruca* in China, *Marseulia* in Middle East, *Metalepta* on the Peruvian plateau, or *Rupilia* in Australia. *Metacycla* occurs in Mexico on *Ambrosia ambrosioides*, a small plant (Asteraceae). In this species, the beetle does not walk on the ground, but the male is flying and active, searching for females. The female, black in the collections, is red and pink in some species when alive and probably it is an aposematic color.

A review of the brachelytrous Chrysomelidae (Galerucinae and Alticinae) has been made by Pierre Jolivet, but due to the numerous galerucine genera affected, the list is not complete. The phenomenon is more frequent among mountain, steppe or desert-inhabiting genera and species,



Brachelytry, Figure 60 **Some additional cases of brachelytry (a) *Galeruca littoralis* (Fabricius). South of France. Pygidium prominent. Winged; (b) *Galeruca monticola* Kiesenwetter. France: Pyrenean mountains. Apterous; (c) *Arima marginata* (Fabricius). South of France. Apterous; (d) *Metacycla marginata* Chapuis. Female. Mexico. Apterous; (after Jolivet P (2005) Brachelytry among Chrysomelidae. Lambilionea 105(3):371–384).**

mostly in the tropics, but it also exists in temperate areas. Life on the edge has its constraints, but such mutants not only survived, but have persisted for a very long time. Other families like Staphylinidae seem more consistent; only in the Arctic, where many apterous or brachypterous species occur, brachelytry is absent. Apparently it can be maintained only under hot or relatively temperate climates. Brachelytry seems ancient and linked to harsh environmental conditions. It is known that wing atrophy helps the female in producing more eggs. That must also be the same for brachelytry. There are many cases where only the female is brachelytrous. We must distinguish between elytra fully developed or truncate (brachelytry), but there are degrees between relictual scales (some Staphylinidae) and relative shortening of the elytra. However, very rarely the elytra disappeared completely. Often scales persist. Among Bruchidae, Alticinae, many Galerucinae, very often the end of the abdomen is apparent, but it is not a case of brachelytry.

Certainly the shortening of elytra helps the mobility of the abdomen among the Staphylinidae. Among the Histeridae, the function for truncated elytra is less clear, but among saprophagous beetles the wings are always covered. This may be a necessity in a dirty and humid environment. In the case of Cerambycidae, mimetism with ants could be responsible, but among floricolous groups the wings can remain free. In many cases, the reason for brachypterism is not clearly understood. The case of the *Metacycla* species (Galerucinae) is unique, having physogastric, brachelytrous, apterous females and, macroelytrous, probably flying males. In some species of this genus, the drawings (yellow bands) of the elytra are printed over the upper side of the abdomen. In most cases of brachyletry, the upper abdomen is strongly sclerotized to replace the absence of protection by the lost elytra.

Brachelytry does not seem to be analogous between the various families of beetles. It has appeared independently, for instance, among Staphylinidae and Histeridae. Wing folding also is different in both families. When the beetles are on their back, the staphylinids use their abdomen to recover and attain their footing, whereas histerids use their elytral stump. For Degallier (pers. comm.), histerid elytra are shortened organs, whereas for staphylinids the elytra could be vestigial in relation to an elongated abdomen. There seems not to be any synapomorphy between the two groups.

Often, brachelytry or apterism are connected with a reduced metasternum and various morphological and anatomical correlations (timarchisation of Rüschkamp, 1927). Among ground Chrysomelidae and others, reflex bleeding, hoemocoelous toxicity, thanatosis, aposematism, extra-sclerotization of the abdominal tergites help in protection against predators for those wingless and relatively unprotected beetles. Most of those beetles are black, as in *Timarcha*, but some are brilliantly colored. Black for a ground insect can be aposematic on grasses. A set of mutations should have produced these conditions, and apterism and brachelytry are generally associated with the many usual morphological conditions.

References

Beutel RG, Leschen RAB (eds) (2005) Coleoptera, Beetles. I. morphology and systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim). Walter de Gruyter. Berlin, New York, 567 pp

Beutel RG, Leschen RAB (2005) Phylogenetic analysis of Staphyliniformia (Coleoptera) based on characters of larvae and adults. Syst Entomol 30:510–548

Crowson RA (1981) The biology of the Coleoptera. Academic Press, London, 802 pp

Jolivet P (2005) Brachelytry among Chrysomelidae. Lambillionea 105(3):371–384

Paulian R (1988) Biologie des Coléoptères. Lechevalier, Paris, 719 pp

Rüschkamp F (1927) Der Flugapparat der Käfer. Zoologica. Stuttgart 28(75):1–88

Seguy E (1967) Der Flugapparat Käfer. Zoologica. Stuttgart 28(75):1–88

Seguy E (1967) Dictionnaire des Termes Techniques d'Entomologie Elémentaire. Lechevalier, Paris, 465 pp

Brachodidae

A family of moths (order Lepidoptera). They also are known as little bear moths.

► Little Bear Moths
► Butterflies and Moths

Brachycentridae

A family of caddisflies (order Trichoptera).

► Caddisflies

Brachypsectridae

A family of beetles (order Coleoptera). They commonly are known as Texas beetles.

► Beetles

Brachypteridae

A family of beetles (order Coleoptera). They commonly are known as short-winged flower beetles.

► Beetles

Brachypterous

Having short wings, that do not cover the abdomen or nearly so. (contrast with macropterous).

► Brachelytry

Brachytosis

A bacterial disease of certain Malacosoma species (tent caterpillars), caused by *Clostridium brevifaciens*.

Brackish

Saline water with a concentration of salt between that of fresh and salt water.

Braconidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies
► Natural Enemies Important in Biological Control

Bradynobaenidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Brahmaeidae

A family of moths (order Lepidoptera) also known as brahmin moths.

► Brahmin Moths
► Butterflies and Moths

Brahmin Moths (Lepidoptera: Brahmaeidae)

JOHN B. HEPPNER
Florida State Collection of Arthropods, Gainesville, FL, USA

Brahmin moths, family Brahmaeidae, are a small family of 28 species, mostly Palearctic and African. There are two subfamilies: Dactyloceratinae and Brahmaeinae. The family is in the superfamily Bombycoidea (series Saturniiformes), in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults medium size to very large (50–180 mm wingspan), with head vertex roughened; haustellum average (rarely vestigial); labial

Brahmin Moths (Lepidoptera: Brahmaeidae), Figure 61 **Example of brahmin moths (Brahmaeidae), *Brahmaea wallichii* (Gray) from Taiwan.**

palpi upcurved or porrect; maxillary palpi vestigial or very small (2-segmented); antennae bipectinate; body robust. Wings broadly triangular but mostly rounded (rarely with apex somewhat falcate); hindwings rounded (Fig. 61). Maculation mostly dark browns with numerous scalloped and concentric light lines, plus other markings; rarely more colorful. Adults nocturnal. Larvae are leaf feeders. Host plants recorded in Asclepiadaceae and Oleaceae.

References

Chu HF, Wang LY (1977) The Brahmaeidae of China (Lepidoptera). Acta Entomologicae Sinica 20:83–84

Holloway JD (1987). Family Brahmaeidae. In: The moths of Borneo. Malay Nat J 3:91–93, pl 7

Nässig WA, Paukstadt U (1990) The Brahmaeidae of Sumatra. In: Heterocera Sumatrana, 6:117–136

Nässig WA, Treadaway CG (1998) The Brahmaeidae (Lepidoptera) of the Philippines. Nachrichten des Entomologischen Verein Apollo Suppl 17:425–440

Rougeot PC (1971) Brahmaeidae. In: Les Bombycoides (Lepidoptera-Bombycoi dea) de l' Europe et du Bassin Méditerranéen. In Faune de l' Europe et du Bassin Méditerranéen, 5: 46–59

Seitz A (1911–1928) Familie: Brahmaeidae. In: Die Gross-Schmetterlinge der Erde, 2:227–228, pl. 35 (1911); 10:521–522, pl. 56 (1928); 14:349–351, pl. 47, 60 (1927)

Brain

The brain of insects consists of three fused ganglionic masses: the protocerebrum, the deutocerebrum, and the tritocerebrum (Fig. 62) (Fig. 63).

► Nervous System

Brain Hormone

An earlier name for the hormone that activates the prothoracic glands to produce molting hormone (ecdysone). It also is known as prothoracicotropic hormone (PTTH). The brain is now known to produce several hormones with different functions.

► Endocrine Regulation of Insect Reproduction
► Diapause

Brauer, Friedrich Moritz

Friedrich Brauer was born in Vienna on May 12, 1832. His professional work began as assistant in the entomological museum of Universität Wien, and he was appointed custodian in 1873. In 1874 he was appointed professor of zoology in that university. He became director of the Naturhistorisches Hofmuseum and published extensively on Neuroptera and Diptera. He died on December 29, 1904.

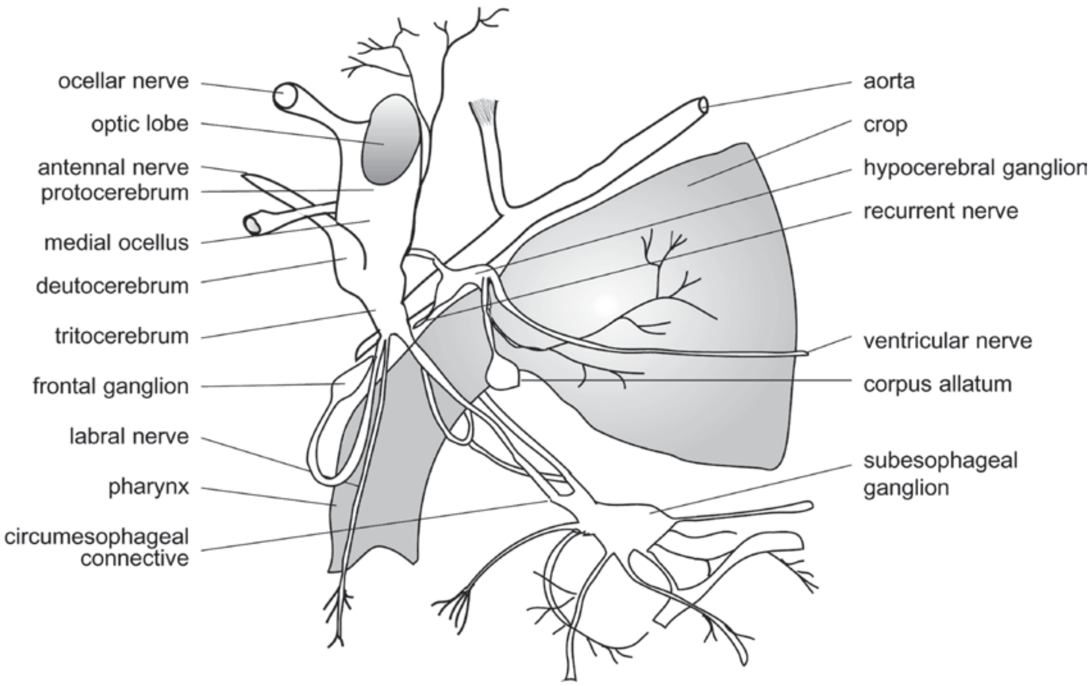
Reference

Poulton EB (1905) Professor Friedrich Moritz Brauer. Entomologist's Monthly Magazine 41:73–74

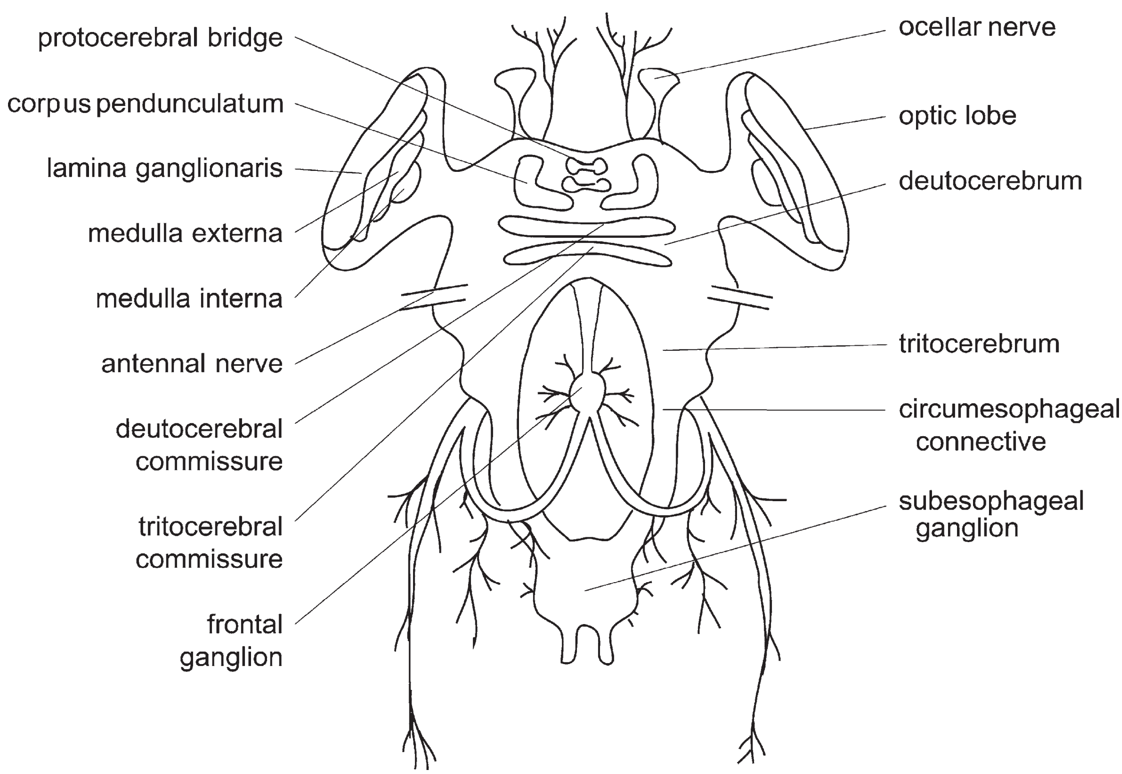
Braulidae

A family of flies (order Diptera). They commonly are known as bee lice.

► Flies
► Bee Louse



Brain, Figure 62 **Lateral view of the insect brain (adapted from Snodgrass, Insect morphology).**



Brain, Figure 63 **Cross section of an insect brain (adapted from Snodgrass, Insect morphology).**

Brentidae

A family of beetles (order Coleoptera). They commonly are known as straight-snouted weevils.

► Beetles

Bristle-Legged Moths (Lepidoptera: Schreckensteiniidae)

JOHN B. HEPPNER
Florida State Collection of Arthropods,
Gainesville, FL, USA

Bristle-legged moths. family Schreckensteiniidae, are a small family of only five known species (three in North America, one in Central America, and one in Europe). Some place the family in its own monobasic superfamily, Schreckensteinoidea. The family is part of the superfamily Tineoidea, in the section Tineina, subsection Tineina, of the division Ditrysia. Adults are small (10–12 mm wingspan), with head smooth-scaled and hind tibiae with long bristles; haustellum naked; maxillary palpi minute, 1-segmented. Maculation is lustrous in shades of gray or brown, with reduced venation and long hindwing fringes. Adults are diurnal. Larvae are leaf skeletonizers on Anacardiaceae or Rosaceae. The family and nominate genus *Schreckensteinia* are named after the German lepidopterist and coleopterist, Baron Friedrich Roth von Schreckenstein (1753–1808).

References

Buszko J, Skalski AW (1980) Schreckensteiniidae. In: Klucze do Oznaczania Owadów Polski. 27. Motyle – Lepidoptera, 23:32–36. Polskie Towardzystwo Entomologiczne [in Polish], Warsaw

Dugdale JS, Kristensen NP, Robinson GS, Scoble MJ (1999) The smaller Microlepidoptera-grade superfamilies. In: Kristensen NP (ed) Lepidoptera, moths and butterflies. vol 1: Evolution, systematics, and biogeography. In: Handbuch der Zoologie. Band IV. Arthropoda: Insecta. Teilband. W. De Gruyter, Berlin, 35:217–232

Falkovitsh MI (1978) Schreckensteiniidae. In: Identification keys to the insects of European Russia. 4. Lepidoptera, 2:526–529. St. Petersburg: Academie Nauk USSR [in Russian], Russia

Heppner JB (2003) Schreckensteiniidae. In: Lepidopterorum Catalogus, (n.s.). Fasc. 29. Association for Tropical Lepidoptera Gainesville, FL, 8 pp

Bristletails (Archeognatha)

This is a primitive order of insects known as Archeognatha or Microcoryphia. The order name is derived from the Greek words *archaios* (primitive) and *gnathos* (jaw). Because these insects are wingless, and none of their ancestors appear to be winged, the order is placed (with the order Zygentoma) in the subclass Apterygota; in this regard they (apterygotes) differ from all other insects.

Classification

There are about 250 species found throughout the world

Class: Insecta
  Apterygota
    Order: Archeognatha
      Family: Machilidae
      Family: Meinertellidae

Characteristics

Like other insects (but unlike some similar-appearing wingless animals such as diplurans, order Entotrophi, and proturans, order Protura), the mouthparts are external (ectognathous). They also lack metamorphosis; they do not change in form as they molt, only increase in size. The number of molts is considerable; 20–70 have been reported. They can live from 1 to 4 years.

Bristletails are small, measuring 10–12 mm in length. The body is cylindrical, but somewhat flattened. The thorax is strongly arched, resulting in a "hump-backed" appearance. Bristletails have large compound eyes that are almost touching, and also ocelli. They are covered with scales, and their color is gray, whitish, or brownish. The mandibles are long. The body segments are well-defined, including the three thoracic segments. The tarsi have three segments, the abdomen 11. The abdomen bears a long median apical filament (a tail-like structure) and two shorter lateral cerci. The antennae are fairly long, and least half the length of the body, and filiform.

Biology

Bristletails are nocturnal, and hide during the day is such cryptic habitats as leaf litter and decaying logs. Some frequent the shorelines water bodies, particularly among rocks near the shore. They are known for their ability to leap. Bristletails feed on algae, lichens, and plant debris. Bristletails do not copulate. They transfer their sperm indirectly by suspending droplets of sperm on strands or threads, which are taken up by the female.

References

Arnett RH Jr (2000) American insects, 2nd edn. CRC Press, Boca Raton, FL, 1003 pp

Remington CL (1954) The suprageneric classification of the order Thysanura (Insecta). Ann Entomol Soc Am 47:277–286

Wygodzinsky P (1987) Order Microcoryphia. In: Stehr FW (ed) Immature insects, vol 1. Kendall/Hunt Publishing, Dubuque, Iowa, pp 68–70

Broadcast Application

The application of a material such as an insecticide to the entire surface of a field.

Broad-Headed Bugs

Members of the family Aldyidae (order Hemiptera).

► Bugs

Broadleaf Plant

One of the major plant groups, with net-veined, broad leaves. Synonymous with dicotyledonous plants. (contrast with grass).

Broad Mite, *Polyphagotarsonemus latus* (Banks) (Acari: Tarsonemidae)

This mite affects several important crops.

► Citrus Pests and Their Management
► Vegetable Pests and Their Management

Broad-Shouldered Water Treaders

Members of the family Veliidae (order Hemiptera).

Bugs

Broad-Winged Damselflies

A family of damselflies in the order Odonata: Calopterygidae.

► Dragonflies and Damselflies

Broad-Winged Thrips

Members of the family Aeolothripidae (order Thysanoptera).

► Thrips

Bromeliad Fauna

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Bromeliads are a family (Bromeliaceae) of monocotyledonous plants with about 2,500 described species assigned to about 60 genera. Almost all of them are native to the neotropics, but the range of a few extends farther north. Sixteen species are native to southern Florida, three of which attain northern Florida, and one of these reaches southeastern Virginia (USA). Many bromeliad species are epiphytic whereas others are terrestrial. Roots of those that are epiphytic do not penetrate their tree hosts, and serve as holdfasts rather than nutrient-absorbing structures. Thus, minerals are absorbed through the leaves, not the roots, and the plants are not parasitic. In contrast, roots of ground-dwelling bromeliads may absorb minerals. Some bromeliads that grow on the ground dwell on rock surfaces (are saxicolous), some in arid habitats and others in marshy soils. Some major genera are *Aechmea*, *Billbergia*, *Brocchinia*, *Bromelia*, *Catopsis*, *Cryptanthus*, *Dyckia*, *Guzmania*, *Hechtia*, *Hohenbergia*, *Neoregelia*, *Nidularium*, *Pitcairnia*, *Tillandsia*, and *Vriesia*.

A remarkable feature of many bromeliad species in many genera is the ability to impound water in the leaf axils. Water thus impounded is rainwater, or rainwater enriched with nutrients leached from tree canopies (throughfall). Large specimens of many species may impound substantial volumes of water, up to many liters. Depending upon architecture of individual species, each of many axils may hold a separate small pool of water, or the axils may combine to form a central tank. These pools of plant-impounded water are called phytotelmata. They serve to provide a reservoir of water for absorption by the plant. Bromeliads under tree canopies contain fallen, decomposing leaves and seeds and twigs of trees. These decomposing materials provide nutrients that can be absorbed by the bromeliad (dendrophilous nutrition). Decomposition is caused by fungal and bacterial action, and by aquatic invertebrate animals. Bromeliads not under tree canopies depend on inputs of wind-blown nutrients (anemophilous nutrition). Typically, algae use these wind-blown nutrients and a food chain depends upon consumption of algae. Epiphytic bromeliads that lack tanks are said to be "aerobic," and have in the USA been labeled as "air plants."

Some authors define tank bromeliads as those that have a central water-impounding tank, perhaps surrounded by additional water-impounding axils. Others include any bromeliads that impound water in their axils, even if the water is distributed among many axils. The latter position is adopted here for convenience, not because the concept has greater merit.

One bromeliad species, *Ananas comosus* L. (pineapple), is a very important agricultural crop in tropical countries worldwide. A few other species are grown locally in the neotropics to provide food or drink (e.g., *Bromelia pinguin* L. and *Puya raimondii* Harms) or fiber (e.g., *Aechmea magdalenae* (André) and *Neoglaziovia variegata* (Arruda da Camara)). Bromelain, extracted from pineapple fruits, has pharmaceutical use as an anti-inflammatory, and is also used as a meat-tenderizer. There is widespread harvesting of bromeliad inflorescences from the wild as decoration for churches on religious holidays in neotropical countries. Very many species and cultivars and hybrids are grown as ornamental plants especially in Europe and North America.

Bromeliads are used in four ways by animals. First, the habitat formed by bromeliad phytotelmata is exploited by some aquatic animals as aquaria. Second, some small animals live permanently or almost so in the non-water-holding axils of bromeliads, the terraria. Third, bromeliads are used as an occasional place of concealment or hunting grounds, or the impounded water is used as a source of moisture, by some terrestrial animals, so these animals are visitors. Fourth, the bromeliads are eaten by some terrestrial animals. Insects exploit the plants in all four ways, and among the insects using each way are specialist species which have no other means of existence or habitat. Bromeliads are therefore essential to the existence of many insect species. Many other invertebrate animals and a few vertebrates also play a role. Additionally, there are three ways in which bromeliads exploit animals: first, as dispersers of seed; second, as pollinators; and third, as food (carnivory).

Aquatic Animals Using Bromeliad Phytotelmata as Habitat for their Immature Stages

The account below is not intended as a catalog, and it omits some groups and mentions few of the individual species.

Rotifera

Rotifers (wheel animalcules) dwell in many freshwater habitats, and some of these habitats are bromeliad phytotelmata. The earliest mention of a rotifer in bromeliads was in Costa Rica in 1913. The most thorough study to date was made in Jamaica in the early 1990s, when 41 of the 211 species reported from Jamaica were documented from bromeliads. They belong to 12 genera including *Lecane*, *Lepadella*, and *Cephalodella*.

Annelida

An aquatic oligochaete worm, *Dero superterrenus* Michaelsen, was first detected and described from Costa Rican bromeliads and found to be an obligate bromeliad inhabitant. Later, it was found to be quite widespread in neotropical countries. The mystery of how it manages to distribute itself among epiphytic bromeliads – when it seems limited to the aquatic environment of bromeliad axils – was solved when worms were seen to be attracted to bromeliad-dwelling frogs. Quite simply, the worm is phoretic on the moist skin of frogs. This method – phoresy, or "hitching rides" – has been detected in other aquatic invertebrates having limited mobility. In contrast, the aquatic insects present in bromeliad phytotelmata have winged adults, so their ability to disperse is assured.

Crustacea

Ostracods (seed shrimps) found in the water in bromeliad phytotelmata include species of the genera *Metacypris*, *Candonopsis*, and *Elpidium*. The first to be described was *Metacypris bromeliarum* Müller, from Brazil. Others have been found in Colombia, Costa Rica, Jamaica, Mexico, Puerto Rica, and Florida. Some are known from no habitat other than bromeliad phytotelmata.

Cyclopoid and harpacticoid copepods have been found in bromeliad phytotelmata in several neotropical countries and at least some of them are specialists to that habitat. The finding of one of the harpacticoid species (*Phyllognathopus viguieri* Maupas) in cultured bromeliads in Indonesia and the United Kingdom, and another (*Attheyella aliena* (Noodt)) in Germany suggested that these organisms had been transported in horticultural specimens. A cyclopoid species, *Bryocyclops anninae* Menzel, also was found in a botanical garden in Indonesia, although its occurrence in Puerto Rico suggests the latter locality or a wider area of the West Indies is its origin.

Cladocera are rare inhabitants of bromeliad phytotelmata; they are represented only by *Daphnia ambigua* Scourfield in Jamaica and *Alona bromelicola* Smirnov in Nicaragua. *Sesarma* and *Metopaulias* are genera of crabs. *Sesarma angustipes* Dana was described from Brazil (later detected in Trinidad), and *Metopaulias depressus* Rathbun from Jamaica, both in the nineteenth century. They reproduce only in the habitat provided by bromeliad axils, and *M. depressus* provides maternal care to its brood. The crabs are able to climb trees to distribute themselves from bromeliad to bromeliad.

Acari

Arrenurus andrewfieldi Orghidan & Gruia is an aquatic mite known from axils of *Aechmea aquilega* in Venezuela. Other aquatic mites of the same family (Arrenuridae), and some attributed to the family Anoetidae, have been reported from bromeliad phytotelmata in other countries.

Odonata

Larvae of dragonflies and damselflies are aquatic and predatory. They have well-developed legs and thereby are able to climb out of the water from one leaf axil and into the water in another. At least 12 species are now reported to have been detected in bromeliad phytotelmata in neotropical countries, and some of them appear to be specialists to this habitat, having been found nowhere else. These specialists are all species of damselflies, especially of the genus *Leptagrion*.

Hemiptera

Aquatic Hemiptera are represented by eight species of seemingly obligate bromeliad-dwellers in the family Veliidae (sometimes called broad shouldered water striders). Four belong to the genus *Paravelia* and four to *Microvelia*. That these genera belong to separate subfamilies suggests that adaptation to the bromeliad habitat occurred independently at least twice. Veliids are predators.

Coleoptera

Larvae of three families of water beetles have been found in bromeliad phytotelmata in neotropical countries. The families are Dytiscidae and Hydrophilidae (both with predatory larvae), and Scirtidae (once known as Helodidae or Cyphonidae) with larvae believed to be filter-feeding detritivores.

Trichoptera

Larvae of most caddis flies live in freshwater streams. One species, *Phylloicus bromeliarum* Müller, has adapted in Brazil to the habitat provided by bromeliad phytotelmata. From Costa Rica there is a record of a stonefly (Plecoptera) in bromeliad phytotelmata. So all three insect orders with strictly aquatic larvae (Odonata, Plecoptera, and Trichoptera) are represented in bromeliads in neotropical countries.

Diptera

It is the order Diptera (flies) which has the record for the largest number of families (at least 15) and species (hundreds) with aquatic larvae reported from bromeliad phytotelmata. They include larvae of Tipulidae, Anisopodidae, Sciaridae, Cecidodomyiidae, and Psychodidae. They include Ceratopogonidae whose adults are important in pollination of cacao, case-making and non-case-making larvae of Chironomidae. They include Tabanidae, Stratiomyiidae, Phoridae, Syrphidae, Borboridae, Aulacigastridae, and Muscidae.

The family Culicidae (mosquitoes) is especially well represented, with well over 200 species reported in the literature. Furthermore, a few of these mosquitoes are among the best studied denizens of bromeliad phytotelmata. This began with the realization that the subgenus *Kerteszia* of the genus *Anopheles* contains several species which develop only in bromeliad phytotelmata, and *Kerteszia* adults are important vectors of malaria. Studies in Trinidad in the late 1940s were followed by studies in the Brazilian state of Santa Catarina, and were aimed at preventing transmission of malaria to workers on cacao plantations and in urban areas surrounded by forest. Unfortunately, the simplest solution appeared to be destruction of bromeliads, and in southern Brazil this took the form of deforestation of a "cordon sanitaire" around urban areas. Public health workers seem to have adopted a concept that bromeliads are a major source of mosquitoes transmitting diseases. Thus, when Old World forms of dengue fever were detected in the Neotropics, beginning in the late 1970s and with continuing problems, public health workers targeted bromeliads as a source of the vector mosquitoes (*Aedes aegypti* (L.) and, beginning in the late 1980s, *Aedes albopictus* (Skuse)). That concept is almost wholly erroneous, because these species of *Aedes* mosquitoes rarely develop in bromeliad phytotelmata. Likewise, public health workers in Florida have erroneously targeted bromeliads as a source of the *Culex* mosquitoes that transmit West Nile virus in the USA, although such larvae of such mosquitoes rarely develop in bromeliad phytotelmata.

In Florida, larvae of two mosquito species, *Wyeomyia mitchellii* (Theobald) and *W. vanduzeei* Dyar & Knab, are highly adapted to existence in the water in bromeliad leaf axils. Typically, few of them survive to adulthood because of food shortage. Thus, they compete with each other in scramble competition, and they are adept at sequestering the small amounts of food available. They are able to survive weeks of starvation which non-specialist mosquito larvae are unable to do. This also allows them to out compete larvae of other mosquitoes that from time to time occur in bromeliad axils. Females of these mosquitoes have color vision and select light-colored (light green) oviposition sites, in contrast to the dark-colored sites (preferably black) typically selected by tree hole-inhabiting mosquitoes. Females hover over bromeliad axils while ovipositing. When they are not ovipositing or blood-feeding, they may be found perched on the trunks of trees harboring bromeliads. Males perform up-and-down flights over small areas of tree trunks when searching for females. Eggs of *W. vanduzeei* are made exceptionally buoyant by having a wax-like coating of minute mushroom-shaped structures that trap a plastron of air; they float vertically at the water surface and may even be washed out of bromeliad axils during heavy rain. In contrast, the eggs of *W. mitchellii* are coated only with a thin layer of a greasy substance, are less buoyant, and they float horizontally. Larvae depend upon input of dead leaves, twigs, and seeds that fall into bromeliad axils from tree canopies above and are decomposed by fungal and bacterial action. Further breakdown of the organic particles and probably digestion of bacteria and fungi in the guts of mosquito larvae make the nitrogenous content more rapidly available for uptake by the bromeliads. Thus, the presence of the mosquito larvae is helpful to the bromeliads, and the bromeliads provide a habitat for the mosquito larvae, so this is a symbiosis. These mosquitoes are not known to transmit any diseases to humans, although they take human blood as well as the blood of other vertebrates such as rabbits. They are viewed by humans as pests. The most appropriate long-term solution to their population control is biological control by competition. Such biological control would introduce organisms that would compete for nutrients with the mosquito larvae. Such competitors would probably be neotropical species of non-biting midges such as Chironomidae. Use of predators against the mosquito larvae would likely provide no solution at all, because survivors of predation would inherit the food resources and thus develop faster and produce larger and thus more fecund adults (Fig. 64).

Anura (frogs)

Tadpoles belonging to at least five frog genera: *Dendrobates* (Dendrobatidae), *Anotheca*, *Hyla*, and *Sphaenorhynchus* (Hylidae), *Syncope* (Microhylidae), and *Eleutherodactylus* (Leptodactylidae) have been reported from bromeliad phytotelmata. Adults of *Physalaemus spiniger* (Miranda-Ribeiro) (Leptodactylidae) may deposit their eggs in foam nests in bromeliad axils in Brazil, but the tadpoles develop elsewhere. In contrast, tadpoles of *Dendrobates pumilio* Schmidt in Central America are carried up trees to bromeliads on the backs of parents, and the tadpoles develop in bromeliad axils feeding on nutritional eggs provided by the female. Regrettably, the bright colors of many dendrobatid frogs ("poison-arrow" or "poison-dart" frogs) has made them popular in the pet trade, no matter that they are poisonous. To supply the popular demand to keep such frogs in aquaria with bromeliads, hunters have plundered them from their natural environment. Consequently, and because of habitat loss, *D. pumilio* is listed in the IUCN Red Book as a threatened species. Other

Bromeliad Fauna, Figure 64 **Schematic representation of a mosquito and a bromeliad: (a) Female *Wyeomyia* mosquito hovering over a *Tillandsia* sp. leaf axil while ovipositing. (b) Male *Wyeomyia* mosquito performing up-and-down flight over a small area of a tree trunk while searching for females. (c) Schematic showing how *Wyeomyia vanduzeei* eggs may be washed out of *Tillandsia* bromeliads during heavy rain. (d) Schematic showing how leaves and seeds from tree canopies fall and are trapped in bromeliad leaf axils, forming the basis of a food chain. Drawings by John Stark.**

strange development is exhibited by tadpoles of *Syncope antenori* Walker, which develop in the leaf axils of a *Guzmania* bromeliad in Ecuador. Here, the tadpoles are born with yolk-filled gastrointestinal tracts, and are able to complete their development without feeding.

Terrestrial Animals Using Bromeliad Terraria as Habitat for their Immature Stages

Bromeliad terraria are the leaf axils that cannot impound water because they leak. Instead, they accumulate moist organic materials. Typically, inner axils form phytotelmata whereas outer axils form terraria. We may also consider the upper parts of those water-impounding axils that are choked with fallen plant debris as terraria. Bromeliad terraria provide habitat for some specialist organisms and many generalists.

Beetles of the genus *Platynus* (Coleoptera: Carabidae) typify this group. Among the several hundred species of this genus, some have specialized to existence in leaf axils of epiphytic bromeliads, and their adults and immature stages occur nowhere else. Although their food has not been investigated, they are most likely predatory in concordance with their closest relatives. So bromeliads serve as hunting grounds for their adults and larvae. These bromeliad specialists occur in Mexico, Central America, and the West Indies.

In eastern Brazil, a scorpion *Tityus neglectus* Mello-Leitão (Buthidae) and a tarantula spider *Pachistopelma rufonigrum* Pocock (Therophosidae) have been found so often in terrestrial water-impounding bromeliads that their association seems to be obligate. Both are predatory. In Brazil, the spider *Psecas chapoda* (Peckham and Peckham) (Salticidae) reproduces only on the non-water-impounding *Bromelia balansae* Mez. In the southern USA, one spider *Pelegrina tillandsia* Kaston (Salticidae) is constantly associated with the atmospheric epiphytic bromeliad *Tillandsia usneoides* (L.) although the growth form of the plant does not provide terraria.

Ants may nest in bromeliad terraria. Some belong to species that also nest on the ground. Some belong to species that typically are arboreal, nesting in hollow twigs and branches. Some bromeliad species in the genus *Tillandsia* (e.g., *T. paucifolia* Baker) have inflated leaf bases providing cavities protected from rain, and the cavities thus formed are often occupied by ants. The ants may cut a small hole in a leaf base for ease of access to the cavity. Investigation may reveal whether such bromeliads and their ant tenants participate in a mutualism in which the plants also benefit.

Terrestrial Animals Using Bromeliads as Occasional Habitat, the Visitors

These visitors are here defined as animals that neither eat nor reproduce in bromeliads. They may be hunting for prey, they may be seeking moisture or concealment from enemies, or they may be present just because their wanderings have taken them there. In Brazil and elsewhere, adult frogs seek refuge during the daytime in bromeliads. Such vertebrates differ from bromeliad specialist frogs found in some parts of the tropics in that their tadpoles develop in other kinds of habitats. But perhaps because of the presence of frogs (potential prey), bromeliads are visited by snakes and other frog-eating vertebrates. Birds may find drinking water there. In tropical areas with pronounced wet and dry seasons, more individuals and species of insects may be present in bromeliad leaf axils in the dry season, when bromeliads provide oases of moisture as well as prey for the predators among these insects.

Terrestrial Animals Eating Bromeliads

Bromeliads in greenhouse cultivation seem more often to be attacked by scale insects than by insects of any other group, and this may be an artifact due to crowding of plants under unnatural conditions that exclude organisms which could control these pests. In Florida, these scale insects belong to the following six families (numbers of species in parentheses): Asterolecaniidae (2), Coccidae (1), Ortheziidae (1), Pseudococcidae (6), and Diaspididae (8). They can be controlled by chemical pesticides or, perhaps, they may be controlled by opening greenhouse walls to allow ingress of tiny parasitoid wasps (if the greenhouse is in a tropical or subtropical area), or by deliberate release of such wasps purchased from biocontrol supply companies (none of the necessary wasp species seems now to be available commercially, but this could change if there were demand).

Among pests of fruits of cultivated pineapple, the most widespread miner is the larva of a butterfly, *Strymon* (=*Thecla*) *basilides* (Geyer) (Lepidoptera: Lycaenidae). Perhaps it also attacks fruits of wild pineapples and perhaps other members of the genus *Ananas*.

Insect larvae that mine stems of bromeliads include Castniidae and Acrolophidae (Lepidoptera) and Curculionidae and Dryophthoridae (Coleoptera). The castniid species concerned seem not to have been identified to species level, but have been detected by this writer in bromeliads in natural areas in Mexico, Honduras, and Panama and doubtless are yet more widely distributed in the tropics. Fully grown larvae are large (~ 5cm), and their mining activities surely result in plant death. They have not been seen to be abundant and their population sizes may be limited by parasitoids, although such parasitoids have not been detected. Larvae of the one acrolophid species implicated, *Acrolophus vigia* Beutelspacher, are parasitized by larvae of at least one unidentified wasp (Hymenoptera: Braconidae). The subject is of academic interest but currently of no economic interest because *A. vigia* has not been detected in the USA Larvae of at least 24 weevil species specialize in mining stems of bromeliads. They belong to three genera, *Cholus*, *Cactophagus*, and *Metamasius*. The life cycle of the weevil *Diastethus bromeliarum* Champion seems unrecorded. All were classified within the family Curculionidae, but recently the part of that family containing *Cactophagus* and *Metamasius* has been considered a separate family (Dryophthoridae). It is unclear whether any of them is a substantial pest in its native ecosystem. However, some of them cause substantial damage to cultivated pineapples in agro-ecosystems. One of them, *Metamasius callizona* Chevrolat, which is native to southern Mexico and Guatemala, also causes enormous damage to Florida's native bromeliad populations after having arrived as a contaminant in one or more shipments of ornamental bromeliads. A biological control project against *M. callizona* is in progress in Florida with intent to reduce its populations (not eradicate them as is sometimes misstated by the news media); the objective of biological control is not to eradicate.

Insects that have specialized to eat the leaves of bromeliads by chewing the surfaces or by mining are surprisingly few. They include a few leaf beetles (Coleoptera: Chrysomelidae) such as *Acentroptera basilica* Thomson and *A. pulchella* Guérin Méneville in southern South America, the abovementioned adult weevils (Coleoptera: Dryophthoridae and Curculionidae), a few caterpillars such as *Napaea eucharilla* Bates (Lepidoptera: Riodinidae), and larvae of a leaf-mining fly, *Melanagromyza rosales* Woodley (Diptera: Agromyzidae), in Costa Rica. Generalist insects that chew bromeliad leaves include cockroaches (Blattaria), whose actions are scarcely noticeable outside a greenhouse environment, and grasshoppers (Orthoptera: Acrididae). In spring in southern Florida (USA), population explosions of "lubber grasshoppers" (*Romalea guttata* Houttyn (Acrididae)) attack many monocotyledonous plants, including bromeliads; although the damage they cause initially appears severe, the plants seem to recover by new growth. In Andean countries, the spectacled bear, *Tremarctos ornatus* (Cuvier), is reported to include a substantial proportion of bromeliads in its diet.

Larvae of *Epimorius testaceellus* Ragonot (Lepidoptera: Pyralidae) develop within the flower pods of the bromeliad *Tillandsia fasciculata* Swartz, causing considerable local damage. A tiny wasp parasitoid attacks these larvae and may limit populations of this moth.

Animals as Dispersers of Bromeliad Seed

Dispersal of seed in the bromeliad subfamily Tillandsioidea is by wind. The fleshy seeds of many Bromelioidea, however, seem designed to attract feeding by vertebrate animals, and indeed birds have been reported to consume the seeds, pass them through alimentary tracts, and disperse them together with feces in new habitats. The subject of seed-dispersal by animals is not well documented.

Animals as Pollinators of Bromeliads

Feeding by animals at bromeliad nectar may be considered as a special case of phytophagy because this does no harm to the plants, unless perhaps the animals should consume nectar without effecting pollination. There are remarkably few observations of nectar feeding. Those that are mentioned most are by hummingbirds at large flowers of some large bromeliads, and these may well be over-emphasized because hummingbirds are diurnal and easy to see, and by butterflies and a few beetles. Bats are documented as pollinators of the genus *Werauhia*. Feeding by moths is nocturnal, hard to observe, and may be vastly underrated. There is much scope for collaboration between entomologists who can identify the insects effecting pollination and botanists who can identify the bromeliads specifically and demonstrate pollination, especially at night.

Animals as Food for Bromeliads (Carnivory)

In just three bromeliad species (one *Catopsis* and two *Brocchinia*) carnivory has developed, because the plants trap insects which are decomposed by bacterial action in their tanks. Although some writers have deemed this to be "proto-carnivory" because the three bromeliads in question do not produce digestive enzymes, the effect is the same. The first detected instance was in the bromeliad *Catopsis berteroniana* (Schultes) in southern Florida, although the plant has a wider distribution in the neotropics. Although it grows epiphytically, it grows typically above tree canopies, so it accumulates little or no organic debris from trees. It seems to have evolved a method of confusing winged terrestrial insects so that they stumble into it, have difficulty escaping, and drown and are decomposed in the water-filled leaf axils. The two *Brocchinia* species are terrestrial and grow in nutrient-poor habitats in inland Venezuela. We may only hope that the gluttonous commercial trade in carnivorous plants will not plunder these plants from the wild. Hobbyists should at least be warned that the two *Brocchinia* species require cool, humid, breezy climatic conditions that are hard to match in cultivation, that populations of *C. berteroniana* in southern Florida are all in protected lands, that the plants are specifically protected by law, and that none of the plants can withstand freezing temperatures.

Conclusion

In pre-Columbian times, bromeliads and their denizens were a huge ecosystem extending in the Americas from southeastern Virginia (USA) to Argentina. Bromeliads and their animal denizens are being destroyed overwhelmingly by encroachment by human populations. This has been called "development." One of the most species-rich areas was Brazil's Atlantic forest, which has been reduced to less than 7% of its former extent, but a similar story prevails everywhere. Some, especially in Trinidad and Brazil, were destroyed in the twentieth century because of an oversimplified concept that bromeliads are a source of malaria-carrying *Anopheles* mosquitoes, and so the simplest method of controlling malaria is to destroy the forest and the bromeliads. This concept has spilled over, irrationally, to other countries, other bromeliads, other mosquitoes, and other diseases (or no diseases), to which it does not apply.

Lesser constraints on bromeliad populations and their denizens have made their mark because so much has been destroyed by "development." Widespread and vast harvesting of bromeliad blooms for church activities is having an affect. The harvesting of bromeliads from nature has unequivocally contributed to the spread of pest insects internationally. Selective harvesting of the rarest bromeliads for the horticulture trade may be having a negative affect, although a counter-argument has been made that they are being propagated and thus will survive in culture. Destruction of native bromeliad populations in Florida by a pest weevil (which arrived as a contaminant of "ornamental" bromeliads from Mexico) is having an overwhelming negative affect on the bromeliad populations – its affect on the bromeliad fauna in Florida has not yet been addressed although it surely must likewise be negative. We have some idea of the reduction of bromeliad populations throughout their former range, but we have no idea of the reduction of populations of the animals that depend upon bromeliads; we can only guess that it is at very least as bad, most likely worse. Harvesting of selected bromeliad-inhabiting animals from nature, such as *Dendrobates* frogs, threatens their very existence but fortunately most bromeliad-dwelling organisms lack appeal to hobbyists, and so are threatened "merely" by development destroying bromeliads.

Involved biologists have four major options. The first is to study the heck out of native bromeliad faunas in numerous neotropical countries while there still is a fauna. The second is political lobbying for the preservation of tracts of land that may preserve part of the fauna (some of it will inevitably be lost with "development"). The third is to persuade churchgoers of Latin American churches not to harvest bromeliads from nature – to use other sorts of decorations instead of destroying the environment. The fourth is to provide public educational support to laws of many countries that already prohibit "harvesting" of bromeliads from nature for commercial purposes.

References

Frank JH (1983) Bromeliad phytotelmata and their biota, especially mosquitoes. In: Frank JH, Lounibos LP (eds) Phytotelmata: terrestrial plants as hosts for aquatic insect communities. Plexus Publishing, Marlton, NJ, USA, pp 101–128

Frank JH (1996) Bromeliad Biota. Available at http://BromeliadBiota.ifas.ufl.edu. Accessed Oct 2006

Janetzky W (1997) Crustacea in bromeliad phytotelmata. Available at http://BromeliadBiota.ifas.ufl.edu/crbrom.htm. Accessed Oct 2006

Janetzky W, Koste W (1997) Rotifera in bromeliad phytotelmata. Available at http://BromeliadBiota.ifas.ufl.edu/robrom.htm. Accessed Oct 2006

Picado C (1913) Les broméliacées épiphytes considerées comme milieu biologique. Bulletin des Sciences de la France et de la Belgique 47:215–360

Polhemus JT, Polhemus DA (1991) A review of the veliid fauna of bromeliads with a key and description of a new species (Heteroptera Veliidae). J New York Entomol Soc 99:204–216

Bronzed Cutworm, *Nephelodes minians* Guenée (Lepidoptera: Noctuidae)

This caterpillar is a pest of turfgrass, and occasionally other crops.

► Turfgrass Insects and Their Management

► Turfgrass Insects of The United States: Biology and Management

Brood

In asocial insects, this generally refers to a cohort of individuals resulting from deposition of a cluster of eggs and developing concurrently. However, sometimes it is used to refer to all the offspring of a parent, which may include several clusters of eggs produced over the lifespan of the female. In social insects, this refers to all the immature offspring of a colony, and may consist of eggs, larvae, nymphs and pupae.

Brood Cell

Among social insects, a cell, chamber or pocket constructed to house the immature stages.

Brooding

A form of parental care wherein the young insects remain near the parent insect (though in some insects surrogate parents are employed). Sometimes the parents actively engage in defense of the young, but often they do not.

Brood Sac

In cockroaches, an internal pouch, usually under the wing covers, where eggs are incubated in females.

Broun, Thomas

Thomas Broun was born in Edinburgh on July 15, 1838. His father and an uncle were naturalists and probably influenced him. At the age of 16, he joined the British army, took part in the Crimean war, and then served in Burma and India during the Indian Mutiny. In 1862 he married and emigrated to New Zealand. At outbreak of the Maori war, he was commissioned as captain, served throughout the war, and attained his majority. After that war, he began to work on New Zealand insects. In 1880 was published his "Manual of New Zealand Coleoptera" which listed 1,140 species. Supplements increased this total to 3,979 species. In 1890 he was appointed Government Entomologist. His type specimens are mainly in the Natural History Museum, London. He died on August 24, 1919 (Fig. 65).

References

Herman LH (2001) Broun, Thomas. Bull Am Mus Nat Hist 265:49

Broun, Thomas, Figure 65 Thomas Broun.

Brown Citrus Aphid, *Toxoptera citricida* (Kirkaldy) (Hemiptera: Aphididae)

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The brown citrus aphid, *Toxoptera citricida*, is believed to originate from China. Until 1900, this insect was confined to southeast Asia, Australia, New Zealand, the Pacific Islands including Hawaii, South Africa, and South America. Since then it has become established in several countries of Central America and many islands in the Caribbean Basin. Brown citrus aphid was first discovered in 1995 in south Florida; in the following two years, this insect had expanded into all citrus production areas in Florida. Because of its ability to transmit citrus tristeza virus (CTV) in an efficient manner, the combina tion of brown citrus aphid and CTV has become an important problem of citrus worldwide. Disastrous epidemics of citrus tristeza virus have occurred in association with brown citrus aphid in Argentina, Brazil, Colombia, and Peru. CTV is known to cause decline and death of citrus trees grafted on sour orange (*Citrus aurantium* L.) rootstock, but some CTV isolates can cause stem pitting regardless of rootstock, and can result in long-term debilitation that reduces yields of sweet orange and grapefruit from 5 to 45%. Currently, there are about 185 million citrus trees in Florida grafted on the susceptible sour orange rootstock. Citrus tristeza poses a real threat not only to Florida's citrus industry, but also to other citrus producing states in the U.S. Brown citrus aphid feeding causes leaf distortion and shortening of terminal growth. Its honeydew provides a good medium for growth of sooty mold. More importantly, brown citrus aphid is the most efficient vector of CTV as compared with other citrus aphids such as *Aphis gossypii*, *A. spiraecola* and *Toxoptera aurantii*. The overall transmission efficiency of CTV by *T. citricida* ranges from 1 to 13% dependent upon CTV isolates and biotypes of vector. Brown citrus aphid reproduces parthenogenetically. Most females start to produce nymphs within 24 h after emergence. Nymphs undergo four instars. The developmental times for nymphal stages vary with temperatures and host plants. Within a temperature range of 8–30°C, the length of nymphal development decreases as temperature increases. The average developmental times for first, second, third and fourth instars are 1–12, 1–13, 2–16 and 2–22 days, respectively. At 5°C, nymphs fail to develop beyond the second instar. At 32°C, the developmental times for all nymphal stages increase compared to those at 28–30°C. The adults can survive and reproduce within the temperature range of 10–32°C (Fig. 66).

The mean longevity of females decline exponentially from 60 days to 7 days as temperatures increase from 10 to 32°C. The maximal longevities of individual females are 90, 62, 47, 30, 19, 15 and

Brown Citrus Aphid, Toxoptera citricida (Kirkaldy) (Hemiptera: Aphididae), Figure 66 Winged and wingless adults of brown citrus aphid, *Toxoptera citricida* (photo P. Choate, University of Florida).

9 days at 10, 15, 20, 25, 28, 30 and 32°C. Fecundity is more affected by temperatures; at 10 and 32°C, the fecundity is adversely affected. The average nymph production by adults within 15–30°C increases to a maximum of 53 nymphs per female at 20°C, then decreases sharply as temperature increases. The daily rate of nymph production varies with adult age. The peaks of reproduction appear at 4 through 10 days after adult emergence, with an average of 2–5 nymphs per day. The duration of reproduction lasts as long as adult longevity within the temperature range of 15–30°C.

The biology of brown citrus aphid is also affected by host plants on which the populations are reared. The average nymphal development periods on rough lemon, sour orange, grapefruit, and key lime are from 5.9 to 6.2 days. However, longer developmental periods (6.5–7.2 days) are required on box orange, calamondin, lime berry and orange jassamine. The average number of nymphs produced per female reared on sour orange, grapefruit, key lime, rough lemon, calamondin, box orange, lime berry and orange jassamine are 59, 43, 34, 43, 33, 18, 21 and 23 nymphs. Female adults live an average of 23 days on these hosts. Because young citrus flush occurs only intermittently in commercial groves, it is believed that plants other than commercial citrus play an important role in sustaining brown citrus aphid populations when young citrus shoots are not available.

Brown citrus aphid can be controlled by a number of pesticides. Hymenopteran insects play a critical role in pollination and fruit set. Pesticide application can greatly affect the pollination process in the blooming season; thus the material and time of application are of great significance in reducing mortality of pollinators. Other biocontrol agents such as parasitoids (*Lysiphlebia* spp., *Aphelinus* sp. and *Lipolexis* sp.), syrphid fly (*Pseudorus clavatus*), ladybeetles (*Cycloneda sanguinea*, *Harmonia axyridis* and *Coelophora inaequalis*), lacewing (*Chrysopa* spp.), and entomopathogenic fungi (*Beauveria bassiana* isolates) show various degrees of effectiveness in control of brown citrus aphid.

► Citrus Pests and Their Management

References

Bar-Joseph M, Roistacher CN, Garnsey SM, Gumpf DJ (1981) A review on tristeza: an ongoing threat to citriculture. Proc ISC 1:419–422

Michaud JP (1998) A review of the literature on the brown citrus aphid, *Toxoptera citricida* (Kirkaldy). Fla Entomol 81:37–61

Michaud JP, Browning HW (1999) Seasonal abundance of the brown citrus aphid, *Toxoptera citricida* (Homoptera: Aphididae) and its natural enemies in Puerto Rico. Fla Entomol 82:424–447

Rocha-Peña MA, Lee RF, Lastra R, Niblett CL, Ochoa-Corona FM, Garnsey SM, Yokomi RK (1995) Citrus tristeza virus and its aphid vector, *Toxoptera citricida*. Threats to citrus production in the Caribbean and Central and North America. Plant Dis 79:437–445

Tsai JH (1998) Development, survivorship, and reproduction of *Toxoptera citricida* (Kirkaldy) (Homoptera: Aphididae) on eight host plants. Environ Entomol 27:1190–1195

Tsai JH, Wang K (1999) Life table study of brown citrus aphid (Homoptera: Aphididae) at different temperatures. Environ Entomol 23:412–419

Brown Dog Tick or Kennel Tick, *Rhipicephalus sanguineus* (Latreille) (Acari: Ixodida: Ixodidae)

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Rhipicephalus sanguineus is the main vector and reservoir of a group of bacteria now called the *Rickettsia conorii* complex. They are causative agents of a number of similar human diseases known earlier as Mediterranean spotted fever, and distributed all around the Mediterranean and Black Seas as well as in India and some countries of southeastern Asia. According to the current data, new varieties of this disease connected with *R. sanguineus* have been distinguished that are caused by different subspecies of *R. conorii*, namely Mediterranean spotted fever (subsp. *conorii*) in the Mediterranean area, including northern Africa and southern Europe; Israeli tick typhus (subsp. *israelensis*) in Israel; Astrakhan fever (subsp. *caspia*) in the lower reaches of the Volga River in Russia; and Indian tick typhus (subsp. *indica*) in Asia. In addition, the brown dog tick was known as the vector of *Rickettsia rickettsii*, the causative agent of Rocky Mountain spotted fever in Central America, mainly in Mexico. Recently, a focus of this disease with *R. sanguineus* as the only vector was described and investigated in Arizona, USA. The broad distribution of this tick raises concern about such foci in adjacent states. Several new species of *Rickettsia* were also isolated from *R. sanguineus*, and *Rickettsia massiliae* was documented as a human pathogen. The brown dog tick was shown to harbor *Coxiella burnetii* (the causative agent of Q-fever) for many years after the death of the tick. *Rhipicephalus sanguineus* transmits several agents pathogenic for dogs. The causative agent of canine ehrlichiosis, *Ehrlichia canis*, originally described in the Mediterranean area, was later found in numerous areas of the world, and today its distribution completely coincides with the tick's range. *Rhipicephalus sanguineus* also transmits protozoan dog pathogens, such as *Babesia canis* endemic in the USA and Africa, and *B. gibsoni* in the Far East and North Africa. Several other pathogens were isolated from this tick, but their epidemiological or epizootiological significance is either small or unclear. Transstadial and transovarial passage of *R. conorii*, *R. massiliae* and *B. canis* has been proven.

The difficulties of species identification in the genus *Rhipicephalus* resulted in subdividing the genus into groups of closely related species. In particular, the *R. sanguineus* group includes about ten species, with *R. turanicus* being the most difficult to distinguish from *R. sanguineus*. At the same time, genetic analysis of ticks from different areas of the world showed that there are distinct patterns for *R. sanguineus* and that the intraspecific variability of sequences within the species is very low. This means that *R. sanguineus* is a valid species.

The brown dog tick is the only cosmopolitan species of ticks. This species originated from Africa where its hosts were local carnivores and ungulates. Later, dogs became its main and often only hosts. Spread of the tick worldwide has been connected with human transport of dogs over the globe. At present, this tick can be found in all continents between the latitudes of 50°N and 35°S, but sometimes even further in association with dogs living indoors (in houses or kennels). It was recorded from all 50 states of the USA, many sites in Canada, as well as from such European countries as Belgium, Denmark, England, Germany, Norway, Poland and some others. Some cases of human infection with *R. conorii* by ticks inside human dwellings were documented.

Being ecologically flexible and tolerant of a large range of climatic conditions, *R. sanguineus* populates various areas, mainly inhabited localities including human dwellings, but also uninhabited environments which may be humid tropical, subtropical or continental (semi-desert). Unfed ticks are active for the whole year in the tropics, indoors as well as in the field. Under tropical conditions, ticks may have three generations during the year. Year round activity has also been observed in ticks living together with dogs in human dwellings in all regions. Unfed ticks living in the field to the north or south of the tropical zone are active from spring until autumn. Here they have two or sometimes only one generation annually. The more temperate the climatic conditions, the shorter is the period of activity of unfed *R. sanguineus* specimens. In Mediterranean countries, the season of adult activity lasts for 6–8 months, from March-April until October-November, depending on the environmental conditions of a particular area.

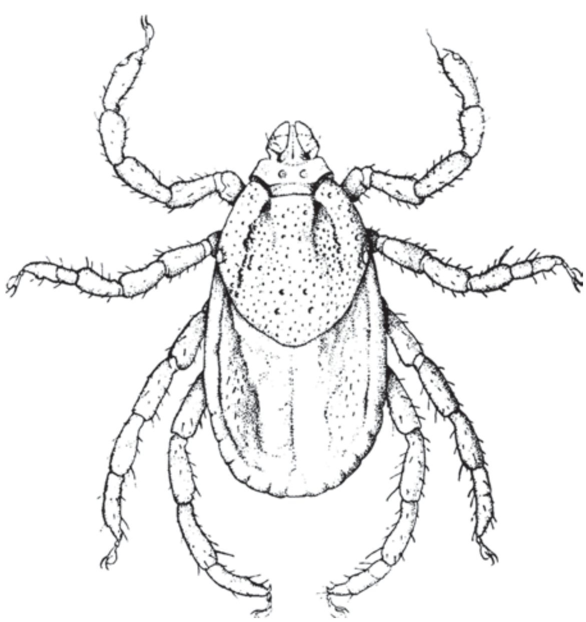
Host seeking behavior of unfed ticks depends on the conditions of their habitation. When the dog ticks live in human localities, they are constantly rather close to their main hosts, often just around the dog's bedding area. When ticks are ready to feed, they migrate a very short distance to their hosts, catch onto them and move over the dog's body looking for an attachment site. In the field, the ticks use an ambush strategy positioning on the vegetation, preferably on the tips of low grass, often in clusters. In the adult ticks, the anterior end of the body usually points towards the ground. Questing ticks can catch onto a passing host or, sensing it from a distance, they move in its direction, rather quickly over the sandy ground. *Rhipicephalus sanguineus* in the open field lives under much more inhospitable conditions than ticks living in dense forests due to low humidity and great fluctuations of ambient temperature. Under such conditions, the ticks are incapable of prolonged questing activity. To replenish their water reserves, ticks must regularly migrate down to the litter and soil where temperature is lower and humidity higher. Dog ticks have eyes and apparently use them effectively both for choice of optimal illumination and for searching for hosts.

The capacity of *R. sanguineus* for active migrations is rather limited. There are no data about tick migrations in tropical areas, but in semi-desert areas the unfed specimens can move upwards up to 20–40 cm, with the difference between ticks of different stages being undetectable. An interesting phenomenon concerning engorged nymphs and females in or near human dwellings has been documented many times: after repletion and detachment, they migrate vertically over the walls looking for suitable sites (cracks, crevices) for molting or egg-laying. The height of such migrations may be up to 2.5 m.

The season of activity for unfed subadults (larvae and nymphs) depends on the seasonality of adult ticks. In the tropical zone, subadults can be active during the entire year, with periodic and sometimes rather small fluctuations in their abundance. Under more temperate climatic conditions, the abundance of unfed subadults increases soon after the decrease in adult abundance, larval activity preceding that of nymphs. The life span of individual adults after molting continues from 3–4 months during summer months, to about 8–9 months if the hibernation followed with behavioral diapause takes place. In continental climates, only engorged nymphs and unfed adults can successfully survive during the winter. Unfed ticks that do not find a host and cannot feed during the activity season die due to complete expenditure of their nutritional reserves.

The brown dog tick (Fig. 67) is a typical exophilic three-host tick. The larva feeds for 3–6 days, the nymph for 4–10 days and an adult female for 6–13 days. Insemination of the adult female takes place on the host after 3–4 days of feeding. Without insemination, the female stops its engorgement and lives in an attached position until insemination, or death from drying. The larvae increase their weight during feeding 10 to 20-fold, while nymphs increase their weight 60 to 75-fold and adult females 70 to 120-fold. The adult males feed for 3–5 days, increasing their weight 1.5 to 2-fold. Henceforth, males migrate over the host body, attaching in different sites. The mass of an unfed larva is 0.02–0.025 mg, whereas the mass of a fully engorged female reaches 200–350 mg and it can lay up to 5,000 eggs. Two main components provide the increase of tick reproductive capacity: minimizing egg size (and, hence, unfed larval mass) and increased capability for interstage growth during nymphal feeding.

The minimal weight of engorgement after which females are capable of laying eggs is about 20 mg. After the female reaches the weight of 170–200 mg,



Brown Dog Tick or Kennel Tick, *Rhipicephalus Sanguineus* (Latreille)Acari: Ixodida: Ixodidae), Figure 67 The brown dog tick, *Rhipicephalus sanguineus.*

the dependence of egg number/mg of engorged female becomes linear and equals approximately 15–17 eggs/mg of the female weight. Weight characteristics and fecundity of the cosmopolitan *R. sanguineus* are different in populations from different regions. The populations from tropical conditions have smaller engorged female weights and, hence, lower fecundity.

The brown dog tick is a host-specific species, having the dog as its main host, though it can also feed on different vertebrates, such as livestock, some carnivores, lagomorphs, rodents, insectivores. All three parasitic stages can use dogs (sometimes the same individual) as hosts. Under conditions of extreme proximity with the host, there are cases where the tick changed from a three-host type of development to a two-host type. Sometimes larvae did not leave the dog after engorgement, and molted to nymphs on the host. In other observations, these were engorged nymphs that molted on the host to adults. Adults actively attack people in the Palaearctic and are the main source of human infection by different pathogens. Until recently, *R. sanguineus* rarely attacked people in the Nearctic, particularly in the USA. However, during the last several decades this tendency seems to have changed and a number of cases of human bites by the brown dog tick have been recorded. The recent outbreak of Rocky Mountain spotted fever in Arizona was connected to heavy infestation of dogs by *R. sanguineus* and numerous ticks of this species in the yards of patients' homesites.

Because the dog is a principal factor in human tick-borne infections, the suppression of ticks on dogs by using systemic acaricides or plastic collars impregnated with acaricides is an effective protection of humans from tick attacks and bites. Dogs heavily infested by ticks are dipped into water mixtures prepared with acaricidal emulsifiable concentrates and wettable or soluble powders. Regular cleaning of kennels, changing beddings, and acaricidal treatment of sites which dogs frequent are necessary measures for tick suppression. Educational programs for dog owners might be useful for increasing their knowledge about tick medical importance. Experiments on the treatment of tick hosts or tick location sites by preparations based on fungi and nematodes have shown that some pathogens have an obvious acaricidal effect. However, it is too early to estimate their real possibility for practical purposes of human protection.

► Ticks

References

Beati L, Keirans JE (2001) Analysis of the systematic relationships among ticks of the genera *Rhipicephalus* and *Boophilus* (Acari: Ixodidae) based on mitochondrial 12S ribosomal DNA sequences and morphological characters. Journal of Parasitology 87:32–48

Goodman JL, Dennis DT, Sonenshine DE (eds) (2005) Tick-borne diseases of humans. American Society for Microbiology, Washington, DC

Ioffe-Uspensky I, Mumcuoglu KY, Uspensky I, Galun R (1997) *Rhipicephalus sanguineus* and *R. turanicus* (Acari: Ixodidae): closely related species with different biological characteristics. J Med Entomol 134:74–81

Ioffe-UspenskyI, Uspensky I, Mumcuoglu KY, Galun R (2005) *Rhipicephalus sanguineus* and *R. turanicus* (Acari: Ixodidae): numerical indices for distinguishing between adults of closely related species in Israel. In:5th international conference on ticks and tick-borne pathogens, programme, proceedings. Université de Neuchâtel Switzerland, pp 171–175

Nicholson WL, Paddock CD, Demma L, Traeger M, Johnson B, Dickson J, McQuiston J, Swerdlow D (2006) Rocky mountain spotted fever in Arizona: documentation of heavy environmental infestations of *Rhipicephalus sanguineus* at an endemic site. Ann N Y Acad Sci 1078:338–341

Parola P, Paddock CD, Raoult D (2005) Tick-borne rickettsioses around the world: emerging diseases challenging old concepts. Clin Microbiol Rev 18:719–756

Pegram RG, Keirans JE, Clifford CM, Walker JB (1987) Clarification of the *Rhipicephalus sanguineus* group (Acari, Ixodoidea, Ixodidae). II. *R. sanguineus* (Latreille, 1806) and related species. Syst Parasitol 10:27–44

Uspensky I, Ioffe-Uspensky I (2002) The dog factor in brown dog tick *Rhipicephalus sanguineus* (Acari: Ixodidae) infestations in and near human dwellings. Int J Med Microbiol 291(Suppl 33): 156–163

Uspensky I, Ioffe-Uspensky I, Mumcuoglu KY, Galun R (1999) Body weight characteristics of some ixodid ticks: reflecting adaptations to conditions of their habitats? In Bruin J, van der Geest LPS, Sabelis MW (eds) Ecology and evolution of the *Acari*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 657–665

Walker JB, Keirans JE, Horak IG (2000) The genus *Rhipicephalus* (Acari, Ixodidae). A guide to the brown ticks of the world. Cambridge University Press, Cambridge, UK

Brown Lacewings

Members of the family Hemerobiidae (order Neuroptera).

► Lacewings, Antlions and Mantidflies

Brown Planthopper, *Nilaparvata lugens* (Hemiptera: Delphacidae)

This is a serious pest of rice in Southeast Asia.

► Area-Wide Insect Pest Management

Brown Rot of Fruit

These are fungal diseases of fruit that are transmitted by insects.

► Transmission of Plant Diseases by Insects

Brown Wheat Mite, *Petrobia latens* (Müller) (Acari: Tetranychidae)

This mite causes injury to wheat.

► Wheat Pests and Their Management

Brown-Banded Cockroach, *Supella longipalpa* (Fabricius) (Blattodea, Blattellidae)

This common cockroach is one of the more important pests in cooler climates.

► Cockroaches

Bruch, Carlos

Carlos Bruch was born in Munich in 1869. He was interested in natural sciences but at age 14 joined his father's business, and then in 1887 followed his father to Argentina. Later that same year he obtained a job providing photographic and printing services to the newly-built Museo de La Plata. The insect collection that he had formed in Germany became the foundation of the entomological section of the museum, and later he became head of that section despite lack of formal training in entomology. In 1906 he was appointed professor of zoology of Universidad de La Plata. In 1913 the title of "doctor honoris causa" was bestowed upon him, followed by other titles. His research and some 200 publications were on diverse groups of insects. He died on July 3, 1943. Pages 48–55 of Revista de la Sociedad Entomologica de Argentina (vol. 43), written by several authors as representatives of several Argentine institutions, laud his accomplishments.

Reference

Herman LH (2001) Bruch, Carlos. Bull Am Mus Nat Hist 265:49–50

Bruchidae

A family of beetles (order Coleoptera). They commonly are known as seed beetles.

► Beetles

Brues, II, Charles Thomas

Charles Brues was born on June 20, 1879, in West Virginia. His high school years were spent in Chicago, but instead of attending the University of Chicago, he went to the University of Texas, persuaded to do so by William Morton Wheeler who had just been appointed head of the zoology department there. A schooldays friendship with A. L. Melander, both of whom had been introduced to entomology by H. E. Walter, was continued in Texas and until the death of Brues many years later. They coauthored entomological papers while at Texas. After graduation with A.B. degree in 1901 and M.S. degree in 1902, Brues went to Columbia University, but then returned to Texas to work for the U.S. Department of Agriculture. In 1905 he moved to the Milwaukee Public Museum to work as Curator of Invertebrate Zoology, but in 1909 relocated to Harvard University to become instructor in economic entomology, with William Morton Wheeler as his supervisor. In 1935 he was promoted to Professor of Entomology and also was Associate Curator of Insects at the Museum of Comparative Zoology. In 1946 he was made Emeritus Professor of Entomology at Harvard. He collected insects throughout the United States, and in the Philippines, East Indies, West Indies, and South America. He was an active member of the Cambridge Entomological Club and editor of its publication (Psyche) from 1910 to 1947. Among his publications are "A key to the families of North American insects" (first published in 1915 and coauthored with Melander, and later revised), "Insects and human welfare" (1921, later revised), and "Insect dietary" (1946). His research was on taxonomy and behavior of phorid flies in ant nests, "parasitic" Hymenoptera, food and feeding habits of insects, medical entomology, and tissue staining, and thermophilous insects. He was a stimulating advisor of his graduate students. He died in Florida on July 22, 1955, survived by his wife and a son and daughter.

Reference

Mallis A (1971) Charles Thomas Brues, II. In American entomologists. Rutgers University Press, New Brunswick, NJ, p 434–435

Brulle, Gaspard Auguste

Auguste Brullé was born in Paris on April 7, 1809. At school he showed a taste for the natural sciences. Then, in 1829 he was able to take part in a French government-sponsored expedition to Moorea, and enthusiastically studied insects. In 1933–1839 he was an assistant at the Muséum National d' Histoire Naturelle in Paris, working for the chairman of entomology. In 1832, with other entomologists, he contributed to founding the Société Entomologique de France. His (1839) professional thesis presented to the Faculté des Sciences of Université de Paris was on deposits of fossil insects. In 1839 he was appointed to a professorship of zoology and comparative anatomy in Dijon. Unfortunately for entomology, his duties in Dijon precluded his further contributions to studies of insects. Nevertheless, from 1831 to 1843, he published on taxonomy of Coleoptera and Hymenoptera, mostly in Annales de la Société Entomologique de France. The (1834–1837) book "Histoire naturelle des insectes"; that he co-authored with Audouin (Brullé wrote for it the sections of Coleoptera, Orthoptera, and Hemiptera) was not completed. He was awarded France's highest medal, the Légion d' Honneur. He died on January 21, 1873.

Reference

Desmarest E (1873) Note sur la vie et les travaux entomologiques d' Auguste Brullé. Annales de la Société Entomologique de France (5)2:513–516

Brunner Von Wattenwyl, Carl

Carl Brunner was born in Bern on June 13, 1823, a member of a notable Swiss family, but moved at an early age to Vienna. His early publications were in chemistry, physics, geology, glaciology, and meteorology. In 1861 he published his first important contribution on Orthoptera, then in 1865 the first of a series of papers on classification of Blattodea. These were followed in 1878 by a paper on classification of Tettigoniidae, then in 1888 on that of Stenopelmatidae and Gryllacrididae. In 1882 was published his encyclopedic work of the European Orthoptera

"Prodromus der Europäischen Orthopteren." In all, he published 27 works on Orthoptera and was one of the most notable of orthopterists. He died on August 24, 1914, at Kirchdorf, Austria, and his Orthoptera collection is in Vienna.

References

Burr M (1900) Brunner von Wattenwyl. Ent Rec J Var 12:12 + pl. 1
Rehn JAG (1915) Carl Brunner von Wattenwyl. Entomol News 26:285–288

Brush-Footed Butterflies (Lepidoptera: Nymphalidae)

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The Nymphalidae is one of five families in the superfamily Papilionoidea (true butterflies) of the order Lepidoptera (moths and butterflies). Although a number of lineages within the family are well circumscribed and have been recognized since the 1800s, the taxonomic rank which such lineages should be accorded and how they should be subdivided remains contentious. A number of currently recognized subfamilies, and even some tribes, have been considered distinct families by some authors. However, continuing morphological and especially molecular research now provides real hope of a stable higher classification in the future. Ten subfamilies are currently recognized, including:

- Order: Lepidoptera
  - Superfamily: Papilionoidea
    - Family: Nymphalidae
      - Subfamily: Libytheinae
      - Subfamily: Calinaginae
      - Subfamily: Morphinae
      - Subfamily: Satyrinae
      - Subfamily: Charaxinae
      - Subfamily: Apaturinae
      - Subfamily: Nymphalinae
      - Subfamily: Danainae
      - Subfamily: Heliconiinae
      - Subfamily: Biblidinae

Distinguishing Characteristics and Relationships

One distinctive and unambiguous character is unique to the Nymphalidae: the ventromesial surface of the antenna has three longitudinal ridges (termed carinae, meaning "keel"; the antenna is hence "tricarinate"), one lying either side and one separating two shallow longitudinal grooves. Two further characters may be the presence of a distinctive structure, von Siebold's organ, in the female genitalia, and a filiform seta in the mature larva that is absent in other papilionoid families.

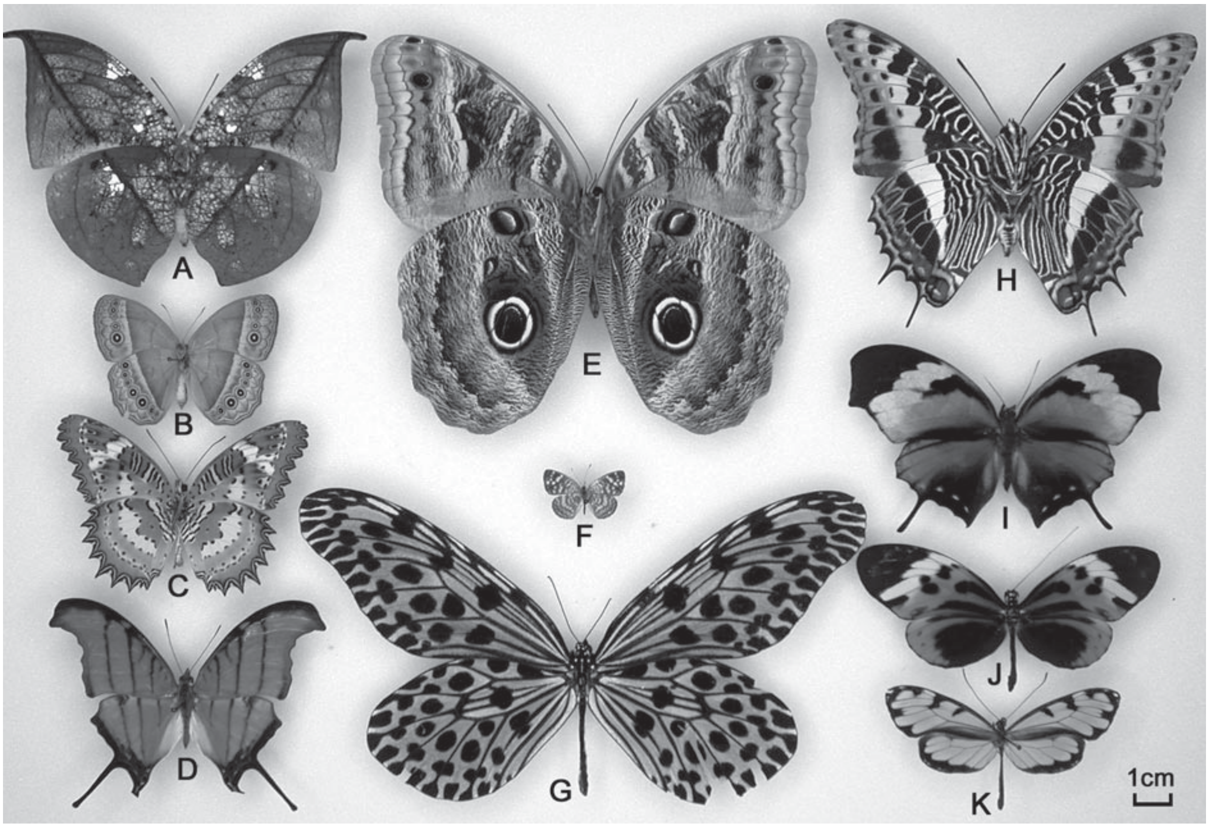
The sister taxon (most closely related group) to the Nymphalidae is thought to be the Lycaenidae plus Riodinidae, which share several thoracic and musculature characters with the family. More obvious characters are provided by the foreleg, which is reduced in adults of most male Lycaenidae plus Riodinidae, and in male and female Nymphalidae (only in male Libytheinae). The male foreleg in all three families lacks tarsal claws and has the original five tarsal segments (tarsomeres) reduced in number through fusion, with the latter feature also occurring in some female Nymphalidae. In male Riodinidae, and both sexes of most Nymphalidae, only four legs are used for walking, and in male Nymphalidae the forelegs are clothed in hair-like scales, inspiring the common familial name "brush-footed butterflies."

All nymphalid subfamilies, except for Libytheinae, are further grouped by the loss of use of the foreleg in the female. Relationships between other nymphalid subfamilies remain obscure, although certain relationships are often found and seem plausible, such as Morphinae plus Satyrinae. While most subfamilies are probably natural (monophyletic) groups, the Nymphalinae, Biblidinae, and Satyrinae have no convincing autapomorphies (uniquely derived characteristics). They will almost certainly be subdivided or merged with other subfamilies as our knowledge of nymphalid phylogeny increases.

Morphology

Adult

Nymphalid butterflies (Fig. 68) range from tiny melitaeines (Nymphalinae), the size of a fingernail, to giant *Caligo* (Morphinae), the size of dinner-plates. The wings may be rounded, elongate (e.g., Heliconiinae, Ithomiini), scalloped (e.g., *Cethosia*), or with long hindwing tails (e.g., *Marpesia*). The simplest nymphalid wing patterns consist of a series of dark lines and ocelli (eyespots, a common feature) on a pale background, which are variably modified through loss, expansion or fusion into a fantastic array of patterns. These patterns range from almost entirely transparent and colorless in ithomiine danaines to the extremely complex patterns of certain *Charaxes* species (Charaxinae), to the brilliant iridescent blue that makes *Morpho* butterflies visible from low-flying aircraft. Many insights into the



Brush-Footed Butterflies (Lepidoptera: Nymphalidae), Figure 68 **Representative nymphalid butterflies. A, *Coenophlebia archidona* (Charaxinae), Ecuador; B, *Mycalesis orseis* (Satyrinae), Malaysia; C, *Cethosia penthesilea* (Heliconiinae), Malaysia; D, *Marpesia petreus* (Biblidinae), Ecuador; E, *Caligo ilioneus* (Brassolinae), Ecuador; F, *Phystis simois* (Nymphalinae), Ecuador; G, *Idea lynceus* (Danainae), Malaysia; H, *Charaxes castor* (Charaxinae), Kenya; I, *Consul fabius* (Charaxinae), Ecuador; J, *Heliconius numata* (Heliconiinae), Ecuador; K, *Oleria baizana* (Danainae), Ecuador.**

developmental genetics and evolution of lepidopteran wing patterns have been gained from comparative study of nymphalid wing patterns.

Wing color pattern signaling functions include crypsis (e.g., the extraordinary leaf-like *Kallima* and *Coenophlebia*; transparent-winged forest understorey satyrines and ithomiines), startle or deflective coloration (e.g., the eyespots of *Caligo* and *Satyrinae*), interspecific recognition (e.g., *Nessaea*, *Catonephele*), and both Batesian (e.g., certain Nymphalinae and Charaxinae) and Müllerian (e.g., Heliconiinae, Danainae) mimetic warning coloration. Color pattern variation includes seasonal polymorphism (e.g., *Junonia*), local genetic polymorphisms (e.g., *Heliconius*, *Hypolimnas*), and often remarkable geographic racial polymorphism (e.g., Danainae, *Heliconius*).

The external morphology is rather uniform, being responsible, at least in part, for the poorly resolved high-level classification of the family. Variation in wing venation, thoracic exoskeletal, leg and labial palpal morphology provides the foundation for the current subfamilial classification. In certain species the veins and basal wing sclerites on either fore or hindwing may be modified to form a tympanal organ (e.g., *Heliconius*, Satyrinae), though its function is poorly understood. At the subtribal, generic and species level genitalic morphology, especially male, has been used extensively, although there is often no variation between closely related species.

The Nymphalidae exhibit a rich diversity of secondary sexual structures. Most commonly these are modified scales with glandular bases, typically confined to the male sex, termed "androconia." Androconial scales usually form patches, fringes, tufts or pockets, and may be flattened or elongate, but often are hair-like and erectile (e.g., Satyrinae, Danainae). Alar androconia are often associated with wing veins, and occur commonly in the Satyrinae and Danainae. Abdominal androconia may be located on eversible glands (e.g., *Vila*) or contained within a membranous sheath that can be everted through an increase in haemolymph pressure (e.g., the coremata that characterize the Danaini). Especially complex androconial systems, such as those in the Danaini, involve abdominal brushes that are remote from glandular alar areas but make contact with them immediately before scent dispersal. Secondary sexual structures also are known for females of some taxa, most notably in some members of the Heliconiinae, which possess a dorsal abdominal gland and associated lateral club-like structures termed stink-clubs or clavatia.

Immature Stages

Nymphalid immature stages are morphologically extremely diverse, and although comparative study is in relative infancy compared to adult morphology, immature stage characters may still provide very significant information for the higher level classification of the family.

The eggs are typically spherical, ovoid, or flattened domes, and almost smooth (e.g., Satyrinae), ribbed (e.g., Danainae), or faceted with interstitial spines (Limenitidini). Larvae may be smooth (e.g., some Danainae), covered with small granulations (e.g., Satyrinae), or decorated with fleshy tubercles (e.g., Danainae), dense spines (e.g., Nymphalinae) that may be modified into highly elongate and branched scoli (some Biblidinae), or hair tufts (e.g., some Brassolinae). In later instars of some neotropical Charaxinae the third thoracic and first abdominal segments also may be expanded to form dorsal or dorsolateral humps. The head capsule may be striped or colored, and may be smooth (e.g., Danainae), or ornamented with chalazae (raised wart-like processes, frequently bearing setae), that often form elaborate dorsal and subdorsal head horns. The ninth abdominal segment is often bifid, forming "tails" (e.g., Satyrinae, Charaxinae, Morphinae). Larvae may be cryptically colored (most Satyrinae, Limenitidini) or black with bright orange, white or yellow markings that suggest warning coloration.

Except for a few satyrines that pupate terrestrially, the pupa is suspended by the cremaster and never has a girdle. Pupae may be smooth, elongate ovoids (e.g., some Satyrinae and Danainae), or highly ornamented with various spines, flanges, and elongate projections (e.g., some Biblidinae). The pupal color pattern ranges from highly cryptic, mottled brown or green, to bright colors that may be aposematic, and many other species are notable for their brilliant opalescent or metallic coloration (e.g., Limenitidini, Danainae).

Diversity, Distribution and Biogeography

The family includes approximately 6,000 to 7,000 species and 350–400 genera. The largest subfamily is the Satyrinae with some 2,500 species, many of which remain undescribed. In contrast, the Calinaginae contains only a single genus of about eight species and the Libytheinae only two genera with 12 species.

The majority of the subfamilies are cosmopolitan, although the Calinaginae are confined to the Sino-Himalayan region and the Morphinae are entirely tropical. However, at the tribal level endemism is much higher, with large tribes confined to or overwhelmingly more diverse in single regions. Notable examples include the Brassolini, Morphini and Ithomiini, restricted to the Neotropics; the Amathusiini, occurring only in the Oriental region; the Acraeini, with its spectacular radiation in the Afrotropical region; and the Danaini, largely confined to the Old World.

Species diversity increases steeply from temperate to tropical regions, reaching a peak in the Neotropical region which contains perhaps 40% of the family. Community species richness is also greatest in the Neotropics, in the foothills of the eastern Andes, where lowland tropical rainforest may contain over 450 species, about a quarter of the butterfly fauna. Species richness decreases with elevation, though richness peaks may occur from 500 to 1,000 m above sea-level, due to overlap of lowland and sub-montane faunas.

The variation in dispersal ability within the Nymphalidae is perhaps more extreme than in any other butterfly family. Certain nymphalids are renowned as great wanderers: the famed Monarch (*Danaus plexippus*, Danainae) occurs throughout much of the globe, even on Hawaii, while the nymphaline *Hypolimnas misippus* is almost as widely distributed. However, the vast majority of species occur only within a single biogeographic region, and a number of species have much more restricted ranges, sometimes down to the level of a single mountain range. Distribution patterns in neotropical montane satyrines (tribe Pronophilini) and the nymphaline genus *Hypanartia* have been used to examine geographic modes of speciation in montane habitats. Ithomiine danaines and heliconiines have featured prominently in studies of the historical biogeography of the Amazon basin.

Habitats

Nymphalid butterflies occur in almost all terrestrial ecosystems. They are found in deserts, grasslands (especially Satyrinae), temperate and tropical lowland and montane forests, ranging from sea-level to over 5,000 m in high ice-fields of the Himalayas and the Andes. They are found in all stages of habitat succession, from primary forest to arid scrub, with varying ecological fidelity.

Ecology

Immature Stages

All nymphalid larvae are phytophagous, with the vast majority concentrating on about 100 families of flowering plants, in addition to a few groups on Cycadaceae (cycads), Selaginellaceae (club-mosses) and Neckeraceae (mosses). The Satyrinae and Morphinae feed largely on monocotyledons, as do a few Charaxinae, with the remainder almost exclusively on dicotyledons.

Eggs may be laid in clusters or singly, varying between species, and on or off the foodplant, or, in some satyrines, be dropped from the air. Larvae of a number of species are gregarious and aposematic, suggesting unpalatability (e.g., Heliconiinae), while others adopt a variety of defensive strategies. These include camouflage through decoration of the early instars with frass pellets (stercophory), maintenance and extension of the leaf mid-rib with frass to form a perch (common in Biblidinae), and construction of a mass of frass and leaf material at the base of the leaf mid-rib to provide additional camouflage, which may be elaborated further into an apparent decoy larva-shaped mass (Limenitidini). Spinose larvae may react violently to disturbance, swinging the body and head (e.g., Biblidini), or curl into a defensive posture with the spines directed outwards (e.g., Limenitidini), while smooth-bodied satyrine larvae may simply drop from the plant into the ground litter. A number of nymphalid larvae hibernate in shelters made from cut and sewn leaves, and in some species (e.g., *Adelpha*), this behavior apparently has been co-opted for protection.

Pupation takes place on or off the foodplant, and some satyrines form a weak cocoon on the ground in which they pupate

Adults

Nymphalids exhibit a broad range of behavior. Unpalatable groups, such as Danainae and Heliconiinae, have a typically slow and even flight, while palatable species in the Apaturinae and Charaxinae are some of the fastest and most agile butterflies. They may be found in open areas (e.g., Satyrinae, Nymphalinae), in shady forest understorey (e.g., Satyrinae, Morphinae, Danainae), and at various levels within forest subcanopy and canopy (e.g., Heliconiinae, Biblidinae, Charaxinae). Throughout the day a succession of different groups becomes active, with the fastest-flying species being active only during the hotter hours of the day.

Adult nymphalids feed on various food substrates including flower nectar, pollen, rotting fruit, carrion, and damp sand. Flower nectar and rotting fruits provide the carbohydrates that power flight, while pollen is used by *Heliconius* butterflies to provide nutrients for egg production. Damp sand and carrion are thought to provide sodium ions, important for neuromuscular activity, which are typically in low concentration in larval food plants. These last two sources may also provide amino acids that are used in manufacturing body proteins. To some extent the preferred food source may be dependent on habitat, with open-country species seeking flowers and damp sand, and forest species feeding on rotting fruit and carrion.

A variety of strategies protect nymphalid butterflies from predators, particularly birds. Many species have cryptic underside markings, especially in the Satyrinae and Morphinae, while bright dorsal coloration in the same species probably confuses predators. Most Biblidinae and Charaxinae probably rely on fast flight to evade predators.

Warningly colored ithomiine danaines and heliconiines were instrumental in the formulation of mimicry theory, providing some of the most outstanding examples of this phenomenon in the animal kingdom. Unpalatable danaines and heliconiines are the basis for numerous Müllerian mimicry rings, in which other nymphalids (e.g., Charaxainae, Nymphalinae), as well as other butterflies and moths, participate as probable Batesian (palatable) mimics.

Unpalatable nymphalids obtain protective chemicals by several means. They may sequester secondary chemicals from larval feeding, such as the cardiac glycosides obtained by Danaini from their apocynaceous foodplants. Alternatively, protective compounds, such as the cyanogenic glucosides in *H`eliconius*, may be synthesized from amino acids in the larval or adult food. More complex precursors also may be stored from the larval stage, or obtained through adult pharmacophagy (literally, "chemical feeding"). Adult danaines obtain dehydropyrrolizidine alkaloids by feeding on Asteraceae flowers (sometimes Boraginaceae), or dried or withered

Boraginaceae plants (sometimes Asteraceae). In ithomiine danaines, it is predominantly males which exploit these alkaloid sources, transferring the compounds to females in the spermatophore during mating.

Nymphalids generally seek females for mating by "patrolling" appropriate areas of habitat (e.g., *Morpho* butterflies may patrol several kilometers along rivers or roads), or by "perching." Perching nymphalids wait for passing females in species-specific locations, such as a forest light-gap or edge, hilltop, riverside, or prominent patch of vegetation, usually at a characteristic height above ground and at a particular time of day. Many satyrines and brassoline morphines are crepuscular, actively perching or patrolling only at dusk and dawn. Ithomiine danaines perch most actively in the middle to late afternoon, while fast-flying forest canopy species, such as the Charaxinae, are active in the middle of the day. The same perching location may be maintained for years. Perching males are territorial and pugnacious, swiftly engaging in high spiraling flights with intruding conspecific males, with the resident male typically winning the encounter to return to the perching site. Some *Charaxes* butterflies have serrate forewing costal margins, which are reported to be used in male-male interactions. Certain species in the genus *Hamadryas* (Biblidinae) are notable for loud crackling sounds that are emitted by perching males in flight, by percussion of the forewings.

Male ithomiine danaines are remarkable in forming dense aggregations, or leks, of up to 20–30 species, which may last several months. Pheromones released through the hindwing hair-pencil androconia attract both sexes, including those of non-conspecific but co-mimetic species, thus providing increased protection from predation and providing a mating place that can be more easily located through the concentrated odor. Aggregations of similar origin and function also are reported in some danaines (*Euploea*).

Males of certain species of Heliconius patrol foodplants and mate with females before eclosion from the pupa, thus avoiding courtship. In those species where courtship has been studied in some detail (Satyrinae, Danainae, Heliconiinae), the importance of androconially disseminated pheromones in achieving successful courtship has been demonstrated. In the Danainae, sex pheromones like danaidone (Danaini) are manufactured from pyrrolizidine alkaloids that also confer protection from predators.

Economic Importance

With the exception of *Brassolis* and *Caligo* (Brassolinae) which may be pests on coconut palm and banana plantations, respectively, and certain Heliconiinae which attack passion fruit plants, few other nymphalid butterflies cause any serious damage to crops. Nymphalid butterflies, however, do have a positive economic value. Nymphalid butterflies are an important component of the dead butterfly specimen trade (e.g., *Agrias*, *Charaxes*), the trade in specimens for education (e.g., the Monarch), and are widely used in butterfly houses in temperate countries (e.g., *Heliconius*, *Caligo*). Butterfly houses import much livestock from butterfly farms in tropical countries, providing an alternative source of income in rural areas.

Conservation

Because of their aesthetic appeal, butterflies may be used as flagship taxa for conservation. Attempts to preserve the spectacular over-wintering colonies of the Monarch butterfly in Mexico have raised awareness of conservation in that region. Butterfly diversity and abundance are increasingly being used at the habitat scale as indicators of disturbance and its effects on biodiversity. Nymphalidae are diverse, one of the easiest groups to identify, and many respond to baited traps, and are thus a principal group in such studies. At the biogeographic scale, the Ithomiini have been proposed as an indicator taxon for neotropical lowland forest butterfly diversity, because of their ease of sampling and apparent close correlation with overall butterfly diversity. Finally, recent shifts in geographic range limits of butterflies, especially nymphalids, have been used as evidence for global climate change.

References

Ackery PR (1988) Hostplants and classification: a review of nymphalid butterflies. Biol J Linn Soc 33:95–203
Ackery PR, de Jong R, Vane-Wright RI (1999) The butterflies: Hedayloidea, and Papilionoidea. In: Kristensen NP (ed) Handbook of zoology 4. de Gruyter, Berlin, Germany, pp 263–300
Brower AVZ (2000) Phylogenetic relationships among the Nymphalidae (Lepidoptera) inferred from partial sequences of the wingless gene. Proc R Soc (Biol Sci B) 267:1201–1211
DeVries PJ (1987) The butterflies of Costa Rica and their natural history. Papilionidae, Pieridae, Nymphalidae. Princeton University Press, Princeton, New Jersey.
Harvey DJ (1991) Appendix B. Higher classification of the Nymphalidae. In: Nijhout HF (ed) The development and evolution of butterfly wing patterns. Smithsonian Institution Press, Washington, DC, pp 255–273
Parsons MJ (1998) The butterflies of Papua New Guinea. Their systematics and biology. Academic Press, London, UK

Brush Organ

Clusters of long setae on the body of certain insects (particularly male Lepidoptera and some Neuroptera). They occur on various parts of the body, but usually on the abdomen. They are associated with exocrine glands, and usually used during courtship to disperse sex pheromones. This term is synonymous with "hair pencils."

Bryopsocidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice and Psocids

B.t.

Abbreviation for the bacterium *Bacillus thuringiensis*.

Bubo

An enlargement of a lymph gland caused by an infection.

► Bubonic Plague
► Plague: Biology and Epidemiology

Bubonic Plague

The dominant form of plague (also known as black death), caused by the bacterium *Yersinia pestis* and vectored by several fleas, but especially *Xenopsylla* spp. It is primarily a disease of rodents, but fleas can spread it to other animals and humans. Bubonic plague is one form of plague, with the others being septicemia plague (infection of the blood) and pneumonic plague (infection of the lungs). Bubonic plague causes headache, elevated temperatures, chills, tiredness, abdominal pains, and painful swellings (buboes) of the lymph nodes. Anyone with large, painful, and tender lymph glands and experiencing extreme tiredness and fever should be considered a possible plague victim, especially if they have had potential exposure to animals capable of harboring plague. People most likely to contract bubonic plague are those living in rural environments, and people active in rural environment such as biologists, campers and hunters.

If untreated, it often is fatal to humans. Treatment is accomplished by application of antibiotics, often streptomycin, but early detection is important. Other important measures to prevent plague are educating the public to avoid places where plague may occur, informing the medical community about diagnosis of plague, and treatment using appropriate medicine. An early warning sign of potential human infection is die-off of rodents. Although rats have historically been implicated in disease transmission, plague is also associated with rock and ground squirrels, wood rats, chipmunks, prairie dogs, mice and voles. To prevent plague problems, it may be useful to use insecticides to kill fleas

during epidemics (e.g., treatment of prairie dog burrows), to apply flea control treatments to pets regularly, to avoid handling sick animals, and to use insect repellents.
▶ Plague: Biology and Epidemiology
▶ Fleas (Siphonaptera)
▶ History and Insects

Buccal Cavity

The entry way to the insect mouth, surrounded by the mouthparts. The oral cavity (Fig. 69).
▶ Alimentary System
▶ Alimentary Canal
▶ Digestion

Bucculatricidae

A family of moths (order Lepidoptera). They are commonly known as ribbed-cocoon maker moths.
▶ Ribbed-Cocoon Maker Moths
▶ Butterflies
▶ Moths

Budding

Among social insects, the same as colony fission: multiplication of colonies by the departure from the parental nest of one or more reproductive forms accompanied by workers. Thus, the parental nest remains functional and new ones are founded.

Buffalo Gnats

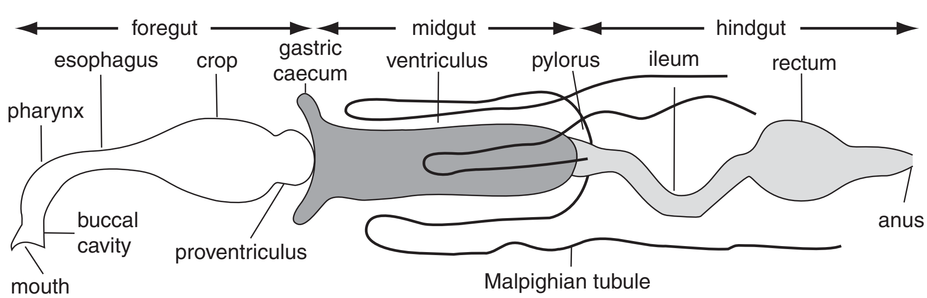
Members of the family Simulidae (order Diptera).
▶ Flies

Buffalograss Chinch Bug, *Blissus occiduus* Barber (Hemiptera: Blissidae)

This insect has become a pest of buffalograss in some areas.
▶ Turfgrass Insects and Their Management
▶ Turfgrass Insects of The United States: Biology and Management

Buffer Zone

This term has different meanings depending on the context. From the perspective of insect control, a buffer zone may be established around a treated field by treating surrounding land and vegetation. This reduces the possibility that an insect can arrive successfully in a susceptible field because nearby insects are eliminated not only in the field, but from surrounding areas. This is most



Buccal Cavity, Figure 69 **Generalized insect alimentary system (adapted from Chapman, The insects: structure and function).**

important for dispersive species, and particularly for disease vectors. From a regulatory perspective, a buffer zone is an area in which a specific pest of concern does not occur, or occurs at a very low level and is controlled, and also encloses, or is adjacent to, an infested area. In both cases, however, the purpose of the buffer zone is to reduce or eliminate spread of a pest.

► Risk Analysis (Assessment)
► Regulatory Entomology
► Invasive Species

Buffon, Georges Louis Leclerc (Comte De)

Georges-Louis LeClerc was born in Montbard, France, on September 7, 1707. He is believed to have been educated in the Jesuit college of Dijon and later received a diploma in law from the Université de Dijon. His early scientific studies were in mathematics and physics, and he performed experiments on the tensile strength of wood. He entered the Academie Royale des Sciences of Paris in 1734. Six years later he was appointed director of the royal garden, which later was called the Jardin des Plantes and was the French center of study not only of botany, but also of zoology, chemistry, and mineralogy. Perhaps he would have studied insects if his eyesight had been adequate. Although he did not do so, he had profound influence on entomology by his founding a huge work (1749–1804) "Histoire naturelle, générale et particulière" in 44 volumes. There were later supplements [see for example, Audinet-Serville above]. The work set out to contradict Linné, because Georges-Louis did not believe in the classification into genera, families, orders and classes that Linné had proposed. The work was very influential especially because so many specialists (including entomologists) became involved in its writing, and because of its completeness (for its time). Furthermore, it was written in French, rather than Latin, breaking the precedent of so many earlier books. He was made a peer of France by Louis XV, king of France, bestowing on him the title of "Comte de Buffon." He died in 1788, leaving his wife Marie and one son.

References

Anon. 1999 Georges-Louis Le Clerc, Comte de Buffon. Thomson Gale: World of scientific discovery, 2nd ed. Farmington Hills, MI, USA

Tuxen SL (1973) Entomology systematizes and describes: 1700–1815. In Smith RF, Mittler, TE Smith CN (ed) History of Entomology. Annual Reviews Inc., Palo Alto, California, pp 95–117

Bugs (Hemiptera)

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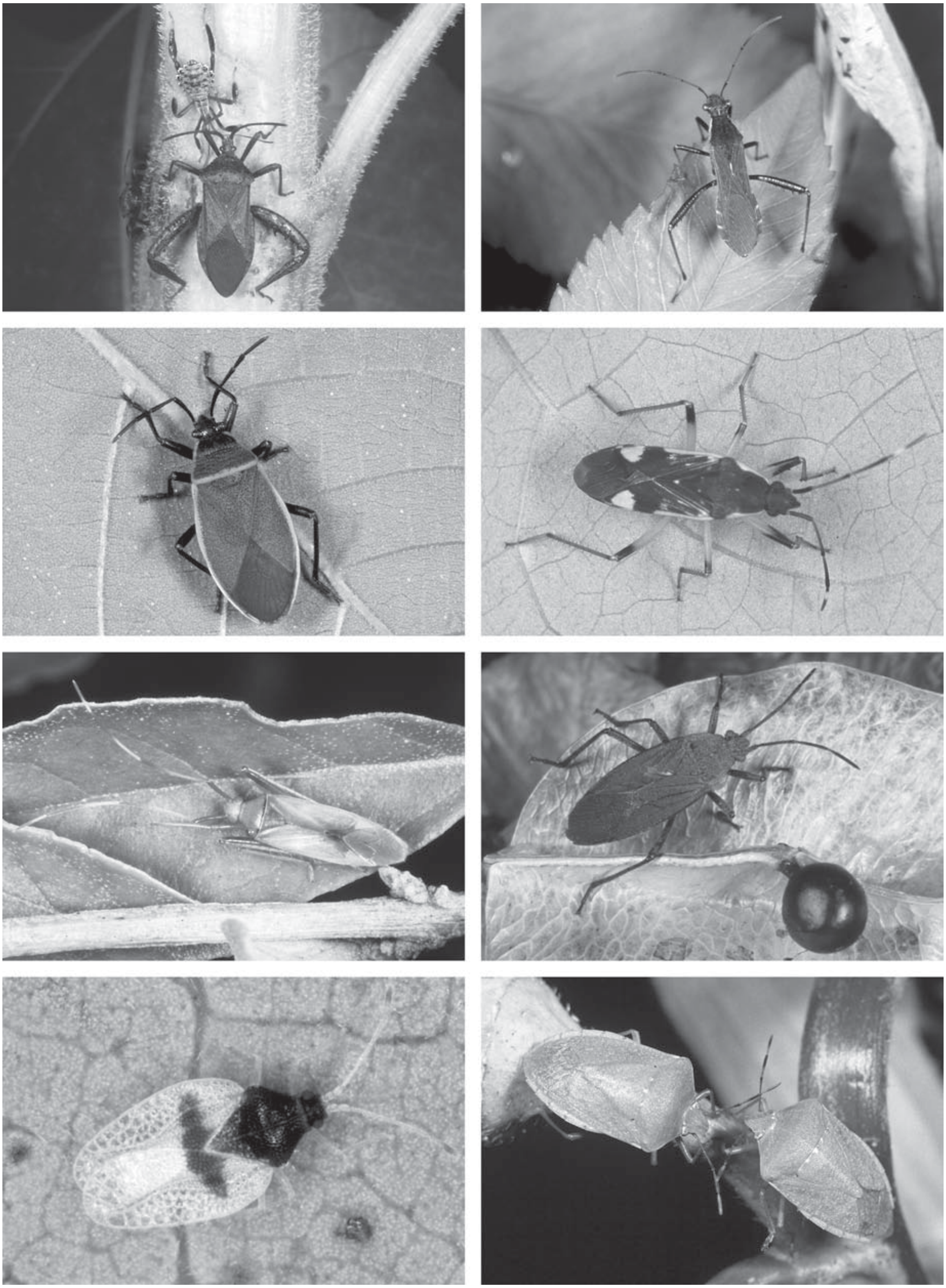
Hemiptera are the largest order of insects with incomplete metamorphosis. This order includes pond skaters, squash bugs, big-eyed bugs, stink bugs, cicadas, leafhoppers, planthoppers, treehoppers, froghoppers, psyllids, aphids, scales, mealybugs, whiteflies, and others (Figs. 70 and 71). Although less well known than beetles or butterflies, they are a diverse group of insects, ubiquitous, interesting, or even spectacular, and in some cases agriculturally and medically important. Approximately 82,000 species have been described worldwide, comprising about 8–10 percent of all known insect species, with an estimated 105,000 species not yet described. They range from minute, wingless scales to fish-eating giant water bugs, which may reach a length of 11 cm. These fascinating insects occur in nearly every type of habitat, including several species that live on the surface of the ocean hundreds of miles from land and others that can be found occasionally drifting in the wind. The majority are plant-feeders, but many species are predatory on other insects, while others feed on



Bugs (Hemiptera), Figure 70 (Continued) the blood of vertebrates and are of great medical importance.

In general, hemipterans have simple or incomplete metamorphosis, in which the young, called nymphs, are similar to adults in shape. The wings develop externally as budlike outgrowths which increase in size at each molt and become functional after the last molt.

The mouthparts of Hemiptera are elongate, forming a slender and usually segmented beak that is used for piercing the host, either plant or animal, and sucking liquids after injecting enzymes that enable extraoral digestion. In many Hemiptera, the basal portion of the front wing is thickened to form a wing cover and the apical portion is thin and usually transparent while the hind wings are entirely membranous. The front wing, or hemelytron (from the Greek words *hemi*, meaning half, and *pteron*, meaning wing), gives the order its name. The name Hemiptera was coined by Linnaeus in 1758.

Classification

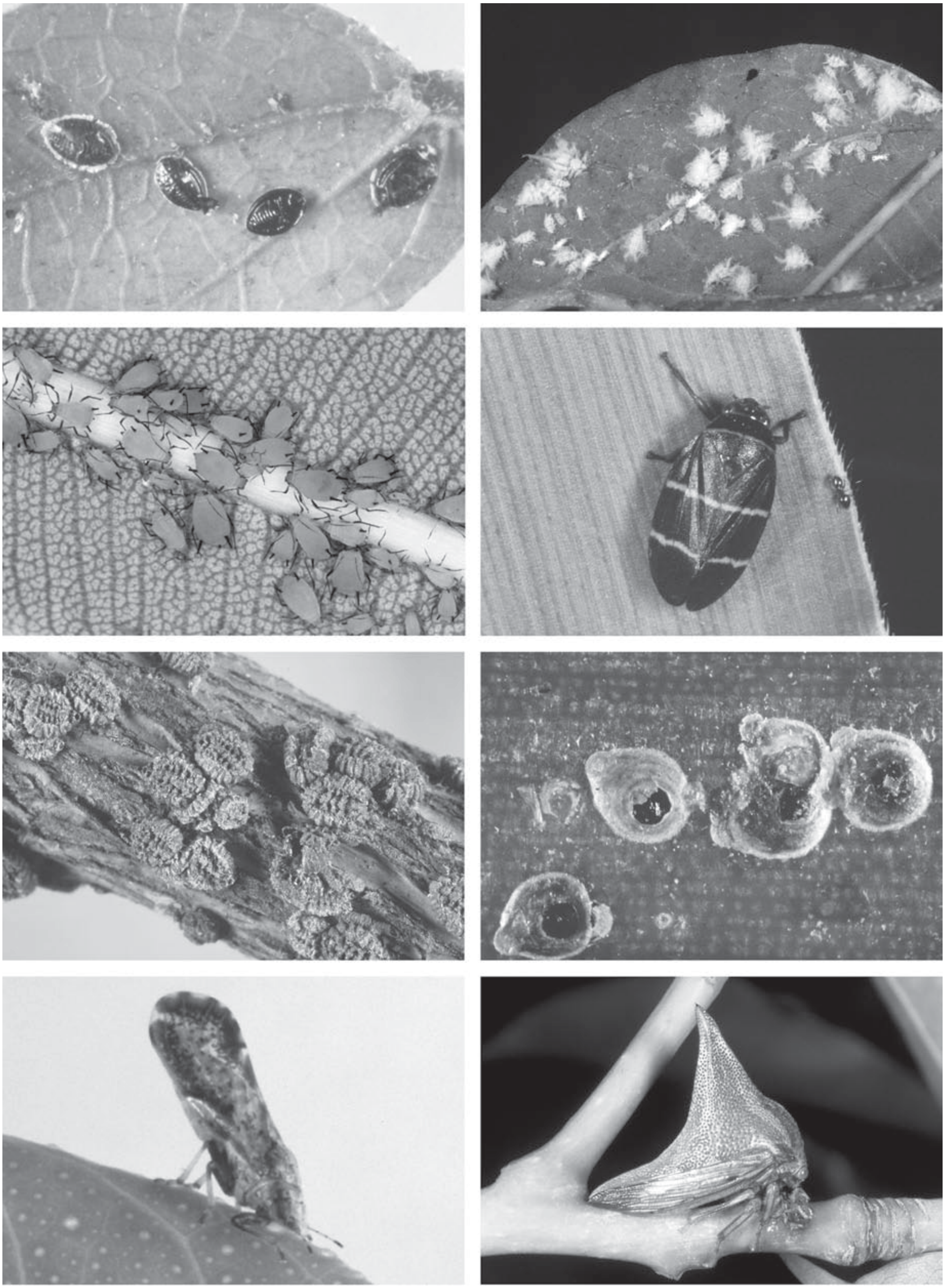
The earliest book to deal exclusively with the Hemiptera was written in 1803 by J. C. Fabricius, a student of C. Linnaeus. He renamed the group Rhyngota, later changed to Rhynchota, a name that is being used today. The term Rhynchota (from the Greek, *rhynchos*, for beak) refers to the morphology of the mouth parts, an elongate structure known as proboscis or rostrum. This name should eventually replace Hemiptera because the rostrum is characteristic to all groups in this order. Up-to-date classifications recognize five suborders within Hemiptera instead of the familiar two suborders, Homoptera and Heteroptera. These suborders are Sternorrhyncha, Fulgoromorpha, Cicadomorpha, Coleorhyncha, and Heteroptera. These names refer to monophyletic groups and will provide stability to the nomenclature within Hemiptera. Some classification schemes present Heteroptera and Coleorhyncha together as Prosorrhyncha, another apparently monophyletic group. The old term Homoptera does not refer to a monophyletic group and has essentially been abandoned. Another classification has four suborders, Sternorrhyncha, Auchenorrhyncha, Coleorhyncha, and Heteroptera; again, the term Auchenorrhyncha refers to a nonmonophyletic taxon and apparently is being abandoned. The arrangement of the various groups (suborders, superfamilies, and families) in the order Hemiptera has been debated for many years. The present classification should not be regarded as fixed.

Order: Hemiptera
- Suborder: Sternorrhyncha
- Suborder: Fulgoromorpha
- Suborder: Cicadomorpha
- Suborder: Coleorhyncha
- Suborder: Heteroptera

Suborder Sternorrhyncha

Sternorrhynchans are common insects found in a wide variety of ecosystems throughout the world. All members of the Sternorrhyncha feed on phloem or xylem from host plants and many are considered plant pests. The group name "Sternorrhyncha" (Greek, *sternon*, chest; *rhynchos*, nose or snout) is derived from the location of the mouthparts occurring between the bases of the front legs. In previous classification schemes, both the Auchenorrhyncha and Sternorrhyncha have been recognized as suborders of the Homoptera. However, the legitimacy

Bugs (Hemiptera), Figure 70 **Representative bugs (Hemiptera): top left, a leaffootted bug, *Acanthocephala femorata* (Coreidae); top right, a broad-headed bug, *Alydus pilosulus* (Alydidae); second row left, a largid bug, *Largus succinctus* (Largidae); second row right, a seed bug, *Dieuches armatipes* (Lygaeidae); third row left, a plant bug, *Creontiades rubrinerus* (Miridae); third row right, Jadera bug, *Jadera haematoloma* (Rhopalidae); bottom left, avocado lace bug, *Pseudacysta persa* (Tingidae); southern green stink bug, *Nezara viridula* (Pentatomidae) (all photos by Lyle Buss).**



Bugs (Hemiptera), Figure 71 **(Continued)**

of the order Homoptera has been and is the topic of many debates. There is taxonomic evidence demonstrating that the "Homoptera" grouping is paraphyletic (derived from a single ancestor but not containing all descendants). Many taxonomists agree that this group should be recognized as part of the Hemiptera but debates occur when discussing placement of the Homopteran groups as suborders within the Hemiptera. For the purpose of this discussion, we will recognize the Sternorrhyncha as a suborder of the Hemiptera. The suborder Sternorrhyncha contains four major superfamilies: Aleyrodoidea (whiteflies); Aphidoidea (aphids); Coccoidea (scale insects); and Psylloidea (jumping plant lice). The classification system is:

Order: Hemiptera
- Suborder: Sternorrhyncha
  - Superfamily: Aleyrodoidea
    - Aleyrodidae-whiteflies
  - Superfamily: Aphidoidea
    - Adelgidae-adelgids
    - Aphidiidae-aphids
    - Phylloxeridae
  - Superfamily: Coccoidea
    - Aclerdidae-flat grass scales
    - Asterolecaniidae-pit scales
    - Beesoniidae
    - Carayonemiidae
    - Cerococcidae-ornate pit scales
    - Coccidae-soft scales
    - Conchaspididae
    - Dactylopiidae-cochineal scales
    - Diaspididae-armored scales
    - Eriococcidae-felt scales
    - Halimococcidae
    - Kermesidae-gall-like scales
    - Kerriidae-lac scales
    - Lecanodiaspididae-false pit scales
    - Margarodidae-margarodid scales
    - Micrococcidae
    - Ortheziidae-ensign scales
    - Phenacoleachiidae
    - Phoenicococcidae-palm scales
    - Pseudococcidae-mealy bugs
    - Putoidae-giant mealy bugs
    - Stictococcidae-false soft scales
  - Superfamily: Psylloidea
    - Calophyllidae
    - Carsidaridae
    - Homotomidae
    - Phacopteronidae
    - Psyllidae
    - Triozidae

One of the most common characters associated with the Hemiptera are the modifications seen in the mouthparts that appear to many as being a "beak." The mandibles, maxillae, labium and labrum are present, but are modified into a rostrum where the mandibles and maxillae are modified into needle-like or thread-like stylets lying within a grooved labium. Hemiptera use their mouthparts to feed on plant or animal tissues. The sternorrhynchans share the mouthpart modifications, but differ by using their stylets to probe plant tissues intercellularly or intracellularly, and forming a protective sheath from secreted saliva around the mouthparts.

Many of the sternorrhyncans are phloem feeders with a diet rich in carbohydrates and deficient in amino acids and other nitrogenous materials. To compensate for this deficiency, sternorrhynchans have endosymbionts (intracellular bacteria or fungi) housed in special tissues and contribute to the nutrition of the insect host. Because many

Bugs (Hemiptera), Figure 71 **Additional representative bugs (Hemiptera): top left, acacia whitefly, *Tetraleurodes acaciae* (Aleyrodidae); top right Asian woolly hackberry aphid, *Shivaphis celti* (Aphididae); second row left, oleander aphid, *Aphis nereii* (Aphididae); second row right, twolined spittlebug, *Prosophia bicincta* (Cercopidae); third row left, grenade scale, *Cerococcus deklei* (Cerococcidae); third row right, ananas scale, *Melanaspis bromeliae* (Diaspididae); bottom left, Asian citrus psyllid, *Diaphorina citri* (Psyllidae); bottom right, thorn bug, *Umbonia crassicornis* (Membracidae) (all photos by Lyle Buss).**

sternorrhynchans feed on phloem, too many carbohydrates are taken in and must be expelled. They expel excess carbohydrates by excreting a sugary substance called honeydew. Honeydew can contaminate foliage and serves as a good growth medium for sooty molds. Sooty molds can detract from the overall appearance of the host plant and can interfere with photosynthesis. Honeydew can also attract ants that may protect the sternorrhynchans from their natural enemies and help in removal of excess honeydew secretions.

Aphidoidea (Aphidoids)

Aphids or aphidoids are probably the most universally recognized members of the Sternorrhyncha due primarily to their presence on ornamental plants and crops. Members of the superfamily Aphidoidea are best recognized by the presence of siphunculi (cornicles) arising from the abdomen. Other key characteristics in recognizing aphidoids include: 2-segmented tarsi with the second segment bearing two claws and the presence of a cauda (equivalent to the lingula found on whiteflies) on the posterior tip of the abdomen. Aphidoids are generally soft-bodied (ranging between 1 and 8 mm in length) and variously pigmented from yellow to green to brown and occasionally red. They tend to be gregarious, and live in colonies or aggregations on their host plants. Both alates (winged) and apterous (without wings) individuals may be present in colonies. Immature stages look like smaller versions of the adults. They typically travel short distances to (or on) host plants by walking or by being transported by ants. Dispersal over great distances can be accomplished through flight or by wind currents. Most aphidoids feed either on phloem or in the parenchyma tissue with most being monoecious but a few species being heteroecious. Many aphidoids are pests of crops and some species are capable of transmitting viruses such as barley yellows, plum pox, and various diseases of cucurbits and melons.

The life cycles of the aphidoids include both asexual (parthenogenic) and sexual reproductive strategies. Life cycles where sexual generations are present are termed holocyclic and those where sexual generations are absent are termed anholocyclic. There are six stages to development for the aphidoids; egg, four nymphal stages and the adult stage. Morphological differences occur between and within families. For example, members of the *Eriosoma* (Aphidae) can produce cottony wax to cover their bodies, whereas other members of the Aphidae produce no wax. There are three families (Aphididae, Adelgidae and Phylloxeridae) with roughly 4,500 known species comprising the Aphidoidea. The Aphididae (aphids) comprise the largest family within the Aphidoidea, containing roughly 4,300 species. As in the higher classification of the Sternorrhyncha, there is much debate on numbers of subfamilies and/or tribes within the Aphididae. There are two genera and roughly 50 species within the Adelgidae. Most adelgids are found on coniferous hosts and readily induce gall formation on their hosts. The Phylloxeridae contain eight genera and approximately 75 species. Most species primarily occur on oaks (Fagaceae) and hickories (Juglandaceae).

Aleyrodoidea (Whiteflies)

Aleyrodids or whiteflies are one of the most recognized plant pests in the world with various diseases being transmitted to crops and with the overwhelming numbers of adults present in infested crops. A tell-tale sign indicating whitefly presence is the white cloud that emerges when plant foliage is disturbed. Adult whiteflies derive their common name (*aleuro*, flour) from the powdery, white wax secretions that cover their bodies. The adults are small, with wingspans being 4 mm or less. There are roughly 1,200 described species within the single family of the Aleyrodoidea. The family Aleyrodidae is recognized as having two subfamilies: the Aleurodicinae and the Aleyrodinae. The

Aleyrodidae are unusual with the subfamilies being defined by both adult and nymphal characters, and the species are defined solely on the characteristics of the puparium. Members of the Aleurodicinae can be distinguished from the Aleyrodinae by having larger adults with more complex wing venation, and also by the presence of large agglomerate wax pores on the puparium.

Whiteflies typically reproduce sexually, with unfertilized eggs becoming males. There are six stages of development for whiteflies: egg, three nymphal instars, pupal instar and the adult. Once mating occurs, whitefly females typically lay their stalked eggs in arcs or circles on the underside of leaves. Once eggs hatch, first instars emerge and generally settle close to deposition sites. Subsequent development occurs on the underside of leaves. Economically important species undergo multiple generations in a season, whereas many benign species usually have only one to two generations per season. Adult males are interesting in that they perform courtship behaviors prior to mating (abdominal oscillations that cause acoustic substrate vibrations).

Many species are considered economically important. They feed from the plant vascular tissues and all feeding stages produce honeydew. Adult whiteflies cue into plant chemicals and colors (green and yellow). Most host plants are angiosperms, with relatively few hosts being herbs, grasses, ferns or palms. Feeding damage from whiteflies can be seen in a myriad of symptoms, including leaf chlorosis, wilting, leaf drop and presence of honeydew. Some species are associated with viral disease transmission and the most serious pests are associated with orchards, crops and greenhouses. Probably the most recognized significant pest of this group is *Bemisia tabaci* (sweetpotato whitefly). This pest is highly polyphagous and is thought to vector more than 70 different viruses (e.g., Gemini virus, melon leaf curl virus). The most virulent form of this species is biotype B or *B. argentifolii* (silverleaf whitefly). Generally control of these whiteflies is realized with the use of non-specific predators (predaceous mites and lacewing larvae) and parasitic wasps that are often specific to the whitefly species that they attack.

Coccoidea (Scale Insects)

The coccoids or scale insects comprise the most diverse group within the Sternorrhyncha. They derive their common name from the presence of a thin layer of secreted wax, resin, or other secreted materials held over or affixed to the body of the insect. Scale insects occur throughout the world on a wide range of host plants, and many are considered economically important plant pests in agricultural crops, urban landscapes, greenhouses and forests. Many have been the focus of a variety of biology and ecology studies over the years. The first example of a successful biological control program was with the vedalia beetle on cottony cushion scale (*Icerya purchasi*). Scale insects (Dactylopiidae) have even been used as biological control agents on prickly pear cacti (*Opuntia* sp). Others such as the pela wax scale (*Ceroplastes pela*), cochineal insects (*Dactylopius* sp.) and lac insects (Kerriidae) have been used to produce commercial products.

Scale insects also have many unique biological and morphological characteristics. They are a good example of gender dimorphism with the adult males resembling small flies, with one pair of true wings and a second, but reduced pair. The classification has primarily been based on the morphology of the adult female. The adult females are usually sedentary and affixed to the host plant. The immature stages are often smaller than the adult life stages with the dispersal stage (or crawlers) ranging from 300 to 700 μm in length and having a flattened ovoid body shape. Perhaps one of the most unique and fascinating morphological oddities within the scale insects can be seen in the ground pearls (Margarodidae). They have a quiescent stage where an immature developmental stage may form a protective covering (cyst) around the body to help in adverse environmental conditions. Scale insects demonstrate a wide range of reproductive systems including: hermaphroditism (cottony cushion scale, *Icerya purchasi*), asexual reproduction (up to seven different types of parthenogenesis) and sexual reproduction. Eggs may be laid outside the body underneath a protective covering such as an ovisac (some Coccidae, Margarodidae, Ortheziidae and Pseudococcidae) or underneath the testa, or scale covering, as seen in many armored scales (Diaspididae). In others cases, eggs are withheld in the body and live birth occurs (some armored scales and members of the Phoenicococcidae).

Taxonomically, scale insects have always been divided into two informal groups, the archaecococcids and the neocococcids. The archaecococcids are comprised of the Margarodidae (roughly 400 species), Ortheziidae (ensign scales, 135 species), Carayonemidae (four species) and the Phenacoleachiidae (two species). The archaeococcid grouping is not monophyletic and members of this group share primitive characteristics (e.g., retention of abdominal spiracles). The neocococcoids comprise the rest of the coccoids (17 families, approximately 7,000 species). This informal grouping is considered monophyletic based on derived features such as apical setae on the labium, loss of abdominal spiracles. The three largest families of neococcoids are the Diaspididae (armored scales, 2,400 species), the Pseudococcidae (mealybugs, 2,000 species) and the Coccidae (soft scales, 1,000 species). Other neococcid families include: Aclerdidae (flat grass scales, approximately 50 species), Asterolecaniidae (pit scales, 200 + species), Beesoniidae (nine species), Conchaspididae (approximately 30 species), Cerococcidae (ornate pit scales, 70 species), Dactylopiidae (cochineal insects, nine species), Eriococcidae (felt scales, 550 species), Halimococcidae (20 species), Kermesidae (gall-like scales, 90 species), Kerriidae (lac insects, 100 species), Lecanodiaspididae (false pit scales, 80 species), Micrococcidae (eight species), Phoenicococcidae (one species) and the Stictococcidae (16 species).

There are species of scale insects that represent every major cyclic system seen in insects. Some species such as pink hibiscus mealybug (Pseudococcidae: *Maconellicoccus hirsutus*) and lobate lac scale (Kerriidae: *Paratachardina lobata lobata*) have multivoltine (numerous generations per year) life cycles. Others, such as European fruit lecanium (Coccidae: *Parthenolecanium corni*) and Indian wax scale (Coccidae: *Ceroplastes ceriferus*) generally are univoltine. Proper environmental conditions, such as prolonged warm periods and high humidity, can allow some univoltine species to have more than one generation per season. After eggs are laid, and once the crawlers or first instars emerge, they will begin searching for suitable feeding sites. They will settle on the natal host plant, or will be dispersed to other hosts via wind currents. Some crawlers have demonstrated behaviors (such as arching their bodies) that aid in their ability to become airborne. Once a suitable host is found, crawlers settle (becoming sedentary in many cases) and begin the feeding process.

Scale insects feed in the phloem or parenchyma of the host plants. The coccoids demonstrate the complete spectrum of feeding preference ranging from monophagous to oligophagous to polyphagous. Primary damage to the host plant is through sap removal. This process can cause the plant to have chlorosis in the foliage, premature leaf drop, twig die back and possibly death of the host plant. Many coccoids produce copious amounts of honeydew. In turn, the honeydew becomes a good growth media for sooty molds that can hinder photosynthesis of the host plant and detract from the aesthetic value of the host.

A key factor in controlling scale insect infestations is detection. Many scale insects are able to slip by inspections by being present in very small population numbers. Growers and homeowners should attempt to thoroughly inspect their plants to insure that populations of scales do not become established. Control of scale insect infestations is realized through a variety of methods: (i) cultural (ii) natural enemies (iii) oils (iv) pesticides. Cultural control methods, such as pruning and destruction of infested material, can be effective when populations are at low levels. In some cases, natural enemies keep populations of scale insects at low levels. The best scale insect predators are the ladybird beetles (Coccinellidae: *Chilocorus*, *Cryptolaemus* and *Rodolia*). When crawlers are present, lacewing larvae can be good predators, but should not be relied upon due to their polyphagous nature. Most parasitoids that attack scale insects are from the Aphelinidae (e.g., *Aphytis* sp.) and the Encyrtidae (e.g., *Metaphycus* sp.). Use of horticultural oils can be a good support treatment when natural enemies are present. Horticultural oils are not as toxic as other pesticides to the natural enemies. Proper application of oils in conjunction with natural enemies can suppress and keep scale populations at levels below the economic threshold. Lastly, chemical control is relied on in many situations with severe infestations to help reduce the scale insect populations.

Psylloidea (Jumping Plant Lice)

The Psylloidea or jumping plant lice are found in most regions of the world, with the majority of species present in tropical regions. Psylloids are the most attractive of the sternorrhynchans, with many possessing brilliant color patterns. Psylloid adults are very small, ranging from less than 1–8 mm in length, and often resemble miniature cicadas. The immature stages closely resemble the adult life stage but lack wings. Immatures from the Psyllidae can occur on the surface of the host plant, within a gall or within "lerps." Lerps are protective coverings formed from exudates from the immatures (liquid feces and wax filaments).

The common name (jumping plant lice) refers to the ability of the adults to jump backwards when disturbed. All members of this superfamily feed primarily on the phloem of woody-dicotylendonous plants. Many members of the Psylloidea are plant pests. Damage from psylloids can be in the form of galls, stunting or poor plant growth. In some instances, psylloids can transmit diseases. Examples include *Cacopsylla pyricola* (transmits fireblight in pears), *Bactericera cockerelli* (vectors psyllid yellows in several garden crops), and *Diaphorina citri* (vectors citrus greening disease in citrus).

There is much discussion concerning the taxonomy and numbers of families within the Psylloidea. Here we recognize six families: Calophyidae, Carsidaridae, Homotomidae, Phacopteronidae, Psyllidae, and the Triozidae. The majority of the families have very select host ranges: Calophyidae feed primarily on plants from the Anacardiaceae; Carsidaridae are restricted to members of the Bombaceae, Malvaceae, and Sterculiaceae; Homotomidae are restricted to the Moraceae; Phacopteronidae feed on plants in the Meliaceae; Psyllidae feed on a wide range of hosts.

Unlike many of the other sternorrhynchans, psylloids reproduce solely through sexual means. They have seven life stages: egg, five nymphal instars and the adult. Many species occurring in tropical to warm temperate regions tend to have multivoltine life cycles. Those species occurring in northern climates tend to have univoltine or occasionally bivoltine life cycles. Psylloids tend to migrate or disperse over short distances by jumping or flying and much like whiteflies or aphids, can travel great distances on air currents.

Many species are specialists as nymphs, often feeding on a particular plant structure on a specific host. Feeding preference exhibited by the adults differs from that of the immature stages. They are typically polyphagous but host plants are generally defined as those that the immature stages can develop. Like other sternorrhynchans, psylloids produce honeydew that attracts ants that benefit the psylloids by potentially driving away their natural enemies.

Suborder Fulgoromorpha

Fulgoromorphans, or planthoppers, are common in nearly all habitats and some are either bizarre or spectacular in form. They occur throughout the world, although most are from the tropical and subtropical regions. All species are plant sap feeders. Some feed on trees or shrubs, others prefer lower-growing grasses or sedges. Some feed underground on plant roots; still others feed on ferns or on fungi growing under bark or on moist logs. Some planthopper species are of agricultural importance because of the plant pathogens they transmit when feeding, or because of the sooty mildew promoted by their sugary exudates (honeydew). One species has caused, if indirectly, cases of poisoning in humans. Analysis of molecular data and new interpretations of morphological characters of both adults and nymphs strongly support the monophyly of the Fulgoromorpha. About 12,000 planthopper species have been described and arranged into 20 families, the largest and most economically important being Delphacidae. Since only a few families have been shown to be monophyletic, this classification will surely be modified in the future.

- Order: Hemiptera
  - Superfamily: Fulgoroidea-planthoppers
    - Fulgoridae
    - Dictyopharidae
    - Flatidae
    - Hypochthonellidae
    - Issidae
    - Acanaloniidae
    - Caliscelidae
    - Nogodinidae
    - Tropiduchidae
    - Delphacidae
    - Cixiidae
    - Derbidae
    - Achilixiidae
    - Achilidae
    - Kinnaridae
    - Meenoplidae
    - Tettigometridae
    - Lophopidae
    - Eurybrachidae
    - Ricaniidae

The most spectacular planthoppers are the fulgorids. Seven hundred and fifty species are known in the family Fulgoridae, all from subtropical and tropical regions. Both adults and nymphs feed above ground on their host plants, which are usually are dicots. These insects range from 4 mm to 10 cm in length with wingspans of up to 15 cm. In some species the hind wings have large colorful eyespots, designed to startle potential predators. The most distinctive feature in many fulgorids is the bizarre shape of their head, which can be long and toothed, slender, or bulbous. In *Fulgora*, the lantern bug, the head resembles a crocodile's head, complete with false eyes, nostrils and teeth. Despite its name, the head of *Fulgora* does not glow. Most likely, though, they mimic lizards, positioning themselves vertically with the head uppermost, just as lizards do. Another family of planthoppers in which both adults and nymphs feed above the ground is Dictyopharidae, the sister group of the Fulgoridae. The 600 described species ranging in length from 3 to 33 mm are found throughout the world. Most dictyopharids are green or brown and have a long head projection referred to as a cephalic horn. A few species have modified front legs that are broad and flat. Most species are monophagous and feed above ground on their hosts, primarily dicots.

Flatids are the next most spectacular hoppers, especially those in the tropics. They range from 4 to 32 mm in length and their front wings, which are broad, blunt-ended and opaque, and have many cross veins in the costal area, may be pink, red, yellow, green, white, brown, black, and plain, stripped, or spotted. Sexual dimorphism is not uncommon. Mostly pantropical but occurring world wide, Flatidae is a large family of more than 1,000 species related most closely to the Tropiduchid group of families, Issidae, Nogodinidae, and Tropiduchidae. Most species of flatids feed on woody dicots, above ground, and many are polyphagous. Nymphs and adults of many species feed together in large groups, the nymphs protecting themselves by producing long, curly wax threads on the surfaces of their bodies. *Metcalfa pruinosa* (Say), a polyphagous species from the United States, was introduced into Italy in the late 1970s and is causing damage especially to grapes in southern Europe. Wax from the nymphs covers the fruit, and their honeydew promotes the growth of sooty mold. Hypochthonellidae, a family composed of only two species in Africa, is presently considered as a subgroup within Flatidae. *Hypochthonella caeca* China & Fennah is the only known true subterranean fulgoroid, and has reduced wings and eyes and lacks ocelli. Both adults and immatures are found in the soil, where they feed on roots of plants.

The majority of the 1,000 described species in the family Issidae feed as adults and nymphs on trees and grasses, above-ground. They are widely distributed, although the majority are found in tropical regions. More issids are monophagous than polyphagous. Most adults, which are between 2 and 8 mm in length, are dark-colored with opaque wings. Some appear beetle-like due to their tough, short front wings. Some even resemble weevils because of a long snout-like structure and expanded forelegs. Acanaloniidae (about 80 species), a group presently considered within Isiidae, are hoppers that resemble flatids, except that they do not have the many cross veins in the costal area of the front wings characteristic of Flatidae. They feed on grasses and herbaceous plants.

Another group of hoppers that resemble weevils is Caliscelidae. They previously were placed within Issidae, and are a small family found worldwide. Caliscelids are small (1–5 mm long) and brachypterous. They are known to feed on grasses, sedges, and palms, and some are associated with ants.

Nogodinidae is a primarily tropical family of approximately 150 species, 4–17 mm long, that feed as adults and nymphs above ground on woody dicots; all known species are monophagous. It is unknown at present if this group is monophyletic.

Tropiduchidae has about 350 species described, ranging in length from 5 to 13 mm; this family is primarily pantropical but occurs worldwide. Tropiduchids usually have an oddly shaped head and wings of variable color patterns. Both adults and nymphs feed above-ground, usually on understory plants in moist, tropical forests. The Dubas Bug, *Ommatissus lybicus* (Bergevin), is the worst pest of date palms in the Middle East because it can result in the death of the plant.

Delphacidae is the largest family in Fulgoromorpha, with nearly 2,000 species worldwide. Delphacids are small (2–10 mm in length), usually brown or greenish planthoppers. They are characterized by a hind tibia with triangular cross-section coupled with an articulated spur at its distal end. Delphacids are important pest species because they feed on monocots that include rice, wheat, corn, and sugarcane. Many of them cause more damage by vectoring viral diseases than by direct feeding.

The most economically important delphacid is the brown planthopper *Nilaparvata lugens* (Stål). Since the early 1970s, this species has been the most serious pest of rice in South East Asia, the Pacific, New Guinea, India and Sri Lanka. It can travel long distances, assisted by strong wings, reaching Korea and Japan from China. It transmits a virus ("grassy stunt disease") to rice, a crop that feeds at least 60% of the world.

The nymphs of cixiids, derbids, achilixiids, achilids, kinnarids, and meenoplids are thought to have their nymphal stages cryptic or associated with soil, or in spaces under bark or on logs, rather than being in the open on the plants as are the adults. With almost 2,000 species, Cixiidae is one of the largest families in Fulgoromorpha. Cixiids are found in all regions of the world. Adults (ranging from 3 to 13 mm in length) look superficially like minute cicadas, being slightly broad and flat and with clear, membranous wings held at a low angle over the body when at rest. The nymphs feed on the roots of grasses and herbaceous plants, on fungi on rotten wood, or on ferns, while adults feed on a variety of tree and shrub species. Some nymphs have been found in association with ants. Nymphs in the genus *Oliarus* are subterranean. In Hawaii, nymphs of *Oliarus* live in caves and feed on roots while protecting themselves with a cocoon of wax filaments. As adults, they move through the caves holding to the rock walls with the help of modified pretarsal claws. Some species are blind, unpigmented, and flightless.

Cixiids are economically important because they can transmit plant diseases. One species, *Myndus crudus* Van Duzee, acts as disease vector for the phytoplasma that causes Lethal Yellowing, a lethal disease of palms, including the coconut palm. It was first reported (1830s) in the West Indies and later appeared in the Florida Keys (1950) and in other areas of the United States. It has now spread to others parts of the world. Other cixiids are suspected of also transmitting this disease.

Derbids (4–mm) are planthoppers with long, narrow, fragile wings, sometimes white or brightly colored. More than 800 species of Derbidae exist worldwide, primarily in the tropical and subtropical regions. Adults of these bugs have been found feeding on fungi associated with plant or wood decay, on flowering plants, on palms and on a few deciduous trees. Nymphs are thought to be obligate fungus feeders. Members in the group called moth derbids congregate on one leaf and sit characteristically with their wings held flat against the underside of the leaf.

More than 350 species of Achilidae (recognized by the overlapping tips of the front wings) have been described throughout the world. Adults, which range from 3 to 13 mm in length, feed on the phloem of trees or shrubs while the nymphs are thought to feed on fungi in holes in logs, or under loose bark, or in decaying vegetation.

Achilixiidae is a small tropical family with 24 described species ranging from 4 to 8 mm in length. Achilixiid planthoppers are known from the Neotropics, Philippines, and Borneo. Some include Achilixiidae within Achilidae, but their placement is uncertain at present.

Forty species have been described in the family Kinnaridae (2–4 mm in length) mostly from the Neotropical and tropical Oriental regions. Nymphs feed on roots and some are cave adapted; most adults feed from the upper portion of plants, usually dicots. Some species lay their egg masses in the soil or on wood, and cover them with water repellent waxes. The nymphs of Meenoplidae, the sister group of the Kinnaridae, are also associated with soil and some, as in Kinnaridae, have been found in caves. Eighty species have been described, mostly from the Ethiopian and Oriental tropical regions. Adult meenoplids are very small, flattened planthoppers that range from 3 to 7 mm in length. Most adults feed on monocots, the majority of the species feeding across several families (they are among the most polyphagous in Fulgoromorpha).

Tettigometridae is a small family of less than 100 species, sized 3–11 mm, that occurs in the Ethiopian and Palearctic regions. The nymphs of most species live underground in groups feeding on plant roots, while adults live on foliage, mostly dicots. In some species ants attend the nymphs.

Lophopidae includes about 140 described species, 5–15 mm long, nearly all from the Old World tropics. Their wings are usually opaque tan or brown. *Pyrilla* spp., which feed on monocots that include sugarcane, corn and rice, are serious sugarcane pests in India.

Eurybrachidae (7–29 mm long) is a tropical family of about 200 species with opaque tan or brown rectangular wings. The group occurs in the Australian, Ethiopian and Oriental regions. Adults and immatures are monophagous and feed above ground; one example is *Platybrachys leucostigma* Walker from Australia, which feeds on *Eucalyptus maculatus*. The front wings of some species are shaped and colored at the apex to look like a head, some complete with false antennae.

Gengid planthoppers are found only in South Africa (two species described), believed by some authors to belong within the family Eurybrachidae.

Ricaniids (380 species) range from 4 to 12 mm long with their wings, when spread, reaching up to 30 mm in some species. These are moth-like planthoppers found in the warmer parts of the eastern hemisphere. They feed above ground primarily on dicots, although some feed on monocots or ferns, with polyphagy common. Some species damage ornamental and agricultural crops. A species that occasionally causes poisoning in humans is *Scolypopa australis* Walker, a ricaniid from Australia, now also found in New Zealand. This species occasionally feeds on the poisonous plant *Coriaria arborea* and produces honeydew that, in time of low nectar, may be collected by honey bees. This honey is poisonous to humans.

Suborder Cicadomorpha

The suborder Cicadomorpha has three superfamilies with about 30,000 species described, all of which are terrestrial plant-feeders. They are extraordinarily diverse and ubiquitous. The most familiar insects in this group are the cicadas (Cicadoidea), the largest and loudest insects in Cicadomorpha. Cercopoidea includes the two-striped froghopper, *Prosapia bicincta* (Say), a cercopid native to the southeastern United States that damages forage and turf grasses and some ornamentals. Within Membracoidea are two important groups, the Cicadellidae, which is considered the tenth largest family of insects, as well as one of the most abundant, and the Membracidae, which includes some of the most fantastically designed insects. Cicadomorpha is considered a monophyletic group. It was previously placed in Auchenorrhyncha together with Fulgoromorpha. The classification of Cicadomorpha is:

- Order: Hemiptera
  - Suborder: Cicadomorpha-cicadas, spittlebugs, leafhoppers and treehoppers
    - Superfamily: Cicadoidea: cicadas
      - Cicadidae-cicadas
      - Tettigarctidae: hairy cicadas
    - Superfamily: Cercopoidea-froghoppers
      - Aphrophoridae
      - Cercopidae-spittlebugs
      - Clastopteridae
      - Machaerotidae
    - Superfamily: Membracoidea-treehoppers and leafhoppers
      - Membracidae-treehoppers
      - Aetalionidae
      - Melizoderidae
      - Cicadellidae-leafhoppers
      - Myerslopiidae

Cicadoidea-Cicadas

Cicadas are large insects, reaching lengths of 10 cm, although some are as small as 1 cm. Approximately 4,000 species are known, if not all described. With a stout body, broad head, large compound eyes, and long, usually transparent wings, they are easily recognized. They are also known for their loud singing, which usually takes place during the day or at twilight, males calling to attract the females. Each species has a characteristic song produced by an enlarged abdomen that serves as the resonating chamber.

Although cicadas occur from the tundra to the tropics, they are most diverse and abundant in the tropical regions. Both adults and nymphs usually feed on xylem from trees and shrubs, and are commonly polyphagous. Nymphs are entirely subterranean, possessing digging front legs, feeding usually on perennial roots, and emerging after several years in the soil to molt into adults. Some cicadas are able to be active at temperatures that would induce torpor in other insects because they are facultatively endothermic. They can warm themselves through shivering of flight and/or tymbal muscles or cool themselves by releasing water (i.e., evaporative cooling). Within the family Cicadidae, the most famous might be the gregarious "periodical cicada" (genus *Magicicada*, seven species) from the eastern United States. Broods emerge simultaneously in millions at intervals of either 13 or 17 years. These cicadas can cause considerable damage to trees. The damage is done by the egg-laying females, which cut slits in twigs to insert their eggs. In Australia, sugarcane can be tremendously damaged (even shredded) when thousands of cicadas oviposit in a single crop. Two species of importance are the Brown Buzzer (*Cicadetta crucifera* [Ashton]), also known as the Brown Sugarcane Cicada, and the Grass Fairy

(*Parnkalla muelleri* [Distant]), also known as the Yellow Sugarcane Cicada, both of which become abundant in sugarcane fields in certain seasons. The former lives in open grasslands, and edges of woodland and mangroves, while the latter species prefers areas of open grassland or woodland/scrub habitats.

Only two species are included in the family Tettigarctidae, both in the genus *Tettigarcta*. One species is found only in southeastern Australia and the second only in Tasmania. Many characters distinguish this family from Cicadidae, including a large pronotum, eyes close together, simple sound-producing organs (timbals) in both sexes rather than only in males; and no true auditory tympana. Rather than communicating with audible songs, these cicadas communicate using vibrations through substrate. They are called hairy cicadas because the underside of their body is densely covered with brown or grey hairs. Also unlike Cicadidae, hairy cicadas remain hidden during daylight hours.

Cercopoidea-Froghoppers

Cercopoidea is the least studied lineage of Cicadomorpha, with about 3,000 species known. They are found almost worldwide, with highest diversity in the tropics. Their anterior wings are coriaceous and many, especially in the tropics, are of contrasting colors of red with black or yellow. Their hind legs are long and adapted for leaping, hence their common name "froghoppers." The hind tibiae are long and have one or two stout spines and a single or double row of spines at the apex. Some species are gregarious. Nymphs are mostly stationary and hidden, protected from desiccation and parasites by a fluid secreted from epidermal glands in the abdomen, which is converted into foam ("spittle") with expelled air. Most species feed on sap from herbaceous plants, but some feed on trees. Some are of economic importance, causing damage to pecans, cotton, clover, and alfalfa. Some species are capable of transmitting pathogens. Most froghoppers live in grasslands with nymphs feeding on roots. Froghoppers, as a group, are considered the most important pest insects of sugar cane in the Neotropics.

Aphrophoridae is a large family of spittlebugs distributed worldwide. Not all species produce froth or foam as immatures. Some species feed on legumes and several are of economic importance. In Australia, the most common and widespread species is *Philagra parva* (Donovan), which has a curved horn on the head.

Nymphs of Clastopteridae also hide within spittle masses. Some clastopterids are of economic importance. For example, the pecan spittlebug (*Clastoptera achatina* Germar, 2 mm long) heavily infests and feeds on terminal shoots of pecan trees, reducing the nut crop.

Cercopidae are found worldwide and are richly represented in the tropics, where they are the most brightly colored. Nymphs live within spittle masses, explaining their common name "spittlebugs." They feed on shrubs, trees, and herbaceous plants, but some prefer grasses. The largest cercopids (including *Megastethodon urvillei* [Le Pelletier and Serville]) are found in Australia and New Guinea, and may reach up to 20 mm. Spittlebugs are considered the most important pest insects of Neotropical sugar cane. A grassland spittlebug, *Prosapia simulans* (Walker), is a threat to sugarcane and forage grasses and also feeds on many of the major forage grasses, including corn, and also on some non-graminoid hosts. It is known from the lowland tropics from Mexico to Panama but has now been found in Venezuela and Colombia. It threatens sugarcane crops in southern United States, which already is under attack from the native froghopper, *Prosapia bicincta* (Say). Cercopids are also important because they are capable of vectoring *Xylella fastidiosa*, a bacterium that affects many economic plants in the world, including citrus, maple, coffee, grape, and others.

Machaerotidae is a small family restricted to the Oriental region, tropical Africa, and Australia. The nymphs do not live within spittle masses, but live instead within calcareous tubes attached to the host plant, immersed in their liquid excretions. A new classification has recently been proposed for Cercopoidea, with three families, Cercopidae, Clastopteridae (including machaerotid froghoppers), and Epipygidae, a new family from the Neotropics. In this classification the family Aphrophoridae is not considered monophyletic and its genera are divided among the other families.

Membracoidea-Treehoppers and Leafhoppers

Membracoidea is a monophyletic group comprised of approximately 25,000 described species in five or more families. It is the most diverse of the Cicadomorpha superfamilies. Membracidae (up to 12 mm long and with 3,200 species) are extremely diverse in tropical America, where they occur in rainforests, savannas, and deserts. Adults have cuticular expansions on the pronotum that often extend over the abdomen. The pronotal modifications range in shape from simple (spines, horns) to fantastic, which sometimes differ in males and females of the same species. Membracids feed primarily on trees and shrubs. Many species are gregarious, with young and adults feeding together. Much has been speculated on the function of the pronotal expansions. Some shapes might provide protection in the form of mimicry of their host, looking like thorns (as in *Umbonia*), seeds, or bark; others mimic ants or wasps, as in *Cyphonia*. Some have aposematic (warning) coloration. Others might be protected from vertebrate predators by their spiny projections; all those with pronotal expansions might survive mutilation from predators. However, the latest theory is that it has a thermoregulatory function, providing large surfaces for water evaporation. Treehoppers tend to be active during the day, when they are exposed to extreme heat and when predators tend to be inactive. For defense, nymphs feed among adults. The nymphs of some species are attended by ants. Parental care is common (egg guarding, principally) in Membracidae.

Aetalionidae also feed on trees, are gregarious, are commonly tended by ants, or by Meliponinae bees, and display parental care. Some are as long as 28 mm; the beak extends to the hind coxae. Their pronotum and sometimes their head have cuticular expansions, but some resemble cicadellidae or cercopidae. This family of 44 described species is Neotropical, except for two species found in the south of the Himalayas. The genus *Aetalion*, which resembles a large cercopid, occurs in Florida, Arizona and California.

Melizoderidae is a very small family of eight species known only from Chile and Argentina. The pronotum has a unique, somewhat conical shape. Nothing is known of their biology. This family is considered a distinct lineage between Cicadellidae and Membracidae.

Cicadellidae, with more than 20,000 described species worldwide, is the largest family in Hemiptera and the tenth largest family of insects. Since most species are likely undescribed, an estimate of the family size is not possible at present. The species richness is highest in the tropics. Cicadellids are 3–22 mm long, with narrow and often colorful wings, with posterior tibia prismatic in cross-section and with spines. For defense they rely mostly on agility, for they jump and fly. Some leafhoppers are Batesian mimics of bees or wasps; that is, by shape, coloration, and even behavior they mimic bees or wasps. For example, leafhoppers in the genus *Lissocarta* and *Propetes* imitate paper wasps (Vespidae), and the genus *Teletusa* imitates bees in the family Megachilidae. A trait unique to Cicadellidae among all insects is the production of brochosomes, small protein-lipid particles of intricate structure produced by cells in the Malpighian tubules. They actively spread this material over their body, wings, and legs and also on their eggs. There is some evidence that this material serves to form a protective layer that repels water or honeydew and prevents fungal infections.

Cicadellid leafhoppers are of major agronomic importance because they can injure plants in several ways, including the transmission of pathogens. *Scaphoideus titanus* Ball (5–6 mm long) is an example of a cicadellid that can cause diseases. It is able to transmit phytoplasmas (unicellular organisms without a rigid wall) to grapevines if they fed previously on infected plants whether as young or as adult. This North American species was accidentally introduced to France in 1960 and has spread throughout southern and eastern Europe, reaching Spain and Portugal in 2000. The phytoplasma disease called Golden Flavescence is of considerable economic importance, and has been already found in Spain, France and Italy.

Pierce's disease is a lethal grapevine disease caused by *Xylella fastidiosa*, one of the most significant disease-causing pathogens in the Americas. This bacterium causes water stress due to vascular occlusions by aggregates of the bacteria. Different strains of this species attack different hosts, which include citrus, coffee, elm, oak, oleander, maple, sycamore, almond, alfalfa, peach, grape, and others. The primary vectors for Pierce's disease are cicadellines, or sharpshooters. *Homalodisca coagulata* (Say) (the glassy-winged sharpshooter) is an important vector of *Xylella fastidiosa* in the southeastern United States. Recently, it has become established in California, where it is threatening the large wine industry because of increased spread of Pierce's disease.

Myerslopiidae are a small family found only in New Zealand and South America. These leafhoppers inhabit forests, and both adults and nymphs living in leaf litter and soil with high organic content. This family has less than 20 species.

A group of archaic cicadellids, with 120 species, is treated by some as a family named Ulopidae. They are 2.5–12 mm long and have stiff front wings that are either plain or that have a simple color pattern. Most species lack hind wings and feed on the roots or root-necks of plants, hiding in the soil, although a few feed on shrubs and trees.

Suborder Coleorhyncha-Moss Bugs

The suborder Coleorhyncha contains the single family Peloridiidae, considered the sister group of the Heteroptera. Their distribution is limited to the Southern Hemisphere. Twenty-five species have been described from eastern Australia, Tasmania, Lord Howe Island, New Zealand, New Caledonia, Chile and Patagonia in Argentina; they may also occur in New Guinea. Peloridiids resemble planthoppers but have hemelytron-like forewings. Adult peloridiids are small (between 2 and 4 mm long), flattened, oval, greenish or brownish. Among their unique characteristics are the broad head and the pronotum with lateral areolate expansions. They are primarily phytophagous on mosses, thus known as moss bugs, and usually live in moist habitats such as damp leaf litter on forest floors with mosses, liverworts, and decaying trunks but a few species have been found in caves.

Suborder Heteroptera

Heteroptera are the only insects correctly called "true bugs." This is the most abundant and biologically diverse group of insects with incomplete metamorphosis. Species of Heteroptera are characterized primarily by having the first pair of their wings divided into two areas (hence the name "Heteroptera," different wings), one part thickened and opaque and the other part membranous and usually transparent. Most true bugs are diurnal plant-feeders with well developed eyes and wings, although many variations and exceptions exist. Some species are of agricultural, veterinary, or medical importance. Heteroptera are a relatively small monophyletic group of approximately 37,000 described species with at least 25,000 yet to be described. Although they are arranged among 88 families, the classification will undergo changes in the future. Presently the suborder Heteroptera is divided into seven infraorders, as follows:

Infraorder: Enicocephalomorpha: unique headed-bugs
- Aenictopecheidae
- Enicocephalidae-unique headed-bugs

Infraorder: Dipsocoromorpha
- Ceratocombidae
- Dipsocoridae-jumping ground bugs
- Hypsypterygidae
- Schizopteridae
- Stemmocryptidae

Infraorder: Gerromorpha: semiaquatic bugs
- Mesoveliidae-water treaders
- Hebridae-velvet water bugs
- Paraphrynoveliidae
- Macroveliidae
- Hydrometridae-marsh treaders
- Hermatobatidae-coral treaders
- Veliidae-small water striders
- Gerridae-water striders and pond skaters

Infraorder: Nepomorpha: water bugs
- Belostomatide-giant water bugs
- Nepidae-water scorpions
- Gelastocoridae-toad bugs
- Ochteridae-velvety shore bugs
- Corixidae-water boatmen
- Potamocoridae
- Naucoridae-creeping water bugs
- Aphelocheiridae
- Notonectidae-back swimmers
- Pleidae-pygmy back swimmers
- Helotrephidae

Infraorder: Leptopodomorpha
- Aepophilidae-marine bugs
- Saldidae-shore bugs
- Omaniidae-intertidal dwarf bugs
- Leptopodidae-spiny shore bugs

Infraorder: Cimicomorpha
- Pachynomidae
- Reduviidae-assassin bugs (includes ambush bugs, kissing bugs, thread-legged bugs)
- Velocipedidae-fast-footed bugs
- Microphysidae
- Joppeicidae
- Thaumastocoridae-palm bugs
- Miridae-plant bugs or leaf bugsTingidae-lace bugs
- Medocostidae
- Nabidae-damsel bugs
- Lasiochilidae
- Plokiophilidae-web lovers
- Lyctocoridae
- Anthocoridae-minute pirate bugs or flower bugs
- Cimicidae-bed bugs
- Polyctenidae: bat bugs

Infraorder: Pentatomorpha

Superfamily: Aradoidea
- Aradidae-bark bugs
- Termitaphididae

Superfamily: Coreoidea
- Alydidae-broad-headed bugs
- Coreidae-leaf-footed bugs
- Hyocephalidae
- Rhopalidae-scentless plant bugs
- Stenocephalidae

Superfamily: Idiostoloidea
- Idiostolidae
- Henicocoridae

Superfamily: Lygaeoidea
- Artheneidae
- Berytidae-stilt bugs
- Blissidae-chinch bugs
- Colobathristidae
- Cryptorhamphidae
- Cymidae
- Geocoridae-big-eyed bugs
- Heterogastridae
- Lygaeidae
- Malcidae
- Ninidae
- Oxycarenidae
- Pachygronthidae
- Piesmatidae
- Rhypharochromidae
- Orsillidae
- Ischnorhynchidae

Superfamily: Pentatomoidea
- Acanthosomatidae-shield bugs
- Aphylidae
- Canopidae
- Cydnidae-burrower bugs
- Dinidoridae
- Lestoniidae
- Megarididae
- Pentatomidae-stink bugs
- Cyrtocoridae
- Phloeidae
- Plataspidae
- Scutelleridae-shield bugs
- Tessaratomidae-giant shield bugs
- Thaumastellidae
- Urostylidae

Superfamily: Pyrrhocoroidea
- Largidae
- Pyrrhocoridae-cotton stainers

Heteropterans differ from other Hemiptera by their characteristic wings, mouthparts, scutellum, and scent glands. They have two pairs of wings; the first pair is held flat over their body, above the second pair of wings, which are membranous and transparent. The design of the forewings is a compromise between the needs for efficient flight and protection. The cuticle of the corium and clavus is thickened for protection but these wing parts are also shaped and hinged for facilitating and controlling flight. The wing membrane is thin and usually transparent. All parts of the wing, including corium, clavus, and membrane, are supported by veins. Some adults have lost their wings entirely, while others are winged but are unable to fly due to flight muscle reduction. Many species of Gerridae (500 species worldwide), an aquatic group known as water striders, are wingless. In other true bugs, the wings are variously modified or strongly abbreviated. An example of a group with modified wings is the rarely encountered family Schizopteridae (120 described species worldwide). Schizopterids resemble tiny beetles due to their near-black coloration, compact and rotund shape, and uniformly sclerotized, shell-like forewings.

The scutellum, which means little shield, is a triangular part of the thorax seen dorsally between the first pair of wings. The shape and size of the scutellum is highly variable among true bugs and is frequently used for purposes of classification. In the Scutelleridae (at least 450 species worldwide), the scutellum is so large that it covers the entire abdomen and wings. These insects, known also as shield bugs, are among the most spectacular of all Heteroptera, some species being iridescent or metallically colored. All shield bugs are plant feeders; some are of agricultural importance.

Heteropterans are characterized by elongate mouthparts in the form of a segmented beak, or rostrum, used for sucking fluids. The beak has two channels, one through which saliva (a fluid with enzymes) is pumped to predigest and liquefy their food and the other through which fluids are sucked. Because their beak is located far forward on the lower surface of the head, in contrast with the other hemipterans, the heteropteran beak is versatile, allowing them to exploit a great variety of resources, including plants, other arthropods, carrion, tadpoles or small fish, and even blood from vertebrates.

Nearly all heteropterans have scent glands that produce pungent chemicals used primarily for defense. In adults, the external openings of these glands are located on each side of the thorax between the second and third pairs of legs. The openings end in a variety of grooves, lobes and spouts that allow the evaporation of the noxious chemicals. These external structures are distinctive in many groups and are commonly used for classification or identification purposes. Some bugs lack functional scent glands; for example, members of the family Rhopalidae (about 210 species described) are commonly referred to as scentless plant bugs.

Defense

Heteropterans are in general highly mobile, diurnal insects with well developed compound eyes. This mobility allows them to find new hosts and allows them to escape potential predators or parasites.

True bugs escape predators by flying (e.g., stink bugs, plant bugs, leaf-footed bugs), dropping (e.g., lace bugs, shield bugs); burrowing (e.g., burrower bugs or cydnids); running (e.g., shore bugs, seed bugs, water striders), moving into narrow places (e.g., flat bugs, chinch bugs, palm bugs, bed bugs), hopping (e.g., toad bugs), jumping (e.g., schizopterids), or swimming (e.g., water boatmen, giant water bugs, velvet water bugs).

Aside from their mobility, the main defense employed by true bugs is the secretion of a noxious chemical which serves to repel enemies, especially ants, which are important predators. Other natural enemies include lizards, birds, frogs, spiders, and other insects. Other defense mechanisms known among Heteroptera are biting (e.g., assassin bugs, damsel bugs, creeping water bugs, and others), sharp spines on the thorax (e.g., some stink bugs, assassin bugs, and others), cryptic shapes and colors (e.g., ambush bugs, most seed bugs, leaf-footed bugs, toad bugs, and others), mimicry (e.g., ant mimetic seed bugs and others), aggregation (e.g., immature leaf-footed bugs, scentless plant bugs, cotton stainers), and aposematic, or warning, coloration (e.g., nymphs of scentless plant bugs, milkweed bugs, assassin bugs). Some bugs simply stay very still to avoid being noticed, such as the narrow-bodied bugs marsh treaders, stilt bugs, water scorpions, and the spider-web inhabiting reduviids. Members of the Coreidae are outstanding in their fantastic shapes and colors. Some designs function as disruptive coloration in which the outline of the insect is obscured by contrasting color patterns.

Feeding

About 60% of all true bug species are plant feeders, some of which are of great economic importance. The remaining 40% are predatory or ectoparasitic. Because of their method of feeding, in which they insert their beak stylets into tissues between cells to suck juices rather than directly into cells, they are generally not effective in the transmission of plant diseases. The damage caused to plants is usually direct, by feeding on the reproductive parts of the plants such as flowers, ovaries, developing fruits, or ripening or mature seeds. Some species, however, cause indirect damage by feeding on stems and roots, forcing the plant to repair damaged tissue. Feeding with a beak allows them to bypass many of the plants' defenses (wax, thorns, spines, setae, tannins) as well as most pesticides, which are most effective against insects that bite and chew. Most of the species in the family Miridae, or plant bugs, (approximately 10,000 described species, or one-third of all Heteroptera), are phytophagous. Many species in this family are of significant economic importance. Most mirids feed on growing portions of the plant such as flowers, buds, pollen, or new foliage. A few, however, feed on both plant and animal material. Most rhyparochromids are mature-seed feeders, injecting enzymes into the seed where the nitrogen-rich contents are liquefied and predigested. Most rhyparochromids feed on fallen seeds, although some feed on mature seeds while still on the plants; some are of occasional economic importance because they can feed in large numbers. *Oncopeltus* are colorful lygaeids that feed on maturing seeds of the milkweed plant, the same plant known as primary host of the Monarch butterfly caterpillars. An example of stem feeding is presented by *Blissus*, the famous chinch bugs, known by homeowners as major lawn pests; they often feed in great numbers and kill large patches, occasionally wiping out entire lawns. Extensive biological studies have been done on this pest. Cydnids are soil-inhabiting bugs that feed on the roots of plants, hence their name, burrower bugs. Aradids, or bark bugs, feed on the mycelia of various fungi under tree bark. Tingidae, or lace bugs, are entirely phytophagous, usually found in large numbers on mature foliage. Many species attack and damage important ornamental plants. All species of lace bugs of economic significance are in the subfamily Tinginae, comprised of delicate and beautiful forms with lacelike appearance.

Of all hemipterans, only heteropterans feed on both other arthropods and on vertebrates. Examples of predaceous bugs are the back swimmers (Notonectidae, 343 species recognized) that feed on insects trapped in the water surface; damsel bugs (Nabidae, 500 species) that feed on insects among foliage and on the ground, or on insects caught in spider webs, and ambush bugs (Phymatinae, 281 species in the family Reduviidae) that commonly hide on or below flowers waiting for pollinating insects such a flies or bees, although other insects are attacked as well. Other reduviids, within the subfamily Emesinae, can walk on spider webs and feed on spiders. Geocorids (219 species described), known as big-eyed bugs, prey on other insects and have proven useful in biological control programs. A unique group of predatory insects are water striders in the subfamily Halobatinae, which inhabit an usual marine habitat, the surface of the ocean, both near the shore or far out at sea. Plokiophilids, or web lovers, live either on spider webs to steal the spider's prey, or with web-spinners (insect order Embioptera) feeding on the eggs and weak or dead individuals; their tarsi (feet) are adapted to walking on webs. Some aquatic bugs (Belostomatidae or giant water bugs, and Nepidae or water scorpions) feed on other insects, on tadpoles and even small fish. All species of Polyctenidae, known as bat bugs, are ectoparasitic, that is, they feed externally on bats. Cimicids and lygaeoids in the tribe Cleradini feed on vertebrate blood.

Medically Important Species

Triatomine bugs (more than 110 species) are nocturnal hematophagous reduviids that feed on the blood of mammals, including humans. The insects tend to feed near the mouth area of sleeping humans and are thus commonly called kissing bugs. Some species transmit Chagas' Disease, an important disease in Latin America caused by *Trypanosoma cruzi* Chagas. The most important triatomine species are *Triatoma infestans*, *T. sanguisuga*, *T. dimidiata*, *T. barberi*, *T. brasiliensis*, *T. maculata*, *T. pseudomaculata*, *T. rubrovaria*, *T. sordida*, and *Rhodnius prolixus*, *ecuatoriensis*, and *pallescens*. All feed at night on humans or their pets, and hide during the day, often inside human habitations. Cimicids, or bed bugs (about 100 species), are hematophagous as well, acting as temporary ectoparasites on bats, humans, and birds or rodents living in groups. All are wingless and the majority feed on bats. They spend most of their time in crevices and other hiding places near their hosts, remaining on the host only while feeding. They can be found in the bedroom, bed, and among the bedclothes. Bed bugs exist wherever humans live. Much research has been conducted on the two cimicid species, both known as the bed bug, *Cimex hemipterus* and *Cimex lectularius*. Most bed bugs do not serve as vectors of pathogens of human or animal disease. Their importance is generally as a nuisance pest, although large populations can result in serious loss of blood. The word "bug" is derived from the Anglo-Saxon *bugge*, which almost certainly referred to the bed bug.

Development and Cytogenetics

Immature heteropterans, called nymphs or larvae, usually pass through five instars or stages before reaching the adult, or winged, form. They usually live in the same habitat as the adults and are commonly similar to them in coloration, shape, and feeding habits. Nymphs of some species form large defensive aggregations.

True bugs seem to show a great deal of cytogenetic diversity, including polyploidy of the autosomes, with the sex chromosome number highly variable as well. Sex determination in Heteroptera is not like that of mammals. The majority of the species have a simple XX:XY system, though many species have XO males, and some have multiple X and Y chromosomes and still are males.

► Aphids
► Cicadas

- ► Lace Bugs
- ► Leafhoppers
- ► Plant Bugs
- ► Planthoppers
- ► Scale Insects and Mealybugs
- ► Spittlebugs
- ► Stink Bugs
- ► Treehoppers
- ► Whiteflies

References

Ben Dov Y, Hodgson CJ (eds) (1997) Soft scale insects: their biology, natural enemies and control, vol 7A & B. World crop pests. Elsevier Press, Dordrecht, The Netherlands, 452 & 443 pp

Bourgoin Th, Campbell BC (2002) Inferring a phylogeny for Hemiptera: falling into the "autapomorphic trap." In: Holzinger WE (ed) Zikaden: leafhoppers, planthoppers and cicadas (Insecta: Hemiptera: Auchenorrhyncha). Denisia 4, Biologiezentrum des Oberösterreichischen Landesmuseums, Austria, pp 67–82

Blackman RL, Eastop VF (2000) Aphids on the world's crops. An identification and information guide, 2nd edn. Wiley, Chichester, 466 pp

Cassis G, Gross GF (1995) Hemiptera: Heteroptera (Coleorrhyncha to Cimicomomorpha). In: Houston WWK Maynard GV (eds) Zoological catalogue of Australia, vol 27.3A. CSIRO, Australia, 506 pp

Denno RT, Perfect TJ (eds) (1994) Planthoppers. Their ecology and management. Chapman & Hall, New York, New York, 799 pp

Dietrich CH, Deitz LL (1993) Superfamily Membracoidea (Homoptera: Auchenorrhyncha). II. Cladistic analysis and conclusions. Syst Entomol 18:297–311

Gillot C 1995 The Hemipteroid orders. In: Entomology. Plenum Press, New York, New York, pp. 195–232

Holzinger WE (ed) (2002) Zikaden. Leafhoppers, planthoppers and cicadas (Insecta: Hemiptera: Auchenorrhyncha). Denisia 4, Biologiezentrum des Oberösterreichischen Landesmuseums, Austria, VIII + 556 pp

McGavin GC (1993) Bugs of the world. Blandford, London, UK, 192 pp

Schaefer CW, Panizzi AR (2000) Heteroptera of economic importance. CRC Press, New York, NY, 828 pp

Schuh RT, Slater JA (1995) True bugs of the world (Hemiptera: Heteropera): classification and natural history. Cornell University Press, Ithaca, NY, 336 pp

Woodward TE, Evans JW, Eastop VF (1970) Hemiptera (bugs, leafhoppers, etc.). In: The insects of Australia. A textbook for students and research workers. Melbourne University Press, Melbourne, Australia, pp 387–457

Bulb Mites, *Rhizoglyphus* (Acari: Acaridae)

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Bulb mites are mite species of the family Acaridae that infests the bulb, rhizome, corm and tuber of plants of Amaryllidaceae, Liliaceae, Iviraceae, Solaneae and Cruciferae. Customarily, it refers only to mites of the genus *Rhizoglyphus*. Seventy-three species are recorded in this genus over the world. However, only two of them, *R. echinopus* and *R. robini*, are found worldwide, causing serious problems to the culture of numerous crops. *R. echinopus* has been reported from Argentina (as *R. callae*), Canada, USA (Texas), Belgium, Denmark, France, Germany, Hungary, Italy, Netherlands, Poland, Romania, Russia, Scotland, Spain, the United Kingdom, Ukraine, Egypt, Israel, China, India, Iran, Japan, Korea and New Zealand. *R. robini* has been reported from Canada, USA, Mexico, China, Japan, Korea, Taiwan, New Zealand, Israel, Egypt, Poland and the United Kingdom. *Rhizoglyphys echinopus* and *Rhizoglyphus robini* were not properly distinguished in earlier years, not until van Eyndhoven set them apart. Consequently, records on these two species in early reports are subject to uncertainty. A third species, *Rhizoglyphus setosus*, is reported to infest various hosts in Taiwan. This species was reported first by Manson in 1972, from New Guinea. It may also be distributed in countries nearby. Another species, *R. hyacinthi*, that appeared in early reports causing heavy loss to gladiolus and lily is probably not a valid species, as there is neither a well-defined description on this species nor specimens available.

Acarid mites, in the genera *Caloglyphus* and *Schwiebea*, were also found to infest bulbs in the 1990s. These mites reproduce on bulbs, and may be as hard as the *Rhizoglyphus* species to control. The term "bulb mite" shall, therefore, include mites of these two genera. Mites reported under the generic name of *Caloglyphus* actually belong to three genera: *Caloglyphus*, *Cosmoglyphus* and *Sancssania*.

Bulb Mites, *Rhizoglyphus* (Acari: Acaridae), Table 10 List of ***Rhizoglyphus*** mites reported as pests, crops and ornamentals affected, and geographic location

Species	Crop affected	Country
algericus	*Gladiolus* sp	Algeria
alliensis	*Allium sativum*	Mexico
allii	*Allium sativum*	China
caladii	*Caladium* sp	New Guinea
costarricensis	*Oryza sativa*	Costa Rica
echinopus	*Allium bakeri*	Japan
	Allium cepa	Argentina (as *R. callae*), India, Russia
	Allium sativum	India, Korea, New Zealand, Romania, Spain
	Capsicum sp	India
	Curcuma domestica	India
	Freesia sp	UK
	Gladiolus sp	Argentina (as *R. callae*), New Zealand
	Hyacinthus sp	Argentina (as *R. callae*), New Zealand, Russia
	Iris sp	New Zealand
	Lolium longiflorum	USA (as *R. hyacinthi*)
	Narcissus sp	Canada, New Zealand, Russia, Scotland, UK
	Solanum sp	France, India, USA (as *R. phylloxerae*)
	Tulipa sp	Netherlands, New Zealand, Russia
engeli	*Freesia* sp	Netherlands
	Lilium sp	Netherlands
	Gladiolus sp	Netherlands
fumouzi	*Narcissus* sp	Canada (from Netherlands)
longispinosus	Taro	Taiwan
	Giant alocasia	Taiwan
narcissi	*Narcissus* sp	China
nepos	*Hypomoea* sp	Italy
robini	*Allium* cepa	Israel, Japan, Mexico, New Zealand, USA
	Allium chinense	Japan
	Allium fistulosum	Taiwan
	Allium porrum	Taiwan
	Allium sativum	Egypt, Israel, New Zealand
	Allium tuberosum	Japan

Bulb Mites, *Rhizoglyphus* (Acari: Acaridae), Table 10 **List of *Rhizoglyphus* mites reported as pests, crops and ornamentals affected, and geographic location (Continued)**

Species	Crop affected	Country
	Daucus carrota	New Zealand
	Freesia sp	Japan, UK
	Gladiolus sp	China, New Zealand, Taiwan, USA
	Iris sp	New Zealand
	Lolium longiflorum	Japan, New Zealand, USA
	Narcissus sp	Canada, New Zealand, UK
	Solanum tuberosum	New Zealand
	Secale cereale	Poland
robustus	*Allium sativum*	Mexico
singularis	*Dioscorea* sp	India, New Zealand (from India)
setosus	*Allium cepa*	Taiwan
	Allium porrum	Taiwan
	Allium sativum	Taiwan
	Caladium sp	New Guinea
	Lilium sp	Taiwan
	Gladiolus sp	Taiwan
solanumi	*Solanum* sp	Pakistan
tacitri	*Citrus* sp	Tahiti
tardus	*Allium cepa*	USSR
tarsalis	Sugar Beets	USA
tsutienensis	Lily	Taiwan
	Green onion	Taiwan
	Leek	Taiwan
	Tuberose	Taiwan

Species of these genera are often found in stored products or materials that are rich in organic substrates. More research is needed to determine exactly how often these species infest bulbs.

Bulb mites are generally polyphagous, with numerous host plants recorded. The recorded host plants of *R. robini*, for example, include at least 28 crops that belong to 14 families. Bulb mites usually inhabit the surface of the bulb where the stems or roots grow. When the population is high, mites can also be located between the tissue layers of the basal part of the stems. Bulb mites can also feed and reproduce on plant debris when there is no adequate host plant, and can maintain their population in the soil for a long time.

The damage caused by bulb mites to plants includes direct infestation and indirect transmission of plant disease. Bulb mites feeding on bulbs or roots can cause yellowing, wilt and early defoliation of lower leaves, dwarfing or even death of the plant. Plant pathogens transmitted by bulb mites include *Fusarium oxysporum*, *Rhizoctonia solani*, *Pythium ultimum*, and *Pseudomonas marginata*, which infest gladiolus and/or lily. Heavy loss can result from the infestation of bulb mites. Destruction of 10–70% of bulbs or plants have been reported for lily, gladiolus, onion and rakkyo. When the bulb mite population is too high, farmers may have to shift to grow non-bulb crops.

The life cycle of bulb mite normally undergoes four stages, namely the larva, protonymph, tritonymph and the adult. When the environment is suboptimal, such as poor quality or quantity of food, crowding or poor environmental quality, the protonymph will molt into a deuteronymph. The deuteronymph stage is also called the hypopus, which does not have a functional mouthpart. The hypopus will actively seek a host, usually an arthropod, to attach to and be transferred to a new environment with plenty of food. The hypopus or deuteronymph will, then, molt into tritonymph and resume the normal life cycle.

Rhizoglyphus mites develop quickly. At 28°C, development from egg to adult only takes approximately nine days. Adult females live about twenty-four days and produce 180–280 eggs. "*Caloglyphus*" mites are similar to *Rhizoglyphus* mites in development rate, but have an even higher fecundity. The populations of these mites can build up to a huge number within a short time period. A single bulb may harbor a population of hundreds or even more than a thousand mites.

Bulb mites are difficult to control. *Rhizoglyphus echinopus, Rhizoglyphus robini*, and *Rhizoglyphus setosus* are all resistant to a large number of acaricides. It appears that *Caloglyphus* mites are as potent as *Rhizoglyphus* mites in the development of acaricide resistance. Additionally, they inhabit a niche below the soil surface, which is difficult for acaricides to reach. A large amount of acaricide must be applied to have it reach bulb mites. Irrigation can affect bulb mites though, some adult females of *R. robini* could survive immersion for 30 days. In the field, the mites can hide in air bubbles among soil particles, and, hence, live even longer. Plowing of fields to expose the interior of soil to solar heat to build up its temperature has been recommended to kill the bulb mites inside. However, some bulb mites may escape by moving down to a depth of thirty cm or more. Fumigation of the soil does not make the crop immune from bulb mites. Applications of acaricide later in the season are still required. There seems no way to eradicate bulb mites from a field once they have invaded the field. The best way to protect the crop is: (i) Treat the bulbs before planting to kill mites that may live on them. (ii) Reducing the bulb mite population in soil before planting by solar heat or fumigating with acaricides. (iii) Apply acaricide sometimes later in the growing season. However, acaricide applied after planting will have a limited effect.

References

Bu GS, Li LS (1998) Taxonomic notes on and key to the known species of the genus *Rhizoglyphus* (Acari: Acaridae) from China. Syst Appl Acarol 3:179–182

Garman P (1937) A study of the bulb mite (*Rhizoglyphus hyacinthi* Banks). Bull Conn A E S 402:889–907

Ho CC (1988) An introduction to the exotic mite-pests in Taiwan. Chin J Entomol (Special Publ.) 2:155–166

Nesbitt HHJ (1988) Three new mites of the subfamily Rhizoglyphine. Can Entomol 76:21–27

Woodring JP (1969) Observations on the biology of six species of acarid mites. Ann Entomol Soc Am 62:102–108

Bulldog Ant or Bull Ant, *Myrmecia* spp. (Hymenoptera: Formicidae)

Bulldog or bull ants are some of the best-known ants in Australia due to their large size, very painful sting, and aggressive behavior. Their mandibles are exceptionally large and well equipped with teeth. Their name is derived from their habit of gripping something with their strong mandibles and hanging on to it. These ants are aggressive and have well developed vision. If disturbed, these large ants will often come swarming rapidly from their nest in the soil straight towards the intruder with mandibles open and ready to use, but they also are quick to sting any intruder after grasping it in its mandibles. Their sting is an important cause of anaphylaxis in Australia, even causing death of humans. There are about 90 species of bulldog ants in Australia, and they range greatly in size. Many are brightly colored red or orange on the head and abdomen.

Bulldog ants are some of the most primitive ant species and only have relatively small colonies.

The workers forage in a solitary manner, and unlike many other ant species do not form scent trails when foraging. Instead, bulldog ants forage independently and upon finding food carry it back to the nest, which is located in the soil. Despite their aggressive nature, adult bull ants feed predominantly on honeydew, nectar and other sweet substances, but their larvae are carnivorous and are fed on insects collected by foraging workers. Bulldog ants are most active during the day and forage either on the ground or on low vegetation. Some of the smaller species are called "jumper ants" due to their tendency to leap; despite their relatively small size they are extremely aggressive.

► Ants (Hymenoptera: Formicidae)
► Venoms and Toxins in Insects
► Bullet Ant, *Paraponera clavata* (Fabricius)

Bullet Ant, *Paraponera clavata* (Fabricius) (Hymenoptera: Formicidae)

Paraponera clavata is best known for its large size and severe sting. Workers are 18–25 mm long and resemble stout, reddish-black, wingless wasps. The pain caused by the sting of this insect is purported to be greater than that of any other wasp or ant, and is ranked as perhaps the most painful insect sting. The pain may persist for a full 24 h. The pain is caused by a paralyzing neurotoxic peptide in the venom called poneratoxin.

The genus *Paraponera* is found in Central and South America, south from Costa Rica and Nicaragua to Brazil and Peru. Bullet ants are used by some indigenous people in their initiation rites to manhood. In this process, the ants are first immobilized, and then hundreds of them are woven into sleeves made out of leaves, with the stinger facing inward. As part of this rite, boys slip the sleeve down onto their arm. The goal of this initiation rite is to keep the sleeve on for a full 10 min. After exposure to the ants, the boys' arms are temporarily paralyzed because of the venom, and they may shake uncontrollably for days.

The ants in this subfamily (Paraponerinae) are primitive, and their stings are morphologically similar to those of some solitary wasps Wasp stings are multi-purpose defensive tools rather than the more specialized weapons of more advanced ants, and tend to be more painful than the stings of ants.

Bullet ant is a relatively primitive ponerine, and unlike more advanced ants, does not display a great deal of polymorphism. Queens are only slightly larger than workers. Mature colonies are small and at most contain a few thousand ants. However, workers exhibit a size-based division of labor, and the smaller ants tend to remain in the nest as nursemaids while larger workers serve as guards and foragers. Colonies consist of several thousand individuals, and are usually found at the bases of trees. The workers forage in the trees in the area directly above the nest, where they search for insect prey and plant nectaries. Extra-floral nectar is an important part of their diet. Water is also collected. Both nectar and water are shared with nest ants, or placed as tiny droplets on feeding larvae. Solid food consists mostly of arthropods, other invertebrates, and occasionally pieces of small vertebrates. Termites are especially attractive prey. Nestmates are recruited using pheromone trails, although experienced foragers also use landmarks. Most foraging activity occurs at dusk and during the night.

► Ants (Hymenoptera: Formicidae)
► Venoms and Toxins in Insects
► Bulldog Ant or Bull Ant, *Myrmecia* spp

Bumble Bees

Members of the family Apidae (order Hymenoptera, superfamily Apoidae).

► Wasps, Ants, Bees and Sawflies
► Bees

Bunchy Top of Papaya

This is an important bacterial disease of papaya that is transmitted by insects.

► Transmission of Plant Diseases by Insects

Buprestidae

A family of beetles (order Coleoptera). They commonly are known as metallic wood-boring beetles.

► Beetles

Burgess, Albert Franklin

Albert Burgess was on October 2, 1873, in Massachusetts. He received a first degree in 1895 and an M.S. in 1897 from Massachusetts Agricultural Academy. From 1899 to 1907 he worked as Assistant in Entomology at the University of Illinois and inspector of nurseries and orchards for the Ohio Department of Agriculture. Then he returned to Massachusetts to work for the U.S. Department of Agriculture in the Gypsy Moth Project, and continued this work until his retirement in 1943. However, in 1916, work on the browntail moth was added to his duties. His American Association of Economic Entomologists, and for years contributed much time to that society and its Journal of Economic Entomology. He died on February 23, 1953, survived by his second wife and two sons from his first marriage (Fig. 72).

Burgess, Albert Franklin, Figure 72 **Albert F. Burgess.**

Reference

Mallis A (1971) Albert Franklin Burgess. In: American entomologists. Rutgers University Press, New Brunswick, NJ, pp 435–437

Burmeister, Carl Hermann Conrad

Hermann Burmeister was born in Stralsund, Germany, on January 15, 1807. His early university education was at Universität Greifwald (1825–1827), whence he moved to Universität Halle. His dissertation at Halle and academic training gave him a doctorate in medicine and a doctorate in zoology in 1929. He did his military service in 1832. He taught in schools in Berlin until, in 1837, he became professor of zoology in Halle. He married in 1836, and had two sons. His first insect collection is in Halle. He published a five-volume textbook, “Handbuch der Entomologie” in 1832–1847. Between 1850 and 1852, with one of his sons, he travelled in eastern Brazil and then returned to Halle. One account of his Brazilian travels was published in 1853 as “Reise nach Brasilien, durch die Provinzen von Rio de Janeiro und Minas Geraes…,” another in 1854–1856 as “Systematische Uebersicht der Tiere Brasiliens,” although it was incomplete and deals only with mammals and birds. He returned to Halle, but in 1856 he left again, this time for Argentina, and spent four years (1857–1860) travelling within Argentina before publishing (1862) a 2-volume book “Reise durch die La Plata-Staaten…” He returned to Halle, but resigned from his position in 1861, divorced his German wife Marie Elise, and travelled once more to Argentina. His previous work resulted in his being offered directorship of the Museo Publico de Historia Natural in Buenos Aires in 1862. His interests were in all areas of natural history, but especially entomology. He wrote on paleontology, insect anatomy, the beetle family Scarabaeidae,

Burmeister, Carl Hermann Conrad, Figure 73
C. Hermann Burmeister.

and many other subjects, and published about 300 titles. He remarried in Argentina and had two sons. He died on May 2, 1892, following an accident in which he fell from a ladder into a glass showcase at the museum (Fig. 73).

References

Essig EO (1931) Burmeister, Hermann Carl Conrad. In: A history of entomology. The Macmillan Company, New York, NY, pp 562–563

Papavero N (1973) Burmeister. In: Essays on the history of Neotropical dipterology, with special reference to collectors (1750–1905). Museu de Zoologia, vol 2. São Paulo, Brazil, pp 292–293

Ulrich W (1972) Hermann Burmeister, 1807 to 1892. Ann Rev Entomol 17:1–20

Burnet Moth Biology (Lepidoptera: Zygaenidae)

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The family Zygaenidae is a member of the order Lepidoptera, suborder Ditrysia and the superfamily Zygaenoidea. Other than Zygaenidae, the superfamily Zygaenoidea consist of the following families: Megalopygidae (Lagoidae), Heterogynidae, Chrysopolomidae, Metarbelidae (Teragriidae), Limacodidae (including Cochlidiidae, Heterogenidae, Eucleidae), Cyclotornidae, and Epipyropidae. The Zygaenidae are further subdivided into seven subfamilies: Zygaeninae (burnet moths), Procridinae (forester moths), Chalcosiinae, Charideinae, Phaudinae, Anomoeotinae and Himantopterinae from which only Zygaeninae and Procridinae (and to a lesser extent Charideinae) are frequently mentioned even though Chalcosiinae are considered to be the largest group living in tropics. It is worth noting that the genus *Zygaena* is the most studied genus of the family.

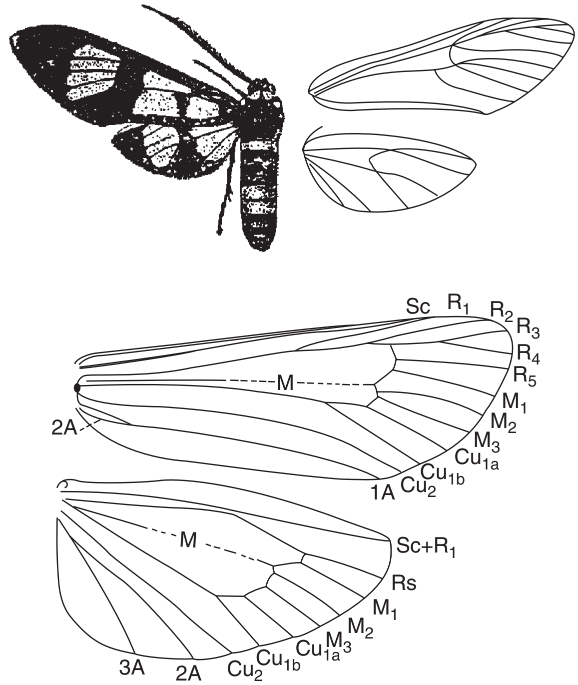
External Morphology

The adults of the family Zygaenidae closely resemble the Ctenuchidae from the superfamily Noctuoidea, but are readily distinguished by the presence of Cu_2 in the hind wings. Many are very brilliantly colored and there is considerable diversity of structure. It is interesting to note that all subfamilies, except Phaudinae and Himantopterinae, have been shown to contain the cyanogenic glucosides linamarin and lotaustralin. The larvae are short and cylindrical and have short hairs protruding from numerous verrucae. The pupae are enclosed in tough, elongate, membranous cocoons aboveground.

Life History and Habits

The zygaenid moths (Figs. 74 and 75) usually are diurnal in habit, though several species are known as nocturnal or are active during both night and day. *Zygaena* (*Mesembrynus*) *nocturna* Ebert, also known as a subspecies of *Z.* (*M.*) *seitzi* Reiss, is an example of the latter case. While it

Burnet Moth Biology (Lepidoptera: Zygaenidae), Figure 74 **The adults of two *Zygaena* species: (above) *Z. fraxini* Mén.; (below) *Z. carniolica* Scop. (After Abivardi C (2001) Iranian entomology–an introduction, 2 vols. Springer Verlag, Heidelberg, Germany, XXXIII, 1033 pp).**



Burnet Moth Biology (Lepidoptera: Zygaenidae), Figure 75 **Resemblance of the family Ctenuchidae (Noctuoidea) (above left) to the family Zygaenidae, but readily distinguished by their wing venation (above right: Ctenuchidae *(Euchromia polymena)*; below: Zygaenidae *(Zygaena filipendulae* L.).**

was originally described as exclusively nocturnal, it is also reported from Yasudj (Iran) to fly during the day.

In general, the zygaenid larvae live exposed on herbaceous plants. The larvae of the genus *Zygaena* show a certain oligophagy: while those belonging to the subgenera *Agrumenia* and *Zygaena* feed exclusively on Fabaceae, those of the subgenus *Mesembrynus* feed, with few exceptions, on Apiaceae. Laboratory studies on the biology of a zygaenid from Iran, *Z.* (*M.*) *tamara* ssp. *Kendevanica* Tremewan, revealed nine larval instars during which two to three stages of diapause were observed. In the final instar, the larvae constructed their cocoons either on the stems and twigs or on the surface of the box provided for pupation. The number of instars varies among species, with *Z.* (*M.*) *lydia* Staudinger displaying seven instars and *Artona chorista* Jordan with seven.

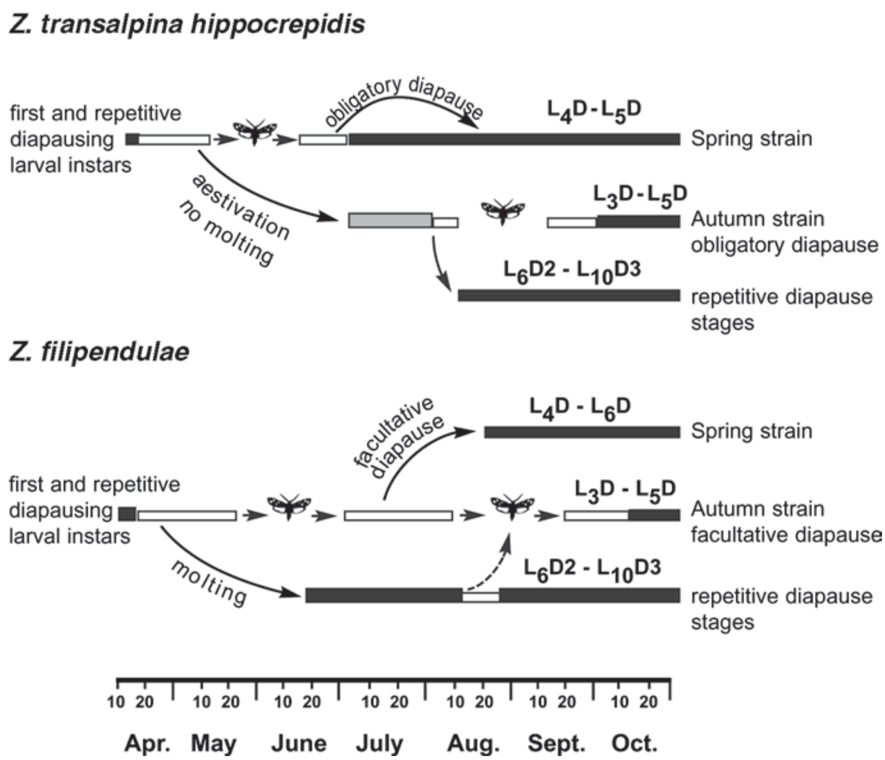
The most interesting life cycle (Fig. 76) strategies have been observed in species of the Palaearctic genus *Zygaena*. Development time varies markedly within a population. This variation is due to repeated larval hibernations between the third to the tenth instar and are due either to repeated or prolonged diapause periods. This phenomenon has been described as "fractionized development." Larvae normally pupate after six or seven feeding instars.The high flexibility in different *Zygaena* life cycle phenologies is based

Burnet Moth Biology (Lepidoptera: Zygaenidae), Figure 76 **External morphology of eggs (a), larvae (b & c; left: dorsal position; right: lateral position) and cocoon (d) of *Z. carniolica* Scop. with its adults (e) resting on thistle flowers. (Courtesy of Professor Clas M. Naumann and Pro Natura- The Swiss Alliance for Nature Conservation, Basel, Switzerland.)**

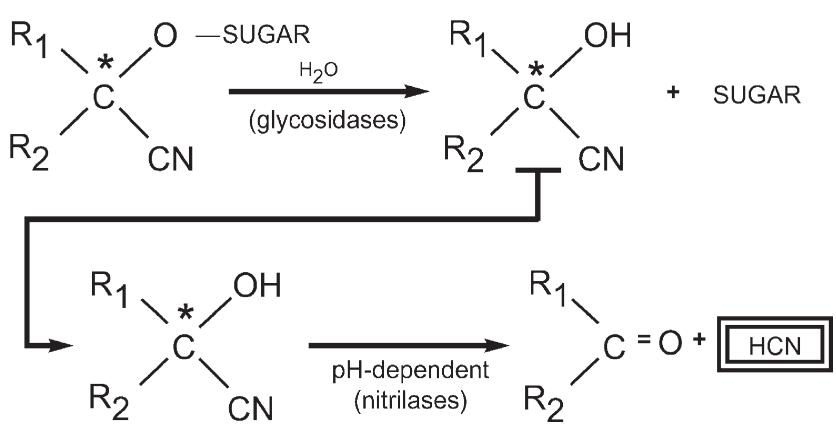
on both exogenous and endogenous factors. The variability in diapause and the consequent variable generation times may (Fig. 77) represent a strategy of spreading of the risk, thereby buffering the populations against adverse and fluctuating climatic conditions.

Cyanogenesis

The phenomenon of cyanogenesis is known to occur in more than 2,500 plant species (including important crop plants such as cassava, sorghum, flax, clovers and almond) as well as in some arthropods. Cyanogenesis is the process by which either plants or animals release hydrogen cyanide (HCN) from endogenous cyanide-containing compounds and is thought to play a role in defense against generalist, natural enemies. In plants, the cyanogenic glucosides and the corresponding enzymes are usually stored in different compartments. When herbivores such as cattle and insects feed on cyanogenic plants, the enzyme comes into contact with the glucoside leading to the release of hydrocyanic acid. Hydrocyanic acid is a powerful toxin that fends off herbivores and thus protects the plants. Within the insects, cyanogenesis occurs in beetles (Coleoptera) and bugs (Hemiptera) and seems to be quite common in Lepidoptera. In the order Lepidoptera, cyanogenesis is reported for several families of butterflies (Nymphalidae, Lycaenidae, Pieridae, Papilionidae and Hesperiidae) and moths (Megalopygidae, Heterogynidae, Limacodidae, Zygaenidae, Thyatiridae, Geometridae, Notodontidae, Arctiidae, Noctuidae and Lymantriidae). Within the family Zygaenidae, five of the seven subfamilies (except the Phaudinae and Himantopterinae) have been shown to contain the cyanogenic glucosides linamarin and lotaustralin (Figs. 78 and 79). Cyanogenesis is closely related to aposematic patterns in both larvae and adults, and mimicry is common. In *Zygaena* larvae there are three defenses against natural enemies: (i) an aposematic coloration that discourages an attack by a

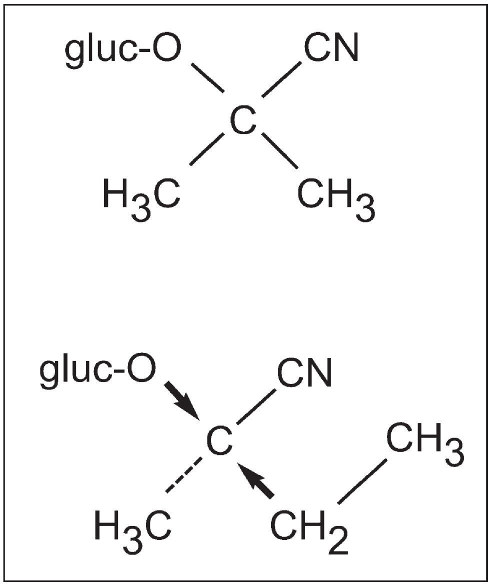


Burnet Moth Biology (Lepidoptera: Zygaenidae), Figure 77 **Fractionized development in *Zygaena* species: *Z. transalpina hippocrepidis* Hueb. and *Z. filipendulae* L. as examples. (Courtesy of Prof. Clas M. Naumann.)**



Burnet Moth Biology (Lepidoptera: Zygaenidae), Figure 78 **The process of cyanogenesis or enzymatic release of hydrogen cyanide (HCN) from endogenous cyanide-containing compounds.**

predator when visual contact is made, (ii) a secretion that is released following a relatively slight touch that fends off enemies by the noxious taste of the cyanogenic glucosides and/or the viscosity of the fluid, and (iii) when a larva is eaten by a predator, the liberated hydrocyanic acid of the hemolymph deters predation of other larvae.



Burnet Moth Biology (Lepidoptera: Zygaenidae), Figure 79 Structure of two cyanogenic glucosides (above: Linamarin; below: Lotaustralin) produced by the members of the family Zygaenidae.

Predators and Parasitoids

Several natural enemies are known. *Ectemnius kriechbaumeri* (Hymenoptera: Sphecidae) parasitizes larvae of the six-spot burnet (*Zygaena filipendulae* L.) in Italy and Spain. In Iran, larvae of *Zygaena* (*Agrumenia*) *esseni* Blom are parasitized by the ichneumonid *Casinaria orbitalis* Gravenhorst. They also are susceptible to infection by the entomopathogenic nematode *Steinernema* sp. Populations of western grapeleaf skeletonizer, *Harrisina brillians*, in southern California appear to be maintained at low levels of abundance by the combined activity of a granulovirus (HbGV) and the parasitoid *Ametadoria misella* (Diptera: Tachinidae).

In Italy, the European grapeleaf skeletonizer (*Theresimima ampellophaga*) is attacked by six species of parasitoids namely, two (chalcidids *Brachymeria intermedia* and *Hockeria unicolor*), a braconid (*Apanteles ultor*), two tachinids (*Zenillia libatrix* and *Exorista* sp.) and the famous *Trichogramma evanescens* (Hymenoptera: Trichogrammatidae). However, the percentage of parasitism was not high enough to control the pest.

Economic Importance

Knowledge about the economic importance of the members of the family Zygaenidae is confined to the subfamily Procridinae (forester moths) and, to a much lesser extent, to the subfamily Zygaeninae (burnet moths). The members of both subfamilies have been reported to play a role in pollination of the orchid *Anacamptis pyramidalis* (Orchidaceae).

Among the serious pests are western grapeleaf skeletonizer, European grape leaf skeletonizer, *Artona chorista* Jordan, and coconut leaf miner.

The western grapeleaf skeletonizer, *Harrisina brillians*, has been the subject of numerous studies in California (USA) and in northwestern Mexico. While the populations of this moth in southern California appear to be maintained at low levels of abundance by the combined activity of a granulovirus (HbGV) and the parasitoid *Ametadoria misella* (Diptera: Tachinidae), outbreaks of this insect have been common in central California. The host plant is damaged as follows: first, the early fourth instar larvae feed on the lower leaf surface, leaving only the veins and upper cuticle. This gives leaves a whitish, paper like appearance. Then, the late fourth and all fifth instar larvae skeletonize the leaves, leaving only the larger veins. In high populations, larvae can defoliate vines by July. When the vines are severely defoliated, larvae will then feed on the grape clusters, which can result in bunch rot. Defoliation can also result in sunburn of the fruit and quality loss. Furthermore, defoliation after harvest may also weaken vines by affecting food reserves.

The European grapeleaf skeletonizer, *Theresimima ampellophaga*, is a bivoltine species in the southern part of its range (south Italy) and univoltine in France, north Italy, Austria, Hungary and the former USSR. The larvae feed on the lower leaf surface and in late July, they abandon the leaves and move to the stumps left after pruning in the previous year where they spin cocoons in which they overwinter. Damage includes injuries to the young leaves by the small larvae in summer, injuries to the unopened buds immediately after hibernation and destruction of the young leaves by the older larvae in spring, which consume the whole leaf except for the midrib.

Artona chorista Jordan is recorded as a major pest of large cardamon plantations in India. Eggs are laid on the underside of leaves in batches of over 300 and hatch after about two weeks. The young larvae skeletonize the leaves, while mature larvae leave only the midribs exposed. There are seven larval instars and the larval and pupal stages last about two months or one month, respectively. Adult males and females live for about one week.

Coconut leaf miner, *Artona catoxantha* Hamps, is an important pest of coconut in Indonesia. Although *Apanteles artonae* (*Glyptapanteles artonae*) has been found to be the most important parasitoid of the pest, hyperparasitism of the parasitoid by other insects reduce the activity of *A. artonae* leading to frequent outbreaks of the coconut leaf miner.

References

Abivardi C (2001) Iranian entomology–an introduction, 2 vols. Springer Verlag, Heidelberg, Germany, XXXIII, 1033 pp

Efetov KA, Tarmann GM (1999) Forester moths. Apollo Books, Stenstrup, Denmark, 191 pp

Franzl S (1992) Synthesis, transport and storage of cyanogenic glucosides in larva of *Zygaena Trifolii* (Esper, 1783) (Lepidoptera: Zyaenidae). In: Dutreix C, Naumann CM, Tremewan WG (eds) Recent advances in burnet moth research (Lepidoptera: Zygaenidae). Koeltz Scientific Books, Champaign, IL, pp 21–31

Naumann CM, Tarmann GM, Tremewan WG (1999) The western Palaearctic Zygaenidae (Lepidoptera). Apollo Books, Stenstrup, Denmark, 304 pp

Stark DM, Purcell AH, Mills NJ (1999) Natural occurrence of *Ametadoria misella* (Diptera: Tachinidae) and the granulovirus of *Harrisina brillians* (Lepidoptera: Zygaenidae) in California. Environ Entomol 28:868–875

Wipking W, Naumann CM (1992) Diapause and related Phenomena in Zyganidae moths. In: Dutreix C, Naumann CM, Tremewan WG (eds) Recent advances in burnet moth research (Lepidoptera: Zygaenidae). Koeltz Scientific Books, Champaign, IL, pp 107–128

Burnet Moths (Lepidoptera: Zygaenidae) Burrower Bugs

Members of the family Cydnidae (order Hemiptera).

► Bugs

Burrowing Water Beetles

Members of the family Noteridae (order Coleoptera).

► Beetles

Bursa Copulatrix

A sac-like modification of the oviduct, or copulatory chamber, that receives the male aedeagus.

► Reproduction

Bursicon

A neuropeptide hormone produced by the neurosecretory cells of the brain that controls sclerotization (tanning) and cuticle expansion.

► Integument: Structure and Function

Bush Crickets

A subfamily of crickets (Eneopterinae) in the order Orthoptera: Gryllidae.

► Grasshoppers, Katydids and Crickets

Butterflies (Lepidoptera: Rhopalocera)

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Among the insect order Lepidoptera, butterflies comprise about 9% of the order worldwide, totaling about 20,400 described species (moths represent the other 91% of all lepidopterans). There are perhaps another 3,500 butterfly species awaiting discovery and naming, mostly from tropical regions of the world, and especially among the smaller species such as skippers (family Hesperiidae) and blues (family Lycaenidae). The Nymphalidae are the largest butterfly family, with about 7,080 known species worldwide; second largest is Lycaenidae with 5,955 known species. Although the name Rhopalocera is not used in modern classification of Lepidoptera, the name can be used to refer to all the butterflies (Heterocera is used as the name for all moths). While most moths are nocturnal (with many exceptions), most all butterflies are diurnal, although some are known to be crepuscular (especially a few tropical skippers).

Out of the total of 125 families of Lepidoptera, there are seven families of butterflies, although many specialists continue to place snout butterflies (family Libytheidae, only 12 known species) among the Nymphalidae and thus have only six families. Likewise, there is controversy about whether skippers (family Hesperiidae) should be in their own superfamily, Hesperioidea, or together with other butterflies in a single superfamily Papilionoidea. One solution to this controversy is to use a sub classification below the superfamily level, thus the series Hesperiiformes and series Papilioniformes are used. The main true butterfly families are Papilionidae (swallowtail butterflies), Pieridae (yellow-white butterflies), Lycaenidae (gossamer-winged butterflies), Riodinidae (metalmark butterflies), Libytheidae (snout butterflies), and Nymphalidae (brush-footed butterflies). Some specialists combine Riodinidae with Lycaenidae. Contrarily, most of the subfamilies in Nymphalidae in the past often have been separated as their own families, like Satyridae, Charaxidae, Morphidae, Amathusidae, Danaidae, Heliconiidae, etc. Butterflies now are thought to be a lineage from ancestors of what remain now as the most primitive of bombycine moths (perhaps resembling Ratardidae and relatives of Southeast Asia), which then evolved to geometer moth ancestors (families Geometridae and Hedylidae) and an alternate lineage that evolved to diurnal lifestyles and modern butterflies.

Butterfly adults typically have large eyes, a large haustellum (or tongue), and knobbed, or clubbed, antennae; but skippers (family Hesperiidae) mostly have the antennae with elongated hooked clubs. Although most butterfly adults have strong thoracic legs, in the family Nymphalidae the first pair of thoracic legs are not used for walking and instead are held folded under the prothorax. The bodies of adult butterflies are typically rather slender, but many groups have very robust bodies, allowing them to be very strong fliers (e.g., charaxine and danaine Nymphalidae). Some groups have scent organs (coremata) on the abdomen that can be everted either for protection or as pheromone releasers during mating behavior. Danainae butterflies (family Nymphalidae) have wing vein scent organs (androconia) in males, and Satyrinae butterflies (family Nymphalidae) have tymbal organs used for hearing within some wing veins. Wings include a pair of forewings and a pair of typically smaller hindwings (some Pieridae have larger hindwings than forewings, particularly in the tropical American subfamily Dismorphiinae), and generally the forewings are rather triangular in shape and the hindwings are more rounded. Great variety of wing shape, however, is known and many groups have hindwing tails (e.g., many Lycaenidae and Papilionidae). A huge variety of color patterns exist among butterflies, from monotone browns or grays, to extremely colorful, to some that even are nearly colorless or transparent (e.g., some tropical glasswings of the subfamily Ithomiinae, family

Butterflies (Lepidoptera: Rhopalocera) , Figure 80 **Representative butterflies (Lepidoptera: Rhopalocera): top left, *Isoteinon lamprospilus formosanus* Fruhstorfer (Hesperiidae) from Taiwan (photo C.C. Lin); top right, *Zerynthia polyxena cassandra* (Geyer) (Papilionidae, Parnassiinae) from France (photo J.H.H.**

Nymphalidae). The *morpho* butterflies of the subfamily Morphinae (family Nymphalidae), from tropical America, are well known for their brilliant blue coloration that is the result of structural scales that reflect light, rather than the typical lepidopteran wing scales that have pigmented colors.

Butterfly caterpillars for the most part are typical lepidopteran caterpillars, with the usual number of prolegs (4 pairs plus a posterior pair), but many different setal vestitures and color forms are known. Caterpillars typically have a hard head capsule, three pairs of clawed thoracic legs, and 4 pairs of abdominal prolegs having crochets (hook-like spines on the base of the prolegs that provide footing when climbing on plants), plus a posterior proleg pair. Most of the Nymphalidae larvae have various kinds of bizarre spined and enlarged setae, called scoli, typically even on the head. Swallowtail larvae, on the other hand, have a unique defensive odiferous and usually brightly colored forked scent organ, called an osmeterium, just behind the head capsule that is extruded to help defend against a predator. Larvae among most Lycaenidae are slug-like and can retract their head into folds of the prothorax. The more primitive skipper caterpillars (family Hesperiidae) have few body setae and mostly feed on grasses and other monocots. Other butterfly larvae feed on a great variety of hostplants, although most individual species have a narrow hostplant preference (e.g., monarch butterfly larvae feed only on milkweed leaves, Asclepiadaceae). Most butterfly larvae pupate as exposed pupae and do not make cocoons. Swallowtail pupae (family Papilionidae) typically use a silken girdle to angle away from a plant stem, while most other butterflies attach their pupae using the cremaster and hang upside down (Lycaenidae pupae tend to be laid flat on a plant surface).

Butterflies, while a small percentage of the order Lepidoptera, have served as the model organisms for a large number of ecological and biological studies of the Lepidoptera, much more than among the moths. Part of this study usage pertains to their being diurnally active, and thus easier to study than the nocturnal moths. Butterflies also are mostly more colorful and larger than typical moths, and are thus the most well known lepidopterans among the general public. Butterflies have complex flight behavior and mating rituals that have been the subject of many detailed studies over the years. Flight among butterflies also involves directed migration in some cases, the most well known example being the yearly mass autumn flights of the American monarch butterfly (*Danaus plexippus*, family Nymphalidae) from as far as southern Canada to wintering refugia in Mexico, and then back again the following spring. There are many other cases of lesser migrations among other species and on all continents. Other studies on butterflies have focused on their life histories, which involve such intricate aspects as commensal myrmecophilous adaptations, as among most larvae of the blues (family Lycaenidae) and metalmarks (family Riodinidae), where ants protect the larvae from predators and the larvae provide the ants with desirable secretions. However, most butterflies still remain unknown biologically, particularly among tropical species.

The largest known butterflies are among the birdwings (family Papilionidae) (Fig. 80) of the Indo-Australian tropics, especially in New Guinea and the Solomon Islands, where the largest females attain wingspans of up to 280 mm. One African

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Thiele); second row left, *Eurytides marcellus* (Cramer) (Papilionidae, Graphiini) from Florida, USA (photo H.O. Hilton); second row right, *Papilio glaucus* Linnaeus (Papilionidae, Papilionini) from Florida, USA (photo H.O. Hilton); third row left, *Pieris canidia* (Sparrman) (Pieridae, Pierinae) from Taiwan (photo C.C. Lin); third row right, *Heliophorus ila matsumurae* (Fruhstorfer) (Lycaenidae, Lycaeninae) from Taiwan (photo C.C. Lin); bottom left, *Libythea celtis formosana* Fruhstorfer) (Libytheidae) from Taiwan (photo C.C. Lin); bottom right, *Agraulis vanillae* (Linnaeus) (Nymphalidae, Heliconiini) from Florida, USA (photo J. B. Heppner).

swallowtail species (*Papilio antimachus*) has males with a wingspan of up to 250 mm (females in this species are smaller than the males). The smallest known butterflies are some of the high altitude or desert blues (family Lycaenidae), where wingspans as small as 6 mm are known. The average butterfly, however, has a wingspan of about 30 mm, not much different from the average moth adult, since there are a large number of very small skippers and blues, and fewer of the larger swallowtails and Nymphalidae in the world.

► Butterflies and Moths

References

D' Abrera B (1980–95) Butterflies of the world, 12th vol. Hill House, Melbourne, Victoria, Australia

Douglas MM (1986) The lives of butterflies. University of Michigan Press, Ann Arbor, Michigan, 241 pp, 16 pl

Feltwell J (1986) The natural history of butterflies. Facts on file, New York, New York, 133 pp

Feltwell J (1993) The illustrated encyclopedia of butterflies. Blandford, London, UK, 288 pp

Kitching RL, Scheermeyer E, Jones RE, Pierce NE (eds) (1999) Biology of Australian butterflies. CSIRO, Canberra, Australia, 395 pp (Monograph of the Australian Lepidopterist's Society 6)

Manos-Jones M (2000) The spirit of butterflies: myth, magic, and art. H. N. Abrams, New York, NY, 144 pp

Nijhout HF (1991) The development and evolution of butterfly wing patterns. Smithsonian Institution Press, Washington, DC, 297 pp, 8 pl

Owen DF (1971) Tropical butterflies: the ecology and behaviour of butterflies in the tropics with special reference to African species. Clarendon Press, Oxford, UK, 214 pp, 40 pl

Vane-Wright RI, Ackery PR (eds) (1984) The biology of butterflies. Royal Entomological Society of London, 429 pp (Reprinted 1989, Princeton University Press, Princeton, NJ)

Watson A, Whalley PES (1975) The dictionary of butterflies and moths in color. McGraw Hill, New York, NY, 296 pp, 144 pl

Butterflies and Moths (Lepidoptera)

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The Lepidoptera, one of the main plant-feeding groups of insects in the world, are well known to most all persons familiar with nature or the garden, as the day-flying butterflies and the mostly nocturnal moths. Included are all the butterflies and skippers (superfamily Papilionoidea), plus such common moth groups as silkworms (or silkmoths) (family Bombycidae), emperor moths (or giant silkmoths) (family Saturniidae), hornworms (or hawk moths) (family Sphingidae), cutworms (or millers and owlet moths) (family Noctuidae), inch worms (or geometer moths) (family Geometridae), clothes moths (family Tineidae), and many others. The spectacular variety of wing coloration and markings of the Lepidoptera has evolved over millions of years, from the rather drab primitive moths that hardly appear much different than the related Trichoptera, to the most brilliantly colored butterflies. The Lepidoptera are notably differentiated from Trichoptera by the scales which cover the wings and all external body parts.

Lepidoptera (or "scaly wings") are perhaps best known for the colorful day-flying butterflies. Such famous species as the American monarch butterfly (*Danaus plexippus*, family Nymphalidae, subfamily Danainae), the swallowtails and the tropical birdwings (family Papilionidae), the many common yellow butterflies (family Pieridae), and blues and hairstreaks (family Lycaenidae), are known by most persons in the world from their earliest school days. The name "butterfly" is thought to come from Old English usage related to yellow butterflies looking like slices of butter on the wing, or "butter-fly" (the Old English or Old German "buterfloege"), or even ancient folklore of fairies stealing butter. Other languages and cultures all have their own common names for butterfly: farfalla (Italian), lepke (Hungarian), Schmetterling or Tagfalter (German), papillon (French), vlinder (Dutch), sommerfugl (Danish), psyche (Greek), chô-chô (Japanese), hú díeh (Chinese), borborleta (Portuguese), mariposa (Spanish), fluture (Romanian), farasha (Arabic), kupu-kupu (Indonesian), rama-rama (Malaysian), titli (Urdu), boboochka (Russian), kipepeo (Swahili), and so on. Many names refer to both butterflies and moths, such as the German word Schmetterling and the French papillon, while moths are sometimes referred to what in English would be "night butterflies," or special words are available just for moths as, for example, Nachtfalter (German), moth (English), and polilla (Spanish).

Most cultures in the world have mythology and words for butterflies and moths. Moths, however, while also having well known common names, have mostly been associated since ancient days with those few species that are destructive to man: thus, cutworms (Noctuidae), clothes moths (Tineidae), rice moths and grain moths (Pyralidae), cankerworms (Geometridae), and so forth. Folklore for Lepidoptera also includes such superstitions as the fear of death associated with the death-head sphinx of Europe and Asia (*Acherontia atropos*, Sphingidae): the large-bodied adults in this genus have markings on the thorax that resemble a human skull, and they also squeak like a mouse when held by their bodies. Likewise, the very large black witch moth (*Ascalapha odorata*, Noctuidae) of tropical America is also feared as an omen of death when one flies into a house through an open window. Many native cultures, like in the Amazon Basin, believe butterflies are the departed souls from recently deceased persons. Contrarily, among all the Lepidoptera, perhaps the most beneficial to man has been the silkworm moth, *Bombyx mori* (Bombycidae), a domesticated variety of a native Chinese silkworm moth which has been cultured for centuries in China to produce fine silk, spun from the strands of its white cocoons.

The Lepidoptera are estimated to number approximately 255,000 extant species in the world, with about 156,100 species already named and cataloged. The order has often been divided into the generalized groupings of Rhopalocera, or butterflies, and Heterocera, or moths. Although this separation has no validity in our modern understanding of the evolution of the order, the simplified divisions nonetheless are a way of referring to each group using Latin names and are still commonly encountered in the popular literature. Likewise, for the terms Microlepidoptera (or the smaller and primitive moths) and Macrolepidoptera (the usually larger and more advanced moths and butterflies): these terms are not universally applicable since some "micro" -moths include very large species (some Hepialidae and Cossidae) and some "macro" -moths also include some very small species (e.g., some Geometridae and Noctuidae). Some butterflies (e.g., some blues, Lycaenidae) are smaller even than some of the average Microlepidoptera.

There is incredible diversity of form, biology, behavior, and feeding habits among the Lepidoptera, which occur in almost all known habitats, from the Arctic to the densest jungles. The only region lacking Lepidoptera is Antarctica, although some small brachypterous species could conceivably be present on the northernmost tip of the continent nearest to Tierra del Fuego. There are also completely different lifestyles between the adults and the larvae of Lepidoptera. For example, while adult butterflies seek nectar for the most part, and most moths at least seek moisture (there are a few that do not feed as adults), there are such strange larval adaptations as the myrmecophilous larvae of many Lycaenidae, where the larvae are tended and protected by ants. As a contrary example, in larvae of Dalceridae, the larvae are protected from ant attacks by an integumental defensive secretion, while the adults of these slug caterpillars lead simple lives in search of mates, as do most moths.

In the overall world fauna of 255,000 species of Lepidoptera, most of the evolutionary development and biodiversity is among the moths (an estimated 231,500 species), while butterflies and skippers total an estimated 23,500 species worldwide, and represent only about 9% of the total extant species of Lepidoptera.

Classification

The order is now divided into four suborders, based on modern studies using cladistics and other techniques for analysis of morphological characters and other evolutionary information: Zeugloptera, Aglossata, Heterobathmiina, and Glossata. Each of the first three suborders include only a single nominate family of primitive moths and all the remainder of the order is under Glossata. There are differing modern classifications adhered to, although in general most lepidopterists now agree on the overall treatment of families and higher categories. In the classification adopted herein, the Glossata are further divided into the cohorts Dacnonypha and Myoglossata. Dacnonypha are subdivided into two infraorders: Dacnonypha and Lophocoronina. Myoglossata are divided into two subcohorts, Myoglossata and Neolepidoptera, with the first containing only the infraorder Neopseustina, and Neolepidoptera having two infraorders: Exoporia, and Heteroneura. Most Lepidoptera are in Heteroneura, which are divided into two divisions: Monotrysia and Ditrysia. Monotrysia have two sections: Nepticulina and Incurvariina. Ditrysia, then, contain the majority of the order, with section Tineina having most of the micro-moths, and section Cossina mostly the larger moths and the butterflies. The remaining classification details in Lepidoptera involve further divisions into subsections, superfamilies, and families.

The following listing gives an overview of the main groupings and superfamilies of Lepidoptera. Butterflies are in Papilionoidea, including skippers which sometimes are placed in their own superfamily, Hesperioidea. Butterflies are placed near the middle of the Bombycina, and not at the end of the order as many older works have them, since the Noctuidae are now considered the most evolutionarily advanced Lepidoptera. Groups preceeding Ditrysia contain the most primitive Lepidoptera, and among these, the first three suborders contain the most archaic relicts of ancient lepidopteran lineages still extant.

- Order: LEPIDOPTERA
  - Suborder: Zeugloptera
    - Micropterigoidea
  - Suborder: Aglossata
    - Agathiphagoidea
  - Suborder: Heterobathmiina
    - Heterobathmioidea
  - Suborder: Glossata
    - Cohort: Dacnonypha
      - Infraorder: Dacnonypha
        - Eriocranioidea
      - Infraorder: Lophocoronina
        - Lophocoronoidea
    - Cohort: Myoglossata
      - Subcohort: Myoglossata
        - Infraorder: Neopseustina
          - Neopseustoidea
      - Subcohort: Neolepidoptera
        - Infraorder: Exoporia
          - Mnesarchaeoidea
          - Hepialoidea
        - Infraorder: Heteroneura
          - Division: Monotrysia
            - Section: Nepticulina
              - Andesianoidea
              - Nepticuloidea
              - Tischerioidea
              - Palaephatoidea
            - Section: Incurvariina
              - Incurvarioidea
          - Division: Ditrysia
            - Section: Tineina
              - Subsection: Tineina
                - Tineoidea
                - Gelechioidea
                - Copromorphoidea
                - Yponomeutoidea
                - Immoidea
                - Pyraloidea
                - Pterophoroidea
              - Subsection: Sesiina
                - Sesioidea
                - Zygaenoidea
            - Section: Cossina
              - Subsection: Cossina

Cossoidea
Castnioidea
Tortricoidea
Subsection: Bombycina
Calliduloidea
Uranioidea
Geometroidea
Papilionoidea
Drepanoidea
Bombycoidea
Sphingoidea
Noctuoidea

The arrangement of the classification of Lepidoptera follows a progression somewhat in line with our knowledge of how the order evolved, from the most primitive moths that resembled Micropterigidae, to what are now considered the most advanced lepidopterans, the Noctuidae. Yet, advanced features are also found in other groups, such as the Sesiidae, with their unique wing locking mechanism that nearly approaches the similar wing locking found in wasps (Hymenoptera), and butterflies, where some have evolved advanced features like the chordotonal organs found in wing veins of Satyrinae (Nymphalidae).

Overall, the order has 32 superfamilies and 125 families in the classification adopted herein. There is still some controversy in terms of how many families and superfamilies there are and how they should be arranged. For example, some other recent classifications for Lepidoptera use 46 superfamilies, splitting many odd families to their own monobasic superfamilies. However, the foundations of the primitive groups (non-Ditrysian groups) are fairly well established now, although new discoveries can still come to light from remote tropical regions of the world: for example, one small family of primitive moths, the Neotheoridae, was only discovered within the past 25 years and was based on a single known specimen from Brazil. Since many specialists elevate odd groups to higher levels, many of the remaining controversies in Lepidoptera classification pertain to how different groups should be treated, i.e., whether as a subfamily or as a separate family, etc. Even some unusual tribes within subfamilies are considered separate families by some specialists. Among the butterflies, nearly all subfamilies have at one time or another been considered separate families, and some of the currently adopted families were listed as their own superfamilies (viz., Nymphaloidea and Lycaenoidea, etc.) in some past classifications.

As the diversity of the Lepidoptera came to light after Linnaeus, as more species were discovered in tropical regions, more and more categories and families were needed to classify the enormous biodiversity discovered in the world. Where Linnaeus had only five "families" of Lepidoptera in 1758, we now have 125 families, 290 subfamilies, and several hundred tribes. As noted above, remaining controversies often involve whether some of the subfamilies should be separate families: for example, in one recent classification, most of the Gelechioidea families have been reduced to subfamilies in one enormous family Elachistidae, which itself is only a small family among several families of Gelechioidea in the classification used herein. Another case involves the slug caterpillar families, which evidently have converged on a common larval habitus while their fundamental evolution, as based on the position of the heart vessel, demonstrates that the different families belong in two different lineages within the Ditrysia: the flannel moths (Somabrachyidae and Megalopygidae), as well as the burnet-type moths (Heterogynidae, Zygaenidae, Himantopteridae, and Lacturidae), all Zygaenoidea, being in Section Tineina, while the other families with slug caterpillars (Dalceridae, Limacodidae, and Chrysopolomidae), of the Cossoidea, belonging in Section Cossina. However, some specialists continue placing all slug caterpillar families together. These differing arrangements often are dependent on the experience of various specialists, since many only study local faunas, for example, and not the entire global fauna of a family, thus limiting their knowledge and often resulting in the view that some unusual tropical species should be in a new family or subfamily, etc., rather than integrating it within existing groups. Yet, since most of the biodiversity of the order is in the tropics, much study is still needed for many Lepidoptera groups, and especially so on their biologies and immature stages. One can note below in the biodiversity section how many entire families remain completely unknown biologically.

Evolution

Lepidoptera are known as fossils from at least as far back as the Lower Jurassic; thus, the split from Trichoptera-like relatives undoubtedly occurred already much earlier. However, fossils of lepidopterans are not as common as they are for other insect orders, so the evolutionary record is little documented. The greatest number of fossil Lepidoptera are known from amber, particularly Eocene aged Baltic amber and the younger Dominican amber from the Caribbean. There are also considerable numbers of Oligocene lepidopteran fossils known from rocky sediments, like from Florissant, Colorado, from Tertiary sediments in Italy and other parts of Europe, and from late Jurassic layers from Central Asia, among others. Most all known fossil Lepidoptera have been found in the Northern Hemisphere, and only a few are known from the Southern Hemisphere, but this may well be the result of more searching in Europe and North America than has been done south of the equator.

The older fossil lepidopterans are all of the kind of species now found in the most primitive families, such as the mandibulate Micropterigidae and other homoneurous groups of primitive Lepidoptera. The oldest known lepidopteran fossil is from Lower Jurassic layers from England, named *Archeolepis mane*. Primitive Hepialidae have been found in Palaeocene British limestone and mid-Miocene Chinese deposits. Butterflies are most well known from deposits found at Florissant, Colorado, of Eocene age. An earlier butterfly has been found in Upper Palaeocene deposits in Denmark. Some of the most primitive of butterflies still extant, like in the genera *Baronia* (Papilionidae) from Mexico and *Calinaga* (Nymphalidae) from Asia, resemble some of the ancient fossil butterflies. Evidence of larval feeding is also known in fossils, as for example, from leafminers. Because almost all Lepidoptera are plant feeders, there has necessarily also been considerable adaptation to various plants, what we now consider as insect-plant coevolution.

The evolution of Lepidoptera lineages to the extant families we have today was undoubtedly very reticulate, rather than a simple linear progression, and this is evident in our classification as well. For example, among Ditrysian groups the families are not related in the sequential manner they are listed on paper, but rather they represent progressions from ancestral divisions that evolved like branches on a tree. Thus, there remain today in each division both primitive elements (e.g., those with spined pupae) and advanced groups. One can see the relictual groups in the basal families of the main divisions, as in the first listed families in Tineoidea, Sesioidea, Cossoidea and Calliduloidea, while advanced families are present in each division as well, each with some advanced features yet in different lineages than what led to the most advanced, the Noctuidae.

Characteristics

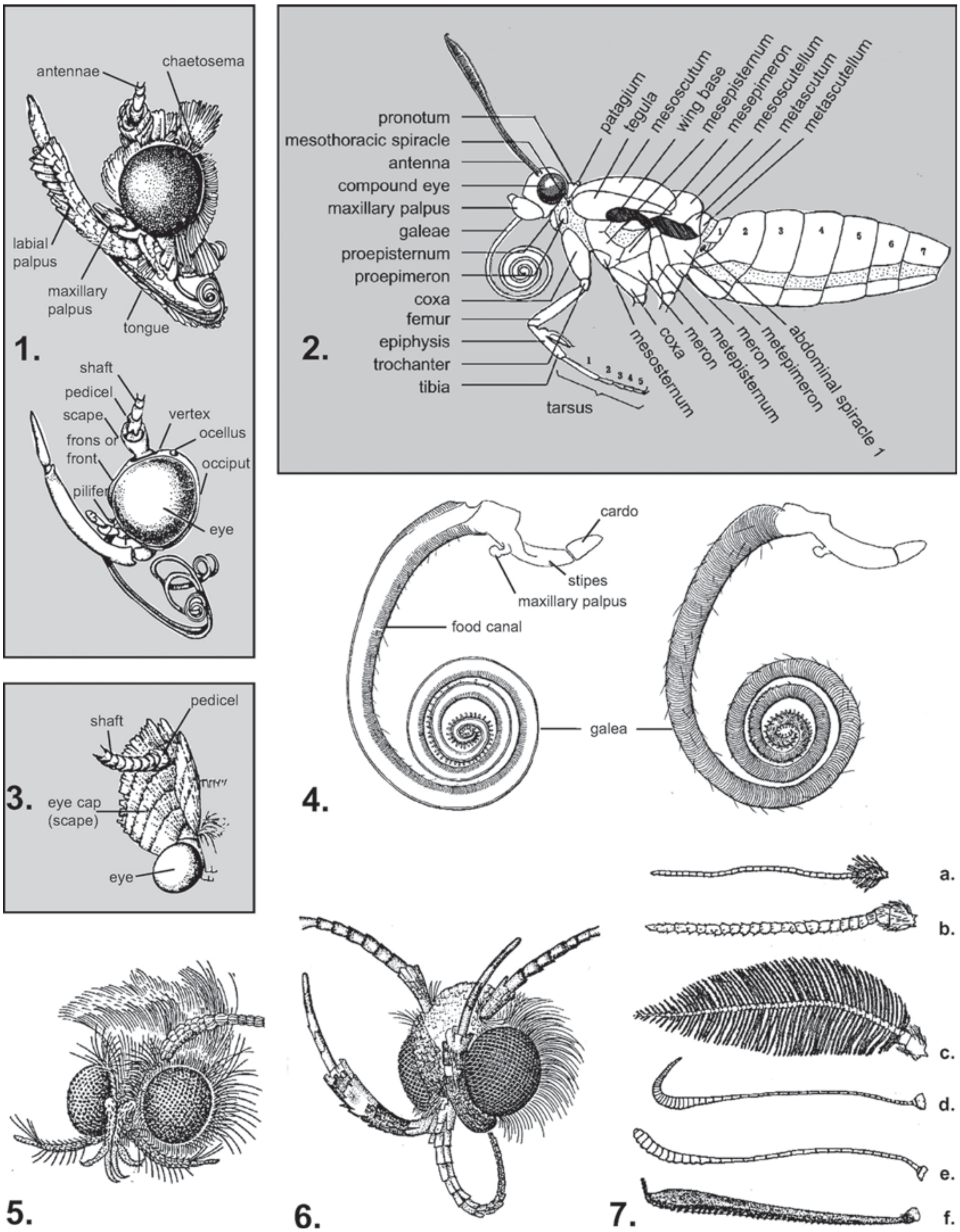
All Lepidoptera have a complete, holometabolous life cycle, with separate egg, larva, pupa, and adult stages. The morphology of the lepidopteran adult and immature stages have been extensively studied, with some of the larger species, like some of the large hawk moths (e.g., *Manduca* sp., Sphingidae) and emperor moths (e.g., the North American cecropia moth, *Hyalophora cecropia*, and the polyphemus moth, *Antheraea polyphemus*, Saturniidae) being used as experimental subjects for anatomy and physiology studies, due to their availability and large size. The monarch butterfly (*Danaus plexippus*, Nymphalidae) has also been used as a model for many morphological studies.

Adults

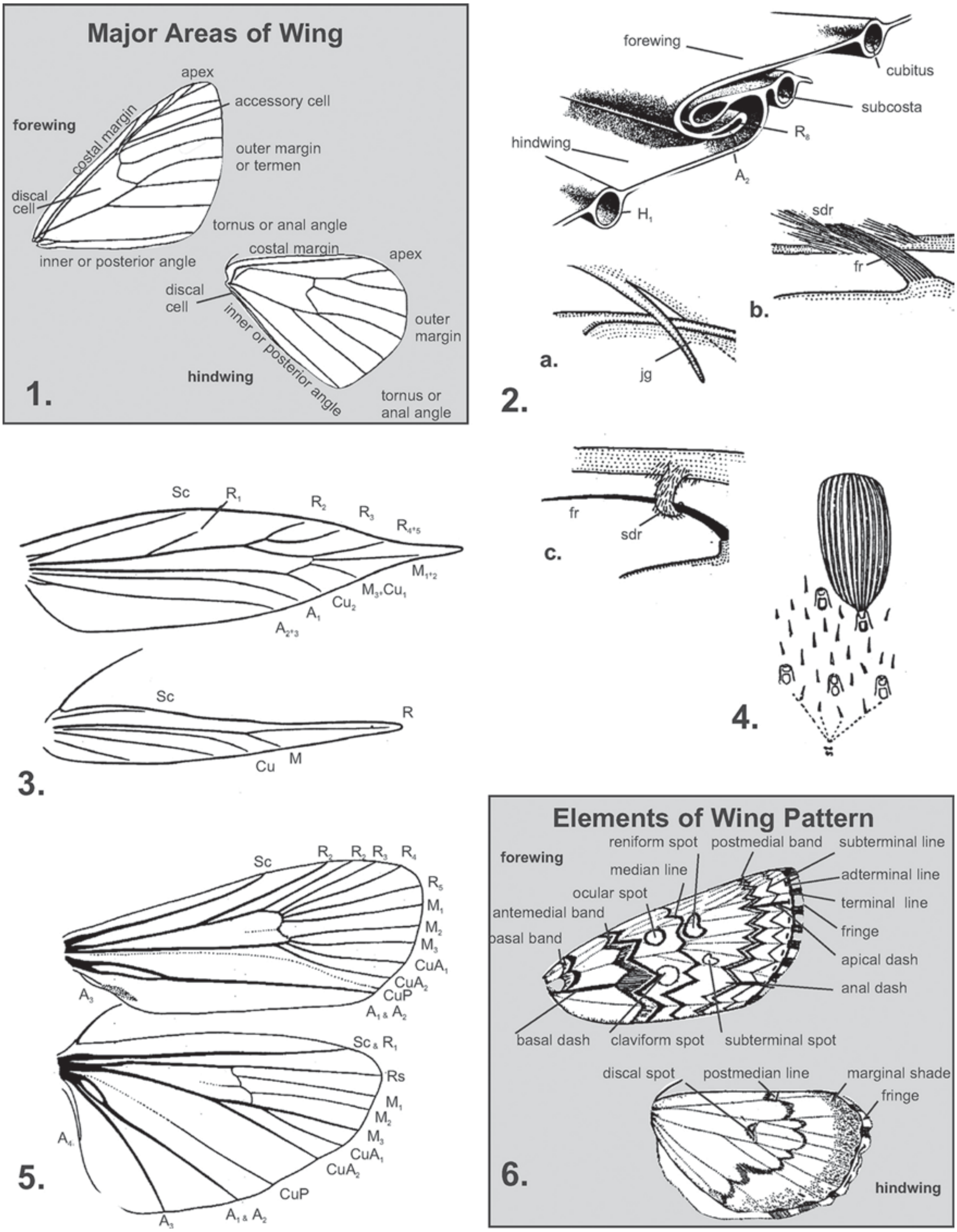
Most Lepidoptera are moderate-sized, winged insects, averaging about 30 mm in wingspan. The (Figs. 81 and 82) smallest known species, as small as 2.5 mm in wingspan, are in the pygmy leafminer family Nepticulidae, while the largest known lepidopterans are about 300 mm in wingspan, as in the emperor moth (or giant silkmoth) family (Saturniidae). The largest moths among these Saturniidae include females of the hercules moth (*Coscinocera hercules*) from Australia, which have large quadrate wings and a large, heavy body, and likewise females of the atlas moth, *Attacus atlas*, and related species of the genus *Attacus* of Southeast Asia; males in these species are somewhat smaller. Some of the larger hawk moths (Sphingidae) also have massive bodies and very thick, strongly veined wings, as do some of the carpenterworm moths (Cossidae), like the Australian *Xyleutes affinis*, where the abdomen in large females attains 70 mm in length. There also are exceptionally large winged species among the primitive ghost moths, family Hepialidae, especially from Australia (e.g., *Zelotypia stacyi*) and South Africa (e.g., *Leto venus*), and such other moth families as the giant butterfly moths (Castniidae) and owlet moths (Noctuidae), as well. An owlet moth (Noctuidae) actually has the record wingspan, where some females of the white witch moth (*Thysania agrippina*) of the Amazon attain wingspans of 305 mm, but the largest emperor moths (Saturniidae) have an overall larger wing area due to their quadrate wing shape.

Butterflies also average about 30 mm in wingspan, since even though many are large sized, there are a great number of smaller species, particularly among the skippers (Hesperiidae), and also the blues and hairstreaks (Lycaenidae). Butterflies range in size from less than 7 mm in wingspan to over 280 mm. Among the smallest blues (Lycaenidae), the genus Itylos from the high Andes of Bolivia and Chile is about 6–10 mm in wingspan, while the genus *Micropsyche*, from Afghanistan, is about 7 mm in wingspan, and some American *Brephidium* specimens are 6–9 mm in wingspan. Many of the Microlepidoptera are larger than these small butterflies. The largest butterflies, such as female birdwings of *Ornithoptera alexandrae* (Papilionidae) from New Guinea, are over 280 mm in wingspan. Another large butterfly is the African swallowtail, *Papilio antimachus* (Papilionidae) where the elongated wings of some males attain 250 mm in wingspan; in this species the females are smaller in size.

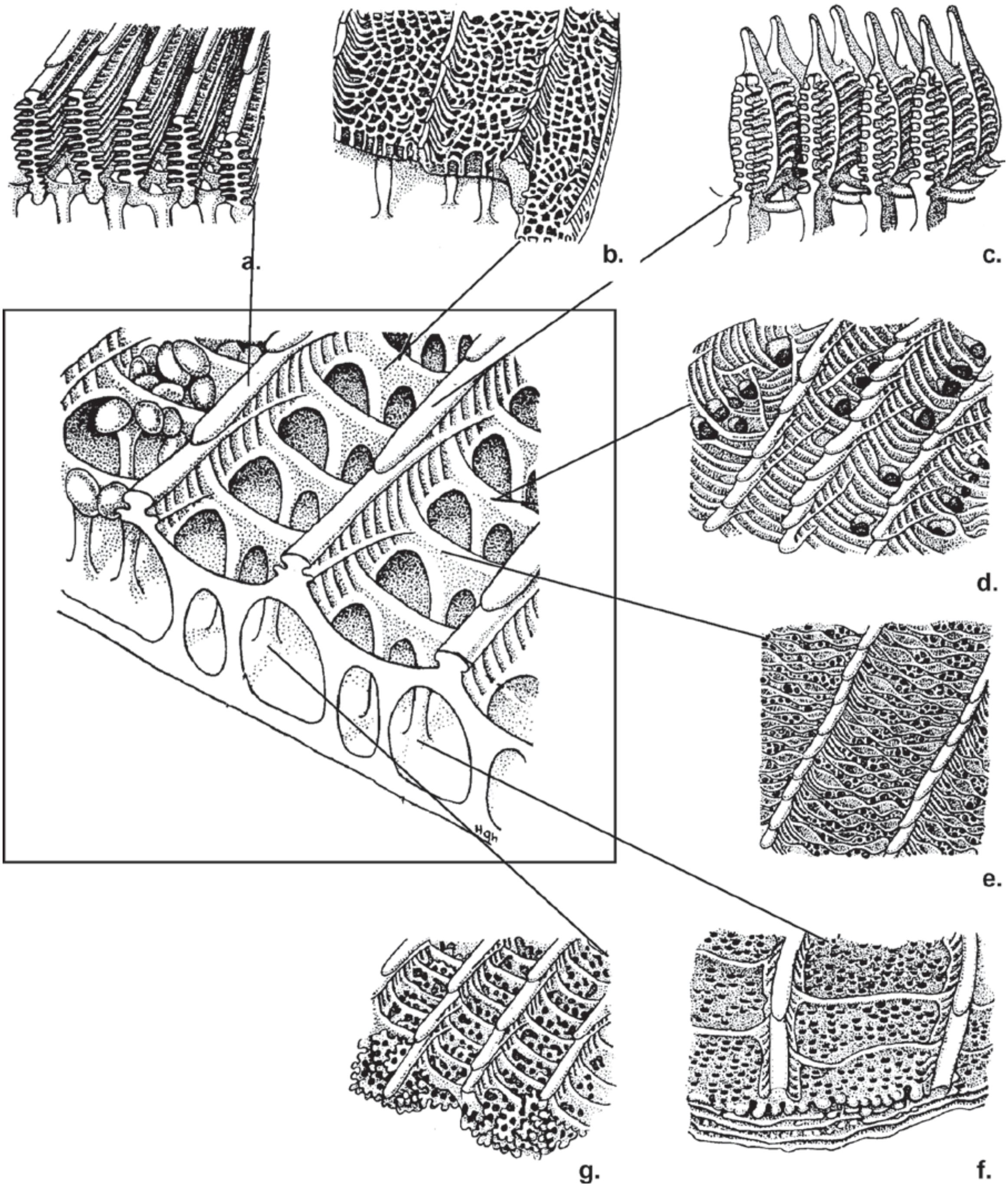
Lepidoptera typically have four wings and scales cover all body parts. Some exceptions occur, whereby various surfaces may be devoid of scales (e.g., so-called eyespots or clear spots in some moths and butterflies), but all Lepidoptera have at least some areas of their external body with the unique lepidopteran scale structures, or squamae (Fig. 83). Trichoptera in rare cases also have some wing scales, but they typically are hair-like and not like scales among lepidopterans and do not cover other body parts. Most lepidopteran scales are flattened and ribbed, containing pigments for color. Other modified scales include androconia, or scent organs, prevalent in such groups as the monarch subfamily Danainae (family Nymphalidae), where they occur as a patch near the central veins of the hindwings. Wing scales in such species as *Morpho* butterflies (subfamily Morphinae, family Nymphalidae) and the metallic-like spots of some day-flying moths, as in the metalmark moth family (Choreutidae), have the scales modified to refract light, thus producing the brilliant iridescent blues seen in male *Morpho* butterflies. Many species also have specialized scales that reflect patterns of ultraviolet light, which wavelengths are in the main spectrum that Lepidoptera actually see. Consequently, the UV pattern of many lepidopteran wings is very different than what we see as their coloration in white light, and the UV pattern is what is actually being used as visual cues in mating behavior which may isolate related species. Lepidopteran UV patterns have mostly been studied



Butterflies and Moths (Lepidoptera), Figure 81 **Lepidopteran head and associated structures: 1. Head morphology (after Hodges, 1971); 2. Lepidopteran morphology; 3. Head details showing eye cap (after Hodges, 1971); 4. Haustellum (galea), with inneraspect of right maxilla (left) and outer aspect of left maxilla (right); 5. Head scaling, rough (Tineidae) (after Falkovitsh and Zagulajev, 1978); 6. Head scaling, smooth (Gelechiidae) (after Falkovitsh and Zagulajev, 1978); 7. Antennal types: (a) filiform (Eriocraniidae), (b) pectinate (Hepialidae), (c) bipectinate (Saturniidae), (d) club-hooked (Hesperiidae), (e) clubbed (Papilionidae), (f) thickened (Sphingidae) (after Zerny and Beier, 1936–38).**



Butterflies and Moths (Lepidoptera), Figure 82 **Lepidopteran wings: 1. Wing regions (after Hodges, 1971); 2. Wing locking mechanisms: Sesiidae double fold (after Heppner and Duckworth, 1981), (a) jugum (Hepialidae), (b) female frenulum and retinaculum (Sphingidae), (c) male frenulum and retinaculum (Sphingidae) (a–c, after Tillyard, 1926), 3. Wing venation, leafminer (Lyonetiidae) (after Seksjeva, 1981); 4. Wing nomenclature (after Hodges, 1971); 5. Wing venation (Brachodidae) (after Heppner, 1981); 6. Lepidopteran wing scale (after Spuler, 1910).**



Butterflies and Moths (Lepidoptera), Figure 83 **Lepidopteran scale morphology (after Ghiradella, 1998): (a) scale ridges may be modified as lamellae for interference coloration (e.g., *Morpho* wings); (b) flats between ridges may be elaborated to produce Tyndall blue coloration (e.g., some *Papilio* sp.); (c) lamellae of complex ridges may be shaped to produce reflective coloration (e.g., for metallic-like spots); (d) inter-ridge microribs may have reduced window-like shapes; (e) flats between ridges may be plate-and-pore configuration (e.g., in androconial scales of Pieridae); (f) scale interiors may have body-lamellae to produce thin-film interference colors; and (g) scale interior may be filled with crystallite lattices that produce diffraction colors. (© Ghiradella, 1998; used with permission from author and John Wiley & Sons, Inc.)**

in butterflies and not in moths, nor even in day-flying moths, but of course all lepidopteran wing maculation is only seen in UV by the mates, other species, and other insects. While most lepidopteran scale colors will fade after some time exposed to light, the structural colors of the modified scales will not fade over time. Most lepidopteran colors are pigment based within the scales, but some is structural. In the yellow and white butterflies, family Pieridae, some of the coloration is from excretory deposits. Color patterns in Lepidoptera have been the subject of extensive studies, especially for butterflies, but also for some of the moths.

Lepidopteran wing shapes can vary considerably, although the typical form is of four similar wings, with the forewings usually larger than the hindwings. Some unusual species have the hindwings greatly reduced in a few cases, or extremely narrowed as in the Old World tropical burnet-like moths of the family Himantopteridae (superfamily Zygaenoidea) and the Amazonian *Copiopteryx* moths (Saturniidae). There are a few rare examples where the hindwings are almost completely atrophied (e.g., some wasp moths, subfamily Ctenuchinae, family Arctiidae), and likewise even for the forewings among a few brachypterous species. For typical lepidopterans there also are a variety of wing shapes that are encountered, from the more average shape as found in most Noctuidae, for example, to the tailed hindwings of swallowtails (Papilionidae), or very pointed wings as in some tropical burnet moths (Zygaenidae), or the split wings found in plume moths (Pterophoridae), and the even more split many-plumed moths (Alucitidae), where each wing vein is separated. Many of the Microlepidoptera have very long hair-like fringe scales along the wing edges, particularly on the hindwings, as in Gelechioidea families and many of the leafminers in particular.

Wing venation in Lepidoptera has been used for classification since the time of Linnaeus. Most families have wing venation that can help to identify them, although we now also use many other characters of the body that often are more reliable, since wing venation can vary to some extent even within some species. The more advanced groups display venation that is more reduced in the number of veins in the hindwings. Some moths, particularly the tiny leafminer groups (e.g., Nepticulidae, Opostegidae, Tischeriidae, Heliozelidae, Gracillariidae, Bucculatricidae, among others), often have greatly reduced venation in both fore- and hindwings. In homoneurous venation, the fore- and hindwings have similar venation, while more importantly, the hindwing is "locked" to the forewing in flight by what is called a jugum, rather than the more evolved and complicated frenulum and retinaculum wing-locking mechanism of the advanced families of Lepidoptera. The most highly evolved wing-locking mechanism is found in most clearwing moths, family Sesiidae, where there is not just a frenulum-retinaculum arrangement but the entire mesal margins of the fore- and hindwings are recurved to interlock. Butterflies have a humeral lobe wing-coupling mechanism.

Body structure in Lepidoptera adults includes a head, thorax and abdomen, as in other insects, but all covered in lepidopteran scales. The head usually has large compound eyes and prominent labial palpi (one tropical Asian family, the Amphitheridae, has the compound eyes of males split in half). Labial palpi typically are 3-segmented and upcurved, but great variation exists in different Lepidoptera families. Maxillary palpi, contrastingly, are mostly small or even vestigial (sometimes absent), while the most primitive groups have 5-segmented maxillary palpi. Lepidoptera have sucking mouthparts as adults, except for the most primitive families (Micropterigidae, Agathiphagidae, and Heterobathmiidae), which have retained mandibular mouthparts (Eriocraniidae have a reduced haustellum and vestigial mandibles). The proboscis, or tongue of typical adult Lepidoptera, more correctly termed a haustellum, is composed of two parts (galeae) that interlock to form a sucking tube, usually curled between or beneath the labial palpi. While some moths have the haustellum greatly reduced and very short (even vestigial or absent in some non-feeding Saturniidae, for example), some moths and butterflies have a very long haustellum, possibly developed to reach nectar sources in long-stemmed flowers. The longest known haustella are in some hawk moth (Sphingidae) species, where lengths of up to 30 cm are known.

The lepidopteran head has various other structures (or lack thereof) in different families, all of which are in part used to define the various families, as for example, ocelli and chaetosemata sensory organs near the antennal bases, and maxillary palpi: these vary in different families and sometimes are atrophied or even completely absent. The antennae also vary among different families, or even among different genera within a family, with short or very long antennae. Although moths typically have antennae of many segments that extend to fine points and butterflies have antennae with terminal knobs or clubs, there are exceptions among some moths (e.g., agaristine Noctuidae and Castniidae have clubbed antennae) and even many skippers (Hesperiidae) have curved clubs that also resemble some moth antennae (e.g., Sematuridae and Uraniidae). Very long antennae are typical of the small long horned fairy moths (family Adelidae), and some others like the Asian double eye moths (family Amphitheridae) and most of the tropical longhorned moths (family Lecithoceridae). Antennal structure also varies considerably, from simple form to complex bipectinate antennae (even quadripectinate) as found in many emperor moths (Saturniidae), or greatly thickened as in most clearwing moths (Sesiidae) and hawk moths (Sphingidae). The antennae of male Saturniidae are particularly complex and attuned to dedect faint pheromone plumes from females.

The thorax of adult lepidopterans has the usual three pairs of thoracic legs, also covered with scales. Butterflies of the family Nymphalidae typically use only the posterior two pairs of thoracic legs for walking, although they possess all three pairs of legs. The tibiae and femora usually have spurs on the end of the segment and this has been used to classify various families, particularly the tibial spurs, which vary in number in different families. The usually 5-segmented tarsi have two hook-like tarsal claws on the last segment. The main thoracic structures of Lepidoptera, however, are the enlarged wings of most species. Brachypterous species were already mentioned earlier, but most Lepidoptera have well developed wings for active flight. Some females, however, are flightless and without wings, particularly in the family Psychidae, and some species of geometer moths (Geometridae) and tussock moths (Lymantriidae). In the bagworm moths, family Psychidae (Tineoidea), the females are even larviform and remain within the larval shelter and cocoon as adults, waiting for the winged males to find them. Like many Lepidoptera, the female bagworm moths emit a pheromone to attract the males. Among the emperor moths (Saturniidae), even faint pheromone scents have been shown to attract males from up to 20 miles downwind from a female.

The abdomen of adult Lepidoptera is typically elongated, composed of up to ten segments, usually with the basal segment and the most distal segments very reduced. The distal segments also usually are reduced to integrate with the genitalic attachments (Fig. 84). The main characters of lepidopteran species identification involve the usually complex genitalia of male and female adults. Lepidoptera have some of the most complex genital structures of any insect group, both in the males and the females. Some of the more bizarre examples of Lepidoptera genitalia involve such things are complicated spines and setae of males, plus variously shaped claspers, and in some females the amazing elongation of the ductus bursae into an extremely long, thin and convoluted tube, as in some Choreutidae (especially the genus *Brenthia*). In Gelechiidae, many of the species have asymmetrical male genitalia, where one clasper is larger than the other. Among butterflies, the parnassians (subfamily Parnassiinae, Papilionidae) and also some Acraeinae (Nymphalidae), have the strange trait of the male adding a post-copulatory plug or covering (called a sphragis) to the female abdomen, preventing further mating by the female.

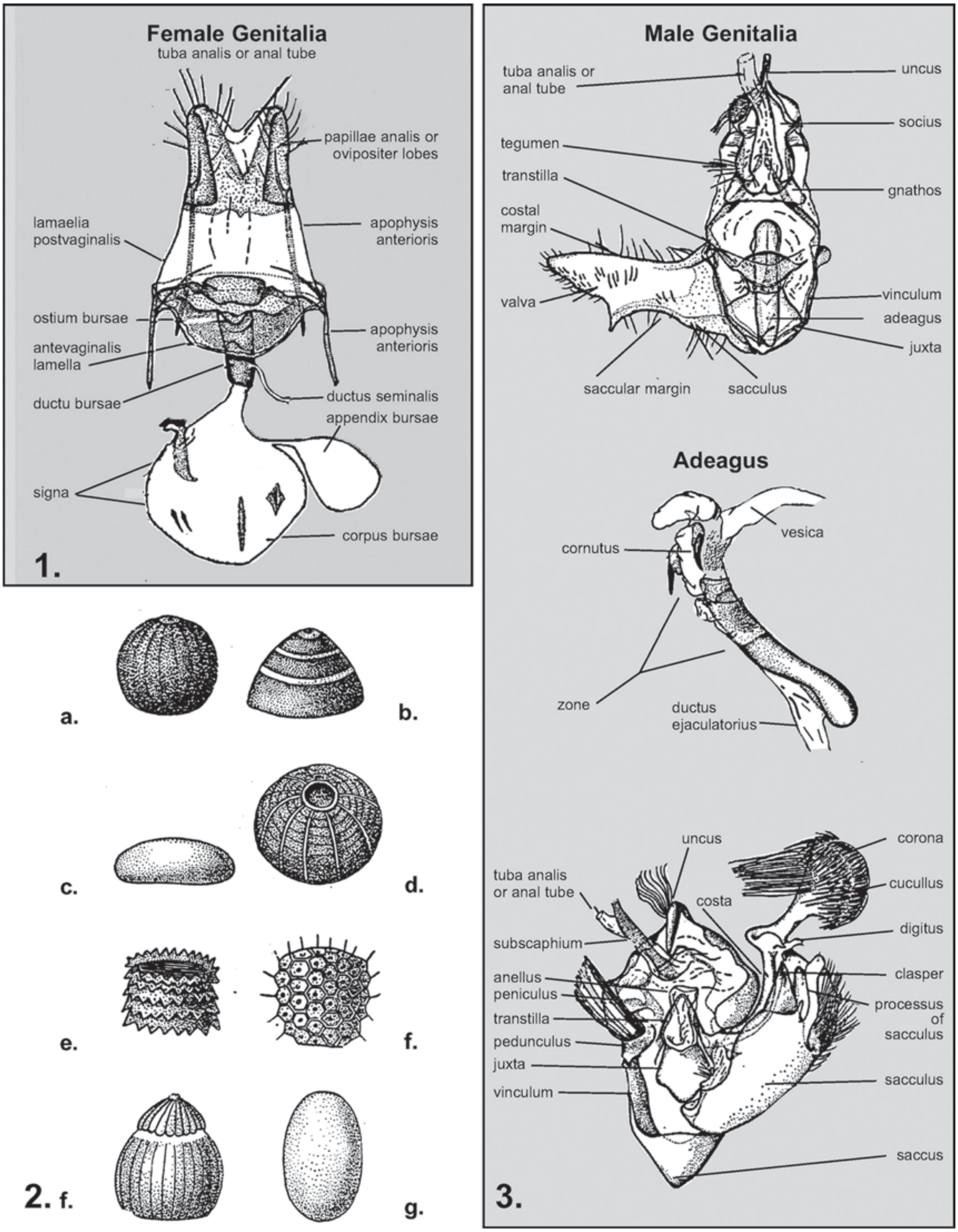
Larvae

While adult Lepidoptera present a large array of characters used in classification, the larvae have a completely different set of characters (Fig. 85). In fact larval classification often conflicts with trends one finds in adult classification. Lepidopteran larvae have mandibles for chewing, and are unique in having specialized abdominal legs, called prolegs, which usually have ventral hooked setae called crochets. While the similar appearing sawflies (Symphyta), in the Hymenoptera, are also caterpillar-like, they do not have the lepidopteran crochets and also have too many prolegs, usually 6–7 pairs plus the rear pair, while Lepidoptera typically have only four pairs of prolegs plus a rear pair. The only known exceptions with supplemental prolegs in Lepidoptera occur in one of the families of slug caterpillars, Dalceridae, where late instar larvae have six pairs of rudimentary prolegs. Contrarily, reduction exceptions are more common, where larvae have fewer prolegs in unusual cases, as in some Noctuidae and most Geometridae where there usually are only a single pair of prolegs plus the rear pair. Most leafminers also have evolved proleg reduction and even thoracic leg reductions, like in Gracillariidae and Nepticulidae, where the minute larvae have three or fewer pairs of vestigial prolegs, or are almost devoid of recognizable prolegs (the feeding style inside of leaves has produced the evolutionary reduction of the unneeded legs in these cases). Likewise, most of the slug-like caterpillars (e.g., Zygaenoidea, Limacodidae, and Megalopygidae) utilize the entire ventral body surface as a moving platform, much like slugs do, such that the prolegs are often reduced to mere bumps on the body.

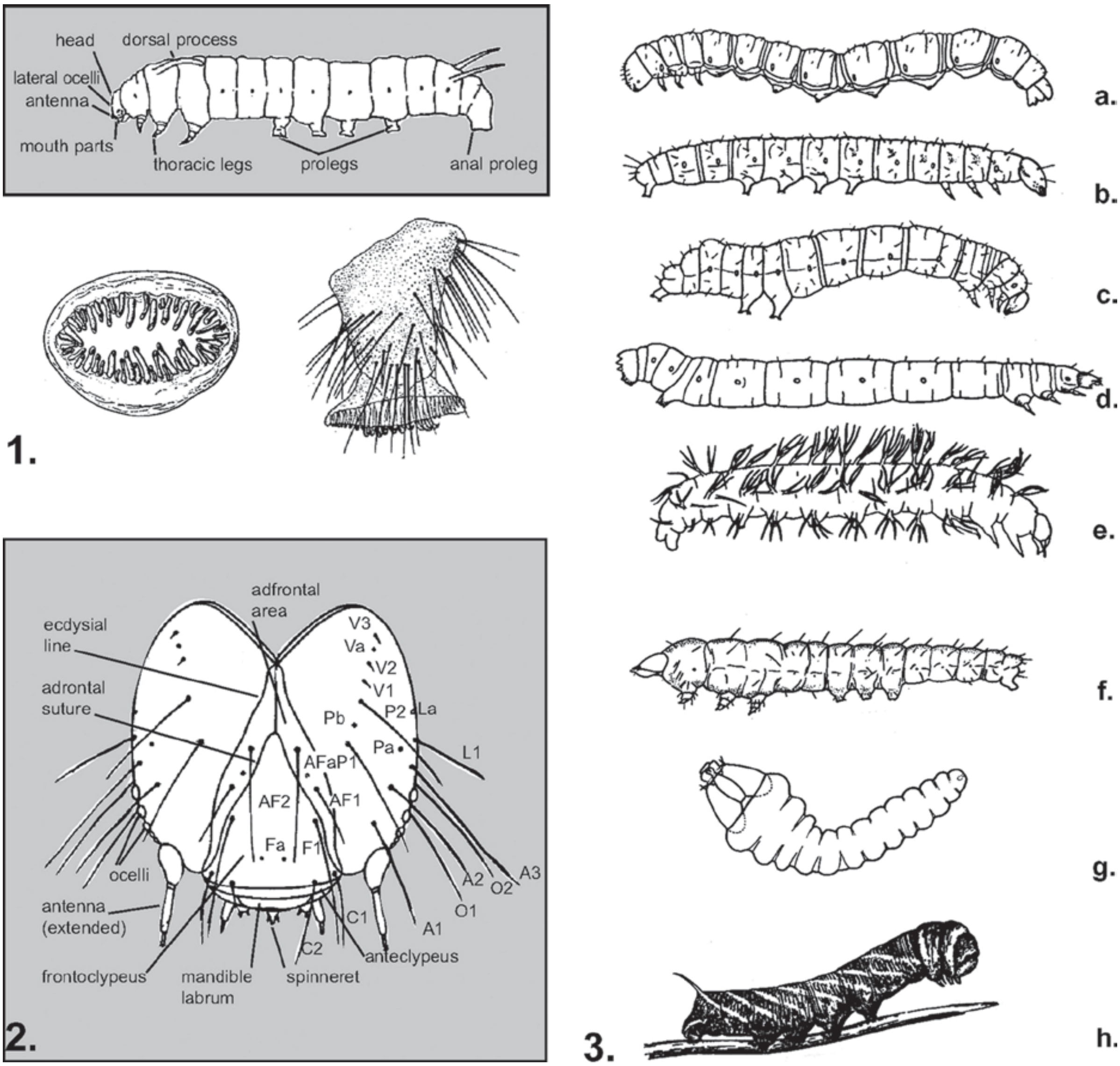
Lepidoptera larvae have their own set of characters, in particular the array of head and body setae and spines that can be mapped (called chaetotaxy) and usually are diagnostic for particular families. Many species can be identified by their larvae, but only for those where the larvae are known and have been studied. Some caterpillars are extremely large and grotesque, like the hickory horned devil, which is the larva of the American regal moth (*Citheronia regalis*, Saturniidae). Some hawk moth larvae, or hornworms (Sphingidae) can also be very large, as well as some of the larger carpenter worm larvae (Cossidae). Leafminers, contrarily, are among the tiniest of Lepidoptera larvae. The vast majority of Lepidoptera, however, remain unknown biologically and their larvae have never been seen or studied, nor are their hostplants known. Thus, much research remains to be done on Lepidoptera larvae and their biologies. It can be noted here that even such large moths as the white witch moth, *Thysania agrippina* (Noctuidae), mentioned earlier as the species with the largest known wingspan of any lepidopteran, remains completely unknown biologically, and that even though the adults are commonly attracted to lights in the Neotropical lowland jungles.

Proposed phylogenies based on adults often are not substantiated when larvae are compared, and this often is the cause of taxonomic argument among specialists, particularly for those unfamiliar with larvae or who do not study larvae but instead rely only on adult characters. The kind of controversies that arise between larval taxonomy and adult taxonomy, where the adult taxonomists may not know the larvae very well or even ignore their characters, can be seen in the Noctuidae, where a recent larval work for European owlet moths has different conclusions for many of the subfamilies from what those studying only adult characters have published.

Since Lepidoptera larvae spend most of their time feeding in microhabitats far different than their adults prefer, larval features are often attuned to their needs with very specific body characters. Thus, larvae that feed inside plants usually have reduced setae and smaller legs than do those that feed externally on plants. Some bizarre shapes and life styles are known among Lepidoptera larvae. For example, the only known aggressively carnivorous lepidopteran larvae occur in Hawaii: species of the genus *Eupithecia* (Geometridae) capture flies as food using massive, modified tarsal claws. A few other moth larvae are also carnivorous on aphids and scale insects, like in the genus



Butterflies and Moths (Lepidoptera), Figure 84 **Lepidopteran reproductive structures and eggs; 1. Female genital morphology (after Hodges, 1971); 2. Typical lepidopteran eggs: upper left) Noctuidae *(Amathes)*, upper right) Notodontidae (Hoplitis), second row left) Notodontidae *(Phoesia)*, second row right) Noctuidae *(Naenia),* third row left) Lycaenidae *(Thecla)*, third row right) Nymphalidae *(Limentis),* bottom row left) Noctuidae *(Spodoptera)*, bottom row right) Zygaenidae *(Zygaena)* (after Zagulajev, 1978); 3. Male genital morphology (two types), with detail of typical aedeagus (after Hodges, 1971).**



Butterflies and Moths (Lepidoptera), Figure 85 **Lepidoptera larvae: 1. Larval morphology, with details of crochets and proleg (after Chapman, 1969; and Mellis and Zocchi, 1958); 2. Larval head morphology (after Common, 1970); 3. Typical lepidopteran larval types: (a) Hepialidae, (b) Tortricidae, (c) Noctuidae, (d) Geometridae, (e) Pyralidae, aquatic (Nymphulinae), (f) Gracillariidae (late instar), (g) Gracillariidae (early instar, Phyllonorycter), (h) Sphingidae) (a-d, after Tillyard, 1926; e, after Bourgogne, 1951; f-g, after Patocka, 1980; h, after Lutz, 1935).**

Pyroderces (Cosmopterigidae), but they do not capture winged insects in rapid attacks like the larvae in Hawaii. Carnivorous butterfly larvae are known in the Asian genus *Liphyra*, one of the more primitive genera in Lycaenidae, where larvae feed on ant larvae yet are tolerated by the ants they live with because of the secretions the larvae give the ants.

Eggs

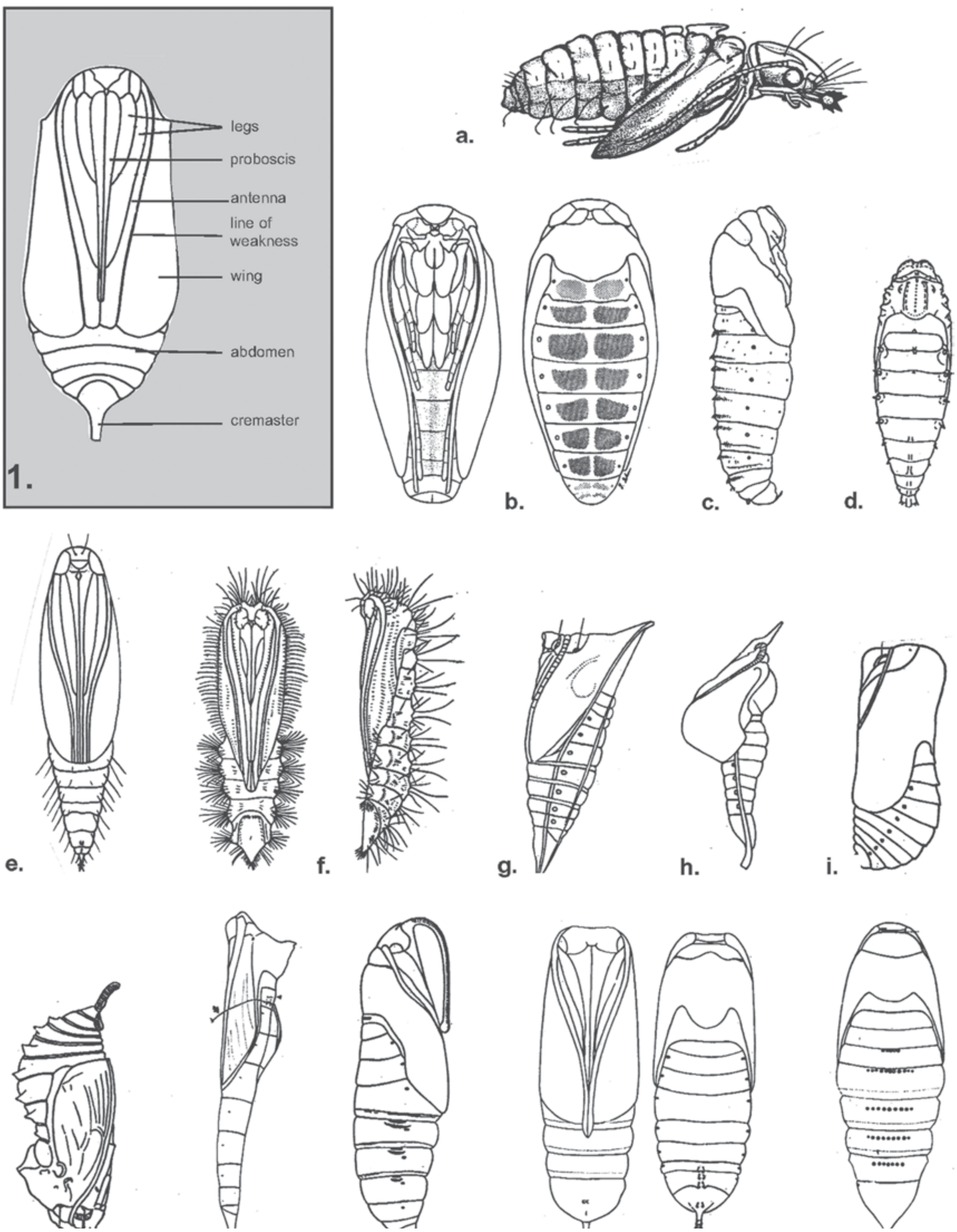
Lepidoptera eggs usually are rounded and relatively small (about 1 mm), but some groups have flattened eggs, as for example among the Tortricidae (Fig. 84). Many butterfly eggs are upright and ribbed. All Lepidoptera eggs have a tough shell, called the chorion, plus various degrees of external sculpturing and usually four sperm entry holes, or micropyles (up to 16 in some Notodontidae). The largest lepidopteran eggs are found among some of the emperor moth species (Saturniidae) and hawk moths (Sphingidae), up to about 4 mm in diameter (e.g., 4 mm in *Argema mittrei* and 3.2 mm in *Attacus crameri*, Saturniidae).

Eggs usually are laid singly or in groups directly onto host leaves or stems, but some moth females insert the eggs into plant tissues using a very strong ovipositor, particularly among the more primitive moths (e.g., Eriocraniidae). The average lepidopteran female lays about 100–200 eggs. Species with the greatest numbers of eggs per female are known among the ghost moths (Hepialidae), where some females have been recorded with close to 50,000 minute eggs: these moths spray their eggs randomly about while flying over likely hosts, leaving it to the young caterpillars to find their hostplants to feed on upon hatching.

Although no lepidopteran has been discovered where the adults care for eggs or larvae, as is known in some beetles, many lay their eggs in secretive sites or devise other protective solutions, and some species have developed protective commensal relationships with other insects. A notable case involves the blue butterflies (Lycaenidae), where ants typically tend to the larvae and protect them from predators and parasitoids while getting desirable secretions from the larvae. Ovovivipary, however, is known in a few groups of lepidopterans, notably a few Tineidae, Psychidae, Coleophoridae, and Cosmopterigidae. Psychidae in particular have numerous species that are parthenogenetic. A modified form of this phenomenon is known among some butterflies (e.g., some *Colias* and *Euchloe* (Pieridae), *Parnassius* (Papilionidae), and *Erebia* (Nymphalidae)), where living larvae (usually only one) are present in the oviduct of the female and presumably remain there until the female dies, as no actual deposition of living larvae has been witnessed in butterflies.

Pupae

The pupal stage varies in form (Fig. 86), from those with loose legs, as in the primitive moths such as Eriocraniidae, to the most advanced groups where the legs of the future adult are fused to the pupal shell. Many of the primitive families, as also Tortricidae and Sesiidae for example, have noticeable dorsal spines on the abdomen of the pupa, used to help the pupa wiggle out of the cocoon when the adult emerges. Most Lepidoptera pupae have a cremaster of strong spines or protrusions at the distal end of the abdomen. Some of the Microlepidoptera pupae have only thin hooked setae as a cremaster-like structure. While most Lepidoptera larvae spin a cocoon before transforming into the pupal stage, many groups have an exposed pupa, as in most butterflies and some advanced moths like Noctuidae. While most pupation and cocoon-making is on the hostplant, many pupate among debris or in the ground, as for example most of the hawk moth larvae (Sphingidae) make a pupal cell in soil, from which the adult must burrow upwards to escape by means of temporarily retaining the hard pupal head covering to push through the soil. The leafminers pupate within their leaf mine for the most part. Many butterflies simply hang their pupae upside down from the cremaster plug of silk the larva spins just before pupation. Some butterfly larvae (mainly Papilionidae) spin a silken girdle for the pupa (also in Hedylidae and some Geometridae), thus keeping it upright at the pupation site. Bagworms (Psychidae) pupate within the larval shelter (or bag), and likewise for such families as the casebearer moths (Coleophoridae) and some sackbearer moths (Mimallonidae). Most leaf



Butterflies and Moths (Lepidoptera), Figure 86 **Lepidoptera pupae: 1. Pupal morphology (after Urguart, 1960), and typical forms: (a) Eriocraniidae, (b) Opostegidae (front and back), (c) Psychidae, (d) Elachistidae, (e) Pyralidae, (f) Pterophoridae (front and side), (g) Papilionidae, (h) Pieridae, 1951), (i) Lycaenidae, (j) Nymphalidae, (k) Hedylidae, (l) Sphingidae, (m) Dioptidae (front and back), (n) Noctuidae (a, e, after Patocka, 1980; b, after Davis, 1989; c, l–n, after Mosher, 1916; d, after Falkovitsh, 1981; f, after Zagulajev, 1986; g–i, after Bourgogne, 1951; j, after Tillyard, 1926; k, after Scoble and Aiello, 1990).**

webbers, leaf tiers, and leafrollers pupate within the larval shelter (mostly in the families Oecophoridae, Gelechiidae, Pyralidae, and Tortricidae).

Ecology

Lepidoptera biology includes many strange behavioral traits and biologies that have evolved in different groups and species. Whereas most lepidopterans have rather drab colors that lend themselves to good camouflaging when at rest on leaves or trees, other species have adopted bright coloration or startle techniques for protection. Butterflies, of course, as some day-flying moths, use bright coloration or color spots for mating behavior as well. For example, the bright blues of the *morpho* butterflies (Morphinae, Nymphalidae), already mentioned for their scale structure, are used by males to keep other males away from their territories, while females may also respond to the bright coloration during mating rituals. Likewise, the bright coloration of *morpho* butterflies also involves startle defense, since roosting males will congregate on a branch and, when disturbed, flash their blue colors together (the "flash and dazzle" defense), probably scaring away many predators in this way. The *morpho* flight pattern, a rather bouncing kind of rapid flight in males, also makes it difficult for predators to find them on the wing, since the blue color flashes only every few seconds or so as the butterfly flaps its wings when flying through the forest, thus showing only intermittantly where the butterfly is at any instant. However, some birds have learned how to capture them anyway. Some butterflies, especially among the hairstreaks (Lycaenidae), use their hindwing tails as "false heads" to confuse predators, and many of the other tailed butterflies may have developed tails for this purpose as well, and likewise for some of the diurnal tailed moths (e.g., Sematuridae and Uraniidae).

Among the moths, eye spots are well known markings among those species that are not completely colored for camouflage. The many emperor moths (Saturniidae) which have large bright eyespots on the hindwings, use startle techniques to evade predators, since these moths will flash their hindwings when distrubed from their normal resting positions where the hindwings are hidden beneath the more camouflaged coloration of the forewings. Butterflies use eye spots for startle effects as well, as for example among the owl butterflies of the genus *Caligo* (Brassolinae, Nymphalidae) of the American tropics, and even such species as the European peacock butterfly, *Inachisio* (Nymphalidae).

Other species, both moths and butterflies, use bright coloration not for startle effects but as warning colors. One of the reasons the warning colors are recognized by predators is that the bodies of these Lepidoptera (or other insects) contain alkaloids their larvae have embibed from their hostplants, and thus the adults are poisonous to most predators like birds and frogs. For example, monarch butterflies (*Danaus plexippus*, Nymphalidae) and relatives contain poisonous alkaloids (heart poisons for predators), and most birds will not eat the adults once they learn that brightly colored insects are distasteful. Likewise, for such moths as the very colorful flag moths, subfamily Pericopinae (Arctiidae), which are believed to all be poisonous as well, due to bodily alkaloids. Such moths as Zygaenidae, which are mostly also very colorful, have phytocyanides in their bodies. Some adults of various Lepidoptera groups also imbibe plant chemicals from nectar sources.

A varied group of lepidopterans have evolved the use of various plant poisons (mostly alkaloids, glycosides, phytocyanides, and cardenolides) as defensive agents. Monarch butterflies (Danainae, Nymphalidae), as already noted, sequester alkaloids from their hostplants, milkweeds (Asclepiadaceae) by the feeding of their larvae. Burnet moths (Zygaenidae) and *Heliconius* butterflies (Heliconiinae, Nymphalidae), among others, do the same for plant cyanides, as already noted for larval defense. In the case of the burnet moths, the adults are even somewhat resistant to the fumes of cyanide gas, since they will survive in a cyanide vial much longer than any other Lepidoptera can. Many of these and other traits in Lepidoptera have evolved as defensive measures against birds and other predators, and parasitoids. There are also many other forms of defense that lepidopterans use, such as death feigning (e.g., many emperor moths will do this if disturbed), and excretion of alkaloids from wing bases or abdominal glands (e.g., many Arctiidae do this, especially in Pericopinae and the wasp moths, subfamilies Ctenuchinae and Syntominae). Additional adult defenses include such things as loud noises, as are found in some brush-footed butterflies in the genus *Hamadryas* (Nymphalidae), where the adults make a clicking or crackling sound when they fly, possibly scaring bird predators in this way.

Mimicry with other insects and among each other is a further use of color and maculation as part of defense strategies in Lepidoptera. Mimicry among Lepidoptera involves various species looking similar to one or more that are poisonous by their bodily alkaloids, as noted earlier. Thus, a poisonous tiger moth (Arctiidae), or butterfly like the monarch, is the model that other lepidopterans have taken the appearance to obtain the same defensive protection yet without themselves being poisonous. For example, in the case of the monarch there is the well known North American mimic, the Viceroy butterfly, *Limenitis archippus* (Nymphalidae), which itself is not distasteful or poisonous to birds and other predators. Extensive mimicry complexes occur, particularly in the tropics, especially modelled around some of the flag moths (subfamily Pericopinae, family Arctiidae). Likewise, there are also mimicry complexes modelled after other insects that are avoided by birds and other predators, such as polistine wasps (Vespidae, Hymenoptera) and stink bugs (Pentatomidae, Hemiptera). Thus, we find many so-called wasp moths, subfamilies Ctenuchinae and Syntominae (family Arctiidae), that appear remarkably like real species of wasps, plus other moths both among Arctiidae and Pyralidae that have modelled themselves after some bugs or beetles. The wasp moths include mimics that are among the most precise to toxic models known in Lepidoptera, and many appear and behave so much like true wasps that on the wing one cannot be sure what they are. All these kinds of cases involve what is called Müllerian mimicry, where the mimic has a clear benefit by looking like the model. There is also simple mimicry, called Batesian mimicry, where the mimics look like various models and each other, but there is no apparent benefit evident like that of having a poisonous model. However, there may be some benefit to mimicking a color pattern that has been found to be advantageous for some reason. For example, there is a large mimicry complex of swallowtail butterflies (Papilionidae) and swallowtail moths (*Urania*, Uraniidae) in the Neotropics, yet where none of the possible models are poisonous but do all have variegated patterns of striped green and black. Likewise, there is a similar mimicry complex in New Guinea involving blue Uraniidae (genus *Alcides*) and several swallowtail butterflies (*Papilio laglaizei*, *P. ulysses*, and *P. pericles*, and even *P. woodfordi*), where all have bands or patches of blue color surrounded by black bands.

Although most Lepidoptera larvae use camouflage for protection, others use startle effects or bright coloration as a protective strategy, much as do some adult lepidopterans. For example, the bright colors of some hawk moth larvae such as the giant gray sphinx of the Neotropics, also called the frangipani sphinx (*Pseudosphinx tetrio*, Sphingidae), where the large larvae are banded in bright yellow and black, with an orange head, are thought to possibly mimic coral snakes, since they also move their bodies rapidly when disturbed and will even "strike" at a predator like a snake. Some make noises if disturbed, as for example in the death-head sphinx, *Acherontia atropos* (Sphingidae), mentioned earlier for its adult noises, which also makes noises in the larval stage using its mandibles; and likewise for some Saturniidae larvae and others. Even some larvae among the Microlepidoptera make noises when disturbed, as for example in the larvae of *Diurnea fagella* (Oecophoridae), of Europe, where larvae scrap their claws on a leaf surface. Pupal noises are also known among some lepidopterans. Some Lepidoptera pupae also can make rasping sounds by moving their abdominal segments together.

Larval defense also takes on the form of ferocious appearance and head movements, as for example in the large hickory horned devil, *Citheronia regalis* (Saturniidae), of North America, which not only has large spined horns but will rear its head swiftly back to hit anything that grabs its body. A number of tropical hawk moth larvae (Sphingidae) rear up when disturbed and retract their head into a large thorax, while thoracic eye spots make them then appear like snake heads. One of the most accurate snake mimics, or "viper worms," is the larva of the Neotropical hawk moth, *Hemeroplanes ornatus* (Sphingidae). As with adults, some larvae also have poisonous alkaloids as defensive measures that back up their bright colors, as in the wasp moths (Ctenuchinae) of the American tropics and their Old World cousins, wasp moths in the subfamily Syntominae (family Arctiidae), and the American flag moth larvae (subfamily Pericopinae), for example, where larvae can also be colorful.

Some larvae also make use of defense in numbers, thus feeding in large masses so any predator finding them will undoubtedly still enable some to escape: for example, many of the tent caterpillars (Lasiocampidae) feed in large masses and make tent protective webs as well. The same massing behavior is also known in other lepidopteran larvae, like the processionary caterpillars of the subfamily Thaumetopoeinae (Notodontidae), famous for traveling in a long single file when moving from one host tree to another, both in Europe and in tropical species of the group. The unusual tropical Himantopteridae (Zygaenoidea) also congregate as masses of larvae.

Other larval defenses include poisonous setae, which can be very potent for persons particularly allergic to the "stings." There are a number of such stinging caterpillars in North America, as also in other faunal regions, particularly in the moth families Limacodidae, Megalopygidae, and Saturniidae. Setae of tussock moth larvae (Lymantriidae) are also irritating in some cases. Even deaths have occurred by persons in the tropics from contact with some caterpillars of the emperor moths (Saturniidae), especially the Brazilian *Lonomia* sp. (even the adults in this group have irritating wing scales). The larvae of this genus have poison glands that inject a chemical, when touched, that triggers human blood coagulation problems and also haemorrhagic reactions in some cases, thus causing some of the reported deaths in Brazil. Another potent genus among the emperor moths, both for larval poisonous spines and irritation from adult scales, is *Hylesia* (Saturniidae). These so-called stinging caterpillars are well protected in this way from most predators, but still can be subject to the tiny parasitoid wasps that can insert their eggs between larval spines, or circumvent their defenses by getting to the egg stage instead.

The topic of stinging caterpillars is called lepidopterism in the medical profession, and deals with allergic reactions to certain poisons. The genus *Lonomia* is part of the New World subfamily Hemileucinae (Saturniidae) and most all of these have poisonous spines, as for example the io moth (*Automerisio*) of North America and the several hundred species in this group from South America. The slug caterpillars, families Limacodidae and Megalopygidae, are likewise well known for their poisonous spines. Some stinging caterpillars even spin the left over spines from their larval skin into their cocoon and protect the cocoon in this way as well, as for example in the *Lonomia* moths from Brazil. Lepidopterism is also known in other families, even in the Australian Anthelidae, where contact with cocoons of one species can cause allergic reactions due to urticating setae.

Commensal relationships among larvae, where some benefit is obtained from the interaction with another insect, is a further form of protection for some lepidopterans. Many blues and relatives (Lycaenidae) have commensal relations as larvae with ants, so-called myrmecophily. The larvae obtain protection from predators and even parasitoids in many cases, and the ants obtain wanted secretions from the larvae, much like we do with milk cows. Some metalmark butterflies (Riodinidae) also have myrmecophilous larvae.

Flight is what is most typical of Lepidoptera, besides their often colorful wing maculation. Some groups, like the clearwing moths (Sesiidae) and hawk moths (Sphingidae), have developed very strong wings used for often exceedingly fast flight. Among the fastest known lepidopterans are some in the family Sphingidae, especially in some of the day-flying species, where flight speeds to 35 mph are known. While most lepidopteran flight is rather slow, with slowly flapping wings and some gliding, the fastest fliers and hoverers have exceedingly rapid wing beats. For example, the hawk moths (Sphingidae) typically fly like hummingbirds and can hover in place while feeding on flower nectar. Butterflies can hover at nectar sources to some extent as well, by flapping their wings, but only hawk moths have the excessively rapid wing beat that allows hummingbird-like steady hovering in place. Even within one family flight behavior can vary considerably among different genera, as for example, in Saturniidae, where most have rather slow lumbering flight behavior, yet in the American genus *Hemileuca* the day-flying males can rival hawk moths in speed of flight. Likewise, male yucca skippers (Megathyminae, family Hesperiidae), mostly in the American Southwest, also typically fly very fast in search of females. Of course, flight in Lepidoptera has been studied extensively, and particularly how this relates to adult mating behavior and migration in butterflies.

Activity regimes among Lepidoptera vary as much as other features of their life histories. While most butterflies are diurnally active as adults and most moths are nocturnal, there are many exceptions. Many butterfly species have particular times of active flight, such as only briefly in the morning or at dusk, or only midday. For example, the Neotropical owl butterflies (*Caligo*, subfamily Brassolinae, Nymphalidae), and their relatives, typically fly at dusk. The related jungle queen butterflies, as in the genus *Stichophthalma* (subfamily Amathusiinae, Nymphalidae) from Southeast Asia, fly in the late afternoon and at dusk, while during most of the day they are to be found at rest in dark thickets in the forest. Likewise, many moths will fly only in the evening hours before midnight, while some fly only before dawn. Some moths are also diurnal and like butterflies, have particular flight periods, as before noon (e.g., most Sesiidae), or at dusk only (most Hepialidae, and some Sphingidae and Saturniidae). Crepuscular moths also include some of the giant butterfly moths (family Castniidae) of the Neotropics, Australia, and Southeast Asia, and also a large number of leafroller moths (family Tortricidae). The Hedylidae, which some consider nocturnal butterflies but are herein retained in Geometroidea, fly at night. All the above is likewise true for larval feeding activity among various groups, with some feeding only at night and others at various times, or only during daylight.

For adults, there is also specialized flight, besides searching for food or mates, like directed migration, as exhibited in such species as the monarch butterfly (*Danaus plexippus*, Nymphalidae) in their migrations in North America to spend winter months in Mexico. Western North American monarchs overwinter in coastal California. Related danaines on Hispaniola, of the genus *Anetia* (Nymphalidae), congregate in the higher elevations of the Dominican Republic. There are many other migratory species recorded, and in all faunal regions. For example, some owlet moths (Noctuidae) in Australia and Europe, snout butterflies (Libytheidae) in North America and Africa, and black danaines (*Euploea* spp., Nymphalidae) in Taiwan, which overwinter in secluded areas protected from sever frosts, like the North American monarchs do. Hawk moths and owlet moths migrate over mountain passes during certain times of the year in Venezuela, as do some butterflies. Some diurnal moths also have migratory flights, like the migrations of *Urania* moths (Uraniidae) in the Neotropics. Many other cases of migrating Lepidoptera are known. Some of the cases of large flights are more seasonal and directed mass movement in relation to population pressure than they are migration in the sense of the complex annual two-way migration sequence as evidenced in the American monarch.

Aggregation is well known with some overwintering butterflies, but there also are mass roostings that some species use during the night, presumably as protection against predators, although this has not been proven conclusively. For example, *Heliconius* butterflies (Nymphalidae) typically roost in large assemblages at night. Likewise, for *morpho* butterflies (Morphinae, Nymphalidae). Roosting behavior has also been documented in other tropical butterflies as well. Few moths have roosting activity like those noted for some butterflies, and most such cases for moths involve resting sites for large groups of adults in one area but not like the dense roosting documented for butterflies. For example, one finds large numbers of grass loopers, genus *Mocis* (Noctuidae), resting together in Florida, which can be startled into mass flight over short distances when disturbed during the day. Likewise, *Nyctemera* tiger moths (Arctiidae) have similar mass startle flight responses in the Oriental tropics when disturbed during the day. Various other owlet moths (Noctuidae), geometer moths (Geometridae), and snout moths (Pyralidae) also rest in groups and fly away in swarms when disturbed during daylight. Most cases of diurnal moths coming to lights at night are due to being disturbed and then going to the nearest light source. There are also cases of cold adaptation techniques where moths at high altitudes or during the winter will mass in large numbers: for example, there are some owlet moths, genus Euxoa (Noctuidae), that do this during cold nights in the North American Rockies, notably recorded as also being a food source for bears.

Among some of the other more bizarre behavior found among the Lepidoptera, one can note the blood sucking activity of one species of owlet moth in the genus *Calyptra* (Noctuidae) from Southeast Asia, which attacks large mammals such as buffalo, cows and deer. This behavior is apparently a development of the eye-frequenting (or lachryphagous) behavior among other Asian moths, mainly Noctuidae and some Geometridae and Pyralidae, but also a few Notodontidae and Thyatiridae, which rest on the edges of the eyes of large mammals and suck eye juices from the surface of the eyes. In the case of the blood sucking species, the haustellum has been modified to pierce skin and suck blood, much as in mosquitoes, a modification from fruit-piercing owlet moths (Noctuidae), like in the Asian genus *Othreis* and the New World *Gonodonta*.

Of all studies on Lepidoptera, besides those on butterfly and moth life histories, those pertaining to population biology and biogeography of butterflies have probably been the most numerous over the years, and include most all aspects of lepidopteran biology, from larval food preferences, to genetics, to mimetic relationships, to seasonality, to taxonomy of the species involved. Many such studies worldwide, many now classic, can be referenced. Among the hundreds of examples are the well known studies on various checkspot butterflies (*Euphydryas* sp., Nymphalidae) in California and other areas of North America. Likewise, studies in North America for Colorado butterflies and the many recent studies on swallowtails (Papilionidae), as well as innumerable similar studies in Japan, Africa, and other regions. In Europe, one has studies like on blues (Lycaenidae), various other British butterflies, and many others. Likewise, innumerable studies have been done on the ecology and population biologies of tropical butterflies. Such studies for moths, however, are much fewer, as for example on European pine looper moths (Geometridae) and California oak moths (Dioptidae), to give just a few examples out of thousands of studies, but mainly on economic species and their control.

Biodiversity

The following notes summarize the main groupings and the 125 extant families of Lepidoptera in the world. The most primitive moths are discussed together, while more advanced families are treated according to their respective superfamilies. Families are listed in the table. The species totals given for each family have been updated to include all valid species described to the year 2000.

The world total number of known species comes to 156,100 species. An estimated additional 100,000 species remain to be discovered and named, mainly from tropical regions of the world, including many of the most imperiled habitats. During the decade from 1990 to 2000, about 8,500 Lepidoptera species were described from all regions, particularly from remote areas of temperate Central Asia and from the tropical forests of Southeast Asia and Central Africa. Thus, the rate of new discoveries and descriptions of new species remains fairly steady, averaging about 850 species per year among Lepidoptera. However, unless larger and more active surveys are made of critical and unknown tropical and other remote regions, and unless the training of more taxonomists to study new material is increased, it will take another 100 years to complete the basic inventory of the remainder of the Lepidoptera not yet identified from among the total extant worldwide fauna of about 255,000 living species. Unfortunately, estimates of yearly forest and other habitat destruction do not leave us 100 years for this inventory to be accomplished in many areas of the world under the most intense human population and development pressures. And likewise, the basic inventories to describe all extant species do not involve detailed biological studies to determine the life histories of these newly discovered species. Even most of the species already described remain unknown biologically, so another larger cadre of researchers is needed to study the biologies involved.

ORDER: LEPIDOPTERA

Suborder: ZEUGLOPTERA

MICROPTERIGOIDEA

MICROPTERIGIDAE - Mandibulate Archaic Moths

Micropteriginae

Sabatincinae

Suborder: AGLOSSATA

AGATHIPHAGOIDEA

AGATHIPHAGIDAE - Kauri Moths

Suborder: HETEROBATHMIINA

HETEROBATHMIOIDEA

HETEROBATHMIIDAE - Valdivian Archaic Moths

Suborder: GLOSSATA

Cohort: DACNONYPHA

Infraorder: DACNONYPHA

ERIOCRANIOIDEA

ERIOCRANIIDAE - Sparkling Archaic Sun Moths

ACANTHOPTEROCTETIDAE - Archaic Sun Moths

Acanthopteroctetinae

Catapteriginae

Infraorder LOPHOCORONINA

LOPHOCORONOIDEA

LOPHOCORONIDAE - Australian Archaic Sun Moths

Cohort: MYOGLOSSATA

Subcohort: MYOGLOSSATA

Infraorder: NEOPSEUSTINA

NEOPSEUSTOIDEA

NEOPSEUSTIDAE - Archaic Bell Moths

Subcohort: NEOLEPIDOPTERA

Infraorder: EXOPORIA

MNESARCHAEOIDEA

MNESARCHAEIDAE - New Zealand Primitive Moths

HEPIALOIDEA

NEOTHEORIDAE - Amazonian Primitive Ghost Moths

ANOMOSETIDAE - Australian Primitive Ghost Moths

PROTOTHEORIDAE - African Primitive Ghost Moths

HEPIALIDAE - Ghost Moths

PALAEOSETIDAE - Miniature Ghost Moths

Infraorder: HETERONEURA

Division: MONOTRYSIA

Section: NEPTICULINA

ANDESIANOIDEA

ANDESIANIDAE - Valdivian Forest Moths

NEPTICULOIDEA

NEPTICULIDAE - Pygmy Moths

Pectinivalvinae

Nepticulinae
OPOSTEGIDAE - Eye-Cap Moths
TISCHERIOIDEA
TISCHERIIDAE - Trumpet Leafminer Moths
PALAEPHATOIDEA
PALAEPHATIDAE - Gondwanaland Moths
Section: INCURVARIINA
INCURVARIOIDEA
INCURVARIIDAE - Leafcutter Moths
Incurvariinae
Crinopteryginae
CECIDOSIDAE - Gall Moths
PRODOXIDAE - Yucca Moths
Lamproniinae
Prodoxinae
ADELIDAE - Longhorned Fairy Moths
Nematopogoninae
Adelinae
HELIOZELIDAE - Shield Bearer Moths
Division: DITRYSIA
Section: TINEINA
Subsection: TINEINA
TINEOIDEA
Series Tineiformes
ACROLOPHIDAE - Tube Moths
Amydriinae
Acrolophinae
TINEIDAE - Fungus Moths
Euplocaminae
Myrmecozelinae
Harmaclоninae
Meessiinae
Dryadaulinae
Scardiinae
Nemapogoninae
Tineinae
Setomorphinae
Perissomasticinae
Hapsiferinae
Hieroxestinae
Erechthiinae
Siloscinae
Stathmopolitinae
Teichobiinae
ERIOCOTTIDAE - Old World Spiny-Winged Moths
Eriocottinae
Compsocteninae
PSYCHIDAE - Bagworm Moths
Lypusinae
Naryciinae
Taleporiinae
Penestoglossinae
Psychinae
Oiketicinae
ARRHENOPHANIDAE - Tropical Lattice Moths
Series Gracillariiformes
AMPHITHERIDAE - Double-Eye Moths
SCHRECKENSTEINIIDAE - Bristle-Legged Moths
DOUGLASIIDAE - Douglas Moths
BUCCULATRICIDAE - Ribbed-Cocoon Maker Moths
GRACILLARIIDAE - Leafminer Moths
Gracillariinae
Lithocolletinae
Phyllocnistinae
GELECHIOIDEA
OECOPHORIDAE - Concealer Moths
Depressariinae
Ethmiinae
Peleopodinae
Autostichinae
Xyloryctinae
Stenomatinae
Oecophorinae
Hypertrophinae
Chimabachinae
Deuterogoniinae
LECITHOCERIDAE - Tropical Longhorned Moths
Ceuthomadarinae
Oditinae
Lecithocerinae
Torodorinae
ELACHISTIDAE - Grass Miner Moths
Perittiinae
Elachistinae
PTEROLONCHIDAE- Lance-Wing Moths
GELECHIIDAE - Twirler Moths
Physoptilinae
Gelechiinae
Pexicopiinae

Dichomeridinae
BLASTOBASIDAE - Scavenger Moths
Holcocerinae
Blastobasinae
COLEOPHORIDAE - Casebearer Moths
Coleophorinae
Batrachedrinae
MOMPHIDAE - Mompha Moths
AGONOXENIDAE - Palm Moths
Agonoxeninae
Blastodacninae
COSMOPTERIGIDAE - Cosmet Moths
Antequerinae
Cosmopteriginae
Chrysopeleiinae
SCYTHRIDIDAE - Flower Moths
COPROMORPHOIDEA
COPROMORPHIDAE - Tropical Fruitworm Moths
ALUCITIDAE - Many-Plumed Moths
CARPOSINIDAE - Fruitworm Moths
EPERMENIIDAE - Fringe-Tufted Moths
Epermeniinae
Ochromolopinae
YPONOMEUTOIDEA
OCHSENHEIMERIIDAE - Cereal Stem Moths
GLYPHIPTERIGIDAE - Sedge Moths
Orthoteliinae
Glyphipteriginae
PLUTELLIDAE - Diamondback Moths
Ypsolophinae
Plutellinae
Scythropiinae
Praydinae
ATTEVIDAE - Tropical Ermine Moths
YPONOMEUTIDAE - Ermine Moths
Saridoscelinae
Yponomeutinae
Cedestinae
ARGYRESTHIIDAE - Shiny Head-Standing Moths
LYONETIIDAE - Lyonet Moths
Cemiostominae
Lyonetiinae
Bedelliinae
ACROLEPIIDAE - False Diamondback Moths
HELIODINIDAE - Sun Moths
IMMOIDEA
IMMIDAE - Imma Moths
PYRALOIDEA
HYBLAEIDAE - Teak Moths
THYRIDIDAE - Picture-Winged Leaf Moths
Simaethistinae
Whalleyaninae
Argyrotypinae
Thyridinae
Siculodinae
Striglininae
PYRALIDAE - Snout Moths
Group Crambinina
Crambinae
Schoenobiinae
Cybalomiinae
Linostinae
Scopariinae
Musotiminae
Midilinae
Nymphulinae
Odontiinae
Noordinae
Wurthiinae
Evergestinae
Glaphyriinae
Pyraustinae
Group Pyralinina
Pyralinae
Chrysauginae
Galleriinae
Epipaschiinae
Phycitinae
PTEROPHOROIDEA
TINEODIDAE - False Plume Moths
OXYCHIROTIDAE - Tropical Plume Moths
PTEROPHORIDAE - Plume Moths
Macropiratinae
Agdistinae
Ochyroticinae
Deuterocopinae
Pterophorinae
Subsection: SESIINA
SESIOIDEA
BRACHODIDAE - Little Bear Moths

Pseudocossinae
Brachodinae
Phycodinae
SESIIDAE - Clearwing Moths
Tinthiinae
Paranthreninae
Sesiinae
URODIDAE - False Burnet Moths
Galacticinae
Urodinae
CHOREUTIDAE - Metalmark Moths
Millieriinae
Brenthiinae
Choreutinae
ZYGAENOIDEA
HETEROGYNIDAE - Mediterranean Burnet Moths
ZYGAENIDAE - Burnet Moths
Zygaeninae
Phaudinae
Charideinae
Chalcosiinae
Anomoeotinae
Callizygaeninae
Procridinae
HIMANTOPTERIDAE - Long-Tailed Burnet Moths
LACTURIDAE - Tropical Burnet Moths
SOMABRACHYIDAE - Mediterranean Flannel Moths
MEGALOPYGIDAE - Flannel Moths
Aidinae
Megalopyginae
Trosiinae
Section: COSSINA
Subsection: COSSINA
COSSOIDEA
Series Cossiformes
COSSIDAE - Carpenterworm Moths
Chilecomadiinae
Cossulinae
Cossinae
Hypoptinae
Zeuzerinae
DUDGEONEIDAE - Dudgeon Carpenterworm Moths
METARBELIDAE - Tropical Carpenterworm Moths
Series Limacodiformes
CYCLOTORNIDAE - Australian Parasite Moths
EPIPYROPIDAE - Planthopper Parasite Moths
Epipyropinae
Heteropsychinae
DALCERIDAE - Tropical Slug Caterpillar Moths
Acraginae
Dalcerinae
LIMACODIDAE - Slug Caterpillar Moths
CHRYSOPOLOMIDAE - African Slug Caterpillar Moths
Ectropinae
Chrysopolominae
CASTNIOIDEA
CASTNIIDAE - Giant Butterfly Moths
Synemoninae
Neocastniinae
Castniinae
TORTRICOIDEA
TORTRICIDAE - Leafroller Moths
Tortricinae
Chlidanotinae
Olethreutinae
Subsection: BOMBYCINA
CALLIDULOIDEA
RATARDIDAE - Oriental Parnassian Moths
PTEROTHYSANIDAE - Parnassian Moths
Pterothysaninae
Hibrildinae
CALLIDULIDAE - Old World Butterfly Moths
Griveaudiinae
Callidulinae
URANIOIDEA
EPICOPEIIDAE - Oriental Swallowtail Moths
Schistomitrinae
Epicopeiinae
APOPROGONIDAE - African Skipper Moths
SEMATURIDAE - American Swallowtail Moths
URANIIDAE - Swallowtail Moths
Uraniinae
Microniinae
EPIPLEMIDAE - Crenulate Moths
Auzeinae

Epipleminae
GEOMETROIDEA
GEOMETRIDAE - Geometer Moths
Archiearinae
Oenochrominae
Orthostixinae
Ennominae
Desmobathrinae
Geometrinae
Sterrhinae
HEDYLIDAE - American Butterfly Moths
PAPILIONOIDEA
Series Hesperiiformes
HESPERIIDAE - Skipper Butterflies
Megathyminae
Coeliadinae
Pyrrhopyginae
Pyrginae
Trapezitinae
Heteropterinae
Hesperiinae
Series Papilioniformes
PAPILIONIDAE - Swallowtail Butterflies
Baroniinae
Parnassiinae
Papilioninae
PIERIDAE - Yellow-White Butterflies
Pseudopontiinae
Dismorphiinae
Pierinae
Coliadinae
LYCAENIDAE - Gossamer-Winged Butterflies
Lipteninae
Poritiinae
Liphyrinae
Miletinae
Curetinae
Lycaeninae
Theclinae
Polyommatinae
RIODINIDAE - Metalmark Butterflies
Styginae
Hamearinae
Euselasiinae
Corrachiinae
Riodininae
LIBYTHEIDAE - Snout Butterflies
NYMPHALIDAE - Brush-Footed Butterflies
Group Nymphalinina
Tellervinae
Danainae
Ithomiinae
Acraeinae
Heliconiinae
Nymphalinae
Group Satyrinina
Calinaginae
Apaturinae
Amathusiinae
Morphinae
Brassolinae
Satyrinae
DREPANOIDEA
AXIIDAE - Gold Moths
THYATIRIDAE - False Owlet Moths
Thyatirinae
Polyplocinae
CYCLIDIIDAE - Giant Hooktip Moths
DREPANIDAE - Hooktip Moths
Drepaninae
Oretinae
Nidarinae
BOMBYCOIDEA
Series Bombyciformes
CARTHAEIDAE - Australian Silkworm Moths
EUPTEROTIDAE - Giant Lappet Moths
Janinae
Eupterotinae
Panacelinae
APATELODIDAE - American Silkworm Moths
Apatelodinae
Epiinae
Phiditiinae
BOMBYCIDAE - Silkworm Moths
Bombycinae
Prismostictinae
MIMALLONIDAE - Sackbearer Moths
ANTHELIDAE - Australian Lappet Moths
Munychryiinae
Anthelinae

LASIOCAMPIDAE - Lappet Moths
Chondrosteginae
Chionopsychinae
Poecilocampinae
Macromphaliinae
Lasiocampinae
Series Saturniiformes
ENDROMIDAE - Glory Moths
Endrominae
Mirininae
LEMONIIDAE - Autumn Silkworm Moths
Lemoniinae
Sabaliinae
BRAHMAEIDAE - Brahmin Moths
Dactyloceratinae
Brahmaeinae
OXYTENIDAE - American Tropical Silkworm Moths
CERCOPHANIDAE - Andean Moon Moths
Cercophaninae
Janiodinae
SATURNIIDAE - Emperor Moths
Arsenurinae
Ceratocampinae
Hemileucinae
Agliinae
Ludiinae
Salassinae
Saturniinae
SPHINGOIDEA
SPHINGIDAE - Hawk Moths
Smerinthinae
Sphinginae
Macroglossinae
NOCTUOIDEA
NOTODONTIDAE - Prominent Moths
Group Oenosandrinina
Oenosandrinae
Group Thaumetopoeinina
Thaumetopoeinae
Group Notodontinina
Pygaerinae
Platychasmatinae
Notodontinae
Phalerinae
Dudusinae
Heterocampinae
Nystaleinae
Meiceratinae
DIOPTIDAE - American False Tiger Moths
Dioptinae
Doinae
THYRETIDAE - African Maiden Moths
LYMANTRIIDAE - Tussock Moths
Orgyiinae
Lymantriinae
ARCTIIDAE - Tiger Moths
Group Pericopinina
Pericopinae
Group Arctiinina
Lithosiinae
Arctiinae
Group Ctenuchinina
Ctenuchinae
Syntominae
NOCTUIDAE - Owlet Moths
Group Aganainina
Aganainae
Group Herminiinina
Herminiinae
Group Noctuinina
Hypenodinae
Rivulinae
Hypeninae
Catocalinae
Euteliinae
Stictopterinae
Sarrothripinae
Chloephorinae
Nolinae
Plusiinae
Acontiinae
Condicinae
Amphipyrinae
Stiriinae
Psaphidinae
Agaristinae
Cocytiinae
Heliothinae
Acronictinae

Pantheinae
Bryophilinae
Cuculliinae
Hadeninae
Noctuinae

Primitive Moths

The families considered the most primitive of all lepidopterans, in the groups up to Myoglossata, include the first six families. The first three superfamilies are all relictual base lineages of the Lepidoptera and also have only one family in each superfamily and each suborder: Micropterigidae (Micropterigoidea, suborder Zeugloptera), Agathiphagidae (Agathiphagoidea, suborder Aglossata), and Heterobathmiidae (Heterobathmioidea, suborder Heterobathmiina). They are all small moths (not over 16 mm in wingspan), concentrated most in what are now considered refugia regions of the world where the oldest faunas remain, so-called Gondwanaland distributions, notably in South Africa, Australia, New Zealand, and Chile, although some are more widespread like the Micropterigidae which occur in all regions. All have homoneurous venation and a jugum for wing coupling of the fore- and hindwings during flight, and the hindwings are mostly about the same size as the forewings. Adults have small mandibles instead of the usual lepidopteran haustellum (or proboscis) of the Aglossata, but the primitive families of the Glossata also have a reduced haustellum in addition to vestigial mandibles. Most of the primitive moths also have large 5-segmented maxillary palpi and the head vertex vestiture with long scales or hair-like scales.

Micropterigoidea

Micropterigoidea contain the single family, Micropterigidae (in the past misspelled as Micropterygidae).

Micropterigidae (mandibulate archaic moths) total 130 species worldwide. There are two subfamiles. Adults are minute to small and diurnal. Larvae feed on mosses, liverworts, or detritus.

Agathiphagoidea

Agathiphagoidea are also a monobasic superfamily, containing the relict family, Agathiphagidae. Adults have chewing mouthparts (haustellum absent) and are similar to Micropterigidae.

Agathiphagidae (kauri moths) total only two known species, from Australia and Fiji. Adults are small and diurnal. Larvae are seed-borers of kauri pines (Araucariaceae).

Heterobathmioidea

Heterobathmioidea are one of the most obscure groups, based on only a single family, Heterobathmiidae. Adults have small mandibles (haustellum absent).

Heterobathmiidae (Valdivian archaic moths) include about nine species, with named thus far all from southern South America. Adults are small and diurnal. Larvae are leafminers of *Nothofagus* trees (Fagaceae).

Eriocranioidea

The superfamily Eriocranioidea contains two families, together comprising the Infraorder Dacnonypha. Adults have a reduced haustellum but retain vestigial mandibles.

Eriocraniidae (sparkling archaic sun moths) are a Holarctic family of 25 species, about half in Europe and half in North America. Adults are small and diurnal. Larvae are leafminers on a variety of hardwood trees and other plants.

Acanthopteroctetidae (archaic sun moths) are very similar to Eriocraniidae, and include only four species, all North American except for one in the Palearctic. Adults are small and thought to be diurnal. Larvae are blotch leafminers on *Ceanothus* (Rhamnaceae) for the single species known biologically.

Lophocoronoidea

Representing the infraorder Lophocoronina, this monobasic superfamily contains the small archaic family, Lophocoronidae. Adults have the haustellum reduced (mandibles vestigial).

Lophocoronidae (Australian archaic sun moths) have six known species in Australia. Adults are small and crepuscular in sclerophyll eucalyptus woods. Biologies and larvae remain unknown..

Myoglossata

The cohort Myoglossata are divided into two subcohorts: Myoglossata and Neolepidoptera, where the subcohort Myoglossata contains only a single infraorder, Neopseustina, and the Neolepidoptera have two infraorders (Exoporia and Heteroneura) which contain all the remaining Lepidoptera.

Neopseustina

This infraorder contains only the single superfamily Neopseustoidea. Wing venation is homoneurous and a jugum is used for wing coupling. Adults have the haustellum short (mandibles vestigial).

Neopseustoidea

This first group of the Myoglossata includes only the single archaic family Neopseustidae.

Neopseustidae (archaic bell moths) include nine known species (six from Southeast Asia and three from Chile). Adults are small (bell-shaped when at rest) and crepuscular or diurnal. Biologies and larvae remain unknown, but species in Chile are thought to possibly feed on native bamboos.

Exoporia

This first infraorder of the Neolepidoptera, Exoporia, has two superfamilies, Mnesarchaeoidea and Hepialoidea, with six primitive moth families in total. Wing venation is homoneurous and a jugum is used for wing coupling.

Mnesarchaeoidea

This superfamily is contains a single family of primitive moths, the Mnesarchaeidae. Adults have the haustellum short (mandibles vestigial).

Mnesarchaeidae (New Zealand primitive moths) occur only in New Zealand, with eight known species. Adults are small and diurnally active in forest clearings and near ferns. Biologies and larvae remain unknown.

Hepialoidea

This superfamily comprises the first group of lepidopterans with several families, although most species are in Hepialidae, the ghost moths. The superfamily comprises 616 known species worldwide. All are relict groups that retain a jugum for wing coupling, and are rather small moths, but Hepialidae also have some of the largest species of the "micro" -moths known (up to 250 mm in wingspan). Adults with reduced haustellum (sometimes absent) and usually with vestigial mandibles (absent in Hepialidae and Palaeosetidae); antennae are mostly short; hindwings tend to be nearly as long as the forewings.

Neotheoridae (Amazonian primitive ghost moths) include a single species from the Mato Grosso area of Brazil (two more species have been discovered recently). Adults are medium size. Biologies and larvae remain unknown.

Anomosetidae (Australian primitive ghost moths) comprise a single genus with one known species from Australia. Adults are small. Biologies and larvae remain unknown

Prototheoridae (African primitive ghost moths) comprise 12 species from southern Africa. Adults are small. Biologies and larvae remain unknown, but a pupa has been found in moss.

Hepialidae (ghost moths, or swifts) comprise about 594 species from all faunal regions, but most are from Australia, South Africa and Chile. Adults are medium size to very large and typically crepuscular or nocturnal, but a few are diurnally active. Larvae feed as borers on roots, trunks or under bark of trees, various bushes, or grasses, or even leaf litter.

Palaeosetidae (miniature ghost moths) comprise eight species worldwide (five in Assam, Thailand and Taiwan, two in Australia, and one in Colombia). Adults are small and crepuscular or active during the day in dark forested areas, typically near wet moss-covered rock faces. Biologies remain unknown but larvae of a species in Taiwan are thought to feed on mosses.

Monotrysian Moths

The division Monotrysia, of the infraorder Heteroneura, comprises sections Nepticulina and Incurvariina, and include the first more evolved moths leading to the main Ditrysian Lepidoptera. All have frenular bristles as the wing coupling mechanism instead of a jugum. The Monotrysia comprise nine families in recent classifications, all with a single genital opening in females (Ditrysia have two female genital openings). Mandibles are not present in any of the species in this group (except Andesianidae and Palaephatidae), nor in any higher lepidopterans. Nepticulina have four families in four superfamilies (Andesianidae, Nepticuloidea, Tischerioidea, and Palaephatoidea) and Incurvariina have five families in the single superfamily, Incurvarioidea.

Andesianoidea

The superfamily was formed in 2003 for odd Valdivian moths formerly considered to be Cossidae. Their female genital morphology, however, was found to be monotrysian. Only one family is known. Adults with head roughened; haustellum very short (with vestigial mandibles present); antennae bipectinate in males; labial palpi elongated; and maxillary palpi 5-segmented (unfolded). Wing venation is somewhat primitive.

Andesianidae (Valdiviar forest moths) total only three known species from southern Andean forest zones of Argentina and Chile. Adults are robust and of medium size, apparently nocturnal (possibly crepuscular). Biologies are unknown, but larvae are likely to be stem borers.

Nepticuloidea

The superfamily Nepticuloidea includes two families of the tiniest leafminer moths known: Nepticulidae and Opostegidae. Adults with haustellum very short; antennae with distinct eye caps; labial palpi reduced; maxillary palpi 5-segmented and folded; and head vestiture very rough-scaled. Wing venation is greatly reduced.

Nepticulidae (pygmy moths) comprise 868 species from all faunal regions, although most (over 510 sp.) are from the Palearctic region; actual world fauna likely exceeds 1,200 species. Two subfamilies are used. Adults are minute and diurnally active. Larvae are leafminers, usually blotch mines, although some also mine other plant parts. A large variety of hostplants are used.

Opostegidae (eye-cap moths) total 122 known species from all faunal regions and especially Australia; actual fauna probably exceeds 175 species. Adults are minute to small and diurnally active. The few larvae known are leafminers, but some are stem borers. Hostplants are in several plant families.

Tischerioidea

The superfamily Tischerioidea includes the single family Tischeriidae Adults with head vestiture rough; haustellum short and scaled; labial palpi short; maxillary palpi minute, 1-segmented, and wing venation is very reduced.

Tischeriidae (trumpet leafminer moths) total 81 known species from all regions except Australia, with most species in the Nearctic (48 sp.); actual fauna likely exceeds 125 species. Adults are small and diurnally active. Larvae are leafminers, usually trumpet-shaped mines or blotch mines, on a variety of hostplants.

Palaephatoidea

The monobasic superfamily Palaephatoidea contains one family from southern refugia regions of the world (except South Africa), the Palaephatidae. Adults with head roughened; haustellum short, naked (vestigial mandibles usually present); labial palpi short; maxillary palpi 5-segmented and folded, and wing venation is heteroneurous.

Palaephatidae (Gondwanaland moths) total 39 described species (28 from Chile and Argentina, and 11 from Australia), but at least 25 more undescribed species are known from Australia alone; actual fauna probably exceeds 90 species. Adults are small to medium size. Biologies little known but adults presumed diurnally active. Larvae tie hostplant twigs together (on Verbenaceae and Proteaceae).

Incurvarioidea

This superfamily is the sole group comprising section Incurvariina of the Monotrysia. Included are a number of odd groups that have been considered families in the past, but only five families are now recognized. The superfamily has 589 known species. All have a scaled haustellum, although mostly reduced; head vestiture is rough-scaled except for Heliozelidae; some have 5-segmented maxillary palpi (Incurvariidae and Prodoxidae, plus rarely in Adelidae), while reduced in others.

Incurvariidae (leafcutter moths) total about 116 species from all regions, but most are Palearctic (64 sp.), divided into two subfamilies. Adults are small and mostly diurnal in shaded habitats. Larvae are leafminers at first, then switch to leaf skeletonizing on a variety of hostplants; some are case bearers or shoot borers.

Cecidosidae (gall moths) total only seven species, with five species from southern South America and two from South Africa. Adults are small and probably diurnal. In Argentina larvae are gall makers on *Schinus* (Anacardiaceae).

Prodoxidae (yucca moths) total 65 species, mostly western Nearctic. There are two subfamilies. Adults are minute to small and diurnal. Larvae are seed, flower stalk, or stem borers; rarely gall makers. Hostplants are various yucca plants (Agavaceae) and other species are on hardwood trees and bushes.

Adelidae (longhorned fairy moths) comprise 295 species worldwide, but most are Palearctic (143 sp.), with two subfamilies; actual fauna probably exceeds 400 species. Adults are minute to small; antennae extremely long (often 2X wing lengths) in males, but of average length in females (sometimes thickened). Adults are usually diurnal but a few are crepuscular. Larvae are leafminers, but in later instars change to casebearers. Hostplants include a number of different plant families.

Heliozelidae (shield bearer moths) total 106 species from all regions, with more than half the species split between North America (31 sp.) and Australia (36 sp.); actual fauna probably exceeds 200 species. Adults are minute to small and diurnal. Larvae make serpentine leaf mines at first, then make blotch mines in later instars. Hostplants include a variety of hardwood trees and bushes.

Ditrysia

This division of the infraorder Heteroneura comprises all the remaining Lepidoptera, divided into the sections Tineina and Cossina. All the remaining Lepidoptera have heteroneurous wing venation (although often with reduced venation in the tiny leafminers) and a frenulum-retinaculum wing coupling (rarely reduced). Typically, they have 3-segmented labial palpi, generally upcurved, and a haustellum (rarely reduced or absent).

Tineina

This section of the Ditrysia involves those groups with a ventral heart vessel in the adult (considered more primitive than the dorsal heart vessel of the Cossina), and are further divided into the subsections Tineina and Sesiina. Most of the Microlepidoptera families are in this section of the Ditrysia, other than the primitive moths and a few groups in Cossina often included among the micro-moths. The subsection Sesiina have a spined pupa, while most of the subsection Tineina have an unspined pupa (Gelechioidea, Copromorphoidea, Yponomeutoidea, Immoidea, Pyraloidea, and Pterophoroidea), other than the basal groups that form the Tineoidea, which also have a spined pupa. (Pterophoridae pupae have scolus-like projections but not "spined" as here defined).

Tineoidea

The superfamily Tineoidea includes the most primitive of the Ditrysia and also are basal groups with ancestors that evolved to the Sesiina groups, Sesioidea and Zygaenoidea, while also having begun the development to the other superfamilies of the subsection Tineina. Tineoidea are split into two series, Tineiformes (Acrolophidae, Tineidae, Eriocottidae, Psychidae, and Arrhenophanidae) and Gracillariiformes (Amphitheridae, Schreckensteiniidae, Douglasiidae, Bucculatricidae, and Gracillariidae), which some specialists consider separate superfamilies. The superfamily total comes to about 5,730 known species. Adults with head vestiture mostly rough-scaled; haustellum naked (unscaled); labial palpi mostly upcurved, 3-segmented (except most Psychidae); maxillary palpi mostly small; antennae mostly filiform (mostly bipectinate in Psychidae); wing venation reduced in some species (mainly leafminers). Larvae with three lateral setae on the prothorax.

Acrolophidae (tube moths) total 270 species in the New World, mostly in the large genus *Acrolophus*; actual fauna likely exceeds 350 species. Two subfamilies are used. Adults are small to medium size, with rather robust bodies and usually large recurved labial palpi. Adults are mostly nocturnal, but some may be crepuscular. Larvae are root feeders, mostly of grasses, and construct long underground silken tubes to feed on hostplant roots.

Tineidae (fungus moths) comprise the first very large family of Lepidoptera, with about 2,160 described species. The actual world fauna probably exceeds 4,000 species. The family is divided into 16 subfamilies. Adults are minute to medium size and nocturnal or crepuscular; rarely diurnal. Larval habits vary greatly, but most are detritus feeders, some making cases, tunnels, or silken tubes; also, odd groups are coprophagous, keratophagous,woolen feeders, and even myrmecophilous and termitophilous larvae are known. Included among Tineidae are some of the most well known household pest species, such as clothes moths and grain moths.

Eriocottidae (Old World spiny-winged moths) are a small family of 212 known species, mostly African (120 sp.) and Oriental (66 sp.), now divided into two subfamiles. Adults are small to medium size and mostly diurnally active, or may be crepuscular. Biologies are little known but some larvae reported to tunnel in the soil, possibly feeding on roots or detritus.

Psychidae (bagworm moths) total 1,001 known species, mostly Palearctic and African, with only 88 known for the New World; actual fauna likely exceeds 1,200 species. The family is now divided into six subfamilies. Adults are minute to medium size and mostly diurnal or crepuscular. Larvae are mostly leaf feeders or feed on lichens, all making distinctive types of larval cases, or bags. Pupation is within the larval case and females often remain there in a wingless or larviform shape, using pheromones to attract the winged males. A number of species are economic and many are general plant feeders.

Arrhenophanidae (tropical lattice moths) total about 30 species, mostly Neotropical, but recently with some Southeast Asian additions; actual fauna probably exceeds 50 species. Adults are small to medium size. Adult activity mostly nocturnal, but some are diurnal. Biologies unknown except for one Neotropical species with case bearing larvae that feed on fungi.

Amphitheridae (double-eye moths) are an unusual and small family of mostly tropical moths, totaling 57 species, mostly Indo-Australian (one genus occurs in Europe and possibly another in South America). Adults are small, with eyes usually divided. Adults active diurnally. Larvae are leafminers, becoming leaf skeletonizers in later instars; host records are mostly in Betulaceae and Aceraceae. The family has been erroneously called Roeslerstammiidae in recent European literature.

Schreckensteiniidae (bristle-legged moths) are a small family of only eight known species (three in North America, one in Central America, and one in Europe). Adults are small and diurnal. Larvae are leaf skeletonizers on Anacardiaceae or Rosaceae.

Douglasiidae (Douglas moths) comprise only 28 known species, mostly Palearctic (20 sp.). Adults are minute to small and crepuscular or diurnal. Larvae are leafminers or borers in petioles or stems. Hostplants are known in Boraginaceae, Labiatae, and Rosaceae.

Bucculatricidae (ribbed-cocoon maker moths) total 247 species worldwide, with most species being Nearctic (103 sp.) or Palearctic (86 sp.); most species are in the genus *Bucculatrix*. Adults are minute to small and mostly diurnal. Larvae are leafminers, with some changing to external leaf skeletonizing in later instars, but a few are gall makers or stem miners. Pupation is in a white spindle-shaped cocoon with a ribbed surface, unique to the family. Many different hostplants are known but many feed on Compositae. Some species are economic.

Gracillariidae (leafminer moths) comprise the major leafmining family of Lepidoptera, with about 1,740 species from all regions. The actual world total probably exceeds 6,000 species. There are three subfamilies. Adults are minute to small and active diurnally. Larvae are usually leafminers but change form in later instars (hypermetamorphism) from sap feeders with reduced legs, to later instars with a 3-proleg pair larval form, which is unique among the Microlepidoptera. Later instars sometimes feed externally as leaf skeletonizers. Hostplants include a great number of plant families. A few species are of economic importance, such as the citrus leafminer (*Phyllocnistis citrella*).

Gelechioidea

This superfamily comprises a huge group of micromoths, all having a scaled haustellum and unspined pupa. There has been considerable turmoil in recent classifications proposed for the group, either with a large family Oecophoridae or with conglomeration of various groups into an enlarged family Elachistidae. In the classification adopted herein, there are 11 families recognized, the largest being Oecophoridae and Gelechiidae. The entire superfamily encompasses about 18,230 described species worldwide, but the actual fauna may well exceed 45,000 species, since there are huge numbers of undescribed tropical species. Adults mostly with head vestiture mostly relatively smooth-scaled (rarely roughened); haustellum always scaled; labial palpi mostly recurved, 3-segmented; maxillary palpi vary but mostly small; antennae mostly filiform. Larvae mostly with three lateral setae on the prothorax (except two in Momphidae).

Oecophoridae (concealer moths) is a large family of about 7,550 described species from all faunal regions, with most species being from Australia; the actual fauna may well exceed 12,000 species worldwide. There are ten subfamilies recognized. Adults are small to medium size and mostly nocturnal but some are diurnal or crepuscular. Larvae include many leaf litter feeders, but also leaf tiers, leaf webbers, bark feeders, and a few leafminers. Hostplants include a large number of plant families, plus lichens, fungi, and detritus or leaf litter. Few are economic.

Lecithoceridae (tropical longhorned moths) total about 1,038 described species, mostly tropical

Oriental, but also with one group in the Palearctic; actual fauna probably exceeds 1,500 species. There are four subfamilies. Adults are small and mostly diurnal and many have the habit of holding the long antennae together to the front when at rest. Larvae may mostly be leaf litter feeders or leaf tiers, but few species are known biologically. A few varied hostplants are recorded.

Elachistidae (grass miner moths) comprise about 723 species worldwide, but most are Palearctic (472 sp.). Two subfamilies are used (or only tribes). Adults are small and often crespuscular or nocturnal, but some are diurnal. Larvae are leafminers (sometimes gregarious) or stem miners, especially on grasses (Gramineae) and related plant groups like Juncaceae and Cyperaceae, but other plant families are also utilized.

Pterolonchidae (lance-wing moths) total only 11 species, mostly Mediterranean, plus two are from South Africa. Adults are small and may be mostly crepuscular. Larvae are root borers as far as is known. Only recorded hostplants are in Compositae.

Gelechiidae (twirler moths) are a very large family, with over 4,830 species described, however, possibly with a fauna exceeding 10,000 species worldwide. Subfamily arrangements have varied but now include 4. Adults are small and mostly nocturnal but some are diurnal or crepuscular. Larvae have a range of feeding habits but most are leaf skeletonizers, using a leaf fold or leaf tie as protection. A large variety of plants are used as hosts. Some species are economically important.

Blastobasidae (scavenger moths) total over 296 species worldwide, with many known from North America and Europe; actual fauna probably exceeds 600 species. There are two subfamilies. Adults are small and nocturnal as far as is known. Larvae are scavengers or detritus feeders, sometimes feeding on plant fruits, flowers, or seeds, among a number of plant families, but few are known biologically. At least one species lives with coccids (Hemiptera) but predation on the coccids has not been confirmed.

Coleophoridae (casebearer moths) comprise about 1,525 species worldwide, with most being Palearctic and in the genus, *Coleophora*. The actual world fauna likely exceeds 2,000 species. Most are in subfamily Coleophorinae, while non casebearers are in Batrachedrinae. Adults are small and may be mostly crepuscular but many are diurnal. Larvae make small cases (except for Batrachedrinae), often distinctly shaped for each species, skeletonizing host leaves, but some are seed borers, leafminers, or stalk borers, or skeletonize leaves beneath frass webs. A few Batrachedrinae are predaceous on scale insects (Hemiptera). Various hostplants are utilized. A few species are economic. Ovovivipary has been recorded for a few species.

Momphidae (mompha moths) total 127 species worldwide, with about half from the Palearctic. Adults are small and mostly diurnal or crepuscular. Larvae mostly leafminers, but some are borers in flowers and stems, or gall makers. Hosts are only known in Onagraceae.

Agonoxenidae (palm moths) are a small family of 68 known species from all faunal regions. Adults are small and diurnal. Larvae are leaf skeletonizers, or borers in leaves, stems, and fruits; rarely gall-makers. Hostplants mostly in Rosaceae or Palmae. A few are economic.

Cosmopterigidae (cosmet moths) total over 1,540 species worldwide, but the extant fauna may encompass 3,500 species. There are three subfamilies. Adults are small and mostly diurnal, but some are crepuscular. Larvae mostly leafminers or needleminers, but some are borers of various plant parts; a few are predaceous on Hemiptera. Hosts are varied. Ovovivipary recorded in a few species. Some economic species are known.

Scythrididae (flower moths) total about 523 species worldwide, but mostly known from Europe. Adults are small and diurnal but some may be crepuscular. Larvae are skeletonizers on leaves, buds, flowers, hiding under webbings. Many plant families are used as hosts, plus some on lichens and mosses.

Copromorphoidea

This superfamily comprises four families related especially by larval characters. The world fauna totals 623 species. Adults with head vestiture mostly smooth-scaled; haustellum naked (unscaled); labial palpi porrect (except for Epermeniidae), 3-segmented; maxillary palpi vary; antennae mostly filiform. Larvae with two lateral setae on the prothorax.

Copromorphidae (tropical fruitworm moths) are a small family of 58 species, mostly tropical; actual fauna probably exceeds 100 species. Adults are small to medium and nocturnal. Larvae are leaf feeders using a leaf web, or are borers (one feeds beneath bark), but few biologies are known. Hostplants include Berberidaceae, Ericaceae, Moraceae, Podocarpaceae, and Rubiaceae.

Alucitidae (many-plumed moths) total about 184 species worldwide. Adults are small; wings with all veins as separate wing clefts to near the wing bases (rarely split only to center of wings). Adults active in deep shade, or may be crepuscular. Larvae are borers or gall makers as far as is known. Various hostplant records are known.

Carposinidae (fruitworm moths) total about 279 species from all regions, but most are Australian and South Pacific. Adults are small to medium and nocturnal or crepuscular. Larvae are borers in fruits, seeds, buds, or trunks and limbs, but a few are leafminers. Hosts include a variety of plants. A few species are economic.

Epermeniidae (fringe-tufted moths) total 102 species, with many being Palearctic (36 sp.) and Australian (23 sp.), in two subfamilies. Adults are small and diurnal or crepuscular. Larvae are leafminers, leaf skeletonizers, or borers of seeds, fruits, or buds; a few are gall makers. Host records include several plant families.

Yponomeutoidea

This superfamily of varied moths includes nine families, some of which have been transferred from Tineoidea, while other previously contained groups are now in other superfamilies. About 1,853 species are known in the superfamily. Adults with head vestiture mostly relatively smooth-scaled (roughened in Ochsenheimeriidae, Argyresthiidae and Lyonetiidae); haustellum developed and naked (unscaled); labial palpi mostly upcurved; maxillary palpi mostly reduced; antennae mostly filiform. Larvae mostly with three lateral setae on the prothorax (two in Glyphipterigidae, and a few Plutellidae and Yponomeutidae).

Ochsenheimeriidae (cereal stem moths) include only 17 species from the Palearctic (one species is from Kashmir), with one species introduced into North America. Adults are small and diurnal. Larvae are leafminers, but become stem borers in later instars, primarily on grasses (Gramineae), sedges (Cyperaceae) and rushes (Juncaceae). One species is economic.

Glyphipterigidae (sedge moths) total 431 species from all regions, mostly in the genus *Glyphipterix*, with the largest number from the Australian-New Zealand region; actual world fauna probably exceeds 600 species. There are two subfamilies. Adults are small and diurnal, usually in proximity to the hostplants. Larvae are mostly borers in seeds, stems, or leaf axils, and a few are leafminers, but most tropical species are unknown biologically. Hostplants are mostly sedges (Cyperaceae), rushes (Juncaceae), and grasses (Gramineae), plus a few other plant families.

Plutellidae (diamondback moths) include 386 species worldwide; actual fauna probably exceeds 600 species. There are four subfamilies. Adults are small to medium size and mostly nocturnal or crepuscular, but some are diurnal. Larvae are leaf skeletonizers, but most remain unknown biologically. Hosts include different plant groups. A few species are economic.

Attevidae (tropical ermine moths) include 48 species, mostly tropical and in the genus *Atteva* (the single partially non-tropical species known occurs across the southern United States and into the Caribbean and Mexico); actual fauna probably at least 60 species. Adults are small to medium size and are diurnal or crepuscular. Larvae are leaf webbers and leaf skeletonizers on Araliaceae and Simaroubaceae. Minor economic species occur on Ailanthus trees in India and the United States.

Yponomeutidae (ermine moths) total 395 species worldwide; actual fauna likely exceeds 500 species. Three subfamilies are recognized. Adults are small to medium size and mostly nocturnal. Larvae are leaf skeletonizers and leaf webbers, but some are leafminers or needleminers. Hosts include many different plant families. A few species are economic.

Argyresthiidae (shiny head-standing moths) include 160 species, mostly from Holarctic region; actual fauna probably exceeds 450 species. Adults are small and mostly crepuscular, but many may be diurnal. Larvae are leafminers and needleminers, and some mine in various plant parts. Numerous plants are recorded as hosts. Several species are economic.

Lyonetiidae (Lyonet moths) total 264 species, mostly Holarctic; the actual fauna probably exceeds 600 species. There are three subfamilies. Adults are minute to small and mostly crepuscular and nocturnal. Larvae are blotch leafminers; rarely mining stems. Many plant groups are recorded as hosts. A few species are economic.

Acrolepiidae (false diamondback moths) include 96 species, mostly Palearctic. Adults are small and crepuscular or diurnal. Larvae mostly leafminers, but some are borers in seeds, stems and flower buds. Several hostplant groups are used, but mostly on Compositae. Very few are economic.

Heliodinidae (sun moths) are a small family of 56 species, mostly Neotropical (31 sp.); actual fauna probably exceeds 100 species. Adults are small and diurnal. Larvae are mostly leaf skeletonizers, but some are borers in fruit racemes. Several plant families are used as hosts.

Immoidea

This is a monobasic superfamily for the single small family Immidae. It is somewhat related to Pyraloidea and may represent relatives of common ancestors. Adults with head vestiture relatively smooth-scaled; haustellum naked; labial palpi upcurved and often prominent, with long second segment; maxillary palpi minute, 1 to 2-segmented; antennae mostly filiform; body robust. Larvae with three lateral setae on the prothorax.

Immidae (imma moths) comprise 246 species, all tropical, and mostly Indo-Australian and South Pacific; actual fauna likely exceeds 450 species. Adults are small to medium size and diurnal, but some may be crepuscular. Larvae are leaf feeders, but only three species have biological data. Hostplants are in Myrtaceae, Podocarpaceae, and Violaceae.

Pyraloidea

This superfamily includes three families but mainly the very large family, Pyralidae. The superfamily comprises about 17,312 species worldwide. Recent specialists have taken to splitting Pyralidae into its two major lineages, as the separate families Crambidae and Pyralidae, but this reversion to what was done over 100 years ago is unnecessary and amply clarified by using the "group" category below the family level within a single family Pyralidae. Some specialists do even more splitting by placing each pyraloid family in its own monobasic superfamily (Hyblaeoidea, Thyridoidea, and Pyraloidea). Adults with head vestiture mostly smooth-scaled; haustellum mostly scaled (not Hyblaeidae and Thyrididae); labial palpi mostly porrect, 3-segmented; maxillary palpi varied; antennae mostly filiform. Larvae have two lateral setae on the prothorax.

Hyblaeidae (teak moths) are a small tropical family of 18 species, mostly Indo-Australian and in the genus *Hyblaea* (one pantropical species is also established in southern Florida). Adults are medium size; body usually robust. Adults are diurnal or perhaps crepuscular. Larvae are leaf rollers. Hostplants are in Bignoniaceae and Verbenaceae. One economic species: the teak leafroller (*Hyblaca puera*).

Thyrididae (picture-winged leaf moths) total 794 species worldwide, nearly all tropical, with nearly half the species Indo Australian (only a few species are in the Nearctic and Palearctic regions); actual fauna likely exceeds 1,200 species. There are six subfamilies. Adults are small to large and diurnal or crepuscular. Larvae are leafrollers (one Australian species is gregarious), or borers in stems and flower racemes; a few are gall makers. A number of hostplants are used. Only a few species are economic.

Pyralidae (snout moths) comprise the third largest family of Lepidoptera, with about 16,500 described species, but a probable fauna of at least 25,000 species worldwide; 19 subfamilies are used in the classification. Adults are small to large and mostly nocturnal, but some are crepuscular and a few are diurnal. Larvae are mostly leafrollers or leaf webbers, but many are borers, root feeders, detritus feeders (including stored products pests), and a few are leafminers, plus rare myrmecophilous species, and even some aquatic groups making cases (Nymphulinae). A large number of economic species are in this family, including pests on virtually all crops and forest trees. Hostplants are in a large number of plant families.

Pterophoroidea

This superfamily includes only three families, but most species are in the Pterophoridae. About 1,309 species are known for the superfamily. Adults with head vestiture average (rather smooth scaled); haustellum naked (unscaled); labial palpi porrect; maxillary palpi mostly short; antennae filiform. Larvae have three lateral setae on the prothorax in Pterophoridae, but only two lateral setae in Tineodidae (not known for Oxychirotidae).

Tineodidae (false plume moths) include only 11 species, all from Australia. Adults are small and possibly diurnal or crepuscular. Larvae are leaftiers, but most are not known biologically. Only recorded hostplants are in Euphorbiaceae and Oleaceae.

Oxychirotidae (tropical plume moths) include only six species, all Indo-Australian and South Pacific. Some specialists include this family as part of the Tineodidae. Adults are small and may be crepuscular. Larva of one species feeds on seeds of white mangrove (Avicenniaceae); remainder unknown biologically.

Pterophoridae (plume moths) comprise about 1,292 species worldwide, with about a third being Palearctic; actual world fauna probably exceeds 1,800 species. Subfamilies number five. Adults are small, usually with hindwings split into three fringed plumes; forewings often entire or split into two parts near the termen (a few species have both wings entire). Adults mostly nocturnal but some crepuscular or in shaded areas during the day. Larvae mostly leaf feeders, or miners and borers of various plant parts; a few are gall makers. Hostplants include many families. Several species are economic.

Sesiina

The subsection Sesiina of the Tineina include two superfamilies: Sesioidea and Zygaenoidea.

Sesioidea

The Sesioidea include four families, although many specialists maintain separate superfamilies for most of them: Brachodidae, Sesiidae, Urodidae, and Choreutidae. Brachodidae are thought to be the basal group, with close ties to Sesiidae. The world fauna totals 1,963 known species in the superfamily. Adults mostly with head vestiture mostly smooth-scaled (rough in most Brachodidae); haustellum mostly naked (scaled in Choreutidae); labial palpi mostly upcurved; maxillary palpi mostly small; antennae vary but many with thickened antennae (Sesiidae). Larvae mostly with three lateral setae on the prothorax, but most Brachodidae and a few Choreutidae with only two lateral setae.

Brachodidae (little bear moths) comprise 140 species, most being Old World tropical, particularly Indo-Australian (none are North American). There are three subfamilies. Adults are small to medium size and diurnal. Larvae are root feeders of grasses (in the European Brachodes, Brachodinae), using silken tubes, or borers in palm trunks and leaf stems, or other plants; some are leaftiers (Phycodinae). Hostplants are in Gramineae, and also Bromeliaceae, Melistomaceae, Moraceae, and Palmae. A few are economic on palms.

Sesiidae (clearwing moths) include about 1,325 species from all regions; the actual number probably exceeds 1,800 species. Subfamilies are three. Adults are small to medium size; antennae usually thickened and with a slight distal club (most also with unique small terminal bristles on antennae). Wings very elongated and with unique wing-locking folding where the margins meet. Adults are diurnal, particularly during morning hours. Many species mimic various wasps (Hymenoptera). Larvae mostly borers on various plant parts, and a few are gall makers; two species are predaceous on scale insects (Hemiptera). Host specificity is high for most species, but overall many plant families are used as hosts. A number of species are economic, including some major pests of fruit trees, forest trees, and grape vines.

Urodidae (false burnet moths) total only about 80 species, primarily Neotropical, but with a few species in North America and in Eurasia. Adults are small and may be crepuscular or mostly nocturnal, but a few possibly diurnal. Larvae are leaf webbers or skeletonizers, but few are known biologically. Pupation is in a specialized filigreed cocoon. Hostplants known in Lauraceae, Leguminosae, Salicaceae, Sapotaceae, and Theaceae. A few are minor pests.

Choreutidae (metalmark moths) comprise 418 species worldwide; actual world fauna probably exceeds 800 species. There are three subfamilies. Adults are small, with haustellum scaled. Adults are diurnal; usually near their hostplants and tend to hop about on leaves. Larvae mostly leaf skeletonizers, but some are budworms; rarely leafminers (Millieriinae). Numerous hostplant families are recorded, but many in Compositae and Moraceae.

Zygaenoidea

This superfamily contains the burnet moth and flannel moth groups, with six families involved (in Europe also called forester moths, which name is used for one of the Noctuidae subfamilies in North America). Some very colorful species are included, especially some of the larger Zygaenidae which in the Oriental region are as large as some butterflies. The superfamily has 1,609 known species from all regions. Adults with head vestiture usually average but often rough-scaled; haustellum naked (unscaled), but sometimes absent or vestigial; labial palpi mostly upcurved; maxillary palpi mostly small or reduced; and antennae mostly bipectinate (sometimes clubbed). Larvae all have three lateral setae on the prothorax and most are slug-like.

Heterogynidae (Mediterranean burnet moths) include only seven species, with three species from the Mediterranean region of southern Europe and northern Africa and four species from South Africa. Adults are small and diurnal, but females are apterous and larviform. Larvae, upon hatching inside the female cocoon, feed first on the dead female and then become external leaf feeders. Hostplants are in Leguminosae.

Zygaenidae (burnet moths) comprise about 1,140 species worldwide, particularly well developed in tropical Asia (450 sp.) where also the largest species occur; actual world fauna likely exceeds 1,500 species. There are seven subfamilies. Adults are small to large, with antennae sometimes clubbed. Adults are diurnal, often flying like butterflies, or commonly on flowers. Larvae are leaf skeletonizers, sometimes feeding communally and usually at night; often slug-like, with concealed head. Hostplants include various plant families. Economic species are mostly pests on grapevines in North America and Europe.

Himantopteridae (long-tailed burnet moths) include 56 species from Africa and tropical Asia. Adults are small to medium size; hindwings with extremely long tails. Adults are diurnal but few are known biologically. Larvae are leaf skeletonizers, often communal; sometimes massing in the 1000s. Known hostplants are in Dipterocarpaceae.

Lacturidae (tropical burnet moths) total 138 species, mostly Indo-Australian but with a few in the southern United States; actual world fauna probably exceeds 250 species. Adults are small to medium size and nocturnal, but some may be crepuscular. Larvae are leaf skeletonizers and are colorful, but most are not known biologically. Hostplants are in families Celastraceae, Moraceae, and Sapotaceae.

Somabrachyidae (Mediterranean flannel moths) include only five species, with three species from southern Europe and north Africa, plus two species from South Africa. Adults are small. Adults are diurnal, but females are larviform and wingless (females of the South African species are unknown). Larvae are leaf feeders (eggs laid on leaves, not in the female cocoon), somewhat slug-like, with concealed head. Hosts are grasses (Gramineae) and Compositae.

Megalopygidae (flannel moths) are a New World family of 263 species, mostly Neotropical; actual fauna likely exceeds 350 species. Adults are small to large and nocturnal. Larvae are leaf feeders, usually communal in early instars; slug-like, with concealed head; with poison spines usually beneath long hair-like setae. A large number of hostplants are recorded, and some species are polyphagous. A few are economic on forest trees and palms, but most are of medical importance due to urticating setae in adults and the poison spines in larvae.

Cossina

This is the second division of the Ditrysia (with a dorsal heart vessel) and includes all the macromoths and butterflies, plus a few more of the Microlepidoptera in subsection Cossina, where the pupae have dorsal spines (tribe Ceracini of Tortricidae are an exception). All the larger moths and butterflies are in subsection Bombycina, where the pupae are unspined. Subsection Cossina has three superfamilies: Cossoidae, Castnioidea, and Tortricoidea. Subsection Bombycina has eight superfamilies: Calliduloidea, Uranioidea, Geometroidea, Papilionoidea (including Hesperioidea), Drepanoidea, Bombycoidea, Sphingoidea, and Noctuoidea. All have the haustellum naked (unscaled), when present.

Cossoidea

This superfamily includes large “micro” -moths, such as in the carpenterworm moths (Cossidae), plus the slug caterpillar moth groups. There are two series used to divide the superfamily: Cossiformes, for the more primitive carpenterworm families (Cossidae, Dudgeoneidae, Metarbelidae, Cyclotornidae, and Epipyropidae), and Limacodiformes, for the slug caterpillar families (Dalceridae, Limacodidae, and Chrysopolomidae). About 2,054 species are known in the superfamily. Adults with head vestiture mostly rough-scaled; haustellum naked (or vestigial); labial palpi upcurved or short; maxillary palpi mostly reduced or absent; antennae mostly bipectinate; body mostly robust. Larvae have three lateral setae on the prothorax.

Cossidae (carpenterworm moths) total 682 species worldwide; actual fauna probably exceeds 750 species. There are five subfamilies. Adults are small to very large and nocturnal. Larvae are borers in trunks and limbs. Hostplants are recorded in a large number of plant families. A number of species are economic pests of forest trees.

Dudgeoneidae (Dudgeon carpenterworm moths) include only six species in the single genus Dudgeonea, with two species from Africa, one from India, and three from Australia. Adults are medium size; abdomen with small tympanal organs. Adults nocturnal as far as is known. Larvae mostly unknown, but one Australian species is a stem borer on Rubiaceae.

Metarbelidae (tropical carpenterworm moths) include 103 species, mainly Afrotropical and Oriental, with one species in the Palearctic region; actual world fauna likely exceeds 150 species. Adults are small to medium size and may be crepuscular. Larvae nocturnal borers on tree bark or in tree trunks, but most species remain unknown biologically. Hostplants include various trees. A few have minor economic status.

Cyclotornidae (Australian parasite moths) include only five known species from Australia, the most primitive of the Limacodiformes group of Cossoidea. Adults are small. Adult activity uncertain but may be crepuscular. Larvae flattened, with lateral protrusions; highly evolved as parasites of leafhoppers, scale insects, or psyllids (Hemiptera) in early instars, and then as predators of ant larvae.

Epipyropidae (planthopper parasite moths) total 40 described species, with at least another 30 known species awaiting naming; most diversity is in Australia. Two subfamilies are known. Adults are minute to small and crepuscular or nocturnal; females are sedentary. Larvae slug-like with rounded dorsum; parasitic on fulgorids and planthoppers (Hemiptera).

Dalceridae (tropical slug caterpillar moths) include 84 Neotropical species (one sp. intrudes from Mexico into southern Arizona). Two subfamilies are known. Adults are small to medium size. Adult activity uncertain; possibly only nocturnal or crepuscular. Larvae slug-like, often with translucent gelatinous wart-like surface; feeding as leaf feeders (early instars as leaf skeletonizers), but few are known biologically. Various hostplants are used and some larvae are polyphagous. Few have any economic status.

Limacodidae (slug caterpillar moths) total 1,104 known species worldwide, the largest family of Cossoidea, mostly tropical and especially biodiverse in the Oriental tropics; likely world total is near 1,600 species or more. Adults are small to medium size. Adults perhaps only nocturnal; many with unique resting postures. Larvae slug-like and mostly polyphagous leaf feeders, usually with an extensive array of poisonous stinging spines dorsally. Large numbers of hostplants utilized. Few species are economic other than medically as stinging caterpillars, but palm defoliators can be a problem in the tropics.

Chrysopolomidae (African slug caterpillar moths) are a small African family of about 30 known species. Two subfamilies are known. Adults are medium size and nocturnal. Larvae leaf-feeding and slug-like, with small spines; often colorful. Hostplants include Celastraceae. No economic species are known.

Castnioidea

This superfamily contains only the single family Castniidae. Often in the past thought of as the progenitor lineage to butterflies, they are now considered only an offshoot of cossoid like ancestors, while butterflies are evolved from geometroid-like ancestors that also developed into Hedylidae. Adults with head vestiture smooth-scaled and eyes large; haustellum naked (rarely vestigial); labial palpi often with distal segment erect; maxillary palpi 2 to 4-segmented; antennae clubbed. Body robust. Larvae with two or three lateral setae on the prothorax.

Castniidae (giant butterfly moths) total 170 known species, mostly Neotropical but with some species also in the Indo-Australian region; likely world total may exceed 180 species. Three subfamlies are known. Adults are medium to large size and diurnal or crepuscular. Larvae are borers of monocot plants, including grasses (Gramineae), Cyperaceae, Bromeliaceae, Marantaceae, Musaceae, and Palmae, among others. A few are economic on banana plants, various palms, and sugarcane.

Tortricoidea

Another monobasic superfamily exclusively for the family Tortricidae. In the past, the tortricid subfamilies were often considered separate families, such as Olethreutidae and Chlidanotidae, and even groups like Ceracidae and Cocylidae which now are only tribes (Ceracini are odd for Tortricoidea also due to their unspined pupae). Adults with head vestiture mostly roughened; haustellum naked (unscaled); labial palpi mostly porrect; maxillary palpi usually 4-segmented; antennae filiform; and body usually relatively stout. Larvae have three lateral setae on the prothorax.

Tortricidae (leafroller moths) are a large family of 8,945 described species from all faunal regions; the actual fauna likely will exceed 12,000 species. Three subfamilies are known. Adults are small (rarely medium sized) and mostly nocturnal or crepuscular, but some are diurnal. Larvae mostly leafrollers, but some are borers in various plant parts, including stems, branches, flowers, and seeds; a rare few are leaf litter feeders. Most species are restricted to certain hostplants among innumerable plant families. Many species are economic.

Bombycina

Remaining larger moths and the butterflies are in this subsection of the Cossina, including eight superfamilies.

Calliduloidea

This superfamily includes three families of ancient lineage with many primitive features: Ratardidae, Pterothysanidae, and Callidulidae. All are Old World and total 131 known species for the superfamily. Ratardidae are sometimes placed in Cossidae by some specialists, but represent a basal relict from cossoid ancestors similar to Metarbelidae, however on the lineage to Callidulidae. Adults with head vestiture average (rough in Ratardidae); haustellum naked (absent in Ratardidae); labial palpi usually porrect; maxillary palpi vestigial; antennae filiform or bipectinate; forewings broadly rounded or quadratic, or more acute; hindwings more rounded. Immature stages remain little known; larvae with two lateral setae on prothorax in Callidulidae.

Ratardidae (Oriental parnassian moths) are butterfly-like moths of the Himalayas and Oriental tropics, with ten described species, plus a few more still undescribed. Adults are medium sized, but males often much smaller than females. Adults are diurnal. Larvae are bark feeders, but biologies and larvae are mostly unknown.

Pterothysanidae (parnassian moths) include 19 species, from southern Africa (seven sp.) and Southeast Asia (12 sp.). There are two subfamilies. Adults are medium size and diurnal, possibly also crepuscular. Biologies and larvae remain unknown.

Callidulidae (Old World butterfly moths) include 102 species, mostly tropical Oriental, in two subfamilies. Adults are medium size and diurnal, flying like some butterflies in quick bursts to alternate leaf perches; resting position with wings held together and upright. Larvae largely unknown, except for two species which are leafrollers of ferns.

Uranioidea

This superfamily encompasses both very large and small moths among five families, mostly Old World: Epicopeiidae, Apoprogonidae, Sematuridae, Uraniidae, and Epiplemidae. Some of these families continue to be mixed up with Drepanoidea and Geometroidea, or have been combined into Epiplemidae. About 814 species are known in the superfamily. Adults with head vestiture mostly roughened (more average in Epiplemidae); haustellum naked; labial palpi mostly upcurved or short; maxillary palpi minute and one segmented; antennae filiform, but also bipectinate and clubbed or thickened in some species; forewings quadratic to triangular and somewhat pointed apically; hindwings usually rounded (some tailed). Larvae with two lateral setae on the prothorax, as far as is known.

Epicopeiidae (Oriental swallowtail moths) are a small family with 25 species known in two subfamilies, mostly Himalayan and East Asian. Adults are medium to large and diurnal. Larvae little known, but leaf feeders with waxy secretions over body. Hostplants are in Clethraceae, Cornaceae, Ericaceae, Theaceae, and Ulmaceae.

Apoprogonidae (African skipper moths) include only a single species from South Africa. Adults are medium size; antennae clubbed (hooked at tip); body robust. Adults presumed diurnal, but nothing is known of the biology or larvae.

Sematuridae (American swallowtail moths) total 36 Neotropical species, one of which just reaches into the United States, in southern Arizona. Adults are medium to large; antennae thickened, with elongated club (slightly hooked at tip). Adults nocturnal but some may be crepuscular. Larvae are leaf feeders, but few known biologically. Hostplants are unrecorded.

Uraniidae (swallowtail moths) comprise about 120 species from all tropical regions, mostly Indo-Australian (85 sp.); one species strays into the United States-Mexican border region (mainly in Texas). Two subfamilies are used. Adults are medium to large and nocturnal or diurnal, with some of the larger diurnal species known to migrate. Larvae are leaf feeders. Hostplants are known in Asclepiadaceae, Myrtaceae, and Euphorbiaceae.

Epiplemidae (crenulate moths) total about 632 species worldwide, with most being Neotropical (230 sp.) and Indo-Australian (301 sp.). Two subfamilies are used. Adults are small to medium size and nocturnal. Larvae are leaf feeders or webbers. Hostplants are in several plant families.

Geometroidea

One of the largest superfamilies of Lepidoptera, mainly with the large family Geometridae, but also including the odd Hedylidae (some specialists place the latter family near the true butterflies, in its own superfamily, Hedyloidea). The superfamily total comes to 21,190 known species. Adults with head vestiture normal; haustellum naked; labial palpi upcurved; maxillary palpi small; antennae mostly filiform (rarely bipectinate); forewings triangular, usually with somewhat pointed forewings (sometimes rounded), but sometimes emarginate or with falcate apex; hindwings more rounded in most species (rarely tailed); and body mostly slender and abdomen with tympanal organs. Larvae with two lateral setae on the prothorax, and most larvae have a reduced proleg number.

Geometridae (geometer moths), also called inch worms, are the second largest family of Lepidoptera, with about 21,150 described species from all faunal regions; the actual fauna probably exceeds 26,500 species. The major biodiversity is in the Neotropics, with over 6,500 species described, and the Indo-Australian region with about 6,670 species. The family is divided into eight subfamilies. Adults are small to large; a number of genera have brachypterous or apterous females. Adults mostly nocturnal, but also some crepuscular and diurnal groups. Larvae mostly leaf feeders, typically moving in looping fashion due to reductions in proleg numbers. Hostplants include most all plant families. Some major defoliating pests are known in this family.

Hedylidae (American butterfly moths) total only 40 known species, all Neotropical. Adults are medium size and nocturnal. Larvae are leaf feeders. Hostplants are recorded in Euphorbiaceae, Malvaceae, Streculiaceae, and Tiliaceae.

Papilionoidea

The butterflies, also called Rhopalocera, include seven families, including the skippers, family Hesperiidae. Skippers are sometimes placed in their own monobasic superfamily, Hesperioidea, but the differences can also be noted by using series Hesperiiformes and Papilioniformes. True butterflies include families Papilionidae, Pieridae, Lycaenidae, Riodinidae, Libytheidae, and

Nymphalidae. In the past, many of the subfamilies, especially in Nymphalidae, have been considered separate families, and the entire superfamily has on occasion been split into several superfamilies, such as Lycaenoidea and Nymphaloidea. Some specialists still include Riodinidae within Lycaenidae, and Libytheidae within Nymphalidae, and controversies about this continue. Extant butterflies number about 20,400 described species, but the actual butterfly fauna probably is about 23,500 species worldwide, due to the numerous still unnamed small skippers (Hesperiidae) and blues (Lycaenidae). Butterflies have 3-segmented, mostly upcurved labial palpi (only long and porrect in Libytheidae), small or vestigial maxillary palpi (1-segmented), head scaling relatively smooth in most groups, and a naked haustellum; antennae with clubs (hooked at tip in Hesperiidae); forewings mostly triangular, while hindwings are usually more rounded (sometimes with tails). Wing coupling via a humeral lobe rather than the frenulum-retinaculum arrangement of most moths. Larvae with two lateral setae on the prothorax.

Hesperiidae (skipper butterflies) include about 4,100 species from all faunal regions; most are Neotropical, with over 2,338 species. The actual world fauna probably exceeds 4,500 species. Seven skipper subfamilies are recognized. Adults are small to medium size and diurnal, usually with very rapid flight, but a few tropical species are crepuscular. Larvae are leafrollers or borers. Hostplants are primarily grasses (Gramineae) and other monocots. A few economic species are known, particularly on rice.

Papilionidae (swallowtail butterflies) total about 589 species worldwide, with about 260 species being Indo-Australian, including the largest of all butterflies, the birdwings. Three subfamilies are recognized. Adults are medium size to very large and diurnal. Larvae are leaf feeders; with an osmeterium defensive gland behind head. Hostplants include many plant groups. Some economic species are known, mainly citrus feeders

Pieridae (yellow-white butterflies) total about 1,275 species worldwide, most being Indo-Australian (ca. 515 sp.). Four subfamilies are recognized. Adults are small to large and diurnal. Larvae are leaf feeding. Various plants are utilized. Some economic species are known, particularly on cabbages amd other crucifers.

Lycaenidae (gossamer-winged butterflies) total about 5,955 species worldwide; the actual fauna probably exceeds 7,000 species. About 1,125 species are Neotropical. The family has eight subfamilies. Adults are small to medium size and diurnal, but a few of the relict genera possibly crepuscular or only in dark forests. Larvae mostly somewhat slug-like, with tubercles and short setae; head usually retractable into thorax. Larvae feed as leaf feeders (some on other plant parts), but many are myrmecophilous and some even are carnivorous on ant larvae or hemipterans. Hostplants are in a wide variety of plant families, but particularly Fagaceae and Leguminosae. A few economic species are known.

Riodinidae (metalmark butterflies) total about 1,419 species worldwide but predominate in the Neotropics (1,322 sp.); the actual world fauna probably exceeds 2,500 species. Five subfamilies are recognized. Adults are small to medium size and diurnal; often with rapid flight. Larvae are leaf feeders, but many are myrmecophilous; one is known to be carnivorous on hemipterans. Larvae mostly slug-like with short setae. Hostplants are recorded in numerous plant families.

Libytheidae (snout butterflies) are a small family of only 12 species, with at least one species in each faunal region. Adults are medium size and diurnal. Larvae are leaf feeders. Hostplants are in Ulmaceae.

Nymphalidae (brush-footed butterflies) are the largest family of butterflies, with about 7,080 described species worldwide; the actual fauna probably exceeds 8,000 species. To represent the division of relict basal groups within the family, the subfamilies are divided into two groups: Nymphalinina, with six subfamilies, and Satyrinina, also with six subfamilies. Adults are medium to large and diurnal, although crepuscular activity is known in a few cases (some Amathusiinae and Brassolinae). Larvae are mostly leaf feeders; a few feeding gregariously. Hostplant records are among almost all higher plants.

Drepanoidea

This superfamily includes four families perhaps most related to Geometroidea. The branching and reticulate nature of evolution places the butterflies first after Geometroidea and before Drepanoidea when listed on paper, representing a more evolved side branch. Some recent classifications have greatly disorganized this superfamily, placing Axiidae in its own monobasic superfamily (Axioidea) and merging Cyclidiidae and Thyatiridae into Drepanidae as subfamilies: the latter three families all have some cohesive features (e.g., abdominal tympanal organs) but also many unique features that provide evidence of family status. The superfamily comprises about 1,056 known species. Adults with head scaling normal; haustellum normal (small or absent in some Drepanidae); labial palpi mostly upcurved; maxillary palpi mostly vestigial; antennae varied but mostly serrate of filiform; body generally robust; forewings mostly triangular or somewhat elongated; and hindwings rounded. Larvae with two lateral setae on the prothorax.

Axiidae (gold moths) are a very small family of only six Palearctic species in the Mediterranean region. Adults are medium size and nocturnal. Larvae are leaf feeders. Hostplants are in Euphorbiaceae.

Thyatiridae (false owlet moths) comprise 224 species from all regions except Australia, but most are tropical Oriental (199 sp.); the actual fauna probably exceeds 275 species. Two subfamilies are recognized. Adults are medium size and nocturnal. Larvae are mostly nocturnal leaf feeders. Hostplants are recorded in a number of plant groups.

Cyclidiidae (giant hooktip moths) are a small family of 14 described species, all Oriental plus one species in the southern Palearctic. Adults are medium to large size and nocturnal. Larvae are leaf feeders. Hostplants recorded so far only in Alangiaceae

Drepanidae (hooktip moths) comprise 812 species worldwide, but predominately Oriental (647 sp.); none are known for the Neotropics and only a few are in the Nearctic; the actual fauna probably exceeds 950 species. Three subfamilies are known. Adults are small to medium size and nocturnal. Larvae are leaf feeders. Hostplants include a variety of plants. A few are economic.

Bombycoidea

This superfamily includes many of the largest moths and encompasses 13 families and about 4,810 known species. The superfamily is divided into two groups: series Bombyciformes (Carthaeidae, Eupterotidae, Apatelodidae, Bombycidae, Mimallonidae, Anthelidae, and Lasiocampidae) and series Saturniiformes (Endromidae, Lemoniidae, Brahmaeidae, Oxytenidae, Cercophanidae, and Saturniidae). Some specialists use the series names for two superfamilies, or even other superfamilies are added (such as Mimallonoidea), and there also is some confusion as to how many families are involved (e.g., Oxytenidae and Cercophanidae are sometimes included among Saturniidae by some researchers). Adults with head scaling often roughened; haustellum mostly absent; labial palpi mostly upcurved but sometimes reduced; maxillary palpi mostly vestigial or absent; antennae mostly bipectinate (also quadripectinate in Saturniidae); body generally robust and often with hair-like setae; forewings mostly triangular and hindwings rounded (some with long tails). Larvae with two lateral setae on the prothorax.

Carthaeidae (Australian silkworm moths) are a monobasic relict family in Bombycoidea with a single species from western Australia. Adults are large and nocturnal (usually flying after midnight). Larvae are leaf feeders, with numerous clubbed setae. Hostplants are only in Proteaceae.

Eupterotidae (giant lappet moths) total 325 species worldwide (except the Nearctic), but most are Oriental (238 sp.); only four species are recorded in the Neotropics. Three subfamilies are known. Adults are small to large and nocturnal. Larvae are leaf feeders. Hostplants among numerous different plants. Few species are economic (e.g., rice or forest pests).

Apatelodidae (American silkworm moths) are exclusively New World, and total 252 species, mostly Neotropical (247 sp.). Three subfamilies are used. Adults are small to medium size and nocturnal. Larvae are leaf feeders. Hostplants are in various plant families.

Bombycidae (silkworm moths) total 166 described species, all Old World and primarily Oriental (146 sp.), with only five species known for Africa. Two subfamilies are involved. Adults are medium size and nocturnal. Larvae are leaf feeders. Hostplants predominate in Moraceae. The silkworm (*Bombyx mori*) is used for silk production.

Mimallonidae (sackbearer moths) total 254 species, all New World and primarily Neotropical (250 sp.). Adults are medium size and nocturnal. Larvae are leaf feeders, with larval cases. Hostplants are recorded in a number of plant families. A few can be economic.

Anthelidae (Australian lappet moths) total 100 species, all from Australia. There are two subfamilies. Adults are medium size to large; rarely with micropterous females. Adults nocturnal, but at least one species with diurnal males. Larvae are leaf feeders and generally colorful. Host plants recorded in several plant families. Some species have urticating larval setae.

Lasiocampidae (lappet moths) include 2,130 species worldwide, with many in Africa (790 sp.). Subfamilies are five. Adults are small to large; some with micropterous females. Adults mostly nocturnal but some males are diurnal. Larvae are leaf feeders, sometimes communally in silken tent-like webbings. Hostplants are various. Some species are economic as tree defoliators.

Endromidae (glory moths) are a monobasic family of four species, from Europe to Central Asia. There are two subfamilies. Adults are medium size. Adult males are diurnal but females are nocturnal. Larvae are leaf feeders. Hostplants recorded in Betulaceae, Caprifoliaceae, Salicaceae, Tiliaceae, and Ulmaceae.

Lemoniidae (autumn silkworm moths) total 21 species, mostly Mediterranean. There are two subfamilies. Adults are medium size and nocturnal, but some males are diurnal; flight periods are often in the autumn in Europe. Larvae are leaf feeders. Hostplants are mostly in Compositae and Euphorbiaceae.

Brahmaeidae (brahmin moths) are a small family of 28 species, mostly Palearctic and African. There are two subfamilies. Adults are medium size to very large and nocturnal. Larvae are leaf feeders. Hostplants recorded in Asclepiadaceae and Oleaceae

Oxytenidae (American tropical silkworm moths) include 60 species, all Neotropical. Adults are medium size to large and nocturnal. Larvae are leaf feeders; some mimic snakes. Hostplants recorded in Rubiaceae.

Cercophanidae (Andean moon moths) include 30 species of mostly austral South American moths. There are two subfamilies Adults are medium size to large and nocturnal. Larvae are leaf feeders. Hostplants recorded in Celastraceae, Lauraceae, Saxifragaceae, and Tiliaceae.

Saturniidae (emperor moths) include 1,435 species worldwide, but are predominately Neotropical (860 sp.). There are seven subfamilies. Adults are medium size to very large and mostly nocturnal or crepuscular, but some are diurnal. Larvae are leaf feeders and many are polyphagous, some being communal or gregarious; many are extremely large. Hostplants are extremely varied. Some species are economic for agriculture, but major urticating larvae are involved in dermatitis and more severe allergic reactions, and in a few cases even from adult scales.

Sphingoidea

This is a monobasic superfamily for the hawk moth family, Sphingidae. Some specialists include the family in Bombycoidea. Adults with head scaling mostly normal (sometimes roughened); haustellum often very long; labial palpi mostly upcurved; maxillary palpi mostly small; antennae mostly clavate or lamellate and thickened; body robust; forewings mostly elongate-triangular and hindwings much smaller. Larvae with two lateral setae on the prothorax.

Sphingidae (hawk moths) total 1,230 species worldwide. Tropical regions of the New World, Africa and Asia have the most biodiversity. There are three subfamilies. Adults are medium size to very large and nocturnal or crepuscular, but some a diurnal. Larvae are leaf feeders, usually with posterior horn-like scolus (thus, the common name, hornworms, for the larvae); many larvae extremely large. Hostplants recorded in numerous plant families. Some are economic.

Noctuoidea

The largest superfamily, containing nearly a third of all lepidopterans, the Noctuoidea comprise about 44,025 described species, mainly in the families Noctuidae and Arctiidae. Six families are included in the superfamily: Notodontidae, Dioptidae, Thyretidae, Lymantriidae, Arctiidae, and Noctuidae. Numerous subfamilies among these families have at various times been considered families, and various specialists are still undecided on the number of families to use. For example, Thyretidae are sometimes included in Arctiidae and Dioptidae are included among Notodontidae. Contrarily, Oenosandrinae, Thaumetopoeinae, and Doinae are often listed as separate families. Adults with head scaling mostly normal (rarely roughened); haustellum naked (sometimes reduced); labial palpi mostly upcurved but many porrect or recurved; maxillary palpi mostly vestigial or absent (some larger in Notodontidae); antennae varied; body mostly robust; forewings mostly elongate triangular and hindwings more rounded; body usually robust and with metathoracic tympanal organs (but absent or vestigial in Syntominae, family Arctiidae). Larvae with two lateral setae on the prothorax.

Notodontidae (prominent moths) total 3,562 species from all faunal regions, particularly from the Neotropics (1,766 sp.); actual world fauna likely exceeds 4,000 species. The subfamily classification varies, but currently involves ten subfamilies, with segregation into three groups: Oenosandrinina (for Oenosandrinae, with three species in Australia), Thaumetopoeinina (for Thaumetopoeinae), and Notodontinina (for the remaining eight subfamilies). Adults are small to very large; some with massive bodies. Adults are mostly nocturnal. Larvae are leaf feeders, sometimes gregarious (especially among Thaumetopoeinae) and feeding nocturnally. Hostplants include a large variety of plant families, especially for broadleaf forest trees. A number of economic species are known.

Dioptidae (American false tiger moths) total 507 species, primarily Neotropical (505 sp.); actual fauna likely exceeds 800 species. Two subfamilies are known. Adults are medium size and mostly nocturnal, but some are diurnal or crepuscular. Larvae are leaf feeders, particularly toxic plants in families like Aristolochiaceae, Euphorbiaceae, Passifloraceae, and Violaceae, but also on various others like Fagaceae. Very few are economic.

Thyretidae (African maiden moths) include 212 species, all African. Adults are medium-size. Adults perhaps mostly diurnal; often wasp mimics. Larvae are thought to be leaf feeders, but most species remain unknown biologically. Hostplant records include Thymelaeaceae and Ulmaceae.

Lymantriidae (tussock moths) total 2,490 species worldwide; actual fauna likely exceeds 3,000 species. Most of the fauna is Old World tropical (ca. 2,090 sp.). Two subfamilies are used. Adults are small to very large and mostly nocturnal, but some are diurnal or crepuscular. Larvae are leaf feeders, sometimes gregariously. Hostplants include many different plant families. Many species are serious defoliators of forest trees.

Arctiidae (tiger moths) include 11,155 species worldwide, primarily Neotropical (ca. 6,000 sp.); actual world fauna likely exceeds 14,000 species.

There are five subfamilies among groups: group Pericopinina (with Pericopinae), group Arctiinina (for Lithosiinae and Arctiinae), and group Ctenuchinina (for Ctenuchinae and Syntominae). Adults are small to large; hindwings greatly reduced in some groups (wasp moths). Adults mostly nocturnal but many are crepuscular or diurnal (Pericopinae, Ctenuchinae, and Syntominae). Larvae are leaf feeders. Hostplants are varied among numerous plant families, including mosses and lichens.

Noctuidae (owlet moths) are the largest family of Lepidoptera, with about 26,310 described species worldwide; actual fauna likely exceeds 30,000 species. Major regions of biodiversity are in the Neotropics (ca. 8,600 sp.) and the Indo Australian region (6,500 sp.). Numerous subfamilies and tribes have been described and the classification is still in flux, but 26 subfamilies are now recognized, mostly in group Noctuinina; also segregated are Aganainae (previously in Arctiidae), in group Aganainina, and Herminiinae, in group Herminiinina. Adults are small to very large and mostly nocturnal, but some are crepuscular and several groups are diurnal. Larvae mostly leaf feeders, but many are borers. Hostplants include numerous plant families, but the majority of owlet moths are not known biologically. Some agricultural pests are included in the family (e.g., cutworms, armyworms, and others).

► Butterflies
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References

Bourgogne J (1951) Order des lépidoptéres. In: Grassé PP (ed) Traité de Zoologie. Anatomie, Systématique, Biologie. Insectes 10:174–448, 3 pl. Masson, Paris, France

Eaton JL (1988) Lepidopteran anatomy. Wiley, New York, NY, 257 pp

Heppner JB (1991) Faunal regions and the diversity of Lepidoptera. Trop Lepid 2 (suppl 1):185

Heppner JB (1998) Classification of Lepidoptera. In: Holarctic Lepidoptera, 5 (suppl 1):1–148 (1998); 14 (suppl 1):149–320 (2003); 15 (suppl 1): (in prep)

Hering EM (1925) Biologie der Schmetterlinge. J Springer, Berlin, Germany, 480 pp

Holloway JD, Bradley JD, Carter DJ (1987) Lepidoptera. In: CIE guides to insects of importance to man. 1. CABI and British Museum of Natural History, London, UK, 262 pp

Kristensen NP (ed) (1999) Lepidoptera, moths and butterflies. Vol. 1: Evolution, systematics, and biogeography. In: Handbuch der Zoologie. Band IV. Arthropoda: Insecta. Teilband 35. W. De Gruyter, Berlin, Germany, 487 pp

Portier P (1949) La biologie le lépidoptères. In: Encyclopédie entomologique (A) 23:1–643, 1 pl. P. Lechevalier, Paris, France

Scoble MJ (1992) The Lepidoptera: form, function and diversity. Oxford University Press, Oxford, UK, 404 pp

Stehr FW (ed) (1987) In Lepidoptera. In: Stehr FW (ed) Immature insects [1]. Kendall-Hunt, Dubuque, Iowa, pp 288–596

Vane-Wright RI, Ackery PR (eds) (1984) The biology of butterflies. Royal Entomological Society of London, London, UK, 429 pp. (Reprinted 1989. Princeton University Press, Princeton, NJ)

Watson A, Whalley PES (1975) The dictionary of butterflies and moths in color. McGraw Hill, New York, New York, 296 pp, 144 pl

Young M (1997)The natural history of moths. T. & A. D. Poyser, London, UK, 271 pp, 16 pl

Butterfly Counts

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The North American Butterfly Association, together with the Xerxes Society, coordinates the annual North American butterfly counts. Participants in this event pick a date, usually within two weeks on either side of July 4. On this date, the aim is to count, in a 24 h period, the number of species of butterflies and the number of individuals of each species within a circle 15 miles in diameter. When the same locations are visited year after year, a long term record of butterfly diversity and abundance is available from each site.

This has been an annual event since 1975 when there were 29 official counts. In 2000, 422 counts were held; 349 in 44 states in the U.S., 66 Canadian counts in five provinces, and seven Mexican counts in three states. The purpose of the counts is to get long term records, over a wide

Butterfly Counts, Table 11 Santa Fe Butterfly Count Results (Glorieta Canyon/Glorieta Peak)[a]*

	1994	1995	1996	1997
SWALLOWTAILS				
Black Swallowtail	1	–		-/5
Anise Swallowtail	–	–		-/1
Western Tiger	14	4		1/3
Two-tailed Swallowtail	5	–		2/1
Pale Swallowtail	5			-/-
WHITES AND SULFURS				
Pine White	–	–	6	-/-
Checkered White	2	44	–	24/-
Mustard White	37	11	–	12/-
Orange Sulfur	13	30	1	19/13
Southern Dogface	2	–	–	-/-
Mexican Yellow	–	14		-/-
Dainty Sulfur	1	29		2/-
LITTLE BUTTERFLIES				
Colorado Hairstreak			1	-/-
Great Blue Hairstreak	1		–	-/-
Coral Hairstreak	–	–	1	-/-
Behr's Hairstreak	7	1	–	-/-
Banded Hairstreak	72	38	2	10/-
Western Pine Elfin	–	1	–	-/-
Thicket Hairstreak	3	–	–	1/-
Juniper Hairstreak	2		–	-/-
Gray Hairstreak	1		–	1/-
Leda Ministreak	1		–	-/-
Marine Blue	4	–	–	-/-
Reakirt's Blue	62	33	–	1/-
Western Tailed-Blue	–	2	1	-/-
Melissa Blue	–	2	–	-/-
Acmon Blue	5	4	–	1/-
BRUSH-FOOTED BUTTERFLIES				
Variegated Fritillary	27	3	–	26/-
Atlantis Fritillary	4	20	7	10/4
Arachne Checkerspot	16	–	–	-/1
Silvery Checkerspot	1	36	1	
Northern Crescent	–	–	2	2/-
Field Crescent	–	–	1	3/-
Mylitta Crescent	–	1	–	6/-

Butterfly Counts, Table 11 (Continued)

Satyr Anglewing	1			
Green Anglewing	1	–	–	
Zephyr Anglewing	6	–	2	2/-
Mourning Cloak	7	11	3	7/2
American Lady	5	7	–	1/-
Painted Lady		20	1	5/7
West Coast Lady		10	–	-/-
Weidemeyer's Admiral	3	3	5	21/1
California Sister	3	–	–	-/-
Goatweed Butterfly				1/-
SATYRS AND WOOD NYMPHS				
Canyonland Satyr	1			1/-
Common Ringlet	2	–		
Small Wood-Nymph	74	45	86	27/7
MILKWEED BUTTERFLIES				
Monarch			–	1/-
SKIPPERS				
Silver-spotted Skipper	1	–	–	-/-
Mexican Cloudywing	2	3		-/1
Northern Cloudywing	2	2		-/-
Rocky Mountain Duskywing	–	2		-/-
Persius Duskywing	–	–	–	-/8
Afranius Duskywing	1	–	–	3/-
Common Checkered-Skipper	10	34	4	49/-
Sootywing sp	–	–	–	1/-
Russet Skipperling	7	7	1	3/-
Garita Skipperling	–	–	–	1/1
Pahaska Skipper	–	–	–	1/3
Tawny-edged Skipper	10	10	4	3/-
Snow's Skipper	6	–	–	
Golden Skipper	41	17	16	4/-
Dun Skipper	60	9	1	2/-
Common Roadside-Skipper	–	2	–	
Total species	36	32	20	35/17 (42)
Total butterflies	519	455	146	258/61(319)

geographical area, of butterfly diversity and abundance. A second, but equally important goal, is to increase public awareness of insect conservation. Consequently, counts are advertised and the general public is invited to participate. Each group records every species seen as well as the number of individuals of each species. Other information recorded is how many people counted, total number of miles covered, and total amount of time in the field as well as information about weather and habitat. Annual results are published by the North American Butterfly Association.

The data obtained in these counts is, due to the uncontrolled conditions, not the most systematic. However, it has still proven to be useful for looking at large trends. For example, the count data from 1989 to 1997 have been used to assess patterns of species richness and abundance across North America. The log of party hours (number of hours spent making observations in the field was used summed across all groups in a single count circle) to standardize species richness and abundance data. The study concluded that (i) species richness is highest in low latitudes and Rocky Mountain longitudes, (ii) total abundance is highest in northern U.S. latitudes and Great Plains longitudes, (iii) species richness increases with greater topographical relief, and (iv) species richness and diversity indices are lower in more disturbed habitats. The North American Butterfly Association magazine, "American Butterflies," publishes a count column which gives information about the counts and analyses of results. Butterfly enthusiasts interested in starting their own counts should visit the NABA web site www.naba.org. At this site information is available on running and reporting a count and who to contact in your region about count locations which already exist.

Butterfly counts are a wonderful way to introduce children, parents, and other interested individuals to butterflies. There does need to be at least one experienced butterfly identifier in the group, but everyone can run around and catch them. There are numerous opportunities to teach about host plants, habitat, habits and behaviors, and of course, butterfly identification. Many people who show up out of curiosity come back year after year and find it a great pleasure to compare results from year to year.

For those who want more precise data generated in a more systematic manner, Pollard transects are a good way to go. This technique uses a transect route which is marked out and followed, usually once per week. The counter walks at a standard pace and all butterflies within a fixed distance of the path are counted. This monitoring scheme is used in Great Britain and the Netherlands, and to a limited degree in the United States.

The accompanying table shows some typical count data from the Santa Fe, New Mexico, butterfly count Butterfly Counts From Areas of New Mexico, USA.

References

Kocher SD, Williams EH (2000) The diversity and abundance of North American butterflies vary with habitat, disturbance, and geography. J Biogeogr 27:785–794

North American Butterfly Association website. Available at www.naba.org

Pollard E, Yates TJ (1993) Monitoring butterflies for ecology and conservation. Chapman and Hall, London, UK

Butterfly Gardening

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Butterfly gardening has become a very popular pastime in recent years. Planting a butterfly garden is a simple and rewarding experience for both children and adults. If you like bird watching or flower gardening, you will love butterfly gardening! Unlike most wildlife, butterflies are not strictly limited to remote natural areas. They are commonly found in both country and city and can easily be attracted with a little know-how and the proper planning. A butterfly garden does not require much land; even a few strategic additions to an existing garden can make a big difference.

Whether it fits in a container on the patio or stretches over several acres, a well-planned butterfly garden can be as simple or as complicated as you want to make it. The same basic concepts and guidelines apply, regardless of the size. The most important thing to understand before you begin is that butterflies have many different behaviors, affinities, and needs. Also, these requirements often change dramatically throughout their life-cycle. A well-planned butterfly garden should provide variety to attract different kinds of butterflies and cater to both adult butterflies and their larvae. Proper choice of plants and landscape design is essential. Such decisions will help determine which butterfly species will be attracted, remain in the area, and ultimately reproduce.

Why You Should Plant a Butterfly Garden

Butterflies are the most popular of all insects. Besides being attractive, they play some important roles in the environment, including:

1. Butterflies help pollinate a wide range of native and cultivated flowering plants.
2. Butterflies provide food for many other organisms. Various small mammals, nesting birds, lizards, spiders, and other insects all feed on adult butterflies or their larvae.
3. Due to their tremendous appeal and popularity, butterflies often serve as "'umbrella'" species. When butterflies are protected, their habitats and the other creatures that live there are also protected.
4. Butterflies are indicator species. They are among the first organisms to show a negative reaction to environmental changes and pollutants. Just like a canary in a coalmine, butterflies can help alert us to problems in the local environment that may affect our own health and well-being.
5. Butterflies are a convenient way for you and your children to learn about insects, an abundant, important, but poorly known group of organisms.

The Butterfly Life Cycle

All butterflies go through a life cycle consisting of four distinct developmental stages: the egg, the larva or caterpillar, the pupa and the adult. Adult females typically deposit small eggs singly or in clusters on or near specific plant species. These host plants provide growing larvae with the proper nutrition they need to complete growth and development. Larval host plants may also furnish shelter, camouflage, and chemicals used for protection, courtship, and reproduction. Caterpillars (larvae) are herbivores (plant feeders) and have very selective tastes. Each butterfly species only feeds on specific plant species. Consequently, butterfly larvae rarely become pests of vegetable and ornamental plants, though they will greedily eat the host plants you provide for them.

Butterfly larvae can grow at an astonishing rate, increasing in size and weight many times over before reaching maturity. To accommodate this tremendous change in proportion, each larva molts numerous times during its life, revealing each time a new and often radically different larval skin. Once fully grown, the larva seeks a safe place to pupate. Most attach themselves to a branch, twig or other support by spinning silk. After a short rest, the larva molts for the last time to reveal the pupa, or chrysalis. Inside, larval structures break down and reorganize to form the adult butterfly. When environmental conditions are right, the pupa splits open and an adult butterfly emerges.

The Elements of a Butterfly Garden

There are several simple guidelines that, if followed, will result in a successful butterfly garden:

Provide a combination of adult nectar sources and larval host plants. A garden with both adult nectar sources and larval host plants can accommodate the entire life cycle of a butterfly. Having both adult and larval resources available will encourage adult butterflies to remain in your yard, reproduce, and build populations year after year.

Plant in both full sun and partial shade if you can. Most butterflies and their adult nectar sources are fond of bright sunlight. However, some butterflies are at home in woodlands or along forest edges and rarely venture out into open, sunny areas. They often are more attracted to nectar sources and larval host plants located in the shadier sections of the garden.

Plan for consistent host plant and nectar availability throughout the growing season. Choose plants that bloom, grow or perform better at different times of the year, as well as plants having one peak season. The added variety insures that your garden will provide continuous food for butterflies.

Plan for diversity. Choose plants that have a variety of different heights and growth habits. A diverse planting scheme helps to increase the number of microclimates and feeding levels available to butterflies. Also, provide a mix of flower colors, shapes, and sizes. Different butterfly species have distinct color preferences, feeding behaviors, and proboscis (tongue) lengths. These factors determine which flowers a butterfly chooses or is able to visit. A wide mix of adult nectar sources provides accessible and attractive food to a greater number of butterfly species.

Plant in groupings. If space allows, try to combine several plants of the same species in a large grouping. Large drifts of color and clusters of vegetation tend to be more apparent and attractive to adult butterflies. Groups of larval host plants provide larvae with additional resources in the event one is depleted, and help to mask leaf damage or defoliation.

Include native plants. Native plants are well adapted to the soil type and climate of the region where they naturally occur and are not as prone to disease or pest attack.

Choose the appropriate plant for each location. Determine the basic light, water, and soil requirements of each plant before planting. For example, avoid putting a sun-loving species in deep shade. This will insure ensure that your plants grow and perform to their maximum potential.

Weeds can be good for your garden. Many common weeds serve as larval host plants. Carefully search each plant for larvae before you pull it out. If larvae are present, leave the plant alone until they have finished feeding.

Learn to identify the butterflies in your area. Become familiar with your local butterfly species. Try to learn which ones are common, which ones are rare, and which ones you most want to attract. Then when it is time to choose the larval host plants for your garden, select your plants accordingly.

Adult Nectar Sources

Adult butterflies are highly active, but short-lived. During their brief adult period, they must find a mate, reproduce, seek out food and shelter, and avoid being. To accomplish all this, most adult butterflies rely on sugar-rich nectar as fuel.

Nectar-rich, colorful flowering plants, therefore, are the backbone of any successful butterfly garden. They draw in adult butterflies from the surrounding environment like a magnet while adding beauty and interest to the landscape. They also attract butterflies rapidly. Therefore, adult nectar sources should always be the first additions to a new butterfly garden.

When selecting flower colors, aim for a variety. While reds, pinks and purples are generally the most attractive adult nectar source colors, a great many butterfly species are also drawn to yellows, blues, and whites. Each butterfly species has its own color preferences.

Flower shape also influences visitation. In acquiring nectar, butterflies are limited by the length of their proboscis, or tongue. As a result, the nectar in long, tubular flowers is typically more accessible to butterflies possessing a longer proboscis. A butterfly's behavior while feeding affects its flower choice as well. Many large swallowtail butterflies, for example, continuously flutter their wings while nectaring. This enables them to feed much like hummingbirds, with access to flowers too delicate to land on. On the other hand, many smaller butterflies such as blues and hairstreaks prefer to feed while at rest. They are strongly attracted to large clusters of small, short-tubed flowers that form a stable platform on which to alight.

The greater the variety of flower colors, shapes, and sizes available, the greater variety of butterfly species will be attracted. Double- and triple-flowered plants are the only major exception to this rule. While such flowers produce spectacular blooms, they have been bred to impress humans, not butterflies. In the process, external features have been artificially manipulated, often at the expense of nectar content or accessibility.

Larval Host Plants

Larval host plants also are key ingredients to any successful butterfly garden. They are generally not as showy, nor are they absolutely necessary to attract adult butterflies. However, a garden composed solely of nectar plants provides nothing more than a simple, fast-food refueling spot. It completely ignores the requirements of the other stages of a butterfly life cycle. Consequently, adult butterflies come into the garden to feed but soon leave.

Larval host plants offer butterflies a reason to stay and not just pass through. Adults drawn into the garden by colorful nectar plants will now find all the necessary resources to reproduce. You will soon notice some of the same individuals returning day after day and many of the same butterfly species becoming garden regulars. Most adult butterflies tend not to wander far from their larval hosts. Thus, you may notice a greater number of butterflies. Instead of just attracting individuals from the surrounding area, your garden will produce new adults from the maturing larvae present.

Other Attractants

Not all butterflies are exclusively attracted to flowers. Many species, such as red-spotted purples, leaf wings, question marks, tawny emperors, hackberry butterflies, mourning cloaks, malachites, buckeyes, as well as some satyrs and wood nymphs are also drawn to or feed solely on tree sap, rotting fruit, dung or carrion.

To accommodate their needs, simply place one or more shallow dishes on the ground at various locations throughout the garden. Fill them with a selection of rotting fruit, banana peels, and melon rinds. Mash large pieces or whole fruit to help increase the available surface area and expose the juicy interior. Once a week or so, rinse out each dish with a garden hose and refill. If ants are a problem, fill a slightly larger dish with water and set the smaller fruit dish in the center. This creates a small moat and prevents the ants but not the butterflies from gaining access to the tasty meal.

Water

Males of many butterfly species commonly gather at water sources such as stream banks, mud puddles, moist gravel or damp sand for access to water, dissolved salts, and amino acids. Such groupings can form rather impressive displays. For the more ambitious butterfly gardener, artificial mud puddles or water stations can be created with varying degrees of effort.

The simplest method is to fill a large plastic container, such as a sweater storage box, with sand. Locate an open, sunlit area of your garden, dig a shallow hole, and place the container into the ground so that the rim is even with the top of the soil. Fill in any gaps around the outside of the container with loose earth and thoroughly wet the sand. The plastic container will hold in the water and keep the sand moist for some time.

The same process can be accomplished on a larger scale by lining an existing depression or newly dug hole with plastic. Simply make sure that the edges of the plastic are covered with soil and fill the center with sand or small gravel. A slightly concave design will help moisture collect from occasional rain and regular garden watering.

The spray from a small garden fountain placed nearby can also help keep the ground consistently moist.

To make the area even more attractive, initially mix in a small amount of table salt with the sand or occasionally add a capful of natural fish emulsion (an organic fertilizer available at most garden centers).

Shelter

In addition to food and water, butterflies often need protection from wind, rain, temperature extremes, and predators. The easiest way to accomplish this in the garden is to include many kinds of plants, including shrubs and small trees. Try also to cluster vegetation and add a few nondeciduous species. Given time, as your garden grows and matures, the diversity of plantings will naturally create several microclimates, or small localized environments, that offer butterflies shelter.

Keeping the Butterfly Garden Productive

There are a few basic steps that will help you keep your garden healthy, productive and looking its best:

Give new plants a good start. New plants can quickly become stressed. As a result, they are more vulnerable to disease and pest attack. They may grow poorly and even die if not properly attended. Therefore, make sure to mulch and regularly water all new plants. This will help reduce weed competition, keep them from drying out, and insure that they become firmly established. Healthy plants will reward you with vigorous growth and healthy blossoms.

Fertilize regularly. Routine fertilizer applications will help produce maximum plant growth and flower production. Consult a local nursery specialist or Extension agent if you have questions about specific fertilizers or particular plant requirements.

Avoid using pesticides. All butterfly life stages are extremely sensitive to pesticides. Even the slightest drift from nearby spraying can be deadly. If you want to have a butterfly garden, you must be willing to tolerate insects, including some that eat the flowers. Try to allow the natural enemies of insects to take care of the insect problems. Even *Bacillus thuringiensis*, or Bt, a natural bacterial disease of caterpillar pests that is normally considered harmless because it does not affect most insects, people, or pests, can be deadly to butterfly larvae. If you must use insect control, always choose the least toxic chemical first. Insecticidal soaps and horticultural oils, for example, can be effective against many small garden pests. They are harmless to humans and generally biodegradable. If the problem persists, move on to a stronger chemical, but apply it selectively. Apply pesticides only to the infested branch or plant and never treat the entire garden. Choose short-lived (non-residual) products. Particularly avoid using systemic pesticides on larval host plants. Unlike contact poisons, systemic pesticides are taken up by the plant. They kill when an insect eats the treated vegetation.

Trim off old blossoms. Periodic "deadheading," or removal of old, spent blossoms on your nectar plants, will encourage the continued production of new flowers. It can also extend the flowering period of some species.

Choice of Butterfly Plants

The choice of plants for your butterfly garden is determined by several factors, including the amount of sun or shade, the soil and moisture conditions, and the climate where you live. Therefore, the preferred plants vary from place to place, and for specific recommendations it is advisable to check with local butterfly gardening publications and educational sources such as the cooperative extension service in your area. As examples, following are lists of plants recommended for a northern climate, Nebraska, and a southern climate, Florida. Note that although some plants are recommended in both locations, few are recommended for both locations.

List of Plants to Attract Butterflies in Nebraska

Source: Nebraska Cooperative Extension Service, Nebguide G93–1183-A

{L} = Larval Food Plants

{N} = Nectar Plants

Annual Flowers

Ageratum - *Ageratum houstonianum* {N}
Common Sunflower - *Helianthus annuus* {L,N}
Cosmos - *Cosmos* spp. {N}
Fetid Marigold - *Dyssodia papposa* {L}
Globe Candytuft - *Iberis umbellata* {N}
Gomphrena - *Gomphrena globosa* {N}
Heliotrope - *Heliotropium arborescens* {N}
Lantana - *Lantana camara* {N}
Marigold - *Tagetes* spp. {N}
Nasturtium – *Tropaeolum* spp. {N}
Nicotiana - *Nicotiana alata* {N}
Petunia - *Petunia* x *hybrida* {N}
Salvia - *Salvia* spp. {N}
Scabiosa - *Scabiosa atropurpurea* {N}
Snapdragon - *Antirrhinum majus* {L,N}
Statice - *Limonium sinuatum* {N}
Sunflower - *Helianthus* spp. {N}
Sweet Alyssum - *Lobularia maritima* {N}
Verbena - *Verbena* spp. {N}
Zinnia - *Zinnia* spp. {N}

Biennials

Catnip - *Nepeta cataria* {N}
Chives - *Allium schoenoprasum* {N}
Dame's Rocket - *Hesperis matronalis* {N}
Dill - *Anethum graveolens* {L,N}
Lavender - *Lavender angustifolia* {N}
Mint - *Mentha* spp. {N}
Parsley - *Petroselinum crispum* {L,N}
Queen Anne's Lace - *Daucus carota* {L,N}
Sweet Fennel - *Foeniculum vulgare* {L,N}
Thistle - *Cirsium* spp. {L,N}

Shrubs

Butterfly Bush - *Buddleia davidii* {N}
Cinquefoil - *Potentilla* spp. {N}
Chokecherry - *Prunus virginiana* {L,N}
Cotoneaster - *Cotoneaster* spp. {N}
Lilac - *Syringa* spp. {N}
Mock Orange - *Philadelphus* spp. {N}
Privet - *Ligustrum* spp. {N}
Spirea - *Spiraea* spp. {N}
Viburnum - *Viburnum* spp. {N}
Wild Plum - *Prunus americana* {L,N}

Perennial Herbaceous Plants

Aster - *Aster* spp. {L,N}
BeeBalm - *Monarda* spp. {N}
Blanketflower - *Gaillardia* spp. {N}
Butterfly Weed - *Asclepias tuberosa* {L,N}
Chrysanthemum - *Chrysanthemum* spp. (open-centered types) {N}
Clover - *Melilotus* spp., *Trifolium* spp. {L,N}
Coreopsis - *Coreopsis* spp. {N}
Daylily - *Hemerocalli s* spp. {N}
Dogbane - *Apocynum* spp. {N}
Gayfeather - *Liatris* spp. {N}
Goldenrod - *Solidago rigida* {N}
Hollyhock - *Alcea rosea* {L}
Ironweed - *Vernonia* spp. {N}
Joe-Pye Weed - *Eupatorium* spp. {N}
Mallow - *Malva* spp. {L}
Milk-vetch - *Astragalus* spp. {L,N}
Milkweed - *Asclepias* spp. {L,N}
Ornamental Onion - *Allium* spp. {N}
Partridge Pea - *Cassia fasciculata* {L,N}
Phlox - *Phlox* spp. {N}
Pinks - *Dianthus* spp. {N}
Prairie Clover - *Dalea* spp. {L,N}

Purple Coneflower - *Echinacea* spp. {N}
Pussy-toes - *Antennaria* spp. {N}
Rudbeckia - *Rudbeckia* spp. {N}
Sedum - *Sedum* spp. {N}
Shasta Daisy - *Chrysanthemum maximum* {N}
Yarrow - *Achillea* spp. {N}

Plants For Butterfly Gardening in Florida

Source: Your Florida guide to butterfly gardening. A guide for the Deep South

Trees

American Plum - *Prunus americana*
Black Cherry - *Prunus serotina*
Chaste Tree - *Vitex agnus-castu*
Chickasaw Plum - *Prunus angustifolia*
Coastal Plains Willow - *Salix caroliniana*
Flowering Dogwood - *Cornus florida*
Hop Tree - *Ptelea trifoliata*
Mimosa - *Albiza julibrissum*
Redbud - *Cercis canadensis*

Shrubs

Azalea - *Rhododendron* sp.
Blackberry - *Rubus* sp
Butterfly Bush - *Buddleia davidii*
Button Bush - *Cephalanthus occidentalis*
Chinese Privet - *Ligustrum sinense*
Fire Bush - *Hamelia patens*
Glossy Abelia - *Abelia* x *grandiflora*
Golden Dewdrop - *Duranta repens*
Hibiscus - *Hibiscus* sp.
Ixora - *Ixora* sp.
Jatropha - *Jatropha integerrima*
New Jersey Tea -*Ceonothus americanus*
Plumbago - *Plumbago capensis*
Pride of Barbados - *Caeselpina pulcherima*
Red Buckeye - *Aesculus pavia*
Sweet Pepperbush - *Clethra alnifolia*
Virginia Willow - *Itea virginica*

Vines

Bougainvillea - *Bougainvillea* sp.
Coral Vine - *Antigon leptopus*
Honeysuckle - *Lonicera* spp.
Mexican Flame Vine - *Senecio*
Morning Glory - *Ipomoea* spp.
Star Jasmine - *Trachelospermum jasminoides*

Herbaceous Perennials

Aster - *Aster* spp
Bachelor's Button - *Centaurea* sp.
Black-eyed Susan - *Rudbeckia hirta*
Blazing Star - *Liatris* spp.
Blue Sage - *Salvia azurea*
Bluebeard - *Caryopteris chandonensis*
Blue-eyed Grass - *Sisyrinchium* sp.
Butterfly Weed - *Asclepias tuberosa*
Cardinal Flower - *Lobelia cardinalis*
Catchfly - *Silene* spp.
Cigar Plant - *Cuphea micropetala*
Coral Vine - *Antigon leptopus*
Coralbean - *Erythrina heracea*
Daylily - *Hemerocallis* sp.
Deer Tongue - *Carphephorus* sp.
Fire Spike - *Odontonema strictum*
Firecracker Plant - *Russelia equisetiformis*
Frogfruit - *Phyla nodiflora*
Garden Phlox - *Phlox paniculata*
Glorybower - *Clerodendrum bungei*
Goldenaster - *Chrysopsis* sp.
Goldenrod - *Solidago* spp.
Groundsel - *Senecio* spp.
Heliotrope - *Heliotropium arborescens*
Indian Blanket - *Gaillardia pulchella*
Indigo Bush - *Amorpha fruticosa*
Ironweed - *Vernonia* spp.
Joe-pye Weed - *Eupatorium fistulosum*
Jupiter's Beard - *Centrantus ruber*
Lantana - *Lantana* sp.

Mexican Heather - *Cuphea hysoppifolia*
Mexican Milkweed - *Asclepias curassavica*
Mist Flower - *Eupatorium coelestinum*
Moss Verbena - *Verbena tenuisecta*
Mountain Mint - *Pycnanthemum* sp.
Obedient Plant - *Physostegia virginiana*
Pentas - *Pentas lanceolata*
Porter Weed - *Stachytarphaeta jamaicensis*
Purple Coneflower - *Echinacea purpurea*
Rattlesnake Master - *Eryngium yuccifolium*
Sandhill Milkweed - *Asclepias humistrata*
Sedum - *Sedum* spp
Shepherd's Needle - *Bidens alba*
Shrimp-plant - *Beloperone guttata*
Society Garlic - *Tulbaghia violacea*
Spotted Beebalm - *Monarda punctata*
Stokes' Aster - *Aster laevis*
Sunflower - *Helianthus* sp
Swamp Milkweed - *Asclepias incarnata*
Tall Wild Verbena - *Verbena brasiliensis*
Tropical Sage - *Salvia coccinea*
Tuber Vervain - *Verbena rigida*
Verbena - *Verbena* sp
Wild Petunia - *Ruellia brittoniana*
Yarrow - *Achillea millefolium*

Some Larval Host Plants and Species Supported:

Beggar's-tick (*Desmodium* sp.), Long-tailed Skipper (*Urbanus proteus*)

Black Cherry (*Prunus serotina*), Tiger Swallowtail (*Papilio glaucus*), Red-spotted Purple (*Limenitis arthemis astyanax*)

Blue Passionflower (*Passiflora caerulea*), Gulf Fritil lary (*Agraulis vanillae*)

Camphor Tree (*Cinnamonum camphora*), Spicebush Swallowtail (*Papilio troilus*)

Cassia (*Cassia* sp.), Cloudless Sulphur (*Phoebis sennae*), Orange-barred Sulphur (*Phoebis philea*), Sleepy Orange (*Eurema nicippe*)

Coastal Plain Willow (*Salix caroliniana*), Viceroy (*Limenitis archippus floridensis*)

Coontie (*Zamia pumila*), Atala (*Eumaeus atala florida*)

Corky-stemmed Passion Vine (*P. suberosa*), Gulf Fritillary (*Agraulis vanillae*), Zebra Longwing (*Heliconius charitonius*), Julia (*Dryas iulia*)

Cudweed (*Gnaphalium* sp.), American Painted Lady (*Vanessa virginiensis*)

Dill (*Anethum graveolens*), Black Swallowtail (*Papilio polyxenes*)

Dutchman's Pipe (*Aristolochia* sp.), Polydamus Swallowtail (*Battus polydamus*), Pipevine Swallowtail (*Battus philenor*)

False Indigo (*Amorpha fruticosa*), Dogface Butterfly (*Zerene cesonia*)

False Nettle (*Boehmeria* sp.), Red Admiral (*Vanessa atalanta*)

Fennel (*Feoniculum vulgare*), Black Swallowtail (*Papilio polyxenes*)

Frogfruit (*Phyla nodiflora*), White Peacock (*Anartia jatrophae*), Phaon Crescent (*Pyciodes phaon*)

Gerardia (*Agalinus* sp.), Buckeye (*Junonia coenia*)

Green Ash (*Fraxinus pennsylvanica*), Tiger Swallowtail (*Papilio glaucus*)

Green Shrimp-plant (*Blechum brownei*), Malachite (*Siproeta stelenes*), White Peacock (*Anartia jatrophe*)

Hercule's-club (*Zanthoxylum clava-hercules*), Giant Swallowtail (*Papilio cresphontes*)

Hop Tree (*Ptelea trifoliata*), Giant Swallowtail (*Papilio cresphontes*)

Indigo Bush (*Indigofera* sp.), Ceraunus Blue (*Hemiargus ceraunus*)

Joint Vetch (*Aeschynemone* sp.), Barred Sulphur (*Eurema daira*)

Live Oak (*Quercus virginiana*), White M Hairstreak (*Parrhasius m-album*)

Maypop (*Passiflora incarnata*), Zebra Longwing (*Heliconius charitonius*), Gulf Fritillary (*Agraulis vanillae*), Julia (*Dryas iulia*), Variegated Fritillary (*Euptoieta claudia*)

Mexican Milkweed (*Asclepias curassavica*), Monarch (*Danaus plexippus*), Queen (*Danaus gilippus*)

Partridge Pea (*Cassia fasciculata*), Cloudless Sulphur (*Phoebis sennae*), Little Sulphur (*Eurema lisa*)

Parsley (*Petroselinium crispum*), Black Swallowtail (*Papilio polyxenes*)

Pawpaw (*Asimina* sp.), Zebra Swallowtail (*Eurytides marcellus*)

Pencil Flower (*Stylosanthes biflora*), Barred Sulphur (*Eurema daira*)
Plantain (*Plantago* sp.), Buckeye (*Junonia coenia*)
Red Bay (*Persea borbonia*), Palamedes Swallowtail (*Papilio palamedes*), Spicebush Swallowtail (*Papilio troilus*)
Rue (*Ruta graveolens*), Black Swallowtail (*Papilio polyxenes*), Giant Swallowtail (*Papilio cresphontes*)
Ruellia (*Ruellia* sp.), Buckeye (*Junonia coenia*), Malachite (*Siproeta stelenes*), White Peacock (*Anartia jatrophe*)
Saltwort (*Batis* sp.), Great Southern White (*Ascia monuste*)
Sassafras (*Sassafras albidum*), Spicebush Swallowtail (*Papilio troilus*)
Shepherd's Needle (*Bidens alba*), Dainty Sulphur (*Nathalis iole*)
Slippery Elm (*Ulmus rubra*), Question Mark (*Polygonia interrogationis*)
Smooth Water Hyssop (*Bacopa monnieri*), White Peacock (*Anartia jatrophe*)
Southern Red Cedar (*Juniperus virginiana*), Swead nerís Hairstreak (*Mitoura gryneus sweadneri*)
Spicebush (*Lindera benzoin*), Spicebush Swallowtail (*Papilio troilus*)
Sugarberry (*Celtis laevigata*), Hackberry Butterfly (*Asterocampa celtis*), Tawny Emperor (*Asterocampa clyton*), Question Mark (*Polygonia interrogationis*), Snout Butterfly (*Libytheana bachmanii*)
Swamp Bay (*Persea palustris*), Palamedes Swallowtail (*Papilio palamedes*), Spicebush Swallowtail (*Papilio troilus*)
Sweet Bay (*Magnolia virginiana*), Tiger Swallowtail (*Papilio glaucus*), Palamedes Swallowtail (*Papilio palamedes*), Spicebush Swallowtail (*Papilio troilus*)
Toadflax (*Linaria* sp.), Buckeye (*Junonia coenia*)
Tree Pawpaw (*Asimina triloba*), Zebra Swallowtail (*Eurytides marcellus*)
Turkey Oak (*Quercus laevis*), Banded Hairstreak (*Satyrium calanus*)
Virginia Peppergrass (*Lipidium virginicum*), Checkered White (*Pontia protodice*), Great Southern White (*Ascia monuste*), Cabbageworm (*Pieris rapae*)
Virginia Snakeroot (*Aristolochia serpentaria*), Pipevine Swallowtail (*Battus philenor*), Polydamus Swallowtail (*Battus polydamus*)
Wax Myrtle (*Myrica cerifera*), Red-banded Hairstreak (*Calycopis cecrops*)
White Ash (*Fraxinus americana*), Tiger Swallowtail (*Papilio glaucus*)
White Oak (*Quercus alba*), Banded Hairstreak (*Satyrium calanus*)
White Sweet Clover (*Melilotus alba*), Gray Hairstreak (*Strymon melinus*), Alfalfa Butterfly (*Colias eurytheme*)
Wild Lime (*Zanthoxylum fagara*), Giant Swallowtail (*Papilio cresphontes*)
Winged Elm (*Ulmus alata*), Question Mark (*Polygonia interrogationis*)
Winged Sumac (*Rhus copallina*), Red-banded Hairstreak (*Calycopis cecrops*)
The butterfly web site: http://www.thebutterflysite.com/gardening.shtml

References

Daniels JC (2000) Your Florida guide to butterfly gardening: a guide for the Deep South. University Press of Florida, Gainesville, FL
Minno M, Minno M (1999) Florida butterfly gardening. University Press of Florida, Gainesville, FL
North American Butterfly Association web site. Available at http://www.naba.org/pubs/bgh.html
Tekulsky M (1985) The butterfly garden. The Harvard Common Press, Boston, MA

Buxton, Patrick Alfred

Patrick Buxton was born in 1892. He attended Cambridge University in 1916–1921, and in those years completed his medical training and qualified with the degrees of M.R.C.S. and L.R.C.P. However, his attendance was disrupted by service in World War I, during which he was stationed in Iraq ("Mesopotamia") and Iran ("northwestern Persia"). He concluded those studies in 1921, with a diploma in tropical medicine and hygiene. Then, he accepted an appointment to the government of Palestine (which later became Israel) as entomologist, and worked there for two years. Next, he joined a medical and scientific expedition to Samoa. From the expedition resulted his publications "Researches in Polynesia and Melanesia"; and "Insects of Samoa." In 1925, he was appointed director of the Department of Entomology of the London School of Hygiene and Tropical Medicine, and from 1931 he also held the chair of medical entomology in the University of London. He took numerous trips to Africa to work on Glossina and sleeping sickness, and from these visits resulted his (1948) "Memoirs on trypanosomiasis in eastern Africa"; and (1955) "History of tsetse flies." He was elected a fellow of The Royal Society in 1947. He died in 1956.

Reference

Hall WJ (1956) The president's remarks. Proceedings of the Royal Entomological Society of London (C) 20:73–77

Byrrhidae

A family of beetles (order Coleoptera). They commonly are known as pill beetles.

► Beetles

Byturidae

A family of beetles (order Coleoptera). They commonly are known as fruitworm beetles.

►Beetles

Cabbage Aphid, *Brevicoryne brassicae* (L.) (Hemiptera: Aphididae)

BEATA GABRYS
University of Zielona Gora, Poland, Zielona Gora

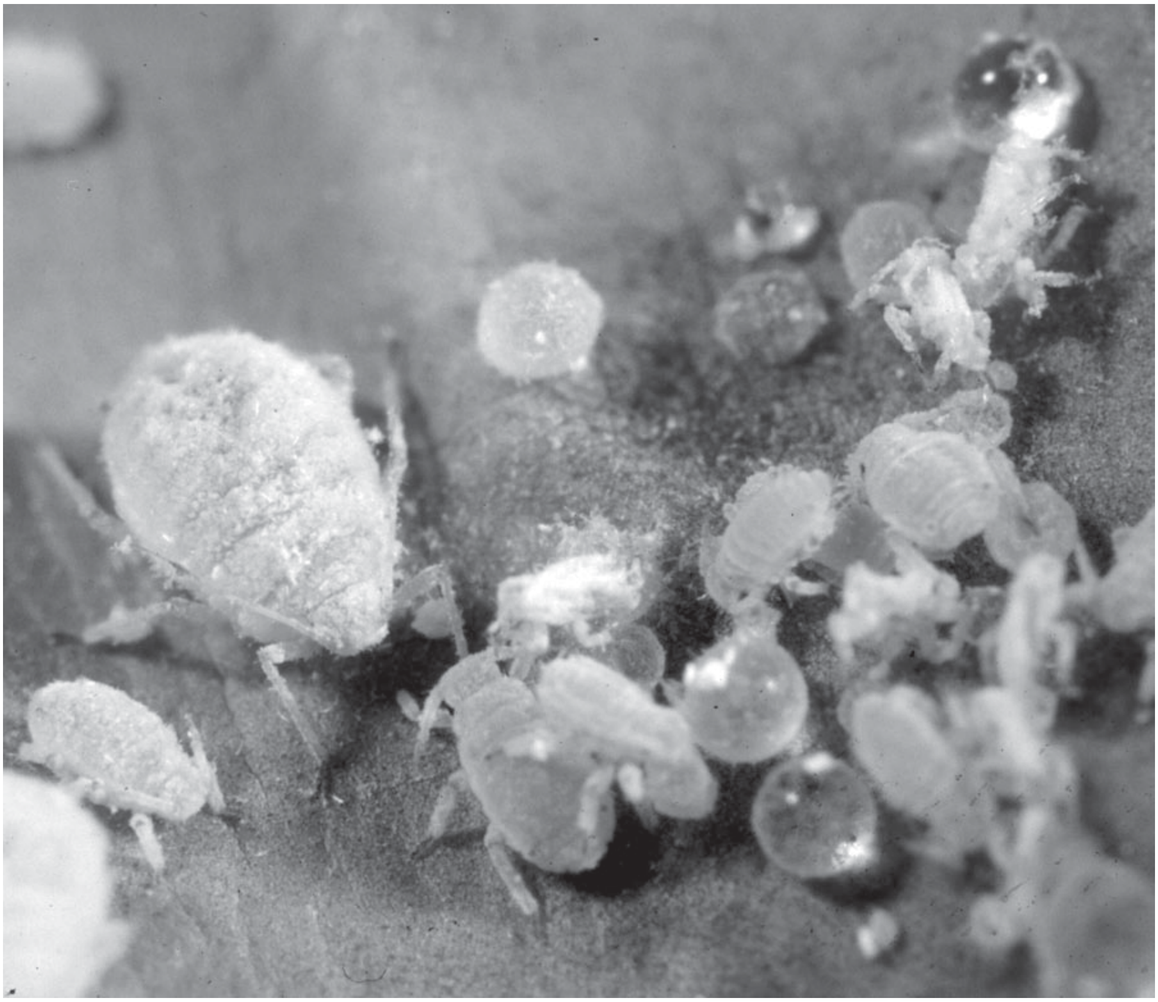
Apterous females (called apterae) are green-yellow or greyish-green, with a dark head and two rows of dark spots dorsally on the thorax and abdomen. The body is covered with a thick greyish-white or bluish mealy wax (Fig. 1). The siphunculi (cornicles) are small and dark. The body is 1.6–2.6 mm long. Winged females (called alatae) are green, with the head and ventral side black, and black transverse bars on dorsal abdomen. The wax layer is thinner in the alatae than in the apterae. The body is 1.6–2.8 mm long. Males are winged. The number of chromosomes is 2n = 16.

Cabbage aphid occurs throughout all the temperate and warm temperate parts of the world. *B. brassicae* lives in colonies that can contain hundreds to several thousand densely packed individuals.

The type of cabbage aphid life cycle depends on the climatic conditions during winter. In colder regions it is holocyclic (sexual forms – winged males and apterous oviparous females (oviparae) – appear in autumn; females release a sex pheromone, nepetalactone, and after mating they lay overwintering eggs). Where the winter is mild, they are anholocyclic (aphids reproduce parthenogenetically the year round). Parthenogenetic females are viviparous (they give birth to nymphs). Depending on the temperature and humidity conditions, one cabbage aphid generation develops in 7–10 days.

Cabbage aphid is monoecious, its host range consisting primarily of plants in the family Brassicaceae (=Cruciferae) in summer as well as in winter, including such important crops as oilseed rape and cabbage vegetables (head cabbage, Brussels sprouts, cauliflower, kale, collards). The host plants may be divided into three groups depending on their ability to support aphid populations: permanent, temporal, and accidental host plants. Permanent host plants support the cabbage aphid population throughout the whole vegetation period. A female may give birth to about 20 nymphs (larvae) in 10 days on these plants (e.g., *Brassica napus* L., *B. oleracea* L., *Sinapis alba* L.). Temporal host-plants support 2–3 aphid generations. A female feeding on temporal host plants produces about ten larvae in 10 days (such plants as *Lepidium sativum* L., *Isatis tinctoria* L.). On accidental host-plants, aphids may develop less than one generation (e.g., *Thlaspi arvense* L. (10 larvae/10 days/female), *Capsella bursa-pastoris* (L.) Med. (5 larvae/10 days/female), *Lunaria annua* L. (4 larvae/10 days/female), *Erysimum cheiranthoides* L. (0 larvae/10 days/female).

Older nymphs and adult apterae leave plants in response to overcrowding and decline in plant quality; they move within a plant or between plants via touching stems or the soil. Winged morphs appear following overcrowding and decline in plant quality, or in reaction to environmental factors such as temperature (below 10–15°C for at



Cabbage Aphid, *Brevicoryne brassicae* (L.) (Hemiptera: Aphididae), Figure 1 **Cabbage aphids on cabbage leaf. Note white waxy exudates on aphid bodies.**

least 24 h), and seasonal changes in day length (photoperiod). Overcrowding alone is not responsible for appearance of winged forms in cabbage aphid colonies.

During flight, cabbage aphid responds to physical and chemical stimuli. Shape, size, and density of plants, as well as light of high intensity (especially wavelengths of 550–590 nm) are significant cues. Particularly important is the contrast between light reflected from bare soil and plants. Summer migrants do not respond to host plant volatiles from large distances; however, they do react positively to host plant volatiles in close proximity, especially the volatile products of glucosinolate breakdown.

While on the plant surface, *B. brassicae* is relatively unaffected by mechanical barriers. However, exceptionally dense hairs can protect plant parts against aphid infestation. Epicuticular wax structure also is important; cabbage aphids drop off smooth surfaces. Glucosinolates typical of a given plant species, and n-alkane mixture in epicuticular waxes present on the plant surface, can be recognized by cabbage aphids. It is not clear whether these chemicals bear any importance in host selection. The existence of external contact chemoreceptors at the tips of aphid antennae is not well documented. It is assumed that aphids tend to initiate stylet probes into plant tissues regardless of the nature of surface chemicals. Landing on an unsuitable plant motivates cabbage aphids for new flights. Flight muscle autolysis occurs several days after settling and the start of reproduction.

When probing (i.e., inserting and moving the stylets within plant tissues), cabbage aphid selects for high turgor and high amino acid, sucrose, and glucosinolate content in young and growing plant parts of its host plants. When aphid stylets are in peripheral tissues (epidermis and mesophyll), the continuation of probing depends on detection of chemical stimulants – glucosinolates – in mesophyll cells. Aphids are able to sample mesophyll cell content during brief cell punctures along the stylet pathway. Feeding deterrents may impede stylet penetration at epidermis and parenchymatous tissues as well as at vascular tissue level. When aphid stylets are in vascular tissues (phloem and xylem), cabbage aphid responds positively to a high content of amino-acid nitrogen, and at the same time it is relatively resistant to its loss. High nitrogen fertilization of soil promotes cabbage aphid population development under field conditions. The development of *B. brassicae* is positively correlated with treonine, tyrosine, alanine, leucine, and glutamic acid content, and negatively correlated with phenylalanine content. A minimum of 15% sucrose content stimulates feeding by the cabbage aphid. Such concentrations occur in phloem sap of growing leaves. Among plant allelochemicals, the glucosinolates are very strong phagostimulants for the cabbage aphid. In phloem sap of young leaves, the glucosinolate concentration reaches 10 mM. However, most glucosinolates do not have direct effect on aphid performance. Cabbage aphid fecundity is positively correlated with some alkenyl glucosinolates (e.g., progoitrin, sinigrin) content, and a negative correlation is found for indole ones (e.g., glucobrassicanapin, neoglucobrassicin). Glucosinolate metabolism in the aphid is not known. Some amount of the ingested glucosinolates is sequestered in cabbage aphid hemolymph. The glucosinolates may also be hydrolyzed by endogenous aphid myrosinases (aphid myrosinases are not identical with plant myrosinases). High lectin content in the phloem sap causes high mortality of *B. brassicae*. The possible mechanism for this toxicity may be binding of lectin to chitinous structures in the stylets and foregut.

Cabbage aphid may reduce plant growth by 35%, the number of side branches by 43%, and the oil content by over 10%. Aphids may cause 85% yield loss and may induce the increase in glucosinolate content in rapeseed. Content of certain amino acids (e.g., methionine) increases in phloem sap due to cabbage aphid feeding. *B. brassicae* transmits about 20 plant viruses.

The natural enemies of the cabbage aphid are primarily generalist insect predators such as Coccinellidae and Carabidae (Coleoptera), Syrphidae (Diptera), Chrysopidae (Neuroptera), and parasitoids. There is only one primary parasitoid species of *B. brassicae* – *Diaeretiella rapae* (Mc Intosh) (Hymenoptera, Aphidiidae). It may reduce aphid populations by 30–40% at the peak infestation.

► Crucifer Pests and their Management

References

Gabrys B (1999) Semiochemicals in the biology and ecology of the cabbage aphid *Brevicoryne brassicae* (L.). Zeszyty Naukowe Akademii Rolniczej we Wroclawiu. Rozprawy. CLXIV. 356. 84 pp

Hafez M (1961) Seasonal fluctuations of population density of the cabbage aphid, *Brevicoryne brassicae* (L.) in the Netherlands and the role of its parasite, *Aphidius (Diaeretiella) rapae* (Curtis).Tijdscrift vor Plantenziekten 67:445–548

Klingauf FA (1987) Host plant finding and acceptance. In: Minks AK, Harrewijn P (eds) Aphids, their biology, natural enemies and control, vol 2B. Elsevier, Amsterdam, pp 209–223

Markkula M (1953) Biologisch-ökologische Untersuchungen uber die Khlblattlaus, *Brevicoryne brassicae.* (L.) (Hem., Aphididae) Ann Soc Zool Bot Fenn Van 15:1–133

Nault LR, Styer WE (1972) Effect of sinigrin on host selection by aphids. Entomol Exp Appl 15:423–437

Cabbage Looper, *Trichoplusia ni* (Hübner) (Lepidoptera: Noctuidae)

The cabbage looper is found in many crucifer-growing areas of the world, including parts of

Africa, Asia, Europe and North America. However, overwintering occurs only in warm-winter regions. The cabbage looper is highly dispersive, and adults have sometimes found at high altitudes and far from shore. Flight ranges of approximately 200 km have been estimated.

Description and Life Cycle

The number of generations completed per year varies from two to three in cool-summer climates to several overlapping generations in warmer climates. Development time (egg to adult) requires 18–25 days when insects are held at 32–21°C, respectively, so at least one generation per month could be completed successfully under favorable weather conditions. There is no diapause present in this insect, and although it is capable of spending considerable time as a pupa, it does not tolerate prolonged cold weather. It reinvades most temperate regions annually after overwintering in warmer latitudes. In the eastern United States, overwintering regularly occurs only in the southern half of Florida.

Egg

Cabbage looper eggs are hemispherical in shape, with the flat side affixed to foliage. They are deposited singly on either the upper or lower surface of the leaf, although clusters of six to seven eggs are not uncommon. The eggs are yellowish white or greenish in color, bear longitudinal ridges, and measure about 0.6 mm in diameter and 0.4 mm in height. Eggs hatch in about 2–5 days.

Larva

Young larvae initially are dusky white, but become pale green as they feed on foliage. They are somewhat hairy initially, but the number of hairs decreases rapidly as larvae mature. Larvae have three pairs of prolegs, and crawl by arching their back to form a loop and then projecting the front section (Fig. 3) of the body forward. The mature larva is predominantly green, but is usually marked with a distinct white stripe on each side. The thoracic legs and head capsule are usually pale green or brown. Dorsally, the larva bears several narrow, faint white stripes clustered into two broad white bands. In some cases the mature larva is entirely green. The body is narrower at the anterior end, and broadens toward the posterior. It measures 3–4 cm in length at maturity. Head capsule width is 0.29, 0.47, 0.74, 1.15, and 1.79 mm, respectively, for instars one through five. Larval development generally requires 19–20 days.

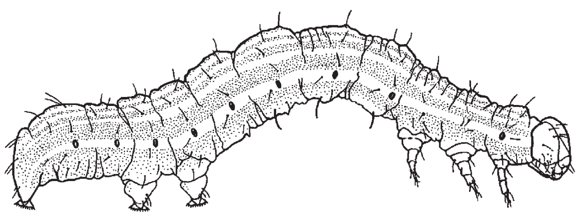
Pupa

At pupation, a white, thin, fragile cocoon in formed on the underside of foliage, in plant debris, or among clods of soil. The pupa measures about 2 cm in length. Duration of the pupal stage is about 4, 6, and 13 days at 32, 27, and 20°C, respectively.

Adult

The forewings of the cabbage looper moth are mottled gray-brown in color; the hind wings are light brown at the base, with the distal portions dark brown (Fig. 2). The forewing bears silvery white spots centrally: a U-shaped mark and a circle or dot that are often connected. The forewing spots, although slightly variable, serve to distinguish cabbage looper from most other crop-feeding noctuid moths. The moths have a wingspan of 33–38 mm. During the adult stage, which averages 10–12 days, 300–600 eggs are produced by females. Moths are considered to be seminocturnal because feeding and oviposition sometimes occurs about dusk. They may become active on cloudy days or during cool weather, but are even more active during the nighttime hours.

Cabbage Looper, *Trichoplusia ni* (Hübner) (Lepidoptera: Noctuidae), Figure 2 Adult of cabbage looper, *Trichoplusia ni*.



Cabbage Looper, *Trichoplusia ni* (Hübner) (Lepidoptera: Noctuidae), Figure 3 Cabbage looper larva.

Host Plants

The cabbage looper feeds on a wide variety of cultivated plants and weeds. As the common name implies, it feeds readily on crucifers, and has been reported damaging broccoli, cabbage, cauliflower, Chinese cabbage, collards, kale, mustard, radish, rutabaga, turnip, and watercress. Other vegetable crops injured include beet, cantaloupe, celery, cucumber, lima bean, lettuce, parsnip, pea, pepper, potato, snap bean, spinach, squash, sweetpotato, tomato, and watermelon. Additional hosts are flower crops such as chrysanthemum, hollyhock, snapdragon, and sweetpea, and field crops such as cotton and tobacco. Surprisingly few common agricultural weeds are frequent hosts. Adults feed on nectar from a wide range of flowering plants, including clover, *Trifolium* spp.; goldenrod, *Solidago canadensis*; dogbane, *Apocynum* spp.; sunflower, *Helianthus* spp.; and others.

Damage

Cabbage loopers are leaf feeders, and in the first three instars they confine their feeding to the lower leaf surface, leaving the upper surface intact. The fourth and fifth instars chew large holes, and usually do not feed at the leaf margin. In the case of cabbage, however, they feed not only on the wrapper leaves, but also may bore into the developing head.

Natural Enemies

The cabbage looper is attacked by numerous natural enemies, and the effectiveness of each seems to vary greatly. Most studies note the effectiveness of wasp and tachinid parasitoids, and a nuclear polyhedrosis virus (NPV). During the latter instars, *Voria ruralis* (Fallen) (Diptera: Tachinidae), a solitary or gregarious endoparasite attacking the medium or large size larvae, often is the dominant cause of death, accounting for an average of about 53% mortality. *Trichoplusia ni* NPV causes about 12% mortality, and undetermined fungi about 10%. *Copidosoma truncatellum* (Dalman) (Hymenoptera: Encyrtidae) is the other significant mortality factor, but accounted for only six to seven percent mortality. Other studies reported that egg parasitism of cabbage looper by *Trichogramma* (Hymenoptera: Trichogrammatidae), while variable, could reach about 35%. Despite the abundance of parasitoids, however, *T. ni* NPV is usually considered the key factor affecting populations. Early signs of larval infection by NPV are a faint mottling of the abdomen in the area of the third to the sixth abdominal segments. This is followed by a more generalized blotchy appearance, and the caterpillar eventually becomes creamy white in color, swollen, and limp. Caterpillars die within 5–7 days of contracting the disease.

Management

Blacklight traps and pheromone traps have been used in an attempt to predict looper population densities. Pheromone releasers and blacklight traps can be combined to increase moth catches. Insecticide resistance has become a problem in cabbage looper control, but susceptibility varies widely among populations. *Bacillus thuringiensis* has long been used for effective suppression of cabbage looper, and has the advantage of not disrupting populations of beneficial insects.

► Crucifer Pests and their Management
► Vegetable Pests and their Management

References

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, 729 pp
Elsey KD, Rabb RL (1970) Analysis of the seasonal mortality of the cabbage looper in North Carolina. Ann Entomol Soc Am 63:1597–1604
McEwen FL, Hervey GER (1960) Mass-rearing the cabbage looper, *Trichoplusia ni*, with notes on its biology in the laboratory. Ann Entomol Soc Am 53:229–234
Oatman ER, Platner GR (1969) An ecological study of insect populations on cabbage in southern California. Hilgardia 40:1–40
Shorey HH (1963) The biology of *Trichoplusia ni* (Lepidoptera: Noctuidae). II. Factors affecting adult fecundity and longevity. Ann Entomol Soc Am 56:476–480
Shorey HH, Andres LA, Hale RL (1962) The biology of *Trichoplusia ni* (Lepidoptera: Noctuidae). I. Life history and behavior. Ann Entomol Soc Am 55:591–597

Cabbage Maggot or Cabbage Root Fly, *Delia radicum* (Linnaeus) (Diptera: Anthomyiidae)

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Cabbage maggot (cabbage root fly) is known as a pest throughout the northern hemisphere. It apparently was introduced accidentally from Europe to North America in the early 1800s. Cabbage maggot thrives under cool conditions, and rarely is reported to be a pest south of about latitude 45 degrees north, and when it is, it usually occurs at a high elevation. Quite cold tolerant, it is found in some of the northernmost agricultural regions.

Life History

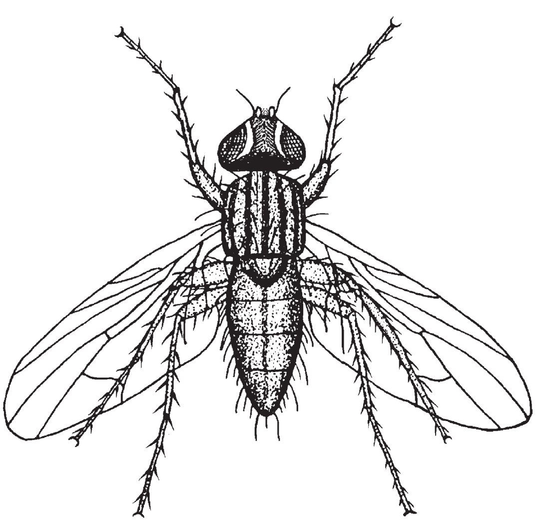
The number of generations occurring annually varies from one in the far north to three in optimal climates, although there are occasional reports of four generations. The generations may overlap considerably. A developmental threshold of about 6°C has been determined for most life stages. The time required for a complete generation is estimated at 40–60 days.

Eggs normally are laid in the soil around the stem of cruciferous plants, but sometimes eggs are deposited directly on the stem of plants. The elongate eggs are white in color, and taper markedly at both ends, but one end is more blunt than the other. One side of the egg is flattened or slightly concave, with the opposite side convex. Eggs measure about 1.1 mm long and 0.34 mm wide. The eggs are often laid in clumps of a few eggs, but sometimes hundreds of eggs are found at the same location, evidence that more than one female may oviposit at the same spot. Females commonly produce 300–400 eggs during their life span of 30–60 days. Eggs hatch in 3–5 days, averaging about 3.5 days at 20°C.

There are three instars. The length of the mouthparts (cephalopharyngeal skeleton) can be used to differentiate instars, with mean lengths of 0.44, 0.80, and 1.24 mm, respectively. The larvae are white in color and attain lengths of about 1.5, 3.7, and up to 8 mm, respectively. The mouth hooks are black. Located immediately behind the head is a pair of brownish fan-like spiracles, each of which is divided into about 12 lobes. Larvae feed externally and internally on roots, and internally on stem tissue. The larval period requires about 18–22 days under field conditions, but development time may be altered by weather. Exposure of first and second instar larvae to cool temperatures or short photoperiods seems to induce diapause in the pupal stage.

The puparium is oval, bluntly rounded at both ends, and brown in color. The average length is 5.5 mm, with a range of 3.5–6.5 mm. The duration of the prepupal stage is about 3–5 days, and the pupa requires 12–25 days during the summer. However, this is the overwintering stage, so it is prolonged for 5–8 months in the overwintering generation(s). Overwintering pupae require at least 22 weeks of temperatures < 6°C to complete diapause development. The puparia from the summer generations are usually found in the soil immediately adjacent to the root on which the larvae last fed. Sometimes they occur within the plant tissue, including the aboveground stem tissue. Aestivation occurs in response to warm temperatures, above 20°C, and especially in response to hot temperatures, 27–30°C. In preparation for overwintering, the larvae seem to disperse further from the plant, and deeper into the soil. Overwintering puparia may be found 12–15 cm from the plant, and commonly are found in the soil at a depth of 10 cm.

The adults are dark with gray markings (Fig. 4). The male bears three blackish longitudinal bands on the thorax, but these markings are less distinct on the female. The flies are quite bristly, and measure 5–7 mm long. Adults feed on nectar from flowering plants. If they obtain adequate food they may persist for 2–4 weeks, whereas they perish in 2–3 days if denied food. Adults are highly attracted to crucifers for oviposition. The preoviposition period of adults is about 6 days.



Cabbage Maggot or Cabbage Root Fly, *Delia radicum* (Linnaeus) (Diptera: Anthomyiidae), Figure 4 Adult cabbage maggot (cabbage root fly), *Delia radicum* (Linnaeus).

Cabbage maggot commonly attacks cruciferous vegetable crops, including broccoli, Brussels sprouts, cabbage, cauliflower, collard, kale, kohlrabi, mustard, radish, rutabaga, turnip, and watercress. It has been reported from noncrucifer crops on occasion, but these are misidentifications that stem from the difficulty in accurately identifying this fly. Cruciferous weeds apparently do not play a significant role in the biology of this insect; although some appear to be suitable hosts, they rarely are mentioned in the economic entomology literature.

Important natural enemies include staphylinids of several genera, particularly *Aleochara* sp. (Coleoptera: Staphylinidae); a wasp, *Trybliographa rapae* (Westwood) (Hymenoptera: Eucoilidae); and a mite, *Trombidium* sp. (Acari: Trombidiidae). *Aleochara* sp. attack the pupal stage of cabbage maggot, *Trybliographa* attacks the larvae, and the mite destroys the eggs.

Natural control has been studied extensively in both Europe and North America. Egg predation by staphylinids and carabids may reach 90–95% annually. *Aleochara* are very effective predators, but become active too late in the spring to have much effect on first generation cabbage maggot. *Trybliographa* is fairly effective at high host densities, often parasitizing in excess of 50% of available hosts. Other natural enemies of the immature cabbage maggot include numerous hymenopterous parasitoids of questionable economic importance, carabids (Coleoptera: Carabidae) and ants (Hymenoptera: Formicidae). General predators undoubtedly attack the adults, but they are not considered to be important.

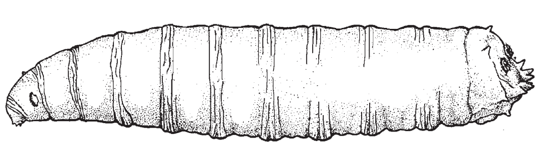
Fungi are commonly observed infecting flies. *Entomophthora muscae* and *Strongwellsea castrans* cause epizootics among adults during wet weather, and though impressive, act too late to prevent early season crop damage.

The spring generation tends to appear consistently, but latter generations are greatly influenced by weather. Rain and cool weather may decrease egg production and egg predation, and cause starvation of flies, but optimal egg production is associated with temperatures of 18–21°C, which corresponds well with the weather occurring during most spring generations. Pupal development is particularly susceptible to delay caused by hot temperatures, which normally is associated with summer generations. Dry soil is lethal to eggs.

Damage

Larvae (Fig. 5) damage crucifers by feeding on the roots and, to a much lesser degree, the stems or petioles of plants. Damage to leaf crops such as cabbage is most evident in the late spring; signs of feeding damage are initially seen as drooping or wilting of a few leaves, and then perhaps the entire plant. Delayed maturity and stunting are common responses to root maggot injury. Plant death often coincides with drought or water stress, when the injury to roots is fully expressed. When plants are small, five to ten maggots are necessary to kill the seedling. However, later in the season densities of 100 maggots or more may be supported satisfactorily if the plant has adequate water.

Cabbage maggot larvae feed on the rootlets or feeder roots, but invariably move to the main or tap root as they mature. They scar the surface and burrow into the root. In the case of crops that are harvested for their root, such as radish and turnip, damage results in severe crop loss, and in this case the autumn generation may be quite important. The summer generation causes little damage. Damage tends to be greater on loamy sand soil than on sand or clay soil, but as a general rule light soils are more problem prone.



Cabbage Maggot or Cabbage Root Fly, *Delia radicum* (Linnaeus) (Diptera: Anthomyiidae), Figure 5 Mature cabbage maggot (larva of cabbage root fly), *Delia radicum* (Linnaeus).

Although most eggs are laid on the soil, a small number are sometimes deposited on plant tissue, resulting in injury by larvae to leaflets, especially to Brussels sprout buttons. Occasionally the growing points of plants are attacked, resulting in multiple heads.

Management

Adult flight periods can be monitored by using cone screen traps baited with crucifers. Baits are more effective than yellow sticky traps, although sticky trap captures are correlated with egg deposition rates. Horizontal surfaces are more suitable than vertical surfaces for landing by flies. Dispensers that release isothiocyanates, naturally occurring odors released by crucifers, can be used as lures. Color, but not leaf pattern, also can influence host selection. Water traps baited with isothiocyanate can be used to monitor population, but trap catches do not predict egg numbers accurately.

Flight activity can be predicted from thermal unit accumulations. The overwintering (partly developed) generation require about 300 day-degrees (above a base temperature of 43°F). Subsequent generations require about 1200 degree-days.

With the introduction of chlorinated hydrocarbon insecticides, damage by cabbage maggot was greatly reduced. Long-lasting insecticides, applied to the soil at planting, protect the roots from larvae. This remains the principal method of plant protection in commercial crucifer production, but the insecticides have been changed over time as resistance to insecticides developed. Loss of insecticide efficacy is due not only to selection for insecticide resistant insects, but enhanced degradation of insecticide by soil microbes.

Insecticides are typically applied as a granular formulation over the seed bed or incorporated into the soil, or as a liquid drench. Foliar applications are sometimes made to suppress adults. Foliar application of insecticides, timed according to temperature accumulations, can be superior to soil applications or calendar-based sprays. Seed treatment can be an effective method of providing protection to seedlings, but it does not work well for all insecticides. Naphthalene has been investigated in Europe for repellency to ovipositing flies; although good protection occurs for about 6 weeks, the cost of application is high.

Modification of planting and tillage practices is often recommended for reduction in cabbage maggot damage. Delayed planting is reported to allow the young plants to escape oviposition by the spring adults. Sanitation also is quite important, as the roots and stems of crucifers left in the field can be very suitable for autumn and early spring generations of cabbage maggot. Crop residues should be deeply buried, or pulled and allowed to dry completely. High plant densities are more attractive than low densities to flies, but because there are more plants on which to distribute the eggs, yield may be equivalent at both plant densities. Introducing diversity into the landscape, as by undersowing portions of a crucifer crop with clover, will disturb the normal host orientation pattern and reduce oviposition. Similarly, single row intercropping of crucifers with unrelated plants will greatly reduce the oviposition rate on crucifers.

Physical manipulations of the crop environment also assist pest suppression. Crops covered tightly with row covers escape injury by cabbage maggot. Tar paper or cardboard discs, or collars made of other weather-resistant material, placed around the stem of seedlings have long been recommended as a physical barrier to reduce the ability of females to deposit eggs at the soil-stem interface. A precise fit is required, however, or the flies will circumvent the barrier.

Reliable biological control techniques have not yet been developed. Entomopathogenic nematodes (Nematoda: Steinernematidae and Heterorhabditidae) have been evaluated for suppression of larvae. Although heterorhabditid nematodes are attracted to cabbage maggot larvae and pupae, under field conditions they have not been shown to be effective. Steinernematid nematodes provide some suppression of cabbage maggot larvae in pot and field trials, but very high densities of nematodes are needed, at least 100,000 nematodes per plant. This is not entirely surprising because fly larvae are less susceptible to nematodes than are many other insects. In Europe, the potential of using the predatory beetle *Aleochara bilineata* (Gyllenhal) (Coleoptera: Staphylinidae) to achieve biological suppression of cabbage maggot is being studied; while technically feasible, the costs thus far are high.

Despite the common name, cabbage is less attractive to cabbage maggots than some other crucifer crops. Chinese cabbage, mustard, rutabaga, and turnip tend to be more severely injured than cabbage. There also is some variation within vegetable crops in resistance to attack; fast growing varieties seem most injured. Overall, not much progress has been made on finding cultivars resistant to cabbage maggot.

► Crucifer Pests and their Management
►Vegetable Pests and their Management

References

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, 729 pp

Finch S (1989) Ecological considerations in the management of *Delia* pest species in vegetable crops. Ann Rev Entomol 34:117–137

Finch S (1993) Integrated management of the cabbage root fly and the carrot fly. Crop Protection 12:423–430

Fulton BB (1943) The cabbage maggot in North Carolina. North Carolina. Agr Exp Stn Bull 335, 24 pp

Cabbageworm, *Pieris rapae* (Linnaeus) (Lepidoptera: Pieridae)

The cabbageworm occurs in temperate regions around the world, and is easily confused with other common cabbage white butterflies. In most temperate areas, it is a serious pest if insecticides are not used to protect cabbage. In North America, it is known as the imported cabbageworm because it is an invader; in Europe it is known as the small white cabbage butterfly.

Life Cycle and Description

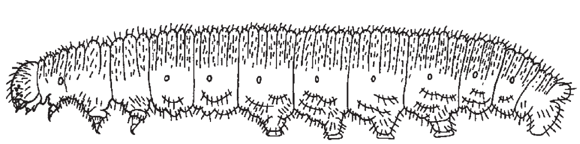
The complete life cycle of this insect requires 3–6 weeks, depending on weather. The number of generations reported annually is two to three in cool climates such as Canada, increasing to six to eight in southern areas.

Egg

Eggs are laid singly, usually on the lower surface of outer leaves of plants. The egg measures 0.5 mm in width and 1.0 mm in length, and initially is pale white in color but eventually turns yellowish. The egg is laid on end, with the point of attachment flattened and the distal end tapering to a blunt point. The shape is sometimes described as resembling a bullet.

Larva

The larva is green, velvety in appearance (Fig. 6), and bears five pairs of prolegs. There are five instars. Head capsule widths are about 0.4, 0.6, 0.97, 1.5, and 2.2 mm, respectively. Body lengths at maturity of each instar averages 3.2, 8.8, 14.0, 20.2, and 30.1 mm, respectively. The larva requires about 15 days to complete its development during August. Average development times for each instar at 19°C was observed to be 4.5, 3.0, 3.3, 4.1, and 7.8 days, respectively. All larval stages except the first instar bear a narrow yellow line running along the center of the back; this stripe is sometimes incomplete on the early instars. A broken yellow line, or series of yellow spots, also occurs on each side.



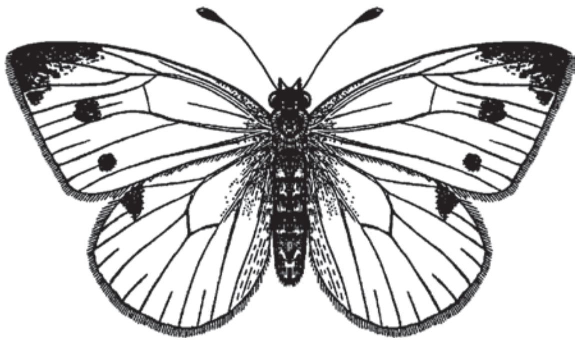
Cabbageworm, *Pieris rapae* (Linnaeus) (Lepidoptera: Pieridae), Figure 6 **Larva of cabbageworm, *Pieris rapae*.**

Pupa

Pupation normally occurs on the food plant. The chrysalis is about 18–20 mm in length, and varies in color, usually yellow, gray, green and speckled brown. A sharply angled, keel-like projection is evident dorsally on the thorax, and dorsolaterally on each side of the abdomen. At pupation, the chrysalis is anchored by the tip of the abdomen to the silk pad, and a strand of silk is loosely spun around the thorax. Pupation during the summer generations lasts about 11 days. The chrysalis is the overwintering stage, however, so its duration may be prolonged for months. The proportion of pupae that diapause increases as autumn progresses, so that at the time of the final generation all pupae are in diapause.

Adult

Upon emergence from the chrysalis the butterfly has a wingspan of about 4.5–6.5 cm. It is white above with black at the tips of the forewings. The front wings are also marked with black dots: two in the central area of each forewing in the female, and one in case of males (Fig. 7). When viewed from below, the wings generally are yellowish, and the black spots usually show faintly through the wings. The hind wing of each sex also bears a black spot on the anterior edge. The body of the butterfly is covered with dense hair, which is colored white in females, but darker in males. The adult typically lives about 3 weeks. The female produces 300–400 eggs. The adult is very active during the daylight hours, often moving from the crop to flowering weeds to feed.



Cabbageworm, *Pieris rapae* (Linnaeus) (Lepidoptera: Pieridae), Figure 7 Adult of cabbageworm.

Damage

Cabbageworms feed on foliage, and if left unchecked often will reduce mature plants to stems and large veins. Although they prefer leafy foliage, larvae may burrow into the heads of broccoli and cabbage, especially as they mature. Larvae are often immobile, and difficult to dislodge, and may be overlooked when cleaning produce. Larvae produce copious quantities of fecal material which also contaminate and stain produce.

Host Plants

Larvae of this insect feed widely on plants in the family Cruciferae, but occasionally on a few other plant families that contain mustard oils. Commonly attacked are vegetable crops such as broccoli, Brussels sprouts, cabbage, cauliflower, collard, horseradish, kale, and kohlrabi. Also sometimes attacked are flowers such as nasturtium and sweet alyssum, and weeds in the family Cruciferae. Adults sip nectar from flowers, and are commonly seen feeding at a number of plants.

Natural Enemies

The imported cabbageworm is subject to numerous predators, parasitoids, and diseases. *Apanteles glomeratus* (L.) (Hymenoptera: Braconidae) attacks the early instars, and emerges from the mature larva as it prepares to pupate. *A. glomeratus* is readily observed in the field, searching diligently on foliage for larvae. Dead cabbageworm larvae are often found with clusters of 20–30 *A. glomeratus* cocoons attached. In some areas tachinids (Diptera: Tachinidae) are more important than wasps.

Virus and fungal diseases of imported cabbageworm have been reported, but the predominant natural disease in a granulosis virus (GV). *P. rapae* GV occurs most commonly under high density conditions, and often among late instar larvae after they have consumed the exterior foliage of plants and are forced into close contact. Over 90% mortality of larvae due to natural occurrence of this disease has been reported. In the early stages of infection, larvae are inactive and paler in color. As the disease progresses, the caterpillar body turns yellow, and tends to appear bloated. After death, the body blackens, the integument ruptures, and the liquefied body contents ooze on the plant foliage. Rainfall has a major roll in assisting the spread of the virus on the plant, and from the soil to the plant.

Management

Imported cabbageworm are readily killed by foliar application of insecticides, including the bacterial insecticide *Bacillus thuringiensis*. Crucifer crops differ is their susceptibility to attack by imported cabbageworm. Chinese cabbage, turnip, mustard, rutabaga, and kale are less preferred than cabbage, collards, Brussels sprouts, broccoli, and cauliflower. Some cultivars of certain crops also have moderate levels of resistance to infestation by imported cabbageworm. Cabbage butterflies avoid ovipositing on red cabbage varieties. However, larval survival is favored by red cabbage, so red varieties are not a satisfactory solution to the caterpillar problem.

► Crucifer Pests and their Management
► Vegetable Pests and their Management

References

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, 729 pp

Chittenden FH (1916) The common cabbage worm. USDA Farmers' Bull 766, 16 pp

Harcourt DG (1963) Biology of cabbage caterpillars in eastern Ontario. Proc Entomol Soc Ontario 93:61–75

Richards OW (1940) The biology of the small white butterfly (*Pieris rapae.*), with special reference to the factors controlling its abundance. J Anim Ecol 9:243–288

Cactus Flies

Members of the family Neriidae (order Diptera).

► Flies

Cactus Moth, *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae)

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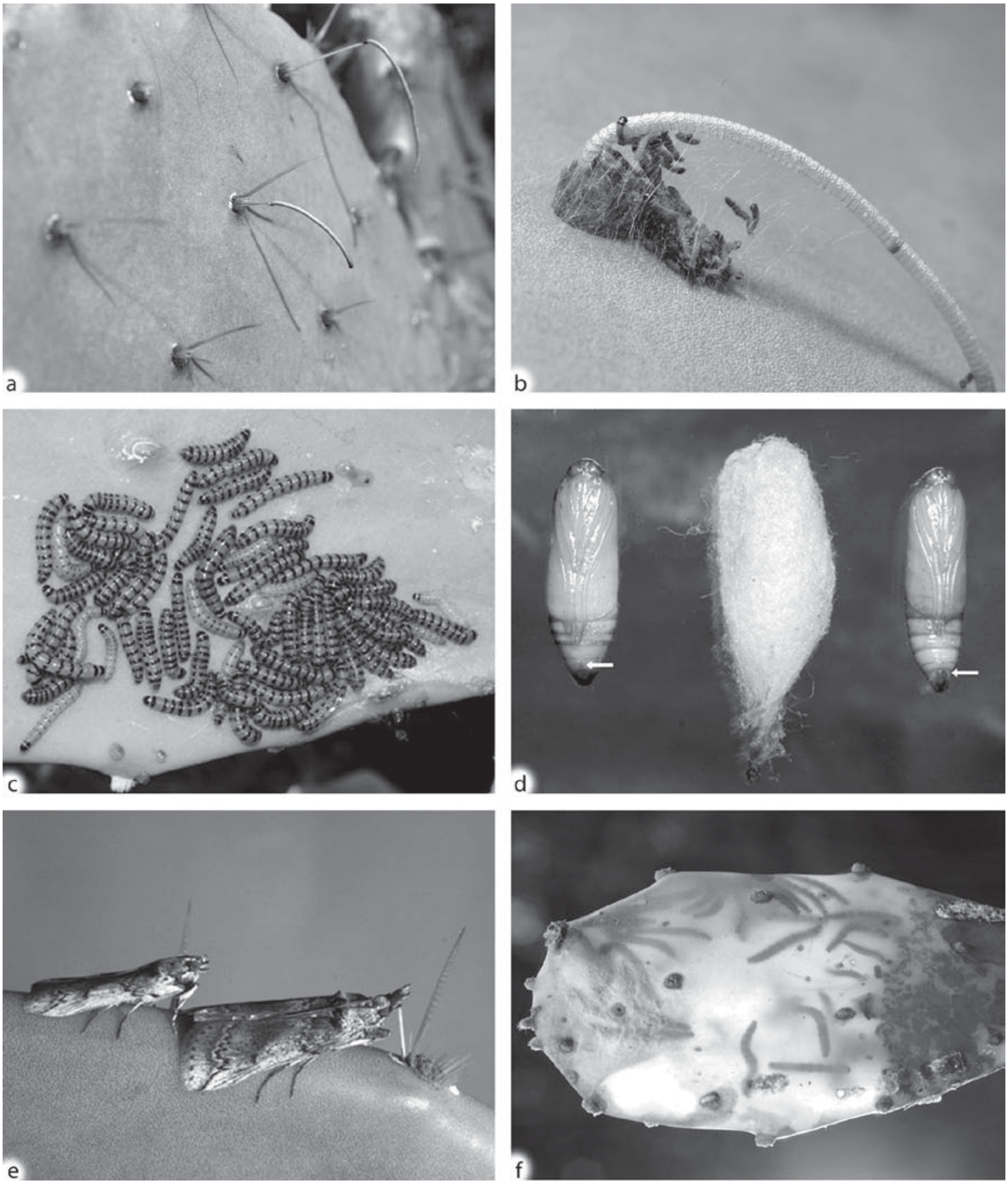
The cactus moth became a textbook example of successful classical biological control after it was imported from Argentina into Australia in 1926 to control invasive *Opuntia* cacti. To date, the moth continues to play an active role in controlling *Opuntia* in Australia. In 1989, *Cactoblastis* was found in Florida (USA), subsequently spreading northward to South Carolina and westward to Alabama by 2004. The arrival of the moth in the United States was cause for concern in the cactus industry. In the United States, cacti are grown primarily as ornamentals in Arizona, California, Nevada, New Mexico, and Texas. Highest nursery production is in Arizona (wholesale and retail values of $4.5 million and $9.5 million, respectively), followed by southern California. Despite attempts to prevent migration to the valuable cactus growing regions in Mexico, *Cactoblastis* was found in Isla Mujeres, Mexico, in August 2006. Over 250,000 ha are cultivated in Mexico producing annual economic revenue of about $50 million (1990–1998).

Although the importations into Australia and the invasion into the USA and Mexico occurred many years apart, the *Cactoblastis* moth has now become a cautionary example in the practice of biological control. Research on the moth has shifted from mass release to control. Here, we attempt to summarize the current state of knowledge on the biology, distribution and control methods against *Cactoblastis*.

Biology

Like other cactus-feeding moths, the *Cactoblastis* female lays its eggs (Fig. 8) on top of each other to form an "eggstick," often averaging 60–100 eggs per eggstick. Young larvae burrow into the cactus cladode through a single entry hole, negating the effect of the cactus secretions. Larvae feed collectively within the cladode for about 2 months in the summer and four in the winter. Afterwards, the larvae exit the plant to pupate in the leaf litter or soil. Adult lifespan is short, about 9 days, or ranging from about 5 days at 34°C to about 12 days at 18°C in females. Sex ratios are typically 1:1. Depending on climate and season, *Cactoblastis* undergoes 2–3 generations per year. In South Africa, summer and winter generation times are 113–132 days and 234–256 days, respectively. In Australia, summer and winter generation times are 100–120 and 235–265 days, respectively. Under laboratory conditions, generation time ranges from 67 days at 30°C to 185 days at 18°C. Duration of lifestages is generally: egg (50 days); larval (130–180 days); pupal (40–70 days). Duration of immature life stages is affected by temperature



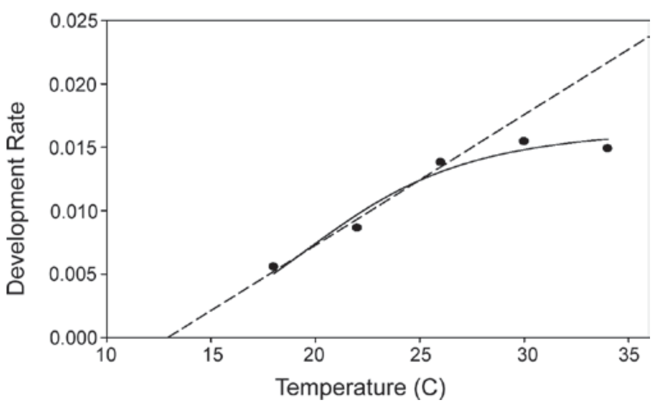
Cactus Moth, *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae), Figure 8 **Life cycle of *Cactoblastis cactorum*: (a) eggs deposited on a cactus spine, forming an "eggstick"; (b) larvae hatching from eggs; (c) mature larvae are strikingly colored orange and black; (d) pupae and a pupal case, with arrows pointing to the genital slit, a character that can be used to sex the pupae; (e) male (left) and female (right) moths; (f) a cactus pad hollowed out by feeding of the larvae. Note that the larvae are visible within the pad (photographs by Ignacio Baez).**

(Table 1, Fig. 9). At 30°C, development from eggs to pupae averages 64.8 days, increasing to 179.9 days at 18°C. Duration of immature life stages was used to generate a development rate curve (Fig. 9) and to calculate a theoretical development threshold temperature of 13.3°C.

Lifetime fecundity is about 172 eggs on *Opuntia ficus-indica*, compared to 138 on *O. aurantiaca* for the summer generation. Respective values for the winter generation were 177 and 159. Total fecundity of winter generations ranges from 88–97 in South Africa, and 99–125 in Australia, although some estimates for total fecundity are as high as 200–300 eggs per female. Total lifetime fecundity changes with temperature, and ranges from about 12 at 34°C to about 100 at 26°C. The combined effects of insect age and temperature are shown using an Enkegaard oviposition rate surface using the equation: eggs = $(-11.241 + 0.854T)\, d \exp(-0.020Td)$; where T is temperature (°C) and d is time (days) (Fig. 10). The estimated parameters p and q describe how quickly maximal oviposition is reached as a function of temperature; and w how quickly it returns to zero. Net reproductive rate (R_0), gross reproductive rate (*GRR*), generation time (*T*), intrinsic rate of increase (*r*), finite rate of increase (λ), and doubling time (*DT*) were 43.68 females/female, 44.02 females/female, 67.14 days, 0.0562 females/female/day, 1.058 females/female/day, and 12.33 days, respectively, at 30°C. The life history parameters of *Cactoblastis* (Table 2) indicate an insect with relatively low reproductive potential and susceptibility to control measures at the egg stage that is exposed for periods of 20–48 days, depending on temperature.

Cactus Moth, *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae), Table 1 Immature development of *Cactoblastis cactorum* (mean ± SE; days)

Life stage	Temperature (°C)				
	18	22	26	30	34
Eggs	47.90 ± 0.28	29.60 ± 0.22	22.50 ± 0.22	20.90 ± 0.23	22.90 ± 0.35
Larvae	78.39 ± 2.58	61.36 ± 2.77	33.52 ± 0.61	29.89 ± 0.80	30.08 ± 1.05
Pupae	53.46 ± 1.52	24.91 ± 0.14	16.28 ± 0.51	13.88 ± 0.66	13.79 ± 0.67
Complete	179.86 ± 2.92	115.96 ± 2.84	72.22 ± 0.79	64.75 ± 0.88	67.04 ± 1.65

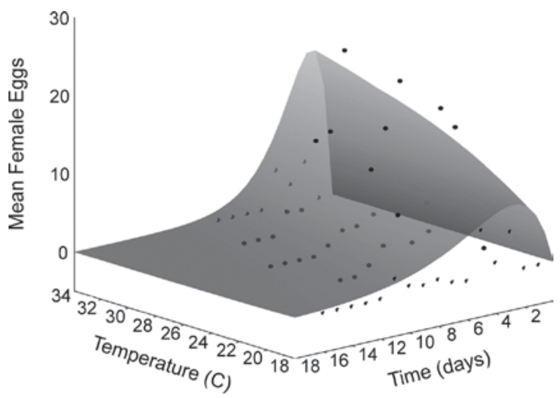


Cactus Moth, *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae), Figure 9 Development rate for *Cactoblastis cactorum* immatures (eggs to pupae). Development rate was fitted to the logistic equation rate = $0.0165/(1 + (T/20.7093)^{-5.8823})$. The linear portion of the curve was used to estimate a lower development threshold temperature of 13.3°C.

Distribution

After importation into Australia from Argentina in 1926, *Cactoblastis* moths dispersed throughout infested areas, exceeding all expectations of the Australian government and resulting in collapse of cactus stands at the original release sites by 1932. In 1956, *Cactoblastis* was shipped from South Africa to the Caribbean island of Nevis where it established and provided successful biological control against a complex of native prickly pear cacti. Successful introductions followed in Montserrat and Antigua in 1960. Through natural migration, intentional or unintentional human action, *Cactoblastis* has been reported throughout the Caribbean (or West Indies; including St. Kitts, the US Virgin Islands, Hispaniola [Haiti], Cuba, the Dominica Republic, the Bahamas, the Cayman Islands, Puerto Rico, Barbados), New Caledonia, Hawaii, Mauritius, St. Helena, and Ascension Island with varying degrees of establishment and success against *Opuntia*. The moth was imported into Pakistan and Kenya but apparently failed to establish.

In 1989, the arrival of *Cactoblastis* in mainland North America was documented by reports in south Florida. *Cactoblastis* likely entered Florida



Cactus Moth, *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae), Figure 10 Enkegaard surface showing simultaneous effects of time and temperature on mean oviposition rate (female eggs). The estimated equation is: eggs = (−11.241 + 0.854T) d exp (−0.020*Td*) (*F* = 16.96; df = 3, 54: P < 0.001; R^2 = 0.35).

Cactus Moth, *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae), Table 2 Life history parameters for *Cactoblastis cactorum* at different temperatures

Parameter	Temperature (°C)				
	18	22	26	30	34
Net Reproductive Rate (R_0)[a]	8.550	46.24	49.20	43.68	5.95
Gross Reproductive Rate (*GRR*)[b]	9.021	48.22	49.38	44.02	6.16
Generation Time (*T*)[c]	185.54	129.58	75.07	67.14	68.95
Intrinsic Rate of Increase (*r*)[d]	0.0116	0.0296	0.0519	0.0562	0.0258
Finite Rate of Increase (λ)[e]	1.0116	1.03	1.053	1.058	1.026
Doubling Time (*DT*)[f]	59.90	23.41	13.32	12.33	26.86

[a]$R_0 = \sum l_x m_x$ expressed in units of female/female; egg numbers divided by 2 because of 1:1 sex ratio
[b]$GRR = \sum mx$ in female/female
[c]$T = (\sum x l^x m^x)/R_0$ in days
[d]$r = \ln R_0/T$ in female/female/day
[e]$\lambda = \exp(r)$ in female/female/day
[f]$DT = \ln(2)/r$ in days

through commercial importations of *Opuntia* from the Dominican Republic into Miami. By 1999, *Cactoblastis* had spread northwards and was found throughout the eastern Florida coastline and as far north as Tampa on the western coast. By 2002, the moth had expanded westward to Pensacola, Florida and northward along the eastern coast to Charleston, South Carolina. In July, 2004, westward migration had reached Dauphin Island, Alabama and Bull Island, South Carolina (about 80 km north of Charleston). The westward migration of *Cactoblastis* in the southeastern United States is estimated at 160 km/year with arrival at the Texas border predicted to occur in 2007. The much-dreaded arrival of *Cactoblastis* in Mexico occurred in August 2006 on Isla Mujeres, a small island off the northeast coast of the Yucatan peninsula in Mexico. The method by which *Cactoblastis* migrated into Mexico is unknown, although speculation centers on winds and hurricanes, or accidental transport via tourists or commercial trade.

The analysis of insect distributions may be assisted through the use of bioclimatic models such as CLIMEX. Bioclimatic models incorporate known ecological and climatic tolerances of organisms in their native habitats to predict potential distribution or densities in other geographical regions. The twofold process typically consists of replicating the known distribution of the target species in its native habitat by estimating biological and stress parameters using experimental data or estimates from the literature. Afterwards, the geographical area of interest is extended or a new area is chosen where the target species may be introduced intentionally, as in a biological control agent, or unintentionally, as in an invasive pest species.

Temperature index parameters were estimated using the laboratory data on development time at different constant temperatures (Table 3). The moisture index parameters were based on those of the Mediterranean fruitfly, *Ceratitis capitata* (Diptera: Tephritidae), with a native South American distribution similar to that of *Cactoblastis*. The target area of distribution was the documented native habitat of Paraguay, Uruguay, southern Brazil and northern Argentina.

Cactus Moth, *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae), Table 3 CLIMEX parameter file for *Cactoblastis*

Parameter	Description	Value
	Temperature Index	
DV0	Lower temperature threshold=	9
DV1	Lower optimum temperature	25
DV2	Upper optimum temperature	30
DV3	Upper temperature threshold	36
	Moisture Index	
SM0	Lower soil moisture threshold	0.1
SM1	Lower optimal soil moisture	0.2
SM2	Upper optimal soil moisture	0.8
SM3	Upper soil moisture threshold	1.0
	Cold Stress	
TTCS	Cold stress temperature threshold	9.0
THCS	Cold stress temperature rate	0
DTCS	Cold stress degree-day threshold	0
DHCS	Cold stress degree-day rate	−0.0001
TTCSA	Cold stress temperature threshold (average)	9.0
THCSA	Cold stress temperature rate (average)	−1.0
	Heat Stress	
SMDS	Dry stress threshold	0.01
HDS	Dry stress rate	−0.1
	Wet stress	
SMWS	Wet stress threshold	1.2
HWS	Wet stress rate	0.0015
PDD	Degree days per generation	1500

Predicted and known worldwide distributions of *Cactoblastis* are shown together in the map. In its native distribution range of Uruguay, Paraguay, south Brazil and north Argentina, *Cactoblastis* appears to be limited by cold stress to the south and along the Andes mountain range, and by wet stress to the north in parts of Brazil. Areas in eastern Brazil may be conducive to moth survival despite the absence of records in that area. The fact that no records of *Cactoblastis* exist in this area may be due to the absence of host *Opuntia* species, or the lack of efforts to find the moth. The model suggests potential distribution may occur in North America (from the Caribbean Islands to Florida, Texas and Mexico), Africa (South Africa, and parts of the eastern coast), southern India, parts of Southeast Asia and in the northeastern coast of Australia. As partial validation of these predictions, the moth was recorded in the Caribbean, including Cuba, Bahamas and Puerto Rico. Furthermore, the moth has been recorded in southern Africa and Australia. *Cactoblastis* was released, but apparently did not establish, in Kenya and Pakistan. Based on the model output, establishment might have been expected in Kenya, but not in Pakistan. New Caledonia, Hawaii and the islands of St. Helena and Ascension did not appear on the maps generated. Based on the current parameter values, the moth is close to its predicted northern range along the Atlantic coast. However, new data and revised parameter values could allow further expansion northwards. Therefore, the current projections are likely to be conservative estimates of *Cactoblastis* range in North America.

Because the potential range is likely to be conservative, more problematic is that the predicted range already encompasses Florida, Texas, eastern Mexico, as well as a bridge of favorable climate linking Florida to Texas along the Gulf Coast. Therefore, even without human intervention such as contaminated shipments of cacti, climatic conditions may support natural migration of the moth from Florida into Texas, provided adequate *Opuntia* populations exist along the Gulf Coast. Other bioclimatic models yield results similar to those from CLIMEX. GARP (Genetic Algorithm for Rule set Prediction) was used to estimate distribution of host cacti. Flora Map predicted potential distribution of *Cactoblastis*. When the distribution maps of both host plant and cactus moth were overlaid, possible invasion routes into Mexico were predicted to be along the northern border through Texas, or less likely, through southeastern Mexico.

The validity and utility of bioclimatic models is controversial. Clearly, distribution of organisms is determined by factors other than climate. The problems encountered in collecting data to both calibrate and validate the CLIMEX model are likely to be typical for most scientists attempting similar studies. Detailed distribution records are difficult to obtain, despite the fact that *Cactoblastis* is a well-documented insect. There is a need to determine definitively whether the absence of records from large regions such as eastern Brazil is because sampling was performed, but no moths were collected, or simply because no sampling efforts were undertaken. Absence data is almost as important as presence data. In addition to problems with distribution record data, weather data may not be available for specific times and locations of interest. In an insect as cosmopolitan as *Cactoblastis*, a potentially significant complication is that strains of different geographical origins have differing bionomics, perhaps as adaptations to local climate. Despite numerous valid criticisms against the climate matching approach, in the absence of appropriate data, climate matching may be the only viable option to predict species distributions.

Control

Currently there are no consistently effective chemical or biological methods to control *Cactoblastis*. To limit *Cactoblastis* infestations, adequate surveillance and early detection are critical. Effective surveillance may require the use of specialized traps such as those baited with virgin female moths. In areas where *Cactoblastis* has established as a pest, the selection of a control agent is determined by considering the value of the crop, the size of the affected area, and if the moth is itself used as a control agent against invasive cactus species. Control methods may include management practices such as the collection and destruction of infested cacti. Systemic insecticides have not proven effective against *Cactobastis*, but selected contact insecticides may be used against early instars, before they penetrate the cactus.

There are many potential biological control agents against *Cactoblastis*, but none appear to be specific. As discussed in the Biology section, the moth is characterized by a relatively low reproductive potential, which suggests that potential biological control agents need not possess extremely high reproductive rates. Candidate agents for evaluation might include egg parasitoids or predators that attack the vulnerable and exposed egg stage. Egg parasitoids belonging to the genus *Trichogramma* have been suggested as agents, possibly in augmentative biological control programs. In Australia, *Trichogramma minutum* Riley caused up to 32% egg parasitism. This egg parasitoid is commercially available. In South Africa and Australia, egg predation by ants is a significant regulatory factor in the *Cactoblastis* populations. Important ant predators include *Crematogaster liengmei* Forel, *Pheidole* sp., *Tetramorium erectum* Emery, *T. bacchus* Forel, *Tetramorium* sp., *Monomorium albopilosum* Emery, *M. minutum* Mayr, and *Camponotus niveosetosus* Mayr. Egg mortality due primarily to ant predation has been found to range from 55 to 78% depending on season and cactus species. Other ant species suspected of being egg predators on *Cactoblastis* are *Technomyrmex albipes* Smith, *Monomorium delagoense* Forel, *Camponotus eugeniae* Forel, and *C. rufoglaucus* (Jerdon).

Alternatively, potential agents might be those specialized for searching and attacking the moth larvae within the cactus plant. Possible classical biological control agents from South America include one braconid larval parasitoid, five to six ichneumonid wasps, and a tachnid fly. *Apanteles alexanderi* Brethes (Hymenoptera: Braconidae) can cause parasitism levels over 30%. The ichneumonid *Temelucha* sp. caused 5–30% larval parasitism. The tachinid fly *Epicoronimyia mundelli* (Blanchard) also attacks other species of cactus moths. The braconid wasp, *Bracon hebetor* Say, parasitized up to 25% of the larvae in South Africa; this wasp can be mass reared on alternate hosts. Larval predators of *Cactoblastis* include ants (*Pheidole* sp. and *Anoplolepis steingroeveri* (Forel)) and a tachinid (*Pseudoperichaeta* sp.). Pupal predation by the ant species *Dorylus helvolus* (L.) has been measured at about 13–34%. Pupal parasitism by chalcid parasites *Invreia* sp. and *Euchalcidia* sp. was estimated at about 5%. In Florida, the chalcid parasite *Brachymeria ovata* Say, attacked 55% of *Cactoblastis* pupae at one site. Limited work has been done on evaluating insect pathogens as a control agent against *Cactoblastis*. *Beauveria* sp. caused high larval death rates in Australia and the species *B. bassiana* may have potential in inundative control programs. The protozoan *Nosema cactoblastis* has been reported from South Africa, but recorded infection levels are only 0–6%. The pathogen *Bacillus thuringiensis* Berliner has demonstrated efficacy against Lepidopteran pests but is not likely to be effective against *Cactoblastis* inside the cactus plant.

The Sterile Insect Technique (SIT) method is being developed to study *Cactoblastis* populations, and possibly for eradication in colonization sites or for controlling dispersal and movement into new areas. SIT may have the most potential in the northern Gulf coast region where cacti are rare and *Cactoblastis* populations are low, although control will be expensive.

Control measures against *Cactoblastis* infestations in the United States will probably be limited in most regions because *Opuntia* species are usually a low value crop. Life history data indicate that the moth does not display particularly high reproduction, so its pest status is due largely to the protection afforded by the cactus plant once the larvae have gained entry into the cactus tissue. The most vulnerable life stage appears to be the egg stage, both because it is exposed, and also because of its relatively long duration. Natural predation by ants may be encouraged. However, even after moth larvae have entered the plant, specialized natural enemies may be effective in seeking and attacking larvae inside the cactus plant. Effective integrated pest management of *Cactoblastis* will require an understanding of all the management options available to develop comprehensive, yet cost-effective strategies under different geographical and socio-economic situations, while limiting detrimental effects against non-target organisms.

► Sterile Insect Technique
► Area-Wide Insect Pest Management
► Biological Control of Weeds
► Foreign Exploration for Insects that Feed on Weeds

References

Legaspi JC, Legaspi BC Jr (2007) Life table analysis for *Cactoblastis cactorum* immatures and female adults under five constant temperatures: implications for pest management. Ann Entomol Soc Am 100:497–505

Mahr DL (2001) *Cactoblastis cactorum* (Lepidoptera: Pyralidae) in North America: a workshop of assessment and planning. Fla Entomol 84:465–473 (and papers contained in this volume)

Sutherst RW, Maywald GF, Bottomley W, Bourne A (2004) CLIMEX v2: user's guide. CSIRO, Queensland Australia

Zimmermann HG, Moran VC, Hoffmann JH (2000) The renowned cactus moth, *Cactoblastis cactorum*: its natural history and threat to native *Opuntia* floras in Mexico and the United States of America. Divers Distrib 6:259–269

Zimmermann HG, Bloem S, Klein H (2004) Biology, history, threat, surveillance and control of the cactus moth, *Cactoblastis cactorum*. International Atomic Energy Agency, Vienna, Austria, 46 pp

Caddisflies (Trichoptera)

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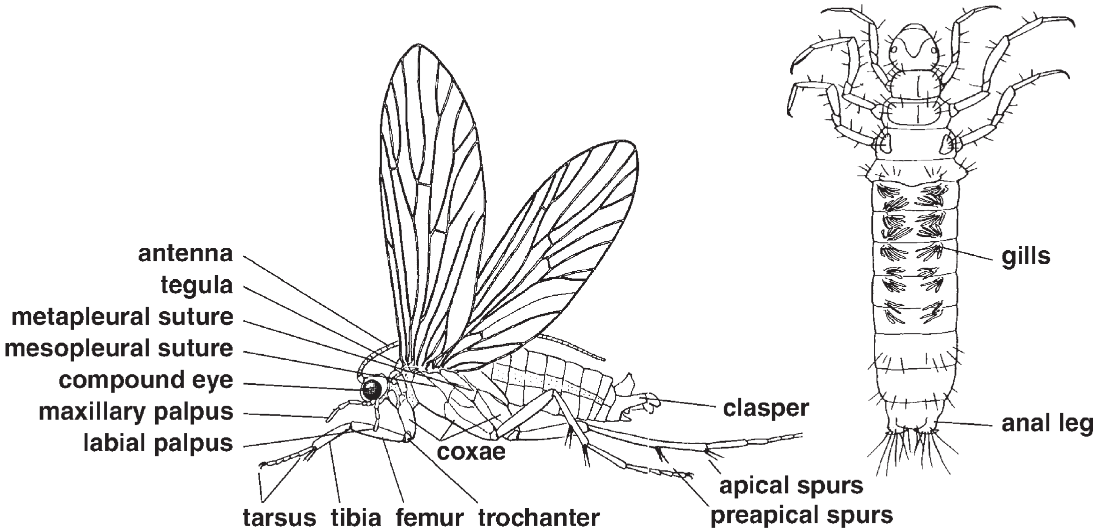
The Trichoptera, or caddisflies, is an advanced order of aquatic insects that, as adults, are easily distinguished by the presence of two pairs of wings covered with hair and held in a roof like manner over the abdomen. They typically exhibit a rather dull appearance (some being distinctly patterned) with long, slender antennae. They possess chewing type mouthparts with reduced mandibles, but feed mainly on liquid diets as adults and are detritivorous or predaceous as larvae. Adults are nocturnal and typically found alongside lakes and streams, but may also be encountered away from bodies of water. Larvae are found in a variety of aquatic habitats, mainly cool swift-flowing streams. Caddisflies are an important component in aquatic food chains and also are used as bioindicators of pollution.

Caddisfly larvae can be distinguished from other aquatic insects by the presence of modified anal prolegs and a portable case or silken retreat that protects their delicate body. Larval cases are constructed from a variety of materials, ranging from stick and leaf fragments to small stones and grains of sand, and are held together by silk produced by labial silk glands. Larval caddisflies (Fig. 11) have a closed respiratory system marked by the absence of spiracles and the presence of abdominal gills in some members. Respiration of larvae occurs through the cuticle and gills (if present). Abdominal undulation and morphological adaptations, mainly humps on the anterior segments of the abdomen and lateral fringes of hair, allow for circulation of water through the case. Larvae go through five to seven instars before pupation. They cease feeding and become inactive for up to several weeks inside the silken pupal cases. Pharate adults use their sharp mandibles to cut away the case, and then float to the surface and emerge from the pupal integument.

Adults live for approximately a month (up to three in some families). After mating, females enter the water to deposit eggs on the underside of rocks. Hairs on the body act as a water-proof layer, essentially allowing the adult to breathe underwater by preventing the spiracles from coming into contact with the surrounding water. The eggs of some species are surrounded by a gelatinous mass that swells to form a protective covering.

Caddisflies are a product of their environment. One reason they are so diverse is their ability to occupy so many diverse habitats, from cool flowing streams to warm still waters. Morphology and behavior of the larvae allow a variety of means to collect food, in addition to several families



Caddisflies (Trichoptera), Figure 11 Diagram of adult male and larval caddisflies.

occupying different feeding guilds. For example, aperture size of the net-spinning caddisfly retreat is directly correlated to the size of their food item: a larger aperture for larger prey, and a smaller aperture for particulate material. Morphological modifications found in some families allow for a diet of diatoms by scraping the surface of rocks, while others are more suited for a filtering collecting lifestyle using forelegs or delicate nets and retreats. Nets, cases and tubes constructed by the larvae also allow for protection and concealment while feeding or during pupation. Cases match the habitat in which the larvae are found, from sand and pebble cases in sandy streams, to plant material found in many springs, lakes and ponds.

Caddisflies are considered the sister group to butterflies and moths(Order Lepidoptera) and are unique in the fact that they are the only holometabolous group of insects that are considered aquatic. Some Trichoptera also share similar pheromone detection systems like these found in some primitive Lepidoptera.

Currently, there are an estimated 1,400 species of caddisflies recognized from North America within 27 families, and approximately 7,000 species in 60 extant families worldwide. Weaver and Morse (1986) reviewed different phylogenies and examined feeding and case-making behavior to hypothesize that an ancestral tube-dwelling caddisfly gave rise to other forms. Keys to caddisfly larvae, pupae and adults of North American species can be found in the publications cited in the "References" section. A worldwide database and current higher classification is available at the website, http://entweb.clemson.edu/database/trichopt/hierarch.htm. An overview of classification is:

Order Trichopteralt
- Suborder Annulipalpia
  - Superfamily: Hydropsychoidea
    - Family: Dipseudopsidae
    - Family: Arctopsychidae
    - Family: Ecnomidae
    - Family: Hydropsychidae
    - Family: Polycentropodidae
    - Family: Psychomyiidae
    - Family: Xiphocentronidae
  - Superfamily: Hydroptiloidea
    - Family: Glossosomatidae
    - Family: Hydroptilidae
  - Superfamily: Philopotamoidea
    - Family: Philopotamidae
  - Superfamily: Rhyacophiloidea
    - Family: Hydrobiosidae
    - Family: Rhyacophilidae
- Suborder: Integripalpialt
  - Superfamily: Limnephiloidea

Family: Apataniidae
Family: Brachycentridae
Family: Goeridae
Family: Lepidostomatidae
Family: Limnephilidae
Family: Rossianidae
Family: Uenoidae
Superfamily: Phayganeoidea
Family: Phryganeidae
Superfamily: Leptoceroidea
Family: Calamoceratidae
Family: Leptoceridae
Family: Molannidae
Family: Odontoceridae
Superfamily: Sericostomatoidea
Family: Beraeidae
Family: Helicopsychidae
Family: Sericostomatidae

A brief synopsis of the more common families follows.

Family: Brachycentridae (Humpless Caddisflies)

The larval cases of this family range from pieces of plant material to small pebbles and grains of sand. Some members of this family are filter feeders, collecting food particles from the current with the use of their hairy forelegs, switching to a predaceous diet in later instars. The genera *Brachycentrus* and *Micrasema* are the two more common genera that are found throughout North America.

Family: Glossosomatidae (Saddle-case Caddisflies)

Larvae of this family form saddle-like cases that are similar to turtle shells. The upper portion of the case is comprised of large stones while the lower portion is generally made up of sand. They are usually found on the upper surface of stones in swift, cool streams. Two common genera are *Glossoma* and *Agapetus*.

Family: Helicopsychidae (Snail-case Cadisflies)

This family is unique within the order with larvae constructing coiled cases similar in appearance to snail shells. They are found primarily in swift flowing waters with sandy substrates and the wave swept shores of lakes and also in springs. *Helicopsyche* is the only genus within the family.

Family: Hydropsychidae (Net-spinning Caddisflies)

These caddisflies are known for their cup-shaped nets that allow for both a secure place to reside and a means of collecting food. The net acts as a strainer and is permanently held in place with pupation occurring inside of the structure. *Hydropsyche*, *Cheumatopsyche* and *Ceratopsyche* are the more diverse and widely distributed genera within this family.

Family: Hydroptilidae (Microcaddisflies)

Microcaddisflies are unique in that the first four instars are free-living with later instars increasing in size and making a purse or flask-shaped case open at each end. Larval case material is varied, ranging from pure silk to plant material and grains of sand. *Hydroptila*, *Ochrotrichia* and *Oxythira* are the most diverse and widespread genera within the family.

Family: Lepidostomatidae (Lepidostomatid Caddisflies)

Generally found in cool headwater streams, these caddisflies are also known from springs. Larvae construct four sided cases or slender tubes of concentric rings, each made up of sticks, twigs and sand. *Lepidostoma* is a common genus, accounting for most of the diversity within the family.

Family: Leptoceridae (Long-horned Caddisflies)

Named for their long antennae in both the larval and adult stages, long-horned caddisflies are primarily detritivorous or predaceous with some members known to feed on freshwater sponges. Larval cases vary, with some resembling short, stout "log cabins" of twigs to slender tubes made of silk and plant material. *Oecetis*, *Ceraclea* and *Triaenodes* are three widespread genera found within this family.

Family: Limnephilidae (Northern Caddisflies)

This is the largest family of caddisflies in North America with more that 300 species, with the widespread genus *Limnephilus* accounting for almost a third of the diversity. Larvae are found in both lentic and lotic habitats and cases differ between young and older larvae.

Family: Molanidae (Hood-case Caddisflies)

This widespread family is only represented by a few species known mainly in eastern North America in lentic habitats. The case is distinctive in that it consists of a tapered tube of sand with a flattened hood, allowing the larvae to feed in the open under concealment. *Molanna* is the more common genus of this family.

Family: Philopotamidae (Finger-net Caddisflies)

The larvae of this family are found primarily on rocks in swiftly flowing, cold streams. The finger shaped tubes have a large upper opening and a much smaller lower opening, which results in the collection of food particles within the net. Pupation occurs in a silk lined pebble case. Three widespread genera, *Chimarra*, *Doliphiloides* and *Wormalida*, are found within this family.

Family: Phyrganeidae (Large Caddisflies)

As the name implies, these are larger than most caddisflies, found primarily in cold, lentic habitats and sometimes along the slow margins of streams. Larval cases consist of portions of grass stems arranged spirally. Representative genera within the family are *Agrypina* and *Ptilostomis*.

Family: Polycentropodidae (Trumpet-net Caddisflies)

These caddisflies are found in a variety of lentic and lotic habitats and within a variety of retreats and cases. Some members construct delicate trumpet-shaped retreats while others have rigid tubes strengthened with sand. Primarily collectors, members of this family are also known to be predaceous. Common genera include *Neureclipsis* and *Polycentropus*.

Family: Rhyacophilidae (Primitive Caddisflies)

This family is caseless, or free-living, until pupation and is typically predaceous. The genus *Rhyacophilia* is a diverse group containing over 100 species and is typically found in swift mountain streams.

References

McCafferty WP (1981) Aquatic entomology. Science book international, Boston, MA, 448 pp

Merritt RW, Cummins KW (eds) (1996) An introduction to the aquatic insects of North America, 3rd edn. Kendall/Hunt, Dubuque, IA

Weaver JS III, Morse JC (1986) Evolution of feeding and case-making behavior in Trichoptera. J North Am Benthol Soc 5:150–158
Wiggins GB (1996) Larvae of North American caddisfly general Trichoptera, 2nd edn. University of Toronto Press, Toronto, Ontario, Canada

Cadelle, *Tenebroides mauritanicus* (Linnaeus) (Coleoptera: Tenebrionidae)

This is a grain and flower-infesting species.
► Stored Grain and Flour Insects

Caeciliidae

A family of psocids (order Psocoptera).
► Bark-Lice, Book-Lice or Psocids

Caecum (pl., caeca)

A sac-like or tube-like structure, opened at one end only.
► Gastric Caecum

Caenidae

A family of mayflies (order Ephemeroptera).
► Mayflies

Calamoceratidae

A family of caddisflies (order Trichoptera).
► Caddisflies

Calcaria

Moveable spurs at the tip of the tibia.

Calibrate

A process designed to standardize or correct the measuring devices on instruments. In pesticide application technology, calibration refers to adjustment of nozzles on a spray apparatus, or determination of the amount of pesticide that is produced by a sprayer when it is operated.

California Red Scale, *Aonidiella auranti* (Maskell) (Hemiptera: Diaspidae)

This is a major pest of citrus in California, USA.
► Citrus Pests and their Management

Calipharixenidae

A family of insects in the order Strepsiptera.
► Stylopids

Callidulidae

A family of moths (order Lepidoptera) also known as Old World butterfly moths.
► Old World Butterfly Moths
► Butterflies and Moths

Calliphoridae

A family of flies (order Diptera). They commonly are known as blow flies, bluebottle flies, and greenbottle flies.
► Flies

Callirhipidae

A family of beetles (order Coleoptera). They commonly are known as cedar beetles.
► Beetles

Callow

Newly molted individuals whose exoskeleton is still relatively soft and lightly pigmented.

Calophllidae

A family of bugs (order Hemiptera, superfamily Psylloidea).

► Bugs

Calopsocidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice or Psocids

Calopterygidae

A family of damselflies (order Odonata). They commonly are known as broad-winged damselflies.

► Dragonflies and Damselflies

Calvert, Philip Powell

Philip Calvert was born in Philadelphia on January 29, 1871, and grew up there, leaving school in 1888 and graduating from the University of Pennsylvania in 1892 with a certificate in biology, and in 1895 with a Ph.D. He then spent a year in Germany, at the universities of Berlin and Jena. In 1907 he began to teach zoology at the University of Pennsylvania, retiring in 1959 with the rank of Emeritus Professor. Teaching played a major role in his life. His research contribution was on Odonata, on which group he published over 300 papers, beginning in 1899. He wrote especially on taxonomy, but also on anatomy, distribution, paleontology, and ecology. Some of his major publications were (1893) "Catalogue of the Odonata (dragonflies) of the vicinity of Philadelphia with an introduction to the study of this group of insects," (1901–1906) "Insecta Neuroptera Odonata" in Biologia Centrali-Americana, (1909) "Contribution to a knowledge of the Odonata of the Neotropical Region, exclusive of Mexico and Central America," and (1944) "The rates of growth, larval development, and seasonal distribution of the genus *Anax*". A book, "A year of Costa Rican natural history" followed his sabbatical leave in Costa Rica in 1909–1910. He was president of the American Entomological Society from 1901 to 1915, editor of Entomological News from 1911 to 1944, and one of the founders of the Entomological Society of America. He died on August 23, 1961.

References

*Mallis A (1971)Philip Powell Calvert. In: American entomologists. Rutgers University Press, New Brunswick, NJ, pp 178–180

Rehn JAG (1962) Philip Powell Calvert (1871–1961). Entomol News 63:113–121

Schmieder RG (1962) Additions to the bibliography of Philip P Calvert, subsequent to 1950. Entomol News 63:121

Schmieder RG, Phillips ME (1951) Bibliography of Philip P Calvert. Entomol News 62:3–40

Calypter (pl., calypteres)

A small fold or lobe in the hind margin of fly wings (Diptera) covering the haltere.

Calyptodomous

Pertaining to nests, particularly wasp nests, in which the combs are surrounded by an envelope.

Camel Crickets

A family of crickets (Rhaphidophoridae) in the order Orthoptera.

► Grasshoppers, Katydids and Crickets

Cameron, Malcolm

Malcolm Cameron was born in London in 1873, and died there on October 24, 1954. He obtained an M.D. degree at The London Hospital and entered the British navy as naval surgeon. He served in the British navy during the Boer War and in the first World War (campaigns in the Falklands and East Africa). He retired in 1920 and devoted the rest of his life to entomology, although he had about 40 publications before retirement. He went to India, where he collected Staphylinidae extensively, but returned in 1925 to London due to a lung illness. His five-volume contribution on Staphylinidae of British India was his major work, but 206 other papers on Staphylinidae worldwide together enabled him to describe 4,136 species and 195 genera in Staphylinidae, making him the most profuse describer of species of this family after Max Bernhauer. Like Bernhauer, he did not provide illustrations or keys for most of his works (the Fauna of British India was an exception), so identification of specimens of the species he described is not easy. His collection of some 55,000 specimens was bequeathed to the British Museum (Natural History), later called The Natural History Museum.

References

Herman LH (2001) Cameron, Malcolm. Bull Am Mus Nat Hist 265:51–52
Puthz V (1986) Bibliographie de Publikationen Malcolm Cameron' s (1873–1954). Philippia 5:301–310

Cambrian Period

A geological period of the Paleozoic era, extending from about 580 to 500 million years ago. Chelicerate arthropods date from this time.
► Geological Time

Camillid Flies

Members of the family Camillidae (order Diptera).
► Flies

Camillidae

A family of flies (order Diptera). They commonly are known as camillid flies.
► Flies

Campestral

Inhabiting open fields.

Campodeidae

A family of diplurans (order Diplura).
► Diplurans

Campodeiform Larva

A term used to describe larvae that are elongate and flattened, with well-developed thoracic legs and antennae, and a prognathous head. Such larvae are usually active and predacious. It is named for *Campodea*, a dipluran. This body form is found in the orders Ephmeroptera, Odonata, Plecoptera, and Neuroptera.

Canacidae

A family of flies (order Diptera). They commonly are known as beach flies.
► Flies

Candeèze, Ernest Charles Auguste

Ernest Candèze was born in Liège, Belgium, on February 27, 1827. He studied medicine in Paris and Liège, and became a physician and director in a hospital for the insane. In Liège he was a pupil of Lacordaire. His taxonomic interest was the study of Elateridae (Coleoptera), in which family he became a world authority, and his most notable achievement (1857–1860) was a four-volume monograph on Elateridae supplemented by papers in Annales de la Société Entomologique de Belgique. Additionally, he published on insect pests of horticulture, was a member of the Academie de Belgique and of the Société Royale des Sciences de Liège, president of the Société Entomologique de Belgique in 1873 and 1874, one of the five commissioners of the Muséum d' Histoire Naturelle of Brussels, and a member of several foreign entomological societies. One of his collections of Elateridae is in the Natural History Museum (London) and another in Brussels. His wife died in 1872; they had five children, of whom Léon Candèze became an entomologist. He died near Liège on June 30, 1898.

References

*EssigEO (1931) Candèze, Ernst Charles Auguste. In: A history of entomology. MacMillan, New York, pp 563–564

Lameere A (1898) Notice sur le Dr. Ernest Candèze. Ann Soc Entomol Belg 42:504–519

Canine Babesiosis

This is a tick-transmitted protozoan disease. It is also known as canine piroplasmosis.

► Piroplasmosis

Canine Piroplasmosis

This is a tick-transmitted protozoan disease. It is also known as canine babesiosis.

► Piroplasmosis

Cannibalism

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Cannibalism is intraspecific predation. It occurs widely among arthropods. It is best known in predatory species, though it also occurs among detritivores and herbivores. Cannibalism is often viewed as a population self-regulatory measure, acting to limit population size and suppress population outbreaks. Shortage of food, high density, or both of these factors contribute to cannibalism. Elimination of competition is considered by some to be the basis for such cannibalism. However, possibly of equal benefit is the fitness advantage resulting from improved nutrition by cannibalistic individuals. Cannibals can benefit from larger food supplies following the elimination of competition, but also from the higher nutritional quality of feeding on arthropod body tissues rather than plant tissues. Probably less important are the benefits derived from reduced predation and parasitism following cannibalism; lower host densities often result in less frequent attack by predators and parasitoids. Cannibalism may select for shorter egg development times, as eggs are a particularly vulnerable stage. Cannibalism likely has contributed to development of parental care. In eusocial insects, cannibalism can be used to adjust caste ratios or sex allocation ratios.

Cannibalism is a normal phenomenon for many arthropods, not an anomaly. Cannibalism has been documented in many insect orders, including Odonata, Orthoptera, Thysanoptera, Hemiptera, Trichoptera, Lepidoptera, Diptera, Neuroptera, Coleoptera, and Hymenoptera. It occurs among predatory species and herbivores, and involves predation by the mobile adults and larvae or nymphs on each other, and on immobile eggs and pupae. Arthropods occurring at high densities, faced with inadequate food availability, or spatially constrained (e.g., limited to feeding within a fruit or stem) more commonly display cannibalism. Also, generalist species are more prone to display cannibalism than are specialist species, and females are more cannibalistic than males. The greater occurrence of cannibalism among females may simply be a manifestation of the greater size of females, allowing them to overpower prey more easily. Cannibalism is common among freshwater insects. Perhaps surprisingly, cannibalism is quite common among some groups of herbivorous insects.

Some adaptations to deter cannibalism are evident. Deposition of eggs on long thin stalks by lacewings (Neuroptera: Chrysopidae) is often given as an example of evolution of a cannibalism-deterring behavior. Synchronous hatching of eggs is much more widespread, and similarly deters the early-hatching individuals from taking advantage of their late-hatching siblings. Dispersion of individuals, particularly of eggs, is another good way to reduce cannibalism.

Population Regulation

Cannibalism can reduce population size before resource (food) shortages occur, thereby averting physiological stress. This is not unlike other population regulation behaviors such as spacing, dispersion, and the benefits resulting from marking pheromones (which serve to deter insects from ovipositing repeatedly into a limited food resource). For many species, cannibalism is correlated with frequency of encounter, and higher levels of cannibalism occur if there is an abundance of susceptible prey. For example, ladybird beetle (Coleoptera: Coccinellidae) larvae often feed on nearby unhatched eggs, but if hatching is simultaneous there is no cannibalism. Cannibalism occurs among herbivorous insects even when normal food is plentiful, as in the ladybird beetle example mentioned above. Hatching *Danaus* spp. (Lepidoptera: Nymphalidae) caterpillars feed readily on their siblings (eggs), even while feeding on foliage.

The importance of cannibalism in population regulation is generally poorly documented. Often such losses are simply attributed to disappearance, and it is unknown whether losses are due to intraspecific or interspecific predation, or dispersion. Cannibalism also is hard to measure because it may be restricted to a short period in time, and often is detectable only via direct observation. As noted above, ladybird beetle larvae often feed on eggs, but once hatch occurs, predation diminishes or disappears because eggs, not other larvae, are the preferred alternate food. It may be necessary to actively seek out cannibalism data to document the relative importance of cannibalism. For example, studies of *Gerris* water striders (Hemiptera: Gerridae) have shown that the presence or absence of older water striders significantly influences survival of young *Gerris*. If broods overlap, the older bugs feed heavily on the younger, but if the older insects are artificially removed, survival of the young bugs is quite high. This effect of cannibalism is not easy to discern without the artificial manipulation of the older age class.

After hatching, the predatory and cannibalistic Mormon cricket (Fig. 12), *Anabrus simplex* Haldeman (Orthoptera: Tettigoniidae), forms groups (called "bands") that move each day, stopping only briefly to feed and to rest at night. The benefit of almost continuous movement is thought to be a mechanism to protect the defenseless molting individuals from being consumed by their siblings, as the molting crickets are left behind while the non-molting and aggressively cannibalistic individuals continue to seek food. If these high-density aggregations were not moving the molting individuals would be easy prey and most would be killed. This may represent an unusual example of the significance of cannibalism, and the evolution of a novel defense against it.

Cannibalism can also be important in maintaining populations during periods of food scarcity. From the perspective of population persistence, it is better to have a few well-fed cannibalistic individuals surviving than to have all individuals die from temporary lack of food. Physiological quality can be as important as abundance. Population stability and persistence is enhanced during periods of food deprivation if the few survivors are well fed and capable of reproduction; the alternative may be more but malnourished individuals incapable of reproducing.

Nutrition

Conflicting data exist on the nutritional benefits of being a cannibal. For example, a study of

Cannibalism, Figure 12 **Cannibalism by Mormon cricket, *Anabrus simplex* Haldeman (Orthoptera: Tettigoniidae). (i) Cannibalism of a cricket; this species attacks congeners whenever the opportunity arises. Perhaps because of this, it forms groups (called "bands") that move each day, stopping only briefly to feed and to rest at night. The benefit of almost continuous movement is thought to be a mechanism to protect the defenseless molting individuals from being consumed by their siblings, as the inactive molting crickets are left behind while the non-molting and aggressively cannibalistic individuals continue to seek food. (ii) When cricket bands cross highways some are killed by the tires of passing vehicles. The other crickets are quick to take advantage of this food source and stop to feast on their killed or injured comrades. They, in turn will be killed by additional vehicular traffic. After several vehicles have passed by, the roadways are marked by slippery, greasy bands marking the paths of vehicle tires.**

predatory ladybird beetles showed that although individuals cannibalizing eggs did not benefit in terms of survival rates, they displayed more rapid development and (in the case of females) a higher final body weight. Both rapid development and higher body weight are considered favorable to population growth. Another study involving *Harmonia axyridis* ladybird beetles found that cannibalism allowed beetle larvae to supplement an otherwise inadequate diet of aphids and to survive to maturity. Cannibalistic willow leaf beetles, *Plagiodera versicolora* (Coleoptera: Chrysomelidae), gain a size advantage and are more successful at initiating feeding sites on tough vegetation as compared to non-cannibalistic individuals. Similarly, many aquatic detritivores supplement their diet with animal material obtained through cannibalism, and a study of caddisflies (Trichoptera) found that individuals with animal material in their diet had higher larval survival, shorter larval and pupal development times, earlier emergence dates, larger adult body mass (30–40%), and higher fecundity (30% more eggs). In contrast, a study of the herbivorous caterpillar *Acsia monuste* (Lepidoptera: Pieridae) found no benefit from cannibalism of eggs or larvae, and study of the caterpillar *Spodoptera frugiperda* (Lepidoptera: Noctuidae) found lower body rates and development times among cannibals. However, many studies do not separate the effects of density *per se* (higher density increases the rate of cannibalism but decreases fitness) from the effects of cannibalism (which sometimes benefits the cannibal).

Herbivorous insects have greater difficulty in obtaining protein than many other insects, particularly predators and parasitoids, due to the relatively low levels of protein in their diet. Not surprisingly, many have evolved supplemental feeding behaviors that provide additional protein, including feeding on pollen, exuviae, and members of the same species (conspecifics). Early stages of development especially benefit from extra protein, and later in life it is not unusual for holometabolous insects to shift toward more carbohydrates in their diet. The level of cannibalism displayed by an herbivorous species can change according to dietary levels of protein. Addition of casein to a laboratory diet of pure cellulose greatly diminished cannibalistic behavior of the Pacific dampwood termite, *Zootermopsis angusticollis* (Isoptera: Hodotermitidae). The level of cannibalism by the beet armyworm, *Spodoptera exigua* (Lepidoptera: Noctuidae), was inversely related with the nitrogen level of the host plant. Thus, armyworm larvae were able to compensate for poor quality diet by increasing cannibalism, with a subsequent boost (Table 4) in egg production.

Cannibalism, Table 4 Levels of cannibalism and subsequent egg production by beet armyworm larvae fed on sugarbeet foliage grown in nutrient solution with nitrogen deficiency (0N), normal nitrogen (1N), or twice the normal level of nitrogen (2N) (adapted from Al-Zubaidi and Capinera (1983) Environ Entomol 12:1687–1689)

	Nutrient level (N)		
	0N	1N	2N
Cannibalism (%)	60	38	24
Mean no. eggs after fed:			
Foliage + pupae	467	512	615
Foliage only	382	481	512

Trophic Eggs

Trophic eggs ar e homologous to fertile eggs but they cannot develop into viable offspring and are normally eaten by siblings. Thus, in a sense, consumption of these eggs is an expression of cannibalism. They are most commonly found in eusocial (social) insects such as Isoptera (termites) and Hymenoptera (wasps, bees, ants) but sometimes in other, non-eusocial groups such as owlflies (Neuroptera), crickets (Orthoptera), ladybird beetles (Coleoptera), psocids (Psocoptera), and spiders (Aranea). Trophic eggs likely evolved due to the survival benefits of having viable or nonviable (sterile) eggs available for offspring to feed upon. Trophic eggs provide a uniform food for offspring, and in the case of colonial species, can be stored for use during unfavorable periods. Trophic eggs are most common among eusocial species due to the interdependency on the different castes and (usually) the ability of the queen to manipulate the members of the colony.

Sexual Cannibalism

This is a special type of cannibalism wherein an insect (usually a female) consumes a conspecific, normally a male, in association with mating. Such cannibalism usually occurs after copulation, and is widespread among mantids (Mantodea) but uncommon in other taxa. In mantids, this has been documented to be a significant source of nutrition for the female. It is easy to understand the benefits of cannibalism to the female, and some have postulated that cannibalism pre-coitus is more likely with unsuitable males and post-coitus more likely with more suitable mates. What is less apparent, however, is why the male is successfully duped into becoming a food resource for his mate. With mantids, the larger size of females perhaps accounts for the female's success; it is easy for her to overpower him. On the other hand, it can be argued that natural selection favors post-coitus sexual cannibalism because the male is making the "supreme" parental investment in his offspring. Perhaps this is consistent with other nuptial gifts such as the large proteinaceous sperm capsule (spermatophylax) provided to females by males of some katydids (Orthoptera: Tettigoniidae) such as the Mormon cricket, Anabrus simplex. If such sacrifice on the part of male mantids occurs willingly, it certainly represents an extreme form of paternal investment. Though not well understood, it appears that males are rather cautious with females, and strive to escape after mating.

Costs of Cannibalism

Cannibalism clearly is not always beneficial. Cannibals risk injury or death from the defensive responses of their prey. Typically, cannibals prey on smaller or younger conspecifics, minimizing their risk of injury. Cannibalism can also result in the transmission of microbial pathogens to the predatory individual. Infected individuals early in the disease cycle are sluggish, and are relatively easy prey, but they may harbor a lethal dose of pathogens if they are ingested. Thirdly, cannibalism often is particularly widespread among siblings because adults deposit clusters of eggs. This can result in reduction of inclusive fitness, because there is little opportunity to distinguish relatives from nonrelatives. Aggressive cannibals may also eliminate prospective mates if they consume all conspecifics. The genetic costs of destroying relatives and eliminating prospective mates are likely very important evolutionary factors in the selection against cannibalistic behavior. Finally, many insects benefit from living in groups. Although most apparent for social insects, even nonsocial insects enjoy benefits from group living such as easier exploitation of food resources or more effective deterrence of predation. Cannibalism works against the accrual of such group-derived benefits.

► Facultative Predators
► Nutrient Content of Insects
► Praying Mantids (Mantodea)
► Mormon Cricket, *Anabrus simplex* Haldeman
► Katydids
► Gregarious Behavior in insects

References

Bernays EA (1998) Evolution of feeding behavior in insect herbivores. Bioscience 48:35–44

Elgar MA, Crespi BJ (1992) Cannibalism. Ecology and evolution among diverse taxa. Oxford University Press, Oxford, UK, 361 pp

Fox LR (1975) Cannibalism in natural populations. Ann Rev Ecol Syst 6:87–106

Joyner K, Gould F (1987) Conspecific tissues and secretions as sources of nutrition. In: Slansky F Jr, andRodriguez JG (eds) Nutritional ecology of insects, mites, spiders, and related invertebrates. Wiley, New York, NY, pp 697–719

Simpson SJ, Sword GA, Lorch PD, Couzin ID (2006) Cannibal crickets on a forced march for protein and salt. Proc Natl Acad Sci 103:4152–4156

Canopidae

A family of bugs (order Hemiptera, suborder Pentamorpha).

► Bugs

Canopy

The leafy part of plants or trees.

Canthariasis

Infestation of the organs of the body, including the alimentary canal, with beetle larvae. This is an unusual condition, and most often occurs by consuming flour or other grain products that are infested with grain beetles.

Cantharidae

A family of beetles (order Coleoptera). They commonly are known as soldier beetles.

► Beetles

Cantharidin

A defensive chemical produced by blister beetles and found in their blood. It can cause blisters on the skin of humans if they crush the beetles. Blisters can also form in the mouth and digestive tract of animals that consume the beetles along with forage plants. Horses are more susceptible to injury and death than other livestock. In North America, alfalfa hay is the principal source of blister beetles, and it is contaminated when hay is crimped (crushed) to hasten drying, as beetles are also killed at this time and incorporated into the hay. Problems occur mostly during or following grasshopper outbreaks because *Epicauta* spp. blister beetle larvae develop on the eggs of grasshoppers, and the adults move to alfalfa blossoms to feed.

► Blister Beetles
► Multifunctional Semiochemicals

Canthus

A chitinous process that, in some insects, divides the eyes into an upper and lower half.

Cape Honey Bees, *Apis mellifera capensis* Escholtz

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The Cape honey bee, *Apis mellifera capensis* Escholtz is a subspecies (or race) of western honey bee, *A. mellifera* Linnaeus, that occurs naturally in the Cape region of South Africa. Upon casual observation, Cape bees look very similar to another race of honey bee present in South Africa, *Apis mellifera scutellata* (the "African" honey bee of the Americas). Yet reproductively, Cape bees differ significantly from *Apis mellifera scutellata* and other honey bee races, making it perhaps the most distinctive race of *A. mellifera* worldwide.

Identification

Cape bees have been distinguished from *scutellata* and other African races of honey bees using morphometric techniques. Genetic analyses are used increasingly as complications with morphometric techniques arise. Most beekeepers in South Africa use other characteristics to identify Cape bees, namely (i) the ability of worker bees to produce female offspring, (ii) the highly developed ovaries in Cape laying-workers, and (iii) small, queenless swarms. Once these phenotypes can be detected, Cape bees usually are established already.

Distribution

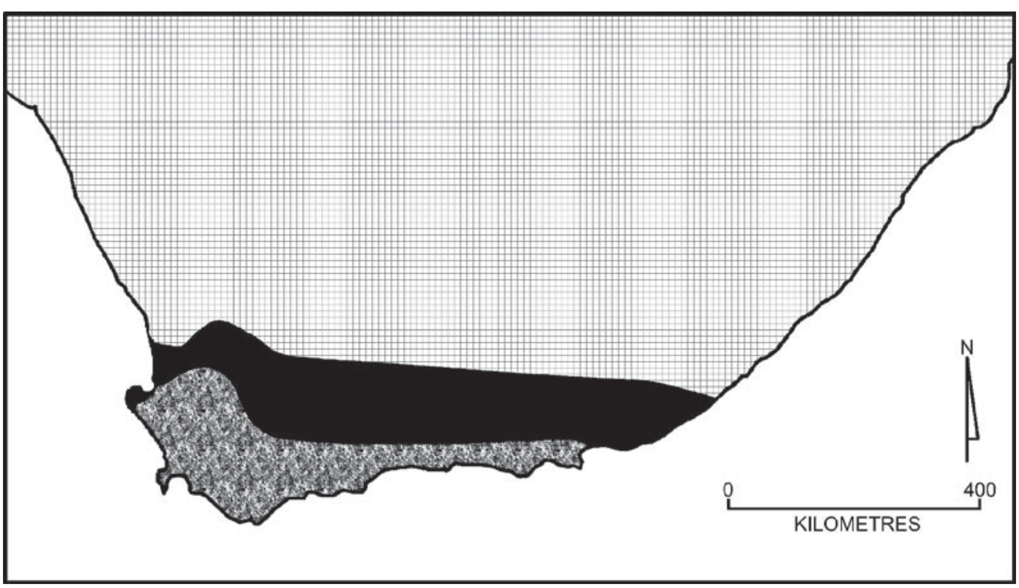
The natural distribution of Cape bees mirrors that of the fynbos region in the southwestern section of South Africa. Part of the Cape Floral Kingdom (one of six floral kingdoms worldwide), the fynbos is a narrow strip of land stretching from the southwestern-most corner of South Africa, eastward to Port Elizabeth. Even though it is small, the fynbos region contains over 80% of the flower diversity found in the Cape Floral Kingdom, and it has more plants species than any area in the world, including tropical rain forests.

Because it is rich in plant biodiversity, the fynbos region is able to support a remarkable diversity of life, from insects to higher animals. Cape honey bees specialize in foraging on plant species found in the fynbos, and beekeepers in this area use Cape bees as their bee of choice. Like other western honey bee races, Cape bees can be managed readily for purposes of pollination and honey production.

Because the fynbos region is limited climatically to the small belt stretching from southwestern South Africa eastward to Port Elizabeth, Cape bee distribution is limited to this area as well (Fig. 13). Here, one can find the "pure" race of Cape bee. However, Cape bees can hybridize with *Apis mellifera scutellata*, and they begin to do so just north of the fynbos belt. This zone of hybridization also encompasses a narrow stretch of land, running the entire length of area just north of the fynbos region. North of the zone of hybridization, one will find the "pure" race of *Apis mellifera scutellata*.

Reproduction in Cape Bees

Understanding reproduction in Cape bees is fundamental to understanding their biology and behavior. For the most part, reproduction in Cape bees follows that of other races of honey bees. Queens are the reproductive individuals in honey bee colonies. When queens emerge from the waxy cells in which they pupate, they spend the first 10–14 days of their lives maturing and mating. During this time, a queen bee will leave the colony in search of drones or male honey bees. Queens and drones mate in the air, following which the drones die. The queen will repeat this process over the course of a few days, mating with anywhere from 10–20 drones. Queens store all of the semen collected from the various drones in an organ called a spermatheca.



Cape Honey Bees, *Apis mellifera capensis* Escholtz, Figure 13 The distribution of Cape honey bees in South Africa (shaded gray). The area shaded black represents where *A.m. capensis* and *A.m. scutellata* hybridize. The checkered area indicates the natural distribution of *A.m. scutellata* (modified from Hepburn and Radloff, 1998).

When a queen bee lays an egg, she can control whether or not the egg is fertilized. If she chooses not to fertilize the egg, the resulting offspring will be a male bee or drone. If she chooses to fertilize the egg, the resulting offspring will be a female bee, either a queen or a worker. This type of reproduction is referred to as haplodiploid reproduction because male honey bees (from unfertilized eggs) are haploid while female honey bees (from fertilized eggs) are diploid.

Queen and worker bees both originate from the same type of egg. The quantity and quality of food they are fed while young determines whether the female larvae will become a queen or a worker. So it is correct to suggest that workers are underdeveloped queens (though, some rightly argue that the reciprocal is most true, at least behaviorally and physiologically) because they were fed less food while developing as larvae.

Worker bees, despite being sexually immature, have ovaries but they are unable to mate. They can, however, lay eggs. Because the eggs cannot be fertilized, workers are able to produce only drone offspring. This leads to an interesting dynamic in honey bee colonies. The presence of a queen in a colony suppresses a worker's desire to reproduce. As long as the colony has a functioning queen, worker bees typically do not oviposit.

However, honey bee colonies may lose their queens for a number of reasons. This event usually results in the rearing of a new queen, a feat accomplished by worker bees that begin to nurture a young female larva originally produced by the now-deceased queen. Despite this safety mechanism, many colonies fail to requeen themselves before the female larvae in the colony become too old to become queens. Because of this, many colonies become hopelessly queenless and are destined to perish.

Despite the fact that the colony will die without a queen, it does have one last chance to pass its genetics on to other honey bees in the area. When a colony has become hopelessly queenless for a period of time (usually > 2 weeks), some workers' ovaries develop, and the workers begin to oviposit. The resulting, haploid offspring all become drones. Drones produced from laying workers are sexually viable, thus they are able to mate with virgin queens from other colonies in the area.

This is the point in the reproductive cycle where Cape bees differ from all other races of honey bees. When a Cape bee colony goes queenless, it attempts to rear a new queen. And if for whatever reason the colony becomes hopelessly queenless, some workers' ovaries will develop and the workers will begin to oviposit. However, unlike eggs produced by laying workers in other honey bee races, eggs produced by Cape laying workers are usually diploid, even though Cape workers cannot mate. This means that Cape workers are fully capable of producing female offspring, both workers and queens.

The process by which Cape workers produce diploid eggs is called thelytokous parthenogenesis – they can produce males and females parthenogenetically. In this system, the egg pronucleus fuses with one of the polar bodies that results from meiosis, thus forming a diploid nucleus that continues to develop normally into a female bee (either a queen or worker). Queenless colonies of Cape bees can survive for some period of time and even rear a new queen from one of the laying worker's eggs. If, however, the colony fails to requeen itself, the population will dwindle and the colony will die. Even multiple laying workers present in a colony cannot maintain the reproductive output of a single queen.

Thelytoky in Cape bees leads to a number of different important considerations. For example, worker offspring produced by Cape laying workers are a type of clone, being genetically identical to their mother (who provided both sets of chromosomes). Furthermore, the ability of workers to lay diploid eggs breeds a type of reproductive conflict not seen in colonies of other races of honey bees. For example, queenless Cape colonies have a number of options: (i) produce a new queen from a queen mother egg, (ii) produce a new queen from a worker-laid egg, (iii) proceed as a laying worker colony, or (iv) proceed as a laying worker colony and later produce a queen from a worker-laid egg.

It is important to note that thelytoky is not unique to Cape bees. It is believed that workers from most (if not all) races of honey bees are capable of laying diploid eggs. However, < 1% of worker-laid eggs are diploid in other honey bee races. So while it is the exception, rather than the rule, in other honey bee races, thelytoky is common and the predominant scenario in Cape bee colonies.

A number of hypotheses have been proposed for the prevalence of thelytoky in Cape bees. Perhaps the leading hypothesis is that because the Cape region of South Africa is very windy, Cape colonies experience a significant queen loss when queens leave the colonies to mate. Colonies with thelytokous capabilities would not suffer the loss of a queen the same way as colonies without thelytokous capabilities, thus favoring the propagation of colonies with thelytokous workers.

Biology and Behavior

Behaviorally, Cape bees are not unlike other African races of honey bees. They are "flighty" on the comb (run on the comb when the colony is disturbed), abscond (completely abandon the nest) readily in response to nest disturbances or diseases/pests, have smaller colonies than European races (an artifact of being in a warmer climate), use copious amounts of propolis (resins collected from trees and plants, used as a weatherproofing agent and antibiotic in the colony), and are well-suited to warm climates. Unlike other African bee races (especially *Apis mellifera scutellata*), Cape bees are docile, at least usually. Yet, there is a key behavioral difference that separates them from all other races of honey bees. Cape bees are considered social parasites.

Social parasitism in Cape bees is not understood fully. In instances of larger numbers of colonies per unit area (e.g., managed-colony situations), worker bees and drones will "drift" between colonies. When the drifting bees are Cape worker bees, the worker bees can takeover or parasitize the "host" colony. In this regard, the mother queen of the host colony is lost (a process not understood fully at this point) and the Cape worker becomes the reproductive individual in the colony. This process can be exacerbated when two or more Cape worker bees drift into the same colony.

Laying workers not only possess the ability to produce female offspring, but their pheromonal bouquet changes from that of a worker to that of a queen. This is especially true with respect to the pheromones of the mandibular glands, which change to a very queen-like scent. This change in scent makes the Cape laying worker become adopted by the parasitized colony as its new queen. That is why it is difficult to requeen a laying worker colony. The bees in the colony think they have a queen. Any introduction of a new queen into a Cape laying worker colony almost always results in the new queen's death.

The ability of Cape workers to produce female offspring elicits another interesting behavior in Cape colonies – worker policing. In worker policing, workers produced from one Cape laying worker can detect eggs oviposited by other laying workers and destroy or eat those eggs. This establishes a dominance hierarchy within Cape laying worker colonies whereby females from the same mother police the colony and destroy their aunts' offspring in favor of their own mother's offspring (their sisters). Research has shown that this behavior has led to territory grabbing within Cape laying worker colonies.

Because a Cape laying worker colony is composed of many laying workers, all whose offspring are working to ensure their mother is the dominant laying force in the colony, bees produced by the same laying worker may congregate in the same area of the colony. So within a colony, one might find smaller "sub-colonies," each headed by a laying worker. This system is truly amazing and has advanced the study of the development of sociality and reproductive castes.

Problems for Beekeepers

Although the biology and behavior of Cape bees are fascinating, they present a problem for beekeepers in South Africa. Cape workers can parasitize colonies of any race of *A. mellifera*. Migratory beekeepers managing *scutellata* in the northern part of South Africa have moved bees into the fynbos region of South Africa where the Cape bee is present (the reciprocal also happens). This has allowed Cape workers to drift into and parasitize *Apis mellifera scutellata* colonies. This action has been a significant problem for beekeepers because Cape-parasitized colonies often dwindle and die. Furthermore, Cape bees are specialist foragers in the fynbos region and they often perform poorly when taken outside of this region. So *Apis mellifera scutellata* colonies parasitized by Cape bees in the northern part of South Africa can become useless to beekeepers.

Beekeepers in South Africa often consider Cape bees more of a serious threat to their colonies than varroa mites (*Varroa destructor*, the most prolific pest of honey bees). Because of this, researchers globally have taken notice of Cape bees. Many fear that if Cape bees ever spread outside of South Africa, they may be a significant problem for beekeepers worldwide.

References

Hepburn HR (2001) The enigmatic Cape honey bee, *Apis mellifera capensis*. Bee World 82:181–191

Hepburn HR, Radloff SE (1998) Honeybees of Africa. Springer-Verlag, Berlin, Germany, 370 pp

Johannsmeier MF (ed) (2001) Beekeeping in South Africa. Plant protection handbook No. 14, Agricultural Research Council, Pretoria, South Africa, 288 pp

Capitate

Having an expanded tip or club-shaped, and usually used in reference to antennae.

► Antennae of Hexapods

Capniidae

A family of stoneflies (order Plecoptera). They sometimes are called small winter stoneflies.

► Stoneflies

Capsid

The protein coat or shell of a virus particle; the capsid is a surface crystal, built of structure units.

Capsids

Some members of the family Miridae (order Hemiptera).

► Plant Bugs

► Bugs

Capsomere

A cluster of structure units arranged on the surface of the nucleocapsid, in viruses possessing cubic symmetry.

Carabidae

A family of beetles (order Coleoptera). They commonly are known as ground beetles.

►Beetles

Carabid Beetles (Coleoptera: Carabidae) as Parasitoids

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Several genera of carabid beetles are ectoparasitoids as larvae. The parasitoid habit is uncommon in beetles; only eleven beetle families include parasitoid species, compared to a much wider diversity of parasitoids in the Diptera and Hymenoptera. The evolution and ecology of these parasitoid beetles is fascinating, but their host associations are poorly known.

Carabid beetles have been stereotyped as ground-dwelling generalist predators, yet in recent years many counter-examples have shown the Carabidae to be more diverse in form, habit, and trophic association. Many carabids, especially tropical species, are arboreal. Granivory, herbivory, and specialized predatory habits are widespread. Three of the 76 recognized tribes are known to have parasitoid species: Brachinini, Peleciini, and Lebiini. All of these are ectoparasitoids on pupae of other beetles or, in one Peleciine genus, on immature millipedes.

In all known parasitoid carabids, the larva passes through three distinct development phases. First, the free-living first larval instar emerges from an egg laid in the host's habitat, and locates a host. Then, the larva feeds on a single pupal or pre-pupal host, while it molts zero to four times. Third, after the host is consumed, the larva undergoes a non-feeding larval stage ("pre-pupa") with zero to two molts; it then pupates next to the remains of the host. The total number of larval instars often deviates from the three molts typical for Carabidae, ranging from one (*Pelecium*) to five instars (some *Brachinus*). The adults live in the host habitat and may have a narrow or broad range of prey, including the immature stages of the host.

The best-known genera of parasitoid carabids are *Brachinus*, *Lebia*, and *Lebistina*. *Brachinus*, the celebrated bombardier beetle, emits a directed, explosive spray of boiling-hot quinone solution, which is considered the most highly evolved defensive secretion of the many types documented in the Carabidae. Studies by Eisner and colleagues have shown the elaborate mechanisms which allow the orchestration of this exothermic reaction while protecting the emitter and instantly repelling potential predators. They have also shown the chain of evolutionary developments leading to this impressive set of defensive organs. North American *Brachinus* are found in littoral habitats near fresh water, where the known beetle hosts in families Hydrophilidae, Dytiscidae, and Gyrinidae emerge to pupate from their larval aquatic habitats. Recently, dryland European *Brachinus* have been associated with carabid hosts of the genus *Amara*, broadening the known hosts to 11 species, for only nine of the approximately 300 *Brachinus* species described.

On the basis of fragmentary observation, it appears that *Pelecium sulcatum* (Pelecinii) develop as parasitoids on chrysomelid pupae and immature millipedes, and have only one larval instar.

Lebia species number over 450 and the genus is cosmopolitan, with 47 in North America. Adults typically seek prey in plant canopies, and all known larvae are ectoparasitoids of chrysomelid beetle pupae, yet only four species' hosts have been documented. Many additional *Lebia* species are reported to be associated (often with adult mimicry) with specific chrysomelids, particularly flea beetles (Alticinae) and casebearers (Cryptocephalinae), implying a host-parasitoid relationship. Two species parasitize economically important hosts: *L. scapularis* on elm leaf beetle, *Xanthogaleruca luteola* in Europe, and *L. grandis* on (Fig. 14) Colorado potato beetle, *Leptinotarsa decemlineata* in North America. Although elm leaf beetle is a significant invasive pest of ornamental elms in North America and elsewhere, *L. scapularis* apparently has not been considered for classical biological control. In contrast, *L. grandis* was introduced to France in the 1930s, and its parasitoid life history discovered, as part of a USA-France

Carabid Beetles (Coleoptera: Carabidae) as Parasitoids, Figure 14 ***Lebia grandis*** **fed first instar larva (top) with its prepupal host, Colorado potato beetle,** ***Leptinotarsa decemlineata*** **(photo by Caroline Chaboo).**

classical biocontrol program. Since the carabid was originally described from North Carolina in 1830, over 60 years before Colorado beetle arrived there, its putative original host was the false potato beetle, *L. juncta*, the only *Leptinotarsa* present. Although the introduction to Europe failed, there is interest in future classical biocontrol because of the apparent host specificity and the fact that the adults are the most voracious predators known on eggs and larvae of Colorado potato beetle. *Lebia* adults are typically found in close association with their host species, and females oviposit in close proximity to the host pupal habitat; in the case of *L. grandis*, this takes place in the soil below infested host plants.

Lebistina, an African genus closely related to *Lebia*, shows adult mimicry of its chrysomelid hosts, a pattern shared with some *Lebia* species. *Lebistina* is one part of a complex anthro-ecological story involving the San indigenous tribe of Southern Africa. San tribe members dig underground for the pupae of chrysomelids and their carabid parasitoids, both associated with the aromatic shrub *Commiphora* in the incense tree family, Burseraceae. Pupae of both the chrysomelid *Diamphidia*, and especially its parasitoid *Lebistina*, are collected for their potent neurotoxic arrow-poisons, which allow San hunters to fell large prey such as giraffes with small bows and arrows, but usually only after several days of tracking the injured animal.

Parasitoid carabids present some fascinating evolutionary questions, not the least of which is why both the impressive arrow-poisons and the explosive exocrine toxins are associated with these genera. Yet, at most, 1% of their hosts are known. In addition, the possible management of predator/parasitoid beetles may offer an interesting opportunity for "double control" of chrysomelid pest species.

References

Eggleton P, Belshaw R (1993) Comparisons of dipteran, hymenopteran and coleopteran parasitoids: provisional phylogenetic explanations. Biol J Linn Soc 48:213–226

Eisner T (2003) For love of insects. Belknap Press, Harvard University, Cambridge, MA, 464 pp

Erwin TL (1979) A review of the natural history and evolution of ectoparasitoid relationships in carabid beetles. In: Erwin TL, Ball GE, Whitehead DR, Halpern AL (eds) Carabid Beetles: their evolution, natural history, and classification. Dr W Junk, The Hague, The Netherlands, pp 479–484

Robertson H (2004) How San hunters use beetles to poison their arrows. Iziko museum of Cape Town. Available at www.biodiversityexplorer.org/beetles/chrysomelidae/alticinae/arrows.htm (accessed 26 March 2008)

Saska P, Honek A (2004) Development of the beetle parasitoids, *Brachinus explodens* and *B. crepitans* (Coleoptera: Carabidae). J Zool (Lond) 262:29–36

Weber DC, Rowley DR, Greenstone MH, Athanas MM (2006) Prey preference and host suitability of the predatory and parasitoid carabid beetle, *Lebia grandis*, for several species of *Leptinotarsa* beetles. J Insect Sci 6:9. Available online at http://insectscience.org/6.09/

Carabiform Larva

This is another term for campodeiform larva.

► Campodeiform Larva

Caraboid Larva

A larval form that is similar to campodeiform, but usually more chitinized and with stronger mandibles and short antennae. It is found in the families Staphylinidae, Carabidae, Dytisidae, and Hydophylidae (all in the order Coleoptera).

► Campodeiform Larva

Carapace

This is not a term used with insects (hexapods). It is used to describe the fused dorsal covering of crustaceans.

Carayonemidae

A family of insects in the superfamily Coccoidae (order Hemiptera).

► Bugs

Carbamate Insecticide

One of a class of cholinesterase inhibiting insecticides derived from carbamic acid.
► Insecticides

Carbohydrate

A large class of carbon-hydrogen-oxygen compounds, including simple sugars (monosaccharides) such as glucose. Glucose is the major fuel for most organisms and is the basic building block of polysaccharides such as starch and cellulose.

Carboniferous Period

A geological period of the Paleozoic era, extending from about 360 to 300 million years ago. The oldest insect fossils date from this period.
► Geological Periods

Carcinogen

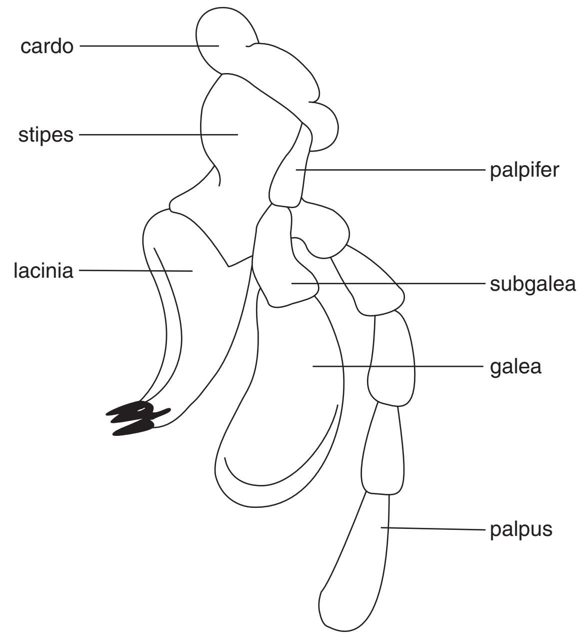
A substance or agent capable of causing cancer.

Carcinophoridae

A family of earwigs (order Dermaptera). They sometimes are called seaside and ring-legged earwigs.
► Earwigs

Cardo

A term that is used differently among orders (Fig. 15) and structures, but most commonly refers to the base or proximal section of a maxillary appendage.
► Mouthparts of Hexapods



Cardo, Figure 15 External lateral aspect of the left maxilla in an adult grasshopper, showing some major elements.

Careers in Entomology

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Entomologists are lucky to have a wide range of career choices. These include research in a wide variety of contexts, from universities, to many government agencies, to private corporations. The following is a summary of the institutions which hire entomologists, the types of work available and the qualifications usually required.

Faculty research, teaching, and extension positions almost always require a Ph.D. in entomology or a related field. Leadership positions in government agencies and heads of research groups in industry and government require a Ph.D. plus related administrative experience.

Research assistant positions are available for most graduate students. These are funded positions to perform research which also include tuition and a stipend. Teaching assistant positions are also available to graduate students. These include helping professors teach lecture and laboratory classes and grade papers and projects. Post doctoral fellowships are available to people with a Ph.D. to perform research on funded projects.

There are a wide variety of research technician jobs that require an M.S. or relevant work experience or a combination of education and work experience. Positions in county extension and many regulatory positions require a B.S. and/or relevant work experience. There are many part time and intern positions which are available to high school or college students without a degree. Jobs in the urban pest control industry rarely require any special education.

Qualifications and Skills

Each job listing will have a list of desired qualifications and skills.

Research

Research requires skills in areas such as devising, setting up, and running experiments, taking data, analyzing and recording data using computer programs, writing up results for publication and presenting results in lectures and conferences.

Teaching

Teaching skills include knowledge of the field and the ability to help students learn through lecture and discussion as well as designing courses and putting together course materials for a class.

Extension

Extension usually requires a combination of research skills and facility interacting with the public and other government organizations.

Regulatory

Regulatory work involves inspection of plants and animals entering an area with the goal of detecting, excluding, containing, or eradicating pathogens, weeds, and other undesirable organisms.

Industry

Industry work may involve research, but also inventing, patenting, and marketing new products. This also involves service oriented skills such as advising clients and providing pest control services.

Opportunities

Educational Institutions

Land Grant Universities and Cooperative Extension

These institutions usually have a focus on agricultural research and teaching with a network of extension stations throughout the state. Faculty positions generally involve a combination of research and teaching, often, but not always, focusing on applied rather than "pure" research. The research portion of the work involves the design and implementation of research projects, identifying sources and applying for research funding, training of graduate students and other students who participate in the research, writing up papers for publications, delivering lectures at conferences, and (if extension) interacting with and advising farmers. These positions usually include teaching in an area of expertise as well as teaching entry level courses in entomology.

Land grant universities have insect collections for reference and research. Positions are available in the museums for taxonomists and collections managers who help identify, sort, label, and collect specimens.

Extension work involves research on agricultural and urban plant and animal husbandry.

Extension positions are available and based in each county to advise people about raising and caring for plants and animals. Extension work involves research and survey work as well as considerable interaction with the public and other government agencies. Extension positions often focus on agriculture and animal husbandry, but increasingly focus on urban landscapes and other urban pests. Positions also are available in the extension research stations connected with the university, but located in agricultural areas.

Other Public and Private Research Universities

There are many other research universities that hire entomologists as part of biology departments or departments of entomology, ecology, behavior, or evolution. Medical and veterinary schools also hire entomologists to do research on insect transmitted diseases and other insect related illnesses. Duties and qualifications are similar to the above.

Undergraduate Colleges and Universities with a Focus on Teaching

There are many smaller universities and colleges where a professor's primary duties are in teaching. In these institutions, teaching duties can be quite various and a person with training in entomology might find herself teaching human anatomy or animal physiology, as well as courses in her specialty. Many professors also have research projects, though these are not as central to advancement as in the aforementioned research universities.

United States Government

U.S. Department of Agriculture

The principal agencies hiring entomologists include the Agricultural Research Service (ARS), Animal and Plant Health Inspection Service (APHIS) and the Forest Service. They hire for research, extension, and regulatory positions.

Armed Forces

The Navy, Army, and Air Force hire entomologists to do research on insects which transmit vector borne diseases such as malaria, dengue fever, and encephalitis as well as pest control specialists who work on ships and bases.

Other Agencies

Other agencies hire specialists in mosquito control and to track and advise on other public health concerns such as bubonic plague. The National Park Service and other government agencies hire entomologists for implementing IPM programs and handling pest control problems.

Industry

Urban Pest Control and Landscape Maintenance

This is a large and diverse industry that services business and residential customers. They need entomologists to do identifications, advise customers, and apply pesticides and other pest controls.

Pesticide and Pest Control Device Manufacturers

These businesses need entomologists to design and run evaluation tests on the pesticides and devices that a company markets. They also need experts to identify areas of need in the pest control industry and to consult with distributors and customers.

Food, Tobacco, and Drug Companies

These industries hire entomologists to research methods of keeping insects out of their packaged products and out of their manufacturing and processing areas. They also hire entomologists to do pest control in processing and packaging areas.

International Aid Organizations

A variety of agencies such as the World Health Organization (WHO), the United States Agency for International Development (USAID), and the International Center for Tropical Agriculture (CIAT) hire entomologists to work on a variety of public health and agriculture projects overseas. There are many non-governmental organizations (NGOs) which hire entomologists for similar projects. These are research and extension positions, generally temporary, and may require foreign language skills.

Independent Entomologists

This section will focus on entomologists who choose not to work for an institution, but who go into business for themselves. It is anticipated that this section will give ideas, inspiration, and some caution to those who are thinking of working independently as an entomologist.

The individuals consulted for this section chose the independent route for a great variety of reasons. Some did not have the formal education to get a job in a university or government following established routes. Others did not like being a part of a large institution, or preferred working by themselves. Others could not realize their ambitions or dreams at a university and so formed their own foundations and businesses. Circumstances of all sorts cause some aspiring entomologists to put together a career in a location that lacks universities or industries that fit their skills or their family situations. Many independent entomologists got their start working at a university or in industry and later struck out on their own. The following are typical examples of the work of independent entomologists. Keep in mind that these categories are rather general and not mutually exclusive. Many independent entomologists work in several of these areas.

This brief survey should show that there are numerous opportunities available to those who prefer to work independently. Undoubtedly, there are some possibilities left out or still to be invented.

The benefits mentioned most frequently of doing independent work are the ability to do what you love all the time, making (more or less) your own hours, the diversity of contacts that are developed, and the ability to conceive of a dream and bring it to fruition, while offering a valuable service not otherwise available. Some, with a lifelong passion for entomology but little or no formal education, have found their way to satisfying careers via the independent route. A few of these people have eventually obtained traditional jobs in universities or industry.

Naturally, there is a downside to such work. Difficulties include the lack of support staff and the necessity of doing everything yourself, including all the bookkeeping, hiring, firing, advertising, phone answering, etc. Also, there is a frequent necessity of looking for new work which may involve lots of phone calls, drawing up of proposals, and periods without much income. On the other hand, many people mentioned that getting started was difficult, but after a few years, the work just keeps coming in with very little necessity to go out and look for it. Many independent entomologists have second jobs on the side ranging from teaching to police officer.

Research and Development of Products

Entomologists working in this area often contract to test and develop products for pest control as well as helping the developers through the complex procedures for registering a new product.

People doing this work generally started out with standard jobs in universities or industry where they received training and made the contacts necessary to run a business on their own.

Lectures, Workshops and Other Courses

Entomologists working in this area design and teach courses on a wide range of topics from parasitic insects to tropical biology to urban pest control to the design, building, and maintenance of insect zoos. Such courses may be for professionals, graduate or undergraduate students, or the general public. They may also develop and sell educational materials.

Lectures and classes on insects are also popular with garden clubs, elementary schools, nature centers, museums, state and national parks, elder hostels, agricultural associations, and many others.

Writing and Photography

Many independent entomologists write field guides, children's books, and other books about animals and insects. A passion for photography or art involving insects frequently is the driving force for those who pursue a career in publishing books on insects.

Urban Pest Control

Perform routine and specialized pest control for home owners and businesses. This involves diagnosing problems, applying pesticides or otherwise controlling pest populations. It may also involve doing home repairs and other preventive measures.

Consultant and Contract Work

Consultants are probably the largest category of independent entomologists. Consulting work can range from pest control in urban or agricultural settings (often involving IPM and other alternatives to traditional chemical control programs), advising about rearing and displaying live insects, and advising industry about development or marketing of products. Many entomologists contract with other organizations to do specific tasks such as curating a particular group of insects for a museum, surveying private or public land for butterflies and other insects, and scouting fields for pests and beneficial insects and making control recommendations.

Non Profit Organizations

These organizations usually are focused on conservation of particular insect groups or insect habitats. These organizations also may include insects and pest control in a larger context such as preserving traditional agricultural techniques.

Retail or Wholesale Business

At least one intrepid entomologist has a store specializing in insect toys, jewelry, food, books, and other products. Other businesses sell insect control devices and chemicals.

Caribbean Fruit Fly, *Anastrepha suspensa* (Loew) (Diptera: Tephritidae)

This fly affects various fruits in the Caribbean region.

► Citrus Pests and their Management
► Tropical Fruit Pests and their Management

Carina (pl., Carinae)

A ridge or keel. This character is evident on many orthopterans, and both lateral and medial carinae occur on the pronotum of some grasshoppers. It has considerable diagnostic value at the species level in grasshoppers.

► Thorax of Hexapods

Carnid Flies

Members of the family Carnidae (order Diptera).
► Flies

Carnidae

A family of flies (order Diptera). They commonly are known as carnid flies.
► Flies

Carnivore

A flesh-eating organism (contrast with herbivore).

Carnivore Fleas

Members of the family Vermipsyllidae (order Siphonaptera).
► Fleas

Carnivorous

Feeding on animals.

Carnivorous Plants

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Carnivorous plants use entrapped animal tissues, mainly insects, as a source of nutrition. There are approximately 600 species of carnivorous plants in six angiosperm subclasses, which include both monocotyledons and eudicotyledons. The multiple, polyphyletic origins of the carnivorous plants suggest that the syndrome is an adaptation to the low nutrient, bright, waterlogged habitats that the plants typically inhabit. Carnivorous plants are found worldwide in varied climates that span extremes of temperature and rainfall. All carnivorous plants are insectivorous except for the few species with aquatic traps.

Among the insectivorous plants, there are three kinds of structures that are responsible for trapping insects: mucilage (sticky) traps (found among the Lentibulariaceae, Roridulaceae, Byblidaceae, Droseraceae and Dioncophyllaceae); pitfall (pitcher) traps (Sarraceniaceae, Nepenthaceae, Cephalotaceae and Bromeliaceae); and snap traps (Droseraceae). Stalked glands bearing a droplet of adhesive liquid are the basis of mucilage traps. The glands are borne on leaf surfaces, and insects become entangled in the mucilage when they alight on or walk onto the glandular surface. Enzymatic juices are released by the plant and digestion of the prey ensues. Pitcher traps are modified leaves that are formed into vase-like structures that are held erect with the aperture uppermost. The lip of the pitcher may bear nectaries and pigment patterns that serve to attract insect visitors. Below the nectaries, the interior surface of the pitcher is smooth and slippery, and may be covered with minute, downward-pointing projections that prevent insect feet from obtaining a firm grip on the surface. The hapless insect visitor falls into the fluid in the base of the pitcher and drowns. Pitcher plants have digestive glands, but the dissolution of the prey is further assisted by various pitcher inhabitants, including microbes and insect larvae. Plants with snap traps have a pair of lobed structures that are capable of movement at the end of certain leaves. The trap responds to stimulation of trigger hairs on the trap surface by rapidly closing the lobes, which have marginal spines that interdigitate and thereby enclose the insect visitor. The trap reopens after the prey is digested by secreted enzymes.

The prey of insectivorous plants typically are small, mobile individuals from a diverse array of taxa: Collembola, Diptera, Hymenoptera, Coleoptera, Hemiptera, Thysanoptera; with less frequent representation from Lepidoptera, Odonata, Orthoptera and other orders. Spiders, mites and isopods are also caught. To attract insects, the traps of some carnivorous plants provide nectar rewards and some are pigmented, scented or glisten in ways that may emulate the attributes of flowers or carrion. Other traps rely simply on the tendency of insects to alight on, or walk across, convenient surfaces. Insect tissues are particularly rich in nitrogenous compounds, and plants reportedly obtain 10–75% of their nitrogen from prey, depending on species and location. Prey capture promotes flower production and the reproductive success of the plant.

All carnivorous plants are pollinated by insects and there is a potential conflict between prey capture and pollination. Many plants have a spatial or temporal separation between their flowers and their traps that promotes segregation of these processes, so evidence for the existence of this conflict is rare.

Pitcher traps often support a "phytotelm," which is a plant-borne pool that comprises an aquatic ecosystem. The volume of phytotelms ranges from a few milliliters in *Sarracenia* pitchers to approximately 2 L in *Nepenthes rajah*. The insect members of the phytotelm community are Dipteran larvae, and different species adopt various lifestyles, such as filter feeding (e.g., mosquito larvae), saprophagy and predation. These inhabitants are sometimes referred to as pitcher "inquilines" or the "infauna." Phytotelms are much studied by community ecologists looking at patterns of coexistence and community structure. There are also non-aquatic associates of pitcher traps. Ants (e.g., genus *Camponotus*) inhabit pitchers in certain pitcher plants (*Nepenthes bicalcarata*) and scavenge from the pitcher fluid. Additionally, spiders occasionally spin webs across pitcher apertures, thus acting as resource parasites.

► Insectivorous Plants

References

Cresswell JE (2000) Resource input and the community structure of larval infaunas of an eastern tropical pitcher plant. Ecol Entomol 25:19–25

Ellison AM, Gotelli NJ (2001) Evolutionary ecology of the carnivorous plants. Trends Ecol Evol 16:623–629

Juniper BE, Robins RJ, Joel DM (1989) The carnivorous plants. Academic Press, London, UK

Carnivory and Symbiosis in the Purple Pitcher Plant

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Pitcher plants are a widely recognized group of carnivorous plants, well known for capturing and digesting small animals to supplement more usual nutrient sources. Carnivorous plants have fascinated biologists for centuries, despite making up only a tiny percentage of the species of flowering plants. Only about 600 species occur in six angiosperm subclasses. They generally inhabit nutrient-poor habitats, and the captured and digested insects provide a source of nitrogen, phosphorus, and micronutrients. Pitcher plants make up a substantial proportion of the carnivorous flora, with known representatives in three unrelated families: the new world Sarraceniaceae (27 + species), the tropical Nepenthaceae (103 + species) and the Australian Cephalotaceae (one species).

The pitcher plants have modified tubular leaves or "pitchers" that act as simple pitfall traps for insects and other small terrestrial animals. Insects are attracted to the plant by color patterns or production of extrafloral nectar, then may lose their footing and fall into the pitcher to drown in fluid retained in the pitchers. In many cases, slippery surfaces and/or downward pointing hairs prevent the insects from climbing out and escaping. Some pitchers exclude rainfall by hoods that cover the pitcher opening (e.g., *Nepenthes*, some *Sarracenia*) and secrete fluids that include digestive enzymes (including proteases, esterases, acid phosphatases, and amylases) that collect at the bottom of the pitcher. Other species (e.g., *Heliamphora* spp. and *Sarracenia purpurea*) collect rainwater and may or may not secrete digestive enzymes into the water.

One reason for the fascination with these plants is that they represent a type of plant/insect interaction that falls outside of the more expected interactions such as herbivory or pollination. Therefore, many studies have concentrated on aspects of carnivory, such as cost-benefit analyses (i.e., cost of attracting insect prey versus nutritional benefit from prey), prey species composition, digestive enzymes, etc. Other researchers have focused on pitcher plants as habitat for a wide variety of organisms. Pitcher plant inhabitants include aquatic taxa that live in the fluid in the pitcher (insects, mites, rotifers, protozoa, and bacteria), but may also include wasps that build nests in the pitchers, ants that live in specialized parts of the plants, and spiders that spin webs across the mouth of pitchers. Because the pitchers function as discrete habitats with clear boundaries between the internal and external environment, they have been the subject of many process-related studies, examining food-web, energy flow, and community questions within entire ecosystems. This is particularly true for the purple pitcher plant, *Sarracenia purpurea*, which is the most widely distributed pitcher plant in North America, and which has relatively long-lived pitcher habitats.

Sarracenia Species in North America

The Sarraceniaceae includes three genera in the New World: *Sarracenia* (8–11 species, depending on taxonomic opinion), *Darlontonia* (a single species in California and Oregon) and *Heliamphora* (at least 15 species in South America). *Sarracenia* is North American, and is mainly a genus of the American southeast (Table 5). As many as five species may occur naturally at a single site along the Gulf coast, but pitcher plant habitat is declining dramatically in these areas, and many species and subspecies in the genus are threatened by habitat loss. One species, *S. purpurea* (the purple pitcher

Carnivory and Symbiosis in the Purple Pitcher Plant, Table 5 ***Sarracenia*** **species in North America**

Species	Common name	Distribution
S. alata	pale pitcher plant, or winged pitcher plant	US Gulf coastal plain; SW Alabama to Texas
S. flava	yellow pitcher plant	US southeastern coastal plain; SW Alabama to SE Virginia
S. leucophylla	white-topped pitcher plant	US Gulf coastal plain; Florida to E Mississippi
S. minor	hooded pitcher plant	Northern Florida to North Carolina
S. oreophila	green pitcher plant	rare in North Carolina, Georgia, and Alabama; protected status
S. psittacina	parrot pitcher plant	US southern Gulf coast; Georgia to Mississippi
S. purpurea	purple pitcher plant	fragmented locations through the eastern US from Florida north to Maine and westward to Minnesota; widespread across Canada from the Atlantic coast to the northern prairie provinces and into northern British Columbia and southern Northwest Territories
S. purpurea var. *burkii* (or *S. rosea*)	Burke's variety	US Gulf coastal plain; some elevate this to species status as *S. rosea*
S. rubra	sweet pitcher plant	SE USA; North Carolina to Florida and Mississippi
S. rubra alabamensis (or *S. alabamensis*)	canebrake pitcher plant	rare in Alabama; protected; some elevate this to species status as *S. alabamensis*
S. rubra jonesii (or *S. jonesii*)	mountain pitcher plant	rare in North and South Carolina; protected; some elevate this subspecies to species status as *S. jonesii*

plant), ranges throughout much of North America, from Florida and Labrador in the east, and northwestward through Minnesota and the Canadian prairie provinces, into northern British Columbia and the southern Northwest Territories. Populations are generally stable in the northern parts of the range, especially in the less human-populated areas of the Canadian boreal zone. Species are perennial, and have tube-shaped leaves that form pitfall traps for small, mobile invertebrates. All species also produce photosynthetic non-tubular leaves in response to light intensity and nutrients.

Sarracenia species interact with insects in four major ways, (i) carnivory, (ii) pollination, (iii) herbivory, and (iv) symbiosis. All pitcher plants are carnivorous and attract insects as prey. The plants can self-pollinate, but several insects, especially bumblebees, are important in providing cross-pollination for the plants. Several insects feed on different parts of pitcher plants, and some of them are obligate pitcher herbivores, especially noctuid moths in the genus *Exyra*. Finally, some insects live inside the pitchers, especially in *S. purpurea*, which provides a relatively long-lasting aquatic habitat. Some wasps and spiders may also build nests in pitchers, and block the capture of prey by the plant. Information on herbivory and pollination ecology of pitcher plants can be found in the excellent review of pitcher plant-arthropod interactions by Debbie Folkerts.

Most *Sarracenia* species secrete a small amount of fluid that collects in the bottom of the pitcher, and prey collects in this moist zone rich in digestive enzymes. The types of prey that are attracted and retained by the plant vary with pitcher morphology, mainly relating to the height of the pitchers and the size of the pitcher opening, but ants are a frequent prey item in most pitcher species. Most species have a hood that covers the pitcher opening, preventing rain from diluting the digestive enzymes. In contrast, pitchers in *S. purpurea* lack this covering hood, so the pitcher fills up with rain, providing a larger and more complex aquatic habitat than other *Sarracenia* species. Most North American studies of carnivory and symbiosis have concentrated on *S. purpurea* because its wide distribution and ability to hold water for relatively long periods of time allow the development of a surprisingly complex community of inhabitants.

The Purple Pitcher Plant, *Sarracenia purpurea*

Sarracenia purpurea is a long-lived herbaceous perennial that is widespread over much of North America. Pitcher-shaped leaves are produced in a rosette, with new pitchers produced every 15 or 20 days. Soon after a new pitcher opens, it fills up with rainwater and begins attracting insect prey, and several new leaves may be produced over the summer. The purple pitcher plant is exposed to a wide variety of conditions throughout a range which encompasses 30° longitude and 70° latitude. In the south, the species grows year round in a variety of nutrient poor habitats, whereas in the north, it has a relatively short growing season and is strongly associated with peatlands. Unlike other pitcher plants, pitchers of *S. purpurea* provide a stable habitat for several months, including over the winter, before degrading and losing water in their second year. In the northern part of the range, the pitcher fluid may freeze during the winter, but the pitcher retains its integrity for at least a few weeks into the new season and continues to hold water. Like most carnivorous plants, purple pitcher plants are associated with habitats where nutrients are not generally available. Interestingly, the plants have been shown to be nutrient limited in localities even where nitrogen amounts do not appear limiting. In these cases, soil microbes and plants such as *Sphagnum* intercept the nutrients before angiosperms like the pitcher plants can assimilate them. The ability to capture and digest animal prey provides nitrogen, phosphorus, and some micronutrients, and though the plant can grow without prey, the added nutrients are thought to be important for plant processes like flowering.

Carnivory in Purple Pitcher Plants

Insects are attracted to the pitchers by both visual and chemical cues. The plant produces extrafloral nectar containing both carbohydrates and amino acids, allowing it to attract a wide variety of insects and other small invertebrates. Nectar, which is most abundant in newer pitchers, is produced in nectaries around the pitcher rim, where it accumulates and entices insects to move downward on the plant. UV light guides and purple streaks are found at the top of the pitchers and these also direct insects into the plant and downward into the pitcher fluid. Downward pointing hairs prevent the insects from escaping, and they eventually drown and are digested by the plant. In most *Sarracenia* species, digestion occurs through the action of digestive enzymes (e.g., proteases, hydrolases) produced in glands in the epidermis. Digestive glands and plant-produced enzymes had not been shown conclusively in *S. purpurea* and digestion was believed to result from proteolytic activity from bacteria and autolytic enzymes from the drowned victims. However, recent study has shown that not only does *S. purpurea* produce digestive enzymes (hydrolases), but that enzyme induction relates to pitcher developmental stage and to the presence of prey. Newly opened pitchers produce hydrolases even before the pitcher fills with water and before any bacteria or prey are present, but hydrolase levels decline if no prey are captured. The production of hydrolases can be re-induced, though, if prey is attracted to the pitcher at a later time. This may be a strategy to minimize the "cost" of carnivory to the plant, since digestive enzymes are produced only during the time when the pitcher is most attractive to prey or when prey are actually present.

Carnivory is usually examined by identifying the captured and decomposing prey found in pitchers. Ants generally make up the majority of the prey items, but flies, bees, wasps, moths, beetles, leafhoppers, grasshoppers, and spiders are also found. Despite all the adaptations that the pitcher shows to attract and retain prey, videotape of actual pitcher plant-insect interactions show that many insects are able to escape from the pitchers and capture efficiency is really quite low. In one study, several thousand insects were recorded in and around the pitcher mouth, but only about 2% were captured, and some groups (e.g., ants) were quite successful in escaping the pitcher trap. Most pitchers that have been evaluated in this author's lab, though, have had significant deposits of decomposing insect detritus in the bottom, and no pitchers were devoid of prey, so even if capture efficiency is low, it is likely still high enough to add nutrients to the plant. Young pitchers attract the most prey, possibly due to the relatively large amounts of nectar produced in new pitchers compared to old ones. Pitchers continue to accumulate prey throughout the summer, however, and the highest overall amounts of detritus are found in the older, overwintered pitchers.

Limnological Characteristics in Pitchers of the Purple Pitcher Plant

Individual pitchers on purple pitcher plants form temporary aquatic habitats that can hold up to about 60 ml of water (for large pitchers), but more typically hold between 20 and 40 ml. The plant maintains a clean water environment in pitchers through uptake of CO_2 and ammonia, and infusion of oxygen during photosynthesis. Oxygen levels are usually maintained at or near saturation for given temperatures (usually 5–10 mg/L), and pitchers rarely go anoxic in the field, and only if prey volumes are unusually high. However, other conditions within pitchers are usually highly variable, on both short and long-term scales, with large fluctuations in pH, temperature, and nutrients. Reported pH levels range from highly acidic (pH of about 3.0) to near neutral, depending on the pH of rainwater that fills the pitchers, the pH of plant secretions, and the pattern of prey decomposition. Several researchers have reported that pitcher pH declines over time as prey is captured, and have related the declines to the decomposition processes in the leaves. We have also found dramatic diurnal variations in pH within individual pitchers, due to low alkalinity conditions and the uptake and release of CO_2 during photosynthesis and respiration by the plant.

Temperature patterns within the pitcher can also be highly variable, both geographically (over the extremely large geographical range of the plant) and seasonally or diurnally within a site. Pitcher plants usually grow in open bogs in full sunlight, so can be exposed to a wide range of ambient temperatures. Conditions within the pitcher usually do not vary as much as in the surrounding bog.

Nutrient levels in the fluid depend on the age of the leaf, mainly because of temporal differences in the amount of prey captured. Hydrolases are secreted as the leaf opens and begins attracting insect prey, and then these enzymes combine with bacterial action and prey-derived autolytic enzymes to release ammonia and other dissolved nutrients. A steady supply of soluble nitrogen is therefore supplied for the plant through the breakdown of prey. Nitrogen fixing bacteria are also found in pitcher fluid, and these provide a further source of nitrogen to the plant. Animals living within the pitchers (arthropods and rotifers) feed on bacteria, protozoa, and the decaying prey and they excrete ammonia, which prevents nutrients from becoming sequestered in the bacteria and protozoa. The ammonia does not accumulate to toxic levels since the plant actively takes it up, especially when temperatures and light are at high levels.

Aquatic Pitcher Inhabitants

All *Sarracenia* species are associated with a suite of organisms (arthropods, rotifers, protozoa, bacteria) that reside within the pitcher and form communities of varying levels of complexity. Since *S. purpurea* pitchers hold water and provide habitat for several months, they form surprisingly complex aquatic communities comprising several trophic levels. The inhabitants have sometimes been referred to as resource parasites, intercepting prey that has been captured by the plant and using it for their own growth and development. However, it is now clear that these species also free up nutrients and prevent them from becoming sequestered in bacteria or protozoa, and can actually enhance release of nutrients to the plant. In return, the pitcher provides habitat and maintains a clean water habitat by actively taking up the toxic ammonia and CO_2 produced by the living organisms in the pitcher.

Several species of aquatic insect have been recorded alive in *S. purpurea* pitchers, but many of these (including stoneflies, caddisflies, midges, etc.) are thought to wash into pitchers during bog flooding events, and survive to emerge but not to actively colonize new pitchers. Three Diptera species (the pitcher plant mosquito, *Wyeomyia smithii*; pitcher plant midge, *Metriocnemus knabi*; and pitcher plant fleshfly, *Fletcherimyia fletcheri*) are obligate inhabitants of *S. purpurea*, and have been widely studied across their range, which approximates the range of the plant. At least eight other sarcophagids are associated with *Sarracenia* spp. pitchers, including *Sarcophaga sarraceniae*, and the other species of *Fletcherimyia*, but these are not as well studied as *Fletcherimyia fletcheri*. Other organisms that have been reported from purple pitcher plants include mites (especially *Sarraceniopus gibsoni*), a rotifer (*Habrotrocha rosa*), and a suite of protozoa and bacteria species.

Wyeomyia smithii (Coquillett) (Diptera: Culicidae): The Pitcher Plant Mosquito

The pitcher plant mosquito is, without doubt, the best studied of the pitcher plant inhabitants. Its range is slightly smaller than that of the pitcher plant itself, but it still extends over a wide area of

North America. The life history patterns vary depending on latitude. The species is univoltine in the north and bivoltine or even multivoltine in the south. It is autogenous for its first ovarian cycle throughout its range, but will take a blood meal to mature additional egg batches. It is an obligate pitcher plant inhabitant and is restricted to the purple pitcher plant in the north, though it will oviposit in other *Sarracenia* species in the south. Adult females are attracted to the pitchers through chemical cues and oviposit preferentially into new pitchers, increasing the chance that the pitcher will retain water throughout the insect's life cycle. In the more northerly parts of the range, adult emergence and oviposition correspond to the period when pitchers are just opening in spring. Adults desiccate easily, and do not travel far from their natal pitchers. In one study in Prince Edward Island, Canada, it took 6 years for mosquitoes to recolonize pitcher plants (Fig. 16) that had been transplanted from another bog, despite a rich supply of pitchers with mosquito inhabitants within a few meters of the transplanted plants.

Wyeomyia smithii larvae (Fig. 17) overwinter as larvae throughout their range, but again, there are differences that relate to latitude. They overwinter as 4th instar larvae in the south, and as 3rd instar larvae in the north (often frozen in the pitcher fluid), and diapause is both initiated and terminated via photoperiod. Recent work has shown that the photoperiodic responses are changing in response to global warming, and that measurable changes in the required daylength to induce diapause have occurred over the last 30 years. Despite their ability to overwinter in the frozen pitcher fluid in northern locations, they are not very tolerant of low temperatures, and will die if winter temperatures are too cold, or if sufficient snow cover is not available for insulation. Therefore, at northern edges of the range, there are many plants, and even entire bogs, where the mosquito is absent. They also die if there isn't enough aquatic habitat for survival, for example, if the fluid dries under drought conditions or if the pitcher develops a hole through which the water escapes.

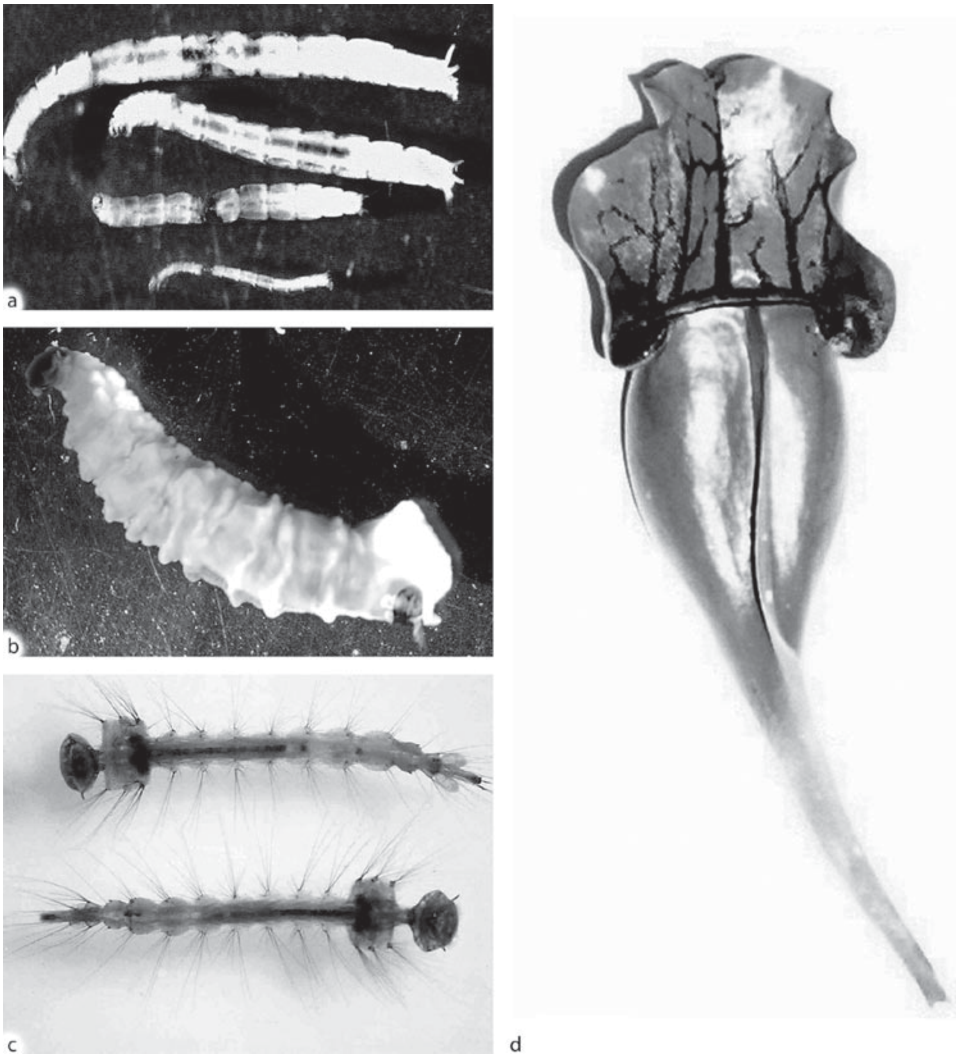
The mosquitoes feed by filtering bacteria, protozoa, and fine detritus from the water column, and they obtain their oxygen directly from the air through a breathing siphon, and through their cuticle. They are tolerant to wide diurnal variations in temperature, oxygen, and pH.

Metriocnemus knabi Coquillet (Diptera: Chironomidae): The Pitcher Plant Midge

The pitcher plant midge has been less studied than the mosquito, but is found in pitchers throughout most of the range of the plant, and is often present in very high numbers in pitchers. Larvae (Fig. 17) can overwinter in more than one instar, depending upon the stage of development when daylength begins to shorten; for example, different cohorts may overwinter as 2nd or 3rd or 4th instar larvae. Life cycles may be univoltine or bivoltine, depending on the summer temperatures during development, and oviposition occurs in both young and older leaves. The midges are more tolerant to cold than the mosquito, and they are found in many northern bogs where the mosquitoes are absent. Similar to the mosquito, the midge requires enough water to maintain an aquatic environment, but if the pitcher loses water (common in older pitchers that can lose their integrity), the midge larva can crawl from one pitcher to another on the same plant. They pupate in a gelatinous mass on the sides of the pitchers, and adults emerge and mate, then search for oviposition sites.

The midge lives in the wad of detritus that collects at the bottom of the pitcher, and feeds by chewing into the bodies of the drowned insects or scavenges on the decomposing particulate material. They respire cutaneously and are relatively intolerant of low oxygen, so will only be found in pitchers with sufficient oxygen for respiration. Few natural pitchers experience anoxia, however, so it is rare to find pitchers in northern peat bogs without a strong complement of pitcher plant midges.

Carnivory and Symbiosis in the Purple Pitcher Plant, Figure 16 **Glenfinnan bog and pitcher plants, Prince Edward Island, Canada: (a) bog habitat; (b) purple pitcher plant, *Sarracenia purpurea*.**



Carnivory and Symbiosis in the Purple Pitcher Plant, Figure 17 **(a) Larvae of pitcher plant midge, *Metriocnemus knabi*; (b) larva of pitcher plant flesh fly *Fletcherimyia fletcheri*; (c) larvae of pitcher plant mosquito, *Wyeomyia smithii*; (d) modified tubular leaves or "pitchers" that act as simple pitfall traps for insects and other small terrestrial animals, and serve as a home to the aforementioned flies.**

Fletcherimyia fletcheri (Aldrich) (Diptera: Sarcophagidae): The Pitcher Plant Flesh Fly

Sarcophagid flies are usually not associated with aquatic habitats, but several species, particularly within the genus *Fletcherimyia*, are found in pitcher plants. *Fletcherimyia fletcheri* is the most aquatic of the suite of pitcher plant species, and is an obligate inhabitant of the purple pitcher plant. Larvae (Fig. 17) are deposited directly into pitcher plants, with larvipositing females preferring new pitchers at the height of their prey attractance. Usually only one larva is found per pitcher, since larvae are aggressive and territorial and will kill or chase away any additional larvae. Not all larvae die after territorial encounters, though, since they are capable of limited movements to other pitchers. They are usually considered to be univoltine in the northern part of the range, and multivoltine in the south. Larvae develop in the pitchers, then crawl out to pupate in the surrounding moss.

Larvae feed at the surface of the water on newly drowned prey items. They attach to the surface tension and breathe surface oxygen through posterior spiracles, so are tolerant to wide variations in oxygen in the water.

Other Pitcher Plant Inhabitants

Mites are often found in pitcher plants, and feed either on the captured prey or on other mite species. It isn't clear how the mites disperse from pitcher to pitcher, but they may travel on the bodies of the adult insect inhabitants or be associated with some of the obligate herbivores of pitcher plants. A species of bdelloid rotifer, *Habrotrocha rosa*, is also common in purple pitcher plants, though it is rarely seen unless pitcher fluid is examined without preservation, since the rotifers don't preserve well and are usually washed through sieves before examination. The rotifers are very active, however, and can be fascinating to watch, if a researcher is patient enough to look for them. The rotifers feed on bacteria and particulate organic matter in the water column, and may be critical in providing soluble nitrogen and other nutrients to the plant. Protozoan and bacterial species diversity have rarely been enumerated, but at least 40 Protozoa species and several bacterial types have been recorded from pitchers.

Pitcher Plants as "Model Ecosystems"

Purple pitcher plant leaves provide ideal systems for investigating a variety of ecological questions. The pitchers form small, discrete, aquatic systems that support complex aquatic communities consisting of at least three trophic levels. Although they are aquatic ecosystems, they are located within terrestrial ecosystems, and therefore provide small "islands" of habitat where colonization and dispersal patterns, as well as food webs and energetics, can be studied relatively easily, and with a degree of replication that is not possible in most habitats. They are also easily manipulated, since it is relatively simple to add or remove food materials or top predators, to monitor population effects. Since purple pitcher plants occur over a vast geographical area, it is also possible to study ecological processes in entire ecosystems over a wide latitudinal range.

The pitcher ecosystem is mainly detritus based, with energy coming from the insects that are captured by the plant, then drown and decay in the pitcher fluid. The lowest level of the food web is therefore made up of detritivores, including bacteria, some mites, the pitcher plant midge, and when present, the flesh fly. The pitchers may also contain phytoplankton. Protozoans and rotifers feed on the bacteria and algae, then are themselves fed on by the top predator in the system, the pitcher plant mosquito. There are usually no predators for the midges and flesh flies, despite their low position in the food web. Manipulations of various food web components have shown that pitcher plant communities respond to a combination of "top-down" and "bottom-up" regulation. Generally, the lower trophic levels are resource limited with respect to both population size and taxonomic richness, so as resources (prey) are added to pitchers, abundance and richness increases. In contrast, predator limitation targets specific groups only, so that addition of mosquito larvae results in a decrease in rotifers, but increases in bacterial abundance and richness.

Many other studies have concentrated on other aspects of community structure, especially the interactions among the pitcher macrofauna (midges, mosquitoes, flesh flies). Some studies have found that the feeding of the midges releases nutrients that support mosquito populations, in a processing chain commensalism. Others have not found relationships among the major insect groups, suggesting that these patterns may relate to food availability. A recent study which evaluated latitudinal trends in species richness across most of the range of the purple pitcher plant found that species richness (mainly of the bacteria and protozoa) increases with increasing latitude, contrary to most predictions of latitudinal patterns. This may also be driven by food web patterns, since the top predator in the system, the mosquito, declines in abundance with increasing latitude.

Summary

The purple pitcher plant is a widespread carnivorous plant which interacts with insects through carnivory and by providing habitat, as well as through herbivory and pollination. The pitchers form discrete aquatic habitats within a terrestrial landscape, and provide a home to a surprisingly complex community of aquatic organisms. Because of the ease of studying and manipulating these habitats, considerable information is available on both the individual taxa and their interactions, over a wide geographical range.

► Carnivorous Plants
► Insectivorous Plants
► Bromeliad Fauna
► Phytotelmata

References

Bradshaw WE, Creelman RA (1984) Mutualism between the carnivorous purple pitcher plant and its inhabitants. Am Midl Nat 112:294–304

Bradshaw WE, Holzapfel CM (2001) Genetic shift in photoperiodic response correlated with global warming. Proc Natl Acad Sci 98:14509–14511

Buckley HL, Miller TE, Ellison AM, Gotelli NJ (2003) Reverse latitudinal trends in species richness of pitcher-plant food webs. Ecol Lett 6:825–829

Dahlem GA, Naczi RFC (2006) Flesh flies (Diptera: Sarcophagidae) associated with North American pitcher plants (Sarraceniaceae), with descriptions of three new species. Ann Entomol Soc Am 99:218–240

Dress WJ, Newell SJ, Nastase AJ, Ford JC (1997) Analysis of amino acids in nectar from pitchers of *Sarracenia purpurea.* (Sarraceniaceae) Am J Bot 84:1701–1706

Fish D, Hall DW (1978) Succession and stratification of aquatic insects inhabiting the leaves of the insectivorous pitcher plant, *Sarracenia purpurea.* Am Midl Nat 99:172–183

Folkerts D (1999) Pitcher plant wetlands of the Southeastern United States: arthropod associates. In: Batzer DP, Rader RB, Wissinger SA (eds) Invertebrates in freshwater wetlands of North America: ecology and management. Wiley, New York, pp 247–275

Gallie DR, Chang S-C (1997) Signal transduction in the carnivorous plant *Sarracenia purpurea*: regulation of secretory hydrolase expression during development and response to resources. Plant Physiol 115:1461–1471

Giberson DJ, Hardwick ML (1999) Pitcher plants (*Sarracenia purpurea*) in eastern Canadian peatlands: ecology and conservation of the invertebrate inquilines. In Batzer DP, Rader RB, Wissinger SA (eds) Invertebrates in freshwater wetlands of North America: ecology and management. Wiley, New York, pp 401–419

Heard SB (1994) Pitcher-plant midges and mosquitoes: a processing chain commensalism. Ecology 75:1647–1660

Juniper BE, Robins RJ, Joel DM (1989). The carnivorous plants. Academic Press, London, UK

Kitching RL (2001) Food webs in phytotelmata: "bottom-up" and "top-down" explanations for community structure. Ann Rev Entomol 46:729–760

Rice BA (2007) Carnivorous plant FAQ v11.0. Available at (http://www.sarracenia.com/faq.html.) Accessed 2 May, 2007

Rymal DE, Folkerts GW (1982) Insects associated with pitcher plants (*Sarracenia*: Sarraceniaceae) and their relationship to pitcher plant conservation: a review. J Alabama Acad Sci 53:131–151

Van Breeman, N (1995) How *Sphagnum* bogs down other plants. Trends Ecol Evol 10:270–275

Carob Midge Complex, *Asphondylia* spp. (Diptera: Cecidomyiidae) in Cyprus

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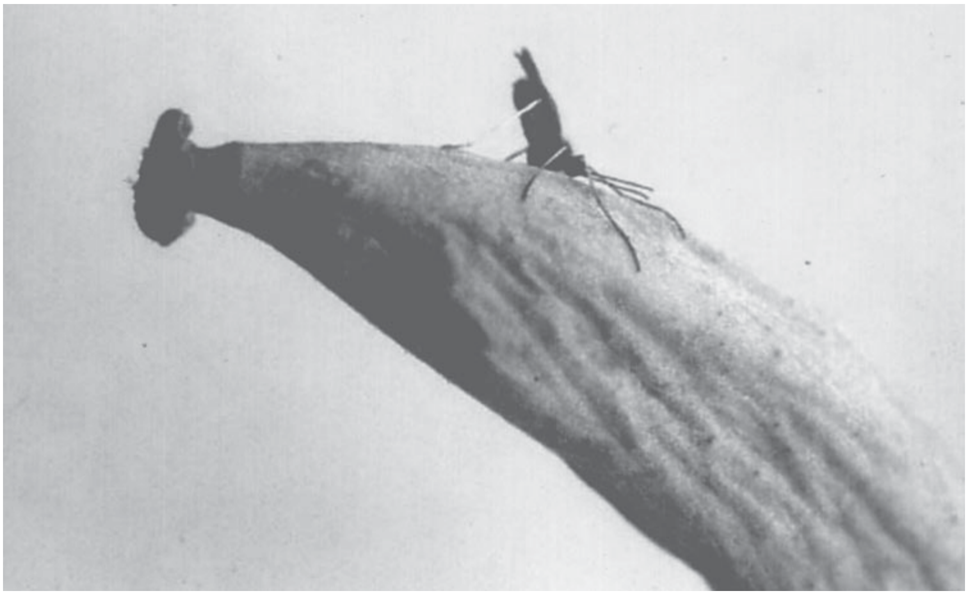
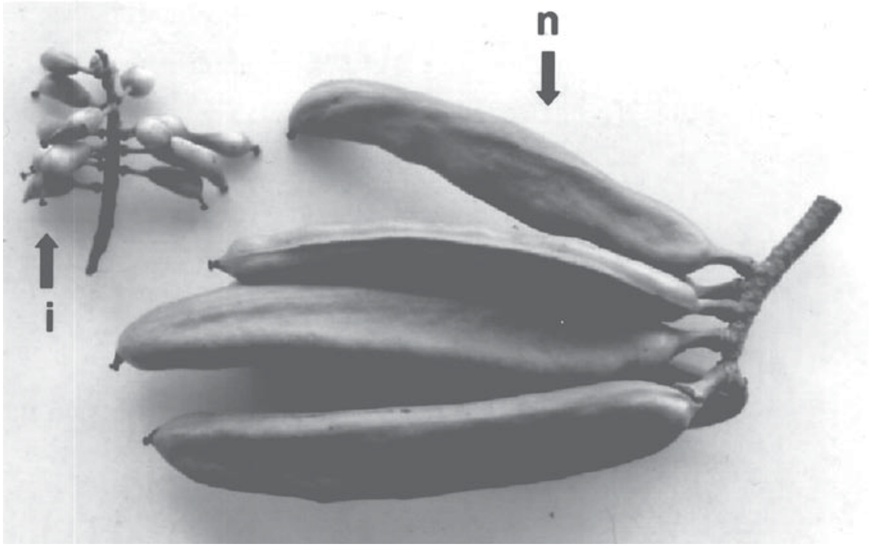
In Cyprus, a cecidomyiid complex, *Asphondylia* spp. attacks the pods of carob, *Ceratonia siliqua*, causing a fruit stunting deformation known as brachycarpia. This malformation is reported to have been noticed on the island for the first time around 1870. The adult female (Fig. 18) inserts the eggs with its ovipositor in the carob pods when these are about 0.5 cm long. Infestation becomes evident 7–10 days later with the pod swelling gradually as the midge larva grows. The pupa is formed in the infested pod in a rather hardened



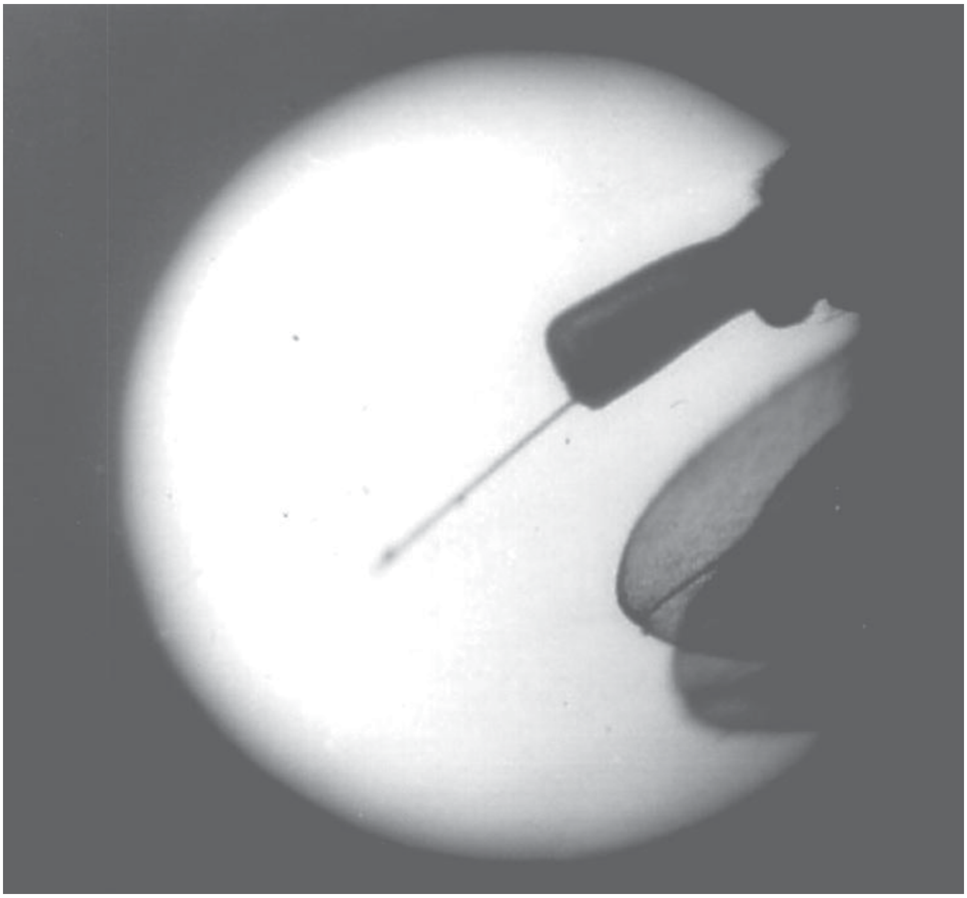
Carob Midge Complex, *Asphondylia* spp. (Diptera: Cecidomyiidae) in Cyprus, Figure 18 **Adult of the carob midge, *Asphondylia* sp.**

whitish niche. Upon completing its development the adult emerges leaving the pupal skins half-protruding from the infested pod. Initially it was believed that the cecidomyiid responsible for brachycarpia was *Asphondylia gennadii* (Marchal) and that it attacked only carobs. Later biological studies in Cyprus, however, revealed that the midges from carob pods (Figs. 19–20) required an alternate host for the summer. The adults of the overwintering generation emerging from carob pods in April would not deposit their eggs in the few out-of-season young carob pods that could sometimes be available. No alternative points of attack on the carob tree could be found. Instead, they would search for secondary host-plants like caper (*Capparis spinosa*), pepper (*Capsicum annuum*), potato (*Solanum tuberosum*), garden rocket (*Eruca sativa*), mustard (*Sinapis* spp.), sea squill (*Urginea maritima*), asphodel (*Asphodelus fistulosus*), and St. Johnswort (*Hypericum crispum*). The successful development of the carob midge on all these host plants was proved experimentally in cages and supported by meticulous observations in isolated areas under natural conditions. On caper the females insert the eggs within the flower bud among the petals, the stamens and on the ovary. On pepper, squill, potato and St. Johnswort they insert their eggs in the ovary during the flower-bud stage (Fig. 21). As a result, infested flower buds harden and never bloom. Five or six generations develop on the secondary plants, which are available for infestation until September–October. At that time, the midges return to carobs to lay their eggs in the newly formed pods of the normal flowering season for the overwintering generation.

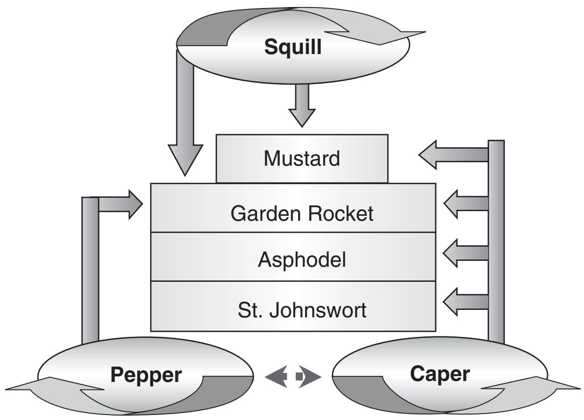
The above findings stimulated a re-examination of the generic placement and the overall taxonomic status of the carob gall midge. Adults, larvae and pupae from all the mentioned host plants are anatomically identical, suggesting that all these midges may belong to one species. However, there is a differential host preference among adults from the various secondary hosts. For example, adult females from pepper readily attacked only pepper and garden rocket, rarely attacked caper and did not attack squill and St. Johnswort. Those from caper readily attacked caper, mustard, garden rocket, asphodel and St. Johnswort, rarely attacked



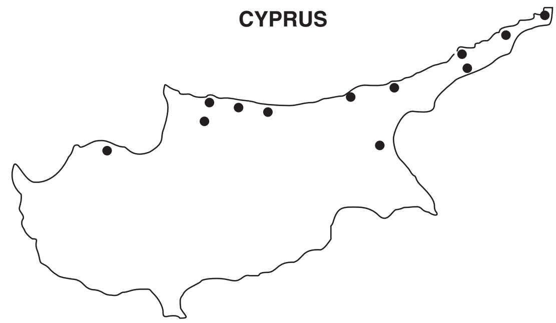
Carob Midge Complex, *Asphondylia* spp. (Diptera: Cecidomyiidae) in Cyprus, Figure 19 **Normal (n) and midge-infested (i) carob pods.**



Carob Midge Complex, *Asphondylia* spp. (Diptera: Cecidomyiidae) in Cyprus, Figure 20 **Ovipositor of the carob midge, *Asphondylia* sp.**



Carob Midge Complex, *Asphondylia* spp. (Diptera: Cecidomyiidae) in Cyprus, Figure 21 **Differential host preference among carob midge adults from squill, pepper and caper.**



Carob Midge Complex, *Asphondylia* spp. (Diptera: Cecidomyiidae) in Cyprus, Figure 22 **Distribution of carob midge infestation on pepper in Cyprus.**

pepper and did not attack squill. Finally, midges from squill readily attacked squill, garden rocket and mustard but did not attack pepper and St. Johnswort.

In an older survey (1970–1972) midge infestation on carobs and caper, in contrast with that on the other host plants, was widely distributed all over the island. A striking difference, however, was observed with the infestation on pepper that occurred only on the northern coast and the whole Karpasia peninsula (Fig. 22). The southern part of the island is still free from midge infestation on pepper. The northern part is now inaccessible to repeat the survey. This characteristic distribution of midge infestation on the different host plants and the midge behavior on host preference indicates that the carob midge complex consists of the overwintering generation of a morphologically homogenous but biologically heterogeneous population of *Asphondylia*. It is possible that there are three races or sibling species of this gall midge.

Damage

On carobs, the estimated loss of yield is significantly lower than the apparent one. The number of carob pods on each inflorescence is generally very large and certainly not all of them reach maturity. All the unfertilized pods drop at an early stage of their development unless the carob midge attacks them. Infested pods do not drop. The majority of the fertilized pods will also drop at their early growing stages because trees cannot bear to maturity all the pods produced. Consequently, it is misleading to calculate the damage by comparing the infested and normal pods because among the infested pods, a significant number would have dropped even in the absence of the carob midge. The relationship between the estimated loss of yield and the observed infestation was found to be described by a second-degree polynomial curve with the equation $\hat{y} = -0.12 + 0.177x + 0.00247x^2$.

Mortality Factors

The natural mortality factors recorded were: (i) the parasites – *Eurytoma* sp. A., *Eurytoma* sp. B., *Pseudocatolaccus nitescens* (Walker), *Tetrastichus brevicornis* (Panzer), *Eupelmus urozonus* Dalm., *Adontomerus* sp. and *Paraholaspis* sp.; (ii) predators – ants, earwigs, spiders; (iii) unidentified molds; and (iv) weather conditions.

Molds appear in the interior part of the infested carob pods, causing the death of the midge larva. Subsequently, the pods drop. Ants have been observed cutting holes through the infested carob pods and earwigs would enlarge these holes. The midge larvae or pupae would then be destroyed either by these predators or by the development of molds or they would dry up. Spiders attack adult midges while the latter rest during the day. The midge mortality occurring from November to April is mainly due to abiotic factors (weather). The effectiveness of the biotic factors (parasites, predators and molds) becomes evident from April onwards.

References

Anon (1914) Entomological notes. Cyprus Agr J 35:805–807

Gagné RJ, Orphanides GM (1992) The pupa and larva of *Asphondylia gennadii* (Diptera: Cecidomyiidae) and taxonomic implications. Bull Entomol Res 82:313–316

Gennadius P (1902) The carob tree. Government Printing Office, Nicosia, Cyprus, 30 pp

Harris KM (1975) The taxonomic status of the carob gall midge, *Asphondylia gennadii* (Marchal), comb. N. (Diptera, Cecidomyiidae), and of other *Asphondylia* species recorded from Cyprus. Bull Entomol Res 65:377–380

Morris HM (1930) Report of the entomologist for 1929. Report of the Director of Agriculture, Cyprus, pp 47–55

Orphanides GM (1975) Biology of the carob midge complex, *Asphondylia* spp. (Diptera, Cecidmyiidae), in Cyprus. Bull Entomol Res 65:381–390

Orphanides GM (1976) Damage assessment and natural control of the carob midge complex, *Asphondylia* spp. (Diptera, Cecidomyiidae) in Cyprus. Bollettino del Laboratorio di Entomologia Agraria "F. Silvestri" 33:80–98

Carotenoids

Carotenoids are among the most common and important natural pigments. They are fat-soluble, and found principally in plants and photosynthetic bacteria, where they are abundant in chloroplasts and play a critical role in photosynthesis. They also occur in some non-photosynthetic microbial organisms. Animals are incapable of carotenoid synthesis, but they obtain them from their diet where they serve as antioxidants, serve as a precursor to vitamin A, and impart bright coloration. Carotenoids are responsible for much of the red, orange, yellow, and brown color found in plants, as well as some of the coloration of animals, including insects.

At least 600 different carotenoids are known. They are derived from a 40-carbon polyene chain, and display alternating single and double bonds. The specific end groups on these molecules affect polarity and help determine how they interact with membranes. The hydrocarbon carotenoids are known as carotenes. The oxygenated carotenoids are called xanthophylls. Beta-carotene is perhaps the best known carotenoid.

In insects, carotenoids are responsible for the yellow color of such insects as pierid butterflies and the orange of ladybird beetles. Combined with blue pigment, carotenoids can produce green color. One of their most important functions is the production of the visual pigment retinene.

Carpenter Ants, *Camponotus* spp. (Hymenoptera: Formicidae)

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Carpenter ants play critical roles in forest ecosystems as predators of defoliating insects, decomposers of cellulose, and as vital links in food webs. They may become serious household pests, however, when they infest structures and damage wood.

Carpenter ants belong to the highly diverse and cosmopolitan genus, *Camponotus*, in the subfamily Formicinae (Table 6). The formicines are characterized by their production of formic acid in the venom gland, a potent alarm pheromone and defensive compound that is sprayed on its victims. There are 19 other subfamilies in the family Formicidae. Of the 288 genera of ants, with approximately 11,800 species described so far, *Camponotus* is one of the most impressive with an estimated 1,000 species worldwide.

In the United States and Canada there are approximately 50 species of *Camponotus*, of which 24 are considered to be structural or nuisance pests. Those causing the most damage belong to the subgenus *Camponotus*. Since the majority of species in this group nest in wood, they are commonly called carpenter ants. Two of the most common species that infest structures are black carpenter ants, *C. modoc* in western states, and *C. pennsylvanicus* in central and eastern states.

Colony Development

The claustral mode of colony founding, wherein the queen seals herself off in a chamber and rears her first brood in isolation, is typical for carpenter ants. After the spring mating flights, inseminated queens search for suitable nest sites in wood where they construct a cavity and lay a clutch of eggs. The queen does not leave the chamber to forage, instead metabolizing her fat bodies and wing muscles to provide nourishment for herself and the growing brood. Depending on temperature and species, complete metamorphosis (development of egg-larva-pupa and adult stages) takes from 6 to 10 weeks before the first workers emerge. These first workers are small due to the limited food supply and are therefore called minims. With their arrival, foraging commences and the colony begins to grow. The queen lays a second clutch of eggs in late summer but these do not complete development until after winter dormancy. After the first year, the queens of *C. modoc* and *C. pennsylvanicus* have two annual periods of oviposition, the first in late winter or early spring and the second in summer. Major (larger) and media (smaller than major, but larger than minim) workers are not produced until the third season, and reproductives only after several years.

Carpenter Ants, *Camponotus* spp. (Hymenoptera: Formicidae), Table 6 Some common species of carpenter ants and their geographic distribution

Camponotus species	Geographical distribution
C. americanus Mayr	Eastern and central USA, SE Canada
C. chromaiodes Bolton	Eastern and central USA, SE Canada
C. herculeanus (Linnaeus)	Northern USA, Canada, Alaska, Europe
C. ligniperdus (Latreille)	Europe
C. modoc Wheeler	Western USA, southwestern Canada
C. novaeboracensis (Fitch)	Northern USA, southern Canada
C. pennsylvanicus (DeGeer)	Eastern and central USA, SE and S central Canada
C. essigi Smith	NW Mexico to S Canada
C. nearcticus Emery	Northern USA, eastern USA, S Canada
C. sayi Emery	Southwestern USA and Mexico
C. floridanus (Buckley)	Southeastern USA
C. castaneus (Latreille)	Eastern central USA
C. variegatus (Smith)	Hawaiian islands
C. vicinus Mayr	Western USA, Mexico to S Canada

Mature colonies are partitioned into a main or parent nest where the queen resides, and into satellite nests that contain workers, mature larvae, pupae, and winged reproductives. Generating satellite nests expands the territory of a colony, while a network of interconnecting trails maintains communication and flow of resources between the nests. The number of satellite nests per colony and their size varies. For example, ten nests were counted in a colony of Florida carpenter ants, *C. floridanus*, and 12,000 workers were found in a satellite nest (Fig. 23) of *C. modoc*. Thus, the total number of ants in a colony may attain over 50,000 in the case of *C. modoc* and more than 100,000 in *C. vicinus*. The difference in size may be attributed to the presence of multiple queens (polygyny) in *C. vicinus* colonies versus a single queen (monogyny) that is typically found in colonies of *C. modoc* and *C. pennsylvanicus*.

Wood with high moisture content is selected for colony initiation by inseminated queens. Moisture is a requirement for the development of eggs and young larvae, and parent nests will often be located in areas outside structures where there is sufficient humidity. Satellite nests are typically found in drier areas because eggs and young larvae are not present. These nests are often found in structures under insulation, in attics, wall voids, and subfloors where higher temperatures and humidity occur.

Home Range

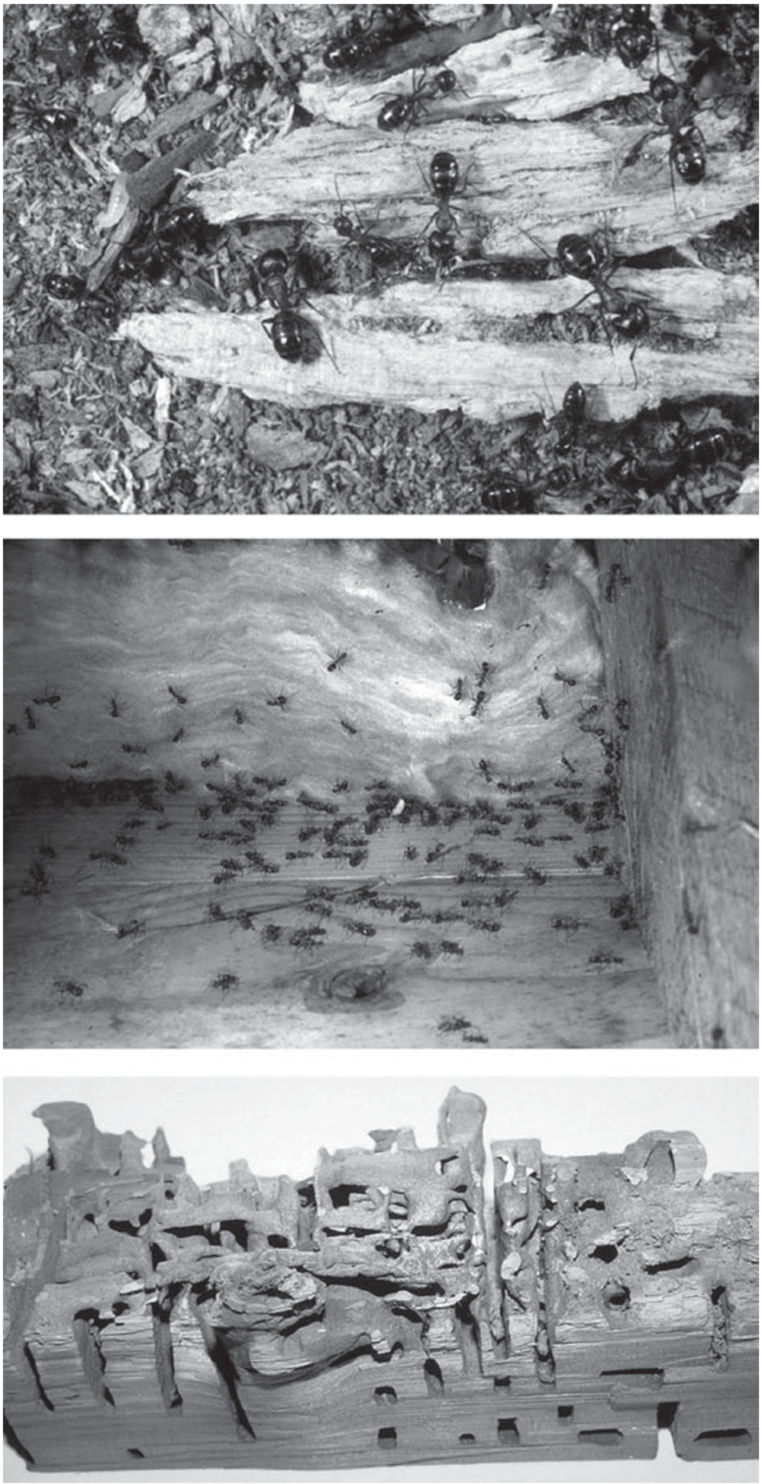
The territory of a colony is determined by its daily activity range, which includes the network of trails connecting its various nests with resource sites. The area covered by a large mature colony may be considerable. For example, in the case of the Florida carpenter ant nest complex mentioned above, it spread over an area measuring 43 m across; and trails 200 m long have been reported for *C. modoc*. Many species of carpenter ants are nocturnal, and they have evolved special adaptations for finding their way in the environment at night. In the case of *C. pennsylvanicus*, for example, odor trails are the primary orientation cue, but workers are also capable of landmark and celestial orientation. As with other ants, tactile cues are also used for orientation, and edge-following is commonly observed in carpenter ants, particularly along structural guidelines in man-made environments.

Foraging

Carpenter ants use group foraging to exploit ephemeral resources. The discovery of a food item too large to handle individually prompts a scout to deposit a chemical trail pheromone on the ground as she returns to the nest. The trail pheromone is produced in the hindgut and, in combination with formic acid, stimulates trail-following by other ants that the scout actively solicits when she arrives back at the nest. Established trails are used for more permanent resource sites such as aphid colonies that may remain in use from one season to the next. It is thought that the foraging population makes up no more than 10% of the colony population. Some of the larger species make prime targets for visual predators such as birds, so it is not surprising that their foraging is conducted primarily at night. The onset of foraging in *C. pennsylvanicus* and *C. modoc* is a dramatic event to observe, with large numbers of ants pouring out of the nest at dusk.

Trophallaxis

Honeydew is a favorite food of carpenter ants. Excreted by homopterans such as aphids, it contains sugars, amino acids, minerals, and vitamins. Carpenter ants have specialized digestive tracts for handling this liquid diet, and removing solids with a filtration mechanism in their mouthparts. The crop, also known as the social stomach, is a distensible sac located in the gaster of the ant which expands to hold liquids that are stored, transported, and finally regurgitated and shared via trophallaxis with other ants. This food-sharing



Carpenter Ants, *Camponotus* spp. (Hymenoptera: Formicidae), Figure 23 **Carpenter ants and damage: workers of *Camponotus vicinus* in a nest (above); satellite nest of *Camponotus modoc* under subfloor insulation (center); damage caused by *Camponotus modoc* to building timber (below) (photos by Laurel Hansen).**

behavior among workers, and from workers to larvae and the queen, is a fundamental bond in the social behavior of ants.

Pest Management

The structural pest management industry ranks carpenter ants as one of the most important economic pests. In certain regions of the United States, such as the Northeast and Pacific Northwest, carpenter ants outrank termites as wood-destroying organisms. They are also notoriously difficult to control.

In order to be effective, a management program for a household infestation of carpenter ants must be based on a thorough inspection. Ideally, all of the nests on the property should be located, both inside and outside. Structural infestations are more commonly caused by satellite nests; however, the original source of the problem often results from a parent nest located outside.

Locating nests is often difficult due to the cryptic behavior of carpenter ants. In this regard, a "feed and follow" technique can be helpful. Chopped insects such as crickets or mealworms are provided to the ants, which are then followed back to their nest. This technique is most effective when conducted at night when the majority of foragers are active. Outdoor nests may be located in live or dead trees, stumps or logs, landscape timbers, firewood piles, and buried wood. Indoors, common nest locations include crawl spaces and attics, often in or under insulation. In addition, satellite colonies will nest in exterior and interior wall voids, and hollow doors. Ant activity is often associated with moist conditions in and around sinks, dishwashers, bathtubs, showers, and toilets.

Once the nests have been located, they can be treated with a contact insecticide appropriate for the situation (e.g., a dust formulation in a wall void, or spray for infested landscape timbers). If nests are not located, there are other treatment options offered by pest control companies. In what is known as a perimeter treatment, a band of insecticide is sprayed around the outside foundation of a structure, along door and window frames, and under the lower edge of siding. Depending on the insecticide used, some act as barriers to the ants while others are non-repellent. In the latter case, the insecticide is picked up by the ant and carried back to the nest where it can be spread to other ants. Toxic baits may be effective if they are sufficiently attractive to the ants. Their recruitment and food-sharing behavior facilitates the distribution of a toxicant throughout the colony.

References

Cannon CA, Fell RD (1992) Cold hardiness of the overwintering black carpenter ant. Physiol Entomol 17:121–126

Hansen LD, Akre RD (1985) Biology of carpenter ants in Washington State (Hymenoptera: Formicidae: *Camponotus*). Melanderia 43:1–63

Hansen LD, Klotz JH (2005) Carpenter ants of the United States and Canada. Cornell University Press. Ithaca, New York, 224 pp

Klotz JH, Greenberg L, Reid BL, Davis L Jr (1998) Spatial distribution of colonies of three carpenter ants, *Camponotus pennsylvanicus*, *Camponotus floridanus*, *Camponotus laevigatus* (Hymenoptera: Formicidae). Sociobiology 32:51–62

Hedges, SA (1998) Field guide for the management of structure-infesting ants. Franzak & Foster Co, Cleveland, OH, 155 pp

Carpenter Bees (Hymenoptera: Apidae: Xylocopinae)

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The common name of these insects is derived from their nesting habits. Although small carpenter bees, *Ceratina* spp., excavate tunnels in pithy stems of various bushes, the large carpenter bees, *Xylocopa* spp., chew nesting galleries in solid wood or in stumps, logs, or dead branches of trees. Obviously, the wood-attacking species are the basis for the "carpenter bee" name designation. The latter bees may become economic pests if nesting takes place in structural timbers, fence posts, and other wood structures. It is *Xylocopa* that most people know about or are concerned about, at least in North America. The easiest method of separating *Ceratina* from *Xylocopa* is by size: *Ceratina* are < 8 mm in length, whereas *Xylocopa* are 20 mm or larger.

At various times, carpenter bees have been placed in the families Anthophoridae, Xylocopidae, or Apidae, though the most recent placement is within the Apidae. This family is characterized, in part, by the jugal lobe of the hind wing being absent or shorter than the submedian cell and by the forewing having three submarginal cells. Within the family, carpenter bees are distinguished most easily by the triangular second submarginal cell, and by the lower margin of the eye almost in contact with the base of the mandible (i.e., the malar space is absent).

Xylocopa spp. generally resemble bumble bees in size and color. They are black, metallic bluish or greenish black, or purplish blue. Some males have yellowish areas on the face. Both sexes may have pale or yellowish pubescence on the thorax, legs, or abdomen, but there tends to be less yellow color than in bumble bees. Sometimes they are unicolorous, ranging from entirely yellow to entirely black. Large carpenter bees are readily distinguished from bumble bees primarily by the absence of pubescence on the dorsum of the abdomen, which is somewhat shiny. They also lack a malar space (present in bumble bees), and the triangular second submarginal cell.

Xylocopa virginica is the species of most concern in the USA, though locally other species can be abundant. *Xylocopa virginica* normally uses dry, coniferous woods as nesting sites, including *Pinus*, *Juniperus*, and *Taxodium* spp., but some deciduous woods used in fence railings are also used. Hardwood timber is usually avoided. *Xylocopa virginica* selects nesting sites in well-lighted areas where the wood is not painted (though they may not be deterred by stains) or covered with bark. In general, these bees are gregarious, often building several tunnels in the same location, and also tending to nest in the same areas for generations. Old nests are refurbished, but new nests are also constructed at old locations. In new nests, female bees chew their way into the wood, excavating a burrow about 15 mm in diameter. Boring proceeds more slowly against the grain (about 15 mm a day) than with the grain. The direction of galleries in the wood appeared to depend on the direction of the grain. If the grain is oriented vertically, the nests are vertical; if horizontally, then the nests tend to be horizontal with respect to the ground. Galleries extend about 30–45 cm in newly completed nests. New tunnels are smooth and uniform throughout, but older galleries show evidence of less uniformity with random depressions and irregularities. Apparently these older galleries are used by several generations of bees. Also, several bees may use a common entry hole connecting to different tunnels. After excavating the gallery, female bees gather pollen, which is mixed with regurgitated nectar. The pollen mass is placed at the end of a gallery, an egg is laid, and the female places a partition or cap over the cell composed of chewed wood pulp. This process is repeated until a linear complement of six to eight end-to-end cells is completed. Females apparently construct only one nest per year in northern locations, with bees emerging in the late summer and overwintering as adults, and with mating taking place in the spring. In warm-weather areas such as Florida, however, at least two generations are produced per year, with broods occurring in February-March and during the summer. In Florida, adult bees are active from November to January and from April to summer.

Several types of "damage" are directly associated with carpenter bees: weakening of structural timbers in barns, sheds and other open structures where bees have ready entry; defacing of wood trim on structures, usually the eves of houses; gallery excavation in wood water tanks (much less a problem now that metal has replaced wood in most instances); and human annoyance. The last point is included because carpenter bee females may sting (rarely, and males do not sting), and male bees may hover or dart at humans who venture into the nesting area. In general, carpenter bees are not much of a threat to people, but this does not prevent people from becoming alarmed because these are large insects. Also, there sometimes is an indirect effect of carpenter bee colonization on structures. Occasionally woodpeckers are attracted to tunnels to feed on the brood. If the tunnels are in a structure, the damage resulting from the woodpecker can be significant.

A buzzing or drilling sound is heard when a carpenter bee is boring into the wood. If the hole is not visible, as often is the case when the bee is boring under the eves of houses, their activities can be detected by the presence of sawdust on the ground under the hole. As noted previously, carpenter bees rarely attack painted or varnished wood. In areas frequented by these insects, damage to structures can often be prevented by painting. If this is not effective or desirable, a small amount of insecticide that is labeled for bees and wasps can be applied to the affected area, including the entryways of the tunnels. Also, the holes could be plugged with caulking, putty, or similar substance, or screened. A common approach is to spray or dust the tunnels with insecticide, allow the bees a day or two to contact the insecticide and move it around the tunnel, and then plug the hole. Alternatively, because the number of bees is usually not great, and because the bees are fairly docile, it is usually possible to capture them all with an insect net and freeze or crush them, thereby avoiding the cost and hazard of insecticides.

Carpenter bees generally are not pests. Even those species considered to be occasional pests, such as *X. virginica*, offset their damage by pollination services, including pollination of economically important plants.

Small carpenter bees are never pests because they excavate nests and provision only the hollowed-out stems of twigs. Like the larger xylocopines, they excavate nests with their mandibles, and use these cavities for both nesting and overwintering sites. The female provisions the nest with pollen and nectar, deposits an egg, then caps the cell with masticated plant material. Typically she repeats the process again and again until several cells are stacked within the hollowed stem. The last cell area is left incomplete, and she uses this area to rest and to defend her nest from intruders. She remains close to the nest until her offspring emerge. Interestingly, because the first laid eggs hatch first, and they are deepest within the hollow stem, the new adults (which do not chew their way laterally through the wall of the stem) must navigate around the younger, less developed siblings stacked above in order to escape. The new adults chew through the cell caps, moving the debris down but being careful not to damage any wasps still in the pupal stage, and moving the pupae up to rest on the new, elevated floor of the cell. It may take several days for the first-hatching wasp to dig its way out, and by this time other wasps likely have hatched, resulting in a trail of adults, all working in tandem to pass cell cap material down.

► Bees (Apidae)

References

Balduf WV (1962) Life of the carpenter bee, *Xylocopa virginica* (Linn.). Ann Entomol Soc Am 55:263–271

Daly HV (1973) Bees of the genus *Ceratina* in America north of Mexico. UC Publ Entomol 74:1–113

Howard LO (1892) Note on the hibernation of carpenter bees. Proc Entomol Soc Washington 2:331–332

Hurd PD Jr (1955) The carpenter bees of California. Bulletin of the California Insect Survey 4:35–72

Hurd PD Jr (1958) Observations on the nesting habits of some new world carpenter bees with remarks on their importance in the problem of species formation. Ann Entomol Soc Am 51:365–375

Hurd PD Jr (1961) A synopsis of the carpenter bees belonging to the subgenus *Xylocopoides* Michener. Trans Am Entomol Soc 87:247–257

Hurd PD Jr, Moure JS (1963) A classification of the large carpenter bees (Xylocopini). UC Publ Entomol 29:1–365

Rau P (1928) The nesting habits of the little carpenter-bee, *Ceratina calcarata.* Ann Entomol Soc Am 21:380–397

Carpenter, Frank Morton

Frank Carpenter was born in Boston, USA, on September 6, 1902. His father, although an employee of a business company, had a strong interest in natural history, and encouraged Frank' s interest in insects. He entered Harvard University in 1922, and graduated with an A.B. degree in 1926, a master' s degree in 1927, and a D.Sc. in 1929. His doctoral thesis on fossil ants was published in 1930, but was preceded by seven of his earlier papers on fossil insects. In 1928 he was appointed at Harvard University as research fellow in applied biology, in 1931 as associate in entomology, in 1932 as assistant curator of invertebrate paleontology, in 1935 as instructor in zoology, in 1936 as curator of fossil insects, in 1939 as assistant professor of entomology, in 1945 as Alexander Agassiz professor of zoology, in 1969 as Fisher professor of natural history, and in 1973 became emeritus professor. This is the man who built the fossil insect collections of Harvard University' s Museum of Comparative Zoology. For nearly 40 years, he taught entomology and paleontology. He was chairman of the Department of Biology in 1952–1959 and had a heavy role in extension. His research in fossil insects spanned 70 years, and he specialized in the Paleozoic fauna. The fossil dragonfly that he described as Meganeuropsis americana, with a wingspan of 29 inches is the largest insect known. In addition to work on fossil insects, he worked on systematics of present-day Neuroptera, Raphidioidea and Mecoptera. After retirement in 1973, he continued voluntarily to curate the collection of fossil insects and to edit Psyche, the journal of the Cambridge [Massachusetts] Entomological Club (a job he held from 1947 to 1990). His wife Ruth, to whom he was married for 64 years, was a constant companion and helper. He died in Massachusetts on January 18, 1994.

Reference

Furth DG (1994) Frank Morton Carpenter (1902–1994): academic biography and list of publications. Psyche 101:126–144

Carpenterworm Moths (Lepidoptera: Cossidae)

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Carpenterworm moths, family Cossidae, total 682 species worldwide; actual fauna probably exceeds 750 species. The group is a relict family which has retained many primitive features and often is classified closer to Tineidae and Psychidae. There are five subfamilies, two of which are exclusively Neotropical (Chilecomadiinae and Hypoptinae): Chilecomadiinae, Cossulinae, Cossinae, Hypoptinae, and Zeuzerinae. The family is in the superfamily Cossoidea (series Cossiformes) in the section Cossina, subsection Cossina, of the division Ditrysia. Adults small to very large (9–240 mm wingspan), with head small and average or slightly rough scaling; labial palpi upcurved; maxillary palpi small, 1–2-segmented; antennae filiform or bipectinate (antennal tips usually thinner). Wings are elongated (Fig. 24) and hindwings often rather small and rounded; body very robust (the largest female cossids rival hawk moths in size and mass).

Carpenterworm Moths (Lepidoptera: Cossidae), Figure 24 Example of carpenterworm moths (Cossidae), *Stygia leucomelas* Ochsenheimer from France.

Maculation usually various dark shades of brown or gray, with various spots or markings; some lighter or colorful. Adults are nocturnal. Larvae are borers in trunks and limbs. Host plants are recorded in a large number of plant families, especially all those with larger tree species. A number of species are economic pests of forest trees.

References

Arora GS (1976) A taxonomic revision of the Indian species of the family Cossidae (Lepidoptera). Rec Zool Surv India 69:1–160

Barnes W, McDunnough JH (1911) Revision of the Cossidae of North America. Contr Nat Hist Lepidoptera North Am 1:(1)1–35, pl 1–7

Buser R, Huber W, Joos R (2000) Cossidae – Holzbohrer. In: Schmetterlinge und ihre Lebensräume: Arten-Gefährdung Pro-Schutz. Schweiz und angrenzenden Gebiete, 3:97–116, pl 2. Pro Natura-Schweizerische Bund fuer Naturschutz, Basel

Schoorl JW Jr (1990) A phylogenetic study on Cossidae (Lepidoptera: Ditrysia) based on external adult morphology. Zoologische Verhandlingen 263:1–295, 1 pl

Seitz A (ed) (1912–1937) Familie: Cossidae. In: Die Gross-Schmetterlinge der Erde, 2:417–431, pl 52–55 (1912); 2(suppl):241–245 (1933); 287, pl 16 (1934); 6:1264–1287, pl 167, 169, 181–184 (1937); 10:807–824, pl 93, 96–99 (1933); 14:540–551, pl 79–80 (1929). A. Kernen, Stuttgart

Carposinidae

A family of moths (order Lepidoptera). They commonly are known as fruitworm moths.

► Fruitworm Moths
► Butterflies and Moths

Carrion Beetles (Coleoptera: Silphidae)

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Despite the association of silphids with carrion, which is often repugnant to humans, the biology of these organisms includes a rich and complex array of fascinating evolutionary and ecological phenomena.

Silphids (Fig. 26) have the largest bodies and are the most conspicuous of the staphylinoid beetles. However, the family is not very species rich by beetle standards, containing only 183 extant species. Commonly, they are known as "carrion beetles" due to their frequent association with vertebrate carcasses. They are sometimes referred to as "large carrion beetles" to distinguish them from other beetles associated with carrion, such as those in the family Leiodidae (which are sometimes called "small carrion beetles"). Most species eat carrion although many will also prey on carrion associated insects, such as maggots, or other carrion beetles. Some species are phytophagous, or exclusively predaceous, while at least one species has been found only in dung. The primary food source for the larvae of most species, however, is vertebrate carrion. A radical departure from this ancestral life history pattern is seen in the species *Nicrophorus pustulatus* which, although capable of breeding on carrion, has recently been discovered to be a parasitoid of snake eggs – perhaps the only known example of a parasite of a vertebrate that kills and consumes its host (in this case, snake embryos).

The family contains two subfamilies, each of which specializes on a different size of carrion. Carrion feeding members of the subfamily Silphinae, which lack parental care, prefer large vertebrate carcasses (>300 g), and are often found on megafaunal carcasses, such as elk, moose, or bison. They must share these carcasses with vertebrate scavengers and a large suite of necrophilous insects such as the larvae of blow- and fleshflies, some of which become prey for the beetles. Adults of the subfamily Nicrophorinae, which display parental care and complex subsocial nesting behaviors, generally only breed by monopolization of a small carcasses (<300 g, usually <100 g) such as those of birds or rodents. These beetles remove small carcasses from the competitive arena of flies, ants, and other scavengers by burial into a subterranean nest – hence their common name of "burying beetles" or "sexton beetles." This remarkable behavior attracted the attention of early naturalists and remains the focus of research today.

Distinguishing Characteristics and Relationships

The family as a whole has only one, somewhat ambiguous, synapomorphy (diagnostic character) – a bulge on the posterior quarter of each elytron. However, silphids can be easily recognized by a combination of characters including their necrophilous habits (most species), their size (usually 1–2 cm), their weakly to strongly clubbed antennae, their very large scutellum, which is sometimes as wide as their head, and their tricostate elytra. There is strong evidence indicating silphids are closely related to members of the family Staphylinidae. Some evidence suggests silphids may actually belong inside the family Staphylinidae (which would require changing the family Silphidae into a subfamily of the Staphylinidae).

Members of the subfamily Nicrophorinae do possess an unambiguous synapomorphy – a pair of stridulatory files on the dorsal surface of abdominal segment 5 which are used for auditory communication between adults before mating (courtship songs) and between adults and larvae during development, and for defense when disturbed. The files are scraped by the underside of the elytral apices when the beetles pump their abdomens forward and backward. Paired stridulatory files are absent from the Silphinae but adults of the basal genera *Ptomaphila* (Australia) and *Oxelytrum* (Neotropics) possess stridulatory morphology – at least one species of *Oxelytrum* has been observed stridulating. These beetles have spines on the underside of the elytra that can be scraped by the abdominal intersegmental membrane when the beetles move their abdomens from side to side – a phenomenon that has yet to be studied in the silphines. Because silphines do not nest, presumably the only function of their stridulation would be defense.

Morphology

Adult

Length 7–45 mm (usually 12–20 mm); ovate to moderately elongate, and slightly to strongly dorsoventrally flattened (Silphinae). Frontoclypeal (epistomal) suture absent (Silphinae), or present as fine line (Nicrophorinae). Antennae are 11-segmented but appear as 10-segmented in Nicrophorinae due to reduced second segment fused to third segment; ending in 3-segmented club, usually preceded by two or three enlarged but sparsely setose segments (Silphinae and basal Nicrophorinae) or antennomeres 9–11 forming a large club (*Nicrophorus*). Pronotum with lateral edges complete, sometimes explanate. Scutellum large – often as wide as head. Elytra truncate, exposing 1–5 abdominal tergites in *Diamesus*, *Necrodes*, and *Nicrophorinae*; not truncate in remaining Silphinae, covering abdomen; never striate; in Silphinae bearing 0–3 raised costae or carinae per elytron (present but indistinct in Nicrophorinae); with raised callus near posterior end of outermost costa; epipleura usually well-developed and with ridge complete almost to apex. The elytra of most *Nicrophorus*, *Ptomascopus* and *Diamesus* species usually have broad colored bands or spots (fascia and maculae) extending laterally to meet epipleura. Abdomen with sternite 2 not visible between hind coxae but visible laterally of metacoxae; sternites 3–8 visible in females, 3–9 visible in males. Legs with five tarsal segments per tarsus. Males usually with broadly expanded protarsal segments and longer protarsal setae (midtarsal also expanded in male *Diamesus*), pro- and midtarsi of female similar.

Larvae

Length 12–40 mm, campodeiform (most Silphinae) or eruciform (Nicrophorinae); elongate, more or less parallel-sided to ovate, slightly to strongly flattened, relatively straight or slightly curved ventrally. Body surfaces heavily pigmented and heavily sclerotized (Silphinae), or lightly pigmented and lightly sclerotized (Nicrophorinae). Stemmata 6 (Silphinae) or 1 (Nicrophorinae) on each side. Mandibles lacking mola. Thoracic terga and abdominal terga and sterna consisting of one or more sclerotized plates, without patches or rows of asperities, each tergum with 1 (Silphinae) or 2 (*Ptomascopus*) lateral tergal processes extending beyond edges of sterna or without such processes (*Nicrophorus*) but with four spinose projections along posterior margin of abdominal terga. One or two segmented, well developed urogomphi.

Classification, Diversity, and Distribution

In recent years there have been some changes to the classification and newly described species added, so a current classification, with updated species counts, and distributional information is provided below (Table 7). The family currently stands at 183 species.

The distribution of an organism is the result of both ecology and evolutionary history. Silphids, especially the nicrophorines, are rare in warmer climates, such as lowland tropical forests, and virtually absent from dry climates like deserts – these ecological constraints certainly have limited their distribution in places like Africa, Australia, and Tibet. A few silphids in northern Africa survive in cooler, wetter mountainous regions but the Sahara presumably prevents southward dispersal. The family Silphidae is thought to have originated in the northern hemisphere on the paleocontinent of Laurasia. The subfamily Nicrophorinae best represents this with only three species in territory once part of the southern landmass of Gondwana. These three species are thought to have radiated down the Andes of South America, having survived in the cooler, montane climate.

The nicrophorines are distributed in the northern hemisphere, with species radiations having occurred in the Malay Archipelago, resulting in various endemic island species restricted to montane habitats, and into South America along the Andes. None are found in Africa south of the Sahara, in Australia (Fig. 25), or Antarctica. These beetles were once thought to be absent from the Indian subcontinent south of the Himalayas, but there may be a population of the recently described species *Nicrophorus sausai* in Meghalaya India, a mountainous region isolated from the Himalayas. This unusual, and perhaps relict, population begs additional study and confirmation.

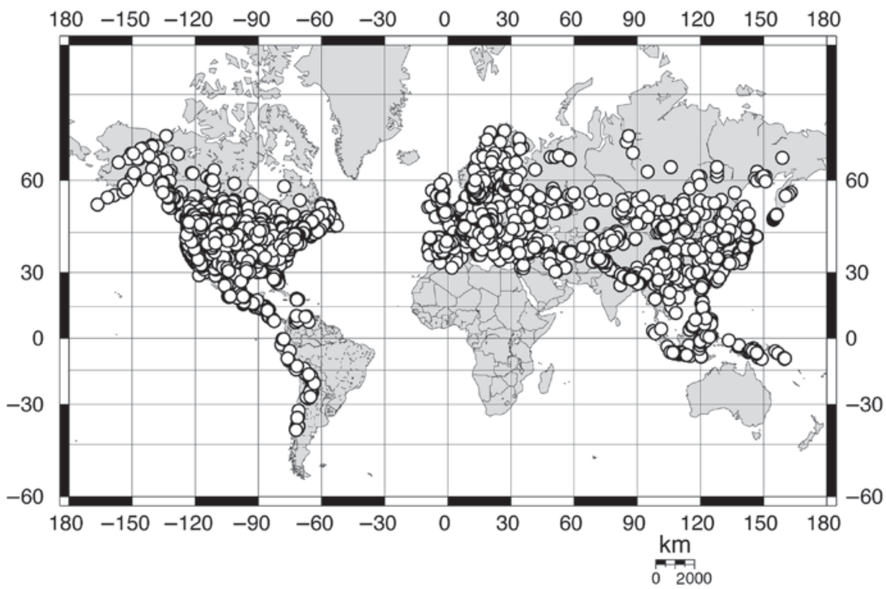
The silphines are more widespread than the nicrophorines, with greater representation on Gondwanan areas. This is thought to be related to their greater generic diversity (12 genera) and possible greater age. There are four species in Australia and New Guinea (*Ptomaphila*, 3 endemic species; *Diamesus* 1 species) and a larger radiation in South America than is seen in the nicrophorines (*Oxelytrum*, 8 species). It has been suggested that this radiation of the Silphinae into South America and consequently Australia (via Antarctica) took place 50–60 million years ago producing these, the only two silphid genera endemic to the southern Hemisphere. There are also three silphine species in South Africa (*Thanatophilus*, 2 species; *Silpha*, 1 species) and an entire silphine genus (*Heterotemna*, 3 species) endemic to the Canary Islands off the northwest coast of Africa. However, as with the nicrophorines, most species of the Silphinae are found in the northern hemisphere, although they seem to be somewhat more tolerant of warm habitats than are the nicrophorines. This tolerance is perhaps due to their preference for larger carcasses which they do not (and could not) defend from competitors. *Nicrophorus* species, probably due to their requirement for small carcasses that can be buried and defended, do not appear to compete well with the ants, flies and carrion-associated scarab beetles that are more abundant in warmer habitats.

Together, the Silphidae show an amphitropical or amphipolar distribution, i.e. they are restricted to northern and southern temperate zones but

Carrion Beetles (Coleoptera: Silphidae), Table 7 Carrion beetle classification, species counts, and distribution

Order Coleoptera	
Superfamily Staphylinoidea	
Family Silphidae Latreille, 1807	15 genera, 183 species
Subfamily Silphinae Latreille, 1807	12 genera, 111 species
Aclypea Reitter, 1884	13 species, Holarctic
Dendroxena Motschulsky, 1858	2 species, Eurasia
Diamesus Hope, 1840	2 species, Asia, Australia
Heterosilpha Portevin, 1926	2 species, West Nearctic
Heterotemna Wollaston, 1864	3 species, Africa: Canaries
Necrodes Leach, 1815	3 species, Holarctic
Necrophila Kirby and Spence, 1828	17 species, Holarctic
subgenus *Necrophila* Kirby & Spence, 1828	
subgenus *Eusilpha* Semenov-Tian-Shanskij, 1890	
subgenus *Calosilpha* Portevin, 1920	
subgenus *Deutosilpha* Portevin, 1920	
subgenus *Chrysosilpha* Portevin, 1921	
Oiceoptoma Leach, 1815	9 species, Holarctic
Oxelytrum Gistel, 1848	8 species, SW Nearctic/Neotropical
Ptomaphila Kirby & Spence, 1828	3 species, Australia, New Guinea
Silpha Linnaeus, 1758	25 species, Eurasia, Africa[a]
subgenus *Silpha* Linnaeus, 1758	
subgenus *Phosphuga* Leach, 1817	
subgenus *Ablattaria* Reitter, 1884	
Thanatophilus Leach, 1815	24 species, Holarctic & Africa, Madagascar
Subfamily Nicrophorinae Kirby, 1837	3 genera, 72 species
Eonecrophorus Kurosawa, 1985	1 species, Nepal
Ptomascopus Kraatz, 1876	3 species, Asia
Nicrophorus Fabricius, 1775	68 species, Holarctic, N Africa, S America, SE Asia

[a]One species of Europe, *Silpha trisits* Illiger, has been introduced and established in North America (southern Quebec)



Carrion Beetles (Coleoptera: Silphidae), Figure 25 **Map of the subfamily Nicrophorinae (Silphidae). 6,736 localities from 17,250 specimens examined showing the known distribution (99% of records are *Nicrophorus*). The lack of records throughout much of Russia is almost certainly a collection artifact whereas the absence of records in Australia, sub-Saharan Africa, most of India and South America is not. A corresponding map for the subfamily Silphinae has not yet been prepared – see text for description of the distribution of the Silphinae.**

generally absent from the intervening tropics (with the exception of tropical montane habitats).

The lesser generic diversity of the nicrophorines (3 genera) compared to the silphines, combined with their almost pure Laurasian distribution, supports preliminary estimates for a younger age of the main radiation in the Nicrophorinae (the genus *Nicrophorus*) based on fossil and molecular divergence dating methods. All known fossils of the genus *Nicrophorus* are Eocene or younger, less than 50 million years old, with the majority being known from the Pleistocene. Molecular dating methods provide a preliminary, and wide, range for the radiation of the genus having happened 50–24 million years ago. The transition to the Oligocene from the Eocene is thought to represent the most dramatic climatic change of the Cenozoic era, in which the Mesozoic "hot house" world was transformed into the Neogene "ice house" world that persists today. Given the absence of *Nicrophorus* from lowland tropical habitats and the preference of these organisms for cooler climates, it seems reasonable to infer these beetles may have radiated during this cooling event of the Oligocene. Roughly concurrent with this cooling event, many modern rodent families appeared and radiated – and these would have been ideal prey items for *Nicrophorus* beetles. In addition to a small-mammal radiation during this time, most modern bird orders and families appeared between the early Eocene and the late Oligocene-early Miocene, during a period of intense diversification. Small birds are also ideal prey items for *Nicrophorus*.

The family is thought to have originated in the Old World, and the subfamily Nicrophorinae certainly shows this pattern in which all but one of the five genera/subgenera are endemic to Asia. The New World has the minority of world species for all groups that are also found in the Old World, and has only two endemic genera: *Oxelytrum* and *Heterosilpha*. One new species of *Nicrophorus*,

Carrion Beetles (Coleoptera: Silphidae), Figure 26 ***Nicrophorus olidus*** **Matthews, a silphid found in Honduras and Mexico; female, dorsal and lateral view.**

N. hispaniola, was recently discovered and described in the Dominican Republic. This was the first *Nicrophorus* described in the New World since 1925, bringing the total to 21 New World species of *Nicrophorus*. There are 25 species of Silphinae in the New World, combined with the 21 species of nicrophorines yielding 46 species of silphids in the New World.

Ecology

Silphids are most frequently encountered at vertebrate carrion but are sometimes found associated with dung or fungi, or at electric lights. Most species will prey on fly larvae or other insects present on carcasses or dung, in addition to eating the carcass itself. Some species are phytophagous (11 species of *Aclypea*) while others are predacious (*Dendroxena*, some *Silpha* and possibly *Ptomascopus zhangla*, a poorly known and recently discovered species from China). The silphine *Necrodes surinamensis* as an adult feeds primarily on fly larvae but can survive on carrion alone. The majority of silphids that have been studied are nocturnal or crepuscular (active at sundown and sunrise), which might help avoid predation by birds.

Some species of the genus *Nicrophorus* have become model organisms for research in ecology, physiology, and behavior – particularly dealing with questions about parental care, the evolution of sociality, competition, and other behaviors of nesting organisms (e.g., brood parasitism). There have been over 150 behavioral ecology studies on these species in the past 25 years. Subjects of these studies include, for example, the ability of adults to regulate their brood size to match the size of the carrion resource via control of the number of eggs produced and subsequent parental culling of "extra" larvae by cannibalism. Other subjects investigated include adult competition and fights to win a carcass, pheromone emission, adult stridulatory communication (between parents and larvae, precopulatory, and defensive), duration and explanation for paternal care, and antimicrobial properties of anal and oral secretions, among many others. Biparental care, as seen in *Nicrophorus,* is rare in insects in general, and has been the focus of much investigation.

The typical progression from discovery to new offspring for *Nicrophorus* species proceeds as follows: A small vertebrate carcass, like that of a mouse, is found soon after nightfall and often on the day of its death. If numerous *Nicrophorus* beetles find the carcass the beetles begin to fight to dominate the resource. Larger bodied beetles tend to win these competitions with losers retreating, sometimes with minor injuries (missing leg parts or cuts in their wing covers). The loser females sometimes lay eggs near the carcass and some of her offspring might enter and develop in the nest of the winning beetles. The beetles' fights usually result in a single species remaining, with smaller bodied species having been excluded. Within the larger species the males fight the males and the females fight the females until the largest male and largest female remain in control of the carcass. Courtship stridulation occurs and can lead to rejection of the male by the female if he cannot stridulate as expected. This may help beetles identify conspecifics but no one has carefully investigated how this is accomplished. The mechanisms by which closely related species avoid hybridization are equally unstudied. The male and female pair work together to bury the carcass by digging beneath it. If the substrate is too tough the pair might move the carcass to more suitable ground by laying beneath it and moving it with their legs. If a male finds a carcass and no females are present he will emit a pheromone to attract a female. Sometimes males without carcasses will emit pheromone to attract females with whom they try to mate. Females, like all insects, can store sperm for later use and sometimes can find and bury carcasses alone, using sperm from prior mating to fertilize her eggs.

It can take 5–24 h for a carcass to be secured below-ground (with smaller-bodied species tending to bury less deeply than larger bodied species). The carcass is rolled into a ball that minimizes its surface area. Fur or feathers are removed and a brood chamber is built that will house the carcass and the developing larvae. The carcass is treated with oral and anal secretions that help preserve the resource from microbial decay. The female will then lay eggs based on the mass of carcass (between 10 and 50 eggs is typical) although more eggs are typically laid than larvae that will be reared. Because body size is critical to winning contests for carcasses, larger bodied offspring will be more likely to successfully reproduce than smaller bodied offspring. A carcass resource can yield either many small burying beetle offspring, or fewer large burying beetle offspring. This selection pressure has resulted in a behavior known as filial cannibalism – the parents kill and consume "extra" larvae that would otherwise lower the average body size of the resulting offspring. These beetles, therefore, regulate the size of their brood carefully – both by laying a clutch size appropriate to the mass of the carrion resource, and by later "fine-tuning" the clutch size if too many eggs hatch by eating the late arriving larvae.

Parent beetles stay with the larvae during their approximate 2-week development period – defending them against possible usurpers (this being the major advantage of paternal care). The parents also tend the larvae, maintain the brood ball and regurgitate food for the larvae. The burying beetles are unusual among insects in having peak levels of juvenile hormone (normally considered a gonadotropic hormone in adult insects) during the early parental period when the ovaries are small. Parental regurgitations to young larvae increase larval growth rates, and in some species, are essential for molting from the first to second instar. The larvae molt between each of three instars and either pupate to adult and overwinter as adults or overwinter as a final larval instar "pre-pupa."

This life history of *Nicrophorus* species is based on finding, concealing and monopolizing small carcasses before their competitors. However, they cannot exclude all interested parties – in addition to a vigilance that prevents usurpation by other *Nicrophorus* adults, the parents must contend with both bacterial and fungal decay of the carcass. Recent studies in both North America and Japan have shown that the treatment of the carcass with oral and anal secretions by *Nicrophorus* adults greatly reduces the microbial decay, and a number of antimicrobial agents have been identified.

Other animals that often accompany the beetles into their nest include both nematodes and mites (Acari). The nematode-beetle relationship is poorly known with considerable potential for future work. At least two nematode species, *Rhabditis stammeri*, and *R. vespillonis,* have been documented as associates of *Nicrophorus vespilloides* and *N. vespillo,* respectively, although it is certain that many more, probably undescribed, nematode species associate with silphids. The nematodes breed on the carrion and their offspring disperse to new carrion resources with the new generation of beetles – traveling in the gut of the beetle larvae and using the adult hindgut and/or genitalia for transport to a new carcass. Nematodes have been observed in laboratory settings to reach enormous population sizes – causing the beetles to abandon the carcass – but it is unknown if this happens in the wild. The new generation of nematodes will form large aggregations on the surface of the carcass, each will arch upwards and start to wave. They will also form small, living, waving towers by climbing on one another. This behavior brings the nematodes in contact with the beetles, onto which they climb. It is not known how or if the beetles have adapted to competitive pressure from these nematodes, nor is it known to what degree the nematodes reduce the beetles' fitness.

The mite-beetle relationship is better understood than that of the nematodes, but remains one of the more complex and rich areas for future research. It is not known how many species of silphids carry mites (phoretic associates) but most of the *Nicrophorus* species that have been studied ecologically carry them. Like the nematodes, the mites' life cycle is tied to that of the beetles with the deuteronymphs (the last pre-adult stage) dispersing phoretically on the adult beetles. Mites present on silphine species probably are using them as alternate hosts opportunistically until they can transfer to a burying beetle. Many of the mites appear to be host-specific, and considerable taxonomic work remains to done with them. Over 14 species of mites from four families (Parasitidae, Macrochelidae, Uropodidae, and Histiomatidae) were found on *Nicrophorus* species in Michigan, USA. The most frequently encountered and well-studied mites in this system are those in the genus *Poecilochirus* (Mesostigmata: Parasitidae). Initial work in the 1960s indicated an apparent mutualistic mite-beetle relationship resulting from the mites' predation on fly eggs that would otherwise hatch and compete with beetle offspring. However, more thorough examination of this relationship has found much greater complexity – including examples of mutualism, commensalism, and parasitism, varying with species and conditions. What was once thought to be a single species of mite, *Poecilochirus carabi*, has since been discovered to be a species complex of several morphologically similar, but reproductively isolated species that are specific to their host beetle species. Only a few of these cryptic mite species have been described or examined in detail. It is likely that most of the 69 known *Nicrophorus* species have their own (probably undescribed) *Poecilochirus* species.

An even more poorly-known symbiotic relationship involving the Silphidae awaits study: nematodes of the family Allantonematidae have been reported as parasites of the burying beetles' *Poecilochirus* mites!

Conservation

In the USA, much attention has been focused recently on the American burying beetle, *Nicrophorus americanus* Olivier, a federally listed endangered species and one of five "giant" species in the genus. As recently as the 1930s, this species was considered to be common over most of the eastern half of the North American continent. However, it now occurs in <10% of its former range (populations are now restricted to a few islands offshore of Rhode Island and Massachusetts and the western periphery of the historic range). This species was first listed in 1989 and represents an unusual case of species endangerment in that there are no apparent causal factors for its decline that simultaneously explain why the eight other co-occurring *Nicrophorus* species have not declined. Many weakly supported hypotheses have been suggested, including DDT contamination, extinction of the passenger pigeon, deforestation, artificial lighting, loss of carrion availability, and an unknown, intrinsic, genetic effect. One important difference between *N. americanus* and its congeners is that this species requires larger carcasses (>80 g) than its congeners to maximize its reproductive success. Subsequent work and review of the literature points to a "best," albeit provisional, explanation of this species' decline based on (i) known population declines of optimally sized carrion "prey" species such as ground nesting birds and the passenger pigeon, and (ii) increased vertebrate scavenger and congener competition for the reduced carrion available. The greater pressure from vertebrate scavengers may have resulted from competitive release after the loss of larger predators (such as the gray wolf [*Canis lupus*] and the mountain lion [*Felis concolor*]) and an increase in habitat fragmentation and edge habitats. *Nicrophorus americanus* may have declined because it is experiencing greater vertebrate and congener competition for a reduced resource base. The species is being bred in captivity and work is underway to establish new populations. The attention it has received due to its federal protection has helped its prospects considerably.

Given the well-documented and recent rise in mean global temperature, some conservationists are worried about montane island endemics that cannot survive in the warmer lowlands. As our climate changes, the size of these cooler, montane habitats will contract as they gradually move higher in elevation. There are at least ten *Nicrophorus* species endemic to the higher elevations of various islands in the Malay Archipelago. These species, among many other similarly adapted organisms, could become threatened with extinction if their cooler, montane habitats start to disappear. Some are already living at the highest elevations available to them.

Recent Research

Recent work on these beetles has resulted in some interesting discoveries. In addition to 11 newly described species since 1999, primarily from Asia, there has been phylogenetic work underway which has suggested that the relatively high species richness of the genus *Nicrophorus* may have resulted from a rapid radiation – a burst of evolution. This radiation was possibly coincident with the global cooling during the Oligocene and the subsequent radiation of small birds and mammals – and possibly caused by the key innovation of small carcass monopolization.

From other recent research we have learned that females with a carcass will not attack males who have recently been in contact with a carcass and typically cared for a brood. These males are considered to have a "breeder's badge", a profile of cuticular hydrocarbons that identifies them as parental – and those males lacking this scent are attacked. This addresses questions of how these social beetles recognize each other.

It had already been determined that adults cannot recognize their own larvae from those of other couples, nor even, of other species of nicrophorines (in Japan, *Ptomascopus* larvae are sometimes brood parasites, mixed into broods of *Nicrophorus concolor* larvae and raised by *Nicrophorus* parents). The mechanism by which parents can minimize such brood parasitism is temporal – they kill larvae that arrive too early or too late around the window of time that their own larvae appear.

Our understanding of the biology and evolution of the Silphidae progresses, with continuing work on the phylogenetics, reproductive behaviors of basal lineages, brood parasitism, communal breeding, endocrinology, use of stable isotopes to determine larval diet, and host shifts, although many questions remain uninvestigated.

► Decomposer Insects
► Beetles (Coleoptera)

References

Ratcliffe BC (1996) The carrion beetles (Coleoptera: Silphidae) of Nebraska. Bull Univ Nebraska State Mus 13:1–100

Peck SB (2001) Silphidae Latreille, 1807. In: Arnett RH, Thomas MC (eds) American beetles: archostemata, myxophaga, adephaga, polyphaga: staphyliniformia, vol 1. CRC Press, Boca Raton, FL, pp 268–271

Scott MP (1998) The ecology and behavior of burying beetles. Ann Rev Entomol 43:595–618

Sikes DS (2005) Silphidae. In: Kristensen NP, Beutel RG (eds) Handbook of zoology, vol IV Arthropoda: Insecta part 38, Coleoptera, Beetles, vol I: Morphology and systematics (Archostemmata, Adephaga, Myxophaga, Polyphaga partim) (RG Beutel RAB Leschen, eds) Walter de Gruyter, Berlin, NY, pp 288–296

Sikes DS, Newton AF, Madge RB (2002) A catalog of the Nicrophorinae (Coleoptera: Silphidae) of the world. Zootaxa 65:1–304

Carsidaridae

A family of bugs (order Hemiptera, superfamily Psylloidea).

► Bugs

Carter, Herbert James

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Narrabeen, NSW, Australia

Herbert James Carter was born on the 23rd of April 1858 in Marlborough, Wiltshire, England. He was educated in England, receiving his Bachelor of Art Degree in Cambridge. At the age of 24 he migrated to Australia and took up the position of Mathematical Master at Sydney Grammar School. Later on, in 1902, he was appointed as Principal of Ascham Girls' School in Sydney where he worked until his retirement in 1914. Although he was a devoted educator, his interest in entomology and his contribution to knowledge of the Australian insect fauna were very significant. He became interested in entomology soon after his arrival in Australia and produced his first paper on Australian Coleoptera in 1905. He traveled and collected extensively in New South Wales, Victoria, Tasmania, South Australia and Western Australia. He collaborated with A.M. Lea and a number of other entomologists of his era, including with K.G. Blair, the Coleopterist of the British Museum. During his long life he published 65 papers, including major works on Tenebrionidae, Buprestidae and Colydiidae. He described 55 genera and 1,234 species new to science. After retirement he continued his entomological work until his sudden death on the 16th of April 1940, in the Sydney suburb of Wahroonga.

References

Carter HJ (1933) Gulliver in the bush – wanderings of an Australian entomologist. Angus & Robertson, Sydney, Australia, 234 pp
Zimmerman EC (1993) Australian weevils, vol 3. CSIRO, East Melbourne, pp 493–494

Carthaeidae

A family of moths (order Lepidoptera) also known as Australian silkworm moths.

► Australian Silkworm Moths
► Butterflies and Moths

Carton

The paper manufactured by Hymenoptera for nest construction.

Carrier

An inert material serving to dilute a pesticide, and to carry it to its target.

Carrying Capacity

The theoretical maximum population size that an area can support indefinitely within defined set of conditions.

Casebearer Moths (Lepidoptera: Coleophoridae)

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Casebearer moths, family Coleophoridae, comprise over 1,525 species worldwide, with most being Palearctic (1,082 sp.) and in the genus,

Casebearer Moths (Lepidoptera: Coleophoridae), Figure 27 Example of casebearer moths (Coleophoridae), *Coleophora* sp. from Florida, USA.

Coleophora. Most are in subfamily Coleophorinae, while non-casebearers are in Batrachedrinae. The family is part of the superfamily Gelechioidea in the section Tineina, subsection Tineina, of the division Ditrysia. Adults small (5–24 mm wingspan), with head smooth-scaled; haustellum scaled; labial palpi recurved; maxillary palpi minute, 2-segmented. Wings usually very elongated and hindwings spindle-shaped with long fringes. Maculation shades of brown or gray, sometimes mostly white, and unicolorous or with various markings or stripes, but rarely more colorful and with iridescence. Adults may be mostly crepuscular but many are diurnal. Larvae make small cases (except for Batrachedrinae), often distinctly shaped for each species (Fig. 27), skeletonizing host leaves, but some are seed borers, leafminers, or stalk borers, or skeletonize leaves beneath frass webs. A few Batrachedrinae are predaceous on scale insects (Hemiptera). Various host plants are utilized. A few species are economic. Ovovivipary has been recorded for a few species.

References

Baldizzone G (1996) A taxonomic review of the Coleophoridae (Lepidoptera) of Australia. Tijdschrift voor Entomologie 139:97–144

Hodges RW (1966) Review of the New World species of *Batrachedra* with descriptions of three new genera (Lepidoptera: Gelechioidea). Trans Am Entomol Soc 92:585–651

Landry J-F, Wright B (1993) Systematics of the nearctic species of metallic-green Coleophora (Lepidoptera: Coleophoridae). Can Entomol 125:549–618

Toll S (1962) Materialien zur kenntnis der paläarktischen arten der familie Coleophoridae (Lepidoptera). Acta Zool Cracoviensia 7:577–720, 133 pl

Vives-Moreno A (1988) Catalogo mundial sistematico y de distribucion de la familia Coleophoridae Hübner, [1825] (Insecta: Lepidoptera). Boletin de Sanidad Vegetal 12:1–196

Casey, Thomas Lincoln

Thomas Casey was born at West Point, New York state, on February 19, 1857. His father was a general of the U.S. army, and he graduated from the U.S. Military Academy in 1879. As a soldier, he traveled widely in the USA, and used every opportunity to collect beetles as well as building his collection by purchase from others. He also was interested in applied astronomy. He was a prolific describer of insect species, publishing 77 papers between 1884 and 1924, and in them describing more than 9,000 species. However, he has been widely criticized not only because his descriptions were brief and lacked illustrations, but because he often selected superficial differences between specimens as the basis of species separation. In other words, he failed to recognize that morphological characters may vary considerably within species. Consequently, many of the species names that he proposed have subsequently been sunk as synonyms. His collection of almost 117,000 specimens including 9,200 holotypes was bequeathed to the U.S. National Museum of Natural History. He died on February 3, 1925.

Reference

Herman LH (2001) Casey, Thomas Lincoln. Bull Am Mus Nat Hist 265:53–54

Cassava Mealybug, *Phenacoccus manihoti* Matile-Ferrero (Hemiptera: Pseudococcidae)

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This is one of many insects that came to the attention of science only after it had been inadvertently transported and established on a new continent. In the early 1970s, mealybug infestations suddenly devastated cassava (in French: "manioc") in the Congo and what is today the Democratic Republic of Congo, around the two capitals Brazzaville and Kinshasa, respectively. From there, this new plague spread rapidly, at a speed of over 100 km per year. It got new footholds in Nigeria, near the border to Benin, then on the border between Gambia and Senegal, and within a few years had covered the entire cassava growing area of Africa from Senegal to Ethiopia and to South Africa. By the mid-1990s, only the Indian Ocean Islands including Madagascar were still free of this pest, and they have remained so up to today (2001).

Wherever this mealybug, which was newly described as *Phenacoccus manihoti* Matile-Ferrero, and belonging to the family Pseudoccocidae, turned up it became the most important cassava pest, threatening the supply of the main staple food for about 200 million Africans.

Morphology and Biology

This is a typical mealybug; pinkish, covered with white waxy dust, oval in shape (3–4 mm length) with no wings, weak legs, and long sucking mouth parts on the ventral side (Fig. 28). Yellowish eggs are laid in daily batches protected by wax filaments, mostly underneath the tip of the abdomen of the female. The tiny first instar larvae disperse all over the plants and can be transported by wind. The three nymphal instars resemble each other and the adult, except for the size increase. This species is parthenogenetic, which means that it reproduces without males.

The life cycle is completed within 1 month and the mealybug reproduces throughout the year, without any resting stages. It attacks cassava, *Manihot esculenta* Crantz (Euphorbiaceae), the related Ceara rubber *Manihot glaziovii* Mull. Arg., as well as the interspecific hybrid of these two plants, which are of South American origin. At extreme outbreak levels the infestation spills over to many other plants of different species which happen to grow in the vicinity of infested cassava, but when infestations are low no other plant species are attacked.

Damage

Mealybugs suck preferentially in the growing tip and on the underside of leaves. During heavy attacks the undersides of leaves are covered with a white mass. Mealybugs eject surplus sugar water, which accumulates on the leaves below as a sticky cover of honeydew, which is subsequently attacked by fungi. The resulting black "sooty-mold" cover reduces photosynthesis, and sucking of the insect in the growing tips leads to stunting. In areas where cassava leaves are eaten as a vegetable, such use is made impossible by heavy mealybug infestation. Accumulation of carbohydrates in the storage tubers, which in cassava is a continuous process, is reduced, and quality is impaired. Tuber yield losses of up to 80% have been recorded. In addition, because of the stunting, planting sticks are of poor quality, which compromises the following year's crop. Thus, cassava cultivation has disappeared from vast areas during the height of the cassava mealybug epidemic.

Control Options

Wherever this mealybug appeared for the first time, extension services tried to combat it with pesticides. As the mealybug is often hidden in the

Cassava Mealybug, *Phenacoccus manihoti* Matile-Ferrero (Hemiptera: Pseudococcidae), Figure 28
The cassava mealybug, *Phenacoccus manihoti*, on a cassava leaf (upper left); the exotic parasitoids *Apoanagyrus lopezi* (upper right) and *A. diversicornis* (middle left); one of the widespread and common indigenous coccinellids, *Hyperaspis pumila* (middle right); and cassava field devastated by cassava mealybug (lower) (from Neuenschwander (2005) In: Evaluating indirect ecological effects of biological control. CABI, Wallingford, UK).

buds, insecticides are generally inefficient, all the more because they also preferentially kill the natural enemies. In fact, it was demonstrated that repeated insecticide applications led to an explosion of the mealybug population.

Similarly, cassava varieties were tested in a quest to find and/or develop resistant varieties. As stand-alone component, resistant/tolerant varieties did, however, not give satisfactory results.

The Solution: Biological Control

Cassava was brought to Africa from South America by Portuguese traders in the sixteenth century, though it acquired today's importance only in the early twentieth century. It was therefore surmised that this new mealybug came from South America and that classical biological control, i.e., the transfer of natural enemies that keep this insect under control in its original home, could bring the solution. "Foreign exploration", i.e., the search for natural enemies, in Latin America was undertaken by several international research organizations, including CAB International and the International Institute of Tropical Agriculture (IITA), but the cassava mealybug remained elusive. In the course of this exploration, another mealybug was discovered, *Phenacoccus herreni* Cox and Williams, but when its parasitoids were tested they did not attack the *P. manihoti* known from Africa.

In 1981, a researcher from the Centro Internacional de Agricultura Tropical (CIAT) finally found *P. manihoti* in Paraguay. Under the leadership of IITA, "foreign exploration" was then concentrated and *P. manihoti* was found on cassava in a few sites in the Rio de la Plata valley in Paraguay, Brazil and Bolivia.

The first natural enemy of *P. manihoti* to be discovered, the parasitic wasp *Apoanagyrus* (*Epidinocarsis*) *lopezi* de Santis (Hymenoptera, Encyrtidae), eventually also proved to be the best biological control agent. Mated females lay their eggs into mealybugs (second to fourth instars), where a larva develops freely floating in the coelom of the mealybug. Sometimes the host tries to mount a defense action by encapsulating the parasitic larva, but this is successful only in about 10% of cases (which might include larvae that died for other reasons). The larva pupates in the sausage-shaped dry remains of the mealybug, called a "mummy", from where the adults emerge, after a total life cycle of about 2 weeks. Because the female determines the sex of its offspring by adding or withholding sperm during oviposition into the host, she can exploit the host to its best. Second instar hosts yield only male parasitoids, which though small are fully functional; fourth instars yield mostly females, which because of their large size can produce more eggs than small females.

Several other natural enemies, among them the wasp *A. diversicornis* Howard and several predatory lady beetles, mainly *Hyperaspis notata* Mulsant and *Diomus hennesseyi* Fürsch (Coleoptera: Coccinellidae), were collected mostly in Paraguay and Brazil in the course of several years and shipped to CABI in the United Kingdom for quarantine. There, the insects were reared and checked to be: (i) free of diseases, (ii) not harmful to plants, (iii) not hyperparasitic, i.e., harmful to indigenous parasitoids, and (iv) not harmful to useful insects like bees and silkworms. They were then sent to IITA in Nigeria, with the necessary Nigerian import permits and under the umbrella approval of the Inter-African Phytosanitary Council of the Organization for African Unity. Further studies, mass rearing with specially developed equipment, and releases followed. In the early 1980s, on the strength of encouraging results in Nigeria, these exotic insects were sent to all African countries requesting them. Releases were executed mostly from the ground and, in a few instances, by aircraft using a specially developed apparatus. Thus, a total of about 150 releases was made by IITA, always in close collaboration with the quarantine authorities and scientists of the various African countries.

By the mid-1990s, *A. lopezi* was established everywhere in Africa where *P. manihoti* occurred. It sometimes had dispersed long distances from the release sites (170 km within ten generations of *A. lopezi* was documented). The other parasitoid failed to establish (i.e., it could not be recovered after 1 year) and the two coccinellids (Fig. 28) established only locally in the Democratic Republic of Congo, Malawi, and perhaps some East African countries, where they had to compete with numerous common indigenous lady beetle species.

A. lopezi became the target of extensive impact studies, using paired sleeve cages, chemical exclusion experiments, simulation modelling on the basis of laboratory studies, and direct monitoring through field surveys in many countries. As a result, this is one of the best-researched examples of classical biological control of an exotic arthropod pest. Wherever *A. lopezi* had been present for about 2 years (3–4 years in the East African highlands), mealybug populations dropped tenfold to non-economic levels, thus validating the model predictions. In local spots with exceedingly poor soils, such as pure sand without any mulch, mealybug populations, though lower than before, remained high enough to cause damage despite the presence of *A. lopezi*. For such conditions, any further release of *A. lopezi* is useless, but strengthening the plants by applying mulch successfully tipped the balance and reduced mealybug infestation considerably.

The key features that made *A. lopezi* such a successful biological control agent (particularly in comparison to *A. diversicornis*) were: (i) an exceptional host finding capacity, higher than any of its exotic or local competitors; (ii) acceptance of a wide range of host stages; (iii) extensive host feeding, whereby the female wounds its host and sucks its hemolymph, thereby killing small hosts outright; (iv) fast development (almost two generations for one by its host; he same as for *A. diversicornis*).

These advantages clearly outweighed the perceived low reproductive rate, low (but density dependent) parasitism rate, and the fact that *A. lopezi* was attacked by local hyperparasitoids. In fact, 16 species of wasps were found to have switched over to *A. lopezi*. They came from parasitoids, mostly *Anagyrus* spp. (Hymenoptera, Encyrtidae), that attack *Phenacoccus madeirensis* Green, a common mealybug on cassava. Except for an odd case, these *Anagyrus* spp. could not reproduce on *P. manihoti*.

Though at the time of the release in the early 1980s no indigenous mealybug species had been tested and the whole concept of non-target effects was not yet prominent, food-web studies after the establishment showed that *A. lopezi* developed on *P. manihoti* only. Environmental effects of this biocontrol project were thus limited to the impact on a ecosystem that had been temporarily disturbed by the invasion of *P. manihoti*, which offered numerous indigenous predators a new and ample food. With the collapse of this food source, the abundance of these general predators, as well as of hyperparasitoids, declined drastically, presumably back to pre-invasion levels.

The population equilibrium of *P. manihoti* has remained low for the last 20 years, with an occasional short-term low peak in abundance. Ten to 15 years after the establishment of *A. lopezi*, extension services and governmental research organizations in most previously affected countries reclassified *P. manihoti* as an insect of minor importance. The stability of the system is only disturbed where insecticide interventions on neighboring crops like cotton, or against grasshoppers, disturb the balance by killing the wasps. This leads to an upsurge in *P. manihoti* populations, a situation well known to practitioners of integrated pest management.

In field experiments, yields under conditions of biological control of *P. manihoti* were compared with those where mealybug infestations had been artificially boosted. In surveys, various factors affecting yield were quantified and their contribution to yield attributed. On the basis of these results, the savings due to biological control of *P. manihoti* were extrapolated to all affected countries and compared with the investment into this project. According to different scenarios of how farmers can cope with loss of cassava, returns for each dollar invested were between $200 and $740. For this evidently successful project, its former leader was honored with the World Food Prize.

► Area-Wide Pest Management

References

Gutierrez AP, Neuenschwander P, Schulthess F, Herren HR, Baumgaertner JU, Wermelinger B, Loehr B, Ellis CK (1988) Analysis of biological control of cassava pests in Africa. II. Cassava mealybug *Phenacoccus manihoti*. J Appl Ecol 25:921–940

Hammond WNO, Neuenschwander P (1990) Sustained biological control of the cassava mealybug *Phenacoccus manihoti* (Hom.: Pseudococcidae) by *Epidinocarsis lopezi* (Hym.: Encyrtidae). Entomophaga 35:515–526

Herren HR, Neuenschwander P (1991) Biological control of cassava pests in Africa. Ann Rev Entomol 36:257–283
Neuenschwander P (1996) Evaluating the efficacy of biological control of three exotic homopteran pests in tropical Africa. Entomophaga 41:405–424
Neuenschwander P (2001) Biological control of cassava mealybug in Africa: a review. Biol Control 21:214–229
Neuenschwander P, Markham R (2001) Biological control in Africa and its possible effects on biodiversity. In: Wajnberg E, Scott JK, Quimby PC (eds) Evaluating indirect ecological effects of biological control, CABI Publishing, Wallingford, UK, pp 127–146
Zeddies J, Schaab RP, Neuenschwander P, Herren HR (2001) Economics of biological control of cassava mealybug in Africa. Agric Econ 24:209–219

Cassava Pests and their Management

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The origin of cassava (Euphorbiaceae: *Manihot esculenta* Crantz) is the Neotropical Americas, where it is estimated that domestication occurred some 7,000–9,000 years ago. At present this perennial shrub is grown throughout the tropical regions of the world. The highest production is in Africa (ca. 55%); while Asia and Latin America account for 27 and 18%, respectively. In the case of yields on an average per-hectare basis, they are highest in Asia (14.1 t/ha) and the Americas (12.7 t/ha) and lowest in Africa (8.5 t/ha). Cassava is cultivated mainly for its starchy roots and is ranked as the sixth most important caloric source in the human diet and the fourth most important staple in the tropics. Cassava leaves may also be consumed and may be an important source of protein in some African countries and Northeast Brazil.

Cassava is vegetatively propagated, has a long growth cycle (8–24 months), is drought tolerant, and is often intercropped with staggered planting dates so it is almost always present in farmers' fields. Most cassava is grown by small-scale farmers in traditional farming systems, often on marginal or fragile soils under rain-fed conditions, using few purchased inputs such as fertilizers and pesticides. As yields are low in these systems, pest control is of low priority due to the high costs and the long crop cycle, which may require various applications.

The dynamics of cassava production are changing, however, as trends in the food, feed and industrial sectors are leading to an increased demand for high-quality cassava starches. In Latin America, there are indications of a shift toward larger scale production units where cassava is grown as a plantation crop, and it is advantageous for farmers to employ a multiple planting and harvesting production system in order to meet the constant market demands of the processing industries. In this type of production system, the cassava crop will be found at several different growth stages in the same or surrounding fields. Evidence now indicates that pest problems will be compounded in these overlapping production systems. Populations of certain pests such as whiteflies, hornworms and mealybugs tend to increase when a constant food supply (e.g., young cassava foliage) is available. Given this trend, with the concomitant increase in pest populations and damage, there will be a greater tendency to apply pesticides to control pest outbreaks.

The Consultative Group for International Agricultural Research (CGIAR) has two research centers – the International Center for Tropical Agriculture (CIAT, Cali, Colombia) and the International Institute of Tropical Agriculture (IITA, Ibadan, Nigeria) – with global and regional (Africa) mandates, respectively, for cassava, oriented toward resource-poor farmers. Today, there is a need to invest in cassava research in order to understand fully the role of pests and diseases in these multiple production systems, where different stages of the crop overlap, providing a constant source of nourishment.

Following is an overview of the cassava arthropod complex, and the corresponding damage to the crop, aspects of biology, behavior, and management of the most important pests are explored for the following categories: foliage feeders, stemborers/stem feeders, soil-borne pests and secondary pests. This is followed by a look at future trends.

The Cassava Arthropod Pest Complex and Crop Damage

Not surprisingly since cassava originated in the Neotropics, the greatest diversity of arthropods reported attacking the crop is from these regions (Table 8). More than 200 species have been reported, many of which are specific to cassava and have adapted in varying degrees to the array of natural biochemical defenses in the host, which include laticifers and cyanogenic compounds.

The pest complex varies greatly among the major cassava-growing areas in the Americas, Africa and Asia. The crop, whose origin is in South America, was introduced into Africa in the 1500s and into Asia in the seventeenth century. In Asia, none of the major Neotropical pests has become established, and native arthropods that have adapted to cassava have not been reported as causing serious economic damage. In Africa, the whitefly *Bemisia tabaci* is presently considered to be the major pest of cassava because it is the vector of cassava mosaic disease (CMD). Moreover, recent reports indicate that *B. tabaci* is also causing root yield reductions due to direct feeding on the crop. There is also the possibility of the accidental introduction of pests via planting material, which can wreak havoc. The cassava green mite (*Mononychellus tanajoa*) and the cassava mealybug (*Phenacoccus manihoti*), which were introduced from South America, have caused considerable crop losses and have been the target of massive biological control efforts.

Studies indicate that several arthropod species can cause considerable yield loss and that the pest complex is not geographically uniform. Two cassava mealybug species offer an example of the geographic influence on crop damage. *Phenacoccus herreni*, which has caused considerable damage in northeast Brazil, was probably introduced from northern South America (Venezuela or Colombia), where mealybug populations are controlled by natural enemies not found in Brazil. *Phenacoccus manihoti*, which has caused severe crop damage in Africa, had, until recently, been reported only from Paraguay, the Mato Grosso area of Brazil, and the Santa Cruz area of Bolivia. In 2005, this species was collected from the states of Bahia and Pernambuco in northeastern Brazil. The spread of *P. manihoti* into the drier, hotter regions of Brazil is probably associated with the movement of cassava planting material (i.e., stem cuttings) from southern Brazil into the northeast.

The cassava pest complex can be divided into two groups: those that have probably co-evolved with cassava, which is their primary or only host; and generalist feeders that may attack the cassava crop sporadically or opportunistically and are often limited in geographic distribution. The first group includes the *Mononychellus* mite complex, mealybugs, the hornworm *Erinnyis ello*, lacebugs, whiteflies, stemborers, fruit flies, shoot flies, scales, thrips and gall midges. The generalist feeders consist mainly of a complex of white grub species, termites, cutworms, grasshoppers, leaf-cutting ants, burrower bugs, crickets, *Tetranychus* mite species and other stemborers.

The most serious pests of cassava – those causing economic damage or yield losses – are generally those that have co-evolved with the crop, including mites, hornworms, whiteflies, mealybugs, lacebugs and stemborers. Generalist feeders reported causing yield losses, often on a localized basis, include burrower bugs, white grubs, leaf-cutting ants and grasshoppers.

Most cassava arthropod pests cause indirect plant damage because they are foliage or stem feeders, reducing leaf area, leaf life or photosynthetic rate. Those pests that can attack the crop over a prolonged period, especially during seasonally dry periods (3–6 months) can cause severe yield losses as a result of decreased photosynthesis, premature leaf drop and death of the apical meristem. Potential yield reduction by these pests can be greater than that by cyclical pests such as hornworms, leaf-cutter ants and grasshoppers,

Cassava Pests and their Management, Table 8 **Global distribution of important arthropod pests of cassava**

Arthropod pest	Major species	Americas	Africa	Asia
Mites	*Mononychellus caribbeanae*	x		
	Mononychellus tanajoa	x	x	
	Tetranychus urticae	x		x
	Oligonychus peruvianus	x		
Stemborers	*Chilomima clarkei*	x		
	Coelosternus spp.	x		
	Lagochirus araneiformis	x		
	Lagochirus spp.	x	x	x
Lacebugs	*Vatiga illudens*	x		
	Vatiga manihotae	x		
	Vatiga lunulata	x		
	Amblystira machalana	x		
Burrower bugs	*Cyrtomenus bergi*	x		
	Pangaeus piceatus	x		
	Tominotus communis	x		
Termites	*Heterotermes tenuis*	x		
	Coptotermes sp.	x	x	x
White grubs	*Phyllophaga menetriesi*	x		
	Phyllophaga obsoleta	x		
	Phyllophaga sneblei	x		
	Leucopholis rorada			x
Hornworm	*Erinnyis ello*	x		
	Erinnyis alope	x		
Tiger moth	*Phoenicoprocta sanguinea*	x		
Leaf-cutter ants	*Atta sexdens*	x		
	Atta cephalotes	x		
	Acromyrmex landolti	x		
Scale insects	*Aonidomytilus albus*	x		
	Parasaissetia nigra	x		
	Ceroplastes sp.	x		
	Saissetia miranda	x		
Pests of dried cassava (stored)	*Araecerus fasciculatus*	x	x	x
	Lasioderma serricorne	x	x	x
	Rhyzopertha dominica	x	x	x
	Tribolium castaneum	x	x	x
	Sitophilus oryza	x		

Cassava Pests and their Management, Table 8 Global distribution of important arthropod pests of cassava (Continued)

Arthropod pest	Major species	Americas	Africa	Asia
	Sitophilus zeamais		x	x
	Prostephanus truncatus		x	x
Gall midge	*Jatrophobia brasiliensis*	x		
Whiteflies	*Aleurotrachelus socialis*	x		
	Aleurothrixus aepim	x		
	Aleurodicus dispersus	x	x	x
	Bemisia afer		x	x
	Bemisia tuberculata	x		
	Bemisia tabaci	x	x	x
	Trialeurodes variabilis	x		
Shootflies	*Neosilba perezi*	x		
	Silba pendula	x		
Fruit flies	*Anastrepha pickeli*	x		
	Anastrepha manihoti	x		
Mealybugs	*Phenacoccus manihoti*	x	x	
	Phenacoccus herreni	x		
	Phenacoccus gossypii	x		
	Phenacoccus madeirensis	x		
	Ferrisia virgarta	x		
Root mealybugs	*Pseudococcus mandio*	x		
	Stictococcus vayssierei		x	
Leafhoppers	*Empoasca bispinata*	x		
	Sacphytopius fuliginosus	x		
	Scaphytopius marginelineatus	x		
Grasshoppers	*Zonocerus elegans*		x	
	Zonocerus variegatus		x	
Thrips	*Frankliniella williamsi*	x	x	x
	Corynothrips stenopterus	x		
	Scirtothrips manihoti	x		
	Scolothrips sp.	x		

which cause sporadic defoliation; however, these highly visible pests often induce cassava producers to apply pesticides.

Few cassava pests damage cassava roots directly. Three exceptions are burrower bugs (*Cyrtomenus bergi*), white grubs (Scarabaeidae) and root mealybugs (e.g., *Pseudococcus mandio*). *Cyrtomenus bergi* causes root punctures during feeding that can introduce fungal pathogens that reduce root yield and quality. White grubs have been found feeding directly on cassava roots causing yield loss and severe root rot. Yield losses of 17% have been reported for *P. mandio* feeding on cassava roots in southern Brazil.

In general, arthropod pests are most damaging during the dry season, being less severe in areas of considerable and consistent rainfall; however, there are exceptions to this rule. Hornworm attacks will frequently occur at the onset of the rainy season when there is considerable new growth and young leaves. Severe whitefly attacks often coincide with the rainy season when young, succulent leaves are preferred for oviposition. Studies have also shown that burrower bugs and white grubs prefer soils with higher soil moisture content.

The cassava plant is well adapted to long periods of limited water and responds to water shortage by reducing its evaporative (leaf) surface rapidly and efficiently and by partially closing the stomata, thereby increasing water-use efficiency. The crop has the potential to recover and compensate for yield losses from seasonally dry periods and pest attack due to the higher photosynthetic rate in newly formed leaves. Younger leaves play a key role in plant carbon nutrition. Most pests prefer the younger canopy leaves; thus, dry-season feeding tends to cause the greatest yield losses in cassava.

Climate change predictions indicate that certain agricultural lands will receive less rainfall in the future. The cassava crop may have a comparative advantage in these extended seasonally drier regions; however, increased cassava production in the Neotropics and Africa could result in more severe pest outbreaks, reducing yields and/or increasing pesticide use.

Management of Cassava Arthropod Pests

Foliage Feeders

Whiteflies

Considered one of the world's most damaging agricultural pest groups, both as direct feeders and virus vectors, whiteflies attack cassava-based agroecosystems in the Americas, Africa and, to a lesser extent, in Asia. Currently, they may be causing more crop damage and yield loss on cassava than any other pest attacking the crop.

There is a large species complex associated with the crop, the importance of which can vary between regions or continents. The largest complex on cassava is in the Neotropics, where 11 species are reported, including *Aleurotrachelus socialis*, *Trialeurodes variabilis*, *Aleurothrixus aepim*, *Bemisia tuberculata* and *Bemisia tabaci* (=*B. argentifolii*). *Aleurotrachelus socialis* and *T. variabilis* cause considerable direct damage and yield losses in northern South America (Colombia, Venezuela and Ecuador) and in certain regions of Central America. *Trialeurodes variabilis* is observed primarily in the higher altitudes (over 1,000 m), while *A. socialis* is confined to lower altitudes (up to 1,200 m). *Aleurothrixus aepim* is found in high populations causing yield loss in Northeast Brazil.

Bemisia tabaci, the vector of CMD, caused by several geminiviruses, has a pantropical distribution, feeding on cassava throughout most of Africa, several countries in Asia and more recently in the Neotropics. It has been speculated that the absence of CMD in the Americas may be related to the inability of its vector to colonize cassava effectively. Prior to the early 1990s, the *B. tabaci* biotypes found in the Americas did not feed on cassava. The B biotype of *B. tabaci*, regarded by some as a separate species (*B. argentifolii*), has been collected from cassava in several regions of the Neotropics. Although seldom observed in high populations, it is now considered that CMD poses a more serious threat to cassava production given that most traditional cultivars grown in the Neotropics are highly susceptible to the disease.

Damage

Whiteflies can cause direct damage to cassava by feeding on the phloem of leaves, inducing leaf curling, chlorosis and defoliation. High populations, combined with prolonged feeding, result in considerable reduction in root yield. Yield losses resulting from *A. socialis* and *A. aepim* activity are common in Colombia and Brazil, respectively. With *A. socialis* feeding, there is a correlation between duration of attack and yield loss. Infestations of 1, 6 and 11 months resulted in a 5, 42 and 79% yield reduction, respectively. More recently, yield losses of 58% due to *T. variabilis* feeding have been recorded in the Andean region of northern South America. In several East African countries, yield losses due to direct feeding by *B. tabaci* have been recorded in recent years as a result of the higher populations observed. In Uganda, over 50% reductions in root yield have been recorded.

Biology and Behavior

Research with *A. socialis* and *A. aepim* indicates that populations of both species can occur throughout the growing cycle (1 year or more) but are usually highest during the rainy season when there is considerable new growth. *Aleurotrachelus socialis* females prefer ovipositing on the undersides of the young apical leaves, reaching a high of 244 eggs (avg. 181, min. 155) per female. The individually oviposited banana-shaped eggs hatch in about 10 days and pass through three feeding nymphal instars and a pupal stage (4th instar) before reaching the winged adult stage. During the third instar the body color changes from beige to black, surrounded by a waxy white cerosine, making this species easy to distinguish from other whitefly species feeding on cassava. *Aleurotrachelus socialis* egg-to-adult development was 32 days under growth chamber conditions (28 ± 1°C, 70% RH). *Aleurotrachelus socialis* may be specific to cassava as populations have not been observed on other plant species.

Control

Integrated management of cassava whiteflies depends on having effective, low-cost, environmentally sound technologies available for farmers. A successful whitefly control program requires continual research input to acquire the basic knowledge needed to develop the technologies and strategies for appropriate implementation. A recent survey in an important cassava-growing region of Colombia showed that 34% of the farmers surveyed applied chemical pesticides for whitefly control versus only 4.6% applying biological products. Farmer field trials in the region revealed a 58% reduction in yield due to whitefly attack; however, 52% of the farmers surveyed employed no control measures. Pesticide applications have not provided adequate control, probably for lack of knowledge of whitefly biology, especially the immature stages (the presence of eggs and early-instar nymphs). Moreover, around 88% of the farmers had little or no knowledge of whitefly biology, behavior and management. This has resulted in inappropriate timing of applications and the misuse of chemical pesticides.

Recent research and field observations on cassava whiteflies in the Neotropics indicate that control measures, especially pesticide applications, are compromised because of the whitefly's capacity for rapid population increases and its ability to develop high levels of pesticide resistance. When *A. socialis* feeds on a susceptible cassava variety, it doubles its population every 4.2 days. When there are overlapping crop cycles (e.g., multiple plantings) and favorable rainfall patterns, the conditions are ideal for a rapid buildup in whitefly populations as a constant food supply of young cassava leaves are available for adult feeding, high oviposition and nymphal development. Field observations indicate that once whitefly populations begin this rapid increase, they are very difficult to control, requiring repeated pesticide applications that disrupt natural biological control and that are also uneconomical for small farmers. This capacity for rapid population buildup makes it urgent to introduce efficient management practices early in the plant growth cycle, possibly during the first month of plant growth and before the economic threshold is reached.

Four methods of whitefly control in cassava are discussed: host plant resistance (HPR), biological, cultural and chemical.

Host Plant Resistance
This form of resistance to whiteflies is rare in cultivated crops. HPR studies initiated at CIAT more than 20 years ago have systematically evaluated the accessions in the CIAT cassava germplasm bank for resistance to whiteflies, especially *A. socialis*. Of approximately 5,500 genotypes evaluated in the field in Colombia, about 75% are susceptible, with damage ratings above 3.5 (1 = no damage, 6 = severe damage). Emphasis is placed on those genotypes with damage ratings under 2.0 (about 8%). As there may be susceptible escapes due to insufficient selection pressure, they are reevaluated in subsequent trials. Several sources of resistance to *A. socialis* have now been identified: Genotype MEcu 72 has consistently expressed a high level of resistance, while MEcu 64, MPer 334, MPer 415 and MPer 273 express moderate to high levels. When feeding on resistant genotypes, *A. socialis* has less oviposition, a longer development period, smaller size and higher mortality than those feeding on susceptible genotypes. *Aleurotrachelus socialis* nymphal instars feeding on MEcu 72 and MPer 334 suffered 72.5 and 77.5% mortality, respectively, mostly in the early instars.

A cross between MEcu 72 (female parent, whitefly resistant) and MBra 12 (male parent, high yielding, good plant type) resulted in 128 progeny, four of which were selected for whitefly resistance, yield and cooking quality. These four hybrids, along with susceptible genotypes and local farmer varieties, were evaluated at three sites in Tolima Province in Colombia by CORPOICA-MADR (Colombian Corp. for Agricultural Research/Ministry of Agricultural and Rural Development) over a 4-year period. CG 489–31 was selected for high whitefly resistance, high yield and good cooking qualities. In 2003, it was officially released by MADR under the name of Nataima-31. It has attained yields of 33 t/ha, outyielding the regional farmers' variety in Tolima by 34% with no pesticide applications. Nataima-31 is now being grown commercially in several areas of Colombia and has been introduced into Ecuador and Brazil.

Given that *B. tabaci* is a pantropical species that is the vector of CMD, which causes severe cassava crop damage in Africa and India, several cassava genotypes were sent by CIAT to NRI (Natural Resources Institute-UK) to be evaluated for resistance to *B. tabaci*. Genotype MEcu 72 had the lowest rate of *B. tabaci* oviposition so it was introduced into Uganda during 2005 and will be included in a breeding program to develop whitefly-resistant varieties.

Biological Control
Numerous natural enemies are found associated with whiteflies on cassava in the Neotropics (Table 9). In recent field explorations in Colombia, Ecuador, Venezuela and Brazil, a complex of parasitoids, predators and entomopathogens were collected from several whitefly species. The most representative group is that of the microhymenopteran parasitoids. The richness of species in Colombia, Venezuela and Ecuador is primarily represented by the genera *Encarsia*, *Eretmocerus* and *Amitus*, frequently associated with *A. socialis*. Gaps in knowledge about this natural enemy complex have limited the determination of their effectiveness in biological control programs. There is little knowledge regarding levels and rates of parasitism by species or specification of the host and its effect on the regulation of whitefly populations.

Eleven species of parasitoids (5 genera) were collected from the cassava-growing regions of Colombia; an additional five species were collected from Ecuador and seven from Venezuela. On the Caribbean Coast of Colombia, *A. socialis* was parasitized by eight species, with the genus *Eretmocerus* comprising 70% of the parasitoids. In Magdalena Province, 73% of *A. socialis* parasitism was by *Amitus macgowni*, followed by *Encarsia* sp. (26%). In the Andean region *Eretmocerus* spp. parasitized all whitefly species, but *Encarsia pergandiella* was the predominant parasitoid of *T. variabilis*.

More than 20 species of entomopathogens have been reported infecting whiteflies on cassava, including *Aschersonia* sp., *Lecanicillium* (*Verticillium*) *lecani*, *Beauveria bassiana* and *Paecilomyces*

Cassava Pests and their Management, Table 9 **Natural enemies of important cassava arthropod pests**

Principal species	Parasitoids	Predators	Entomopathogens
Aleurotrachelus socialis	*Amitus macgowni*	*Delphastus* sp.	*Beauveria bassiana*
	Encarsia sp.	*D. quinculus*	*Lecanicillium lecani*
	Encarsia hispida	*D. pusillus*	*Aschersonia aleyrodes*
	E. bellotti	*Chrysopa* sp. nr. *cincta*	
	E. sofia	*Condylostylus* sp.	
	E. luteola		
	E. americana		
	E. cubensis		
	Metaphycus sp.		
	Euderomphale sp.		
	Signiphora aleyrodis		
	Eretmocerus spp.		
Aleurothrixus aepim	*Encarsia porteri*		*Cladosporium* sp.
	E. aleurothrixi		
Aleurodicus dispersus	*Encarsia* sp.		
	E. haitiensis		
	Aleurotonus vittatus		
	Eretmocerus sp.		
Bemisia tuberculata	*E. hispida*	*Condylostylus* sp.	
	E. pergandiella		
	Euderomphale sp.		
	Encarsia sp. prob. *variegata*		
	Metaphycus sp.		
	Eretmocerus sp.		
Bemisia tabaci	*Encarsia sophia*	*Delphastus pusillus*	
	E. lutea	*Condylostylus* sp.	
	E. formosa		
	E. mineoi		
	Eretmocerus mundus		
Trialeurodes variabilis	*Encarsia* sp.	*Chrysopa* sp. nr. *cincta*	*Aschersonia aleyrodes*
	E. pergandiella	*Condylostylus* sp.	*B. bassiana*
	E. Sophia		*L. lecani*
	E. luteola		
	E. strenua		

Cassava Pests and their Management, Table 9 **Natural enemies of important cassava arthropod pests (Continued)**

Principal species	Parasitoids	Predators	Entomopathogens
	E. hispida		
	E. bellotti		
	E. nigricephala		
	Eretmocerus spp.		
Aleuroglandulus malangae	*Encarsia guadeloupae, Encarsia desantisi*	*Nephaspis namolica*	
Mononychellus tanajoa		*Insects:*	*Hirsutella thompsoni*
		Stethorus tridens	*Neozygites floridana*
		S. darwin	*N. tanajoae*
		S. madecasus	
		Oligota minuta	
		O. gilvifrons	
		O. centralis	
		O. pigmaea	
		Delphastus argentinicus	
		Chrysopa sp.	
		Mites/Phytoseiidae:	
		Typhlodromalus manihoti	
		T. aripo	
		Neoseiulus idaeus	
		Galendromus annectes	
		Euseius concordis	
		Euseius ho	
Phenacoccus manihoti	*Apoanagyrus lopezi*	*Cleothera onerata*	
	Acerophagus sp.	*Hyperaspis* sp.	
		Nephus sp.	
		Chrysopa sp.	
		Sympherobius sp.	
		Typhlodromalus aripo	
Phenacoccus herreni	*Acerophagus coccois*	*Ocyptamus* sp.	*Cladosporium* sp.
	Apoanagyrus diversicornis	*Sympherobius* sp.	*Neozygites fumosa*
	Aenasius vexans	*Hyperaspis* sp.	
	Anagyrus insolitus	*Nephus* sp.	
	A. thyridopterygis	*Cleothera onerata*	
	A. pseudococci	*C. notata*	

Cassava Pests and their Management, Table 9 **Natural enemies of important cassava arthropod pests (Continued)**

Principal species	Parasitoids	Predators	Entomopathogens
	Anagyrus sp. nr. *Greeni*	*Diomus* sp.	
	Aenasius sp. nr. *putonophylus*	*Coccidophylus* sp.	
	Prochiloneurus dactylopii	*Scymnus* sp.	
	Chartocerus sp.	*Olla* sp.	
	Hexacnemus sp.	*Curinus colombianus*	
	Eusemion sp.	*Cycloneda sanguinea*	
		Hippodamia convergens	
		Azya sp.	
		Chrysopa sp.	
		K. coccidarum	
		Zelus sp.	
Phenacoccus gossypii	*Anagyrus* sp.	*Curinus colombianus*	*Cladosporium* sp.
	Apoanagyrus sp.	*Cleothera onerata*	
	Aenasius masii	*Coccidophylus* sp.	
	Acerophagus coccois	*Scymnus* sp.	
	Hexacnemus sp.	*Olla* sp.	
	Eusemion sp.	*Hippodamia convergens*	
	Haltichella sp.	*Azya* sp.	
	Prospaltella sp.	*Chrysopa* sp.	
	Signiphora sp.	*K. coccidarum*	
		Pentillia sp.	
		Sympherobius sp.	
		Ocyptamus sp.	
		Kalodiplosis coccidarum	
		Zelus sp.	
		Emesaya sp.	
Frankliniella williamsi		*Orius* sp.	
Scirtothrips manihoti		*T. aripo*	
Vatiga illudens		*Zelus* sp.	
Vatiga manihotae		*Zelus nugax*	
Erinnyis ello	*Trichogramma* spp.	*Chrysopa* spp.	*Bacillus thuringiensis*
	Telenomus sphingis	*Podisus nigrispinus*	baculovirus of *E. ello*
	Cotesia americana	*P. obscurus*	*Metarhizium anisopliae*
	Cotesia sp.	*Polistes carnifex*	*Beauveria bassiana*
	Euplectrus sp.	*P. erythrocephalus*	*Paecylomices* sp.

Cassava Pests and their Management, Table 9 Natural enemies of important cassava arthropod pests (Continued)

Principal species	Parasitoids	Predators	Entomopathogens
	Drino macarensis	*P. versicolor*	*Nomuraea rileyi*
	Drino sp.	*P. canadensis*	*Cordyceps* sp.
	Euphorocera sp.	*Polybia emaciata*	
	Sarcodexia innota	*P. sericea*	
	Thysanomia sp.	*Zelus nugax*	
	Belvosia sp.	*Zelus* sp.	
	Forciphomyia eriophora	*Calosoma* sp.	
	Cryptophion sp.	*Dolichoderus* sp.	
	Ooencyrtus sp.	*Alcaeorrhynchus grandis*	
	Chetogena scutellaris		
		Spiders:	
		Tomicidae	
		Salticidae	
Erinnyis alope	*Trichogramma* spp.	Spiders:	
	Telenomus sp.	Tomicidae	
		Salticidae	
		Chrysopa sp.	
Chilomima clarkei	*Brachymeria* sp.		*Metarhizium anisopliae*
	Tetrastichus howardi		*Beauveria bassiana*
	Trichogramma sp.		undetermined virus
Aonidomytilus albus		*Prodilis* sp.	
Saissetia miranda	*Anagyrus* sp.		
	Metaphycus sp.		
	Scutellista cyanea		
Anastrepha pickeli	*Opius* sp.		
Anastrepha manihoti	*Opius* sp.		
Cyrtomenus bergi		*Nerthra* sp.	*Heterorhabditis* sp.
			Metarhizium anisopliae
			Steinernema sp.
Phyllophaga menetriesi		*Campsomeris dorsata*	*Metarhizium anisopliae*
			Beauveria bassiana
Stictococcus vayssierei		*Anoplolepis tenella*	
Zonocerus elegans			*Metarhizium anisopliae*

Cassava Pests and their Management, Table 9 Natural enemies of important cassava arthropod pests (Continued)

Principal species	Parasitoids	Predators	Entomopathogens
			Beauveria bassiana
Zonocerus variegatus			*Metarhizium anisopliae*
			Beauveria bassiana
Iatrophobia brasiliensis	*Torymoides sulcius*		

fumosoroseus; however, there has to be a careful selection of the species, as well as the identification of native isolates of entomopathogenic fungi. Greenhouse experiments at CIAT with an isolate of *L. lecani* resulted in 58–72% *A. socialis* nymphal mortality and 82% egg mortality. The *L. lecani* isolate has been formulated into a commercial biopesticide BioCanii®. The commercial biopesticide Mycotrol®, (isolate of *B. bassiana*, a product of Laverlam S.A.), gave very effective control (over 90% mortality of the egg and first two nymphal instar stages) of *A. socialis* in greenhouse experiments at CIAT. Mycotrol®, which is also effective against *B. tabaci* and *T. variabilis*, is presently being evaluated in field trials.

The most frequently observed predators feeding on cassava whiteflies are chrysopids (Neuroptera: Chrysopidae). These generalists feed on the eggs and immature stages of numerous arthropods. *Chrysoperla carnea* is frequently collected feeding on *A. socialis* in cassava fields. In lab studies at CIAT, *A. socialis* egg and nymphal consumption by *C. carnea* were measured by recording the time required for 50% consumption of the prey state being offered. *Chrysoperla carnea* adults required 80 h to consume 50% of the nymphal instars and pupae and 77 h to consume 50% of the eggs.

Cultural Control

In traditional cropping systems cassava is often intercropped, a practice that has been shown to reduce populations of certain pests. Intercropping cassava with cowpeas reduced egg populations of *A. socialis* and *T. variabilis* by 70% compared to those in monoculture. Yield losses in cassava/maize, cassava monoculture and mixed cultivar systems were ca. 60% versus only 12% in cassava/cowpea intercrops.

When cassava is grown in overlapping cycles or multiple plantings, it is difficult to break the whitefly development cycle so rapid population buildups occur. Upon emerging from the pupal stage, adults migrate to feed and oviposit on recently germinated young plants in adjacent fields. A successful tactic for countering this situation is to implement a "closed season," defined as an interdiction or prohibition when cassava cannot be present in the field. Field observations at CIAT have shown that a 1- to 2-month period with no cassava in the field decreases whitefly populations dramatically over a 4-year period. The success of this ban is enhanced by the fact that *A. socialis* does not appear to have efficient alternate hosts so their populations "crash" when adults cannot find an alternate host species to sustain or increase populations. Nevertheless, the economic practicality of this strategy for the producers is debatable. In many regions a constant supply of cassava roots is economically desirable for meeting the demands of local fresh and processing markets. This same tactic would not be as effective for a species such as *B. tabaci*, which has numerous alternate hosts where its populations can be sustained and multiply.

Chemical Control

Several products with new or novel active ingredients have been evaluated for controlling

A. socialis and *T. variabilis*. Foliar applications of theamethoxam and imidacloprid were most efficient in reducing whitefly populations. Best control was obtained when applied as a drench at a high doses (0.8 and 0.6 l/ha) on young plants. The treatment of cassava planting material (stem cuttings) with a 7-min emersion in a solution of theamethoxam (Actara®) (1 g/l H_2O) is also giving promising results. More than two pesticide applications during the crop cycle should be avoided. Field experiments have shown that pesticides need not be applied after 6 months of crop growth as yield loss due to whitefly attack will not occur. A cost-benefit analysis indicates that chemical pesticide applications for whitefly control in cassava are generally uneconomical for small farmers and only slightly beneficial for large farmers who can generally receive a higher price for the product. Research is under way to evaluate the feasibility of substituting entomopathogens as biopesticides to replace chemical pesticide applications.

Cassava Mites

More than 40 species of mites have been reported feeding on cassava in the Americas, Africa and Asia. The most important are *Mononychellus tanajoa* (syn. = *M. progresivus*), *Mononychellus caribbeanae*, *Tetranychus cinnabarinus* and *Tetranychus urticae* (also reported as *T. bimaculatus* and *T. telarius*). Cassava is the major host for the *Mononychellus* spp., while the *Tetranychus* spp. have a wide host range. *Mononychellus tanajoa*, the cassava green mite (CGM), is the most important species, causing crop losses in the Americas and Africa. It is native to the Neotropics, first being reported from northeast Brazil in 1938. It is presently found in most cassava-growing regions in the Americas, especially in seasonally dry regions of the lowland tropics in Brazil, Colombia and Venezuela.

Damage

In experimental fields in Colombia, *M. tanajoa* attacks of 3, 4 and 6 months resulted in yield losses of 21, 25 and 53%, respectively. Under high mite populations on the Colombian Atlantic Coast, yields were reduced by 15% in resistant cultivars compared with an average 67% loss in susceptible cultivars. In Africa, *M. tanajoa* was first reported from Uganda in 1971; within 15 years it had spread across most of the cassava-growing belt, occurring in 27 countries and causing estimated root losses of 13–80%. CGM has been the objective of a major biological control effort since the early 1980s.

Biology and Behavior

Mites, especially the cassava green mite, are dry-season pests that can cause yield losses where there is a seasonally dry period of at least 3 months. At the onset of the rainy season, mite populations decrease and cassava plants produce new foliage. If the rains do not persist, cassava green mite populations will again increase, causing defoliation and more severe yield losses. This pattern has been observed in the semiarid cassava-growing regions of Northeast Brazil. Cassava green mite populations prefer to feed on the undersides of young emerging leaves, which develop a mottled whitish to yellow appearance and may become deformed or reduced in size. Heavy infestations will cause defoliations, beginning at the top of the plant, often killing apical and lateral buds and shoots.

The adult is green in color with an average body length of about 350 μm. Females oviposit on the leaf undersurface; eggs hatch in 3–4 days (30°C and 70 ± 5% RH). At 15, 20, 25 and 30°C, the egg-to-adult stage is 41.4, 19.5, 10.3 and 7.8 days, respectively. These data indicate that cassava green mite populations can increase rapidly in warm regions of the lowland tropics. At 30°C, each female oviposits 90–120 eggs; during the initial population buildup, mostly females are produced, adding to the rapid population increase.

Management

Pesticide applications for controlling mites on a long-cycle crop such as cassava are not a feasible or economic option for low-income farmers. Moreover, even low doses of pesticides have adverse effects on natural enemies. Cultural control methods have not been explored, and there is little mention of their use in the literature. Research into the control of *M. tanajoa* has followed two main thrusts: HPR and biological control. It is expected that these two complementary strategies can reduce cassava green mite populations below economic injury levels.

Host Plant Resistance

It is hypothesized that in the presence of efficacious natural enemies, only low-to-moderate levels of HPR are needed to reduce CGM populations below economic injury levels. A level of resistance that would hinder, delay or suppress the initial buildup of cassava green mite populations could provide sufficient opportunity for establishing effective natural enemy populations that would prevent an eruption of the cassava green mite population. Therefore an important objective of an HPR strategy is to develop cultivars that are not highly susceptible to the cassava green mite and that hopefully contain low-to-moderate levels of resistance. Immunity or even high levels of resistance do not appear to be available in *M. esculenta* germplasm.

A considerable effort has been made to identify cassava green mite resistance in cultivated cassava. CIAT, IITA and several national research programs in the Americas and Africa have screened cassava germplasm for cassava green mite resistance. Of the more than 5,000 landrace cultivars in the CIAT cassava germplasm bank, only 6% (300 cultivars) were identified as having low-to-moderate levels of resistance. A select number of cultivars with moderate levels of resistance have been released to farmers after a considerable effort by plant breeders and entomologists. Two hybrids (ICA Costeña and Nataima 31), both with low levels of mite resistance, are being grown by cassava farmers in Colombia.

Most mite-resistance field evaluations by CIAT have been carried out in the lowland tropics with a prolonged dry season (4–6 months) and high mite populations (Colombian Atlantic Coast). In Brazil, cassava green mite evaluations were conducted by CNPMF/EMBRAPA, primarily in the semiarid regions of the northeast. Of the 300 cultivars identified by CIAT as promising for CGM resistance (over several years and 2–7 field cycles), 72 have consistently had damage ratings below 3.0. Low-to-moderate levels of resistance are indicated by 0–3.5 (0–6 damage scale).

Mite resistance-mechanism studies indicate strong antixenosis (preference vs nonpreference) for oviposition, as well as moderate antibiosis. In lab studies, *M. tanajoa* displayed a strong ovipositional preference for susceptible varieties. When paired with the moderately resistant cultivars MEcu 72, MPer 611 and MEcu 64 in free-choice tests, 95, 91 and 88%, respectively, of the eggs were oviposited on the susceptible cultivar CMC 40. Antibiosis is expressed by mites having lower fecundity, a longer development time, a shorter adult life span, and higher larval and nymphal mortality when feeding on resistant versus susceptible cultivars.

Biological Control

Beginning in the early 1980s, extensive evaluations of the natural enemy complex associated with cassava mites were conducted at more than 2,400 sites in 14 countries of the Neotropics. The primary target in most of these field and lab studies was the cassava green mite. These ongoing extensive surveys indicate that the cassava green mite is present throughout much of the lowland Neotropics. High populations, which can cause significant yield loss, occur most frequently in Northeast Brazil and can be localized.

Geographic regions of the Americas were identified and prioritized using GIS support to assist in targeting specific areas for exploration. Homologous maps based on agrometeorological data and microregional classification comparing Africa and the Neotropics were prepared as one of the major targets for biological control in those areas of Africa where the cassava green mite was causing economic damage.

A total of 87 phytoseiid species were collected and stored: 25 are new or unrecorded species; 66

were collected from cassava. The current predator mite reference collection held at CIAT conserves primarily those related to phytophagous mites found on cassava. A taxonomic key on the species associated with cassava is being prepared with Brazilian colleagues. The CIAT-Brazil collection is a true reference collection with accompanying database and can be readily used for species description. Explorations also identified several insect predators of cassava green mite, especially the staphylinid *Oligota minuta* and the coccinellid *Stethorus* sp. After extensive lab and field studies of this cassava green mite predator complex, it was generally agreed that the phytoseiid predators offer the best potential for controlling mites, especially when occurring in low densities. The phytoseiid development cycle is shorter than that of the cassava green mite. In studies at CIAT with the species *Neoseiulus anonymus*, the egg-to-adult development period at 25 and 30°C was 4.7 and 4.0 days, respectively. This is approximately half the development period for the cassava green mite at those temperatures. Survey data also revealed that cassava green mite densities were much higher in northeast Brazil than in Colombia, but the richness of phytoseiid species was greater in Colombia.

Field data from experiments in Colombia demonstrated that a rich phytoseiid species complex could reduce cassava green mite populations and prevent cassava yield loss. When natural enemies were eliminated by applying low doses of an acaricide that did not affect the cassava green mite population, cassava root yields were reduced by 33%. Application of an acaricide did not increase yields, indicating the effectiveness of biological control.

A major objective of the surveys for cassava green mite natural enemies and the substantial research that followed was to identify the key phytoseiid species controlling cassava green mite populations and introduce them into Africa. This was a collaborative effort between CIAT and EMBRAPA in the Americas and IITA in Africa. Of the phytoseiid species identified as feeding on CGM, those most frequently collected were *Typhlodromalus manihoti* (found in over 50% of the fields surveyed), *Neoseiulus idaeus*, *Typhlodromalus aripo*, *Galendromus annectens*, *Euseius concordis* and *Euseius ho*.

More than ten species of phytoseiids were shipped from Colombia and Brazil to Africa, via quarantine in England (IIBC-International Institute of Biological Control). None of the Colombian species became established, but three of the Brazilian species did (*T. manihoti*, *T. aripo* and *N. idaeus*). *Typhlodromalus aripo*, the most successful of the three species, has now spread and is found in more than 14 countries. *Typhlodromalus aripo* inhabits the apex of cassava plants during the day and forages on leaves at night; it can persist during periods of low cassava green mite densities by consuming alternative food sources (e.g., maize pollen). On-farm trials in Africa indicate that *T. aripo* reduces CGM populations by 35–60% and increases fresh root yield by 30–37%.

Neozygites sp. is a fungal pathogen (Zygomycetes: Entomophthorales) found on mites throughout cassava-growing regions of the Neotropics. Isolates of *Neozygites floridana* from Brazil and Colombia, and from *M. tanajoa* from Brazil and Benin were evaluated on the cassava green mite in Africa. Laboratory and field studies indicate that the Brazilian strain of *N. floridana* was the most virulent. Although this fungus shows considerable promise for biological control of the cassava green mite, further research and field evaluations are needed.

Exotic phytoseiid mite predators can play an important role in reducing CGM populations in Africa; however, field observations in the Neotropics indicate that they are very sensitive to disturbances in the agroecosystems, especially the use of pesticides. For example, when insecticides were applied at CIAT for controlling thrips, cassava green mite populations erupted, and few phytoseiid predators were detected in the fields. Studies in Colombia showed that low acaricide doses that did not cause mortality to cassava green mite were lethal to phytoseiids, causing a considerable increase in mite populations and cassava yield losses. In the Neotropics, especially on larger plantations, cassava farmers may use pesticides to control hornworm, whitefly or thrips outbreaks. This could result in mite outbreaks and yield losses if biological control is the only control measure, and highly susceptible cultivars are being grown.

Cassava Mealybugs

Although more than 15 species are reported attacking the crop, only two are important economically, *Phenacoccus herreni* and *P. manihoti*, both of Neotropical origin. *Phenacoccus manihoti* was introduced inadvertently into Africa in the early 1970s, where it spread rapidly across the cassava-growing regions of that continent, causing considerable yield loss. This species has been the object of a successful biological control program. In the Americas *P. manihoti* was first found in Paraguay in 1980 and later collected from certain areas of Bolivia and Mato Grosso do Sul state in Brazil, causing no economic damage. More recently (2005), *P. manihoti* was collected from two northeastern states, Bahia and Pernambuco.

The origin of *P. herreni* is probably northern South America, where it was found in cassava-growing regions of Colombia and Venezuela. It was first reported in northeast Brazil during the mid-1970s, where high populations caused considerable yield losses. Surveys in the region found few parasitoid natural enemies, suggesting that *P. herreni* is an exotic pest, probably coming from northern South America where parasitoids are frequently observed.

Damage

Both species cause similar damage: adult and nymph feeding causes leaf yellowing, curling and cabbage-like malformation of the apical growing points. High populations lead to leaf necrosis, defoliation, stem distortion and shoot death. Reductions in photosynthetic rate, transpiration and mesophyll efficiency – together with moderate increases in water-pressure deficit, internal CO_2 and leaf temperature – were found in infested plants. Yield losses in experimental fields at CIAT ranged from 68–88%, depending on cultivar susceptibility. Farmers in northeast Brazil estimated their losses to be over 80%, and cassava production decreased in the region during the 1980s. In Africa, yield losses due to *P. manihoti* feeding and damage were around 80%.

Biology and Behavior

Both species are morphologically similar and originally thought to be only one species. *Phenacoccus manihoti* is parthenogenic, whereas males are required for reproduction of *P. herreni*. The females deposit ovisacs containing hundreds of eggs on the undersides of leaves and around apical and lateral buds. Eggs hatch in 6–8 days, and there are four nymphal instars; the first instars are highly mobile and will spread over the plant or between plants. The fourth instar is the adult stage for females, while males have four nymphal instars plus the adult stage. The third and fourth instars occur in a cocoon, from which the winged male adults emerge, living only 2–4 days. The life cycle of the female is 49.5 days; that of the male, 29.5. The optimal temperature for female development is 25–30°C. Populations of both species peak during the dry season. The onset of rains reduces pest populations and plant damage, permitting some crop recovery.

Mealybug dissemination between regions, countries or continents is probably through infested stem cuttings. The introduction of *P. manihoti* into northeast Brazil from southern Brazil can probably be traced to the movement of cassava varieties between these two regions.

Management

Cassava mealybug management is a well-documented example of classical biological control, both in Africa and the Americas. In Africa, *P. manihoti* is being controlled successfully after introducing the parasitoid *Anagyrus lopezi* from the Neotropics. After several years of exploration in the Neotropics by scientists from IIBC, IITA and CIAT, the target species *P. manihoti* was finally located by a CIAT scientist (A.C. Bellotti) in Paraguay in 1980. IIBC collected natural enemies of *P. manihoti* that were sent via quarantine in London to IITA in Benin for multiplication and release in Africa. The encyrtid parasitoid *A. lopezi* and the coccinellid predators *Hyperaspis notata*, *Hyperaspis raynevali*, and *Diomus* sp. became established in Africa. The parasitoid is credited with being the principal agent reducing the mealybug populations. *Anagyrus lopezi* became established in all ecological zones occupied by *P. manihoti* and is now found in 27 countries, covering an area of 2.7 million km^2. Cassava losses have been reduced by 90–95% with an estimated savings of US$7.971–20.226 billion.

Surveys in Colombia and Venezuela identified numerous parasitoids, predators and entomopathogens associated with *P. herreni*. Several parasitoids show a specificity or preference for *P. herreni*: *Acerophagus coccois*, *Anagyrus diversicornis*, *Anagyrus putonophilus*, *Anagyrus isolitus*, *Anagyrus elegeri* and *Aenasius vexans*. Based on numerous field and lab studies, three encyrtid parasitoids (*A. diversicornis*, *A. coccois* and *A. vexans*) were identified as effective in *P. herreni* infestations. Comparative life-cycle studies show that they completed two cycles for each cycle of *P. herreni*. This is a favorable ratio for biological control. *Anagyrus diversicornis* prefers third instar nymphs, where as the smaller *A. coccois* parasitizes male cocoons, adult females and second instar nymphs. *Aenasius vexans* prefers second and third instar nymphs. Field studies with natural populations of *A. diversicornis* and *A. coccois* estimated *P. herreni* mortality at 55% for their combined action.

Through the combined efforts of CIAT and CNPMF/EMBRAPA, these three parasitoids were exported from CIAT to EMBRAPA, Brazil, where they were mass reared and released into *P. herreni*-infested cassava fields, primarily in the northeastern states of Bahia and Pernambuco from 1994 to 1996. More than 35,000 parasitoids were released, and all three species became established. Studies prior to release had determined that none of these species existed in this region. In Bahia, *A. diversicornis* dispersed 120 km in 6 months after release and 304 km in 21 months. *A. coccois* was recovered in high numbers 9 months later, 180 km from its release site. *Aenasius vexans* was consistently recaptured at its release site in Pernambuco, having dispersed only 40 km in 5 months.

Personal observations in recent years indicate that *P. herreni* populations have decreased considerably as cassava farmers in the region have not reported severe outbreaks and cassava cultivation has returned to areas where it had been previously abandoned due to *P. herreni* damage. However, the recent introduction of *P. manihoti* into the region has resulted in reports of severe mealybug damage in Bahia, causing alarm among cassava producers. An effort by local institutions and researchers is needed to determine if key *P. manihoti* parasitoids are present or need to be introduced into the region.

Thrips

Several species of thrips are reported feeding on cassava, primarily in the Americas. The most important include *Frankliniella williamsi*, *Corynothrips stenopterus*, *Scirtothrips manihoti*, *Caliothrips masculinus* and *Scolothrips* sp. More recently a new species of thrips (*Thrichinothrips strasser*) associated with cassava was reported from Costa Rica. *Frankliniella williamsi* is reported feeding on cassava in Africa, and high populations of *S. manihoti* have recently been reported from central Brazil. *Frankliniella williamsi* appears to be the most important species and the only one reported causing yield losses.

Damage

Frankliniella williamsi larvae and adults feed on the growing points and young leaves of cassava, which do not develop normally; leaflets are deformed and show irregular chlorotic spots. The rasping-sucking stylet-like mouthparts damage leaf cells during expansion, causing deformation and distortion; and parts of the leaf lobes are missing. Brown wound tissue appears on the stems and petioles, and internodes are shortened. Growing points may die, causing growth of lateral buds, which may also be attacked, giving the plant a witches'-broom appearance that can be confused with viral disease symptoms.

Yield reductions induced by *F. williamsi* range from 5–28%, depending on varietal susceptibility. The average reduction for eight varieties in Colombia was 17.2%. Thrips damage and yield reduction are especially pronounced in the seasonally dry tropics where the dry season is at least 3 months. Plants recover with the onset of the rainy season.

Management

Frankliniella williamsi is not considered a major pest of cassava as it is not often reported causing yield losses in farmers' fields. It can be controlled easily by using resistant pubescent cultivars. Approximately 50% of the CIAT cassava germplasm bank are pubescent, and resistant to *F. williamsi*. Resistance is based on leaf bud pilosity, and increasing pubescence of unexpanded leaves increases thrips resistance. Observations indicate that most landrace varieties grown by farmers in the seasonally dry lowland tropics are pubescent. It is hypothesized that cassava growers may have selected pubescent varieties over time for the absence of thrips damage.

Cassava Lacebugs

Reported as pests of cassava only in the Neotropics, five species of the genus *Vatiga* show a decided preference for feeding on cassava: *Vatiga illudens*, *V. manihotae*, *V. pauxilla*, *V. varianta* and *V. cassiae*. The first two are the most widely distributed and the most damaging to cassava. *Vatiga illudens* predominates in Brazil but also occurs throughout the Caribbean region and may be present in other areas. *Vatiga manihotae*, the most widespread lacebug, is consistently found on cassava in Colombia and Venezuela, but is also reported from Cuba, Trinidad, Peru, Ecuador, Paraguay, Argentina and Brazil. *Vatiga* spp. have also been reported feeding on wild species of *Manihot*. In 1985 the black lacebug, *Amblystira machalana*, was first observed causing damage to cassava in different regions of Colombia, Venezuela and Ecuador.

Damage

Lacebug adults and nymphs feed on the undersurface of lower and intermediate leaves, but can also damage upper leaves. Feeding by *Vatiga* spp. causes leaves to form yellow spots that eventually turn reddish brown, resembling *Tetranychus* mite damage. *Amblystira machalana* feeding is characterized by white feeding spots that increase in area until leaf centers turn white and eventually darken. High lacebug populations will cause leaves to curl and die, often resulting in defoliation of lower leaves. Higher populations are observed on younger plants (4–5 months) but decline as plants age.

The relationship between damage and population density and duration is not entirely understood. In recent field trials with natural populations of *A. machalana* at CIAT, yield losses ranged from 8.1–42.7%, depending on cultivar susceptibility and duration of lacebug attack.

Populations of *V. illudens* in Brazil are endemic and appear to be causing yield losses, especially in the central Campo Cerrado regions, although high populations are also reported from the south and northeast.

Biology and Behavior

Prolonged dry periods favor high populations of *V. illudens* and *V. manihotae*. In contrast, *A. machalana* attack can occur during both wet and dry seasons, but is more likely during rainy periods. Observations in Colombia indicate shifts in lacebug populations. *Vatiga manihotae* was the predominant species in the Cauca Valley until the mid-1980s. By 1990, *A. machalana* populations dominated. More recently, *V. manihotae* increased and is once again the predominant species, while *A. machalana* is difficult to find. The cause for this shift in populations is unknown. In Ecuador, populations of *A. machalana* remain high.

The egg stage of *V. manihotae* is 8–15 days, followed by five nymphal instars averaging 16–17 days; adult longevity was 40 days under field conditions. Laboratory studies with *V. illudens* in Brazil reported a nymphal duration of 13.5 days and an average adult longevity of 27 days. In lab studies with *A. machalana*, the egg stage averaged 8.2 days; the five nymphal instars, 14 days; average adult longevity was 22 days.

Management

Lacebugs are the least studied of the important cassava pests, so considerable research is required before sound and efficient management practices can be recommended. These studies should be conducted in Brazil where *V. illudens* is endemic. Lacebug control appears difficult as few natural enemies have been identified, and chemical control should be avoided. In Colombia and Ecuador, observations indicate that *V. manihotae* or *A. machalana* populations are not high enough to warrant pesticide applications. Preliminary screening of cassava germplasm in Brazil and Colombia indicates that HPR may be available, but no germplasm development program is attempting to develop resistant cultivars. In insectary studies in Brazil using caged *V. illudens*-infested plants, isolates of the fungal entomopathogens *Metarhizium anisopliae* and *Beauveria bassiana* caused 100 and 74% mortality of the lacebugs, respectively, indicating the potential of these fungi for lacebug control.

Cassava Hornworms

Several lepidopterans feed on cassava, the most important being the cassava hornworm, *Erinnyis ello*, which causes serious damage to cassava in the Neotropics and has a broad geographic range, extending from southern Brazil, Argentina and Paraguay to the Caribbean Basin and southern USA. The migratory flight capacity of *E. ello*, its broad climatic adaptation, and wide host range probably account for its wide distribution. Several other species of *Erinnyis* (*E. alope*, and subspecies *E. ello ello*, *E. ello encantado*) are reported feeding on cassava in the Neotropics, but they appear to be of minor importance and do not cause economic damage to the crop.

Damage

Hornworm larvae feed on cassava leaves of all ages, and high populations will also consume young, tender stems and leaf buds. Severe attacks cause complete plant defoliation, bulk root loss and poor root quality. In farmers' fields, natural attacks resulted in 18% yield loss; simulated damage studies resulted in 0–64% root loss, depending on number of attacks, plant age and edaphic conditions. Repeated attacks are more common when poorly timed pesticide applications fail to destroy fifth instar larvae or prepupae. Frequent attacks often occur on larger plantations (over 100 ha), where subsequent populations can oviposit and feed on areas not previously defoliated. Severe attacks and complete defoliation do not kill cassava because carbohydrates stored in the roots enable recovery, especially during the rainy season.

Biology and Behavior

Although hornworm outbreaks are sporadic, they mostly occur during the rainy season when foliage is abundant. The grey, nocturnal, migratory adult moths have strong flight abilities. *Erinnyis ello* females oviposit small, round, light green to yellow eggs individually on the upper surface of cassava leaves. In field cage studies, females oviposited an average of 450 eggs, although as many as 1,850 eggs/female were observed. This high level oviposition, combined with the mass migratory behavior of adults, helps explain the rapid buildup of hornworm populations and their sporadic occurrence. During the larval period, each hornworm consumes about 1,100 cm^2 of foliage, about 75% of this during the fifth instar. At 15, 20, 25 and 30°C, the mean duration of the larval stage is 105, 52, 29 and 23 days, respectively, indicating that their peak activity may occur at lower altitudes or during the summer in the subtropics. When considerable leaf area is present, up to 600 eggs may be found on a single plant, and larval populations may exceed 100 per plant. It is estimated that 13 fifth instar larvae can defoliate a 3-month-old plant in 3–4 days, especially on low fertility soils. Given the foregoing, hornworm outbreaks must be controlled when populations are in the early larval stage.

Management

The migratory behavior of hornworm adults makes effective control difficult to achieve and reduces the impact of natural biological control. Insect migration has been described as an evolved adaptation for survival and reproduction, and some researchers speculate that the hornworm's migration evolved as a mechanism to survive low food availability, unfavorable environmental conditions and attack by natural enemies. It is important to detect hornworm outbreaks while in the early development stages. Successful control requires monitoring field populations to detect migrating adults, oviposition or larvae in the early instars. This can be done with black light traps for adults or by scouting fields for the presence of eggs and larvae.

Pesticides give adequate control if applied when hornworm populations in the early larval instar stages are detected and treated. Larval populations in the fourth and fifth instars are difficult to control. Farmers often react only when considerable defoliation has occurred, with excessive, ill-timed costly applications that can lead to repeated or more severe attacks. Pesticide use may also disrupt natural enemy populations, leading to more frequent attacks, a common occurrence on larger plantations.

More than 30 species of parasites, predators and pathogens of the egg, larval and pupal stages have been identified and reviewed extensively; however, their effectiveness is limited, most likely due to the migratory behavior of hornworm adults. Eight microhymenopteran species of the families Trichogrammatidae, Scelionidae and Encryrtidae are egg parasites, of which *Trichogramma* and *Telenomus* are the most important. In recent field surveys during a hornworm outbreak at CIAT, egg parasitism reached 68%, 57% due to *Trichogramma* sp. and 11% to *Telenomus* sp. Tachinid flies are important dipteran larval parasitoids and the Braconidae, especially *Cotesia* spp., are the most important hymenopteran. *Chrysopa* spp. are common egg predators while important larval predators include *Polistes* spp. (Hymenoptera: Vespidae) and several spider species. Important entomopathogens include *Cordyceps* sp. (Aconycites: Clavicipitaceae), a soil-borne fungus that invades hornworm pupae causing mortality. Recent lab studies show that certain isolates of *Beauveria* sp. and *Metarhizium* sp. cause high larval mortality. Hornworm outbreaks can be controlled with timely (early instars) applications of commercial biopesticides of *Bacillus thuringiensis*.

The effectiveness of biological control agents in a hornworm management strategy depends on the ability to synchronize the release of large numbers of predators or parasitoids to augment natural biological control. Predator and parasitic effectiveness in hornworm control is limited by poor functional response during outbreaks, which are of short duration (15 days). In the absence of a reliable commercial source of *Trichogramma* or other parasitoid or predator species, the cost of maintaining these natural enemies in continuous culture to guarantee availability when an *E. ello* outbreak occurs is economically prohibitive and impractical for most cassava farmers.

The complexities of inundatory releases of parasitoid and predator species suggest the need for a cheap, storable biological pesticide. A granulosis virus of the family Baculoviridae was found attacking *E. ello* in cassava fields at CIAT in the early 1970s. Pathogenicity studies using virus material extracted from infected larvae collected in the field were carried out on cassava plants in the lab and field. Larval mortality reached 100% at 72 h after application. Studies on the effect of virus concentration on mortality of larval instars showed a sigmoidal relationship for the first, second and forth instars. LD_{50} studies show that progressively higher concentrations are needed for adequate control of each succeeding larval instar. Most fifth instar larvae reached the prepupal stage, but few female adults emerged and those that did had wing deformities and died without producing progeny.

Although the baculovirus can be managed by small farmers, this technology has been most successful with larger producers or where research and extension services have provided access to it. Growers can collect and macerate diseased larvae and apply the virus suspension to cassava fields. The virus can be stored for several years under refrigeration, and for a few months at room temperature. Hornworm management with the baculovirus was implemented in southern Brazil during the late 1980s and early 1990s. Researchers and extension workers trained farmers in the handling and use of the virus and distributed free samples. By 1991 the virus was being applied on about 34,000 ha in Paraná state at a cost of only about US$1/ha. In Santa Catarina state, virus applications to early instars resulted in almost complete control, and pesticide applications were reduced by 60%.

In Venezuela, where the hornworm is endemic, the virus preparation was applied (70 ml/ha) to large cassava plantations (7,000 ha) via overhead sprinkler irrigation systems when larvae were in the first and second instars. This not only resulted in 100% control but also eliminated pesticides; the cost of gathering, processing, storing and applying the virus preparation was only US$4/ha.

In Colombia, a baculovirus biopesticide was developed by a private company (Biotropical) in collaboration with CIAT. The product has been approved for commercial release by MADR and is available as a wettable powder. Field trials to evaluate the efficacy of this product (Bio Virus Yuca®) were carried out in two locations in Colombia: the provinces of Tolima and Risaralda. During natural hornworm attacks, the baculovirus applications (300 g/ha) resulted in 93% hornworm mortality in Tolima and 85% in Risaralda.

The key to effective hornworm control is training farmers to detect outbreaks through light trapping of adults or field monitoring combined with the timely application of a biopesticide (or chemical insecticide) when larvae are in their early instars (1–3).

Stemborers and Stem Feeders

Numerous insect species can feed on and damage cassava stems and branches. Although some species are nearly worldwide in distribution, the most important are in the Neotropics. Four pests will be discussed in this section: stemborers, scale insects, fruit flies and shoot flies. Several other pests can also damage the stem (e.g., mites, thrips, mealybugs, hornworms and grasshoppers); however, they are primarily leaf feeders and are discussed elsewhere. Dipteran fruit flies (*Anastrepha* spp.) and shoot flies (*Neosilba* sp.) can also bore into the stem and are discussed here.

Stemborers can damage cassava in two ways; they can (i) weaken the plant by tunneling in the stems, causing breakage that will reduce yields, and (ii) destroy or reduce the quality of stem cuttings, thereby affecting germination and vigor of the planting material.

Stemborers

A complex of arthropod stemborers that includes both lepidopteran and coleopteran species feed on and damage cassava. In the Neotropics stemborers are most important in Colombia, Venezuela and Brazil. Seven species of *Coelosternus* (Coleoptera: Curculionidae) can reduce cassava yields and quality of planting material in Brazil; however, the damage is generally sporadic and localized, and significant yield losses are not reported. Although stemborer species have been identified in Africa, there are no reports of severe damage or yield losses.

Populations of the stemborer *Chilomima clarkei* (Lepidoptera: Pyralidae) have increased dramatically in Colombia and Venezuela in recent years, to the point where it is now considered an important pest of cassava, causing yield losses and damage to stem cuttings. On the Atlantic coast of Colombia (provinces of Magdalena and Cesar), *C. clarkei* damage was detected in 85% of the cassava plantations surveyed.

Damage

Chilomima clarkei populations can occur throughout the year but are higher during the rainy season. From 4–6 overlapping cycles can occur during the 1-year crop cycle, increasing potential damage and making control more difficult. Stem breakage can occur when there is extensive tunneling by larvae. When over 35% of the plants suffer stem breakage, yield losses range from 45–62%. Larval tunneling can also lead to stem rot and a reduction in the quantity and quality of planting material. Attacks are easily detected by the presence of excreta, sawdust and exudates ejected from burrows made in infested stems.

Biology and Behavior

Adult females are nocturnal and oviposit in cassava stems, usually around the bud or node. The tan-colored females can oviposit more than 200 eggs in a 5–6 day period. The egg stage averages 6 days (28°C). The highly mobile first instar larvae feed on the outer bark or stem epidermis. Upon finding an appropriate feeding site, usually around lateral buds, the larvae form a protective web, under which the first four instars feed, enlarging the web with each instar. Stem penetration occurs during the fifth instar larval stage. Extensive tunneling can occur as the larval cycle is completed (6–12 instars). Pupation occurs in the stem and winged adults emerge. The larval stage is 32–64 days, followed by the pupal stage (12–17 days). Female adults live 5–6 days; males, 4–5 days.

Management

Stemborer control is difficult once the larvae enter the stem and tunneling begins. In addition, the web formed by the early larval stages acts as a protective devise against natural enemies and pesticide applications. The mobile first instar larvae are vulnerable and more exposed to both natural enemies and pesticides. Biopesticides such as *Bacillus thuringiensis* (Bt) are recommended; however, with overlapping generations, several applications may be required, which would be too costly for small producers. Intercropping with maize will reduce *C. clarkei* populations, but only until the intercrop is harvested.

Cultural practices such as selection of clean cuttings and burning plant residues, especially stems and branches, are recommended for reducing stemborer populations. Natural enemies such as hymenopteran parasitoids (*Bracon* sp., *Apanteles* sp., *Brachymeria* sp., *Tetrastichus howardi* and *Trichogramma* sp.) have been identified, but their role in regulating stemborer populations has not been investigated. The fungal entomopathogens *Metarhizium anisopliae* and *Beauveria bassiana* have been identified as possible biological control agents.

CIAT has worked on identifying cassava germplasm resistant to *C. clarkei*. More than 1,000 genotypes have been evaluated on the Colombian Caribbean coast, where *C. clarkei* populations are consistently high. Evaluations are based on the number of holes and tunnels and percent stem breakage. Genotypes with 0–1 holes/stem indicate varietal influence and the need for further evaluation. As natural field populations of *C. clarkei* are used in these evaluations, results may be misleading because genotypes exhibiting low infestation may be "escapes" (i.e., have avoided damage by chance). CIAT has initiated research to introduce insect-resistant Bt genes through *Agrobacterium*-mediated transformation into cassava embryonic tissue to develop resistant cultivars.

Scale Insects

Several species of scales are reported attacking cassava stems and leaves in the Americas, Africa and Asia. Although reductions in yield due to scale attack have been reported, they are not considered to be serious pests of cassava. The most important species are *Aonidonytilus albus* and *Saissetia miranda*. *Aonidonytilus albus* has been reported on cassava throughout most of the cassava-growing regions in the world and is considered the most widely distributed cassava pest. It is easily disseminated from one region to another through stem cuttings, which probably accounts for its wide distribution.

Damage

Outbreaks are more severe during the dry season. Their incidence increases when scale-infested stem cuttings are used for planting material. High *A. albus* populations may cover the stem and lateral buds. Leaves on heavily infested stems yellow, and defoliation can occur. With severe attacks the plants are stunted and stems can desiccate, leading to plant mortality. Some scale species can attack the leaves, but the greatest damage appears to be the loss of planting material. The germination of heavily infested cuttings is greatly reduced; when they do germinate, the roots are poorly developed, reducing plant vigor. Yield losses of 19% were recorded at CIAT on plants heavily infested with *A. albus* and there was a 50–60% loss in germination.

Management

The most effective means of control is through the use of clean, uninfested planting material and destroying infested plants to prevent the spread of infestation. Stem cuttings for vegetative propagation should be carefully selected from uninfested plants. The mussel-shaped *A. albus* grey to white female is difficult to detect, especially when populations are low and attached to stems around the lateral buds.

Treating stem cuttings that have originated from fields with scale attack is highly recommended. Dipping the cuttings in a pesticide emulsion for 5 min is effective against light *A. albus* infestations. Heavily infested cuttings should not be sown as they will germinate poorly even if treated with a pesticide. Storing healthy cuttings with infested ones will increase dissemination and infestation as the first nymphal instars (crawlers) are highly mobile.

Fruit Flies

Two species of fruit flies, *Anastrepha pickeli* and *Anastrepha manihoti* (Diptera: Tephritidae:), whose origin is the Neotropics, are reported to attack cassava fruits from several regions of Central and South America. *Anastrepha montei* is reported infesting seed capsules in Costa Rica. Infestation of cassava fruits causes no economic damage and is of no concern to cassava producers. When oviposition occurs in the fruit, the larvae bore throughout the fruit, destroying the developing seed, which is a problem for plant breeders.

With respect to damage, the tan to yellow colored females will oviposit in the tender upper portion of the cassava stem in certain areas during the rainy season. The developing larvae become stemborers, tunneling into the apical stem, which provides an entrance for soft rot bacteria such as *Erwinia caratovora*, resulting in severe rotting of stem tissue and apical dieback. Several larvae may be found in one stem; their presence can be noted by the white liquid exudate that flows from their tunnel. Damage is more severe on younger (2–5 months) plants. Nevertheless, the plants can recover from fruit fly damage. Yield losses have not been reported, but there is a reduction in the quality of stem cuttings for planting material. When there is severe damage to the pith region of the stem, there is a reduction in germination. Yield losses can occur if severely damaged cuttings are used as planting material. It is therefore important that only stem cuttings without damage to the pith regions be sown for vegetative propagation.

Shoot Flies

Damage has been observed in most of the cassava-growing regions of the Americas but has not been reported from Africa or Asia. The most important species are *Silba pendula* and *Neosilba perezi* (Diptera: Lonchaeidae). Severe attacks have been reported from Cuba, southern Brazil and parts of Central America, especially Costa Rica.

Damage

Larval feeding damage is manifested by a white to brown exudate flowing from cassava growing points, which eventually die. This breaks apical dominance, retards plant growth, and causes germination of side buds which leads to excessive branching. The dark metallic blue *S. pendula* adults deposit eggs in the growing points between the unexpanded leaves, and the young larvae tunnel in the soft tissue, eventually killing the apical bud. Attacks may occur throughout the year but are more prevalent at the onset of the rainy seasons and on recently germinated or young plants, resulting in a reduction in growth of the stems used for planting material. Yield is seldom affected.

Management

If plants are being grown for quality cuttings, the crop needs to be protected only during the first 3 months of growth. Usually one timely pesticide application suffices to protect the crop.

Soil-Borne Pests

The majority of the arthropod pests of cassava are "source" pests, feeding on leaves and stems, which causes indirect damage by reducing root yield. Few are "sink" pests, which cause direct, irrevocable damage to the edible roots. The most important and damaging root feeders appear to be generalists, and there is a hypothesis that cyanogenic potential in cassava is a defense mechanism against them. All cassava varieties have a high cyanogenic potential in leaves, stems and root peel. It can also be theorized that the root peel acts as a protective device, especially in those varieties with low cyanogen levels in the root parenchyma. Three soil-borne pests are discussed here: the burrower bug, white grubs (several species) and root mealybugs.

Cassava Burrower Bug

First recorded as a pest of cassava in Colombia in 1980, *Cyrtomenus bergi* (Hemiptera-Heteroptera: Cydnidae) appears to be native to the Neotropics, is a polyphagous feeder that attacks a wide range of crops, and is one of the few arthropod pests that feeds on the tuberous root of cassava. Additional hosts include onions, peanuts, maize, potatoes, *Arachis pintoi* (forage peanuts), sorghum, sugarcane, coffee, asparagus, beans, peas, pastures and numerous weeds. It has also been reported feeding on cassava in Venezuela, Costa Rica, Panama and Brazil (states of São Paulo and Pará).

Cassava is not the optimal host for *C. bergi*. Fecundity, survival and intrinsic rate of population increase were highest on peanuts and forage peanuts, followed by maize. Sweet cassava, sorghum and onions are not favorable hosts, and *C. bergi* could not complete its life cycle on bitter cassava.

Damage

Cyrtomenus bergi nymphs and adults feed on cassava roots by penetrating the peel and parenchyma with their strong thin stylet, leaving fine lesions in the plant tissue. This feeding action permits the entrance of several soil-borne pathogens (e.g., *Aspergillus*, *Diplodia*, *Fusarium*, *Genicularia*, *Phytophthora* and *Pythium* spp.), causing local rot spots on the parenchyma. The brown to black lesions begin to develop within 24 h after feeding is initiated.

In cassava, a quantitative scale to assess root damage was established, using a 1–5 rating based on the percentage of the parenchyma surface covered by rot lesions (1 = no damage, 2 = 1–25%, 3 = 26–50%, 4 = 51–75% and 5 = 75–100%). Studies show that even low *C. bergi* populations (close to zero) can cause more than 20% of the root to be covered with rot lesions. The darkened lesions on the white root parenchyma are not acceptable for the fresh consumption market; middlemen reject shipments of root with 20–30% damage, which translates into 100% loss for the farmers. Field trials in Colombia showed that damage can reach 70–80% of total roots, with more than a 50% reduction in starch content, thereby reducing the commercial value for the processing industry. As damage is not detected until roots are harvested and peeled, producers can lose the value of the crop as well as labor, time and land use.

Biology and Behavior

Cyrtomenus bergi has five nymphal instars. It had a lifespan of 286–523 days when fed on slices of low-HCN cassava roots in the lab (23°C, 65 ± 5% RH). Egg eclosion averaged 13.5 days; mean development time of the five nymphal stages was 111 days; mean longevity for adults was 293 days.

Cyrtomenus bergi is strongly attracted to moist soils, and populations can occur in the soil throughout the crop cycle. It will migrate when soil moisture content is below 22% and is most persistent when it exceeds 31%. Thus, the rainy season greatly favors adult and nymphal survival, behavior and dispersal, whereas there is increased nymphal mortality during the dry season.

Feeding preferences may be related to levels of cyanogenic glucosides in the cassava roots. Adults and nymphs that fed on high-HCN (>100 mg/kg) cultivars had longer nymphal development, reduced egg production and increased mortality. Oviposition on CMC 40 (43 mg HCN/kg) was 51 eggs/female versus only 1.3 on MCol 1684 (627 mg HCN/kg). Adult longevity on CMC 40 (235 days) was more than twice that on MCol 1684 (112 days). Additional studies indicate that the earliest instars are most susceptible to root cyanogenic potential (CNP). Due to the short length of the stylet, feeding during the first two instars is confined mainly to the root peel, whereas third to fifth instars can feed on the root parenchyma. CMC 40 has a low cyanogen level in the root parenchyma, but a high level in the root peel (707 mg HCN/kg). Feeding experiments in the lab resulted in 56% mortality of first and second instar nymphs feeding on CMC 40 and 82% for those feeding on MCol 1684. The high cyanogen level in the peel of CMC 40 is probably responsible for the high mortality.

Feeding preference studies carried out in the field in Colombia show that low HCN cultivars suffer more damage than high-HCN ones. Three cassava varieties – MCol 1684 (high CPN), MMex 59 (intermediate CPN) and CMC 40 (low CPN) – were evaluated in field studies to determine the effect of CPN on *C. bergi* root damage. Ten months after planting, root damage on the low, intermediate and high CPN varieties was 85, 20 and 4%, respectively. These data indicate that CPN may act as a feeding deterrent and that *C. bergi* should not be a problem where cassava with high CNP is cultivated (i.e., northeast Brazil and many parts of Africa). However, in many cassava-producing regions, low CNP or "sweet" varieties are preferred, especially for fresh consumption or starch markets.

Management

Cyrtomenus bergi can be the target of extensive chemical control, given the nature of the damage it causes to cassava as well as other crops. For example, in Colombia, control of *C. bergi* on crops such as onions, peanuts and coriander requires considerable pesticide use, with only marginal results. In cassava, pesticide use can reduce populations and damage; however, frequent applications may be required and they are costly and often fail to reduce damage below economic injury levels.

Cyrtomenus bergi control is difficult due to the polyphagous nature of the pest and its adaptation to the soil environment. As the initial damage can occur early in the crop cycle, control methods should be implemented either prior to or at planting, or during the first 2 months of crop growth. Intercropping cassava with *Crotalaria* sp. (sunn hemp) reduced root damage to 4% versus 61% damage in cassava monoculture. This practice also reduces cassava yields by 22%; because *Crotalaria* has little commercial value, this technology has not been readily adopted by producers.

Recent research indicates that there is considerable potential for biological control of *C. bergi*. Isolates of native Colombian strains of the entomopathogenic fungi *Metarhizium anisopliae* and *Paecilomyces* sp. have been evaluated in the laboratory. An isolate of *M. anisopliae* infecting *C. bergi* in the field resulted in 61% mortality of fifth instar nymphs and an overall mortality of 33%. More recent studies with *M. anisopliae* strains CIAT 224 and CIAT 245 caused mortalities of 34.7% and 49.3%, respectively.

Applications of *M. anisopliae* (Isolate CIAT 224), combined with a sublethal dose of the insecticide imidacloprid, were evaluated in the laboratory and greenhouse. *Cyrtomenus bergi* nymphal mortality was always significantly higher when *M. anisopliae* was applied in combination with imidacloprid, compared to applications of the fungus alone (80.3% vs. 34.2%). Thus, entomopathogens combined with sublethal doses of insecticides such as imidacloprid can be an effective tool in an IPM strategy for controlling *C. bergi* or other soil-borne pests; however, field studies are required before acceptable technologies can be recommended.

Several species of nematodes have been identified parasitizing *C. bergi*. *Steinernema carpocapsae* successfully infected *C. bergi* in the laboratory, resulting in 59% parasitism after 10 days. Strains of *S. feltiae* and a native species of Colombia, *Heterorhabditis bacteriophora*, were compared in greenhouse studies with *C. bergi* adults. The penetration rate for *S. feltiae* was 93.9%, compared to 72.1% for *H. bacteriophora*. However, *H. bacteriophora* caused higher mortality (42.2%) than *S. feltiae* (8.6%) after 15 days. Field studies are needed to evaluate the potential of *H. bacteriophora* and other nematode species in an IPM strategy.

White Grubs

A complex of rhizophagous white grubs (Coleoptera: Scarabaeidae) is associated with the cassava crop in many regions of the Americas, Africa and Asia. White grubs are classified as hemi-edaphic (along with ants and termites) as they spend only a portion of their life cycle in the soil. It is during their larval stages in the soil that they can damage the cassava crop; the adult scarab beetles are not reported feeding on the aboveground organs of the plant. Recent surveys in cassava-growing regions of Colombia showed that white grubs were well represented in the edaphic communities associated with the crop. In Risaralda province, 1,858 white grubs (eight species) were collected from cassava plots. It is often difficult to distinguish the species actually causing damage to the crop. The genus commonly associated with damage to cassava in the Neotropics and Africa is *Phyllophaga* spp. *Leucopholis rorida* is reported causing damage to cassava in Indonesia and other countries in Asia.

Damage

Severe attacks of white grubs can destroy the stem cuttings used to establish new plantations. In one field study in Colombia there was a 95% loss in stem cutting germination due to white grub attack. Grubs feed on the bark, pith and buds of stem cuttings, hindering germination. They also can cause plant death by feeding on the basal part of young stems.

Recent studies in Colombia on *Phyllophaga menetriesi* with potted cassava plants under controlled conditions showed that one larva caused a 30% reduction in plant survival and three larvae per plant destroyed 50% of the plants in 56 days. White grub feeding damage has also been observed on the roots including the swollen tuberous root.

Biology and Behavior

Laboratory studies with *P. menetriesi* resulted in an average of 13 days for the egg stage and 19, 27 and 175 days for the first, second and third instars, respectively. After the third instar, the larvae entered a diapause stage averaging about 30 days, followed by a pupal stage averaging 34 days. Adults remained in the pupal chamber for about 73 days, followed by a 15-day flight period. The complete egg-to-adult cycle of *P. menetriesi* averaged 386 days.

Phyllophaga menetriesi is mostly observed at altitudes between 1,000–1,600 m, and damage to cassava is primarily during the rainy months when the crop is planted and early growth occurs.

Management

White grubs populations can often be detected during land preparation prior to planting. Farmer surveys in a major cassava-growing region in Colombia (Risaralda and Quindio provinces) disclosed that 71% of the farmers applied pesticides to control soil pests, while only 14% used biological control. Biological control through the use of entomopathogenic nematodes and fungi offers promise for white grub control. A native Colombian strain of *Heterorhabditis* sp., when applied in high doses (10,000 infective juveniles/ml) to first and second instar larvae of *P. menetriesi* in lab studies, resulted in 88.3 and 83.4% mortality, respectively. In lab studies at CIAT, several isolates of *M. anisopliae* caused high levels of mortality of *P. menetriesi*. Two isolates (CIAT 515 and CIAT 418) caused more than 60% white grub mortality. Isolate CIAT 515, in combination with a low rate of imidacloprid, resulted in 90% mortality of second instar larvae. The effectiveness of these biological control agents needs to be tested in farmers' fields before they can be recommended as part of a white grub management strategy.

Cassava Root Mealybugs

Two mealybug species have been reported feeding on and causing damage to cassava roots. In South America, *Pseudococcus mandio* (Hemiptera: Pseudococcidae) has been recorded from southern Brazil, Paraguay and Bolivia; it is reported as causing root damage only in Brazil. *Stictococcus vayssierei* (Hemiptera: Stictococcidae) is reported from the Cameroon and neighboring Central African countries. *Stictococcus vayssierei* is referred to in the literature as the root mealybug, the root scale or the brown root scale insect of cassava.

Pseudococcus mandio can result in reduced quality of tuberous roots and cause some plant defoliation. Females have three nymphal instars, and adults oviposit an average of 300 eggs, indicating a capacity for rapid population increases. The life cycle from oviposition to adult was 25 days for females and 30 for males. Yields losses of 17% have been reported in southern Brazil.

Stictococcus vayssierei larvae and adults attack young feeder roots on germinating stem cuttings, resulting in defoliation, wilting, tip dieback and plant death. Mature tuberous roots are often small, covered with mealybugs, and unattractive for the commercial market. Females (males are rare) are dark red in color, circular and flattened. Eggs are protected by wax threads secreted beneath the female body. Larvae are creamy white and mobile. *Stictococcus vayssierei* infestation is severest during the dry season and on unfertile, lateritic and clay soils. Infestations were more severe when cassava was planted on flat lands than when planted on ridges. Plant vigor and root yield improved by approximately 22% when planted on ridges. Intercropping favored higher mealybug infestations than cassava grown in monoculture.

Adequate control measures have not been determined for either species. Recommendations for management of *S. vayssierei* in the Cameroon include planting on ridges and monocropping cassava.

Secondary Pests

Numerous species of arthropods feed on cassava without causing major economic damage to the crop. These occasional or incidental pests may occur sporadically or at such low population levels that yield is not affected. If their populations increase or outbreaks occur in localized areas, some of these pests could cause yield losses. These secondary pests discussed briefly here include gall midge, termites, leaf hoppers, leaf-cutting ants and grasshoppers.

Grasshoppers

Zonocerus elegans and *Zonocerus variegatus* are potentially the most destructive of this group. They attack cassava primarily in Africa and are rarely reported feeding on cassava in the Neotropics (occasionally from Brazil). Several African countries including Nigeria, Congo, Benin, Uganda, Ivory Coast, Ghana and Central Africa report thousands of hectares of cassava defoliated in some years, probably causing yield reductions.

Damage

Grasshoppers feed on the leaves, causing defoliation, but during outbreaks the young tender bark can be stripped. Young plants are preferred and attacks are more severe during the dry season. Yield losses as high as 60% have been estimated.

Biology and Behavior

In Nigeria, grasshopper oviposition usually occurs at the onset of the rainy season; eggs hatch at the start of the dry season (6–7 months later). This population attacks cassava as the dry season progresses when other preferred herbaceous food plants become scarce. Experiments show that large amounts of HCN in the leaves can act as a deterrent to grasshopper feeding. The early instars (1–4) will not consume growing cassava, while instars 5 and 6 will eat it only if deprived of other food sources. Wilted cassava leaves are readily consumed by all stages and result in a high grasshopper growth rate.

Control

Chemical control of grasshoppers is feasible but may not be financially or ecologically sustainable, especially for small, resource-limited farmers. It is not considered an effective mid- or long-term solution as pesticide applications may lead to a resurgence of other pests such as the cassava mealybug or the cassava green mite when their natural enemies are killed indiscriminately.

Biological control with fungal entomopathogens offers a more effective long-term solution for grasshopper control. *Metarhizium anisopliae* var. *acridum* (also known as *M. flavoviride*), *Beauveria bassiana* and *Entomophaga grylli* have been identified infecting *Z. variegatus*. Efforts are currently underway to develop effective biopesticides for grasshopper control. Results with *M. anisopliae* have been encouraging.

Gall Midges

Iatrophobia brasiliensis (Diptera: Cecidomyiidae) has been recorded on cassava only in the Americas. They are considered of little economic importance and do not require control. However, the yellowish green or red galls on the upper leaf surface are highly visible to farmers, who may apply pesticides. A severe attack, especially on young plants, may cause leaf yellowing, and retarding of plant growth has been reported. Destruction of infested leaves is recommended to reduce midge populations.

Leaf-cutter Ants

Several species of leaf-cutter ants (genera *Atta* and *Acromyrmex*) are reported feeding on cassava in the Neotropics, especially in Brazil. Commonly reported species are *Atta sexdens*, *Atta cephalotes* and *Acromyrmex landolti*. Ants cut semicircular pieces of leaves, which they carry to their underground nests. Cassava plants can be completely defoliated when a large number of worker ants attack a crop. Outbreaks occur most frequently during the early months of crop establishment, but plants usually recover from ant damage. Recent field trials in Venezuela resulted in a 55% reduction in root yield due to leaf-cutter ant defoliation. Ant nests are usually visible because of the mound of soil deposited around the hole. Control of leaf-cutter ants is difficult; toxic baits are recommended.

Termites

Termites are reported as pests in several cassava-growing regions of the world, but primarily in Africa. They attack cassava mainly in the tropical lowlands, feeding on stem cuttings, feeder roots, swollen roots or growing plants. In Colombia, termites have been observed causing losses in germination as well as death of young plants, especially in regions with sandy soils. Feeding on swollen roots can lead to root rot (due to soil pathogens) damage. Losses in germination of 30% and 50% loss in stored planting material have been recorded. Control in the field is difficult, but stored planting material can be protected with an application of an insecticide dust.

Leafhoppers

Several species have been collected feeding on cassava. Several collections have been made by CIAT in Colombia, and numerous specimens from three families (Cicadellidae, Cixiidae and Delphacidae) are being identified. None is considered to be a pest causing yield losses, and all are usually observed in low populations. However, several of these species are being studied as possible vectors of cassava frog skin disease (CFSD), which probably originated in the Amazon regions of South America and has now spread to several countries in the region causing considerable crop loss. The disease has been described as a virus of the family Reoviridae and/or phytoplasm. Damage is characterized by the suberization and thickening of the swollen root epidermis, resulting in low production of little commercial value. Several species have now been mass reared, and vector-transmission studies are being carried out.

Future Trends and Considerations

The success of an ecologically oriented IPM program for cassava requires the implementation of a strategy that minimizes or prevents chemical pesticide use. Given the increased emphasis on commercial-scale plantations, where the crop has a high commercial value, there is a tendency to apply pesticides when noticeable crop damage occurs. Pests that trigger pesticide application include the cassava hornworm, whiteflies, mites, white grubs, burrower bugs, mealybugs and thrips.

Crop-protection technologies based on host plant resistance, microbial and arthropod biological control agents, together with appropriate agronomic practices, should be developed and implemented. This holistic approach has formed the basic philosophy for IPM research at international agricultural research centers such as CIAT and IITA, as well as in several national research programs such as EMBRAPA (Brazilian Agricultural Research Corp., Brasilia, Brazil), NARO (National Agricultural Research Organization, Uganda).

CIAT, IITA and the Brazilian national program EMBRAPA maintain large germplasm banks that offer entomologists and breeders a potential pool for pest-resistance genes. Traditional farmers will adopt new varieties cautiously if they are adapted to local agroecological and socioeconomic conditions. New or introduced varieties should not be highly susceptible to major pests in a given region. In the Neotropics this is especially true for mites, whiteflies, thrips and mealybugs.

Biological control agents have been identified for many of the cassava arthropod pests; however, the efficacy of naturally occurring biocontrol agents to maintain pests below economic damage levels has not been well documented. Classical biological control has been successful in Africa against two introduced pests from the Americas, the cassava mealybug (*P. manihoti*) and the green mite (*M. tanajoa*). Although natural biological control is probably effective in controlling some pests in the Neotropics, pest outbreaks and subsequent yield losses continue to occur. For example, the hornworm *Erinnyis ello* has a large complex of natural enemies including predators, parasites and pathogens; however, they are not effective in maintaining the hornworm below the economic injury level. The adult's migratory abilities and sporadic attacks serve as a defense against the more than 30 natural enemies. The stemborer *Chilomima clarkei* causes considerable damage in certain regions of Colombia, but effective natural enemies have not been identified. In recent years whitefly populations and damage have increased in several regions of the Neotropics as well as in Africa, causing considerable yield reduction. Several natural enemies have been identified, but their role in a biological control program has not been determined.

It should be kept in mind that in cropping systems where cassava is grown as a functional perennial, certain pests and their associated natural enemies may be in equilibrium. When cassava is grown year round in the tropics, often with overlapping cycles, pest species may be present throughout and thereby able to increase rapidly when environmental conditions become favorable to their dynamics. Natural enemy populations may not respond rapidly enough to suppress the increasing pest populations so outbreaks occur. Populations of mites, mealybugs, lacebugs and whiteflies, although present in the subtropics of the Americas, do not increase as rapidly or reach the levels of their counterparts in the tropical regions. During the "winter" months in subtropical regions, cassava will lose most or all its foliage. This can cause considerable reduction in pest populations so any increases may be retarded when warmer, more favorable, growing conditions return in the spring.

Biotechnology tools offer the potential for developing improved pest-resistant cultivars and enhancing the effectiveness of natural control organisms including parasitoids and entomopathogens. Wild *Manihot* species are a rich source of useful genes for the cultivated species *M. esculenta* and for resistance to pests and diseases. Their use in regular breeding programs is restricted by the long reproductive breeding cycle of cassava and "linkage drag" associated with the use of wild relatives in crop improvement. This source of resistance genes has been exploited for controlling CMD in Africa. CMD resistance was obtained by intercrossing cassava varieties with *Manihot glaziovii*, which resulted in interspecific hybrids that were backcrossed to cassava until CMD-resistant varieties were produced.

Several wild *Manihot* species have been evaluated in the greenhouse and field for resistance to mites (*M. tanajoa*), mealybugs (*P. herreni*) and whiteflies (*Aleurotrachelus socialis*). Genotypes (accessions) of the wild species *Manihot flabellifolia* and *Manihot peruviana* displayed intermediate levels of resistance to *M. tanajoa* and *P. herreni* and high levels of resistance to *A. socialis*. In addition, *M. tanajoa* oviposition was greatly reduced when feeding on accessions of *Manihot alutacea* and *Manihot tristis*. Interspecific crosses between these wild *Manihot* species and *M. esculenta* landrace varieties have resulted in numerous interspecific progeny, which are being evaluated for pest resistance. Initial results indicate that the resistance is heritable as numerous progeny have been identified with resistance to *M. tanajoa* and *A. socialis*. Three polymorphic molecular markers for *M. tanajoa* that showed clear differences between resistant and susceptible individuals were identified in *M. flabellifolia*. A project is under way to develop low-cost tools for accelerated marker-aided introgression of useful pest-resistance genes into cassava gene pools.

It is predicted that cassava production in Africa, Asia and the Americas will increase considerably during the next decade. This growth will be market driven and influenced by the processing and private sectors. Cassava can provide the raw material for the animal feed, starch and bio-fuel industries, as well as remaining an important food for human consumption. Pest management will continue to play an important role in sustaining high cassava-production levels. This will require continued research input to develop new integrated pest management (IPM) technologies.

In order to meet the demand for increased cassava production, farmers will seek new higher yielding varieties. This will increase the movement of germplasm – usually vegetative stem cuttings – between regions, countries and even continents. Quarantine measures to prevent the movement of pests, especially into Asia, are an important issue. Cassava pests have shown the ability to disseminate great distances as shown by the introduction of the mite and mealybug into Africa from the Americas. There are several additional pests that could cause severe crop losses if introduced into Africa or Asia, including several mite species, lacebugs, whiteflies, stemborers, mealybugs and thrips. Moreover, what may be considered a secondary pest in the Neotropics could become a major pest outside its center of origin, as evidenced by the mealybug, *P. manihoti*.

References

Bellotti AC (2002) Arthropod pests. In: Hillocks RJ, Thresh JM, Bellotti AC (eds) Cassava: biology, production and utilization. CABI Publishing, Wallingford, Oxon, UK, pp 209–223

Bellotti AC, Arias B (2001) Host plant resistance to whiteflies with emphasis on cassava as a case study. Crop Protect 20:813–823

Bellotti AC, Riss L (1994) Cassava cyanogenic potential and resistance to pests and diseases. Acta Hortic 375:141–151

Bellotti AC, Arias B, Guzmán OL (1992) Biological control of the cassava hornworm *Erinnyis ello* (Lepidoptera: Sphingidae). Fla Entomol 75:506–515

Bellotti AC, Peña J, Arias B, Guerrero JM, Trujillo H, Holguín C, Ortega A (2005) Biological control of whiteflies by indigenous natural enemies for major food crops in the Neotropics. In: AndersonPK, Morales F (eds) Whitefly and whitefly-borne viruses in the tropics: building a knowledge base for global action. CIAT Publication No 341, Cali, Colombia, pp 313–323

Bellotti AC, Smith L, Lapointe SL (1999) Recent advances in cassava pest management. Ann Rev Entomol 44: 343–370

Braun AR, Bellotti AC, Guerrero JM, Wilson LT (1989) Effect of predator exclusion on cassava infested with tetranychid mites (Acari: Tetranychidae). Environ Entomol 18:711–714

Braun AR, Bellotti AC, Lozano JC (1993) Implementation of IPM for small-scale cassava farmers. In: Altieri MA (ed) Crop protection strategies for subsistence farmers. Westview, Boulder, Colorado, pp 103–115
El-Sharkawy MA (1993) Drought-tolerant cassava for Africa, Asia, and Latin America. BioScience 43:441–451
Herren HR, Neuenschwander P (1991) Biological control of cassava pests in Africa. Ann Rev Entomol 36:257–283
Holguin CM, Bellotti AC (2004) Efecto de la aplicación de insecticidas químicos en el control de la mosca blanca *Aleurotrachelus socialis* Bondar en el cultivo de yuca *Manihot esculenta* Crantz. Rev Colomb Entomol 30:37–42
Melo EL, Ortega-Ojeda CA, Gaigl A, Ehlers RV, Bellotti AC (2006) Evaluación de dos cepas comerciales de entomonematodes como agentes de control de *Cyrtomenus bergi* Froeschner (Hemiptera: Cydnidae). Rev Colomb Entomol 32:31–38
Neuenschwander, P (2004) Cassava mealybug, *Phenacoccus manihoti* Matile-Ferrero (Hemiptera: Pseudococcidae). In: Capinera JL (ed) Encyclopedia of entomology. Kluwer, Dordrecht, The Netherlands, pp 464–467
Ngeve JM (2003) The cassava root mealybug (*Stictococcus vayssierei* Richard) [Hom: Stictococcidae]: present status and future priorities in Cameroon. Afr J Root Tuber Crops 5:47–51
Onzo A, Hanna R, Sabelis MW (2005) Biological control of the cassava green mite in Africa: Impact of the predatory mite *Typhlodromalus aripo*. Entomol Beric 65:2–7
Yaninek JS, Onzo A, Ojo JB (1993) Continent-wide releases of Neotropical phytoseiids against the exotic cassava green mite in Africa. Exp Appl Acarol 17:145–160

Caste

A form or type of individuals in social insects. Castes may be distinguished by different morphology and behavior.

Castes

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Castes can be defined as subsets of individuals within a species that are morphologically or biologically distinct. Although "polymorphism" usually is understood to mean the occurrence of discretely different morphotypes and biologies within a species, and therefore overlaps with this definition of castes, within the social insects the term "castes" is always used to describe this condition. In social insects, there may or may not be marked differences in appearance of the subsets, but they definitely display differences in behavior and biology. An alternate term for describing the discretely different (lacking intermediate forms) intraspecific variation occurring within insects is "polyphenism." (In contrast, phenotypes that show gradual change in response to environmental variation, without producing discretely different subsets, are called "reaction norms.") Regulation of caste is determined by hormones, which trigger different patterns of gene expression, leading to alternative phenotypes. Ultimately, however, it is the environment, acting through hormone intermediaries, that promotes development of polyphenisms such as castes. In social insects, the castes cooperate with each other in a nest to accomplish tasks benefiting the entire colony. Some of the castes are sterile, serving as workers or soldiers to facilitate reproduction by a small number of reproductives. The sterile castes presumably have evolved through the process of kin selection.

Phenotypic plasticity occurs in all organisms, and the phenotype that is expressed depends on environmental conditions. Interestingly, the environment to which the alternative phenotype is an adaptation is often not the same as the environment that induces the development of that phenotype. As noted above, some phenotypes display incremental changes in response to environmental variables. Others display discrete changes, resulting in two or more discrete alternative phenotypes. In either event, it can be advantageous to an organism to have the ability to develop multiple phenotypes without requiring genetic polymorphism.

The developmental switch that leads to production of alternative phenotypes is regulated by hormones. For morphological expression of polyphenism, a molt is normally required. Thus, the developmental trigger typically is in the instar preceding the expression. Within that sensitive period when change can be triggered, often there is only a brief period when hormones can alter developmental pathways. The relevant hormones generally are juvenile hormone and ecdysone, but sometimes other hormones are involved.

Ants

Among the ants, female castes are usually expressed as worker, soldier and queen castes. Males do not display different castes. Soldiers are often referred to as major workers, with the coexisting smaller members called minor workers. Not all castes occur in all species. Castes are determined by a number of factors, including larval nutrition, winter chilling, post-hibernation temperature, egg size, queen age, and queen influence. The function of castes or "caste polyethism" is well described by the aforementioned designations. Queens are mostly concerned with production of eggs, though early in the life of the colony the queen may perform various tasks, and some grooming of workers may occur indefinitely. Soldiers are specialized for colony defense, and often bear a large head and oversized mandibles to aid in this task. Workers repair the nest, gather food, and tend larvae and pupae, and the other colony members. Workers may also be involved in colony defense, especially the larger workers. Males exist only to fertilize queens. Temporal changes also occur over the course of the ant's lifespan; this is called "age polyethism." For example, young workers tend to work inside the nest, whereas older workers tend to forage outside.

Over the years, some authors have recognized variants, phases, or anomalies within castes in an attempt to recognize small differences in behavior and morphology, and this has led to confusion. Castes can be defined by both morphological and behavioral characteristics, of course, and E.O. Wilson has proposed a system of caste naming that integrates both types of characters: The males play no direct role in colony maintenance, being only sperm donors. The queen or "gyne" is the principal reproductive, although "gyne" sometimes is used to include all reproductive females. She is anatomically distinctive due to an enlarged abdomen. The worker ordinarily is a sterile female. Such females have reduced ovarioles and lack spermathecae for sperm storage. So if they eventually become reproductives, they can only reproduce parthenogenetically. The worker caste is often subdivided into subcastes such as "minor," "media," and "major," and is based on size. When workers are specialized for defense, they are called soldiers. The ergatogyne is a reproductive caste intermediate between worker and queen. It can be subdivided into "intercaste" which is anatomically intermediate between workers and queens, but lacks a spermatheca so cannot mate, and "ergatoid queen" which also is intermediate but possesses a spermatheca and can replace the queen. The gamergate is not common, but occurs in a few groups of ants, and is strictly a physiological caste. In this case, the reproductive is morphologically indistinguishable from the worker, but can be inseminated and produce eggs. The most distinguishing feature of the dichthadiiform ergatogyne is that it possesses an extremely enlarged gaster, but this reproductive also has some additional minor morphological modifications. The final caste would be considered to be the temporal caste. In the temporal caste, differentiation is based solely on behavior and age.

Social Bees and Wasps

Among social bees and wasps, the more primitively eusocial groups lack mophological differences but display different behaviors. More interesting is the general lack of the worker subcastes such as those that are found in ants and termites. This is despite the fact that bees and wasps, at least the species with very large colonies, display a sophisticated division of labor (polyethism). In bees and wasps, however, the division of labor is based less on production of castes, and more on temporal polyethism. In temporal polyethism the same individual passes through different stages of specialization as it grows older. Some differences exist based on size, however, with larger individuals tending to forage more and smaller individuals tending to conduct nest work and brood care.

In social bees and wasps, there is a correlation between caste evolution and colony size. E.O. Wilson divides this into four steps:

1. Colony size of 2–50 adults – the females are semisocial or begin life as workers and later become egg layers.
2. Colony size of 10–400 adults – externally, the queen is still identical to the worker caste, but there is functional differentiation of the worker caste from the queen. The egg-laying females maintain the workers in a subordinate position by aggressive dominance behavior. This can be expressed by the stealing and eating of eggs laid by rivals. Temporal poyethism is weakly developed among workers.
3. Colony size of 100–5,000 adults – some external differentiation of queens and workers is evident, and this is under the control of nurse workers that feed larvae differently. Queens do not display dominance behavior. Temporal polyethism is weak among workers.
4. Colony size of 300–80,000 adults – queen and worker dimorphism is strong. Queen dominance is absent and queens maintain control with pheromones. Temporal polyethism is strongly developed among workers.

Termites

Superficially, termites and ants have similar caste systems. However, these taxa are phylogenetically remote from each other, and careful examination shows some important differences, so it is clear that sociality and caste systems evolved separately in Hymenoptera and in Isoptera. Both ants and termites have evolved a soldier caste with specialized head structure and behavior, and both are populated primarily by similar-looking but behaviorally versatile workers. Their systems of temporal polyethism also are similar. Termites differ, however, in that males do not exist solely for fertilization. Termite workers can be either sex, whereas in the holometabolous social insects (ants, bees, wasps) the workers are always female. Also, termite immatures are workers, whereas immatures of the other social insects require continual care by adult workers.

Termite castes have some unique features. In the lower termites, the reproductives secrete sex-specific pheromones that inhibit metamorphosis of the immatures into additional reproductives. Termites also are capable of producing "supplementary reproductives." If the primary reproductives are removed, fertile but wingless individuals of both sexes develop in the colony. Thus, termite colonies display "immortality"; they may never completely perish because reproductives can be generated as necessary. Termite soldiers seem to be capable of suppressing the development of workers into soldiers, maintaining a larger number of termites arrested in the worker stage, probably to the benefit of the colony.

The classification of termite castes is as follows: The larva (a wingless nymph, as these are hemimetabolous insects) lacks evidence of wings and of the features that characterize soldiers. The nymph (brachypterous nymphs) develops from the larval stage but possesses wing buds initially, and wing pads after some molts. Eye differentiation also occurs at this stage. A worker stage occurs in the higher termites, but not the lower. Workers lack wings, and eyes are reduced or lacking. The head and mandibles are well developed. Lacking the worker stage, the lower termites have instead a stage called pseudergate. Pseudergates develop from nymphal stages or larvae. Soldiers have morphological features that are specialized for defense. This includes large mandibles, large heads, and glands capable of discharging defensive secretion. Primary reproductives are derived from colony-founding queens and males. If the primary reproductives are removed from the colony, often supplementary reproductives can appear. The supplementary reproductives take three forms: (i) the adultoid reproductive, found in the higher termites only, which appears identical to the primary reproductive and may already exist but changes behavior in the absence of the primary reproductive; (ii) the nymphoid reproductive is a supplementary male or female derived from a nymph and retaining wing buds; (iii) the ergatoid reproductive is also a supplementary male or female, but is larval in form and lacks wing buds.

The primary reproductives construct an initial cell and rear the first brood, providing them not only with food but the protozoans necessary for independent feeding on cellulose. The first brood workers (or worker-like pseudergates or nymphs) soon take over responsibilities for foraging, nest construction and nursing. The queen and male become specialized reproductive organisms. Interestingly, the worker caste is morphologically uniform but behaviorally diverse when species are compared. The soldier caste is morphologically diverse but behaviorally uniform. Soldiers can use their mandibles effectively in defense against insects their own size, or in the case of those practicing chemical defense, their glands can secrete or spray a number of bioactive substances to deter intruders.

► Polyphenism
► Termites
► Bees
► Ants

References

Ananthakrishnan TN, Whitman D (eds) (2005) Insect phenotypic plasticity. Diversity of responses. Science Publishers, Enfield, New Hampshire, 213 pp

Hölldobler B, Wilson EO (1990) The ants. Belknap Press, Cambridge, MA, 732 pp

Miura T (2004) Proximate mechanisms and evolution of caste polyphenism in social insects: from sociality to genes. Ecol Res 19:141–148

Miura T (2005) Developmental regulation of caste-specific characters in social insect polyphenism. Evol Dev 7:122–129

Nijhout HF (1999) Control mechanisms of polyphenic development insects. Bioscience 49:181–192

Wilson EO (1971) The insect societies. Belknap Press, Cambridge, MA, 548 pp

Zhou X, Oi FM, Scharf ME (2006) Social exploitation of hexamermin: RNAi reveals a major cast-regulatory factor in termites. Proc Natl Acad Sci 103:4499–4504

Castniidae

A family of moths (order Lepidoptera) also known as giant butterfly moths.

► Giant Butterfly Moths
► Butterflies and Moths

Caterpillar

The larva of a butterfly, moth (Fig. 29), sawfly, and some scorpionflies.

Cat Flea, *Ctenocephalides felis felis* Bouché (Siphonaptera: Pulicidae)

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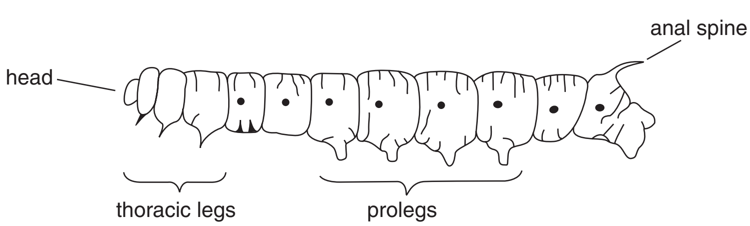
Cat fleas are the most common ectoparasite on both dogs and cats in North America. These small (2 mm), reddish brown, wingless insects have bodies that are laterally compressed (i.e., flattened side-to-side) and covered with many backward-projecting spines, making them, like a cocklebur, difficult to remove from the animal's coat. Their



Caterpillar, Figure 29 **Lateral view of a moth caterpillar (Lepidoptera: Sphingidae).**

hind legs are long and well adapted for jumping. Adult fleas feed exclusively on blood and their mouthparts are equipped for sucking blood from the host. Cat fleas attack a variety of warm-blooded hosts, including humans and pets, making them both a veterinary problem and household pest. Although cat fleas have been collected from more than 30 species of urban and suburban wildlife, most of these animals are not satisfactory hosts.

Cat fleas do not commonly serve as disease agent vectors. However, they are capable of transmitting the causative agents of flea-borne typhus (*Rickettsia typhi*) and cat scratch disease (*Bartonella henselae*). The cat flea is the intermediate host for the dog tapeworm, *Dipylidium caninum*, which can affect small children as well as dogs and cats. It is supposedly capable of transmitting plague (*Yersinia pestis*), but has been important in epidemic situations only outside the U.S.

Probably the most common flea symptom is that pets bite and scratch themselves repeatedly. Severely flea-infested puppies and kittens risk life-threatening anemia. Sensitized people suffer pruritus stimulated by antigens in flea saliva, and resultant scratching opens the skin to infection. Flea saliva has been described as one of the most irritating substances known to man, and very small amounts cause great irritation and itching.

Flea allergy dermatitis (FAD) is a severe condition found primarily in dogs, but also occasionally seen in cats. In a flea-allergic animal, flea salivary antigens stimulate intense itching that results in self-inflicted trauma such as scratching and biting. Affected animals display obsessive grooming behavior, hair loss, and weeping sores with secondary infection. Until successful FAD immunotherapy is developed, treatment involves flea elimination from the animal's environment and flea bite prevention. But only one bite can stimulate a full cascade of symptoms in sensitive animals.

Fleas and their associated diseases can constitute over half a veterinary practice's caseload in some regions. More energy and money are spent battling these insects than any other problem in veterinary medicine.

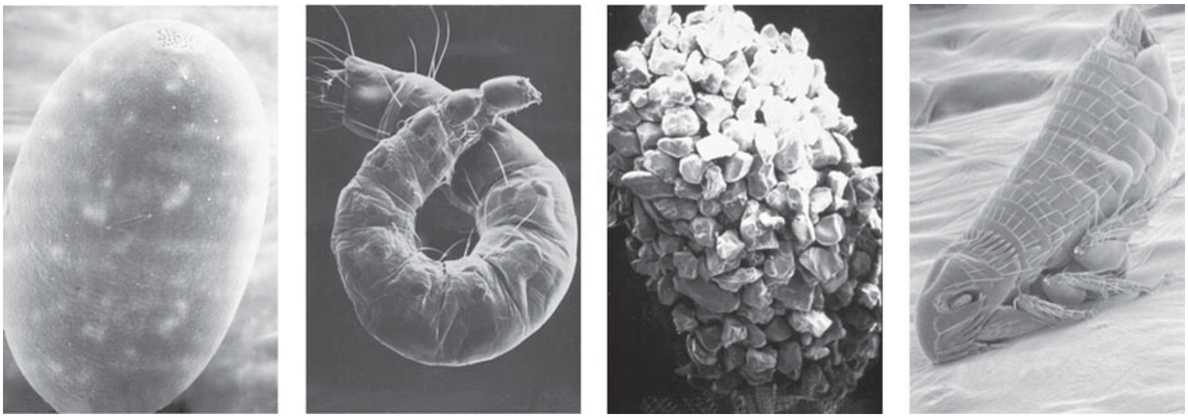
The cat flea is a cosmopolitan, eclectic species, having been recorded from over three dozen species, including opossums, raccoons, skunks, coyotes, and even birds. Infested wildlife can move flea infestations from infested premises to previously non-infested areas. The combination of wide host range and movement of fleas by urban wildlife explain the fleas' ability to repopulate domestic animals following suppression efforts. Because it lacks host specificity and tends to feed on humans, the cat flea is a pest of both companion animals and their homes.

Once adult cat fleas locate a host, they tend to remain on that animal unless dislodged. They feed readily, taking several blood meals every day. They not only feed, but mate and lay eggs while on the host, unlike rat fleas that hide in rodent burrows between blood meals. Flea eggs (Fig. 30) are not sticky so they readily fall off into the host's environment, with large numbers accumulating in areas frequented by the animal. Scratching caused by saliva in flea bites speeds the drop of eggs from the host. Once the adult flea finds a host, it begins to feed. The female mates and begins oviposition within a couple of days. On the host, a female flea averages about one egg per hour and, as a female flea can live on the host for several weeks, potential production can amount to hundreds of eggs in her lifetime. Only the adult stage is parasitic; all other life stages develop off the host.

Cat flea eggs are approximately one mm in length, with little surface structure. Typically eggs hatch within 24–48 h following oviposition, with more rapid hatching at warm temperatures.

Small, white, eyeless, legless larvae emerge from the eggs with chewing mouthparts. They graze through their habitat, feeding on organic debris and adult flea feces (partially digested blood). As they seldom travel far from where they hatch, cat flea larvae are usually found in furniture, carpeting, or outside in areas frequented by host animals. In efforts to avoid light, flea larvae typically burrow deep into carpet or, outdoors, into duff.

Flea larvae are highly subject to desiccation and dry out rapidly. Humidity over 50% in the larval environment is essential for development,



Cat Flea, *Ctenocephalides felis felis* Bouché (Siphonaptera: Pulicidae), Figure 30 The cat flea life cycle: (left) a flea egg is not sticky so readily falls from the host and hatches a few days later; (second from left) flea larvae coil when disturbed; (third from left) within the cocoon the larva completes development through the pupal stage to an adult flea; (right) adult fleas feed exclusively on blood.

and this susceptibility to heat and desiccation makes it unlikely that flea larvae survive outdoors in sun-exposed areas. Because hosts prefer shaded areas, flea eggs are more likely to be deposited in shade, and flea larvae develop where the ground is shaded and moist. Likewise, indoors flea larvae are protected under the carpet canopy where air movement is minimized and humidity is highest. Most flea larvae, therefore, tend to be located in areas where pets spend most of their time.

Under favorable conditions, flea larvae can complete development in as little as 10 days. Cool temperatures, food shortages, or other unsuitable environmental conditions may extend larval developmental time to several weeks or a month. In areas like south to central Florida, flea larvae can develop outdoors from egg to pupal stage, even during the winter months of November to March, due to the mild temperatures and high humidity. When mature, the larva locates an appropriate site for pupation and spins a silk cocoon to which adheres environmental debris, making the cocoon appear as a small dirt clod or lint ball.

Within its cocoon, the larva molts to the pupa and continues metamorphosis, becoming an adult flea within about 4 days under favorable conditions. The pre-emerged adult stadium has the most variable length of any stage in the flea life cycle, ranging from days to several months (or perhaps over a year). The pre-emerged adult flea within the cocoon is more resistant to desiccation than either eggs or larvae. Stimuli such as pressure, carbon dioxide, and warmth (triggers associated with mammalian hosts) cause adult fleas to emerge from their cocoons. This emergence from the cocoon causes many problems in homes and apartments where infested pets previously lived. When the hosts are removed from a residence, the eggs and larvae all develop to the pre-emerged adult stage, waiting for a host. As soon as a new resident occupies the house, thousands of fleas emerge at once, stimulated by the movement, warmth, and carbon dioxide. Emergence of these adults from their protective cocoons may persist for 3–6 weeks despite all efforts to control them.

Most fleas emerge within a couple of weeks following cocoon formation. Upon emergence, the flea can survive for approximately 7–10 days (or longer under high humidity and low temperature conditions) if it does not locate a host.

Because fleas must have blood from a mammal host to survive, treating host animals to use them as “bait” is the most efficient and successful suppression tactic. There are several on-animal products that are effective for flea control. Many contain pyrethrins, which are safe, effective products but kill only fleas on the animal at time

Cat Flea, *Ctenocephalides felis felis* Bouché (Siphonaptera: Pulicidae), Figure 31 **Fleas are ornamented with spines and combs that help anchor them in the host's coat.**

of treatment and do not provide residual control. Other over-the-counter compounds include spot-on permethrin products, which are limited to canine use as they can be lethal to cats.

Veterinarians can prescribe products that provide several weeks of control with a single application. These are applied in a small volume (a few milliliters) on the back of the animal's neck and distribute over the body surface in skin oils. In addition to spot-on formulations, some products are available as sprays. These adulticides kill fleas on the animal within a few hours, then provide residual flea suppression for several weeks.

After pets are treated, fleas will continue to emerge and hop onto the animal; the host will "harvest" fleas from the surrounding environment until they have been killed and no more are emerging. Because it will take a while for fleas in the environment to die off, some fleas may be seen on the animals for up to a month following treatment, but that does not indicate product ineffectiveness. When used prior to flea population build up, insect growth regulators can break the flea life cycle. While these compounds do not kill adult fleas, they do prevent eggs and larvae from completing development, ensuring that any fleas brought into the area will not establish a sustaining population.

Due to their wide host range, fleas can continually move into homes and reinfest. Homes without pets can develop severe cat flea problems if wild or feral animals (raccoons, opossums, skunks, etc.) nest in the crawl space or attic and share their fleas. Typically migrants den under the structure in the spring; as their young abandon the nest, fleas left behind climb up through subflooring, seeking a blood meal from any warm-blooded host. Excluding potential carriers from the property will reduce opportunities for reinfestation.

Sanitation is an important flea suppression tactic; by eliminating larval development sites and destroying immature stages before they develop to the pestiferous adult stage (Fig. 31), pets and people can be protected from fleas. Areas frequented by pets accumulate flea eggs and larval food, so these microhabitats should be vacuumed and treated with insect growth regulators or borate products to prevent flea infestations. Such areas include under furniture, animal bedding and sleeping quarters, and utility rooms or other locations where the pet spends time.

► Fleas

References

Durden LA, Traub R (2002) Fleas (Siphonaptera). In: Mullen GR, Durden LA (eds) Medical and veterinary entomology. Academic Press, San Diego, CA

Dryden MW, Broce AB, Cawthra J, Gnad D (1995) Urban wildlife as reservoirs of cat fleas, *Ctenocephalides felis*. In: American Association of Veterinary Parasitologists, 40th Annual Meeting. Pittsburgh, PA, p 65

Holland GP (1964) Evolution, classification, and host relationships of Siphonaptera. Ann Rev Entomol 9:123–146

Rust MK, Dryden MW (1997) The biology, ecology, and management of the cat flea. Ann Rev Entomol 42:451–473

Cattle Grub, *Hypoderma* spp. (Diptera: Oestridae)

Livestock-infesting flies that migrate through the host's body.

► Myiasis
► Veterinary Pests and their Management

Cattle Ticks

Several ticks can be important parasites of cattle.

► Ticks
► Area-Wide Pest Management

Cauda

The pointed tip of the abdomen, the modified ninth abdominal tergum, in aphids. It is sometimes called the "tail."

► Abdomen of Hexapods

Caudal

Pertaining to the anal end of the body.

Caudal Filaments

Thread-like processes at the tip of the abdomen (Fig. 32), often referred to as "tails" by non-entomologists.

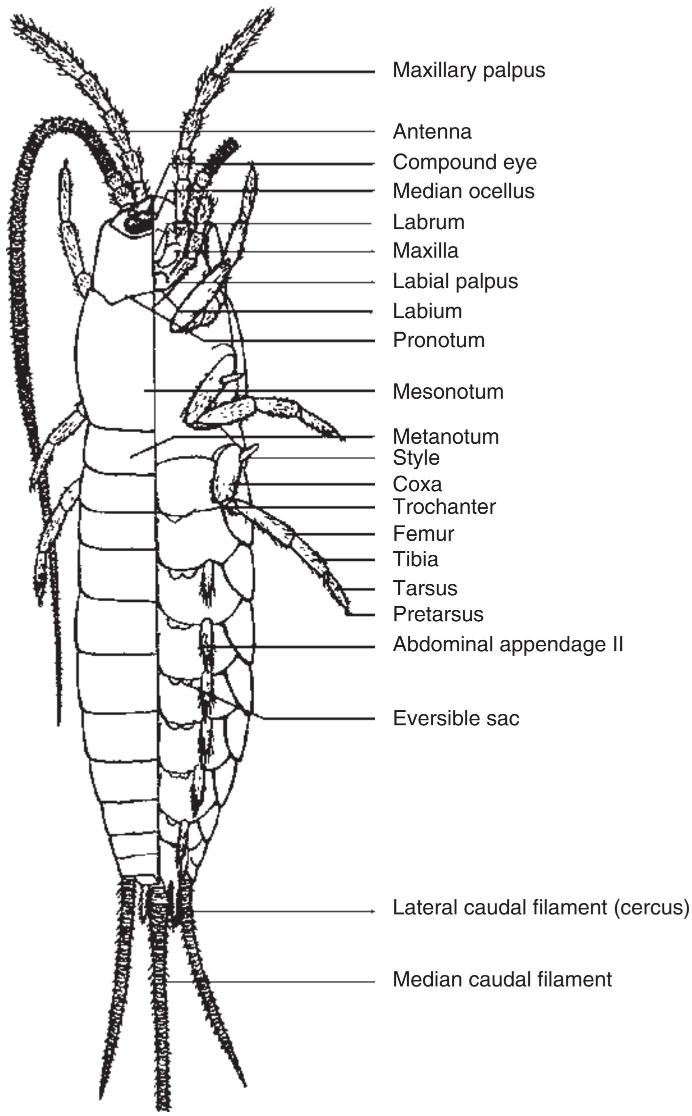
► Abdomen of Hexapods

Caudal Lamellae

The caudal gills of damselflies.

Caudate

Having a tail-like process at the anal end of the body.



Caudal Filaments, Figure 32 **Dorsal (left) and ventral (right) view of a silverfish (Collembola).**

Caudell, Andrew Nelson

Andrew Caudell was born in Indianapolis on August 18, 1872, and moved with his parents to a farm in Oklahoma where he grew up. He became interested in insects and later studied at Oklahoma Agricultural College. After a brief employment in Massachusetts with the Gypsy Moth Project, in 1898 he joined the U.S. Department of Agriculture, studied Orthoptera, and became custodian of Orthoptera at the U.S. National Museum. Study of this group of insects, but including Zoraptera, became his life's work, and he published numerous papers on it. His other accomplishments included being president of the Entomological Society of Washington in 1915, and publishing with Nathan Banks "The Entomological Code. A code of nomenclature for use in entomology". Married, and with one daughter, he died on March 1, 1936.

Reference

Mallis A (1971) Andrew Nelson Caudell. In: American entomologists. Rutgers University Press, New Brunswick, NJ, pp 198–200

Cave Adapted Insects

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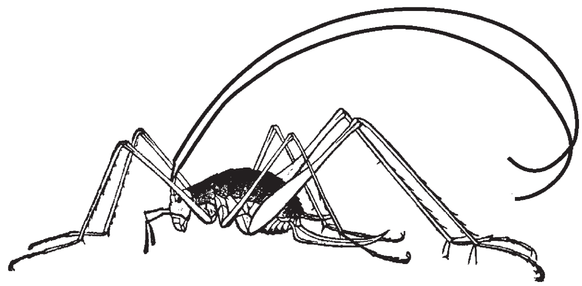
Insects inhabit nearly every conceivable habitat on earth and often exhibit unique adaptations corresponding to these environments. Caves are certainly among the more unusual and fascinating of these habitats. Insects and other organisms living in caves have evolved to deal with a set of unique environmental conditions, and the species of cave inhabiting insects vary in the degree to which they are limited to life in caves. Species that must spend their entire lives within caves are called troglobites. Environmental conditions typical of habitat deep within caves include:

- Complete absence of light
- Stable and usually very high (>95%) humidity
- Relatively low levels of available nutrients
- Nearly constant temperature

Troglobites are among the most interesting of the cave-adapted species. Because they live in the absence of light, many troglobitic insects have non-functional eyes. Most commonly, this is evidenced by the reduction or even complete loss of the compound eyes. Instead, troglobitic insects may have greatly elongated antennae and legs (Fig. 33) relative to their nearest epigean (aboveground) relatives. Equipped with elongate setae, these appendages allow the insects to detect nearby potential prey or predators in the absence of light. Troglobitic insects also may be particularly attuned to detecting vibrations and chemosensory cues.

There is little selective pressure for elaborate coloration (camouflage, warning coloration) in the absence of light, and, as a result, many troglobitic insects are whitish or pale brown in coloration. The high humidity of the caves, often in excess of 98%, means that moisture retention is less of a problem than in many epigean habitats. Consequently, many cave insects have a thinner, less waxy cuticle



Cave Adapted Insects, Figure 33 ***Haedonoecus subterraneus*** **(Orthoptera: Rhaphidophoridae), adult female. Note extremely long legs, palps, and antennae – adaptations that are advantageous in a cave. (Source: Packard AS (1888) Cave fauna of North America. Memoirs Natl Acad Sci 4:1–156 + 27 plates.)**

than their nearest surface relatives, further enhancing the often pale appearance we associate with cave-adapted animals.

Perhaps the most important aspect of cave life relating to the absence of light is its effect on the availability of energy. In the dark zone of caves there are no primary producers – no photosynthesizing plants. Interesting exceptions to this do occur, but by and large, cave communities depend on organic debris that falls or washes into caves, the bodies of organisms that accidentally fall or wander into caves, and fecal material and sometimes the bodies, eggs, or young of trogloxenes (species that live in caves but must leave the cave for part of their life cycle) that bring in energy from outside the caves, such as bats and cave crickets. The cave community, then, is basically a decomposer community. In many caves, insects play important roles in this community.

The relatively low levels of energy available in many caves means that life is sparse, and, consequently, predators are rare. In comparison to their surface kin, troglobitic insects often move more slowly, live longer, and produce fewer and larger eggs, all adaptations to deal with the lower energy levels of the cave environment. For example, the European catopid cave beetle, *Speonomus longicornis*, may live more than 3 years.

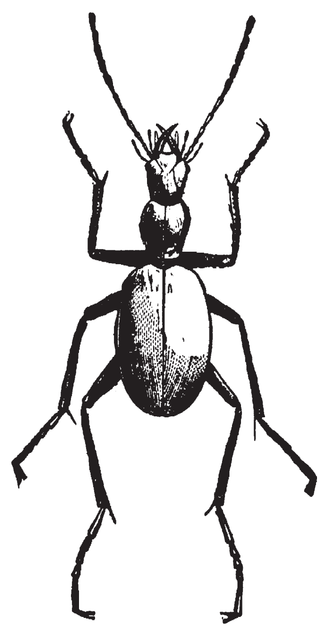
The near constant conditions in the cave usually mean that troglobites do not have very pronounced circadian rhythms of activity. This does not, however, mean that there are no environmental cues to indicate the passing of days or seasons. Many caves "breathe," taking in air or releasing it as the barometric pressure changes or as the temperature above ground rises and falls. The movements of trogloxenes, such as cave crickets and bats, also may be informative to the cave-limited species. Seasonal flooding of cave streams also can provide information about seasons (as well as provide an influx of new nutrients).

What specific organisms, then, live under the above environmental conditions and exhibit these sorts of adaptations?

The hexapod order Collembola (Springtails) contains many troglobites; a few of the genera with cave-inhabiting species include *Pseudosinella*, *Onychiurus*, and *Folsomia*. These tiny organisms feed on minute organic debris and the ubiquitous fungi that break down leaf litter, twigs, and fecal material. Springtails sometimes are found on the surface film of drip pools on cave floors (e.g., some *Arrhopalites* species). Troglobitic springtails are sometimes present in large numbers, visible to us as tiny white flecks moving about on the substrate.

Trogloxenic cave or camel crickets of the genus *Ceuthophilus* are one of the more prominent insect inhabitants of many Nearctic caves. These orthopterans roost in caves, usually high on walls or on ceilings where they are less susceptible to predation by cave visitors such as mice and raccoons. At night, some portion of the cave's population of *Ceuthophilus* sp. will emerge from the cave (often about dusk) to forage for food above ground. Most cave-inhabiting *Ceuthophilus* species exhibit adaptations that suit them both for their nighttime excursions (mottled brown and black coloration, large powerful legs for jumping out of harm's way) and for life in the cave (most notably, their long, attenuated appendages, especially the antennae). Other genera of Rhaphidophoridae occur in caves in the United States (e.g., *Haedonoecus*), in Europe (e.g., *Troglophilus*), in Australia and New Zealand (where cave-dwelling species of *Gymnoplectron* and other genera are known as "cave wetas") and elsewhere.

The feces of the roosting crickets provide food for other cave organisms, and the adult female crickets typically deposit their eggs in the protection of the cave, inserting their ovipositor into the soft sandy cave soils. These eggs, of course, are a dense source of nutrients, and in some areas there are troblobitic beetles of the family Carabidae. In the United States, common beetle genera that are cave cricket (*Ceuthophilus*, and the more cave-adapted but less widespread *Haedonoecus*) egg predators include ground beetles of the genera *Rhadine* and *Neaphaenops* (Fig. 34). Troglobitic carabid beetles are often a pale rusty red in color, and the more cave-adapted species have no eyes, or compound eyes reduced to only a few facets. Some cave-adapted carabid predators of cricket eggs have a narrowed and elongated head and

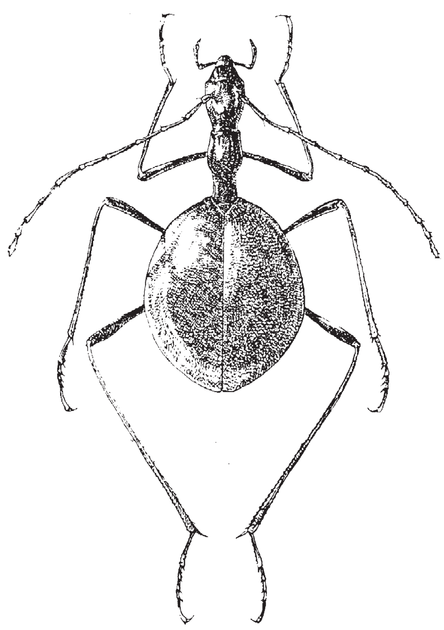


Cave Adapted Insects, Figure 34 ***Neaphaenops tellkampfi*, a cave cricket egg predator found in some Kentucky, USA, caves. (Source: Packard AS (1888) Cave fauna of North America. Memoirs Natl Acad Sci 4:1–156 + 27 plates.)**

thorax, which presumably facilitate reaching deep into holes where cricket eggs may be found.

The Coleoptera are one of the most successful insect orders in caves, especially the families Carabide, Leiodidae, and Staphylinidae. The first cave invertebrate to be described (in 1832) was a carabid beetle, *Leptodirus hohenwarti* (Fig. 35), in Europe. Many of the troglobitic carabids (ground beetles) are predators. The North American carabid genera *Rhadine* and *Neaphaenops* contain troglobitic species that may spend many hours searching for the eggs, which they extract from the ground and consume. *Psudanophthalmus* is another carabid beetle genus frequently found in caves of the eastern United States, where they feed on a variety of different things. Southern European caves harbor an unusually diverse cave carabid fauna.

Another group of beetles with some success in the cave environment is the rove beetles (Staphylinidae). While significantly fewer species of staphylinids are troglobites, they commonly are



Cave Adapted Insects, Figure 35 ***Leptodirus hohenwarti*** **Schmidt, 1832. (Source: Jeannel (1949) Reprinted in Vandel, A (1965) Biospeleoeology: the biology of caverniculous animals. Pergamon Press, New York, NY, 524 pp)**

found in caves, especially in the Mediterranean region. In the United States, the staphylinid *Quedius spelaeus* frequently is encountered, especially in association with cave stream riparian zones and leaf litter. One rather distinctive looking group of rove beetles, the Pselaphinae (mold beetles), contains a number of very small, narrowly endemic troglobitic species of *Batrisodes*, found in caves of south-central Texas. Round fungus beetles (Leiodidae) of the genus *Ptomophagus* include several troglobitic species in North America.

A surprising number of flies are found in caves. Most famously, the larvae of the New Zealand cave glow-worm (*Arachnocampa luminosa*, Mycetophilidae) are found on the ceilings of sometimes spacious caverns. They are bioluminescent, and dangle sticky threads down from the ceiling which capture prey items attracted to the light. In the United States, the predatory larva of the mycetophilid *Macrocera nobilis*, commonly known as the "monorail worm," also makes sticky, web-like structures on walls and floors of caves and moves effectively both forward and backward along these narrow strands. In temperate North American caves, adults of several species of troglophilic heleomyzid flies commonly are found on cave walls and ceilings. Another common cave fly in the eastern United States is *Megaselia cavernicola* (Phoridae). In the winter, it is not unusual to encounter large numbers of mosquitoes (Culicidae) overwintering in the relatively stable and moderate conditions of a cave.

This brief look at cave insects certainly does not represent the true diversity of taxa and interesting adaptations that exist. While some of the more common inhabitants of temperate North American caves are emphasized here, the fauna of tropical caves has been short-changed, as have the incredible faunas of the lava tubes of the Canary and Hawaiian islands, where pale, stilt-legged emisine reduviids stalk their prey and cixid hemipterans feed on tree roots and produce vibratory signals intended for potential mates. Nor have the other arthropods found in caves been discussed. These include an amazing array of arachnids (spiders, mites, opilionids, ricinuliids, etc.) and, especially in aquatic habitats, crustaceans (copepods, crabs, crayfish, isopods, amphipods, etc.). The citations below serve as an introduction to the large body of literature on cave invertebrates.

► Cave Habitat Colonization

References

Camacho AI (ed) (1992) The natural history of biospeleology. Monografias Museo Nacional de Ciencias Naturales, Madrid, Spain, 680 pp

Chapman P (1993) Caves and cave life. HarperCollins, London, UK, 224 pp

Culver DC (1982) Cave life evolution and ecology. Harvard University Press, Cambridge, MA, 189 pp

Mohr CE, Poulson TL (1966) The life of the cave. McGraw-Hill, New York, NY, 232 pp

Vandel A (1965) Biospeloeology: the biology of caverniculous animals. Pergamon Press, New York, NY, 524 pp

Cave Habitat Colonization

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Over the centuries people have keenly studied the animals found in the sea, in rivers, and on the land, but little attention has focused on animals that inhabit caves. The ancient Greeks believed that caves were the abode of the dead, and this may have led to the belief that caves could not possibly harbor life. However, large numbers of cave dwelling animals representing a wide diversity of groups, such as insects, millipedes, amphipods, isopods, fish, and spiders, have been described over the last 200 years. The first published work on biospeleology appeared in 1845, by the Danish zoologist, J.C. Schiödte, describing animals he collected from caves in Italy. Thereafter, biospeleological research began in earnest, focusing on European and North American temperate caves. One of the key questions that researchers have debated over the last 150 years is how animals came to live in caves, and how they have subsequently evolved. These two processes, cave colonization and speciation, are frequently confused in the literature. Here we describe models of cave colonization, and refer the reader to Taylor (this volume) and references below for further details on speciation.

One of the first modern hypotheses for the origin of cave organisms was that of Vandel (1965), who put forward the "Pleistocene-effect" model for the evolution of terrestrial troglobites (obligate cave dwellers) in temperate regions. This model has also been termed the "relictual," "isolation," "refugium" or "climate-relict" model. Vandel proposed that troglobites evolved allopatrically from epigean (surface dwelling) species, which had adapted to the cool climatic conditions of the Pleistocene ice ages (1.5 million–10,000 years ago). When the glaciers retreated, these organisms were subsequently restricted to more favorable climatic habitats, such as deep wooded ravines, cool and moist forest floors and caves. Over time, with continued climatic variability and subsequent surface habitat changes, the epigean populations became extinct. Under this model the resulting geographic isolation of cave populations leads to the allopatric speciation of cave dwelling organisms. Vandel's model has been the traditional view for the origin of cave populations, especially in temperate regions such as Europe and North America where major climatic changes during the Pleistocene have occurred.

But what about tropical caves? Biological investigation of the worlds' tropical caves did not receive much attention until the 1970s. Before this, scientists working in the Pleistocene-effect paradigm believed that troglobites were virtually nonexistent in tropical caves. The paucity of troglobites in these regions was explained by the lack of past climatic extremes required to restrict epigean populations to cave habitats. However, since the 70s both the discovery of large numbers of terrestrial troglobites in tropical regions such as Australia, the Canary and Galápagos Islands, Hawaii, and

Jamaica, combined with the mounting evidence that significant past climatic fluctuations occurred in much of the world during the Pleistocene, has made biologists reconsider the evolutionary origins of troglobites in the tropics. For example, it is postulated that cavernicolous species of cockroaches in North Queensland have arisen as a result of isolation in moist refugia during periods of increasing aridity in Australia in the late Cenozoic.

In 1973 Howarth proposed the "adaptive-shift" model to account for the origin of tropical troglobites in lava tubes of the Hawaiian Islands where epigean congeners of the cave dwelling species have been found. This model has also been termed the "local habitat shift" or "invasion" model. Howarth proposed that pre-adapted species move into newly developed cave habitats to exploit the resources not otherwise available on the surface, with troglobites evolving parapatrically or sympatrically through an adaptive-shift rather than by isolation induced by climatic change. Under this model caves do not act as refugia from episodic climatic changes, instead their colonization is a continuing process. Speciation follows as a result of isolation of organisms brought about by an adaptive-shift, and does not relate directly to climate change. As with Vandel's model, Howarth's model incorporates both processes of colonization and of speciation.

A related model to the adaptive-shift model is the "active colonization" model put forward by members of the Laboratoire Souterrain du CNRS in France, which applies to temperate as well as tropical caves. In addition to cave habitats, the researchers have studied the colonization of interstitial voids found in soil and screes (termed the "milieu souterrain superficiel" or superficial hypogean compartment). They suggest that climatic events may not be the primary factors of cave colonization, but that colonization is an active phenomenon in new biotypes. Climatic changes are considered as a localized model, with organisms colonizing caves as a result of a number of biological interactions. This model is a variant of Howarth's adaptive-shift theory, but includes the possibility of subsequent events, including climatic changes, leading to speciation. The biological interactions that lead to colonization may include invasion as an immediate refuge from surface abiotic stresses, opportunism (caves as new niches to be colonized) or a result of competition or predation pressure in surface habitats.

Hypotheses for the evolution of subterranean organisms are still debated today, with a regular re-elaboration of the fundamental scenarios described above. To date research evidence has failed to falsify any alternative models, and no generalized single theory has been put forward. The origin of a particular cave dwelling organism should perhaps best be interpreted based on the evidence that explains the origin of that organism, and may invoke a combination of biological and or abiotic factors leading to colonization (and speciation) in those individual circumstances.

► Cave Adapted Insects

References

Barr TC Jr (1968) Cave ecology and the evolution of troglobites. Evol Biol 2:35–102

Culver DC (1982) Cave life: evolution and ecology. Harvard University Press, Cambridge, MA

Howarth FG (1973) The cavernicolous fauna of Hawaiian lava tubes. Pacific J Insects 15:139–151

Howarth FG (1987) The evolution of non-relictual tropical troglobites. Int J Speleology 16:1–16

Rouch R, Danielopol DL (1987) L' origine de la faune aquatique souterraine, entre le paradigme du refuge et le modéle de la colonisation active. Stygologia 3:345–372

Slaney DP (2001) New species of Australian cockroaches in the genus Paratemnopteryx Saussure (Blattaria, Blattellidae, Blattellinae), and a discussion of some behavioural observations with respect to the evolution and ecology of cave life. J Nat Hist 35:1001–1012

Vandel A (1965) Biospeleology: the biology of cavernicolous animals (translated by Freeman BE). Pergamon Press, Oxford, UK, 524 pp

Weinstein P (1994) Behavioural ecology of tropical cave cockroaches: preliminary field studies with evolutionary implications. J Aust Entomol Soc 33:367–370

Cayenne Tick, *Amblyomma cajennense* Fabricius (Ixodida: Ixodidae)

This disease vector is found throughout the Americas.

► Ticks

cDNA

The double-stranded DNA copy of a eukaryotic messenger RNA molecule, produced in vitro by enzymatic synthesis and used for production of cDNA libraries or probes for isolating genes in genomic libraries.

cDNA Library

A collection of clones containing dsDNA that is complementary to the mRNA. Such clones lack introns and regulatory regions of eukaryotic genes. Once cDNA molecules are transcribed, they are inserted into a vector and amplified in *E. coli*.

Cecidomyiidae

A family of flies (order Diptera). They commonly are known as gall midges.

► Flies

► Gall Midges (Diptera: Cecidomyiidae)

Cecidosidae

A family of moths (order Lepidoptera). They also are known as gall moths.

► Gall Moths

► Butterflies and Moths

Cedar Beetles

Members of the family Callirhipidae (order Coleoptera).

► Beetles

Cell

The fundamental unit of life. Each multicelled organism is composed of cells. Cells may be organized into organs that are relatively autonomous but cooperate in the functioning of the organism. This term also is used to describe any area of a wing that is between or bounded by veins. Wing cells are named after the vein forming the upper margin, and are numbered from the base outward.

Cell Culture

The growing of cells in vitro, or in an artificial container rather than in an organism.

Cell Culture of Insects

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Insect tissue culture was initiated by R. Goldschmidt in 1915. He cultured spermatocytes of *Hyalophora cecropia* (Lepidoptera: Saturniidae) in hemolymph of the same species. He could maintain the spermatocytes for more than 3 weeks, and observed spermatogenesis in vitro. His culture may be taken as organ culture, because he did not aim to proliferate cultured cells. Later, W. Trager (1935) established standard methods for insect cell culture. He devised media proper for insect cell culture, and with it he successively cultured *Bombyx mori* (Lepidoptera: Bombycidae) ovarian cells for several weeks. In 1956, Wyatt formulated a synthetic medium based on the chemical composition of insect hemolymph. The composition of her medium is still used at present as the base of formulation of new media. In 1962, the first insect continuous cell line (a cell population which continues to proliferate unlimitedly) was established by Grace. He obtained permanently growing cells from the culture of the ovarian cells of *Antheraea eucalypti* (Lepidoptera: Saturniidae). Since then, more than 400 insect cell lines have been established. They include 172 dipteran cell lines (115 from *Drosophila melanogaster* and 47 from 22 mosquito species), 147 lepidopteran cell lines, 16 coleopteran cell lines, 15 hemipteran cell lines, 13 hymenopteran cell lines, 11 blattarian cell lines, and 1 orthopteran cell line. The history of insect tissue culture development before 1962 was reviewed by Day and Grace (1959).

Standard methods to initiate primary culture of insect tissues are as follows: The insects used should be aseptic or surface-sterilized. Tissues or organs to be cultured are excised under sterile conditions. The excised tissues or organs are washed in saline, and cut into small pieces. The resulting tissue fragments are washed again, and transferred into culture flasks with culture medium (explant culture). In some cases, especially *D. melanogaster* cell culture, excised tissues are often dissociated further into single cells by means of partial digestion with an enzyme, and are seeded as separated single cells. Generally, explant culture is common in insect cell culture, and gives better results. At present, techniques for insect cell culture are far from one which enables scientists to make cell culture from any tissue of any species, and improvement of the techniques continues.

In explant culture, cell migration from explants begins soon after the culture is established. These migrated cells generally consist of epithelial-like, fibroblast-like and hemocyte-like cells. The epithelial-like cells and fibroblast-like cells often form cell sheets and cellular networks, respectively, while the hemocyte-like cells do not form any structure. The migrated cells may proliferate by mitoses, and subculture may become possible, if the culture conditions are appropriate. However, usually it takes several months or even years for the cells to proliferate enough to be subcultured. By repeating subcultures, a cell line may become a permanently growing cell population, which is called a continuous cell line.

Physical Conditions

Culture conditions may be divided into physical conditions and chemical conditions. As the former, temperature, pH, osmotic pressure and illumination will be considered. The insect cells are usually cultured. Between 20 and 30°C, the growth rate increases with the rise of temperature. Most of insect cells, however, deteriorate above 30°C. Usually insect cells are not affected by the change in the pH of the culture media between 6.0 and 7.5, and are rather resistant to the change of osmotic pressure. Most insect cell culture media have osmotic pressure between 300 and 400 mOsmol/kg. However, cells may survive even in the medium diluted to half strength. Illumination does not affect on cell survival or growth, although UV or sunlight is harmful to the cells. Photoperiodism has no effect on insect cells either, i.e., long night photoperiod does not induce arrest of cell growth.

Chemical Conditions

For chemical conditions, composition of culture media and gaseous phase will be considered. Cells require inorganic salts for maintaining ion balance, sugars as energy source, amino acids for protein synthesis, vitamins and some growth factors for survival and proliferation. Usually approximately six inorganic salts are used. Na^+, K^+, Ca^{++}, Mg^{++}, PO_4^-, and Cl^- will be required. As energy sources, glucose satisfies the requirement. Usually 20 amino acids, which are constituents of proteins, are incorporated into a medium, although the essential amino acids are arginine, cystine, glutamine, glycine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, proline, serine, threonine, tryptophan, tyrosine, and valine. As vitamins, water-soluble B group vitamins are commonly used. They are, in most media, thiamine, riboflavin, calcium pantothenate, niacin, pyridoxine, biotin, folic acid, *p*-aminobenzoic acid, isoinositol and choline chloride. However, some of them are not essential. For example, the flesh fly

(Diptera: Sarcophagidae) embryonic cell line, NIH-SaPe-4, requires only thiamine, riboflavin, calcium pantothenate and either of niacin or niacinamide. The vitamin requirement by insect cells in culture may depend on cell line species. Most insect cells do not require added lipid-soluble vitamins, such as vitamin A, D, E, and K.

Instead of using individual chemicals, natural substances, which contain necessary substances for cell growth, may be used. Seawater may be used instead of mixtures of inorganic salts. Some protein hydrolysates, such as lactalbumin hydrolysate, casein hydrolysate, egg albumin digest and so on, are used in lieu of mixture of 20 or 21 individual amino acids. Water-soluble yeast extract products contain usually sorts and amounts of vitamins for insect cell growth, and are used instead of the mixture of individual vitamins. The media containing natural substances are called "natural media" whereas those contain only known chemicals are called as "synthetic media".

However, both types of media need to be fortified by addition of sera or some other growth-promoting substances. As sera, heat-treated insect hemolymph or fetal bovine serum (FBS) is used. Among commercially available vertebrate sera, only FBS is markedly growth-promotive. Other sera, such as calf serum bovine serum, horse serum, turkey serum and sheep serum are either ineffective or even detrimental. Other than sera, growth factors or some other growth-promoting substances are used as an additive. As growth factors, only one insect growth factor has been isolated from the flesh fly cell line, so far, NIH-SaPe-4. This growth factor is a polypeptide and acts in autocrine manner, and seems to be species specific, or to have narrow spectrum. Vertebrate growth factors are ineffective on insect cells, except insulin, which is reported to be growth stimulative for *D. melanogaster* cells.

For the gas composition in gaseous phase as well as in media, oxygen is required in large-scale culture of cells. In small-scale culture, insect cells do not consume much oxygen, and the cells can be cultured in tightly capped flasks. For large-scale culture (several liters to several 100 L), however, oxygen supply is necessary, and it is performed by oxygen sparger directly into the media. The control of CO_2 concentration in gaseous phase is not necessary for insect cells, because insect cells are insensitive to the change in the pH of the culture media.

Characteristics of Cells

The structure of the cultured cells varies even in a cell line. The shape and the size of the cells are not uniform. Also, karyotype of the cells varies. Tetraploid cell lines are common among lepidopteran cell lines. The karyotype may change by repeating subculture. Some insect cell lines are substrate-dependent, and form cell sheets. Others are substrate-independent and can grow in suspension. Growth rate is different in different cell lines. The population doubling time distributes from 20 h to several days. Insect cell lines cannot be distinguished morphologically from each other. However, they can be distinguished each other by analyses of karyotype, isozyme pattern, PCR, DNA finger printing, and the combination of these techniques.

Insect cell culture is a good tool for basic studies in various fields. Established cell lines are more or less different from cells in intact insects. The cell lines, however, retain many characteristics that they had when they were in insect bodies. Therefore, cell lines can be used as excellent experimental materials, if one keeps the difference of cells in vivo and in vitro in mind. Insect cell lines have been used in various fields, such as cell physiology, cytogenetics, biochemistry, endocrinology, toxicology, gene technology and pathology. Among them insect cell cultures have been used frequently in the studies of insect pathology, especially virus diseases, for a long time.

Practical Applications

For practical use, insect cell culture is being used in combination with insect viruses for production of foreign protein, and viral insecticides. In the former case, baculovirus vector systems are now widely used to produce proteins not originating from insects. For example, gene encoding human interferon-β is inserted into the polyhedrin gene sequence of NPV, which is previously inserted into an *Escherichia coli* plasmid. The resulting plasmid is transfected with wild virus genome to the NPV-sensitive insect cell line. In this way, recombinant NPV, which contains the human interferon-β gene in the sequence of polyhedrin gene, is obtained. The human interferon-β can be produced by inoculating the recombinant virus to the NPV-sensitive cell culture.

For the production of viral insecticides, the process of cell culture, preparation of inoculum, inoculation, maintenance of infected cells, and harvest of replicated viruses have been almost established. However, when one tries to increase the scale of culture, various problems arise, and the production of viruses by means of large scale culture of insect cells and viruses has not yet been industrialized. The problems to be solved include oxygen supply, avoidance of shear force, and cost of culture media. The insect cell lines may be used for toxicity tests. In the screening tests for insecticides, cultured cells are good materials for screening chemicals, which act on metabolic pathways. Drugs for human such as anti-cancer drugs may be tested at the screening level by the use of insect cells. Insect cells can be cultured without a CO_2 incubator, and are tolerant to the change in pH, osmotic pressure and temperature. These are advantages of using insect cell culture over mammalian cell culture.

References

Day MF, Grace TDC (1959) Culture of insect tissues. Ann Rev Entomol 4:17–38

Goldschmidt R (1915) Some experiments on spermatogenesis in vitro. Proc Natl Acad Sci USA 1:220–222

Grace TDC (1962) Establishment of four strains of cells from insect tissues grown in vitro. Nature 195:788–789

Trager W (1935) Cultivation of the virus of grasserie in silkworm tissue cultures. J Exp Med 61:501–513

Wyatt SS (1956) Culture in vitro of tissue from the silkworm, *Bombyx mori.* LJ Gen Physiol 39:841–852

Celyphidae

A family of flies (order Diptera).

► Flies

Cement

This is a very thin lipid or shellac-like layer of integument outside the wax layer. It serves to protect the wax layer from disruption.

► Integument: Structure and Function

Cenchrus (pl., Cenchri)

A roughened section of the metanotum in sawflies; it serves to hold the wings in place when they are folded over the body.

Census

Complete enumeration of every individual within a defined sample universe. (contrast with sample).

► Sampling Arthropods

Centipedes (Class Chilopoda)

The centipedes are not numerous, numbering about 3,000 species around the world. However, they are widely distributed in both temperate and tropical regions, where they are found in soil, under litter, and beneath stones and bark.

Characteristics

Centipedes usually are 1–10 cm in length, but may be larger in the tropics, where they can attain a length of up to 26 cm. They possess but one pair of legs per segment, a feature that allows them to be easily distinguished from the superficially similar millipedes (Diplopoda). Like many other arthropods (millipedes, pauropods, symphylans), but unlike insects, the centipedes bear a head and a long trunk with many leg-bearing segments. The head bears a pair of antennae, and sometimes ocelli, but not compound eyes. The mouthparts are ventral, and positioned to move forward. Gas exchange is through a tracheal system in which the spiracles cannot be closed. Excretion takes place through malpighian tubules, and unlike insects and arachnids, centipedes excrete ammonia.. The heart is a dorsal tube with paired ostia at each segment. The ventral nerve cord has a ganglion for each body segment. Sperm transfer is indirect, using a spermatophore. Structures called Tömösváry organs are found at the base of the antennae in some centipedes. Apparently it is used to detect vibrations. The orders Geophilomorpha and Scolopendromorpha exhibit epimorphic development; the young have the full complement of segments when they hatch. Development of the other orders is anamorphic; the young have only a portion of their eventual complement of segments upon hatching, and add them as they grow.

Covering the mouthparts of centipedes is a pair of structures called maxillipeds or poison claws. They are derived from the first pair of trunk appendages, but are involved in feeding. Each claw consists of four segments and is curved inward toward the midventral line. A poison gland is found within the base of the claw. Centipedes are well known for their poison claws, but they have other defenses as well. In some, the posterior-most legs may be used for pinching, and repugnatorial glands on the last four legs are common. As with millipedes, defensive secretions may include hydrocyanic acid. Except for the geophilomorphs, centipedes are adapted for running. Interestingly, the legs of some long-legged centipedes are progressively longer toward the posterior of the body, which helps to prevent interference with leg movement. The soil dwelling geophilomorphs do not use their legs for running, and these animals move through the soil using extension and contraction of the body trunk, much the same as earthworms.

Classification

As is the case with many taxa of arthropods, the classification of centipedes is subject to debate. Following is a recent classification system:

Phylum: Arthropoda
Subphylum: Atelocerata
- Class: Chilopoda
  - Subclass: Epimorpha
    - Order: Geophilomorpha
      - Family: Himantariidae
      - Family: Schendylidae
      - Family: Oryidae
      - Family: Mecistocephalidae
      - Family: Geophilidae
      - Family: Chilenophilidae
      - Family: Eriphantidae
      - Family: Dignathodontidae
      - Family: Aphilodontidae
      - Family: Gonibregmatidae
      - Family: Neogeophilidae
    - Order: Scolopendromorpha
      - Family: Scolopendridae
      - Family: Cryptopidae
  - Subclass: Anamorpha
    - Order: Lithobiomorpha
      - Family: Lithobiidae
      - Family: Ethopolidae
      - Family: Watobiidae
      - Family: Gosibiidae
      - Family: Pseudolithobiidae
      - Family: Pterygotergidae
      - Family: Henicopidae
    - Order: Craterostigmomorha
    - Order: Scutigeromorpha
      - Family: Scutigeridae

The Epimorpha are longer centipedes, usually consisting of at least 21 leg-bearing segments. Young epimorphs, upon hatching, bear a full complement of long or short legs. Tömösváry organs are absent. In contrast, the Anamorpha are shorter, usually with 15 leg-bearing segments. Young anamorphs, when the hatch, bear 4–7 pairs of long or very long legs. Tömösváry organs are present. The order Geophilomorpha consists of about 1,000 species, order Scolopendromorpha of a bout 550 species, Lithobiomorpha of about 1,100 species, order Craterostigmomorpha only two species, and Scutigeromorpha about 130 species. The geophilomorphs are long worm-like animals, highly specialized, dwelling in soil, and not primitive, whereas the scutigeromorphs are long-legged forms, commonly found around human habitations, and clearly are primitive. The Scolopendromorpha and Lithobiomorpha both consist of heavy-bodied animals that live beneath stone, bark and logs.

Ecology

Life histories of centipedes are poorly known, but 5–6 instars occur in many species. Longevity is often 3–6 years, and it commonly takes more than a year to attain maturity. It is difficult to separate instars, but head capsule width is most reliable.

The centipedes are predaceous. Most feed on arthropods, snails, earthworms and nematodes, but even toads and snakes are consumed by some. The antennae and legs are used to detect prey. The poison claws are used to stun or kill the prey. Though painful, the bite of centipedes is normally not lethal to humans, resembling the pain associated with a wasp sting.

Centipedes require a humid environment. Their integument is not waxy, and their spiracles do not close. Hence, they are found belowground, in sheltered environments, or active above-ground principally at night. Some centipedes have adapted to a marine existence, living among algae stones and shells in the intertidal zone. Apparently they can retain sufficient air during high tides, or capture a sufficiently bubble of air to allow submersion.

Some centipedes (scolopendromorphs and geophilomorphs) produce a cavity in soil or decayed wood in which to brood their egg clutch, which often numbers 15–35 eggs. The female guards the eggs until the young hatch. Inte remaining taxa, the eggs are deposited singly in the soil.

Reference

Lewis JGE (1981) The biology of centipedes. Cambridge University Press, Cambridge, UK, 476 pp

Central Body

A region in the center of the protocerebrum that serves as an integration point for different types of information, and for activation of body movements associated with the thoracic region. The central body is located between the bases of the stalks of the mushroom bodies. It receives input from both sides of the brain, and from the optic lobes.

► Central Body

Central Dogma

The Central Dogma was proposed by F. Crick in 1958. It states that the genetic information is contained in DNA, which is transcribed into RNA, which is translated into polypeptides. The transfer of information was proposed to be unidirectional from DNA to polypeptides: polypeptides are unable to direct synthesis of RNA, and RNA is unable to direct synthesis of DNA. The Central Dogma was modified in 1970 when RNA viruses were found to transfer information from RNA to DNA.

Central Nervous System (CNS)

In insects, the central nervous system consists of the brain, ventral ganglia, and the ventral nerve cord. The ventral ganglia and connecting nerve cord usually lie close to the cuticle on the ventral side of the body. The brain occurs on top of the esophagus, and is sometimes called the supraesophageal ganglion.

► Nervous System

Centromere

A region of a chromosome to which spindle fibers attach during mitosis and meiosis. The position of the centromere determines whether the chromosome will appear as a rod, a J, or a V during migration of the chromosome to the poles in anaphase. In some insects, the spindle fibers attach throughout the length of the chromosome and such chromosomes are called holocentric. Centromeres are usually bordered by heterochromatin containing repetitive DNA.

Cephalothorax

The fused head and thorax of Arachnida and Crustacea, and of coccids.

Cephidae

A family of sawflies (order Hymenoptera, suborder Symphyta). They commonly are known as stem sawflies.

► Wasps, Ants, Bees and Sawflies

Cerambycidae

A family of beetles (order Coleoptera). They commonly are known as longhorned beetles.

► Beetles
► Longicorn, Longhorned, or Round-headed Beetles (Coleoptera: Cerambycidae)

Cerambycoid Larva

A larval body form that is straight, somewhat flattened or cylindrical, smooth or naked, and distinctly segmented. They tend to be found in wood or soil, and occur in the families Cerambycidae, Buprestidae, and Elateridae (all in order Coleoptera).

Ceraphronidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Ceratocanthid Scarab Beetles

Members of the family Ceratocanthidae (order Coleoptera).

► Beetles

Ceratocanthidae

A family of beetles (order Coleoptera). They commonly are known as ceratocanthid scarab beetles.

► Beetles

Ceratocombidae

A family of bugs (order Hemiptera).

► Bugs

Ceratophyllidae

A family of fleas (order Siphonaptera). They sometimes are called bird and rodent fleas.

► Fleas

Ceratopogonidae

A family of flies (order Diptera). They commonly are known as biting midges, punkies or no-see-ums midges.

► Flies
► Biting Midges, *Culicoides* sp. (Diptera: Ceratopogonidae)

Cercoccidae

A family of insects in the superfamily Coccoidae (order Hemiptera).

► Bugs

Cercophanidae

A family of moths (order Lepidoptera) also known as Andean moon moths.

▶ Andean Moon Moths
▶ Butterflies and Moths

Cercopidae

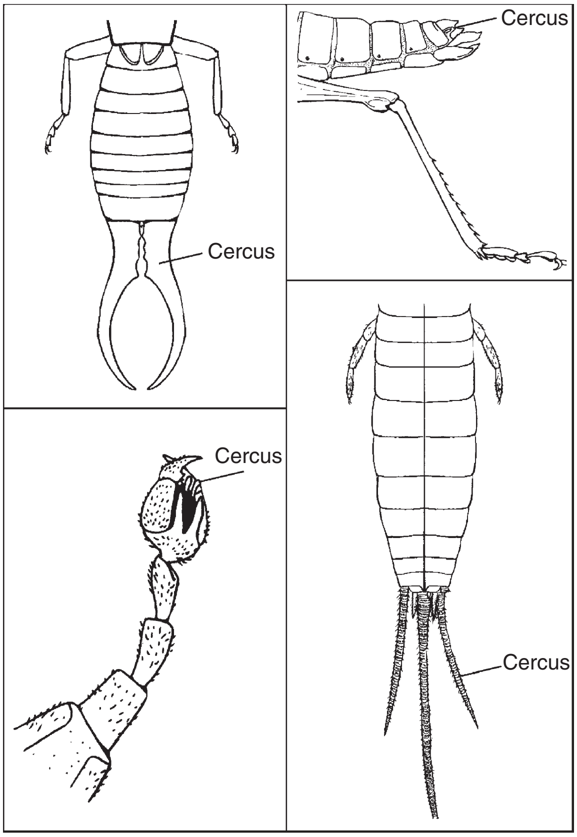
A family of insects in the order Hemiptera. They sometimes are called froghoppers or spittlebugs.

▶ Bugs

Cercus (pl., cerci)

A sensory appendage (Fig. 36) located near the tip of the abdomen, usually on abdominal segment ten. In many insects the c erci are antenna-like in shape, paired and jointed.

▶ Abdomen of Hexapods



Cercus, (pl., cerci) Figure 36 Diagrams of the tip of the abdomen in various hexapods, showing various forms of the cercus. Top left, earwig; top right grasshopper, lower left, scorpionfly; lower right silverfish.

Cereal Leaf Beetle, *Oulema melanopus* (Linnaeus) (Coleoptera: Chrysomelidae)

This leaf-feeding beetle is a pest of small grain crops.

▶ Wheat Pests and their Management

Cereal Stem Moths (Lepidoptera: Ochsenheimeriidae)

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Cereal stem moths, family Ochsenheimeriidae, include only 17 species from the Palearctic (one sp. is from Kashmir), with one sp. introduced into North America. The family is part of the superfamily Yponomeutoidea in the section Tineina, subsection Tineina, of the division Ditrysia. Adults small (9–17 mm wingspan), with head very roughened; eyes large; haustellum short and naked; labial palpi tufted; maxillary palpi 2-segmented; antennae often basally swollen in males. Wings rather elongated but fringes average. Maculation somber hues of brown or gray, with indistinct markings. Adults are diurnal. Larvae are leafminers, but become stem borers in later instars, primarily on grasses (Gramineae), sedges (Cyperaceae) and rushes (Juncaceae). The common name for the family is derived from the single economic species, the cereal stem moth. Some place the family as a subfamily of what is grouped as the "family" Ypsolophidae (the latter actually a subfamily of Plutellidae). The family and nominate genus *Ochsenheimeria* are named after the German lepidopterist Ferdinand Ochsenheimer (1767–1822).

References

Davis DR (1975) Review of Ochsenheimeriidae and the introduction of the cereal stem moth *Ochsenheimeria vacculella* into the United States (Lepidoptera: Tineoidea). Smithsonian Contrib Zool 192:1–20

Davis DR (1998) Ochsenheimeriidae. In Lepidopterorum Catalogus, (n.s.). Fasc 48. Association for Tropical Lepidoptera, Gainesville, FL, 12 pp

Karsholt O, Nielsen ES (1984) A taxonomic review of the stem moths, *Ochsenheimeria* Hübner, of northern Europe (Lepidoptera: Ochsenheimeriidae). Entomol Scand 15:233–247

Réal P (1966) Famille des Ochsenheimeriidae. In: Balachowsky AS (ed) Entomologie Appliquée à l' Agriculture. Tome 2: Lépidoptères, 254–255. Paris, 1057 pp

Zagulajev AK (1988) Family Ochsenheimeriidae. In: Fauna SSSR. 4. Lepidoptera, 7: 70–177. Acad. Nauk. [in Russian], St. Petersburg

Cerebellum

The subesophageal ganglion, a portion of the visceral nervous system that innervates many of the appendages associated with feeding.

► Nervous System

Cerebrum

The portion of the brain above the esophagus; the region before the subesophageal ganglion. There are three recognized portions, the proto-, deutero- and tritocerebrum.

► Nervous System

Cerococcidae

A family of insects in the superfamily Coccoidae (order Hemiptera). They sometimes are called ornate pit scales.

► Bugs

Cerumen

A brown mixture of wax and propolis used by social bees for nest construction.

Cervical Shield

A plate on the dorsal surface of caterpillars just behind the head. It is also known as the prothoracic plate or shield.

Cervix

The membranous region between the head and thorax (Fig. 37). The cervix is analogous to the neck in vertebrates.

Cervical Sclerites

Small chitinous plates on the membrane between the head and the thorax.

Cerylonidae

A family of beetles (order Coleoptera). They commonly are known as minute bark beetles.

► Beetles

Cestodes or Tapeworms

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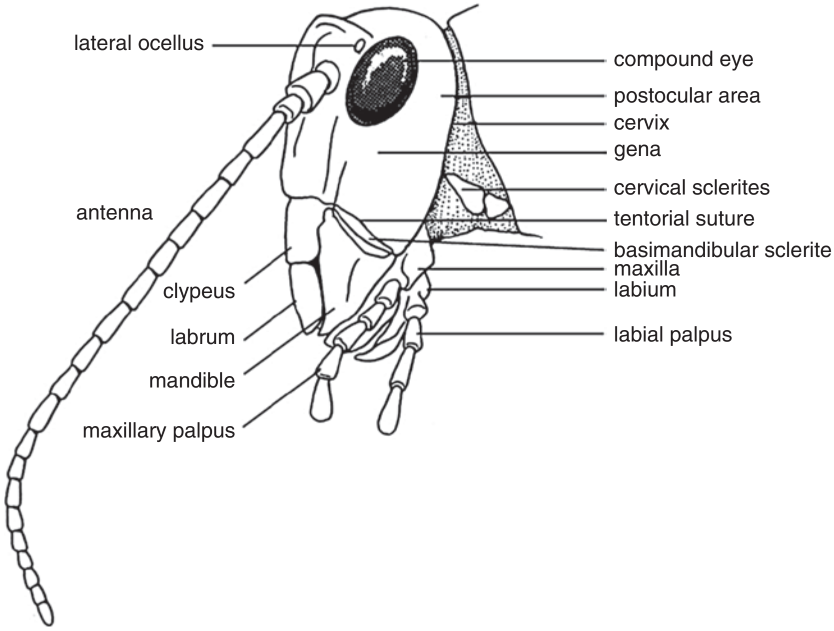
The majority of tapeworms (phylum Platyhelminthes, order Cestoda) that have terrestrial life cycles utilize two hosts. The adult worms are found in the gut lumen of the final, or definitive host, where they undergo sexual reproduction and produce eggs that contain a developing embryo protected



Cervix, Figure 37 **Side view of the head of an adult grasshopper, showing some major elements.**

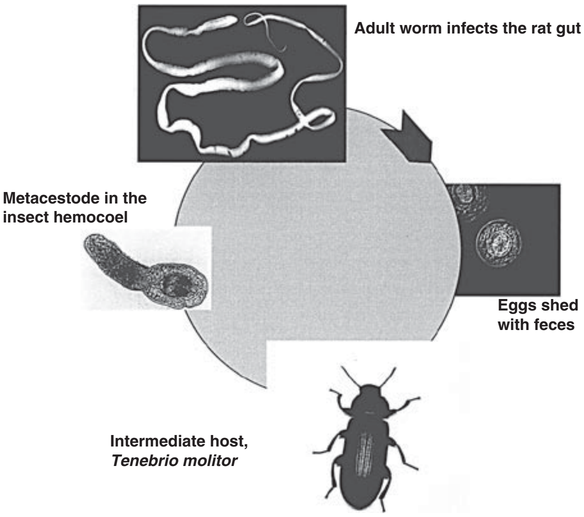
by several membranes. These eggs are shed into the environment with the host feces, either still contained within the tapeworm segment, or proglottis, in which they developed, or free from it. The life cycle continues when eggs are ingested by an intermediate host, often a coprophagous insect or other arthropod. They hatch within the insect gut and burrow through the gut wall with the help of 3 pairs of curved hooks and the lytic contents of a pair of glands. In the hemocoel, they transform into a metacestode and, once mature, will be transmitted and the life cycle completed if their intermediate host falls prey to another definitive host.

Fecal material from infected definitive hosts may be more attractive to insects than that from uninfected hosts, as is the case for feces from rats infected with a rate tapeworm, *Hymenolepis diminuta*. This enhances the chances of the cestode's life cycle being completed. Another rat tapeworm, *Raillietina celebensis* (also an occasional parasite of humans), provides an example of the means whereby a non-coprophagous insect becomes an intermediate host. Gravid proglottides, detached from the main tape and remaining intact, are picked up from the fecal material by ants, carried to the nest and fed to the ant larvae. Some larval fleas also ingest tapeworm eggs when feeding on host feces. The immature worms develop with the larval flea and are ingested by the definitive host when the adult flea is accidentally eaten during grooming. Dogs become infected with the dog tapeworm, *Dipylidium caninum*, in this way and, for the latter species, so do cats and occasionally humans.

Prevalence of cestode infection in the definitive host may be linked with seasonal changes in feeding patterns. Thus, a study of the shrew *Sorex araneus araneus* in Poland demonstrated that a spring and summer diet including the coprophagous beetle, *Geotrupes stercorosus*, gave rise to infections with *Ditestolepis diaphana* and *Staphylocystis furcata* in the summer and autumn. Whereas in the winter and spring, the predominance of *Pseudodiorchis prolifer* infections in the shrew reflected a change of diet in the autumn and winter to the myriopod intermediate host of this latter cestode, as beetles were difficult to find.

Due to the trophic nature of tapeworm transmission, definitive hosts of cestodes associated with insects are partially or entirely insectivorous. Thus, with the possible exception of cestode infections in the poultry industry, tapeworms that utilize insect intermediate hosts are of no medical or veterinary importance and have, therefore, attracted little research attention. The exception is the rat tapeworm, *H. diminuta*, which has been the doyen of cestode laboratory research models due to the ease with which its life cycle can be maintained.

Several insects act as intermediate hosts for the rat tapeworm including fleas and cockroaches (Fig. 38), but laboratory studies have focused upon the effect of infection on the flour beetles, *Tribolium* spp. and *Tenebrio molitor*. Long-term studies have revealed that infection results in a 50% depression in the equilibrium population of *T. confusum* as a result of fecundity reduction in the females. The mechanism underlying fecundity reduction has been extensively studied in *T. molitor*, and appears to result both from the host response to the presence of the parasite and to the direct action of a factor(s) produced by the early developmental stages of the parasite. Several aspects of the process of vitellogenesis or the production and uptake of yolk protein are affected. In the ovary, yolk uptake by developing follicles is retarded and they contain less protein than their equivalents from uninfected beetles. The presence of a competitive inhibitor of the binding site of juvenile hormone to the follicular epithelium results in a retardation in the development of patency in the follicular epithelium, thereby affecting yolk uptake. Synthesis of yolk protein in the fat body also is inhibited but, in this case, by a factor of parasite origin that is peptidergic in nature. The effect of infection on male reproductive physiology is not as well studied. An increase in the size, protein and trehalose content of the bean-shaped accessory glands has been reported and this may account for an increase in protein and trehalose content of spermatophores produced by infected males. In contrast, male response to female sex pheromone is decreased by infection. The effect of these changes on the number of offspring produced by females mated with infected males is yet to be established unequivocally.



Cestodes or Tapeworms, Figure 38 The life cycle of *Hymenolepis diminuta*, an example of an insect-associated cestode.

Although cestodes cause a reduction in the reproductive fitness of beetles, it has been demonstrated that the life span of infected female *T. molitor* is increased by 40% and males by 25%. This may be due to changes in resource management such that longevity is increased when fewer resources are devoted to reproduction.

The production of aggregation pheromones is down-regulated by infection, and several aspects of behavioral response to environmental cues are altered, although this does not appear to increase the chance of host predation by rats. However, defensive glands are everted less frequently, and toluquinone and m-cresol production are reduced, possibly accounting for the greater likelihood that infected beetles will be eaten by rats. This may thus represent an example of host manipulation that will enhance transmission prospects.

References

Blankespoor CL, Pappas PW, Eisner T (1997) Impairment of the chemical defence of the beetle, *Tenebrio molitor*, by metacestodes (cysticercoids) of the tapeworm, *Hymenolepis diminuta*. Parasitology 115:105–110

Carver FJ, Gilman JL, Hurd H (1999) Spermatophore production and spermatheca content in *Tenebrio molitor* infected with *Hymenolepis diminuta*. Insect Physiol 45:565–569

Hurd H (2001)Parasite regulation of insect reproduction: similar strategies, different mechanisms? In: EdwardsJP, Weaver RJ (eds) Endocrine interactions of parasites and pathogens. Bios Scientific Publishers, Oxford, UK

Kisielewska K (1961) Circulation of tapeworms of *Sorex araneus araneus* L. in biocenosis of Bialowieza National Park. Acta Parasitol Pol 9:31–369

Webb TJ, Hurd H (1999) Direct manipulation of insect reproduction by agents of parasite origin. Proc R Soc Lond B Biol Sci 266:1537–1541

Chaeta (pl., chaetae)

An outgrowth of the cuticle originating in a pit. It is an articulated spine-like process.

Chaeteessidae

A family of praying mantids (Mantodea).

► Praying Mantids

Chaetotaxy

The arrangement and nomenclature of chaetae (setae). This is used to create a setal map.

Chaff Scale, *Oulema melanopus* (Linnaeus) (Coleoptera: Chrysomelidae

This is an occasional pest of citrus trees.

► Citrus Pests and their Management

Chafers

Members of the subfamily Melolonthinae, family Scarabaeidae (order Coleoptera).

► Beetles

Chagas, Carlos Justiniano Ribeiro

Carlos Chagas was a Brazilian physician who discovered Chagas disease (Chagas' disease), or American trypanosomiasis. Chagas disease is an endemic insect-borne disease found in Central and South America from Mexico to Argentina. It is caused by the protozoan *Trypanosoma cruzi*. In discovering this malady, he became the only individual investigator so far who described completely all elements of the disease: the pathogen, vector, host, clinical manifestations, and epidemiology. He also developed a new and effective approach to malaria control, a technique that remains the principal method for malaria suppression around the world.

Chagas was born on July 9, 1879 in Oliveira, in the state of Minas Gerais, Brazil. He was the son of upper-class parents who owned a small coffee plantation. His ancestors had come to Brazil in the seventeenth century. His father died when Carlos was only 4 years old, and at the age of seven he was sent to a Jesuit boarding school. There he was befriended by a priest who instilled in him a love of natural history. Following his mother's wishes that he should become an engineer, at the age of 14 he enrolled in the School of Mining Engineering in Oro Pieto, Minas Gerais. However, at the age of 16 he was afflicted with beri-beri and spent some time with his uncle Carlos Ribeiro de Castro, an M.D. who had just established a new hospital. Brazil at this time was struggling to develop because it had so many endemic diseases. For example, many European ships refused to dock in Brazil for fear of their crews contracting yellow fever, bubonic plague, smallpox and other diseases. Chagas' uncle convinced him that through the practice of medicine he could perform important national service. Influenced by his uncle, in 1897 Chagas abandoned the plan to become an engineer and entered the Faculty of Medicine of Rio de Janeiro where he received his M.D. in 1903.

Chagas had opportunity early in his career to conduct research, but was attracted by clinical practice in a hospital in Jurujuba. Following financial problems, in 1905 Chagas accepted a position with a company in the interior of the state of São Paulo, where malaria was a serious problem for workers. Studying the transmission cycle closely, he realized that workers were being bitten while sleeping. Up to this time, the only known effective preventative approach for malaria control was destruction of larvae in breeding areas (swamps). As this was not effective, he began to use the insecticide pyrethrum to disinfect houses. This approach proved to be very successful.

Chagas moved to the Oswaldo Cruz Institute in 1906, which became his base of operations for the remainder of his career. In 1909, Cruz asked Chagas to undertake an antimalaria campaign in Lassance, Brazil, where railroad construction was stalled because so many workers had succumbed to malaria. There he remained for 2 years, living and working in a railroad car. He soon noticed disease symptoms that were not consistent with malaria, and later some locals pointed out to him a blood-sucking bug called "vinchuca" that commonly were found in the huts of workers. This blood-sucking insect, an assassin bug or kissing bug (Hemiptera: Reduviidae), was later determined to be in the genus *Triatoma*, several species of which transmit a disease later named Chagas disease. Chagas dissected the *Triatoma* bugs and found within them a trypanosome (Protozoa). Allowing the bugs to feed on marmoset monkeys, he found that the trypanosome could be transmitted. He identified the trypanosome and named it *Schizotrypaum cruzi* after his mentor and friend Oswaldo Cruz. Later it became known as *Trypanosoma cruzi*. Suspecting that these bugs could be transmitting the trypanosome to people due to their great abundance in rural homes, and their blood-feeding habits, Chagas soon found tryanosomes in the blood of a young girl. He also conducted autopsies of workers dying with acute and chronic forms of the disease, and found brain and myocardium abnormalities accounting for the involvement of these organs in the new disease. He conducted surveys of animals in the area, and determined that armadillos were the likely reservoir of the trypanosomes.

The acute phase of Chagas disease occurs in the first few weeks or months of infection. Often it is symptom-free or exhibits only mild symptoms and signs that are not unique to Chagas disease. The symptoms noted by the infected individual may include fever, fatigue, aches of the head or body, rash, loss of appetite, diarrhea, and vomiting. The signs of infection include mild enlargement of the liver or spleen, swollen glands, and local swelling (a chagoma). The most easily recognized indication of acute Chagas disease is called Romaña's sign, which includes swelling of the eyelids on the side of the face near the bite wound or where the bug feces were deposited or accidentally rubbed into the eye. Symptoms, if present, usually fade away after a few weeks or months. However, if untreated, the disease persists. Occasionally young children die from severe inflammation of the heart muscle or brain. The acute phase is more severe in immuno-compromised people. The chronic phase of infection may result in no signs of infection for decades or even for life. However, some people develop heart problems including an enlarged heart, heart failure, altered heart rate or rhythm, and cardiac arrest. Also, intestinal problems can occur, including an enlarged esophagus or colon, which can lead to difficulties with eating or defecation.

Chagas was widely recognized for his noteworthy achievements. He was elected to the National Academy of Medicine in 1910, and in 1912 he received the Schaudinn Prize for outstanding work in protozoology and tropical medicine. He was twice nominated for the Nobel Prize, but never received the award. In 1922, Chagas was recognized with the Great Prize of the Pasteur Centenary Commemorative Exposition in Strasbourg. He was awarded honorary doctorate degrees from Harvard University and the University of Paris.

Chagas took over direction of the Institute in 1917 following the death of Oswaldo Cruz, and remained in this position until 1934. During this period the Brazilian government asked him to organize a campaign against Spanish influenza, which was devastating Rio de Janeiro, and also to reorganize the Department of Health in Brazil (he also served as director from 1920–1924). There he introduced many innovations and created centers of preventative medicine. He died in Rio de Janeiro from a heart attack on November 8, 1934.

► Chagas Disease or American Trypanosomiasis
► Trypanosomes

References

Lewinsohn R (1979) Carlos Chagas (1879–1934): the discovery of *Trypanosoma cruzi* and of American trypanosomiasis (foot-notes to the history of Chagas's disease). Trans R Soc Trop Med Hyg 73:513–523

Lewinsohn R (2003) Prophet in his own country: Carlos Chagas and the Nobel Prize. Perspect Biol Med 46:532–549

Chagas Disease: Biochemistry of the Vector

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Chagas disease is caused by the parasitic protozoan *Trypanosoma cruzi*, which is transmitted by blood-feeding insects in the subfamily Triatominae (Hemiptera: Reduviidae), with 130 species forming five tribes, among them only the tribes Triatomini and Rhodniini possess relevant vector capacity. *Triatoma infestans* (Klug) (Fig. 39) and *Rhodnius prolixus* (Stål) are representative examples of each tribe, and the most thoroughly studied, as they are the major ones responsible for Chagas disease transmission. Triatomins are called kissing bugs or assassin bugs; local names are *vinchuca*, *chinche* or *picudo*. *Trypanosoma cruzi* infects some 16–18 million people, with another 90 million at risk in regions of South and Central America. There is neither a vaccine against it, nor a safe and effective drug to cure it. Fundamental research in insect physiology was pioneered by V.B. Wigglesworth using *R. prolixus*. Most biochemical studies in Triatominae are focused on blood intake, digestion, fat body and integumental lipid metabolism and transport, and molting.

Chagas Disease: Biochemistry of the Vector, Figure 39 ***Triatoma infestans*, a major vector of Chagas disease in South America.**

Feeding

Insect blood feeding impacts directly on human and animal health. When a blood meal is taken, the pathogen *T. cruzi* might be transmitted via excreta deposited on the host skin. *Rhodnius prolixus* is capable of ingesting 300 mg of blood in 15 min. Such highly efficient blood intake is made possible by a special mouthpart developed to avoid blood coagulation and platelet aggregation. Purification, cloning, expression, and mechanism of action of a novel platelet aggregation inhibitor from the salivary gland of *R. prolixus* was recently reported. Serotonin and other major biogenic amines in insects, dopamine and octopamine, have been reported to modulate a variety of physiological and behavioral functions, including the control of feeding behavior in insects. Feeding was found to be a natural stimulus for the release of serotonin into the hemolymph of *R. prolixus*, and serotonin depletion led to a reduced blood meal size in this insect. Triatomins produce bioactive molecules in their salivary glands that are inoculated into host skin via saliva during feeding. Four closely related proteins found in *Rhodnius saliva* behave as immunomodulators, countering their host's haemostatic, inflammatory and immune responses to facilitate blood feeding, exhibiting vasodilator, anticoagulant and antiplatelet aggregation activity. Because they bind nitric oxide, and act as a storage and delivery system for it, they are named nitrophorins. As a consequence of hematophagia, triatomins feed on a protein- and lipid- rich diet, with fatty acids as the major source for energy production. This results in a much larger yield in the amounts of ATP produced, as compared to that of insects consuming carbohydrate. The fat body is the major metabolic factory, as well as the main storage depot of fat, glycogen and protein. Its metabolites are transported to target organs via hemolymph.

Protein Metabolism

Many of the proteins that are crucial in the life of insects are biosynthesized in the fat body. Protein synthesis is often under control of juvenile hormone (JH).

Complete hydrolysis of blood-meal proteins is mediated by exo- and endo-peptidases. Endoproteinases cleave proteins to smaller segments that are finally completely degraded to amino acids by exopeptidases. Triatominae midgut also contains endopeptidases B and D, involved in hemoglobin hydrolysis. Salivary glands have acid phosphatase activity with anticoagulant properties to destroy hemoglobin; large amounts of sialidase activity are also detected after a blood meal, rich in sialic acids. Hemoglobin digestion and detoxification of the free haem by its sequestration into an insoluble pigment known as haemozoin (Hz) were recently detected in the midgut of *R. prolixus*.

Blood meals trigger the onset of diuresis after the diuretic hormone is released by the neurosecretory cells of the mesothoracic ganglionic mass. Insects then undergo a rapid elimination of urine during which time the insect may lose 40% of the weight of the meal. Multiple diuretic peptide factors have been suggested, and the serotonin role is well described. Uric acid is the most important nitrogenous waste material excreted by triatomins. It is formed through the uricotelic pathway by *de novo* synthesis from protein.

Reproduction

Egg production is under hormonal and nutritional control; a blood meal is required to start vitellogenesis, and juvenile hormone (JH) secretion by the corpora allata (CA) regulates oocyte development. The amount of blood required for oviposition varies from 5 to 8 mg/egg for R. prolixus to 16–25 mg/egg for *T. infestans*. Vitellogenins (VG) are high molecular weight lipoproteins synthesized in the fat body of adult females. They enter the oocytes by pinocytosis to be converted into vitellins (VN). A molecular weight around 4×10^5 was estimated for different species, after characterization by immunodiffusion (ID), immunoelectrophoresis (IEP), and electrophoresis in polyacrylamide gel (PAGE). Vitellogenin synthesis also has been detected in *R. prolixus* ovaries.

Lipid Composition, Metabolism, and Transport

A high lipid content (7–8%) is characteristic of eggs, and remains high through the first instar in *T. infestans*. It is close to 1.5% throughout the whole nymphal cycle to adult stage. Major insect and egg lipids are triacylglycerols (85%) with energy storage function; phospholipids (4–8%), mainly phosphatidylethanolamine and phosphatidylcholine, are involved in cell membrane formation and metabolic events; and the major sterol component is cholesterol, sequestrated from host blood and stored as cholesterol esters or free (5–8%), which contributes to lipid bilayer fluidity regulation. Small amounts of saturated hydrocarbons (straight and multiple methyl-branched chains of 27 to >41 carbons), primary fatty alcohols (straight chains of 24–34 carbons) and wax esters (44–48 carbons) confer water-proofing properties to the cuticular surface, also preventing chemicals and microorganism penetration.

The major whole-body insect fatty acid components are oleic (18:1) and palmitic (16:0), with minor amounts of linoleic (18:2), stearic (18:0), palmitoleic (16:1) and arachidonic (20:4) acids. Minor components play specific functions; for example, volatile fatty acids of short chains (VFA) formed in the Brindley glands, are released upon disturbance and serve as defensive secretion, with isobutyric acid accounting for most of their characteristic stink odor.

Very long chain fatty acids (VLCFA), up to 34 total carbons, are also present in the triatomin integument, and are detectable precursors to hydrocarbon and fatty alcohol formation. Specific fatty acids precursors to cuticular waxes formation are detected in minute amounts in the integument: methyl-branched fatty acids of 16 and 18 carbons in the straight carbon chain are intermediates in methyl-branched hydrocarbon synthesis.

Dietary lipids are the only source of 18:2 and 20:4 acids in Triatominae, which lack both Δ 5 and Δ 6 desaturating enzymes. These polyunsaturated components contribute to membrane fluidity and they are precursors to the eicosanoids prostaglandins, molecules of significance in reproduction. Large amounts of 20:4 acids are stored in male testes. They are metabolized into prostaglandins (PG) and transferred to females via spermatophores during copulation. Eicosanids also participate in the immune response, i.e., to help clear bacteria from contaminated hemolymph, and to regulate fluid balance.

Fatty acid biosynthesis was extensively studied in the whole insect, the fat body, the integument and reproductive organs, both in tissue slices and after subcellular fractionation. *De novo* fatty acid assays employed radioactive precursors such as [^{14}C]acetate or [^{14}C]propionate by injection into the hemolymph for in vivo or tissue slice assays; [^{14}C]acetyl-CoA or [^{14}C]malonyl-CoA were used in cell-free assays. Whole insect, fat body or integumental tissue mostly metabolize [^{14}C]acetate into triacylglycerols (ca. 80%) and phospholipids (>10%). The major fatty acids formed are 16:0, 18:1, 18:0 and 16:1, produced by a cytosolic fatty acid synthetase (FAS) and a Δ 9 desaturase.

Metabolites are incorporated into hemolymph lipoproteins (Lp) that serve multiple functions in insect development and reproduction. They transport nutrients from the site of absorption or the site of synthesis to the site of utilization and storage in target tissues. Other than vitellogenin, three lipoproteins have been identified in triatomins, a high density lipoprotein (HDL) also named lipophorin, and two very high density lipoproteins, VHDL-1 and VHDL-2. Their apo-proteins are polypeptides from 17 to 210 kdaltons (kDa), with a 86 kDa common component. Lipid transport is mediated by lipophorin, an ubiquitous lipoprotein, that is widely distributed among insects. It functions as a reusable shuttle for neutral and polar lipid transport in Triatominae. HDL from the hemolymph of *T. infestans* has an apparent molecular weight of 670 kDa, with an isoelectric point of 7.0 and a density (δ) of 1.10 g/ml. It contains 53% protein and 47% lipid. The protein moiety consists of two apoproteins: apoLp-I (255 kDa) and apoLp-II (70–80 kDa), rich in the amino acids aspartic acid, glutamic acid, and leucine. Diacylglycerols constitute 41% of the total lipids, and satisfy the major energy requirement in insects. HDL is also the vehicle for transport of phospholipids, hydrocarbons, and cholesterol. It also behaves as a free fatty acid donor to VHDL, a hexameric storage protein (δ = 1.27 g/ml) with a putative role related to amino acid and free fatty acid supply involved in molting, metamorphosis and reproduction events. Lipophorin binding sites located on the surface of the oocyte, mainly at the microvilli, mediate phospholipid transfer from the hemolymph to the oocytes.

The Integument

The bulk of triatomins cuticular proteins are soluble in urea 7 M, with eight major bands separated by electrophoresis. They contain large amounts of hydrophobic and polar uncharged amino acids. The abdominal cuticle is extensible through the fifth instar, and chitin accounts for <20% (w/w). When *Rhodnius* takes a blood meal, a plasticizing factor is secreted which lowers the pH of the cuticle, and this changes the degree of bonding between cuticular proteins. Therefore, the cuticle becomes more flexible and the abdomen is dramatically expanded up to nearly four times, with the cuticle becoming very thin. Chitin synthesis is started by depletion of glycogen and trehalose from storage sites for conversion to UDP-N-acetylglucosamine units, which are further polymerized to chitin, an aminopolysaccharide. Chitin synthesis occurs mostly in the fat body; its formation is under ecdysteroid regulation. Chitin is not responsible for the hardness of the integument; instead this attribute is associated with tanned proteins, their degree of sclerotization and their distribution among the polysaccharide matrix.

Molting evokes major biochemical changes in the cuticle of Triatominae. In preparation for molting, chitinase and proteinase are secreted to digest the less sclerotized cuticle, but have no effect either on exocuticle or on the surface lipids. The oenocytes, modified epidermal cells, are the site of integumental lipid synthesis. They transfer newly formed hydrocarbons to hemolymph, which functions as a selective shuttle, storing methylbranched chains while releasing to the site of deposition, the epicuticular surface, straight and methylbranched chains in a 1:1 ratio. Inhibition of cuticular lipid synthesis in *T. infestans* was shown to raise detrimental effects on hatch and insect development, water barrier properties, and to enhance chemical and microbial insecticide penetration; complete degradation of *T. infestans* hydrocarbons by fungal pathogens was recently shown.

► Assassin Bugs
► Area-Wide Pest Management
► Chagas Disease or American Trypanosomiasis

References

Brenner RR (1987) Chagas disease vectors. Lipid composition and metabolism. In: Brenner RR, Stoka AM (eds) Chagas disease vectors. Biochemical aspects and control, vol 3. CRC Press, Boca Raton, FL, USA, pp 9–35

Juárez MP (1994) Hydrocarbon biosynthesis in *Triatoma infestans* eggs. Arch Insect Biochem Physiol 25:193–206

Champagne DE, Nussenzveig RH, Ribeiro JM (1995) Purification, partial characterization, and cloning of nitric oxide-carrying heme proteins (nitrophorins) from salivary glands of the blood-sucking insect *Rhodnius prolixus*. J Biol Chem 270:8691–8695

Rimoldi OJ, Córsico B, Gonzalez MS, Brenner RR (1996) Detection and quantification of a very high density lipoprotein in different tissues of *Triatoma infestans* during the last nymphal and adult stages. Insect Biochem Mol Biol 26:705–713

Wigglesworth VB (1933) The physiology of the cuticle and of ecdysis in *Rhodnius prolixus*. Q J Microsc Sci 76:269–318

Chagas Disease or American Trypanosomiasis

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Chagas (or Chagas') disease is named after its discoverer, the Brazilian physician Carlos Chagas. It is caused by the trypanosome (protozoan) parasite *Trypanosoma cruzi*. This pathogen is transmitted to animals and people by kissing bugs (Hemiptera: Reduviidae: Triatominae) (Table 10). The disease occurs in the western hemisphere from Mexico to Argentina (Fig. 40), primarily in rural areas where poverty is widespread. It is estimated that as many as 18 million people in Mexico, Central America, and South America have Chagas disease. Interestingly, most of these victims do not know they are infected because the acute symptoms fade away. If the disease remains unrecognized and untreated, however, there can be serious consequences later in life and the disease ultimately can be life threatening. About 50,000 people die each year from complications caused by Chagas disease.

Chagas Disease or American Trypanosomiasis, Table 10 The major vectors of Chagas disease and their distribution

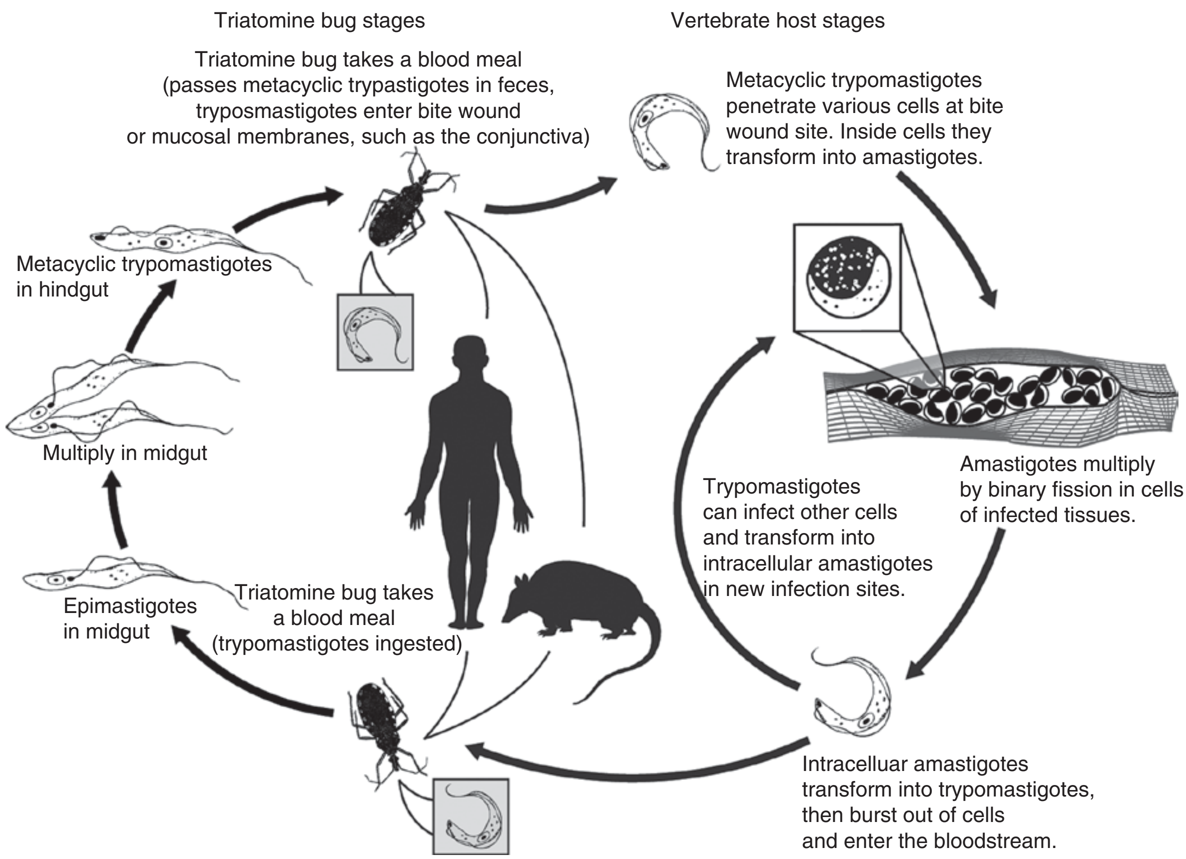
Species	Geographic distribution
Panstrongylus herreri	northern Peru
Panstrongylus megistus	Brazil, Paraguay, Argentina, Uruguay
Rhodnius prolixus	southern Mexico south to Colombia and Venezuela
Rhodnius pallescens	Panama, Colombia
Triatoma infestans	Peru, Bolivia, Brazil, Paraguay, Argentina, Uruguay, Chile
Triatoma dimidiata	Mexico south to Ecuador and Peru
Triatoma pallidipennis	Mexico
Triatoma phyllosoma	Mexico
Triatoma maculata	Colombia, Venezuela, Guyana, Suriname
Triatoma brasiliensis	Brazil
Triatoma guasayana	Bolivia, Paraguay, Argentina
Triatoma sordida	Bolivia, Brazil, Paraguay, Uruguay, Argentina

Chagas Disease or American Trypanosomiasis, Figure 40 The distribution of Chagas disease in Latin America; shaded areas indicate regions where Chagas disease is most likely to occur.

The acute phase of Chagas disease occurs in the first few weeks or months of infection. Often it is symptom-free, or exhibits only mild symptoms and signs that are not unique to Chagas disease. The symptoms noted by the infected individual may include fever, fatigue, aches of the head or body, rash, loss of appetite, diarrhea, and vomiting. The signs of infection include mild enlargement of the liver or spleen, swollen glands, and local swelling. The most easily recognized indication of acute Chagas disease is called Romaña's sign, which includes swelling of the eyelids on the side of the face near the bite wound or where the bug feces were deposited or accidentally rubbed into the eye. Symptoms, if present, usually fade away after a few weeks or months. However, if untreated, the disease persists. Occasionally young children die from severe inflammation of the heart muscle or brain. The acute phase is more severe in immunocompromised people. The chronic phase of infection may result in no signs of infection for decades or even for life. However, some people develop heart problems including an enlarged heart, heart failure, altered heart rate or rhythm, and cardiac arrest. Also, intestinal problems can occur, including an enlarged esophagus or colon, which can lead to difficulties with eating or defecation. A toxin is responsible for the destruction of tissues.

Although Chagas disease occurs primarily in the rural areas in Latin America, the movement of large numbers of people from rural to urban areas of Latin America, and to other regions of the world, has increased its geographic distribution. It is a growing threat in the United States and the Caribbean region, where Chagas disease is not endemic; it is estimated that about 500,000 unknowingly infected immigrants now live in these more northern countries. In these areas, where kissing bugs are not common or not likely to bite humans, Chagas management should focus on preventing transmission from blood transfusion, organ transplantation, and mother-to-baby (congenital) transmission. Nevertheless, there are ominous reports of *Trypanosoma cruzi* occurring in wild animal (raccoon, opossum) populations as far north as North Carolina. The triatomine bugs indigenous to North America are capable of transmitting Chagas disease (Fig. 41). The failure of Chagas to be a problem in the USA is attributed to the low incidence of infected bugs (6%) and vertebrate hosts (15%), but also to the habit of the northern species not to defecate immediately after feeding, so even if humans are bitten the bugs are less likely to defecate on humans in North America than in Central and South America.

In Chagas-endemic areas, the principal route of infection is by being bitten by triatomine bugs, primarily *Triatoma* spp., and especially *T. infestans*. The bugs contract the typanosomes by feeding on infected animals or people. The bite of kissing bugs typically produces little or no pain, so the



Chagas Disease or American Trypanosomiasis, Figure 41 The Chagas disease cycle in triatomine bugs and animal hosts (adapted from CDC).

sleeping host is usually unaware of the blood-feeding episode. Once infected, the bugs pass *T. cruzi* parasites in their feces. The bugs frequently aggregate in barns, sheds or houses if they are not insect-proof. In rural areas, many houses are made from materials such as mud, adobe, straw, and palm thatch, and lack window screening and in some cases, doors. Thus, there is nothing to prevent entry of the bugs. During the day, the bugs hide in crevices in the walls and roofs. If the roof is straw or another material with cracks and crevices, the bugs can hide easily and are not readily detected. Then, during the night, when the inhabitants are sleeping, the bugs emerge to feed. (Bugs may feed during the day if their hosts are nocturnal, such as bats.) Because they tend to feed on people's faces, triatomine bugs have also come to be known as "kissing bugs." After they bite and ingest blood, they commonly defecate on the person. The person becomes infected if *T. cruzi* parasites in the bug feces enter the victim's body through mucous membranes or breaks in the skin. The unsuspecting, sleeping person may accidentally scratch or rub the feces into the bite wound, eyes, or mouth, facilitating entry of the trypanosomes. This is the principal form of *T. cruzi* entry into humans, but disease transmission also occurs through consumption of uncooked food contaminated with feces from infected bugs, congenital transmission (from a pregnant woman to her baby), blood transfusion, organ transplantation, and (rarely) accidental laboratory exposure. Animals can contract the disease by consuming infected prey, as in consumption of mice by household cats.

The natural reservoirs of *Trypanosoma cruzi* are wild animals such as monkeys, opossums, amphibians, lizards, armadillos, sloths, bats, porcupines and ground squirrels. These natural hosts do not develop pathologies. However, *T. cruzi* is also harbored in infected humans, and domestic animals like cats, dogs, rabbits, and guinea pigs. Canine trypanosomiasis is of veterinary importance in Latin America. In nature, kissing bugs are found in hiding places such as caves, tree holes, hollow trees, fallen logs, palm fronds and epiphytes. Though kissing bugs feed on birds, and the bugs can be quite numerous in chicken houses on farms, birds seem to be immune against infection and therefore are not considered to be a *T. cruzi* reservoir. The different vectors of Chagas disease have differing host preferences, so the disease transmission cycle varies accordingly.

The generalized infection cycle is as follows: The infected triatomine bug ingests blood and defecates feces containing trypomastigotes near the feeding site. The victim, irritated by the bite, scratches the area, thereby rubbing the trypomastigote-containing feces into the wound or into intact but susceptible mucosal membranes, such as the conjunctiva. Once inside the host, the trypomastigotes invade cells, where they differentiate into intracellular amastigotes. The amastigotes multiply by binary fission and differentiate into trypomastigotes, which are released into the bloodstream. Cells from a number of different tissues are susceptible to infection by the trypomastigotes, and once inside, they transform into intracellular amastigotes at new infection sites. Intracellular amastigotes destroy tissues such as the intramural neurons of the autonomic nervous system in the intestine and heart, leading to digestive and heart problems, respectively. Replication resumes only when the parasites enter another cell or are ingested by another vector. The final step in the cycle is infection of the vector, which occurs when the bug feeds on an infected host containing trypomastigotes. Once ingested by the bug, the ingested trypomastigotes multiply and differentiate (amastigote and epimastigote forms) in the midgut and transform into infective metacyclic trypomastigotes in the hindgut. The feces may contain thousands of metacyclic tryptomastigotes.

Management of bugs to disrupt disease transmission is possible. In many areas of Latin America, the interiors of houses are treated with pyrethroid insecticides to eliminate kissing (*Triatoma*) bugs. At least two South American countries have rid themselves of the problem in this manner. However, complete control is difficult to accomplish, and houses are often reinfested because some bugs escape the insecticide within the homes by hiding, or because the homes are reinvaded from nearby, untreated areas. Animal shelters are often good harborages for *Triatoma*, and if they are not adequately treated and are near homes, the bugs quickly disperse to the treated home. A distance of at least 1,500 m is considered necessary as a buffer zone between untreated and treated harborages. An economic and effective alternative to chemical control is bed nets, though the edges of the net must be tucked beneath the mattress to assure that bugs cannot enter. Also, the net and mattress must be large enough that the human sleeping beneath the net does not come into contact with the bed netting, because there is risk that bugs will feed through the netting if the human is immediately adjacent. The logistics and cost of meeting these requirements often prove daunting to poor people, so insecticide treatment is more practical. Likewise, improved housing and sanitation would virtually eliminate this problem, but achieving this is presently not possible due to the cost.

Detection of infection is often done by examining the patient's blood to look for trypanosomes or *T. cruzi*-specific antibodies. However, a procedure called "xenodiagnosis" is sometimes used, wherein laboratory-reared bugs free of trypanosomes are fed on patients, incubated, and then examined for presence of trypanosomes in the alimentary tract. Xenodiagnosis is very sensitive because the trypanosomes, even if few in number in the human host, build up to large numbers in the bug and are easily detected.

Treatment of infected people is difficult because medication is usually effective only if administered during the acute phase, and many victims are unaware of their condition. This issue is compounded by the resistance of the trypanosome to medication is some regions, and by the toxicity and side effects of the drugs. During the chronic phase of infection, treatment consists mostly of treating the symptoms, and both heart replacement and intestinal surgery are practiced. Treatment in either the acute or chronic phase does not guarantee a cure. A vaccine was developed in the 1970s and it proved fairly successful, but implementation is constrained by the high cost of production.

The effect of Chagas disease is measured less by mortality and more by morbidity. Chronically infected people often suffer decades of weakness and fatigue that effectively removes them from the workplace and prevents them from enjoying a normal life. This results in considerable social disruption and economic loss. A survey of the incidence of Chagas disease found that about 12% of the residents of Chile and Paraguay were infected, and in Argentina and Bolivia the rate was 8%.

► Assassin Bugs, Kissing Bugs and Others (Hemiptera: Reduviidae)
► Chagas
► Chagas Disease: Biochemistry of the Vector
► Trypanosomes
► Area-Wide Pest Management

References

Beard CB, Gordon-Rosales C, Durvasula RV (2002) Bacterial symbionts of the Triatominae and their potential use in control of Chagas disease transmission. Ann Rev Entomol 47:123–141

Brenner RR, Stoka AM (eds) Chagas disease vectors, vols 1–3. CRC Press, Boca Raton, FL

Dias JCP, Schofield CJ (1999) The evolution of Chagas disease (American Trypanosomiasis) control after 90 years since Carl Chagas discovery. Memorias do Instituto Oswaldo Cruz 94:103–121

Kirchhoff LV (1993) American trypanosomiasis (Chagas disease) – a tropical disease now in the United States. N Engl J Med 329:639–644

Zeledón R, Rabinovich JE (1981) Chagas' disease: an ecological appraisal with special emphasis on its insect vectors. Ann Rev Entomol 26:101–133

Chalaza (pl., chalazae)

A pimple-like protuberance of the body wall bearing a seta. Chalazae are commonly found on larvae.

Chalcididae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Chalkbrood

A fungus disease of honey bee larvae caused by *Ascosphaera apis*. The disease causes the larvae to become mummified, and usually to take on chalky white appearance, but sometimes gray or black. Early in the infection process the larvae are covered with a fluffy white growth of mycelia, but later they shrink and acquire the chalky appearance. Though not usually considered serious, occasionally it can be damaging. It occurs widely, though often going unnoticed. Young bees are susceptible to infection, and normally are infected after being fed spores and then exposed to cool weather. Because the chilling is necessary, it is usually the cells at the periphery of the hive that are infected.

Bees usually acquire the disease by ingestion of honey or pollen, and the spores successfully overwinter and remain infective for many years. Poor ventilation and excessive precipitation and humidity are associated with greater expression of this disease. Poor nutrition is also a factor, as is colony weakening due to other diseases, mites, and poor beekeeping practices. The pathogen can also be acquired from native bees.

Management is usually accomplished by reversing the conditions that bring about expression of the disease: improved ventilation, better nutrition, keeping the hives closed during winter, and better sanitation. Destruction of infected hives is helpful. Antibiotics are not usually suggested.

► *Ascosphaera API*

► Honey Bees

► Apiculture

Reference

Morse RA, Nowogrodzki R (1990) Honey bee pests, predators and diseases, 2nd edn. Cornell University Press, Ithaca, NY, 474 pp

Chamaemyiidae

A family of flies (order Diptera). They commonly are known as aphid flies.

► Flies

Chaoboridae

A family of flies (order Diptera). They commonly are known as phantom midges.

► Flies

► Aphids

Charipidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Chaudoir, Maximilien Stanislavovitch De

Maximilien de Chaudoir was born on September 12, 1816, at Ivnitza, a village in the Ukraine. He inherited the title of Baron which had been conferred on his grandfather by King Maximilien Joseph of Bavaria, and had later been made hereditary by Czar Nicholas I of Russia. His private tutor was Jean Wavre, who interested him in natural history. In 1831 he was sent to study law to Dorpat (Tartu), but there spent most of his time working on the insect collections assembled by J.F. Eschholtz. In 1834 he was made a member of the Société Entomologique de France, and the following year (at the age of 18) presented his first entomological paper at one of its meetings. After his return to the Ukraine, his entomological collection, especially of Carabidae, grew by purchase from collectors and dealers and from his own collecting expeditions in the Ukraine and other Russian territories in the Caucasus. He published frequently in the Bulletin de la Société Imperiale des Naturalistes de Moscou. In 1863 he moved to

France, later transporting his worldwide collection of Carabidae there and working on it until his death on May 6, 1881. His publications include 108 works on Carabidae including major taxonomic revisions, and are written mainly in French, although he knew Russian, German, English, and Italian. His collection was acquired in 1952 by the Muséum National d' Histoire Naturelle of Paris.

References

Ball GE, Erwin TL (1982) The Baron Maximilien de Chaudoir: inheritance, associates, travels, work, and legacy. Coleopt Bull 36:475–501

Basilewsky P (1982) Baron Maximilien de Chaudoir (1816–1881) [including a bibliography]. Coleopt Bull 36:462–474

Champion, George Charles

George Champion was born in London on April 29, 1859. He became interested in beetles early in his life, and was employed in his late twenties by Frederick Godman and Osbert Salvin to collect beetles for the Biologia Centrali-Americana project in Central America. Later, he wrote for the project and assisted in editing its publications. His taxonomic work on beetles then continued, and he wrote many publications on specimens collected by his son H.G.C. Champion in India, eventually publishing more than 420 papers. He died in Woking, England, on August 8, 1927.

Reference

Herman LH (2001) Champion, George Charles. Bull Am Mus Nat Hist 265:54–55

Chapman, Reginald Frederick

ELIZABETH A. BERNAYS
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Reg Chapman was born at London, England on July 2, 1930. He obtained a bachelor's degree in zoology in 1951 at Queen Mary College of London University, United Kingdom. Then, with a scholarship from the Anti-Locust Research Centre he studied factors governing roosting behavior in locusts, first in the laboratory in London and later in Africa. Chapman lived and worked in a locust outbreak area in one of the smaller valleys of the East African rift system from 1953 to 1957. There was no town, electricity, phone or radio. He was one of the first to make quantitative observations on insect behavior in the field, and one of few combining field and lab work (he built his own house and lab). He soon learned that the locusts did not sundown, and if he really wanted to understand what was governing their behavior he needed to work as they demanded – a lesson he passed on to many. In this remote place Reg Chapman made his first contributions to behavior of locusts and grasshoppers (and lizards), including relationships between hemolymph potassium levels and feeding activity. He was strongly influenced by three extremely rigorous scientists who guided his PhD – Boris Uvarov, Donald Gunn, and John Kennedy.

At the University of Ghana he studied host-finding by tsetse flies for 2 years. In 1959, Reg was appointed to a faculty position at Birkbeck College (another college of the University of London). His main responsibility was to teach invertebrate zoology and advanced entomology. Subsequently, he developed a masters course which he taught single-handed, and this led to what he is best known for – The Insects – Structure and Function. First published in 1969, this book with its various revisions and finally a total rewrite (1998) has been a major resource for students, teachers, and researchers round the world.

At Birkbeck, Chapman extended his interests in insect feeding to include the sensory system, with locusts and grasshoppers as models with a small, but quite productive, research group including Liz Bernays who was to become his wife. One finding, that insects can differentiate between plants on the basis of the surface wax on the leaves, was quite novel at the time, and his interest in the plant surface continued. He initiated work on chemoreceptor physiology with another student, Wally Blaney, and on the significance of receptor numbers among other things. He was successively, lecturer, University Reader and University Professor in the University of London.

In 1970, Chapman became Director of the Research Division at the Anti-Locust Research Centre and as well as continuing research, directed studies on other topics such as insect flight, plant chemistry and insects and crop plant resistance. As the Centre increased its coverage of insect pests in developing countries, he developed and was responsible for, a wide range of research programs in many parts of the world – groups in the Philippines working on brown planthopper of rice, in India on varietal resistance of sorghum to pests, in Botswana on sorghum pests, in Nigeria on a pest grasshopper, the impact of soil termites on grasslands, and the impact of pesticide use on non-target organisms, and in Mali a radar group studying grasshopper migration. He spent a week at a time with each, examining data and discussing the next steps. As well as revising The Insects at that time, he wrote a small book on locust biology.

When Liz Bernays was offered a position in Berkeley in 1983, Reg Chapman, in his usual way of putting others first, went with her to an unsalaried situation. However, in 1987, the University of Arizona made irresistible offers to both, and Chapman was a professor of insect neurobiology until his retirement in 2001. In Arizona, his work on taste physiology was productive, with the help of several postdocs and students.

Besides The Insects, and A Biology of Locusts, Reg wrote Host-plant Selection by Phytophagous Insects with Liz, edited four books, and wrote 20 critical reviews, ten book chapters, 110 research papers, and twenty entries for encyclopedias and other popular books. Reg's research accomplishments and reviews, especially in the area of feeding behavior and physiology, are a major contribution, but much of the work he did is under the authorship of others – he always wanted his students and coworkers to get the credit. Similarly, he was a major influence on hundreds of graduate students; he loved to help them, and constructively criticize all who came to him, not just the 37 he formally guided. His breadth of knowledge and his ability to quickly see to the heart of a problem was legendary. He cared deeply about getting it right and doing it properly. He will be remembered as one of the most modest, yet broadly knowledgeable and critical entomologists, and a great classroom teacher. Reg Chapman died at Tucson, Arizona on May 2, 2003.

Checkered Beetles

Members of the family Cleridae (order Coleoptera).

► Beetles

Cheek

The lateral part of the head between the compound eye and the mouth.

Chela

The terminal portion of a limb that bears a claw-like structure. This term is sometimes used to describe the forelegs of mantids, which effectively grasp prey.

Chelating Agent

A molecule capable of binding metal atoms; one example is EDTA, which binds Mg^{++}.

Chelicera (pl. chelicerae)

The pincer-like first pair of mouthpart appendages in arachnids.

Chelisochidae

A family of earwigs (order Dermaptera). They sometimes are called black earwigs.

► Earwigs

Chelonariidae

A family of beetles (order Coleoptera). They commonly are known as turtle beetles.

► Beetles

Cheloniform Larva

A larva that is oval or circular, strongly flattened, and with a concealed head; resembling a turtle.

Chemical Ecology of Insects

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Ecology is the study of the effects on organisms of their biotic (i.e., living) and abiotic (i.e., nonliving) environments. Chemical ecology is simply the study of the effects on organisms of chemicals produced by living organisms in their environment (i.e., their biotic environment). Thus, chemical ecology is a sub-discipline of ecology, emphasizing interactions within and among species that are mediated by chemicals. The behavior and/or physiology of all major groups of organisms examined to date, from bacteria to plants to insects to humans, are to some extent influenced by chemicals produced and released into the environment by other organisms.

Chemical ecology as a recognized scientific discipline came into being in the early 1970s. At this time there was increasing interest in non-pesticidal methods of insect control because of the growing awareness of environmental problems caused by persistent, toxic pesticides. Simultaneous rapid advances in the instrumentation required to analyze minute amounts of chemicals found in nature (i.e., gas chromatographs, mass spectrometers and nuclear magnetic resonance spectroscopes) spurred the development of chemical ecology.

Over the last 30 years, the breadth of insect chemical ecology has increased from the study of insects interacting within one trophic level to two-trophic level interactions involving insects and their food organisms to multitrophic-level interactions. Chemical ecologists work on problems ranging from applied to basic in nature. For many chemical ecologists, the primary goal of their research is to find ways to reduce insect populations to acceptable levels without using broad-spectrum insecticides by changing the insects' behavior so that they inflict less harm on our food, our livestock and us. Other chemical ecologists study the chemical ecology of insects to understand better the more basic aspects of their species of interest; who is related to whom, why they eat a particular food plant and not others, how they defend themselves, etc…

The chemicals that mediate interactions between organisms in nature are termed semiochemicals. This comes from the Greek word "semeon" which means a mark or a signal. The semiochemicals that mediate interactions between organisms of the same species (intraspecific interactions) are pheromones whereas semiochemicals that mediate interactions occurring between different species (interspecific interactions) are allelochemicals.

Pheromones were the first semiochemicals that received intense scientific study and to date, well over 500 have been identified, most of these being sex attractant pheromones of Lepidoptera. Insects use pheromones to communicate with members of their species to facilitate reproduction (sex pheromones), locate food sources (trail pheromones), warn of danger (alarm pheromones) and maintain the function and cohesion of large colonies (many pheromones of social insects). We can use pheromones to disrupt communication among members of a pest species so that they do less damage to our crops and animals. We can also use pheromones to detect the presence of insect pests, monitor their changes in population size, and time applications of insecticides or other control measures.

Interspecific interactions, involving insects and other insects, plants or other organisms, are mediated by allelochemicals. These chemicals are significant to organisms of a species different from their source, for reasons other than food. Three types of allelochemicals are recognized: allomones, kairomones, and synomones. The designation of a particular chemical depends on which species in the interaction benefits and which, if any, is harmed after perceiving the chemical. For example, an allomone is a chemical that is produced or acquired by one organism that causes a behavioral or physiological response in the receiver of another species that is beneficial to the emitter but not to the receiver. The organism, either plant or insect, releasing the allomone is benefited by preventing a potential predator from eating it. The receiver of the allomone is harmed because it is denied what would otherwise be a suitable meal.

Many plants produce allomones that repel herbivorous insects and protect their tissues from herbivore damage. Ecologists, such as Gottfried Fraenkel, Paul Erhlich and Peter Raven, in the 1950s and 1960s suggested that the huge diversity of insect-repellent and deterrent chemicals found within angiosperm plants might actually have evolved in response to the selection pressure of feeding by herbivorous insects. Today, most ecologists believe that these secondary plant compounds, so named because they did not appear to have a function in the primary metabolism of plants as nutrients or structural compounds, probably arose as defenses against plant pathogens and to help in plant-plant competition rather than as defenses against insects; however, their effects on insects are undisputed.

Allomones in the cabbage plant family (the Brassicaceae) are the reason that relatively few insects feed on these plants. Most members of this plant family produce sulfur-containing compounds called glucosinolates that deter feeding of herbivores. These chemicals give mustard, collard and turnip greens their distinct taste (which many humans consider an "acquired" taste). Volatile breakdown products of the glucosinolates, the isothiocyanates and other compounds, which repel most insects, give the condiment mustard its pungent aroma. Plants in the squash, pumpkin and melon family (the Cucurbitaceae) are well defended with exceedingly bitter large steroid-type molecules called cucurbitacins. Most insects will not feed on wild species of the Cucurbitaceae because of the bitter cucurbitacins. However, when humans began domesticating these crops for human consumption, they selectively bred out the bitter taste and reduced the levels of the allomones that the plants use to defend themselves. Thus, cucurbit species grown for human consumption are non-bitter and are readily attacked by many pest insects.

Chemical ecologists can apply their knowledge of plant-produced allomones for pest management by developing them as biopesticides or by increasing their levels in non-edible portions of a crop with the help of plant breeders. Azadirachtin from the Indian neem tree *Azadirachta indica*, oils of various herbs such as mint, rosemary, and thyme, pyrethrum from chrysanthemums, and rotenone from the roots of the legume *Derris*, among others, have all been developed as botanical insecticides or plant protectants because of their toxic or repellent effects on insects.

Many insect species produce allomones, often surprisingly similar in structure to those of plants, which repel or deter predators that may try to eat them. For example, *Heliconius* butterflies and *Zygaena* moths release the cyanogenic glycosides, linamarin and lotaustralin, which break down to release hydrogen cyanide, when predators threaten them. Coincidently, clover and birdsfoot trefoil also rely on the same cyanogenic glycosides to deter herbivores and grazers. The venoms of wasps, bees and ants are allomones that are highly deterrent to predators, including the human variety. The list of allomones synthesized or acquired by insects to defend themselves is lengthy and is reviewed elsewhere.

A second group of allelochemicals is the kairomones. A kairomone is a semiochemical that is produced or acquired by an organism that causes a behavioral or physiological response in the receiver of a different species that is beneficial to the receiver but not to the emitter. We know that many species of predators and parasitoids are attracted to their hosts or prey by volatile chemicals (kairomones) released by the prey or from by-products of the prey (e.g., pheromones and excretory products such as frass and honeydew). For example, some species of ant-decapitating flies in the genus *Pseudacteon* (family Phoridae) are attracted to their hosts, worker fire ants in the genus *Solenopsis* (family Formicidae), by the odor of the ants' alarm pheromone. Specialist herbivorous insects (those that oviposit on and whose larvae feed on only a narrow range of plant species) use distinct chemicals produced by their host plants as signposts or guides to their plants. For example, moths that specialize on plants in the cabbage family, such as the cabbage white butterfly *Pieris rapae*, are attracted to the volatile isothiocyanates, which are allomones for most other insects that do not feed on cabbage. Thus a kairomone can be a chemical cue that the emitter legitimately uses as a pheromone or an allomone but that an illegitimate receiver turns to its advantage. A single chemical compound could be called a pheromone, a kairomone or an allomone, depending on who benefits, the emitter or the receiver.

The last class of semiochemicals that is recognized today is the synomones. This term was proposed for chemicals that mediate mutualistic interactions in which both the emitter and the receiver benefit. For example, the blend of chemicals released by plants when under attack by herbivorous insects may properly be called a synomone when it attracts parasitoids or predators that then parasitize the insect herbivore, thus reducing the damage to the plant. The receiving organism, the parasitoid, benefits by being provided an additional source of cues with which to help it locate a potential host. For example, the braconid parasitoid, *Cardiochiles nigriceps*, is attracted to tobacco, cotton and corn plants that have been damaged by larvae of its host, the tobacco budworm *Heliothis virescens* (Noctuidae), by volatile chemicals that are released by the damaged plants. Interestingly, the synomonal blend released by the plant is specific to the herbivorous insect that is feeding on it; the parasitoid ignores plants that have been damaged by larvae of a closely related noctuid, the corn earworm *Helicoverpa zea*, which is not a viable host for this parasitoid.

The odor of flowers that attracts pollinating insects can also be considered synomonal because it is beneficial to both the flower whose pollination is ensured and, usually, to the receiving insect, which is guided to a necessary resource – nectar, pollen, or some other reward. However, some plants have turned their synomones into allomones, by attracting insects and then providing them with nothing in return. For example, many species of orchids in the Mediterranean and other places in the world attract male bees and wasps of certain species with floral odors that mimic the sex pheromone of their own species. The males are attracted to the flower and attempt to mate with it. During this "pseudocopulation", the flower is pollinated but the male insect gains nothing, and is perhaps even harmed by wasting its time and energy on an activity that will not increase its genetic fitness.

► Alarm Pheromones
► Allelochemicals
► Attraction of Insects to Organic Sulfur Compounds in Plants
► Host Location in Parasitic Wasps
► Host Marking Pheromones
► Host Plant Selection by Insects
► Natural Enemy Attraction to Plant Volatiles
► Pheromones
► Plant Secondary Compounds and Phytophagous Insects

► Pyrrolizidine Alkaloids and Tiger Moths
► Sex Attractant Pheromones
► Social Insect Pheromones
► Tritrophic Interactions

References

Bell WJ, Cardé RT (eds) (1995) Chemical ecology of insects 2. Chapman & Hall, New York.
De Moraes CM, Lewis WJ, Paré PW, Alborn HT, Tumlinson JH (1998) Herbivore-infested plants selectively attract parasitoids. Nature 393:570–573
Dicke M, Grostal P (2001) Chemical detection of natural enemies by arthropods: an ecological perspective. Ann Rev Ecol Syst 32:1–23
Harborne JB (2001) Twenty-five years of chemical ecology. Nat Prod Rep 18:361–379
Haynes KF, Yeargan KV (1999) Exploitation of intraspecific communication systems: illicit signallers and receivers. Ann Entomol Soc Am 92:960–970
Morehead SA, Feener DH Jr (2000) Visual and chemical cues used in host location and acceptance by a dipteran parasitoid. J Insect Behav 13:613–625
Schiestl FP, Ayasse M, Paulus HF, Löfstedt C, Hansson BS, Ibarra F, Francke W (1999) Orchid pollination by sexual swindle. Nature 399:421–422

Chemigation

Application of agricultural chemicals, including insecticides, through the irrigation system.

Chemokinesis

A kinesis response with respect to a chemical gradient.

Chemoreceptor

A sense organ that perceives chemical stimuli.

Chemotaxis

A taxis with reference to a chemical gradient (taste, odor).

Chestnut Gall Wasp Classical Biological Control in Japan

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The chestnut gall wasp, *Dryocosmus kuriphilus* Yasumatsu (Hymenoptera: Cynipidae), is one of the most serious chestnut-tree pests. It is thelytokous and univoltine. This wasp is now thought to have originated in China and to have been accidentally introduced from there into Japan around 1940. Chestnut gall wasp was also introduced into South Korea and Georgia, in the southeastern United States, in 1958 and 1974, respectively, probably via Japan.

The adult emerges from the gall during a relatively brief part of the early summer, and immediately lays eggs inside chestnut buds (Fig. 42) When the buds start to develop the following spring, immature larvae that hatched in the previous year resume their growth, and the galls begin to swell rapidly. Consequently, in heavily infested trees, the yields of chestnuts are diminished, and the trees themselves may die.

Chestnut Gall Wasp Classical Biological Control in Japan, Figure 42 ***Dryocosmus kuriphilus*** **ovipositing on the bud of a chestnut tree (photo by S. Moriya).**

After entering Japan, the pest spread so fast that it was distributed throughout most of Japan by the end of the 1950s, seriously damaging chestnut production. Because the larva of chestnut gall wasp is protected by the thick wall of the gall, no method of chemical control was feasible. But chestnut gall wasp could be controlled very effectively at first by using resistant chestnut varieties. Therefore, all of the susceptible varieties of chestnut trees were rapidly replaced by resistant ones. However, a stronger strain of chestnut gall wasp emerged, and the galls began to appear again around 1960, even on the highly resistant varieties. The breakdown of resistance alarmed chestnut growers, because the use of resistant varieties was the only available method of controlling the pest.

After diplomatic relations between Japan and China were re-established in 1972, a Japanese entomologist found that chestnut gall wasp had been recorded on a Chinese chestnut, *Castanea mollissima* Blume, much earlier in China than in Japan. Furthermore, it was found that chestnut gall wasp had not been a serious pest in China even though Chinese chestnut varieties were highly susceptible to chestnut gall wasp. Thus, a Chinese parasitoid, *Torymus sinensis* Kamijo (Hymenoptera: Torymidae), was selected for introduction to Japan. In the spring of 1982, a mere 260 mated females were released onto Japanese chestnut trees, *C. crenata* Sieb. et Zucc., growing on the grounds of the National Institute of Fruit Tree Science (NIFTS), Tsukuba, about 50 km northeast of Tokyo. Like chestnut gall wasp, the parasitoid is univoltine, and yet the population of *T. sinensis* in Japan increased steadily year after year. The density of *T. sinensis* females in 1989 was more than 25 times higher than that in 1983. *T. sinensis* is now completely dominant among the native parasitoids of chestnut gall wasp at NIFTS. The effect of the 1982 release of *T. sinensis* on the chestnut gall wasp population was evaluated by observing gall formation ratios (Fig. 43) on chestnut trees. Infestation of chestnut gall wasp steadily decreased after the release until it reached a level of about 3% in 1988, then decreased to < 1% in the early 1990s.

Chestnut Gall Wasp Classical Biological Control in Japan, Figure 43 ***Torymus sinensis*** **attacking a gall of** ***Dryocosmus kuriphilus*** **(photo by S. Moriya).**

Thus, the single release of *T. sinensis* at NIFTS ultimately reduced chestnut gall wasp infestation to a level far below that which chestnut trees can tolerate (the tolerable injury limit is about 30% infestation of current shoots). The rate at which *T. sinensis* expanded its distribution range was also determined. The parasitoid spread gradually during the first few years, at a rate of <1 km/year, followed by more rapid and accelerated spreading in the next few years. In the spring of 1989, *T. sinensis* was detected in an area more than 12 km from NIFTS. Since then, a steady expansion, at a constant rate of about 60 km per year (=per generation), has been observed. Consequently, the parasitoids seem to have dispersed by themselves several hundred kilometers from the point of release by the mid-1990s.

In Kumamoto Prefecture, in southwestern Japan, *T. sinensis* was also released in 1982 and was later confirmed to have become established there. However, unlike the case in Tsukuba, the population density did not increase significantly. This delay in population increase might be attributable to the high mortality of *T. sinensis* associated with the activity of native facultative hyperparasitoids.

A native Japanese parasitoid, *T. beneficus* Yasumatsu et Kamijo, which is closely related to *T. sinensis*, consists of at least two strains that differ from each other only in the time of the adult emergence period. The female of either strain of *T. beneficus* has a shorter ovipositor sheath than does the female of *T. sinensis*, whereas the male *T. beneficus* cannot be distinguished morphologically from the male *T. sinensis*. The emergence period of *T. sinensis* is in between those of the two strains of *T. beneficus* and more or less overlaps them. Thus, it should be noted that crossing between *T. sinensis* and *T. beneficus* occurs under natural conditions. When these two torymids were artificially crossed, morphologically intermediate females were observed among the offspring, and they were fertile. Although there was no evidence of direct competition between *T. sinensis* and *T. beneficus*, the number of *T. beneficus* apparently decreased after *T. sinensis* was introduced into the chestnut groves at NIFTS.

References

Moriya S, Inoue K, Mabuchi M (1989) The use of *Torymus sinensis* to control chestnut gall wasp, *Dryocosmus kuriphilus,* in Japan. Food Fertilizer Technology Center Technical Bull 118:1–12

Moriya S, Inoue K, Shiga M, Mabuchi M (1992) Interspecific relationship between an introduced parasitoid, *Torymus sinensis* Kamijo, as a biological control agent of the chestnut gall wasp, *Dryocosmus kuriphilus* Yasumatsu, and an endemic parasitoid, *T. beneficus* Yasumatsu et Kamijo. Acta Phytopathol Entomol Hung 27:479–483

Murakami Y (1997) Natural enemies of the chestnut gall wasp: approaches to biological control. Kyushu University Press, Fukuoka, Japan, 308 pp (in Japanese)

Murakami Y, Gyoutoku Y (1995) A delayed increase in the population of an imported parasitoid, *Torymus (Syntomaspis) sinensis* (Hymenoptera: Torymidae) in Kumamoto, southwestern Japan. Appl Entomol Zool 30:215–224

Shiga M (1997) Classical biological control of the chestnut gall wasp, *Dryocosmus kuriphilus:* present status and interactions between an introduced parasitoid, *Torymus sinensis,* and native parasitoids. In: Yano E, Matsuo K, Shiyomi M, Andow DA (eds) Biological invasions of ecosystem by pests and beneficial organisms. National Institute of Agro-Environmental Sciences, Tsukuba, Japan, pp 175–188

Chevrolat, Louis Alexandre Auguste

Auguste Chevrolat was born in Paris on March 29, 1799. He had numerous sisters, and was brought up not by his parents but by his grandmother and a maternal aunt in the town of Melun. He showed an early interest in natural history, collecting birds and all sorts of insects, but decided to specialize in beetles. He made friends with notable entomologists (Latreille, Duméril, Dejean, and Guérin) and began to publish descriptions of new species of insects, the first being Doryphora 21-punctata published in Magasin de Zoologie. He was charged by Duponchel to edit the section on chrysomelids for the dictionary directed by d' Orbigny. In 1832 he was a founding member of the Société Entomologique de France, and in 1875 was elected an honorary member of it. He published more than 180 papers during his lifetime, his two most frequent outlets were Annales de la Société Entomologique de France, and Magasin Zoologique, and he published more on Curculionidae (in the broad sense) than on any other insect family. He died on December 16, 1884.

Reference

Reiche L (1884) Notice necrologique sur Auguste Chevrolat. Ann Soc Entomol Fr (6) 4:357–360

Chewing and Sucking Lice (Phthiraptera)

This order of wingless ectoparasitic insects is thought to have evolved from barklice (Psocoptera).

Certainly it is not difficult to imagine insects dwelling *in* animal nests (many Psocoptera) evolving into insects that dwell *on* birds and mammals (Phthiraptera), and morphologically they are similar. Traditionally, the order Phthiraptera has been treated as two separate orders (or two suborders), the chewing lice (Mallophaga) and the sucking lice (Anoplura). However, modern treatment of this group has Mallophaga divided into three suborders (Amblycera, Rhyncophthirina, Ischnocera), with Anoplura the fourth suborder. Both chewing and sucking lice are obligate parasites, and cannot survive long off their hosts. They are the only truly parasitic group among the exopterygote insects. They display remarkable host specificity, and most individuals spend their entire life cycle on a single host. They relocate opportunistically only when individuals are in close proximity, and so they have developed diverse morphology due to their high degree of isolation. Their basic specializations are based on feeding on skin debris, fur, feathers, and blood. The order name (Phthiraptera) is derived from the Greek words "phtheir" (louse), plus "a" (without), and "pteron" (wing).

Classification

About 3,000 species of chewing lice from around the world are distributed in three suborders, and often associated with specific bird hosts, but sometimes mammals. There are about 15 families of sucking lice, containing only about 500 species, though many species probably remain to be described. Most species of lice are quite host specific. Some families have common names that reflect their hosts.

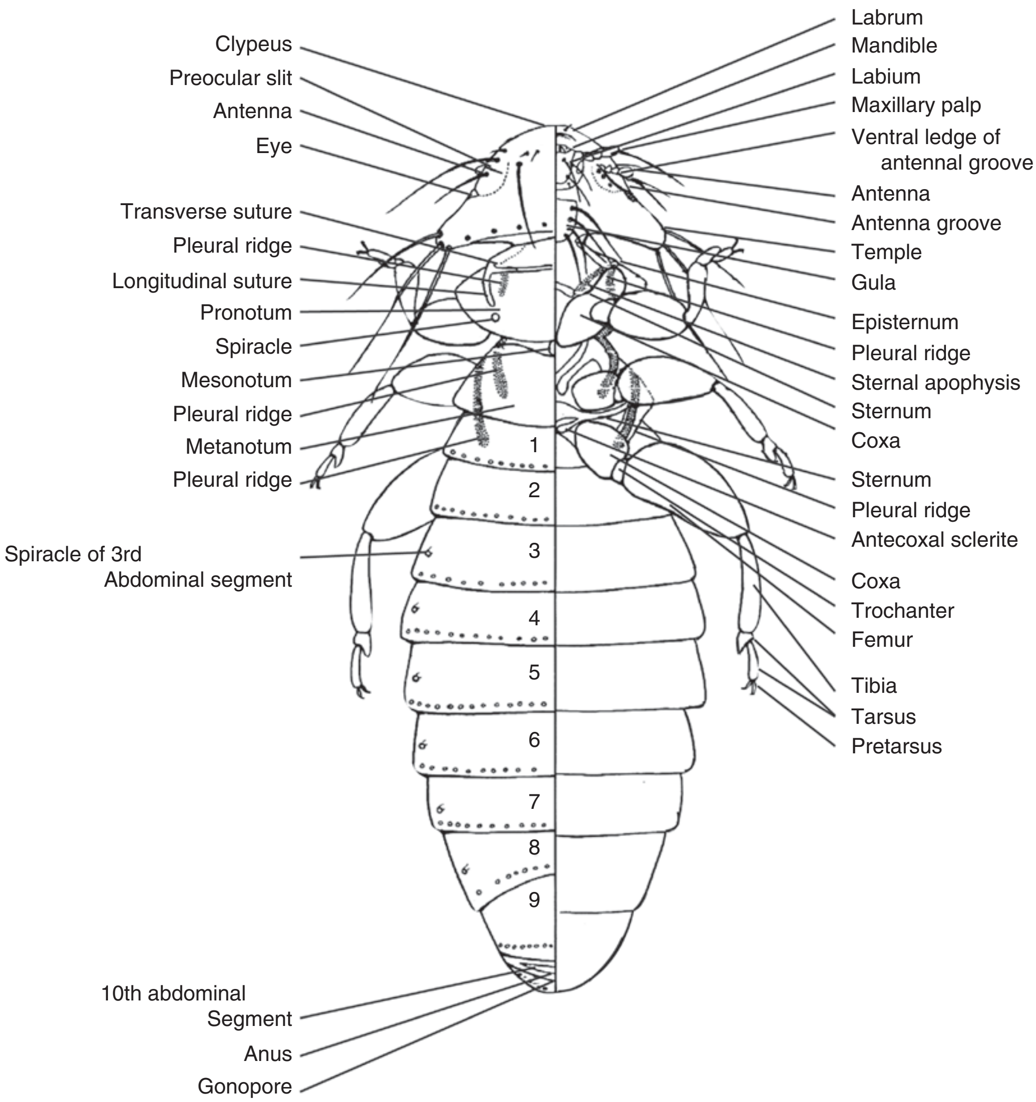
Class Insecta
Order Phthiraptera
  Suborder Amblycera
    Family Menoponidae – poultry lice
    Family Trinotonidae
    Family Laemobothriidae – hawk lice
    Family Ricinidae – hummingbird lice
    Family Trochiliphagidae
    Family Boopidae – marsupial chewing lice
    Family Gryropidae – guinea pig lice
    Family Trimenoponidae – marsupial lice
    Family Abrocomophagidae
  Suborder Ischnocera
    Family Trichodectidae – mammal chewing lice
    Family Philopteridae – bird lice
    Family Heptapsogasteridae
  Suborder Rhyncophthirina
    Family Haematomyzidae
  Suborder Anoplura
    Family Polyplacidae – spiny rat lice
    Family Linognathidae – pale lice
    Family Enderleinellidae – squirrel lice
    Family Hoplopleuridae
    Family Neolinognathidae
    Family Hamophthiriidae
    Family Ratemiidae
    Family Microthoraciidae
    Family Echinophthiriidae – seal lice
    Family Pthiridae – pubic lice
    Family Pedicinidae
    Family Pecaroecidae – peccary lice
    Family Hybothiridae
    Family Haematopinidae – ungulate lice
    Family Pediculidae – body lice

The hosts of the chewing lice, other than those suggested by the aforementioned common names, are hummingbirds for trochiliphagids; ducks, geese and swans for trinotonids; a rodent for the only known abrocomophagid; many birds for heptapsogasterids; and elephants and warthogs for haematomyzids. The sucking lice feed on mammals. Interestingly, although humans have domesticated animals for thousands of years, they have rarely acquired lice from them. Instead, the lice associated with humans are in the genera *Pthirus* and *Pediculus*, which they share with the higher primates, particularly the apes.

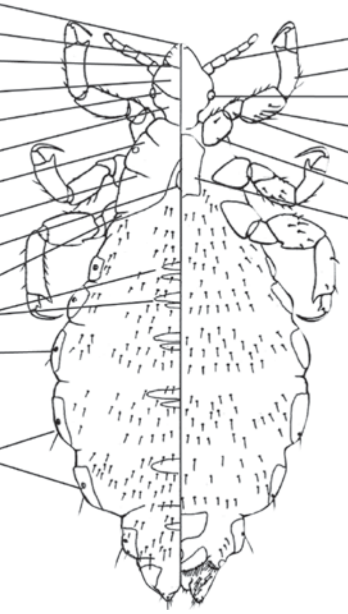
Characteristics

Chewing lice are small ectoparasites, generally measuring 0.5–6 mm long, and wingless. The head is wide, or at least wider than the thorax (Fig. 44), and bears small eyes and short antennae(3–5 segments). The form of the antenna varies; in the suborder Amblycera they normally are capitate, whereas in the suborder Ischnocera they are filiform. Ocelli are absent. The mouthparts, as suggested by the common name, are the chewing type. The body is flattened and has six or fewer spiracles. The legs have one or two claws. Cerci are lacking. The metamorphosis is incomplete (hemimetabolous development). These hemimetabolous insects have three nymphal instars.

Sucking lice also are small ectoparasites, measuring only 0.5–5 mm in length, and oval in shape. Their head is narrow, a distinguishing character relative to the chewing lice (Fig. 45). Their eyes are reduced or absent; ocelli are absent. The antennae are short, and 3–5 segmented. The mouthparts, which are about as long as the head, are highly modified and are adapted for piercing and sucking. The mouthparts are retracted into the head when not in use. The body is dorsoventrally flattened. The segments of the thorax are fused, and the thoracic spiracles located dorsally. The abdominal



Chewing and Sucking Lice (Phthiraptera), Figure 44 **A diagram of a chewing louse showing a dorsal view (left) and a ventral view (right).**



Chewing and Sucking Lice (Phthiraptera), Figure 45 **A diagram of a sucking louse showing a dorsal view (left) and a ventral view (right).**

segments are distinct. The tarsi consist of only one segment, and there is only one large claw on each tarsus. Cerci are absent. Metamorphosis is incomplete, as with the chewing lice.

Biology

Probably all species of birds are affected by chewing lice, but only about 20% of mammals host these lice. The eggs are attached to the feathers or hairs of the host with glue. The nymphs and adults feed on feathers, hair, skin, blood, and the oils produced by the skin. Blood feeding seems to be of minor importance, and substantial infestations can occur with little ill effect, though the common behavior among birds of taking a "dust bath" is probably an attempt to rid themselves of lice. However, when populations are very high, they can be of veterinary importance, especially to young fowl. They are not important in disease transmission. They spread from animal to animal by body contact, and often leave their host soon after it perishes.

Sucking lice feed only on blood of mammals. Two (or three, depending on how *Pediculus humanus* is treated) species affect humans, and about 12 species affect domestic animals. The families tend to contain lice with very similar feeding habits. For example, the echinophthiriids feed on seals, sea lions, walruses and river otter; the enderleinellids on squirrels; the haematopinids on ungulates such as pigs, cattle, horses and deer; the hoplopleurids on rodents and insectivores; the linognathids on even-toed ungulates such as cattle, sheep, goats, reindeer and deer, and on canids such as dogs, foxes and wolves; the pecaroecids on peccaries; the pediculids on the head and body of humans; the polyplacids on rodents and insectivores; and pthirids on gorillas and humans. The eggs generally are cemented to the hairs of the host. There are three nymphal instars in nearly all species.

Because lice are co-evolved (co-speciated) with their specific hosts, the extinction of hosts results in extinction of lice species as well. Due to pervasive host extinction (for example, about 67% of the genera of mammals are thought to be extinct), many species of lice likely have disappeared. However, lice do not preserve well, and are virtually absent from the fossil record, so their history is not well known.

► Human Lice

References

Arnett RH Jr, (2000) American insects, 2nd edn. CRC Press, Boca Raton, FL, 1003 pp

Ash JS (1960) A study of the Mallophaga of birds with particular reference to their ecology. Ibis 102:93–110

Durden LA, Musser GG (1994) The sucking lice (Insecta, Anoplura) of the world; a taxonomic checklist with records of mammalian hosts and geographical distributions. Bull Br Mus Nat Hist 218:1–90

Grimaldi D, Engel MS (2005) Evolution of the insects. Cambridge University Press, Cambridge, UK, 755 pp

Hopkins GHE (1949) The host-associations of the lice of mammals. Proc Zool Soc Lond 119:387–605

Kim KC, Ludwig HW (1978) The family classification of Anoplura. Syst Entomol 3:249–284

Kim KC (1987) Order Anoplura. In: Stehr FW (ed) Immature insects, vol 1 Kendall/Hunt Publishing, Dubuque, IA, pp 224–245

Kim KC, Pratt HD, Stpjanovich CJ (1986) The sucking lice of North America. An illustrated manual for identification. Pennsylvania State University Press, University Park, Pennsylvania.

Price MA, Graham OH (1997) Chewing and sucking lice as parasites of mammals and birds. U.S. Department of Agriculture Technical Bulletin 1849, 309 pp

Price RD (1987) Mallophaga. In: Stehr FW (ed) Immature insects, vol 1. Kendall/Hunt Publishing, Dubuque, IA, pp 215–223

Chewing Mouthparts

Mouthparts that consist of opposable, non-sucking structures; biting mouthparts.

► Mouthparts of Hexapods

Chiang, Huai C.

Huai Chiang was born February 15, 1915, in Sunjiang County, Jiansu Province, China. He attended Tsinghua University in Beijing, where he was first exposed to entomology. During the Sino-Japanese war of 1937–1945, his studies were disrupted and he relocated to the Temporary University in Ghangsha, Hunan, and then to Southwestern Associated University in Kunming, Yunan. The latter involved an incredible 68-day overland trek by Chiang and his fellow students. After graduating, he joined the Agricultural Research Institute in Kunming. Kunming was the terminus of the Allied Forces air supply route from India, and Chiang interacted with a military anti-malaria unit, which allowed him to make important contacts and to improve his English. Chiang contacted the University of Minnesota and enrolled in 1945. He completed his graduate studies in 1948, and accepted a temporary position studying European corn borer. This, and a temporary stint as an instructor of entomology at Minnesota, led to a permanent faculty position where he worked until retiring in 1984.

Huai Chiang is best known for his work on corn pests, and he authored about 250 publications, including two articles in the Annual Review of Entomology. He was considered an expert in biological control and insect ecology. He was active in international and government agencies and programs, and was honored by several universities and countries for his research and service. He died on March 30, 2005, in Ithaca, New York.

Reference

Radcliffe T (2005) Huai C. Chiang. Am Entomol 51:126–127

Chigger

A mite of the family Trombiculidae.

► Mites

Chikungunya

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Chikungunya is an *Alphavirus* in the family Togaviridae. It is an arthropod-borne virus (arbovirus) transmitted to humans primarily by *Aedes aegypti*, the yellow fever mosquito. Togaviruses replicate in the cytoplasm and mature by budding out from the cell membrane. They are not very stable in the environment and are easily destroyed or inactivated by disinfectants. The genus *Alphavirus* has 27 member viruses, all of which are mosquito-borne. Eleven of these viruses cause disease in humans, and eight of them produce significant epidemics: Chikungunya, Ross River virus, eastern, western, and Venezuelan equine encephalitis, O'nyong-nyong, Mayaro, and Sindbis. Chikungunya virus is widespread throughout Africa, India, and Southeast Asia, including the Philippines. Devastating epidemics, sometimes lasting for months or years, have occurred and reoccurred in Africa and Asia. A majority of an urban population can be infected within a few months. Under these circumstances *A. aegypti* can maintain the virus in a human-mosquito-human cycle.

Symptoms, Treatment, and Prevention

Chikungunya received its name from a Swahili or Makonde term meaning "that which bends up," referring to the stooped posture of patients afflicted with severe joint pain associated with this disease. Chikungunya is a debilitating but generally self-limiting febrile viral disease. It is characterized by arthralgia or arthritis, typically in the small joints of the extremities, such as ankles, knees, toes, wrists, and fingers. Other symptoms include high fever, headache, nausea, vomiting, photophobia, maculopapular rash, buccal and palatal enanthema, myalgia, chills, flushed face, lymphadenopathy, stooped posture, and, in some cases, bleeding from the nose and mild hemorrhaging. The incubation period can range from 2–12 days, but is usually 3–7 days. The onset of this disease is sudden, and is marked by a rapid increase in body temperature followed by severe pain in the limbs and spine. These symptoms usually last 3–5 days followed by recovery in 5–7 days. However, the virus has shown signs of greater virulence in the recent Indian Ocean epidemic. Occasionally joint pain can reoccur intermittently for months or even years. Unapparent Chikungunya infections do occur, but how commonly this occurs is unknown. It is thought that life-long immunity is conferred through clinical or unapparent infection with the Chikungunya virus.

Chikungunya is diagnosed based on symptoms and serological testing. At this time there is no cure for the disease. Vaccine trials were carried out in 2000, but funding for the project was eliminated and the project was discontinued. There is no vaccine or antiviral treatment available for Chikungunya fever. The illness is generally self-limiting and the symptoms usually resolve over time. Symptomatic treatments are recommended after excluding other more dangerous diseases, such as dengue and yellow fever. These treatments include rest, plenty of fluids, and acetaminophen, naproxen, ibuprofen, or paracetamol to relieve fever and aching. Aspirin should not be taken to treat Chikungunya fever. An infected person should stay indoors to protect against further mosquito exposure and transmission of the disease to other people during the first few days of illness. Other measures to reduce the spread of Chikungunya fever include use of insecticides to kill adult and larval mosquitoes. Measures that can be taken by individuals include elimination of standing water where mosquitoes can breed, use of insect repellents containing permethrin or DEET, wearing long pants and long-sleeved shirts, and use of screens on windows and doors to prevent entry by mosquitoes.

The present strain of the Chikungunya virus in the Indian Ocean region appears to be more virulent than those causing previous epidemics. A number of patients have developed complications and died. The death of a 10 year old boy had no other plausible explanation; Chikungunya virus was the only pathogen present in his blood. The death toll from the Chikungunya virus continues to increase. In the Indian Ocean region, 77 death certificates issued in January through March 2006 state

Chikungunya as the cause of death, although for most cases co-morbidity played a significant role.

Epidemiology

Aedes aegypti is the most important vector of the viruses of Chikungunya, dengue, and yellow fever. This mosquito is widely distributed between 40°N and 40°S latitude. *Aedes aegypti* does not thrive in hot dry climates and is vulnerable to extreme temperatures. The primary food source for female *A. aegypti* is blood from a vertebrate host; male mosquitoes do not suck blood. The blood meal for *A. aegypti* is commonly human blood, but they will also feed on other mammals and birds. *Aedes aegypti* has been recognized as the chief vector of Chikungunya for approximately 50 years, although other species of *Aedes* (see below) and *Culex* have also been implicated.

In the 1950s an aggressive mosquito control campaign greatly reduced *A. aegypti* on the island of Réunion, east of Madagascar in the Indian Ocean. Reducing the primary vector of Chikungunya should have reduced or eliminated the spread of this disease. This proved not to be the case. *Aedes albopictus*, the Asian tiger mosquito, was not viewed as a significant threat, and remained abundant due to lack of control measures. This mosquito is of Asian origin, and is usually found far away from human habitation. *Aedes albopictus* feeds readily on many species of mammals and birds. It was assumed to be an inefficient vector of Chikungunya in nature because of its habit of feeding on non-susceptible hosts that do not contribute to the transmission cycle. However, the recent outbreak and epidemic of Chikungunya on Réunion, with roughly 265,000 people infected (34% of the total population of the island), indicates that *A. albopictus* can be an effective vector of Chikungunya.

The Chikungunya virus was first isolated from the blood serum of a febrile human by R.W. Ross in 1953 in the Newala district of Tanzania. It was later recovered in Bangkok in 1958, and has more recently caused massive epidemics in many countries. The Chikungunya virus is geographically distributed in Africa, India, and Southeast Asia. The virus is maintained in Africa through a sylvatic transmission cycle between *Aedes luteocephalus*, *Aedes furcifer*, or *Aedes taylori* mosquitoes and wild primates. The Chikungunya virus is transmitted among baboons and humans by *A. furcifer*. In Africa, baboons are the primary vertebrate host from which the virus extends into the human population. In Asia, the Chikungunya virus is transmitted from human to human by *A. aegypti* through an urban transmission cycle. Because neither a vertebrate reservoir nor a sylvan transmission cycle has been identified outside of Africa, it is thought that the Chikungunya virus originated in Africa and was later introduced into Asia and other parts of the world. The Chikungunya virus has caused outbreaks and epidemics in East Africa (Tanzania and Uganda), Austral Africa (Zimbabwe and South Africa), West Africa (Senegal and Nigeria), and Central Africa (Central African Republic and Democratic Republic of the Congo) since its discovery in 1953.

Chikungunya virus in the Indian Ocean region has recently caused one of the largest epidemics reported in the last 40 years, involving hundreds of thousands of people. The severity and magnitude of the epidemic has surprised public health specialists and the governments. Chikungunya virus infection has steadily increased within the human population. In 2005 there were an estimated 12,400 cases reported, whereas in 2006 there were over 200,000 cases reported through April alone. These numbers do not include cases that are misdiagnosed or unreported.

It has been suggested that many cases of Chikungunya fever are misdiagnosed as dengue fever. The clinical symptoms of Chikungunya infection often mimic those of dengue fever, and Chikungunya virus is present in regions where dengue virus is endemic. There have been documented cases of simultaneous co-infection with dengue and Chikungunya viruses. A human-mosquito-human cycle has sustained urban epidemics involving *A. aegypti* as the vector, and Chikungunya-dengue and Chikungunya-yellow fever outbreaks have been described. The association of Chikungunya, dengue, and yellow fever is likely due to transmission by the same vector species, *A. aegypti*. *Aedes aegypti* is not limited to Africa and Asia, so there is the possibility that the Chikungunya virus could spread elsewhere.

In 2006, six complete genome sequences of selected Chikungunya viral isolates were studied. Results of this study suggest that the Chikungunya virus can adapt to new environmental conditions, and can evolve the ability to survive in vectors that it was incapable of surviving in previously. These results underscore the possibility that the Chikungunya virus can spread to other parts of the world. The Chikungunya virus continues to be a growing problem since its discovery in 1953.

References

Enserink M (2006) Massive outbreak draws fresh attention to little-known virus. Science 311:1085

Effler PV, Pang L, Kitsutani P, Vorndam V, Nakata M, Ayers T, Elm J, Tom T, Reiter P, Rigau-Perez JG, Hayes JM, Mills K, Napier M, Clark GG, Gubler DJ (2005) Dengue fever, Hawaii, 2001–2002. Emerg Infect Dis 11:742–749

Higgs S (2006) The 2005–2006 Chikungunya epidemic in the Indian Ocean. Vector Borne Zoonotic Dis 6:115–116

Jupp PG, McIntosh BM (1988) Chikungunya disease. In: Monath TP (ed) The arboviruses: epidemiology and ecology. CRC Press, Boca Raton, FL, pp 137–157

Kettle D (1995) Medical and veterinary entomology, 2nd edn. CABI Publishing, New York.

McIntosh BM, Jupp PG, Dos Santos I (1977) Rural epidemic of Chikungunya in South Africa with involvement of *Aedes furcifer* and baboons. S Afr J Sci 73:267–269

Myers RM, Carey DE (1967) Concurrent isolation from patient of two arboviruses, Chikungunya and dengue type 2. Science 157:1307–1308

Reiter P, Fontenille D, Paupy C (2006) *Aedes albopictus* as an epidemic vector of Chikungunya virus: another emerging problem? Lancet Infect Dis 6:463–464

Ross RW (1956) The Newala epidemic. III. The virus: isolation, pathogenic properties and relationship to the epidemic. J Hyg 54:177–191

Salvan M, Mouchet J (1994) *Aedes albopictus* and *Aedes aegypti* at Ile de la Réunion. Ann Soc Belg Med Trop 74:323–326

Tesh RB, Gubler DJ, Rosen L (1976) Variation among geographic strains of *Aedes albopictus* in susceptibility to infection with Chikungunya virus. Am J Trop Med Hyg 25:326–335

World Health Organization. Chikungunya and dengue in the south west Indian Ocean. Available at http://www.WHO.int/csr/don/2006_03_17/en. Accessed 25 May 2007

Chilli Thrips, *Scirtothrips dorsalis* Hood (Thysanoptera: Thripidae)

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The common names of *Scirtothrips dorsalis* are chilli thrips, chili thrips, castor thrips, Assam thrips, strawberry thrips and yellow tea thrips. Taxonomists now regard *Neophysopus fragariae* Girault, *Heliothrips minutissimus* Bagnall, *Anaphothrips andreae* Karny and *S. dorsalis* var. *padmae* Ramakrishna as synonyms of *S. dorsalis* Hood.

Economic Importance

Scirtothrips dorsalis has long been a pernicious pest of various vegetable crops, cotton, citrus and other fruit and ornamental crops in its principal range in southern Asia, where it may kill newly emerged seedlings, severely distort leaves and scar the surface of fruits of its favored hosts. In India, *S. dorsalis* is a serious pest of castor bean (*Ricinus communis* L.), chilli pepper (*Capsicum annum* L. var. *annum*), peanut (*Arachis hypogaea* L.), cotton (*Gossypium* spp.), onion (*Allium cepa* L.), rose (*Rosa* spp.) and other flowers. In Taiwan, *S. dorsalis* is a significant pest of citrus, especially satsuma mandarin (*Citrus unshui* Marc), tea (*Camellia sinensis* [L.] O. Kuntze), and the rubber tree (*Hevea brasiliensis* Müll. Arg.). In Japan, *S. dorsalis* is notorious for its damage to citrus, tea, and grapevine (*Vitis vinifera* L.). In Côte d'Ivoire, it is a serious pest of cotton. In Indonesia, *S. dorsalis* is a serious pest of soybean (*Glycine max*

[L.] Merr.). In Queensland, Australia. *S. dorsalis* is a significant pest of strawberry (*Fragaria ananassa* Duchesne X *F. virginiana* Duchesne).

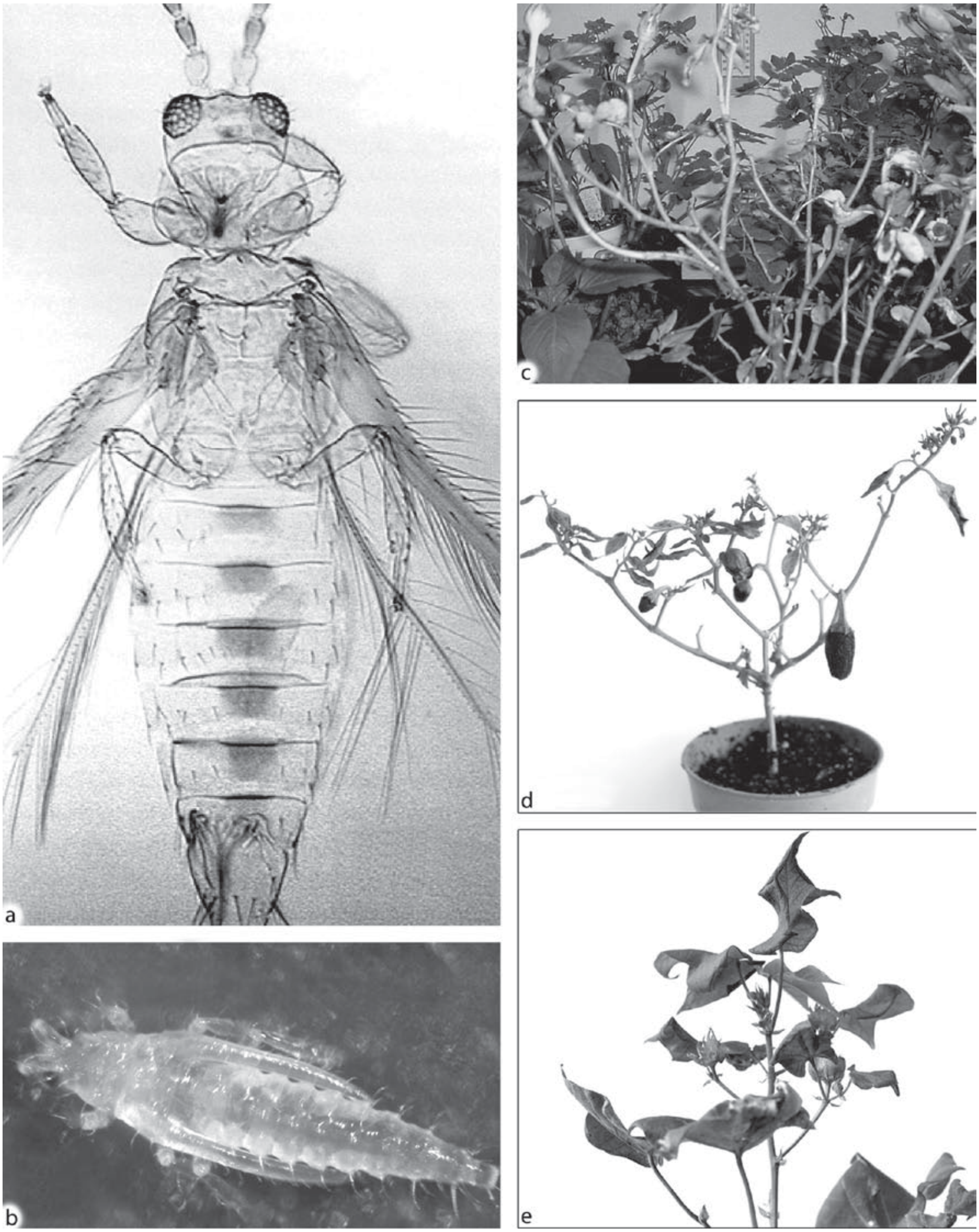
Scirtothrips dorsalis has spread to South Africa, Côte d'Ivoire, Kenya, Oceania, Australia (Queensland), Papua New Guinea, Indonesia, and the Solomon Islands; in 2003 it was found to be established on St. Vincent, an island in the Caribbean Sea. Since 2003, *S. dorsalis* has emerged as a major pest in certain Caribbean islands, Suriname, Venezuela, Florida and southern Texas. The pest is still absent from the European and the Mediterranean Region. In the New World, *S. dorsalis* is now damaging crops as follows – St. Vincent and St. Lucia: commercial fields of chili pepper; Barbados: sea island cotton (*Gossypium barbadense* L.), and carrot (*Daucus carota* L.); Florida: *Celosia argentea* L., coleus (*Plectranthus scutellaroides* [L.] R. Br.), *Coreopsis* spp., geranium (*Pelargonium* x *hortorum* Bailey), Gerber daisy (*Gerbera jamesonii* H. Bolus ex hook f.), "Knockout" rose, pepper transplants (*Rosa* spp.), impatiens (*Impatiens* spp.), Japanese privet (*Lagustrum japonicum*), lisianthus (*Eustoma russellianum*), pentas (*Pentas lanceolata* [Förrsk.] Deflers), petunia (*Petunia* x *hybrida*), pittosporum (*Pittosporum* spp.), plumbago (*Plumbago auriculata*), snapdragon (*Antirrhinum majus*), verbena (*Grandualaria* x *hybrida* [Gönland & Rűmpler] Neson & Pruski), Victoria blue (*Salivia farinacea*), pansy *Viola* x *wittrockiana* Gams, zinnia (*Zinnia elegans*) and many other ornamental plants. Lawn care operators and other landscape management firms in Florida regard *S. dorsalis* to be nearly as threatening as insecticide-resistant western flower thrips, *Frankliniella occidentalis* (Pergande). Thus, where the two species both occur, it is important that measures taken against one species do not exacerbate the difficulty of suppressing the other. Also in Florida, *S. dorsalis* has been found frequently on pepper seedlings in retail outlets, but it has not yet become problematic in the commercial production of pepper or any other vegetable crop.

Scirtothrips dorsalis is a vector of various viral and bacterial diseases, including peanut bud necrosis virus (PBNV), peanut chlorotic fan virus (PCFV), tobacco streak virus (TSV) and tomato spotted wilt virus (TSWV).

Recognizing *S. dorsalis* Infestations

Scirtothrips dorsalis feeds on the meristems of host plants' terminals and on other tender above-ground parts, and creates damaging feeding scars, distortions of leaves and discolorations of buds, flowers and young fruits (Fig. 46). It does not feed on mature tissue. *Scirtothrips dorsalis* causes damage by sucking the contents out of individual epidermal cells, which leads to necrosis of the tissue. Initially such tissue has a silvery sheen, but soon the damaged areas turn brown or black. In heavily infested pepper fields the appearance of the plants is known as "chilli leaf curl." Heavy feeding causes the tender leaves and buds to become brittle, so that total defoliation and severe crop loss may occur.

Usually, *S. dorsalis* adults are no longer than 1.2 mm and have pale bodies and dark wings. Dark spots are found dorsally on the abdomen, forming an incomplete stripe. Typically, the first instar larvae, second instar larvae and pupae are 0.37–0.39, 0.68–0.71 and 0.78–0.80 mm long, respectively, and all have pale bodies. The presence of distorted or discolored plant parts is suggestive of presence of *S. dorsalis*. Larvae feed on the undersides of young tender pepper leaves, and cause the leaf edges to curl upwards and brownish areas to develop between the veins. Corky tissue develops on infested fruits. *Scirtothrips dorsalis* larvae and adults tend to aggregate along the midvein or at the borders of damaged leaf tissues. In some instances, *S. dorsalis* infested plants superficially resemble broad mite infested plants, but broad mites cause pepper leaves to curl downwards and become narrow. On the other hand, when *S. dorsalis* populations become dense, the pest then feeds on the upper sides of the leaves of a number of host plants.



Chilli Thrips, *Scirtothrips dorsalis* Hood (Thysanoptera: Thripidae), Figure 46 **Chilli thrips and damage: (a) adult of chilli thrips (photo by L. Mound), (b) larva of chilli thrips (photo by C. Sabines), (c) chilli thrips-infested rose plants (photo by C. Sabines), (d) chilli thrips damage on a pepper plant (photo by I. Maguire) (e) chilli thrips damage on a cotton plant (photo by I. Maguire).**

Scirtothrips dorsalis individuals can be dislodged onto a white or black paper or plastic sheet on which they are readily visible. Samples can be taken by rinsing these thrips from plant material using 70% ethanol. The ethanol solution is then poured onto a fine sieve, and the specimens can be removed from the latter with a camel hair brush and mounted on slides for examination under a microscope. Adults are attracted to yellow sticky cards and perhaps to a lesser extent to yellowish-green, green or white surfaces. In Japan sticky suction traps above the canopies of tea plants are used to monitor the flight of *S. dorsalis* and other thrips.

Life History

The life cycle stages of *S. dorsalis* are egg, first instar larva, second instar larva, prepupa, pupa and adult. The microscopic eggs are creamy white, kidney shaped and about 0.075 mm long and 0.070 mm wide. They are deposited inside plant tissue above the ground, and they hatch in 2–5 days. Larvae and adults tend to aggregate along the midvein or at the borders of damaged leaf tissues. Usually the pupae are found in the axils of the leaves, in curled leaves, under calyces of flowers and fruits, although they may also be found in the leaf litter or soil. Larval development requires 8–10 days and prepupal and pupal development together require 2.6–3.3 days. At about 28°C, the period spanning the first instar to the adult ranged from 11.0 days on pepper to 13.3 days on squash. *S. dorsalis* adults lived 13.6 days on tomato and 15.8 days on eggplant. The base and upper development temperatures of *S. dorsalis* are 9.7°C and 33.0°C, respectively. The species has a thermal requirement of 265 degree days from egg to adult and 281 degree days from egg to egg. Thus, the species is believed to undergo up to 18 generations per year in warm subtropical and tropical areas and about eight generations per year in warm temperate areas. It is believed that *S. dorsalis* cannot overwinter outdoors in areas where the minimum temperature reaches −4°C for 5 or more days. *Scirtothrips dorsalis* tends to become more abundant during prolonged dry periods than during rainy periods, and its abundance is negatively affected by torrential rainfall events. The flight activity of *S. dorsalis* is greatest between noon and 2 p.m. Not all eggs are fertilized as a result of mating. Fertilized eggs develop into females, and unfertilized eggs develop into males. The sex ratio is often shifted in favor of female progeny.

Host Plants

Before *S. dorsalis* became established in the Western Hemisphere, it was already known to attack a wide range of hosts belonging to 112 plant taxa in about 40 families; as the pest invades new territory it attacks many additional taxa of plants. Economically important hosts of *S. dorsalis*, include the following: banana (*Musa* spp.), bean (*Phaseolus vulgaris* L.), cashew (*Anacardium occidentale* L.), castor (*Ricinus communis* L), Chinese bitter cucumber (*Momordica charantia* L.), citrus (*Citrus* spp.), corn (*Zea mays* L.), cocoa (*Theobroma cacoa* L.), cotton (*Gossypium* spp.), eggplant (*Solanum melongena* L.), golden dew drop (*Duranta erecta* Lindl.), grape (*Vitis* spp.), kiwi (*Actinidia chinensis* Planch), litchi (*Litchi chinensis* Sonn.), longan (*Dimocarpus longan* Lour.), mango (*Mangifera indica* L), melon (*Cucumis melo* L.), onion (*Allium cepa* L.), passionfruit (*Passiflora edulis* Sims), peach (*Prunus persica* L. Batsch), peanut, (*Arachis hypogaea* L.), pepper (*Capsicum* spp.), poplar (*Populus* spp.), sacara (*Sacara* spp.), sacred lotus, (*Nelumbo nuciferae* Gaertn.), soybean (*Glycine max* L.), strawberry (*Fragaria ananassa* Duchesne X *F. virginiana* Duchesne), sweet potato (*Ipomoea batatas* L.), tea (*Camellia sinesis* L.), tobacco (*Nicotianum* spp.), tomato (*Lycopersicon esculentum* L.), viburnum (*Viburnum suspensum* Lindl.), wild yam (*Discorea* spp.), and yedda hawthorn (*Rhaphiolepis umbellata* (Thunb.).

Monitoring and Management

Host crops such as bean, corn and cotton, are produced from seed and should be monitored as soon as the seedlings emerge, because the seedlings are especially attractive and very susceptible to severe damage by *S. dorsalis*. Hosts that appear to serve as preferred, such as pepper, "Knockout" rose, lisianthus, etc., should be monitored for symptoms of *S. dorsalis* infestation at least twice per week. Samples of symptomatic plant tissues should be sent to a professional for confirmation.

The development of systems for managing *S. dorsalis* is still in its infancy. The World Vegetable Center (AVRDC) recommends the removal of any weeds that may serve as hosts, rotation of crops, fostering the activities of predators and parasites, and rotating insecticides. In Japan the use of reflective synthetic films to cover the ground between rows of citrus trees is fairly effective.

Thrips are attacked by an array of predators, parasitoids and pathogens. Practical use in managing thrips populations in the field has been made of minute pirate bugs, *Orius* spp. (Hemiptera: Anthocoridae) and of the entomopathogenic nematodes, *Thripinema* spp. (Tylenchida: Allantonematidae). *Orius* adults and nymphs eat all stages of thrips, and suppress rapidly growing thrips populations. Since *Orius* also feed on aphids, spider mites, moth eggs, and pollen, *Orius* populations tend to persist long after thrips populations have been decimated. *Thripinema* are tiny parasitic worms, which render parasitized female thrips incapable of laying eggs. Male and female thrips parasitized with *Thripinema* tend to feed sparingly, cause little feeding damage and spread pathogens weakly.

Whether releases of *Orius* or *Thripinema* should be made will depend on the value of the plant material to be protected. Also since releases may be less effective outdoors than in greenhouses and shadehouses, the cost of releases outdoors may be prohibitive. Nevertheless every effort should be made to conserve valuable natural enemies in field situations.

Other predators of thrips, which have not been adequately studied to determine their practical suppression value, include lacewings, *Chrysoperla* spp., several mired bugs, ladybird beetles, and a number of predatory thrips including *Franklinothrips vespiformis*, the black hunter thrips, the six spotted thrips (*Leptothrips mali*), *Scolothrips sexmaculatus*, the banded wing thrips (*Aeolothrips* spp.), and the predatory phytoseiid mites, *Amblyseius* spp., *Euseius hibisci* and *Euseius tularensis*.

In India the known predators of both larvae and adults of *S. dorsalis* are *Carayonocoris indicus, Erythrothrips asiaticus, Franklinothrips megalops, Geocoris ochropterus, Mymarothrips garuda, Orius maxidentex,* and *Scolothrips indicus*. Most of the known parasitoids of thrips are in the genera *Ceranisus, Goetheana, Thripobius,* and *Entedonastichus*.

Under experimental conditions, *S. dorsalis* can be suppressed with several entomopathogens including *Beauveria bassiana*, *Metarhizium anisopliae* and *Fusar ium semitectum*. The first two of these pathogens have been used for insect control for several decades, whereas the latter was recently found to be effective in the laboratory studies in India.

The advent of *S. dorsalis* into the Caribbean and Florida stimulated research on its biology and management. Notably the pyrethroid insecticides proved to be only weakly effective. The most effective materials evaluated to date (Table 11) are shown in the table. In order to forestall the development of resistance to any insecticide, materials belonging to different classes should be used in a rotation. Formulations of imidacloprid applied to the soil as a drench are effective, and they do not kill predators and parasites. In instances where another pest, such as the western flower thrips in Florida, has already developed incipient resistance to a given insecticide, great care must be exercised in choosing an insecticide to suppress *S. dorsalis*. Possibly this problem may be avoided by the application of entomopathogenic fungi, such as *Beauveria bassiana*, and *Metarhizium anisopliae*, but the efficacy of these preparations still requires field evaluation.

The insecticide data in the table does not constitute control recommendations. All materials

Chilli Thrips, *Scirtothrips dorsalis* Hood (Thysanoptera: Thripidae), Table 11 Recently developed insecticides with high effectiveness against *Scirtothrips dorsalis*

Class of material	Trade name	Common name	Approximate % control	Method of application
Neonicotinoid	Actara	thiamethoxam[a]	70	Foliar
	Provado; Marathon;	imidacloprid[a]	70–80	Foliar
	Admire	imidacloprid[a]	>90	Soil
Organophosphate	Orthene	acephate[a]	>80	Foliar
Pyrrole	Pylon	Chlorofenapyr[a]	>90	
Fermentation product: nicotinic acetylcholine receptor activator	Spintor; Conserve	Spinosyn A + B[a]	>90	Foliar
	Radiant	Spinetoram	>90	Foliar
Fermentation product: GABA inhibitor	Agrimek; Avid	Abamectin[a]	70–80	Foliar
Entomopathogenic Fungi	BotaniGard	*Beauveria bassiana*	>80	Foliar
	Tick EX	*Metarhizium anisoplae*	70–80	Foliar

[a]This indicates that efficacy was measured in field trials; absence of "a" indicates that efficacy was measured in laboratory or greenhouse trials

must be used in strict accordance with the registration label. Use of biologically based preparations such as spinosyn A + B, spinetoram and abamectin will allow continuation of the activity of naturally occurring predators and parasites.

► Thrips (Thysanoptera)

References

Ananthakrishnan TN (1984) Bioecology of thrips. Indira Pub House, West Bloomfield, MI, 233 pp

Ananthakrishnan TN (1993) Bionomics of thrips. Ann Rev Entomol 38:71–92

CABI/EPPO (1997) Quarantine pests for Europe, 2nd edn. CAB International, Wallingford, UK, 1440 pp

CABI (2003). Crop protection compendium: global module. Commonwealth Agricultural Bureau International, Wallingford, UK

Chang NT (1995) Major pest thrips in Taiwan. In: Parker BL, Skinner M, Lewis T (eds) Thrips biology and management. Plenum Press, New York, NY, pp 105–108

Moritz G, Morris D, Mound L (2001) Thrips ID. Pest thrips of the world. An interactive identification and information system. CSIRO Publishing, Australia

Mound LA, Palmer JM (1981) Identification, distribution and host plants of the pest species of *Scirtothrips* (Thysanoptera: Thripidae). Bull Entomol Res 71:467–479

Seal DR, Ciomperlik M, Richards ML, Klassen W (2006) Distribution of the chilli thrips, *Scirtothrips dorsalis* Hood (Thysanoptera: Thripidae), within pepper plants and within pepper fields on St. Vincent. Fla Entomol 89:311–320

Chimaeropsyllidae

A family of fleas (order Siphonaptera).

► Fleas

Chinaberry, *Melia azedarach* L., A Biopesticidal Tree

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Biopesticides are chemicals derived from a biological source. They are described as agents that include natural plant metabolites, microbial pest control agents such as entomopathogens, insect growth regulators and behavior-modifying chemicals. Biopesticides are generally nontoxic to vertebrates and plants and are called biorational insecticides in Integrated Pest Management programs. Biorationals are based on natural products and synthetic analogues of naturally occurring biochemicals and are more acceptable than conventional insecticides because they are environmentally less hazardous to humans and other non-target organisms.

Botanical insecticides are plant-derived chemicals used in insect control. Plants synthesize secondary compounds that act as a defense against pests and diseases. The plant family Meliaceae was identified as one of the most promising sources of compounds with insect-control properties. In particular, some members of the generas *Melia* and *Azadirachta* were outstandingly effective against insects, and their components also were useful in many other respects. These components are considered important from economical, environmental and ecotoxicological standpoints because, in general, only 20–50 g of the active principle is sufficient to treat one hectare of area to achieve a satisfactory reduction in pest populations, and also because the products are readily biodegradable. The non-conventional effects of these preparations can include: partial reduction or complete inhibition of fecundity and sometimes egg hatchability, reduction of adult life span, oviposition deterrence, direct ovicidal effects, antifeedant and repellent effects against larvae, nymphs and adults, and action as an insect growth regulator.

Insecticidal active ingredients from the neem tree, *Azadirachta indica* A. Juss, a member of the mahogany family (Meliaceae) and other related trees, specifically *Melia azedarach* L., fulfill most of the strict requirements for modern pesticides. These ingredients are non-toxic to mammals and are readily degraded on plants and in the soil. The high efficacy of these substances and their rapid biodegradability completely fulfill the requirements of toxicological and environmental safety.

Classification

The name *Melia* is the Greek name for the ash-tree *Fraxinus ornus* L. It belongs to the family Meliaceae, subfamily Meloideae, and tribe Melieae. *Melia azedarach* also is called Persian lilac, lilac, chinaberry, paradise tree, white cedar, umbrella tree, bead tree, syringa, hoop tree, China tree, pride of India, etc. In India, the most common name is Dharek. The names *azadirachtin* and *azedarach* are said to be derived from Persian azadirakht, which means "the tree azadirachtin" (azadirachtin = ash), similar to the derivatization of *Melia* from the Greek name for ash (μ ε λ κ). Its common names in the Mediterranean region are Zinzalakht and Azadarakht (Day).

"Species"/forms/variations/cultivars of the *Melia* complex in Asia and the Pacific region were all considered to be *M. azedarach*. Consequently, *Melia dubia* CAV, *M. australasica* A. Juss, *M. toosendan* Sieb. and Zucc., *M. volkensii* Gürke, *M. conchinchinensis* M.J. Roem., *M. superba* Roxb., *M. floribunda* Morr., *M. azedarach* var. *sempervirens* Sw., *M. azedarach* var. japonica Don., and numerous others are synonyms of *M. azedarach*. The Texas umbrella tree, *M. azedarach* var. *umbraculiformis*, Berkmans which grows in the southern USA, is considered a mutation of *M. azedarach*. In contrast to all other *M. azedarach* variations/forms, it has a flattened crown of branches.

Geographic Distribution

The origin of *Melia azedarach* L., the chinaberry tree, is from northwestern India, where it is found up to approximately 1,800 m above sea level. It is indigenous to Baluchistan and the Jhelum valley in Kashmir. However, it is cultivated and naturalized throughout India, Burma, and the Malay Peninsula. It occurs also in Persia and China.

It is a deciduous tree often grown for shade or ornament on roadsides, parks and other open places. It is found in nearly all warm climatic areas. Due to its relatively low temperature requirements, it grows in southern Europe and in the Mediterranean region as well as southern France, northern Italy, and Croatia. It can be found as an avenue tree in Algeria, Cyprus, Greece, India, Lebanon, Palestine, Syria, Tunisia, etc. In northern Argentina, it is planted for firewood and timber production. In Uganda, Kenya, and South and West Africa, it is planted as a drought resistant ornamental and shade tree. Although the chinaberry tree is a native to tropical Asia, it is now widely distributed in dry regions of the southern and western United States. In some parts of the southern USA, *M. azedarach* is regarded as an "invasive" plant because its seeds are rapidly spread by birds.

Botanical Characteristics

Melia azedarach L. is a tree reaching up to 30 m (about 90 ft), with a thick trunk, spreading branches and furrowed bark. Chinese and Indian cultivars usually attain a height of 8–15 m whereas in certain areas in the Southern Hemisphere, such as Sri Lanka, Malaysia and Indonesia, the tree may reach 25–30 m. The blossoming time is March-May in the Northern Hemisphere, but some "forms" blossom throughout the summer or even the whole year round. The flowers are fragrant, are purplish or lilac, in long peduncles and axillary panicles which are shorter than the leaves and are glabrous or sparsely puberulent. The bi- to tri-pinnate alternate leaves are usually up to 45 cm (1–3 ft) long, while in young trees often longer (< 1 m). The leaflets are ovate and elliptic to lanceolate, acute, sharply serrate or lobed or have a crenate to serrate margin and are 1.2–5 cm (1–2 in) long. Leaf shedding takes place in the Mediterranean region during October and November. Some ecotypes in the wet tropics (Malaysia) do not regularly shed their leaves. The girth can reach more than 3.2 m. The bark is relatively smooth and the heartwood is reddish. Fruits are nearly globular, yellow and smooth. The ripe yellow fruits, or drupes, are about the size of a cherry, globular to oval, 1/2– 3/4 in. in diameter, and are enclosed in a very hard endocarp, which contains 3–5 elongate-oval seed kernels. The ripe fruits can remain for several months on the trees. The kernels have an oil content of approximately 40%. The number of chromosomes is the same as in the neem tree, n = 14.

Phytochemical Properties

More than 280 limonoids have been isolated and identified from Meliacae plants. The most active constituents of *M. azedarach* are classified as azadirachtin-type C-seco limonoids and apo-euphol limonoids as trichilins with a 14,15-epoxide and a C-19/C-29 lactol bridge.

The limonoid *azadirachtin* is absent from *M. azedarach*; it exists only in *Azadirachta* sp. The toxic tetranortriterpenoids (meliatoxins A_1, A_2, B_1, B_2) were isolated from the fruit of *M. azedarach*. Meliatoxin A_2 was found to be identical to A_1 except that ester moiety at C-28 is 2-methylpropionyl in place of the 2-methylbutanoyl group in A_1. Meliatoxins B_1 and B_2 are isomeric with A_1 and A_2, respectively except the epoxide ring in B_1 and B_2 is replaced by a 5-member ring ketone at C-15. The chemical structure of the meliatoxins differs from trichilin, only in the lack of the hydroxyl substituent at C-12.

Using bioassay guided fractionation and isolation technique, the principal insecticidal constituents of *M. azedarach* were isolated from methanolic extracts of green chinaberry fruits and were found to be two very potent insecticidal tetranortriterpenoids. These terpenoids include novel meliacin, called 1-cinnamoyl melianone, and a new derivative of meliacarpine called 1-cinnamoyl-3, 11-dihydroxymeliacarpin. Azadirachtin analogs were found in *M. azedarach* fruit extracts. These isolated compounds were 1-cinnamoyl-3-feruloyl-11-hydroxymeliacarpin, 1-cinnamoyl-3-feruloyl-11-hydroxy 22, 23-dihydro-23-β-methoxymeliacarpin, and 1-tigloyl-11-methoxy-20-acetylmeliacarpine. Other limonoids that have been found in *M. azedarach* are: azedarchol, nimbin, santonum, sandolactone, ochinal and ochinine actetate, sandanol, melianone, mellanin, melianol and many others such as flavonoids, melianoninol, meliandiol, vanillic acid, vanillin and toosendanin. It was found that saponification of the oil from green berries of *M. azedararch* yielded 65% linoleic acid and approximately 20% oleic acid. Apart from palmitic and stearic acid, only very low quantities of other fatty acids, saturated or unsaturated, were also detected. The limonoids salanin and volkensin were isolated from the fruits of *M. volkensii*.

Salanin, meldenin and a limonoid glycoside, established as 6-acetoxy-11-hydroxy-7-oxo-14-epoxymeliacin-1,5-diene-3-O-L-rhamnopyraside, were isolated from 5 kg of powdered *M. azedarach* seeds extracted in 30 l of ethanol. *M. azedarach* leaves were also found to contain santonum, melianone, sandolactone, ochinal and ochinine acetate and 1-cinnamoyl melianone. Rutin and 3-O-L rhamnoside were isolated from *M. azedarach* in India. The two flavonol diglycosides, rutin and kaempferol-3-O-β rutinoside, were also isolated in high yields from the leaves of *M. azedarach* in Spain.

Three trichilin type limonoids with the three known limonoids, trichilins B and D and meliatoxin A_2, were isolated from ether-extracted root bark of the Chinese *M. azedarach* L., namely trichilin H, 12-acetyltrichlin B, and 7,12 diacetyltrichilin B. A biogenetically interesting ring-C seco limonoid, salannal, and a potent insect antifeedant, meliacarpine E, were also isolated from the root bark of the Chinese *M. azedarach*, along with four other seco-limonoids, salanin, deacetyl salanin, nimbolinin B, and nimbolidin B. Sandanol, melianol, mellanine A, and meldenin were isolated from the seeds.

Production of Meliaceous Trees

The trees are easily propagated both sexually and vegetatively. They can be reproduced using seeds, seedlings, saplings, root suckers or cuttings.

Clean seeds, without the pulp, are planted in nurseries in prepared plastic sacks. Germination takes place after 8–15 days, depending on temperature and water supply. Shade usually is not required, but a partially shaded nursery may be advantageous. Ordinary seeds are ready for transplanting in 12 weeks, when they reach a height of 7.5–10 cm and their taproot is approximately 15 cm long. Transplanting is done during the rainy season with a high survival rate. It has been reported that trees produced through seed germination exhibit considerable variation. Hence, tissue culture technology was adopted to raise uniform plantation permitting multiplication of superior genotypes.

Medicinal and Other Uses

Melia azedarch is a medicinal plant used in Eastern medicine. It has been used in many places for the treatment of a variety of human disorders. On the Island of Maritius and in China, an extract of the bark is used as an antihelminthic. In Algeria, the plant is used as a tonic and antipyretic, and in South Africa, it is used for the treatment of leprosy, eczema and the relief of asthmatic attacks. In Asia, leaves are used as an antipyretic while the leaves, fruits and bark are used as an antihelminthic, however, certain "forms" are known to be poisonous to humans and livestock. The oil of *M. azedarach* is also used as an antihelminthic and antiseptic.

Ripe fruits are known to be more toxic to mammals than green ones. Leaves seem to be less toxic, as they are used as fodder for goats in India. It was reported that children have died after eating six to eight ripe fruits. Records also show that *M. azedarach* is toxic to livestock, commonly affecting pigs, but the poisoning of cattle, sheep, goats and poultry has been reported with symptoms of nausea, vomiting, constipation or scouring, often with blood. It was found that the approximate oral LD_{50} values of purified ethanolic solutions of the meliatoxins attributed to be the cause of high toxicity to pigs, was 6.4 mg/kg. Meliatoxins A_1, A_2, B_1 and B_2 have been shown to be responsible for the acute nervous system dysfunction and death in pigs. Toxicity may vary with location and stage of growth and may be entirely absent in some trees.

Melia azedarach provides a multipurpose, termite-resistant heartwood which is used for tea-boxes, furniture, ceilings and other building purposes. The "white cedar" leaves in Australia are used by aborigines as a fish poison.

Bioactivity of the *Melia azedarach* Tree Against Insects

Persian lilac trees remained unharmed during severe invasion by the desert locust *Schistocera gregaria* both in Palestine in 1915 and during the locust plague in India in 1926–27. It was proposed that *M. azedarach* does not kill acridids but repels them for several days and is unpalatable to *Schistocerca gregaria*.

In Punjab, leaves of *M. azedarach* used as soil treatment at a rate of 7 tons/acre reduced the termite attack on wheat to 0.7% as compared with 8% in untreated plots.

M. azedarach is not a good host for the sweetpotato whitefly, *Bemisia tabaci* (Gennadius). Host preference bioassays indicated a significantly lower number of live whiteflies on the leaves of the chinaberry tree versus the leaves of beans, cucumbers, and tomatoes after 24 h.

Bioactivity of Extracts of Melia azedarach

Leaf extracts of *M. azedarach* protected plants against locust feeding and the activity was found to be higher in these extracts than in pulp and the very small seed kernels. Chloroform extracts of *M. azedarach* leaves were found to retard the growth of first instar larvae of the corn earworm *Heliothis zea* and the fall armyworm *Spodoptera frugiperda*. At a concentration of 30 mg-eq/g diet fed to test larvae, 100% mortality occurred and larvae died before pupation, retarding development in both insect species. Significant weight reduction in larvae was observed due to feeding deterrence of the extract.

Aqueous extracts of *M. azedarach* applied on bean plant leaves interfere with the longevity and development of adults and immature stages of *B. tabaci*. The interference of the extract, in a field test, reduced transmission of viruses by 45–60% compared to control plants. This was attributed to the phago-deterrent effect of the plant extract against adults. Toxicity of aqueous emulsions of *M. azedarach* fruits prepared from 5% solutions in acetone containing also Triton X-100 (0.5%) against adults of *Sitotroga cerealella* was approximately 0.2% that of malathion, and activity of 4-day-old residues was 20–40%. The extract lost its toxicity nearly totally by the 8th day after the spray.

Fruit and leaf extracts of *M. azedarach* showed a comparable and potential repellent effect against *B. tabaci* adults. Fruit and leaf aqueous extracts caused a significantly lower number of live adult whiteflies to be encountered on treated bean leaves than the control after 24 h, regardless of whether these plant parts were crushed or boiled in water. *M. azedarach* aqueous extracts at the rate of 1:5 (w/v) caused a possible antifeedant action against adult *B. tabaci* as indicated by fewer eggs laid by treated adults and fewer pupae produced.

The growth of 2nd and 4th larval instars of the oak processionary caterpillar *Thaumetopoea processionea*, was retarded after being sprayed by an enriched *M. azedarach* fruit extract; and after 4 days of spraying, the larvae became quite lethargic. Even with lower concentrations of 0.01%, mortality of 100% was attained within a period of 1–2 weeks. Death was mainly caused by moult disruption because the larvae were not able to shed the old exuviae. Younger larvae were more sensitive to the plant extracts than older ones.

The *Melia* fruit aqueous extract significantly lowered the number of larvae of the pea leafminer, *Liriomyza huidobrensis* (Blanchard), per Swiss chard plant as compared to the control, at 15 days after first spray when two consecutive sprays were performed under field conditions. The *Melia* fruit extract significantly decreased the number of live larvae per cucumber leaf compared to the control, 10 days after each spray under greenhouse conditions. *Melia* fruit extracts and cyromazine caused the formation of deformed larvae which were partially brown rotted and oozing. This indicates that the fruit extract may have a growth-regulating activity similar to that of cyromazine, a triazine insect growth regulator selective to the genus *Liriomyza*. The aqueous leaf extract was found to keep the number of live larvae per leaf at a significantly lower density than the control only at 20 days after the second treatment application. This indicates that the leaf extract might need a longer period of time to reveal its effect. Increasing the number of consecutive sprays enhances the activity of these extracts under field conditions due to the known ultraviolet degradation of botanical extracts.

The activity of mixed function oxidases in the midgut of 5th-instar larvae of *Pieris rapae* was reduced to half its value after feeding on toosendanin, an extract from the bark of *M. azedarach* or *M. toosendan*. Esterase activity in the midgut was also markedly reduced, but not in the hemolymph.

Simple preparations from *M. azedarach* include: drying of the fruit, milling of the seeds, preparation of aqueous extracts, and of a seed dust diluted with 25% zeolite. The main pests controlled by these preparations were: *S. frugiperda*, *Spodoptera* sp., *B. tabaci*, *Plutella xylostella*, *Mocis latipes*, *Diaphania* sp., *Herse cingulata*, *H. virescens*, *Sitophibus oryzae*, *Cyclas formicarius elegantulus*, *Aphis gossypii* and *Myzus persicae*.

Methanolic extracts of *M. azedarach* of high concentrations (25% and 12.5%) caused about 100% mortality of *A. fabae* nymphs within 4 days. Extracts of 25%, 12.5%, and 1.25% also deterred alates in choice experiments from ovipositing on treated *Vicia faba* plants.

Adults of *B. tabaci* were significantly more repelled from tomato plants treated by the undiluted methanol, acetone or water extracts when compared to the control after 72 h. There were significant differences in percent mortality (23.0–48.9%) of nymphal instars when exposed to the undiluted extracts compared to the other diluted extracts and the control. *M. azedarach* leaf and fruit extracts were found to be repellent to the whitefly adults, while the fruit extracts specifically have shown a significant detrimental effect against early nymphal instars. The undiluted methanol extracts caused a very low number of live adult whiteflies on treated plants in comparison to the undiluted water and acetone extracts. This indicates that methanol seems to extract more of the bioactive components from Melia compared to that of acetone or water. Similarly, aqueous and methanol extracts of leaves, fruits and callus of *M. azedarach* have shown significant repellent activity of 58.9–67.7% and have decreased significantly the oviposition rate of the insect without affecting the adult whitefly emergence compared to the control. Extracts of frozen samples were found to be as effective against the pest as fresh samples, thus allowing storage of *Melia* parts to be used in case of shortage. The antifeedant action of the *M. azedarach* extract was observed and it was found that the rate of adult mortality of *B. tabaci* on plants sprayed with *M. azedarach* leaf or fruit extracts (1:5, w/v) were not significantly different from the mortality rate when *B. tabaci* were kept unfed.

The two highest concentrations: 10,000 and 2,000 ppm of the ethanol extract of fruits of *M. azedarach* were incorporated into artificial diet of the fall armyworm, *S. frugiperda*. This caused 100% mortality of the insect before pupation, but the hexane extracts tended to be less effective. Treated larvae showed significant weight loss and delay in the time needed for pupation. Ethanol extracts of the fruits of *M. azedarach* containing 32mg/100ml caused 97%–98% mortality of the cabbage aphid, *Bervicoryne brassicae* in 48 h. Ethanol seed kernel extract of *M. azedarach* inhibited feeding of the rice noctuid *Spodoptera abyssina* by 99.8%.

Petroleum ether extracts of *M. azedarach* fruits are strong antifeedants against nymphs of the brown planthopper, *Nilaparvata lugens*. Rice plants treated with a hexane extract of *M. azedarach* were not only repellent to adults of the green rice leafhopper, *Nephetettix nigropictus*, and the macropterous brown planthopper in choice test against control plants, but they also reduced the feeding time of the insects. Petroleum-ether extract (2%) of both *Melia toosendan* and *M. azedarach* caused respectively 100% and 89.5% feeding deterrence of third-instar larvae of Spodoptera litura.

The petroleum-ether, ethanol and methanol extracts of *M. azedarach* and *M. toosendan* seed kernels have bioactivity against several insect pests such as the rice yellow stem borer *Schirpophaga incertulas*, the fifth instar of the cabbage butterfly *Pieris rapae*, the female rice gall midge *Orseolia oryzae*, the citrus leafminer *Phyllocnystis citrella*, the polyphagous beetle *Anomala cupripes*, and the Asiatic corn borer *Ostrinia furnacalis*. High oviposition deterrence and reduction of adult emergence of the rice hispa and the pulse beetle was detected when exposed to leaf or seed extracts of Chinaberry.

The food intake of newly emerged females of the brown planthopper, and the whitebacked planthopper, *Sogatella furcifera*, on rice plants sprayed with *M. azedarach* seed oil, was reduced starting from the dosage of 5 mg/plant. The $_{32}$P isotope tracer technique was used to verify the antifeedant effect of *M. azedarach* seed oil emulsion against the citrus aphid, *Aphis citricola*. The nymphal period of the cicadellid *Nephotettix nigropictus* was prolonged and mortality was obtained when the insects were fed on seedlings treated with the oil extract.

The 0.5% emulsified seed oil extract of *M. azedarach* gave good control of the orange spiny whitefly, *Alevrocanthus spiniferus* (Quaintance), and its efficacy was comparable to that of the potent acaricides amitraz or cyhexatin in controlling the citrus red mite, *Panonychus ulmi* on citrus. The chinaberry seed oil is also highly toxic to the Formosan subterranean termite.

Bioactivity of *Melia azedarach* components against insects

Meliatoxins and trichilin type limonoids were found to be antifeedants against certain insect pests. Meliatriol isolated from fruits of *M. azedarach* showed strong antifeedant properties against 5th instar of the desert locust *Schistocerca gregaria* Forsk. Meliatine, an exceedingly bitter substance isolated from the leaves of *M. azedarach*, was found to effectively protect crop leaves against the locust attack.

The steroid, estrer azaderachol, isolated from the ether extract of the root bark of *M. azedarach* var. *japonica*, showed antifeedant activity against larvae of *Agrotis segetum*. The antifeedant properties of *M. azedarach* constituents: salannal, meliacarpine E, salanin, deacetyl salanin, nimbolinin B and nimbolidin B were examined with the larvae of *Spodoptera eridania*. Meliacarpinin E showed the most potent activity at 50 ppm, similar to meliacarpinins A-D. Other C-seco limonoids showed only weak activities at 500–1000 ppm. Three trichilin type limonoids from the ether extract of the root bark of the Chinese *M. azedarach* L., namely trichilin H, 12-acetyl, and 7,12 diacetyltrichilin B. were found to be antifeedants active against the Japanese pest *Spodoptera exigua*.

Meliatoxin A_2 isolated from the fruit of *M. azedarach* induced a significant level of antifeedant activity against *Spodoptera lituralis* larvae, while the meliatoxin B_1, lacking the epoxide ring, was much less active. The salannins and salannols isolated from *M. azedarach* have shown antifeedant activity toward the Mexican bean beetle.

The two tetranortriterpenoids: 1-cinnamoyl melianone and 1-cinnamoyl-3, 11-dihydroxymeliacarpin were found to have growth inhibitory effects for first instar larvae of the Lepidoptera *Heliothis viriscens* and *S. frugiperda*. Other highly oxidized tetranorterpenoids that are azadirachtin analogs have impaired metamorphosis of the Mexican bean beetle, *Epilachna varivestis*.

Integration With Natural Enemies

Adults of the predator *Coccinella septempunctata* showed no mortality after being allowed to consume adults of the mustard aphid, *Lipaphis erysimi*, that had been exposed for 5 h to mustard leaves treated with 1.5% alcoholic extract of the drupe of *M. azedarach*.

Leaves infested with *Epilachna vigintioctopunctata*, and treated with a petroleum ether extract of the drupes of *M. azedarach*, were less parasitized by *Pediobius foveolatus* than the control. However, on exposure to parasitization 24 h after treatment, larvae were parasitized normally and the parasites that emerged from treated hosts were normal.

M. azedarach oil did not affect the survival and behavior of the larvae of *Coccinella undecimpunctata*, but there was prolongation of the fourth larval instar while the *Aphis gossypii* aphid consumption was unchanged. The oil of *M. azedarach* seeds was found to be only slightly toxic against the predatory mirid bug *Cyrtorhinus lividipennis* and non-toxic against the spider *L. pseudoannulata*, natural enemy of the white-backed planthopper, *Sogatella furcifera*, the brown planthopper, *N. lugens*, and the green leafhopper, *Nophotettix virescens*. A massive dosage of the seed oil of *M. azedarach* applied topically to the wolf spider *Lycosa pseudoannulata*, a natural enemy of the brown planthopper, *Nilaparvata lugens*, had no effect on the spider.

Potentials in Sustainable Systems

Extracts of tissue culture of *Melia* have shown repellency to different insect species similar to extracts of *Melia* leaf or fruit. The synthesis of secondary plant compound(s) in such undifferentiated cells of *Melia* is clearly occurring. It may be possible to enhance production of meliaceous allelochemicals in tissue cultures to the extent that culture extracts could eventually be used for production of botanical insecticides. As an alternative to harvesting an ecologically important tree, cell-culture systems can be used to provide a continuous supply of those biopesticidal extracts through the propagation of *Melia* all year round and using them easily and conveniently.

The different ecotypes of *M. azedarach* are a potential natural resource that can be utilized, as raw material and extracts, in low-input agroecosystems. Cultivation of this meliaceous tree is an economically feasible practice, as it is usually planted as a common shade tree. The efficacy of *M. azedarach* extracts might be enhanced by investigating the timing and frequency of application of the plant extracts on crops for management of major economical agricultural pests. These extracts could provide a relatively inexpensive and readily available insecticide to combat the pest resistance to insecticides.

► Botanical Insecticides

References

Abou-Fakhr Hammad EM, Zournajian H, Talhouk S (2001) Efficacy of extracts of *Melia azedarach* L. callus, leaves and fruits against adults of the sweetpotato whitefly *Bemisia tabaci* (Hom. Aleyrodidae). J Appl Entomol 125:425–488

Ascher KRS, Shmutterer H, Zebitz CPW, Nagvi SNH (1995) The Persian lilac chinaberry tree: *Melia azedarach* L. In: Schmutterer H (ed) The neem tree. VHC Publishers, New York, NY, pp 602–642

Kraus HS, Baumann M, Bokel U, Klenk A, Klingele S, Pohnl M, Schwinger M (1987) Control of insect feeding and development by constituents of *Melia azedarach* and *Azadirachta indica*. In: Schmutterer H, Ascher KRS (eds) Natural pesticides from the neem tree and other tropical plants. Proceedings of the Third International Neem Conference, Rauiscchholzhausen, Germany, pp 111–125

Lee MS, Klocke JA, Barnby MA, Yamasaki RB, Balandrin MF (1991) Insecticidal constituents of *Azadirachta indica* and *Melia azedarach* (Meliaceae). In: Hedin PA (ed) Naturally occurring pest bioregulators, ACS Symposium Series 449, pp 293–304

Nakatani M, Huang RC, Okamura H, Naoki H, Iwagana T (1994) Limonoid antifeedant from Chinese *Melia azedarach*. Phytochemistry 36:39–41

Nardo EAB, De Costa AS, Lourencao AL (1997) *Melia azedarach* extract as an antifeedant to *Bemisia tabaci* (Homoptera: Aleyrodida). Fla Entomol 80:92–94

Oelrichs PB, Hill MW, Valley OJ, Macleod JK, Molinski TF (1983) Toxic tetranortriterpenes of the fruit of *Melia azedarach*. Phytochemistry 22:531–534

Tewari GC, Moorthy PNK (1985) Plant extracts as antifeedants against *Henosepilachna vigintioctopunctata* (Fabricius) and their effect on its parasite. Indian J Agr Sci 55:120–124

China, William Edward

William China was born in London on December 7, 1895. His university education was in London and Cambridge, but was interrupted by World War I. In that war, he served in France, first in the British army, later in the Royal Air Force. He returned to Cambridge University and earned a degree in zoology. In January 1922, he was appointed assistant in the Department of Entomology of the British Museum (Natural History), in 1930 assistant keeper, and eventually in 1955, keeper. His subject of research was the taxonomy of Hemiptera, in which he eventually published 265 papers, describing 98 new genera and 248 species. During World War II, he was deeply involved in temporarily moving the national insect collections out of London to prevent damage or loss. His research resulted in his award in 1948 of a D.Sc. degree by Cambridge University. He retired in 1970 to a little fishing village in the county of Cornwall, where he died on September 17, 1979, survived by his wife Lita and three children.

Reference

Knight WJ (1980) Obituary and bibliography. Entomologist's Monthly Magazine 115:164–175

Chinch Bug, *Blissus leucopterus* (Say) (Hemiptera: Blissidae)

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The chinch bug, *Blissus leucopterus*, is found through much of the eastern United States and southern Canada, west to about the Rocky Mountains. However, it is absent from the Gulf Coast region, where it is replaced by a closely related species, the southern chinch bug, *Blissus insularis* Barber. The two species have overlapping ranges in portions of the southern states from North and South Carolina through central Georgia and west to Texas. Southern chinch bug feeds only on lawn and forage grasses, particularly St. Augustine grass, and is not a food crop pest. Other species of *Blissus* occur in both eastern and western states but they are of little consequence. The *Blissus* spp. may have dispersed northwards from South America, but if so they apparently dispersed in precolonial times, as there is no record of their introduction.

The range of *B. leucopterus* can be subdivided because two discrete subspecies exist; *B. leucopterus hirtus* Montandon in the northeast, and *B. leucopterus leucopterus* (Say) in the central region of the eastern states. In eastern Canada, the New England states, and south to about northern Virginia and eastern Ohio, the northeastern form, *B. leucopterus hirtus*, is a pest of lawn grasses, but not of food crops. This subspecies is also called "hairy chinch bug" to distinguish it from the food crop-attacking subspecies, *B. leucopterus leucopterus*, which is known simply as "chinch bug." Chinch bug occurs from Virginia to Georgia in the east, extending to South Dakota and Texas in the west. Chinch bug generally is not damaging throughout its entire range, and is considered to be a pest mostly in the midwestern and southwestern states from Ohio in the east to South Dakota and Texas in the west.

Life History

There are at least two generations per year throughout the range of *B. leucopterus leucopterus*. The first generation commences in the spring with oviposition by overwintering adults, usually in April or May. The second generation begins in June–August. Second generation adults overwinter, often in the shelter of clump-forming wild grasses, dispersing in the spring to early-season crops, and then in early summer to later-developing crops where the second generation develops. Generations overlap considerably due to prolonged oviposition, and in the southwestern states there is some evidence of a third generation. A complete life cycle can occur in 30–60 days.

The elongate-oval eggs are rounded at one end, truncate at the other, and measure about 0.85 mm long and 0.31 mm wide. The truncate end bears three to five minute tubercles, 0.1 mm in length. The eggs are whitish initially, turning yellowish brown after a few days and reddish before hatching. Eggs are deposited in short rows at the base of the plant on roots, on the lower leaf sheaths and stems, and on the soil near the plant. Females deposit eggs at a rate of 15–20 per day over a 2–3 week period, producing up to 500 eggs. Duration of the egg stage is about 16 days at 27°C and 8 days at 31°C.

There are five instars. Duration of the instars is about 5, 6, 5, 4, and 6 days for instars 1–5, respectively, when reared at 29°C. Under field conditions, the development time may be extended, with a developmental period of about 30–40 days normal, and 60 days not unusual. During the early instars, the head and thorax are brown, the legs pale. These structures become darker as the nymphs mature, so that the mature nymph is blackish. The first two segments of the abdomen are yellowish or whitish, the remainder red except for the tip of the abdomen, which is black. The reddish abdomen becomes progressively darker, however, appearing almost black at nymphal maturity. The wing pads become visible in the third instar, but are difficult to discern. In the fourth instar the wing pads extend about half the width (Fig. 47) of the first abdominal segment. In the fifth instar the wing pads extend to the third abdominal segment. The nymphal body lengths are about 0.9, 1.3, 1.6, 2.1, and 2.9 mm for instars 1–5, respectively. Nymphs prefer to feed in sheltered locations such as curled leaves and on roots, but are often found aggregated on the stem near the base of the plants. When not feeding they may hide under clods of soil and rubbish, or in loose soil.

The body and legs of the adult are blackish in color (Fig. 48). The wings of *B. leucopterus leucopterus* nearly attain the tip of the abdomen, and are white in color with a pronounced blackish spot found near the center and outer margin of the

Chinch Bug, *Blissus leucopterus* (Say) (Hemiptera: Blissidae), Figure 47 **Adult of chinch bug, *Blissus leucopterus* (Say).**

Chinch Bug, *Blissus leucopterus* (Say) (Hemiptera: Blissidae), Figure 48 **Fourth instar of chinch bug, *Blissus leucopterus* (Say).**

forewings. The adult measures 3.5–4.5 mm in length. In the related form called hairy chinch bug, the wings generally are abbreviated, usually not extending beyond the middle of the abdomen.

Hosts of chinch bug consist solely of plants in the family Gramineae, but include both wild and cultivated grasses. It is known principally as a pest of such grain crops as barley, corn, millet, oat, rye, sorghum, and wheat, but oat is only marginally suitable. However, it also damages forage grasses including sudangrass and timothy, and feeds on wild grasses such as foxtail, *Setaria* spp.; crabgrass, *Digitaria* spp.; and goosegrass, *Elusine indica*.

Females select sorghum for oviposition over wheat and corn; barley is intermediate in preference. Crop suitability, as measured by development time, is similar to oviposition preference.

Numerous natural enemies have been observed. Among avian predators feeding on chinch bugs are common birds as barn swallow, *Hirundo erythrogastra* Boddaert; horned lark, *Otocoris alpestris* (Linnaeus); meadowlark, *Sturnella magna* (Linnaeus); redwinged blackbird, *Agelaius phoeniceus* (Linnaeus); and kingbird, *Tyrannus tyrannus* (Linnaeus). Insect predators of special importance are insidious flower bug, *Orius insidious* (Say) (Hemiptera: Anthocoridae), an assassin bug, *Pselliopus cinctus* (Fabricius) (Hemiptera: Reuviidae), and various ants (Formicidae). Ladybird beetles (Coleoptera: Coccinellidae) and lacewings (Neuroptera: Chrysopidae) frequently have been observed on plants infested with chinch bugs, but their effects are uncertain.

Parasitoids are sometimes found in these small insects, but rarely are they considered to be significant mortality factors. An egg parasite, *Eumicrosoma benefica* Gahan (Hymenoptera: Scelionidae), the nymphal or adult parasite *Phorocera occidentalis* (Walker) (Diptera: Tachinidae), and an unspecified, naturally occurring nematode have been reported. The egg parasitoid, which is found throughout most of the range of the chinch bug and is active during much of the season when chinch bug occurs, was reported to parasitize up to 46% of the eggs in Nebraska, so it may be of considerable value in biological control.

The most important natural mortality factor is fungal disease, particularly *Beauveria bassiana*. Interestingly, this fungus was intensively redistributed, particularly in Kansas, during the late 1880s in an effort to increase suppression. However, it eventually became apparent that the disease spread naturally, and that the effectiveness of the fungus was related more to weather than to the efforts of agriculturalists and entomologists to foster epizootics. The fungus is invasive and pathogenic at relative humidities of at least 30–100%, but fungal replication and conidia production require humidities of at least 75%. Clumps of such bunch grasses as little bluestem, *Andropogon scoparius*, serve to harbor not only overwintering bugs, but *Beauveria* as well, and may be important in initiating fungal epizootics. The food plant of the chinch bug affects susceptibility to *B. bassiana*, with a diet of corn and sorghum suppressing fungus development and bug mortality.

Weather has significant impact on chinch bugs. The overwintering period is moderately critical. Adults seek shelter in stubble and debris, but one of the most favorable locations is among the stems of bunch grasses. Bunch grasses provide food in the autumn before the onset of winter temperatures, and again in the spring before it is consistently warm and the bugs disperse. Bunch grasses also serve to break the wind by reducing desiccation and the severity of the wind, and by keeping excessive rainfall from the insects. Thus, in the absence of bunch grasses or similar shelter, survival can be poor. Heavy snow cover is favorable, keeping the bugs warmer and sheltered from the drying wind.

Summertime weather is perhaps even more critical. Chinch bugs thrive in warm, dry conditions, at least in the midwestern states. Heavy rainfall can kill many bugs, and wet, humid weather fosters epizootics of fungal disease. In the southwest the situation is different because dry weather is usually assured, but the absence of summer rain causes premature senescence of plants, depriving bugs of green food late in the summer.

Damage

Chinch bug is a plant sap-feeding insect, causing a reddish discoloration at the site of feeding and death of that portion of the plant. Plant growth can be stunted, or plants killed when fed upon by large numbers of bugs. Their destructiveness is attributable, in part, to their gregarious nature. Not only do large numbers aggregate on certain plants, but they also disperse in tremendous numbers from field to field. When plants are infested while young, they suffer more damage than if infested later in growth.

Management

Granular and liquid insecticides are used to protect plants, particularly plants that are invaded by nymphs or adults dispersing from senescent early-season crops. Systemic insecticides can be applied at planting time, and either contact or systemic materials after the crop has emerged from the soil. Liquid insecticides should be directed to the base of the plants, a location favored by the insects.

Historically, most damage occurred when early-season small grain crops matured, and large numbers of first generation nymphs dispersed by walking to adjacent crops, usually corn. This was combated by erecting barriers, usually in the form of a ditch, between crops. Also, some destruction of overwintering bugs in wild grasses was accomplished by burning, though it was rarely more than 50% effective. These practices are largely obsolete, and insecticides are now used effectively. However, it remains advisable to rotate among susceptible and nonsusceptible crops, and to grow susceptible crops in isolation from alternate hosts. Because the combination of small grains and corn leads to damage by chinch bugs, it may be desirable to eliminate one of these crops and thereby eliminate an important food from the chinch bug life cycle. In southern states the crop sequence is different, with both wheat and corn invaded by overwintering bugs early in the season.

Cultural practices that promote dense growth and shade will increase humidity and decrease chinch bug numbers. Thus, fertilization and irrigation can be detrimental to chinch bug survival.

There is considerable difference among crops in susceptibility to injury, and within crops the level of resistance also is variable. Measurable levels of difference in bug longevity and development occur when they feed on different varieties of wheat, though there is not a practical level of resistance. In contrast, a resistant variety of sorghum has been identified, and there is considerable resistance in grain corn.

► Turfgrass Insects and their Management
► Vegetable Pests and their Management

References

Leonard DE (1968) A revision of the genus *Blissus* (Heteroptera: Lygaeidae) in eastern North America. Ann Entomol Soc Am 61:239–250

Swenk MH (1925) The chinch bug and its control. Nebraska agricultural experiment station circular 28, 34 pp

Chironomidae

A family of flies (order Diptera). They commonly are known as midges.

► Flies

Chironomids as a Nuisance and of Medical Importance

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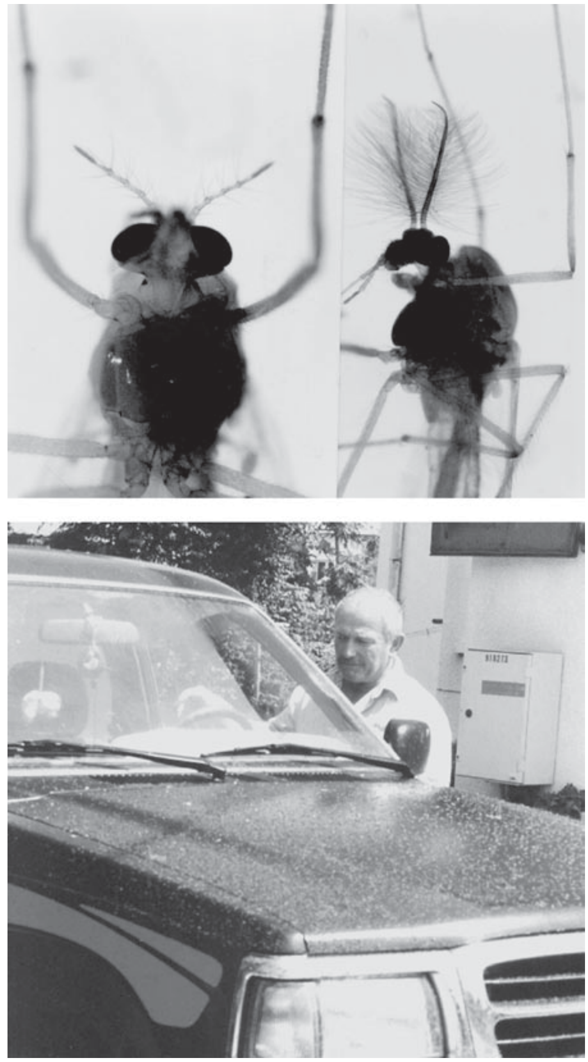
Chironomids, the "non-biting midges" (Diptera: Chironomidae) are one of the most important groups of insects worldwide in freshwater, aquatic ecosystems. Chironomids can be found on all continents, including Antarctica. They are abundant in terms of the number of species that are known to exist (estimated number between 15,000 and 20,000), their relative biomass or both. They play an important role in the decomposition process.

Large populations of midges with densities amounting to several thousand larvae/m^2 (usually on the floor of freshwater habitats) have been reported. They are a source of economic burden, nuisance, and health problems. Large midge population densities create conflict with nearby human settlements. This phenomenon is recognized worldwide, in the United Kingdom, United States, Japan, Italy, Spain, Israel, New Zealand and Sudan.



Chironomids as a Nuisance and of Medical Importance, Figure 49 **Nuisance midges: above, *Chironomus* sp. female (left) and male (right); below, accumulation of midges on an automobile after only a few minutes of travel.**

Chironomidae (particularly *Chironomus*) emerging from polluted natural and man-made aquatic habitats, near or in urban districts, can become intolerable (Fig. 49). During the spring and midsummer, evening breezes carry large swarms of adult midges to nearby cities and communities where they can become a severe nuisance to the residents. Adult midges are most active during the evening and they may enter the mouth, eyes and ears, thus limiting evening activities outdoors and indoors. In 1998, a population estimated at 40–50 billion individuals/night emerged from 200 acres of waste stabilization ponds near Tel Aviv, Israel. Such swarms may be economically important due to the damage they can cause to vessels, pumps and aeroplane engines.

Chironomid larval populations ("red-worms") contaminate municipal drinking water supply systems. This problem has been reported in the United Kingdom since the 1970s, in the U.S.A., Israel and elsewhere. In both the U.K. and U.S.A., the chironomid inhabiting the water systems was identified as the parthenogenetic species *Paratanytarsus grimmi*. After entering the pipe system, the pupal stage circulates in the water and may produce egg masses without emerging as airborne adults. Because pesticides cannot be used in a water supply, a food-grade coagulant and water disinfectant were suggested as control agents.

Besides the unacceptable appearance of red-worms in the water supply, the larvae also may cause technical problems by blocking water filtration systems. In countries where recycled water is used for irrigation, the larvae may adhere to the inner surface of pipes and contribute to the build-up of biofilm on these surfaces. As a result of such accumulations, greater amounts of energy may be needed for water transport.

Many insect vectors of serious human diseases are flies. This includes nematoceran flies in which the females feed on a vertebrate blood meal. Chironomids are non-biting midges, and it may seem surprising to find that they are of medical significance. However, they are now recognized as causing severe allergic reactions in humans. The most thoroughly investigated case of an allergic disease associated with chironomids comes from the Sudan. People living south of the Aswan Dam suffer from the mass emergence of chironomids from Lake Nasser. In the dry winds, large numbers of dead insects are blown into the air, causing allergic reactions such as asthma and rhinitis. The town of Wadi Halfa located near Lake Nasser has been particularly plagued since the building of the dam on the Nile. A few cases also have been reported from the U.S.A. For example, an employee at a hydroelectric plant in Alabama developed seasonal hay fever in response to the mass emergence of chironomids from the dam. It has been shown that chironomid larval hemoglobin, which contaminates adults during metamorphosis, is a potent human allergen. It is believed that midges are potentially the cause of many allergic reactions worldwide.

As well as causing allergies, midges may play a role in the maintenance and transmission of infectious diseases. Chironomid egg masses have been reported to serve as a natural reservoir for the cholera bacterium, possibly raising the chironomid problem from a nuisance level to a life-threatening hazard. Cholera is a severe diarrheal disease that kills thousands of people each year and affects the lives of millions of others. The disease is caused by the bacteria *Vibrio cholerae*, which is pathogenic to humans only. At present, the disease is most common in the Indian subcontinent and less developed countries in Asia, Africa and South America.

References

Ali A (1994) Pestiferous Chironomidae (Diptera) and their management. In: Rosen D, Bennett FD, Capinera JL (eds) Pest management in the subtropics: biological control – a Florida perspective, Intercept Ltd, Andover, UK, pp 487–513

Armitage P, Cranston PS, Pinder LCV (eds) (1995)The Chironomidae: the biology and ecology of non-biting midges. Chapman & Hall, London, UK, 572 pp

Benke AC (1998) Production dynamics of riverine chironomids: extremely high biomass turnover rates of primary consumers. Ecology 79:899–910

Broza M, Halpern M, Teltsch B, Porat R, Gasith A (1998) Shock chloramination: a potential treatment for Chironomidae (Diptera) larvae nuisance abatement in water supply systems. J Econ Entomol 91:834–840

Broza M, Halpern M (2001) Chironomids egg masses and *Vibrio cholerae*. Nature 412:40

Chitin

A tough insoluble structural polysaccharide material that comprises variable portions of the insect cuticle. It is a water-insoluble polysaccharide that forms the exoskeletons of arthropods, and is one of the most widely occurring polysaccharides in nature. Chitin molecules are long-chain sugars consisting of *N*-acetyl-glucosamines attached together with beta-glucosidic linkages.

Chitinase

An enzyme that degrades chitin.

Chitinous

Consisting of, or containing, chitin.

Chittenden, Frank Hurlbut

Frank Chittenden was born in Ohio on November 3, 1858, and grew up in a small town there. He studied entomology at Cornell University. Next, he worked at the Brooklyn Museum and was one of the founders of the Brooklyn Entomological Society and an editor of Entomologica Americana. In 1891 he was hired by the U.S. Department of Agriculture (Fig. 50) and embarked on his life's work as an applied entomologist, contributing greatly to the knowledge of pests of vegetables and stored products. In 1904 he was awarded an honorary degree of doctor of sciences by Western University of Pennsylvania. He died in Washington, DC, on September 15, 1929.

Chittenden, Frank Hurlbut, Figure 50 **Frank H. Chittenden.**

Reference

*Mallis A (1971)Frank Hurlbut Chittenden. In: American entomologists. Rutgers University Press, New Brunswick, NJ, pp 100–102

Chlorinated Hydrocarbons

A class of synthetic insecticides containing chlorine as one of the constituents. Chlorinated hydrocarbon insecticides are typically very persistent and formerly were used widely for soil and seed treatments. These chemicals also are known as organochlorines.

► Insecticides

Chloroperlidae

A family of stoneflies (order Plecoptera). They sometimes are called green stoneflies.

► Stoneflies

Chloropidae

A family of flies (order Diptera). They commonly are known as frit flies or grass flies.

► Flies

Chlorosis

Yellowing or bleaching of normal green plant tissue, usually caused by the loss of chlorophyll.

Choreutidae

A family of moths (order Lepidoptera). They are commonly known as metalmark moths.

► Metalmark Moths
► Butterflies and Moths

Cholinesterase

An enzyme that is present in the synapse region of nervous tissue, and which is necessary for normal functioning of nerves in animals. Cholinesterase inhibiting chemicals such as insecticides of the organophosphate and carbamate classes disrupt nerve transmission in insects.

Chordotonal Sensory Organs

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Insects have a plethora of sensory organs scattered over and within their body. Many of the sensory structures are mechanical sensors that bend, indicating contact with a surface or wind and air movement over the structure. Other mechanoreceptors detect stress in the exoskeleton, the cuticle, caused by movement of legs, wings, or antennae, and enable insects to know the position of their body and limbs. Still others detect vibrations in the substrate on which the insects may be resting, and vibrations in the air, which we usually call sound. Sound detectors are typically called tympanal organs. The simplest of mechanoreceptors may consist of a single hair or seta that projects from the cuticle surface. Such a simple receptor, usually with only one sensory neuron connecting it to the central nervous system (CNS) is called a sensillum.

More complex sensory organs are composed of many sensilla, i.e., they have many sensory neurons connecting to the CNS. Although there are numerous morphological variations in a mechanoreceptor, from the simple, single hair receptor to very complex receptors such as Johnston's organ on the antennae of most insects, they tend to have certain common features. Whether one or many, each sensory neuron is enclosed in one to several sheath cells, and connected by a relatively long axon to the central nervous system. In mechanoreceptors the dendrites, that part of the sensory neuron nearest the site of the stimulus, typically are enclosed within a sclerotized cap cell, called the scolopale. The scolopale is attached to, or in contact with, the site where stimulation will occur, usually some internal structure or the cuticular surface. Any stretching or movement of the structure to which the scolopale is attached will stimulate the dendrites of the sensory neuron and may set up a series of nerve impulses going into the CNS. If only one sensory neuron and scolopale is present, the single unit is called a scolopodium, or chordotonal sensillum. These terms are used interchangeably. More complex mechanoreceptors contain many scolopidia or multiple scolopale units, or chrodotonal sensilla, again terms that refer to the same things.

The subgenual organ is a complex chordotonal organ composed of multiple scolopidia. The name "subgenual" means below the knee, from Latin for knee (*genu*), and this complex chordotonal organ usually is located near the joint between the femur and tibia. Subgenual organs may contain as few as three scolopidia in some earwigs (*Forficula* spp.), but in most insects usually contains more scolopidia. It acts as a proprioceptor (a receptor of internal stimuli) and detects vibrations of the substrate on which the insect rests. The subgenual organ is especially well developed in crickets (Gryllidae) and katydids (Tettigonidae) and is closely associated with a tympanal organ, with both organs located on the tibia. The two organs have separate sensory innervation, however, and probably have separate functions. In some insects, the scolopidia in the subgenual organ vary in length, suggesting that different scolopidia might respond to vibrations of different amplitude according to length. The subgenual organ of the American cockroach *Periplaneta americana* is sensitive to vibrations that would displace the foot of the insect by as little as 10^{-9}–10^{-7} cm. The subgenual organ generally is less well developed in Lepidoptera, Hymenoptera, and Hemiptera than in the Orthoptera, and some Hemiptera, Coleoptera, and Diptera do not have subgenual organs. Those without a subgenual organ display only low sensitivity to high frequency vibrations. Probably all insects have, in addition to the subgenual organ, additional more simple chordotonal sensilla on the legs, particularly at or near the leg joints, and some insects lacking a subgenual organ have a similar organ at the distal end of the tibia that may serve much the same function as the subgenual organ.

Johnston's organ is another large complex chordotonal organ that typically consists of many scolopidia. Johnston's organ is located between the second (the pedicel) and third joints of each antenna of most adult insects. Some hexapods (Collembola and Diplura) do not have a Johnston's organ. A simplified form of the organ occurs in some larvae. Johnston's organ responds to several kinds of stimuli in different insects, including acting as a proprioceptor to indicate movement of the antennae, monitoring wing-beat frequency in relation to flight speed in some Diptera, serving as a gravity indicator, indicating ripples at the water surface in gyrinid beetles, and functioning as a sound reception in mosquitoes and perhaps other insects. With its location in the second antennal segment, Johnston's organ is positioned to monitor movements of the antennal flagellum, whether due to muscles controlled by the insect, or displacements of the antennae by wind and flight. Radially arranged scolopidia are attached to the wall of the pedicel at one end and to the intersegmental membrane between the pedicel and flagellum. Johnston's organ seems to have reached its apex of development in Chironomidae and Culicidae (Diptera), in which the pedicel is much enlarged and filled with scolopidia. It seems to function in successful swarming and mating. Male mosquitoes detect the sound of the female in flight when the arista on the male antenna vibrates in resonance to the wing beats. Long hairs on the antennae of males also vibrate, causing the flagellum (the major portion of the antenna) to resonate in response to the flight sounds of females. Males of the mosquito *Aedes aegypti* are most sensitive to frequencies from 400 to 650 Hz, corresponding closely to the natural wing-beat frequency of females. Johnston's organ functions as a flight speed indicator in adult *Calliphora erythrocephala*, and probably also in some other insects such as the housefly, honeybee, and related insects. It is probably an important gravity indicator for most insects, enabling them to have a sense of their body in relation to horizontal and vertical planes because the weight of the antenna excites scolopidia depending upon the pull of gravity relative to the body.

Many insects produce sounds, are sensitive to sounds, and utilize sounds in courtship, mating, prey location, and predator avoidance. Detection of high frequency sound waves in the air is accomplished by a tympanum, a chordotonal organ containing scolopidia. Tympanal organs are located at various places on the body of insects, including near the sternum of the first abdominal segment of Acrididae (grasshoppers) and Cicadidae (cicadas), on the tibia of Tettigoniidae (long-horn grasshoppers) and Gryllidae (crickets), on the thorax of Notonectidae (water beetles), and on the thorax or abdomen of some Lepidoptera. Tympanal organs are specialized for air-borne sound pressure waves, and permit sound detection over a relatively long distance. They are sensitive to a wide range of frequencies from 2 kHz up to about 100 kHz. Typically in insects, as well as in other animals, tympanal organs are paired. A single pressure receptor is not very efficient at detecting the directionality of the sound source, but two receptors, preferably well separated from each other, can detect directionality by differences in reception at the two locations. Tympanal ears typically have a minimum of three components, (i) a thin cuticular tympanum on the cuticular surface, (ii) an air sac or other tracheal structure behind the tympanum, and (iii) sensory neurons organized in scolopidia attached to the tympanal membrane or attached near it, so that they vibrate in response to the vibrations of the tympanum. Airborne sound waves cause the tympanum to vibrate, and sensory neurons enclosed in the scolopale cells detect the vibrations and respond by sending nerve signals to the CNS. The air cavity or tracheal sac plays an important role as a resonating chamber. Some insects have a tympanum that can respond to sound waves striking it from the inside of the air chamber as well as from outside; such tympanal organs are pressure-difference receivers, and they are especially sensitive to directionality of the sound. Some tympanal organs have scolopidia of different length, suggesting sensitivity to various frequencies, but function is unproven. Tympanal organs probably evolved from some early form of mechanoreceptor, probably a stretch-registering proprioceptor, but they evolved independently among the seven orders of insects having tympanal hearing. In addition to tympanal organs, some insects also may hear some sounds with other organs including Johnston's organ, subgenual organs, scattered simple chordotonal sensilla, and simple hair sensilla.

References

Bailey WJ (1991) Acoustic behaviour of insects: an evolutionary perspective. Chapman & Hall, London, 225 pp

Hoy RR, Robert D (1996) Tympanal hearing in insects. Ann Rev Entomol 41:433–450

Nation JL (2002) Insect physiology and biochemistry. CRC Press, Boca Raton, FL, 485 pp

Yack JE, Fullard JH (1993) What is an insect ear? Ann Entomol Soc Am 86:677–682

Choriogenesis

Production of a thin vitelline membrane and chorion by the follicle cell, the last step in production of the egg.

Chorion

The outer layer of an insect egg. The egg "shell."

Choristidae

A family of insects in the order Mecoptera.

► Scorpionflies

Christophers, (Sir) Samuel Rickard

Rickard Christophers was born in Liverpool on November 27, 1873. He graduated in medicine in 1896, and then spent some time on the Amazon. In 1898 he joined the Malaria Commission, which had been established jointly by The Royal Society and the (British) Colonial Office; that was the year in which final proof was obtained of transmission of malaria by Anopheles mosquitoes. In West Africa, he concluded quickly that people who survive malaria are the main reservoirs of the disease, allowing it to be transmitted by mosquitoes to uninfected people. After that, he worked in India, on malaria and the various Anopheles species that transmit it, showing that successful control requires knowledge of the habits and larval habitat of each implicated Anopheles species. He developed standards for malarial surveys. He investigated the anatomy and behavior of mosquitoes, including the development of mosquito eggs. Later he worked at the London School of Tropical Medicine and Hygiene, and then at Cambridge University. His landmark book (1960) "*Aedes aegypti* (L.), the yellow fever mosquito" was published when he was 87. At the age of 90 he retired and moved to the county of Dorset in the west of England. He died on February 19, 1978.

Reference

Gillett JD (1978) Sir Rickard Christophers. Antenna 2:33

Chromatids

Chromosome components that have duplicated during interphase and become visible during the prophase stage of mitosis. Chromatids are held together at the centromere.

Chromomere

A region on a chromosome of densely packed chromatid fibers that produce a dark band. Chromomeres are readily visualized on polytene chromosomes.

Chromosome Imprinting

The mechanisms involved in chromosomal imprinting, or labeling of DNA, is associated with methylation of DNA in many organisms. Imprinting is a reversible, differential marking of genes or chromosomes that is determined by the sex of the parent from whom the genetic material is inherited.

Chromosome Puffs

A localized swelling of a region of a polytene chromosome due to synthesis of DNA or RNA. Puffing is readily seen in polytene salivary gland chromosomes of dipteran insects.

Chromosomes

Units of the genome with many genes, consisting of histone proteins and a very long DNA molecule; found in the nucleus of every eukaryote.

Chronic

In pathology, of long duration; not acute. This is usually used to describe a debilitating disease that slowly infects a population as opposed to one that quickly and dramatically infects the population.

Chronic Bee Paralysis

A disease of bees caused by a RNA virus (but not a picornavirus). Symptoms include flightlessness and a distended abdomen. (contrast with acute bee paralysis)

Chronic Toxicity

The toxic effect of a chemical following long-term or repeated sublethal exposures.

Chronotoxicology

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All eukaryotic organisms, including insects, have developed rhythmic behavioral, physiological or biochemical patterns synchronized with particular periods of the day, to adapt to their ecological niches in the most optimal manner. Those oscillations, circadian rhythms, have evolved with a periodicity approximating 24 h, are of endogenous nature and may be adjusted to lighting stimuli. Chronotoxicology is the study of the adverse effects of chemicals on living organisms in relation to their circadian rhythms. In particular, it examines toxicants' chronotoxicity, i.e., periodic changes in sensitivity of living organisms to toxicants.

Historical Perspective

Circadian changes in sensitivity to toxicants were first reported in mice by Halberg and Stephens as early as 1958. Five years later, Stanley Beck showed that the German cockroach, *Blatella germanica* (L.) exhibits a 24-h susceptibility rhythm when administered a standard dose of potassium cyanide at different times of the day. Within a little more than a year of Beck's report, two papers on insecticide chronotoxicity appeared in the prominent journal *Science*. Cole and Adkisson reported diurnal variations in mortality from a standard dose of trichlorfon applied to the beetle, *Anthonomus grandis*, and Polcik and colleagues, in a paper on dichlorvos chronotoxicity to the mite, *Tetranychus urticae* (Koch) posed an important and novel concept that "the findings of a marked sensitivity pattern should emphasize the importance of considering circadian organization [of the pest] in the evaluation and interpretation of toxicological experiments with insecticides." Soon, Nowosielski et al. reported daily changes in susceptibility of the house cricket, *Acheta domesticus* (L.) and *T. urticae* to anesthetics (ethyl ether, chloroform and carbon tetrachloride).

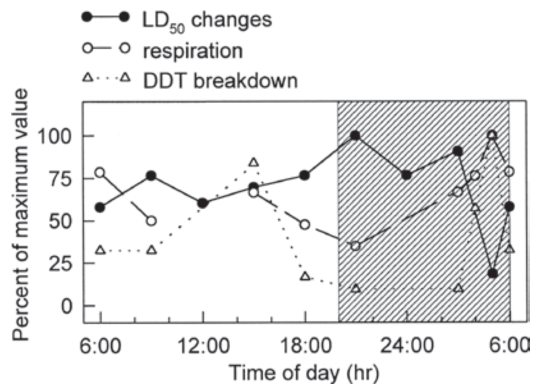
These pioneering papers demonstrated that susceptibility to toxicants fluctuate during the day, and are dependent not only on properties of the toxicant, but also on endogenous rhythmic changes in pest physiology. One might have predicted that by now, monitoring the diurnal susceptibility to toxicants (and, in particular, to insecticides) would be an experimental routine for establishing toxicity parameters. However, recent inquiry suggests that papers on the chronotoxicity of insecticides are rarities.

Forty years after pioneering publications of Beck, Polcik and colleagues and Cole and Adkisson, Pszczolkowski and associates inspected representative databases (Medline, Toxline, Agricola, and Internet Database Service-Biological Sciences) in search of papers on pesticide chronotoxicity to insects. The search, followed by paper-to-paper inquiry yielded only 16 reports referring to diurnal or circadian changes in insecticide toxicity in insects. Four more were found more recently. Ten of them examined difference between the highest and the lowest mortality percent after application of a standard dose of insecticide at various times of the day, in the remaining reports diurnal variations in LD_{50} were reported. However, even these scanty data show that insect mortality can be as much as nine times higher than if the same, standard dose is applied at some other time or times, and that, depending on the time of testing, the highest LD_{50} may be up to 7.5 times higher than the lowest LD_{50} for the same toxicant.

Coincidence of Insecticide Susceptibility Rhythms and Other Biological Rhythms

Theoretically, periodic changes in insecticide sensitivity should reflect periodic changes in ratios of penetration, ratios of detoxification (including metabolism, elimination from hemolymph and excretion of a given toxicant), periodic alterations at the site of action (for instance, periodic over- or underexpression of target receptors) or their combinations. This assumption was reiterated in publications devoted to physiological and behavioral aspects of insect biological rhythms, e.g., in fundamental "Insect clocks." Unfortunately, this hypothesis did not attract attention of many researchers.

Perhaps the most extensive analysis of physiological and biochemical events that underlie circadian sensitivity to an insecticide was research on house fly, *Musca domestica* (L.). Mean LD_{50} values for DDT were established as a function of application time in the house fly, kept in a specific photoperiodic regimen. Flies tested topically with DDT had a significantly lower LD_{50} value when treated at the end of the dark phase, and increased tolerance to DDT during the early part of the dark phase. This distribution was apparently caused by some endogenous oscillations, because the flies kept in total darkness exhibited similar pattern of DDT susceptibility. This rhythmic response was not caused by changes in cuticle permeability to the insecticide, for regardless of the time of application, about 40% of DDT was absorbed within 2 h. However, comparison of DDT susceptibility rhythm and rhythmic changes in respiration and DDT breakdown to DDE do not support the hypothesis that elevation of DDT toxicity (Fig. 51) was caused by decrease in dynamics of detoxification mechanisms. The data

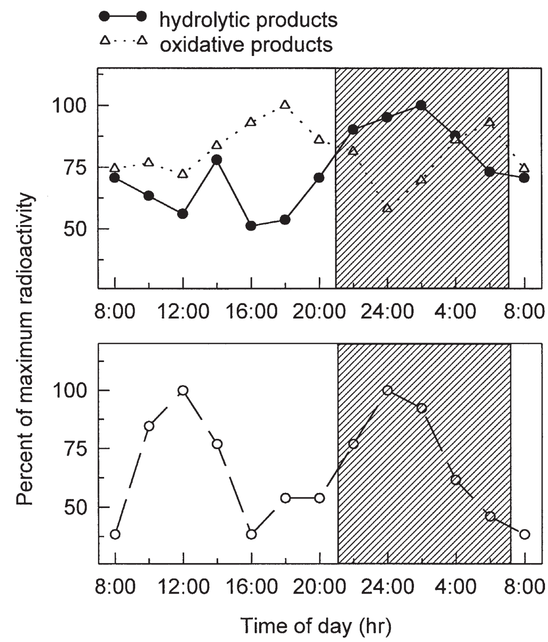


Chronotoxicology, Figure 51 Diurnal distributions of LD_{50} from DDT versus diurnal changes in respiration and DDT breakdown in WHO strain of the house fly *Musca domestica*. Generally, low respiratory rates and low DDT metabolism correspond with high tolerance to DDT, and high levels of detoxification correspond with high susceptibility to DDT, which is an unexpected correlation. For the sake of clarity, the original measurements are normalized and expressed as percent of the maximum value obtained for diurnal toxicity, respiration and DDT breakdown pattern, respectively. Shaded areas mark the dark phase of the photoperiod. (Collated and modified from Shipp E, Otton J (1976) Circadian rhythms of sensitivity to insecticides in *Musca domestica* (Diptera, Muscidae). Entomol Exp Appl 19:163–171; Shipp E, Otton J (1976) Diel changes in DDT absorption and breakdown rates and respiratory rhythm in the housefly, *Musca domestica*. Entomol Exp Appl 19:235–242.)

show an opposite trend: relatively low ratios of DDT breakdown and respiration correspond with relatively high ratios of DDT tolerance, and vice versa. Only at 15:00 P.M. high tolerance to DDT is correlated with high levels of respiration and DDT breakdown. Thus, circadian changes in susceptibility of *Musca domestica* to DDT were generally independent of ability to detoxify DDT. Perhaps the oscillations in this insecticide tolerance were caused by some alterations at the target site.

Time-dependent events in insect systems involved in insecticide toxicity and metabolism may be even more complex, given the mode of action of insecticide studied. Research on metabolism of di-syston (0,0-diethyl S-2 (ethylthio) ethyl phosphoditioate) in larvae of *Heliothis zea* (Boddie) is a good example. Di-syston requires biological oxidation to become active; thus, in addition to periodic changes in ratios of insecticide penetration, detoxification, or periodic alterations at the site of action one must consider periodic changes in activity of oxidative enzymes which are necessary to activate the insecticide. In this study, the experimental insects were maintained in a specific photoperiodic regimen (14 h of light- and 10 h of dark phase) and controls were exposed to constant light. The treatments aimed to synchronize larval biochemical processes to photoperiod, or keep them de-synchronized, respectively. In both groups, the larvae were injected with standard dose of isotope-labeled insecticide in various times of the day. Radioactivity of hydrolytic or oxidative metabolites of di-syston was determined in larval tissues and excreta, 4 h after injection, revealing three distinct rhythms. Oxidation (and therefore toxicity) of di-syston (Fig. 52) reached the highest ratios at the end of the light phase and at the end of the dark phase of the photoperiod, and dropped to the lowest values soon after lights on and after lights off. The rhythm of hydrolase activity was bimodal too, with peaks in the middle of either dark or light phase of the photoperiod. The latter rhythm roughly corresponded with the rhythm of di-syston metabolite excretion. Control larvae, maintained in desynchronizing lighting conditions, did not show rhythmic patterns of di-syston metabolism.

This work has two important implications. First it shows that sometimes a researcher should consider at least one more rhythmic organismal event influencing toxic potential of an insecticide administered at various times of the day; in this case time dependent changes in activation of toxic properties of the insecticide. Second, it shows that lighting conditions may influence periodic responses to insecticide toxicity (in their study, periodic changes in di-syston activation and degradation were abolished in constant light). It is a pity that they did not provide information about diurnal changes in mortality of *H. zea* larvae due to di-syston. I am not aware of this information being available in literature.

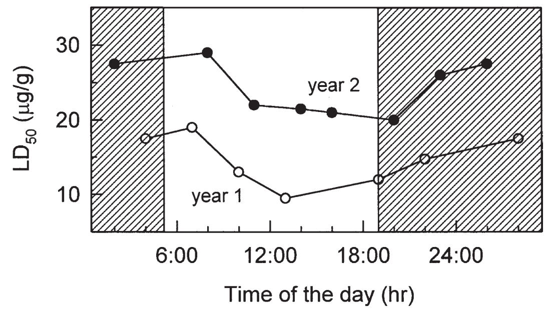


Chronotoxicology, Figure 52 **Diurnal changes in oxidation and hydrolysis of isotope-labeled Di-syston by *Heliothis zea* last instar larvae. Standard doses of this insecticide were applied at various times of the day. Di-syston requires biological oxidation to become insecticidally active, thus diurnal changes in its oxidation reflect its actual toxic potential. Changes in hydrolysis reflect dynamics of detoxification. B. Diurnal changes in concentrations of Di-syston metabolites in excreta of *Heliothis zea* last instar larvae. High activity of hydrolytic enzymes is correlated with low concentrations of toxic products of Di-syston oxidation (A) and products of Di-syston detoxification are excreted immediately (B), showing bimodal diurnal pattern of detoxification. Shaded areas mark the dark phase of the photoperiod. (Modified from Bull DL, Lindquist DA (1965) A comparative study of insecticide metabolism in photoperiod-entrained and unentrained boll-worm larvae *Heliothis zea* (Boddie). Comp Biochem Physiol 16:321–325.)**

Because periodic changes in physiological or biochemical processes are difficult to monitor, a number of reports have suggested that circadian rhythms in insect sensitivity to toxicants could be correlated to locomotor activity rhythms, which are relatively easy to record. For example, it has been noted by several investigators that there is a general trend of a time of greatest susceptibility occurring at about the time of onset of increased activity. However, the scanty data published on coincidence of daily changes in susceptibility to insecticide treatment and rhythms of locomotor activity do not support this assumption. There is no universal rule that would allow predicting the time of the greatest sensitivity to insecticides by monitoring circadian patterns of locomotor activity. It seems that the time of greatest sensitivity depends on the species, mode of treatment and the insecticide tested rather than a specific moment in the insect's activity pattern.

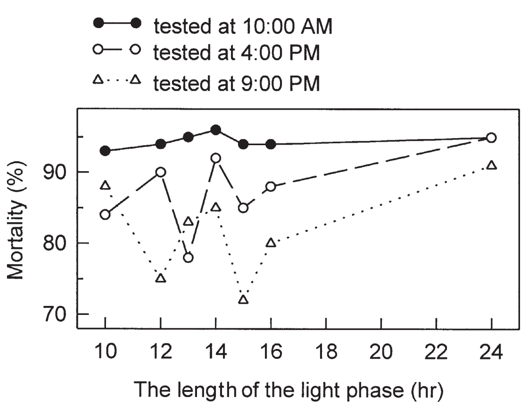
Biological Rhythms and Measuring Toxicity Parameters

Thus, it appears that insect toxicologists should concern themselves with not only the usual parameters of insecticide toxicity, but also with diurnal distribution of toxicity. At the very least, circadian time of treatment should be indicated in reports on mortality tests, particularly if toxicity parameters are used for comparative study of insecticide resistance. For example, in one study two samples of the beetle *Diabrotica virgifera virgifera* (LeConte) were collected, one in August 1967 and the other 12 months later, from the same location, which was meanwhile exposed to routine sprays with diazinon. Daily distributions of LD_{50} (Fig. 53) were established for either population of the beetles. If the author had limited himself to one toxicity assay at 7:00 A.M. in 1967, and one toxicity assay at 11:00 A.M. in 1968, he would have probably concluded that no resistance has been built up between 1967 and 1968. In fact, the field populations of *Diabrotica* increased resistance to diazinon by about 70% during that period of time, and only investigation of diurnal pattern of susceptibility revealed increase in resistance against this insecticide.

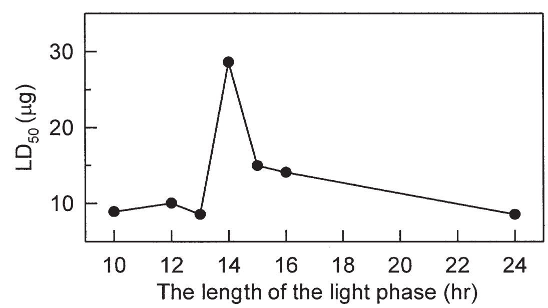


Chronotoxicology, Figure 53 Diurnal patterns of Diazinon toxicity to field populations of adult *Diabrotica virgifera virgifera*. The photoperiod shown is the naturally occurring photoperiod under which the beetles were living when collected. Upper curve shows LD_{50} distribution for the population collected in 1968. The lower curve reflects susceptibility of the population collected 12 months earlier. Only determination of diurnal LD_{50} distributions and maintaining the same photoperiodic regimen and similar timing of insecticide treatment allowed demonstration of increased resistance to Diazinon (further explanations in text). Shaded areas mark the dark phase of the photoperiod. (Modified from Ball HJ (1969) Diurnal rhythm of sensitivity to diazinon in adult western corn rootworms. J Econ Entomol 62:1097–1098.)

Precautionary measures should also be taken if insecticide resistance is compared between populations of the same age, and the same history of toxicant exposure, but kept under different breeding or testing regimens. Because insects are known to synchronize their endogenous rhythms to exogenous stimuli such as photo- or thermoperiod (a phenomenon called "entraining to a rhythm" in chronobiological nomenclature) the diurnal distribution of insecticide sensitivity may be synchronized to external conditions too. This was observed when house flies were reared through multiple generations, each experimental population in a different photoperiod. Seven different photoperiods were used, including constant light throughout 24-h cycle. In the first set of experiments the flies were treated with standard doses of trichlorfon at various times of the day. Next, the flies were returned to their respective photoperiodic regimens and percent mortality was recorded 48 h later. Mortality depended both upon the time of treatment commencement and the photoperiodic regimen the insects were kept in. For instance, mortality from trichlorfon administered at 10:00 A.M. almost did not vary, oscillating between 96 and 93 % regardless of the photoperiod to which the flies were synchronized, and maintained in, during the exposure (Fig. 54) to the insecticide. However, in the groups treated with trichlorfon in other times of the day, marked differences in mortality were observed. For instance, in group treated at 4:00 P.M., the mortality varied from 78 to 95%, depending on the length of the light phase of the photoperiodic regimen used. When the flies were exposed to the insecticide at 9:00 P.M. the differences were even greater. In another experiment, the flies were similarly reared in various photoperiodic regimens, and therefore their endogenous rhythms had synchronized to external light:dark oscillations of their specific photoperiodic regimens. Next, the flies were treated with various doses of trichlorfon at a fixed time of the day, corresponding not only to a fixed time of their own photoperiodic regimen (for instance 9 h after the onset of light) but also to a fixed time of the astronomical day (in this case 4:00 P.M.). Subsequently the flies were transferred to constant lighting conditions, where no oscillating stimuli could have influenced insects' endogenous rhythms. After 48 h of exposure to trichlorfon (Fig. 55), the LD_{50}



Chronotoxicology, Figure 54 Susceptibility of house flies to standard dose of trichlorfon at various times of the day as a function of the length of the light phase of the photoperiod. The flies were reared in specific photoperiod for several generations before and during exposure to the insecticide. The light in each experimental group came on at the same time (7:00 A.M.), trichlorfon was administered in various times of the day. The flies tested at 10:00 A.M. exhibited almost the same mortality ratios regardless of photoperiod they were reared and tested under. The flies tested at 4:00 P.M. or 9:00 P.M. showed marked variations in mortality from standard dose of trichlorfon, dependent on the photoperiod they had experienced prior to the tests and during exposure to the insecticide. (Modified from Fernandez AT, Randolph NM (1967) Photoperiodic effect on the daily susceptibility of the house fly to trichlorfon. J Econ Entomol 60:1633–1635.)



Chronotoxicology, Figure 55 Variability of LD_{50} from trichlorfon administered at fixed time of the day to the flies that had been synchronized to various photoperiods before the testing took place. The flies were kept in various photoperiods for several generations, and then exposed to the insecticide for 48 h under constant lighting conditions. Beginning of insecticide treatment commenced 9 h after lights on (4:00 P.M.), in each group. The flies that had experienced photoperiod light:dark 14:10 prior to the test were markedly more resistant to trichlorfon than those that had been kept in photoperiod light:dark 13:11. (Drawn on the basis of data by Fernandez and Randolph, 1967.)

was calculated. The flies entrained to the photoperiod consisting of 13 h of light phase and 11 h of dark phase were three times more susceptible to trichlorfon than the flies entrained to only slightly different photoperiod (14 h of light phase and 10 h of dark phase). Analogous experiments with DDT, endrin and dieldrin yielded similar results.

These remarkable results show that some insects entrained to a photoperiod maintain their characteristic rhythmicity of detoxification under constant lighting conditions, and their diurnal distribution of susceptibility to toxicants are determined by synchronizing stimuli from the past. Entraining, as a feature of circadian organization of insect physiology and behavior, clearly should be taken into consideration while planning toxicity tests, but many insect toxicologists do not realize how sensitive to entraining insect physiological systems can be.

Insect populations do not need to be exposed to certain photoperiodic conditions for several successive generations to synchronize their organismal oscillations to external lighting regimen. For instance, short-lasting exposures to light during the dark phase of the rhythm also effectively synchronize rhythms in adult insects of some species (e.g., many dipterans). Such a stimulus may shift the insect endogenous rhythms by several hours in comparison to original pattern of physiological oscillations, inducing a response (so-called phase response) that lasts for days if not weeks under continuous lighting conditions. Even temporary changes in insect breeding conditions may have profound effects on detoxification rhythms and, consequently, diurnal distribution of mortality in toxicity tests.

Concluding Remarks

An entomologist aware of time-dependent changes in toxicity of insecticides, toxicants or narcotic agents finds himself in a frustrating situation. On one hand, it is reasonable to propose that circadian organization of mechanisms that underlie insecticide uptake, detoxification, action on the target sites or at least diurnal distribution of mortality should be carefully studied before ultimate toxicity parameters are established and released as a basis for further use. On the other hand, chronotoxicological experiments are labor expensive and time intensive. The scarcity of published data does not allow any generalization as to methodology of experimenting: there is no universal correlation of susceptibility patterns with daily distribution of locomotor activity. Dynamic detoxification processes sometimes do not correlate with toxicity changes in an expected manner; the same photoperiodic conditions may abolish cyclic changes in insecticide metabolism (and, presumably, toxicity) in one species, such as *H. zea* larvae, or permit changes in susceptibility to occur in another, such as adult house flies. Research in insecticide chronotoxicology apparently does not attract funding, and its results are not easy to interpret, discuss and publish, since there is not much literature on this topic. Nor has monitoring the diurnal distribution of pest susceptibility to insecticides become an experimental routine for establishing insecticide toxicity parameters.

Impressive progress in knowledge of insect toxicology, insecticide resistance mechanisms and insect chronobiology has been made, but these disciplines need integration. Perhaps younger generations of entomologists will charge themselves with such a task.

► Rhythms in Insects
► Insecticides
► Insecticide Toxicity
► Insecticide Bioassays

References

Bainbridge CA, Margham P, Michael T (1982) Diurnal fluctuations in susceptibility to insecticides in several strains of the yellow fever mosquito (*Aedes egypti* L.). Pest Sci 13:92–96

Ball HJ (1969) Diurnal rhythm of sensitivity to diazinon in adult western corn rootworms. J Econ Entomol 62:1097–1098

Beck SD (1963) Physiology and ecology of photoperiodism. Bull Entomol Soc Am 9:8–16

Bull DL, Lindquist DA (1965) A comparative study of insecticide metabolism in photoperiod-entrained and unentrained boll-worm larvae *Heliothis zea* (Boddie). Comp Biochem Physiol 16:321–325

Cole CL, Adkisson PL (1964) Daily rhythm in the susceptibility of an insect to a toxic agent. Science 144:1148–1149
Crystal MM (1969) Changes in susceptibility of screw-worm flies to the chemosterilant *N′*, *N′*-tetramethylenebis (1-aziridinecarboxamide), with time of administration. J Econ Entomol 62:275–276
Eesa NM, Cutkomp LK (1995) Pesticide chronotoxicity to insects and mites: an overview. J Islam Acad Sci 8 (1):21–28
Fernandez AT, Randolph NM (1967) Photoperiodic effect on the daily susceptibility of the house fly to trichlorfon. J Econ Entomol 60:1633–1635
Halberg F, Stephens AN (1958) 24-hour periodicity in mortality of C mice from *E. coli* lipopolysaccharide. Fed Proc17:439
Halberg J, Halberg F, Lee JK, Cutcomp LK, Sullivan WK, Hayes DK, Cawley BM, Rosenthal J (1974) Similar timing of circadian rhythms in sensitivity to pyrethrum of several insects. Int J Chronobiol 2:291–296
Kermarrec A, Abud-Autun A (1978) Variations de la sensibilité au parathion selon l'heure chez *Acromyrmex octospinosus* Reich (Formicidae, Attini). Ann Zool Ecol Anim 10:29–35
Nowosielski JW, Patton RL, Naegele JA (1964) Daily rhythm of narcotic sensitivity in the house cricket, *Gryllus domesticus* L., and the two-spotted spider mite, *Tetranychus urticae* Koch. J Cell Comp Physiol 63:393–398
Polcik B, Nowosielski JW, Naegele JA (1964). Daily sensitivity rhythm of the twospotted spider mite, *Tetranychus urticae*, to DDVP. Science 145:405–406
Pszczolkowski MA, Dobrowolski M, Spencer C (2004) When did you last test your insects? The forgotten importance of chronotoxicology. Am Entomol 50:72–74
Saunders DS (1982) Insect clocks, 2nd edn. Pergamon Press, New York, NY, 408 pp
Shipp E, Otton J (1976a) Circadian rhythms of sensitivity to insecticides in *Musca domestica* (Diptera, Muscidae). Entomol Exp Appl 19:163–171
Shipp E, Otton J (1976b) Diel changes in DDT absorption and breakdown rates and respiratory rhythm in the housefly, *Musca domestica*. Entomol Exp Appl 19:235–242

Chrysalis

The pupal stage of a butterfly.

Chrysididae

A family of wasps (order Hymenoptera). They commonly are known as cuckoo wasps.

► Wasps, Ants, Bees and Sawflies

Chrysomelidae

A family of beetles (order Coleoptera). They commonly are known as leaf beetles.

► Beetles
► Leaf Beetles (Coleoptera: Chrysomelidae)

Chrysopidae

A family of insects in the order Neuroptera. They commonly are known as green lacewings.

► Lacewings, Antlions and Mantidflies
► Natural Enemies Important is Biological Control

Chrysopolomidae

A family of moths (order Lepidoptera) also known as African slug caterpillar moths.

► African Slug Caterpillar Moths
► Butterflies and Moths

Chyromyid Flies

Members of the family Chyromyidae (order Diptera).

► Flies

Chyromyidae

A family of flies (order Diptera). They commonly are known as chyromyid flies.

► Flies

Cibarium

The preoral cavity; an external space in front of the head that is surrounded by the mouthparts but in front of the true mouth or stomodeum.

Cicada Parasite Beetles

Members of the family Rhipiceridae (order Coleoptera).

► Beetles

Cicadas (Hemiptera: Cicadoidea)

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The members of the superfamily Cicadoidea Westwood are four-winged insects with sucking mouthparts that possess three ocelli and a rostrum that arises from the base of the head.

Classification

The classification within the superfamily has had a varied history. There have been as many as six families described within the superfamily. The major characters used to separate these families are structures of the sound production system, e.g., the timbal covers and stridulatory apparatuses. The separation of the two major historical families was based primarily on the presence or absence of timbal covers. However, the variation in the timbal cover anatomy is not related to a monophyletic ancestry within the groups. Similarly, the stridulatory structures have evolved as a means to isolate species reproductively and, therefore, appear to have evolved independently more than once. As a result, the structures of the sound apparati were a poor choice of characters on which the higher taxonomy should be based. The recent analysis of the higher taxonomy of the Cicadoidea suggests only two families are justified within the Cicadoidea, the Tettigarctidae and the Cicadidae.

Order: Hemiptera
Infraorder: Cicadomorpha
Superfamily: Cicadoidea

Family Tettigarctidae White

Contains two species in the genus *Tettigarcta* White (Fig. 56). The extant members of this family are restricted in their distribution to Australia. The Tettigarctidae exhibit ancestral morphology showing many similarities in their structure to fossil cicadas. They have a expanded pronotum that lacks paramedial and lateral fissures and a pronotal collar and conceals much of the mesonotum along with peculiar wing venation. The mesonotum lacks a cruciform elevation. The hind coxae overhang the abdomen. In addition, both sexes of the Tettigarctidae have a timbal apparatus but the structures are poorly developed and they lack tympana. Males lack an acoustic resonating chamber in the abdomen. They have recently been shown to communicate through vibrational rather than airborne signals.

Family Cicadidae Latreille

Members of this family (Fig. 57) represent the vast majority of extant cicadas. Characters that separate members of the family include: a pronotum that includes a pronotal collar, paramedial and lateral fissures and is smaller than the mesonotum; the mesonotal scutellum forms a cruciform elevation; timbals if present only found in males; males have an abdominal resonating chamber; both sexes have tympana. The extant genera have been divided into three subfamilies based on the

Cicadas (Hemiptera: Cicadoidea), Figure 56 ***Tettigarcta crinita*** **Distant, 1883, a member of the family Tettigarctidae.**

Cicadas (Hemiptera: Cicadoidea), Figure 57 ***Cicada orni*** **Linnaeus, 1758, a representative of the family Cicadidae.**

structure of the male genitalia, wing venation, timbal covers, and opercula. It includes the members of all previously described families except the Tettigarctidae.

Chararacteristics

Adults

Cicadas show a large range in adult body size. The smallest species have body lengths of 1 cm and wingspans of <2 cm while the largest species have body lengths of 7 cm and wingspans of almost 20 cm. The body coloration varies from a uniform reddish, green, brown, or black to a mixture of colors. The coloration pattern of the pronotum and mesonotum is especially useful in determining species. The head is dominated by the two compound eyes. Three ocelli form a triangle on the dorsal surface of the head between the compound eyes. This arrangement of the ocelli is one of the distinguishing characteristics separating cicadas from other bugs. The antennae are short and are located between the postclypeus and the compound eyes. The mouthparts form a needle-like rostrum that is inserted into plants to obtain xylem fluid. The postclypeus houses the pumping musculature. The thorax is divided into the three segments characteristic of insects. Each thoracic segment has a pair of legs and wings are attached to the mesothorax and metathorax. The wings can be hyaline, they may be infuscated, or they may be opaque or pigmented. Wing venation is another significant character used in taxonomy. The opercula are another diagnostic character that originate on the ventral metathorax but extend toward and often cover large portions of the abdomen. The abdomen is clearly segmented with the terminal segments modified to form the reproductive organs. The genitalia are one of the most important structures in identifying species. The abdomen of male cicadas is generally hollow and acts as a resonating organ to increase the song intensity. In addition, the timbal covers may be found covering the timbal organ of the male.

Immature Stages

Documented life cycles of cicadas range from 1 to 17 years. The life cycle can be variable within a species and emergence may be determined by the quality of the food source for the nymph, or all the individuals of a population may emerge synchronously as in the periodic cicadas (*Magicicada* spp.). Eggs are laid in twigs or stems of the host plants. The nymphs will crawl out of the egg and fall to the ground after hatching. The nymph will then burrow into the ground and attach to a root to obtain nourishment. The nymph will construct a chamber around the root in which it will grow and proceed through its hemimetabolous development. When it is mature, the nymph will emerge from the soil, find a vertical surface on which it can attach and then the adult encloses from it.

Natural History

Cicadas are found on all continents except Antarctica. They have a broad distribution in the tropical and temperate latitudes and can be found wherever permafrost is absent. As is common in the animal kingdom, the tropics are rich with species diversity. There is a correlation between the described cicada diversity for particular geographic regions and where cicada taxonomists have concentrated their efforts during their individual careers either through repeated expeditions or by living in a particular region.

One of the most distinguishing characteristics of cicadas is their acoustic behavior. The sounds produced by cicadas are species specific and are becoming useful tools in species identification. The sounds are generally produced by males but females have evolved acoustic responses to male signals. The major male sound production system is a timbal organ. The timbal organ is a rib-strengthened, chitinous membrane located in the first abdominal segment that is buckled by contraction of a timbal muscle. Structures such as the abdominal air sacs, opercula, and timbal covers can modify the sound emitted by the cicada. Stridulatory apparati have evolved in several genera as an accessory sound production system. The stridulatory systems are generally associated with the wings and the mesothorax but a genital system has also been described. Finally, crepitation is used as the primary communication signal by two genera of North American cicadas. The stridulatory and crepitation systems permit two way communication between the sexes in contrast to the unidirectional timbal system.

Birds are major predators of adult cicadas. Emergences of periodical cicadas represent a superabundant food source and many animals (e.g., fish, amphibians, reptiles, birds and mammals) change their foraging habits to include the cicadas. Cicada killers (family Sphecidae) are natural parasites that provision their nests with adult cicadas as food for their offspring. Nymphs burrowing into the ground are prey for ants whereas underground nymphs are prey for animals like moles and boars. Predators such as spiders, mantids, robber flies, and bats also take adult cicadas as prey.

There are also several genera of entomopathogenic fungi that use cicadas as hosts. Some fungi grow on nymphs (e.g., *Cordyceps* spp.) while others grow on the adults (e.g., *Massospora* spp.).

Agricultural Importance

The main source of agricultural damage occurs when the females oviposit in their host plants. Large emergences of cicadas (i.e., periodic cicadas) and their corresponding oviposition can cause small trees to wilt and small branches to break off trees. In addition, the loss of nutrients to the host tree in supporting a heavy infestation on its roots can lead to decreased growth and fruit production. These effects have been well documented in apple orchards located near old growth forests that support a large cicada population. There are several contact insecticides that can kill the adults but they cannot be relied upon to protect the trees completely. The slow action of the pesticides makes controlling the damage caused by the adults difficult. Pruning trees prior to cicada emergence decreases the availability of preferred oviposition sites. Covering small trees with cheesecloth or some form of netting to prevent access has been a successful strategy to protect trees particularly susceptible to damage.

Several species around the world have moved from natural grasses as their host plant to sugarcane. These species decrease the yield of the sugarcane fields they infest. A successful control strategy has been to till the soil which kills the nymphs. Adults can also be controlled with contact insecticides.

There have been reports of cicadas ovipositing in other food crops such as dates, asparagus, citrus trees, cotton, grapevines, etc. These reports are generally isolated, and cicadas do not appear to be major agricultural pests with the exceptions noted above.

► Sound Production in the Cicadoidea

References

Boulard M (2001) Higher taxonomy and nomenclature of the Cicadoidea or true cicadas: history, problems and solutions (Rhynchota Auchenorhyncha Cicadomorpha). Ecole Pratique des Hautes Etudes, Travaux du Laboratoire Biologie et Evolution des Insectes Hemipteroidea 14:1–48

Duffels JP (1993) The systematic position of *Moana expansa* (Homoptera: Cicadidae), with reference to sound organs and the higher classification of the superfamily Cicadoidea. J Nat Hist 27:1223–1237
Moulds MS (1990) A guide to Australian cicadas. New South Wales University Press, Kensington, Australia, 217 pp
Moulds MS (2005) An appraisal of the higher classification of cicadas (Hemiptera: Cicadoidea) with special reference to the Australian fauna. Rec Aust Mus 57:375–446
Myers JG (1929) Insect singers: a natural history of the cicadas. George Routledge and Sons, Limited, London, UK, 304 pp

Cicadellidae

A family of bugs (order Hemiptera). They commonly are known as leafhoppers.

► Leafhoppers
► Bugs

Cicindelidae

A group of beetles (order Coleoptera), sometimes treated as a separate family, here considered part of Carabidae. They commonly are known as tiger beetles.

► Beetles
► Tiger Beetles

Cigarette Beetle

► Stored Grain and Flour Insects

Ciidae

A family of beetles (order Coleoptera). They commonly are known as minute tree-fungus beetles.

► Beetles

Cimbicidae

A family of sawflies (order Hymenoptera, suborder Symphyta).

► Wasps, Ants, Bees and Sawflies

Cimicidae

A family of bugs (order Hemiptera). They sometimes are called bed bugs.

► Bugs
► Bedbugs (Hemiptera: Cimicidae)

Circadian Rhythm

An endogenous biological rhythm with a recurrence of about 24 h. Changes in biological or metabolic functions that show periodic peaks or lows of activity based on or approximating a 24-h cycle. This also is known as a circadian clock.

► Biological Clock of the German Cockroach, *Blatella germanica* (L.)

Circulative Virus

A virus that systemically infects its insect vector and usually is transmitted for the remainder of the vector's life.

Circumesophageal Connective

The bilateral neural connective between the tritocerebrum and the subesophageal ganglion. Usually the alimentary canal passes between the circumesophageal connectives.

► Nervous System

Citricola Scale, *Coccus pseudomagnoliarum* (Kuwana) (Hemiptera: Coccidae)

This species is a citrus pest in California, USA.

► Citrus Pests and Their Management

Citrus Blackfly, *Aleurocanthus woglumi* (Ashby) (Hempitera: Aleyrodidae)

This citrus pest is a black-colored whitefly.

► Citrus Pests and Their Management

Citrus Greening Disease

This psyllid-transmitted disease is a serious hazard to citrus crops.

► Transmission of Plant Diseases by Insects

Citrus Leafminer, *Phyllocnistis citrella* (Stainton) (Lepidoptera: Gracillaridae)"

This leaf-mining caterpillar is a pest of young trees.

► Citrus Pests and Their Management

Citrus Mealybug, *Planococcus citri* (Risso) (Hempitera: Pseudococcidae)

This mealybug threatens citrus crops in USA.

► Citrus Pests and Their Management

Citrus Peelminer, *Marmara gulosa* (Guillen and Davis) (Lepidoptera: Gracillaridae)

This is a minor citrus pest in USA.

► Citrus Pests and Their Management

Citrus Pests and their Management

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Botanically, the genus *Citrus* L. is an evergreen tree in the family Rutaceae. As a commercial tree, it is composed of a scion (the variety) and the rootstock. These two parts are budded or grafted together, with the goal of combining the best properties of each to make a tree that produces plenty of quality fruit. The genus *Citrus* contains many species and hybrids. Some of the more common fruits are citron (*C. medica* L.), sour orange (*C. aurantium* L.), pummelo (*C. maxima* Merril), lemon (*C. limon* (L.) Burm. f.), mandarin or tangerine (types with red-orange skin) (*C. reticulata* Blanco), common, Mexican, West Indian, or Key lime (*C. aurantifolia* (Christm. et Panz.) Swingle, Tahiti lime (*C. latisfolia* Tanaka), sweet lime (*C. limettioides* Tanaka), grapefruit (*C. maxima* var. *racemosa*, formerly *C. paradisi* MacFayden), and orange or sweet orange (*C. sinensis* (L.) Osbeck). Species in *Citrus* can readily interbreed or hybridize. Many combinations are commercially available, such as tangelo (mandarin X grapefruit), mandarin lime (lemon X mandarin), and tangor (mandarin X sweet orange). Other species or hybrids of *Citrus* are used as rootstocks.

History of Citrus

Citrus species probably originated in southeast Asia and India. Various citrus fruits, such as lemons, limes, and oranges, were cultured in the Indus Valley over 4,000 years ago. The modern citrus varieties most likely came from China. Conquering armies, traders, and explorers from the Romans to the Arabs to the western Europeans transported citrus fruits and seeds from Asia through southern Europe, northern Africa and to the New World. Christopher Columbus brought sour orange, lemon, and citron seeds when he established colonies in Haiti and the Caribbean. Spanish explorers brought oranges to St. Augustine, Florida, from 1513 to 1565, and Ponce de Leon brought seeds and ordered sailors to plant them wherever they landed. Grapefruit arrived in Florida much later, when a grove was planted near Tampa in 1823. Spanish missionaries introduced citrus to California in 1769.

Pest Descriptions

This section includes the important mite and insect species (Table 12, Figs. 58–60) that attack citrus in the continental United States (Arizona, California, Florida, and Texas), though many are cosmopolitan. Pest management considerations are discussed at the end of this section.

Acari

Citrus is infested by several groups of mites including rust and bud mites (Eriophyidae), spider mites (Tetranychidae), false spider mites (Tenuipalpidae) and broad mites (Tarsonemidae). Mites have piercing-sucking mouthparts that physically injure leaves and fruit by removing cell contents and by injecting plant toxins and viruses. Mite management depends principally on protecting biological control agents, secondarily on application of horticultural oils to foliage, and as a last resort applications of miticides.

Eriophyidae

Citrus rust mites, *Phyllocoptruta oleivora* (Ashmead), are small, light yellow, and elongated mites. They are serious pests in Florida, Texas, and California coastal districts. These mites injure leaves by penetrating the lower epidermal layer of cells promoting dry necrotic areas called mesophyll collapse. This "russeting" results in leaf drop, especially during dry periods. Feeding in fruit destroys rind cells and on oranges this injury is also referred to as russeting. Injury to grapefruit, lemons, and limes during early fruit growth causes "silvering" of the peel and, if severe, results in a condition called "shark skin." These blemishes lower the grade of fresh fruit, reduce fruit size, and increase fruit drop. There are several natural enemies of citrus rust mites including the parasitic fungus *Hirsutela thompsonii* Fisher.

Pink citrus rust mite, *Aculops pelekassi* (Keifer), is similar to citrus rust mites in feeding and injury. They can coexist on the same leaves, but *A. pelekassi* can develop larger, more damaging populations earlier in the season. Pink citrus rust mites are usually pink and are narrower than citrus rust mites.

Citrus bud mite, *Eriophyes sheldoni* Ewing, is primarily a pest of coastal lemons in California. They feed within leaf axil buds and developing blossoms, causing formation of multiple buds and abnormal growth of subsequent leaf foliage or flowers.

Several other eriophyid mites are pests in other world citrus areas, the citrus grey mite, *Calacarus citrifolii* Keifer, in southern Africa, and the brown citrus mite, *Tegolophus australis* Keifer, in coastal New South Wales and Queensland, Australia.

Tetranychidae

Citrus red mite, *Panonychus citri* (McGregor), was recognized as a pest in Florida in 1885, but was not identified in Texas until the early 1980s. In California, it was initially a pest in coastal areas, but by the 1930s spread to more inland districts. It is considered a sporadic pest, and occurs mostly on lemons and grapefruit. Adult mites are red or purple with large pink to white hairs (setae) on the body. Adults and immatures feed on leaves, fruit, and green twigs, but prefer the upper surface of young leaves. Injury to leaves and fruit is caused by extraction of chlorophyll. This "stippling" causes a grayish or silvery appearance, and severe stippling can lead to mesophyll collapse. High populations may cause leaf drop and twig dieback, and fruit sunburn in summer. During dry, cold, windy conditions, high mite populations may cause a condition known as "firing," "blasting," or "burning" of the foliage. There are many natural enemies of citrus red mites including lady beetles (species of *Stethorus*) and predaceous mites (species in the genera *Galendromus*, *Typhlodromalus*, and *Euseius*).

Citrus Pests and their Management, Table 12 Citrus arthropod pests, geographical area affected, and site of injury

Taxa scientific/Common name	Geographic area	Site of injury
Arachnida		
Acari		
Eriophyidae		
Phyllocoptruta oleivora (Ashmead) citrus rust mite	world (humid areas)	twigs, leaves, fruit
Aculops pelekassi (Keifer) pink citrus rust mite	world (humid areas)	twigs, leaves, fruit
Eriophyes sheldoni (Ewing) citrus bud mite	world	blossoms, fruit
Tetranychidae		
Panonychus citri (McGregor) citrus red mite	world	leaves, fruit, green
Eutetranychus banksi (McGregor) Texas citrus mite	western hemisphere	leaves
Eotetranychus sexmaculatus (Riley) sixspotted mite	western hemisphere, Asia	leaves
E. lewisi (McGregor) Lewis spider mite	southern California	fruit
E. yumensis (McGregor) Yuma spider mite	southern California, Arizona	leaves, fruit, green twigs
Tetranychus urticae (Koch) twospotted spider mite	world	leaves
T. pacificus (McGregor) Pacific spider mite	western U.S.	leaves, fruit, green twigs
T. tumidus (Banks) tumid spider mite	southeastern U.S.	leaves
T. mexicanus (McGregor) Mexican spider mite	southern North America to South America	leaves
Tenuipalpidae		
Brevipalpus phoenicis (Geijskes) red & black flat mite	world	fruit, leaves, twigs
B. obovatus (Donnadieu) privet mite	world	fruit, leaves, twigs
B. californicus (Banks) false spider mite	world	fruit, leaves, twigs
B. lewisi (McGregor) citrus flat mite	California, Japan	fruit, leaves, twigs
Tarsonemidae		
Polyphagotarsonemus latus (Banks) broad mite	world	leaves, fruit
Hexapoda		
Orthoptera		
Acrididae		
Romalea guttata (Houttuyn) eastern lubber grasshopper	southern U.S.	leaves, fruit
Schistocerca americana (Drury) American grasshopper	North America	leaves, fruit

Citrus Pests and their Management, Table 12 Citrus arthropod pests, geographical area affected, and site of injury (Continued)

Taxa scientific/Common name	Geographic area	Site of injury
Tettigoniidae		
Scudderia furcata (Brunner von Wattenwyl)	North America	leaves, fruit peel
Microcentrum retinerve (Burmeister) angularwinged (lesser angle-wing) katydid	eastern U.S.	leaves, fruit peel
M. rhombifolium (Saussure) broadwinged (greater angle-wing) katydid	North America	leaves, fruit peel
Gryllidae		
Hapithus agitator (Uhler) restless bush cricket	eastern U.S.	leaves, small fruit
Orocharis luteolira (Walker) false jumping bush cricket	southeastern U.S.	leaves, small fruit
Isoptera		
Rhinotermitidae		
Reticulitermes flavipes (Kollar) eastern subterranean termite	eastern North America	roots, tree bark
R. hesperus (Banks) western subterranean termite	western North America	roots, tree bark
Heterotermes aureus (Snyder) desert subterranean termite	southwestern U.S., Mexico	roots, tree bark
Kalotermitidae		
Paraneotermes simplicicornis (Banks) desert dampwood termite	southwestern U.S.	roots, tree bark
Kalotermes minor (Hagen) common drywood termite	southwestern U.S., Mexico	roots, tree bark
Termitidae		
Gnathamitermes perplexus (Banks) desert termite	southwestern U.S., Mexico	roots, tree bark
Termopsidae		
Zootermopsis angusticollis (Hagen) common dampwood termite	western North America	tree bark
Hemiptera		
Coreidae		
Leptoglossus gonagra (F.) citron bug	western hemisphere	fruit
L. phyllopus (L.) leaffooted bug	North America	fruit
L. zonatus (Dal.) western leaffooted bug	North America	fruit
Lygaeidae		
Nysius ericae (Schillling) false chinch bug	North America, Europe	young stems

Citrus Pests and their Management, Table 12 Citrus arthropod pests, geographical area affected, and site of injury (Continued)

Taxa scientific/Common name	Geographic area	Site of injury
N. raphanus (Howard) false chinch bug	North America	young stems
Pentatomidae		
Nezara viridula (L.) southern green stink bug	world	young stems and fruit
Cicadellidae		
Homalodisca coagulata (Say) glassy-winged sharpshooter	U.S., French Polynesia	green stems
Empoasca fabae (Harris) potato leafhopper	world	fruit
Flatidae		
Metcalfa prunivora (Say) flatid planthopper	world	twigs
Psyllidae		
Diaphorina citri (Kuwayama) Asiatic citrus psyllid	Asia, South America, Florida	young leaves
Aleyrodidae		
Aleurocanthus woglumi (Ashby) citrus blackfly	Asia, western hemisphere, world	leaves
Dialeurodes citri (Ashmead) citrus whitefly		leaves
D. citrifolii (Morgan) cloudywinged whitefly	Asia, western hemisphere, world	leaves
Aleurothrixus floccosus (Maskell) woolly whitefly		leaves
Parabemisia myricae (Kuwana) bayberry whitefly	Asia, Israel, Venezuela, California, Florida	leaves
Siphoninus phillyreae (Haliday) ash whitefly	world, Arizona, California, Nevada	leaves
Aphididae		
Toxoptera citricida (Kirkaldy) brown citrus aphid	world (not Mediterranean), Florida	leaves
T. aurantii (Boyer de Fonscolombe) black citrus aphid	world	leaves
Aphis spiraecola (Patch) spirea aphid	world	leaves
A. gossypii (Glover) melon or cotton aphid	world	leaves
A. craccivora (Koch) cowpea aphid	world	leaves
Margarodidae		
Icerya purchasi (Maskell) cottonycushion scale	world	leaves, twigs, branches

Citrus Pests and their Management, Table 12 Citrus arthropod pests, geographical area affected, and site of injury (Continued)

Taxa scientific/Common name	Geographic area	Site of injury
Coccidae		
Coccus hesperidum (L.) brown soft scale	world	twigs, leaves
C. pseudomagnoliarum (Kuwana) citricola scale	world, California	leaves, twigs
Saissetia neglecta (De Lotto) Caribbean black scale	world, Florida	leaves, twigs, fruit
S. miranda (Cockerell & Parrott) Mexican black scale	world	leaves, twigs
S. oleae (Olivier) black scale	world	leaves, twigs
Parasaissetia coffeae (Walker) hemispherical scale	world	leaves, twigs
P. nigra (Nietner) nigra scale	world	leaves, twigs
Ceroplastes floridensis (Comstock) Florida wax scale	world	leaves, twigs
C. cirripediformis (Comstock) barnacle scale	western hemisphere	leaves, twigs
Diaspididae		
Aonidiella aurantii (Maskell) California red scale	world	leaves, fruit, branches
A. citrina (Coquillett) yellow scale	world	leaves, fruit
Parlatoria ziziphi (Lucas) black parlatoria scale	world	leaves, twigs, fruit
P. pergandii (Comstock) chaff scale	world	leaves, fruit, branches
Cornuaspis (=*Lepidosaphes*) *beckii* (Newman) Purple scale	world	leaves, fruit, branches
Lepidosaphes gloveri (Packard) glover scale	world	leaves, fruit, branches
Unaspis citri (Comstock) citrus snow scale	world	branches, leaves, fruit
Chrysomphalus aonidum (L.) Florida red scale	world	leaves, green twigs,
Pinnaspis aspidistrae (Signoret) fern scale	world	leaves, fruit
Pseudococcidae		
Planococcus citri (Risso) citrus mealybug	world	fruit, leaves, twigs
Pseudococcus calceolariae (Maskell) citrophilus mealybug	world	fruit, leaves, twigs
P. comstocki (Kuwana) Comstock mealybug	world	fruit, leaves, twigs
P. longispinus (Targioni-Tozzetti) long-tailed mealybug	world	fruit, leaves, twigs
Maconellicoccus hirsutus (Green) pink hibiscus mealybug	Africa, Asia, Australia, Caribbean, Florida	fruit, leaves, twigs

Citrus Pests and their Management, Table 12 **Citrus arthropod pests, geographical area affected, and site of injury (Continued)**

Taxa scientific/Common name	Geographic area	Site of injury
Thysanoptera		
Thripidae		
Frankliniella bispinosa (Morgan) flower thrips	southeastern U.S.	flowers
F. kelliae (Sakimura) flower thrips	southeastern U.S.	flowers
Scirtothrips citri (Moulton) citrus thrips	California, Arizona	flowers
S. auranti (Faure) citrus thrips	southern Africa	flowers
S. dorsalis (Hood) citrus thrips	Japan, Africa, Florida	flowers
S. perseae (Nakahara) avocado thrips	California	flowers
Heliothrips haemorrhoidalis (Bouché) greenhouse thrips	world	leaves, fruit
Chaetanaphothrips orchidii (Moulton) orchid thrips	tropics, Florida	leaves, fruit
Danothrips trifasciatus (Sakimura) orchid thrips	tropics, Florida	leaves, fruit
Coleoptera		
Curculionidae		
Diaprepes abbreviatus (L.) diaprepes root weevil	Caribbean, Florida	roots, leaves
Pachnaeus litus (Germar) southern blue-green citrus root weevil	Caribbean, Florida	leaves, roots, fruit
P. opalus (Oliver) northern blue-green citrus root weevil	Caribbean, Florida	leaves, roots, fruit
Artipus floridanus (Horn) little leaf notcher	Caribbean, Florida	leaves, roots
Asynonychus godmani (Crotch) Fuller rose beetle	world	buds, leaves, roots
Diptera		
Cecidomyiidae		
Prodiplosis longifila (Gagné) citrus gall midge	Florida, Caribbean, South America	flowers
Tephritidae		
Anastrepha suspensa (Loew) Caribbean fruit fly	Florida, Caribbean	fruit
A. ludens (Loew) Mexican fruit fly	southwestern U.S., Mexico to South America	fruit
A. obliqua (Macquart) West Indian fruit fly	Caribbean, Texas, Central and South America	fruit
A. fraterculus (Wiedemann) South American fruit fly	Texas south to Chile and Argentina	fruit

Citrus Pests and their Management, Table 12 Citrus arthropod pests, geographical area affected, and site of injury (Continued)

Taxa scientific/Common name	Geographic area	Site of injury
A. serpentina (Wiedemann) sapote fruit fly	Texas south to Argentina	fruit
Bactrocera correcta (Bezzi) guava fruit fly	southern Asia	fruit
B. dorsalis (Hendel) oriental fruit fly	Asia and the Pacific	fruit
B. tryoni (Froggatt) Queensland fruit fly	Australia	fruit
B. tsuneonis (Miyake) Japanese orange fly	eastern Asia	fruit
Ceratitis capitata (Wiedemann) Mediterranean fruit fly	world	fruit
C. rosa (Karsch) Natal fruit fly	throughout Africa	fruit
Lepidoptera		
Gracillariidae		
Phyllocnistis citrella (Stainton) citrus leafminer	world	leaves
Marmara gulosa (Guillen & Davis) citrus peelminer	California, Mexico	fruit
Tortricidae		
Archips argyrospilus (Walker) fruittree leafroller	North America	fruit, leaves
Argyrotaenia citrana (Fernald) orange tortrix	North America, Europe	fruit, leaves
Megalopygidae		
Megalopyge opercularis (J. E. Smith) puss caterpillar	North America	leaves, nuisance
Papilionidae		
Papilio cresphontes (Cramer) orangedog	western hemisphere	leaves
P. zelicaon (Lucas) California orangedog	western North America	leaves
Hymenoptera		
Formicidae		
Atta texana (Buckley) Texas leafcutting ant	western hemisphere	leaves
Solenopsis invicta (Buren) red imported fire ant	western hemisphere	twigs, bark
S. geminata (F.) fire ant	western hemisphere	twigs, bark
S. xyloni (McCook) southern fire ant	southern U.S.	twigs, bark
Linepithema humile (Mayr) Argentine ant	western hemisphere	leaves (interferes with biological control)
Formica aerata (Francouer) native gray ant	western U.S.	leaves (interferes with biological control)

Citrus Pests and their Management, Table 12 Citrus arthropod pests, geographical area affected, and site of injury (Continued)

Taxa scientific/Common name	Geographic area	Site of injury
Gastropoda		
Pulmonata		
Helicidae		
Helix aspersa (Müller)	world	fruit, leaves, bark

Texas citrus mite, *Eutetranychus banksi* (McGregor), occurs throughout the Western hemisphere. It has been a pest in Texas citrus for many years, but was first detected on citrus in Florida in 1951. Since 1955 it has increased in abundance to where it is the dominant spider mite species. Adults are tan to brownish-green with dark green to black spots on the sides. Unlike citrus red mites, Texas citrus mites have short, stout setae on their upper surface. This species is abundant during periods of prolonged dry weather. They feed on upper leaf surfaces, rarely on the fruit and never on twigs, and their injury is similar to that of citrus red mites.

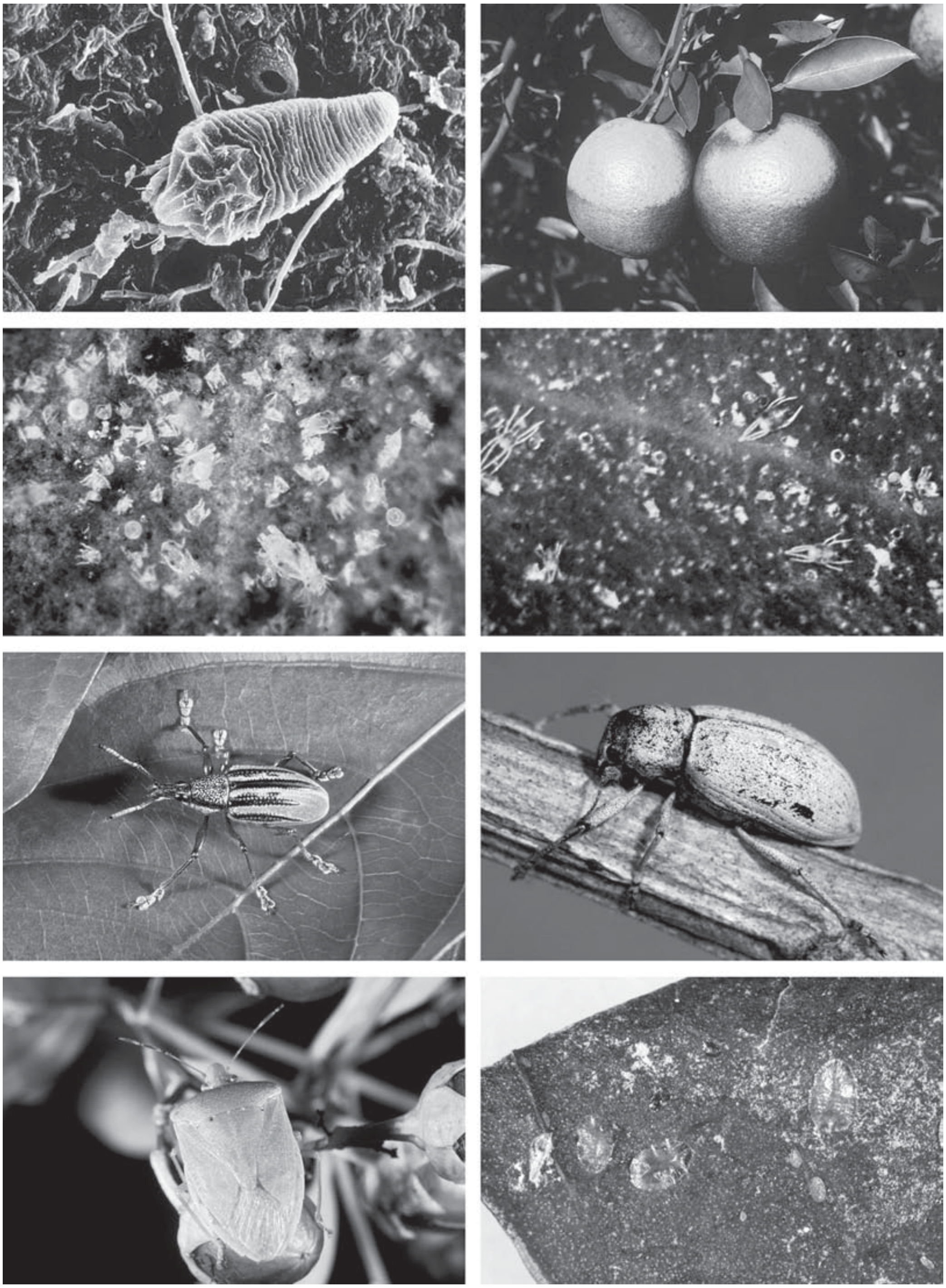
Sixspotted spider mite, *Eotetranychus sexmaculatus* (Riley), was first mentioned as a sporadic pest in Florida in 1886 and continues as a spring season pest particularly on grapefruit and orange. In California, these mites occur in coastal growing areas. Adults are pale yellow to green with one to three pairs of dark spots on the upper surface which can sometimes be indistinct or missing. Sixspotted spider mites differ from citrus red mites and Texas citrus mites in that they feed on the lower leaf surface. They initially infest the petiole and midvein area, causing a slight depression. At higher densities, raised yellow areas develop on the upper leaf surface opposite that of the established lower leaf surface colonies, and severe defoliation can follow.

Two other *Eotetranychus* species, Lewis spider mite, *E. lewisi* (McGregor), and Yuma spider mite, *E. yumensis* (McGregor), occur on grapefruit and lemon in California and Arizona. Lewis spider mite was found on navel oranges in southern California in 1942 and continues to be a pest in the southern citrus districts except in desert areas. Adults are various shades of pale amber or green with black spots along the lateral margin. Lewis spider mite generally damages fruit. Yuma spider mite is distributed in the Coachella and Imperial valleys of California and the Yuma citrus district of Arizona. Adults are light straw to dark pink and are most numerous in winter and late spring. These mites feed on leaves, fruit and green twigs.

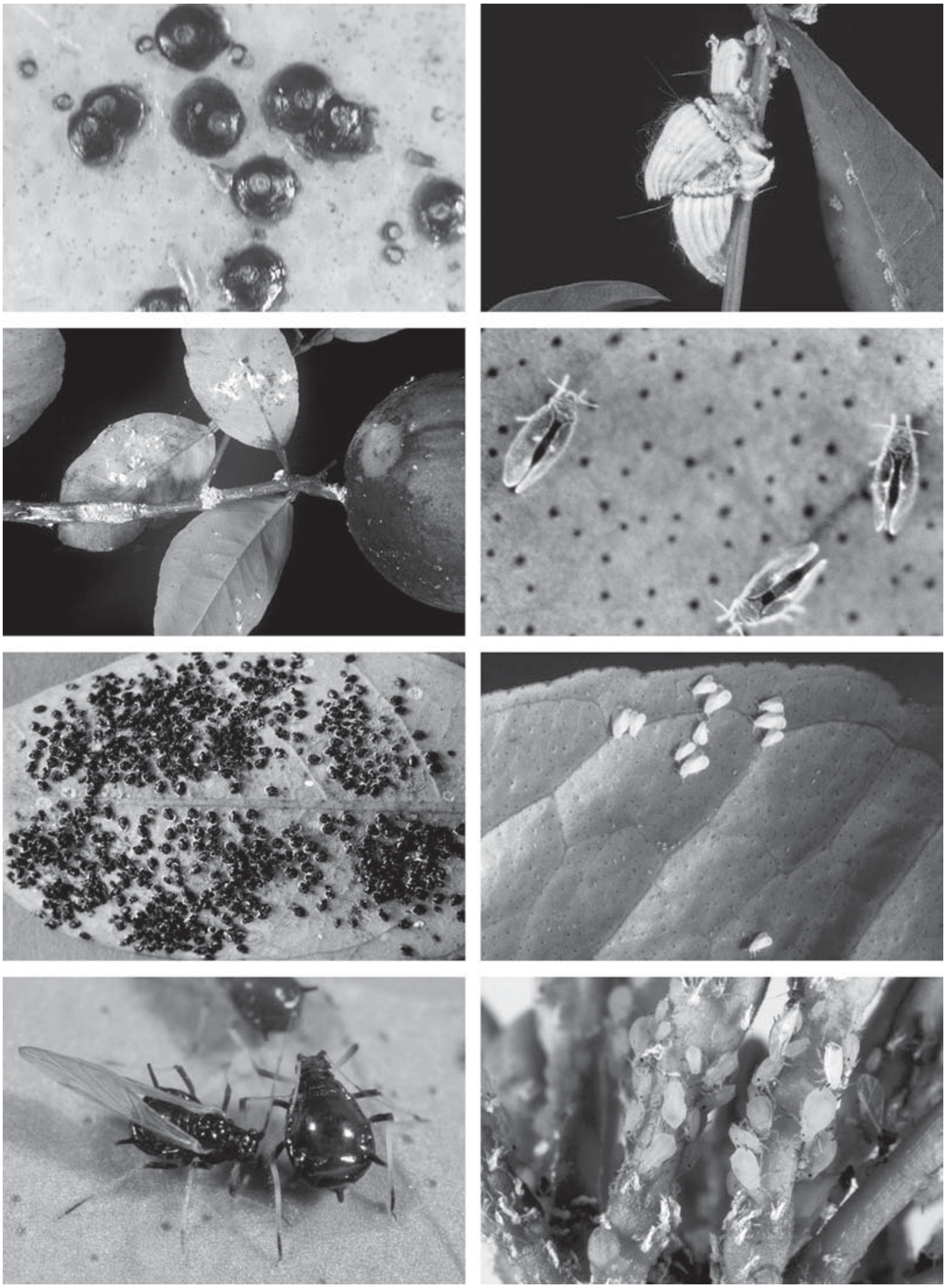
Twospotted spider mite, *Tetranychus urticae* Koch, is a serious pest of many crops but is only an occasional pest of citrus, particularly in the San Joaquin Valley of California. It first appears on the underside of the leaves, but as populations increase, can be found infesting the upper leaf surface and fruit. Conspicuous webbing similar to that of *Eotetranychus* species can occur in areas of heavy infestation. As with all spider mites, damage potential of *T. urticae* varies from citrus species to citrus species, from year to year, and is related to weather conditions such as heat and to water stress.

Several other *Tetranychus* species rarely attack citrus in the U.S. Pacific spider mite, *T. pacificus* McGregor, is more of a pest of deciduous tree fruits, but has caused damage in the central valleys of California. Tumid spider mite, *T. tumidus* Banks, is present in the southeastern U.S. and *T. mexicanus* (McGregor) is occasionally a pest of citrus in Texas.

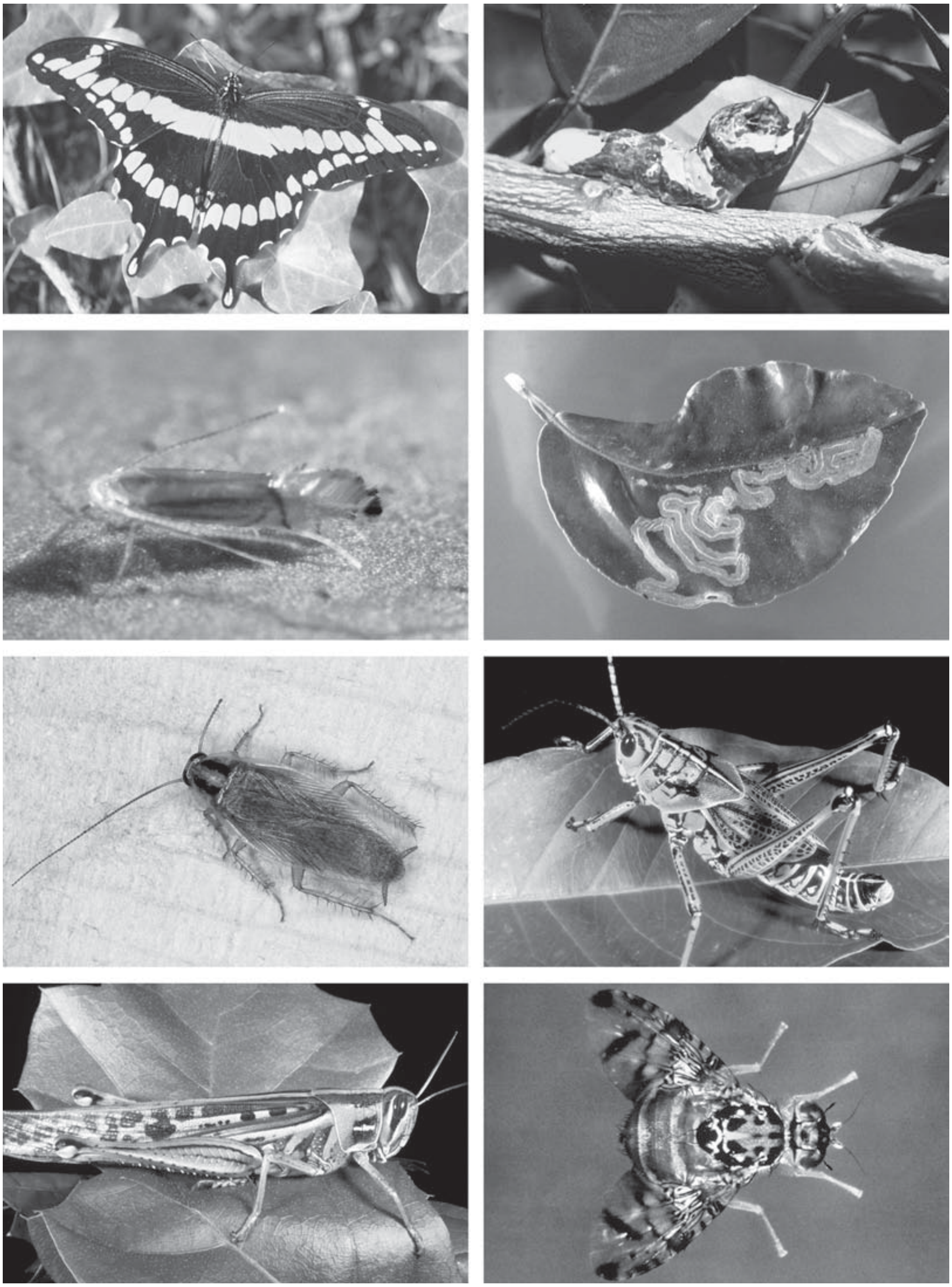
Worldwide, other members of Tetranychidae are citrus pests. This list includes four *Eutetranychus* species: oriental red mite, *E. orientalis* (Klein), occurring in the Mideast and Asia, and three African species, lowveld citrus mite, *E. anneckei* Meyer, *E. africanus* Klein, and *E. sudanicus* Elb., *Eotetranychus cendanci* Rimando from southeast Asia, and *Schizotetranychus hindustanicus* (Hirst) from southern India.



Citrus Pests and their Management, Figure 58 **Some common insect and mite pests of citrus. Top left, scanning electron micrograph of citrus rust mite (photo, J. C. Allen); top right, feeding injury (dark areas where surface temperatures did not inhibit mite feeding) by citrus rust mite (photo, J. C. Allen); second row left, sixspotted spider mites (photo, J. Knapp); second row right, Texas citrus mite (photo, J. Knapp); third row left, *Diaprepes* (citrus root) weevil (photo, J. L. Capinera); third row right, blue-green citrus weevil (photo, P. M. Choate); bottom left, southern green stink bug (photo, J. L. Capinera); bottom right, brown soft scale (photo, L. J. Buss).**



Citrus Pests and their Management, Figure 59 Some common insect and mite pests of citrus. Top left, Florida red scale (photo, J. L. Castner); top right, cottony cushion scale adults (on stem) and immatures (on leaf) (photo, L. J. Buss); second row left, citrus mealybug (photo, J. Knapp); second row right, adult citrus blackflies (photo, J. Knapp); third row left, immature citrus blackflies (photo, J. Knapp); third row right, citrus whitefly (photo, J. Knapp); bottom left, brown citrus aphid (photo, P. M. Choate); bottom right, spirea aphid (photo, J. L. Capinera).



Citrus Pests and their Management, Figure 60 **Some common insect and mite pests of citrus. Top left, giant swallowtail, adult form of orange dog (photo, J. L. Castner); top right, orange dog, larval form of giant swallowtail (photo, J. Knapp); second row left, adult citrus leaf miner (photo, J. L. Castner); second row right, leaf mines caused by citrus leaf miner larvae (photo, J. L. Castner); third row left, Asian cockroach (photo, J. L. Castner); third row right, eastern lubber grasshopper (photo, J. L. Capinera); bottom left, American grasshopper (photo, J. L. Capinera); bottom right, Mediterranean fruit fly (photo, J. Knapp).**

Tenuipalpidae

Four species of false spider mites in the genus *Brevipalpus* attack citrus in the United States. Three of these, *phoenicis* (Geijskes), *obovatus* Donnadieu, and *californicus* (Banks), are cosmopolitan and occur on citrus in most parts of the world. Infestations usually begin in the interior of the tree canopy on the underside of leaves near the midrib, but false spider mites are also found on fruit and woody tissue (twigs and branches). *Brevipalpus* mites are flat, reddish, and difficult to notice because they are small and slow moving. They have a relatively long life cycle compared with other phytophagous mites. *Brevipalpus* mites are economically important because they vector a bacilliform virus that causes leprosis. This disease can be found on fruit, leaves, and tree branches, and is commonly referred to as nailhead rust. The fourth species, *B. lewisi* McGregor, is found in the desert and interior valleys of California's citrus growing region. It is a secondary invader that feeds on rind tissue damaged by other insects. *B. phoenicis* mites have gained fame lately when it was discovered that they only exist in the haploid state (one copy of chromosomes).

Tarsonemidae

Broad mite, *Polyphagotarsonemus latus* (Banks), is a very important pest of "Tahiti" lime in Florida and an infrequent pest of coastal lemons in California. They are distributed across the world and feed on many horticultural plants. Adult females are light yellow, amber, or green with an indistinct white median stripe on the back, and males are similar in color but without the stripe. Broad mites are found on newly formed leaves or on young fruit. Heavy infestations on leaves cause distortion, curling, or stunting, but the most important damage is russeting on young fruit. Fruit that are severely russeted are not available for the fresh market and must be used for processing. Natural enemies include several predatory mite species.

Orthoptera

Several species of grasshopper, katydid, and cricket cause minor damage to citrus due to feeding with their chewing mouthparts. These species rarely warrant control actions, but when they do foliar insecticides are employed.

Acrididae

Two grasshopper species, eastern lubber grasshopper, *Romalea guttata* (Houttuyn), and American grasshopper, *Schistocerca americana* (Drury), are sporadic pests in citrus groves. Lubber grasshopper adults are yellow with red and black markings and American grasshoppers are light brown with black markings. Injury is caused by nearly full grown nymphs which feed on foliage and occasionally fruit and the most serious damage occurs when young citrus trees are defoliated.

Tettigoniidae

Three species of katydid attack citrus. In Florida, only broadwinged katydid, *Microcentrum rhombifolium* (Saussure), causes economic damage. In California, forktailed katydid, *Scudderia furcata* Brunner von Wattenwyl, is the species that causes damage, although angularwinged katydid, *M. retinerve* (Burmeister), is also present. Katydid feeding resembles that of grasshoppers and is mostly restricted to foliage. When fruit rinds are attacked, large, smooth, sunken areas on the fruit surface result.

Gryllidae

Two species of bush cricket, restless bush cricket, *Hapithus agitator* Uhler, and false jumping bush cricket, *Orocharis luteolira* Walker, may be present in large numbers in Florida citrus groves. Both species feed on small fruit, leaves, and twigs in the lower canopy. Fruit drop and peel blemishes may result in economic damage.

Isoptera

Rhinotermitidae

The only termite species in Florida that attacks citrus is eastern subterranean termite, *Reticulitermes flavipes* (Kollar). Attack starts below ground where they feed on bark and cambium of young trees. They can become serious pests of citrus in groves where nearby pine woods support large populations. Two other species, desert subterranean termite, *Heterotermes aureus* (Snyder), and western subterranean termite, *R. hesperus* Banks, have damaged citrus in California.

Kalotermitidae

Desert dampwood termite, *Paraneotermes simplicicornis* (Banks), has damaged grapefruit trees in the Coachella Valley of California by feeding on the taproot and lateral roots. This species has also damaged young trees in Texas. Common drywood termite, *Kalotermes minor* Hagen, has damaged citrus in California by feeding either below ground or above ground by gaining entry through wounds or crevices. Two other termite species, desert termite, *Gnathamitermes perplexus* (Banks) (Termitidae), and common dampwood termite, *Zootermopsis angusticollis* (Hagen) (Termopsidae), occasionally damage citrus in California.

Hemiptera

At least 12 families have been documented to occasionally cause economic damage on citrus, and some of the most important pests are found in this group. All Hemiptera have piercing-sucking mouthparts, and are usually controlled by improved management of plants in the ground cover of groves, protection of predators and parasitoids, application of horticultural oils, and foliar insecticide applications.

Coreidae

Citron bug, *Leptoglossus gonagra* F., leaffooted bug, *L. phyllopus* (L.), and western leaffooted bug, *L. zonatus* (Dal.), are three plant bug species that puncture the fruit rind and suck the juices from underlying vesicles. Citron bug (Figs. 58–60) is dark brown to black with the front margin of the thorax yellow. Populations build on nearby melons and weeds in the grove during spring and summer, and injury to citrus usually occurs by fall. Leaffooted bug occurs in Arizona, the Gulf states, and Florida, where its principle host plants are thistles (*Cirsium* spp.). It is dark brown with a pale yellow line across the wings. Damage by plant bug feeding can cause fruit drop and also may provide access for various pathogens. Damage is more common on citrus fruit with thinner rinds. Western leaffooted bug is primarily a pest of pomegranates in California, although they will occasionally attack tangerines, oranges, and grapefruit.

Lygaeidae

Two false chinch bug species, *Nysius ericae* (Schil.) and *N. raphanus* Howard, occasionally are very destructive to young trees in California. Adults are small and light to dark gray. Nymphs and adults sometimes congregate in large numbers on younger wood.

Pentatomidae

Southern green stink bug, *Nezara viridula* (L.), is green and is abundant in the fall and early winter. Although other species of stink bugs attack citrus, this species is usually the only one found in high numbers. Most stink bugs breed on a variety of weed plants. In Florida, this insect is most destructive to tangerines.

Cicadellidae

Glassy-winged sharpshooter, *Homalodisca coagulata* (Say), is native to the southeastern United States, but recently has invaded California. Specimens from a citrus grove in Ventura County were identified in 1989. This large leafhopper is dark brown to black with yellowish spots on its head and back. Glassy-winged sharpshooters vector the bacterium *Xylella fastidiosa* which causes many plant diseases. Infections affect the xylem of the plant and is known as Pierce's disease (grape), almond leaf scorch, phony peach disease, alfalfa dwarf, and oleander leaf scorch. Citrus variegated chlorosis, a serious disease of oranges in South America vectored by *H. coagulata*, is not currently present in the U.S. In California, the major concern is transmission of Pierce's disease in vineyards. Although the disease has been present in California for many years, glassy-winged sharpshooter is a more efficient vector than the native sharpshooters because of higher mobility and the ability to occupy a wide range of new habitats and host plants.

Potato leafhopper, *Empoasca fabae* (Harris), is a common insect that attacks over 100 crop plants throughout the U.S. It is an occasional pest of citrus in California, especially in groves near tomato or cotton fields in the San Joaquin Valley. Adults are small, greenish, and very active insects. Potato leafhopper feeds on fruit by puncturing rind cells, causing yellowish to light brown scars.

Flatidae

One flatid planthopper species, *Metcalfa prunivora* (Say), is an occasional pest of citrus in Texas. It is grayish-white and feeds on twigs. This insect only completes one generation per season. Grapefruit trees appear to be favored over orange trees.

Psyllidae

Asiatic citrus psyllid, *Diaphorina citri* Kuwayama, was found in southeastern Florida in 1998 and in southern Texas in 2001. Its native range includes much of southern Asia, although it has been found in Brazil and Honduras. African citrus psyllid, *Trioza erytreae* (Del Guercio), is the only other psyllid worldwide that is an economic pest of citrus. *D. citri* is a small active insect with a brown, mottled appearance and is found on the lower sides of new flush leaves. Damage caused by this insect is either direct feeding injury resulting from the withdrawal of fluids from the foliage, development of sooty mold on leaves, and/or transmission of organisms that cause citrus greening disease, though this disease is not yet known from American populations. Greening symptoms include mottling and yellowing of leaf veins, irregular leaf and flower production, abnormal fruit drop, and an unpleasant flavor in the juice. Asiatic citrus psyllid management in Florida is being conducted using classical biological control, wherein parasitoids from Asia are collected and released.

Aleyrodidae

There are eight whitefly species that are considered citrus pests. Whitefly nymphs extract phloem sap from leaf tissues causing leaves to wilt and drop if there are large populations. Feeding on such a sugary liquid diet means that the waste product, honeydew, is also a very sugary liquid substance. The creation of honeydew provides a food source for sooty mold fungus which "blackens" the leaves and interferes with the tree's ability to make food through photosynthesis. Honeydew also attracts ants, which sometimes interfere with biological control. The combined effects of feeding by nymphs and associated sooty mold can result in death of young trees and serious fruit yield reductions for producing trees. Fruit that has sooty mold on it ripens later than normal fruit and is also discolored. Many of these whitefly species that attack citrus are also pests of horticultural crops in greenhouses in northern states.

Citrus blackfly, *Aleurocanthus woglumi* Ashby, is of Asian origin that was first detected in the Western Hemisphere in Jamaica in 1913 and then in Key West, Florida, in 1935. It was rediscovered in Ft. Lauderdale, Florida, in 1976 and spread to neighboring citrus-producing counties. It first invaded the lower Rio Grande Valley of Texas in 1955 on residential citrus, and again in Brownsville in 1971 in both residential and commercial groves. Adults are slate-blue with a median white band; the abdomen and head are bright red. Females lay eggs on the underside of leaves in a characteristic spiral pattern. This insect has over 300 host plants, but citrus is one of its favorites. There is a very successful history of both classical and augmentative biological control of citrus blackfly through release of two parasitic wasps in many areas of the Western Hemisphere including Mexico, Florida, and Texas.

Citrus whitefly, *Dialeurodes citri* (Ashmead), and cloudywinged whitefly, *D. citrifolii* (Morgan), are two other Asian pests that invaded Florida in the late 1800s. In the 1920s, whiteflies were considered the most serious pests of citrus in Florida. They can still be a serious pest, although not at the same level that they once were. Both species are found in Texas citrus, and citrus whitefly also is found in California. Both citrus and cloudywinged whitefly adults are small and white, although cloudywinged adults have a darkened area at the end of each wing. Many natural enemies are used in biological control of both whitefly species, including fungi, predators, and parasitoids.

Woolly whitefly, *Aleurothrixus floccosus* (Maskell), was first found in Florida in the early 1900s and also is found in Texas and California. Adults are yellowish-white and seldom fly. The last nymphal stage (pupa) is surrounded by waxy filaments. Adult females lay eggs in a circle on mature leaves. Like other whiteflies on citrus, they are mostly controlled by natural enemies.

Barberry whitefly, *Parabemisia myricae* (Kuwana), is an Asian species first discovered in California in 1978 and Florida in 1984. Like other whiteflies, they have several hosts other than citrus. Adults are small, whitish-yellow insects. Females prefer to lay eggs on young, tender foliage. Several natural enemies attack barberry whitefly, and the first populations found in Florida were already under natural biological control, apparently because the parasitoids were introduced with the whitefly.

Ash whitefly, *Siphoninus phillyreae* (Haliday), is a species from temperate and subtropical regions of Europe, northern Asia and north Africa. It was first collected in southern California in 1988, and is now present in Arizona and Nevada. It has arboreal hosts, including several fruit trees, and in Europe this pest causes severe damage to pear and apple. Adults are small, whitish insects with a light dusting of wax. Natural enemies from Israel and Italy were imported to California for biological control.

Aphididae

Aphids comprise a large and diverse group of small, fragile insects that are economically important because of direct damage and transmission of plant diseases. Many species are winged (alate) and wingless (apterae), depending on the season. Their biologies are complex because a species may contain both sexual and parthenogenetic (able to reproduce without fertilization by males) forms at different times of the season or on different host plants.

Brown citrus aphid, *Toxoptera citricida* (Kirkaldy), is one of the world's most serious pests of citrus. It is found in southeast Asia, southern Africa, Australia and New Zealand, South America, the Caribbean, and since November 1995, in Florida. These aphids are larger than other species on citrus and have slender antennae. Wingless adults are shiny black, while nymphs are dark reddish-brown and reproduce parthenogenetically by producing nymphs, thus, there are no males and no eggs. They damage citrus by producing copious amounts of honeydew so that leaves and fruit become black with sooty mold. However, their most serious damage to trees is by vectoring a phloem-limited virus called citrus tristeza closterovirus. This virus causes tristeza stem pitting disease. One of the most devastating citrus crop losses ever reported followed the introduction of this aphid into Brazil and Argentina, where 16 million trees on sour orange rootstock were killed. Several different management measures are being studied in Florida, including cultural control through rootstock improvement, biological control, and chemical control.

Black citrus aphid, *Toxoptera aurantii* (Boyer de Fonscolombe), is a related species and is found throughout the world where citrus is grown. It is found in all citrus areas of the U.S. It is smaller than brown citrus aphid, with the adult apterae dull black. The antennae and legs appear to be striped. Black citrus aphid is not a serious pest of citrus and is either a poor or nonvector of citrus tristeza.

Spirea aphid, *Aphis spiraecola* Patch (formerly known as *A. citricola* Van der Goot), is a small green aphid that originated in eastern Asia. It was found in Florida and California in the 1920s, and now is present in Texas. Aphids attack new growth leaves, causing them to curl or roll, and cause damage by retarding the growth of young trees, reducing fruit set, and production of sooty mold. Winged forms develop when the aphid colony becomes crowded or when leaves mature. Spirea aphid reproduces parthenogenetically throughout the season, and may spend the summer on alternate (non-citrus) host plants.

Melon or cotton aphid, *Aphis gossypii* Glover, is a cosmopolitan pest that feeds upon and injures many horticultural and agronomic crops. It is about the same size as spirea aphid, but on citrus is generally dark gray or dull black. It infests citrus during the spring flush of growth. Melon aphid can transmit citrus tristeza virus, but apparently is not an efficient vector.

Several other aphid species occasionally are found on citrus in Florida, including cowpea aphid, *Aphis craccivora* Koch, oleander aphid, *A. nerii* (Boyer de Fonscolombe), potato aphid, *Macrosiphum euphorbiae* (Thomas), and green peach aphid, *Myzus persicae* (Sulzer).

Margarodidae

Only one member of this family is a pest on citrus. Cottony cushion scale, *Icerya purchasi* Maskell, is a large scale insect originally from Australia but that has now dispersed throughout the world wherever citrus is grown. It was first discovered in California in 1868 and by the late 1880s was severely damaging citrus in the southern part of the state. A coccinellid predator from Australia, vedalia beetle [*Rodolia cardinalis* (Mulsant)], was imported to the Los Angeles area and released in 1888–1889. The beetle multiplied quickly and the cottony cushion scale was brought under control. This was the first successful use of a classical biological control agent in the U.S. Cottony cushion scale was accidentally sent to Florida in a shipment of vedalia beetles in 1893. Vedalia beetle provides effective control nearly everywhere. Mature female scales have bright orange-red, yellow, or brown bodies that are partially covered by wax. The body is also covered by a large, fluted egg sac filled with red eggs. Females are actually hermaphrodites, having the sex organs of both males and females. Males are rare and are winged. When females self-fertilize, only hermaphrodites are produced, whereas if a hermaphrodite mates with a male, more males and hermaphrodites are produced. Cottony cushion scales congregate along the midrib of leaves and on trees. They damage citrus by decreasing tree vitality, increasing fruit drop and defoliation.

Coccidae

Unarmored or soft scales are represented by several species on citrus. They have no protective covering like armored scales but do secrete a wax-like substance which protects them. Female soft scales do not have wings, but are mobile until eggs start to form. Adult males usually have one pair of wings, and don't live very long. Young scales are called crawlers, and they either hatch from eggs or are born alive. Later stages produce large amounts of honeydew upon which sooty mold fungus grows and, along with armored scales, are among the most serious pests of citrus in the world. Many parasitoid species attack and control soft scales, but ants will protect scale populations from their natural enemies.

Two species of *Coccus* are citrus pests. Brown soft scale, *Coccus hesperidum* L., has a worldwide distribution on a variety of plants. In Florida, it is not a pest of concern, but is the most serious soft scale pest in Texas. The scale body is flat and oval, light brown to yellowish. Females give birth to pale yellow crawlers. Brown soft scale is a more serious problem on young trees due to feeding and honeydew production. Mature trees suffer from reduced vigor, twig dieback, and reduced fruit yields. There are several parasitic wasps that attack brown soft scale.

Citricola scale, *C. pseudomagnoliarum* (Kuwana), is found in California. It is more of a serious pest in the San Joaquin Valley than other citrus districts. Young citricola scale are very flat and more transparent looking than young brown soft scale, while mature citricola scales are gray. Crawlers appear in late April and settle on the underside of leaves. By November, they migrate to twigs, where their development speeds up. By the next spring, mature female scales lay eggs which hatch into crawlers. Damage to citrus is similar to that of brown soft scale.

Three species of black scale, *Saissetia*, are citrus pests. Caribbean black scale, *S. neglecta* De Lotto, is a pest in Florida. Adult females are brown to black and have a tough circular or hemispherical shell. Two lateral ridges and one longitudinal ridge create an "H" shaped pattern. Crawlers move from leaves to small twigs and fruit stems. Females lay eggs and usually reproduce without fertilization by males (parthenogenesis). Mexican black scale, *S. miranda* (Cockerell & Parrott), is found in the southern U.S. and Mexico on a wide variety of plants. It is seldom found in Florida. Black scale, *S. oleae* (Olivier), a pest of olive trees and oleander, is found in the southern citrus districts of California and in Florida. This scale's appearance is similar to that of other black scales. Excreted honeydew supports growth of sooty mold and feeding reduces tree vigor and causes leaf and fruit drop.

Four other species of soft scales are occasional pests in the U.S. Hemispherical scale, *Parasaissetia coffeae* (Walker), is widely distributed across the world and is found in the coastal sections of southern California. Nigra scale, *P. nigra* (Nietner), is a tropical species that is found rarely in California. Florida wax scale, *Ceroplastes floridensis* Comstock, is an important pest of citrus in the Mideast and Asia, and is occasionally a problem in Florida. Adults are highly convex, somewhat angular, and oval. Males have not been reported. Barnacle scale, *C. cirripediformis* (Comstock), is an occasional pest of citrus in California, Texas, Florida, and Mexico. The thick wax coat is dirty white and is divided into distinct plates, one on top and six on the side.

Diaspididae

Armored scales are represented by several species on citrus. Females and immature males are covered by coatings of wax and cast skins (exuviae) of earlier instars. As crawlers, females insert their mouthparts into the plant and never move again. They will lay either eggs or live young under the armor (cover), depending on species. Armored scales injure citrus by feeding, not by production of honeydew and resulting sooty mold. The level of damage varies greatly among armored scale species.

California red scale, *Aonidiella aurantii* (Maskell), and yellow scale, *A. citrina* (Coquillett), are two armored scales that are major pests in the citrus-growing districts of California. California red scale is found also in Texas, while yellow scale is found in Florida. Adult females have circular covers. Immature male covers are more elongated, and adults are small, two-winged insects that live for only a few hours. Females give birth to live young (crawlers), which search for locations to settle. California red scale infest all parts of the tree, including leaves, twigs, branches, and fruit. Yellow scale is found rarely on twigs and branches. Plant tissue is injured as a result of plant fluid removal and injection of toxic substances. Damage is caused by leaf yellowing, leaf drop, and fruit drop, and serious damage to trees occurs when twigs and branches are killed. Biological control is an important management tactic used against these scales, with *Aphytis* and *Comperiella* parasitoids mass reared and released.

Black parlatoria or ebony scale, *Parlatoria ziziphi* (Lucas), was discovered infesting citrus in southern Florida in 1985. It is considered a major pest in countries bordering the Mediterranean, tropical Asia, parts of South America, and the Caribbean. The female covering is black, rectangular, and with a fluted surface while the male covering is white, except at one end, flat, and elongate. The armor is almost impossible to remove from host tissues. Scales infest leaves, twigs, and fruit, and because they adhere so strongly, cause rejection of fresh fruit in markets. Large populations cause chlorosis and early drop of leaves, dieback of twigs and branches, and distortion of fruit.

Chaff scale, *Parlatoria pergandii* Comstock, has a similar distribution as black parlatoria scale, except that it is also found in the Gulf states. This is the most common armored scale in Texas. The scale covering is circular to elongated, thin, and brown to gray. The female body, eggs and crawlers are purplish. Chaff scales often are found in depressions on fruit or along midribs on leaves, and are also found on tree bark. When fruit mature, areas around the scale remain green, rendering the fruit unsuitable for the fresh market.

Purple scale, *Cornuaspis* (=*Lepidosaphes*) *beckii* (Newman), was the most common and damaging armored scale in Florida prior to 1960 and the introduction of a parasitoid (*Aphytis lepidosaphes* Compere). It is found in Texas and in more humid areas of California. Adult females are curved and oyster-shaped (broad and tapering), with a purplish-brown cover and a white scale body color. Immature male covers are shorter and more slender than those of the female. Adult males are small winged insects. Females lays eggs under her scale cover. Purple scales prefer trees with a dense canopy and infest leaves, wood, and fruit. On leaves, they cause yellow chlorotic spots which lead to defoliation. Fruit quality is affected because fruit infested with scales do not change color.

Glover scale, *Lepidosaphes gloveri* (Packard), also known as "long" scale, is found in association with purple scale. It is found in Florida, Texas, and limited areas in California. Adult female covers are long and narrow, purplish-brown, with white to purple colored scale bodies. They infest leaves, twigs, bark, and fruit, and when on woody bark, orient with the grain of the bark. Parasitic wasps generally keep this species under biological control.

Citrus snow scale, *Unaspis citri* (Comstock), was known to infest citrus since 1880, but became an important pest in Florida in the early 1960s. Replacement of trees after a severe freeze in 1962 brought thousands of infested nursery stock to groves. Female covers are oyster-shaped with a longitudinal ridge, and are purplish-brown with a gray border. Immature male covers are white with a center ridge and fainter ridges on either side. Adult males are winged and yellowish. Although they infest all parts of a tree, citrus snow scales primarily attack the trunk and large branches. Declining tree vigor and lower fruit production result from high populations.

Florida red scale, *Chrysomphalus aonidum* (L.), affects citrus in Florida and Texas, but is seldom found in groves in California. It was introduced into Florida from Cuba in 1874 and was a major pest until release of the parasitoid *Aphytis holoxanthus* DeBach in 1960. In Texas, California red scale and Florida red scale can be misidentified. Florida red scale female covers are more circular, are dark reddish-brown, and have a conspicuous light brown nipple. The female's body is yellow, and the female's cover is more easily removed than those of California red scale. Adult males are winged insects that fertilize adult females. Females lay eggs which hatch into very active, bright yellow crawlers. Unlike other armored scales, Florida red scales attack only leaves and fruit. On leaves, they cause yellow chlorotic spots which lead to defoliation. They also cause yellow spots on fruit which render it unmarketable as fresh fruit.

Fern scale, *Pinnaspis aspidistrae* (Signoret), is found in Florida, South America, and Japan. Female scale covers are pale brown, flat, and pear-shaped. Immature males are white and elongated, resembling male citrus snow scale. They are found only on leaves and fruit. They have a wide host range and never cause economic damage to citrus.

Pseudococcidae

Mealybugs are soft, oval, flat, distinctly segmented insects covered with a white, mealy wax that extends into spines (filaments) along the body margin and the posterior end. Unlike scales, mealybugs remain motile throughout their life cycle. Species differ in external appearance by the waxy covering and the thickness and length of filaments. Mealybugs injure plants by extracting sap from trees and secreting large amounts of honeydew, which serves as a food source for sooty mold. Feeding on foliage and twigs reduces the vigor of trees and may result in defoliation. Feeding on fruit results in distortions and scars which lower the grade of the produce.

Citrus mealybug, *Planococcus citri* (Risso), occurs in Florida, Texas, and in the coastal citrus districts in California. They have pinkish bodies that are visible under the powdery wax. Adult males are winged insects. Eggs are laid in a white cottony mass, and nymphs are light yellow. Citrus mealybugs prefer protected areas such as the calyx of fruit or along the stem. Feeding along the stem usually results in fruit drop. There are several natural enemies including pathogens, parasitoids, and the ladybird beetle, *Cryptolaemus montrouzieri* (Mulsant). This predator was imported from Australia to California in 1891.

Three species of *Pseudococcus* are citrus pests. Comstock mealybug, *P. comstocki* (Kuwana), a native of Asia, is primarily a pest on lemons in the San Joaquin Valley of California. It differs from citrus mealybug by having a thicker wax cover and two spines at the posterior end. The citrophilus mealybug, *P. calceolariae* (Maskell), and longtailed mealybug, *P. longispinus* (Targioni-Tozzetti), are present in California. Longtailed mealybugs differ from other species because young are born as active nymphs. They are usually not a problem on citrus because of the work of natural enemies.

An exotic species, pink hibiscus mealybug, *Maconellicoccus hirsutus* (Green), is a serious pest of citrus and other plants in Africa (Egypt), southeast Asia and northern Australia. It was found in the Caribbean in 1994, in southern California in August 1999, and just recently in Florida in June 2002. It has a high reproductive rate and infests many horticultural, ornamental, and agronomic crops. This mealybug feeds on soft tissues of plants and injects a toxin which causes leaf curling and distortion. Feeding also promotes growth of sooty mold because of honeydew excretion.

Thysanoptera

Thrips are a group of small, elongated insects with fringed wings. Their mouthparts have been described as "rasping-sucking," but it is likely that certain parts pierce rather than rasp leaf and flower tissue. The majority of thrips species feed on plants, but some feed on fungus and others are predaceous on small arthropods. Life cycles consist of an egg stage, two larval stages that feed, one prepupal stage that doesn't feed, one non-feeding pupal stage, and an adult stage that feeds. Several species are pests on citrus.

Thripidae

Two species of flower thrips are found on citrus in Florida. *Frankliniella bispinosa* (Morgan) occurs throughout the state, while *F. kelliae* Sakimura is found in central and southern growing areas. Both species have wide host ranges, but on citrus have been shown to injure navel and "Valencia" oranges. Flower thrips migrate aerially during the flowering cycle from January through April. They have been documented to feed, oviposit, and develop on various flower parts, such as the ovary, style, petals, anthers, pistil, and calyx. Resulting damage is by reducing fruit set. Recently a relationship between thrips feeding and the fungal pathogen *Colletotrichum acutatum* J. H. Simmonds was associated with post bloom fruit drop.

Three *Scirtothrips* species are recognized as citrus pests, *S. auranti* Faure in South Africa, *S. dorsalis* Hood in Japan and Africa, and citrus thrips, *S. citri* (Moulton), in California and Arizona. Citrus thrips is an important pest on navel oranges in the San Joaquin Valley, on desert citrus including grapefruit and tangerine, and on lemons grown in the coastal districts. They are small, yellowish-orange, and have fringed wings. They feed on leaves, young fruit (especially under the sepals), and green twigs. Leaf injury is along the midrib or leaf margins, causing leaf deformities, and injury to fruit is by puncturing epidermal cells, leaving uniform scars. Scars in young fruit form a ring around the stem, and as the fruit grows, the ring increases and is found further from the stem. Natural enemies include several predators including mites (*Eusieus tularensis* Congdon). A fourth species, *S. perseae* Nakahara, recently was found infesting avocado in southern California. It is not known if this Central American native will attack citrus.

Greenhouse thrips, *Heliothrips haemorrhoidalis* (Bouché), is a New World species that is also found in Europe, the Mideast and north Africa. In the U.S. it is found in central and southern Florida and southern California along the coast. Adult females are black with a reticulated body surface and yellow-white legs. Greenhouse thrips develop parthenogenetically. They injure rind tissue by feeding on epidermal cells, which may cause ring spotting or irregular russeting. Injury occurs where fruits, fruits and leaves, or fruits and twigs are in contact. In Florida economic loss to growers is restricted to red grapefruit varieties, but in California greenhouse thrips attack "Valencia" oranges, lemons, and avocados. Feeding from fruit epidermal cells removes pigment. No scars or deformities develop, but fruit may be downgraded.

Two other thrips species occur in Florida citrus. *Chaetanaphothrips orchidii* (Moulton) females are yellow with distinctive dark banding on the wings. They are most common on grapefruit and are present throughout the year. Fruit injury resembles that of greenhouse thrips. *Danothrips trifasciatus* Sakimura is present in low numbers in association with *C. orchidii.*

Coleoptera

Beetles represent the largest order of insects in number of species. As might be expected, this is an extremely diverse group with species that specialize in phytophagy (plant feeding), zoophagy or carnivory (feeding on animals, usually as predators or parasitoids), fungivory (fungus-feeding), and saprophagy (feeding on dead material). However, relatively few species specialize or infest citrus. The primary family of beetles that attack citrus is Curculionidae, the weevils.

Diaprepes weevil, *Diaprepes abbreviatus* (L.), has several other common names such as "Apopka weevil" and "sugarcane rootstalk borer weevil." It is native to the Caribbean, and is only found in the U.S. in Florida and Texas. It was first reported in central Florida (Apopka) in 1964 and since has spread over the southern two-thirds of the state. Adults are black with white, reddish, or yellowish scales on the wing covers (elytra). This is the largest weevil species that infests citrus in Florida. Eggs are laid on new flush leaves that have been clustered or glued together by females using an adhesive material. Young larvae fall to the soil and begin feeding on roots. During the course of its development, which can last anywhere between 6 and 24 months, larvae may consume any part of the tree's root system. Diaprepes pupate in the soil and then emerge to find mates. Although adults fly, they do not disperse far from their emergence site. Adults may nibble or "notch" the margin of leaves, but important injury is caused by larval feeding. Young trees can be killed by a single larva and older trees suffer when major roots or the taproot is girdled. Feeding on roots also allows for the introduction of plant pathogens, which injure an already stressed tree. There is a considerable amount of research being conducted by federal and state entomologists in Florida in detecting, controlling, and preventing damage by this insect.

Two species of blue-green citrus root weevils are found in Florida. *Pachnaeus litus* (Germar) is found in south-central to southern Florida; *P. opalus* (Oliver) is commonly found in north and north-central Florida. At least two *Pachnaeus* species also occur in Texas citrus groves. Adults of both species are gray-green to aqua and can be separated by structures on the wing covers. Larvae are root feeders and will attack all root parts except the crown. Adults feed by notching the leaf margins. As with other citrus root weevils, many other plant species can be used as hosts.

Fuller rose beetle, *Asynonychus godmani* Crotch, is found in Florida, Texas and California. It was reported in Florida in 1916 and has been known as *Pantomorus cervinus* (Boheman) and *A. cervinus* (Boheman). Its distribution in Florida ranges from the southern tip to north-central areas. Adults are brownish-gray, flightless, and are all females that develop parthenogenetically. Eggs are usually laid under the calyx of the fruit. Larvae take from 9 to 12 months to develop and feed on all root parts except for the crown. Fuller rose beetle is not a serious economic pest by itself, but because eggs are laid on fruit, they are a quarantine pest when fruit is to be exported. One management tactic developed in California is the use of parasitic nematodes [*Steinernema carpocapse* (Weiser)] for biological control.

The smallest root weevil in Florida is the little leaf notcher, *Artipus floridanus* Horn. This insect was reported as early as 1876 and is found mostly along the east coast. Adults are grayish-white, flightless, and are all female. Unlike the other species discussed in this group, *A. floridanus* has a much shorter life cycle. Larvae can complete development in as little as 35 days. Also unlike the other species, larvae feed only on smaller root parts such as pioneer and fibrous sections.

Diptera

This large, diverse order contains two families that attack citrus. Gall midges (Cecidomyiidae) are infrequent pests of citrus buds and flowers. Fruit flies (Tephritidae) from the genera *Anastrepha*, *Bactrocera*, and *Ceratitis* attack fruits and vegetables. Females insert eggs under the skin of fruit and larvae feed within, causing direct injury and decay. Fruit fly species are also quarantine pests, where whole loads or even a season's worth of produce may be denied entry within regions of a country or among countries because of the threat of infestation.

Cecidomyiidae

The citrus gall midge, *Prodiplosis longifila* Gagné, is a small black-yellowish fly that attacks citrus, tomatoes, potatoes, and cotton in Florida, the Caribbean, and South America. Large populations developed in 1984 on limes in southern Florida. Eggs are laid in flower buds and larvae feed on flowers, injuring several flower structures. Larvae complete development, drop to the ground, and pupate in the soil. Damage occurs when flowers are killed and drop from the tree.

Tephritidae

Three genera, *Anastrepha*, *Bactrocera*, and *Ceratitis*, contain fruit fly species that are considered serious citrus pests. Eggs are inserted under the skin of various fruits, berries, nuts, and vegetables. Larvae then mine the host, promoting decay and causing the fruit to be unmarketable. Fruit flies are direct pests in countries where they are established, but are also regulatory or quarantine pests in countries where particular species are not established. There has been much research worldwide into detection or monitoring of adults, and management tactics other than insecticide sprays, such as bait stations, sterile insect technique (releasing sterile flies to mate with wild flies) and biological control.

Species in the genus *Anastrepha* are New World flies that attack tropical and subtropical fruits. The Mexican fruit fly, *A. ludens* (Loew), is important in the United States because it is subtropical rather than tropical. It is found in southern Texas, California and Arizona, where continuous detection and eradication programs, such as sterile insect technique, are in place. It was detected in Florida in 1934 and again in 1972, but did not become established. This relatively large yellow-brown fly is native to Mexico but can be found as far south as northern South America. In Texas, grapefruit appears to be the preferred host, and several deciduous hosts such as peach, pear and apple also can be attacked.

The Caribbean fruit fly, *A. suspensa* (Loew), is a yellow-brown fly that is native to the West Indies. This species has an interesting history in Florida. It was documented in Key West in 1931, although was believed to have been established for many years. This "strain" attacked guavas (*Psidium guajava* L.) and noneconomic fruits but did not infest citrus. This strain differed from populations found in Puerto Rico that did feed on citrus. The Key West populations apparently were eradicated through fruit removal and insecticide sprays and died out sometime after 1936. Since 1965, a new introduction into Florida spread from southern areas to central Florida groves. It attacks mature and overripe citrus, and its seriousness as a pest is still being investigated. Exports require an elaborate fly-free zone system that requires several million dollars a year to maintain. Even so, in some years up to 16,000 hectares (40,000 acres) of grapefruit have been lost to export markets because of fly captures within protocol areas.

Three other *Anastrepha* species are pests in the Western Hemisphere and are potential pests in Florida if they become established. The West Indian fruit fly, *A. obliqua* (Macquart), is nearly identical to *A. suspensa* and occurs throughout the Caribbean, southern Texas, and south to Argentina. It was found in Key West in the 1930s during surveys for *A. suspensa*. It was also eradicated and hasn't been found in Florida since 1935. This species has a long host list, but mangos (*Mangifera indica* L.) and guavas can be economically damaged. It rarely attacks citrus. The South American fruit fly, *A. fraterculus* (Wiedemann), is economically the most important species in South America (Brazil, Argentina, Peru), but is also found in Central America northward to southern Texas. However, this species may be part of a species complex since specimens identified as *A. fraterculus* vary widely from populations in Brazil, Mexico, and Texas. It also has a wide host range that includes tropical, subtropical and temperate fruits including sweet orange and peach. The sapote or serpentine fruit fly, *A. serpentina* (Wiedemann), is a brown fly that is common from southern Texas to Mexico, Central America and South America. It can be a severe pest of ripened sapote (*Calocarpum* spp.) and sapodilla (*Manilkara zapota* L.) in Mexico. Although many flies are trapped in south Texas, there is only one record of an infestation in grapefruit.

Species in the genus *Bactrocera* (formerly *Dacus*) are flies native to Africa, the Mediterranean, Asia and the Pacific. None of the citrus-infesting species are currently established on the mainland United States, but several are occasionally trapped in California and Florida. The oriental fruit fly, *B. dorsalis* (Hendel), is a variably colored medium-sized fly that infests fruits and vegetables throughout Asia (Pakistan, India, Vietnam, Philippines, Japan, etc.) and the Pacific, including Hawaii. It was introduced into Hawaii in the mid-1940s by returning servicemen that were stationed on several Pacific islands, but has become partially under control through the introduction of parasitoids. In Japan, several management tactics including the use of attractant baits and sterile male release has been successful. Guava fruit fly, *B. correcta* (Bezzi), is a small, brightly colored, predominately black fly that occurs in southern and southeastern Asia. Adults have been trapped in California and Florida but it hasn't established. It is a potential pest of citrus, peach, and other subtropical and tropical fruits. Queensland fruit fly, *B. tryoni* (Froggatt), is a small brown-yellow fly that is wasplike in appearance. The distribution of this species includes the eastern half of Australia, although flies have been trapped in Western Australia, New Guinea, and several Pacific islands. It is a pest of pome and stone fruits as well as citrus. Biologically, this species is more temperate in distribution and does not breed continuously but overwinters as an adult. Japanese orange fly, *B. tsuneonis* (Miyake), infests orange, grapefruit and mandarin orange in Japan, southwestern China and probably Taiwan. There have been no interceptions of this fly in the U.S., mostly because of an embargo of citrus from infested areas. Changes to the embargo laws may increase the chances of introducing this pest.

Species in the genus *Ceratitis* are originally from sub-Saharan Africa, but now some have a worldwide distribution. Mediterranean fruit fly, "Medfly," *C. capitata* (Wiedemann), is a yellowish brown fly that is one of the world's most destructive fruit pests. It has been established in Hawaii since 1910, and has been detected at different times in California, Florida, and Texas. For instance, Medfly has been detected in Florida 16 times since 1929, and only massive and expensive eradication programs have kept it from becoming established in the continental U.S. As with other tephritid fruit flies, eggs are laid slightly beneath the fruit's surface. Larvae feed within the fruit, and generally the fruit drops to the ground and larvae move into the soil to pupate. Over 260 species of hosts have been recorded, with peach, nectarine, orange, grapefruit, apricot, and pear being some of the Medfly's favorites. In addition to the reduction in citrus yield, infested areas have the additional expense of control measures and costly sorting for fresh and processing fruit. Detection and control of the Medfly has included trapping, quarantines, cultural control (waste removal and disposal of culls), release of sterile males, and biological control. Much research has been completed designing traps and lures for detection of Medfly.

Two other *Ceratitis* species are pests in Africa. The Natal fruit fly, *C. rosa* Karsch, is slightly larger than the Medfly and similar in appearance. It is distributed throughout sub-Saharan Africa and on the Indian Ocean islands of Mauritius and Réunion. This fly overwinters in the adult stage and can withstand below-freezing temperatures. It attacks many temperate stone and pome fruits including peach, nectarine, apricot, apple and pear. Although the Natal fruit fly has been intercepted in the United States in produce, it has never been captured as an escapee. If accidentally introduced, it could prove to be a serious pest. *C. malagassa* Munro damages citrus fruit on the island of Madagascar. It has a smaller geographical distribution than the other two *Ceratitis* species discussed.

Lepidoptera

There are several families of moths and butterflies that attack the fruit or foliage of citrus. Fruit-piercing moths (Noctuidae) are pests in southern Africa, Australia, and east Asia. They include species in the genera *Achaea*, *Calpe*, *Emaenas*, *Ercheia*, *Gonodonta*, *Othreis*, and *Serrodes*. None of these are apparently established in the U.S. Other noctuids, such as cabbage looper, *Trichoplusia ni* (Hübner) and beet armyworm, *Spodoptera exigua* (Hübner) can cause considerable damage to nursery stock and young citrus. Bollworm, *Helicoverpa zea* (Boddie), is a pest of citrus in Africa in areas when cotton is planted nearby, but is seldom a problem on citrus.

Gracillariidae

Two species in this family are pests of citrus in the U.S. Citrus leafminer, *Phyllocnistis citrella* Stainton, is an Asian species that has recently spread to northern Africa, Central America and the United States. It was found in late May 1993 in Dade County, Florida, late August 1994 in the Rio Grande Valley of Texas, and in 2000 in Imperial County, California. Hosts include citrus and related species within the plant family Rutaceae. Eggs are laid on the underside of leaves and green-yellow larvae enter leaves and begin forming mines. Pupation is within the mine and white and silver-colored adults emerge during the morning. Injury to foliage and fruit can be extensive with large populations, and damage is more serious to nursery trees or newly planted groves. This pest appears to be able to be controlled through the use of natural enemies. Several Asian parasitoid species have been collected from Australia and released in the United States, but native natural enemies also show promise in reducing populations.

Citrus peelminer, *Marmara gulosa* Guillen Davis, has seriously damaged citrus in several areas in California including the Coachella and San Joaquin valleys and Kern County. Larvae burrow within the epidermal surface of the fruit causing serpentine mines. It often attacks fruit located near alternate hosts such as oleander and willows. Although it seldom affects more than 5% of the fruit, in 2000 citrus peelminer infested almost 70% of the fruit in some groves. It also expanded its geographic and host ranges in California. Research is now being conducted to see if infested fruit imported from Mexico during 1998 included a new biotype or species of peelminer.

Tortricidae

Two species can cause extensive injury to citrus. Fruittree leafroller, *Archips argyrospilus* Walker, has been a pest of citrus in California for many years. This species is widespread across the United States feeding on a wide variety of hosts. It has damaged apples in Michigan, New York and Pennsylvania, and bald cypress in Louisiana. On citrus, it feeds on spring flush growth of leaves, flowers, newly set fruit, and later on mature fruit. Unlike many tortricids, eggs are generally laid on woody tissue. Orange tortrix, *Argyrotaenia citrana* (Fernald), is primarily a pest of "Valencia" and navel oranges in southern California. Eggs are laid on stems, fruit and upper leaf surfaces, and larvae primarily feed on new growth leaves and fruit. Fruit feeding is around the sepals and holes can be eaten in the peel.

Several other tortricid species occasionally can attack citrus in the United States. These include garden tortrix, *Ptycholama peritana* (Clemens), variegated leafroller, *Platynota flavedana* Clemens, omnivorous leafroller, *Platynota stultana* Walsingham, and western avocado leafroller, *Amorbia cuneana* (Walsingham). These species are not specific to citrus and attack several other crops and ornamentals. Tortricids found in other citrus-producing countries include *Archips occidentalis* (Walsingham) and *Tortrix capensana* Walker, pests in South Africa, *Archips rosanus* (L.) in Greece, and *Epiphyas postvittana* (Walker) in Australia. Like the other leafrollers, these species have relatively wide host plant ranges.

Megalopygidae

Puss caterpillars, *Megalopyge opercularis* (J. E. Smith) are pests more because of their medical importance than through defoliation. This caterpillar is the larval form of the southern flannel moth, which is found throughout the southeast and into Texas. Human disease from puss caterpillars usually arises from direct contact to their urticating hairs. Field workers pruning or harvesting fruit are usually the people who come in contact with these insects.

Papilionidae

A large number of species of swallowtail butterfly larvae (orangedogs) feed on citrus foliage throughout the world. Orangedogs are named because when disturbed, larvae stick out orange-colored osmeteria (scent organs located behind the head) and give off a strong, disagreeable odor. Two species are common in the U.S. Giant swallowtail, *Papilio cresphontes* Cramer, is distributed throughout the U.S. except in the far west. It is an occasional pest of citrus in Florida and Texas, where young trees in groves or nurseries can be quickly defoliated. Adults are large dark butterflies with diagonal yellow bars on the forewings. Adults can be attracted to plants in butterfly gardens. Citrus California orangedog or black anise swallowtail, *P. zelicaon* Lucas, is a native butterfly that feeds on perennial anise (sweet fennel) and citrus. Like other *Papilio* larvae, these larvae are more damaging to young trees.

Hymenoptera

This order contains ants, wasps, and bees. Wasps and bees can be pests when fruit workers contact colonies in the field.

Formicidae

In the Rio Grande Valley, the Texas leafcutting ant, *Atta texana* (Buckley), is the most serious ant pest. These reddish-brown ants remove leaves from trees to culture fungus for food. In areas of large colonies, single trees may be defoliated in a single night. Large areas underground are excavated and may present problems for farm machinery. Multiple defoliation of young trees can slow growth or cause tree death.

Fire ant species in the United States can be citrus pests and include red imported fire ant, *Solenopsis invicta* Buren, native fire ant, *S. geminata* (F.), and southern fire ant, *S. xyloni* McCook. Fire ants injure trees by attacking twigs, bark, and leaves, and young trees can be completely girdled. Young trees also can be damaged when bark beneath tree wraps are injured and provide a point of entry for fungi.

Several ant species are problems on citrus because of their interference in the development of biological control programs. Argentine ants, *Linepithema humile* (Mayr) (formerly known as *Iridomyrmex humilis*), and native gray ants, *Formica aerata* Francouer, feed on honeydew excreted by soft scales, mealybugs, whiteflies, and aphids. In this relationship, they protect these species from natural enemies. They even protect other scales species that don't produce honeydew, such as California red scale, from potential biological control agents.

Gastropoda: Pulmonata

Helicidae

Although snails are not insects, they can be serious pests of citrus by feeding on leaves, buds, flowers, fruit and bark. The brown garden snail, *Helix aspersa* Müller, is a European species that is found in California and in most southeastern states. However, it is not established in Florida. This species is hermaphroditic (having both male and female organs), so during mating mutual fertilization can occur. Large populations can be found in citrus groves where extensive damage to leaves and fruit may occur. At one time, snails were only found in California's humid and cool coastal areas, but because of drip irrigation and no-till weed control, snails are now found in several citrus-growing districts.

Citrus Pest Management

Fresh or Processing Market

One of the most important decisions citrus growers make at the beginning of a season is whether to market their fruit for the fresh market or processed market. For maximum profitability of fresh market fruit, a high level of pest control is needed to reduce the number of external blemishes. This level of quality is not needed for fruit destined for the processing market. Several factors are involved in the decision-making process for market destination:

grove location and accessibility of markets, fruit variety grown, grove history for pests, and profitability desired. Growers may decide that their fruit will be managed for the fresh market, but after spring bloom several abiotic (weather-related) or biotic (tree health, disease pressure, high pest densities) factors may change that decision. Therefore, the market decision that growers make impact the management input in groves.

Sampling and Thresholds

Citrus growers need to be able to identify and provide estimates of the numbers of pests and natural enemies present in their groves. The frequency and methods used to sample or monitor for pests and natural enemies varies depending on the pest being sampled and the time invested. For instance, it is suggested that sampling for citrus rust mites be every 2 weeks during the season because their populations can expand quickly. Most other pests are monitored on a monthly basis. Sampling may involve trees randomly selected for each period or permanently designated station trees. Trees that are randomly selected should be dispersed sufficiently to be representative of the grove. Station trees are representative trees that are flagged and visited each sampling period. In both cases, accurate and descriptive records should be kept. Action thresholds are pest population densities that, when reached, signal to the grower that some type of corrective action is needed. Thresholds for a certain pest species will vary depending on the fruit market destination, time of season, and abundance of appropriate natural enemies. Thresholds have been developed by entomologists for many of the important citrus pests, and are designed to provide enough time for growers to take corrective action.

Management Strategies

Growers use three general approaches for control of citrus pests. Cultural control is defined as using horticultural techniques to reduce the likelihood of pest problems. Several cultural control techniques may be completed before or during grove establishment, such as site selection, rootstock choice, and the use of virus-free budwood. Techniques accomplished after grove establishment include tree nutrition, irrigation, plant waste removal, pruning practices, and harvesting practices.

The second management strategy that growers may employ is biological control, which is the use of naturally occurring or imported parasitoids, predators, or pathogens to reduce pest populations. The citrus industry historically has encouraged the use of natural enemies, therefore, many citrus pests are partially or fully under biological control. However, biological control systems are easily disturbed by pesticide use.

The third management strategy used by citrus growers is chemical control. The products that are used include synthetic chemicals such as insecticides, acaricides, and horticultural oils, which have different ways of killing arthropods (mode of action). Biological products such as bacteria, fungi, or viruses also are available and can be used in a similar fashion as chemicals. Before chemical control is used, several factors must be considered. Is the pesticide labeled for use against the target pest and is it efficacious? What is the cost effectiveness of the product and what are the hazards to natural enemies, the environment, the fruit, and the applicators? Finally, what is the impact of the intended product on the development of pest resistance. All citrus-producing states have guides available each season for growers. These guides contain lists of labeled products and directions on how to use them against the important pests in those areas. Each state also has entomologists who compare the efficacy of new and existing products under the conditions of the local growing areas.

References

Hui S (1999) Sweet oranges: the biogeography of *Citrus sinensis*. Available at http://www.aquapulse.net/knowledge/orange.html. Accessed 4 April, 1999

Morton JF (1987) Fruits of warm climates, Media Incorp, Miami, FL. Available at http://www.hort.purdue.edu/newcrop/morton/index.html
Reuther W, Calavan EC, Carman GE (eds) (1989) The citrus industry, vol 5: crop protection, postharvest technology, and early history of citrus research in California. Division of Agriculture and Natural Resources, University of California, 374 pp
Texas A&M University. Available at http://aggie-horticulture.tamu.edu/citrus/industry.htm
University of California. UC pest management guidelines – pests of Citrus. Available at http://axp.ipm.ucdavis.edu/PMG/selectnewpest.citrus.html
University of Florida. Available at http://creatures.ifas.ufl.edu/ and http://edis.ifas.ufl.edu/MENU_CH5A for Insect Pests of Citrus and /MENU_CG for Pest Management Guides

Citrus Rust Mites (Acari: Eriophyidae)

Several mites cause russeting of citrus.

► Citrus Pests and Their Management

Citrus Snow Scale, *Unaspis citri* (Comstock) (Hemiptera: Diaspididae)

This is an important citrus pest in Florida, USA.

► Citrus Pests and Their Management

Citrus Stubborn Disease

This is a leafhopper-transmitted disease of citrus.

► Transmission of Plant Diseases by Insects

Citrus Whitefly, *Dialeurodes citri* (Ashmead) (Hemiptera: Aleyrodidae)

This was once a very serious pest of citrus, but is now considered a minor pest.

► Citrus Pests and Their Management

Cixiidae

A family of insects in the superfamily Fulgoroidae (order Hemiptera). They sometimes are called planthoppers.

► Bugs

Cladistic Analysis

A technique that groups taxa based on the relative recency of common ancestry.

Clade

A monophyletic group of taxa that share a closer common ancestry with one another than with members of any other group.

Cladiopsocidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice or Psocids

Cladistics

A school of thought that uses only evolutionary relatedness (phylogenetics) in assigning taxonomic groupings in classification systems.

Cladogenic Speciation

Branching evolution of new species.

Cladogram

A term used two ways by different authors. Either a dendrogram (tree) produced using the principle of parsimony, or a tree that depicts inferred historical relationships between organisms.

Clambidae

A family of beetles (order Coleoptera). They commonly are known as fringe-winged beetles.

► Beetles

Class

A major subdivision of a phylum, and containing a group of orders.

► Classification

Classical Biological Control

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Biological control is a method of pest control that employs parasitoids, predators, microbial pathogens and, sometimes, nematodes to reduce pest populations. Pests that are targets of biological control include insects, mites, and weeds. [See the section on Natural Enemies for a description of natural enemies used in biological control programs.]

Biological control is part of natural control, which maintains populations within more or less regular upper and lower limits over time. Natural control factors may be biotic (living) or abiotic (nonliving). Biotic control factors include the effects of natural enemies, food quantity and quality, interspecific and intraspecific competition for resources, and requirements for space or territory.

All insects and mites have a diverse array of natural enemies. Microorganisms, invertebrates, and vertebrates all affect them, causing debilitation or death. Pathogens attacking arthropods include viruses, bacteria and fungi. Many vertebrates (including birds, lizards, fish and frogs) feed on pest arthropods. Nematodes belonging to several families attack insects. However, by far insects are the most numerous and diverse natural enemies of other insects, with hundreds of thousands of species feeding on other insects.

Abiotic factors that affect insect and mite populations include weather (heat, cold, rain, drought) and other physical factors. Biotic and abiotic control factors usually act together to limit population growth by reducing birth rates or increasing mortality or dispersal, although one may be more important than the other in certain situations.

Most organisms produce more progeny than the environment can sustain, yet many natural populations maintain characteristic densities over long periods of time. This state of dynamic equilibrium is achieved by an interaction between the biotic potential of the species and the resistance of biotic and abiotic factors in the environment. Some ecologists have focused on the importance of natural population regulation by biotic factors (particularly natural enemies), while others have emphasized the importance of abiotic factors (especially weather). Still other ecologists have emphasized the importance of interspecific competition in regulating population densities. The relative importance of these factors continues to be debated, but it is likely that each is important and potentially capable of regulating population densities in specific situations. Under most circumstances both biotic and abiotic factors together influence population densities, and it is the degree to which any one factor affects natural control in specific situations that differs.

Physical factors generally influence populations in a density-independent manner. This means that the intensity of the effect of physical factors is not related to the target population's density. Thus, a severe freeze usually will kill approximately the same proportion of large populations as of small populations. By contrast, biotic factors may influence population densities in a more density-dependent manner, with their effect increasing in intensity as populations become larger and decreasing in intensity as populations decrease. Density-dependent population regulation acts as a negative feedback process between population density and rate of increase. For example, the availability of plant hosts may exert density-dependent pressure on insect populations, with a small number of plants being sufficient for a small population but inadequate for a large one.

Parasitoids, predators and pathogens potentially are capable of affecting pest populations in a density-dependent fashion because they can respond to changes in host population density. Some natural enemies may increase their activities and reproductive rates as the density of their insect host increases, and reduce these activities as the density of their hosts declines. If natural enemies increase their numbers with increasing pest/host population densities, this is termed a numerical response. Numerical responses occur because prey or hosts are readily available so that the reproductive rates of natural enemies are enhanced. A functional response is another important component of a density-dependent response by parasitoids and predators. A functional response is the change in number of prey or hosts consumed or parasitized per natural enemy in response to changing prey or host density. Functional responses are influenced by several factors, including: (i) rate of successful search, (ii) the amount of time the natural enemy and target pest are exposed to each other, and (iii) the time spent by the natural enemy handling each prey or host. If pest populations increase and, as a consequence, are more aggregated, natural enemies may not have to spend as much time searching for prey or hosts. Natural enemies also can increase their functional response by consuming only part of their prey at high densities, thus killing more prey per unit time.

Naturally Occurring Biological Control

Many insects or mites are not pests because native natural enemies keep them suppressed with no assistance from humans. Naturally occurring biological control often is discovered only after natural enemy populations have been disrupted and insect or mite populations have increased dramatically to become pests. Biological control also includes an applied technology through which humans attempt to restore, enhance, or mimic a natural phenomenon by three basic tactics: classical biological control, augmentation, or conservation.

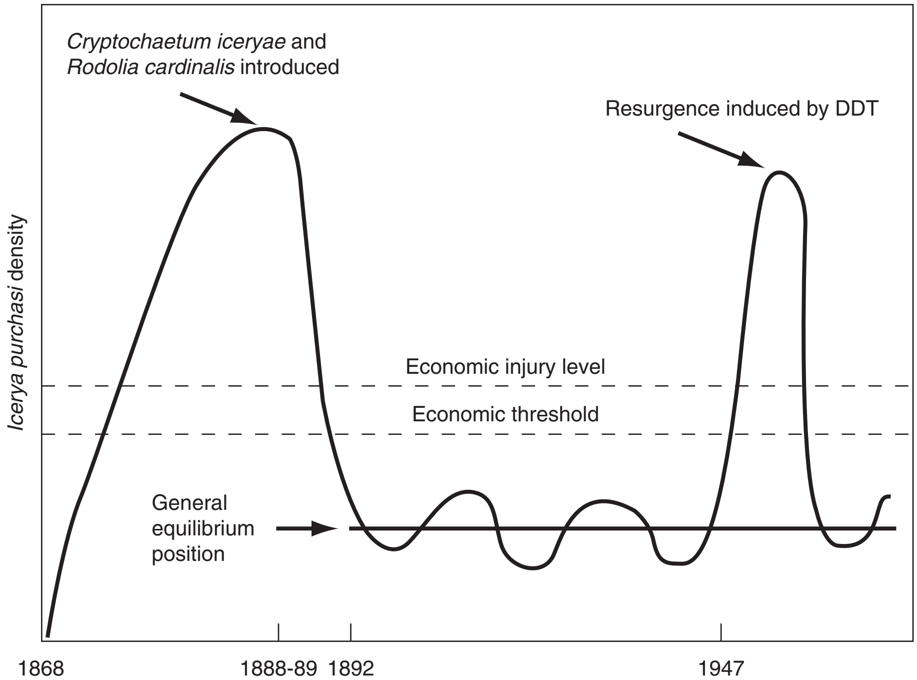
Classical Biological Control

This approach involves importing and establishing natural enemies in order to assist in the long-term control of newly introduced, foreign pests. Classical biological control involves a series of steps and usually takes a number of years. Most programs require more than 10 years of effort.

Classical biological control in the U.S.A. was demonstrated to be a useful pest management tool over 100 years ago after two natural enemies were introduced and established in 1888 against the cottony cushion scale, *Icerya purchasi*, in California's citrus industry. The cottony cushion scale was accidentally introduced into California. It rapidly established, spread and multiplied. The severe effects of its feeding on citrus trees threatened the survival of the citrus industry. In one of the more dramatic classical biological control programs ever recorded, the Vedalia lady beetle *Rodolia cardinalis* and a fly *Cryptochetum iceryae* were imported and released. Within 2 years, these natural enemies had established, multiplied, and spread to reduce populations of the cottony cushion scale (Fig. 61) to an insignificant level. These natural enemies have continued to provide effective control in California ever since unless disrupted by applications of pesticides. Furthermore, these natural enemies have been distributed to more than 25 additional countries, where they have established and provided excellent control of the cottony cushion scale.

Assumptions of Classical Biological Control

Insects or mites that establish in a new environment often are much more serious pests than they are in their native range where they are suppressed by a complex of natural enemies. If a foreign pest arthropod evades regulatory and quarantine barriers to become established in a new environment and cannot be eradicated, the feasibility of classical biological control should be evaluated immediately.



Classical Biological Control, Figure 61 **The cottony cushion scale, *Icerya purchasi*, increased its population dramatically after its introduction in 1868 into California citrus groves. In 1888, the parasite *Cryptochetum iceryae* and the predator *Rodolia cardinalis* were introduced. Within a year after their establishment, they reduced the scale populations below the economic injury level, where it fluctuated around a general equilibrium position until DDT applications were made in the 1940s, which allowed a resurgence because the natural enemies were disrupted.**

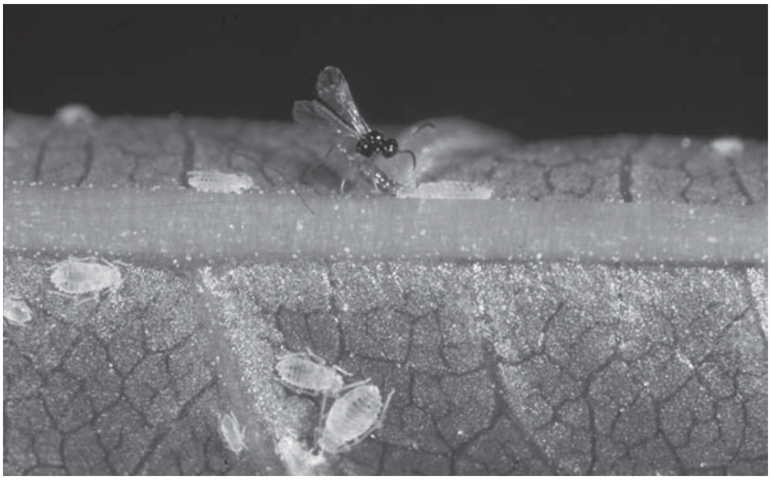
The assumptions of classical biological control are: (i) pest populations are suppressed by natural enemies in their native land, (ii) pest populations have escaped suppression after their introduction without their natural enemies into a new environment, and (iii) introduced natural enemies may be more effective in a new location if introduced free of their own natural enemies (e.g., predators and parasitoids may have their own natural enemies that reduce their effectiveness against the target pest). Another assumption is that the existing natural enemies present in the new geographic environment will be generalists, and therefore less effective than natural enemies that have specialized on the target pest in their original environment.

Classical biological control programs typically require a number of years to execute, and there are no guarantees that the pest populations will be suppressed to a satisfactory level in the new environment. However, if classical biological control is successful, it can provide cost-effective and environmentally benign pest management for a long time.

Steps in Classical Biological Control

Classical biological control involves a series of steps, beginning with identifying the pest as native or foreign in origin. If foreign, it is important to identify the origin of the pest, because this area may provide the most extensive array of natural enemies for evaluation and possible importation.

Once the biology and behavior of the pest have been reviewed, specific natural enemies are identified as potential targets of a collecting trip. Sometimes, a long list of natural enemies is available; sometimes, only a few natural enemy species



Classical Biological Control, Figure 62 **Endoparasitoid female, *Trioxys pallidus* (Hymenoptera: Aphelinidae), inserting an egg into the walnut aphid, *Chromaphis juglandicola*. (Photo provided by J. K. Clark.)**

are known. Typically, only a few species are collected, shipped and evaluated further. Once the natural enemies are obtained and shipped to a quarantine facility, their identity is verified by taxonomic specialists and the colonies are screened to eliminate undesirable hyperparasitoids (parasitoids of the primary parasitoid) or pathogens. Permission to release the natural enemies must be obtained from state and or federal regulatory agencies after a risk analysis has been conducted. Natural enemies are then mass reared and released (Figs. 62 and 63) with the goal of permanently establishing them in the new environment to provide continuing control of the target pest.

Classical biological control programs are dependent upon having taxonomic specialists to correctly identify immigrant pests, provide information on their geographic distribution, and identify natural enemies in the country of origin. Correct identification (Fig. 64) of pests and their origins is important when planning collection trips. Natural enemies also must be correctly identified before they can be released from quarantine into the new environment. Some effective biological control programs have been delayed because taxonomic information was lacking or incorrect. Because financial support for systematics is declining, fewer such specialists are being trained which could lead to delays or failures in future classical biological control programs. Taxonomic specialists also can provide information on the host or prey range of the natural enemy, which is important when risk assessments are being conducted prior to releasing the natural enemies.

Classical biological control is an important component of pest management programs because foreign pests invade new environments on a continuing basis. For example, by 1971 at least 1,683 species of insects or mites found in North American forests, rangelands, or agricultural fields were illegal aliens. Some were pests, some were beneficial, and some had no known economic importance. At least 235 major pests in the U.S.A. are foreign, coming from nearly all geographic regions of the world. Another 630 foreign arthropod species are listed as lesser pests. In Florida, at least 209 species of foreign insects have been found since 1970; approximately 20 are major pests, including the Mexican fruit fly, *Anastrepha ludens*, Mediterranean fruit fly, *Ceratitis capitata*, Asian tiger mosquito, *Aedes albopictus*, citrus blackfly, *Aleurocanthus woglumi*, citrus leafminer, *Phyllocnistis citrella*, Asian citrus psylla, *Diaphorina citri,* brown citrus aphid, *Diaphorina citri*, and the melon thrips, *Thrips palmi*.

Classical Biological Control, Figure 63 **Endoparasitoid female, *Cardiochiles diaphaniae* (Hymenoptera: Braconidae), inserting an egg into the melonworm, *Hyalinata hyalinata*. This parasitoid was introduced from Colombia, South America into Puerto Rico and Florida, successfully establishing in the former location.**

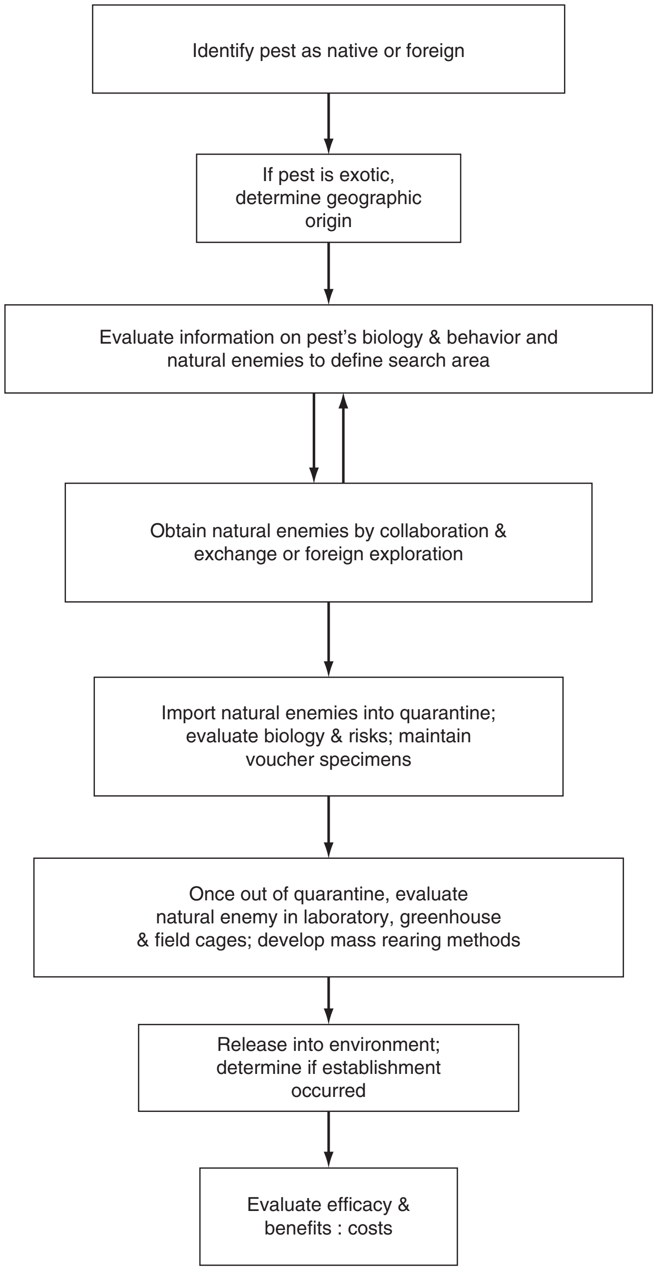
Based on past history, foreign insect and mite species will continue to immigrate to the U.S.A. at the rate of about eleven species per year. Of the eleven, seven are likely to be pests of some importance and about every third year a pest of major significance will be discovered. Assuming that few of these pests can be eradicated, classical biological control remains a potentially effective method for providing cost-effective pest suppression.

Classical biological control can be effective against different types of pests. For example, in the continental U.S.A. and Hawaii insects in the orders Lepidoptera, Coleoptera, Hemiptera, Hymenoptera, Diptera and Orthoptera have been suppressed by arthropod natural enemies in classical biological control programs. Nearly complete control was obtained in some cases, while in others only partial control was achieved. Sometimes a single natural enemy provided substantial control; in other circumstances several natural enemy species were required. Effective biological control can be achieved with a specific natural enemy in the entire geographic region that the pest inhabits in some cases, or this natural enemy may be effective only in a limited part of the new geographic distribution.

Some classical biological control programs can be accomplished without a collecting trip; if a natural enemy has been established in one region, scientists there can collect it and ship it to a new region where the pest has invaded. Once the natural enemy has been processed through quarantine, reared and released, it may provide relatively rapid and inexpensive control (Table 13).

Cooperation Between Scientists Aids in Citrus Blackfly Project

Classical biological control of the citrus blackfly, *Aleurocanthus woglumi*, in Texas and Florida provides an example of highly successful projects that benefited from cooperation between scientists in different regions. The citrus blackfly invaded Texas in the late 1960s and caused serious damage in citrus groves there. Eradication efforts began in 1971, but were unsuccessful. Joint efforts between scientists in Texas and Mexico resulted in the importation, evaluation and release of two parasitoids, *Amitus hesperidum* and *Encarsia opulenta*, that provided complete biological control of the citrus blackfly.



Classical Biological Control, Figure 64 **Classical biological control involves a series of steps before a foreign pest can be controlled by the introduction and establishment of one or more natural enemies. From start to finish, classical biological control programs require sustained funding and personnel over several years.**

The citrus blackfly subsequently invaded Florida in 1976, and huge populations developed rapidly. The honeydew produced by the blackflies caused entire citrus groves to become blackened by sooty mold growth. Again, eradication of the pest was attempted, but after $15 million dollars had been spent, the blackfly was still present and increasing its distribution.

Classical Biological Control, Table 13 **Some cases of successful biological control of pest arthropods by imported arthropod natural enemies in the Continental USA and Hawaii**

Pest[a] control	Crop or host	Principal natural enemies[a] (P) = parasitoid (Pred) = predator	Project results[b] C = complete S = substantial P = partial
Oriental mole cricket, *Gryllotalpa orientalis*	Sugarcane	*Larra polita* (P)	P
alfalfa weevil, *Hypera postica*	Alfalfa	*Bathyplectes curculionis* (P)	P-S
		Microctonus aethiops (P)	P-S
		Tetrastichus incertus (P)	P-S
American cockroach, *Periplaneta americana*	Household pest	*Ampulex compressa* (P)	P
armyworm, *Pseudaletia unipuncta*	Sugarcane	*Apanteles militaris* (P)	C
		Archytas cirphis (P)	S
Asiatic rice borer, *Chilo suppressalis*	Rice	*Amyosoma chilonis* (P)	P
		Dioctes chilonis (P)	P
		Trichogramma japonicum (P)	P
asparagus beetle, *Crioceris asparagi*	Asparagus	*Tetrastichus asparagi* (P)	P-S
Australian cockroach, *Periplaneta australasiae*	Household pest	*Ampulex compressa* (P)	P
barnacle scale, *Ceroplastes cirripediformis*	Passion fruit	*Coccidoxenus mexicanus* (P)	S
birch leaf-mining sawfly, *Heterarthrus nemoratus*	Birch, Alder	*Chrysocharis laricinellae* (P)	C
		Phanomeris phyllotomae (P)	C
black scale, *Saissetia oleae*	Citrus, Olive, Ornamentals	*Metaphycus helvolus* (P)	S
		Diversinervus elegans (P)	S
		Encyrtus infelix (P)	S
		Metaphycus luteolus (P)	S
		Coccophagus capensis (P)	P-S
		Coccophagus cowperi (P)	S
browntail moth, *Euproctis chysorrhoea*	Forest, shade trees	*Apanteles lacteicolor* (P)	S
		Townsendiellomyia nidicolor (P) and others	S ?
California red scale, *Aonidiella aurantii*	Citrus	*Aphytis lingnanensis* (P)	P
		Aphytis melinus (P)	P
		Comperiella bifasciata (P)	P
Chinese grasshopper, *Oxya chinensi*	Sugarcane	*Scelio pembertoni* (P)	S

Classical Biological Control, Table 13 Some cases of successful biological control of pest arthropods by imported arthropod natural enemies in the Continental USA and Hawaii (Continued)

Pest[a] control	Crop or host	Principal natural enemies[a] (P) = parasitoid (Pred) = predator	Project results[b] C = complete S = substantial P = partial
Chinese rose beetle, *Adoretus sinicus*	Vegetables, ornamentals	*Campsomeris marginella modesta* (P)	P
		Tiphia segregata (P)	P
citrophilus mealybug, *Pseudococcus fragilis*	Citrus, Acacia	*Coccophagus gurneyi* (P)	C
		Hungariella pretiosa (P)	C
citrus blackfly, *Aleurocanthus woglumii*	Citrus	*Amitus hesperidum* (P)	C
		Encarsia opulenta	
citrus mealybug, *Planococcus citri*	Citrus	*Cryptolaemus montrouzieri* (Pred)	P
		Leptomastidea abnormis (P)	P
citrus leafminer, *Phyllocnistis citrella*	Citrus Florida Coconut palm	*Ageniaspis citricola* (P)	S
coconut scale, *Pinnaspis buxi*		*Telsimia nitida* (Pred)	S
Comstock mealybug, *Pseudococcus comstocki*	Apple	*Allotropa burrelli* (P)	C
		Pseudaphycus malinus (P)	C
cottony cushion scale, *Icerya purchasi*	Citrus	*Cryptochetum iceryae* (P)	S-C
		Rodolia (=Vedalia) cardinalis (Pred)	C
Egyptian alfalfa weevil, *Hypera brunneipennis*	Alfalfa	*Bathyplectes curculionis* (P)	P
European corn borer, *Olstrinia nubilalis*	Corn	*Lydella thompsoni* (P)	P
		Macrocentrus gifuensis (P) and others	P
European earwig, *Forficula auricularia*	Gardens	*Bigonicheta setipennis* (P)	P
fern weevil, *Syagrius fulvitarsis*	Native Hawaiian Tree ferns	*Doryctes syagrii* (P)	P
Florida red scale, *Chrysomphalus aonidum*	Citrus	*Aphytis holoxanthus* (P)	C
gypsy moth, *Lymantria dispar*	Forest, shade trees	complex of parasitoids, predators and pathogens	P
Japanese beetle, *Popillia japonica*	Turf, pasture, fruits, ornamentals	*Tiphia vernalis* (P)	P
longtailed mealybug, *Pseudococcus adonidum*	Citrus, Avocado	*Anarhopus sydneyensis* (P)	P
		Cryptolaemus montrouzieri (Pred.)	P
		Hungariella peregrina (P)	P

Classical Biological Control, Table 13 **Some cases of successful biological control of pest arthropods by imported arthropod natural enemies in the Continental USA and Hawaii (Continued)**

Pest[a] control	Crop or host	Principal natural enemies[a] (P) = parasitoid (Pred) = predator	Project results[b] C = complete S = substantial P = partial
Mediterranean fruit fly, *Ceratitis capitata*	Fruits, Coffee	*Opius tryoni* (P)	P
		Opius fullawayi (P)	P
melon fly, *Dacus cucurbitae*	Melons Cucumber	*Opius fletcheri* (P)	P
New Guinea sugarcane weevil, *Rhabdoscelus obscurus*	Sugarcane	*Lixophaga sphenophori* (P)	S-C
nigra scale, *Saissetia nigra*	Ornamentals	*Metaphycus helvolus* (P)	S
nutgrass armyworm, *Spodoptera exempta*	Sugarcane, pasture	a complex of parasitoids	P-C
olive scale, *Parlatoria oleae*	Olive, ornamentals, deciduous fruit	*Aphytis maculicornis* (P) *Coccophagoides utilis* (P)	S S-C
oriental beetle, *Anomala orientalis*	Sugarcane	*Campsomeris marginella modesta* (P)	P-S
		Tiphia segregata (P)	
oriental fruit fly, *Dacus dorsalis*	Fruits	*Opius oophilus* (P)	S-C
		Opius vandenboschi (P)	S
oriental fruit moth, *Grapholitha molesta*	Peach, pome fruits	*Macrocentrus ancylivorus* (P)	P
oriental moth, *Cnidocampa flavescens*	Shade trees, fruit trees	*Chaetexorista javana* (P)	S
pea aphid, *Acyrthosiphon pisum*	Alfalfa	*Aphidius smithi* (P)	S
pine tip moth, *Rhyacionia frustrana bushnelli*	Pine trees	*Campoplex frustranae* (P)	P
pink sugar cane, mealybug *Trionymus sacchari*	Sugarcane	*Anagyrus saccharicola* (P)	S
purple scale, *Lepidosaphes beckii*	Citrus	*Aphytis lepidosaphes* (P)	S-C
Rhodesgrass scale, *Antonina graminis*	Orange grasses	*Neodusmetia sangwani* (P)	S
San Jose scale, *Quadraspidiotus perniciosus*	Deciduous fruit	*Prospaltella perniciosi* (P)	P

Classical Biological Control, Table 13 Some cases of successful biological control of pest arthropods by imported arthropod natural enemies in the Continental USA and Hawaii (Continued)

Pest[a] control	Crop or host	Principal natural enemies[a] (P) = parasitoid (Pred) = predator	Project results[b] C = complete S = substantial P = partial
satin moth, *Stilpnotia salicis*	Forest trees	*Apanteles solitarius* (P)	S-C
		Meteorus versicolor (P)	S-C
spotted alfalfa aphid, *Therioaphis maculata*	Alfalfa	*Aphelinus semiflavus* (P)	S
		Praon palitans (P)	S
		Trioxys utilus (P)	S
southern green stink bug, *Nezara viridula*	Vegetables, fruits, ornamentals	*Trissolcus basilis* (P)	S-C
sugarcane aphid, *Aphis sacchari*	Sugarcane	complex of parasitoids and predators	S
sugarcane borer, *Diatraea saccharalis*	Sugarcane	*Lixophaga diatraeae* (P)	P
		Agathis stigmaterus (P)	P
sugarcane leafhopper, *Perkinsiella saccharacida*	Sugarcane and others	*Tytthus mundulus* (Pred)	C
sweet potato leaf miner, *Bedellia orchilella*	Sweet potato	*Apanteles bedelliae* (P)	P-C
taro leafhopper, *Tarophagus proserpina*	Taro	*Cyrtorhinus fulvus* (Pred)	S
torpedo bug planthopper, *Siphanta acuta*	Coffee, Mango, Citrus	*Aphanomerus pusillus* (P)	S-C
walnut aphid, *Chromaphis juglandicola*	Walnuts	*Trioxys pallidus* (P)	P-C
western grape leaf skeletonizer, *Harrisina brillians*	Grape	*Apanteles harrisinae* (P)	S
		Sturmia harrisinae (P)	
wooly apple aphid, *Eriosoma lanigerum*	Apple	*Aphelinus mali* (P)	S-C
wooly whitefly, *Aleurothrixus floccosus*	Citrus	*Amitus spiniferus* (P)	S-C
		Eretmocerus paulistus (P)	C
yellow scale, *Aonidiella citrina*	Citrus	*Comperiella bifasciata* (P)	S-C

[a]Not all examples are cited; success ratings and scientific names of pests and natural enemies vary in different lists.
[b]Complete successes (C) refer to complete biological control obtained and maintained against a pest over an extensive area so that pesticide applications rarely are necessary. Substantial (S) successes include cases in which insecticidal control is sometimes required. Partial successes (P) are those in which chemical controls are applied, but the intervals between applications or lengthened or the outbreaks occur less often. ? refers to situations in which the results are unknown or controversial.

As the result of cooperation between scientists from Texas and Mexico, *A. hesperidum*, *E. opulenta*, *E. clypealis* and *E. smithi* were introduced into Florida in 1976. Both *A. hesperidum* and *E. opulenta* became established. *Amitus hesperidum* provided rapid control of blackfly populations, but *E. opulenta* eventually replaced *A. hesperidum* as the dominant parasitoid after citrus blackfly populations had been reduced. Both parasitoids are given credit for providing complete biological control of the blackfly in Florida by 1981. The program cost approximately $US 2.2 million dollars, but the benefits continue to accrue, and were estimated to be $9.3 million in 1980 alone.

Effective classical biological control depends upon the establishment of one or more foreign natural enemies in a new environment. Establishment of natural enemies in new environments is not guaranteed, with estimates of successful establishment ranging from 16 to 34%. There is intense interest in learning how to increase establishment rates and the use of climate-matching computer programs may allow scientists to increase the establishment rate. After release, the introduced natural enemy must find adequate hosts and other resources as well as suitable climatic conditions in the new environment. Natural enemies must be released in adequate numbers, in a healthy condition, at an appropriate time, and in the presence of suitable hosts or prey if establishment is to succeed.

In some cases, different populations (biotypes) of a particular species have different biological attributes that make them more or less likely to establish and be effective in the new environment. For example, a parasitoid called *Trioxys pallidus* originally was collected in France and released in California to control the walnut aphid *Chromaphis juglandicola*. The French biotype established, but was only effective in the cooler, more humid coastal areas of California. A biotype of *T. pallidus* from Iran was subsequently established and provided highly effective control of the walnut aphid in the hot, dry Central Valley of California.

Although classical biological control can yield complete and lasting pest population suppression in a many situations, many past efforts have been only casual or have involved use of an unsuitable natural enemy. In general, relatively little classical biological control has been directed against pests of range, forage, grain crops or row crops. For example, of 110 pest species under partial to complete control by classical biological control, only 13 involved pests of row crops. This relatively poor record has been attributed to the instability of the row crop environment. Row crops persist only for weeks or months, during which time the natural enemy must discover and move into the crop, find, attack, and build up numbers on the pest, then be subjected to abrupt disruption at the end of the crop season.

A large number (ca. 40%) of the pests targeted in classical biological control programs have been scales (Hemiptera), and about 20% have been Lepidoptera, Coleoptera, or Hemiptera other than coccids. Many of the successes have been achieved in warmer climates, particularly in Hawaii and California, although it is likely that these successes are due to the extensive efforts employed in classical biological control. Other trends include an emphasis on employing parasitoids rather than predators, with a majority of successful classical biological control programs involving highly host-specific natural enemies. Establishment of host-specific parasitoids is considered to be lower risk than release of natural enemies with a broad host or prey range. Such host specificity is important in alleviating concerns about unintended effects of these natural enemies on nontarget native species.

Successful classical biological control is dependent on two critical elements: (i) establishing the natural enemy in the new environment, and (ii) the efficacy of the natural enemy in the new environment. Usually, a particular pest will have more natural enemies attacking it than are feasible to evaluate and release. Some guidelines have been suggested for choosing between different natural enemy species to evaluate and release.

Potentially effective natural enemies generally exhibit as many of the following attributes as possible:

- Fitness and adaptability in the target environment
- High searching capacity for the target species
- High reproductive rate relative to that of the host or prey
- Synchronization with the host or prey and its habitat
- Host or prey specificity
- An ability to increase its effectiveness as the host or prey density increases (density-dependent response to the pest)

A natural enemy that behaves in a density-dependent manner can respond to changes in the population density of its host or prey, leading to an increasing percentage of kill with increasing host or prey density and a decreasing percentage of kill with decreasing host or prey density. It is difficult to document experimentally that, in fact, a natural enemy is behaving in a density-dependent manner because it is likely that most natural enemy-pest interactions exhibit a time lag, and thus are behaving in a delayed density-dependent manner. Delayed density dependence occurs when the response of natural enemies to the pest population is delayed for some reason.

In many situations classical biological control programs result in substantial pest population reductions. However, some large, lengthy, and expensive projects have been unsuccessful for unknown reasons. As an example, a classical biological control project directed against the gypsy moth, *Lymantria dispar*, has been slow to result in adequate pest population suppression despite extensive and long-term efforts involving the importation and release of predators, parasitoids and pathogens. Gypsy moth populations are preyed on by native natural enemies, including vertebrate predators. Despite the effects of native and imported natural enemies, suppression of gypsy moth populations in North America to levels that are considered acceptable has been slow in coming.

Classical Biological Control and the Gypsy Moth

The gypsy moth is an important forest defoliator that was introduced into North America in 1869. Large classical biological control projects were initiated during three different intervals, with the first beginning in 1905 after efforts to eradicate the gypsy moth were abandoned. That project continued through 1914 and the second ran from 1922 until 1933. Efforts intensified again in 1963.

During these three intervals, more than 40 species of parasitoids were introduced into North America against the gypsy moth; ten established, including two that attack eggs, two that attack small larvae, four that attack larger larvae, and two that attack pupae. In addition, the predaceous ground beetle, *Calosoma sycophanta*, and a nuclear polyhedrosis virus (a virus specific to the gypsy moth) were established.

Despite the effects of these parasitoids, predators and pathogens, and the depredations of a variety of native natural enemies such as mice, shrews, birds, spiders, stink bugs, hornets, preying mantids, ants and bacterial and fungal diseases, the gypsy moth continued to expand its range in North America and cause periodic defoliations over thousands of acres of forest and shade trees.

Recently, a fungus native to Japan, *Entomophaga maimaiga*, was found causing dramatic and unexpectedly high levels of mortality to gypsy moth larvae in the northeastern United States. The mortality was unanticipated because the fungus is believed to have been introduced into North America nearly 80 years ago, but was not discovered until 1989. No one knows why it apparently was ineffective until recently; some speculate that the fungus was introduced recently, although the introduction was not conducted with an established program and did not go through risk evaluation.

Despite the pleasant surprise of discovering another microbial disease agent, it is unclear whether *E. maimaiga*, in combination with the other exotic and native natural enemies, can provide adequate suppression of gypsy moth populations in North America. Gypsy moth populations apparently are influenced by both biotic and abiotic factors, including vertebrate and invertebrate natural enemies, weather, host tree species, foliage chemistry and plant quality. Because gypsy moth populations synchronously reach outbreak densities over large areas, it is possible that a combination of weather and other mortality factors is responsible for the onset of periodic outbreaks. There is considerable debate over the degree and type of control exerted by various vertebrate and invertebrate natural enemies, and it is unclear whether establishment of additional foreign natural enemies would contribute significantly to suppressing the still-expanding distribution of the gypsy moth in North America.

Even in southern Europe, where an extensive array of natural enemies occur and the gypsy moth is a native, gypsy moth populations reach damaging levels periodically. Thus, the gypsy moth appears to represent a foreign pest that may be managed only by a multi-tactic pest management program.

Sometimes, classical biological control programs can reduce the pest population to a level that can be lived with over a very large area. The cassava mealybug classical biological control program is one of the most successful and large scale programs ever conducted. This program has gone through all the steps involved, including an economic analysis of the costs and benefits.

Continent-Wide Control of the Cassava Mealybug in Africa

Cassava, *Manihot esculenta*, was brought to Africa about 300 years ago from South America. Cassava serves as a subsistence crop for 200 million people because it is hardy, and adapted to a variety of farming systems and to sub-Saharan climatic conditions. Cassava is estimated to provide up to 50% of the daily caloric intake of 200 million people in Africa and, because cassava roots can remain in the ground for up to 2 years, provides an even higher proportion of the diet when other crops fail. Cassava is an insurance crop against famine.

In the early 1970s, the cassava mealybug *Phenacoccus manihoti* was accidentally introduced into Africa, probably because quarantines were ignored and planting material was introduced illegally. The cassava mealybug spread rapidly across much of the sub-Saharan region of Africa and caused devastating losses (10–100%) by the early 1980s, estimated to be at least $2 billion per year.

Chemical control was not ecologically, economically, or logistically feasible. Famine was possible if control was not achieved. A breeding program was initiated to develop resistant varieties, but this was recognized to be a potential solution that would take at least 10–20 years.

At the same time as the breeding program was initiated, a classical biological control program was begun. Surveys in Central and South America were conducted for natural enemies of the cassava mealybug and an encyrtid parasitoid *Apoanagyrus lopezi* was introduced, reared and released by the Africa-Wide Biological Control Programme of the International Institute for Tropical Agriculture and by national agencies of many African countries. Subsequent to its first release in 1981 and 1982, *A. lopezi* has established in at least 19 countries and is providing effective control of the mealybug throughout most of its distribution in Africa.

The economic benefits of this classical biological control program were estimated from 1977 through 2002, using the following very conservative assumptions: that cassava has a value of US $60/ton; production would remain stable at 1980 levels; an average yield loss of 20% would occur due to mealybug; and *A. lopezi* would reduce losses due to mealybugs by only 60%; by 2002 other control methods (plant resistance, integrated pest management programs) would provide effective control.

An estimated $2,205,000,000 are estimated to have been saved by the introduction of *A. lopezi*, as compared to the classical biological control program which cost $14,800,000. This produced a benefit to cost ratio of 149:1, which is unusually high. The benefits are so high because the program was developed quickly, was unusually effective across a wide geographic region, and cassava is a very important crop. This estimate demonstrates how well classical biological control can work and has encouraged its use against another pest of cassava introduced into Africa, the cassava green mite.

Conservation of Natural Enemies

Conservation of natural enemies involves protecting and maintaining natural enemy populations. Conservation is crucial if either native or introduced natural enemies are to be maintained in agricultural crops. Conservation most often involves modifying pesticide applications.

As a general principle, pesticide applications should be made only when pest populations exceed specified levels and when no other control tactic is available. In some cases, changing the active ingredients, rates, formulations, timing, and/or location of pesticide applications can allow natural enemies to remain effective. Maintaining untreated refuges also protects natural enemy populations; for example, alternate rows are treated with pesticides so that the lady beetle *Stethorus punctum* can survive to control European red mites, *Panonychus ulmi*, in Pennsylvania apple orchards.

Effective Natural Enemies

The effectiveness of natural enemies in controlling pest populations depends on the characteristics of the specific system. However, as a general rule, the most effective natural enemies:

- Exhibit a high degree of prey or host specificity
- Have a high relative reproductive rate compared to their prey or host, and
- Exhibit a tolerance of abiotic factors similar to that of the host or prey

The host or prey searching ability of arthropod natural enemies has been studied rarely in the field. What we know about their behavior usually comes from observations in the laboratory or other artificial situations. Arthropod natural enemies respond to physical and chemical cues from the host or prey itself, from its host plant, and from an interaction of the two.

Prey/host selection has been divided into four steps: (i) habitat selection, seeking a particular environment where an appropriate host plant occurs; (ii) prey or host finding, identifying prey or host individuals on the plant; (iii) prey or host acceptance, examining individual hosts or prey in the environment to determine whether to feed on or parasitize it; and (iv) prey or host suitability, the ability of the parasitoid to develop on or within the host or the predator to feed on the prey.

Biological Control in Relation to Other Pest Management Approaches

The goal in pest management is to reduce a pest's density to a lower density than would otherwise occur. Fluctuations in density are expected to occur over time, which may be either small or large. Ideally, the average density remains below the level that causes economic injury. However, the degree of biological control achieved is not always sufficient to provide economic pest suppression.

The term strategy describes the long-term plan or theoretical framework of an operation. The term tactics describes the methods used to attain or fulfill that strategy. There are several strategies for managing pests, including: exclusion or quarantine of foreign pests, eradication, suppression of pest populations by plant resistance, biological control or chemical control, and integrated pest management (IPM). Within each strategy, there are various methods or tactics employed.

Exclusion or quarantines can prevent or delay the introduction of foreign pests into a new geographic region. Eradication of foreign pests by means of pesticide applications, release of sterile males, or removal of suitable host plants is feasible in some circumstances. Plant resistance can provide substantial to partial suppression of many insect or mite pests, but resistant plant varieties are not available for all pests. Furthermore, insects and mites can evolve resistance to plant resistance mechanisms. Thus, each strategy is valuable but may be limited in scope.

Classical biological control can provide effective suppression of many invasive insects, mites and weeds. However, it is rare that all invasive pests can be controlled by the importation and release of natural enemies in classical biological control programs. Nor is chemical control able to suppress all pests because resistance to pesticides and concerns about damage to the environment and health hazards are increasing. As a result, integrated pest management is an increasingly important approach; it involves deploying several approaches, perhaps including the use of transgenic (pest resistant) plants, releases of sterile male insects, cultural controls, and release of pheromones (chemicals used to communicate between individuals within a species, such as mating pheromones), in a harmonious manner to control pests.

Classical biological control should always be considered when a new pest invades because classical biological control generally is compatible with nonchemical management tactics in IPM such as plant resistance, cultural controls, and a variety of biorational methods. Biorational pest management methods include tactics such as pest mating disruption by release of pheromones, disruption of normal development of pests after application of insect hormones, or applications of antifeedant materials. Techniques that are compatible with the use of biological control, or have little impact on natural enemies, are often considered biorational.

Under many circumstances, pest managers will need to employ multiple tactics to achieve economic suppression of all the pest populations. Tactics used in IPM programs include plant resistance, biological control, chemical control, cultural controls, or biorational controls. How should the pest manager prioritize the pest management tactics to be evaluated and employed? One principle should be that all tactics considered should be examined for their effects on natural enemies.

The conceptual basis for organizing an IPM program with biological control as a key component was spelled out over 45 years ago. That project, designed for California alfalfa, demonstrates some of the concepts and complexities of creating such programs. The spotted alfalfa aphid, *Therioaphis maculata*, invaded California and was detected in 1954. The aphid spread rapidly throughout the state, causing millions of dollars of crop loss damage. Shortly after the aphid became established, research was initiated to find or develop varieties of alfalfa resistant to the aphids; to develop a classical biological control project; and to identify pesticides that would control this pest at a reasonable cost. An important component of the IPM program included the introduction and establishment of the spotted alfalfa aphid parasitoids *Praon pallitans* and *Trioxys utilis* in a classical biological control project. However, classical biological control was combined with other tactics to achieve effective pest management in alfalfa.

A variety of alfalfa was identified that was able to tolerate feeding by the aphid and several pesticides were found that controlled the aphids. Analysis of the effects of insecticide treatments on a complex of native predators, as well as the introduced parasitoids *Praon pallitans* and *Trioxys* *utilis*, indicated that parasitoids of the spotted alfalfa aphid could survive many pesticides if the parasitoids were in the pupal stage when treated. Importantly, because the aphid was not the only alfalfa pest and the alfalfa caterpillar *Colias eurytheme* had to be controlled as well, a polyhedrosis virus was found to be effective in controlling the alfalfa caterpillar either alone or in combination with a selective chemical insecticide. Monitoring was recognized to be a key component in the program. Population levels of the alfalfa caterpillar and its parasitoid, *Apanteles medicaginis*, were monitored regularly and chemical control was recommended only if the pest: parasitoid ratio was unfavorable. Thus, both the aphid and the caterpillar could be controlled without disrupting control of the aphid by natural enemies.

This project laid out a number of concepts that remain central to designing an effective IPM program in which biological control is a central component. This study defined integrated control as "…applied pest control which combines and integrates biological and chemical control…," and emphasized that chemical control should be used only as necessary and in a manner which is least disruptive to biological control, cautioning that when "…chemicals are used, the damage from the pest species must be sufficiently great to cover not only the cost of the insecticidal treatment but also the possible deleterious effects, such as the harmful influence of the chemical on the ecosystem," thereby introducing economic and ecological considerations into the pest management equation. Thus, biological control and chemical control were shown to be potentially complementary or, with adequate understanding, made to augment one another.

This project also articulated an important principle: the ideal pest suppression tactic is not one that eliminates all individuals of the pest while leaving all of the natural enemies. Pest elimination would force the host- or prey-specific natural enemies to leave the treated area or starve. The goal should be to suppress pest populations rather than eliminate them.

Evaluating Classical Biological Control Programs

The degree and quality of evaluations of classical biological control programs vary dramatically. In some cases, detailed documentation has been provided (for example, the cassava mealybug project), but in other cases few records were kept.

Classical biological control programs can be difficult to evaluate; sometimes the results are so spectacular that assessment appears to be unnecessary. At the least, however, assessments of pest status "before" and "after" need to be made, although such evaluations provide only circumstantial evidence that natural enemies are effective.

Designing controlled experiments to document the effectiveness of classical biological control is particularly difficult when there are no untreated plots because natural enemies have dispersed rapidly. Also, low pest populations are difficult to monitor. When no reduction in pest populations occurs, it is easy to assume that the natural enemies were ineffective, although the natural enemies may, in fact, be providing some degree of suppression. Partial suppression is even more difficult to evaluate; natural enemies often behave differently at high and low host or prey densities.

Identifying the reasons for changes in pest population density is difficult because natural enemies are but one of the mortality factors influencing populations of pests. Both biotic and abiotic factors influence pests and in many crops several to many species of natural enemies influence pest populations, but unraveling the impact of each is difficult. Even the simplest ecosystem is sufficiently complicated that population models developed to describe them are not easily tested in the field.

Two questions are often asked when evaluating natural enemies: (i) are natural enemies controlling a pest, and (ii) how is the control achieved? Three major approaches are employed to answer the first question. These may be used either singly or in combination. Research efforts to answer the second question are more complex.

Exclude, Eliminate, or Reduce Natural Enemies

Several exclusion techniques have been employed to demonstrate that one or more natural enemies can control a pest population. A branch, tree, or other whole plant can be isolated to prevent movement of natural enemies into the system. Isolation can be achieved by hand picking, providing sticky barriers for nonflying natural enemies, or by cages. The size of mesh on cages can be modified to exclude different natural enemies based on size. Evaluation of natural enemies by exclusion has been most useful when combined with other evaluation methods such as behavioral observations or population sampling.

Unfortunately, none of these techniques is completely satisfactory. Cages may alter the microclimate (light intensity, temperature, humidity and wind speed) and this change can influence the effects of the natural enemies. For example, cooler temperatures can reduce the growth and activity rates of pests or natural enemies. Few have the time and patience to hand pick natural enemies, and the area which can be manipulated by this method is relatively small. Most natural enemies are able to fly over sticky barriers. It is usually difficult to identify which members of the predator or parasitoid complex are essential for the suppression of the pest population unless the complex consists of one or a few easily segregated species.

Natural enemies can be eliminated by application of pesticides that are nontoxic to the pest and, if an outbreak occurs subsequently the natural enemy or natural enemies can be assumed to have been controlling the pest. This approach was accidentally employed when effective control of the cottony cushion scale by the Vedalia beetle was disrupted by application of DDT; this pest has been under excellent control for nearly a century and the control agents have been effective when introduced elsewhere. However, relatively few pesticides are nontoxic to pests, and subtle sublethal effects can alter the pest's response.

Natural enemies can be added to one plot and not to another and changes in pest density in the release site can be attributed to the effects of the natural enemies. Likewise, prey or hosts can be added to a field plot and the efficiency of natural enemies can be estimated by changes in pest density. Direct observation of predation is useful in identifying prey and predator species; observations reveal where and when a predator searches, which is useful in designing a sampling scheme. Direct observation requires no manipulation of the environment and pests or natural enemies can be added or removed to determine the responses of the natural enemy to changes in pest density. Unfortunately, this method is time consuming and difficult to employ if the natural enemy is cryptic, active only at night, or easily disturbed.

A variety of biochemical methods also have been employed to determine whether predators are preying on specific prey, including the enzyme-linked immunosorbent assay (ELISA), precipitin tests, polyacrylamide gradient gel electrophoresis, and prey marking by labels.

Correlation

Another approach is to correlate the damage exerted by the pest, or the crop yield, with natural enemy population levels. If high natural enemy populations are correlated with low damage levels or high crop yields, the natural enemies may be providing effective pest suppression. However, correlation is not causation and other changes in crop management practices such as crop cultivar or cultural methods may influence the amount of damage inflicted or the amount of crop yield. Ideally, blocks with the natural enemies of interest are compared to blocks lacking them. However, if the natural enemies are highly mobile, such comparisons may be possible only for a very short period of time.

Modeling

There are many kinds of models (including mathematical, statistical, simulation, and analytic), and many uses to which models can be put. Computer models have been developed which attempt to forecast and understand pest and natural enemy populations. Some models include crop-pest-natural enemy interactions with the goal of understanding the role of natural enemies in regulating pest densities.

Risk Assessments

Classical biological control in recent years is receiving increased scrutiny regarding possible environmental risks associated with the importation and release of foreign natural enemies. Claims have been made that parasitoids and predators released into Hawaii have had a detrimental effect on native butterflies and moths. Unfortunately, it is not clear that the observed changes in native insect populations can be attributed to classical biological control because the critics failed to discriminate between the effects of habitat destruction, pesticide use, and the possible negative effects of released arthropod natural enemies. The release of the tachinid parasitoid *Compsilura concinnata* in the classical biological control program directed against the gypsy moth is thought to have had negative effects on native populations of Lepidoptera, including the beautiful native silk moths. Because *C. concinnata* is known to attack over 200 species of Lepidoptera, it is unlikely to be considered suitable for release under current risk assessments in classical biological control programs.

Practitioners of biological control are convinced that classical biological control of arthropod pests or weeds is environmentally safe and low risk if carried out by trained biological control specialists. Concerns about preservation of native flora and fauna have led some to recommend restrictions on the importation of all foreign species.

During the debate on the potential negative effects of classical biological control, it should be remembered that the use of natural enemies in classical biological control programs directed against invasive insect, mite and weed pests could result in reduced pesticide use, reduced ground water contamination by pesticides, reduced negative effects on nontarget organisms from pesticides, reduced pesticide residues on food, reduced crop production costs, improved control of pests, and increased farm worker safety due to reduced pesticide use.

References

Clausen CP (1978) Introduced parasites and predators of arthropod pests and weeds: a world review. Agricultural handbook 480. U.S. Department of Agriculture, Washington, DC

DeBach P (ed) (1964) Biological control of insect pests and weeds. Reinhold, New York, NY

DeBach P, Rosen D (1991) Biological control by natural enemies, 2nd edn. Cambridge University Press, Cambridge, UK

Frank JH, McCoy ED (1992) The immigration of insects to Florida, with a tabulation of records published since 1970. Fla Entomol 75:1–28

Herren HR, Neuenschwander P (1991) Biological control of cassava pests in Africa. Ann Rev Entomol 36:257–283

Huffaker CB (ed) (1971) Biological control. Plenum Press, New York, NY

Sailer RI (1983) History of insect introductions. In: Wilson CL, Graham CL (eds) Exotic plant pests and North American agriculture. Academic Press, New York, NY, pp 15–38

van Driesche RG, Bellows TS Jr (1996) Biological control. Chapman & Hall, New York, NY

Classification

In sampling, this refers to a sampling plan that classifies population density as being either above or below some predetermined level (e.g., economic threshold), or belonging within some density class (e.g., low, medium, high). Commonly used in pest management decision making application (contrast with estimation).

In systematics, a natural arrangement of taxa that organizes like organisms into categories. Membership in groups traditionally has been based on structural features, but also biological features, and increasingly on molecular features. Sometimes classification is considered "artificial," because the classification is based on features that are convenient to see or to score, but have no phylogenetic significance. In contrast, "natural" classifications systems rely on features that are shared due to common evolutionary descent. The principal categories used in classification of insects, in descending (most inclusive to least) order, are:

- Phylum
  - Class
    - Subclass
      - Infraclass
        - Series
          - Superorder
            - Order
              - Suborder
                - Infraorder
                  - Family
                    - Subfamily
                      - Tribe
                        - Genus
                          - Species

In practice, all these categories are not often used; the most commonly used taxa are class, order, family, genus and species. Other categories also exist; for example, the class Insecta is sometimes placed in the superclass Hexapoda and the superphylum Ecdysozoa, and related families are often grouped into superfamilies. The subclass Pterygota is sometimes divided into two divisions, consisting of the hemimetabolous orders and the holometabolous orders. Possibly the only level that can be assessed objectively is the species. Species are grouped into genera, genera into families, and so forth, but taxonomists differ in the importance of characters used to cluster the taxa, so different arrangements are possible. The names of most orders end in – ptera; of families in – idea; of subfamilies in -inae, and of tribes in – ini.

The classification of insects is often debated, but a common arrangement and the derivation (from Greek or Latin) for the class Insecta follows. The order names generally are logical if you consider the appearance of the insects in that group. Perhaps the only obscure name is Zygentoma, which was introduced by Carl Börner, in 1904. He viewed these insects to be an evolutionary "bridge" or connection between the apterygote (wingless) and pterygote (winged) insects, hence the name.

Subclass Apterygota: Greek *a* (without) = *pteron* (wings)

Order Archeognatha: Greek *archaios* (primitive) + *gnathos* (jaw)

Order Zygentoma: Greek *zyg* (bridge) + *entoma* (insect)

Subclass Pterygota: Greek *pteron* (wing)

Infraclass Paleoptera: Greek *palaios* (ancient) + *pteron* (wing)

Order Ephemeroptera: Greek *ephermeros* (short-lived) + *pteron* (wing)

Order Odonata: Greek *odon* (tooth) (referring to the mandibles)

Infraclass Neoptera: Greek *neos* (new) + *pteron* (wing)

Series Exopterygota: Greek *exo* (outside) + *pteron* (wing)

Superorder Plecopteroidea

Order Plecoptera: Greek *plecos* (plaited) + *pteron* (wing)

Order Embiidina: Latin *embios* (lively)

Superorder Orthopteroidea

Order Phasmatodea: Latin *phasma* (apparition or specter)

Order Mantodea: Greek *mantos* (soothsayer)

Order Mantophasmatodea: from Mantodea + Phasmatodea

Order Blattodea: Latin *blatta* (cockroach)

Order Isoptera: Greek *iso* (equal) + *pteron* (wing)

Order Grylloblattodea: Latin *gryllus* (cricket) + *blatta* (cockroach)

Order Orthoptera: Greek *orthos* (straight) + *pteron* (wing)

Order Dermaptera: Greek *derma* (skin) + *pteron* (wing)

Order Zoraptera: Greek *zoros* (pure) + *a* (without) + *pteron* (wing)

Superorder Hemipteroidea

Order Psocoptera: Latin *psocos* (book louse) + Greek *pteron* (wing)

Order Hemiptera: Greek *hemi* (half) + *pteron* (wing)

Order Thysanoptera: Greek *thysanos* (fringed) + *pteron* (wing)

Order Phthiraptera: Greek *phtheir* (louse) + *a* (without) + *pteron* (wing)

Series Endopterygota: Greek *endo* (inside) + *pteron* (wing)

Superorder Neuropteroidea

Order Megaloptera: Greek *megalo* (large) + *pteron* (wing)

Order: Raphidioptera: Greek *raphio* (a needle; referring to the ovipositor) + *pteron* (wing)

Order Neuroptera: Greek *neuron* (nerve) + *pteron* (wing)

Superorder Coleopteroidea

Order Coleoptera: Greek *coleos* (sheath) + *pteron* (wing)

Order Strepsiptera: Greek *strepti* (twisted) + *pteron* (wing)

Superorder Panorpoidea

Order Mecoptera: Greek *mecos* (length) + *pteron* (wing)

Order Trichoptera: Greek *trichos* (hair) + *pteron* (wing)

Order Lepidoptera: Greek *lepido* (scale) + *pteron* (wing)

Order Diptera: Greek *di* (two) + *pteron* (wing)

Order Siphonaptera: Greek *siphon* (tube) + *a* (without) + *pteron* (wing)

Superorder Hymenopteroidea

Order Hymenoptera: Greek *hymen* (membrane) + *pteron* (wing)

Variations on this System of Classification

Among the principal variations on this system of classification are the grouping of Phasmatodea and Mantodea into a single order, Dictyoptera; the grouping of Megaloptera, Raphidioptera and Neuroptera into Neuroptera; the splitting of Hemiptera into two orders, Hemiptera and Homoptera; the grouping of Mallophaga and Siphunculata into Phthiraptera; and the grouping of Strepsiptera with Coleoptera. Also, some additional groups of arthropods such as the Collembola, Diplura and Protura are sometimes considered to be insects. Classification systems (Figs. 65 and 66) are based on morphological similarities (phenetics) and evolutionary relatedness (phylogenetics), as well as comparative anatomy, physiology, and behavior. Increasingly, the genetic component of insects is being used to establish relatedness.

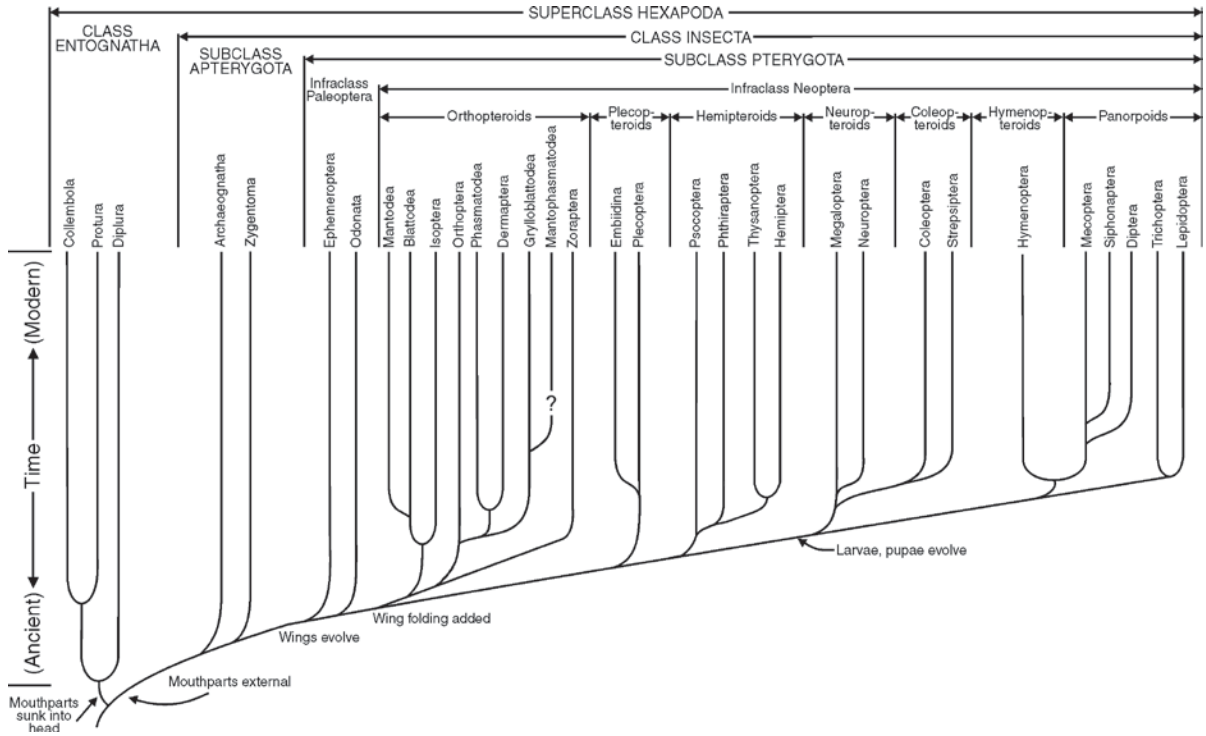
Characteristics of the Major Groups

The major groups are characterized by a number of fundamental differences. The members of subclass Apterygota lack wings, possess rudimentary abdominal appendages, practice indirect insemination, and molt throughout their life, whereas the subclass Pterygota possess wings (or did at one time), generally lack abdominal appendages, practice direct insemination via copulation, and molt only until sexual maturity is attained.

Infraclass Paleoptera consists of primitive insects. The wings cannot be flexed over the back when the insect is at rest. The immature stages of existing paleopterans live in aquatic habitats. The Neoptera, on the other hand, are a diverse group of relatively modern insects. They can flex their wings over the body. They display development in which the immatures are similar to the mature form (Exopterygota), or the immatures differ markedly in appearance from the adults (Endopterygota).

Superorder Plecopteroidea, consisting of Plecoptera and Embiidina, is closely related to superorder Orthopteroidea. Both suborders have chewing mouthparts; complex wing venation, with the hindwings larger than the forewings; and cerci. They differ, however, in that the forewings are not thickened, and external male genitalia are lacking.

The members of superorder Orthopteroidea (Polyneoptera) have chewing mouthparts, long antennae, complex wing venation, large hindwings, thickened forewings, large cerci, and nymphs with ocelli. Several orders are considered to be orthopteroids: Phasmatodea, Mantodea,



Classification, Figure 65 **Diagram of the possible phylogeny of the hexapods, showing relationships among the major groups (principally insect orders) and the temporal occurrence of major evolutionary steps in insect structure and development.**

Mantophasmatodea, Blattodea, Isoptera, Grylloblattodea, Orthoptera, Dermaptera, and Zoraptera. In many older classification systems, they were all considered to be part of the order Orthoptera. This is a relatively primitive group.

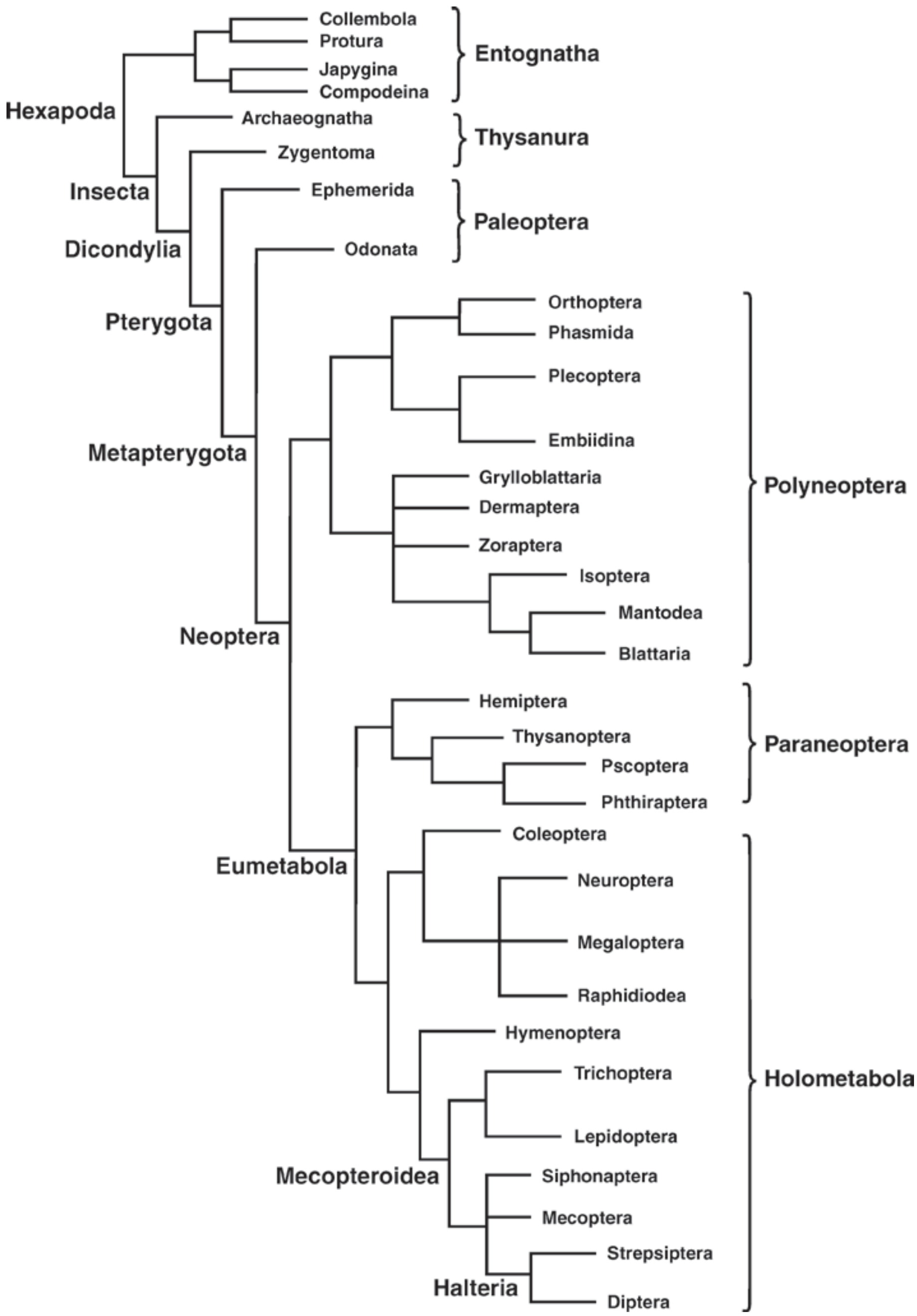
Superorder Hemipteroidea (Paraneoptera) is also a large group, consisting of the orders Psocoptera, Hemiptera, Thysanoptera, and Phthiraptera. Unlike the Orthopteroidea, they lack cerci, and have stylet-like structures associated with their mouthparts (though in Psocoptera, chewing mouthparts are preserved). Some groups are well designed for piercing the host and sucking liquids. Though this and the preceding superorders are considered to be hemimetabolous, a few members of Thysanoptera and Hemiptera are physiologically holometabolous.

The superorder Neuropteroidea is holometabolous, and consists of the orders Megaloptera, Raphidioptera, and Neuroptera. Both aquatic and terrestrial forms occur in this superorder. The wings tend to bear numerous cells.

Superorder Coleopteroidea consists of the orders Coleoptera and Strepsiptera. They are similar in that the metathorax is developed for flight, and bears functional wings. The forewings of the Coleoptera are reduced to hard wing coverings, and even more reduced in the Strepsiptera, to small club-like appendages. They contrast strongly in that the Coleoptera is the largest order, and Strepsiptera one of the smaller orders.

Panorpoidea is another large superorder, consisting of the orders Mecoptera, Trichoptera, Lepidoptera, Diptera, and Siphonaptera. They share few common characters, however, such as a tendency for a reduced meso- and metasternum, the media and cubitus of the hind wing arise from a common stem, and the terminal abdominal segments tend to function as an ovipositor.

Lastly, the superorder Hymenopteroidea consists only of the order Hymenoptera, though



Classification, Figure 66 A recent assessment of phylogenetic relationships within Hexapoda based on both morphological and some molecular characters (adapted from Wheeler et al., 2001, Cladistics 17:113–169).

this is a very divergent, complex group. They bear numerous Malpighian tubules, unlike all other endopterygotes, which have only four to six tubules. Also, their wing venation is often greatly reduced.

► Each Individual Order
► Phylum
► Orders
► Sampling Arthropods

Clastopteridae

A family of bugs (order Hemiptera, suborder Cicadomorpha).

► Bugs

Claustral Colony Founding

A process of colony founding in which the initial reproductives seal themselves of in cells, and proceed to rear the initial brood using nutrients obtained from their own tissues.

Clavate

Thickening toward the tip. This term is usually used to describe antennae with expanded tips.

► Antennae of Hexapods

Clavate Larva

This term is sometimes used to describe a larva with an enlarged thoracic region, particularly buprestid, cerambycid, and eucnemid larvae.

Clavola

The antenna beyond the pedicel. The flagellum.

► Antennae of Hexapods

Clavus

This term has several meanings, including the angular hind margin of the hemelytra in Hemiptera (Fig. 67); the club of an antenna; the knob at the end of the stigmal or radial wing veins in Hymenoptera; and the rounded or finger-like process in the male genitalia of Lepidoptera.

Claw

A hollow, sharp, curved organ, located at the tip of the tarsus (foot).

► Legs of Hexapods

Clearwing Moths (Lepidoptera: Sesiidae)

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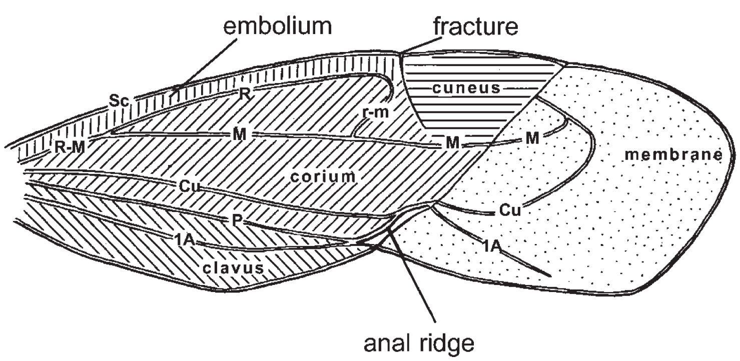
Adults of the family Sesiidae(formerly Aegeriidae) are called clearwing mothsbecause a part of the wings, especially the hindwings, lacks overlapping scales and is therefore transparent. The body typically is dark-colored, but most species have contrasting yellow, orange, or reddish bands or markings on the abdomen, legs, or both. Males and females often differ in coloration, and in some



Clavus, Figure 67 Front wing of a bug (Hemiptera: suborder Heteroptera), thickened basally and membranous distally.

cases the amount of clear area in the wings. Virtually all species are day-flying. The moths may be seen sipping nectar from flowers or resting on foliage on sunny days. Many adult sesiids bear a striking resemblance to wasps, especially paper wasps (*Polistes* spp.) or yellow jackets. Being moths, they cannot sting; however, this mimicry doubtless discourages insectivorous birds and other vertebrate predators. The moths' hovering flight and tendency for some species to move the abdomen in a wasp-like posture contributes to the deception.

Sesiid larvae tunnel in living branches, trunks, root collars, or roots of trees and shrubs, and in canes and vines of woody and some herbaceous plants. Granular, sawdust-like frass usually is expelled from the site of attack. Damage to the inner bark and cambium can contribute to the decline and death of host plants. Some species are economically important pests of forest and landscape trees, or fruit crops. The squash vine borer, *Melittia cucurbitae*, is a pest of squash, gourds, and pumpkins. A few species induce plant galls, or feed as inquilines within galls of other insects. Most clearwing species exploit only a few closely-related species of trees, shrubs, or vines as hosts. A few, such as the dogwood borer, *Synanthedon scitula*, attack a broad range of plants.

The family Sesiidae belongs to the order Lepidoptera, suborder Ditrysia (Frenatae), and superfamily Sesioidea. Clearwing moths have a world wide distribution with about 170 genera containing more than 1000 described species. Nineteen genera and 155 species of sesiids are known from North America, including such important pests as the raspberry crown borer, *Pennisetia marginata*; grape root borer, *Vitacea polistiformis*; squash vine borer, *Melittia cucurbitae*; lesser peachtree borer, *Synanthedon pictipes*; peachtree borer, *Synanthedon exitiosa*; dogwood borer, *Synanthedonscitula*; and lilac borer, *Podosesia* syringae.

Adult clearwings are slender-bodied, small to medium-sized moths, wingspan 1.4 to 4.6 cm. The forewings are narrow, at least four times as long as wide, with anal veins reduced. The hind wings are shorter and somewhat more broad, with all three anal veins present. The forewings fold downward along their inner, rear margin, with a row of tiny curved spines that interlock with the fold; similar spines along the hindwing costa help to hold the wings together. The antennae are simple to bipectinate, widening gradually and then narrowing again to the tip. The larvae are ivory white or cream-colored except for a brownish, sclerotized head and lighter thoracic shield. Each thoracic segment has one pair of small jointed legs. Abdominal segments 3 to 6, and 10, have fleshy lobes (prolegs), each ending in two transverse bands of tiny hooklike crochets.

Many clearwing species have a 1-year life cycle. Others require two years to complete a generation, whereas a few species have two generations per year. Winter is spent as a partially grown larva within a gallery under the bark of the host plant, or within stems, canes, or roots. Several sizes of larvae may overwinter, reflecting the fact that the eggs from which they eclosed were laid by different females over a number of weeks. Active feeding resumes in early spring. Some species pupate in late winter or spring, whereas others feed longer and pupate later in the growing season. Before pupating, the larva extends its tunnel to the bark surface except for a paper-thin cover. Pupation occurs within a cocoon made from frass and bits of bark or soil held together with silken strands. The pupal stage lasts about 3 weeks. Empty pupal skins often are left partially protruding from exit holes in the bark after the moths have emerged.

Flight activity, mating, and egg-laying by a particular species usually are finished within 4 to 6 weeks after initial emergence. Adults of different species emerge at certain times during the growing season, and their flight activity often is restricted to a specific time of day. These temporal differences likely are important for reproductive isolation, especially since females of a number of species emit chemically-similar sex pheromones to attract males.

After mating, females deposit eggs singly in bark crevices, often around wounds, cankers, or old larval feeding galleries. They seem to be attracted to plants that are injured or weakened by root pruning, transplant shock, insect or disease injury, drought, or other stress factors. Individual females typically live only about a week, during which they may lay several hundred eggs. Eggs hatch in about 2 weeks, and larvae then bore into the bark and mine in the phloem and cambium, lengthening and enlarging the tunnel as they grow. Many species later enter the sapwood. Branch dieback, limb and trunk swellings, moist sap spots on the bark, gum exudates, expulsion of larval frass, or protruding pupal skins all may indicate that borers are present.

Woodpeckers are important in natural control. Ants, and in some cases field mice, moles and skunks, prey upon the pupae. Eggs, larvae, and pupae are attacked by various parasitic wasps or flies. A fungus, *Beauveria* sp., sometimes infects and kills the larvae.

In the early 1970s, scientists identified and synthesized two major isomeric pheromone components, the Z, Z- and E, Z- isomers of 3,13-octadecadien- 1-ol-acetate, from the peach tree borer and lesser peach tree borer, respectively. Subsequent field testing soon revealed cross-attraction of other clearwing species to these pure isomers, their corresponding alcohols, or to various blends of these compounds. This breakthrough allowed entomologists to learn more about the flight periods of a number of clearwing moth species, to survey local sesiid fauna, and to develop effective attractants for some of the key pest species.
Traps baited with commercial synthetic pheromones are used by nursery operators and landscape managers to monitor clearwing moth activity. This helps them to fine-tune timing of control actions. Entomologists also are evaluating use of such attractants for mass trapping or mating disruption of pests such as peachtree borer in orchards. The most important management strategy is to minimize plant stress, because healthy trees, shrubs, and vines are less likely to be attacked by borers.

References

Eichlin TD, Duckworth WD (1988) Sesioidea: Sesiidae. In RB Dominick et al (eds) The moths of America north of Mexico. Fasicle 5.1. 176 pp

Englehardt GP (1946) The North American clearwing moths of the family Aegeriidae. Bulletin 190. U.S. National Museum, Washington, DC

Johnson WT, Lyon HH (1988). Insects that feed on trees and shrubs, 2nd ed. Cornell University Press, Ithaca, New York

Solomon JD (1995) Guide to insect borers of North American broadleaf trees and shrubs. Agricultural Handbook 706. USDA Forest Service, Washington, DC. 735 pp

Taft WH, Smitley D, Snow JW (1991) A guide to the clearwing borers (Sesiidae) of the north central United States. USDA North Central Regional Publication 394

Cleptobiosis

A relationship in which one species robs the food stores, or scavenges in the refuse piles, of another species – but does not nest in association with the host.

Cleptoparasite

An organism that consumes the stored food of another from its nest.

Cleridae

A family of beetles (order Coleoptera). They commonly are known as checkered beetles.

► Beetles

Click Beetles

Members of the family Elateridae (order Coleoptera).

► Beetles

Clicking by Caterpillars

Although acoustic communication is well known among certain moths (mostly in the context of detecting ultrasonic cries of insectivorous bats), acoustic communication is widespread in Lepidoptera. Vibrational signals are used by some butterfly and moth larvae in communication with mutualistic ants, conspecifics, and predators. However, sounds made by at least 12 families, including Tortricidae, Oecophorida, Notodontidae, Saturniiidae, and Sphingidae, may be involved in defense. Saturniid and sphingid larvae produce audible (to the human ear) clicks that have been described as "cracking" or "crackling." Closure of the mandibles produces the "click" sounds, and it follows disturbance of the larvae as may occur when the insects are grasped or pecked by birds. The clicking sound often precedes regurgitation by the larvae, and regurgitation is known to be repellent to both vertebrate and invertebrate predators.

► Vibrational Communication
► Acoustic Communication in Insects
► Acoustic Aposematism (Clicking) by Caterpillars

Reference

Brown SG, Boettner GH, Yack JE (2007) Clicking caterpillars: acoustic aposematism in *Antheraea polyphemus* and other Bombycoidea. J Exp Biol 210:993–1005

Climatic Release

The release of a population from climatic constraints by a favorable change in weather, allowing it to attain a population increase or outbreak.

Climax

The end point of an ecological successional sequence; the community has reached a steady state.

Cline

A geographic gradient in the frequency of a gene.

Cloaca

The rectum, a common chamber into which the anus and gonopore open; the vagina.

► Reproduction
► Vagina

Clone

A population of identical cells often containing identical recombinant DNA molecules. Also a group of organisms produced from one individual cell through asexual processes. The offspring are identical. The word may be used either as a noun or a verb.

Closed Cell

A cell bounded on all sides by wing veins.

Clothes Moths

Members of the family Tineidae (order Lepidoptera).

► Fungus Moths
► Butterflies and Moths

Clothodidae

A family of web-spinners (order Embiidina).

► Web-Spinners

Clover Mite, *Bryobia praetiosa* Koch (Acari: Tetranychidae)

These clover and grass-feeding mites damage vegetation and also enter homes, becoming a nuisance.

► Mites

Club Fleas

Members of the family Rhopalopsyllidae (order Siphonaptera).

► Fleas

Clubtails

A family of dragonflies in the order Odonata: Gomphidae.

► Dragonflies and Damselflies

Clumped Distribution

A distribution of organisms in which there is some aggregation of individuals that exceeds the clumping that would occur randomly. This is the most common distribution displayed by insects.

Clusiid Flies

Members of the family Clusiidae (order Diptera).

► Flies

Clusiidae

A family of flies (order Diptera). They commonly are known as clusiid flies.

► Flies

Cluster Analysis

A method of hierarchically grouping taxa or sequences on the basis of similarity or minimum distance. UPGMA is an unweighted pair group method using the arithmetic average. WPGMA is the weighted pair group method using the arithmetic average.

Cluster Fly, *Pollenia rudis* (Fabricius) and *P. pseudorudis* Rognes (Diptera: Calliphoridae)

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The name cluster fly (or loft fly) is given to two species of Northern Hemisphere blowflies (Calliphoridae) *Pollenia rudis* and *P. pseudorudis* that preferentially breed in earthworms of the genera *Allolobophora*, *Eisenia* (= *Helodrilus*) and *Lumbricus*. Many other members of the genus breed in earthworms, but so far as is recorded, only *P. rudis* and *P. pseudorudis* invade buildings in large numbers in autumn, achieving pest status, leaving again in spring. The identities of these flies have been confused until recently. Only in 1985 was *Pollenia pseudorudis* recognized as distinct from both *P. rudis* and *P. angustigena*, and the previously named *P. obscura* was subsumed in *P. pseudorudis*.

Apart from New Zealand records, there is no clear indication that *P. pseudorudis* invades houses elsewhere in the world, because in the Northern Hemisphere and Hawaii, only *P. rudis* is recorded as the nuisance species, although it may just be that no effort has been made to gauge whether *P. pseudorudis* is present as well. It is possible that both species (and perhaps others) occur together in houses in North America, and perhaps elsewhere, as they do in the wild, but possibly because of the *P. obscura* synonymy no distinction has been attempted. Lofts are a common sanctuary, hence one of the common names, and the flies cling together, often in ropy clusters. They have been described as "the most frustrating of … structural insect pests."

First reports of cluster flies as a household nuisance appeared in the mid nineteenth century, although the first published mention of a fly associated with earthworms was in 1881, when Charles Darwin, in his treatise on earthworms reported an earlier observation by Perrier.

In the 1930s, a link between earthworms and swine influenza was postulated, with a view that "the virus of swine influenza is a surviving prototype of the agent responsible for the great human pandemic of 1918" and that hogs and earthworms may serve as the source of future epidemics. Because of its links with earthworms, the cluster fly was regarded as a possible vector of human influenza, an hypothesis that has not been supported by subsequent research.

The tribe Polleniini to which the cluster flies belong occurs in four distinct geographical groups, the Palearctic (with at least 30 species), the Nearctic and Austro-Oriental regions, each with at least eight species in the genus *Melanodexia* and two in *Pollenia*. The Australasian and Oceanian regions have three genera, *Anthracomyia* (which is monotypic), *Dexopollenia* (five species) and *Pollenia* (43 species, the majority in New Zealand). However, there are still a further 17 species unnamed in New Zealand designated as species "a" to species "q" inclusive. It appears that only the two Northern Hemisphere (widely distributed throughout the Nearctic and Palearctic) species, *P. rudis* and *P. pseudorudis*, congregate in houses, although further work may alter this view. Both species have been intercepted in New Zealand, but only *P. pseudorudis*, which reached New Zealand in the early to mid-1980s, appears to have established and, over the next 20 years or so, subsequently dispersed throughout both main islands.

In the Holarctic, a *P. rudis* species group is recognized, and contains six species of *Pollenia*: *P. angustigena*, *P. rudis*, *P. pseudorudis*, and three exclusively in the Palearctic: *P. hungarica* (Central Europe and southern parts of Scandinavia), *P. longitheca* (eastern Mediterranean) and *P. luteovillosa* (Algeria and Morocco). There is a seventh species of doubtful status.

The adult flies (Fig. 68) are slow-flying, easily-caught insects; they are active in spring and summer in pasture and gardens, and then, as ground temperatures begin to drop in autumn (fall), the flies move towards shelter, usually houses or other buildings that act like large flytraps. In the afternoon they settle on the upper parts of walls and on roofs, facing towards the setting sun. As the sun sets, the flies crawl into any crevice and into roof spaces, and may enter rooms, using drapes, pictures, etc., as hiding places. For a few days, the flies will go back outside, and then return at night, but this behavior eventually ceases, except if there is a spell of mild weather during winter. Mild weather will break the fragile hibernation of the flies and they will become sluggishly active. Outside of human habitations, the overwintering locations of cluster flies are not well known, although they have been recorded from the tunnels made by beetles in timber and fungi and also in animal burrows. The flies return to the outside in spring, again causing a nuisance as they do so.

Cluster Fly, *Pollenia rudis* (Fabricius) and *P. pseudorudis* Rognes (Diptera: Calliphoridae), Figure 68 **A recently emerged cluster fly. Normally the fly at rest has the wings folded back more than is shown here, and they obscure the abdomen (photo courtesy of Lynnette Schimming).**

The cluster fly *P. rudis* is frequently seen in very large numbers in spring moving over moist grass. The female deposits a batch of eggs on the soil surface and then moves some distance away and deposits another batch, about 100–130 eggs in all. Three days later the eggs hatch and the larvae descend into the soil by following natural pore spaces, such as gaps between plant stems and soil and worm burrows, although not if the latter are blocked by casts. It seems the larvae locate a host by a random locomotion through the soil pores rather than following any product of the host. Some species of earthworms emerge from their burrows at night and move freely about on the surface, and after rain many worms can be seen above ground. This surface movement could be a mechanism that would improve the potential for cluster fly larvae to encounter potential hosts.

Adult flies are on the wing from early spring in the Northern Hemisphere (February, March) to late autumn (October, November). They are sometimes attracted to horse and human feces, but are more attracted to meat and fruit, with banana reported to be especially good bait.

Larvae enter the earthworm through almost any point in the body wall, but mostly on the dorsal side and sometimes through spermiducal and other pores. Larvae must penetrate a worm within 3 days after hatching if they are to survive. Penetration is attempted under the influence of a substance present in both the slime and coelomic fluid, which has been named "penetration-inducing factor." They have been reported to re-emerge after a short period to produce an opening through which they protrude the posterior spiracles. It has been reported that during the first two stadia the larva acts as an internal parasite, and during the last it feeds on the host from the outside. Larvae may also leave the host and commence feeding on healthier parts of the same worm or on a fresh worm. Up to seven larvae may occur in a single worm, although a single larva will feed on as many as three earthworms, resulting in larger pupae than usual. The larvae can eventually eat the entire body of the worm and pupate in the soil nearby.

Development times vary with climatic conditions. In Canada, total development time is 25–30 days at 23°C, of which 11–14 days are spent in the pupal stage. There are three or four generations per year. In Europe, after wintering in a dormant state in the body cavities of earthworms, the larvae molt twice over about a 20 day period and then pupariate outside the host. The pupal stage typically lasts from 32 to 45 days, although it can be as short as 7 days at high temperatures (e.g., 27°C).

A number of species of worms are variously reported as hosts. In Europe, cluster flies attack *Allolobophora chlorotica*, *A.* (latterly *Eisenia* formerly *Helodrilus*) *rosea*, and *L. terrestris*, whereas in North America both of the *Allolobophora* spp. as well as *A. caliginosa* are parasitized. But *A. rosea* and *A. chlorotica* seem to be the most common hosts in North America; both are surface-dwelling species occurring mainly in the top 10 cm of the soil. In general, attempts to experimentally infest worms with *P. rudis* larvae have met with mixed success and only *A. rosea* was infested in all attempts. It is possible to rear *P. rudis* in the laboratory using *A. rosea* as a host. Parasitism in the field in North America is said to occur only in *A. chlorotica* and *A. rosea*, although other species (*A. caliginosa*, *L. terrestris*, *L. rubellus*, *Eiseniella tetraedra*, *Eisenia foetida*, *Octalasium lacteum*) in a crushed form will support first instar larvae. Studies in Hungary showed that *P. rudis*, *P. pseudorudis* and *P. hungarica* could be bred out of *A. rosea*.

The sexes of overwintering flies are approximately equal in numbers and the abdomen of flies at this time is full of fat globules, possibly the remnants of larval fat bodies. The following spring, the flies possess a shrunken or desiccated appearance because the fat has been used up during the winter.

It has been reported that there are important differences in the life history of *P. rudis* in Europe compared with North America, with the first instar larva as the over-wintering stage in Europe, rather than the adult as in North America. In addition, there is only one generation a year reported from Europe. However, apparently there are three species in the "*rudis*" species complex in North America and the life cycle of each may differ. Discrepancies between North American and European reports with regard to cluster fly biology (and coincidentally larval morphology) may be because early work may not apply to any *rudis* group member and it is possible that the authors worked with different species.

Enlargement of the distribution of *P. rudis* into the Oceanic and Australasian regions has occurred relatively recently, with Hawaii recording its first flies in 1955, with *A. caliginosa* serving as the host. *Pollenia rudis* was intercepted at the New Zealand border in 1981. This species does not appear to have broached the border, as no specimens have been subsequently found in the wild. However, in 1984 a species soon to be recognized as *P. pseudorudis* was found in a house in Auckland, New Zealand, and over the next 19 years spread throughout the country, but up to 2007 no worm hosts have yet been identified.

During the first 12 years after its discovery in New Zealand, *P. pseudorudis* populations established themselves throughout the North Island, being more numerous in some years and districts that at other times. Simultaneously, in 1996 with the end of this initial expansion period, the first South Island populations were recorded. Further expansion in the South Island took place over the next 7 years to the southernmost districts. It appears that *P. pseudorudis* is not found in either Hawaii or Australia at present, although *P. rudis* occurs in the former. The clustering habit of adult flies would provide an opportunity for them to collect in shipping containers and facilitate their trans-hemispheric movement.

It might be thought that the large numbers of cluster flies appearing each year would have a detrimental effect on local earthworm faunas. In Europe and North America, four species of earthworms are used as hosts: *A. chlorotica*, *A. caliginosa*, *A. rosea* and *L. terrestris*. However, there have been no reports of notable reductions in earthworm numbers or any horticultural consequences. Given the enormous numbers of earthworms in pasture, variously estimated from 70,000 to around 10 million per hectare, there would seem to be enough to spare for cluster fly population maintenance.

Apart from this unresolved question of whether earthworm numbers suffer as a consequence of cluster fly activity, the insects evoke strong emotional responses in humans and present a major housekeeping nuisance. If swatted they leave greasy spots. There can also be economic effects if businesses decide to close because of fly activity, and such closures have been recorded. In addition, there is a potential public health nuisance, and a town water supply contained in a large wooden reservoir tank in New Zealand had to be drained after cluster flies settled inside and an excess of fecal coliform bacteria was found in the water. Invasion of a hospital in Europe provoked concern and although no bacteriologically sterile flies could be found, an enrichment culture technique had to be used to provide sufficient bacteria for identification. This suggests that cluster flies may be a low health threat.

Keeping cluster flies out of houses can be difficult, although finding possible entry points and blocking them with appropriate materials such as wire mesh can work. The flies are capable of squeezing through very small crevices, however, and even the most assiduous search may miss openings. The principal control method favored by pest control firms involves insecticide application on outside walls of buildings, fogging of interiors, such as roof spaces, and even treatment of vegetation and soil. Overuse of insecticides both inside and outside is not a particularly safe option for either humans or other animals. Simply vacuuming flies up as they enter houses is safe and effective, especially because flies killed by insecticides would have to be cleared up in some manner in any event.

References

Heath ACG, Marris JWM, Harris AC (2004) A cluster fly, *Pollenia pseudorudis* Rognes, 1985 (Diptera: Calliphoridae): its history and pest status in New Zealand. NZ J Zool 31:313–318

Oldroyd H (1964) The Natural history of flies. Weidenfeld & Nicolson, London

Rognes K (1987) The taxonomy of the *Pollenia rudis* species-group in the Holarctic region (Diptera: Calliphoridae). Syst Entomol 12:475–502

Thomson AJ (1973) The biology of *Pollenia rudis*, the cluster fly (Diptera: Calliphoridae). I. Host location of first-instar larvae. Can Entomol 105:335–341

Thomson AJ, Davies DM (1973) The biology of *Pollenia rudis*, the cluster fly (Diptera: Calliphoridae). II. Larval feeding behaviour and host specificity. Can Entomol 105:985–990

Yahnke W, George JA (1972) Rearing and immature stages of the cluster fly (*Pollenia rudis*) (Diptera: Calliphoridae) in Ontario. Can Entomol 104:567–576

Clypeofrontal Suture

The suture marking the division between the clypeus and the epicranium. The clypeal suture.

Clypeus

A part of the head below the front (Fig. 69) to which the labrum is attached.

► Head of Hexapods

Coarctate Larva

This term usually is applied to the third phase of hypermetamorphic development in Meloidae. At this point in development, which corresponds approximately to instar six, the larva typically is strongly sclerotized, immobile, and the legs are greatly reduced. Sometimes it is used to describe a larva that is similar to the puparium of a fly, in which the cuticle of the preceding instar is not completely shed but remains attached to the posterior end of the body.

Coarctate Pupa

A pupa that is enclosed in the hardened shell formed by the last larval cuticle. This is usually called a puparium.

Coccidae

A family of insects in the superfamily Coccoidae (order Hemiptera). They sometimes are called soft scales, wax scales, and tortoise scales.

► Bugs

► Scale Insects and Mealybugs

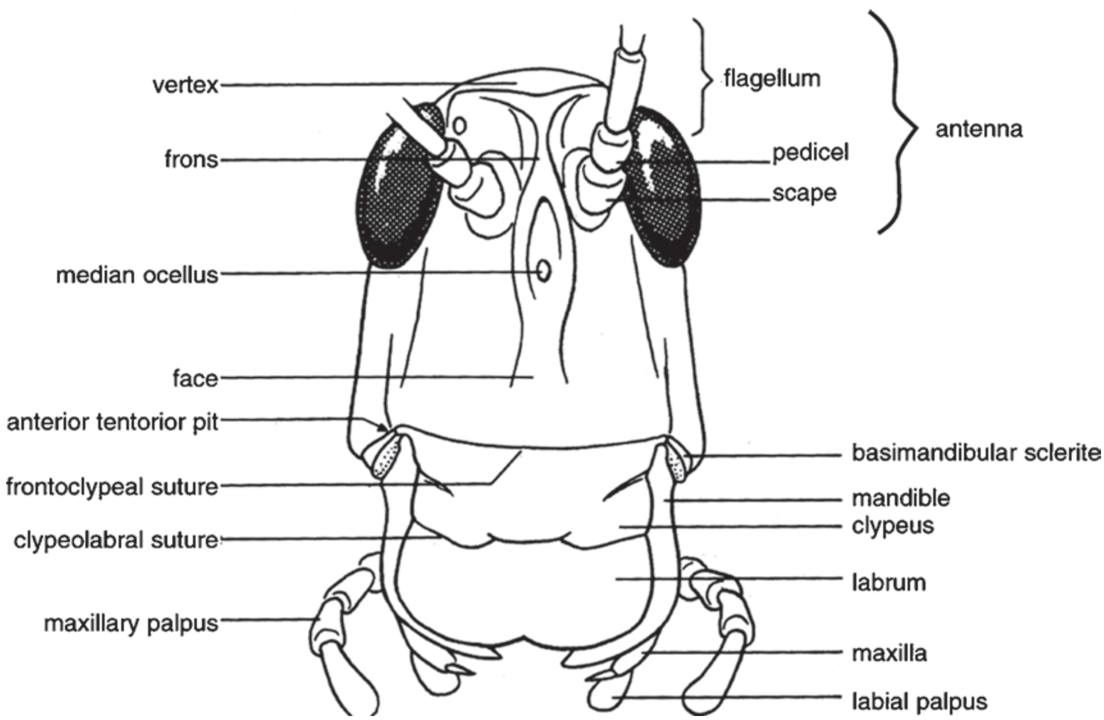
Coccinellidae

A family of beetles (order Coleoptera). They commonly are known as ladybird beetles.

► Beetles

Coccoidae

A superfamily of insects in the order Hemiptera. They sometimes are called scale insects, though



Clypeus, Figure 69 Front view of the head of an adult grasshopper, showing some major elements.

mealybugs also are found in this superfamily. This superfamily contains such families as Margarodidae, Ortheziidae, Kerridae, Coccidae, Acleridiidae, Cryptococcidae, Kermesidae, Asterolecaniidae, Lecanodiaspididae, Cercoccidae, Dactylopiidae, Diaspididae, Conchaspididae, Phoenicococcidae, Pseudococcidae, and Eriococcidae.

► Scale Insects and Mealybugs
► Bugs

Cochineal Insects

Members of the family Dactylopiidae, superfamily Coccoidae (order Hemiptera).

► Bugs
► Scale Insects and Mealybugs
► Lacquers and Dyes from Insects

Cockerell, Theodor Dru Alison

Theodor Cockerell was born in London on August 22, 1866, and became interested in natural history at an early age with parental encouragement. This interest extended to insects and slugs and snails and was further encouraged after the death of his father by a trip to Madeira. Upon finishing school, he was employed by a flour company, but developed tuberculosis. At the age of 20 he sailed to the United States and journeyed to Colorado to find a climate that would cure his illness. That climate was beneficial and his health recovered. In Colorado he worked on a catalogue of the flora and fauna there, but returned to London in 1890 to work in the British Museum (Natural History). He was invited by Alfred Russel Wallace to help in the preparation of a new edition of the latter's book "Island Life." In 1891 he was appointed Curator of the Public Museum (now Institute of Jamaica) in Kingston and became interested in scale insects. Unfortunately, his tuberculosis had returned by 1893. Fortunately for him, he was able to trade jobs with C.H.T. Townsend of the New Mexico College of Agriculture, and he moved to Las Cruces to become entomologist at the Experiment Station and Professor of Entomology and Zoology. But there his wife died giving birth to a second son, who died at the age of eight, the first son having died in infancy in Jamaica. Later, he took an American wife, Willmatte. In New Mexico, he developed an interest in wild bees, studied their taxonomy and behavior, and eventually published description of 5,480 new names for species, subspecies and varieties, together with 146 new names for genera and subgenera. In 1903 he returned to Colorado and took a position as Curator of the Museum of Entomology at Colorado College. Here, he continued his work on bees but also developed an interest in paleoentomology and paleobotany and numerous other natural history subjects, and even art, poetry and politics. He traveled to Europe, Japan, Thailand, India, Siberia, Australia, Morocco and other parts of Africa, Canada, and Honduras. Upon retirement, he divided his time between Colorado and southern California. His published works amount to over 3,000 items, in which he described over 7,000 species of plants and animals, extant and fossil. He died on January 26, 1948, in California.

Reference

*Mallis A (1971) Theodore Dru Alison Cockerell. In: American entomologists. Rutgers University Press, New Brunswick, NJ, pp 357–362

Cockroaches (Blattodea)

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The cockroaches (also called roaches) are members of an ancient order of insects. The order name is derived from the Latin word *blatta*, or cockroach. They are closely related to the praying mantids (Mantodea), and often are grouped with them (as suborders) to form the order Dictyoptera. Though the mantids evolved from the cockroaches, they are a specialized group of predatory insects that warrant individual recognition. Termites

(Isoptera) can also be placed in the order Dictyoptera, and are considered by some to be social cockroaches. The order name for cockroaches sometimes is given as Blattaria.

Classification

About 4,000 species are found throughout the world, though most are tropical. They usually are grouped into six families.

Order: Blattodea
- Superfamily: Blattoidea
  - Family: Blattidae
- Superfamily: Blaberoidea
  - Family: Polyphagidae
  - Family: Cryptocercidae
  - Family: Nocticolidae
  - Family: Blattellidae
  - Family: Blaberidae

Characteristics

The cockroaches are small to large in size, measuring from about 2 mm to over 60 mm. The largest, *Megaloblatta blaberoides*, measures 100 mm when the tegmina are included in the measurement, and has a wing span of 185 mm. They are flattened, oval, and often dark or reddish brown, though some are black or green. Species that live under bark or rocks sometimes are extremely flattened, though this degree of compression also is useful for defending against attack by ants because the cockroaches cling so tightly and closely that the ants cannot get beneath them to their more vulnerable under-surface. The head is concealed (when viewed from above) by the pronotum. Compound eyes are usually present and well-developed, though absent in some cave-dwelling species and myrmecophiles. The filiform antennae are long. They possess chewing mouthparts. Both males and females usually bear two pairs of wings, though the front wings are thickened. Both short-winged and wingless species are known. The cursorial legs are not greatly modified, and only moderately long, but some species run quite rapidly. There are five tarsal segments. Cerci are present, though varying in length, and consisting of one to five segments. Some species burrow, and these are among the heaviest of the cockroaches. *Megoblatta rhinoceros*, for example weighs over 30 g. Burrowers are often wingless, heavy-bodied, hard, and bear spines. On the other end of the scale, some cockroaches inhabiting the nests of social insects (mostly ants and termites) are only 2.7 mm long. Indeed, it is surprising to most people that small species predominate, but they are easily overlooked.

The accessory glands of female cockroaches produce oothecae, or egg cases, which contain few to many eggs. The eggs are usually are arranged in two rows, and in many cases the *ootheca* is surrounded by a thick, protective covering. The ootheca may be inserted into a protected location or just dropped by the female in the general environment in which she lives, but others carry the ootheca until the eggs are ready to hatch. Cockroaches in the family Blaberidae retain their eggs internally and give birth to living young.

Sexual dimorphism is sometimes quite pronounced. The sexes are so different in some species that they were originally described as separate species. These differences suggest that competition to win a mate is quite keen. The abdomen of the female, not surprisingly, is more elongate.

As with other hemimetabolous insects (incomplete metamorphosis), the immatures resemble the adults in general appearance, differing primarily by the absence of the tegmina and wings in immatures (nymphs). Immatures also have poorly developed genitalia, and lack characters useful for identification. Some are colored quite differently from the adult stage.

Although we tend to think of cockroaches as nocturnal, some are active during the day. Not surprisingly, their color is quite different. Day-active cockroaches often sport bright colors: some are brightly colored; others are aposematically colored because they are chemically defended; still others mimic other species (Batesian mimics). They commonly mimic beetles, including such brightly colored species as ladybird beetles (Coccinellidae), carrion beetles (Silphidae), and metallic wood-boring beetles (Buprestidae). Cave-dwelling species are typically depigmented, and have a thin cuticle, elongated appendages and loss of vision.

The cockroaches are basically terrestrial insects, though some semi-aquatic species are known. Flight is not well known for most species, but most seem to fly poorly, despite the presence of large wings. The presence of wings is the primitive condition, and wings have been reduced or lost in many taxa. Those living below-ground or in burrows, galleries or crevices are most prone to winglessness, as are those living in stable habitats. The absence of wings in the adult form of some species is associated with retention of juvenile characters (paedomorphosis).

Habitats and Food

Cockroaches are found in nearly all habitats, from the forest canopy to the soil, within burrows and caves, within logs and detritus, and in nests of social insects, rodents, reptiles and birds. They are most numerous in the hot, humid tropics, between 30°N and 30°S. They are also more common at sea level (where temperatures are warmer) rather than at high altitudes. In the tropics, there is considerable vertical stratification on trees at night, with most species returning to the ground litter during the day. The species that inhabit the most elevated portions at night are also the best fliers; not surprisingly, the flightless species are lowest on the trees.

Favored habitats of cockroaches are dark, humid, poorly ventilated, and cramped or crowded. Thus, they are commonly found with loose substrate such as leaf litter and clods of soil. Some force themselves into small voids such as spaces under bark, within the bases of palm trees, or under rocks. Only a few excavate burrows in wood or compacted soil, but rotting logs are popular habitats. Caves may or may not be populated. The presence of vertebrate guano maintains large numbers of cockroaches in caves. Despite the aforementioned preferences, some cockroaches have not only managed to exploit desert environments, but have become some of the most abundant mesofauna present. Many desert dwellers live beneath the sand, at least for a portion of the day. They also take advantage of natural burrows created by rodents and vertebrates. Only a few species actually inhabit the water, though many favor the water-vegetation interface.

Cockroaches are usually thought of as scavengers or omnivores. However, this mostly reflects our knowledge of domiciliary pest species, plus the tendency of cockroaches to behave abnormally when constrained to the laboratory environment. Most display some degree of preference, though they are by no means highly selective (Table 14). For example, in a natural environment such as a tropical rain forest, there seem to be three dominant night-time feeding strategies: they forage on the forest floor, feeding on decaying vegetation but also ingesting nematodes, fungi, insects, and other invertebrates; they emerge from crevices and tree holes, ascend to a preferred height in the trees, and feed on material that has fallen onto the leaves or is growing on the leaves; they emerge from harborages and flit about the vegetation irrespective of height, scraping algae and other microvegetation from the tree foliage, bark, or elsewhere. Cockroaches search actively for food but also use olfaction to locate suitable food. They usually consume the food as they find it, though some species will transport food elsewhere. They can learn where food is located and return after an absence. Juvenile cockroaches require more nitrogen than do older cockroaches so they initially favor meals from animal or microbial sources. Females consume more than males. Generally cockroaches are not thought of as plant pests, but there are important exceptions. In a closed environment such as a greenhouse, any species can be damaging if they become sufficiently abundant. Others, such as *Pycnoscelus surinamensis* and *Blatella asahinai*, commonly are associated with plant injury, even under field conditions. Cockroaches are quite tolerant of starvation, living from five to over 40 days without

Cockroaches (Blattodea), Table 14 Diet of four species of *Parcoblatta* based on nocturnal observations (after Gorton REJ (1980) The University of Kansas Science Bulletin 52:21–30)

Food source	*P. pennsylvanica*	*P. uhleriana*	*P. lata*	*P. virginica*
Mushrooms	+	+		+
Cambium			+	
Flower petals			+	
Moss		+		
Sap	+		+	
Cercopid spittle	+			
Live insects	+			
Bird feces		+		
Mammal feces	+			
Mammal cartilage		+		

water and food. Water is a more critical resource, and they can survive longer without food than without water, perhaps 60–90 days. Dead conspecifics and shed cuticles are a common food resource; not surprisingly, biting and cannibalism are reported.

The digestive system of cockroaches is well equipped with a diversity of microbiota. The resident fauna and flora, plus the microbes ingested along with food, comprise a rich microbial "brew" that enhances fermentation. They also contribute cellulases, though endogenous cellulases also occur. It has been postulated that cellulose ingestion indirectly benefits cockroaches by fueling their microbial gut inhabitants, with the microbes and their products being the primary source of nutrition. The significance of microbes in the gut of cockroaches is seen in the regular coprophagous (feces-feeding) behavior of young cockroaches, which provides an important inoculum for the young insects. The wood-feeding cockroaches in the family Cryptoceridae are the link to termites. Not surprisingly, digestion is about the same in cryptocerids and termites, the principal difference between the two groups being the evolution of a higher level of sociality in termites.

Fecal pellets are attractive to cockroaches. Fecal chemicals function as short-distance attractants and arrestants. Cockroaches may aggregate in locations with these chemicals. The response is not species specific: they prefer the chemicals produced by their own species, but will aggregate at sites contaminated by other species, including distant relatives. Due to their lack of specificity, the chemicals are not usually considered to be aggregation pheromones, but they clearly are a form of behavior-eliciting chemicals. Other factors such as acoustic, tactile, visual and olfactory stimuli also influence aggregation, as do environmental stimuli such as light, humidity, temperature, and air movement.

Parental Care

Most cockroaches display some form of parental care, though the degree of care differs (Table 15). Care of eggs is most widespread; carrying and hiding oothecae, and defense of oothecae, are examples of care. Brooding behavior is a short-term association of the mother and neonates. In some species, the young cluster around, under and on the mother, though this behavior may only persist for about a day. Though often not lasting long, this behavior allows the cuticle of neonates to harden. The transfer of gut microbiota also may occur at this time, probably via a fecal meal.

Cockroaches (Blattodea), Table 15 **Parental care in cockroaches where offspring are provided with bodily secretions by adults (adapted from Nalepa, Bell (1997) Social behavior in insects and arachnids)**

Species	Offspring	
	Location	Food source
Perisphaerus sp.	Cling ventrally	Hemolymph
Trichoblatta sericea	Cling ventrally	Sternal exudate
Pseudophoraspis nebulosa	Cling ventrally	?
Phlebonotus pallens	Under tegmina	?
Thorax porcellana	Under tegmina	Tergal exudate
Gromphadorina portentosa	Abdominal tip of female	Secretion from brood sac
Salganea taiwanensis	Mouthparts of adult	Stomodeal fluids
Cryptocercus punctulatus	Abdominal tip of adult	Hindgut fluids
Cryptocercus kyebangensis	Abdominal tip of adult	Hindgut fluids
Blatella vaga	Under tegmina	Tergal exudate

Sometimes the brooding behavior is extended for a longer period of time, perhaps 2 weeks. Females may accommodate offspring during this period by allowing young cockroaches to cling to her body, and some have evolved external brood chambers under their wing covers. An example of a higher level of brood care is found in *Thorax porcellana*, which maintains its young in a brood pouch for about 7 weeks. It seems that the young feed on a pinkish material secreted by the dorso-lateral regions of the tergites. Parental feeding of young is not unusual. Usually it is only the female that is involved in parental care.

Ecological Importance

Cockroaches contribute to ecosystem functioning by breaking down organic matter and aiding in release of nutrients. They are aided both by their endogenous cellulases and their microbial symbionts. Cockroaches can be considered to be soil fauna, though they rarely are acknowledged as such. The principal diet of cockroaches is organic material, and in living and feeding in the litter, soil and decaying trees, they contribute to the make-up of the soil. Their role is not in the direct mineralization of soil, because that is the role of microorganisms. Rather, it is to put the organic material in contact with the microbes. This is done by fragmenting litter, exposing litter to microbes, and by transporting microbes to new resources. Cockroaches are less dependent on water for functioning than are microbes, and microbes in the gut are afforded the correct conditions for activity. Also, the fecal pellets produced by cockroaches are an important substrate for microbes, and speed the return of above-ground productivity to the soil. Microfauna such as mites, springtails, nematodes and protozoa utilize the bacteria and fungi growing on the pellets as a principal food resource. The importance of litter decomposers for soil formation and enrichment is widely acknowledged. What is not known, however, is the relative importance of cockroaches. We can likely assume that it is quite significant in tropical forests, but in temperate forests they also are abundant, often comprising about half of the soil macrofauna.

Domiciliary Cockroaches

Some "domiciliary" species invade dwellings, and a few species are well-adapted to living in buildings and on ships, where they can become numerous enough to be considered pests. Lack of hygiene is normally associated with cockroach infestation in temperate areas, though in tropical and subtropical regions cockroaches live out-of-doors and invade dwellings irrespective of hygiene. Cockroaches often produce an odor that is unpleasant, and are implicated in a limited amount of disease transmission. They are a major source of allergens. Cockroaches are often the target of chemical suppression efforts, especially in food establishments. Thus, it is not surprising that insecticide resistance is widespread in some species. Cockroaches may be eaten by predatory vertebrates, and parasitized by nematodes and mites, but the most important natural enemies are egg parasitoids. About six families of wasps, but particularly Evaniidae and Eulophidae, parasitize cockroach eggs, sometimes quite effectively.

Cockroaches as Pests

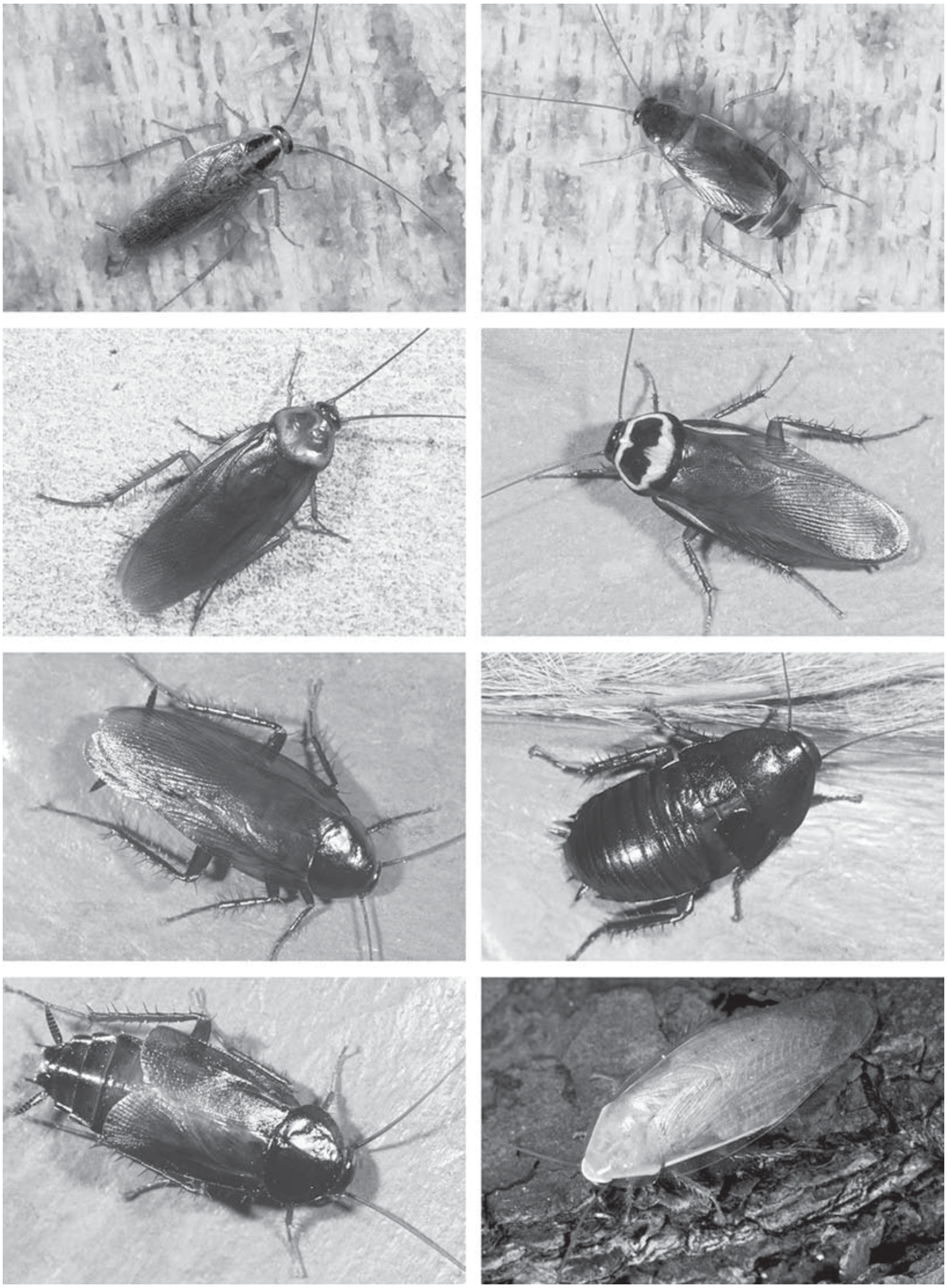
Traditionally, efforts to suppress cockroach populations in the urban environment have relied almost exclusively on repeated applications of synthetic pesticides. However, the chemical approach to cockroach control has become increasingly less popular. This is primarily due to the development of multi-chemical resistance among German cockroach populations and increased public concern about pesticide exposure in their living environment. These two issues have led to development of less toxic approaches to cockroach management.

The Principal Cockroach Pest Species

The predominant pest cockroach species in the world is the German cockroach, *Blattella germanica* (Fig. 70). German cockroaches are small, with adults <1.5 cm in length. They are gold in color and have two dark longitudinal bands on their pronotum near the head. Immature German cockroaches are smaller than adults, wingless and dark brown in color. German cockroaches are primarily indoor pests. They have strict moisture requirements so they are usually found in kitchen and bathroom areas. Adults live about 6 months, and during this time the female produces from 4 to 8 oothecae. The female carries the egg case throughout embryonic development (3–4 weeks) often releasing it from her body only hours before the nymphs hatch. Each female produces about 28 nymphs in each egg case. German cockroaches are the most prolific cockroach pest species, most likely to be insecticide resistant, and therefore the most difficult to control.

An increasingly important species is the brown-banded cockroach, *Supella longipalpa*. Although it is favored by warm climates, it can be quite abundant in more temperate environments, and has replaced German cockroach as the dominant pest species in some areas. It is more tolerant of low humidity than German cockroach, so it is found inhabiting areas without a ready source of water, such as bedrooms and closets. The common name is most descriptive of the nymphal stage, though even the adult has two dark bands on the wings. It lacks the two parallel dark stripes found on the prothorax of German cockroaches. The female carries an egg capsule with up to 18 eggs initially, but after a day or two she attaches it to an object. The incubation period of eggs is about 70 days, and time to complete development is about 160 days.

Some other pest species include the American cockroach, *Periplaneta americana*, Australian cockroach, *P. australasiae*; brown cockroach, *P. brunnea*; smoky-brown cockroach, *P. fuliginosa*; Oriental cockroach, *Blatta orientalis*; and the Florida woods cockroach, *Eurycotis floridana*. These other species of cockroaches (Fig. 70) are much larger and heavier than German and brown-banded cockroaches. Adults range in size from 3 to 4 cm in length and are reddish brown to black in color. Some of these large cockroaches can live up to 2 years in the adult stage. Adult females can produce an egg case about every 1–2 weeks. A typical female will produce about 20–80



Cockroaches (Blattodea), Figure 70 **Some common cockroaches: top left, German cockroach, *Blatella germanica*; top right, brown-banded cockroach, *Supella longipalpa*; second row left, American cockroach, *Periplaneta americana*; second row right, Australian cockroach, *Periplaneta australasiae*; third row left, smoky-brown cockroach, *Periplaneta fulginosa*; third row right, Florida woods cockroach, *Eurycotis floridana*; bottom left, Oriental cockroach, *Blatta orientalis*; bottom right, Cuban cockroach, *Panchlora nivea* (photos by J. L. Castner, University of Florida).**

oothecae during her lifetime, each containing 15–20 nymphs. Peridomestic females release the egg case from their body soon after it has developed. They then glue the egg case to a surface, usually in a hidden, moist area. In contrast, German cockroach females continue to carry the egg case throughout embryonic development.

Some cockroaches live both indoors and out-of-doors, especially in warm climates, and are called "peridomestic" cockroaches. Peridomestic cockroaches normally breed outdoors in sewers, palm trees, tree holes, piles of firewood, water meters, well pumps, mulch, and flower beds. These cockroaches usually enter homes only occasionally, when foraging for food, water or warmth. In some situations, however, they will establish breeding populations in attics, crawl spaces, wall voids and other indoor areas.

Management

Exclusion and Sanitation

Long-term prevention of cockroach infestation is the best means of ensuring a cockroach free environment. This is most easily accomplished by exclusion (preventing cockroach entry) and sanitation (elimination of cockroach resources). Not only will these measures prevent a future infestation, they will also help to reduce an existing cockroach problem. Methods of preventing cockroach entry include:

- Cockroaches migrate easily through multi-unit dwellings via plumbing and electrical connections. Sealing gaps around plumbing, wall outlets and switch plates will prevent cockroaches from migrating from infested units to others.
- Keep doors and windows closed and screened. Also, caulk cracks and gaps that may allow peridomestic cockroaches to invade from outdoors.
- Peridomestic cockroaches frequently enter homes by coming up through dry drain traps. Periodically run the water in spare bathrooms, utility tubs and toilets to keep the drain trap filled and off limits to cockroaches.
- Covering vent pipes on the roof with fiberglass window screen will prevent cockroaches from migrating up from sewer connections and gaining ready access to the roof, and hence to attics and windows.
- Groceries, produce and other packaged food products may have been stored in infested locations before they were purchased. Make an effort to visibly scan all grocery items for evidence of cockroachs before putting them away.
- Children can transport cockroaches from school to home in book bags and lunch pails. Inspect these items on a regular basis.

Sanitation is critically important. For example, German cockroaches can remain alive for approximately 2 weeks with no food or water and for 42 days if only water is available. Therefore, it is important to realize that cockroaches can survive on minute amounts of food such as crumbs, grease or food residue.

- Indoor trash containers should be emptied frequently, and kept clean both inside and out. Plastic bags lining trash containers can be kept closed with twist ties. This will prevent cockroaches from being attracted to the garbage area.
- Filled indoor garbage containers should be removed from the dwelling immediately and placed in outdoor containers with tight fitting lids or dumpsters.
- Keeping the area around dumpsters or other outdoor garbage storage areas clean and free of debris will also prevent peridomestic cockroach infestations in the area.
- Frequent emptying of sink strainers and running of the garbage disposal and will prevent food build up in the sink drain.
- Washing dishes immediately after a meal will prevent cockroaches from consuming food residue on dishes. Unwashed dishes are a major source of food for German cockroaches.
- Kitchen appliances (toasters, toaster ovens, microwaves, ovens, stoves, and refrigerators) should be kept clean and free of food particles

and grease. Additionally, the areas underneath and behind these appliances should be kept grease and crumb free.

- If pets are present, dry food should be kept in resealable containers. Do not leave food and water out all the time. Feed your pet at particular times and clean up after every meal.
- All foods products should be resealed after opening, stored in plastic snap-lid containers, or kept in the refrigerator.
- Regular sweeping/vacuuming of floors and furniture helps to eliminate cockroach food sources.
- Regular cleaning of food storage areas and shelves not only eliminates spilled or scattered food, but disrupts cockroach populations that may be using the area as a harborage.

The single most important factor in determining cockroach survival is availability of water. German cockroaches live <2 weeks without a supply of free water, even if food is abundant. During periods of drought, the incidence of peridomestic cockroaches indoors will often increase as these large cockroaches invade structures in search of moisture. Therefore, it is important to eliminate all sources of moisture that contribute to cockroach survival. Important steps in water management include:

- Tightening loose pipes, patch plumbing leaks and replace used washers in the kitchen sink and bathroom areas. Outdoor water spigots and sprinklers should also be checked for drips and leaks.
- Water left in the sink or bathtub after dish washing or bathing also provides moisture for cockroaches. These sources are eliminated by drying out sinks and bathtubs after use.
- A common source of moisture is condensation under the refrigerator. This area should be frequently wiped dry or, if possible, a pan should be placed under the appliance to collect water. The collection pan should be emptied frequently. Condensation on pipes (under the sink or in wall voids) is also a problem. Insulate these pipes, if possible.
- Pet drinking dishes and aquariums are also sources of moisture. Empty pet water dishes at night when cockroaches are foraging but the pet is indoors or asleep. Aquariums should have tight fitting lids or screens to prevent cockroach entry.
- Be careful not to over-water indoor plants, because excess water is available to cockroaches.
- Glasses, cups and soda cans containing water or liquid residue are common sources of moisture for cockroaches. Be sure not to leave these containers in bedrooms, sinks, on counter tops or other areas. Rinse and invert cups and glasses to dry immediately after use, and dispose of soda cans in trash containers.
- Steps should be taken to eliminate places where water collects outdoors (tires, cans, tree holes, etc.). This will not only eliminate cockroach moisture sources but also mosquito breeding habitat.

The third critical element for cockroach survival is harborage. By nature, cockroaches avoid open, well-lighted areas with frequent air movement. They prefer dark, warm cracks and crevices. Excess clutter provides numerous locations suitable for cockroach habitation. The elimination of these harborages (clutter) is important in controlling infestations. Practices that reduce harborage include:

- Adult cockroaches can fit into cracks only 1.6 mm wide (about 1/16 of an inch). Any small gap or hole that leads to a void is a prime cockroach harboring area. Cracks and crevices of this kind should be sealed with a tube of caulking.
- Removing clutter (boxes, bags, clothing, toys, food, books, papers, etc.) eliminates cockroach harborages and breeding areas. It is essential to keep all areas of the home, especially the kitchen and bathroom, uncluttered and free of useless debris.
- Outside, remove debris and trash from around the house.
- Stack firewood far away from the house, as this is a prime harborage area for peridomestic cockroaches.
- Filling in tree holes with cement also eliminates peridomestic cockroach harborage.
- Keep shrubbery and ornamentals well trimmed. In particular, keep palm trees free of loose and dead palm branches and remove all palm debris.

Toxicants

Usually it is desirable to eliminate the need for toxicants, but this is not always possible. Reduced chemical control methods currently are available for indoor and outdoor cockroach control. The traditional approach of cockroach control based on application of liquid insecticides to floor, wall, and fixture surfaces has been supplanted by more selective application techniques. The most recent technological advances in reduced toxic and non-toxic cockroach control have been in bait formulations, and in insect growth regulators. Other currently used non-toxic measures include desiccating dusts, traps and biological controls. Each of these treatment methods can contribute to an effective cockroach management program. On the other hand, although ultrasonic devices are frequently advertised as a non-toxic method of cockroach control, extensive research has shown that these devices neither kill nor repel cockroaches.

Cockroach Baits

Cockroach baits consist of a toxicant mixed with a food source. Some baits also contain attractants or feeding stimulants designed to make the bait more attractive to cockroaches than other food sources that may be available in the immediate area. Current indoor bait formulations are applied as dusts, pastes, gels or bait stations. The bait station is one of the more popular application methods for cockroach baits. This is because the stations are easy to put out, safe around children and pets and have residual activity. Gel and dust bait formulations are formulated for injection into cracks and crevices, which reduces the potential contact of people with toxicants, and places the toxicants in areas frequented by cockroaches.

Bait stations for peridomestic cockroaches are simply larger versions of those used for German cockroach baiting. The problem with this baiting system is that peridomestic species live and breed outdoors in palm trees, woodpiles, tree holes and other areas where bait station placement is difficult. The homeowner will often want the large bait stations placed inside the structure in order to kill peridomestic cockroaches that are caught foraging inside. This, however, does nothing about the population of cockroaches that continues to breed outdoors.

Outdoor baiting products are used primarily for the control of peridomestic cockroaches. Spreadable granular baits or bait stations are the most common formulations used for peridomestic cockroach control. Spreadable baits are usually applied as a perimeter band around a structure, and can effectively suppress populations and reduce invasion rates of households. However, it is difficult to determine the residual longevity of these products, particularly in areas where precipitation is frequent. Even "weatherized" baits have difficulty retaining their residual properties where there is heavy rainfall or irrigation. This is particularly true in the southeastern United States where precipitation can ruin bait effectiveness in a single day.

Insect Growth Regulators

Insect growth regulators (IGRs) are a group of compounds that disrupt the normal growth and development of insects. The IGRs are considered to be reduced-risk tools. They generally have very low toxicity to mammals because they act by disrupting the hormonal processes that are specific to insects. IGRs that mimic the juvenile hormones of insects are called juvenile hormone analogues (JHAs). JHAs are chemical compounds with structural chemistry that is very similar to the hormones that the immature cockroach produces naturally. JHAs interfere with the proper development of last instar cockroach nymphs. Instead of the nymphs molting into reproductive adults they molt into "adultoids," which often have twisted wings and are sterile. Because the adultoids are unable to reproduce, over the course of time the cockroach population will decline. JHAs are an effective method of long term German cockroach control. However, because JHAs eliminate reproduction but do not kill existing cockroaches, they are very slow acting (from 4 to 9 months to achieve control). JHAs are often combined with residual insecticides. In this manner most of the population can be eliminated quickly by the insecticide, and cockroaches that survive the insecticide treatment are then sterilized by the JHA. Insect growth regulators are available in spray formulations or point source dispensers, where the IGR is released on a filter paper contained in a permeable plastic station then transmigrates throughout the infested area.

Chitin synthesis inhibitors (CSIs) are another type of insect growth regulator that is being developed for use in management programs targeting a variety of insect pests. Exposure to CSIs results in the abnormal molting of nymphs, causing them to die during the molting process. CSIs also cause adult cockroaches to form abnormal egg cases and interferes with the hatching process.

Inorganic Dusts

Inorganic dusts such as silica gel and boric acid have been used frequently for indoor cockroach control. The dusts are applied with a squeeze-bulb duster into cracks and crevices under sinks, stoves, behind refrigerators, along baseboards, in electrical outlets, cabinets and wall voids. Silica gel is simply a finely ground sand-like product that adheres to, and absorbs, the protective waxes on the cockroach cuticle, resulting in cockroach death from dehydration. Boric acid is a stomach poison that is picked up by cockroaches walking across dusted areas. The boric acid adheres to the cockroach cuticle so when the cockroach grooms itself it ingests the boric acid and soon dies.

Traps

One of the non-chemical tactics available for reducing a cockroach infestation involves the use of traps. Sticky traps can be purchased and placed indoors, near the garbage, under the sink, in the cabinets, under and behind the refrigerator, and in the bathroom. Outdoors, sticky traps are not recommended because they tend to capture many non-target animals (snakes, lizards etc.), and are not resistant to weathering.

A second trapping method is the use of baited jars. Any empty jar (pickle, mayonnaise, peanut butter, etc.) with a rounded inside lip will suffice. Coat the inner lip of the jar with a thin film of Vaseline (to keep trapped cockroaches from escaping). The jar should then be baited with a quarter slice of bread soaked in beer (a cockroach favorite). If beer and bread are unavailable try other foods like cookies, dog food, apples, etc. The outside of the jar should be wrapped in paper towel so cockroaches have a surface to grasp as they climb up the sides of the jar. To kill trapped cockroaches simply pour dishwashing detergent into the jar and add hot water. The cockroaches can then be dumped outside or in the garbage. Wash out the jar and repeat the process every 2–3 days. Indoor jar traps should be placed in the same locations as those listed for sticky traps. When trapping outdoors, jars should be placed in trees, tree holes, mulched areas, firewood, near trash cans, compost piles, air conditioning units and storage sheds. Covering the jars with a dome-shaped piece of aluminum foil taped to the sides will prevent rain from filling the traps. Jar traps are very suitable for outdoor use because they present little threat to non-target organisms, and are not easily damaged by weather.

Biological Control

Natural controls do play an important role in managing cockroach populations. Natural cockroach enemies include wasps, nematodes, spiders, toads and frogs, centipedes, birds, lizards, geckos, beetles, mantids, ants and small mammals (mice). It is very important that these populations of natural enemies be maintained to help keep cockroach populations in check. Often, the importance of natural enemies in keeping the cockroach problem in check is overlooked.

Oothecal Parasitoids

Parasitic wasps are an important natural enemy of cockroaches. The wasps are parasitoids of the cockroach egg case (ootheca) and can have a significant negative impact on outdoor cockroach populations. Most species of parasitoid wasps are associated with peridomestic cockroaches. The majority of these wasps are minute (1–5 mm) and do not sting humans. Peridomestic cockroaches like the American and smoky-brown live in outdoor harborages such as palm trees, tree holes, and woodpiles. The parasitoids live with the cockroaches in the harborage parasitizing their egg cases. When the adult male and female wasps emerge they mate immediately. The female then begins to sting other oothecae, laying her eggs inside them. The wasp offspring eat the cockroach embryos inside the ootheca before hatching. This natural system results in 60–70% of all cockroach egg cases being parasitized without any human interference.

Oothecal wasp parasitoids have been tested for potential indoor use. Domestic populations of brown-banded cockroaches were successfully controlled in a California animal rearing facility by these wasps. However, it is doubtful that parasitoid wasps will ever be reared for commercial use. Very few individuals would welcome a population of 200,000 wasps in their home even if they promised to eliminate a severe cockroach infestation. Wasp parasitoids are extremely susceptible to pyrethroid insecticides. When attempting to eliminate an outdoor cockroach infestation, it is important to realize the insecticide applications in peridomestic cockroach harborages may not kill all of the cockroaches but it certainly will eliminate the parasitoids. This can result in future cockroach problems because surviving cockroaches can reproduce unchecked once the parasitoids are eliminated. The application of bait around an infested area is the best way to treat a population of peridomestic cockroaches and preserve the wasp parasitoids.

► Boric Acid
► Diatomaceous Earth
► Baits for Insect Control
► Insecticides
► Insecticide Resistance
► Urban Entomology

References

Arnett RH Jr (2000) American insects, 2nd edn. CRC Press, Boca Raton, FL, 1003 pp

Bell WJ, Roth LM, Nalepa CA (2007) Cockroaches: ecology, behavior, and natural history. The Johns Hopkins University Press, Baltimore, MD, 230 pp

Cornwell PB (1968) The cockroach, vol 1. Hutchinson & Company, London, UK, 391 pp

Fisk FW (1987) Order Blattodea. In: Stehr FW (ed) Immature insects, vol 1. Kendall/Hunt Publishing, Dubuque, IA, pp 120–131

Miller DM, Koehler PG (1999) Least toxic methods of cockroach control. Florida Cooperative Extension Service Publication ENY-258

Roth LM, Willis ER (1960) The biotic associations of cockroaches. Smithsonian Miscellaneous Collections, vol 141, pp 1–470

Cockroaches and Disease

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The importance of domestic cockroaches (those invading our buildings) as public health pests, especially as vectors of disease, is somewhat uncertain. Although many pathogenic organisms have been isolated from cockroaches, there is only circumstantial evidence to link diseases in human beings to the causal agents of those disorders known to be present on and in cockroaches closely associated with humans (Table 16).

Cockroaches rank with termites as the most important insects found in association with humans. Cockroaches can be found in most any place humans inhabit, especially where food is stored, processed, prepared, or served. They seek not only our food, but also putrefied and decaying matter, virulent discharges, and feces. Cockroaches

Cockroaches and Disease, Table 16 Pathogens associated with cockroaches[a]

Pathogen type	Pathogen	Potentially associated disease	Cockroach species
Bacteria	*Alcaligenes faecalis*	wound infection, gastroenteritis	American, Oriental
	Bacillus spp.	food poisoning, conjunctivitis	American, Oriental
	Campylobacter jejuni	enteritis	American, Oriental
	Clostridium spp.	gas gangrene, food poisoning	Oriental
	Escherichia coli	diarrhea, wound infection	American, Oriental, German
	Klebsiella pneumoniae	pneumonia, urinary infections	Unspecified cockroaches
	Mycobacterium leprae	leprosy	German, American, Australian
	Nocardia spp.	actinomycetoma	American
	Proteus spp.	wound infection	American, Oriental
	Pseudomonas aeruginosa	respiratory infections, gastroenteritis	American, Oriental, German
	Salmonella spp.	food poisoning, gastroenteritis	American
	Salmonella typhi	typhoid	Oriental
	Streptococcus pyrogenes	pneumonia	Oriental
	Serratia marcescens	food poisoning	American, Oriental, German
	Shigella dysenteriae	dysentery	German
	Staphylococcus aureus	wound, skin and internal	German
		infections	Oriental
	Streptococcus faecalis	pneumonia	American, Oriental, German
	Yersinia pestis	plague	Oriental
Fungi	*Aspergillus* spp.	respiratory infections	American, Oriental
Helminths	*Ancylostoma duodenale*	hookworm	American
	Ascaris lumbricoides	giant human roundworm	American
	Ascaris spp.	roundworm	Oriental
	Enterobius vermicularis	pinworm	Oriental, German
	Hymenolopsis spp.	tapeworm	American
	Necator americanus	hookworm	American
	Trichuris trichuria	whipworm	American, Oriental, German
Molds	*Aspergillus niger*	otomycosis	Oriental

Cockroaches and Disease, Table 16 Pathogens associated with cockroaches[a] (Continued)

Pathogen type	Pathogen	Potentially associated disease	Cockroach species
Protozoans	*Entamoeba hystolytica*	amebiasis	Oriental, Australian, German, American
	Giardia spp.	giardiasis	Unspecified cockroaches
Viruses	*Poliomyelitis*	paralytic polio	German, American, brown-banded

[a]Extracted from Roth LM, Willis ER (1960) The biotic associations of cockroaches. Smithsonian Institute, Washington, DC, 439 pp

readily move from garbage disposal areas, to sewers, to toilets, to food ready for consumption. This movement creates the opportunity for the contamination of food and food preparation surfaces with disease-causing organisms.

Important Species

Cockroaches are tropical or subtropical in origin. Species that have adapted to living indoors originated in tropical Africa. Cockroaches probably became domesticated in prehistoric times when humans were cave dwellers. As humans evolved to more sophisticated structures, the cockroach also moved, readily adapting to new surroundings. Homes, restaurants, hospitals – any place that has warmth, food and water available – form ideal environments for the proliferation of these pests.

Only a small number of species have moved from the fields and forests to take up residence in our structures. And of these domestic species, the German, Oriental, and American cockroaches are the most important species because of their wide distribution and common occurrence in buildings. The German cockroach is most often found in close association with kitchens and other food areas. American and Oriental cockroaches may also be found in food areas, but more often are found in basements, sewers, crawl spaces, and outdoor areas. Each of these species is routinely found in areas of filth and decaying organic matter. Thus, filth organisms are found both on their bodies and within their digestive tracts.

Public Health Importance of Cockroaches

Numerous published papers recount the incidence of cockroaches, their association with disease and filth organisms, their production of odorous secretions that can contaminate and affect the flavor of foods, the socially unacceptable nature of cockroaches in homes, and in some cases, the fear and anxiety some individuals have of cockroaches. These problems are justification for the large sums of money spent each year to control these pests.

Domestic Nuisance

Cockroaches are among the most common insects found associated with humans. They breed in our buildings and share our food, water, warmth and shelter. They consume the same food that we eat, as well as dead plant or animal materials, leather, glue, hair, wallpaper, fabrics, book bindings, and feces. They contaminate food by crawling around and defecating on it, or by leaving cast skins, empty egg cases, or dead bodies in foodstuff. They regurgitate saliva and intestinal fluids from their mouths while feeding and deposit fecal droppings as they crawl around on food. The nasty habits of this pest cause fear and social embarrassment for homeowners.

Cockroach Bites

Cockroaches have been reported to bite humans, although such instances are rare and not serious. They have been noted to gnaw on the skin and nails of sailors aboard heavily infested ships. Cockroaches are most likely to nibble on the eyelashes, fingernails, and toenails of sleeping children and the infirm, and in cases of heavy infestations they can cause small wounds on softer skin.

Accidental Invasion of the Body

Numerous accounts of cockroaches entering the ear, nose, or other body orifices have been recorded. These invasions usually occur at night when the human "host" is sleeping and when cockroaches are most active. There have also been instances of intestinal invasion by cockroaches, usually in young children in severely infested living conditions. As cockroaches forage for food in heavily infested areas, it certainly is possible for them to enter orifices of the body, especially when the person is sleeping and quite still.

Disease Carriers

Published papers recount the incidence of cockroaches and their association with disease organisms. They document the evidence that cockroaches carry pathogens in and on their bodies and in their excreta, but are unable to establish any cause and effect relationship with disease in humans. So to date, cockroaches can only be viewed with suspicion.

Incriminating evidence is difficult to find linking cockroaches as vectors of disease outbreaks. There are many anecdotal stories, such as the one about an epidemic of food poisoning caused by *Salmonella* among children in the nursery of a hospital in Brussels. The infection persisted for 2 months, despite isolation of the patients. Cockroaches were considered as carriers only after a night nurse drew attention to an infestation of *Blattella germanica*, the German cockroach. The insects were observed running over the bed clothing and over the children at night. Among the cockroaches caught, one was found to be carrying numerous bacteria identified as *Salmonella*. When the cockroach infestation was eliminated, the food poisoning epidemic stopped immediately. Thus, the circumstances were very suspicious, but there was no conclusive evidence that the cockroaches were involved in the disease outbreak.

It is important to note that over 30 species of bacteria, most of them potentially pathogenic, have been found on cockroaches collected from public buildings, along with numerous viruses, protozoans, mold fungi, intestinal helminths (pinworms, tapeworms, etc.), and secretions which "may have" mutagenic and carcinogenic effects. So there certainly is not a lack of pathogens found on and in cockroaches.

Allergies

Some people are allergic to cockroaches. Cockroach secretions, body parts, and excrement contain a number of allergens to which many people exhibit allergic responses, such as skin rashes, watery eyes, and sneezing. For some very allergic individuals, and particularly for those who also have a lung disease such as asthma, allergic reactions to cockroach allergens can be very serious and even life threatening. "Cockroach asthma" is caused by the inhalation of any one of a number of protein fractions found in cockroaches that can cause allergies.

High- and low-molecular-weight proteins that have been isolated from cockroach extracts have been used to illicit bronchospastic allergy responses in humans, with allergies to cockroaches being the second most common allergy in asthmatics (with even more important sensitivity occurring in asthmatic children in severely infested homes). Dermatitis and conjunctival edema also occur in asthmatic and skin-sensitive populations.

Exposure to cockroaches increases the incidence of reaction to cockroach allergens. Sensitivity is quite high among asthmatic children in severely infested homes. Any conditions favorable to an increase in cockroach populations, as well as the lack of fresh airflow to remove airborne allergens, will lead to greater allergy problems. Thus, it is important to create living environments free of cockroaches, as well as those that have a good supply of fresh air.

Focus on Sanitation

Cockroach infestations do have the potential for serious health consequences. Acceptable hygiene standards (including cockroach elimination) must be implemented to avoid the social unacceptability of cockroaches, the potential contamination of foodstuffs, and the health problems that they can cause.

► Cockroaches

References

Alcamo IE, Frishman AM (1980) The microbial flora of field-collected cockroaches and other arthropods. J Environ Health 42:263–266

*Cornwell PB (1968) Diseases. In: The cockroach, vol 1. Hutchinson, London, UK

Ebeling W (1975) Pests on or near food. In: Urban entomology. University of California, Los Angeles, CA

Kang B, Chang JC (1985) Allergenic impact of inhaled arthropod material. Clin Rev Allergy 3:363–375

Roth LM, Willis ER (1957) The medical and veterinary importance of cockroaches. Smithsonian miscellaneous collection, vol 134, pp 1–147

Cocoon

A sheath, usually of silk, formed by an insect larva as a chamber for pupation.

Coconut Mite, *Aceria guerreronis* (Acari: Eriophyidae)

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The coconut mite, *Aceria guerreronis* Keifer (Acari: Eriophyidae), attacks fruits of the coconut palm, *Cocos nucifera* L., feeding in extremely dense aggregations that cause scarring and distortion of the fruits. This mite is the only eriophyid mite that is a serious pest of coconut palm, and it is considered one of the worst arthropod pests of this palm, whether grown as a crop tree or as an ornamental. It is distributed in many tropical countries.

Distribution

The coconut mite was described in 1965 from specimens collected in Guerrero, Mexico. The same year it was found near Rio de Janeiro, Brazil. Within the next several years it was found in many countries of Tropical America and also in West Africa. The native home of the species, which is especially of interest in searching for biological control agents, has been enigmatic. However, it was recently reported that DNA sequence data from disparate populations of coconut mite in the tropics of the Eastern and Western Hemispheres revealed that populations from the Americas were the most diverse, while those from Africa and Southern Asia were virtually uniform. This suggests that the mite evolved and diversified in the Americas, and spread in the tropics of the Eastern Hemisphere from a single introduction (presumably in West Africa). The coconut mite has not been found in the South Pacific Region, the original home of the coconut.

Although the coconut mite is apparently native to the Americas, coconut palms are native to the South Pacific. Earlier introductions were brought first to the Caribbean Region and then elsewhere in the American Tropics from West Africa by Europeans in the 1500s. During this same period, a small population of coconut palms was found on the Pacific coast of Panama, but these are thought to have been introduced naturally or by seafarers from the South Pacific shortly before the arrival of the Spanish. As a worldwide agricultural industry developed around the coconut in the 1800s, additional coconut varieties were introduced to many localities.

It is not known how long this mite has been associated with coconut, but based on anecdotal evidence provided by farmers and other observers in various localities of the Americas, local people had been familiar with the damage typical of this mite long before it was discovered and described taxonomically. The greatest diversity of cocosoid palms, i.e., genera related to the monotypic *Cocos*, is found in South America. It has thus been suggested that the original host of the coconut mite may have been a *Cocos* relative native to the Americas.

The most dramatic extension of the range of coconut mite in recent years occurred in the late 1990s, when it was found for the first time on coconuts in Tanzania (East Africa), India, and Sri Lanka.

Description

The adult female of coconut mite, which is the largest stage, is 205–255 μm long and 36–52 μm wide. The mites are white and translucent. Like eriophyid mites in general, they are elongate and possess two pairs of legs, instead of four pairs as is typical of mites in general. Massive colonies of the mites, but not individual mites, can be detected with difficulty with a 10X hand lens. At this magnification, the colonies appear as vague silvery patches.

Hosts

In nearly all localities where coconut mite is present, its only reported host is coconut palm. Rare exceptions include a record of this mite on fruit of *Lytocaryum weddellianum* (H.A. Wendland), and on queen palm, *Syagrus romanzoffiana* Chamisso (Glassman), both of which are cocosoid palms native to Brazil. Coconut palm varieties differ in their susceptibility to coconut mite. Almost all varieties have some level of susceptibility.

Biology and Ecology

The mites infest the abaxial (lower) surfaces of the tepals and that part of the fruit surface that is covered by the perianth. They are able to penetrate between the perianth and fruit surface a month after the fruit begins development. Prior to this, the tepals are too tightly appressed to allow entry of the mites.

The coconut mite has inefficient host-finding capabilities that are compensated for by a high reproductive rate and rapid development. Presumably, a population on a fruit is initiated by one or more fertilized females usually from either infested fruits on the same palm, perhaps even the same raceme, or from a nearby infested palm. The mites feed by piercing the superficial plant tissue to elicit juices which they then imbibe. A coconut mite develops from egg to adult in 10 days; thus, populations can build up rapidly. Often, thousands of mites in each of several aggregations occupy the same fruit. Massive populations of coconut mites may be present among the tepals and on the fruit surface beneath the perianth until about the sixth month of the coconut's development, after which populations decline. They are no longer present on mature (12-month old) fruits.

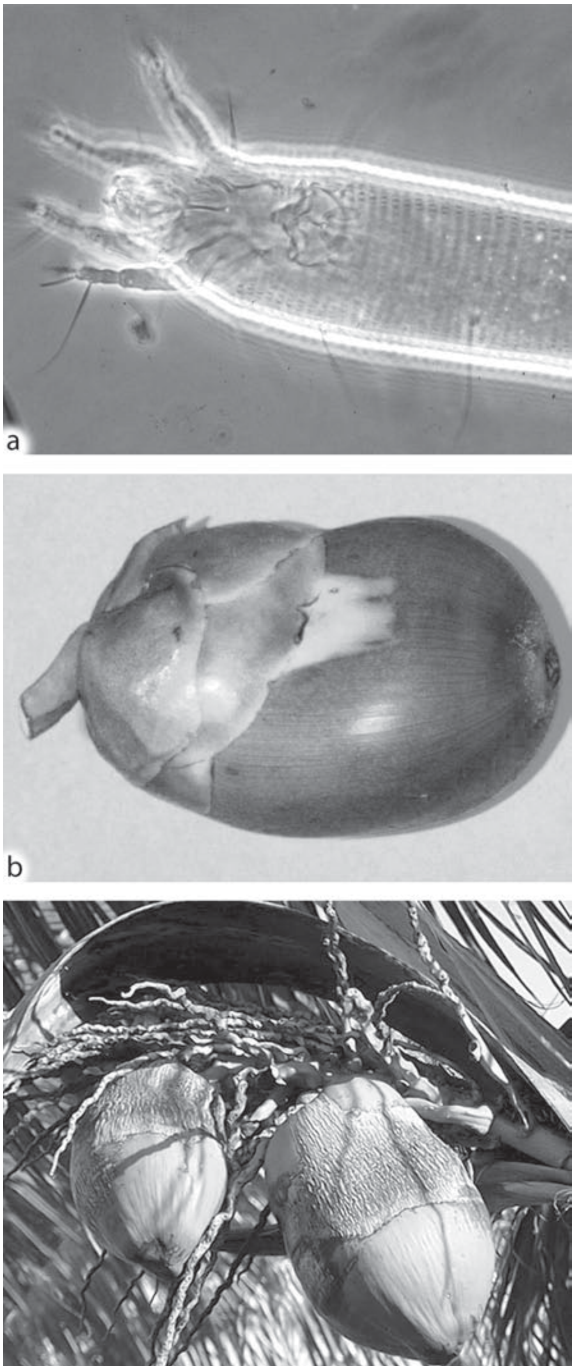
Coconut mites are probably capable of dispersing from one palm to the other on air currents or by phoresy (e.g., riding on insects or birds that visit palm flowers). Where coconut palm plantings are dense, the mites may disperse to new hosts by being blown a short distance, and in some cases probably crawl from one palm to another on foliage that is in contact, ultimately arriving on a fruit. Thus, their potential to spread to new host palms is greater where the palms are in close proximity. In densely planted coconut plantations, up to 100% of the palms are often infested, while the percentage infested is typically lower in more widely spaced plantings of coconut palm. However, isolated coconut palms may sometimes be highly infested.

Some researchers indicate that the coconut mite is most damaging to palms under dry conditions, i.e., growing in relatively dry regions or during the dry season in tropical areas with pronounced wet and dry seasons. Potential explanations for this relationship include that under dry conditions the perianth may open slightly so as to allow mites to enter more easily, that the coconut may develop more slowly and thus remain longer in a susceptible stage, or that fungi that help regulate the mites may be suppressed. However, other researchers have reported that coconut mite attack increases in wet periods, or that there is no clear association between seasonal rainfall patterns and coconut mite populations.

Damage and Economic Importance

The feeding site of the coconut mite is on the surface of the meristematic zone of the coconut fruit. This is a circular whitish zone covered by the perianth. The fruit expands from this zone, so that the young fruits of about 2.5–3.0 cm in length and diameter develop to the mature coconut of up to 25 cm long during the period of about 1 year.

An early-stage infestation of a young coconut by coconut mites (Fig. 71) is often detectable as a small pale area, often triangular but sometimes broader, extending on the fruit surface from beneath the perianth. With exposure to the air, the pale area turns brown within a few days. The location of damaged sites on individual coconuts is partly determined by the arrangement of tepals of the perianth. Damage tends to be greater under tepals that overlap adjacent tepals at both ends, because mites find more space there than under tepals whose ends are overlapped. As an infested coconut develops, the tissue extending from beneath the perianth continues to incur damage, thus the damaged area eventually covers a large portion of the surface. In older damage, the affected surface is suberized (cork-like), with deep longitudinal fissures which may be intersected by horizontal cracks. If intense mite feeding is concentrated on one side of the fruit meristem, the fruit may develop unevenly,



Coconut Mite, *Aceria guerreronis* (Acari: Eriophyidae), Figure 71 **(above) A coconut mite, *Aceria guerreronis*; (center) young coconut fruit with early damage (pale triangular area) due to feeding of the coconut mite, *Aceria guerreronis*; (below) coconuts with suberized surfaces due to feeding of the coconut mite, *Aceria guerreronis*.**

forming a distorted coconut. Highly severe damage stunts the fruits. Some observers report that damage to young fruits causes excessive numbers of them to drop, but other researchers suggest that some fruit shedding is normal and in many cases the additional fruit shedding that may be caused by coconut mites may not significantly affect yield of copra and other coconut products.

Copra, a main product of the coconut industry, is the white kernel, or coconut "meat" after it is dried. In one study, coconut mite damage was found to cause a loss of up to 30% of the copra. Other researchers have reported a less serious impact on copra production.

In many tropical countries, millions of coconuts are sold fresh in roadside stands and farmers' markets for coconut water, i.e., the clear liquid in the coconut that serves as a beverage and is sometimes erroneously called "coconut milk." (In the coconut industry, the latter term applies to the paste made by grinding the kernel.) Data is not available on the possible impact of the coconut mite on the production of coconut water, but the unappealing appearance of mite-damaged coconuts has been shown to adversely affect sales of this product.

Coconut palms are an essential feature in the landscape of tropical resort areas, and are treasured by many residents of the tropics. Damage by coconut mite does not affect the vigor of the palm and the scarred coconuts are not highly noticeable from a distance, but the aesthetic damage is important to homeowners or managers of areas where coconuts are seen up close, such as in the landscaping around hotel swimming pools.

Coconut mite damage can be spotted at a distance, but must be confirmed by closer examination. At maturity, the surface tissues of a coconut dry and become a tan color. Prior to maturing, coconuts are green, yellow, bronze, apricot, or a blend of these colors, depending on variety. Thus, the dark brown color of coconut mite damage is most noticeable when the fruit is young. Any kind of mechanical damage can result in browning of the surface of young coconuts, but coconut mite damage consistently extends from beneath the perianth, which is not true of other kinds of mechanical damage.

Colomerus novahebridensis Keifer is an eriophyid mite present in southeast Asia and the Pacific that causes damage to coconuts that is similar but much lighter and less frequent than that of *A. guerreronis*. In Florida, Puerto Rico, and presumably elsewhere in the Caribbean Region, *Tarsonemus* sp. (Acari: Tarsonemidae), causes damage similar in appearance to early coconut mite damage. However, this mite is rare, and apparently does not remain long on coconut fruits, as the damage never advances beyond the early stage. *Stenotarsonemus furcatus* DeLeon, which has been found in association with damage on coconut fruits in Brazil, may be the same or a similar species.

Management

Chemical Control

Some acaricides have been shown to kill coconut mites. However, most chemicals applied topically had to be repeated indefinitely to maintain control. Systemic acaricides might persist longer in the plant, but such chemicals could result in residues in the fruits, and coconuts are harvested throughout the year. Chemical control is perhaps the least viable option for control of coconut mite.

Mechanical Control

A simple mechanical form of control practiced by some plantation managers is to prune all of the coconuts in all stages of development. This is said to result in a plantation free of coconut mites for an extended period. However, this method would cause a disruption in the economic benefits of the plantation.

Cultural Control

As mentioned above, results of studies of environmental factors influencing coconut mite populations, including wet or dry conditions and nutrient levels, have been thus far controversial. Future research may provide a basis for economically feasible cultural control of the coconut mite.

Host Plant Resistance

Common coconut varieties in the Americas, *viz*., 'Jamaica Tall,' 'Panama Tall,' 'Malayan Red Dwarf,' 'Malayan Yellow Dwarf,' and 'Malayan Green Dwarf,' are all highly susceptible to coconut mite. Some observers have reported that certain varieties of coconut in some countries appear to be resistant to coconut mite. A highly resistant Cambodian variety was reported on a research station in Africa. It was suggested that the spherical shape of the fruit of this variety perhaps resulted in a very tight perianth that excluded coconut mites. In a study in St. Lucia, West Indies, highly spherical coconuts had less coconut mite damage than elongated coconuts on the same palm. However, extensive damage of coconut mites on some spherical-fruited coconut varieties has been observed.

Biological Control

Predatory mites found beneath the coconut perianth and in some cases observed to prey on coconut mites have been reported in various localities. They include *Bdella distincta* Baker and Balock (Bdellidae); *Amblyseius largoensis* Muma, *Neoseiulus mumai* Denmark, *N. paspalivorus* DeLeon (Phytoseiidae); *Lupotarsonemus* sp. (Tarsonemidae); and *Proctolaelaps bickleyi* Bram. (Ascidae). Under natural conditions, predatory mites have a minor effect at best on populations of the coconut mite, but researchers continue to explore the possibilities of biological control of coconut mite.

The fungus *Hirsutella thompsonii* (Fisher), which is widely distributed and known to attack various species of mites, has been isolated from coconut mites in various countries, as has *H. nodulosa* Petch in Cuba. Control of several species of mites with fungus has been attempted, but success has often depended greatly on environmental conditions. In general, these efforts have been most successful under humid conditions favoring the development of the fungi. However, some recent advances in myco-acaricide development have been encouraging.

Because coconut mites are almost microscopic and pass almost all of their life cycle in a cryptic habitat, it appears possible that in some regions the mite may be present at undetected levels. If such regions were known (e.g., if surveys in the South Pacific Region should reveal the presence of the coconut mite at extremely low levels), they would be promising sources of effective natural enemies of the coconut mite.

References

Navia D, de Moraes GJ, Roderick G, Navajas M (2005) The invasive coconut mite *Aceria guerreronis* (Acari: Eriophyidae): origin and invasion sources inferred from mitochondrial (16S) and nuclear (ITS) sequences. Bull Entomol Res 95:505–516

Fernando LCP, Moraes GJ, Wickramananda IR (2002) Proceedings of the international workshop on coconut mite (*Aceria guerreronis*), Sri Lanka, 6–8 January, 2000. Coconut Research Institute, Sri Lanka, 117 pp

Howard FW, Abreu-Rodriquez E, Denmark HA (1990) Geographical and seasonal distribution of the coconut mite, *Aceria guerreronis* (Acari: Eriophyidae), in Puerto Rico and Florida, USA. J Agr 74:237–251

Howard FW, Moore D, Giblin-Davis R, Abad R (2001) Insects on palms. CABI Publications, Wallingford, UK, 400 pp

Moore D (2000) Non-chemical control of *Aceria guerreronis* on coconuts. Biocontrol News Inform 21:83N–87N

Moore D, Howard FW (1996) Coconuts. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyid mites – their biology, natural enemies, and control. Elsevier, Amsterdam, The Netherlands, pp 561–569

Cocoon Breaker

A structure found on Lepidoptera pupae, usually on the head, that enables the insect to escape from the cocoon.

Coding Strand

The strand of the DNA molecule that carries the biological information of a gene and which is transcribed by RNA polymerase into mRNA.

Codling Moth, *Cydia pomonella* (Linnaeus) (Lepidoptera: Tortricidae)

This is one of the most important pests of apple fruit.

► Apple Pests and Their Management

Codon

A triplet of nucleotides that code for a single amino acid.

Coelomomyces

The phylum Chytridiomycota, once considered a member of the Mastigomycotina, is now included with the Oomycota in the kingdom Protoctista. Within the Chytridiomycetes, *Coelomomyces* (order = Blastocladiales) is the most notable insect pathogen. This genus contains more than 70 species and has been found worldwide. *Coelomomyces* is unique among the entomopathogenic fungi in that it requires two different hosts to complete its life cycle. The insect hosts are usually mosquito larvae, although other dipterans such as black flies and midges, as well as some backswimmers (Hemiptera), also can become infected. The alternate hosts are other aquatic arthropods (microcrustaceans) such as copepods and ostracods. Alternation between hosts is obligatory, i.e., zoospores produced in mosquitoes will not infect other mosquitoes, and zoospores from infected microcrustaceans will not infect other Microcrustaceae. This development of different parasitic stages within two unlike hosts is termed heteroecism and was observed in the phytopathogenic rust fungi before it was discovered in *Coelomomyces*. Heteroecism may be considered similar to the terms digenetic or heteroxenous, used to describe certain protozoa (*Amblyospora*) that require two or more hosts for survival. *Coelomomyces* has not yet been cultured in vitro through its entire, two-phase life cycle. The in vivo culture of several species of *Coelomomyces* has been successfully achieved by cycling the fungus through its respective host systems, which in some cases can be maintained in small containers.

The occurrence of *Coelomomyces* epizootics is dependent on the presence of both hosts, the relative sizes of their populations, and the age of host mosquito larvae. Studies have shown that infection of anopheline larvae with *C. punctatus* correlates with the seasonal abundance of the alternate copepod hosts, and that early-instar larvae are more readily infected than those from later instars. In the field, it has been observed that the larvae become infected primarily at dusk. This is apparently due to the dual photoperiodicity of gamete release from the alternate hosts, which, under laboratory conditions, also occurs at this time. Environmental factors such as pH and temperature of the water appear to be much less important in infection rates of mosquito larvae and in the progress of epizootics of *Coelomomyces* than the relationship between the two host systems. Finally, with respect to host range, some species of the fungus may infect several genera of mosquitoes, while others are specific for a single species.

It is significant that under natural conditions, mosquito larvae from later instars can become infected with *Coelomomyces*. Older larvae particularly are susceptible just after molting, when the cuticle is not yet completely hardened. Infection in older larvae and even in some younger instars exposed to a low level of inoculum may not necessarily kill the insect. Heavily infected larvae do not pupate and starve to death due to the depletion of nutritional reserves from the fat body by the fungus. In contrast, larvae with light infections may pupate and develop into infected adults. The fungal hyphae migrate from the hemocoel and penetrate the ovaries. Conversion of the fungal hyphae into resting sporangia is apparently stimulated by hormones (e.g., 20-hydroxyecdysone) produced by the mosquitoes after a blood meal; in healthy mosquitoes, the same hormones influence egg maturation. It has been observed that adult *Aedes aegyptii* mosquitoes infected with *C. stegomyiae* display normal reproductive behavior with respect to copulation, sperm transfer and storage, and oviposition. However, no eggs are produced because oocytes of infected ovaries do not endocytose vitellogenin and, as a result, vitellin yolk granules cannot form. During oviposition, infected females therefore discharge piles of *Coelomomyces* resting sporangia, which fill the ovaries rather than eggs. Obviously, this provides an excellent means of dispersal of the pathogen to its alternate host.

Meiosis occurs in the germinating, resting sporangia, and the wall-less zoospores generated during this reduction division often are referred to as meiospores. Meiospores are posteriorly uniflagellate and are released from sporangia in masses covered by thin vesicles consisting of the inner regions of mature sporangial walls. Meiospores serve as the infective propagules of the alternate microcrustacean hosts. In the case of *C. dodgei*, the copepod hosts release substances recognized by the meiospores, increasing the probability of their attachment to the host cuticle. Meiospore attachment can be consolidated by secretion of adhesive material from cytoplasmic vesicles. At the time of attachment, the meiospores encyst and invade the host via a penetration germ tube. In *C. psorophorae*, appressoria may be produced and may function as an additional mechanism for attachment of the fungus to host surfaces; attachment of this species to host *Cyclops vernalis* takes place primarily in intersegmental regions. Meiospores are of opposite mating types, and each meiospore develops a thallus that will form a male or female gametangium within the alternate host. In *C. dodgei*, the male gametangia are bright orange due to the presence of carotene, and the female gametangia are light amber. Both types can occur within an individual copepod, and gametes, i.e., the haploid zoospores released as products of gametangial cleavages, therefore can fuse during swarming within the host. Alternatively, gametes may escape from the microcrustacean cadaver to mate outside the host. The biflagellate zygotes that result from mating of the gametes are the infective propagules of mosquito larvae.

Susceptibility of mosquito larvae to infection by *Coelomomyces* varies and appears to depend upon the ability of the zygotes to attach to host cuticle. Attachment of *C. psorophorae* zygotes to the cuticle of a susceptible host occurs preferentially at intersegmental membranes, on head capsules, at the bases of anal gills, and around the anus. Attachment is closely associated with encystment of the zygotes. Germination is initiated at one end of the cyst, where an appressorium forms and functions in further attaching the cyst to the host. As germination continues, a penetration tube grows from the appressorium and traverses the cuticle to the epidermal region, where the infecting fungal protoplasts are deposited into host cells. After penetration, the thalli appearing as irregularly shaped, protoplast-like thalli (hyphal bodies) invade other larval tissues, especially the fat body and the hemocoel. There is no apparent host hemocytic response to *Coelomomyces* hyphal bodies, at least in the case of *C. punctatus* infecting *Anopheles quadrimaculatus*. This could be due to masking of the fungal surface by host material or to production of fungal surface components which are interpreted as self by host defense cells. As a *Coelomomyces* infection progresses within host mosquito larvae, extensive growth and branching of hyphae occurs, and resting sporangia, which will eventually cleave into the meiospores infectious to the alternate host, form to complete the life cycle.

References

Federici B (1981) Mosquito control by the fungus *Culicinomyces*, *Lagendium*, and *Coelomomyces*. In: Burges HD (ed) Microbial control of pests and plant disease. Academic Press, London, UK, pp 555–572

Lucarotti CJ (1992) Invasion of *Aedes aegypti* ovaries by *Coelomomyces stegomyiae*. J Invertebr Pathol 60:176–184
Travland LB (1979) Structures of the motile cells of *Coelomomyces psorophorae* and function of the zygote in encystment on a host. Can J Bot 57:1021–1035
Whisler HC, Zebold SL, Shemanchuk JA (1975) Life history of *Coelomomyces psorophorae*. Proc Natl Acad Sci 72:693–696

Coelopidae

A family of flies (order Diptera). They commonly are known as seaweed flies.

► Flies

Coenagrionidae

A family of damselflies (order Odonata). They commonly are known as narrow-winged damselflies.

► Dragonflies and Damselflies

Coevolution

Reciprocal, adaptive changes in traits of two populations.

Coffee Bean Rot

Stink bugs introduce fungi into coffee berries while feeding.

► Transmission of Plant Diseases by Insects

Coffee Berry Borer, *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae: Scolytinae)

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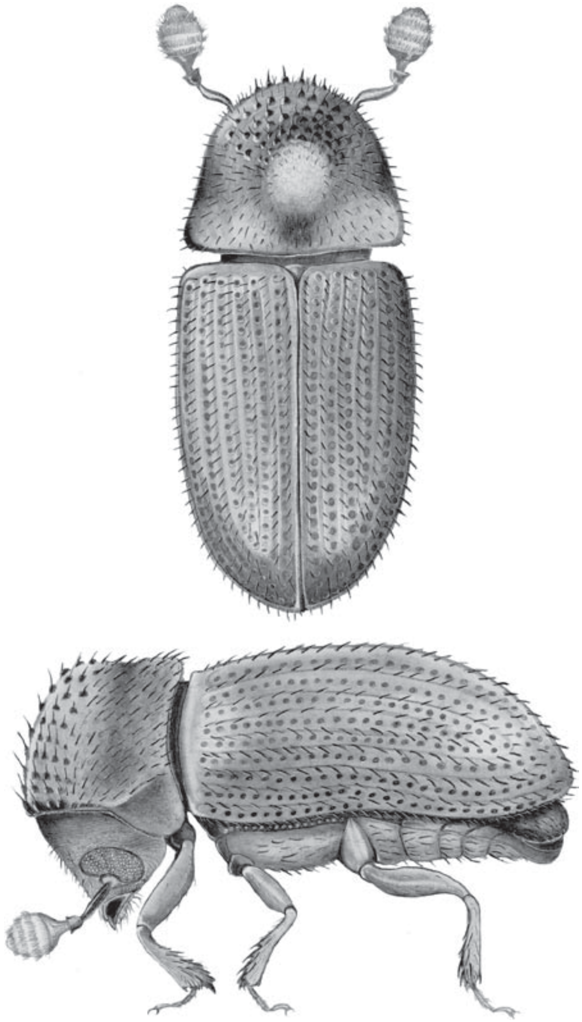
The coffee berry borer, *Hypothenemus hampei* (Ferrari), known throughout Latin America as "la broca del café," is the most devastating insect pest of coffee throughout the world. This minute insect (0.5–0.8 mm length and 0.2 mm wide) is endemic to Central Africa, and has now spread to most coffee growing regions throughout the world. Infestation levels can be quite high (e.g., Uganda 80%, Colombia 60%, Jamaica 58–85%, Tanzania 90%, Malaysia 50–90%, and Mexico 60%). It is striking that out of more than 850 insects reported on coffee, the coffee berry borer is the only one that has adapted to use the seed of *Coffea arabica* and *Coffea canephora* (=*robusta*) as its food source.

Damage begins when an adult female (Fig. 72) bores a hole into the coffee berry and deposits her eggs; larvae feed on the coffee seed, lowering its quality and possibly causing abscission of the berry. An interesting aspect of the insect's biology is the highly skewed sex ratio favoring females (10:1), which contributes to a high reproductive capacity. *Wolbachia*, a maternally inherited bacterium known to induce parthenogenetic development and skewed sex ratios favoring females, has been detected in coffee berry borers from 11 different countries.

When larvae molt into adults, they mate with their siblings inside the berry; therefore, once females emerge, they are inseminated and ready to deposit eggs into another coffee berry. In contrast to females, males remain in the berry, and are unable to fly. Thus, insect development inside the coffee berry makes this insect very difficult to control. The highly toxic chlorinated hydrocarbon endosulfan has been widely used against the coffee berry borer but some countries have banned its use. Also, the insect has developed resistance to this product. The lack of safe and effective chemical control strategies has led to strong efforts by coffee scientists in many countries to develop biological control methods relying on parasitoids and fungal entomopathogens.

Four of the most common coffee berry borer parasitoids originate in Africa: two bethylids (*Prorops nasuta* Waterston and *Cephalonomia stephanoderis* Betrem), one eulophid (*Phymastichus coffea* La Salle), and one braconid (*Heterospilus coffeicola* Schmiedeknecht). Some of these have been introduced



Coffee Berry Borer, *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae: Scolytinae), Figure 72 Adult coffee berry borer, *Hypothenemus hampei*. Drawing by Ann Simpkins (USDA).

in coffee producing countries (e.g., Colombia, Jamaica, Mexico) in an attempt to reduce coffee berry borer damage, but their mass production remains expensive due to the need for coffee seeds in which to rear the coffee berry borers used to rear the parasitoids.

The most common fungal entomopathogen isolated from the coffee berry borer is *Beauveria bassiana*, although *Isaria fumosorosea*, *Paecilomyces lilacinus*, and *Metarhizum anisopliae* have also been reported to a lesser extent. The use of *B. bassiana* as a fungal endophyte to control the coffee berry borer is being aggressively studied. The insect has also been shown to be associated with 40 species of fungi in 22 genera. Two nematodes have been reported as parasites of the coffee berry borer: *Panagrolaimus* sp. in India and *Metaparasitylenchus hypothenemi* in Mexico.

Cultural practices such as complete collection of berries on the tree and ground immediately after harvest could greatly reduce coffee berry borer population levels. However, this laborious strategy is not considered a feasible or cost-effective alternative.

► Coffee Pests and their Management

References

Baker PS (1999) The coffee berry borer in Colombia. Final report of the DFID – Cenicafé – CABI Bioscience IPM for Coffee Project, DFID – Cenicafé, Chinchiná, Colombia, 154 pp

Brun LO, Marcillaud C, Gaudichon V, Suckling DM (1989) Endosulfan resistance in *Hypothenemus hampei* (Coleoptera: Scolytidae) in New Caledonia. J Econ Entomol 82:1311–1316

Bustillo PAE, Cárdenas MR, Villalba GA, Benavides MP, Orozco HJ, Posada FFJ (1998) Manejo integrado de la broca del café *Hypothenemus hampei* (Ferrari) en Colombia. Centro Nacional de Investigaciones de Café (Cenicafé), Chinchiná, Colombia, 134 pp

Le Pelley RH (1968) Pests of coffee. Longmans, Green and Co, London, UK, 590 pp

Pérez J, Infante F, Vega FE, Holguín F, Macías J, Valle J, Nieto G, Peterson SW, Kurtzman CP, O'Donnell K (2003) Mycobiota associated with the coffee berry borer (*Hypothenemus hampei*) in Mexico. Mycol Res 107:879–887

Poinar G Jr, Vega FE, Castillo A, Chavez IE, Infante F (2004) *Metaparasitylenchus hypothenemi* n. sp. (Nematoda: Allantonematidae), a parasite of the coffee berry borer, *Hypothenemus hampei* (Ferrari) (Curculionidae: Scolytinae). J Parasitol 90:1106–1110

Posada F, Aime MC, Peterson SW, Rehner SA, Vega FE (2007) Inoculation of coffee plants with the fungal entomopathogen *Beauveria bassiana* (Ascomycota: Hypocreales). Mycol Res 111:749–758

Varaprasad KS, Balasubramanian S, Diwakar BJ, Ramarao CV (1994) First report of an entomogenous nematode, *Panagrolaimus* sp. from coffee berry borer, *Hypothenemus hampei* (Ferrari) from Karnataka, India. Plant Protect Bull 46:42

Vega F, Benavides P, Stuart J, O'Neill SL (2002) *Wolbachia infection* in the coffee berry borer (Coleoptera: Scolytidae). Ann Entomol Soc Am 95:374–378

Coffee Pests and their Management

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The perennial and evergreen nature of the coffee plant (*Coffea* spp.) favors attack by a number of insects and mites (Table 17, Figs. 73 and 74). All portions of the plants are susceptible to attack, and damage may appear at the seed bed, nursery, plantation, or in the warehouse. Certain pests affect the coffee plant only temporarily, while others live for several generations on the plant. In some instances, the attack may cause the death of the plant, but in most cases the pests only weaken the plant, reducing yield. When the bean is attacked, quality also may be affected.

Insects constitute the most numerous group of coffee pests; of more than 850 species of insects that feed on coffee in the world, approximately 200 (23.5%) have been reported in the tropical and sub-tropical areas in America. Out of these, hardly thirty species, mostly indigenous, cause losses considered important. The pests and the seriousness of the problems they cause vary from one country to another, and from one area to another. The coffee pest that is considered the most important in tropical America is the coffee berry borer, *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae: Scolytinae), now cosmopolitan but originating in Africa. The coffee leaf miner, *Leucoptera coffeella* Guérin-Méneville (Lepidoptera: Lyonetiidae), and the root mealybugs (Pseudococcidae) are causing serious problems in several countries. Bugs of the genus *Antestiopsis* (Pentatomidae), which are very harmful in Africa, have not yet been reported in the American hemisphere.

Most of the insects that are found in coffee plantations are beneficial because they contribute to plant pollination, degrade organic matter, or feed on phytophagous organisms. A study conducted in Mexico showed that parasitic and predatory organisms, which regulate the populations of many pests, represented 42% of the total of species collected in a coffee plantation. For this reason, it is important to protect and maintain the natural enemies of pests, avoiding the indiscriminate use of chemical pesticides and some agronomic practices that are harmful to natural control. The goal of this section is to describe the biological and ecological characteristics of the main insects and mites of *C. arabica* L. and *C. canephora* Pierre ex Froehner, the damage caused by these pests, their natural enemies, and pest management in coffee growing countries of tropical America. The pests to be described are listed in Table 17, which also includes the parts of the plant that are damaged and the development stage of the coffee plant that they damage. The criterion applied to include these organisms in the category of "major pests," was that they were reported in at least one of the manuals on coffee pests that have been published in Brazil, Colombia, Costa Rica, Cuba, El Salvador, Guatemala, Honduras, Jamaica, Mexico or Venezuela.

Coffee Berry Borer, *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae: Scolytinae)

Distribution

This is the most serious insect pest of coffee worldwide. It originated in Africa. In the Americas, it is found in coffee plantations from Mexico to Brazil, including some countries in the Caribbean region such as Cuba, Jamaica, the Dominican Republic and Puerto Rico.

Damage and Economic Importance

Coffee berry borer (Fig. 73) is a direct pest because it causes direct damage to the product to be harvested, the coffee bean. The attacked green, ripe and dry fruits or berries usually show a hole

Coffee Pests and their Management, Table 17 The most common phytophagous insects and mites of coffee in tropical America

Taxon (scientific and common name)	Country where the insect/mite is reported as coffee pest	Developmental stage feeding in/on the plant	Plant parts affected
Acari: Tarsonemidae			
Polyphagotarsonemus latus (Banks)	Brazil	Nymph, adult	Leaves
Acari: Tenuipalpidae			
Brevipalpus sp.	Brazil, Jamaica, Mexico	Nymph, adult	Leaves
Acari: Tetranychidae			
Olygonychus coffeae (Nietner)	Guatemala, Mexico	Nymph, adult	Leaves
Olygonychus ilicis (McGregor)	Brazil, Guatemala	Nymph, adult	Leaves
Olygonychus punicae (Hirst)	El Salvador	Nymph, adult	Leaves
Olygonychus yothersi (McGregor)	Colombia, Costa Rica, Venezuela	Nymph, adult	Leaves
Coleoptera: Anthribidae			
Araecerus fasciculatus (DeGeer)	All coffee growing countries in America	Larva, adult	Bean
Coleoptera: Cerambycidae			
Plagiohammus maculosus (Bates)	Costa Rica, El Salvador, Guatemala, Honduras, Mexico	Larva	Stem, root
Plagiohammus mexicanus Breuning	Mexico	Larva	Stem, root
Plagiohammus spinipennis (Thomson)	Mexico	Larva	Stem, root
Coleoptera: Curculionidae			
Brachyomus quadrinodosus (Lacordaire)	Venezuela	Adult	Leaves
Cleistolophus similis Sharp	Costa Rica	Adult	Leaves
Compsus sp.	Colombia	Adult	Leaves
Epicaerus capetillensis Sharp	Guatemala, Honduras, Mexico	Adult	Leaves
Hypothenemus hampei (Ferrari)	Mexico to Brazil, including Cuba, Jamaica, Dominican Republic, and Puerto Rico	Larva, adult	Fruit, bean
Lachnopus buchanani Marshall	Cuba	Adult	Leaves
Macrostylus boconoensis Bordón	Colombia, Venezuela	Adult	Leaves
Pantomorus femoratus Sharp	Costa Rica	Adult	Leaves

Coffee Pests and their Management, Table 17 The most common phytophagous insects and mites of coffee in tropical America (Continued)

Taxon (scientific and common name)	Country where the insect/mite is reported as coffee pest	Developmental stage feeding in/on the plant	Plant parts affected
Pantomorus godmani Crotch	Brazil	Adult	Leaves
Steirarrhinus sp.	Costa Rica	Adult	Leaves
Xylosandrus morigerus (Blandford)	Mexico to Brazil	Larva, adult	Young stems, branches
Coleoptera: Scarabaeidae			
Anomala sp.	El Salvador	Larva	Root
Dyscinetus picipes Burmeister	Cuba	Larva	Root
Phyllophaga spp.	Widely distributed in coffee plantations in America	Larva	Root
Phyllophaga latipes (Bates)	El Salvador	Larva	Root
Phyllophaga menetriesi (Blanchard)	El Salvador	Larva	Root
Phyllophaga obsoleta (Blanchard)	El Salvador	Larva	Root
Phyllophaga sanjosecola Saylor	Costa Rica	Larva	Root
Phyllophaga vicina Moser	Costa Rica	Larva	Root
Hemiptera: Aphididae			
Toxoptera auranti (Boyer de Fonscolombe)	Tropical and sub-tropical areas of the Old World. Widely distributed in coffee plantations in America	Nymph, adult	Leaves, buds and other tender parts of the plant
Hemiptera: Coccidae			
Coccus spp.	Mexico	Nymph, adult female	Aerial part of the plant
Coccus hesperidum L.	Guatemala, Mexico	Nymph, adult female	Aerial part of the plant
Coccus viridis (Green)	Brazil, Colombia, Costa Rica, Cuba, Ecuador, El Salvador, Guatemala, Honduras, Jamaica, Mexico, Puerto Rico, Surinam, Venezuela	Nymph, adult female	Aerial part of the plant
Parasaissetia sp.	Colombia	Nymph, adult female	Aerial part of the plant
Parasaissetia nigra (Nietner)	El Salvador, Guatemala, Puerto Rico, West Indies	Nymph, adult female	Aerial part of the plant
Saisettia spp.	El Salvador, Mexico	Nymph, adult female	Aerial part of the plant

Coffee Pests and their Management, Table 17 The most common phytophagous insects and mites of coffee in tropical America (Continued)

Taxon (scientific and common name)	Country where the insect/mite is reported as coffee pest	Developmental stage feeding in/on the plant	Plant parts affected
Saisettia coffeae (Walker)	Brazil, Costa Rica, Cuba, El Salvador, Guatemala, Honduras, Mexico, Dominican Republic, Venezuela	Nymph, adult female	Aerial part of the plant
Saisettia olae (Oliver)	Brazil, Cuba, Guatemala, Mexico	Nymph, adult female	Aerial part of the plant
Toumeyella sp.	Venezuela	Nymph, adult female	Root
Toumeyella liriodendri (Gmelin)	Guatemala	Nymph, adult female	Root
Hemiptera: Cerococcidae			
Cerococcus catenarius Fonseca	Brazil	Nymph, adult female	Aerial part of the plant
Hemiptera: Diaspididae			
Chrysomphalus sp.	Guatemala	Nymph, adult female	Aerial part of the plant
Chrysomphalus dictyospermi (Morgan)	Guatemala	Nymph, adult female	Aerial part of the plant
Ischnaspis longirostris (Signoret)	Colombia, Cuba, Guatemala	Nymph, adult female	Aerial part of the plant
Lepidoshaphes beckii (Newman)	Venezuela	Nymph, adult female	Aerial part of the plant
Selenaspidus articulatus (Morgan)	Colombia, Ecuador, Mexico	Nymph, adult female	Aerial part of the plant
Hemiptera: Margarodidae			
Icerya purchasi Maskell	Venezuela	Nymph, adult female	Aerial part of the plant
Hemiptera: Ortheziidae			
Insignorthezia insignis Browne	Brazil, Colombia	Nymph, adult female	Aerial part of the plant
Praelongorthezia praelonga (Douglas)	Brazil	Nymph, adult female	Aerial part of the plant
Hemiptera: Pseudococcidae			
Brevicoccus sp.	Guatemala	Nymph, adult female	Root
Ceroputo sp.	Costa Rica	Nymph, adult female	Root
Dysmicoccus sp.	Colombia, Ecuador	Nymph, adult female	Root
Dysmicoccus bispinosus (Beardsley)	Brazil, Guatemala, Honduras, Mexico	Nymph, adult female	Root
Dysmicoccus brevipes (Cockerell)	Costa Rica, El Salvador, Guatemala, Honduras, Mexico	Nymph, adult female	Root

Coffee Pests and their Management, Table 17 The most common phytophagous insects and mites of coffee in tropical America (Continued)

Taxon (scientific and common name)	Country where the insect/ mite is reported as coffee pest	Developmental stage feeding in/on the plant	Plant parts affected
Ferrisia virgata (Cockerell)	Brazil, Mexico, West Indies	Nymph, adult female	Aerial part of the plant
Geococcus sp.	Mexico, Venezuela	Nymph, adult female	Root
Geococcus coffeae Green	El Salvador, Guatemala, Honduras, Surinam	Nymph, adult female	Root
Geococcus radicum Green	El Salvador	Nymph, adult female	Root
Neochavesia caldasiae (Balachowsky)	Colombia	Nymph, adult female	Root
Rhizoecus sp.	Mexico, Venezuela	Nymph, adult female	Root
Rhizoecus andensis Hambleton	Colombia	Nymph, adult female	Root
Rhizoecus coffeae Laing	Costa Rica	Nymph, adult female	Root
Paraputo sp.	Guatemala	Nymph, adult female	Root
Planococcus citri (Risso)	Brazil, Colombia, Costa Rica, Cuba, El Salvador, Guatemala, Honduras, Jamaica, Mexico, Puerto Rico	Nymph, adult female	Root, aerial part of the plant
Planococcus halli Ezzat & McLonnell	Guatemala	Nymph, adult female	Root
Pseudococcus elisae (Borchsenius)	Guatemala	Nymph, adult female	Root
Pseudococcus longispinus (Targioni-Tozzeti)	Guatemala	Nymph, adult female	Root
Pseudococcus jongispinus Targioni-Tozzetti	Mexico	Nymph, adult female	Aerial part of the plant
Puto sp.	Costa Rica	Nymph, adult female	Root
Puto antioquensis (Murillo)	Guatemala	Nymph, adult female	Root
Rhizoeccus campestris (Hambleton)	Guatemala	Nymph, adult female	Root
Rhizoeccus caticans (Hambleton)	Guatemala	Nymph, adult female	Root
Rhizoeccus kondonis Kuwana	Guatemala	Nymph, adult female	Root
Rhizoeccus nemoralis Hambleton	El Salvador, Honduras	Nymph, adult female	Root
Hymenoptera: Formicidae			
Acromyrmex spp.	Venezuela	Adult	Leaves
Acromyrmex coronatus (F.)	Brazil	Adult	Leaves
Acromyrmex octospinosus (Wheeler)	Trinidad	Adult	Leaves

Coffee Pests and their Management, Table 17 **The most common phytophagous insects and mites of coffee in tropical America (Continued)**

Taxon (scientific and common name)	Country where the insect/mite is reported as coffee pest	Developmental stage feeding in/on the plant	Plant parts affected
Atta spp.	Guatemala, Ecuador, Nicaragua, Venezuela	Adult	Leaves
Atta cephalotes (L.)	Colombia, Costa Rica, Mexico, Surinam, Trinidad	Adult	Leaves
Atta fervens Say	Mexico	Adult	Leaves
Atta insularis Guérin-Méneville	Cuba	Adult	Leaves
Atta laevigata Smith	Brazil	Adult	Leaves
Atta mexicana (Smith)	Guatemala, Mexico	Adult	Leaves
Atta sexdens (L.)	Brazil	Adult	Leaves
Atta sexdens rubropilosa Forel	Brazil	Adult	Leaves
Lepidoptera: Apateloididae			
Olceclostera moresca (Schaus.)	Colombia	Larva	Leaves
Lepidoptera Arctiidae			
Estigmene acrea (Drury)	Colombia	Larva	Leaves
Lepidoptera: Dalceridae			
Dalcera abrasa Herrich-Schaeffer	Brazil	Larva	Leaves
Zadalcera fumata Schaus	Brazil	Larva	Leaves
Lepidoptera: Elachistidae			
Stenoma cecropia Meyrick	Colombia	Larva	Leaves
Lepidoptera: Geometridae			
Glena sp.	Brazil	Larva	Leaves
Oxydia spp.	Colombia	Larva	Leaves
Oxydia saturniata Guenée	Brazil	Larva	Leaves
Lepidoptera: Limacodidae			
Phobetron hipparchia (Cramer)	Brazil, Colombia	Larva	Leaves
Sibine spp.	Colombia	Larva	Leaves
Lepidoptera: Lyonetiidae			
Leucoptera coffeella (Guérin-Méneville)	Widespread wherever coffee is grown in the Neotropical area	Larva	Leaves
Lepidoptera: Megalopygidae			
Megalopyge lanata (Stoll)	Brazil, Colombia	Larva	Leaves
Podalia sp.	Brazil	Larva	Leaves

Coffee Pests and their Management, Table 17 The most common phytophagous insects and mites of coffee in tropical America (Continued)

Taxon (scientific and common name)	Country where the insect/mite is reported as coffee pest	Developmental stage feeding in/on the plant	Plant parts affected
Lepidoptera: Noctuidae			
Agrotis spp.	Colombia, Costa Rica, Ecuador, El Salvador	Larva	Stems of small plants in germinating seedbeds or recently transplanted plants
Agrotis ipsilon (Hufnagel)	Brazil	Larva	Stems of small plants in germinating seedbeds or recently transplanted plants
Agrotis repleta Walker	Venezuela	Larva	Stems of small plants in germinating seedbeds or recently transplanted plants
Feltia spp.	Costa Rica, El Salvador, Venezuela	Larva	Stems of small plants in germinating seed-beds or recently transplanted plants
Pseudoplusia includens (Walker)	Honduras	Larva	Leaves
Spodoptera sp.	Colombia, Costa Rica, Ecua-dor, El Salvador	Larva	Stems of small plants in germinating seedbeds or recently transplanted plants
Spodoptera eridania (Stoll)	Venezuela	Larva	Stems of small plants in germinating seed-beds or recently transplanted plants
Spodoptera frugiperda (Smith)	Costa Rica, Brazil	Larva	Stems of small plants in germinating seedbeds or recently transplanted plants; leaves
Trichoplusia ni (Hübner)	Colombia	Larva	Leaves
Lepidoptera: Psychidae			
Oiketicus geyeri (Berg)	Brazil	Larva	Leaves
Oiketicus kirbyi Lucas	Brazil, Cuba	Larva	Leaves
Lepidoptera: Saturniidae			
Automeris sp.	Brazil, Colombia	Larva	Leaves
Automeris complicata Walker	Brazil	Larva	Leaves

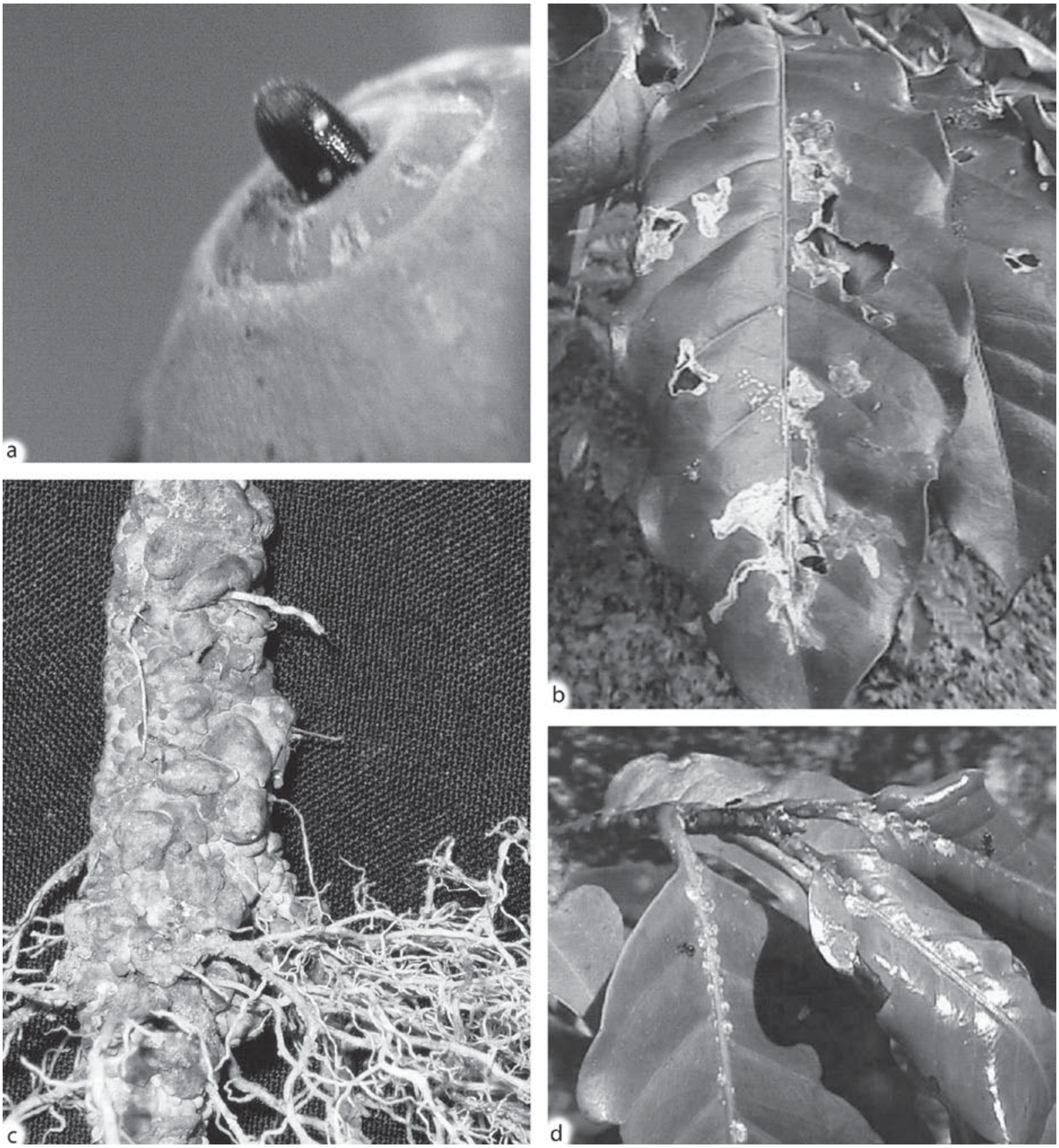
Coffee Pests and their Management, Table 17 The most common phytophagous insects and mites of coffee in tropical America (Continued)

Taxon (scientific and common name)	Country where the insect/ mite is reported as coffee pest	Developmental stage feeding in/on the plant	Plant parts affected
Automeris coresus Boisduval	Brazil	Larva	Leaves
Automeris illustris Walker	Brazil	Larva	Leaves
Eacles imperialis magnifica (Walker)	Brazil	Larva	Leaves
Eacles masoni Schaus	Ecuador	Larva	Leaves
Lonomia circunstans (Walker)	Brazil	Larva	Leaves
Orthoptera: Gryllidae			
Paroecanthus guatemalae Saussure	Guatemala, Honduras	Adult female	Stem, branch
Paroecanthus niger Saussure	El Salvador, Guatemala	Adult female	Stem, branch
Orthoptera: Tettigoniidae			
Gongrocnemis sp.	Guatemala	Nymph, adult	Leaves, buds, fruit pulp, beans
Idiarthron atrispinum (Stål)	Costa Rica, Guatemala	Nymph, adult	Leaves, buds, fruit pulp, beans
Idiarthron subquadratum Saussure & Pictet	Colombia, Guatemala, El Salvador, Honduras, Mexico	Nymph, adult	Leaves, buds, fruit pulp, beans

on its apical portion. The hole is located at the center or ring of the berry's ostiole and the emission of sawdust can be observed through this hole. Its attack reduces the yield and affects the bean quality. Characteristic damage includes the rotting of developing beans as a result of saprophytic microorganisms that enter through the hole, the drop of young berries due to attack, and the loss of bean weight due to insect feeding. The borer can cause bean yield losses of 30–35% with 100% of perforated berries at harvest time; nevertheless, damage can be greater if harvest is delayed. All the commercial coffee varieties and species are attacked by this insect. However, it shows preference for *C. canephora*, and its multiplication is also higher on beans of this coffee species. Recently it was suggested that *H. hampei* serves as a vector for *Aspergillus ochraceus* Wilh., which produces ochratoxin A, a potent toxin that sometimes contaminates green coffee beans, roasted coffee, and coffee brews, including instant coffee.

Description

The egg is elliptical, crystalline and yellowish toward maturity. Its length varies from 0.52 to 0.69 mm. The larva is white-yellowish, without legs, with a "C"-shaped body and a wide thoracic region. The head is light brown, with visible and forward-extending mandibles. Visible hairs spread over the head and body. Females molt twice and males once. The length of the last larval instar is from 1.88 to 2.30 mm. The pre-pupa is similar to the larva, but its color is milky-white,



Coffee Pests and their Management, Figure 73 Some coffee pests: (a) Coffee berry borer, *Hypothenemus hampei* (Curculionidae) infesting a coffee berry; (b) Damage of coffee leaf by coffee leaf miner, *Leucoptera coffeella* (Lyonetiidae); (c) Root mealybugs (Pseudococcidae); (d) Scale insects on coffee leaf (Coccidae).

its body is less curved, and it does not feed. The pupa is milky-white and yellowish towards maturity. Many of the adult's characteristics can be seen in the pupal stage. The pupa varies from 1.84 to 2.00 mm long. The adult is elongated with a cylindrical body slightly arched towards the end of the abdomen. It is about 1.50–1.78 mm long and its body is bright black, although

Coffee Pests and their Management, Figure 74 **Some additional coffee pests: (a) Coffee branch perforated by *Xylosandrus morigerus* (Curculionidae); (b) Coffee stem attacked by a stem borer, *Plagiohammus maculosus* (Cerambycidae); (c) Aphids on coffee leaf; (d) Adults of a katydid, *Idiarthron subquadratum*; (Tettigoiidae) (e) Oviposition by a bush cricket, *Paroecanthus* (Gryllidae) on the stem of a coffee bush.**

yellowish when emerging from the pupa. The head is ventrally located and is protected by the pronotum. The antennae are elbowed and clubbed at the ends. Mouthparts are the typical chewing type and the elytra are convex and possess longitudinal grooves that alternate with longitudinal series of bristles. Females have well-developed wings that allow them to fly, while the males' wings are atrophied. Females are easily differentiated from males because they are larger.

Biology and Ecology

Adult females initiate the infestation. In general, a berry is infested by a single female. If the coffee bean is watery or milky, the insect tends to abandon it and the bean usually rots. But if the bean consistency is hard enough, the founding female constructs a gallery where she lays the eggs. The eggs are oviposited one by one, forming small groups within the coffee bean. The female lays from 1 to 3 eggs per day during the first 15–20 days; afterwards, the egg laying diminishes gradually. Both the founding female and the larvae build tunnels in the bean, where they also feed. Pupation takes place within the coffee bean where the larva hatched. The duration of the biological cycle, from egg to adult, varies according to the temperature: 21 days at 27°C, 32 days at 22°C and 63 days at 19.2°C. As the first adult offspring appear, the population inside an infested bean typically consists of 25–30 individuals in all stages of development, of which there are approximately 10 females for each male. Mating is conducted between siblings inside the bean. The mated females leave the bean where they developed to look for another where they will oviposit. Several generations occur while berries are available. After coffee harvest, the borer continues to reproduce in the non-harvested berries located on the plant and on the ground. In locations with low rainfall, where there is a clearly defined period between harvests, the adults find refuge in the black, dry berries. Adult females emerge massively from these old berries with first rainfall, initiating the infestation by attacking berries from the earliest flowerings of the new harvest.

Natural Enemies

Coffee berry borer is attacked by several natural enemies. Four parasitoid species from Africa are the best known: *Prorops nasuta* Waterston (from Cameroon, Ivory Coast, Zaire, Kenya, Tanzania, Togo, Uganda) and *Cephalonomia stephanoderis* Betrem (Ivory Coast, Togo) (both Hymenoptera: Bethylidae), and two solitary ectoparasitoids of the larva, pre-pupa and pupa, *Heterospillus coffeicola* Schimideknecht (Hymenoptera: Braconidae) (Cameroon, Zaire, Kenya, Tanzania, Uganda) (a free-living wasp that deposits a single egg near a borer's egg cluster in a recently attacked berry) and *Phymastichus coffea* LaSalle (Hymenoptera: Eulophidae) (Togo, Kenya) (a gregarious endoparasitoid of *H. hampei* adults which parasitizes the borer during the berry perforation). Other parasitoids that have been reported attacking *H. hampei* include *Aphanogmus dictyna* (Waterston) (Hymenoptera: Ceraphronidae) (Uganda), *Sclerodermus cadavericus* Benoit (Hymenoptera: Benthylidae) (Uganda, Zaire, Kenya), *Cephalonomia hyalinipennis* Ashmead (Mexico) and *Cryptoxilos* sp. (Hymenoptera: Braconidae) (Colombia). In Brazil and Colombia, there are reports of an undescribed species of *Cephalonomia* parasitizing *H. hampei*.

Some of the predators that have been recorded include *Dindymus rubiginosus* (F.) (Hemiptera: Pyrrhocoridae) (Indonesia), *Calliodes*, *Scoloposcelis* (Hemiptera: Anthocoridae) (Colombia), and *Leptophloeus* sp. near *punctatus* Lefkovich (Coleoptera: Laemophloeidae) (Togo, Ivory Coast). However, most of the predators of *H. hampei* reported from around the world (most of them anecdotal records) have been ants (Hymenoptera: Formicidae), including *Azteca instabilis* (F. Smith), *Crematogaster curvispinosa* Mayr, *C. torosa* Mayr, *Dolichoderus bituberculatus* Mayr, *Pheidole radoszkowskii* Mayr, and *Solenopsis geminata* (F.). Unknown species of *Azteca*, *Brachymyrmex*, *Paratrechina, Pheidole, Prenolepis* and *Wasmannia* have been recorded as well.

Several entomopathogenic fungi attack the coffee berry borer, but *Beauveria bassiana* (Balsamo) Vuillemin is the most common species infecting *H. hampei* adults under natural conditions. Other fungi recorded infecting *H. hampei* are *Fusarium oxysporum* Schlechtend, *F. avenaceum* (Fr.) Sacc., *Hirsutella eleutheratorum* (Nex ex Gray) Petch., *Metarhizium anisopliae* (Metschnikoff) Sorokin, *Nomuraea rileyi* (Farlow) Samson, *Paecilomyces amoenoroseus* (Hennings) Samson, *P. farinosus* (Holm. ex S.F. Gray), *P. fumosoroseus* (Wize) Brown & Smith, *P. javanicus* (Friederichs & Bally) Brown & Smith, *P. lilacinus* (Thom.) Samson, and *Verticillium lecanii* (Zimmerman). Some of these fungi, such as *M. anisopliae* and *P. lilacinus*, have been isolated from *H. hampei*-infested berries collected from the soil.

Metaparasitylenchus hypothenemi Poinar (Tylenchida: Allantonematidae), an entomopathogenic nematode attacking *H. hampei* adults, has been reported in Mexico and appears to have a wide distribution in coffee plantation in Mexico and Central America

This nematode cause sterility in female borers. The natural parasitism by an undescribed species of *Panagrolaimus* (Rhabditida: Panagrolaimidae) has been reported in *H. hampei* in India and Mexico. *M. hypothenemi* and *Panagrolaimus* sp. were found infecting the same *H. hampei* adults in Mexico. Species from Heterorhabditidae and Steinernematidae (Rhabditida) are able to infect *H. hampei* in the laboratory, but this has not been observed in the field.

In Colombia, infections in the coffee berry borer caused by bacteria such as *Bacillus* sp. and *Serratia* sp. were observed. Also, infections of proteobacterium *Wolbachia* in *H. hampei* adults have been reported from samples around the world. The microsporidian *Mattesia* sp. was observed in a population of laboratory-reared insects.

Management

An integrated pest management strategy is used against the coffee berry borer. The principal tactics are cultural control, biological control, use of traps baited with attractants, and chemical control with synthetic insecticides. Sampling infested berries is used for pest control decision-making.

Sampling Infested Berries

The proportion of infested berries is calculated based on the following sampling protocol: in an area of 1–5 ha, 20 uniformly distributed sites are selected; at each site five coffee plants in a row are selected; 20 berries of each coffee plant are examined (without tearing them off), and the number of perforated berries is recorded.

Cultural Control

There are a number of cultural practices that may be used to minimize damage by borers. The berries left on the plant before maturity and on the ground after harvest are collected and boiled for 5 min to eliminate the borers in them. This practice is also called "manual control" or "rere." Weeds are controlled after the harvest in order to facilitate the collection of berries from the ground and to increase the mortality of *H. hampei* by dehydration of the berries. The coffee and shade plants are pruned to create less favorable environmental conditions for multiplication of the borer. Coffee plant density is decreased because high sowing densities favor infestation. The coffee plants are fertilized so that they have more uniform flowerings. Varieties with the same fruiting pattern are used because the early flowering varieties are an infestation source for late flowering varieties; however, coffee varieties or species which flower earlier or later than the main variety can be used as "trap crops," if managed properly. The harvest is conducted as the fruits ripen.

Biological Control

The natural enemies most often used against the borer in tropical America have been the parasitoids *C. stephanoderis*, *P. nasuta* and *P. coffea*, and the entomopathogenic fungus *B. bassiana*. These three parasitoids were introduced to tropical America from Africa. They are established in most of the countries where they have been released. Nevertheless, classical biological control with these African parasitoids has not been sufficient to reduce the borer population below the economic injury level. Yearly inoculative and inundative releases of parasitoids have been used with better results. However, inundative releases are expensive because mass rearing methods and facilities have not been developed for area-wide releases. Parasitoids are produced for inoculative releases in laboratories where the borer is reared mostly in parchment coffee (35% humidity) for use in rearing the parasitoids. A rearing system for *H. hampei* in an artificial diet has been developed; however, its application for mass production of parasitoids is not fully employed. An alternative and less intensive rearing system to produce parasitoids for inoculative releases is production of the parasitoids in rural areas, also known as "parasitoid rural rearing." In this system, the coffee growers rear the parasitoids at their farms or communities. Such rearing is conducted using coffee berries infested by the borer in the field. Regardless of the rearing method used, annual releases of parasitoids are needed to manage the borer population.

The use of *B. bassiana* for borer control is more developed than is the use of parasitoids. Its success has resulted from the relatively easy propagation, formulation and application of this fungus. Strains of *B. bassiana* are commonly collected for mass production from infected *H. hampei* females in the field. Rice grains are used as the propagation substrate for this entomopathogen. The fungus requires high relative humidity for germination of the spores and it is very susceptible to sunlight. Early in the morning is the most effective time to apply it in the field, when the borer is starting to penetrate the coffee berry.

Insect Traps

Traps are used for monitoring and control of the coffee berry borer. They are made using 2 L plastic bottles into which one or more windows have been cut to allow the entry of flying females. Borers are attracted by a mixture of methanol and ethanol (1:1 or 3:1) and they are caught and drowned in the water placed at the bottom of the trap. Typically, 16–25 traps are deployed per hectare. Each trap is suspended from a branch of a coffee plant at 1.2–1.5 m above the ground. Borers captured are removed from the traps and counted weekly. The best time to use the traps for *H. hampei* control is after the harvest, during the massive emergence of females from old berries. Better results for suppression of insect infestation in the next harvest can be obtained by combining the use of traps with strict sanitation.

Chemical Control

There are several chemical insecticides used for borer control, among which endosulfan is outstanding for its ability to cause high mortality of *H. hampei*. However, this organochlorine insecticide is being seriously questioned for negative side effects (it is highly toxic to fish and bees, and it causes secondary pest outbreaks by eliminating the natural enemies); borer resistance (apparently this pest is not resistant to endosulfan in tropical America; nevertheless, there is concern about the development of resistance, as in the case of New Caledonia); and sanctions in the international market due to the possible presence of residues in the coffee bean. The insecticide should only be used if the borer population reaches the economic threshold. The best time for spraying is when the adult borer starts penetrating the fruit, at the so-called semi-consistency stage of development (about 20% dry weight in the bean). This period varies, according to the temperature, from 90 to 140 days after the main flowering. Formerly, treatments were throughout the plantation, but now sprays are directed only at infested areas.

Coffee Leaf Miner, *Leucoptera coffeella* (Guérin-Méneville) (Lepidoptera: Lyonetiidae)

Distribution

This species is found in the Neotropics: Mexico, Central America, South America and the Caribbean region. It is widespread wherever coffee is grown.

Damage and Economic Importance

In some areas of tropical America, the coffee leaf miner is considered to be the principal insect pest of coffee; certainly this is the case in some coffee-growing areas in Brazil. Leaves are the only plant organs damaged by this insect. The damage is caused by the larva. Four larvae per leaf may cause leaf drop. The affected leaves show irregular light-brown spots. If the damaged surface of the leaf is rubbed, the leaf separates into two layers and between them is found a small white worm, from 2 to 5 mm in size. The coffee leaf miner lesions may be confused with the symptoms of Anthracnose (*Colletotrichum* sp.), but in the latter case the leaf layers do not separate when rubbed. Four months after flowering, a reduction in the rate of growth of the coffee berries and an increase in leaf production take place; this allows the plant to compensate for the damage caused by the miner. But when the fruit growth starts again, if there is more than one leaf miner lesion per leaf it will result in economic damage. The damage increases if simultaneously the plant is under drought stress. Attack of coffee by leaf miner can cause severe defoliation. In Ecuador, defoliation between 70 and 90% has been reported on *C. arabica* and from 30 to 40% on *C. canephora*. The lack of leaves on the plant reduces the photosynthetic activity, and consequently the availability of nutrients for the fruits. In Brazil, when 94–95% of the leaves were mined, a reduction in yield between 68–80% has been observed.

Description

The egg is oval, translucent yellow and similar to a flattened volcano in profile. It is 0.28 mm long, 0.18 mm wide, and 0.08 mm tall. The larva has a dorsoventrally flattened body with a more pronounced flattening of the head and the first thoracic segment. The true legs are found on the 1st, 2nd and 3rd thoracic segments but four pairs of prolegs occur on the 6th, 7th, 8th and 13th abdominal segments. It has four larval instars. The larva attains a length of 4.5 mm. The pupa is white in the initial stage and ochre towards maturity, except for the dorsal portion, which remains white. The pupa is covered by a white cocoon which resembles an elongated "H" or "X." The adult is a small moth between 2.0 and 3.0 mm long with its body covered by silvery scales. The antennae are long and thin. The front wings possess a gray oval point distally, surrounded by a black line and edged by a yellow stripe that extends along the margin. Males tend to be slightly smaller than females.

Biology and Ecology

The female usually lays its eggs irregularly on the upper surface of the darkest, most mature leaves, particularly on the middle and lower parts of the coffee plant. Eggs are laid individually or in small clusters of up to seven eggs, with a total fecundity that varies between 30 and 80 eggs. Upon hatching, the larva makes a semi-circular cut at its base and penetrates rapidly into the leaf, where it moves about, mining the palisade parenchyma tissue. When ready to pupate, the fully developed larva leaves the gallery very early in the morning, making a semi-circular cut on the face of the leaf, through which it slips down by a silk thread which it secretes from the mouth. Cocoon formation and pupation take place on the lower face of the coffee leaf, often on a curvature of the leaf or close to a protruding vein. The duration of the life cycle, from egg to adult, lasts between 25 and 75 days, depending on the temperature. Several generations occur annually, particularly in coffee plantations with full sunlight or only lightly shaded. The abundance of *L. coffeella* is significantly affected by the onset of rainfall, and by natural enemies, which are very numerous after the end of the dry season.

Natural Enemies

The coffee leaf miner is attacked by a large number of parasitoids; predators and some insect pathogens have also been recorded. More than 20 morphospecies of parasitoids wasps (Hymenoptera) have been reported in tropical America. Eulophidae are the most common parasitoids of *L. coffeella*; this group is largely unknown because keys for neotropical species do not exist. In Mexico, *Neochrysocharis* was the genus with the greater number of morphospecies, and also the one that was collected most frequently. It was followed, in order of abundance, by *Pnigalio*, *Closterocerus*, and *Zagrammosoma*. Of two braconids collected in Mexico, *Stiropius letifer* (Mann) was the most abundant and most widely distributed. Wasps (Vespidae) are the most important predators of coffee leaf miner in Brazil, but in Mexico, the most important predators are ants (Formicidae). The bacteria *Pseudomonas aeruginosa* (Schroeter) Migula and *Erwinia herbicola* (Löhnis) Dye, and the fungus *Cladosporium* sp., have been reported infecting *L. coffeella*.

Management

There are several useful approaches to management of coffee leaf miner. population. Sampling is recommended prior to initiating chemical control.

Sampling Damaged Leaves

The recommended sampling protocol follows: sampling is initiated when the coffee flowers, and is conducted monthly until the berries stop growing. The coffee plantation to be sampled is divided into areas not larger than one hectare. The sampling is conducted by selecting a zigzag path across the coffee plantation and by selecting 12 coffee plants at random. From each coffee plant, 25 leaves are selected at random, and the number of leaves with mines is recorded. The first two pairs of leaves at the tip of the branches are not sampled.

Cultural Control

The shade canopy of coffee plantation should not be trimmed immediately after harvest; it should be thinned only when the onset of the rainy season is imminent. Adequate soil fertilization is important. Thick mulch coverage of the soil should be maintained. High coffee plant densities should be avoided. The coffee plant should be pruned to stimulate vigorous growth. Damaged leaves should be collected and placed in containers that allow the escape of parasitoids but not of the coffee leaf miner.

Biological Control

The introduction of natural enemies into new areas has not been widely explored. The most important action conducted so far has been to protect the already existing natural enemies by avoiding the use of broad-spectrum, residual contact insecticides. The natural control exerted by the coffee leaf miner's natural enemies varies from 2 to 70%; however, in most cases it is unnecessary to resort to the use of chemical control. Regrettably, the use of chemical insecticides may eliminate a large portion of the beneficial organisms, causing pest resurgence and making it difficult to implement control. In certain countries like Honduras, high and recurring *L. coffeella* infestations have diminished significantly when the use of chemical control is not applied for several years and the beneficial fauna is restored. This supports the idea that coffee leaf miner control should not be based on use of insecticides in order to avoid disrupting the actions of parasitoids and predators.

Chemical Control

Numerous chemical insecticides can be used for suppression of *L. coffeella* and protection of foliage. These products include both organophosphate and pyrethroid insecticides. They are inexpensive and can be applied at the same time with other agrochemicals, but they are highly toxic and they are more likely to cause ecological disturbances. Organophosphorates are often applied twice at an interval of 30–45 days, with an additional application in cases of severe attack. In the case of pyrethroids, one or two applications at an interval of 45–60 days are recommended. The application of granular insecticides with systemic action to the soil is also recommended in cases where it is difficult to apply foliar sprays. Soil applications interfere much less with the natural enemies of the coffee leaf miner, and this approach can be used to control pests and soil diseases simultaneously. Granular insecticides should be shallowly buried at the drip line of the plant once a year during the rainy season. Where this type of product is used, it is recommended that harvest occur 90 days after application.

Root Mealybugs (Hemiptera: Pseodococcidae)

Distribution

Root mealybugs are found in Neotropical countries where coffee is grown. The principal root mealybugs affecting coffee plants in tropical America are shown in Table 17.

Damage and Economic Importance

These insects attack the coffee plant roots and some species also affect the foliage. The foliage of attacked coffee plants appears withered, the color of the leaves fade, and they have copper, brown or necrotic edges. Additionally, total or partial leaf drop may occur. These symptoms are more evident during the dry season. In case of serious attacks by *Dysmicoccus bispinosus* (Beardly), a thick, cork-like, dark crust covers the main and secondary roots; the attacked roots lose their absorbent root hairs. Heavily attacked plants perish. Infestation appears to be associated with ants (Formicidae). The symptoms may be confused with the symptoms of fungal diseases and with physiological plant problems. In the case of *Neorhizoeccus coffeae* (Laing) and *D. brevipes* (Ckll.) infestations, the branches turn whitish and the affected root seems to be covered with flour, the crust separates easily, and considerable deteriorated tissue appears. The attacked plants have little anchorage and are easily dislodged.

Root mealybugs have become important coffee pests in some areas of tropical America during the last 20 years. In Guatemala, the most harmful species is *D. bispinosus*; in Costa Rica, *N. coffeae* and *D. brevipes*; in El Salvador, *D. brevipes*, *Rhizoeccus nemoralis* Ham. and *Geococcus coffeae* Green; and in Colombia, *Chavesia caldasiae* (Balachowsky). At some coffee plantations in Colombia, *Planococcus citri* (Risso) has also appeared as a pest, causing up to 30% yield loss in the attacked trees. Other forms of damage caused by root mealybugs include excessive extraction of potassium, destruction of the absorbent root hairs, development of small rotting areas which tend to atrophy, and enhanced entry of plant pathogens. This damage creates a general condition of weakness, slow growth and plant death in many cases.

Dysmicoccus brevipes weakens the coffee plants but it rarely kills them. In Costa Rica, plants with more than 20 mealybugs per liter of soil are more susceptible to infection by the fungus *Cercospora coffeicola* Berk & Cooke. Damage is more apparent on nutrient-deficient soils, and where weeds are abundant. Plants in seed beds and tree nurseries are also attacked. The varieties of *C. arabica* grown in Central America (e.g., Caturra, Catuaí, Bourbon) are susceptible to the mealybug attack, while tolerance has been observed on *C. canephora*, *C. dewevrei* De Wild. & Durand, and *C. excelsa* Chev.

Description

Mealybug eggs are small (0.5 mm). The nymphs are oval, slightly swollen, usually white, yellow or pink-colored, and covered by a white waxy-mealy dust with waxy filaments projecting laterally. The female nymphs molt three times, and the males, contrary to the females, form a waxy cocoon in the third instar, where they pupate. The adult females have no wings and they are similar to the nymphs but larger. Smaller species, such as *Geococcus* and *Rhizoecus*, are from 1.5 to 2.0 mm long and the larger ones, such as *Dysmicoccus* and *Pseudococcus*, are from 2.5 to 5.0 mm long. Males are white, fragile-looking, smaller than the females, and they possess a pair of wings and a pair of terminal filaments.

Biology and Ecology

Mealybugs generally live attached to the coffee root, forming numerous colonies. Their reproduction may be sexual or parthenogenetic (partial or total). Eggs are laid in groups and covered by a layer of cotton-like wax or by an egg sac of crystalline wax filaments. A single female may deposit 300–600 eggs. Other species, such as *Pseudococcus adonidum* (L.) are oviparous. Females die shortly after the eggs hatch. Upon eclosion, the small nymphs start looking for an appropriate place to settle on the plant root; at the selected site, they insert their mouthparts, and feed by suctioning the sap from the root. Some of them settle down permanently on a site until they reach maturity, and others may change their feeding site by moving short distances. Depending on the type of soil, the humidity, aeration and age of the coffee plant, they usually place themselves between 10 and 60 cm under the soil surface, their population diminishing as the soil depth increases. Different species prefer different parts of the root. For example, *D. brevipes* and *R. nemoralis* prefer the main and the lateral roots, while *G. coffeae* attacks the absorbent roots; the smaller species attack the whole root system near the soil surface.

As they feed and develop, the nymphs and adults excrete their characteristic waxy cover and form compact colonies. Mealybugs excrete sugary substances (honeydew), which supports the growth of fungi (i.e., *Bornetina*), which contribute to formation of the thick, cork-like, dark crust covering and sheltering the mealybug colony; a succession of crusts give a knotty appearance to the root. The sugary substances also attract certain ant species, which live in a symbiotic association (trophobiosis) with the mealybugs. In exchange for the sugary foodstuff, the ants give them protection and transportation from one root to another and from one plant to another. The ants that associate with mealybugs in South America and in some of the Caribbean Islands are in the genus *Acropyga*. In Colombia, the Hope ant (*A. robae* Donisthorpe) and the Amagá ant (*A. fuhrmanni* Forel) are associated with *N. coffeae* and *C. caldasiae*, respectively. In Guatemala, *D. bispinosus* seems to be associated with the presence of the ant *Solenopsis geminata* (F.). *P. citri* does not produce large quantities of sugary excretions when it lives on the plant roots, and is not attractive to ants. In certain cases, the mealybugs have lived for more than a year in the absence of ants.

The life cycle, from egg to adult, requires from 30 to 120 days, according to the species and the temperature. Five generations develop per year in the case of *D. bispinosus*. Root mealybugs develop better during the rainy season, particularly in low or medium altitude plantations in Central America. Other conditions that favor their development are sandy, acid pH, and medium moisture soils. In Colombia, the damage caused by *Rhizoecus* sp. seems to increase in old, poorly fertilized plantations, and in Guatemala *D. bispinosus* is found most frequently in 1–5 year-old plantations. Mealybugs are polyphagous, also attacking other plants such as shade trees (*Inga* spp.), cassava (*Manihot esculenta* Crantz), sugarcane (*Saccharum*), banana trees (*Musa*), lemon trees (*Citrus*) and some herbs that grow on the coffee plantation. In Costa Rica, *Anredera ramosa* (Moq.) Eliasson is an alternate host of *D. brevipes*; in El Salvador, *D. bispinosus* has been found associated with *Lantana camara* L.

Natural Enemies

In general, the literature on coffee mealybugs in tropical America does not make reference to their natural enemies. In Cuba, *Coccidoxenoides peregrinus* (Timberlake) (Hymenoptera: Encyrtidae) is cited as a solitary, primary endoparasite of the pseudococcid complex in coffee. Other natural enemies of mealybugs reported in Cuba are *Diadiplosis cocci* Felton (Diptera: Cecidomyiidae), *Leptomastix dactylopii* Howard (Hymenoptera: Encyrtidae) and *Signiphora* sp. (Hymenoptera: Signiphoridae).

Management

There are management options for mealybugs, but insecticides are normally used once pest populations develop.

Sampling

Sampling should preferably be conducted on young coffee plantations (up to 6 years old). Plants near ant nests should be examined critically; from 15 to 20 plants/ha should be checked, paying more attention to those that are close to the ant nests and/or possess yellow leaves. The surrounding shade trees and bushes should also be checked. The plants are checked by moving the stems in all directions in order to gain visibility of the base of the roots.

Cultural Control

Mealybugs should not be present in the seed bed and tree nursery. The limits of any infestation sites should be determined and marked. Adequate fertilization should be provided, including addition of organic matter to the soil. Physical conditions of the soil should be improved in order to avoid floods. Planting coffee trees on land previously supporting plants that are highly susceptible to mealybugs (e.g., cassava, sugarcane) should be avoided. Alternate host plants should be eliminated from the plantation. Severely damaged plants should be removed and burned.

Biological Control

This is practically unexplored in the coffee growing countries of tropical America.

Plant Resistance to Insects

In Guatemala, some research has been conducted which supports the use of plants grafted on resistant rootstocks of *C. canephora* (genotypes 3757, 3754, 3751, 3581, 3752 and 3756) and *C. dewevrei*.

Chemical Control

Systemic organophosphorate and carbamate insecticides produce good results, although they are expensive. The presence of mealybugs in seed beds or on plants younger than 1 year old is sufficient justification for insecticide application. On plantations older than 3 years, insecticide application is made if more than 1.6 colonies per plant, on average, are found. In no case should the damage be allowed to exceed 25% of the absorbent roots. Insecticides are applied on the drip line of the plant if the damage is on the small roots. If the damage is on the main root a funnel-shaped hole should be made around the tree trunk, the insecticide should be poured in and the hole should be covered again with soil, adding also a layer of dead leaves. Application of granular insecticides is made at the beginning of the rainy season or 3 months before starting the harvest.

Scale Insects, Mealybugs and Related Foliage Pests (Hemiptera)

Distribution

Different scale insects, mealybugs and related foliage pests live on the coffee plant. The geographic distribution of some is restricted to a few countries of tropical America, whereas others are distributed more widely. Some are reported attacking the coffee plant only in South America, others only in Central America or the Caribbean (Table 17).

Damage and Economic Importance

Scale insects, mealybugs and related species attack the aerial part of the coffee plant and, in some species, also the root (e.g., *Planococcus citri* [Risso]). The leaves, fruit, branches and young tissues of the aerial part of the attacked coffee plant often support colonies or groups of circular, oval or elongated scales, which may be flattened or swollen, with a soft or hard consistency. In other cases, colonies of insects have a soft body covered with white, cotton-like filaments. These insects cause damage by removing large quantities of sap, which causes plant malnutrition. Also, sticky honeydew and blackish molds can be found covering the foliage. When *Capnodium* (sooty mold) and *Meliola* (black mildew) fungi grow on the honeydew excreted by the scales, they interfere with photosynthesis. Ants are present where scale insects are feeding.

In cases of severe attack, a dirty appearance on the plant, general weakening, growth delay, yellowing and drop of foliage and fruit are observed. With the articulated scale, *Selenaspidus articulatus* (Morgan), old attacks may be recognized because the site where the scales were located turns yellow or discolored, resembling infection by the coffee rust fungus (*Hemileia vastatrix* Berk. and Br.). Some species, such as the green scale, *Coccus viridis* (Green), are considered to be quite important to coffee production, though some attack a number of different cultivated plants. Severe infestations of *C. viridis* may kill young tree nursery plants. The incidence of these pests is highest on coffee plantations lacking adequate shading.

Pest Description

The following cases are presented as examples: *C. viridis* – adult females are motionless, oval, sometimes asymmetric, very flat and pale yellow. They have some black spots centrally, and they tend to be soft and elastic. They are about 2.2 mm wide and 4.0 mm long. The presence of males is very rare. *Saisettia coffeae* (Walker) – adult females are motionless, almost spherically shaped and dark brown. They are 2.0–3.5 mm in diameter. The males are winged. *P. citri* – adult females are mobile, oval, pale yellow or dark orange, with very clear segments on the body, and 4.0 mm in size. They are covered with a dusty white glandular secretion except for a longitudinal stripe dorsally. They have filaments laterally. Males are smaller (1.0 mm), violet to yellow in color, and they have well-developed wings.

Biology and Ecology

The biology of these insects varies among species and can be quite complex. The first instar has legs and antennae and is very active. To feed, the insects attach and insert their mouthparts. After the first molt, they generally lose their legs and antennae and the insect becomes sessile. By then, it begins to secrete a waxy, scale-shaped layer that covers the body. In the case of scales of the family Diaspididae, this layer of scale is almost always separated from the insect's body. Adult females remain under this cover and they produce their eggs or directly give birth to the nymphs therein. The location on the plant, and the age of the plant they prefer to attack, depends on the species of scale: *C. viridis* is commonly located along the leaf veins, on the back of the leaves, on young buds and on seed bed coffee fruits of nursery plants; *S. articulatus* is found mainly on the leaves and fruits of production plants; the round scale, *Parasaissetia* sp., mostly attacks the stems and branches of coffee plants younger than 1 year; the black scale, *Ischnaspis longirostris* (Signoret), infests the leaves, branches and fruits of old, poorly attended coffee plantations; *Cerococcus catenarius* Fonseca gathers in the form of a line or chain along the trunks and branches; *P. citri* attacks new branches, leaves, flower buds, fruit peduncles and fruits; *Orthezia* spp. attack branches, leaves and fruits, mostly of robusta coffee in Brazil. The males develop very much like the females except that in the last stage, before transforming into adults, they go through a pupal stage; the wings develop externally over the pupa. Most of the scales reproduce parthenogenetically. Some species are oviparous (*S. coffeae*, *S. olae* [Oliver]) and others are viviparous (*Coccus hesperidum* L.). The total number of eggs produced per female varies among the species; for example: *C. viridis*, between 50 and 600 eggs; *Orthezia praelonga* Douglas, more than 200 eggs; *C. catenarius*, about 900; *S. coffeae* can lay up to 1,600 eggs. The complete life cycle, from egg to adult, lasts between 40 and 60 days. The scale insects are more abundant during the dry season and at the onset of the rainy period. Hard rains and natural enemies are important factors in the mortality of these pests.

Natural Enemies

These insects are susceptible to a large number of parasites, predators and pathogens as natural enemies.

Management

Sampling

During the dry season, inspections should be conducted to check for the presence of scales and related species in the coffee plantation, as well as on other plants cultivated nearby or at the same time.

Cultural Control

The nursery shading should be reinforced during the dry season. Affected plants should not be transplanted. Weeds should be suppressed. The pests should be kept under control on host plants existing in or near the coffee plantations. Sanitary pruning should be performed to eliminate (by burning) old and unproductive branches infested by the pests.

Biological Control

Natural enemies should be protected and preserved, using insecticide only if necessary.

Chemical Control

Chemical control is directed only at infested plants, after checking to determine that the scale colonies are alive. For better control, mineral oil is added to the insecticide solution, with applications made every 15 days until the problem is corrected. The oil should not be used during flowering or during sunny periods of the day. During the rainy season, granulated insecticides may be used.

Cutworms and Armyworms (Lepidoptera: Noctuidae)

Distribution

These insects are widely distributed in the coffee plantations of tropical America (Table 17).

Damage and Economic Importance

Cutworms and armyworms constitute an economically important pest for many crops. Damage is caused during the night by the larval stage. The larvae attack the stems of small coffee plants in germinating beds, seedbeds or plant nurseries, and recently transplanted plants. On seed beds and plant nurseries, plant damage typically takes the form of plants cut at the soil level or slightly above, or withered plants. In the case of recently transplanted coffee plants, defoliated and sometimes dead coffee plants can be observed. *Spodoptera frugiperda* (Smith) larvae feed on the stem, causing withering and finally death of the small plants during the first year of their lives. In other cases, the stem breaks at the site of the ring formed by the larval feeding. When the infestation is severe, many plants are killed and re-sowings are needed, which increases the coffee plantation set-up costs. Damage is more frequent in plantations that are close to fields where corn, beans, vegetables, cassava or pasture are grown.

Pest Description

The following species are presented as examples: *S. frugiperda* – the larvae have a well-contrasted, inverted "Y" on the head; neonate larvae are white with a black head, but as they grow they turn dark. Large worms are light brown to dark green in color and they are about 4.0 cm long. *Agrotis ipsilon* (Hufnagel) – small larvae are brown with paler back marks, and large ones, which may be as be as large as 4.0–5.0 cm, are shiny black-gray in color, with a pale gray line on the back and black tubercles on each of the segments.

Biology and Ecology

Adults are moths that are active at night, laying their eggs individually (*A. ipsilon*) or in groups (*S. frugiperda*). During the first two larval stages, they feed on leaves that are at soil level, and in the last three they act as cutting worms. During the day, they remain hidden in the soil. In some species, such as *A. ipsilon*, the larvae coil up when disturbed. Larvae pupate in the soil.

Natural Enemies

There are many natural enemies (parasitoids, predators and pathogens) of these pests. In Ecuador, the larval parasitoids *Bonetia* sp. (Diptera: Tachinidae) and *Chelonus* sp. (Hymenoptera: Braconidae) and the predatory ground beetle *Calosoma* sp. (Coleoptera: Carabidae), are cited.

Management

Sampling

Night-time inspection of seedbeds and the young plantations should be made to detect initial infestations.

Cultural Control

Seedbeds or plant nurseries should be kept clean of weeds and dead leaves, since the larvae seek shelter there.

Mechanical Control

Larvae should be eliminated by hand during the night-time inspections. Heavy watering should be applied to get the larvae out of their hiding places, followed by manual elimination. Light traps can be used to capture the adults.

Biological Control

Biological insecticides such as *Bacillus thuringiensis* Berliner should be used, particularly at the beginning of infestations, when the larvae are small.

Chemical Control

Insecticides can be incorporated into the soil, before or after sowing, for cutworm control. Granular products are used in a preventive manner. The use of poisoned baits during the night and dry weather is also recommended.

Brown Coffee Borer, *Xylosandrus morigerus* (Blandford) (Coleoptera: Curculionidae: Scolytinae)

Distribution

This pest comes from the Oriental region, having its distribution center in the Indomalayan area. It was detected in the western hemisphere in 1958–1959, and it is now found from Veracruz, Mexico to Brazil.

Damage and Economic Importance

Various tree species can be attacked by *X. morigerus* (e.g., avocado, cacao, cedar, coffee). This insect displays a strong preference for attacking robusta coffee, *C. canephora*. Some reports indicate that it may also infest *C. arabica*; however, this has not been confirmed in Mexico. The attacked coffee plant branches and young stems typically display a few or many holes of about 1.0 mm diameter. Blackening of the tissues may be seen around the perforations. A longitudinal cut of an affected branch reveals a gallery in which the whitish larvae can be observed, along with reddish brown adults. The attacked young branches and stems dry up distally and then die. Apparently, the mortality of the branches and stems is caused by microorganisms that invade the plant tissues through the feeding sites formed by the brown coffee borer. Ants, termites or mites can be found in the abandoned galleries. Often the ants cause the death of branches or stems when enlarging the abandoned galleries of *X. morigerus* to construct their own nests. If death of branches or stems does not occur, the yield is reduced as a result of damage to the flowering and development of the fruit. The symptoms can be observed more frequently on weak coffee plants, but attacks may also be seen on the young stems of pruned plantations. This pest is particularly important in Ecuador. In Mexico, *X. morigerus* is also an important pest in the Soconusco region in Chiapas.

Description

The egg is oval, white and very small. The larva is milky white, with a yellowish head, and lacks legs. The pupa is white initially, turning cream to brown toward maturity. The adult is cylindrical and from 1.40 to 1.90 mm long. It is differentiated from other species of the same genus by the bright brown-reddish color, by the stouter body and because the declivity commencing only on-third of the elytral length from the base, and by the near absence of punctures on the sides of the elytra (variable). Females have well-developed wings and fly, but males are incapable of flight. Females are larger than males.

Biology and Ecology

Mated females take flight during the day, leaving the gallery where they developed in search of branches or stems, which they penetrate to construct the new galleries. The female lays from 20 to 60 eggs in 8–10 days. *X. morigerus* is an ambrosia beetle. The adults and larvae get more nutrition by feeding on fungi (e.g., *Ambrosiaemyces zeylanicus* Trotter is reported from Ecuador;

Raffaelea tritirachium Batra from Mexico) than from the coffee plant tissues. These fungi grow inside the gallery, which is inoculated by the founding female. The larvae have three instars. The life cycle, from egg to adult, is 20–40 days. A gallery may contain more than 80 individuals in all stages of development. The sex ratio in galleries is female-dominated; various studies have found only one male for each 7, 11 or 20 females. Mating occurs within, or very close to the gallery. Infestation is apparently less evident under drought conditions, because the ambrosia fungi require moisture. Nevertheless, reports from Ecuador indicate that the populations are larger during the dry season of the year. *X. morigerus* is a pest which frequently attacks healthy plants; however, very strong attacks may be observed when the coffee plants have been weakened by droughts, malnutrition, nematode attacks and competition with weeds. The attacks may be accompanied by attacks from other Scolytinae.

Natural Enemies

No native parasitoids of this pest have been reported in coffee growing countries in tropical America. However, it should be mentioned that in Indonesia, a *Tetrastichus* sp. (Eulophidae) has been reported, and also probably a bethylid parasitoid. In Ecuador, ants (Formicidae) have been recorded as predators of the brown coffee borer, including species of *Crematogaster*, *Leptothorax*, *Pheidole*, *Pseudomyrmex* and *Solenopsis*. The entomopathogenic fungus *B. bassiana* has been reported infecting this insect pest.

Management

Sampling

No sampling methods have been developed in coffee plantations; however, some studies indicate that penetrated branches and stems have an aggregated distribution in the field. Traps baited with ethanol have been used for monitoring flying females in robusta coffee plantations.

Cultural Control

Infested vegetative material, particularly in young or pruned plantations, should be cut and burned periodically. Adequate fertilization should be applied. Shade of coffee should be regulated by pruning. Weeds should be suppressed by shading, mulching, use of ground cover, and by selective weeding by hand.

Biological Control

This approach has not yet been attempted for this species.

Chemical Control

This is recommended when the beetle population has undergone a marked increase and natural and cultural control cannot restrain it. Insecticides are useful only when adults are out of the galleries or are boring on the branches; once they have taken refuge within the galleries, insecticides have little or no effect on *X. morigerus*.

Stem Borers *Plagiohammus* spp. (Coleoptera: Cerambycidae)

Distribution

Three species of *Plagiohammus* have been reported attacking the stem of coffee plants in Mexico and Central America. *P. maculosus* (Bates) has the wider geographic distribution (Costa Rica, El Salvador, Guatemala, Honduras, Mexico), while *P. mexicanus* Breuning and *P. spinipennis* (Thomson) have been recorded attacking coffee only in Mexican plantations.

Damage and Economic Importance

A pile of white-yellowish sawdust or powder present at the base of coffee plants, at the soil level, in a good indication of infestation by *Plagiohammus*. Infested plants may have a withered, yellow-like and decaying appearance. Careful observation at the stem base may help identify the hole or holes (ca. 5.0 mm in diameter), where the sawdust originates. A longitudinal cut of the stem and root may uncover a large, white or creamy-colored larva with long gallery containing powder; the gallery begins at the stem and may go as low as the tip of the central tap root. These borers are one of the most destructive coffee plant pests in certain areas of tropical America. The damage is caused by the larva when it bores into the stem and the root. The borer attack delays the plant growth and it may cause death directly by damaging its root, or indirectly, by facilitating stem breakage following wind action or other factors.

Description

The egg is unknown. The larva is creamy-white, with the thorax wider than the abdomen, and legless. Its head is light brown with strong and visible mandibles extended forward. A well-developed larva is about 4.5 cm long. The pupa is brown and similar in size to the adult. The adult has an elongated body, cylindrical, from 2.0 to 3.5 cm long by 0.8 cm wide. The body is light brown with two white lines on the prothorax and with irregular white spots on the elytra. The antennae are longer than the body (4.0 cm).

Biology and Ecology

Not much is known about the bionomics of *Plagiohammus* spp. Adult females lay eggs on the bark of coffee plant stems, at a height below 30.0 cm. Upon eclosion, the larva penetrates the stem and bores longitudinally all the way to the root, while it feeds, grows and develops. The larvae may be found in the stem, from the base to a height of one meter. When ready to pupate, the larva moves close to the excretory opening, which has been made close to the ground, and it isolates itself within the stem in a chamber surrounded by sawdust. The larval period lasts from 2 to 3 years. Adults are more visible at the beginning of the rainy season (April through June), the period when egg laying occurs. The abundance of these cerambycids is higher in high-altitude coffee plantations (>1,000 m) and in places with long summers or with lack of rain. Abandoned coffee plantations are more severely attacked.

Natural Enemies

There is no information on the natural enemies of the *Plagiohammus* spp.

Management

Sampling

Coffee plants having sawdust as the base of the trunk should be searched for. If damage is recent, the sawdust is white or pale yellow.

Cultural Control

Infested stems should be removed. Adequate fertilization should be applied. Weeds should be managed by shading, mulching, ground cover, and mechanical removal.

Biological Control

This has not been attempted yet.

Chemical Control

In places where the pest appears yearly, a preventive insecticide application with a brush or a manual pump is recommended, treating from the stem base up to 60.0 cm high. Application may be repeated once or twice every 20 days. In order to kill the larva within the stem, a cotton ball soaked in an insecticide can be inserted through the respiration and excretion opening made by the larva, or insecticide solution can be injected into the opening with a syringe. When treating in this manner, the orifice is enlarged, the product is applied and the orifice is sealed with mud, clay or any other material that solidifies. This step, though effective, can be expensive due to the labor it may require.

White Grubs (Coleoptera: Scarabaeidae)

Distribution

Phyllophaga is a well-represented genus of white grubs in coffee plantations in tropical America (Table 17). In El Salvador, *P. latipes* (Bates), *P. menetriesi* (Blanch) and *P. obsoleta* (Blanch) are found, whereas in Costa Rica *P. sanjosecola* Saylor and *P. vicina* (Moser) are reported. Other white grubs recorded in coffee are *Anomala* sp. (El Salvador) and *Dyscinetus picipes* Burmeister (Cuba).

Damage and Economic Importance

White grubs attack the coffee plant root. The damage is caused by larvae that live in the soil and feed on the root system of the plant. In the seedbed and plant nursery, the plants wither and die rapidly; in the coffee plantation, irregular areas on one or several coffee plants, usually young, may be observed, which show symptoms of yellowishness, limited growth, scarce fruits and mummified fruits. When the affected plants are taken out of the soil, lesions, very few small roots and partial or total bark peeling on the main and secondary roots are observed. In some coffee growing areas, these pests can be economically important, because they may cause death of the plants. The attacks are more severe in plant nurseries, on recently transplanted coffee bushes and on 1 year-old plants, although mature plantations may also suffer the attacks of these pests. In some plantations it is estimated that 2 or 3% of the transplanted coffee plants may be lost to white grub attack. Coffee plantations located in the vicinity of pastures are most affected.

Pest Description

The egg is white; when recently laid, they are elongated, and later on they adopt a round shape. The larva has a milky-white colored body with a "C" shape, with long thoracic legs covered with hair. The head is dark or light, with strong mandibles. There are three larval stages; the last stage grows up to 3.5–4.0 cm long. The pupa is brown-golden in color, with a size that varies between 1.8 and 2.0 cm. The adult is a strong, heavy bodied scarab. Depending on the species, they may be light or dark brown or reddish-brown in color, measuring from 0.5 to 2.5 cm in length; the antennae are enlarged distally, with the apical expansion consisting of several laminated segments. They are able to fly.

Biology and Ecology

Adult females, which have twilight habits, come out at the beginning of the rainy season and they lay their eggs within the first 10.0 cm of depth in the soil, close to pastures or fodders. The eggs are laid one by one or forming small groups. A female may lay up to 200 eggs. Small larvae feed themselves with organic matter and small roots, and when they reach the last development stage, they are voracious root eaters. They are found at different depths, according to the soil temperature and humidity. They are common in areas that have been gramineous pastures. The larval stage lasts about 6 months. Pupation takes place in a chamber or cell located in the soil at a depth between 10.0 and 20.0 cm. The duration of the life cycle, from egg to adult, varies from 9 to 10 months. Adults are strongly attracted by artificial light and they feed from the leaves of some plants, such as cassava, African oil palm and *Erythrina* trees (Fabaceae).

Natural Enemies

The larval parasitoids *Campsomeris*, *Elis* and *Tiphia* (Hymenoptera: Scoliidae) have been reported in coffee plantations. Parasitism of bacteria *Micrococus* sp. on larvae and parasitism of fungi *Spicaria* sp. and *Metarhizium* sp. on pupae has been observed. Nematodes as parasites of larvae have been observed as well. A robber fly *Diogmites* species (Diptera: Asilidae) has been recorded predating larvae in the soil. Several mammal, reptile and bird species predate on the adults.

Management

Sampling

Root and soil samples at a depth of up to 20.0 cm should be taken, in order to determine the infestation sources. The samples are taken from three coffee plants, at 30.0 m intervals. On areas <7 ha, sampling should be taken diagonally and for larger areas sampling should be taken in parallel.

Cultural Control

Weeds should be suppressed principally by shading, by mulching, by ground cover vegetation, by slashing back and by selective weeding by hand. Shade trees should be pruned.

Physical-Mechanical Control

During preparation of the seedbed or plant nursery, the soil to be used for bag filling should be sifted, and the larvae found therein killed manually. Light traps, preferably 40 watt black-light traps, should be used to capture and eliminate adults. The use of a trap for every 10–15 ha is recommended, which should be turned on from 18:00 to 21:00 o'clock. This procedure has the disadvantage of attracting a number of other night habit insect species, which should not be eliminated.

Biological Control

Biological control has not been attempted in coffee plantations.

Chemical Control

In the case of plant nurseries and recently transplanted coffee plants (<1 year old), one larva per plant justifies the use of granular insecticides. The application can also be made at sowing time. With three large larvae or seven small larvae per square meter, insecticides are recommended for young plants. Three year old plants withstand up to eight larvae; for 4 year-old plants, 12–15 larvae; well-attended mature plantations withstand up to 20 larvae per coffee plant.

Black Citrus Aphid, *Toxoptera aurantii* (Boyer De Fonscolombe) (Hemiptera: Aphididae)

Distribution

This aphid comes from the tropical and sub-tropical areas of the Old World. It is widely distributed in coffee plantations in tropical America.

Damage and Economic Importance

T. aurantii attacks leaves, buds and other tender parts of the coffee plant. Coiled, deformed and curled leaves and tender buds are signs of infestation;

also, reduced growth, and leaf and flower drop occur. Damage may occur in seedbeds, plant nurseries, and on adult coffee plants. Yellow, green or black insect colonies, more or less round shaped, can be found on the lower surface of foliage. They are easily excited, producing a characteristic noise which may be audible if the colonies are very large. The infestation may be accompanied by a fungus, called sooty mold, on the foliage, and also by the presence of ants. In general, this aphid is not very important as a pest; however, a considerable yield reduction may appear when severe and prolonged attacks occur, particularly if the infestation appears during the flowering and fruiting season. The damage is often more severe in the plant nursery, on growing plants. *T. aurantii* is reported to be responsible for the transmission of pathogens to coffee plants in Costa Rica and Guadeloupe.

Description

The nymphs are similar to adults, but smaller and dark-brown in color. The adults have a globoid, dark green or black body, and they may or may not have wings; apterous females are larger (2.0–2.1 mm) than winged ones (1.7–1.8 mm). They bear a pair of cornicles on the back of the body.

Biology and Ecology

Adult females generally reproduce by parthenogenesis and are viviparous. Males are winged and rarely seen. An apterous female may produce 50 female nymphs in 7 days. The life cycle, from nymph to adult, is 6 days at 25°C. These aphids excrete honeydew on which the sooty mold fungus grows. The fungus gives a blackish appearance to the plant. The honeydew is highly appreciated by ants; hence the association of ants with aphids, providing them with protection and transport to other plants. *T. aurantii* finds conditions more favorable during the dry season. When conditions are adverse, winged females are produced in order to disperse and colonize new plants. Infestations appear in a cyclic manner.

Natural Enemies

More than 70 species of natural enemies have been reported on *T. aurantii* around the world. In coffee plantations in tropical America, the following have been reported: the braconid parasitoids *Diaretus* sp. and *Lysiphlebus testaceipes* (Cresson); the entomopathogenic fungus *Acrostalagmus albus* Preuss; the coccinellid predators *Hippodamia* sp. and *Cycloneda* sp.; the syrphid predators *Allograpta* sp., *Paragus borbonicus* Macquart and *Baccha clavata* Fabricius; and the green lacewing predator *Chrysopa* sp. (Chrysopidae).

Management

Sampling

Growers are advised to monitor young leaves throughout the dry season for aphids or damage.

Cultural Control

Reinforce shade of coffee plantation during the dry season. Affected plants should not be transplanted.

Biological Control

It is generally acknowledged that natural enemies contribute importantly to prevent *T. aurantii* from having greater economic impact. Natural enemies should be conserved.

Chemical Control

If chemical control becomes necessary, either insecticidal oil or an insecticide may be used. Chemical control should only be applied at the first signs of damage during periods of young leaves' growth. Young leaves should be completely moistened after application of chemicals.

Leaf-Cutting Ants, *Atta* and *Acromyrmex* (Hymenoptera: Formicidae)

Distribution

Leaf-cutting ants of the *Atta* and *Acromyrmex* genera are found in Neotropical countries where coffee is grown. The principal leaf-cutting ant species affecting coffee plants in tropical America are shown in Table 17.

Damage and Economic Importance

Leaf-cutting ants attack leaves, tender buds and flowers of the coffee plant. The leaves of attacked coffee plants have semi-circular cuts or these plants are completely defoliated. Leaf fragments dispersed on the ground are seen around the defoliated plants. In recent attacks, the presence of ants carrying leaf and flower pieces may be observed. It is possible to detect earth mounds (nests) nearby or relatively far away.

Situations in which ants are direct plant pests are rare; however, in the tropical and sub-tropical areas of America, ants of the *Atta* and *Acromyrmex* genera can constitute important pests of many cultivated and wild plants. In tropical America, cutting ants constitute the dominant group of herbivorous animals, because they consume much more vegetation than any other animal group. In the case of coffee, these ants are generally considered of minor importance. Nevertheless, in some areas like the Turrialba region of Costa Rica, *A. cephalotes* attacks on coffee plants can be severe in monocultures. The damage is caused by the worker caste when they cut the coffee foliage and flowers with their mandibles. In some *Atta* species, from 5 to 28 colonies/ha have been observed, with the possibility of having one or more millions of workers in each colony. The nests they construct may have dimensions that vary between 30 and 600 m^2. From one day to the other, one or more coffee plants may be completely defoliated by these ants. Coffee plantations near woody or weedy areas are attacked more commonly.

Pest Description

Atta cephalotes (L.) is hereinafter described. Their colonies contain three castes: queens, males and workers. Queens are big (16 mm), with a strong brown-reddish color, and they have wings (although they lose them after the nuptial flight); also, they have a pair of horns on the occipital lobules and another pair on the lower part of the head, close to the mandibles. Males are winged but smaller (13 mm) than the queens, and they do not have the aforementioned horns. Workers are wingless. Soldier workers present abundant yellowish hair on the forehead sides, and they are about 13–15 mm long. Forager workers have less hair and they are about 9–10 mm long; fungus-cultivator workers are lighter colored and smaller (from 2 to 4 mm).

Biology and Ecology

Atta and *Acromyrmex* ants are social insects that use plant leaves to cultivate symbiotic fungus (*Leucoagaricus gongylophorus* (Möller) Singer; *Attamyces* spp.), which serves as their foodstuff. They form colonies constituted of three castes: queens, males and workers; the latter are sterile and present acute polymorphism and functions (soldiers, foragers, cultivators). The mating of queens with males takes place outside the nest during the nuptial flight, at the beginning of the first rains. Newly mated females dig their nests in the soil and begin to cultivate the fungi which will serve as their food and to lay their first eggs. The eggs give birth to the larvae and after 40–60 days, the first adult workers emerge. New colonies have a single tower-like mound of small size of <200 cm^2 in area, and with a small entrance hole, whereas older colonies are flattened, with larger entrance holes and a colony surface area >200 cm^2. The growth of the colony is very slow at the beginning, but during the second and third year it accelerates rapidly and then it diminishes as the colony starts production of males and winged queens. Towards the end of the third year, the population is enormous, and it is possible to observe more than 1,000 entrance/exit holes on the nest. The *Acromyrmex* nests are simpler than those of *Atta*. In order to reach the plants which serve as their food, the forager workers move from the nest, which is often in non-cultivated fields, through narrow paths which can go more than 100 m in distance. The workers' activity is more intense during the night.

Natural Enemies

Apparently these ants have few natural enemies. Several predators, such as birds, toads, lizards and anteaters feed on the queens and males during the nuptial flight. In Colombia, other carnivorous ants have been observed to be predators of leaf-cutting ants. The importance of all these natural enemies in regulating leaf-cutting ant populations is unknown.

Management

The optimal time of the year to control leaf-cutting ants has not been determined. However, the nuptial flight period, a crucial event within the ant life cycle, should be taken into account. Considering the ecological importance of leaf cutting ants as plant population regulators in woody and grazing areas, and taking into account that in certain areas they are eaten by humans, it is recommended that population regulation, not elimination, be the primary goal.

Sampling

No sampling techniques have been developed for leaf-cutting ants in coffee plantations. The nests can be located by following the narrow paths used by the ants. Ant colony density can be estimated by sampling four 125-m^2 plots at each edge of a farm (north, west, east and south), and a single 500-m^2 area in the center of the farm (a total area of 1,000 m^2).

Cultural Control

Queens should be eliminated at the recently formed nests using a grub hoe. Repellent plants (e.g., sorghum) should be sown. Because coffee on farms with low vegetational diversity is at greater risk of attack by *A. cephalotes*, it is recommended that shade trees be planted in order to increase shade levels and therefore to decrease ant colonization. Also, it may be desirable to plant shade trees that are palatable to leaf-cutting ants, but that should be either not commercially valuable (e.g., *Erythrina poeppigiana* [Walp]. Cook, *Cordia alliodora* (Ruiz & Pav.) Oken, *Swietenia macrophylla* King, *Cedrela odorata* L.), or that are tolerant of ant attack, in order to divert ants from foraging coffee plants.

Biological Control

Some entomopathogenic (e.g., *Paecilomyces* sp. and *M. anisopliae*) and antagonist (*Trichoderma viride* Persoon ex Gray) fungal strains have proved to be successful against leaf-cutting ant colonies in experimental studies. However, the practicality of these fungi has not been assessed in commercial coffee plantations.

Chemical Control

Insecticides are applied directly through some of the entrance/exit holes of the nests, taking the precaution of plugging or closing most of them before. The "ant hill beating" procedure may also be used, which consists of digging in the nest with a shovel in order to uncover the ant brood, and spraying them with insecticide. Also, leaf-cutting ants can be successfully controlled using baits containing insecticides. Treatment results can be improved by basing the amount of insecticide applied on an estimate of the colony volume, instead of surface colony area. An experimental study shows that mounds of dump material can be used as a highly effective small-scale deterrent to protect *Hibiscus* plants from defoliation by *A. cephalotes*, but this method has not been tested in coffee.

Long-Horned Grasshoppers or Katydids (Orthoptera: Tettigoniidae)

Distribution

Two *Idiarthron* species, *I. subquadratum* Saussure & Pictet and *I. atrispinum* (Stål), and one unknown *Gongrocnemis* species have been reported attacking coffee in Mexico and Central America; apparently, *I. subquadratum* is present in Colombia too. Of these, *I. subquadratum* is the most important katydid pest in coffee because very high infestations have been reported in some coffee plantations in El Salvador and Mexico. Most of the information available on katydids comes from this species.

Damage and Economic Importance

Attacked coffee leaves show irregular holes marginally and centrally; feeding can also be observed on the tender buds, shoots and branch tips. A characteristic symptom of katydid damage is the appearance of green and ripe fruits with damaged pulp, so that the coffee beans are exposed. The damage is caused by both the nymphs and adults. In coffee plantations where heavy attacks of *I. subquadratum* occur, complete destruction of leaves, buds and small branches, the fall of tender fruits and the destruction of fruits can be observed. In general, *I. subquadratum* is not an economically important problem in coffee, although it sometimes may create some concern in certain areas of Central America and Mexico. In southeastern Mexico (Siltepec, Chiapas), the most critical attack period is from June through November. Damage is more important in very shaded and abandoned coffee plantations. In addition to direct damage caused by *I. subquadratum,* plant pathogenic fungi may be involved in the damage (e.g., *Phoma costarricensis* Echandi).

Description

The eggs of *I. subquadratum* are brown in color, elongated, with a hard chorion; they are oviposited in compact clusters. There are six nymphal instars. Newly emerged nymphs are fragile and gray in color. Nymphs resemble adults, but are smaller, lighter colored, and lack wings. Nymphs and adults have strong and large mandibles and the antennae are very thin and longer than the body. Adults have a heavy set, more or less cylindrical body, greenish, brown-gray or light gray in color, with females from 5.0 to 6.0 cm long. Males are smaller. With their thorny, strong and long back legs, they can jump. Their ability to fly is limited and in general their movements are clumsy. Females have an ovipositor, from 1.0 to 2.3 cm long, at the tip of the abdomen, which looks like a spur or a knife point.

Biology and Ecology

Idiarthron subquadratum is arboreal, polyphagous, and nocturnally active. Both nymphs and adults leave their daytime shelters at night and disperse by jumping between tree and bush canopies. They hide in shady places, such as dead leaves, rotten trunks and weeds; in particular, they take refuge in plants of wind-breaks, izote (*Yucca guatemalensis* Baker) barriers, banana plants (*Musa* spp.) and *Sanseviera* sp. This species feeds on leaves and fruits of several plants, including coffee (*Coffea* spp.), banana (*Musa* spp.), orange (*Citrus* spp.), chayote [*Sechium edule* (Jacq.) Swartz], and pacaya (*Chamaedorea* sp.). Mating occurs in plant canopies at night or in daytime shelters. Adult females place their eggs in the soil and, in some cases, under the bark. The eggs are placed in a mass (from 5 to 50), and one female may lay several hundred. In Siltepec, Chiapas, Mexico, mating usually occurs in October, and oviposition occurs in November and December. Adults are killed by low temperatures in January and February, and eggs undergo diapause. At the beginning of the rainy season, between May and June, nymphs emerge and start to feed on coffee plants. Generations are overlapping in warmer regions. The life cycle from egg to adult is about 80 days at 28°C. In El Salvador, this pest is especially common in high altitude coffee plantations.

Natural Enemies

Birds, spiders, parasitic nematodes and an unknown tachinid fly species (Diptera: Tachinidae) have been reported in Mexico.

Management

Sampling

"Shelter traps" made with a 10-cm-diameter by 30-cm-long bamboo (*Bambusa vulgaris* Schrad.) internode closed at one end, can be used for sampling *I. subquadratum*. The bamboo traps are placed on coffee bushes upon the first rainfall events, and during daytime are checked every week for captured insects.

Cultural Control

Weed control should be applied. The shade should be regulated. Trash and rotten trunks in the coffee plantation should be prevented. Dry banana and plantain leaves should be eliminated.

Mechanical Control

Bamboo traps as described earlier for sampling can be used for elimination of *I. subquadratum*. The traps are placed in dark spots of the plantation and in the vicinity of the plants that are normally used as refuge. The traps are checked weekly and the insects are killed manually and/or used as food for domestic animals (e.g., chickens and dogs).

Biological Control

Some strains of *B. bassiana* kill nymphs in the laboratory. However, the use of this biocontrol agent has not been attempted in field.

Chemical Control

When infestations are heavy, the application of chemical insecticides at the places of refuge is recommended. Toxic baits placed inside the bamboo traps are also recommended. The most convenient period for chemical control is 1 month after the beginning of rainfall and before oviposition takes place. Because high infestations of the pest have been related to low populations of natural enemies, insecticide use should be avoided in order to conserve natural control.

Bush Crickets, *Paroecanthus* spp. (Orthoptera: Gryllidae)

Distribution

Bush crickets appear sporadically, affecting coffee plants and shade trees in coffee plantations in some areas of Central America and Mexico. The reported species are *Paroecanthus guatemalae* Saussure (Guatemala, Honduras) and *P. niger* Saussure (El Salvador, Guatemala). The *Paroecanthus* species in Mexico remains unknown. Recently, high infestations of bush crickets have been reported in Honduras.

Damage and Economic Importance

Paroecanthus spp. attack lignified stems and branches of coffee bushes and shade trees. The affected plants show small marks or holes, 3.0 mm in diameter by 1.0 mm in depth, distributed in line throughout the affected stems and branches. This mark along the stem gives it the appearance of a flute; hence this damage is known as "flute disease." If the stem or branch bark is lifted right below each hole, an "X" shaped scar on the wood may be observed. The damage is caused when the adult female of the cricket lays its eggs. Heavy attacks of the bush cricket (when there are many holes), may cause physiological disorders in the coffee plant, which affects its development. The cricket can be a pathogen vector, or perhaps the lesions may favor the penetration of diseases. A severe infestation can kill the coffee plant. In Honduras, where high infestations have been reported, the affected plants develop a yellowish color and they lose leaves and fruits.

Description

The egg is white with elongated shape (1.0 by 5.0 mm). Nymphs are similar to adults, but their wings are not well developed and they are smaller than adults. The adult has a cylindrically shaped body and is 2.0–2.5 cm long. The legs are yellowish in color and the abdomen is dark brown. The antennae are filiform and their length is almost twice the size of the body. In the female, the wings do not cover all of the abdomen, which at its tip shows the cerci and a long pin-shaped ovipositor.

Biology and Ecology

The bush cricket is active at night, while during daytime it takes refuge in dark places in the weeds, dead leaves and some plants such as bananas (*Musa* spp.) and izotes (*Y. guatemalensis*). Only on cloudy days and when it is very abundant can it be seen during the day. The female lays about eight eggs in each oviposition hole, distributing two on each end of the scar it makes on the wood, in an "X" shape. The nymphs emerge in about 3 weeks, and they go through several molts for 3 months before becoming adults. Nymphs and adults can feed from the coffee plant. Three or four generations appear per year. The attacks are more severe in unshaded coffee plantations. In Honduras, acute infestations have been reported in the dry season in plantations located between 900 and 1,250 m above sea level.

Natural Enemies

An egg parasitoid wasp, *Acmopolynema* sp. (Hymenoptera: Mymaridae), has been reported in Honduras and Mexico.

Management

Sampling

Scouting should be conducted to determine the limits of the infestation during the dry season. Upon detection of damage, the trunk bark should be scratched in search of the insect's eggs. If the damage is recent, the perforations are white and unhatched eggs shall be observed; if the damage is old, the perforations are dark and the eggs have hatched.

Cultural Control

Weeds should be controlled within and on the edges of the plantation. Severely damaged plants should be re-planted, or pruned of the affected stems, and burned thereafter to eliminate the eggs.

Biological Control

This has not been attempted.

Chemical Control

In plantations that are close to the affected plantations, a preventive insecticide application with a brush or a manual pump is recommended, treating from the stem base up to 60.0 cm high. Application may be repeated once or twice every 20 days. Also, an insecticidal dust can be directed to the main stem, to the soil, and to the plantation edges during the dry season.

Leaf-Eating Caterpillars (Lepidoptera)

Distribution

There is a large and diverse group of leaf-eating caterpillar species in tropical American countries affecting coffee. The principal leaf-eating caterpillars are shown in Table 17.

Damage and Economic Importance

Coffee bushes affected by leaf-eating caterpillars show totally or partially consumed leaves. Sometimes the fruits are also affected. Eventually, voracious worms or caterpillar larvae, as well as, their feces, can be observed. Some of these are urticating caterpillars. These insects are frequently mentioned in the coffee pest manuals of South American countries, such as Brazil and Colombia. Some species even defoliate entire sections of the coffee plantation.

Description

As example of leaf-eating caterpillars, *Oxidia* sp. (Geometridae), is described. When small, they are black, and when large, they are light gray. These caterpillars attain a length of 5.0–6.0 cm. The larvae are called inchworms or measuringworms.

Biology and Ecology

Adults lay their eggs individually or in groups on the foliage of various plants. The larvae or worm feeds on the foliage. The caterpillar goes through several molts, and as it grows, feeds itself voraciously. Some species, such as *Phobetron hipparchia* (Cramer), *Sibine* spp., *Olceclostera moresca* (Schaus), *Megalopyge lanata* (Stoll & Cramer) and *Automeris* sp., among others, have urticating hairs which cause painful lesions to anyone touching them. Measuringworms, which are active nocturnally, possess camouflage which allows them to go unnoticed during the day. In general, the pupation takes place in the soil. In Ecuador, *Automeris* sp. and *Eacles masoni* Schaus appear cyclically during the rainy season. The adults or moths have nocturnal habits. Insecticide abuse and climatological changes can affect the natural enemies of leaf-eating caterpillars, so their populations may increase and become damaging.

Natural Enemies

There are many natural enemies of leaf-eating caterpillars. Among them, birds, parasitic Hymenoptera and Diptera, and fungal, bacterial and viral diseases are notable.

Management

Sampling

Regular inspection of the coffee plantation should be made to detect initial infestation sources.

Mechanical Control

The larvae of urticating worms should be eliminated manually using gloves. In the case of measuringworms, the same can be done, but at night. Adults should be eliminated with light traps.

Biological Control

Bacillus thuringiensis Berliner can be used, particularly at the beginning of infestations when the caterpillars are small.

Chemical Control

Some organophosphates and pyrethroids are recommended. In general, the use of chemical insecticides is not necessary, because the natural enemies provide regulation of the populations of these leaf-eating caterpillars. Thus, it is important to preserve the natural enemies, and use insecticides only in extreme cases.

Leaf Weevils (Coleoptera: Curculionidae)

Distribution

Various leaf weevils are present in coffee plantations in tropical America (Table 17).

Damage and Economic Importance

Leaf weevils attack the coffee bush leaves. The leaves show irregular holes, tearing and notches on their edges, often beginning at the tip and from the edge towards the vein. The most affected parts are new leaves and shoots. The damage is caused by the adults, which feed on the coffee foliage. The attack of these weevils can become important when they affect the buds of recently pruned plants and of trees <1 year old. The lesions caused by this pest on the leaves may favor the infection of *P. costarricensis*.

Description

Larvae are whitish and legless. The color of adults varies according to the species, being off-white (*Compsus* sp.), light brown with yellow spots (*Macrostylus* sp.), grayish, light brown or black (*Epicaerus capetilensis* Sharp.) or green. Their size varies from 9.0 to 13.0 mm. The snout is fairly well developed in these insects.

Biology and Ecology

Adults feed from the foliage of coffee and other plants. A distinctive characteristic of these weevils is that when they feel threatened they contract their legs and snout and let themselves fall to the ground where they seemingly disappear. Their eggs are laid in the soil and the larvae lead a subterranean life (between 10.0 and 20.0 cm deep), feeding from weed roots, including the coffee plant root. The weevil populations are higher from June through August in Honduras. In Brazil, *Pantomorus leucoloma* (Boheman) is more frequent in the summer and it attacks both *C. arabica* and *C. canephora*. In Honduras, the most frequent attacks appear in the highest altitude areas. Very weedy areas favor infestation.

Natural Enemies

Predation by assassin bugs (Hemiptera: Reduviidae) is reported in Costa Rica.

Management

Sampling

Tender buds and new leaves of the coffee plants should be checked. When the damage only appears on old leaves and not new ones, no control measure should be initiated.

Cultural Control

Weeding should not be complete, so that adult and larvae weevils have a feeding source and abstain from attacking the coffee plants.

Biological Control

It has not been attempted.

Chemical Control

When the populations are large, applications of insecticides to the foliage and then to the soil are recommended.

Coffee Bean Weevil, *Araecerus fasciculatus* (De Geer) (Coleoptera: Anthribidae)

Distribution

Present in all coffee growing countries in America.

Damage and Economic Importance

Araecerus fasciculatus attacks stored coffee beans. Coffee beans stored in warehouses, coffee mills and other places used to gather the harvest will show perforations and irregular and relatively large galleries caused by this weevil. Accumulation of a fine yellowish powder is also observed. Highly infested warehouses will have a large number of little beetles, +the walls, roofs and windows. This weevil, which attacks a wide variety of grain in storage, is considered as one of the few economically important pests of stored coffee in the American countries, particularly in South America. It creates problems in warehouses that store poorly processed coffee containing more than 12% humidity. The damage is caused by the weevil larvae, which live in and feed on the grains. The attack is also favored when the warehouse temperature is higher than 27°C and relative humidity is above 60%. In 6 months of infestation, losses of 30% have been estimated. *C. arabica* apparently is more susceptible than *C. canephora*. The fruits that remain on the plant after harvest may also be attacked.

Description

The larva is without legs, white, with a "C" shaped body and a relatively wide thorax. The head is small, light brown in color. They measure from 5.0 to 7.0 mm. They have about five molts. Pupal size varies from 3.0 to 4.0 mm. The adult is oval, with an arched body, covered by hairs and with a length of 2.5–4.5 mm. The head has round prominent eyes, with a short, wide, curved-downwards "snout" and the mouthparts distally.

Biology and Ecology

Adult females lay eggs on the parchment coffee grooves, placing one per grain and approximately three per day. The average number of eggs laid is 52. Larvae create galleries in the seed, and they pupate there also. The life cycle, from egg to adult, is 35–40 days. Between 55 and 74% of the descendants are composed of females. Infestation is more acute on softened coffee beans. Up to ten generations are reported per year.

Natural enemies

In Colombia, the following natural enemies of *A. fasciculatus* have been reported: *Aniseptoromalus calanadrae* (Howard) (Hymenoptera: Pteromalidae), *Cephalonomia gallicola* (Ashmead) (Hymenoptera: Bethylidae), *Cheyletus* sp. (Acari: Cheyletidae) and *Monieziella* sp. (Acari: Tyroglyphidae).

Management

Sampling

Fortnight visits should be made to the storehouses to check the presence of weevils, particularly in the wet season and in places with very humid weather.

Cultural Control

Adequate fertilizing, harvesting and pulp extraction should be conducted. Coffee should be stored with adequate humidity. Warehouses and storage places should be kept clean. Infested lots should be set aside and placed in the sunlight.

Bilogical Control

It is not conducted.

Chemical Control

In the case of preventive treatments and the treatment of infested lots, fumigation is recommended. After fumigation, spraying of a 3-month residual effect pyrethroid with motorized equipment is recommended. The preventive treatment should be conducted when there are 1–2 weevils/m^2 of sacks. Treatment of the walls, floor and roof of the warehouse where the coffee is going to be stored is also recommended.

Spider Mites (Acari)

Distribution

At least, six spider mite species have been recorded in coffee in tropical America (Table 17). *Olygonychus* (Acari: Tetranychidae) is the most representative genus.

Damage and Economic Importance

Spider mites attack coffee foliage in all their stages of development. Attacked plants present yellowish, brown or copper colored leaves, with more undulated edges. Sometimes the attacked leaves may dry up and fall. Also, the leaves lose their shine and present a dirty appearance. The symptoms take place in large patches in the coffee plantation, and more frequently in old, poorly attended coffee plantations, and near the roads. These symptoms are easily recognized at a distance. Upon examination of the upper face of the leave with a magnifying glass, little animals moving on the leave can be observed, and in general, silky threads which retain dust and other residues. The damage, which consists of the destruction of superficial cells of the leaf, is caused by immature and adult mites when they feed. Spider mites may be especially important in some areas of tropical American countries during abnormally dry weather. In severe attacks the leaf functions are interrupted and they may drop. Leaf defoliation and yield decreases may occur when more than 30 mites per leaf are present, particularly under dry weather conditions. The economic importance of some species of mites on coffee, for example, *Polyphagotarsonemus latus* (Banks) (Acari: Tarsonemidae) in Brazil, is unknown.

Description

The egg is elliptic or spherical, bright orange, reddish or red in color, depending on the species. Its length varies from 0.100 to 0.127 mm. The larva has three pairs of legs, an almost circular body, and according to the species, orange or yellow colored when hatching, turning green-yellowish as they feed. They are from 0.15 to 0.16 mm long. Nymphs (protonymph and deutonymph) have four pairs of legs, and they are ovoid and about 0.20 mm long. In the deutonymph, which is larger, females (0.20–0.26 mm) can be differentiated from males (0.18–0.23 mm). Adult females are larger (0.28–0.50 mm) and more oval than the males (0.25–0.35 mm). Color varies according to the species and the sex; however, colors such as red and orange are blended, and in some cases the mites have spots. The broad mite, *P. latus*, has a white-milky color and it is smaller than the other species (0.15–0.20 mm).

Biology and Ecology

Adult females reproduce sexually and parthenogenetically. The eggs are laid one by one, preferentially on the upper face of leaves, close to the veins, although *P. latus*, unlike the others, prefers the lower side of the leaves. The eggs may be fixed to the leaf with the silk threads (cobweb) produced by the mites and which serves for protection and for moving from one leaf to another. Unlike the Tetranychidae, Tenuipalpidae (*Brivipalpus* sp.) do not produce silky threads. Egg laying, in the case of *Olygonychus coffeae* (Nietner), occurs at a rate of 4–6 eggs/day/female for 2 or 3 weeks. Upon eclosion, the larvae feed from cells that they puncture with their chelicerae, and in time they become protonymphs and the latter become deutonymphs. At the end of their development, both protonymphs and deutonymphs go through an inactive stage called "quiescence." An accumulation of various residual materials such as dust and the old exuviae of spider mites can be observed in the cobweb producing species. The egg to adult life cycle varies from 8 to 28 days, according to the temperature. Females mate with one or more males, and a male may fertilize several females. Females, which are more abundant than males, disperse from one leaf to another and from one coffee plant to another, by the use of silk threads. However, the factors that contribute the most to dispersion are the wind, humans and other animals. Spider mites prefer to colonize the sunlit coffee plants and the older leaves, although in severe infestations they also attack the young leaves.

Natural Enemies

Predators such as ladybirds (Coleoptera: Coccinellidae) and rove beetles (Coleoptera: Staphylinidae) are reported. However, the literature on coffee pests is not clear about the predator species present.

Management

Sampling

The plantation should be checked during the summer or dry periods, preferably on roadsides. The infestation of a coffee plantation plot is determined by making parallel inspection routes 25 m apart from each other, and examining 24 leaves at random from four coffee plants every 25 m.

Cultural Control

Shade trees should be planted in very sunlit areas. Weed control should be conducted. Adequate fertilizing should be applied.

Biological Control

Not applied.

Chemical Control

Some pesticides have a selective action, affecting only mites, and others (non-selective) kill mites and insects. In case of a simultaneous attack by mites and leaf miners, non-selective products are recommended. However, the overuse of this practice can negatively affect the beneficial parasitoids and predators. Applications should be made only to infested areas. Various pesticides are recommended, making one application and sometimes a second one. A population of 30–40 spider mites per leaf in the dry season cause defoliation, so this density must be avoided.

References

Barrera JF (ed) (2002) Tres plagas del café en Chiapas. El Colegio de la Frontera Sur. México, 198 pp

Cárdenas-M R, Posada-F FJ (2001) Los insectos y otros habitantes de cafetales y platanales. Comité Departamental de Cafeteros del Quindío. Armenia, Colombia, 250 pp

Castillo-Ponce G, Contreras-J A, Zamarripa-C A, Méndez-L I, Vázquez-M M, HolguínM F, Fernández-R A (1996) Tecnología para la producción de café en México. Instituto Nacional de Investigaciones Forestales y Agropecuarias. México. 88 pp. Primera reimpresión. Folleto Técnico Núm 8

Coffee Industry Development Company Ltd (1986) Growing coffee in Jamaica. Jamaica, 103 pp

García-G A, Campos-A O, Barrera-S CA, Meoño-R JE (1998) Manual de caficultura. Tercera edición. Asociación Nacional del Café, Guatemala, 218 pp

Le Pelley RH (1973) Las plagas del café. Editorial Labor, SA, Barcelona, 693 pp

Matiello JB (1991) O café. Do cultivo ao consumo. Publicações Globo Rural. Coleção do Agricultor. Grãos. Editora Globo, SA, Brasil, 320 pp

Muñoz-H R (2001) Plagas insectiles del cafeto. In: Manual de caficultura. Instituto Hondureño del Café, Honduras, pp 115–142

Páliz-S V, Mendoza-M J (1993) Plagas del cafeto. In: Manual de caficultura. Estación Experimental Pichilingue. GTZ, FUNDAGRO, Quevedo, Ecuador, pp 144–166

Cold Tolerance in Insects

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Exposure to low temperatures is among the most important abiotic factors limiting the range of insects in temperate climates. The relationship between insects and cold is dynamic, particularly when considering the actual temperature at the surface of the integument versus internal and/or ambient conditions, the length of exposure to low temperature, and the degree of temperature fluctuation over a defined period of time (e.g., day, week or winter season). These issues make it challenging to categorize insect tolerance to a specific set of temperatures, particularly in terms of survival. As poikilotherms, although some are heterothermic under specific conditions, insects have adapted to cold environments resulting in extension of locomotor and/or reproductive activity during low temperature exposure, enhancement of metabolic rate, and maintenance of a positive energy balance. The implications to many of these insects are a lengthening of the life cycle and a requirement for individuals to overwinter one or more times. The actual mechanisms associated with these adaptations have received extensive study in recent years, including attempts to decipher the underlying genetic basis of individual and population responses to low temperatures and seasonal change.

Classification of Cold Tolerance

Insect cold tolerance classifications have traditionally been divided into freezing tolerance and freeze intolerant strategies. This division has been criticized in recent years by a number of investigators. The arguments for the classification scheme have depended on the definitions applied to the two terms, and it is how freezing tolerant and freeze intolerant species have been defined that evokes the controversy. For example, in freeze tolerance, these insects are said to be capable of withstanding ice formation in some or nearly all parts of the body and associated fluids. Most insects in this grouping usually freeze at temperatures between −5 and −10°C, though others require lower temperatures. Once frozen, these species can tolerate cooling to much lower temperatures, and upon thawing, the insects recover and apparently resume normal development and behaviors. Some experts, however, have contended that this example of freeze tolerance is at the extreme end of cold tolerance and only represents insects which are most suited to survive low temperatures. An examination of some 60–70 species of insects classified as freezing tolerant has led to the suggestion that there are distinct freeze tolerance strategies that allow insects to be grouped based on supercooling points (SCPs) and lower lethal temperature (LLT): (i) partially freeze tolerant species that survive a small portion of their body water converted to ice; (ii) moderately freeze tolerant species, if the exposure is sufficiently long, die at temperatures <10° below their SCP; (iii) strongly freezing tolerant insect species display LLT twenty degrees or more below their SCP; and (iv) freezing tolerant species possess very low SCPs and freeze at extremely low temperatures. Insects in this latter group are capable of surviving at temperatures a few degrees below their SCP.

Insects that are not tolerant of any ice formation in their bodies are generally termed freeze intolerant species. The natural tendency has been to assume that these insects will die if tissues or body fluids freeze, and presumably if they avoid the frozen state, these insects will survive. Such classification appears to be an oversimplification of the freeze intolerant strategy, because most species of insects found in temperate regions are susceptible to injury and possibly death at non-freezing temperatures. For these insects, the more correct terminology for their low temperature survival strategy is freeze susceptible (avoidance). In this classification, a distinction is made between freezing and chilling, recognizing that injury and death may result from low-temperature processes occurring at non-freezing temperatures. Even in this system of classification, there is further division in which freeze avoiding species are distinguished from those insects susceptible to chilling. Freeze avoidance is defined as both a low temperature survival strategy and a description of a specific circumstance under which the insect will die, that is, when it freezes. Chill tolerant species possess extensive supercooling ability and a high level of cold tolerance, but is distinguished from the freeze avoiding insects by displaying some mortality above the SCP, which in most cases increases with decreasing temperatures and increasing length of exposure. Some insects are strongly influenced by the severity of the preceding winter conditions, indicating that the cold tolerance of these species is not as well developed as those that seem to be independent of yearly variations in winter temperatures. These insects are referred to as chill susceptible and are characterized by extensive supercooling that allows them to survive moderate low temperature exposure (0–5°C), but only brief exposure to temperatures below −5°C can induce death. SCPs are not indicators of cold temperature tolerance in these species. The final category of cold tolerance is termed opportunistic survival. It is used to describe insects that originate in tropical or semi-tropical regions, which implies that these species are deficient in cold hardiness adaptations or characteristics, and as such, are not likely to survive at temperatures below the threshold that permits "normal metabolism." These insects may have extensive supercooling but can only survive low temperatures by opportunistic exploitation of a favorable habitat or location. Essentially such insects are non-hardy since they possess no physiological adaptations to survive low temperatures.

Mechanisms of Cold Tolerance

Cold adapted insects have developed a complex of strategies that allow survival at their physiological temperature minimum. These strategies broadly include (i) morphological (e.g., melanism, hair/pubescence, reduction in size, physical barriers); (ii) behavioral (migration, opportunistic exploitation, parasitism); (iii) physiological (depression of SCPs, removal or acquisition of ice nucleators); and (iv) biochemical (synthesis of antifreeze proteins and/or polyhydric alcohols) adaptations. The latter two adaptations have received considerable attention, resulting in a fairly clear picture of the mechanisms characteristically associated with freeze tolerant versus freeze susceptible strategies. In freeze-tolerant insects, potent ice-nucleating agents are produced or acquired in the extracellular fluids, promoting a protective extracellular freezing at a few degrees below zero. Polyhydroxy alcohols (polyols) and sugars accumulate in extracellular fluids to cryoprotect partially frozen tissues. In addition, fat body and localized tissues synthesize antifreeze proteins that function to inhibit secondary recrystallization of ice. Collectively, these adaptations sharply drop the lower lethal temperature to −40°C or below.

Other adaptations used by freeze tolerant insects include changes in membrane composition to maintain the liquid crystalline state at low temperatures, a process referred to as homeoviscous adaptation. These changes can occur at low temperatures through an increase in points of unsaturation along phospholipids fatty acid chains. Membrane composition changes have also been shown to occur by increasing the cholesterol content or changes in the distribution of phospholipid classes composing plasma membranes. Changes in membrane composition are not restricted to freezing strategies and can occur with freeze susceptible species as well.

In contrast, freeze susceptible species generally attempt to remove or inactivate ice nucleators, most commonly through purging the contents of the digestive tract. Many of these insects have the ability to maintain a liquid state at temperatures well below the equilibrium freezing point (FP) of their body fluids through manipulation of the colligative properties of their body fluids. This can be achieved by increasing the solute concentration of extracellular fluids (directly or through a reduction of water mass), accumulation of cryoprotective polyols and sugars, and through supercooling. Production of thermal hysteresis factors function to stabilize the supercooled state. Some species also elicit a rapid cold-hardening (RCH) response that protects insects against non-freezing (cold shock) injury. Rapid cold-hardening is a swift physiological response elicited by exposure to mild chilling to turn on one or more of the above mechanisms to enhance the cold hardiness of insects, thereby affording protection from exposure to subsequent low temperature exposures. Together, these adaptations contribute to a depression of the SCP and lower the temperatures that promote freezing.

► Diapause
► Overwintering in Insects
► Thermoregulation in Insects

References

Bale JS (1996) Insect cold hardiness: a matter of life and death. Eur J Entomol 93:369–382
Lee RE Jr, Denlinger DL (1991) Insects at low temperatures. Chapman & Hall, New York, 513 pp
Lencioni V (2004) Survival strategies of freshwater insects in cold environments. J Limnol 63:45–55
Sinclair BJ (1999) Insect cold tolerance: how many kinds of frozen? Eur J Entomol 96:157–164
Zachariassen KE (1985) Physiology of cold tolerance in insects. Physiol Rev 65:799–832

Cole Crops

Crops of the family Cruciferae, such as cabbage, broccoli, and collard. Cole crops are also called crucifers.

Collectors

In an aquatic community, insects that collect fine particles of organic matter from the water.

Coleophoridae

A family of moths (order Lepidoptera). They commonly are known as casebearer moths.

► Casebearer Moths
► Butterflies and Moths

Coleoptera

An order of insects. They commonly are known as beetles.

► Beetles

Collecting and Preserving Insects

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Insects provide many opportunities for biological studies, ranging from detailed research to casual field observations. Frequently the need arises for collecting specimens to accurately identify the species of interest. Collecting techniques and methods of preservation of insects vary considerably. A few of these techniques are described here.

Key elements to successful insect collecting

Collectors frequently wish to find as many different insects as possible. In order to accomplish this, the greater the diversity of collection techniques employed and habitats explored, the greater the diversity of insects that will be collected.

Most entomology textbooks present an overview of collecting and preserving insects for study. There are two major categories of information dealing with these subjects, collecting techniques and preservation techniques (how to deal with the insects once collected).

Collecting Techniques

Collecting techniques are limited only by the imagination of the student or researcher. Practically any technique will yield a few insects. Here are a few:

Hand-collecting, turning over logs and rocks and other objects
Unbaited pitfall traps
Pitfall traps baited with carrion, dung, yeast, or fermented fruits
Hand-collecting, or use of sweep nets, beating trays, aspirators
Cutting sections of plants to place into containers within which the insects will later emerge, breaking logs apart with an ax or chisel, stripping bark of dead trees to find subcortical insects
Hand-held nets
Passive intercept traps: Malaise and window traps
Attractant traps with mercury-vapor or ultraviolet light, or carbon dioxide, or specific insect pheromones as bait
For Subterranean Insects
Sifting soil or debris with a sieve
Placing debris into a Berlese or Tullgren funnel to extract insects by heat, or light, or a chemical repellent
Aquatic nets

Living Insects

If your objective is to collect insects alive for study alive, then your best option to prevent damage is to chill them as soon as they are collected. To do this, place them into suitable containers in an insulated chest with ice or other refrigerant, and transport them as soon as you can. If your objective is to kill them to obtain preserved specimens, kill rapidly to prevent damage.

Killing Methods

Large specimens typically are killed in a jar with a closely fitting lid using a volatile toxicant such as ethyl acetate absorbed onto plaster or sawdust or cotton. Small specimens may be killed in vials using the same toxicant. Alternatively, if they will not be damaged by immersion in liquid, they may be killed in 70% alcohol or soapy water. Freezing (several hours) also is an option, though it may result in certain deformities.

Recording

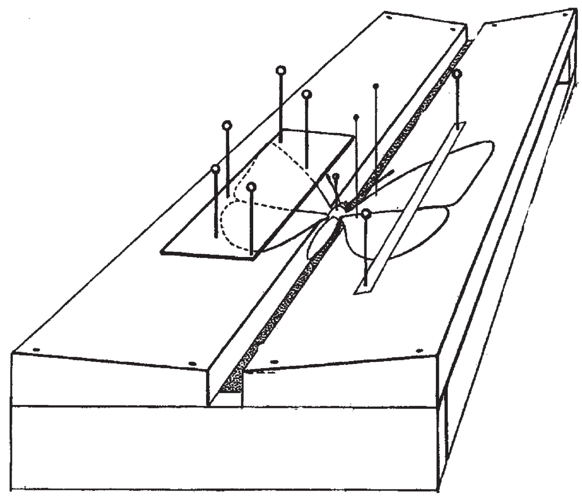
Vials or other containers should be labeled in the field as the specimens are collected. Never use a ball-point pen for insect labels; if you do not have a pen with India ink available in the field, make a temporary label with pencil. Record at least all the information you may eventually need (see section below on Labeling specimens).

Preserving Insects

Small and soft-bodied insects should be stored in 70% alcohol (either ethanol or isopropanol) in tightly sealed glass vials. Isopropanol (rubbing alcohol) is inexpensive and readily obtained in most countries. Ethanol may be subject to excise laws because it may be used for human consumption, so typically is more expensive and more difficult to obtain, and there seems to be no point in going to that trouble if isopropanol can be obtained. A label should be placed in the vial, with information printed or written in insoluble ink. An additional label may be taped to the outside of the vial. Insect larvae may need brief insertion in boiling water before they are preserved in alcohol, without which they will blacken.

Vials

These are available in many shapes and sizes. Plastic vials are useful in the field because they are less subject to breakage than are glass vials, but glass vials are very much preferable for long-term storage. When specimens are stored in alcohol in vials, be aware that the type of vial and type of stopper is important. Straight-sided glass vials ("shell vials") are thinner-walled and more fragile than other types. Vials stoppered with screw-caps or corks will sooner or later allow the liquid contents to evaporate. Thick-walled glass vials with necks ("homeopathic vials"), when fitted with natural rubber stoppers, seem to offer the greatest permanence, but the rubber will eventually crack and decompose. Stoppers of neoprene or other synthetic materials have not yet shown an advantage over natural rubber. If using homeopathic vials with rubber or neoprene stoppers, it is important to seat the stopper firmly; this may be done by inserting a straightened-out steel paper clip alongside the stopper as the latter is inserted, then withdrawing the paper clip to release trapped air. All vials should be checked periodically for leakage and loss of preservative.



Collecting and Preserving Insects, Figure 75
Spreading board used to prepare moths and butterflies.

Mounting Techniques

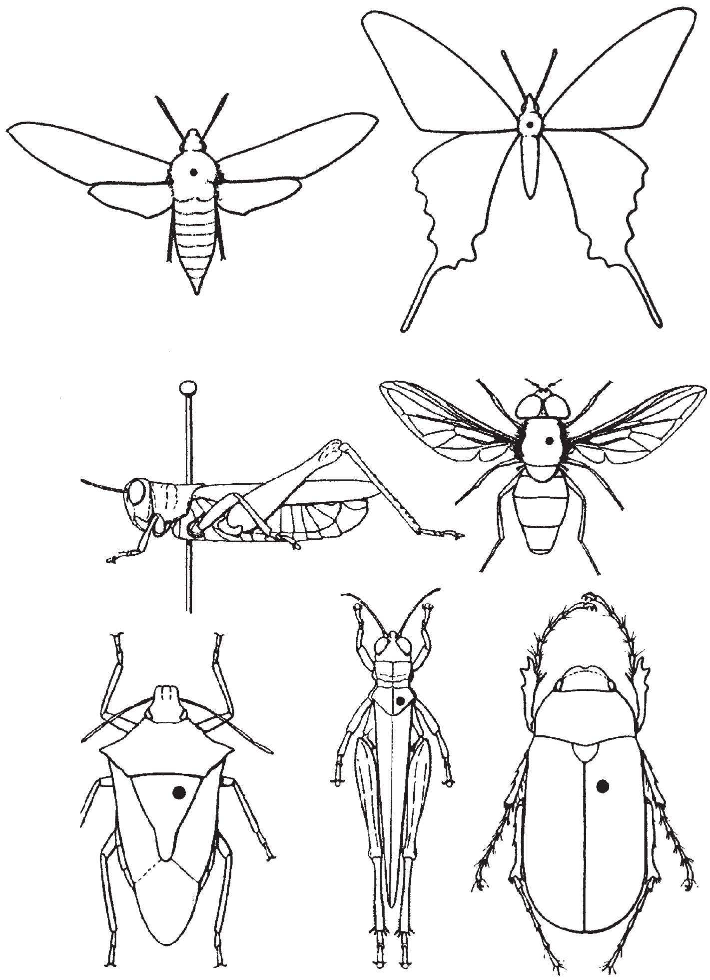
Different insects require different mounting techniques. Large moths and butterflies and some other winged insects are mounted with wings neatly (Fig. 75) spread on a spreading board.

Pinning

Insects of average size usually are mounted on pins. In many countries, steel pins of 3.5 cm length are used; the best quality is stainless steel with nylon heads. Lacquered steel pins may rust, and brass pins may corrode (become covered with green verdigris) in humid climates. Pin widths are numerically designated, with standard sizes 0–3 increasing in thickness with increase in numerical value. Extremely narrow pins are of size 00, and extremely thick pins are of sizes 4–7 but are longer. Most insects large enough to be pinned may be pinned on sizes 2 or 3. Insects are pinned in specific locations depending on their classification. Large beetles are pinned in the middle of their right wing cover, close to the front margin. Other examples of pin positions are included in the diagrams provided in the accompanying figures. (In the United Kingdom, white brass pins once were used; their length varied with width). Minuten pins (from a German adjective meaning minute) are very small, fine pins used for pinning tiny insects into a small block of pinning material, which is in turn pinned by a standard pin.

Storage in Transparent Envelopes

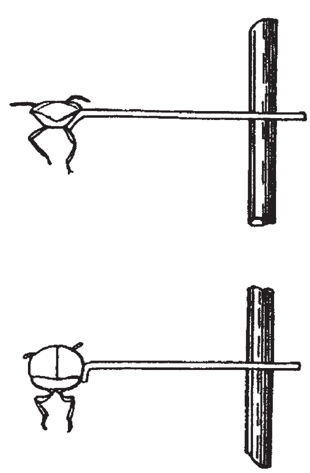
Some Odonatologists (dragonfly collectors) stuff their specimens into semi-transparent (Glassine) envelopes. This is an alternative to pinning (Fig. 76) specimens, saving much museum space. However, this is not necessarily the most desirable method of storage because the specimens are prone to breakage.



Collecting and Preserving Insects, Figure 76 Position of pins in various kinds of insects.

Pointing

Insects too small to be pinned safely may be mounted on cardboard points, glued to the point on their right side. Points should be bent down slightly to better attach to the side of each specimen. Such points may be purchased, or may be made by a hand-held device called a point press, which cuts points (Fig. 77) from a sheet of cardboard. Care should be taken not to cover the underside of the insect with glue, obscuring key characters. This is the standard mounting technique in the USA, and it is claimed to be better because underside characters are visible. However, there are two major problems: (i) insects thus mounted are very susceptible to physical damage,



Collecting and Preserving Insects, Figure 77 Examples of how to position mounting point under right side of insect specimen.

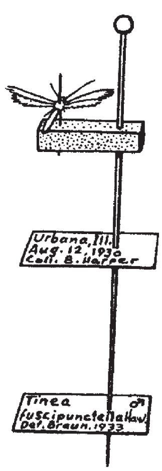
and (ii) adhesives used to obtain secure adhesion to the small surface may be soluble only in harsh solvents (benzene, toluene, xylene, acetone, etc.). Subsequent attempts to dissect soft body tissues are thwarted because these are destroyed.

Card Mounts

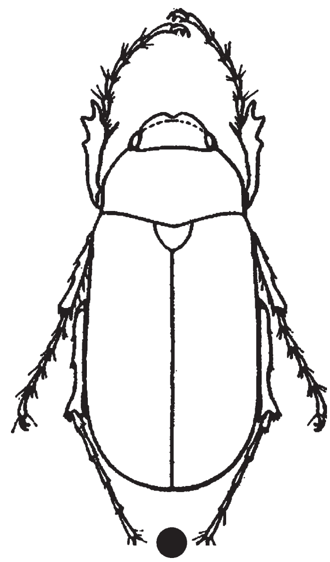
Some groups of insects are better mounted on tiny (Figs. 78–80) rectangular cards. Cards of standard sizes are sold by some supply houses. This technique is popular with European entomologists. It is claimed to be better because the specimens are better-protected from physical damage and because they may be viewed in one plane against the white background of the card (as contrasted with specimens that may be drooped over card points), and because they may later be removed easily for dissection. Only water-soluble adhesives should be used. There are perhaps two problems:

(1) The underside characters are not visible without removal from the card. However, preparators with a series of specimens available will mount some dorsal side up, and some ventral side up.

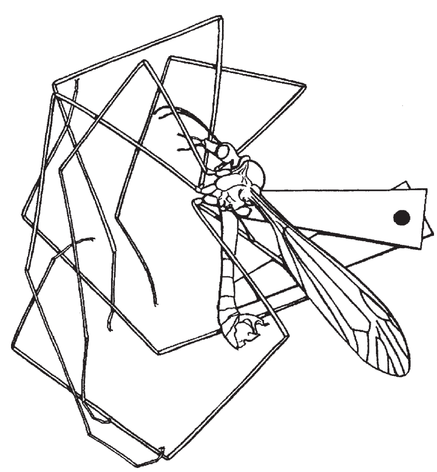
(2) It is said that such a method of preparation is more time-consuming. This may be true, but it varies with the expertise of the preparator. More importantly, if the specimen is rare and from a distant locality, it makes far more sense to spend a few seconds more to prepare it this way (better-protected)



Collecting and Preserving Insects, Figure 78 Minuten pin used to position small insect above piece of cork. This technique is frequently used for delicate flies and very small moths and butterflies.



Collecting and Preserving Insects, Figure 79 Card-mounted specimen (European fashion).



Collecting and Preserving Insects, Figure 80 Large long-legged flies such as crane flies may need to have their body supported with an extra large point. Alternatively, the specimen could be place on a card mount, which will offer much more protection from damage by protecting the legs, too.

than to face the days or weeks and expense necessary to collect more specimen from the distant locality, even assuming that a replacement specimen can be found for a rare species.

Adhesives

Many kinds of adhesives are used to secure insects to card points. The objective is to secure the insect firmly to the point. It is recommended that only water-soluble or alcohol-soluble adhesives be used. When other kinds of adhesives are used, there will arise questions about the necessary solvents to remove the specimens (it is virtually impossible to guess what adhesive some collector may have used and what its solvent is). For specimens adhered to card mounts, only water-soluble adhesives should be used. When card-mounting, the strength of the adhesive is less important because much more surface area is used. Many water-soluble adhesives are available, although the two most commonly sold in stationery stores in the USA are unsuitable, one because it dries hard, cracks and turns brown, and the other because it is not truly transparent and dries from the outside inward, forming first a sticky "skin."

Card Mounts, Card Points, and Labels

Use only a heavy weight, high quality, non-yellowing, 100% rag card stock for making these items. Some years ago, "Bristol board," a laminated card, was recommended. We see no advantage to such laminated card stock.

Genitalia

It is often desirable to dissect specimens to make the genitalia evident for identification purposes. With card-mounted specimens, the genitalia (if large enough and well-sclerotized) may be mounted on the same card as the specimen, a great advantage. If, however, they are feebly sclerotized or too small, they may be mounted (after dehydration through alcohols to xylene) in a drop of Canada balsam on a small celluloid rectangle pinned directly below the specimen (no cover slip is needed). When specimens are card-pointed, the usual method is to place them in "genitalia vials" pinned through the stopper below the specimen. Such genitalia vials are tiny, of glass or plastic, and contain a cork or stopper of some synthetic material; typically, they contain alcohol, glycerine, or a mixture of the two. When genitalia almost fill the vial, and when such vials are checked frequently for leakage, the method may have merit. Otherwise they can be disastrous: extremely small genitalia in a vial can be lost when the stopper is pulled, or the vial can leak and desiccate the parts. Such genitalia vials are to be avoided wherever possible.

Slides

Some insect specimens are best mounted on microscope slides. These include very small and soft-bodied insects as well as dissections of insect parts. The most permanent mountant available is Canada balsam. Some insects (scale insects, aphids and lice, minute parasitic Hymenoptera, and many insect larvae) typically are prepared by clearing and differential staining before being mounted on microscope slides.

Soft-Bodied Specimens

Because of their hard exoskeleton, very many insects will maintain their shape when dead and dry. Some, however, will not – they tend to shrivel. Techniques have been developed for maintaining the shape of dried specimens (one alternative was to preserve them in alcohol, another to mount them on microscope slides). For decades, the preferred method for preserving large Orthoptera (grasshoppers and crickets), Phasmida (stick-insects) and Mantodea (mantids) was to eviscerate them and stuff their abdomen with cotton before pinning and drying. For Odonata (dragonflies and damselflies), the method was to eviscerate them and stuff a toothpick-shaped object into the abdominal cavity. For larvae of butterflies and moths (caterpillars), the method was to roll the abdominal contents out through the anus, then inflate the abdomen (by blowing into it) while drying the inflated skin in a tiny oven. Mosquitoes and some other flies, and Trichoptera, having feeble exoskeletons, could not be dealt with by such rough physical methods because they are covered in scales, and the scales would be lost by such treatment; they were destined to shrivel as they dried. Many of these methods have now been abandoned because of the availability of critical-point drying. A critical-point drier is an expensive piece of equipment and may be unavailable in some institutions and to amateur collectors.

Labeling Specimens

Specimens without accurate and complete collection data are of little value. A proper label contains locality data, date of collection, collector's name, method of collection, and identification label with determiner's name. Additional information may be included (host plant, behavior, etc.). Computer-generated laser-printed labels in general seem entirely adequate. Such labels with a font size of 3 or 4 are suitable for pinned specimens. Labels with larger font (10 or 12) can be used in vials with alcohol. Most laser-printer inks seem stable in alcohol (you may want to test labels made with the laser printer available to you before relying upon them), and printed labels are far easier to read than are most hand-written labels, Use them wherever you can for pinned and alcohol-preserved specimens (provided that the ink is not alcohol-soluble).

Information on Labels

Labels for pinned insects should be placed beneath specimens, aligned parallel with the insect's body. The top label should contain (i) country, (ii) province or state, etc., (iii) township, etc., (iv) route information when known if the collection was a result of a route followed, (v) date of collection, and (vi) collector's name(s). A second label should contain method of collection (bait, technique, trap) and habitat. Dates should be written in order day-month-year (the international standard) with month either in letters or in Roman numerals and the year with four digits. For example, a date of the 4th of July 2002 should thus be written as 4-JUL-2002 or 4-VII-2002, and not as 7/04/02 (as in commonly done in the USA) or as 4/7/02 (as is commonly done in most of the world) or as 2002/7/4 as is commonly done in the Far East. A third label may contain rearing information. A fourth label may contain determination information, species name, determiner, and date of determination.

Pinning Blocks

Supply houses sell blocks on which specimens and labels may be pinned. These achieve a standard height for each specimen and label and make a resultant collection appear more uniform. Unfortunately, we have not seen a block from a supply house with more than three steps. If the steps are (i) specimen, (ii) dissections of genitalia from the specimen, (iii) locality information, (iv) habitat information, and (v) identification information, then five steps are needed. The only current option seems to be for collectors to manufacture their own pinning blocks (one of us has done so).

Storing Collections

Insect collections require protection from atmospheric conditions such as humidity and pests capable of destroying specimens. Such pests include cockroaches, silverfish, ants, dermestid and anobiid beetles, booklice, and mice. Tight containers, with a fumigant, will deter most pests. Be sure not to use chemicals toxic to humans or pets. The safest method is to store in or donate a collection to a recognized museum where it will be maintained safely. Museum curators often will provide space for your materials, hoping that at some time in the future you will donate your collection to them.

Storage Containers and Cabinets

Insect specimens are typically housed in wooden storage boxes (in the USA called Schmit or Schmitt or Schmidt boxes) or in cabinets with drawers. The storage boxes have tightly-fitting lids, and the floor is lined with a material into which pins can easily be thrust. Traditionally, this material was cork, usually lined with paper, but now is normally some white synthetic foam. European cabinets were and are of numerous sizes, each drawer lined with a pinning material. The disadvantage of the European system is that dozens or hundreds of specimens may have to be moved one by one to make way for a few new specimens. Additionally, drawers of some cabinets are exceptionally shallow, allowing vertical space only for short pins. In the USA, another system arose in which drawers of standard size were designed to accept a standard number of cardboard unit trays, the unit trays (not the drawers themselves) are lined with a pinning material, and all drawers accept standard 3.5 cm pins. Unit trays are manufactured in a range of complementary sizes so that a combination of small and large trays, as need arises, will fit precisely into a drawer. The trays make it easy to move groups of specimens about a drawer or from drawer to drawer, and protect specimens from physical damage. The "US system" was a good idea, but, unfortunately, the "system" is at least three systems, not one, and developed at competing museums, which differ in dimensions of drawers and size of unit trays so that they are not interchangeable.

Supply Houses

Several companies maintain an inventory of entomological supplies and sell by mail order. They sell nets, beating sheets, light traps, vials, pins, forceps, lenses, pinning blocks, storage boxes, cabinets, microscopes, microscope illuminators, microscope slides, preservatives, light traps, numerous other items, and assorted entomological literature.

Permits

A very few species of insects have been declared to be endangered species. They may not be collected, even on your own property, without a very hard-to-obtain permit. In many countries, you may collect any other insect (apart from endangered species) on your own property, or (with permission from the landowner) on someone else's property. If the landowner is a government agency and the property is a park or preserve, you may need a written permit from that agency. In a few countries you may not collect insects of any kind without a government permit; even if you use a pesticide to kill pests on your property, and along with the pests you kill harmless or beneficial insects, you may not collect any of these insects without a permit. So, be aware of the laws in your country.

References

Hatch M (1926) Concerning the insect collection. Entomol News 37:329–332

Lehker GE, Deay HO (1969) How to collect, preserve, and identify insects. Extension circular 509. Cooperative Extension Service, Purdue University, Lafayette, IA, 43 pp

Ross HH (1962) How to collect and preserve insects. Illinois State Natural History Survey Circular 39, Urbana, IL, 71 pp

Smart J (1954) Instructions for collectors. No 4A Insects. British Museum (Natural History), London, UK, 178 pp

Steyskal GC, Murphy WL, Hoover EM (eds) (1986) Insects and mites: techniques for collection and preservation. US

Department of Agriculture, Miscellaneous Publication No 1443, Washington, DC, 103 pp. Available Online at http://www.sel.barc.usda.gov/Selhome/collpres/contents.htm

Collembola

An order of hexapods in the class Entognatha, and sometimes considered to be insects. They commonly are called springtails.

► Springtails

Colleterial Glands

Female insects commonly secrete glue that attaches the egg to a substrate. Also secreted in some cases are jelly-like materials, oothecae, or pods containing the individual eggs. The glands that secrete these are known by various names, including accessory, mucous, cement, and colleterial glands.

Colletidae

A family of bees (order Hymenoptera, superfamily Apoidae). They commonly are known as plasterer bees and yellow-faced bees.

► Wasps, Ants, Bees and Sawflies
► Bees

Collophore

A tube-like structure located ventrally on the first abdominal segment of springtails (Collembola).

Colobathristidae

A family of bugs (order Hemiptera, suborder Pentamorpha).

► Bugs

Coloburiscidae

A family of mayflies (order Ephemeroptera).

► Mayflies

Colonization

The introduction and establishment of a species, usually a beneficial insect, in a new geographic area or habitat.

Colony

A group of individuals, other than a mated pair, which rears offspring in a cooperative manner, and may construct a nest. (contrast with aggregation)

Colony Fission

Among social insects, the same as budding: multiplication of colonies by the departure from the parental nest of one or more reproductive forms accompanied by workers. Thus, the parental nest remains functional and new ones are founded.

Colony Odor

The odor specific to a particular colony. This odor allows social insects to identify their nestmates among others of the same species.

► Social Insect Pheromones

Colorado Potato Beetle, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae)

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Colorado potato beetle is the most important insect pest of potatoes in the northern hemisphere. Larvae and adults feed on potato foliage, and under many agricultural conditions the pest will completely defoliate the crop if not controlled. It is also a major pest of eggplant (aubergine) and tomato in some regions, as well as feeding on solanaceous weeds such as horsenettle, *Solanum carolinense*. Although it is occasionally found on other nightshade crops such as peppers (*Capsicum*), tobacco, and husk tomato (*Physalis*), it cannot complete its life-cycle on these hosts.

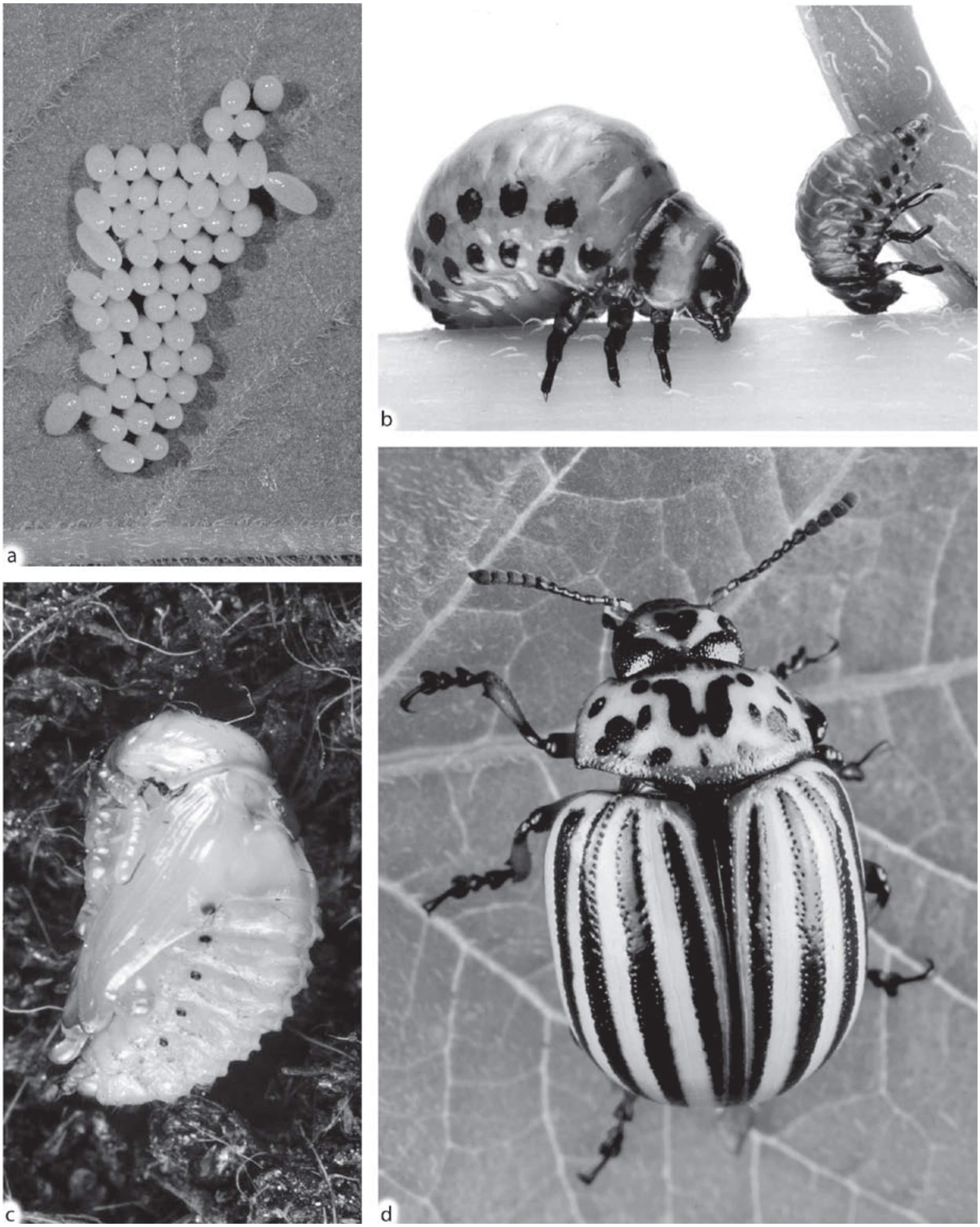
The original range of Colorado potato beetle was probably restricted to southwestern USA and/or northern Mexico, where the host plants were the spiny nightshade herbs *Solanum rostratum* (buffalobur) and *Solanum elaeagnifolium* (silverleaf nightshade). The species was described in 1824, but the first occurrence on potato was not reported until 1859 in Nebraska. From there it spread rapidly, especially eastward, reaching the Atlantic coast of North America in 1874. By then the potato crop was a staple food, and the spread of Colorado potato beetle infestation prompted early development of arsenical pesticides and application methods in the USA.

In 1870, responding in part to the threat of Colorado potato beetle introduction, Germany established the first-ever quarantine law followed within several years by other European countries. Following the eradication of numerous isolated European introductions, its establishment into France in 1921 initiated another rapid geographic invasion which now includes all of Europe (except for the United Kingdom, Ireland, and Scandinavia), continues through central Asia eastward into China, and threatens to spread into east and south Asia, where one-third of the world's potatoes are grown. The range is now about 8 million km^2 in North America and a like area in Eurasia. Climatically favorable areas not yet infested include east Asia, parts of south Asia temperate South America and Africa, Australia and New Zealand.

Colorado potato beetle adults are approximately 10 mm long, convex, with cream-yellow and black striped elytra, and variable black markings (Fig. 81) in the pronotum. Larvae are typically orange with two rows of black lateral spots, and as later instars are characteristically hump-backed in shape. Colorado potato beetle overwinters as the adult in the soil, and has from one to several generations per year, depending on temperature, photoperiod, and availability and quality of host plants. In the spring, overwintered adults emerge from the soil and begin their search for host plants to feed upon. This commences with walking, but after a few days beetles may take to flight. The yellow-orange eggs, laid on leaf undersides in masses of 20–60 (several hundred to a few thousand total per female), soon hatch into leaf-feeding larvae which eat about 40 cm^2 of foliage. The fourth instar larva drops to the ground and digs down a few cm to pupate in the soil, emerging 10–20 days later as a callow adult. Also a voracious leaf feeder, the imago consumes up to 10 cm^2 per day. Depending on food, photoperiod, and temperature, this young adult may mate and reproduce, or after feeding, bury itself 10–50 cm deep in the soil to spend months in diapause before emerging the next spring.

In areas where tomatoes abound, it has evolved an improved fitness on this plant, as in the southeastern USA and Uzbekistan. Even where it does not thrive on tomato, large numbers may damage this valuable crop. In contrast, potato plants can tolerate light to moderate defoliation at certain times of year, but without control, major to complete crop loss is common. A typical economic threshold is one adult equivalent per plant, where small larvae are counted as equivalent to 1/4 of one adult, and large larvae (3rd and 4th instars) equate to 2/3 of an adult. Yield impact is dependent on timing, variety, and other crop stresses.

In early years, control relied on hand-picking, but this gave way to arsenical insecticides and in the 1940s the more powerful synthetic chemical controls. No other agricultural pest better exemplifies evolution of resistance to insecticides. Within the first decade of DDT use, it was failing against Colorado potato beetle in the intensive potato-growing region of Long Island, New York, USA. Resistance followed to numerous other chlorinated hydrocarbons, organophosphates, carbamates, and pyrethroids. This sustained evolution of pesticide resistance has prompted development and use of additional novel chemical controls such as neonicotinoids and ecdysteroids, as well as transgenic crops incorporating high levels of beetle-specific



Colorado Potato Beetle, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae), Figure 81
Colorado potato beetle (a) egg mass, (b) larvae, (c) pupa and (d) adult. (Egg mass photo by D. Weber; others by Doro Röthlisberger, Zoological Museum, University of Zurich.)

Cry3A BT toxins (derived from *Bacillus thuringiensis*). Transgenic potatoes were developed and introduced as the cultivar "Newleaf" in the 1990s, later also incorporating resistance to important aphid-transmitted potato viruses. Yet this highly effective tactic met with a mixed and then negative reception, first because it was introduced contemporaneously with an effective and broader-spectrum systemic insecticide, imidacloprid, and later because large multinational processors decided that using transgenic potatoes would risk consumer opposition across their global markets. Two years after registration in the US, major buyers announced plans to discontinue Newleaf purchases, and commercial sales have been discontinued. Transgenic technology continues with limited field trials in eastern Europe, and may be commercialized in the future. One prerequisite for sustainable use, as with chemical controls, is the implementation of resistance management plans.

Periodic failure of chemical controls has prompted research into a variety of alternatives ranging from pedestrian to peculiar. These include native and introduced biological controls, crop rotation, cover crop mulches, trap crops, trenches to disrupt crop colonization, early planting, late planting, and multi-row propane-fueled flamers and crop vacuums. Collectively and as complements to chemical control, these are essential tactics to manage the pest and help avert resistance.

For an insect that is the focus of thousands of published scientific articles, there is still surprisingly much to learn. In just the past few years, plant-based attractants as well as a male-produced aggregation pheromone, (*S*)-3,7-dimethyl-2-oxo-6-octene-1,3-diol, have been discovered. The exact role that these behaviorally active substances will play in Colorado potato beetle management remains to be seen, but perhaps in combination with selective toxins and/or antifeedants, a push-pull behavioral strategy can succeed in suppressing the Colorado potato beetle instead of whole-field treatments which have historically failed due to selection of resistance.

Natural enemies of Colorado potato beetle may sometimes keep the pest below economic threshold, but not reliably in most current cropping systems. Predatory stink bugs (*Podisus* and *Perillus*) as well as several species of generalist Coccinellidae and Carabidae, spiders and harvestmen are common predators. During the 1980s, the egg parasitoid wasp *Edovum puttleri* was introduced to the USA from Colombia (where it is native on *L. undecemlineata* (Stål)), and enjoyed success as an inundative biocontrol in the high-value eggplant crop. This parasitoid is not winter-hardy. Rearing efforts ceased with the advent of the systemic neonicotinoid imidacloprid.

Two of the most promising natural enemies native to North America are quite poorly studied. *Lebia grandis* is a carabid ground beetle predator of Colorado potato beetle eggs and larvae as an adult, whose larvae are ectoparasitoids of Colorado potato beetle pupae. The newly hatched larvae locate the Colorado potato beetle host soon after it buries itself to pupate, then obtain their entire larval food requirement from a single host pupa, emerging weeks later as blue-metallic and orange, very mobile and hungry adult predator beetles. Two species of tachinid parasitoid flies of the genus *Myiopharus* attack larvae or in the fall even Colorado potato beetle adults, where they overwinter as an early-instar larva inside their host, then develop and emerge the next season as an adult fly. *Beauveria bassiana* has potential to suppress Colorado potato beetle populations under some conditions, and commercial formulations have been developed. If the agroecosystem can somehow better nurture natural enemies, especially early in the season before Colorado potato beetle damage the crop, then Colorado potato beetle management may not so frequently require costly and sometimes troublesome insecticidal inputs.

Crop rotation is consistently an effective means to delay and reduce colonization of overwintered adults. But in many cases, land tenure and intensive culture may prevent farmers from rotating the several hundred meters which constitute an effective separation in successive years. Yet even unrotated crops are amenable to border treatments, trap crops or trenches to thwart beetle colonization, because many adults overwinter in wooded or other non-crop areas adjacent to crop fields. Physical controls of flaming and vacuuming have enjoyed limited success against the pest. Rye straw or other killed cover crops suppress Colorado potato beetle populations, probably by a combination of abiotic and biotic effects. One novel cultural-physical control uses late-maturing trap crops to attract beetles to concentrated overwintering areas which are then stripped of their snow and mulch covering in midwinter to enhance diapause mortality.

Colorado potato beetle is one of the most frequently used bioassay insects for toxicological and physiological research, and usually the first beetle to be tested with candidate insecticides. It is easily maintained on a potato diet, hosting few diseases in the lab, and is also amenable to semi-artificial diet, which aids in precisely controlling its nutrition. Colorado potato beetle has played a key role in development of concepts of host-plant location and selection, host shifts, molecular and population mechanisms of pesticide resistance, gene flow, and integrated pest management. There is also active research on conventional and engineered crop resistance, neurophysiology, dispersal behavior, biochemical and molecular reaction of host plants to Colorado potato beetle feeding, digestive, microbial and immunological defenses of Colorado potato beetle and, of course, novel natural and synthetic toxins and antifeedants.

Providing sustainable control options requires not only laboratory and molecular insights into the mechanisms, but also ecological and behavioral insights, especially into the movement of beetles within and between fields which could lead to the spread or suppression of pesticide resistance genes in agricultural populations. The quantification of gene flow and frequencies, which in turn depends on selection, dispersal and reproduction, provides the basis for rational deployment of refugia in resistance management. Questions of movement are also critical to effective employment of crop rotation and pest colonization in a variety of regional cropping systems. In some areas, the beetle flies frequently. In others, it flies rarely. In Siberia, it buries deeply over winter, while in milder areas, it buries less deeply. Some beetles delay emergence from diapause for years at a time. Researchers express both reverence and frustration at the variability in its behavior.

Just why is the Colorado potato beetle so flexible in responding to changing ecology and toxicology? The reason may lie in its evolutionary history of genetic and biochemical diversity in ecological and evolutionary pursuit of toxicologically complex and ephemeral groups of host plants. This beetle reinforces the need for flexible and integrative thinking in developing pest management strategies: one tactic alone will not quell it for long. Witness the latest entry, the chloronicotinyl imidacloprid, starting to fail after about 10 years of intensive use in the eastern USA. Integration of multiple effective tactics will continue to be essential for an intelligent and sustainable approach to management of the formidable Colorado potato beetle.

► Potato Pests and Their Management
► Vegetable Pests and Their Management

References

Boiteau G, Alyokhin A, Ferro DN (2003) The Colorado potato beetle in movement. Can Entomol 135:1–22
Casagrande RA (1987) The Colorado potato beetle: 125 years of mismanagement. Bull Entomol Soc Am 33:142–150
Chang GC, Snyder WE (2004) The relationship between predator density, community composition, and field predation of Colorado potato beetle eggs. Biol Control 31:453–461
Dickens JC, Oliver JE, Hollister B, Davis JC, Klun JA (2002) Breaking a paradigm: male-produced aggregation pheromone for the Colorado potato beetle. J Exp Biol 205:1925–1933
Ferro DN, Logan JA, Voss RH, Elkinton JS (1985) Colorado potato beetle (Coleoptera: Chrysomelidae) temperature-dependent growth and feeding rates. Environ Entomol 14:343–348
Grapputo A, Boman S, Lindström L, Lyytinen A, Mappes J (2005) The voyage of an invasive species across continents: genetic diversity of North American and European Colorado potato beetle populations. Mol Ecol 14:4207–4219
Jermy T (1994) Hypotheses on oligophagy: how far the case of the Colorado potato beetle supports them. In: Jolivet PH, Cox ML, Petitpierre E (eds) Novel aspects of the biology of Chrysomelidae. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 129–139

Hough-Goldstein JA, Heimpel GE, Bechmann HE, Mason CE (1993) Arthropod natural enemies of the Colorado potato beetle. Crop Protect 12:324–334
Mota-Sanchez D, Hollingworth RM, Grafius EJ, Moyer DD (2006) Resistance and cross-resistance to neonicotinoid insecticides and spinosad in the Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae). Pest Manag Sci 62:30–37
Weber DC (2003) Colorado beetle: pest on the move. Pest Outlook 14:256–259

Colorado Tick Fever

A viral disease transmitted by ticks in the USA.

► Ticks

Columnar Cells

The tall, and generally most numerous cells, of the midgut. They conduct most of the enzyme secretion and absorption of digested products.

Colydiidae

A family of beetles (order Coleoptera). They commonly are known as cylindrical bark beetles.

► Beetles

Comb

A layer of brood cells or cocoons produced by social insects and clustered together in a regular arrangement.

Comb-Clawed Beetles

Members of the family Alleculidae (order Coleoptera).

► Beetles

Commensalism

An association between two organisms from distant taxa that harms neither and benefits at least one.

Common Fleas

Members of the family Pulicidae (order Siphonaptera).

► Fleas

Common Name

A vernacular name, reflecting the language of a particular country, as opposed to a scientific name, which is universal.

► Common (Vernacular) Names of Insects

Common Oviduct

A median tube (median oviduct) of the female genital tract (Fig. 82) that leads from the lateral oviducts to the cloaca (vagina).

► Reproduction

Common Sawflies

Members of the family Tenthredinidae (order Hymenoptera, suborder Symphyta).

► Wasps, Ants, Bees and Sawflies

Common Scorpionflies

Members of the family Panorpidae (order Mecoptera).

► Scorpionflies

Common Skimmers

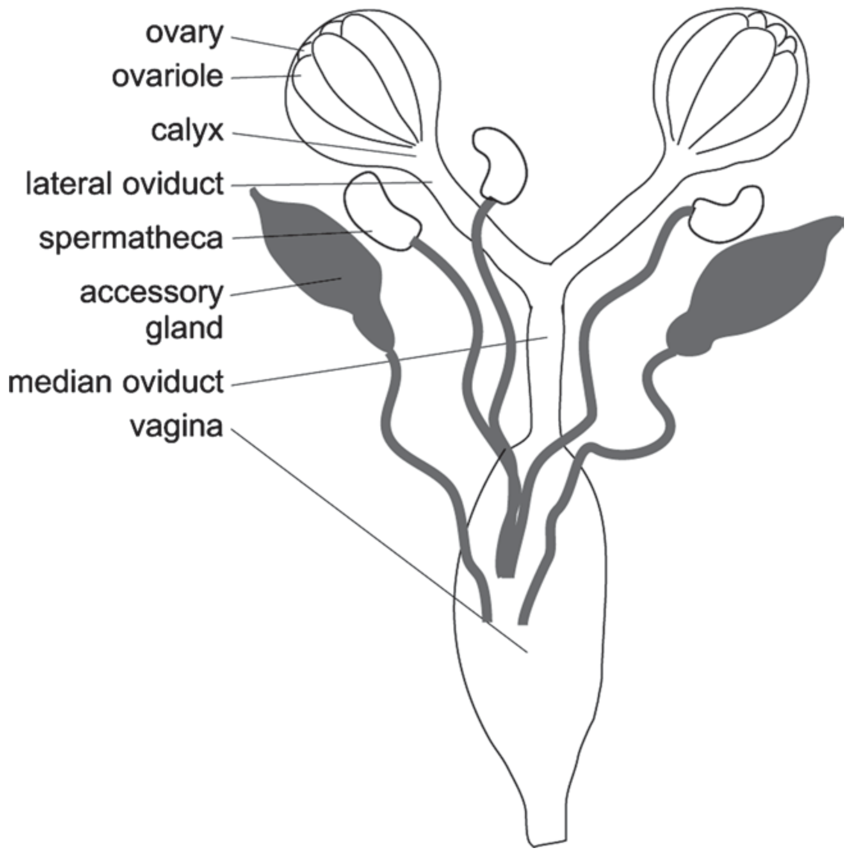
A family of dragonflies in the order Odonata: Libellulidae.

► Dragonflies and Damselflies

Common Stoneflies

Members of the stonefly family Perlidae (order Plecoptera).

► Stoneflies



Common Oviduct, Figure 82 **Diagram of female reproductive system, as found in *Rhagoletis* (Diptera) (adapted from Chapman, The insects: structure and function).**

Common Thrips

Members of the family Thripidae (order Thysanoptera).

► Thrips

Common (Vernacular) Names of Insects

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There are two meanings of the word "common" as applied to names. One is that a name is abundant or widespread. Quite another is that a name is written in the vernacular language of the place where it is used, rather than in Latin. Take, for example, the species *Danaus plexippus* whose common name in the USA is monarch butterfly. That name is common on both counts. But take instead the scarab species *Serica rhypha* which has been assigned the invented English language name "crooked silky June beetle." That "common" name is unlikely to be known to more than a handful of people anywhere; it is a vernacular name that is not commonly used.

Very few vernacular names are common in the sense of abundantly used and widespread. A more appropriate term for this entry would be vernacular names, but this expression itself is not common (in the sense of being widely used and abundant), although it deserves to be so.

The English language has a few true common names for insects. Ant, bee, beetle, butterfly, and cricket are some of them. They are old names, having come into use before entomologists began to classify the five or six million insect species that may exist. In medieval bestiaries, such names were used as if they applied to individual species, so that we may read in bestiaries about the habits of "the ant" alongside habits of "the lion."

Entomologists soon realized that they were dealing with many species of ants, and by 1990 had described about 8,800 species of them, with the task of description still unfinished. Together, they are classified as the family Formicidae, they have 8,800 + scientific species names, and entomologists call them "the ants." In contrast, "the lion" of medieval bestiarists remains the one species *Panthera leo*.

The general public seems to have little grasp of this complexity. News writers, when interviewing an entomologist about ants, typically insist that the entomologist provide a "common name" for whatever ant species is being discussed. Then, the news writer typically uses this "common name" and writes about it being "a variety of ant[s]." By using the expression "variety" instead of species, the news writer seems to be drawing on a medieval classification (that "the ant" is the classificatory equivalent of "the lion"), refusing to acknowledge that there may be more than one species of ant. It is a sad reflection on public education that news writers may have only a medieval knowledge of insect classification and, that with such [lack of] knowledge, their task is to inform the public.

Entomologists, when challenged with the question of "what is the common name of the insect you are talking about?," invented some names in vernacular English. They invented such names as "the wood ant," "the carpenter ant," "the black imported fire ant," "the red imported fire ant," "the Argentine ant" and a few others. But those names do not go very far in listing the 8,800+ species of ants known worldwide. Even those few names became cumbersome for news writers who preferred greater simplification. Thus, "the red imported fire ant" got simplified to "the fire ant" (by which "the black imported fire ant" became "downsized").

There is no hope for systematically providing "common" (vernacular) names for all the approximately one million insect species that have now been described (and have scientific names) much less the three to five million that have not yet been described. Nor is there any point in doing so in English or the world's other over 900 current written languages. The emphasis should instead be on providing scientific (Latin) names for all species. Then we will have at least one name that may be used worldwide for each species, as was the intent of scientific names. For any group of people insisting on a name in its own language for some particular insect species where none exists, one may be invented on the spur of the moment.

Conventionally, "common names" are not capitalized in English. If, however, a proper noun (such as a geographical name or the name of a person or a month) is incorporated in that "common name," then that word (a proper noun) alone needs capitalization (for example, "a June beetle").

Vernacular Names Derived from Scientific Names

For higher taxa of insects and any other animals, there are accepted methods of deriving English

Common (Vernacular) Names of Insects, Table 18 Examples of common (vernacular) names

Classification	Name	Common name	Derived singular	Derived plural
1 tribe	Brachinini	bombardier beetles	brachinine	brachinines
2 subfamily	Cicindelinae	tiger beetles	cicindeline	cicindelines
3 family	Culicidae	mosquitoes	culicid	culicids
4 order	Plecoptera	stoneflies	plecopteran	plecopterans
5 class	Insecta	–	insect	insects
6 phylum	Arthropoda	–	arthropod	arthropods

vernacular names ("common names") from the scientific names. The table below gives the scientific name of a tribe, a subfamily, a family, an order, a class, and a phylum. English vernacular names have been derived as shown.

It is unfortunate that the derived vernacular names in rows 1 and 2 are identical in ending.

The same method may be used for deriving vernacular names from all names of higher taxa. These derived names are English (not Latin) and are typically written with all letters in the same case, which is to say that there is no more reason to capitalize the first letter than there is to capitalize the first letter of the English words bird or cat. Editorial guidelines of major entomological journals, with no exceptions, require that they not be capitalized, to avoid confusion with scientific names.

The same method is used to derive vernacular names in other languages using the Latin alphabet, but with twists according to the language in question. In French, the singular and plural from Culicidae are culicide and culicides, but many French texts do capitalize the first letter. In Italian they are culicido and culicidi, and it seems permissible although not required in at least some Italian entomological journals to capitalize the first letter. In Spanish they are culícido and culícidos, and the tendency, as in English, is not to capitalize the first letter. In German the plural is Culiciden, and this word must be capitalized because all German nouns must have the first letter capitalized; the singular should be Culicid (capitalized), but such a word is avoided by circumlocution.

"Official" Common Names

The Entomological Society of America has taken an unusual step of publishing a list of "common names." The names selected for this list and their form are due to opinions of a committee. By 1989 this list had a few more than 2,000 "common names," and they applied to selected taxa at various levels from subspecies to class, including some non-insect invertebrates. The list was developed because "standardized common names are useful when communicating with the public and with other entomologists." The list includes names of "species [that], in most cases, will inhabit the United States, Canada, or their possessions and territories." To promote adoption of these approved names, the ESA requires that only they be used in manuscripts submitted to that society for publication. More than 100,000 species of insects inhabit the United States and/or Canada, and far fewer than 2% of species have been given approved "common names."

ESA's printed list of common names was recently supplemented with an online capability by which common names or scientific names may be searched (http://www.entsoc.org/pubs/common_names/index.htm). Long delay in implementing this online search ability, meanwhile requiring purchase of the printed edition, may have contributed to lack of adoption of the approved names by other organizations within the United States. For example, in the mid-1990s, this writer used the ESA-approved "common name" for *Apis mellifera* (honey bee) in a manuscript submitted as a book chapter for publication by a commercial publishing house. That name was changed to "honeybee" by the editorial staff on grounds that "honeybee" is the "house style" of that publishing house. Outside the United States, the ESA-approved "common names" have even less weight, because contrasting "common names" may be commonly used. For example, the ESA-approved "common name" for the butterfly *Pieris rapae* is "imported cabbageworm" (based upon the medieval concept that its larva is a "worm," and the more recent concept that it was "imported" from Europe [in fact, it probably arrived as an immigrant, which is to say that it may have been a contaminant or hitchhiker on some cargo, never deliberately imported, but the possibility that it arrived by a combination of winds and flight from Europe or eastern Asia is hard to rule out]) but, in the United Kingdom where it is native, it has been called "small white" or "small white butterfly" perhaps since the eighteenth century.

Australia's CSIRO and the Entomological Society of Canada list "common" names of insects on websites http://www.ento.csiro.au/aicn and http://esc-sec.org/menu.htp, respectively, with free public access.

Reference

ESA (1989) Common names of insects and related organisms. Entomological Society of America, Lanham, MD, 199 pp

Common Walkingsticks

A family of walkingsticks (Heteronemiidae) in the order Phasmatodea.

► Walkingsticks and Leaf Insects

Communal Behavior

A level of sociality less than eusocial behavior. A type of presocial behavior. It involves members of the same generation sharing a nest, but without brood care.

► Presocial
► Solitary
► Subsocial
► Communal
► Quasisocial
► Semisocial
► Eusocial Behavior

Community

A group of populations that interact within a certain geographic area. The biotic portion of an ecosystem. This is also called an ecological community.

Companion Planting

The interplanting of repellent and susceptible host plants, affording protection to the susceptible plants.

Competitive Displacement

Replacement of one species by another. Species that replace other species typically are ecological homologues, or nearly so. This also is known as competitive exclusion.

► Gause's Principle

Complex Metamorphosis

A change in body form in which the insect displays a striking change in appearance over the course of its development. This is also referred to as holometabolous development. The developmental process consists of the egg, larval, pupal and adult stages. Complex metamorphosis is also known as complete metamorphosis.

► Metamorphosis
► Incomplete Metamorphosis

Compliance Procedure (for a Consignment)

From a regulatory perspective, this is an official procedure that is used to verify that a consignment (usually of plants or other regulated articles) complies with stated phytosanitary procedures.

► Risk Analysis (Assessment)
► Regulatory Entomology
► Invasive Species

Compound Eyes

The principal organs of visual reception in most insects, consisting of individual functional units (ommatidia), each of which is marked externally by a facet. The number of ommatidia present in an eye varies greatly among taxa. Species with great visual acuity may have thousands of ommatidia per eye, whereas others with poor vision may have as few as a dozen ommatidia per eye. Compound eyes are very effective at detecting motion, but less suitable for discerning form. Color vision apparently in present in most insects, and polarization of light can be detected by some.

► Head of Hexapods

Compsocidae

A family of psocids (order Psocoptera).

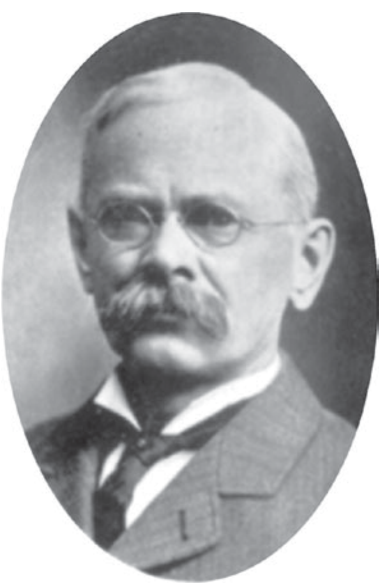
► Bark-Lice, Book-Lice or Psocids

Compound Nest

A nest containing more than one species of social insect. Although there may be intermingling by the adults, the broods are maintained separately.

Comstock, John Henry

Henry Comstock was born on a farm in Wisconsin on February 24, 1849. His father, in attempt to pay off the farm's mortgage, decided to search for gold in California, but died of cholera on the journey, leaving his mother to support the family. She became ill after she moved with her son to New York in 1853, and John was first placed in an orphanage, then cared for by unsympathetic relatives, then taken in by a farming/sailing family. He became a cook on sailing ships on the Great Lakes to earn his living. In 1869 he entered Cornell University, and in summer 1870, after reading Thaddeus Harris' book "Insects injurious to vegetation" he determined to become an entomologist. Unfortunately for him no course in entomology was being offered at Cornell University, so in summer 1872 he studied entomology at Harvard University with Hermann Hagen. After this brief introduction, he returned to Cornell University and there taught entomology while he was still a student. Until that time, he had supported himself by working as a laborer and at other part-time jobs. Now, he was paid as a lecturer. He continued his studies and graduated in 1874 with a B.S. degree, the only degree that he ever earned. He continued to lecture at Cornell University and in 1876 was appointed (Fig. 83) Assistant Professor of Entomology. In 1878 he married Anna Botsford, one of his students. But by then he had accepted and acted upon an invitation by Charles Riley to study *Alabama argillacea*, a pest of cotton, and the following year he became Chief Entomologist in the U.S. Department of Agriculture. In the winter of 1879–1880 he began studies of scale insects on citrus in Florida and continued them in California. He returned to Washington, was replaced as Chief Entomologist by Charles Riley, who reoccupied the position, then returned to academic life at Cornell University. His wife graduated from Cornell in 1885, and by then had taught herself wood-engraving, which she used with acclaim to illustrate her husband's (1888) first part of his "An introduction to entomology" and other works. This was followed (1894) by "Manual for the study of insects," a book which was so successful that the "Comstock Publishing Company"



Comstock, John Henry, Figure 83 **John Henry Comstock.**

was formed, and it continues to this day as a branch of Cornell University Press and outlet for major entomological works. Later works (1904) "How to know the butterflies" and (1912) "The spider book" followed. Anna Comstock's "Handbook of nature study" was published in 1911 and her "Pet book" in 1914. His "Introduction to entomology" was published in full in 1920. He resigned from his university position in 1913 and died in 1931, surviving his wife by less than a year, having suffered a brain hemorrhage in 1926 and merely existing for the next 5 years.

Reference

*Mallis A (1971) John Henry Comstock and Anna Botsford Comstock. In: American entomologists. Rutgers University Press, New Brunswick, NJ, pp 126–138

Concealer Moths (Lepidoptera: Oecophoridae)

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Concealer moths, family Oecophoridae, are a large family of about 7,550 described species from all faunal regions, with most species being from Australia; the actual fauna may well exceed 12,000 species worldwide. There are ten subfamilies recognized: Depressariinae, Ethmiinae, Peleopodinae, Autostichinae, Xyloryctinae, Stenomatinae, Oecophorinae, Hypertrophinae, Chimabachinae, and Deuterogoniinae. Many of the subfamilies have at various times been considered separate families (e.g., Ethmiinae, Stenomatinae, Xyloryctinae). Even some of the odd tribes of Oecophorinae have been considered separate families, such as the tribe Stathmopodini. The family is part of the superfamily Gelechioidea in the section Tineina, subsection Tineina, of the division Ditrysia. Adults small to medium size (5–80 mm wingspan), with smooth head (rarely slightly roughened); haustellum scaled; maxillary palpi 3–4-segmented and folded over haustellum base (or reduced to one segment). Maculation varies from somber to very colorful and iridescent, and variously marked; venation (Fig. 84) usually complete (rarely reduced as in such narrow-winged groups as Stathmopodini). Adults mostly nocturnal but some are diurnal or crepuscular. Larvae include many leaf litter feeders, but also leaf tiers, leaf webbers, bark feeders, and a few leafminers, with a very diverse assemblage of biologies involved. Host plants include a large number of plant families, plus lichens, fungi, and detritus or leaf litter. Some groups are recorded more on some plants, such as Ethmiinae, which have many host records in Boraginaceae, and the Australian Hypertrophinae, which are mostly on Myrtaceae.

Concealer Moths (Lepidoptera: Oecophoridae), Figure 84 Example of concealer moths (Oecophoridae), *Alabonia geoffrella* (Linneaus) from Italy.

References

*Common IFB (1994–1997) Oecophorine genera of Australia. In: Monographs on Australian Lepidoptera 3:1–390 (1994); 5:1–407 (1997), CSIRO, Canberra
*Gaede M (1938–1939) Oecophoridae. In: Lepidopterorum catalogus, 88, 92:1–476. W Junk, The Hague
Gozmány L (2000) In: Microlepidoptera Palaearctica, Band 10: Holcopogonidae. Goecke & Evers, Keltern, 174 pp, 8 pl

Hodges RW (1974) Gelechioidea. Oecophoridae. In: Dominick RB (eds) The moths of America North of Mexico including Greenland, Fasc 6.2. EW Classey, London, 142 pp, 8 pl

Powell JA (1973) A systematic monograph of New World ethmiid moths (Lepidoptera: Gelechioidea). Smithsonian Contrib Zool 120:1–302

Sattler K (1967) Ethmiidae. In: Amsel HG, Gregor F, Reisser H (eds) Microlepidoptera Palaearctica, vol 2. G Fromme, Vienna, 185 pp, 106 pl

*Toll S (1964) Oecophoridae. In: Klucze do Oznaczania Owadów Polski. 27. Motyle – Lepidoptera, 35:1–174. Polskie Towardzystwo Entomologiczne [in Polish. Engl transl 1975. 176 pp. National Science Foundation, Washington]

Conchaspididae

A family of insects in the superfamily Coccoidae (order Hemiptera).

► Bugs

Conditional Lethal

A mutation that may be lethal only under certain environmental conditions.

Conditioned Stimulus

A stimulus that evokes a response that was previously elicited by an unconditioned stimulus.

Condyle

A process by means of which an appendage is articulated at the point of attachment, and particularly the point of articulation of the mandible and the head.

Confused Flour Beetle, *Tribolium confusum* Jacquelin du Val (Coleoptera: Tenebrionidae)

This important grain pest feeds on flour, but not on whole grain kernels.

► Stored Grain and Flour Insects

Congeners

Member of the same genus.

Congo Floor Maggot, *Auchmeromyia senegalensis* (*luteola*) (Diptera: Calliphoridae)

The larvae of this curious fly feed on the blood of humans and other mammals, though they do not infest the tissues. The normal hosts are warthogs, hyenas and other animals. Occasionally the females deposit eggs on the floor of huts and the larvae live within the earthen floor or in the bedding of primitive habitations in sub-Saharan Africa. The larvae become active at night, feeding on sleeping inhabitants. They repeatedly feed for periods of 15–20 min, and then retreat to their hiding places. Inhabitants can avoid this pest by sleeping above the floor, in beds or hammocks.

► Myiasis

Congener

This has several meanings, but generally means an organism belonging to the same genus as another organism. Congeners within the same geographical region tend to compete with one another so many adaptations can be observed that mitigate this pressure on populations. Congenic organisms are organisms with very similar genomes.

Conidiophore

A specialized hypha on which one or more conidia are produced.

Conidium

A sexual fungus spore formed at the end of a conidiophore.

Conifer Bark Beetles

Members of the family Boridae (order Coleoptera).
► Beetles

Conifer Sawflies

Some members of the family Diprionidae (order Hymenoptera, suborder Symphyta).
► Wasps, Ants, Bees and Sawflies

Coniopterygidae

A family of insects in the order Neuroptera. They commonly are known as dustywings.
► Lacewings, Antlions, Mantidflies

Conjunctiva

A membraneous infolded portion of the body wall (Fig. 85) that connects two segments.

Connexivum

In Hemiptera, the junction of the dorsal and ventral abdominal plates, which is marked by a pronounced ridge.

Conopidae

A family of flies (order Diptera). They commonly are known as thick-headed flies.
► Flies

Conservation Biological Control

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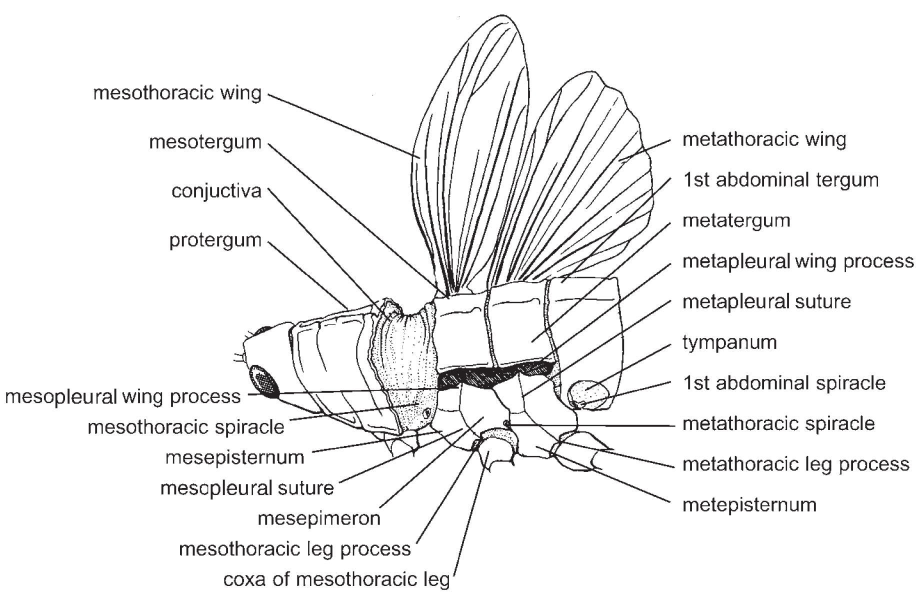
Conservation biological control is the implementation of practices that maintain and enhance the reproduction, survival, and efficacy of natural enemies (predators, parasitoids, and pathogens) of pests. Natural enemies are important in regulating populations of many agricultural and forest insect pests. Approaches to conservation of these natural



Conjunctiva, Figure 85 **Head and thorax of a grasshopper (Orthoptera).**

enemies involve avoidance of practices harmful to them, as well as adoption of practices that benefit them. Like other animals, insect natural enemies require food, water, and shelter, and protection from adverse conditions. To achieve the goals of conservation biological control, fundamental knowledge of the biology and requirements of natural enemies is needed.

Practices Detrimental to Natural Enemies

Perhaps the most important rule of conservation biological control is the physician's maxim, "first, do no harm." Many insecticides can have both direct and indirect effects on natural enemies. Direct effects include acute or chronic mortality as a result of direct contact with pesticides. Direct sublethal effects, such as decreased adult fecundity, reduced viability of offspring, and changes in feeding habits or other behaviors can also occur. Indirect effects can result from mortality in populations of alternate prey or hosts of the natural enemies. Use of broad-spectrum insecticides that have detrimental effects on natural enemies can lead to rapid resurgence of targeted pest populations. In addition, secondary pest outbreaks (rapid increase to pest status of populations of non-target arthropods) can result if naturally occurring biological control of these secondary arthropods is disrupted. Use of more selective "biorational" insecticides, or insecticides with short residual activity, can be an effective strategy for conservation of biological control agents. Timing insecticide applications when natural enemies are absent or in life stages that are not susceptible to the insecticide can also aid in natural enemy conservation. Recent research involving development of pesticide-resistant natural enemies holds promise as well.

Conservation biological control also includes implementation of agricultural and silvicultural practices compatible with maintenance of natural enemy populations. Monoculture environments are highly advantageous to many herbivorous pests, but are usually very poor environments for natural enemies. Plowing, mowing, and harvesting operations, dust from these practices, burning of crop residues, and poorly timed irrigation practices can cause direct mortality of natural enemies. Of greater importance, however, is the habitat disruption associated with these practices. This disruption can create harsh conditions for natural enemies. Alternate hosts or prey, nectar and pollen sources, free water, and refugia are generally found in greater quantities in habitats with greater diversity of vegetation. Microclimatic conditions are generally more moderate as well. However, increasing reliance on intensive agriculture and forestry practices has tended to decrease habitat heterogeneity as well as genetic diversity of crops. Densities of parasitoids, as well as parasitism rates of pest species, have been found to be higher in mixed species habitats and in agricultural field edges near mixed species habitats. Avoidance or modification of cultural practices that disrupt natural enemy populations is an important strategy for maintaining natural enemy effectiveness.

Practices that Enhance Natural Enemy Effectiveness

Incorporating practices that are beneficial to natural enemies requires fundamental knowledge of natural enemy ecology and life history. These practices can be divided into two broad categories: (i) alternate foods or hosts of natural enemies, and (ii) shelter and refugia.

Many predators and parasitoids require alternate food sources. For instance, certain ladybird beetles (Coccinellidae), which are important aphid predators, feed on plant pollen before switching to aphids. Many adult parasitoids require food in the form of pollen, nectar, or honeydew. Availability of such foods has been found to increase fecundity, longevity, survival, and effectiveness of many species. Availability of plant food sources may also increase the host searching efficiency of parasitoids, since degree of hunger can influence whether the parasitoids spend more time searching for hosts or for food. Starved parasitoids have demonstrated greater attraction to flower odors over host-associated odors. Maintenance of non-crop plants in or around agricultural fields or forest plantations can provide these foods, and also harbor alternate hosts or prey of natural enemies, helping to maintain natural enemy populations when pest populations are low. Provision of artificial supplementary food sources has also been shown to increase longevity of some agricultural and forest parasitoids in the laboratory and field.

Natural enemies also require shelter from the elements. Artificial shelters have been found to increase winter survival of various peach orchard predators, allowing them to provide improved control of early season peach pests. Windbreaks and shelterbelts may increase searching efficiency and oviposition of parasitoids and predators adversely affected by high winds. Within-field and border refugia in the form of mixed species habitats can also increase the natural enemy: pest ratio by providing overwintering and aestivation sites.

Conservation biological control is likely to increase in importance as agricultural and commercial forest systems become more intensively managed and restrictions on the use of conventional insecticides increase. It is an approach that requires integration of fundamental insect life history and natural enemy/pest interactions with knowledge of the ecology of the systems in which these interactions take place. This combination of factors makes conservation biological control research and implementation a challenging, but potentially rewarding, endeavor.

References

Barbosa P (ed) (1998) Conservation biological control. Academic Press, New York, NY, 396 pp
Croft BA (1990) Arthropod biological control agents and pesticides. Wiley, New York, NY, 723 pp
Landis DA, Wratten SD, Gurr GM (2000) Habitat management to conserve natural enemies of arthropod pests in agriculture. Ann Rev Entomol 45:175–201
Pickett CH, Bugg RL (eds) (1998) Enhancing biological control: habitat management to promote natural enemies of agricultural pests. University of California Press, Berkeley, CA, 422 pp

Conservation of Ground Beetles in Annual Crops

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Ground beetles (Coleoptera: Carabidae) are an important and diverse group of ground-dwelling insects with over 2,500 species known from North America alone, and more than 40,000 known species worldwide. They occur in many habitats including forests, riparian areas, grasslands, orchards, and crop fields. As immatures, carabid beetle larvae usually live in litter or the upper soil layers and have ten well-defined body segments tapering towards their posterior end. Adult beetles are primarily nocturnal, with a body size ranging from a few millimeters up to 3–4 cm. Adult beetles have relatively long legs and are black or dark reddish, although several species are colored.

Adult and larva beetles feed on insects, snails, slugs, and weed seeds. Because of their voracious feeding behavior and their abundance in agricultural settings, carabid beetles are considered important biological control agents with the potential of restricting the abundance of many pest species. Among the different pests carabid beetles are known to consume are: black cutworms, *Agrotis ipsilon* Rottemburg; gypsy moth, *Lymantria dispar* (Linné); cabbage maggot, *Delia radicum* (Linné); armyworm, *Pseudaletia unipuncta* (Haworth); European corn borer, *Ostrinia nubilalis* (Hübner); western corn rootworms, *Diabrotica virgifera virgifera* LeConte; and many aphid species. Several species of ground beetles are omnivorous, consuming not only insects, but also seeds of common agricultural weeds such as giant foxtail (*Setaria faberi* Herm.), velvetleaf (*Abutilon theophrasti* Medicus), redroot pigweed (*Amaranthus retroflexsus* L.), and common lambsquarters (*Chenopodium album* L.).

Due to the potential of ground beetles as biological control agents, their biology and ecology have been widely studied. However, ground beetles are not commercially available for augmentation and several studies have demonstrated that common agricultural practices such as tillage, pesticide applications, and harvest reduce ground beetle abundance and alter carabid beetle community characteristics. As a result, pest control by predatory ground beetles in conventionally managed annual crop fields is usually diminished. Moreover, the current tendency of increasing agricultural landscape simplification, where farmers manage large monocultures with high mechanical and chemical inputs, increases the impact of management practices on carabid beetle survivorship.

In row crop systems, to fully exploit the potential of ground beetles as biological control agents, it is necessary to generate an environment that allows their survivorship and reproduction. Habitat management represents a viable approach to reduce the negative impact that several agricultural management practices have ground beetles. Habitat management is defined as a series of practices aimed to alter habitats to improve availability of resources required by natural enemies for optimal performance. Several habitat management practices have been shown to encourage carabid populations, including no-tillage or conservation tillage practices, cover crops, and maintenance of refuge habitats in close spatial association with crop fields. The goal of these practices is to provide ground beetles with the ecological infrastructure necessary for their survivorship and reproduction.

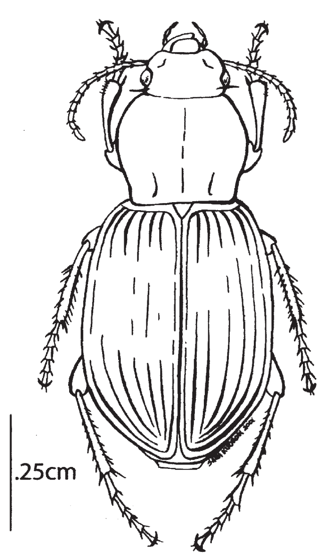
Several studies have evaluated the impact of tillage on ground beetle abundance and diversity. In general, lower number of individuals are found in conventional tillage than in no-tillage or reduced tillage systems. This could be due to either a direct mortality inflicted by soil disturbance, or the indirect effect caused by removal of resources and food. The impact that tillage has on carabid beetles depends on the species, but it has been found that species diversity and evenness tends to increase in reduced tillage fields when compared to conventionally tilled ones.

Cover crops have also been shown to be a suitable habitat management practice to enhance ground beetle abundance. Cover crops are crops not grown for harvest, but rather for other benefits they provide, including protection from soil erosion, improving soil structure, supplying soil nutrients, suppression of weed germination and weed growth, and contribution to management of insect pests and plant pathogens. From an insect's point of view, cover crops can increase humidity, reduce temperature, and serve as a host for alternate prey species. In total, cover crops often provide a favorable habitat for generalist predators such as carabid beetles. However, it is important to note that the increase in surface plant material occurring in cover crop systems may be responsible for a decrease in carabid beetle mobility.

Due to the ephemeral characteristics of annual crop systems, it is critical to assure the overwinter survivorship of ground beetles. Providing refuge habitats in close association with crop fields has been shown to be a promising approach to conserving ground beetles. Examples of refuge habitats include non-crop sites such as woodlands, hedgerows, riparian buffers, cross wind trap strips, perennial pastures, and grassy strips. Crop field edges not sprayed with pesticides can also act as refuge habitats for carabid beetles. Refuge habitats benefit carabid beetles through several mechanisms. First, refuge habitats provide suitable overwintering sites for carabid larvae and adults. Several studies have shown that the density and diversity of overwintering carabids is higher in refuge strips than in adjacent crop fields. Possible mechanisms for these differences include a differential mortality and/or a preferential selection of habitat. Second, refuge habitats act as a stable resource of food such as aphids and springtails.

This is particularly important early in the growing season when prey have not colonized crop fields and has been observed to correlate with an increase in the weight and reproductive output of female carabid beetles. Third, refuge strips provide favorable microclimates during hostile weather conditions such as high temperature and low humidity. Finally, refuge habitats protect carabid beetles from disruptive management practices. If pesticide applications, cultivation, or harvest damage carabid populations, refuge habitats can serve as sources of natural enemies that colonize agricultural fields, inflict mortality on pests, and return to refuges.

A common denominator among all habitat management practices aimed at conserving carabid beetles in row-crops is an increase in the planned biodiversity (organisms purposely included in the agroecosystem by the farmer) and the associated biodiversity (all soil flora and fauna, herbivores, carnivores, etc. that colonize the crop fields (Fig. 86) but are not intentionally established by farmers). However, it is not increasing diversity per se the final objective of habitat management. A key component is to identify the elements of diversity that enhance ecological services necessary to secure the establishment, survivorship, and reproduction of this diverse group of beneficial organisms. This knowledge should be combined with an understanding of the spatial scale over which habitat management operates (within-field, farm-level, agricultural landscape), any potential negative aspect associated with the addition of new plants into the systems (i.e., increasing the risk of pest outbreak or weed invasion), and the associated economic costs and benefits.



Conservation of Ground Beetles in Annual Crops, Figure 86 ***Anisodactylus sanctaecrusis*** **(F.), a ground beetle commonly found in agricultural fields (Drawing by S. Kudrom).**

References

Desnder K, Dufrene M, Loureau M, Luff ML, Maelfait JP (1994) Carabid beetles: ecology and evolution. Kluwer Academic Publishers, Dordrecht, The Netherlands

Landis DA, Wratten SD, Gurr GM (2000) Habitat management to conserve natural enemies of arthropod pest in agriculture. Ann Rev Entomol 45:175–201

Lee JC, Menalled F, Landis D (2001) Refuge habitats modify impact of insecticide disturbance on carabid beetle communities. J Appl Ecol 28:472–483

Lovei GL, Sunderland KD (1996) The ecology and behavior of ground beetles. Ann Rev Entomol 41:231–256

Stork NE (1990) The role of ground beetles in ecological and environmental studies. Intercept, Andover, UK

Conservation of Insects

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Insect conservation is a relatively new concept. Traditionally, invertebrates are the lowest priority for conservation organizations due to their relative inconspicuousness to the public eye and the lack of showy charismatic flagship species among the large invertebrate numbers. Even our most basic scientific knowledge of insects is relatively poor. Some taxonomists estimate that there are more than four million insect species alone, but other entomologists believe the number could be as high as 50 million. Of these insect species, only 5–10% have scientific names. Even for described and well known species, the information on their biology and population dynamics is scarce, which makes it harder to determine their conservation status. There is also a misconception among the general public that a good bug is a dead one, which makes it more difficult to obtain public money for insect conservation projects.

At the same time, the roles that the insects play in our lives can hardly be overestimated. They are responsible for reproduction of most plants, and are essential food sources for many vertebrates from fish to birds and even mammals. Though most pest species indeed belong to the Insecta, there also are many insect species that keep pests under control through predation and parasitism. Though we consider conservation of the pollinators and of the natural enemies to be as essential as conservation of endangered insect species, here we discuss only conservation of endangered and threatened species, and focus on the diurnal Lepidoptera as an example of the problems and opportunities inherent in the overall field of insect conservation.

Cites

The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) was signed in 1973 and entered into force in 1975. The treaty now has 152 Parties.

CITES species are listed in Appendices according to their conservation status. In addition, listed species must meet the test that trade is at least in part contributing to their decline. CITES regulates international trade in species of animals and plants according to their conservation status.

Appendix I species are species in danger of extinction, for which all commercial trade is prohibited.

Appendix II species are not necessarily threatened with extinction, but may become so unless trade is strictly regulated. These include species that are in international trade and are vulnerable to overexploitation. Regulated trade is allowed provided that the exporting country issue a permit that includes a finding that the trade will not be detrimental to the survival of the species or its role in the ecosystem. This regulation includes a requirement for documentation from the country of export, monitoring of imports and, in some cases, export quotas.

Appendix III. A country may unilaterally (without a vote) list in Appendix III any species which is subject to regulation within its jurisdiction for which the cooperation of other Parties is needed. Importing countries must check for export permits for the species issued by the country of origin for Appendix III species.

The Importance of Subspecies

The U.S. Endangered Species Act is written to allow the preservation of any recognized unique taxonomic entity, subspecies included. Indeed, preserving a subspecies is as important as conservation of a species as a whole. Not only do subspecies frequently turn out to be separate species with thorough study, but most insect populations thrive on the gene flow that occurs between populations in the intergrade zones and through migration. Unique morphological characteristics of subspecies reflect the genetic diversity that allows species to survive. These morphological features are often linked with various ecological and physiological characteristics. Many local populations go extinct at one time or another, and such extinction events are becoming more and more frequent with shrinking of the average population size. Occasional repopulating from an extant neighboring population is therefore required for long-term survival of most populations. It is not enough to conserve a species in a single locality, but in as many localities as possible, connected by corridors of habitat. A distribution range containing as wide variability as possible should ideally be designated in a successful conservation effort. Subspecies, under current legislation, play an instrumental role in achieving these goals.

Butterflies as an Index Group in Conservation

Despite the large numbers of insects that have been placed on various lists of threatened or endangered species, and even larger numbers that have already become extinct or are on the verge of extinction, by far the most interest and funding have been attracted by the butterflies. The latter group accounts for only 20,000 species, or half a percent of the total insect diversity, but there are probably more books written on that group than on the rest of the insects combined. This popularity, the result of butterflies' esthetic appeal, is also responsible for the amount of knowledge on them that has been accumulated since the time of Linnaeus, mostly by amateur naturalists. The last two decades have seen publication of books on the butterfly fauna of nearly every country of the world, and there also are numerous books that cover worldwide faunas of particular groups or different aspects of butterfly biology. These works, combined with the efforts of hundreds of regional butterfly-enthusiast organizations, provide a significant framework for conservation. We should note that this knowledge is far from complete, as life histories and survival requirements are still not understood for the majority of species.

As with many conservation movements, the conservation of butterflies takes many, sometimes contradictory forms. For instance, some ill-informed people, driven by good intentions focus their efforts almost entirely on prohibition of collecting. Collecting, however, has been repeatedly demonstrated to play no important role in endangering butterfly populations. Indeed, quite the opposite is true: collecting is instrumental in acquiring scientific information, as well as in attracting new people into the movement for butterfly conservation. By far outweighing all other factors that threaten butterflies (or any other species) are those of habitat degradation and pollution, in that order.

The highest diversity of insects on the planet is found in the Amazonian rainforest, the equatorial area which has had no recent major cataclysms such as glaciation leading to mass extinction. Lesser, but nevertheless impressive, diversity of insects is found in the tropical forests of West Africa, Asia, and New Guinea. Despite the rapid disappearance of these forests, these are not the habitats that contain most of the species placed on the "endangered" lists. Instead, that dubious distinction falls to the temperate zones. Here, conservation efforts are much more extensive in the developed countries, such as United States, Japan, and the countries of Western Europe, where ecological awareness and general education level are higher. This creates a misleading impression, as most of the potentially threatened or truly endangered species actually occur in the developing tropical countries.

Another peculiar phenomenon is that many species are given preference in being declared endangered because of the demand they attract from collectors. Normally, these are the larger and more attractive species. Even when these species are in decline, this decline is caused by loss of habitat, and has little to do with collecting. Habitat, at least in the developing countries, often is not provided protection from such legislation. The focus on collecting occurs mostly because people who create insect conservation legislation are general wildlife biologists, whose primary focus as well as education and training are in the area of large vertebrate animals.

Wildlife biologists tend to extrapolate their experiences with large vertebrates to insect conservation. Thus, they don' t take into account that even the smallest insect population consists of thousands of individuals, and that most insects reproduce with large numbers of eggs from a single female, and have very high biotic potentials.

The population numbers can naturally vary tremendously from year to year, which is also rarely taken into account by those monitoring them. The threat from collectors seems obvious to vertebrate wildlife biologists because it is parallel to their experience with hunters and game animals. However, it is sometimes enough to just mow a meadow or burn the grass in it to destroy the whole insect population consisting of thousands of individuals: a task that could never be even deliberately accomplished by a dozen collectors. Nevertheless, over- collecting in rare populations that are already greatly diminished in size by habitat degradation could be a problem, and no commercial collecting should be allowed in such localities.

Even in the tropics, some habitats are more threatened and contain more endangered species than others. Mountain chains and the islands create the conditions of isolation that are often responsible for new species formation. Mountains also support a wide variety of unique habitats associated with elevation change, with correspondingly unique or specialized and highly localized species of plants and animals inhabiting them. In the tropics, these habitats are often claimed for settlements and agriculture because they have much more favorable climatic and soil conditions than the lowlands. Reforestation in such areas, when it occurs, often is conducted with exotic fast-growing tree species, such as temperate pines and Australian eucalyptus, which only contributes to exotic replacement and extinction of the native insect species. The fauna of tropical islands, such as those of Oceania, the Antilles or Madagascar, are composed of mostly endemic species. Some of the most threatened insect species are found on these islands, where overpopulation of humans often leads to deforestation and erosion. Even in the areas where population densities are low, the demand for cheap timber that can be easily hauled away by sea, as well as weakness of environmental laws and governmental corruption, lead to deforestation and extinction.

Case Studies of Four Endangered Swallowtail Butterflies (Papilionidae) from Different World Regions

Ornithoptera alexandrae, New Guinea, and other birdwing butterflies

The first specimen of the Queen Alexandra's birdwing, *Ornithoptera alexandrae* (Fig. 87), the largest butterfly in the world, was discovered in New Guinea at the turn of the century. Recognizing it was something new, but always flying high and out of reach, the collector, A. S. Meek, had to fire a shotgun blast at the insect to bring it down in 1906.

Today, the butterfly persists only in small patches of primary forest left around Popondetta. Population surveys of this species are difficult, as adults fly in the canopy. It is extremely local and its distribution even before recent habitat destruction was apparently restricted, perhaps by host specificity of the species, which feeds on three related *Aristolochiaceae* vine species: *Aristolochia dielsiana*, *Paraaristolochia alexandriana* and *P. meridionaliana*.

Ornithoptera alexandrae has had the legal status of Endangered since 1967 in Papua New Guinea, and is listed as a CITES Appendix I species. As a result, ironically, it does not enjoy the protection of habitat that accrues to other *Ornithoptera* species from local people who could be ranching it for sale to collectors, if it were not so listed. (Papua New Guinea and Australia are now jointly planning a ranching project, which may require re-listing it to Appendix II status.) In addition, restoration of the rainforest habitat that was lost to oil-palm plantations and volcanic devastation (in 1951) is underway, and eventually *O. alexandrae* might see removal of present restrictions on its commercial propagation and marketing.

Several other species of that colorful butterfly genus, as well as many other insects of New Guinea, are already raised for sale. This activity is under the centralized control of IFTA (Insect Farming

Convervation of Insects, Figure 87 **Adult of Queen Victoria's birdwing, *Ornithoptera victoriae* (photo by Andrei Sourakov).**

and Trading Agency) at the town of Bulolo. The individual ranching incomes from this activity, though low by the standards of the western countries, often exceed the national income average by ten-fold. This fact provides strong incentive for planting host plants and preserving habitat for the species being ranched.

Ranching requires very little effort and no initial investment. Wild female butterflies from the surrounding forest lay eggs on their respective host plants. Most birdwing species, for example, feed on the widespread pipe vine, *Aristolochia tagala*, which readily grows in small farm plots. Caterpillars are allowed to feed and pupate freely, while pupae are collected and brought inside a hut. No cages are used to hold the emerged butterflies or to keep ants and parasitic wasps away because ranchers usually do not have money to buy these much-needed supplies. Instead, they wait for a pupa to turn dark, and then watch it closely until the butterfly emerges. Then it is killed and papered for sale to IFTA, and further commercial distribution abroad.

Following the example of Papua New Guinea, other countries in the region have established similar programs with different degrees of success. For example, two birdwing species are found exclusively on the Solomon Islands. Smaller than *O. alexandrae*, they are nevertheless among the world's largest and most beautiful butterflies. Males are valued by collectors for their dazzling coloration, females for their immense size. Queen Victoria's birdwing, *Ornithoptera victoriae*, displays different shades of brilliant green, while the wings of d' Urville's birdwing, *Ornithoptera priamus urvillianus* (Fig. 88), are sky-blue. The females are colored inconspicuously brown and are slow fliers that mostly stay inside the forest.

In the Solomons, butterfly specimens are sold to a middleman in Honiara, who accumulates a sufficient number of butterflies to fill an order from a Western dealer. Ranchers receive a fraction of what a butterfly will be actually sold for in the developed world. With more coordination brought into the program, perhaps by the Solomon Islands Development Trust organization, some middlemen could be bypassed, and the ranching would become more economically important to the farmers. Now that local people have been introduced to ranching, which is a much more efficient way of acquiring

Conservation of Insects, Figure 88 **Adult of d' Urville's birdwing, *Ornithoptera priamus urvillianus* (photo by Andrei Sourakov).**

high-quality specimens than collecting, the trade (and thus conservation effort) is being hampered by the fact that these birdwings are presently prevented from normal trade in the largest potential market in the U.S. by a desire of some CITES officials there to punish the Solomon Islands government "for not doing enough for conservation." The environmental threat to birdwing survival comes from the destruction of their forest habitat through logging and slash-and-burn agriculture, activities which disregard the presence of endangered butterflies and for which there is no punishment because the local people own the land and can develop it as they wish. Without the economic impetus to preserve these forests for butterfly ranching and other sustainable activities, there is no local incentive to resist the lucrative logging concessions requested by foreign timber companies. Thus, outside political pressure in the form of a unilateral U.S. trade embargo, which is not endorsed by other CITES nations, is having an anti-conservation outcome and inhibiting insect conservation measures undertaken in the Solomon Islands.

Homerus swallowtail, *Papilio homerus*, Jamaica

This is the largest swallowtail in the Americas. Once it inhabited seven of the thirteen parishes of the island of Jamaica in the West Indies, but now it is found only in St. Thomas and Portland parishes at the junction of the Blue Mountains and the John Crow Range. In the late 1930s, *P. homerus* butterflies (Fig. 89) were relatively common. By 1945, the species was rapidly disappearing from its larger stronghold in the eastern Blue Mountains. It is now one of four endangered swallowtail species listed in the IUCN Red Data Book "Threatened Swallowtail Butterflies of the World."

The rugged Blue Mountains run approximately one-third the length of the island. The climate is uneven throughout the island. For instance, the northern parish of Portland receives heavy rainfall of 381 cm, while the south is much drier (89 cm). *Papilio homerus* larvae require humidity to be close to 100% to survive. Thus, the species only inhabits wet limestone forest at the western end of Jamaica, and lower montane rain forest at

Conservation of Insects, Figure 89 **Adult of Homerus swallowtail, *Papilio homerus* (photo by Thomas C. Emmel).**

the eastern end. The first area is characterized by trees such as Jamaican cedar, prickly yellow and figs. Secondary succession areas frequently have bracken ferns and citrus trees. The second area supports mountain guava, Santa Maria, cobywood, roadwood and tree ferns. *Papilio homerus* normally occur below an elevation of 1,000 m. *Hernandia catalpifolia*, locally known as water mahoe or water wood, and *H. jamaicensis* (pumpkin wood, suck axe) are the larval host plants, in the family Hernandiaceae. *Ocotea* nr. *leucoxylon* (loblolly sweetwood in the Lauraceae) may also be used by larvae.

Forest reserve areas were established in these mountains, including prohibition of cutting trees. However, FIDCO (Forest Industries Development Company), formed by the Jamaican government in 1979, began cutting 2,000 hectares of rainforest per year to plant Caribbean Pine to help the charcoal production industry. With the rapid disappearance of the wet streamside rain forests, this activity presented the major threat to P. homerus survival. In 1984 the film "*Papilio homerus*, the vanishing swallowtail," was produced. This film and other similar publicity efforts over the potential national symbol represented by this rare flagship species, have created a positive movement of preservation, culminating in the establishment of Blue and John Crow Mountains National Park in 1991, with *Papilio homerus* as the official symbol of the Park Service. Subsequent educational efforts have continued annually in Jamaica's elementary schools, with written materials on the butterfly's life history and the manifold importance of the montane rain forest habitat to watershed protection, wildlife, recreation, and tourism-based economic benefits. After Hurricane Gilbert destroyed most of the planted Caribbean Pines at the end of the 1980s, the establishment of the montane rain forest park has allowed natural succession to begin reclaiming these areas. Fortuitously, Hernandia species are among the foremost recolonizing rain forest trees, rapidly increasing the potential habitat for the Homerus Swallowtail.

Parnassius apollo, Europe

This is the first butterfly species that was placed on the CITES list for prevention of trade. While numerous cases of local extinction are known for the species throughout Europe, none of them has been linked to collecting. Acid rains were blamed for its demise in the 1970s in Germany and the Alps, while around Moscow the mass spraying for gypsy moth might be a key factor for its disappearance. Everywhere, habitat loss is also a significant factor. In our view, one of the weaknesses of the current conservation legislation concerning *P. apollo* (Fig. 90) (as well as of all other endangered butterfly species) is that it targets the species rather than the habitat. Additionally, this legislation recognizes all subspecies of *P. apollo* as endangered, despite the fact that many of them, particularly in Central Asia mountain ranges, are very common. Some captive breeding and reintroduction programs for the endangered European subspecies are being developed locally.

Schaus' Swallowtail, *Heraclides aristodemus ponceanus* Schaus, Florida

The Schaus' swallowtail is the resident *H. aristodemus* subspecies that is found in South Florida and the Florida Keys. An assortment of other distinct subspecies is found on some of the Bahamian and Caribbean islands. Only a few of the Keys have suitable hardwood hammock habitat today, and even fewer support the Schaus butterflies. This is one of the cases where pollution by mosquito control practices has evidently contributed significantly to the demise of the species. Were it not for this impact since 1972, the population (though impaired by the loss of habitat) would be substantially above present precarious levels.

The adult butterflies (Fig. 91) emerge from their pupae after the first rains in May, following a long dry season. The major population is that on Elliott Key, an isolated, seven-mile-long and quarter-mile-wide island, where there are no recent human developments or mosquito control practices. The annual number of adults flying there has usually hovered at several hundred to as many as a thousand, though it varies from summer to summer.

Schaus' swallowtail was once widespread throughout south Florida, but its population size and distribution have been reduced by the growth of Miami and urbanization of the Keys, and, later, by the spraying of Dibrom and Baytex pesticides. Prior to the development of the area, butterflies migrated freely around the northern Keys and mainland. Capture/recapture data shows individuals fly as much as 3.5 miles within a few hours. This movement supported the genetic diversity of each of the smaller populations, and ensured population of new sites and natural repopulation of those suffering a temporary extinction.

Today, Elliott Key has the only large population of the butterfly, and the area is currently protected as a part of Biscayne National Park. When Schaus' swallowtail was recognized as an endangered species by the U. S. Fish and Wildlife Service in 1984, a research group from the University of Florida began looking for ways to secure its future. Although now protected, the Schaus' swallowtail, even on Elliott Key, remains at risk. The small size of this sanctuary, and the absence of secure populations outside it, make the Elliott population vulnerable. Should it be wiped out by an ecological disaster, there would be no natural source of Schaus' swallowtails to repopulate the islands.

Schaus' swallowtail shares Elliott Key with two similar-looking swallowtails: the Bahama swallowtail, *Heraclides andraemon bonhotei*, apparently a very low-level resident population or an occasional visitor, and the Giant swallowtail, *H. cresphontes*, which forms a persistent but smaller resident population. The Giant swallowtail flies synchronously with Schaus', but can easily be identified by its larger size and more powerful flight. Schaus' swallowtails usually have slow fluttering flight to maneuver through the dense jungle of tropical hardwood hammock while avoiding lethal spider webs. It is

Conservation of Insects, Figure 90 **Adult of *Parnassius apollo* (photo by Alexander Dantchenko).**

not uncommon to see a Schaus' even "backing up," a rarity among butterflies. While giant swallowtail larvae would feed on any citrus (Rutaceae) tree, Schaus' larvae can complete development only on wild lime (*Zanthoxylem fagara*) and torchwood (*Amyris elimifera*). Females especially prize the latter for Therefore, Schaus' require these host plants and the thick hardwood hammock, which provides a relatively cool, shady microclimate in the hot Keys.

When Hurricane Andrew hit south Florida in August 1992, the hammock on Elliott Key was devastated: no canopy was left to protect the delicate undergrowth of torchwood and wild lime

Conservation of Insects, Figure 91 **Adult of Schaus' swallowtail, *Heraclides aristodemus ponceanus* (photo by Andrei Sourakov).**

from the desiccating rays of the sun. Elliott Key's wild Schaus' population survived Hurricane Andrew in very low numbers (only 17 in 1993), and was later buttressed by releases of captively reared individuals. Fortuitously, 100 wild Schaus' eggs had been removed to establish a captive colony at the University of Florida just 2 months before the hurricane. This colony was expanded to produce several thousands of Schaus' swallowtails that were then released back in the wild at a series of sites on the south Florida mainland and the Florida Keys in 1995, 1996, and 1997. Capture-recapture data showed (Fig. 91) recovery to about 1,200 adults flying in 1996 and 1997. However, the possible genetic bottleneck that the population went through during the immediate post-hurricane years could cause serious problems for the population in the future. Additionally, a 5-year drought (1998–2002) in South Florida reduced the Schaus populations to, at most, 200 adults by mid 2002.

In captivity a female can live up to 32 days and lay up to 430 eggs; in nature, she lays at most 80 eggs before dying at an average age of 3.6 days. Most of the eggs in nature are eaten by predators such as ants, or parasitized by wasps. Thus, captive propagation can work well with this species. The females can easily be hand-paired, and lay eggs on either torchwood or wild lime. The young larvae are raised in vials with fresh torchwood leaves, and later can be placed on potted trees. At maturity they are transferred back into individual plastic cups, in which the larvae pupate. Then, either pupae or emergent adults are released into the wild at suitable sites.

Future studies will tell whether the 13 wild populations that were established after Hurricane Andrew through this captive propagation program are viable. In addition to monitoring the success of the introductions, there is a need for continuing the search for remnants of suitable, reintroduction-worthy habitat. The program's survival greatly depends on funding, which has so far been provided by the U.S. Fish and Wildlife Service and private donations.

► Endangered Species

References

Collins M, Morris MG (1985) Threatened swallowtail butterflies of the world. The IUCN red data book. IUCN, Cambridge, UK, 401 pp
New TR (ed) (1993) Conservation biology of Lycaenidae (Butterflies). IUCN, Gland, Switzerland, 173 pp
New TR (1997) Butterfly conservation. Oxford University Press, Oxford, UK, 248 pp
Samways MJ (1994) Insect conservation biology. Chapman & Hall, London, UK, 358 pp

Conspecific

Organisms belonging to the same species.

Construction Behavior of Insects

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One of the most complex and exciting areas of insect biology is that of nest architecture and construction behavior. There are four major groups of insects that are well-recognized builders, while there are individual species in other groups that also build structures. The four major groups of builders are the Isoptera (termites), the Hymenoptera (ants, bees and wasps), the Lepidoptera (butterflies and moths, though only moths build), and the Trichoptera (caddisflies). The moths and caddisflies build individual cases, cocoons, or group retreats, but the termites, ants, social bees and social wasps build the most elaborate structures. Some nests are enormous relative to the size of the builders (several miles high if the height is made proportional to human dimensions), able to maintain nearly constant temperature and humidity, and able to withstand years of harsh sun and driving tropical rains. Small insect groups that build, or with only a few building species, include the Diptera (flies), Embioptera (webspinners), Orthoptera (grasshoppers, crickets), Hemiptera (cicadas, hoppers), Neuroptera (lacewings, antlions, mantispids), and Coleoptera (beetles).

Types of Structure and Nest Architecture

Of the many different types of structures built by insects, some of the simplest structures are the bubble nests of the froghoppers (Hemiptera). Bubble nests function in anti-predator defense and water conservation and are produced by frothing up secretions of the Malpighian tubules into a tight bubble mound around the builder.

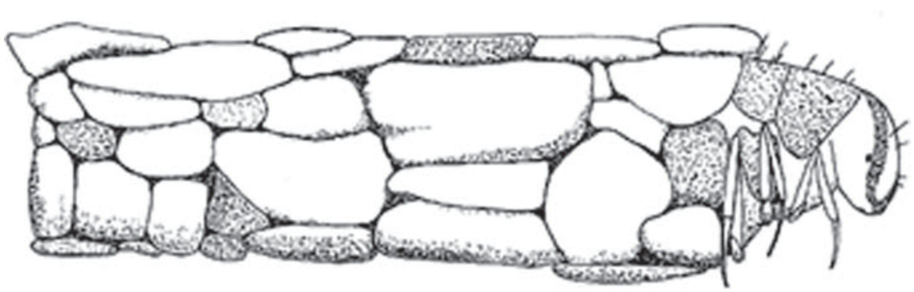
Another very simple form is the cocoon built by a moth caterpillar preparing for pupation. The larva finds a spot for this transitional stage to take place and begins the process of building the cocoon. The larva has large salivary or labial glands that produce a remarkable material called silk. This complex protein is drawn from the glands forming a durable and water resistant thread. The larva touches the substrate and attaches the end of the silk to one side and then draws out a length of silk in an arch and attaches the silk to the substrate on the other side of its body. Repeatedly attaching and looping over itself, the larva creates a covering that will protect and attach the denser cocoon pouch on the inside. Once the outer layer is in place, the larva will spin silk around and around itself to create the protective cocoon. In a cocoon of the silkworm moth, the length of the single thread is 500–1,300 m long. Silk material is made from the threads that are unwound from these cocoons. The cocoons are soaked in hot water and the loose outer thread is caught on a turning spool. The cocoon unwinds as one very long silk thread. Multiple strands are collected at the same time and combined to create a remarkably strong thread that can then be dyed and woven into a beautiful cloth. The larvae of other moth groups, such as the bagworms and the case making clothes moths, build individual silk cases with fragments of their food material or vegetation incorporated in the walls. The case is dragged around, serving to protect the larva as it feeds, and is spun closed during pupation.

Other Lepidoptera species, including some tent caterpillars, lay their eggs in clusters. When the larvae hatch, they work together to spin a common retreat. The silk in the walls of the retreat is so tightly layered that it takes on an almost leather-like appearance and texture. Some individuals are more active foragers and lay down silken trails to foraging locations, which the others follow. During the day, they return to the safety of the multi-layered retreat that protects them from predators and dampens temperature and humidity fluctuations.

The Embioptera or webspinners are members of a small order of insects, but unique in that they use silk from tarsal glands in their front legs to spin silken passageways. Groups of individuals live together in what becomes a network of galleries.

The caddisfly larva is the immature form of the Trichoptera. This insect group is closely related to the butterflies and moths, but it has little hairs instead of scales on its wings. Although the adult is a terrestrial insect, its immature larva is aquatic, living in streams among the rocks and vegetation at the bottom. As in the Lepidoptera, this group builds using silk produced by the salivary or labial glands. The caddisfly larvae build a variety of structures, depending on the species. Some build a silken web, which they use in straining food from the water flowing around them. Others build retreats by attaching small pebbles (Fig. 92) or plant material to silk in a case surrounding their body. As they grow, they add more building material on the front lip of the case, always keeping it just large enough to draw back into for safety, but small enough to drag around. The type of material and the form that the case takes is species-specific, so the characteristics of the case can help in identifying the animal that made it. Studies have shown that the larvae are very careful in their selection of building material, turning each item around repeatedly before rejecting or accepting it. If accepted, the item is then carefully oriented and glued with silk into position. *Macronema transversum* is a species of caddisfly that builds a more elaborate, curved case. This U-shaped case, which has an incurrent funnel facing upstream and a smaller excurrent funnel immediately downstream, not only provides a safe retreat, but also is used to support a web spun across the interior chamber and to filter food particles from the water.

There are some insects that use the leaves of plants to create safe feeding locations for their developing brood. The females of a group of leaf-rolling weevils (Coleoptera) first use the mandibles at the end of a long proboscis to chew into the leaf petiole just at the base of the leaf. The female then moves out on the leaf and begins to break open the epidermal layer with tarsal claws and mouthparts until the leaf begins to curl with loss of turgor pressure. The female then aligns herself with the edge of the leaf and using the legs on one side, pulls the leaf edge over to begin the tight curl. The leaf is rolled to completion and glued tight with anal secretion. During the construction of the curl, the female enters the curl and lays an egg through a slit she makes in the inner layer. Thus, multiple leaf layers protect the egg, and when it hatches, the larva has a secure feeding spot.



Construction Behavior of Insects, Figure 92 **Caddisfly case built of small pebbles and silk by the larva. They are found in streams and other bodies of flowing water.**

Many different types of animals, both vertebrate and invertebrate, build burrows, insects included. These burrows may be simple, consisting of a tube dug into the ground with a single chamber, or they may be quite complex in structure. Regardless of complexity, the burrows may serve a variety of functions including predator avoidance, brood rearing, feeding and vocalization enhancement.

Immature cicadas, members of the order Hemiptera, live in burrows. The length of the nymphal stage varies with the species, but may extend as long as 17 years. During that time, they live underground and feed on roots accessed from their burrows.

Some members of the order Orthoptera build burrows, but none more elaborate than that of the mole cricket, *Gryllotalpa vineae*. The male of this species builds a burrow with two adjacent, horn-shaped entrances. The double-barreled burrow curves downward where the two entrances join in a single, somewhat enlarged passage leading to the deeper blind retreat. The male calls from the enlarged passage while facing away from the entrance. He rubs his forewings producing a loud call, which is greatly amplified by the burrow design and can be heard by a person more than 400 m away. The call frequency with maximum energy is 3–4 kHz, while the call can reach over 100 dB at approximately a half meter above the burrow.

The antlions of the order Neuroptera build prey-capturing traps in sandy soil, which at times can be spotted along hiking trails. The larva has large mandibulate mouthparts and builds its cone-shaped pit by throwing sand up and out of the hole with its flat head and mandibles. It buries itself at the bottom of the pit and lies in wait for an unsuspecting ant or other small insect to slide down the side of the pit. By tossing sand up the edge of the pit, the antlion creates a mini-avalanche that causes the struggling prey to slide further down the side of the pit, whereupon it is bitten and sucked dry. There is a group of flies, the worm-lion, *Vermileo comstocki*, that also builds a similar trap to catch prey.

Those that build underground burrows to protect immature offspring are members of the Orthoptera, Coleoptera and Hymenoptera. Parental care may exist in the form of guarding the burrow, or provisioning the young. In the dung beetles, male and female pairs dig out a burrow and then pack the end of it with a ball of fresh dung (some collect the dung first, tap it into a ball and push it with the hind legs to a desirable location where they then cover it with dirt). An egg is laid on the ball of dung, or the ball may be subdivided a number of times and eggs laid on each of the balls. In some species, there is little parental care, while in others, the burrow is defended and the dung ball is kept from desiccating and molding. After hatching from the eggs, the young feed on the dung within the protective environment of the burrow.

Burrow construction is most elaborate among the ants, bees and wasps. In some wasps and bees, multiple chambers are built either singly or in clusters off the main tube, or off branching tubes. Each chamber or cell houses one developing larva that feeds on food provisioned within the sealed cell. Some species, like *Paralastor* sp., build a mud tube elaboration on the burrow entrance that helps prevent parasitoids and predators from entering during the construction and provisioning of cells. In the stingless bees, the nest entrance has wax added to form a chamber for guard bees and a landing platform for returning foragers. The large nest chamber houses wax cells where the brood is reared and the reserves of honey and pollen are stored. In these insects, the honey and pollen are fed to the young and they are progressively provisioned. Tubes leading deeper into the ground provide space for water drainage and garbage disposal.

One group of amazing underground builders is the leaf cutter ants, of the tribe Attini. The colonies of these extraordinary ants start with the founding queen who has been fertilized prior to sequestering herself in a newly formed blind burrow. She takes a small amount of fungus from her parental nest, plants it with a bit of her anal secretion, and carefully tends this small fungal garden. She lays a few eggs, which are destined to become the first workers for the colony. From this obscure beginning, the colony grows until it has a fully formed caste system with sterile workers and soldiers numbering in the millions. Separate chambers are built to grow fungal gardens and rear brood. These ants forage for leaves, which they bring back to the colony along cleared paths. They attach the leaves to the fungal garden, sometimes using small amounts of anal fluid. Mycelia of the fungus are planted on the leaves where they grow and soon cover the entire leaf. The ants tend the fungal gardens, which in turn produce spherical swellings that are eaten by the ants. An *Atta* leafcutter queen is estimated to live ten or more years. By the time her colony is mature, the nest will have more than several million workers, will have thousands of chambers and over a thousand entrances. Nests have been described that reach as deep as 6 m below the surface and extend over 100 m^2.

Although termite nests typically start out underground, they are built up with loads of building material until they have some structures above ground. Even the termites with the simplest nests have covered passages made by gluing pieces of mud together with fecal material. Their building process includes creating an arch and then extending that arch to form the tunnel, which protects them from predators, the sun and desiccation. The mounds of some termites get to be enormous, with chimneys that extend 9–10 m above the ground. The mound of *Macrotermes bellicosus* is one of the most complex yet described. The mound has a central living area with chambers for the king and queen, the brood and the fungal gardens (like the leaf cutter ants). Surrounding this central living area is an open chamber that allows air to circulate around the inner core. The outer protective wall is filled with passages that act like capillaries and maintain a constant temperature within the mound, while decreasing potential water loss from evaporation. Warm air, produced by the termites and gardens within the core, rises and passes out to the air passages within the outer protective wall. The air cools in these outer passageways and sinks downward. The cooler air is then drawn into the core area as the warm air rises. Millions of workers and chambers filled with fungal gardens generate a great deal of heat, yet the architecture of the mound keeps the temperature constant, within one degree Celsius.

The shape of the termite mounds may also contribute to colony thermoregulation. For example, the mounds of the compass termite stand about 4 m high and are long and thin. The broad surfaces face east and west, while the thin sides face north and south. Thus, during the cool mornings and evenings, there is a broad surface facing the sun to collect solar energy, while during the heat of the day, only a narrow surface is exposed to the sun, minimizing the heat uptake. The nests of other species have tall towers or buttresses, which also help to cool down the nest.

There is a group of solitary wasps that are referred to as mud daubers. This group includes the potter wasps, which build single or clusters of small mud cells, each one built to house one developing offspring and the provisioned, paralyzed insects or spiders to feed it. In some cases, the pots truly look like a clay pot molded into a jug-shape with an outwardly curving lip at the entrance. After the jug has been stuffed full with paralyzed caterpillars and an egg laid, the jug is sealed with a mud plug. Because these wasps are small, their nests are often overlooked, and most homeowners are more likely to notice the long mud tubes of the organ-pipe wasp (*Trypoxylon* spp.) (Fig. 93) or the large cell clusters of the common mud dauber (*Scelephrons* spp.). The organ pipe nest is built by the female, as is typical in the Hymenoptera. She adds mud to form arching mud strips in a long half-tube attached along the edges to the substrate. The tube is long enough to house approximately six cells. She lines the inside, smoothing out the interior walls and adding to the tube along the substrate junction. She then begins the process of provisioning the cells with spiders, laying an egg on one of the spiders and sealing off the individual cells with mud in sequence down the length of the tube. This is one group in which

Construction Behavior of Insects, Figure 93 **Organ-pipe mud dauber female constructing a mud tube. She will line the tube and then construct a series of cells down its length. Each cell will be provisioned with spiders, have an egg laid on one spider, and be sealed off with a mud wall. The fly in the photograph is a nest parasite of this wasp.**

Construction Behavior of Insects, Figure 94 ***Polistes*** **wasp female building a petiole and the side of the first cell. Building material is a combination of plant fibers and glandular secretion.**

the male contributes to the process of construction and brood provisioning by guarding the tube entrance from nest parasites that would otherwise sneak one or several of their own eggs into the cells. The male is then well placed to mate with the female when she is ready to lay her eggs.

Social wasps usually use plant material of some sort to build aerial or underground nests, but some species use mud. Each nest is typically made of one or more combs of hexagonal cells in rows, and the nest may have one or many enclosing envelopes. The architecture of the nests made by wasps is typically cryptic in that the nests are thin and built on the underside of tree trunks, or leaves, or in cavities, have the color of the surrounding substrate and are easily overlooked. The nests of some social wasps have no enclosing envelope and are attached to the substrate by a narrow petiole (Fig. 94).

The nests of a unique group of wasps, *Microstigmus*, are made using plant hairs from the underside of leaves. *Microstigmus comes* has been extensively studied; these small (4 mm long) tropical wasps begin by locating a nesting spot on the underside of a leaf of a species-specific host plant in the genus *Chryosophila*. A single female, or small group of cooperating females, then begins to chew up plant hairs in a wide circle. The hairs are pulled inward and a growing mound of hairs wrapped in silk forms around the edge of the circle. The wasp or wasps keep working until a ball of plant hairs and silk is located at the center of the area cleared of plant hairs. The base of the ball is worked into a long slender spiraling petiole, which suspends the ball that will form the actual nest. The wasps create an entrance near the base of the petiole and excavate a space called the vestibule. This will be an area for adult wasps to gather that is located above the cells. The remaining ball is worked into 1–14 cells, which are lined with silk and provisioned with Collembola. Although some *Microstigmus* are progressive provisioners, *M. comes* is a mass provisioner. Prior to laying an egg, these wasps stuff each cell with enough Collembola to supply a developing larva through pupation. The entire nest is only approximately 1 cm^3 in size.

Building Materials

The study of the building materials that insects use is still far from complete. There are two key ways the building material supports the weight of the structure, (i) compression, in which the nest bears the weight of the overlying structure like the bricks in the wall of a building, and (ii) tension, in which the weight of the structure is suspended and hangs. Insects use both methods.

Silk, often used in suspension construction, is a polypeptide that is highly diverse in structure as well as in gland of origin when compared across species. However, in general, it is a remarkable type of material in that it is extremely light weight yet has a tensile strength 2–3 times that of steel. Its strength comes from its structure. Silk, in most arthropods, is a fibroin– a protein with long, unbranching polypeptides. Although the sequence and make up of the polypeptide chains vary between species, glycine, alanine and serine make up about 80% of most types of silk. Crystalline or highly organized regions are interspersed with amorphous or unorganized regions. The organized areas have tightly packed polypeptide chains that are in tightly linked pleats through hydrogen cross bonding. The amorphous areas give silk its flexibility.

When building, bees use a second type of glandular secretion. Epidermal glands along the anterior edges of the abdominal sternites and/or tergites produce bees' wax in thin scales. Wax is a component of the insect integument. During the course of evolution, it is likely that clusters of cells that produced wax for the integument became specialized for greater wax production. The bees scrape the wax off the wax producing surfaces of the abdomen and work it into a ball of material for adding to the comb. In some species, the wax is mixed with plant resins to make a mixture called cerumen. Although wax and cerumen are both water resistant and pliable, cerumen is more pliable than wax and is used for building the softer parts of the nest such as the storage pots and brood cells. In some species, wax is also mixed with other glandular secretions or even mud. Resins may even be used without the addition of wax to produce supporting pillars and protective layers. Thus, construction material for bees varies dramatically in the wax content and in the nature of the additives, depending on the species, the component of the nest under construction and the type of support the structure provides.

Mud is often mixed with water and glandular secretions or fecal material and used in building. Insects building with mud usually use fine, moist soil. In some species such as the mud-daubing wasps, the builder vibrates as it collects and applies the mud. This has the effect of suspending the mud particles and liquefying the material, thus making it easier to manipulate and shape.

The use of plant fibers and fragments requires the addition of glandular secretion, as well. Analysis of the building material of *Polistes* paper wasps shows that the glandular secretion adds a mix of more than 20 amino acids to the plant fibers, including glycine, serine, alanine, valine and proline. The combined material is pliable, strong, lightweight and water resistant. Not only is the glandular secretion added to the building material, but it also is added to the outer surface of the nest, especially around the petiole and comb back. The wasps apply the pure oral secretion by licking the nest and this often results in a shiny, dark outer layer.

Function and Evolution of Insect Structures

Protection is the primary function of all insect-made structures. The structure separates the insect from the exterior world and thus, may help to lessen fluctuations in temperature and humidity and may act as a protective barrier between developing brood and predators, parasitoids and parasites. The bubble nests of the spittle bug, the caddisfly case, the galleries of the Embioptera and the towering nests of termites all share the functional role of protection. However, the structures often have additional functions. For instance, the bubble nests of the spittle bug help the nymph avoid desiccation; the caddisfly case assists in feeding in some species, and helps move water over the gills. As previously described, the termite mound controls thermoregulation and humidity regulation, and shelters the colony from rain. It provides housing for the members of the colony and their sources of food.

One feature of many social insect combs that has attracted attention is the hexagonal array of cells. This pattern of cells occurs in the combs of honey bees and many social wasps and appears to be the result of packing circular cells as closely as possible with a minimum use of building material. The builders actually build circular cells initially, which are possible to see along the edge of the comb, but as they add on additional cells, the adjoining walls straighten out. Once a cell is completely surrounded by other cells, it takes on the hexagonal shape. Occasionally cells are four- or five-sided, but this occurs when the cell arrangement is being adjusted for a confined space, or the rows of cells are out of alignment.

The brood developing in the hexagonal cells of the comb is a rich food source for a number of predators, both vertebrate and invertebrate. The enclosing envelope that the nests of many species have helps to hide the comb, and the small entrance hole is easy to defend against ants (Fig. 95), which are an important invertebrate predator of social insect colonies. In addition, the envelope layers of some wasp nests help to insulate the brood on the inside by creating a cushion of air around them.

Construction Behavior of Insects, Figure 95
Polybia occidentalis **nest showing the enclosing envelope and small entrance hole that aids in nest defense against ants (photo R. L. Jeanne, Univ. Wisconsin).**

Nests with no enclosing envelope have a narrow attachment to the substrate as an anti-predatory defense. The comb appears to hang from this narrow petiole in a precarious manner, but the petiole is strengthened with many layers of glandular secretion or silk. The narrow petiole provides protection from marauding ants because it is difficult for them to find, and the wasps can defend it both physically and with applied chemical barriers.

It is possible to compare nest structure among groups of related species and formulate hypotheses about the evolution of the different species-specific structures. For instance, in the social wasps, all of the variation in nest architecture was shown to be a derivation of the basic horizontal comb (cell openings facing down) hung from the substrate by a somewhat narrowed extension of the comb top or back. In one derived set of nests, the comb top has become narrowed to form a petiole of variable length and combs take a variety of angles and forms. Another derived group developed envelopes that are the extension of the outer walls of the outer row of cells of the comb. Petioles may or may not be present and the envelope serves to protect the brood from predators. A third group of distinctive nests have narrowed petiole attachments, multiple combs and a separate envelope that is not an extension of the cell walls. It can only be hypothesized that predation, environmental pressures and evolving modifications in the building material combined to produce the larger, complex nests of the highly eusocial wasps. It has been suggested that the evolution of building material capable of holding together a large nest was a critical precursor to the development of highly eusocial behavior and large colony size. The building behavior has had to change as well, because as nests become larger, more construction material is needed for the nest attachment and supporting walls. As a result, mature nests are often structurally quite different from incipient nests.

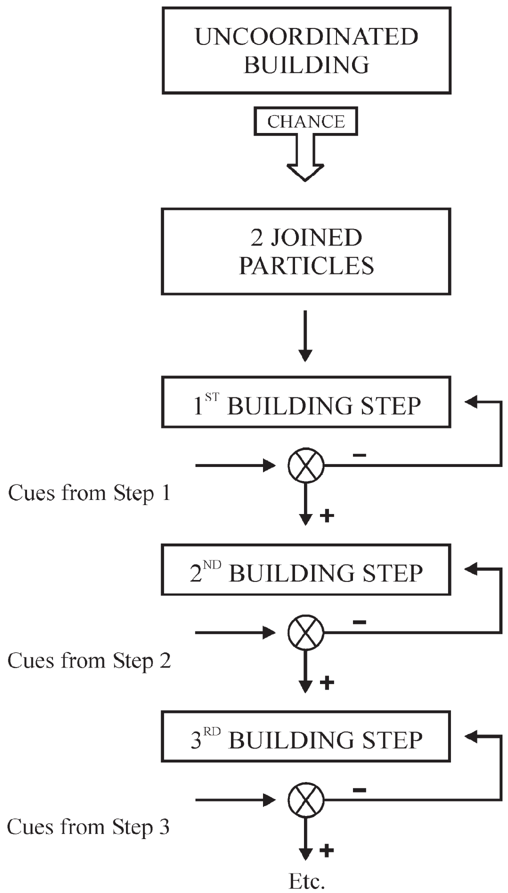
Regulation of Construction Behavior

As shown in previous sections, the nests of most insects are species-specific in design and the nests can thus be used to enhance phylogenetic studies. There are several hypotheses attempting to explain how species-specific construction information is transmitted between generations. Insects could inherit a blueprint of the finished nest design and then build toward creating a structure that matches the blueprint. There is no support for this hypothesis, and intuitively one can consider a small termite building in the pitch-black galleries of the developing nest and see the difficulty. There is little possibility that such an insect could comprehend the entire structure and coordinate its construction with that of many other builders. A second possibility is that there are certain individuals that inherit the design blueprint, and these lead builders then direct the construction of others based upon information they have gathered while moving systematically about the nest. There is again no evidence supporting this hypothesis, and it would be difficult for an individual to compare what others are building to a blueprint design of the finished product. In all insects studied thus far, the only direction observed is by the queen or king (if present), and they simply act as pacemakers.

A third hypothesis is that each individual inherits a construction program of sorts. This program consists of the steps of construction and a sensitivity to certain cues that regulate that construction process. When an insect builds, it has no sense of the finished product and is simply responding to the immediate cues, some of which come from previously completed construction. The process of building in response to previous construction is referred to as "stigmergy," a word coined by P. Grassé.

In solitary insects, the building program follows a linear series of steps with the completion of one step triggering the next. Cues associated with the completion of an act are tested with the addition of a load. A simple decision is made – is the previous step done? If no, add building material in the same way as before, if yes, go on to the next step of construction. By building through a specific set of construction steps and responding in a species-specific way to certain cues, the results are a species-specific nest. Because each individual (Fig. 96) is independently responding to the cues in its surroundings, no coordination among individuals is necessary.

With social insects, nests develop over a longer period of time. Throughout the nesting season, cells are progressively lengthened as the brood grows, entrances, chambers and cells are added, and petioles and envelopes are enlarged. Although the building may start out with a linear series of construction steps, this soon can no longer describe the process where building can take place in any of many different sites simultaneously. Builders must evaluate competing locations and



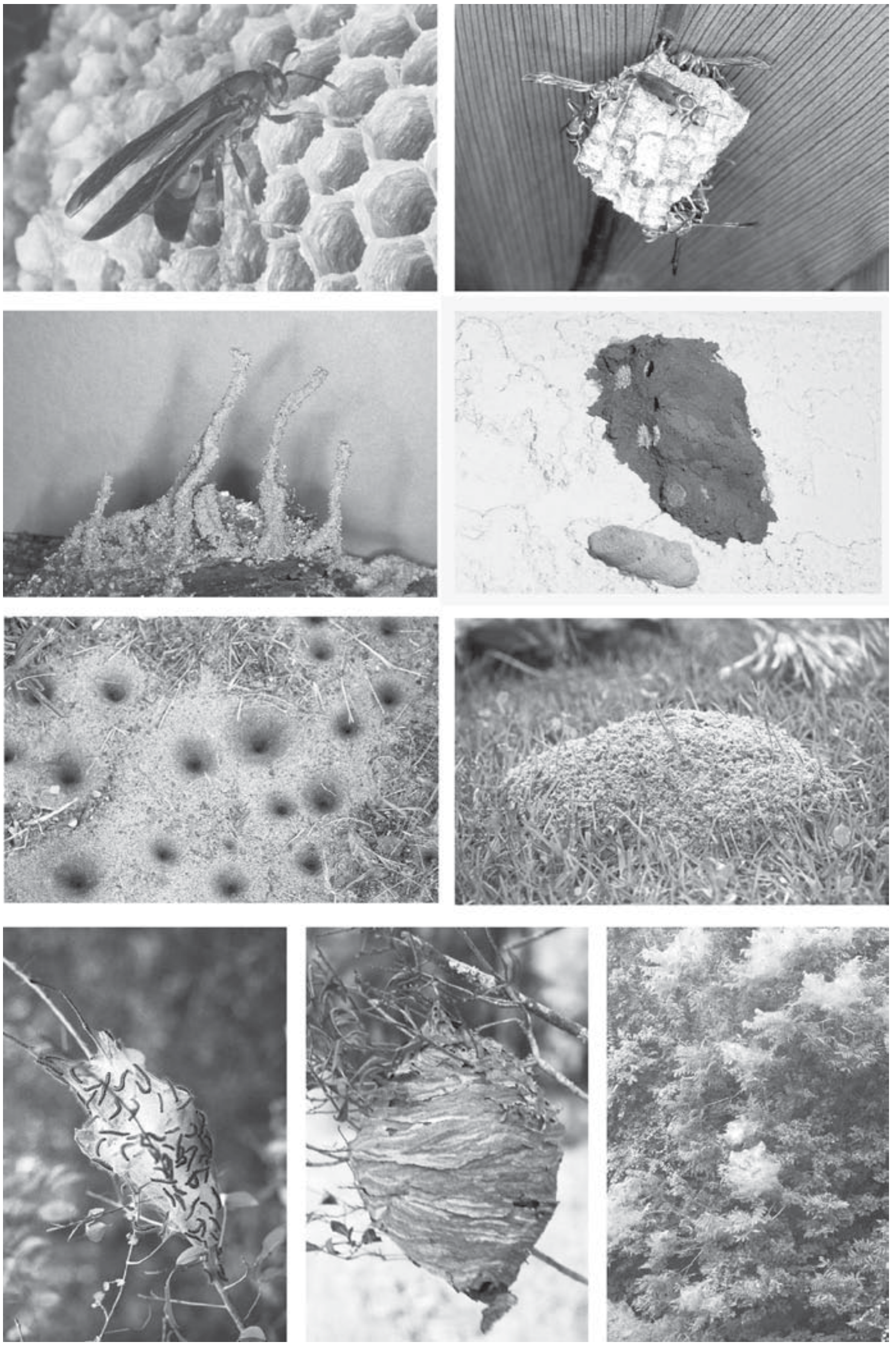
Construction Behavior of Insects, Figure 96
Diagrammatic representation of a building program.

choose one site for building. In large complex nests, like those built by termites, different areas of the nest have distinct structures added at certain times in the colony's reproductive cycle (e.g., platforms are built for dispersing reproductive allates.) This array of different structural components challenges stigmergy because the builders cannot just keep building based on previous construction and must switch to different building programs at appropriate times. Thus, building in highly eusocial insects must have a more complex regulatory mechanism or additional components to their building program. Nonetheless, stigmergy has been shown to be an important means for explaining the regulation of construction in a wide array of species, insect and non-insect, social and non-social. Studies of construction behavior in different organisms can help identify common construction mechanisms. Where species differ, these comparisons can lead to insights into the evolution and regulation of this behavior.

The building process actually involves two types of decisions: (i) where to build next, and (ii) how to shape the building material in that location. For instance in the paper wasp, *Polistes fuscatus*, which builds a comb suspended by a petiole, brood size and cell mouth angle impact the decision about which cell to lengthen next, while the antennae are used to measure the width of the cell as pulp is added. By constantly rotating the antennae in adjacent cells, wasps maintain a species-specific cell diameter. Cut one of the antennae and the cell wall measurements are altered. Most behavioral studies of construction have investigated the first type of decision only. The second type of decision and its relationship with the first have been studied in only a few insect species and many questions still remain to be investigated.

Individual building decisions are a part of the larger phenomenon of colony wide activity. The regulation of the pace of construction and how the tasks of foraging for water, collecting wood pulp for building and building itself are partitioned has been studied in the swarm founding wasps. *Polybia occidentalis* has been shown to have complex interactions among the builders, pulp foragers and water foragers, with smaller colonies having longer queuing delays that result in less efficient task partitioning. In another swarm founding species of wasp, *Metapolybia* spp., water or water saturation of the colony appears to be a critical regulator of task partitioning dynamics, with water availability affecting water foraging, pulp foraging, and consequently, the number of builders.

As it has become clear that among insects, individuals build by rather simple rules and act independently of one another, it has become apparent that colony wide behavior can be understood as a culmination of all of these individual building events. Self-organization is an epi-phenomenon seen in some aspects of social insect behavior. The



Construction Behavior of Insects, Figure 97 Some diverse types of insect construction: *top left*, paper wasp nest showing detail of brood cells; *top right*, paper wasp nest early in construction showing early formation of cells; *second row left*, tubes constructed by subterranean termites to maintain high humidity as they seek food; *second row right*, mud dauber nest; *third row left*, pits for capture of ants constructed by ant lion larvae; *third row right*, mound constructed by imported red fire ants; *bottom row left*, tent constructed by eastern tent caterpillar larvae; bottom row center, paper wasp nest; *bottom row right*, nests constructed by fall webworm larvae. (All photos by J. L. Castner, University of Florida.)

honey, pollen and brood storage pattern seen in honey bee combs can be explained through a self-organizing process. Likewise, positive feedback during construction can amplify small differences in worker behavior, and can lead to the distinct and repeated patterns of galleries observed in both ant and termite nests. Computer modeling studies have shown that, indeed, relatively simple rules and a programmed responsiveness to the location and activity of other colony units within the virtual nest can lead to clustered building and a chamber pattern of walls and spaces similar to those of real nests and other repeating patterns seen in nature. Modeling studies have also shown that relatively small changes in the building program can lead to pronounced differences in the appearance of nests. These results suggest a mechanism for the evolution of the diversity in nest structures observed in nature.

Conclusions

Much of behavior is transient, with little in the way of a permanent record left behind. Construction behavior (Fig. 97), however, does leave physical evidence behind that has even been fossilized. These trace fossils include burrow remains, nests and such things as the dung balls made by beetles some 30–35 million years ago. The amazing fact is that fossilized ant nests from 60 million years ago show little variation from those seen today, suggesting that at least some social insects have not changed their behavior over extremely long periods of time. Thus, the complex behaviors associated with insect construction have been around for millions of years. Some of the evolutionary process and the regulation of construction behavior is now understood, but this area of insect biology remains a vital and fertile area for ongoing and future research.

References

Hansell MH (1984) Animal architecture and building behaviour. Longman, New York, NY, 324 pp
Matthews RW, Matthews JR (1978) Insect behavior. Wiley, New York, NY, 507 pp
Ross KG, Matthews RW (eds) (1991) The social biology of wasps. Cornell University Press, Ithaca, NY, 678 pp
Turner JS (2000) The extended organism. Harvard University Press, Cambridge, MA, 235 pp
Von Frisch K (1974) Animal architecture. Harcourt Brace Jovanovich, New York, NY, 306 pp

Consumption Efficiency

The proportion of energy available that is consumed at a trophic level. In the case of herbivorous insects, it is the proportion of net primary productivity that is ingested.

Contact Poison

A pesticide that acts after external contact of the insect with the toxicant, and does not require ingestion to be effective.

► Insecticides

Contagious Disease

A disease which is naturally transmitted by hosts of the disease; synonymous with communicable disease.

Containment

From a regulatory perspective, containment consists of phytosanitary measures in and around an infested area to prevent spread of a pest.

► Risk Analysis (Assessment)
► Regulatory Entomology
► Invasive Species

Contamination

Harboring of, or contact with, microorganisms (or other organisms such as insect parasites).

Continental Drift

The separation and movement of land masses in geologic time.

Controlled Atmosphere Technologies for Insect Control

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Controlled atmosphere treatments have been employed to control stored products pests for centuries. The first example is the storage of grains in ancient Egypt, where the cribs were sealed tightly to prevent the propagation and growth of insects through the use of lowered oxygen environment. Historically, controlled atmosphere treatments were designed to preserve commodity quality during long-term storage. The secondary effect of providing some level of insect control was serendipitous. Sometimes the controlled atmosphere provides extra time to store a commodity at low temperatures, and the low temperatures have an effect on insect mortality, while at other times the controlled atmosphere directly affects the desired insect control. Reported effects of controlled atmosphere on insect physiology include the reduction of NADPH levels in hypercarbonic (>10% CO_2) environments, a reduction in energy charge as a result of slower production of ATP, the production of glutathione is reduced, and the inhibition of the regeneration of choline to acetylcholine under hypercarbonic environments. There is also an observed reduction of high temperature tolerance in insects exposed to anoxic environments.

Controlled atmosphere can also mean controlling the environment surrounding an insect, meaning the temperature, light, humidity, pressure, and atmospheric gases. Any postharvest situation allows for the manipulation of the environment for pest control. Traditionally, controlled atmospheres means the alteration of atmospheric gases, such as oxygen and carbon dioxide. This can be achieved through the use of flow-through systems in which oxygen is lowered by a nitrogen purge and carbon dioxide is increased by injection of this gas. The levels of oxygen and carbon dioxide

Controlled Atmosphere Technologies for Insect Control, Table 19 USDA-APHIS approved controlled atmosphere treatments for fresh fruits as of 2007

Commodity	Pest	Percentage		Temperature	Heating rate	Total
		O_2	CO_2	°C	°C/hr	Time
Apple	Codling Moth & Oriental Fruit Moth	1	15	46	12	3 h
Cherry	Codling Moth & Western Cherry Fruit Fly	1	15	47	>200	25 min
Cherry	Codling Moth & Western Cherry Fruit Fly	1	15	45	>200	45 min
Nectarines & Peaches	Codling Moth & Oriental Fruit Moth	1	15	46	24	2.5 h
Nectarines & Peaches	Codling Moth & Oriental Fruit Moth	1	15	46	12	3.0 h

Controlled Atmosphere Technologies for Insect Control, Table 20 Some potential controlled atmosphere treatments to control arthropod pests in fresh fruits and vegetables

Commodity	Pest	Percentage		Temperature	Time
		O2	CO2	(°C)	(Days)
Apple	San Jose scale	<1	>90	>12	2
Apple	San Jose scale	0	96	22	1
Apple	Codling moth	1.5–2	<1	0	91
Apple	Mites	1.0	1.0	20.8	160
Apple	4 tortricid pests	0.4	5.0	40	>0.6
Asparagus	Aphid & thrips	8.4	60	0–1	4.5
Strawberry	Thrips	1.9–2.3	88.7–90.6	2.5	2
Sweet potato	Sweetpotato weevil	4	60	25	7
Sweet potato	Sweetpotato weevil	2	40	25	7
Sweet potato	Sweetpotato weevil	2	60	25	7
Table grapes	Mites, thrips, omnivorous leafroller	11.5	45	2	13
Walnut	Codling moth	8.4	60	25	7
Mango	Fruit flies				
Broccoli	Thrips	0.0025			
Lettuce	Thrips	0.0025			

used in controlled atmosphere treatments vary in relation to commodity tolerance and insect intolerance. The levels of atmospheric gases necessary to kill a target pest will vary in relation to the pest/commodity complex.

Controlled atmosphere technologies have unique terminology associated with them. Some of the important terms/acronyms and their definitions are:

Controlled atmosphere (CA): Alteration of the chemical content of the air environment from that normally experienced at STP.

Chilling mortality: Death of an organism due to cumulative, non-freezing, low temperature damage.

Anoxic: Low oxygen to no oxygen environment.

Hypercarbonic: High carbon dioxide environment.

MAP: Modified atmosphere packaging.

Vacuum: Reduction of atmosphere through evacuation. Reduction of atmospheric pressures below STP.

STP: Standard temperature and pressure. Internationally, the current STP defined by the IUPAC (International Union of Pure and Applied Chemistry) is an absolute pressure of 100 kPa (1 bar) and a temperature of 273.15°K (0°C).

Hypobaric treatments: Reduction of atmospheric pressures below STP.

Hyperbaric treatments: Increase of pressure above STP.

Film wraps: Plastic impermeable or semi-permeable wraps of fresh fruits and vegetables to reduce respiration and dehydration.

Coatings: Usually wax or shellac type mixtures that cover fruits and vegetables to reduce respiration and dehydration.

Low Oxygen

The most common types of controlled atmosphere treatments are those that employ low oxygen environments. In the case of apples, oxygen levels vary from 1 to 5%, and carbon dioxide levels can vary from 0.3 to 3%. Other treatments use ultra low levels of oxygen, such as the case with broccoli, which employs oxygen levels of 0.0025%. Both of these treatments are performed at temperatures well below 5°C.

Low oxygen treatments can be effective in killing insects provided that the temperature is high enough to put a stress on the metabolic system of the insect. Reduced O_2 consumption leads to a decreased rate of ATP production. As a result of energy insufficiency, the membrane ion pumps fail, leading to K^{+2} efflux, Na^{+} influx, and membrane depolarization. The voltage-dependent Ca^{+2} gates are then opened, causing Ca^{+2} influx. The high Ca^{+2} concentration in the cytosol activates phospholipases and leads to increased membrane phospholipid hydrolysis. The cell and mitrochondrial membranes become further permeable, causing cell damage or death.

Omnivorous leafroller pupae use metabolic arrest as a major response to hypoxia. The pupae's O_2 consumption rate and metabolic heat rate decrease slightly with decreasing O_2 concentration until a critical concentration is attained, below which the decrease become rapid. The critical concentration points are 10, 8 and 6 kPa at 30, 20 and 10°C, respectively. Although the pupae's metabolism decreases quickly below the critical concentration points, the pupae do not initiate anaerobic metabolism until the O_2 concentration is below 2 kPa at 20°C. Concentrations of O_2 below the anaerobic compensation point appear to be in the insecticidal range.

High Carbon Dioxide

There are other treatments that use carbon dioxide levels of 60% or greater, with the oxygen level not being regulated. These treatments have been used at temperatures within the normal growing range (10–40°C). High carbon dioxide treatments have been shown to be very effective in controlling mites and diapausing insects. However, when elevated carbon dioxide is used in combination with low oxygen levels, the results on insect mortality have been variable. Combination high temperature and controlled atmosphere treatments used effectively against lepidopteran pests do not work as effectively against fruit flies. This may be due to the differences in the respiratory systems and regulatory mechanisms of terrestrial (Lepidoptera) and semi-aquatic (fruit fly larvae) insects. At low temperatures, near 0°C, mortality of the moth *Platynota stultana* is greater with 45 kPa O_2 + 11.5 kPa O_2 (air) as compared with 45 kPa CO_2 + 0.5 kPa O_2. In some cases, when only a small amount of CO_2 is present in an O_2-deficient atmosphere, it can enhance mortality by up to ten-fold.

Elevated CO_2 (hypercapnia) can reduce the rate of insect respiration. High levels of CO_2 can reduce oxidative phosphorylation by inhibiting respiratory enzymes such as succinate dehydrogenase and malic enzyme. Reduced oxidative phosphorylation leads to reduced ATP generation, which in turn leads to a failure of membrane ion pumps, membrane depolarization and eventual cell death, as described for hypoxia.

Elevated CO_2 levels can decrease pH through the formation of carbonic acid. Reduced pH can increase intercellular Ca^{2+} concentration, which causes the cell and mitochondrial membranes to become more permeable, suggesting that high CO_2 can increase membrane permeability. High CO_2 levels can alter the ratio of pyruvate to lactate by 25% of normal, changing the redox potential and a lesion in the electron transport chain, presumably by a modification in the permeability of mitochondrial membranes.

Modified Atmosphere Packaging

Controlled atmosphere can also be achieved through the use of semi-permeable membranes, called modified atmosphere packaging, which reduces the movement of oxygen and carbon dioxide. Modified atmosphere packaging is generally performed at temperatures between 0–20°C, with 1–18% O_2, and 0–10% CO_2, and is of a long duration, generally weeks to months. Modified atmosphere packaging can also be generated using film wraps. Also, film coverings and coatings can form modified atmospheres in fresh horticultural commodities. These treatments are usually carried out at 20–27°C, for long durations, with variable levels of atmospheric gases, depending on commodity respiration rates and film permeability. The commodity will consume oxygen and increase carbon dioxide during normal respiration processes. Normally, the reduction of oxygen and elevation of carbon dioxide are not as severe because there is a point where either the level of oxygen will no longer support commodity respiration or the level of elevated carbon dioxide is inhibitory to commodity respiration. Therefore, modified atmosphere packaging often takes longer to kill the target pest.

Temperature Combinations

Temperature control has been a traditional means of controlling the environment to affect insect mortality. Typically, low temperature has been the means used to control postharvest pests. Low temperatures work because they are usually below the optimal growth and development temperatures of most insect species. Low temperature causes mortality through cumulative, systemic tissue and metabolic damage, and the inability to repair that damage. Unfortunately, low temperature controlled treatments require a significant time, measured in days, weeks, or even months, to affect insect mortality. The advantage of low temperature controlled atmosphere is that it could be applied during marine transit. A 13 day treatment with 45 kPa CO_2 (11.5 kPa O_2) at 2°C or lower has been developed for control of Pacific spider mite, western flower thrips and omnivorous leafroller on table grapes. Although table grapes tolerate this treatment, exposure to insecticidal atmospheres for this length of time, even at low temperatures, would not be tolerated by many fresh commodities.

There has been considerable research on controlled atmosphere at intermediate temperatures (10–28°C), but interest in this approach has been diminishing due to increasing research on high temperature CA treatments (40–55°C). The advantage of intermediate temperature controlled atmosphere treatments is that they range from hours to days, much faster than low temperature controlled atmosphere treatments. However, high temperature controlled atmosphere treatments have gained popularity because the treatments are relatively short and easy to apply. High temperature controlled atmosphere applies two simultaneous stresses, which greatly reduces total treatment time and minimizes commodity phytotoxicity due to elevated temperatures. In fact, high temperature controlled atmosphere treatments may be beneficial for climacteric fruits (fruits that continue to ripen after harvest) because the elevated temperatures knock out many of the enzymes involved in fruit ripening, and therefore extends shelf life. High temperature controlled atmosphere treatments appear to block thermal acclimation by blocking the synthesis of heat shock proteins due to lack of oxygen, wherein the elevated carbon dioxide inhibits respiration and alters internal pH, causing systematic breakdown of oxidative phosphorylation and electron transport.

Hot water dips not only raise temperature, but alter the levels of atmospheric gases in the commodity. As temperature rises, oxygen level in the commodity is reduced and carbon dioxide is elevated. This is due to the interaction of cuticle permeability and ability of the gases to dissolve in water.

Ozone, Other Chemicals and Processes

Ozone has typically been used for control of postharvest diseases. However, the advances in ozone generation and application of vacuum has allowed for treatments to be developed for arthropod pests. The problem with ozone is that it is non-penetrating and can only effectively control external pests. Also, ozone penetration is inhibited by water. So, wet commodities are poor candidates for ozone treatments. In addition, there may be some problems with ozone if the commodities have green stems and leaves. Ozone decomposes chlorophyll and may cause a "bleaching" effect of green commodities.

Hypobaric treatments have been gaining popularity. These treatments work by reducing atmospheric pressures below STP (Standard Temperature and Pressure), and in turn reduce both the availability of oxygen and the ability of the spiracles to remain closed. This may cause anoxia and desiccation stress, resulting in mortality of the insect.

Only recently, hyperbaric or hydrostatic pressures have been tested for controlling internal feeding insects. This technology uses very high pressures of 10,000–80,000 psi, pressures experienced in the deep ocean environments, to disinfest and decontaminate foods. It is not known how these very high pressures kill insects, but it is presumed that it causes protein denaturation and wide-scale tissue break-down.

Machinery

The most attractive feature of controlled atmosphere treatments is the wide range of locations and situations where it can be applied. Controlled atmosphere treatments can be applied in huge warehouses, individual pallets in cold rooms, specially designed heat/controlled atmosphere chambers, hot water dipping tanks, shipping containers in transit, in individual boxes (via modified atmosphere packaging), and in individual fruits (via wraps and coatings). With today's technology, controlled atmosphere is becoming more affordable and portable. Nitrogen generators needed to form low oxygen environments are becoming more compact and affordable. Compressed tanks of carbon dioxide are still relatively inexpensive, and are needed only when the protocol calls for CO_2 levels higher than the commodity can produce. Modified atmosphere packaging is found in every aspect of the fresh food market. Each modified atmosphere packaging system provides an affordable and portable controlled atmosphere system.

Approved Treatments

To date there are only a few controlled atmosphere treatments in the USDA, APHIS treatment manual (see "approved controlled atmosphere" table). These treatments were the first to be approved and were only entered into the Federal Register on April 16, 2007. These treatments employ a combination of controlled atmosphere (Fig. 98) and hot forced air (called CATTS for "Controlled Atmosphere Temperature Treatment System"). Other controlled atmosphere treatments have been developed (see "potential controlled atmosphere" table), but are not yet in the APHIS treatment manual.

Adoption of controlled atmosphere quarantine treatments by industry has been slow because of the wide availability of chemical fumigants like methyl bromide. Although methyl bromide was identified as an ozone depleter under the Montreal Protocol, its use for commodity disinfestations is still allowed while other uses, such as soil and structural fumigations, are restricted. The cost of methyl bromide has rapidly increased from US$5 for a 100 lb. tank in 1995 to nearly US$1,000 in 2007. As fumigation costs rise, alternative, non-chemical quarantine treatments will gain industry support and become more common.

References

Edwards LJ (1968) Carbon dioxide anaesthesia and succinic dehydrogenase in the corn earworm, *Heliothis zea*. J Insect Physiol 14:1045–1048

Fanestil DD, Hastings AB, Mahowald TA (1963) Environmental carbon dioxide stimulation of mitochondrial adenosine triphosphate activity. J Biol Chem 238:836–842

Controlled Atmosphere Technologies for Insect Control, Figure 98 A commercial CATTS (controlled atmosphere temperature treatment system) can accommodate various types of produce and packaging, and produce insect-free products.

Fleurat-Lessard F (1990) Effect of modified atmospheres on insects and mites infesting stored products. In: Calderon M, Barkai-Golan R (eds) Food preservation by modified atmospheres. CRC Press, Boca Raton, FL, pp 21–38

Friedlander A (1983) Biochemical reflections on a non-chemical control method. The effect of controlled atmospheres on the biochemical processes in stored product insects. In: Proceedings of the third international working conference on stored product entomology. Kansas State University, Manhattan, Kansas, pp 471–486

Herreid CF (1980) Hypoxia in invertebrates. Comp Biochem Physiol (A) 67:311–320

Hochachka PW (1986) Defense strategies against hypoxia and hypothermia. Science 231:234–241

Mitcham EJ, Zhou S, Bikoba V (1997) Controlled atmosphere for quarantine control of pests of table grape. J Econ Entomol 90:1360–1370

Neven LG, Mitcham EJ (1996) CATTS (controlled atmosphere/temperature treatment system): a novel tool for the development of quarantine treatments. Am Entomol 42:56–59

Neven LG (2005) Combined heat and controlled atmosphere quarantine treatments for control of codling moth, *Cydia pomonella*, in sweet cherries. J Econ Entomol 98:709–715

Neven LG, Rehfield-Ray LM (2006) Combined heat and controlled atmosphere quarantine treatment for control of western cherry fruit fly in sweet cherries. J Econ Entomol 99:658–663

Neven LG, Rehfield-Ray L, Obenland D (2006) Confirmation and efficacy tests against codling moth and oriental fruit moth in peaches and nectarines using combination heat and controlled atmosphere treatments. J Econ Entomol 99:1610–1619

Neven LG, Rehfield-Ray L (2006) Confirmation and efficacy tests against codling moth, *Cydia pomonella*, and oriental fruit moth, *Grapholitha molesta*, in apples using combination heat and controlled atmosphere treatments. J Econ Entomol 99:1620–1627

Zhou S, Criddle RS, Mitcham EJ (2000) Metabolic response of *Platynota stultana* pupae to controlled atmospheres and its relation to insect mortality response. J Insect Physiol 46:1375–1385

Zhou S, Criddle RS, Mitcham EJ (2001) Metabolic response of *Platynota stultana* pupae during and after extended exposure to elevated CO_2 and reduced O_2 atmospheres. J Insect Physiol 47:401–40

Convergent Evolution

The evolution of unrelated species or lineages resulting in similar structures and behaviors.

Cooloola Monsters

A family of crickets (Cooloolidae) in the order Orthoptera.

► Grasshoppers, Katydids and Crickets

Cooloolidae

A family of crickets (order Orthoptera). They commonly are known as cooloola monsters.

► Grasshoppers, Katydids and Crickets

Cooties

A popular term applied to human body lice.

► Human Lice

► Chewing and Sucking Lice (Phthiraptera)

Coppers

Some members of the family Lycaenidae (order Lepidoptera).

► Gossamer-Winged Butterflies

► Butterflies and Moths

Copromorphidae

A family of moths (order Lepidoptera). They commonly are known as tropical fruitworm moths.

► Tropical Fruitworm Moths

► Butterflies and Moths

Coprophagous

Feeding on fecal material.

Coprophagy

Feeding on dung or excrement by animals. Such arthropods are said to be coprophagous or coprophages.

► Food Habits of Insects

Coptopsyllidae

A family of fleas (order Siphonaptera).

► Fleas

Copularium

The initial chamber constructed by a pair of colony-founding termites.

Coquillett, Daniel William

Daniel Coquillett was born on a farm in Illinois on January 23, 1856. He collected insects while a youth, and published his first entomological paper "On the early stages of some moths" in the Canadian Entomologist in 1880. However, he developed an incipient tuberculosis, and his parents moved the family to Anaheim, California, in 1882. There, he began to specialize in flies. His entomological activities drew the attention of C.V. Riley who appointed him as a U.S. Department of Agriculture field agent in 1885. He worked on chemical control of pest insects (Fig. 99) and on part of the cottony cushion scale biological control program. At the same time, he continued his studies of Diptera, especially bee flies and robber flies. When C.V. Riley's relationships with California growers become strained in 1893, Coquillet was called to Washington, DC, and was made an honorary

Coquillett, Daniel William, Figure 99 **Daniel W. Coquillett.**

custodian of the Diptera collections in the U.S. National Museum. There, he published extensively on Tachinidae, Simuliidae, Culicidae, and other flies, eventually describing about 1,000 species. A major work was his (1910) "Type species of North American Diptera." He died on July 7, 1911, and his Diptera collection became part of the US National Museum.

Reference

Mallis A (1971)Daniel William Coquillet. In: American entomologists. Rutgers University Press, New Brunswick, NJ, pp 389–391

Coral Treaders

Members of the family Hermatobatidae (order Hemiptera).

► Bugs

Corazonin

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Corazonin is a neuropeptide that is found in many insects. It consists of 11 amino acid residues, and three molecule types are known (Fig. 100). [Arg^7]-corazonin was the first molecule discovered, from the cockroach *Periplaneta americana*, and is a potent cardio-stimulating neuropeptide. It has been found in other species including other cockroaches, a cricket, and moths, but no cardio-stimulating action is found in any of these other insects. In the sphinx moth, *Manduca sexta*, this molecule plays a role in controlling eclosion. [Thr^4, His^7]-corazonin occurs in the European commercial honey bee, *Apis mellifera*, but its function is yet to be elucidated. The last molecule is [His^7]-corazonin that has been identified from a stick insect, a grasshopper, and locusts. Immunohistochemical observations indicate that corazonin is synthesized in the brain and sent via the axon to the corpus cardiacum where it is presumably secreted into the hemolymph in some insects. In locusts and grasshoppers, corazonin induces melanization and also has other physiological functions, as described below in association with phase polyphenism.

Role of Corazonin in the Control of Body-Color Polymorphism in Locusts

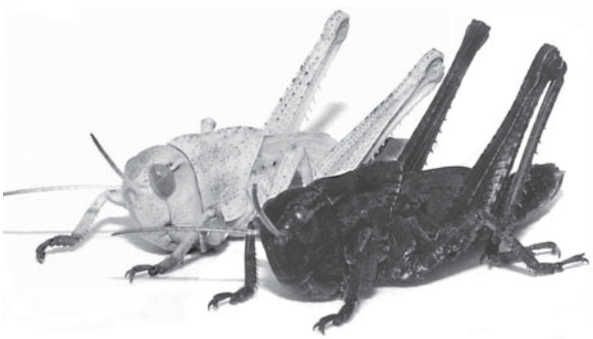
In 1921, B.P. Uvarov proposed the phase theory to explain that locusts that had been regarded as two distinct species (*Locusta danica* and *L. migratoria*) belonged to the same species, which was designated as *L. migratoria*. According to his theory, locusts display body-color polyphenism in response to population density and some environmental factors. Locusts under low population density are called solitarious phase, whereas those under high population density are called gregarious phase. Solitarious nymphs are uniformly colored. Their body color is cryptic and assumes green, brown, yellow, reddish, grey, or black depending on the background color of their habitat. In contrast, gregarious

pGlu-Thr-Phe-Gln-Tyr-Ser-**Arg**-Gly-Trp-Thr-Asn-amide	**[Arg^7]-corazonin**
pGlu-Thr-Phe-**Thr**-Tyr-Ser-**His**-Gly-Trp-Thr-Asn-amide	**[Thr^4, His^7]-corazonin**
pGlu-Thr-Phe-Gln-Tyr-Ser-**His**-Gly-Trp-Thr-Asn-amide	**[His^7]-corazonin**

Corazonin, Figure 100 **Corazonin molecule types. Different amino acids are emphasized.**

nymphs develop black patterns with an orange background color. Locusts growing under intermediate population densities are often called transient phase and display intermediate body coloration. Juvenile hormone (JH) is responsible for the induction of green color. Because the green body color is common among solitarious locusts, JH was once believed to control the phase-related body-color polyphenism. The administration of JH to gregarious nymphs causes them to lose the black patterns and induces green color, but destruction of the corpus allatum, the gland producing JH, does not induce black patterns. An albino mutant strain of *L. migratoria* was used to study the hormonal control of body color polyphenism. This strain was derived from a laboratory culture in Japan, and the albinism is a recessive trait controlled by a simple Mendelian unit. The possible involvement of a neuropeptide in the control of body-color polymorphism was noticed in *L. migratoria* in which albino nymphs turned darker after receiving an injection of methanol extracts of brains and corpora cardiaca taken from normal (pigmented) nymphs. The extracts are heat-stable, but lose the dark-color inducing activity after incubation with a proteinase. This dark-color inducing factor was later demonstrated to be identical to [His^7]-corazonin. The albinism of the above strain is caused by deficiency of this neuropeptide.

Albino nymphs injected with [His^7]-corazonin (Fig. 101) develop not only black patterns but also various other colors depending on the dose and the timing of the injection. Nymphs with a completely black body color appear if they are injected with a high dose of the neuropeptide at the beginning of the previous stadium, whereas those injected with lower doses at the same stage turn brown, light brown or yellow in the following nymphal stadium. Uniformly reddish body coloration appears in nymphs injected with the hormone shortly before the previous ecdysis. These body colors are similar to those normally observed in solitarious nymphs of *L. migratoria* in the field. Green solitarious nymphs are brownish or reddish in the ventral side of the body as well as some portions of the legs. Such body coloration can be induced in albino nymphs when both JH and corazonin are injected. As previously mentioned, gregarious nymphs typically develop black patterns with an orange background color. This type of body coloration can also be induced by injection of [His^7]-corazonin at a certain stage in albino nymphs. It is highly likely that changes in corazonin concentration control the expression of body coloration in the locust. For a certain type of body coloration to be maintained in successive nymphal stadia, the specific changes in corazonin and JH concentrations required for the expression would be repeated



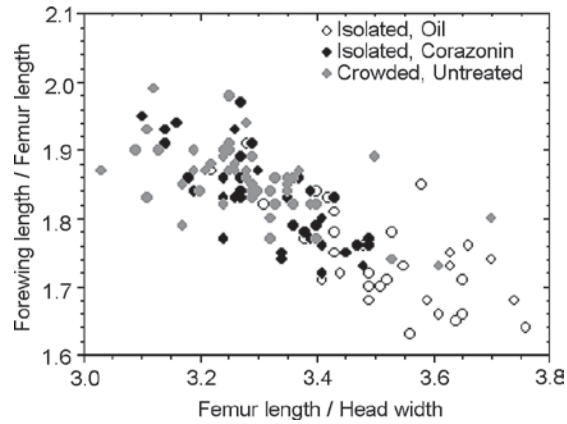
Corazonin, Figure 101 **Albino *Locusta migratoria* nymphs. The individual on the right was injected with corazonin in the previous stadium.**

in each stadium. The hormonal induction of solitarious and gregarious body coloration is independent of the rearing density.

Other locusts and grasshoppers also show body-color polyphenism and corazonin appears to be present in their central nervous system and corpora cardiaca. Transplantation of their brain and corpora cardiaca into albino *L. migratoria* induces darkening in the latter. Injection of [His^7]-corazonin causes darkening in all locusts and grasshoppers so far tested. In the desert locust, *Schistocerca gregaria*, and the American grasshopper, *S. americana*, [His^7]-corazonin has been isolated and is responsible for the induction of black patterns, but not the background color. An albino strain is known for *S. gregaria* that is inherited by a simple Mendelian unit, as in the case for *L. migratoria*. However, the albinism in the former is caused by some unknown mechanism other than deficiency of [His^7]-corazonin, because this neuropeptide is present in this strain. Some katydids display body-color variation. The albino bioassay suggests that their brain also contains corazonin or a similar compound, but injection of [His^7]-corazonin has no biological activity on the body color in the katydids.

Effect of Corazonin on Body Shape

The body dimensions of locusts are affected by crowding. Morphometric ratios (Fig. 102) of F/C and E/F (F = hind femur length; C = maximum head width; E = forewing length) are often used to evaluate the degree of "gregarization" or "solitarization." Gregarious adults have a smaller F/C ratio and a larger E/F ratio than solitarious adults. In the laboratory, similar values can be obtained by rearing locusts in a group or in isolation. Neither JH nor molting hormone influences these ratios in a consistent manner, indicating that these hormones play no major role in the control of phase-related changes in body shape. On the other hand,

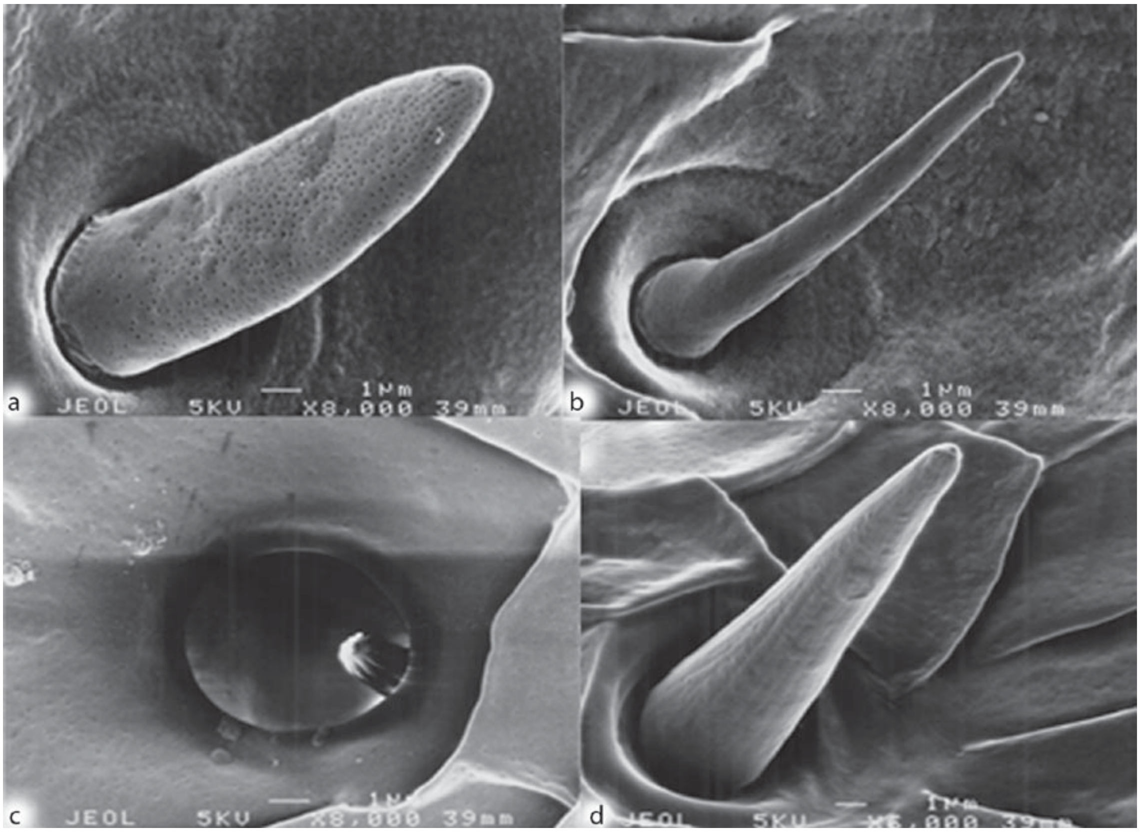


Corazonin, Figure 102 **Effect of corazonin injection on morphometric ratios in *Locusta migratoria*. (Based on data of Tanaka et al., 2002. Reproduced with permission of *Journal of Insect Physiology*.)**

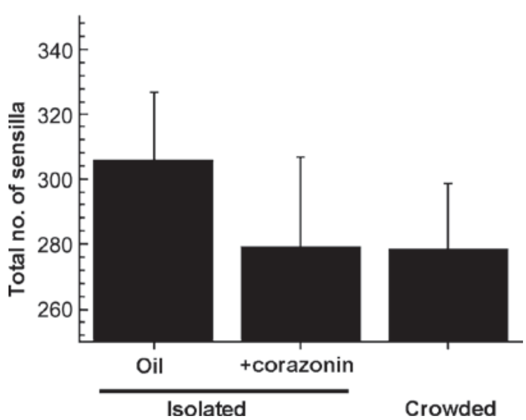
injection of [His^7]-corazonin induces morphometric gregarization in isolated-reared adults of *L. migratoria* and *S. gregaria*. This gregarizing effect is greater as the injections are made earlier during nymphal development.

Effect of Corazonin on the Formation of Antennal Sensilla

Locusts have several types of sensilla on the antennae. In *S. gregaria* and *L. migratoria*, the total number of antennal sensilla is greater in solitarious adults than in gregarious ones, although the significance of this difference is unknown. Corazonin causes locusts reared in isolation to develop fewer antennal sensilla when injected during the nymphal stage as compared with oil-injected counterparts, and the total number of antennal sensilla in the former becomes similar to that for locusts reared in groups. Among the four major antennal sensilla (Figs. 103 and 104), basiconic sensilla do not show a phase-specific difference in abundance. Injection of corazonin does not influence the abundance of this sensillum. As in the case for



Corazonin, Figure 103 **Four types of antennal sensilla in *Schistocerca gregaria*. A: basiconic sensillum type with high density of pores; B: basiconic sensillum type B with low density of pores; C: coeloconic sensillum; D: trichoid sensillum with a terminal pore in the inset. (After Maeno and Tanaka, 2004. Reproduced with permission of *Journal of Insect Physiology*.)**

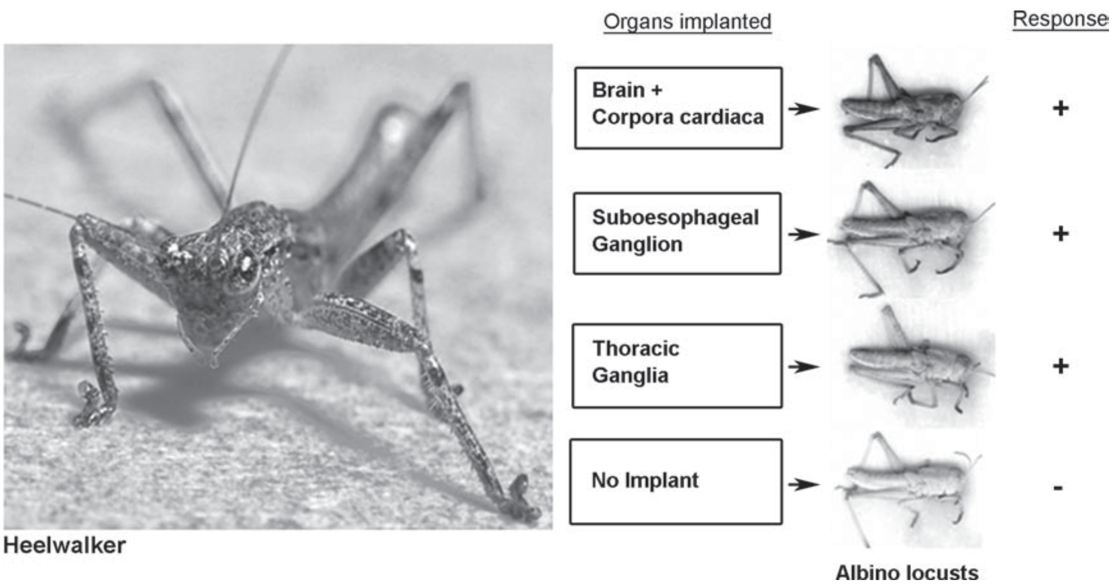


Corazonin, Figure 104 **The number of sensilla. (After Maeno and Tanaka, 2004. Reproduced with permission of *Journal of Insect Physiology*.)**

morphometric gregarization, the earlier the injection of corazonin during nymphal development the greater the effect on the total abundance of antennal sensilla in the adult stage.

Corazonins in Other Insects

Corazonins have been chemically identified in only a small number of species. It is highly likely that more than three molecular types of corazonin exist in insects. Immunohistochemical observations are a powerful tool to visualize the presence and localization of corazonin and similar compounds in many species, although this technique still requires laborious



Corazonin, Figure 105 **Dark-color inducing activity of various organs from a heelwalker, *Hemilobophasma montaguensis* when implanted into albino nymphs of *Locusta migratoria*. (After Tanaka, 2006. Reproduced with permission of *Applied Entomology and Zoology*.)**

procedures. Probably the easiest and fastest method to detect corazonin is use of the albino *L. migratoria* strain as a bioassay. As mentioned earlier, implantation of a brain or corpora cardiaca taken from normal locusts into albino nymphs causes the latter to turn darker. Using this method, more than 90 species of insects have been checked. The results indicate that insects belonging to a total of 19 insect orders have been shown to have a dark-color inducing activity (Table 21) when their brain or/and corpora cardiaca were implanted into albino locusts. This includes both pterygote and apterygote orders of insects, indicating that corazonin or a corazonin-like compound is old in origin. Interestingly, no coleopterans show a sign of corazonin activity, which is also supported by immunohistochemical evidence. Brains and corpora cardiaca taken from twisted-winged parasites, Strepsiptera, which are often placed in the order Coleoptera, display a dark-color inducing activity when implanted into albino locusts. Heelwalkers, belonging to a recently discovered new insect order, Mantophasmatodea, also have a positive response (Fig. 105). These observations suggest that corazonin or a similar molecule is widespread in the Insect class including pterygote and apterygote insects except for the Coleoptera.

► Polyphenism in Insects and Juvenile Hormone (JH)
► Phase Polymorphism in Locusts
► Grasshoppers and Locusts

References

Pener MP (1991) Insect phase polymorphism and its endocrine relations. Adv Insect Physiol 23:1–79

Pener MP, Yerushalmi Y (1998) The physiology of locust polyphenism, an update. J Insect Physiol 44:365–377

Tanaka S (2001) Endocrine mechanisms controlling body-color polymorphism in locusts. Arch Insect Biochem Physiol 47:139–149

Tanaka S (2006) Corazonin and locust phase polyphenism. Appl Entomol Zool 41:179–193

Uvarov B (1966) Grasshoppers and locusts, vol 1. Cambridge University Press, Cambridge, UK, 481 pp

Uvarov B (1977) Grasshoppers and locusts, vol 2. Centre for Overseas Pest Research, London, UK, 475 pp

Veenstra JA (1991) Presence of corazonin in three species and isolation and identification of [His7] corazonin from *Schistocerca americana*. Peptides 12:1285–1298

Corazonin, Table 21 A list of insects tested by the albino bioassay for dark-color inducing activity.

Class	Order	No. species tested[a]
Insecta	Thysanura	1/1
	Ephemenoptera	2/2
	Odonata	3/3
	Orthoptera	18/18
	Phasmatidae	1/1
	Mantophasmatodea	1/1
	Dictyoptera	6/6
	Dermaptera	1/1
	Isoptera	2/2
	Plecoptera	2/2
	Hemiptera	9/9
	Neuroptera	1/1
	Mecoptera	1/1
	Trichoptera	6/6
	Lepidoptera	11/11
	Diptera	7/7
	Hymenoptera	7/7
	Strepsiptera	2/2
	Coleoptera	0/13

[a]No. of species with a positive response/No. of species tested.

Corbicula

A pollen basket. A specialized scopa, or pollen holding apparatus, found in bumble bees and honey bees. The corbicula consists of the broad, concave hind tibia surrounded by a fringe of long hairs.

Cordulegastridae

A family of dragonflies (order Odonata). They commonly are known as biddies.

► Dragonflies and Damselflies

Corduliidae

A family of dragonflies (order Odonata). They commonly are known as green-eyed skimmers.

► Dragonflies and damselflies

Coreidae

A family of bugs (order Hemiptera). They sometimes are called leaf-footed bugs.

► Bugs

Coreid Bugs and Relatives: Coreidae, Stenocepahidae, Alydidae, Rhopalidae, and Hyocephalidae (Hemiptera: Coreoidea)

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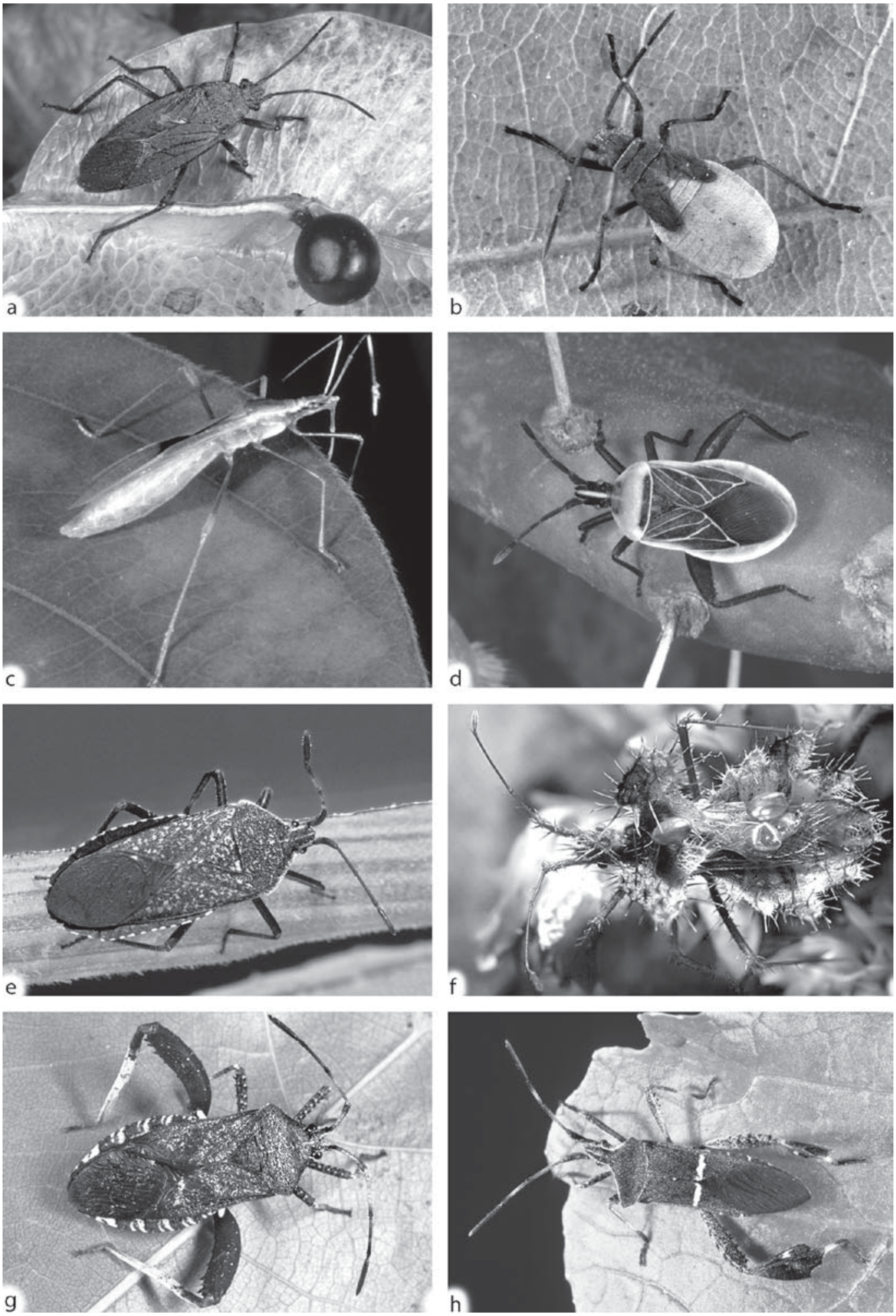
The superfamily Coreoidea of the suborder Heteroptera includes principally phytophagous bugs, but also some coprophagous and carrion feeding species. Ocelli are present on the head and the antennae are four-segmented (Fig. 106). Usually their metapleural scent-gland peritremes (plates on the metapleural scent glands) are well developed, with showy orifices that emit a strong scent. Coreoidea consists of five families:

- Order Hemiptera
  - Suborder Heteroptera
    - Infraorder Pentamorpha
      - Superfamily Coreoidea
        - Family Stenocephalidae
        - Family Coreidae
        - Family Alydidae
        - Family Rhopalidae
        - Family Hyocephalidae



Coreid Bugs and Relatives: Coreidae, Stenocepahidae, Alydidae, Rhopalidae, and Hyocephalidae (Hemiptera: Coreoidea), Figure 106 **Coreoid bugs: (a) adult red-shouldered bug, *Jadera haematoloma* (Rhopalidae) by golden rain tree seed, a favorite food; (b) nymph of *J. haematoloma*; (c) adult**

Stenocephalidae

The small family Stenocephalidae, with two genera and over 30 species, possesses intermediate characters between Lygeidae and the Coreidae. This family is restricted to the Eastern Hemisphere. The greatest species diversity occurs in the Afrotropical Region. Stenocephalids are phytophagous, and often polyphagous. Many species in the Palaearctic region live in association with Euphorbiaceae.

Stenocephalidae are slender bugs, 8–16 mm long. The head is elongated, subtriangular, with mandibular plates longer than the clypeus. The bucculae are short and explanate (flat and spreading). The antennae four segmented. Metathoracic glands are present. The abdominal spiracles are located ventrally. Females oviposit on plant surfaces.

Coreidae

This family consists of over 1,800 species and 250 genera, and is worldwide in distribution. Various groups are commonly called leaf-footed bugs, squash bugs or pod bugs. The family Coreidae was established by Leach in 1815 and included the present families Alydidae and Rhopalidae. All of them plus the Stenocephalidae have numerous veins in the membrane of the hemelytra.

Coreids vary in size from 5 mm to more than 4 cm and although most have a robust body, some are thin or display peculiar legs and antennae and even spiny or hairy bodies. In some species, males use the modified hind legs for territorial combat. They show varied coloration, though in temperate climates they are generally brown or gray, and more or less dark. In tropical and subtropical countries, they sometimes are colorful. In coreids, the head tends to be small in relation to the body and generally is shorter than the pronotum. The antennae are four segmented. Metapleural scent-gland peritremes are well developed.

Currently, the family is considered to consist of four subfamilies: Agriopocorinae, Coreinae, Meropachydinae and Pseudophloeinae. Agriopocorinae contains Australian coreids that are flattened and generally wingless. They possess spiracles on abdominal segments 2 and 3 that are visible from above. The vast majority of coreid bugs are contained on the Coreinae. They display very different shapes and sizes. They have a median sulcus (groove) on the head in front of the eyes. The tibiae possess deep grooves on the outer surface. The abdominal spiracles are not visible from above. This subfamily includes many tribes throughout the world, but mainly in warmer regions. The Meropachydinae include over 12 genera with a small head, the hind femora large, and hind tibiae with the distal end produced into a spine or tooth. The abdominal spiracles are not visible from above. This subfamily is restricted to the Neotropical Region. The Pseudophloeinae are relatively small in size. Their head does not have a medial sulcus in front of the eyes, the tibiae are not grooved (sulcate) on the outer surface, and the abdominal spiracles are not visible from above. This subfamily consists of about 28 genera and 165 species, and is mainly old-world in distribution.

***Stenocoris* sp. (Alydidae), sometimes known as broad-headed bugs or rice bugs; (d) adult of cactus bug, *Chelinidea vittiger* (Coreidae), a species commonly associated with prickly pear cactus (*Optuntia* spp.) in North America; (e) adult of squash bug, *Anasa tristis* (Coreidae), a serious pest of squash in North and Central America; (f) adult golden egg bug, *Phyllomorpha laciniata* (Coreidae) with eggs carried on its back; (g) adult *Euthochtha galeator* (Coreidae) is found widely in eastern North America where it occasionally can become a pest, feeding on such plants as oranges and roses; (h) adult *Leptoglossus phyllopus* (Coreidae), one of the most damaging of the leaffooted bugs in North America, where it feeds on fruits, vegetables, grains and other crops. (photo credits: a, b, d, g, Lyle Buss; f, Arja Kaitala; c, e, h, John Capinera).**

Most coreids are phytophagous, feeding on seed or fruit. A few species are considered to be of economic importance. Cucurbits, various nut and fruit trees, rice, legumes and greenhouse vegetables are crops damaged by coreids worldwide. They even can attack conifers, junipers and *Eucalyptus*. Among the economically important species is the squash bug, *Anasa tristis*, which occurs from Brazil to Canada, and is especially a pest in Mexico and the USA. The genus *Leptoglossus* has more than 40 species and variable feeding habits. Formerly this genus was restricted to the Western Hemisphere, but there have been introductions to Europe (Italy and Spain) and to northern Africa. Some species are serious pests, such as the polyphagous *Leptoglossus occidentalis* and *L. phyllopus*. Coreids are not generally thought of as plant virus vectors, but their feeding secretions can be toxic, causing phytotoxicity. Also, they are associated with the transmission of fungi and other pathogens.

Few behavioral studies have been done on Coreidae, although it is known that some males with large femora fight for territory, and that some employ pheromones for sexual attraction or aggregation. Of special interest is the behavior associated with parental care displayed by some coreids. Golden egg bug (*Phyllomorpha laciniata* Villiers) shows a very peculiar oviposition behavior. Females can lay eggs on plants (*Paronychia argentea*), or on the bodies of conspecifics of both sexes, where they remain until hatching. Egg carrying on *P. laciniata* has been known for over a century. It is common to see both males and females carrying 1–15 eggs/individual glued to their backs. The eggs laid on plants experience high rates of predation and attacks by parasitoid wasps. However, when the eggs are carried by an adult, fewer eggs are attacked by parasitoid wasps. Female oviposition choice may be adaptive and minimizes offspring mortality. The golden egg bug is not unique among insects in the sense that males carry eggs (it is also known in belostomatid bugs) but rather it is unique because there are different explanations for this behavior. Some authors have interpreted this behavior as parental care. Others have suggested alternative explanations, such as the notion that this behavior results from the egg-laying female behaving as an intraspecific parasite.

Alydidae

The Alydidae, which are called broad-headed bugs, are a cosmopolitan family known worldwide. It includes about 42 genera and over 250 species, with most living in the subtropical and tropical regions. Many alydid nymphs are dark red-brown, and some adults look like ants or wasps.

Alydidae includes three subfamilies: Alydinae that feed mainly on Fabaceae, and Micrelytrinae and Leptocorisinae that feed predominantly on grasses. The body and appendages of alydids are elongated. The head is subtriangular. The head relatively broad, with the width greater than half the width of the posterior margin of the pronotum. The bucculae is shorter than the antennal insertion. Two ocelli are present, but they are not found on tubercles. The metathoracic glands have distinct external peritremes, and they often produce a foul odor. The wing membrane has numerous veins. Some species are economically important, including *Leptocorisa acuta* on Poeacea, and *Riptortus linearis* and *R. serripes* on Fabaceae.

Rhopalidae

The family Rhopalidae includes 20 genera and about 210 species in two subfamilies: Serinethinae and Rhopalinae. These subfamilies are represented in both the Eastern and Western Hemispheres. Rhopalinae are most diverse in the Palaearctic Region whereas Serinethinae are more tropical in distribution.

In Rhopalidae, the clypeus extends beyond the mandibular plates. Two ocelli are present on tubercles. Rhopalidae have greatly reduced metapleural scent-gland peritremes; for this reason they are called scentless plant bugs. The hemelytral membrane contains numerous veins. The secondary dorsal abdominal scent gland opens close to that of the first gland. All of the rhopalids are phytophagous on herbs and woody plants, but are not known to be economic pests of any significance. However, in Florida, USA, the rhopalid bug *Jadera haematoloma* feeds on golden rain tree, *Koelreuteria* spp. (Sapindaceae) and other plants in this family, becoming so abundant as to become a significant nuisance around homes. *Niesthrea lusitanica* (Sailer) is beneficial, and is used to control the invasive weed velvetleaf, *Abutilon theophrasti*.

Hyocephalidae

The small family Hyocephalidae includes only two genera and three species from Australia: *Hyocephalus aprugnus* Bergroth and *Moevius* with two species. The adults are large, elongate, and mostly dark in color. The head is very extended. The bucculae are enlarged, extending posteriorly to the eyes. The gula has a labial groove. The pronotum is trapezoidal. The scutellum is small. Macropterous and brachypterous morphs are known. The wing membrane contains four veins forming three basal cells. All spiracles occur ventrally. Hyocephalids live under stones in sandy and gravelly areas and may be associated with *Acacia* and *Eucalyptus*.

► Bugs (Hemiptera)
► Paternal Behavior in Heteroptera
► Squash Bug, *Anasa tristis* (Degeer) (Hemiptera: Coreidae)

References

Brailovsky H (2002) A new species of *Maevius* Stål from Australia and some notes on the family Hyocephalidae (Hemiptera: Heteroptera). Proc Entomol Soc Washington 104:41–50

Dolling WR (1991) The Hemiptera. Oxford University Press, Oxford, UK, 274 pp

Göllner-Scheiding U (1983) General-Katalog der Familie Rhopalidae (Heteroptera). Mitteilungen aus dem Zoologischen Museum in Berlin 59:37–189

Kaitala A (1996) Oviposition on the back of conspecifics: an unusual reproductive tactic in a coreid bug. Oikos 77:381–389

Lansbury I (1966) A revision of the Stenocephalidae Dallas 1852 (Hemiptera-Heteroptera). Entomologists' Monthly Magazine 101:145–160

Mitchell PL (2000) Leaf-footed bugs (Coreidae). In: Schaefer CW, Panizzi AC (eds) Heteroptera of economic importance. CRC Press, Boca Raton, FL, pp 337–403

Moulet P (1995) Hémiptères Coreoidea (Coreidae, Rhopalidae, Alydidae), Pyrrhocoridae, Stenocephalidae, Euro-Méditerranéens. Faune de France 81:1–336

Schaefer CW (1965) The morphology and higher classification of the Coreoidea (Hemiptera: Heteroptera). III. The families Rhopalidae, Alydidae, and Coreidae. Misc Publ Entomol Soc Am 5:1–76

Schuh RT, Slater JA (1995) True bugs of the world (Hemiptera: Heteroptera). Classification and natural history. Cornell University Press, Ithaca, NY, 336 pp

Vázquez MÁ (1985) Los Coreoidea ibéricos. Tesis Doctoral. Publicaciones de la Universidad Complutense de Madrid, 322 pp

Coremata

Long eversible tubes found at the tip of the male's abdomen is some Lepidoptera (Fig. 107). These structures are inflated pneumatically, and release pheromones. The pheromones released from the coremata are thought to be aphrodisiacs, and to function in courtship.

Coremata, Figure 107 Fully inflated coremata in a specimen of a tiger moth (Arctiidae) (photo by A. Sourakov).

Corethrellidae

A family of flies (order Diptera)

► Flies

Corioxenidae

A family of insects in the order Strepsiptera

► Stylopids

Corium

The thickened basal region (Fig. 108) of the front wing in Hemiptera.

► Wings of Insects

Corixidae

A family of bugs (order Hemiptera). They sometimes are called water bugs

► Bugs

Corn Delphacid, *Peregrinus maidis* (Ashmead) (Hemiptera: Delphacidae)

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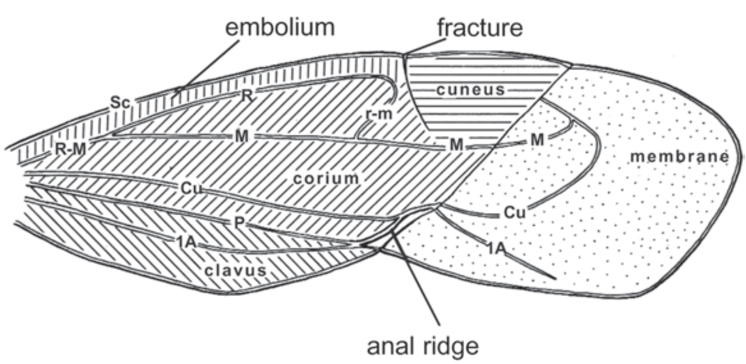
The corn delphacid, *Peregrinus maidis* (Ashmead) (Fig. 109) is known to be a vector of at least two viral diseases of maize (*Zea mays* L.), and is of particular economic importance in the lowland humid tropics. It has even been suggested that its introduction into Central America resulted in the collapse of the Mayan civilization.

P. maidis is pantropical, having been recorded from most tropical regions, including the West Indies, Central and South America, Africa, islands in the Indian and Pacific Oceans, India, Malaysia, Taiwan, Indonesia, China and Australia. In the United States, it has been recorded from Washington, DC, south to Florida, and west to Ohio and Texas.

P. maidis is the only known vector of two major viral diseases of maize, maize mosaic virus and maize stripe virus. The former is a tropical and subtropical disease and is found in Hawaii and in southern Florida. Maize stripe virus, also a tropical and subtropical disease, has been known to occur in southern Florida.

The corn delphacid feeding causes damage to corn and sorghum (*Sorghum bicolor* Moench) extracting a large quantity of sap and excretion of honeydew. Both nymph and adult are efficient vectors of maize stripe and maize mosaic viruses. In general, the nymph is a more efficient transmitter than the adult. The virus can be acquired in less than an hour. The average incubation period of virus in *P. maidis* is 10–14 days,



Corium, Figure 108 Front wing of a bug (Hemiptera: suborder Heteroptera), thickened basally and membranous distally.

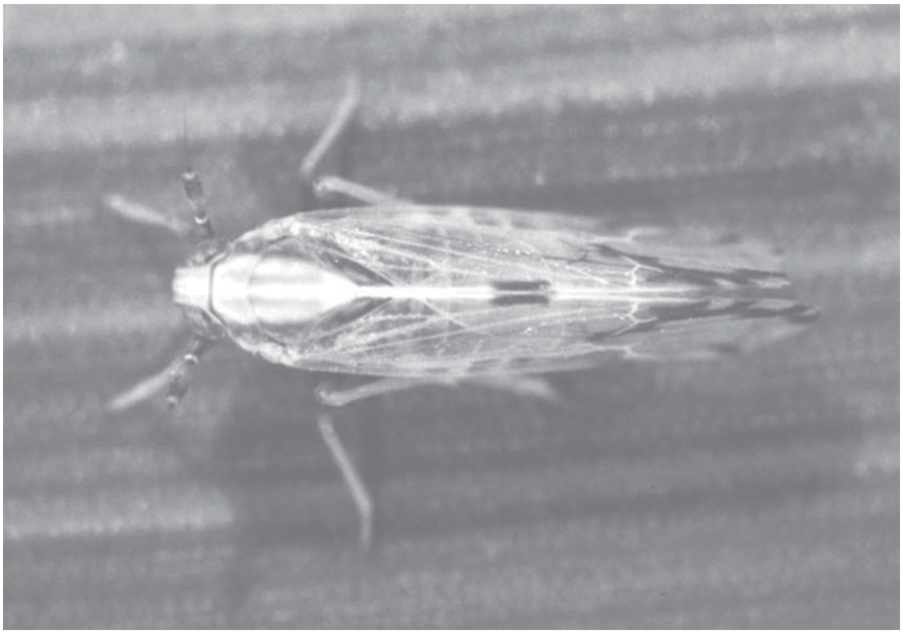
depending on age of vector and virus titre in the infected plant. Once the viruses are acquired by *P. maidis,* they are retained for life. Both viruses multiply in the vector, and only maize stripe virus is transovarially transmitted by *P. maidis*. Corn plants and *P. maidis* can be doubly infected, bearing both viruses.

The life cycle of corn delphacid varies with temperature and host plant. The average developmental periods at 10–32°C are 2–10 days for first instar nymph, 4–20 days for second instar, 4–24 days for third instar, 17–19 days for fourth instar and 4–13 days for fifth instar. Nymphs undergo five instars within the range of 16–27°C. The adult longevity averages 10–97 days for males, and 19–108 days for females, within the temperature range of 17–32°C. At 27°C, the average number of eggs laid per day per female range from 15 to 25 eggs and a mean of 605 eggs, ranging from 297 to 938 eggs per female. The preoviposition period ranges from 3 to 6 days, and the oviposition period ranges from 11 to 48 days. The developmental period of immature stages is also affected by the host plants on which they are reared. At 27°C, the respective average length of nymphal development on corn, itch grass (*Rottboellia exaltata* L.), sorghum (*Sorghum bicolor* (L.) Moench), goose grass (*Eleusine indica* (L.) Gaertn.), barnyard grass (*Echinochloa crusgalli* L.), and gamma grass (*Tripsacum dactyloides* L.) is 17, 18, 20, 25, 27 and 61 days. The adult longevity on these respective plants averages 20, 28, 8, 8, 7 and 43 days.

The number of eggs laid daily per female on corn, itchgrass and gamma grass is 21, 6 and 4 eggs, respectively. The number of eggs per female per life on these three plants averages 612, 146 and 46 eggs.

The eggs are deposited under the epidermal cells along the leaf sheath and midrib. The egg is lined in one or more rows numbering 4–7 eggs. The egg is elongate and curved with a round posterior end. The average size of egg measures 1.06 mm long and 0.28 mm wide. Freshly laid eggs are translucent white with red eye suffusion at posterior end.

Young nymphs are mostly aggregated and feed on the inside of the leaf sheath. It is very common to find adults attending the nymphal



Corn Delphacid, *Peregrinus maidis* (Ashmead) (Hemiptera: Delphacidae), Figure 109 Adult corn delphacid, *Peregrinus maidis* (photo J. Tsai).

aggregations in the field. The average size of the first instar measures 1.4 mm long and 0.4 mm wide. The average measurement of second instar is 1.7 mm long and 0.6 mm wide. The average size of third instar is 2.3 mm long and 0.8 mm wide. The fourth and fifth instars measure 2.8 and 4.0 mm long, and 1.2 and 1.7 mm wide, respectively. The morphological characters such as number of tarsomeres on metatarsi and the development of metatibial spur and wingpad are useful in distinguishing the instars. Both adult males and females typically are dimorphic, containing macropterous and brachypterous forms. In rare case, the adult can be completely wingless.

P. maidis can be controlled by the use of pesticides that are routinely used for control of lepidopteran pests affecting corn. Most research emphasis is placed on breeding corn hybrids resistant to the viral pathogens instead of the insect vector.

► Maize (Corn) Pests and their Management

References

Bradfute OE, Tsai JH (1983) Identification of maize mosaic virus in Florida. Plant Dis 67:1339–1342

Falk BW, Tsai JH (1998) Biology and molecular biology of viruses in the Genus *Tenuivirus*. Ann Rev Phytopathol 36:139–163

Tsai JH (1996) Development and oviposition of *Peregrinus maidis* (Homoptera: Delphacidae) on various host plants. Fla Entomol 79:19–26

Tsai JH, Wilson SW (1986) Biology of *Peregrinus maidis* with description of immature stages (Homoptera: Delphacidae). Ann Entomol Soc Am 79:395–401

Tsai JH, Zitter TA (1982) Characteristics of maize stripe virus transmission by the corn delphacid. J Econ Entomol 75:397–400

Tsai JH, Steinberg B, Falk BW (1990) Effectiveness and residual effects of seven insecticides on *Dalbulus maidis* (Homoptera: Cicadellidae) and *Peregrinus maidis* (Homoptera: Delphacidae). J Entomol Sci 25:106–111

Cornea

The cuticular part of an eye.

Corn Earworm, *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae)

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Corn earworm is found throughout North America except for northern Canada and Alaska. In the eastern United States, corn earworm does not normally overwinter successfully in the northern states. It is known to survive as far north as about 40 degrees north latitude, or about Kansas, Ohio, Virginia, and southern New Jersey, depending on the severity of winter weather. However, it is highly dispersive, and routinely spreads from southern states into northern states and Canada. Thus, areas have overwintering, both overwintering and immigrant, or immigrant populations, depending on location and weather. In the relatively mild Pacific Northwest, corn earworm can overwinter at least as far north as southern Washington.

Life Cycle and Description

This species is active throughout the year in tropical and subtropical climates, but becomes progressively more restricted to the summer months with increasing latitude. In northeastern states dispersing adults may arrive as early as May or as late as August due to the vagaries associated with weather; thus, their population biology is variable. The number of generations is usually reported to be one in northern areas such as most of Canada, Minnesota, and western New York; two in northeastern states; two to three in Maryland; three in the central Great Plains; and northern California; four to five in Louisiana and southern California; and perhaps seven in southern Florida and southern Texas. The life cycle can be completed in about 30 days.

Egg

Eggs are deposited singly, usually on leaf hairs and corn silk. The egg is pale green when first deposited, becoming yellowish and then gray with time. The shape varies from slightly dome-shaped to a flattened sphere, and measures about 0.5–0.6 mm in diameter and 0.5 mm in height. Fecundity ranges from 500 to 3,000 eggs per female. The eggs hatch in about 3–4 days.

Larva

Upon hatching, larvae wander about the plant until they encounter a suitable feeding site, normally the reproductive structure of the plant. Young larvae are not cannibalistic, so several larvae may feed together initially. However, as larvae mature they become very aggressive, cannibalizing other larvae. Consequently, only a small number of larvae (often only one) are found in each ear of corn. Normally, corn earworm displays six instars, but five is not uncommon and seven to eight have been reported. Mean head capsule widths are 0.29, 0.47, 0.77, 1.30, 2.12, and 3.10 mm, respectively, for instars 1–6. Larval lengths are estimated at 1.5, 3.4, 7.0, 11.4, 17.9, and 24.8 mm, respectively. Development time averaged 3.7, 2.8, 2.2, 2.2, 2.4, and 2.9 days, respectively, for instars 1–6 when reared at 25°C.

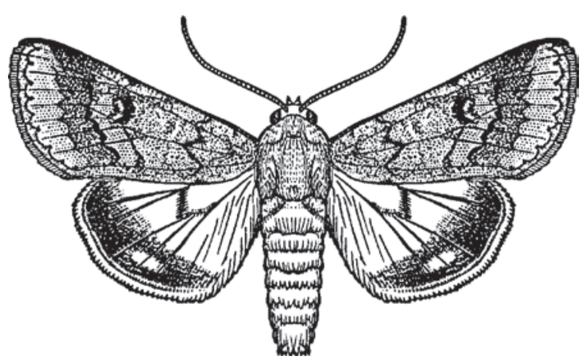
The larva (Fig. 111) is variable in color. Overall, the head tends to be orange or light brown with a white net-like pattern, the thoracic plates black, and the body brown, green, pink, or sometimes yellow or mostly black. The larva usually bears a broad dark band laterally above the spiracles, and a light yellow to white band (Fig. 111) below the spiracles. A pair of narrow dark stripes often occurs along the center of the back. Close examination reveals that the body bears numerous black thorn-like microspines. These spines give the body a rough feel when touched. The presence of spines and the light-colored head serve to distinguish corn earworm from fall armyworm, *Spodoptera frugiperda* (J.E. Smith), and European corn borer, *Ostrinia nubilalis* (Hubner). These other common American corn-infesting species lack the spines and have dark heads. Tobacco budworm, *Heliothis virescens* (Fabricius), is a closely related species in which the late instar larvae also bear microspines. Although it is easily confused with corn earworm, it rarely is a vegetable pest and never feeds on corn. Close examination reveals that in tobacco budworm larvae the spines on the tubercles of the first, second, and eighth abdominal segments are about half the height of the tubercles, but in corn earworm the spines are absent or up to one-fourth the height of the tubercle.

Pupa

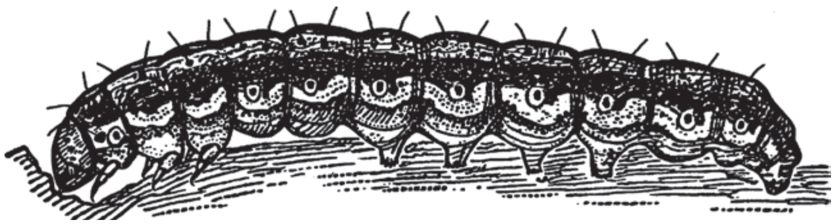
Mature larvae leave the feeding site and drop to the ground, where they burrow into the soil and pupate. The larva prepares a pupal chamber 5–10 cm below the surface of the soil. The pupa is mahogany-brown in color, and measures 17–22 mm in length and 5.5 mm in width. Duration of the pupal stage is about 13 days (range 10–25) during the summer.

Adult

As with the larval stage, adults (Fig. 110) are quite variable in color. The forewings of the moths usually are yellowish brown in color, and often bear a small dark spot centrally. The small dark spot is especially distinct when viewed from below. The forewing also may bear a broad dark transverse band distally, but



Corn Earworm, *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae), Figure 110 Adult of corn earworm, *Helicoverpa zea*.



Corn Earworm, *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae), Figure 111 **Corn earworm larva.**

the margin of the wing is not darkened. The hind wings are creamy white basally and blackish distally, and usually bear a small dark spot centrally. The moth measures 32–45 mm in wingspan. Adults are reported to live for 5–15 days, but may survive for over 30 days under optimal conditions. The moths are principally nocturnal, and remain active throughout the dark period. During the daylight hours they usually hide in vegetation, but sometimes can be seen feeding on nectar. Oviposition commences about 3 days after emergence, continuing until death. Fresh-silking corn is highly attractive for oviposition but even ears with dry silk will receive eggs. Fecundity varies from about 500–3,000 eggs, although feeding is a prerequisite for high levels of egg production. Females may deposit up to 35 eggs per day.

Host Plants

Corn earworm has a wide host range; hence, it is also known as tomato fruitworm, sorghum headworm, vetchworm, and cotton bollworm. In addition to corn and tomato, perhaps its most favored vegetable hosts, corn earworm also attacks artichoke, asparagus, cabbage, cantaloupe, collard, cowpea, cucumber, eggplant, lettuce, lima bean, melon, okra, pea, pepper, potato, pumpkin, snap bean, spinach, squash, sweet potato, and watermelon. Not all are good hosts, For example, a study of relative suitability of crops and weeds in Texas found that although corn and lettuce were excellent larval hosts, tomato was merely a good host, and broccoli and cantaloupe were poor. Other crops injured by corn earworm include alfalfa, clover, cotton, flax, oat, millet, rice, sorghum, soybean, sugarcane, sunflower, tobacco, vetch, and wheat. Among field crops, sorghum is particularly favored. Cotton is frequently reported to be injured, but this generally occurs only after more preferred crops have matured. Fruit and ornamental plants may be attacked, including ripening avocado, grape, peaches, pear, plum, raspberry, strawberry, carnation, geranium, gladiolus, nasturtium, rose, snapdragon, and zinnia. In studies conducted in Florida, corn earworm larvae fed on all 17 vegetable and field crops studied, but corn and sorghum were most favored. In cage tests earworm moths preferred to oviposit on tomato over a selection of several other vegetables that did not include corn. Such weeds as common mallow, crown vetch, fall panicum, hemp, horsenettle, lambsquarters, lupine, morningglory, pigweed, prickly sida, purslane, ragweed, Spanish needles, sunflower, toadflax, and velvetleaf, have been reported to serve as larval. Crimson clover and winter vetch, which may be both crops and weeds, are important early season hosts in Mississippi. Cranesbill species were particularly important weed hosts in this area. In North Carolina, especially important wild hosts are toadflax and deergrass. Adults collect nectar or other plant exudates from a large number of plants. Trees and shrub species are especially frequented. Among the hosts are *Citrus*, *Salix*, *Pithecellobium*, *Quercus*, *Betula*, *Prunus*, *Pyrus* and other trees, but also alfalfa; red and white clover; milkweed, and Joe-Pye weed and other flowering plants.

Damage

Corn earworm is considered by some to be the most costly crop pest in North America. It is more damaging in areas where it successfully overwinters, however, because in northern areas it may arrive too late to inflict extensive damage. It often attacks valuable crops, and the harvested portion of the crop. Thus, larvae often are found associated with such plant structures as blossoms, buds, and fruits. When feeding on lettuce, larvae may burrow into the head. On corn, its most common host, young larvae tend to feed on silks initially, and interfere with pollination, but eventually they usually gain access to the kernels. They may feed only at the tip, or injury may extend half the length of the ear before larval development is completed. Such feeding also enhances development of plant pathogenic fungi. If the ears have not yet produced silk, larvae may burrow directly into the ear. They usually remain feeding within a single ear of corn, but occasionally abandon the feeding site and search for another. Larvae also can damage whorl-stage corn by feeding on the young, developing leaf tissue. Survival is better on more advanced stages of development, however. On tomato, larvae may feed on foliage and burrow in the stem, but most feeding occurs on the tomato fruit. Larvae commonly begin to burrow into a fruit, feed only for a short time, and then move on to attack another fruit. Tomato is more susceptible to injury when corn is not silking; in the presence of corn, moths will preferentially oviposit on fresh corn silk. Other crops such as bean, cantaloupe, cucumber, squash, and pumpkin may be injured in a manner similar to tomato, and also are less likely to be injured if silking corn is nearby.

Natural Enemies

Although numerous natural enemies have been identified, they usually are not effective at causing high levels of earworm mortality or preventing crop injury. For example, in a study conducted in Texas, <1% of the larvae were parasitized or infected with disease. However, eggs may be heavily parasitized. *Trichogramma* spp. (Hymenoptera: Trichogrammatidae), and to a lesser degree *Telenomus* spp. (Hymenoptera: Scelionidae), are common egg parasitoids. Common larval parasitoids include *Cotesia* spp., and *Microplitis croceipes* (Cresson) (all Hymenoptera: Braconidae); *Campoletis* spp. (Hymenoptera: Ichneumonidae); *Eucelatoria armigera* (Coquillett) and *Archytas marmoratus* (Townsend) (Diptera: Tachinidae). General predators often feed on eggs and larvae of corn earworm; over 100 insect species have been observed to feed on *H. zea*. Within-season mortality during the pupal stage seems to be important, and although overwintering mortality is often very high, the mortality is due to adverse weather and collapse of emergence tunnels rather than to natural enemies. In Texas, *Steinernema riobravis* (Nematoda: Steinernematidae) has been found to be an important mortality factor of prepupae and pupae, but this parasitoid is not yet generally distributed.

Epizootics caused by pathogens may erupt when larval densities are high. The fungal pathogen *Nomuraea rileyi* and the *Helicoverpa zea* nuclear polyhedrosis virus are commonly involved in outbreaks of disease, but the protozoan *Nosema heliothidis* and other fungi and viruses also have been observed.

Management

Sampling

Eggs and larvae often are not sampled on corn because eggs are very difficult to detect, and larvae burrow down into the silks, out of the reach of insecticides, soon after hatching Moths can be monitored with blacklight and pheromone traps. Both sexes are captured in light traps whereas only males are attracted to the sex pheromone. Both trap types give an estimate of when moths invade or emerge, and relative densities, but pheromone traps are easier to use because they are selective. The pheromone is usually used in conjunction with an inverted cone-type trap. Generally, the presence of five to ten moths per night is sufficient to stimulate pest control practices.

Insecticides

Corn fields with more than 5% of the plants bearing new silk are susceptible to injury if moths are active. Insecticides are usually applied to foliage in a liquid formulation, with particular attention to the ear zone, because it is important to apply insecticide to the silk. Insecticide applications are often made at 2–6 day intervals, sometimes as frequently as daily. Because it is treated frequently, and over a wide geographic area, corn earworm has become resistant to many insecticides. Susceptibility to *Bacillus thuringiensis* also varies, but the basis for this variation in susceptibility is uncertain. Mineral oil, applied to the corn silk soon after pollination, has insecticidal effects. Application of about 0.75–1.0 ml of oil 5–7 days after silking can provide good control in the home garden. Trap cropping is often suggested for this insect; the high degree of preference by ovipositing moths for corn in the green silk stage can be used to lure moths from less preferred crops. Lima beans also are relatively attractive to moths, at least as compared to tomato. However, it is difficult to maintain attractant crops in an attractive stage for protracted periods. In southern areas where populations develop first on weed hosts and then disperse to crops, treatment of the weeds through mowing, herbicides, or application of insecticides can greatly ameliorate damage on nearby crops. In northern areas, it is sometimes possible to plant or harvest early enough to escape injury. Throughout the range of this insect, population densities are highest, and most damaging, late in the growing season. Tillage, especially in the autumn, can significantly reduce overwintering success of pupae in southern locations.

Biological Control

The bacterium *Bacillus thuringiensis*, and steinernematid nematodes provide some suppression. Entomopathogenic nematodes, which are available commercially, provide good suppression of developing larvae if they are applied to corn silk; this has application for home garden production of corn if not commercial production. Soil surface and subsurface applications of nematodes also can affect earworm populations because larvae drop to the soil to pupate. This approach may have application for commercial crop protection, but larvae must complete their development before they are killed, so some crop damage ensues. Trichogramma spp. (Hymenoptera: Trichogrammatidae) egg parasitoids have been reared and released for suppression of H. zea in several crops. Levels of parasitism averaging 40–80% have been attained by such releases in California and Florida, resulting in fruit damage levels of about 3%.

Host Plant Resistance

Numerous varieties of corn have been evaluated for resistance to earworm, and some resistance has been identified in commercially available corn. Resistance is derived from physical characteristics such as husk tightness and ear length, which impede access by larvae to the ear kernels, or chemical factors such as maysin, which inhibit larval growth. Host plant resistance thus far is not completely adequate to protect corn from earworm injury, but it may prove to be a valuable component of multifaceted pest management programs.

► Vegetable Pests and Their Management
► Maize (Corn) Pests and their Management

References

Archer TL, Bynum ED Jr (1994) Corn earworm (Lepidoptera: Noctuidae) biology on food corn on the high plains. Environ Entomol 23:343–348

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, CA, 729 pp

Harding JA (1976) *Heliothis* spp.: seasonal occurrence, hosts and host importance in the lower Rio Grande Valley. Environ Entomol 5:666–668

Hardwick DF (1965b) The corn earworm complex. Entomological Society of Canada Memoir 40, 246 pp

Neunzig HH (1964) The eggs and early-instar larvae of *Heliothis zea* and *Heliothis virescens* (Lepidoptera: Noctuidae). Ann Entomol Soc Am 57:98–102

Oatman ER, Platner GR (1971) Biological control of the tomato fruitworm, cabbage looper, and hornworms on processing tomatoes in southern California, using mass releases of *Trichogramma pretiosum*. J Econ Entomol 64:501–506

Cornicles

Two tubular structures located on the posterior part (fifth or sixth abdominal segment) of an aphid's abdomen. They vary greatly in structure, and are the source of aphid alarm pheromone. They are also called siphunculi.

► Abdomen of Hexapods
► Aphids

Corn Leaf Aphid, *Rhopalosiphum maidis* (Fitch) (Hemiptera: Aphididae)

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This species may be of Asiatic origin, but now has a world-wide distribution in temperate areas. However, corn leaf aphid does not persist in areas with severe winters, so it dies out from cold areas such as most of Canada, and northern Europe and Asia, and re-invades large areas of temperate regions annually.

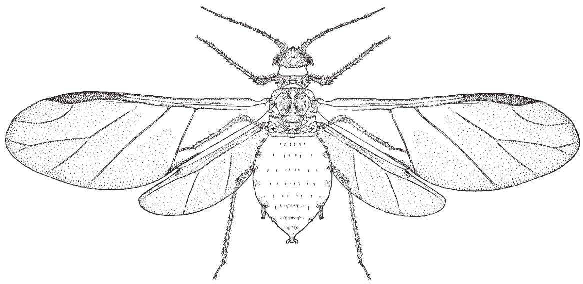
Life History

This species overwinters as viviparous females (displaying parthenogenetic reproduction) in warm winter areas (such as the southern USA). During mild winters, there is evidence that such overwintering may occur in moderately cold winter regions, too (such as the mid-western USA). Overwintering does not occur in cold winter areas (such as most of Canada). Oviparous (egg producing) forms and males are rare, though in Pakistan, eggs overwinter on *Prunus* sp. The northern areas of North America and southern Canada are thought to be invaded annually, with the timing of invasion and the number of subsequent generations in an area a function of weather. The short life cycle of this aphid, normally 6–12 days, allows production of 20–40 generations per year in such southern locations as Texas and about nine generations in Illinois, but fewer further north.

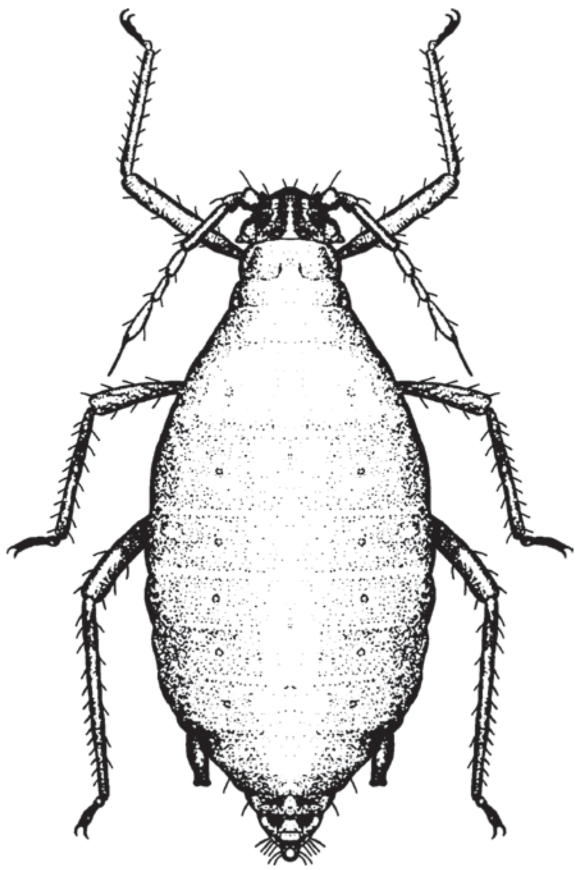
There are 4 instars. The young nymph initially is pea green in color, with red eyes and colorless antennae and legs, and measures about 0.5 mm long. Body length increases to about 0.9, 1.1, and 1.3 mm, the green body color becomes darker, and the appendages gain some dark pigmentation as the nymph progresses through instars 2–4. Mean development times are 4.5, 4.5, 4.5, and 4.7 days, respectively, for instars 1–4 among nymphs destined to grow into apterae, when cultured at 11°C. The corresponding development times for 19 and 29°C are 1.7, 1.8, 1.7, and 1.9 days; and 1.2, 1.2, 1.5, and 1.7 days, respectively. Development times for alatae are quite similar, except that instar 4 tends to require an additional day.

The viviparous females generally are bluish green, although they become darker with time, some becoming almost black. Fine white powder covers the entire body. The winged form (alatae) has a black thorax and head, whereas in the wingless form (apterae) only the head is black (Figs. 112 and 113). The winged form also tends to bear three black spots laterally on the abdomen, and the base of the cornicles is enveloped in a small area of purple or black color. In both female forms the appendages are black. The alatae measure about 1.7 mm long, the apterae about 2.4 mm. The adult male aphid measures about 1.5 mm long. The head, thorax, and legs are black. The abdomen is dark bluish green, with a dark spot laterally on each segment.

Corn leaf aphid feeds on numerous grasses in addition to corn, and is considered to be a serious pest of cereal grains due to its ability to transmit virus diseases. The crops fed upon, in addition to corn, include barley, chufa, oat, rye, millet, sorghum, Sudan grass, and sugarcane. Barley is the



Corn Leaf Aphid, *Rhopalosiphum maidis* (Fitch) (Hemiptera: Aphididae), Figure 112 **Winged female corn leaf aphid, *Rhopalosiphum maidis* (Fitch).**



Corn Leaf Aphid, *Rhopalosiphum maidis* (Fitch) (Hemiptera: Aphididae), Figure 113 **Wingless female corn leaf aphid, *Rhopalosiphum maidis* (Fitch).**

most important early season host. While the leaf blades are rolled, aphid colonies develop within the furled barley leaves. However, once the corn is about 30 days old it also becomes very suitable for aphids; the tassels forming within the furled leaves are particularly suitable for aphid population growth. As the tassel extends, aphids disperse over the entire plant to feed.

Among weeds and prairie grasses known to serve as hosts are barnyardgrass, *Echinochloa crus-galli*; buffalo grass, *Buchloe dactyloides*; crabgrass, *Digitaria sanguinalis*; foxtail, *Setaria* spp.; grama grass, *Bouteloua* spp.; and Johnson grass, *Sorghum halepense*.

These aphids feed on exposed areas of the plant and often are subject to significant levels of predation and parasitism. Numerous species of ladybird beetles attack corn leaf aphid. Despite their abundance, however, the ladybird beetles generally are numerous and effective predators only after the aphid populations attain high and damaging densities. Other common predators include various flower flies (Diptera: Syrphidae), predatory midges (Diptera: Cecidomyiidae), minute pirate bugs (Hemiptera: Anthocoridae), and lacewings (Neuroptera: Chrysopidae).

Several wasps parasitize corn leaf aphid. *Lysiphlebus testaceipes* (Cresson) (Hymenoptera: Braconidae) is the most widespread and common parasitoid, but *Aphelinus varipes* (Foerster) (Hymenoptera: Aphelinidae) is an important parasitoid in Texas. Other parasitoids include *Diaeretiella rapae* (M'Intosh) and *Ephedrus persicae* (Froggatt) (both Homoptera: Aphidiidae) and *Aphelinus asychis* Walker (Hymenoptera: Encyrtidae).

Damage

Corn leaf aphid is commonly found feeding on the tassel and silk of the corn plant in addition to the leaves. It interferes with pollen production and fertilization, resulting in poor kernel fill of the ears. Infestation also can cause a delay in plant maturity, and reduced plant size. Honeydew secreted by the aphids supports growth of sooty mold fungus, causing an unsightly appearance of the ears and interfering with photosynthesis in small grains. In general, crop plants are very tolerant of aphids, and only extremely dense infestations cause injury. If soil moisture conditions are inadequate, however, then the damage by the aphids is increased, and yield reductions are more likely.

The ability to transmit plant viruses greatly exacerbates the damage potential of this aphid. Several diseases, including barley yellow dwarf, beet yellows, cucumber mosaic, lettuce mosaic, maize streak, maize dwarf mosaic, and maize stripe are transmitted. Even in crops not successfully colonized by the aphids, corn leaf aphid is implicated in the transmission of numerous stylet-borne viruses.

Management

Sampling for corn leaf aphids on young leaf tissue is usually done by visual examination of the whorls. As the aphids disperse from the whorls, they are readily apparent on other plant structures. As populations increase and honeydew accumulates, remote detection of aphid populations is possible by examination of photographs taken by aircraft using infrared-sensitive film; sooty mold growing on honeydew impedes the reflectance of infrared radiation. It is advisable to monitor populations in barley early in the season, as incidence in this favored crop may reflect potential incidence in corn later in the season. Populations of alate aphids may be monitored with yellow water pan traps or sticky traps, though aphids collected on sticky traps are often damaged and difficult to identify.

Systemic insecticides applied to the young plants or to the soil soon after plant emergence from the soil are particularly effective at controlling aphids. They may be killed by contact insecticides as well, though the increase in crop yield does not justify spraying on some low value grain crops.

Early plantings can escape injury, especially in northern areas where aphids do not overwinter. In New York, for example, corn planted before June 10 escape injury by corn leaf aphid and maize dwarf virus, but incidence of aphids and disease increase thereafter. Little work on the management of corn leaf aphid as a virus vector has been reported, other than the assessment of corn varieties for resistance.

► Maize (Corn) Pests and their Management

References

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, CA, 729 pp

Kring TJ (1985) Key and diagnosis of the instars of the corn leaf aphid *Rhopalosiphum maidis* (Fitch). Southwest Entomol 10:289293.

Straub RW (1984) Maize dwarf mosaic virus: symptomatology and yield reactions of susceptible and resistant sweet corns. Environ Entomol 13:318–323

Straub RW, Boothroyd CW (1980) Relationship of corn leaf aphid and maize dwarf mosaic disease to sweet corn yields in southeastern New York. J Econ Entomol 73:92–95

Wildermuth VL, Walter EV (1932) Biology and control of the corn leaf aphid with special reference to the southwestern states. USDA Technical Bulletin 306, 21 pp

Corn Leafhopper, *Dalbulus maidis* (Delong and Wolcott) (Hemiptera: Cicadellidae)

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The corn leafhopper, *Dalbulus maidis* (Delong and Wolcott) is found only in subtropical and tropical areas of America. Its host range is limited to maize and its relatives.

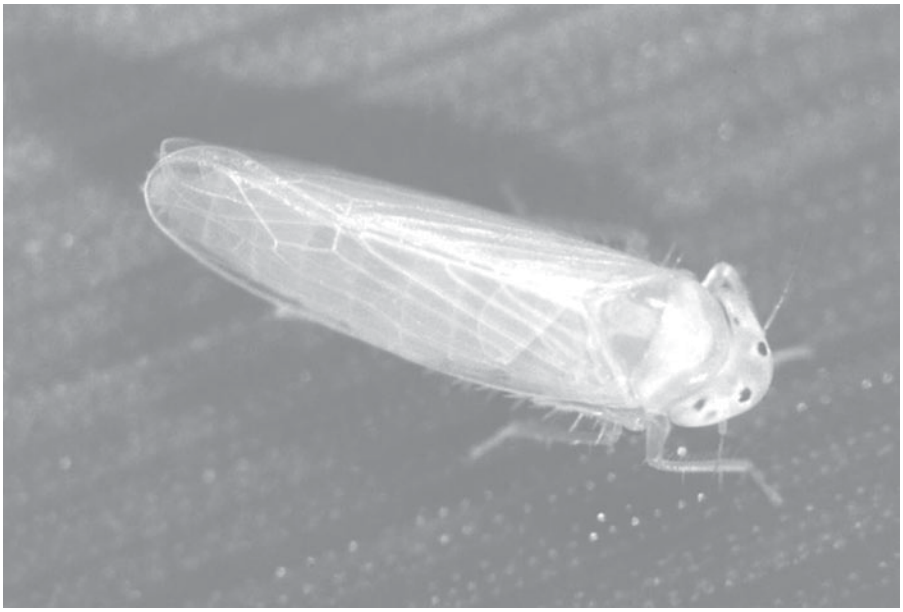
Maize (*Zea mays* L.) is one of the major cereal crops; it ranks third in production following wheat and rice with an average of 380 million tons produced annually on 120 million ha by 53 countries. It is the world's most widely grown crop in almost all tropical areas of the world including tropical highlands over 3,000 m in altitude, to temperate areas as far north as the 65th latitude. In tropical and subtropical areas of America, maize is often infected with at least three serious phytoplasmal and viral agents. They are known as corn stunt spiroplasma (CSS), maize bushy stunt phytoplasma

(MBP) and maize rayado fino virus (MRFV). These three pathogens are all transmitted by *D. maidis* in a persistent manner. However, the former two pathogens are known to multiply in the *D. maidis*. In Florida, corn plants often have been infected by any two of these pathogens. Occasionally, multiple pathogens can be found in the same corn plants in the field. CSS can be acquired by *D. maidis* in 15 min. All these pathogens require a protracted incubation period in the vector, ranging from 14 to 21 days, depending upon the isolate and titre of pathogen, and biotype and age of vector.

The life cycle of *D. maidis* varies with temperature and host plant. In general, nymphs undergo five instars; an additional instar is often noted. The average developmental times for first through fifth instars range from 12 to 34 days at 10°C, 6 to 13 days at 16°C, 3 to 4 days at 27°C and 2 to 4 days at 32°C. The adult (Fig. 114) longevity averages 67 days for males and 38 days for females at 10°C, 107 days for males and 52 days for females at 16°C, 78 days for males and 30 days for females at 27°C, and 16 days for males and 10 days for females at 32°C. There is a minimum of one day preoviposition period, and it is affected by rearing temperature. The number of eggs oviposited per day per female averages 4 eggs at 16°C, and 15 eggs at 27°C. The number of eggs laid per female per life averages 402 eggs at 16°C and 611 eggs at 27°C.

Other plants such as *Tripsacum dactyloides* L., *Tripsacum* sp., *Rottboellia exaltata* L., *Secale cerale* L., and *Avena sativa* L. can be used as temporary feeding hosts, but not for rearing hosts. Besides corn, *T. dactyloides* var. *meridonale* is suitable for continuous rearing of *D. maidis*. Eggs are mainly deposited in the mesophyll tissue of the midrib. The egg is elongate, and curved with a round posterior end. The average size of egg measures 1.04 mm long and 0.25 mm wide. Young nymphs often are found aggregating more on leaves than stems. The average size of instar I through V measures 0.87 mm long and 0.27 wide, 1.14 mm long and 0.37 mm wide, 1.69 mm long and 0.49 mm wide, 2.14 mm long and 0.62 mm wide, 2.82 mm long and 0.81 mm wide, respectively. The average size of male and female measures 2.80 mm long and 0.81 mm wide, and 3.18 mm long and 0.88 mm wide, respectively. *D. maidis* can be controlled by the use of pesticides that are commonly used for control of lepidopteran pests of corn.

► Maize (Corn) Pests and their Management



Corn Leafhopper, *Dalbulus maidis* (Delong and Wolcott) (Hemiptera: Cicadellidae), Figure 114 **Adult corn leafhopper, *Dalbulus maidis* (photo J. Tsai).**

References

Falk BW, Tsai JH (1998) Biology and molecular biology of viruses in the Genus *Tenuivirus*. Ann Rev Phytopathol 36:139–163

Nault LR, Bradfute OE (1979) Corn stunt: involvement of a complex of leafhopper-borne pathogens. In: Maramorosch K, Harris KF (eds) Leafhopper vectors and plant disease agents. Academic Press, New York, NY, pp 561–586

Tsai JH (1987a) Bionomics of *Dalbulus maidis* (DeLong and Wolcott). A vector of mollcutes and virus (Homoptera: Cicadellidae). In: Maramorosch K, Raychaudhuri SP (eds) Mycoplasma diseases of crops: basic and applied aspects. Springer-Verlag, New York, NY, pp 209–221

Tsai JH (1987b) Mycoplasma diseases of corn in Florida. In: Maramorosch K, Raychaudhuri SP (eds) Mycoplasma diseases of crops: basic and applied aspects. Springer-Verlag, New York, NY, pp 317–325

Tsai JH, Falk BW (1988) Tropical corn pathogens and their associated vectors. In: Harris KF (ed) Advances in disease vector research. Springer-Verlag, New York, NY, pp 177–201

Tsai JH, Steinberg B, Falk BW (1990) Effectiveness and residual effects of seven insecticides on *Dalbulus maidis* (Homoptera: Cicadellidae) and *Peregrinus maidis* (Homoptera: Delphacidae). J Entomol Sci 25:106–111

Corn Stunt

A disease transmitted by leafhoppers to maize (corn).

► Transmission of Plant Diseases by Insects
► Corn Leafhopper, *Dalbulus maidis*

Corpora Pedunculata

The mushroom bodies of the brain. These are large bilateral integrative centers located in the protocerebrum. They are thought to function in olfactory learning.

► Nervous System

Corpus Allatum (pl., Corpora Allata)

Small endocrine glands behind the brain (Fig. 115), with nervous connections to the brain, and the source of juvenile hormone.

► Endocrine Regulation of Insect Reproduction
► Juvenile Hormone
► Reproduction
► Corpus Cardiacum
► Nervous System

Corpus Cardiacum (pl., Corpus Cardiaca)

Small organs between the corpus allata (Fig. 115) that releases PTTH to the hemolymph.

► Endocrine Regulation of Insect Reproduction
► Reproduction
► Corpus Allatum
► Nervous System

Corpus Pendunculatum

A portion of the protocerebral region of the brain, also called "mushroom bodies." The size of the corpus pendunculatum is correlated with the occurrence of complex behaviors in insects, and seems best developed in social insects.

► Nervous System
► Learning in Insects
► Learning in Insects: Neurochemistry and Localization of Brain Functions

Corydalidae

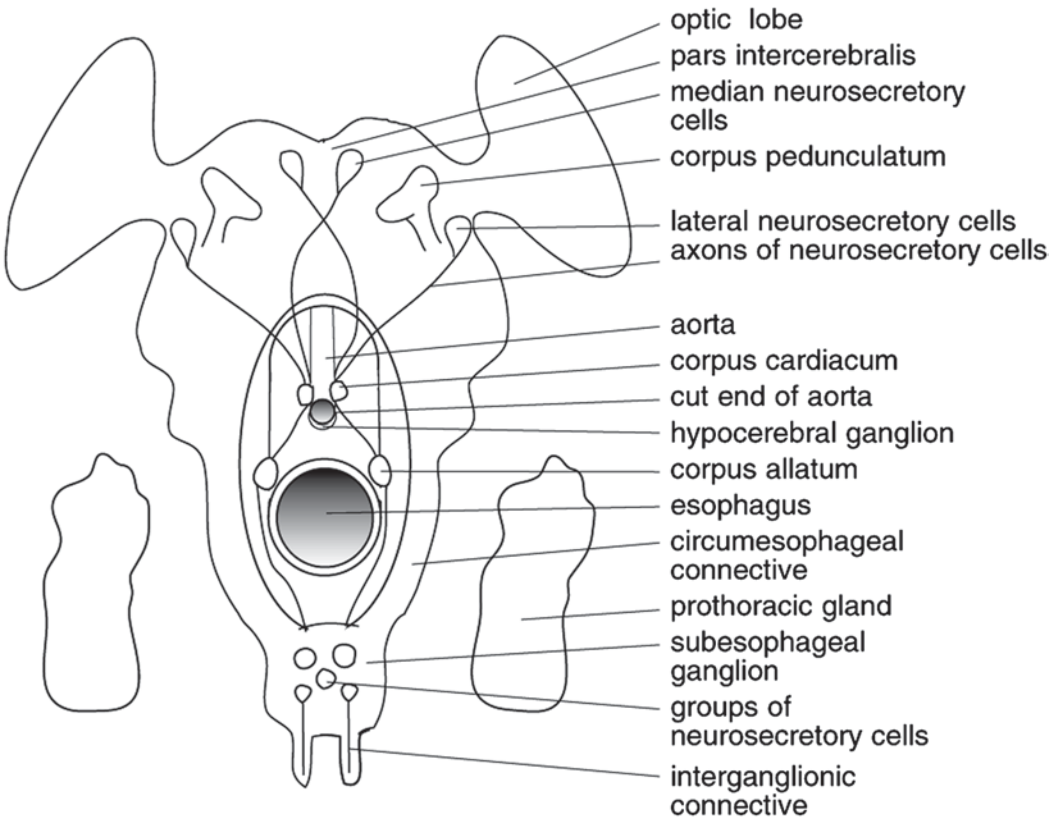
A family of insects in the order Megaloptera. They commonly are known as dobsonflies and fishflies.

► Alderflies and Dobsonflies

Corylophidae

A family of beetles (order Coleoptera). They commonly are known as minute fungus beetles.

► Beetles



Corpus Allatum (pl., Corpora Allata), Figure 115 Cross section showing the relationships of the principal endocrine glands with the brain (adapted from Chapman, The insects: structure and function).

Cosmetic Damage

Superficial injury that affects the appearance, and hence the value of a crop, though leaving the quantity and nutritional value unaffected.

Cosmet Moths (Lepidoptera: Cosmopterigidae)

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Cosmet moths, family Cosmopterigidae, total over 1,540 species worldwide, but the extant fauna may encompass 3,500 species. Three subfamilies are used: Antequerinae, Cosmopteriginae, and Chrysopeleiinae. The family is part of the superfamily Gelechioidea in the section Tineina, subsection Tineina, of the division Ditrysia. Adults small (6–32 mm wingspan), with head smooth-scaled; haustellum scaled; labial palpi recurved; maxillary palpi 4-segmented. Wings very linear and with long fringes on hindwings. Maculation varies greatly (Fig. 116) but many have various spots or lines, often with metallic-iridescence. Adults mostly diurnal, but some are crepuscular. Larvae mostly leafminers or needleminers, but some are borers of various plant parts; a few are predaceous on Hemiptera. Hosts are varied but many records are for Leguminosae. Ovovivipary has been recorded in a few species. Some economic species are known.

Cosmet Moths (Lepidoptera: Cosmopterigidae), Figure 116 Example of cosmet moths (Cosmopterigidae), *Ithome concolorella* (Chambers) from Florida USA.

References

Clarke JFG (1965) Cosmopterigidae. In: Clarke JFG (ed) Catalogue of the type specimens of Microlepidoptera in the British Museum (Natural History) described by Edward Meyrick, 5:471–559. British Museum (Natural Hisory), London

Hodges RW (1978) Gelechioidea. Cosmopterigidae. In: Dominick RB (eds) The moths of America north of Mexico including Greenland. Fasc. 6.1. E. W. Classey, London, 166 pp, 6 pl

Mariani M (1935) Monografie sulle Cosmopteryx d' Europa. Giornale del Sciencia Naturale Economica Palermo 38:1–54 (1934)

Riedl T (1962–69) Matériaux pour la connaissance des Momphidae (Lepidoptera) paléarctiques. Polski Pismo Entomologica, 32:69–75 (1962); 33:101–106 (1963); 35:419–468 (1965); 36:75–84 (1966); (B) 1–2:115–118 (1966); 37:25–46 (1967); 39:635–923 (1969) [mostly Cosmopterigidae]

Cosmopolitan

Distributed throughout the world, or nearly so.

Cossidae

A family of moths (order Lepidoptera). They commonly are known as carpenterworm moths, goat moths, and leopard moths.

► Carpenterworm Moths
► Butterflies and Moths

Costa

The basal segment of the leg, articulating with the body. Also the thickened anterior-most vein that forms the anterior margin of the wing.

► Legs of Hexapods

Costal Break

A section of the costal vein where the sclerotization is weak or absent, and the vein appears to be broken.

► Wings of Insects

Costal Cell

The wing space between the costal and subcostal veins.

► Wings of Insects

Costal Margin

The anterior margin (Fig. 117) of the wing.

► Wings of Insects

Costs and Benefits of Insects

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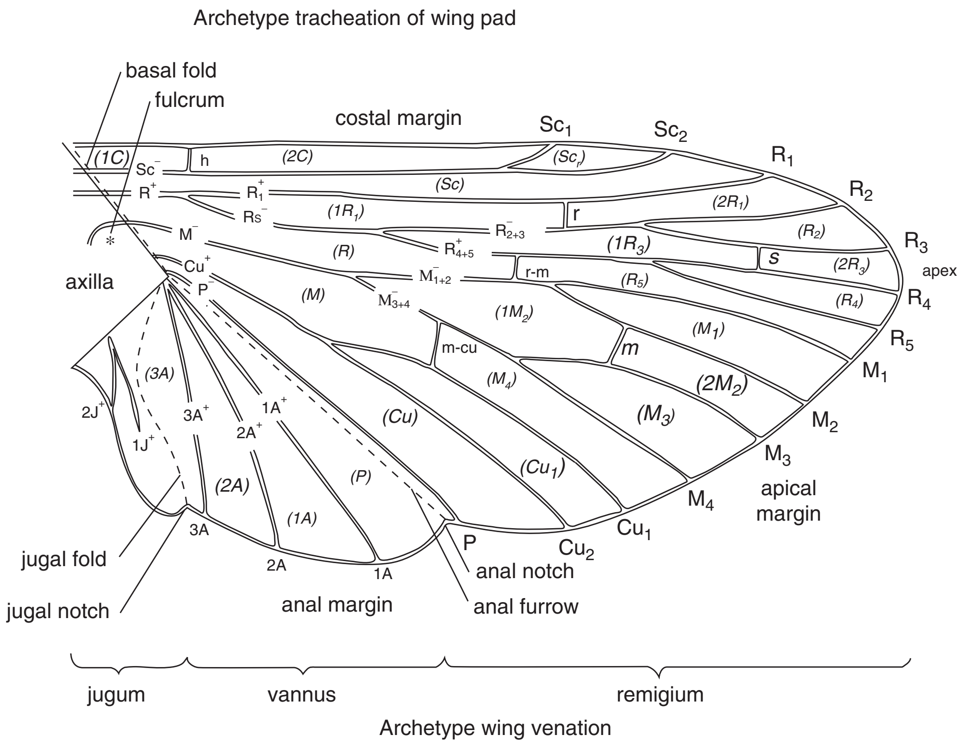
Insects (arthropods) have a well-deserved reputation for significant economic and ecological effects, but there tends to be over-emphasis on negative effects and under-emphasis on beneficial effects. The emphasis on negative effects results from well-known insect competition with humans for food and fiber resources, and the role of insects in transmitting diseases to humans, domesticated and wild animals, and to crop and forest plants. The negative effects of insects are due not only to their direct damage (usually by feeding) and indirect



Costal Margin, Figure 117 **Hypothetical ancestral pattern of wing venation.**

effects (often by transmission of plant and animal diseases), but by the costs of preventing or reducing damage (Table 21). There is a rich literature purporting to provide documentation of losses attributable to pests, though some of it has been challenged. In contrast, the beneficial effects are less well documented. In part, there has not been much incentive to document the beneficial effects of insects. However, the under-appreciation of insects is also due to the difficulty in assigning monetary value to the benefits derived from insect pollination (next to items of commerce such as silk and honey, probably the best-documented benefit), the decomposition of plant materials and animal dung, the biological suppression of pest insects and weeds, and the role of insects in recreation, or as food for fish and other wildlife. The benefits of insects as food for humans, and in production of silk, shellac, and pigments is worth mentioning, but small in comparison to some other benefits.

The Negative Effects of Insects on Crops and Livestock

Yield Loss

The reduction in crop yields and costs of preventing damage attributable to insects are notoriously difficult to obtain. Even in the USA, where considerable efforts to estimate loss have been made, there is considerable variation among loss estimates, and concern about their reliability. Studies of the major crops conducted in the USA indicate that without insecticides, 50% or more of the major crops could be lost to insects. Generally, crop losses in the USA due to insect and mite pests (with pest control practices) are estimated to be 13–15%, a value of perhaps $35 billion annually (1998 estimate). In developing countries, however, losses are greater, usually 20–30% of preharvest yield, and then additional losses during storage. The cost of pesticides for prevention of crop

Costs and Benefits of Insects, Table 21 **Losses associated with some nonindigenous pests in the USA (adapted from Pimentel et al. 2000). NA signifies information not available**

Type of organism	Losses ($ millions)	Control costs ($ millions)	Total costs ($ millions)
Plants			
Purple loosestrife	NA	45	45
Aquatic weeds	10	100	110
Melaleuca tree	NA	3–6	3–6
Crop weeds	23,400	3,000	26,400
Pasture weeds	1,000	5,000	6,000
Turfgrass weeds	NA	1,500	1,500
Mammals			
Wild horses and burros	5	NA	5
Feral pigs	800	0.5	800.55
Mongooses	50	NA	50
Rats	19,000	NA	19,000
Cats	17,000	NA	17,000
Dogs	250	NA	250
Birds			
Pigeons	1,100	NA	1,100
Starlings	800	NA	800
Reptiles and amphibians			
Brown tree snake	1	4.6	5.6
Fishes	1,000	NA	1,000
Arthropods			
Imported fire ant	600	400	1,000
Formosan termite	1,000	NA	1,000
Green crab	44	NA	44
Gypsy moth	NA	11	11
Crop pests	13,900	500	14,400
Turfgrass pests	NA	1,500	1,500
Forest pests	2,100	NA	2,100
Molluscs			
Zebra mussel	NA	NA	100
Asian clam	1,000	NA	1,000
Shipworm	205	NA	205
Microbes			
Crop plant pathogens	21,000	500	21,500
Turfgrass pathogens	NA	2,000	2,000
Forest plant pathogens	2,100	NA	2,100

Costs and Benefits of Insects, Table 21 **Losses associated with some nonindigenous pests in the USA (adapted from Pimentel et al. 2000). NA signifies information not available (Continued)**

Type of organism	Losses ($ millions)	Control costs ($ millions)	Total costs ($ millions)
Dutch elm disease	NA	100	100
Livestock disease	9,000	NA	9,000
Human disease	NA	6,500	6,500
All organisms			136,630

damage in the USA is estimated at $3 billion annually (2003 estimate). Because about 40% of pests are nonindigenous, their contribution to the loss is estimated at about $15 billion. However, nonindigenous pests are more likely to be serious pests than are indigenous species, so this is likely an underestimate of the effects of invaders. Also, considerable effort is directed to preventing movement of pests from country to country, and in eliminating (eradicating) or suppressing newly arrived pests, so these costs should be added to the losses associated with nonindigenous species. The losses to livestock are estimated to total an additional $9 billion annually.

Nonindigenous (Invasive) Pests

The monetary cost of only the nonindigenous insect pests affecting the USA was estimated in 2000 to total about 15% of the total cost of nonindigenous organisms. The effects of nonindigenous weeds, mammals, and plant pathogens were each estimated to be greater than the effects of insects, but insects reportedly accounted for more loss than birds, reptiles and amphibians, fishes, molluscs, livestock diseases, and human diseases. Monetary loss due to nonindigenous arthropods is considered to be about $16 billion in both the USA and in India, and is variously considered to represent 40–60% of the losses due to arthropods. Sometimes the damage attributable to nonindigenous species is partitioned according to proportions of indigenous and nonindigenous species in the pest species assemblage. This approach has been used, but it likely underestimates the effects of nonindigenous species, which often account for disproportionately large amounts of damage. For example, of the total crop losses attributable to arthropods in three states of the USA, Hawaii, Florida and California, the proportions due to nonindigenous species are estimated to be 98, 95, and 67%, respectively, much higher than the proportions of species that are nonindigenous.

The effects of nonindigenous insects are much greater than the simple monetary loss. For example, the woolly adelgid, *Adelges piceae* (Ratzeburg) (Hemiptera: Adelgidae), has killed about 90% of Fraser fir (*Abies fraseri*) trees in the southern Appalachian Mountains, disrupting local ecosystems and leading to local shifts in avifauna. In New England, the occurrence of gypsy moth defoliation in oak-dominated forests is apparently contributing to the decline in abundance of Saturniidae and other large summer moths, although it is debatable whether the decline is due to loss of favored food, enhanced abundance of generalist parasitoids, or nontarget effects of gypsy moth suppression. Although biodiversity is obviously affected, it is not possible to affix a monetary value to these changes.

Pesticides

An important negative effect of pests is the cost of preventing their damage. These costs include the economic, environmental, and health effects of pesticides. The world market for pesticides is estimated at about $31 billion (2005 estimate). The

USA is the biggest market, both in terms of costs (33%) and amount of active ingredients applied (22%). After North America, the next biggest consumer of pesticides is Southeast Asia, followed by Europe, South America, and finally Africa and the Middle East. However, herbicides are used more extensively than insecticides. The use of insecticides, as measured by amount of active ingredient, is about 20% of all pesticide use. In North America, insecticide use in agriculture has been decreasing for some time due to both the shift to products that are effective at lower rates of application, and the recognition that overuse of insecticides has many detrimental effects. In many other areas of the world, however, insecticide use continues to increase. The cost of insecticides used worldwide is $7.7 billion (2005 estimate), about 25% of the cost of all pesticides. For comparison, the cost of other pesticides (in $ billions) is herbicides, 14.8; fungicides, 7.5; and other, 1.1. Nearly everywhere, the agricultural sector is the principal consumer of pesticides. In the USA, for example, agriculture uses about 77% of the pesticides applied, whereas the urban pest control industry (structural, building interiors, and landscape) and government use about 14%, and consumer use (self-applied home and garden) is only about 9%.

The Negative Effects of Insects on Wildlife

Biting and Stinging

Insects can be detrimental to wildlife due to direct effects (biting, stinging, disease transmission) or indirect effects (nontarget effects of insecticides). Blood feeding by mosquitoes (Diptera: Culicidae), deer flies (Diptera: Tabanidae), ticks (Acarina: Ixodida) and other wildlife parasites undoubtedly causes considerable annoyance, and sometimes determines suitability of habitat or affects feeding behavior. For example, birds have been known to abandon their nests and fledglings due to the abundance of blood-feeding ticks or mites, and many ticks can cause paralysis of mammals. Predation of ground-nesting bird nestlings, sea turtle eggs, and other small wildlife by red imported fire ant, Solenopsis invicta Buren, is of considerable concern in the southeastern USA, as is predation by Argentine ant, *Linepithema humile* (Mayr) (formerly *Iridomyrmex humilis* Mayr), on the west coast of the USA.

Disease Transmission

Of particular importance to wildlife is the transmission of diseases by arthropods. Eastern equine encephalitis is an example of a common wildlife disease transmitted by mosquitoes. Found in eastern North America and south to Argentina and Peru, the disease is due to a virus that is harbored most commonly in passerine and other perching birds, which serve as the amplification hosts. Mosquitoes feeding on these birds when they are viremic obtain high concentrations of virus in the ingested blood, and in turn become infected. Upon feeding on other birds, the mosquitoes transmit the disease. Wildlife differ greatly in susceptibility. Nonindigenous species such as pheasants, chukar partridge, and pigeon are most susceptible, but an endangered native bird, whooping crane, readily succumbs to the disease. Symptoms of infection can include lethargy and lack of coordination; surely such animals are more susceptible to predation even if they survive infection. Other examples of diseases affecting wildlife include tularemia (rabbit fever) caused by *Francisella tularensis*, which is transmitted by tick and insect bites and infects over 100 species of mammals and 25 species of birds; bubonic plague caused by *Yersinia pestis*, which is transmitted by fleas to rodents, rabbits and other mammals; Lyme disease caused by *Borrelia burgdorferi*, which is transmitted by *Ixodes* ticks to deer, mice, bats, squirrels, weasels, and others, including reptiles and birds; and West Nile virus caused by a flavivirus, and which is transmitted by mosquitoes to 250 species of birds and 18 species of mammals.

Pesticides

Insects can be considered detrimental to wildlife by virtue of stimulating use of insecticides; exposure to pesticides can be deleterious to all wildlife, but particularly to birds. A simple example is the presence of seed-feeding flies, *Delia* spp. (Anthomyiidae), which damage crop seeds planted in the spring. To prevent damage by insects while the seed is germinating, coatings containing insecticides are commonly applied to seeds before they are planted. Seed treatment with insecticides (and often fungicides) not only protects the germinating seed, but if the insecticide acts systemically it may also impart protection to young plants, particularly from piercing-sucking insects such as aphids. Unfortunately, birds will often feed on seeds that have been recently planted, and thereby ingest a lethal dose of insecticide. Another problem results from broadcast application of granular insecticides to the soil surface. Probably because sand is sometimes consumed by birds to aid in grinding up seeds, birds sometimes feed on granular insecticide, again resulting in bird mortality. Lastly, application of liquid insecticides sometimes results in a lethal dose of insecticide being applied directly to wildlife. Though this seems unlikely, when aircraft are used to apply insecticides, extensive land area is treated quickly and wildlife may not have adequate time to escape. Not only are crop fields treated, but often adjacent border areas (hedge rows, fence rows, irrigation ditches, road margins) are treated deliberately or inadvertently. In the case of nestling birds, there is no opportunity to avoid exposure. There is also a problem with birds flying into fields that were recently treated, perhaps to feast on dying insecticide-containing insects, thereby ingesting a lethal dose of insecticide. Other vertebrates are not immune to such poisoning, but it is most pronounced in avifauna and fish. The United States Fish and Wildlife Service estimates that over 670 million birds are exposed to pesticide on farmlands in the USA, and that about 10% die immediately as a result. This does not include those that are sickened and die later, or eggs left unhatched or nestlings left to starve. Organophosphate and carbamate insecticides are most commonly implicated.

The use of persistent lipophilic insecticides, which tend to accumulate in animals that are higher on the food chain, has long been known to affect hatching success in predatory birds (raptors). The widespread use of DDT, in particular, was linked to production of abnormally thin egg shells and subsequent declines in successful raptor reproduction. DDT and related products interfere with calcium metabolism. Less well known, but not at all surprising, are the effects of DDT and dicofol on alligators. Male alligators living in Lake Apopka, Florida, have low testosterone levels. Lake Apopka was the site of a DDT and dicofol (which is closely related to DDT) spill, and the insecticides had estrogen-like effects, resulting in feminization of the males. The penises of male alligators were 25% smaller, bone density was affected in females, and egg hatching was reduced. Alligator numbers plummeted in the years after the pesticide spill. DDT was widely used before its adverse effects were fully appreciated, and though its use is prohibited in many areas of the world, it remains in use elsewhere due to its effectiveness, persistence, and low cost. Birds that migrate long distances may move into and out of countries where DDT is used, so it remains a continuing threat even where it is not currently used. The benefits of DDT to humans are not trivial, especially in countries plagued by malaria and other mosquito-vectored diseases, so there remains considerable interest in continuing its use. Consequently, there is extensive literature for and against DDT.

Although the use of DDT has attracted considerable attention as a disruptor of wildlife populations, its direct toxicity is quite limited. Certain cyclodiene insecticides, particularly heptachlor, dieldrin and aldrin, are similarly persistent and more toxic. Indeed, it is the cyclodiene insecticides that accounted for most of the direct mortality to birds in the 1950s–1960s, not DDT. Generally, use of DDT, cyclodienes, and similar lipophilic products that accumulate in wildlife has declined greatly. Where use of these products has been reduced, wildlife populations have recovered.

Pesticide use also affects wildlife indirectly, and these indirect effects may be more important than the direct exposure of wildlife to insecticides. One important indirect effect is the depletion of insect populations caused by insecticide use. Broad-spectrum insecticides cause treated fields to become almost sterile, and if the products are persistent the fields may remain depleted of insect life for weeks. Birds will attempt to compensate for loss of insect food by foraging elsewhere, but there are limits as to how far they can fly and then return regularly to a nest with food for nestlings. If the distance is too great, the nest will be abandoned. Due to the high cost of insecticide development and registration, agrochemical companies favor development of broad-spectrum products because, once registered, they can be used extensively and generate large profits before the patent expires. The nonselective nature of such products is particularly damaging to bird populations; if only the pests were affected, some insect fauna would remain to support bird life.

Another indirect effect of pesticides on wildlife is the change in floral diversity (loss of edible weeds, weed seeds, or fungi, and also depletion of habitat or cover) caused by herbicide (and to a lesser degree by fungicide) application. Grass and weed seed can be an important food resource, and clean culture of crops – though beneficial in terms of plant growth efficiency, energy efficiency and water conservation – can greatly reduce food abundance for bird life. This problem is exacerbated by the ever-increasing scale (field size) in agriculture, which usually results from merging smaller fields, reducing crop heterogeneity, and in destroying hedge-row and other border area habitat. The results of the combined effects are often dramatic. In Britain, for example, two-thirds of farmland bird species have shown declines in abundance.

The Negative Effects of Biting Pests and Vectors of Human Disease

Many people are killed annually by diseases that are vectored by arthropods, and even more suffer chronic infections that impair their ability to work efficiently and live normal lives. Probably the top arthropod-transmitted diseases are malaria, leishmaniasis, sleeping sickness, lymphatic filariasis, and dengue. These also are among the most important diseases in tropical areas of the world. Some of the important arthropod-transmitted diseases, the vector, and human pathogen are:

African relapsing fever (*Ornithodorus* spp. (*Borrelia* spp.)
Amoebic dysentery (*Musca domestica*) (*Entamoeba histolytica*)
Chagas' disease (*Triatoma* spp.) (*Trypanosoma cruzi*)
Cholera (flies) (*Vibrio cholerae*)
Dengue (*Aedes aegypti*) (virus)
Encephalitis (mosquitoes) (virus)
Epidemic fever (*Pediculus humanus*) (*Rickettsia prowazeki*)
Epidemic relapsing fever (*Pediculus humanus*) (*Borrelia recurrentis*)
Filariasis (mosquitoes) (*Wuchereria bancrofti*)
Sleeping sickness (*Glossina* spp.) (*Trypanosoma* spp.)
Leishmaniasis (*Phlebotomus* spp.) (*Leishmania* spp.)
Loasis (*Chrysops* spp.) (*Loa loa*)
Lyme disease (ticks) (*Borrelia burgdorferi*)
Malaria (*Anopheles* spp.) (*Plasmodium* spp.)
Murine typhus (*Xenopsylla cheopis*) (*Rickettsia typhi*)
Onchocerciasis (*Simulium* spp.) *(Onchocerca volvulus)*
Plague (*Xenopsylla cheopis*) (*Pasturella pestis*)
Rocky Mountain spotted fever (ticks) (*Rickettsia rickettsii*)
Scrub typhus (*Trombicula* spp.) (*Rickettsia tutsugamushi*)
Trench fever (*Pediculus humanus*) (*Rickettsia quintana*)
Tularemia (*Chrysops* spp.) (*Francisella tularensis*)
Typhoid fever (flies) (*Salmonella typhi*)
Yaws (flies) (*Treponema pertenue*)
Yellow fever (*Aedes aegypti*) (virus)

Likely the most important arbovirus is dengue, which is found throughout the world in tropical areas. According to the USA's Centers for Disease Control and Prevention (CDC), as of 2005 tens of millions of people were being infected, and tens of thousands of people were contracting dengue hemorrhagic fever. Though dengue usually is not lethal, the closely related but more severe dengue hemorrhagic fever can be very dangerous, often resulting in mortality of about 5% of its victims. Yellow fever remains an important arbovirus in the tropics, with perhaps 200,000 cases per year, and 30,000 deaths. Similarly, Japanese encephalitis causes about 40,000 cases per year, inflicting 10–15,000 deaths annually in Asia. West Nile virus recently gained access to North America, and though only a few thousand people have contracted this disease thus far, like other encephalitis diseases, survivors often suffer significant neurological impairment. Malaria remains the most important insect-vectored disease, infecting 300–500 million people per year, and resulting in about one million deaths per year. The economic and sociological consequences of this disease are devastating.

Domestic animals are a very important source of food and companionship for humans, and they also can succumb to diseases transmitted by arthropods. Among the important diseases of domesticated animals, the vector, and the animal pathogen are:

African horse sickness (*Culicoides* spp.) (virus)
Anthrax (*Musca domestica*) (*Bacillus anthracis*)
Blue tongue of sheep (*Culicoides* spp.) (virus)
Cattle filariasis (blackflies) (*Onchocerca gutturosa*, etc.)
Dirofilariasis (mosquitoes) (*Dirofilaria* spp.)
Fowl spirochaetosis (*Dermanyssus gallinae*) (*Borrelia anserina*)
Heartwater of cattle (*Amblyomma hebraeum*) (*Rickettsia ruminantium*)
Mal de caderas (*Stomoxys calcitrans*) (*Trypanosoma equinum*)
Nagana (*Glossina* spp.) (*Trypanosoma* spp.)
Surra (Tabanidae) (*Trypanosoma evansi*)
Texas cattle fever (*Boophilus annulatus*) (*Babesia bigemina*)

The Negative Effects of Urban (Structural, Household, and Landscape) Pests

Urban pests are among the most important because they affect so many people, not only those in rural/agricultural environments. Also, the pesticide market for structural, household and landscape pests is large and unusually lucrative for pesticide companies. Thus, pesticide use is actively promoted at the same time that major efforts are under way to reduce pesticide use in crops. In some cases there is justification for pest control in the urban environment, particularly in the case of termite and red imported fire ant control. Other examples of important urban pests, and the basis of their importance, include cockroaches (mostly a sanitation issue), flies (sanitation), household ants (sanitation), stored grain insects (sanitation), carpet beetles and clothes moths (damage to wool products), lice and fleas (human and pet health), and turf and ornamental plant pests (aesthetics).

Termites can be extremely destructive by attacking wood buildings, compromising their structural integrity. Even buildings constructed largely of concrete can be damaged because subterranean termites will tunnel over concrete to get to wood roof supports, and because drywood termites and some subterranean termites will alight on roofs and attack from above. In addition to structural materials, damage may be inflicted to cabinetry, furniture, and wood paneling and trim. Damage by termites is a severe problem in all but the northernmost climates, but is especially acute in warmer areas because termites are active for longer periods of time. The economic effect of termites is estimated at $5–6 billion per year (2006 estimate) in the USA, with most of the damage occurring in the warm-weather, southern states from Florida to California, and also in Hawaii.

Arthropods living indoors, such as house dust mites and cockroaches, can be an important source of allergens. Cockroach allergens are proteins shed by cockroaches, and also found in their feces. Exposure by children to cockroach allergens is believed to be a major risk factor for asthma. Currently, about 20% of American children are allergic to cockroach allergens, and asthma rates are particularly high in inner-city areas where cockroach problems frequently occur. Such children miss more school and have more hospitalizations for asthma. Cockroach allergy is not limited to children, however. In addition to allergy/asthma issues, about $200 million is expended annually in the USA for cockroach suppression in homes and businesses, particularly in the food/restaurant industries.

Red imported fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae), is an interesting and complex case because not only is it a very important urban pest, but it also affects agricultural and natural environments, and even has beneficial aspects. A native of South America, it entered the USA without its natural enemies and has proliferated largely unchecked. Because it stings, it threatens the lives of people, pests, livestock and wildlife. The economic effect in the USA is estimated at $5.6 billion per year, with the principal impacts being to residential households ($3.6 billion), disruption of electric and communication systems ($637 million), crop destruction ($428 million), golf course damage and treatment ($318 million), and effects on schools and school yards ($130 million) (2004 estimates). Other ants can be a nuisance, and carpenter ants can cause structural damage, but none approach the impact of *S. invicta*. On the other hand, *S. invicta* is an effective predator of insects, and in some cropping systems such as sugarcane, this species contributes significantly to the biological suppression of other pest species.

The Benefits of Pollination and Honey Production

Pollination

Pollination is accomplished by insects, vertebrates (birds and bats), and wind, but certain crops are mostly dependent on insects, and bees in particular, for successful pollination. Notable among crops requiring pollination are most fruits and nuts, many vegetables, and a few field crops. The grain crops, including corn (maize) are wind-pollinated. Wild pollinators can be quite important for plants requiring insect pollination, and may be completely effective for isolated plants or small fields. However, in modern crop production the high density of crops and the long distance of crops from uncultivated areas may limit the ability of wild pollinators to effectively provide pollination of crop plants. Therefore, hives of bees (usually Hymenoptera: Apidae and specifically *Apis mellifera*) are often moved adjacent to the crops requiring pollination. In the USA, about 2.5 million hives were rented for pollination services in 1999, clearly indicating the importance of pollination. Nearly 85% of the rentals occurred in only seven crops (in descending order of importance): almond, apple, melons, alfalfa seed, plum/prune, avocado, and blueberry.

Estimates of the dependence of crops on pollination, and the proportion of pollination accomplished by wild pollinators versus domesticated honey bees, are shown in Table 22. Note that dependence varies considerably from crop to crop, and even within related crops (e.g., compare grapefruit to lemon, which are both citrus crops). The value of pollination is estimated at over $3 billion in the USA alone (2001 estimate), though there are earlier estimates of $5.7 billion in pollination benefits. Though this is a small value relative to the total value of crops, these insect-pollinated crops account for important diversity in our diet. Imagine subsisting on corn, wheat and barley, spiced up with an occasional potato; a bland diet, indeed! The benefits of fruit and vegetables are considerable, both for nutrition and appetite.

However, some caution should be used in interpreting pollination data. Sometimes "insect pollinated crops" can be produced without pollination. Thus, with asparagus, carrots and alfalfa (for example) a crop can be obtained in

Costs and Benefits of Insects, Table 22 **The value of crop production in the USA resulting from pollination, 2001–2003, in relation to the source of pollinators (adapted from Losey and Vaughn, 2006)**

Crop	Mean annual value ($ millions)	Dependent on pollination (%)	Domesticated nonindigenous bees (%)	Indigenous bees (%)	Mean value from indigenous bees ($ millions)
Fruits and nuts					
Almond	1120.0	100	100	10	158.51
Apple	1585.1	100	90	20	4.2
Apricot	30.0	70	80	10	38.24
Avocado	382.4	100	90	10	2.31
Blueberry, wild	23.1	100	90	10	19.29
Blueberry, cultivated	192.9	100	90	10	0.31
Boysenberry	3.9	80	90	10	0.31
Cherry, sweet	290.6	90	90	10	26.15
Cherry, tart	56.3	90	90	10	5.07
Citrus					
Grapefruit	278.4	80	90	10	22.27
Lemon	286.1	20	10	90	51.50
Lime	2.0	30	90	10	0.06
Orange	1713.6	30	90	10	51.41
Tangelo	10.8	40	90	10	0.43
Tangerine	112.0	50	90	10	5.60
Temple	6.1	30	90	10	0.18
Cranberry	159.7	10	90	10	15097
Grape	2774.8	10	10	90	249.73
Kiwifruit	16.7	90	90	10	1.50
Loganberry	158.0	50	80	20	15.80
Macadamia	31.1	90	90	10	2.80
Nectarine	121.2	60	80	20	14.54
Olive	66.5	10	10	90	5.99
Peach	487.9	60	80	20	58.55
Pear	263.9	70	90	10	18.47
Plum & prune	197.8	70	90	10	13.85
Raspberry	95.8	80	90	10	7.19
Strawberry	1187.6	20	10	90	213.77
Vegetables					
Asparagus	164.3	100	90	10	16.43
Broccoli	543.4	100	90	10	54.34
Carrot	575.5	100	90	10	57.55

Costs and Benefits of Insects, Table 22 The value of crop production in the USA resulting from pollination, 2001–2003, in relation to the source of pollinators (adapted from Losey and Vaughn, 2006) (Continued)

Crop	Mean annual value ($ millions)	Dependent on pollination (%)	Domesticated nonindigenous bees (%)	Indigenous bees (%)	Mean value from indigenous bees ($ millions)
Cauliflower	219.8	100	90	10	21.98
Celery	256.5	100	80	20	51.30
Cucumber	379.5	90	90	10	34.16
Cantaloupe	401.0	80	90	10	32.08
Honeydew	94.1	80	90	10	7.53
Onion	808.0	100	90	10	80.80
Pumpkin	75.5	90	10	90	61.16
Squash	192.3	90	10	90	155.76
Vegetable seed	61.0	100	90	10	6.10
Watermelon	315.9	0.7	0.9	0.1	22.11
Field crops					
Alfalfa hay	7212.8	100	95	5	360.64
Alfalfa seed	109.0	100	95	5	5.45
Cotton lint	3449.5	20	80	20	137.98
Cotton seed	689.3	20	80	20	27.57
Legume seed	34.1	100	90	10	3.41
Peanut	793.1	10	20	80	63.45
Rapeseed	0.3	100	90	10	0.03
Soybean	15095.2	10	50	50	754.76
Sugar beet	1057.3	10	20	80	84.58
Sunflower	312.7	100	90	10	31.27
Total					3074.13

the absence of pollinators, but they require pollinators for propagation (seed production). A relatively small area of carrots, if properly pollinated, can produce enough seed for all the carrots grown as vegetables. In the case of alfalfa, the crop can be harvested several times per year, and for several years, before replanting. The extreme case is asparagus, which is normally harvested for a decade before replanting. Thus, although the existence of these crops (and many others) is dependent on insect pollination, the production of any particular field may not require the presence of pollinators. In contrast, for other crops (e.g., apple, avocado, and blueberry) every fruit harvested requires visitation by an insect pollinator.

We take for granted that pastures and prairies will be populated by wildflowers. A spring walk through woodlands is a wonderful way to see small herbaceous plants in their full glory. And what would a tropical landscape be without a profusion of flowers? Without insects to perform pollination services, these and many other environments would seem sterile, lacking in the bright colors we normally expect in our landscapes. Most plants that produce colorful flowers do so to attract insects, and without these pollinators the plants would decline or disappear. Biodiversity would decline tremendously, and highly coevolved systems, such as some orchids, would certainly disappear. It is difficult to assign economic or even aesthetic values to the loss of insect pollination, but it certainly would represent a very different world than we now enjoy.

Honey

Honey is an important by-product of pollination. At one time, honey production was more important; farmsteads routinely produced their own supply of sweetener from their own hives. Later, an industry grew up to supply honey, often manned by migratory beekeepers who kept hundreds or thousands of hives and followed the availability of nectar for their bees. While this still occurs to some extent, in many instances the importance of honey has been supplanted by other sweeteners (from sugar cane, sugar beet, or corn). Nevertheless, honey production is an important supplement to pollination services for many beekeepers, and the only product for some. The value of honey produced in the USA was $157 million in 2005, coming from 2.4 million colonies. But about 60%of the honey consumed in the USA was imported from other countries, so this value underestimates its importance. World honey production in 2005 was estimated by the Food and Agriculture Organization of the United Nations to be slightly over 1.4 billion kg. Production has increased steadily over the last decade or so, with most of the increases coming from Asia and South America, while honey production in the USA continues to decline, along with the number of beekeepers and colonies of bees. It is difficult to estimate the value of honey throughout the world due to differing currencies, but it likely was about $3 billion in 2005.

The Benefits of Animal Dung Decomposition

Although it is difficult to estimate the benefits of insect decomposition of plant products, in a qualitative sense it is certain that insects speed up plant matter decomposition, allowing more light to reach the forest floor and increasing the rate of nutrient recycling. By hastening the demise of senescent vegetation, especially trees, insect decomposers allow the forests to boost productivity. Averaged across ecosystems, insects consume about 5% of available (not including woody tissues) biomass. Thus, herbivores can affect ecosystem productivity by regulating the rate of energy input. Saprophytic species (feeding on feces and honeydew) cannot directly affect primary productivity, but can regulate it indirectly by affecting the rate of nutrient recycling. Feces and honeydew allow premature release of nutrients, boosting nitrogen flow to the plants.

One aspect of decomposition that has been studied is consumption of dung by insects, particularly by dung beetles (Scarabaeidae: Scarabaeinae). Cattle produce large quantities of dung, about 9,000 kg (about 21 cubic meters) per animal per year. Scarab beetles are quite efficient at decomposing this waste, which otherwise smothers vegetation, fouls vegetation leading to avoidance by grazing animals, and ties up nitrogen in an unusable form. Decomposition also reduces the breeding of parasites and nuisance and biting flies that would otherwise breed in the dung.

The accelerated decomposition of dung by dung beetles in the USA is estimated to provide at least $380 million in benefits annually (2006 estimate). The economic benefits attributable to specific actions include reduction in fouling of forage, $122 million; reduced volatilization of nitrogen, $58 million; reduced parasitism, $70 million; and reduced numbers of pest flies, $130 million. Dung beetle activity is not as great in the USA as it is in many other countries due to the animal husbandry practices of the USA. Specifically, large numbers of cattle are pastured in feedlots (beef cattle) or on concrete (dairy cattle) rather than on rangeland, and dung beetles do not inhabit these areas. Also, over half of the cattle in the USA are treated with avermectin pesticides to control parasites, and the avermectin residues in the dung inhibits development of dung beetles. Thus, the benefits due to dung beetles are likely considerably greater in countries that maintain their livestock in pastures or do not treat with avermectins.

The benefit of dung beetles is perhaps best seen in Australia, a continent that lacked mammals (and mammal dung) until cattle were introduced during settlement by Europeans in 1788. The abundance of cattle in Australia (about 20 million currently) produces an abundance of dung that is slow to decompose, which allows bush fly, Musca vetustissima Walker (Diptera: Muscidae), to breed in huge numbers in the dung. Marsupial dung, the natural food source of bush fly, is much smaller and tends to dry out quickly and become unsuitable for fly larvae. To deal with the reduction in pasture by the slowly decomposing dung, and to reduce fly breeding, many species of dung beetles from Africa and Europe were introduced. The result has been an 80% reduction of bush flies. This approach has only recently been extended to target dog dung, a problem in urban areas.

Losses attributed to forage fouling are derived from the concept that cattle will not, or cannot, consume forage covered with dung. Studies conducted in California, USA, determined that the presence of dung beetles would increase the decomposition rate of dung by about 20%. Projected over cattle on pasture and rangeland throughout the country, it is possible to estimate a $122 million saving due to dung beetles. This assumes that stocking rates are optimized to use all food. However, this is not always a realistic assumption. The California data may not be applicable universally. In Australia, for example, the benefits are much greater because dung retention time was reduced from as long as four years to as little as 48 h.

Drying of dung causes marked reduction of its inorganic nitrogen content, with the nitrogen being released into the atmosphere. In contrast, if the dung is incorporated into the soil, the nitrogen is available to plants and thus functions as a fertilizer. The difference is considerable, about an 80% difference in nitrogen content. The enhanced plant growth associated with incorporation of dung into the soil by dung beetles is estimated to increase available forage by about $58 million per year in the USA. As in the previous example, this is only true if the stocking rate is adjusted appropriately to take advantage of the additional forage.

The availability of dung allows survival of parasites and pests, and reducing the longevity of the dung should reduce survival of the parasites and pests as well. The economic benefits have been calculated to be $70 million and $380 million per year, respectively, in the USA. As noted earlier, however, avermectins are widely used in the USA, so the benefit of beetles might be better in regions not using these pesticides. Also, these calculations are based only on beef cattle, but benefits also accrue to other livestock such as dairy cattle, horse, goats, and sheep, so these certainly are low estimates of the economic benefit of dung beetles.

The Benefits of Insects for Recreation

Insects are quite important as food for wildlife populations that, in turn, support recreational activities such as hunting, fishing, and wildlife viewing. The importance of insects relative to wildlife populations is often overlooked, except for freshwater fish, where there is considerable appreciation for the role of insects in supporting fish populations. The importance of wildlife in technologically advanced countries is often limited mostly to recreation, and the analyses reported below (2005 estimates) relate only to such values, and are limited to calculations made only for the USA. However, in some parts of the world wildlife is an important part of the human diet, so the effects of insects would be proportionally greater in such locations.

Small game, but not large game, is often critically dependent on insects for food. Chicks of such popular game birds as pheasant, quail and grouse cannot survive without insects as a nutritional resource. Therefore, the economic effects of insects, based on the proportion of expenditures related to hunting these birds, is about $1.48 billion annually in the USA (Table 23). Waterfowl also eat insects, but to a lesser degree than the terrestrial species. Thus, the economic effect of insects as food for waterfowl is estimated at only $0.58 billion. Other vertebrates that are popular with hunters, such as squirrels and raccoons, also consume insects as part of their diet, but their contribution to the hunting economy has not been calculated.

The majority of freshwater fish are insectivorous, so the entire value of the freshwater fishing (recreational fishing) economy can be attributed to insects (Table 24). This value is $27.9 billion. Although saltwater fish are not normally thought of as insectivorous, about 25 species spend part of their life in freshwater habitats where they feed on insects. If the proportion of the marine fisheries (commercial fishing) due to these species is calculated, it represents about $0.22 billion.

Wildlife watching is an important form of recreation, and birdwatching is central to wildlife observation. Wildlife viewers often also appreciate opportunities to view small mammals, reptiles and amphibians, which often use insects as well, and many make efforts to view insects. Nevertheless, the benefits of wildlife watching are calculated only on the basis of birdwatching, and only on the basis of species of North American birds that are primarily insectivorous. Thus, this is a very conservative estimate, but still accounts for an economic impact of $19.8 billion.

The Benefits of Biological Control by Insects

As noted previously, insecticides are often used to suppress pests and their damage, and this is a costly undertaking. However, pest control would be vastly more expensive were it not for control of insects by their natural enemies, principally other insects. As with other estimates of insect effects, it is difficult to assess the benefits of natural biological control. However, it has been estimated that 65% of insects are being maintained in a non-damaging status relative to their host plants by the action of natural enemies, and only about 7% attain damaging levels (the others do not feed on plants). In the USA, the benefit (in 2005) of beneficial insects (predators and parasitoids) to cropping systems has been calculated to be about $4.5 billion annually, whereas the benefits due to the actions of other factors (insect diseases, weather, etc.) working in conjunction with beneficial insects totals about $13.6 billion.

Other Benefits of Insects

Silk production (sericulture)

Silk is produced by special glands (generally modified salivary glands) in the larvae of some Lepidoptera, and by other structures in some immatures and adults of mites and spiders. Only moth larvae, however, have been exploited by humans for their ability to produce silk commercially. The silk naturally serves various functions, such as larval dispersal in the wind, leaf rolling, anchoring of pupae, and construction of cocoons. It is this latter function, which consists of production of a single long strand of silk, which allows the silk to be unwound from the pupal case and harvested.

In different parts of the world, various species have been used to produce silk, but generally it involves insects of the superfamily Bombycoidea, and particularly *Bombyx mori* L. Silk has been harvested by humans from *Bombyx mori* at least since 2600 B.C. It was one of the first, and most valuable, trade commodities between China and Europe. Though originating in China, once the insect was smuggled out of China it was quickly spread around the world, where its cultivation was limited only by the ability to produce mulberry trees, its natural host. Besides China, Japan and India are the most important production centers. Now it can be produced on artificial diet as well. Silk is a valuable commodity, valued at over $1 billion annually.

Costs and Benefits of Insects, Table 23 **Insectivory in North American bird species (adapted from Losey and Vaughan, 2006)**

Order	Common name	No. species	No. primarily insectivorous	No. partially insectivorous	No. not insectivorous
Gavliiformes	Loons	5	0	5	0
Podicipediformes	Grebes	7	5	2	0
Procellariiformes	Tubenoses	6	1	4	1
Pelicaniformes	Pelicans & allies	11	0	5	6
Ciconiiformes	Herons & allies	20	5	12	3
Phoenicopteri-formes	Flamingos	1	1	0	0
Anseriformes	Waterfowl	44	19	24	1
Falconiformes	Vultures, hawks, & falcons	31	3	18	10
Galliformes	Quail, grouse & allies	22	2	20	0
Gruiformes	Cranes & allies	13	8	5	0
Charadriiformes	Shorebirds & gulls	108	51	22	35
Columbiformes	Pigeons & doves	11	0	3	8
Cuculiformes	Cuckoos & roadrunners	6	6	0	0
Strigiformes	Owls	19	6	11	2
Caprimulgi-formes	Goatsuckers	8	8	0	0
Apodiformes	Swifts & hummingbirds	20	6	14	0
Trogoniformes	Trogons	1	1	0	0
Coraciiformes	Kingfishers	3	0	1	2
Piciformes	Woodpeckers	22	22	0	0
Passeriformes	Perching birds	285	251	34	0
Total		643	395	180	68
%			61	28	11

Shellac

Several scale insects (Hemiptera: Kerriidae) can be grown on trees in Southeast Asia and used as a source of lac, a resin that is the principal ingredient of shellac. *Laccifer lacca* Kerr is the species most commonly cultured for this purpose. India produces the largest proportion of the shellac on the world market, though production has fallen greatly due to the availability of synthetic resins.

Costs and Benefits of Insects, Table 24 Value of commercially landed fish that rely on insects as a critical nutritional resource (adapted from Losey and Vaughan, 2006)

Species	Fish weight (kg landed)	Fish value ($)
Alewife	1,675,935	384,968
Mullet, striped	15,473,230	9,504,673
Mullet, white	509,887	241,064
Mullets	444,000	310,680
Mummichog	4,590	13,221
Perch, white	2,482,006	1,082,354
Perch, yellow	1,714,342	2,914,078
Salmon, chinook	27,345,066	32,633,445
Salmon, chum	92,031,758	16,900,456
Salmon, coho	32,256,133	15,261,440
Salmon, Pacific	176	538
Salmon, pink	334,080,474	24,758,990
Salmon, sockeye	184,505,904	109,897,597
Shad, American	2,074,686	1,190,072
Shad, gizzard	5,306,259	700,916
Shad, hickory	88,339	23,199
Smelt, eulachon	1,081,152	160,842
Smelt, rainbow	489,467	730,685
Smelts	480,212	150,728
Suckers	157,164	45,384
Tilapias	5,482,778	1,223,061
Trout, lake	558,129	228,773
Trout, rainbow	308,306	189,625
Walleye	25,810	42,396
Whitefish, lake	8,604,823	6,048,110
Total	–	224,637,295

Dyes

Commercially important dyes have been extracted from insects. Probably best known is cochineal dye, obtained from the bodies of cochineal scales, *Dactylopius coccus* (Hemiptera: Dactylopiidae). Cultivated on *Opuntia* cactus, it can be used to produce a bright red dye that once was very popular, declined in importance as synthetic materials became available, and now is becoming more popular again as a "natural" dye. It also is useful in cosmetics and food. Lac dye is a byproduct of shellac production. It has been used as a skin cosmetic, in medicine, and for dyeing wool, silk and leather.

Human and Animal Food

Insects are not ordinarily a major source of nutrition for humans in western societies. In some societies, however, insects are consumed if they are especially available or provide needed nutrition during times of famine (e.g., locusts in Africa), or as part of cultural tradition (e.g., as a condiment – canned grasshoppers in Southeast Asia or Maguey worms in Mexico). In Africa, Asia, Oceania, and Latin America it is not unusual to find a great diversity of insects in local marketplaces, and in some countries children are especially likely to eat insects opportunistically. Insects are good sources of proteins, lipids, and vitamins, but it is difficult to raise them economically. Thus, they tend to be eaten opportunistically rather than cultured. The economic value of insects as food has not been assessed, but likely is relatively low. In a few societies, insects have been prized as food. For example, the emperor Montezuma and the Aztec kings who preceded him prized the eggs of aquatic Hemiptera (called "ahuahutle"), where it was the equivalent of caviar, and transported at great effort and expense to Tenochtitlan for ceremonies. Surely if more of the world's leaders would set an example of consuming insects, others would be induced to follow, setting the stage for a new insect-based food industry!

Insects often are useful for maintenance of pets, as they are readily accepted and nutritious. Easily cultured insects are most generally used, including house cricket, *Acheta domesticus*; mealworm, *Tenebrio molitar*; waxworms, *Galleria mellonella*; and various flies (Muscidae and Calliphoridae). They are most often used as food or a food supplement for amphibians, reptiles and birds, but rodents and some small mammals also accept them. They are sold in various forms at pet shops, including alive, dried, and frozen. In recent time, dehydrated insects have been included in some types of wild bird food, although this is still relatively unusual. Also, zoos often seek live insects for their exhibit animals, both due to their nutritional value and also because higher animals often suffer from boredom in a zoo environment, and it is healthy to provide variety and diversion, which can be provided in the form of live insects. Thus, large mobile insects such as grasshoppers provide diversion as well as nutrition for some zoo animals, including monkeys. Lastly, but importantly, insects are used as a lure (bait) for fishing, as some fish take live insects preferentially. The same insects used for pet food tend to be used as fish bait.

Medical Treatment

Though more widely used for medical treatment in ancient societies, insects retain some uses in contemporary treatment of human ailments, most notably for apitherapy (bee venom therapy) and for maggot therapy. Apitherapy is sometimes recommended for rheumatic diseases, including arthritis and multiple sclerosis. Traditionally, bees were stimulated to sting the affected area, but injected venom is now also used as a form of treatment. Bee venom is also applied topically in creams, liniments and ointments. Maggot therapy is more well-founded scientifically, and takes advantage of the propensity of some fly larvae (usually *Lucilia* maggots) to feed on dead and decaying flesh, but to avoid feeding on living tissue. Thus, live maggots are introduced to wounds of humans or pets to clean out necrotic tissue. Also, maggots excrete products that inhibit growth of microbes that lead to infection of living tissue and stimulate regrowth of healthy tissue. More commonly used prior to the advent of modern antibiotics (the 1940s and 1950s), maggot therapy continues to be used for wounds that display difficulty in healing, and with the emergence of antibiotic-resistant bacteria, there is potential of renewed interest by the medical community.

► Apiculture
► Pollination and Flower Visitation
► Bees
► Ants

► Invasive Insects
► Natural Enemies Important in Biological Control
► Insecticides
► History and Insects
► Lyme Borreliosis
► Eastern Equine Encephalitis
► West Nile Fever
► Plague: Biology and Epidemiology
► Silkworms
► Eri Silkworm
► Sericulture
► Shellac
► Lacquers and Dyes from Insects
► Entomophagy: Human Consumption of Insects
► Maggot Therapy
► Midges as Human Food
► Native American Culture and Insects
► Nutrient Content of Insects

References

Cox C (1991) Pesticides and birds: from DDT to today's poisons. J Pestic Ref 11:(4)2–6
DeFoliart GR (1989) The human use of insects as food and as animal feed. Bull Entomol Soc Am 35:(1)22–35
DeFoliart GR (1999) Insects as food: why the western attitude is important. Annu Rev Entomol 44:21–50
Hill DS (1997) The economic importance of insects. Chapman and Hall, London, UK
Hodkinson ID, Hughes MK (1982) Insect herbivory. Chapman and Hall, London, UK
Lind PM, Milnes MR, Lundberg R, Bermudez D, Orberg J, Guillette LJ Jr (2004) Abnormal bone composition in female juvenile American alligators from a pesticide-polluted lake (Lake Apopka, Florida). Environ Health Perspect 112:359–362
Losey JE, Vaughan M (2006) The economic value of ecological services provided by insects. Bioscience 56:311–323
Pimentel D, Lach L, Zunia R, Morrison D (2000) Environmental and economic costs of nonindigenous species in the United States. Bioscience 50:53–65
Rosenstreich DL, Eggleston P, Kattan M, Baker D, Slavin RG, Gergen P, Mitchell H, McNiff-Mortimer K, Lynn H, Ownby D, Malveaux F (1997) The role of cockroach allergy and exposure to cockroach allergen in causing morbidity among inner-city children with asthma. N Engl J Med 336:1356–1363
Southwick EE, Southwick L Jr (1992) Estimating the economic value of honey bees (Hymenoptera: Apidae) as agricultural pollinators in the United States. J Econ Entomol 85:621–633
Ware GW, Whitacre DM (2004) The pesticide book. MeisterPro Information Resources, Willoughby, OH

Cost-Benefit Analysis

An assessment of the total costs of an activity in comparison to its total benefits. Although environmental and societal aspects may be considered, all costs and benefits are usually expressed in monetary terms.

Cotton or Melon Aphid, *Aphis gossypii* Glover (Hemiptera: Aphididae)

This species is an important pest of crops and has a wide host range.
► Aphids
► Melon Aphid, *Aphis gossypii*

Cotton Leafworm, *Spodoptera littoralis* (Boisduval)

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This insect occurs in Africa, Madagascar, Europe and the Middle East. A very similar but allopatric insect, *Spodoptera litura* (Fabricius) (taro caterpillar or tobacco cutworm), is found in Asia, Australia, and the Pacific region. For many years these two species were thought to be the same, and although they have been considered to be separate species by most authorities since 1962, confusion lingers. Other common names applied to *S. littoralis* include Egyptian cotton leafworm or Egyptian cotton worm, tomato caterpillar, tobacco caterpillar, and Mediterranean climbing cutworm, just to name a few.

Life History

The number of generations displayed by this species depends on temperature. In southern Europe, for example, three generations are commonly observed, whereas in Egypt seven generations are not unusual. Warm, but not excessively hot, weather favors this species. Development ceases when temperature are less than about 10.5°C. This species lacks the ability to diapause and is intolerant of cold winters, so in Europe, for example, it occurs regularly only in the southernmost regions.

Eggs are spherical, somewhat flattened, and measure about 0.4–1.0 mm in diameter. They are deposited in clusters of 100–300 eggs, in fairly regular rows comprising three layers, and covered with whitish scales from the abdomen of the female moth. The eggs are yellowish or green initially, but turn black before hatching. Eggs persist for 2–3 days in the summer, but considerably longer under cooler condition, up to 25 days. Females have been shown to produce 1500–2000 eggs.

Larvae initially are pale green with black heads. The older larvae are more variable, often appearing gray, brown or almost black and with dark markings. The latter instars bear triangular spots laterally on each body segment, and dorsal stripes. They attain a length of 40–50 mm. Young larvae feed in groups, but after the third instar they disperse and become solitary. Normally there are six instars. Larvae are inactive during the day, with the older instars seeking shelter in the soil but the younger larvae remaining motionless on the foliage. Larval development may require only 12–18 days under hot conditions, but requires up to 85 days under cool conditions.

Larvae burrow into the soil to a depth of 3–5 cm in preparation for pupation. Pupae are dark red to reddish brown, and are found in cells buried in the soil. The pupae are 15–20 mm in length, and the last segment bears two hooks. Pupal development time is only 5–10 days under warm conditions, but requires up to 30 days under cool conditions.

The appearance of adults are typical of *Spodoptera* moths, with the forewings bearing brown, yellow and white markings, and the hind wings white with a narrow brown margin. The wing span is about 30–44 mm. It is nearly identical to the yellowstriped armyworm, *S. ornithogalli* (Guenée), of North America. Adults are active at dusk and during the evening. They mate immediately upon emergence and can begin to deposit eggs within two days of mating, though sometimes several days elapse before egg deposition. The adults are short-lived, rarely surviving seven days under warm conditions, though persisting for three weeks under cool conditions. Sex pheromones are produced and have been identified for use in traps.

Many naturally occurring biological control agents have been identified, especially parasitoids (Braconidae, Encyrtidae, Tachinidae, and Ichneumonidae) and general predators. Several disease agents, including a baculovirus, microsporidia, fungi, and nematodes have been observed.

Damage

Cotton leafworm, like most *Spodoptera* species, is highly polyphagous. It attacks nearly 90 species of importance in 40 plant families, including virtually all vegetables; many flowers; avocado, citrus, and mulberry trees; coffee; grapes; field crops such as alfalfa, clover, cotton, grain amaranth, peanut, rice, soybean, sugarcane, and tobacco; and many other plants. Larvae feed on the foliage and the fruits or pods of plants. It is considered to be an extremely damaging agricultural pest where it occurs.

Management

Insecticides are commonly applied for control of this insect, particularly in cotton. However, it can be managed by using *Bacillus thuringiensis*, insect growth regulators and slow-release pheromones, thereby preserving natural enemies.

When management procedures are used in an integrated manner, the number of chemical insecticide applications can be greatly reduced. Insecticide resistance is a frequent problem when insecticides are used excessively. Not all strains of *Bacillus thuringiensis* are effective.

► Taro Caterpillar or Tobacco Cutworm, *Spodoptera litura* (fabricius) (Lepidoptera: Noctuidae)
► Yellowstriped Armyworm, *Spodoptera ornithogalli* (Guenée) (Lepidoptera: Noctuidae)
► Fall Armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae)
► Beet Armyworm, *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae)
► Vegetable Pests and their Management

References

Baker CRB, Miller GW (1974) Some effects of temperature and larval food on the development of *Spodoptera littoralis.* (Boisd.) (Lep., Noctuidae)Bull Entomol Res 63:495–511

*CABI and EPPO (1997) Spodoptera littoralis and Spodoptera litura. In: Quarantine pests for Europe, 2nd edn. CABI International, Wallingford, UK, pp 518–525

Kehat M, Gordon D (1975) Mating, longevity, fertility and fecundity of the cotton leaf-worm, *Spodoptera littoralis.* (Boisd.) (Lepidoptera: Noctuidae) Phytoparasitica 3:87–102

Cotton Stainers

Members of the family Pyrrhocoridae (order Hemiptera).

► Bugs

Cotton Whitefly, *Bemisia tabaci* Gennadius (Hemiptera: Aleyrodidae)

This species is also known as sweetpotato whitefly and silverleaf whitefly, and is a serious pest worldwide.

► Whiteflies (Hemiptera: Aleyrodidae)

Cottony Cushion Scale, *Iceryi purchasi* Maskell (Hemiptera: Margarodidae)

This is an important citrus pest if predators are absent.

► Citrus Pests and their Management
► Scale Insects and Mealybugs (Coccoidae)
► Hemiptera
► Area-Wide Pest Management

Cover, Border and Trap Crops for Pest and Disease Management

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Natural pest control provides a safer and more sustainable approach for managing pest populations. This type of control relies heavily on complex communities, natural enemies and the integration of cultural tactics including the use of mulches, trap crops, cover crops and other mechanisms that modify insect behavior to reduce the effect of insect herbivores on crop plants. This is also called "ecological management." Two hypotheses have been proposed to explain the reduction in herbivore damage in complex crop communities. The "natural enemies" hypothesis proposes that more diverse food sources (nectar, pollen, prey host species) allow for the establishment of higher densities of predators and parasites, which regulate pest populations in diverse habitats. Secondly, the "resource concentration" hypothesis predicts that herbivores will not want to remain in sparsely populated plant stands because fewer resources are available.

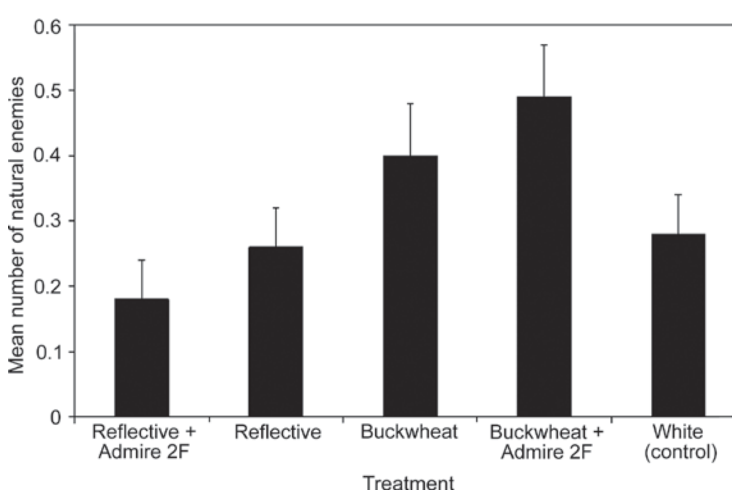
Conventional pest control programs rely heavily on monoculture environments with high usage of broad-spectrum pesticides. However, total reliance on chemical tactics to control pests can lead to resistance of arthropod pests, reduction in natural enemies, and resurgence of pest populations. In addition, this strategy is harmful to the environment and it increases the cost of production. These effects have led to the search for other management alternatives, which are sustainable and cost effective. Such practices include use of mulches, cover crops, trap crops and border crops.

The Role of Mulches for Suppression of Pest Populations

Mulching is the art of using soil barriers to improve plant growth. This helps to reduce arthropod pest populations, disease symptoms and regulate soil temperatures. Generally, there are two types of mulches, which can be used to suppress pests: organic and synthetic (Figs. 118 and 119).

Organic mulches

These types of mulches are composed of lawn clippings, leaves, straw, sawdust, bark nuggets, wood chips, brown paper and living mulches. They are used extensively in the production of ornamental landscape plants but high usage also occurs within the fruit and vegetable industry. One common example of an organic mulch is living mulch. A living mulch is a minor crop that grows within a major crop. Living mulches are low-cost alternatives to synthetic mulches and are safe for the environment. Common living mulches include buckwheat, *Fagopyrum esculentum* Moench, white clover, *Trifolium repens* L., and wheat, *Triticum aestivum* L. Living mulches (Fig. 119) reduce the number of insect herbivores that alight onto crop plants. This is accomplished by modification of insect behavior. For instance, alate aphids locate their hosts by contrasting the soil background with the green color of the foliage. The establishment of living mulches will alter the appearance of the soil surface, subsequently reducing the image that is recognized by aphids. In addition, living mulches provide supplemental resources that support higher numbers of natural enemies (Fig. 118) contributing to pests' regulation. Living mulches have also been shown to reduce the number of whiteflies, delay the onset of insect-borne viruses and increase yields in vegetable plants. It is, however, important to select the appropriate living mulch suited for the crop to be planted and the pest to be controlled. In some instances competition between the crop and the living mulch can result in reduced yields.



Cover, Border and Trap Crops for Pest and Disease Management, Figure 118 Occurrence of natural enemies in plots containing the living mulch buckwheat, *Fagopyrum esculentum*, compared with plots treated with synthetic mulch; note greater abundance in the presence of living mulch.

Cover, Border and Trap Crops for Pest and Disease Management, Figure 119 **Types of mulch: (*above*) living mulch: buckwheat intercropped with zucchini squash; (*center*) zucchini squash growing on reflective plastic mulch; (*below*) Sunn hemp cover crop in an organic field in Citra, Florida.**

Synthetic Mulches

Various colors of synthetic mulches including clear, white, black, yellow and silver-colored plastic (Fig. 119) are used commercially to grow vegetable crops. In semi-tropical regions, conventional growers use white in the summer, white on black (white top surface with black bottom) in the fall, and black in the winter and early spring. Black mulches increase soil temperatures during the cool season and white mulches reduce soil temperatures during the warm season. Ultraviolet light (UV)-reflective mulches, used by some growers, have the added benefit of reducing pests and the occurrence of viral diseases. They can reduce abundance of whitefly and aphid vectors that transmit viruses such as tomato spotted wilt virus and mosaic virus among various vegetable crops. UV-reflective mulches work by reflecting short-wave light, which repels incoming insect herbivores, thus reducing their potential for alighting on crop plants. However, these mulches lose their effect on insects once the reflecting surfaces are covered by the crop canopy. UV-reflective mulches have an added advantage of increasing plant vigor and growth, which eventually results in increased yields. However, they do not decompose easily in the environment, which may limit their use in some farming systems.

The Role of Cover Crops in Suppressing Pest Populations

Cover crops can be annual, biennial or perennial herbaceous plants grown singly or within mixed stands throughout the year to cover the bare soil. Cover crops become green manures when they are plowed back into the soil specifically to improve soil nutrient quality. In addition to suppressing weeds and nematode populations, cover crops can influence insect population dynamics by diverting generalist pests, confusing specialist pests, reducing the success of the pest by changing the quality of the host plant, and by increasing natural enemy abundance by providing supplemental resources (food, water, and overwintering sites).

In temperate climates, cover crops are usually winter annuals that are planted in late summer to give soil cover during the winter. Barley, *Hordeum vulgare*, and rye, *Secale ceceale*, are excellent examples of winter grass-like cover crops whereas hairy vetch, *Vicia villosa*, is a very common winter legume cover crop.

Summer grass-like cover crops include sorghum, *Sorghum bicolor*, and sudan grass, *Sorghum sudanense*, whereas leguminous summer cover crops include cowpeas, *Vigna unguiculata*, sunn hemp, *Crotalaria juncea*, and velvet bean, *Mucana deeringana*. In the United States, summer cover crops are planted in June, July and August and are termed warm-season crops. In well-managed orchards, the combination of leguminous and graminaceous cover crops can provide improved cover crop benefits as opposed to using only one pure stand cover crop.

Cover crops are an important part of sustainable organic agriculture and provide good potential for managing economically important pests. Crops that produce high glucosinolate levels have been effective in reducing nematode populations when they are incorporated into the soil and allowed to decompose. For instance, residues of nematode-resistant radish proved to be effective in suppressing the sugarbeet nematode, *Heterodera schachtii*. A significant decline in the nematode population as well as the rate of nematode infection has been observed in sugarbeet crops when fodder radish, *Raphanus sativus* L., and white mustard, *Sinapsis alba* L., were used as cover crops.

The Role of Barrier or Border Crops in Suppressing Pest Populations

Barrier or border crops have been used as a cultural strategy for reducing pest populations for more than half a century. It involves establishing another minor crop on the perimeter of the main crop for pests and disease suppression. Several theories have been suggested to describe the mechanisms by which barrier crops reduce pest populations. Barrier crops reduce pest and related problems (incidence of pepper veinal mottle virus disease) by acting as a physical barrier for vectors. However, factors including plant height can affect the effectiveness of the barrier crop. Barrier crops also may act as a "sink" for virus invading new environments. For instance, aphids landing on the barrier crop will lose their virus charge while probing, consequently preventing them from transmitting diseases.

The Role of Trap Crops in Suppressing Pest Populations

Trap crops are plants grown before or with the main crop to attract pests from the main crop into a smaller area (the trap crop). Trap crops are the more-preferred host when grown with the main crop. The ecological behavior of the target pests should be considered when selecting the trap crop. In addition, the agronomic compatibility between the main crop and trap crop should be known to prevent competition for natural resources (nutrients and water). Trap crops can increase the efficiency of control by concentrating the pests in one location and by applying a chemical treatment without spraying the main crop, or by destroying the trap crop and associated pests through tillage or burning. It is also possible to release biological control agents into the trap crop, using it as a nursery for beneficial organisms that will then spread into the main crop. The overall cost of management can be significantly reduced because pesticide treatments or other management tactics are only applied to areas on the trap crop, where the pest congregates. Monitoring the pest population density on the trap crop is necessary in order to prevent the pest from migrating to the main crop.

Planting a few rows of squash ahead of the main planting can be used to protect from pickleworm, *Diaphania nitidalis*, infestation because the invading moths are attracted to the blossoms of the older plants. Squash can also be planted in conjunction with tomato to protect against silverleaf whitefly, *Bemisia argentifolii*, because squash is more preferred. In both cases, however, the squash must be sprayed with insecticide or destroyed before the insects disperse to the main crop.

Economics of Sustainable Agriculture

Ecological management of arthropod and nematode pests is a practical sustainable approach to achieving effective pest control while protecting the environment. The primary economic focus of sustainable agriculture is the input cost savings from reduced pesticide usage and fertilizer applications. In some instances, it can be less expensive since many of the tactics employed (mulching, cover crops, trap crops, etc.) are not imported and are tied directly into daily farming activities. Also, incorporating leguminous cover crops into different cropping systems may decrease the amount of N applications, and the energy needed for crop production. However, this may not necessarily result in increased profits for farmers because of two important factors affecting the profitability of cover crops: (i) the ability to improve crop yield, and (ii) the establishment cost of the cover crop. Overall, more research is needed to determine the long-term profitability of these sustainable practices.

References

Alegbejo MD, Uvah I (1986) Effect of intercropping pepper with tall crops on the incidence of pepper veinal mottle virus disease on pepper. Niger J Entomol 7:82–87

Cradock RK, da Graca JV, Laing MD (2002) Studies on the control of virus diseases in zucchini crops. S Afr J Sci 98:225–227

Csizinszky AA, Schuster DJ, Kring JB (1995) Color mulches influence yield and insect populations in tomatoes. J Am Soc Hortic Sci 120:778–784

Frank DL, Liburd OE (2005) Effects of living and synthetic mulch on the population dynamics of whiteflies and aphids, their associated natural enemies, and insect-transmitted plant diseases in zucchini. Environ Entomol 34:857–865
Hilje L, Costa HS, Stansly PA (2001) Cultural practices for managing *Bemisia tabaci* and associated viral diseases. Crop Prot 20:801–812
Liburd OE, Frank DL (2007) Synthetic and living mulches for control of homopteran pests and diseases in vegetables. In: Saxena G, Mukerji KG (eds) Management of nematode and insect-borne plant diseases. The Haworth Press Inc., New York, NY pp 67–86
Lu Y, Watkins B, Teasdale JR, Abdul-Baki AA (2000) Cover crops in sustainable food production. Food Rev Int 16:121–157
Smith HA, Koenig RL, McAuslane HJ, McSorley R (2000) Effect of silver reflective mulch and a summer squash trap crop on densities of immature *Bemisia argentifolii* (Homoptera: Aleyrodidae) on organic bean. J Econ Entomol 93:726–731
Zitters AT, Simons JN (1980) Management of viruses by alteration of vector efficiency and by cultural practices. Annu Rev Phytopathol 18:289–310

Cover Crops

Cultivation of a second type of crop, principally to improve the production system for a primary crop (e.g., legumes or rye maintained during the winter season to improve soil condition), to suppress weeds, or to harbor beneficial insects.

►Cover, Border and Trap Crops for Pest and Disease Management

Coxa

The basal-most segment of the insect leg (Fig. 120), attaching to the thorax.

► Legs of Hexapods

Crab Lice, *Phthirus pubis* (Linnaeus) (Phthiraptera: Pthiridae)

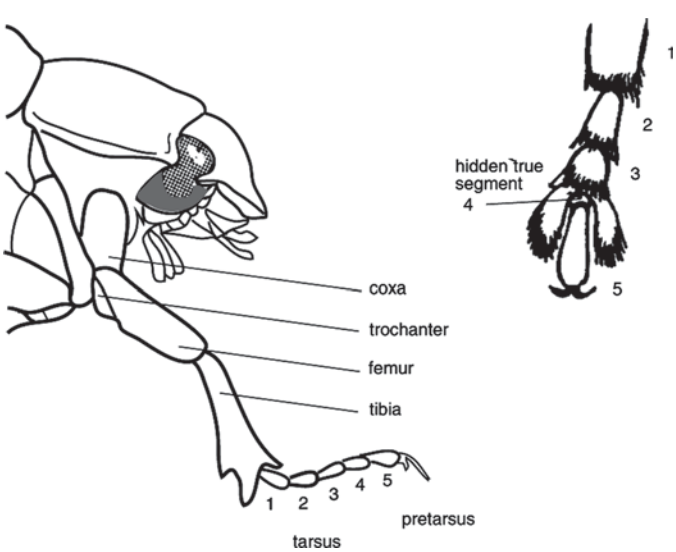
These lice infest the genital regions of humans.

► Human Lice

Crabronidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies



Coxa, Figure 120 **Leg of a beetle (Coleoptera: Scarabaeidae) leg showing its component parts, and a close-up of one type of beetle tarsus (foot).**

Cranberry Fruitworm, *Acrobasis vaccinii Riley* (Lepidoptera: Pyralidae)

This is a pest of blueberries in eastern North America.

► Small Fruit Pests and their Management

Cranberry Girdler, *Chrysoteuchia topiaria* (Zeller) (Lepidoptera: Pyralidae)

This species affects both cranberries and turfgrass.

► Small Fruit Pests and their Management

Cranberry Tipworm, *Dasineura oxycoccana* (Johnson) (Diptera: Cecidomyiidae)

Cranberry tipworm affects both cranberries and blueberries.

► Small Fruit Pests and their Management

Crane Flies (Diptera: Tipulidae and Others)

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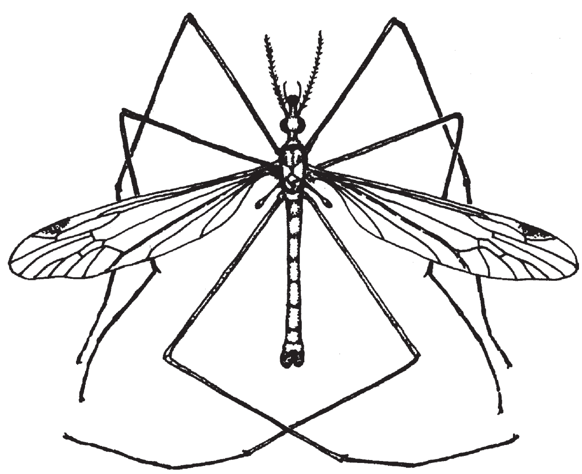
Largest of the families of true flies (Order Diptera) in number of known species, the crane flies (Family Tipulidae, of suborder Nematocera) are abundantly represented on all continents except Antarctica. Some 15,000 species have been named and described, more than 10,000 of these through the work of one man, Prof. Charles P. Alexander, of the University of Massachusetts. Over 1,600 species are known from North America.

Crane flies can be differentiated from most other nematocerous flies by the presence on the dorsum of the thorax of a broadly V-shaped, transverse suture between mesonotal prescutum and scutum, or roughly at the level of the wing bases. Three other, relatively small families share this characteristic. The Tanyderidae, or primitive crane flies, have five branches of the radial vein reaching the wing margin. Tipulidae have four or fewer. Trichoceridae, or winter crane flies, possess ocelli, while tipulids have none. Ptychopteridae, or phantom crane flies, have a single anal vein in each wing, compared to two in Tipulidae.

Most adult crane flies are slender-bodied, with elongate, membranous wings and conspicuously long, slender legs (Fig. 121). People not familiar with insects often mistake crane flies for large mosquitoes. In fact, the colloquial term "gallinipper" has been applied to both crane flies and mosquitoes. However, no crane flies are able to bite. In size, crane flies range from two species of *Holorusia* (originally *Ctenacroscelis*) of southeastern Asia, with a wing span of over 100 mm, or *Holorusia hespera* in western United States, with approximately a 70 mm wing span, to the tiny *Tasiocera ursina*, with wingspread of only 4.5–5.0 mm, smaller than that of mosquitoes. Wings of many crane flies are unmarked except for the somewhat darkened stigma, while many other species have the wings spotted, transversely



Crane Flies (Diptera: Tipulidae and Others), Figure 121 Adult male of *Tipula* sp., dorsal aspect. Body length 18 mm, wing length 21 mm. Legs are arranged unnaturally to show relative lengths of segments.

banded, or with a mottled or clouded pattern of brown, gray or black. The slender legs of some species are banded with dark brown, while those of others may be partially white (for example, *Brachypremna* or some *Hexatoma*). While most kinds of flies, indeed most insects, have the trochanter firmly attached to the adjacent femur, the legs of crane flies are readily broken off between trochanter and femur, possibly so that a leg seized by a predator can quickly be shed, to spare the fly.

The adult life of most crane flies is brief. The adults emerge from the pupal skin, often at night in order to have the body hardened, the wings fully extended and the insect capable of flight by sunrise when birds and other predators become active. Males usually appear a night or two before females. Males of many species form swarms to which females are attracted. Following mating, females disperse and oviposit. Oviposition is often completed in two or three nights. Thus, an adult life of a few days is ordinarily adequate. Adults of *Chionea*, rendered inactive by night time chill, and forced to seek shelter from severe cold, may survive a few weeks.

The adults of most crane flies do not feed but subsist on energy acquired and stored by the larva. Those of a few, such as species of subgenus *Geranomyia* of the large genus *Limonia*, possess elongate mouthparts or a proboscis and are known to obtain nectar from certain flowers.

Ecology

Adult Tipulidae are most often found in low, leafy vegetation in shaded, somewhat damp areas, such as along small woodland streams. However, there are a few species living in grasslands or even in semi-desert habitats. At temperate latitudes, they are usually the most common in spring and late summer and may have two annual generations. Adults of Chionea, virtually wingless and almost spider-like in appearance, may be found on the surface of snow, in winter, in Eurasia and North America.

The larvae of crane flies are subcylindrical and somewhat tapered toward the ends (Fig. 122). The head, variously sclerotized according to the species, can be withdrawn into the thoracic segments. The larvae occur in a great variety of moist to wholly aquatic, even marine intertidal microhabitats. Those of aquatic species may be found in decomposing plant material near the shore or in shallow water near sandbars. Larvae in aquatic situations may respire by means of a pair of large spiracles on the ninth abdominal segment that are raised to the surface from time to time. Others have such spiracles but appear to obtain sufficient oxygen through the skin. A few (e.g., larvae of *Antocha* and *Hesperoconopa*) have a closed tracheal system and lack spiracles. Most aquatic tipulid larvae leave the water to pupate. While some aquatic and semi-aquatic larvae are detritivores, many others are carnivorous. The larvae of *Pedicia*, *Limnophila* and *Hexatoma*, for example, feed on midge larvae, other insect larvae and other small, aquatic invertebrates. Terrestrial crane fly larvae may occur in and feed upon rotting wood, fungi, or decomposing plant debris, in mosses and liverworts, among rootlets of grasses and other plants, and a few (e.g., *Cylindrotoma*) feed on leaves of herbaceous plants. The only larval Tipulidae that are of direct economic importance are those that eat rootlets of range-land grasses or seedling crops (particularly some species of *Tipula* and *Nephrotoma*).

Crane Flies (Diptera: Tipulidae and Others), Figure 122 Larva of *Tipula* sp., left lateral aspect. Body length 29 mm.

Geological Record

The oldest fossil remains described as Tipulidae are of upper Triassic age, perhaps 180 million years old. In North America, the earliest remains, similar to modern Tipulidae, are in the fine-grained shale of the Green River formation, of the Eocene age, approximately 50 million years old. The Baltic amber of northern Europe, which is upper Eocene to Oligocene in age (about 45 million years old), contains numerous species of crane flies, preserved in fine detail.

Taxonomic Divisions

The family Tipulidae has been divided into three subfamilies, Tipulinae, Cylindrotominae and Limoniinae. Most large crane flies belong to the Tipulinae, but there are a few large Limoniinae. For identification keys (North America), see Alexander 1942 (somewhat revised and reprinted in 1966) or Alexander 1967. In fairly recent years, European authors have elevated these three subfamilies and tribe Pediciini of Limoniinae to full family status.

References

*Alexander CP (1942) Family Tipulidae. In: The Diptera or true flies of Connecticut. Connecticut State Geological and Natural History Survey, Bulletin 64, pp 196–509

Alexander CP (1967) The crane flies of California. Bull Calif Insect Survey 8:1–269

Cranium

The head capsule of an insect.

► Head of Hexapods

Crapemyrtle Aphid, *Sarucallis kahawaluokalani* (Kirkaldy) (Hemiptera: Aphididae)

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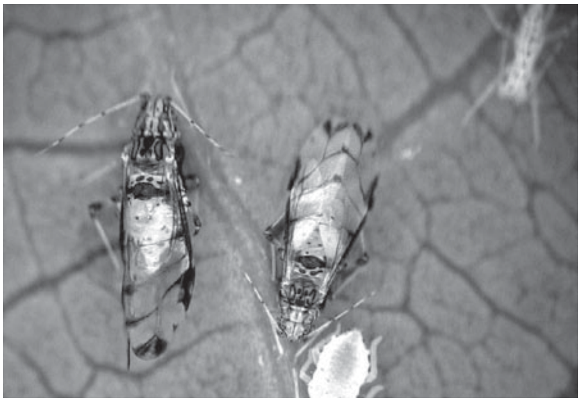
The crapemyrtle aphid, *Sarucallis kahawaluokalani* (Kirkaldy), is native to Southeast Asia but may be found anywhere that crape myrtles, *Lagerstroemia* spp,. are grown. With the exception of henna and pomegranate, *S. kahawaluokalani* is host specific, feeding exclusively on species of *Lagerstroemia*. Interestingly, other aphid species are not known to attack or infest crape myrtles. Crape myrtles are popular ornamental plants throughout tropical and subtropical areas of the world. Because aphids can be extremely difficult to detect on plants during shipping, *S. kahawaluokalani* has been transported throughout the world on shipments of crape myrtle. When aphid numbers are high, *S. kahawaluokalani* damages crops via a fungus that grows on its excrement. Several insect predators attack crapemyrtle aphids, but most are unable to provide permanent control of aphid populations.

Crapemyrtle aphids (Fig. 123) reproduce at an astonishing rate, giving the impression that an infestation suddenly occurred overnight. Each adult *S. kahawaluokalani* gives birth parthenogenetically to several offspring per day, and the growth of crapemyrtle aphid populations is further accelerated by the process of telescoping generations. Parthenogenesis is a form of asexual reproduction where offspring are produced without mating. Furthermore, crapemyrtle aphids are viviparous, meaning they give live birth to their offspring. Telescoping generations refers to the process in which nymphs or immature aphids begin to develop offspring inside of them before they become adults. In many aphid species, a nymph that is developing inside of its mother has already begun to develop offspring



Crapemyrtle Aphid *Sarucallis Kahawaluokalani* (Kirkaldy) (Hemiptera: Aphididae), Figure 123
Winged adults and nymph of crape myrtle aphids, *Sarucallis kahawaluokalani*.

inside of itself. Telescoping generations allows aphids to reproduce immediately upon becoming an adult, and *S. kahawaluokalani* give birth within a few hours of reaching the adult stage. Crapemyrtle aphids exhibit a life cycle that is more complex than simple parthenogenesis, and under some environmental conditions, crapemyrtle aphids practice sexual reproduction.

The life cycle of *S. kahawaluokalani* begins when overwintering eggs hatch in the spring. Aphids hatching from overwintering eggs are all female, and such mature wingless stem mother aphids that hatch from overwintering eggs are called fundatrices (singlular, fundatrix). Fundatrices reproduce through parthenogenesis, giving rise to a second generation known as virginoparae. Virginoparae reproduce through parthenogenesis and subsequent generations of aphids throughout the summer are also called virginoparae. In late summer and early fall, virginoparae produce a special generation of aphids known as sexuparae. Sexuparae give birth to both male and female aphids. The female aphids of this generation are known as oviparae, and after mating with males, oviparae deposit their eggs on the branches of crape myrtle. Eggs are deposited in loose clusters within the crevices of bark and remain on the plant until the following spring when the eggs hatch and the cycle restarts.

Nymphs of *S. kahawaluokalani* are yellow in color with black hair-like projections protruding from their abdomen. Adult *S. kahawaluokalani* are yellow, mottled with black spots, and have two large black tubercles that project from their dorsum. Many aphids produce winged adults for dispersal, but usually do so in response to overcrowding of the host plant or a sudden drop in host plant quality. *Sarucallis kahawaluokalani* is unusual among aphids in that all adults, except for oviparae, are winged and capable of dispersing. Fecundity and development of *S. kahawaluokalani* are dependent on ambient temperature, and under optimal conditions, *S. kahawaluokalani* adults can produce over six offspring per day, and nymphs can mature in as little as five days. Adults can live up to 21 days, producing more than 150 offspring within their lifetime.

Successful reproduction and development are dependent on the assimilation of nutrients. Crapemyrtle aphids acquire their nutrition by feeding on the phloem sap of their host plant. Phloem is rich in sucrose and other sugars, but contains low concentrations of amino acids. In addition to having small amounts of amino acids, phloem does not contain all of the amino acids required for successful growth, development, and reproduction. Crapemyrtle aphids have evolved several mechanisms to circumvent the disadvantages of feeding on phloem. To obtain the necessary quantity of nutrients, aphids feed on large volumes of phloem and use a special filter chamber in the gut to remove necessary nutrients. Furthermore, aphids harbor endosymbionts within the gut that manufacture amino acids that are required by the aphid but not present in the phloem. The most common endosymbiont of aphids are members of the genus *Buchnera*. Phloem contains large quantities of sucrose, which causes it to be a hypertonic solution. Thus, even though aphids feed on a liquid diet, they are confronted with the problem of becoming dehydrated from their source of food. Aphids can overcome this is by changing simple sugars into more complex sugars, which in turn lowers the osmotic pressure by creating fewer sugar molecules per molecule of water. Feeding on large quantities of phloem, followed by filtering and changing of sugar composition, creates a large amount of unused sugar and water. Crapemyrtle aphids excrete unused or transformed sugars, along with water, from the anus in a droplet known as honeydew. To avoid becoming coated and entangled in sticky honeydew, crapemyrtle aphids forcefully eject honeydew away from their feeding site. Honeydew can be easily spotted in the field as a shiny sticky substance on the leaves of crape myrtles.

Honeydew is rich in sugars and promotes the growth of fungi and other microorganisms. The honeydew of *S. kahawaluokalani* promotes the growth of an undescribed black sooty mold in the genus *Capnodium*. *Capnodium* sp. can turn the entire plant an unsightly black color, detracting from the visual aesthetics. Furthermore, thick carpets of *Capnodium* sp. interfere with photosynthesis, causing the abscission of leaves and in some cases complete defoliation of the plant. Established plantings of crape myrtle do not show signs of long term damage and bloom beautifully the following year. Damage to crape myrtles is influenced by crape myrtle cultivar and interactions with aphid natural enemies.

Crapemyrtle aphids are attacked by a variety of insect predators, but are not known to harbor any parasitoids. Lacewings (Chrysopidae), flower flies (Syrphidae), lady beetles (Coccinellidae), and other generalist predators feed on crapemyrtle aphids, especially when other prey are scarce. Predatory and parasitic hymenoptera of other insect pests feed on honeydew, allowing them to search for prey over greater distances. Because crapemyrtle aphids do not cause permanent damage to crape myrtles, and provide food for insect natural enemies, the use of chemical pesticides is strongly discouraged. If aphids reach high populations and control is necessary, the use of soapy water or power washing is usually sufficient for removing aphids from a particular plant. These methods are less harmful to insect natural enemies and help contribute to biological and natural control of crapemyrtle aphid and other insect pests.

References

Alverson DR, Allen RK (1991) Life history of the crapemyrtle aphid. Proc SNA Res Conf 36:164–167

Alverson DR, Allen RK (1992) Bionomics of the crapemyrtle aphid (Homoptera: Aphididae). J Entomol Sci 27:445–457

Dixon AFG (1998) Aphid ecology. Chapman and Hall, London, UK, 300 pp

Mizell RFI, Schiffhauer DE (1987) Seasonal abundance of the crapemyrtle aphid, *Sarucallis kahawaluokalani*, in relation to the pecan aphids, *Monellia caryella* and *Monelliopsis pecanis* and their common predators. Entomophaga 32:511–520

Mizell RF, Knox GW (1993) Susceptibility of crapemyrtle, *Lagerstroemia indica* L., to the crapemyrtle aphid (Homoptera: Aphididae) in North Florida. J Entomol Sci 28:1–7

Craw, Alexander

Alexander Craw was born on Ayr, Scotland, on August 3, 1850. He emigrated to California, USA, when he was 23, and by 1875 was placed in charge of a very large orange grove near Los Angeles. He helped D.W. Coquillett in investigations of chemical control of the new pest cottony cushion scale. He was the first to suggest use of natural enemies for control of this pest when chemicals failed. In 1890, he was appointed quarantine inspector at the port of San Francisco by the California Board of Agriculture, and it was he who developed and put into practice the principles of horticultural quarantine. In 1904 he accepted a position as Superintendent and Inspector of the Hawaiian Board of Agriculture and Forestry in Honolulu, where he remained until his death in 1908. Most of his publications were about control of pests and about exclusion of new pests by quarantine, but he did describe a few new species of insects.

Reference

*Essig EO (1931) Craw, Alexander. In: A history of entomology. The Macmillan Company, New York, NY, pp 593–595

Crawler

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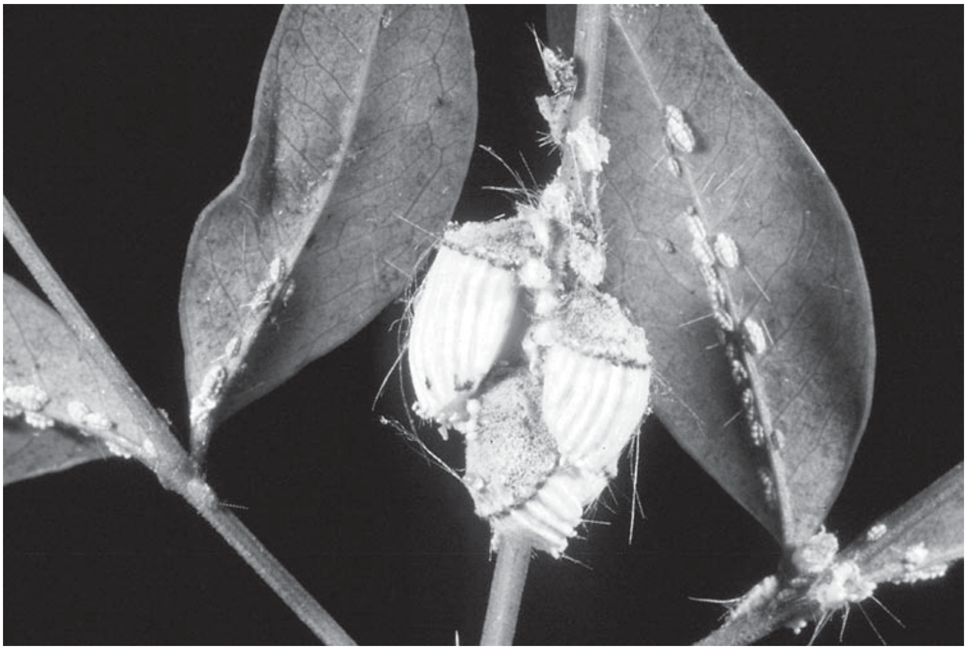
Crawler is the active stage of an insect immediately after egg hatch (first instar) found among certain insects in the order Hemiptera. The term crawler is most commonly used to describe first instar scale insects, but may also describe similar stages found among mealybugs and whiteflies. The crawler stage is noted for mobility allowing distribution within and among host plants. Many species that have a crawler period (e.g., Diaspididae and Aleyrodidae) subsequently produce (Fig. 124) immature stages that move little, if at all, following the crawler period.



Crawler, Figure 124 **Cottony cushion scale adults and crawlers. The adults (large with a white, fluted, waxy secretion on the stem) are easily observed, whereas the small crawlers (small insects along the mid-vein on the leaf) are harder to detect. (Photo by Lyle Buss, University of Florida.)**

In management of insects, the crawler stage is often one that is targeted for control because crawlers are small and have a relatively thin wax coating that makes them easier to kill with pesticides.

Crawling Water Beetles

Members of the family Haliplidae (order Coleoptera).

► Beetles

Creeping Myiasis

Infestation of humans by bot fly larvae that ultimately cannot complete their development and perish in the abnormal human host. The larvae typically die in the first instar after burrowing beneath the skin, causing little serious injury but causing itching and creeping eruptions. Species of *Gasterophilus* are usually implicated, and follow close association of humans with livestock, particularly horses and mules.

Creeping Water Bugs

Members of the family Naucoridae (order Hemiptera).

► Bugs

Cremaster

In Lepidoptera, a process at the tip of the abdomen, usually bearing spines or hooks, by which pupae are suspended from silk attached to a substrate surface.

Crenulate

A tem used to indicate a wavy or scalloped appearance.

Crenulate Moths (Lepidoptera: Epiplemidae)

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Crenulate moths, family Epiplemidae, total about 632 species worldwide, with most being Neotropical (230 sp.) and Indo-Australian (301 sp.). The common name for the family refers to the often scalloped, or crenulate, margins of the wings. Two subfamilies are known: Auzeinae, with about 25 sp. (mostly Indo-Australian), and Epipleminae for all others. The family is in the superfamily Uranioidea, in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults small to medium size (9–47 mm wingspan), with head scaling normal; labial palpi upcurved; haustellum naked; maxillary palpi minute, 1-segmented. Wings (Fig. 125) triangular, typically with distinct marginal emarginations and marginal points, and forewing tip often somewhat falcate; hindwing generally rounded to triangular and also usually with emarginations and marginal points or tail-like projections. Maculation mostly shades of brown with few markings and hindwings usually matching the forewing coloration; rarely more colorful; some are leaf-like. Adults nocturnal. Larvae leaf feeders or webbers.

Crenulate Moths (Lepidoptera: Epiplemidae), Figure 125 Example of crenulate moths (Epiplemidae), *Epiplema castanea* Warren from Taiwan.

Host plants in several plant families, including Bignoniaceae, Caprifoliaceae, Olacaceae, Oleaceae, Rosaceae, Rubiaceae, and others.

References

*Boudinot J (1982) Insectes Lépidoptères Epiplemidae. In: Faune de Madagascar. 60:1–55. Paris: Off. Rech. Sci. Tech. Outre-Mer, France

* von Dalla Torre KW (1924) Epiplemidae. In: Lepidopterorum catalogus. 30:1–57. W. Junk, Berlin.

*Holloway JD (1998) Subfamily Epipleminae. In: The moths of Borneo, 8:78–82, 92–132, pl.1, 6–8. Malayan Nature Society, Kuala Lumpur (Malayan Nature Journal, 52).

Seitz A (ed) (1912–33) Familie: Epiplemidae. Die Gross-Schmetterlinge der Erde, 2:277–280, pl. 48 (1912); 2(suppl.):171–172 (1933); 6:1141–1170, pl. 169–172 (1930); 10:577–600 (1929), 601–604, pl. 58–59 (1930); 14:390–394, pl. 67 (1928). A. Kernen, Stuttgart

*Stehr FW (1987) Epiplemidae (Geometroidea). In: Immature insects [1], 507. Kendall/Hunt, Dubuque

Crepuscular

Organisms in which the period of activity is twilight, either pre-dawn or dusk.

Cresson, Ezra Townsend

Ezra Cresson was born on June 18, 1838, in Pennsylvania, USA. He attended public schools in Philadelphia through the eighth grade, but then had to drop out to help support the family. Little of his paid employment was in entomology, and one of his positions was as clerk in the treasurer' s office of the Pennsylvania Railroad Company, another was as secretary to a wealthy patron of the Philadelphia Academy of Sciences, and a third was with a fire insurance company. His interest in insects was kindled by his future father-in-law, James Ridings. He, Ridings, and George Newman, in 1859, were the founding members of an entomological society which, in 1867, changed its name to the American Entomological Society, and is now the oldest existing entomological society in the United States. The society, under its original name, began in 1863 to publish Proceedings of the Entomological Society of Philadelphia. Cresson was one of the society members who set the type for the printing: this was truly an in-house publication. In that first issue of the Proceedings appeared Cresson' s "Catalogue of the Cicindelidae of North America," after which he confined his own publications to works on Hymenoptera. Between 1861 and 1882 he published 66 papers on Hymenoptera including catalogs and descriptions. In 1901 his collection, including 2,367 type specimens representing 3,511 species, was presented to the American Entomological Society. He died on April 19, 1926. Two of his five children displayed a strong interest in entomology. These were Ezra T. Cresson, Jr., who specialized in Diptera, and George Binghurst Cresson, who specialized in ants.

Reference

*Mallis A (1971) Ezra Townsend Cresson. In: American entomologists.Rutgers University Press, New Brunswick, NJ, pp 343–348

Cretaceous Period

A geological period at the end of the Mesozoic era, extending from about 170 to 65 million years ago.

► Geological Periods

Cribellum

In spiders, a sieve-like structure found just in front of the spinnerets.

Cribrate

This describes a structure or surface that is pierced by narrowly spaced small holes, resembling a sieve or strainer, or that functions as a sieve.

Crickets

Certain members (suborder Ensifera, superfamily Grylloidae) of an order or insects (Orthoptera).

► Grasshoppers, Katydids and Crickets

Criddle, Norman

Norman Criddle was born in Addlestone, Surrey, England, on May 14, 1875 and moved to Canada in 1882 with his parents. The Criddle family established a homestead in Aweme, Manitoba. From his early childhood, Criddle had a strong interest in flora and fauna. This was expressed, in part, by drawing and painting, which he developed to great proficiency. His artistic skills were "discovered" only after he developed a poison bait, a mixture that came into wide use for grasshopper control during periodic outbreaks on the Canadian prairie. The bait brought the attention of Dominion Entomologist James Fletcher, who came to admire Criddle's artistic and entomological abilities. They coauthored a publication on weeds in Canada in 1905. This pioneer entomologist received a government appointment in 1913, and investigated the cause of grasshopper plagues, attributing them to cycles of weather correlated with changes in the numbers of sunspots. Over the years, he also came to mentor several of Manitoba's foremost entomologists. His entomological interests extended well beyond grasshoppers, of course, and he was a major proponent of understanding the biology of insects as a basis for their control. Norman Criddle received an honorary degree in Agriculture from the Manitoba Agricultural College shortly before his death on May 4, 1933 in Brandon, Manitoba.

Crimean-Congo Hemorrhagic Fever

This virus affects humans, and is transmitted by several species of ticks.

► Ticks

Cristate

A term used to indicate the presence of a high ridge or crest.

Critical Period

The notion that the brain is needed for a period of time (the critical period) if the insect is to develop properly. The brain synthesizes PTTH that activates the prothoracic gland to secrete ecdysone. Removal of the brain after PTTH produced (after the critical period) does not disrupt development.

Crochets

The minute hooks found on the prolegs, mostly of caterpillars. They usually are arranged in rows or circles.

Crop Diversity and Pest Management

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Contemporary theories concerning the relationship between crop diversity and arthropod damage originated from observations made during the early decades of the twentieth century in temperate tree plantations and mixed farming systems in the tropics. Seminal studies of insect damage on collards by Pimentel and Root provided a broad ecological framework for examining arthropod damage under mixed and simple cropping systems. The classic experiments of Risch and Bach in Costa Rica demonstrated that the relationship between mixed cropping systems and pest damage is ultimately determined by the specifics of arthropod behavior.

Crop diversity can take many forms. Traditional farming systems in the tropics are often characterized by intercropping, in which different crops are arranged in alternating rows, or mixed together without regard to row. Mixed cropping systems in both temperate and tropical regions can resemble a mosaic-like patchwork of distinct crops. Trees, hedgerows, cover crops and even weeds can increase the plant diversity on a farm. Modern examples of crop diversity include the intentional mixing of resistant and non-resistant wheat hybrids for Hessian fly management in the midwest of the USA.

Several hypotheses have been put forward to explain why pest damage is sometimes less in polycultures, as mixed cropping systems are called. The "enemies" hypothesis, defined by Root, suggests that polycultures offer greater resources than monocultures to parasitoids and predators in the form of nectar and pollen, alternate hosts and prey, and habitat. Populations of natural enemies are hypothesized therefore to be more stable in mixed cropping systems than in simple ones, and so better able to keep herbivore populations below economically damaging levels.

A complementary idea put forward by Root is the "resource concentration" hypothesis. This proposes that resources provided by a crop are more easily exploited by herbivores when "concentrated" in a uniform stand. It may become more difficult for the herbivore to find and exploit the crop when it is mixed with other crops. This is because the volatiles, appearance, and leaf characteristics of non-host plants may interfere with the host-finding mechanisms of certain arthropods. According to the "resource concentration" hypothesis, once an herbivore has found a suitable host within a polyculture, within-stand effects such as shading, increased humidity, and the presence of non-host crops may influence the arthropod to feed and oviposit less than it would in a monoculture, and to emigrate from the crop patch sooner than it would from a large uniform stand.

Trap cropping is another form of polyculture that has been used to reduce pest damage. The pest is drawn away from the crop being protected by the presence of a more attractive crop – the trap crop. Trap crops are often sprayed with pesticides to keep pest populations from building up and moving on to the main crop.

Neither the enemies hypothesis, resource concentration hypothesis or trap cropping has been shown consistently to predict how an arthropod will behave in a mixed cropping system. In the 1970s, mathematical theories were proposed to suggest that diverse systems should be more stable than simple ones, and therefore that polycultures should experience less pest damage than monocultures. The misconception that crop diversity in itself reduces pest damage has persisted in spite of the fact that it is inconsistent with empirical observation. Stability is not a characteristic of most annual cropping systems, which tend to begin and end with the complete destruction of all vegetation in the field. Whether one or several crops are grown in the field in the interim may have little bearing on the long-term stability of the cropping system.

Reviews of the literature indicate that in over fifty percent of the cases studied, intercropping reduced arthropod damage compared to monoculture. Fifteen to eighteen percent of the time, damage was worse in intercropped systems, and in twenty percent of the cases the results were variable. A significant trend revealed by reviews of the intercropping literature is that damage by monophagous insects tends to be reduced in polyculture, while damage by polyphagous insects is more likely to be increased or unaltered in mixed cropping systems. Under traditional mixed cropping conditions in Costa Rica, densities of a monophagous species of leaf beetle are reduced under polyculture, while densities of a polyphagous leaf beetle species are not reduced. Studies such as this indicate that the damage caused by an arthropod species in polyculture will be determined by the quantity and quality of host plants in the mix rather than by crop diversity in the taxonomic sense.

In addition to host range, the host-finding mechanisms and the mobility of an arthropod will determine how its behavior is influenced by a given polyculture. In Costa Rica, populations of a monophagous chrysomelid were reduced in polyculture because they tended to emigrate more quickly from the mixed stands. Arthropods with sensitive host-finding mechanisms may be more easily deterred by the presence of non-host plants than arthropods that do not rely on specific visual or olfactory host-finding cues. Highly mobile insects such as certain grasshoppers or beetles may abandon a patch in which suitable hosts are hard to find more quickly than weak fliers such as whiteflies or thrips.

Host-finding, mobility, and host range also influence how natural enemies will behave in a complex cropping system. Generalist predators and parasitoids are probably better adapted than specialized natural enemies to search the varied visual and olfactory landscape presented by a polyculture. Like monophagous herbivores, natural enemies with a narrow host range may be more efficient when searching in a uniform environment.

By influencing probing behavior, mixed cropping systems may also affect the transmission rates of insect-vectored diseases. For example, crop combinations that encourage vectors of non-persistent viruses such as aphids to probe more frequently and for a shorter duration may increase the likelihood of non-persistent virus transmission. By contrast, the transmission of persistent viruses tends to require longer probing periods, and so might be reduced by a cropping environment that stimulates vectors such as whiteflies to probe for shorter periods.

Recent efforts in biological control have emphasized the introduction of perennial refugia or nursery crops for natural enemies in and around cropped areas. This is a form of polyculture. Refugia crops are planted to maintain stable populations of natural enemies in a cropping system by providing habitat, pollen, nectar, and alternate victims, so that predators and parasitoids will be available near the crop to suppress incipient pest populations. Region-wide approaches to managing major pests such as whiteflies and certain Lepidoptera have included the establishment of refugia for natural enemies.

Standard methods of field research that have been established for studying and managing pest populations in large monocultures may require modification for use in complex polycultures. Conventional field plot research designs require replication under uniform conditions that are often difficult to achieve in a heterogeneous environment. The reduction of field plot variability required for standard statistical analysis is also difficult to accomplish in polycultures, which are by definition highly variable environments. Elucidation of the relationship between polyculture and pest management may require the adaptation of multiple regression methods and spatial diversity analysis.

Similarly, methods for establishing scouting protocols and calculating economic injury levels have been designed to address pest behavior in homogeneous environments, and may require adaptation for mixed cropping systems. The population dynamics and feeding behavior of both herbivores and natural enemies may be different on a crop when that crop is grown in polyculture as opposed to monoculture. The resources that can be allocated to scouting and managing the pest complex of a crop that represents only one component of a diverse farm may differ from the resources available to manage the pest complex of a large monoculture.

References

Andow D (1991) Vegetational diversity and arthropod population response. Annu Rev Entomol 36:561–86

Bach CE (1980) Effects of plant density and diversity in the population dynamics of a specialist herbivore, the striped cucumber beetle, *Acalymma vittata*. Ecology 61:1515–1530

Bach CE (1980) Effects of plant diversity and time of colonization on an herbivore-plant interaction. Oecologia 44:319–326

Pimentel D (1961) Species diversity and insect population outbreaks. Ann Entomol Soc Am 54:76–86

Risch SJ (1980) The population dynamics of several herbivorous beetles in a tropical agroecosystem: the effect of intercropping corn, beans and squash in Costa Rica. J Appl Ecol 17:593–612

Risch SJ (1981) Insect herbivore abundance in tropical monocultures and polycultures: an experimental test of two hypotheses. Ecology 62:1325–1340

Risch SJ, Andow D, Altieri MA (1983) Agroecosystem diversity and pest control: data, tentative conclusions, and new research directions. Environ Entomol 12:625–629

Root R (1973) Organization of a plant-arthropod association in simple and diverse habitats. The fauna of collards. Ecol Monogr 43:95–124

Crop

A portion of the foregut in the alimentary canal of insects. The crop receives the insect’s meal, and in insects that feed only infrequently it may be greatly expanded to accommodate the occasional meal. Although lined with a thick lining that inhibits digestion, in some insects the digestive enzymes secreted from the mouth or regurgitated from the midgut pass into the crop and perform partial digestion.

► Alimentary Canal and Digestion

Crop Loss Assessment

This refers to the procedure for assessing arthropod impact on crop yield and quality.

► Methods of Measuring Crop Losses

Crop Residue

A portion of the crop that is not harvested, and usually is returned to the land by tillage or as mulch.

Crossing Over

The reciprocal exchange of polynucleotides between homologous chromosomes during meiosis.

Cross-Resistance

In pest management, the resistance of a pest population to a pesticide to which it has not been exposed that accompanies the development of resistance to a pesticide to which it has been exposed.

Cross-Striped Cabbageworm, *Evergestris rimosalis* (Guenée) (Lepidoptera: Pyralidae)

This is an important crucifer pest in the southern USA.

► Crucifer Pests and their Management

Cross Vein

Short crosswise veins between the lengthwise wing veins and their branches. Most insects have only a few cross veins, but the netwinged species have numerous cross veins.

► Wings of Insects

Crotch, George Robert

George Crotch was born in Cambridge in 1842 and obtained his undergraduate education at Cambridge University. While still a student he was deeply involved in collecting insects. By the time he received an M.A. degree (1863) he had concentrated on Coleoptera, and he published a Catalogue of British Coleoptera. The next year he collected insects in the Canary Islands and, on return to England, obtained a job in the university library at Cambridge. In 1865 and 1870 he made collecting trips to Spain, and meanwhile had published several entomological papers including works on Coccinellidae and Erotylidae and had become sub-editor of Zoological Record. In the autumn of 1872 he sailed to the USA and traveled overland to California in the spring of 1873. A collecting expedition to British Columbia, Oregon and parts of California followed. In the autumn of 1873 he returned to Philadelphia (his point of arrival in the USA), having accepted an appointment from Louis Agassiz to curate insects in the Museum of Comparative Zoology at Harvard University. However, he had been infected with "consumption" (tuberculosis), of which he died on June 16, 1874. Despite his travel and illness, he published eight papers on North American Coleoptera in 1873! One can only wonder at what he might have accomplished had he not died so young. The insects that he collected in the Azores are in the Natural History Museum (London), whereas his Coccinellidae and Erotylidae are in the Museum of Comparative Zoology, Harvard University.

Reference

*Essig EO (1931) Crotch, George Robert. In: History of entomology. The Macmillan Company, New York, pp 598–600

Crowson, Roy Albert

Roy Crowson was born in the county of Kent, England, on November 22, 1914. He graduated from University College, London, in 1936, and then began anatomical research on Coleoptera. He worked as assistant curator of the Tunbridge Wells Museum until World War II, when he served in the Royal Air Force. In 1948, he joined the Department of Zoology of Glasgow University. Numerous publications on structure of beetle adults and larvae followed, with more on classification, until his death. Major works were a series called "The natural classification of the families of Coleoptera" which (1955) were republished as a book, a (1971) book "Classification and biology," and a (1981) book "The biology of the Coleoptera." He died on May 13, 1999, survived by his wife, Betty.

Reference

Wheeler Q (2000) Professor Roy Albert Crowson 1914–1999. Coleopterists Bull 54:120–121

Crucifer

A plant in the family Cruciferae, such as cabbage, broccoli, or collard. Crucifers also are called cole crops.

Crucifer Flea Beetle, *Phyllotreta cruciferae* (Goeze) (Coleoptera: Chrysomelidae)

This species is a pest of several crucifer crops.
► Flea Beetles (Coleoptera: Chrysomelidae)

Crucifer Pests and their Management

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Crucifer crops are members of the family Cruciferae and include cabbage, cauliflower, Brussels sprouts, broccoli, rape and mustard. Grown commercially or as garden vegetables, they attract a large number of insects. Since the common crucifer crops are introduced vegetables, most of the insect feeders originated in Europe or are species native to the United States that feed on a wide range of plants. The importance and abundance of a given insect species changes with location. Insects attacking crucifers can be divided into three groups: (i) leaf or foliage feeders, (ii) sap feeders, and (iii) root feeders.

Leaf or Foliage Feeders: Caterpillars and Flea Beetles

Caterpillars of moths, skippers, and butterflies in the order Lepidoptera are important leaf feeders. The adults have four large wings usually covered with brightly colored scales. The most common are the cabbage looper, the imported cabbageworm, and the diamondback moth. Two others with potential of becoming major pests are the cross-striped cabbageworm and the cabbage webworm. The rank of species importance generally varies with latitude. In the more southern areas of the United States, the cabbage looper is the most abundant, followed by the imported cabbageworm and the diamondback moth. In the more northern latitudes, the cabbage looper populations become more variable and the imported cabbageworm becomes the dominant species. Both the cross-striped cabbageworm and the cabbage webworm are generally localized, occasional pests.

The Imported Cabbageworm, *Pieris rapae* (L.) (Pieridae)

The imported cabbageworm was first discovered in North America in 1860 when a single specimen was captured in Quebec. Nearly 30 years later, it had spread north to Hudson Bay, south to the Gulf of Mexico, and west to the Rocky Mountains. It now occurs throughout most of North America. It spends the winter as a cocoon in or near crucifer crops. In spring, the white adult (Fig. 126) butterfly emerges. The male butterfly has one black spot and the female has two black spots on each front wing. After mating, the female lays eggs within 24 h of emergence. Eggs are laid singly on the underside of the outer leaves of the plant. They hatch into caterpillars in four to eight days. The caterpillars molt four times and pass through five stages in 12–33 days. The dark velvety green caterpillars (Fig. 127) have a faint yellow stripe down the back and along the sides. They feed voraciously on leaves and reach 25 mm in length. When full grown, the caterpillar changes into a cocoon. Each cocoon changes to an adult butterfly in 8–20 days. The butterfly lives for approximately three weeks. Females generally lay 200–300 eggs. They generally have two to four generations a year, but as many as six generations have been observed in the southern portions of its range. A tiny wasp parasite, *Cotesia glomerata* (L.) (Hymenoptera: Braconidae), attacks the first three caterpillar stages. It lays 20–50 eggs into a caterpillar. The eggs hatch into parasite grubs that feed within the caterpillar. When the parasite grubs complete feeding on the caterpillar, they emerge as a group from the late fifth stage of the caterpillar, and spin yellow cocoons. The caterpillar dies. *Cotesia rubecula* (Marshall) is an exotic solitary wasp that is a close relative of *C. glomerata*. It generally attacks the first three caterpillar stages,

Crucifer Pests and their Management, Figure 126 **Imported cabbageworm adult.**

but it kills the imported cabbageworm caterpillar soon after it molts to the fourth caterpillar stage. The single *C. rubecula* grub inside it exits, and spins a white cocoon. Another parasitic wasp, *Pteromalus puparum* (L.) (Hymenoptera: Pteromalidae) attacks the cocoon stage of the imported cabbageworm. *P. puparum* is a gregarious internal parasite of the imported cabbageworm, attacking the newly formed cocoon. The parasitic grubs develop within the host and emerge as adult wasps through a small hole cut in the cocoon case.

The Cabbage Looper, *Trichoplusia ni* (Hübner) (Noctuidae)

The medium sized adult moth (Fig. 128) is grayish brown, about 25 mm long, with wing span of 38 mm. There is a silver figure 8 design near the center of each front wing. The back wings are light brown with a dark margin. In spring, about 300 eggs laid by a female singly on the upper and lower surfaces of leaves, hatch in three days into caterpillars. The caterpillar eats holes in leaves and reaches (Fig. 128) full size in two to four weeks. The green caterpillar forms a characteristic loop as it moves. It reaches 40 mm long when full grown and has a thin white line along each side of the body and two near the middle line of the back. It spins a cocoon and passes the winter in this stage. It emerges as an adult in spring. There are three to six generations a year. A parasitic fly, *Voria ruralis* (Fallén) (Diptera: Tachinidae), attacks the caterpillar. There are three parasitic wasps that attack the cocoon stage: *Gambrus ultimus* (Cresson), *Stenichneumon culpator cincticornis* (Cresson), and *Vulgichneumon brevicinctor* (Say) (Hymenoptera: Ichneumonidae).

Diamondback Moth, *Plutella xylostella* (L.) (Plutellidae)

The diamondback moth is a cosmopolitan insect. It is slender and grayish brown, 8.5 mm long, with

Crucifer Pests and their Management, Figure 127 **Imported cabbageworm caterpillars.**

wing expanse of about 14 mm. When folded, the wings display three diamond-shaped yellow spots along the line where the wings meet. The colors of the female are lighter, and the markings less distinct than the males. The back or hind wings have a fringe of long hairs. The moth passes the winter under leaves. In spring, the moth lays an average of 160 small yellowish-white eggs that hatch in three to five days. The greenish caterpillars feed on the leaves and complete development in 10–30 days. The full-grown caterpillar (Fig. 129) is yellowish green with erect long black hairs. It forms a fine white mesh cocoon and the adult emerges in about a week. There are four to six generations a year in North America depending on temperature. In the tropics, there can be as many as 15–18 generations a year. The most common parasite of the caterpillar is a wasp, *Diadegma insulare* (Cresson) (Hymenoptera: Ichneumonidae), that is capable of killing up to 70% of the caterpillars.

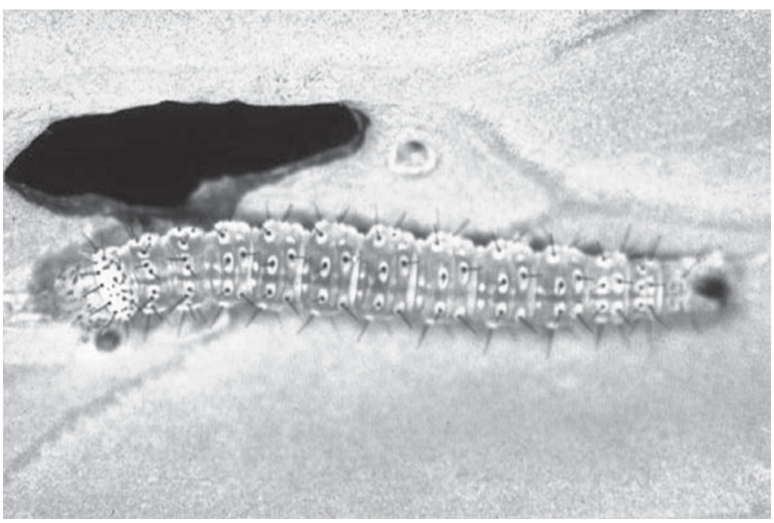
Cross-striped Cabbageworm, *Evergestis rimosalis* (Guenée) (Pyralidae)

The adult is a small yellowish brown moth (Fig. 130) with a dark patch towards the end of the front margin of the front wing. The female lays about 80 eggs in small overlapping masses on the host plant leaf. The eggs are yellow, flattened, and hatch in three to seven days. There are four caterpillar stages that complete (Fig. 131) development in 6–17 days and change into a cocoon. The caterpillar is gray on the back and yellow on the lower side, with a broad distinctive black band on each side separating the gray from the yellow. The cocoon stage lasts for 9–10 days, before changing into the adult. There are three to four generations a year. This insect has the potential to be a very serious and destructive pest of crucifer crops in the eastern United States. The young caterpillars feed on leaves but the mature caterpillars migrate to the heart or head of the plant and can riddle the head with feeding holes making the plant unmarketable. It is naturally kept in check by a parasitic wasp, *Cotesia orobenae* Forbes (Hymenoptera: Braconidae), that feeds on the caterpillar. Indiscriminate use of insecticides that kill off the parasite will result in outbreaks of the cross-striped cabbageworm.

Crucifer Pests and their Management, Figure 128 **Cabbage looper adult.**

Cabbage Webworm, *Hellula rogatalis* (Hulst) (Lepidoptera: Pyralidae)

The cabbage webworm is a sporadic but destructive pest of crucifer crops in the southeastern United States. It is potentially the most serious pest of broccoli. The front wing of the moth is light brown and gray. The newly emerged adults start laying eggs in three to four days and can deposit up to 161 eggs per female. Newly laid eggs are yellowish green, and turn pink as they mature.

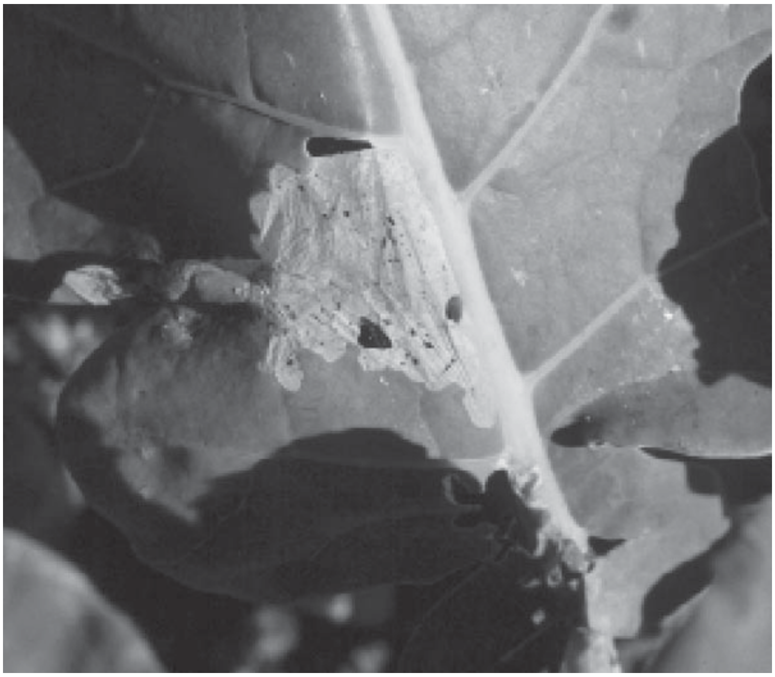


Crucifer Pests and their Management, Figure 129 **Diamondback moth caterpillar.**

Crucifer Pests and their Management, Figure 130 **Cross-striped cabbageworm adult.**

Crucifer Pests and their Management, Figure 131 **Cross-striped cabbageworm caterpillars.**

Most of the eggs are laid on the upper surface of the leaf, and hatch in three to eight days. There are five caterpillar stages and they complete development in 15–35 days. The first two caterpillar stages mine the leaf between the upper and lower leaf surface (Fig. 132). The larger caterpillars feed on the underside of the leaf causing them to curl and roll up. They also spin webs among the rolled leaves. The webs protect them from insecticide sprays. The last two caterpillar stages feed on the leaf and midrib, breaking it into two. The caterpillar moves to the heads after eating the leaves. The cocoon stage lasts for 7–17 days before changing to adult. The adult lives for 11–25 days. There are



Crucifer Pests and their Management, Figure 132 **Cabbage webworm damage.**

one to two generations per year. It is difficult to control cabbage webworms because the caterpillars are protected and there are no effective parasites that attack them.

Occasional Caterpillar Pests

Caterpillars that are occasional or minor pests include the corn earworm *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae); fall armyworm, *Spodoptera frugiperda* (J. E.Smith) (Lepidoptera: Noctuidae); green cloverworm, *Plathypena scabra* (Fabricius) (Lepidoptera: Noctuidae); yellow-striped armyworm (Lepidoptera: Noctuidae), and southern cabbageworm, *Pontia protodice* (Boisduval & LeConte) (Lepidoptera: Pieridae). Severe feeding on the leaves by these caterpillars results in loss of crop yield. All plant stages, from seedling to heading, are susceptible to attack. Before a management program is initiated, it is important to have an understanding of the occurrence of the individual species and their life stages during the growing season.

Flea Beetles (Coleoptera: Chrysomelidae)

Flea beetles are small elongate, oval, black beetles of 1.6–3.2 mm with back legs enlarged for jumping. When disturbed, they jump up resembling fleas bouncing up and down, hence their common name, flea beetles. The adult beetle is a general feeder of leaves, leaving tiny pits or small holes. When they are present in large numbers, their feeding can cause pitted areas and numerous holes on leaves. There are two common species among crucifers, the potato flea beetle *Epitrix cucumeris* (Harris) and the tobacco flea beetle *Epitrix hirtipennis* (Melsheimer). Eggs of flea beetles are very tiny and difficult to see. The potato flea beetle scatters its eggs in the soil close to roots of host plants. The tobacco flea beetle eggs are laid in batches or clusters. They hatch in about 10 days into whitish, slender, cylindrical worms that feed on the roots of weeds and crucifer plants. The worms or grubs usually do not cause as much damage as the adults. When full grown in about four weeks, the worms are 3.2–8 mm long, and have tiny legs and brownish heads. They change into the cocoon stage that lasts for 7–10 days before emerging as adults. There are usually one to two generations a year. Flea beetles are very common on new plantings and can cause severe damage to young seedlings or plants. They often infest weeds near crucifer crops and move onto young plants. Heavy infestations cause young plants to dry up.

Sap Feeders: Harlequin Bugs, Aphids

Harlequin bugs and aphids are the most serious sap feeders of crucifers. They can be especially damaging to young plants that cannot withstand as much damage as the larger plants. Thus, they are often serious pests during the early plantings or transplantings of crucifers. Both the adults and young nymphs suck sap from the plants.

Harlequin Bug, *Murgantia histrionica* (Hahn) (Heteroptera: Pentatomidae)

The harlequin bug (Figs. 133 and 134) is an exotic pest originating in Central America. It was first recorded in the United States in 1864. It passes the winter south of the 40°N latitude. Individuals found north of the 40°N latitude most likely are carried by wind currents or are due to seasonal migration. It was considered the most destructive insect pest of crucifers in the United States before the use of synthetic insecticides because it is capable of destroying entire crops. After the advent of synthetic insecticides, the importance of the harlequin bug declined. However, the harlequin bug has often caused substantial damage in crucifers during the past decade when insecticides were not used. The harlequin bug has a wide host range and has been reported to feed on over 50 species of plants, including crucifers. Cabbage, collards, broccoli, Brussels sprouts, kale, mustard, turnip, and cauliflower are a few of the economically important crops attacked by this pest. It also has been found on many wild plants, allowing the bugs to survive when crucifers are not present. The number of harlequin bug generations per year varies by location. There are two generations in the north and up to five generations in the South. In the North, the adult finds shelter in cabbage stalks, grass or other debris. In the South, the insects feed and breed during the entire year. The adults become active in spring when they start feeding on weeds, and are ready to lay an average of 150 eggs when garden plants or crucifers are available. The tiny white eggs that look like kegs are laid mostly on the underside of leaves in two rows. There are normally 12 eggs per batch, and each egg has two broad black loops. They hatch in 4–29 days, depending on temperature into young (nymph) bugs. The young bugs molt after five days. Each developing bug molts four times and passes through five nymphal stages in about 45 days to reach the adult stage. Feeding damage results in death of young plants. The younger plants succumb to feeding injury sooner than the older plants. Time to death is shorter when larger numbers of harlequin bugs feed together on the same plant.

Cabbage Aphids, *Brevicoryne brassicae* (L.) (Hemiptera: Aphididae)

Cabbage aphids are green, soft-bodied insects often referred to as plant lice because of the large numbers and their rapid rate of reproduction. They are 1.6–3.2 mm in length. They feed by inserting their sharp needle-like stylets in their beaks into plant tissues and suck sap from the plant. Affected leaves (Fig. 135) curl and crinkle or become deformed. During severe infestations, they cover the whole plant, causing the plant to wilt and die. Infested plants that survive are shorter and grow more slowly, and cabbage heads that are formed are light in weight and are not suitable for marketing. The aphid can reproduce by normal sexual reproduction and asexually without

Crucifer Pests and their Management, Figure 133 **Harlequin bug adults on rape.**

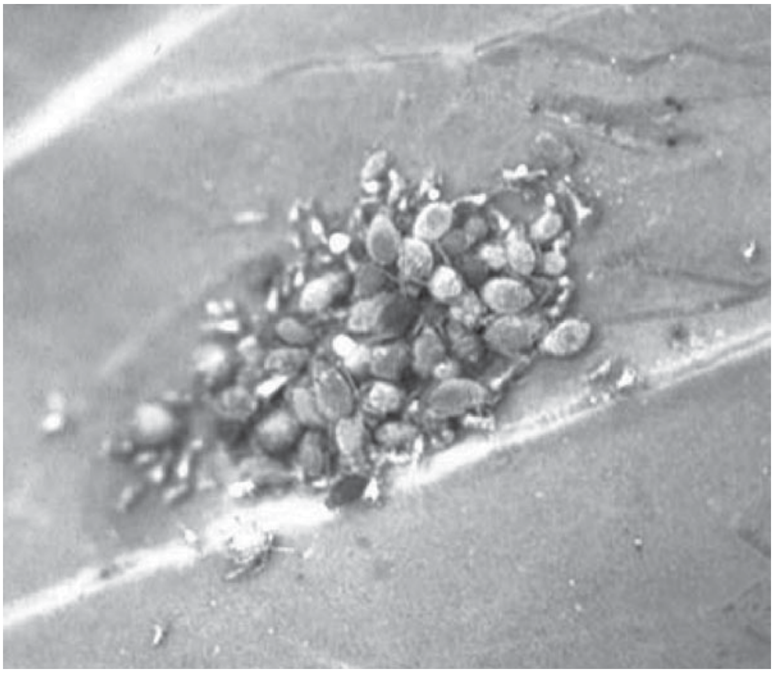
mating. Sexual reproduction occurs in the fall when winged males and females are formed. These are the fall migrants that leave the summer host. The winged females produce wingless females that mate with the males of the previous generation. After mating, the true female lays small black fertilized eggs in a sheltered place to pass the winter. From these eggs rise the stem mother the next year. The eggs hatch into small nymphs (young aphids) and grow to full size as stem mothers with warmer weather. These stem mothers are wingless. Each can reproduce without mating and gives rise to 50–100 eggs that hatch while they are still inside the stem mother and emerge as active nymphs in 7–14 days. These young nymphs can reproduce just like their stem mothers within a week. Each generation takes about a month. The number of generations depends on temperature, and in the far south, they continue to breed year round. Several natural enemies feed on aphids. The most common predators are grubs and adults of ladybird beetles and green lacewings, and the maggots of the flower (syrphid) fly. These usually keep the aphid population down. During heavy infestations, chemical sprays or insecticidal soaps may have to be used. For chemical sprays to be effective, they have to reach the underside of the leaves where the aphids usually lodge.

Root Feeder: Cabbage Maggot

Cabbage Maggot, *Delia radicum* (L.) (Diptera: Anthomyiidae)

This is a serious pest in the northern states above 40°N latitude, and in Canada. The adult fly resembles a housefly and is dark ash gray in color, but is smaller, 6.4 mm long. It lays its eggs in cracks and crevices in the soil near the roots. The eggs hatch in three to seven days into small maggots. The maggots feed on the roots of crucifers below ground level and thus are not easily seen. Small

Crucifer Pests and their Management, Figure 134 Harlequin bug nymph.



Crucifer Pests and their Management, Figure 135 Cabbage aphids.

roots are entirely eaten and larger roots show feeding tunnels caused by the maggots. Heavy feeding causes the plant to wilt and become stunted. Such plants have a sickly color. The maggots are white, 6.4–8.5 mm and without legs, and feed for three to four weeks to reach full size. They move away from the root to the soil and form a brown casing called the puparium within the top few inches of the soil. The puparium stage lasts for two to three weeks. The adult fly that emerges begins laying eggs. There are two to four generations a year. The winter is passed in the quiescent pupa stage inside the puparium casing. To control this fly, it is best to cover the seedbeds of crucifers with thin cloth or fine mesh gauze. Insecticidal drenches also can be used at the time of planting or transplanting.

References

Chamberlin JR, Kok LT (1986) Cabbage lepidopterous pests and their parasites in southwestern Virginia. J Econ Entomol 79:629–632

Kok LT, Acosta-Martinez JA (2001) Development of Cotesia orobenae Forbes (Hymenoptera: Braconidae) in its host, *Evergestis rimosalis* (Gueneé) (Lepidoptera: Pyralidae). J Entomol Sci 36:9–16

Kok LT, McAvoy TJ (1989) Fall broccoli pests and their parasites in Virginia. J Entomol Sci 24:258–265

Lasota JA, Kok LT (1989) Seasonal abundance of imported cabbageworm (Lepidoptera: Pieridae), cabbage looper (Lepidoptera: Noctuidae), and diamondback moth (Lepidoptera: Plutellidae) on cabbage in southwestern Virginia. J Econ Entomol 82:811–818

Ludwig SW, Kok LT (2001) Harlequin bug, *Murgantia histrionica* (Hahn) (Heteroptera: Pentatomidae) development on three crucifers and feeding damage on broccoli. Crop Prot 20:247–251

Mays WT, Kok LT (1997) Oviposition, development, and host preference of the cross-striped cabbageworm (Lepidoptera: Pyralidae). Environ Entomol 26:1354–1360

Crypsis

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Crypsis is a Greek word meaning camouflage. An animal that is cryptic is one that is camouflaged so that it is difficult to discern from its background. The advantage of crypsis in most animals is that it gives protection against predators that detect prey by eyesight. For example, many green caterpillars are camouflaged on leaves, giving them protection against insectivorous birds. Some predators are also cryptic which enables them to get close to prey that detect predators visually. For example, a lion or a leopard crouching in yellow-brown grass is well camouflaged so its prey may inadvertently wander close to it. Among arthropods, the flower mantids *Pseudocreobotra* and *Hymenopus*, and the crab spider *Misumena* (Thomisidae), are all cryptic when resting on flowers while waiting to grab insects that visit the flower for nectar or pollen. Crypsis here could be both a defense against predators (Figs. 136 and 137) and also an aid for capturing insects that visit the flowers but do not see them. However, it has not been demonstrated that fewer insects visit flowers with conspicuous rather than with cryptic predators on them, so this suggestion remains unproven.

The simplest form of camouflage involves the animal's color matching that of its background, e.g., green lacewings, *Chrysopa* (Neuroptera), on green leaves or transparent mosquito larvae in the plankton of ponds. However, birds and some other vertebrate predators have excellent eyesight and can recognize a simply camouflaged insect either by the shadow on its lower surface or by its characteristic outline. Two evolutionary responses of cryptic insects to such predators are "countershading" and "disruptive coloration."

Green grasshoppers are cylindrical so, when sunlight comes from above, the ventral surface will be in shadow and hence appear to be darker green than the dorsal surface. Countershaded grasshoppers are paler green ventrally so that this shadow is reduced and the crypsis is improved because the animal appears uniformly green in side view. Green hawkmoth caterpillars usually rest upside down under leaves and stems and have reversed countershading with the upper ventral surface dark green and the lower dorsal surface pale green.

Crypsis, Figure 136 **The eyed hawkmoth (*Smerinthus ocellata*) larva showing reverse countershading. When the larva rests in its normal orientation (left), the body appears flat due to the lighter coloration of the dorsal surface of the insect. When the twig bearing the larva is inverted (right), the larva becomes very conspicuous as the sun shining on the light dorsum increases the contrast between the insect's dorsal and ventral surfaces (photos by M. Edmunds).**

Crypsis, Figure 137 **Shorthorn grasshoppers mating, with disruptive black markings that break-up the body outline and conceal the eye (photo by M. Edmunds).**

Many green grasshoppers have black streaks and stripes on their bodies which draw the eyes of predators to these marks rather than to the contour of the insect. These are disruptive colors. Similar disruptive markings occur in caterpillars, shield bugs and many other cryptic insects. Large compound eyes are possibly a feature by which vertebrate predators can recognize an otherwise well camouflaged insect. One way of concealing the eye is for disruptive lines to pass through it so that attention is drawn away from the eye to the line which does not look like insect prey. Disruptive eyestripes occur in many grasshoppers. It is probable that disruptive colors increase the probability that a prey insect will not be found by a predator, but this has not been demonstrated experimentally.

Crypsis can also be perfected by morphological adaptations, e.g., by flattening of the body so there is no ventral shadow, or by resembling a specific part of the environment, such as a stick or a leaf. Some (Figs. 138 and 139) green lycaenid caterpillars, the green Australian mantid *Neomantis* (both on green leaves) and the brown mantis *Theopompa* and bug *Dysodius* (both on bark) are all flattened so there is no ventral shadow. Other insects have excrescences that break up the body outline, e.g., the grass-living mantis *Pyrgomantis* and the grasshopper *Cannula* are both long and slender with a pointed vertex on the head so they resemble a blade of grass, while the mantids *Phyllocrania* and *Hemiempusa* both have foliose excrescences (leaf-like outgrowths) on the legs and head (Fig. 140).

Looper caterpillars of geometrid and noctuid moths are usually brown with minute legs which are barely visible close to the head, and a slender, cylindrical body that may be rugose like the bark of a twig. They rest with the posterior claspers gripping a branch and the body extended in a straight line like a broken twig. Stick insects (Phasmida) and some praying mantids (e.g., *Danuria*, *Heterochaeta*, *Angela*) also have slender bodies and appropriate resting postures such that they closely resemble sticks, while leaf insects (Phasmida) and some mantids (*Choerododis, Phyllocrania*), butterflies (*Kallima*), and grasshoppers (*Zabilius*) closely resemble individual leaves. Some caterpillars rest conspicuously on the upper surfaces of leaves and closely resemble black and white bird droppings. Since insectivorous birds normally ignore droppings this probably gives good protection. However, as the caterpiller grows it becomes too large to mimic a bird dropping. The final instar of the alder moth (*Apatele almi*) is black and yellow (either aposematic or mimicking a wasp), that of *Trilocha kolga* changes to resemble the brown and black feces of a large lizard or bird. In *Oxytenis naemia* the final instar resembles brown leaf detritus fallen from the canopy, while in species of *Papilio* it is disruptively colored green and black and no longer rests on top of leaves. There is also a cicada, *Ityraea*, where a cluster of insects resembles a spike of flowers. These highly specific resemblances have been called stick mimicry, leaf mimicry, bird dropping mimicry, etc. However, since they have presumably evolved from simple camouflage by

Crypsis, Figure 138 The brown chrysalis of the hawkmoth, *Atemnora westermanni*, resembles a dead leaf lying amongst brown leaves on the forest floor of Ghana (photo by M. Edmunds).

Crypsis, Figure 139 **The mantid, *Neomantis australis*, from Queensland, Australia, shows cryptic green coloration and a flattened body that reduces shadow (photo by M. Edmunds).**

predator selection progressively eliminating the more easily found insects, they are probably better considered as extreme forms of crypsis, and Cott called them examples of "special resemblance."

A cryptic insect is only well camouflaged when on the correct background, but if it moves somewhere else or if the background changes it is immediately vulnerable to predation. Many cryptic insects move until they find a suitable background on which to rest, typically one on which they are cryptic. Thus, when the polymorphic grasshopper *Acrida turrita* was given a choice of backgrounds, significantly more green than yellow insects rested on a green background and significantly more yellow than green insects rested on a yellow background ($p<0.001$ in both cases). Similar background choice occurs in other polymorphic grasshoppers and in praying mantids, resulting in green insects tending to rest on green substrates and brown ones to rest on brown substrates. Bark-resting moths with disruptive markings adopt resting postures which align their markings with similar marks on the tree. The geometrid moth *Melanolophia canadaria* normally rests sideways with its markings running vertically parallel to striations in the bark. Given a choice of resting on a white surface with vertical or horizontal black tape strips, Sargent found that significantly more insects rested with the markings parallel to the strips ($p<0.001$) giving excellent camouflage, but equal numbers rested sideways and vertically (with head up or down), so the moth adjusts its resting position to coincide with the strips. When the experiment was repeated with the strips covered with acetate so that there was no difference in texture, the resting positions of the moths were random with respect to the strips, with equal numbers facing sideways and vertically, so Sargent concluded that the resting position of this moth is determined by tactile rather than visual stimuli. The noctuid moth *Catocala ultronia* normally rests with the head down and the markings parallel with vertical ridges on the bark. In a similar experiment, significantly more insects rested with their markings aligned to the strips giving good camouflage ($p<0.05$), and almost all moths rested head vertically down rather than horizontally ($p<0.001$). The resting positions were unchanged if the strips were covered with acetate, so in this species, resting posture is innate and not modified by substrate pattern or texture.

Crypsis, Figure 140 **The brown leaf mimicking preying mantid, *Phyllocrania paradoxa*, rests on brown dead vegetation in Ghana. Note the frills on head, body, and legs which break up the outline of the insect (photo by M. Edmunds).**

Some cryptic insects can change color (Fig. 141) so that they match their background, but this change usually takes several days or occurs only when the insect moults. Some swallowtail and other butterfly pupae can be either green or brown, usually matching their substrate. Details vary in different species, but in *Papilio polyxenes* short daylength induces most caterpillars to turn into brown pupae which are well camouflaged during the winter on deciduous shrubs. However, with a long photoperiod (i.e., in summer), pupae were usually brown on thick branches but green on thin twigs, giving good camouflage both on brown branches and on green twigs close to green leaves. Final instar poplar hawkmoth caterpillars (*Laothoe populi*) can be green or white depending on whether they are resting on green or white-leaved food plants. When reared on two different

Crypsis, Figure 141 **This satyrid butterfly, *Paralaza nepalica*, from Nepal blends into a sandy background (photo by A. Sourakov).**

plants significantly more sibling poplar hawk caterpillars on green leaved *Salix fragilis* became green rather than white while significantly more reared on white-leaved *Populus alba* became white. Similarly, various grasshoppers and praying mantids can be green or brown depending on whether their substrate is green or brown. In all examples that have been studied, the specific cue that determines which color the insect becomes is not substrate color but some other factor such as humidity (in the mantid *Miomantis paykullii* and the grasshopper *Syrbula admirabilis*), light intensity (in the mantid *Sphodromantis lineola*), or substrate reflectance (in the hawkmoth *Laothoe populi*).

Finally, there is abundant experimental evidence that crypsis does indeed reduce predation on insects. Most experiments involve placing some insects on a background where they are camouflaged and others on one where they are conspicuous and then exposing them to predators either in the laboratory or in the field. Polymorphic insects are especially good experimental subjects because the two morphs can be placed on two backgrounds, one of which matches the color of each morph. Experiments of this type have shown the selective advantage of resting on a background where the insect is cryptic in the peppared moth (*Biston betularia*), caterpillars of the pine looper (*Bupalus piniarus*) and poplar hawkmoth (*Laothoe populi*), grasshoppers (*Acrida turrita*), and praying mantids (*Mantis religiosa*). Experiments have also shown that countershaded green pastry prey were found significantly less often by wild birds than were uniformly green prey, so demonstrating the selective advantage of countershading.

It is tempting to ask why, if crypsis is of such great advantage to an animal, many more animals are not cryptic. The main reason is because cryptic animals must remain motionless, and adaptations that perfect crypsis may conflict with other essential activities such as feeding, escape by running or flying, or finding a mate. However, predators can become more proficient at finding cryptic prey by developing a "searching image" for specific insects. One evolutionary response to this aspect of predator behavior is for the prey to evolve several different color forms (polymorphism) such that the density of each morph remains low and the predator must acquire several different searching images if it is to fully exploit the prey population. Cryptic polymorphic insects occur among grasshoppers (*Acrida*), mantids (*Mantis*, *Sphodromantis*), hemipterans (*Philaenus spumarius*), caterpillars (*Bupalus piniarus*, *Herse convolvuli*), and moths (*Biston betularia*).

References

Cott HB (1940) Adaptive coloration in animals. Methuen, London, UK, 508 pp

Edmunds M (1974) Defence in animals: a survey of anti-predator defences. Longman, Harlow, UK, 357 pp

Edmunds M, Evans DL, Schmidt JO (eds) (1990) Insect defences. State University of New York, Longman, Harlow, UK, pp 3–21

Edmunds M, Dewhirst RA (1994) The survival value of countershading with wild birds as predators. Biol J Linn Soc 51:447–452

Edmunds M, Grayson J (1991) Camouflage and selective predation in caterpillars of the poplar and eyed hawkmoths (*Laothoe populi* and *Smerinthus ocellata*). Biol J Linn Soc 42:467–480

Wickler W (1968) Mimicry in plants and animals. Wiedenfeld & Nicholson, London, UK, 255 pp

Cryptobiosis

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Cryptobiosis is defined as the state of organism when it shows no visible signs of life and when its metabolic activity becomes hardly measurable, or comes reversibly to a standstill. Cryptobiosis is a generic term for ametabolism, and can be further divided into five categories based on factors inducing them: cryobiosis (induced by freezing), thermobiosis (low and high temperatures), osmobiosis (high osmolarity), anhydrobiosis (lack of water) and anoxybiosis (lack of oxygen).

So far, the African chironomid *Polypedilum vanderplanki* is the only insect species exhibiting cryptobiosis (anhydrobiosis, in this case). The larvae of this chironomid live in small and shallow rock pools. When the pool dries up during the dry season, the larvae become completely desiccated. When the rainy season comes and the pool fills with water, they may revive after rehydration. The desiccated larvae also become resistant to extreme temperature conditions. So far, 17 years is the longest record of dormancy for this insect. When given water, the larvae quickly become active, usually within one hour, with no ill effects.

Slow dehydration is more beneficial for the insect than rapid dehydration. Larvae make tubes by incorporating detritus and soil with their sticky saliva. The tube serves not only as a physical barrier against enemies and aids in feeding, but also reduces the dehydration rate. In the absence of tubes, larvae do not survive rehydration. During the dehydration process, larvae accumulate large amounts of trehalose (up to 20%), which provides effective protection against desiccation because of its high capacity for water replacement and vitrification. Although membranes are impermeable to trehalose, a trehalose transporter is expressed in the fat body, allowing trehalose production and transport into the hemolymph. Trehalose also serves to protect proteins and cell membranes. Late embryogenesis abundant (LEA) proteins occur in the dehydrating larvae, preventing protein aggregation when concentrated upon desiccation. The anhydrobiotic larvae attain tolerance to several extreme conditions to such an extent that they can revive after expose to -270 to + 103°C, irradiation up to 9 k Gy, and submersion in pure ethanol.

References

Clegg JS (2001) Cryptobiosis – a peculiar state of biological organization. Comp Biochem Physiol B 128:613–624

Crowe JH, Hoekstra FA, Crowe LM (1992) Anhydrobiosis. Annu Rev Physiol 54:579–599

Kikawada T, Minakawa N, Watanabe M, Okuda T (2005) Factors inducing successful anhydrobiosis in the African Chironomid *Polypedilum vanderplanki*: Significance of the larval tubular nest. Integr Comp Biol 45:710–714

Kikawada T, Saito A, Kanamori Y, Nakahara Y, Iwata K, Tanaka D, Watanabe M, Okuda T (2007) Trehalose transporter 1, a facilitated and high-capacity trehalose transporter, allows exogenous trehalose uptake into cells. Proc Natl Acad Sci USA 104:11585–11590

Watanabe M, Kikawada T, Yukuhiro F, Okuda T (2002) Mechanism allowing an insect to survive complete dehydration and extreme temperatures. J Exp Biol 205: 2799–2802
Watanabe M, Nakahara Y, Sakashita T, Kikawada T, Fujita A, Hamada N, Horikawa D, Wada S, Kobayashi Y, Okuda T (2007) Physiological changes leading to anhydrobiosis improve radiation tolerance in *Polypedilum vanderplanki* larvae. J Insect Physiol 53:573–579

Cryptoceridae

A family of cockroaches (order Blattodea).

► Cockroaches

Cryptochetid Flies

Members of the family Cryptochetidae (order Diptera).

► Flies

Cryptochetidae

A family of flies (order Diptera). They commonly are known as cryptochetid flies.

► Flies

Cryptophagidae

A family of beetles (order Coleoptera). They commonly are known as silken fungus beetles.

► Beetles

Cryptorhamphidae

A family of bugs (order Hemiptera, suborder Pentamorpha).

► Bugs

Crystalliferous

Producing or bearing crystals. This term is applied to a number of *Bacillus* and *Paenibacillus* species which, in addition to the endospore, produce a discrete, characteristic crystal or crystal-like inclusion in the sporulating cell.

Csiki, Ernõ; (Ernst Dietl)

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Ernst Dietl was born on the October 22, 1875 at Zsilvajdejvulka, Hunyad Shire, Transylvania, Hungary, today Vulcan, Romania. In 1897 he graduated at the College of Veterinary in Budapest and shortly afterwards gained employment in the Hungarian National Museum's Zoological Collections as assistant curator. He was mainly responsible for the library and the beetle collection. In 1898 he changed his original German name to the Hungarian "Csiki." He remained in the service of the museum until his retirement in 1933, eventually ascending to the position of Departmental Head or Director. After his retirement he withdrew from active work for a few years but as World War II ended, he returned to the museum as an outside consultant to continue with his entomological activities. In 1953, at the age of 78 he received the Doctor of Biological Sciences degree. He has passed away in Budapest, on the 7th of July 1954. Ernő Csiki was probably the first Hungarian museum entomologist who could devote his entire active life to his chosen group of insects, the Coleoptera. During his years the museum's beetle collection grew from 120,000 to well over one million specimens. This unprecedental growth was partially due to the personal collecting activities of Csiki which yielded more than 60,000 beetles and partially to the fact that in those years the museum had sufficient funds for purchasing valuable collections. One of the most notable acquisitions was Reitter's European and Asian collection, containing over 200,000 specimens and more than 5,000 types. Ernő Csiki was one of the most prolific Hungarian coleopterists, describing more than 400 species, publishing 451 works containing over 9,000 pages. He had a wide interest, although the Carabidae was his favorite group. His major work, *Die Käferfauna des Karpaten-Beckens*, 1946 is still considered a fundamental monograph of the Central-European Carabidae. He was a major contributor to the Junk- Schenkling *Coleoptorum Catalogus*. He wrote 4,748 pages for the volumes published between 1910 and 1940. During his life he received numerous awards and prizes, and earned the respect of all his colleagues. In the Second District of Budapest, where he lived, a street was named Beetle Street, (Bogár utca) in honor of Ernő Csiki.

References

Sachtleben H (1955) Gestorben Dr. Ernő Csiki. Beiträge zur Entomologie 5:454

Székessy Vilmos (1954) Dr. Ernő Csiki (1875–1954). Folia enomologica hungarica (S. N.) 7:1–20

Székessy Vilmos (1955) Csiki Ernő emlékezete. állattani Közlemények 45:7–10

Ctenidium (pl. ctenidia)

A comb-like structure found on any part of an insect, but particularly the comb of flat spines found in fleas and certain beetles.

Ctenoplectidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees, and Sawflies

Ctenostylidae

A family of flies (order Diptera).

► Flies

Cubitus

The fifth longitudinal wing vein. It extends from the wing base and usually is two-branched before reaching the wing margin.

Cuckoo Bees

Members of the family Anthrophoridae (order Hymenoptera, superfamily Apoidae).

► Bees
► Wasps, Ants, Bees, and Sawflies

Cuckoo Wasps

Members of the family Chrysididae (order Hymenoptera).

► Wasps, Ants, Bees, and Sawflies

Cucujidae

A family of beetles (order Coleoptera). They commonly are known as flat bark beetles.

► Beetles

Cucurbit

A plant in the family Cucurbitaceae, such as cucumber, squash, and watermelon.

Cucurbit Yellow Vine Disease

This disease occurs in North America, and squash bug is thought to be the vector.

► Transmission of Plant Diseases by Insects

Culicidae

A family of flies (order Diptera). They commonly are known as mosquitoes.

► Mosquitoes
► Flies

Culicifuge

A mosquito repellent. This term is derived from the family name for mosquitoes (Culicidae) and the Latin verb "fugere" (to flee).

Culicinomyces clavisporus

One species of the genus *Culicinomyces*, *C. clavisporus*, includes Australian, American and Canadian strains isolated from the mosquitoes *Anopheles hilli*, *A. quadrimaculatus*, and *Culiseta inornata*, respectively. The fungus is able to infect mosquito genera that transmit diseases in higher animals (e.g., *Anopheles*, *Culex*, and *Aedes*). *Culicinomyces clavisporus* also is pathogenic to some other aquatic dipteran larvae in the families Chironomidae, Ceratopogonidae, Simuliidae, Syrphidae, and Ephydridae. The three strains vary with respect to colony morphology, conidial development, and growth rates in different media; all three exhibit conidial dimorphism, with the smaller type of conidia more abundantly produced in the Australian and American strains. In addition, conidia can be generated on polyphialides, phialides with more than one neck, in all of the isolates. The gray-white colonies can appear more darkly pigmented in all of the strains depending upon culture conditions. *Culicinomyces* has been targeted as a potential biocontrol agent because it is easily cultured under surface or submerged conditions, and because it can recycle within mosquito populations. Recycling is due to the formation of external spores on dead, infected larvae which infect later generations of larvae either from the same genus or a different one.

Culicinomyces clavisporus is unusual because its submerged conidia are produced both *in vitro* and *in vivo*, and it invades host larvae through the digestive tract (foregut) rather than the outer integument. Ingested conidia adhere to the cuticle of the digestive tract via their sticky outer coating. This bonding between the conidia and host epicuticle is strong enough to resist mechanical disruption by movements of the gut wall. Growth of *C. clavisporus* germ tubes through host cuticle takes 6–18 hours. Melanized areas can form in the cuticle around the advancing hyphae, and the fungus is then forced to grow around this resistant material. As in the cuticle, zones of melanization also can develop in the hypodermis. Cylindrical blastospores form by budding from the hyphae and circulate in the hemolymph. Mycelial formation follows, and conidiophores eventually grow out through the thorax, abdomen, mouthparts, and bases of antennae. A dense layer of conidia is produced on the cadaver; however, the degree of sporulation depends upon the time of larval death. If the larvae die before they are completely filled with mycelia, external conidia may not form. It is speculated that toxins released by the high concentration of penetrating hyphae contribute to such rapid larval death because normally, up to one week is required for larvae to succumb to a *Culicinomyces* infection.

References

Cooper RD, Sweeney AW (1986) Laboratory studies on the recycling potential of the mosquito pathogenic fungus *Culicinomyces clavisporus*. J Invertebr Pathol 48:152–158

Goettel MS, Sigler L, Carmichael JW (1984) Studies on the mosquito pathogenic hyphomycete *Culicinomyces clavisporis*. Mycologia 76:614–625

Sweeney AW, Inmann AO, Bland CE, Wright RG (1983) The fine structure of *Culicinomyces clavisporus* invading mosquito larvae. J Invertebr Pathol 42:224–243

Cultivar

An agricultural plant variety or strain developed for specific horticultural properties.

Cultivation

A tillage operation used to prepare land for cultivation. Cultivation also disrupts pest populations, including weeds and soil insects.

► Cultural Control of Insect Pests

Cultural Control of Insect Pests

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Cultural control is using the production or utilization methods of a commodity with a concern for insect management. Cultural control practices are usually multipurpose technical procedures that create environments that either avoid high-risk situations for infestations or develop unfavorable conditions for pests. The operations are often the foundation of preventive control strategies in integrated pest management (IPM) programs. Cultural controls are not usually intended to suppress insect outbreaks, but are designed to prevent infestations from developing. These control methods are usually inexpensive because they are generally necessary for producing or using a commodity often with pest management as a secondary priority. Designing and implementing cultural control in IPM programs may call for greater professional competence, because greater knowledge of insect biology and behavior is usually required as compared to other insect management methods (e.g., control with insecticides). Patience and perseverance are important because the preventive nature of cultural control tactics often does not show tangible results other than a lack of pest problems on a commodity. Several cultural control methods are frequently combined with other pest management techniques in IPM programs for a commodity.

Examples of cultural control methods used independently or in concert with other insect management tactics in IPM programs are:

Sanitation is destroying the habitat associated with a commodity so that insect pests are deprived of shelter, protection from natural enemies, overwintering sites, etc. Sanitation also refers to methods that destroy or remove insects directly from the commodity environment. Examples include destruction of infested weeds and crop debris in and around crop fields, use of vacuums and/or high pressure water or air to clean machinery in food processing areas and warehouses, removal of potential termite-infested wood around homes, and composting garden debris to eliminate pests.

Pest endurance practices are methods designed to aid commodity tolerance of pests without economic damage. Examples of agricultural methods that stimulate optimum health and vigor in crops for tolerance of insect injury include using vigorous seed, good seedbed preparation, optimal fertilization, irrigation and weed control, thinning, pruning, etc.

Pest preventive maintenance practices are procedures that keep commodity environments clean and free of materials where pests can build up and methods that ensure rapid movement of commodities through production, storage, and shipment in order not to allow time for pests to increase.

Crop and cultivar selection is choosing crops and cultivars with consideration of their susceptibility or resistance to the insect pests, along with high yield, produce quality, and other desirable agronomic characteristics. It is using adapted crops and cultivars that have the greatest profit potential with the least hazard for insect problems. Crop and cultivar selection includes the use of insect resistant varieties (including insecticidal transgenic plants), but it also includes decisions to avoid high-risk crops or cultivars that could produce insect outbreaks. Examples include use of cotton and corn varieties that express insecticidal Cry proteins derived from the bacterium *Bacillus thuringiensis* Berliner or the use of wheat containing native resistant genes to the Hessian fly, *Mayetiola hibiscella* (Swazey).

Crop rotation is switching plant species within an environment in order that a resident insect population which is adapted to one of the crops cannot survive when the other is planted into the field. An example would be using corn and soybean as field crops in alternate years so that larvae of western corn rootworm, *Diabrotica virgifera virgifera* LeConte, cannot survive the shift from host corn to non-host soybean. Crop rotation is applicable to other situations such as in greenhouses, plant nurseries, etc. and can be used during the same year in fields where multicropping is used. Crop rotation is also applicable for stored products as when soybean and corn are alternated in grain bins to discourage the build up of granary weevils, *Sitophilus* spp., and meal moths, *Pyralis farinalis* L.

Disruption of phenological synchrony is interfering with a pest population's natural association with susceptible growth stages of a crop. Alternating planting and harvest dates and using cultivars of desirable maturity are ways that crop growth can be manipulated to avoid peak levels of pests during the season, for example, early planting of sweet corn to avoid high populations of corn earworm, *Helicoverpa zea* Boddie, and fall armyworm, *Spodoptera frugiperda* (J.E. Smith).

Deception and concealment practices is using lures, trap crops, or polyculturing crops to either decoy or hide a commodity from infestations. Examples include placing Japanese beetle, *Popillia japonica* Newman, traps in the backyard to help lure adults away from landscape plants; using an early maturing soybean cultivar around the periphery of a soybean field as a trap crop for stinkbugs, *Nezara* spp.; and companion planting various herbs and aromatic plants to hide garden plants from pests.

► Cover, Border and Trap Crops for Pest and Disease Management

References

All JN (1999) Ruberson JR (ed) Handbook of pest management. Marcel Dekker Inc., New York, pp 395–415

Rabb RL, (1984) Defoliart GK, Kennedy GG, Huffaker CB, Rabb RL (eds) (1984) Ecological entomology. Wiley, New York, pp 697–728

Rajendran B, Pimentel D (ed) (2002) Encyclopedia of pest management. Marcel Dekker, Inc., New York, 929 pp

Cultural Entomology

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Entomology has long been concerned with two general areas of study. The first is the study of insect pests and useful insects which falls into the realm of economic or applied entomology. The second is the study of the biology of insects for the sake of knowing without practical application, which is generally referred to as basic entomology. However, recently a distinct field of entomology has been recognized called cultural entomology. Cultural entomology is the study of the influence of insects and other terrestrial arthropods in literature, languages, music, the arts, interpretive history, religion, and recreation. Because the term "cultural" is narrowly defined, some aspects normally included in studies of human societies are excluded. Thus, ethnoentomology, which is concerned with all forms of insect-human interactions in so-called primitive societies, is not completely synonymous with cultural entomology. For example, practical uses of insects such as entomophagy as part of the diet, in pharmacology, or in other wholly practical uses of insects, are not the subject matter of cultural entomology. Where primitive societies have employed insects in cultural activities such as art and religion, ethnoentomology and cultural entomology overlap.

Reference

Hogue CL (1987) Cultural entomology. Annu Rev Entomol 32:181–99

Culture of Natural Enemies on Factitious Foods and Artificial Diets

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The use of arthropod predators and parasitoids in augmentative biological control programs necessitates the availability of cost-effective mass rearing systems, allowing the production of large numbers of beneficials at the lowest possible price.

In many cases, suppliers of beneficial arthropods must resort to employing so-called natural rearing systems. Here, the beneficial is cultured on its natural host or prey, which itself is maintained on one of its food plants. Natural rearing systems can be economically viable, like the production of the parasitoid, *Encarsia formosa*, on tobacco plants infested with the greenhouse whitefly, *Trialeurodes vaporariorum*. In many cases, however, the necessity to maintain three trophic levels (natural enemy, host and host's food plant) leads to problems of discontinuity and the high costs of rearing facilities and labor result in a high price of the natural enemies, making them more expensive than chemical controls. Costs may be lowered when the herbivorous host used for natural enemy production can be reared on an artificial diet in lieu of plants, which is the case for many lepidopteran larvae.

Costs may be further reduced when natural enemies can be produced on unnatural or factitious hosts that are easier and less expensive to rear than the natural host. Factitious hosts are organisms that are not normally attacked by the beneficial, mostly because they do not occur in its natural habitat, but do sustain its development. Eggs of the lepidopterans *Ephestia kuehniella* and *Sitotroga cerealella*, are routinely used in the commercial production of various natural enemies including coccinellid beetles, lacewings, predaceous heteropterans, and egg parasitoids of the genus *Trichogramma*. Hatching of the eggs is prevented by gamma- or UV-irradiation or by freezing. Although these moths are easily produced on inexpensive foods (wheat flour or grains), there are substantial monetary investments for the mechanization of rearing procedures and for the health care of workers (repeated inhalation exposure to scales is known to cause allergies). Because of a continuously high demand, this has led to high market prices especially for *Ephestia kuehniella* eggs, amounting to $800 to $1,200 (U.S.) per kilogram by the end of the 1990s. Other insects that are frequently used as factitious food in commercial insectaries and research labs include larvae of the greater wax moth, *Galleria mellonella* (for several ichneumonid, braconid and tachinid parasitoids and for predatory stink bugs), and of the yellow mealworm, *Tenebrio molitor* (e.g., for reduviids and predatory stink bugs). *Trichogramma* wasps can also be successfully mass produced on eggs of the rice moth, *Corcyra cephalonica* and a number of silkworms, such as the Chinese oak silkworm, *Antheraea pernyi*. Commercial suppliers routinely use astigmatid mites such as *Tyrophagus putrescentiae* and *Carpoglyphus lactis* as prey for culturing a number of phytoseiid mites. Some non-insect materials also may hold promise for use as foods in insect mass culturing. It has been shown that the anthocorid *Orius laevigatus* and the mirid *Macrolophus caliginosus* can be reared on cysts of the brine shrimp, *Artemia franciscana*, with similar developmental and reproductive success as on *Ephestia kuehniella* eggs. Given that *Artemia* cysts are at least an order of magnitude cheaper than flour moth eggs, they may be an economically viable alternative food for the mass propagation of these heteropteran predators and possibly other predaceous insects.

The availability of an artificial diet that supports the growth and reproduction of a natural enemy offers a further alternative for the rationalization and automation of mass rearing procedures. Ideally, biochemical analyses of the natural food along with studies of the digestive and absorptive physiology of the insect should be used as guidelines for diet definition, but in fact, many successes with artificial diets were based on a mere trial-and-error approach. A nutritionally adequate artificial diet should contain the basic nutrients (proteins or amino acids, lipids, carbohydrates) in appropriate proportions. In addition, some specific minor components may be needed as growth factors, like sterols, vitamins, minerals and nucleic acids. Further, the diet has to be formulated and presented in a manner that makes it acceptable for feeding or oviposition. Therefore, physical properties such as shape, hardness, texture, homogeneity and water content are important considerations. Inert filling or gelling agents, like agar, cellulose and gelatin, have been used to obtain adequate consistency mainly in diets for insects with chewing mouthparts. Several materials have been used to wrap or encapsulate liquid and semi-liquid media, like paraffin, Parafilm and certain polymeric coatings. Measures can be taken to prevent spoilage of the food by micro-organisms. This can be done by adding anti-microbial or anti-fungal agents (provided they are non-toxic to the insect), by adjusting pH or by sterilizing the diet.

Artificial diets have been classified in three general types: (i) holidic diets, in which all ingredients are known in chemical structure, (ii) meridic diets, which have a holidic base supplemented with one or more unrefined or chemically unknown substances (e.g., liver extracts, yeast products), and (iii) oligidic diets, which are mainly made up of crude organic materials (like meat diets). It is, however, not always easy to discriminate between these three diet types and, in fact, only a complete description of its composition is able to fully characterize an artificial diet. A more relevant criterion to categorize a diet is the presence or absence of insect components. Many artificial diets still contain host materials to fulfill the need for certain growth factors, or to supply feeding or oviposition stimuli. Insect additions can vary from small quantities of host hemolymph to whole host bodies. Supplementing artificial diets with insect materials again implies the dependence on parallel host cultures, which may lead to an increase in production costs. In some cases, however, insect components are inexpensive and easy to obtain, like the hemolymph from silkworms in the silk-producing areas of Asia and Latin America. As an alternative to hemolymph or host extracts, insect cell cultures have been used to serve as a source for essential host factors in the artificial rearing of certain parasitoids.

A number of arthropod natural enemies have been reared with variable success on artificial media. Several predatory heteropterans, chrysopids and coccinellids have been reared for consecutive generations on diets devoid of insect materials. Promising results have also been obtained with artificial diets for hymenopterous egg and pupal parasitoids and for tachinid larval parasitoids. Endoparasitoids (i.e., parasitoids which develop inside their hosts) are generally more difficult to rear on artificial media than ectoparasitoids or predators; for the larvae of endoparasitoids, the diet is not only their food, but also their living environment. In diets for endoparasitoids, oxygen supply, osmotic pressure and pH are major concerns. The situation is even more complex for koinobiontic endoparasitoids. These parasitoids do not immediately paralyze or kill their hosts, allowing them to continue to develop for some time after oviposition. As a consequence, the developing parasitoid larva has strong physiological interactions with the still living host, that often supplies it with specific growth factors. Finally, understanding interactions with microbial symbionts may be the key to success in developing an adequate artificial food for a number of entomophagous insects.

The main concern for natural enemies produced on artificial (or factitious) food is their quality as biological control agents. Artificially fed natural enemies may diverge biologically from their naturally fed counterparts and may have impaired abilities to find or kill their natural host. Biological, biochemical, physiological and behavioral parameters can be used to assess the fitness of an artificially reared beneficial in the laboratory, but excellent field performance against the target pest remains the ultimate quality criterion. In the early 1990s, *Trichogramma* egg parasitoids were already being produced on artificial eggs at an industrial scale in China; the parasitoids were being released on thousands of hectares resulting in excellent control of different lepidopterous crop pests. In the United States and Europe, biocontrol companies have also started to integrate artificial diets in their production process and some beneficials are at least partially being reared on artificial foods.

► Augmentative Biological Control
► Rearing of Insects

References

Arijs Y, De Clercq P (2001) Rearing *Orius laevigatus* on cysts of the brine shrimp *Artemia franciscana*. Biol Control 21:79–83

Cohen AC (2004) Insect diets. Science and technology. CRC Press, Boca Raton, FL, 324 pp

Etzel LK, Legner EF, Bellows TS, Fisher TW (eds) (1999) Handbook of biological control. Academic Press, San Diego, CA, pp 125–197

Grenier S, De Clercq P, van Lenteren JC (eds) (2003) Quality control and production of biological control agents. Theory and testing procedures, CABI Publishing, Wallingford, UK, pp 115–131

Thompson SN (1999) Nutrition and culture of entomophagous insects. Annu Rev Entomol 44:561–592

Waage JK, Carl KP, Mills NJ, Greathead DJ, Singh P, Moore RF (eds)(1985) Handbook of insect rearing, vol I. Elsevier, Amsterdam, The Netherlands, pp 45–66

Cuneus

In Hemiptera, the small triangular area at the end of the corium on the hemelytra. In Odonata, the small triangular structure (Fig. 142) between the compound eyes.

Cupedidae

A family of beetles (order Coleoptera). They commonly are known as reticulated beetles.

► Beetles

Curculionidae

A family of beetles (order Coleoptera). They commonly are known as snout beetles or weevils.

► Beetles

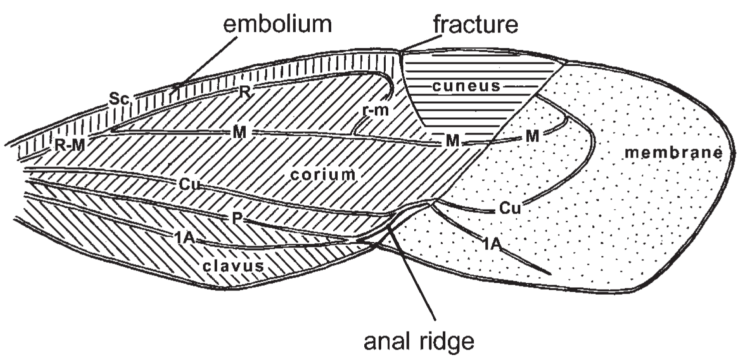
► Weevils, Billbugs, Bark Beetles and Others (Coleoptera: Curculionidae)

Curculionoid Larva

A larval body form that is robust, C-shaped, with a well-developed head. It is found in the weevils (Curculionidae) and the first instar of Bruchidae (both Coleoptera).

Curran, Charles Howard

Howard Curran was born in the province of Ontario, Canada, on March 20, 1894. He became interested in insects by the age of seven and built a collection, but left school at the age of 12. He worked in the newspaper-publishing business, at first in his father's office and later in the province of Saskatchewan. In 1915 he was employed as an assistant in the Dominion Entomology Branch at Vi0neland Station, Ontario. He went to Europe with Canadian troops in 1917, served in France in Word War I, was wounded and invalided out. He returned to Vineland Station in 1919–1921, and in 1921 received a B.S.A. degree from Ontario Agricultural College (now the University of Guelph). At the college, he met C.J.S.



Cuneus, Figure 142 Front wing of a bug (Hemiptera: suborder Heteroptera), thickened basally and membranous distally.

Bethune, who encouraged his interest in Syrphidae. At the annual meeting of the Entomological Society of America in Toronto in 1921, he was encouraged to apply for a fellowship at the University of Kansas for graduate studies. This he did, was successful, and obtained his M.Sc. degree in 1923 with a thesis on North America Syrphidae in partial fulfillment of the requirements. Meanwhile, in 1922, his father's firm began printing The Canadian Entomologist. In 1923–1928, Howard was entomologist in charge of Diptera and stored products insects, and published many papers in the pages of The Canadian Entomologist. In 1928 he joined the staff of the American Museum of Natural History, rose in its ranks, retired in 1960, and then became Curator Emeritus. He received a D.Sc. degree from the University of Montreal in 1933 after a thesis "The families and genera of North American Diptera." His primary entomological contribution was the description of 2,648 taxa in 62 families of Diptera. From the 1940s, he undertook much consulting work and his output of publications lessened. After retirement, he moved to Florida and was appointed entomologist with the University of Florida Agricultural Experiment Station at Leesburg. He died in Leesburg on January 23, 1972, survived by his second wife, Ethel, and three children.

Reference

Arnaud PH, Owen TC (1981) Charles Howard Curran (1894–1972). Myxia 2:1–20

Cursorial

Adapted for running. This term is used to describe legs adapted for running.

Curtis, John

John Curtis (Fig. 143) was born in Norwich, England, on September 3, 1791. During his school years he developed a talent for drawing, and began to collect butterflies. In 1807, he began to work for a solicitor. However, through contact with insect collectors, he found employment as curator and illustrator of insects. After some 12 years he began work on his series of books on "British entomology," whose first part was published in 1824, with the last, part 16, in 1839. These works were illustrated by his 769 magnificent color plates. He also (1829) published "A guide to an arrangement of British insects." In 1841 he became editor of the insect part of "Gardener's Chronicle" and wrote over 100 articles for it, under the pseudonym "Ruricola." He died on October 6, 1862, in London.

Curtis, John, Figure 143 John Curtis.

Reference

Herman LH (2001) Curtis (Ruricola), John. Bull Am Mus Nat Hist 265:56–58

Curtonotid Flies

Members of the family Curtonotidae (order Diptera).

► Flies

Curtonotidae

A family of flies (order Diptera). They commonly are known as curtonotid flies.

► Flies

Cushman, Robert Asa

Robert Cushman was born in Massachusetts on November 6, 1880. He studied at the University of New Hampshire and at Cornell University. In 1906 he was employed by the U.S. Department of Agriculture and worked in part on applied entomology (boll weevil, pests of fruits, pests of grapes) and on taxonomy (ichneumonid and chalcidid wasps). He was active in the Entomological Society of Washington, and its president in 1925. He died in California on March 25, 1957.

Reference

*Mallis A (1971)American entomologists. Rutgers University Press, New Brunswick, NJ, pp 372–373

Cuticular Lipids

Lipids comprise an important component of the cuticle of insects.

► Metabolism of Cuticular Lipids

Cuticle

The noncellular outer layer of the integument, which is the outer covering of an insect. The cuticle serves as the exoskeleton, the site for muscle attachment and a barrier against predation, parasitism, and infection by pathogens. The cuticle consists of several layers, including the epicuticle, exocuticle, and endocuticle (Fig. 144). The exocuticle or endocuticle may be reduced or even absent on some parts of the insect, but the epicuticle and epidermis are always present. During molting, the inner layers of the new cuticle (the future exocuticle and endocuticle) are not sclerotized into distinct layers, and is called the procuticle, but this is a temporary condition.

► Juvenile Hormone

Cuticulin

The very thin outer layer of the epicuticle. Cuticulin is a tough, insoluble and inelastic layer of cross-linked protein and lipid molecules.

Cutworm

Any of a number of caterpillars in the family Noctuidae that hide in the soil, feeding there or emerging at night to feed on foliage or seedlings.

► Potato Pests and their Management

► Vegetable Pests and their Management

► Maize (Corn) Pests and their Management

Cutworm Moths

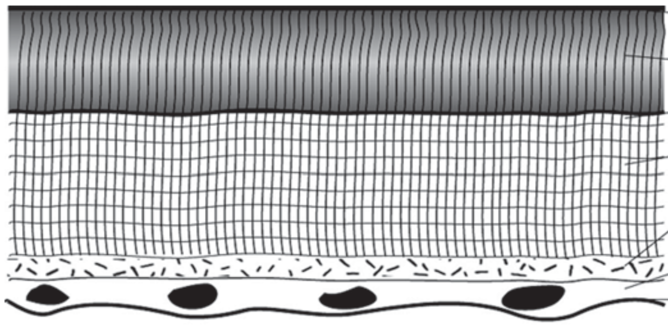
Members of the family Noctuidae (order Lepidoptera).

► Owlet Moths

► Butterflies and Moths

Cuvier, (Baron) Georges Léopold Chretien Frédéric Dagobert

Georges Cuvier was born in Montbéliard, at that time in Württemberg (later absorbed into France, and now in Germany) on August 23, 1769. He was therefore born a Württemberger and became French. Actually, he was christened Jean Léopold Nicolas Frédéric Cuvier, but after the early death of his elder brother, Georges, he was renamed Georges. He studied theology and anatomy in



Cuticle, Figure 144 **Cross section of the insect cuticle and epidermis (adapted from Chapman, The insects: structure and function).**

Stuttgart. In 1795 he moved to Paris and was employed as assistant in comparative anatomy at the Jardin des Plantes (later known as Muséum National d' Histoire Naturelle). Much later he became professor at the Collège de France and chancellor of the Université de Paris. His contributions to entomology consisted of his first small publications, and the entomological part of his (1799–1805) work "Leçons d' anatomie compare." The entomological part of his (1816) book "Règne animal" was written not by him, but by Latreille. He had great influence on zoological anatomy, but little directly on entomology. Much of his influence, however, was by his stance that animal species are immutable – they do not evolve. Thus, his ideas contrast with those of Lamarck, who believed that evolution does take place, but by heredity of acquired characters. They contrast just as much with the later ideas of Charles Darwin about evolution. Cuvier's ideas were adopted by Louis Agassiz (see above). He was made grand officer of France's Legion d' Honneur in 1826. He was made a peer of France (Baron) in 1831 by the king Louis Philippe. He died in France on May 13, 1832.

Reference

Tuxen, SL (1973) Smith RT, Mittler TE, Smith CN (eds) History of Entomology. Annual Reviews Inc., Palo Alto, CA, pp 95–117

Cyclical Polymorphism

A complex life cycle characterized by the occurrence of several to many morphs. Many morphs are seasonally related, and are most clearly manifested in aphids, which produce various forms of winged and wingless, a nd asexual and sexually reproducing forms, over the course of a season.

► Aphids
► Polyphenism
► Polyphenism and Juvenile Hormone (JH)
► Phenotypic Plasticity

Cyclidiidae

A family of moths (order Lepidoptera) also known as giant hooktip moths.

► Giant Hooktip Moths
► Butterflies and Moths

Cycloalexy

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Cycloalexy is a form of gregarism, and involves group reactions. The name is derived from the Greek "kuklos" = circle and "alexo" = I defend, I protect. It is the attitude adopted at rest by some insect larvae, both diurnal and nocturnal, in a tight circle when either the heads or ends of the abdomen are juxtaposed at the periphery, with the remaining larvae at the center of the circle. It can also be named the ring defense behavior. Coordinated movements such as the adoption of threatening attitudes, regurgitation, reflex bleeding and biting are used to repel predators or parasitoids. If for any reason, the circle is broken, ants or pentatomids can easily catch some larvae. The system is more efficient against predators than against parasitoids that have all found a way to turn the defense. Cycloalexy has analogy in vertebrates, penguins and muskoxen, for instance, living in familial groups and sometimes adopting a circular formation of males protecting the young and females from potential predators. Cycloalexy is mainly known among Coleoptera: Chrysomelidae, (Cassidinae, Chrysomelinae, Criocerinae), Coleoptera: Curculionidae, sawflies, and several other insect orders (Diptera, Ceratopogonidae, Neuroptera, Lepidoptera, etc.).

Generally, the individuals in a colony disperse to feed upon foliage by night (or by day when they rest during the night), one behind the other, to reaggregate before dawn. In Pergidae, to reaggregate the larvae communicate by means of low frequency vibrations created by tapping the uropod upon the substrate. Paropsine (Coleoptera: Chrysomelidae) larvae in Australia also tap the substrate with the abdomen to reunite the dispersed colony. All the insects demonstrating cycloalexy are subsocial in the larval stage and also often exhibit maternal care of eggs and larvae. Some cycloalexic leaf beetles like *Platyphora* in Brazil are viviparous. When dropped one by one by the mother, the larvae congregate immediately.

Cycloalexy, like maternal care, can only be the result of a long evolutionary history. The behavior efficiently protects the larvae during their most vulnerable periods (at rest, during molting). However, the defense is not always perfect. Trigonalyid parasitoids have succeeded in having their eggs swallowed by the sawfly larvae, thus obviating the need to confront the defensive ring.

Younger larvae sometimes seem to be protected inside the circle, and this could be interpreted as altruism on the part of the larvae at the periphery (Fig. 145). Also, reciprocal altruism may take place when the inner and outer larvae exchange positions. However, this interpretation has been challenged. In Australian sawflies in the genus *Perga* (*Perga dorsalis* Leach), some 20% of the larvae preferentially occupy the outer positions in the resting colony and appear to lead the foraging expeditions. Leaders are quick to regain outer positions if removed and placed in the center of the colony. So there seem to be differences in the dispersal behavior of larvae in time and space.

Small colonies of larvae sometimes show non-viability (e.g., pergids). However, when larvae of *Coelomera* spp. (Coleoptera: Chrysomelidae) on a leaf of a *Cecropia* tree are divided into two or three subgroups, those groups seem as efficient as big ones in repelling predators.

► Gregarious Behavior in Insects

References

Jolivet P, Vasconcellos-Neto J, Weinstein P (1990) Cycloalexy: a new concept in the larval defense of insects. Insecta Mundi 4:133–141

Vasconcellos-Neto J, Jolivet P (1988) Une nouvelle stratégie de défense: la stratégie de défense annulaire (cycloalexie) chez quelques larves de Chrysomélides brésiliens. Bulletin Societé Entomologique France 92:291–299

Vasconcellos-Neto J, Jolivet P (1989) Ring defense strategy (cycloalexy) among Brazilian chrysomelid larvae (Col.). Entomography 67:347–354

Verma KK (1996) Cycloalexy in leaf-beetles (Col. Chrys.). Insect Environ 2:82–84

Weinstein P (1989) Cycloalexy in an Australian pergid sawfly (Hym. Pergidae). Bull R Belg Entomol Soc 125:53–60

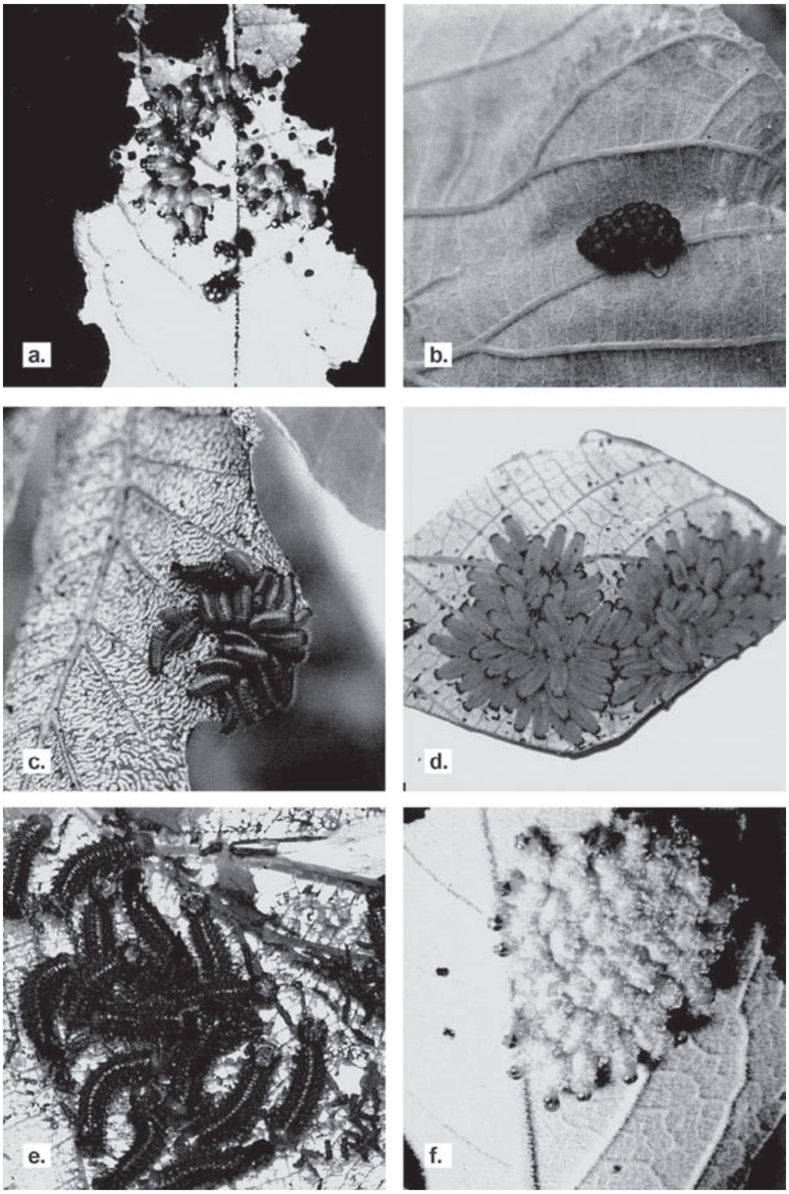
Weinstein P, Maelzer DA (1997) Leadership behaviour in sawfly larvae, *Perga dorsalis*. Oikos 79:450–455

Cyclo-Developmental Transmission

Transmission of an arthropod transmitted disease wherein the causal organism undergoes cyclical changes but does not multiply in the body of the arthropod vector.

► Mechanical Transmission

► Cyclo-Propagative Transmission, and Propagative Transmission



Cycloalexy, Figure 145 **Cycloalexy:(a) Third instar of *Platyphora conviva* Stål, 1858 (Coleoptera: Chrysomelinae). Rupture of the cycloalexic ring and predation by a bug of one larva. (photo J. Vasconcellos-Neto, 1986.) Itatiaia National Park, RJ, Brazil. (b) Eggs of *Coelomera lanio* Dalman Coleoptera: Galerucinae), laid on the underside of the folioles of *Cecropia adenopus* (Cecropiaceae). The newly hatched larvae will aggregate. (photo Jolivet, 1990.) Viçosa, MG, Brazil. (c) First instar larvae of *Coelomera lanio* Dalman (Coleoptera: Galerucina). Cycloalexic ring. (photo Jolivet, 1990.) Viçosa, MG, Brazil. (d) Second instar larvae of *Coelomera lanio* Dalman (Coleoptera: Galerucinae), on a leaf of *Cecropia adenopus*. The ring has been doubled. (photo Jolivet, 1990.) Viçosa, MG, Brazil. (e) Third instar of *Coelomera lanio* Dalman (Coleoptera: Galerucinae), on a leaf of *Cecropia adenopus*. The cycloalexic ring is near to be broken and the larvae to go feeding (Coleoptera: Galerucinae). (photo Jolivet, 1990.) Viçosa, MG, Brazil. (f) Cycloalexic ring of *Platyphora conviva* Stål (Coleoptera: Chrysomelinae). First instar. The larvae have covered themselves with the hair of the underside of the leaves for extra protection. (photo J. Vasconcellos-Neto, 1986.) Itatiaia National Park, RJ, Brazil.**

Cyclo-Propagative Transmission

Transmission of an arthropod transmitted disease wherein the causal organism undergoes cyclical changes and multiplies in the body of the arthropod vector.

► Mechanical Transmission
► Cyclo-Developmental Transmission, and Propagative Transmission

Cyclorrhapha

A term sometimes applied to the higher flies (Diptera), usually treated as an infraorder, and also known as Muscamorpha. The cyclorrhaphous Diptera differ from the other (lower) flies in that pupation and the formation of the adult form occur within the old, hardened third instar cuticle.

► Flies (Diptera)

Cyclotornidae

A family of moths (order Lepidoptera) also known as Australian parasite moths.

► Australian Parasite Moths
► Butterflies and Moths

Cydnidae

A family of moths (order Hemiptera). They sometimes are called burrower bugs.

► Bugs

Cylindrical Bark Beetles

Members of the family Colydiidae (order Coleoptera).

► Beetles

Cymidae

A family of bugs (order Hemiptera, suborder Pentamorpha).

► Bugs

Cyphoderidae

A family of springtails in the order Collembola.

► Springtails

Cypselosomatid Flies

Members of the family Cypselosomatidae (order Diptera).

► Flies

Cypselosomatidae

A family of flies (order Diptera). They commonly are known as cypselosomatid flies.

► Flies

Cyrtocoridae

A small family of bugs in the order Hemiptera, suborder Heteroptera. It is treated by some as a subfamily of Pentatomidae.

► Bugs

Cystocyte

A type of hemocyte, also known as coagulocytes, that participates in the coagulation process of hemolymph.

► Hemocytes of Insects: their Morphology and Function

Cytochrome

The complex protein respiratory enzymes occurring within plant and animal cells in the mitochondria, where they function as electron carriers in biological oxidation.

Cytoplasm

The fluid components of the cell, outside the nucleus.

Cytoplasmic Incompatibility

Reproductive incompatibility between two populations caused by factors that are present in the cytoplasm. Often associated with microorganisms.

Cytoplasmic Polyhedrosis Virus

An RNA virus associated with inclusion bodies found in cytoplasm of cells.

Cytosol

The fluid portion of the cytoplasm, excluding the organelles in a cell.

D

Dactyl

A tarsal segment, after the first segment, that is expanded and finger-like in appearance. The dactyls on the front legs of mole crickets (Orthoptera: Gryllotalpidae) are an adaptation that facilitates the insect burrowing, mole-like, though the soil.

► Mole Crickets and their Biological Control
► Grasshoppers, Katydids and Crickets

Dactylopiidae

A family of insects in the superfamily Coccoidae (order Hemiptera). They sometimes are called cochineal insects.

► Bugs

Daddy Long-Legs

This term is applied to several arthropods, principally craneflies (Diptera: Tipulidae), spider-like harvestmen (Arachnida: Opiliones or Phalangida), and several true spiders in the family Pholcidae (Arachnida: Aranea), but most often *Pholcus phalangioides*. What they all have in common is that they have long, slender legs; otherwise, they are not closely related.

Dahlbom, Anders Gustav

Anders Dahlbom was born in Ostgothland, Sweden, on March 3, 1806. He studied in Lund and earned a doctorate in philosophy in 1829. Then he became an instructor in natural history and preparator in the zoological museum in Lund in 1830. Three promotions made him professor of entomology in Lund in 1858. He explored his native Sweden to collect zoological specimens and also traveled abroad to Germany and Denmark, and there visited museums. He married Wilhelmine Krey, and they had six children. His area of research was the taxonomy of Hymenoptera. His first two publications appeared in 1829, and were monographs on pompilid wasps and chrysidid wasps. For almost 30 years he maintained an output of books and papers on Hymenoptera while maintaining correspondence with entomologists in his own country and in Britain, France, and Germany. He died in Lund on May 6, 1859.

Reference

Anon (1859) Nekrolog Entomol Ztg (Stettin) 20:337–340

Dalceridae

A family of moths (order Lepidoptera). They commonly are known as tropical slug caterpillar moths.

► Tropical Slug Caterpillar Moths
► Butterflies and Moths

Dampwood Termites

A group of termites in the families Kalotermitidae and Rhinotermitidae that are known to attack moist dead wood.

► Termites

Damsel Bugs

Members of the family Nabidae (order Hemiptera).

► Bugs

Damselflies

Certain members (suborder Zygoptera) of an order of insects (order Odonata).

► Dragonflies and Damselflies

Dance Flies, Balloon Flies, Predaceous Flies (Diptera: Empidoidea, Exclusive of Dolichopodidae)

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The dance flies, balloon flies and other predaceous flies that have traditionally been placed in the family Empididae are now classified in four families of Empidoidea along with the long-legged flies of the family Dolichopodidae. With approximately 11,400 described species and many more undescribed species, the Empidoidea are one of the largest superfamilies of Diptera and the most diverse lineage of predaceous flies. The four families that were formerly classified as the single family Empididae are listed below with their included subfamilies.

Order: Diptera
- Superfamily: Empidoidea (exclusive of Dolichopodidae)
  - Family: Empididae
    - Subfamily: Empidinae
    - Subfamily: Hemerodromiinae
    - Subfamily: Clinocerinae
  - Family: Atelestidae
    - Subfamily: Nemedininae
    - Subfamily: Atelestinae
  - Family: Hybotidae
    - Subfamily: Trichininae
    - Subfamily: Ocydromiinae
    - Subfamily: Oedaleinae
    - Subfamily: Tachydromiinae
    - Subfamily: Hybotinae
  - Family: Brachystomatidae
    - Subfamily: Trichopezinae
    - Subfamily: Ceratomerinae
    - Subfamily: Brachystomatinae

Together these families include nearly 4,500 described species worldwide and comprise a morphologically diverse array of taxa, although *Homalocnemis*, *Iteaphila*, *Anthepiscopus* and *Oreogeton* are still unplaced to family within this classification. The vast majority of species are predators as adults with the few exceptions being obligate flower-feeding groups that consume pollen as their only protein source. They are found in a variety of forested and open habitats where they breed in moist soils, decaying wood, dung, and in aquatic habitats. All known larvae appear to be predators on invertebrates.

Distinguishing Characters

Most adult Empidoidea (exclusive of Dolichopodidae) can be easily differentiated from the very similar Dolichopodidae by their lack of green metallic body coloration. However a few non-dolichopodid Empidoidea (e.g., most *Lamprempis*) are metallic green and some dolichopodids are not metallic. However, all Dolichopodidae have the Rs wing vein originating at or near the level of crossvein h and have crossvein r-m situated in the basal fourth of the wing, unlike other Empidoidea that have the Rs vein originating well distal to the level of crossvein h and have crossvein r-m distal to the basal fourth of the wing. In addition, male dolichopodids have their terminalia rotated forward beneath the preceding segments of the abdomen, unlike other empidoids. Some bee flies (Bombyliidae) and asiloid groups (e.g., therevids *sensu lato*) can also be confused with non-dolichopodid Empidoidea, but these flies generally have a larger anal (cu*p*) cell that reaches, or nearly reaches, the margin of the wing and they lack any predaceous modifications on either the legs or mouthparts. A few platypezid cyclorrhaphan flies (e.g., *Microsania*) can also be confused with non-dolichopodid Empidoidea, but their arista is comprised of three articles rather than two, and the acrostichal setae are uniserial rather than biserial or absent.

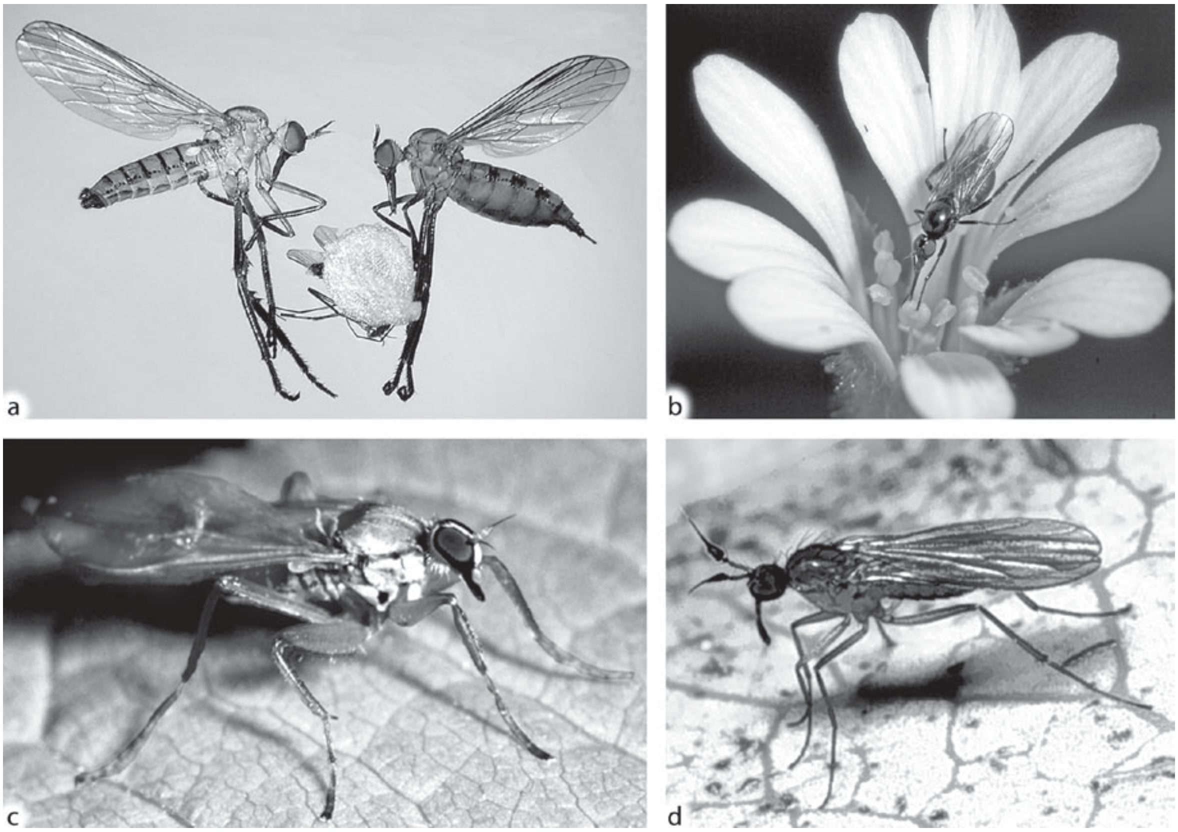
Morphology – Adults

Adult Empidoidea (exclusive of Dolichopodidae) are small to medium-sized flies (1–12 mm) that are darkish to light in color and are rarely metallic green (Fig. 1). The head is variously shaped, but is not large and is usually narrower than the thorax. The compound eyes are generally large, with the males often holoptic (i.e., eyes meeting above in the middle of the head) and the females dichoptic (i.e., eyes separated). However in some groups the males are dichoptic, and in one major lineage (the Hybotinae) the females are also holoptic like the males. The antenna consists of a scape, pedicel, postpedicel (1st flagellomere) and a stylus. The pedicel is usually without the thumb-like conus seen in most cyclorrhaphan flies that inserts into the postpedicel. The postpedicel appears as a single article that is variously shaped. The stylus is usually comprised of two articles, is short to elongate, and is either apical or more dorsally situated on the postpedicel, such that it appears arista-like. The proboscis is short to elongate, with a one-segmented palpus, and a labrum that is usually armed at the apex with paired epipharyngeal blades. The chaetotaxy (bristling) of the head is limited, and usually includes a pair of ocellar bristles, postoculars, and sometimes additional vertical bristles.

The thorax is generally rectangular in dorsal outline and is extended anteriorly in some groups. The mesonotum is nearly flat to greatly arched and dome-like. The chaetotaxy of the thorax includes notopleurals and scutellars, and various other dorsal bristles depending upon the group, and the acrostichal and dorsocentral setae tend to be differentiated. The wings are of varied shape and size, sometimes broadened, sometimes narrowed, rarely reduced, with the alula and anal lobe often lacking. The wing color varies from clear to darkened, and is seldom patterned with markings. The wing venation is exceedingly varied from relatively complete to markedly reduced. The anal cell is closed and never reaches the wing margin. The legs are varied in length, thickness and armature, and often at least one pair bears raptorial modifications. The legs are sometimes sexually dimorphic, with rows of pinnate bristles in females and clasping or glandular structures in males. The empodium between the claws is usually setiform, but is pulvilliform in some aquatic groups.

The abdomen is subcylindrical and usually elongate, with at least some tergites bearing abdominal plaques. The male terminalia are either unrotated or twisted 45–90° to the right. The male genital capsule is symmetric or asymmetric and has a lever-like ejaculatory apodeme that usually articulates ventrally against the base of the phallus. The female terminalia are with or without spine-bearing acanthophorites and there is one spermatheca internally.

The family Empididae (Fig. 1a) includes small to relatively large flies (2–12 mm in length) that usually have fairly complete wing venation, with vein R_{4+5} often forked and cell dm usually present. The prosternum is enlarged to form a precoxal bridge and the legs are usually strong, long and



Dance Flies, Balloon Flies, Predaceous Flies (Diptera: Empidoidea, Exclusive of Dolichopodidae), Figure 1
Representative Empidoidea (a) *Empis aerobatica* (Empididae); left – male, right – female, center – balloon with prey (a midge) attached, USA (photograph by Eric Fisher); (b) *Acarteroptera licina* (Atelestidae); female feeding on flower, Chile (photograph by Stephen Marshall); (c) *Platypalpus holosericus* (Hybotidae), female, Canada (photograph by Stephen Marshall); (d) *Ceratomerus* sp. (*virgatus* group) (Brachystomatidae), female, New Zealand (photograph by Stephen Marshall).

slender without a fore tibial gland. The male terminalia are unrotated and the cerci are often enlarged and developed for clasping. The female abdomen is telescopic and pointed apically, and lacks acanthophorite spines on tergite 10.

The Atelestidae (Fig. 1b) are small flies (2–4 mm) with venation characterized by an unbranched vein R_{4+5} and a relatively long anal cell. They lack predaceous modifications on the mouthparts (i.e., epiphyngeal blades) and the legs are not raptorial. The fore tibial gland is also lacking. The male terminalia are unrotated and the gonocoxal apodemes are distinctively elongated. The female abdomen is telescopic and lacks tergite 10.

The family Hybotidae (Fig. 1c) includes very small to medium-sized flies (1–9 mm) that generally have reduced venation, with vein R_{4+5} unbranched and cell dm often absent. Usually at least one set of legs (fore, mid, or hind depending on the group) is raptorial and a fore tibial gland is present. The male terminalia are normally twisted 45–90° to the right and are often asymmetric. The female abdomen is telescopic and lacks acanthophorite spines on tergite 10.

The Brachystomatidae (Fig. 1d) are small to relatively large flies (2–11 mm) that tend to have fairly complete wing venation, with vein R_{4+5} often forked and cell dm always present. The legs are usually strong, long and slender and lack a fore tibial gland. The male terminalia are unrotated (asymmetrically twisted to the left in some Trichopezinae), and the ejaculatory apodeme is plate-like and narrowly fused to the base of the phallus. The female abdomen is truncate, and usually bears a fringe of setae along the posterior margin of tergite 7 as well as acanthophorite spines on tergite 10.

Morphology – Immatures

The immature stages of all Empidoidea are poorly known, but larvae are generally maggot-like with reduced head sclerites and a unique mandible made up of four to six components. Non-dolichopodid empidoid immatures are known for relatively few groups, but for those that are known the larvae possess either an amphipneustic, metapneustic, or apneustic respiratory system depending on the taxon. Prolegs are generally present on some abdominal segments of aquatic or semi-aquatic groups, whereas creeping welts tend to be present on the abdominal segments of more terrestrial taxa.

Unlike Dolichopodidae, most other empidoid larvae do not appear to spin a cocoon before pupating. There is a single report of a cocoon having been spun by a larva of a species of *Drapetis* (Tachydromiinae). However, no cocoon was spun by a larva in the related genus *Megagrapha* that was observed pupating, suggesting that cocoon production is not common to all Tachydromiinae as has been speculated.

Non-dolichopodid empidoid pupae vary considerably depending on the genus and the habitat they occupy. Some genera (*Drapetis*, *Megagrapha*) possess a pair of lengthened anterior respiratory organs that arise from the anterior dorsal surface of the thorax, whereas others (*Hemerodromia*, *Chelifera*) possess lengthened lateral abdominal respiratory processes; *Neoplasta* has both types of lengthened respiratory processes. Several aquatic genera (*Oreogeton*, *Hemerodromia*, *Clinocera*, *Roederiodes*, *Wiedemannia*) have relatively stout spines along the dorsal surface of each abdominal segment with the terminal segment ending in a pair of strong hooks.

Ecology

The Empidoidea (exclusive of Dolichopodidae) represent a large group of predaceous flies, including a few flower-visiting species. They are often found in various forest habitats, on leaves, tree trunks, damp depressions and aquatic vegetation, and are a dominant component of running water habitats such as streams and seeps. However, some taxa are associated with more open areas such as agricultural fields, grasslands, marshes, coastal zones and beaches. Many groups exploit a variety of habitats for completion of their life cycles, using different sites for larval development, swarming and mating, and adult feeding. Adults capture various arthropod prey, including small to medium-sized Diptera, Hemiptera, Thysanoptera, Lepidoptera, Trichoptera, Hymenoptera, Neuroptera, Ephemeroptera, Plecoptera, Coleoptera, Collembola, and Acari. Because of their vast species diversity and wide habitat range, predaceous empidoid flies are important natural and potential biological control agents of various pest insects.

A number of adult non-dolichopodid Empidoidea also visit flowers (Fig. 1b), presumably in most cases to obtain nectar, but at least a few groups (e.g., *Iteaphila*, *Anthepiscopus*, *Anthalia*, *Allanthalia* and *Euthyneura*) obtain all their protein requirements by feeding on pollen.

Larvae are generally found in damp soil, rotten wood, dung, running water, seeps and tidal zones, depending on the group. They appear to be predaceous on various arthropods, particularly other Diptera larvae.

As a group, Empidoidea have the potential to be useful bioindicators for conservation programs and for site quality assessment. Fifteen species of non-dolichopodid Empidoidea have been listed in the Red Data Book as critically endangered, endangered or vulnerable in Great Britain, whereas 33 species have been listed for Northern Belgium. Due to their predominantly predaceous habits, they are normally not considered to be threatened unless their breeding biotopes or microhabitats are endangered.

Mating Behavior

Many species of non-dolichopodid Empidoidea mate on the ground or on vegetation (e.g., Hemerodromiinae, Clinocerinae, Tachydromiinae and Hybotinae) while others gather in aerial mating swarms (Atelestinae, Ocydromiinae, most Empidinae, and many Trichopezinae). The synchronized movement of adult flies within these mating swarms is the basis for the common name "dance flies." In a few genera, such as *Trichina* (Trichininae), *Oedalea* (Oedaleinae) and *Bicellaria* (Hybotinae), aerial aggregations have been observed even though mating apparently takes place on the ground. These aerial aggregations that occur without mating have been termed "relict swarms."

Members of one large subfamily, the Empidinae, transfer nuptial gifts from male to female during courtship and mating. Depending on the species, these nuptial gifts include prey, various types of inedible objects, and/or secreted balloons (Fig. 1a), which is why the entire group is sometimes referred to as "balloon flies." Within the Empidinae mate choice is generally made by females that visit male-dominated swarms. Males in these species compete for females using these nuptial gifts, often enhanced with various secondary sexual characters. However, many species of Empidinae exhibit sex-role reversed courtship behavior where females gather in swarms to await males that choose their mates. Females of these species exhibit many different secondary sexual characters used in courting males, such as enlarged wings, pinnate leg scales, eversible abdominal pleural sacs and silvery abdomens.

Diversity, Evolution and Distribution

The Empidoidea (exclusive of Dolichopodidae) are worldwide in distribution and comprise approximately 4,500 species classified in over 160 genera. In addition, numerous fossil genera and species have been described from several Mesozoic and Tertiary deposits, particularly in amber inclusions from Lebanon, Spain, New Jersey, Myanmar (Burma), Siberia, Canada, the Baltic Region, Dominican Republic and Mexico. In terms of generic diversity, the entire group is richest in western North America, southern Africa, New Zealand and southern South America. This is also reflected in species diversity, where non-dolichopodid Empidoidea are seemingly more diverse in temperate rather than tropical regions.

The Empididae are a large family of well over 2,000 described species worldwide that include the Empidinae, Hemerodromiinae, and Clinocerinae, as well as the *Ragas* group, *Hesperempis* group, *Philetus* and *Brochella*. The monophyly of this diverse heterogeneous family is still somewhat uncertain. The immature stages of Clinocerinae and most Hemerodromiinae are aquatic whereas the immature stages of the other groups are primarily terrestrial.

The Atelestidae are a small distinctive family of nine extant species that are classified in four genera. The Palaearctic genus *Nemedina* is assigned to its own subfamily Nemedininae whereas the other genera *Atelestus* (Palaearctic), *Meghyperus* (Holarctic) and *Acarteroptera* (Chilean) belong to the Atelestinae. The immature stages of Atelestidae are unknown, but are believed to be terrestrial.

The Hybotidae are a diverse family of approximately 2,000 described species currently classified into five subfamilies, namely the Trichininae, Ocydromiinae, Oedaleinae, Tachydromiinae, and Hybotinae. The family is well defined by several synapomorphies and its monophyly is not in doubt. All of the included subfamilies are virtually cosmopolitan in distribution, except for Trichininae and Oedaleinae, which are essentially Holarctic. The entire family is terrestrial and many species are found in some of the driest habitats occupied by empidoid flies.

The Brachystomatidae are a moderate-sized family of about 150 described species worldwide. The family includes the nearly cosmopolitan Trichopezinae with 14 recognized genera, the Southern Hemisphere Ceratomerinae with three currently recognized genera, and the primarily Holarctic Brachystomatinae with three genera. The monophyly of this morphologically diverse family is based primarily on synapomorphies associated with modifications of the female terminalia. Based on limited information obtained from rearing records and habitats occupied by adults, the immature stages of Brachystomatidae are believed to include both terrestrial and aquatic representatives.

► Flies

References

Chvála M (1983) The Empidoidea (Diptera) of Fennoscandia and Denmark. II. General Part. The families Hybotidae, Atelestidae and Microphoridae. Fauna Entomol Scand 12:1–279

Collin JE (1961) Empididae. British flies, vol 6. University Press Cambridge, UK, 782 pp

Cumming JM (1994) Sexual selection and the evolution of dance fly mating systems (Diptera: Empididae; Empidinae). Can Entomol 126:907–920

Cumming JM, Sinclair BJ (2007) Family Empididae. In: Brown BV, Borkent A, Cumming JM, Wood DM, Woodley NE, Zumbado M (eds) Manual of Central American Diptera, vol 1. NRC Research Press, Ottawa, Canada (in press)

Sinclair BJ, Cumming JM (2006) The morphology, higher-level phylogeny and classification of the Empidoidea (Diptera). Zootaxa 1180:1–172

Smith KGV (1969) The Empididae of southern Africa (Diptera). Annals Natal Mus 19:1–342

Steyskal GC, Knutson LV (1981) Chapter 47. Empididae. In: McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR, Wood DM (eds) Manual of Nearctic Diptera, vol 1. Agriculture Canada Monograph 27, Biosystematics Research Institute, Ottawa, Canada, 674 pp

Dark Mealworm, *Tenebrio obscurus* Fabricius (Coleoptera: Tenebrionidae)

This is a stored grain insect, and very similar to the more common yellow mealworm, *Tenebrio molitor* Linnaeus.

► Stored Grain and Flour Insects
► Darkling Beetles

Darkling Beetles (Coleoptera: Tenebrionidae)

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The family Tenebrionidae belongs to the suborder Polyphaga of the order Coleoptera (beetles). The superfamily Tenebrionoidea includes the families Anthicidae, Colydiidae, Melandryidae, Monomidae, Salpingidae, Mycetophagidae, Tetratomidae, Mordellidae, Rhipiphoridae, Prostomidae, Synchroidae, Oedemeridae, Stenotrechelidae, Meloidae, Mycteridae, Ciidae, Boridae, Pythidae, Aderidae, Scraptiidae, Archeocrypticidae, and Zopheridae, as well as the large family Tenebrionidae.

Order: Coleoptera
 Suborder: Polyphaga
  Superfamily: Tenebrionoidea
   Family: Tenebrionidae

Tenebrionidae are the fifth largest family of Coleoptera with 14,641 species worldwide and 1,345 occurring in the United States. These numbers are low since in the past three decades, many changes have been made in the classification of the family and many new taxa have been described. The Zopheridae and Archeocrypticidae have been removed and given family status, and the former families Alleculidae and Lagriidae are now considered subfamilies within Tenebrionidae. Adding species from those two groups raises the total world species to 16,267 with 1,540 in the United States. The current classification recognizes twelve subfamilies worldwide, eleven of which occur in the United States.

Tenebrionidae is one of the most highly evolved and diverse families of Tenebrionoidea and, indeed, in the order Coleoptera itself. It is a difficult group to characterize because of the many exceptions that exist in most characters. Discounting the exceptions, the following combination of morphological characters separate adult tenebrionids from other Tenebrionoidea: tarsal formula 5-5-4; procoxal cavities closed; antennae eleven-segmented and inserted under lateral expansion of the genae; abdomen with basal three visible sterna connate, 4 and 5 movable.

Adults

The length of adult tenebrionids ranges from slightly more than one to more than 60 mm. While the popular concept of the family is somber coloration (shades of black or brown), there are some (i.e., *Strongylium*, *Cuphotes*, *Poecilisthus*, *Platydema*) that are vividly colored. There are many species in a number of different subfamilies which lack metathoracic wings (sometimes there are apterous and alate members within the same genus, and occasionally even within a population of a single species (i.e., *Blapstinus*). The elytra usually completely cover the abdomen but in some (i.e., *Corticeus*, *Phaleria*) the pygidium is exposed.

Immature Stages

Tenebrionid larvae are usually elateroid (wireworm-like) or C-shaped, elongate and cylindrical, 5–40 mm in length, hard-bodied, with five-segmented thoracic legs. The head is exserted with a frontoclypeal suture present. The apical abdominal segment is usually rounded or triangular, urogomphi, concave plates, or other armature present or absent.

The larvae of some tenebrionids (e.g., *Eleodes*) are sometimes called "false wireworms" because of their resemblance to the larvae of Elateridae which are known as "wireworms." Both do similar damage to underground portions of plants. The most conspicuous difference between them is that tenebrionid larvae have a less flattened head and unfused labrum. Larvae of elaterids usually have the labrum absent or fused with the clypeus, forming a median sclerotized projection called a "nasale."

Habitats

There are few macrohabits from which tenebrionids are excluded. In the deserts of the world, they are among the most conspicuous occupants, sometimes occurring in enormous numbers. All of them have evolved remarkable water conserving mechanisms, and survive principally on metabolic water derived from their foods. Essentially all of these desert dwellers lack metathoracic wings and are therefore flightless. The elytra usually are fused, forming a subelytral cavity, and the integument is thick, both factors helping to control water loss through the spiracles.

Desert tenebrionids escape the extreme daytime temperatures of arid regions by hiding under debris or in mammal burrows, venturing out only at dusk. They are probably not truly nocturnal but opportunists, taking advantage of cooler nighttime temperatures. The experienced darkling beetle collector works mostly at night.

At the other extreme are many genera, rich in species, which inhabit moist environments throughout the world. Genera such as *Strongylium*, *Helops*, *Tarpela* and *Statira* are almost entirely confined to tropical and subtropical regions and are more diurnally active.

Several genera in the tribe Phaleriinae (e.g., *Phaleria*, *Chaerodes*) are found only on ocean beaches where they congregate beneath organic debris. There are a number of interesting relationships between tenebrionids and other insects. Members of the genus *Corticeus* inhabit the galleries of bark beetles (Scolytinae) and others (e.g., *Araeoschizus*, *Bycrea*) occur in ant nests.

Many species are subcortical but usually occur under bark of a number of tree species. There are few that are host specific and none are defoliators. At least one species, *Palembus ocularis* Casey, appears to be intimately associated with a plant, *Tamarindus indica*, and another, *Sciophagus pandanicola* (Boisduval), occurs on *Pandanus* in Hawaii. Those are exceptions.

There are a number of genera in several widely separated phylogenetic groups (e.g., *Bolitotherus*, *Rhipidandrus*, *Neomida*, *Platydema*) which inhabit fungi. It appears that both the larvae and adults feed directly on the fungi.

A number of darkling beetle species live in caves or rock fissures and apparently nowhere else. Some (e.g., *Alphitobius laevigatus* (Fab.), *Zophobas* spp.) often are associated with bat guano in caves.

Food

Darkling beetles are mostly omnivorous and only a few appear to be host specific. Many species (e.g., *Eleodes*, *Blapstinus*) are root feeders. Wherever stored grain products are stored, a number of cosmopolitan tenebrionids are secondary pests. None of them are able to attack unbroken grain kernels but feed on ground or milled farinaceous materials; these insects are collectively known as "bran bugs." The genera *Tribolium*, *Gnatocerus*, *Palorus*, *Sitophilus* and *Latheticus* are secondary pests of cereal products throughout the world. All of these are thought to be of tropical origin and probably were fungus feeders originally. They tend to favor stored products that are not in the best condition (wet, moldy, etc.).

References

Doyen JT (1972) Familial and subfamilial classification of the Tenebrionoidea (Coleoptera) and a revised generic classification of the Coniontini (Tentyriinae). Quaestiones Entomol 8:357–576

Doyen JT, Lawrence JF (1979) Relationships and higher classification of some Tenebrionidae and Zopheridae (Coleoptera). Syst Entomol 4:333–377

Doyen JT, Tschinkel WR (1982) Phenetic and cladistic relationships among tenebrionid beetles (Coleoptera). Syst Entomol 7:127–183

Watt JC (1974) A revised subfamily classification of Tenebrionidae (Coleoptera). NZ J Zool 1:381–452

Watt JC (1967) A review of classifications of Tenebrionidae (Coleoptera). Entomologist's Monthly Magazine 102:80–86

Dark-Winged Fungus Gnats

Members of the family Sciaridae (order Diptera).

► Flies

Darlington, Jr., Philip J

Philip Darlington was born in Philadelphia, USA, on November 14, 1904. The family moved to the state of Connecticut, and Philip spent the rest of his life in the New England states (Connecticut, Massachusetts, Maine, New Hampshire and Vermont) except when he was on field trips or in military service. His parents were interested in nature, which influenced Philip in his career. In 1922, he entered Harvard University, gained a first degree and continued to graduate school, gaining a Ph.D. in 1932. An explanation for his lengthy studies is that he took the year 1928–1929 to work in Colombia for the United Fruit Company. Ostensibly he worked as entomologist to solve a problem in applied entomology. He returned to Harvard University with a large collection of insects and bird skins. Then he worked on his Ph.D. dissertation on carabid beetles of New Hampshire. But in 1931–1932 he joined an expedition, led by W.M. Wheeler, to Australia, from which he returned with an extraordinarily large collection of insects plus 341 specimens of mammals. On his return to Harvard University, he was appointed assistant curator of insects. During the next few years he made several expeditions to the West Indies, collecting insects and other animals in the high mountains of the Greater Antilles. In 1940 he was appointed curator of Coleoptera, and 2 years later he married Elizabeth Koch. However, in World War II he enlisted in the U.S. Army and served in a malaria survey in New Guinea, the Bismarck Archipelago, and the Philippines. He returned to Harvard University in 1944. Other collecting expeditions followed, such as to the southern extremes of South America in 1962–1963, but he was also appointed Alexander Agassiz Professor of Zoology at Harvard University. His published works were on zoogeography and natural selection, mimicry, and taxonomy. His three books were (1957) "The geographical distribution of animals," (1965) "Biogeography of the southern end of the world…," and (1980) "Evolution for naturalists…" In recognition of his works he was elected to the (U.S.) National Academy of Sciences, to the American Academy of Arts and Sciences, and was awarded two Guggenheim fellowships. He died on December 16, 1983.

References

Ball GE (1985) The contributions of Philip J. Darlington, Jr. to the study of carabid beetles in the Americas and a bibliography of his publications. In: Ball GE (ed) Taxonomy, phylogeny and zoogeography of beetles and ants. A volume dedicated to the memory of Philip Jackson Darlington, Jr. (1904–1983). Dr W. Junk (Series Entomologica vol 33), Dordrecht, xiii + 514 pp

Brown WL (1985) Philip Darlington's contributions to evolutionary theory. In: Ball GE (ed) Taxonomy, phylogeny and zoogeography of beetles and ants. A volume dedicated to the memory of Philip Jackson Darlington, Jr. (1904–1983). Dr W. Junk (Series Entomologica vol 33), Dordrecht, xiii + 514 pp

Carpenter FM (1985) Philip Jackson Darlington, Jr.: A biographical sketch. In: Ball GE (ed) Taxonomy, phylogeny and zoogeography of beetles and ants. A volume dedicated to the memory of Philip Jackson Darlington, Jr. (1904–1983). Dr W. Junk (Series Entomologica vol 33), Dordrecht, xiii + 514 pp

Darners

A family of dragonflies in the order Odonata: Aeshnidae.

► Dragonflies and Damselflies

Darwin, Charles

Charles Darwin was born in Shrewsbury, England, on February 12, 1809. He was educated at Shrewsbury Grammar School, Edinburgh University (1825–1827), and Cambridge University (1828–1831), obtaining B.A. and M.A. degrees. His real interest at Cambridge was in collecting insects, especially beetles. Then he served as naturalist aboard H.M.S. Beagle during that ship's round-the-world cruise in 1831–1836. Insects were prominent among the organisms that he observed and collected, but many of the new species that he collected were not named by him, but by specialists (C.C. Babington, F.W. Hope, W.W. Saunders, J.O. Westwood, and G.R. Waterhouse). He did spend 8 years (1846–1854) monographing barnacles (Cirripedia). His leaving of the descriptive work on insects to specialists allowed him to concentrate on producing his greatest works, "The origin of species" (1859) and "The descent of man" (1871). He died on April 19, 1882, in the county of Kent.

References

Remington JE, Remington CL (1961) Darwin's contributions to entomology. Ann Rev Entomol 6:1–12

Smith KGV (1982) Charles Darwin and the Royal Entomological Society of London. Antenna 6:200–201

Darwinism

This term is synonymous with the Theory of Natural Selection, which explains that speciation results from differential survival and reproduction in response to selective forces (both biotic and abiotic). Organisms that are well adapted to selective forces can survive and reproduce, with the progeny of these survivors likely inheriting these adaptations. In contrast, organisms that are not well adapted to these same selective forces may not survive or reproduce, leading to their elimination and loss of progeny. Thus, small mutations interact with these selective forces and allow organisms to change over time.

► Darwin, Charles

Dascillidae

A family of beetles (order Coleoptera).

► Beetles

Date Palm Stem Borer, *Pseudophilus testaceus* Gah. (=*Jebusea hammershmidti* Reiche) (Coleoptera: Cerambycidae)

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The adult date palm stem borer is 21–40 mm in length and the females usually are longer than the males. The beetle is reddish brown in color and the body is covered by short pubescence. The eyes are perspicuous. The antennae have twelve segments and are as long as the body. The hind margin of the last sternite is straight in the male and round with a small depression in its middle in the female. The eggs are white and elongated, measuring about 3.5–4.3 mm long and less than 2 mm wide. The larvae are long and cylindrical, about 45–50 mm in length, light in color with dark brown heads, and are legless with well-formed dorsal pseudopods. The pupae are 36–45 mm in length.

Geographic Distribution

The date palm stem borer is found in India, Iraq, Iran, Saudi Arabia, the Gulf States and Egypt.

Symptoms and Economic Importance

This pest is more serious in humid areas than dry ones. Older trees are more susceptible to infestation than young trees. Infestation is more serious in neglected farms and the potential damage could reach up to 90% in humid areas. The main damage symptoms caused by this pest are the cylindrical, oblique emergence holes of the adults made when the beetles emerge after burrowing in the trunk of the palm trees.

Biology

The life cycle of the date palm stem borer is 1 year in most cases, but sometimes a single generation may take longer. Adults are active from April to July. The number of eggs per female varies from 30 to 150. The eggs are laid singly under the frond base with an incubation period of up to 2 weeks. The larvae feed first on the frond base and then bore into the stem (trunk) of the tree where they spend the winter months. The larvae have four to five instars in about 10 months. The larvae construct an oval pupal cell 25–30 mm long and 10–15 mm wide, and the pupal stage lasts about 3 weeks.

Control

Pest control measures are mainly focused on the adults. Light traps are recommended to capture adults and to provide notice to farmers about the presence and density of this pest. The capture rate is the highest from early-May to mid-June. If the pest is causing serious economic damage, dusting with contact insecticides is recommended. The growing point of the tree and the base of the fronds are the preferred site for insecticide application. The fungus *Beauveria bassiana* yielded promising results, experimentally, against the larvae in Iraq.

References

Talhouk N (1984) The most common agricultural pests in Saudi Arabia. Ministry of Agriculture and Water, 121 pp (in Arabic)

Hussain A (1974) Pests of date palm trees and dates in Iraq. Baghdad University, 190 pp (in Arabic)

Hammad SM, Kadous AA (1989) Studies on the biology and ecology of date palm pests in the eastern Province of Saudi Arabia. Research Grants Program, Technical Report No. 25. KACST, Riyadh, Saudi Arabia, 142 pp

Davis, William Thompson

William Davis was born in New York on October 12, 1862, and developed an interest in natural history, encouraged in entomology by Augustus Grote. He had no college education, but went to work at the age of 20 as a clerk. He joined the Brooklyn Entomological Society and the New York Entomological Society and obtained an education by learning from other members and by his own observations. His special interest was in cicadas, and he named and described more than 100 of the roughly 170 species known in America north of Mexico. He traveled little, but obtained specimens from all over the USA by purchase. At the age of 46, he retired from his job, having been able to save enough money, and spent the rest of his life on his hobbies, mainly entomology, but including other areas of natural history, as well as history. He and Charles Leng together wrote two books on the history of Staten Island, the second of which (1930) appeared in four volumes. He was a major donor of funds to the Staten Island Institute of Arts and Sciences, and left the type specimens of the insects he described to the American Museum of Natural History. He married in 1900, but his wife died 13 months later. He died on January 22, 1945.

Reference

Mallis A (1971) Willian Thompson Davis. In: American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Day-Degree

A physiological unit combining temperature and time, and used to measure and predict growth of organisms. Also commonly called degree-days.

► Bioclimatic Models in Entomology

DDT

This is an acronym for dichloro-diphenyl-trichloroethane, more correctly known as 2,2-bis-(cholorophenyl)-1,1,1-trichloroethane), a compound first synthesized in 1873 but not used as an insecticide until much later. It was not until 1939 that the Swiss chemist Paul Müller discovered its insecticidal properties, and Geigy Chemical Company began producing it for control of insect pests. This product, though not universally effective, was much more effective than any previous insecticide and revolutionized chemical-based insect management. It proved very effective in control of medically important insects and saved thousands of civilian and military lives in wars of that era by improving sanitation and blocking disease transmission by insects during and following warfare. In the crop production sector, DDT also created a new level of expectation among producers and consumers, who came to expect higher crop yields, and undamaged and uncontaminated produce.

DDT is an organochlorine insecticide, and is related to dicofol (a miticide) and methoxychlor (an insecticide) among other products. Its major breakdown products are DDD and DDE, although DDD was registered as an independent insecticide. DDT has low volatility, is insoluble in water, but is soluble in nonpolar solvents. It degrades under alkaline conditions, but is relatively stable in sunlight. Like most insecticides of the era and since, it affects transmission by nerves. Specifically, it disrupts sodium ion channels resulting in spontaneous firing of nerves, leading to spasms and death. In terms of acute toxicity, it is only moderately toxic to mammals, though very toxic to many insects and some other aquatic organisms such as crayfish and shrimp. In some cases, it apparently caused acute mortality to birds.

Most importantly, DDT was very persistent, with a half-life of 30–60 days in water and 2–15 years in soil. Persistence was useful in protecting against insect damage, but proved to be a feature that allowed accumulation of DDT or its DDD and DDE products in animal tissues. Because predators tend to be long-lived and consume numerous prey over time, they were exposed to large quantities of DDT and it products, and it persisted in their bodies and built to high concentrations. Exposure to these chemicals was associated with egg thinning in several raptors such as peregrine falcon, bald eagle, and brown pelican. Calcium deposition was found to be impaired when birds were exposed to DDT. The thin eggs could not support the chicks, resulting in high mortality and rapid population decline in these and some other birds. This led the United States Environmental Protection Agency to ban the use of DDT in the USA in 1972, though left open was the possibility of its use for medical emergencies. Many other countries followed the lead of the USA, and DDT use has declined in much of the world, though it remains available and popular in some countries. With the re-emergence of malaria and some other tropical arthropod-borne diseases as serious problems for humans in warm areas of the world, a resurgent interest in DDT for use against mosquitoes is developing. The evidence for DDT causing health problems in humans, particularly cancer, is weak.

► Insecticides
► Costs and Benefits of Insects

Dead-End Hosts

Hosts that do not allow amplification of a disease, thereby interrupting transmission, and serving as an end point in the disease cycle. This is usually used in the context of arboviruses.

► Amplification Hosts

Dead Log Bark Beetles

Members of the family Pythidae (order Coleoptera).

► Beetles

Dealate

An individual that has shed its wings, usually after mating. This is common among some groups of social insects.

Dealation

Among social insects, the removal of the wings by the reproductives during or after the nupital flight, and prior to colony founding.

Death Feigning

A behavior displayed by defenseless insects when threatened or disturbed, wherein they become inactive and appear to be dead.

Death-Watch Beetles

Members of the family Anobiidae (order Coleoptera).

► Beetles

Debach, Pau l Hevener

Paul DeBach was born in the state of Montana, USA, on December 28, 1914. With his parents, he moved to California at an early age. His university training began at the University of California at Los Angeles, but he transferred to the Berkeley campus, and completed his B.A. degree in entomology in 1938. Next, for his graduate studies, he moved to Riverside, worked with H.S. Smith, and was awarded a Ph.D. degree in 1940. His first appointment was with the U.S. Public Health Service (1942–1943) in malaria control, and his second was with the U.S. Department of Agriculture (1943–1945) in control of whitefringed beetle. After World War II, he returned to California as assistant entomologist with the Department of Biological Control, Citrus Experiment Station, of the University of California at Riverside. He remained there for the rest of his career. He organized the first formal courses there in biological control. His major research was on homopterous pests of California citrus. He undertook foreign exploration for biological control agents. To conduct his work, he needed reliable identifications of pests and biocontrol agents alike and, when these could not be obtained rapidly from taxonomists, he undertook the taxonomy himself, focusing on minute wasps, and published (1979) a monograph on the genus *Aphytis.* His work also included artificial selection of more efficient strains of biocontrol agents. Together with Carl Huffaker, he developed the University of California International Center for Biological Control. Again with Carl Huffaker, he developed an Integrated Pest Management Program designed to develop pest management strategies with minimal use of chemical pesticides, in which 18 universities and the U.S. Department of Agriculture collaborated. He published more than 200 papers and four books. The (1964) "Biological control of insect pests and weeds" that he edited with Carl Huffaker and to which he contributed key chapters was for years the leading textbook on biological control. He died in California in February 1992.

Reference

Gordh G, Huffaker CB, Luck RF (1992) Paul Hevener DeBach, Biological control: Riverside. Available at http://sunsite.berkeley.edu:2020/dynaweb/teiproj/uchist/inmemoriam/inmemoriam1993 (accessed Aug 2002)

Decomposer Insects

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In any natural or semi-natural habitat, three types of organisms exist: producers, consumers and decomposers. Good functioning of the ecosystem will depend on their suitable action and interaction. Organisms capable of catching energy and synthesizing organic matter from inorganic compounds constitute the producers. Though chemosynthetic bacteria exist, most producers are plants. Green plants use solar energy and fix CO_2, producing organic compounds rich in energy. Most of this accumulated energy will get used in the ecosystem by respiratory processes and other vital functions, whereas some organisms of the community such as the consumers and decomposers will use the energy accumulated by other organisms.

The consumers are heterotrophic organisms that obtain food from producers or from other consumers, with the possibility of several levels of complexity inside an ecosystem. Primary consumers feed directly on the producers. Secondary consumers feed on primary consumers, etc. Finally, we have the decomposers, saprophytic organisms feeding on dead matter or decaying remains derived from producers and consumers. Thus, the organic matter synthesized by producers goes on to other levels of organisms across the trophic chains, though much of the energy will be used in respiratory processes at all levels.

In these trophic processes, an important element to take into account is that the decomposers operate at all the levels. Thus, all energy not used by the consumers and producers, as well as that accumulated in excretory products, is used by the decomposers and recycled into the ecosystem. This process constitutes the energy cycle, and good functioning and subsistence of the ecosystems depends on effective energy cycling.

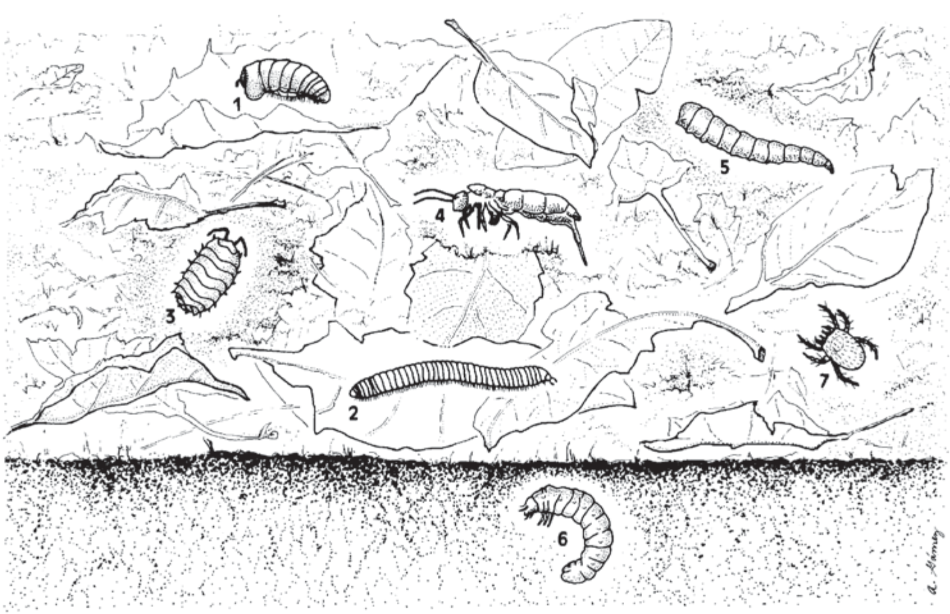
In a terrestrial ecosystem, more than 90% of the organic matter synthesized by the green plants remains unconsumed, and it passes to the level of decomposers as plant material decaying on soil, together with the remains of animal corpses, and the excretory products of all levels.

The process of decomposition is one of the most important events in the functioning of ecosystems. Decomposition can be defined as the process by means of which a dead organism or its remains are broken down into the parts or elements that comprise it, and at the end of the process the animal or plant remains will have gradually disintegrated until their structures cannot be recognized, and their complex organic molecules will have fragmented. This involves a complex process in which biotic and abiotic agents interact within the ecosystem. To sum up, the decomposition processes cause the liberation of energy and mineralization of chemical nutrients, turning the organic matter into inorganic elements.

In the process of decomposition, there are two phases, sometimes difficult to distinguish, that we could call "destruction" and "degradation" of the organic matter. The process of destruction refers to the initial phase of the decomposition cycle and is characterized by breaking down the organic remains by mechanical means so that at the end of this process small-sized particles are obtained. During this initial phase both abiotic (rain, wind, temperature, etc.) and biotic elements (decomposer fauna) play an important role. In the second phase, degradation of the organic matter occurs, resulting in the disintegration of the small particles into molecules, producing CO_2, H_2O and mineral salts as final products.

The destruction phase also results in dispersion of the organic matter, because the small resulting particles can be taken by means of diverse mechanisms out of the initial source (dragging by wind and water, or direct action of animals such as burial, ingestion, movement, etc.). It is important to note that nutrients released by decomposers constitute a food source for numerous animal species, extending the cycle by means of incorporation of the nutrients into tissues, and eventually constituting new corpses and excrements.

The groups of arthropods involved in the processes of decomposition of animals and plants remains belong to many taxa (Fig. 2). They are considered to be mesofauna when their size ranges between 100 and 200 mm (such as mites (Acari), springtails (Collembola) and small insects), or macrofauna when they are larger, such as some beetles (e.g., Scarabaeidae, Geotrupidae or Silphidae), Diptera larvae (e.g., Muscidae, Sarcophagidae, Scatophagidae or Calliphoridae), centipedes (Diplopoda), woodlice (Isopoda), etc. All these groups are responsible for the fragmentation of plant or animal remains, contributing to the destruction phase. They contribute both to the redistribution of the organic remains and formation of soil elements. These groups of arthropod



Decomposer Insects, Figure 2 The arthropods involved in the process of decomposition of animal and plant remains belong to such taxa as Diplopoda (1 and 2), Isopoda (3), Collembola (4), Diptera larvae (5), Coleoptera (6), Acari (7).

decomposers are present in nearly all terrestrial habitats, and generally in very high numbers. In some cases, millions of individuals belonging to hundreds of species have been identified in just one square meter. Especially in temperate areas, arthropods are the major decomposers, playing a very important role in degradation of waste. Thanks to the action of the arthropods during the initial phase of fragmentation, organic remains can be degraded, and eliminated from the soil surface.

When a suitable community of decomposers exists, it prevents the appearance of potential bottlenecks in the recycling of basic elements in the ecosystem. Thus, when entomofauna capable of acting effectively on plant and animal remains does not exist in a terrestrial ecosystem, serious alterations in the ecosystem arise, with a reduction in energy flow and great loss of biodiversity.

Decomposers of Plant Remains

Arthropods play an important role in degradation processes of plant remains. Nevertheless, most lack the ability to develop enzymatic processes for degrading the fundamental components of any plant: lignin and cellulose. Degradation of cellulose requires the presence of the enzyme cellulase, which most arthropods lack. Many insects have solved this problem by means of mutualistic relations with micro-organisms, having bacteria or symbiotic protozoa in the intestinal tract. Others take advantage the cellulase produced by external microflora. Among the well-known insect decomposers are termites (Isoptera) and cockroaches (Blattodea). The termites possess symbiotic bacteria and protozoa, and in their absence wood cannot be assimilated by these insects.

In many ecosystems millipedes (Diplopoda) have special importance as decomposers. These arthropods, which specialize in leaf litter consumption, sometimes are abundant, concentrated in relatively small areas, and active during a great part of the year.

Another important group in the degradation of plant remains is woodlice (Isopoda), which also possess symbiotic microorganisms in their intestine that allows them to degrade cellulose.

Not all arthropods assimilate cellulose by means of symbiotic bacteria, but they make use of woody materials that are pre-digested by extraintestinal microorganisms. Included in this group are some species of springtails such as *Tomocerus* (Collembola), ambrosia beetles (Coleoptera: "Curculionidae" Scolytinae), ants of the genus *Atta* (Hymenoptera: Formicidae) and termites (Isoptera) that cultivate fungi.

All plant remains do not always present the same difficulty of digestion for arthropods. Fruits are extensively exploited by arthropods, thanks to the existence of yeasts that enhance fruit decomposition, allowing many arthropods such as flies (*Drosophila* is probably the best known example) and wasps (Hymenoptera: Vespidae) to feed into the product resulting from the fermentation. Nevertheless, a fact that must be remembered is that the relationship between micro-organisms (bacteria, fungi and protozoa) and plant remains is very close, and therefore, in most cases it is inevitable that the arthropods consume both resources simultaneously. In some cases, the ingested biomass of micro-organisms is more important nutritionally than the ingested plant remains.

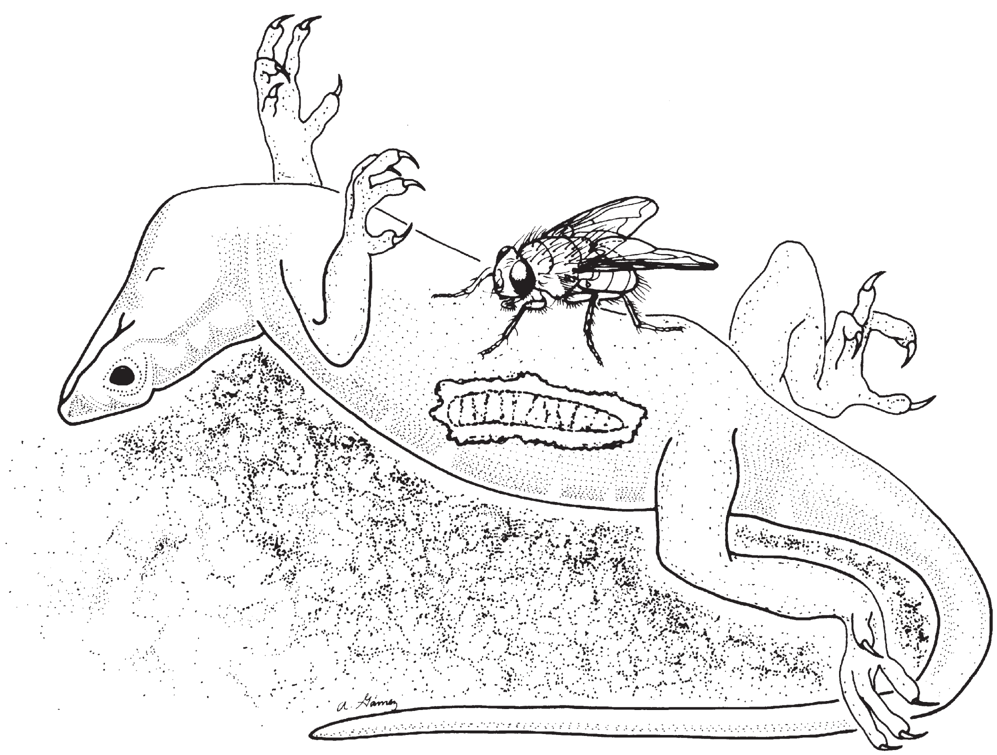
The Entomofauna of Excrement and Corpses

The studies of ecosystems have generally paid preferential attention to the decomposition processes of vegetative remains, due to the importance that litter has in the composition of the soil and the contribution of its nutrients. The process of decomposition of carrion and dung, though sometimes not well known and little studied in many ecosystems, is also important.

To understand the processes of degradation of corpses and excrements, and the attractiveness of this decaying matter to arthropods, we must consider that they are very rich resources of organic components that have very special microclimatic conditions. Dung and carrion represent not only a rich source of energy, but also a very specialized habitat that is exploited, in most cases, by very specific entomological fauna. This fauna obtains food either directly, such as in the case of the coprophages and carrion-eating arthropods, or indirectly, such as in the case of the predators that feed on the decomposers.

It is generally difficult to establish the limits of an arthropod community, but when we study carrion or dung we meet a perfectly defined ecological unit, limited in both space and time. Carrion (Fig. 3) and dung present many special characteristics that influence the composition and dynamics of the set of species using them. These resources constitute isolated microhabitats inside an ecosystem in which they are deposed, forming a patchy system. These microhabitats are relatively small in size (except for corpses of large vertebrates), rich in nutrients, and with a short existence (generally not more than one insect generation). Carrion and dung are special microhabitats characterized fundamentally by their rapid ecological successions, being extremely ephemeral micro-ecosystems that are rapidly destroyed by the action of the arthropods that colonize them. Arthropod species are sometimes very abundant in these resources, and thousands of individuals belonging to a set of arthropod decomposers may be attracted to an isolated unit. For example, more than 100 species of arthropods belonging to 16 orders and 48 families have been found in just one rabbit corpse, or 16,000 dung beetles found in elephant dung.

The arthropods involved in succession vary according to geographical areas, even in places with similar climates. Also, the number of individuals and the species colonizing these microhabitats vary enormously from one patch to another, and also through time. Typically, these species are more or less aggregated in these limited resources, with interspecific differences in foraging and breeding behavior. The aggregated



Decomposer Insects, Figure 3 **Adult and larva of a blow fly (Diptera: Calliphoridae) on a lizard cadaver. Blow flies constitute the first wave of insects colonizing corpses.**

spatial distribution and resource partitioning allow a great number of decomposer species to coexist in an ecosystem, but great differences in numbers of individuals and species composition are generally found among similar amounts of carrion or dung. However, the broad taxonomic categories of carrion or dung specialists are similar worldwide.

Sometimes it is difficult to discern whether the arthropod fauna involved in decomposition processes contributes directly to the recycling of organic matter or, as in leaf debris systems, they make the substrate more available to the microorganisms (bacteria and fungi) considered by some authors to be the true decomposers. The action of the larvae of flies and other insects, for example, produces liquefaction of corpse tissues, preparing the substratum for the intervention of microbial decomposers. On the other hand, the mechanical action associated with removal of excrement by beetles, and in making tunnels by both beetles and fly larvae, enhances microbial activity. The existing studies show that the action of decomposer species of arthropods and microorganisms is complementary, but not purely additive.

Vertebrates are often considered to be important scavengers, and many species feed on carrion. Vertebrates may not distinguish between freshly killed prey and a freshly dead animal, and many predators eat both of them. It is not easy to know how much organic matter is recycled in this manner, but depending on the period of the year, many of the small animal corpses can be totally destroyed by scavengers. However, during summer and autumn in temperate regions, and in the rainy period in tropical areas, corpses are rapidly colonized by arthropods. As a result, rapid decay is observed, with the vast majority of carrion being consumed by various arthropod species, principally fly larvae.

The process of decomposition among excrement and corpse systems varies as a result of the particular composition of the remains, which attracts its own specialist community of arthropod decomposers. Likewise, differences between the entomological fauna of excrement are found, especially between the excrement of carnivores and those of herbivores. This occurs because the composition of nutrients is totally different between carnivore and herbivore excrement. While the excrement of herbivores contains a great number of vegetative components that are little changed from the plants ingested (80–75% of the ingested weight), the digestive system of carnivores is much more efficient and the excrements contain less organic matter suitable for exploitation by arthropod species. The fauna feeding on the carnivore excrement is generally depauperate, and decay often results exclusively from the actions of microorganisms.

Decomposers of Corpses

Arthropod species attracted to corpses change according to the ecosystem and environmental conditions. The importance of necrophagous arthropods is not only the ingestion of carrion, but also in making the carrion available to microorganisms. Many insects, principally fly larvae, secret enzymes directly into the carrion, producing liquefaction of the tissues. Likewise, adult and larval beetles, and fly larvae, make tunnels through the carrion, increasing aeration and microbial activity. The dominant groups, both in number of individuals and diversity, are dipterous and coleopterous species. Also, in geographic areas where ants are abundant, the corpses are removed rapidly by these insects, specially the corpses of invertebrates. Nevertheless, the arthropods involved in this processes, and the intensity of the action of these animals, vary according the spatial location of the corpse, type of soil and depth of burial. The number of insects living in carrion diminishes with depth of burial.

The arthropods colonizing corpses form a sequential succession of groups and species that depends on the size of the carrion, and on the climatic and edaphic conditions of the area where they live. Very few species are widespread throughout the world, and each geographical area and ecosystem has its specialist species feeding on carrion.

The colonization of a corpse is a sequence of arthropods arriving as successive waves at the carrion. The form, nature and timing of the succession depend on the geographic area, the surrounding non-biological environment, and the size of the carrion. The first waves involve blow flies (Diptera: Calliphoridae) and house flies (Diptera: Muscidae) arriving for a few hours to oviposit or drop live larvae. Later, there is a second wave of sarcophagid flies (Diptera: Sarcophagidae) that together with species of calliphorid and muscid flies, deposit their eggs or live larvae on the corpse. The larvae of these flies are, in turn, consumed by larvae and adults of predatory beetles living in corpses. Staphylinids (Coleoptera: Staphylinidae), histerids (Coleoptera: Histeridae) and silphids (Coleoptera: Silphidae), all are predators of flies, though they also feed on carrion. When the viscera decompose and the fat of the corpse turns rancid, a third wave of insects starts, with some species of phorids (Diptera: Phoridae), drosophilids (Diptera: Drosophilidae) and hover flies of the subfamily Eristalinae (Diptera: Syrphidae) arriving. The fourth wave consists of cheese skipper species (Diptera: Piophilidae) and related families of flies. Finally, a fifth wave occurs, the larvae and adults from some groups of beetles such as dermestids (Coleoptera: Dermestidae), trogids (Coleoptera: Scarabaeoidea: Trogidae) and clerids (Coleoptera: Cleridae) and tineid caterpillars (Lepidoptera: Tineidae) that eat keratin and feed on the remaining hair and feathers.

Diptera are among the most important decomposers, especially some of the Calliphoridae (e.g., *Lucilia*, *Calliphora*, *Chrysomyia*, etc.), followed by some Muscidae (e.g., *Fannia*), and Sarcophagidae (e.g., *Sarcophaga*). Though the adults feed on the fluids of the corpse, the larvae are the true decomposer organisms, secreting enzymes directly into the carrion and helping with the liquefaction of the corpse tissues while assisting the increase of microbialactivity. These families of Diptera are more abundant from early summer to mid autumn in temperate regions, and also in the rainy season in tropical areas.

The biology of all the Diptera species is similar. Females of blow flies and house flies lay eggs or drop live larvae on to the surface of the fresh corpses, generally at the base of the hairs or near to the natural holes. Such natural openings facilitate the penetration of larvae into the inner regions of the corpse. The ovoviparous females of sarcophagids are less fecund than blow flies and house flies, and do not deposit all their larvae in the same carrion, rather distributing them evenly among several corpses. Development of fly larvae is normally very fast (3–6 days during the favorable periods of the year) and pupation takes place away from the corpse, in the soil surrounding it. Sometimes the mature larvae may migrate more than one meter from the carrion. Ten to 30 days after pupation, the new adults emerge and fly off to search for new corpses, starting a new life cycle.

Among Coleoptera, a principal group in many temperate ecosystems is Silphidae (e.g., *Nicrophorus*, *Silpha*). It is a group specifically adapted to living in carrion and its action is comparable to that of the Diptera. The adults of *Nicrophorus* species show a very special biology. When a species of this genus arrives at the fresh corpse, the male and female bury the carrion (Fig. 4) underground, thereby reducing the risk of colonization by other insects. Once the carrion is safe in the burial chamber, and the beetles have copulated, they make the corpse into a ball. The eggs are deposited into a short chamber above the carrion ball. The female makes a conical depression on the top of the ball, and defecates and regurgitates droplets of partially digested food, and stridulates, attracting the larvae to the depression in the carrion. The female, and sometimes the male, give parental care and provide food by regurgitating into this depression. Thus, they ensure the survival of the offspring and avoid predation and competition.

In tropical forests, many species of Scarabaeidae are attracted to both carrion and dung. Availability of resources for dung beetles in most

Decomposer Insects, Figure 4 **Male and female *Nicrophorus* (Coleoptera: Silphidae) burying a mouse corpse underground. These insects are specifically adapted for living in carrion.**

Neotropical forests is low because of the low density of large mammals and the low availability of any particular type of dung. This absence can probably be attributed to the absence of suitable numbers of large herbivores in the forests of Central and South America, and the few natural pastures of this region (except where cattle have been introduced). In African forests, where large herbivores are present in relatively large numbers, many dung beetles specialized in the use of excrement may be found.

Forensic Entomology

Knowledge of the succession of species taking place in a corpse following death has been used in studies of forensic entomology. This rather consistent succession has been used for medical legal analyses to estimate the time elapsed since death of an animal. The study of arthropod species from a cadaver gives us information about the location, time, and conditions to which the corpse was exposed before being found. The generalized sequence of fly colonization is most frequently used. The first colonizing species are the bigger flies belonging to the blow fly family (Calliphoridae) followed by sarcophagids (Sarcophagidae) and house flies (Muscidae). The adults of the lesser-sized families such as Psychodidae, Scatopsidae, Sciaridae, Phoridae, Sepsidae and Sphaeroceridae come to the corpse in the last phase of decomposition, after the corpse has been abandoned by the larvae of the first colonizing flies. Their larvae leave the corpse to pupate away from the larval site, normally in the ground or substrate below carrion. The development of larvae is temperature dependent, and knowledge of the larval cycle and its relationships at different temperatures, can be used to estimate the age a cadaver. Forensic entomology is an important instrument in criminal investigation; however, we must take into account that each succession will consist of different species in different geographical regions. This is true even in sites with similar climatic conditions, because few species are widespread in distribution, and each area may have its own carrion-feeding species. Nevertheless, the broad taxonomic levels of decomposers of carrion are constant worldwide. Also, some differences may be found as a result of variation in ambient temperatures that may speed the process (sunlight and high temperatures) or retard it (shelter and cold conditions), variation in exposure of the carrion, possible burial of the corpse, cause of death, etc.

Some carrion-feeding flies can cause myiasis, an infestation of live vertebrates by larvae of Diptera, particularly blow flies of the genera *Lucilia*, *Chrysomyia*, *Cochlyomyia*, etc., that feed on live or dead tissues of the host. This infestation causes problems in some farming areas, and may be of considerable economic importance. Probably one of the best known examples of myiasis is with *Cochliomyia hominivorax* (Diptera: Calliphoridae), a species living in neotropical regions. Larvae of *C. hominivorax* develop on wounded animals and humans, and can provoke the death of the host.

Decomposers of Excrement

The excrement of vertebrates generally is a rich source of nutrients, and insects play an important role in the rapid recycling processes of feces. However, carnivorous excrement contains little material useable by insects because of their efficient digestive process. In contrast, the digestive system of herbivores is less efficient, and the dung produced is quite similar to the original leaf material. More than half the food consumed by herbivorous animals is returned to the ground in the form of unassimilated material, i.e., dung. Because it is abundant in organic matter and moist, herbivore dung is an ideal medium for establishment of a specific, rich entomofauna involved in the process of decomposition and elimination of feces. Quantitatively, large herbivore dung pats are the most important resource for dung beetles in most regions, and this fauna is especially abundant in historic grazing areas.

Excrement is a very special habitat for coprophagous species, and the spatial distribution of dung increases the tendency of these insects to concentrate in a limited space. The process of colonization of excrement typically consists of three waves of insects. The first wave of colonizers involves certain flies arriving within hours to lay eggs or larviposit on the dung before a crust is formed on the pat. The second wave is several families of beetles. Lastly, mites become abundant.

The main groups of flies are Muscidae and Scatophagidae, followed by Fanniidae and Calliphoridae. Most adults and larvae of flies are coprophagous, but feeding also on the microorganisms present in the dung. Others are facultative or obligate predator species. Many species are attracted to any decaying matter, but others only feed and breed in dung. Throughout the world, muscid coprophages such as *Musca domestica*, *Musca vetustissima* and *Haematobia irritans* are pests of cattle. But some muscids are facultative predators (e.g., *Muscina* spp.) and obligate predatory larvae (e.g., *Mydaeae* spp.). The best-known species of Scatophagidae is probably *Scatophaga stercoraria*, a species frequently found visiting dung anywhere in the Northern Hemisphere, and also in northern and southern Africa. *Scatophaga stercoraria* has coprophagous larvae, but adults are primarily predators or nectar feeding, only occasionally feeding on liquefied dung.

Females of flies may lay eggs in batches of about 150, which hatch in from 8 to10 h, to 3 days, depending on the environmental conditions and the species involved. Muscid larvae may complete their development within 2 days in favorable environmental periods, or delay several weeks in the colder temperatures.

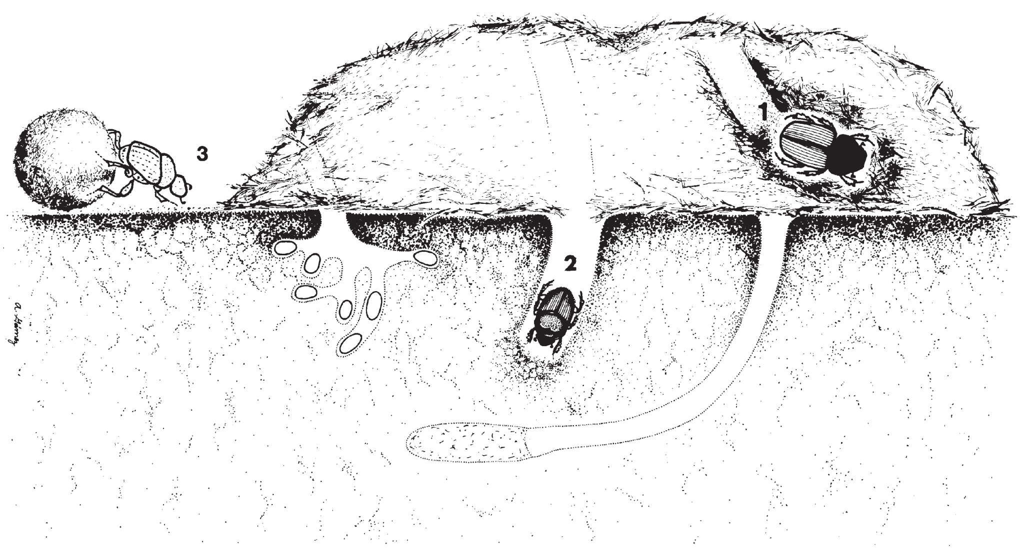
Among beetles that use dung resources, the dung beetles belonging to the Scarabaeidae (Scarabaeinae, Geotrupinae and Aphodiinae) are the most important and numerous. Not all scarab larvae are strictly coprophagous, and some ingest soil organic matter or feed on roots of plants. However, many are coprophages, and often exceedingly abundant. Thousands of individuals from many species may be found colonizing single dung pats in temperate and tropical grazing ecosystems. Most Aphodiinae are saprophagous and within the Geotrupinae coprophagy is the rule for the Geotrupini. Only Scarabaeinae has coprophagy as a characteristic of most of its species. In this case, most of the nutrients eaten by the adults are derived from eating microbes or colloids suspended in dung. The larvae feed on the dung supplied by their parents in a nest chamber.

Various other groups of beetles visit dung but they are primarily predators. Coleoptera of the families Hydrophilidae, Staphylinidae, and Histeridae are associated with carrion as predators of larvae of flies and dung-beetles. However, the two former families also include coprophagous species. In the temperate region, the hydrophilids *Cercyon* and *Sphaeridium* (Coleoptera: Hydrophilidae) are coprophagous, arriving within the early hours after deposition of dung.

The behavior of dung beetles (Coleoptera: Scarabaeidae) is specialized and diversified in response to exploitation (Fig. 5) of excrement by adults and larvae. The Scarabaeidae consist of approximately 7,000 species (5,000 Scarabaeinae, 1,900 Aphodiinae and 150 Geotrupinae). Many species of Scarabaeinae and Geotrupinae have developed special feeding and breeding strategies that allow them to remove dung rapidly the soil surfaces by digging burrows below the dung pad to store fragments of dung in tunnels. They also may form dung into balls and roll them away from the pad for burial far from the food source. The importance of these habits is the protection of food for adult or larvae, avoiding competitors, predators and unfavorable climatic conditions. Only Aphodiidae do not make a nest. Aphodiidae eat directly into the dung and many species deposit theirs eggs directly in dung pads without nest chamber or in the surrounding soil. Geotrupinae and many tribes of Scarabaeinae are tunnelers. These species dig a tunnel below the dung pat and accumulate dung in the bottom of the burrow; this food can be used either for adult or for larval feeding. Finally, some species of Scarabaeinae are rollers, making a ball of dung that is rolled away from the pat for a variable distance before burying.

One of the most important aspects of the biology of Scarabaeinae and Geotrupini is their nesting behavior. Geotrupini nests are the most primitive and consist of simple burrows filled with "sausages" of dung, usually containing one egg each.

The reproductive biology of Scarabaeinae has several distinct patterns, which have been reviewed and compiled in comprehensive and wonderful books by Halffter and Matthews (1966) and



Decomposer Insects, Figure 5 **Behavior of dung beetles (Coleoptera: Scarabaeidae) is both specialized and diversified to allow exploitation of excrement. Aphodiinae do not make nests, and dwell within the dung (1). Geotrupinae and many tribes of Scarabaeinae are tunnelers (2). Some tribes of Scarabaeinae are rollers (3), making a ball of dung that they roll away from the dung pat.**

Halffter and Edmonds (1982). The process of nesting involves the creation of a place in the soil where a supply of dung is accumulated for development of larvae.

Scarabaeinae nesting frequently involves bisexual cooperation of a pair of beetles, for either short or long periods of time, and parental care sometimes exists. The adults make brood balls in the protected nest, each of which contains the amount of food required for larvae to enable them to complete larval development. Nesting behavior is considered as an adaptation to isolate immature larvae from each other and from adults, increasing the survival of offspring. Obviously this is a process that requires the investment of considerable time and energy on the part of the parents. Nesting derives from feeding behavior and basically corresponds to food relocation: tunneling and ball rolling.

The tunneling scarabs take food from the dung pat and bring it into a previously excavated gallery. Various types of nesting have been described for tunnelers, and it is sometimes difficult to ascribe a particular type of nesting to a species.

The most primitive and simplest nest behavior is observed in some genera of Dichotomini, Oniticellini, Onitini, and also Onthophagini. A female digs a simple burrow, fills it with food, forms a brood mass and provides a single egg. In this case, there is no bisexual cooperation or maternal care, and the species involved show relatively high fecundity.

Other groups of dung beetles make nests containing several or many brood masses such as those observed in some species of Dichotomini, Onitini, Onthophagini and Oniticellini. The brood masses are constructed in series, in the same tunnel or separated in individual side branches. In this type of nesting, bisexual cooperation may exist, but the role of the male is restricted to introducing food into the tunnel. These species have relatively high fecundity, and there is no maternal care.

Coprini and several Dichotomini, Onitini and Oniticellini species construct nests that contain several spherical brood masses arranged in a single or branched tunnel with or without separation.

Some scarabs produce a nest containing only a few brood balls in a chamber, and physically separated from other chambers. This nesting behavior is present in species with low fecundity: Phanaeni (without maternal care), several Dichotomini (with or without maternal care), and several Coprini (with maternal care).

Finally, the species of *Oniticellus* (Oniticellini) show endocoprid nesting behavior: digging burrows and making brood chambers in the dung pat, where nesting takes place. The species of this genus present moderate to extensive maternal care.

The roller habit of food relocation is only present in some tribes of Scarabaeinae: Scarabaeini, Chantonini, Gymnopleurini and Sisyphini. Species of these groups make a brood ball that is rolled away from the pat. The weight of the ball can be up to more than fifty times the weight of the beetle. The process is initiated by one partner and the ball acts as a sexual display to the other sex. The brood ball also may be rolled by two partners, but sometimes the female is transported on the ball. Combat is common between members of the same species when rolling balls. Generally, sexual cooperation finishes when copulation takes place in the burrow, after which the male leaves the female. Females prepare four to five pyriform brood balls and lay eggs in a narrow cavity at the upper end of each pair. The female may abandon the nest after oviposition, such as in Scarabaeini, Canthonini, Gymnopleurini and Sisyphini, or they can remain in the nest until the offspring emerge, as has been described for the African genus *Kheper*.

Finally, there are some species of dung beetles that demonstrate special feeding and nesting biology. They are species using part of the food resources accumulated by other dung beetle species in burrows or a breeding chamber. These species are called kleptoparasites, and examples are found in Aphodiidae and Scarabaeidae. These species live as parasites in the nest prepared by either roller or tunneler dung beetles.

Beneficial Actions of Decomposer Insects in Ecosystems

The viability of every ecosystem is based on the normal functioning of its nutrient cycle. This is a very complex ecological process with a great number of components, including decomposer organisms. The activity of decomposers benefits humus formation in the soil, and the availability of nutrients for plants. This feature is especially evident in pasture ecosystems, where an indispensable condition for correct functioning is that the cattle dung is rapidly used and transformed. If this does not occur, dung deposited on the soil may eventually cause serious damage because it deteriorates the pastureland by preventing plant growth.

When pats are not removed, they cover the pasture, inhibiting the growth of grass. The effect is a loss of available surface for cattle. Several authors have reported several estimates of the loss of pasture. In the U.S.A., for example, Fincher (1981) reported that cattle continuously covered more than 300 hectares of pasture with dung each year.

Dung pats remaining on pasture have a noxious effect because cattle do not graze on the rank growth around these cowpats. Refusal by cattle to graze on pasture grass growing near dung is a response to the offensive properties of the dung itself. Furthermore, most of the valuable nutrients of the unburied pats are lost. For example, 80% of the nitrogen content in a pat may be lost, but when adequate numbers of dung beetles are present and efficient burial by dung beetles exist, the nitrogen loss is reduced by 15%, with the nitrogen held by soil colloids. Another potential benefit of dung beetle activity is the increase in pasture by the incorporation of organic matter into the soil and increases in soil aeration and water content.

Several authors have mentioned the possible role of dung beetles in reducing infestation of livestock by worm parasites. Feces remaining on the soil could be an incubator for parasite worm larvae. If dung beetles bury these feces before parasites reach the infectious stage, the parasitism of cattle can be minimized. Dung beetles are also useful agents in the control of flies breeding in dung. The scarabs compete with fly larvae for food, reducing the amount of breeding by depriving the flies of food.

Some authors have calculated the economic value of the role recovered by dung beetles in pastures. Fincher (1981) estimated that the agricultural sector in the U.S.A. would have potential benefits of more than 2,000 million dollars a year if suitable fauna were present for rapid burial of cattle dung. The value of dung beetles in pasture ecosystems was first observed in Australia, where dung beetles were introduced to help solve the problems of loss of pasture surface and increase of flies breeding in dung. The Australian pasture was profoundly disturbed by domestic animals brought by the first European settlers who arrived 200 years ago. The native dung beetles were adapted to the dung pellets of kangaroos and other marsupials, not to the large grazing and browsing herbivores. The large, voluminous accumulated dung of horses, cattle, and sheep generated a pollution problem as a result of its unattractiveness for the native beetle fauna. In Australia, a program of dung beetle species introduction was proposed by Bornemissza about 1960 and several species of scarabs from South Africa, France and Spain, adapted to use the dung of domestic cattle in open pastures, were established successfully. These beetles were introduced to help solve the problems of pasture degeneration and increase of populations of fly pests breeding in dung.

► Forensic Entomology

References

Bornemissza GF (1979) The Australian dung beetle research unit of Pretoria. S Afr J Sci 75:257–260

Byrd JH, Castner JL (2001) Forensic entomology. The utility of arthropods in legal investigations. CRC Press, New York, NY, 440 pp

Fincher GT (1981) The potential value of dung beetles in pasture ecosystems. J Georgia Entomol Soc 16 (suppl):316–333

Halffter G, Edmonds WD (1982) The nesting behaviour of dung beetles (Coleoptera: Scarabaeidae). An ecological and evolutive approach. Publication of the Institute of Ecology, Mexico
Halffter G, Matthews EG (1966) The natural history of dung beetles of the subfamily Scarabaeinae. Folia Entomologica Mexicana. México 12–14 (Reprint for Medical Books di Cafaro C (1999) Palermo, Italy)
Hanski I, Cambefort Y (eds) (1991) Dung beetle ecology. Princeton University Press, Princeton, NJ
Putman RJ (1983) Carrion and dung. The decomposition of animal wastes. Edward Arnold, London, UK

Decumbent

A term used to indicate a structure that is bent downward (contrast with decurved.

Decurved

A term that is used to indicate a structure that is bend upward (contrast with decumbent.

Deer Flies

Members of the genus *Chrysops*, in the family Tabanidae.

► Horse Flies and Deer Flies
► Flies (Diptera)

Deer Fly Fever

Also known as Tularemia or rabbit fever, this is a serious infectious disease caused by the bacterium *Francisella tularensis*. The disease is endemic in North America, and parts of Europe and Asia. The primary vectors are ticks and deer flies, but occasionally the disease can also be spread through other arthropods. Animals such as rabbits and muskrats serve as reservoir hosts. The disease is named after Tulare County, California, where in 1911 the disease was studied in squirrel and human populations.

► Ticks

Deer Keds

Some deer-associated members of a blood-sucking family of flies generally known as louse flies (Diptera: Hipposboscidae). Both winged and wingless forms occur, and this family includes sheep keds, bird ticks, wallaby flies, and tick flies.

► Flies (Diptera)

Deer Midges

Members of the family Tabanidae (order Diptera).

► Flies

Deficiency Disease

A nutritional disease resulting from lack of carbohydrates, proteins, amino acids, fatty acids, vitamins, or trace minerals, or other essential constituents and elements of the diet.

Deflection Marks

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Deflection marks are thought to divert the attack of a predator away from the most vulnerable part of an animal to where it will do minimal damage, such as the wings of a butterfly. Markings that are thought to function in this way occur in many butterflies but have not been described from most other insect taxa. The reason for this may be that butterfly wings can suffer considerable damage (Fig. 6) yet the insect is still able to fly, while in insects from most other orders, damage to the wings severely impairs flight. Deflection marks

Deflection Marks, Figure 6 **Meadow brown butterfly, *Maniola jurtina*, with a beak-shaped piece of its wing removed by a bird in France. Note that the peck was directed at the black and white eyespot on the forewing (photo by M. Edmunds).**

Deflection Marks, Figure 7 **The "false head" of the lycaenid butterfly *Hypolycaena dubia* from Ghana deflects predator attacks to the less vital areas of the body (photo by A. Sourakov).**

might also be expected to occur in moths, but most moths are nocturnally active when visually oriented predators are unable to see the markings, or else they are aposematic, in which case such markings would be of no obvious advantage. Two well-known examples that have been studied experimentally are the false head at the tip of the hind wings of many lycaenid butterflies and the small black and white eyespots on the wings of satyrid butterflies.

The false head at the tip of the hind wing of lycaenids may have the following components: long tails resembling (Fig. 7) antennae, the anal angle at the base of the tail bent outward from the plane of the wing, bright spots of color on the anal angle which may resemble eyes, and convergent lines on the wing leading toward the tail. The butterfly *Arawacus aetolus* (= *Thecla togarna*) has all four of these morphological components of a dummy head while other lycaenids have zero, one, two, or three components. Lizards have been shown to attack the posterior end of lycaenids (rather than the head) but they are only successful if they grab part of the body. If they only grab wings, these usually tear and the butterfly escapes, albeit with a symmetrical piece torn from its wings. In a sample of over 1,000 lycaenids from Columbia belonging to ca. 125 species, Robbins found that butterflies with more false head components had higher incidences of symmetrical damage caused by predators than did butterflies with few false head components ($p < 0.001$). This suggests that the false head is successful in diverting attacks away from the true head. However, this is a measure of butterflies that successfully escaped from predators. It does not indicate whether there is a difference in the numbers of successful captures of butterflies with and without false heads.

Wourms and Wasserman added painted convergent lines, painted anal spots and pasted tails to dead white butterflies (*Pieris rapae*), and offered these to blue jays (*Cyanocitta cristata*). One, two or all three of these additions had no effect on the part of the butterfly initially seized by the jays, but during subsequent handling, the birds pecked more often at the dummy head, especially if this comprised all three of the added components ($p < 0.001$). When live butterflies with added dummy heads were presented to jays, significantly more of these than of the control, non-manipulated insects escaped after being seized ($p < 0.05$). This suggests that the dummy head increases the chances of a butterfly escaping once it has been seized by a bird.

Lycaenids with false heads may also have specific behaviors that enhance the mimicry of a true head, e.g., agitating the hind wings so that the false head and antennae move in a life-like way, and swiveling 180 degrees after landing so that a watching predator may anticipate that the butterfly will fly off in one direction when it will actually fly off in another. For most of these behaviors, there is no evidence that they increase the survival chances of the insect, and the 180-degree swiveling occurred only rarely in *A. aetolus*.

Small, circular, black eyespots with a white central dot occur near the edges of the fore and hind wings of many satyrid butterflies which also may divert attacks away from the body of the butterfly to the edge of the wing. Carpenter found that many wild caught east African butterflies had triangular markings on the wings that appeared to have been made by bird beaks, and where the insect had eyespots, these beak-marks were close to them. Carpenter interpreted this as a measure of successful escape from predators. Swynnerton painted small eyespots on the wings of *Charaxes* butterflies, released them, and then recaptured them a few days later. He found that many had beak marks at or close to the eyespots implying that birds had attempted to seize the insect by its wings rather than by its body. Finally Blest offered yellow buntings (*Emberiza citrinella*) mealworms with either the head or the tail painted black or painted white with a black eyespot. Birds pecked significantly more often at the painted rather than the unpainted end of the insect, and they pecked more often at a painted end with an eyespot than at one without an eyespot. He concluded that small eyespots do attract birds to peck at them, and that eyespots on wings can therefore successfully divert attacks away from the butterfly's head.

References

Cott HB (1940) Adaptive coloration in animals. Methuen, London, UK, 508 pp

Edmunds M (1974) Defence in animals: a survey of anti-predator defences. Longman, Harlow, UK, 357 pp

Robbins RK (1980) The lycaenid "false head" hypothesis: historical review and quantitative analysis. J Lepid Soc 34:194–208

Robbins RK (1981) The "false head" hypothesis: predation and wing pattern variation of lycaenid butterflies. Am Nat 118:770–775

Wourms MK, Wasserman FE (1985) Butterfly wing markings are more advantageous during handling than during the initial strike of an avian predator. Evolution 39:845–851

Defoliant

A chemical used to remove foliage from a plant. In agriculture it usually is used to enable easier harvesting of certain crops such as cotton or potatoes, but also to cause the starvation of leaf-feeding insects.

Defoliation

Removal of leaves or portions of leaves, a frequent result of high densities of leaf-feeding insects.

DeGeer, Carl (Carolus, Karl, Charles)

Carl DeGeer was born in Finspang, Sweden, on February 10, 1720. His birth in a noble family gave

DeGeer, Carl (Carolus, Karl, Charles), Figure 8 **Carl DeGeer.**

him the hereditary title of Baron, and his family was wealthy, allowing him to indulge his interests in natural history. He was educated in the Netherlands, and later became a pupil of Linné in Uppsala. He was a good student, and in 1752–1778 published a five-volume work, "Memoirs pour servir à l'histoire des insectes." It included excellent descriptive writing. A problem, however, was that (Fig. 8) DeGeer had assigned Latin names to many insect species following Linné's methods. The International Code of Zoological Nomenclature has decreed that the (1758) 10th edition of Linné's "Systema naturae" contains the first valid scientific names for animals, and so the names published by DeGeer before 1758 are not valid and have been suppressed. The student had been too far ahead of the teacher in assigning names! DeGeer died in Stockholm on March 8, 1778.

Reference

*Essig EO (1931) DeGeer, Carl. In: A history of entomology. Macmillan, New York, NY, pp 601–602

Degree-Day

A physiological unit combining temperature and time, and used to measure and predict growth of organisms. Also called day-degrees.

► Bioclimatic Models in Entomology

Delimiting Survey

From a regulatory perspective, this is a survey to determine the boundaries of an area considered to be infested by, or free from, a pest. It differs from a detection survey in that it is much more comprehensive.

► Risk Analysis (Assessment)
► Regulatory Entomology
► Invasive Species

Dejean, Pierre François Marie Auguste

Pierre François Dejean was born in Amiens, France, on August 10, 1780. It has been stated that he was the greatest coleopterist of his time, although he had another occupation. This other occupation was as a soldier: he became Lieutenant General and aide-de-camp to Napoleon Bonaparte, and he fought in (Fig. 9) Napoleon's final battle at Waterloo. He even collected beetle specimens on battlefields. His specialty was the beetle family Carabidae, and he assembled specimens from many parts of the world. By 1837, his collection numbered 22,239 species. He employed Boisduval as his private curator. His greatest publications were catalogues of his collection, which underwent four editions between 1802 and 1836. These catalogues were good guides to a systematic ordering of his collection. However, he did not believe in the principle of priority in naming species, often coined new names for the species represented in his collection (instead of using names that had been published earlier by others), and his catalogues did not contain descriptions; consequently, names that he coined are nomina nuda without validity. He died in Paris on March 17, 1845. His collection was divided, and parts of it are in various European museums.

Dejean, Pierre François Marie Auguste, Figure 9
Pierre Dejean.

Reference

*Essig EO (1931) Dejean, Pierre François Marie Auguste. In: A history of entomology. The Macmillan Company, New York, NY, pp 601–602

Delphacidae

A family of insects in the superfamily Fulgoroidae (order Hemiptera). They sometimes are called planthoppers.

► Bugs

Delusory Parasitosis

Imagined cutaneous parasitosis by insects and mites. This is an emotional disorder in which invisible or nearly invisible organisms are present on, or in, the body. This mental disturbance is not uncommon, and is often associated with stress in the patient's life, and unusual or abnormal behaviors. Sometimes there is an actual physical basis for the problem, such as sensitivity to dust, pollen, fiberglass, paper splinters, static electricity, etc., so it is difficult to diagnose. Sometimes invisible "cable mites," "paper mites," and "computer mites" are implicated in the office workplace environment.

Individuals experiencing delusory parasitosis (also known as hallucinatory parasitosis) typically claim that the problem has survived repeated pesticide applications, and attempts at body cleansing and household cleansing. They may claim that the insects disappear, or that they retreat into the skin or body orifices during the day, only to reappear at night. Evidence of infestation is often presented in the form of skin flakes, dried blood, hair, pieces of tissue, dust, and insect fragments – but the insect fragments are usually normal household pests or insects that are accidental invaders. Frequently such individuals make numerous visits to medical doctors and dermatologists, but resist seeing a psychologist.

► Entomophobia
► Psychiatry and Insects

Deme

An interbreeding group in a population; a local population.

Deimatic Behavior

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Deimatic behavior is designed to intimidate predators and dissuade them from attacking. It typically involves the display of some conspicuous color or structure. It has also been called dymantic, frightening or startle behavior. Deimatic displays cause attacking predators to hesitate, and perhaps withdraw, thereby giving the prey animal a chance to escape. Deimatic behaviors occur in both aposematic and cryptic animals so that they can be either a genuine warning of unpleasantness or a bluff.

Many large praying mantids and phasmids have dramatic deimatic displays. These insects are typically cryptic but, if disturbed, they expose previously hidden brightly colored hind wings in a static display which is maintained for perhaps a minute or more. Large mantids also often expose bright colors on the inside of the forelegs and they may stridulate by rubbing the abdomen between the raised wings making a hissing noise. The large grasshopper *Phymateus* has a similar deimatic display exposing red and yellow on the hind wings, but while the displays of mantids and most phasmids are pure bluff, this grasshopper has repellent glandular secretions from the thorax and is distasteful to some insectivorous predators. Some arctiid and ctenuchid moths also have deimatic displays exposing bright colors on the hind wings or the abdomen. These insects are also chemically protected and some are aposematic, so the display is a reinforcement to warn predators of their nastiness. The arctiid *Melese laodamia* stridulates when it is handled, while species of *Haploa* and *Halisidota* emit clicks in response to the sonar pulses of hunting bats. Both are thought to be warnings to deter possible predation. Some pupae of butterflies and moths also emit squeaks or clicks when they are molested (e.g., pupae of the death's head hawkmoth *Acherontia atropos*) which may intimidate predators. In sphingids and some other moths, bright colors on the hind wings exposed in a static display are a bluff, not a genuine warning. In the eyed hawkmoth (*Smerinthus ocellata*), the hind wings have enormous eyespots that are gently agitated during display much like the eyes of an owl or other large predator.

There is some anecdotal evidence that deimatic displays really do frighten off predators. For example, the displays of Neotropical mantids successfully frighten off a variety of species of monkeys and lizards, and the stridulation of scorpions also intimidates hedgehogs. However, other examples are unsuccessful. Displays do not prevent African mammals (civet, kusimanse and bush-baby) from eating mantids. The startle display of the giant South American mantid *Stagmatoptera biocellata* successfully intimidated two species of insectivorous bird. In a rigorous experimental study, Blest trained birds to take dead mealworms from a perch on a small box. When the bird landed on the box, a pattern lit up on either side of the mealworm. Blest found that the sudden appearance of a bright color frightened some of the birds and so was of survival value. The more the color and pattern resembled a vertebrate eye, the more effective it was in frightening away the bird. He then experimented with the peacock butterfly (*Nymphalis io*) that has large eyespots on both fore and hind wings. He presented yellow buntings with normal butterflies and with butterflies in which all the color scales of the eyespots had been rubbed off. He found that the birds gave significantly more escape responses to the normal insects than to the ones lacking eyespots ($p < 0.001$). So the sudden display of any bright color is frightening, but the more the color and pattern resemble a vertebrate eye the more intimidating it is. This shows how the near-perfect, large eyespots of some insects have evolved progressively with each improvement being more effective in warding off predators.

Reference

Edmunds M (1974) Defence in animals: a survey of anti-predator defences. Longman, Harlow, UK, 357 pp

Denaturation

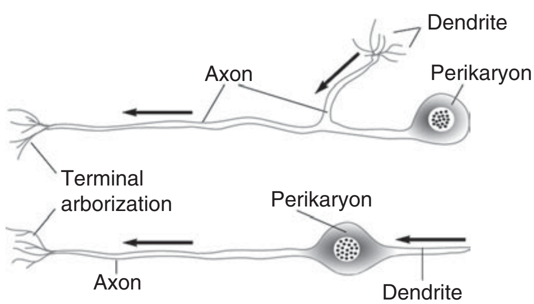
Breakdown of secondary and higher levels of structure of proteins or nucleic acids by chemical or physical means.

Dendrites

Branching projections of the cell body in nerve cells that serve to (Fig. 10) enhance synaptic connections between nerves.

Dendrogram

A branched diagram that represents the evolutionary history of a group of organisms.
► Classification



Dendrites, Figure 10 Diagrams of insect nerve cells showing direction of nervous impulse (adapted from Chapman, The insects: structure and function).

Dengue

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Dengue fever and its more severe outcome, dengue hemorrhagic fever, emerged as the most important viral disease transmitted by arthropods to man during the last decade of the twentieth century. In the past 20 years, global incidence of dengue has increased approximately fivefold. An estimated 50–100 million annual cases of dengue fever and several hundred thousand cases of dengue hemorrhagic fever were occurring worldwide at the start of the twenty-first century. The current pantropical distribution of this disease is primarily a consequence of the global transport of dengue virus by infected humans and population expansions of its primary mosquito vector, *Aedes aegypti*.

The Pathogen and Disease

Dengue virus is classified as a species in the family Flaviviridae, which includes other pathogens, such as yellow fever virus. Four serotypes of dengue virus are recognized and referenced numerically (often as DEN-1 through DEN-4). The prevalence of the four serotypes varies geographically, despite the widespread exchanges of viral variants by human travel. DEN-2, for example, has been and remains the most common serotype found in Africa, although some outbreaks on that continent have been caused by other serotypes. Strains of dengue virus differ substantially in their pathogenicity to man.

Many infections of humans with dengue virus cause no overt symptoms and do not result in disease. In Thailand and Singapore, for example, 87–95% of infections with this virus are asymptomatic or very mild. Symptomatic infections lead to either undifferentiated fever, dengue fever, or dengue hemorrhagic fever.

Undifferentiated fever, accompanied by a rash, is an outcome of dengue infection more common among infants and young children. Older children and adults are more likely to suffer the classical symptoms of dengue fever, which include a high fever with abrupt onset, severe headache, pain behind the eyes and in muscles and joints (which gave dengue its alternate name of "breakbone fever"), and a skin rash. Reductions in white blood cell counts are common, and skin hemorrhages may occur. The bleeding complications that sometimes accompany classical dengue during epidemics are differentiated clinically from those of dengue hemorrhagic fever. The case fatality rate of dengue fever is very low.

Typical dengue hemorrhagic fever is manifested clinically by high fever, hemorrhagic phenomena, liver enlargement, and circulatory failure. Hemoconcentration during dengue hemorrhagic fever is associated with a reduction in red blood cell platelets. Leakage of plasma differentiates dengue hemorrhagic fever from dengue fever, and its extent affects the severity of the disease.

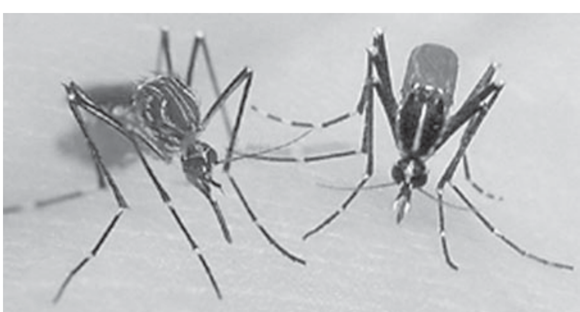
Dengue hemorrhagic fever is categorized into four grades of increasing disease severity. Grade I is characterized by fever accompanied by non-specific constitutional symptoms; a positive tourniquet test is the only hemorrhagic manifestation. Grade II adds symptoms of spontaneous bleeding, usually from skin or other hemorrhages. Grades III and IV represent levels of dengue shock syndrome, regarded as the most severe form of dengue hemorrhagic fever. Grade III is marked by a weak and rapid pulse, cold skin, and restlessness. Pulse and blood pressure are undetectable in the state of profound shock characteristic of Grade IV. The case fatality rate of dengue hemorrhagic fever is 1–5%, dependent on patient care.

Vectors

Throughout most of the range of endemic dengue, and especially in urban areas, the yellow fever mosquito, *A. aegypti*, is the primary vector (Fig. 11) from man to man. The Asian tiger mosquito *Aedes albopictus*, another container-inhabiting species dispersed transcontinentally, like its close relative *A. aegypti*, by shipping, is considered an important secondary vector and may be the sole vector of dengue virus to man where the yellow fever mosquito is absent. If both these aforementioned species are absent, other members of the same *Stegomyia* subgenus, such as *Aedes polynesiensis* on Pacific islands, may transmit dengue virus to man.

In both Asia and Africa, sylvan cycles of dengue are maintained among forest-dwelling, container-inhabiting mosquitoes and arboreal primates. In Malaysia and Vietnam, species of the Niveus Group of the genus *Ochlerotatus* (formerly *Aedes*) are involved in the forest maintenance cycle of dengue. In West Africa, isolates of DEN-2 have been made from treehole dwellers *Aedes africanus*, *Aedes opok*, and *Aedes luteocephalus* of the subgenus *Stegomyia* and *Aedes taylori* and *Aedes furcifer* of the subgenus *Diceromyia*. Interestingly, these same mosquito species are implicated in sylvatic maintenance cycles of yellow fever virus in West Africa. There is yet no evidence for the presence of a sylvan maintenance cycle of dengue in the Americas.

Dengue virus does not replicate in mosquitoes of other genera, such as *Culex* or *Anopheles*, which are thus not considered to be potential vectors. In the laboratory, *A. albopictus* is a more efficient vector of dengue virus than *A. aegypti*. This observation, and the native presence of *A. albopictus* in the original range of endemic dengue in Asia, supports an older association between dengue and *A. albopictus* than with *A. aegypti*. Extensions of this reasoning postulate that the higher viremia required to infect the more recent vector *A. aegypti* has led to a selection for epidemic viral strains carried by the yellow fever mosquito. By contrast, the more ancient vector *A. albopictus* is believed to be more involved in passage and maintenance of endemic dengue strains that cause milder or asymptomatic infections in humans.



Dengue, Figure 11 Adult females of the two most important mosquito vectors of dengue, *Aedes aegypti* (left) and *Aedes albopictus* (right).

Evolution, History, and Spread

The isolation of all four serotypes from nonhuman sylvan reservoirs in Malaysia suggests a tropical Asian origin of the virus previous to involvement of humans in its life cycle. Molecular genetic comparisons of viral envelopes of epidemic and endemic dengue strains suggest that human infections originated from 100 to 1,500 years ago.

The first historical accounts that may represent human cases of dengue are records around A.D. 992 of disease in China with symptoms of fever, rash, eye pain, arthralgia, and hemorrhage. By the eighteenth century, dengue had spread around the world by shipping, which transported both infected humans and *A. aegypti*, whose immature stages stowed away in water storage vessels. The first recorded outbreaks of a dengue-like disease in the New World occurred in the French West Indies in 1635 and in Panama in 1699.

The name dengue is purportedly derived from a Swahili term applied to the disease during epidemics in 1823 and 1870 in East Africa. However, the term dengue appears in Spanish literature of 1801, arguing for an earlier origin of the name. Although transmission of the disease by mosquitoes was demonstrated in 1903, dengue viruses were not isolated until the 1940s. The four serotypes of the virus were identified by the mid-1950s.

World War II created social and ecological disruption that led to the spread and increases of dengue fever and *A. aegypti* in Asia, the South and Central Pacific, and Australia, and to the emergence of dengue hemorrhagic fever. Major outbreaks of dengue in the New World were delayed by reductions in the abundance and range of *A. aegypti* attributable to an eradication campaign targeted at this vector of urban yellow fever in the USA, Central, and South America. However, early in the 1980s, following the recovery of *A. aegypti* populations, major epidemics of dengue fever and dengue hemorrhagic fever began to appear routinely in the Americas. In 1981, over 344,000 cases with 158 deaths were attributed to dengue in Cuba, and in the first 30 weeks of 2002, over 711,000 cases of dengue were recorded in Brazil. Dengue currently is endemic in most countries of the tropical Americas, with seasonal outbreaks associated with rainfall and concomitant increases in *A. aegypti* numbers.

Maintenance and Transmission

Viremic humans in the acute phase of the diseases are the primary sources of infection for *A. aegypti*. The rate of virus passage and replication in susceptible vectors depends on ambient temperature, and female *A. aegypti* are capable of transmitting virus 7–25 days after an infectious meal.

Transovarial transmission of dengue virus has been demonstrated for several species of *Aedes*, but the rates of passage from mothers of eggs to *A. aegypti* and *A. albopictus* are low. However, vertical transmission of dengue has been documented in the field for several species of sylvan vectors in West Africa. These observations suggest that maintenance by transmission of virus from female mosquitoes to their offspring may play a more important role in sylvatic cycles of dengue. Sexual transmission between male and female *A. albopictus* has been demonstrated experimentally for all four serotypes of dengue virus.

Risk Factors for Dengue

Broad factors that increase dengue risk include (i) the spread and population growth of *A. aegypti*, (ii) a lack of mosquito control, (iii) urbanization, (iv) transport of dengue viruses by infected travelers, and (v) deterioration of public health infrastructure. Geography and rainfall influence the distribution of dengue, which is more likely to prevail in tropical climates with moderate to high rainfall.

Despite the role of *A. aegypti* as primary vector, indices of urban abundance of this species have not proven useful for predicting dengue outbreaks. Blood-feeding by infected *A. aegypti* on multiple hosts and a relatively high daily survival rate of adult females are thought to contribute to efficient transmission of dengue virus by this species.

Dengue cases tend to cluster in houses, possibly because infected *A. aegypti* often take blood from several occupants of the same house. Housing quality, human population densities, and water storage practices also are correlated with dengue incidence. Thus, slum conditions that permit vectors ready access to human hosts, and water in containers suitable for the growth and development of *A. aegypti*, both favor the occurrence of dengue. The critical human deme size needed to maintain endemic transmission has been variously estimated from 150,000 to one million persons.

At the individual level, host age, sex, general health, and antibody status influence the outcome of infection with dengue. Strains of dengue virus differ in their virulence, and levels of viremia vary among vector species; both of these factors therefore influence risks of infection to humans.

Although the causes of dengue hemorrhagic fever and dengue shock syndrome are not well understood, it is believed that the risk of these serious complications increases with sequential infection of individuals with different dengue serotypes. Other determinants of dengue hemorrhagic fever risk are viral virulence, individual susceptibility, and local intensity of dengue transmission.

Economic Impact and Prevention

The economic burden of dengue hemorrhagic fever in Thailand is estimated to cost that country 31.5–51.5 million dollars annually, and the 1981 dengue epidemic in Cuba cost that island nation about 103 million dollars. However, these estimates do not include economic losses attributable to reductions in productivity from absenteeism, lost tourism, or social disruptions. Recent reassessments that calculate "disability-adjusted life years" (DALYs) have shown that dengue has an economic impact comparable to more heralded infectious diseases, such as malaria and tuberculosis.

Although research towards a dengue vaccine is in progress, a pediatric vaccine to prevent dengue in areas of epidemic dengue fever and dengue hemorrhagic fever is still some years off. In the meantime, the best prophylaxis remains control of *A. aegypti*. Although adulticides sprayed during epidemics have not proven effective, community-based programs targeted at reducing the incidence of *A. aegypti* immatures have shown promise in lessening risks in dengue-endemic countries, such as Vietnam.

References

Gubler DJ (2002) Epidemic dengue/dengue hemorrhagic fever as a public health, social and economic problem in the 21st century. Trends Microbiol 10:100–103

Gubler DJ, Kuno G (eds) (1997) Dengue and dengue hemorrhagic fever. CABI Publishing, New York, NY, xi + 477 pp

Density

The number of individuals in relation to the space (area) in which they occur.

Density Dependence

Changing in effect in proportion to population density. This term usually is used to describe population mortality factors that increase in severity as population density rises.

Density Independence

Not changing in effect in proportion to population density. This term usually is used to describe population mortality factors that act independent of population density.

Dentate

Bearing teeth or tooth-like projections (denticles).

Dentition

This refers to the presence and arrangement of denticles (teeth). Dentition formulas based on denticles of the hypostome are used to distinguish among ticks.

Denver Billbug, *Sphenophorus cicastriatus* Fabricius (Coleoptera: Curculionidae)

This billbug affects cool season turfgrasses in the western USA.

► Turfgrass Insects and their Management

Deoxyribonucleic Acid (DNA)

The molecule that carries genetic information.

Deposit

The residual insecticide impacting the target, or missing the target pest but remaining on the substrate (in the latter case, residual deposit or residue are better terms). In the case of a residual deposit, the insecticide only becomes effective as insects move around and encounter it.

Depressed

A term used to describe structures that are flattened from top to bottom.

Derbidae

A family of insects in the superfamily Fulgoroidea (order Hemiptera). They sometimes are called planthoppers.

► Bugs

Dermal

Pertaining to the skin or absorption through the skin. Dermal exposure is a major route of pesticide poisoning. Dermal toxicity assessments for pesticides involve skin treatment of the test animals.

Dermaptera

An order of insects. They commonly are known as earwigs.

► Earwigs

Dermatitis Linearis

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This is an affliction of human skin caused by toxin from some species of the subtribe Paederina (Coleoptera: Staphylinidae: Paederinae). The toxin also has a severe effect on human eyes. The 28 species thus far shown experimentally or observationally to produce such a toxin belong to three of the 14 genera of Paederina, namely *Paederus*, *Paederidus*, and *Megalopaederus*, yet these 28 represent only a small fraction of the 623+ species currently classified within the subtribe. The distribution of the species known to produce such a toxin includes Europe and Asia (although human affliction has been reported only in the south of these continents, from Italy east to Japan), Africa, Central and South America, and Australia. There are numerous published reports of the affliction, and some of them describe "epidemics" of hundreds of people afflicted. There are no reports from the West Indies, and reports from Mexico and the southern USA are not yet fully proven.

The affliction has been given numerous names in several languages. The first name used, "dermatite vesiculeuse saissonière," coined in 1915 in what was then the Belgian Congo, is in French and doubtless for that reason was ignored by writers of English, Italian, and Spanish. The second name used, "dermatitis linearis," serves well as an international name because it is a Latinized name, coined first in Japan in 1917. All other names came later, and the most popular of these function only in English (it is no more appropriate to force writers of French, Italian, Spanish, etc., to use an English-language name than it is to force writers in English to use the original French name). A currently popular name "Paederus dermatitis" (1967) is inaccurate because the affliction can be caused by members of Paederina other than *Paederus*, and the name functions only in English. Other currently popular names "rove beetle dermatitis" (1963) and "Staphylinidae dermatitis" (1968) are likewise inaccurate because the species that cause it belong only to some genera of the subtribe Paederina, not to the remaining 45,000+ species of the family Staphylinidae. As an example of the complications these latter names cause, this writer was twice (independently, and spaced a few years apart) asked to supply to Iranian medical workers, who were investigating dermatitis linearis in their country, photocopies of all publications on Staphylinidae! But I had already published a review of all information I had detected about dermatitis linearis and *Paederus* sensu lato (Paederina) (<400 relevant publications, translated where necessary from 15 languages other than English), and the remaining >45,000 papers or books on other species of the family Staphylinidae were irrelevant! These Iranian workers were misled by the names "rove beetle dermatitis" and "Staphylinidae dermatitis," which expressions should be expunged from the literature, into believing that all rove beetles produce a medically important toxin. The expressions "Nairobi eye" (used in eastern Africa, 1935) and "whiplash dermatitis" (used in Australia, 1954) are whimsical, and of no more general use than the original French name or other names such as "fuetazo" (used in Ecuador, 1945), "fuoco selvatico" (used in Italy, 1935), "quemas" (used in Venezuela, 1946) and numerous others. The expression dermatitis linearis is here highly recommended as the most appropriate term to use.

In fact, three toxins have been identified. The first, pederin, is reported from *Paederus fuscipes* Curtis, *P. columbinus* Laporte, *P. littoralis* Gravenhorst, *P. melanurus* Aragona, *P. riparius* (L.), *P. rufocyaneus* Bernhauer, *P. sabaeus* Erichson, and *Paederidus rubrothoracicus* (Goeze), whereas the second, pseudopederin, is reported from *P. fuscipes*, and the third, pederone, from *P. fuscipes* and *P. columbinus*. Other species have been reported to cause the affliction, but their toxins have not been specifically identified. Pederin is an amide with two tetrahydropyran rings, pederamide and pedaldehyde (see PEDERIN).

Pederin is expressed from adult beetles when they are crushed. This occurs frequently when adult beetles of some species fly to light (incandescent and fluorescent), inadvertently land on humans adjacent to the light, and are crushed (by human body parts) against the skin. The beetles do not attack people – instead, the harm is self-inflicted by humans. Typically, a hand is used to crush a beetle, and smears the exudate (pederin) in a line across the skin. Within 24-h a linear red mark of dermatitis is seen on the skin, thus the name dermatitis linearis. That contaminated hand may be used inadvertently to transfer the toxin to other body parts.

The exuded toxin penetrates the skin without any abrasion. Public health authorities should be proactive in warning the public about the risks and their avoidance as soon as the flying insects are detected. The best avoidance is not to stand or sit outdoors by lights when the insects are flying. If an insect lands on the skin, it should be blown off by a breath of air, not crushed. If an insect is crushed, immediate washing of the skin with soap and water after contact with the insect(s) averts penetration of the skin by the toxin. Eyes contaminated by the toxin should be washed immediately. Treatments after dermatitis has developed (beginning 24-h or so after skin contact) are little more than palliative. Healing occurs naturally after weeks or even months. Antibiotics may help those patients at risk of bacterial infection following lesions.

Effects of the toxin include not just a severe skin rash, which may persist for months, but also, in severe cases, fever, neuralgia, arthralgia, and vomiting. Secondary infections, rhinitis, and even tympanitis may occur. Ocular manifestations include pain and lachrymation, edema, corneoconjuctivitis, exfoliation of the cornea, and iritis, some of which cause temporary blindness.

► Paederus
► Paederina
► Pederin
► Rove Beetles (Coleoptera: Staphylinidae)

References

Frank JH, Kanamitsu K (1987) *Paederus* sensu lato (Coleoptera: Staphylinidae): natural history and medical importance. J Med Entomol 24:155–191

Pavan M (1982) Summary of the present data on pederin. Pubblicazioni dell'Istituto di Entomologia dell'Università di Pavia (23), 61 pp

Dermestid Beetles

Members of the family Dermestidae (order Coleoptera).

► Beetles
► Stored Grain and Flour Insects

Dermestidae

A family of beetles (order Coleoptera). They commonly are known as skin or dermestid or skin beetles.

► Beetles

Derodontidae

A family of beetles (order Coleoptera). They commonly are known as tooth-necked fungus beetles.

► Beetles

Desensitization

The elimination or reduction of allergic sensitivity. This usually is accomplished by a course of antigen treatments. It also is known as immunotherapy.

Desert Locust, *Schistocerca gregaria* Forskål (Orthoptera: Acrididae) Plagues

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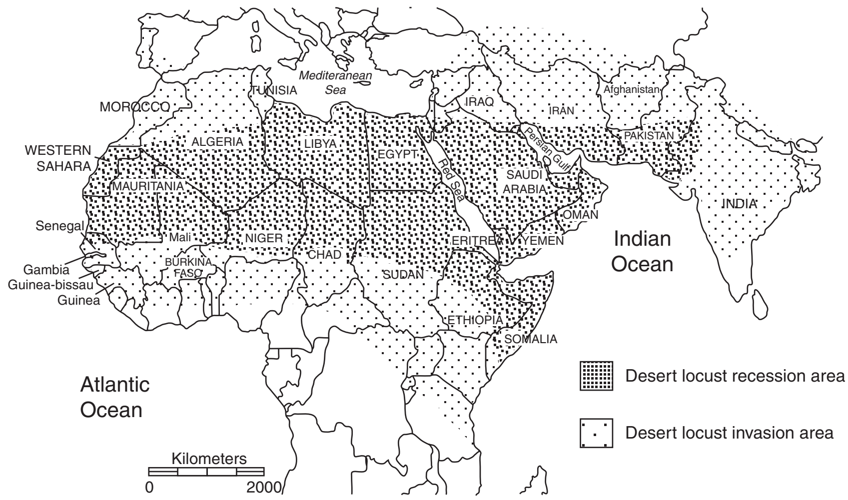
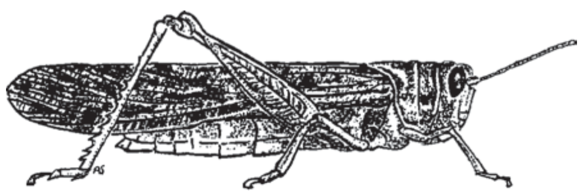
Normally, the desert locust, *Schistocerca gregaria* Forskål (Orthoptera: Acrididae), is a solitary insect that occurs in desert scrub regions of northern Africa, the African Sahel, the Arabian Peninsula, and parts of western Asia to western India. Each locust is 7–8 cm in length, weighs about 2 g, and undergoes five molts after emerging from egg pods deposited several cm beneath the soil (preferably sandy) surface. The adult is a faded tannish yellow with wings that are mottled with black blotches. During the solitary phase, desert locust populations are low and present no economic threat to agriculture. After periods of drought, when vegetation flushes occur in major desert locust breeding areas, rapid population buildups and competition for food occasionally result in transformation from solitary phase to gregarious behavior on a regional scale. Following this transformation, which can occur over two or three generations (there are generally three to five generations per year), desert locusts can form dense bands of flightless nymphs and swarms of winged adults. Gregarious adults are brownish gray with a pink tinge while sexually immature, and bright yellow when sexually mature. Nymphs are usually yellow with heavy black markings on the body, head, legs, and wings but their coloration can range from greenish to tan. The transition from the innocuous solitary phase to the plague stage is termed an outbreak and as it spreads to involve one or more regions, it is often called an upsurge. A desert locust plague occur when swarms and bands are found on an interregional scale (regions generally refer to the Red Sea area, West Africa, the Arabian Peninsula, and southwestern Asia) and originate from a number of breeding areas as part of a widespread but interrelated locust breeding and migrating dynamic than can continue for years.

There are several areas within the desert locust's recession (solitary phase, low population densities) distribution (Figs. 12 and 13) that are referred to as key breeding areas because they are known historically to favor large scale gregarization when conditions are conducive. These areas are, from east to west, the southern desert area astride the border of Pakistan and India, the Tihama Red Sea coastal area of Yemen and Saudi Arabia, the Red Sea coasts of Eritrea and Sudan, the interior Eritrean and Sudanese deserts, the Tibesti Mountains of northwestern Chad, the Aär Mountains and Temesna of north central Niger, the Adrar des Iforas Mountains of Mali, and large areas of Mauritania's coastal and interior desert.

Reference to locust plagues are found in the Bible and the Koran, and in some places along the Mediterranean coast locust plagues have been held responsible for epidemics of human pathogens, such as cholera (this is because of massive



Desert Locust, *Schistocerca Gregaria* ForskåL (Orthoptera: Acrididae) Plagues, Figure 12 **Distribution of the desert locust during recession (solitary phase, low density populations) and potential distribution during plagues (gregarious phase).**



Desert Locust, *Schistocerca Gregaria* ForskåL (Orthoptera: Acrididae) Plagues, Figure 13 **The desert locust, *Schistocerca gregaria* (Forskål) (solitary vs. gregarious coloration is not discernable in a black and white drawing).**

quantities of decomposing locust cadavers that accumulated on beaches after swarms had drowned in the sea). Written accounts of desert locust plagues in North Africa date back to about A.D. 811, but more precise records were not kept until the twentieth century. Since then, it is known that desert locust plagues have occurred sporadically to the present.

A single swarm of locusts can be small (hundreds of square meters) or large, composed of billions of locusts, with up to 80 million per square kilometer over an area of more than 1,000 km^2. In 1 day, a swarm of desert locusts can fly as much as 100 km in the general direction of prevailing winds. Bands of nymphs can advance about 1.5 km per day. Plagues often involve hundreds of swarms, and the locusts' invasion area can expand to involve the Middle East, western Asia to Bangladesh, the sub-Sahel from Guinea to Tanzania, and parts of southern Europe.

Desert locust adults can consume approximately 2 g of green vegetation each day, including leaves, flowers, bark, stems, fruit, and seeds. Nearly all crops, and non crop plants, are at risk, including millet, rice, vegetables, banana, cotton, barley, wheat, date palm, pine, rangeland grasses, acacia, sugarcane, maize, and sorghum. Crop loss as a result of desert locust infestation is difficult to quantify, but it is important for developing control strategies on a cost-effective basis.

At this point, however, crop loss estimates are primarily anecdotal rather than having been determined through systematic empirical means. Two of the more well established anecdotal examples include more than $50 million (in 1994 dollars) lost to desert locust infestation in 6 weeks in the Sousse Massa Valley of Morocco in 1954, and the loss of 167,000 tons of grain in 1958 in Ethiopia, said to be enough to feed a million people for a year. Determination of the impacts of desert locust plagues and control campaigns have been challenged by the complexities of intertwining commercial economics, the predominance of subsistence farming, concurrent outbreaks of other pests (e.g., African migratory locust, armyworm, and quelea birds), international assistance from aid agencies, environmental impacts of conventional pesticide applications, and differences among the economies, resources, infrastructures, and cropping zones in physical relation to key desert locust breeding areas. Damage caused by locusts, in addition to occurring very sporadically, is geographically patchy because of the mobile nature of swarms. Where swarms land and feed, losses can reach 100% within hours.

Monitoring locust populations during recession periods to anticipate the onset of gregarious behavior and to locate locust bands and swarms for control operations during outbreaks and plagues is a challenging task that has become increasingly technologically sophisticated. Model-generated forecasts of desert locust population events and general patterns of swarm movement during outbreaks and plagues are simulated using weather and vegetation index information gathered from satellite platforms, meso-scale and synoptic-scale weather patterns, soil mapping, and probabilities based upon historical knowledge about locust population dynamics throughout the recession and plague distributions. Though useful, forecasts are not always accurate or timely. The actual search for desert locust bands and swarms is accomplished through visual surveillance from terrestrial vehicles, fixed wing aircraft, helicopters, and by military and police outposts, nomads, farmers, and fire lookouts.

Controlling large bands and swarms of desert locusts has been attempted in different ways with varying degrees of success. Trenches can be dug near agricultural perimeters to catch nymphal bands marching toward crops where they can be buried. Smoke putatively repels swarms, but evidence of its efficacy is lacking. In some societies, a magic or holy man is summoned to dispel the bands and swarms with icons and incantations.

Natural enemies exist, including predatory and parasitic flies and wasps, predatory beetle larvae, birds, and reptiles, but they are easily overwhelmed by the magnitude of most swarms. Locusts are, in some African and Asian cultures, a dietary item sold on the open market, and in parts of Francophone Africa they are referred to as "crevettes du Sahara," or Sahara desert shrimp. Large scale harvest of desert locusts during outbreaks and plagues, however, is not practiced, whether for human consumption or for animal feed. Also, because of the current reliance on conventional insecticides for locust control, harvest of locusts for human or animal consumption is generally discouraged during campaigns.

Following the bans on organochlorines in the late 1980s because of environmental concerns, application of conventional short residual insecticides, sprayed directly onto hopper bands or settled swarms, has been the sole tactic for lack of viable alternatives. During the last two decades of the twentieth century, various organophosphorus, carbamate, or pyrethroid insecticides were used against desert locusts (ultra-low volume formulations were increasingly favored). Although the use of contact insecticides can be effective when populations are detected early, widespread spraying has been controversial for environmental, human safety, and economic reasons. Significant advances in tactics have been sparse during the last two decades of the twentieth century, with the possible exception of the development of a longer residual pyrazole insecticide, formulation of some mycopesticides (especially *Metarhizium* spp.), studies on botanical extracts, including neem oil and Melia extracts, and testing of various insect growth regulators. Applied studies involving the use of desert locust pheromones have not been conducted.

Generally, a successful control operation would result in the elimination of at least 80% of a swarm or band. On a more regional scale, however, the relative numbers of swarms or bands that must be eliminated to stop the various stages of outbreaks or plagues have not been determined.

Aside from the environmental conditions that contribute toward the development of outbreaks and plagues, other factors can affect the efficacy of control efforts. Remote key breeding areas, much of which are in the vast and rugged Sahara desert, make timely deployment of resources at critical times difficult. Armed conflict in the desert locust's recession distribution area is chronic and, in many cases, it precludes intervention against locusts in key breeding areas that are contested by national governments, controlled by rebel forces, endangered by bandits or clans, or strewn with buried antitank and antipersonnel mines. Unpreparedness of crop protection services in the affected countries has at times made it easier for desert locust populations to overwhelm control capabilities; some regional desert locust control organizations have been unable to respond to sudden locust infestations because of inadequate funding by member nations and failures to address internal problems. Ill-defined responsibilities among some desert locust affected countries, especially between countries with key breeding areas far from important agricultural areas in the same country and adjacent countries where croplands are the most immediately threatened by swarms from those breeding areas, have resulted in failures to intervene when outbreaks were developing. Competing pressures on agricultural production posed mostly by drought and other pests compound the challenges posed to crop protection services by locust outbreaks. Lack of funds for deploying human and material resources and maintaining preparedness for desert locust operations chronically challenges national and local capacities for surveillance and control particularly in the Sahel, Sudan, Djibouti, Eritrea, Ethiopia, Somalia, and Yemen.

During the last two decades of the twentieth century there were three notable episodes of desert locust gregarization. In 1986, a desert locust outbreak occurred in Sudan and Eritrea (then, northern Ethiopia). Largely because of armed conflict in both areas, adequate control could not be conducted, and resulting massive swarms moved west across the Sahel. More breeding occurred in Chad, Niger, Mali, Mauritania, Morocco, Saudi Arabia, and southern Algeria until early 1989. Desert locust infestations were reported from 23 countries, and control operations covered about 26 million ha mostly with the aim of protecting cropping zones at immediate risk. Serious economic losses were not reported.

Another desert locust outbreak began in late 1992 along the Red Sea coastal plains of Sudan and Eritrea. Swarms that escaped late control operations moved across the Red Sea to the Tihama where breeding continued. Desert locust populations increased on both sides of the Red Sea and swarms then moved across the Sahel to Mauritania and to the desert border of India and Pakistan. Control operations mainly focused on breeding areas, and about 4 million ha were involved in the campaign in 18 countries.

In late 1997, gregarious desert locust populations were detected early on the coasts of Sudan and Eritrea. Fast intervention in Eritrea averted the development of swarms, but armed conflict on the southern coast of Sudan permitted swarms to move from rebel held territory to Egypt, Saudi Arabia, and three other countries in the Red Sea region reported desert locust infestations before all swarms were apparently eliminated over a collective area of about 430,000 ha.

Outbreaks, upsurges, and plagues can decline to recession status for a variety of reasons, and often the cause involves more than one of the following factors. Storm fronts can carry swarms over the sea where many can drown or reach lands that are not conducive to survival. In October 1988, for example, a storm front moving west out of Mauritania and Senegal carried swarms across the Atlantic Ocean to Caribbean islands from Trinidad to the Virgin Islands. Those locusts that did not drown en route did not survive in the areas of the Western Hemisphere that they encountered. A cold winter in North Africa, 1988–1989, stopped an eastward movement of swarms along the Mediterranean coast before they could move south with spring northerlies to breeding areas in the Sahel. Dry weather is likely to be the most important natural cause of locust population declines because vegetation recedes and rain is needed for desert locust eggs to hatch. Drying weather was probably the most responsible for the decline of the 1986–1989 plague, and it played a significant role in ending the 1992–1994 upsurge. Human intervention can, if applied appropriately, contribute toward averting plague status from being reached, and human intervention has been identified as an important factor in ending the 1992–1994 upsurge and the 1997–1998 outbreak.

In theory, there are four general approaches to desert locust infestations. Inaction has been promoted by those who claim that insurance covering desert locust disasters would make control efforts superfluous, but it has never been instituted. A reactive approach is mostly adopted on an emergency basis to protect crops after plague status has been reached and crop or rangeland is under threat. The 1986–1989 desert locust campaign was conducted reactively; the perception of imminent agricultural catastrophe kept control teams around cultivated areas and interventions did not occur in the key breeding areas. Proaction means early intervention to mitigate or avert further development of a problem. In the context of desert locusts, proaction entails intervention against localized outbreaks before plague status is reached. This requires early detection of bands and swarms, preferably in breeding areas, and strategic prepositioning of resources. Without empirical intervention threshold levels, timing of intervention is determined through a blend of estimated gregarizing locust populations, local capacity for control, experience, intuition, and political pressure. The 1992–1994 and the 1997–1998 campaigns represent proactive approaches, even when locust populations did spread to other regions during the 1992–1994 campaign. Prevention, like inaction, has not been implemented (though claims have been made by those who used long-residual organochlorine insecticides prior to the mid-1980s). Ideally, desert locust control should occur at or before the onset of gregarious behavior when locusts, preferably in the less mobile and nonreproductive nymphal stage, have amassed in small patches no more than several square meters in diameter in breeding areas. Success would likely require that a critical, though as yet undetermined, proportion of these patches be controlled with the ultimate aim of holding locust populations in the recession phase indefinitely.

Desert locust control operations, whether conducted reactively or proactively, usually involve several sources of funding and assistance. At the national level, control is mostly carried out by district and national elements of the Ministry of Agriculture sometimes with farmers and nomads assisting. In some North African countries, however, the military was responsible for conducting campaigns. Regional desert locust control organizations (presently limited to the Desert Locust Control Organization for Eastern Africa) conduct surveillance and control operations in some countries in eastern Africa.

There are disparities between the economies of countries in the recession distribution area. Relatively wealthy countries like Morocco and Saudi Arabia that can unilaterally conduct large control campaigns are often adjacent to poorer neighbors like Chad, Eritrea, Niger, and Yemen that depend to some extent on foreign aid have been sources of swarms that invaded their neighbors. Foreign aid, in kind or in cash, is provided by regional (e.g., the Arab Organization for Agricultural Development, and the Inter Governmental Authority for Development), multilateral (e.g., the Food and Agriculture Organization of the United Nations, and the International Fund for Agricultural Development), bilateral (e.g., the U.S. Agency for International Development, Swedish International Development Agency), and nongovernmental (e.g., Africare, Norwegian Church Aid) organizations to some of the less wealthy countries.

References

Krall S, Peveling R, Ba Diallo D (1997) New strategies for locust control. Birkhäuser, Basel, Switzerland
Showler AT (1995) Desert locust control, public health, and environmental sustainability in North Africa. In: Swearingen WD, Bencherifa A (eds) The North African environment at risk. Westview Press, Boulder, Colorado, pp 217–239
Showler AT (1995) Locust (Orthoptera: Acrididae) outbreak in Africa and Asia, 1992–1994: an overview. Am Entomol 41:179–185
Showler AT, Potter CS (1991) Synopsis of the 1986–1989 desert locust (Orthoptera: Acrididae) plague and the concept of strategic control. Am Entomol 37:106–110
Steedman A (1988) Locust handbook. Overseas Development Agency/Natural Resources Institute, London, UK

Desert Longhorned Grasshoppers

A family of grasshoppers (Tanoceridae) in the order Orthoptera.

► Grasshoppers, Katydids and Crickets

Detection Survey

From a regulatory perspective, this is a survey to determine the presence of a pest in an area. It differs from a delimiting survey in that the extent (boundaries) of infestation are not precisely determined.

► Risk Analysis (Assessment)
► Regulatory Entomology
► Invasive Species

Deterministic Model

A mathematical model in which the relationships are fixed, and the element of probability is not considered. Thus, a given input produces a given output consistently. (contrast with stochastic model)

Deterrent

Broadly, this term refers to something that provides protection against bodily harm, but from an entomological perspective it usually is used in the context of preventing feeding or oviposition. Thus, in a practical sense it is nearly synonymous with "repellent."

► Repellents of Biting Flies
► Allelochemicals
► Plant Secondary Compounds and Phytophagous Insects

Dethier, Vincent Gaston

Vincent Dethier was born in Boston, USA, on February 10, 1915. His three degrees A.B. (1936), A.M. (1937) and Ph.D. (1939) are from Harvard University. He was employed (1937–1938) as an entomologist at the G.W. Pierce Laboratory in Franklin, New Hampshire, then (1939) as an assistant at the Cruft Physics Laboratory of Harvard University. In 1939–1941 he taught biology at John Carroll University in Cleveland, Ohio. In 1946, he was employed as a research physiologist by the U.S. Army Chemical Corps. In 1946–1947 he was a professor at The Ohio State University, before moving to The Johns Hopkins University (1947–1958) where he investigated chemoreception in blowflies. Next (1958–1967), he worked as professor of zoology and psychology at the University of Pennsylvania and concurrently was an associate at the Institute of Neural Science School of Medicine. He worked (1967–1975) as professor at Princeton University, and finally (1975) was a faculty member of the University of Massachusetts. He made major contributions to insect physiology and published several books, including short stories for adult and juvenile readers. His best-known entomological books are perhaps (1961) "Animal behavior: its evolutionary and neurological basis," (1976) "The hungry fly: a physiological study of the behavior associated with feeding," and (1992) "Crickets and katydids, concerts and solos." He died in 1993.

Reference

Anon. Available at http://search.biography.com/ bio_browse (accessed Aug 2002)

Detoxification Mechanisms in Insects

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Insects are faced with numerous toxins (xenobiotics) as they go through life, some produced naturally by plants (sometimes called allelochemicals) and some produced by humans (insecticides). To survive the natural toxins, insects have evolved various detoxification mechanisms. These same mechanisms also sometimes allow insects to overcome insecticides, and the level and type of mechanisms differ greatly. This results in differing toxicity among different stages, populations, and species of insects. Knowledge of detoxification allows us to better incorporate chemical resistance mechanisms in crop plants, and to better select insecticides that will be effective when applied.

Normally, a lipophilic xenobiotic that enters an animal's body is rapidly detoxified. Detoxification can be divided into phase I (primary) and phase II (secondary) processes. Phase I reactions consist of oxidation, hydrolysis and reduction. The phase I metabolites are sometimes polar enough to be excreted, but usually are further converted by phase II reactions. In phase II reactions, the polar products are conjugated with a variety of endogenous compounds such as sugars, sulfate, phosphate, amino acids or glutathione, and subsequently excreted. Phase I reactions usually are responsible for decreasing biological activity of a toxicant and therefore the enzymes involved are rate limiting with respect to toxicity.

Phase I Reactions

Oxidation

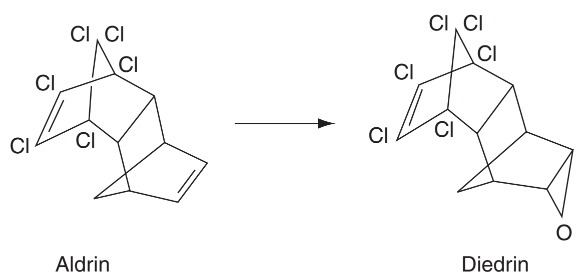
Oxidation is considered the most important among the phase I reactions. The oxidative reactions are carried out by a group of enzymes called microsomal cytochrome P450 monooxygenases [also known as mixed-function oxidases (MFO) or microsomal oxidases]. These enzymes, located in the endoplasmic reticulum of eukaryotic cells, commonly are found in mammals, birds, reptiles, fish, crustaceans, molluscs, insects, bacteria, yeast and higher plants. Microsomal monooxygenases are a three-component system comprised of cytochrome P450, NADPH-cytochrome P450 reductase and a phospholipid (phosphatidylcholine). The details of catalytic events mediated by cytochrome P450 are not fully understood. The substrate first binds to oxidized cytochrome P450 (Fe^{3+}); the enzyme-substrate complex undergoes reduction and then interacts with oxygen. Finally, the hydroxylated substrate and a molecule of water are released. Electrons from NADPH are transported by NADPH-cytochrome P450 reductase and provide reducing equivalents to the ferric cytochrome P450-substrate complex. The overall reaction occurs according to the equation:

$$RH + NADPH + H^+ + O_2 \rightarrow ROH + NADP^+ + H_2O$$

where RH is a substrate. In some cases, the second electron may originate from NADH via cytochrome b_5. Cytochrome b_5 is involved in fatty acid desaturation and in certain microsomal monooxygenase activities, including methoxycoumarin *O*-demethylation, ethoxycoumarin *O*-deethylation, benzo[*a*]pyrene hydroxylation and cypermethrin hydroxylation in house flies. The exact role of phosphatidylcholine in microsomal oxidation is not known. The phospholipid is essential for electron transfer from NADPH to cytochrome P450 but it does not function as an electron carrier. It appears to be involved in the coupling of

NADPH-cytochrome P450 reductase and cytochrome P450 and in the binding of the substrate to the cytochrome.

It is well established that insect cytochrome P450, the terminal oxidase of the monooxygenase system, exists in multiple forms as found in mammals. As many as six forms were isolated from the house fly, *Musca domestica*, four forms from the flesh fly, *Sarcophaga bullata*, and the black blow fly, *Phormia regina*, three forms from the pomace fly, *Drosophila melanogaster*, and two forms from the black swallowtail, *Papilio polyxenes*. The multiplicity of cytochrome P450 would explain why the microsomal monooxygenase system possesses a broad substrate specificity capable of oxidizing various functional groups of lipophilic organic molecules. Each form is coded for by its own gene. To date, several hundred cytochrome P450 genes have been identified, including the house fly (*CYP6A1*, *CYP6A3*, *CYP6A4*, *CYP6A5*, *CYP6C1*, *CYP6D1*), the pomace fly (*CYP6A2*, *CYP4D1*, *CYP4D2*, *CYP4E1*), the bollworm, *Helicoverpa amigera* (*CYP6B2*, *CYP4G8*, *CYP9A3*, *CYP6B2*), the tobacco budworm, *Heliothis virescens* (*CYP9A1*), the black swallowtail (*CYP6B1*, *CYP6B3*) and the cockroach, *Blaberus discoidalis* (*CYP4C1*). Among the reactions performed by the microsomal monooxygenase system, epoxidation, hydroxylation, *N*-dealkylation, *O*-dealkylation, desulfuration and sulfoxidation are most important with respect to pesticide metabolism.



Detoxification Mechanisms in Insects, Figure 14 **Epoxidation of aldrin.**

Epoxidation

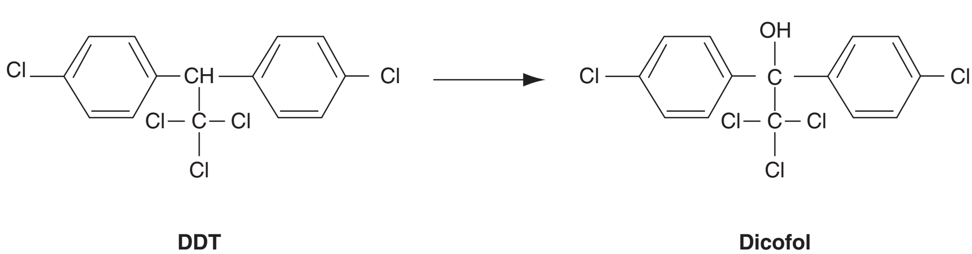
Epoxidation is an important microsomal reaction. For example, the cyclodiene (Fig. 14) insecticide aldrin can be oxidized to its epoxide dieldrin which is more environmentally persistent than its precursor. Epoxides are usually highly unstable and can undergo rapid enzymatic hydration to dihydrodiols catalyzed by epoxide hydrolases. These highly reactive epoxides can form adducts with cellular macromolecules such as proteins, RNA and DNA, often resulting in chemical carcinogenesis.

Hydroxylation

Hydroxylation can occur with an aliphatic or aromatic carbon atom. DDT and the carbamate insecticide carbaryl are known to be hydroxylated by microsomal monooxygenases as shown in the accompanying figure (Figs. 15 and 16). Microsomal hydroxylation usually results in detoxification.

N-Dealkylation

N-Dealkylation is a common reaction in the metabolism of xenobiotics including organophosphorus

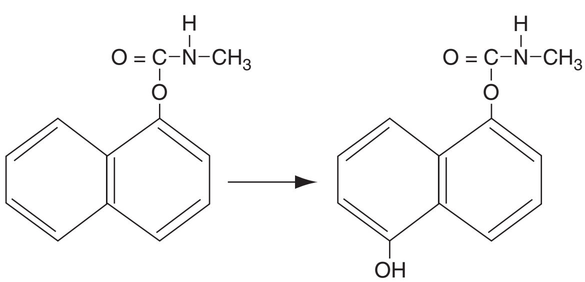


Detoxification Mechanisms in Insects, Figure 15 **Aliphatic hydroxylation of DDT.**

and carbamate insecticides. The reaction is believed to proceed by an unstable α-hydroxy intermediate which spontaneously releases an aldehyde in the case of the primary alkyl group. For example, the carbamate insecticide (Fig. 17) propoxur is *N*-demethylated to 2-isopropoxyphenyl carbamate via 2-isopropoxyphenyl *N*-hydroxymethyl carbamate. Microsomal *N*-dealkylation results in detoxification.

O-Dealkylation

O-Dealkylation of alkyl groups of the ester or ether structures of insecticides occurs frequently but it also involves an unstable α-hydroxy intermediate as found in *N*-dealkylation. For example, methoxychlor (Fig. 18) is *O*-demethylated by the system. *O*-Dealkylation is known to occur with a wide variety of organophosphates including certain dimethyl triesters. *O*-Dealkylation results in detoxification.



Carbaryl

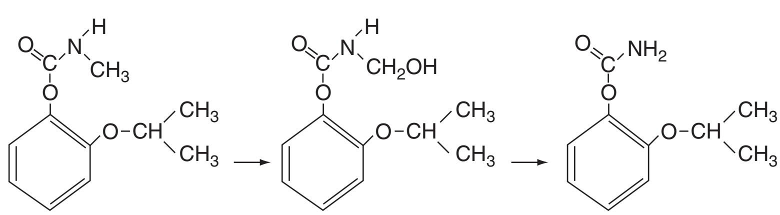
Detoxification Mechanisms in Insects, Figure 16 **Aromatic hydroxylation of carbaryl.**

Desulfuration

Organophosphorus insecticides with the P = S group are desulfurated by microsomal monooxygenases of insects to their corresponding P = O analogues. This reaction results in activation because the product, P = O, binds more tightly to the acetylcholinesterase and are thus more potent acetylcholinesterase inhibitors. For example, parathion (Fig. 19) is desulfurated to paraoxon.

Sulfoxidation

Many thioether-containing insecticides such as organophosphorus compounds and carbamates are oxidized by microsomal monooxygenases of insects to their corresponding sulfoxides. In general, sulfoxide formation represents an oxidative activation process leading to an increase in anticholinesterase activity. For example, phorate (Fig. 20) is oxidized to phorate sulfoxide. In the fall armyworm, *Spodoptera frugiperda*, sulfoxidation of phorate requires NADPH and is inhibited by carbon monoxide and piperonyl butoxide, and induced by cytochrome P450 inducers (e.g., indole 3-carbinol and indole 3-acetonitrile). In mammals, thioether-containing insecticides (e.g., phorate and disulfoton) can be oxidized by a microsomal FAD-dependent monooxygenase to their corresponding sulfoxides. The FAD monooxygenase system requires NADPH and oxygen for



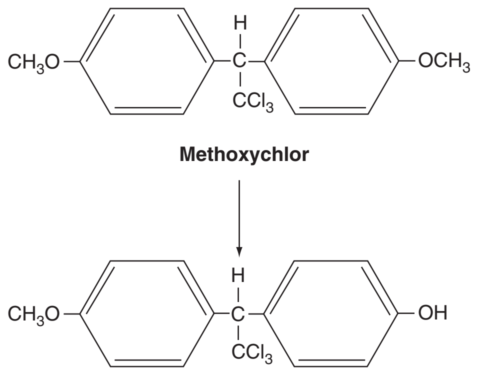
Propoxur

2-Isopropoxyphenyl *N*-hydroxymethyl carbamate

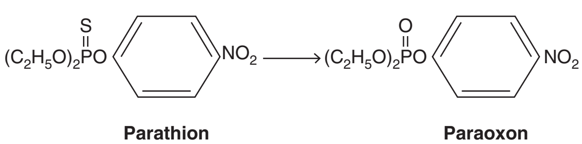
2-Isopropoxyphenyl carbamate

Detoxification Mechanisms in Insects, Figure 17 ***N*-Demethylation of propoxur.**

activity but is insensitive to methylenedioxyphenyl compounds. Recently, the FAD-dependent monooxygenase system has been demonstrated in insects.



Detoxification Mechanisms in Insects, Figure 18
***O*-Demethylation of methoxychlor.**



Detoxification Mechanisms in Insects, Figure 19
Desulfuration of parathion.

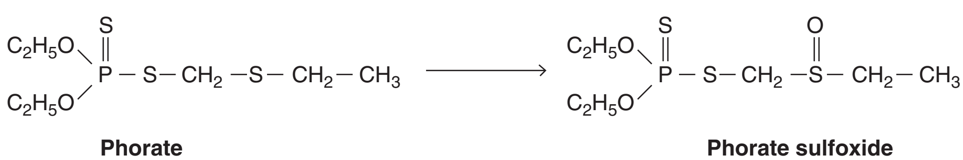
Reduction

Although insects contain reductases catalyzing the reduction of xenobiotics, reduction is less common than oxidation. Three types of reduction reactions, i.e., nitro reduction, azo reduction, and aldehyde/ketone reduction are known to occur in insects.

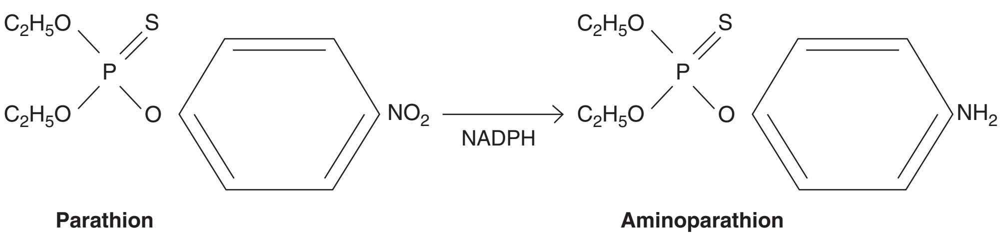
An NADPH-dependent nitroreductase has been reported in the soluble fraction (cytosol) of adult female house flies (Fig. 21) which reduces parathion to aminoparathion. The reductase activity is not affected by the presence of oxygen.

Nitrobenzene reductase activity (Fig. 22) has been detected in the fat body, gut and Malpighian tubules of the Madagascar cockroach, *Gromphadorhina portentosa*. Anaerobic conditions are essential for activity. The enzymes in the microsomes are strongly NADH dependent, whereas those in the soluble fraction are strongly NADPH dependent. Activity is enhanced by the addition of FAD, FMN or riboflavin. It appears that the true substrate for the nitroreductase is FMN and that the reduction of the nitro compounds occurs nonenzymatically. Similar results are obtained using azofuchsin as substrate.

Aldehyde reductases, which catalyze the reduction of (Fig. 23) aldehydes and ketones, are widely distributed in animal species including



Detoxification Mechanisms in Insects, Figure 20 **Sulfoxidation of phorate.**



Detoxification Mechanisms in Insects, Figure 21 **Nitro reduction of parathion.**

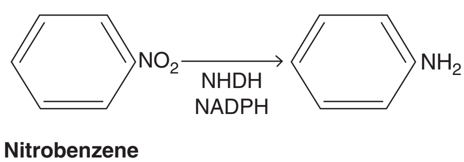
insects (e.g., *D. melanogaster* and *B. discoidalis*). These enzymes catalyze as in the accompanying reaction.

Aldehyde reductases are cytosolic enzymes requiring NADPH as cofactor. They reduce naturally occurring compounds such as benzaldehyde and daunorubicin as well as synthetic chemicals.

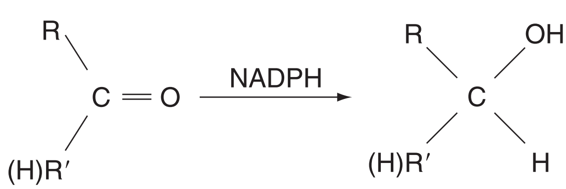
Hydrolysis

Insecticides such as organophosphates, carbamates, pyrethroids and some juvenoids, which contain ester linkages, are susceptible to hydrolysis. Esterase are hydrolases that split ester compounds by the addition of water to yield an acid and an alcohol.

$$R^1COOR + H_2O \rightarrow R^1COOH + ROH$$



Detoxification Mechanisms in Insects, Figure 22 Nitro reduction of nitrobenzene.



Detoxification Mechanisms in Insects, Figure 23 Aldehyde/ketone reduction.

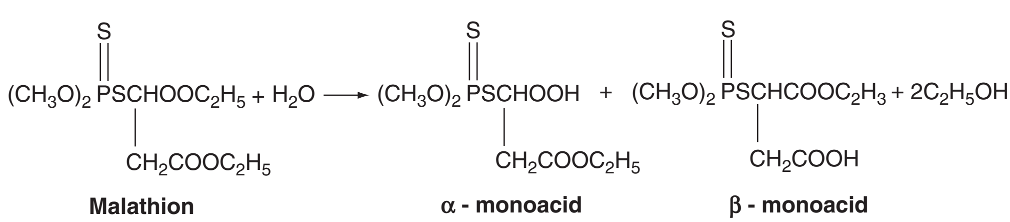
Esterases which metabolize organophosphates can be divided into three groups: A-esterases are not inhibited by organophosphates but hydrolyze them; B-esterases are susceptible to organophosphate inhibition; and C-esterases which are uninhibited by organophosphates but do not degrade them.

There are two types of esterases that are important in metabolizing insecticides, namely, carboxylesterases and phosphatases (also called phosphorotriester hydrolases). Carboxylesterases which are B-esterases play significant roles in degrading organophosphates, carbamates, pyrethroids and some juvenoids in insects. The best example (Fig. 24) is malathion hydrolysis, which yields both α- and β-monoacids and ethanol.

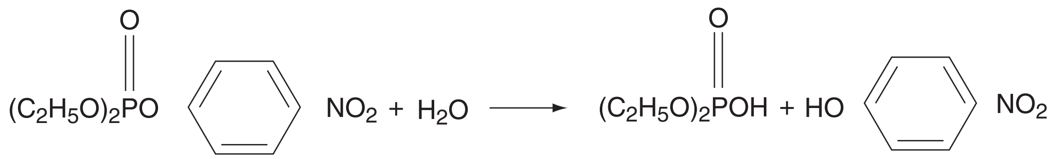
Carboxylesterase is responsible for the selective toxicity of malathion which favors mammals over insects. Carboxylesterase hydrolyzing *trans*-permethrin has been found in numerous insect species, including the fall armyworm, velvetbean caterpillar (*Anticarsia gemmatalis*), cabbage looper (*Trichoplusia ni*), tobacco budworm, corn earworm (*Helicoverpa zea*), and spined soldier bug (*Podisus maculiventris*).

Phosphatases are A-esterases which detoxify many organophosphorus insecticides especially phosphates in insects. In house flies, paraoxon (Fig. 25) can be hydrolyzed to diethyl phosphoric acid as in the accompanying reaction. Phosphatases also hydrolyze the alkyl groups of organophosphates. Paraoxon was hydrolyzed by the enzyme in house flies.

Several amide-containing organophosphorus insecticides such as dimethoate and acephate have (Fig. 26) been shown to be hydrolyzed by carboxylamidases to their corresponding carboxylic acid derivatives.



Detoxification Mechanisms in Insects, Figure 24 Hydrolysis of malathion.



Paraoxon

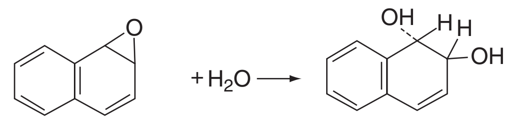
Detoxification Mechanisms in Insects, Figure 25 **Hydrolysis of paraoxon.**

dimethoate   dimethoate acid

Detoxification Mechanisms in Insects, Figure 26 **Hydrolysis of dimethoate.**

Carboxylamidase activity toward *p*-nitroacetanilide has been detected in different insect species from the orders Lepidoptera, Orthoptera and Dictyoptera. The carboxylamidase from fall armyworm larvae has been purified. The purified enzyme is a monomer with a molecular weight of 59,000–60,000 Da. The enzyme is inhibited by the hydrolase inhibitors paraoxon, triphenyl phosphate, eserine and phenylmethylsulfonyl fluoride, showing I_{50} values of 4.7 μM, 0.2 mM, 16 μM and 90 μM, respectively. Activity also is inhibited completely by the organophosphorus insecticides profenfos and dichlorvos at 0.1 mM. The enzyme is active toward other amides, such as acetanilide and phenacetin, and various α- and β-naphtholic esters. Based on the purification factor, substrate specificity, and sensitivity to hydrolase inhibitors, the carboxylamidase appears to be different from carboxylesterases in this insect.

Epoxide rings of alkene and arene compounds are hydrated to form *trans*-diols. The enzymes which catalyze the addition of a molecule of water to an epoxide ring to yield diols are known as epoxide hydrolases. Epoxide hydrolase activity (Fig. 27) has been detected in numerous species of insects. Enzymatic epoxide hydration of certain cyclodiene insecticides and their analogues has been demonstrated in the house fly, blow fly (*Calliphora erythrocephala*), yellow mealworm (*Tenebrio molitor*), Madagascar cockroach, southern armyworm (*Spodoptera eridania*), and red flour beetle (*Tribolium castaneum*). Epoxide hydrolase is important also in the metabolism of juvenile hormone, which contains the 10,11-epoxy ring, in several insect species including the southern armyworm, house fly, black blow fly, and flesh fly.



naphthalene 1,2-oxide   naphthalene dihydrodiol

Detoxification Mechanisms in Insects, Figure 27 **Epoxide hydration of naphthalene 1,2 oxide.**

Among the phase I reactions, oxidation mediated by microsomal monooxygenases is the most important in insects. Resistance to insecticides caused by enhanced microsomal monooxygenase activities has been reported in numerous insects.

Phase II Reactions

Phase I reactions with xenobiotics result in the addition of functional groups such as hydroxyl, carboxyl, and epoxide. These phase I products can undergo further conjugation reactions with endogenous molecules. These conjugations are called phase II reactions. The endogenous molecules include sugars, amino acids, glutathione, phosphate and sulfate. Conjugation products usually are more polar, less toxic and more readily excreted than their parent compounds. Thus, the process, with only a few exceptions, results in detoxification.

Three types of conjugation reactions occur in insects. Type I requires an activated conjugating agent which then combines with the substrate to form the conjugated product. Type II involves the activation of the substrate to form an activated donor which then combines with an endogenous molecule to yield a conjugated product. In type III, conjugation can proceed directly between the substrate and conjugating agent without involving activation. Thus, types I and II require formation of high energy intermediates before conjugation reactions proceed.

The chemical groups required for type I are OH, NH_2, COOH and SH (glucose conjugation, sulfate conjugation and phosphate conjugation); for type II, COOH (amino acid conjugation); and for type III, halogens, alkenes, NO_2, epoxides, ethers and esters (glutathione conjugation).

Glucose Conjugation

Glucose conjugation is found commonly in insects and plants but rarely in mammals. Glucoside formation is accomplished by a reaction between an activated intermediate, uridine diphosphate glucose (UDPG), and the xenobiotic, with the enzyme glucosyl transferase as catalyst (Fig. 28). In insects, *O*-glucosides have been identified from some insecticide metabolism studies, including carbaryl, propoxur, carbofuran, DDT and allethrin.

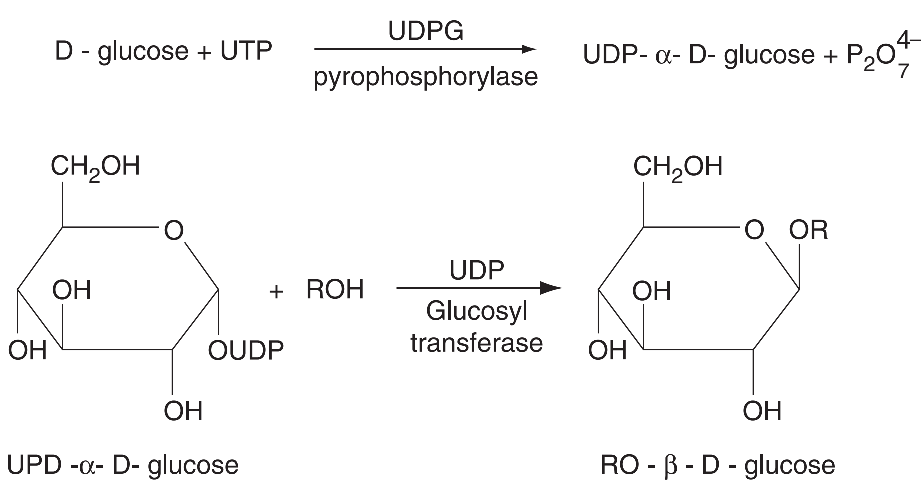
Sulfate Conjugation

Sulfate conjugation requires the prior activation of inorganic sulfate by adenosine triphosphate to an active intermediate, 3'-phosphoadenosine-5'-phosphosulfate (PAPS), from which the sulfate group is transferred to a substrate (ROH). The final step is catalyzed by an enzyme called sulfotransferase. The three-step reaction (Fig. 29) sequence is illustrated in the accompanying reaction.

Sulfate conjugates have been detected *in vivo* in numerous insect species following exposure to phenolic compounds. A sulfotransferase prepared from gut tissues of southern armyworm larvae has been shown to be active toward *p*-nitrophenol and steroids including cholesterol, ecdysone and β-sitosterol.

Phosphate Conjugation

Conjugation of xenobiotics with phosphate is rare in animals. Insects and arachnids are the major groups of animals in which phosphate conjuga-



Detoxification Mechanisms in Insects, Figure 28 Glucose conjugation.

$$ATP + SO_4^{2-} \underset{\text{adenylyl transferase}}{\overset{\text{ATP-SULFATE}}{\rightleftharpoons}} APS + PP_i$$

$$APS + ATP \xrightarrow[\text{3}'\text{-phosphotransferase}]{\text{ATP-adenylyl sulfate}} PAPS + ADP$$

$$ROH + PAPS \xrightarrow{\text{sulfotransferase}} ROSO_3H + PAP$$

Detoxification Mechanisms in Insects, Figure 29 **Sulfate conjugation.**

tion has been demonstrated. Phosphate conjugates have been detected in house flies, blow flies (*Lucilia sericata*) and New Zealand grass grubs (*Costelytra zealandica*) when treated with 1-naphthol, 2-naphthol or *p*-nitrophenol. An active phosphotransferase (Fig. 30) prepared from the gut of the Madagascar cockroach requires ATP and Mg^+ for phosphorylation of *p*-nitrophenol.

Amino Acid Conjugation

Aromatic acids often are conjugated with amino acids in animals, glycine being the most frequently used amino acid. Conjugation of aromatic acids with glycine has been demonstrated in several species of insects. Glycine conjugation occurs in two steps. The first involves the activation of the substrate (RCOOH) by an enzyme system requiring ATP and coenzyme A and the second the condensation of the activated substrate with glycine.

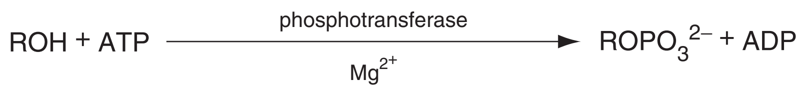
$$\text{RCOOH} + \text{ATP} + \text{HSCoA} \rightarrow \text{RCOSCoA} + \text{AMP} + \text{PPi}$$

$$\text{RCOSCoA} + \text{H}_2\text{NCHRCOOH} \rightarrow \text{RCONHCHRCOOH} + \text{HSCoA}$$

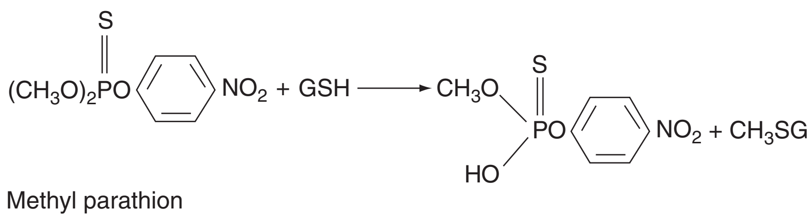
Glutathione Conjugation

Glutathione conjugation is performed by a group of multifunctional enzymes known as glutathione *S*-transferases. These enzymes catalyze the conjugation of reduced glutathione (GSH) with electrophilic substrates. Glutathione *S*-transferases perform a variety of reactions including (i) the *S*-alkylation of GSH by alkyl halides and related compounds; (ii) the replacement of labile aryl halogen or nitro groups by GSH; (iii) the replacement of labile arakyl halogen and ester groups by GSH; (iv) the addition of GSH to various epoxides; (v) the addition of GSH to α, β-unsaturated compounds including aldehydes, ketones, lactones, nitriles and nitro compounds; and (vi) the *O*-alkyl and *O*-aryl conjugation of phosphorothiates and phosphates with GSH. The glutathione conjugate is subsequently transformed to a mercapturic acid through the stepwise loss of glutamic acid and glycine to a cysteine conjugate which is finally acetylated before excretion. Because of their broad substrate specificities, glutathione *S*-transferases are responsible for the detoxification of numerous toxicants.

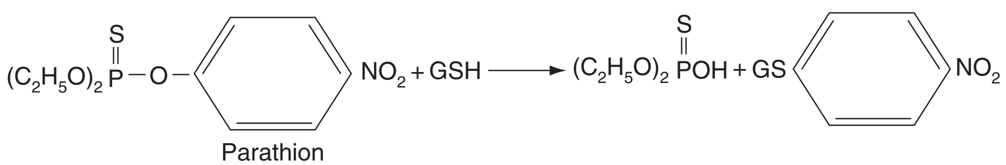
Glutathione *S*-transferases are important in the metabolism of organophosphorus insecticides resulting in detoxification. For example, methyl parathion (Fig. 31) is dealkylated by glutathione *S*-transferase to form desmethyl parathion and methyl glutathione. On the other hand, parathion (Fig. 32) can be dearylated by glutathione *S*-transferase to produce diethyl phosphorothioic acid and *S*-(*p*-nitrophenyl) glutathione. Interestingly, a glutathione *S*-transferase isozyme isolated from the house fly exhibits DDT-dehydrochlorinase activity,



Detoxification Mechanisms in Insects, Figure 30 **Phosphate conjugation.**



Detoxification Mechanisms in Insects, Figure 31 **Glutathione conjugation of methyl parathion.**



Detoxification Mechanisms in Insects, Figure 32 **Glutathione conjugation of parathion.**

showing that DDT-dehydrochlorinase is one of glutathione *S*-transferases. DDT-dehydrochlorinase converts DDT to DDE resulting in detoxification.

Glutathione *S*-transferases have received considerable attention due to their roles in insecticide detoxification and resistance in insects. Cytosolic glutathione *S*-transferases have been purified from more than two dozen insect species, including Lepidoptera, Diptera, Coleoptera, Dictyoptera and Hymenoptera. These transferases exist in multiple forms, and as many as nine isozymes were found in midguts and fat bodies of fall armyworm larvae. Insect glutathione *S*-transferases consist of two subunits (homodimers and heterodimers) of molecular weight between 19,000 and 35,000 Da. Recent studies also show that purified cytosolic and microsomal glutathione *S*-transferase isozymes from fall armyworm larvae all possess cumene hydroperoxide peroxidase activity. Thus, insect glutathione *S*-transferases might play a significant role in the protection of biological membranes against oxidative damage.

Induction of Detoxification Enzymes

Detoxification enzymes possess a capacity for rapid increase in activity in response to chemical stress, a phenomenon called enzyme induction. In insects, microsomal monooxygenases can be induced by a variety of organic chemicals in insects including insecticides such as DDT, cyclodienes; insect hormones and growth regulators such as 20-hydroxyecdysone and juvenile hormone; organic solvents such as pentamethylbenzene; drugs such as phenobarbital and 3-methylcholanthrene, butylated hydroxytoluene and triphenyl phosphate; and allelochemicals such as terpenoids, indoles, flavonoids and furanocoumarins. On the other hand, glutathione *S*-transferases are induced by various xenobiotics including insecticides such as DDT and dieldrin; barbiturates such as phenobarbital; and allelochemicals such as xanthotoxin, and indole 3-acetonitrile. Interestingly, many methylenedioxyphenyl compounds commonly used as insecticide synergists are inducers of DDT-dehydrochlorinase in house flies.

Hydrolases also are induced by xenobiotics in insects, but to a small extent. Juvenile hormone and juvenoids are inducers of juvenile hormone esterase in *Hyalophora gloveri* and *T. ni*. 1-Naphthyl acetate esterase is induced by a range of allelochemicals including α-pinene, menthol, indole 3-acetonitrile, indole 3-carbinol and flavone in fall armyworm larvae. In the same insect, epoxide hydrolase (toward styrene oxide) is moderately induced by allelochemicals such as indole 3-carbinol, peppermint oil and phenobarbital. Moreover, juvenile hormone epoxide hydrolase can be induced by phenobarbital in house flies.

Very little is known about the induction of reductases in insects. Juglone reductase is induced by allelochemicals such as α-pinene, peppermint oil, flavone, indole 3-acetonitrile and indole 3-carbinol in the fall armyworm.

It is now well established that the induction of microsomal monooxygenase activity involves synthesis of new enzyme, i.e., *de novo* protein synthesis, rather than activation of pre-existing enzyme or a block in the rate of degradation. The exact mechanism of induction in insects is not yet clear. In mammals, it appears that certain exogenous inducers enter the cell and bind to a semi-specific cytosolic receptor protein. The inducer-receptor complex is then transferred to the nucleus. The complex activates the appropriate structural genes which results in the production of the cytochrome P450 and associated components.

Enzyme Induction as Detoxification Mechanism

The importance of the microsomal monooxygenases, glutathione *S*-transferases, carboxylesterases and epoxide hydrolases in insecticide metabolism and detoxification as well as in insecticide resistance is well documented. It is, therefore, logical to expect that an increase in these enzyme activities resulting from induction by xenobiotics would decrease the toxicity of an insecticide due to enhanced metabolism.

Dietary α-pinene causes southern armyworm larvae to become more tolerant to a botanical insecticide, nicotine. Enhanced tolerance to synthetic insecticides also has been demonstrated in phytophagous insects fed plants capable of inducing microsomal monooxygenase activity. Variegated cutworm larvae fed peppermint leaves are more tolerant of the insecticides carbaryl, acephate, methomyl, and malathion than larvae fed snap bean leaves. Increased tolerance for carbaryl and methomyl also has been observed in larvae of the cabbage looper and alfalfa looper (*Autographa californica*) fed peppermint plants instead of their favored host plants broccoli and alfalfa.

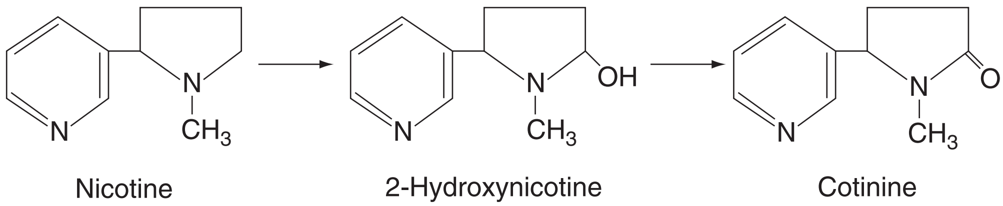
Further studies reveal that corn leaves, which is a potent inducer of microsomal monooxygenases, cause fall armyworm larvae to become less susceptible to the insecticides methomyl, acephate, methamidophos, diazinon, trichlorfon, monocrotophos, permethrin and cypermethrin than soybean-fed larvae.

Induction of glutathione *S*-transferases by phenobarbital in house flies provides some protection against the toxicity of methyl parathion, methyl paraoxon, azinphosmethyl and methidathion. Similarly, induction of glutathione *S*-transferase in fall armyworm larvae protects the larvae against organophosphorus insecticides. Larvae fed cowpeas, a potent inducer of the transferase, are twice as tolerant of diazinon, methyl parathion and methamidophos as those fed soybeans.

Induction of carboxylesterases and epoxide hydrolases also would affect the toxicity of insecticides. For example, host plant induction of 1-naphthyl acetate esterase would decrease the toxicity of certain insecticides containing an ester linkage, such as organophosphates, pyrethroids, and some juvenile hormone analogs, and, possibly, carbamates.

Metabolism of Allelochemicals by Detoxification Enzymes

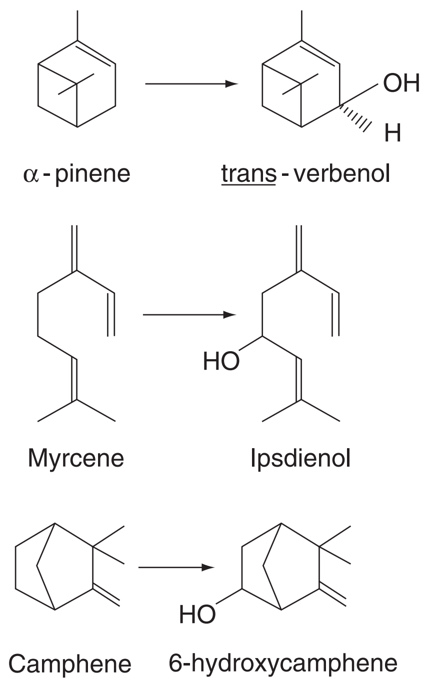
Many allelochemicals are known to be metabolized by detoxification enzymes in insects. It has



Detoxification Mechanisms in Insects, Figure 33 **Metabolism of nicotine in insects.**

been shown that the botanical insecticides, nicotine, pyrethrins and rotenone, are metabolized by microsomal monooxygenases in insects. Nicotine is hydroxylated (Fig. 33) at the C-2 position to produce 2-hydroxynicotine followed by alcohol dehydrogenation to yield cotinine in tobacco feeding insects. Pyrethrin I is hydroxylated at the trans-methyl group and the side chain in house flies. As for rotenone, it is oxidatively metabolized to rotenolone I and II, 6',7'-dihydro-6',7'-dihydroxyrotenone and 8'-hydroxyrotenone in house flies.

A variety of monoterpenes (Fig. 34) are oxidatively metabolized by bark beetles. α-Pinene is hydroxylated to trans-verbenol (a pheromone) in *Dendroctonus terbranus* and *Dendroctonus frontalis*, myrcene to ipsdienol in *Ips* spp. and camphene to 6-hydroxycamphene in *Dendroctonus* and *Ips* spp. α-Pinene also is oxidized to α-pinene epoxide by microsomal monooxygenases in bark beetles. Pulegone is oxidized to 9-hydroxypulegone and 10-hydroxypulegone by microsomal monooxygenase from southern armyworm larvae.

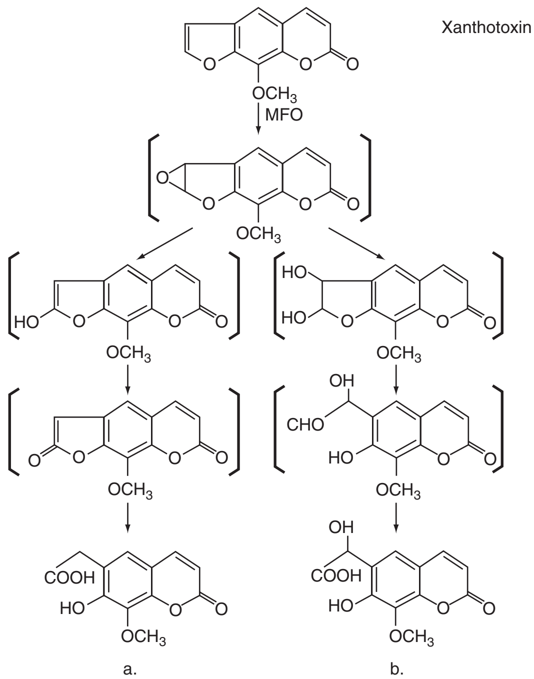


Detoxification Mechanisms in Insects, Figure 34 **Microsomal oxidation of monoterpenes.**

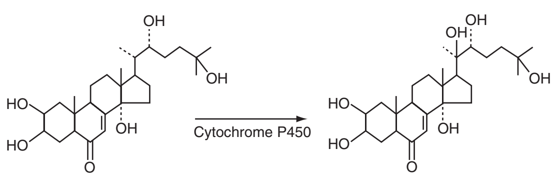
The metabolism of xanthotoxin, a furanocoumarin (Fig. 35) found in the Umbelliferae, has been studied in the black swallowtail. Two metabolites, 7-hydroxy-8-methoxy-2-oxo-2H-1-benzopyran-6-acetic acid (metabolite a) and α,7-dihydroxy-8-methoxy-oxo-2H-1-benzopyran-6-acetic acid (metabolite b), are believed to be formed through microsomal oxidation. The ability of black swallowtail to rapidly detoxify this compound would explain why this insect is able to feed on xanthotoxin-containing plants without being poisoned.

The phytoecdysone, ecdysone, which is (Fig. 36) found in certain plants such as ferns, has been shown to be hydroxylated by microsomal monooxygenases at the C-20 position to become 20-hydroxyecdysone in various insects. This C-20 hydroxylation has been reported in the African migratory locust (*Locusta migratoria migratortoriodes*), the tobacco hornworm (*Manduca sexta*), the gypsy moth (*Lymantria dispar*), the pomace fly and the fall armyworm. The enzyme responsible for this hydroxylation, ecdysone 20-monooxygenase, is active in the midgut, fat body and Malpighian tubules.

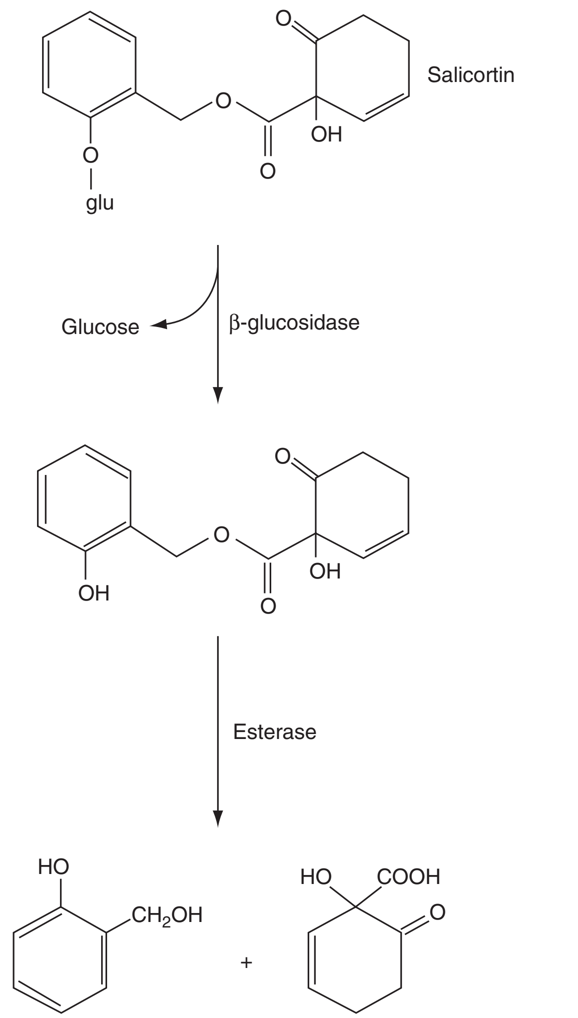
The juvenile hormone antagonist, precocene II, is shown to be attacked primarily by microsomal monooxygenases from fat body homogenates of cabbage looper larvae to become two isomeric dihydrodiols. Although precocene 3,4-epoxide has



Detoxification Mechanisms in Insects, Figure 35
Microsomal oxidation of xanthotoxin.



Detoxification Mechanisms in Insects, Figure 36
Microsomal oxidation of ecdysone.



Detoxification Mechanisms in Insects, Figure 37
Hydrolysis of salicortin.

not been detected in this study, its formation is believed to be essential as an intermediate for both diols. Because of the extreme reactivity of the epoxide, it is suggested that the epoxide is involved in the allatotoxication of precocene II.

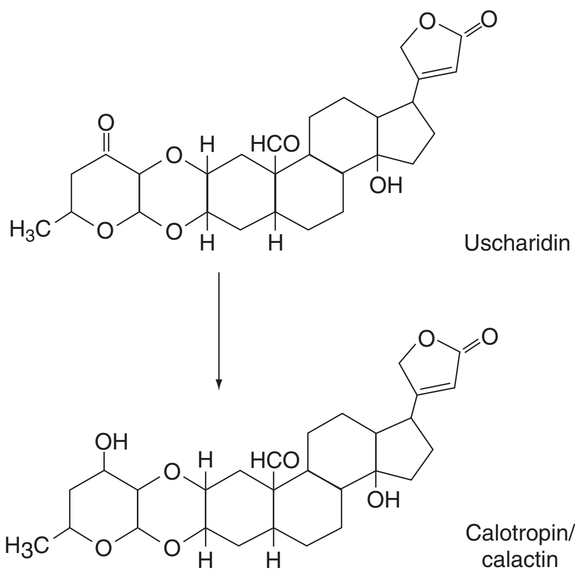
Plants produce a variety of allelochemical glycosides including glycoalkaloids, glucosinolates, cyanogenic, phenolic, iridoid and triterpenoid glycosides. A glycoside consists of a glycone (sugar moiety) and an aglycone (nonsugar moiety), the most common glycone being glucose in plants. Nearly all naturally occurring plant glycosides are β-linked *O*-glycosyl compounds. Glycosidases are a group of hydrolytic enzymes which catalyze the hydrolysis of glycosidic linkages in glycosides. Thus, β-glycosidases are very important in the metabolism of plant glycosides. Although insect β-glycosidases are capable of hydrolyzing glycosides to release carbohydrates, allelochemical aglycones generally are toxic to insects. Therefore, insects must have enzymes that can detoxify the aglycone. It has been shown that the ability of peachtree borer (*Synanthedon exitosa*) larvae to survive well on prunasin-containing peach tree is because they can metabolize cyanogenic glycosides through β-glucosidase and detoxify the released cyanide by β-cyanoalanine synthase. Another example is larvae of the tiger swallowtail (*Papilio glaucus*) that feed on quaking aspen which contains various phenolic glycosides (e.g., salicortin). These larvae (Fig. 37) hydrolyze the glycosides by β-glucosidase and detoxify the released phenolic aglycone by a highly active esterase, thereby allowing them to survive on aspen.

Certain reductases are important in the detoxification of allelochemicals. For example, the milkweed cardenolide, uscharidin, is metabolized (Fig. 38) by aldehyde reductase to calactin or calotropin (an enantiomer) in the monarch butterfly (*Danaus plexippus*) larvae. Milkweeds contain a complex mixture of cardenolides. Monarch butterfly larvae feed on milkweed and store cardenolides that make adults unpalatable to most bird predators.

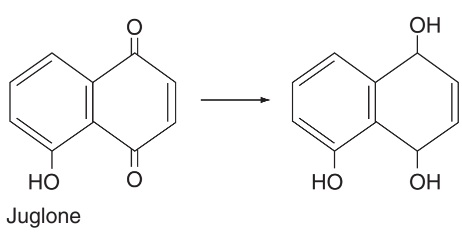
Moreover, juglone (a 1,4-naphthoquinone), which is commonly found in members of the Juglandaceae, is toxic to insects. Juglone is metabolized by quinone reductase (Fig. 39) in several species of Lepidoptera including the fall armyworm, corn earworm, tobacco budworm, velvetbean capterpillar and luna moth (*Actias luna*). Variation in susceptibility of these insects to juglone appears to be correlated with reductase activity.

Some toxic alleochemicals are metabolized by glutathione *S*-transferases. For example, α, β-unsaturated carbonyl allelochemicals including benzaldehyde, *trans*-2-hexenal and *trans*, *trans*-2, 4-decadienal (Fig. 40) are metabolized by glutathione *S*-transferases from fall armyworm larvae. These allelochemicals commonly are found in corn, wheat and oats, all of which are preferred host plants for the fall armyworm.

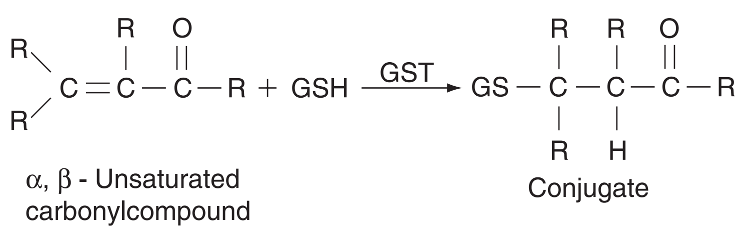
Glutathione *S*-transferases of lepidopterous larvae also metabolize toxic isothiocyanates (RNCS) commonly found in cruciferous plants. The reaction occurs as in the (Fig. 41) accompanying figure. These allelochemicals include allyl, benzyl and 2-phenylethyl isothiocyanate. Allyl and benzyl isothiocyanate are metabolized by glutathione *S*-transferases from the two generalists, fall armyworm and cabbage looper, but no activity is detected with the specialist, velvetbean caterpillar. Apparently, glutathione



Detoxification Mechanisms in Insects, Figure 38
Reduction of uscharidin.



Detoxification Mechanisms in Insects, Figure 39
Reduction of juglone.



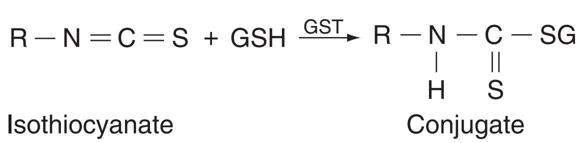
Detoxification Mechanisms in Insects, Figure 40 **Metabolism of a carbonyl compound by glutathione *S*-transferases.**

S-transferases play an important role in their survival since the generalists, but not the specialist, are adapted to feeding on isothiocyanate-containing crucifers.

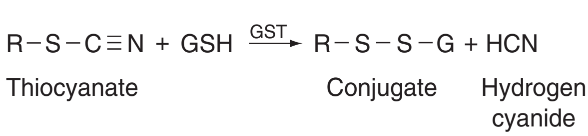
In addition, organothiocyanates (SCN) such as benzyl thiocyanate (Fig. 42) also are metabolized by glutathione *S*-transferases from lepidopterous larvae. The reaction occurs as in the accompanying figure.

The glutathione-dependent metabolism of an organothiocyanate results in the liberation of toxic HCN. Thus, the glutathione conjugation is an intoxication process which is an undesirable system for phytophagous insects. Lepidopterous insects vary greatly in both their ability to metabolize organothiocyanates (via glutathione conjugation) and to detoxify its toxic metabolite, HCN. Obviously, a high cyanide detoxification capacity would be essential to insects feeding on thiocyanate-containing plants.

Moreover, highly polyphagous insects possess multiple forms of midgut glutathione *S*-transferase, whereas the more specialized insects have a single form of the enzyme. These results suggest strongly that glutathione *S*-transferases play an important role in allelochemical resistance in phytophagous insects.



Detoxification Mechanisms in Insects, Figure 41 Metabolism of isothiocyanates by glutathione *S*-transferases.



Detoxification Mechanisms in Insects, Figure 42 Metabolism of organothiocyanates by glutathione *S*-transferases.

Role of Detoxification Enzymes in Insecticide Resistance

Insecticide resistance is one of the major obstacles to the successful control of insects. Insecticide resistance has been shown to involve three mechanisms, i.e., enhanced detoxification, reduced penetration and target site insensitivity. Generally, these resistance factors do not occur alone and are known to interact with each other, especially penetration and metabolism, to enhance the level of resistance. In the case of enhanced detoxification, a number of enzymes have been shown to be involved in resistance. They are the microsomal monooxygenases, carboxylesterases and glutathione *S*-transferases.

Enhanced microsomal monooxygenase activity has been shown to be a major mechanism of resistance for all insecticide classes except the cyclodienes in numerous insects especially house flies. In house flies and mosquitoes, resistance is due to constitutive overexpression of cytochrome P450 genes resulting in the production of more cytochrome P450 enzymes.

Carboxylesterases are involved in resistance to ester-containing insecticides such as organophosphorus, carbamate and pyrethroid insecticides. Resistance to malathion caused by enhanced carboxylesterase activity has been demonstrated in the mosquito (*Culex tarsalis*) and the bedbug (*Cimex lectularus*). In green peach aphids, brown planthoppers (*Nilaparvata lugens*) and mosquitoes (*Culex* spp.), resistance to various types of insecticidal esters is caused by amplification of esterase genes, i.e., the presence of multiple copies of the structure genes that direct the synthesis of enzymes.

Glutathione *S*-transferases play a significant role in resistance to organophosphorus insecticides in insects, especially house flies and mosquitoes. In mosquitoes, increased gene expression, rather than gene amplification, is the primary molecular basis of glutathione *S*-transferase-based resistance. Resistance to parathion, diazinon and diazoxon in a resistant strain of house fly is caused by an increased glutathione *S*-transferase activity via deethylation of these insecticides. DDT-dehydrochlorinase, a glutathione *S*-transferase, also is responsible for DDT resistance in DDT-resistant insect species.

References

Brattsten LB (1992) Metabolic defenses against plant allelochemicals. In: Rosenthal GA, Berenbaum MR (eds) Herbivores: their interactions with secondary plant metabolites, 2nd edn. Academic Press, New York, NY, pp 175–242

Dauterman WC (1985) Insect metabolism: extramicrosomal. In: Kerkut GA, Gilbert LI (eds) Comprehensive insect physiology, biochemistry and physiology, vol 11. Pergamon Press, New York, NY, pp 713–730

Hodgson E (1985) Microsomal mono-oxygenases. In: Kerkut GA, Gilbert LI (eds) Comprehensive insect physiology, biochemistry and physiology, vol 11. Pergamon Press, New York, NY, pp 225–326

Nakatsugawa T, Morelli MA (1976) Microsomal oxidation and insecticide metabolism. In: Wilkinson CF (ed) Insecticide biochemistry and physiology. Plenum Press, New York, NY, pp 61–104

Terriere LC (1984) Induction of detoxication enzymes in insects. Ann Rev Entomol 29:71–88

Yang RSH (1976) Enzymatic conjugation and insect metabolism. In: Wilkinson CF (ed) Insecticide biochemistry and physiology. Plenum Press, New York, NY, pp 177–225

Yu SJ (1986) Consequences of induction of foreign compound-metabolizing enzymes in insects. In: Brattsten LB, Ahmad S (eds) Molecular aspects of insect-plant association. Plenum Press, New York, NY, pp 153–174

Yu SJ (2008) The toxicology and biochemistry of insecticides. CRC Press, Boca Raton, FL, 296 pp

Detritivore

An organism that feeds on detritus (decaying debris).

► Decomposer Insects
► Food Habits of Insects

Detritivory

Feeding on detritus or fragments (usually plant fragments, but also detritus from animals such as skin or feathers). Such arthropods are said to be detritivorous or detritivores.

► Food Habits of Insects
► Decomposer Insects

Deutocerebrum

The portion of the brain that innervates (Fig. 43) the antennae. The middle section of the brain.

► Nervous System

Deuterophlebiidae

A family of flies (order Diptera). They commonly are known as mountain midges.

► Flies

Deutonymph

The third instar mite.

► Mites (Acari)

Developmental Threshold

The threshold at which growth will occur, usually taken to mean the lowest temperature at which growth commences (i.e., lower developmental threshold or developmental zero) but also a high temperature above which development ceases (i.e., upper developmental threshold).

► Bioclimatic Models in Entomology

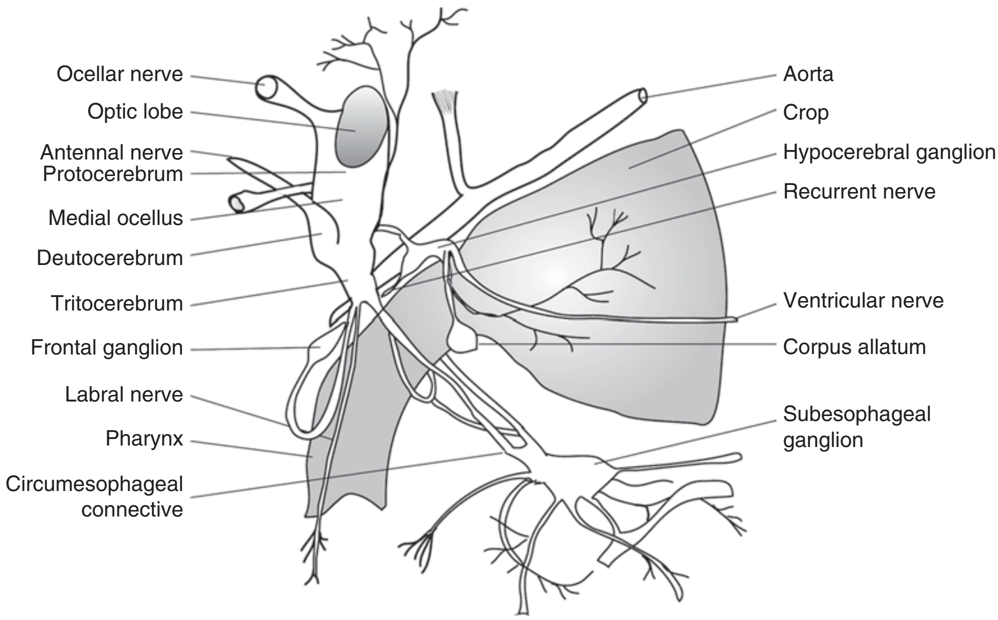
Diadocidiidae

A Family of flies (order Diptera).

► Flies

Diagnosis

In pathology, the process of distinguishing one disease from another. The determination of a disease from its signs, symptoms, etiology, pathogenesis, physiopathology, morphopathology, etc.



Deutocerebrum, Figure 43 **Diagram of the insect brain, lateral view (adapted from Snodgrass, Insect morphology).**

Diamondback Moth, *Plutella xylostella* (Linnaeus) (Lepidoptera: Plutellidae)

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Diamondback moth is probably of European origin but has become rather cosmopolitan, and is now found throughout the Americas, Europe, Southeast Asia, Australia, and New Zealand. By virtue of its ability to feed on cruciferous weeds, diamondback moth is sometimes abundant even in some areas where cruciferous crops do not occur. It is highly dispersive, and is often found in areas where it cannot successfully overwinter, such as most of Canada.

Life History

Total development time from the egg to pupal stage averages 25–30 days, depending on weather, with a range of about 17–51 days. In cooler climates such as Ontario, Canada, diamondback moth is present from May to October, but is most abundant in July and September. There are four to six generations annually, but discrete broods are not apparent. In mid-latitude climates such as Colorado, USA, the number of annual generations is estimated to be seven, and overwintering survival is positively correlated with the abundance of snowfall. There is continuous breeding in the southern, warm weather regions of USA, so the number of generations is likely 12–15 per year there and in tropical climates.

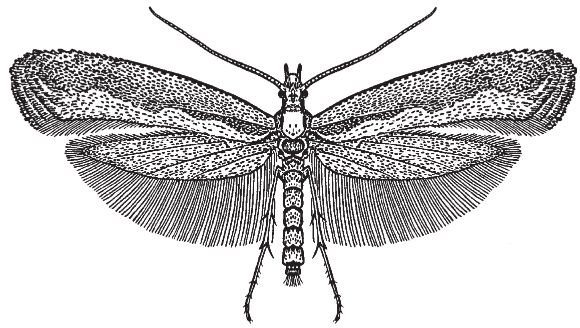
Diamondback moth eggs are oval and flattened, and measure 0.44 mm long and 0.26 mm wide. Eggs are yellow or pale green in color, and are deposited singly or in small groups of two to eight eggs in depressions on the surface of foliage, or occasionally on other plant parts. Females may deposit 250–300 eggs early in the year, but the number decreases in later generations by 90%; average total egg production is probably 150 eggs. Development time averages 5.6 days, with a range of 4–8 days.

Diamondback moth has four instars. Average and range of development time is about 4.5 (3–7), 4 (2–7), 4 (2–8), and 5 (2–10) days, respectively. Throughout their development, larvae remain quite small and active. If disturbed, they often wriggle violently, move backward, and spin down from the plant on a strand of silk. Overall length of each instar rarely exceeds 1.7, 3.5, 7.0, and 11.2 mm, respectively, for instars 1–4. Mean head capsule widths for these instars are about 0.16, 0.25, 0.37, and 0.61 mm. Larval body (Fig. 45) form tapers at both ends, and a pair of prolegs protrudes from the posterior end, forming a distinctive "V." The larvae are colorless in the first instar, but thereafter are green. The body bears relatively few hairs, which are short in length, and most are marked by the presence of small white patches. There are five pairs of prolegs. Initially, the feeding habit of first instar larvae is leaf mining, although they are so small that the mines are difficult to notice. The larvae emerge from their mines at the conclusion of the first instar, molt beneath the leaf, and thereafter feed on the lower surface of the leaf. Their chewing results in irregular patches of damage, and the upper leaf epidermis is often left intact.

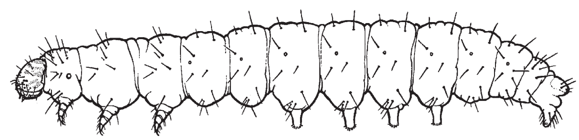
Pupation occurs in a loose silk cocoon, usually formed on the lower or outer leaves. In cauliflower and broccoli, pupation may occur in the florets. The yellowish pupa is 7–9 mm in length. The duration of the cocoon averages about 8.5 days (range 5–15 days), but during a portion of this time the insect is in the prepupal rather than the pupal stage.

The adult (Fig. 44) is a small, slender, grayish-brown moth with pronounced antennae. It is about 6 mm long, and marked with a broad cream or light brown band along the back. The band is sometimes constricted to form one or more light-colored diamonds on the back, which is the basis for the common name of this insect. When viewed from the side, the tips of the wings can be seen to turn upward slightly. Moths usually mate at dusk, immediately after emergence from the cocoon. Flight and oviposition take place from dusk to midnight, and moths can be found feeding at blossoms on nectar. Adult males and females live about 12 and 16 days, respectively, and females deposit eggs for about 10 days. The moths are weak fliers, usually flying within 2 m of the ground, and not flying long distances. However, they are readily carried by the wind. The adult is the overwintering stage in temperate areas, but moths do not survive cold winters such as is found in most of Canada. They routinely reinvade these areas each spring, evidently aided by southerly winds.

Diamondback moth attacks only plants in the family Cruciferae. Virtually all cruciferous vegetable crops are eaten, including broccoli, Brussels sprouts, cabbage, Chinese cabbage, cauliflower, collard, kale, kohlrabi, mustard, radish, turnip, and watercress. Not all are equally preferred, however, and collard will usually be chosen by ovipositing moths relative to cabbage. Several weeds are important hosts, especially



Diamondback Moth, *Plutella Xylostella* (Linnaeus) (Lepidoptera: Plutellidae), Figure 44 Adult of diamondback moth, *Plutella xylostella* (Linnaeus).



Diamondback Moth, *Plutella Xylostella* (Linnaeus) (Lepidoptera: Plutellidae), Figure 45 Larva of diamondback moth, *Plutella xylostella* (Linnaeus).

early in the season before cultivated crops are available. Yellow rocket, *Barbarea vulgaris*; shepherdspurse, *Capsella bursa-pastoris*; pepperweed, *Lepidium* spp.; and wild mustards, *Brassica* spp. are commonly cited as important weed hosts.

Natural enemies are important mortality factors, though weather also determines population trends. Large larvae, prepupae, and pupae are often killed by the parasitoids *Microplitis plutellae* (Muesbeck) (Hymenoptera: Braconidae), *Diadegma insulare* (Cresson) (Hymenoptera: Ichneumonidae), and *Diadromus subtilicornis* (Gravenhorst) (Hymenoptera: Ichneumonidae). All are specific on *P. xylostella*. In Ontario, Canada, *D. insulare* was considered most important except during diamondback moth population outbreaks, when the other species assumed greater importance. *D. insulare* was also important in California, USA. Nectar produced by wildflowers is important in determining parasitism rates by *D. insulare*. Egg parasites are unknown. Fungi, granulosis virus, and nuclear polyhedrosis virus sometimes occur in high-density diamondback moth larval populations.

A large proportion of young larvae is often killed by rainfall. However, an important factor determining population trends is reported to be adult mortality. Adult survival was thought to be principally a function of weather, although this hypothesis has not been examined rigorously.

Damage

Damage is caused by larval feeding. Although the larvae are very small, they can be quite numerous, resulting in complete removal of foliar tissue except for the leaf veins. This is particularly damaging to seedlings, and may disrupt head formation in cabbage, broccoli, and cauliflower. The presence of larvae in florets can result in complete rejection of produce, even if the level of plant tissue removal is insignificant.

Diamondback moth was long considered a relatively insignificant pest. Its impact was overshadowed by such serious defoliators as imported cabbageworm, *Pieris rapae* (Linnaeus), and cabbage looper, *Trichoplusia ni* (Hübner). However, in the 1950s the general level of abundance began to increase, and by the 1970s it became troublesome to crucifers in many areas. Although this shift in abundance was attributed to increased availability of alternate weed hosts or destruction of parasitoids, insecticide resistance was suspected to be the major factor responsible for the increased problem. This was confirmed in the 1980s as pyrethroid insecticides began to fail, and soon thereafter virtually all insecticides were ineffective. Relaxation of insecticide use, and particularly elimination of pyrethroid use, can return diamondback moth to minor pest status by favoring survival of parasitoids.

Management

Populations are usually monitored by making counts of larvae, or by the level of damage. In Texas, USA, average population densities of up to 0.3 larvae per plant are considered to be below the treatment threshold. In Florida and Georgia, treatment is recommended only when damage equals or exceeds one hole per plant. When growers monitor fields and subscribe to these treatment thresholds rather than trying to prevent any insects or damage from occurring in their fields, considerably fewer insecticide applications are needed to produce a satisfactory crop. Pheromone traps also can be used to monitor adult populations, and may predict larval populations 11–21 days later. However, because of variation among locations, each crop field requires independent evaluation.

Protection of crucifer crops from damage often requires application of insecticide to plant foliage, sometimes as frequently as twice per week. However, resistance to insecticides is widespread, and includes most classes of insecticides including some *Bacillus thuringiensis* products. Rotation of insecticide classes is recommended, and the use of *B. thuringiensis* is considered especially important because it favors survival of parasitoids. Even *B. thuringiensis* products should be rotated, and current recommendations generally suggest alternating the *kurstaki* and *aizawa* strains because resistance to these microbial insecticides occurs in some locations. Mixtures of chemical insecticides, or chemicals and microbials, are often recommended for diamondback moth control. This is due partly to the widespread occurrence of resistance, but also because pest complexes often plague crucifer crops, and the insects vary in susceptibility to individual insecticides.

Sex pheromone, although not usually considered to be an insecticide, can also be used as a chemical crop protectant. Continuous release of pheromone has been investigated as a technique to suppress diamondback moth mating activity. The number of insecticide treatments can be reduced from 13 to 15 to only 3 per crop cycle when crops are grown in the continuous presence of diamondback moth pheromone.

Rainfall has been identified as a major mortality factor for young larvae, so it is not surprising that crucifer crops with overhead sprinkle irrigation tend to have fewer diamondback moth larvae than drip or furrow-irrigated crops. Best results are obtained with daily evening applications.

Crop diversity can influence abundance of diamondback moth. Larvae generally are fewer in number, and more heavily parasitized, when crucifer crops are interplanted with another crop or when weeds are present. This does not necessarily lead to reduction in damage, however. Surrounding cabbage fields with two or more rows of more preferred hosts such as collard and mustard can delay or prevent the dispersal of diamondback moth into cabbage crops.

Crucifer transplants are often shipped long distances prior to planting, and diamondback moth may be included with the transplants. In the USA, many transplants are produced in the southern states, and then moved north as weather allows. Cryptic insects such as young diamondback moth larvae are sometimes transported, and inoculated in this manner. The transport of insecticide-resistant populations also may occur. Every effort should be made to assure that transplants are free of insects prior to planting.

Crucifer crops differ somewhat in their susceptibility to attack by diamondback moth. Mustard, turnip, and kohlrabi are among the more resistant crucifers, but resistance is not as pronounced as it is for some other cabbage-feeding Lepidoptera. Varieties also differ in susceptibility to damage by diamondback moth, and a major component of this resistance is the presence of leaf wax. Glossy varieties, lacking the normal waxy bloom and therefore green rather than grayish green, are somewhat resistant to larval feeding. Larvae apparently spend more time searching, and less time feeding, on glossy varieties.

► Crucifer Pests and their Management
► Vegetable Pests and their Management

References

Bach CE, Tabashnik BE (1990) Effects of nonhost plant neighbors on population densities and parasitism rates of the diamondback moth (Lepidoptera: Plutellidae). Environ Entomol 19:987–994

Biever KD, Boldt PE (1971) Continuous laboratory rearing of the diamondback moth and related biological data. Ann Entomol Soc Am 64:651–655

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, CA, 729 pp

Harcourt DG (1955) Biology of the diamondback moth, *Plutella maculipennis* (Curt.) (Lepidoptera: Plutellidae), in eastern Ontario. Report of the Quebec Society for the Protection of Plants, Report No. 37, pp 155–160

Harcourt DG (1957) Biology of the diamondback moth, *Plutella maculipennis* (Curt.) (Lepidoptera: Plutellidae), in eastern Ontario. II. Life-history, behaviour, and host relationships. Can Entomol 89:554–564

Harcourt DG (1960) Biology of the diamondback moth, *Plutella maculipennis* (Curt.) (Lepidoptera: Plutellidae), in eastern Ontario. III. Natural enemies. Can Entomol 92:419–428

Harcourt DG (1961) Design of a sampling plan for studies on the population dynamics of the diamondback moth, *Plutella maculipennis* (Curt.) (Lepidoptera: Plutellidae). Can Entomol 93:820–831

Harcourt DG (1962) Design of a sampling plan for studies on the population dynamics of the imported cabbageworm, *Pieris rapae* (L.) (Lepidoptera: Pieridae). Can Entomol 94:849–859

Harcourt DG (1963) Biology of cabbage caterpillars in eastern Ontario. Proc Entomol Soc Ontario 93:61–75

Talekar NS, Yang HC, Lee ST, Chen BS, Sun LY (eds) (1985) Annotated bibliography of diamondback moth. Asian Vegetable Research and Development Center, Taipei, Taiwan, 469 pp

Diamondback Moths (Lepidoptera: Plutellidae)

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Diamondback moths, family Plutellidae, include 386 species worldwide; actual fauna probably exceeds 600 species. There are four subfamilies (Ypsolophinae are erroneously considered a family by some): Ypsolophinae, Plutellinae, Scythropiinae, and Praydinae. The family is part of the superfamily Yponomeutoidea in the section Tineina, subsection Tineina, of the division Ditrysia. Adults small to medium size (7–55 mm wingspan), with head usually smooth-scaled; haustellum naked; labial palpi porrect (rarely upcurved); maxillary palpi 4-segmented (rarely 1–2-segmented); antennae sometimes thickened at middle. Wings elongated, sometimes with longer fringes (Fig. 46) on hindwings, and forewings sometimes appearing apically falcate due to fringe arrangement. Maculation varied but generally subdued, with various markings or bands, but a few are colorful. Adults mostly nocturnal or crepuscular, but some are diurnal. Larvae are leaf skeletonizers, but most remain unknown biologically. Hosts include different plant groups, but many are on Cruciferae. The main economic species, the diamondback moth from Europe, gives the family its common name. Several other economic species are known, particularly in the genus *Prays* (Praydinae are often classified in Yponomeutidae, but belong in Plutellidae).

Diamondback Moths (Lepidoptera: Plutellidae), Figure 46 Example of diamondback moths (Plutellidae), *Plutella xylostella* (Linnaeus) from Taiwan.

References

Agassiz DJL (1996) Yponomeutidae. In: Emmet AM (ed) The moths and butterflies of Great Britain and Ireland, vol 3, pp 39–114, pl 9–11

*Meyrick E (1914) Plutellidae. In: Lepidopterorum Catalogus, vol 19. W. Junk, Berlin, pp 1–64 [part]

Moriuti S (1964) Studies on the Yponomeutidae (VIII). Ypsolophus (Lepidoptera: Plutellidae) of Japan. Kontyu 32:197–210, pl 7

Moriuti S (1977) Yponomeutidae s. lat. (Insecta: Lepidoptera). In: Fauna Japonica. Keigaku, Tokyo, 327 pp, 95 pl

Zagulajev AK (1981) Plutellidae. In: Identification keys to insects of European Russia, vol 4, part 2: Lepidoptera. Academie Nauk [in Russian], St. Petersburg, pp 359–397

Diamphipnoidae

A family of stoneflies (order Plecoptera).

► Stoneflies

Diapause

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There is practically no corner of Earth that has not been colonized by insects. The most remarkable aspect of this extremely varied environmental adaptation is the capacity of insects to survive adverse or extreme environmental conditions. What kind of strategy for survival do these organisms possess to withstand harsh North American winters or scorching tropical conditions?

Most people associate the terms "hibernation" with cold winter conditions and "aestivation" with hot summer conditions. Until the end of the nineteenth century these two terms were generally used to describe seasonal environmental adaptations by all animal forms. In 1893, the German entomologist Wheeler coined the word "diapause" to describe a period of immobility during the embryonic development of an insect. He had noticed that insect embryos rotate within the egg shell, first in a clockwise and then, in a counterclockwise direction. The pause between these two rotations was reported as diapause.

The use of this new term was extended by Hennéguy in 1904 to all the stages of an insect's life cycle where there is an arrest in their development. Consequently, insects may exhibit embryonic (or egg), larval, pupal and adult diapause. Simply stated then, diapause is a state of arrested development. However, it is a fairly complex phenomenon which has been expertly used by insects to colonize various environmental niches.

To understand the specificity of diapause, it has first to be compared not only with hibernation and aestivation, but also with what is known as "dormancy." This general term is actually applicable to all situations where a living organism (plant or animal) is in a state of quiescence or torpor. Dormancy refers to a seasonably recurring period in the life of an organism during which growth, development, and reproduction are suppressed. Houseflies exhibit cold torpor or dormancy in the winter. When conditions warm up, they become active again.

Strictly speaking, the word hibernation describes a mammalian physiological adaptation to winter. Bears hibernate and do so as a result of specific physiological adjustments. During their hibernation they have short wake-up periods. Unfortunately, many books and other publications talk about hibernating insects when they actually mean overwintering insects in a state of diapause or torpor. The distinction between hibernation and diapause will become clearer as we further describe the latter.

One hundred years after Hennéguy we now know that diapause is: (i) a photoperiodically controlled phenomenon; (ii) a temperature-dependent syndrome; and (iii) a phenomenon subject to dietary, hormonal and genetic influences.

A Photoperiodically Controlled Phenomenon

Every single day of the year living things experience an alternation of light and darkness. This is referred to as the photoperiod: a "photophase" (light), and a "scotophase" (darkness). Many physiological functions are directly affected by this daily switching of light and dark because all organisms possess what are known as biological clocks, i.e., systems capable of registering changes in light intensity and reacting accordingly. Each living tissue, therefore, possesses an environmental periodicity which allows organisms to perform functions with a selective advantage, at the right time.

Insects have a photoperiodic counter that seems to accumulate successive long day/short night or short day/long night cycles and that determine when is the appropriate time to prepare for winter or adverse summer conditions. Therefore, using the photoperiod changes, they can anticipate adverse seasonal conditions, and undergo physiological and behavioral adjustments to withstand environmental extremes. Upon receipt of the appropriate signals, they can search for a convenient site to overwinter or aestivate in a state of diapause, or they can migrate to a more favorable climate.

Most summer-active insects like the European corn borer, *Ostrinia nubilalis*, respond to a decreasing photophase (the shorter days of late summer or early fall) to enter diapause. Others like the European pine sawfly, *Neodiprion sertifer*, have both a winter diapause in the egg stage and a summer diapause in the cocoon stage. The egg diapause is triggered by decreasing photophases while the summer diapause is brought about by the increasing photophases of early summer. An interesting third type of photoperiodically controlled diapause is exhibited by the Colorado potato beetle, *Leptinotarsa decemlineata*, an insect capable of entering its adult diapause under all photoperiod conditions except a narrow window of long photophases.

The insects mentioned above have a facultative diapause: under laboratory conditions one can modify photoperiod regimes and prevent diapause from occurring altogether. This becomes very useful when large numbers of insects are required, on a continual basis, for experimental purposes, or for biological control programs.

But there are insects whose diapause is obligatory. Whatever the photoperiod or other environmental conditions, they always enter diapause at a specific time of their life cycle. This is the case with the cinnabar moth, *Tyria jacobae*, an important biological control agent of the weed tansy ragwort, which always enters diapause in the pupal stage, even under controlled laboratory conditions which would prevent diapause in other species.

There is a definite time period over which photoperiod acts: the photosensitive and the photoresponsive stages. These may occur within the developmental interval at which diapause sets in (e.g., in the larval stage), or may precede the instar during which diapause begins (e.g., a photosensitive larva with a pupa in diapause). According to the late professor Stanley Beck, who has contributed significantly to our understanding of how insects respond to light and photoperiods, "the insect accumulates daily photoperiodic input until the required number of inductive photoperiods results in diapause determination."

A Temperature-Dependent Syndrome

While photoperiod is the primary regulator of diapause induction, temperature and other factors may modify the diapause-regulating role of light/darkness alternation. Some authors consider that, for some species, temperature is the major diapause-inducing factor. The influence of temperature is exerted not only for the onset of diapause, but also throughout the duration of the phenomenon and its termination.

1. Temperature normally modifies the insect's response to diapause-inducing photoperiods. In long-day insects (such as the European corn borer), low temperatures tend to promote larval diapause while high temperatures tend to prevent it;
2. Below some threshold temperatures (e.g., 15°C), a high incidence of pupal diapause will be observed in other species if the larvae are continually maintained at such temperatures, indicating that the photoperiod primary effect has been overrun;
3. Temperature is definitely critical for diapause maintenance. It actually regulates what is known as diapause development, i.e., the sequence of physiological events characteristic of the time spent in diapause;
4. Temperature can be an active diapause-terminating stimulus. In the banded woollybear, *Pyrrharctia isabella*, a minimum chilling period is required before the larva will come out of diapause;
5. Temperature plays a major role in regulating the breaking of diapause. A minimum temperature threshold must be reached and maintained to ensure that development will proceed at the end of diapause.

It should be noted that thermoperiods, i.e., the alternation of high/low temperature regimes (e.g., 14 h at 25°C and 10 h at 10°C) may enhance or diminish the effect of diapause-inducing photoperiod. Thermoperiodic induction curves fit photoperiodic induction curves almost exactly.

Influence of Food

Diet may act as a diapause-regulating factor, particularly in aestival and imaginal (adult) diapauses. The older leaves of potato plants help induce adult diapause of Colorado potato beetle, while the older needles of pines seem to favor the incidence of prolonged diapause in sawflies. Prolonged diapause is a form of diapause that lasts more than a year. The jack pine sawfly, *Neodiprion swainei*, has been known to stay in diapause in the cocoon stage for up to 7 years.

While the food available prior to diapause can be a factor in the induction, maintenance and termination of diapause, it must be recognized that the prevailing temperature conditions, photoperiods (particularly in imaginal diapause) and genetic factors all act concurrently.

Genetic Control of Diapause

Since there are different strains of the same insect species that exhibit obligatory or facultative diapause (e.g., the banded woollybear), it is obvious that diapause is a genetically controlled phenomenon. This is still one of the least studied and understood aspects of diapause. But as molecular techniques work their way into the study of insect development, the genetic mechanisms governing diapause characteristics and expression will be better understood.

Genes controlling the number of generations per year (voltinism) are no doubt associated with the presence or absence of diapause. The expression of such genes is subject to the prevailing environmental conditions, which explains why, for instance, only the last of two or three generations of the European corn borer within the same year enters diapause.

It is currently believed that several genes determine the insect's response to the length of the critical photoperiod, the percentage of individuals entering diapause, and the duration of diapause. This could be a case of supergenic inheritance where the polygenes controlling diapause are inherited as a supergene. The quantitative aspects of diapause (duration of critical photoperiods, percentage of individuals entering diapause, length of the diapause period) are considered to be under polygenic control.

Hormonal Aspects of Diapause

The development and metamorphosis of insects is under the control of hormones secreted by specific organs and cells. Diapause being such a periodically occurring phenomenon, and because it is synonymous to arrested development, it is natural to think of the immediate cause of diapause as a change in endocrine status associated or not with the presence of a diapause hormone.

Inactivation of the brain hormone, which controls all the other hormonal events in insects, is one of the ways in which diapause is triggered, particularly in larvae and pupae, making it, in this case, an endocrine deficiency syndrome. The larva then exhibits reduced metabolic rate, reduced water content, increased fat, and behavioral changes necessary for a period of dormancy. But it is also believed that, once the phenomenon has been initiated, a cepahalic factor maintains the diapause state in some insects.

But diapause can also be the result of modifications in the titre and activity level of ecdysones and juvenile hormone. There are examples of retention of a functional endocrine system when larvae undergo molts in a diapause-maintaining photoperiod, changing from a spotted form to an immaculate form, as illustrated by the sugarcane borer, *Diatrea saccharalis*.

In cases of embryonic diapause, a hormone from the subesophageal ganglion has been reported to be secreted by the adult female and passed on to the embryo which enters diapause. This has been particularly demonstrated in the silkworm, *Bombyx mori*.

While embryonic, larval, and pupal diapauses affect the whole organism, adult diapause is an organ-related phenomenon: the reproductive system is turned off. This cessation of gamete production and of reproductive activity has been referred to as "gonotrophic dissociation." The expression "reproductive diapause" is also used. The brain hormone fails to stimulate the corpora allata which secrete juvenile hormone. In adults juvenile hormone plays a major role in gametogenesis. If juvenile hormone is applied topically to adults in diapause, the production of eggs and sperm is resumed.

In the absence of a specific diapause hormone in the great majority of insects, one should not be surprised that there is a great diversity of opinion in the scientific literature regarding the role of ecdysones, juvenile hormone and brain hormone in the onset maintenance and termination of diapause. But it is also a reflection of the tremendous biological variety characteristic of the insect world.

A comprehensive description and understanding of diapause goes far beyond the simple definition of the phenomenon as a state of arrested development. This system of anticipatory regulation has provided insects, through their evolution, with the tools necessary to exploit a diversity of environments which, to this day, remain hostile to other forms of life. It is therefore appropriate to end with the definition provided by Nechols et al. (1999): diapause is a hormonally mediated state of low metabolic activity associated with reduced morphogenesis, increased resistance to environment extremes, and altered or reduced behavioral activity.

► Ecdysteroids
► Juvenile Hormone
► Metamorphosis
► Prothoraciotropic Hormone
► Embryogenesis

References

Beck SD (1980) Insect photoperiodism, 2nd edn. Academic Press, New York, NY

Danks HV (1987) Insect dormancy: an ecological perspective. Biological Survey of Canada (Terrestrial Arthropods), Ottawa, Canada

Nechols JR, Tauber MJ, Tauber CA, Masaki S (1999) Adaptations to hazardous seasonal conditions: dormancy, migration, and polyphenism. In: Huffaker CB, Gutierrez AP (eds) Ecological entomology, 2nd edn. Wiley, New York, NY, pp 159–200

Saunders DS (1982) Insect clocks, 2nd edn. Pergamon Press, Oxford, UK

Tauber MJ, Tauber CA, Masaki A (1986) Seasonal adaptations of insects. Oxford University Press, New York, NY

Diapause Hormone

A hormone that induces the tendency of insects to enter diapause. In silkworms, the diapause hormone is present in the pupal stage of females, and causes the eggs to diapause after they are deposited.

► Diapause

Diaprepes Root Weevil, *Diaprepes abbreviatus* (L.) (Coleoptera: Curculionidae)

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The tropical root weevil *Diaprepes abbreviatus* was described by Carl Linnaeus as *Curculio abbreviatus* in the tenth edition of his *Systema Naturae* in 1758 from specimens collected in the West Indies. *Diaprepes abbreviatus* is found on Puerto Rico and Hispaniola and in the Lesser Antilles from Grenada and Barbados in the south to the Virgin Islands in the north, Hispaniola, and possibly Cuba. The species appears to be absent from Trinidad and Tobago, and from Jamaica. *Diaprepes abbreviatus* was discovered in Orange County, Florida, USA, in 1964. Since then, this highly polyphagous weevil has established in 23 Florida counties. In 2000, *D. abbreviatus* was found in a citrus grove in the Rio Grande Valley of Texas. In 2005, it was discovered infesting ornamental palms in an urban area of Orange County, California, USA, and subsequently found in Los

Angeles County and San Diego County. Several putative species of *Diaprepes* that vary in coloration and elytral striation have been synonymized with *D. abbreviatus*. A questionable species, *D. rohrii*, is reported only from St. Croix, U.S. Virgin Islands, while *D. abbreviatus* is apparently absent from that island. *Diaprepes rohrii* may simply be another color morph of *D. abbreviatus*. By 1933, it was recognized that the various forms of *Diaprepes* found throughout Hispaniola, Puerto Rico, and the Lesser Antilles were most likely a single species, fundamentally similar both structurally and behaviorally. Puerto Rico is the most likely center of origin because of the high degree of distinct, stable phenotypes on the island.

Host Plants

Some of the earliest mentions of *D. abbreviatus* refer to it as a common pest of sugarcane as early as the latter half of the nineteenth century on the island of Barbados. The weevil has an extremely wide host range and has been reported to attack over 200 plants including economically important crops from diverse botanical families (e.g., banana, bean, cacao, cassava, citrus, corn, cotton, mango, onion, peanut, pecan, potato, sugarcane, sweet potato, yam), ornamentals (palms and many others), and exotic weeds in the U.S. (e.g., kudzu and Brazilian pepper). In 1900, *D. abbreviatus* was reported in large numbers on Puerto Rico attacking guava and young coffee plants. In 1915, it was reported to be generally distributed over the island of Puerto Rico but causing particular damage to sugarcane. In Florida, *D. abbreviatus* has become a principal pest of orange and grapefruit and only low levels of host plant resistance within sexually compatible citrus germplasm have been reported. Its ability to infest ornamental plants in commercial nurseries, especially species of palm produced in southern Florida for interstate shipment, apparently accounts for its recent appearance in Texas and California.

Natural Enemies

The toad, *Bufo marinus*, was imported to Puerto Rico from Barbados in 1920 and again from Jamaica in 1924 to control white grubs (*Phyllophaga* spp.) and *D. abbreviatus*. It was alleged at the time that the introduction of the mongoose for control of rats resulted in an increase of populations of *D. abbreviatus*. Although the mongoose failed to control its intended victims, apparently it was more effective at destroying species of reptiles and birds that preyed on insects. More recent efforts at classical biological control in Florida introduced five species of egg parasitoids from the Caribbean for control of *D. abbreviatus*. Two eulophid species (*Quadrastichus haitiensis* Gahan, an endoparasitoid from Puerto Rico, and *Aprostocetus vaquitarum* Wolcott, an ectoparasitoid from Dominican Republic) are considered to be established in parts of southern Florida. The trichogrammatid *Ceratogramma etiennei* Delvare from Guadeloupe failed to establish. Two species have been recently introduced: *Fidiobia dominica* Evans (Platygastridae) from Dominica and *Haeckeliania sperata* Pinto (Trichogrammatidae) from St. Lucia. While reports refer to percent parasitism of egg masses, there is little evidence to indicate that egg parasitoids have been effective in reducing economically damaging populations of *D. abbreviatus*. No parasitoid of adults or larvae has been reported.

Species of entomopathogenic nematodes (*Steinernema riobrave* and *Heterohabditis indica*) are commercially available for use in Florida citrus to control *D. abbreviatus*. Efficacy of nematode treatments is associated with soil characteristics, with better control reported on lighter, sandy soils compared with heavier, poorly drained soils. Nematodes are formulated in products for delivery in irrigation water (nemagation).

Life Cycle and Description

The entire life cycle (egg to egg) can occur in approximately 154 days under ideal conditions but may be considerably longer in the field where temperature and moisture conditions vary. Generations overlap, with adults emerging throughout the year in the tropics and southern Florida. In central Florida, adults are absent during the coldest months. No evidence of diapause has been found, although larvae can endure long periods of low soil moisture. Emergence of adults in the Caribbean was observed to occur following onset on spring rains. In Florida, adults are most active during the period of high rainfall and temperature from June through October. Northern expansion of this species appears to be constrained by winter soil temperatures below 12°C for periods >30 days.

Eggs

Eggs are laid in masses of approximately 100 between leaf surfaces apposed and cemented in place by the female. Eggs complete development in approximately 7 days at 26°C with a lower developmental threshold of 12°C and an upper thermal limit between 30 and 32°C. The niche created by the female apparently provides conditions of temperature and humidity required for egg development.

Larva

Neonate larvae fall to the ground where they disperse and burrow into the soil. The lower threshold for development of neonates was estimated to be 15°C. Larval development to pupation occurs in approximately 125 days at 26°C. At the onset of pupation, larvae reared on artificial diet can weigh as much as 600 mg, depending on conditions of temperature and humidity experienced during larval development.

Pupa

The pupa creates a chamber in the soil by means of a writhing motion. Pupation is completed in approximately 3 weeks at 26°C. Initially, the exarate pupa is callow, becoming darker as pupation proceeds.

Adults

Adults vary in size between approximately 1 and 2.5 cm in length. Mean male length and mass are less than mean female size. Adults produced on artificial diet vary in weight from about 250 –350 mg. Males engage in prolonged bouts of guarding behavior and can remain mounted and intromitted for hours. There is anecdotal evidence for adult aggregation, presumably mediated by an as yet undiscovered pheromone. *Diaprepes* adults are largely black but covered with colored scales that range from ashy white to dull orange and bright yellow. Distinct phenotypes occur within defined geographic regions, marked by varying colors and patterns of elytral stripes. The length and number of raised ridges on the elytra devoid of scales varies between populations. On St. Lucia and Puerto Rico, there is subspecific variation in color and elytral ridges linked by intergrades. On Puerto Rico, western lowland populations of *D. abbreviatus* tend to have whitish elytra. They are brownish in southern and eastern lowlands including Culebra and Vieques. In the western central mountains, there is a larger phenotype often with yellow elytra and an additional strip per elytron; in the eastern mountains, a smaller, grayish, sometimes greenish variety prevails. On Barbados, the weevil was described in 1912 as pale-green with dark, bronze stripes. Emergent adults require 24–48h to fully sclerotize within the pupal chamber in the soil. Initially, adults possess a deciduous mandibular spur that likely facilitates adult emergence from the soil and is subsequently lost. Females have been estimated to produce on the order of 5,000 eggs over the adult lifespan that may be as long as 3–4 months in the field. Females cease oviposition at temperatures below 15°C.

Damage

Diaprepes abbreviatus was described in 1987 as the single most serious insect pest of agriculture, horticulture, and silviculture on Puerto Rico. In the 1930s, *D. abbreviatus* rivaled the sugarcane borer, *Diatraea saccharalis*, as the most serious pest of sugarcane in Barbados. The weevil, an apparently indigenous insect, did not infest sugarcane for centuries despite its extensive cultivation on Barbados. Infestations on sugarcane and sweet potatoes were not observed prior to 1901. By 1904 it had become fairly abundant, but not serious until 1909, and since that date it has increased in virulence every year. In 1922, loss was estimated at 3.5 tons and in 1929 at 5–6 tons of cane/acre on Barbados. Adult feeding damage consists of notching of leaf margins. Adult damage to citrus is considered minor. Larval damage to citrus is a function of direct damage to roots and secondary infection of wounds by pathogenic fungi, particularly *Phytophthora* spp. For this reason, damage is more severe in poorly drained soils conducive to fungal pathogens. While larvae remain external to citrus roots, they bore into and inhabit subterranean parts of sugarcane, sweet potato, potato, cassava, and other plants with tuberous roots or tubers.

Management

Sampling

A modified Tedders trap, consisting of a base of two interlocking vanes topped by a mesh receptacle has been used to estimate relative adult density. Since no pheromone or attractant is known for this species, such traps are inefficient and yield only very small numbers of weevils. The trap is based on the tendency for newly emerged adults to walk over the soil surface to dark vertical shapes. A more productive, active sampling method uses a beat sheet to sample individual trees.

Insecticides

Chlorinated hydrocarbon and other highly persistent insecticides were used as barriers to neonate weevils, for control of larvae in the soil, and as adulticides until the removal of such materials from the market. The waning of the era of persistent insecticides coincided with the introduction of *D. abbreviatus* into the United States. Several modern insecticides are effective against adults. However, because of the short residual effectiveness of foliar sprays and the prolonged period of adult emergence, adulticides may only be effective when used frequently over large areas. Porous soils and a vulnerable water table in Florida limit the use of soil insecticides on citrus. At least two species of entomopathogenic nematodes are marketed as bioinsecticides for this species.

Cultural Practices

Publications from the Caribbean in the early 1900s recommended pulling cane stumps after harvest to expose larvae and suggested "a few head of poultry" be kept on hand during the operation. It was suggested that fully developed larvae disperse from the cane stools in search of moist soil to pupate, sometimes moving a considerable distance in the soil. Large numbers of adults emerged after the first heavy rains of May/June. In 1939, a system of cash payments was advocated for collection and destruction of adult weevils. It was noted that continuous cropping of cane increased damage from *Diaprepes*. In 1911, school children on Barbados, St. Kitts and Antigua were enlisted to collect and destroy adults – 30,000 were captured and destroyed on one estate during 1 month. Adult weevils were reported from pigeon pea, corn, bean, and sweet potato (considered an especially good host for the weevil). Cooperative campaigns over a decade to reduce populations on Barbados were deemed successful due to the fact that the island is small, densely populated, and had a minimal amount of uncultivated land.

Manual collection of newly emerged adults, especially from cane fields, was facilitated by planting attractive host plants such as pigeon pea (*Cajanus cajan*) or other fast-growing shrubs or trees on field borders. A "bare-root method" has been suggested wherein soil is removed from the roots at the base of citrus stems thereby limiting access by larvae to the crown and thereby reducing the possibility of girdling. Kaolin-based particle films have shown some promise in reducing oviposition in field trials in Florida.

Host Plant Resistance

Only low levels of plant resistance to *D. abbreviatus* have been reported from sexually compatible citrus genotypes. Higher levels of resistance occur in related citroid fruit trees and some nonhost legumes. Recently, active isolates of *Bacillus thuringiensis* (Bt) have been discovered, raising the possibility of a genetically engineered rootstock transformed to express a *Diaprepes*-active toxin gene.

Biological Control

The toad *Bufo marinus* was imported to Puerto Rico from Barbados in 1920 and again from Jamaica in 1924 to control white grubs (*Phyllophaga* spp.) and *D. abbreviatus*. Two species of egg parasitoids have been established and two other species have recently been released in southern Florida but are constrained by prey availability during the winter months at more northern latitudes. They are not expected to establish in central Florida, Texas, or California unless periodic releases are made. Entomopathogenic nematodes are the only other biological control methods currently used.

References

Hall DG, Peña J, Franqui R, Nguyen R, Stansly P, McCoy C, Lapointe SL, Adair RC, Bullock B (2001) Status of biological control by egg parasitoids of *Diaprepes abbreviatus* (Coleoptera: Curculionidae) in citrus in Florida and Puerto Rico. BioControl 46:61–70

Lapointe SL (2000) Thermal requirements for development of *Diaprepes abbreviatus* (Coleoptera: Curculionidae). Environ Entomol 29:150–156

Lapointe SL, Bowman KD (2002) Is there meaningful plant resistance to *Diaprepes abbreviatus* (Coleoptera: Curculionidae) in citrus rootstock germplasm? J Econ Entomol 95:1059–1065

Lapointe SL, McKenzie CL, Hall DG (2006) Reduced oviposition by *Diaprepes abbreviatus* (L.) (Coleoptera: Curculionidae) and growth enhancement of citrus by Surround particle film. J Econ Entomol 99:109–116

Shapiro DI, McCoy CW (2000) Virulence of entomopathogenic nematodes to *Diaprepes abbreviatus* (Coleoptera: Curculionidae) in the laboratory. J Econ Entomol 93:1090–1095

Weathersbee AA, III Lapointe SL, Shatters RG, Hall DG (2006) Activity of *Bacillus thuringiensis* isolates producing novel endotoxins as measured by an innovative bioassay against neonate *Diaprepes abbreviatus* (Coleoptera: Curculionidae). Fla Entomol 89:441–448

Diaprepes Weevil, *Diaprepes abbreviatus* (Linnaeus) (Coleoptera: Curculionidae)

Best know as a citrus pest, this weevil has a wide host range.

► Citrus Pests and their Management
► Diaprepes Root Weevil

Diapriidae

A family of wasps (order Hymenoptera). See also.

► Wasps, Ants, Bees and Sawflies

Diaspididae

A family of insects in the superfamily Coccoidae (order Hemiptera). They sometimes are called armored scales. See also,

► Bugs

Diastatidae

A family of flies (order Diptera). They commonly are known as diastatid flies.

► Flies

Diastatid Flies

Members of the family Diastatidae (order Diptera). See also,

►Flies

Diatomaceous Earth

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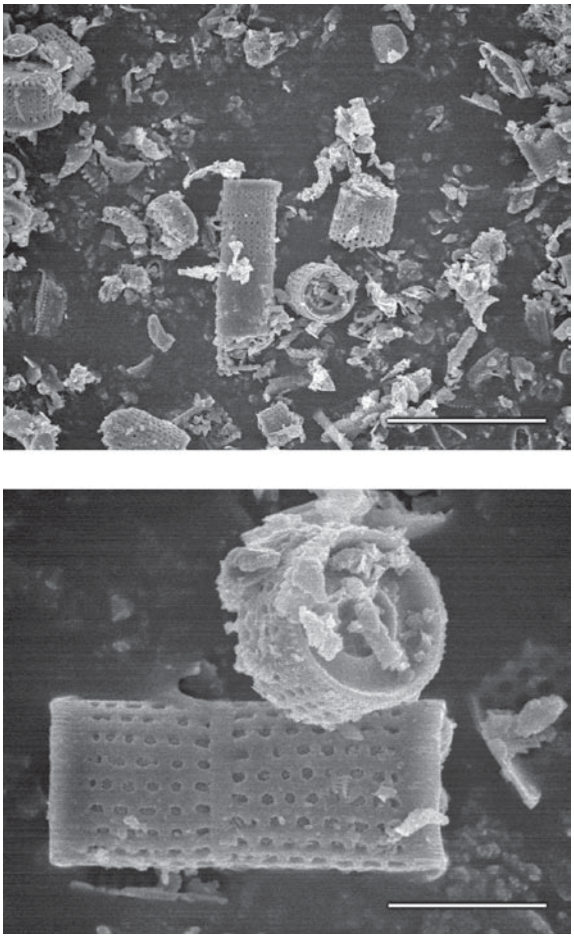
Diatoms are microscopic algae that live in both fresh and saltwater environments. They become impregnated with silicon from their environment as they grow, leaving a "skeleton" consisting of silicon dioxide (SiO_2) when they die. These diatoms are small. Many elongate forms are only 10–15 microns in length and 5 microns in diameter; others are spherical. They usually are free-floating, and a major component of oceanic plankton. They can be extremely numerous, and comprise the most important primary producers for small animal life in oceans. It is estimated that 25% of all organic carbon fixation (conversion of carbon dioxide and water into sugars by photosynthesis) on earth occurs in oceans due to diatoms. They also are a major source of oxygen. Most are not consumed, of course, and when the algae perish, their bodies accumulate, leaving silica deposits of up to 300 m thick in some areas. These compressed silicaceous deposits, consisting of 85–95% silicon dioxide, are mined for various industrial purposes such as abrasives for polishing, brightening agents in paint, and as filtering or insulating agents.

Why is Diatomaceous Earth Insecticidal?

Diatomaceous earth (also called diatomite), dust, and other small particulate matter have been used for thousands of years to protect stored grain from insects. Diatomaceous earth and dust kill insects by absorbing the waxy fats and oils from the epicuticle of insects. If sufficient waxy material has been absorbed, the insect cannot maintain proper water balance, and perishes due to dehydration. To a lesser degree, diatomaceous earth affects insects through abrasion, though this attribute is very compatible with the effects of oil sorption. Lastly, some repellency effects have been documented, though this is the least important attribute.

Environmental Interactions

Diatomaceous earth and dust are more insecticidal in arid environments. Moist grain (greater than about 15%) or humid storage conditions (> about 70%) can negate much of the benefit due to wax loss by insects. High temperatures enhance effectiveness of diatomaceous earth by increasing the rate of water loss. Insects also differ in their innate susceptibility; diatomaceous earth particles (Fig. 47) are more likely to adhere to hairy or rough-bodied species. Insects with these characteristics, and smaller species (with a large surface-to-volume ratio), or species with a thin epicuticle or thin wax coating, are more susceptible to death from diatomaceous earth. Insects that imbibe food in a liquid form (e.g., sucking insects or mites) are less likely to suffer the effects of diatomaceous earth than those that metabolize water from their food. Efficacy of diatomaceous earth interacts with high temperature (e.g., 50–60°C), but some insect species exposed to a combination of diatomaceous earth and high temperatures perish more rapidly than those exposed to diatomaceous earth and lower temperatures, whereas in other species exactly the opposite response is observed.



Diatomaceous Earth, Figure 47 Diatomaceous earth particles viewed with a scanning electron microscope; in the upper image, the bar at the lower right represents 30 microns; in the lower image, the bar represents 7.5 microns.

Variability Among Diatomaceous Earths

The size and shape of diatomaceous earth varies according to the dominant species living in the ocean or lake, and so the wax-absorption properties vary as well. Diatomaceous earth often possesses oil absorption values of about two to three times its own mass. The properties that define oil holding capacities are not well known, but particles of 45 microns or greater seem to be inferior. In addition to silicon dioxide, diatomaceous earth deposits may contain any of several contaminants, including aluminum, magnesium, iron, phosphorus, sulfur, salt, moisture, volcanic ash, clay, chert, and limestone. Diatomaceous earth products usually contain at least 90% silicon dioxide, however. Diatomaceous earth may be heated to high temperatures (called calcined diatomaceous earth) or left unheated (uncalcined); only uncalcined material is used as an insecticide. Aqueous solutions of sodium silicate can be dried and formulated into very light powders that are more effective (require less material); this is called silica aerogel. Silica aerogel, with its low density, is difficult to apply because it tends to float in the air, so is not often used. Diatomaceous earth is not flammable, is odorless, and is insoluble. Its color varies. Most deposits consist principally of amorphous silica, but a small proportion of crystalline silica occurs, and at a higher proportion in marine deposits.

What is Affected by Diatomaceous Earth?

Diatomaceous earth has been shown to kill ants, bedbugs, silverfish, caterpillars, crickets, termites, fleas, earwigs, beetles, ticks, mites and many other arthropods. However, the usual target is stored grain insects. *Cryptolestes* spp. are the most susceptible, followed by *Sitophilus*, and then by *Oryzaephilus*, *Rhyzopertha*, and *Tribolium* spp. Efficacy seems to be related to physical properties of the dust, rather than its chemical composition. As noted previously, high moisture levels reduce its effectiveness. Some diatomaceous earth formulations contain a low percentage of some other insecticide, commonly pyrethrum and piperonyl butoxide. Diatomaceous earth is usually applied as a dust, but sometimes as a water-based slurry. In addition to functioning as a grain protectant, diatomaceous earth is sometimes used to protect fabric and wood structures.

Safety

Diatomaceous earth is considered to lack acute or chronic health effects when consumed by mammals.

Sometimes diatomaceous earth is fed to livestock to control worms and other internal parasites. Thus, residues on food are not considered hazardous to humans. The known deleterious effects of diatomaceous earth derive from chronic inhalation of dust, as might occur among miners and processors. Amorphous silica is classified as not carcinogenic, but crystalline silica can cause lung problems. Applicators should be provided with protection of eyes, lungs, and skin. Slurry formulations also reduce the risk of inhalation.

References

Fields P, Korunic Z (2000) The effect of grain moisture content and temperature on the efficacy of diatomaceous earths from different geographical locations against stored-product beetles. J Stored Prod Res 36:1–13
Golub P (1997) Current status and future perspectives for inert dusts for control of stored product insects. J Stored Prod Res 33:69–79
Korunic Z (1998) Diatomaceous earths, a group of natural insecticides. J Stored Prod Res 34:87–97
Quarles W, Winn PS (2006) Diatomaceous earth alternative to stored product fumigants. IPM Practitioner 28(1/2):1–10

Dichotomous Keys

A system of using a series of statements about specimen-related characters to identify an unknown. The user is presented a series of two choices, and asked to choose the correct one (best fit), which leads to other paired choices, and eventually leads to the correct identification.

► Identification of Insects

Dicondylic Articulation or Joint

A joint with two points of articulation between the adjacent segments. Having two condyles.

► Condyle
► Legs

Dicot

A plant with seedlings having two cotyledons. Dicots (dicotyledenous plants) are broadleaf plants.

Dicteriadidae

A family of damselflies (order Odonata).

► Dragonflies and Damselflies

Dictyopharidae

A family of insects in the superfamily Fulgoroidae (order Hemiptera). They sometimes are called planthoppers.

► Bugs

Dictyoptera

The orthopteroid insects (crickets, katydids, grasshoppers, grylloblatids, stick insects, cockroaches, mantids, termites, and earwigs) have been divided into numerous groups, and one of these is called Dictyoptera. Dictyoptera is usually considered to be an order comprised of the mantids, cockroaches, and sometimes the termites. They seem to share a common origin, and have filiform antennae, are mandibulate, often are winged and have thickened forewings, possess concealed genitalia, and possess pronounced cerci. In one scenario, the Blattodea or Blattaria (cockroaches), Mantodea (mantids), and Isoptera (termites) are considered to be suborders. Some consider mantids and termites to be families of cockroaches, however. In another scenario, Dictyoptera is considered to be a superorder, with these same groups as orders rather than suborders. Though acknowledging the relatedness of these taxa, we treat the roaches, mantids, and termites as orders, and ignore the term Dictyoptera.

Differential Grasshopper, *Melanoplus differentialis* (Thomas) (Orthoptera: Acrididae)

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In North America, this grasshopper occurs widely in the central and western regions of the United States, and in northern Mexico; in Canada it occurs in southern Saskatchewan and British Columbia. Within the United States it is absent from the Atlantic and Gulf Coast region, except that it occurs in Pennsylvania, New Jersey, and Maryland. It is infrequent in the Pacific Northwest area. Also, within the large geographic area generally inhabited by differential grasshopper, it is rare in arid environments.

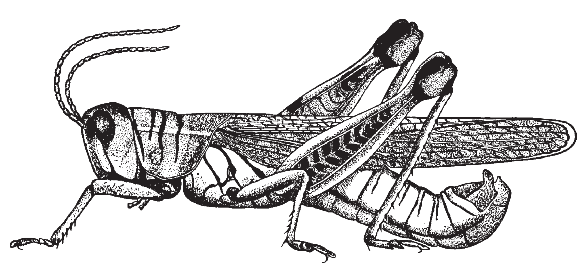
Life History

Melanoplus differentialis has a single generation annually, with the egg stage overwintering. This is a late-season species, with eggs hatching about 3 weeks after those of twostriped grasshopper, *Melanoplus bivittatus* (Say), and 2 weeks after *Melanoplus sanguinipes* (Fabricius). In Colorado, eggs hatch in June, usually within a 2-week period. Nymphs complete their development in July-August; adults are present from August-October.

The eggs are creamy white, yellowish, or light brown in color. They are elongate-cylindrical in shape, tapering to a blunt point at each end. The eggs are about 4–5 mm long and 0.85 mm in diameter. Eggs are clustered within an elongate, cylindrical pod consisting of 40–200 eggs arranged in four columns and held together by frothy material. The eggs are deposited in the soil, and the upper portion of the pod is plugged with additional froth. Eggs are normally deposited among the roots of grasses and weeds, especially along edges of fields, and in moist soil. Embryonic development occurs in the autumn after eggs are deposited, but the embryo enters diapause at about the point of 50% development, and must endure a period of cold before commencing growth.

The nymphs normally develop during the warmest period of the summer, and complete their development in about 30 days, though development times are extended if weather is cool. There are six instars, and the nymphs are not distinctive in appearance. First instars are greenish, yellowish or brownish with an indication of a black stripe on the outer face of the hind femora. Instars two through six are similar but possess a curved dark stripe extending from the back of the eye across the pronotum, and bordered below by a narrower white stripe. The black stripes on the femora are pronounced. The hind tibiae are light green or gray. The nymphs increase in body length from 5.3–6 mm in the first instar, to 5.2–6.8, 9.4–12.6, 12–14, 18–21.5, and 22–32 mm in instars 2–6, respectively. The number of antennal segments is 12, 14–17, 19–20, 21–22, 25–26, and 26 in instars 1–6, respectively.

The adults are fairly large grasshoppers, the males measuring 28–34 mm in length, the females 32–44 mm. They display more color variability than most grasshoppers. They may be principally brownish green, or yellow, or almost entirely black, though the yellow form is most abundant. The most distinctive feature of these grasshoppers is the row of black marks, arranged in herring-bone fashion (Fig. 48) on the outer face of the hind femora. These markings are not so evident in the infrequent black form, which instead bears four white blotches on its otherwise black hind femora.



Differential Grasshopper, *Melanoplus differentialis* (Thomas) (Orthoptera: Acrididae), Figure 48
Adult of differential grasshopper, *Melanoplus differentialis* (Thomas).

The forewings in all except the black form are uniform grayish or brownish; the hind wings in all forms are colorless. The males bear large, boot-shaped cerci.

Like many other grasshoppers, differential grasshopper tends to roost on elevated locations at night. This allows them to bask in the morning sun, and to assume activity early in the day. Bushes and other tall vegetation are favorite perches.

The host plants preferred by differential grasshopper are tall broadleaf plants such as those typically associated with fence rows, irrigation ditches, and fallow fields. It prefers plants in the family Compositae such as ragweed, *Ambrosia* spp.; sowthistle, *Sonchus asper*; sunflower, *Helianthus annuus*; and prickly lettuce, *Lactuca scariola*; though it will feed on other broadleaf plants such as kochia, *Kochia scoparia*; and smartweed, *Polygonum* sp.; and on such grasses as bermudagrass, *Cynodon dactylon*; slender oat, *Avena barbata*; barley, *Hordeum* sp.; and Johnsongrass, *Sorghum halepense*. In North Dakota alfalfa fields, differential grasshopper reportedly ate kochia, *Kochia scoparia*; quackgrass, *Agropyron repens*; squirreltail grass, *Hordeum jubatum*; bristly foxtail, *Setaria* spp.; and field bindweed, *Convolvulus repens*, in addition to alfalfa. On prairie, they ate mostly stickseed, *Lappula echinata*; wavyleaf thistle, *Cirsium undulatum*; quackgrass, *Agropyron repens*; and pepperweed, *Lepidium densiflorum*.

Crops sometimes injured include alfalfa, clover, corn, cotton, soybean, sugarbeet, timothy, and small grains such as barley and wheat. However, during periods of great abundance all crops are at risk because under such conditions virtually all green vegetation may be consumed.

Weather affects the distribution of differential grasshopper, but in a manner somewhat different from some other grasshopper species. Differential grasshopper is associated with dense vegetation, so it follows that it would thrive in areas with adequate moisture to support lush growth of plants. It is a common, and damaging, species on the eastern edge of the Great Plains, where rainfall is plentiful, and relatively infrequent along the drier western edge of this region. Sometimes, during periods of higher than normal precipitation, its abundance expands into areas of the Great Plains normally dominated by species better adapted to dry conditions, such as migratory grasshopper, *Melanoplus sanguinipes* (Fabricius). When weather returns to normal, however, migratory grasshopper resumes its status as the dominant species.

High levels of precipitation are not entirely advantageous for differential grasshopper. Precipitation during the warm months leads to outbreak of disease in differential grasshopper populations. This is a short-term response, and disease outbreaks occur only when grasshoppers are abundant. Differential grasshopper seems to be more susceptible to disease than some other species, including migratory grasshopper. Precipitation accompanied by cool weather during the hatching period is detrimental to differential grasshopper, as is the case for all grasshoppers, largely because it disrupts feeding during the critical early life of the grasshopper. The late onset of winter can favor grasshopper population increase because it allows adults additional time to produce eggs.

Damage

This species seemingly has benefited from agricultural practices more than most grasshoppers, with grasshopper survival increased by the abundance of weeds associated with crops, and the irrigation practices of western farms. It also readily exploits disturbed sites in cities and towns. Unlike some of the arid environment-loving species, its numbers and damage may increase following long-term increases in precipitation. The damage caused by differential grasshopper principally takes the form of leaf removal. Plants may be completely defoliated, or left ragged. Because this grasshopper tends to roost in elevated locations at night, where they may nibble while resting, trees and shrubs outside the normal dietary range are sometimes severely injured.

Management

Liquid formulations of insecticides are commonly applied to foliage to protect against damage. Because grasshoppers rarely develop in crops, but instead invade from weedy areas, it is often the edges of crop fields that are most injured. Therefore, application of insecticide to the borders of crop fields is often adequate to protect an entire field. It is even better to apply insecticides to the developing grasshopper populations in weedy areas before they move to crops. This not only minimizes damage to crop plants, but often results in younger grasshoppers being targeted for elimination. Younger grasshoppers are more susceptible to insecticides, with large nymphs and adults sometimes difficult to kill.

Application of insecticide-treated bait is an effective alternative to foliar treatments for *Melanoplus* spp. because these grasshoppers spend considerable time on the soil where they come into contact with baits. Bait formulations are bulky and more difficult to apply than liquid products, so they are less often used, but have the advantage of limiting exposure of crops to insecticide residue and of minimizing mortality of beneficial insects such as predators and parasitoids due to insecticide exposure. Also, the total amount of insecticide active ingredient necessary to obtain control is usually considerably less when applied by bait because the grasshoppers actively seek out and ingest the toxin. Finally, for relatively expensive products that must be ingested to be effective, such as microbial insecticides, baits are the most effective delivery system.

The attractant used most commonly for grasshopper bait is flaky wheat bran, though other products such as rolled oats are sometimes suggested. No additives, other than insecticide (usually 5% active ingredient), are necessary because the wheat bran alone is quite attractive to *Melanoplus* grasshoppers. Other additives such as sawdust, water, vegetable or mineral oil, molasses, amyl acetate, salt, or sugar have been suggested, but provide little or no additional benefit over dry bran. The bait should be broadcast widely to maximize the likelihood of grasshopper contact, and should be applied while grasshoppers are in the late instars because adults ingest less bait.

Elimination of weeds within, and adjacent to, crops is the most important cultural practice, and can have material benefit in preventing damage to crop borders. However, during periods of weather when grasshoppers become numerous they may move long distances and invade crops.

Tillage is an effective practice for destruction of eggs. Deep tillage and burial are required, shallow tillage having little effect. All the crop-feeding *Melanoplus* species deposit some eggs in crop fields, especially during periods of abundance, but it is fence row, irrigation ditch, field edge, and roadside areas that tend to be the favorite oviposition sites, so tillage is not entirely satisfactory unless other steps are taken to eliminate grasshopper egg pods from these areas that cannot be tilled. Though providing suppressive effects, deep tillage is not consistent with the soil and water management practices in many areas, so may not be a good option.

Row covers, netting, and similar physical barriers can provide protection against grasshoppers. This approach obviously is limited to small plantings, and can interfere with pollination. Also, grasshoppers are capable of chewing through all except metal screening, so this approach does not guarantee complete protection.

The natural enemies of differential grasshopper don't seem to offer much promise for effective suppression. The microsporidian pathogen *Nosema locustae* is well studied as a microbial control agent of *Melanoplus* spp. and is available commercially. It is fairly stable, and easily disseminated to grasshoppers on bait. However, its usefulness is severely limited by the long period of time that is required to induce mortality and reduction in feeding and fecundity. Also, the level of mortality induced by consumption of *Nosema* is quite low, often imperceptible. It is best used over very large areas, not just on individual farms, and should be applied at least 1 year in advance of the development of potentially damaging populations.

Fungi have also been investigated for grasshopper suppression. A grasshopper strain of *Beauveria* *bassiana* has been effective in some trials, and *Metarhizium anisopliae* var. *acridum* has worked well for grasshopper and locust suppression in Africa and Australia, so it may prove useful for *Melanoplus* spp. Behavioral thermoregulation by grasshoppers, wherein they bask in the sun and raise their body temperatures, is potentially a limiting factor for use of fungi. Basking grasshoppers easily attain temperatures in excess of 35°C; such high temperatures decrease or even prevent disease development in infected grasshoppers. Inconsistent quality control in production of fungi also limits use of these organisms for grasshopper control.

► Grasshopper Pests in North America
► Grasshoppers and Locusts as Agricultural Pests
► Grasshoppers, Katydids and Crickets (Orthoptera)

References

Capinera JL, Scott RD, Walker TJ (2004) Field guide to the grasshoppers, katydids, and crickets of the United States. Cornell University Press, Ithaca, New York, 249 pp

Parker JR (1939) Grasshoppers and their control. USDA Farmers' Bulletin 1828, 37 pp

Parker JR, Shotwell RL (1932) Devastation of a large area by the differential and the two-striped grasshoppers. J Econ Entomol 25:174–187

Pfadt RE (2002) Field guide to common western grasshoppers. Wyoming Agricultural Experiment Station Bulletin 912, 288 pp

Shotwell RL (1941) Life histories and habits of some grasshoppers of economic importance on the Great Plains. USDA Technical Bulletin 774, 48 pp

Digger Bees

Members of the family Anthrophoridae (order Hymenoptera, superfamily Apoidae).

► Bees
► Wasps, Ants, Bees and Sawflies

Digitate

Pertaining to structures with finger-like processes.

Dilaridae

A family of insects in the order Neuroptera. They commonly are known as pleasing lacewings.

► Lacewings, Antlions and Mantidflies

Dimboa

An acronym for 2,4-dihydroxy-7-methoxy-1,4,-benzoxazin-3-one, a naturally occurring compound in corn (maize) that provides some resistance against caterpillars.

Dimorphic

Having two distinct forms. Among insects, winged and wingless forms are a common example of dimorphism.

Dinidoridae

A family of bugs (order Hemiptera, suborder Pentamorpha).

► Bugs

Diopsidae

A family of flies (order Diptera). They commonly are known as stalk-eyed flies.

► Flies

Dioptidae

A family of moths (order Lepidoptera). They commonly are known as American false tiger moths and oakworms.

► American False Tiger Moths
► Butterflies and Moths

Diphyllostomatid Beetles

Members of the family Diphyllostomatidae (order Coleoptera).

► Beetles

Diphyllostomatidae

A family of beetles (order Coleoptera). They commonly are known as diphyllostomatid beetles.

► Beetles

Diploid

Having two copies of each chromosome.

Diplurans (Diplura)

This is an order of hexapods in the class Entognatha. These hexapods are sometimes considered to be insects (class Insecta). This order is also known as Entotrophi.

Classification

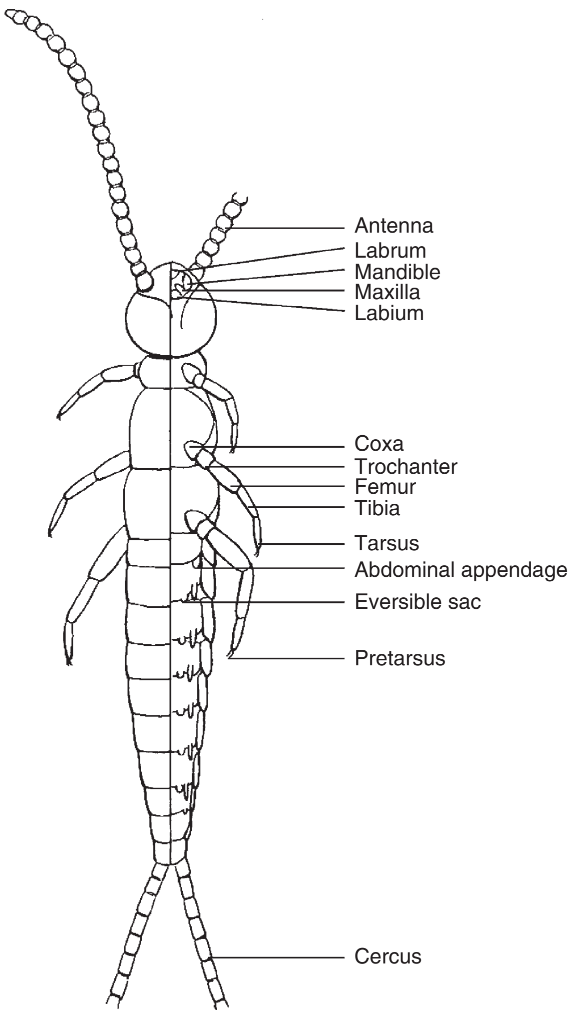
About 660 species are known from throughout the world, though this groups is not well known. The Campodeidae is well represented in the Holarctic region, with the other families more common in the subtropics and tropics. The taxonomy of Diplura is confused, but six families in two suborders are sometimes recognized:

Class: Entognatha
- Order: Diplura
  - Suborder: Rhabdura
    - Superfamily: Projapygoidea
      - Family: Anajapygidae
      - Family: Projapygidae
    - Superfamily: Campodeoidea
      - Family: Procampodeidae
      - Family: Campodeidae
  - Suborder: Dicellurata
    - Superfamily: Japygoidae
      - Family: Japygidae
      - Family: Parajapygidae

Characteristics

Diplurans resemble symphylans (class Symphyla), or perhaps silverfish (order Thysanura), bristletails (order Archeognatha), or proturans (order Protura). However, they have only three pairs of legs, so they are easily distinguished from the (Fig. 49) many-legged Symphyla. Also, the presence of only two cerci rather than three caudal filaments distinguishes diplurans from silverfish and bristletails. They are distinguished from proturans (order Protura) by the presence of antennae.

Diplurans are usually less than 10 mm in length, though their size range is 2–50 mm. They are elongate, soft-bodied, and brownish. The integument is thin, and few scales are found on these animals. The body regions, including the three thoracic segments, are distinct. The head is distinct, and the antennae long, many-segmented, and slender. Compound eyes and ocelli are absent. The biting and chewing mouthparts are entognathous (recessed in the head). The mandibles are elongate. They are wingless, and the three pairs of legs are similar in appearance and moderately short. The tarsi are one-segmented. The abdomen consists of ten well-developed segments and a small 11th segment. The tip of the abdomen bears a pair of cerci. The cerci vary greatly among the taxa, from long, many-segmented antenna-like appendages to stout, strongly sclerotized forceps used for prey capture. Most of the abdominal segments also bear small appendages. Trachea are present, but Malpighian tubules are vestigial or absent. The immatures greatly resemble the adult stage, differing principally in the number of antennal segments. They are considered to have incomplete metamorphosis.



Diplurans (Diplura), Figure 49 **A diagram of a dipluran showing a dorsal view (left) and a ventral view (right). Note that the cerci are abbreviated.**

Biology

These small animals are found among fallen leaves and in decaying vegetation, under logs and stones, and in soil and caves. They vary in dietary habits; some feed on vegetation whereas others eat other small soil-inhabiting arthropods. Sperm transfer is indirect, with males producing stalked spermatophores which the female takes up without courtship. Eggs are deposited in the soil. They can be long-lived, with the life span requiring 2–3 years in some species. The number of molts is considerable; up to 20 molts per year are known.

References

Arnett RH Jr (2000) American insects, 2nd edn. CRC Press Boca Raton, FL, 1003 pp
Allen RT (1994) An annotated checklist and distribution records of the subfamily Campodeiinae in North America (Insecta: Diplura: Rhabdirura: Campodeidae) Trans Am Entomol Soc 120:181–208
Paclt J (1956) Biologie der primär flügenllosen Insekten, Fischer, Jena, 258 pp
Paclt J (1957) Diplura, Genera Insectorum, Fascicle 212, 123 pp
Wygodzinsky P (1987) Class and order Diplura. In: Stehr FW (ed) Immature insects, vol 1. Kendall/Hunt Publishing, Dubuque, IA, pp 65–67

Diprionidae

A family of sawflies (order Hymenoptera, suborder Symphyta). They commonly are known as conifer sawflies.

► Wasps, Ants, Bees and Sawflies
► Sawflies (Symphyta)

Dipsocoridae

A family of bugs (order Hemiptera).

► Bugs

Diptera

An order of insects. They commonly are known as flies.

► Flies

Dipteromimidae

A family of mayflies (order Ephemeroptera).

► Mayflies

Direct Flight Muscles

Muscles that connect directly to the wing bases and power the wings directly.

Directive Coloration

Colors or marks on potential prey organisms that divert the predator from the more vital regions of an organism. Thus, for example, a bird might be induced to grasp a butterfly in the wing region rather than the abdomen.

Direct Pests

Pests that inflict injury directly on the portion of the commodity that is harvested for sale.

Dirofilariasis

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Dirofilariasis is a complex of veterinary diseases caused by nematodes (round worms) belonging to the phylum Nematoda, order Filarioidea, family Onchocercidae and genus *Dirofilaria*. The genus *Dirofilaria* is divided into two subgenera: *Dirofilaria* and *Nochtiella*. The subgenus *Dirofilaria* contains *Dirofilaria immitis* that causes canine cardiovascular disease (dog or canine heartworm disease) in dogs and dog like carnivores, cats, domestic ferrets, and rarely in humans causing pulmonary dirofilariasis. The subgenus *Nichtiella* contains *Dirofilaria repens* that occurs in dogs and cats, *D. tenuis* in raccoons, *D. ursi* in bears, and *D. striata* in bobcats and panthers. The first three species of *Dirofilaria* in the subgenus *Nochtiella* cause subcutaneous nodules in their vertebrate hosts and in humans. All parasites belonging to this family complete their development in two hosts. The vertebrate is the final host and the mosquito is the intermediate host/vector, except in *D. ursi* where the hosts/vectors are blackflies.

The distribution of *Dirofilaria immitis* is worldwide, thus canine or dog heartworm disease occurs all over the world, especially in tropical and temperate zones. In the United States, it was once limited to the south and southeast regions. However, the disease has spread and is now found in most regions of the United States and Canada, particularly where mosquitoes are prevalent. The distribution is influenced by a reservoir population of animals (usually dogs) that have adult worms in their hearts and microfilariae circulating in the blood, and a mosquito vector in which the early larval stages can develop to the infective larval stage. The distribution of parasites belonging to subgenus *Nochtiella* is more restricted, for example, *D. repens* occurs in Europe, Asia, Africa, and Mediterranean countries, *D. tenus* and *D. striata* occur in southeast U.S.A. and *D. ursi* occurs at the U.S.-Canadian border.

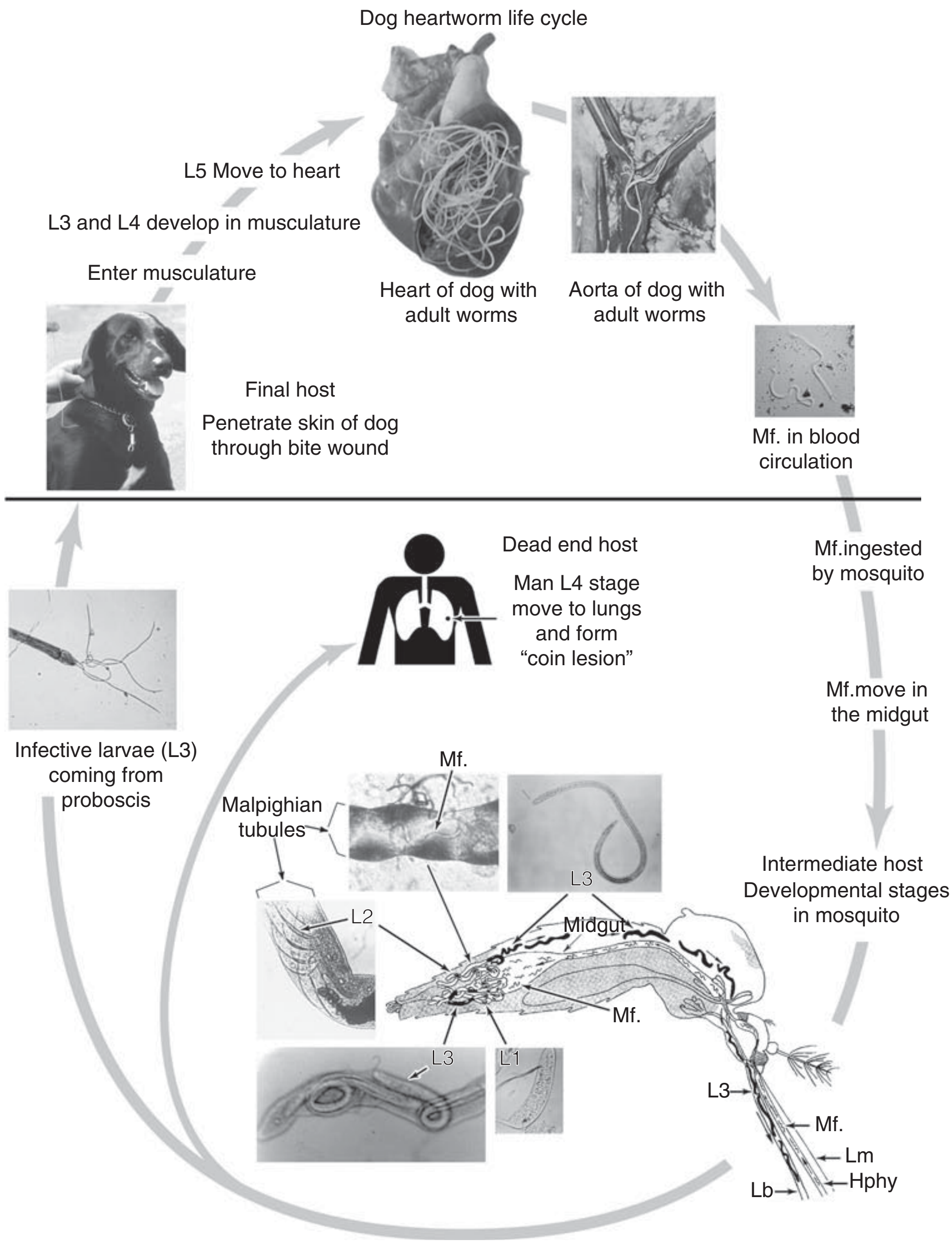
Dog heartworm disease (dirofilariasis) is a serious and potentially fatal disease in dogs and cats. In dogs and other carnivores, the adult worms normally reside in the heart and large adjacent vessels. Adult worms are long, slender and white. Males are 12–16 cm long and have a corkscrew tail, and females are 25–30 cm long. Adult worms cause disease by clogging the heart and major blood vessels leading from the heart. They interfere with the valve action in the heart. By clogging the main blood vessels, the parasite reduces the blood supply to other organs of the body, particularly the lungs, liver, and kidneys, leading to malfunction of these organs. Most dogs infected with heartworms do not show any signs of disease for as long as 2 years. Unfortunately, by the time signs are seen, the disease is well advanced. The signs of heartworm disease depend on the number of adult worms present, the location of the worms, the length of time the worms have been present, and the degree of damage to the heart, lungs, liver, and kidneys from the adult worms and the microfilariae. The most obvious signs are: a soft, dry, chronic cough, shortness of breath, weakness, nervousness, listlessness, and loss of stamina. All of these signs are most noticeable following exercise, when some dogs may even faint and die.

Once infected, a dog is infected for life. The sexually mature nematodes mate in the right ventricle of the heart and discharge unsheathed microfilariae into the bloodstream. Microfilariae are 290–330 μm long and 6–7 μm wide, with tapered anterior end and straight posterior end, without cephalic hooks. They cannot develop further in the dog, but can survive in the blood stream for up to 2–3 years. They circulate throughout the body but remain primarily in the small blood vessels and capillary beds. Because they are as wide as the small capillaries, they may block blood flow. The body tissues and cells being supplied by these capillaries are thus deprived of the nutrients and oxygen normally supplied by the blood. The lungs and liver are primarily affected and destruction of lung tissue that leads to coughing. Cirrhosis of the liver causes jaundice, anemia, and general weakness because this organ is essential in maintaining a healthy animal. The kidneys may also be affected and allow poisons to accumulate in the body.

These circulating microfilariae must be ingested by a mosquito (the vector) during blood-feeding on the infected dog before they can develop further. Soon after the blood meal, the microfilariae move from the mosquito's midgut to the Malpighian tubules where they become intracellular. At a temperature of about 27°C the microfilariae become immobile, shorten and thicken, and develop into the so-called "sausage form" larvae in about 4–5 days, with the first stage larvae continuing until a molt at about 8 days. During the second larval stage, the internal organs of the worm are formed. The second molt occurs at 11–12 days, resulting in the third stage (L3) (Fig. 50) of infective larvae that resemble miniature adults. During the next 2–3 days, they increase in length, break out of the Malpighian tubules, migrate to the hemocoel then move into the head capsule and accumulate in the labium (a mouthpart of the proboscis continuous with the hemocoel). The development in the mosquito can be as short as 10 days at 30°C or as long as 28 days at 18°C. Thus, in 2–3 weeks, microfilariae transform into infective larvae that are about 1300 μm long. As the infected mosquito feeds, the labium is bent back and L3 escape in a pool of hemolymph onto the skin. When the stylets are withdrawn, the L3 enter through the wound. Up to 10 to 12 L3 can be transmitted by a single mosquito. Further development of the infective larvae only takes place in the dog and related species after mosquitoes feed on the vertebrate host. Spread of the disease therefore coincides with the mosquito season. The number of dogs infected and the length of the mosquito season are directly correlated with the incidence of heartworm disease in any given area.

In the dog and other carnivores, infective larvae (L3) after penetrating the skin move in the subcutaneous tissue and molt to L4 in about 10 days post infection. The L4 migrate to muscle bundles (fascial planes, muscle sheaths) and start to grow during the next 60 days and then molt to L5. The L5 migrate through venule walls by 70 days post-infection and are carried through the right ventricle of heart to pulmonary arterioles, most of them arriving there by 3–4 months post-infection. L5 mature to adults after migrating to the right ventricle and pulmonary trunk. If both sexes are present, they mate and the female can produce microfilariae after approximately 6 months post-infection, thereby completing the life cycle. These females can continue producing microfilariae for 5–7 years, which can survive for about 2 years in the blood circulation.

It takes a number of years before dogs show outward signs of infection. Consequently, the disease is diagnosed mostly in 4–8 year old dogs. The disease is seldom diagnosed in a dog under 1 year of age because the larvae take up to 7 months to mature following establishment of infection in a dog. In endemic areas, the average worm burden in the dog is about 15. High worm burdens



Dirofilariasis, Figure 50 Life cycle of dog heartworm (*Dirofilaria immitis*). Stages of filarial worm in dog: L3 = third stage larvae and L4 = fourth stage larvae in musculature and adult worms in heart and aorta of dog. Stages of filarial larvae in the mosquito: Mf = microfilariae, L1 = first stage larvae (sausage stage), L2 = second stage larvae, and L3 = third stage larvae in Malpighian tubules and microphotographs. Lm = labium, Lb = labrum, and Hphy = hypopharynx.

(more than 75) can be demonstrated in acute post-caval syndromes and chronic ascites from tricuspid valve dysfunction. Because of the increased resistance of most animals from repeated exposure to L3 over time, high worm burdens are most likely to occur in dogs which have not been exposed to any mosquitoes with L3 previously and are then bitten by many mosquitoes over a 3 month period. In that case, a dog may have as many as 300 worms.

Feline dirofilariasis is a complex pathological disease, which is principally subclinical. It produces among others, pulmonary vascular disorders with complications caused by clinically significant heart, lung, liver, kidney and thoracic duct diseases as well as CNS signs and symptoms. Generally, the common signs in acute and severe cases include fainting, dyspnea, seizure, intermittent vomiting, diarrhea, blindness, rapid heart beat or syncope. The signs of the chronic stage include stress intolerance, dyspnea, lethargy, loss of appetite, quilothorax, rapid heart beat, abdominal distention (in the case of congestive right heart failure), cyanosis, abnormal liver sounds, systolic murmur (extremely rare), occasional nose bleeding, urinary retention and ascitis. In endemic areas, the average worm burden in the cat is 1–3 worms. In cats, adult worms live for approximately 2 years and sometimes produce very few microfilariae, if at all.

Dirofilaria immitis microfilariae can develop to the infective stage larvae in more than 100 species of mosquitoes, out of more than 3,000 species present worldwide, and these species are considered as potential vectors. In order to be a heartworm vector, besides being resistant to infection but yet susceptible enough to allow larval development, a mosquito species must feed on infected dogs, be well adapted to the region and be abundant and preferably multivoltine. However, about 25 mosquito species mostly belonging to *Aedes* and *Culex* have been collected worldwide with developing larvae in their Malpighian tubules, hemocoel and mouthparts and they have been identified as natural vectors. These are: in North America – *Aedes canadensis*, *Ae. cantators*, *Ae. excrucians*, *Ae. sierrensis*, *Ae. sticticus*, *Ae. stimulans*, *Ae. sollicitans*, *Ae. taeniorhynchus*, *Ae. trivittatus*, *Ae. vexans*, *Culex nigripalpus*, *Cx. quinquefasciatus*, *Cx. salinarius, Anopheles puntipennis,* and *Psorophora ferox*; in Australia – *Ae. annulipes*, *Ae. notoscriptus*, *Ae. vigilax*, *Cx. annulirostris*, and *Cx. quinquefasciatus*; in Japan – *Ae. albopictus*, *Ae. togoi*, and *Cx. quinquefasciatus*; in South Pacific – *Ae. pseudoscutellaris*, *Cx. annulirostris*, and *Cx. quinquefasciatus*.

Dirofilaria immitis is also an occasional parasite of humans, causing pulmonary dirofilariasis. Because infective larvae develop to a limited extent in humans, the latter are referred to as the dead end hosts. The filarial nematodes enter the subcutaneous tissue after a bite from an infected mosquito, develop to the L4 stage, and travel to the right ventricle where they die and embolize the pulmonary vasculature, causing small pulmonary infarctions that subsequently appear as solitary nodules. Although these nodules are usually identified incidentally by chest radiography in asymptomatic patients, the lesions are generally presumed to be neoplastic. The nodules of dirofilariasis are usually round called "coin lesions" in the lungs but sometimes they are dumbbell-shaped. Microscopically, the nodules are granulomas composed of central coagulation necrosis and peripheral fibrosis with round cell infiltration, histiocytes, and multinucleated giant cells. Because these nodules are difficult to be differentiated from primary or metastatic lung carcinomas and the inflammation exists around the nodule, the nodule should be removed surgically. During the last 40 years, approximately 150 cases of human pulmonary dirofilariasis have been reported worldwide.

Three other parasites that cause dirofilariasis, belong to subgenus *Nochtiella,* produce subcutaneous nodules which may be migratory both in their vertebrate hosts and in humans, are *D. repens*, *D. tenuis* and *D. ursi*.

Dirofilaria repens, a parasite of the subcutaneous tissues of dogs and cats, is found in Europe, Asia, and Africa, especially in Mediterranean countries, Russia and Japan. Human infections by *D. repens* are being reported with increasing frequency in all these countries. Both males and females of this parasite are about half the size of *D. immitis*, the females measuring 100–170 mm in length and 0.46–0.65 mm in width and males 50–70 mm in length and 0.37–0.45 mm in width with two to six preanal papillae to the right of the anus and four to five to the left. The microfilariae of *D. repens* occur in the subcutaenous lymph spaces and in the peripheral blood. The microfilariae range in length from 268–360 μm and overlap in size that reported for *D. immitis*. They can be distinguished from *D. immitis* microfilariae by the relative positions of somatic structures such as nerve ring, the excretory cell, the G1 cell, and the anal space along the length of the microfilariae. Development of *D. repens* in mosquitoes follows a similar pattern as that of *D. immitis* in mosquitoes. However, the mosquitoes that support development of the larval stages of these parasites belong to *Aedes* and *Culex* species found in Europe, Asia, and Africa.

Dirofilaria tenuis is a parasite of the subcutaneous tissues of raccoons in the southeastern United States but humans are also infected. More than 20 human cases have been reported from Florida and most of them were from southern Florida. The microfilariae are 370 ± 9 μm long and ca. 7 μm wide and are comparable in size to *D. striata* microfilariae. Development of *D. tenuis* in mosquitoes follows a similar pattern as that of *D. immitis*. The natural vectors of *D. tenuis* in south Florida is *Ae. taeniorhynchus*, however, several other species of mosquitoes, such as *An. quadrimaculatus*, *Ae. triseriatus*, *Psorophora columbiae* and *Ps. Ferox*, are considered potential vectors.

Dirofilaria species causing subcutaneous infections in vertebrates and humans are identified primarily on the basis of structure and arrangement of the ridges. Longitudinal ridges of adult *D. repens* are conspicuous and sharp, separated by a space three to four times the width of the ridge itself. *Dirofilaria tenuis* has a distinctive pattern of low, rounded ridges in a branching network with spaces appearing narrower than the ridges themselves. The cuticle of *D. immitis* is smooth with ridges occurring only on the ventral aspect of the caudal extremity of the male worm.

Dirofilaria ursi is a parasite of the peritracheal and perirenal tissues of bears in North America and Japan and Russia, and rarely of dogs in these areas. Human infections with *D. ursi* causing subcutaneous nodules have been reported in the states and provinces along the U.S.-Canadian border. The intermediate host of *D. ursi* is the blackfly, *Simulium venustum* and perhaps other simuliids in Canada. Development of *D. ursi* microfilariae in simuliids is similar to that observed for other *Dirofilaria* species in mosquitoes, i.e., all species of *Dirofilaria* complete their development in the Malphighian tubules of their vector.

Dirofilaria striata is found in panthers and bobcats in Florida. The adults of this species occur in the intermuscular fascia or free in the peritoneal cavity. The females of *D. striata* are 25–28 cm long and males are 8–9 cm wide. Microfilariae of *D. striata* are significantly longer and more slender than those of *D. immitis* (348 μm × 4–5 μm vs. 299 μm × 5–6.5 μm) and exhibit within the cephalic space two prominent nuclei separated from the main body of the nuclear column. *Dirofilaria striata* has been reported as an accidental parasite of dogs in Florida and adults have been recovered from deep intramuscular fascia of dogs. The potential mosquito vectors of *D. striata* in south Florida are *Ae. taeniorhynchus*, *An. quadrimaculatus*, *Cx. nigripalpus* and *Cx. quinquefasciatus*.

Since canine cardiovascular dirofilariasis is primarily a disease of dogs and cats that are household pets, several diagnostic and preventive measures are used by veterinarians. Canine dirofilariasis can not be controlled unless the mosquito populations are completely controlled. Several diagnostic tests to determine if cats and dogs are infected are as follows: (i) demonstration of the microfilariae of *D. immitis* in a blood sample by concentration techniques, (ii) the detection of circulating microfilarial antigen, (iii) thoracic radiographs can be a screening tool for dogs and cats with suggestive clinical signs of heartworm disease, and (iv) echocardiograms are diagnostic with the typical "double parallel" white lines are noted in the pulmonary arteries or right ventricles of dogs or cats. Routine therapy included: (i) Pre-therapy diagnostic to determine sub-clinical disease, especially of the liver and kidney. (ii) Adulticidal therapy (Immiticide®, Caparsolate®, Filaramide®) to eliminate mature worms. (iii) A rest period of 4–6 weeks to allow the animal to recover from the lung injury associated with worm death. (iv) Microfilaricidal therapy (Heartgard®, Interceptor®) if required. (v) Post-Microfilaricidal check. (vi) Antigen test to determine success of adulticidal therapy. (vii) Preventative medications (Filaribits®, Heartgard®, Interceptor®). Information on all these aspects can be obtained from your practicing local veterinarians.

References

Boreham PFL, Atwell RB (1988) Dirofilariasis. CRC Press, Boca Raton, FL, 249 pp

Nayar JK, Knight JW (1999) *Aedes albopictus* (Diptera; Culicidae): an experimental and natural vector host of *Dirofilaria immitis* (Filarioidea: Onchocercidae) in Florida, USA. J Med Entomol 36:441–448

Shah MK (1999) Human pulmonary dirofilariasis: review of literature. South Med J 92:276–279

Tarello W (1999) Canine Dirofilariasis due to *Dirofilaria (Nochtiella) repens*. Review from literature and a clinical case. Rev Med Vet 150:691–702

Discal Cell

A cell, usually enlarged, that is found near the center of the wing.

Discrete Generations

A series of generations in which one generation is completed before the next commences. This is common place for insects with a single generation per year, separated by a period of diapause. With insects having more than one generation per year, however, it is common to have overlapping generations, wherein the early life stages of the succeeding generation overlap the final stages of the preceding generation.

Disease

A process that represents the response of the body to injury or insult. A pathogen is not a disease, but it may cause one.

Diseases of Grasshoppers and Locusts

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The importance of grasshoppers and locusts as pests, and the increased concerns over the deleterious environmental and health effects of using chemical insecticides to control their outbreaks, recently has drawn much attention to the possibility of exploiting their pathogens as microbial control agents. Disease often is responsible for suppression of grasshopper and locust outbreaks. Disease causing agents include bacteria, fungi, protozoa and viruses.

Bacteria

Two species of bacteria, *Serratia marcescens* Bizio and *Pseudomonas aeruginosa* (Schroeter) Migula have been implicated in disease epizootics observed in field populations and laboratory-reared locusts and grasshoppers. These bacteria infect their host after being ingested and often spread rapidly in laboratory colonies. However, their role in the natural suppression of grasshopper and locust populations remains unclear.

Bacterial pathogens of locusts and grasshoppers received considerable attention as potential microbial control agents in the early 1900s and in the 1950s. Several attempts were made to use these bacteria to manage grasshoppers and locusts, but these studies never proceeded beyond the stage of surveys and laboratory trials. Concerns over human and environmental safety at the time, as well as product stability, led to the termination of this work.

The commercial success of certain serovars of *Bacillus thuringiensis* as microbial control agents of numerous insect pests has spawned several attempts to isolate related spore-forming bacteria pathogenic to locusts and grasshoppers. Although some toxins, such as the β-exotoxin of *B. thuringiensis*, have a broad activity against a large number of insects, including locusts and grasshoppers, strains producing more species-specific δ-endotoxins highly active against orthopterans have not been discovered to date. However, the continued discovery of new strains of *B. thuringiensis* with specific activity against a broader range of pests and the recent commercial development of a new species of *Serratia* (*Serratia entomophila*) for control of grass grubs provides incentive to continue the search for orthoperan-active bacteria. But at the moment, there is no evidence of naturally occurring bacterial species or strains that would warrant exploitation for locust or grasshopper control.

Fungi

Unlike most other pathogens which must be ingested to cause disease, entomopathogenic fungi generally enter their host via the external cuticle. A handful of species are common in grasshoppers and locusts and these include *Beauveria bassiana* (Balsamo) Vuillemin, *Entomophaga grylli* (Fresenius) Batko species complex, *Metarhizium anisopliae* (Metschnikoff) Sorokin, *Metarhizium anisopliae* var *acridum* (syn = *Metarhizium flavoviride*) and *Sorosporella* spp.

Beauveria bassiana

There are numerous records of *B. bassiana* infecting grasshoppers and locusts and it has been documented causing epizootics amongst locust populations in Africa. The fungus is ubiquitous and infects a wide variety of insects from most orders. Aerial conidia, the infective spore stage of the fungus, adhere to the cuticle of the host, germinate, penetrate through the external cuticle, rapidly proliferate within the host body via hyphal growth and production of yeast-like hyphal bodies or blastospores, killing the host within 4–10 days of infection. Soon after the host dies, and under appropriate moisture conditions, the fungus emerges through the body wall and quickly sporulates, producing numerous conidia on the host surface, often appearing like a white powder completely engulfing the host cadaver.

The fungus has been commercially developed and registered as a microbial control agent against numerous pest insects throughout the world. Field trials with inundative applications of an American isolate against grasshoppers in North America and Africa produced mixed results. Several studies have demonstrated that infected grasshoppers and locusts are able to escape lethal infection by basking in the sun, thereby increasing their body temperature above the thermal threshold for growth of the fungus (see below).

Entomophaga grylli Complex

Fungi in the *Entomophaga grylli* complex are obligate grasshopper pathogens responsible for numerous widespread epizootics worldwide, and are regarded as a key factor in regulating many grasshopper populations. This complex contains several pathotypes that vary in their ability to produce both conidia and resting spores within a single season. The fungus overwinters as resting spores in the soil. A portion of the resting spores germinate each spring, while others remain dormant for two or more seasons. Germinating resting spores produce specialized spores which are forcibly ejected from the soil into the lower canopy where grasshoppers encounter them. Once these spores contact a grasshopper host they germinate, penetrating the body wall, and the fungus then rapidly proliferates within the grasshopper body cavity as protoplastic bodies. Approximately 1 week after initial exposure, infected grasshoppers climb to the top of the plant canopy where they die grasping firmly onto the plant substrate. For this reason, this disease is often referred to as the "summit disease." Depending on the pathotype, at this point, either resting spores are exclusively produced and the insect eventually falls to the ground, the cadaver disintegrates and the resting spores are released into the soil, or alternatively, the cadaver produces either resting spores or aerial conidia, which are responsible for within-season epizootic development.

Natural epizootics of the fungus often produce high levels of mortality, and have been credited for ending grasshopper outbreaks in many North American grasshopper species. There have been several attempts at inundative application of conidia in an effort to induce epizootics (inundative microbial control), however, none were able to achieve satisfactory results. The most important limiting factors were lack of adequate mass production and application techniques and the specific environmental requirements of the fungus for survival and infectivity. Attempts at inoculative introduction (classical biological control) also were not successful. Introductions of North American isolates into Australia and vice versa failed to establish, although the introductions into North America initially were followed by population declines of key pest species. These initial studies suggest that these pathogens have potential for use in biological control, however, further studies are required.

Metarhizium anisopliae var *acridum*

There are records of *M. anisopliae* var *acridum* (formally referred to as *Metarhizium flavoviride*) from grasshoppers in Africa, Australia and Brazil, and natural epizootics have been documented in Africa. The mode of pathogenesis and infection cycle is essentially the same as described above for *B. bassiana*, except that cadavers are covered with a powdery covering that is dark olive green rather than white.

The fungus has been the subject of much research in the last decade and several commercial products for grasshopper and locust control now are available in Africa and Australia. A multinationally funded project, LUBILOSA, spearheaded by CABI and the International Institute of Tropical Agriculture, resulted in the discovery and development of this fungus as a commercial microbial insecticide (Green Muscle™). During this project, many improvements in the formulation, mass production and application of this fungus were made. These developments have resulted in a commercial formulation that can be stored up to 4 years that can be applied through Ultra Low Volume (ULV) application in an oil formulation, and that also offers the conidia some protection from the sun's harmful rays.

Protozoa

Protozoans that infect grasshoppers are mainly microsporidians, but certain Amoebida, Eugregarina, Neogregarina and Ciliophora also are known from grasshoppers. Among the Microsporidia, *Heterovesicula cowani* Lang et al., *Johenrea locustae* Lange et al., *Nosema acridophagus* Henry, *N. cuneatum* Henry, *N. locustae* Canning, *N. montanae* Wang et al., *N. pyrgomorphae* Toguebaye et al., and *Perezia dicroplusae* have been described. No doubt, many more await discovery and description.

The most studied microsporidian of grasshoppers has been *N. locustae*, and it was the basis for the first microbial pesticide (Nolobait™) developed against grasshoppers and locusts. Ingested spores germinate in the gut whereby they release a binucleate sporoplasm into a host cell through quickly extruded polar filaments. Sporoplasms subsequently spread to and replicate in the fat body, eventually depleting the host of its fat reserves.

Spores are mass produced *in vivo* in grasshoppers. Because the spores need to be ingested to initiate disease, commercial formulations are formulated on a wheat bran bait carrier. Extensive field-testing has taken place in North America, Argentina, China and Africa. Although at times application of spores has resulted in considerable decline in grasshopper or locust populations with subsequent carry over in treated areas, in other trials such impacts were not observed. Application of a pathogen such as *N. locustae* can be expected to result in sublethal effects such as delayed development, lower reproduction and reduced feeding. Unfortunately, many assessments measured only short term impact of *N. locustae* rather than long term benefits. Several other microsporidians with greater virulence than *N. locustae*, such as *N. cuneatum*, may better fit the microbial insecticide paradigm. There is also great potential of using microsporidians in the classical sense (inoculative releases) which await exploration.

Viruses

Entomopoxviruses are the only DNA viruses that have been found naturally infecting grasshoppers and locusts. Nearly 15 grasshopper and locust entomopoxviruses have been reported. The most extensively studied among these has been the *Melanoplus sanguinipes* EPV (MsEPV). Although the precise mode of infection of grasshopper viruses has not been studied in detail, pathogenesis probably is similar to that of other entomopoxviruses; ingested viral occlusion bodies break down in the alkaline medium of the gut, releasing the individual virions which then infect midgut cells, presumably replicate, and progeny virus is then released into the hemocoel, eventually infecting the fat body tissues. Virions replicate within the fat body cells and are packaged in proteinaceous crystalline matrices, the occlusion bodies.

Effects of infection vary according to dosage received. In heavily infected grasshopper populations, death can occur in two distinct modes. An initial mortality takes place between 2 and 10 days post exposure, subsides and then mortality increases again during the second mode, 14 days after initial exposure. Occlusion bodies are produced only in grasshoppers dying during the second mode. Infected grasshoppers that escape the early mortality experience a profoundly longer development period, and few develop to the adult stage. During this delayed development period, there is a concomitant reduction of feeding. Prevalence rates of the virus in field populations are extremely low and very little is known about its epizootiology.

Field evaluations on the potential of using grasshopper entomopoxviruses as microbial insecticides were carried out in the United States. The virus was mass produced by injecting grasshoppers and incubating them in an insectary. Infected cadavers were crushed and formulated in a starch granule and then dispersed in the field. Maximum prevalence levels in treated fields reached 23%, however, it is speculated that due to grasshopper dispersal between experimental plots, this may be a rather conservative estimate. At this time, the *in vivo* production is cost prohibitive and feasibility of developing these viruses as grasshopper control products remain questionable.

Grasshopper Thermal Ecology

Locusts and grasshoppers optimize their body temperature through behavioral responses, such as basking in the sun. Recent research has demonstrated that individuals infected with a pathogen will attempt to increase their temperature even further, a phenomenon termed "behavioral fever." Even though behavioral fever has been demonstrated in ectotherms from various taxa in response to infection by a variety of pathogens, to date only *Nosema* and fungi have been found to elicit such behavioral fevers in grasshoppers and locusts. Behavioral fever can result in augmentation in body temperature to the vicinity of 40°C, which usually is well above the upper limits for growth of most pathogens. Furthermore, behavioral fever may enhance the insect immune response by stimulating the production of hemocytes. Consequently, speed of kill and overall mortality can be affected drastically, depending on the environmental conditions prevalent that may or may not allow optimal thermoregulation (e.g., sun, cloud, wind, rain). In microbial control of grasshoppers and locusts, it may be possible to overcome such constraints through application of pathogen cocktails containing pathogens or pathotypes selected for a wide range of thermal possibilities according to the environment that is being treated (e.g., day length and day/night temperatures).

References

Bidochka MJ, Khatchatourians GG (1991) Microbial and protozoan pathogens of grasshoppers and locusts as potential biocontrol agents. Biocontrol Sci Technol 1:243–259
Gardner SN, Thomas MB (2002) Costs and benefits of fighting infection in locusts. Evol Ecol Res 4:109–131
Goettel MS, Johnson DL (eds) (1997) Microbial control of grasshoppers and locusts. Memoirs of the Entomological Society of Canada, vol. 171. The Entmological Society of Canada, Ottawa, Canada, 400 pp
Inglis GD, Goettel MS, Erlandson MA, Weaver DK (2000) Grasshoppers and locusts. In: Lacey LA, Kaya HK (eds) Field manual of techniques for the application and evaluation of entomopathogens. Kluwer Academic Press, Dordrecht, The Netherlands, pp 651–679
Kleespies RG, Huger AM, Stephan D (2000) Diagnosis and pathology of diseases from locusts and other orthopterans. Deutsche Gesellschaft fur Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Germany, 43 pp
Lomer CJ, Bateman RP, Johnson DL, Langewald J, Thomas M (2001) Biological control of locusts and grasshoppers. Ann Rev Entomol 46:667–702
Lomer CJ, Prior C (eds) (1992) Biological control of locusts and grasshoppers. CAB International, Wallingford, UK, 394 pp
Mason PG, Erlandson MA (1994) The potential of biological control for management of grasshoppers (Orthoptera: Acrididae) in Canada. Can Entomol 126:1459–1491
Streett DA, McGuire MR (1990) Pathogenic diseases of grasshoppers. In: Chapman RF, Joern A (eds), Biology of grasshoppers. Wiley, New York, NY, pp 483–516

Disjunct Populations

The geographical distribution of a species (or other taxon) consists of widely separated populations.

Disk

A soil cultivator made up of many circular blades that act to break up the soil into smaller aggregates.

Dispersal

Displacement to a new habitat. Dispersal usually is multidirectional and passive, taking advantage of wind currents.

The spatial patterning of individuals in a population in their habitat. This pattern can be broadly described as uniform, random or, most commonly, aggregated.

Dispersion

Dispersion or distribution is a spatial property that can be quantified by explicit spatial indices, or more typically by probability models (e.g., Poisson, Negative-binomial) or empirical models (e.g. Taylor's power law). The measurement of dispersion is dependent on the sample unit size and population density. Dispersion is an important element in the development of a sampling plan.

► Sampling Arthropods

Disruptive Coloration

Color patterns on an animal that confer protection by obscuring the outline of the animal. Typically it consists of strongly contrasting colors. The classic example is the black and white stripes of zebra. In insects, it may be manifested in stripes or bands, especially on larvae, on in spotted or blotchy patterns.

Distal

Pertaining to the part of an appendage furthest from the body.

Distiproboscis

The distal third of the proboscis in muscoid flies; this is the labellum.

Ditomyiidae

A family of flies (order Diptera).

► Flies

Diuretic Hormones

Neuropeptide hormones that promote fluid formation and rapid excretion by Malpighian tubules. In *Rhodnius*, the hormone is released from abdominal nerves associated with the mesothoracic ganglion, but this is not the case with all insects.

Diurnal

Organisms in which the period of activity occurs during daylight hours.

Diverticulum

An invagination or extension of the wall of the alimentary canal with the distal portion closed. Diverticula, when present, typically are associated with the anterior region of the alimentary canal. They are useful for food storage, and especially important when an insect takes infrequent but large meals.

Dixid Midges

Members of the family Dixidae (order Diptera).

► Flies

Dixidae

A family of flies (order Diptera). They commonly are known as dixid midges.

► Flies

DNA

Deoxyribonucleic acid, the genetic molecule.

DNA Probe

Also called a gene probe or genetic probe. Short, specific (complementary to the desired DNA sequence) artificially produced segments of labeled DNA are used to combine with and detect the presence of a specific gene or DNA sequence within the chromosome. The presence of this labeled probe usually is detected visually.

DNAse

Deoxyribonuclease, an enzyme that degrades DNA.

Dobsonflies

Some members of the family Corydalidae (order Megaloptera).

► Alderflies and Dobsonflies

Dobzhansky, Theodosius Grigorievich

Theodosius Dobzhansky was born in Nemirov, Ukraine, on January 25, 1900. While he was still a boy, he collected butterflies and intended to study the systematics of Coccinellidae once he had an education in biology. His university education was in Kiev, where he became an instructor in 1921–1924, and began Mendelian research on *Drosophila* and field research on Coccinellidae. Then he moved to Russia, and taught at the University of Leningrad in 1924–1927 while continuing research on *Drosophila* and Coccinellidae. Then, he moved to the USA. For a year, he worked at Columbia University. He became a researcher

(1928–1940) at the California Institute of Technology where he published his groundbreaking book (1937) "Genetics and the origin of species." He moved (1940–1962) back to Columbia University, then (1962–1971) to Rockefeller University, and finally (1971–1975) to the University of California at Davis. His contribution was to demonstrate that there is much genetic variability in a population, and that this includes many potentially lethal genes. Such genes, however, confer versatility when the population is exposed to environmental change [this theme is reiterated in the work of Edmund Brisco Ford, see below]. His work on population evolution in *Drosophila* fruit flies and humans gave the evidence that linked Darwin's theory with Mendel's law of heredity. He died on December 18, 1975.

Reference

Anon. Available at http://www.biography.com/search/article.do?id=9275931, accessed 26 March 2008

Dockage

Reduction in value of a crop or product due to damage, as may occur when infested with insects before or after harvest.

Dog Heartworm

A mosquito-transmitted cardiovascular disease of dogs caused by infection with the nematode *Dirofilaria immitis*.

► Dirofilariasis

Dolabellopsocidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice or Psocids

Dolichopodidae

A family of flies (order Diptera). They commonly are known as long-legged flies.

► Flies
► Long-legged Flies

Dominance Hierarchy

The physical domination of some individual by others, usually for a long period of time.

Dominant

A gene is dominant when it produces the same phenotype whether it is heterozygous or homozygous. The trait is expressed even if only one copy of the gene is present in the genome.

Dominant Species

A species that makes up a large proportion of the assemblage, or community, biomass or numbers.

Donisthorpe, Horace St. John Kelly

Horace Donisthorpe was born in 1870 and lived in various places in southern England, mainly London suburbs. He was an amateur entomologist, in the sense that amateur means he was not paid for entomological studies. He joined the Entomological Society of London in 1891 (and served in various capacities) and the Zoological Society. His major interests were in beetles, ants, and the fauna living in ant and bird nests. He was an inveterate insect collector with a curious philosophy that the only specimens he would put in his collection were those he had collected himself. His publications range from numerous small notes to books, and the total list amounts to about 800 items. His major works were (1913) a supplementary volume (VI) to Fowler's "Coleoptera of the British Islands," (1915) "British ants," and (1927) "Guests of British ants." The first edition of "British ants" was privately published, and in its endpages has a list of the subscribers who bought copies; perhaps because the initial edition was small, a second edition was published in 1927. "Guests of British ants" is an account of the fauna, including even reptiles, found in ant nests. He died on April 22, 1951, in a hospital in the London area.

Reference

Blair KG (1951) Horace St. John Kelly Donisthorpe. Entomologist's Monthly Magazine 87:215

Dormant

To become inactive during periods of cold weather.

Dormant Oil

An oil formulation that is applied to plants during the dormant season (usually winter) when the foliage is not present and thus not susceptible to injury (phytotoxicity). It is usually directed to small arthropods or their eggs, and apparently causes suffocation.

► Horticultural Oil

Dorsal

Referring to the upper surface.

Dorsal Diaphragm

A thin cellular layer beneath the heart that aids in blood flow. It is an incomplete wall of muscle and thin cells that separates the region around the dorsal vessel from the rest of the hemocoel.

Dorsal Longitudinal Muscles

Longitudinal muscles located dorsally in insect thoracic segments that power the downstroke of wings during insect flight. These are indirect flight muscles and are not attached to the wings. They are attached to apodemes at the anterior and posterior of the meso- and metathorax. When contracted, the dorsal longitudinal muscles slightly arch the thorax, causing he wings to move downward.

► Dorsoventral Muscles

Dorsal Vessel: Heart and Aorta

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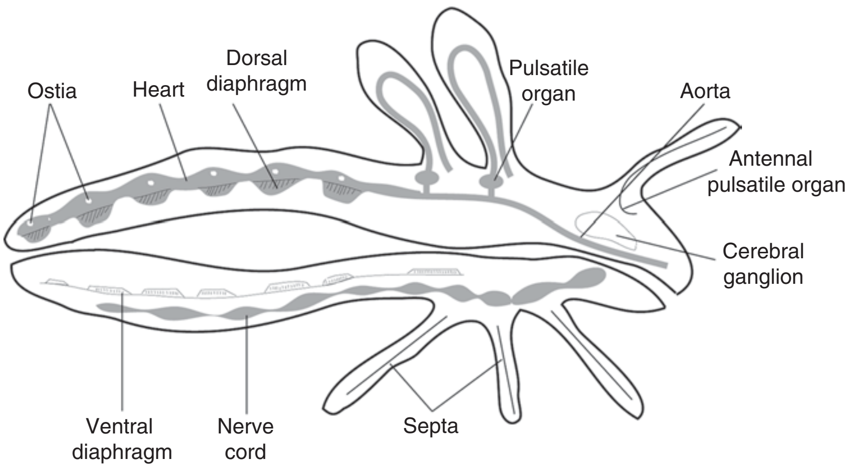
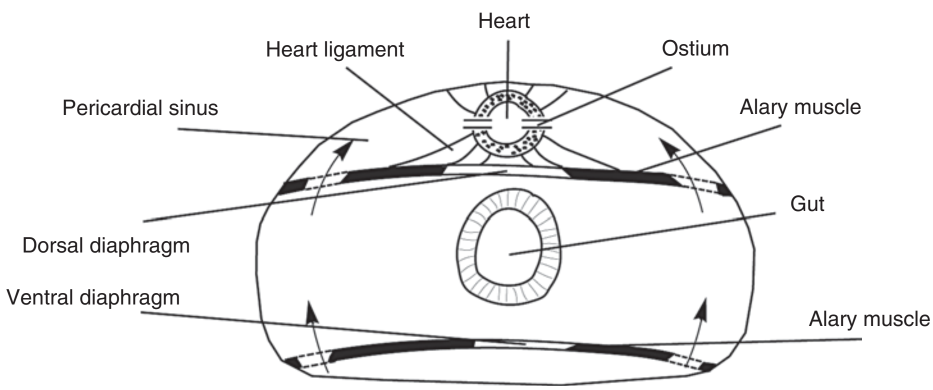
The circulatory system of insects is an open system, with the hemolymph pumped by a dorsal vessel that usually (Figs. 51–53) opens into the head. From the head the hemolymph simply percolates backward, bathing all the internal organs, eventually completing the circuit by entering the dorsal vessel through small openings, the ostia. The vessel is often described as consisting of two parts, the "heart" and the "aorta." These terms are borrowed from vertebrate cardiology, but they have little physiological meaning in describing the dorsal vessel of insects. The abdominal portion of the dorsal vessel is often referred to as the heart while the thoracic portion is the aorta. The major criteria for deciding when the heart ends and the aorta begins are the presence of alary muscles and incurrent ostia in the heart portion. The aorta does not have alary muscles and lacks incurrent ostia, but it may have excurrent ostia. Both alary muscles and incurrent ostia occur in the thoracic portion of the vessel in many Orthoptera, and nearly the entire length of the vessel can be called the heart, with a short aorta leading into the head. Typically the dorsal vessel is a simple tube, but in Orthoptera and Dictyoptera the heart has several pairs (four pairs in *Blaberus* sp.) of long diverticula passing



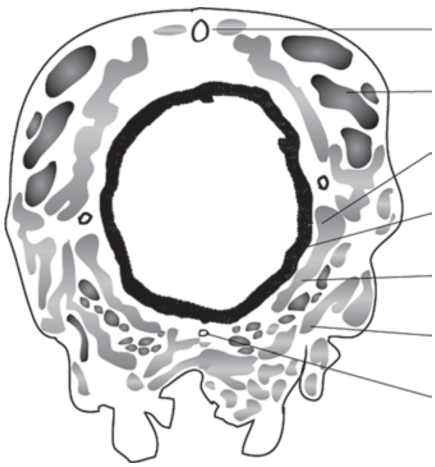
Dorsal Vessel: Heart and Aorta, Figure 51 Diagram of the components of the insect circulatory system; hemolymph moves through the heart and aorta to the head, filtering back through the body cavity and back into the heart via the ostia. Pulsatile organs assist in moving hemolymph through the appendages, especially the wings (adapted from Chapman, The insects: structure and function).



Dorsal Vessel: Heart and Aorta, Figure 52 Cross section of an insect abdomen, showing components of the insect circulatory system and direction of hemolymph flow (adapted from Evans, Insect biology).

out and branching around the laterally located tergo-sternal muscles and ending in fat body tissue. The posterior end of the heart is usually closed, but it is open in immatures of craneflies (Tipulidae), and in Ephemeroptera (mayflies) it divides into three branches, with one passing into each of the three caudal filaments.

In the abdomen, the dorsal vessel (Fig. 53) is located just beneath the tergal cuticle, but in the thorax of some insects portions may be helical (honeybee adults) or meander in long loops through the thoracic musculature in Lepidoptera and Coleoptera adults. The flow of hemolymph in some insects aids in thermoregulation, with thoracic loops acting as a heat exchanger to pick up heat from the thoracic musculature. Some insects can slow down the entry of relatively "cool" hemolymph from the abdomen so that the temperature of the thorax can be kept high for flight on cooler days. Many moths "shiver" by contracting the flight muscles before taking flight on cool days, utilizing the heat generated by muscle action to provide



Dorsal Vessel: Heart and Aorta, Figure 53 Cross section of a caterpillar showing the location of the dorsal vessel (here labeled heart) (adapted from Chapman, The insects: structure and function).

a favorable thoracic temperature for flight. Conversely, the thorax may need cooling on very hot days when muscle action creates too much thoracic heat. At high environmental temperatures large-bodied adult Lepidoptera such as *Manduca sexta* generate too much heat in the thorax, and the abdomen acts as a cooling radiator as hemolymph is allowed to flow rapidly to the abdomen which is less well insulated with scales than is the thorax. Heat is dissipated to the air surrounding the abdomen, and the cooler hemolymph is pumped back to the thorax by the heart.

References

Heinrich B (1996) The thermal warriors. Strategies of insect survival. Harvard University Press, Cambridge, MA, 221 pp

Heinrich B (970) Thoracic temperature stabilization by blood circulation in a free-flying moth. Science 16:580–582

Dorsoventral Muscles

Muscles running from the dorsal to the ventral components of thoracic segments that power the upstroke of wings during insect flight. These are indirect flight muscles, and they are not attached directly to the wings.

► Dorsal Longitudinal Muscles

Dorsum

The anatomical upper surface of a body; opposite of ventral. The legs are considered to be associated with the lower or ventral surface, and the dorsum is the opposite surface, the top of the head and the "back" of the thorax and abdomen.

Double-Eye Moths (Lepidoptera: Amphitheridae)

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Double-eye moths, family Amphitheridae, are an unusual and small family of mostly tropical moths, totaling 57 species, mostly Indo-Australian (one genus occurs in Europe and another in South America). The family is part of the superfamily Tineoidea, in the section Tineina, subsection Tineina, of the division Ditrysia. Adults small (11–22 mm wingspan), with head rough-scaled and eye usually divided; haustellum naked; maxillary palpi 1-segmented. Maculation is colorful and iridescent or duller and pale, and variously marked. Adults active diurnally. Larvae are leafminers, becoming leaf skeletonizers in later instars; host records are mostly in Betulaceae and Aceraceae. The family has been erroneously called Roeslerstammiidae, based on the single European genus, *Roeslerstammia*, named after the Austrian lepidopterist Joseph E. Fischer von Röslerstamm (1787–1866).

References

*Heppner JB (2003) Amphitheridae. In: Lepidopterorum Catalogus, (n.s.). Fasc 28. Association for Tropical Lepidoptera, Gainesville, FL, 8 pp

Kyrki J (1983) *Roeslerstammia* Zeller assigned to Amphitheridae, with notes on the nomenclature and systematics of the family (Lepidoptera). Entomol Scand 14:321–329

Moriuti S (1978) Amphitheridae (Lepidoptera): four new species from Asia, *Telethera blepharacma* Meyrick new to Japan and Formosa, and *Sphenograp tis* Meyrick transferred to the family. Bull Univ Osaka Prefecture B 30:1–17

Moriuti S (1987) Amphitheridae (Lepidoptera) of Thailand. Microlepidoptera Thailand 1:87–95

Viramo J (1968) Über die Verbreitung und die Wirtspflanzen von *Roeslerstammia erxlebeniella* F. (Lep., Acrolepiidae). Aquilo (Zool.) 6:12–17

Double Sampling

A sampling approach in which an initial sample (usually small) is drawn and used to determined the necessary sample size for a subsequent sample within the same time period.

► Sampling Arthropods

Douglas-Fir Beetle, *Dendroctonus pseudotsugae* Hopkins (Coleoptera: Curculionidae, Scolytinae)

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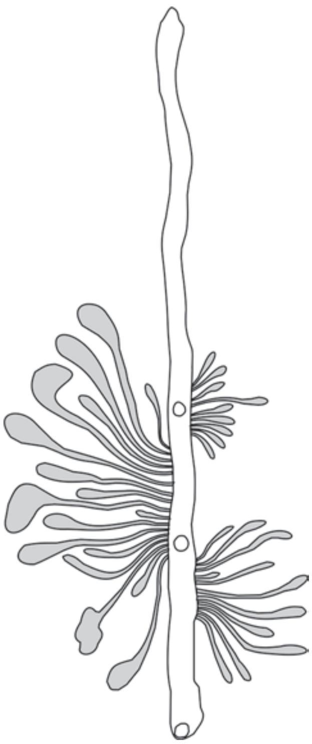
The Douglas-fir beetle, *Dendroctonus pseudotsugae*, is a bark beetle that attacks and can cause extensive mortality of its host Douglas-fir, *Pseudotsuga menziesii*, throughout most of its range in British Columbia, the western United States, and south to Mexico. The insect can also attack and reproduce in downed western larch, *Larix occidentalis* and subalpine larch, *L. laricina*, but is not able to complete development on standing larch trees. Western hemlock, *Tsuga heterophylla,* is also reported as a host. Just like with other tree-killing bark beetles, tree mortality results when the insects utilize the phloem of the tree for habitat and nourishment which results in girdling of the tree disrupting the translocation of nutrients. As the tree succumbs to the attack it changes in coloration within a year to a light yellow then to a bright orange before the needles begin to drop. The insect also inoculates attacked trees with blue-stain fungi *Ophiostoma pseudotsugae* and *Leptographium abietinum*, which may assist the insect in overcoming tree defenses.

Under endemic population levels the insect infests scattered trees downed by windstorms or stressed by root disease, defoliation, or fire injury. As populations increase healthy trees can be killed from small groups consisting of a few trees to groups of hundreds of trees. Epidemics can be quite devastating, but they usually only last about 4 years. Initial symptoms of attack include an accumulation of brown-reddish boring dust at the base of the tree and in bark crevices. Resin flow is also often observed, but not always, as it drains from attacks higher in the tree. Attacks are not always successful as the tree is often able to repel the insects from entering the tree by the copious exudation of resin.

The Douglas-fir beetle has one generation per year. There is a variation in flight periodicity from year to year and from one location to another but the primary dispersal flight usually occurs in mid- to late spring. Colonization of new trees is mediated by chemical attractants. Females initiate attacks on new hosts and after mating with a single male, begin constructing an egg gallery (Fig. 54) by tunneling up in the phloem parallel to the grain of the wood. The males assist in gallery construction at first by clearing boring dust and frass at the beginning of the gallery and then helping pack the rest of the gallery with frass. The egg galleries are usually 20–25 cm in length. As the females construct the gallery they lay eggs in niches alternately on both sides of the gallery in clusters of 5–24 eggs. The eggs are white and about 1 mm in length. Eggs hatch in 7–21 days. The larvae are white, c-shaped, and legless with shiny light brown heads. There are four larval instars. Through the summer each larva constructs its own larval gallery leading away from the egg gallery at approximately a



Douglas-Fir Beetle, *Dendroctonus pseudotsugae* Hopkins (Coleoptera: Curculionidae, Scolytinae), Figure 54 **Douglas-fir beetle egg gallery (drawing by Joyce VanDeWater).**

Douglas-Fir Beetle, *Dendroctonus pseudotsugae* Hopkins (Coleoptera: Curculionidae, Scolytinae), Figure 55 **Douglas-fir beetle adult (drawing by Joyce VanDeWater).**

right angle, pupates in a chamber at the end of the gallery, and later transform into the adult. Pupation usually occurs by August with transformation into the adult stage occurring late August-September. As the larvae develop they spread out forming a fan-shaped pattern that is distinctive of this species of bark beetle. The adult is the primary overwintering stage although some larvae may also overwinter. Newly emerged adults (Fig. 55) are light brown but later become dark brown to black with reddish elytra. Older beetles darken with time and become completely black. Adults are stout, cylindrical beetles, 4–6 mm in length.

A number of natural enemies help regulate populations of the Douglas-fir beetle. The most notable include clerid beetle predators *Enoclerus sphegeus* and *Thanasimus undulatus*, the predatory fly *Metedera aldrichii*, parasitoid wasps in the genus *Coeloides* and various woodpeckers.

Infestations of Douglas-fir beetle occur most commonly in overmature stands, with high stocking, and a high proportion of Douglas-fir. The largest trees in the stands are preferred. In downed trees the insect prefers to attack the underside of the tree. Because insect populations may increase rapidly in downed trees, rapid removal of downed trees may help reduce populations. Maintaining vigorously growing stands with adequate stocking levels can help mitigate tree mortality.

► Bark Beetles in the Genus *Dendroctonus*

References

Bedard WD (1950) The Douglas-fir beetle. U.S. Department of Agriculture Circular No. 817

Furniss MM, Johnson JB (2002) Field guide to the bark beetles of Idaho and adjacent regions. Idaho Forest, Wildlife, and Range Experiment Station, University of Idaho, Moscow, Idaho

Ross DW, Solheim H (1997) Pathogenicity to Douglas-fir of *Ophiostoma pseudotsugae* and *Leptographium abietinum*, fungi associated with the Douglas-fir beetle. Can J Forest Res 27:39–43

Schmitz RF, Gibson KE (1996) Douglas-fir beetle. Forest insect and disease leaflet #5. U.S. Department of Agriculture Forest Service

Douglasiidae

A family of moths (order Lepidoptera). They commonly are known as douglas moths.

► Douglas Moths

► Butterflies and Moths

Douglas, John William

John Douglas was born in London on November 18, 1814. At the age of 15, he was the victim of a practical "joke" by a schoolfellow, who set alight his pocket full of firecrackers. His extensive burns kept him bedridden for 2 years and required numerous operations throughout his life. While he was bedridden, he turned to the study of botany and drew plant specimens, at which he became proficient. He found employment at Kew Botanical Garden for a few years, but his father obtained for him a better-paying job at the Customs House. He married in 1843. While at Kew, he began collecting insects, and in 1837 published his first entomological paper. Much of his work was directed to Lepidoptera. His major work, coauthored with John Scott, was perhaps "The British Hemiptera, Volume 1, Hemiptera-Heteroptera," published by the Ray Society. Additions and corrections to this work were published from time to time in Entomologist's Monthly Magazine, of which he became editor in 1874. He joined the Entomological Society of London and held several posts, becoming president in 1861. He died on August 28, 1905.

Reference

Saunders E (1905) In memoriam. Douglas JW. Entomologist's Monthly Magazine 41:221–222

Douglas Moths (Lepidoptera: Douglasiidae)

JOHN B. HEPPNER

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Douglas moths, family Douglasiidae, comprise only 28 known species, mostly Palearctic (20 sp.). The family is part of the superfamily Tineoidea, in the section Tineina, subsection Tineina, of the division Ditrysia. Adults minute to small (6–15 mm wingspan), with head smooth-scaled; haustellum naked; labial palpi short; maxillary palpi reduced, 1-segmented. Maculation dull with bands of gray or tan, with venation reduced (especially in the hindwings) and with long hindwing fingers. Adults are crepuscular or diurnal. Larvae are leafminers or borers in petioles or stems. Host plants are known in Boraginaceae, Labiatae, and Rosaceae. The family and nominate genus *Douglasia* are named after the British lepidopterist and hemipterist John W. Douglas (1814–1905).

References

Gaedike R (1974) Revision der paläarktischen Douglasiidae (Lepidoptera). Acta Faunistica Entomol Mus Natl Prague 15:79–101

*Toll S (1956) Douglasiidae. In: Klucze do Oznaczania Owadüw Polski. 27. Motyle – Lepidoptera, 40:37–50. Polskie Towardzystwo Entomologiczne [in Polish]

Dragonflies

Certain members (suborder Anisoptera) of an order of insects (order Odonata).

► Dragonflies and Damselflies

Dragonflies and Damselflies (Odonata)

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Adult dragonflies and damselflies are two of the most beautiful and better-known insects of world. Their kaleidoscope of colors and aerobatic abilities have fascinated people for many centuries, and much has been written about them. They are conspicuous members of most permanent lakes, ponds, and wetlands. Nymphs of many species are also found in lotic habitats. Nymphs of some species are found in water filled leaf axils of plants, moist leaf litter, and even brackish water. Some species also occur in temporary habitats. Two North American species (family Petaluridae) are found among wet leaves in seepage areas.

Adults are medium to large in size, having wingspans ranging from 20 to 115 mm. Local names that have been applied to this order include, mosquito hawk, devil's darning needle and horse stinger. The order name is Odonata, which means tooth, and refers to the large prominent jaws or mandibles of the adults.

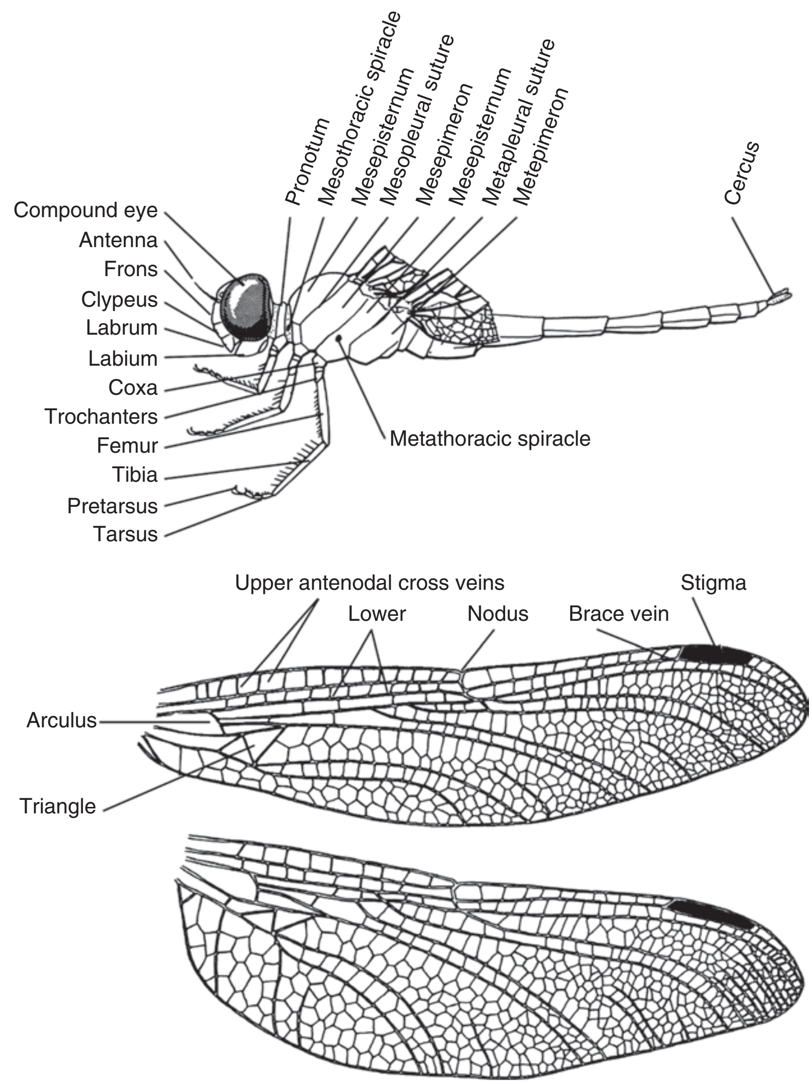
Adult dragonflies (Fig. 56) are easily recognized by two pairs of membranous elongate wings with many veins, long abdomen, bristle-like antennae and large head occupied mostly by the compound eyes. The nymphs are unique as compared to all other insect immatures by having the lower lip (labium) modified into a grasping structure that is elbowed and can be folded. The order includes two distinctive suborders in both the adults and nymphs in North America, the dragonflies or Anisoptera, and the damselflies or Zygoptera. The only other suborder of Odonata, the Anisozygoptera, includes one family, the Epiophlebiidae. This subfamily has two species, one distributed through the islands of Japan and the other in the eastern Himalayas in Nepal. Dragonfly adults are distinguished by hind wings (Fig. 57) that are wider at the base than the front wings, the abdomen long and stout, and when at rest wings are held outstretched. Nymphs are recognized by a long or oval body, and no gill plates at the end of the abdomen (Fig. 57) (instead there are three short pointed structures). Adult damselflies have both the front and hind wing of the same shape and size, a long thin abdomen, and wings held "roof-like" over the body at rest. Damselfly nymphs have elongate and slender bodies and three flat, elongate gill plates at the apex of the abdomen.

All Odonata adults are predators of flying insects, often small flies, but also larger insects such as wasps, butterflies, and even other dragonflies or damselflies. They use the front legs as a "basket" to scoop their prey out of the air. Sometimes adults will pick prey off plants or other substrates. Dragonfly and damselfly nymphs are accomplished visual predators of almost anything they can overpower, including microcrustaceans, other aquatic insects, to tadpoles, and even fish. They use the unique lower lip or labium to grab the prey and bring it to their mouthparts for consumption. Nymphs are either climbers or crawlers stalking their prey or, sprawlers and burrowers ambushing their prey.

Dragonfly nymphs pump water in and out of a gill chamber inside the posterior portion of the abdomen. This type of "jet propulsion" can be easily observed in a pan of water. Damselfly nymphs have three flat gill plates at the apex of the abdomen, providing a larger surface area for oxygen diffusion.

About 5,500 species of Odonata are known from the world grouped in 28 families, of which eleven are recorded from North America. Approximately 440 species have been recorded from North American. A summary of the North American species can be located at the website http://www.afn.org/~iori/nalist.html. Additionally, many useful links to other Odonata websites can be found at http://www.ent.orst.edu/ore_dfly/links.html.

Order: Odonata
- Suborder: Zygoptera
  - Family: Dicteriadidae
  - Family: Polythoridae
  - Family: Amphipterygidae
  - Family: Calopterygidae
  - Family: Lestidae



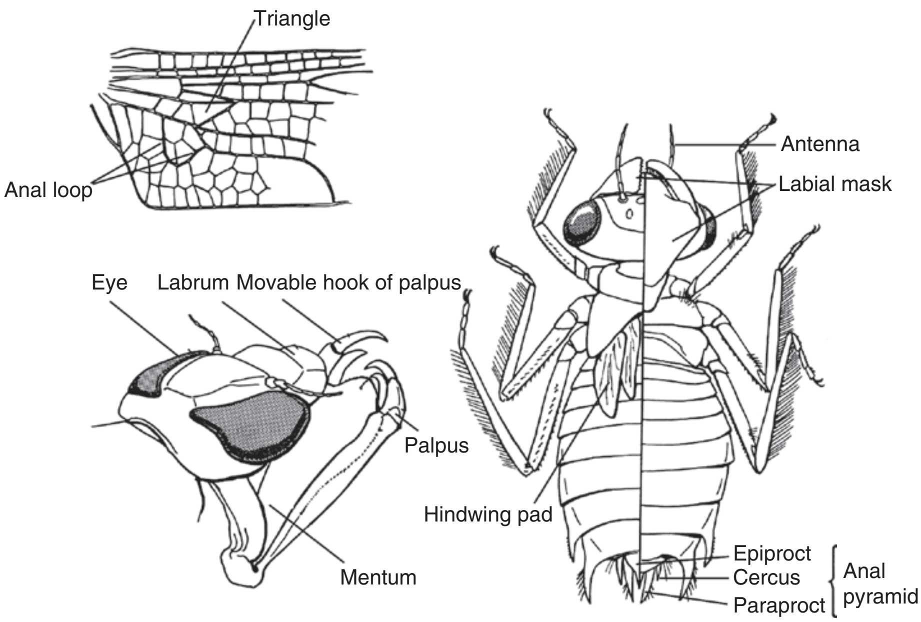
Dragonflies and Damselflies (Odonata), Figure 56 **Adult dragonfly: lateral view of female (above); front and hind wings (below).**

Family: Perilestidae
Family: Synlestidae
Family: Megapodagrionidae
Family: Pseudostigmatidae
Family: Platystictidae
Family: Protoneuridae
Family: Coenagrionidae
Suborder: Anisoptera
Family: Petaluridae
Family: Austropetaliidae
Family: Aeshnidae
Family: Gomphidae
Family: Neopetaliidae
Family: Cordulegastridae
Family: Corduliidae
Family: Libellulidae

A brief synopsis of common North American families is presented below.

Family Calopterygidae (Broad-winged Damselflies)

These well-known groups of familiar stream damselflies are known as the jewelwings (*Calopteryx*)



Dragonflies and Damselflies (Odonata), Figure 57 **Base of dragonfly hind wing (above, left) showing anal loop, a diagnostic character. Diagram of dragonfly nymph (right) showing dorsal (left portion) and ventral (right portion) perspective. Head of immature dragonfly showing the mouthparts (lower left), which are modified for grasping.**

and the rubyspots (*Hetaerina*). The large adults have metallic green bodies, the wings are not abruptly stalked at the base, and they have a skipping type of flight. The long-legged nymphs have a flat, pentagonal head, a very long first antennal segment, and are usually associated with instream aquatic plants, woody debris, and exposed roots of streamside plants. Species are characteristically associated with small to medium sized streams (*Calopteryx*) and larger rivers (*Hetaerina*). Only one generation per year is known for this group. Adults perch horizontally on twigs at the shore. The courtship behaviors of the adults have been extensively studied. The dancing flights are characteristic. Males have distinctive territorial display flights.

Family Lestidae (Spreadwinged Damselflies)

Nymphs of most species inhabit marshes and swamps, temporary standing water, and slow moving streams. The adults of these damselflies are easily recognized by their perching posture, at an oblique angle with partially spread wings. The long abdomen and petiolate part of the lower lip (prementum) easily distinguish the nymphs. One generation per year has been reported for the North American species. The two genera *Archilestes* and *Lestes* are widely distributed. *Archilestes* are usually found in streams of a slow current, even in isolated desert canyons of the Southwest.

Family Coenagrionidae (Narrowwinged or Pond Damselflies)

This family is the most successful of all damselflies in terms of the number of different species and types of aquatic habitats occupied. These are the red, orange, yellow and blue small adult damselflies commonly seen around ponds and various types of wetlands. The adults are known by such common names as sprites (genus *Nehalennia*), forktails (genus *Ischnura*), dancers (genus *Argia*), and bluets (genus *Enallagma*). Nymphs are usually associated with living or dead aquatic vegetation and debris. Nymphs of the genus Argia are often within rocky substrates of riffle reaches of streams. Egg-laying habits of the adult female are often astounding, with some species completely submerging and crawling about. Most species lay eggs just a few centimeters below the surface in plant material, both living and dead.

Family Aeshnidae (Darner Dragonflies)

The adults of these soaring dragonflies include the largest species in North America. Genera such as *Anax* (green darners), *Coryphaeschna* (pilot darners), and *Epiaeschna* (swamp darners) are the giants of this group. Many darners have long slender bodies resembling a darning needle, hence the name. The adults are easily identified by the large eyes meeting on top of the head, with the bodies brown, black and striped or spotted with blue. Nymphs are easily distinguished by the combination of a flat mentum and 6 or 7-segmented antennae. Adults are strong fliers, with some species migrating long distances. Often they feed in swarms. Nymphs are climbers, and are found among living and dead submerged plant material, including woody debris. Some species that occur in streams may be found clinging to submerged logs. Adult females insert eggs into underwater portions of plants. Nymphs may require 2–4 years to complete one generation.

Family Gomphidae (Clubtail Dragonflies)

Adults of clubtails get their name from the enlarged end of the abdomen in males of many species. Adults are beautifully camouflaged with brown or black marked with yellow or green. The eyes are widely spaced on top. Nymphs, like the family Aeshnidae, have a flat mentum, but the antennae are only 4-segmented. Adults usually perch on the ground horizontally and, unlike the darners, they do not soar but skulk around trees or make short distance flights in nearby fields, squatting on stones, sometimes branches of shrubs or on logs. Nymphs are burrowers in soft silt, sand or gravel of streams of all sizes or ponds. Nymphs of the huge dragonhunter, *Hagenius brevistylus*, are found among accumulations of leaves in quiet margins of streams. Most species require 2 years to complete their life cycle.

Family Libellulidae (Skimmer Dragonflies)

The skimmers include some of the most common dragonflies in North America. Almost every pond, lake or wetland has an assemblage of these species. A few species are found in streams. Adults of many species have prominent wing patterns, and many have brightly colored abdomens of red, blue and other colors. Adults can be easily distinguished by the characteristic boot-shaped anal loop of the hind wing. Adults usually perch on tips of stems, and have a gliding type of flight. Nymphs can be usually recognized by the scoop-like labial palps with the distal margins relatively smooth. However, nymphs are often difficult to distinguish from the Corduliidae (in some classifications only recognized as a subfamily, the Corduliinae). Nymphs are sprawlers or climbers, and found in all types of standing water, from hoof prints to the edges large lakes or reservoirs. A few species are even found in brackish water and other estuarine environments. Well-known genera are *Libellula* (king skimmers), *Sympetrum* (meadowhawks), *Erythrodiplax* (dragonlets), *Perithemis* (amberwings), *Erythemis* (pondhawks), *Tramea* (saddlebags gliders), and *Celithemis* (small pennants).

References

Abbott JC (2005) Dragonflies and damselflies of Texas and south-central United States. Princeton University Press, Princeton, NJ, 344 pp

Beaton G (2007) Dragonflies and damselflies of Georgia and the southeast. University of Georgia Press, Athens, Georgia, 355 pp
Corbet PS (1999) Dragonflies. Behavior and ecology of Odonata. Comstock Publishing Associates, Ithaca, New York, 829 pp
Dunkle SW (2000) Dragonflies through binoculars: a field guide to dragonflies of North America. Oxford University Press, New York, NY, 252 pp
Garrison RW, von Ellenrieder N, Louton JA (2006) Dragonfly genera of the New World. An illustrated and annotated key to Anisoptera. Johns Hopkins University Press, Baltimore, MD, 368 pp
Needham JG, Westfall MJ Jr, May M (2000) Dragonflies of North America. Scientific Publishers, Gainesville, FL, 939 pp
Silsby J (2001) Dragonflies of the world. Smithsonian Institution Press, Washington, DC, 216 pp
Westfall MJ Jr, May ML (1996) Damselflies of North America. Scientific Publishers, Gainesville, FL, 649 pp

Drake, Carl John

Carl Drake was born on a farm in Ohio on July 28, 1885. He obtained a B.S. degree (and a Bachelor of Pedagogy) from Ohio State University in 1912, then in 1914 an M.S. degree and in 1921 a Ph.D. degree from the same institution. He worked for 4 years as specialist in entomology in the School of Forestry, Syracuse University, then from 1922 to 1946 in the Department of Zoology and Entomology at Iowa State University. In this last position, he was not only departmental head, but also head of the entomology section of the Iowa Agricultural Experiment Station. His taxonomic interests were in lace bugs and semiaquatic Hemiptera, of which he built a large collection. His experiment station obligations as applied entomologist had him working on grasshoppers, chinch bug, Hessian fly, and European corn borer. He was a member of the Central States Plant Board, the National Plant Board, and the American Association of Economic Entomologists. On retirement in 1946, he concentrated on his taxonomic interests, and in 1957 moved to work as an honorary Research Associate of the U.S. National Museum in Washington, DC. By working at the museum 61/2 days per week (he never married), his lifetime publications list grew to exceed 500 papers. He died on October 2, 1965, in Washington, DC.

Reference

*Mallis A (1971) Carl John Drake, In: American entomologists. Rutgers University Press, New Brunswick, NJ, pp 238–239

Drench Treatment

Application of a liquid insecticide to an area, usually soil, until it is completely penetrated.

Drepanidae

A family of moths (order Lepidoptera). They commonly are known as hook-tip moths.

► Hootktip Moths
► Butterflies and Moths

Driver Ants (*Dorylus* subgenus *Anomma*) (Hymenoptera: Formicidae)

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Driver ants are those army ant species in the afrotropical subgenus *Dorylus (Anomma)* that hunt by massive swarm raids on the forest floor and up in the vegetation. Any animal capable of moving fast enough and lacking other effective protective mechanisms flees from such an advancing swarm of hundreds of thousands or even millions of ant workers in search of prey. Hence the raid swarm “drives” many animals before it. Due to their ferocious nature, these ants are recognized by their own name in many tribal languages in sub-Saharan Africa. In Ghana, for example, they are called "Nkran" in the Twi language. In Kenya, people in the Meru tribe use the term "Thuraku" for them. Their common English name was originally coined in 1847 by Dr. Thomas Savage in the description of his observations of *D. (A.) nigricans* colonies in present-day Liberia. Although other authors have subsequently applied the term to all species in the subgenus *Anomma* (as currently recognized) or even to all species in the genus, it is best to stick with its original meaning to avoid confusion.

Taxonomy and Phylogeny

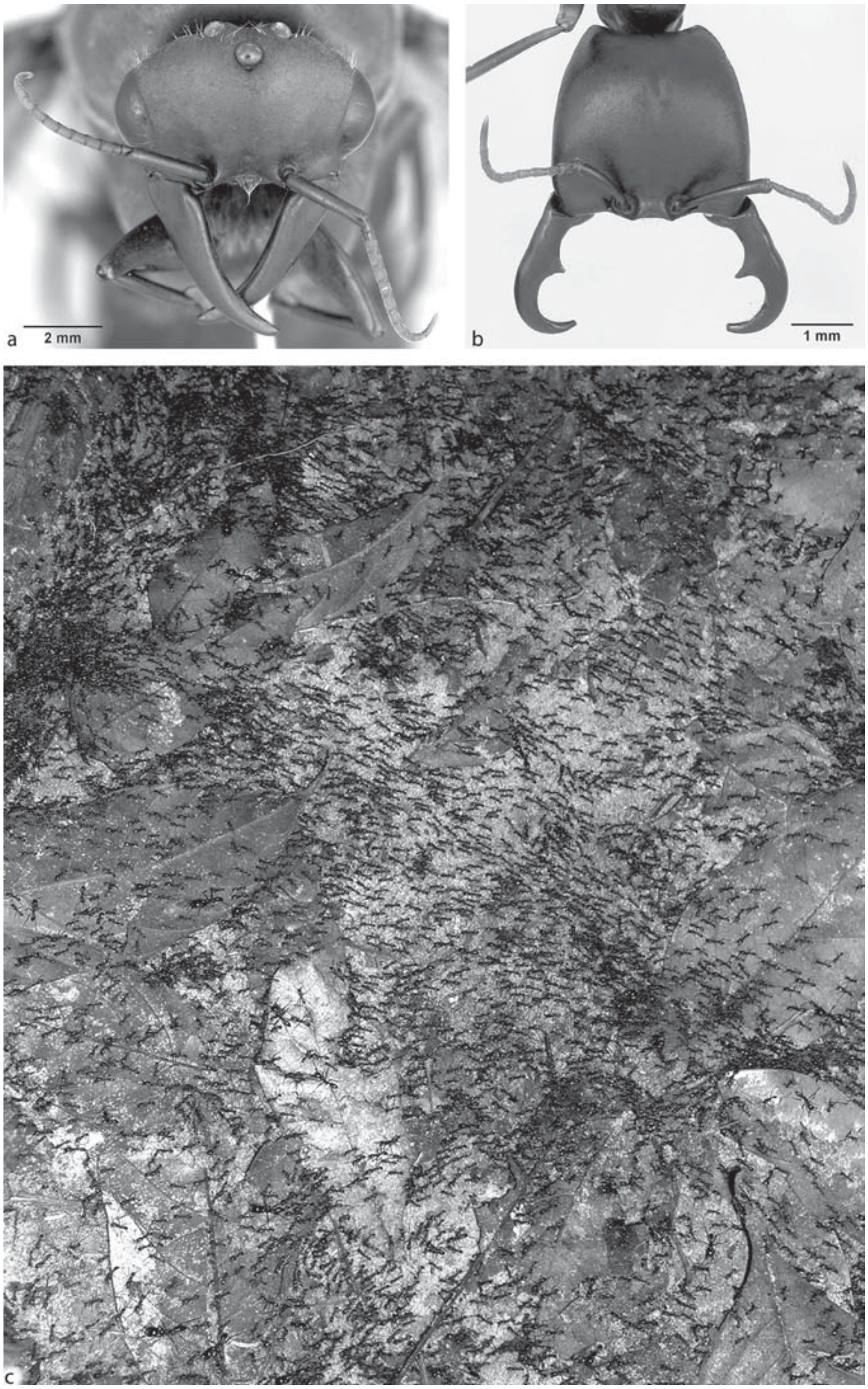
Many species in the genus *Dorylus* (as well as many other army ants) were described based only on a single caste or sex and the associations between these different forms have been hard to establish. Therefore, delimitating the subgenus *Anomma* proved difficult and several other species not showing the typical "driver ant" hunting behavior but foraging less conspicuously in the leaf-litter were also described as species in the subgenus *Anomma* after 1847. But recent evidence from a molecular phylogeny indicates that the subgenus *Anomma* as currently defined is actually paraphyletic. The species that forage in the leaf-litter are more closely related to subterranean species of the subgenus *Dorylus* s.s. than to the driver ants (in the sense of Savage's original functional definition), which form a well-supported clade. This result thus indicates that the foraging in massive surface swarms evolved only once within the genus *Dorylus*. Since the type species for the subgenus *Anomma* is a driver ant, the species hunting in the leaf-litter stratum will have to be removed from *Anomma* in a revised subgenus classification of the genus *Dorylus*. Although more than thirty nominal forms have been described under *Anomma* (including those taxa that turn out to be more closely related to *Dorylus* s.s.), there are probably only about ten species of driver ants.

Morphology

Workers

Driver ant workers can be distinguished from the workers of all other *Dorylus* species by several qualitative and quantitative traits (these apply mostly to the largest individuals). The qualitative traits are the presence of basisternal spines, frontal carinae reduced, mesonotum in lateral view impressed, petiole long and slender, and strongly (Fig. 58) trapezoidal head shape (head width much wider anteriorly than posteriorly). Moreover, driver ant workers have relatively (i.e., for a given worker dry mass) longer mandibles, legs and antennae, and these features are probably adaptations associated with the derived driver ant foraging mode. While their longer mandibles can inflict more painful bites and thus provide better protection against predators, longer legs allow faster and more efficient locomotion, the transport of larger prey items (prey is carried slung underneath the body) and finally perhaps also better climbing of vegetation. Longer antennae, on the other hand, will help workers to follow pheromone trails at higher speed while avoiding collisions in spite of dense traffic. Being more exposed to sunlight during foraging, driver ant workers also tend to be darker than workers of species hunting in leaf-litter and soil. Like workers of all other *Dorylus* species, driver ant workers lack eyes.

The degree of worker polymorphism in driver ants (and other *Dorylus* species) is among the most extreme in ants. In some species the largest workers have a dry mass 200-fold that of the smallest workers. These extreme differences in size are associated with striking differences in the number of antenna segments (varying between eight in the smallest workers and 11 in the largest), hairiness, mandible structure (with many teeth in the smallest workers and only an apical and subapical tooth in the largest), head shape (from rectangular in the smaller individuals to trapezoidal in the largest), coloration (from light brown to very dark or black) and in the relative



Driver Ants (*Dorylus* Subgenus *Anomma*) (Hymenoptera: Formicidae), Figure 58 **Driver ants: (a) Head of a *Dorylus* (*Anomma*) *nigricans* male in frontal view. The mandible is very long and slender and the head is high (photograph by April Nobile, from www.antweb.org); (b) Head of a large *D.* (*A.*) *sjoestedti* worker in frontal view. The head is much wider anteriorly and the mandible has only two teeth (photograph by April Nobile, from www.antweb.org); (c) A raid swarm of *D.* (*A.*) *nigricans* advancing on the forest floor in the Taï forest, Ivory Coast (photograph by Caspar Schöning).**

sizes of several other body parts. In general, it is fair to say that the morphological diversity in a driver ant colony is larger than in some other entire ant genera. This substantial variation has contributed to the confusion in driver ant taxonomy because some species were described more than once based on workers belonging to different size-classes.

Males

In Africa, *Dorylus* males are collectively referred to as sausage flies and the first *Dorylus* males to be found were described as a *Vespa* wasp species by Linné. *Dorylus* males possess a pair of compound eyes and three ocelli. The mandibles of driver ant males are relatively longer and more slender than those of other *Dorylus* species, and their heads are relatively longer than the extremely broad heads of other *Dorylus* males. Moreover, they are much darker.

Queens

Driver ant queens are perhaps the largest ants in the world, those of *D. wilverthi* may be up to 6 cm long and may lay as many as 3–4 million eggs every month. Driver ant queens, like workers, do not possess eyes. It is unclear which characters in the driver ant queen caste are actually apomorphies because the queens of many *Dorylus* species are unknown so that comparative studies are difficult but the shape of the hypopygium of driver ant queens seems to be unique within *Dorylus*.

Behavior

The raiding swarms of driver ants are one of the most fascinating examples of coordinated group activity shown by animals with hundreds of thousands or even a few million ant workers forming a dense carpet acting as a dragnet that sweeps through areas of 1,000 m^2 or more in a single day in search of prey. Workers climb vegetation up to a height of several meters. The swarms can be 30 m or more wide and move forward at a speed between 7 and 25 m per hour depending on the species. The foraging distances of *D. wilverthi* colonies may be up to 220 m. Driver ants are almost exclusively carnivorous but they are also attracted to oily vegetative products such as palm nuts and avocadoes. Their raids appear to be an efficient strategy to harvest abundant and evenly distributed small prey (such as solitary insects) as well as rare and very patchily distributed large prey (such as mammal carcasses). Driver ant prey spectra are therefore extremely diverse. Although quantitative data are lacking, driver ant species are likely to be the most polyphagous predators on earth. Solitary insects (especially their less mobile immature stages) and earthworms make up the majority of the biomass retrieved. Most vertebrates easily escape, but sometimes small amphibians (e.g., frogs), mammals (e.g., mice) and reptiles (e.g., chameleons) fall victim to the raid swarms. Large captive animals such as snakes and monkeys have been reported to be eaten to the bones by driver ants. In the hunting behavior it becomes evident that the extreme worker polymorphism is linked to a pronounced, yet flexible, division of labor. While the proportion of larger workers is very small in the swarm, they are crucially important and disproportionately overly represented in the tasks of pinning down, dismembering and retrieving larger prey. Workers can cooperate in the transport of large prey items with large workers grabbing the item at the front and one or more small workers lifting it off the ground at the back. In the species examined so far, most of the prey biomass is transported by such groups.

At irregular intervals, the entire colony migrates to a new nest site, most probably as a result of resource depletion around the nest. Migrations can last up to 4 days and include the movement of the colony's queen, its workers and its brood carried by the workers. Unlike some army ant species in the subfamily Ecitoninae, the temporal emigration pattern is not linked to a rhythm in the queen's egg-laying activity. Some migrations are triggered by predator attacks on the nests.

Colonies nest in the soil, usually at the base of trees. Over the period of a nest stay, workers may bring up large amounts of soil (40 kg or more) to the surface. In the nest, the workers form a big cluster that hangs suspended from roots and contains the brood and queen. Quite often, colonies reoccupy old nests that they or other colonies had used before.

Driver ants reproduce by colony fission like honeybees. Colony fission directly creates colonies with worker populations large enough for conducting swarm raids. When a colony has grown to a large enough size, the queen lays eggs that develop into queens and males. The sex ratio is highly male-biased. Only a few (two to fifty) queens, but several hundreds or up to a few thousand males, are reared. After about 4 weeks, the queen pupae hatch and all but one of the virgin queens are killed in ways not yet understood. At this point the old queen leaves the nest with about half the worker population. The remaining queen will subsequently mate with several males that fly in from foreign colonies. The males in this nest hatch after about 8 weeks and then in turn fly off at night in search of foreign nests with virgin queens ready to mate. When the males have flown off, the new queen and the remaining workers form a new functional colony and are free to migrate to new foraging grounds. Although there is a tendency for colonies to reproduce towards the end of the dry season, colony fissions take place throughout the year. In two species, colonies have been observed to produce males without a subsequent colony fission.

Ecology

With a worker population of up to nine million individuals, driver ant colonies form the largest single-family insect societies on earth, and thus have a voracious appetite. The immediate effect of their raids is a reduction of the biomass and perhaps the diversity of invertebrates in the foraging areas. Driver ants therefore create a mosaic of patches in different stages of recovery from prey extraction. By this mechanism, they may promote diversity in the invertebrate communities, but to date studies examining the effect of driver ant raids on the prey population dynamics are lacking. This issue becomes both more complex and interesting when one considers that up to three driver ant species can coexist at a site. Depending on the degree of resource partitioning between them, the combined impact on the invertebrate communities in the vegetation and on the forest floor may be very strong.

Driver ant colonies are hosts to diverse assemblages of so-called myrmecophiles. These are animals (such as certain staphylinid beetles and isopods) that have evolved mechanisms to integrate into the colonies without the ants identifying them as non-nestmates. These mechanisms represent either chemical or tactile camouflage (or both). It is difficult to examine what exactly all these species are doing in the colony but it seems likely that the majority are parasitic, while others are commensals. Blind snakes of the genus *Typhlops* parasitize driver ant colonies by feeding on the brood or on the prey brought in by the foraging workers.

The number of bird species specializing in attending the raid swarms to catch animals flushed by the advancing ants (and sometimes stealing prey from them) is much smaller than in South America where many dozens of "ant-birds" are closely associated with two swarm-raiding ant species in the subfamily Ecitoninae. The paucity of specialized ant-following birds in Africa is puzzling in view of the higher colony density and diversity of driver ants.

In spite of their painful bites, driver ants are preyed on by several mammals, including pangolin, honey badger, aardvark, gorilla, Jackson's mongoose and the common chimpanzee. The last species is the only one known to employ tools when taking driver ant prey. After opening the nest with the hands, so-called ant-dipping wands are inserted into the mass of ants in the central nest cavity. When enough ants have climbed the wand, it is removed and the ants are swiped off the tool with the hand or mouth and then hastily eaten. The effect of mammal predation on the growth and fitness of driver ant colonies has not yet been studied. *Dorylus* species in the subgenus *Typhlopone* are the most important invertebrate predators of driver ants. They attack driver ant colonies in their nests through tunnels in the soil and sometimes destroy them.

Finally, driver ants are also ecologically important because they move large amounts of soil, not only in nest construction but also when preparing their foraging and migration trails as "roads" with an even surface or as trenches and tunnels. The soil carried to the surface during nest construction is enriched with the indigestible prey remains and thus presumably rich in nitrogen and other plant nutrients.

Habitat and Distribution

Driver ants are restricted to sub-Saharan Africa. Within this vast region, they occur primarily in forests and other humid habitats. Some species appear to depend strictly on forest, while others such as the East-African *D. (A.) molestus* live in a wide range of habitats such as scrubland in proximity to rivers, woodland, agroforestry systems (e.g., banana, cocoa and coffee) and forests from sea level up to 3,000 m altitude.

Economic Importance

Driver ants provide a valuable pest-control service when invading houses and hunting in cultivated land. However, these benefits are probably outweighed by the damage they cause when attacking humans and livestock. Unlike termite alates, driver ant males are not eaten by people, although they would appear to be nutritiously rewarding. The reason is probably that their availability is far less predictable and that termite alates are much softer and easier to roast and chew.

References

Gotwald WH Jr Army ants – the biology of social predation. Cornell University Press, Ithaca, New York

Kronauer DJC, Schöning C, Vilhelmsen LB, Boomsma JJ (2007) A molecular phylogeny of *Dorylus* army ants provides evidence for multiple evolutionary transitions in foraging niche. BMC Evol Biol 7:56; http://www.biomedcentral.com/1471–2148/7/56

Leroux JM (1982) Ecologie des populations de dorylines *Anomma nigricans* dans la région de Lamto (Côte d'Ivoire). Publications du Laboratoire de Zoologie, No. 22. Ecole Normale Supérieure, Paris

Raignier A (1972) Sur l'origine des nouvelles sociétés des fourmis voyageuses Africaines (Hymenopteres, Formicidae, Dorylinae). Insectes Soc 19:153–170

Raignier A, van Boven JKA (1955) Étude taxonomique, biologique et biométrique des *Dorylus* du sous-genre *Anomma* (Hymenoptera, Formicidae). Annales Musée Royal du Congo Belge Nouvelle Série in Quarto Sciences Zoologiques 2:1–359

Savage TS (1847) On the habits of the "drivers" or visiting ants of West Africa. Trans R Entomol Soc Lond 5:1–15

Schöning C, Njagi WM, Franks NR (2005) Temporal and spatial patterns in the emigrations of the army ant *Dorylus (Anomma) molestus* in the montane forest of Mt. Kenya. Ecol Entomol 30:532–540

Droplet Spermatophore

A spermatophore (capsule containing sperm) that is attached to a thread-like stalk, which in turn has an adhesive base for placement on a substrate. Male Collembola often distribute their sperm in this manner.

Drosophilidae

A family of flies (order Diptera). They commonly are known as small fruit flies, vinegar flies, or pomace flies.

► Flies

Drumming Communication and Intersexual Searching Behavior of Stoneflies (Plecoptera)

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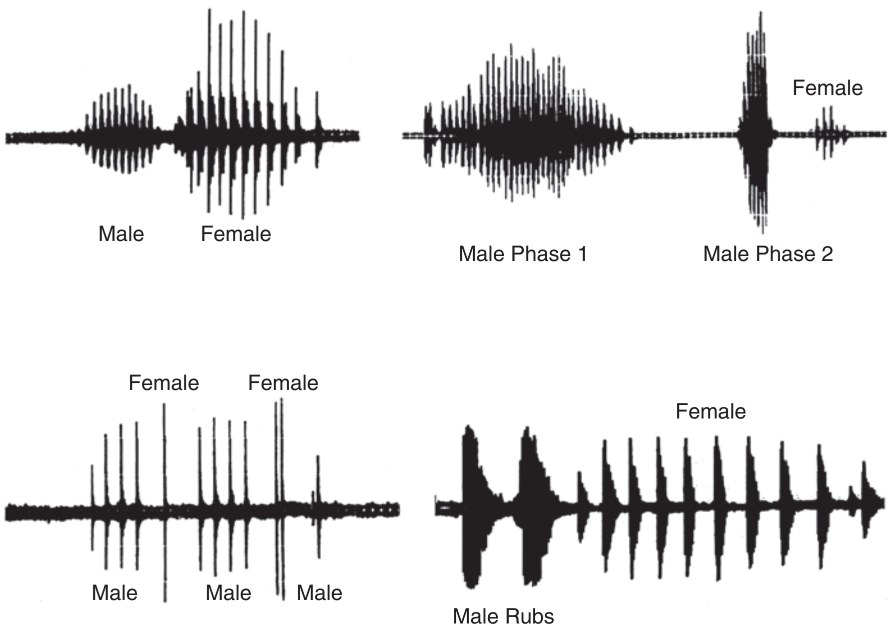
Stoneflies of the Northern Hemisphere suborder Arctoperlaria have evolved the most diverse and complex system of vibrational communication known in insects. Only leafhoppers and delphacid planthoppers possibly have evolved signals as complex as those of stoneflies, but relatively few species of those two groups have been studied. The first studies in the 1960s and 1970s that were designed to quantify the drumming communication of stoneflies established that: (i) vibrational signals were produced by percussion, with either the unmodified or specialized distal, ventral portion of the abdomen, (ii) duets were either "2-way" (male call-female answer sequences) or "3-way" (male call-female answer-male reply sequences), (iii) male calls were more complex than female answers or male replies, (iv) the signals of both sexes and their duet pattern were species-specific and therefore probably fixed action behaviors, and (v) during duetting, males searched for stationary females, establishing that the behavior was part of the mate-finding system. Intensive research in the past three decades has revealed that signals are produced in some groups by methods other than percussion, that the rhythms and exchange characteristics of both males and females vary in complex ways and that the search behaviors in relation to drumming are more than simple "bee-line homing" of the male on females.

The entire mating system of stoneflies involves both their intersexual communication with vibrational signals and the associated aggregation and movement (searching-related) behaviors of both sexes. The typical system in Arctoperlaria involves the sequence of: (i) encounter site aggregation of sexes, (ii) species-specific calling by males with vibrational signals during a ranging, non-oriented search, (iii) duet establishment when females within communicable range answer with vibrational signals, then (iv) a localized, oriented search by the moving male toward the now stationary female until location and mating are accomplished. Males are polygamous and continue calling and searching during their short reproductive lives. Typically, only virgin females answer males and, once mated, reject subsequent male advances by raising and curving their abdomens.

There is obviously no fossil record for vibrational communication in stoneflies, so formulation of a paradigm on how the behavior originated and has been further developed has of necessity depended on patterns revealed from modern species. Out-group comparisons with the Grylloblattodea, other orthopteroid groups and the Southern Hemisphere stonefly suborder Antarctoperlaria, indicate that ancestral stoneflies were non-drummers. The first trace of the behavior probably resulted from males accidentally bumping their unmodified abdomen while searching for females, followed by the possible defensive response of females to the vibrations by becoming motionless and stationary. Selection progressively reinforced the male bumping and female response into behavioral actions until a relatively simple, sequenced duetting (male calls-female answers) developed, that represents an ancestral pattern. The signals of both sexes were produced by percussion and were monophasic volleys of even spacing and little amplitude modulations (Fig. 59).

Out-group comparisons have indicated further that species-specificity and behavioral isolation were then derived from this ancestral pattern (and are represented in modern species) by either: (i) retention of the ancestral pattern with slight modifications of signal characteristics (number of beats, overlap of the male-female duet, changing the beat interval rhythm or amplitude modulation) in both male and female signals; (ii) major rhythm changes, particularly in male calls, by phasing or grouping of signal beats; (iii) changes in the method of signal vibration



Drumming Communication and Intersexual Searching Behavior of Stoneflies (Plecoptera), Figure 59
Patterns of signaling among stoneflies: upper left, ancestral-type signaling duet of *Pictetiella expansa;* upper right, duet with a diphasic male call of *Acroneuria abnormis;* lower left, symphonic exchange with grouped male call and grouped-interspersed female answers of *Isogenoides zionensis;* lower right, signal exchange with a 2-rub male call and female percussion answer of *Doroneuria baumanni.*

production from ancestral percussion to abdominal substrate stridulation (rubbing), or in rare cases, body jerking or pushups without touching the substrate (tremulation); or (iv) combinations of these changes. The result in modern arctoperlarian stonefly species is an exciting and highly derived and complex array of signal and duet patterns, each unique to particular species, and in some cases fairly uniform in pattern among particular genera or families.

The most specialized male calls involve his rubbing the substrate with a specialized, and probably co-evolved, abdominal knob or hammer. Each rub probably represents a modified and prolonged ancestral percussion stroke, using the knob or hammer that may be uniquely ridged or dimpled. This produces a squeaking sound on resonant substrates. Males of various species produce one to seven rubs, always answered by their females with percussion-produced signals.

Little is known about the searching behaviors of species once duet communication between males and females has been established. Recent studies have established that the vibrational communication definitely functions to reduce the time required for males to find females, and that females can be sexually selective by not answering males that call with abortive calls, or by remaining stationary only for some specified time that allows a more fit drumming-searching male to find her. Males generally search by triangulation during duetting with females on flat surfaces. On naturally branched surfaces, such as live or dead plant stems, a male progressively calls on the main stem and on each branch just beyond each bifurcation toward an answering female, effectively determining whether her answering vibrational signal comes from in front or behind him, and therefore whether she is out on that branch or on a branch further away on the main stem. In species that use tremulation, males fly and land on riparian shrubs and call on leaves; if a female sitting on another leaf responds, he moves toward her, testing leaf by leaf just beyond each petiole junction. Females in this case move to the petiole-leaf junction and become stationary, effectively insuring that once the male finds her correct leaf location, he does not have to search the entire leaf surface to finally make contact with her. This can be described as a "fly-tremulate-search" pattern. All stonefly species that have been studied appear to utilize an initial and specific type of sexual encounter site for initial aggregation of the sexes. This is followed by a ranging search with males intermittently calling for females, then beginning a more localized and oriented search once females answer with signals that reveal her location. Mating of stoneflies ensues almost immediately after males find females; no elaborate courtship behaviors have been discovered.

► Vibrational Communication
► Acoustic Communication in Insects

References

Stewart KW, Maketon M (1991) Structures used by nearctic stoneflies (Plecoptera) for drumming, and their relationship to behavioral pattern diversity. Aquat Insects 13:33–53

Stewart KW (1994) Theoretical considerations of mate finding and other adult behaviors of Plecoptera. Aquat Insects 16:95–104

Stewart KW (1997) Vibrational communication in insects, epitome in the language of stoneflies? Am Entomol 43:81–91

Stewart KW (2001) Vibrational communication (drumming) and mate-searching behavior of stoneflies (Plecoptera); evolutionary considerations. In: Dominguez E (ed) Trends in research in Ephemeroptera and Plecoptera. Kluwer Academic/Plenum Publishers, Dordrecht, The Netherlands, pp 217–225

Zeigler DD, Stewart KW (1977) Drumming behavior of eleven Nearctic stonefly (Plecoptera) species. Ann Entomol Soc Am 70:495–505

Dry Bark Beetles

Members of the family Bothrideridae (order Coleoptera).

► Beetles

Dry-Fungus Beetles

Members of the family Sphindidae (order Coleoptera).

► Beetles

Dryinidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Dryopidae

A family of beetles (order Coleoptera). They commonly are known as long-toed water beetles.

► Beetles

Drywood Termites

A group of termites in the family Kalotermitidae known to attack dry wood that is not in contact with the soil. (contrast with dampwood and subterranean termites)

► Termites

dsDNA

► Double stranded DNA

Dubas Bug (Old World Date Bug), *Ommatissus lybicus* Bergerin (Tropiduchidae: Hemiptera)

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The Dubas bug or Old World date bug feeds on the leaves of the date palm trees, *Phoenix dactyifera*, in Iraq, Iran, Saudi Arabia, Bahrain, Oman, Egypt, Lybia, Algeria and Trinidad. It is closely related to *Ommatissus binotatus* DeBerg, which attacks the wild palm, *Chamaerops humilis*, in

North Africa, Spain, and in the southeastern region of the former Soviet Union.

Description

The adult female is about 5–6 mm in length, yellowish green and has up to ten dark spots on the head and 7th and 8th abdominal segments. The adult male is about 3–3.5 mm in length. It differs from the female by the absence of the dark spots on the 7th and 8th abdominal segments, the more tapered abdomen and the greater length of the wings relative to the abdomen. The eggs are elongated, cucumber like and about 0.5–0.8 mm in length. They are bright green in color at deposition, then change to yellowish white and later to bright yellow. The nymphs are bright brown and have dark stripes on the dorsal surface of the thorax and abdomen. The tip of the abdomen terminates in an extension or cauda-like structure and has 16 white waxy filaments, each about 3 mm long. The eyes are red and the nymphs can walk and jump up to 60 cm.

Symptoms and Economical Importance

The adults and nymphs feed on the sap of the leaflets and midribs of the date palm frond. At high levels of infestation, Dubas bugs attack the fruit stalks and the fruit. Dubas excrete heavy honeydew and dust sticks to it. The infested leaflets become light green and yellow green in color. Necrotic areas (damage) are noticeable on the infested fronds and are caused by egg-laying. Dubas bug is an occasional pest, meaning that it becomes an important pest for a season or two, followed by less damage in the coming seasons. At high levels of infestation, 50% of the date yield may be lost. Dubas bugs may cause indirect damage to crops that are grown under the infested date palm trees due to the dripping of honeydew.

Biology

Dubas bugs have two generations per year, a spring and autumn generation. Dubas bugs hibernate in the winter and aestivates in the summer as eggs in the axial veins and midrib of the date palm fronds. A female deposits an average of 100 eggs during its life-span. Eggs hatch in April and in September in the spring and autumn generations, respectively. Newly hatched nymphs disperse into the frond folds or onto young fruits, and commence feeding. The nymphs pass through five instars. Nymphal duration is about 6 weeks. The adults can fly, and their habitat is the same as the nymphs.

Control

A small chalcidiod wasp parasitizes the eggs of the Dubas bug. The larvae of lacewings also prey on the Dubas nymphs and adults. The adult beetles of three species of the coccinellids attack the nymphs and adults of the Dubas bugs.

Certain cultural practices help to keep the trees healthy. Good drainage and windbreaks help to reduce injury by this pest. Systemic insecticides can be used at high levels of infestation. Aerial application of insecticides is most useful for wide-ranging infestations, or when the height of the date palm trees makes it difficult to apply chemical pesticides from the ground. However, aerial application increases scale insect infestations because the pesticide kills their natural enemies.

References

Talhouk N (1984) The most common agricultural pests in Saudi Arabia. Ministry of Agriculture and Water, 121 pp (in Arabic)

Hussain A (1974) Pests of date palm trees and dates in Iraq. Baghdad University, 190 pp (in Arabic)

Hammad SM, Kadous AA (1989) Studies on the biology and ecology of date palm pests in the eastern Province of

Saudi Arabia. Research Grants Program, KACST, Riyadh, Technical Report No. 25, 142 pp
Kranz JH, Schmutter, Koch W (eds) (1977) Diseases, pests and weeds in tropical crops. Verlage Paul Parey, Berlin

Dudgeon Carpenterworm Moths (Lepidoptera: Dudgeoneidae)

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Dudgeon carpenterworm moths, family Dudgeoneidae, includes only six species in the single genus *Dudgeonea*, with two species from Africa, one from India, and three from Australia. The family is in the superfamily Cossoidea (series Cossiformes) in the section Cossina, subsection Cossina, of the division Ditrysia. Adults medium size (28–72 mm wingspan), with head somewhat rough-scaled; haustellum absent; labial palpi upcurved; maxillary palpi 3-segmented; antennae pectinate (rarely bipectinate). Body robust; abdomen with small tympanal organs. Wings elongated; forewings rounded at termen (Fig. 60). Maculation dark with golden or light spots; hindwing pale. Adults nocturnal as far as is known. Larvae mostly unknown, but one Australian species is a stem borer on Rubiaceae. The family and genus *Dudgeonea* are named after the British lepidopterist Gerald C. Dudgeon (18??-1930), who published mostly on Indian Lepidoptera.

Dudgeon Carpenterworm Moths (Lepidoptera: Dudgeoneidae), Figure 60 Example of dudgeon carpenterworm moths (Dudgeoneidae), *Dudgeonea leucosticta* Hampson from South Africa.

References

*Holloway JD (1986) Family Dudgeoneidae. In: Moths of Borneo, 1:41, pl 4. Malayan Nature Society (Malayan Nature Journal 40:41, pl 4), Kuala Lumpur
Roepke W (1955) Notes and description of Cossidae from New Guinea (Lepidotera: Heterocera). Trans R Entomol Soc Lond 107:281–288, 2 pl [part: Dudgeonea]
Schulze CH, Fiedler K (1996) First record of the family Dudgeoneidae (Lepidoptera, Ditrysia) for Borneo. Tinea 15:74–77

Dudgeoneidae

A family of moths (order Lepidoptera). They also are known as Dudgeon carpenterworm moths.

► Dudgeon Carpenterworm Moths
► Butterflies and Moths

Dudich, Endre

GEORGE HANGAY
Narrabeen, NSW, Australia

Endre Dudich was born on the March 20, 1895 at Nagysallü, in Bars Shire, Hungary. At an early age his interest was influenced by his father, who was a medical practitioner and liked zoology. He attended college in Esztergom (Northern Hungary) continuing his studies at the Pázmány Péter University of Science. During World War I, his university studies were interrupted with three and a half years of military service, during which he served on the front. He received his diploma in 1920 and in 1922 the doctorate. Due to the friendship and encouragement of Elemér Bokor, he focused his research on the Coleoptera and the invertebrate fauna of caves. However, one of his main achievements was a major work on zoological taxonomy (Rendszeres állattan. Pécs, 1927), which has established him as a leading scientist of that field. In 1934 he was commissioned to establish the Institute of Zoological Taxonomy. He worked in this institute until his death. Endre Dudich pioneered modern taxonomical and zoogeographical research in Hungary and created the country's first underground research station in the Baradla Cave (northeastern Hungary). He became a leading expert in the biological research of caves and from 1958 until 1970 he directed scientific work at the Danube Research Station at Alsü Göd, north of Budapest. He kept working until his death on the February 5, 1971.

References

Balogh J (1971) Endre Dudich. Magyar Tudomány, Budapest, 6
LOKSA I (1971) Dr Dudich Endre. Karszt és Barlang. Budapest, 1
Soüs Á (1972) Megemlékezés dr. Dudich Endrérôl. Állattani Közlemények, Budapest

Dufour, Léon Jean Marie

Léon Dufour was born at Saint-Sever, France, on April 11, 1780. He was a veteran of the French army, with service in Spain during the Napoleonic wars. He married and had children. His publications spanned the years 1811–1864, reported work on the anatomy, behavior, development, physiology, and taxonomy of filarial nematodes, earthworms, crustaceans, arachnids, and insects (Orthoptera, Coleoptera, Diptera, and Hymenoptera), and numbered over 230. He was awarded France's highest medal, as an officer of the Legion d' Honneur. He died on April 18, 1865.

References

Grenier A (1865) [Mort de M. Dufour]. Bulletin de la Société Entomologique de France (1865): xx–xxi
Laboulbène A (1865) Paroles d' adieu adressées a M. Léon Dufour. Annales de la Société Entomologique de France 4(5):214–215
Laboulbène A (1865) Travaux d' entomologie publiés de 1811 à 1864 par M. Léon Dufour. Annales de la Société Entomologique de France 4(5):216–252

Dufour's Gland

A gland on the posterior part of the abdomen in female Hymenoptera that is a source of various pheromones.

Dulosis

A parasitic relationship wherein a parasitic (dulotic) ant species raids the nest of another species, captures brood, and raises them as slaves.

Dung Beetles

Members of the subfamily Scarabaeinae, family Scarabaeidae (order Coleoptera).

► Beetles

Dung Flies

Members of the family Sarcophagidae (order Diptera).

► Flies

Dunnage

Wood used to package or support cargo. Wood crates and packing are an important entry route for invading wood-boring insects. However, wood crates can also be a harborage for egg masses and pupae of arthropods, and all motile stages of snails, facilitating movement of pests across international boundaries.

► Regulatory Entomology
► Risk Analysis (Assessment)
► Invasive Species

Duponchel, Philogène August-Joseph

Philogène Duponchel was born in France toward the end of 1774. At the age of 16 he was in the French army during the Revolutionary War, after his parents fled from France. He became a bureau chief in the war administration. He was not discharged from the army until 1816, but he used his free time for entomological studies. He married and had two children. His interest was especially in Lepidoptera. He was a friend of Latreille, Dejean, and Duméril, and was guided in his studies by them. He was a co-founder of the Société Entomologique Française, at one time a president of it, and held other roles in it at various times. With Chevrolat as co-author, he contributed to d' Orbigny's (1842) "Dictionnaire universel d' histoire naturelle…" He died in Paris on January 10, 1846.

References

Guérin-Méneville FE (1846) Discours prononcé par M. Guérin-Méneville aux funerailles de M. Duponchel. Bulletin de la Société entomologique de France (2)4:iv–vi

Duméril C (1846) Allocution de M. Constant Duméril sur la tombe de M. Duponchel. Bulletin de la Société entomologique de France 2(4):vii–viii

Dust

A dry pesticide formulation consisting of finely divided powder, used without additional dilution, and normally applied by a stream of air.

Duster

Equipment used to apply a dust formulation of pesticide.

Dustywings

Members of the family Coniopterygidae (order Neuroptera).

► Lacewings, Antlions and Mantidflies

Dutch Elm Disease

This fungal disease of elm trees is transmitted by bark beetles.

► Transmission of Plant Diseases by Insects

Dyar, Harrison Grey

Harrison Dyar was born in New York on February 14, 1866. He obtained a B.S. in chemistry from Massachusetts Institute of Technology in 1889, and an A.M. and Ph.D. From Columbia University in 1894 and 1895, respectively. His Ph.D. research was "On certain bacteria from the area of New York City," but before that he had published (in 1894) "A classification of lepidopterous larvae," and for that evidence of training and interest, he was offered in 1897 an unpaid position as Custodian of Lepidoptera at the U.S. National Museum. He occupied the position for the next 31 years, publishing constantly on Lepidoptera, and receiving no financial compensation for his work: he was independently wealthy. However, his other interest was in nematocerous Diptera, and he studied Culicidae, Simuliidae, Psychodidae, and Chaoboridae. With Frederick Knab, he published a four-volume work "The mosquitoes of North and central America" which was initiated as the result of a grant from the Carnegie Institution to L.O. Howard who was another of the authors. "Dyar's rule" was the result of his studies on the growth of caterpillars, in which he stated that the "width of the head capsule of the larva follows a regular geometric progression in the successive instars." He has been remembered by some as a cantankerous man who was quick to criticize others. He owned and edited the entomological journal Insecutor Inscitiae Menstruus, which was published from 1913 to 1927. He died on January 21, 1929.

References

Epstein ME, Henson PM (1992) Digging for Dyar. Am Entomol 38:148–169
*Mallis A (1971) Harrison Grey Dyar. In: American entomologists. Rutgers University Press, New Brunswick, NJ, pp 323–326

Dyar's Rule

The width of the insect head capsule increases by a factor of 1.2–1.4 from one molt to another.

Dytiscidae

A family of beetles (order Coleoptera). They commonly are known as predaceous diving beetles.

► Beetles

E

Ear Tag

A popular method of distributing insecticide to livestock. The insecticide is impregnated in a plastic dispenser, which is fastened to the ear of an animal. The dispenser releases the insecticide slowly, and the animal, by moving its head, contacts other parts of its body and the body of other animals, resulting it widespread distribution of the insecticide.

Earth-Boring Dung Beetles

Members of the family Geotrupidae (order Coleoptera).

► Beetles

Earwigflies (Mecoptera: Meropeidae)

JAMES C. DUNFORD, LOUIS A. SOMMA, DAVID SERRANO
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There are two known extant members of the family Meropeidae worldwide. The North American earwigfly, *Merope tuber* Newman, is found in eastern North America, and the Australian earwigfly, *Austromerope poultoni* Killington, is found in Western Australia. One additional species, *Boreomerope antiqua* Novokschonov, is an extinct, fossil meropeid known from the Middle Jurassic of Siberia. The vernacular name for earwigflies is derived from the male genital claspers that superficially resemble the forficulate cerci of earwigs (Dermaptera).

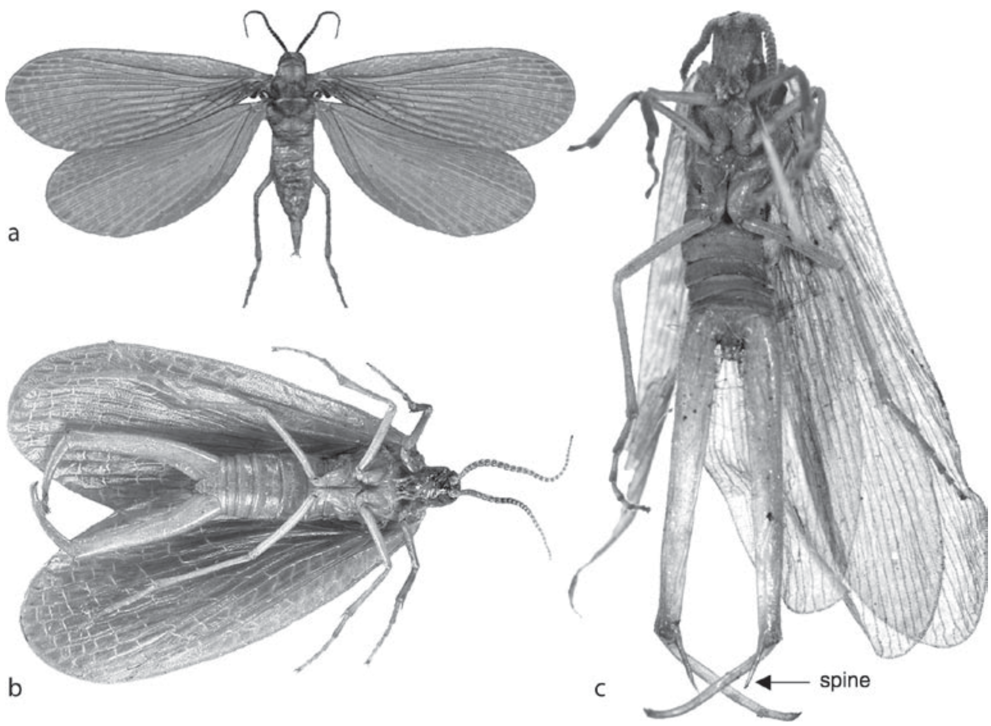
Meropeid genera are hypothetically closely related to Eomeropidae, probably basal to more derived mecopterans (e.g., scorpionflies, *Panorpa* spp.), and could provide a clue to the phylogenetic link between Mecoptera and Siphonaptera. Meropeid larval and pupal stages remain undescribed and may be an important link in better understanding the evolution of advanced holometabolous insects.

The specific epithet for the North American earwigfly, *tuber*, Latin for swelling, knob, hump or protuberance, is a reference to the jugum, a distinct lobe on the basal posterior margin of the forewings. The jugum of *M. tuber* was originally described as a "*tubere*" and "knob" by Newman in 1838, and is used to produce audible stridulations by rubbing against a ridged portion of the thorax, or could function as part of a wing interlocking mechanism.

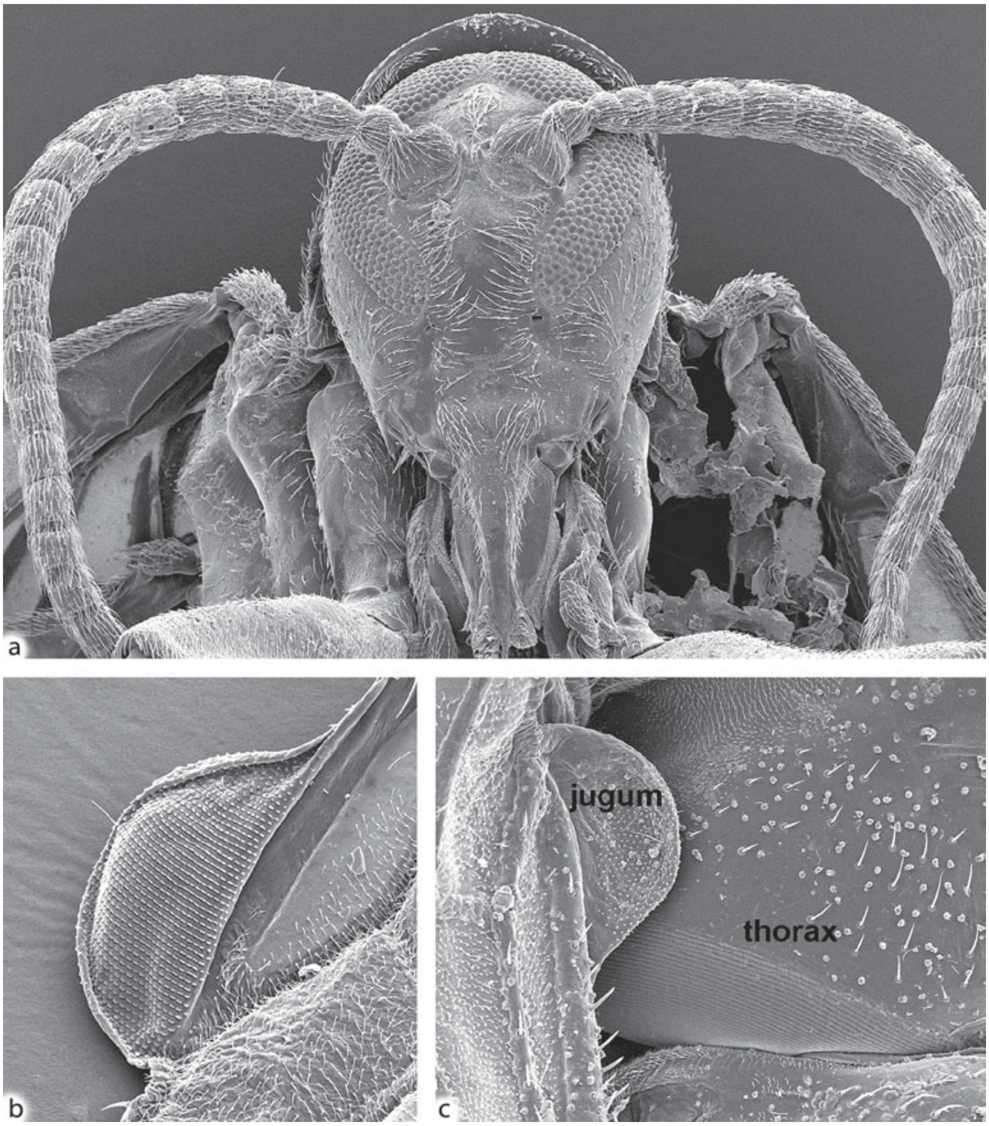
The Australian earwigfly was named in honor of E.B. Poulton, who first collected it in southwest Western Australia in 1914. There are several morphological features that separate the two extant meropeid genera, namely wing venation and the presence of an apical spine on the basal segment of the male genital claspers of *A. poultoni*. *Austromerope* adults also bear a lobe or jugum on the base of each forewing but they are much smaller than the juga on *Merope*.

At present, meropeid immature stages have not been described, and much of their general biology remains unknown. *Merope tuber* (Fig. 1a, b) adults are apparently nocturnally active and have been recorded primarily from deciduous, mesic woodlands, usually near streams. Seasonal records reported for *M. tuber* include dates encompassing early May through late November. For more than 150 years *M. tuber* were considered rare, but recent collection methods (i.e., pitfall, light, and various flight traps) reveal that this secretive mecopteran is more abundant than what was once thought. Published records of *Merope* previous to 1954 were for localities in or east of the Appalachian Mountains. Since that time, specimens have been collected increasingly farther west. Through 1993, the recorded range of *M. tuber* was from southeastern Canada to northern Georgia, west to Kansas, Minnesota and eastern Iowa, largely restricted to environmental conditions similar to those known along the Appalachian range and eastern mesic forests. However, more recent collection records indicate that *M. tuber* is also found further south (e.g., Alabama and Florida) suggesting that it may have found refuge in some of these disjunct areas during glacial advances.

Austromerope poultoni have been (Fig. 1c) collected in light and pitfall traps containing alcohol preservatives and taken in a wide variety of somewhat xeric habitat types, including Jarrah and Karri forests, Wandoo woodland and heath. Seasonality records for adult *A. poultoni* include a range of dates between July (midwinter) and December (early summer). Adults likely live within or below the litter layers in these habitats and they are not commonly encountered, but like *M. tuber* have recently been collected in greater numbers due to more thorough sampling efforts.
► Scorpionflies



Earwigflies (Mecoptera: Meropeidae), Figure 1 **(a) Female *Merope tuber* (dorsal view); North Carolina, USA; body length 11 mm (image by David Serrano); (b) Male *Merope tuber* (ventral view); Tennessee, USA; body length (excluding claspers) 8.5 mm (image by David Serrano); (c) Male *Austromerope poultoni* (ventral view); NE of Collie, Western Australia; body length (excluding claspers) 7.7 mm (image by Allan Wills)**



Earwigflies (Mecoptera: Meropeidae), Figure 2 (a) Scanning electron micrograph of *Merope tuber* head; Tennessee, USA (image by Louis A. Somma); (b) Jugum (ventral view) located on basal posterior margin of *Merope tuber* forewing; Wisconsin, USA (image by Louis A. Somma); (c) Ridges located on *Merope tuber* thorax (dorsal view); Wisconsin, USA (image by Louis A. Somma).

References

Abbott I, Burbidge T, Wills A (2007) *Austromerope poultoni* (Insecta, Mecoptera) in south-west Western Australia: occurrence, modelled geographical distribution, and phenology. J R Soc West Aust 90:97–106

Byers GW (1993) Autumnal Mecoptera of southeastern United States. Univ Kansas Sci Bull 55:57–96

Dunford JC, Kovarik PW, Somma LA, Serrano D (2007) First state records for *Merope tuber* (Mecoptera: Meropeidae) in Florida and biogeographical implications. Fla Entomol 90:581–584

Faithfull MJ, Majer JD, Postle AC (1985) Some notes on the occurrence and seasonality of *Austromerope poultoni* Killington (Mecoptera) in Western Australia. Aust Entomol Mag 12:57–60
Fitch A (1872) Fourteenth report on the noxious, beneficial, and other insects of the State of New York. Trans N Y State Agric Soc 1870 30:355–381
Grimaldi DA, Engel MS (2005) Evolution of the insects. Cambridge University Press, Cambridge, UK, 755 pp
Novokschonov V(G) (1995) Der älteste Vertreter der Meropeidae (Mecoptera, Insecta). Paläeontologische Zeitschrift (Stuttgart) 69:149–152
Richards AG (1965) The proventriculus of adult Mecoptera and Siphonaptera. Entomol News 76:253–256
Sanborne PM (1982) Stridulation in *Merope tuber* (Mecoptera: Meropeidae). Can Entomol 114:177–180
Whiting MF (2002) Phylogeny of the holometabolous insect orders: molecular evidence. Zool Scr 31:3–15

Earwigs (Dermaptera)

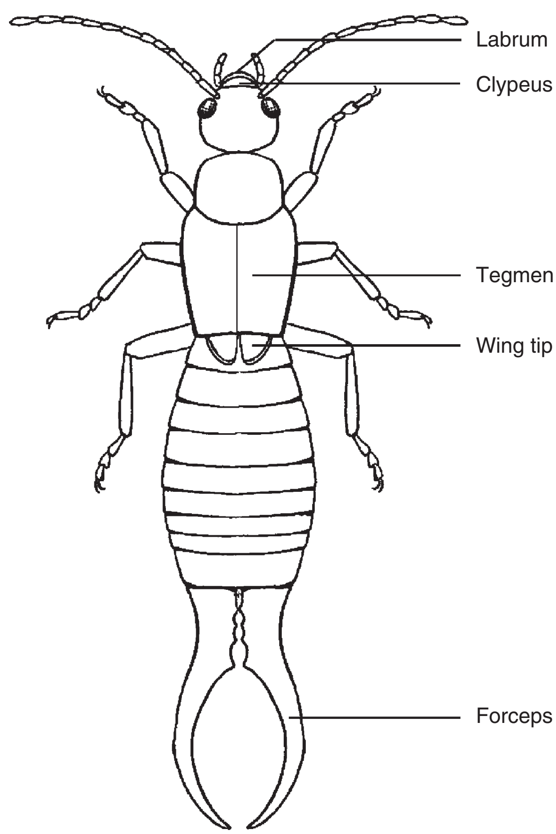
Earwigs are, in some respects, one of the most readily recognized orders of insects. However, this applies only to the "typical" earwigs bearing forceps-like cerci. There are some animal-parasitic groups that lack the forceps-like cerci. The order name is based on the Greek words *derma* (skin) and *pteron* (wing).

Classification

There are three suborders of earwigs, but two are very small. Nearly all the 1,500 known species occur in a single suborder, Forficulina. Suborder Hemimerina consists of ten blind, wingless species that live on giant rats in tropical Africa. They have small filiform cerci. Suborder Arixenina consists of five species that live on bats in Southeast Asia. Similarly, they are nearly blind, wingless, and have straight cerci.

Characteristics

Earwigs are elongate insects with biting/chewing mouthparts. They range in size from 4 to 80 mm. Earwigs usually are uniform black or brown, but some are striped. The antennae are moderately long, consisting of 6–15 segments. They may bear two pairs of wings, or be wingless. The forewings (when wings are present) are modified into short, thickened covers (called tegmina) for the functional hind wings. The hind wings fold beneath the tegmina and are unusually oval, with veins radiating from the central region of the wing. The legs are moderately short and unspecialized. The tarsi consist of three segments. Both males and females bear cerci. The cerci are undivided, and in most species are modified into heavily sclerotized forceps-like structures called, appropriately enough, forceps (Fig. 3). The shape of the cerci can be used to distinguish species, sex, and sometimes age. Metamorphosis is incomplete. Earwigs are predominantly tropical insects.



Earwigs (Dermaptera), Figure 3 Diagram of an earwig, shown dorsally.

Biology

Earwigs tend to be nocturnal, hiding during daylight in soil, leaf litter, under bark, and other cryptic, humid locations. Most are omnivorous, but a few are predatory or live on vertebrates as ectoparasites. The common name "earwig" likely is derived from the tendency of earwigs to crawl into dark crevices including, perhaps, a human ear. This rarely, if ever, occurs. Females earwigs display some elements of sociality, specifically maternal care for eggs and young earwigs. The female protects and cleans the eggs and young from her mate as well as other potential predators, but the nymphs disperse when about half grown. There are 4–5 nymphal instars. They nymphs are hard to distinguish from the wingless adults except by size. The cerci also are not completely developed, tending to be less curved than as adults. However, females display a similar tendency of having less curved cerci, relative to males, so the age of earwigs can be difficult to ascertain.

References

Arnett RH Jr (2000) American insects, 2nd edn. CRC Press, Boca Raton, FL, 1003 pp
Brindle A (1987) Order Dermaptera. In: Stehr FW (ed) Immature insects, vol 2. Kendall/Hunt, Dubuque, Iowa, pp 171–178
Steinmann H (1989) World catalog of Dermaptera. Kluwer Academic Publishers, Dordrecht, 933 pp

East Coast Fever

This is a tick-borne protozoan disease of cattle.
► Piroplasmosis

Eastern Equine Encephalitis

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Eastern equine encephalitis (also known as EEE, eastern encephalitis, and eastern equine encephalomyelitis) was first recognized in North America in horses from Virginia, Delaware, New Jersey, and Maryland in 1933. The virus that causes EEE was first isolated from brains of animals in 1933 and recovered from human central nervous system (CNS) tissue in 1938. The virus is transmitted through the bite of an infected mosquito. Infection in mosquitoes, wild birds, horses, and humans is uncommon, but causes a high mortality in susceptible hosts. Infection with the EEE virus can cause a range of CNS complications from mild or none at all, to severe encephalitis (swelling of the brain). EEE is sometimes referred to as eastern equine encephalomyelitis, meaning swelling of the brain and spinal cord. Vertebrate hosts that are most susceptible to severe complications include humans, horses, and some exotic birds. EEE virus has been isolated in eastern North America, eastern Canada, Central and South America, Jamaica, Trinidad and Tobago, Cuba, Haiti, and Dominican Republic.

Virus

Eastern equine encephalitis virus is an RNA Alphavirus in the family Togoviridae. The virus is transmitted to mammalian hosts by mosquitoes. Avian hosts may acquire the virus from mosquitoes and in some instances, without the mosquito vector. In pheasants, the virus can spread from one bird to another through cannibalism and pecking.

Mosquito Vectors

In the enzootic cycle (mosquito-bird-mosquito, present in the animal community at all times), the mosquito vector of EEE virus in the eastern United States is *Culiseta melanura*, a mosquito that prefers to feed on birds. *Ochlerotatus* (formerly *Aedes*) *sollicitans*, a salt-marsh mosquito, may be the main vector during outbreaks in humans and horses, as it will feed on birds, humans, and horses.

Studies suggest that *Coquilletidia perturbans*, *Ochlerotatus* (formerly *Aedes*) *canadensis*, and *Aedes vexans* may be important vectors in southeastern Massachusetts. In tropical countries, the primary mosquito vectors are *Culex nigripalpus*, *Culex taeniopus*, and *Ochlerotatus* (formerly *Aedes*) *taeniorhynchus*.

Bird Hosts

Birds naturally infected with EEE virus include ring necked pheasants, pigeons, chukar partridge, Pekin ducks, turkeys, a number of passerines, owls, whooping cranes and shore birds. Antibodies to EEE virus have been found in some of these bird hosts, and EEE virus has been isolated from others.

Transmission Cycle

Eastern equine encephalitis virus is an arbovirus (arthropod-borne virus) that is passed from one host to another through the bite of an infected mosquito. In the eastern United States, the EEE virus circulates between birds and mosquitoes in freshwater swamps. The mosquito acquires the virus from an infected bird. Wild birds may have a viremia (the occurrence of viruses within the peripheral bloodstream of the host) without the signs of infection seen in other animals. After an incubation period in the mosquito, other hosts may then be infected when the female mosquito takes a blood meal. Mosquitoes that feed strictly on birds will maintain a local enzootic cycle of EEE. Mosquitoes that feed on a wider range of hosts may infect humans and horses, which serve as a dead-end for the virus. Neither infected humans nor horses have enough circulating virus to infect mosquitoes. The virus has an incubation period of 4–10 days once it has entered a previously uninfected vertebrate host. During the incubation period, the virus may invade the spinal cord and brain. Infection can potentially lead to death of the vertebrate host.

Disease in Humans

Symptoms in humans can be mild, flu-like symptoms to severe encephalitis manifested by fever, headache, and nausea followed by drowsiness, convulsions, and coma. The case fatality rate is 35–65% of clinical cases. Some humans who are infected with the virus develop neutralizing antibodies but do not develop clinical illness. In children under 5 who survive the disease, mental retardation, convulsions, and paralysis often are observed. Estimated total costs associated with each human case is from $21,000–$3 million for severe infections. There is no human vaccine for EEE virus. There is no specific treatment for eastern equine encephalitis. This combined with the lack of a human vaccine emphasizes the importance of personal protection from mosquito bites. Personal protection using mosquito repellent is the best method for preventing infection.

Disease in Horses

The disease in horses is often biphasic with fever starting 18–24 h after infection that lasts about 1 day. Four to six days post-infection, fever starts again and lasts from 1 to 4 days and nervous system signs appear: depression, head close to the ground, flaccid lips, weight loss, and a legs-apart stance. Death occurs within 5–10 days post-infection and the mortality rate is 75–90% with brain damage occurring in animals that survive. There is no specific treatment for EEE in horses. The method of prevention in horses is in the form of an effective horse vaccine that is available to all horse owners.

Disease in Birds

Pheasants exhibit signs including fever, depression, diarrhea, ataxia, tremors, and paralysis of one or both extremities. Initially, infections in pheasants occur from mosquito bites. Later on, the disease can be spread from bird to bird through pecking and cannibalism.

Emus are susceptible to EEE virus and exhibit acute onset of depression, profuse hemorrhagic diarrhea, anorexia and ataxia. Terminally, these birds show extreme exhaustion, hemorrhagic diarrhea and vomiting. Infection in emus causes moderate morbidity and high mortality. Treatment is supportive only, and there is some degree of immunity provided with the equine bi- or tri-valent vaccines.

Detection/Diagnosis

In humans, diagnosis of EEE is based on signs of encephalitis and virus isolation from CNS tissues or blood. A confirmed case of EEE includes the following: a clinically compatible disease (febrile illness, encephalitis) and onset of illness during a period when arbovirus transmission is likely to occur and either a stable elevated antibody titer to an arbovirus or specific IgM (antibody formed early in an immune response; it is a less persistent antibody that indicates recent or chronic infections) antibody in serum, and either a fourfold or greater change in serum antibody titer, viral isolation from tissue, blood or spinal fluid, or specific IgM antibody in the cerebrospinal fluid.

Diagnosis of EEE in horses includes a history of the animal, physical exam, and lab tests to analyze blood or cerebrospinal fluid for antibodies or virus. Since the disease progresses rapidly in horses, EEE confirmation is usually made after the horse' s death. At this point, examination of brain tissue is required to confirm brain lesions or attempt virus isolation.

Epidemics and Epizootics

Massachusetts experienced an epidemic of EEE in 1938 with 38 human cases (74% mortality) and 248 horse cases (90% were fatal). In 1947, an epidemic occurred in Louisiana that killed 90% of the approximately 14,000 infected horses and 9 of 15 humans with the virus died. The Dominican Republic reported 9 deaths among 13 infected humans and 516 horse cases in 1948–1949. An accurate mortality rate in horses during that epidemic is not obtainable as all sick animals were ordered killed when the cause of the epizootic was determined. From 1939 to 1954, there were 27 reported epizootics in pheasants in New Jersey. An epizootic occurred in Panama in 1973 causing 40 deaths in 100 infected horses. The Centers for Disease Control reports 153 confirmed human cases spread throughout 20 states from 1964 to 1997. Fifty of the human cases occurred in Florida (33%). Small outbreaks and sporadic cases in humans continue to occur in various locations throughout the known transmission zone.

The numbers of EEE horse cases are probably severely under-reported. The United States Department of Agriculture reported 26,468 cases of encephalitis in horses from 1956 to 1970. Of the mere 2,620 that could be specifically diagnosed, 605 cases were due to the EEE virus. Many horses are euthanized before a confirmation can be made. Because brain tissue is required for confirmation of EEE in horses, some horse owners are reluctant to provide the necessary tissues or to incur the expense of the laboratory confirmation.

Future Outlook

EEE virus transmission likely will continue in the known transmission zones. There will be some years with many horse and human cases. As humans and animals move into EEE endemic areas near marshes and swamps, and natural wetlands are preserved, contact with infected mosquitoes is likely to continue and perhaps expand the areas of transmission. The susceptibility to EEE virus for many exotic animals is unknown; importation of such animals into EEE virus transmission zones may also subject them to the levels of mortality seen in emus, pheasants, and horses. Prevention of EEE through the use of vaccines in animals and personal protection in humans is increasingly more important as source reduction of mosquito larval habitats is discouraged or illegal in natural wetlands and mosquito control professionals have fewer methods for controlling the vectors of EEE virus.

References

Eldridge BF, Edman JD (eds) (2000) Medical entomology. A textbook on public health and veterinary problems caused by arthropods. Kluwer Academic Publishers, Dordrecht, The Netherlands

Pedro NA, Szyfres B (1987) Zoonoses and communicable diseases common to man and animals, 2nd ed, Scientific Publication No. 503. Pan American Health Organization, Washington, DC

Morris CD (1992) Eastern equine encephalitis. J Fla Mosq Cont Assoc 63:23–34

Rivers TM, Horsefall FL Jr (eds) (1959) Viral and rickettsial infections of man, 3rd edn. J.B. Lippincott Company, Philadelphia, PA

Eastern Lubber Grasshopper, *Romalea microptera* (Beauvois) (Orthoptera: Acrididae)

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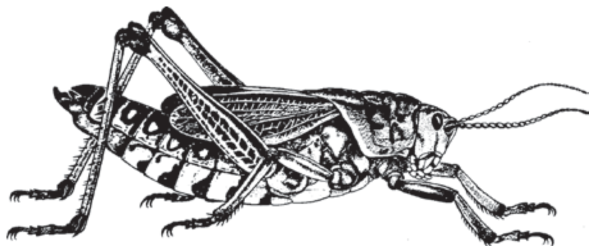
This grasshopper is common in the southeastern United States from North Carolina to eastern Texas, including the entire peninsula of Florida. It is common in many areas of the southeastern USA, and well known to the populace due to its large size and use in biology classrooms for dissection exercises. Unfortunately, the scientific community uses two different scientific names for the same species, and *R. microptera* is also called *R. guttata* (Houttuyn). The latter is probably the correct name, but because the former designation was used for many years, this proposed "correction" is introducing unnecessary confusion.

Life History

There is one generation per year, with the egg stage overwintering. These grasshoppers are long-lived, and either nymphs or adults are present throughout most of the year in the southern portions of Florida. In northern Florida and along the Gulf Coast they may be found from March–April to about October–November.

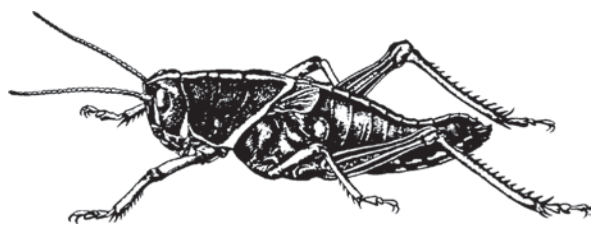
The eggs of lubber grasshoppers are yellowish or brown in color. They are elongate elliptical in shape and measure about 9.5 mm in length and 2.5 mm in width. The are laid in neatly arranged clusters, or pods, which consist of rows of eggs positioned parallel to one another, and held together by a secretion. Normally there are 30–50 eggs in each pod. Ovipositing females are reported to prefer mixed broadleaf tree-pine habitats with intermediate soil moisture levels, avoiding both lowland, moist, compact soil and upland, dry, sandy soil. The female deposits the pod in the soil at a depth of 3–5 cm and closes the oviposition hole with a frothy secretion or plug. The plug allows the young grasshoppers easy access to the soil surface when they hatch. Duration of the egg stage is 6–8 months.

Young nymphs (Fig. 4) are highly gregarious, and remain gregarious through most of the nymphal period, though the intensity dissipates with time. Normally there are five instars, though occasionally six instars occur. The nymphs are mostly black with a narrow median yellow stripe along the pronotum and abdomen, along the edges of the pronotum, and on the lower side of the abdomen. The legs are well marked with red. Their color pattern is distinctly different from the adult stage, and so the nymphs commonly are mistaken for a different species than the adult form. The early instars can be distinguished by a combination of body size, the number of antennal segments, and the form of the developing wings. The nymphs measure about 10–12, 16–20, 22–25, 30–40, and 35–45 mm in length during instars 1–5, respectively. Antennal segments,



Eastern Lubber Grasshopper, *Romalea microptera* (Beauvois) (Orthoptera: Acrididae), Figure 4 Adult of eastern lubber grasshopper, *Romalea microptera* (Beauvois).

which can be difficult to distinguish even with magnification, number 12, 14–16, 16–18, 20, and 20 per antenna during instars 1–5, respectively. The shape of the plates immediately behind the pronotum changes slightly with each molt. During the first instar the ventral surface is broadly rounded; during the second instar the ventral edges begin to narrow slightly and point slightly posteriorly, and also acquire slight indication of venation; during the third instar the ventral edges of the plates are markedly elongate, point strongly posteriorly, and the veins are pronounced. At the molt to the fourth instar the orientation of the small, developing wings shifts from pointing downward to pointing upward and posteriorly. In instar four the small forewings and hind wings are discrete and do not overlap, though the forewings may be completely or partly hidden beneath the pronotum. In instar five, the slightly larger wings overlap, appearing to be but a single pair of wings. Nymphs can complete instars 1–4 in about 7 days each, with the terminal instar requiring 10 days. However, under cool conditions 60 days are required for nymphal development.



Eastern Lubber Grasshopper, *Romalea microptera* (Beauvois) (Orthoptera: Acrididae), Figure 5 Nymph of eastern lubber grasshopper, *Romalea microptera* (Beauvois).

Adults often are colorful, but the color pattern varies. Often the adult eastern lubber normally is mostly yellow or tawny (Fig. 5), with black on the distal portion of the antennae, on the pronotum, and on the abdominal segments. The forewings extend two-thirds to three-fourths the length of the abdomen. The hind wings are short and incapable of providing lift for flight. The forewings tend to be pink or rose in color centrally whereas the hind wings are entirely rose in color. Darker forms of this species also exist, wherein the yellow color becomes the minor rather than the major color component, and in northern Florida a predominantly black form is sometimes found. Adults attain a large size, males measuring 43–55 mm in length and females often measuring 50–70 mm, sometimes 90 mm. Both sexes stridulate by rubbing the forewing against the hind wing. When alarmed, lubbers will spread their wings, hiss, and secrete foul-smelling froth from their spiracles. They can expel a fine spray of toxic chemicals for a distance of 15 cm. The chemical discharge from the tracheal system is believed to be an anti-predator defense, and to consist of chemicals both synthesized and sequestered from the diet. Vertebrate, but not invertebrate, predators are affected.

Eastern lubber grasshopper has a broad host range. At least 26 species from 15 plant families containing shrubs, herbs, broadleaf weeds, and grasses are eaten. A preference has been observed for pokeweed, *Phytolaca americana*; tread-softly, *Cnidoscolus stimmulosus*; pickerel weed, *Pontederia cordata*; lizard's tail, *Saururus* sp.; sedge, *Cyperus*; and arrowhead, *Sagittaria* spp. Though its preferred habitat seems to be low, wet areas in pastures and woods and along ditches, lubbers disperse long distances during the nymphal period. They are gregarious and flightless, their migrations sometimes bringing large numbers into contact with crops where they damage vegetables, fruit trees, and ornamental plants. Lubbers seemingly display little preference among vegetable crops, feeding widely on whatever is available. In choice tests they favor broccoli, Brussels sprout, carrot, pea, and squash relative to other common vegetables. Under field conditions, they seem to display preference for corn, cowpea, and peanut. Also, they seek out and defoliate amaryllis, Amazon lily, crinum, narcissus, and related plants in flower gardens. In Florida, they sometimes damage young citrus trees.

The natural enemies of lubber grasshoppers are poorly documented. Vertebrate predators such as birds and lizards learn to avoid these insects due to the production of toxic secretions. Naïve vertebrates gag, regurgitate, and sometimes die following consumption of lubbers. However, loggerhead shrikes, *Lanius ludovicianus* Linnaeus, capture and cache lubbers by impaling them on thorns and the barbs of barbed wire fence. After 1–2 days the toxins degrade and the dead lubbers become edible to the shrikes. Undetermined flies and nematodes have been reported from lubbers, and it is possible to infect lubbers experimentally with the grasshopper-infecting nematode *Mermis nigrescens*.

Damage

Lubber grasshoppers are defoliators, consuming the leaf tissue of numerous plants. They climb readily, and because they are gregarious they can completely strip foliage from plants. More commonly, however, they will eat irregular holes in vegetation and then move on to another leaf or plant.

Management

Management practices are not well developed. Insecticides applied to the foliage or directly to the grasshopper will prove lethal. However, due to their large size they often prove difficult to kill. Insecticide treatment is more effective for young grasshoppers. Because they are dispersive, and may continue to invade an area even after it is treated with insecticide, it is difficult to afford protection to plants.

► Grasshopper Pests in North America
► Grasshoppers and Locusts as Agricultural Pests
► Grasshoppers, Katydids, and Crickets (Orthoptera)

References

Capinera JL, Scott RD, Walker TJ (2004) Field guide to the grasshoppers, katydids, and crickets of the United States. Cornell University Press, Ithaca, NY, 249 pp

Hunter-Jones P (1967) The life-history of the eastern lubber grasshopper, *Romalea microptera* (Beauvois), (Orthoptera: Acrididae) under laboratory conditions. Proc R Entomol Soc London (A) 42:18–24

Jones CG, Whitman DW, Compton SJ, Silk PJ, Blum MS (1989) Reduction in diet breadth results in sequestration of plant chemicals and increases efficacy of chemical defense in a generalist grasshopper. J Chem Ecol 15:1811–1822

Rehn JAG, Grant HJ Jr (1961) A monograph of the Orthoptera of North America (north of Mexico), vol 1. Monograph 12, Academy of Natural Sciences of Philadelphia, 257 pp

Ecdysial Line

A line of weakness that breaks during molting (ecdysis). This is found at the top of the head capsule, or a nearby area.

Ecdysis

The shedding of the old cuticle during the molting process.

Ecdysone

A steroid hormone secreted by the prothoracic glands and responsible for inducing molting and the sequential expression of stage-specific genes. It is produced from cholesterol.

► Endocrine Regulation of Insect Reproduction
► Reproduction
► Diapause
► Metamorphosis

Ecdysone Agonists, A Novel Group of Insect Growth Regulators

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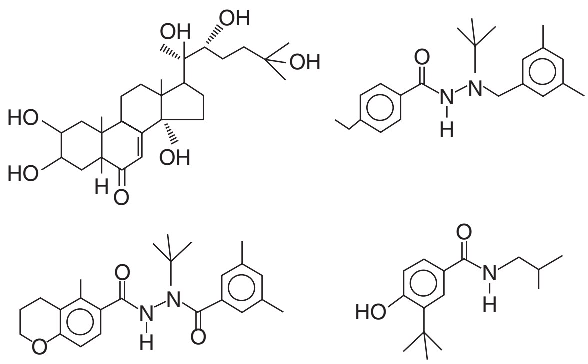
The diacylhydrazines are a novel class of chemically and mechanistically new insect control agents that were discovered and characterized by researchers of the Rohm and Haas Co. (Pennsylvania, USA) in the mid-1980s. The first member of this group was RH-5849 (N-tert-butyl-N'-benzohydrazide) that had interesting foliar and root-systematic insecticide activities against a range of lepidopteran, coleopteran and dipteran pests. More recently, another more commercial analog was introduced, tebufenozide (N-tert-butyl-N'-(4-ethylbenzoyl)-3,5-dimethylbenzo-hydrazide; RH-5992; Mimic™, Confirm™, Rondam™) that is a more potent and selective foliar caterpillar control agent. In addition, halofenozide (N-tert-butyl-N'-(4-chlorobenzoyl)benzohydrazide; RH-0345; Mach 2™) that is a more effective soil insecticide for white grub and caterpillar control in turf, and methoxyfenozide (N-tert-butyl-N'-(3-methoxy-o-toluoyl)-3,5-xylohydrazide; RH-2485; Runner™, Intrepid™, Prodigy™) exhibits high insecticide efficacy and selectivity against Lepidoptera including Pyralidae, Pieridae, Tortricidae and Noctuidae. In this respect, Rohm and Haas was granted a "Presidential Green Chemistry Award" from the U.S. Government for the discovery of these non-steroidal ecdysone agonists. Due to the commercial success, screening bioassays were initiated to discover new 20E acting compounds, e.g., chromafenozide (Nippon Kayaku Co., Japan) and benzamide (3,5-di-*tert*-butyl-4-hydroxy-N-isobutyl-benzamide, DTBHIB, Sumitomo Co., Japan).

Chemistry and Physical Properties

The dibenzoylhydrazines can be readily synthesized from tert-butylhydrazine hydrochloride and the corresponding substituent benzoyl chloride using Schotten-Bauman conditions. The presence of the bulky tert-butyl group on the hydrazine allows the acid chlorides to be reacted in a sequential and highly regio-specific manner.

The dibenzoylhydrazines (Fig. 6), although not steroids, mimic actions of the insect molting hormone, 20-hydroxyecdysone, binding directly to the binding sites of 20-hydroxyecdysone and acting as full agonist at that site. As a consequence, treated larvae express all the classic symptoms of an untimely and severe overdose with 20-hydroxyecdysone, called hyperecdysonism. Treatment induces premature apolysis, which is the primary mode of action, and larvae stop feeding. Within 3–12 h after uptake, molting was initiated, and by 24 h, intoxicated larvae prematurely slip their old head capsules in an attempt to ecdyse. However, normal successful ecdysis was inhibited. In addition, abnormal cuticle deposition and other molting irregularities were seen, such as a lack of sclerotization and tanning of the new cuticle, absence or conspicuous low number of endocuticular lamellae, hindgut extrusion and loss



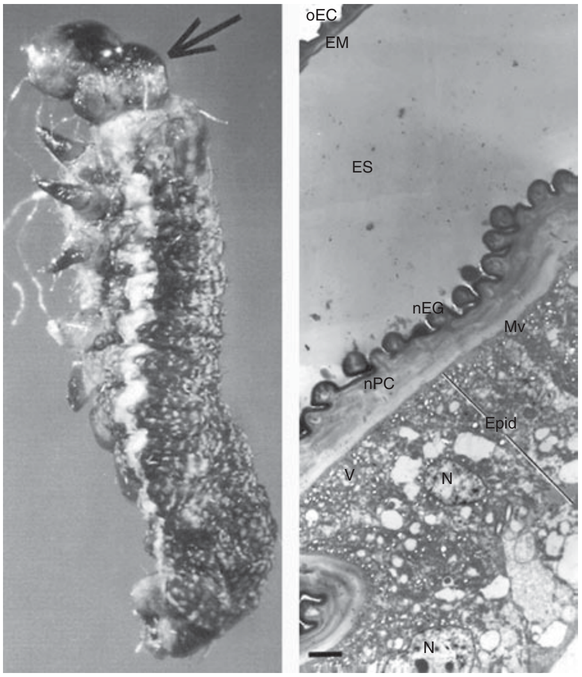
Ecdysone Agonists, A Novel Group of Insect Growth Regulators, Figure 6 **Chemical structures of 20-hydroxyecdysone (upper left), tebufenozide (upper right), chromafenozide (lower left) and DTBHIB (lower right).**

of hemolymph and molting fluid, that results in desiccation and ultimate death.

Insecticidal Mode of Action

The dibenzoylhydrazines manifest these typical effects via interaction with the molting hormone receptor complex that consists of a heterodimer of two steroid receptor superfamily members, i.e., the ecdysteroid receptor (EcR) and the Ultraspiracle (USP) protein. This hormone-protein complex binds then to the ecdysone responsive elements on the DNA. These chemicals permit the expression of genes and behavioral events that are dependent upon the presence of 20-hydroxyecdysone. However, those processes that are dependent upon the absence of 20-hydroxyecdysone, such as the expression of dopa-decarboxylase enzyme for tanning and the ecdysis behavior (production/release of the neuropeptide eclosion hormone), are prevented due to the persistence in the insect tissues (Fig. 7).

In adults, the dibenzoylhydrazines caused a reduction of egg production and fertility in various target Lepidoptera, Coleoptera and Diptera. However, the exact mechanism of action is not clear.



a b

Ecdysone Agonists, A Novel Group of Insect Growth Regulators, Figure 7 **Last instar of the beet armyworm, *Spodoptera exigua* (Lepidoptera), 24 h after treatment with 1 ppm methoxyfenozide. (a) Panel A is a lateral view under the light microscope with the arrow showing slipped head capsule and the unsclerotized new cuticle over the head and mouth parts. (b) Panel B is a transmission electron micrograph of the integument, showing the presence of a double cuticle, the conspicuous absence of a high number of procuticular lamellae underneath the newly secreted epicuticle and signs of epidermal cell degeneration. BL: basal lamina, DB: dense body, Epid: epidermal cell, EM: ecdysial membrane, ES: ecdysial space, MV: epidermal microvilli, N: epidermal nucleus, nEC: new epicuticle, nPC: procuticle of the new cuticle, oEC: old epicuticle of the particularly digested cuticle, V: vacuoles, bar = 3 μm.**

Insecticidal Properties and Efficacy Against Target Pests

The dibenzoylhydrazines were tested in larvae and adults from at least 16 different insect orders, and toxicity is most pronounced when exposure and uptake occur via ingestion. Tebufenozide and methoxyfenozide perform a high selective toxicity against Lepidoptera. These compounds are marketed around the world for control of important agricultural caterpillar pests in cotton, vegetables, top fruit, grapes, ornamentals, forestry and rice. Targets are, for instance, beet armyworm, *Spodoptera exigua*, cabbage looper, *Trichoplusia ni*, codling moth, *Cydia pomonella*, grape berry moth, *Lobesia botrana*, spruce budworm, *Choristoneura fumiferana*, rice leafroller, *Cnaphalocricis medinalis*, and others. Use rates typically range between 30 and 300 g of active ingredient/ha depending on the target crop and pest.

Safety to Non-target Organisms

Tebufenozide and methoxyfenozide had little or no effect on a panel of non-lepidopteran pests (Coleoptera, Hemiptera, mites and nematodes) when tested at high rates (from 18 to 1500-fold greater than that producing 90% mortality in Lepidoptera). Likewise, laboratory and field experiments showed that there are little or no adverse effects at normal rates on a wide range of non-lepidopteran beneficial insects such as honeybees and bumblebees (Hymenoptera), many predatory insects (Hemiptera, Coleoptera, Neuroptera, Odonata, Plecoptera, Trichoptera, Ephemeroptera) and mites (Acarina), several caterpillar endoparasitoids (Hymenoptera) and certain insect predators such as spiders (Arachnida). These compounds appear to be highly caterpillar selective and highly compatible for integrated pest management (IPM). Treatment also was found to be safe towards several non-arthropod invertebrates such as earthworms and nematodes, and has a low acute toxicity for a representative crustacean (*Daphnia magna*).

For vertebrates, several representative mammals, bird and fish species (rat, quail and trout) were, at a minimum, four orders of magnitude less susceptible to methoxyfenozide and tebufenozide than is a representative lepidopteran species. These compounds are non-irritating (rabbit), non-sensitizing (guinea pig), non-mutagenic and non-oncogenic (mouse, rat and dog). Methoxyfenozide has a dietary no effect level (NOEL) of 1950 mg/kg in a two-generation rat development bioassay. In retrospect, this relative lack of vertebrate toxicity might have been anticipated since such organisms do not synthesize or utilize 20E, the ecdysone receptor complex (EcR and USP) or any other closely homologous substances.

► Ecdysteroids
► Metamorphosis
► Endocrine Regulation of Insect Reproduction
► Diapause
► Insecticides

References

Carlson GR (2000) Tebufenozide: a novel caterpillar control agent with unusually high target selectivity. In: Anastas PT, Heine LG, Williamson TC (eds) ACS Symposium Series 767, Green chemical syntheses and processes. American Chemical Society, Washington, DC, pp 8–17

Carlson GR, Dhadialla TS, Hunter R, Jansson RK, Jany CS, Lidert Z, Slawecki R (2001) The chemical and biological properties of methoxyfenozide. Pest Manag Sci 57:115–119

Dhadialla TS, Carlson GR, Le DP (1998) New insecticides with ecdysteroidal and juvenile hormone activity. Annu Rev Entomol 43:545–569

Mikitani K (1996) A new nonsteroidal chemical class of ligand for the ecdysteroid receptor 3,5-di-tert-butyl-4-hydroxy-N-isobutyl-benzamide. Biochem Biophys Res Commun 227:427–432

Palli SR, Retnakaran A (2001) Ecdysteroid and juvenile hormone receptors: properties and importance in developing novel insecticides. In: Ishaaya I (ed) Biochemical sites of insecticide action and resistance. Springer-Verlag, Berlin, Germany, pp 107–132

Smagghe G, Degheele D (1998) Ecdysone agonists: mechanism and biological activity. In: Ishaaya I, Degheele D (eds) Insecticides with novel modes of action. Springer-Verlag, Berlin, Germany, pp. 25–39

Williams CM (1968) Ecdysones and ecdysone analogues. Their assay and action on diapausing pupae in the Cynthia silkworm. Biol Bull 134:344–355

Ecdysozoa

The concept of a superphylum called Ecdysozoa was proposed only in 1997, following molecular analyses that suggested close relatedness among some invertebrates that shed their three-layered cuticle periodically. However, a similar concept had been proposed 100 years earlier based on morphology. The characteristics that link the ecdysozoans, in addition to the three-layered sheddable cuticle composed of organic material, include the absence of locomotory cilia, production of amoeboid sperm, and the absence of spiral cleavage in the embryonic stage. There are two major groups within this scheme of classification, encompassing several phyla. Only the Arthropoda (over 6 million species) and Nematoda (over 20,000 species) are speciose, the other phyla being fairly minor in importance. The phyla involved are:

- Ecdysozoa
  - Panarthropoda
    - Arthropoda
    - Onychophora
    - Tardigrada
  - Cycloneuralia
    - Kinophora
    - Priapulida
    - Loricifera
    - Nematoda
    - Nematomorpha

This grouping has yet to win wide acceptance, as these taxa seem to be polyphyletic.

Reference

Aguinaldo AMA, Turbeville JM, Linford LS, Rivera MC, Garey JR, Raff RA, and Lake JA (1997) Evidence for a clade of nematodes, arthropods and other moulting animals. Nature 387:489–493

Ecdysteroids

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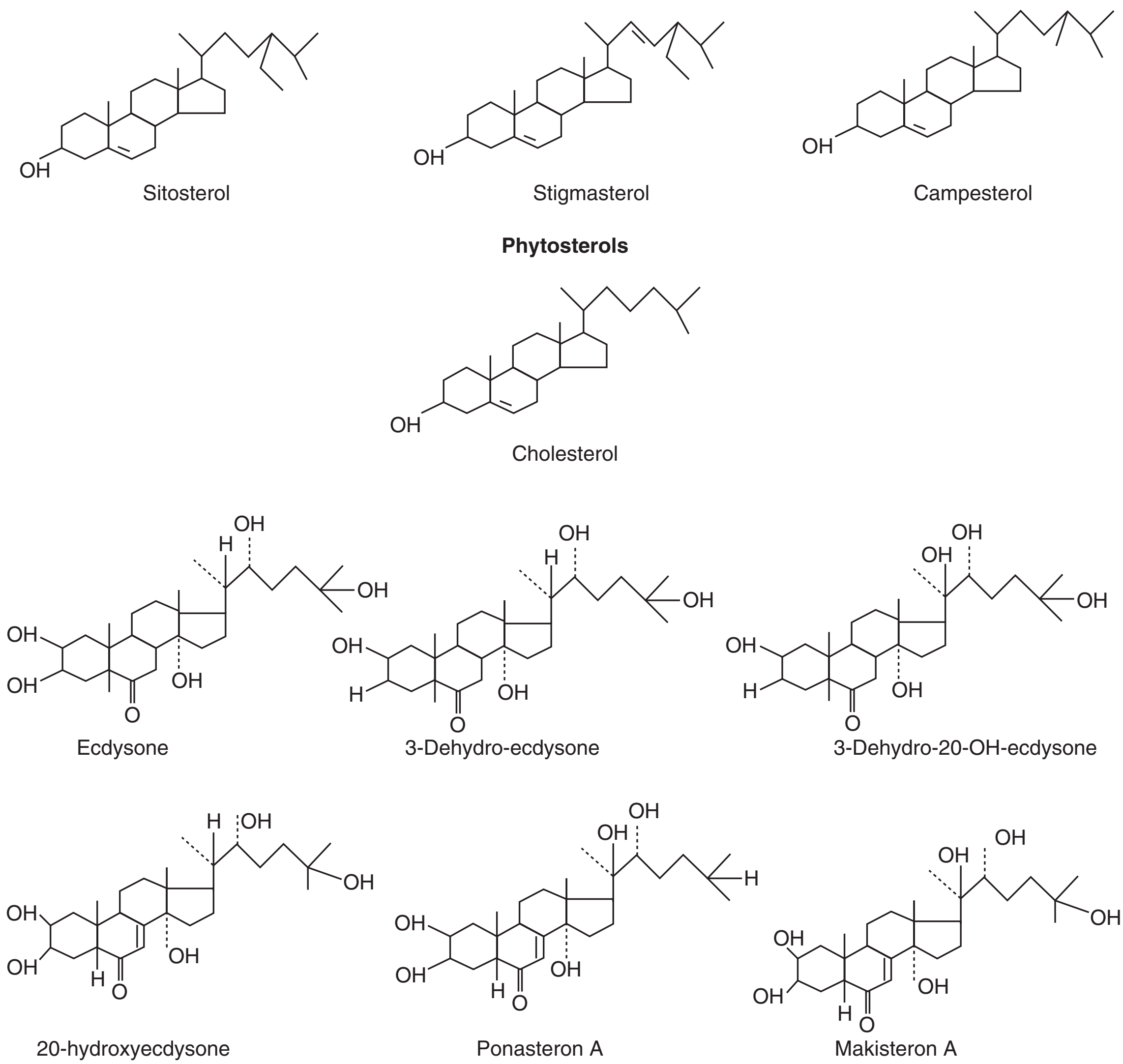
Ecdysteroids are hormones that regulate a wide variety of cellular processes in the life cycle of arthropods. Pulses of ecdysteroids coordinate the complex events during molting and metamorphosis in postembryonic development which are essential in the life of the insects. Two of the most common and studied ecdysteroids hormones in insects are ecdysone = (α -ecdysone) and 20-OH-ecdysone = (ecdysterone, crustecdysone).

Research on insect hormones began in 1934, when V.B. Wigglesworth, in his study on the physiology of ecdysis in the Hemipteran *Rhodnius prolixus* described the metamorphosis in this blood sucking bug. One year later, G. Fraenkel published a study of the hormone causing pupation in the blowfly *Calliphora erythrocephala*. From P. Karlson's autobiography we learn that, in 1943 he started the work on the isolation of the molting hormone of insects, and only in 1954, Bütenandt and Karlson had succeeded in isolating a crystalline form of ecdysone. In order to obtain reasonable amounts of the hormone, they had to use 500 kg of male silk worm pupae, (*Bombyx mori*). The exact structure of ecdysone was fully elucidated in 1965, independently by the Karlson group, and the crystallographers Hüber and Hoppe. Later, in the year 1966, the structure of 20-OH-ecdysone(20E), which is regarded in most arthropods as the predominant active hormone, was sequentially established by Dennis Horn' s group as crustecdysone and Hoffmeister group as ecdysterone. The concept of steroid hormone action on gene expression was first developed by studies on the mode of action of ecdysteroids in Dipteran flies. This was due to the findings in 1960 of Clever and Karlson, that ecdysteroids can activate transcription in polytene chromosomes of the midge, *Chironomus tentans*. Evidence to support this concept was the visible enlargement of specific regions of polytene chromosome puffs of the target cells.

Origin and Site of Synthesis

Cholesterol, originating either from the insect diet or from the conversion of dietary C28 and C29 phytosterol, is the common precursor of ecdysteroids (Fig. 8). All insects and other arthropods are unable to synthesize de novo the steroid nucleus, therefore require exogenous or dietary source of sterol for normal growth. The prothoracic glands, comprising a single steroidogenic cell type in most insects, are the predominant site of ecdysteroids biosynthesis during postembryonic development. In flies, higher insects, the prothoracic glands is a part of an organ, the ring gland, which also includes the corpus cardiacum and corpus allatum. The latter is the site of ecdysteroids release to the hemolymph. In some insects, epidermal, oenocytes and gonadal cells are alternative sites for ecdysteroids production, especially during adult life, at a time the prothoracic glands are no longer present. In female ovaries, the epithelium of the follicle cells produces ecdysteroids, which play a crucial role in the induction of vitellogenesis. During embryogenesis, in the absence



Ecdysteroids, Figure 8 **Structural formulae of some important phytosterols, ecdysteroids and cholesterol.**

of any differentiated site of ecdysteroids biosynthesis, many insects are able to elevate their ecdysone titer by metabolizing maternal ecdysteroid conjugates to active hormones.

In crustaceans, ecdysteroids are produced by the Y-organ glands, and control a number of processes in the life cycle of the animals, similar to insects.

The Regulation of Ecdysteroid Synthesis

The regulation of ecdysteroids synthesis is very complex, and under the control of peptide hormones as well as the sesquiterpenoid juvenile hormone (JH). Ecdysteroids are mainly synthesized by the prothoracic glands and released into the hemolymph upon stimulation by the prothoracicotropic hormone (PTTH), a neuropeptide produced by the insect brain. The periodic increase in ecdysteroids titer critical to insect development reflect to a large degree the activation of the prothoracic gland by PTTH. The structure and mode of action of PTTH has been investigated in a number of insects. PTTH is synthesized as a preprohormone and it is expressed in a number of neurosecretory cells of the brain. It occurs in multiple forms large and small, some are active others not, depending on the insect species. Binding of PTTH to the membrane receptor elevates intracellular Ca^{2+} influx, and the action in turn enhances cAMP formation. As a consequence cAMP-dependent protein kinase is stimulated. The activated kinase stimulates ecdysteroid production. PTTH acts at critical steps in the regulation of ecdysteroids levels in developing insects. The concentration of active ecdysteroids is modified by target cell specific hormone metabolism. The prohormones ecdysone, 3-dehydroecdysone and 3-dehydro-20 hydroxyecdysone, which are secreted into the hemolymph, are metabolized to the more active compound 20E, which is in most arthopods the predominant active hormone. In various species of Hemiptera, Makisterone A is regarded as the major molting hormone. Like vertebrates, a series of cytochrome P450 is involved in the various steps of 20E synthesis from cholesterol. There are indications that at least two cephalic factors are able to stimulate ovarian ecdysteroidogenesis in the blow fly: one acting via cAMP independent mechanism, and the other using cAMP as a second messenger. Although the ecdysteroids have been characterized, ecdysteroids biosynthetic pathways and enzymes involved in the hormones biosynthesis are not yet fully elucidated. Also, little is known about the genes involved in the biosynthesis of the hormones.

PTTH is not the sole regulator of ecdysone biosynthesis. JH exerts an indirect tropic effect on the prothoracic glands, probably mediated by a stimulatory protein in the hemolymph, possibly a precursor steroid carrier. Also, the developmental state of the prothoracic glands to respond to the regulatory effectors appears to be a key factor in the regulation of ecdysone synthesis. During larval-pupal development, regulatory effectors, hormone interactions, and competence of the prothoracic glands may all be integrated to regulate the ecdysteroid titers. There is experimental evidence for the existence of a neuroendocrine regulation of ecdysteroid synthesis in ovaries of *Aedes ageptii* and *Locusta migratoria*. It may be significant to mention that in *Locusta* there are structural similarities between the larval (PTTH) and adult ecdysiotropins.

In crustaceans, ecdysteroid synthesis is regulated by molt-inhibiting hormone (MIH). This neurohormone exerts opposite effects compared to PTTH in insects by inhibiting ecdysteroid synthesis in the Y-organs. MIH also increases cAMP second messenger which activates protein kinases, following alteration of cellular Ca^{2+} levels. The contrasting steroidogenic effects of PTTH and MIH probably arises from differences in the cellular kinase substrates. In insects such substrates enhance ecdysteroid secretion by increasing the translation of granular protein. In crustacea, MIH stimulates changes leading to the inhibition of both protein synthesis and steroidogenesis.

Ecdysteroids Metabolism

Activation

The metabolism of the prohormones ecdysone, 3-dehydroecdysone and 3-dehydro20-hydroxyecdysone to 20-hydroxyecdysone, is regarded as an activation mechanism, converting the poorly active precursors, to the highly active 20-hydroxyecdysone, the principle molting hormone. This refers mainly to higher insect species like Dipterans. Other insect species use both ecdysone and 20-hydroxyecdysone as hormonal messengers. There are speculations that during evolution in higher insects ecdysone lost its hormonal role and is merely a prohormone.

Inactivation Mechanism

Inactivation mechanisms of ecdysteroids are common in the various insects tested. Ecdysone and/or 20-hydroxyecdysone are inactivated primarily by:

1. Esterification, acetylation, posphorylation.
2. Epimerization, oxidation followed by isomeric reduction of the C-3 hydroxyl group.
3. Hydroxylation of the C-26 methyl group followed by oxidation to ecdysonoic acid.
4. To a lesser extent by esterification of the C-2 hydroxyl group on the A nucleus of the molecule.

Inactivation of ecdysteroids varies according to the tissue and developmental stage. In other arthropods, the inactivation mechanism of the active ecdysteroids is similar to insects.

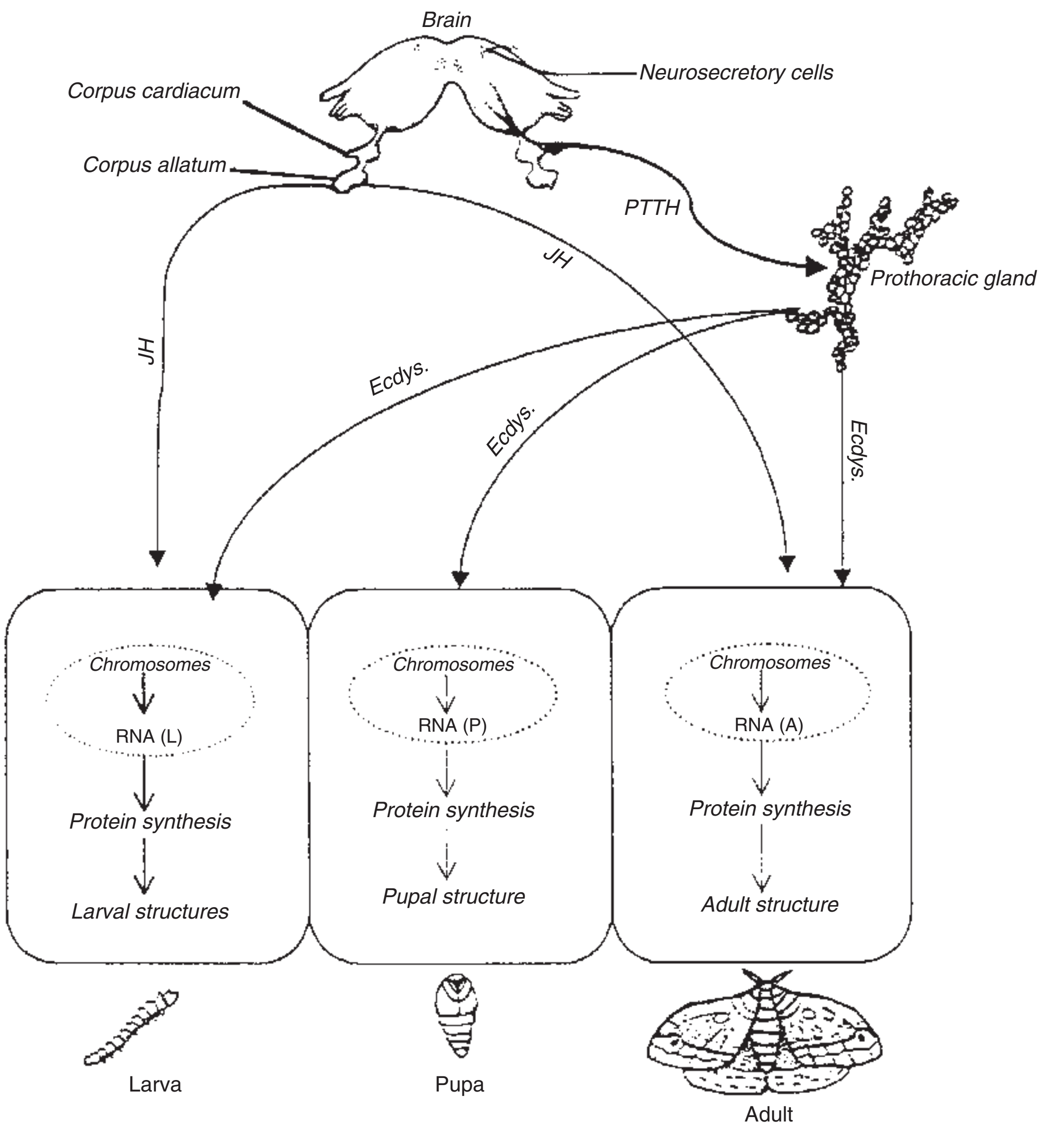
Storage Mechanisms

A large portion, up to 98% in some insect spp., of the ovarian ecdysteroids are esterified to phosphate conjugates at the C-22 hydroxyl group. Occasionally, more complex conjugates bearing nucleotides on the phosphates are found together with the 22-phosphates. These ovarian conjugates are present in newly laid eggs, and gradually metabolized during embryogenesis to the active hormone. It may be relevant that the eggs contains enzymes involved in ecdysteroid metabolism.

Mode of Action of Ecdysteroids: Molecular Aspects

Metamorphosis transforms the insect larva into a reproductive adult through a complex series of developmental events involving cell proliferation, differentiation, remodeling of structures for new functions, and finally programmed cell death. In insects, these developmental processes are coordinated by pulses of ecdysteroids that include the principle hormone 20E and in some insects ecdysone, which have morphogenetic functions of its own, and also JH. The ecdysteroids cause molting (Fig. 9) and also are responsible for the changes in the genetic programs that are necessary for metamorphosis, whereas the presence of JH in the larva prevents these changes from taking place, but does not prevent the molting response. Thus, metamorphosis ensues when ecdysteroids rise in the absence of JH in the final larval instar. In most insects, exogenous JH at this time causes the formation of a supernumerary larva, but in the higher Diptera JH does not prevent pupariation nor pupation, but disrupts the development of the adult organs, thereby causing the death of the insect. The target tissues of ecdysteroids contain proteins which bind to the hormone. The binding has a high affinity for the hormone, and a limited number of binding sites per target cell, which is characteristic of steroid hormone receptors. In addition, the binding proteins exhibit a differential affinity for the various ecdysteroids, depending on their biological activity.

Determination of the mode of action of ecdysteroids at the genomic level was based on a series of pioneering studies using *Chironomus* and *Drosophila* which showed that in polytene



Ecdysteroids, Figure 9 Schematic diagram of the principal endocrine organs of Lepidopteran insects and the regulation of metamorphosis by their hormones. Ecdys. = ecdysteroids; JH = juvenile hormone.

chromosomes certain stage-dependent puffs could be induced by exogenous ecdysone. This model interaction of the hormone with the hormone-receptor complex recognizes specific DNA response elements, and triggers a cascade of gene activity that directs the molting process. Over one hundred different genes are known to be regulated by ecdysteroids. Hormonal regulation is gene and tissue specific, and is modified according to the developmental stage of the insect. The general molecular mechanism of steroid hormone action must be diversified to adapt hormone action according to the physiological needs. Target cell specific hormone metabolism is one way to adapt molting hormone action in a tissue specific manner. Beside molting, ecdysteroids regulate a large number of processes including spermatogenesis, oogenesis, reproduction, embryogenesis, diapause, change in insect color, behavior, metabolism and cell death. Ecdysteroids also regulate the concentration of enzymes responsible for the synthesis and degradation of 20E, and thus modulate ecdysteroid titer; regulate the central nervous system sensitivity to eclosion hormone and ecdysis triggering hormone; and the regulation of melanization by the induction of the enzyme dopa decarboxylase. The relatively simple ecdysone-inducible genes of salivary gland glue proteins or larval serum proteins-1 of fat body, for example, have a single transcript. However, other ecdysone-inducible genes show a complex pattern of transcription and stretch over regions of 50 kb or more.

Involvement of Ecdysteroids in the Control of Reproduction and Embryogenesis

Vitellogenic ovaries synthesize ecdysteroids at a given stage of their development. In some dipteran species, ecdysteroids synthesis starts at almost the same time as the onset of vitellogenin synthesis, whereas in other species like orthopterans the synthesis starts only towards the end of vitellogenin uptake. These ecdysteroids are either released into the blood of the female or accumulate inside the oocytes and are transferred in the newly laid eggs. This situation is common in most insect species. However, the ratio of the amounts released into the blood, to those retained in the oocytes seem to vary between insect orders. In locusts, for example, only 2% of the ecdysteroids produced by the ovary is released into the blood of the female, the other 98% accumulates in the newly laid eggs. In *Galleria* (Lepidoptera), this ratio is 1:1. It should be mentioned, however, that in most insect species most ovarian ecdysteroids are conjugates, and may escape detection.

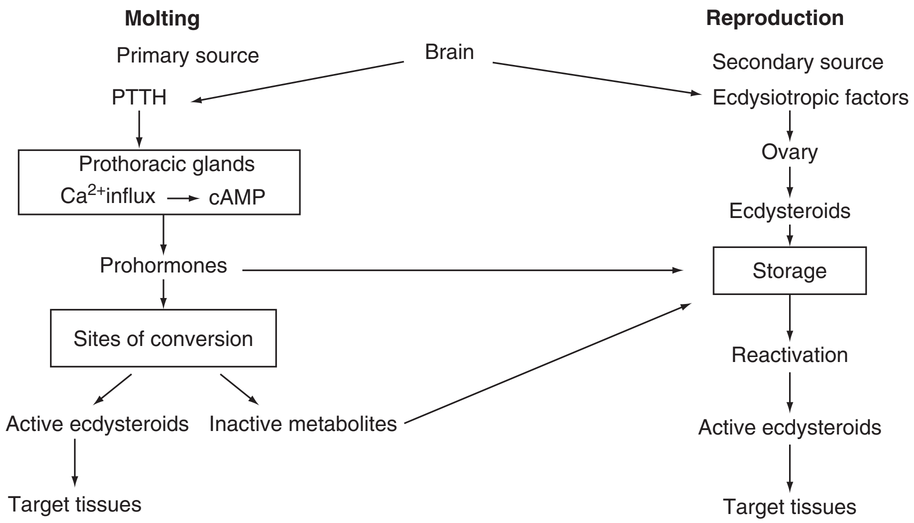
In higher insect orders, like the Diptera, ovarian ecdysteroids play a role in the control of vitellogenin synthesis, whereas in other orders they play a role in the early events of embryogenesis. Ecdysteroids also control additional events in a variety of insect species. For example, in mosquitoes, separation of incipient follicles from the germarium, and control of release of ovulation hormone, is controlled by ecdysteroids.

As regards the possible involvement of ecdysteroids in the control of vitellogenesis in dipterans, ecdysteroids can stimulate the synthesis of vitellogenin mRNA, both in females and males. In female Diptera, ecdysteroids stimulate the fat body to synthesize increased amounts of vitellogenin; it is possible that the fat body has to be primed by JH to become responsive to ecdysteroids.

The involvement of ovarian ecdysteroids (Fig. 10) in the early events of embryogenesis is based on the remarkably high concentrations, about 10^{-4} M of ecdysteroid conjugates of ovarian origin, present in newly laid eggs. As embryogenesis proceeds, the conjugates are then hydrolyzed by enzymatic activity, resulting in the surge of free ecdysteroids. The presence of enzymes responsible for these transformations has been monitored in a number of insects. In the newly laid eggs, the maternal conjugate first is hydrolyzed to the active ecdysteroid needed to trigger some specific processes, then it metabolized to an inactive molecule. Indeed, during embryogenesis there are a certain number of peaks of ecdysone and/or 20-hydroxyecdysone which coincide with cuticle deposition, either by the serosa or by the embryonic epidermis. Thus, via a large supply of ecdysteroid conjugates, the mother controls ecdysone-triggered events of embryogenesis which occur prior to the stage when the embryo has acquired its own capacity to biosynthesize ecdysone *de novo*.

Ecdysteroids in Non-arthropods Metazoans

Many protostomians contain ecdysteroids; the main ecdysteroids which were identified in non-arthropods are similar to those found in the different insects such as ecdysone, 2-deoxy-ecdysone, Ponasterone A, 20-hydroxyecdysone and 20, 26-dihydroxyecdysone. As in arthropods, these ecdysteroids are found both in free or esterified (polar or non-polar) forms. The concentration of



Ecdysteroids, Figure 10 Simplified scheme of ecdysteroid production in insect molting and reproduction.

ecdysteroids recorded in non-arthropods are generally lower than those found in arthropods. Titre fluctuations have been recorded in relation to reproductive cycles, embryonic metamorphosis and integumental events. This indicates that in non-arthropods ecdysteroids might play roles similar to those that they exert in arthropods.

It is of interest to mention that human patients infested by trematodes, cestodes and nematodes contained ecdysteroids in their blood and urine. The potential of this finding for diagnosis, and possibly even for interfering with the parasite' s development or reproduction, is of interest. The detection of ecdysteroids in sera or urine of humans may contribute to diagnosis of helminth infection. It is premature to speculate that these finding open a novel way of fighting parasitic infection. It is questionable whether or not these parasites use ecdysteroids for the control of their reproduction and development.

Phytoecdysteroids

Analogues of ecdysteroids occur in a variety of plants: pteridophyta, gymnosperms, and angiosperms. The ecdysteroids isolated from plants are ecdysone, 20E, 3-epi-20-hydroxyecdysone, 20-hydroxyecdysone 22 acetate, ponasteron A and many others of less importance. The physiological relevance of these phytoecdysteroids in the plants, which are identical to the zooecdysteroids, is not thoroughly studied. A high concentration of ecdysteroids may contribute to the protection of the plant against invertebrate predators by mimicking the natural hormones and disturbing the hormonal balance within the insect. They can act as antifeedants or antagonize the action of the ecdysteroid hormones.

► Ecdysone Agonists
► Prothoraciotropic Hormone
► Diapause
► Endocrine Regulation of Insect Reproduction
► Metamorphosis

References

Barker GC, Chitwood DJ, Rees HH (1990) Ecdysteroids in helminthes and annelids. Invertebr Reprod Dev 18:1–11
Dinan L (2001) Phytoecdysteroids: biological aspects. Phytochemistry 57:325–339
Gilbert LI, Ryberynski R, Warren TJ (2002) Control and biochemical nature of the ecdysteroidogenic pathway. Annu Rev Entomol 47:883–916

Harshman LG (1998) Differential gene expression in insects. Annu Rev Entomol 43:671–700
Henrich VC, Rybezynski R, Gilbert LI (1999) Peptide hormones, steroid hormones and puffs: mechanisms and models in insect development. Vitam horm 55:73–125
Lafont R (2000) Understanding insect endocrine systems: molecular approaches. Entomol Exp Appl 97:123–136
Smith AW, Sedlmeier D (1990) Neurohormonal control of ecdysone production: comparison of insects and crustaceans. Invertebr Reprod Dev 18:77–89

Echinophthiriidae

A family of sucking lice (order Phthiraptera). They sometimes are called seal lice.

► Chewing and Sucking Lice

Eclosion

Egg hatching. Escape of the immature insect from the egg chorion. This term also is sometimes used to describe emergence of the adult from the pupal stage.

Eclosion Hormone

A neurosecretory polypeptide produced by the brain and released into the hemolyph, stimulating molting.

► Metamorphosis

Ecnomidae

A family of caddisflies (order Trichoptera).

► Caddisflies

Ecological Community

A group of populations that interact within a certain geographic area. The biotic portion of an ecosystem. It is also called a community.

Ecological Homologues

Species that have niche parameters that are almost identical. Such species typically do not coexist, and evolve in different geographic regions.

Ecological Management

This term is equivalent to cultural management or cultural control. This is the manipulation of the environment or practices to prevent invasion, minimize damage, or eliminate pests. It depends on the use of normal planting, production, harvesting practices rather than specialized equipment or techniques. A good example of ecological management would be manipulation of planting dates, making them either earlier or later depending on circumstances, to avoid infestation.

► Cultural Control of Insect Pests

Ecological Niche

The role of an organism including the resources used and habitat occupied.

Ecological Succession

Replacement of members of a community over time in response to community change. This process is normally thought of as a botanical phenomenon, wherein grasses are replaced by small shrubs, then large shrubs, then small trees, and finally large trees. However, insects display corresponding changes as other members of the community change. It is also called succession.

Ecology

The study of organisms in relation to their environment. News writers often substitute the term ecology when they mean environment.

Economic Injury Level (EIL)

A level of pest abundance or damage at which the cost of control equals the crop value gained from instituting the control procedure.

► Economic Injury Level (EIL) and Economic Threshold (ET) Concepts in Pest Management

Economic Damage

Damage that exceeds a visual or aesthetic effect, causing a monetary loss.

► Economic Injury Level (EIL) and Economic Threshold (ET) Concepts in Pest Management

Economic Injury Level (EIL) and Economic Threshold (ET) Concepts in Pest Management

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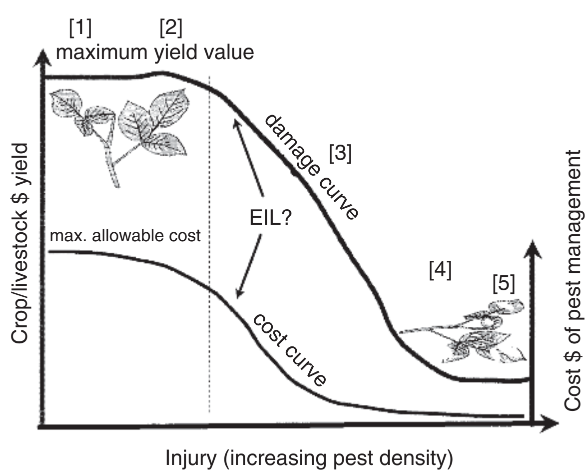
One of the fundamental concepts of integrated pest management is that each pest species has a definable relationship in terms of damage to the plant or animal host that it attacks. This relationship is often referred to as the damage curve (Fig. 11), which is often determined relative to yield loss. This damage curve can take several forms, but was summarized by Higley and Peterson as having a tolerance or overcompensation phase ([1] no yield response, or [2] positive yield response to injury), a linearity phase ([3] e.g., yield loss = – a (unit injury) + b), and a desensitization and an inherent impunity phase ([4] decreasing and finally [5] no additional yield loss per unit injury). The curve can be used with various methods to determine whether or not any action or pest management tactic (e.g., pesticide, biological control, cultural control, etc.) is needed to reduce the damage associated with this pest. Also, this relationship is uniquely characterized by a critical point, the economic injury level (EIL), or the point in the agricultural production system where the costs associated with pest management equal the benefits from the pest management actions. In other words, below the pest population represented by the EIL there is no need to take pest control actions because they are not economically justified, but economic damage can occur when the pest population densities are above the EIL.

A simple, robust model of the EIL relationship between pest control costs and benefits from control actions was developed by Pedigo et al. as:

where C = management cost per production unit, V = market value per production unit, D = damage per unit injury, I = injury per pest equivalent, and K = proportional reduction in injury with management. They later combined D + I into a single variable, D′ = percent yield loss per pest. A variation on this formula that is often used that assumes 100% control is: EIL = (C × N)/(V × I), where N = the number of pests causing injury, and I = percent yield loss (similar to the D′ value above). In an example using the EIL = C/VD′ K formula, if a seasonal average of one insect/plant causes a



Economic Injury Level (EIL) and Economic Threshold (ET) Concepts in Pest Management, Figure 11 **Example of a pest damage curve (thick line) and associated cost of pest control (thin line) used to estimate at economic injury level (EIL).**

10% reduction in yield, the market value of the crop is \$0.4/lb fruit and you expect 5 lb fruit/plant yield, the cost of control is \$0.04/plant, and you can count on a 75% reduction in damage with the control tactic used, then:

EIL = \$0.04 cost per plant/(\$0.4/lb×0.5lb/insect × 0.75)
= 0.27 insects/plant

Notice that if you halve the number of insects required to inflict 10% yield loss, you halve the EIL value. In contrast, if you double the cost of control you double the EIL value, again balancing the tradeoff between control costs and benefits. In reality, the EIL value can be difficult to calculate exactly because of the temporal and dynamic nature of pest damage and crop value. In the example above, an early season average of one insect might result in 15% yield while late season results in only 5% yield, so the estimate based on a seasonal mean would not be very precise for a given period during the season. One way to avoid large seasonal differences is to calculate an early-season and a late-season EIL, for example:

$EIL_1 = C/VD_1'K$ and $EIL_2 = C/VD_2'K$
or
EIL_1 = \$0.04 cost per plant/(\$0.4/lb×0.75 lb/insect × 0.75)
= 0.18 insects/plant
EIL_2 = \$0.04 cost per plant/(\$0.4/lb×0.25lb/insect × 0.75)
= 0.5 insects/plant

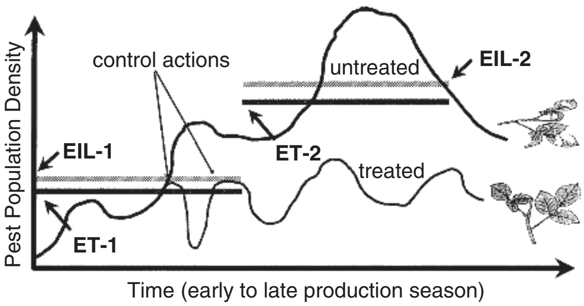
The EIL can be based on a single, seasonal mean, based on periods during the season with similar responses (e.g., seedling, vegetative, fruit formation, or simply early versus late season), or be accurately calculated over time for the life span of the affected host. This latter determination of a dynamic EIL requires a great deal of data and is seldom accomplished for most crop or livestock systems. In addition, the EIL formulas often assume a linear response to injury at any given time during the season, which may not be entirely accurate. Even so, an assumption of linearity can be generally sufficient for the range of pest injury critical for an EIL determination.

Estimates based on the aforementioned EIL formulas are in use for many agricultural pests and have successfully provided pest management decision criteria for many production systems, mainly because of both their effectiveness and ease of use. It should be noted that in commercial production systems, economic injury levels are likely to be close to a maximum allowable pest management cost because these systems have traditionally focused on maximizing returns and reducing risks to production. What is often lacking in these estimates of EILs is an environmental cost factor. The environmental cost would adjust the pest management cost by taking into consideration not just what the farm spends on management tactics, but also an estimated average cost to the environment or agro-ecosystem where the farm exists. Using the environmental economic injury level:

$$EIL = (C+EC)/VDIK$$

proposed by Higley and Wintersteen and adding an environmental cost of \$0.04/plant would increase the EIL to 0.53 or double its previous level in the aforementioned example. There will likely be a high degree subjectivity in this kind of environmental cost estimate. Even with its complications, the EIL is fundamental for understanding the interaction of pests with their host, but the calculation of economic thresholds from these data is quite a different problem, which will be discussed in the next section.

An economic threshold (ET) is typically the pest population density at which a pest control action (e.g., pesticide, biological control, cultural control, etc.) should be taken in order to prevent an increasing pest population from reaching economically damaging levels, which is the economic injury level (EIL). As shown in the diagram of the two-level fixed economic threshold (Fig. 12), two different fixed economic thresholds are esti-



Economic Injury Level (EIL) and Economic Threshold (ET) Concepts in Pest Management, Figure 12 **A two-level, fixed economic threshold with treated (narrow line), i.e., effectively controlled to stay below the EIL, and untreated (thick line) pest populations.**

mated for a single pest in a given cropping season depending on if the time frame is early season (ET-1) or late season (ET-2) as:

$$ET_1 = 90\% \times EIL_1 = 0.16 \text{ insects/plant}$$
$$ET_2 = 90\% \times EIL_2 = 0.48 \text{ insects/plant}$$

Also as an example, the pest population levels of a treated field (control actions taken) versus an untreated field (no control action) are indicated by the narrow and solid lines, respectively (Fig. 12). What can be seen from this example is that, on several levels, time is as critical a component in the estimation of economic thresholds as pest numbers. Also, it is clear that frequent pest monitoring or scouting will be required to track pest population density through time with some accuracy. In this example, it is assumed that approximately twice as many insects are required to cause an equal amount of yield loss in late season (EIL-2) as early season (EIL-1). Another aspect of time is that there may be an increase in the pest population or damage over time, and will tend to increase at a determined rate, excluding massive emigration events, as the season progresses. Finally, there is a time component in the duration of delay from when a pest population reaches an economic threshold, when control actions are actually implemented, and when the reduction of the pest population begins to occur. This can directly affect the threshold value, because the purpose of the threshold is to prevent the pest population density from reaching the EIL. As Pedigo stated, "the ET actually represents the time for taking action against a pest; population density serves as a convenient index of that time."

Economic thresholds for agricultural pests vary greatly in their accuracy (how close the estimate is to a true ET) and their precision (degree of variation around an estimated value) depending on the method used for its development. In the broadest sense, thresholds in the literature are either more subjective (based on an educated guess or "guesstimate") or more objective (based on research data used to estimate an EIL and an effective method for relating the EIL to a threshold level for initiating pest management actions). In either case, the objective is to prevent the pest population from reaching an economically damaging level. However, a low level of accuracy, often associated with subjective estimates called "nominal thresholds," can lead to either underestimating or overestimating the pest population level where action should be taken. An underestimate will result in more control costs than is economically justified, whereas an overestimate will result in crop or livestock damage that could have been avoided economically with the appropriate timing of an effective control tactic. Even though an objective ET can be more accurate than a subjective ET, the objective ET' s precision can be greatly influenced by the method in which an EIL is calculated. An EIL based on seasonal population means relative to final yield loss can be very accurate, but not very precise for individual dates during the season. Using the previous example of 15% yield loss during early season and 5% yield loss during late season for an equal number of pests, the calculated EIL values for early and late season are 0.18 and 0.53, respectively. If a single EIL = 0.27 is used for the entire season, then there will be an overestimated ET early in the season and an underestimated ET late in the season, causing the same problem as a lack of accuracy, even if it is likely to a lesser degree.

A subjective ET can be based on effective observational data as, for example, by adjusting the threshold higher or lower after each production season based on yield response, so that a reasonably accurate ET is developed through a long term process of iteration. Generally, a subjective ET is fixed at a value or named by consensus for a given use period and is thus referred to as a nominal threshold. In fact, a significant number of thresholds in use today are based on this method. The problem with this method is that it does not define the mechanism behind the EIL and ET, and can thus be affected by changes in production factors, e.g., crop variety, climate, market-driven planting dates, etc., to some unknown degree from year to year. At the very least, a subjective ET can be a starting point for threshold development, and potentially provide significant pest management benefits.

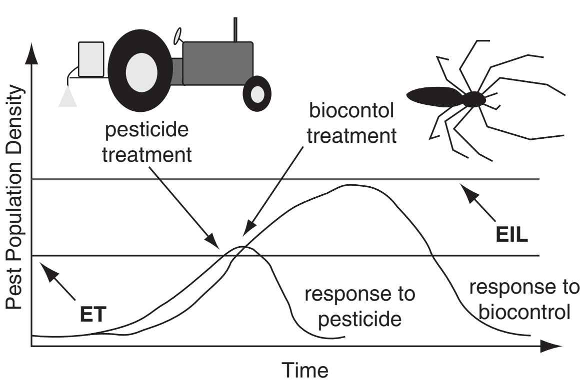
Although objective determinations of ET are research-based, they also can have a range of sophistication and complexity beginning with a simple fixed ET. The fixed ET is set at a specific percentage of the determined EIL, usually based on conservative estimates for preventing significant crop loss. In the example for a single seasonal EIL determination described in the previous section, the estimated EIL = 0.27 insects per plant would result in 2.7% yield loss that cannot be economically prevented within the conditions of the example. If there was a relatively high risk of loss, for example above 10%, a conservative threshold might be set at half, regardless of whether or not the additional control actions are economically justified. High levels of threats of injury can even lead to abandoning the ET altogether. In the other direction, if a new, highly effective (100% control) and inexpensive ($0.01/plant) control product is introduced into the system, not only does the EIL drop to 0.05, the expected yield loss at this level is so low at 0.5% that the tendency will be to leave the ET at or even above the EIL = 0.05. In this case, increasing the EIL could be justified by using other decision criteria, like environmental costs that have not been included in the initial EIL determination. Subjective judgments on the overall percentage crop loss that can be tolerated tend to vary more at the low injury levels than the high injury levels since high injury levels are not commercially tolerated. What is not considered in detail with the fixed ET is the actual time between control actions and the time it takes for the pest population to increase to the predicted EIL. In most cropping systems, weekly scouting reports are followed by weekly curative actions in the form of pesticide applications. If a cultural or biological control tactic is used that needs time to affect the overall pest population, the estimation of this time becomes critical. In this case, more descriptive thresholds based on the mechanisms of pest population dynamics are needed to accurately predict when the population level will reach the EIL.

Descriptive thresholds are of two general types, stochastic and deterministic. The deterministic model assumes a fixed and unique outcome, whereas a stochastic model incorporates probabilities based on demographics. Thus, the stochastic ET is based on an estimated pest population growth based on average population dynamics, with an associated probability of error. An economic threshold based on sequential sampling of a pest population is a good, fairly complex example of a stochastic ET. A simple example, based on highly predictable pest population dynamics, would be if a pest population prior to reaching an EIL is known to increase at a given exponential rate that doubles the population ($y = 2^x$ where y = pest numbers and x = generation time) after each generation time and the scouting interval (e.g., 7 days), is equal to one generation time. Then using the EIL = 0.27, the threshold would simply be:

$$\text{ET} = \text{EIL} - (\text{EIL}/2) = 0.27 - (0.135)$$

This simplistic example only works if the control action and response can occur between scouting intervals, that you can accurately predict that the EIL will be reached by the next scouting event, and that there is no great need to modify the value to include an additional margin of error based on a probability analysis.

The deterministic ET relies on knowledge of age-specific parameters and life processes of the pest population. It can still require probability estimates for specific processes, such as the average mortality of a beneficial insect that would affect the estimate of "K" in the calculation of an EIL, but the key mechanisms that determine pest population growth are defined. Biological control or long term cultural control tactics could benefit from the use of this type of threshold. A typical difference in the response time for a biological control tactic versus a chemical control tactic is illustrated in Fig. 13. In this example, both tactics provide equally high levels of control, but the response to the pesticide is fast, so the ET could be set closer to the EIL value than it can with the biological control. To estimate the biological control response it might be necessary to calculate life table data for both the predator and prey species (crop pest) and relate this to temperature, time and spatial dynamics; a fairly complex proposition. As the time increases between the initiation date of an effective control action and the



Economic Injury Level (EIL) and Economic Threshold (ET) Concepts in Pest Management, Figure 13 Delayed response to a biological control tactic.

control response of the pest, these descriptive thresholds can become more crucial.

References

Higley LG, Pedigo LP (1996) The EIL concept. In: Higley LG, Pedigo LP (eds) Economic thresholds for integrated pest management. University of Nebraska Press, Lincoln, NE, pp 9–21

Higley LG, Peterson RKD (1996) The biological basis for the EIL. In: Higley LG, Pedigo LP (eds) Economic thresholds for integrated pest management. University of Nebraska Press, Lincoln, NE, pp 22–40

Higley LG, Wintersteen WK (1992) A novel approach to environmental risk assessment of pesticides as a basis for incorporating environmental costs into economic injury levels. Am Entomol 38:34–39

Pedigo LP, Higley LG (1992) A new perspective of the economic injury level concept and environmental quality. Am Entomol 38:12–21

Pedigo LP (1996) General models of economic thresholds. In: Higley LG, Pedigo LP (eds) Economic thresholds for integrated pest management. University of Nebraska Press, Lincoln, NE, pp 41–57

Southwood TRE (1978) Ecological methods. Chapman and Hall, New York, NY, 524 pp

Stern VM, Smith RF, van den Bosch R, Hagen KS (1959) The integrated control concept. Hilgardia 29:81–101

Economic Threshold (ET)

The point at which corrective measures must be taken to prevent damage from attaining or exceeding the economic injury level; a level of damage or insect abundance that warns the agriculturist of impending problems.

► Economic Injury Level (EIL) and Economic Threshold (ET) Concepts in Pest Management

Ecosystem

A complex of organisms and their physical environment that interact as a defined ecological unit. Ecosystems may be natural, or modified by human activity. Ecosystems generally are not defined by political boundaries. The biotic and abiotic components and their interactions within a certain geographic area. Ecological communities pluts their physical environment.

Ecotone

The transition zone between two different communities. An example of an ecotone is fresh water marshes that serve as a transition between grassland and lakes.

Ectadene (pl. ectadenia)

Accessory glands of ectodermal origin found in the male reproductive system of some insects.

► Accessory Gland
► Reproduction

Ectophagous

Feeding on the outside of a host.

Ectopsocidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice or Psocids

Ecotype

A subspecies or race that is adapted to a particular set of environmental conditions.

Ectognathous

A hexapod with mouthparts that are not recessed into the head; rather, they are exposed. This is also known as ectotrophus. Such mouthparts are typically found in insects. This type of mouthparts distinguishes them from some related hexapods, the Entognatha (collembolans, diplurans, proturans), which have recessed mouths.

Ectotherm

An organism that uses energy from the environment rather than metabolic heat to regulate its body temperature. Insects are generally considered to be ectotherms, but some display endothermic behavior and physiology.

► Thermoregulation in Insects

Ectoparasite

A parasite that develops externally on the host. Typical ectoparasites include fleas, lice and ticks of vertebrates. However, some ectoparasites affect insects, particularly some mites. Insects that develop externally on their insect hosts (usually wasps) are more correctly called ectoparasitoids, but usually are called ectoparasites, too.

Edaphic

Pertaining to the soil.

Edwards, Henry

Henry Edwards was born in the country of Herefordshire, England, on August 27, 1830. He studied law, but he worked as an actor and his hobby was the collection of butterflies, in both of which occupations he became nationally rated in the US. In 1853, he travelled with a theatrical company to Australia, Peru, Panama, California, and Mexico, and managed to collect butterflies (and various other invertebrates) in all these places. From 1865, he lived in California, and was associated with the "Old California Theatre." His butterfly collection, eventually consisting of 250,000 specinmens, became one of the finest in the US. In 1867 he was elected member of the California Academy of Sciences, and he published a series of papers entitled "Descriptions of Pacific coast Lepidoptera." In 1877, he moved to the U.S. east coast, joined the New York Entomological Society, and edited the journal "Papilio" (1881–1883). In 1881–1882 he published an important paper on Aegeriidae, and in 1889 (after a sojourn in Australia), he published a "Bibliographical catalogue of the described transformations of North American Lepidoptera." He died in New York city on June 9, 1891. His butterfly collection was bought by his friends (for benefit of his wife) and presented to the American Museum of Natural History in New York.

Reference

Essig Eo (1931) Edwards Henry, 611– 613 in *A history of entomology*. The Macmillan company, New York, 1029 pp

Edwards, William Henry

William Edwards was born in the state of New York on March 15, 1822, and took an early interest in natural history. He attended Williams College in Massachusetts, graduating in 1842. Then in the city of New York he studied law and was admitted to the bar in 1847. In 1846, after leaving college, he journeyed to Brazil to collect birds, butterflies, and other specimens. This resulted in his first book, "Voyage up the Amazon" in 1847, which influenced soon-to-be travellers Bates and Wallace. As a practicing lawyer, he had time to indulge his passion for butterfly collecting, and later for rearing butterflies from their eggs, and during his lifetime published some 200 papers. His major work was a three-volume book "The butterflies of North America" which appeared between 1872 and 1897, and received accolades. He died on April 2, 1909.

Reference

Mallis A (1971) William Henry Edwards, pp. 288–292 in American entomologists. Rutgers University Press, New Brunswick, New Jersey, 549 pp

Eelworm

A nematode.

Efficiency

A measure of the level of precision or accuracy per unit of cost (time or currency).

► Sampling Arthropods

Egg

The first free-living stage of most insects, contained within a chorion (shell).

Egg Burster

A raised area such as a ridge or bump on the head of an embryo that is used to mechanically rupture an egg shell during hatching.

Egg Case

The case or covering secreted by an insect that contains or protects the egg cluster. It is most commonly found in orthopteroid insects. The egg case is also known as an oötheca.

Egg Pod

A clutch of eggs surrounded by a capsule. Also called egg case or ootheca. This term is generally reserved for orthopteroid insects.

► Eggs of Insects

Eggs of Insects

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Nearly all insects produce eggs (oviparity) during the adult stage, though some seemingly can produce living offspring (viviparity) indefinitely, and a few retain their eggs internally until after they hatch (ovoviviparity), depositing partly grown progeny (e.g., sheep keds and tsetse flies). Eggs are a common means of passing through unfavorable (dry season or winter) periods when food is unavailable, though because other stages of insects can enter diapause, egg-overwintering is by no means universal. Most eggs are spherical, oval, or elongate. The degree of sculpturing and ornamentation varies, as does their color. They may have ancillary structures such as anchors (e.g., wasp parasitoids) or floats (e.g., mosquitoes). They may be deposited singly or in batches, but typically a species is consistent in its pattern of oviposition.

The Egg Shell

The egg shell, or chorion, of insects is proteinaceous. It apparently lacks chitin, the polysaccharide responsible for the hardness of the exoskeleton. The insect egg shell suffers from the same problem faced by other terrestrial egg-layers: because the water molecule is smaller than the oxygen molecule, the gas exchange needed for respiration also results in dehydration (water loss). There is no ready means to allow gas exchange without some moisture loss. Thus, insects have evolved various means to facilitate gas exchange while minimizing water loss. Their challenge is appreciably more difficult than for birds and reptiles because their eggs are much smaller and therefore have a much larger surface to volume ratio, leading to greater potential for water loss. Insects tend to have mores complex egg shells than birds and reptiles to accommodate this challenge.

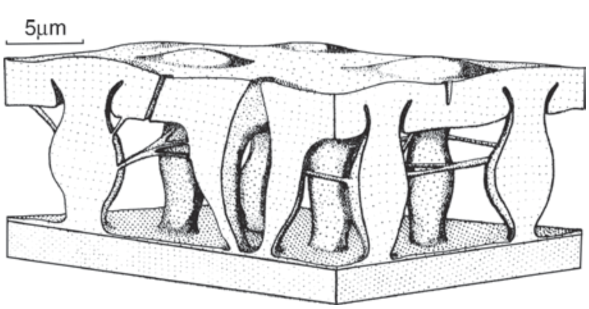
In general, insects have solved the surface area to volume ratio problem with respect to their larval and adult forms by evolving a waxy covering over their entire body. To solve the gas exchange problem, they have closable spiracular openings that allow bursts of gas exchange with minimal water loss. However, insects generally have opportunity to feed and ingest additional moisture, so the spiracle-based system does not have to be absolutely efficient. It does require that the insects be well enough developed that the closure mechanisms function reliably. With embryos and their chorion, this solution does not work, necessitating a modification. This is not to say that the eggs do not have a waxy covering, because they do, but there are no functional spiracles associated with the chorion.

Most terrestrial eggs, but not most eggs laid in water, have air-containing meshworks within the chorion. The chorionic meshwork contains a layer of gas, and has holes (aeropyles) that connect it to the outside. The holes, which measure less than a micron to several microns in size, provide continuity with the ambient atmosphere, allowing gas exchange. Their small size and small number help in water conservation. Often there are vertical columns within the chorion; they connect the external, relatively impervious layer of the chorion with the internal serosa (membrane covering of the embryo), and between the columns the gas is free to move. Not surprisingly, the chorionic meshwork system has undergone considerable modification in the different taxa, ranging from complex multi-layered systems to stalked aeropyles and the absence of meshwork.

Eggs that are found in water or likely to be submerged often are adapted to function with the aid of a plastron. A plastron is a film (bubble) of gas that has an extensive water-air interface that aids in the extraction of oxygen from water. The plastron is usually held in place by hairs or meshworks, and largely maintains its volume during use. It functions as a physical gill; as the insect withdraws oxygen from the plastron the relative concentration of nitrogen increases, stimulating more oxygen to flow into the plastron from the surrounding water, and nitrogen to flow out of the plastron into the water. Aquatic insects with plastron respiration in their eggs are normally found in fast-flowing, oxygen-rich water or along the edges of ponds and lakes where the water level changes. It may seem surprising that terrestrial eggs also often have adaptations that allow plastron function, but it is not unusual for rain to wet eggs and the eggs to remain wet for hours or even days, so it is a useful adaptation even in the terrestrial environment.

In addition to facilitating gas exchange and water conservation, the chorion must, in some cases, allow uptake of water or liquid nutrients from the environment. Hydropyles, structures that allow the uptake of water, are found on some eggs. Water is absorbed when the embryo is rapidly growing, and the egg enlarges in size. The eggs of most aquatic insects absorb water, but terrestrial insects that deposit their eggs where moisture may occur (e.g., grasshopper eggs in soil) also may have eggs that enlarge. The hydropyle is formed interiorly from the serosal (Fig. 14) layer, but may be visible externally by an extension of the chorion. Uptake of water sometimes causes the chorion to crack, leaving the embryo protected principally by the membranes. Some moisture can be absorbed from the air; partly desiccated eggs may reabsorb moisture from the air if the humidity is adequately high.

On the outside of the chorion the female may also secrete glue that attaches the egg to a substrate. Also secreted in some cases are jelly-like materials, oothecae, pods, or egg cases containing the individual eggs. The glands that secrete these are known by various names including accessory, mucous, cement, and collateral glands.



Eggs of Insects, Figure 14 **Cross section of an egg shell of showing air-containing meshwork. Note that the chorionic columns support the outer layer of the eggshell (above) above the internal serosa (below). The air in the meshwork is connected to the outside by small holes (aeropyles) as shown (left center of diagram) (adapted from Hinton 1981).**

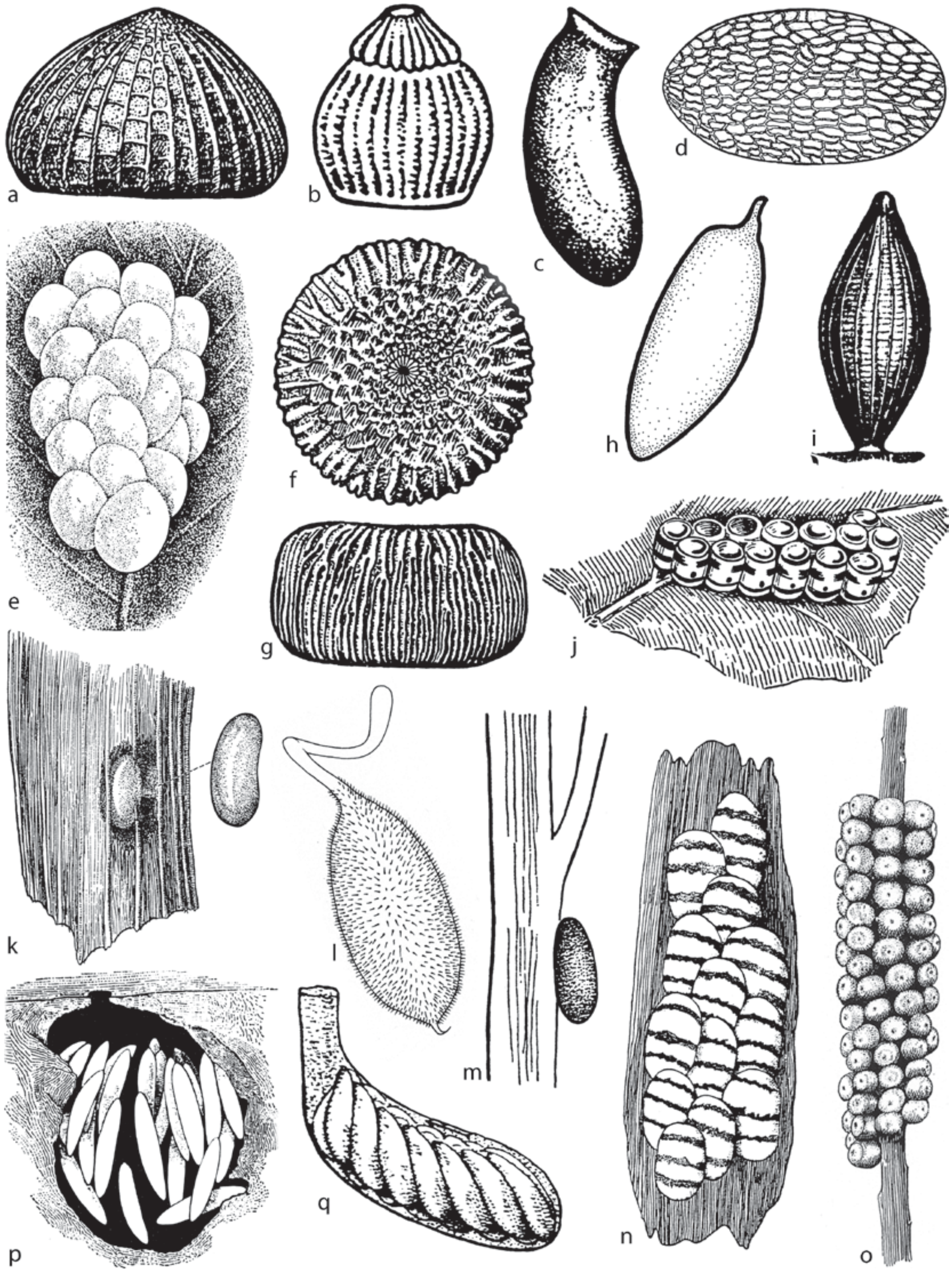
Defenses of Eggs

Various protective devices are evident in eggs, mostly to avoid predation. The defenses against predation can be grouped into three general types: deceptive devices, chemical protection, and mechanical protection.

Most species seek to conceal their eggs. They may be deposited in soil, plant tissue, or beneath stones, for example. They may be cryptically colored to avoid being seen. Some are essentially transparent, so they resemble the substrate. Several Lepidoptera have eggs with a black spot apically, purportedly resembling eggs from which a parasite has emerged. Eggs strung together resemble plant organs such as tendrils. Egg deposited apically on a plant may appear to be seeds. Some eggs resemble plant galls (Fig. 15).

Insects are sometimes poisonous or distasteful, so it is not surprising that chemicals are sometimes found on or in the eggs. For example, adult blister beetles (Coleoptera: Meloidae) are well known to contain cantharidin, and this occurs in the egg stage as well. Similarly, cardiac glycosides from milkweed plants deter birds from eating caterpillars, and their eggs are not only invested with these chemicals but they advertise their presence by being bright yellow colored. A few moths use the poisonous setae from the molted exoskeleton of the larval stage to protect their eggs by spreading the setae over the eggs.

Mechanical protection of eggs can be gained by layering eggs with non-poisonous setae or scales. The moth *Aesicopa patulana* (Lepidoptera: Tortricidae) rings its eggs with a palisade of erect scales. The ootheca of cockroaches (Blattodea) and mantids (Mantodea) deter predation by all but the most determined predators. Plant structures are useful mechanical barriers against predation. Bark beetles (Coleoptera: Curculionidae: Scolytinae) oviposit



Eggs of Insects, Figure 15 **Representative insect eggs: (a) fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae); (b) beet armyworm, *Spodoptera exigua* (Lepidoptera: Noctuidae); (c) garden fleahopper, *Halictus brachtatus* (Hemiptera: Miridae); (d) beet leafminer, *Pegomya betae* (Diptera: Anthomyiidae); (e) garden webworm, *Achyra rantalis* (Lepidoptera: Crambidae); (f) hop vine borer, *Hydraecia immanis* (Lepidoptera: Noctuidae) dorsal view; (g) hop vine borer, *Hydraecia immanis* (Lepidoptera: Noctuidae) lateral view; (h) greenhouse whitefly, *Trialeurodes vaporariorum* (Hemiptera:**

beneath bark, making access by predators difficult. Adults of the sugarcane rootstalk borer weevil, *Diaprepes abbreviatus* (Coleoptera: Curculionidae) oviposit between two leaves that are glued together; for access to the eggs, predators and parasitoids must penetrate the leaf tissue first. The chorion of a few eggs, such as those of range caterpillar, *Hemileuca oliviae* (Lepidoptera: Saturniidae) are so hard that many predators avoid feeding on them.

Size of Eggs

Formerly, it was postulated that hemimetabolous (exopterygote) insects had proportionally more yolk available to the developing embryo and the neonates were well advanced in development, producing a young insect that closely resembled the adult form. In concert with this logic, holometabolous (endopterygote) insects were considered to be yolk-deficient, and the young were forced to hatch earlier in development, and therefore forced to produce young that were not miniature adults, but more embryonic in form. This line of reasoning is no longer accepted, and indeed there is no evidence that hemimetabolous insects produce larger eggs than holometabolous insects.

Insect egg size is best correlated with the size of the female parent; large insect species typically produce larger eggs (Table 1). This is only a correlation, however, and there is considerable variation, as can be seen in the accompanying table, in which egg length is presented as a function of adult body length. Thus, micro type tachinid eggs are only about 1% of the length of the adult body, whereas at the other extreme, aphid eggs average 44% of the length of the adult.

To give insect egg size some perspective, consider that the length of a newborn human is about 50 cm, or 30% the size of the average human mother. If a human were to give birth to offspring in proportion to the size of aphids, it would measure 73 cm, nearly 50% larger. On the other hand, if humans gave birth to babies on the scale of some tachinid flies, they would measure only 2.2 cm, less than 5% of the length of the average newborn. Surely the range in insect egg size is considerable.

It is difficult to determine which insects produce the smallest and largest eggs, due in part to

Eggs of Insects, Table 1 Mean insect egg length as a proportion (%) of adult body length

	No. of species	Mean	S.D.
Tachinidae (microtype)	3	1.35	1.3
Ephemeroptera	17	2.15	1.1
Tachinidae (macrotype)	5	8.66	1.9
Pentatomidae	5	11.30	1.5
Tenebrionidae	4	11.56	3.8
Acrididae	5	13.09	2.9
Staphylinidae	5	13.90	1.8
Aphelinidae	4	14.34	3.1
Dermestidae	10	16.84	5.2
Psocidae	6	20.50	5.8
Tettigoniidae	12	22.26	8.6
Muscidae	9	25.61	5.9
Lathridiidae	6	26.98	5.1
Anisotomidae	5	34.60	6.6
Aphididae	6	44.00	12.8

Adapted from Hinton 1981

Aleyrodidae); (i) alfalfa caterpillar egg, *Colias eurytheme* (Lepidoptera: Pieridae); (j) harlequin bug, *Murgantia histrionica* (Hemiptera: Pentatomidae); (k) southern corn billbug, *Sphenophorus callosus* (Coleoptera: Curculionidae); (l) *Eurytoma* sp (Hymenoptera: Eurytomidae); (m) spotted asparagus beetle, *Crioceris duodecimpunctata* (Coleoptera: Chrysomelidae); (n) southwestern corn borer, *Diatraea grandiosella* (Lepidoptera: Crambidae); (o) range caterpillar, *Hemileuca oliviae* (Lepidoptera: Saturniidae); (p) Mediterranean fruit fly, *Ceratitis capitata* (Diptera: Tephritidae); (q) migratory grasshopper, *Melanoplus sanguinipes* (Orthoptera: Acrididae).

the paucity of data but also because it can be calculated based on actual dimensions or on a proportional basis. Likely the smallest eggs are the microtype tachinid eggs, both in absolute terms and proportionally. For example, the eggs of *Zenilla pullata* (Tachinidae) are only 0.027 by 0.020 mm. However, more data on (Fig. 15) the eggs of some of the smallest insects such as trichogrammatids and mymarids (Hymenoptera) should be obtained, as these are especially minute insects. On the other extreme, the eggs of carpenter bees (Hymenoptera: Apidae: Xylocopinae) are reputed to be the largest, at least in terms of absolute size. For example, *Xylocopa auripennis* and *X. latipes* produce eggs that measure about 3.0 mm in width and 16.5 mm in length. These are large bees, but by no means are they particularly large insects. As noted previously, aphids likely produce the largest eggs if the size of the female is considered.

Egg size is affected by latitude, particularly by mean temperatures. Insects occurring in cooler climates (closer to the north or south pole) tend to produce larger eggs than those inhabiting warm climates (closer to the equator), at least if comparisons are made within a species or closely related forms. At the coldest part of the range inhabited by insects, however, which is perhaps less hospitable, egg size begins to diminish. Thus, for most species, optimal (largest) egg size is at the cooler end of the range, but not the very coldest.

Intraspecific variation in egg size at a single location or within a single egg cluster also occurs, though it is less well documented. Environmental quality affects mean egg size, as does maternal age. With poor food quality, inadequate food availability, or old age, insects tend to produce smaller eggs. There is also a heritability component to egg size; individuals developing from smaller eggs have longer development times, develop into smaller individuals, have a higher mortality rate, and produce smaller eggs. One might expect, then, that resource-limited female insects would produce only a smaller number of large eggs rather than produce any small eggs. However, optimal egg size (i.e., that which confers increased fitness), varies with environmental conditions. Thus, the traditional view that progeny from large eggs are qualitatively superior or more vigorous, though largely true, is subject to qualification. Phenetic variation results in production of progeny that are able to cope effectively with unpredictable but recurrent instabilities in their environment. In short, there are some circumstances when smaller eggs produce individuals that are more, not less, fit under those particular circumstances. Under cool weather conditions the larvae from some insects have been shown to be more fit. Also, the slower growing larvae from small eggs sometimes live longer, grow larger, and produce more eggs. Thus, there is selective pressure for variation in egg size.

Number of Eggs

The number of eggs produced by a female insect (fecundity) varies considerably (Table 2). Undoubtedly, social insects are the most fecund. Although data on fecundity of social insects is often lacking, data on honey bees are reliable, so the estimate of up to 2,000 eggs per day, or 220,000 per year, or about 600,000 eggs in a lifetime seems reasonable. Termites, on the other hand, can produce 30,000 eggs per day and live 15–20 years, so their reproductive output is likely unsurpassed. Ants have a more modest reproductive output, perhaps several hundred eggs per year and 5,000–6,000 over the course of a lifetime.

To maintain a stable population, a female need produce only two eggs that will result in reproductively successful adults. However, some species encounter extraordinary mortality, so they produce large numbers, as mentioned above. On average, most insects produce 50 to several hundred eggs, and their reproductive output is correlated with their life style (niche). The effects of life style and mortality rate are clearly demonstrated by beetles in the family Meloidae. Those that feed on grasshopper eggs (principally *Epicauta* spp.) are deposited by females after she

Eggs of Insects, Table 2 The mean number of eggs deposited by different insects

	Number of eggs
Aeropus sibericuas (Orthoptera: Acrididae)	30
Schistocerca gregaria (Orthoptera: Acrididae)	317
Locusta migratorioides (Orthoptera: Acrididae)	1000
Anechura bipunctata (Dermaptera: Forficulidae)	55
Pediculus pubis (Phthiraptera: Pthiridae)	26
Rhodococcus bulgariensis (Hemiptera: Coccidae)	1135
Geocoris punctipes (Hemiptera: Geocoridae)	178
Chrysopa oculata (Neuroptera: Chrysopidae)	185
Oryctes rhinoceros (Coleptera: Scarabaeidae)	90
Lyctus linearis (Coleoptera: Bostrichidae)	20
Carpophilus hemipterus (Coleoptera: Nitidulidae)	1071
Coccinella septempunctata (Coleoptera: Coccinellidae)	750
Leptintarsa decemlineata (Coleoptera: Chrysomelidae)	1300
Pediobius foveolatus (Hymenoptera: Eulophidae)	30
Ooencyrtus kuwanai (Hymenoptera: Encyrtidae)	224
Diatraea saccharalis (Lepidoptera: Crambidae)	300
Trichoplusia ni (Lepidoptera: Noctuidae)	500
Aedes aegypti (Diptera: Culicidae)	1360
Delia antiqua (Diptera: Anthomyiidae)	123

Adapted from Hinton 1981.

has located a grasshopper egg pod in the soil. Thus, the likelihood of survival is relatively good because the meloid offspring do not have to search to find a host, and the female may deposit less than 100 eggs per batch. In contrast, those species that feed on bees must climb up on flowers and attach to a visiting bee to obtain a ride back to the bee's cell where it can attack larval bees. This obviously is a more precarious existence, and such meloids produce 2,000–3,000 eggs per batch. Similarly, those tachinids that oviposit directly on hosts lay a few hundred eggs over the course of their life span, whereas those that scatter them about on food plants in hope that they will be consumed and infect a host insect produce many more eggs, perhaps 5,000–6,000. Some examples of fecundity are shown in the following table.

When considering intraspecific variation in fecundity, reproductive output is positively correlated with the size of the insect pupa or adult. High fecundity can lead to crowding and intraspecific competition for food resources, however, causing a reduction in pupal or adult mass and reduction in fecundity. Thus, in the absence of regulatory mechanisms such as specific parasitoids and disease, populations tend to cycle markedly, with periods of high fecundity preceding crowding and reduction of fecundity following crowding. The resulting low population, then, is freed from the competition and fecundity again cycles upward. Some insects seem to be competition limited, and demonstrate violent swings in abundance. More commonly, however, the swings in abundance are ameliorated by natural enemies.

Mating normally stimulates oviposition, and females that are not mated usually delay oviposition, scatter their eggs in an abnormal manner, and lay fewer eggs. Not all species display this pattern of oviposition, however. Not surprisingly, those that display facultative parthenogenesis may not be influenced by mating status. But, surprisingly, some insects oviposit normally even when not mated and producing nonviable eggs.

Oviposition

The site of egg deposition is incredibly varied, reflecting the vast diversity of life styles displayed by insects. Deposition ranges from apparently random, as when stick insects (Phasmida) drop eggs to the ground while feeding in tree tops, to highly selective, as when wasp (Hymenoptera) hyperparasites select specific locations on specific ages of parasitoids within specific hosts in specific habitats, and also check to determine that the prospective host is not already parasitized before ovipositing. Some of the interesting locations for egg deposition include:

- Under water, glued to a substrate such as plant tissue. This is common among insects where both the adult and immature stages dwell in the water such as predaceous diving beetles (Coleoptera: Dytiscidae) and backswimmers (Hemiptera: Notonectidae).
- Dropped into water, or near the water and in a location likely to be flooded. This occurs in mosquitoes (Diptera: Culicidae), horse flies and deer flies (Diptera: Tabanidae), and caddisflies (Trichoptera).
- Deposited on or in a host insect. This is common among parasitic Hymenoptera and Diptera, and they may deposit their egg free within the host insect's hemocoel, within a specific organ, attached to the body wall internally or externally, or only within a certain stage (e.g., the host egg).
- The parasitic insect oviposits on the host while the latter is flying. This requires that the female be equipped with claspers to hold the host while egg deposition occurs, as in thick-headed flies (Diptera: Conopidae).
- The insect is phoretic rather than parasitic, and oviposits on an insect to take advantage of the phoretic insect's behavior. This occurs with human bot flies (*Dermatobia hominis* [Diptera: Oestridae]) in South America, which oviposit on mosquitoes that then seek out humans and other mammals, the eventual host of the bot fly. The truly clever aspect of this is that the bot fly egg hatches when the mosquito is blood-feeding, and falls onto the host where it burrows in and feeds.
- The female deposits her eggs on the back of the male, as in some giant water bugs (Hemiptera: Belostomatidae), which then provide aeration and protection for the eggs.

Distribution of Eggs

Eggs can be deposited individually, in small clusters, or in large clusters. Often, ovipositional cues stimulate egg laying, and the cues may be physical, chemical or biological. Aggregation pheromones are among the best-known stimuli affecting oviposition. For example, bark beetles (Coleoptera: Curculionide: Scolytinae) release pheromones that, in conjunction with host plant volatiles, stimulate mass attack and oviposition, allowing the beetles to overcome the innate resistance of trees to attack, and facilitating survival of their brood. Indeed, many insects benefit from the mutual stimulation of feeding siblings, and are better able to overcome structural defenses of plants when they feed as part of a group. There may also be some benefits to gregariousness of young larvae because they are able to present a collective defense against predation. Plant allelochemicals deter feeding by generalist herbivores, but herbivore species that adapt to such chemical defenses often come to use the defensive chemicals as attractants, feeding stimulants and oviposition stimulants. Other factors affecting egg laying include host sex pheromones, host-produced sounds, surface texture, surface color, and light intensity.

▶ Allelochemicals
▶ Embryogenesis
▶ Oogenesis
▶ Gregarious Behavior in Insects
▶ Mosquito Oviposition
▶ Parental Care in Heteroptera
▶ Phenotypic Plasticity

References

Capinera JL (1979) Qualitative variation in plants and insects: effect of propagule size on ecological plasticity. Am Nat 114:350–361

Fox CW, Czesak ME (2000) Evolutionary ecology of progeny size in arthropods. Annu Rev Entomol 45:341–369

Hinton HE (1981) The biology of insect eggs. Pergamon Press, Oxford, UK, 1500 pp

Ehrlichiosis

A disease caused by one of several rickettsial organisms in the genus *Ehrlichia*.

▶ Ticks

Eickwort, George C

George Eickwort was born in New York City on June 8, 1940. An early interest in entomology persuaded him to study at the University of Michigan, where he obtained a B.S. in 1962 and M.S. in 1963. He then went to the University of Kansas and obtained a Ph.D. in 1967. He was hired as assistant professor in the Department of Entomology of Cornell University. He was heavily involved in teaching at undergraduate and graduate levels, and in 1986 received a Distinguished Achievement Award in teaching from the Entomological Society of America. He guided 24 Ph.D. and six M.S. students. His research centered on Halictidae (sweat bees). In summers, he taught at the Rocky Mountain Biological Laboratory. He died in a car accident in Jamaica on July 11, 1994.

Reference

Brown WL, Franclemont JG, Tauber MJ, Liebherr JK (1995) George C. Eickwort. Am Entomol 41:190–191

Ejaculatory Duct

A median duct or tube (Fig. 16) that carries sperm from the region of the testes to the exterior of the insect.

▶ Reproduction
▶ Testis

Elachistidae

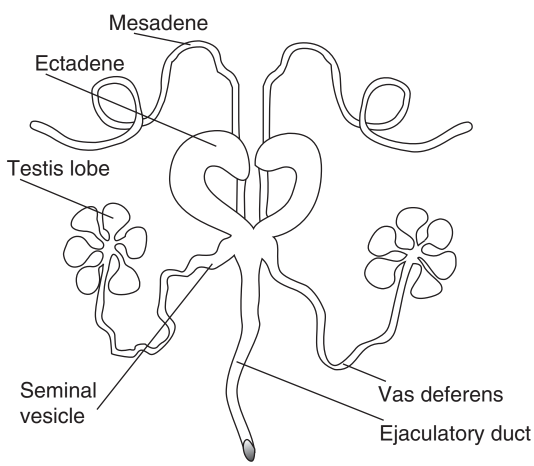
A family of moths (order Lepidoptera). They commonly are known as grass miner moths.

▶ Grass Miner Moths
▶ Butterflies
▶ Moths

Elasmidae

A family of wasps (order Hymenoptera).

▶ Wasps



Ejaculatory Duct, Figure 16 **Diagram of a male reproductive system as found in *Tenebrio* (Coleoptera) (adapted from Chapman, The insects: structure and function).**

► Ants
► Bees
► Sawflies

Elateridae

A family of beetles (order Coleoptera). They commonly are known as click beetles, though many of the larvae are known as wireworms.
► Beetles

Elateriform Larva

A larva that is heavily sclerotized, with few body hairs and short legs. Such larvae resemble wireworms (Elateridae).

Elaters

Members of the family Elateridae (order Coleoptera).
► Beetles

Elbowed Antennae

Antennae with a long basal segment, and additional smaller segments extending at a distinct angle (sometimes ninety degrees) from the basal segment. Such antennae are common among ants.
► Antennae of Hexapods

Electrophoresis

The separation of molecules in an electric field. Electrophoresis can be used to separate proteins or DNA molecules.

Elenchidae

A family of insects in the order Strepsiptera.
► Stylopids

Elephantiasis

Obstruction of the lymphatic vessels due to infection by nematodes that are transmitted by mosquitoes.
► Human Lymphatic Filariasis

Elfins

Some members of the family Lycaenidae (order Lepidoptera).
► Gossamer-Winged Butterflies
► Butterflies
► Moths

Elipsocidae

A family of psocids (order Psocoptera).
► Bark-Lice, Book-Lice or Psocids

Elmidae

A family of beetles (order Coleoptera). They commonly are known as riffle beetles.
► Beetles

Elm Leaf Beetle, *Xanthogaleruca (=Pyrrhalta) luteola* (Müller) (Coleoptera: Chrysomelidae).

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The elm leaf beetle is the primary defoliator of elm trees. Its range includes Canada, Central Asia, Europe, the Middle East, North Africa, Siberia and the United States. More recently, this insect has become established in Australia and South America.

The elm leaf beetle feeds only on elms (*Ulmus* spp.) and occasionally, on *Zelkova serrata*, also an Ulmaceae. Other key pests that attack only elms include the European elm scale, *Gossyparia spuria*

(Modeer); the European elm bark beetle, *Scolytus multistriatus* (Marsham); and Dutch elm disease, *Ophiostoma* (=*Ceratocystis*) *ulmi* (Buisman), a pathogen vectored by the elm bark beetle. However, there is great variability in pest susceptibility among and within elm species. Elms of Asian origin generally are more resistant (in some instances virtually immune) to both the elm leaf beetle and Dutch elm disease, while many Eurasian and North American elms are highly susceptible. Many pest-resistant elm cultivars have been developed and elms continue to be selectively bred to replace the hundreds of thousands of American elms, *Ulmus americana*, killed by Dutch elm disease.

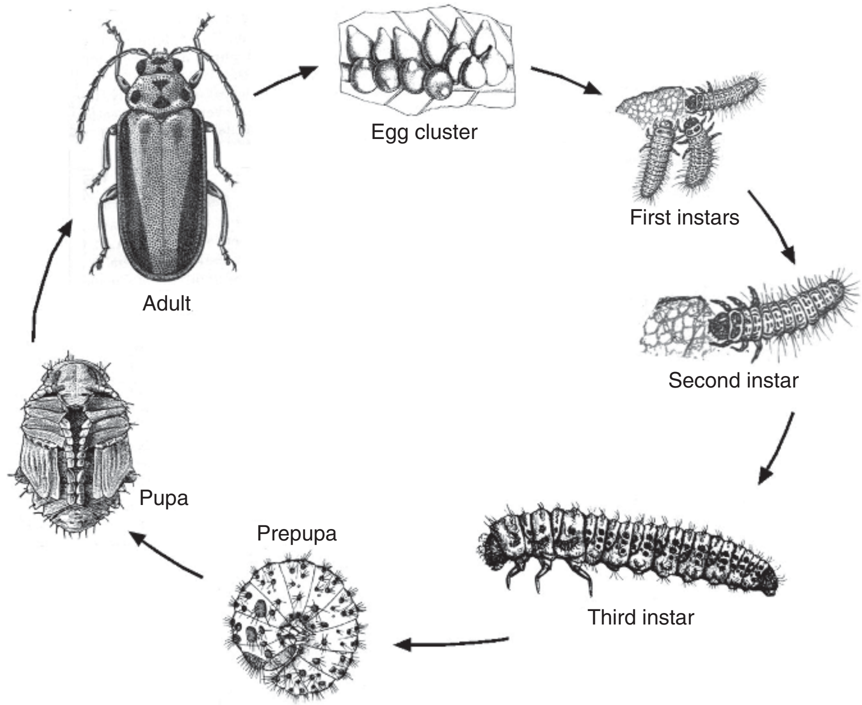
Elm leaf beetle larvae skeletonize the lower leaf surface, while the adults chew entirely through the leaf, often in a shot hole pattern. Defoliation eliminates summer shade, reduces the aesthetic value of trees and causes annoying leaf drop. Repeated, extensive defoliation weakens elms, causing the trees to decline. Severe defoliation possibly increases tree susceptibility to elm bark beetles and Dutch elm disease.

The adult beetles are about 8 mm long and are olive-green with black margins on each wing cover. The females lay yellowish eggs in double rows of about 5–25 on the underside of leaves. Each egg is about 1 mm wide and 1.5 mm tall and becomes grayish before hatch. The larvae appear black initially, but after feeding, become a dull yellow or green with rows of tiny, dark tubercles (projections). The larvae develop through three instars (Fig. 17). Third instars are up to about 1 cm long and have dense rows of dark tubercles that resemble a black stripe down each side, making them easy to distinguish from first- and second-instar larvae. The pupae are about 6 mm long and are bright yellow to dull orange in color.

Adult elm leaf beetles commonly overwinter in bark crevices, litter, woodpiles, or in buildings. The adults fly to foliage in the spring to feed and lay eggs. After feeding in the canopy for several weeks, mature larvae crawl down the tree trunk, become curled inactive prepupae, and then develop into yellowish pupae. After about 10 days, the adult beetles emerge from the pupae around the tree base and fly to the canopy to feed and (during spring and summer) lay eggs. The elm leaf beetle has about two annual generations in much of its range, but this varies with weather and location. For example, typically there is only one complete generation a year in northeastern California, while up to three generations can occur in central and southern California. Temperature monitoring can predict the seasonal emergence of adults and when each life stage occurs in the field, but are location-specific.

Good cultural care of trees is an essential component of integrated pest management. Many European and American elm species are adapted to summer rainfall and require proper irrigation to grow well in Mediterranean climates such as California and parts of Australia. Avoid pruning elms during the spring and summer as the European elm bark beetle is attracted at this time to fresh pruning wounds, and can introduce Dutch elm disease. If planting or replacing elms, consider using cultivars resistant to both Dutch elm disease and the elm leaf beetle (e.g., "Frontier," "Prospector"). Avoid elms that are highly susceptible to both the elm leaf beetle and Dutch elm disease (e.g., English elm, *Ulmus procera*, and Scotch elm, *U. glabra*).

Several natural enemies kill elm leaf beetles, but generally do not provide adequate control by themselves. A small, black tachinid fly, *Erynniopsis antennata*, oviposits on larvae, feeds inside, and emerges from mature beetle larvae or prepupae. *Erynniopsis antennata* is native to Eurasia and has been introduced in parts of the United States. Its black to reddish, cylinder- or teardrop-shaped pupae occur during spring and summer at the base of trees. *Erynniopsis antennata* overwinters in adult beetles, emerging as adults in spring, although this is not readily observed. *Erynniopsis antennata* is the most important elm leaf beetle parasitoid in California, but its effectiveness is limited by a secondary parasitoid, *Baryscapus* (=*Tetrastichus*) *erynniae*, and some apparent asynchrony between the host and the parasite life cycles.



Elm Leaf Beetle, *Xanthogaleruca (=Pyrrhalta) Luteola* (Müller) (Coleoptera: Chrysomelidae), Figure 17 **Elm leaf beetle stages and life cycle. adult, larvae: L.O. Howard. 1895. The shade-tree insect problem in the eastern United States. The Yearbook of Agriculture. USDA. Washington, DC. eggs, prepupa: F. Silvestri. 1910. Contribuzioni alla conoscenza degli insetti dannosi e dei loro simbionti. Bollettino del Laboratario di Zoologia Generale e Agraria Portici 4:246–288. pupa: G.W. Herrick. 1913. Control of two elm-tree pests. Cornell University Agricultural Experiment Station Bulletin 333.**

Oomyzus (=*Tetrastichus*) *brevistigma* parasitizes mature elm leaf beetle larvae and pupae. One or more small, round holes in the beetle pupae can indicate where this parasitoid has emerged. This species is of uncertain origin, but is the most important elm leaf beetle parasitoid in the eastern United States. *Oomyzus brevistigma* can be laboratory-reared in large numbers and cold-stored for several weeks, suggesting it is a good candidate for inundative biological control of its host.

An egg parasitoid, *Oomyzus* (=*Tetrastichus*) *gallerucae*, occurs in Eurasia and scattered locations where it has been introduced in the United States. It leaves round holes when it emerges from the beetle eggs, which remain golden. When the beetle larvae have emerged, the egg shell is whitish with more ragged holes. *Erynniopsis antennata* and *Oomyzus brevistigma* have been introduced to Australia and Argentina in an effort to provide classical biological control of the elm leaf beetle.

Historically, this pest was managed by foliar application of broad-spectrum insecticides, including lead arsenate beginning in the late 1800s, DDT starting in the 1940s, and more recently, various organophosphates (e.g., acephate and malathion), carbamates (carbaryl) and pyrethroids (e.g., bifenthrin, fluvalinate). Current recommendations are to use an integrated program that incorporates resistant elms, good cultural practices, conservation of natural enemies and regular monitoring. For example, presence-absence egg sampling can be used in California to predict the extent of defoliation and treatment need based on the percentage of one-foot branch terminals infested with beetle eggs. If needed, controls include foliar spraying with *Bacillus thuringiensis* subspecies *tenebrionis*, or spot application to bark (bark banding) with a broad-spectrum insecticide to kill larvae migrating down the trunk. Systemic insecticides (e.g., abamectin, imidacloprid) that are applied without spraying minimize environmental contamination, and if applied to soil, avoid the tree injury that occurs during injecting or implanting insecticide into roots or trunks. Where beetles entering buildings to overwinter is a problem, they can be excluded by screening openings and sealing exterior cracks and crevices. University Cooperative Extension services can provide more specific pest management recommendations.

References

Dahlsten DL, Rowney DL, Lawson AB (1998) IPM helps control elm leaf beetle. Calif Agric 52:18–24

Dreistadt SH, Dahlsten DL (1990) Relationships of temperature to elm leaf beetle (Coleoptera: Chrysomelidae) development and damage in the field. J Econ Entomol 83:837–841

Dreistadt SH, Dahlsten DL, Lawson AB (2001) Elm leaf beetle. University of California DANR Pest Notes Publication 7403. Available at http://www.ipm.ucdavis.edu/PMG/PESTNOTES/pn7403.html (accessed 10 March 2008), http://www.ipm.ucdavis.edu/PMG/selectnewpest.home.html

Hamerski MR, Hall RW, Keeney GD (1990) Laboratory biology and rearing of *Tetrastichus brevistigma* (Hymenoptera: Eulophidae), a larval-pupal parasitoid of the elm leaf beetle (Coleoptera: Chrysomelidae). J Econ Entomol 83:2196–2199

Miller F, Ware G (1999) Resistance of elms of the *Ulmus davidiana* complex to defoliation by the adult elm leaf beetle (Coleoptera: Chrysomelidae). J Econ Entomol 92:1147–1150

Elongate-Bodied Springtails

A family of springtails (Hypogasturidae) in the order Collembola.

► Springtail

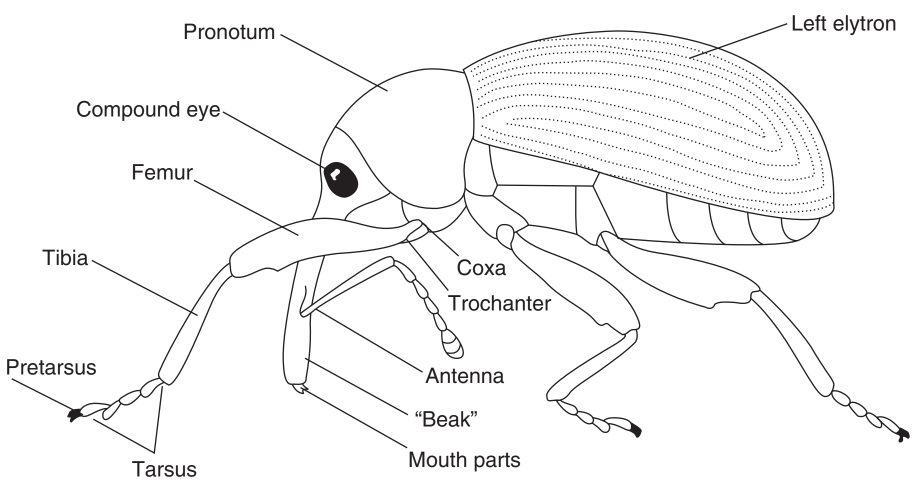
Elytron (pl. elytra)

The thickened front (Fig. 18) wing of beetles, serving primarily for protection of the hind wings or flight wings.

► Wings of Insects

Elytron/Femur Ratio (E/F)

The ratio of the length of the front wing (more correctly called tegmen) to the length of the femur.



Elytron(pl. elytra), Figure 18 **Side view of a weevil (Curculionidae).**

This character is used to determine the morphological phase status of locusts.

Emarginate

A structure that is indented or notched.

Embiidae

A family of web-spinners (order Embiidina).
► Web-Spinners

Embiidina

An order of insects, formerly known as Embioptera. They commonly are known as web-spinners.
► Web-Spinners

Embolium

The leading edge of the corium region (Fig. 19) on the hemelytra of Hemiptera.
► Wings of Insects

Embioptera

► Embiidina

Embryogenesis

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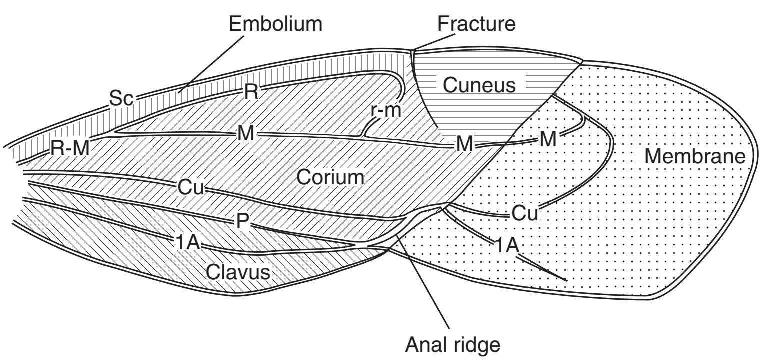
Embryogenesis in insects starts with an intricate, ordered building of the egg by the female. The female fills an egg with cytoplasm and yolk, beginning with the future posterior end of the embryo. The egg also is supplied with cytoplasmic determinants by the mother, and specific types of determinants are more concentrated in one end of the egg than the other. Cytoplasmic determinants are ribonucleic acid particles (RNPs) that code for transcription or translation factors, gene regulators, growth factors, kinases and other enzymes. These cytoplasmic determinants specify the anterior-posterior and the dorsal-ventral body axes: they initiate a developmental sequence that activate specific zygotic regulatory genes in a region-specific pattern. This pattern narrows and becomes refined with time, because each new set of activated genes allows the establishment of more developmental fates, and for an increasingly precise allocation of fates within each region.

In many holometabolous insects, the basic body plan of the larva is specified very early in development, before and during the cellular blastoderm stage. Some of the genes that regulate early development are known as "gap genes," "pair rule genes" and "homeobox genes." Along the ventral-dorsal axis in hemimetabolous and



Embolium, Figure 19 **Front wing of a bug (Hemiptera: suborder Heteroptera), thickened basally and membranous distally.**

holometabolous insects, the future mesoderm lies ventral-most. Ventrolaterally lies a band of nuclei/cells committed to neural development, and located more dorsally is the ectoderm and extraembryonic ectoderm. Endoderm is derived from a small region anterior and posterior to the mesoderm as well as from the inner yolky region of the egg.

The initial allocation of fates along the anterior-posterior axis is set by gap genes, which code for regulatory proteins. Gap genes divide the embryo into several large regions (loss of a functional gap gene leads to a loss of a large portion of the body). Gap genes induce, but also restrict the expression domains of primary pair rule genes, narrowing these domains to a bisegmental pattern. The primary pair rule genes induce other pair rule genes. Each pair rule gene has a bisegmental pattern of activity that overlaps some, but not all, of the other domains. Their combined expression patterns create a series of stripes and establish the segmental nature of the insect body. Pair rule genes activate segment polarity genes that maintain anterior to posterior patterning within each segment. Segment polarity genes must remain active until the adult stage. Gap genes and pair rule genes also activate homeobox genes (e.g., selector genes) that regulate the anatomical characteristics of segments. Within each insect segment, one finds that each nucleus has received an almost unique developmental address. Such positional information collectively builds an organized body plan.

A number of genes that set up the body axes and segments in *Drosophila* have conserved functions in a diversity of animals from centipedes and horseshoe crabs to other hemimetabolous and holometabolous insects, and likewise vertebrates and humans. Although developmentally crucial genes in hemimetabolous orders are similar to those in holometabolous embryos, their temporal expressions are different. Hemimetabolous embryos may take more than two months to complete embryogenesis at room temperature. In hemimetabolous insects, the onset of pattern formation is not simultaneous across the entire body, but proceeds in an anterior to posterior direction. In orders such as Blattodea, Dermaptera, Isoptera, and Embiidina, segments are added by means of posteriorly directed growth and must include *de novo* DNA synthesis. In others orders such as Phasmida, Orthoptera and Hemiptera, the basic body regions are unrefined but present. Segments develop larger size and anatomical complexity one by one. In contrast, a *Drosophila* larva breaks out of its egg shell approximately 22 h after fertilization. In such quickly developing insects, segmentation proceeds almost simultaneously across the body.

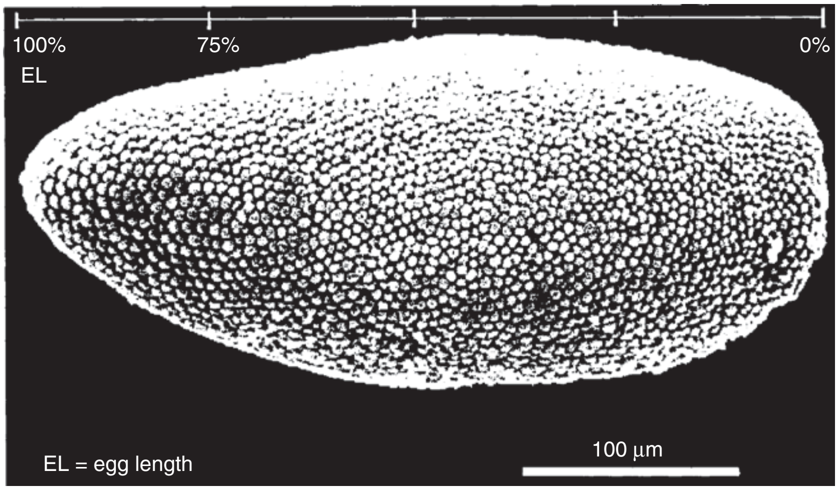
Insect cells have been thought of as having a mosaic form of development, that is, exhibiting a fixed and invariant commitment to a particular fate that is not altered by, for example, transplantation to other regions of the embryo, even during early embryogenesis. In holometabolous orders, this specificity is due to the flurry of genetic activity that occurs during early development (described briefly above). However, some embryonic tissues from holometabolous insects are able to regulate, i.e., develop variably in response to the surrounding cells. For instance, cell-cell communication between different cell types is essential for normal development of the midgut and mesoderm. In hemimetabolous insects, there is a far greater ability within the egg to regulate the cells' final fate. Krause's experiments with stone crickets (Gryllacrididae, Orthoptera) induced embryonic twinning, partial duplications, and triplications, thereby demonstrating that embryonic cells produced flexible responses to new developmental circumstances.

Early development in animals is characterized by cleavage divisions, whereby the single large egg is subdivided into a host of small cells, which is followed by morphogenetic movements that reshape the embryo. Insects are special in that they undergo 10–13 rounds of nuclear divisions before forming cells. Most nuclei migrate to the periphery of the egg, and cells are formed when the egg's plasma membrane folds inward to separate and enclose individual nuclei. The cellularization process takes approximately one hour in *Drosophila* (Fig. 22), but in other insects there can be region-specific differences in the onset of cell formation. The cellularization process produces the cellular blastoderm, consisting of an embryonic and extra-embryonic component. In termites (Isoptera) and walking sticks (Phasmida), an uneven distribution of nuclei precedes the separation into the embryo and extraembryonic tissue after the cellular blastoderm stage. In other hemimetabolous orders (for example, Odonata, Plecoptera, Orthoptera) and in most holometabolous insects, the distribution of nuclei is practically uniform. However, in parasitic Hymenoptera, cleaving nuclei associate into clusters and form cells. Each cluster gives rise to one embryo, and two (as in Platygastridae) to 1,500 (as in Encyrtidae) young can emerge from a single egg. This phenomenon of polyembryony is another example of regulative, as opposed to mosaic development, within holometabolous orders.

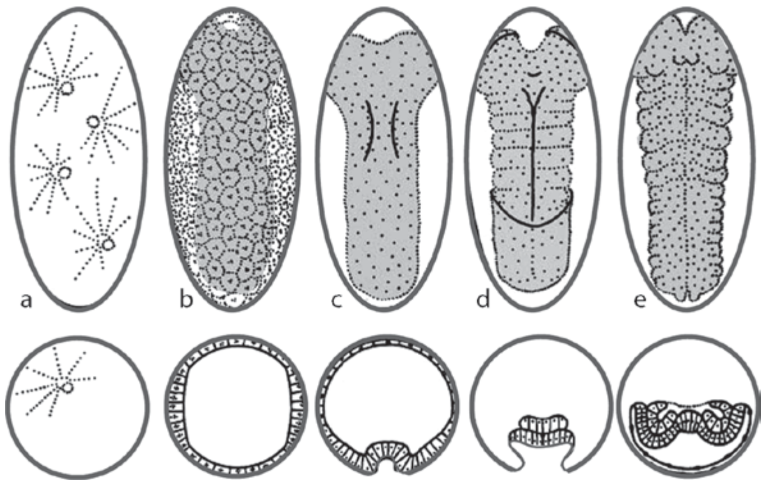
Most insect eggs have a substantial amount of yolk that lies to the interior of the cellular blastoderm (Fig. 20). Eggs of hemimetabolous insects tend to contain more yolk than eggs of holometabolous insects. Insects are defined as engaged in meroblastic cleavage – incomplete cleavage of the yolky region, and in superficial cleavage – the yolk lies interior to the cellular blastoderm, filling the central region of the egg.

Extraembryonic cells develop into the serosa that line the inner surface of the egg, the amnion that encloses the embryo, and vitellophages and yolk cells. Vitellophages will form a provisional inner lining of the future midgut and aid in the digestion of yolk. They are usually digested before hatching, but may become incorporated into the epithelial lining of the gut in Odonata. In *Drosophila*, signals from yolk nuclei (vitellophages or yolk cells) are essential for the proper cell migration by prospective gut tissue so that a digestive tube is formed.

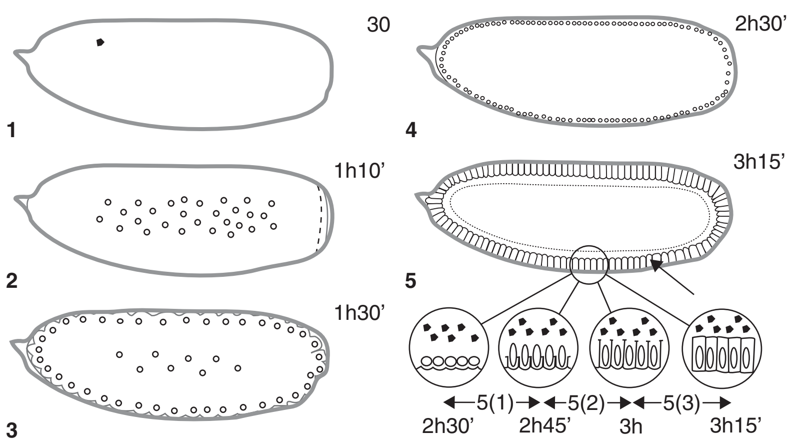
Morphogenesis, the creation of form, describes the cell movements that must take place to create an ordered body plan. At the blastoderm stage (Fig. 21), the embryo consists of a single layer of cells. In hemimetabolous insects, the separation between the extraembryonic component and the embryo involves a convergence of the embryonic cells toward the ventral and posterior side of the egg. In holometabolous insects like coleopterans, lepidopterans and dipterans, embryonic cells also converge toward the ventral side, but this



Embryogenesis, Figure 20 **Cellular blastoderm stage in the fruit fly *Drosophila melanogaster*. Anterior region is to the left and the dorsal side is up (Scanning electron micrograph by S. Dyby).**



Embryogenesis, Figure 21 **Steps in the early embryogenesis of insects. Top row: ventral view of egg, anterior end up. Bottom row: diagrammatic cross sections at the levels indicated by bars in top row. (a) Multiplication and migration of nuclei within the ooplasm. (b) Cellularization of the superficial part of the ooplasm. The resulting blastoderm initially consists of uniform cells but soon regional differences in cell density and shape indicate segregation into germ anlage and prospective embryonic covers. (c) The prospective mesoderm starts to invaginate along the midline of the germ anlage (gastrulation). (d) Germ band after gastrulation, with segment borders and amniotic folds forming. The folds shown over head lobes (top) and abdomen approach each other and finally fuse, thereby closing the amniotic cavity. (e) Advanced germ band stage, with appendage buds, transient coelom anlagen, and amniotic cavity (Modified from Sander, 1976).**



Embryogenesis, Figure 22 **Early development of a fly embryo, showing stages from 1 to 5 (Modified from Lawrence, 1992).**

migration movement occurs in concert with an extension movement along the anterior-posterior axis that dramatically lengthens the embryo, now described as the germ band. Germ band elongation allows for body segmentation to take place without a process of segment-by-segment addition. This is defined as a long-germ band development. In contrast, when the majority of body segments forms one after the other, this is described as the short-germ band type.

The germ band develops an inner mesodermal and outer ectodermal cell layer during gastrulation. The entire mesodermal cell sheet invaginates, that is, the cell sheet buckles inward in some species; in others, mesodermal cells ingress individually once a midventral groove has formed by means of cell shape changes. The mesodermal cells rearrange to line the inner surface of the ectoderm, then engage in cell divisions. They form segmentally reiterated clusters of cells called somites. The ventral-most component of the somites – the visceral or splanchnic mesoderm – will differentiate into the musculature of the midgut, fat body, gonads, and blood, whereas the rest – the somitic mesoderm – form segmental muscles, the dorsal vessel (heart muscle), and musculature of the foregut, hindgut and genitalia. Limb musculature is derived from the ventrolateral region of the somites. Cephalic mesoderm contributes to the musculature of the head, pharynx, mouthparts and the anterior portions of the foregut.

A ventrolateral region of the ectoderm is neurogenic and gives rise to the nervous system. In hemimetabolous embryos, neuroblasts generally ingress while the mesodermal somites are forming and each region of the germ band matures. In holometabolous embryos, neuroblasts ingress just after the mesoderm cells line the inner surface of the ectoderm, that is, after gastrulation and an accompanying rapid elongation of the germ band. In the procephalic region where the brain develops, the neuroblasts stay on the surface longer. Ingressed neuroblasts divide several times and give rise to ganglion mother cells. The latter divide symmetrically or asymmetrically, with the asymmetrical division producing a ganglion cell or neuron. Neuroblasts and ganglion cells associate into neuromeres, which are segmentally reiterated cell clusters separated by intersegmental ridges. The neuromeres become connected by axonal bundles that build longitudinal connectives and transverse commissures. This early arrangement of the central nervous system is altered by fusion of specific neuromeres to bring about the final arrangement of ganglia. The optic lobes of the brain connect to two thickened ectodermal cell plates that develop into lateral ocelli. An extensive peripheral nervous system is established, beginning with the appearance of somatic muscle cells and the progenitors of sensory cells.

The rest of the ectoderm turns into epidermis, apodemes, glands, sensory organs, tracheal system, Malpighian tubules, and epithelia of the foregut and hindgut. The non-neurogenic ectoderm cells tend to stay connected as a cell sheet (epithelium) so that the primary morphogenetic changes occur by epithelial invaginations or evaginations. Limb formation and gnathal appendages begin as an evagination or a budding outward by the ectoderm. The Malpighian tubules begin as flat outpocketings of the hindgut epithelium and elongate into long convoluted tubes during late embryogenesis. The salivary glands derive and invaginate from the labium. They elongate into two long tubes that join into a common duct by the labium. The first invaginations of the tracheal system appear as tracheal pits, one for each thoracic and abdominal segment. Further internal tracheal branching continues by invagination, cell migration, and rearrangements. Cell fusions produce the final tracheal network, followed by deposition of cuticle and tanning.

The insect gut consists of the foregut, midgut and hindgut. Aspects of gut development are similar across most insect orders, although the final anatomy and physiology of the gut vary with the type of food that the juvenile insect ingests, digests, absorbs, and excretes. The gut primordia are found at the anterioventral side of the embryo and at its posterior extremity. The primordia invaginate and involute during or just after gastrulation, forming hollow sacs. The innermost part of these sacs is endoderm, which dissociates from the prospective foregut and hindgut and migrates along the inner body wall and comes in contact with the visceral mesoderm that becomes the musculature of the midgut. Together with the visceral mesoderm, the midgut endoderm forms a tube around the yolk that lies inside the embryo. The encircling of the yolk proceeds in a ventral to dorsal direction. The foregut and hindgut epithelium are ectoderm derivatives, whereas most of the midgut epithelium is endodermal in origin. The anterior portion of the midgut epithelium has both endoderm and ectoderm contributing to gastric caeca, outpocketings of the gut that often harbor a bacterial community. The foregut and hindgut musculature differentiates before the midgut is entirely formed. In lepidopterans, the contractions of foregut and hindgut help turn and reposition the embryo within the extraembryonic membranes during mid-embryogenesis. The stomodael nervous system derives from the dorsal roof of the foregut, and develops into the endocrine glands, corpora cardiaca and corpora allata, a frontal ganglion, connectives, and a recurrent nerve that loops back to the brain.

The germ band is open dorsally in both hemi- and holometabolous orders. The amnion covers this dorsal opening, and is replaced by embryonic cells during a process called dorsal closure. The ectodermal cells rearrange and migrate dorsally, as do the cardioblasts and the midgut mesoderm and endoderm. In insects with long-germ band development, dorsal closure is preceded by germ band shortening. The germ band not only shortens, but also expands, and the embryo takes up room previously occupied by yolk. Once dorsal closure is completed, it is tissue organization and differentiation, rather than morphogenetic reshaping of the germ band, that occupies most the time left before the juvenile insect hatches from its egg. In lepidopterans and other orders, an embryonic molt of newly formed cuticle occurs during late embryogenesis. Tanning and pigmentation occur in the tracheal tree, mouthparts, head capsule, setae, integument, and other cuticular elements.

Diapause is common during the egg stage. A complex mix of environmental and genetic factors influence the female's laying of eggs that are capable of diapause. The stage of developmental arrest is usually determined genetically and may occur during early, mid-, or late embryogenesis. Some insects can withstand drying-out. The eggs of some African locusts, for example, remain viable after three years of desiccation.

► Diapause
► Endocrine Regulation of Insect Reproduction
► Oogenesis
► Nervous system
► Reproduction
► Sterile Insect Technique

References

Anderson DT (1972) The development of hemimetabolous insects. In: Counce SJ, Waddington CH (eds) Developmental systems: insects, vol 1. Academic Press, London, UK, pp 95–163

Anderson DT (1972) The development of holometabolous insects. In: Counce SJ, Waddington CH (eds) Developmental systems: insects, vol 1, Academic Press, London, UK, pp 165–242

Campos-Ortega JA, Hartenstein V (1985) The embryonic development of *Drosophila melanogaster*. Springer Verlag, Berlin, Germany, 405 pp

Counce SJ (1972) The causal analysis of insect embryogenesis. In: Counce SJ, Waddington CH (eds) Developmental systems: insects, vol 2. Academic Press, London, UK, pp. 2–125

Kalthoff K (1996) Genetic and molecular analysis of pattern formation in the *Drosophila* embryo, Ch 21. Analysis of biological development, 1st edn. McGraw-Hill, New York, NY, pp 493–542

Patel NH, Hayward DC, Lall S, Pirkl NR, DiPietro D, Ball EE (2001) Grasshopper hunchback expression reveals conserved and novel aspects of axis formation and segmentation. Development 129:3459–3472

Sander K (1984) Embryonic pattern formation in insects, Ch 10. In: Malacinski GM, Bryant SV (eds) Pattern formation: a primer in developmental biology. Macmillan, New York, NY

Walker SS, Lee KK, Descai RN, Erickson JW (2000) The *Drosophila melanogaster* sex determination gene *sisA* is required in yolk nuclei for midgut formation. Genetics 155:191–202

Embolemidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Embonychidae

A family of web-spinners (order Embiidina).

► Web-Spinners

Emergence

Escape of the adult from the body covering of the terminal immature stage or pupa; sometimes used to describe eclosion.

Emerson, Alfred Edwards

Alfred Emerson was born in the state of New York, USA, on December 31, 1896. He moved with his parents to Chicago in 1905. In a family of artists, he was the first scientist. In 1914 he went to Cornell University with the objective of studying poultry science, but chose entomology instead. While he was at Cornell, he visited the New York Zoological Station in Guyana, met zoologist William Beebe, and at the latter's suggestion began to study termites. In 1920, he completed his M.A. degree, married, and took his new wife on his second trip to Guyana. A third trip followed, in 1924, but meanwhile he had in 1921 accepted a position as instructor at the University of Pittsburgh. He completed requirements for a Ph.D. degree from Cornell in 1925, then moved to the University of Chicago, where he stayed for the rest of his career. His major contribution to entomology was the over 100 papers he published on the systematics, phylogeny, distribution and natural history of termites, including fossil species. He co-authored (1949) "Principles of animal ecology" which was the major North American text on the subject of its time. But, his first wife died of a heart condition that year. He received numerous awards and was elected to the National Academy of Sciences in 1962. He died in New York state on October 3, 1976, survived by two children from his first marriage and by his second wife, Eleanor, whom he married in 1950. His termite collection of about a million specimens, representing 1,745 species, was given to the American Museum of Natural History.

Reference

Wilson EO, Michener CD (1982) Alfred Edwards Emerson December 31, 1896 – October 3, 1976 [with bibliography]. National Academy Press, Biogr Mem 53:159–176

Emery's Rule

This postulates that in colonies of social insects, their social parasites are similar in appearance to the hosts and closely related phylogenetically.

Emigration

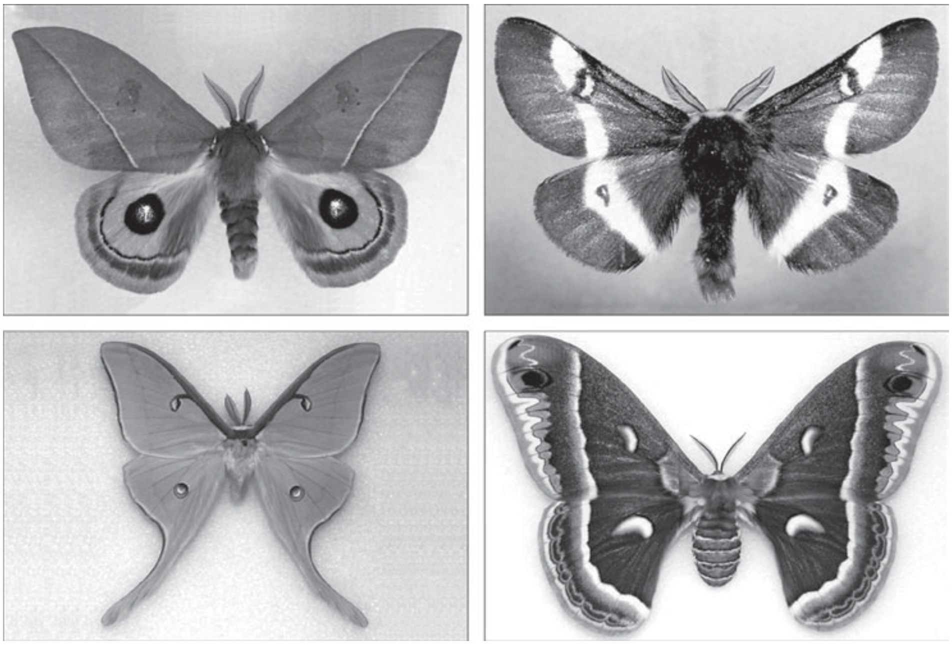
Movement of individuals out of an area to another location (contrast with immigration).

Emperor Moths (Lepidoptera: Saturniidae)

JOHN B. HEPPNER
Florida State Collection of Arthropods,
Gainesville, FL, USA

Emperor moths, family Saturniidae (also called giant silk moths, and including Buck moths, io moths, and royal moths), include 1,435 species worldwide, but are predominately Neotropical (860 sp.). The family is in the superfamily Bombycoidea (series Saturniiformes), in the section Cossina, subsection Bombycina, of the division Ditrysia. There are seven subfamilies: Arsenurinae, Ceratocampinae, and Hemileucinae are all New World, plus Agliinae (Palearctic), Ludiinae (Afrotopical), Salassinae (Oriental), and Saturniinae.

The larger species, in the subfamily Saturniinae, are more diverse in Africa (225 sp.) and tropical Asia (125 sp.), yet are the only subfamily found in all regions of the world. Hemileucinae forms the largest subfamily, with 630 species, mostly Neotropical. Adults medium size to very large (30–300 mm wingspan), with head vertex roughened; haustellum absent or short; labial palpi short; maxillary palpi vestigial; antennae bipectinate (some actually quadripectinate), smaller in females; body robust, with long hair-like scales. Wings broadly triangular, often with apex falcate (especially in males of some genera), or more rounded; hindwings rounded but sometimes with tails (sometimes extremely long) (Fig. 23). The longest hindwing tail lengths are about 130 mm (not counting the basal area of the hindwing), equally long and thin in the Neotropical genus *Copiopteryx* and in the African genus *Eudaemonia*, and long but wider tails in the giant Madagascan *Argema*. Maculation various, but mostly shades of brown with eyepots (sometimes hyaline) and terminal border bands, or white with spots, or other coloration; hindwings often with large eyespots (especially in Hemileucinae). Adults mostly nocturnal or crepuscular, but some are diurnal. Larvae are leaf feeders and many are polyphagous, some being communal or gregarious; many are extremely large. Many larvae have bizarre spines and scoli; many are urticating (especially in Hemileucinae). Host plants are extremely varied, particularly in broadleaf forest tree families, but at least 48 plant families are involved. Some species are economic for agriculture, but major urticating larvae are involved in dermatitis and more severe allergic reactions (the most toxic seem to be the genus *Lonomia* in Brazil), and in a few cases even from adult scales.



Emperor Moths (Lepidoptera: Saturniidae), Figure 23 Examples of Emperor moths (Saturniidae): top left, (subfamily Hemileucinae), *Automeris cecrops* (Boisduval) from Arizona, USA; top right, *Hemileuca* maia (Drury) from Florida, USA; lower left, (subfamily Saturniinae), *Actias luna* (Linnaeus) from Florida, USA; lower right, *Hyalophora cecropia* (Linnaeus) from Florida, USA.

References

D' Abrera B (1995–1998) Saturniidae mundi: saturniid moths of the world, 2 vol. Goecke & Evers, Keltern

Lemaire C (1978–2002) Les Saturniidae Américains, the Saturniidae of America. Los Saturniidae Americanos, Neuilly-sur-Seine (1978 vol 1; 1980 vol 2); Museo Nac. Costa Rica, San Jose. (1988. Vol. 3); Goecke & Evers, Keltern (2002. Volume 4).

Peigler RS, Wang HY (1996) Saturniid moths of Southeastern Asia. Taiwan Museum, Taipei, 262 pp

Pinhey ECG (1972) The emperor moths of South and Central Africa. C. Struik, Capetown, 150 pp, 43 pl

*Seitz, A. (ed.). (1911–1928). Familie: Saturniidae. In: Die Gross-Schmetterlinge der Erde, 2:209–226, pl. 31–34 (1911); 2 (suppl.):129–133, pl. 11, 14 (1932); 6:713–827, pl. 101–137, 142 (1929–30); 10:497–520, pl. 52–56 (1926–28); 14:313–347, pl. 48–59 (1927). A. Kernen, Stuttgart

Tuskes PM, Tuttle JP, Collins MM (1996) The wild silk moths of North America: a natural history of the Saturniidae of the United States and Canada. Cornell University Press, Ithaca, NY, 250 pp, 30 pl

Empididae

A family of flies (order Diptera). They commonly are known as dance flies.

► Flies

Empusidae

A family of praying mantids (Mantodea).

► Praying Mantids

Empodium

A single spine or pad-like structure found between the tarsi of Diptera.

► Legs of Hexapods

Emulsifier

A surfactant used to stabilize the distribution of one liquid in another (i.e., create an emulsion).

Emulsion

A pesticide formulation in which droplets of one liquid are dispersed within another liquid (e.g., oil in water).

Emulsifiable Concentrate

An insecticide formulation in which an emulsifying agent has been added to allow an active ingredient and solvent that normally would not mix with water to be effectively dispersed in water.

Encapsulated Pesticide

Enclosure of a small amount of pesticide within a covering such as polyvinyl to provide controlled (prolonged) release of the toxicant. Such formulations are also referred to as micro-encapsulated.

Encapsulation

The enclosure of an invader, usually a parasitoid larva, within the blood of the host insect by a layer of hemocytes.

Encephalitis

A group of arthropod-borne viruses (arboviruses) affecting the nervous system of vertebrate animals, including humans. Often these viruses are spread by mosquitoes. Signs and symptoms of infection include stiff neck, headache, confusion, rash, fever, arthritis, inflammation of the brain, coma, paralysis, and death. Some of the viruses and diseases include:

Alphaviruses

Eastern equine encephalitis

Western equine encephalitis
Venezuelan equine encephalitis
Flaviviruses
St. Louis encephalitis
Japanese encephalitis
West Nile fever
Yellow fever
Dengue
Bunyaviruses
LaCrosse encephalitis
Reoviruses
Colorado tick fever
African horse sickness viruses

Although vaccines are available for some arboviruses, prevention hinges mostly on limiting or eliminating exposure to blood-feeding arthropods.

► Dengue
► Eastern Equine Encephalitis
► Japanese Encephalitis
► Lacrosse Encephalitis
► St. Louis Encephalitis
► Yellow Fever
► West Nile Fever
► African Horse Sickness Viruses
► Mosquitoes
► Mosquitoes as Vectors of Viral Pathogens

Encyrtidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Endangered Area

An area where ecological factors favor the establishment of a pest that, if established, will cause an economically important loss in the area.

► Invasive Species
► Regulatory Entomology
► Risk Analysis (Assessment)

Endangered Species

Endangered species are those considered to be at risk of extinction in a relatively short period of time. Other species experiencing population decline are considered to be at less risk, and are classified as threatened, or are placed in another category to designate that they or their habitat is at risk. Following (Table 3) is a list of insects "of concern" established by the United States Fish and Wildlife Service. [STATUS: E is endangered; T is threatened; C is candidate taxon, ready for proposal; DA is delisted taxon; PE is proposed endangered; EmE is emergency listing, endangered; PE is proposed endangered.

Endemic

Populations occurring at low levels of abundance in an area, though on occasion they may move to a more abundant state (an outbreak or epidemic). This term is sometimes, but incorrectly, used to describe indigenous or precinctive populations.

Endemism

The condition of being indigenous to, and restricted to, a specific area.

► Precinction

Enderleinellidae

A family of sucking lice (order Phthiraptera). They sometimes are called squirrel lice.

► Chewing and Sucking Lice

Endocrine Gland

A gland that discharges its products, generally hormones, into the inside of an insect (Fig. 24) (contrast with exocrine gland).

► Endocrine Regulation of Insect Reproduction

Endangered Species, Table 3 **Threatened and endangered insect species in the United States**

Inverted common name	Scientific name	Listing status	Current range
Beetle, American burying	*Nicrophorus americanus*	E	AR, MA, MI, NE, OH, RI, SD, Canada (Ont.)
Beetle, Coffin Cave mold	*Batrisodes texanus*	E	TX
Beetle, Comal Springs dryopid	*Stygoparnus comalensis*	E	TX
Beetle, Comal Springs riffle	*Heterelmis comalensis*	E	TX
Beetle, delta green ground	*Elaphrus viridis*	T	CA
Beetle, Hungerford's crawling water	*Brychius hungerfordi*	E	MI, Canada
Beetle, Kretschmarr Cave mold	*Texamaurops reddelli*	E	TX
Beetle, Mount Hermon June	*Polyphylla barbata*	E	CA
Beetle, Tooth Cave ground	*Rhadine persephone*	E	TX
Beetle, valley elderberry longhorn	*Desmocerus californicus dimorphus*	T	CA
Beetle, Warm Springs Zaitzevian riffle	*Zaitzevia thermae*	C	MT
Bug, Wekiu	*Nysius wekiuicola*	C	HI
Butterfly, Bahama swallowtail	*Heraclides andraemon bonhotei*	DA	FL
Butterfly, bay checkerspot	*Euphydryas editha bayensis*	T	CA
Butterfly, Behren's silverspot	*Speyeria zerene behrensii*	E	CA
Butterfly, callippe silverspot	*Speyeria callippe callippe*	E	CA
Butterfly, Corsican swallowtail	*Papilio hospiton*	E	France (Corsica), Italy (Sardinia)
Butterfly, El Segundo blue	*Euphilotes battoides allyni*	E	CA
Butterfly, Fender's blue	*Icaricia icarioides fenderi*	E	OR
Butterfly, Homerus swallowtail	*Papilio homerus*	E	Jamaica
Butterfly, Karner blue	*Lycaeides melissa samuelis*	E	IL, IN, MI, MN, NH, NY, OH, WI, Canada (Ont.)
Butterfly, Lange's metalmark	*Apodemia mormo langei*	E	CA
Butterfly, lotus blue	*Lycaeides argyrognomon lotis*	E	CA
Butterfly, Luzon peacock swallowtail	*Papilio chikae*	E	Philippines
Butterfly, Mariana eight-spot	*Hypolimnas octucula mariannensis*	C	GU
Butterfly, Mariana wandering	*Vagrans egestina*	C	GU, MP
Butterfly, mission blue	*Icaricia icarioides missionensis*	E	CA
Butterfly, Mitchell's satyr	*Neonympha mitchellii mitchellii*	E	IN, MI, OH
Butterfly, Myrtle's silverspot	*Speyeria zerene myrtleae*	E	CA

Endangered Species, Endangered Species, Table 3 **Threatened and endangered insect species in the United States (Continued)**

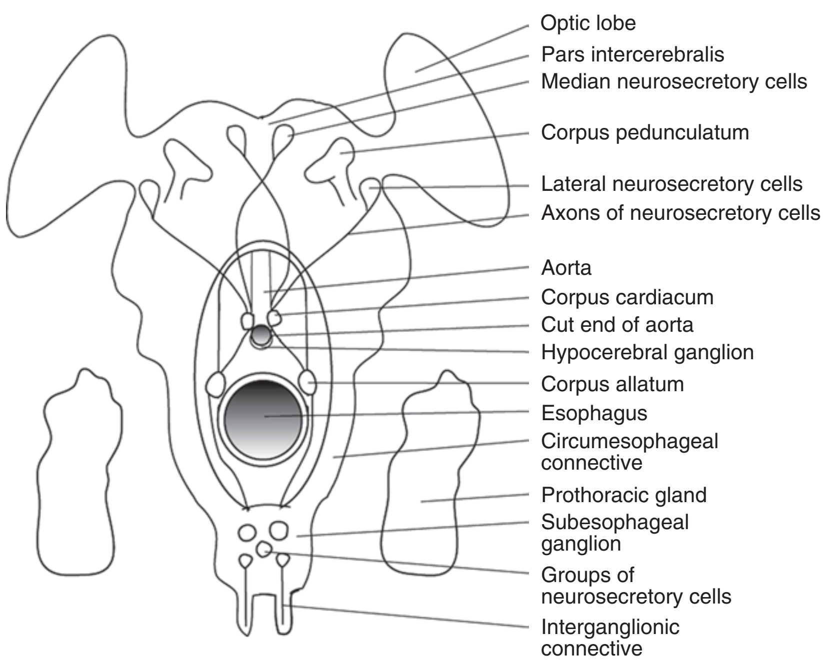
Inverted common name	Scientific name	Listing status	Current range
Butterfly, Oregon silverspot	*Speyeria zerene hippolyta*	T	CA, OR, WA
Butterfly, Palos Verdes blue	*Glaucopsyche lygdamus palosverdesensis*	E	CA
Butterfly, Queen Alexandra's birdwing	*Troides alexandrae*	E	Papua New Guinea
Butterfly, Quino checkerspot	*Euphydryas editha quino (=E. e. wrighti)*	E	CA, Mexico
Butterfly, Sacramento Mountains checkerspot	*Euphydryas anicia cloudcrofti*	PE	NM
Butterfly, Saint Francis' satyr	*Neonympha mitchellii francisci*	E	NC
Butterfly, San Bruno elfin	*Callophrys mossii bayensis*	E	CA
Butterfly, Schaus swallowtail	*Heraclides aristodemus ponceanus*	E	FL
Butterfly, Smith's blue	*Euphilotes enoptes smithi*	E	CA
Butterfly, Uncompahgre fritillary	*Boloria acrocnema*	E	CO
Butterfly, Whulge checkerspot (=Taylor's)	*Euphydryas editha taylori*	C	No data
Caddisfly, Sequatchie	*Glyphopsyche sequatchie*	C	TN
Cave beetle, beaver	*Pseudanophthalmus major*	C	KY
Cave beetle, Clifton	*Pseudanophthalmus caecus*	C	KY
Cave beetle, greater Adams	*Pseudanophthalmus pholeter*	C	KY
Cave beetle, Holsinger's	*Pseudanophthalmus holsingeri*	C	VA
Cave beetle, icebox	*Pseudanophthalmus frigidus*	C	KY
Cave beetle, inquirer	*Pseudanophthalmus inquisitor*	C	TN
Cave beetle, lesser Adams	*Pseudanophthalmus cataryctos*	C	KY
Cave beetle, Louisville	*Pseudanophthalmus troglodytes*	C	KY
Cave beetle, surprising	*Pseudanophthalmus inexpectatus*	C	KY
Cave beetle, Tatum	*Pseudanophthalmus parvus*	C	KY
Damselfly, blackline Hawaiian	*Megalagrion nigrohamatum nigrolineatum*	C	HI

Endangered Species, Endangered Species, Table 3 Threatened and endangered insect species in the United States (Continued)

Inverted common name	Scientific name	Listing status	Current range
Damselfly, crimson Hawaiian	*Megalagrion leptodemus*	C	HI
Damselfly, flying earwig Hawaiian	*Megalagrion nesiotes*	C	HI
Damselfly, oceanic Hawaiian	*Megalagrion oceanicum*	C	HI
Damselfly, orange black Hawaiian	*Megalagrion xanthomelas*	C	HI
Damselfly, Pacific Hawaiian	*Megalagrion pacificum*	C	HI
Dragonfly, Hine's emerald	*Somatochlora hineana*	E	IL, OH, WI
Fly, Delhi Sands flower-loving	*Rhaphiomidas terminatus abdominalis*	E	CA
Gall fly, Po' olanui	*Phaeogramma* sp.	C	HI
Grasshopper, Zayante band-winged	*Trimerotropis infantilis*	E	CA
Ground beetle, [unnamed]	*Rhadine exilis*	E	TX
Ground beetle, [unnamed]	*Rhadine infernalis*	E	TX
Mold beetle, Helotes	*Batrisodes venyivi*	E	TX
Moth, Blackburn's sphinx	*Manduca blackburni*	E	HI
Moth, Kern primrose sphinx	*Euproserpinus euterpe*	T	CA
Naucorid, Ash Meadows	*Ambrysus amargosus*	T	NV
Pomace fly, [unnamed]	*Drosophilia aglaia*	PE	HI
Pomace fly, [unnamed]	*Drosophila attigua*	C	HI
Pomace fly, [unnamed]	*Drosophila differens*	PE	HI
Pomace fly, [unnamed]	*Drosophila digressa*	C	HI
Pomace fly, [unnamed]	*Drosophila hemipeza*	PE	HI
Pomace fly [unnamed]	*Drosophila heteroneura*	PE	HI
Pomace fly [unnamed]	*Drosophila montgomeryi*	PE	HI
Pomace fly [unnamed]	*Drosophila mulli*	PE	HI
Pomace fly [unnamed]	*Drosophila musaphila*	PE	HI
Pomace fly [unnamed]	*Drosophila neoclavisetae*	PE	HI
Pomace fly [unnamed]	*Drosophila obatai*	PE	HI
Pomace fly [unnamed]	*Drosophila ochrobsis*	PE	HI
Pomace fly [unnamed]	*Drosophila substenoptera*	PE	HI
Pomace fly [unnamed]	*Drosophila tarphytrichia*	PE	HI
Riffle beetle, Stephan' s	*Heterelmis stephani*	C	AZ
Skipper, Carson wandering	*Pseudocopaeodes eunus obscurus*	EmE, PE	EmE = CA, NV, Washoe Co., NV and Lassen Co., CA; PE = CA, NV, Washoe Co., NV and Lassen Co., CA

Endangered Species, Endangered Species, Table 3 Threatened and endangered insect species in the United States (Continued)

Inverted common name	Scientific name	Listing status	Current range
Skipper, Dakota	*Hesperia dacotae*	C	MN, ND, SD, Canada
Skipper, Laguna Mountains	*Pyrgus ruralis lagunae*	E	CA
Skipper, Mardon	*Polites mardon*	C	CA, OR, WA
Skipper, Pawnee montane	*Hesperia leonardus Montana*	T	CO
Tiger beetle, Coral Pink Sand Dunes	*Cicindela limbata albissima*	C	UT
Tiger beetle, highlands	*Cicindela highlandensis*	C	FL
Tiger beetle, northeastern beach	*Cicindela dorsalis dorsalis*	T	CT, MA, MD, NJ, RI, VA
Tiger beetle, Ohlone	*Cicindela ohlone*	E	CA
Tiger beetle, Puritan	*Cicindela puritana*	T	CT, MA, MD, NH, VT
Tiger beetle, Salt Creek	*Cicindela nevadica lincolniana*	C	NE



Endocrine Gland, Figure 24 Cross section showing the relationships of the principal endocrine glands with the brain (adapted from Chapman, The insects: structure and function).

Endocrine Regulation of Insect Reproduction

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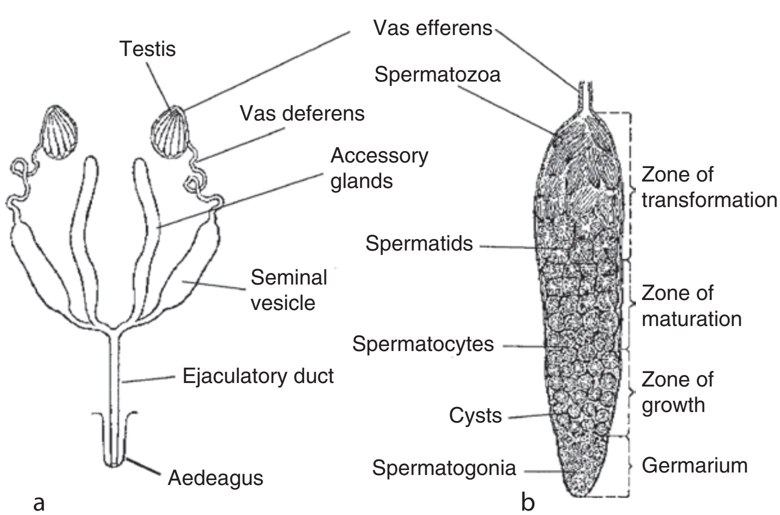
Insects dominate our planet largely because of their enormous reproductive capacity, which is made possible by a most efficient reproductive system. This reproductive efficiency results from the synchronization of the endocrine system that controls reproduction with both environmental signals and the internal physiological state of the insect, so that reproduction is triggered only when it is environmentally and biologically appropriate.

Sites Where Hormones are Released in insects

Insects release hormones from conventional endocrine glands, which are tissues that specialize in the secretion of hormones that are transported by the blood and that act on receptor-bearing target tissues elsewhere in the body. Examples of endocrine glands in insects are the prothoracic glands, which produce ecdysteroids, and the corpus allatum, which produces juvenile hormones (JH). Insects also have hybrids of endocrine glands and nerve cells that are called neurosecretory cells. These cells synthesize neurohormones and release them from specialized neurohemal organs into the bloodstream, affecting distant target tissues. Examples of neurosecretory cells are the medial neurosecretory cells of the brain that release the neurohormone prothoraciotropic hormone from the corpus cardiacum, its neurohemal organ. Receptors present on target cells specifically bind the hormones and produce a biological effect, but non-target cells that lack these receptors are unable to receive the message.

Endocrine Regulation of Male Reproduction

The production of spermatozoa occurs within the follicles of the male testes (see diagram of male reproductive system). Apical stem cells in the anterior stem cell niche of the follicle divide mitotically to form spermatogonia. As these spermatogonia move down through the testes (Fig. 25), they become enclosed by somatic cells that produce cysts around them. The remainder of the



Endocrine Regulation of Insect Reproduction, Figure 25 **(a). The generalized male reproductive system. (b). A single testicular follicle showing the zones of sperm maturation (From Snodgrass, 1935).**

testicular follicle can be divided into zones containing these cysts in successive regions of sperm development. In zone I, the zone of growth, the spermatogonia divide mitotically six to eight times within each cyst to form spermatocytes, each of which remains connected by cytoplasmic bridges, or ring canals. The number of divisions within a cyst is species specific; in *Rhodnius* the spermatocyte stage is reached at eight divisions, or 128 cells per cyst. In zone II, the zone of maturation, the spermatocytes divide meiotically to form haploid spermatids. The cysts continue to move toward the vas deferens within zone III, the zone of transformation, and the haploid spermatids within them differentiate into flagellated spermatozoa. As this differentiation proceeds, the cysts elongate and eventually rupture, releasing the spermatozoa into the vas efferens. These spermatozoa then migrate to the seminal vesicles where they remain until mating takes place. Spermatogenesis is thus a multi-step process of meiotic and mitotic divisions and cell differentiation.

In some short-lived insect species that do not feed as adults, spermatogenesis may occur early during the larval and pupal stages. Sperm are produced throughout the adult lives of longer-lived males. Because the hormonal conditions that exist during these immature and adult periods are vastly different, it has been difficult to generalize a scheme for the hormonal control of insect spermatogenesis. Indeed, it has been suggested that insect spermatogenesis may be a sequential process of differentiation that is completely independent of hormones. There have been some reports of the effects of hormones in a few species of insects, but relatively little is known compared to our knowledge of how hormones control the reproductive system in females.

The few studies that have examined the endocrine control of spermatogenesis suggest that the rate of mitotic divisions of spermatogonia to form spermatocytes is increased by high levels of 20-hydroxyecdysone, but when JH titers are also high, this increase is abolished. In some larval insects, the meiotic divisions of spermatocytes are arrested at prophase until they reach the end of their larval period. A release of 20-hydroxyecdysone unblocks meiosis and allows the cells to proceed to metaphase. An ecdysiotropin produced by the brain induces the synthesis of ecdysteroids by the testis sheaths of several lepidopteran species. While most effects of JH on spermatogenesis are inhibitory, JH has been reported to accelerate spermatogenesis in some insects. The release of mature spermatozoa from the cysts in the testes may display a circadian rhythmicity that is initially inhibited by 20-hydroxyecdysone. The decline of 20-hydroxyecdysone is thus necessary in order for sperm to be released.

The male accessory glands are involved in the synthesis of seminal fluid, the spermatophore, and vaginal mating plugs. They also produce various peptides that have physiological effects on the female when they are transferred during mating. The development and secretions of the male accessory glands are often controlled by JH. The accumulation of some secretory peptides in the glands is enhanced by JH and inhibited by 20-hydroxyecdysone.

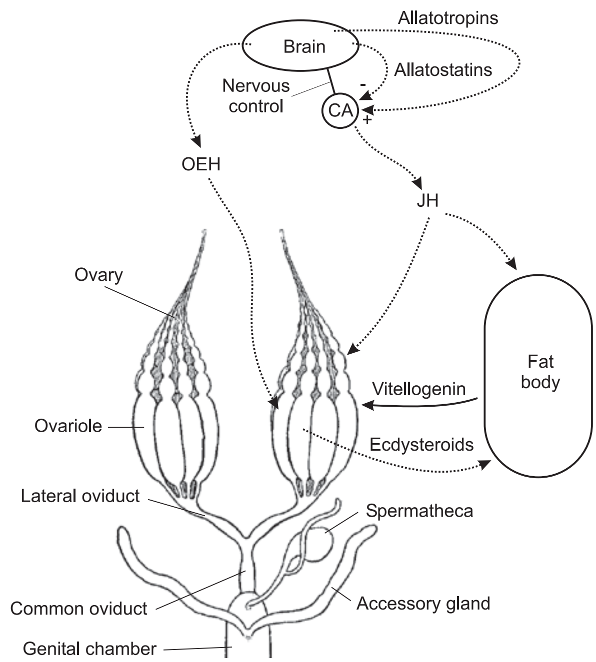
Many insect species undergo a diapause, which is a physiologically programmed developmental arrest that occurs prior to the onset of unfavorable environmental conditions. Spermatogenesis is interrupted in those lepidopterans that undergo a larval or pupal diapause but it resumes once diapause has been completed. It is the lysis of developing gametes before they become mature, rather than any developmental activity, that causes this interruption. The renewal of spermatogenesis occurs as a result of the increasing titers of 20-hydroxyecdysone that occur when diapause is terminated.

There are two different kinds of sperm produced by the single fused testes of lepidopterans. The conventional eupyrene sperm fertilize the egg, but the apyrene sperm have no nuclei and thus no genetic function in fertilization. It has been speculated that by traveling with the eupyrene sperm, they may increase their motility within the female reproductive tract, or provide the eupyrene sperm with nutrients. The differentiation of apyrene sperm from eupyrene sperm in the testis occurs as a result of their exposure to a hemolymph-borne apyrene-spermatogenesis-inducing factor. In some other species, individual males produce sperm of varying lengths, a factor that may contribute to speciation.

Endocrine Regulation of Female Reproduction

The production of oocytes in the female begins within the germarium of the ovariole, where the haploid oocytes are produced from stem cells (see Fig. 26). As they descend through the vitellarium, they take up the vitellogenin that is deposited in the cytoplasm as yolk. The yolk is used by the developing embryo as precursors and energy for growth. Vitellogenin is usually produced by the fat body and released into the hemolymph, from where it is specifically taken up by the oocyte by receptor-mediated exocytosis. The process of vitellogenesis is closely regulated by hormones to insure that reproduction only occurs when all systems are ready.

There is a tremendous amount of ecological variability among insect species and it is not surprising that there is a comparable variability and complexity in the systems that regulate their reproduction. There are but a few generalizations that can be made regarding the endocrine control of female insect reproduction. In short-lived insects that do not feed as adults, the yolk must be derived from reserves that are acquired during the larval stage. In these insects, vitellogenesis occurs while the pharate adult is still within the pupal skin and the adult emerges with a full complement of eggs. In the lepidopteran *Hyalophora cecropia*, this pre-emergence egg development appears to occur in the absence of any identifiable hormonal controls and may simply be a developmental program that is followed by the fat body. In longer-lived insects that undergo multiple cycles of reproduction, vitellogenesis occurs when the fat body is activated by hormones that allow the vitellogenins to be produced cyclically.



Endocrine Regulation of Insect Reproduction, Figure 26 The generalized female reproductive system. The brain regulates the production of JH by nervous control as well as with the various peptides that activate JH synthesis (allatotropins) and inhibit JH synthesis (allatostatins). The JH acts on both the fatty body and the ovaries. An ovarian ecdysteroidogenic hormone (OEH) released by the brain activates the synthesis of ovarian ecdysteroids that act on the fat body to cause the transcription of vitellogenin genes (Modified from Snodgrass, 1935).

The specific hormones that are involved in cyclical vitellogenesis vary considerably among insects, and again there is no single mechanism of hormonal control that can be described. However, there are two general approaches to cyclical egg production. In some insects, the production of vitellogenins is dependent on JH alone, such as in grasshoppers, cockroaches, some lepidopterans, and *Rhodnius*. JH acts directly on the fat body cells, causing them to initiate the translation and secretion of vitellogenin. In contrast, there are a few other insects, including the gypsy moth, *Lymantria dispar*, where low or declining titers of

JH in the last larval instar have been shown to be necessary for vitellogenin production by the fat body. The release of JH from the corpora allata is controlled by the brain, either neurally or hormonally by its production of allatotropins that turn the corpora allata on and allatostatins that turn the corpora allata off.

In many other insects, including most dipterans, both JH and 20-hydroxyecdysone are involved in reproduction. JH regulates the formation of new endoplasmic reticulum in the fat body and the sequestration of the vitellogenin produced, while 20-hydroxyecdysone regulates the rate of its production. Variations in the control of vitellogenesis by 20-hydroxyecdysone are common. Vitellogenin production in the Indian meal moth, *P. interpunctella*, coincides with a decline in the ecdysteroid titer of the pharate adult. Vitellogenin synthesis in the silkworm, *Bombyx mori*, coincides with a rise of 20-hydroxyecdysone.

The control of vitellogenesis in the female mosquito is a good example of the complexity of the mechanisms that have evolved to coordinate reproduction with nutritional state. Vitellogenesis only occurs in female mosquitoes after a blood meal has been periodically acquired, so blood ingestion consequently serves as an experimental method of synchronizing the reproduction of many individuals so that the coordinated events can be better observed in the laboratory. The blood meal provides the precursors for yolk synthesis that are lacking after larval development is completed.

After the adult female emerges, the JH that is released by the paired corpora allata during the first few days of life prepare both the fat body and the ovary for vitellogenesis. In response to an early peak of JH, the fat body cells become polyploid to provide more templates for DNA synthesis during vitellogenesis. JH also stimulates the induction of mRNA in fat body cells, the proliferation of ribosomes, and a development of its responsiveness to 20-hydroxyecdysone. The follicle cells that surround the oocyte-nurse cell syncytium are relatively undifferentiated at emergence, but in response to JH, they begin to differentiate and increase in size.

There are endocrine cells dispersed throughout the midgut epithelium, and in response to the ingestion of a blood meal these cells may trigger the release of the neurohormone ovarian ecdysteroidogenic hormone from the brain, which acts on the ovaries to increase their synthesis of protein and stimulate their production of ecdysone. Although the prothoracic glands, the site of ecdysteroid synthesis in larvae, degenerate and are absent in adult insects, the follicular epithelium of the ovary produces these ecdysteroids in adults. The 20-hydroxyecdysone then activates the transcription of vitellogenin genes in the fat body. The most abundant fat body transcript is a 6.5 kb vitellogenin mRNA that is translated into a 224 kDA pro-vitellogenin and subsequently cleaved and then repackaged into a 380 kDa vitellogenin. The 20-hydroxyecdysone peak also stimulates the follicle cells of the ovary to synthesize the vitelline envelope, the inner layer of the chorion, and acts again on the germarium to cause the creation of a new, secondary follicle. During the later stages of egg development, an oostatic hormone is produced that prevents the maturation of any secondary follicles until the maturing eggs have been laid, and avoids the burden of developing so many eggs that the female could no longer fly.

► Reproduction
► Ecdysteroids
► Diapause
► Embryogenesis
► Meiotic Drive in Insects
► Reproduction
► Oogenesis
► Juvenile Hormone
► Nervous System
► Prothoraciotropic Hormone

References

Brown MR, Graf R, Swiderek KM, Fendley D, Stracker TH, Champagne DE, Lea AO (1998) Identification of a steroidogenic neurohormone in female mosquitoes. J Biol Chem 273:3967–3971

Davey KG (1997) Hormonal controls on reproduction in female heteroptera. Arch Insect Biochem Physiol 35:443–453
Davey KG, Sevala VL, Gordon DRB (1993) The action of juvenile hormone and antigonadotropin on the follicle cells of *Locusta migratoria*. Invertebr Reprod Dev 24:39–46
De Cuevas M, Lily MA, Spradling AC (1997) Germline cyst formation in *Drosophila*. Annu Rev Genet 31:405–428
Dumser JB (1980) The regulation of spermatogenesis in insects. Annu Rev Entomol 25:341–369
Friedlander M (1997) Control of eupyrene-apyrene sperm dimorphism in Lepidoptera. J Insect Physiol 43:1085–1092
Gade G, Hoffmann KH, Spring JH (1997) Hormonal regulation in insects: facts, gaps, and future directions. Physiol Rev 77:963–1032
Gillott C (2003) Male accessory gland secretions: modulators of female reproductive physiology and behavior. Annu Rev Entomol 48:163–184
Happ GM (1992) Maturation of the male reproductive system and its endocrine regulation. Annu Rev Entomol 37:303–320
Klowden MJ (1997) Endocrine aspects of mosquito reproduction. Arch Insect Biochem Physiol 35:491–512
Klowden MJ, Chambers GM (2004) Production of polymorphic sperm by anopheline mosquitoes and their fate within the female genital tract. J Insect Physiol 50:1163–1170
Koch EA, Smith PA, King RC (1967) The division and differentiation of *Drosophila* cystocytes. J Morphol 121:55–70
Meola R, Lea AO (1972) Humoral inhibition of egg development in mosquitoes. J Med Entomol 9:99–103
Raikhel AS, Snigirevskaya ES (1998) Vitellogenesis. In: Harrison FW, Locke M (eds) Microscopic anatomy of invertebrates, vol 2c. Wiley-Liss, New York, NY. pp 933–955
Raikhel AS, Miura K (1999) Nuclear receptors in mosquito vitellogenesis. Am Zool 39:722–735
Sappington TW, Raikhel AS (1998) Molecular characteristics of insect vitellogenins and vitellogenin receptors. Insect Biochem Mol Biol 28:277–300
Yamashita YM, Fuller MT, Jones DL (2005) Signaling in stem cell niches: lessons from the *Drosophila* germline. J Cell Sci 118:665–672

Endogenous

A property inherent in an organism (contrast with exogenous).

Endogenous Rhythm

Biological rhythms that arise independently of external stimulation.

Endomychidae

A family of beetles (order Coleoptera). They commonly are known as handsome fungus beetles.

► Beetles

Endoparasite

A parasite that lives inside the host.

Endophagous

Feeding within the body of a host, often on the internal organs.

Endophallus

The eversible inner lining of the aedeagus.

Endophytic Fungi and Grass-Feeding Insects

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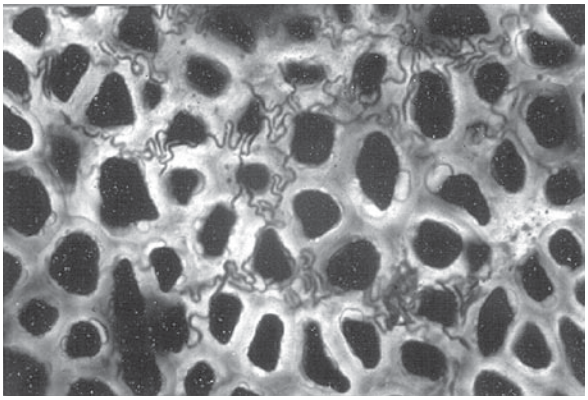
Nature had shaped plant defense mechanisms for warding off attack by plant-feeding insects long before humans started domesticating wild plants for food production about 10,000 years ago. As early farmers began developing agrarian societies, they probably observed that cultivated plants differed in their abilities to resist insect attacks. It remained, however, for twentieth century science to determine that variation in plant susceptibility to insect herbivores is often genetically based and results from natural plant chemistry and plant morphological traits (thorns, trichomes). Today, a rich body of literature exists on these plant defense mechanisms and abiotic (light, temperature, moisture, plant nutrient status, air pollutants) factors that influence plant susceptibility to insect attack.

The role of plant microorganisms in determining the outcome of some plant/insect encounters was not widely recognized by entomologists and other scientists until the 1980s. By the beginning of the twenty-first century, however, microorganisms were included in major scientific discussions of plant defensive mechanisms against insect attack. Fungal endophytes (*Epichloë* species and their asexual *Neotyphodium* forms) of grasses are one of the best known microbial groups that adversely affect insect survival. These endophytes (endo [within] and phyte [plant]) live for some or all of their life cycle within grasses and are mostly self-perpetuated through maternal transmission in seed. They are invisible because their host plants show no outward signs of infection.

It was not until microbiologists and animal scientists associated *Neotyphodium* infection (Fig. 27) in pasture grasses with toxic disorders of grazing cattle and sheep in the late 1970s and early 1980s that entomologists and grass breeders linked these fungal endophytes with enhanced grass resistance to insect pests. The first reports appeared in 1982 (New Zealand) and 1983 (United States) and documented enhanced field resistance to the Argentine stem weevil, *Listronotus bonariensis*, and

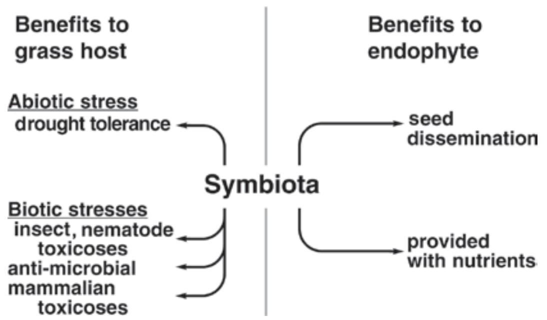


Endophytic Fungi and Grass-Feeding Insects, Figure 27 Section through a tall fescue seed showing mycelium of *Neotyphodium coenophaialum* between the aleurone cells (X100).

sod webworm, *Crambus* sp., in *Neotyphodium*-infected forage and turf perennial ryegrasses, *Lolium perenne*, compared to endophyte-free plants. Interestingly, before endophytes were implicated in ryegrass resistance to the Argentine stem weevil, some investigators attributed variability among ryegrass lines for susceptibility to weevil attack to traits based on plant genes.

After the first reports of *Neotyphodium* based resistance to insects, entomologists and other scientists accelerated the pace of research to generate more information on the extent and nature of specific grass/endophyte/insect associations. These efforts greatly expanded the list of insects negatively affected by endophyte-infected grasses, so, by the year 2000, it contained more than 40 species in five orders (Coleoptera, Lepidoptera, Diptera, Hemiptera, and Orthoptera) of the class Insecta. Concurrent research isolated and identified the chemical constituents (i.e., indole diterpenes, peramine, and pyrrolizidine and ergot alkaloids) of endophyte/host grass associations and characterized the responses of endophyte-infected grasses to a range of abiotic and biotic stresses. An outgrowth of research on the anti-mammalian and anti-insect properties of endophyte-infected grasses was the "defensive mutualism hypothesis," which viewed alkaloids produced by endophytes as defense chemicals that provide adaptive advantage to the infected host grass. Under this hypothesis, the fitness enhancing and anti-herbivore properties of endophyte infection would lead to higher frequencies of infected plants in grass populations. The accompanying figure (Fig. 28) illustrates the known benefits of grass/endophyte associations, which are viewed as symbiota to reflect the intimate association of the two partners. Most of the existing information about grass/*Neotyphodium* symbiota comes from work on forage and turf grasses in the genera *Lolium* (especially perennial ryegrass) and *Festuca* (especially tall fescue, *F. arundinaceae*, and fine fescue species).

Although researchers are far from fully understanding the range of insect responses to endophyte-infected grasses, they have developed a



Endophytic Fungi and Grass-Feeding Insects, Figure 28 **Known benefits to each symbiotic partner. Not every *Neotyphodium*-infected grass host has all of the benefits shown.**

good information base on the outcome of many interactions between grasses, endophytes, and insects. For example, research has shown that both insect deterrence and toxicity result from the production of alkaloids, and that the host grass genotype or species, and the endophyte strain involved in the interaction affect the expression and the type of insect resistance. Three examples illustrate the diversity of responses by plant-feeding insects. As previously mentioned, the first linkage between endophyte infection and insect resistance involved the Argentine stem weevil. This weevil maintains a close association with perennial ryegrass throughout its life cycle in New Zealand, where it is a significant pest of this important pasture grass. Adult weevils prefer to feed and oviposit on ryegrass plants that are free of endophytes, compared to endophyte-infected plants. A chemical, peramine, in endophyte-infected plants appears to be a powerful feeding deterrent to adult weevils. In another example, young larvae of the fall armyworm, *Spodoptera frugiperda*, a caterpillar that feeds on many grass species, prefer feeding on endophyte-free tall fescue, whereas older larvae do not display preference with respect to endophyte infection. This example shows that different life stages of some insects are affected differently by exposure to endophyte-infected grasses. Finally, *Neotyphodium* infection in wild barley, *Hordeum* spp., does not always kill the Russian wheat aphid, *Diuraphis noxia*, a primary pest of wheat and barley, as experiments showed that the aphid was sensitive to some, but not all, *Neotyphodium*/wild barley associations.

Although most of the early insect work emphasized the protective role of endophytes, a few studies documented insect insensitivity to endophyte infection in the late 1980s. Researchers continue to add to the list of insects unaffected by *Neotyphodium* infection in host grasses, thus revealing the variable nature of grass/endophyte/insect interactions, and the fact that endophyte-produced alkaloids do not always function as plant defensive chemicals. The absolute function of most chemicals produced by endophytes is still very much open for discussion and more scientific investigation.

Grass breeders and seed companies quickly developed and marketed *Neotyphodium*-infected *Lolium* and *Festuca* turf grasses after they recognized the benefits associated with endophyte infection. Today, turf grass professionals and homeowners in the United States routinely establish endophyte-infected grasses on golf courses, lawns, and playfields for better stand persistence and insect resistance. Additionally, scientists and commercial seed companies are beginning to take advantage of a vast diversity of *Neotyphodium* species and strains that differ in their ability to produce particular alkaloids. They are doing this by developing and marketing new forage grasses that are *Neotyphodium* combinations with "non-toxic endophytes" that do not produce toxins (e.g., ergot alkaloids) harmful to mammals, but do produce the necessary metabolites for better stand persistence and insect resistance. An expanding area of investigation involves biotechnological manipulations of endophytes for the commercial production of large pools of new grass-endophyte associations for specific purposes, including insect resistance.

References

Clay K (1988) Fungal endophytes of grasses: a defensive mutualism between plants and fungi. Ecology 69:10–16

Clement SL, Kaiser WJ, Eichenseer H (1994) Acremonium endophytes in germplasms of major grasses and their utilization for insect resistance. In: Bacon CW, White JF Jr (eds) Biotechnology of endophytic fungi of grasses. CRC Press, Boca Raton, FL, pp 185–199
Clement SL, Wilson AD, Lester DG, Davitt CM (1997) Fungal endophytes of wild barley and their effects on *Diuraphis noxia* population development. Entomol Exp Appl 82:275–281
Popay AJ, Rowan DD (1994) Endophytic fungi as mediators of plant-insect interactions. In: Bernays EA (ed) Insect-plant interactions, vol 5. CRC Press, Boca Raton, FL, pp 83–103
Saikkonen K, Faeth SH, Helander M, Sullivan TJ (1998) Fungal endophytes: a continuum of interactions with host plants. Annu Rev Ecol Syst 29:319–343

Endocuticle

The inner portion of the procuticle (Fig. 29), a region that is softer and lighter in color than the exocuticle. The endocuticle is not sclerotized, so it can be resorbed prior to the insect molt, and used to make new cuticle.

► Integument: Structure and Function
► Epicuticle

Endoplasmic Reticulum (ER)

A system of sacs (cisternae) in the cytoplasm of eukaryotic cells in which the ER is continuous with the plasma membrane and the outer membrane of the nuclear envelope. If the outer surfaces of the ER membranes are coated with ribosomes, the ER is “rough-surfaced”; otherwise it is called smooth-surfaced.

Endoproteases

Protein digesting enzymes that attack large proteins internally at the linkage between certain amino acids, breaking the protein into smaller polypeptides.

Endopterygota

A division of Insecta in which the wings develop internally during the immature stages. Holometabolous insects.

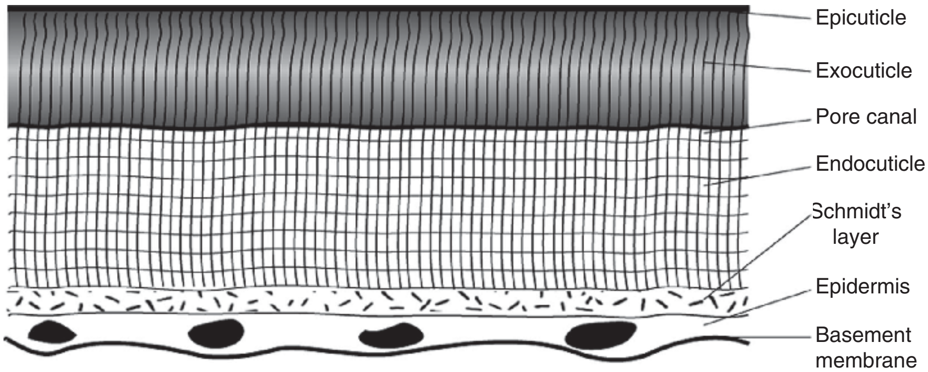
► Metamorphosis

Endoskeleton

An internal portion of the skeleton. The chitinous processes extending internally.

Endotherm

An organism that produces metabolic heat for thermoregulation. Mammals and birds are common



Endocuticle, Figure 29 **Cross section of the insect cuticle and epidermis (adapted from Chapman, The insects: structure and function).**

examples of endotherms, and although insects generally are considered to be ectotherms rather than endotherms, some display endothermic behavior and physiology.

► Thermoregulation in Insects

Endotoxins

Substances produced by microorganisms which are not secreted into the surrounding medium but are confined within the microbial cell; they are released after autolysis.

Endrő di, Sebő (Sebastian Endrő di)

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Sebő Endrő di was born on the October 18, 1903 in Kassa, Hungary, now Kosice, Slovac Republic. He graduated in law from the Pázmány Péter University of Science, Budapest in 1931. He was a keen amateur coleopterist, working as a lawyer for the Danube Steamship Company from 1931 until 1948, then as a lecturer at the College of Horticulture, Budapest (1949–1956) and at the University of Agricultural Science at Göd, North of Budapest (1956–1961). From 1961 until his retirement in 1966 he was employed by the Ministry of Agriculture's Plant Protection Service in Budapest. After his retirement he had a room in the Hungarian Natural History Museum's Zoological Collections, where he conducted research until his death. His first entomological research focused on the beetle fauna of the Börzsöny Mountains, North of Budapest, where his family had a summer house. He set out to explore the beetles of this area together with his son, Sebastian Endrő dy-Younga. Through his long and productive life as a coleopterist, he has studied various sections of the beetle fauna of the Carpathian Basin and of the lands of historical Hungary as well as the scarabaeoid fauna of the World, publishing 222 scientific works. His achievements were highly respected by his colleagues and he was awarded with the Frivaldszky Memorial Plaque (Silver) by the Hungarian Entomological Society in 1967 and with the "In Scientia Entomofaunistica Excellenti" medal by the VIII. Central-European Entomofaunistic Symposium in 1979. Sebő Endrő di is known mainly by his work on the Scarabaeoidea, especially the Dynastinae. His greatest work was the revision of this subfamily of beetles, which was published in the German language in 20 sections, and consisted of 1,600 pages in eight journals. A shorter version of 800 pages in English was published in 1985 (The Dynastinae of the World, Budapest-Hagen, 1985). Dr. Endrő di passed away on the of December 12, 1984 in Budapest. He was a kind and helpful man with an immense knowledge of beetles.

References

Kaszab Z (1984) Dr. Endrő di Sebő (1903–1984). Folia Entomol Hung 46:2, 5–16
Kaszab Z, Papp CS (1986) Sebő Endrő di (1903–1984). Entomography 4:379–397
Kaszab Z, Zunino M (1986) L' opera scarabeologica di Sebő Endrő di (1903–1984). Mem Soc Entomol Ital 64:45–52

Endrő dy-Younga, Sebastian (Sebestyén Endrő dy-Younga, Sebestyén Endrő dy)

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Sebestyén Endrő dy was born on the 26th of June, 26 1934 in Budapest. He became interested in beetles early in his life, following the footsteps of his father, Sebő Endrő di with whom he studied the coleoptera fauna of the Börzsöny Mountains, a wilderness region North of Budapest. He completed his formal studies by receiving his doctoral degree at the Eötvös Lóránt University of Science in Budapest, in 1958. From 1957 until 1965 he was employed by the Hungarian Natural History museum and worked closely with Dr. Zoltán Kaszab. He also published some papers regarding the beetles of the Börzsöny Mountains. In order to distinguish father and son, his father changed the spelling of their family name by replacing the last letter of *Endrődy* with an *i*, consequently he became *Endrődi* and Sebastian added his mother's maiden name by a hyphen to the original family name, thus forming the name *Endrő dy-Younga*, by which name he was known for the rest of his life. His Christian name *Sebestyén* is the Hungarian equal to *Sebastian*. He used the former in his Hungarian publications and the latter in his many works in English and German as well as in everyday life after he left Hungary. For his family and friends he was known as *Sebő*. In 1965, he accepted the position of senior research officer at the Ghana Academy of Science's Crops Research Institute in Ghana, and in 1973 together with his family he moved to the Republic of South Africa. He joined the Transvaal Museum in Pretoria in the same year, and became the Chief Curator of its Coleoptera Department in 1974. He held this position until 1998 when he resigned from it due to ill health. Endrő dy-Younga was a gifted coleopterist, blessed with a sharp mind and extraordinary memory. He was athletic and therefore a very effective, never-tiring field worker, well and truly belonging to the "Kaszab School" of extremely hard-working field entomologists. While in Ghana, he collected hundreds of thousands of specimens, which were sent back to the museum in Budapest. His beetle studies were chiefly focused on the Clambidae, Cybocephalidae and Tenebrionidae but he also researched the coleoptera fauna of the Carpathian Basin, publishing on various families. His 93 publications include major monographs and revisions. From the material that he collected through his life, 1,318 new species were described either by him or by colleagues, and 153 species and six genera were named after him. He received the Frivaldszky Memorial Plaque from the Hungarian Entomological Society. This seemingly frugal formal recognition does not reflect on his popularity as a colleague and friend, and the respect given to him as a coleopterist of immense knowledge. The international community of coleopterists suffered a great loss when he passed away on the February 26 1999.

References

*Bellamy CL, Jäch M (1999) In: memoriam Sebastian Endrő dy-Younga (1934–1999). Koleopterol Rundsch 69:209–214

Brain R (2000) Tribute to Dr Sebastian Endrő dy-Younga. Ann Transvaal Mus 37: 4–5

Breytenbach E (2000) Sebastian Endrő dy-Younga. 1934–1999. Afr Entomol 8:1, 151–156

Merkl O (1999) Dr. Endrő dy-Younga Sebestyén (1934–1999). Rovarász Híradó 25:1–3

Anon E-Y (2000) Publications of Sebastian E.-Y. Ann Transvaal Mus 37: 6–8

Endromidae

A family of moths (order Lepidoptera) also known as glory moths.

► Glory Moths
► Butterflies and Moths

Enemy Impact Hypothesis

The concept that community stability is enhanced by diversity, and that plant diversity favors the presence of natural enemies which can moderate the abundance of herbivores.

English Grain Aphid, *Sitobion avenae* (Fabricius) (Hemiptera: Aphididae)

This is an important pest of small grain crops world wide.

► Wheat Pests and their Management

Enhanced Biodegradation of Soil-Applied Pesticides

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Pesticides are broken down in the environment by physical action such as heat and light, but biological degradation is often a primary means of dissipating such compounds. This is particularly the case for pesticides applied into soil. Microbes usually cause such biological breakdown.

In the past, many pesticides were not readily degraded by either physical or biological action because of their molecular structure. The most notable examples of such persistent compounds were the chlorinated hydrocarbon and cyclodiene insecticides. Since the 1970s these compounds have gradually been phased out by regulation and replaced by toxic, yet biodegradable, pesticides.

While agricultural producers and environmentalists could feel relieved that the major problem of persistent residues in soil, waterways and produce, and accumulation in animal tissue, was now a thing of the past, a strange new twist occurred in some situations. Some pesticides, particularly those applied to soil to control soil-borne pests and diseases, were no longer controlling pests as effectively as they once had. The problem was first noticed in agricultural systems that required preventative application and longevity of pesticide to protect plant roots from insect damage, such as where soil-dwelling pest insects colonized the crop during the course of its growth.

The phenomenon was puzzling – the pests could be shown to still be susceptible to the pesticide (i.e., they had not developed resistance because of prolonged or repeated exposure) and it seemed related only to particular fields, leading to them being labeled "problem" soils. It was some time, and some disastrous pest damage to many crops, before an explanation for these pesticide failures was revealed. It was all to do with repeated applications of a pesticide to the same area of soil.

Enhanced Biodegradation

Soil is a diverse ecosystem intimately involved in the cycling of organic matter, nutrients and moisture. Since it is known that pesticides are mainly dissipated from soil by microbiological metabolism, it is clear that some microbes can utilize apparently toxic compounds as a nutrient or carbon source. Microbes form a highly diverse component of the soil biota, intricately linked to soil processes and complex food webs. By the very nature of their rapid reproduction by cell division, populations of microbial organisms such as bacteria can respond and adapt very quickly to changes in their environment.

This is the basis of enhanced (also known as accelerated) biodegradation. Repeated applications of a pesticide to soil can stimulate the microbes that are able to metabolize the compound. This enrichment of the microbial population can reach a point where degradation of the pesticide occurs too fast to allow it to exert its desired pest control effect. The paradox is that the apparently positive general effect of biodegradation can be transformed into the negative local problem of enhanced biodegradation. Unfortunately, once enhanced biodegradation is induced, there is very little that can be done to cure the problem short of sterilizing the soil – hardly a desirable thing to do.

Enhanced biodegradation differs fundamentally from resistance to pesticides. In situations where resistance develops as a result of repeated exposure to a pesticide, individuals within the pest population carrying the genetic capacity to detoxify the compound have a selective advantage and gradually come to dominate the population. Enhanced biodegradation does not involve the pest directly. The causative organisms are otherwise innocuous members of the soil microbial community that "feed" on the pesticide and take it out before it can exert its toxic action sufficiently on pests to prevent crop damage.

Pesticide resistance comes at a metabolic cost to an organism – energy must be expended to detoxify a compound that has no intrinsic nutritional worth to the organism. Consequently, pesticide resistant genotypes are less fit and will diminish in the population once the selection pressure is removed. Enhanced biodegradation, on the other hand, is a consequence of a nutritional benefit causing proliferation of the adapted organisms. Although they too will diminish in response to reduction in the favored source of nutrition, it is simply a response to resource shortage and not because they are less fit.

A characteristic of enhanced biodegradation is that the effect gradually diminishes if the affected soil is given no further treatments of the pesticide. However, bacteria are mainly responsible and they can form resting stages. Consequently, the phenomenon can rapidly reactivate at an immediately high level if the pesticide is once again applied to the soil. Prevention of the phenomenon is the only sure way of avoiding it.

Unfortunately, enhanced biodegradation approaches by stealth and it is difficult to know what rate of removal of a pesticide from the environment will constitute a problem for control of a pest. The issue will most likely be crop and pest-specific. Acutely toxic pesticides applied when the pest is present are unlikely to suffer the problem, whereas pesticides that need to be applied prophylactically pre-planting to act later in the life of the crop will be at much greater risk.

Soil characteristics affect the risk of onset of enhanced biodegradation. A major factor increasing the risk is high soil pH, which favors proliferation of bacteria over fungi. However, it is known that calcium is an important element in the nutrition of bacteria and calcium content of soil is normally positively correlated with elevated pH. Recent studies confirm that the combined effect of calcium and high pH is required to enhance the risk of enhanced biodegradation. Generally, it seems that sandy soils are more at risk of the phenomenon but this is a broad characteristic that is not easily quantified.

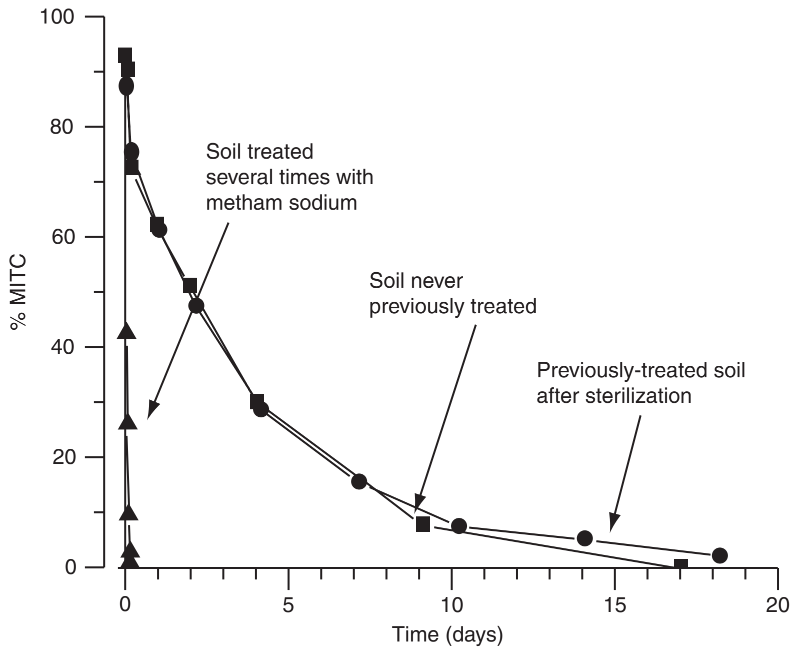
A significant related issue is the phenomenon of cross-degradation, where other pesticides are degraded at an accelerated rate in soil in which they have never been used, but which has enhanced biodegradation to another pesticide. Usually this occurs to structurally related compounds, meaning that new variations of a family of pesticides may be rendered ineffective before being used. This is what occurred to many of the carbamate insecticides used for control of corn rootworm in the American Corn Belt.

An Example

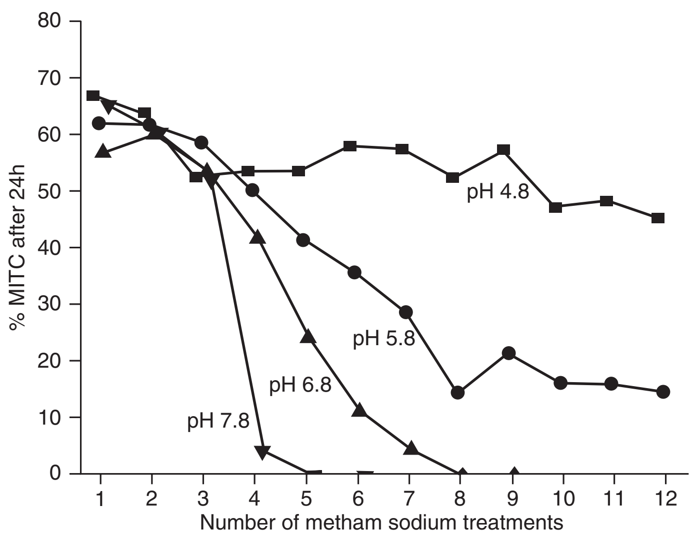
Metham (metam) sodium is a fumigant-like broad-spectrum pesticide widely used for the control of soil-borne pests and diseases. The principal use is in horticulture, which is often characterized by intense production systems with little or no crop rotation. Metham sodium is a somewhat unusual pesticide in that it is not the active pesticidal compound. Rather, it reacts in moist soil to form the toxin methyl isothiocyanate (MITC). Metham sodium, or more accurately the MITC, has been shown to suffer severely from enhanced biodegradation in an intensive horticultural production system where the soil is sandy and its pH is relatively high. It offers a good example of the principles of the phenomenon of enhanced biodegradation.

The accompanying figure shows the percentage of MITC produced and its fate when metham sodium is applied to soil that has either not been previously treated (Fig. 30) and the same type of soil from an adjacent field (Fig. 31) that had been treated approximately annually for about ten years. In the previously untreated soil the MITC was formed at almost 100% of theoretical within about one hour, and it degraded slowly over about 17 days. In contrast, in the previously treated soil only around 45% of the potential MITC was formed and it was completely dissipated within a mere seven hours.

The biological origin of the phenomenon was confirmed by sterilizing a sample of the degrading soil by autoclaving. When subsequently treated with



Enhanced Biodegradation of Soil-Applied Pesticides, Figure 30 **Production and fate of MITC toxin after application of metham sodium to soil never previously treated, soil treated numerous times in the previous ten years, and the previously treated soil after being sterilized.**



Enhanced Biodegradation of Soil-Applied Pesticides, Figure 31 **Amount of MITC remaining in soil 24 h after treatment with metham sodium for a single soil type amended to four pH levels.**

metham sodium, the production and fate of MITC in the soil was identical to the pattern in the soil that had never previously been exposed to the pesticide. Several species of bacteria that could be readily maintained in culture with MITC as the sole nutrient source were isolated from the degrading soil.

The clear influence of high pH (including non-limiting calcium) in exacerbating the risk of enhanced biodegradation is shown in the other figure. Sub-samples of a naturally acidic (pH 4.8) soil were modified to a range of higher pH values and then treated with metham sodium at monthly intervals, with the MITC being measured after 24 h. The highest pH soil developed enhanced biodegradation after only four applications, and the effect was proportional to pH in the other soils.

Implications

The most important aspect of enhanced biodegradation is for those involved in pesticides applied to soil to recognize the reality of the issue, be alert to the warning signs and to understand key risk factors (e.g., high soil pH). Too often in the past the control failures were put down to such things as unfavorable weather, poor application techniques, insufficient chemical or pesticide resistance. This can lead to repeated applications or increased doses – both of which simply exacerbate the problem.

The only option for management of enhanced biodegradation is prevention. One way that this can be achieved is by rotation of pesticides, so long as different types are alternated. However, this often requires a cooperative approach by competing pesticide manufacturers. Other methods that farmers can adopt is lengthening the time between applications of the same pesticide to an area of land through the use of longer crop rotations, and avoiding reliance on a pesticide-only approach by using rotation crops antagonistic to pest organisms.

► Detoxification Mechanisms in Insects

References

Felsot AS (1989) Enhanced biodegradation of insecticides in soil: implications for agroecosystems. Annu Rev Entomol 34:453–476

Racke KD, Coats JR (1990) Enhanced biodegradation of pesticides in the environment. American Chemical Society, Washington, DC

Enicocephalidae

A family of bugs (order Hemiptera). They sometimes are called gnat bugs or unique-headed bugs.

► Bugs

Ensiform

This term is usually applied to structures that are sword-like in appearance. They are flattened with thin edges and taper to a point distally. Most often this term is applied to antennal structures.

Ensign Coccids

Members of the family Ortheziidae, superfamily Coccoidae (order Hemiptera).

► Bugs

Ensign Wasps

Members of the family Evaniidae (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Enteric

This term refers to the digestive system or alimentary canal.

Entognatha

This is a taxon of superclass Hexapoda containing the primitive arthropods closely related to insects. Entognatha is usually considered to be a class, corresponding to the class Insecta, and consisting of the orders Collembola, Protura, and Diplura

(Entotrophi). However, these orders are sometimes considered to be classes, or orders within Insecta.

Entognathous

Mouthparts that are sunk into the head. This is also known as entotrophous. Such mouthparts are found generally in hexapod organisms that are close relatives of insects, such as Collembola, Diplura, and Protura. This is a major feature differentiating these insect-like groups from true insects, which have ectognathous (extruded) mouthparts.

Entomobryidae

A family of springtails in the order Collembola. They commonly are known as slender springtails.

► Springtails

Entomodeltiology

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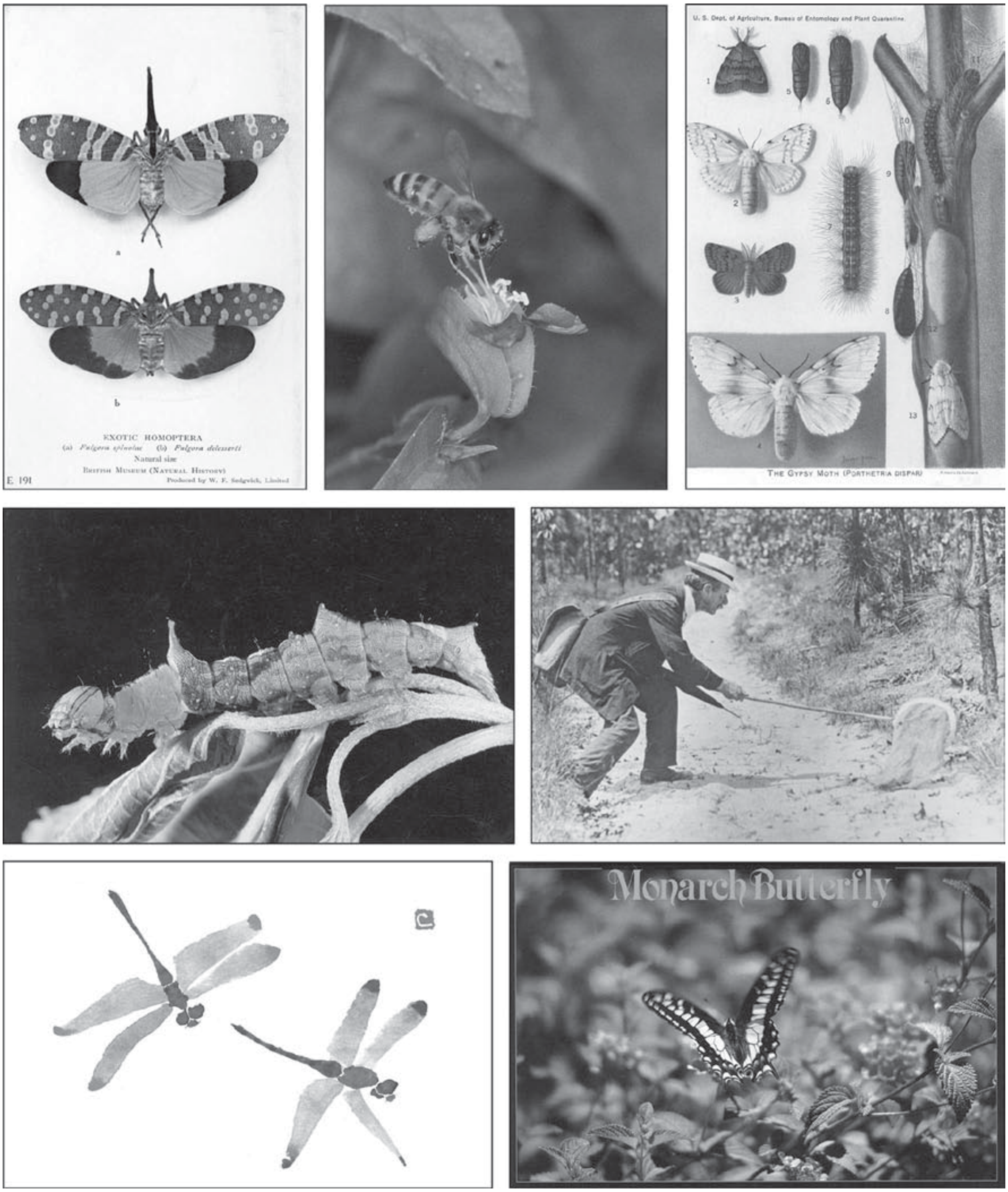
Many entomologists, ecologists, naturalists and amateurs collect insects because they find insects fascinating. Entomodeltiology, a combination of entomo = insect and deltiology = the hobby of collecting postcards, is another way to collect insects. Just as catching rare or unusual insects is challenging, finding postcards is equally challenging. Insects can be found on regular postcards and even on postcards made of leather, wood or ceramic.

Picture postcards were placed on sale at the Columbian Exposition in Chicago, Illinois, on May 1, 1893. Although there were earlier scattered issues, this was the real beginning of the postcard. Illustrations were placed on government printed cards or privately printed souvenir cards. The back of the card was for address only. In 1898, private printers in the U.S. were allowed to print and sell cards with the inscription "Private Mailing Card," and in 1901, private printers were granted permission to use the words "Post Card." Writing on the back was still limited to the address.

Postcards as we know them, with a vertical line down the middle of the back side with a space for the address on the right and a message on the left, were permitted beginning March 1, 1907. Millions of cards were printed from 1907 to 1915, mostly in Germany, where lithographic processes were far superior to those in America. The First World War stopped the printing and importation of post cards from Germany. Most cards were printed in England and the United States. Several other eras followed including the white border era (1915–1930). Printers saved ink by leaving a white border around the picture or illustration. These cards were of poor quality and many publishers went out of business. This was followed by the linen era (1930–1944) where cards with a high rag content caused the cards to have a linen-like finish. Many historical events were depicted on these cards. Finally (1945 to the present), the photochrome era. These color photographs are very appealing to the collectors and some postcard dealers specialize only in chromes.

Deltiology from 1915 to 1970 was not a popular hobby. Around 1970, interest began to grow. At present there are over 100 postcard clubs worldwide. Numerous postcard shows are held each year where collectors can peruse hundreds of thousands of postcards. Two magazines, Barr's Post Card News and Postcard Collector, are published. Subject interest is highest in geographic areas (cities, counties, states). Others limit their collecting to churches, schools, hotels, etc., in a particular area. There is hardly a topic that someone doesn't collect and that includes animals from the largest mammals to insects as diverse as butterflies and fleas.

Interest in insect postcards appears to be increasing as more and more dealers have an insect category in their topical offerings. A few years ago, if you inquired about insects on postcards, you would probably be referred to the animal category. The number of dealers who have a butterfly



Entomodeltiology, Figure 32 **Some postcards depicting insects: top row and second row left, educational postcards showing important or particularly interesting insects; second row right, postcards showing the "art" of capturing tiger beetles; bottom row, portrayal of insects for aesthetic value in oriental art (left) or photography (right). Note that the bottom right postcard is incorrectly labeled; this is a swallowtail rather than a monarch.**

Entomodeltiology, Figure 33 Additional postcards depicting insects: top two rows show humor, which often is associated with mosquitoes, particularly oversized mosquitoes; third row left, insects attired as humans; third row right, a "giant" grasshopper, a common source of humor in areas commonly infested with grasshoppers; bottom left, ladybeetles harnessed, another example of humor; bottom right, a colorful holiday greeting.

category has increased in recent years and it is unusual to find a dealer without such a category.

Considering the beauty of butterflies and moths, it is not surprising that they are favorites among insect postcard collectors. Examples range from chromes of live butterflies and sometimes their larvae, to artistic renderings of butterflies to the inclusion of small non-descript butterflies added to scenery pictures. Monarch butterflies are a favorite subject, especially on the newer chrome cards.

Butterflies and other insects (especially lady beetles and various bees and wasps) may be depicted on general greeting postcards (Fig. 32, Fig. 33) as well as birthday, Easter, Valentines, with only a few on Christmas, Thanksgiving, New Years, and St. Patrick' s Day.

Mosquitoes are frequently found on postcards in areas where tourists abound. A fairly common card has a giant stylized mosquito labeled as the state bird of (insert any state or province). Amazingly, these are usually labeled as *Aedes vexans*, apparently the only species known to postcard illustrators. Other old cards depict mosquitoes attacking people. Honey bees are not left out. Most are humorous with someone being attacked by a swarm of angry bees. Another comic card shows a man fighting bed bugs. Germany produced many postcards with scarab beetles performing as people.

Other themes found among insect postcards include fantasy (e.g., children with butterfly wings), exaggeration (e.g., giant grasshoppers), stamps, Asian art (insects are nearly as common as flowers), humor, and education (e.g., series of images produced by scientific institutes, government, and agrochemical companies).

New postcards may be found in any store that sells cards. Another good source is in the gift shops in natural history museums and butterfly houses. The British Museum of Natural History has issued over two dozen sets of insect postcards based on their vast worldwide collection of insects. Old postcards are often found in antique shops or at postcard shows. Postcard prices range from 25 cents up to hundreds of dollars depending on rarity, condition, topic and age.

Collecting postcards with insects is a challenging hobby. Unlike collecting insects on stamps, where catalogs are available listing every issue, the insect postcard collector is on his own.

Entomogenous

Refers to microbes or nematodes growing in or on the bodies of insects. This term connotes parasitic or other intimate symbiotic relationship, but not necessarily a pathogenic one. Though popular in recent history, this term is now rarely used, and is best considered obsolete (contrast with entomophilous and entomopathogenic).

Entomoparasitic

This term denotes a parasitic relationship between an insect and a parasite, though it usually is used to describe the relationship with insect parasitoids. Although entomoparasitic insects kill their hosts (i.e., they are pathogenic), they are never referred to as entomopathogenic. Some nematodes (the ones that do not kill quickly, instead functioning more like insect parasitoids) are correctly referred to as entomoparasitic (contrast with entomopathogenic, entomophilic).

Entomopathogenic

A relationship between an insect and a microbe, or an insect and a nematode, that results in the death of the insect. It is best considered a subset of entomophilic organisms. Some prefer to limit this term to insect-killing nematodes which harbor and release a pathogenic bacterium: nematodes in the families Steinernematidae and Heterorhabditidae. Although entomoparasitic insects kill their hosts (i.e., they are pathogenic), they are never referred to as entomopathogenic (contrast with and entomophilic).

Entomopathogenic Fungi and their Host Cuticle

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Entomopathogenic fungi are a very diverse group of insect pathogens that include approximately 700 species in almost 100 genera. They occur in most fungal taxonomic groups, with an ample variation in host range, thus providing a large number of microorganisms potentially useful as control agents against different insect orders. Insect pests infesting areas where it is difficult or unsafe to implement control using currently available insecticides are particularly good targets for mycoinsecticides. Among them, there is interest in targeting disease vectors that co-habit with humans (mosquitoes, flies and kissing bugs), mostly due to the health risk of toxic chemical use in human dwellings. There also is growing interest in use of mycoinsecticides to control pests affecting greenhouses, small orchards and organic farms (particularly aphids, whiteflies, a variety of beetles and caterpillars). Unlike other insect-pathogenic microorganisms that must be ingested to initiate the disease (virus, bacteria, nematodes and protozoa), entomopathogenic fungi normally invade by penetrating through the host cuticle. Surface structure and the chemical composition of the cuticle are both believed to affect the attachment of fungal propagules. Initial events can be divided into three successive stages:

(i) Adsorption at the interface between the propagules and the insect epicuticle. This first step involves physical and chemical characteristics of both propagules and host surfaces. The process may involve specific receptor-ligand and/or nonspecific hydrophobic and electrostatic mechanisms. This stage is characterized by the secretion of mucus by fungal cells and the initial dissolution of the surrounding epicuticle by this mucoid substance. Ungerminated conidia deposited on the cuticular surface are able to produce esterases, lipases, and N-acetylglycosaminidase. Thus, enzymatic activities might be implicated early in adhesion processes.

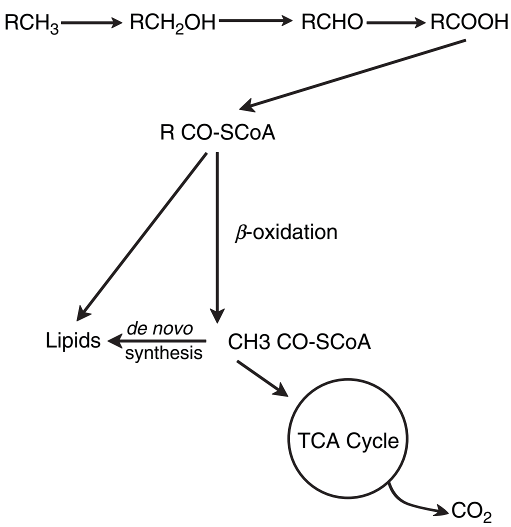
(ii) Fungal germination and development on the insect cuticle. Early events in spore germination require an exogenous carbon source. Both germination stimulators and inhibitors have been detected on the cuticle. In general, high relative humidity (over 90%) is needed for germination. However, an adequate microclimate to promote infection can be found on the intersegmental membranes of the insect's cuticle.

Both adsorption and germination must occur, but success here does not guarantee successful fungal infection. Fungal germination on non-host cuticle, without further penetration into the insect internal tissues, has been reported.

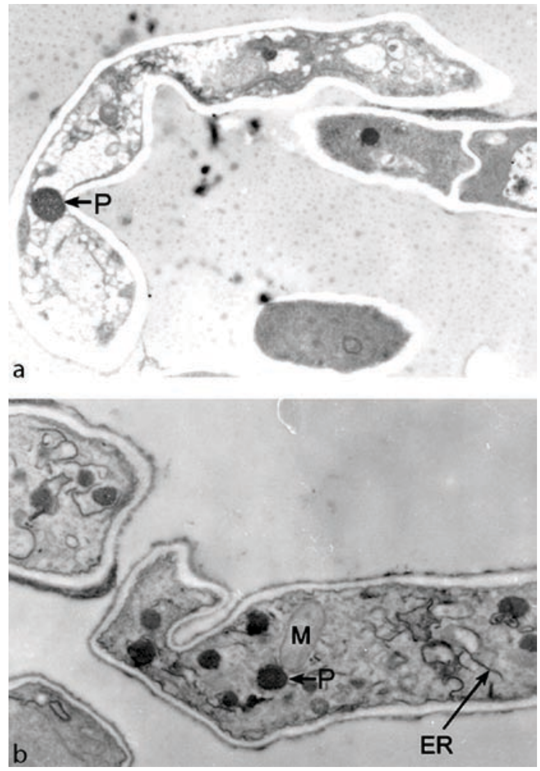
(iii) Fungal penetration. Germ tubes must pass through the different cuticular layers. This process depends both on the intrinsic properties of the germ tube and on the physiological state of the host and is essential for infection occurrence. The most common cuticular reaction to fungal penetration is a localized melanization around and in front of the penetration peg. Successful pathogens overcome any defensive reaction and penetrate into the hemocoel. Finally, the fungus replicates as budding hyphal bodies invading the entire cavity; insect death takes place shortly after.

Fungal Enzymes Involved in Cuticle Degradation

Although the major bulk components of the insect cuticle are protein and chitin, the outermost epicuticular surface layer comprises a complex mixture of non polar lipids, mainly composed by very long chain hydrocarbons (20 to more than 40 carbons). Entomopathogenic fungi are also able to degrade insect epicuticular hydrocarbons, incorporating them into cellular components (Fig. 34) as well as utilizing them for energy



Entomopathogenic Fungi and their Host Cuticle, Figure 34 Proposed pathway for hydrocarbon degradation by entomopathogenic fungi. RCH3: hydrocarbon, RCH2OH: fatty alcohol, RCHO: fatty aldehyde, RCOOH: fatty acid, RCO-SCoA: fatty acyl-CoA, CH3CO-CoA: acetyl-CoA, TCA: tricarboxylic acid.

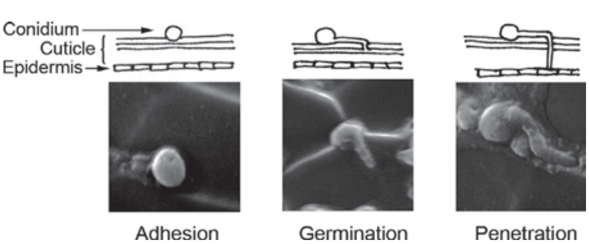


Entomopathogenic Fungi and their Host Cuticle, Figure 35 Electron micrographs of *Beauveria bassiana* comparing fungi grown either in an easily usable carbon source (glucose) or in insect-like hydrocarbon as the sole carbon source. Diaminobenzidine was used to stain peroxisomes. (a) Glucose-grown cells show scarce peroxisomes; (b) Hydrocarbon-grown cells show a large number of small size peroxisomes. P: peroxisomes, M: mitochondrion, ER: endoplasmic reticulum.

production. Insect hydrocarbons were shown to be the preferred cuticular lipid fraction for fungal growth. Employing radiolabeled analogues of insect hydrocarbons, they were shown to be incorporated into a variety of fungal lipid components. Depending on the substrate assayed, complete oxidation (CO_2 production) was also detected. The fungal enzymes involved in insect-like hydrocarbon breakdown have not yet been identified and characterized. In analogy to yeast systems, the first oxidation round is presumably carried out by a microsomal cytochrome P450 enzyme system, producing a fatty alcohol as the primary oxidation product. The alcohol, or eventually the fatty acid, will traverse the peroxisomal membrane, and after successive transformations by the concerted action of alcohol dehydrogenase, aldehyde dehydrogenase, and acyl-CoA synthetases, will eventually provide the appropriate fatty acyl-CoA for degradation in the peroxisomes, the site of β-oxidation in fungi. In *Beauveria bassiana*, development of peroxisomes is clearly stimulated in alkane-grown fungi; electron micrographs (Fig. 35) show diaminobenzidine-stained peroxisomal particles closely associated to endoplasmic reticulum. Furthermore, peroxisomal marker enzymes (i.e., catalase and acyl CoA oxidase) are induced in fungi grown on media containing insect-like hydrocarbons as the sole carbon source.

Penetration of exocuticle and endocuticle involves both physical and enzymatic activities.

The lack of data on the former makes it difficult to envisage its precise role in the whole process. To study enzyme production, fungal preparations are incubated either with insect cuticle or with chemical analogues, thus providing the required carbon and/or nitrogen sources. A variety of hydrolytic enzymes responsible for the degradation of the major cuticular components are induced sequentially: proteases and esterases are produced within the first day, whereas chitinase and lipase activities appear substantially later (4–5 d). Some of them act synergistically during degradation events. First, proteases hydrolyze most of the protein crosslinkages of the procuticle; afterwards, the chitinolytic complex is activated. A number of proteases and chitinases have been identified after expressed sequence tag (EST) analyses of cDNA libraries obtained from fungal cultures incubated with insect cuticle. In this growth condition, at least three kinds of proteases are expressed: subtilisin-like proteases, trypsin-like serine proteases and thermolysin-like metalloproteases. Subtilisin-related enzymes show the greatest activity against insect cuticle, having a crucial role in pathogenesis. Trypsin-related proteases have no ability to degrade intact cuticle, but act on partially hydrolyzed cuticular proteins. Their association with (Fig. 36) appressoria suggests they might be available during early stages of cuticle colonization. Both types of proteases might be part of a cascade of pathogen reactions facilitating the penetration of host cuticles. A similar situation is found with the complex mixture of endo- and exo-chitinases produced by entomopathogenic fungi during growth on the insect cuticle. Helping penetration, endo-chitinases are likely to be the most effective degrading cuticle polymers. Oligomers released by the endoacting enzymes might be further degraded by exo-chitinases resulting in small molecules (i.e., N-acetylglycosamine) usable for nutrition.



Entomopathogenic Fungi and their Host Cuticle, Figure 36 **Initial events of the interaction between entomopathogenic fungi and insect cuticle.**

Mycoinsecticide Improvement

Fungal virulence can be understood as the degree of pathogenicity against a potential insect host. Variation in fungal virulence toward a variety of insect hosts is related to enzyme production, growth conditions, temperature, relative humidity, and the presence of other microorganisms, among other factors. Insect mortality, the time period required achieving this goal, or fungal dose are frequently used as virulence parameters. The potential to enhance virulence has been addressed either by fungal adaptation to grow on a cuticle-like medium, or in a more sophisticated way, by adding insecticidal genes encoding specific cuticle-degrading enzymes (chitinases and proteases). These approaches resulted in 25–50% reduction in the time to kill and/or a similar percentage reduction in other mortality parameters.

The major barrier role of the cuticle in insect survival is well known; furthermore, the ability of fungal degrading enzymes to breach the insect cuticle is already recognized. Improving this set of tools by favoring the initial steps of fungal penetration will help increase mycoinsecticide performance. This goal may be attained through genetic modification, in addition to formulation optimization. Several methods can be applied for genetically improving strains, and recently, transformation methods have been used for the insertion of homologous or heterologous genes in fungal biocontrol agents. Overexpression of virulence-related fungal enzymes will be advantageous, since no safety concern to using genetically modified fungi has been provided, and hence it is an ecologically safe alternative to chemical pesticides.

References

Fargues J (1984) Adhesion of the fungal spore to the insect cuticle in relation to pathogenicity. In: Roberts DW, Aist JR (eds) Infection processes of fungi. The Rockefeller Foundation, New York, NY, pp 90–110

Lomer CJ, Bateman RP, Johnson DL, Langewald JL, Thomas M (2001) Biological control of locusts and grasshoppers. Annu Rev Entomol 46:667–702

Pedrini N, Crespo R, Juárez MP (2007) Biochemistry of insect epicuticle degradation by entomopathogenic fungi. Comp Biochem Physiol C 146: 124–137

Roberts DW, Humber RA (1984) Entomopathogenic fungi. In: Roberts DW, Aist JR (eds) Infection processes of fungi. The Rockefeller Foundation, New York, NY, pp 1–12

St Leger RJ, Screen S (2001) Prospects for strain improvement of fungal pathogens of insects and weeds. In: Butt TM, Jackson C, Morgan N (eds) Fungal biocontrol agents: progress, problems and potential. CAB International, Wallingford, UK, pp 219–238

Entomopathogenic Nematodes and Insect Management

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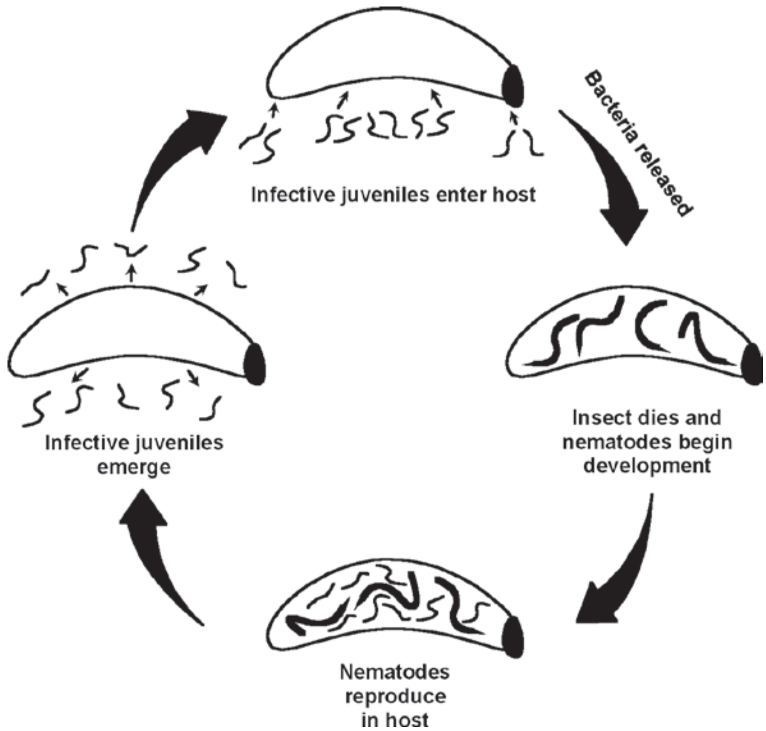
Entomopathogenic nematodes are small round worms comprising three genera in the order Rhabditida: *Heterorhabditis* Poinar, *Steinernema* Travassos, and *Neosteinernema* Nguyen and Smart. More than 35 species of entomopathogenic nematodes have been described. These nematodes are widespread and have been isolated from soil or natural hosts in every continent except Antarctica. In nature, these nematodes are obligate pathogens of insects, and thus have been developed as bioinsecticides to suppress arthropod pests. Entomopathogenic nematodes kill their hosts with the aid of a symbiotic bacterium. Heterorhabditid nematodes are associated with the bacteria *Photorhabdus* spp. And steinernematids are associated with *Xenorhabdus* spp. The bacterial symbiont associated with neosteinernematids has yet to be described.

Biology

A generalized life cycle of entomopathogenic nematodes is depicted in the accompanying figure (Fig. 37). The infective (Fig. 38) juvenile nematode, which is the only free-living stage, enters the host via natural openings, i.e., mouth, anus, spiracles, or occasionally through the insect cuticle. Once the nematodes penetrate into the host' s hemocoel, the symbiotic bacteria (carried in the infective juvenile' s intestine) are released and multiply rapidly, nematode development is initiated, and the host dies within 24–72 h. After the nematodes complete one to three generations within the insect cadaver, infective juveniles exit to find new hosts. The nematode life cycles differ among the genera in that the steinernematids contain only amphimictic forms (males and females), whereas the first generation of heterorhabditids (arising from infective juveniles) contain only hermaphrodites, and subsequent generations may contain amphimictic and hermaphroditic forms. Only one species of neosteinernematids has been described to date; their life cycle is similar to the steinernematids except that only one generation occurs in the host, and infective juveniles arise in female nematodes that have exited the host cadaver.

The relationship between the nematodes and their natural bacterial symbionts is mutualistic. The bacteria provide nutrients to the nematodes, produce antibiotics that inhibit competing microbes, and kill the host through septicemia (occasionally a bacterial toxemia precedes septicemia). Although the nematodes may also contribute to host death through suppression of the immune system and toxin production, the most important role they play in the mutualism is serving as vectors for the



Entomopathogenic Nematodes and Insect Management, Figure 37 **A generalized life cycle of entomopathogenic nematodes.**

Entomopathogenic Nematodes and Insect Management, Figure 38 **An infective juvenile steinernematid nematode.**

bacteria. Without the nematodes the bacteria cannot survive well outside of the host, e.g., in soil, and the nematodes are required for entry into the host hemocoel (few bacteria strains are pathogenic when ingested by a host). The relationship between nematode and bacterium is highly specific. Each steinernematid or heterorhabditid species is primarily associated with a single bacterial species, although some (Fig. 38) bacterial species can be associated with more than one nematode. The specificity of particular bacteria for growth and compatibility with nematodes can vary further on a strain level. The bacteria cells occur as two phenotypic variants: primary and secondary, which differ in dye absorption, response to biochemical tests, and antibiotic production. Although entomopathogenic nematodes have been reported to grow on secondary cells or even on certain non-symbiotic bacteria, the primary cells are most conducive to nematode growth. Infective juveniles only retain the primary cells.

Commerical Develoment and Efficacy

Entomopathogenic nematodes possess many positive attributes as biological control agents. They are safe to humans and are generally safe to other non-target organisms and the environment. Additionally, entomopathogenic nematodes have a wide host range, a durable infective stage, and can be applied using standard agricultural and horticultural equipment.

Another beneficial quality that entomopathogenic nematodes possess as biological control agents is amenability to mass production. The nematode-bacteria complex is mass-produced using *in vivo* (i.e., in insects) or *in vitro* methods (solid or liquid fermentation). *In vivo* production requires a low level of technology and relatively little capital outlay. However, cost efficiency using *in vivo* methodology is low due to space and labor requirements. Some of the factors that can affect nematode yield *in vivo* include choice of insect host and nematode species, nematode inoculum concentration, and environmental factors (humidity and temperature). The most common host used for in vivo production is the greater waxmoth, *Galleria mellonella* (L.); depending on nematode species, yields in *G. mellonella* vary from approximately 40,000 to 300,000 infective juveniles per insect. *In vitro* solid culture, i.e., growing the nematodes and bacteria on crumbled polyurethane foam infused with a liquid medium, offers an intermediate level of technology and costs between *in vivo* and liquid culture. Nematode yield using solid fermentation is affected by inoculum size, culture time, and media composition. Yields can vary from approximately 200,000 to 500,000 infective juveniles per gram of media. *In vitro* liquid culture is the most cost efficient production method but requires the largest startup capital outlay. Factors that affect nematode yields in liquid fermentation include nematode species, mixing (bioreactor design), aeration, and media. Entomopathogenic nematodes have been successfully cultured in bioreactors with capacities as large 80,000 liters, and yields of up to 300,000 infective juveniles per ml have been reported.

For small-scale or laboratory purposes, entomopathogenic nematodes are generally produced *in vivo* and stored in aqueous suspension (with sufficient exposure to oxygen) prior to use. Commercially produced nematodes, however, must be formulated prior to delivery and application. An effective formulation provides a suitable shelf life, stability of product from transport to application, and ease of handling. Increased shelf life, in most entomopathogenic nematode formulations, is obtained by reducing nematode metabolism and immobilization, which may be accomplished through refrigeration and partial desiccation. Optimum storage temperature for formulated nematodes varies according to species: generally, steinernematids tend to store best at 4–8°C whereas heterorhabditids have longer shelf life at 10–15°C. Various formulations for entomopathogenic nematodes have been reported, including activated charcoal, alginate and polyacrylamide gels, baits, clay, peat, polyurethane sponge, vermiculite, and water-dispersible granules. Depending on the formulation and nematode species, successful storage under refrigeration ranges from one to seven months.

The efficacy of entomopathogenic nematodes in suppressing insects depends on selection of the appropriate nematode for the target pest. A suitable nematode must possess a high degree of virulence (killing power) to the host. The nematode must be able to effectively invade and overcome the host immune system under field conditions (laboratory virulence does not necessarily predict field efficacy). Although many entomopathogenic nematodes possess a broad host range spanning several taxonomic orders, the nematode most suited to a particular pest will often be species and strain dependant. Not all entomopathogenic nematodes have broad host ranges, e.g., *S. kushidai* Mamiya appears to be specific for scarab beetles (Coleoptera: Scarabaeidae) and *S. scapterisci* Nguyen and Smart is most suitable to two-clawed mole cricket hosts (*Scapteriscus* spp.).

The ability of entomopathogenic nematodes to persist in the environment may also contribute to host suitability. Indeed, in some cases enhanced persistence may even compensate for lower virulence. Generally, high levels of efficacy persist for only two to six weeks following nematode application. However, there have been some reports of prolonged pest control over several seasons or years. Nematode persistence depends on the nematode species or strain, host density, and environmental factors (e.g., temperature, moisture, etc.).

Additionally, the suitability of an entomopathogenic nematode to control a particular pest depends on the nematode' s foraging strategy. Foraging strategies exhibited by entomopathogenic nematodes exist along a continuum from ambushers to cruisers. Ambushers use a sit and wait strategy; they usually stand on their tails (nictating) and wait until a host comes close before infecting. Cruisers actively seek out their hosts and cue into certain target volatiles (e.g., CO2) prior to contacting the host. Examples of nematodes that exhibit foraging behavior characteristic of ambushers include *S. carpocapsae* (Weiser) and *S. scapterisci*, those exhibiting behavior typical of cruisers include *H. bacteriophora* Poinar, *H. megidis* Poinar, Jackson, and Klein, and *S. glaseri* (Steiner), and those with intermediate search behavior include *S. feltiae* (Filipjev), and *S. riobrave* Cabanillas, Poinar, and Raulston. Ambushers tend to be most successful at infecting mobile insects on or near the soil surface, whereas cruisers tend to be most successful at infecting sessile insects below the soil surface.

Abiotic factors are critical in determining efficacy of entomopathogenic nematode applications. These nematodes are highly sensitive to desiccation and ultraviolet light. Thus, applications made to soil or other cryptic habitats (and made during the early morning or evening) tend to be most successful. Temperature extremes (e.g., below 20°C and above 30°C) can be detrimental to nematodes. The optimum temperature for maximum efficacy depends on nematode species or strain; some nematodes are relatively heat tolerant such as *H. indica* Poinar, Karunakar, and David, and *S. riobrave*, whereas others are relatively cold tolerant, e.g., *H. megidis* and *S. feltiae*. Soil characteristics can also be important in determining efficacy, e.g., coarse soils with high sand content facilitate nematode movement and allow for air exchange. Nematodes require oxygen for survival, and thus factors that reduce airflow such as compacted or water-saturated soil are detrimental. Other pesticides or fertilizers used in conjunction with entomopathogenic nematodes may affect efficacy antagonistically, additively, or synergistically, depending on the agent(s) involved.

Following is a list of some insect pests for which high levels of suppression (greater than or equal to 80%) were achieved under field conditions using entomopathogenic nematodes (Table 4). A high degree of efficacy in pest suppression, however, does not necessitate an opportunity for successful application on a commercial scale; economic factors are also important. Generally, to achieve a high degree of efficacy, at least 25 infective juveniles must be applied per cm^2 of treated area (= 2.5 × 109 per hectare). Based on the number of nematodes required for successful pest control, and current production methods, the cost of entomopathogenic nematodes tends to be relatively high compared with many chemical insecticides. Therefore, commercial use of entomopathogenic nematodes has been cost prohibitive in many low-value crops (e.g., row crops such as cotton and corn), and has been most successful in certain high value crops or niche markets. Some examples of pests and markets where entomopathogenic nematodes have been successfully commercialized include billbugs (*Sphenophorus* spp.) in turf, black vine weevil, *Otiorhynchus sulcatus* (F.), in cranberries and ornamental plants, diaprepes root weevil, *Diaprepes abbreviatus* (L.), in citrus, fungus gnats (Diptera: Sciaridae) in mushrooms, *Scapteriscus* mole crickets in turf, and white grubs (Coleoptera: Scarabaeidae) in turf and ornamental plants.

Several measures can improve entomopathogenic nematode efficacy. Advances in production, formulation, and application technology can enable more viable nematodes to be applied to the same area for an equal or lower cost. Discovery of new nematode strains or species with superior beneficial traits such as virulence, persistence, or environmental tolerance, can enhance the potential for successful pest suppression. Beneficial traits may also be developed in entomopathogenic nematodes through genetic methods, i.e., artificial selection, hybridization, mutagenesis, and genetic transformation.

Entomopathogenic Nematodes and Insect Management, Table 4 A list of some pests for which at least 80% suppression was reported using entomopathogenic nematodes under field conditions[a]

Pest common name	Pest scientific name	Nematode(s)[b]
Artichoke plume moth	*Platyptilia carduidactyla* (Riley)	Sc
Banana moth	*Opogona sachari Bojer*	Hb, Sc
Banana root borer	*Cosmopolites sordidus* (Gemar)	Sc, Sf, Sg
Black cutworm	*Agrotis ipsilon* (Hufnagel)	Sc
Black vine weevil	*Otiorhynchus sulcatus* (F.)	Hb, Hm
Borers	*Synanthedon* spp.	Hb, Sc, Sf
Codling moth	*Cydia pomonella* (L.)	Sc
Corn earworm	*Helicoverpa zea* (Boddie)	Sr
Diamondback moth	*Plutella xylostela* (L.)	Sc
Fungus gnats	Diptera: Sciaridae	Sf, Hb
Japanese beetle	*Popillia japonica* Newman	Hb, Sg
Leafminer	*Liriomyza* spp.	Sc
Mole crickets	*Scapteriscus* spp.	Sc, Sr, Ss
Root-knot nematodes	*Meloidogyne* spp.	Sc, Sf, Sr

[a]At least one scientific paper reported ≥80% suppression of these pests.
[b]Hb = *Heterorhabditis bacteriophora*, Hm = *H. marelatus*, Sc = *Steinernema carpocapsae*, Sf = *S. feltiae*, Sg = *S. glaseri*, Sr = *S. riobrave*, Ss = *S. scapterisci*.

Through continued research the use of entomopathogenic nematodes is expanding. In addition to controlling harmful insect pests, novel uses of entomopathogenic nematodes, and more so, their symbiotic bacteria or associated metabolites, are being pursued to suppress plant parasitic nematodes, and as anti-microbial agents in pesticide and pharmaceutical applications. Furthermore, toxins produced by the bacteria are being studied for their suitability as alternatives to other orally active insecticides such as toxins produced by *Bacillus thuringiensis*.

References

Gaugler R (ed) (2002) Entomopathogenic nematology. CABI, New York, NY, 388 pp

Gaugler R, Kaya HK (eds) (1990) Entomopathogenic nematodes in biological control. CRC Press, Boca Raton, FL, 363 pp

Georgis R, Gaugler R (1991) Predictability in biological control using entomopathogenic nematodes. J Econ Entomol 84:713–720

Kaya HK, Gaugler R (1993) Entomopathogenic nematodes. Annu Rev Entomol 38:181–206

Kaya HK, Stock SP (1997) Techniques in insect nematology. In: Lacey LA (ed) Manual of techniques in insect pathology. Academic Press, San Diego, CA, pp 281–324

Shapiro-Ilan DI, Gaugler R (2002) Production technology for entomopathogenic nematodes and their bacterial symbionts. J Ind Microbiol Biotechnol 28:137–146

Entomophagous

Insectivorous; the consumption of insects or their parts. Though formerly used to describe a broad range of associations that resulted in insects being killed, it now is used mostly to indicate predation of insects. Parasitic relationships are best described as entomoparasitic (for parasitoids) or entomophilic/entomopathogenic (for nematodes and microbial pathogens).

Entomophagy

Consumption of insects by other animals and carnivorous plants.

Entomophagy: Human Consumption of Insects

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In ancient times, when humans first appeared on the earth, insects might have been important foods for them, because they had neither tools to hunt large animals, nor techniques for agriculture. Since then, entomophagy has continued up to the present time all over the world. Human coprolites, which were found in some caves in the USA and Mexico, give evidence to the above consideration. From the coprolites found in caves of the Ozark Mountains located between Arkansas and Missouri, ants, larvae of beetles, lice, ticks and mites were isolated. On the wall of a cave of Artamila in North Spain, a picture showing the collection of wild bee nests was found. It is said that the picture was drawn about 9,000 to 30,000 years B.C. At that time people might have eaten bee larvae and pupae together with the honey. In Shanxi Province, China, cocoons of a wild silkworm, *Theophila religiosae*, were found from the ruins of 2,000 to 2,500 years B.C. Each cocoon had a large hole on it, suggesting that people ate pupae of the silkworms. People ate various insects everywhere in the world, and this developed into traditional entomophagy. Some traditional entomophagy has been handed down to the present.

Most insect species are edible, but some are toxic. More than 1,000 species have been consumed as foods. However, identification of the species is difficult, because in many cases edible insects are given vernacular names. Some of more important groups include grasshoppers; caterpillars; beetles (larvae and adults); termites; bee, wasp and ant brood (larvae, pupae and sometimes winged adults); cicadas; and various aquatic insects.

Present entomophagy may be divided into two categories. One is consumption of insects as necessary nutrients, and the other is uptake of insects as a condiment. In the former case, insects are consumed as protein sources in the area where malnourished people live, or at the time of famine. For example, locust outbreaks are common in Africa and the Middle East, and edible plants are scarce after migration of locusts. Under these circumstances, people catch locusts for their food. However, sometimes local government sprays insecticides against locusts. The insecticide-sprayed locusts are no longer suitable for food. Then there will be conflicts between people and the government.

In the latter case, insects appear as cuisine in restaurants in big cities, and are also sold as processed food. In restaurants, insect dishes are always more expensive than beefsteak. The popular insects served in restaurants are maguey worms (*Cossus redtenbachi* and *Aegiale hesperiaris*), ants (*Liometopum apiculatum*) in Mexico; wasps (*Vespa sorror*), wild silkworm pupae (*Antheraea pernyi*), and pyralid moth larvae (*Chilo fuscidentalis*) in China; wasps (*Vespa* sp.), bees (*Apis dorsata*), giant water bugs (*Lethocerus* (*Belostoma*) *indicus*), pyralid moth larvae (*C. fuscidentalis*) in Thailand.

The processed insects also are expensive compared with other food. As processed insect foods, the followings are commercially available; canned rice grasshoppers (*Oxya yezoensis*), wasps (*Vespa lewisi*), silkworm pupae and adults (*Bombyx mori*), and larvae of Trichoptera from Japan; canned silkworm pupae (*B. mori*) from Korea; canned spice (namphric) containing giant water bugs (*L. indicus*) from Thailand; canned mopany worms (*Goninbrasia belina*) from South Africa; bottles of mezcal containing maguey worms (*C. redtenbachi*) from Mexico; canned soup containing witjuti (witchetty) grubs (larvae of large cossid moth) from Australia; candies containing mealworms (*Tenebrio molitor*) or crickets (*Acheta domesticus*) and fried snacks of some lepidopteran larvae from the USA.

Insects are eaten raw or cooked. In tropical regions where palm weevils (Coleoptera: Rhynchophoridae) are distributed, the larvae are eaten raw by native people joyfully at the moment when captured. In Papua New Guinea, children eat small grasshoppers as a favorite food. Many other species are consumed raw by people in developing countries.

The simplest and most primitive form of food preparation is roasting. It is common to roast insects in a fire or to throw them into hot ash. A more subtle way is to smother by burying insects in the soil with heated stones. Roasting insects by skewering them is popular too. Insects are also boiled or simmered in water or soup. They are often cooked with some vegetables and spices. Frying is also a popular cooking way of insects. Any species or any stage of edible insects can be eaten by frying. In many cases, fried insects with a bit of salt or spices are acceptable. Insects are also fried with vegetables. Some edible insects can be preserved by desiccation. In some places dried insects are commercially available in markets: e.g., mopany worms in South Africa, chipmi (*Gynanisa maja*, Saturniidae) in Zambia, small water bugs (ahuahutle) and their eggs in Mexico.

Although cooking methods for insects are similar in many places, traditions have developed in some areas. Some examples of traditional entomophagy follow. In Japan, rice grasshoppers, wasps (*V. lewisi*), silkworm pupae and trichopteran larvae have been consumed from old times. All these insects are cooked with soy sauce, sugar and rice wine. These insects were used as a protein source by people who lived in mountainous areas and had limited access to fish.

In Africa, termites are widely consumed. People collect termites when these insects swarm out of their nests at the first rain after the dry season. People eat them raw or fried. In Africa there are very many species of Saturniidae, whose larvae are large. Among these species, the mopany worm is famous. The mopany worm is distributed in southern Africa (i.e., South Africa, Botswana, Zimbabwe and Zambia). The worms are relished, and people collect them to a greater extent when the worms reach full-grown stage. In addition to the consumption by the collector themselves, many dried larvae are exported to neighboring areas where the mopany worm does not occur. The mopany worm is prepared mostly by stewing. In Lake Nyassa, when the midge *Chaoboris edulis* is very abundant, Tanzanians collect flies, press them into cakes, and dry them under the sun. The products are called "kungu," and are said to have taste of caviar. Also, Malawians collect ephemeropteran adults, and make cakes. This is also called kungu.

In Thailand and surrounding areas, giant water bugs have been consumed widely. People not only eat intact insects, but also make spices (namplaa sauce or namphric) from the scent glands of males.

In Australia, the aboriginal people still keep the custom of eating witjuty grubs (large cossid moth larvae) and a honey pot ant, *Camponotus inflatus*. People eat the witjuty grubs by roasting them, while the honey pot ants are consumed raw. The bogong moth, *Agrotis infusa*, is a well-known insect food for Aborigines. Every year, the adults migrate to the Australian Alps for summer estivation. Aborigines gather in the Alps to collect the estivating moths in interstices of rocks. They eat the moths by roasting them on heated ash.

In the USA, the Paiute Indians living in the Sierra and Cascade Mountains used to collect the pandora moth larvae, *Coloradia pandora lindseyi*, from conifer trees. Like mopany worms, pandora moth larvae are consumed by roasting or by boiling (the boiled larvae are called "pe-ag-gie" or "piuga"). Modoc Indians in California used to consume the adult of a fly, *Atherix* sp., which is easily collected along rivers. People eat them by making loaves and roasting them. It is said that the taste is similar to headcheese. In California, Mono Lake Indians who lives near alkaline and saline lakes used to consume pupae of a brine fly, *Ephydra hianus*. A colossal number of the pupae are thrown up on the shore of the lake in late summer. The Indians harvested the pupae, removed puparia by rubbing, and ate them. This food is called "koo-chah-bee."

In Thailand, especially in northern part of the country, many insect species are consumed as food. One weaver ant, *Oecophylla smaragdina*, is commonly eaten raw or rubbed with salt, chili or pepper. A grasshopper, *Patanga succincta*, is also a popular edible insect and consumed by frying. A cricket, *Brachytrupes portentosus* has been commonly consumed.

In China, cicadas, ants and wasps have been consumed since ancient times, and these insects are still served in restaurants.

Insect foods can generally be said to be nutritious, because insects are rich in protein, lipid and vitamin. Although the chemical composition of insects varies with developmental stages and sexes even in the same species, protein is about 30–75% and lipid 5–60% of dry weight of insects. Among amino acid constituting insect protein, leucine, lysine and aspartic acid are said to be rich, while cystine and tryptophan are poor. However, some insect protein (for example, that of the house fly, *Musca domestica*) is said to have similar amino acid composition to beef protein. Lipids contained in insects resemble the lipids we take from usual food. For examples, fatty acid composition of the house fly pupae is said similar to that of fish fat. Carbohydrate is minor component of the insect body and is not an important nutrient in insect food. In general, insects contain a few percent of ash. Among minerals, the content of phosphate is commonly high. Insects contain considerable amount of Na, but only a little NaCl. Insects are rich in vitamins A, B1, B2 and D. Larvae of the bee, *Apis mellifera*, are said to have vitamin D ten times of that of cod liver oil, and vitamin A several times of that of egg yolk. These facts suggest that insects will be considered as a source of protein in the future.

Most medicinal use of insects is a part of entomophagy. However, only a few substances have been identified as effective components of the insects used for medicines. Some insects are apparently used as medicines based on the superstition. Cantharidin from meloid beetles, and pederin from a staphilinid beetle, *Paederus paralelus*, are known to have fungistatic action. The former was once used as aphrodisiac, too. Crickets are said to contain a substance called grypin, which acts as antifebrile. A scale insect, *Dactylopius coccus*, contains red pigment called cochineal, which is used as cough medicine, and for trouble with nerves and kidneys. *Cordyceps* is not an insect but entomogenous fungus. It is used for various diseases; an effective substance, cordycepin, has been identified. There are many insect medicines based on superstition. For example, a cicada is used as a diuretic, because a cicada often excretes urine when it flies away, and people who have disuria might want to be able to urinate easily. Silkworm moths copulate soon after adult emergence, and for a long time. People used silkworm adults as an aphrodisiac, because impotent people envy their sexual strength.

► Midges as Human Food
► Native American Culture and Insects
► Nutrient Content of Insects
► Blister Beetles
► Bogong Moth

References

Bodenheimer FS (1951) Insects as human food. Dr. W. Junk Publishers, The Hague, The Netherlands, 352 pp

Comby B (1990) Delicieux insectes. Editions Jouvence, Geneve, Switzerland, 156 pp

Mitsuhashi J (1984) Edible insects of the world. Kokon Shoin, Tokyo, Japan, 270 pp (in Japanese)

Paoletti MG, Bukkens SGF (eds) (1997) Minilivestock. Ecol Food Nutr (Special Issue) 36:95–346

Ramos-Elorduy J (1991) Los insectos como fuente de proteinas, 2nd edn. Editorial Limusa, Mexico City, Mexico, 148 pp

Taylor RL (1975) Butterflies in my stomach. Woodbridge Press Publishing Co., Santa Barbara, CA, 224 pp

Entomophilic

This term denotes an association of microbes or nematodes with insects (and also known as entomophilous). It is used to describe a phoretic or mutualistic association, but sometimes includes pathogenic associations. Thus, it is a very broad category that includes many types of associations, and for that reason, is not very descriptive. It is better to describe pathogenic associations as entomopathogenic rather than entomophilous or entomophilic.

Entomophobia

Abnormal fear of insects and mites. It may be manifested in dermatitis induced by physical irritants or allergens, but also may result in hysterical reactions caused by the sight of the actual or purported organisms. The occurrence of invisible "cable mites," "paper mites," and "computer mites," are sometimes associated with this affliction.

► Delusory Parasitosis

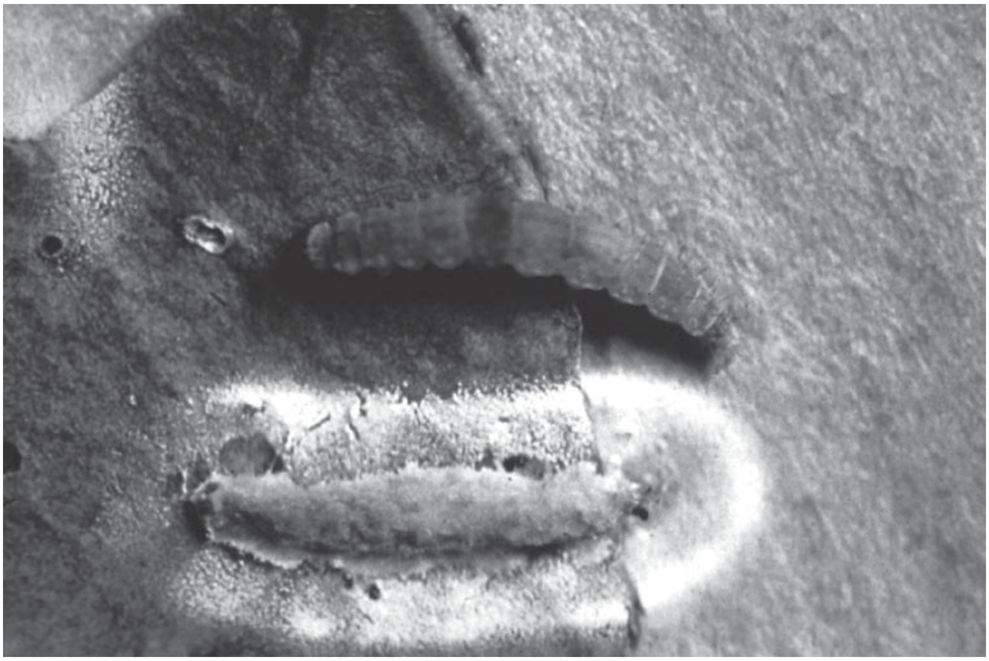
Entomophthorales

Most of the entomopathogenic genera within the Zygomycetes belong to a large order, the Entomophthorales. A second order in the Zygomycetes is the Mucorales, most of which are saprophytic; one genus, *Sporodiniella*, however, does infect membracids. Members of the Entomophthorales, with the exception of the genus *Massospora*, are characterized by the presence of forcibly discharged conidia; in *Massospora*, conidia are formed within the abdomens of periodical cicadas in the genus *Magicicada*. In addition to conidia, the Entomophthorales also produce zygospores (sexual) and azygospore-type resting spores, and mycelia are usually coenocytic, i.e., non-septate. The order is separated into six families depending upon nuclear cytology, characteristics of vegetative cells, and the modes of formation and germination of resting spores. Most notably, species in the genus *Entomophthora* (Entomophthoraceae), which was once the largest genus in the order, have been separated and moved into other genera.

Members of the Entomophthorales can attack a wide variety of insect hosts, including species from Hemiptera, Diptera, Lepidoptera, Coleoptera, Orthoptera and Hymenoptera. The host range of some fungal species may be limited to a specific host insect or may be broad enough to extend to non-target insects. A fungus tentatively identified as *Entomophthora* was found on a termite (Isoptera) embedded in 25 million-year-old amber. The Entomophthorales are especially important pathogens of aphids, grasshoppers, muscoid flies and lepidopteran larvae, and can function as biocontrol agents against these pests. Interestingly, one species of Entomophthorales, *Entomophaga maimaiga*, was introduced into New England from Japan in 1910–1911 in order to control the gypsy moth (*Lymantria dispar*). At this time, the fungus could not be grown in the lab, so researchers depended upon its overwintering in the field to produce new spores for inoculum. However, the fungus disappeared until 1989, when it was recovered from the field in areas with established gypsy moth populations. It is suggested that either the fungus introduced in 1910 developed into a more aggressive strain that has only recently caused obvious, widespread outbreaks, or that a more aggressive strain has been introduced at some point.

Some Entomophthorales will attack animals other than arthropods and can even infect mammals, including humans. Entomophthoromycosis in humans is caused by species of *Conidiobolus* or *Basidiobolus*, and occurs most often in tropical and subtropical regions. Infections usually are restricted to subcutaneous tissues such as those overlaying the paranasal sinuses, but it also has been reported to disseminate into the deep organs, i.e., lymph nodes, lungs, liver and intestines.

As entomopathogens, the Entomophthorales can infect larvae, pupae or adult hosts. Some species have broad host ranges while others, such as *Massospora*, can infect only one insect species. Insects attacked by some Entomophthorales may not show any symptoms until late in the infection process. Infected grasshoppers and Lepidopteran



Entomophthorales, Figure 39 **Entomophthorales infected *Plutella* larvae. Note the halo of primary conidia that have been actively discharged from conidiophores on the diseased insect. For comparison, see healthy insect above the cadaver surrounded by discharged conidia.**

larvae often display summit disease syndrome, meaning they have a tendency to climb to high positions, where they attach and die. Conidia from such cadavers then can disseminate easily to uninfected insects closer to the ground. The appearance of Entomophthorales-infected cadavers also depends upon whether they have surface conidia or internal resting spores. Insects from which conidia have been forcibly discharged may be surrounded by a halo of these propagules that forms as they settle on the substrate (Fig. 39). Diseased insects that produce the resting spore stage darken and liquefy internally.

References

Andreadis TG, Weseloh RM (1990) Discovery of *Entomophaga maimaiga* in North American gypsy moth, Lymantria dispar. Proc Natl Acad Sci USA 87:2461–2465

Brobyn PJ, Wilding N (1983) Invasive and developmental processes of *Entomophthora muscae* infecting houseflies (*Musca domestica*). Trans Br Mycol Soc 80:1–8

Humber RA (1989) Synopsis of a revised classification for the Entomophthorales (Zygomycotina). Mycotaxon 34:441–460

Latgé J-P, Cole GT, Horisberger M, Prevost M-C (1986) Ultrastructure and chemical composition of the ballistospore wall of *Conidiobolus obscurus*. Exp Mycol 10:99–113

Samson RA, Evans HC, Latgé J-P (1988) Atlas of entomopathogenic fungi. Springer-Verlag, Berlin, Germany

Entomopoxvirus

At present, the family Poxviridae is divided into two subfamilies: the *Chordopoxvirinae*, composed of eight genera of vertebrate viruses, and the *Entomopoxvirinae*, containing three genera, A, B, and C, of insect poxviruses. Comparative analysis among the vertebrate and Entomopoxvirus groups has suggested low levels of genomic homology. To date, over 30 insect poxviruses have been detected in Coleoptera (A), Lepidoptera (B), Orthoptera (B), and Diptera (C), and have been placed in genera A, B, or C on the basis of virus morphology. Members within genus A are characterized by oval-shaped virus particles containing a unilateral concave core region and a single lateral body. Members of genus B, isolated from both lepidopteran and orthopteran hosts, have oval-shaped virus particles with a rectangular core region that lacks a discrete lateral body. Genus C members possess a cuboidal or cushion-shaped virus particle, a dumbbell-shaped core region, and two lateral regions.

Poxviruses are the largest and most complex viruses. Poxviruses encapsidate large (130–375 kbp) linear dsDNA molecules. The typical oval-shaped poxvirus measuring 200–400 nm in length may contain over 100 structural proteins. The biconcave or dumbbell-shaped core region contains tightly compressed nucleoprotein. The function of the lateral bodies is unknown. Surrounding the core and lateral body is a lipid bilayer referred to as the outer membrane. Extracellular poxviruses, released via budding, contain a second lipoprotein envelope. The majority of entomopoxviruses produce occlusion bodies at the late stage of infection. These Type B occlusions, also termed spheroids, are composed of the 115 kDa matrix protein spheroidin and numerous enveloped virus particles. The spheroidin component of the different entomopoxviruses appears to be conserved and all entomopoxviruses are sensitive to alkali treatment. It should be mentioned that the vertebrate poxviruses produce acid-sensitive Type A inclusions composed of individual viral particles encoated by a late viral protein. In addition to spheroids, members within genera A and B of the entomopoxviruses may produce virus-free, spindle-shaped inclusions. The 50 kDa protein fusolin (French fuseau = spindle) is the major component of spindles and represents, when present, one of the most abundant EPV proteins.

The entomopoxviruses, like other poxviruses, replicate in the cytoplasm of host cells. This property mandates that poxviruses encapsidate a complete transcriptional system capable of producing functional viral m-RNAs. Poxviruses contain a DNA-dependent RNA polymerase composed of multiple subunits which transcribes only ssDNA. Several of the subunits have been demonstrated to be homologous to eukaryotic RNA polymerases. A second enzyme is the multifunctional capping and methylation complex. This enzyme transfers guanosine and catalyzes the methylation of the terminal ribose molecules of the viral RNAs. The poly-A-polymerase, comprised of two subunits, adds adenylate residues (poly-A) to the 3′ end of the viral m-RNAs. Several encapsidated enzymes, including the monomeric DNA topoisomerase (333 aa), modify the topology via breaking and rejoining of DNA that allows the relaxation of the + and − strands of the supercoiled DNA. The topoisomerase of the AmEPV possesses structural features similar to the vaccinia virus enzyme. Various nucleotide triphosphate phosphohydrolases (NPH 1, 2), including a DNA-dependent ATPase (NPH1), are present in poxviruses. The NPH1 and NPH-II cleave the NTPs into NDPs and free phosphate. A virally encoded protein kinase functions to phosphorylate several virion-specific proteins. Additional enzymes affiliated with poxvirus particles include endoribonucleases, deoxyribonucleases, and alkaline proteases. The endogenous alkaline protease, associated with the entomopoxvirus viral inclusions (spheroids), is derived from host insects. This host-derived protease, activated by alkaline gut conditions, assists in the degradation of the spheroidin (115 kDa) and the subsequent release of virus particles. Tissue culture-produced spheroids lack such alkaline protease activity.

References

Bawden AL, Glassberg KJ, Diggans J, Shaw R, Farmerie W, Moyer RW (2000) Complete genomic sequence of the *Amsacta moorei* entomopoxvirus: analysis and comparison with other poxviruses. Virology 274:120–139

Mitsuhashi W (2002) Further evidence that spindles of an entomopoxvirus enhance its infectivity in a host insect. J Invertebr Pathol 79:59–61

Moss B (1990) Poxviridae and their replication. In: Fields BN, Knipe DM (eds) Virology, 2nd edn. Raven Press, New York, NY, pp 2079–2111

Entotrophi

An order of hexapods in the class Entognatha, but sometimes considered to be insects. This is an alternate name for the order Diplura. They commonly are called diplurans.

► Diplurans

Enumeration Sampling

Sampling based on the complete counting of all individuals in the sample unit (contrast with binomial sampling).

► Sampling Arthropods

Envelope

A covering of carton or wax around the nest of a social insect, especially a social wasp.

Envenomization

The toxic effects caused by stings, secretions, bites, stinging (urticating) hairs or other effects of poisonous arthropods. The same term is used to describe poisoning by other animals, including vertebrates.

Environmental Sex Determination

A method of sex deternmination in which the environment, such as temperature, has a significant effect on the developmental process leading to one or the other sex.

Environmental Influences on Behavioral Development in Insects

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Information stored in the genome cannot be altered over the course of a lifetime, but only across a multitude of generations. Thus, the genome can give rise to developmental programs that will result in an organism, but it cannot optimize this organism for the conditions it may meet during its particular lifetime. It has long been assumed that if that lifetime is short, such optimization may not be necessary and that such short-lived animals as insects are developmentally inflexible, ensuring genetic survival by fecundity, rather than by investment in the perfection of individuals. As we shall see, this is not the case; like vertebrates, insects steer, rather than aim, development, even of behavior, which will be our special focus here. Developmental plasticity of behavior is especially significant to the organism, indeed to the whole community, since even subtle changes in behavior can have significant effects on an animal's success in obtaining food, escaping predation, or finding a mate. And we are now coming to realize that in insects, even as in vertebrates, behavioral development is the result of a series of "dialogs" between the nervous system and the outside world.

Background

In vertebrates, early experience is known to affect development of brain and behavior; impoverishment of stimulation generally diminishes performance of the adult, while enhanced stimulation can be beneficial. "Normal" early experience is important for normal vision, social interaction, homing, development of song… the list is very long. But what of the invertebrates, especially the small, short-lived ones? Because of the above mentioned assumption of inflexibility, they have received little study; indeed they represent a new and hitherto unexplored world, one holding immense promise for broadening our understanding of the development of behavior.

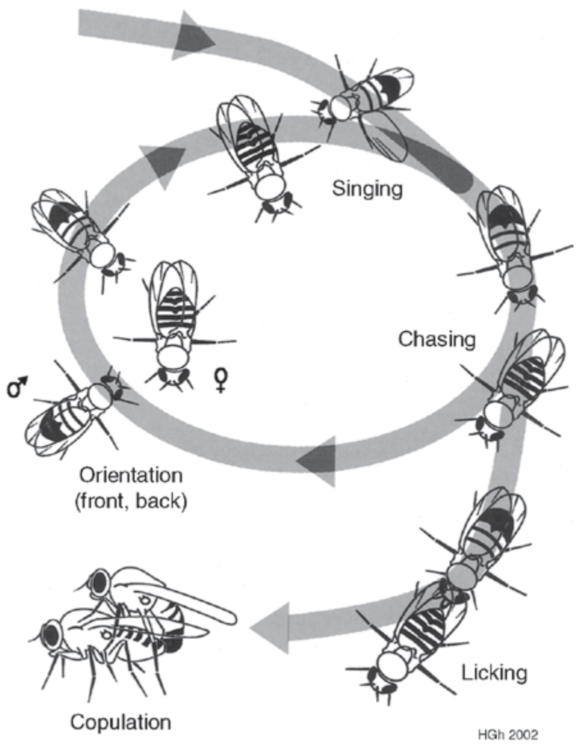
The common laboratory fruit fly, *Drosophila melanogaster*, is a wonderful starting point for such a journey of discovery and will allow us to explore the importance of environmental factors – sensory, social and chemical – in guiding development. *Drosophila* has many advantages as a model system for an analysis of developmental plasticity. First it has a rich and varied repertoire of behaviors that are both reproducible and quantifiable. Second, its short generation time (~10 days at 25°C), the ease with which it can be cultured and the large numbers of individuals that can be maintained under the same environmental conditions at different stages of the life cycle, help pinpoint the nature of the inputs needed for optimum development and the timeframes within which they are effective (the so-called sensitive or critical periods). Third, there are numerous *Drosophila* nervous system mutants, many affecting vision and learning, which are useful tools in determining the mechanisms of experience-dependent development. Fourth, the *Drosophila* nervous system consists of a relatively small number (perhaps a few hundred thousand) of neurons many of which are identifiable and can be compared across individuals raised in different environments. Finally, we "higher animals" share many genes with *Drosophila* – for example genes critical to visual development in *Drosophila* have similar function in mice, zebra fish, frogs, turtles, quail, rats, squid, and even nematodes, so that it is not unlikely that genes involved in developmental plasticity in *Drosophila* are conserved. For these reasons, we propose that *Drosophila* can make yet another contribution to biology by serving as a model of experience-dependent plasticity of brain and behavior.

In *Drosophila*, courtship seems particularly appropriate for the study of developmental plasticity. It has obvious significance in the organism's life history, it is easily studied in the laboratory and, because of its complexity, there is a good chance that even relatively subtle environmental variations may alter its expression. And, of course, what we are studying in the laboratory are manifestations of a neural plasticity that has long been selected for because it is advantageous in the flies' natural habitat.

Courtship matures gradually during the first few days of the adult stage; flies do not become fully competent to court or to be receptive to copulation until several days after they eclose from their pupal cases. This makes it possible that experience before and during the appearance of these behaviors could play a role in their development, much as it does for singing and mate choice in birds. Let us now look at the actual behaviors involved in *Drosophila* courtship.

Courtship Behavior in *Drosophila*

Courtship of *Drosophila* can easily be studied under a dissecting microscope by placing two or more flies into a small (0.2 cm^3) chamber. Shortly after being placed into the chamber, the male approaches the female, chases her, maintains his focus on her if she moves about, and orients his body so that he is facing her abdomen. He taps her abdomen with one of his foretarsi and (Fig. 40) vibrates the wing closest to her to produce a courtship song. After a few minutes, he may lick the female's genitalia, attempt to copulate, or suddenly move in a semicircle to wind up in front of her, "eye-to-eye." If his courtship stimulates her to become receptive, she slows down and eventually permits copulation by opening her vaginal plates.



Environmental Influences on Behavioral Development in Insects, Figure 40 **Diagrammatic representation of some common male courtship behaviors in *Drosophila melanogaster*. Early stages are characterized by chasing, orientation-back, and singing by the male; if the female becomes more receptive and slows down, the male will engage in orientation-front, licking, and making repeated copulation attempts until the female finally opens her vaginal plates, permitting him to mate.**

We can view these behaviors, which involve visual, auditory, chemical and tactile stimulation, as an exchange of sensory information. Males use visual, and to a lesser extent chemical, information to identify and to orient to the female; the absence of this information (as in a male with mutation-induced sensory losses) reduces the likelihood of copulation. Female receptivity is also influenced by such visual cues as the reflection from, and shape of, the male's eyes. Obviously, in a complex environment many agents may modify the development of courtship behaviors. We will look at three: effects on a newly emerged male of the presence of adult males, effects of the presence or absence of early visual stimulation on courtship effectiveness, and effects of low levels of the neurotoxin lead on courtship behavior.

Effects of Homosexual Courtship During the First Hours of Adult Life on the Male

Drosophila melanogaster males do not court only virgin females, they also court newly eclosed males (The young males do gradually lose their "sex appeal" and by the time they are sexually mature are no longer attractive to other males.) One obvious question is why this behavior exists; this "homosexual" courtship expends time and energy and renders the courting male more vulnerable to predation, so it must have some positive evolutionary significance. With such experience, immature males grow up to mate more quickly than do males without homosexual courtship experience. The courtship song, produced by vibration of the courting male' s wing, is one of the stimuli that affect the immature male, which suggests that early exposure to the visual and/or auditory stimuli associated with courtship song is important for development of effective courtship in males.

The observation that adult male flies that experience homosexual courtship during early adult life perform better when courting females has striking similarities to what others have observed studying the development of bird song. In both cases, the immature male receives the stimulation during early life (Fig. 41), before he expresses the behaviors that are influenced by the exposure. In birds, this has been explained by postulating that the young male lays down an auditory template and later compares his own output to that template, modifying the output until there is an adequate match. We suggest that male *Drosophila* may be engaged in a similar process. During the episodes of homosexual courtship, they may be storing something analogous to a neural template

Environmental Influences on Behavioral Development in Insects, Figure 41 **Latency to begin copulation with a female of males raised in the absence of older males, with older males that courted them but could not sing, with older males that courted them and could sing. Note that males copulate faster when they have been reared with older males that can sing while they court; other stimuli must also be important because being courted without singing is better than nothing (Data summarized in Hirsch and Tompkins, 1994).**

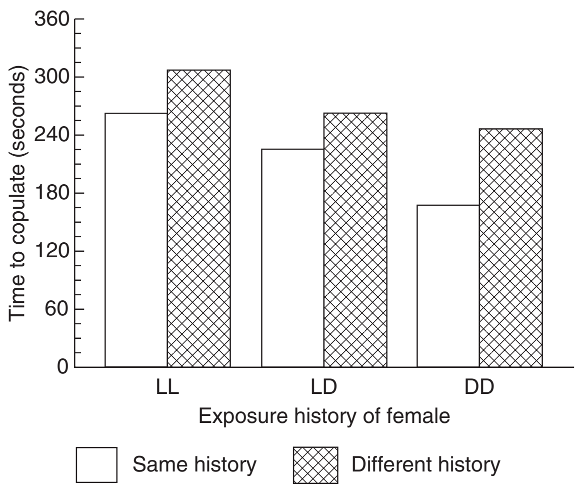
of courtship; when they mature, this template in some way facilitates their own behavior. This remains an open question, as the relevant experiments remain to be done.

Effects of Visual Experience During the First Days of Adult Life

Vision is important during courtship, and to determine whether early visual experience is important for the normal development of courtship behavior, during the first four days of adult life we kept flies either in total darkness (dark-rearing - DD), in constant illumination (light-rearing - LL), or as a control in normal cycling illumination (12 h light/12 h dark-LD). We subsequently scored (Fig. 42) them for copulation latency, i.e., the time taken from the initiation of courtship to copulation. Surprisingly, what affects this most is the similarity in the experience of both members of the pair. Pairs in which the male and the female received the same visual exposure (both LD, both LL, or both DD) mate more quickly than do those whose early experience differed, i.e., "culturally" similar flies mated more readily. Furthermore, these studies revealed the presence of a critical period during which alterations in normal exposure are particularly effective in causing behavioral changes.

Ecological Implications of Mate Choice

The influence of genotype on mate choice is well-documented, while that of early experience is less well understood, except for a few studies on effects of early social interactions on mate preferences of avian and mammalian females. From the studies discussed above, we conclude that otherwise normal *Drosophila* raised in any of our three light regimes (LL, LD, DD) prefer to mate with partners with similar experience. Since females typically copulate on their food source, and then lay eggs in it, their newly eclosed offspring will find themselves in the same environment in which their parents chose mates. Given that flies growing up in this environment are apparently well adapted to it, then perhaps preference for mates with similar backgrounds, including environmental exposure histories, will enhance the fitness of their offspring, assuming the environment has not changed drastically. Thus, what we have learned about developmental plasticity of mate choice may help us to better understand the mechanisms regulating fitness in this species.



Environmental Influences on Behavioral Development in Insects, Figure 42 **Latency to begin copulation with a male of females raised in constant light (LL), in normal cycling illumination (LD), and in total darkness (DD). Note that the less light exposure, the faster females tend to copulate, and that independent of exposure history females copulate faster with males sharing their "culture." (Redrawn from Hirsch et al., 2001.)**

Developmental Effects of Exposure to Low Levels of Lead

As a result of human activity, lead has become ubiquitous in the biosphere. At higher concentrations it can be very toxic, but even at very low concentrations chronic exposure during early life can have significant effects, including cognitive effects, in humans and in other mammals. Given that developmental plasticity is not exclusive to vertebrate animals, does developmental exposure to lead affect complex behaviors of *Drosophila*, in particular courtship?

We choose courtship because it may provide an assay of cognitive function for *Drosophila*, in effect a fly equivalent of an IQ test. Courtship requires that male and female assess one another and reach a decision about whether to mate. Since consequences of this decision can have important consequences for both participants, and especially for the female who does not mate very often in her lifetime, factors influencing the decision-making process can affect fitness of the male and the female.

The effects of lead exposure during development of *Drosophila* may be tested by exposing flies from egg stages until well into adulthood to a lead-contaminated food source. One then assays courtship by seeing how many flies will mate in a given time interval. The results are both striking and significant: the number of pairs mating after exposure to low concentrations of lead is greater than in controls, while after exposure to higher concentrations of lead it is lower. One possible explanation for the increase in mating speed after exposure to low concentrations of lead is that it reduces the female's selectivity in choosing a mate; she may mate more indiscriminately than do control females. Exposure to higher lead concentrations, on the other hand, may debilitate both sexes sufficiently that courtship is slowed down. Lead also has a non-linear (in this case biphasic) effect on fecundity of *Drosophila*, increasing it at low concentrations, and having no clear effect at higher concentrations.

The details of insect response to such toxicants as lead are as yet barely studied, but it is clear that insects such as *Drosophila* are indeed good model systems for the studies that need to be done.

Conclusions

We began by noting that developmental programs that are limited to information in the genome are limited in their ability to optimize the organism for the conditions prevailing during its particular lifetime. We argue that a first step in optimizing development is by providing it with sensitivity to environmental experience. Learning and sensory adaptation enable the process of optimization to continue throughout the organism's lifetime. In effect, these processes match the nervous system to those features of its environment which cannot be predicted far enough in advance to be incorporated into the genetic information base. Genetic information, which reflects adaptation to past conditions, is combined and integrated with epigenetic information, which is more immediately predictive of future conditions.

There are clear precedents for such interpretation of developmental processes. For example, it is known that in the cat, initial development of nerve cells responding to the orientation of a visual image is under genetic control, but completion of development requires visual experience, which fine-tunes the system to respond best to those orientations it saw during the first months of life. In effect, these cells become an internal model of the animal's early visual world. Because it was generated during a critical period after which it cannot be changed, this model has a life-long influence on the animal's behavior. In the fly, initial development of the photoreceptors and of their connections with a target structure, the lamina, is likely to be under control of intrinsic developmental programs, whereas experience modifies both the synapses from the photoreceptors onto special lamina cells, the monopolar cells, and the feedback synapses going back to the photoreceptors themselves. Thus, there is a flexible link between the sensor and the nervous system, a link that can be optimized on the basis of information about the prevailing environment. Consistent with this idea, some behavioral sensitivities are enhanced under test conditions that mimic those present during the animal's early life. Flies deprived of light exposure are more sensitive to light than controls, and the operating range of their visual systems is shifted to allow a better response at lower light levels. These effects are apparently long-term, being present three weeks later. The findings for both cat and fly support the hypothesis that during early stages of adult life the response properties of the visual system are adjusted to function optimally under the conditions prevailing in the animal's visual world; other sensory systems undoubtedly show similar tunability.

The last forty years, which have seen great changes in our understanding of how experience might affect the developing nervous system, have also witnessed the discovery of many model systems for the study of such development. These first included the retinogeniculocortical pathway in the cat, and to a lesser degree in the monkey. In the early 1980s it became clear that lower vertebrates, such as fish and frogs, also constituted good model systems for studying experience-dependent development, and now it is clear that invertebrates can also serve this role. Experience-dependent behavioral plasticity, once assumed to be a curiosity playing at most a minor role in the development of insect brain and behavior, is known to exist in many regions of the adult brain in *Drosophila* and in other invertebrates. Indeed, it seems to be the rule rather than the exception that in all animals experience is needed to complete development of adult brain structures. A corollary of this view is that the ability to undergo experience-dependent development is itself heritable, and that it should be possible to select strains of flies or other invertebrates that are more or less modifiable by early experience, thereby generating additional models for studying developmental plasticity.

One major task will now be to unravel the molecular mechanisms underlying the developmental adjustments in model systems such as *Drosophila*, and thereby to learn more about the often less accessible mechanisms underlying plastic processes in vertebrate brains. On a molecular level, there are likely to be several systems responsible for structural plasticity (for example, in *Drosophila* the cyclic AMP cascade seems to be involved in the central brain, but not in the optic lobes). There is a rich future for research in unraveling the genes involved in the plasticity of the visual system, and *Drosophila* is likely to continue to be a central figure in attempts to identify and characterize these genes. Among the many powerful techniques available with *Drosophila* is the capability of selectively expressing any cloned gene in specific regions of the fly, thus providing very fine "molecular scalpels." The usefulness of these lessons from the world of insects will underscore the basic unity of the mechanisms that appear to govern the link between brain and behavior in all organisms.

A very important lesson that we can learn as we come to understand more about brains and about what is needed to ensure their development, is that "higher" and "lower" animals have much more in common than had been thought possible 20 years ago. This commonality in our origins, and especially the realization that we are all affected by our environment during development, and that we update the information in the genome and enhance our ability to make accurate predictions about the world we live in, means that we have much to learn not only from our closest relatives, but from those who appear on the surface much more distant, and even alien. We hope it means also that our respect for these life forms – so like us in their vulnerability during development – will be enhanced, for in protecting and conserving them we are protecting and conserving ourselves.

References

Greenspan RJ, Ferveur J-F (2000) Courtship in *Drosophila*. Annu Rev Genet 34:205–232

Hirsch HVB, Tompkins L (1994) The flexible fly: experience-dependent development of complex behaviors in *Drosophila melanogaster*. J Exp Biol 195:1–18

Hirsch HVB, Tieman SB, Barth M, Ghiradella H (2001) Tunable seers: activity-dependent development of vision in fly and cat. In: Blass E (ed) Developmental psychobiology, handbook of behavioral neurobiology, vol 13. Kluwer Academic/Plenum Publishers, New York, NY, pp 81–142

Waddell S, Quinn WG (2001) Flies, genes, and learning. Annu Rev Neurosci 24:1283–1309

Enzootic Disease

A disease (usually in low prevalence) which is constantly present in a population.

Enzyme

A protein catalyst that is not itself used up in a reaction. Enzymes are produced by living cells to catalyze specific biochemical reactions. Enzymes may also contain nonprotein components called coenzymes that are essential for catalytic activity.

Eomeropidae

A family of insects in the order Mecoptera.

► Scorpionflies

Eosentomidae

A family of proturans (order Protura).

► Proturans

Epermeniidae

A family of moths (order Lepidoptera). They commonly are known as fringe-tufted moths.

► Fringe-Tufted Moths
► Butterflies and Moths

Ephemerellidae

A family of mayflies (order Ephemeroptera).

► Mayflies

Ephemeridae

A family of mayflies (order Ephemeroptera).

► Mayflies

Ephemeroptera

An order of insects. They commonly are known as mayflies.

► Mayflies

Ephemerythidae

A family of mayflies (order Ephemeroptera).

► Mayflies

Ephydridae

A family of flies (order Diptera). They commonly are known as shore flies.

► Flies

Epicopeiidae

A family of moths (order Lepidoptera) also known as Oriental swallowtail moths.

► Oriental Swallowtail Moths

► Butterflies and Moths

Epicranial Suture

A Y-shaped suture on the upper surface of the head. The arms of the "Y" diverge toward the front of the head.

► Head of Hexapods

Epicranium

The upper portion of the head.

► Head of Hexapods

Epicuticle

The thin, outermost layer of cuticle. It is rich in lipid and protein but lacking in chitin. It consists of a shellac-like cement layer externally (Fig. 43, Fig 44) as well as a proteinaceous layer imbedded with lipids called the cuticulin layer.

► Cuticle

► Integument: Structure and Function

Epicuticular Filaments

Lipoprotein running from the epidermal cells through the pore canals and fusing with the inner edge of the cuticulin. The filaments (and the pore canal) can serve as a conduit for transport of materials such as wax from the epidermal cells to the procuticle and epicuticle.

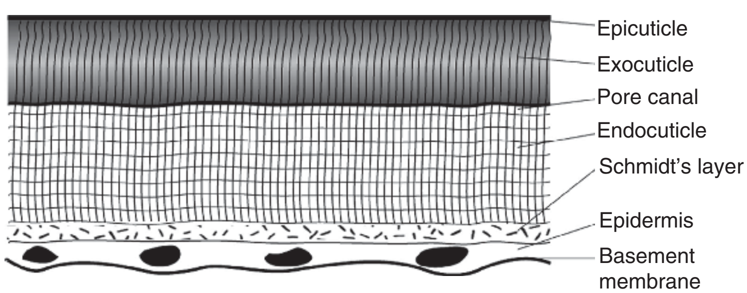
Epidemic

A period of unusually great abundance, especially of pests such as microbial disease agents.

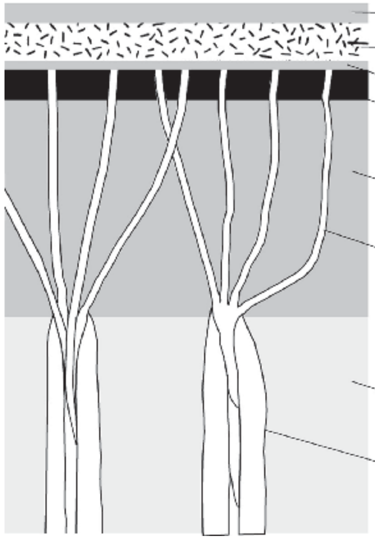
Epidemic Hemorrhagic Fever

A form of hemorrhagic fever endemic to northeastern Asia that is caused by a Hantavirus arbovirus transmitted by mites. It is characterized in its early stages by fever, sweating, thirst, abdominal pain, nausea, and vomiting, and in its later stages by hemorrhage, shock, and kidney failure. It is also called "Korean hemorrhagic fever."

► Mites



Epicuticle, Figure 43 Cross section of the insect cuticle and epidermis (adapted from Chapman, The insects: structure and function).



Epicuticle, Figure 44 Cross section of the insect epicuticle (adapted from Chapman, The insects: structure and function).

Epidemic Relapsing Fever

This disease is caused by a spirochete (*Borrelia recurrentis*) and is transmitted by human body lice. Once common in eastern Europe and Russia, it now occurs mostly in eastern Africa, China, and South America. An endemic form is caused by several forms of spirochete and is transmitted by *Ornithodorus* ticks. Symptoms include chills, fever, headache, muscle pain, nausea, vomiting, and weight loss.

► Chewing and Sucking Lice

Epidemic Typhus

A rickettsial disease (*Rickettsia prowazekii*) transmitted to humans by the human body louse. It occurs most frequently in cooler climates, where heavy clothing is commonly worn. It becomes epidemic during periods of strife, when warfare results in crowding and poor sanitation. It also can develop in prisons and on ships due to lack of sanitation and crowding, where it is known as "prison fever" and "ship fever." The disease is transmitted through the feces of the lice when humans scratch and rub the louse or louse feces into a wound. The lice are not affected by the *Rickettsia*. A variant of this is transmitted from flying squirrels to humans when squirrels take up residence in cabins or houses. Symptoms of epidemic typhus include chills, fever, headache, rash, stupor, and delirium.

► Chewing and Sucking Lice

Epidemiology

In entomology, the study of diseases affecting insects, especially the factors affecting outbreak and spread of the disease, or of diseases spread by insects to animals (humans, wildlife, livestock) or plants.

Epidermis

The layer of living cells (epidermal cells) of the integument, situated beneath the cuticle (Fig. 43), that secretes the cuticle at each molt. In addition, the epidermal cells secrete lipids (waxes), cement, and additional cuticular components.

► Cuticle
► Integument: Structure and Function

Epigaeic

Living, or at least foraging, primarily above-ground (contrast with hypogaeic).

Epigynum

In spiders, the external female genitalia.

Epimeron

The posterior portion of a thoracic pleuron. It is usually small, narrow, or triangular.

Epimorphosis

A type of development wherein the insect ecloses from the egg with a full complement of body segments (the opposite of anamorphosis).

Epipharynx

A mouthpart structure attached to the inner surface of the labrum or clypeus.

Epiphysis

A pad occurring on the inner aspect of the front tibiae in some Lepidoptera.

Epiplemidae

A family of moths (order Lepidoptera). They commonly are known as crenulate moths.

► Crenulate Moths
► Butterflies and Moths

Epipleura (pl. epipleurae)

The lateral margins of the eytra, which are bent downward.

Epiproct

The dorsal portion of the eleventh abdominal segment in insects. This is also known as the supraanal plate and the pygidium. This tergite often covers the anus.

Epipsocidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice or Psocids

Epipyropidae

A family of moths (order Lepidoptera). They commonly are known as planthopper parasite moths.

► Planthopper Parasite Moths
► Butterflies and Moths

Episternum (pl. episterna)

The anterior-most sclerite of the thoracic pleuron.

► Thorax of Hexapods

Epistoma

The portion of the lower face between the eyes and the mouth.

Epizootic

An outbreak or widespread occurrence of disease in which there is an unusually large number of cases. A disease, or a phase of a disease, with high morbidity, and one that is only irregularly present in recognizable form.

Epizootic Bovine Abortion

A bacterial disease transmitted by ticks to cattle in the western USA.

► Ticks

Epizootiology

The field concerned with the study of diseases of animals and their pattern of occurrence.

Equilibrium Position (EP)

An expression used to describe the average density of pests relative to the economic injury level and economic threshold. Some insects have a low equilibrium position and rarely cause damage, whereas others have a high equilibrium position and regularly inflict injury if they are not managed. The concept of EP is most useful when considering insects that do not vary greatly in density or damage, but some insects display highly variable densities, and the equilibrium position is not very descriptive of their population tendencies.

Eradication

Elimination of an organism after it has become established.

Ergatogyne

Among social insects, a form that is intermediate between the worker and queen.

Eremiaphilidae

A family of praying mantids (Mantodea).
► Praying Mantids

Ergatoid Reproductive

Among termites, a supplementary reproductive that is larval in form, without any trace of wing buds, and with a distinctly rounded head.

Ergot of Cereals

A fungal disease of grains that can be transmitted by insects.
► Transmission of Plant Diseases by Insects

Erichson, Wilhelm Ferdinand

Wilhelm Erichson was born on November 26, 1809, in Stralsund, Germany, the son of a senator. After education at the Gymnasium ["high school"] of Stralsund, he entered the Universität zu Berlin in October 1928, obtaining by December 1832 a degree "Doktor der Medizin und Chirurgie" ["Doctor of Medicine and Surgery"]. By April 1834 he was licensed as a medical practitioner. During his university years, he was heavily involved in entomological studies, publishing (with J.F. Brant) in 1831 "Monographia generis Meloes" and then in 1832 "Genera Dyticeorum." In 1837 he obtained a degree "Doktor der Philosophie" from Universität Jena. In 1838, he was awarded the degree of "Privatdocent" [a degree permitting him to lecture at a university] from the philosophical faculty of the Universität zu Berlin, and in 1842 was appointed adjunct professor. The scholastic requirements at German and other European universities were much more rigorous at that time than in the USA. Then, leaving medicine behind, his lectures concentrated on entomology and helminthology. He has been acclaimed by Herman (2001) as a genius, the equivalent of a Mozart in music and, like Mozart, dying young, perhaps the most important entomologist of all time. Although he died before he was 40, his works were prodigious and profoundly important. He worked on Arachnida and Myriapoda as well as on the insect orders Coleoptera, Hymenoptera, Neuroptera, Hemiptera, Strepsiptera, Thysanoptera, Thysanura, and Siphonaptera. He published about 45 books and other papers. Two of them were "Die Käfer der Mark Brandenburg" (740 pages) and "Genera et species Staphylinorum" (954 pages) in which he proposed for the first time a classification that in general still stands of the huge family Staphylinidae. He died in Berlin on November 18, 1849.

Reference

Herman LH (2001) Erichson, Wilhelm Ferdinand. Bull Am Mus Nat Hist 265:60–61

Eriococcidae

A family of insects in the superfamily Coccoidae (order Hemiptera).
► Bugs

Eriocottidae

A family of moths (order Lepidoptera). They also are known as Old World spiny-winged moths.
► Old World Spiny-Winged Moths
► Butterflies and Moths

Eriocraniidae

A family of moths (order Lepidoptera). They commonly are known as sparkling archaic sun moths.
► Sparkling Archaic Sun Moths
► Butterflies and Moths

Eri Silkworm, *philosamia ricini* (Lepidoptera: Saturniidae)

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Kasetsart University, Nakhon Pathom, Thailand

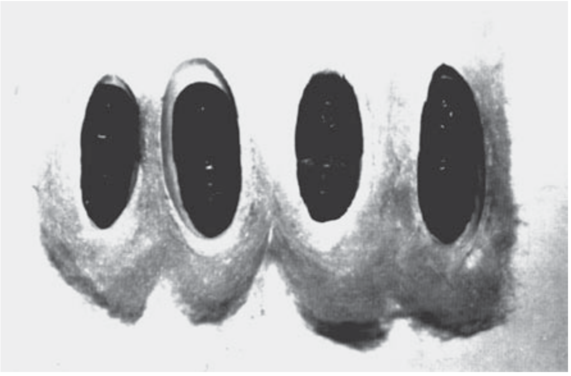
Silk is a smooth, shining, fabulous and unique natural fiber produced by several species of silkworm. Silk fiber generally is produced by the mulberry silkworm, *Bombyx mori*, which was domesticated nearly 2,000 years ago in China. Silkworm rearing and silk weaving, called sericulture, is an environmentally sustainable agro-industrial activity practiced in four major regions globally, with the highest production in Asia and the Pacific. Sericulture provides substantial contributions to a number of national economies while preserving the centuries-old history and tradition of many countries. It is beneficial to the rural population in climatically suitable agricultural sectors because it provides either a primary or secondary source of income for many workers, regardless of age and gender.

In addition to the renowned mulberry silkworm, Bombyx mori, there are at least eight species of wild silkworms that provide silk of high economic and commercial values. They are: *Antheraea pernyi*, *A. yamamai*, *A. proylei*, *A. assamensis*, *A. mylitta*, *A. proylei*, *Philosamia ricini* and *P. cynthia*. The eri silkworm, *P. ricini*, is the only completely domesticated silkworm that is not dependent on mulberry for food. This polyphagous insect feeds on several varieties of food plants in the family Euphorbiaeae, including castor (*Ricinus communis*), kesseru (*Heteropanax fragrans*), payam (*Evodia flaxinifolia*) and tapioca (*Manihot utilissima*). Castor is, by far, the best food plant to promote cocoons that are large in size and rich in silk content.

Eri silkworm has four stages: the egg, larva, pupa (encased in the cocoon), and the adult or moth. The moth lays white eggs which turn grey and then black just before hatching. Eggs hatch in seven days in hot weather, but may take as long as 24 days in cold weather. Female moths lay eggs in clusters that may contain as many as 100 or more eggs. The number of eggs per moth varies, however, the average for a well-fed, healthy moth is about 300.

Eri silkworm molts four times during its larval stage. When molting, the larvae stop eating and become motionless. This state may last for 24–48 h. Toward the end of this state, the larvae begin to cast their skins off by continued undulatory movements and wriggling. During the first to third larval stage, the head is black and shiny but eventually will turn greenish-yellow or yellow with a blackish patch on each cheek when they reach the fourth and fifth stages. On each thoracic and abdominal segment, there are four to six conspicuous tubercular spines mounted with a varying number of hairs and arranged in longitudinal rows. In the fifth stage, the larvae eat enormously and grow very quickly to reach their maximum stage of development. The well-fed (Fig. 45), full-grown

Eri Silkworm, *philosamia ricini* (Lepidoptera: Saturniidae), Figure 45 Larvae of eri silkworm, *Philosamia ricini* feed on cassava leaves.

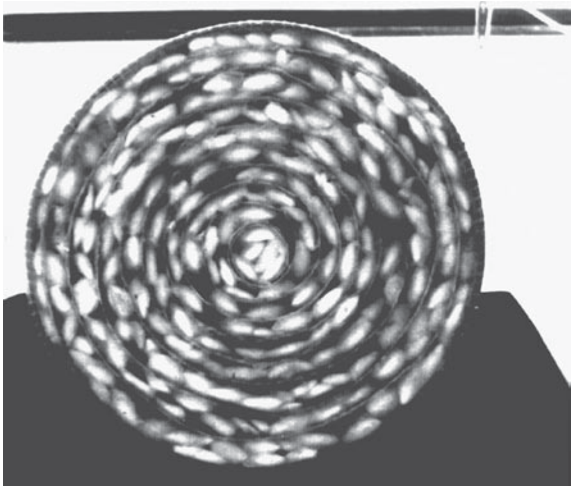


Eri Silkworm, *philosamia ricini* (Lepidoptera: Saturniidae), Figure 46 Cocoons of eri silkworm cut to show the pupae inside.

larvae are cylindrical and about 95–100 mm long. The general body color is white which turns yellow before spinning.

When the larvae get ready for spinning, they cease feeding and empty their digestive tract. The larvae then become active and roam about in search of a suitable place, and settle down to form cocoons. The cocoon is formed by exuding secretion from the silk gland through the spinneret which forms a fine filament of thread when it comes in contact with the air. The larvae finish spinning in about three days and rest inside the cocoon before turning into pupae (Fig. 46 and 47). The thread of the cocoon consists of a core of fibroin and a covering of sericin or gum. The eri cocoon is tapered at one end and is slightly flat and round at the other. It can not be reeled because the cocoon is not formed of a long continuous thread as in mulberry silk, but instead is spun by the larvae in layers. It is also an open cocoon in which the moth can push its way through one end without softening or cutting the fibers. Since eri cocoons are unreelable, they can only be spun by hand. They form a good and highly desirable raw material for millspun silk which is in high demand all over the world.

Moth emergence from the cocoon takes place after about two weeks from the cocoon formation. Male moths emerge earlier than female moths. The eri moth is a big moth with a wingspread of



Eri Silkworm, *philosamia ricini* (Lepidoptera: Saturniidae), Figure 47 Container provided to eri silkworm for cocoon formation.

100–125 mm. The wings are blackish-brown, crossed in the middle with a white band. In the middle of each wing is a crescent-shaped yellow and white spot bordered with a black line. The abdomen of the male is narrower than that of the female. After emergence, the males are more active. They flutter their wings rapidly and rest for an hour or two in a vertical position until their wings are dry. The male moths then start fluttering their wings again in search of female moths to mate with. Mating (Fig. 48) occurs a few hours after moth emergence and female moths lay eggs during the night. The oviposition

Eri Silkworm, *philosamia ricini* (Lepidoptera: Saturniidae), Figure 48 **Male and female eri silkworm shown mating. The female lays eggs on the wood stick.**

can go on for two or three nights. The moths do not fly away and do not eat.

The complete life cycle of the eri silkworm lasts about 44 days in the summer and 85 days in the winter. It is a multivoltine species which can be reared four to five generations all year round where the climatic conditions are favorable.

Eri silkworm cultivation has several profitable advantages. Since the worms feed on castor and tapioca or cassava leaves, eri silkworm cultivation can be practiced as a subsidiary cottage industry by the castor and cassava growers. With its excellent blending properties with both cotton and synthetics, the fabrics made from eri silk yarn are very soft and silky, far more durable than mulberry silk and far more resistant to perspiration and dust. Eri silk is also readily dyed with a large range of colors. All these unique characteristics make the cloths suited not only for dresses but also for shawls, cloaks, rugs, etc. In addition to finished fabrics, eri silk can also become the source of other essential products such as medicines and cosmetics.

Eri silkworms play a significant role in the research on the biological control of noxious insects. Eri egg and larva can be used to mass produce some parasitic and predatory insects. The predatory bug, *Eocanthecona furcellata*, which preys on several species of noxious lepidopteran insects, can be raised in laboratories using eri larvae as food. Furthermore, due to their high protein content, eri larva and pupa are eaten by people, especially those in the Asian countries. They also can be developed as animal feeds or food supplements for poultry, swine and fish which help to reduce production costs in these farms. The eri silkworm, therefore, can create several operations of high income potential. Many countries, therefore, are highly interested in the national industrialization of eri silkworm culture.

References

Maxwell-Lefroy H, Ghosh CC(1912) Eri silk. Memoirs of the Department of Agriculture in India, Entomological Series 4, vol 1, 130 pp

Sarkar DC (1988) Eri culture in India. Central Silk Board. Grafo Printers, Bangalore, India, 51 pp

Sengupta K (1985) Non-mulberry sericulture – its problems and prospects. Sericologia 25:89–94

Ermine Moths (Lepidoptera: Yponomeutidae)

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Ermine moths, family Yponomeutidae, total 395 species worldwide; actual fauna likely exceeds 500 species. Three subfamilies are recognized: Saridoscelinae, Yponomeutinae, and Cedestinae. The family is part of the superfamily Yponomeutoidea in the section Tineina, subsection Tineina, of the division Ditrysia. Adults small to medium size (8 to 31 mm wingspan), with head mostly smooth-scaled; haustellum naked; labial palpi upcurved; maxillary palpi 1 to 2-segmented (rarely reduced). Wings elongated, sometimes with long hindwing fringes (Fig. 49) in species with more lanceolate hindwings. Maculation is often white or gray with many small dark spots, or more monotone shades of brown or gray. Adults are mostly nocturnal. Larvae are leaf

Ermine Moths (Lepidoptera: Yponomeutidae), Figure 49 **Example of ermine moths (Yponomeutidae), *Yponomeuta cagnagella* (Hübner) from Italy.**

skeletonizers and leaf webbers, but some are leafminers or needleminers. Hosts include many different plant families. A few species are economic, particularly in the genus *Yponomeuta* (often misspelled as *Hyponomeuta* in older literature).

References

Clarke JFG (1965) Hyponomeutidae [sic]. In: Clarke JFG, Catalogue of the type specimens of Microlepidoptera in the British Museum (Natural History) described by Edward Meyrick, vol 5, 257–413 [part]. British Museum (Natural History), London

Gershenson ZS, Ulenberg SA (1998) The Yponomeutinae (Lepidoptera) of the world exclusive of the Americas. Nederl. Academie Wetensch, Amsterdam, 202 pp, 3 pl

Huemer P, Tarmann G (1991) Westpaläarktische Gespinstmotten der Gattung Kessleria Nowicki: Taxonomie, Ökologie, Verbreitung (Lepidoptera, Yponomeutidae). Mitteilungen der Münchner Entomologische Gesellschaft 81:5–110

Martouret D (1966) Sous-Famille des Hyponomeutinae [sic]. In: Balachowsky AS (ed) Entomologique Appliquee a l' Agriculture, vol 2. Masson, Paris, pp 102–199

*Moriuti S (1977) Yponomeutidae s. lat (Insecta: Lepidoptera). In: Fauna Japonica. Keigaku, Tokyo, 327 pp, 95 pl

Erotylidae

A family of beetles (order Coleoptera). They commonly are known as pleasing fungus beetles.

► Beetles

Eruciform Larva

A larval body form with a cylindrical body, well developed head, and usually with thoracic legs and abdominal prolegs. Often they are sluggish, and found in the soil or living in burrows within fruit, seeds or wood. Caterpillars and white grubs are typical of eruciform larvae.

Esaki, Teiso

Teiso Esaki was born in Tokyo on July 15, 1899. His father was a government forestry official. Teiso grew up at first in Tokyo and then in Osaka. He published his first entomological note at the age of ten, in the journal Gifu ("Insect World"), which may be a record for young entomologists. He continued studying insects, especially Hemiptera, and publishing on them, while he was in middle school in Osaka. In 1920 he entered the Imperial University of Tokyo, and studied zoology. In 1923 he was appointed associate professor in Kyushu Imperial University, and in 1924–1927 was sent to Europe (especially Budapest and London) to study in the main museums and institutions. Then with his new, German, wife Charlotte, he returned to Japan via the USA. Eventually they had four children. He was elected to the council of the entomological society of Japan, and in 1951 was its president. In 1928, he was appointed chairman of entomology in Kyushu Imperial University, and in 1930 professor of entomology. He was appointed Japanese representative and commissioner to the International Commission of Zoological Nomenclature. He was interested in many aspects of natural history, and especially in zoogeography, zoological nomenclature, the history of biology, Hemiptera, Lepidoptera, and fossil insects, but his specialty was in aquatic Hemiptera, on which he became a world authority. He published about 130 important papers on Hemiptera. He died in Fukuoka, Japan, on December 14, 1957.

Reference

China WE (1958) Obituary. Entomologist's Monthly Magazine 94:132

Esophagus

A portion of the foregut behind the pharynx and leading to the crop.

Essential Amino Acids

The amino acids that insects must have in their diet (i.e., they cannot synthesize these). They are the same as those required by rats: arginine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan, and valine. However, some insects benefit from inclusion of so-called nonessential amino acids, which are actually essential for some species.

Essential Oils

These are terpenes distilled or pressed from plants. They are hydrophobic, and generally aromatic. Many repel insects, and some are insecticidal. In their unrefined state, they often are the basis for folk remedies for repelling insects. Examples include peppermint oil, white cedar oil, red thyme oil, bourbon geranium oil, and linalool.

Estimation

A sampling plan that numerically estimates population density or intensity. Commonly used for detailed population dynamic and experimental studies (contrast with classification) The term can also denote the process of calculating various statistical parameters such as variance.

► Sampling Arthropods

Estuarine Community

A group of organisms inhabiting an estuary (edge/inlet of the sea or juncture of a river and an ocean), as opposed to the open sea (called pelagic).

Ethiopian Realm

The zoogeographic region of Africa, though this does not include northernmost Africa, which is more similar to Europe (and considered to be part of the Palearctic realm). The Ethiopian realm is characterized by having antelopes, giraffes, elephants, rhinoceros, gorillas, dogs, and cats.

► Zoogeographic Realms

Etiology

The study of the causes of disease.

Eucharitidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Eucinetidae

A family of beetles (order Coleoptera). They commonly are known as plate-thigh beetles.

► Beetles

Eucnemidae

A family of beetles (order Coleoptera). They commonly are known as false click beetles.

► Beetles

Eucoilidae

A family of wasps (order Hymenoptera).
► Wasps, Ants, Bees and Sawflies

Eukaryote

An organism with cells containing a membrane-bound nucleus that reproduces by meiosis. Cells divide by mitosis.

Eulichadid Beetles

Members of the family Eulichadidae (order Coleoptera).
► Beetles

Eulichadidae

A family of beetles (order Coleoptera). They commonly are known as eulichadid beetles.
► Beetles

Eulophidae

A family of wasps (order Hymenoptera).
► Wasps, Ants, Bees and Sawflies

Eumastacidae

A family of grasshoppers (order Orthoptera). They commonly are known as monkey grasshoppers.
► Grasshoppers, Katydids and Crickets

Eupelmidae

A family of wasps (order Hymenoptera).
► Wasps, Ants, Bees and Sawflies

Euplantulae

Small pad-like structures beneath the tarsal segments.

Eupterotidae

A family of moths (order Lepidoptera) also known as giant lappet moths.
► Giant Lappet Moths
► Butterflies and Moths

Eurasian Spruce Bark Beetle, *Ips typographus* Linnaeus (Coleoptera: Curculionidae, Scolytinae)

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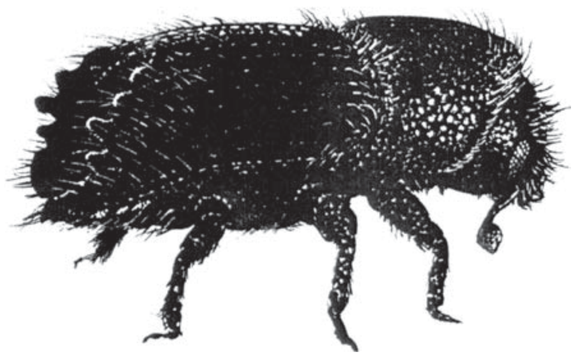
Among thousands of bark beetle species worldwide, only a handful is able to attack and kill trees on a large scale. One of these is the 8-toothed spruce bark beetle, *Ips typographus* L., indigenous to the Palaearctic forests and recently introduced into North America (Fig. 50). In Europe, the main host is the Norway spruce, *Picea abies* (Linnaeus) Karsten; in Eastern Asia, including Japan, the main hosts are spruces of the *P. jezoensis* group. In unmanaged forests, these beetles play an important ecological role by killing old trees and stands, thus promoting biomass recycling and ecosystem rejuvenation. Foresters who are faced with extensive tree mortality do not, however, welcome this activity: managed forests of Europe have lost hundreds of millions of trees in recurring outbreaks.

Hibernation

In the colder areas, the beetles emerging from killed, standing trees most often hibernate in the



Eurasian Spruce Bark Beetle, *Ips typographus* Linneaus (Coleoptera: Curculionidae, Scolytinae), Figure 50 ***Ips typographus*** **adults are 5 to 6 mm long, hairy, and dark brown to black. The tip of each elytron has four teeth.**

litter of the forest floor where a good snow cover offers protection. Beetles hatching from grounded stems or logs more often remain under the bark during the winter. In warmer parts of its range, the spruce beetle is more prone to stay in standing trees. The adult beetles in Finland tolerate temperatures down to −30°C, while the larvae will die at temperatures around −15°C. The mortality rate during hibernation is generally not well known.

Voltinism

The beetles leave their winter quarters in early spring, but flight only occurs when maximum air temperatures exceed 20°C. In Central Europe where flight may occur as early as mid-April, a new generation of beetles may hatch by midsummer to start a second annual generation. A third generation may be initiated in unusually hot summers. In colder areas such as Fennoscandia, spring flight occurs in May and June and only one generation is produced per year. Here, an occasional second generation that remains in the larval stage at the onset of winter will die in the low temperatures.

Breeding

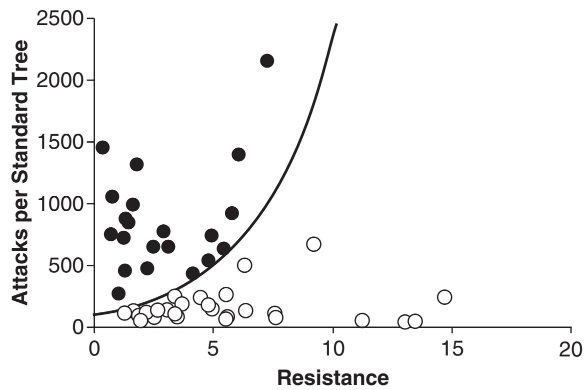
During the flight period, the beetles search for a breeding site. Flight distances are highly variable depending on energy reserves and the availability of fresh breeding substrate; i.e., timber with bark, logging debris, windfalls and live trees. Healthy trees have powerful defense mechanisms, but can be overcome when beetle populations reach epidemic levels.

In this polygamous species, gallery construction starts with the male excavating a nuptial chamber in the phloem, and is joined by one to four females. After mating, each female excavates a gallery and deposits her eggs singly in little niches as she moves along. Maternal galleries, running in the axial direction of the stem, are about 6–15 cm long, depending on attack density. The males remove frass from the galleries and also guard the entrance holes. Space permitting, a female may lay her full complement of about 100 eggs in one gallery. The 5–10 cm long larval mines start at right angles from the maternal gallery. The phloem, in which the larvae feed, is high in stored energy, and larval densities may exceed 500 galleries per square meter of bark surface. *I. typographus* often utilizes most of the stem, but shuns the lower 1–1.5 m as well as the top where the bark becomes too thin for gallery construction. In the upper stem, the galleries overlap with those of other bark beetles, particularly the smaller *Pityogenes chalcographus* (L.), which most often utilizes the thin-barked top section.

During an ongoing attack, parent beetles may be induced to re-emerge after a couple of weeks, particularly in warm weather and when crowding occurs. Males dominate among the re-emerging beetles. They may re-attack the tree from which they emerged, or fly to adjacent ones. Females are more prone to stay in their original host tree, but may also leave to construct new galleries, giving rise to “sister broods.” Occasionally, a second re-emergence may take place, resulting in a third sister brood. As a consequence, cohorts in different stages of development may occur simultaneously, even in areas with only one annual generation.

Pheromones Govern Beetle Attacks

During their initial search for a breeding site, volatile substances emanating from host material guide the beetles. However, upon successfully entering a suitable substrate, a "pioneer" male will emit a chemical bouquet of three volatiles, which act as population aggregation pheromones, summoning both sexes for a joint attack. At a later stage of the attack, two other substances with a repellent effect may be produced. This apparently contributes to the regulation of attack density by inducing latecomers to seek out other sites. The pheromones of the spruce bark beetle were isolated and identified in the 1970s, and have subsequently been used for bait in beetle traps. To some extent, they also attract other scolytids, and also act as kairomones for predators such as clerids.



Eurasian Spruce Bark Beetle, *Ips typographus* Linneaus (Coleoptera: Curculionidae, Scolytinae), Figure 51 **Threshold of successful attack on Norway spruce by *Ips typographus*. Black dots represent killed trees, white dots are surviving trees. A standard tree is 20 cm in diameter at breast height. Resistance is defined by growth efficiency, as measured at breast height, i.e., previous year's increment of stem cross-sectional area as a percentage of sapwood cross-sectional area. Redrawn by Alan A. Berryman after Mulock and Christiansen, 1986.**

The Epidemic Threshold

At low population levels, the beetles are unable to kill trees with intact defenses, and their breeding is therefore restricted to undefended substrates such as logging debris, windfalls and timber. High standards of forest hygiene may help to maintain this non-epidemic state. However, environmental calamities such as large-scale wind-felling and prolonged drought may upset even the best regime of hygiene (Fig. 51), boosting the beetle population to exceed the "Threshold of Successful Attack." Above this level, healthy trees can be overwhelmed in a mass-attack. The threshold is lowered when tree defenses are weakened by prolonged periods of drought, or when tree roots are damaged by strong winds.

When *Ips typographus* attacks a living tree, only two outcomes are possible: the tree is killed and the beetles produce a new generation, or the tree survives and no offspring are generated. In other words: if the number of assailants exceeds the "Threshold of Successful Attack," the beetles win, if not, they are driven away or die.

Fungal Associates

During attack and gallery construction, *Ips typographus* spreads spores of a variety of micro-organisms, among which, species of the fungal family Ophiostomataceae are particularly important. Because concentrations of hyphae often give a bluish stain to the wood, the fungi are referred to as "blue-stain fungi." When a new generation of beetles emerges, the sticky spores adhere to the body surface. Spores are also ingested by callow adults and carried in their guts. Some blue-stain fungi are capable of growing in fresh bark and wood and at least one species, *Ceratocystis polonica* (Siem.) C. Moreau, may kill healthy trees when artificially inoculated into the bark. Blue-stain fungi do not attack cell walls, but rather utilize the contents of bark and wood parenchyma cells, which are storage organs for starch, sugars and lipids and hence, the primary target for both beetles and fungi.

Host Tree Defense

Over the eons, conifers have developed elaborate defense mechanisms to cope with wounding and infection. Thick cork bark, often with abundant stone cells, is an obstacle to invasion. Also inside the living phloem, chemical defenses of both preformed and inducible nature await intruding organisms. An interconnected system of ducts stores constitutive resin, which may repel or immobilize attacking insects. Moreover, the phloem parenchyma cells, a primary energy source for both beetles an fungi, are active in synthesis, storage and modification of phenolics in response to wounding and infection. This renders the phloem inhospitable to intruders. Parenchyma cells may form new periderms including cork layers, thus compartmentalizing the infected area where they release fungistatic substances. Superficial wounds and infections, including aborted beetle attacks, are enveloped and rendered harmless by these reactions. Moreover, the underlying cambium produces numerous traumatic resin ducts in the xylem. Above the "Threshold of Successful Attack," the host defenses collapse. This critical level is defined by the host tree's genetic constitution and by the environment surrounding it. Sub-lethal beetle attacks may rise the threshold level thereby inducing local acquired resistance in attacked stems.

Control of Damage

By maintaining a high standard of forest hygiene, foresters attempt to keep beetle populations in a permanent non-epidemic state. Forest hygiene is generally dependent on the removal of potential breeding material. Ideally, no such material should be found in the forest when the beetles fly, and a minimum requirement is that any breeding substrate should be removed from the forest before the next generation emerges. However, even the most painstaking efforts may be in vain when a gale strikes, most often in winter, leaving large numbers of fallen trees. In rugged terrain with no roads, even dedicated managers may not be able to salvage all fallen trees before the onset of the beetles' flight season. Under such circumstances, downed breeding material may boost propagation, pushing the population across the "Threshold of Successful Attack." Trap trees and beetle traps may be useful for keeping non-epidemic populations down and for mopping up restricted, local populations of beetles, but in case of a full-fledged epidemic, these measures must be combined with large-scale salvage/sanitation cutting.

References

Annila E (1969) Influence of temperature upon the development and voltinism of *Ips typographus* L. (Coleoptera, Scolytidae). Annales Zoologici Fennici 6:161–208

Bakke A, Frøyen P, Skattebøl L (1977) Field response to a new pheromonal compound isolated from *Ips typographus*. Naturwissenschaften 64:98

Christiansen E, Bakke A (1988) The spruce bark beetle of Eurasia. In Berryman AA (ed), Dynamics of forest insect populations. Plenum Press, New York, NY, pp 479–503

Horntvedt R, Christiansen E, Solheim H, Wang S (1983) Artificial inoculation with *Ips typographus*-associated blue-stain fungi can kill healthy Norway spruce trees. Meddelelser fra Norsk institutt for skogforskning 38:1–20

Mulock P, Christiansen E (1986) The threshold of successful attack by *Ips typographus* on *Picea abies*: a field experiment. For Ecol Manage 14:125–132

Solheim H (1991) The early stages of fungal invasion in Norway spruce infested by the bark beetle *Ips typographus*. Can J Bot 70:1–5

Thalenhorst W (1958) Grundzuge der Populationdynamik des grossen Fichtenborkenkafers *Ips typographus* L. SchrReihe forstl. Fak. University of Gottingen 21:1–126

European Castor Bean Tick, *Ixodes ricinus* (Linnaeus) (Acari: Ixodidae)

This species transmits several diseases to livestock in Europe and nearby areas

► Ticks

European Chafer, *Rhizotrogus majalis* Razoumowsky (Coleoptera: Scarabaeidae)

This species has become an important turfgrass pest in eastern North America.

► Turfgrass Insects and their Management

European Cherry Fruit Fly, *Rhagoletis cerasi* (L.) (Diptera: Tephritidae)

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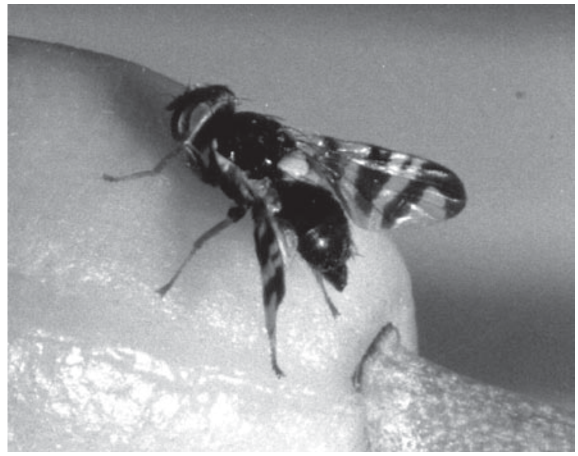
The European cherry fruit fly is a univoltine, oligophagous, carpophagous species. Its larvae develop in the pulp of ripening or ripe wild and cultivated sweet (*Prunus avium* L.) and sour cherries (*P. cerasus* L.) (Rosaceae) as well as into honeysuckle berries (*Lonicera* spp. Caprifoliaceae), especially *L. xylosteum* L. and *L. tartarica*. L. This insect is native to the temperate West Palearctic Regions, including all European countries where its hosts occur (from southern parts, such as Cyprus, to as far North as Norway and Sweden) as well as in some Asian countries (such as Turkey and Iran). Races of the fly specializing in *Prunus* or *Lonicera* spp. may occur, and the existence of geographic races exhibiting unidirectional cytoplasmatic incompatibility has been demonstrated.

The adult is about 3–5 mm in body (Fig. 52) length, glossy black in color with characteristic patterned wings and a peculiar yellow scutellum (metathorax). The elongated larva (three instars) is



European Cherry Fruit Fly, *Rhagoletis cerasi* (L.) (Diptera: Tephritidae), Figure 52 ***Rhagoletis cerasi*** **female.**

typical of cyclorrhaphous Diptera. The last instar is about 5–6 mm long. The pupae are coarctate.

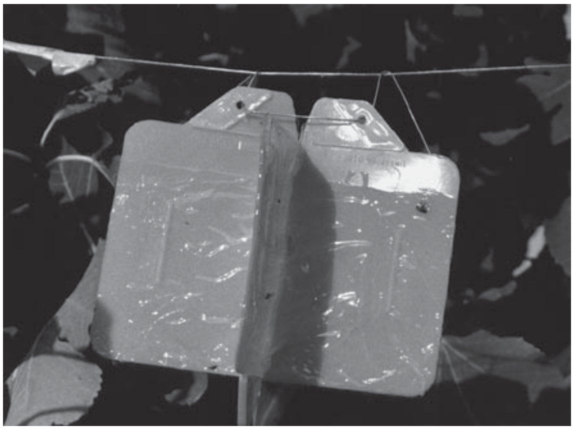
The fly overwinters in the pupal stage in the soil beneath its host plants. Adults emerge in spring and their appearance coincides with the presence of fruits suitable for oviposition. A few days after emergence, the males release a volatile sex pheromone to attract virgin females for mating. Adults feed upon plant exudates and honeydews from other insects. Mating occurs when females are about 5–10 days old. Visual stimuli are of predominant importance for host location. The shape, size and color of host fruits are important cues for their location by gravid females. Oviposition takes place into ripening host fruit. Usually only one egg is deposited into each fruit. After oviposition, the female deposits onto the fruit surface a non-volatile, long persisting, host marking pheromone, which discourages further egg laying into already oviposited fruits. Due to this pheromone, which also plays a role in the mating behavior by functioning as a male arrestant, a uniform distribution of eggs among available fruits in achieved and hence an optimal use of the resources available for larval development. The possibility of using natural or synthetic host marking pheromone for control purposes has been assessed with promising results.

Adults live about two months under optimal conditions (25°C) and each female lays about

200–250 eggs in her lifespan. Under field conditions, first instar larvae hatch in about 5–10 days after oviposition and larval development lasts two to three weeks. Developed larvae leave the fruit and drop to the soil where they pupate at a shallow depth. They undergo diapause and most adults emerge in the next spring. However, a small proportion may emerge after two or even three years, thus assuring persistence of the population during years of fruit scarcity or absence.

The European cherry fruit fly is the most important pest of cherries in Europe, causing fruit damage that may reach 100% of fruit production. Therefore, control measures are frequently required. Early ripening cherry varieties usually escape infestation. In late-ripening varieties, however, control measures are required frequently. This is usually made using insecticides either in the form of proteinaceous bait sprays or as a cover spray applied three weeks before harvest.

Based on the strong attraction of the fly to yellow panels reported, an effective, sticky-coated, 3-dimensional visual trap (the Rebell trap, Fig. 53) has been developed in Switzerland by E.F. Boller and his collaborators. The effectiveness of this trap can be enhanced by adding food attractants such as a dispenser containing ammonium acetate. The Rebell trap is widely used in Europe for adult population monitoring and mass trapping (in non commercial orchards). Intervention thresholds for late varieties are very low (one to two flies per trap or mere presence of flies).



European Cherry Fruit Fly, *Rhagoletis cerasi* (L.) (Diptera: Tephritidae), Figure 53 **Rebell visual trap.**

References

Aluja M, Boller EF (1992) Host marking pheromone of *Rhagoletis cerasi*. Field deployment of synthetic pheromone as a novel cherry fruit fly management strategy. Entomologia Experimentalis et Applicata 65:141–147

Boller EF, Bush GL (1974) Evidence for genetic variation in populations of the European cherry fruit fly, *Rhagoletis cerasi* (Diptera: Tephritidae) based on physiological parameters and hybridization experiments. Entomologia Experimentalis et Applicata 17:279–273

Katsoyannos BI (1975) Oviposition-deterring, male-arresting, fruit-marking pheromone in *Rhagoletis cerasi*. Environ Entomol 4:801–807

Katsoyannos BI, Boller EF (1976) First field application of oviposition-deterring marking pheromone of European cherry fruit fly. Environ Entomol 5:151–152

Katsoyannos BI, Papadopoulos NT, Stavridis D (2000) Evaluation of trap types and food attractants for *Rhagoletis cerasi* (Diptera, Tephritidae). J Econ Entomol 93:1005–1010

Prokopy RJ (1969) Visual responses of European cherry fruit flies, *Rhagoletis cerasi* L. (Diptera, Trypetidae). Bull P Entomol Soc 39:539–566

European Earwig, *Forficula auricularia* Linnaeus (Dermaptera: Forficulidae)

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European earwig is native to Europe, western Asia, and northern Africa, but also has been introduced to Australia, New Zealand, and North America. Once introduced, it can spread very rapidly. For example, European earwig was first observed in North America at Seattle, Washington, in 1907. It spread quickly across the United States, being discovered in Rhode Island in 1911, New York in 1912, and most other provinces of Canada and northern states in the USA in the 1930s and 1940s. Presently it occurs south to North Carolina, Arizona and southern California, but due to its preference for temperate climates it is unlikely to become abundant in the southeastern states. Also, it is not very tolerant of arid environments, but survives where irrigation is practiced.

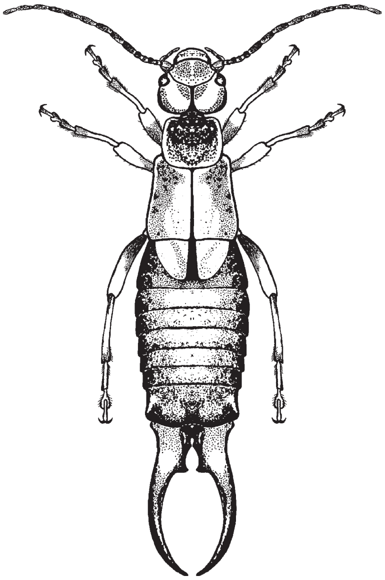
Life History

One generation is completed annually, and overwintering occurs in the adult stage. In British Columbia, Canada, eggs are deposited in late winter, hatch in May, and nymphs attain the adult stage in August. The overwintering females may also produce an additional brood; these eggs hatch in June and also mature by the end of August. In Washington, USA, these events occur about one month earlier. In colder climates such as Quebec, Canada, only a single brood of eggs is produced.

The egg is pearly white, and oval to elliptical. The egg measures 1.13 mm long and 0.85 mm wide when first deposited, but absorbs water, swells, and nearly doubles in volume before hatching. Eggs are deposited in a cell in the soil, in a single cluster, usually within 5 cm of the surface. Mean number of eggs per cluster is reported to range from 30 to 60 eggs in the first cluster. The second cluster, if produced, contains only half as many eggs. Duration of the egg stage under winter field conditions in British Columbia averages 72.8 days (range 56–85 days). The second or spring brood of eggs requires only 20 days to hatch. Eggs are attended by the female, which frequently moves the eggs around the cell, and apparently keeps mold from developing on the eggs. Females guard their eggs from other earwigs, and fight with any intruders.

The nymphal stages, which are four in number, have the same general form as adults except that the wings increase in size with maturity. The body color darkens, gradually changing from grayish brown to dark brown, as the nymph matures. The legs are pale throughout. The wing pads are first evident in the fourth instar. Mean head capsule width is 0.91, 1.14, 1.5, and 1.9 mm in instars 1–4, respectively. Mean body length is 4.2, 6.0, 9.0, and 9–11 mm, respectively. The number of antennal segments is 8, 10, 11, and 12 in instars one to four. Mean duration (range) of instars under laboratory temperatures of 15–21°C is 12.0 (11–15), 10.2 (8–14), 11.2 (9–15), and 16.2 (14–19) days for instars one to four. However, development time is considerably longer under field conditions, requiring 18–24, 14–21, 15–20, and about 21 days for the corresponding instars. Young nymphs are guarded by the mother earwig, which remains in or near the cell where the eggs are deposited until the nymph's second instar is attained.

The adult normally measures 13–14 mm in length, exclusive of the pincher-like cerci (forceps), though some individuals (Fig. 54) are markedly smaller. The head measures about 2.2 mm in width. Adults, including the legs, are dark brown or reddish brown in color, though paler ventrally. The antennae have 14 segments. The pronounced cerci are the most distinctive feature of earwigs; in the male the cerci are strongly curved whereas in the female they curve only slightly. Despite the appearance of being wingless, adults bear long hind wings folded beneath the abbreviated forewings. When ready to fly, adults usually climb and take off from an elevated object. The hind wings are opened



European Earwig, *Forficula auricularia* Linnaeus (Dermaptera: Forficulidae), Figure 54 **Adult male of European earwig, *Forficula auricularia* Linnaeus.**

and closed quickly, so it is difficult to observe the wings. Adults bear a set of cerci at the tip of the abdomen. Adults can use the cerci in defense, twisting the abdomen forward over the head or sideways to engage an enemy, often another earwig.

Earwigs are nocturnal, spending the day hidden under leaf debris, in cracks and crevices, and in other dark locations. Their nighttime activity is influenced by weather. Stable temperature encourages activity, and activity was favored by higher minimum temperatures but discouraged by higher maximum temperatures. High relative humidity seemed to suppress movement whereas higher wind velocities and greater cloud cover encouraged earwig activity. They produce an aggregation pheromone in their feces that is attractive to both sexes and to nymphs, and release quinones as defensive chemicals from abdominal glands.

Social behavior is weakly developed in the European earwig. Males and females mate in late summer or autumn, and then construct a subterranean tunnel (nest) in which they overwinter. The female drives the male from the nest at the time of oviposition. The eggs are manipulated frequently, apparently cleaning them to prevent growth of fungi. She will relocate the eggs in an attempt to provide optimal temperature and humidity for the eggs. Although the female normally keeps the eggs in a pile, as the time for hatching approaches she spreads the eggs in a single layer. After hatching, females continue to guard the nymphs and provide them with food. Food is provided by females carrying objects into the nest, and by regurgitation. Thus, there is parental care, but no cooperative brood care.

Several natural enemies are known, including some that were imported from Europe in an attempt to limit the destructive habits of this earwig in North America. Some authors have suggested that the most important natural enemy is the European parasitoid *Bigonicheta spinipennis* (Meigen) (Diptera: Tachinidae), which has been reported to parasitize 10–50% of the earwigs in British Columbia; others, however, report low incidence of parasitism. Another fly, *Ocytata pallipes* (Fallen) (Diptera: Tachinidae) also was successfully established, but causes little mortality. Under the cool, wet conditions of Oregon, Washington, and British Columbia, the fungi *Erynia forficulae* and *Metarhizium anisopliae* also infect earwigs. The nematode *Mermis nigrescens* appears to be an important mortality factor in Ontario, where 10–63% of earwigs were infected during a 2-year period; however, this nematode has not been reported from earwigs elsewhere. Avian predation can be significant.

Damage

This insect is omnivorous, feeding on a wide variety of plant and animal matter. Although its predatory habits do offset its phytophagous behavior to some degree, on occasion European earwig can inflict significant injury to vegetables, fruit, and flowers. Bean, beet, cabbage, celery, chard, cauliflower, cucumber, lettuce, pea, potato, rhubarb, and tomato are among the vegetable crops sometimes injured. Seedlings and plants providing the earwigs with good shelter, such as the heads of cauliflower, the stem bases of chard, and the ears of corn, are particularly likely to be eaten, and also to be contaminated with fecal material. Among the flowers most often injured are dahlia, carnation, pinks, sweet william, and zinnia. Ripe fruit such as apple, apricot, peach, plum, pear, and strawberry are sometimes reported to be damaged.

European earwig is reported to consume aphids, caterpillar pupae, scale insects, spiders, and springtails as well as vegetable matter. Aphid consumption is especially frequent and well documented. In addition to the higher plants mentioned above, earwigs consume algae and fungi, and often consume vegetable and animal matter in equal proportions.

The economic status of earwigs is subject to dispute. Undoubtedly earwigs sometimes damage vegetable and flower crops, both by leaf consumption and fruit injury. Foliage injury is usually in the form of numerous small holes. Tender foliage may be completely devoured except for major veins. However, the physical presence of earwigs as crop contaminants is perhaps even more important, because most people find their presence and odor to be repulsive. The annoyance associated with their presence is exacerbated by the tendency of earwigs to aggregate, often in association with human habitations; most people simply find them to be annoying. Their propensity to consume other insects, particularly aphids, is an important element in offsetting their reputation as a crop pest. However, augmenting the earwig population by field release, and providing them with additional shelter to enhance survival, have had mixed success in suppressing aphid populations.

Management

Population monitoring can be accomplished with baits and traps. Small piles of baits distributed in dense vegetation often attract large numbers of earwigs, which can be checked during the evening. Wheat bran or oatmeal can serve as bait. Traps take advantage of the natural tendency of earwigs to hide in crevices and dark spots, and can be used to detect presence of earwigs, and to estimate abundance.

Residual foliar insecticides and baits containing toxicants can be used to suppress earwigs. Of numerous baits evaluated, wheat bran flakes plus toxicant and a small amount of fish oil is reported to be optimal. However, others have suggested that fish oil is unnecessary but suggested addition of glycerin and molasses. Commercial products are rarely formulated specifically for earwigs because they rarely are a severe problem. Rather, products sold for grasshoppers, cutworms, slugs, and sowbugs are applied for earwig control. Bait is most effective if applied in the evening.

On residential property or in small gardens, persistent trapping can be used to reduce earwig abundance, though this approach is not likely to be effective if the initial earwig density is high. Boards placed on the soil will be attractive to earwigs seeking shelter. Even more earwigs will accumulate if there are narrow grooves or channels in the board. Moistened, rolled-up newspaper placed in the garden in the evening and disposed of in the morning makes a convenient earwig trap for home gardens. A particularly effective technique is to fill a flower pot with wood shavings and invert the pot over a short stake that has been driven into the soil. Traps can also be placed in trees because earwigs favor this habitat.

► Vegetable Pests and their Management
► Earwigs (Dermaptera)

References

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, 729 pp
Crumb SE, Eide PM, Bonn AE (1941) The European earwig. USDA Tech Bull 766, 76 pp

European Corn Borer, *Ostrinia nubilalis* (Hübner) (Lepidoptera: Crambidae)

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European corn borer is native to Europe, where it is widespread. It also occurs in northern Africa. In neither area is it a serious pest. However, it gained access to North America near Boston, Massachusetts, in 1917 where it quickly became troublesome. European corn borer quickly spread to the Great Lakes region. By 1948 it was established throughout the midwestern corn-growing region and eastern Canada. It now has spread as far west as the Rocky Mountains in both Canada and the United States, and south to the Gulf Coast states. The North American European corn borer population is thought to have resulted from multiple introductions from more than one area of Europe. Thus, there are at least two, and possibly more, strains present. The presence of an eastern or New York strain, and a mid western or Iowa strain, is evident because different pheromone blends are required to capture moths from each population. Both strains sometimes occur in the same area.

Host Plants

European corn borer has a very wide host range, attacking practically all herbaceous plants with a stem large enough for the larvae to enter. However, the eastern strain accounts for most of the wide host range, with the western strain feeding primarily on corn. Crops other than corn tend to be infested if they are abundant before corn is available, or late in the season when senescent corn becomes unattractive for oviposition; snap and lima beans, pepper, and potato are especially damaged. In North Carolina, for example, potato is more attractive than corn at peak emergence of the first moth flight, and more heavily damaged. Other crops sometimes attacked include buckwheat, grain corn, hop, oat, millet, and soybean, and such flowers as aster, cosmos, dahlia, gladiolus, hollyhock, and zinnia. Corn is the most preferred host, but many thick-stemmed weeds and grasses also will support European corn borer, especially if they are growing amongst, or adjacent to, corn. Some of the common weeds infested include barnyardgrass, *Echinochoa crusgalli*; beggarticks, *Bidens* spp.; cocklebur, *Xanthium* spp.; dock, *Rumex* spp.; jimsonweed, *Datura* spp.; panic grass, *Panicum* spp.; pigweed, *Amaranthus* spp.; smartweed, *Polygonum* spp.; and others.

Natural Enemies

Native predators and parasites exert some effect on European corn borer populations, but imported parasitoids seem to be more important. Native parasitoids include *Bracon caulicola* (Gahan), *B. gelechiae* Ashmead, *B. mellitor* Say, *Chelonus annulipes* Wesmael, *Macrocentrus delicatus* Cresson, and *Meteorus campestris* Viereck (all Hymenoptera: Braconidae); *Gambrus ultimus* (Cresson), *G. bituminosus* (Cushman), *Itoplectis conquisitor* (Say), *Campoletis flavicincta* (Ashmead), *Nepiera oblonga* (Viereck), *Rubicundiella perturbatrix* Heindrich, *Vulgichneumon brevicinctor* (Say) (all Hymenoptera: Ichneumonidae); *Dibrachys carus* (Walker) and *Eupteromalus tachinae* Gahan (both Hymenoptera: Pteromalidae); *Syntomosphyrum clisiocampe* (Ashmead) (Hymenoptera: Eulophidae); *Scambus pterophori* (Ashmead) (Hymenoptera: Hybrizontidae); *Trichogramma nubilale* Ertle and Davis and *T. minutum* Riley (both Hymenoptera: Trichogrammatidae); and *Archytas marmoratus* (Townsend) and *Lixophaga* sp. (both Diptera: Tachinidae). Although many species of native parasitoids are known, native parasitoids rarely cause high levels of corn borer mortality.

Exotic parasitoids numbering about 24 species have been imported and released to augment native parasitoids. About six species have successfully established. Among the potentially important species is *Lydella thompsoni* Herting (Diptera: Tachinidae), which may kill up to 30% of second generation borers in some areas, but has disappeared or gone into periods of low abundance in other areas. Other exotic parasitoids that sometimes account for more than trivial levels of parasitism are *Eriborus terebrans* Gravenhorst (Hymenoptera: Ichneumonidae), *Simpiesis viridula* (Hymenoptera: Eulophidae), and *Macrocentris grandii* Goidanich (Hymenoptera: Braconidae).

Avian predators such as downy woodpecker, *Dendrocopos pubescent* (Linnaeus); hairy woodpecker, *D. villosus* (Linnaeus); and yellow shafted flicker, *Colaptes auratus* (Linnaeus) have been known to eliminate 20–30% of overwintering larvae.

Several microbial disease agents are known from corn borer populations. The common fungi *Beauveria bassiana* and *Metarhizium anisopliae* are sometimes observed, especially in overwintering larvae. The most important pathogen seems to be the microsporidian *Nosema pyrausta*, which often attains 30% infection of larvae and sometimes 80–95% infection. It creates chronic, debilitating infections that reduce longevity and fecundity of adults, and reduces survival of larvae that are under environmental. Unfortunately, *N. pyrausta* also infects the parasitoid *M. grandii*.

Life table studies conducted on corn borer populations in Quebec with a single annual generation perhaps provide insight into the relative importance of mortality factors. These workers demonstrated that egg mortality (about 15%) was low, stable and due mostly to predators and parasites. Similarly, mortality of young larvae, due principally to dispersal, dislodgement, and plant resistance to feeding was fairly low (about 15%) but more variable. Mortality of large larvae during the autumn (about 22%) and following spring (about 42%) was due to a number of factors including frost, disease and parasitoids, but parasitism levels were low. Pupal mortality (about 10%) was low and stable among generations. The factor that best accounted for population trends was survival of adults. Dispersal of moths and disruption of moth emergence by heavy rainfall are thought to account for high and variable mortality (68–98%, with a mean of 95%), which largely determines population size of the subsequent generation. Overall generation mortality levels were high, averaging 98.7%.

Life Cycle and Description

The number of generations varies from 1 to 4, with only one generation occurring in northern New England and Minnesota and in northern areas of Canada, three to four generations in Virginia and other southern locations, and usually two generations in the northern United States and southern Canada. In many areas generation number varies depending on weather, and there is considerable adaptation for local climate conditions even within strains. For example, although the developmental rates of single-generation strains are lower than multiple-generation strains, at northern locations such as Prince Edward Island the single-generation strain develops quickly. European corn borer overwinters in the larval stage, with pupation and emergence of adults in early spring. Diapause apparently is induced by exposure of last instar larvae to long days, but there also is a genetic component. Moth flights and oviposition usually occur during June to July, and August to September, in areas with one to two generations annually. In southern locations with three generations, moth flights and oviposition typically occur in May, late June, and August. In locations with four generations, adults are active in April, June, July, and August-September.

Egg

Eggs are deposited in irregular clusters of about 15–20. The eggs are oval, flattened, and creamy white in color, usually with an iridescent appearance. The eggs darken to beige or orangeish tan. Eggs normally are deposited on the underside of leaves, and overlap like shingles on a roof or fish scales. Eggs measure about 1.0 mm in length and 0.75 m in width. The developmental threshold for eggs is about 15°C. Eggs hatch in four to nine days.

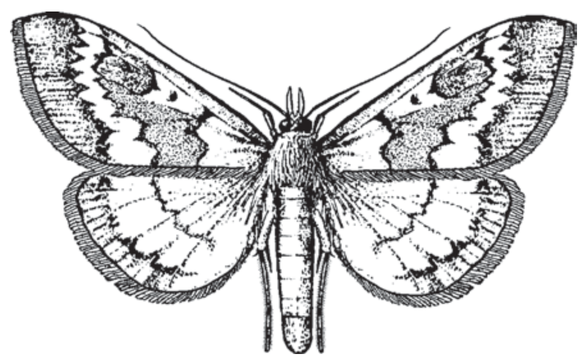
Larva

Larvae are light brown or pinkish gray in color dorsally, with a brown to black head capsule and a yellowish brown thoracic plate. The body is marked with round dark spots on each body segment. The developmental threshold for larvae is about 11°C. Larvae normally display six instars, but four to seven instars have been observed. Head capsule widths are about 0.30, 0.46, 0.68, 1.03, 1.66, and 2.19 mm in instars one to six, respectively. For populations with only five instars, mean head capsule widths are 0.29, 0.44, 0.80, 1.27, and 2.00 mm, respectively. Young larvae tend to feed initially within the whorl, especially on the tassel. When the tassel emerges from the whorl, larvae disperse downward where they burrow into the stalk and the ear. Mortality tends to be high during the first few days of life, but once larvae establish a feeding site within the plant survival rates improve. Larvae in the final instar overwinter within a tunnel in the stalk of corn, or in the stem of another suitable host. Duration of the instars varies with temperature. Under field conditions in New York, development time was estimated at 9.0, 7.8, 6.0, 8.8, 8.5, and 12.3 days for instars one to six, respectively, for a mean total development period of about 50 days. In contrast, during the next year development time at the same site was 4.4, 4.3, 4.6, 5.8, 8.5 and 9.0 days for the six instars, for a mean total larval development period of about 35 days.

European Corn Borer, *Ostrinia nubilalis* (Hübner) (Lepidoptera: Crambidae), Figure 55 **Adult male of European corn borer, *Ostrinia nubilalis*.**

Pupa

Pupae usually occur in April or May, and then later in the year if more than one generation occurs. The pupa is yellowish brown in color. The pupa measures 13–14 mm in length and 2–2.5 mm in width in males and 16–17 mm in length and 3.5–4 mm in width in females. The tip of the abdomen bears five to eight recurved spines that are used to anchor the pupa to its cocoon. The pupa is ordinarily, but not always, enveloped in a thin cocoon formed within the larval tunnel. Duration of the pupal stage under field conditions is usually about 12 days. The developmental threshold for pupae is about 13°C.



European Corn Borer, *Ostrinia nubilalis* (Hübner) (Lepidoptera: Crambidae), Figure 56 **Adult female of European corn borer, *Ostrinia nubilalis*.**

Adult

The moths are fairly small, with males measuring 20–26 mm in wingspan, and females 25–34 mm. Female moths (Fig. 56) are pale yellow to light brown in color, with both the forewing and hind wing crossed by dark zigzag lines and bearing pale, often yellowish, patches. The male (Fig. 55) is darker in color, usually pale brown or grayish brown, but also with dark zigzag lines and yellowish patches. Secondary host plants and adjacent grassy areas play a significant role in the mating behavior of adults, as adults rest and mating takes place in such areas of dense vegetation, called "action sites." Retention of droplets from rainfall and dew in this dense vegetation stimulates the sexual activity of females. Moths are most active during the first 3–5 h of darkness. The sex pheromone has been identified as 11-tetradecenyl acetate, but eastern and western strains differ in production of Z and E isomers. The western strain produces a blend that approximates 97:3 Z:E, whereas the eastern strain uses a blend of 3:97 Z:E. The preoviposition period averages about 3.5 days. Duration of oviposition is about 14 days, with oviposition averaging 20–50 eggs per day. The female often deposits 400–600 eggs during her life span, though there are also estimates of mean fecundity of about 150 eggs in some locations. Total adult longevity is normally 18–24 days.

Damage

This is a very serious pest of both sweet corn and grain corn, and before the availability of modern insecticides this insect caused very marked reductions in corn production. Young larvae feed on tassels, whorl and leaf sheath tissue; they also mine midribs and eat pollen that collects behind the leaf sheath. Sometimes they feed on silk, kernels, and cobs, or enter the stalk. Older larvae tend to burrow into the stalk and sometimes the base of the corn ear, or into the ear cob or kernels. Feeding by older larvae is usually considered to be most damaging, but tunneling by even young larvae can result in broken tassels. The presence of one to two larvae within a corn stalk is tolerable, but the presence of any larvae within the ear of sweet corn is considered intolerable by commercial growers, and is their major concern. European corn borer is considered to be the most important sweet corn pest in northern production areas of North America, and second-generation borers are the principal source of ear damage. Heavily tunneled stalks of grain corn suffer from lodging, reducing the capacity for machine harvesting. Lodging is not a serious threat to sweet corn. Boring by corn borers also allows several fungi to affect corn plants.

In crops other than corn, the pattern of damage is variable. European corn borer larvae damage both the stem and fruit of beans, pepper, and cowpea. The temporal occurrence of fruit affects susceptibility to injury, of course; in Wisconsin, snap beans 14–30 days from harvest were susceptible to damage by larvae, but young plants and fruit near harvest suffered little damage. In celery, potato, rhubarb, Swiss chard, and tomato, it is usually the stem tissue that is damaged. In beet, spinach, and rhubarb, leaf tissue may be injured. Entry of borers into plant tissue facilitates entry of plant pathogens. The incidence of potato blackleg caused by the bacterium *Erwinia carotovora atroseptica*, for example, is higher in potato fields with stems heavily infested by corn borers. Direct damage by corn borers to potato vines, however, results in negligible yield loss.

Management

Sampling

Moths can be sampled with blacklight and pheromone traps, and catches by these traps are correlated. Pheromone-baited water pan traps seem to be the most efficient method of adult. Trap catches are usually used to initiate intensive in-field scouting for egg masses, as moth catches are only roughly correlated with density. Thermal summations are also highly predictive. Moths seek shelter during the daylight hours in dense grass and weeds near corn fields. Flushing moths from such habitats gives an estimate of population densities. Eggs can be sampled by visual examination, but this is a very time-consuming effort.

Insecticides

Liquid formulations of insecticide are commonly applied to protect against damage to sweet corn, particularly from the period of early tassel formation until the corn silks are dry. Recommendations vary from a single application prior to silking, to weekly. Liquid applications are usually made to coincide with egg hatch in an effort to prevent infestation. If corn borers are present in a field, however, the critical treatment time is just before the tassels emerge, or at tassel emergence from the whorl. This plant growth period is significant because the larvae are active at this time and more likely to contact insecticide. A popular alternative to liquid insecticides is the use of granular formulations, which can be dropped into the whorl for effective control of first generation larvae because this is where young larvae tend to congregate. Insecticide is more persistent when applied in a granular formulation.

Cultural practices

Destruction of stalks, the overwintering site of larvae, has long been recognized as an important element of corn borer management. Disking is not adequate; plowing to a depth of 20 cm is necessary for destruction of larvae. Mowing of stalks close to the soil surface eliminates greater than 75% of larvae, and is especially effective when combined with. Minimum tillage procedures, which leave considerable crop residue on the surface, enhance borer survival.

Early planted corn is taller and attractive to ovipositing female moths, so late planting has been recommended, but this is useful mostly in areas with only a single generation per year. If a second generation occurs, such late-planted corn is heavily damaged. Planting border rows of a highly attractive variety of corn to surround a less attractive variety has been investigated in France. The attractive variety, especially if it is an early-flowering cultivar, receives most of the eggs of moths dispersing into the field. If treated with insecticide or destroyed, this border row trap could provide protection for the main corn crop.

Host plant resistance

Extensive breeding research has been conducted, and resistance has been incorporated into grain corn, especially against corn borer populations with only a single annual generation. A principal factor in seedling resistance to young larvae is a chemical known as DIMBOA, which functions as a repellent and feeding deterrent. It has proven difficult to incorporate the known resistance factors into sweet corn without degradation of quality. However, some progress has been made in producing commercially acceptable resistant cultivars, especially when host plant resistance is complemented by use of other suppressive tactics such as application of *Bacillus thuringiensis*.

Biological control

Biological control has been attempted repeatedly in sweet corn and other vegetables susceptible to European corn borer attack. *Bacillus thuringiensis* products can be as effective as many chemical insecticides, but often prove to be less effective. Most single-factor approaches, with the exception of newer formulations of *Bacillus thuringiensis*, have proven to be erratic.

► Vegetable Pests and their Management

References

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, CA, 729 pp

Hudon M, LeRoux EJ (1986) Biology and population dynamics of the European corn borer (*Ostrinia nubilalis*) with special reference to sweet corn in Quebec. I. Systematics, morphology, geographical distribution, host range, economic importance. Phytoprotection 67:39–54

Hudon M, LeRoux EJ (1986) Biology and population dynamics of the European corn borer (*Ostrinia nubilalis*) with special reference to sweet corn in Quebec. II. Bionomics. Phytoprotection 67:81–92

Hudon M, LeRoux EJ (1986) Biology and population dynamics of the European corn borer (*Ostrinia nubilalis*) with special reference to sweet corn in Quebec. III. Population dynamics and spatial distribution. Phytoprotection 67:93–115

Hudon M, LeRoux EJ, Harcourt DG (1989) Seventy years of European corn borer (*Ostrinia nubilalis*) research in North America. In: Russell GE (ed) Agricultural zoology reviews, vol 3. Intercept, Wimborne, Dorset, UK, pp 53–96

European Honey Bee

This is *Apis mellifera mellifera* Linnaeus (Hymenoptera: Apidae), the common honey bee in most parts of the world. The species originated in the tropics of Africa, but the European strain, bred to be docile and an effective producer of honey, was developed in Europe. It is also known as the Italian honey bee. It has been replaced by the African strain (*Apis mellifera scutellata*) in South and Central America, and is now spreading in North America where it is replacing the European strain.

► Honey Bee
► Apiculture
► African Honey Bee

European Foulbrood

Unlike American foulbrood, European foulbrood is not considered to be a serious disease of honey bees. It is caused by the bacterium *Melissococcus pluton*, often appearing in the spring and early summer, then dissipating over the summer. It is found throughout the world. This disease affects very young larvae, and prevents the colonies from growing. It is initiated when the larvae feed on contaminated brood food, and by hive robbing. Infected bees are sometimes discarded by the nurse bees, but it is these nurses that also transmit the disease while feeding the larvae. Bacteria overwinter in the hives. The disease is also spread by contaminated equipment. It also tends to affect colonies that lack adequate nutrition.

Infected bees are discolored, but lack the distinct ropiness of bees infected with American foulbrood. The presence of a sour odor and damaged or uncapped cells is symptomatic, but does not serve to distinguish European foulbrood from American foulbrood. However, the dead bee larva forms a rubbery scale in the bottom of the cell, unlike the hard scale of American foulbrood. Often beekeepers do not treat European foulbrood, but antibiotics are curative.

► Honey Bees
► Apiculture

Reference

Morse RA and Nowogrodzki R (1990) Honey bee pests, predators and diseases, 2nd ed. Cornell University Press, Ithaca, New York. 474 pp

European Red Mite, *Panonychus ulmi* (Koch) (Acari: Tetranychidae)

This is a foliar pest of fruit trees.

► Apple Pests and their Management

European Sheep Tick, *Ixodes ricinus* (Linnaeus) (Acari: Ixodidae)

This species, also known as European castor bean tick, is a livestock pest in Europe.

► Ticks

European Wheat Stem Sawfly

► Wheat Pests and their Management

Eurybrachidae

A family of bugs (order Hemiptera, suborder Fulgoromorpha). All members of the suborder are referred to as planthoppers.

► Bugs

Eurychoromyiidae

A family of flies (order Diptera).

► Flies

Eurytomidae

A family of wasps (order Hymenoptera). They commonly are called seed chalcids.

► Wasps, Ants, Bees and Sawflies

Eusocial Behavior

Advanced social behavior that entails nest sharing; division of labor including a caste system with sterile worker caste caring for offspring of the reproductive caste; and overlapping generations so that offspring assist parents. The truly social insects displaying eusocial behavior, include the termites, the ants, and some of the highly organized bees and wasps.

► Solitary
► Subsocial
► Communal
► Quasisocial

- ► Semisocial
- ► Parasocial Behavior
- ► Sociality in Insects
- ► Castes

Eustheniidae

A family of stoneflies (order Plecoptera).
► Stoneflies

Euthyplociidae

A family of mayflies (order Ephemeroptera).
► Mayflies

Evagination

An outward extension or sac-like structure on the outside of a structure; the opposite of invagination.

Evaniidae

A family of wasps (order Hymenoptera).
► Wasps, Ants, Bees and Sawflies

Evans, Howard Ensign

Howard Evans was born in Hartford, Connecticut, on February 23, 1919. He received M.S. and Ph.D. degrees from Cornell University in 1941 and 1949, respectively, and served in the U.S. army from 1942 to 1945. He was a faculty member of Kansas State University (1949–1952), Cornell University (1952–1960), Harvard University (1960–1973), and Colorado State University (1973–1986). His awards included his appointment at Harvard University as Alexander Agassiz Professor of Zoology, his appointment at Colorado State University as Distinguished Professor, an award in 1976 of the Daniel Giraud Medal from the National Academy of Sciences for recognition of published work in zoology or paleontology, and his appointment as a fellow of the National Academy of Sciences (1977). His main research was on systematics and behavior of Hymenoptera, especially the families Sphecidae, Pompilidae, and Bethylidae, and he described one family (Scolebythidae), 31 genera, and almost 800 species. He published more than 255 scientific papers, 13 books and some dozens of popular articles. Two of his books, "Wasp farm" (1963) and "Life on a little-known planet" (1968) achieved popular acclaim. He died on July 18, 2002, survived by his wife, Mary Alice, and three children.

Reference

Kondratieff BC (2002) Howard Ensign Evans. American Entomologist 48:188–189

Eversible

Capable of being turned inside out, everted, or projected outward.

Excitorepellency

The tendency of some insecticides to excite insects so that they fly away prior to acquisition of a dose adequate for knockdown. This property is seen especially with DDT and some pyrethroids.

Ex Larva

A Latin phrase meaning out of the larva. It is normally encountered mostly on insect labels in museums, and is used to designate specimens that were reared from the larval stage of the host. The similar term "ex ovum" designates specimens reared from host eggs.

Eye-Cap Moths (Lepidoptera: Opostegidae)

JOHN B. HEPPNER
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Eye-cap moths, family Opostegidae, are minute moths with a total of 122 known species, and known from all faunal regions but with many from the Australian region. The likely world total is over 175 species. The family, together with Nepticulidae, forms the superfamily Nepticuloidea, in the section Nepticulina of division Monotrysia, in the infraorder Heteroneura. Adults minute to small (3–16 mm wingspan), with head rough-scaled, with very large eye-caps on the antennal bases; haustellum short and naked (unscaled); labial palpi short and drooping and 3-segmented; maxillary palpi 5-segmented and folded. Wing venation is very reduced, with pseudofrenular bristles as the wing coupling. Maculation is generally white with bands or wing tip iridescences, although some species are dark. Adults are diurnally active. The few larvae known are leafminers, but some are stem borers.

References

Davis DR (1987) Family Opostegidae. In: Stehr FW Jr (ed) Immature insects, vol 1. Kendall/Hunt Publishing, Dubuque, IA
Davis DR (1989) Generic revision of the Opostegidae, with a synoptic catalog of the world' s species (Lepidoptera: Nepticulidae). Smithson Contrib Zool 478:1–97
Eyer JR (1964) A pictorial key to the North American moths of the family Opostegidae. Journal of the Lepidopterists' Society 17:237–242 (1963)
Puplesis R, Robinson GS (1999) Revision of the Oriental Opostegidae (Lepidoptera) with general comments on phylogeny within the family. Bull Nat Hist Mus, Entomol 68:1–92

Eye Gnats

These are *Hippelates* species (Diptera: Chloropidae) flies. They are found in the New World and as the name suggests, frequent the eyes (also sores and wounds) of mammals, where they feed at secretions. Their persistence makes them a nuisance, and they also have been implicated in the mechanical transmission of some diseases such as pinkeye.

► Flies
► Veterinary Pests and their Management

Exarate Pupa

A pupa in which the appendages are free, and not attached or adhering to the body (contrast with obtect pupa).

Excretion

The process of elimination of materials from the body. Excreted materials include metabolites and wastes, excessive and unnecessary nutrients, water, and allelochemicals. The principal organs of excretion are the Malpighian tubules and the hindgut.

Exocrine Gland

A gland that discharges its products to the outside of the insect (contrast with endocrine gland).

Exocuticle

The layer of sclerotized cuticle between the endocuticle and the epicuticle.

Exogenous

Originating outside an organism; extrinsic (contrast with endogenous).

Exogenous DNA

DNA from an outside source. In genetic engineering, DNA from one organism is often inserted into another by a variety of methods.

Exopeptidases

Protein digesting enzymes that attack small pieces of proteins by cutting off the terminal amino acid.

Exopterygota

A division of Insecta in which the wings develop externally during the immature stages. Hemimetabolous insects.

► Metamorphosis

Exoskeleton

A skeleton on the exterior of the body. The muscles are attached on the interior surfaces. A general term used to describe the hard body covering of insects, as is the term cuticle.

Exotic

Organisms that are native of elsewhere. Other terms used to describe this condition are alien and foreign.

Exotoxins

Poisonous substances produced by the microbial cell and liberated into the surrounding environment without destruction of the cell.

Exploratory Learning

Orientation behavior of social insects as they first leave the nest and become oriented to their surroundings.

Exploratory Trail

An odor trail produced continuously by advance workers from a foraging group (contrast with recruitment trail).

Exponential Growth

Population growth under ideal circumstances, without limitation. The population size increases at an increasing rate. The curve describing this relationship (number of individuals and time) is J-shaped.

Expression Vector

Vectors that are designed to promote the expression of gene inserts. Usually an expression vector has the regulatory sequence of a gene ligated into a plasmid that contains the gene of interest. This gene lacks its own regulatory sequence. The plasmid with this new combination (regulatory sequence + gene) is placed into a host cell such as *E. coli* or yeast, where the protein product is produced.

Extra-oral Digestion

Digestion of food before it is taken into the insect's body. This is accomplished by injection of hydrolytic enzymes into the food source, and then sucking up the digested products. Some insects continuously reflux the digestive enzymes by continuously re-injecting and sucking up the liquified juices.

Extrafloral Nectary

A nectar-producing gland found outside the flower.

► Plant Extrafloral Nectaries

Extrinsic Factors

Factors outside an organism, such as weather and other organisms. Exogenous elements.

Exuviae

The discarded or shed body covering after molting. Sometimes the terms “exuvium” or “exuvia” are used for the singular form, but this is not correct.

Eyes

The organs of sight in insects. The principal eyes of insects are (usually) large, multi-faceted “compound eyes.” Auxiliary organs of vision, with much less utility for the insect, are the “simple eyes”; these are more correctly called “ocelli.” Also, there are small, simple eyes found on the side of the head of larvae of holometabolous insects; these are more correctly called stemmata.

► Head of Hexapods

Eyes and Vision

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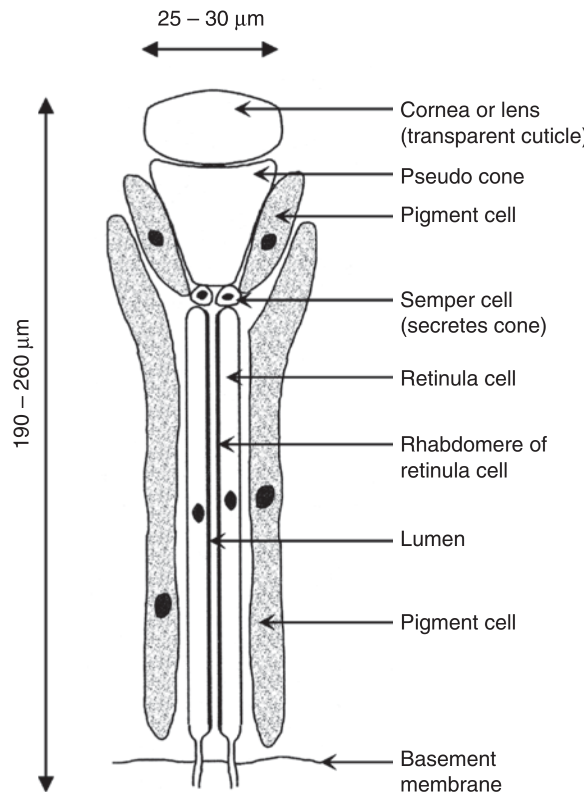
The ultimate source of light on earth is the sun, and both plants and animals evolved physical and biochemical mechanisms to capture light and make responses to its presence or absence. Light causes phototropic movements of leaves and stems and timing of flowering in many plants, and wavelengths in the 600–700 nm range promote photosynthesis. Light often influences sexual reproductive cycles, biological and seasonal rhythms, color changes in the skin, hormone secretion, and various chemical reactions (for example, synthesis of vitamin D in the skin of humans) in animals. Even the simplest plant and animal forms have pigments that enable them to respond to light. The electromagnetic radiation from the sun encompasses a wide spectrum from gamma rays and x-rays (<0.1 nm) to ultraviolet (UV), visible, infrared (IR), radio waves, and other longer wavelengths. Electromagnetic radiation from the sun that reaches the earth spans the range of about 300–900 nm, but the peak in intensity is near 500 nm wavelength. Wavelengths around this 500 nm peak are the only wavelengths that penetrate very deeply into water; even a few meters of water absorb most of the visible spectrum with the exception of wavelengths near 500 nm, which can penetrate clear water to about 100 m. Beyond this depth, little light penetrates. Ozone in the stratosphere strongly absorbs short wavelengths in the cosmic ray and UV range, which is very fortunate for all living things, because they cause chemical changes in DNA. Infrared radiation (IR) is strongly absorbed by water vapor, carbon dioxide, methane and other gases in our environment. Light that is visible to insects ranges from about 350 nm (UV) into the red range about 700 nm; this range is similar to human color vision, but humans do not have UV sensitive photoreceptors.

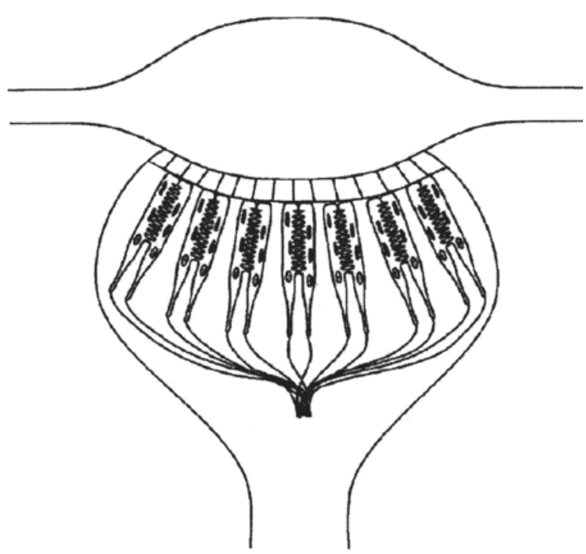
Although the main subject treated here will be insect eyes and vision, parallels and contrasts are noted with the eyes of other arthropods and vertebrates. Some extraordinary parallels in the independent development of visual systems occurred during the evolution of animals, with image-forming eyes evolving in flatworms, annelid polychaetes, coelenterates, echinoderms, insects, arachnids, crustaceans, cephalod molluscs, and vertebrates. Visual receptors, at least in terms of anatomy and structure, evolved independently in different groups of animals, possibly as many as seven times. However, all use the same chromophore, 11-*cis*-retinal or a very similar compound, and the transmembrane protein, opsin. Opsin and the chromophore combine to form rhodopsin, the visual pigment in invertebrate and vertebrate photoreceptors. Opsin is species-specific, as determined by its amino acid composition. Thus, even though the anatomical structure of eyes often evolved independently, it appears that some form of rhodopsin may have been present in very ancient organisms. The basic structure of compound eyes, in which a lens focuses light on photoreceptive cells, evolved 500–600 million years ago in trilobites in the Cambrian period. It is possible that UV, blue, and green photoreceptors existed in insects by the time of the Devonian period, about 300 million years ago.

Among the invertebrates, crustaceans have the most diversity in eye structure of any group of organisms, and at least one noted authority indicates that some of the eyes in crustaceans may have evolved several times independently. Some crustaceans have very simple eyes, but many have compound eyes very similar in structure and physiology to those in insects. Isopods, and some crabs, have apposition eyes (the eye restricts dispersal of light from one ommatidium to another due to a pigmented ommatidium wall) similar to the apposition compound eye in diurnal insects. Superposition eyes (the eye permits passage of light from one ommatidium to another through the unpigmented wall) occur in shrimp, crayfish, and lobster. Molluscs show a range of eyes from very simple eye-cups of limpets to image forming eyes with a lens in squid and octopus. Some scallops have compound eyes similar to apposition eyes in insects.

There are three types of visual receptors in insects: compound eyes, ocelli, and stemmata. Compound eyes are excellent (Fig. 57) motion detectors, responding to the movement of objects across the many small facets in the compound eyes, and in many insects this may be their most important function. Ocelli (Fig. 58) are found on immatures and adults of some insects. The cuticular covering forms a single lens over an ocellus. Beneath it are the photosensitive cells. Compound eyes, ocelli, and stemmata have the necessary structure to form an image. However, it is not



Eyes and Vision, Figure 57 A diagrammatical representation of a longitudinal view of a single facet in the compound eye of the Caribbean fruit fly, *Anastrepha suspensa*.

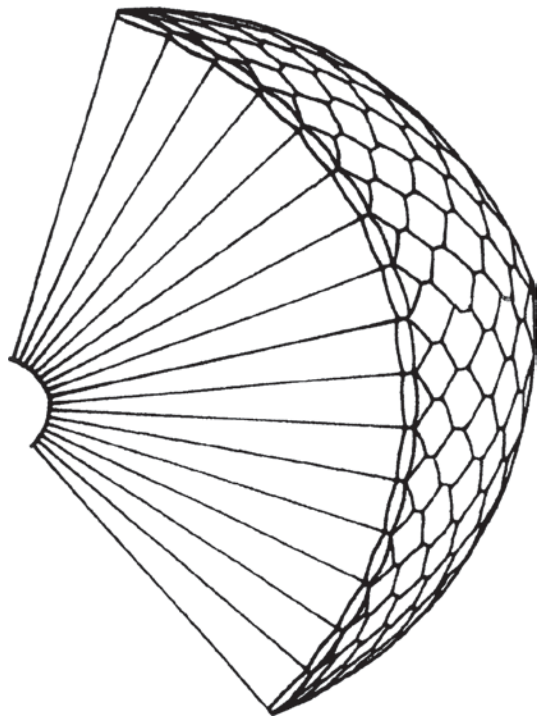


Eyes and Vision, Figure 58 A diagrammatical view of an ocellus showing a single lens, and pairs of retinula cells, each with a rhabdomere region.

possible to say what sort of image the insect sees, because it really sees with the integrative centers in the brain. Does the insect see dozens or perhaps hundreds of small images at once, or does the brain synthesize the incoming data into a single image? No one really knows. Ocelli have the necessary structure to form images, but in cases where detailed studies have been done, the images are focused below the level of the photosensitive cells, so it seems unlikely that insects actually receive an image in the brain from ocelli. Ocelli probably function mainly in detecting the quality and intensity of light, and its presence or absence. Stemmata, the visual receptors in larvae of many holometabolous insects, also can form an image, but stemmata are very small, and it is likely that any image is fuzzy and poorly resolved. The immature stage of grasshoppers, bugs, cockroaches, and other hemimetabolous insects have compound eyes similar to the adult compound eyes. Compound eyes, ocelli, and stemmata follow the same basic structural plan, with a lens to focus the light, light sensitive cells, and axons from the photoreceptive cells projecting to the brain. In all three types of eyes the photoreceptive cells have a rhabdomere region with many membrane layers that contain the visual pigment molecules.

Compound Eye Structure

Viewed from the surface, a compound eye has the appearance of being composed of hexagons. The hexagonal shape is created by the fitting together of multiple facets or units of the compound eyes called ommatidia. A single ommatidium is composed of the dioptric structures (cornea, lens, cone and sometimes other structures that bend and focus the light) the photoreceptor cells, and (Fig. 59) usually additional cells that contain shielding pigments that shield the photoreceptor cells from light entering adjacent facets. The photoreceptor cells actually are the cell bodies of specialized nerve cells, and their axons pass into the brain of the insects. The photoreceptor cells contain the photosensitive pigment, rhodopsin, which is synthesized from a chromophore and a protein (opsin). When light strikes the rhodopsin, it excites the chromophore, leading to a nerve impulse that is passed into the brain by the axons from the photoreceptor cells.



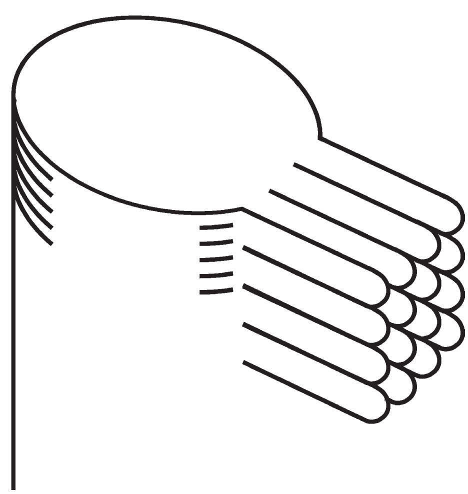
Eyes and Vision, Figure 59 A representation of a section through a compound eye showing multiple facets.

The size of the compound eyes and the number of facets or ommatidia in each eye are variable. A silverfish (*Lepisma* spp., order Zygentoma [Thysanura]) has only 12 ommatidia in each of its small eyes, but a dragonfly has big eyes, each containing thousands of ommatidia. Collembola, Zygentoma, Siphonaptera, and Strepsiptera do not have compound eyes, but they do have light-sensitive structures similar to ocelli.

Compound eye structure evolved adaptively in slightly different ways in diurnally active and nocturnally active insects. Diurnal insects are active during the day when light is bright, and have photopic or apposition eyes; those active in dim light, such as at dusk or at night, have scotopic or superposition eyes. In photopic eyes, the photoreceptor cells are located just below the dioptric structures and extend to the basement membrane. Pigment in accessory cells arranged in a circle around the photoreceptor cells shields the rhodopsin in the photoreceptor cells from light in adjacent facets, and ensures that only light that enters directly from above can strike the visual pigment in a given ommatidium. This arrangement is thought to make for a sharper image focused on the rhabdom of the photoreceptor cells in a particular ommatidium.

When light is very dim, sharpness of vision may not be as important as perception of form and movement. Scotopic eyes in nocturnal and crepuscular insects show light and dark adaptation. In dark adaptation, the pigment in shielding cells migrates or clumps in one end of the cells, leaving them more transparent to light from adjacent ommatidia, and allowing light from several ommatidia to strike the rhabdom of nearby photoreceptive cells. Thus, a particular photoreceptor cell may receive light and images superposed upon each other from nearby facets. Hence, the older name "superposition eye." This arrangement allows more light to enter each facet, but probably makes for a very fuzzy or blurred image because it is unlikely that all the images will be perfectly superimposed upon each other. Brighter light and higher temperatures (both typical of earlier in the evening for night active insects) cause the pigment in shielding cells to disperse throughout the shielding cells, thus shielding the photoreceptor cells from much or all light from adjacent facets. This converts the superposition eye into something that more nearly functions like a photopic eye, possibly with sharper images (as long as the light is brighter). Migration of the pigment to cause shielding of the photoreceptor cells may protect the visual pigment from being bleached by bright light. Nocturnally active insects usually have a network of tracheal tubes (called the "tapetum") beneath, and sometimes as a part of, the compound eyes, and the white, shiny tracheal tissue reflects light back up into the eye. This structural arrangement allows additional light to interact with the visual pigment in the photoreceptors, but also likely makes any image very fuzzy. The reflected light from the tapetum produces the eye shine seen when a light shines on a moth or other night active insect. The eye shine may be variously colored because of the shielding pigments in the eye.

The light-sensitive cells that contain the visual pigment are called "retinula cells" in the entomological literature. They are primary (Fig. 60) receptors, which simply means that their axons project into the optic lobe of the brain before synapsing. By way of contrast, the rods and cones in the human eyes are secondary receptors because their axons synapse several times before reaching the brain. Typically there are eight retinula cells arranged in a rough circle in each ommatidium, but some Lepidoptera have as many as 10–11; honeybees have nine. Sometimes the compound eye is divided into dorsal and ventral parts; adult dragonflies have four retinula cells in each ommatidium in the dorsal part of the eye, and six in the ventral part. Usually the eighth cell, or in honeybees the ninth cell, is short and extends only in the more proximal region (i.e., towards the brain) of an ommatidium. Retinula cells vary greatly in length. They are 60–100 μm long in *Drosophila melanogaster*, about 100 μm long in the American



Eyes and Vision, Figure 60 A representation of the microtubules composing the rhabdomere of a retinula cell.

cockroach, and from 150 to >200 μm long in the tephritid fruit fly *Anastrepha suspensa*.

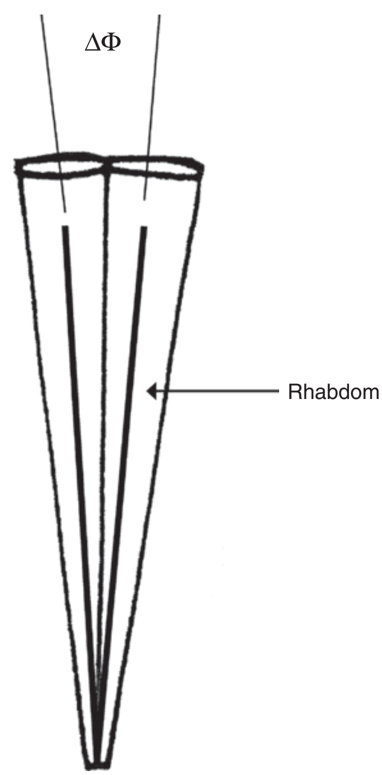
The visual pigment, rhodopsin, is contained in the rhabdomere, a special region of retinula cells that is convoluted into thousands of microvilli or microtubules ending blindly near the center of the circle formed by the retinula cells in a single ommatidium. The tubules typically are about 40–120 nm in diameter along all or part of the length of the cell. In *D. melanogaster*, there are about 60,000 microvilli along the length of each retinula cell, and about 80,000 in each rhabdomere of the American cockroach. A vast surface area is presented by these numerous folds of the cell membrane, and it is in the membrane of these tubules that the molecules of visual pigment, estimated by some researchers to be up to 100 million molecules of rhodopsin per cell, occur.

In some insects, the rhabdomeres of retinula cells in an ommatidium touch or fuse at the center of the circle to form a closed or fused rhabdom, as in honeybees, Lepidoptera, and many other insects. In Diptera and Hemiptera the rhabdomeres do not fuse, but face a central hollow cylinder in the ommatidium. When light strikes the visual pigment, the retinula cell undergoes a depolarization. The depolarizing effect of light is in contrast to the polarizing effect that light has upon the receptors in vertebrate eyes. Resting potentials ranging from 25 to 70 mv have been recorded across the membranes of retinula cells. The inside of the cell is negative relative to the outside during resting conditions in the dark. An electroretinogram (ERG) of electrical activity in response to stimuli can be recorded by placing one electrode on or into the eye and the reference electrode somewhere else in the head. An ERG is a summation of potentials from many retinula cells, and possibly of electrical activity within the optic lobe.

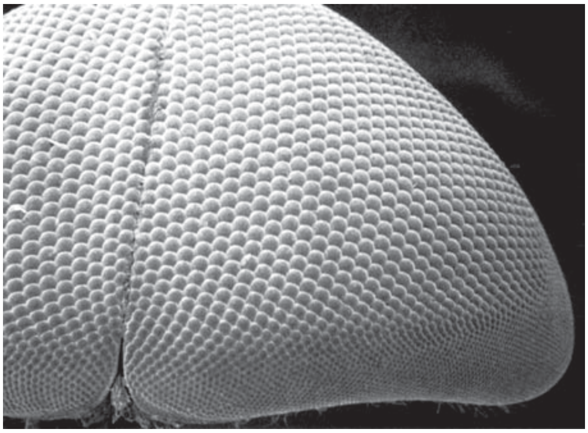
Visual Acuity

Visual acuity is a measure of how well objects can be resolved. Put simply, higher visual acuity means better ability to see objects in the environment and to navigate, capture prey, and chase a potential mate in flight. Insect eyes, however, do not even come close to having the acuity and resolving power of human eyes. The principal factors that determine visual acuity of compound eyes include the angle between two adjacent ommatidia, the optical quality of the dioptric structures that focus the light, dimensions of the rhabdom, the light level, and speed of movement across facets of the eye. The small size of facets of the compound eyes severely limits visual acuity, and larger facets increase visual acuity. The diameter of facets in compound eyes of many insects vary over different parts of the eyes.

The angle between two adjacent ommatidia (Fig. 61) is one important factor that determines acuity of vision. Dragonflies are among the insects that have the most acute vision, with an



Eyes and Vision, Figure 61 The interommatidial angle between two adjacent ommatidia or facets in the compound eye. Smaller values for the angle $\Delta\phi$ increase the possibility for greater visual acuity.



Eyes and Vision, Figure 62 **A scanning electron micrograph of the left compound eye, and a portion of the right eye, of a male horsefly *Tabanus lineola* showing the larger facets in front and extending to the top of the eye. Note smaller facets near the lower rim of the eye. Larger facets represent a fovea or area of the compound eyes with greater visual acuity. The eyes from each side of the head meet in males, but not in females (Photo courtesy of Dr. Jerry Butler, University of Florida.)**

interommatidial angle as small as 0.24°. Most insects have considerably larger interommatidial angles of several degrees up to tens of degrees. The smaller the interommatidial angle, all other factors being equal, the greater the distance at which objects such as prey, a predator, or the surrounding vegetation can be resolved. The very small nature of the lens in compound eyes severely limits resolving power because of diffraction. A human eye has much greater resolving power than a single facet of a compound eye because it is larger, has a larger opening to let light in, and has a single lens. Compound eyes are excellent motion detectors, but the fast movement of objects over the eyes causes any image to be blurred, just as movement of objects, or of the camera, causes blurring in photographs.

Insect compound eyes perform poorly in very dim light, but insects that are active at night or at dusk have special adaptations for vision in dim light. These may include wider facets and wider rhabdoms that increase sensitivity by up to 1–2 log units.

Some insects have variations that provide zones of greater acuity of vision (a "fovea") in certain parts of the eye than other parts. The fovea refers to the region in the human eye with the greatest density of cones (color and bright light sensitive) where resolution is greatest when the eyes are focused directly on the object. An "acute zone" has evolved in the forward facing, and sometimes upward looking, part of the compound eyes in some fast flying insects, particularly those that capture prey in flight, or chase flying potential mates. An insect in relatively straight line flight has a relatively stationary field of view straight in front, but highly blurred vision at the sides of the eyes as objects in the environment flash across the field of view. Bees, butterflies and some acridid grasshoppers have an acute zone in the front of the compound eyes, and better vertical acuity in a band around the equator of the eye. Male blowflies, drone honeybees, male hoverflies, some tabanid flies, and some other male insects that look for potential mates while flying have an acute zone that probably enables them to see the female better, particularly against the sky as a background. Both sexes of mantids, dragonflies, and robber-flies have higher visual acuity near the forward part of the eye that likely enable them to see and capture prey more effectively. The fast flying dragonfly *Anax junius* has 28,672 ommatidia per compound eye, with the smallest known interommatidial angles, and they have an acute zone in the dorsal part of the eye with relatively large facets as much as 62 μm across. This gives the dragonfly ability to catch mosquitoes and other small insects in flight.

Another insect with good vision is the praying mantis *Tenodera australasiae*. Facet diameters in the acute visual zone in the front of the eyes measures up to 50 μm across and they have overlapping acute zones in the large binocular looking eyes that enable them to determine distance of a prey object by binocular triangulation. They strike and capture the prey with the prothoracic pair of forelegs.

The Optic Lobe

The optic lobes extending out toward the compound eyes are large in those insects with large eyes. These optic lobes are part of the protocerebrum, the dorsal part of the brain. Three large neuropils in the optic lobes are sites of synaptic connections. The largest of the neuropils is the lamina ganglionaris, and it is the first synaptic region for incoming axons from the photoreceptors. There is a great deal of crossing of axons as they pass from the retinula cells to the lamina ganglionaris, so that axons from the same ommatidium do not converge upon a single monopolar interneuron. Additional crossing of axons occurs after synaptic connections in the next two neuropils, so that the signals from the individual ommatidia are not conveyed to the integrative centers of the brain as a direct representation of each ommatidium. Although we cannot know exactly what image an insect sees, it is reasonable to assume that its brain synthesizes the information into some sort of whole rather than seeing 28,672 little images (the number of ommatidia in each compound eye of the dragonfly *Anax junius*). The large amount of crossing of neural fibers in the optic lobe of insects is not peculiar to insects, but it is a general feature of visual systems in other animals including humans. Its function is not clearly understood, but it would appear to provide a great deal of back-up security if only some parts of either the external eye or brain receiving the input suffer damage.

Ocelli and Stemmata

Ocelli and stemmata share some similarities with a single ommatidium in a compound eye. The cuticle covering the ocelli and stemmata acts like a lens, focusing the light. Retinula cells below the cuticlar covering have a rhabdomere region of tubules where the visual pigment occurs. The axons from the retinula cells in an ocellus are gathered into the ocellar nerve that projects into the protocerebrum. The evidence suggests that any image formed is focused beneath the layer of retinula cells in an ocellus, and thus probably cannot be transmitted to the brain. Retinula cells show spontaneous electrical activity in the dark, and stimulation by a light beam leads to a more stable and increased transmembrane electrical potential rather than a depolarizing effect as shown by retinula cells in the compound eye. Ocelli likely function to signal light on-off information, intensity of illumination, and possibly in some insects they convey wavelength of stimulating light. The number of retinula cells in an ocellus is variable in different insects; honeybees, for example, have three ocelli and each contains about 800 retinula cells.

Stemmata are eyes in the larvae of some holometabolous insects, with one to six occurring on the head of different larvae. Stemmata have an overlying transparent cuticle and a few retinula cells with rhabdomere regions. Some stemmata have a crystalline lens, and some larvae have two separate rhabdoms, a distal one and a proximal one. An image that falls on the rhabdomere surfaces seems likely, but because of so few photosensitive cells, it is probably poorly, if at all, represented in the brain of the larva. Caterpillars frequently move the head from side to side, which may be a behavior that aids them in obtaining a wider field of view with small, multiple stemmata.

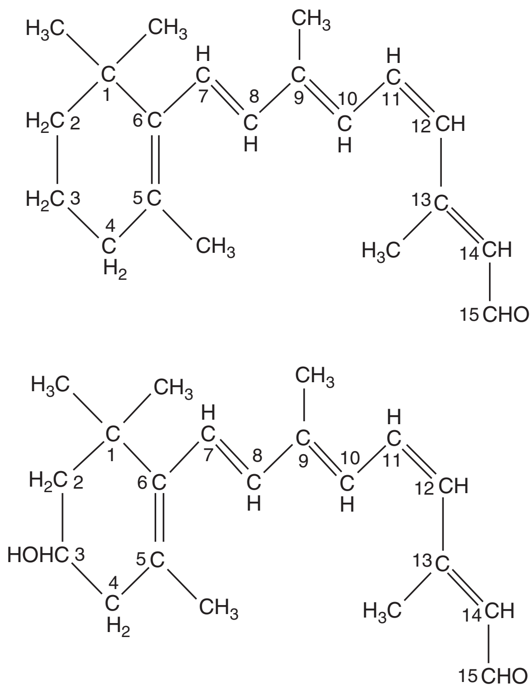
The Chemical Cascade Leading to Vision

The chromophore in insect eyes is 11-*cis*-retinal, or in some insects, 11-*cis*-3-hydroxyretinal. When a photon of light is absorbed by rhodopsin, 11-*cis*-retinal is isomerized to 11-*trans*-retinal. Contrary to the light absorbing reaction in vertebrate eyes, retinal and opsin do not separate from each other in light-activated insect eyes. Light stimulated rhodopsin in insects is called metarhodopsin, and it is a catalyst that activates a fast cascade of chemical reactions in the retinula cells, resulting in generation of a nerve impulse. This signaling pathway is extremely fast, and can be turned on and off, and repeated, many times per second. Measurements in *D. melanogaster* indicate that it takes only several tens of milliseconds to proceed from light activation of rhodopsin to the generation of a nerve impulse. The fact that portions of the visual cascade involves a number of enzyme reactions means that an initial stimulus is amplified as much as 100–1,000 times, turning a few photons of light into a barrage of nerve impulses to the optic lobe. In vertebrate eyes the 11-*trans*-retinal must be reconverted through a series of enzymatic steps in the dark part of the eye into 11-*cis*-retinal, which is combined with opsin to form a new molecule of rhodopsin. In insects, rhodopsin and metarhodopsin are in a dynamic state of equilibrium, and another photon of light can be absorbed by the metarhodopsin/11-*trans*-retinal complex and become converted into rhodopsin/11-*cis*-retinal, a process called photoisomerization. Although the anatomical structure of eyes seems to have evolved a number of times independently, the chemistry of vision is nearly the same in all organisms, and thus provides a link between invertebrates and vertebrates.

Color Vision

Color vision is the ability to discriminate between two wavelengths of light. Color vision may have existed in some insects since the Devonian period, about 300 million years ago. Many insects probably have color vision, but only a few have been studied enough to be certain. Behavior tests, electrophysiology, and molecular characterization of the visual pigment molecules have been used to characterize color vision.

Retinal is held to the opsin in a "pocket" by the ε-amino group of the amino acid lysine in the opsin molecule. The absorption maximum of 11-*cis*-retinal alone is at 380 nm and it absorbs little light longer than 400 nm. When complexed with opsin, however, the opsin tunes the absorption from 360 nm to about 640 nm. Certain amino acid substitutions in locations near the binding pocket for the chromophore influence the absorption spectrum as well, and screening pigments in the cells surrounding the circle of retinula cells in some insects seem to be able to alter the spectral sensitivity of rhodopsin. Insects usually have at least three, and sometimes more rhodopsins, each showing a different absorption maximum. All insect orders that have been tested have green-sensitive photoreceptor cells, and probably most have UV sensitive rhodopsin, which explains why entomologists can use UV lights to attract many kinds of insects. Most, but not all, insects also seem to have a blue-sensitive rhodopsin, but some appear to have lost the blue sensitive pigment over time. The painted lady butterfly, *Vanessa cardui*, has one rhodopsin that absorbs light maximally in the UV region at 360 nm, another absorbs in the blue region maximally at about 470 nm, and one is maximally sensitive in the green part of the spectrum at about 530 nm. The nymphalid butterfly *Heliconius erato* has three rhodopsins, with peak absorptions in the UV range, one in the blue-green range, and one absorbing maximally at long wavelengths between 590 and 640. Although the butterfly has only one rhodopsin for absorption in the red region, it has been shown experimentally that the butterfly can discriminate colored light at 590 nm, 620 nm, and 640 nm. This means it can distinguish yellow-orange from orange from orange-red with only one rhodospin, which would not be expected to give this ability to discriminate shades of red; *Vanessa atalanta*, another lady butterfly, can distinguish red color from green and blue, but cannot distinguish the differences in the red part of the spectrum as can *H. erato*. The Japanese yellow swallowtail butterfly, *Papilio xuthus*, has receptor cells in which rhodopsins are present that absorb maximally in the UV at 360 nm, violet range at 400 nm (sensitivity to violet color may be because the receptor pigment is being tuned by filtering pigments; a rhodopsin with a spectral peak at 400 nm is not common in insects), blue range at 460 nm, green range at 520 nm,



Eyes and Vision, Figure 63 **Chemical structure of 11-*cis*-retinal (above) and 11-*cis*-3-hydroxy retinal (below). When combined with the protein opsin, the visual pigment rhodopsin is formed.**

and red range at 600 nm. The butterflies were trained by Japanese workers to feed on sugar water from dishes placed on colored discs of paper in the laboratory. The butterflies most easily learned to look for food on red and yellow colors, but training to other colors required more training time, and they lost the ability to distinguish blue when the intensity of the color was reduced to 80% of the training intensity (intensity was reduced by placing neutral density filters over the color). Another swallowtail, *Papilio glaucus*, has rhodopsins with maximal absorption at approximately the same maxima as *P. xuthus*, except it does not have one absorbing in the violet range at 400 nm. Most moths are not sensitive to red. Sensitivity may not be very important in dim light because it cannot be distinguished from black; humans lose the ability to distinguish most colors in dim light because the cone cells in the retina that contain the rhodopsins sensitive to color do not work well in dim light. The tobacco hornworm, *Manduca sexta*, has UV, blue, and green receptors, but no red receptor.

Honeybees have color vision and were one of the first insects in which perception of color was demonstrated with behavioral tests. The German scientist and behaviorist Karl von Frisch (who received the Nobel prize for this and subsequent behavioral work with bees) trained honeybees to come to sugar water in a small dish placed on a sheet of blue paper lying on a table outdoors. After the bees had communicated the location to others in their hive (by the bee dance) and had recruited a regular stream of visitors to the dish, von Frisch replaced the blue paper with a clean one and an empty dish (the bees might have left an odor on the previous paper after alighting on it many times, and they might somehow smell the sugar solution or have added some olfactory cue to it by their feeding). He also made a checkerboard arrangement around the blue paper with gray papers of the same size as the blue one and graded in intensity from white to black. Each paper contained an empty dish. Von Frisch reasoned that color blind bees would confuse the blue paper with one or more of the gray papers, and probably would alight on the wrong dish or paper in their search for sugar solution. They were not confused, however, but flew directly to the dish (now without sugar water) on the blue paper. He performed many variations of this experiment, and found that the bees could be trained to come to sugar water on some other colored papers, but they could not distinguish red from black or dark gray colored papers. Subsequent work including electrophysiological analysis of the spectral sensitivity of the honeybee compound eye demonstrated that they have receptors that show maximum sensitivity at 344 nm (UV), 436 nm (blue), and 544 nm (green). They do not have a red-sensitive receptor, which explains why von Frisch could not train them to discriminate red papers containing sugar water.

Evolution of red receptors in insects has been relatively recent, and sporadic with respect to which groups have red receptors. Red receptors evolved at least four times in Lepidoptera, but some Lepidoptera may have subsequently lost the red receptor. Duplications of the green sensitive opsin, and occasional substitution of amino acids at crucial sites in some of the duplicates, probably led to the evolution of a red-sensitive rhodopsin in some insects.

Visual stimuli have been shown to be important to insects in various behavioral experiments. In flight tunnel tests, *M. sexta* moths responded best by flying up wind when visual cues (a white paper flower) were presented with an olfactory stimulus (oil of bergamot, a known attractant for the moths). When the two stimuli were presented spatially or temporally separate from each other, the moths showed a response to both, but less than to both presented together. The authors of the study concluded that the visual stimulus was the ultimate indicator of a nectar (food) source. The pine weevil, *Hylobius abietis*, when seeking an oviposition site, also showed the best (walking) response when a visual stimulus (a green wire with green plastic twigs to simulate a young pine seedling) was presented with pine odor. The response to the two together was additive, with reduced response to either stimulus presented alone. Attraction to the visual stimulus alone was clearly demonstrated, however.

Detection of Plane Polarized Light by Insects

Many invertebrates are able to detect plane polarized light, but humans can only detect it with instruments, not with their eyes. Most of the light from the sun is not polarized, and the waves vibrate in every conceivable direction, but a small percentage of the light becomes polarized by molecules and particles in the atmosphere. Light reflected from waxy and shiny surfaces, such as leaves, or other objects in the environment, also has a polarized component. Polarized waves vibrate in a specific plane, and the e-vector (vibration plane) and intensity of polarization vary with the position of the sun above the horizon, and consequently they change constantly. It is remarkable that so many invertebrates have evolved the ability to detect the plane of polarization, and some, such as honeybees, use a celestial (sun) clock to track both time and plane of polarization. When honeybees fly out from the hive to collect nectar, they often wander from site to site and spend considerable time away from the hive. The plane of polarization and the position of the sun above the horizon will have changed since their outbound flight, and they cannot find the hive again by following the old data from the outward flight. They update the data and fly back in the so-called "bee line" dictated by the new position of the sun and new plane of polarization. Houseflies, *Photurus pennsylvanicus*, fireflies, Japanese beetles, and several species of ants orient to plane polarized light under conditions that prevent them from using background reflections as orientation cues, but whether they use it in a sophisticated manner as do honeybees has not been demonstrated. Another insect that uses celestial navigation and polarization for homing after foraging is the ant *Cataglyphis bicolor*, which is found in North African deserts. It uses plane-polarized light to travel a direct path to its nest in the ground after having wandered, with many turns, up to 100 m in search of food. In most, if not all cases observed, it is the UV sensitive photoreceptor cells in the dorsal rim area of the compound eyes that seem to most often be the cells that detect the plane of polarization. When a UV absorbing shield was held over ants in the field, they began to wander aimlessly, unable to locate their underground nest. The red wood ant, *Formica polyctena*, of northern Europe uses polarized light as a compass. The precise way in which these insects determine the plane of polarization and how they measure time lapse is not known with certainty. The desert locust, *Schistocerca gregaria*, responds to polarized light, especially with two identified neurons named Tutu1 and LoTu1. These neurons respond to both polarized and ordinary light, and their response to plane polarized light is based on blue-sensitive photoreceptors in the dorsal rim area of the compound eyes. The LoTu1 neurons showed approximately two log units greater sensitivity to polarized light than to nonpolarized light.

In what ways other than homing could polarized light be useful to invertebrates? Desert locusts, for example, do not show homing behavior, but they might use polarized light during migrations, and reflected polarized light from plant food sources may be processed by the polarization receptors. The red swamp crayfish (not an insect of course), is sensitive to plane polarized light in behavioral tests. How the crayfish might benefit from detecting polarized light is not clear from experiments, but they may be able to detect transparent prey by the reflection of polarized light from their bodies, and may detect predator fish by reflection of polarized light from their silvery scales. Their compound eyes are similar to the compound eyes in insects, and the dorsal rim area of the eyes appears to be a site for detection of plane polarized light.

Monarch butterflies use a time-compensated sun compass during long migratory flights to Mexico, but behavioral experiments in a flight simulator that allowed the butterflies to take off in flight when exposed to patch of naturally polarized light from the sky, to artificial polarizers, or to the open sky did not indicate that the plane of polarization made any difference in their orientation. When the dorsal rim area of the compound eyes was painted with black paint, they still used their time-compensated sun compass in orientation, but presumably could not detect the plane of polarization. The authors of these experiments concluded that the butterflies do not need polarized light cues to orient in their flight, but the ability to detect the e-vector of polarization might still be useful in some ecological way that these experiments did not probe.

Neotropical butterflies (family Nymphalidae) in Costa Rican tropical forests appear to use polarized light reflected from the shiny surfaces of leaves and the surface of insects to detect forage and oviposition sites, and to identify conspecifics in the low light intensity of the forest foliage. Polarized light may be useful in motion detection, particularly in dim light. Mayflies (order Ephemeroptera) probably use reflected polarized light to identify water surfaces where they can lay their eggs. Unfortunately, they also can be fooled into laying them in the wrong place; mayflies in one location were discovered laying masses of eggs on asphalt road surfaces near the stream from which they emerged. Measurements with instruments designed to measure polarized light indicated that the asphalt surface with the sun shining on it reflected plane polarized light in much the same way that the sunlit water surface in their stream did. Thus, some mayflies were laying their eggs in an environment where they had no chance to hatch.

The dung beetle *Scarabaeus zambesianus* forages for fresh animal dung around sunset, a time when light intensity is low and the polarization pattern in the sky is the simplest of the day, with light of the entire sky polarized in one direction. When the beetles locate fresh dung, they quickly make a ball and roll it away in a straight line, apparently an adaptive mechanism to avoid competition and possible predator or parasite detection at the fresh dung. Experiments with polarization filters that change the e-vector of polarization, show that the beetles are sensitive to the e-vector and reorient their rolling behavior in response to an experimental change in the e-vector. The dorsal rim area of the compound eyes has photoreceptor cells with large rhabdom surfaces, a lack of screening pigments in surrounding cells, and the microvilli in the rhabdoms oriented orthogonal to each other (perpendicular to each other), all features providing the best arrangement for detecting the contrast in e-vector of polarized light. The beetles cease foraging about 40–50 min after sunset, when the degree of polarization at the zenith of the sky decreases from 45% to 5% within 15 min. The change in polarization, of course, might not be the sole factor involved in their behavior.

In the field cricket *Gryllus campestris*, photoreceptor cells have orthogonally oriented microvilli in the dorsal rim area of the compound eyes with a blue-sensitive rhodopsin (λmax about 440 nm).

The cells show strong sensitivity to the e-vector of polarized light, and their input converges on polarization sensitive neurons in the optic lobes of the brain. Inputs from about 200 ommatidia converge upon the optic lobe neurons, which increases the signal-to-noise ratio and sensitivity to the e-vector.

References

Briscoe AD, Chittka L (2001) The evolution of color vision in insects. Annu Rev Entomol 46:471–510

Douglas JM, Cronin TW, Chiou T-H, Dominy NJ (2007) Light habitats and the role of polarized iridescence in the sensory ecology of neotropical nymphalid butterflies (Lepidoptera: Nymphalidae). J Exp Biol 210:788–799

Gilbert C (1994) Form and function of stemmata in larvae of holometabolous insects. Annu Rev Entomol 39:323–349

Kinoshita M, Pfeiffer K, Homberg U (2007) Spectral properties of identified polarized-light sensitive interneurons in the brain of the desert locust *Schistocerca gregaria*. J Exp Biol 210:1350–1361

Land MF (1997) Visual acuity in insects. Annu Rev Entomol 42:147–177

Wolken JJ (1995) Light detectors, photoreceptors, and imaging systems in nature. Oxford University Press, New York, NY, 259 pp

Zaccardi G, Kelber A, Sison-Mangus MP, Briscoe AD (2006) Color discrimination in the red range with only one long-wavelength sensitive opsin. J Exp Biol 209:1944–1955

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Fabre, Jean-Henri Casimir

Jean-Henri Fabre was born at Saint-Léons, southern France, on December 22, 1823. He received little education in school, and taught himself several subjects as a trainee teacher in Avignon. For this, he received a diploma, and found low-paying jobs as a schoolteacher. He married Marie Villard, another teacher. Now, he devoted his free time to studying insects. This gained him no recognition from his employers, but brought him attention from scientists. He was recognized in Paris, and given a high award: the Légion d' Honneur medal. Relations with his employers worsened and, in 1870, when he admitted girls to his science classes, he was fired. An English economist, philosopher and friend, John Stuart Mill, lent him money. Royalties from his numerous popular books on scientific subjects, and his teaching of evening classes, allowed him to live with his family, repay Mill, and even buy a small house on a plot of land. In 1879 he retired from teaching, and went to live in that house, and published the first of what became a series of works on entomology, called "Souvenirs entomologiques." But his wife Marie, who had borne five children, died. "Souvenirs entomologiques," which eventually ran to 10 volumes, contains careful accounts of insect behavior and life cycles, made from his field observations close to his home, and for that are admirable. At the age of 65, he married Marie-Joséphine Daudel, and they had three children. Unfortunately, his books were selling poorly, now because of his antievolutionary viewpoint. Then, in 1909, his fortunes changed. He was "discovered" by national writers and lauded. He was awarded a government pension, and his books began to sell again. But his second wife died in 1912, and he on October 11, 1915.

References

Favret F (1999) Jean-Henri Fabre: his life experiences and predisposition against Darwin. Am Entomol 45:38–48

Teale EW (1949) The insect world of J. Henri Fabre. Dodd, Mead & Co, New York, xvi + 333 pp

Fabricius, Johann Christian

Johann Fabricius (Fig. 1) was born in Tondern, Denmark, on January 7, 1745. He obtained his university education in Copenhagen and Uppsala, at the latter being a student of Linné. He worked as a professor at the universities of Copenhagen (1770) and Kiel (1775). These professorships (at both universities) were in natural history, economy and finance, evidencing the philosophy of the times. Whereas Linné had general interests in the description and classification of plants and animals, Fabricius specialized in insects. With this specialization, he described and named almost 10,000 species of insects contrasted with the 3,000 named by Linné. He also developed insect classification substantially; whereas Linné used characters provided by the wings, Fabricius added characters provided by the mouthparts to do this. He wrote several books, developing and expanding his

Fabricius, Johann Christian, Figure 1 **Johann C. Fabricius.**

classification of insects. They were (1775) "Systema entomologiae," (1776) "Genera insectorum," (1781) "Species insectorum," (1787) "Mantissa insectorum," (1792–1799) "Entomologia systematica" and "Supplementum," (1801) "Systema rhyngotorum" (Hemiptera), (1804) "Systema piezatorum" (Hymenoptera), (1805) "Systema antliatorum" (Diptera), and (1807) "Systema glossatorum" (Lepidoptera, which was never finished). They were written in Latin, which was then the international language of science. The major ones were published in Copenhagen, Kiel, and Leipzig, whose Latinized names are Hafnia, Kilia, and Lipsia. The title pages of the books, following names of the publishing companies, give these Latinized names in the genitive case, Hafniae (meaning "of Copenhagen"), Kiliae, and Lipsiae, a detail that eludes many modern bibliographers. In other words, a book may be said to have been published in Copenhagen (English spelling, used if you are writing in English) or København (Danish spelling, used if you write in a Scandinavian language) or even (if you must be incredibly pedantic this spelling is not wrong) "in Hafnia," but it is an error to say that it was published "in Hafniae."

References

Herman LH (2001) Fabricius, Johann Christian. Bull Am Mus Nat Hist 265:61–62

Tuxen SL (1967) The entomologist J.C. Fabricius. Ann Rev Entomol 9:1–16

Face

The front of the head, below the frontal suture (Fig. 2).

► Head of Hexapods

Face Fly, *Musca autumnalis* De Geer (Diptera: Muscidae)

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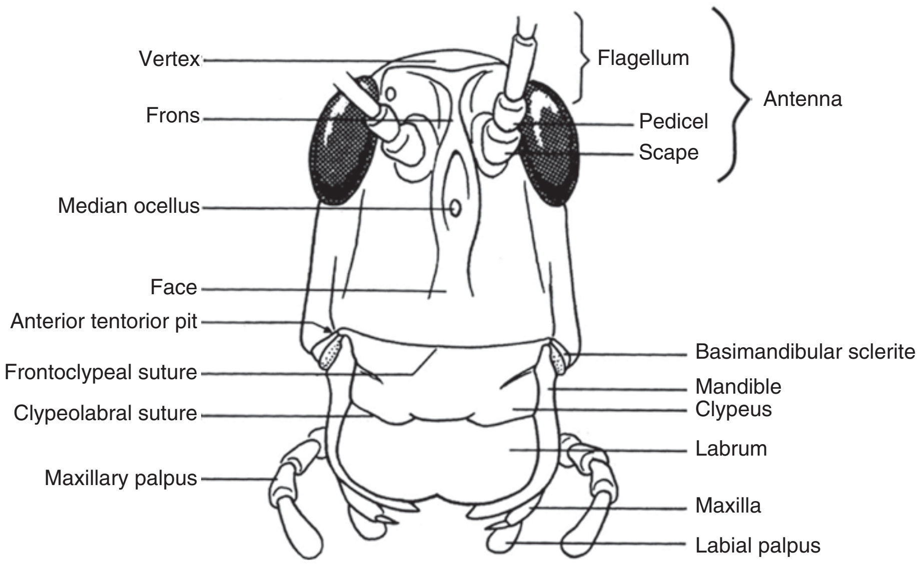
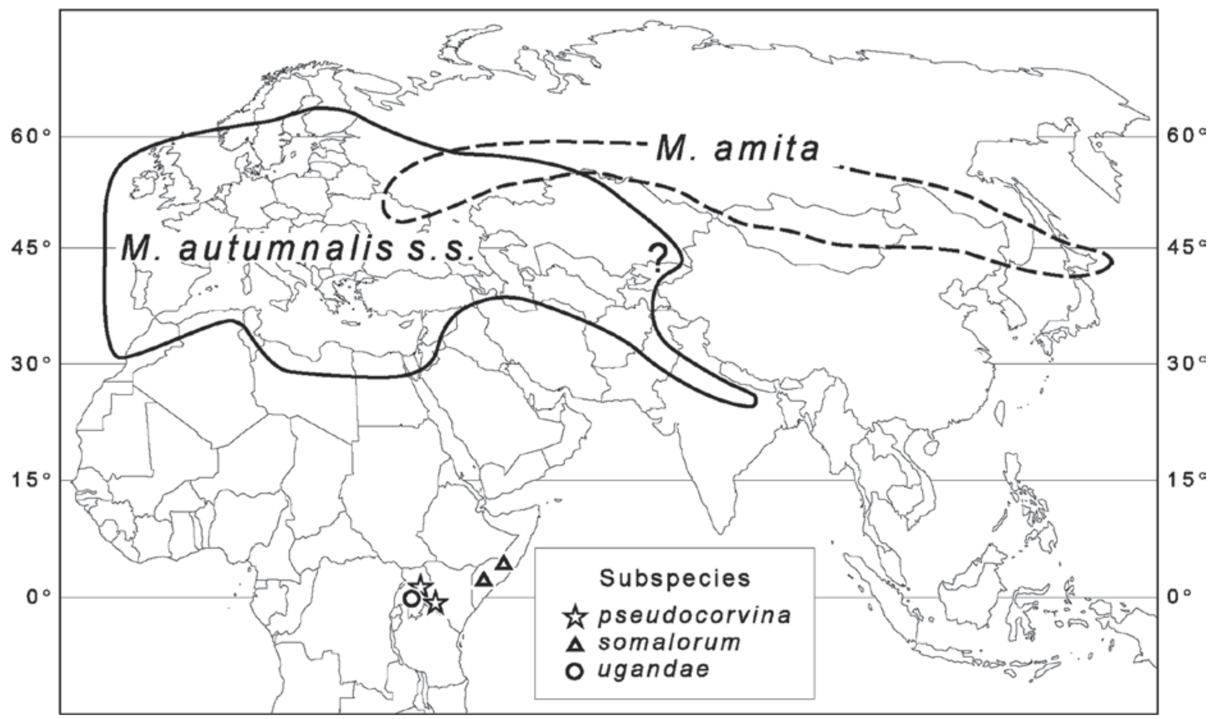
Face fly, *Musca* (*Eumusca*) *autumnalis* De Geer, is one of only two *Musca* species recorded in North America, the other being the house fly, *M.* (*Musca*) *domestica* L. Three *M. autumnalis* subspecies have been described; two occur in Uganda and a third in Somalia (Fig. 3). We doubt their status because of the great distance from other conspecific populations, all of which occupy temperate regions and undergo a facultative reproductive diapause when daylengths approach 12 h. Recent genetic research utilizing mitochondrial nucleotide sequence variation suggests the occurrence of a morphologically indistinguishable sibling species in southeastern Kazakhstan.

In gross appearance, face flies look much like house flies but they tend to be larger and are found in different habitats. Eyes of female face flies are more completely holoptic than in house flies, and the male face flies are completely holoptic, unlike house flies. The basal abdominal pleuron of female



Face, Figure 2 **Front view of the head of an adult grasshopper, showing some major elements.**



Face Fly, *Musca autumnalis* De Geer (Diptera: Muscidae), Figure 3 **Old World distribution of *Musca autumnalis*. The occurrence of a presumptive sibling species to *M. autumnalis* is indicated by the question mark in Kazakhstan (modified after Krafsur and Moon, Annu. Rev. Entomol. 42).**

face flies is yellow, and succeeding pleura are gray-black, whereas the lateral pleura of house fly females more frequently are cream in color. The abdominal pleura of male face flies are bright yellow against a distinctly black dorsal stripe, a trait not commonly shown by male house flies.

Face flies differ greatly from house flies in habits and biology. Face flies are exophagic and exophilic, occurring around bison, pastured cattle and horses. They oviposit only in fresh bovine dung where larval development occurs. Only overwintering face flies in diapause may be found in human or livestock dwellings. In contrast, house flies are ubiquitous in and around human and animal habitations and oviposit and develop as larvae in many kinds of fermenting organic matter.

The veterinary and economic importance of face flies is related to the feeding habits of females, which seek protein from the eyes, noses and other orifices of cattle and horses. In so doing they can serve as vectors of eyeworms (*Thelazia* spp.), hemorrhagic bovine filariasis (*Parafilaria bovicola*), and the agents of "pinkeye" or infectious bovine keratoconjunctivitis (*Moraxella bovis*). When abundant, face flies annoy cattle and horses and are said to disrupt grazing patterns, but the economic significance of this remains to be demonstrated. Female face flies seek protein to support egg development and they do so in each successive gonotrophic cycle. Thus, the vectorial capacity of a face fly is related to her reproductive age. Sex ratios of adults around hosts are highly biased during the breeding season, from April to mid-September. Male face flies do not seek protein but can be found near animals albeit in much smaller numbers than the females. Males are found in much greater numbers perching at the margins of woods, on fences, and other sunlit surfaces. In these locations females are comparatively few and most are virgins. In very late summer, autumn, winter, and early spring, face flies may also be found on sunlit windows and walls in some human dwellings where diapausing flies are thought to have sought overwintering sites. Here the sexes occur in equal numbers.

Distribution and Colonization of North America

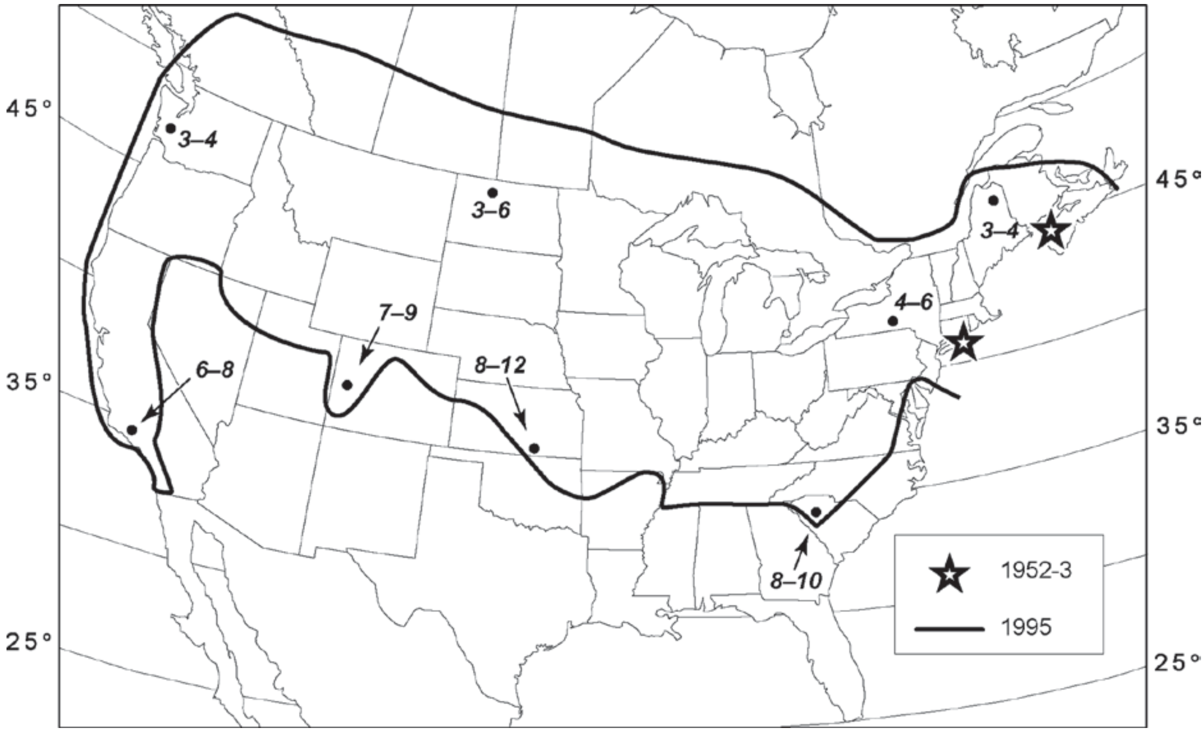
Musca autumnalis s.s. is Palearctic, occurring from the British Isles south to northern Africa and east to Pakistan, Kazakhstan, northern India, and Nepal. Face flies colonized North America only recently. They were first detected in Nova Scotia in 1952, and secondarily recorded in New York in 1953. They rapidly spread through the northern tier of states in North America and southern regions of Canada, to about 53°N and were detected in the Pacific Northwest in 1967, having spread westward at a yearly average rate of c. 250 km per year. Spread southward was much slower. Their current North American distribution extends as far south as about 35°N, including Georgia, Tennessee, Arkansas, Oklahoma, Utah, northern Nevada, and southern California (Fig. 4).

Genetic diversities in North American populations are substantial and indicate a large founding population of the order 10^2–10^3 or more reproducing females, a conclusion supported by the simultaneous introduction of the entomopathic nematode *Paraiotonchium autumnalis* (Tylenchida: Allantonematidae) that is found in about 2–4% of adult face flies. North American populations exhibit little genetic differentiation, testifying to their rapid spread from a likely single, genetically diverse population. Old World populations, however, showed much genetic diversity partitioned among English, Russian, and Kazakhstan populations. Mitochondrial sequence variation suggests the origin of New World face flies was the United Kingdom or Western Europe and a likely scenario is that a large cluster or clusters of diapausing flies were introduced via wartime or postwar shipping between the UK and maritime provinces of Canada.

Reproductive Biology

Face fly females become inseminated only once. Thereafter, females require exogenous protein to undergo vitellogenesis. Ovaries are paired, and average 12–13 ovarioles each. Hence, mean egg production per clutch is about 25, averaged over the breeding season.

Ovarioles develop in synchrony, and flies may undergo repeated cycles of vitellogenesis and oviposition. Ovariole number varies with body size



Face Fly, *Musca autumnalis* De Geer (Diptera: Muscidae), Figure 4 North American distribution of *Musca autumnalis*. The first detections of face flies are indicated. Seasonal numbers of generations are shown, estimated by calculating degree-day sums (modified after Krafsur and Moon, Annu. Rev. Entomol. 42).

and body size varies with the quality of larval nutrition. Late spring and early summer flies tend to be the largest and, therefore, have the most ovarioles.

Microscopic examination of female reproductive systems and chemical analysis of their heads provides the means to estimate reproductive ages and phenology. Because ovarian development is temperature dependent, it is possible to estimate, to a rough approximation, the calendar ages of flies in a sample if the temperature history of the sampling location is known. The first ovipositions in spring require about 77 degree-days (DD) above a threshold of 12°C. The previtellogenic phase requires 30 degree-days and vitellogenesis another 47 DD. Subsequent ovipositions require about 40 DD above the 12°C threshold. Calendar ages may be estimated more accurately by measuring spectrofluorometrically the concentration of pteridines in flies' head capsules. These substances accumulate in the eyes at a rate determined by temperature integrated over time. The pteridine method, applied to flies in the upper Midwestern states, indicated that during the main breeding season males lived an average of 10 days and females 11 days and completed two to three gonotrophic cycles. Development of eggs, larvae, and pupae also are temperature dependent, requiring 57 DD above a 10°C threshold for egg hatch and larval development and a further 134 DD for pupal development. Thus, egg to adult development requires an average 14 days at summer temperatures. Day degree summations indicate that the number of generations annually varies from about three to four in the northernmost part of the range to 8–12 in the south.

Phenology and Overwintering

Face flies overwinter as adults in reproductive diapause. In the field, short day lengths induce reproductive diapause. Both sexes develop hypertrophied fat bodies and do not demonstrate sexual behavior. They become increasingly photonegative and seek out hibernaculae, which may include human dwellings. It is unlikely, however, that many of the flies that enter buildings in autumn survive over winter, because they are unable to replace water and easily escape to the outdoors. Moreover, diapausing flies are killed by exposures to −10°C (14°F) for 7 h or longer. In much of their northern temperate range, temperatures often drop below −10°C for many hours to days. Thus, successful overwintering in heated or unheated structures seems unlikely in the northern regions of face fly distribution. It is more plausible that successful face fly overwintering in the cold climates occurs in subnivean environments or below ground where temperature extremes are much more moderate.

In late winter and early spring, diapausing flies can be found perching outdoors on sunny days when air temperatures approach 12°C. Spring warmth allows the flies to break diapause and seek mates. Females then obtain proteinacious meals from cattle and horses. Gravid flies oviposit on fresh bovine dung. These overwintered flies have survived approximately 7–8 months as adults. Larval and pupal development is temperature dependent. First generation flies then appear about a month later and undergo the same mating, feeding, and gonotrophic cycle, giving rise to overlapping generations. Repeated cycles occur until day lengths decline to 12.5 h in September. Then, newly eclosed flies undergo facultatively gonadotrophic dissociation and develop hypertrophied fat body. Annually replicated studies in Iowa have shown that sharp variations in prevailing daily temperatures have no detectable effects on the sudden switch to diapause development.

Veterinary Significance

The importance of face flies is related to the feeding habits of females on the eyes of cattle (Fig. 5) and horses. They will also imbibe saliva, blood from wounds, and discarded placenta and fetal membranes (afterbirth). Face flies are obligate developmental vectors of eyeworms *Thelazia gulosa*, *T. scrjabini*, and *T. lacrymalis*. The former two species occur in cattle, whereas the latter species

Face Fly, *Musca autumnalis* De Geer (Diptera: Muscidae), Figure 5 Face flies clustered around the head of a cow, where they feed on secretions of the eyes and nose.

occurs in horses. Adult nematodes reside in the lachrymal ducts of their hosts and shed eggs that develop to infective larvae that develop in the hemocoele of face flies. Third stage larvae migrate to the head of adult flies and depart when flies feed on cattle or horses. The clinical significance of *Thelazia* spp. is considered to be small. All three species are endemic in the Old World, and have been introduced into North America.

In Europe, the face fly is also the developmental host and vector for *Parafilaria bovicola* (Nematoda: Filaroidea). This nematode, detected in quarantined imported Charolais cattle in Ontario, causes cutaneous bleeding in cattle and lesions in the surfaces of carcasses, thereby reducing their value. *Parafilaria bovicola* has been recorded in France, Sweden, Eastern Europe, India, Pakistan, the Philippines, North, West and East Africa, and South Africa.

Reports in North America of increased pinkeye incidence after the appearance of face flies led to research focused on the causes and transmission of pinkeye, caused largely by the bacterium *Moraxella bovis*. Converging evidence is that *Moraxella* does not infect and replicate in face flies. Rather, the flies are readily contaminated with *Moraxella* from infected animals, and contaminated flies can assist in mechanical spread of the bacterium from infected to susceptible cattle. Similarly, the agent of bovine brucellosis, *Brucella abortis*, cannot replicate in face flies and ingested bacteria are rapidly degraded. Apart from causing annoyance when populations are dense, face flies do not seem to cause detectably significant economic damage.

Management

Extensive studies of ear tags of various formulations for face fly control have been carried out for 25 years. Backrubbers and dustbags charged with various insecticides have also been evaluated. Treatments are usually assessed by comparing visual counts of flies on animals' faces among treated and untreated herds. No treatment has proved particularly efficacious. It is probable that face fly populations were not effectively reduced largely because females spend little time directly on host animals, which minimizes exposure to insecticides on treated animals. The sterile insect technique (SIT) has been considered as a means of eradication. Treatment of puparia containing pharate adults to 21 Gy of ionizing radiation in an anoxic atmosphere induced 95% sterility in both sexes with minimal cost in reduced longevity and competitiveness compared with unirradiated flies. Although a release strategy has been developed, simulation modeling and methods for mass rearing and genetic sexing remain to be developed. The great propensity for dispersal demonstrated by face flies does not favor SIT as an efficacious way of eliminating face flies and the economic benefits of doing so are not likely to justify costs of the rearing, sterilization and release methods currently available.

References

Cummings MA, Moon RD, Krafsur ES (2005) North American face flies Old World origins: mitochondrial evidence. Med Vet Entomol 19:48–52

Hall RD (1984) Relationship of the face fly (Diptera: Muscidae) to pinkeye in cattle: a review and synthesis of the relevant literature. J Med Entomol 21:361–365

Krafsur ES, Moon RD (1997) Bionomics of the face fly, *Musca autumnalis*. Ann Rev Entomol 42:503–523

Facet

The external surface of an individual ommatidium on a compound eye.

Factitious

An abnormal host for a parasitoid, specifically a non-normal host that biological control prac– titioners use to culture biological control agents in the laboratory because it is more convenient than the natural host.

Factitious Host

Abnormal host. Insects, and biological control agents of insects or plants, sometimes are produced on abnormal hosts due to ease or economy of culture.

Facultative Agents

A term used by Howard and Fiske to describe mortality factors that increase in intensity as population density rises; density-dependent mortality factors.

Facultative Diapause

Optional occurrence of diapause (arrested development), brought about by adverse conditions or conditions signifying the onset of adverse conditions. Facultative diapause occurs where adverse conditions do not occur regularly or predictably, or where insects have several generations per year and continue with their life cycle until some trigger stimulates induction of diapause.

► Diapause
► Obligatory Diapause

Facultative Myiasis

Myiasis in which the maggots dwell for some time in the gut or nasal passages of living animals if they are able to gain access.

► Myiasis

Facultative Parasitism

Optionally a parasite. A condition in which normally free-living organisms may become parasites.

Facultative Predators

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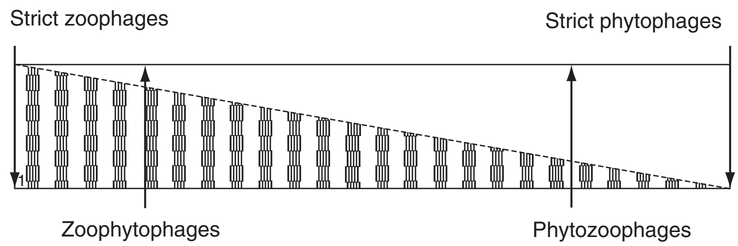
Omnivory, or trophic omnivory, is defined as the capacity of organisms to feed on more than one trophic level. True omnivory is a special case of trophic omnivory in which the consumer feeds on both plants and animal prey. The alternation of prey-feeding and plant-feeding stages during development is relatively common among animals. For example, many predatory insects feed upon plants at the adult stage by consuming floral or extra-floral nectar, pollen, seeds, plant saps and other plant materials, whereas they are carnivorous in juvenile stages. Less frequently, but not rarely, other insect predators may feed on plants and/or on prey at the same developmental stage; these are called facultative predators. The key feature that characterizes facultative predators is their capacity to feed on both plants and prey. Other closely related terms that are sometimes used to describe facultative predators are zoophytophages, phytozoophages, plant-feeding omnivores and opportunistic predators. More recently, omnivory has been structured into three types: life-history, temporal, and permanent omnivory.

The differences between these terms come from the prevalent feeding regime observed in each species. Thus, zoophytophages eat mostly prey, but also take vegetable resources. Conversely, in phytozoophages, the diet is mainly composed of plant materials to which prey are added. In practice, however, the relative amount of vegetable and animal consumption has rarely been determined, and the term applied to a species seems to reflect the perception of the observer rather than the real proportion of plant versus prey food ingested. In fact, species that may feed facultatively on both plants and prey are located in a continuum of feeding



Facultative Predators, Figure 6 **Trophic continuum of feeding habits by predators according to the relative consumption of animal and plant resources.**

habits (Fig. 6) between strict zoophagy and strict phytophagy.

Some authors use the term facultative predator to refer to predators that usually have a well-defined diet, but may also consume a broader range of prey. Parasitoids that are able to feed on the host may be regarded as facultative predators, as females can switch between predation and parasitism when a host is found.

Insect and Arachnid Groups Containing Facultative Predators

It is difficult to review the cases of facultative predation contained in the literature because many references report occasional observations of predators feeding on plants, or of phytophages feeding on animals, but rarely are there more continuous observations on the concurrence of plant and prey feeding at the same developmental stage. However, a list is provided of insect and arachnid groups containing at least one species with facultative predaceous habits (Table 1). Cases of cannibalism, hematophagy and host-feeding parasitoids have not been considered, whereas the cases of saprophagy are included. The list includes 18 orders and 84 families of mostly insects, but also arachnids. This would mean that facultative predation is more widespread among terrestrial insect predators than might be thought, due to the scarcity of studies on this feeding behavior.

Functions and Role of Facultative Predation

To understand functions of the capacity to feed on both plants and prey, it is important first to understand the benefits and costs derived from feeding on plants in facultative predators. At least some of the benefits confer adaptive advantages because a number of facultative predators have retained or acquired morphological (particularly mouth parts), or physiological (amylases, pectinases, symbiotes) traits of herbivores. Consequently, trophic switching capacity may itself constitute an adaptive strategy of some predators living in habitats with high variability in food type abundance.

Benefits may derive from nutritional considerations. Facultative predators may obtain complementary or supplementary nutrients, or other substances like vitamins, water, minerals, symbiotes, or enzymes from alternative plant or prey food. As a result of mixing prey and plant diets, facultative predators enhance one, or several, of their fitness components such as developmental rate, survival, fecundity, and longevity. These benefits in some fitness components, however, may be counterbalanced by costs in the decrease of other components as a result of the poorer quality of plant food. Another cost of facultative predation is a narrower range of prey as a consequence of their greater dependence on host plants than non-plant feeding predators (e.g., *Orius* species avoid foraging on tomato though it hosts suitable prey). The possibility of switching from prey to plant feeding may represent an additional benefit as it

Facultative Predators, Table 1 The known distribution of facultative predation in insects and arachnids

Order/Family	Source	Order/Family	Source
Acariformes			
Tydeidae	(3)	Blattidae	(4)
Parasitiformes		Mantidae	(4)
Phytoseiidae	(3)(4)	Diptera	
Araneida		Tipulidae	(1)
Anyphaenidae	(4)	Ceratopogonidae	(1)
Araneidae	(4)	Empididae	(1)
Coleoptera		Mydaidae	(1)
Anthribidae	(4)	Antohmyiidae	(1)
Anthicidae	(1)	Calliphoridae	(5)
Brentidae	(1)	Muscidae	(5)
Cleridae	(1)	Phoridae	(5)
Endomycidae	(1)	Syrphidae	(3)
Melyridae	(1)	Hemiptera	
Colydiidae	(1)	Anthocoridae	(1)
Cantharidae	(4)	Berytidae	(1)
Carabidae	(3)(4)	Lygaeidae	(1)
Cerambycidae	(2)(4)	Mesoveliidae	(1)
Chrysomelidae	(4)	Miridae	(1)
Coccinellidae	(1)(3)(4)	Nabidae	(1)
Curculionidae	(4)	Pentatomidae	(2)(3)(4)
Lampyridae	(1)	Phymatidae	(5)
Pedilidae	(1)	Reduviidae	(1)(4)
Pyrochroidae	(1)	Aphidoidae	(2)(4)
Silphidae	(1)	Hymenoptera	
Lathridiidae	(1)	Anthophoridae	(2)
Elateridae	(1)(4)	Chalcidoidea	(4)
Malachiidae	(4)	Eurythomidae	(4)
Staphylinidae	(3)	Vespidae	(1)
Tenebrionidae	(4)	Eumenidae	(1)
Collembola		Formicidae	(1)
Entomobryidae	(1)	Lepidoptera	
Isotomidae	(1)	Arctiidae	(2)(4)
Dermaptera		Geometridae	(2)(4)
Carcinophoridae	(3)	Lycaenidae	(4)
Forficulidae	(1)(3)(4)	Noctuidae	(2)(4)
Labiduridae	(3)	Psychidae	(4)
Dictyoptera		Tortricidae	(2)(4)

Facultative Predators, Table 1 The known distribution of facultative predation in insects and arachnids (Continued)

Order/Family	Source	Order/Family	Source
Neuroptera		Psocoptera	
Chrysopidae	(1)(3)(4)	Atropidae	(1)
Myrmeleontidae	(1)	Caeciliidae	(1)
Nemopteridae	(1)	Liposcelidae	(1)
Osmylidae	(1)	Thysanoptera	
Coniopterygidae	(1)	Aeolothripidae	(3)
Mantispidae	(4)	Phlaeothripidae	(1)
Orthoptera		Thripidae	(3)
Acrididae	(1)(2)(4)	Thysanura	(4)
Gryllidae	(1)(2)(3)(4)	Lepismatidae	(1)
Gryllotalpidae	(4)	Tricoptera	
Gryllacrididae	(1)	Limnephilidae	(4)
Pyrgomorphidae	(4)	Zoraptera	(1)
Tettigoniidae	(1)		

Sources: (1) Hagen (1987); (2) Whitman et al. (1994); (3) Hagen et al. (1999); (4) Coll and Guershon (2002); (5) Original additions

diminishes competition among predators for prey. Other benefits come from the feature that most facultative predators are generalists and are better adapted to changing and ephemeral habitats.

The occurrence of facultative predation in food webs influences various interactions among components of the system. For instance, predator and prey may share a common resource and competition may thus occur (e.g., intraguild predation). Systems with facultative predators differ in four ways from those with strict predators: (i) it is unlikely that the relative sizes of prey and plants have a major effect on the tendency of a plant-feeding omnivore to switch between plant and prey feeding; (ii) unlike animal prey, plants are not usually removed after a feeding event, thus the probability of finding a plant does not change; (iii) the location of plant and prey sources is not independent: plants define the prey's habitat; and (iv) the chemical properties of plants and prey differ greatly, and their relative nutritional values for the facultative predator are likely to be a major determinate of the proportion of its plant and prey consumption in the continuum between herbivorous and predaceous habits.

Facultative predators may make different and contradictory contributions to the stability of food webs. As they can link species in the community that would otherwise be unconnected, the occurrence of facultative predators may stabilize systems. Their role in shortening food chains may also contribute to stability. The possibility of switching between prey and plant feeding may allow prey populations to escape predation at low density, resulting in a stabilizing mechanism for the prey population. Other stabilizing and destabilizing effects of facultative predators come from their characteristics as generalist predators.

Facultative Predators for Biological Pest Control

The potential of facultative predators for biological pest control has traditionally been neglected, mainly due to the risk that feeding on the crop may result in economic damage or because predation has been overlooked when compared to plant feeding. However, facultative predators have some advantages for use in biological control, so management programs must minimize their risks and maximize their benefits.

Facultative predators have two main advantages for their use in biological control. One is their capacity to establish themselves early in the crop fields and thus prevent pests from building up high populations. This is a particularly positive trait of biocontrol agents in ephemeral crops such as annual crops that have to be recolonized every season. A second advantage of facultative predators concerns their possibility of feeding on plants when prey are at low density, thus preventing predator extinction or migration. Most observations on the role of plant feeding in early predator establishment and persistence on the crop relate to pollen-feeding predators such as many phytoseiid mites or anthocorids and coccinellids. For instance, the establishment and persistence of *Orius insidiosus* at low prey densities may be due to the ability of the predator to feed on pollen. Similarly, the failure and success of establishing and maintaining *O. laevigatus* on cucumber and pepper has been attributed to the lack or presence of pollen in the flowers, respectively. However, such behavior has proved to be less evident in non-pollen feeding predators. For instance, the foraging times of adults of the facultative predator *Dicyphus tamaninii* in cucumber patches of low and high prey density were compared and no differences were found even though this predator spent some time feeding on the plant.

The main disadvantage of facultative predators for biological control stems from their capacity to damage crops during plant feeding. Such a risk depends on various factors such as the relative amount of plant vs. prey feeding, the host-plant species and cultivar, the time of plant feeding and crop phenology, and the plant tissue fed on by the predator. Relationships between the amount of plant and prey feeding are a function of the nature of nutrients derived from plants by facultative predators. When the nutrients derived from the plant are complementary to those obtained in the prey, plant feeding occurs independently of prey feeding, as has been found in *Campylomma verbasci*, which feeds on apple fruitlets regardless of the availability of prey. When predators switch between plant and prey as alternative sources, the relationship between the two types of feeding will be negative. If prey are preferred to plants, phytophagy will only occur when prey are scarce. This is the case for the mirid bug *D. tamaninii*, which only feeds on tomato fruit when its main prey, greenhouse whitefly, is not abundant. On the other hand, plant feeding may increase with prey feeding when plants provide an element (e.g., water) that is needed for prey consumption, as noted for *D. hesperus*. Consequences of plant feeding on pest suppression, and thus success of facultative predators in biological control, are difficult to predict. Positive effects of plant feeding on facultative predator performance do not necessarily lead to enhanced biological control because per capita prey consumption may be reduced by ingestion of plant food. On the other hand, reduced per-capita prey consumption can be balanced by improved numerical response. Further investigations should address relationships between plant feeding, prey consumption and pest suppression.

Some facultative predators show clear preferences to feed on some crop species and cultivars, which are thus more exposed to their injury than the less preferred ones. Such is the case for *D. tamaninii*, which may damage tomato, but rarely French cucumber varieties. Similarly, *C. verbasci* nymphs injure apples – differently according to the variety – by feeding on the flower parts and fruitlets, whereas injuries are rarely observed on pears. The influence of plant-feeding timing on crop damage can be exemplified by *C. verbasci*, which causes the greatest damage during the bloom period, whereas little or no damage occurs after the fruit reaches a certain size. Finally, risk of crop damage is determined by the plant tissue that is preferred by the facultative predator. Feeding on pollen or extra floral nectar, for example, will rarely lead to high crop damage, whereas damage will be high if fruit is the plant part preferred by the facultative predator, or moderate or even nil if leaves are preferred.

Most facultative predators that have been studied are also generalists regarding prey range. As such, they have traditionally been considered as unable to regulate pests and thus of little use in biological control. This belief, however, is not fully supported by the theory, and is refuted by detailed studies on the role of single species or assemblages of generalist predators. In contraposition with specific natural enemies, generalist predators have positive traits – e.g., quick response to sudden pest population increases, high dispersal capacity, aggregative responses to patched prey distribution, ability to survive at low target-prey density – in essence, for adaptation to changing environments and prey densities, such as those found in ephemeral crops.

Conclusions

Facultative predation is defined as a special case of true omnivory in which plant and prey feeding co-occur within the same developmental stage so that individuals may choose between the two types of food. Facultative predation is relatively common among terrestrial predaceous arthropods as it is found in at least 18 orders and 84 families. The functions of zoophytophagy are still poorly understood, but there are many examples of fitness enhancement in the literature when diets mix vegetable and animal resources. The occurrence of facultative predation in food webs influences various interactions among components of the system and its contribution to stability may be contradictory.

The role of facultative predation in biological control has been neglected mainly due to the risks of damage to the crop. These are functions of various factors that should be better known in order to develop programs for managing facultative predator populations in order to minimize risks and benefit from their advantages as agents of conservation biocontrol. In particular, understanding when facultative predators switch from prey to plant consumption, and how biological control is affected, are of crucial importance.

► Predation: The Role of Generalist Predators in Biodiversity and Biological Control

References

Albajes R, Alomar O (1999) Use and potentialities of polyphagous predators. In: Albajes R, Gullino ML, van Lenteren JC, Elad Y (eds) Integrated pest and disease management in greenhouse crops. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 265–275

Alomar O, Wiedenmann RN (eds) (1996) Zoophytophagous Heteroptera: implications for life history and integrated pest management. Proceedings of the Thomas Say Publications in Entomology, Lanham, MD, 202 pp

Coll M, Guershon M (2002) Omnivory in terrestrial arthropods: mixing plant and prey diets. Ann Rev Entomol 47:267–297

Hagen KS (1987) Nutritional ecology of terrestrial insect predators. In: Slansky F, Rodríguez JG (eds) Nutritional ecology of insects, mites, spiders and related invertebrates. Wiley, New York, NY, pp 533–543

Hagen KS, Mills NJ, Gordh G, McMurtry JA (1999) Terrestrial arthropod predators of insect and mite pests. In: Bellows TS, Fisher TW (eds) Handbook of biological control. Academic Press, San Diego, CA, pp 383–503

Wäckers FL, van Rijn PCJ, Bruin J (eds) (2005) Plant-provided food for carnivorous insects: a protective mutualism and its applications. Cambridge University Press, Cambridge, UK, 356 pp

Whitman DW, Blum MS, Slansky F Jr (1994) Carnivory in phytophagous insects. In: Ananthakrishnan TN (ed) Functional dynamics of phytophagous insects. Science Publishers, Lebanon, New Hampshire, pp 161–205

Fairchild, Alexander Graham Bell

Alexander Fairchild, known to family and friends as Sandy, was born in Washington, DC, on August 17, 1906. His father, David Fairchild, was a botanist with the U.S. Department of Agriculture, who was interested in many aspects of natural history and had even published a book of insect photographs. It was he who encouraged Sandy's interest in nature. In 1921 and again in 1924 he visited Panama, where his father was working. From September 1924 to 1926 he accompanied his parents on a voyage to England and thence to Indonesia, with many stops and side-trips to parts of western Europe, and northern Africa. His opportunities to collect insects were not wasted, and he knew by then that he wanted to become an entomologist. His education to this point had been slight, and in 1926 he entered a preparatory school to acquire enough education to enter university. In 1928 he entered Harvard University, and received a B.S. degree in biology in 1932. At Harvard he encountered Charles Brues, Frank Carpenter, and Joseph Bequaert. One of the latter's interests was Tabanidae, and it was this that inspired Sandy's decision to study tabanid taxonomy for his graduate research at Harvard. Requirements for his Ph.D. degree were completed in 1934, but the dissertation was not completed until 1941. In the intervening 6 years, he held several jobs, and he married Elva Whitman in 1938. The first job (1934–1935) at the University of Florida's Agricultural Experiment Station at Monticello, was as entomologist studying control of insect pests of pecan. In 1935–1937 he worked for the International Health Division of the Rockefeller Foundation, studying insect vectors of "jungle" yellow fever in Brazil. With his wife, in September 1938, he moved to Panama, and began a 32-year association with the Gorgas Memorial Laboratory. His work continued to be on the taxonomy of biting insects (and ticks). He worked on phlebotomine sand flies, simuliid black flies, and tabanids. During World War II he held a U.S. army commission, and he focused on control of mosquitoes, black flies, and sand flies. This took him to Peru and Guatemala as well as Panama. In 1949–1950 he took a leave of absence to teach medical entomology at the University of Minnesota. In 1953, his work on tabanids progressed with visits to examine type specimens in the museums of London and Paris, in 1959 to Rio de Janeiro, and in 1964 to Denmark, The Netherlands, Belgium, Germany, France, Austria and Italy. This work on the type specimens was published in several papers, and in 1971 was crowned with his catalog of Neotropical Tabanidae. He retired from Gorgas Memorial Laboratory in 1970 and moved to Gainesville, Florida, where he was given an office which he used until 1988 for further tabanid studies (and for guidance to graduate students). Then, in 1988 he moved some blocks away to the Florida State Collection of Arthropods in a building of the Florida Department of Agriculture's Division of Plant Industry. Here, his large collection is housed. He died on February 10, 1994, a few days before putting the finishing touches to a revised catalog of Neotropical Tabanidae which, coauthored with J. F. Burger, was published later that year. Elva and their two children survived him.

Reference

Burger JF (1999) Alexander Graham Bell ("Sandy") Fairchild: a biography. In: Burger JR (ed) Contributions to the knowledge of Diptera. A collection of articles on Diptera commemorating the life and work of Graham B. Fairchild, pp 1–41. Memoirs on Entomology, International 14: i–viii, 1–648

Fairmaire, Léon

Léon Fairmaire was born in Paris on June 20, 1820. He received training in law, but the 1848 war ruined his family financially, so he became a public servant, eventually retiring as a hospital administrator. He became an active member of the Société Entomologique de France, was president, and honorary president from 1893 to 1906. Most of his very numerous publications (more than 450) contained unintegrated species descriptions of beetles, not just from Europe but from worldwide localities. However, with Laboulbène he published in 1854 the Coleoptera section of "Faune entomologique française," which was a major analytical work. He collaborated with Jacquelin du Val in "Genera des coléoptères d' Europe" and with Germain in "Coléoptères du Chili." His collection is housed at the Muséum National d' Histoire Naturelle in Paris. He died in Paris on April 1, 1906.

Reference

Herman LH (2001) Fairmaire, Léon. Bull Am Mus Nat Hist 265:63–64

Fairyflies (Hymenoptera: Mymaridae)

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The family Mymaridae is cosmopolitan, occurring in all terrestrial habitats and also in freshwater ponds and streams. The greatest generic diversity occurs in Australia, New Zealand and South America, but the greatest number of species is probably in tropical forests. The northern hemisphere, particularly Europe, is relatively depauperate, with about one quarter of the genera. Mymarids form an important component of any chalcid fauna, making up at least 5–10% of the individuals of Chalcidoidea collected by methods such as Malaise traps or pan traps.

This family is one of the few chalcids groups with a common name – fairyflies – derived from the fact that individuals of most of the species are such small insects that most people have never seen them. Indeed, the family includes the smallest recorded insect: the wingless, eyeless males of *Dichopomorpha echmepterygis* Mockford, that live as parasites in barklouse (Psocoptera) eggs. Four males lined up end to end would extend the diameter of a period.

Diagnosis

Mymaridae are small to minute, mostly delicate wasps that are 0.13–5.4 mm long (average 0.5–1.0 mm), usually without metallic coloration, and usually winged but sometimes wingless. The antennae are usually at least as long as the body, those of the females have a distinct club, and those of the males are filiform. The most important diagnostic feature distinguishing mymarids from other Hymenoptera is the head structure. Dark bars of cuticle (trabeculae) and associated sutures arranged in an H-like pattern divide the vertex and the frons into two distinct sclerites. Mymarid wings are also characteristic, with long fringes of hairs. The forewing usually has a distinct, backward projecting seta (hypochaeta) on the ventral surface of the wing blade in front of the marginal vein. The hind wing is almost always very narrow and stalked, and the wing membrane does not extend the wing base.

Classification

The family contains about 1,400 described species, currently classified in about 100 genera. These have been grouped into tribes and subfamilies based upon either tarsal number or metasomal attachment. Depending on which character is used first, the five tribes and two subfamilies will contain different groupings of genera. A different classification, with three subfamilies, has also been proposed, based on male genitalia. One fossil subfamily was also described, based on a fossil genus in Canadian Cretaceous amber. Regardless of the system followed, the previously proposed tribes and subfamilies need to be critically reviewed to take into better account the diverse fauna from the Australian region, which includes the most primitive genera.

Keys to genera are given by Annecke & Doutt (1961) for the world (outdated), Yoshimoto (1990) for the Western Hemisphere, Schauff (1984) for the Holarctic Region, Subba Rao & Hayat (1983) for the Oriental Region, and Noyes & Valentine (1989) for New Zealand.

The largest and most common genera are *Anagrus*, *Anaphes*, *Gonatocerus*, and *Polynema*. These four account for over half of all the species. Another five, *Alaptus*, *Camptoptera*, *Erythmelus*, *Ooctonus*, and *Stethynium* make up another quarter of the species.

Life History and Habits

Mymarids are found in all terrestrial habitats from deserts to rainforests, and in most cultivated areas. Members of the genus *Caraphractus* live in ponds where the adults use their wings as paddles to swim under water. Many species can be collected in great numbers using Malaise traps or pan traps, but because of their small size, they are rarely seen and are difficult to study when alive. As a result, there is a tremendous amount of new information to be discovered about every aspect of their life history. The biology of very few species (in *Alaptus*, *Anagrus*, *Anaphes*, *Caraphractus*, *Gonatocerus*, and *Polynema*) has been studied in detail. Otherwise, most information on hosts, habits, or microhabitats occupied can be obtained only from the little biological information associated with specimens in museum collections. Hosts are known for species in only about one quarter of the genera, mainly in the four largest ones. Many host records need confirmation, however. Host records suggest that Hemiptera, especially Auchenorrhyncha, are the most commonly used hosts, but this could be because this group has been better studied than other hemimetabolous orders. Other host orders known for certain are Coleoptera, Diptera, Odonata, Psocoptera, and Thysanoptera.

All mymarids are internal, solitary or gregarious, egg parasitoids of other insects. Development is completed entirely within a host egg. There may be several generations per year, often on different hosts. As holometabolous insects, mymarids are unusual because they often have two different types of larval instars and two different kinds of preimaginal development. In *Anaphes*, a secondary immobile sacciform larva follows an active first instar "mymariform" larva. In *Anagrus*, the opposite occurs – an immobile first instar followed by a second, very active "hystriobdellid" instar.

Economic Importance

Most of the biological literature on mymarids focuses on *Anagrus* and *Anaphes* species because these two genera are the most used in biological control against economically important pests. About ten species of mymarids have been used in classical biological control attempts against insect pests such as Curculionidae, Chrysomelidae, Cicadellidae and Delphacidae. *Anagrus* is most important in vineyards against leafhoppers (Cicadellidae) in North America and Europe (where up to 90% egg parasitism may occur) and against planthoppers (Delphacidae) and leafhoppers of rice in Asia and Central America. *Anaphes* spp. are among the most effective parasitoids of leaf beetles (Chrysomelidae) in cereals and carrots in North America, often with 50–90% parasitism rates. The best-known example of successful biological control using mym arids is that of *Anaphes nitens* Girault) against the eucalyptus snout beetle, *Gonipterus scutellatus* Gyllenhal, in parts of Africa, South America and southern Europe. *Anaphes iole* Girault and *Anagrus atomus* L. are commercially reared for sale and mass release against Lygus bugs and leafhoppers in North America and Europe, respectively.

References

Annecke DP, Doutt RL (1961) The genera of the Mymaridae. Hymenoptera: Chalcidoidea. Entomology Memoirs. Department of Agricultural Technical Services, Republic of South Africa, vol 5, pp 1–71

Huber JT (1986) Systematics, biology, and hosts of the Mymaridae and Mymarommatidae (Insecta: Hymeno-ptera): 1758–1984. Entomography: Ann Rev Biosyst 4:185–243
Noyes JS, Valentine EW (1989) Mymaridae (Insecta: Hymenoptera) – introduction, and review of genera. Fauna of New Zealand, vol 17, 95 pp
Subba Rao BR, Hayat M (1983) Key to the genera of Oriental Mymaridae, with a preliminary catalog (Hymenoptera: Chalcidoidea). Contrib Am Entomol Inst 20:125–150
Yoshimoto CM (1990) A review of the genera of New World Mymaridae (Hymenoptera: Chalcidoidea). Flora & fauna handbook no. 7. Sandhill Crane Press, Gainesville, FA, 166 pp

Falciform

This term is used to express a sickle-shaped appearance.

Fall Armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae)

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The fall armyworm is native to the tropical regions of the western hemisphere from the United States to Argentina. It normally overwinters successfully in tropical areas; in the United States overwintering occurs only in southern Florida and southern Texas. The fall armyworm is a strong flier, and disperses long distances annually during the summer months. Thus, in the USA it is recorded from virtually all states east of the Rocky Mountains. However, as a regular and serious pest, its range tends to be mostly the southeastern states.

Life Cycle and Description

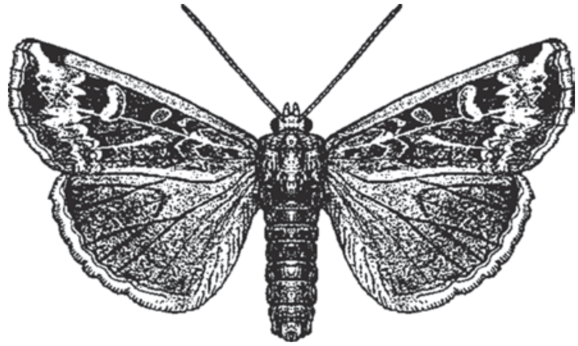
The life cycle is completed in about 30 days during the summer, but 60 days in the spring and autumn, and 80–90 days during the winter. The number of generations occurring in an area varies with the appearance of the dispersing adults. The ability to diapause is not present in this species. In northern areas, where fall armyworm moths do not appear until August, there may be but a single generation. The number of generations is reported to be one to two in Kansas, three in South Carolina, and four in Louisiana. In coastal areas of north Florida, moths are abundant from April to December, but some are found even during the winter months.

Egg

The egg is dome shaped; the base is flattened and the egg curves upward to a broadly rounded point at the apex. The egg measures about 0.4 mm in diameter and 0.3 m in height. The number of eggs per mass varies considerably but is often 100–200, and total egg production per female averages about 1,500. The eggs are sometimes deposited in layers, but most eggs are spread over a single layer attached to foliage. The female also deposits a layer of grayish scales between the eggs and over the egg mass, imparting a furry or moldy appearance. Duration of the egg stage is only 2–3 days during the summer months.

Larva

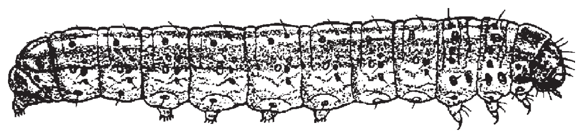
There usually are six instars in fall armyworm. Head capsule widths are about 0.35, 0.45, 0.75, 1.3, 2.0, and 2.6 mm, respectively, for instars 1–6. Larvae attain lengths of about 1.7, 3.5, 6.4, 10.0, 17.2, and 34.2 mm, respectively, during these instars. Young larvae are greenish with a blackhead, the head turning orangish in the second instar. In the second, but particularly the third instar, the dorsal surface of the body becomes brownish, and lateral white lines begin to form. In the fourth to the sixth instars the head is reddish brown, mottled with white, and the brownish body bears white subdorsal and lateral lines (Fig. 8). Elevated spots occur dorsally on the body; they are usually dark in color, and bear spines. The face of the mature larva is also marked with a white inverted "Y" and the epidermis of the larva is rough or granular in texture when examined closely. However, this larva does not feel rough to the touch, as does corn earworm, *Helicoverpa zea* (Boddie), because it lacks the microspines found in the similar appearing corn earworm. The appearance of this insect is quite variable. Duration of the larval stage tends to be about 14 days during the summer and 30 days during cool weather. Mean development time was determined to be 3.3, 1.7, 1.5, 1.5, 2.0, and 3.7 days for instars 1–6, respectively, when larvae were reared at 25°C.



Fall Armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), Figure 7 **Adult fall armyworm, *Spodoptera frugiperda*.**

Pupa

Pupation normally takes place in the soil, at a depth 2–8 cm. The larva constructs a loose cocoon, oval in shape and 20–30 mm in length, by tying together particles of soil with silk. If the soil is too hard, larvae may web together leaf debris and other material to form a cocoon on the soil surface. The pupa is reddish brown in color, and measures 14–18 mm in length and about 4.5 mm in width. Duration of the pupal stage is about 8–9 days during the summer.



Fall Armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), Figure 8 **Fall armyworm larva.**

Adult

The moths have a wingspan of 32–40 mm. In the male moth, the forewing generally is shaded gray and brown, with a triangular white spots at the tip and near the center of the wing (Fig. 7). The forewings of females are less distinctly marked, ranging from a uniform grayish brown to a fine mottling of gray and brown. The hind wing is iridescent silver-white with an narrow dark border in both sexes. Adults are nocturnal, and are most active during warm, humid evenings. After a preoviposition period of 3–4 days, the female normally deposits most of her eggs during the first 4–5 days of life, but some oviposition occurs for up to 3 weeks. Duration of adult life is estimated to average about 10 days.

Host Plants

This species seemingly displays a very wide host range, with over 80 plants recorded, but clearly prefers grasses. The most frequently consumed plants are field corn and sweet corn, sorghum, Bermudagrass, and grass weeds such as crabgrass, *Digitaria* spp. When the larvae are very numerous they defoliate the preferred plants, acquire an “armyworm” habit and disperse in large numbers, consuming nearly all vegetation in their path Field crops are frequently injured, including alfalfa, barley, Bermuda grass, buckwheat, cotton, clover, corn, oat, millet, peanut, rice, ryegrass, sorghum, sugarbeet, sudangrass, soybean, sugarcane, timothy, tobacco, and wheat. Among vegetable crops, only sweet corn is regularly damaged. Other crops sometimes injured are apple, grape, orange, papaya, peach, strawberry and a number of flowers. There is some evidence that fall armyworm strains exist, based primarily on their host plant preference. One strain feeds principally on corn, but also on sorghum, cotton and a few other hosts if they are found growing near the primary hosts. The other strain feeds principally on rice, Bermudagrass, and Johnson grass.

Damage

Larvae cause damage by consuming foliage. Young larvae initially consume leaf tissue from one side, leaving the opposite epidermal layer intact. By the second or third instar, larvae begin to make holes in leaves, and eat from the edge of the leaves inward. Feeding in the whorl of corn often produces a characteristic row of perforations in the leaves. Larval densities are usually reduced to one to two per plant when larvae feed in close proximity to one another, due to cannibalistic behavior. Older larvae cause extensive defoliation, often leaving only the ribs and stalks of cornplants, or a ragged, torn appearance. In corn, they sometimes burrow into the ear, feeding on kernels in the same manner as corn earworm, *Helicoverpa zea*. Unlike corn earworm, which tends to feed down through the silk before attacking the kernels at the tip of the ear, fall armyworm will feed by burrowing through the husk on the side of the ear.

Natural Enemies

Cool, wet springs followed by warm, humid weather in the overwintering areas favor survival and reproduction of fall armyworm, allowing it to escape suppression by natural enemies. Once dispersal northward begins, the natural enemies are left behind. Therefore, although fall armyworm has many natural enemies, few act effectively enough to prevent crop injury. Numerous species of parasitoids affect fall armyworm. The wasp parasitoids most frequently reared from larvae in the United States are *Cotesia marginiventris* (Cresson) and *Chelonus texanus* (Cresson) (both Hymenoptera: Braconidae), species that are also associated with other noctuid species. Among fly parasitoids, the most abundant is usually *Archytas marmoratus* (Townsend) (Diptera: Tachinidae). However, the dominant parasitoid often varies from place to place and from year to year.

Management

Sampling

Moth populations can be sampled with blacklight traps and pheromone traps; the latter are more efficient. Pheromone traps should be suspended at canopy height, preferably in corn during the whorl stage. Catches are not necessarily good indicators of density, but indicate the presence of moths in an area. Once moths are detected it is advisable to search for eggs and larvae.

Insecticides

Insecticides are usually applied to sweet corn in the southeastern USA to protect against damage by fall armyworm, sometimes as frequently as daily during the silking stage. In Florida, fall armyworm is the most important pest of corn. It is often necessary to protect both the early vegetative stages and reproductive stage of corn. Because larvae feed deep in the whorl of young corn plants, a high volume of liquid insecticide may be required to obtain adequate penetration.

Cultural Techniques

The most important cultural practice, employed widely in southern states, is early planting and/or early maturing varieties. Early harvest allows many corn ears to escape the higher armyworm densities that develop later in the season. Partial resistance is present in some sweet cornv arieties, but is inadequate for complete protection.

Biological Control

Although several pathogens have been shown experimentally to reduce the abundance of fall armyworm larvae in corn, only *Bacillus thuringiensis* presently is feasible, and success depends on having the product on the foliage when the larvae first appear.

► Vegetable Pests and Their Management
► Turfgrass Pests and Their Management

References

Ashley TR, Wiseman BR, Davis FM, Andrews KL (1989) The fall armyworm: a bibliography. Fla Entomol 72:152–202
Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, CA, 729 pp
Luginbill P (1928) The fall armyworm. USDA Tech Bull 34, 91 pp
Sparks AN (1979) A review of the biology of the fall armyworm. Fla Entomol 62:82–87

Fall, Henry Clinton

Henry Fall was born in New Hampshire on December 25, 1862. In 1884 he received a B.S. degree from Dartmouth College, New Hampshire. For the next 5 years he taught physics and mathematics in Chicago schools, and for the 28 after that, physics and chemistry at schools in California. In 1917, he retired to New England. He had numerous hobbies, among which was collecting beetles. He accumulated about 250,000 specimens, described 1,484 species, and wrote 144 publications. He received an honorary Ph.D. degree from Dartmouth College in 1929 and died in Massachusetts in 1939. His insect collection and papers were left to the Museum of Comparative Zoology of Harvard University.

Reference

*Mallis A (1971) Henry Clinton fall. In: American entomologists. Rutgers University Press, New Brunswick, NJ, pp 266–269

Fallow

Cultivated land allowed to remain free of crops during the normal growing season.

False Blister Beetles

Members of the family Oedemeridae (order Coleoptera).

► Beetles

False Burnet Moths (Lepidptera: Urodidae)

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False burnet moths, family Urodidae, total only about 80 species, primarily Neotropical (mostly the genus *Urodus*), but with a few species in North America and in Eurasia (subfamily Galacticinae).

False Burnet Moths (Lepidptera: Urodidae), Figure 9 **Example of false burnet moths (Urodidae), *Urodus isthmiella* (Busck) from Panama.**

Only two subfamiles are named: Galacticinae and Urodinae. The family is in the superfamily Sesioidea in the section Tineina, subsection Sesiina, of the division Ditrysia. Adults small (10–37 mm wingspan), with head smooth-scaled; haustellum naked; labial palpi upcurved; maxillary palpi 1–2-segmented. Wings somewhat elongated (Fig. 9). Maculation mostly unicolorous in shades of gray, but a few with various spots; some with metallic-iridescence or lustrous scales. Adults may be crepuscular or mostly nocturnal, but a few possibly diurnal. Larvae are leaf webbers or skeletonizers, but few are known biologically. Pupation is in a specialized filigreed cocoon. Host plants known in Lauraceae, Leguminosae, Salicaceae, Sapotaceae, and Theaceae. A few are minor pests.

References

Frost SW (1972) Notes on *Urodus parvula* (Herny Edwards) (Yponomeutidae). J Lepid Soc 26:173–177

Heppner JB (1997) *Wockia asperipunctella* in North America (Lepidoptera: Urodidae: Galacticinae). Holarctic Lepid 4:81–82

*HeppnerJB (2003) Urodidae. In: Lepidopterorum Catalogus (n.s.), Fasc 66. Association for Tropical Lepidoptera, Gainesville, FL, 16 pp

Kyrki J (1988) The systematic position of *Wockia* Heinemann, 1870, and related genera (Lepidoptera: Ditrysia: Yponomeutidae auct.). Nota Lepid 11:45–69

Moriuti S (1963) Remarks on the *Paraprays anisocentra* (Meyrick, 1922) (Plutellidae), with descriptions of its larva and pupa. Trans Lepid Soc Jpn 14(3):52–59 [in Japanese]

False Click Beetles

Members of the family Eucnemidae (order Coleoptera).

► Beetles

False Clown Beetles

Members of the family Sphaeritidae (order Coleoptera).

► Beetles

False Darkling Beetles

Members of the family Melandryidae (order Coleoptera).

► Beetles

False Diamondback Moths (Lepidoptera: Acrolepiidae)

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Florida State Collection of Arthropods,
Gainesville, FL, USA

False diamondback moths, family Acrolepiidae, include 96 species, mostly Palearctic. The family is part of the superfamily Yponomeutoidea in the section Tineina, subsection Tineina, of the division Ditrysia. Adults small (10–25 mm wingspan), with head smooth-scaled; haustellum naked; labial palpi upcurved; maxillary palpi 4-segmented. Wings elongated, with longer fringes (Fig. 10) on the pointed hindwings. Maculation various shades of brown with lighter markings. Adults are crepuscular or diurnal. Larvae mostly leafminers, but some are borers in seeds, stems and flower buds. Several hostplant groups are used, but mostly on Compositae. Very few are economic.

False Diamondback Moths (Lepidoptera: Acrolepiidae), Figure 10 **Example of false diamondback moths (Acrolepiidae), *Acrolepia autumnitella* Curtis from Austria.**

References

Gaedike R (1970) Revision der paläarktischen Acrolepiidae (Lepidoptera). Entomol Abhandlungen 38:1–54

Gaedike R (1984) Revision von nearktischen und neotropischen Acrolepiidae (Lepidoptera). Entomol Abhandlungen 47:179–194

Gaedike R (1986) Die Typen der orientalischen, australischen und äthiopischen Acrolepiidae (Lepidoptera). Beiträge zur Entomol 36:63–68

Gaedike R (1988) Beitrag zur Kenntnis afrikanischer Acrolepiidae (Lepidoptera). Beiträge zur Entomol 38:83–87

*Gaedike R (1997) Acrolepiidae. In: Lepidopterorum catalogus, (n.s.). Fasc 55. Association for Tropical Lepidoptera, Gainesville, FL, 16 pp

False Firefly Beetles

Members of the family Omethridae (order Coleoptera).

► Beetles

False Flower Beetles

Members of the family Scraptiidae (order Coleoptera).

► Beetles

False Ground Beetles

Members of the family Trachpachidae (order Coleoptera).

► Beetles

False Katydids

A subfamily (Phanopterinae) of katydids in the order Orthoptera: Tettigoniidae.

► Grasshoppers, Katydids and Crickets

False Long-Horned Beetles

Members of the family Stenotrachelidae (order Coleoptera).

► Beetles

False Metallic Wood-Boring Beetles

Members of the family Throscidae (order Coleoptera).

► Beetles

False Owlet Moths (Lepidoptera: Thyatiridae)

JOHN B. HEPPNER
Florida State Collection of Arthropods, Gainesville, FL, USA

False owlet moths, family Thyatiridae, comprise 224 species from all regions (absent in Australia), but most are tropical Oriental (199 sp.); the actual fauna probably exceeds 275 species. Two subfamilies are recognized: Thyatirinae and Polyplocinae. The family is in the superfamily Drepanoidea, in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults medium size (28–52 mm wingspan), with head scaling normal; maxillary palpi vestigial; antennae serrate or filiform; body robust. Wings elongate-triangular, mostly with acute forewing apex; hindwings subtriangular and rounded. Maculation varies but mostly (Fig. 11) shades of brown and gray, with various spotting and striae; sometimes more colorful and with

False Owlet Moths (Lepidoptera: Thyatiridae), Figure 11 **Example of false owlet moths (Thyatiridae), *Thyatira batis* (Linnaeus) from Taiwan.**

lustrous color patches or iridescence; hindwings mostly unicolorous and pale or dark. Superficially, the moths appear similar to owlet moths, thus the derivation of their common name. Adults are nocturnal. Larvae are mostly nocturnal leaf feeders. Host plants are recorded in a number of plant groups with forest trees, including Betulaceae, Caprifoliaceae, Cornaceae, Ebenaceae, Fagaceae, Juglandaceae, Rosaceae, and Salicaceae.

References

Bryner R (1997) Thyatiridae – Wollrückenspinner. In: Schmetterlinge und ihre Lebensräume: Arten-Gefährdung-Schutz. Schweiz und angrenzenden Gebiete, 2:477–512, pl 12. Pro Natura-Schweizerische Bund fuer Naturschutz, Basel

Clarke JFG, Benjamin FH (1938) A study of some North American moths allied to the thyatirid genus *Bombycia* Hübner. Bull Southern California Acad Sci 37:55–73

*Houlbert C (1921) Revision monographie de la famille des Cymatophoridae. In: études de Lépidoptères Comparée, 18(2):23–244, pl 988–989. Rennes

Seitz A (ed) (1912–36) Familie: Cymatophoridae. In: Die Gross-Schmetterlinge der Erde, 2:321–33, pl 49, 55–56 (1912); 2(suppl):187–195, 286, pl 11, 14–15 (1933–34); 6:1171–1175, pl 172 (1936); 10:657–663, pl 85 (1930). A. Kernen, Stuttgart

Soltys E (1965) Thyatiridae. In: Klucze do Oznaczania Owadów Polski. 27. Motyle – Lepidoptera, 49:1–53 [part]. Polskie Towardzystwo Entomologiczne [in Polish], Warsaw

False Pit Scales

Members of the family Lecanodiaspididae, superfamily Coccoidae (order Hemiptera).

► Bugs

False Plume Moths (Lepidoptera: Tineodidae)

JOHN B. HEPPNER
Florida State Collection of Arthropods, Gainesville, FL, USA

False plume moths, family Tineodidae, include only 11 species, all from Australia. The family is in the superfamily Pterophoroidea in the section Tineina, subsection Tineina, of the division Ditrysia. Adults small (15–34 mm wingspan), with head scaling average; haustellum naked; labial palpi porrect; maxillary palpi 4-segmented. Forewings elongate (Fig. 12) and pointed termens can be falcate. Maculation mostly mottled shades of tan and gray. Adults possibly diurnal or crepuscular. Larvae are leaftiers, but most are not known biologically. Only recorded host plants are in Euphorbiaceae and Oleaceae.

False Plume Moths (Lepidoptera: Tineodidae), Figure 12 Example of false plume moths (Tineodidae), *Tineodes adactylis* Guenée from Australia.

References

*Common IFB (1990) Family Tineodidae. In: Moths of Australia, 322–325 [part]. Melbourne University Press, Melbourne.

*Heppner JB (1998) Tineodidae. In: Lepidopterorum Catalogus, (n.s.). Fasc. 61. Association for Tropical Lepidoptera, Gainesville, FL, 8 pp

False Skin Beetles

Members of the family Biphyllidae (order Coleoptera).

► Beetles

False Soft Scales

Members of the family Stictococcidae, superfamily Coccoidae (order Hemiptera).

► Bugs

False Wireworm

False wireworms are beetle larvae in the Family Tenebrionidae. So-called "true" wireworms are beetle larvae in the Family Elateridae.

► Wheat Pests and Their Management

Family

A subdivision of an order, containing a group of related genera. Family names end in -idae.

► Classification

Fanniidae

A family of flies (order Diptera).

► Flies

Fast-Footed Bugs

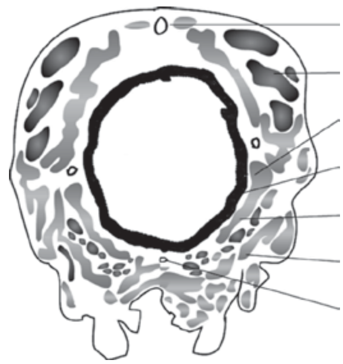
Members of the family Velocipedidae (order Hemiptera).

► Bugs

Fastigium

The anterior dorsal surface of the head, below the antennae. In many insects, this is the extreme anterior point.

► Head of Hexapods



Fat Body, Figure 13 Cross section of caterpillar larva showing distribution of fat tissue (adapted from Chapman, The insects: structure and function).

Fat Body

An aggregation of large cells in the body cavity that stores metabolites (Fig. 13) and is a center of intermediary metabolism.

► Internal Anatomy

Fatty Acid Binding Proteins

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The flight muscles of insects usually depend on fatty acids to fuel migratory flight. These fatty acids are obtained prior to migration from the diet and stored as triacylglycerol in the fat body. During flight, the lipids are converted to diacylglycerol that is released into the hemolymph and transported by the lipoprotein lipophorin to the flight muscle. There, diacylglycerol is hydrolyzed, and free fatty acids enter the muscle cell. Once fatty acids have crossed the plasma membrane, they need to move through the hydrophilic cytosol to the mitochondria where β-oxidation takes place. Because fatty acids are only poorly soluble in water, an intracellular mechanism in needed for their transport through the cytosol. Similarly, a transport process is required in the midgut cells, to facilitate the uptake of fatty acids from the diet and their subsequent delivery to the fat body. The intracellular transport of fatty acids is mediated by fatty acid binding proteins (FABPs).

FABPs are ubiquitous proteins in many vertebrate and invertebrate tissues, with separate genes encoding the FABPs found in various tissues. In insects, distinct FABPs have been identified and characterized in midgut cells and in flight muscle cells. Two midgut FABPs have been isolated from *Manduca sexta,* and their amino acid sequence and tertiary structure have been determined. Best characterized of the muscle FABPs is the FABP from flight muscles of locusts (*Schistocerca gregaria* and *Locusta migratoria*), but analogous proteins have also been found in Lepidoptera (*Helicoverpa zea*, *Acherontia atropos*), Hymenoptera (*Apis mellifera*), and Heteroptera (*Dipetalogaster maximus*). Their structures and function in insect metabolism are described below.

Locust muscle FABPs are very similar in their characteristics to mammalian FABPs. They are small, acidic proteins (Mr 15,000; pI 5.2–5.8) with a single binding site for fatty acids. Locust FABP was crystallized and its structure solved at 2.1 Å resolution. The protein displays the characteristic β-barrel motif common to all FABP. Two perpendicularly oriented β-sheets form a barrel-like structure; within this barrel the fatty acid binding site is located. The β-barrel itself is open to one side, but this (Fig. 14) opening is closed off by a helix-turn-helix motif. The overall structure is similar to the midgut FABPs from *Manduca sexta*, and their mammalian counterparts.

Locusts metabolize fatty acids at extremely high levels during migratory flight, and FABP is required for their rapid transport. Indeed, FABP is the most prominent flight muscle protein in mature adult locusts, amounting to as much as 20% of all cytosolic proteins. Yet, it is completely absent in immature locusts and in newly emerged adults. FABP expression commences immediately after adult ecdysis, and continues at high rates for almost 2 weeks. During this period, the FABP concentration gradually increases to its final concentration. This increase in the FABP concentration is concomitant with the

Fatty Acid Binding Proteins, Figure 14 Structure of locust muscle FABP. All FABPs have a typical beta-barrel structure. The binding site for a single fatty acid molecule is in the cavity formed by the beta-strands; the site is closed by a helix-turn-helix motif. Structure drawn from Brookhaven Protein Data Bank file ftp1.

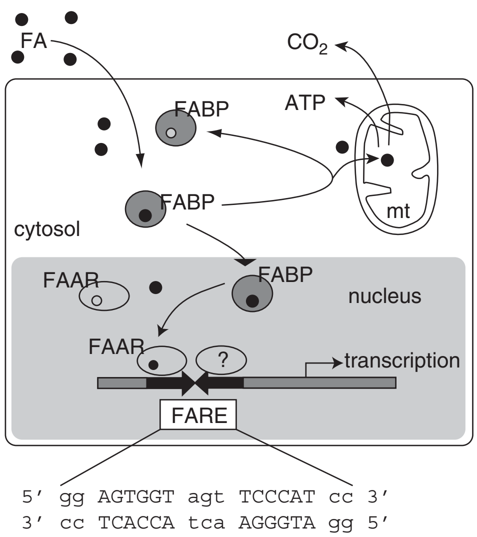
flight ability of the insect. Locusts cannot fly for longer time periods during the first 10 days of adult life, and one of the reasons for this may be the lack of an efficient intracellular fatty acid transport mechanism. Once FABP reaches a significant concentration, it becomes possible to use large amounts of fatty acids and hence to fly for long time periods. In mature adults, flight activity for periods exceeding 2 h further increases FABP expression. When 20 day-old locusts were exercised in tethered flight, the levels of FABP mRNA increased more than 12-fold. Flight times shorter than 1 h, however, had no influence on FABP expression. The latter flights are fueled by carbohydrates, while longer flight periods depend on the β-oxidation of lipids, and hence an efficient fatty acid transport. It was shown that a similar, strong accumulation of FABP mRNA could be induced by adipokinetic hormone, which mobilizes fatty acid from the fat body and stimulates their transport to the flight muscle, and even by an increased lipid supply alone. Thus, it appears that FABP expression is stimulated when the concentration of free fatty acid in the cell exceeds the amount of available FABP.

The molecular mechanisms by which this activation occurs have been partially elucidated.

The promoter of the FABP gene of the locust contains a fatty acid response element that is necessary for the induction of gene expression by fatty acids. The fatty acid response element is a 19 basepair inverted repeat with two hexanucleotide halfsites interspersed by three nucleotides, similar to steroid hormone response elements. It is likely that two different factors bind to the fatty acid response element, at least one of these is activated by the binding of long chain fatty acids. Fatty acids (Fig. 15) are required for full activity, and their availability to nuclear proteins depends on the intracellular concentration of FABP. FABP appears to have free access to the nuclear lumen, and thus this proteins contribution must be considered.

While for many FABP-types the exact functions have not been elucidated, it is generally accepted that muscle FABP serves the following three purposes: FABP increases the solubility of fatty acids and thus lead to a more rapid transport through the cytosol. Moreover, it serves as an intracellular acceptor for free fatty acids that have passed through the plasma membrane. Without such an acceptor, fatty acids would mostly remain in the membrane and not dissolve in the aqueous cytosol. Finally, the binding protein acts as a buffer for free fatty acids, both to assure the presence of fuel molecules prior to muscle activity, and to prevent the build-up of high concentrations of unbound fatty acids afterwards. With their hydrophilic carboxy-group and the hydrophobic tail, free fatty acids are amphiphilic molecules that, by detergent-like interactions, could destroy membrane structures within a muscle cell. The extremely high concentrations of FABP found in locust flight muscle support these functions, and the up-regulation of FABP gene expression by fatty acids represents an elegant physiological mechanism to handle high fatty acid fluxes safely and efficiently.

► Locomotion and Muscles



Fatty Acid Binding Proteins, Figure 15 Regulation of the locust muscle FABP gene. Shown is a schematic drawing of a muscle cell. Most of the fatty acid is bound by FABP and delivered to the mitochondrion for beta-oxidation. FABP also acts as a sensor of the fatty acid concentration in the nucleus. In the presence of an excess of fatty acid, nuclear transcription factors are activated, and the FABP gene is expressed. Abbreviations: FA = Fatty acid, FAAR = fatty acid activated receptor, FARE = fatty acid response element, mt = mitochondrion.

References

Haunerland NH (1997) Transport and utilization of lipids in insect flight muscles. Comp Biochem Physiol 117B:475–482

Haunerland NH (1994) Fatty acid binding protein in locust and mammalian muscle. Comparison of structure, function and regulation. Comp Biochem Physiol 109B:199–208

Smith AF, Tsuchida K, Hanneman E, Suzuki TC, Wells MA (1992) Nucleotide, protein isolation, characterization, and cDNA sequence of two fatty acid-binding proteins from the midgut of *Manduca sexta* larvae. J Biol Chem 267:380–384

Wu Q, Haunerland NH (2001) A novel fatty acid response element controls the expression of the flight muscle FABP gene of the desert locust, *Schistocerca gregaria*. Eur J Biochem 268:5894–5900

Fauriellidae

A family of thrips (order Thysanoptera).

► Thrips

Fauvel, Charles Adolphe Albert

Charles Adolphe Albert Fauvel was born in Caën, France, in 1840 and died there on January 4, 1921. A lawyer by profession, he was a prolific describer of insects, founding the journal "Revue d' Entomologie" as an outlet for many of his works. By 1900, under the name Albert Fauvel, he had published at least 246 papers, mostly on Coleoptera, and on Staphylinidae in particular. His major book was "Faune gallo-rhénane," in several volumes, which, unfortunately, was never completed. Other major works are on the staphylinid faunas of northwestern Africa, Australia and Polynesia, the Moluccas and New Guinea, and New Caledonia, material for which he obtained from collectors in those areas. In 1910, he abruptly stopped publication of Revue d' Entomologie, withdrew from scientific contacts, and remained secluded until his death. He described 96 genera and 1,851 species of Staphylinidae. His collection is now in the Institut Royal des Sciences Naturelles de Belgique.

Reference

Herman LH (2001) Fauvel, Charles Alphonse Albert. Bull Am Mus Nat Hist 265:65–66

Feather-Winged Beetles

Members of the family Ptilinidae (order Coleoptera).

► Beetles

Feces

The excrement of insects produced by the digestive system and passed out the anus. It is also known as excreta. When it is mixed with an abundance of indigestable plant fragments it is commonly called frass.

► Frass
► Alimentary Canal
► Digestion

Fecundity

The reproductive capacity of an organism, often taken to mean the number of eggs produced by a female during her lifetime (contrast with fertility).

Feeding Deterrents

Chemicals that inhibit feeding but do not necessarily repel insects

► Host Plant Selection by Insects

Felt, Ephraim Porter

Ephraim Felt was born in Massachusetts on January 7, 1868. He graduated from Massachusetts State Agricultural College with a B.Sc. degree in 1891 and then became assistant to Fernald and studied the gypsy moth. In 1892 he was awarded a fellowship to Cornell University, studied with Comstock, and received a D.Sc. in 1894. From 1893 to 1895 he taught natural science at the Clinton Liberal Institute, and then worked in the office of the State Entomologist (Fig. 16) of New York, becoming State Entomologist (a job he held for 30 years) when the incumbent, J.A. Lintner, died in 1898. In 1904 appeared in print his "The mosquitoes or Culicidae of New York State" and in 1906 his two-volume "Insect affecting park and woodland trees." His work on gall midges (Cecidomyiidae) was copious, and in his life he described 1,060 species of them, publishing in 1940 "Plant galls and gall makers." Additionally, he wrote several books on trees, and worked on wind-borne insects, the role of insects as vectors of human diseases, and gypsy moth. He was editor of Journal of Economic Entomology from 1908 to 1935, an active member of the New York Entomological Society, a frequent contributor to the New York Times, and

Felt, Ephraim Porter, Figure 16 **Ephraim P. Felt.**

entomological editor of "Country Gentleman." He married in 1908 and had four children. He died on December 14, 1943.

Reference

*Mallis A (1971) Ephraim Porter Felt. In: American entomologists. Rutgers University Press, New Brunswick, NJ, pp 399–402

Femur (pl., femora)

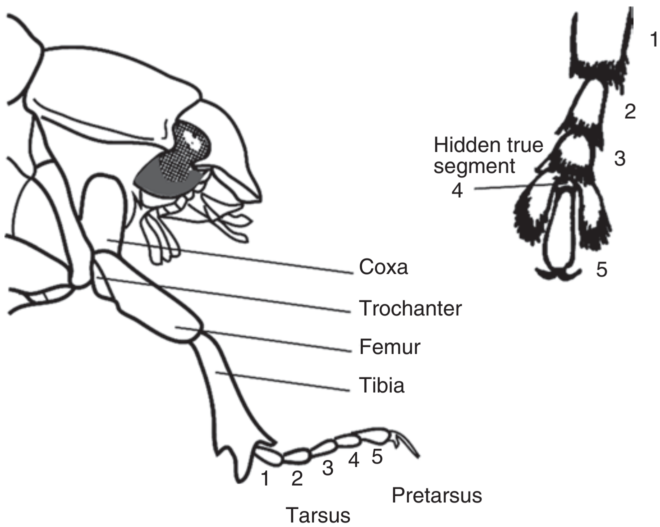
A segment of the leg between the trochanter and tibia. The third leg segment and one of the two largest portions (Fig. 17) of the insect leg, often expanded to enhance leaping or prey capture.

► Legs of Hexapods

Fenichel, Sámuel

GEORGE HANGAY
Narrabeen, NSW, Australia

Sámuel Fenichel was born on the 25th of August 1868 in Nagyenyed, Alsó-Fehér Shire, in Transylvania, then Hungary, now Romania. He received excellent education in natural history in the highly respected Bethlen College of his hometown. In 1888, he was invited to join the Museum of Archaeology in Bucharest, Romania. For 2 years he lead the excavations and research of the ruins of Tropea, a fortress and settlement built by the Romans in Dobrudja (Romania). During this work he met Albert Grubauer, a naturalist from Munich, who was planning a zoological expedition to New Guinea. Fenichel was young, with a keen interest of natural history and an expert preparator of zoological specimens; therefore, he seemed to be an ideal companion to Grubauer, who consequently asked him to join his expedition. Fenichel resigned from his museum post and travelled to Budapest (Hungary) where he received further training in the Hungarian National Museum. The museum also commissioned him to collect zoological and ethnographical material for its collections. Grubauer and Fenichel arrived to German New Guinea (Kaiser Wilhelmsland) in December 1891. Fenichel started to work immediately by collecting zoological specimens, mainly insects, but Grubauer fell ill and left the island. He also took with him the 200,000 Marks, which were to support the expedition, leaving only 100 Marks for Fenichel. Despite this setback, Fenichel stayed and continued his work alone. He concentrated on entomological work mainly, accumulating more than 25,000 specimens. He explored the country around Astrolabe Bay, Friedrich-Wilhelmshafen (today Madang), Konstantinhafen, Erima and Stephansort. He collected in the Finisterre Mountains, where only two other European naturalists worked before him, the Russian N.N. Mikhulo-Maklai (1846–1888) and the German Otto Finsch (1839–1917). As most field zoologists of that age, he also collected ethnographical objects, the number of items in his collection were over 3,000. Most of Fenichel's specimens reached the Hungarian National Museum and a few went to his Alma Mater in Nagyenyed. His promising carrier as an entomologist and



Femur (pl., femora), Figure 17 Leg of a beetle (Coleoptera: Scarabaeidae) leg showing its component parts, and a close-up of one type of beetle tarsus (foot).

naturalist was cut short by malaria. Fenichel died in Stephansort on the March 12, 1893. A memorial plaque on the wall of the Port Moresby University commemorates the life and work of Sámuel Fenichel, the first Hungarian entomologist in New Guinea.

Reference

Balogh J, Allodiatoris I (1972) In Memoriam Lajos Bíró and Sámuel Fenichel. Acta Zoologica, XVIII:1–2. Budapest, Hungary

Fennah, Ronald Gordon

Ronald Fennah was born in Ludlow, England, in 1910. He graduated from Cambridge University in 1935 with a bachelor's degree and was appointed lecturer in zoology at the Imperial College of Tropical Agriculture, Trinidad. While employed there, he was seconded in 1937–1942 as citrus entomologist and in 1942–1948 as food crop pests entomologist to the Windward Islands, and then (1948–1951) entomologist to the Trinidad Department of Agriculture and (1951–1958) entomologist to the cocoa research scheme, Trinidad. These postings involved him in surveys for citrus pests, a (1947) book "The insect pests of food crops in the Lesser Antilles," trials of the resistance of sugarcane varieties to froghoppers (Cercopidae), and studies of the insect pests of cacao in relation to cacao physiology. In 1944, he tested DDT against insect pests of food crops. To test its safety to humans, he deliberately ingested DDT, and painted an emulsion on his skin, during a period of 13 months. He detected no effect. In Trinidad, he developed an interest in the taxonomy of Hemiptera and began publishing on this subject, ultimately producing over 120 papers on this subject, mostly on Fulgoroidea. In 1958 he was appointed assistant director of the Commonwealth Institute of Entomology in London, its director in 1969, and he retired in 1975. Retirement did not stop his taxonomic contributions. Cambridge University awarded him an Sc.D. degree in 1967. He died on August 19, 1987, survived by his wife, Louie May.

References

Wilson MR (1988) Dr. Ronald Gordon Fennah (1910–1987) [with bibliography]. Entomologist's Monthly Magazine 124:167–176

Wilson MR, Harris KM (1988) Ronald Gordon Fennah (1910–1987) Antenna 12:4

Feral

Animals or plants that have escaped domestication and reverted to natural behavior. In entomology, this is used most commonly in reference to swarms of honey bees that escape domestication.

Fergusoninidae

A family of flies (order Diptera).
► Flies

Fernald, Charles Henry

Fernald, Charles Henry, Figure 18 **Charles H. Fernald.**

Charles Fernald was born in Maine on March 16, 1838. At 21, he entered Maine Wesleyan Seminary with the intent of becoming a ship's captain. After 3 years of study he joined the Union Navy and served 3 years during the American Civil War. In the Navy, he also was able to take courses, completing the requirements of Bowdoin College for a B.A. degree, which he received. After the war he became principal of Litchfield Academy, then of Houlton Academy, both in Maine. In the last of the positions, he studied geology, botany, zoology and entomology on his own, and then received in 1871 a M.A. degree from Bowdoin College. That same year, he was made a professor of natural history in Maine State College. In addition to teaching, he studied and published on insects. In 1886 he moved to Massachusetts Agricultural College as professor of zoology and lecturer (Fig. 18) in veterinary science, and occupied this position until his retirement in 1910. The Hatch Act made Federal funds available to state agricultural colleges for experiment stations, and Charles was appointed entomologist to the Massachusetts station. This gave him responsibility for research in applied entomology. A main part of his research was aimed at the gypsy moth, whose presence in Massachusetts was due to its importation by Leopold Trouvelot and subsequent escape from confinement. This research, and Fernald's teaching of entomology made Massachusetts a center for the training of entomologists. His wife, Maria, made her own mark on entomology, with moths of the families Tortricidae and Tineidae, and especially by publication of "A catalogue of the Coccidae of the world." Their son, Henry Torsey Fernald, born on April 17, 1866, in Maine, became first head of the Department of Entomology at Massachusetts Agricultural College in 1899 while his father was professor of zoology. Charles Fernald died on February 22, 1921.

Reference

*Mallis A (1971) Charles Henry Fernald and Henry Torsey Fernald. In: American entomologists. Rutgers University Press, New Brunswick, NJ, pp 141–150

Fern Scale, *Pinnaspis aspidistrae* (Signoret) (Hemiptera: Diaspididae)

These scale insects affect the foliage and fruit of citrus.

► Citrus Pests and Their Management

Ferris, Gordon Floyd

Gordon Ferris was born in Kansas on January 2, 1893, then moved to Missouri with his family and four siblings. His mother died there in childbirth. Gordon moved at the age of 13 to live with his brother Leslie on a farm in Kansas. In 1909, he entered Ottawa University in Kansas but soon dropped out and went to work for a power company in Colorado. The power company funded education for its employees, and in 1912 sent Gordon to Stanford University in California. In 1917, he obtained the degree of M.A., became a teaching assistant there, and remained there for the rest of his 42-year academic career. He was a taxonomist and teacher. He worked on Anoplura, Mallophaga, Coccoidea, Diptera-Pupipara, Cimicidae, and Polyctenidae, being an excellent collector of the insects that he studied. His collecting trips took him throughout the southwest of the USA, and to Mexico and China, and his museum study trips took him to the Natural History Museum (London) and to Cambridge University. He published 275 works, of which his 4-volume "Atlas of the scale insects of North America" (1950–1953) is one of the most outstanding. He died on May 21, 1958.

Reference

*Mallis A (1971) Gordon Floyd Ferris. In: American entomologists. Rutgers University Press, New Brunswick, NJ, pp 169–173

Ferruginous

A rusty or reddish brown color.

Fertility

The number of offspring produced, often taken to mean the number of eggs that hatch (living offspring) during the lifetime of the female. (contrast with fecundity)

Fertilization

The union of the haploid male and female gametes to produce a diploid zygote, marking the start of the development of a new individual and the beginning of cell differentiation.

Festoons

Uniform rectangular regions, separated by sulci (grooves), and located on the posterior margin of most hard ticks.

Fetid

A disagreeable or offensive odor to humans, though such odors may be quite attractive to insects. Such odors are often associated with decaying animals or plant material, but some plants produce fetid odors to attract pollinators.

Fibroin

A proteinaceous component of insect silk. It usually is covered by seracin.

► Silk

Fideliidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Field Capacity

A property of soils. Soil that contains all the moisture it can retain after draining freely under gravity. Saturated soil.

Field Crickets

A subfamily of crickets (Gryllinae) in the order Orthoptera: Gryllidae.

► Grasshoppers, Katydids and Crickets

Fig Rots

Several fungi affect fig fruit, causing the fruit to rot. Insects are implicated in causing these diseases.

► Transmission of Plant Diseases by Insects

Fig Wasps

HANNAH NADEL
USDA-ARS, San Joaquin Valley Science Center, Parlier, CA, USA

Miniscule wasps (order Hymenoptera) that breed exclusively in association with the flask-shaped floral receptacle (fig, syconium) of fig plants (*Ficus* spp.). The group is composed of about 3,000 species of Chalcidoidea in the families Agaonidae, Pteromalidae, Torymidae, Ormyridae, Eurytomidae, and the unplaced subfamilies Epichrysomallinae and Sycophaginae. The Agaonidae are mutualistic partners of figs, pollinating the flowers while laying their eggs in the ovules inside the receptacle. The other species feed on syconial tissues, parasitize the Agaonidae or each other, or parasitize a small number of other insects developing in the syconia. Non-pollinators mostly oviposit from the exterior of the fig wall, and hence have long ovipositors that evolved in length to match the thickness of the fig wall. Some resemble pollinators in form and habit, entering the syconia to lay their eggs. Many have apterous or dimorphic males. Only 20–30% of fig wasp species have been described. A few species of Braconidae (Ichneumonoidea) have also been reared from syconia.

► Wasps, Ants, Bees and Sawflies
► Agaonidae

References

Bouček Z (1993) The genera of chalcidoid wasps from *Ficus* fruit in the New World. J Nat Hist 27:173–217
Weiblen GD (2002) How to be a fig wasp. Ann Rev Entomol 47:299–330
West SA, Herre EA, Windsor DM, Green PRS (1996) The ecology and evolution of the New World non-pollinating fig wasp communities. J Biogeogr 23:447–458

Filariasis

Disease caused by infection with nematodes (filarial worms), and transmitted by flies.

► Dirofi lariasis
► Onchocerciasis
► Human Lymphatic Filariasis (Elephantiasis)

File

A file-like ridge on the underside of the tegmina, near the base. The file is part of the stridulating mechanism in katydids and crickets.

Filiform

Thread-like, slender, and nearly uniform in diameter. A term usually used in reference to antennae.

► Antennae of Hexapods

Filter Chamber

A modification of the gut in sap-feeding insects that allows much of the water and some of the excess carbohydrate ingested by the insect to bypass the midgut, resulting in production of honeydew.

► Alimentary Canal and Digestion

Filter Feeders

Insects in aquatic communities that collect particulate matter from water with the aid of mouth brushes, leg brushes, or webs.

Filter Rearing System for Sterile Insect Technology

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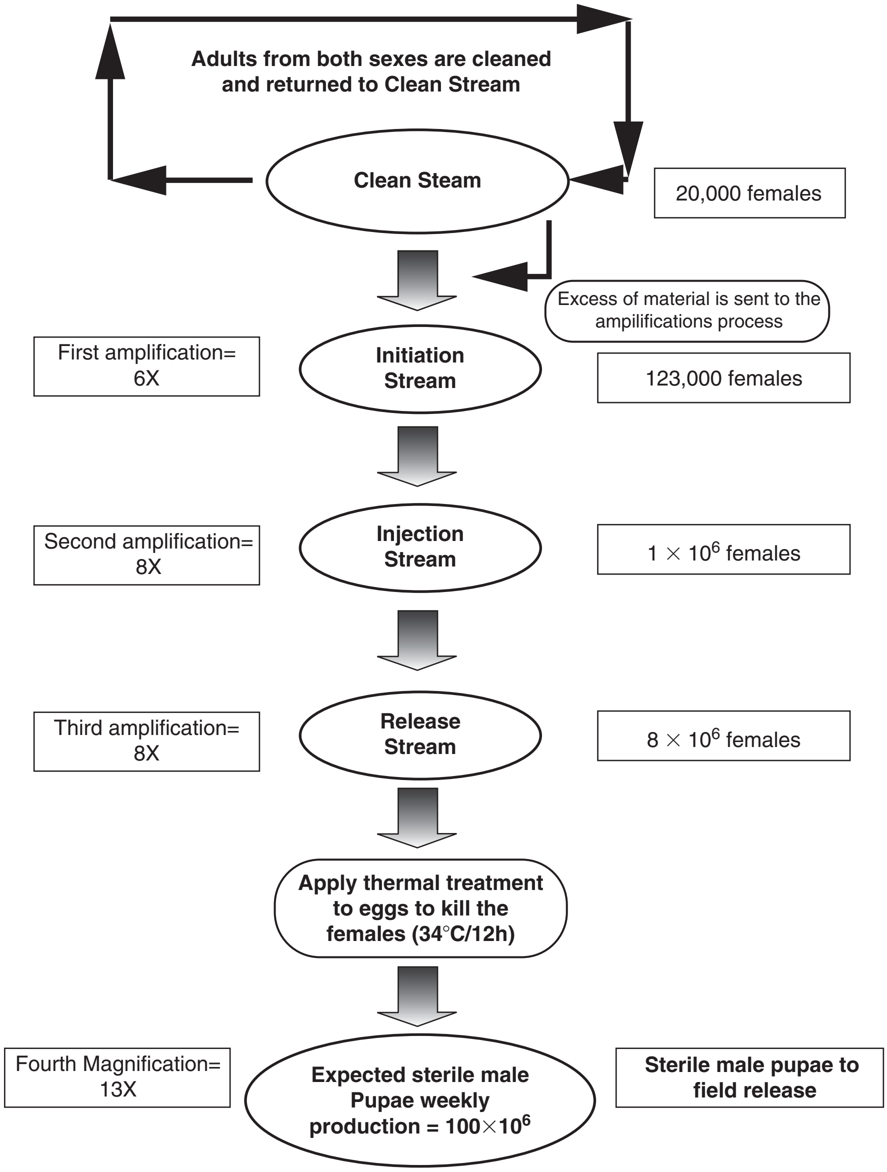
Genetic sexing strains (GSS), which produce only males, are now being used on a large scale for the control of the medfly, *Ceratitis capitata* using the sterile insect technique (SIT). The use of these strains has had a major impact on the overall efficiency of the technique by increasing significantly the amount of sterility induced in field populations and by reducing operational costs. GSS are based on the use of male linked chromosomal translocations, which make possible the linkage of selectable marker genes to the male sex. Two selectable genes have been incorporated into functional sexing strains specifically, *white pupae* (*wp*), which allows males and females to be discriminated based on pupal color, and *temperature sensitive lethal* (*tsl*), which allows the females to be killed by an increase in ambient temperature. GSS are not 100% stable due to the occurrence of a low level of genetic recombination between the selectable marker and the translocation breakpoint. This results in the loss of the sexing characteristics of the strain.

The Filter Rearing System (FRS) was designed to solve the problem of genetic recombination (Fig. 19) when GSS are mass reared for SIT programs. The principle of the FRS is to maintain a small colony of a GSS, with zero recombination, which can continually be amplified to rear a large colony from which males are produced for irradiation and release. In principle, the FRS creates a one-way system for production to ensure that any recombinants are not reintroduced into the colony. The FRS also has other applications for improving the quality of mass reared insects.

In a GSS, males emerge from brown pupae and females from white pupae. In the filter, any flies emerging from the wrong colored pupae are removed every generation. Pupae are separated by color 2–3 days before adult emergence and individual pupae are placed in plastic grids with 100 holes/grid. The holes are 1 cm^2. The grid is covered with a transparent plexiglass lid and the bottom of the grid is sealed with metal gauze. After adults have emerged, they are examined under a magnifying glass and recombinant individuals are killed with a burst of compressed air through the metallic grid. The adult flies emerging from the correct pupal color are transferred to a cage to start the amplification of the population for the subsequent release of sterilized males.

Since it is impossible to screen the very large colonies for operational programs the FRS is based on the sequential amplification of a relatively small backup colony which is cleaned of recombinant individuals. The backup colony (Clean Stream) must be cleaned each generation, but must be large enough to produce sufficient offspring to provide for itself and to initiate the colony amplification sequence. The number of amplifications (Initiation and Injection Streams) depends upon the size of the backup colony in relation to the size of the final colony (Release Stream) required to produce the desired number of males for release, and the rate at which recombinants accumulate at each amplification stage.

The FRS has now been introduced into all of the facilities rearing medfly GSS where it has been shown to be a viable and operational



Filter Rearing System for Sterile Insect Technology, Figure 19 **The continuous Filter Rearing System (FRS) for medfly male-only production.**

system to guarantee the accurate production of only males (> 99.5% males) during release operations.

References

Caceres C, Fisher K, Rendon P (2000) Mass rearing of the medfly temperature sensitive lethal genetic sexing strain in Guatemala. In: Tan KH (ed) Area-wide control of fruit flies and other pests. Penerbit Universiti Sains Malaysia, Penang, Malaysia, pp 551–558

Fisher K, Caceres C, Rendon P (2000) A filter rearing system for mass reared sexing strains of Mediterranean fruit fly (Diptera: Tephritidae). In: Tan KH (ed) Area-wide control of fruit flies and other pests. Penerbit Universiti Sains Malaysia, Penang, Malaysia, pp 543–550

Robinson AS, Franz G, Fisher K (1999) Genetic sexing strains in the medfly, *Ceratitis capitata*: development, mass rearing and field applications. Trend Entomol 2:81–104

Filth Fly Parasitoids (Hymenoptera: Pteromalidae) in North America

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Chalcidoid wasps (Hymenoptera: Chalcidoidea) of the family Pteromalidae comprise the principle parasitoids of pest flies (Diptera) associated with livestock. At least 15 native species of filth fly parasitoids have been identified and a few foreign species have been introduced into North America for classical biological control. Species reported to occur, or which may occur, in North America are listed in Table 2.

Several surveys have been conducted throughout North America to determine species compositions, which appear to be influenced by climatic conditions. Species of *Spalangia* typically are associated with warmer regions and, with species of *Muscidifurax*, dominate the parasitoid complexes in the United States and parts of Canada. The non-chalcidoid species, *Phygadeuon fumator* Gravenhorst (Hymenoptera: Ichneumonidae), also is important in northeastern United States and Canada, and *Trichomalopsis sarcophagae* (Gahan) is common in Alberta, Canada. Microhabitat conditions, such as type of substrate, moisture and light levels also influence species composition within different regions.

Natural levels of parasitism typically are low, with season-long values usually <5%. To enhance parasitism, several species have been commercialized for sale as biological control agents, primarily for the house fly, *Musca domestica* L. and the stable fly, *Stomoxys calcitrans* (L.) (Diptera: Muscidae). Commercialized species include *Muscidifurax raptor* Girault & Saunders, *M. raptorellus* Kogan & Legner, *Nasonia vitripennis* Walker, *Spalangia endius* Walker and *S. nigroaenea* Curtis. These species are mass-reared by insectaries in the United States and shipped to customers throughout North America. Parasitoids normally are packaged in units of 10,000 parasitized house fly pupae, which may contain up to 80,000 parasitoids depending on the species mix. *Muscidifurax raptorellus* and *N. vitripennis* are gregarious species that produce several offspring per parasitized pupae. A common mix includes species of *Muscidifurax* and *Spalangia*. *Spalangia* are reported to search deeper into the substrate for fly pupae than do *Muscidifurax*, but are less active at cooler temperatures than are *Muscidifurax*.

Purchased parasitized fly pupae are scattered in fly breeding sites, such as rotting piles of hay, straw or bedding, accumulations of manure, or spilled silage. Wasps emerging from the pupae then locate and parasitize natural fly pupae in the surrounding area. Release studies in feedlots show that *M. raptorellus* may disperse out to 100 or more meters to locate hosts. Because the flies have a shorter generation time and produce more eggs than the wasps, releases of the wasps are recommended every week or every second week throughout the fly season. Recommended release rates are based either on a per unit area, or on the number of animals in the livestock facility. Effective fly control relies upon a regular program of sanitation to remove fly breeding sites and possibly the occasional use of insecticides to target adult flies.

Research to improve the efficacy of these wasps as biological control agents of filth flies includes: (i) surveys to locate more effective species for commercialization, (ii) matching the release of commercialized species to regional climates, (iii) optimizing release rates and (iv) reducing the costs of mass-production. Research also is underway to increase the production of female wasps using infections of bacteria in the genus *Wolbachia*.

References

Blume RR (1985) A checklist, distributional record, and annotated bibliography of the insects associated with bovine droppings on pastures in America north of Mexico. Southwest Entomol (Suppl 9): 55

Filth Fly Parasitoids (Hymenoptera: Pteromalidae) in North America, Table 2 Pteromalid parasitoids (Hymenoptera: Chalcidoidea) of filth flies (Diptera: Muscidae)[a] in North America, or which may occur in North America

Pteromalidae
Dibrachys cavus (Walker)[b]
Muscidifurax raptor Girault & Sanders[b]
Muscidifurax raptorellus Kogan & Legner
Muscidifurax raptoroides Kogan & Legner
Muscidifurax uniraptor Kogan & Legner
Muscidifurax zaraptor Kogan & Legner[b]
Nasonia vitripennis (Walker)[b]
Pachycrepoideus vindemiae (Rondani)[b]
Psycophagus omnivorus (Walker)[b] [based on a single rearing record]
Spalangia cameroni Perkins[b]
Spalangia drosophilae Ashmead[b]
Spalangia erythromera Förster[b]
Spalangia endius Walker[b]
Spalangia gemina Bouček
Spalangia haematobiae Ashmead[b]
Spalangia longepetiolata Bouček
Spalangia nigra Latreille[b]
Spalangia nigripes Curtis[b]
Spalangia nigroaenea Curtis[b]
Spalangia subpunctata Förster[b]
Toxeumorpha nigricola (Ferrière) (=*Sphegigaster* sp.)
Trichomalopsis americana (Gahan)[b]
Trichomalopsis dubia (Ashmead)[b]
Trichomalopsis sarcophagae (Gahan)[b]
Trichomalopsis tachinae (Gahan)[b]
Trichomalopsis viridescens (Walsh)[b]
Urolepis maritima (Walker)[b] [recorded as filth fly parasitoid in Europe]
Urolepis rufipes (Ashmead)[b]

[a]*Musca domestica* L. (house fly), *M. autumnalis* DeGeer (face fly) or *Stomoxys calcitrans* (L.) (stable fly)
[b]Reported from Canada in addition to the United States

Floate KD, Khan B, Gibson GAP (1999) Hymenopterous parasitoids of filth fly (Diptera: Muscidae) pupae in cattle feedlots of Alberta, Canada. Can Entomol 131:347–362

Floate KD, Coghlin P, Gibson G (1999) Dispersal of the filth fly parasitoid *Muscidifurax raptorellus* (Hymenoptera: Pteromalidae) following mass-releases in cattle confinements. Biol Control 18:172–178

Legner EF (1994) Biological control of Diptera of medical and veterinary importance. J Vector Ecol 20:59–120

Rueda LM, Axtell RC (1985) Guide to common species of pupal parasites (Hymenoptera: Pteromalidae) of the house fly and other muscoid flies associated with poultry and livestock manure. North Carolina Agricultural Research Service Technical Bulletin 278, 88 pp

Smith L, Rutz DA (1991) Microhabitat associations of hymenopterous parasitoids that attack house fly pupae at dairy farms in central New York. Environ Entomol 20:675–684

Finger-Net Caddisflies

Members of the family Philopotamidae (order Trichoptera).

► Caddisflies

Fingerprinting

DNA fingerprinting relies on the presence of simple tandem-repetitive sequences that are present throughout the genome. The regions show length polymorphisms, but share common sequences. DNA from different individuals is cut and separated by size on a gel. A probe containing the core sequence is used to label those fragments that contain the complementary DNA sequences. The pattern of each gel is specific for a given individual, and can be used to establish parentage.

Fire Blight

This important bacterial disease of rosaceous plants is transmitted by many insects.

► Transmission of Plant Diseases by Insects

Fire-Colored Beetles

Members of the family Pyrochroidae (order Coleoptera).

► Beetles

Fireflies (Coleoptera: Lampyridae)

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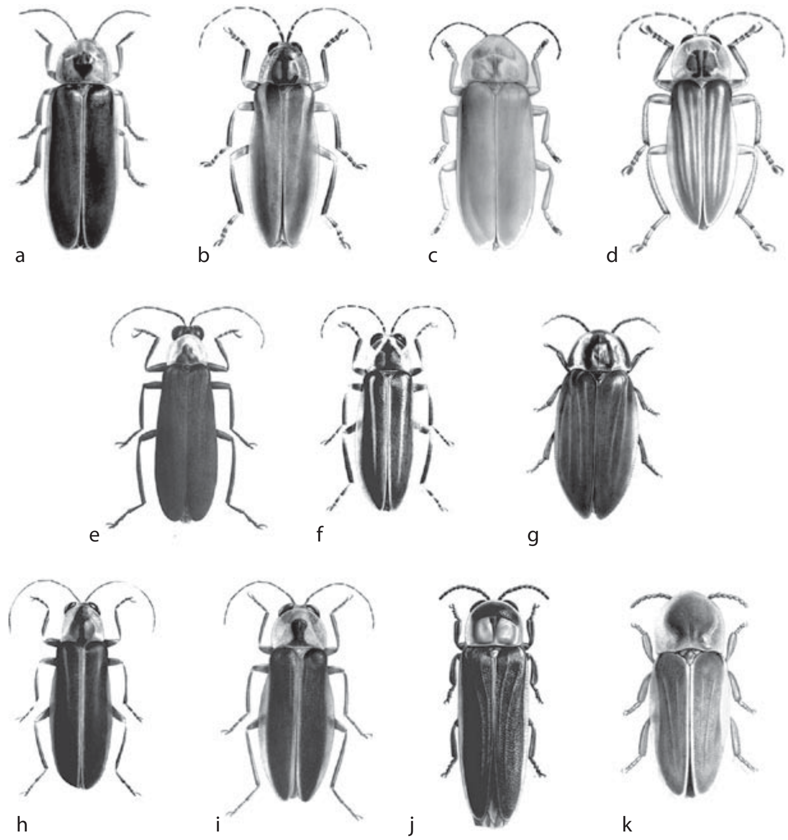
Fireflies occur on all continents except Antarctica, and are best known for the biochemical light they emit. In some regions of North America the common flashing species are known as lightningbugs; in rural Jamaica fireflies are called blinkies but in Kingston they are peenywallies; in Latin America they are luciernaga; in Japan hotaru; in Great Britain and northern Europe, including Hamlet's Denmark (Act 1, Scene V), the single or more common resident species *Lampyris noctiluca* (L.) is known as "the glowworm" ("Glühwürmchen"); and in New Guinea pidgin they are "binatang em i gat lait bilong as." Fireflies appear in folk culture and tradition old and recent around the world: an Asian myth relates a burning grass origin, and one from Europe says that if a glowworm enters the house it warns of impending infant death; in colonial Hispanic America fireflies were used and subsequently outlawed as signals for romanti c trysts (this is more commonly told of luminescent click beetles, family Elateridae). North American children capture them at twilight and put them in jars for bedtime viewing, though some sell them to a company that extracts and processes their light-emitting chemicals for use in research and medicine. Another company transplanted the key gene (for the enzyme, luciferase) from the most common lawn firefly into a bacterium, simplifying commercial production and saving millions of fireflies – and hopefully returning childhood perspectives to the poetic value of fireflies. Children catching fireflies and looking at them in jars, and flying fireflies attracted to glowing time-pieces are TV images with commercial appeal.

With their presumptive kin (superfamily Cantharoidea) fireflies are sometimes informally referred to as leather-winged beetles, from the pliable texture of their wing-covers (forewings, elytra). This group includes soldier beetles, net-winged beetles, giant glowworm beetles, long-lipped beetles, false-fireflies (respectively, beetle families Cantharidae, Lycidae, Phengodidae, Telegeusidae, certain Omethidae), and a few additional rare and unfamiliar forms. Because ever more is learned of DNA content and patterns within and among these taxa, expect that significant changes in formal classification and theoretical framework may be forthcoming.



Fireflies (Coleoptera: Lampyridae), Figure 20 **Some fireflies: (a) *Photinus pyralis* (L.) is the best known firefly in eastern North America, and often appears in considerable numbers. It is the species children chase across lawns at twilight. Its distinctive dipping then rising yellow flashes earned it the appellation "Big Dipper Firefly." (b) *P. pennsylvanica* (DeGeer) was the name used for most North American *Photuris* species from early in the nineteenth century until 1951. Through studies of male flash patterns, several additional species were recognized. The firefly with a distinctive dot-long-dash pattern now claims the DeGeer name of 1774. (c) *Photinus pallens* (Fabricius), a common "blinky" in Jamaica, forms huge aggregations on Asian ginger lilies in fallow fields. (d) An unusual six-lined *Photuris* from Guatemala and southern Mexico. (e) An unnamed montane Photurinae from Colombia, South America, with wasp-like coloration suggesting it may be exposed to potential predators during daylight. (f) *Photuris lloydi* McDermott is presently known with certainty only from its type locality in a hydric hammock in the highlands of south-central Florida. (g) *Ellychnia corrusca* (L.) pupates in the fall and adults are found on tree trunks in the dead of winter, though mating occurs the following spring. (h) Several species with the general appearance of this Florida "variety" of *Photuris versicolor* (Fabricius) occur by the hundreds/thousands in various "grasslands" from the Atlantic to Kansas. (i) *Photuris frontalis* LeConte is one of the flash-synchronizing species in North America. Along with five other species, it forms a distinctive subset of North American *Photuris*. (j) *Photinus collustrans* LeConte, Florida's twilight lawn firefly, is identical in appearance to this one, except the yellow inner-margins of its elytra are continuous around the apices. This one, *P. tanytoxus* Lloyd, has green light and flies later in the evening. (k) *Pleotomodes knulli* Green, an ant-living firefly, occurs throughout peninsular Florida. A congener is found only in central Florida and another in Arizona.**

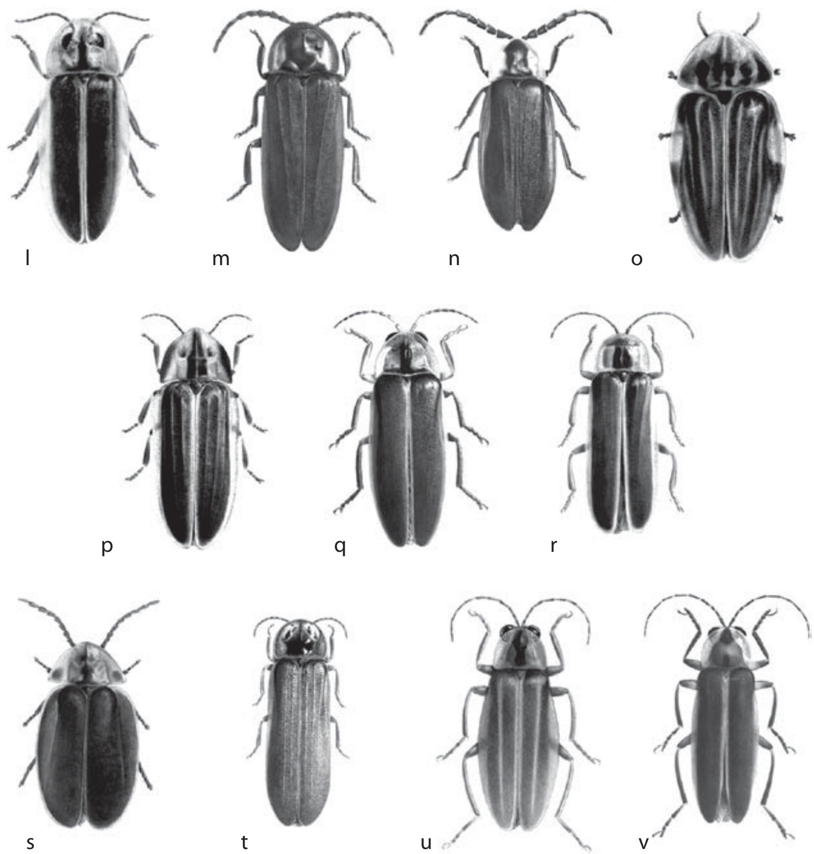
Worldwide, nearly 2,000 lampyrid species have been formally described and named in nearly 80 genera (Figs. 20 and 21). About half of these occur in tropical America and many also occur in tropical Asia, but, curiously, few are known from tropical Africa. The actual number of firefly species in the world, if competent museum naturalist/taxonomists had the opportunity to make a complete collection, might be nearly 8,000. About 120 species in 17 genera are presently named from North America, but in actuality, based on extensive field and bench study, there could be as many as 225 nameable entities in 19 genera, with several additional transitional and problematic populations and reports. The situation will be properly outlined only after their mating signals, ecology, and population inter-connections and genetics are studied in intimate detail. What is especially exciting about such research is that, because some species are so localized, a new (i.e., undescribed) species may be encountered at any time, as each unexplored valley or ancient lake bed is reconnoitered by a taxonomist-fireflyer (Fig. 22).

Carl Linnaeus, the Swedish originator of the basic system used for organismic classification, named the first North American species in 1758, and one of them was the ubiquitous *Photinus pyralis* (L.). The oldest actual firefly remnants presently known from North America are pronotal sclerites of specimens that are closely related to, if not actually, ancestors of today's day-active *Ellychnia corrusca* (L.). These fossils were found in post-glacial sphagnum bogs in southern Ontario, Canada, and dated at about 10,000 B.P. (before the present). Much older remnants of fireflies occur in amber from the Dominican Republic, including specimens that resemble *Robopus* species that now live on Caribbean islands, and a pair in a sexual coupling that has endured about 19 million years.

Although some Florida residents believe that fireflies don't occur in their state, more species are present in Florida than in the north, but conspicuous flashing displays that catch the human eye are rare. Georgia and Florida each have at least 56 species, and as easily seen from a good atlas (one with climate, vegetation, and topographic maps), these two states have a diversity of ecological situations. A 100-mile-wide swath along the border between the two states from the Atlantic to the Gulf may be the richest firefly space in North America. Northern and western states have fewer species. Fireflies in the central Atlantic and midwestern states get more attention because a few rather large species flourish in urban parkland, suburbs, farmland, and other disturbed grasslands, and these frequently flash in huge space-sweeping, eye-catching populations (Fig. 23).

The grandest of all flashing panoramas in the world occur in tidal swamps of mangrove and nippa palm in Southeast Asia, where species of the bentwinged fireflies (genus *Pteroptyx*) gather by the thousands, perhaps formerly in the millions, in broadleaved trees and bushes along brackish waterways and a little inland along canalways. Native boatmen once used 'firefly trees' as navigational beacons, but now there are industries and human habitations occupying the shorelines of many rivers. Such developments are sources of pollution, which flows downstream and sometimes returns on the incoming tide, and which can seep into and poison adjacent bentwing firefly habitat. In recent years, interest in preserving these fireflies has been expressed by local governments.

Some of these species, such as *Pteroptyx malaccae* (Gorham) and *P. tener* (E. Olivier) invite a 'beacon' appellation because perched males emit their flashes in precision synchrony – which western 'scientific' thought once considered to be 'unnatural,' hence not to be believed, and there is a considerable and occasionally silly literature on the subject. Visitors to Malaysia can take a tourist boat ride on the Kuala Selangor (River) and see synchronizers up close. Males of other tree-swarming southeast Asian species such as *Pteroptyx valida* E. Olivier and relatives in New Guinea emit more complex signals, and though they appear to flash independently, they are certainly influenced by near neighbors, which, of course,



Fireflies (Coleoptera: Lampyridae), Figure 21 **Some additional fireflies: (l) *Micronaspis floridana* Green occurs only in salt marshes along Florida's coasts and in the Keys. (m) *Pyropyga nigricans* (Say) occurs in wet grassy areas, and along streams and shorelines. Short-winged individuals occur at a few scattered localities, sometimes with the typical long-winged individuals. (n) *Lucidota atra* (G.A. Olivier) is the common large, black daytime firefly of midsummer in the eastern U.S. (o) *Aspisoma* fireflies are neotropical, but have been collected in extreme southern Texas and Florida. Some members of this genus may be semi-aquatic and pupate on emergent vegetation. (p) *Pyractomena angulata* (Say) sometimes is seen in numbers over marshes, but the amber candle-like flicker of this firefly is more often seen winding slowly around the boughs of treetops. (q) *Bicellonycha wickershamorum* Cicero in Arizona is the only member of this large neotropical genus known to occur north of Mexico. (r) *Photinus indictus* (LeConte) a daylight firefly is without a lantern, and virtually indistinguishable in dorsal view from the flashing species shown here, *P. macdermotti* Lloyd; it differs from all but one other daytime-dark species by having a pale border around each elytron. (s) *Tenaspis angularis* LeConte is a tropical firefly that is collected from time to time in North America, but rarely, and so far only singly judging from museum collections. Perhaps individuals occasionally arrive from Mexico, but they and progeny, if any, survive only a short time. (t) *Phausis reticulata* (Say) is known only from scattered localities across North America to Oklahoma, but can be seen in abundance in the Appalachian Mountains. (u) *Photuris lucicrescens* Barber is a very common firefly across much of eastern North America, and has a distinctive crescendo flash. This illustration is of a related though smaller Florida species that is virtually indistinguishable from "Big Lucy." (v) *Photuris lineaticollis* (Motschulsky) is one of several large species with a tawny rather than yellow trim and a broken pronotal vitta, and found in the southern U.S. from Florida to Texas.**

are rivals for females that approach and enter their illuminated arenas (leks?). There are a few species in North America in which males precisely synchronize their flashes, though these do it only while flying in especially close proximity, typically in open woodlands and hammocks. These include *Photuris congener* LeConte and *Photuris brunnipennis* Jacq.-DuV. in Florida, *Photuris frontalis* LeConte from Georgia north to Maryland and west into Tennessee, and *Photinus concisus* Lloyd in Texas.

Life history

Fireflies are holometabolous insects, and have four life stages: egg, larva, pupa, and adult.

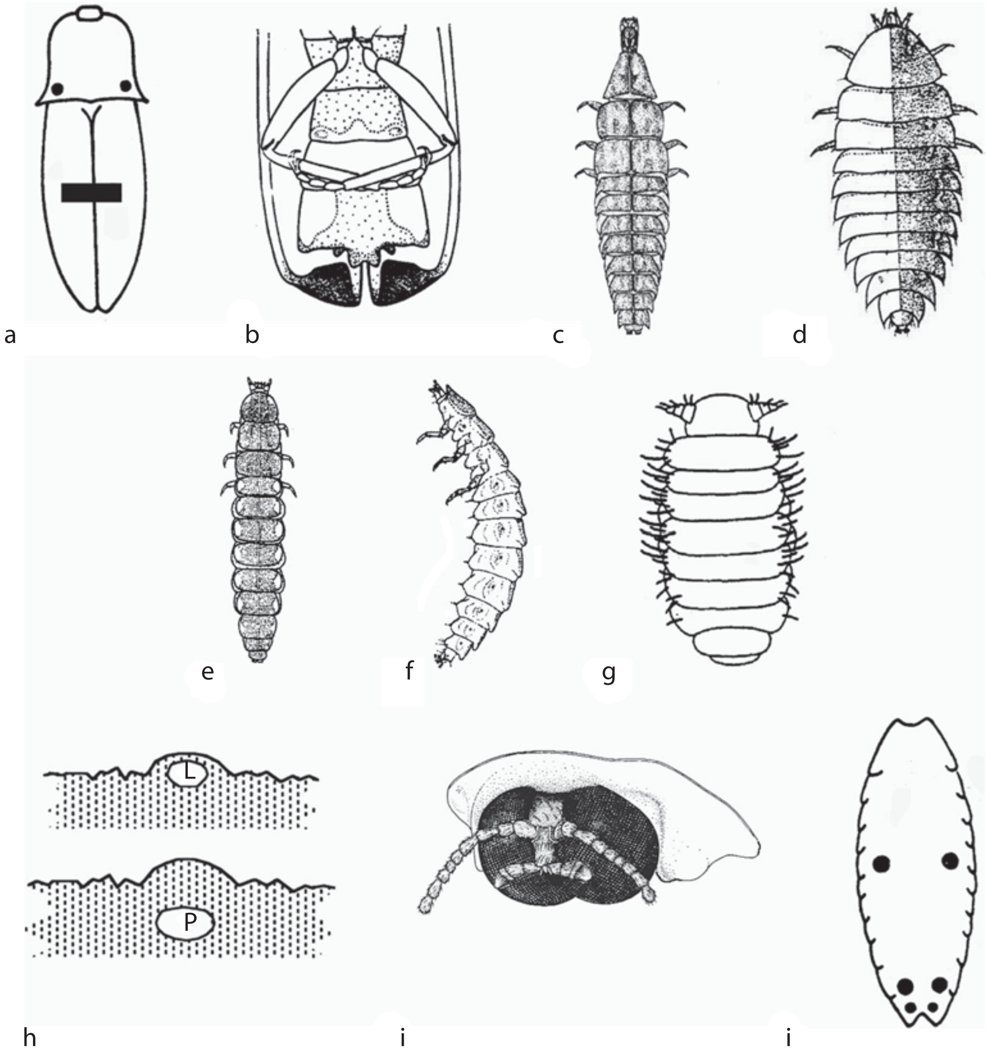
Eggs

In some lampyrid species eggs are deposited a few at a time over several days or weeks. This is probably the case in *Photuris* species in which adult females are hunters and travel among suitable locations seeking prey, and perhaps in early-successional (and ecologically tolerant) "weed" species such as *Photinus pyralis*. In some species, eggs are laid together at one time. Females of *Photinus collustrans* LeConte die in their burrows after ovipositing there. Unfortunately, no species in North America compares with certain Japanese species with respect to egg biology. In the stream-living Japanese Gengi firefly (*Luciola cruciata* Motschulsky), mated females fly upstream and lay their eggs communally in masses near the stream. When larvae hatch they fall, tumble and crawl into the stream, and during the next year, as they gradually are carried downstream, they eat snails and grow. In this firefly, which takes its common name from a samurai warrior family, the life cycle is thus intimately coupled with the hydrologic cycle. Ovipositing Gengi females locate the eggs of other females by the glow the "piles" emit. The eggs of some North American species also glow, but only dimly. In some cases, this glow comes from luminous material that is smeared on the eggs in the mother's egg canal, but later in development the light organs of developing embryos glow within the eggs.

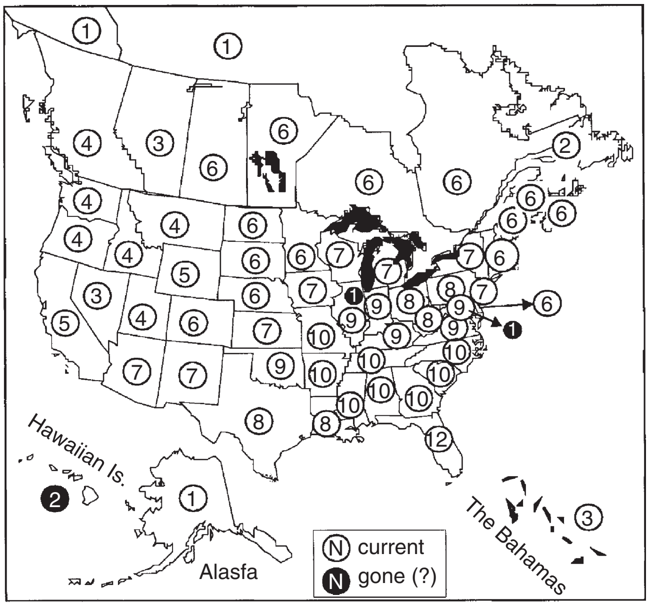
Larvae

Though larvae of only a few species have actually been observed, those of all fireflies are expected/presumed to be luminescent, even larvae of day-active species such as *E. corrusca*, in which the adults do not have lanterns, glow brightly from two points under the tail. The function of larval luminescence has been the source of human speculation for centuries, but now there is seemingly general agreement, and some experimental, comparative, and theoretical evidence as well, to indicate that it is a warning of unpleasant taste, with sometimes emetic or lethal consequences to prospective predators. Likewise, so far as is known, larvae of all fireflies are predaceous, and seek and subdue soft-bodied prey. The larvae of some, such as the European *L. noctiluca* and American *Pyractomena* species, are snail/slug specialists, such gastropods perhaps being the ancestral prey of the family. *Lampyris noctiluca* larvae are reported to follow 2-day-old slime-trails forward, tracking the snails, presumably and remarkably demonstrating that they are able to detect polarization in dry, if not stale, trails. *Photinus* species possibly are annelid specialists, and in captivity have been reared on minced earthworms. *Photuris* larvae are omnivores and scavengers, and reported to eat snails, worms, insect larvae, dead insects, and ripe berries (Fig. 27).

Larvae of a firefly from Sri Lanka (formerly Ceylon) was imported into New Britain (Solomon Islands) and Hawaii to prey upon and thus control the African snail, a pest of sugar cane. Also in the 1950s, two *Luciola* species from Japan were released in Hawaii for the control of fluke parasites of livestock. Because these flatworms (Platyhelmintheses,



Fireflies (Coleoptera: Lampyridae), Figure 22 **Attributes of "fireflies": (a) Outline of a click beetle (family Elateridae) with black dots showing positions of pronotal lanterns, which are visible above and below, and a black bar showing approximate position of the abdominal lantern which shines ventrally and is exposed only when in flight. (b) Ventral view of the abdomen of a male *Pteroptyx* firefly showing the bent elytral tips that form one jaw of a clamp that holds the female during copulation. (c) *Pyractomena borealis* larva, showing the distinctive canoe-like outline of larvae of this genus (from a study by M.A. Archangelsky and M. Branham). (d) *Photuris* sp. larva, showing the distinctively broad (sub-oval) outline of larvae of this genus (after A. Peterson). (e) *Pyropyga nigricans* larva, with a narrowly elongate form more suitable to a burrowing life (from a study by M.A. Archangelsky and M. Branham). (f) Side view of a *Lucidota atra* larva (after A. Peterson). (g) A rough sketch of a *Neanura barberi* collembolan (family Poduridae), about 0.9 mm in length; they occur in pale yellow and pink, and "milk-glass" white (diet?). (h) *Photuris* earthen chambers: top, larval molting chamber; bottom, pupation chamber (after L. Buschman). (i) Head of a *Microphotus angustus* LeConte male, the California pink-glowworm firefly, showing its huge eyes and small antennae and mouthparts. (j) Dorsal outline of female *Phausis reticulata* with dots showing positions of some lanterns; lanterns are variable and not visible unless illuminated.**



Fireflies (Coleoptera: Lampyridae), Figure 23 **Number of genera present in various states and provinces in North America, from current records and conservative interpolative, geographic assumptions. Exotic introductions, two into Hawaii from Asia in the 1950s and another to Maryland and Illinois from Europe before 1850, did not become established. West of the Rockies most species are day-active pheromone users (e.g., *Ellychnia*) or glowworm fireflies (e.g., *Phausis, Microphotus*); both types occur in the east with many lightningbug fireflies.**

Trematoda) spend part of their life cycle as internal parasites of snails, it was hoped that the larvae would eat these intermediate hosts. Apparently, none of the three exotic lampyrids survived in Hawaii. Larvae of Florida's *Pleotomodes* species live in ant nests and possibly feed on the food or young of the ants, or perhaps other nest visitors or inhabitants. Larvae of *Micronaspis floridana* Green live in salt marshes along coastal Florida, among the fiddler crabs and stranded, glowing comb-jellies (phylum Ctenophora). Generalizations on firefly life histories of American species are, with a few notable and noble exceptions, based on fragmentary and incidental observation because it is difficult and ultra-labor-intensive to rear them in captivity. In Japan, the success of hydroponically produced fireflies was critical to a national conservation program that restored vanishing stream species.

Photinus larvae of most species are subterranean and occasionally are dug up in gardens, but only rarely sighted above ground. Larvae of *Pyractomena* and *Photuris* species often are seen glowing. The former are sometimes arboreal, and on rainy nights can be found on twigs and branches of low woody plants. Larvae of marsh- and pond-inhabiting *Pyractomena* species are found on emergent vegetation, and occasionally are seen glowing underwater where they seek aquatic snails. *Photuris* larvae are the glowworms most commonly encountered by nocturnal sojourners in North America, along damp roadsides and paths, along streams and adjacent low wet meadows, and sometimes on lawns near lakes, streams, and ponds. Because adult *P. pennsylvanica* often are seen over marshes and soggy ground, near rivulets and around farm ponds, we can venture that when northeastern

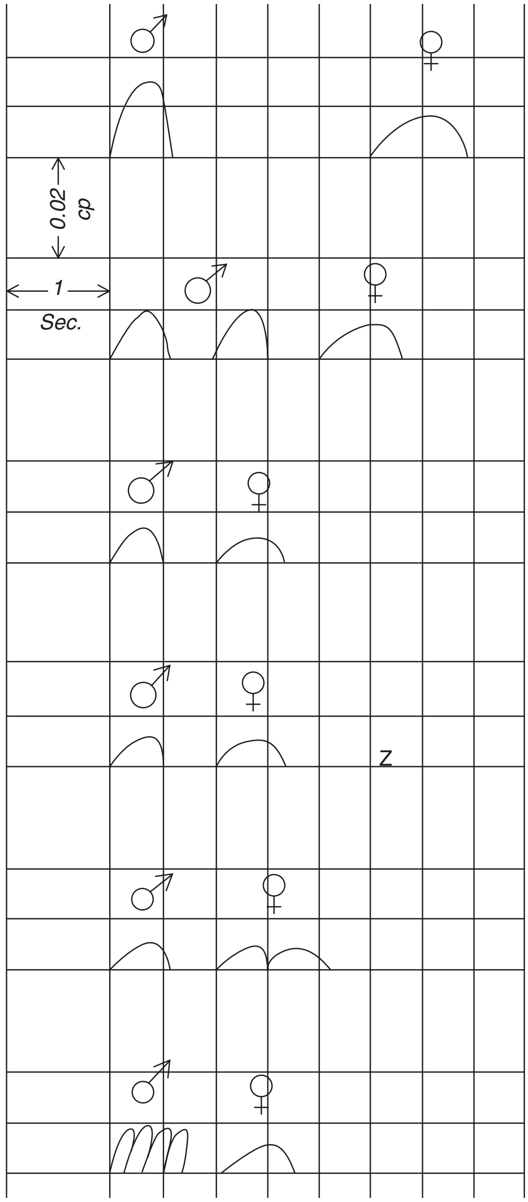
Fireflies (Coleoptera: Lampyridae), Table 3 Flightless females occur in several North American lampyrid species

Genus	Species	
	Flightless	Winged
Aspisoma (LB)	0	2
Bicellonycha (LB)	0	1
Brachylampis	0	2?
Ellychnia (DD)	0	12
Lucidota (DD)	1	2
Micronaspis (LB)	0	1
Microphotus (GW)	7	0
Paraphausis (GW?)	1?	0
Phausis (GW)	10	0
Phosphaenus (DD)	1	0
Photinus (LB)	12	34
Photuris (LB)	0	64
Pleotomodes (GW)	3	0
Pleotomus (GW)	3	0
Pollaclasis (DD)	0	1
Pyractomena (LB)	0	21
Pyropyga (DD)	1?	4
Tenaspis (DD)	0	1
Total	40	145

Sometimes the condition is obvious because the wings are shortened or absent: *Photinus scintillans* (Say), *Photinus collustrans* and others in its species group except *P. umbratus* LeConte, all those of the glowworm firefly genera, and *Lucidota luteicollis* LeConte, a daytime-dark firefly. Females of other species actually may be flightless but this has not been recognized because their wings are little reduced. Flightlessness often is associated with stabile habitats.
(DD = daytime-dark fireflies; GW = glowworm fireflies; LB = lightningbug fireflies)

North America was well-forested, this firefly often may have been associated with beaver dams and their wetlands.

Larvae of the three mentioned lightningbug genera, *Photinus*, *Photuris*, and *Pyractomena*, are the most commonly seen, but those of other genera can be found with some directed effort. Seek *Pyropyga nigricans* (Say) larvae along the shores of northern lakes and streams, on sandy strands and amongst and under stones; *Lucidota atra* (Fabricius) and *E. corrusca* juveniles occur in rotting logs, the latter perhaps especially in pine, and near the horizon with the forest soil (these genera are illustrated in the accompanying plates). When firefly larvae are sought at night in and under rotting logs, sometimes constellations of points of light will flash and quickly disappear. Not to be confused with lampyrids, these are the flashes of luminescent, springless springtails (Order Collembola), presently identified as *Neanura barberi* James, family Poduridae. It is possible that their flashes may mean something to the lampyrid larvae living there.

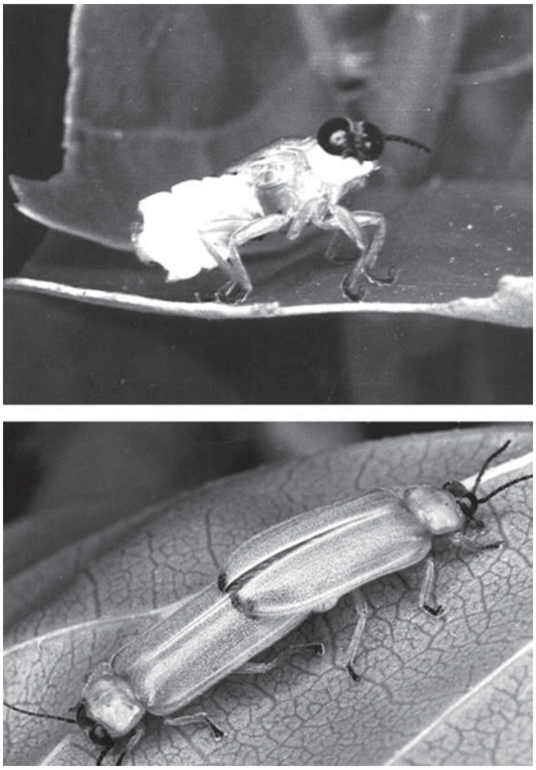


Fireflies (Coleoptera: Lampyridae), Figure 24 **The first known chart of firefly flashes, from the pioneering studies of Frank A. McDermott early in the twentieth century. While afield pursuing an interest in bioluminescence chemistry, he discovered that the flash patterns of male fireflies could be used to identify the species. For naturalist/taxonomists this compares with the discovery of the chemical nature of bioluminescence. Though some names "Mr. Mac" used in his chart were incorrect, this was because the taxonomy of North American fireflies was poorly known in 1914. McDermott later became a highly productive firefly taxonomist.**

Pupae

When ready to pupate, larvae seek or make sheltered places. During pupation the larva, a hunting/eating specialist, becomes the adult form and breeding specialist. Thus, pupation is not a resting stage, as sometimes stated, but a period of considerable phenotype reconstruction, a

Fireflies (Coleoptera: Lampyridae), Figure 25
A pair of mating fireflies (possibly *Robopus*) in Dominican amber, overwhelmed in resin about 19 million years ago. (Photo by T. Nguyen, courtesy of M. Branham, American Museum of Natural History.)



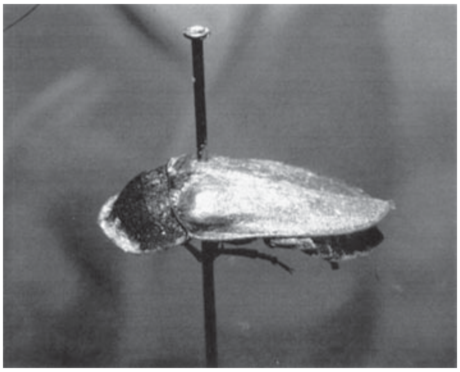
Fireflies (Coleoptera: Lampyridae), Figure 26 ***(top)*** **Male of a bent-wing firefly, *Pteroptyx valida* E. Olivier, perched at the edge of "his" leaf in a Thai swarm tree, aiming his lantern. His flashes attract females and may warn neighbors to stay off his leaf. (bottom) Copulating *P. valida*. The male (*left*) has pushed his elytral tips under those of the female and locked her genital region in the jaws of his clamp; his bent elytral tips form its upper jaw.**

process that results in a body form that is adapted to a completely different lifestyle and range of activities. Pupation lasts from 1 to 3 weeks, depending upon ambient temperature and species. *Photuris* and *Photinus* larvae, like most others that are known, pupate in chambers they make under or at the surface of soil. In contrast, *Pyractomena* larvae hang up in vegetation like chrysalids of some lepidopterans. Perhaps this is an adaptation for living in sites where rising water would flood chambers in the soil, as in river forests. Neotropical relatives of *Pyractomena* that live on emergent vegetation, and in marsh inhabiting *Pyractomena* in North America (*P. lucifera* Melsheimer, *P. linearis* LeConte, *P. dispersa* Green, *P. angulata* (Say)), this would avoid a difficult and perhaps dangerous walk to shore to dig an earthen chamber. In north-central Florida, larvae of *Pyractomena borealis* (Randall) pupate on the southern exposure of tree trunks in February. Development is accelerated by additional heat from the sun (insolation), and after sunset from sun-warmed tree-water, which allows them to become adults and reproduce before other species become active.

Adults

As far as is known from observation and can be predicted from present knowledge, adult fireflies

Fireflies (Coleoptera: Lampyridae), Figure 27 **Larva of *Pyractomena borealis* (Randall) attacking a snail. At this point, the larva is extended under the foot, with head reaching up to bite and inject poison. The snail has detected the larva and has turned its head slightly down and to its left, toward the larva's bite (note the turned position of the lower pair of tentacles). At the upper right, another larva is on the shell and barely visible around the contour of the shell.**



Fireflies (Coleoptera: Lampyridae), Figure 28 **Adult male of *Lamprigera tenebrosus* (Walker), a species introduced into Hawaii to control a snail pest of sugar cane. Apparently rare in collections, this museum specimen was probably collected from a spider web because it was wrapped in silk, which was removed for this photo (loaned by N. Ohba, Yokosuka City Museum, Japan).**

are concerned only with reproduction, including mate-finding and selection, copulation, oviposition, and dispersal, though egg dispersal is problematic in species that have short-winged, hence

Fireflies (Coleoptera: Lampyridae), Figure 29 **The larva of *Photinus pyralis* found glowing on a damp, dirt road in northern Virginia, and placed in a bed of moss to be photographed. Its curled-under tail shows a few fingers of the pygopodium, an eversible "rubber-glove"-like structure that is used for grooming and locomotion.**

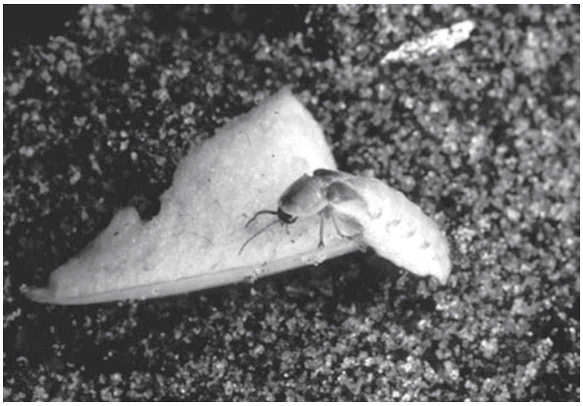
flightless, females. Only one species, *Pyropyga nigricans*, is known to have both short- and fully-winged females, but that this is a complex of species cannot be ruled out. In the case of *Photuris* fireflies, and neotropical relatives such as *Bicellonycha* spp., a singular dramatic exception to the "adult-fasting" rule is found: females of some Photurinae including most North American *Photuris* species augment the nutritional supplies they store as larvae by hunting, and are specialized predators of other fireflies. Some incorporate the protective poisons of their prey's blood into their own bodies and eggs for defense (Fig. 32).

Sexual Communication

Daytime-Dark Fireflies

In day-active species (for example, *Lucidota atra*, *Pyropyga nigricans*, *Photinus indictus* (LeConte)), males detect their females' pheromone, the chemical signal that drifts in a plume downwind, and fly upwind (anemotaxis), hence in the direction

Fireflies (Coleoptera: Lampyridae), Figure 30 **Pupal skin of *Pyractomena borealis* (Randall) hangs from its larval skin which is fastened to the tree bark. The recently eclosed adult is not yet tanned and is pearly white.**



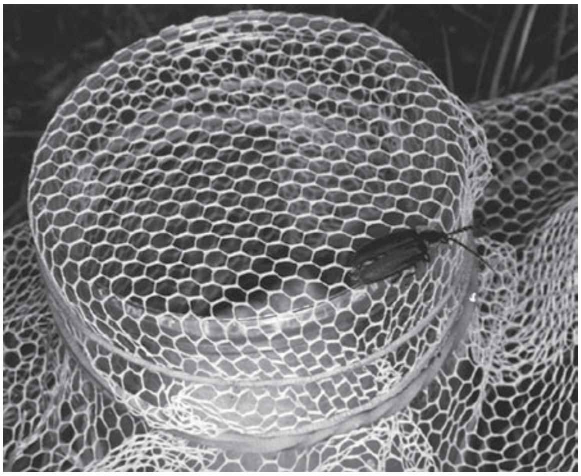
Fireflies (Coleoptera: Lampyridae), Figure 31 **Brachypterous (short-winged) female of *Photinus brimleyi* Green, showing the abbreviated elytra and wings found in a few North American *Photinus* species, including those of *P. collustrans*.**

Fireflies (Coleoptera: Lampyridae), Figure 32 **A female of *Photuris* unnamed-species "B" eating the male of *Pyractomena angulata*, near Lake Alice on the campus of the University of Florida.**

of the signal source. Some species probably use visual information when they near the pheromone emitter, such as a dark silhouette against a pale leaf background. The broad, black form of the rarest of all North American daytime fireflies, *Tenaspis angularis* LeConte is especially conspicuous whether on a leaf or on the wing. This cue was found to be important in the mate search of *P. pyralis* males during twilight. The chemical nature and structure of firefly pheromones has not been reported.

Glowworm Fireflies

In nocturnal species in which females emit light but mate-seeking males do not (for example, *Pleotomodes*, *Microphotus*, and most *Phausis* species), males fly about their habitat. The glowworm



Fireflies (Coleoptera: Lampyridae), Figure 33
A male *Lucidota atra* attracted out of a forest by the species' sexual pheromone and guided by the wind, walks on the netting over the emitting (calling) female.

Fireflies (Coleoptera: Lampyridae), Figure 34 Branched antennae and multifaceted and huge eyes of male *Pleotomus pallens* LeConte.

signal system is thus similar, even analogous to the daytime firefly pheromone system, except that in glowworms males orient to the actual signal, whereas daytime fireflies initially orient to the vehicle, the airflow. It is interesting and useful to consider the differences, the advantages, disadvantages, and consequences of signals that travel in straight lines but have a limited range (bioluminescence), and chemical signals that travel a long distance but only downwind, and in plumes composed of concentration filaments that stream on zephyrs, in spirals and twists up and down and around obstructions and stagnant air pockets (Fig. 33). *Pleotomus* species are glowworm fireflies, but perhaps use both of these signal channels: males may detect a female pheromone a long distance downwind with extensive arrays of sensors on their branched antennae, and at close range orient precisely to the female glow with their huge, abundantly-faceted and multi-directional eyes (Fig. 34). The glowworm fireflies *Microphotus*, *Phausis*, and *Pleotomodes* also may use pheromones, but their antennae are filamentous and do not give a hint of this. *Phausis reticulata* (Say) is an unusual glowworm in that searching males do emit light; their eerie green sparks are commonly seen gliding slowly and silently over the forest floor in the Appalachian Mountains. Sometimes the larva-like *Phausis* females are found glowing in the absence of male activity, but unlit females turn on their four or more tiny points of glow when a glowing male or penlight passes overhead. Perhaps the ability to douse their light permits females to hide from light-orienting predators until a legitimate receiver (a potential mate) is near. The "turn-on" response of these females, initiated upon detection of a male glow, is a key behavioral response that is highly developed in the lightningbug fireflies.

Lightningbug Fireflies

Males of many genera throughout the world emit their bioluminescence in patterns that require more complex lanterns and neural control than do the rather dim glows and slow ON-OFFs of glowworm fireflies. In North America, these species are in the genera *Photinus*, *Photuris*, *Pyractomena*, *Bicellonycha*, and *Micronaspis*.

In some species the male signal is a single flash, and in others it is a group of flashes. Such patterns are repeated at fairly regular "advertising" intervals by flying males. The male flash pattern is only one part of the signal code of such species. In the basic signaling system found in North American lightningbugs, when females see the flash pattern that is characteristic of their males, they flash an answer. During the ensuing dialogue, if the females choose to keep answering, the males fly, walk and climb toward, mount and touch/taste their respondents, and connect with them.

Signaling/courting behavior found in some flashing species in other parts of the world, in particular in certain paleotropic species of the subfamily Luciolinae, is quite different. In New Guinea forests, males and females of *Luciola obsoleta* (E. Olivier) gather in loose swarms beginning at dusk, and emit flickers and flashes for several hours. Finally, glowing females here and there take off and fly through or away from the swarm, and one or more flashing males take up pursuit. Aerial encounters with collisions between males ensue, and the female is repeatedly bumped in flight until she finally alights on a leaf with a male. After courtship dancing and chasing, they couple and remain connected tail-to-tail until the following evening. A great variety of mating behaviors and signal patterns has been described for Japanese and other Asian fireflies.

Flash Pattern Specificity

Because males of a lightningbug species emit a flash pattern that is characteristic of their species, as they fly about the habitat and activity space that is characteristic of their species, in their species' season and time of night, male flashing behavior can be used to identify species. For many in the genus *Photuris*, flash patterns provide the only reliable characters for identification. With practice, it is possible to identify local species from flashing behavior alone. But note that during the final approach of a male to a female, especially after touchdown, flash patterns sometimes become variable. Until the specifics of such pattern variations are known for a species, the flash patterns of perched or walking males cannot be used reliably for identification.

Female Flash Response

When a lightningbug female sees the flash pattern of a male of her species, she answers with a flash-response. Female signals are typically single flashes, and females of some species turn their lantern to face the approaching male. In many species, the answer is emitted within a second of the male signal, but in others there is a conspicuous delay. Females of *P. pyralis* delay 2–4 sec, and those of *Photinus ignitus* (Fig. 35) Fall delay 5–10 sec, depending upon temperature. Males can be attracted to a penlight by placing its tip against the ground and flashing a short flash after each pattern they emit; as a male approaches and flashes, answer each with the penlight tip pushed further into the soil to reduce its apparent brightness to the male.

Fireflies (Coleoptera: Lampyridae), Figure 35
A wolf spider in grass with firefly prey, a female *Photuris* that probably was blinking as she oviposited. A simple experiment is to bait pitfall traps with blinking, light-emitting diodes.

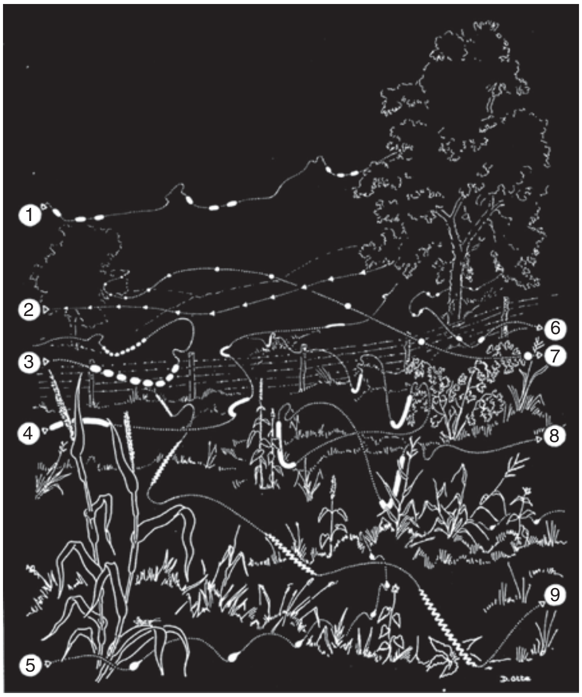
Females can be found by walking about their habitat flashing a penlight simulating the timing of the male flash pattern.

Supernumerary Flash Patterns, Pattern Change-Over and Defaulting

In his pioneering Photuris studies in the 1920s, H. S. Barber observed that males of *P. tremulans* Barber and *P. lucicrescens* Barber each emit two distinctive flash patterns. Since then, many other *Photuris* species have been found to use more than one pattern during mate search. For example, in some populations males of *P. pennsylvanica* emit a short flash for a few minutes after they begin evening activity, and then gradually change over until all are emitting the dot-long-dash pattern described by H. S. Barber. However, during early evening when a male receives an answer to his short flash he switches (defaults) to the dot-dash pattern during his approach to his respondent. Other species with this defaulting behavior include *P. quadrifulgens* Barber, *P. tremulans* Barber, and a New England relative in the same species group. When an observer sees a *Photuris* emitting a green flicker flash pattern, like the one described for *P. tremulans*, to identify the species the observer must become an experimenter and simulate a female answer with a penlight and thus elicit the default (species ID) flash pattern. In early spring in northwestern peninsular Florida, males of a variety of *Photuris lineaticollis* (Motschulsky) search with a continuous glow, presumably mimicking the signal of *Pyractomena angustata* LeConte males; when they are shown a female-like glow response, glowing *P. lineaticollis* males switch to their own short-flash pattern.

Miscellaneous Flashes

Firefly adults, especially those of *Photuris*, emit a variety of flashes (Fig. 36), glows, and twinkles under circumstances that are not connected with mate search, courtship, and rapprochement: from spider webs, puddles, tangles of grass and spanish moss, when encumbered with grasping pseudoscorpions, when held by spiders, when walking on the ground, when perched on wind-blown tips of vegetation, and when landing and taking off. The last mentioned seem to be used for illumination, but others are open for conjecture and study, for what now-hidden revelations they may avail us. In one other situation the meaning of the flashes is clear. *Photuris* females emit flashes as lures when hunting in what has been called "aggressive mimicry."



Fireflies (Coleoptera: Lampyridae), Figure 36 Diagrams of flashes of several species of *Photinus*. Not all of these species occur together. To identify a male from his signal, the observer must know where he is, and also, sometimes, the time of year. *P. pyralis* is number 8 and *P. collustrans* is number 4. Number 6 is a species in the *P. consanguineus* group, but identification is not possible because there is no precise clue to the timing of the two pulses in the pattern.

Aggressive Mimicry

Females of many *Photuris* species take perches in the activity spaces of other species and flash responses to passing males like those the males would receive from their own females. Duped males approach the *Photuris* females, are pounced on and eaten. *Photuris* females also attack flying male fireflies, using the emissions of the males to guide their attacks. Such predations by these females will have been a major influence on the signaling behavior of prey species: in aiming aerial attacks at flash patterns of flying males, predators have certainly influenced the patterns, particularly pattern duration, and flying behavior; with their signal mimicry they are inside their prey's coding system, forcing species to evolve deceptive codes or counter-measures. It was once thought that signaling evolved primarily in the context of avoiding mating mistakes, but a mating mistake is not lethal, and a predator attack can be. Since neither *Photuris* nor predator specialists like them occur in Asia, fireflies provide a natural intercontinental experiment to explore the impact such focused predation may have on signaling behavior.

What goes around comes around, and it would seem that just as prey species have been forced into changing, the communication of predator species also has been influenced by this turn of coevolutionary events, as suggested in the following section.

Flash Pattern Mimicry

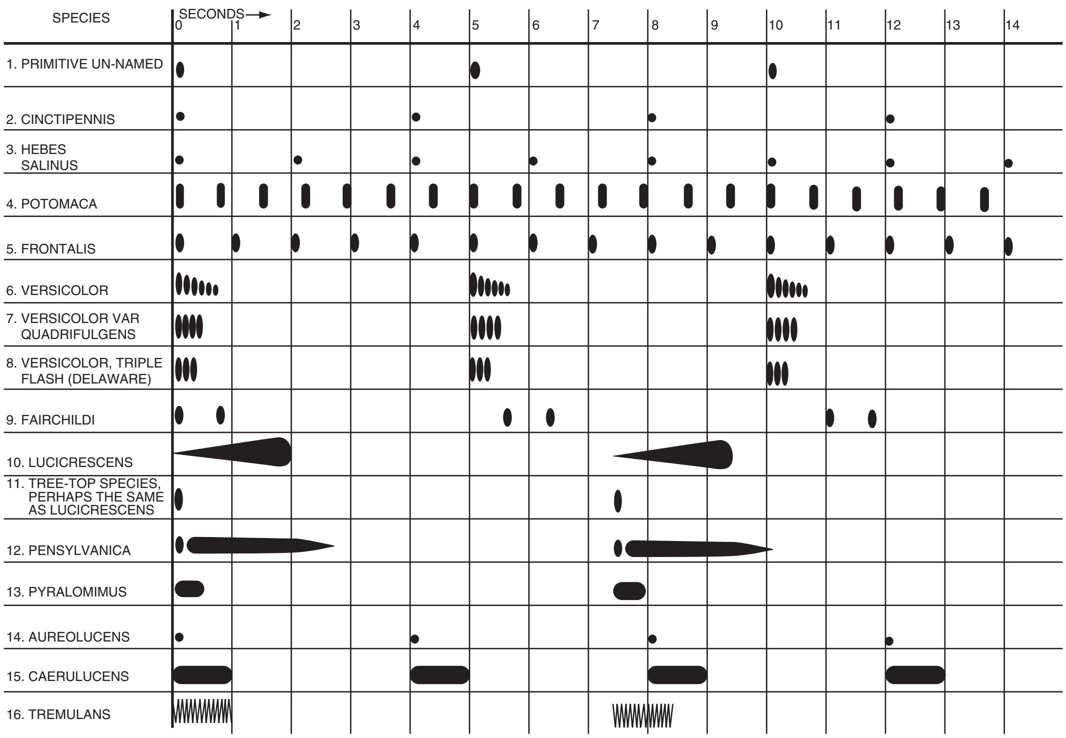
With this general discussion of female-response flashes, and specifically the aggressive mimicry of *Photuris* females, we now return to the supernumerary flash patterns of *Photuris* males. They clearly seem to be related to the aggressive mimicry of *Photuris* females. In several instances, the supernumerary patterns of *Photuris* males are nearly indistinguishable from the flash patterns of other firefly species. When *P. tremulans* and *P. quadrifulgens* males seek mates with the flicker pattern described for *P. tremulans*, they are using a flash pattern that is identical to that of *Pyractomena angulata*, except for its green color; *P. angulata* flickers are amber. The working explanation is this: when males default to their own pattern, they identify themselves to their own females, prospective mates that are hunting and narrowly tuned (gated) to a prey flash pattern. This system presents an interesting and educational, though difficult, problem in sexual selection. In seeming irony, when Barber chose the specific epithet for *Photuris tremulans*, he used not this species' own signal, but one it "borrowed," one being used by other *Photuris*, too, and perhaps one that they all acquired from the same ancestor (Figs. 37 and 38).

Conclusion

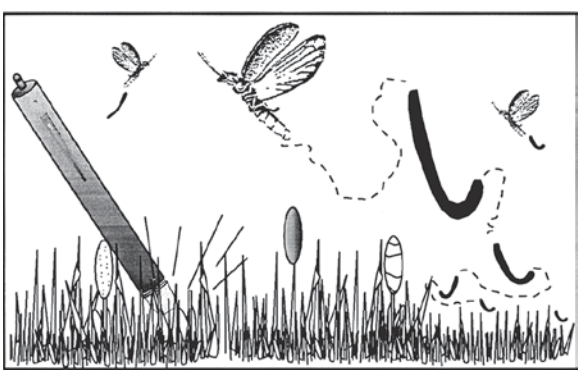
When considering environmental features that have influenced the signaling of fireflies, among the obvious are meteorological elements such as ambient temperature, ambient illumination, and wind; physical certainties, such as the fact that light travels in straight lines, will not pass through opaque objects, and rapidly decreases in visibility with (the square of) distance; and the biological certainty that most organisms and especially predators have photoreceptors. But the signals of other fireflies with which mating mistakes might be made, the signal mimicries of predaceous fireflies, and aerial attack certainly have been of major importance, too. The impact of these elements varies among sites, habitats, seasons, and population densities. When studying the natural history of animals, the naturalist is looking at a chronicle, and when the subjects are fireflies much is written in lights.

Fireflies and Intrusive Light

Suitable firefly habitats today are often bathed, if not drenched or washed out, in artificial light.



Fireflies (Coleoptera: Lampyridae), Figure 37 **Flash pattern chart accompanying Barber's *Photuris* study.**



Fireflies (Coleoptera: Lampyridae), Figure 38 **Method of attracting males to a penlight. Put the tip of the penlight against soft ground. As the male approaches, push the tip further into the ground, as a bright penlight will deter an approaching male.**

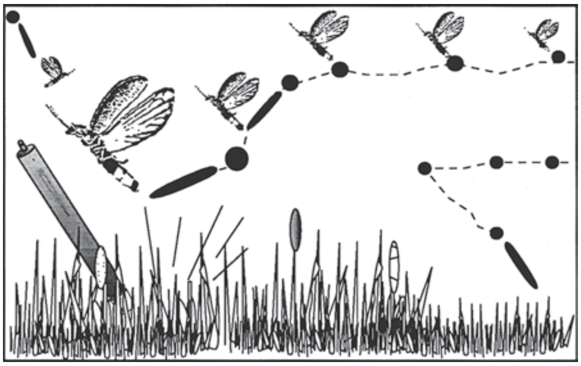
Because of the unique relationship that fireflies have with light, intrusive light may be expected to have especially serious consequences for them. There are several sources, but three main contexts of impact that foreign light can have: noise, illumination, and misinformation. When these combine with other environmental insults, the consequences can be deadly for the fireflies.

Noise

Intrusive illumination as from skyglow, especially that of clouds reflecting light from urbanization below, and direct illumination from streetlights, business or industrial lights, and residential lights make bioluminescent emissions less readily detected by intended (legitimate) receivers. Bioluminescence will be less efficient in mating signals, less attractive for predator-trappers, and less visible as aposematic warnings to attackers. The light intensity that fireflies normally emit is tuned to operate in darker surroundings, and though some may facultatively increase their luminous output to compensate, this decreases stored energy supplies (ATP, adenosine triphosphate), one molecule per emitted photon, that formerly was put more directly into gamete success. When females of the twilight firefly *Photinus collustrans* are delayed in mating and oviposition, it costs them about seven eggs per day of delay. A special consideration is the yellow light of recent, energy-efficient, sodium-vapor highway illumination; it may be of special concern because some fireflies have tuned their lights and eyes to operate in this range of frequencies. Also, if some of the subtle complexities of male signals are important in female mate choice (say, as they reveal good genes, health, and vigor), they could be obscured by intrusive light.

Illumination

Examples of intrusive light as a revealer of naturally hidden actors and activities is obvious to nocturnal naturalists who prowl woods and fields by moonlight and headlamp. Obviously, it will reveal targets to roving predators such as wolf spiders, but consider the attacks of *Photuris* females on other fireflies. These specialists attack flying, flashing males by aiming at their flash patterns and leaking glows from their lanterns. In particular, when attracting foreign males via mimicry, females sometimes leave their perches to attack. Increases in ambient light may shift the balance in these interactions, because it will reveal both perched respondents and approaching hawkers to the males, and also negate one of the few defenses that flying males have, that of hiding in the dark between flash emissions.



Fireflies (Coleoptera: Lampyridae), Figure 39
When early-flying, single-flashing males of *P. pennsylvanica* are answered, they default to their dot-dash (species ID) pattern. Knowing this, the naturalist can recognize at a distance what is happening (right). At the upper left, a distant and potentially interloping male, upon detecting the flash-response interaction, approaches.

Such illumination can have more subtle and obscure effects and results on firefly behavior. The onset of flight in twilight fireflies such as *P. pyralis* and *P. scintillans* (Say) is triggered by diminishing light intensity. Males of such species become active several minutes, even an hour earlier, in shady places and on cloudy days. Also, individual males of late-twilight species become active within shrubs and under herbaceous canopies, but land or return inward when their flight brings them out of the shade into the open. Adults of such species may be confused by intrusive light and initiate, continue, or terminate their evening mate search inappropriately. *Photinus collustrans* reveals another response to ambient light level that may be influenced by intrusions of stray light. Early in their 20-minute window of evening flight, which begins about 20 min after sunset, males fly <1 m above the ground, but as the light-level falls, they gradually fly higher and flight altitudes average above 1 m. This response can be seen when early-flying males pass through the shade of trees and adjust their altitude accordingly. Other manifestations and the significance and consequences of these responses invite fireflyer attention.

Misinformation

Natural light provides information to organisms as timing cues and triggers, and for orientation. Thus, artifical light can interfere with firefly life in several ways. Because light travels in straight lines, rays from celestial sources are used by various animals in their navigation over the earth. By maintaining a fixed angle on the parallel light rays arriving from remote ("infinite") sources, night flyers are able to steer and maintain straight flight over long distances. As an adaptation explanation (behavioral ecology), males could maximize their opportunity to intercept downwind-streaming female pheromone plumes by flying across the wind on star-oriented straight lines. Without a remote orientation reference, nocturnal flyers would tend to stray off course, perhaps fly in circles. When night flyers take a fixed bearing on a local light source with its diverging rays they will spiral into the light. Males of glowworm fireflies (e.g., *Pleotomus*, *Pleotomodes*) track pheromone plumes, and males sometimes are taken in light-traps in considerable numbers.

The orientation of the larvae of *P. borealis* on tree trunks is important for gaining heat from the sun (see above). If larvae use the visible light of the sun rather than, say, using the warmed bark of the trees to determine southern exposure, nearby streetlights may disorient them. A related species, *P. limbicollis* Green, occurs in many of the same forests, but pupates with a north-facing orientation and ecloses a few weeks later. Another potential source of photic misinformation for *P. borealis* was suggested when larvae were brought into the lab in early December and, by chance, were exposed to continuous room light connected with other research. The larvae climbed and pupated a few days after they were brought into the lab and soon eclosed as adults, 2–3 months too early! If continuous light triggered their metamorphosis, in other words caused them to break diapause, field populations exposed to continuous artificial illumination from skyglow or local lights may likewise eclose early or make other developmental miscalculations.

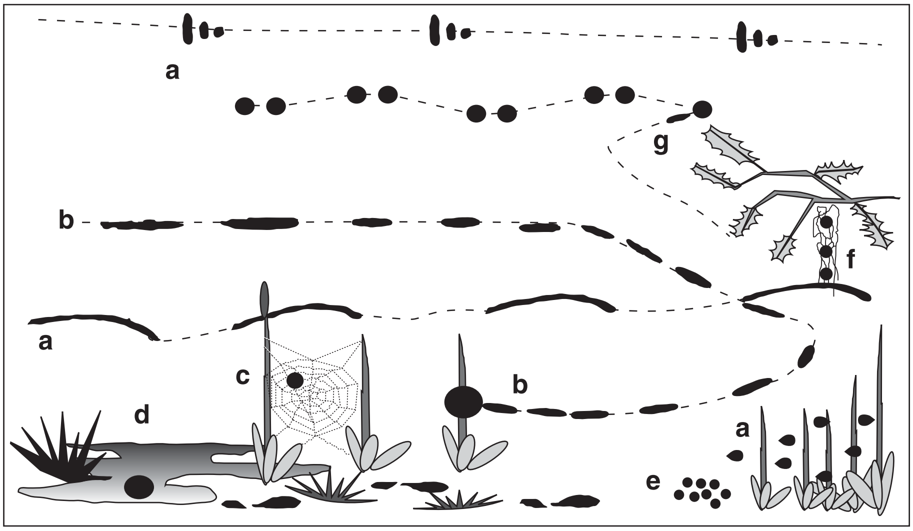
Artificial light sources may be attractive to colonizing and site-changing fireflies if it is mistaken as the glow of the collective emissions of fireflies in suitable habitats, "suitable" being defined as good for mate seeking by male and suitable for oviposition by female emigrants. This could be most significant and deadly for swarming *Pteroptyx* fireflies in Asia.

Intrusive Light as a Synergistic Aggravator

Two of the major ecological changes that have had an impact on firefly populations are: (i) the loss of suitable natural areas, including woodlands, meadows, and bottom-land near streams and rivers, and (ii) the lowering of water tables, resulting in fewer creeks and their floodplain forests, ponds and pond edges, marshes and wet meadows. To this we might add the trapping-out of beavers, if they indeed were once responsible for making firefly habitats in every place possible. This is really to say that the normal patchwork of populations of firefly species that existed in former times now has many holes in it. As more and more populations are lost, the holes get larger, and remaining local populations become less well connected by migrants. When local populations disappear, as they will naturally from time to time, neighbor populations that formerly would have reseeded empty sites are much further away. Thus, there is an ever larger separation of fewer and fewer suitable sites, with inhospitable spaces between remaining sites punctuated and bathed by noisy, revealing, and misinforming bright lights. This must present a formidable formula for extinction. A mathematical ecologist modeled the extinction of local populations and concluded that total extinction of species was retarded or prevented by the chaotic (in the formal, mathematical sense) nature of local extinction and the repopulation of suitable sites. I expect that formal chaos models for fireflies will now predict less optimistic outcomes.

Essences of Lumens

The nature of firefly light is misunderstood by many: laymen, journalists, and entomologists alike. Bioluminescence is the term given to chemiluminescence when it is produced by organisms, and is sometimes poetically referred to as "living light." It is but one of several forms of light emission collectively known as luminescence, which occurs when atoms of a

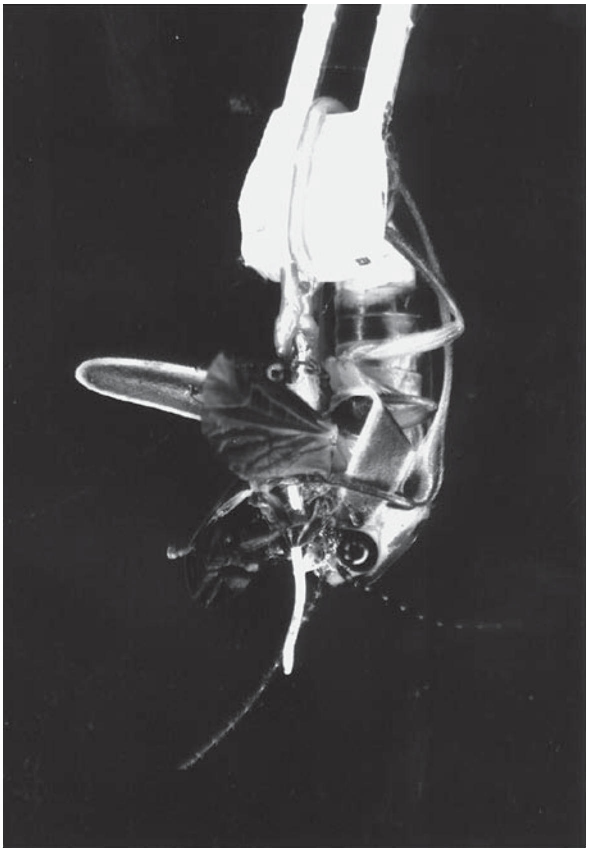


Fireflies (Coleoptera: Lampyridae), Figure 40 **Sampler of contexts in which adults flash. *Photuris* fireflies are responsible for most of the "odd" ones: (a) Male flash patterns, 4 species shown; (b) landing *Photuris* female; (c) ensnared in a spider web; (d) stuck in a water puddle; (e) walking, ovipositing; (f) in a tangle of Spanish moss; (g) female attacking an aerial target.**

Fireflies (Coleoptera: Lampyridae), Figure 41
A *Photuris* unnamed-species "C" female eating a *Photinus* male she has attracted by mimicking the sexual signals of his own females. Sometimes capturing females hang beneath leaves while eating, and hold their victims away from the perch, and sometimes they remain on their hunting platforms. Typically, they are so much larger than their prey that "they can eat anywhere they want."

substance emit photons (packets of light energy) as their electrons return to their stable state after having been lifted to a higher and unstable energy level by input energy. Chemiluminescence does not depend upon, nor come from, light or other electro-magnetic energy currently shining on, or that has previously shone upon, the emitter, as do luminescences such as fluorescence and phosphorescence, respectively. The physics of luminescence differs from that of incandescence, such as the glow of campfire coals and the yellow flame above them, in which molecules emit light because they have been heated to a high temperature and made to vibrate vigorously.

Terms for luminescences sometimes used in older texts and references have various historical and physical explanatory origins, with different terms sometimes having been applied to natural phenomena that have the same physical basis. For example, the sparks seen when certain hard candy is crushed between the teeth, and the sparkly glow observed along the line of separation when transparent tape is snatched from its roll (in the dark) are emitted by ionized atoms of nitrogen, though these two phenomena were once known by different names. The most common error in older biological and modern popular-press living-light literature is the use of the term phosphorescence when the term bioluminescence is correct.



Fireflies (Coleoptera: Lampyridae), Figure 42 **Flashing LED targets suspended from fishpoles by thin electrical wire elicit attacks from *Photuris* females. This one attacked the light (white rectangle at her tail), found an impaled male below, and is chewing on him. Note his elytra and flight wings, and one eye peering from behind the crumpled flight wing above.**

Fireflies (Coleoptera: Lampyridae), Figure 43 **Two *Photuris* females simultaneously attacked a flashing experimental target. The one on the right has severed the head and prothorax of the other. The impaled male hangs below. In this illustration, the macro-photo was superimposed on a time-lapse exposure that showed how the target was trolled and flashed along bushes at the edge of this sandy road; the image of the experimenter was not recorded because he was moving. Attacks were viewed in silhouette against the city skyglow in the background.**

Applications of Firefly Chemistry

The light-producing chemicals taken from the tails of fireflies, or mass-produced by organisms that have received firefly genes, have been used in a variety of ways. Here is a sampler, but new ones appear in cascade:

1. NASA has considered using firefly bioluminescence to search for life in space. Because light production requires luciferase, luciferin, ATP, and magnesium (a cofactor) in a water solution, if one ingredient is withheld no light is produced. If extraterrestrial life occurs, it may use a high-energy phosphate bond as in ATP. If, for example, a soil sample is scraped from the surface of Mars by a robot, mixed with firefly glow ingredients without ATP, and then light is detected, life may be present and the site should be given closer scrutiny.
2. Similarly, bacterial contamination of food can be quickly ascertained without the delay of culturing by swabbing a sample from meat in a packing plant, applying the firefly-test solution, and looking for a glow.

3. The photon-detection technique can find trace amounts of environmental pollution, such as ions of heavy metals. A luciferase gene is fused to the gene in a bacterium that provides specific resistance to the metal. A culture of the bacterium is immersed in a solution of luciferin and the environmental sample to be tested. If the ion is present, the resistance gene is activated, also activating the luciferase gene, and photons are emitted.
4. Animals with mutant genes for their circadian rhythm can be identified by observing their daily activity cycles. Detection of such mutants in plants is not accomplished as easily. To find plant mutants, the firefly luciferase gene is placed with a gene sequence that is turned on by the circadian rhythm gene. With luciferin available, mutant plants emit light out of the normal circadian phase for their species.
5. To determine whether genes can be picked up and coded into the genomes of mammalian tissue, because of the considerable potential of the technique in medicine, dog leg arteries were exposed then flushed (bathed) with genes for luciferase. After allowing time for the luciferase gene to be incorporated into the genome, luciferin was added to the solution. In brief, the leg glowed.
6. Tuberculosis is a serious, dreaded disease, caused by several strains of the bacterium *Mycobacterium tuberculosis*. Antibiotic medications are strain-specific, but diagnosis via culturing a sample from a patient can take 3 months, sometimes a lethal delay for the patient. Firefly solution: insert the luciferase gene into the genome of a bacterial sample from the patient (using a virus). After a short delay, add luciferin and get a glow; then apply various antibiotics to samples of the now-glowing infectious culture; the antibiotic that turns off the glow is the one to give to the patient. Time elapsed: 2–3 days.

Common Questions Asked About Fireflies

Here are answers to the most commonly asked questions about fireflies:

1. Why is firefly light said to be cold? Restatement: When the energy of ATP is converted to radiated electromagnetic energy, why is virtually all of it in the visible light range of wavelengths, and none outside this narrow window of the energy spectrum, including what would be felt as sensible heat? Natural selection has tuned the system of reacting molecules (perhaps in the context of conserving energy) to the wavelengths that are detected by the visual systems of significant receivers. Indirect support for such tuning comes from the finding that adults of early twilight species have made ecological adjustment and have yellow light and yellow-tuned eyes to better contrast with the abundant green in their environment.
2. Why are there no fireflies in California? Restatement: Why are there no lightningbug fireflies in California? The fact that California has other members of the family Lampyridae, glowworm and daytime-dark fireflies, with similar life histories and diets, is evidence that the region is not completely inhospitable to a lampyrid scheme of life. Since eggs, larvae, and adults of eastern U.S. lightningbug species certainly must arrive there from time to time (for example, in cyclonic storms, in root- and potting-soil with nursery stock, and with uninformed firefly enthusiasts), we must suspect that their absence is not because of perfect geographic isolation and such physical barriers as deserts and mountains. It is an interesting ecological puzzle that deserves attention. Perhaps the climate of California is generally too dry for the species that live in the east that are transported there, or the fireflies that presently occur there occupy and completely fill very narrow, highly specialized niches. There is one century-old record from southern California of an otherwise unknown *Photinus* firefly.
3. Why are fireflies disappearing? Restatement: Why do certain flashing fireflies that were formerly seen in eastern United States now appear to be much less abundant or absent altogether? There are standard answers that may be suggested, but there is no documentation or evidence in specific cases. Air, soil, water, and light pollution from a variety of

sources may affect them and their prey: earthworms, snails, slugs, etc. There is much less natural area available due to the ever-increasing amount of land development by humans. Lowered water tables, with the resulting loss of ponds and edges, marshes and general soil moisture, may be a factor in the loss of habitat. Increased sources of run-off such as highways, parking lots and rooftops, with increased volumes of water flowing over the ground causes surface contaminants, such as vehicle hydrocarbons, fertilizers, poisons and salt, to be carried and deposited in remaining natural areas. But we will continue to see certain fireflies for a long time to come, because a few species, such as *Photinus pyralis* and *Photuris tremulans*, are able to live, and apparently thrive, in sites that humans have altered, and these species have extensive geographic distributions. However, many North American species can be expected to become extinct during the next century.

4. How can I attract fireflies to my lawn and garden? Restatement: How can I increase the likelihood that mated firefly females will find and accept vegetation spaces around my home and lay eggs there, and that their progeny will survive, reach adulthood, and remain there for mate-seeking and oviposition? There are standard answers that may be suggested, but there are no specific studies to cite. To provide cues to attract and retain adults, prevent the intrusion of artificial light and enhance the growth of herbaceous vegetation to prevent the soil from becoming dry and hard-packed. Clues for success are provided by the abundance of fireflies in agricultural fields that have been abandoned. In such weedy-field spaces, which are termed old fields by classical ecologists, there has been pioneering by various herbaceous plants which form rich, damp, and sheltering habitats for a few years, with worms, snails, and other soft-bodied prey for firefly larvae. However, woody pioneers (sumac, aspen, locust) eventually invade, and in a few years they will exclude the herbs and grasses, and so on, through successional stages that are characteristic of the region. Encourage old fields in your spaces, and their continued existence where you see them now, by removing woody pioneers as they enter; mowing with the blade (cutter bar) set quite high, once or twice a year, should be sufficient. Occasional sprinkling of former gardens and lawns, and planting lush native herbs and grasses will encourage the development of suburban, experimental old fields. Then, plant some native annelid worms and terrestrial snails.

Fireflies and Human Culture

Emitters of living light, and in particular fireflies, are more than organisms, insects or beetles; they are a special part of human culture. The Japanese have for centuries used them as metaphors for emotional and personal experiences belonging to the human condition, and to punctuate subtle points of a reverent and shared natural philosophy. A firefly becomes a short poem, the keyword "Fireflies" may guide you to a book of short poems, and *A Net of Fireflies* is a collection of poems to be read before sleep, after the mosquito net is drawn up over the bed. It is an unworthy collection of summer haikus that does not have several firefly fireflies; the trick is to discover a meditative connection with the author. "Flash" may not translate directly, any more than a frog's "kerplunk" hits the mark in translation, according to some knowledgeable poetry critics. In pastoral North America of yesterday, FireflyFun was one operative word, but this now lives mostly in memory, with a country grandma and grandpa. Truly, fireflies go beyond science, and, in one of their incarnations, belong to the humanities.

► Fireflies: Control of Flashing
► Beetles

References

Eisner T, Goetz MA, Hill DE, Smedley SR (1997) Firefly "femmes fatales" acquire defensive steroids (lucibufagins) from their firefly prey. Proc Natl Acad Sci 94:9723–9728

Herring P (ed) (1978) Bioluminescence in action. Academic Press, New York, NY
Lloyd JE (1966) 1966 Studies on the flash communication system in *Photinus* fireflies. University of Michigan Museum of Zoology Miscellaneous Publication No. 130. 96 pp
Lloyd JE (1971) Bioluminescence and communication in insects. Ann Rev Entomol 16:97–122
Lloyd JE (1983) Bioluminescence and communication in insects. Ann Rev Entomol 28:131–160
Lloyd JE (1997) Firefly mating ecology, selection, and evolution. In: Choe JC, Crespi BJ (eds) The evolution of mating systems in insects and arachnids. Cambridge University Press, New York, NY, pp 184–192
Lloyd JE (2002) Lampyridae (with overview and key to North American genera). In: Arnett RH Jr, Thomas MC, Skelley PE, Frank JH (eds) American beetles; Polyphaga: Scarabaeoidea through Curculionoidea. CRC Press, New York, NY, pp 187–196
Ohba N (1983) Studies on the communication system of Japanese fireflies. Science Report of the Yokosuka City Museum No. 30.

Fireflies: Control of Flashing

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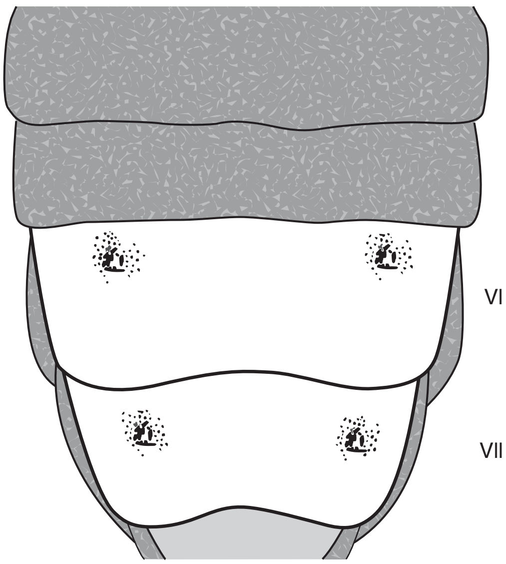
The remarkable ability of biological systems to control light is particularly evident in the phenomenon of bioluminescence, the production of light by living organisms. Many bioluminescent organisms "borrow" their light from luminescent bacteria that are cultured and maintained in special structures. Others produce their own light and in the insects, modulation of these lantern systems runs the control gamut from steady glows to the complex flash patterns of adult fireflies (see Buck, 1948, for a classic and authoritative review of firefly lantern capabilities, and Lloyd [this publication] for a taxonomic and behavioral review of firefly biology). Over literally centuries of study, especially of the lampyrid beetles *Photuris* and *Photinus*, scientists made great progress in working out the chemistry and neurobiology of the firefly light reaction. In basic chemical terms, a substrate, firefly luciferin, complexes with an enzyme, firefly luciferase, and ATP in the presence of Mg^{2+}; once oxygen is added, the system forms a cyclic peroxide which releases light as it decomposes. All ingredients can be mixed in a test tube and the system will stay lit until it runs out of a reactant. Adult fireflies, however, can turn the light both on and off; they can practice flash control.

Years of accumulated evidence suggest strongly that flash control is essentially oxygen control. Certainly insects appear for several reasons uniquely suited to have evolved the ability to use oxygen as a control mechanism. The light, strong and versatile exoskeleton that covers or lines all surfaces abutting on or interfacing with the environment enables their respiratory system to bring air directly to all tissues. The lantern nerves have their final synapses in the tracheal system rather than on the photocytes, the cells that actually produce the light. In the test tube, only addition of oxygen to a premixed "active intermediate" (that contains other ingredients of the flash reaction) initiates the flash rapidly enough (within msec) to approximate the flash *in vivo*. But until recently we have remained ignorant of any mechanism by which gaseous molecular oxygen could be controlled or gated by a biological system. But recent studies broke the log jam with two different but not mutually exclusive models for oxygen control. More recently, however, the current authors have realized that any oxygen control theory may be lacking an important link, and we have therefore developed yet a third model. This chapter will consider all three theories; in order to do so, we must start with a review of the distinctive anatomy of an adult lampyrid lantern (in this case that of *Photuris*). Along the way we will meet an unusual cell, and two respiratory organelles, one believed to be ancient (the peroxisome) and one that was perhaps more recently evolved (the mitochondrion). We will also consider the function of a signaling molecule (NO) relatively new to science for a purpose that may be very new to science. As usual, on considering and trying to answer old questions, we will be raising new ones.

Morphology and Physiology of the *Photuris* lantern

Adults of both *Photuris* sexes have lanterns located under windows of clear cuticle on the ventral layers of the sixth and seventh abdominal segments. Those of the male virtually fill the sterna of these segments (Fig. 44), while those of the female are smaller, but in ultrastructure and physiology they appear identical.

Each lantern is a flat slab of tissue that consists of a dorsal and a ventral layer. The dorsal layer, often referred to as the "reflective layer," consists of large cells filled with granules whose content and purpose are to our knowledge as yet undetermined, although many authors speak of them as urate crystals. The ventral "photogenic" layer consists of the photocytes and their tracheal and nerve supplies. The figure of the photogenic layer presents a view in frontal section (Fig. 45) of the adult lantern; it shows the concentric (rosette) arrangement of the photocytes around the channels, or cylinders, through which run the main tracheae, their finer branches, and (importantly) the closely associated nerve supply. Also shown is a figure presenting a diagrammatic representation of part of a cylinder and its associated structures. Let us now identify some of the cellular players in the system.

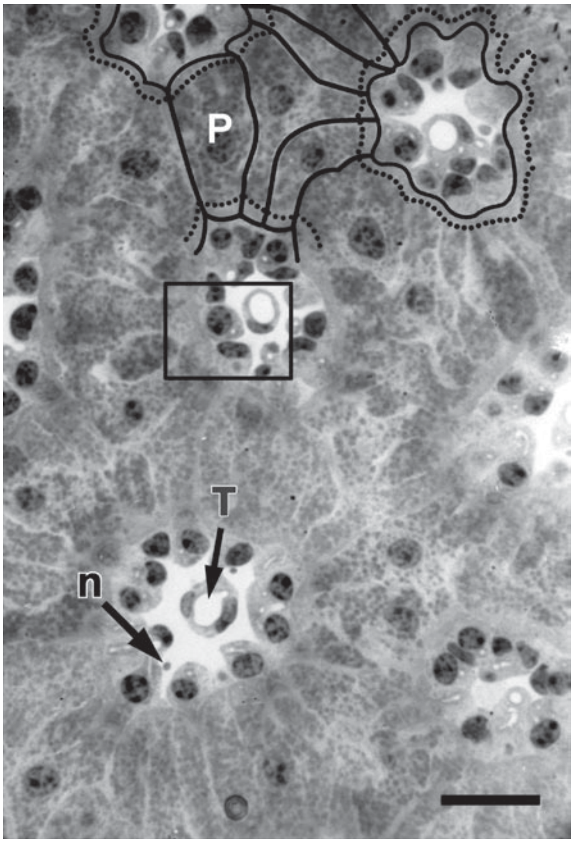


Fireflies: Control of Flashing, Figure 44 Diagrammatic ventral view of several abdominal segments of a male *Photuris*. The cream-colored lantern occupies the sternites of segments VI and VII, which have clear "windows" of cuticle. The depressions in each segment are external pits at the sites of internal attachment of respiratory muscles.

The light-emitting photocytes stretch from cylinder to cylinder so that they have access to tracheae at either end. They are unusual in that they are highly compartmentalized: the interior of each contains huge numbers of granular peroxisomes and little else other than the nucleus. Peroxisomes are cellular organelles that typically contain (among other things) catalases and peroxidases by which they can oxidize substrates by the use of peroxide intermediates. They are believed to have been important in the early development of biological mechanisms for detoxifying and eventually harnessing oxygen in respiration, which latter function was to be largely superceded by the rise of mitochondria and their attendant aerobic respiration. Where peroxisomes appear in contemporary eukaryotic cells, they may be involved in a host of functions, including lipid metabolism, generation of heat, and breakdown of amino acids (including D-amino acids, of which firefly luciferin is an analog). In the firefly photocyte, they contain the luciferin and luciferase and constitute the compartment of the cell that actually lights up.

As an aerobic cell, the photocyte also contains mitochondria, but these are restricted to so-called "differentiated zones" that line the cylinders, forming a "boundary" layer wherever the photocyte abuts on any part of the tracheal system. The photocytes also contain a type of granule, the so-called "differentiated zone granule," which remains to be characterized.

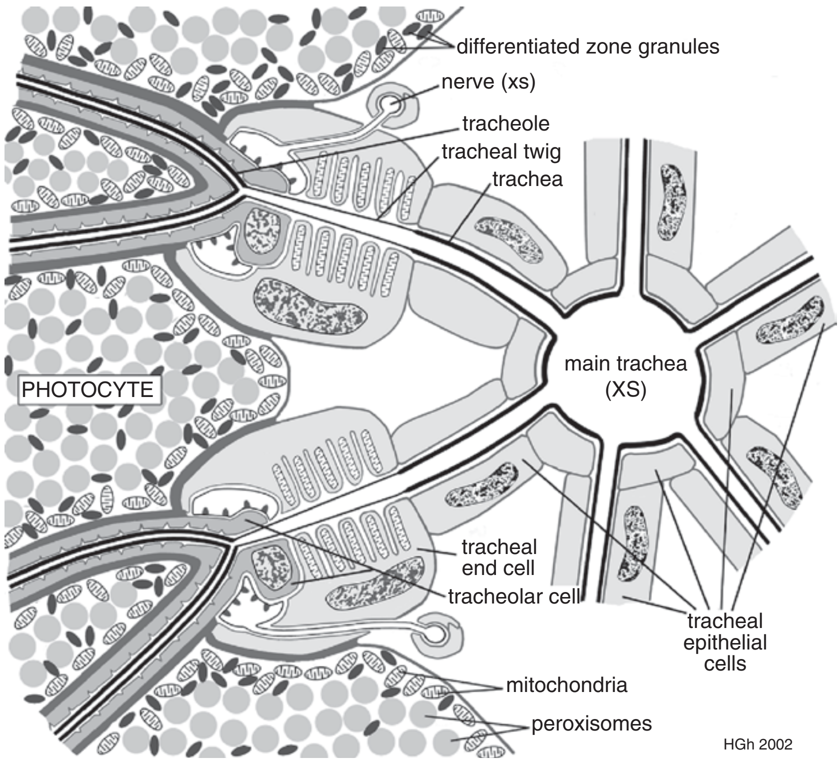
The standard insect tracheal system receives air through paired openings, the spiracles, that periodically open and close under neuromuscular control. From these extend inwards the



Fireflies: Control of Flashing, Figure 45 **Frontal (parallel to the lantern surface) section of the photogenic layer, showing several cylinders and their associated rosettes of peroxisome-laden photocytes. The borders of several photocytes (P) are outlined (solid lines); their collective borders also form the borders of the cylinders (the peripheral photocyte differentiated zones are set off by the dotted lines). The darker granules virtually filling the photocyte interiors are the peroxisomes. The cylinders contain the main tracheae (central signet-ring figures-T), nerves (n – small dot at end of arrow) and the tracheal end organs, which consist of tracheal end cells, tracheolar cells, and nerve endings. The rectangle shows an approximate location of the diagrammatic representation of a part of a cylinder and surrounding structures in the next figure. Bar = 10 μm.**

tracheae (here defined as the non-living cuticular intimae that actually carry the air – some authors use the term to include the attendant tracheal epithelial cells as well); these are sometimes elaborated into air sacs that aid in ventilation. The tracheae ramify throughout the interior, bringing the air directly to the tissues. As the system branches into finer and finer tubes, the number of tracheal cells associated with each tube is correspondingly reduced until at the narrow end of each trachea, each fine cuticular branch is wrapped in a single epidermal cell. Eventually each trachea gives rise to one or more tracheoles, the permeable "capillaries" of the system; these penetrate between the tissue cells to assure adequate ventilation. This transition point has associated with it a single tracheal end cell which is somewhat larger than the other tracheal cells and which hands the system off to a single tracheolar cell, which makes and maintains the tracheoles, All through the system, the cuticular tubes are usually wrapped in one or more spiral cuticular threads, the taenidia, which are presumed to provide reinforcement against distention or collapse.

The tracheal system in the adult lantern has these basic elements, but it is modified in four important ways. First, it is exceptionally richly and extensively branched. Second, the tracheal twig, the section of each trachea just proximal to the beginning of the tracheoles, lacks reinforcing taenidia; in whole mounts showing the cuticular elements alone, the twig appears flimsy and collapsable. However, in fixed and sectioned material, the tracheal twig invariably appears open and surrounded with what looks like a calyx of cuticular fibrils that extend back into crypts of the tracheal end cell (*vide infra*). Third, the tracheoles are also highly modified, but in the other direction, being stiff and resistant to bending or collapse. They (and the branches of their attendant tracheolar cells) penetrate between the photocytes and extend deep into the lantern, where their blind ends abut on those of their opposite numbers from the adjacent cylinders. Their course between the photocytes is matched by extensions of the differentiated zones of the photocytes, suggesting strongly that there is a functional importance for the juxtaposition of these two elements. Fourth, the tracheal



Fireflies: Control of Flashing, Figure 46 Diagrammatic representation of part of a cylinder and surrounding structures. The tracheae, surrounded by their epithelial cells, branch from the main trachea and approach the walls of the cylinder. As they reach the end cells, they shed their taenidia and become the thinner-walled and more flimsy tracheal twigs, which in turn branch into clusters of stout and reinforced tracheoles that penetrate between the photocytes. Each tracheal twig is surrounded by the distinctive tracheal end cell, whose luminal border contains mitochondria-lined folds separated by deep crypts. The tracheal end cell also envelops the body of the tracheolar cell, which makes and maintains the tracheoles. The nerve ending wraps around and appears to synapse (shaded semicircles) on the tracheolar cell. The photocyte is conspicuously compartmentalized: the surfaces abutting on the tracheal system contain the cell's mitochondria whereas the interior of the cell is filled with peroxisomes. The as-yet uncharacterized "differentiated zone granules" are more generally distributed.

end cell is large and specialized (v.i.); it wraps around and enfolds both the body of the tracheolar cell and the nerve ending, which latter synapses on the tracheolar cell. The complex of tracheal end cell, nerve ending and tracheolar cell body is referred to as the tracheal end organ.

The tracheal end cell is particularly specialized in that its luminal surfaces are thrown into deep crypts lined with mitochondria. This morphology is often referred to as "ion pump" morphology because it is commonly associated with such tissues as insect Malpighian tubules and rectal pads, tissues that are known to move ions, thereby moving fluid as well. This morphology is more faintly echoed in the proximal lumina of the tracheolar cells.

In sum, in the adult firefly an extensive and highly modified tracheal system penetrates deep into the lantern. Part (the tracheal twig) seems flimsy and collapsible, while other parts (the tracheoles) are stiffened and reinforced. The tracheal end cells and to a lesser extent the tracheolar cells have the deep mitochondria-lined infoldings that are usually associated with insect ion pumps. Let us now put the lantern nerves into the picture.

The lantern innervation *per se* is not remarkable; the patterning of the flashes apparently is controlled by a "pacemaker" that resides in the brain, and bursts of patterned impulses travel down the nerve cord to produce patterned flashes in the lantern. The lantern nerves travel alongside the tracheae, but they do not reach the photocytes (not in our North American species; although in some Asiatic fireflies, there may be limited contact between nerve endings and photocytes). The axons end not on the photocyte, as one would expect, but within the tracheal end organ, in calyces wrapped around the tracheolar cells. The transmitter that has been identified so far is octopamine, common in invertebrates, and application of octopamine can cause the lantern to glow.

The compartmentalized morphology of the photocyte and the location of nerve endings in the highly modified tracheal system suggested to many investigators that flash control must involve control of oxygen access to the photocyte. In other words, a lantern without these special features may glow, but it will not flash.

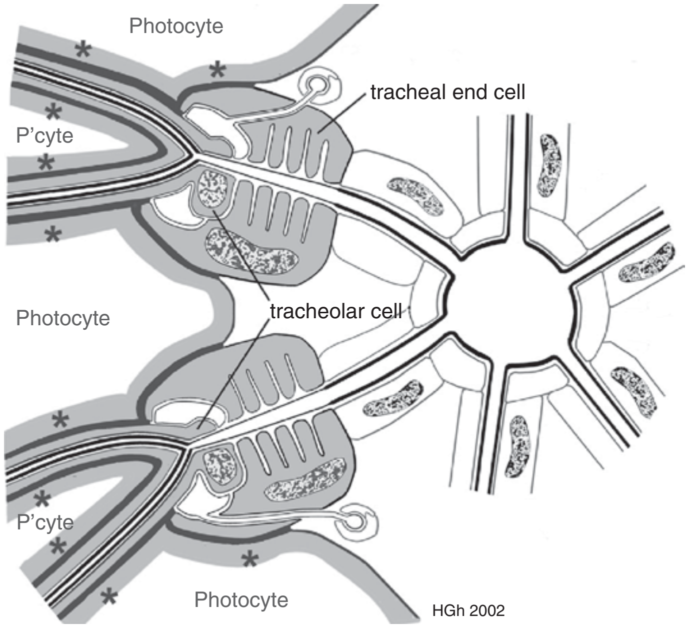
We find such a non-flashing lantern in larval *Photuris*. Like the adult lantern, it is bilayered. The dorsal layer is not that different from that in the adult, but the photogenic layer is. Its photocytes contain peroxisomes, mitochondria, and differentiated zone granules, but these are mixed in together, i.e., the cells are not compartmentalized. The nerves synapse directly on the photocytes rather than in the tracheal system, and the latter shows no particular specialization. Significantly, the larval lantern produces a less articulated signal, a simple glow that slowly rises and falls.

Firefly Flash Control

The increasing acceptance of oxygen as the key to flash control brought with it various suggestions as to mechanisms for this. All revolved around the possibility that a pulse of oxygen arriving via the tracheal system might reach the peroxisomes and set off the light reaction, either by directly providing an oxygen charge or possibly by causing the peroxisomes to make peroxide which in turn would complete the reaction. On the basis of the lantern morphology, Ghiradella pointed out that for oxygen to be the controlling factor, it itself must be controlled and kept from the peroxisome until flash time. The deployment of the mitochondria at the interface with the tracheal system suggested that they might serve as "gatekeepers," absorbing (and presumably using up) any incoming oxygen until the synaptic transmitter sets off a cascade of events that somehow opens the gate.

A mechanism for such a change was provided by Trimmer et al. who realized that the gaseous transmitter nitric oxide (NO) might be the "missing link." NO has several pertinent properties. It can be produced quickly by the enzyme nitric oxide synthetase (NOS) in response to calcium transients raised by the action of the transmitter at the cell surface, and it shuts down mitochondrial function by complexing with and inactivating the mitochondrial enzyme cytochrome c oxidase, without which a mitochondrion cannot bind and use oxygen. If, as it leaves the tracheole, the oxygen is not captured and used up by mitochondrial respiration within 1–2 μm of entering the photocyte, it should be free to diffuse further into the photocyte and reach the peroxisomes. In short, a gaseous transmitter would regulate transmission of another gas to control the flash. This action of NO is completely reversible; the gas degrades and diffuses away quickly, at which point mitochondrial respiration could immediately resume using up the oxygen supply. Trimmer et al. state that the time courses of all reactions are fast enough to account for the behavior of the intact lantern.

In several behavioral tests, Trimmer et al. confirmed that the lantern behaved as predicted with respect to NO manipulations (turned on in presence of NO gas and inhibited in presence of NO scavengers). They further showed via histochemical staining that NOS is roughly localized in the region of (Fig. 47) the tracheal end cells, the tracheolar cells, and the differentiated zones of the photocytes – the technique is not accurate enough



Fireflies: Control of Flashing, Figure 47 As in the preceding figure, part of a cylinder and its surround. Shaded regions show the approximate localization of the nitric oxide synthetase in the tracheal end organ and the differentiated zones (**) of the photocytes.

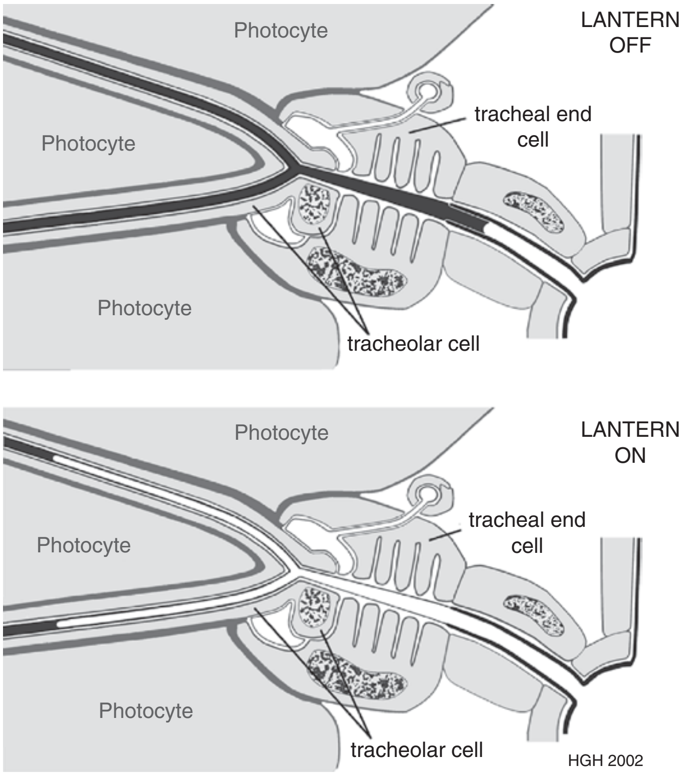
for precise subcellular localization. Trimmer et al. report that, given the abundant histochemical localization of the NOS, NO should be produced in "robust amounts."

Several pieces were now in place for these authors to model a mechanism. While the lantern is off, the mitochondria absorb and presumably utilize any entering oxygen to make ATP by oxidative phosphorylation. The crypts and mitochondria of the end cells and tracheolar cells present a large surface area that may provide an additional "outer gate," similarly absorbing and using any incoming oxygen. When the nerve fires, the transmitter activates the NOS to produce NO. The NO diffuses quickly into the mitochondrial regions of the end cells, tracheolar cells and photocytes. Here it complexes with and renders inactive the cytochrome c oxidase of the mitochondria, turning them "transparent" to the oxygen being delivered by the tracheal system. Oxygen can now diffuse through to the peroxisomes and initiate the flash.

The NO model also provided for flash termination, another hitherto troubling question. NO is labile and easily degraded. The elevated levels of oxygen that result from NO inhibition of cytochrome oxidase would help the process by negative feedback, both chemically and by competition with NO for the cytochrome c oxidase binding sites. Furthermore, studies with mammalian mitochondria suggest that light itself reverses the inhibitory action of the NO on the cytochrome c oxidase, so that the flash could function as a negative feedback system and actually contribute to its own termination. Studies on isolated firefly mitochondria suggest that the inhibitory effect of NO on respiration can be reversed by shining a bright light into the assay.

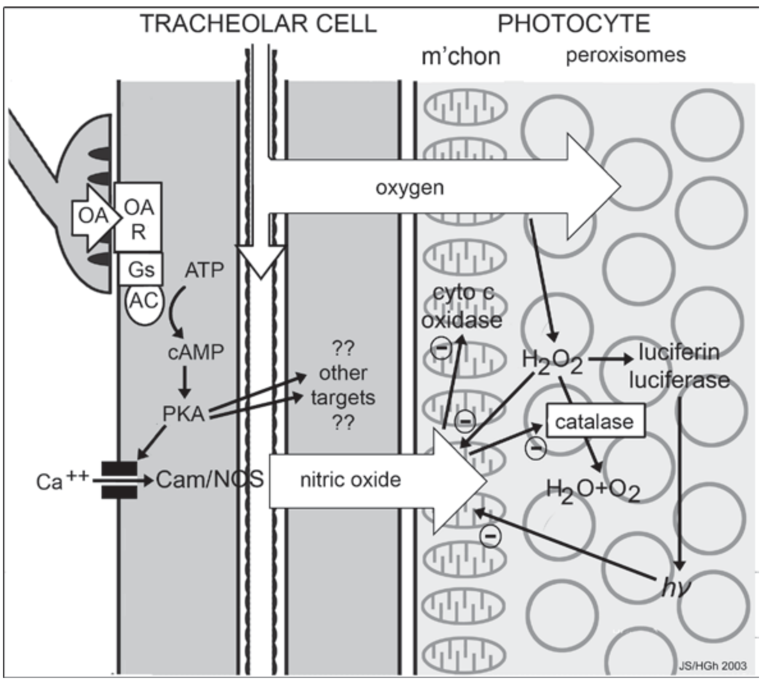
Robust as the model is, it doesn't take into account the putative ion pump morphology of the tracheal end and tracheolar cells and the collapsible nature of the tracheal twig. On the basis of this morphology, a different group of investigators (Timmins et al.) proposed an oxygen control model based on the higher (by a factor of 10^4) diffusion coefficient of oxygen in air than in water. These workers remind us that in any typical resting insect tissue the fine tracheoles are typically filled with fluid drawn from the tissue by capillary action. Anaerobic glycolysis causes the breakdown of glucose to more numerous end products, thereby raising the tissue osmotic pressure, which in turn draws the fluid out of the tracheoles. These then fill with air. In effect, anaerobic activity reduces the path length the oxygen must travel in liquid, greatly speeding up its access to the needy tissues. Timmins et al. extended this observation to the lantern by defining the kinetics of oxygen diffusion in the tracheoles under different conditions. For example, a switch from normal air to pure O_2 caused the lantern to light up continuously after a delay, and this delay was shorter if the firefly was already in flashing mode. Likewise changing from anoxic conditions (a stream of either pure N_2 or pure He) to an air stream caused a "pseudoflash" with different latencies for N_2 and He, which allowed the diffusion lengths in air and water to be calculated. The authors concluded that the O_2 diffusion data was consistent (Fig. 48) with an osmotic control mechanism, namely that tracheal end and tracheolar cells could be responding to the nerve action potentials by pumping ions and could thereby move the fluid out of the tracheoles to clear them for fast oxygen entry. By their calculations, the system should be able to perform this osmotic shift fast enough to account for the rise time of the flash, although the molecular details have not been given.

This proposal raises several questions about how such a model could work, of which speed is only the most prominent problem. Since any

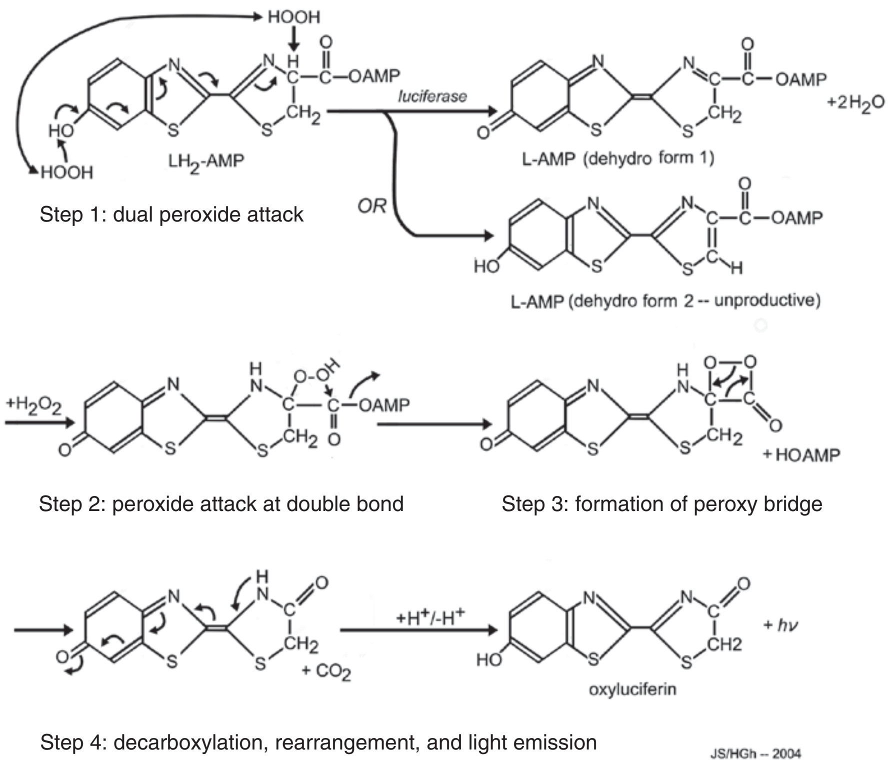


Fireflies: Control of Flashing, Figure 48 "Fluid switch" model for osmotic control of oxygen access to the photocyte. Top – inactive, dark lantern: The tracheae and tracheoles are filled by capillary action with tissue fluid, thereby creating a fluid barrier to the access of oxygen to the photocytes. Bottom – activated lantern: As a result of the nerve impulse, parts of the respiratory tubes are cleared of fluid, thereby permitting rapid diffusion of oxygen to the photocytes to initiate the production of light.

osmotic shift should generally be a relatively slow process (e.g., as in the original hypothesis of metabolic control), this mechanism would appear to be more suited to readying the lantern for flashing than to initiating and quenching each individual flash. Some features, in addition to the anatomical ones, actually fit well into this mechanism. Mosquito tracheolar cells, for instance have water channels called "aquaporins" which allow water to move through the membrane. The lantern is particularly rich in octopamine-sensitive adenyl cyclase and has high cAMP levels, which in mammalian kidney regulate water channel permeability as part of the AntiDiuretic Hormone (ADH) control. But cAMP production and cAMP kinase regulation are slow processes. What signal from the synapse would turn on the pumps (which are not known to be regulated in this



Fireflies: Control of Flashing, Figure 49 **The model mechanism for the control of the lantern flash. The nerve synapses onto the tracheolar cell, releasing octopamine (OA). Octopamine receptors (OAR) both depolarize tracheolar cells to fire spikes and also activate adenylate cyclase (AC), which makes cAMP from ATP. The activated cAMP-dependent kinase (PKA) can phosphorylate voltage dependent calcium channels to enhance Ca^{2+} to enter the cytoplasm (as well as other substrates that may enhance the excitability of this cell). The Ca^{2+} binds to calmodulin (Cam), activating nitric oxide synthetase (NOS) to release nitric oxide (NO), which can readily diffuse across cell membranes to carry the message into the photocytes. (Photocytes may also have calcium channels and NOS for their own NO synthesis as well.) NO binds to and inhibits cytochrome c oxidase, preventing its binding and use of oxygen; oxygen is then free to diffuse beyond the mitochondria to the peroxisomes, where it is converted into hydrogen peroxide. Hydrogen peroxide is normally quickly degraded by catalase, but NO also binds and inhibits catalase, further contributing to the rise in peroxide levels. We hypothesize that it is the fast rise in hydrogen peroxide, rather than a slow rise in oxygen, that activates the luciferin-luciferase to emit light. As time goes by, NO is degraded by light and by action of the catalase in the presence of peroxide, and rising oxygen. These changes terminate the action of the NO, the transient rise in peroxide, and the flash (from Ghiradella and Schmidt, 2004).**



Fireflies: Control of Flashing, Figure 50 **Proposed chemistry of the light reaction, starting with the luciferin-AMP intermediate that forms in the absence of oxygen. Hydrogen peroxide attacks both the 6´ OH and the C4 carbon, removing two hydrogens. No free radicals are left at each site because the double bonds rearrange (arrows) to produce a neutral conjugated dehydro form of L-AMP (form 1). An alternative dehydro form (classical dehydro form 2) does not result in light emission. After peroxide attack on the double bond (step 2), the peroxy-bridge structure forms by attack on the carbonyl, driving off AMP (step 3). This structure then disintegrates, releasing CO_2 and the ketone form of oxyluciferin, still in the rearranged form (C = O not conjugated with other double bonds). This spontaneously rearranges to give the original configuration (with the Ketone now included in the conjugated double bond system) and emits light (from Ghiradella and Schmidt, 2004).**

fashion elsewhere)? How would the pumps and channels be arranged for trans-tubular transport? In vertebrates such transport is accomplished by Na^+ channels on the luminal surface and Na^+ pumps on the external surface. In insect Malpighian tubules, transport is accomplished in the luminal surface using H^+ pumps to establish a gradient and H^+/Na^+ cotransport to utilize the resulting H^+ gradient (in addition to the Na/K pumps on the external surface) to complete the transport across the epithelium. This can account for the clustering of mitochondria at both luminal and external surfaces. It is doubtful, however, that a set of pumps limited essentially to the region of the tracheal twig can account for removal of tissue fluid from the entire length of the standard tracheoles (>100 mm of tubules) effectively enough to open an airway to the photocyte border within milliseconds.

The simplest way to combine the two models is to hypothesize that the osmotic control is the mechanism for readying the lantern for flashing and the NO production is the mechanism for actual flash control. Any such model also needs to explain the collapsible nature of the tracheal twig and the perversely reinforced nature of the tracheoles. We should like to look at that now. If the pumps in the tracheal end cell are in fact helping to move fluid out of the outer border of the cell, they would be reducing its turgor. If we assume that all tracheal elements upstream of the tracheoles themselves are impermeable (as suggested by osmium tetroxide penetration studies), the tracheal twig might very well be functioning as a mechanical valve (a suggestion raised almost a century ago by Dahlgren, 1917), perhaps involved in keeping the lantern dark while the animal is quiescent. If the calyx material seen around it in the sectioned material is in fact linking it with the crypts in the luminal border of the tracheal end cell, any shrinkage in the latter should open the twig. This is presumably what we see in the sectioned material, whose preparation usually causes some unavoidable tissue shrinkage and whose twigs are always wide open.

This ability to remain open or shut is exactly what we might predict of a system that has to change state at certain times of day, and the lantern certainly does this; during the first few minutes of active duty in the evening, it produces erratic and uncoordinated scintillation, almost as though the animal must wake and prime the system before it can start working.

We now return to the basic question we asked at the beginning: What really controls the flash? Any explanation needs to take into account the specialized morphology and the biochemical concomitants, including the NO. We here elaborate on a previous model. In the following discussion, we are assuming that all tracheoles deliver their oxygen efficiently to their tissues, i.e., that there is minimal "leaked" oxygen floating free in the hemolymph. We make the following observations:

- A cut lantern glows briefly at the cut surfaces and then quickly extinguishes. Oxygen must be diffusing in through the cut surfaces, but it does not raise a light response, suggesting that control must in fact be very local in the lantern tissue.
- Case and Strause report action potentials on the lantern surface, even though the nerves end within the tracheal end organs and not at the photocytes; the only other potential conductors are the branches of the tracheolar cells, which are certainly morphologically set up to spread the excitation deep within the lantern.
- The proximity of the photocyte differentiated zones to the air delivery system is exactly what we would expect if lantern mitochondria control lantern oxygen. But the flash does not rise in these regions but in the mysterious peroxisome-rich cell interior. Could there be yet another link in the flash process? Given the great concentration of peroxisomes, and the siting of the other flash ingredients on these, an obvious candidate is peroxide.

With these factors in mind, we proposed a model by which it is hydrogen peroxide, rather than oxygen, that completes the light reaction. As proposed by Trimmer et al., the NO would shut down mitochondrial function, allowing oxygen to reach the peroxisomes, where the oxidases that characterize these organelles would make hydrogen peroxide. The peroxisomal catalase, which would normally break down the peroxide, is also shut down by NO, and peroxide would accumulate explosively, completing the light reaction and raising the flash.

In more detail, our scenario is as follows (Fig. 49). Starting with flash onset:

- The transmitter depolarizes the tracheolar cell, which fires the afore-mentioned action potentials along its branches. This may require a second set of octopamine receptors, coupled to ionic channels, in contrast to those coupled to cAMP production; this is known to occur elsewhere in insects. The action potentials open calcium channels, and calcium enters the tracheolar cell and activates the NOS to produce NO.
- The NO shuts down the mitochondria, opening the photocyte to the entrance of the oxygen, which is in high supply because (we posit) both tracheal twigs and tracheoles are open and gas-filled. But at the same time, the NO reaches the peroxisomes and inhibits the peroxisomal catalase, the

combination of high oxygen and low catalase activity causes peroxide levels to skyrocket and peroxide completes the light reaction.

- As the light reaction runs its course, the NO diffuses out quickly and its inhibition of mitochondrial cytochrome c is reversed both by the high oxygen levels and by the light itself. Furthermore, in the presence of peroxide, NO is degraded by catalase. Thus, a series of feedback reactions undo what was done by the original entrance of NO and oxygen, and the system "tips back" to its interflash state.

This model is of course built around peroxide action and the question now is whether peroxide can also possibly complete the flash reaction, i.e., whether what is known about flash chemistry allows such a revision. We believe that it can: the final figure presents such a revision (details outlined in the caption).

We present this model as a next step, rather than a complete answer, especially since biological systems are rarely even this simple. It is becoming apparent that the oxygen not only travels as molecular O_2 but also as various free radicals and other highly reactive forms and, further, that cells can control and even use many of these. Furthermore, other questions still remain to be answered. Are we accurate in suggesting that the function of the tracheal end cell/tracheal twig complex is to ready the lantern for the night's activity by opening and holding open the tracheal twig to allow free access of oxygen to flash control machinery downstream? Precisely which oxidases are specific to firefly peroxisomes? Does the dorsal layer in fact contain urate, (which is characteristic of insect fat body, from which the lantern is believed to be derived, and if so, what part does the urate play in the flash chemistry? Where are the controls for multiple and flickering flashes? What can the larval lantern, which is developmentally distinct from that of the adult, tell us about the functioning of both types of lantern? And finally, how has this biological control of stored light evolved from what must have been antecedents common to most, or perhaps all, insects, and undoubtedly other organisms as well? We look forward to a bright future for firefly research as the firefly community continues to study this centuries-old mystery.

References

Aprille JR, Lagace CJ, Modica-Napolitano JS, Trimmer BA (2004) Role of nitric oxide and mitochondria in control of firefly flash. Integr Comp Biol 44:213–219

Bradley TJ (1998) Malpighian tubules. In: Harrison FW, Locke M (eds) Microscopic anatomy of invertebrates, vol 11B: Insecta. Wiley-Liss, New York, NY, pp 809–829

Buck JB (1948) The anatomy and physiology of the light organ in fireflies. Ann NY Acad Sci 49:397–482

Case JF, Strause LG (1978) Neurally controlled luminescent systems. In: Herring PJ (ed) Bioluminescence in action. Academic Press, London, UK, pp 331–366

Dahlgren U (1917) The production of light by animals. J Franklin Inst 183:593–624

Ganong WF (1995) Review of medical physiology. Appleton & Lange, East Norwalk, Connecticut, 928 pp

Ghiradella H (1998) The anatomy of light production: the fine structure of the firefly lantern. In: Harrison FW, Locke M (eds) Microscopic anatomy of invertebrates, vol 11A: Insecta. Wiley-Liss, New York, NY, pp 363–381

Ghiradella H, Schmidt JT (2004) Fireflies at one hundred plus: a new look at flash control. Integr Comp Biol 44:203–212

Greenfield MD (2001) Missing link in firefly bioluminescence revealed: NO regulation of photocyte respiration. BioEssays 23:992–995

Hess WN (1922) Origin and development of the light organs of *Photuris pennsylvanica* De Geer. J Morphol 36:245–277

Hoffman R (2004) The story of O. Am Sci 92:23–26

Nathanson JA (1979) Octopamine receptors, adenosine 3´, 5´-monophosphate, and neural control of firefly flashing. Science 203:65–68

Noble-Nesbitt J (1998) Hindgut with rectum. In: Harrison FW, Locke M (eds) Microscopic anatomy of invertebrates, vol 11B: Insecta. Wiley-Liss, New York, NY, pp 759–808

Peterson MK, Buck J (1968) Light organ fine structure in certain Asiatic fireflies. Biol Bull 135:335–348

Pietrantonio PV, Jagge C, Keeley LL, Ross LS (2000) Cloning of an aquaporin-like cDNA and *in situ* hybridization in adults of the mosquito *Aedes aegypti* (Diptera: Culicidae). Insect Mol Biol 9:407–418

Smith DS (1963) The organization and innervation of the luminescent organ of the firefly, *Photuris pennsylvanica* (Coleoptera). J Cell Biol 16:323–359

Timmins GS, Robb FJ, Wilmot CM, Jackson SK, Swartz HM (2001) Firefly flashing is controlled by gating oxygen to light-emitting cells. J Exp Biol 204:2795–2801

Trimmer BA, Aprille JR, Dudzinski DM, Lagace CJ, Lewis SM, Michel T, Qazi S, Zayas RM (2001) Nitric oxide and the control of firefly flashing. Science 292:2486–2488
Wigglesworth VB (1973) The physiology of insect tracheoles. In: Berridge M, Treherne JE, Wigglesworth VB (eds) Advances in insect physiology, vol 17. Academic Press, New York, NY, pp 85–148
Zeng H, Loughton BG, Jennings KR (1996) Tissue specific transduction systems for octopamine in the locust (*Locusta migratoria*). J Insect Physiol 42:765–769

First Grub

The second phase of development in hymermetamorphic larvae of Meloidae. This generally corresponds to instars two to five. Such insects are scarabaeiform in appearance.

Fischer Von Waldheim, Gotthelf

Gotthelf Fischer von Waldheim was born in Lepzig, Germany, on October 3, 1771. He graduated from Universität Freiburg at the age of 26 with a doctoral degree. Then, in 1797, he accompanied von Humboldt to Vienna, intending to study medicine, but studied zoology instead. He then made a scientific journey through Germany and Switzerland, and moved to Paris, where he aided Cuvier. In 1804, he accepted a position as professor and director of the museum in Moscow, Russia. There, he was the leading entomologist and founded the Société Impériale des Naturalistes de Moscou. He described many of the insects collected in voyages by Russian explorers to North America. He published about 50 papers, mainly on Coleoptera and Orthoptera, but with some on Hymenoptera. He died in Moscow on October 18, 1853. His collection is mainly in Moscow, but with some materials in the hands of private collectors.

References

*Essig EO (1931) Fischer von Waldheim, Gotthelf. In: A history of entomology. Macmillan, New York, pp 611–613
Newman E (1854) The president's address. Trans Entomol Soc Lond 2(2):142–153

Fishflies

Some members of the family Corydalidae (order Megaloptera).

► Alderflies and Dobsonflies

Fitch, Asa

Asa Fitch was born on February 24, 1809, in the state of New York. At 17, he entered the Rensselaer School (now Rensselaer Polytechnic Institute) and graduated with honors in 1826. After this 1 year of college training, he entered the Vermont Academy of Medicine in 1827, receiving an M.D. degree in 1829. Next, he attended lectures at Rutgers Medical College in New York City, and then worked in the office of an established medical practitioner in the town of Albany. During the time of his medical studies and practice (1827–1838) he seems to have spent much time collecting insects and, in 1838 he abandoned medicine and returned to Salem, the town of his birth, to manage his father's business. He had married in 1832. In 1845 he published his first entomological paper, on *Cecidomyia*, in 1847 he was appointed as insect collector (Fig. 51) and identifier to the state of New York, and in 1854 his role was expanded to study "Insects injurious to vegetation." He was required to write annual reports on applied entomology, and these appeared in Transactions of the New York State Agricultural Society from 1855 through 1872. His title was not officially "State Entomologist of New York," but he was generally recognized as such. He died on April 8, 1879. His insect collection was in part sold to collectors or to the U.S. National Museum, and in part is deposited in the New York State Museum at Albany.

Reference

*Mallis A (1971) Asa Fitch. In: American entomologists. Rutgers University Press, New Brunswick, NJ, pp 37–43

Fitch, Asa, Figure 51 Asa Fitch.

Fixed-Sample Size Sampling Plan

A sampling plan in which a predetermined number of sample units is collected based on a prescribed level of desired precision, classification accuracy, or level of confidence. (contrast with sequential sampling).

► Sampling Arthropods

Flabellate

A structure that has fan-like or lobe-like processes.

Flabellum

A fan or leafed structure. The lobe at the tip of the glossa in bees.

Fitness

The relative ability of an individual to contribute its genes to the next generation.

Flacherie

A term used to describe the flaccid condition (flaccidity) seen in silkworm larvae suffering from dysentery caused by bacteria, including *Bacillus thuringiensis*.

► Viral Flacherie

Flagellomere

One of the segments of the distal portion of the antenna. A portion of the flagellum.

► Antennae of Hexapods

Flagellum

The outermost region of the antenna, beyond the (Fig. 52) scape and pedicel, and consisting of many segments or subdivisions (flagellomeres).

► Antennae of Hexapods

Flannel Moths (Lepidoptera: Megalopygidae)

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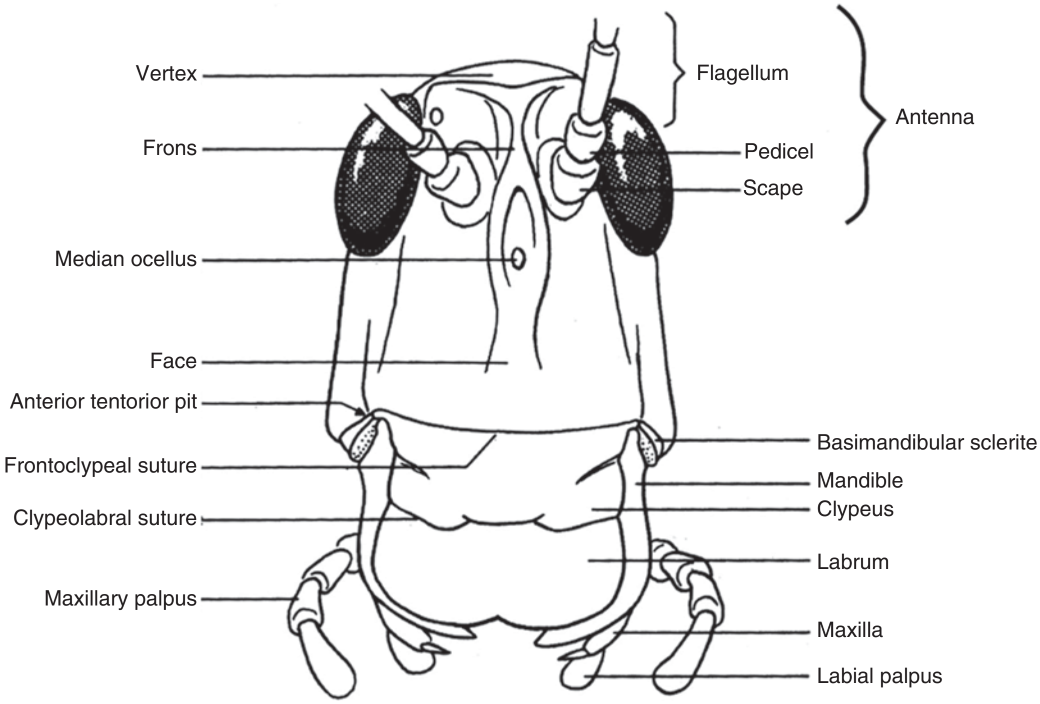
Florida State Collection of Arthropods, Gainesville, FL, USA

Flannel moths, family Megalopygidae, are a New World family of 263 species, mostly Neotropical; actual fauna likely exceeds 350 species. There are three subfamilies (sometimes elevated to separate families): Aidinae, Megalopyginae, and Trosiinae. The family is in the superfamily Sesioidea in the section Tineina, subsection Sesiina, of the division Ditrysia. Adults small to large (10–90 mm wingspan), with head rough scaled; haustellum vestigial; labial palpi minute; maxillary palpi absent; antennae bipectinate. Wings mostly rounded (Fig. 53) and quadrate; body robust. Maculation variable, with shades of brown and



Flagellum, Figure 52 **Front view of the head of an adult grasshopper, showing some major elements.**

Flannel Moths (Lepidoptera: Megalopygidae), Figure 53 **Example of flannel moths (Megalopygidae), *Edebessa purens* (Walker) from Brazil.**

gray, or white, but a few are colorful; scales often long and hair-like on some wing areas. Adults are nocturnal. Larvae are leaf feeders, usually communal in early instars; slug-like, with concealed head; with poison spines usually beneath long hair-like setae. A large number of host plants are recorded, and some species are polyphagous. A few are economic on forest trees and palms, but most are of medical importance due to urticating setae in adults and the poison spines in larvae.

References

Clench HK (1956) Contribution to the study of the neotropical Megalopygidae (Lepidoptera). 1. The genera of the "Trosia" group. Neotropica 2:9–14

Epstein ME (1996) Megalopygidae Herrich-Schäffer, 1855 (Megalopyginae and Trosiinae). pp 72–75 In: Revision and phylogeny of the limacodid-group families, with evolutionary studies on slug caterpillars (Lepidoptera: Zygaenoidea). Smithsonian Contributions to Zoology 582:1–102

Epstein ME (1996) Aididae Hopp, 1927, new status. pp 75–79 In: Revision and phylogeny of the limacodid-group families, with evolutionary studies on slug caterpillars (Lepidoptera: Zygaenoidea). Smithsonian Contributions to Zoology 582:1–102

Hopp W (1927–1929) Die Megalopygiden Unterfamilie der Trosiinae (Lep. Megalopyg.). Mitteilungen des Zoologischen Museums Berlin 13:206–336 (1927); 15: 41–51 (1929)

Seitz A (ed) 1934–35 Familie: Megalopygidae. pp. 1071–1101 In Die Gross-Schmetterlinge der Erde. Teil 6. Die amerikanischen Spinner und Schwärmer, pl. 160–163 (1934–35), 9 pl. A. Kernen, Stuttgart.

Flapping Flight

The most common form of insect flight, wherein flapping movement of the wings generates thrust and movement. Insects can produce forward flight and hovering flight. They can also glide, which is called passive flight.

Flash Colors

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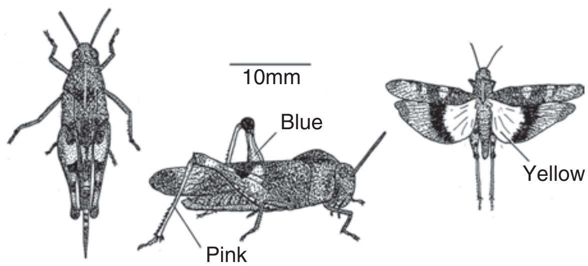
University of Central Lancashire, Preston, United Kingdom

Flash colors are colors that are exposed when an animal moves but are hidden when it is at rest, e.g., the bright hind wings of underwing moths (*Catocala*, *Triphaena*), hawkmoths (*Macroglossum*), and grasshoppers (*Trilophidia*, *Oedipoda*) all make the insect conspicuous while it is flying but as soon as it comes to rest and folds its hind wings beneath the cryptic forewings, the color vanishes. It is thought that predators may initially be startled when a hitherto cryptic insect is disturbed and flies off, suddenly exposing bright colors. The predator may then follow the bright color as it flies, preparing to attack it, but when it lands and the color vanishes the predator is baffled because it was following the color rather than the insect. This is how flash colors are thought to work; they certainly deceive humans in this way, so it is reasonable to suppose that birds also may be deceived, but there has been no experimental demonstration that they reduce predation by natural predators.

Some butterflies have brightly colored upper sides to their fore wings which may be flash colors since these are hidden when the wings are folded together at rest. Other insects (e.g., some bugs and mantids) have bright colors (Fig. 54) on the dorsal surface of the abdomen which are hidden by the cryptically colored wings when at rest. These, too, may be flash colors.

Many grasshoppers stridulate as they jump or fly and then remain silent on landing. It is possible that predators follow the noise and are then baffled when the noise ceases and there is no sign of the insect. If this is indeed the function of stridulation in a flying grasshopper then, by analogy with flash coloration, it could be called flash behavior.



Flash Colors, Figure 54 The grasshopper *Trilophidia tenuicornis* is cryptically brown with disruptive markings when at rest (left and center). When it flies (right), bright colors are exposed on the hind wings which vanish when it lands (flash colors). The pink and blue marks on the hind legs may attract a predator to the most dangerous part of the insect; it can give a painful kick with these legs, which have sharp spines (reproduced from Edmunds, 1974, fig. 6.3).

References

Cott HB (1940) Adaptive coloration in animals. Methuen, London, UK, 508 pp
Edmunds M (1974) Defence in animals: a survey of anti-predator defences. Longman, Harlow, UK, 357 pp

Flat Bark Beetles

Members of the family Cucujidae (order Coleoptera).

► Beetles

Flat Bugs

Members of the family Aradidae (order Hemiptera).

► Bugs

Flat Flies

Some members of the family Hippoboscidae (order Diptera).

► Flies

Flat Grain Beetle, *Cryptolestes pusillus* (Schönherr) (Coleoptera: Laemophloeidae)

This stored grain insect commonly is a pest under cold conditions.

► Stored Grain and Flour Insects

Flat-Footed Flies

Members of the family Platypezidae (order Diptera).

► Flies

Flatidae

A family of insects in the superfamily Fulgoroidae (order Hemiptera). They sometimes are called planthoppers.

► Bugs

Flea Beetles

Members of the subfamily Alticinae of the beetle family chrysomelidae. These insects have strongly developed hind femora, enabling they to jump, flea-like, long distances.

► Beetles

Flea Beetles (Coleoptera: Chrysomelidae: Alticinae)

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Flea beetles are members of the subfamily Alticinae in the leaf beetle family Chrysomelidae, one of the most destructive of insect families. The Alticinae, the largest chrysomelid subfamily, has 6,000 species worldwide, most of which are phytophagous. Flea beetles are small, leaf-feeding beetles with greatly enlarged hind femora (thighs) and a propensity to jump when disturbed, from whence their common name originated. Many species of flea beetles are economic pests of vegetable and field crops, while some have been utilized as biological control agents of noxious weeds.

Although a few are generalist feeders on a wide range of host plants, most species of flea beetles are monophagous or oligophagous, feeding on plants in only one or a few related families. Thus, flea beetles in the genus *Chaetocnema* feed on sweet corn and grasses, others in the genus *Altica* feed on alder, dogwood, elm, grapevine, rose and willow, while another group feeds on potatoes, tomatoes, eggplant and pepper. Because of the variety of flea beetle species, host plants, and habitats, this entry will focus on one species, *Phyllotreta cruciferae* (Goeze), the crucifer flea beetle or cabbage flea beetle, which has many attributes of flea beetles in general.

Crucifer Flea Beetle, *Phyllotreta cruciferae* (Goeze)

The genus *Phyllotreta* Chevrolat is one of the largest alticine genera, with 250 species worldwide. *Phyllotreta* species are principally north temperate in distribution, occurring mostly in Eurasia and North America. Few species occur in tropical habitats. Along with the species in the genus *Psylliodes* Latreille, *Phyllotreta* encompasses the main flea beetle genus that feeds on crucifers. In addition to *P. cruciferae*, 14 other *Phyllotreta* species are injurious to cruciferous crops in Canada, with 12 of these distributed across North America. Many of the 150 Palearctic species of *Phyllotreta* are likewise economically important pests of crucifers. Several *Psylliodes* flea beetles are similar in appearance, biology, and crucifer damage patterns to *Phyllotreta cruciferae*. *Psylliodes crysocephala* (L.), the cabbage stem flea beetle, is one of the most injurious flea beetles to cultivated crucifers in the Palearctic region, while *P. punctulata* Melsh., the hop flea beetle, is commonly found in crucifer field crops in North America.

A native of Eurasia, the crucifer flea beetle, *P. cruciferae,* is the dominant flea beetle pest of oilseed crops in India and eastern Europe, although of sporadic occurrence in western Europe. It was first found in North America in 1923 near Agassiz, British Columbia, Canada. It spread rapidly, and is now distributed throughout the continent. Along with the striped flea beetle *P. striolata* (Fab.), *P. cruciferae* is the most economically important pest of crucifer vegetable and field crops in North America.

Morphology

Phyllotreta cruciferae adults are small, oblong-ovate or oval-shaped leaf-feeding beetles 2–3 mm long (Figs. 55a and 56). They are usually entirely black, or black with a bronze, metallic green or blue luster. Like other *Phyllotreta* species and unlike *Psylliodes*, which has 10, *P. cruciferae* has an 11-segmented, filiform-shaped antenna. The elytra are dorsally flat, and the punctae on them are not deep and arranged in rows as in *Psylliodes punctulata*, but are arranged randomly over the wings.

The creamy white to yellow eggs are oval in shape and about 0.35 mm by 0.20 mm in size. They are laid singly or in small numbers in the soil around the crown of host plants.

The three larval instars are creamy white, slender, cylindrical and worm-like in general appearance, with three pairs of very small legs, a brown head capsule and tan posterior segment (Fig. 55b). The third instar reaches a length of 3–5 mm. Just prior to pupation, third instar larvae form plump quiescent prepupae in an earthen cell in the soil near host roots. *Phyllotreta cruciferae* larvae, like most but not all *Phyllotreta* larvae, are root feeders and, as such, are rarely seen.

The whitish-yellow pupae are about 2.5 mm long, with free body appendages and dark-colored eyes. As they near eclosion to adult state, the pupae darken to black.

Host Range and Food Selection

Nearly all species of *Phyllotreta* feed on plants in the families Cruciferae, Resedaceae, or Capparidaceae. These plant families contain glucosinolates, sulfur-rich, anionic secondary plant compounds that produce several different products through hydrolysis by endogenous myrosinases. These hydrolysis products have different biological roles, acting as defense compounds in some instances and attractants in others. *Phyllotreta cruciferae* flea beetles are strongly attracted to allyl isothiocyanate, a volatile metabolite of the secondary plant compound allyl glucosinolate. The flea beetle feeds on cultivated and wild crucifers that contain glucosinolates, with host crops including the oilseed rapes, canolas, and mustards *Brassica rapa*, *B. napus*, *B. juncea*, *Crambe abyssinica*, *Camelina sativa*, *Eruca sativa*, *Sinapis alba*; host crucifer vegetables *B. chinensis*, *B. oleracea* including kale, Chinese cabbage, cauliflower, cabbage, Brussels sprouts, kohlrabi, broccoli, turnip, and radish; other host crops including *Alyssum*, *Hesperis matronalis*, *Cleome* spp., *Nasturtium officinale*, and *Tropaeolum minor*; and host wild species including *Arabis* spp., *Arabadopsis thaliana*, *Berberea vulgaris*, *Berteroa* sp., *Brassica amplexicaulis*, *B. balearica*, *B. barreliere*, *B. drepanensis*, *B. elongata*, *B. gravinae*, *B. incana*, *B. macrocarpa*, *B. maurorium*, *B. nigra*, *B. tournefotii*, *Cardamine* spp., *Diplotaxis* sp., *Descurainia* spp., *Erucastrum gallicum*, *Lepidium campestre*, *Neslia paniculata*, *Rorippa islandica*, *Sinapis allioni*, *S. ancheri*, *S. flexuosa*, *S. arvense*, and *S. pubescens*. The flea beetle does not feed readily on *Capsella*, *Erysimum*, *Iberis*, or *Thlaspi* species. In stress situations in the absence of suitable crucifer hosts *Phyllotreta* has been observed feeding on such diverse plants as garden peas *Pisum sativum* and red-root pigweed

Amaranthus retroflexus, but it is unlikely that *P. cruciferae* can survive and reproduce on such non-cruciferous hosts.

Biology

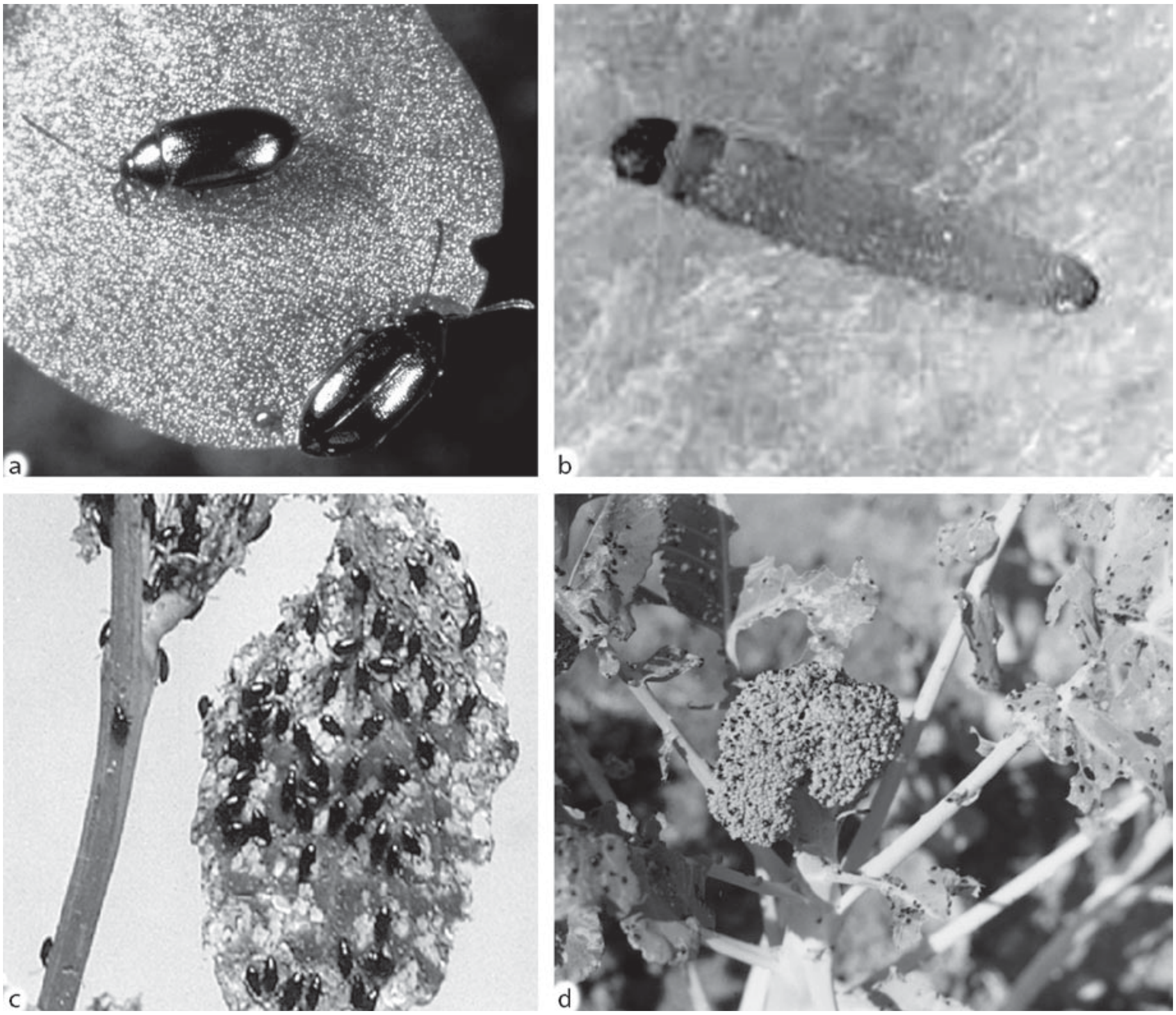
While some flea beetle species may have two to three generations per year, crucifer-feeding flea beetles have one complete generation a year in north temperate climates. *Phyllotreta cruciferae* overwinter as adults in leaf litter or occasionally in soil in protected places such as field margins, fence rows, hedges, tree rows or, less frequently, within cultivated fields. Winter mortality is generally very low, although populations can decline after several consecutive severe winters. Emergence from overwintering sites begins with the first extended period of warm weather in spring. In Alberta, Canada, peak emergence occurs near the end of May when ground temperatures reach 15°C. Overwintered *P. cruciferae* fly when daily maximum air temperatures exceed 14°C. Flea beetle emergence, movement, and feeding is maximized in periods of warm, sunny, dry and calm weather, and is curtailed in cold wet conditions. Flea beetles begin feeding on winter annual weeds or volunteer crucifers early in the spring. They move into fields of preferred host plants such as *Brassica napus* or cruciferous vegetables as these are seeded and germinate. After feeding for a period, each mated female will lay up to 25 eggs at the base of host plants or sometimes on plant roots from April to early July, whereupon the overwintered generation dies off. Larvae hatch in 10 days–2 weeks, and feed on root hairs and small roots, chewing circular pits or penetration holes into the root epidermis. The beetles develop through three larval instars. After feeding for a week to 10 days, the third instar larvae cease feeding and enter a quiescent prepupal resting stage in an earthen cell in the soil. After a pupal period of 1–2 weeks, adult beetles emerge from late July onward, and feed on green cruciferous plants until cold temperatures cause them to leave fields and seek overwintering sites. Univoltinism, one generation per year, appears to be facultative rather than obligate in flea beetle biology. With development from egg to adult being temperature dependent and occurring in as little as 7 weeks under favorable conditions, the event of a complete second generation may become more frequent with increasing global temperatures.

Damage

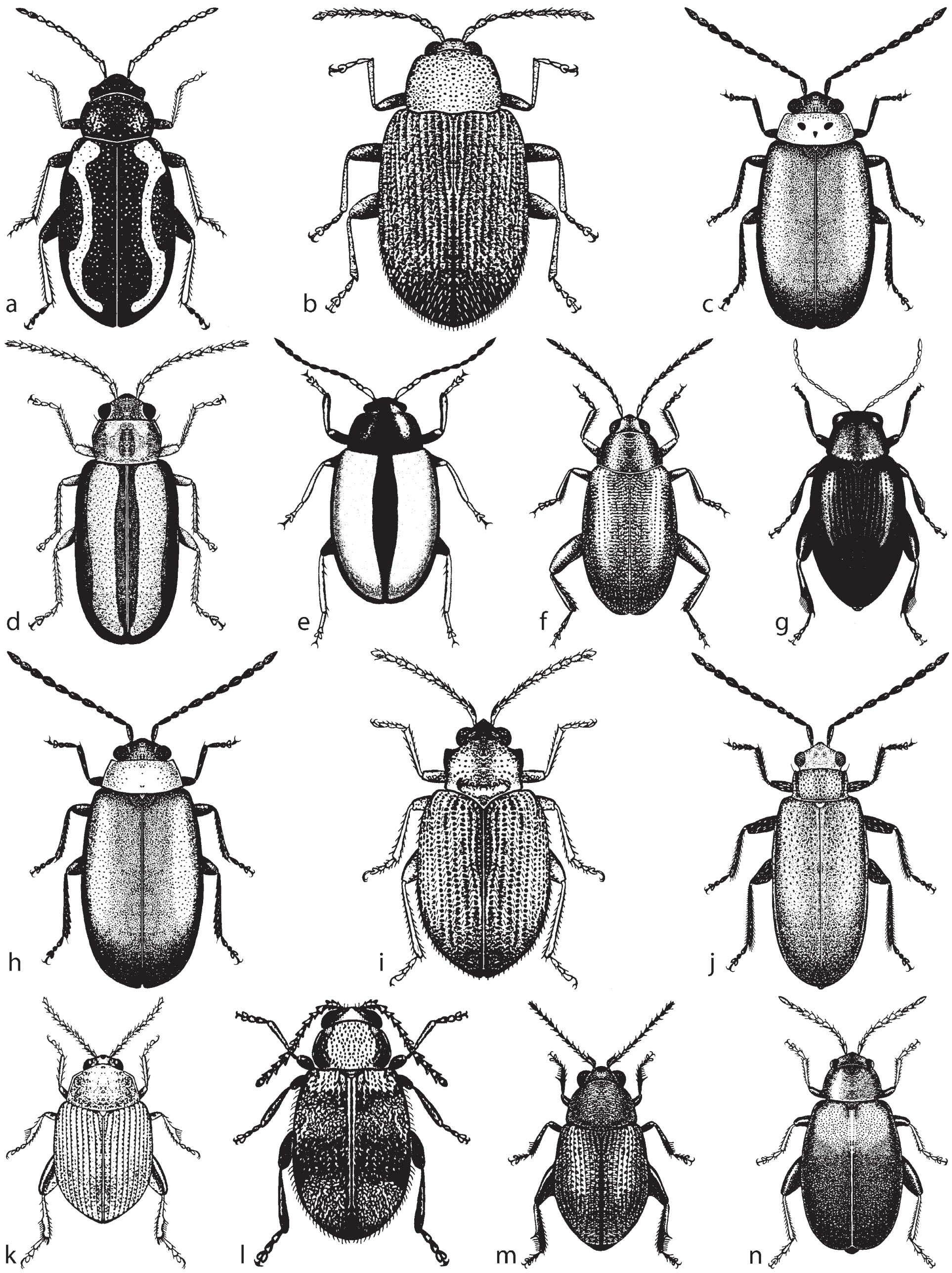
Phyllotreta cruciferae causes the greatest economic damage to cultivated crops through adult beetle feeding on the epidermis of cotyledons and young true leaves. Although each circular feeding pit is small and rarely perforates the leaves, tissue around each feeding lesion dies and, under heavy feeding pressure, the sheer number of feeding pits can give the fragile young leaves a sieve-like or shot-hole appearance (Fig. 55c). In large numbers, flea beetles can rapidly defoliate and kill seedling plants. During cold, inclement weather and periods of slow plant growth flea beetles can feed on seedlings at or below the soil surface as these emerge, destroying the apical meristem and, ultimately, the seedling. Light feeding on older leaves is often restricted to the leaf edges, where it causes browning and curling. Flea beetle feeding can result in decreased plant stand if meristems are severed or if foliar damage is extreme; if plants are not killed directly, flea beetle feeding can result in reduced vigor and delayed plant growth, stunted plants, uneven stands and protracted plant maturity. Under warm sunny conditions flea beetle movement into fields and feeding can be rapid and severe; under heavy flea beetle feeding, entire fields can be destroyed. Damage is often most severe along field edges, where the flea beetles are entering the field. Damage may be worse on light, sandy soils that exacerbate plant desiccation. Once past the three to fourth leaf stage, most crucifers are tolerant to flea beetle foliar feeding. Crucifer vegetable transplants are less affected than direct-seeded crucifer vegetable crops, but they, too, can be killed or severely stunted by heavy feeding during warm, dry weather. Once vegetables reach the six-leaf stage or are taller than 15 cm, only severe defoliation will affect head weight and quality.

Larvae of *P. cruciferae* and most cruciferous flea beetles feed on root hairs and small roots. By this time host plants can tolerate root pruning, and economic damage by *P. cruciferae* larvae to oilseed crops is considered negligible. However, in some cases the value of cruciferous vegetable crops such as radishes can be reduced because of cosmetic damage caused by flea beetle larvae. The larvae of a few species of European flea beetles such as *Phyllotreta nemorum* (L.) and *Psylliodes chrysocephala* (L.) bore into stem and leaf tissue, feeding on leaf mesophyll, petioles and stems. Thus, it is the larval stage of these species that is the most economically detrimental.

As adult populations of *P. cruciferae* emerge in summer, their debarking of the epidermis of green oilseed pods can cause increased chlorophyll content of seed, shriveled or "pepper seed," decreased seed weights, increased pod shattering, and fungal growth within pods in wet weather. Youngest pods and later-seeded crops are most affected. Feeding on heads of crucifer vegetables



Flea Beetles (Coleoptera: Chrysomelidae: Alticinae), Figure 55 **Crucifer flea beetle: (a) adult *Phyllotreta cruciferae* (Goeze); (b) *Phyllotreta cruciferae* larva (3 mm); (c) severe defoliation of crucifer leaves; (d) cosmetic damage to a broccoli head.**



Flea Beetles (Coleoptera: Chrysomelidae: Alticinae), Figure 56 **Some important crop-feeding flea beetles (not drawn to scale): (a) striped flea beetle, *Phyllotreta striolata* (Fabricius); (b) eggplant flea beetle, *Epitrix fuscula* (Crotch); (c) threespotted flea beetle, *Disonycha triangularis* (Say); (d) palestriped flea beetle, *Systena blanda* Melsheimer; (e) horseradish flea beetle, *Phyllotreta armoraciae* (Koch); (f) crucifer flea beetle, *Phyllotreta cruciferae* (Goeze); (g) desert corn flea beetle, *Chaetocnema ectypa* Horn; (h) spinach flea beetle, *Disonycha xanthomelas* (Dalman); (i) potato flea beetle, *Epitrix cucumeris* (Harris); (j) redheaded flea beetle, *Systena frontalis* (Fabricius); (k) sweetpotato flea beetle, *Chaetocnema confinis* Crotch; (l) tobacco flea beetle, *Epitrix hirtipennis* (Melsheimer); (m) corn flea beetle, *Chaetocnema pulicaria* Melsheimer; (n) cabbage flea beetle, *Phyllotreta albionica* (LeConte). (From Capinera 2001, Handbook of Vegetable Pests, Academic Press.)**

can result in brown flecks on curds or florets, creating cosmetic damage and downgrading in crops such as cabbage and broccoli (Fig. 55d). Although rare as a vector of disease in North America, the crucifer flea beetle has been reported to vector the bacterium that causes black rot in cabbage. In Europe flea beetles are known to transmit turnip mosaic.

Economic Impact

The cost of flea beetle damage to oilseed crucifer crops in North America exceeds $300 million annually. Direct losses to oilseed production average 8–10% of the annual crop yield. Because more than 90% of the 5 million ha sown to oilseed crucifer crops in Canada utilize insecticide-fungicide seed dressings, indirect costs include environmental and non-target exposure to pesticides for flea beetle control. Significant damage can occur to young cole crops, especially if these are direct-seeded rather than transplanted, and cosmetic damage by late season feeding can also reduce farm receipts appreciably.

Management

Economic Thresholds

Because of their propensity to move at the least disturbance, flea beetle numbers on plants are difficult to count accurately, and the impact of the number of feeding pits varies with the area of the leaf. Instead of numbers of beetles or feeding pits, economic thresholds in seedling oilseed crucifer crops in Canada are established as defoliation levels of >25% of the leaf area eaten at the cotyledon to third true leaf stage. Economic thresholds at crop maturity have not been determined, but if oilseed pods are still green, heavy feeding on them may decrease seed yields or quality. In cole crop production, late feeding can cause cosmetic damage that will downgrade head quality. An average of 75 beetles per plant can result in severe damage to a mature cabbage crop.

Monitoring

Crop monitoring is the first step in averting losses from flea beetle feeding. Often flea beetle infestations may be localized or sporadic. Examination of seedlings for the appearance of shot-hole feeding should be done daily from emergence until the crop reaches the three to four leaf stage, with special care taken to monitor field boundaries next to grassy or wooded areas. Yellow sticky cards can be used to monitor flea beetle presence, but they may not be suitable for estimating population levels or the need for control. A flea beetle aggregation pheromone has been developed that may allow for early detection of overwintering flea beetles, for population monitoring, and for estimating their densities. Crucifer crops should be monitored especially closely in hot, dry weather, when flea beetle numbers can increase exponentially, and feeding levels and plant stress are high.

Cultural Practices

Any practice that encourages rapid germination, increased seedling vigor and plant growth, and minimization of the seedling vulnerability period will aid in decreasing the susceptibility of young crucifer crops to flea beetle feeding. Thus, good seed bed preparation, proper fertilization, shallow seeding into warm soil with adequate moisture or irrigation will promote rapid seedling growth and lessen flea beetle damage to crucifer seedlings. Cruciferous weeds and volunteer crucifers should be controlled prior to seeding. Canola grown in a zero till cultivation regime with minimal soil disturbance, at high seeding rates and wide row spacings has been shown to suffer less flea beetle damage than crops grown under conventional tillage. Late planting can avoid the spring peak in flea beetle numbers, but may not be practical for agronomic reasons. Seeding rate and date does not significantly affect the abundance of new generation flea beetles. For cole vegetable and salad greens production, such cultural methods as the use of vigorous transplants, row covers, and exclusion fencing can protect seedlings physically until they become large enough to withstand feeding. Irrigation applied under warm, dry conditions may drown beetles when they are most active. Crop rotation and intercropping crucifers with plants from other families such as clovers, marigolds, or tomatoes may decrease flea beetle numbers. Protection of brassica greens such as arugula or bok choi from cosmetic damage may be necessary throughout the season, but is difficult by cultural means.

Host Plant Resistance

Host plant resistance holds potential as a means of effective flea beetle management. *Brassica napus* oilseed rape is less damaged by the crucifer flea beetle than is *B. rapa*, while yellow mustard *Sinapis alba* can outyield both *Brassica* species under heavy flea beetle feeding pressure. Intergeneric crosses between *B. napus* and *S. alba* are being undertaken to introduce mustard flea beetle resistance into oilseed rape. Transgenic *B. napus* with elevated levels of trichomes on the first true leaves also has potential for deterring flea beetles from feeding. Some cruciferous vegetable varieties are variable in susceptibility to flea beetle feeding. Red or purple colored cole varieties may be less preferred than green ones when mature. In general, there is less flea beetle feeding on vegetable cultivars with a heavy, waxy bloom on their leaves.

Biological Control

Three species of braconid parasitoid wasps, and an allantonematid and two mermithid nematodes have been recorded attacking eight *Phyllotreta* species in an intensive European study. The braconid wasp *Townselitis bicolour* (Wesm.) parasitized up to 50% of adult flea beetles in summer in Germany. Microsporidean, eugregarine, and nematode infections have been reported from *Phyllotreta* species in Sweden. In North America, crucifer flea beetles are attacked but not controlled by a suite of natural enemies, including predators such as lacewing (*Chrysopa*) larvae, big-eyed bug (*Geocoris*) sp., *Collops vittatus* Say beetles, and field crickets (*Gryllus* spp.). The native braconid wasp *Microctonus vittatus* Mues. normally parasitizes <5% of crucifer flea beetle populations. An attempt to introduce *T. bicolour* from Europe into western Canada in the 1980s was not successful.

Chemical Control

More than 90% of the oilseed rape crops in Canada are planted with seed that has been treated with an insecticide-fungicide combination. If flea beetles are not controlled by the seed dressings and feeding is severe, or in jurisdictions without registered seed treatments, various foliar insecticides are used for flea beetle control. Some new chemistry insecticides such as thiamethoxam and spinosad are effective in flea beetle control, but the plant-derived products azidiractin and pyrethrin, along with kaolin clay, may not provide adequate protection. New biological, botanical or reduced-risk synthetic insecticides are being investigated for efficacy of control of crucifer flea beetles.

References

Andersen CL, Hazzard R, Driesche R, van Mangan FX (2006) Alternative management tactics for control of *Phyllotreta cruciferae* and *Phyllotreta striolata* (Coleoptera: Chrysomelidae) on *Brassica* crops in Massachusetts. J Econ Entomol 99:803–810

Campbell JM, Sarazin MJ, Lyons DB (1989) Canadian beetles (Coleoptera) injurious to crops ornamentals, stored products, and buildings. Research Branch, Agriculture Canada Publication 1826, Ottawa, Ontario, Canada, 491 pp

Dosdall LM, Dolinski, MG Cowle NT, Conway PM (1999) The effect of tillage regime, row spacing, and seeding rate on feeding damage by flea beetles, *Phyllotreta* spp. (Coleoptera: Chrysomelidae), in canola in central Alberta, Canada. Crop Protect 18:217–224

Feeny P, Pauwe K, DeMong NJ (1970) Flea beetles and mustard oils: host specificity of *Phyllotreta cruciferae* and *P. striolata* adults (Coleoptera: Chrysomelidae). Ann Entomol Soc Am 63: 832–841.

Hill DS (1987) Agricultural insect pests of temperate regions and their control. Cambridge University Press, Cambridge, UK, 659 pp

Lamb RJ (1983) Phenology of flea beetle (Coleoptera: Chrysomelidae) on the survival, growth, seed yield and quality of canola, rape and yellow mustard. Can Entomol 116:269–280

Palaniswamy P, Lamb RJ (1992) Host preferences of the flea beetles *Phyllotreta cruciferae* and *P. striolata* (F.) (Coleoptera: Chrysomelidae) for crucifer seedlings. J Econ Entomol 85:743–752

Sommer G (1981) Biologie und parasitenkomplex der halticinen gattung Phyllotreta. Ph.D. thesis, Albert-Ludwigs-Universitat zu Freiburg in Breslau, Germany.

Flea Collar

A collar containing slowly released fumigant insecticide that is worn by cats and dogs to prevent infestation by fleas. Once popular, though not entirely effective, it has largely been replaced by systemic products that are dabbed on the animal or fed to the animal periodically.

► Veterinary Pests and Their Management
► Cat Flea

Fleas (Siphonaptera)

The fleas are a well known order of blood feeding insects, attacking mammals and birds. They bear some similarities to Mecoptera and Diptera, but their relationship to other insects is uncertain. The order name is based on the Greek words *siphon* (tube), a (without), and *pteron* (wing).

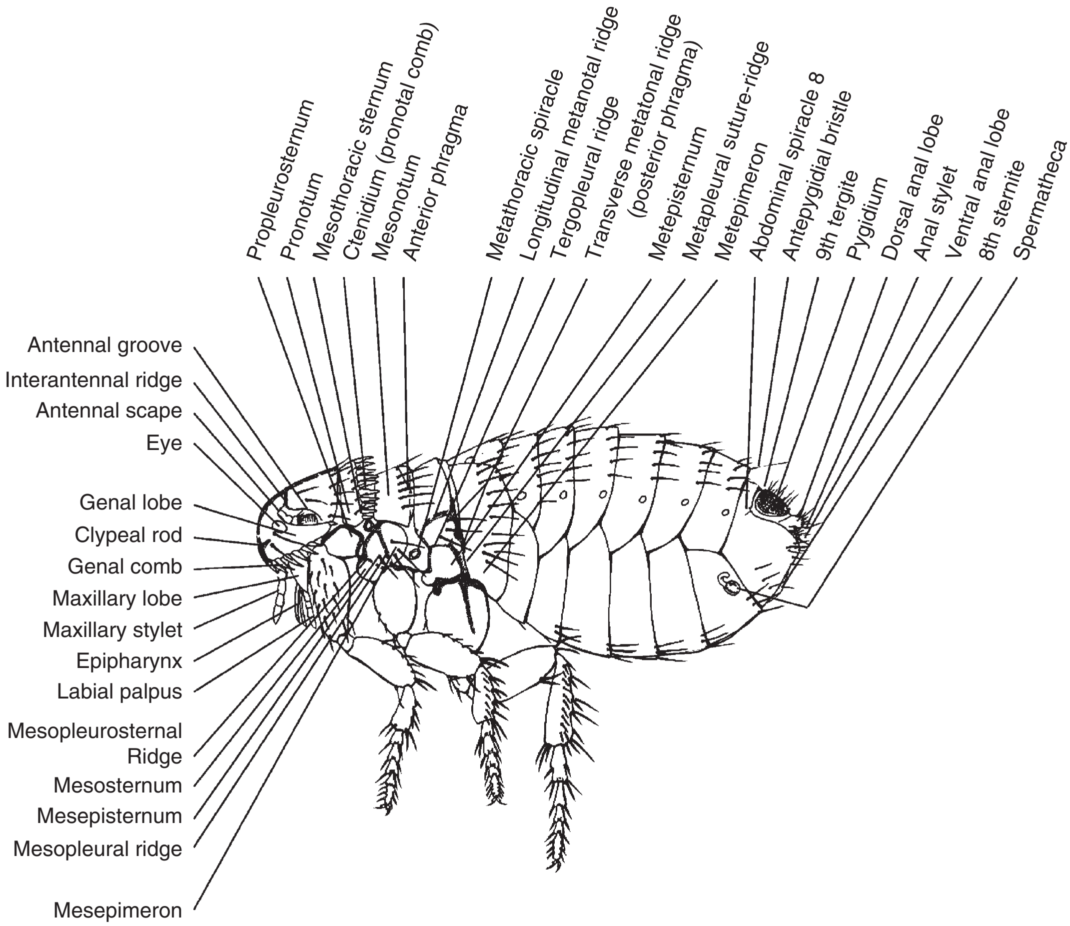
Classification

There are several classification systems available, with anywhere from five to ten superfamilies containing about 16 families. Following is a list of families containing about 2,300 species:

Class: Insecta
- Order: Siphonaptera
  - Family: Pulicidae – common fleas
  - Family: Tungidae
  - Family: Rhopalopsyllidae – club fleas
  - Family: Malacopsyllidae
  - Family: Vermipsyllidae – carnivore fleas
  - Family: Hystrichopsyllidae – rodent fleas
  - Family: Coptopsyllidae
  - Family: Pygiopsyllidae
  - Family: Stephanocircidae
  - Family: Macropsyllidae
  - Family: Xyphiopsyllidae
  - Family: Ancistropsyllidae
  - Family: Chimaeropsyllidae
  - Family: Ischnopsyllidae – bat fleas
  - Family: Leptopsyllidae – scaled fleas
  - Family: Ceratopsyllidae – bird and rodent fleas

Characteristics

Adult fleas are laterally compressed, wingless insects. They generally measure only 1–5 mm in length. They body is dark, normally brown or black, and well sclerotized. The antennae are short and held in grooves at the side of the head. The mouthparts are of the piercing-sucking type, but fairly short. The head often bears a row of large spines laterally; this is called the genal comb and the spines are called ctenidia. Fleas are adorned with numerous spines and setae. Fleas are renowned for their jumping ability, and some can leap up to 30 cm high and 20 cm distance in a single jump. Legs are of moderate size, though the coxae and the hind femora are enlarged. The abdomen consists of ten segments. Fleas display complete metamorphosis. Larvae are elongate (Fig. 57) and legless, resembling fly larvae, but they have a



Fleas (Siphonaptera), Figure 57 **Diagram of a flea showing a lateral view.**

distinct head capsule and moderately long setae. Larvae produce a small silken cocoon that often incorporates sand grains or other debris in its construction.

Biology

Adult fleas are obligate ectoparasites that feed on blood from birds and mammals; blood is required for development of eggs. They tend to be phototactic, and sometimes are attracted to shadows. In contrast, larvae often feed on organic debris, including the blood-containing feces of the adults. Both adults and larvae are often found principally in the nest of their host. The eggs are not normally glued to hair or feathers, and normally fall the nest of sleeping area of the host. Most species are quite specific, feeding on a single host species or related species of hosts. When lacking a preferred host, fleas may accept others, as is the case with rat fleas. Rats are quite susceptible to bubonic plague, and when the rats perish the fleas feed on other available hosts, including humans. Fleas infected with plague bacterial sometimes regurgitate into the host, thereby inoculating the (human) host with plague. Inoculation also is accomplished when the host scratches, and rubs feces containing bacteria into wounds. Rodents are the predominant host of fleas; 74% of fleas are known to feed on rodents. Fewer fleas attack birds. Only 6% of fleas feed on birds. Fleas have an unusual ability to remain for protracted periods of time in the pupal stage, and then to emerge quickly in response to mechanical stimulation. This is an excellent adaptation to conserve energy in the absence of hosts.

Problems Associated With Domestic Fleas

The primary importance of cat flea is its nuisance to humans and pets. They are not picky about their meals; they will feed on almost any warm-blooded animal. Bites usually cause minor itching, but may be more irritating to those with sensitive skin. Some people and pets suffer from flea allergy dermatitis, which can persist for up to 5 days and is characterized by intense itching, reddening at the sight of feeding, hair loss, and secondary infection. Cat fleas also serve as intermediate hosts of the dog tapeworm (*Dipylidium caninum*). This intestinal parasite is transmitted to the pet while grooming when it eats an adult flea carrying a tapeworm cyst. The flea is infected by ingestion of the cyst during its larval stage. The parasite segments resemble small pieces of rice and often are discovered around the anal region of the infected pet, though they may be elsewhere, and may drop from the animal.

Domestic Fleas

The most common domestic flea of both cats and dogs is the cat flea (*Ctenocephalides felis felis*). The dog flea (*Ctenocephalides canis*) appears similar to the cat flea, but is not common on household pets. The sticktight flea (*Echidnophaga gallinacea*) can become a problem if pets frequent areas associated with poultry.

The eggs of fleas are oval, and smooth. They are minute, measuring only about 0.5 mm in length, but visible to the naked eye. Their small size and white color may prevent them from being seen on lightly colored fabric. Small worm-like larvae, 1.5–5 mm in length, hatch from the eggs. Though they also are visible to the naked eye, they are not often observed. They are eyeless, legless and sparsely covered with hairs. The larval body is translucent white with a dark-colored digestive tract that can be seen through the skin. Eventually the larvae mature and spin silken cocoons in which they pupate, and develop into adult fleas. Cocoons are sticky, attracting dirt and debris. Adult fleas are 1–3 mm in length, reddish-brown to black, wingless, and laterally compressed They possess powerful hind legs, are well adapted for jumping onto hosts, and for running through hair and feathers.

Cat flea adults, unlike many other fleas, remain on their host. Females require a fresh blood meal in order to produce eggs. The eggs drop from the host. Adult fecal matter consists of relatively undigested blood. This dried blood falls from the pet and serves as food for the newly hatched larvae. The young fleas will hatch within 2 days and feed on dandruff, grain particles, and skin flakes found on the floor around them, in addition to the fecal matter provided by adult fleas. They develop best in areas protected from rainfall, irrigation, and sunlight, where the relative humidity is at least 75% and the temperature is 70–90°C. The larval stage lasts 5–15 days.

Larvae spin silken cocoons among carpet fibers, in floor crevices, or protected outdoor areas where they develop. Under optimal conditions, new adults are ready to emerge within 2 weeks. They develop faster at higher temperatures, but can remain in their cocoons up to 12 months. Vibrations and/or an increase in carbon dioxide stimulate adults to emerge. Adults live 4–25 days and are the only stage that lives on the pet and feeds on fresh blood.

Management of Fleas Affecting Household Pets

Effective control requires elimination of fleas from the pet, the home, the yard, and control of the flea life cycle. Removal of fleas from the pet alone is futile; immature fleas (eggs, larvae, pupae) develop off the pet and new adults quickly re-infest the animal. Historically, flea management was a very difficult problem in warm humid areas that favored their survival. However, new and safe chemical products are now available that can be used as part of a flea control program. There are three complimentary elements associated with flea management.

Treating the Pet

Removing fleas from pets may be done by a veterinarian, grooming parlor, or by the pet owner. A flea comb may be used, but is not very effective; only 10–60% will be collected. Fleas should be dropped in soapy water and then discarded. This method is very time consuming.

Shampooing the pet removes the dried blood and skin flakes that fall to the ground and serve as food for flea larvae. The animal's body must be thoroughly lathered, and it is recommended that the lather remain for up to 15 min before the pet is rinsed. Flea shampoos contain various insecticides. Some pets, however, may exhibit allergic reactions to these products.

The newest approach to topical flea control applications is spot treatment with products such as imidacloprid (Advantage) or fipronil (Frontline). Both are available as spot-on oils which are applied to the shoulder area of the pet and distribute over the body within a few hours. They are non-toxic to mammals and kill almost all fleas on the pet within 24 h of treatment, and provide effective suppression for 3–6 weeks. These products help reduce the symptoms of flea allergy dermatitis by killing fleas and reducing the number of flea bites on the animal, there may still be some allergic reaction because fleas are able to bite before they die.

Insect growth regulators (IGRs) and insect development inhibitors (IDIs) work by interfering with egg development, and molting of young fleas. They disrupt the flea life cycle but do not kill adult fleas. Methoprene (Precor) and pyriproxyfen (Nylar, Archer) are examples of IGRs available for pet treatment in sprays and flea collars. Lufenuron (Program), an IDI, is orally administered to the pet. The IGR and IDI products do not take immediate effect because they affect flea egg and larval development. Use of one of these products along with use of Advantage or Frontline will kill adults and prevent development of immature fleas.

Ultrasonic flea collars have also been proposed for use to keep fleas off pets, but are completely ineffective. Insecticidal flea collars also are not very effective.

Treating the Home

Indoor treatment should be concentrated on areas frequented by pets, as this is where most of the eggs and larvae will be located. Vacuuming the entire house and disposing of the vacuum bag will help eliminate fleas. Vacuuming will not only remove flea eggs, but may stimulate new adults to emerge from their cocoons, exposing them to any insecticide residue on the floor. Steam cleaning carpets is even more effective than normal vacuuming and should be considered if infestation is severe. In addition to sanitation, borate carpet treatment, applied either by the homeowner or a professional exterminator, works as intestinal poison when it is eaten by flea larvae. The powder is sprinkled and worked into the carpet. Overall risk of danger to pets and humans is unknown, but appears to be low. This treatment, however, is not recommended for homes with infants.

Treating the Yard

Flea larvae develop in shaded, humid areas, but will drown in a flooded environment. Rainfall is often enough to curb larval development outdoors. In addition to drowning, the fecal dried blood meal provided by adult fleas is no longer available if the lawn is wet. Sprays containing insecticides registered for outdoor use, such as pyrethroids, may be applied during dry seasons every 2–3 weeks to shaded areas where pets frequent, and flea larvae abound. Insect growth regulators are also available for outdoor use. If possible, control access of feral animals (opossums, skunks, etc.) to the yard as they bring new fleas with them. Sheds and dog houses should be treated the same as the house. Restricting pet access from areas that are difficult to treat (e.g., beneath porches, inside crowded sheds) may also help flea control.

► Cat Flea

References

Hopkins GHE, Rothschild M (1953–1971) An illustrated catalog of the Rothschild collection of fleas (Siphonaptera) in the British Museum (Natural History), vols 1–5. British Museum, London

Lewis RE (1972–1993) Notes on the geographical distribution and host preferences in the order Siphonaptera. J Med Entomol 9–30

Richman DL, Koehler PG (1997) Fleas: what they are, what to do. Florida Cooperative Extension Service publication ENY-291

Flesh Flies

Members of the family Sarcophagidae (order Diptera).

► Flies

► Myiasis

Fletcher, James

James Fletcher was born on March 28, 1852, in the county of Kent, England. In 1874 he emigrated to Canada and worked for 2 years in the Bank of Montreal. He then became an assistant in the Library of Parliament in Ottawa. In this position he was able to continue his studies in botany and entomology, and he joined the Entomological Society of Canada in 1877. He married in 1879 and later had two daughters. In 1878 he published his first entomological paper, "An outline sketch of the Canadian Buprestidae" and in 1879–1880 a botanical paper "Flora Ottawaensis." His expertise in insects and plants was recognized in 1884 by his appointment as Dominion Entomologist (Fig. 58) to the Canadian Department of Agriculture. Then, he turned his attention to applied entomology, and published annual reports on this subject. His efforts persuaded the Committee of Agriculture of the Canadian House of Commons to establish Experimental Farms in 1887. He then received the title of Entomologist and Botanist, and was transferred from the Library of Parliament to the staff of the Experimental Farms. For the next 21 years his time was occupied with applied entomology and applied botany. In 1896, he received an honorary LL.D. degree from Queen's University, Ontario, for his contributions to agricultural science. He died in Montreal on November 8, 1908.

Reference

*MallisA (1971) James Fletcher. In: American entomologists, Rutgers University Press, New Brunswick, NJ, pp. 113–116

Fletcher, James, Figure 58 James Fletcher.

Flies (Diptera)

Flies are an order of fairly small, relatively frail, two-winged insects. Despite these characteristics, however, they are extremely important, both for their direct biting effects, and because they may transmit diseases to animals. The name of this order is based on the Greek words *di* (two) and *pteron* (wing).

Classification

About 100,000 species of flies are known. Various classification systems exist for this large and diverse order. Two suborders usually are presented: Nematocera with long, many-segmented antennae, and Brachycera with short, apparently 3-segmented antennae. The larvae of the Nematocera also are distinguished by possessing large heads with mandibles that move laterally. In contrast, the larvae of Brachycera tend to have small heads bearing mouth hooks that move vertically. Pupae of the Brachycera also differ in that the pupal stage is passed inside the hardened cuticle of the last larval instar; this is called a puparium. The numerous muscoid families are divided into those with lobes (calypteres) at the base of the wing, and those lacking them.

Class: Insecta
- Order: Diptera
  - Suborder: Nematocera
    - Infraorder: Tipulomorpha
      - Family: Tipulidae – crane flies
      - Family: Cylindrotomidae
      - Family: Limoniidae
      - Family: Trichoceridae – winter crane flies
    - Infraorder: Psychodomorpha
      - Family: Psychodidae – moth and sand flies
    - Infraorder: Ptychopteromorpha
      - Family: Tanyderidae – primitive crane flies
      - Family: Ptychopteridae – phantom crane flies
    - Infraorder: Culicomorpha
      - Family: Dixidae – dixid midges
      - Family: Corethrellidae
      - Family: Chaoboridae – phantom midges
      - Family: Culicidae – mosquitoes
      - Family: Thaumaleidae – solitary midges
      - Family: Simuliidae – black flies
      - Family: Ceratopogonidae – biting midges
      - Family: Chironomidae – midges
    - Infraorder: Blephariceromorpha
      - Family: Nymphomyiidae – nymphomyiid midges
      - Family: Deuterophlebiidae – mountain midges
      - Family: Blephariceridae – net–winged midges
    - Infraorder: Bibionomorpha
      - Family: Axymyiidae – axymyiid flies
      - Family: Bibionidae – March flies
      - Family: Hesperinidae
      - Family: Pachyneuridae – pachneurid gnats
      - Family: Ditomyiidae
      - Family: Diadocidiidae
      - Family: Bolitophilidae
      - Family: Lygistorrhinidae
      - Family: Manotidae
      - Family: Keroplatidae
      - Family: Mycetophilidae – fungus gnats
      - Family: Sciaridae – dark-winged fungus gnats
      - Family: Cecidomyiidae – gall midges
      - Family: Perissommatidae
      - Family: Scatopsidae – minute black scavenger flies
      - Family: Canthyloscelididae
      - Family: Anisopodidae
  - Suborder: Brachycera
    - Infraorder: Xylophagomorpha
      - Family: Xylophagidae – xylophagid flies
    - Infraorder: Stratiomyomorpha
      - Family: Panthophthalmidae
      - Family: Xylomyidae – xylomyid flies
      - Family: Stratiomyidae – soldier flies
    - Infraorder: Tabanomorpha
      - Family: Rhagionidae – snipe flies
      - Family: Pelecorhynchidae – pelecorhynchid flies
      - Family: Athericidae – athericid flies
      - Family: Tabanidae – horse flies and deer flies
      - Family: Vermileonidae
      - Family: Acroceridae – small–headed flies
      - Family: Nemestrinidae – tangle-veined flies

Family: Bombyliidae – bee flies
Family: Apystomyiidae
Family: Mythicomyiidae
Family: Hilarimorphidae – hilarimorphid flies
Family: Therevidae – stiletto flies
Family: Scenopinidae – window flies
Family: Apioceridae – flower flies
Family: Mydidae – mydas flies
Family: Asilidae – robber flies
Family: Empididae – dance flies
Family: Dolichopodidae – long-legged flies
Infraorder: Cyclorrhapha (Muscomorpha)
Division: Aschiza
Family: Lonchopteridae – pointed-winged flies
Family: Opetiidae
Family: Platypezidae – flat-footed flies
Family: Ironomyiidae
Family: Sciadoceridae
Family: Phoridae – hump-backed flies
Family: Pipunculidae – big-headed flies
Family: Syrphidae – flower flies
Division: Schizophora
Section: Calyptrate
Family: Mormotomyiidae
Family: Scathophagidae – dung flies
Family: Anthomyiidae – anthomyiid flies
Family: Fanniidae
Family: Muscidae – house flies
Family: Glossinidae – tsetse flies
Family: Hippoboscidae – louse flies
Family: Calliphoridae – blow flies
Family: Sarcophagidae – flesh flies
Family: Rhinophoridae – rhinophorid flies
Family: Tachinidae – tachinid flies
Family: Oestridae – bot and warble flies
Section: Acalyptratae
Family: Cypselosomatidae – cypselosomatid flies
Family: Megamerinidae
Family: Micropezidae – stilt-legged flies
Family: Neriidae – nerid flies
Family: Diopsidae – diopsid flies
Family: Gobryidae
Family: Nothybidae
Family: Psilidae – rust flies
Family: Somatiidae
Family: Syringogastridae
Family: Tanypezidae – tanypezid flies
Family: Conopidae – thick–headed flies
Family: Lonchaeidae – lonchaeid flies
Family: Pallopteridae – pallopterid flies
Family: Piophilidae – piophilid flies
Family: Platystomatidae – platystomatid flies
Family: Pyrgotidae – light flies
Family: Richardiidae – Richardiid flies
Family: Tachiniscidae
Family: Tephritidae – fruit flies
Family: Ulidiidae
Family: Ctenostylidae
Family: Celyphidae
Family: Chamaemyiidae – chamaemyiid flies
Family: Eurychoromyiidae
Family: Lauxaniidae – lauxaniid flies
Family: Coelopidae – seaweed flies
Family: Dryomyzidae – dryomyzid flies
Family: Helosciomyzidae
Family: Ropalomeridae – ropalomerid flies
Family: Sciomyzidae – marsh flies
Family: Sepsidae – sepsid flies
Family: Acartophthalmidae – acartophthalmid flies
Family: Agromyzidae – leaf miners
Family: Anthomyzidae – anthomyzid flies
Family: Asteiidae – asteiid flies
Family: Aulacigastridae – aulacigastrid flies
Family: Clusiidae – clusiid flies
Family: Fergusoninidae
Family: Marginidae
Family: Neminidae
Family: Neurochaetidae
Family: Odiniidae – odiniid flies
Family: Opomyzidae – opomyzid flies
Family: Periscelididae – periscelidid flies
Family: Teratomyzidae
Family: Xenasteiidae
Family: Australimyzidae
Family: Braulidae – bee lice
Family: Canacidae – canacid flies
Family: Carnidae – carnid flies
Family: Chloropidae – frit flies

Family: Cryptochetidae – cryptochetid flies
Family: Milichiidae – milichiid flies
Family: Tethinidae – tethinid flies
Family: Chyromyidae – chyromyid flies
Family: Heleomyzidae – heleomyzid flies
Family: Sphaeroceridae – small dung flies
Family: Camillidae – camillid flies
Family: Curtonotidae – curtonotid flies
Family: Diastatidae – diastatid flies
Family: Drosophilidae – small fruit flies
Family: Ephydridae – shore flies

Characteristics

Adult flies normally bear a single pair of membraneous wings, though some are brachypterous, and a few are wingless. The second pair of wings is reduced to stubby, knobbed balancing organs called halteres. The eyes are large, and three ocelli usually are present. The antennae are variable, though flies in the suborder Nematocera tend to have long, multi-segmented antennae whereas those in suborder Brachycera tend to have short antennae, often with the third (and final) segment bearing a process called an arista or style. The arista is variable in appearance, but usually hair-like or plume-like. The mouthparts generally are of the sucking type, but some are piercing-sucking whereas others are lapping or sponging. The legs tend not to be unusual or specialized in form, though some are quite long. The terminal tarsal segment often bears a structure called the empodium between the tarsal claws, or pads called pulvilli at the base of the claws. The wings, which number only two if present, often have reduced venation. Most often the wings are colorless. The base of the wing often bears a small lobe called the alula, and basal to the alula may be two lobes, the calypteres. Flies display complete metamorphosis (holometabolous development). Larvae of the Brachycera are often called maggots, and usually headless, legless and worm-like, though those of the Nematocera have head capsules. The pupae of Nematocera are obtect, while those of Brachycera are coarctate. The number of instars tends to be 4–9 in the Nematocera, but only three in Brachycera.

Biology and Importance

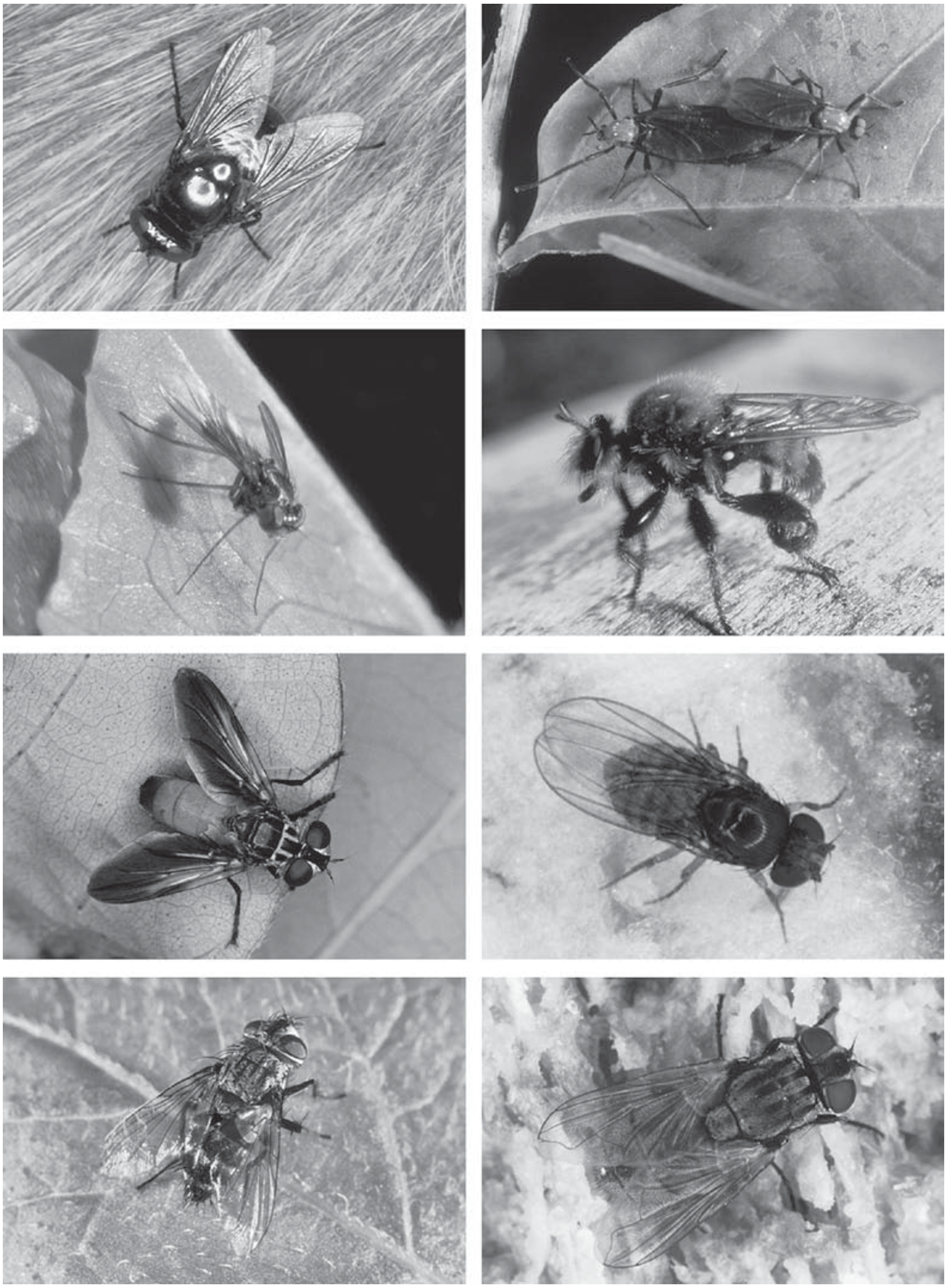
Adults flies generally are excellent fliers. Most of the adult flies feed on nectar or decaying organic matter. However, a considerable number are predatory or fed on blood of animals. Eggs are often deposited in wet habitats, though it ranges from aquatic to terrestrial. Soil and dung are often suitable. Larvae similarly are found in many habitats, and though many lack legs they may be quite mobile. Some attack living vertebrate animals, or recently killed animals.

Diptera is a very large and diverse group of insects, and many are of considerable importance. Some are beneficial, including the carrion and dung-feeding species (Figs. 59 and 60) such as blow flies (Calliphoridae) that quickly assist in the degradation of animal bodies and fecal matter, the predatory species such as flower flies (Syrphidae) that feed on other insects such as aphids, and the parasitoids such as tachinid flies (Tachinidae) that parasitize other insects such as caterpillars. Some flower-feeding species assist with pollination.

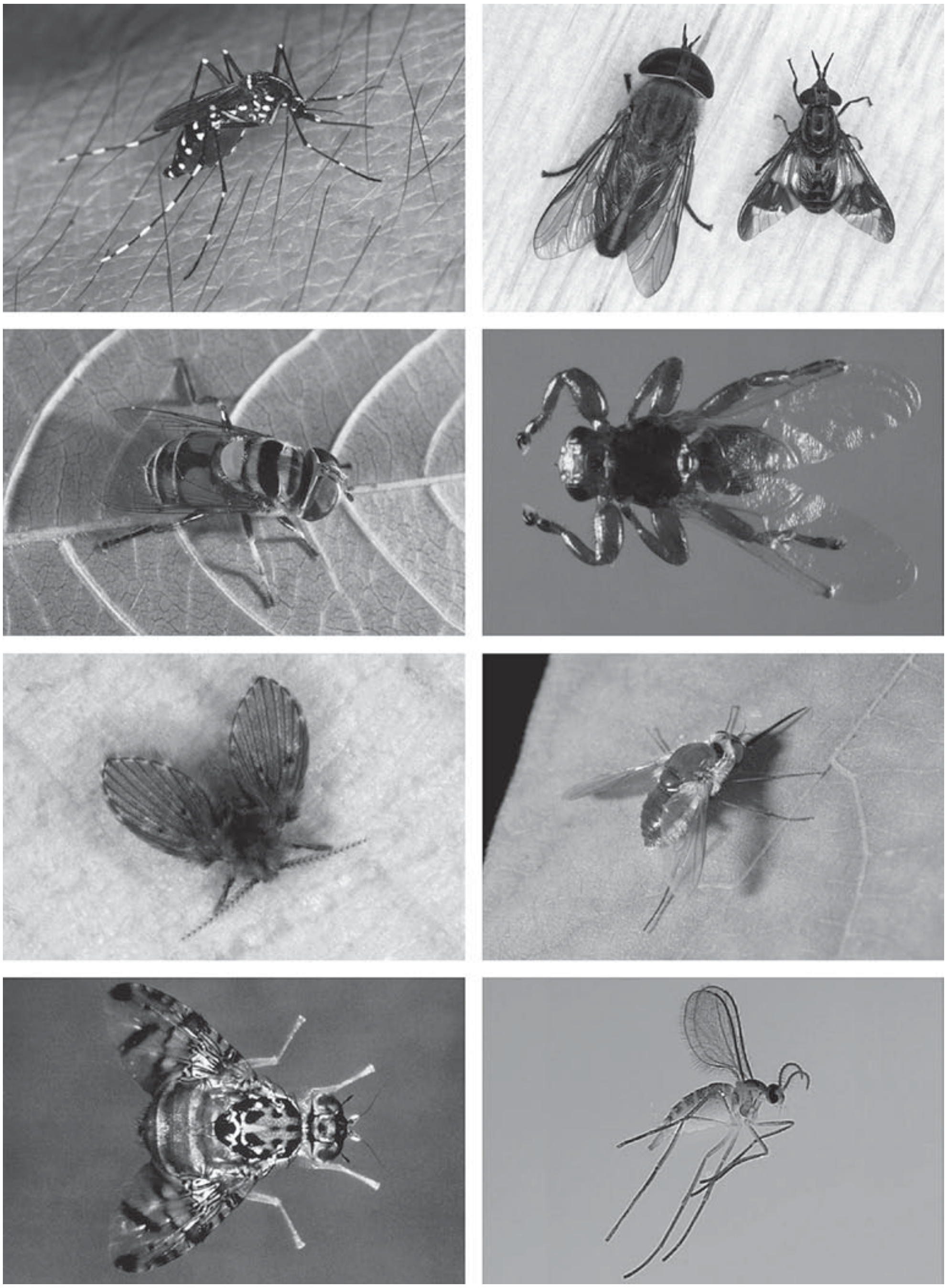
Flies are better known as pests, and often are associated with pestilence. Some feed directly on plants, including root maggots (Anthomyiidae), large fruit flies (Tephritidae), and leaf miners (Agromyzidae). Animal-biting flies include deer flies (Tabanidae), black flies (Simuliidae), tsetse flies (Glossinidae) and mosquitoes (Culicidae). The latter flies are the most important because they are widespread, and efficient vectors of many diseases to humans.

Important Taxa

Following are brief profiles of some of the largest and most important families of flies. Many additional taxa could be included.



Flies (Diptera), Figure 59 **Representatives of the order Diptera. *Top row, left*: green bottle fly, *Phaenica sericata* (family Calliphoridae) (photo, J.L. Castner); *top row, right*: lovebugs, *Plecia nearctica* (Bibionidae) (photo, J.L. Capinera); *second row*, *left:* a longlegged fly, (Dolicopodidae) (photo, J.L. Capinera); *second row*, *right*: a robber fly (Asilidae) (photo, Whitney Cranshaw); *third row*, *left*: feather-legged fly, *Trichopoda pennipes* (Tachinidae) (photo, J.L. Castner); *third row*, *right*: a small fruit (vinegar) fly (Drosophilidae) (photo, J.L. Castner); *bottom row, left:* a tachinid fly, *Myiopharus doryphorae* (Tachinidae) (photo, J.L. Capinera); *bottom row*, *right*: house fly, *Musca domestica* (Muscidae) (photo, J.L. Castner).**



Flies (Diptera), Figure 60 **Representatives of the family Diptera. *Top row, left*: Asian tiger mosquito, *Aedes albopictus* (family Culicidae) (photo, J.L. Castner); *top row*, *right*: a horse fly, *Tabanus* sp. (*left*) and a deer fly, *Chrysops* sp. (*right*) (Tabanidae) (photo, J.L. Castner); *second row*, *left*: a flower fly, *Palpada* sp. (Syrphidae) (photo, J.L. Capinera); *second row, right*: a louse fly, *Lipoptena mazamae* (Hippoboscidae) (photo, L.J. Buss); *third row*, *left*: a moth fly, *Psychoda* sp. (Psychodidae) (photo, J.L. Castner); *third row*, right: a bee fly (Bombyliidae) (photo, J.L. Capinera); *bottom row, left*: Mediterranean fruit fly, *Ceratitus capitata* (Tephritidae) (photo, J.L. Castner); *bottom row, right*, blueberry gall midge, *Dasineura oxycoccana* (Cecidomyiidae) (photo, Erin Finn).**

Crane Flies (Tipulidae)

These long-legged flies are also called daddy-long-legs (some spiders also bear this common name), mosquito hawks and giant mosquitoes (both misnomers as they neither feed on mosquitoes nor feed like mosquitoes). They are some of the largest of the Nematocera, but usually quite harmless. The large size and long legs (easily detached by handling) usually distinguishes them immediately. The adults are not blood feeders. Some plant root and foliage-feeding feeding larvae, often called leatherjackets, are elongate, possess a sunken head, and are relatively amorphous. Few crane flies are damaging to plants. This is the largest family of flies, with about 15,000 species described from around the world.

Mosquitoes (Culicidae)

Mosquitoes are probably the most important insects. About 1,600 species are known. These slender flies possess long piercing-sucking mouthparts. Females, but not males, are commonly blood feeders. Both accept nectar. Larvae are aquatic filter-feeders, often feeding on algae and other particles, though some are carnivorous. Pupae also are aquatic, and are active. Water is the key to mosquito abundance. Temporary water, lacking predaceous insects and fish, is often a prerequisite for mosquito abundance. Eggs are deposited in the water, or on soil that is likely to be flooded. Snow melt, unusually heavy rainfall, and abnormally high tides often provide the temporary water that allows mosquitoes to breed and reach high numbers. Mosquitoes can cause injury by nuisance biting, by blood removal, and by transmission of diseases, particularly viruses and protozoa.. Insecticides have been used extensively to protect against mosquitoes and mosquito-transmitted diseases, and resistance to insecticides is a problem in some areas. Species richness is greatest in the tropics, but abundance is often greatest in arctic regions.

Black Flies (Simuliidae)

These are stout-bodied flies with short legs. They also are called buffalo gnats. The mandibles are a piercing type, but not as elongate as in mosquitoes. The females of some species are blood feeders, and sometimes black flies are a severe problem for people and animals. They are damaging because of their extremely high numbers, their tendency to bite viciously, and their tendency to penetrate orifices of the body such as nostrils, ears, and eye margins. Their feeding can cause the death of birds (especially poultry), and some transmit worms causing filariasis. The larvae are aquatic, and require swiftly flowing, clean water for their development. Ironically, when streams and rivers are cleansed of pollutants, frequently there is a upsurge of black fly problems, making the area less than pleasant during the spring months. About 1,500 species are known world-wide.

Biting Midges (Ceratopogonidae)

These small insects are also known as sand flies, no-see-ums and punkies. Despite their small size, they are vicious biters, often proving to be a serious nuisance along seashores, rivers, and lakes. Some areas are virtually uninhabitable during periods of the year if these midges are not managed. They feed on both vertebrate and invertebrate animals, including other insects. Larvae are semiaquatic, usually living in mud and decaying vegetation. The most important of these midges from the human perspective are in the genus *Culicoides*.

Fungus Gnats (Mycetophilidae)

Fungus gnats tend to be small insects, rather delicate, and widespread. About 3,000 species have been described. In adults, the antennae are long (12–17 segments) and the coxae are well developed. In larvae, the body is worm-like usually whitish with a small, dark sclerotized head, and relatively free of hairs and appendages. The larvae often live in damp places such as decaying organic matter or fungi; adults favor damp, shaded habitats. They tend to be gregarious, and unjustified damage to fruit and vegetables is sometimes attributed to these flies when, in fact, they are attracted to fungus-infected organic matter. Some fungus gnats are serious pests, however, and damage to mushrooms and the roots of potted plants is common. Fungus gnats are unremarkable in appearance, often muted in color

Gall Midges (Cecidomyiidae)

Gall midges are very small, delicate flies with long antennae. About 4,000 species are known. The wings have simplified venation. The larvae often feed on plants, inducing the formation of abnormal growth called galls. The galls provide shelter, and enhanced nutrition, for the larvae. These galls often are unique in shape, and symptomatic of the species. Some gall midges are very damaging, including Hessian fly, *Mayetiola destructor*, sorghum midge, *Contarinia sorghicola*, and chrysanthemum gall midge, *Diarthronomyia chrysanthemi*. Not all members of the family form galls, and some feed on detritus and a few are important predators of other insects.

Horse or Deer Flies (Tabanidae)

Tabanids have acquired many common names, including horse flies, deer flies, yellow flies, stouts, breezeflies, dunflies and clegs. They are heavy-bodied, flattened, and of moderate to large in size. The eyes are very large. The third antennal segment lacks an arista (style). The proboscis projects, and in the female it is used to pierce animal flesh and feed on blood. Males feed on honeydew and on flowers. Tabanids are swift flyers, and often trouble livestock and people. Though eggs are deposited on foliage, the larvae are found in moist soil and decaying debris, where they prey on small animals such as worms and other insects. About 3,500 species are known.

Robber Flies (Asilidae)

The flies of this large family are moderate to large-sized, bristly or densely hairy, and with long, stout legs. The proboscis protrudes, and is particularly hairy. Adults are predatory, sometimes capturing flying insects. The larvae live in the soil and feed on other insects, or are scavengers. Although often considered to be beneficial because they feed on other insects, sometimes they inflict heavy predation on other flies that are parasitoids of grasshoppers, thereby interfering with biological control. About 4,000 species are known.

Bee Flies (Bombyliidae)

Bee flies are often densely pubescent, with long, thin legs and a projecting proboscis. This appearance, plus the hovering behavior of the adults, accounts for the common name. The adults scatter their eggs about the soil. The larvae are parasitoids, attacking bees, wasps, some caterpillars, and grasshopper eggs. The young larvae display hypermetamorphosis, initially actively seeking prey, but then settling down once food is located. About 3,000 species have been described world-wide.

Flower or Hover Flies (Syrphidae)

These tend to be colorful flies, and moderate to large in size. The black and yellow coloration of many species causes them to be confused with bees or wasps. The adults are associated with flowers, where they hover in the air or feed, and they often are quite important as pollinators of flowers. The larvae are variable in their feeding habits; some feed on plants, others on detritus or in aquatic habitats, and many are important as predators of insects. Some are beneficial, feeding on aphids, scale insects and other pests, but others feed within the nests of social insects. A comprehensive treatment of this family has never been published, so although it is certainly one of the largest families of Diptera, with over 5,000 species described, their diversity remains uncertain.

Small Fruit Flies (Drosophilidae)

These small flies are also known as vinegar flies and pomace flies. About 2,800 species are known world-wide. They are often associated with decay, and apparently are attracted to the by-products of fermentation. Because they are easily reared, with rapid generation time, they (particularly *Drosophila melanogaster*) have become favorites for laboratory genetic studies. However, their biology is quite variable, and their feeding habits also include predation, sap and nectar feeding, and leaf mining in addition to feeding on decaying materials. Though commonly emerging from fruit and vegetables, few species are capable of direct damage to plants. Rather, most take advantage of openings or breaks in the fruit surface caused by physiological disorders, cultivation, and harvesting to gain entry. Most species are tropical.

Warble or Bot Flies (Oestridae)

This is a comparatively small family of flies, but it is important because larvae are endoparasites of animals, including humans and livestock. The larvae have swollen bodies and bear numerous stout spines encircling the body. The adults are stout and hover bee-like about their hosts, often causing great excitement or alarm among livestock. Some flies develop within the nasal and pharyngeal cavities, but others migrate through the body, completing their development on the back of the host. The human warble, *Dermatobia hominis*, seizes mosquitoes and deposits its egg on the mosquito; the egg hatches when the mosquito bites a human, and the warble fly larva then penetrates the host at the site of the mosquito bite.

Blow Flies (Calliphoridae)

Blow flies are medium to large in size, and usually metallic blue or green in color. This is a fairly large family, widely distributed, and often quite abundant. They often are scavengers, and become apparent when a freshly killed animal becomes available. Many species lay their eggs on fresh carcasses, with the larvae feeding on the decaying tissues, and contributing significantly to the rapid degradation of carrion. Some, such as the screwworm fly *Cochyliomyia hominivorax*, attack living tissue and can be serious livestock pests. In Australia, sheep blow flies in the genera *Calliphora* and *Lucilia* are severe problems for the livestock industry. Blow flies also are capable of causing cutaneous myiasis, and infesting the nasal cavity or the intestine of living animals. Others feed on animal excrement or similar materials. Some calliphorids are parasitoids of land snails, or predators of grasshopper eggs, and others attack frogs, toads and young birds. The cluster fly, *Pollenia rudis*, attacks earthworms and sometimes becomes so abundant as to be a nuisance in buildings where they collect on ceilings or at windows.

Tachinid Flies (Tachinidae)

This large family of about 8,200 species is relatively indistinct morphologically, but adults tends to be bristly. They are very important as endoparasitoids of other insects, particularly caterpillars, but also sawflies, beetle larvae, orthopterans, and hemipterans. Some species are specific, while others have a very broad host range. They scatter their eggs where they may be consumed, or deposit their eggs on their hosts. Some appear to deposit larvae, but these are actually eggs that hatch immediately upon deposition. Tachinids also attack silkworm larvae, so despite being largely beneficial, at least a few can be considered to be pest.

Leaf Miners (Agromyzidae)

This is a large family of small flies, consisting of about 2,500 flies world-wide. The larvae are miners of leaf tissue and stems, though some are gall formers. The larvae often are flattened, and create a mine of increasing size as they mature. Pupation can occur within the mine, on the leaf surface, or in the soil. Adults often feed at oviposition/feeding punctures. Some species, particularly those in the genus *Liriomyza*, have been the target of extensive insecticide use. As a result, they have evolved resistance to most insecticides. Such flies can become very numerous and damaging when insecticides are used inappropriately. Wasp parasitoids usually can keep leaf miners at low to moderate levels in the absence of insecticides, which disrupt the parasitoids more than the flies.

Large Fruit Flies (Tephritidae)

The large fruit flies often are colorful, and have well-marked wings; the pattern may be diagnostic. Many are important plant pests, most because the larvae burrow into fruit, flowers and stems. Among the damaging species are Mediterranean fruit fly, *Ceratis capitata*, melon fly, *Dacus cucurbitae*, and apple maggot, *Rhagoletis pomonella*. Some of these flies have been relocated accidentally to fruit-growing areas around the world, where they cause great damage to fruit. In other cases they cause loss indirectly because produce is quarantined and cannot be shipped to potential markets. Considerable success has been attained in the suppression and eradication of these fruit flies by using sterile male release techniques and area-wide management. Although the fruit-infesting flies are best known, they comprise only a small proportion of the tephritids, with the majority feeding on flowers. About 5,000 species are known.

► Biting Midges
► Black Flies
► Chironomid as a Nuisance and of Medical Importance
► Crane Flies
► Fruit Flies
► Horse Flies and Deer Flies
► Mechanical Protection of Humans from Arthropod Attacks and Bites
► Mosquitoes
► Mosquitoes as Vectors of Viral Pathogens
► Myiasis Pathogen Transmission by Arthropods, Repellents of Biting Flies
► Tsetse Flies
► Sugar-Feeding in Blood-Feeding Flies

References

Arnett RH Jr (2000) American insects, 2nd edn. CRC Press, Boca Raton, FL, 1003 pp

Evenhuis NL (ed) Catalog of the Diptera of the Australasian and Oceanian regions. http://hbs.bishopmuseum.org/aocat/(accessed 12 April 2008)

McAlpine JF (ed) 1981–1989. Manual of Nearctic Diptera, Volumes 1–3. Agriculture Canada Research Branch, Monographs 27, 28, and 32

Oldroyd H 1964 The natural history of flies. Weidenfeld and Nicolson, London. 324 pp

Stehr FW 1991 Immature insects, Vol. 2. Kendall/Hunt Publishing, Dubuque, Iowa. 974 pp

Flocculant

This term is applied to describe items that resemble soft flakes. Infestation by scale insects, mealybugs, whiteflies, and aphids that extrude wooly, waxy material are sometimes described as flocculant, and the waxy material called flocculence.

Florida Red Scale, *Chrysomphalus aonidum* (L.) (Hemiptera: Diaspididae)

These insects damage citrus foliage in North America.

► Citrus Pests and their Management

Floristic Kingdoms

The biogeographic distribution of unlike plants. A system of displaying the occurrence of indigenous flora, corresponding (in principle) to the zoogeographic realms, and separated by water or mountains. The principal foci of distribution (called kingdoms) are Boreal (most of North America, Europe, and northern Asia), Neotropical (Mexico and most of South America), Paleotropical (most of Africa, India, Southeast Asia), Australian (Australia), South African (the southwestern region of Africa), and Antarctic (Antarctica and the southernmost tip of South America).

Flour Beetle

This refers to *Tribolium* spp. (Coleoptera: Tenebrionidae). They are common pests of grain and flour.

► Stored Grain and Flour Insects

Flowable

A pesticide formulation in which finely divided dry particles of toxicant are suspended in a liquid carrier.

Flower Beetles

Members of the subfamily Cetoniinae, family Scarabaeidae (order Coleoptera).

► Beetles

Flower Flies

Members of the family Syrphidae (order Diptera).

► Flies

Flower Moths (Lepidoptera: Scythrididae)

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Flower moths, family Scythrididae, total about 523 species worldwide, but mostly known from Europe. The family is part of the superfamily Gelechioidea in the section Tineina, subsection Tineina, of the division Ditrysia. Adults small (5–22 mm wingspan), with head smooth-scaled; haustellum scaled; labial palpi recurved; maxillary palpi 4-segmented. Wings (Fig. 61) elongated, with long fringes. Maculation usually rather dark with various spots; some have metallic-iridescence and a few are more colorful. Adults are diurnal but some may be crepuscular. Larvae are skeletonizers on leaves, buds, flowers, hiding under webbings. Brachypterous species are known which make long silken tubes. Many plant families are used as hosts, plus some on lichens and mosses, but particularly Chenopodiaceae, Crassulaceae, Compositae, and Gramineae.

Flower Moths (Lepidoptera: Scythrididae), **Figure 61** **Example of flower moths (Scythrididae), *Scythris tributella* (Zeller) from Italy.**

References

Bengtsson BA (1984) The Scythrididae (Lepidoptera) of northern Europe. E. J. Brill, Leiden; Scandanavian Science Press, Copenhagen, 117 pp (In Fauna Entomologica Scandinavica, vol 13)

Bengtsson BA (1997) Scythrididae. In: Microlepidoptera of Europe, vol 2. Apollo Books, Stenstrup, 301 pp (14 pl)

Jäckh E (1977–78) Bearbeitung der Gattung *Scythris* Hübner (Lepidoptera, Scythrididae). Deutsche Entomologische Zeitschrift 24:261–271 (1977); 25:71–89 (1978); Zeitschrift der Arbeitsgemeinschaft österreichischer Entomologen 29:81–84 (1978); Bolletino del Museo Civico Storia Naturale 5:1–14 (1978)

Landry J-F (1991) Systematics of Nearctic Scythrididae (Lepidoptera: Gelechioidea): phylogeny and classification of supraspecific taxa, with a review of described species. Mem Entomol Soc Can 160:1–341

Passerin d' Entrèves P (1974–95) Revisione degli Scitrididi (Lepidoptera, Scythrididae) palearctici. Bolletino dell' Istituto di Museo Zoologica dell' Universita di Torino, 1974(7):45–56; 1976(3):27–70; 1977(5):57–76; 1979(3):83–90; 1980(5):41–60; Nota Lepidopterologica 18:139–159 (1995)

Flower Strips as Ecological Compensation Areas for Pest Management

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There are many practices designed to make agriculture more sustainable, reduce agrochemical use, and enhance biodiversity in agricultural ecosystems. Organic farming, crop rotation, small-scale fields, and maintenance of natural areas between agroecosystems are some examples. The latter, sometimes referred to as ecological compensation areas, consists of separate or interconnected fields that form buffer zones. Ecological compensation zones act as refuge areas and/or dispersal centers and offer many species adequate niches, compensating, at least partly, for the negative effects of agriculture.

A significant decrease in the use of fertilizers and pesticides occurred as a result of ecological compensation areas in Europe. For example, under integrated production or organic farming systems in Switzerland, farmers have to set aside at least 7% of their farmland as ecological compensation areas (e.g., meadows, hedgerows, traditional orchards, and wild flower strips).

Ecological compensation areas in agriculture not only enhance biodiversity of rare and threatened species, but also support biological control of agricultural pests by increasing the diversity and abundance of beneficial arthropods. This is of particular importance for integrated production and biological farming because almost all spiders and predatory beetles active in crop fields in spring and summer depend on semi-natural habitats for overwintering.

Flower Strips

Flower strips (also known as wild flower strips, sown flower strips or sown weed strips) are a type of ecological compensation areas. Flower strips have found particular favor in central Europe, where they were introduced to increase biodiversity in intensively used arable land. Although flower strips, like the agricultural landscape, are artificial habitats, they have many advantages and offer good opportunities to combine agricultural use and nature conservation. These strips are highly attractive for many species of insects, and increase biodiversity. Even rare species can occur in intensively managed agricultural landscape if the minimum habitat area they require is available and their specific ecological requirements can be fulfilled using a strip-management program. Increasing biodiversity is the primary function of flower strips, and they are proven to enhance the species number of several beneficial arthropod groups. Flower strips, ideally, should occupy at least 5–10% of an agricultural landscape.

Establishment of Flower Strips

Flower strips usually are planted to a width of 3–8 m and sown with native weed-seed mixtures (Fig. 62). The strips are situated at a border of a

Flower Strips as Ecological Compensation Areas for Pest Management, Figure 62 **Photo showing a flower strip sown inside a wheat field in Switzerland (courtesy of Dr. Dieter Ramseier, Swiss Federal Institute of Technology, Zurich, Switzerland).**

field or divide large fields into small parts so that the distance between strips does not exceed 50–100 m. The length of the strip, however, depends on the field length and may be in the range of several hundred meters. Flower strips should start or end at other ecological compensation areas such as road sides, field margins, hedges, forest remnants, dry slopes, and so on. Thus, the total system of flower strips forms a network of ecological compensation areas which connects several types of natural, semi-natural, and artificial habitats. The fields are, therefore, embedded into this network and profit from its high diversity.

Seed Mixtures

The composition of the mixtures is based on the results of a long screening process in which specific characters of over 100 species of wild flowers and cultivated plants have been considered. Seed mixtures for flower strips should be chosen based on properties such as insect diversity and abundance of beneficial insect species in patches of the plant species, length of flowering period, survival capacity in agricultural soils, longevity in a complex plant mixture, the lesser tendency to dispersal into adjacent fields, and seed costs. A good technique to reduce the seed costs is by allowing a maximum amount of natural reseeding of weeds.

The recommended seed mixtures currently used for establishment of flower strips in Switzerland include a complex mixture of wild flowers and cultivated plants and are available from several commercial seed distributors (Table 4). The selected species cover a wide range of low, middle sized, and tall plants. They include early to late flowering plants as well as annuals, biennials, and perennials. Since the commercial production of wild flower seeds is not inexpensive there is a particular need to reduce the costs of the wild flower seed mixture. Much simpler seed mixtures also have been tested consisting of only one to four non-crop species (mixtures of clover and grass, *Phacelia*, sunflowers, etc.), but their usefulness is not yet established.

Maintenance

Maintenance of the vegetation mix, which consists of both the multispecies seed mixture and additional wild species initiated by the seed reservoir in the soil, is a difficult task. Sown strips maintain a high diversity at least in the first 3 years, but weedy grasses may become more common under some circumstances. Problem weeds (e.g., *Cirsium* sp., *Rumex* sp.) may need to be controlled by individual treatments of the plants. To slow down succession towards grasses and to prevent the dominance of only a few species or the appearance of woody plants, it may be desirable to alternate mowing half the strip every second year. In the United Kingdom, flower strips (used as field margin strips) are drilled with a mixture of wild flowers and managed using herbicide applications and by cutting to aid plant establishment. In Switzerland, however, herbicides are not often used.

When these habitats become less and less diverse some kind of regeneration technique must be applied. This may be accomplished by some kind of a minimum soil treatment or by complete plowing followed by additional, or new, sowing.

Flower Strips as Ecological Compensation Areas for Pest Management, Table 4 An example of official seed mixtures used for sowing flower strips in Swiss agriculture

Plant species	Federal Research Station for Agroecology and Agriculture – Mixture 1997	University of Berne – Mixture 1997
Achillea millefolium	□	O
Agrostemma githago	□□	□
Anchusa arvensis	O*	
Anthemis tinctoria	□*	□
Arctium lappa		O
Carum carvi	□	
Centaurea cyanus	□□	□
Centaurea jacea	□	□
Chrysanthemum leucanthemum	□□	□
Cichorium intybus	□	□
Daucus carota	□	□
Dipsacus silvestris	O	O
Echium vulgare	□	□
Hypericum perforatum	□	□
Fagopyrum exdulentum	□□	□□□
Foeniculum vulgare		O
Legousia speculum-arvensis		O
Lythrum salicaria	□*	
Malva moschata	O	
Malva silvestris	□	□
Medicago lupulina		□
Melilotus alba		O
Melilotus officinalis		O
Oenothera biennis		□
Onobrychis vicaefolia		□
Origanum vulgare	□*	□
Papaver rhoeas	□□	□
Pastinaca sativa	□	O
Picris hieracioides	□*	
Reseda luteola	□*	
Silene alba	□	□
Sinapis alba		□
Stachys annua	□*	
Tanacetum vulgare	O	O
Tragopogon orientalis	□	

Flower Strips as Ecological Compensation Areas for Pest Management, Table 4 An example of official seed mixtures used for sowing flower strips in Swiss agriculture (Continued)

Plant species	Federal Research Station for Agroecology and Agriculture – Mixture 1997	University of Berne – Mixture 1997
Verbascum densiflorum	□	□
Verbascum lychnitis	□	
Amount of Seed (kg/ha)	10.-	20.-
Price per kg	CHF234.90	CHF66.30
Price per ha	CHF2349.–	CHF1326. –

Availability of seeds in mixture: O = trace; □= low; □□= frequent; □□□= dominant; * = in addition to the standard mixture.

Flower Strips as Ecological Compensation Areas for Pest Management, Table 5 The extent of penetration of different carabid species into wheat field at different distances from the field margin (after Welling et al., 1994, integrierte Pflanzenproduktion II. Research Report)

Carabid species	No. collected from the field margin	No. collected in the field with regard to distance from the field margin			
		50 m	100 m	150 m	200 m
Carabus granulatus L.	234	12	17	6	5
Pterostichus melanarius Illiger	452	2	2	1	1
Platynus dorsalis Pont.	4497	11	5	1	1
Poecilus cupreus L.	947	32	16	1	0
Carabus auratus L.	47	3	8	0	0
Harpalus aeneus F.	522	3	0	0	0
Loricera pilicornis F.	268	4	0	0	0

The objective, in the long-term, is to attain a steady state between young and old sown weed strips within a landscape. This provides the type of mosaic in which landscapes naturally regenerate and represents an important feature which stabilizes agricultural landscapes.

Flower Strips and Farmers

Organic farmers of Switzerland consider the main advantage of ecological compensation areas (including flower strips) to be the increase in biodiversity. The main disadvantage is believed to be the increase in pests. Other farmers consider the main advantage to be protection against soil erosion and the disadvantages to be the loss of production area and the limitation of free management.

The concept of flower strips has been developed primarily for use where increase of productivity is not a major concern. Because agricultural yields in many areas already are high, actual efforts should aim not at increasing the production, but at stabilizing the yield with respect to an environmentally friendly and sustainable practice.

Weeds

In Switzerland, the density of sown plants often is not high enough to suppress problematic weeds (i.e., *Chenopodium album*, *C. polyspermum*, *Galium aparine*, *Galeopsis tetrahit*, *Polygonum lapathifolium*, *L. persicaria*, *Raphanus raphanistrum* and *Sinapis arvensis*). The suppression of root-propagated weeds (i.e., *Cirsium arvense*, *Convolvulus arvensis* and *Agropyron repens* [*Elymus repens*]) as well as *Rumex obtusifolius* and *Galium aparine* is generally insufficient. A continuous decline in the number of weed species from the 1st to the 4th year, a maximum diversity of flowers in the 2nd year and continuous increase in the percentage of grass occurs on the majority of sites. A dominance of *Anthemis tinctoria*, *Centaurea jacea* and *Leucanthemum vulgare* in the 2nd, and *Achillea millefolium* and *Tanacetum vulgare* in the 3rd year can be observed. In addition, yields in neighbouring crops may be reduced up to a total loss within 2 m distance of the strips due to bad fertilizer spread, insufficient herbicide efficacy, extensive tillage and slug damage. There is neither a positive nor negative yield effect measurable further away in the crop. Weed problems commonly noted by farmers include *Cirsium arvense* (the most serious weed). *Rumex obtusifolius*, *Agropyron repens* [*Elymus repens*] and *Convolvulus arvensis*. The sown flower species are not considered to be problems. The acceptance of ecological compensation area concept is reduced considerably when farmers encounter weed problems.

Slug species (such as *Arion lusitanicus* and *Deroceras reticulatum*) can cause damage adjacent to flower strips in Switzerland and France. Yield loss in the edge rows of the crop has been observed in maize, wheat, peas, and sugarbeet.

Response of Beneficial Insects to Flower Strips

Many weeds attract beneficial insects in high numbers, as pollinators, on green parts of the plants, and overwintering on or in dead plant structures or in the soil below the plants.

For instance, a study conducted in Germany revealed that the flower strips adjacent to wheat fields serve as habitats for several weeds and animals, including beneficial arthropods. Aphids were the most important pest in cereals, and carabids and epigeic spiders were important polyphagous predators. In boundary strips the spectrum of species of both carabids and spiders was more diverse compared to the adjacent wheat fields. In herbicide-free crop edges with a high amount of arable weeds, 10–60% more carabid and spider species were found as in the sprayed control edges. When comparing wheat fields with "rich" marginal structures on one side (broad, diverse boundary strips and hedges) and "poor" marginal structures on the opposite side (narrow, monotone boundary strips), the infestation with cereal aphids was up to 50% lower on the "rich" side. This reduction of aphids was not only at the edges, but also up to 10–20 m inside the fields. By means of mark/recapture-experiments it was shown that most of the carabid species could immigrate 100–150 m into the fields. However, a great number of carabids remained inside wild vegetation. Thus, carabids are mainly retained inside the strips and their penetration into field in a right time and in a sufficient number is doubtful (Table 5).

Similarly, the flower strips offer an haven for attraction and accumulation of syrphids and bees important in pollination of crop plants. For instance, Swiss researchers examined the attractiveness of flower strips towards hoverflies (Diptera: Syrphidae), butterflies (Lepidoptera: Rhopalocera), wild bees (Hymenoptera: Apoidea) and thread-waisted wasps (Hymenoptera: Sphecidae). Insects were quantified visually and/or caught with yellow pan traps. Visual observation indicated that the strips hosted the largest number of these species. In all groups of flower-visiting insects, numbers of species and individuals were higher in the flower strips than in the fields. Interestingly, twelve percent of all species of these insect groups belonged to endangered species. Thus, flower strips provided suitable shelter and nutritional conditions for flower-visiting insects and were therefore very attractive habitats for all insect groups investigated in this study.

Economic Impact of Flower Strips

Wingeier reporting on economic impact of flower strips sown into fields, considers the strips as a method of stabilizing agricultural ecosystems and of reducing the need for pesticides. These strips remain intact throughout the year whereas the crop is harvested at the usual time. His experiments on the economic impact of flower strips were conducted in the Swiss lakes regions (Grosses Moos) in 12 winter wheat, 6 winter barley, 4 winter oat and 4 rye fields in summer 1990. No significant correlations were found between the distance of the strip from the field border and crop yield for any of the cereals studied. Flower strips entailed both an increase and a reduction of field maintenance operations: on the one hand, the strips need to be managed (to prevent excess proliferation), but on the other, savings arise from the smaller field area for cultivation (an area reduction of about 1.2% for 5-ha fields and 2.1% for 1-ha fields with a single 1.5-m wide strip). No adverse effects of flower strips on the grain quality of adjacent wheat plants were noted and only a small increase was determined in the duration of cropping operations. Nevertheless, with ecologically desirable strip distances of 24 m and strip widths of 1.5 m, yield penalties of about 4.5% were recorded for both 1-ha and 5-ha fields with 2 and 4 strips, respectively. These yield reductions would have to be compensated by state subsidies.

Although the establishment of flower strips in an agricultural landscape acts as a haven for the natural enemies (as well as for the pests, e.g., slugs), we cannot overlook their great potential as a sink for accumulation of beneficial insects (e.g., ground beetles) as well as important pollinators. Therefore, these strips can only be of benefit to agroecosystems when they can enhance dispersal of beneficial agents, at the right time and at a significantly high number, into the field.

► Cultural Control of Insect Pests
► Conservation Biological Control

References

Frank T (1998) Attractiveness of sown weed strips on hoverflies (Syrphidae, Diptera), butterflies (Rhopalocera, Lepidoptera), wild bees (Apoidea, Hymenoptera) and thread-waisted wasps (Sphecidae, Hymenoptera). Mitteilungen der Schweizerischen Entomologischen Gesellschaft 71:11–20

Frank T (1999) Density of adult hoverflies (Dipt., Syrphidae) in sown weed strips and adjacent fields. J Appl Entomol 123:351–355

Friedli J, Frank T (1998) Reduced applications of metaldehyde pellets for reliable control of the slug pests *Arion lusitanicus* and *Deroceras reticulatum* in oilseed rape adjacent to sown wildflower strips. J Appl Ecol 35:504–513

Letourneau DK (1998) Conservation biology: lessons for conserving natural enemies. In: Barbosa P (ed) Conservation biological control. Academic Press, San Diego, CA, pp 9–38, 133–153

Marshall EJP, Moonen C, Cooper A (1997) Patterns of plant colonisation in extended field margin strips and their implications for nature conservation. In: Species dispersal and land use processes. Proceedings of the Sixth Annual IALE (UK) Conference, Ulster, Northern Ireland, United Kingdom, 9–11 September 1997. IALE (UK), Aberdeen, Scotland, UK, pp 221–228

Nentwig W, Frank T, Lethmayer C (1998) Sown weed strips: artificial ecological compensation areas as an important tool in conservation biological control. In: Barbosa P (ed) Conservation biological control. Academic Press, San Diego, CA, pp 133–153

Wingeier T (1992) Economic impact of weed strips sown into fields. Agrarokologie 2:1–97 (in German)

Flower Thrips, *Frankliniella* spp. (Thysanoptera: Thripidae)

These insects can interfere with fruit production.

► Small Fruit Pests and their Management

Flower-Loving Flies

Members of the family Apioceridae (order Diptera).

► Flies

Flutter Flies

Members of the family Pallopteridae (order Diptera).

► Flies

Fly Paper

Sticky strips of paper use to capture flies. Adult flies tend to alight on elevated areas where they can obtain a good view of their surroundings. Use of fly paper takes advantage of this behavior; by hanging fly paper from the ceiling or other elevated locations, when flies land they adhere to the sticky paper. The fly paper is often yellow in color, which may provide a visual stimulus for landing, though this is not necessary. Once commonly used in both indoor and outdoor markets, barns, and milking parlors, they largely have been replaced by black-light, electrocuting grid traps where electric power is available.

► Traps for Capturing Insects

Focus (pl., foci)

In epidemiology, the area where the disease is prevalent.

Foliar Application

Application of a pesticide to leaves or plants.

Folivory

Arthropods that feed on foliage, though sometimes this is more narrowly defined to mean insects that chew on foliage, thereby excluding sap-sucking arthropods. Such arthropods are said to be folivorous or folivores.

► Food Habits of Insects
► Phytophagy
► Herbivory

Follicular Epithelium

A layer of epithelial cells that surround the oocyte.

Food-Based Poisoned Baits for Insect Control

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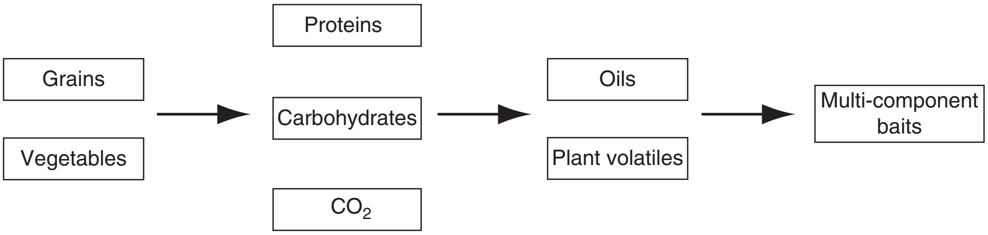
Food-based baits are an effective and selective method of insect control. Typically, a bait consists of a base material called a carrier (often grain or animal protein) plus a toxicant (most often insecticides such as organophosphates, carbamates or pyrethroids) and sometimes an additive (usually oil, sugar or water) to increase attractiveness. The toxicant part of a bait can also be biological rather than chemical. Examples of biological toxicants are *Bacillus thuringiensis* (Bt), parasitic nematodes and fungi. Many baits are not highly attractive to the insect, but instead function as an arrestant. The insect is not attracted to the base material, but finds it palatable and will eat it when encountered. Therefore, baits are distributed by either ground or aerial broadcast application in order to ensure broad dispersion. Toxic baits are often environmentally friendly, inexpensive methods of insect control. Little or no insecticide drift is associated with baits, and there is minimal insecticide residue on crops being attacked by the pest insect. Baits are beneficial because the reduction of pesticide use provides more safety to the pesticide applicator and to the environment.

History

The evolution of bait technology shows a trend (Fig. 63) over time of increased complexity. Simple products such as grains and vegetables comprise the early baits. Grains and vegetables were



Food-Based Poisoned Baits for Insect Control, Figure 63 **Evolution of bait technology, showing the trend of increasing complexity of baits over time.**

Food-Based Poisoned Baits for Insect Control, Figure 64 **For suppression of insects with food-based bait, the volume of bait can be a logistical problem. Shown here is wheat bran-based bait, mixed by hand and machine, and prepared for a grasshopper suppression effort in Colorado, USA, in 1937.**

eventually refined to their specific attractive components such as proteins, carbohydrates, and carbon dioxide. As science and technology advanced, oils and plant volatiles could be extracted and identified from whole plants. Grain (Figs. 64–66) and vegetable bait types present a low cost method of insect control while multi-component baits are more costly, technologically advanced baits. Baits that are made of basic grains and vegetables would be appropriate in situations where cost is a concern such as in low value crops or in less developed countries. Conversely, bait types that are made of plant volatiles and multi-component baits would be more appropriate in high value crops, or in more technologically advanced societies where cost is less of an issue. Nevertheless, relatively simple bait systems tend to predominate throughout the world.

The result of years of research, many modern-day baits are made with synthetic attractants such as pheromones (which are chemical substances

Food-Based Poisoned Baits for Insect Control, Figure 65 **Bait can be distributed by hand, as shown here in the Colorado grasshopper suppression effort of 1937, but it is a formidable task if large areas are involved.**

Food-Based Poisoned Baits for Insect Control, Figure 66 **If bait distribution is to be accomplished on a large scale, some type of machinery is usually needed. Shown here is a primitive (but effective) bait spreader used in the 1937 grasshopper suppression effort in Colorado. Ground distribution of bait was soon replaced by aerial application, and both solid and liquid baits are now generally applied by air if the land area to be treated is extensive.**

used for communication between insects), or kairomones (host plant extracts). Bait carriers used for the formulation of insect control agents can include baits that encourage insect feeding, or inert particles that help carry the insecticide to the target site. Different combinations of bait carriers and attractants are successful on certain insects and not on others.

Food-Based Poisoned Baits for Insect Control, Figure 67 **An assortment of modern food-based bait formulations. The mole cricket and slug/snail baits are an old but effective approach using relatively simple grain or oil-based baits. The ant and cockroach baits involve more complex formulations (the "ant bait system" has separate baits that attract sugar feeding or oil feeding ants; the "roach killing gel" allows placement in hard-to-reach places; and the "roach controller" keeps the bait away from children and pets). The Amdro® fire ant bait ant and the unlabeled, plastic Sentricon® termite bait holder are examples of products that contain slow-acting toxicants that are transported back to the queen.**

Different Types of Baits

The proper bait to use on a specific insect is based on the behavior of the insect and the type of hosts that it finds attractive. Most insect baits are based on one of three categories: food, sex, or shelter. Food baits often use the properties of odor, color, taste, shape, or moisture as the basis of attraction. Sex-based baits utilize odor, color, shape and oviposition behavior as attractants, while baits where shelter is the basis often use visual and tactile stimulation to attract the targeted insect. Because insect behavior is quite different when seeking food, sex, or shelter, these different baits are not usually combined. There are exceptions however. For example, plant volatiles (food) and pheromones (sex) are combined to attract elm bark beetle and Japanese beetle to sticky traps.

Baits used for insect control are usually made of materials that are inexpensive and readily available. The most common baits are those containing grain as the attractant, and some type of toxicant. The composition of baits may contain common household items such as Doritos®, peanut butter, sugar and milk or ingredients as simple as carbon dioxide, a natural by-product of humans and animals. Baits are sometimes specific to the species of insect that they are intended to control. For example, wood is used to monitor for termites in the Sentricon® termite colony elimination system and other similar products. Sentricon® stations are placed in the ground around a building and are baited with untreated wood. If termites are found in the stations, the untreated wood is then replaced with a Baitube™ containing the active ingredient hexaflumuron. The termites feed on the treated wood, tunnel out and send other termite colony members back to feed on the bait. Once the colony is eliminated, the untreated wood is replaced and the process begins again. Slow-acting insecticides are an important component of the bait systems for termites and many other social insects. Slow kill allows the toxicant to be transported back to the queen, thereby eliminating the entire colony. With non-social insects, rapid mortality is usually desirable.

Advantages of Baits

There are several advantages to using dry baits over liquid insecticide formulations. The potential of chemical exposure by direct contact or inhalation of pesticides by non-target organisms is small. When dry baits are used, many beneficial species are not affected directly because the bait is eaten only by a subset of arthropod species. The amount of insecticide active ingredient applied per unit area in dry baits is lower than in liquid sprays. Dry baits may also reduce negative, indirect effects on non-target insectivores (insects that feed on other

Food-Based Poisoned Baits for Insect Control, Table 6 **Examples of food-based bait and the insects they attract**

Bait Type	Insect	Scientific Name	(Order: Family)	Life Stage
Grain baits				
distiller's grain and cat chow	cockroach	various	(Blattodea)	adult/nymph
dried distiller's grain	cockroach	various	(Blattodea)	adult/nymph
starch, rice bran, and molasses	cockroach	various	(Blattodea)	adult/nymph
oatmeal	wireworm	various	(Coleoptera: Elateridae)	larva
corn seeds, Doritos® corn chips, corn-wheat mix, wheat seeds, sorghum	wireworm	various	(Coleoptera: Elateridae)	larva
corn grits	pharaoh ant	*Monomorium pharaonis*	(Hymenoptera: Formicidae)	adult
bran	corn rootworm	*Diabrotica virgifera*	(Coleoptera: Chrysomelidae)	larva
corn starch	corn rootworm	*Diabrotica virgifera*	(Coleoptera: Chrysomelidae)	larva
whole wheat bread dough	dusky sap beetle	*Carpophilus lugubris*	(Coleoptera: Nitidulidae)	adult
corn protein, tortula yeast	South American cucurbit fruit fly	*Anastrepha grandis*	(Diptera: Tephritidae)	adult
defatted corn grits	red imported fire ant	*Solenopsis invicta*	(Hymenoptera: Formicidae)	adult
	pharaoh ant	*Monomorium pharaonis*	(Hymenoptera: Formicidae)	adult
tortula yeast	Anastrepha fruit fly	*Anastrepha* spp.	(Diptera: Tephritidae)	adult
brewer's malt	house fly	*Musca domestica*	(Diptera: Muscidae)	adult
poultry mash	mole cricket	*Scapteriscus borelli*	(Orthoptera: Gryllotalpidae)	adult
		Scapteriscus vicinus	(Orthoptera: Gryllotalpidae)	adult
laying mash, finely cracked corn	mole cricket	*Scapteriscus* spp.	(Orthoptera: Gryllotalpidae)	adult
wheat bran	mole cricket	*Scapteriscus* spp.	(Orthoptera: Gryllotalpidae)	adult
barley	black field cricket	*Gryllus* spp.	(Orthoptera: Gryllidae)	adult/nymph
wheat bran	greasy cutworm	*Agrotis ipsilon*	(Lepidoptera: Noctuidae)	larva

Food-Based Poisoned Baits for Insect Control, Table 6 Examples of food-based bait and the insects they attract (Continued)

Bait Type	Insect	Scientific Name	(Order: Family)	Life Stage
wheat bran	grasshopper	various	(Orthoptera: Acrididae)	adult/nymph
sawdust, bran, maize bran	grasshopper	various	(Orthoptera: Acrididae)	adult/nymph
wheat bran, bran-corncob mix	grasshopper	various	(Orthoptera: Acrididae)	adult/nymph
cornstalks, corncobs	grasshopper	various	(Orthoptera: Acrididae)	adult/nymph
wheat bran, bran-corncob mix	armyworm	*Pseudaletia unipunctata*	(Lepidoptera: Noctuidae)	larva
Wheast® (predator attractant)	lady beetle	*Coleomegilla maculata*	(Coleoptera: Coccinellidae)	adult
Protein baits hydrolyzed torula yeast	Mexican fruit fly, Mediterranean fruit fly	*Anastrepha ludens* *Ceratitis capitata*	(Diptera: Tephritidae), (Diptera: Tephritidae)	adult adult
ammonium bicarbonate, linolenic acid, methyl hydrogen succinate, pyrrolidine, methylamine, putrescine, ethanolamine, phenethylamine, and 5-hydoxy-2-pyrrolidinone	melon fly	*Bactrocera cucurbitae*	(Diptera: Tephritidae)	adult
tuna fish	red imported fire ant	*Solenopsis invicta*	(Hymenoptera: Formicidae)	adult
boiled ham	German yellow jacket	*Vespula germanica*	(Hymenoptera: Vespidae)	adult
tuna cat food	yellow jacket	*Vespula* spp.	(Hymeoptera: Vespidae)	adult
Staley's Protein Insecticide Bait #7	oriental fruit fly	*Bactrocera dorsalis*	(Diptera: Tephritidae)	adult
beef liver	screwworm fly	*Cochliomyia macellaria*	(Diptera: Calliphoridae)	adult
granulated silkworm pupae (Maxforce®)	Argentine ant	*Linepithema humile*	(Hymenoptera: Formicidae)	adult
mouse cadaver	soybean nodule fly	*Rivellia quadrifasciata*	(Diptera: Platytomatidae)	adult
cat feces	calliphorid fly	*Phormia regina*	(Diptera: Calliphoridae)	adult

Food-Based Poisoned Baits for Insect Control, Table 6 Examples of food-based bait and the insects they attract (Continued)

Bait Type	Insect	Scientific Name	(Order: Family)	Life Stage
peanut butter	cockroach	various	(Blattodea)	adult/nymph
manure	house fly	*Musca domestica*	(Diptera: Muscidae)	adult/larva
Oil baits				
canola oil	grasshoppers	various	(Orthoptera: Acrididae)	adult/nymph
cottonseed oil	boll weevil	*Anthonomus grandis*	(Coleoptera: Curculionidae)	larva
	pink bollworm	*Pectinophora gossypiella*	(Lepidoptera: Gelechiidae)	larva
peanut oil	pharaoh ant	*Monomorium pharaonis*	(Hymenoptera: Formicidae)	adult
soybean oil	red imported fire ant	*Solenopsis invicta*	(Hymenoptera: Formicidae)	adult
Vegetable baits				
carrots, turnips, potatoes	wireworms	*Melanotus depressus Limonius dubitans*	(Coleoptera: Elateridae)	larva
cabbage palmetto crown tissue	palmetto weevil	*Rhynchophorus cruentatus*	(Coleoptera: Curculionidae)	adult
Plant extract baits				
cotton plant extract	pink bollworm	*Pectinophora gossypiella*	(Lepidoptera: Gelechiidae)	larva
cucurbitan	corn rootworm	*Diabrotica virgifera*	(Coleoptera: Chrysomelidae)	larva
buffalo gourd root	corn rootworm	*Diabrotica virgifera*	(Coleoptera: Chrysomelidae)	larva
cotton plant extracts	boll weevil	*Anthonomus grandis*	(Coleoptera: Curculionidae)	adult
Coax® and diflubenzuron	fall armyworm	*Spodoptera frugiperda*	(Lepidoptera: Noctuidae)	larva
Coax®, starch and flour	European corn borer	*Ostrinia nubilalis*	(Lepidoptera: Pyralidae)	larva
phenylacetaldehyde	soybean looper	*Pseudoplusia includens*	(Lepidoptera: Noctuidae)	adult
Carbohydrate baits				
agar and grape jelly	red imported fire ant	*Solenopsis invicta*	(Hymenoptera: Formicidae)	adult
sucrose and honeysyrup	honey bee	*Apis mellifera*	(Hymenoptera: Apidae)	adult
sugar and milk	black carpenter ant	*Camponotus pennsylvanicus*	(Hymenoptera: Formicidae)	adult

Food-Based Poisoned Baits for Insect Control, Table 6 Examples of food-based bait and the insects they attract (Continued)

Bait Type	Insect	Scientific Name	(Order: Family)	Life Stage
honey water/sucrose water	Argentine ant	*Linepithema humile*	(Hymenoptera: Formicidae)	adult
flour and sugar	cockroach	various	(Blattodea)	adult/nymph
Carbon dioxide baits				
CO_2	relapsing fever tick	*Ornithodoros turicata*	(Acari: Argasidae)	adult
man CO_2/cow CO_2	mosquito	*Anopheles* spp.	(Diptera: Culicidae)	adult
CO_2 and live rabbit	mosquito	*Anopheles sierrensis*	(Diptera: Culicidae)	adult
CO_2 and ox sebum	tsetse fly	*Glossina pallidipes*	(Diptera: Glossinidae)	adult
CO_2, acetone, 1-octen-3-ol	tsetse fly	*Glossina pallidipes*	(Diptera: Glossinidae)	adult
		Glossina morsitans	(Diptera: Glossinidae)	adult
cattle silhouette traps with CO_2	black fly	*Simulium arcticum*	(Diptera: Simuliidae)	adult
CO_2 from corn roots	corn rootworm	*Diabrotica virgifera*	(Coleoptera: Chrysomelidae)	larva
Multi component baits				
phenethyl propionate, eugenol, geraniol, Japonilure	Japanese beetle	*Popillia japonica*	(Coleoptera: Scarabaeidae)	adult
cucujolides and wheat	cucujid and tenebri-onid, stored grain beetles	*Oryzaephilus surinamensis*	(Coleoptera: Silvavidae)	adult
		Oryzaephilus mercator	(Coleoptera: Silvavidae)	adult
		Tribolium castaneum	(Coleoptera: Tenebrionidae)	adult
		Tribolium confusum	(Coleoptera: Tenebrionidae)	adult
(2E,4E,6E,8E)-7-ethyl-3,5-dimethyl-2,4,6,8-undecatetraene and whole wheat bread dough	dusky sap beetle	*Carpophilus lugubris*	(Coleoptera: Nitidulidae)	adult
pupa powder, onion, eggs and wine	cockroach	various	(Blattodea)	adult/nymph
bread and garlic	cockroach	various	(Blattodea)	adult/nymph
acetic acid, flour, potato, fish meal	cockroach	various	(Blattodea)	adult/nymph

Food-Based Poisoned Baits for Insect Control, Table 6 Examples of food-based bait and the insects they attract (Continued)

Bait Type	Insect	Scientific Name	(Order: Family)	Life Stage
alfalfa powder, powdered milk, and sugar	cockroach	various	(Blattodea)	adult/nymph
stale beer	cockroach	various	(Blattodea)	adult/nymph

insects) by preserving their food supply because fewer arthropod groups are affected.

The benefits of baits are clearly demonstrated by a mathematical model developed by USDA researchers. The model developed predicts the dose of bait that would likely provide the desired degree of initial kill in grasshopper populations. Bait treatments can be made more economical by increasing the efficiency of individual flakes and by reducing the rate of application. In this study, the model predicted that six flakes of 1.96% carbaryl wheat would kill one grasshopper.

Baits are often necessary when insect control programs are conducted near water, where threatened and endangered species occur, or where preservation of a beneficial species of arthropod is important. Baits reduce the problems encountered when applied pesticides drift. When baits are applied, they fall straight down and little dispersion is encountered, unlike liquid or dust insecticides. Considerably less toxic chemicals per unit area is needed as a bait compared with sprays to reduce pest populations to non-economic levels, and baits can be less expensive. Baits often target a particular pest species; therefore, environmental hazards are reduced.

References

Capinera JL, Sechrist TS (1982) Grasshoppers (Acrididae) of Colorado: identification, biology and management. Colorado State University Experiment Station Bulletin 584S, 161 pp

George TL, McEwen LC, Fowler A (1992) Effects of a carbaryl bait treatment on nontarget wildlife. Environ Entomol 21:1239–1247

Jech LE, Foster RN, Colletto D, Walgenbach DD, Roland TJ, Rodriguez GD, Bohls R, Houston RD, Meeks WK, Queener RL, Jackson CL, Dines JL, Puclik MJ, Scott AK (1993) Field evaluation of diflubenzuron and carbaryl bran baits against grasshopper (Orthoptera: Acrididae) populations in South Dakota. J Econ Entomol 86:557–565

Onsager JA, Henry JE, Foster RN (1980a) A model for predicting efficacy of carbaryl bait for control of rangeland grasshoppers. J Econ Entomol 73:726–729

Onsager JA, Henry JE, Foster RN, State RT (1980b) Acceptance of wheat bran bait by species of rangeland grasshoppers. J Econ Entomol 73:548–551

Su NY, Scheffrahn RH (1996) Fate of subterranean termite colonies after bait applications-an update and review. Sociobiology 27:253–275

Food Canal

A longitudinal groove found in the maxillary stylets of Hemiptera. The groove forms a tube for passage of plant sap from the plant to the head. Also found in the stylets of Hemiptera (but not Thysanoptera) is a smaller salivary canal for secretion of saliva as an aid to digestion. Some types of plant viruses are injected into plants through this latter canal.

► Mouthparts of Hexapods
► Plant Viruses and Insects

Food Chain

A pyramid of numbers among species in a community. Species in the community differ in their niche parameters. Members of the lowest level (producers) are most abundant and are consumed by a less abundant higher level (primary consumers), which are in turn consumed by an even less abundant higher level (secondary consumers), etc. Insects typically comprise the primary and secondary consumer levels.

Food Habits of Insects

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The million or so insects that occur in nature come in an astounding array of sizes, shapes and colors and exhibit a wealth of adaptations. They are found virtually everywhere, and some reach staggering numbers of individuals. Their exceptional variability, ubiquity and great numbers, in combination with the wide assortment of plant and animal foods that nature makes available to them, contribute to an almost infinite variety in feeding. Nevertheless, one can sort out a few of their generalized feeding trends, or food habits, as outlined below.

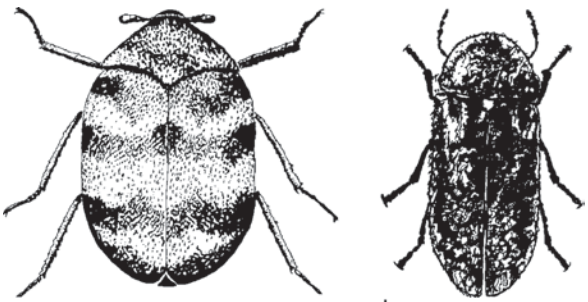
What do Insects Eat?

Insects eat an astonishingly wide array of materials, a few extreme examples of which are worth mentioning. Adult carpet beetles of the genus *Anthrenus* (Fig. 68), are innocuous pollen feeders generally found out-of-doors on flowers, yet they enter homes and lay eggs that soon hatch into larvae. These voracious juveniles eat wool, feathers and hair and, in the process, ruin expensive carpets, upholstery and clothing. Clothes moths including *Tineola bisselliella* (Hummel) and *Tinea pellionella*, L. the skin and larder beetles of *Dermestes* spp., and biting lice also eat hair, wool, feathers, epidermal scales and horn, which all contain the remarkably indigestible substance keratin, a material that does not otherwise form the basis of the diet in animals. Certain larger skin beetles frequent tanneries where they eat skin, hoofs and hair, and vertebrate zoologists rear cultures of the hide beetle, *Dermestes maculatus*, De Geer to clean the bones of museum specimens for study and exhibition. The smaller dermestid, *Anthrenus verbasci*, L. is the acknowledged scourge of entomological collections because of its destructiveness to pinned, dried, unprotected museum specimens.

The cigarette beetle, *Lasioderma serricorne* (Fabricius), is one of a number of common household pests that infest spices including pepper, paprika and chili powder, as well as cereals and pet foods, but it is best known for its consumption of dry, cured tobacco, often in fully formed cigarettes and cigars, which are rendered unusable. This food habit is remarkable in that nicotine, the tobacco plant's secondary substance, is so effective in thwarting insect attack that, in the early twentieth century, it was a commonly used insecticide.

The lead-cable borer, *Scobicia declivis* (Le Conte), and certain other powderpost beetles damage metals causing short-circuiting and service interruption as they bore through oak, maple and other woods. Other members of this heterogeneous group of beetles, the powderpost beetles, infest dry, seasoned wood that is not in contact with the soil. They pose a special problem in barns, cabins and older homes with hardwood flooring, beams, sills, studs, siding and rafters, and they damage lumber, tool handles, furniture, etc., unless the wood has been previously painted or varnished. The beetles drill through the wood, peppering it with pin- or pencil-sized tunnels, and unceremoniously heap the powdery residues outside the exit holes. Those powderpost beetles called deathwatch beetles, especially *Xestobium rufovillosum* (De Geer), make a gnawing or ticking sound as they bore through wood. This sound is audible during periods of (Fig. 68) quiet, especially at night during a wake, from which the name "deathwatch" is derived.

The large milkweed bug, *Oncopeltus fasciatus* (Dallas), the milkweed beetle, *Tetraopes femoratus* Le Conte, and the monarch butterfly, *Danaus*



Food Habits of Insects, Figure 68 (a) *Anthrenus verbasci,* one of the destructive carpet beetles often found in houses where its larvae attack carpets, upholstery, clothing and other fabrics; (b) the deathwatch beetle, *Xestobium rufovillosum*, one of the powderpost beetles that makes a ticking sound as it damages the dry, seasoned wood of old houses, barns, etc. (a is modified and redrawn from Arnett; b is modified and redrawn from Ohio Biological Survey.)

plexippus (L.), are colorful aposematic insects that not only frequent, but actually eat, plants of the poisonous milkweed family Asclepiadaceae and gain a measure of protection thereby. Milkweeds have a milky sap containing cardiac glycosides that these feeders not only tolerate but sequester, rendering them unpalatable to potential predators, most of which find the glycosides emetic. Not only the milkweed-feeding larvae, but also the adults that arise from them, are protected by the glycosides that concentrate particularly on the wings so that birds attempting to eat them vomit violently. Though they do not die, the birds learn to avoid monarchs and other butterflies that resemble monarchs. For example, the viceroy butterfly, *Basilarchia archippus* (Cramen), mimics the distasteful monarch and is protected by its monarch-like appearance though its body fluids lack the offensive glycosides.

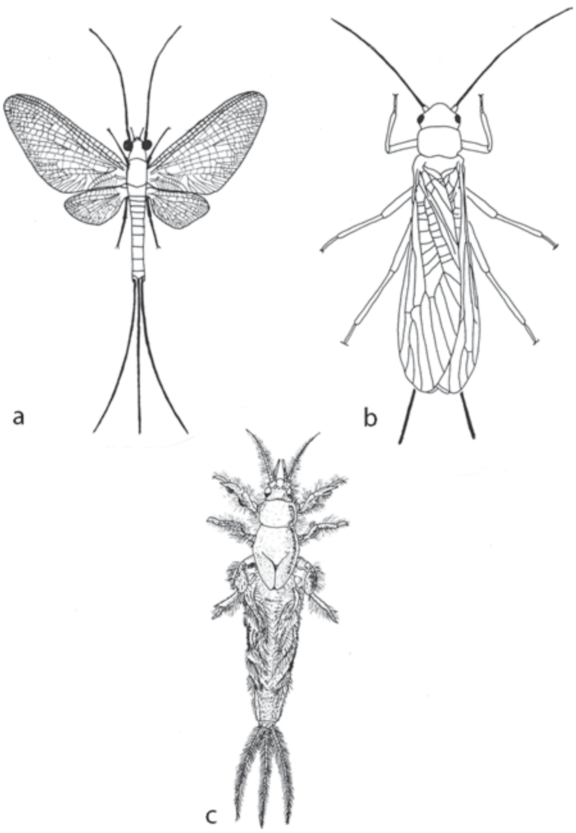
Tumblebugs, or dung beetles, especially of the genus *Canthon*, are among the insect scavengers of feces, and cockroaches such as *Periplaneta americana*, (L.), and the field crickets of genus *Gryllus*, consume feces, mucus and dead animals in varying stages of decomposition, as well as fresh and decayed vegetation. These and other insect scavengers play an important role in nature's decomposition process without which, the world would be a far different, much more loathsome place than that about us today.

Pygmy grasshoppers, or grouse locusts, of the genera *Tettigidea* and *Tetrix*, literally eat dirt. They ingest rich, moist pond and lake soil and the algae, lichens and plant constituents found in it, thereby nourishing themselves on the organic component as they egest the sand and other non-organic components.

Insects That do not Eat

Several kinds of adult insects are aphagous; they do not eat. Mayflies of the genus *Ephemera*, and certain stoneflies with reduced, non-functional mouthparts in the adult stage are examples of aphagous insects (Fig. 69). Their sole purpose in life is to procreate. The naiads, or juveniles, of mayflies such as *Hexagenia limbata* (Serville) eat heartily of algae and aquatic debris found in the clear, unpolluted lakes, ponds and streams, but cease feeding upon reaching maturity. Their adult life is necessarily short because they are obliged to live off the limited food reserves stored during the juvenile stage. Mayfly naiads are easily recognized by their usual three feathery caudal gills as well as plumose gills along the sides of the abdomen. Stonefly naiads superficially resemble mayfly naiads, but have two caudal gills as well as branched gills on the thorax and about the leg bases. Stonefly naiads are plant feeders, predators, or omnivores in cool, rocky stream and lake habitats. Those stonefly adults that eat, consume algae, but other stoneflies resemble mayfly adults in their inability to feed.

The feeding habits of some adult insects are like that of their juveniles, whereas other insects take on completely different food habits upon (Fig. 69) reaching maturity. The change in food habits is correlated with their development. More primitive insects, such as orthopteroids and most hemipteroids, undergo a gradual metamorphosis involving juveniles called nymphs that resemble



Food Habits of Insects, Figure 69 (a) *Ephemera* sp., an adult mayfly, (b) *Isoperla confusa*, an adult stonefly. Although mayflies and certain stoneflies do not eat as adults, their naiads eat heartily and (c) *Hexagenia limbata*, a juvenile mayfly (a is modified and redrawn from Needham; b is modified and redrawn from Frison; c is modified and redrawn from Burks.)

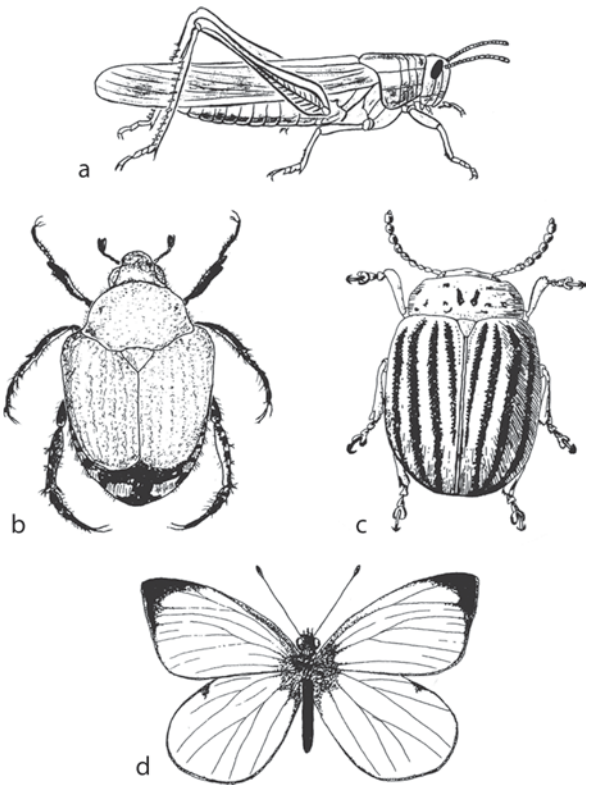
one another and also the adult, differing mainly in size, body proportions and incompletely developed genitalia and wings. These nymphs and the adults into which they grow occupy a similar environmental niche in which the available foods do not change appreciably, even with the season. Moreover, the nymphal mouthparts and digestive tracts are little different from those of the adults and are well adapted for handling a similar kind of food.

In contrast to the above generalized insects are the more advanced insects such as beetles, neuropterans, moths and butterflies, bees, wasps, true flies and certain others. They undergo a complete metamorphosis characterized by dissimilar larval, pupal and adult stages. The larva is essentially a feeding and growing stage often characterized by reduced eyes, antennae and body sclerotization. Its suppression of adult characteristics imparts to it a complete dissimilarity from the structure, physiology and behavior of the adult. The larvae often occupy a different environmental niche and use a different kind of mouthpart and a different digestive tract to take advantage of foods other than those that the adults eat. The adult stage is a dispersal and reproductive stage where adults often select foods that are different from those eaten by the larvae and, occasionally, do not even eat. So dissimilar are the larva and the adult in these advanced insects that a pupal stage has evolved to bridge the structural and physiological transition between them.

One might surmise from the preceding that insect food habits are almost as varied as are the creatures themselves. Fortunately, the picture can be simplified by breaking insect foods into three basic categories: living plants, living animals and dead plants and animals.

Insects That Eat Living Plants

Herbivory or phytophagy, i.e., plant-feeding, is one of the most common food habits among insects. Perhaps half of the living insect species eat vegetation, though their selectivity among the innumerable available host plants varies widely. Plague locusts, their grasshopper relatives, gypsy moth caterpillars, the Japanese beetle and many leaf beetles are examples of polyphagous plant feeders (Fig. 70). Polyphagous species eat plants belonging to widely divergent taxonomic groups, both related and unrelated. They select host plants largely on the basis of availability, abundance, texture, succulence and other physical and chemical attributes. The desert locust, *Schistocerca gregaria* (Forskal), other plague locusts and certain related North American grasshoppers are examples. The desert locust (Fig. 70) sometimes reaches outbreak populations



Food Habits of Insects, Figure 70 **(a) The grasshopper *Schistocerca* sp., a North American relative of the Old World desert locust *Schistocerca gregaria*, and (b) the Japanese beetle, *Popillia japonica*. These two insects are polyphagous. They consume plants belonging to numerous host groups, both related and unrelated.**
(c) The Colorado potato beetle, *Leptinotarsa decemlineata*, which eats members of the potato family and (d) the cabbage butterfly, *Artogeia* (formerly *Pieris*) *rapae*, which eats cruciferous plants. These two insects are oligophagous. They eat host plants belonging either to a single taxonomic group or to several closely related groups. (a is redrawn from Riley; b is modified and redrawn from Essig; c is modified and redrawn from USDA; d is modified and redrawn from Viedma et al.)

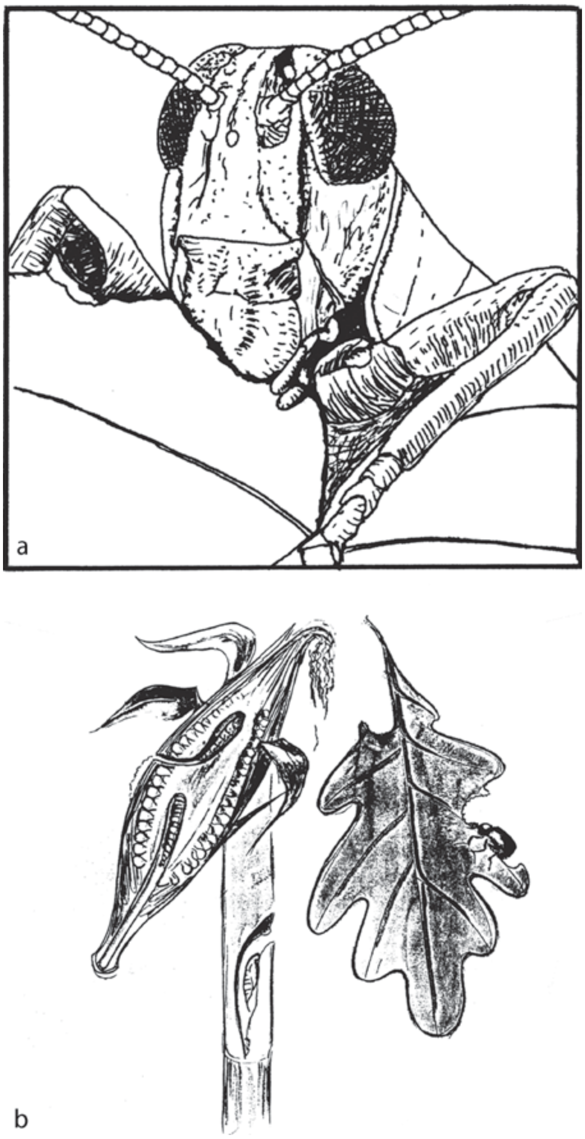
in which it becomes cannibalistic and almost indiscriminately attacks grains, garden crops, trees, native grasses, forbs, dung, dead animal carcasses, and, under starvation pressure, it even turns to perspiration-stained cloth, rake handles, wooden fences and other non-food items. The gypsy moth, *Lymantria dispar* (L.), a well-known pest of shade trees in Europe, was introduced into Massachusetts in the late 1800s in an ill-conceived attempt to cross-breed it with several other silk producers. It accidentally escaped captivity and soon spread throughout New England and westward thereafter until today it is distributed throughout much of northeastern United States. Female gypsy moths are flightless and lay their eggs in silken masses on tree trunks. They die shortly afterward without having traveled far, so most dispersal is by the larvae, which have become one of our most serious pests of oak, birch, ash, and other shade trees. The attractively colored Japanese beetle, *Popillia japonica* Newman, is another introduced pest insect, in this case, one that was accidentally imported on nursery stock from Japan. The larvae eat roots of grass and other herbs until, by midsummer, the adults emerge and begin attacking the foliage and flowers of more than 250 plant species, including roses and many other economically important plants.

Oligophagous insects are more selective and less common than the polyphagous ones just described. They select host plants belonging either to a single taxonomic group, or to several closely related groups. Examples include the monarch butterflies mentioned earlier with respect to milkweeds (their sole source of food), the Colorado potato beetle that is restricted to eating members of the potato family and the imported cabbageworm, which consumes only mustards. The Colorado potato beetle, *Leptinotarsa decemlineata* (Say), a handsome yellow beetle striped with black, is a serious pests of cultivated potato. Originally from Mexico, it was an innocuous member of the Rocky Mountain fauna and attracted little attention eating only a few species of nightshade, which are wild members of the Solanaceae, or potato family. With the advent of railroads and other advances in transportation and communication, the American west came under heavy settlement following the Civil War, whereupon the beetle began invading local gardens to attack potatoes, tomatoes, eggplant and a few other solanaceous plants that it found attractive.

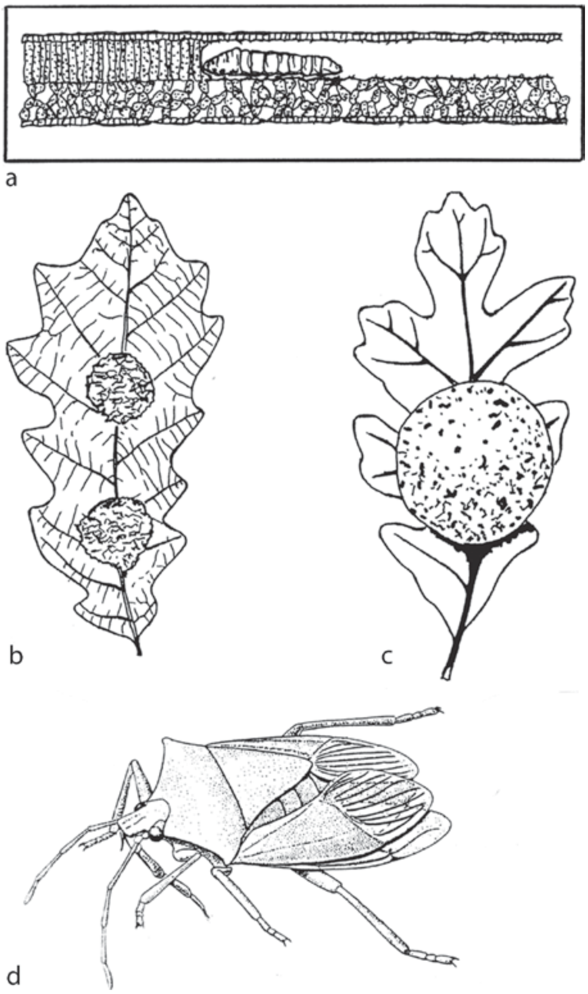
It quickly spread from potato patch to potato patch, reaching the east coast of the United States before the turn of the century and invading Europe afterward. The imported cabbage butterfly, *Artogeia* (formerly *Pieris*) *rapae* (L.), is one of our most common whites. Its larvae eat members of the family Cruciferae, particularly cabbage, riddling the outer leaves of the head. The several cultivated crucifers (cabbage, brussels sprouts, cauliflower, etc.) contain mustard oils with a distinctive, pungent odor and taste that most potential feeders find repulsive. The cycle begins when the female butterfly seeks out and oviposits in a cabbage patch. The larvae hatch, eat and grow to maturity on the particular host species that the parent selected. They refuse plants to which they are not accustomed, and starve in absence of the preferred host. Interestingly, however, they accept the foliage of certain non-host plants if the accustomed mustard oil is first smeared on the strange foliage.

Only a few insects are monophagous, i.e., restricted to a single host. An example is the silkworm moth; its natural food is mulberry. The silkworm moth, *Bombyx mori* (L.), is an Asian native that was introduced into Europe in the sixth century and into the Americas in the eighteenth century. Through the years, this domestic insect has been used in sericulture, and is commercially reared for silk. The larvae eat mulberry leaves until grown and able to spin their cocoons, the strands of which, when unwound, may be used to provide silk. Adult silkworm moths rarely fly and, like mayflies, live only a few days as they are unable to eat.

Insects eat roots, stems, leaves, flowers, fruits, pollen, spores, sap and other plant parts or plant secretions in a manner that varies widely (Figs. 71 and 72). Many beetles, most butterfly and moth caterpillars, grasshoppers, many katydids and some other insects excavate morsels from the edges or center of their chosen foliage or flowers; larval long-horned beetles and other borers tunnel deep within their host plants consuming tissues, fungi, or wood fragments; certain larval caterpillars and flies mine within the upper and/or lower surfaces of the host leaves consuming palisade tissue and/or parenchymatous cells; gall midges and gall gnats stimulate their host to form distinctive, tumor-like plant growths, or galls, in which they sequester themselves and feed; and



Food Habits of Insects, Figure 71 Different types of feeding by insects: (a) the grasshopper, *Melanoplus femur-rubrum*, excavating escalloped morsels from a leaf edge; (b, right leaf) a scarab beetle excavating the leaf edge of an oak and (b, left) larval corn borers attacking an ear and a stalk of corn. (a is modified and redrawn from the Illinois Natural History Survey; b is modified and redrawn from USDA.)



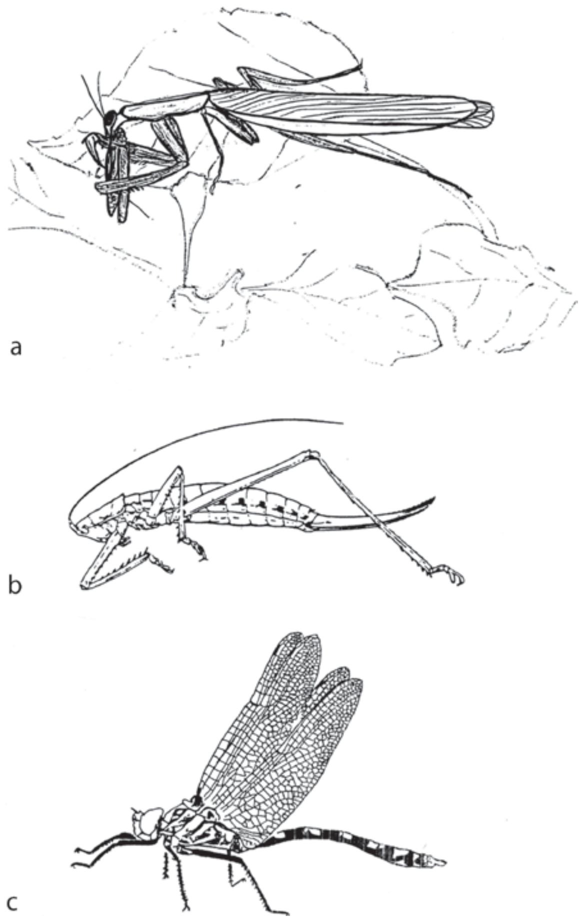
Food Habits of Insects, Figure 72 Different types of feeding, continued: (a) a leaf miner coursing through the interior of a leaf, consuming cells as it goes, but leaving intact the upper and lower leaf surfaces; (b, c) two kinds of galls in which live and feed the respective insect occupants whose influence has stimulated the plants' tumor-like growth; (d) a stink bug showing the typical hemipteran suctorial beak between the fore legs. (a is modified and redrawn from Evans; b and c are modified and redrawn from Atkins; d is by courtesy of the Illinois Natural History Survey.)

aphids, leafhoppers, scale insects, stink bugs and other true bugs are among the phytoparasitic insects that suck plant fluids using their elongate beak in much the same manner as do many blood-feeding animal parasites in their attacks on animal hosts.

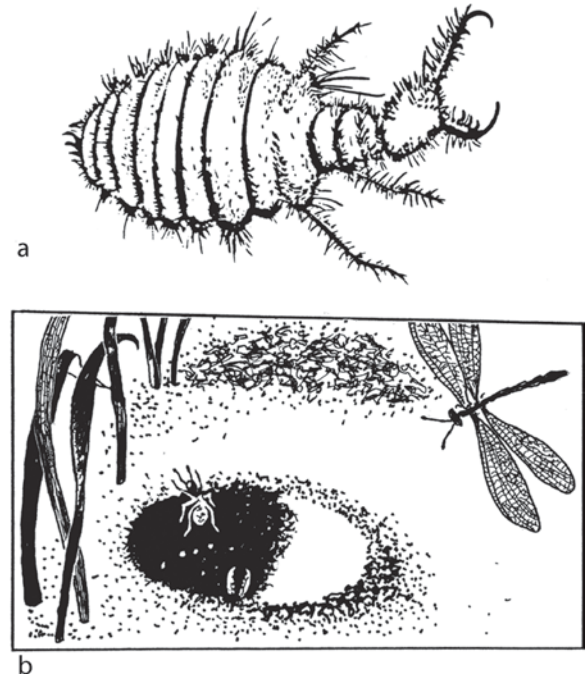
Insects That Eat Living Animals

A number of aggressive, relatively powerful or specialized insect predators attack, overpower and eat other animals (called prey), generally resulting in the latters' death. The prey usually consists of species other than that of the predator, although some strongly predacious insects also feed on their own species, the act of cannibalism. Rapacious katydids such as *Saga pedo*, *Macromia magnifica* MacLachlan and other dragonflies, robber flies, ladybird beetles and mantises are representative predators. Mantises such as *Tenodera* sp., use stealth and (Figs. 73 and 74) ambush to attack, capture and eat, alive and kicking, practically any moving animal of the right size that they can catch and overpower and are even cannibalistic on their own species. Older, larger mantises often devour newly hatched young mantises when given the opportunity, and the larger, stronger adult female mantises may consume the smaller adult males attempting to mate with them. Dragonflies prey on their animal hosts in much the same manner as mantises and carnivorous katydids except they pursue their prey on the wing. Both larval and adult ladybirds are rapacious hunters of aphids and scale insects. *Myrmeleon* sp. and certain other antlions entrap their prey by excavating a pitfall in loose, sandy soil where they bury themselves, with only the rapier-like jaws exposed. In this position, they are able to fall upon and suck dry any ants that blunder into the trap.

Parasites are another kind of animal feeder. Insect parasites differ from insect predators in that they are usually smaller and less powerful than their hosts, and the predator-host relationship usually does not involve the latter's death. *Anopheles maculipennis* Meigen (Fig. 75) and certain other mosquitoes, the females of which may be responsible for the transmission of malaria, yellow fever and other important human diseases, are ectoparasites that live apart from the host except to feed. They are little specialized for their parasitic existence aside from possession of an elongate beak used to suck blood. The human louse, *Pediculus humanus* L., and other sucking lice and



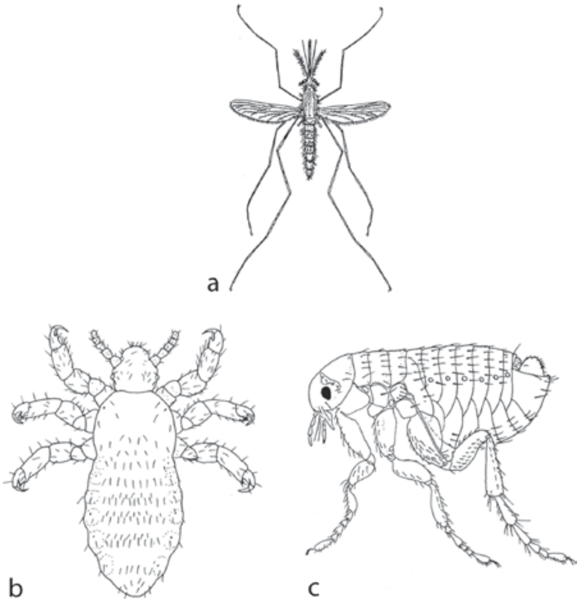
Food Habits of Insects, Figure 73 **(a) The mantis, *Tenodera* sp., eating a prey insect that it has ambushed and is holding by its raptorial fore legs; (b) *Saga pedo*, a predacious Mediterranean katydid that pursues and catches its prey by powerful armed legs; (c) the dragonfly, *Macromia magnifica*, which captures its prey on the wing. (a is modified and redrawn from various sources; b is modified and redrawn from Chopard; c is modified and redrawn from Kennedy.)**



Food Habits of Insects, Figure 74 **(a) *Myrmeleon* sp., an antlion larva, and (b) an overall view of its pitfall. The rapier-like jaws of the buried antlion are exposed at the bottom of the pit, and an ant that has blundered into the trap is attempting to escape at the periphery, as an adult antlion flies overhead. (Figures are modified and redrawn from Buchsbaum.)**

the human flea, *Pulex irritans* L., and other fleas represent another kind of ectoparasite. Unlike mosquitoes, this kind of ectoparasite lives on or near the chosen mammalian host and may require close, continued association with its body warmth. This more intimate parasitism typically involves a highly specialized, wingless, flattened insect with a suctorial beak. The host-parasite relationship is often so specific that, for example, a monkey-feeding louse given access only to a human host starves to death, being unable to accept human food.

Parasitism grades into predation in a number of other insects called parasitoids, of which tachina flies and *Lysiphlebus testaceipes* (Cresson) and (Fig. 76) other parasitic wasps are representative. Parasitoidism is characteristic of larval stages only, not of adults. It is a relationship in which, unlike true parasitism, the larva eventually kills the host. The parasitoid is also relatively large-bodied, sometimes almost as large as the host that it attacks. (It cannot be larger, of course, because it must be able to complete development on the tissues of that single individual). Adult parasitoids lay their eggs on or within the prospective host, and the newly hatched young then eat tissues of their hosts' body cavity, bloodstream or digestive

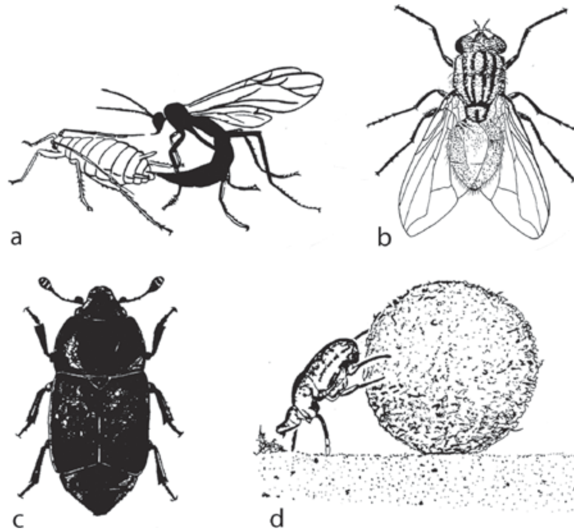


Food Habits of Insects, Figure 75 **(a) The adult mosquito, *Anopheles maculipennis*, an ectoparasite that lives apart from its host, which it approaches only to feed; (b) the human louse, *Pediculus humanus*; (c) the human flea, *Pulex irritans*. The two latter are ectoparasites that, unlike mosquitoes, live in close association with their human host. (a is modified and redrawn from Nuttall and Shipley; b and c are modified and redrawn from Essig.)**

tract. They feed on non-vital parts at first before turning to vital ones, eventually killing the host.

Insects That Eat Dead Plants and Animals

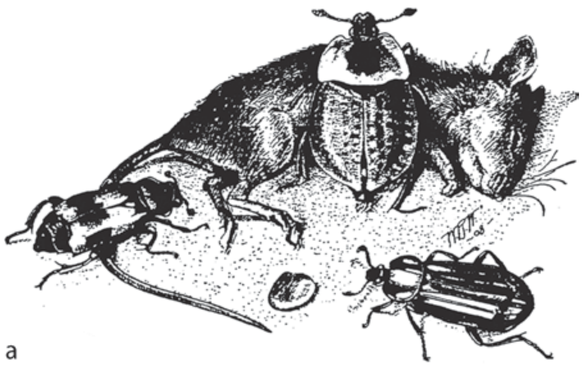
Sap beetles, such as *Carpophilus lugubris* Murray, a serious pest of corn, and certain members of the genus *Glischrochilus*, are likely found in putrefying watermelon rind, fruits or other garbage. These attractive little black insects that are spotted with yellow, as well as the house fly, *Musca domestica* L., and other insect scavengers, may frequent tables at local picnic grounds. Maybe their antics are amusing, but they likely have come from their most recent repast at adjacent garbage dumps, piles of feces, or other equally loathsome waste deposits.



Food Habits of Insects, Figure 76 **At the top is (a) an adult of the parasitoid, *Lysiphlebus testaceipes*, ovipositing in an aphid; in the middle are two scavengers, (b) the house fly, *Musca domestica,* a medically important pest distributed virtually worldwide, and (c) the sap beetle, *Carpophilus lugubris*; and at the bottom is (d) *Kheper aegyptiorum*, a tumblebug using its legs to roll its carefully molded ball of dung to a suitable oviposition and feeding site. (a is modified and redrawn from Crossman; b is modified and redrawn from Turtox Key Cards; c is modified and redrawn from Borror et al.; d is modified and redrawn from Heinrich & Bartholomew.)**

The tumblebug, *Kheper aegyptiorum*, and other dung beetles and carrion beetles including the genera *Silpha* and *Nicrophorus*, are scavengers (Fig. 77) of even more specialized habit than sap beetles and house flies. They are able to eat and develop only when provided their respective food, either dung or carrion. So closely associated are they with their particular food that entomologists who wish to collect them do not look for them directly, but seek out the stools or carrion in which they are likely to be found.

Periplaneta americana (L.) and other cockroaches are insect omnivores par excellence. The American, German, Oriental and other domestic cockroaches are cosmopolites whose individuals



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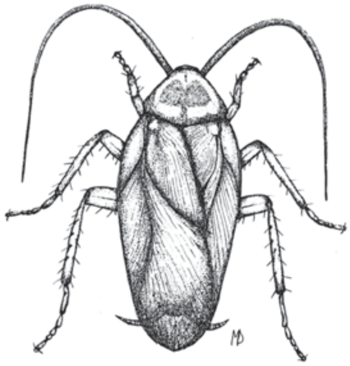


b

Food Habits of Insects, Figure 77 **(a) At left (resting on the host tail) is the carrion beetle, *Nicrophorus* sp., and at right (both on the body and below it) are two different species of the carrion beetle genus, *Silpha*, eating a dead mouse; (b) the domestic cockroach, *Periplaneta americana*. Carrion beetles are carrion specialists, eating only carcasses; cockroaches are generalists, being scavengers that eat most any available living or dead plant or animal or the tissues thereof. (a is after Walton; b is by courtesy of M. Dababneh.)**

frequent kitchens, restaurants, bakeries, grocery stores, hospitals and other places with warmth, humidity and organic debris to eat. They prefer soft, starchy foods but eat a vast array of other substances, fresh or decayed, animal or plant in origin. They even gnaw cardboard, glue, paste, clothing, book bindings, hair, leather, garbage and the secretions and wastes of vertebrates. Their wild cockroach relatives, seldom seen in human dwellings, are secretive nocturnal insects found under bark or leaves, or within woodland debris. These wild cockroaches attack roots, stems, foliage, flowers and fruits both of living and of dead plants, but apparently prefer living to dead tissues. They also prey on small, weak insects, are occasionally cannibalistic, and are attracted to all types of vertebrate wastes and secretions.

References

Bernays EA, Chapman RF (1994) Host-plant selection by phytophagous insects. Contemporary topics entomology, vol 2, Chapman & Hall, New York, NY, 312 pp

Brues CT (1946) Insect dietary. An account of the food habits of insects. Harvard University Press, Cambridge, MA, 466 pp

Brues CT (1952) How insects choose their food plants. In: Stefferud A et al (eds) Insects. The yearbook of agriculture, 1952, U.S. Department of Agriculture, Washington, DC, pp 37–42

Gangwere SK (1972) Host finding and feeding in the Orthopteroidea, especially as modified by food availablity: a review. Rev Univ Madrid 21:107–158

Snograss RE (1967) Insects. Their ways and means of living. Dover Publications, 362 pp (Unabridged republication of article from 1930 Smithsonian Institution Series)

Food Web

A representation of the feeding relationships (dietary links) among all the members of a community.

Foote, Richard H.

Richard Foote is remembered as an authority on the taxonomy of fruit flies (Diptera: Tephritidae). He was born on May 2, 1918 in Bozeman, Montana, and graduated from Montana State University in 1941 before serving in the armed forces during World War II. He earned a Sc.D. in parasitology from Johns Hopkins University in 1952 and immediately joined the United States Department of Agriculture in what was to become the Systematic Entomology Laboratory. Although initially working on mosquitoes, he soon devoted himself to tephritid fruit flies. He devoted his entire career to this agency, and is perhaps best known for his 1993 publication, "Handbook of the Fruit Flies of America North of Mexico." Foote is also known for his early acceptance and promotion of computers for entomological data retrieval. He was active in society activities, particularly in journal editing, and served as president of several scientific societies. He died on February 9, 2002.

Reference

Norrbom AL, Thompson FC (2002) Richard H. Foote. Am Entomol 48:124–125

Footman Moths

Some members of the family Arctiidae (order Lepidoptera) also known as tiger moths.

► Tiger Moths
► Butterflies and Moths

Foramen Magnum

The opening in the posterior surface of the head (Fig. 78) that allows passage of organs (e.g., the alimentary and circulatory organs) that extend from the head into the thorax.

► Head of Hexapods

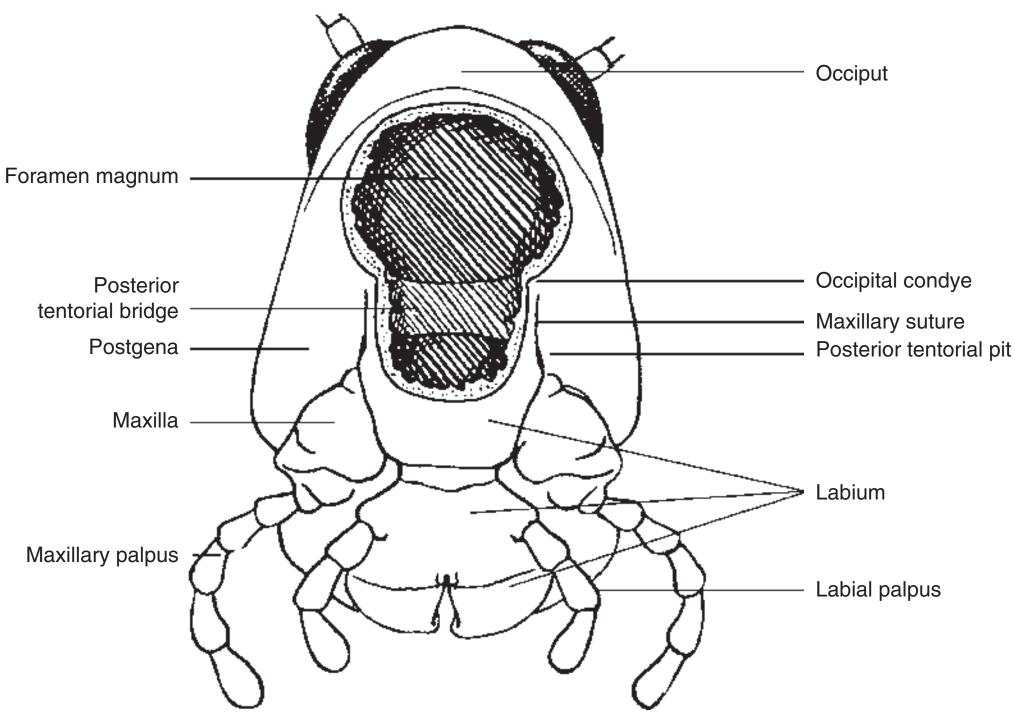
Forbivory

Feeding on broad-leaf plants (i.e., forbs), but not grasses. Such arthropods are said to be forbivorous or forbivores.

► Food Habits of Insects
► Herbivory
► Graminivory
► Phytophagy

Forbes, Stephen Alfred

Stephen Forbes was born in Illinois on a small pioneer farm on May 29, 1844, one of six children.



Foramen Magnum, Figure 78 **The posterior view of the head of a grasshopper (Orthoptera).**

His father died when Stephen was ten, and it was Stephen's older bother, Henry, who sacrificed his own education to send Stephen to Beloit Academy in 1860, a short-lived endeavor because the funds could not be continued. Henry and Stephen served as soldiers in the American Civil War (during which Henry died) and, afterwards, in 1865, Stephen went to study medicine at Rush College in Chicago, but dropped out because of shortage of funds and an aversion to conducting surgery without anaesthetics. He then became infatuated with botany and other aspects of natural history, and worked for some time as a schoolteacher. When J.W. Powell resigned as curator of the Illinois Natural History Society in 1872, Stephen succeeded him. He was appointed in 1877 Director of the State Laboratory of Natural History, a position that he held for the next 40 years, at which time he was made head of the Illinois Natural History Survey, a newly-organized entity. Additionally, he was appointed professor of zoology at the Normal University in 1875–1878, and in 1882 Illinois State Entomologist. But in 1884 he became Dean of the College of Science at the University of Illinois (Fig. 79) and in the same year Indiana University bestowed upon him the title of doctor of philosophy. His interests were not just in entomology, but extended to birds, fishes, crustaceans, leeches, bacteria, rotifers, the parasites of swine, museum methods, and teaching. He was one of those rare individuals who can survive on few hours (five in his case) of sleep each night. His entomological efforts were applied especially to applied entomology, and he worked on Hessian fly, and pests of maize ("corn"), strawberries, sugarbeet, the chinch bug, white grubs, San Jose scale, armyworms, codling moth, black flies, and diseases of insects. He was twice (1893 and 1908) president of the American Association of Economic Entomologists, and also served as president of the Ecological Society of America and of the Entomological Society of America. He died on March 13, 1930, surviving his wife Clara (with whom he had five children) by a few weeks.

Forbes, Stephen Alfred, Figure 79 **Stephen A. Forbes.**

Reference

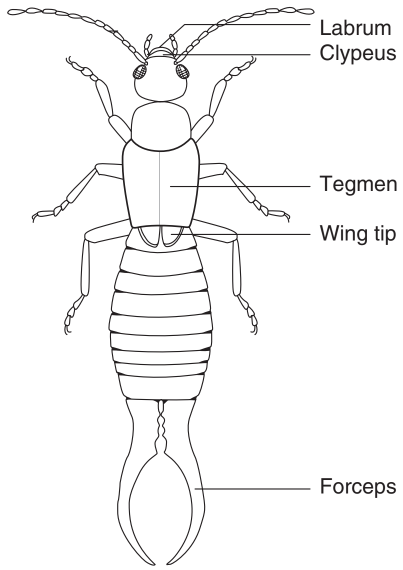
Mallis A (1971) Stephen Alfred Forbes. In: American entomologists. Rutgers University Press, New Brunswick, NJ, pp 55–60

Forceps

These are pincer-like processes found at the tip of the abdomen. They are particularly well developed in earwigs (Fig. 80), where they are used in defense, but also occur in some other insects where they are less noticeable and aid in clasping during copulation.

Ford, Edmund Brisco

Edmund Ford was born in the county of Cumbria, England, on April 23, 1901. In 1920 he entered Oxford University as an undergraduate. He never left, and after his degrees became lecturer in zoology and comparative anatomy. His interests turned toward genetics, he became director of the genetics laboratory within the Zoology Department and, from 1963 to 1969, professor of ecological genetics. One of his interests was in archaeology. A second interest, in wildlife conservation, led to establishment in England of the Nature Conservancy



Forceps, Figure 80 **Dorsal view of an adult earwig (Dermaptera), showing the forceps.**

Council, on which he served from 1949 to 1959. His special contribution in genetics was as "inventor" of ecological genetics, but his contributions to medical genetics led to his nomination as an honorary fellow of the Royal College of Physicians in 1974. Already in 1946 he had been elected a fellow of The Royal Society. His work in ecological genetics involved especially numerical fluctuations in populations of butterflies, and the concurrent changes in genetic structure. Some of his books are (1945) "Butterflies," (1955) "Moths," (1964) "Ecological genetics," (1965) "Genetic polymorphism," (1976) "Genetics and adaptation," and (1984) "The biology of butterflies." [His work on population genetics is mirrored in the work of Theodosius Dobzhansky, see above]. He died in Oxford on January 21, 1988.

Reference

Placito P (1988) Professor Edmund Brisco Ford, FRS. Antenna 12:91–93

Foregut

The anterior region of the gut, consisting of the buccal cavity, pharynx, esophagus and crop, and terminating with the proventriculus (Fig. 81), which controls passage of food into the midgut.

► Alimentary System

Foreign Exploration for Insects that Feed on Weeds

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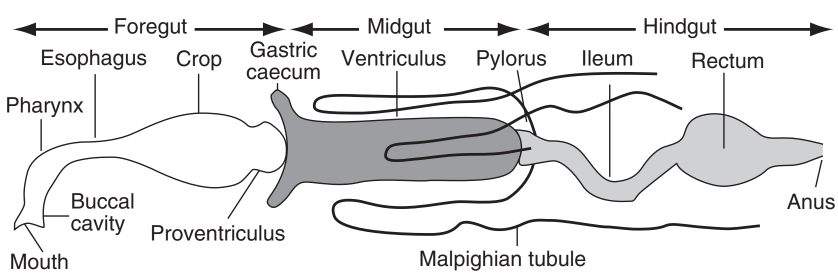
The principal reason to conduct foreign exploration for insects that feed on weeds is to identify exotic natural enemies for their prospective use in biological control programs. Indeed, importation of natural enemies is the most common approach to the biological control of pests, and is often called "classical" biological control. This type of pest control requires exploration for beneficial organisms in the home country of the pest to be controlled, with the intent of introducing the beneficial organism to the country where the plant has become a weed. It should be noted that in this case we consider the target plants – the weeds – to be the pests, and phytophagous insects to be



Foregut, Figure 81 **Generalized insect alimentary system (adapted from Chapman, The insects: structure and function).**

beneficial organisms (not pests, as commonly perceived). So we are reversing the way we usually consider insects and plants as pests and crops in agriculture.

Criteria for Successful Exploration

The target plant usually is not a problem in its area of origin and in its natural area of distribution, where as a matter of fact it may even be beneficial and very important for local ecosystems. The goal of biological control of weeds is to reproduce, in the new environment, a natural balance among the plant and its natural enemies. If successful, this process will reduce the populations of the weed to below the injury level, or minimize their impact on the environment. Foreign exploration is the first, and one of the most critical, steps for the success of any introductory biological control program. The exploratory entomologist should possess multidisciplinary expertise, especially in entomology (various fields), plant and insect pathology, field biology, botany and ecology. In addition, the explorer needs foreign language skills, field and travel experience, organizational ability, tact, self-reliance, stamina and resourcefulness, because exploration is often conducted under difficult conditions.

Plant Ecology

The nature of the weed problem, and the ecological basis for the spread of the plant in the new environment, provide the background for subsequent studies. The plant may have been introduced accidentally, or intentionally (as, for example, an ornamental that spread to become a noxious weed). The mode of introduction of the plant, the mode of spread, size of the area infested, type of habitats invaded and their soil and climate, the species of plants displaced, and impact on native flora and fauna, all contribute to defining the ecology of the target plant and its aggressiveness in its introduced range. One crucial aspect is the exact characterization of the taxonomy of the target plant. It is important to consider the existence of hybrids, biotypes, and other variations in the genetics, morphology, or biochemical traits of the plant. This is essential to obtain the desired effective biological agents for the target plant. Also, all information available from taxonomy of the insect can provide an important contribution to assess the potential as biological control agents of the organisms discovered during the survey. In all cases, a high level of host specificity is required to prevent damage to other species of plants.

Geographic Origin and Climate

Determination of the area to explore is dependent on the information available before starting such exploration. The plan for the survey should be designed on a case by case basis, based on the biology of the plant and its natural enemies, once they are known. The area for exploration should be within the native range of distribution of the target plant, and usually the center (or centers) of origin of the plant is considered the most promising area to explore, because it normally represents the main source of diverse and better adapted natural enemies. However, depending on the nature of the weed problem, evolutionary history and characteristics of the plant, geographical range, and the existence of distinct populations, it may be more important to consider the possible area from which the plant was originally introduced into the new environment. Also, effective natural enemies may occur in other parts of the range of distribution of the plant, as new parasite-host associations. The area explored should be large enough to offer considerable ecological and genetic variation, and therefore a diversity of natural enemies. Careful consideration should be given to the climates in the range of distribution of the plant, as well. The climate or physical environment at the source of biological control agents should be similar, as far as possible, to those of the areas where the plant is a weed problem. Generally speaking, climate matching is a good predictor of successful establishment of biological control agents. Nevertheless, there are cases of successful biological control agents that have been effective in controlling weeds in areas that were not ecoclimatically homologous; the new habitats did not match with the environmental characteristics of their area of origin. Also, it is possible to conduct foreign exploration for insects whose native area of distribution is not in the same hemisphere in which they should be released for biological control. In this case, it is necessary to synchronize their life cycle with the season in the area of introduction.

In conclusion, the identification of the geographical area where it will be more likely to find effective natural enemies is a major step for the success of the exploration. The study of the ecological relationships between the plant and its natural enemies and the importance of other biotic and abiotic factors helps to understand the role and potential effectiveness of the weed-feeding insects discovered during the exploration. The taxonomic position of the plant, along with its relatives and its evolutionary patterns, are important elements to consider during the survey and when evaluating the natural enemies associated with the plant. The exploration may be extended to plant species related to the target plant, since this can provide important information about the degree of specificity and potential of the insects associated to the plant as candidate agents for biological control. Also, in some cases, insects attacking other species of plants that are close relatives of the target weed, may prove to be suitable and successful biological control agents.

► Host Specificity of Weed-Feeding Insects

References

Debach P, Rosen D (1991) Biological control by natural enemies. Cambridge University Press, Cambridge UK

Bosch R, van den Messenger PS (1973) Biological control. Intext Educational Publishers, New York, NY

Forel, Auguste Henri

Auguste Forel was born in 1848 at Morges on Lake Geneva in Switzerland. As a boy, he became interested in insect natural history, influenced by his entomologist great uncle. At the age of 11, his special interest in ants developed as a result of his reading an old book by Pierre Huber. By the age of 12, he had begun to investigate thievery (later called by him lestobiosis) in the little ant *Solenopsis fugax*. After leaving school, he went to study medicine in Zurich and became interested in neurology and psychopathology. Thereupon he went to Vienna and worked on a doctoral dissertation on the morphology of the optic thalamus. Next, he went to Munich and worked for 5 years as assistant in psychology, being much involved in the development of microscopy. Meanwhile, his studies of ants continued, and in 1869 he published his first entomological paper on the behavior of *Solenopsis fugax*. This was followed in 1874 by a groundbreaking book on Swiss ants, "Les fourmis de la Suisse." In 1879 he was appointed professor of psychiatry in Zurich and his career in psychiatry continued to develop with numerous publications. However, it was not surprising that he, a neurologist, should also have studied neurology and sensory perception in ants. His work on chemosensory perception by the antennae of ants was published in 1902, and he worked on the development of castes (polymorphism), the organization of social instincts and their morphological basis, colony development, slavery, and parabiosis in ants. He also worked on collections of tropical ants and phylogeny of ants, and succeeded in describing 3,500 new taxa of ants. He espoused pacificism during World War I, and then socialism. He died in Yvorne, Switzerland, on July 27, 1931.

Reference

Brun R (1931) August Forel. Mitteilungen der Deutschen Entomologischen Gesellschaft 2:129–136 + 1 pl

Forensic Entomology

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Forensic entomology is the intersection between insect science and the legal system. Although most recent attention has focused on the subspecialty known as "medicocriminal entomology," where insect development and succession on a corpse are used to estimate how long the decedent has been dead, there are additional areas where entomology is of legal interest.

Urban entomology includes a variety of important insects with legal implications. Obviously, termites and the damage they cause are at the center of many legal controversies. Other wood-destroying insects, such as powder post beetles, can have similar effects. Dermestid larvae can damage or destroy hides, animal specimens, and furs. Clothes moth larvae can damage stored garments. All of these situations may result in lawsuits.

Another legal implication under the rubric of urban entomology is nuisance. Although often paradoxically rural in nature, flies and other insects emanating from livestock or poultry facilities can annoy nearby residents and result in claims for damages or to enjoin further livestock operations.

Insecticide applications against pest insects can result in drift, run-off or unanticipated outcomes and therefore claims for negligence or recklessness. Cockroaches or flies can adversely affect infants in nurseries or the elderly in nursing homes and result in claims of neglect. Poisonous spiders, especially the brown recluse, are frequently the focus of lawsuits brought under landlord-tenant, worker's compensation or invitee theories.

Insects, insect parts or insect debris in food or similar materials fall under the category of stored products entomology. The typical case involves beetles or moths in flour, cereals or other foodstuff; however, products such as herbal pharmaceuticals may also be involved. Much litigation involves insects associated with restaurants and especially fast-food establishments. Customers finding insects in hamburgers or other foods may sue under various legal theories, but the rigid procedures followed by most national chains typically offer thermal protection against insect and microbial contamination. Not infrequently, customers may try to defraud restaurants or markets by deliberately putting insects into food purchases. These attempts are typically identified by inconsistencies in behavior or biology between the species chosen and the facts of the case.

Medicocriminal entomology is the principal forensic emphasis of insect science. Two major approaches are typically employed to facilitate estimates of postmortem interval or situs (place) of death. Insects are cold-blooded, or poikilothermic, animals that develop, within limits, proportionately more rapidly as temperatures increase. The biologies of most common necrophilous species of flies have been well studied and developmental data are readily available. As the insect "buzzards" of decomposition, female blow flies (Diptera: Calliphoridae) oviposit on carrion in a predictable manner. Many species appear at dead bodies within a few minutes after death has occurred; others exhibit delays in appearance. Therefore, if certain conditions are met, these flies can reflect the length of time someone has been dead. Obviously, the method is best applied during the season of the year when flies are active, and the flies must have access to the corpse. Corpses inside automobile trunks, inside buildings, wrapped in plastic, or in other unique circumstances may be totally or partially protected from flies. Most common blow flies cease oviposition during nighttime hours. Thus, in a straightforward application where a decedent is found outdoors during summer, the procedure is to collect representative samples of the insects present and to assess the most mature stages present. If the species are known, the measured rates of development can be compared to retrospective temperatures obtained from proximate weather stations and the amount of time required to progress from the stage deposited on the decedent by the female fly to the stage collected can be estimated. This period is known as the "minimum postmortem interval," because the decedent in question had to be dead for at least that period.

It is well established that insects and other arthropods appear at dead animals and humans in a predictable succession of species, depending on how long the decedent has been dead. Local studies of the succession of necrophilous arthropods can facilitate mostmortem estimates.

Medicocriminal entomology has enjoyed more than a century of judicial acceptance. It has a solid foundation of insect taxonomy, physiology and behavior and thus passes the "good science" test that is part of evidentiary admissibility. The same is true of the other fields in forensic entomology, and these techniques are often useful as controversies are resolved within the judicial system.

► Decomposer Insects

References

Byrd JH, Castner JL (eds) (2000) Forensic entomology: the utility of arthropods in legal investigations. CRC Press, Boca Raton, FL, 418 pp

Catts EP, Haskell NH (eds) (1990) Entomology and death: a procedural guide. Joyce's, Clemson, South Carolina

Catts EP, Goff ML (1992) Forensic entomology in criminal investigations. Ann Rev Entomol 37:253–272

Hall RD, Haskell NH (1995) Forensic entomology: applications in medicolegal investigations. Chapter 25C in Wecht C (ed) Forensic sciences. Matthew Bender, New York, NY

Smith KGV (1986) A manual of forensic entomology. Cornell University Press, Ithaca, NY

Forest Flies

Some members of the family Hippoboscidae (order Diptera).

► Flies

Forficulidae

A family of earwigs (order Dermaptera). They sometimes are called spine-tailed earwigs.

► Earwigs

Formicary

A nest of ants, an ant mound, or artificial nest used to house ants.

Formicidae

This family consists of the ants (order Hymenoptera).

► Ants
► Wasps, Ants, Bees and Sawflies

Formosan Subterranean Termite, *Coptotermes formosanus* Shiraki (Isoptera: Rhinotermitidae)

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Termites are primarily wood feeding insects, and occur throughout the world. Out of about 2,300 known species, 183 are responsible for significant economic damage. The subterranean termites, as the name suggests, live mostly underground and are major pests of wood and wood products. Most of the destructive species belong to the family Rhinotermitidae, with their center of origin and dispersal primarily in the Oriental region. In this family three genera, *Coptotermes*, *Reticulitermes* and *Heterotermes* are of enormous significance because of the damage they cause. *Coptotermes*, essentially a tropical and subtropical genus, is distributed in the Far East, South Asia, Australia, parts of southern Africa, southern regions of the U.S. (Fig. 82) and Hawaii. Some of the most destructive species include *C. formosanus* (Far East and USA), *C. parvulus* (Indian subcontinent), *C. havilandi* (Thailand, Indonesia and Malaysia) and *C. frenchi* (Australia). In the continental USA, the Formosan termite, *C. formosanus*, was first detected in 1965

Formosan Subterranean Termite, *Coptotermes formosanus* Shiraki (Isoptera: Rhinotermitidae), Figure 82 World distribution of *Coptotermes* spp.

Formosan Subterranean Termite, *Coptotermes formosanus* Shiraki (Isoptera: Rhinotermitidae), Figure 83 A 1-year-old incipient colony of *Coptotermes formosanus,* with the primary reproductives, a soldier, workers and eggs.

around Houston, Texas, and was probably introduced between 1944–1946 in ships returning from the Pacific arena.

The Formosan termite, being a social insect, has a complex caste system. A mature colony comprises a queen and a king, eggs, larvae, workers, soldiers (Fig. 83) and brachypterous nymphs. Each year, for a period of about 6–8 weeks, the mature colonies produce huge swarms of winged adults or primary reproductives. After a short flight to the nearest source of light, the alates land on the ground, shed their wings and form tandem pairs with males closely following the females. The link between the sexes is facilitated by a contact sex pheromone produced by the female. Most of these adults are killed by predators or die of other natural causes. Surviving pairs find a suitable place (need wood and moisture) and form fully enclosed nuptial chambers. Mating takes place within these chambers. There are no external genitalia and the tail to tail mating lasts only about 30 s. Sperm are circular in shape and lack the characteristic tail. Each reproductive pair can mate repeatedly and egg laying follows within a couple of days. After laying 30–40 eggs over a period of about 2 months the pair spends the next 2–3 months feeding and grooming the young larvae. Egg-laying is then resumed and the cycle is repeated about four times over a period of 2 years. After this period, egg-laying is almost continuous and the female grows to an enormous size. Such a female is called a physogastric queen and is essentially a bag of eggs. Various estimates suggest that a physogastric queen may lay over 1,000 eggs/day. The larvae, after molting three times, become either workers or pre-soldiers, the latter molting to soldiers. Typically, a Formosan termite colony has about 5% soldiers, whose primary function is to protect the colony from invaders. The workers build galleries and forage for food. They also feed and groom the newly hatched larvae. Once a colony is 8–10 years old, it starts producing brachypterous nymphs which have small wing pads. After several molts, the brachypterous nymphs give rise to the alates. The factors that regulate formation of various castes, particularly brachypterous nymphs, are not fully understood. Termites are unable to digest wood on their own, and require the help of flagellates and spirochetes present in large numbers in their gut to digest cellulose to usable sugars.

The Formosan subterranean termite, with very high reproductive capacity and resulting colony size (1–4 million termites/mature colony), has tremendous potential for destroying wooden structures, live trees and selected crops. Damage due to subterranean termites in the U.S. is estimated at around $1 billion and the control measures could easily add another $1.5 billion annually. In heavily infested areas, *C. formosanus* can cause major structural damage to an unprotected home in 6 months and almost complete destruction within 2 years.

Detection of termite infestations is the first step in the war against this menacing pest, and remains a critical issue for pest control operators and homeowners alike. As cryptic organisms, subterranean termite infestations remain hidden below the ground, inside trees and within building structures. Traditional methods of detecting infestations of subterranean termites include the use of a flashlight and a sharp probe to determine whether termites are present, but this is useful only in areas accessible to inspection. Other methods that have been studied for detection of termites include use of acoustic signals, odor detection using electronic devices, video probes and infrared imagery. In addition, light and/or sticky traps are used to monitor alates that can suggest the presence of termites in a general area. In-ground monitors, usually in the form of wooden stakes or plastic stations containing wood placed at regular intervals around structures to be protected, have been used to detect infestations. Discovery of termites in the monitors, with regular monitoring, indicates their presence in the structures or surrounding soil; however, the converse is not necessarily true.

Subterranean termites have been around for millions of years and are well adapted to environmental stresses. Being underground, they are fairly well protected from common hazards and the possibility of direct pesticide application. Until recently, termite management practices had focused on protecting individual structures through application of physical or chemical barriers to exclude termites from the structure, while doing little to mitigate populations of the termites in the surrounding area. Present management paradigms have changed with the advent of new termite control methods to that of reducing termite populations below economic threshold while protecting houses, wood products and trees. The new management paradigm can only be achieved through a combination of existing technologies and continued development of new technologies and integrated pest management concepts.

Anything non-chemical that would stop foraging termites from getting to a potential host is a physical barrier. Physical barriers are primarily used to protect buildings and involve the use of particulate matter or metal screens. Pre- and post-construction soil treatment with persistent chemicals such as cyclodienes (aldrin, dieldrin, etc.) was fairly effective against subterranean termites. Some of these chemicals had residual lives of 25–35 years in the soil. However, environmental and health concerns led to the cancellation of their use in mid-1980s. The newer chemicals besides being less mobile in the soil than the organochlorine pesticides require greater precision and frequent application to provide a uniform barrier to termite penetration.

Because of the short life of currently used liquid termiticides, the relative difficulty of providing a complete chemical barrier, and because of continuing health and environmental reasons, monitoring/baiting technologies have been developed to detect the presence of termites and deploy insecticide only when termites are present. Termite presence is monitored using cellulose substrates examined on a regular basis. Several monitoring/baiting systems are commercially available for both in ground and above ground use. Soil monitoring stations are regularly spaced around the structure to be protected. Once termite activity is detected in a monitoring station, the bait is replaced with a toxin-laced substrate. To effectively use baiting technology as a control, the toxicant must be non-repellent and a slow-acting toxin so that termites do not die at the site of treatment and become secondarily repellent. Further, such a slow-acting toxin allows termites to distribute the toxin more widely throughout the colony before they die by grooming and trophollaxis. One group of such chemicals includes the chitin synthesis inhibitors (CSI). The CSIs disrupt ecdysis resulting in the death of the colony.

The subterranean termites live in warm and damp habitats which can be very conducive to the establishment of pathogenic bacteria, fungi and nematodes. However, none of these organisms have proven effective in controlling the termite infestations under field conditions.

Contrary to the practice of treating buildings, chemical treatment of trees is a more recent phenomenon. This is particularly important in the attempt to save valuable trees in urban landscapes. Holes are drilled into a tree trunk and termiticides injected into the termite galleries, usually formulated into a foam to allow movement of the pressurized stream both upward and downward within tree hollows and the termite galleries.

Wood and moisture are two primary requisites for successful establishment of subterranean termite infestations. Sanitation, associated with termite control is a special case in which removal of one or more factors required for termite survival can provide protection by limiting their ability to colonize the area.

References

Higa SY (1981) Flight, colony foundation, and development of the gonads of the primary reproductives of the Formosan subterranean termite, *Coptotermes formosanus*. Ph.D. Dissertation, University of Hawaii, Honolulu, Hawaii, 173 pp

King EG (1971) Biology of the Formosan subterranean termite, *Coptotermes formosanus* Shiraki, with primary emphasis on young colony development. Ph.D. Dissertation, Louisiana State University, Baton Rouge, Louisiana, 190 pp

Krishna K, Weesner FM (1969) Biology of termites, vols 1 & 2. Academic Press, New York, NY

Formulation

The manner in which a pesticide is prepared for sale. Additional steps may or may not be required by the applicator before the product is ready to be applied. A formulation typically consists of a toxicant and adjuvants, and may contain a synergist and a diluent.

► Insecticides
► Insecticide Formulations

Fossil Record of Insects

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Insects have a relatively extensive fossil record, with approximately 1,263 families in 30 commonly recognized orders having been identified. Although only a few fossil insects (such as Collembola) are known from the lower Devonian, a massive radiation began sometime during the early Carboniferous, more than 325 million years ago (mya). The first insects lack wings, but winged insects (the pterygotes) soon radiated into stem groups of all major lineages, including ephemeroids, odonatoids, plecopteroids, orthopteroids, blattoids, hemipteroids, and endopterygotes. The number of orders present by the upper Permian was similar to that today although some of the orders are now extinct and new orders have evolved. Insects, as measured by the number of families, increased in diversity during the late Carboniferous and middle Permian (Table 7).

Insects are highly diverse and ancient arthropods. For example, within the phylum Arthropoda the subphylum Crustacea was present in the Cambrian (about 600 million years ago, mya). A bristletail (Archaeognatha) from the Early Devonian resembles modern archaeognathans. Clear remains of a Collembolan have been found in Devonian deposits and arthropods have apparently been found on land since Devonian times. Two Collembola species were found in the lower Devonian (400 mya) that resemble recent extant Isotomidae and Neanuridae, suggesting that terrestrial arthropods already had radiated in the Ordovician (ca. 500 mya).

A number of extinct and extant orders of primitive insects have been found in a diverse late Paleozoic fauna. During the Carboniferous (which began 360 mya) a diverse array of extinct (in italics) and extant insects were present, including the: Diplura, Monura, Diaphanopterodea, Palaeodictyoptera, Megasecoptera, Permothemistida, Ephemoptera (mayflies), Protodonata, Paraplecoptera, Plecoptera (stoneflies), Orthoptera (grasshoppers

Fossil Record of Insects, Table 7 **Geological time scale in millions of years and types of fossil insects found**

Era	Period	Epoch	Began mya	Extinct and extant fossil insect orders first found
Cenozoic	Quaternary	Recent		Protura, Zoraptera, and Phthiraptera first appeared in fossil record.
		Pleistocene	1.6	
	Tertiary	Pliocene	5	
		Miocene	25	
		Oligocene	35	
		Eocene	60	Mantodea first appeared in fossil record.
		Paleocene	65	
Mesozoic	Cretaceous		145	Isoptera first appeared in fossil record.
	Jurassic		210	Dermaptera first appeared in fossil record.
	Triassic		245	Odonata, Titanoptera, Grylloblattodea, Trichoptera, Lepidoptera and Hymenoptera first appeared in the fossil record.
Paleozoic	Permian		285	Permothemistida, Plecoptera, Embioptera, Protelytroptera, Glosselytrodea, Psocoptera, Thysanoptera, Hemiptera, Antliophora, Mecoptera, Diptera, Amphiesmenoptera, Neuroptera, Megaloptera, and Coleoptera first appeared in the fossil record.
	Carboniferous		360	Pterygotes radiated into stem groups of all major lineages, with seven surviving to modern times (ephemeroids, odonatoids, plecopteroids, orthopteroids, blattoids, hemipteroids, and endopterygotes). Diplura, Monura, Thysanura, Diaphanopterodea, Megasecoptera, Permothemistida, Protodonata, Paraplecoptera, Orthoptera, Blattodea, Caloneurodea, Blattinopsodea, and Miomoptera were present.
	Devonian		400	Collembola (*Rhyniella praecursor*) and Archaeognatha
	Silurian		440	Mites, opilionids, scorpions, pseudoscorpions, centipedes, spiders found in preDevonian strata.
	Ordovician		500	
	Cambrian		600	

and crickets), Blattodea (cockroaches), Caloneurodea, Blattinopsodea and Miomoptera.

During the Permian (which began 285 mya), additional extinct and extant insect groups are found in the fossil record, including Plecoptera (stoneflies), Embioptera (webspinners), Protelytroptera, Glosselytrodea, Thysanoptera (thrips), Hemiptera (true bugs and leafhoppers), Antliophora, Mecoptera (scorpionflies), Diptera (true flies), Asmphiesmenoptera, Neuroptera (lacewings, antlions), Megaloptera (dobsonflies), and Coleoptera (beetles).

By the Triassic (245 mya), nearly all modern orders of insects are found in the fossil record, including Lepidoptera (butterflies and moths), Trichoptera (caddisflies), and Hymenoptera (bees and wasps). By the Jurassic (210 mya), many current families were present. Tertiary insects (65 mya) are essentially modern and include genera nearly indistinguishable from living fauna.

The great diversity of insects was achieved by low extinction rates rather than by high origination rates. The great radiation of modern insects began 245 million years ago and was not accelerated by the expansion of the angiosperm plants during the Cretaceous period.

There are more than 700,000 living species of living insects classified in at least 29 orders and more than 750 families, with the orders Coleoptera (>300,000 named species), Lepidoptera (>120,000 species), Hymenoptera (>120,000 species), and Diptera (>150,000 species) containing the most species. Insects are diverse, numerous, and ancient. An understanding of their systematics and phylogeny will require the combined use of the fossil record, traditional morphological data, and molecular methods.

References

Jarzembowski E, Ross A (1994) Progressive palaeontology. Antenna 18:123–126

Kukalova-Peck J (1991) Fossil history and the evolution of hexapod structures. In: The insects of Australia, 2nd edn. Melbourne University Press, Melbourne, Australia, vol 1, pp 141–179

Labandeira CC, Sepkoski JJ Jr (1993) Insect diversity in the fossil record. Science 261:310–315

Labandeira CC, Beall BS, Hueber FM (1988) Early insect diversification: evidence from a lower Devonian bristletail from Quebec. Science 242:913–916

Fossorial

Adapted for digging; usually used in reference to legs.

Founder Effect

The genetic pattern resulting from introduction of a small population into a new area, and the subsequent divergence from the parental stock. The new population, after a period of time, may no longer be compatible with the original population and is incapable of interbreeding.

Foundress

Among social insects, a fertilized female that founds a new colony. All the offspring in the colony are the sons and daughters of the foundress.

Fourcroy, Antoine-François (Comte De)

Antoine-François Fourcroy was born in France in 1755 and grew up in poverty. He studied medicine, assisted financially by a benefactor, and received a medical degree in 1780. He was appointed professor of chemistry in 1784 at the Jardin du Roi, later Jardin des Plantes, and still later Museum National d' Histoire Naturelle in Paris. He worked with Lavoisier and others in studying chemicals of animal and plant products, classifying them, and reforming the system of chemical nomenclature. He published major works on chemistry in 1792 and 1801. He also was interested in the classification of animals, and published (1785)

"Entomologia Parisiensis; sive catalogus insectorum quae in agro Parisiensi reperiuntur; secundum method Geoffraeanam…" in two volumes; Geoffroy contributed descriptions of new species in pages 1–231 of the first volume. He was a strong supporter of the French revolution, held public offices in it, and became director-general of public education in 1901. In 1908, he was made a count, and became known as Antoine-François de Fourcroy. He died in 1809.

Reference

Nordenskiöld E (1935) The history of biology: a survey. Tudor, New York, 629 pp

Four-Legged Mites (Eriophyoidea or Tetrapodili)

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The Eriophyoidea or Tetrapodili are unusual mites because they have only two pairs of legs as adults instead of the normal four pairs. Eriophyoid mites are second only to the spider mites in their economic importance as plant pests around the world. Eriophyoid mites are minute, and highly specialized to feed on plants. They are the smallest arthropods that feed on plants, averaging 100–500 μm in length and, despite their very small size which could lead to rapid water loss, some can survive in relatively exposed environments on leaves. The mouthparts of eriophyoids consist of a pair of stylet-like chelicerae and a pair of accessory stylets which are modified palps. The small size of the stylets allows eriophyids to penetrate only about 5 μm into the leaf, so feeding occurs in the plant epidermis (Fig. 84).

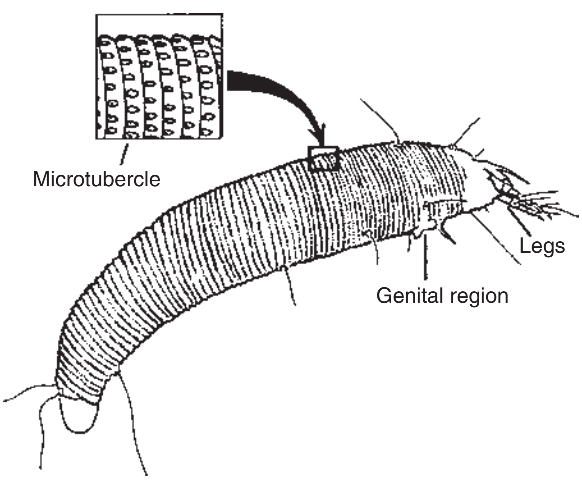
The Eriophyoidea contain three families, the Phytoptidae (consisting of about 20 species of primitive forms often found on conifers), the Eriophyidae (consisting of about 85% of the known species) and the Diptilomiopidae (consisting of about 16 species that are vagrants on leaves). Approximately 3,000 species in 230 genera of eriophyoid mites have been described, yet the biology of many remains relatively unknown.

Most eriophyoid females deposit eggs, from which larvae hatch. After larvae feed they enter a quiescent resting stage from which a nymph emerges and feeds. After another resting stage, adults emerge. The spheroid eggs are laid on leaves or on buds and very small (about 20–60 μm in diameter), but large in comparison to the size of the female depositing them. Immatures are similar to adults in appearance, but smaller and lacking external genitalia. The immatures of many species have never been studied. Adults consist of females and males, but females are more numerous and males of some species have not been found. Males are usually similar to females, although smaller. The basic life cycle consists of egg, larva, nymph, adult, but eriophyoids may have more complex life cycles, with two different types of adult females.

Females of species in which there are two types of adult females are called protogyne and deutogyne. The protogyne female form usually is similar to that of the male. The second type of adult female is the deutogyne, and she often looks very different from the protogyne. This has created taxonomic confusion. This type of life cycle was discovered in the plum nursery mite, *Aculus foceui*; the deutogyne female is the overwintering or hibernating form of *A. foceui*, developing when the foliage begins to harden in the hottest part of the summer. Deutogynes do not deposit eggs prior to overwintering and have a different body form than the protogynes. In the buckeye rust mite, *Tegonotus aesculifoliae*, the two forms were sufficiently different that they were given different genus names. In general, the main differences between proto- and deutogynes is in the microtuberculation (shape of micro ridges on the exoskeleton, which are important taxonomic characters); deutogynes have a reduced microtuberculation, or the microtubercles are a different shape. Deutogynes appear to be adapted to survive adverse conditions perhaps because the reduced microtubercles limit water loss.

Leaf hardening, particularly in the case of eriophyoid species that are leaf vagrants or rust mites, triggers the production of deutogynes in late spring or summer, usually in association with rising temperatures. In some species, particularly those in erinea or galls, the trigger is the onset of cool conditions in the fall of the year and the deutogynes appear later in the year. Deutogynes move off leaves into sheltered crevices on twigs, under bud scales, or other protected sites where they hibernate or aestivate. The deutogyne females mate prior to entering the protected sites and the males don' t go with them. If females fail to mate, they produce only male progeny, indicating that they are arrhenotokous.

Initially, it was assumed that deutogynes were produced only in those species that lived on deciduous host plants. Later, however, it was discovered that deuterogyny occurs in species on evergreen plants and in species on tropical plants. The deutogynes in the tropical or subtropical species differ from the deutogynes in temperate climates. For example the mango-leaf-coating eriophyid, *Cisaberoptus kenyae*, is found on mango leaves and is widespread in the tropics; in *C. kenyae*, however, the deutogynes deposit eggs. In this species, the deutogyne is the commonest form seen and seems to tend the white coating, keeping the coating raised enough to provide space for other colony members. Finally, some species have less distinctive forms of deutogynes, making it difficult to resolve whether there are actually two types of females. It is possible that the less-distinctive deutogynes are suited for dispersal rather than hibernation or aestivation. Only a relatively few eriophyoid species have been studied in sufficient detail that their biology and ecology is well known.



Four-Legged Mites (Eriophyoidea or Tetrapodili), Figure 84 **Eriophyoid mites are wormlike, with only two pair of legs (*right*) close to the chelicerae, the piercing mouthparts. The posterior of the mite has anal pads that allow the mites to adhere to the leaf surface. The exoskeleton has distinctive microtubercles that are useful in identifying eriophyoids. The size and shape of these tubercles may differ between the two types of females, called protogynes and deutogynes, found in some species.**

Eriophyoids disperse by walking, or are wind distributed. At least one, *Aceria litchii*, can be moved about on the bodies of honeybees after the bees forage in infested flower panicles of lychees in Australia. Eriophyoid mites can be transported easily on plant materials, as well. Wind dispersal in some species appears to be a matter of choice with mites assuming a distinctive upright posture to facilitate their aerial dispersal.

Eriophyoids are called blister mites, rust mites, bud mites or gall mites because their feeding causes distinctive damage to plants (Table 8). Fusiform eriophyoids are found wandering on the leaf or bud surfaces of their hosts and are classified as rust mites or leaf vagrants. Examples include the citrus rust mite, a pest of citrus in many parts of the world. Soft bodied worm-like eriophyoids also are found within buds, in blisters, or in galls, and are called bud or gall mites. They are most often found on perennial plants and are generally quite host specific. In fact, eriophyoids are sufficiently host specific that a key is available that shows photographs of the damage on each host plant; this key allows one to identify the species in North

Four-Legged Mites (Eriophyoidea or Tetrapodili), Table 8 Some eriophyoid mite species, their hosts, and damage in North America

Host plant species	Mite species	Damage
Acer campestre, hedge maple	*Eriophyes macrochelus*	Leaf gall
Acer rubrum, red maple	*Eriophyes major*	Erineum, or hairy growth on leaf surface
Avena sativa, oats and other grasses	*Eriophyes tulipae*	Wheat-streak-mosaic virus disease
Carya illinoinensis, pecan	*Eriophyes caryae*	Leaf edge, spotting
Citrus spp., citrus	*Phyllocoptruta oleivora*	Bronzing, russeting of fruit, leaves and twigs
	Eriophyes sheldoni	Deformed buds, flowers, fruit and leaves
Corylus avellana, hazelnut	*Phytocoptella avellanae*	Big bud or bud gall
Cynodon dactylon, Bermuda grass	*Eriophyes cynodonis*	Leaf blade and terminal shoot distortion
	Eriophyes cynodoniensis	Leaf sheath and stem gall
Fagus grandifolia, American beech	*Acalitus fagerinea*	Erineum
Ficus carica, fig	*Eriophyes ficus*	Mosaic-virus disease
Fraxinus americana, white ash	*Eriophyes chondriphora*	Leaf gall
Gossypium spp., wild and cultivated cotton	*Acalitus gossypii*	Bud injury, foliage deformation, leaf blister
Juglans californica, California walnut	*Eriophyes neobeevori*	Catkin gall
	Eriophyes brachytarsus	Leaf gall
Juglans nigra, black walnut	*Eriophyes caulis*	Petiole gall
Juglans regia, English walnut	*Eriophyes erineus*	Erineum
Lycopersicon lycopersicum, tomato also *Datura*, *Petunia*, nightshade and potato	*Aculops lycopersici*	Foliage browning, withering and fruit russeting
Malus pumila, apple	*Calepitrimerus baileyi*	Browning underside of leaves
	Aculus schlechtendali	Injured terminal growth, leaf curl, russeting
Medicago sativa, alfalfa	*Eriophyes medicaginis*	Witch's broom
Pinus clausa, sand pine	*Trisetacus floridanus*	Aborted buds, rosette gall, stunted needles
Pinus monticola, Western white pine	*Trisetacus alborum*	ditto
Prunus domestica, plum	*Acalitus phloeocoptes*	Bud gall
	Phytoptus emarginatae	Leaf gall
Quercus agrifolia, California live oak	*Eriophyes paramackiei*	Brooming at lower tree level
	Eriophyes mackiei	Erineum
Rhus radicans, poison ivy	*Aculops toxicophagus*	Leaf gall
Tulipa sp., tulip	*Eriophyes tulipae*	Bulb damage

Four-Legged Mites (Eriophyoidea or Tetrapodili), Table 8 Some eriophyoid mite species, their hosts, and damage in North America (Continued)

Host plant species	Mite species	Damage
Vaccinium spp., blueberry	*Acalitus vaccinii*	Bud blister, rosette fruit deformation
Vitus spp., grape	*Calepitrimerus vitus*	Abnormal growth, bunched foliage, injured flowers, short internodes
	Colmerus vitus	Deformed bud clusters and leaves, erineum

America (unless the mite is a new invasive pest). Even where two eriophyoids occur on a plant, their feeding damage and location on the plant usually is so distinctive that the different species can be discriminated easily. These very tiny mites cannot be seen readily on leaf surfaces without magnification, however. Because galls or blisters remain on leaves even after the mites have died or dispersed, feeding damage can be seen until the deciduous plant defoliates.

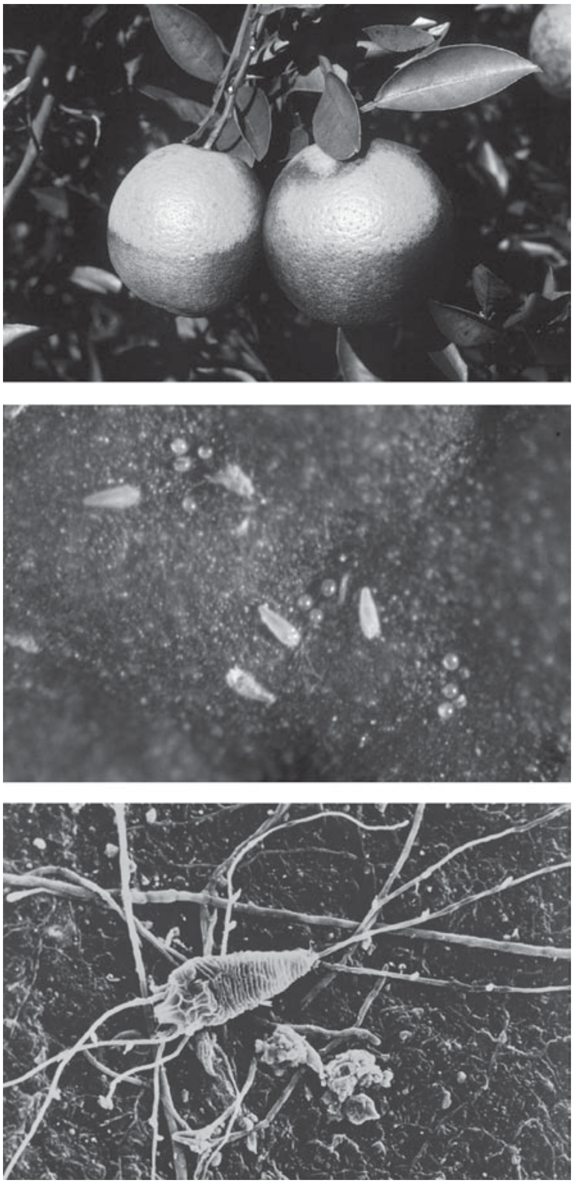
Leaf injury

Injury caused by eriophyoid feeding affects the surface (epidermis) of the leaf because the stylets (modified chelicerae) of these mites are short. Damage to foliage may be quite specific to the mite and host plant: the peach rust mite, *Vasates cornutus*, causes browning or silvering of the peach leaf surfaces by its feeding. *Aceria brachytarsus* causes pocketing of leaf tissues (purse galls) on walnut leaves. *Eriophyes pyri*, the pear blister mite, invades the mesophyll of pear leaves and causes serious injury. Hairy patches, called erinea, on the underside of grape leaves infested with *Eriophyes vitis* represent open galls in which the pocketing of the leaf tissue is minimal. Eriophyoids also injure buds by feeding on their surface and can cause gall formation. The citrus bud mite, *Aceria sheldoni*, causes fruit and leaf malformation in California citrus groves. Eriophyoids also cause "witches broom" of twigs, flower galls, shortening of internodes, or secondary development of leaf hairs.

Vectors of Plant Disease

Eriophyoids are vectors of plant viruses (potyviruses from the genus *Rymovirus*). Each virus has a limited host plant range and a single mite vector species usually is known for each virus. The best studied eriophyoid-virus relationship is the wheat-streak-mosaic virus and the wheat-spot-mosaic viruslike pathogen, both of which are transmitted by *Eriophyes* (= *Aceria*) *tulipae*. These viruses can be acquired after a few minutes of feeding, but longer access to plants results in higher transmission rates. Viruses are retained by the mites following a molt, but are not transovarially transmitted. The virus persists (Fig. 85) about one week at room temperature or for several weeks at lower temperatures in the vectors and must be acquired by one of the two nymphal stages if subsequent transmission by adults is to occur. Because adults cannot acquire and transmit virus, spread of the virus must originate from the original host of the individual mite. Dispersal of eriophyoids, and thus spread of virus, depends on temperature and wind. Although eriophyoids are wingless, during daylight hours they "stand up" on their anal papilla and allow themselves to be distributed by wind. *Aceria tulipae* transmits kernel-red streak of corn as well as wheat-spot, and wheat-streak mosaic viruses.

Other important plant-disease vectors include: *Aceria ficus* transmits fig-mosaic virus; currant-reversion virus is transmitted by *Phytoptus ribis*; peach-mosaic virus is transmitted by *Eriophyes insidiosus;* and ryegrass-mosaic virus is transmitted by *Abacarus hystrix*. The disease called "High Plains



Four-Legged Mites (Eriophyoidea or Tetrapodili), Figure 85 **Citrus rust mite and damage. (*above*) Discoloration of oranges caused by citrus rust mite feeding. (*middle*) Citrus rust mites as seen under a light microscope. (*below*) Citrus rust mite killed by *Hirsutella* fungus as seen under a scanning electron microscope.**

disease" is now known to be consistently associated with a virus and an eriophyoid mite, *Aceria tosichella*. Prior to 1993, no corn virus diseases were found in Colorado but a disease, initially diagnosed as wheat-streak mosaic, was found. The host range of the virus appears to include corn, wheat, barley, rye and oats, as well as cheat grass (*Bromus secalinus*) and yellow foxtail (*Setaria glauca*). The virus can be seedborne. Resistant cultivars have been identified and integrated pest management is possible using host plant resistance, elimination of volunteer plants, isolation from small grains (sources of the virus and vector), and modification of planting date.

Some Major Pests

Phyllocoptruta oleivora (Citrus Rust Mite)

The citrus rust mite is one of the most important and widespread citrus pests in the world. It reproduces rapidly and causes damage to the exterior of the fruit, which causes fresh market fruit to be downgraded. The interior quality of the fruit is not affected, so if the fruit is grown for juice, mite densities are less important.

Citrus rust mite eggs are laid in groups in indentations on fruits and on the ventral surfaces of leaves. The life cycle requires about 7–10 days in summer and females live about 20 days, depositing 20–30 eggs. The mites do well in warm, humid conditions. Severely infested fruits have a powdery appearance as a result of the exuviae left behind by the molting immatures. Mites do not tolerate bright sunlight well, so they choose undersurfaces of leaves and shaded areas of the fruit, which can result in a typical damage pattern in these areas. Feeding damage affects only the surface of the fruit and damaged fruits become silver, reddish brown or purplish black depending on the mite density. The rust mite is able to colonize very young fruit and, thus, control measures should be applied early, if natural enemies such as predator mites or the fungal pathogen *Hirsutella* is not suppressing populations sufficiently. In South Africa, the predatory mite *Amblyseius citri* feeds on rust mite, although it is not fully effective. In Florida, the rust mite is controlled in part by the fungus *Hirsutella thompsoni*. Unfortunately, the fungus often is eliminated if sprays are applied to control fungal pathogens of citrus. The rust mite is thought to have originated in southeast Asia, but little information is available on the natural enemies of this pest there.

Aculus cornutus (Peach Silver Mite)

This mite attacks peaches and almonds. The mites are found on leaves and their feeding causes the leaf surface to appear silvery when high populations are found. High densities can reduce tree growth and reduce fruit size. These mites can serve as prey for phytoseiid predators, such as the phytoseiid *Metaseiulus occidentalis* in California almond orchards, and thus rarely becomes a pest in almond orchards where these predators are abundant.

Aculops lycopersici (Tomato Rust Mite)

Tomato rust mites are pests of tomatoes around the world. Unlike many other eriophyoid mite species, the tomato rust mite attacks various plant species in the family Solanaceae. It can easily kill tomato plants and damages peppers, potatoes, egg plants, tobacco, and petunias. It is often found on *Ipomoea purpurea* (morning glory) in field margins. The morning glory is a natural host and these weeds can serve as a reservoir of the pest.

Tomato rust mites are dispersed by the wind and also by farm workers and agricultural tools. When the tomato plant begins to die, the rust mites migrate to the top of the plant, holding their bodies perpendicular to the leaf surface and adhering to the surface by the anal lobes. In this posture, they are more likely to be blown off the leaf surface. On occasion they form chains by crawling up each other to disperse. Tomato rust mites prefer warm weather and are able to feed on the upper surfaces of leaves in direct sunlight. Symptoms of rust mite damage on tomatoes include: bronzing of leaves, withering, and change of stem color from green to brown. Defoliation takes place, so eventually only young growth remains. The fruits are then sunburned, plant growth is slowed, and fruit production is reduced. If the fruits are attacked, the skin becomes brown. On potatoes, the tomato rust mite does not cause browning, but the leaves may become dry and the whole plant can die. Sulfur dusts or oils can be used to control the tomato rust mite.

Aculus schlechtendali (Apple Rust Mite)

These mites feed on flowers, fruits and leaves of apple. It causes apple leaves to roll up longitudinally and become rusty brown on the lower side and russeting of fruit. Aculus schlechtendali is considered a beneficial species in Washington apple orchards under an integrated mite management program because these mites serve as prey for the predatory phytoseiid *Metaseiulus* (= *Typhlodromus* or *Galendromus*) *occidentalis*. Apple rust mites provide alternative food for these important and effective predators early in the growing season and allow predator populations to increase so they can suppress the spider mite pests (*Panonychus ulmi* and *Tetranychus* spp.) on apples later in the growing season. Apple rust mite populations must become relatively large before they cause significant damage. Likewise, in the northeastern USA, *A. schlechtendali* is an alternative food source for the phytoseiid *Typhlodromus pyri* early in the growing season; this phytoseiid is an important predator of European red mite, *Panonychus ulmi*, in this apple-growing area.

Pesticides and Pesticide Resistance

Various insecticides, fungicides and miticides (acaricides) can be used to control eriophyoid mite pests. Generally, oils and sulfur are effective and have been used against eriophyoid mites for many years, although care must be taken to avoid phytotoxicity from both products.

Eriophyoid mite populations that are exposed to repeated and consistent applications of pesticides can develop a genetically based resistance to particular products. For example, some populations of the peach silver mite (*Aculus cornutus*) in

North America have become resistant to organophosphorous insecticides, and the apple rust mite (*Aculus schlechtendali*) in British Columbia and Washington state in the USA has become resistant to a variety of pesticides used in apple orchards. Likewise, the pear rust mite (*Epitrimerus pyri*) in Washington state is resistant to various pesticides. In citrus groves around the world, the citrus rust mite (*Phyllocoptruta oleivora*) has become resistant to several pesticides, including zineb, dicofol and chlorobenzilate, making control difficult. Developing effective management programs for these agricultural pests may require several tactics in order to delay the development of resistance in eriophyoid pest populations.

Invasive Species

The small size of eriophyoids makes them easy to transport on fruits and foliage without detection and eriophyoids can invade new geographic regions regularly. For example, the eriophyoid *Tegolophus perseaflorae* was found recently in flowers and fruits of avocado in Dade County, Florida. The mites feed on buds, causing necrotic spots on apical leaves and subcircular, irregular openings on mature leaves. Mites are also found on petioles and the undersides of leaves and fruitlets. The feeding causes fruit deformation and discoloration. It was speculated that avocado grafting material was the source of this new pest.

Biological Control of Weeds by Eriophyoids

Not all eriophyoids are considered pests. Many species remain unnoticed, while others are used for biological control of weeds. Attributes that contribute to their success as natural enemies of weeds include: eriophyoids are often host-specific, even to the level of race of plant and host tissue they attack. They are easily distributed by the wind; they can be used with other biological control agents; and some species are able to transmit specific plant viruses to the weed. Negative aspects include the fact that they are relatively slow-acting and must often be used in conjunction with other natural enemies. They are also quite sensitive to low relative humidities because of their small size.

The eriophyoid *Aceria chrondrillae* has been used in the biological control of the Eurasian rush skeleton weed, *Chrondrilla juncea*, in Australia and in the USA. Feeding on skeleton weed induces gall formation in the vegetative and flower buds, causing plant stunting, reduction in seed formation and weakness. Mites appear to be very specific to particular geographic races of the weed; a strain originating from Greece was most suitable against the weed in Australia, but this strain did not perform well in the USA. An Italian strain has been introduced to control the weed population in the USA.

Other eriophyoids have been considered as control agents of weeds, including *Aceria acroptiloni* which suppressed Russian knapweed (*Centaurea repens*) and was introduced into the Crimea from Central Asia. *Aceria centaureae* and *A. thessalonicae* have been evaluated for control of diffuse knapweed (*Centaurea diffusa*) in the USA and Canada. *Eriophyes boycei* was shipped from the USA to Russia for ragweed (*Ambrosia* spp.) control and *Aceria convolvuli* has been released for control of field bindweed (*Convolvulus arvensis*) in the USA. The European St. John's wort, *Hypericum perforatum*, is a weed in eastern Australia and, although the defoliating beetle *Chrysolina quadrigeminata* has become established and provides substantial control, the mite *Aculus hyperici* has been evaluated as an additional natural enemy. Host specificity trials indicate that *A. hyperici* is specific to the genus *Hypericum*.

Other species of eriophyoid mites could become useful natural enemies of weeds once additional information on their taxonomy, host range, and detrimental effects on target weeds have been obtained. In addition, the combination of a host-specific eriophyoid mite as a vector of a specific viral disease of the weed could result in enhanced biological control of weeds.

Identification of Eriophyoids

If you know the plant species and the location of the mite on the plant, you are likely to be able to identify the eriophyoid mite to species. For example, it is usually possible to identify North American eriophyoids without having to use a key because a list of host plants, symptoms of injury, and mite species in North America is available. Of course, this method won't work if the eriophyoid you are trying to identify is a new pest in the USA.

References

Keifer HH, Baker EW, Kono T, Delfinado M, Styer WE (1982) An illustrated guide to plant abnormalities caused by eriophyid mites in North America. USDA handbook 573, 178 pp

Lindquist EE, Sabelis MW, Bruin J (1996) Eriophyoid mites. Their biology, natural enemies and control, Elsevier Science, vol 6. Amsterdam, The Netherlands, 822 pp

Nault LR (1997) Arthropod transmission of plant viruses: a new synthesis. Ann Entomol Soc Am 90:521–541

Oldfield GN (1970) Mite transmission of plant viruses. Ann Rev Entomol 15:343–380

Fovea

A deep pit or depression on the integument of insects. A small pit is called a "foveola." Surfaces bearing fovea or foveola are said to be "foveolate."

Frass

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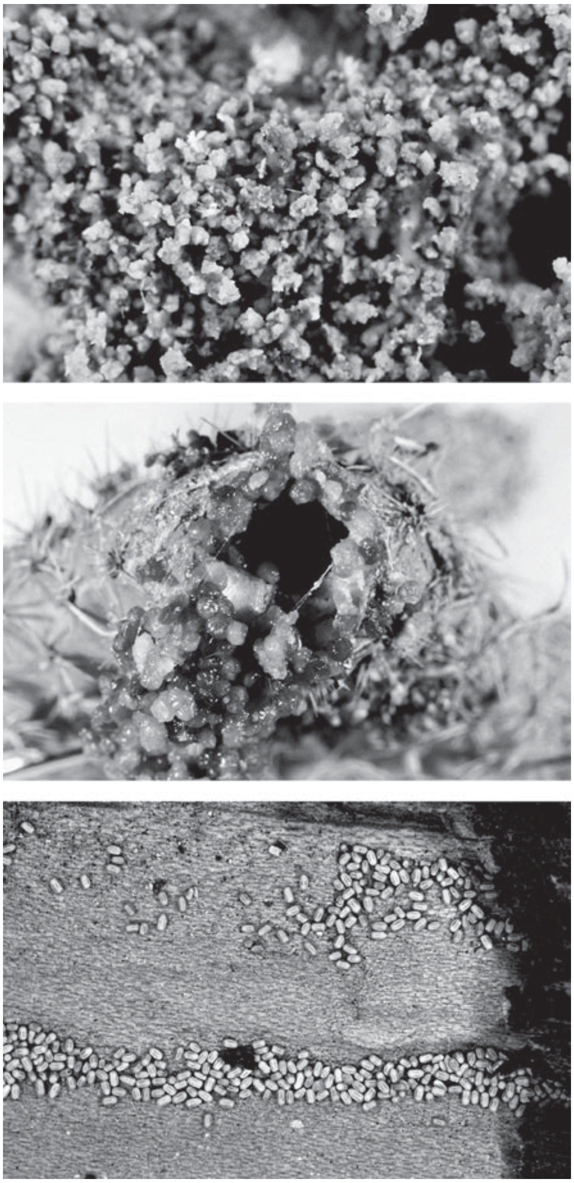
Frass is the solid excrement (fecal material) produced by various insects that feed on wood, foliage and other solid materials. Frass is produced in various shapes (Fig. 86), and moisture content varies with the diet. It is commonly produced in pellet form by various leaf-feeding caterpillars, sawflies



Frass, Figure 86 Frass, or excrement, can be of diagnostic value. Above is termite frass produced by subterranean termites; note that it has irregular edges and is dry. Middle image is moist frass produced by the blue cactus borer, and extruded from the tunnel by the larva; it is very moist. Bottom image is frass from drywood termites; it is produced in smooth-edged pellets and is very dry. (Termite frass photos by J.L. Castner, University of Florida; cactus borer frass photo by J.L. Capinera, University of Florida.)

and beetles, and the shape can be diagnostic of certain genera. The term is probably more widely used to describe excrement produced by various wood boring beetles and certain termites.

Frenate

Bearing a frenulum.

Frenular Hook

A hook or fold into which the frenulum is fitted. This structure occurs in the males of some Lepidoptera.

► Wings of Insects

Frenulum

A spine-like process in Lepidoptera in which the spine arises from the base of the hind wing, protrudes beneath the forewing, and serves to couple the fore- and hind wings during flight.

► Wings of Insects

Fringe-Tufted Moths (Lepidoptera: Epermeniidae)

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Florida State Collection of Arthropods,
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Fringe-tufted moths, family Epermeniidae, total 102 species, with many being Palearctic (36 sp.) and Australian (23 sp.). There are two subfamilies: Epermeniinae and Ochromolopinae. The family is part of the superfamily Copromorphoidea in the section Tineina, subsection Tineina, of the division Ditrysia. Adults small (8–20 mm wingspan), with head smooth-scaled; haustellum naked; labial palpi upturned; maxillary palpi 3-segmented. Wings narrow, with fringes longer on hindwings and scale tufts on forewing margin (Fig. 87). Maculation rather somber shades of brown, with various mostly darker markings. Adults are diurnal or crepuscular. Larvae are leafminers, leaf skeletonizers, or borers of seeds, fruits, or buds; a few are gall makers. Host records include several plant families.

Fringe-Tufted Moths (Lepidoptera: Epermeniidae), Figure 87 Example of fringe-tufted moths (Epermeniidae), *Sinicaepermenia taiwanella* Heppner from Taiwan.

References

Buszko J, Skalski AW (1980) Epermeniidae, Schreckensteiniidae. In: Klucze do Oznaczania Owadów Polski. 27. Motyle–Lepidoptera,22–23:1–35.Polskie Towardzystwo Entomologiczne [in Polish]
Gaedike R (1966) Die Genitalien der europäischen Epermeniidae (Lepidoptera: Epermeniidae). Beiträge zur Entomologie 16:633–692
Gaedike R (1976) Die Epermeniidae der äthiopischen Region (Lepidoptera). Beiträge zur Entomologie 26:451–454
Gaedike R (1977) de Revision der nearktischen und neotropischen Epermeniidae (Lepidoptera). Beiträge zur Entomologie 27:301–312
Gaedike R (1996) de Epermeniidae. In: Lepidopterorum Catalogus, (n.s.). Fasc 48 [47] Association for Tropical Lepidoptera, Gainesville, 20 pp

Fringe-Winged Beetles

Members of the family Clambidae (order Coleoptera).

► Beetles

Frisch, K. Von

Karl von Frisch was born in Vienna on November 20, 1886. After his schooling, he entered Universität Wien to study medicine, at the insistence of his father, although he preferred zoology. After 3 years of study in Vienna, his father relented and allowed him to transfer to Munich to study zoology. Now with a degree, he returned to Vienna in 1909 as a graduate student. In 1910 he was awarded a Ph.D. for a thesis on color changes in fishes. He returned to Munich as assistant professor of zoology, was promoted to associate professor by 1912. During World War I he worked at a Red Cross hospital in Vienna. In 1921 he became professor and director of the zoological institute of Universität Rostock, in 1923 he moved to a similar position at Breslau (now Wroclaw in Poland), and in 1925 he returned to Munich. That last city was heavily damaged in World War II, and he transferred to Graz in Austria. However, in 1950 he returned to Munich to help reconstruct the institute. His official retirement was in 1958, but he continued to publish research results until shortly before he died. He performed research and published on sensory physiology and animal behavior, producing 158 papers and 16 books. His best-known work is on the means by which bees navigate and communicate. His book (English edition 1966), "The dancing bee" and (English edition 1967) "Dance language and the orientation of bees" gained him much acclaim. His awards included a Nobel prize, six honorary doctorates, the Austrian medal of honor, and many others. He died on June 12, 1982.

Reference

Fergusson NDM (1983) Karl von Frisch, 1886–1982. Antenna 7:63

Frit Fly, *Oscinella frit* (L.) (Diptera: Chloropidae)

This insect damages the stem of wheat plants, principally in Europe.

► Wheat Pests and Their Management

Frivaldszky, Imre

GEORGE HANGAY
Narrabeen, NSW, Australia

Imre Frivaldszky was born on the 6th of February 1799 at Bacskó, in Zemplén Shire, Hungary. He began his studies in the highly regarded Piarist College in Sátoraljaújhely where he met the greatest Hungarian botanists of the time. During the many botanical excursions his interest toward natural history deepened and although in 1816 he enrolled as a student in the Budapest University of Medical Sciences, he spent most of his spare time outdoors, studying plants and animals. In 1823, he was awarded with the Doctor of Medicine degree, but he never became a practitioner. Instead, he devoted his life to natural history, especially to the study of Coleoptera. He became a curator of the Hungarian National Museum's natural history section, and he spent the first 10 years in this office by surveying the flora of the country. The resulting collection was outstanding by European standards, but Frivaldszky – and consequently Hungarian science - benefited even more from this work, as during the years of plant collecting, he gradually became a committed entomologist. In 1838 he was admitted into the Hungarian Academy of Science. His achievements in entomology were awarded by many learned societies in Hungary and abroad, and in 1847 he became the Director of the Hungarian National Museum. He expanded his sphere of interest to other countries as well. He organised a number of collecting expeditions to the Balkans, the Near East, the Mediterranean region and the neighbouring lands. His last expedition, at the age of 74, took him to Turkey. Shortly after this journey, on the 19th of October 1870, he passed away. Frivaldszky's life achievement was not only a huge natural history collection that formed the backbone of the museum, but also his tremendous fundamental work, which established entomology as a science in his country. His impetus to Hungarian entomology was so great that it was unparalleled for almost a century, until Zoltán Kaszab's directorship begun in the Hungarian Natural History Museum.

References

Balázs D (ed) (1993) Magyar utazók lexikona. Panoráma. Budapest, Hungary, pp 126–127

Szinnyei J (1980) Magyar írók élete és munkái. I-XIV. 1891–1914 Budapest, Facsimile edition. Budapest, Hungary

Frivaldszky, János

George Hangay
Narrabeen, NSW, Australia

János Frivaldszky was born on the 17th of June 1822, at Rajec, in Trencsén Shire, Hungary. He was introduced to natural history at an early age by his uncle, Imre Frivaldszky. He completed his formal studies at the University of Technology and received his diploma of engineering. But, he didn't become an engineer, instead choosing the study of zoology as his life-long career. He assisted his uncle in the processing and researching of the various collections brought back from his expeditions and became an expert entomologist and conservator. From 1850 onwards he often acted in his frequently sick uncle's museum position. Upon Imre Frivaldszky's retirement, in 1852 he became the assistant director of the Hungarian National Museum's Zoological Collections. János Frivaldszky was especially interested in the arthropods of Hungary and he set out to survey the country's fauna, with special attention to cave dwelling organisms. Due to his labors the museum's collections and entomological knowledge of the Hungarian fauna increased considerably. When the great collections of János Xántus arrived at the museum, Frivaldszky curated them and published the results (*Rövid vázlata azon szerzeményeknek, melyekkel Xántus János az MNM állattani osztályát gazdagította*. Pest, 1865.). Later in his life he studied ornithology and produced a concise work on the avifauna of Hungary (*Aves Hungariae* (*Magyarország madarai*). Budapest, 1891.). In recognition of his life-time achievements in zoology he was admitted in to the Hungarian Academy of Science, first as a corresponding member in 1865 and finally in 1875 as full member. He passed away on the 29th of March 1895 in Budapest.

Reference

Horváth G (1897) Emlékbeszéd Frivaldszky Jánosról. Akadémiai Értekezések, VIII. Budapest, Hungary

Froggatt, Walter Wilson

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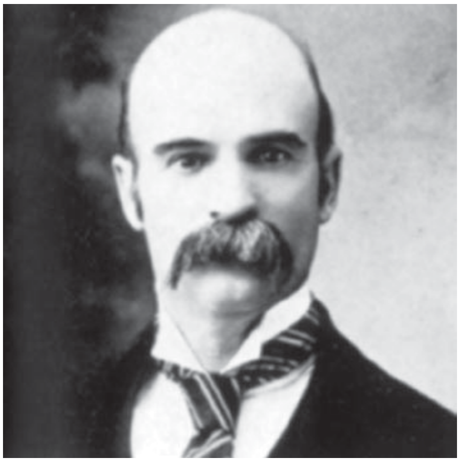
Walter Wilson Froggatt was born in 1858 in Melbourne, Australia. He had a keen interest in natural history, especially entomology, and led the adventurous life of a professional collector. In 1885 he joined the Royal Geographical Society's New Guinea Expedition and not much after that he was employed by Sir William John Macleay as a collector. Beginning in April 1887 he spent more than a year in the wildest parts of northwest Australia, working for Macleay. He spent most of his life in the field, either as a free-lance entomologist or in the service of institutes, museums or private collectors. Usually he traveled alone either by horse or on foot, carrying his equipment and supplies. He collected an enormous number of specimens, which are distributed amongst the many collections in Australia and overseas. In 1907, he published a popular book, the "*Australian Insects*" and in 1923 another on "*Forest Insects of Australia*." He was an avid writer, producing a record number of published entomological articles. From 1923 until 1927



Froggatt, Walter Wilson, Figure 88 **William Froggatt.**

he was Forest Entomologist (Fig. 88) of the New South Wales Forestry Commission. He passed away in 1937 in Croydon, New South Wales, Australia. Froggatt had a remarkably adventuresome life and he is remembered as a pioneer of Australian Entomology.

References

Froggatt WW (1934) A Naturalist in Kimberley in 1887. Aus Nat 9:69–92
Walkom AB (1942) Walter Wilson Froggatt (1858–1937) Proc Linn Soc NSW 67:77–81
Wilson FE (1929) The Froggatt entomological collection. Vic Nat 45:117–119

Froghoppers

Members of the family Cercopidae (order Hemiptera).

► Bugs

Frons

The front of the head capsule, below the base of the antennae (Fig. 89) and above the mouth parts. This is also called the front.

► Head of Hexapods

Front

The front of the head capsule, below the base of the antennae and above the mouth parts. This is also called the frons (Fig. 89).

► Head of Hexapods

Frontal Suture

A suture shaped like an inverted "U," with the base of the "U" positioned just above the antennal bases and the arms of the "U" extending downward.

► Head of Hexapods

Frugivory

Feeding on fruit. Such arthropods are said to be frugivorous or frugivores.

► Food Habits of Insects

Fruit Flies (Diptera: Tephritidae)

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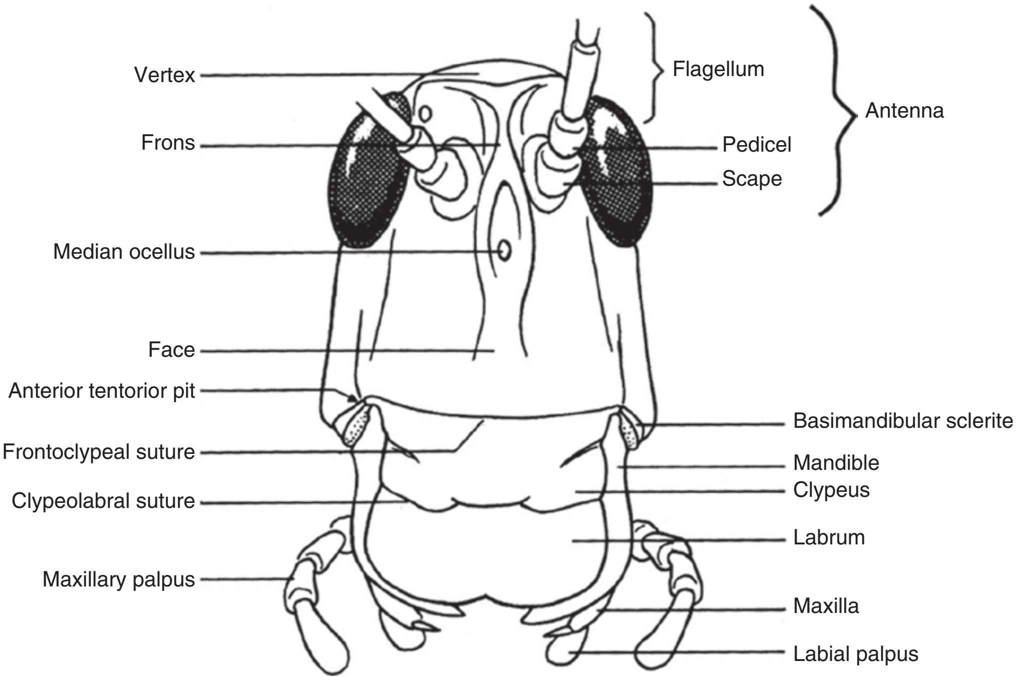
The family Tephritidae is a member of the large and phylogenetically complicated group known as acalyptrate flies.

Order: Diptera
  Suborder: Brachycera
    Infraorder: Muscomorpha
      Section: Schizophora
        Subsection: Acalyptratae
          Superfamily: Tephritoidea

Other families included in the same superfamily are Lonchaeidae, Pallopteridae, Piophilidae, Platystomatidae, Pyrgotidae, Richardiidae, and Ulidiidae (= Otitidae).

The family comprises over 4,300 described species, which are distributed throughout temperate and tropical regions of the world. The Tephritidae may be further subdivided into six subfamilies,



Frons, Figure 89 **Front view of the head of an adult grasshopper, showing some major elements.**

Tachiniscinae, Blepharoneurinae, Phytalmiinae, Trypetinae, Dacinae, and Tephritinae. Only the subfamilies Trypetinae and Tephritinae are represented in all of the major biogeographic regions.

Other insects are sometimes called "fruit flies," particularly the Drosophilidae, but they are not closely related.

Adult

One of the prominent features of the family is the presence in females of a chitinized ovipositor sheath and a needle-like ovipositor that allows them to oviposit into healthy plant tissues. Most species have "picture wings" that are prominently patterned with stripes or spots, and bodies with strongly contrasting colors, such as yellow stripes or spots on a dark background, as in species of *Toxotrypana*, which likely mimic wasps, or bold black stripes on the wings, as in some species of *Rhagoletis* and *Zonosemata*, that mimic jumping spiders. Identification to species level in some groups, including important pest groups such as *Anastrepha*, relies on features specific to the female sex (ovipositor). Sexual dimorphism is common, in which males may be ornamented with specialized combs or bristles on the legs (e.g., some *Ceratitis* species) or elaborate antler-like projections on the head (e.g., some *Phytalmia* species). Adult size varies from about 2–25 mm in length.

Immature stages

Eggs are typically white and elongate-cylindrical, sometimes with long, tail-like extensions. The egg stage lasts only a few days for most species. Active feeding and growth occurs during three larval instars inside the host plant tissues. Body shapes range from vermiform in stem-mining species to globose in gall-makers. Identification to genus or species level usually requires knowledge of the host and may be possible using characteristics of the spiracles, the cephalic segment and various surface features. Larvae may pupate inside the host plant, as is common in many flower infesters and gall makers, or they may exit the host to pupate in the soil, as is typical for most fruit infesters.

Plant Relationships

The family Tephritidae is best known for its pest species that attack a wide array of commercial and wild fruits and vegetables in many different plant families (Figs. 90 and 91). However, the great majority of species are not pests, and the majority are not even fruit infesters. Over half of the members of the family use non-fruit plant tissues as larval feeding sites. These include a large number of flower and seed feeders, and also gall-makers, and stem- and leaf-miners that infest members of the plant family Asteraceae. Members of the tribe Gastrozonini breed in bamboo stems. A few saprophagous and parasitic species are also known.

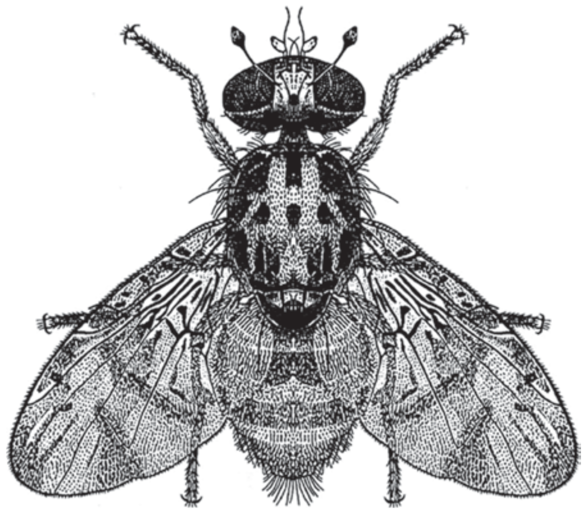
Life History

The duration and timing of the various life stages of tephritid flies depend on their host plant relationships. Many polyphagous, tropical fruit infesters, for example, breed year round, and have long-lived (several months) adults that are able to use a series of different host fruits for oviposition; their egg to pupa stages last only a few weeks, and all life stages are present simultaneously and throughout the year. Other species, both temperate and tropical, are restricted to a single host plant, they are univoltine, and most of their developmental stages are of short duration and synchronized. The adult flight period lasts only a few weeks during the period when the appropriate developmental stage of its host plant is available for oviposition. For most such species, most of the year is passed in the pupal stage. Some temperate species undergo obligatory diapause in the pupal stage that may last for several years.

Behavior

Courtship and mating behavior are very complex and elaborate in some species and may continue for hours. The behavior of many species is linked to the host plant, which may be used as a meeting site for males and females and may be a defendable resource for males. Males of many species display territorial behavior on the host plants and some engage in "boxing" matches to defend them. Lek-like mating aggregations, in which males compete for females, have been described for a number of fruit infesters including the Mediterranean fruit fly, *Ceratitis capitata* (Figs. 90 and 91). Many other aspects of fly behavior are also tightly linked to their host plants, for example, dispersal, feeding, pheromone release and response,

Fruit Flies (Diptera: Tephritidae), Figure 90
Oriental fruit fly, *Bactrocera dorsalis*.



Fruit Flies (Diptera: Tephritidae), Figure 91
Mediterranean fruit fly, *Ceratitis capitata*.

oviposition, and co-occurrence of other tephritid species that utilize the same host plant.

Control

Because of their economic importance, a great deal of effort has gone into study of the biology, genetics and control of pest species. The sterile insect technique (SIT) is widely used in population suppression and eradication programs, especially for the Mediterranean fruit fly. This involves mass rearing of fruit flies, sometimes by the hundreds of millions and sometimes using genetically modified all-male strains, followed by irradiation during the pupal stage to induce sterility. These flies are released into infested areas where sterile males outnumber their wild, fertile counterparts, thus reducing the number of successful matings and limiting population growth or even driving the population to extinction. Another control/eradication technique, known as "male annihilation," is based on attraction of males to highly potent parapheromones, such as methyl eugenol. "Bait stations" using a mixture of the attractant and an insecticide can quickly remove most or all males from a population and drive it to extinction. This technique has been used very successfully against the Oriental fruit fly, *Bactrocera dorsalis*. Classical biological control using hymenopteran parasitoids that attack the immature stages of fruit flies has been used with varying degrees of success.

Evolutionary Studies

The genus *Rhagoletis* has figured prominently in studies of evolutionary biology as a possible model of sympatric speciation. Because the mating, phenology, and biology of tephritid flies is so tightly linked to their host plants, it has been proposed that a shift in host-plant relationships could effectively isolate subpopulations even within a geographic area and lead to genetically distinct host races and ultimately to separate species.

Importance to Humans

Nearly all known members of the family are intimately associated with their host plant taxa, which serve as a feeding substrate for the larval stages. For this reason, many species of Tephritidae are highly damaging plant pests, and are widely known as "fruit flies." Some of the most important genera and examples of fruit and vegetable pest species are: *Anastrepha* with over 200 species occurring in the Americas, including *A. fraterculus*, the South American fruit fly, and *A. ludens*, the Mexican fruit fly; *Bactrocera* with over 500 species mostly in tropical Asia, Australia and islands of the Pacific Ocean, including *B. dorsalis*, the Oriental fruit fly, *B. cucurbitae*, the melon fly, and *B. oleae*, the olive fly; *Ceratitis* with about 80 species, all African in origin, including *C. capitata*, the Mediterranean fruit fly; *Dacus* with about 250 species, mostly African, including *D. bivittatus*, the pumpkin fly; *Rhagoletis* with more than 60 species, mostly Holarctic, but also present in Central and South America, including *R. pomonella*, the apple maggot; and *Toxotrypana* with 13 or more species in tropical America, including *T. curvicauda*, the papaya fruit fly.

Some tephritid host plants are invasive weeds with severe impact especially in pasture and rangelands. Various tephritid flies whose larvae feed on buds or seeds or produce galls have been intentionally promulgated into these weed populations as biological control agents, for example various *Urophora* species that attack thistles.

► Mediterranean Fruit Fly
► Melon Fly

References

Aluja M, Norrbom AL (eds) (1999) Fruit flies (Tephritidae): phylogeny and evolution of behavior. CRC Press, Boca Raton, FL

Foote RH, Blanc FL, Norrbom AL (1993) Handbook of the fruit flies (Diptera: Tephritidae) of America north of Mexico. Cornell University Press, Ithaca, New York

Robinson AS, Hooper G (eds) (1989) In: Helle W (ed) Fruit flies. Their biology, natural enemies, and control. World crop pests, vol 3(A) & vol 3(B). Elsevier, Amsterdam, The Netherlands

Tan KH (ed) (2000) Area-wide control of fruit flies and other insect pests. Penerbit Universiti Sains Malaysia, Pulau Pinang, Malaysia
Thompson FC (ed) (1999) Fruit fly expert identification system and systematic information database, Myia, vol 9. Backhuys Publishers, Leiden, The Netherlands
White IM, Elson-Harris M (1992) Fruit flies of economic significance: their identification and bionomics. International Institute of Entomology, London, UK

Fruit Stalk Borer, *Oryectes elegans* Prell (Coleoptera: Scarabaeidae)

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The fruit stalk borer is found in the Arabian Peninsula as well as in Iraq and Iran. The adult is a stoutly built rhinoceros beetle that is shiny and reddish brown in color. The body length is about 34–36 mm in the female and 28–34 mm in the male. Adults have a horn-like structure on the head which is longer in females. The dorsum of the first thoracic segment has a depression that is deep and large in the female and shallow and small in the male. Mature larvae are about 55–65 mm in length, creamy white in color with brown heads, curved in shape and the last three abdominal segments are thicker than the remaining segments. Two cellulose destroying fungi, *Chaetomium elatum* and *C. murorum*, are found in the frass of fruit stalk borer larvae. The adults hide during the day in damp, organic soils. The adults are attracted to light from April to September and do great damage by boring through the leaf-bases and stems of inflorescences in the crown of the tree.

Importance and Damage

The importance of the fruit stalk borer as a pest varies from year to year. It causes severe damage in damp and neglected fields. The adults cause more damage than the larvae. However, the larvae may cause a huge cavity in the infested trunk that will ultimately cause its collapse. The adults make surface mines in the midrib of the fronds and the fruit stalks. Attacked fruit stalks may be broken or the fruits may be small and droop and shrivel. The adults also make holes at the base of the growing heart leaves and enter the stem.

The larvae do not cause real damage unless they are numerous in one trunk. The larvae also feed on decomposing materials in the soil.

There are other problems that the stalk borer might cause. The most common one is the tapered cut (crosscut) at the lower part of the fruit stalk fruit. However, it was reported from the United States of America, Pakistan, Iraq and a few other countries in the Middle East that these cuts are due to a physiological disorder. Another problem is the detachment of the fruit stalk from the growing point of the tree. There is no strong evidence that such damage is caused by the fruit stalk borer.

Biology

The life-cycle of the fruit stalk borer may require more than 1 year. Females start laying eggs a week after emergence. The eggs are laid singly in wet soil around the roots of date palm trees or on rotten trunks. The eggs that are laid in early spring may reach the adult stage in autumn, while those laid later may reach the adult stage the following spring. The larval stage may take up to 10 months. Pupal longevity is up to three weeks.

Control

In most cases, there is no need for control. But under certain conditions such as high humidity due to rainfall, the fruit stalk borer may cause serious damage. Also, damage by the fruit stalk borer facilitates entry by the red palm weevil, *Rhynchophorus ferrugineus*.

A light trap can be used to reduce the number of flying adults, and to predict the occurrence of the fruit stalk borer outbreak. Most captures usually occur in April, a time when the greatest damage occurs. Food or shelter traps also can be used. These traps consist of wet organic materials mixed with wet, small pieces of date palm trunk covered by fronds. The adults are attracted to this trap in the early morning as a hiding place during the day, and females may even lay eggs in these traps. Pesticides may be added to the traps to kill the attracted adults.

References

Talhouk N (1984) The most common agricultural pests in Saudi Arabia. Ministry of Agriculture and Water, 121 pp (in Arabic)

Hussain A (1974) Pests of date palm trees and dates in Iraq. Bagdad University, 190 pp (in Arabic)

Hammad SM, Kadous AA (1989) Studies on the biology and ecology of date palm pests in the eastern Province of Saudi Arabia. Research Grants Program, Technical Report No 25. KACST, Riyadh, Saudi Arabia, 142 pp

Fruitworm Beetles

Members of the family Byturidae (order Coleoptera).

► Beetles

Fruitworm Moths (Lepidoptera: Carposinidae)

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Fruitworm moths, family Carposinidae, total about 279 species from all regions, but most are Australian and South Pacific. The family is part of the superfamily Copromorphoidea in the section Tineina, subsection Tineina, of the division Ditrysia. Adults small to medium (10–40 mm wingspan), with head smooth-scaled; haustellum naked; labial palpi porrect; maxillary palpi 1-segmented. Wing venation has reduction of two median veins in the hindwings and hindwings somewhat pointed apically. Maculation shades of gray and brown on forewings, plus some scale tufts; hindwings mostly pale. Adults are nocturnal or crepuscular. Larvae are borers in fruits, seeds, buds, or trunks and limbs, but a few are leafminers. Hosts include a variety of plants. A few species are economic.

References

Cho S, Park KT (1990) The systematics of Korean Carposinidae (Lepidoptera). Insecta Koreana 7:87–103

Davis DR (1969) A revision of American moths of the family Carposinidae (Lepidoptera: Carposinoidea). Bull United States Natl Mus 289:1–105

Diakonoff AN (1989) Revision of the Palaearctic Carposinidae with description of a new genus and new species (Lepidoptera: Pyraloidea). Zool Verhandlingen 251:1–155

Kuznetsov VI (1986) Carposinidae. In: Identification Keys to Insects of European Russia. 4. Lepidoptera, 3:18–25 Academie Nauk [in Russian], St. Petersburg

Zimmerman EC (1978) Carposinidae In: Insects of Hawaii 9:792–876

Fulgoridae

A family of insects in the superfamily Fulgoroidae (order Hemiptera). They sometimes are called planthoppers.

► Bugs

Fulgoroidea

A superfamily of insects in the order Hemiptera. Included in this superfamily are families such as Delphacidae, Derbidae, Cixiidae, Kinnaridae, Dictyopharidae, Fulgoridae, Acilidae, Tropiduchidae, Flatidae, Acanalonidae, and Issidae. They sometimes are called planthoppers.

► Bugs

Fuller Rose Beetle, *Asynonychus godmani* (Crotch) (Coleoptera: Curculionidae)

Though not a serious pest, this species affects the ability of North American citrus producers to ship their products.

► Citrus Pests and Their Management

Fumigant

A liquid or solid chemical that forms toxic gas or vapor upon exposure to air, and is used to disperse insecticide in difficult-to-penetrate substrates such as stored grain and soil.

Fumigation

Treatment that uses a pesticide applied in a gaseous form.

Functional Genomics

Study of what traits/functions are conferred on an organism by specific DNA sequences. Typically functional genomics occurs after the DNA sequences have been identified.

Functional Response

A behavioral response of predators or parasitoids to the presence of prey. Searching and prey handling behavior is modified, resulting in increased efficiency of prey destruction. Learning, and more active search in the presence of prey, are implicated in functional responses. (contrast with numerical response)

Fundatrix (pl., fundatrigeniae)

In aphids, the stem mother or first viviparous parthenogenetic generation developing from the fertilized egg.

► Aphids

Fungal Pathogens of Insects

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Fungi are eukaryotic, heterotrophic, absorptive organisms. Most grow vegetatively as fine hyphal filaments and reproduce by means of spores. Fungi are vital parts of ecosystems, often playing a valuable role in decomposition. They include common important organisms such as bread and wine yeasts, edible mushrooms, the causative agents of ringworm and athlete's foot, and fungi which produce antibiotics such as penicillin.

The classification of fungi is complicated and still imperfectly understood. Many different classifications and names have been proposed. Current authorities place the fungi in their own Kingdom, the Fungi or Eumycota. There are more than 56,000 described species placed in four phyla: the Ascomycota, Basidiomycota, the Chytridiomycota, and the Zygomycota. The Deuteromycota is an additional informal polyphyletic phylum. Aquatic entomopathogenic fungi, such as *Lagenidium* (Oomycota) that infect aquatic insects, are no longer considered fungi by some mycologists and are placed in the Kingdom Chromista.

Modern classification schemes no longer consider the Oomycota to be a phylum in the Fungi, but instead members of the Kingdom Chromista.

Fungi and insects interact symbiotically in many ways including mutualism, parasitism, commensalism, and predation. Some insects are totally dependent on fungi for their food. For instance, the leaf-cutting ants *Acromyrmex* and *Atta* spp., and termites in the Macrotermitinae, are mutualists with the fungi *Attamyces* and *Termitomyces*, respectively. These important groups of insects are utterly dependent on fungi for their survival, and similarly, these fungal species are found only in association with their insect "farmers." On the other hand, many fungi exploit and "feed" on insects. Such fungi are called pathogens and are the subject of this section (Table 9).

Fungal entomopathogens are microorganisms that are capable of causing disease in otherwise healthy host insects. They possess the ability to invade, reproduce in, and escape from a host, while overcoming or avoiding the host's defenses. In order to do this, fungal pathogens have spores that are able to mechanically and enzymatically penetrate an insect's exoskeleton, and vegetative hyphae that can survive and grow within a host. After killing a host, the fungus produces spores that are dispersed to new hosts. Often fungi that have little or no ability to infect living healthy insects are found growing on dead insects. These are called

Fungal Pathogens of Insects, Table 9 Simplified classification of entomopathogenic fungi and their arthropod hosts

Phylum/Order	Genus	Hosts
Oomycota		
Lagenidiales	*Lagenidium*	mosquito larvae
Saprolegniales	*Leptolegnia*	mosquito larvae
Chytridiomycota		
Blastocladiales	*Coelomomyces*	mosquito larvae
	Coelomycidium	black fly larvae
Zygomycota		
Entomophthorales	*Conidiobolus*	aphids and others
	Entomophaga	moths, grasshoppers
	Entomophthora	adult flies, aphids
	Erynia	many insects
	Massospora	periodical cicadas
	Neozygites	aphids, thrips, mites
	Strongwellsea	adult flies
	Zoophthora	many insects
Basidiomycota		
Septobasidiales	*Septobasidium*	scales
Ascomycota		
Laboulbeniales	many genera	many insects
Ascosphaerales	*Ascosphaera*	bee larvae
Sphaeriales	*Cordyceps*	many insects
Deuteromycota		
Sphaeropsidales	*Aschersonia*	scales and whiteflies
Moniliales	*Beauveria*	many insects
	Hirsutella	mites and scales
	Metarhizium	many insects
	Nomuraea	Lepidoptera larvae
	Paecilomyces	many insects
	Verticillium	aphids, whiteflies

saprophytic fungi. Most microbial pathogens, such as viruses, protozoa and bacteria, enter the host via the mouth during ingestion, an entry method called *per os*. Fungi, along with certain nematodes, have the ability to directly penetrate the exoskeleton of an arthropod. This makes the fungi particularly important pathogens of insects such as aphids, cicadas, and other sucking insects that do not chew leaves and other substrates, and are, therefore, unlikely to ingest microbial pathogens.

Life Cycle and Invasion of the Host

The life cycle of fungal pathogens begins with a spore. Spores vary in size and shape, and these characteristics are important in determining the species of a fungus. When a spore contacts a suitable host, it attaches to the host integument, forms an appressorium, and penetrates the insect's integument via a germ tube or penetration peg. Usually, enzymes are produced by the spore to soften or dissolve the insect's cuticle, then a germ tube mechanically penetrates the host's exoskeleton. This can be a complicated process. In some fungal species, adhesion of spores is non-specific, while in others the spores "recognize" an appropriate host's integument and begin the germination process. Once inside the host, the fungus grows vegetatively as filaments, called hyphae, or as yeast-like hyphal bodies. Within 3–7 days, the fungus has filled the host's body cavity (hemocoel), resulting in the host's death. Fungal toxins are sometimes involved, particularly with *Beauveria* and *Metarhizium*. *Beauveria* produces a number of toxic metabolites: beauvericin, a cyclic depsipeptide which is toxic to mosquito larvae; bassianolide, which is toxic to lepidopteran larvae; and cyclosporin, an immunosuppressant. *Metarhizium* produces toxins called *destruxins* that can paralyze insect larvae.

Usually after the host's death, the fungus produces spore-bearing hyphae called conidiophores that grow out of the host. Depending on the fungal species, spores are either explosively discharged (as in the Zygomycota: Entomophthorales) or are passively discharged (as in the Deuteromycota and Ascomycota). In some genera, such as *Massospora* in periodical cicadas and *Strongwellsea* in various adult flies, conidia (spores) are produced while the host is still living and mobile. The host in such cases helps disseminate the pathogen.

Epizootics, Biological Control, and Population Regulation

Fungal pathogens that prey on insects often cause readily observed epizootics. An epizootic is defined as an unexpectedly large proportion of diseased insects in a population. Fungal epizootics are often spectacular because: (i) large numbers of insects may be killed; (ii) insects killed by fungi are frequently held in elevated sites by fungal holdfasts; (iii) fungi sporulating on insect hosts are often colorful (white, green, or other colors); and (iv) because insects killed by fungi are usually firm, mummified, and persist for days to months.

Because fungal pathogens kill large numbers of many insect pests, they are frequently important regulators of insect populations and are valuable biological control agents. Fungi are among the most important natural enemies of arthropods such as gypsy moth larvae, periodical cicadas, whiteflies, aphids, spider mites, and many others (Table 10).

Why are fungi so efficient at causing epizootics? First, because their life cycles are usually relatively short compared to the host; sometimes, as is the case with *Neozygites fresenii*, a pathogen of aphids, they kill the host within 3–4 days. Second, many spores, thousands to millions, are produced from each infected host. Third, because many entomopathogenic fungi have developed specialized structures, such as rhizoids, that fasten a host where the opportunities are maximized for spores to contact new hosts. Fourth, spores of many fungi are rapidly spread by air or water to new hosts.

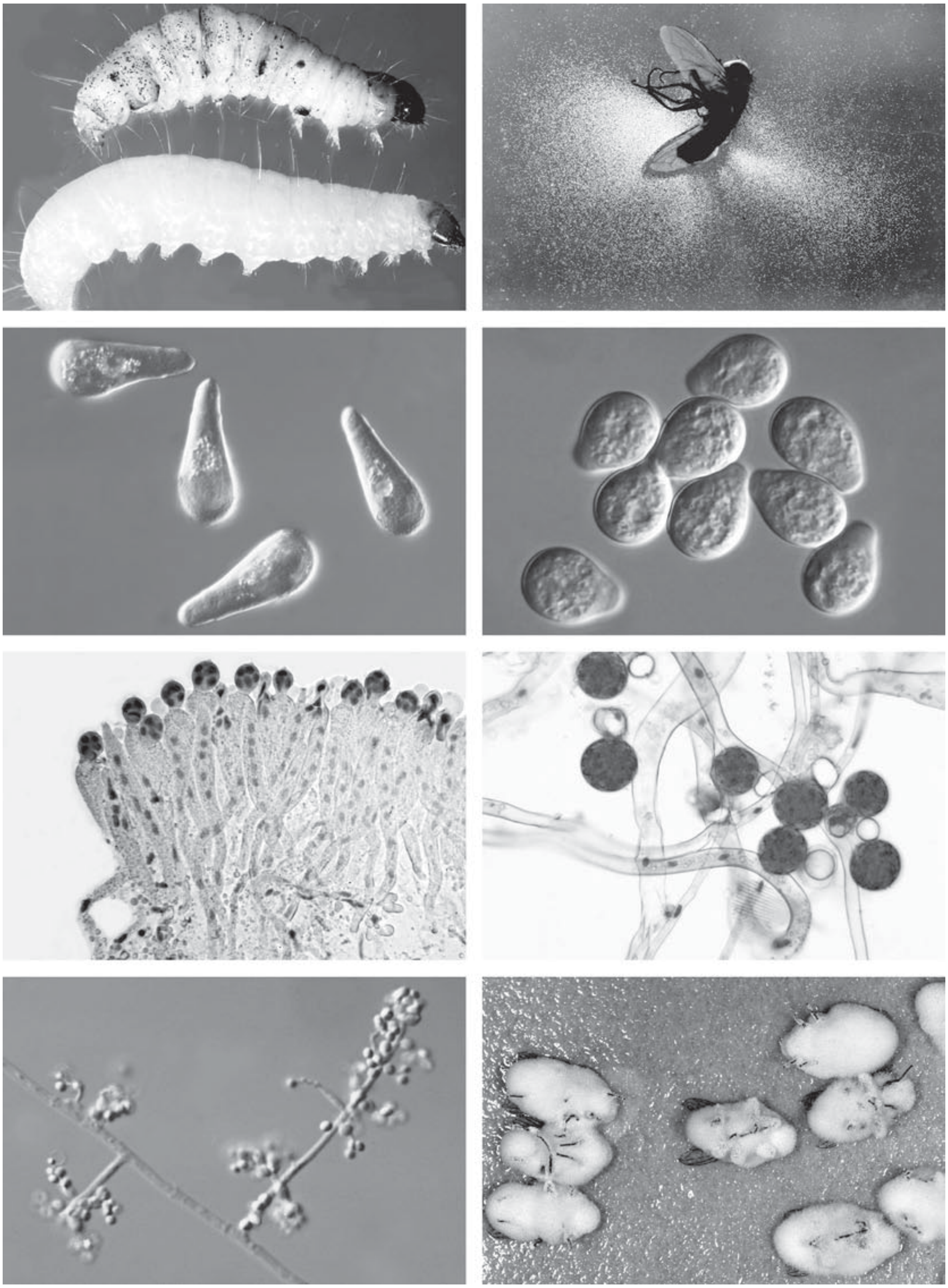
Importantly, many fungal pathogens (Figs. 92 and 93) of insects have a narrow host range, infecting insects in only a limited number of insect species. A limited host range is beneficial because

Fungal Pathogens of Insects, Table 10 Examples of fungi that cause natural epizootics in important insects and mites

Host	Host name	Fungal species
Twospotted spider mite	*Tetranychus urticae*	*Neozygites floridana*
Citrus rust mite	*Phyllocoptruta*	*Hirsutella thompsonii*
Caddisfly adults	Trichoptera	*Erynia rhizospora*
Gypsy moth larvae	*Lymantria dispar*	*Entomophaga maimaiga*
Grasshoppers	Acrididae	*Entomophaga grylli*
Aphids	Aphididae	*Neozygites fresenii*
Aphids	Aphididae	*Erynia neoaphidis*
Aphids	Aphididae	*Condiobolus obscurus*
Aphids	Aphididae	*Entomophthora planchoniana*
Periodical cicadas	*Magicicada* spp.	*Massospora cicadina*
House fly	*Musca domestica*	*Entomophthora muscae*
Mosquito larvae	Culicidae	*Erynia aquatica*
Mosquito larvae	Culicidae	*Coelomomyces* spp.
Mosquito larvae	Culicidae	*Lagenidium* spp.
Black fly larvae	Simuliidae	*Coelomycidium* spp.
Noctuid moths	Noctuidae	*Nomuraea rileyi*
Whiteflies	Aleyrodidae	*Aschersonia aleyrodis*
Diverse insects	Lepidoptera, Aleyrodidae	*Paecilomyces* spp.
Aphids, Whiteflies	Aphididae, Aleyrodidae	*Verticillium lecanii*
Honey bees	*Apis mellifera*	*Ascosphaera apis*
Solitary bees	Megachilidae	*Ascosphaera aggregate*
Diverse insects	Scarabaeidae, Formicidae	*Cordyceps* spp.
Alfalfa weevil	*Hypera postica*	*Zoophthora phytonomi*

non-target organisms such as plants, beneficial insects, and vertebrates are not harmed. Nearly all fungal pathogens of insects are safe for man, his animals and plants. For instance, *Neozygites floridana* and *Hirsutella thompsonii* have a host range limited to mites, *Neozygites fresenii* is limited to aphids, and *Nomuraea rileyi* is limited to lepidopteran larvae. However, fungal entomopathogens are not risk free. There are rare reports of *Beauveria* causing fatal respiratory infections in cold-blooded animals such as alligators and crocodiles, causing allergic reactions in people, and infections in the nasal passages of mammals. *Beauveria* does not grow well at temperatures above 37°C, which limits its dangers to mammals and birds. Strains of entomopathogenic fungi that grow well at 37°C or above could pose risks and probably should not be used in biological control programs.

Fungal species and structures within a species vary widely in their sensitivity to, and ability to survive, environmental conditions such as temperature, relative humidity, and sunlight. Conidia are relatively short-lived in the environment. Therefore, many fungi have the capability to produce longer-lived, environmentally resistant spores, called resting spores. In some cases these can remain viable for years before infecting a host. Fungal pathogens also can survive in the mummified bodies of their hosts (Fig. 92).



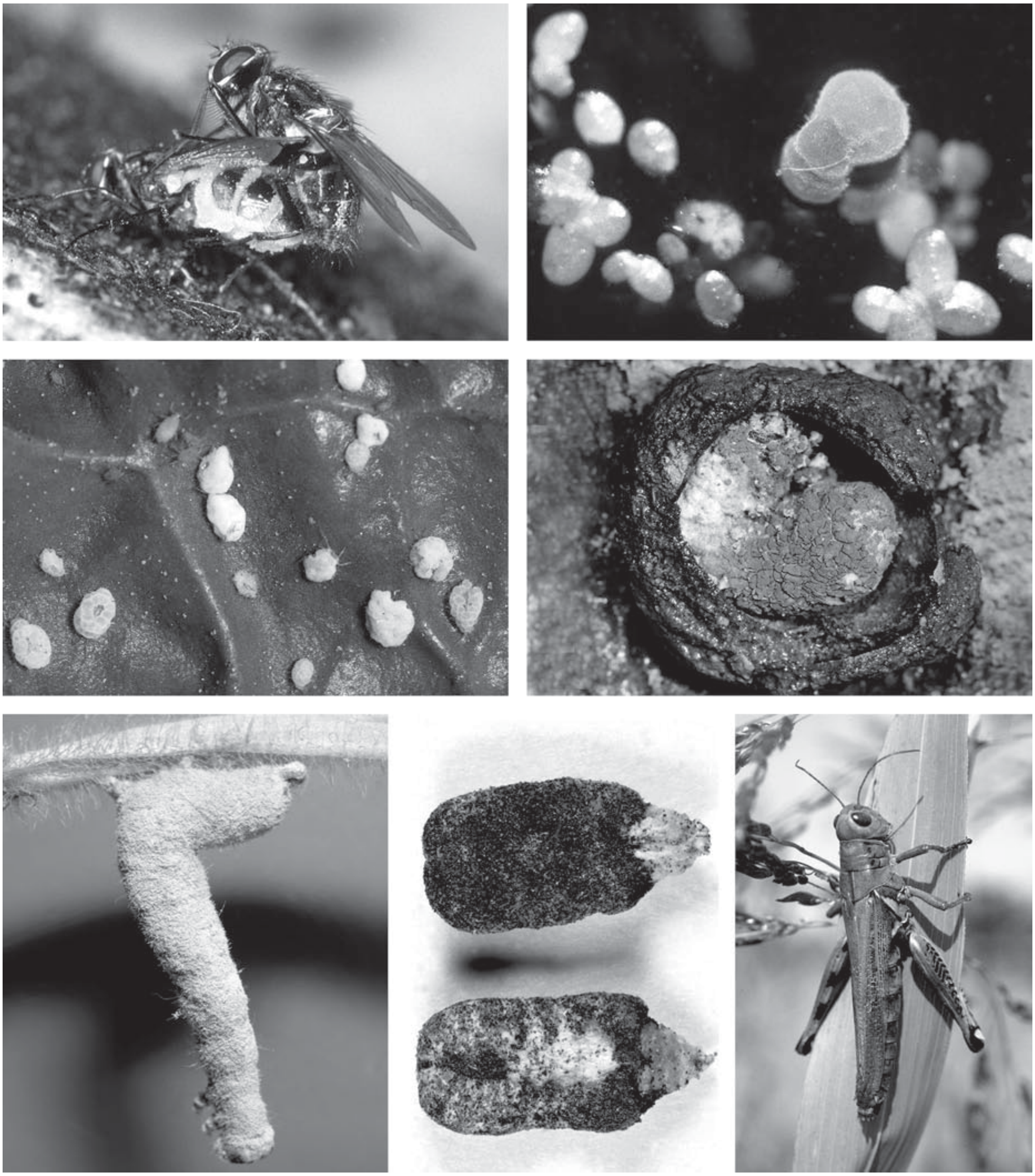
Fungal Pathogens of Insects, Figure 92 **Some insect pathogens: (*upper left*) Larvae of the Indian meal moth, *Plodia interpunctella* (Pyralidae). The top larva was inoculated with spores of *Paecilomyces* sp. (Deuteromycota: Hyphomycetes) and the lower larva was not inoculated. Note the black spots on the integument of the inoculated larva. Each spot represents a melanization defense response of the host to the penetration activity of a *Paecilomyces* spore. This is one example of host defenses against infection;**

Ecology

Entomopathogenic fungi occur in many habitats, including lakes, streams, ponds, snowpools, woodlands, tropical rain forests, agricultural landscapes, and the soil. *Lagenidium giganteum* (Oomycota) is highly pathogenic to mosquito larvae. *Lagenidium* produces motile zoospores that encyst on the cuticle of young mosquito larvae, and penetrate mechanically and enzymatically into the host hemocoel. Mosquito larvae defend themselves by producing melanin at the encystment sites. Mycelia of *Lagenidium* fills the body of the mosquito larva, breaking down the host tissues with fungal protease enzymes. No toxins are thought to be involved. Other fungal pathogens occur adjacent to aquatic habitats. *Erynia rhizospora* is a pathogen of adult Trichoptera; *Erynia conica* attacks various adult Tipulids and Chironomids; *Erynia curvispora* attacks black fly adults; and *E. aquatica* is a pathogen of mosquito pupae and adults. Frequently, infected insects can be discovered attached to rocks and logs near streams, waterfalls, and lakes (Fig. 93).

Forests, both tropical and temperate, are habitats for a variety of entomopathogenic fungi. *Cordyceps* spp. are fascinating pathogens of many insects in tropical and subtropical forests. These Ascomycota produce interesting club-like fruiting bodies (stromata) that emerge from infected hosts (often larvae or pupae of

(*upper right*) A house fly, *Musca domestica* (Muscidae), killed by and held to a window by the fungus, *Entomophthora schizophorae* (Zygomycota: Entomophthorales). When the fly died, specialized hyphal rhizoids (fungal holdfasts) grew out of the mouthparts of the fly and glued it to the glass. Then spore-bearing hyphae grew out of the host and produced thousands of spores (primary conidia) that were explosively discharged and are visible as a white halo around the dead fly. Fungal-mediated changes in host behavior and structures, such as holding the host in an elevated position, improve the odds of spores contacting new hosts; (second row left) Conidia of *Erynia aquatica* (Zygomycota: Entomophthorales), a pathogen of mosquitoes. Each spore is about 35 μm long. Note the difference in size and shape compared to the conidia of *Entomophaga grylli;* (second row right) Primary conidia of the grasshopper pathogen, *Entomophaga grylli* (Zygomycota: Entomophthorales). These spores are about 30 μm long. The shape and size of fungal spores are important characters used in their identification; (third row left) Photomicrograph of spore-bearing hyphae (conidiophores) of *E. schizophorae*. At the tips of the conidiophores the primary conidia are formed and then explosively discharged into the air. Each conidium contains 5 nuclei and is about 23 μm long. Nuclei, visible within the conidiophore, move into the developing conidium, prior to conidial discharge; (third row right) Resting spores of *E. aquatica*. Thick-walled resting spores can remain viable in mud and debris near mosquito breeding sites during the winter, then germinate and infect mosquito larvae in the spring; (bottom left) Spores of *Beauveria bassiana* and other Deuteromycota tend to be smaller than those of the Entomophthorales. These conidia, still attached to their conidiophores, are about 2–4 μm and are globose in shape. The spores of the Deuteromycota, unlike the Entomophthorales, are not explosively discharged from the host into the air; (bottom right) *Beauveria bassiana* (Deuteromycota) is one of the most commonly encountered entomopathogenic fungi, particularly in soil insects. This fungus has a very wide host range (several hundred species of insects at least) and there are several commercial products based on it. Commercialization of *B. bassiana* is possible because it is easily cultured in vitro, its spores are relatively small and easily formulated, and it has a wide host range. The dead hosts, in this case house flies, are covered by a white layer of fungal spores and mycelium. Note the similar appearance of these infected flies. Host insects killed by entomopathogenic fungi usually do not present a shaggy appearance, like saprophytic fungi do.



Fungal Pathogens of Insects, Figure 93 **Some additional insect pathogens: (*upper left*) *Entomophthora schizophorae* causes epizootics in muscoid flies, especially the house fly. Like the grasshopper killed by *E. grylli*, hosts killed by *E. schizophorae* are held to substrates, in this case by fungal rhizoids that grow out of the mouthparts (the lobes of the labellum) of the fly. In addition, dead infected flies appear life-like, have raised wings, and the infected females are attractive to males, who will sometimes engage in copulation with dead females, with obvious implications for the spread of the pathogen. Here you see a male house fly copulating with a dead infected female; (*upper right*) Entomophthoralean fungi in the genus *Erynia* are commonly found infecting insects that occur in moist situations, such as along stream**

Lepidoptera or Coleoptera) in the soil. In China, larvae of hepialid moths infected with *Cordyceps sinensis* have been collected and used medicinally for thousands of years. Especially important in the temperate forests of North America is the fungus *Entomophaga maimaiga*, which causes large-scale epizootics in larval populations of the gypsy moth, *Lymantria dispar*. This fungus is one of the most valuable natural enemies of this pest. Various other Entomophthorales cause epizootics in tent caterpillars, aphids, and other forest pests.

In agricultural habitats, fungi play an important role in regulating populations of various pests: whiteflies are attacked by *Aschersonia* spp.; spider mites are attacked by *Neozygites floridana*; and citrus rust mites by *Hirsutella thompsonii*. Various lepidopteran larvae are frequently decimated on soybean by *Nomuraea rileyi*, while the alfalfa weevil, *Hypera postica*, is heavily attacked by *Erynia phytonomi*.

Techniques for Studying Fungal Pathogens of Insects

Identification of entomopathogenic fungi is best accomplished when the host species is known, the gross signs of the fungus on the host (such as color, texture, attachment structures) are noted, and when microscopic fungal structures (spores, rhizoids, hyphae, cystidia) are examined with a phase microscope. Small amounts of fungal material are removed from the host, using an insect pin or minuten mounted in a wooden dowel, placed in a mounting medium (such as lactophenol) on a glass slide under a coverslip. The coverslip may be sealed with nailpolish to make it semi-permanent. Phase microscopes (usually at 100–400x) are used to examine the spores (conidia), conidiophores (spore-bearing hyphae), rhizoids, hyphae or hyphal bodies, and other structures. The size, shape, and color of spores are particularly important in identification using appropriate keys.

banks, waterfalls, and lakes. *Erynia aquatica* infects mosquitoes (Culicidae) that breed in snow pools. Here you see a mosquito that died in the pupal stage from this fungus. The dead mosquito pupa floats on the water surface, the spores are discharged from the dead host, and infect newly emerged mosquito adults; (second row left) *Pandora neoaphidis* (Zygomycota: Entomophthorales) is one of the most important pathogens of aphids. These are green peach aphids, *Myzus persicae*, killed during an epizootic of *P. neoaphidis*, in a spinach field. The infected aphids are held firmly to the leaf by fungal rhizoid holdfasts; (second row right) *Metarhizium anisopliae* (Deuteromycota) is a very common pathogen of soil insects and has a wide host range. The photograph shows a green June beetle larva, *Cotinus nitida* (Scarabaeidae), in its pupation chamber, killed by *M. anisopliae*. Note the white areas of hyphae where the fungus has not yet sporulated. The mature spores cover the host with millions of green spores; (bottom left) *Nomuraea rileyi* (Deuteromycota: Hyphomycetes) is a common pathogen of Lepidoptera larvae in southern field crops. Host larvae are covered with pale green spores. Note that this host larva, a soybean looper, is attached to a leaf, is firm, is covered with powdery light green masses of spores; (bottom center) *Ascosphaera apis* (Ascomycota: Ascosphaerales) causes chalkbrood in honey bee larvae (brood). The mummified bee larvae resemble pieces of chalk in front of the hive, hence the name chalkbrood. Note the firm, "preserved" appearance of the dead insect. Other diseases of bee larvae, such as American foulbrood, caused by a bacterium, result in the larva becoming "gooey" and having a foul smell; (bottom right) *Entomophaga grylli* attacks grasshoppers. Infected hosts often are found clinging to the tops of grasses, and the dead hosts appear to be alive. There are no fungal holdfasts produced. However, the fungus mysteriously makes its grasshopper victim tightly grasp a plant with its legs before it dies. Upon dissection, large numbers of resting spores were found within the host's abdomen. Another *Entomophaga* sp., *E. maimaiga*, is the cause of major epizootics in gypsy moth larvae and is considered one of the most important natural enemies of this pest.

Many entomopathogenic fungi can be cultured *in vitro* on mycological media, such as Sabouraud dextrose agar. Some such as *Beauveria*, *Metarhizium*, and *Paecilomyces* grow readily on media. Others such as *Pandora neoaphidis* and *Erynia curvispora* can be grown relatively easily *in vitro*, while others such as *Entomophthora muscae* are difficult to culture, and yet others, such as *Neozygites fresenii* are almost impossible to culture in vitro.

Isolating pure cultures of entomopathogenic fungi can be difficult depending on the species of fungus involved and the state of the host. Contamination of cultures by bacteria or unwanted fungi is a frequent problem. Selective media, such as oatmeal agar amended with dodine, are frequently used to isolate fungi such as *Beauveria*, while Entomophthorales are frequently isolated on coagulated egg yolk media. Most media used for isolation include broad spectrum antibiotics such as tetracycline and streptomycin to reduce the chance for bacteria to contaminate the culture. Fungal spores can be transferred from the host to the culture media using a needle. One of the best methods to isolate Entomophthorales is to place the sterile isolation media above the host cadaver, so that conidia are discharged from the host onto the media surface above.

Cultures can be preserved by regular serial transfers onto fresh media, by storing culture slants under a layer of sterile mineral oil, by freeze-drying, or in ultra cold freezers. The USDA maintains a collection of entomopathogenic fungal cultures called the USDA-ARS Collection of Entomopathogenic Fungal Cultures, in Ithaca, New York.

► Pathogens of Whiteflies
► Diseases of Grasshoppers and Locusts
► *Beauveria*
► Coelomomyces
► Culicinomyces
► Hirsutella
► Metarhizium
► Nomurea
► Paecilomyces
► Trichomyces
► *Verticillium lecanii*

References

Boucias, DG, Pendland JC (1998) Principles of insect pathology, 1st edn. Kluwer, Boston, MA, pp 181–183

Lacey LA (ed) (1997) Manual of techniques in insect pathology. Academic Press, San Diego, CA

Lacey LA, Kaya HK (2000) Field manual of techniques in invertebrate pathology. Kluwer, Boston, MA

Keller S (1987) Arthropod-pathogenic Entomophthorales of Switzerland. I. *Conidiobolus, Entomophaga* and *Entomophthora*. Sydowia 40:122–167

Pell JK, Eilenberg J, Hajek AE, Steinkraus DC (2001) Biology, ecology, and pest management potential of Entomophthorales. In: Butt TM, Jackson C, Magan N (eds) Fungi as biocontrol agents, progress, problems and potential. CABI Publishing, Wallingford, UK, pp 71–153

Samson RA, Evans HC, Latgé JP (1988) Atlas of entomopathogenic fungi. Springer-Verlag, Berlin, Germany

Steinkraus DC (2000) Documentation of naturally-occurring pathogens and their impact in agroecosystems. In: Lacey LA, Kaya HK (eds) Field manual of techniques in invertebrate pathology. Kluwer Academic, Dordrecht, The Netherlands, pp 303–320

Tanada Y, Kaya HK (1993) Insect pathology. Academic Press, San Diego, CA

Wilding N, Collins NM, Hammond PM, Webber JF (eds) (1989) Insect-fungus interactions. Academic Press, London, UK

Fungicide

A pesticide used to manage growth of fungi.

Fungivorous

Feeding on fungi.

Fungivory

Fungus or mushroom feeding. Such arthropods are said to be fungivorous or fungivores.

► Food Habits of Insects

Fungus Beetles

Members of the family Anthribidae (order Coleoptera).

► Beetles

Fungus Gnats (Diptera: Mycetophilidae and Others)

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Fungus gnats (Mycetophilidae, Bolitophilidae, Ditomyiidae, Diadocidiidae, Keroplatidae, and Lygistorrhinidae) are a diverse and abundant group of insects in the order Diptera, suborder Nematocera. Adults are usually recognized by their hump-backed appearance, stout and elongate coxae and well-developed tibial spurs (Figs. 94–98). Fungus gnats are primarily forest dwellers but can be found in a variety of ecosystems, often in association with fungal habitats, although most of their natural history secrets remain untold. They occur on all continents except Antarctica. The adults often attain large populations and play an important role in the food web of forest environments.

Traditionally, fungus gnats have been treated as a single family, the Mycetophilidae, and along with Sciaridae (dark-winged fung,us gnats) and Cecidomyiidae (gall midges), make up the superfamily Sciaroidea, within the infraorder Bibionomorpha. Fungus gnats formerly placed in Mycetophilidae, however, have been shown to be composed of several distinct lineages that are now treated as six separate families: Mycetophilidae, Bolitophilidae, Ditomyiidae, Diadocidiidae, Keroplatidae, and Lygistorrhinidae. More families may be recognized in the near future as more study and greater understanding of the *Heterotricha*-group taxa is developed. The *Heterotricha*-group is a heterogeneous assemblage of at least 12 genera

Fungus Gnats (Diptera: Mycetophilidae and Others), Figure 94 An adult male fungus gnat, *Mycetophila* sp. (Mycetophilidae) (photo by P.H. Kerr).

Fungus Gnats (Diptera: Mycetophilidae and Others), Figure 95 Adult male of *Sceptonia johannseni* Garrett (Mycetophilidae) (photo by P.H. Kerr).

Fungus Gnats (Diptera: Mycetophilidae and Others), Figure 96 **Adult female of *Novakia miloi* Kerr (Mycetophilidae) (photo by P.H. Kerr).**

Fungus Gnats (Diptera: Mycetophilidae and Others), Figure 97 **Adult male of *Macrocera* sp. (Keroplatidae) (photo by P.H. Kerr).**

that are now *incertae sedis* within the superfamily Sciaroidea.

Order: Diptera
Infraorder: Bibionomorpha
Superfamily: Sciaroidea

Fungus Gnats (Diptera: Mycetophilidae and Others), Figure 98 **Adult male of *Platyura pectoralis* Coquillett (Keroplatidae) (photo by P.H. Kerr).**

Family: Mycetophilidae
Family: Bolitophilidae
Family: Ditomyiidae
Family: Diadocidiidae
Family: Keroplatidae
Family: Lygistorrhinidae

In total, approximately 5,000 species of fungus gnats have been formally named and described. Mycetophilidae remains the largest family in terms of species number with approximately 3,500 species worldwide, in approximately 136 genera. Undoubtedly the number of fungus gnat species will increase significantly as more study is devoted to the family. The number of genera is also expected to increase. Currently, there are at least several genera that are widely suspected to be artificial groupings of two or more disparate lineages (e.g., *Boletina*, *Dziedzickia*, *Sciophila*). These genera are in need of systematic revision. The largest genus, *Mycetophila*, contains over 700 species and is distributed worldwide. The Palearctic Region is the area of greatest fungus gnat diversity. This may be a result of heightened local interest and expertise in the group more than actual taxonomic diversity but it is interesting to note that in Europe, fungus gnat diversity does not increase as one approaches lower latitudes (a typical pattern for many groups) and it may be that in general, the temperate regions are more diverse for fungus gnats than the tropics. Currently, Finland has the richest fauna of Mycetophilidae recorded among the nations of Europe.

In forested areas throughout the world, fungus gnats are both abundant and diverse. Even in North America, it is not uncommon for two dozen or more fungus gnat genera to be collected over the course of a season from a single Malaise trap. In Finland, one survey effort captured 209 different species of mycetophilid gnats in a single trap in one season. This represents over 30% of the entire mycetophilid species total recorded for Finland. Fungus gnats are sensitive to forestry practices however, and the diversity of gnats may be suppressed for many decades or even permanently after clear-cutting forests.

As their name implies, most fungus gnats are dependent on fungi for their development, either in mushroom fruiting bodies themselves, in the ground on mycorrhizae, or in or on wood or decomposing hummus where they feed on fungal mycelia. Many species appear restricted to certain ecological or systematic groups of fungi. Furthermore, within a particular host fungus, there may be a succession of fungus gnat species that specialize in particular decomposition stages. However, fungus gnats are not restricted to fungal environments. Larvae have also reportedly been found in birds' nests and mammals' burrows (where they may be mycetophagous), and on algae, mosses, liverworts and possibly on lichens. Curiously, field mushrooms (*Agaricus* spp.) do not serve as hosts. Some larvae, such as members of the genus *Leptomorphus* (Mycetophilidae), spin webs underneath bracket fungi where fungal spores are caught and eaten. Some members of Keroplatidae (e.g., *Asindulum* and others) take this one step further and also spin webs to capture small living invertebrate prey. Possibly the most famous of all fungus gnat larvae, the New Zealand glow worm, *Arachnocampa luminosa*, is predaceous and uses its own bioluminescence to lure midges and other small flies into a sticky silk thread that the larva spins and hangs from overhanging rocks (e.g., in caves and hollows). The glow worm silk strands may be up to 50 cm long and are coated with sticky poisonous droplets that paralyze trapped prey so that the surrounding snares remain intact. Other keroplatids, such as some *Orfelia* spp. also have predaceous, bioluminescent larvae and may be found in caves in North America. Still other keroplatid larvae are associated with ant-plants. Perhaps most outlandish of all fungus gnat lifestyles is exhibited by the larva of *Planarivora insignis* (Keroplatidae), a Tasmanian species that lives endoparasitically in land planarians. Approximately 80% of fungus gnat hosts are still unknown.

Fungus gnat larvae are usually slender and white, with ventral welts and a dark head capsule. Larvae pass through five instars. Development time for larvae may be rapid and passed in as little time as a week if the host fungus is ephemeral or in as long as 8–9 months for some keroplatids.

Pupation usually takes place in the ground but may be within the host fungus or hanging from the host fungus in a web of salivary threads. The form of the cocoon is generally dependent on the pupal environment; the pupa is enclosed in a dense or weak cocoon or may be encased within a web, without a cocoon. Many cocoons may be found together within the tissue of non-deliquescent fungi. Fungus gnats may have several generations in summer and fall and generally overwinter in the larval or pupal stage, although some troglophilic species may overwinter as adults.

Adults are slender to moderately robust flies that are black, brown, orange, yellow or a combination of these colors, and may have dark markings on the wings. Some are quite showy and probably mimic Hymenoptera (e.g., *Platyura*, Keroplatidae).

They range in size from 2 to 13.5 mm. Most are crepuscular. During the day, many species prefer moist dark places such as caves, overhanging stream banks, or cavities under tree roots. These areas often support dancing swarms of gnats. Sometimes species of several genera, in one or more families appear to swarm together and can be swept up in one motion with a collecting net. The adults of some genera, especially those with elongate mouthparts (e.g., *Antlemon* and *Asindulum*, Keroplatidae; *Gnoriste*, Mycetophilidae; *Lygistorrhina*, Lygistorrhinidae), presumably visit flowers to feed on nectar. Fungus gnats may be drawn to red or yellow pan traps and/or to light traps (mercury vapor or blacklight) by night. They may also be readily collected by sweeping in the appropriate habitat with an insect collecting net. However, the best way to collect high numbers of fungus gnats is by Malaise trapping.

In the fossil record, the earliest fungus gnats appear in the late Jurassic, at least 150 million years ago. Fungus gnats are rare but already well diversified in Cretaceous ambers, and by the Eocene it appears they were quite abundant. Fungus gnats belonging to recent genera are relatively common in Baltic amber.

References

Blagoderov V, Grimaldi D (2004) Fossil Sciaroidea (Diptera) in Cretaceous ambers, exclusive of Cecidomyiidae, Sciaridae, and Keroplatidae. Am Mus Novitates 3433:1–76

Hutson AM, Ackland DM, Kidd LN (1980) Mycetophilidae (Bolitophilinae, Ditomyiinae, Diadocidiinae, Keroplatinae, Sciophilinae and Manotinae) Diptera, Nematocera. Handbook for the Identification of British Insects Royal Entomological Society of London, vol 9(3), pp 1–109

Jaklovlev J, Siitonen J (2004) Finnish fungus gnats (Diptera, Mycetophilidae, etc.): faunistics, habitat requirements and threat status. Lammi Notes 30:3–7

Matile L (1990) Recherches sur la systematique et l'evolution des Keroplatidae (Diptera, Mycetophiloidea). Memoires du Museum National d'Histoire Naturelle Serie A Zoologie 148:1–682

Økland B (1994) Mycetophilidae (Diptera), an insect group vulnerable to forestry practices? A comparison of clearcut, managed and semi-natural spruce forests in southern Norway. Biodivers Conserv 3:68–85

Søli GE (1997) The adult morphology of Mycetophilidae (s. str.), with a tentative phylogeny of the family (Diptera, Sciaroidea). Entomol Scand Suppl 50:5–55

Vockeroth JR (1981) Mycetophilidae. In: McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR, Wood DM (eds) Manual of nearctic Diptera, vol 1, Monograph 27. Research Branch Agriculture Canada, Ottawa, ON, pp 223–247

Fungus Moths (Lepidoptera: Tineidae)

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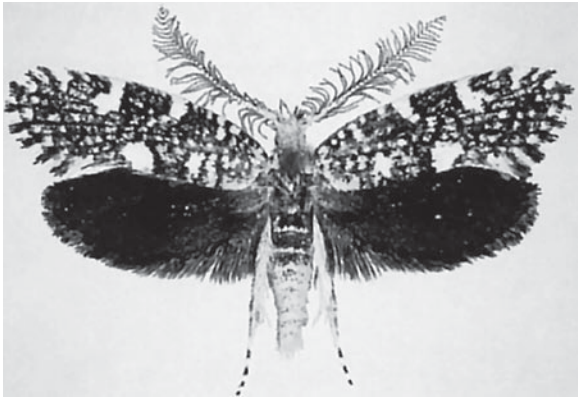
Fungus moths (Fig. 99), family Tineidae, comprise the first very large family of Lepidoptera, with about 2,160 described species; actual world fauna probably exceeds 4,000 species. The family is part of the superfamily Tineoidea, in the section Tineina, subsection Tineina, of the division Ditrysia. The family is divided into 16 subfamilies (many have been considered as separate families by some specialists in the past): Euplocaminae, Myrmecozelinae, Harmacloninae, Meessiinae, Dryadaulinae, Scardiinae, Nemapogoninae, Tineinae, Setomorphinae, Perissomasticinae, Hapsiferinae, Hieroxestinae, Erechthiinae, Siloscinae, Stathmopolitinae, and Teichobiinae. Adults minute to medium size (5–54 mm wingspan), usually with rough head scaling (a few have smooth-scaled heads); haustellum naked (unscaled); maxillary palpi long, 5-segmented (rarely 3-segmented). Maculation mostly somber grays or brown shades, with various speckling spots, but some tropical species colorful (e.g., genus *Coryptilum* from Southeast Asia). Adults are nocturnal or crepuscular; rarely diurnal. Larval habits vary greatly, but most are detritus feeders, some making cases, tunnels, or silken tubes; also, odd groups are coprophagous, keratophagous, woolen feeders, and even myrmecophilous and termitophilous larvae are known. The smooth-headed and more colorful Hieroxestinae and related groups are leafminers. Included among Tineidae are some of the most well



Fungus Moths (Lepidoptera: Tineidae), Figure 99 **Example of fungus moths (Tineidae), *Euplocamus ophisa* (Cramer) from Albania.**

known household pest species, such as clothes moths and grain moths.

References

Davis DR (1978) The North American moths of the genera *Phaeoses, Opogona*, and *Oinophila,* with a discussion of their supergeneric affinities (Lepidoptera: Tineidae). Smithsonian Contrib Zool 282:1–39

Gozmány LA, Vári L (1973) The Tineidae of the Ethiopian region. Transvaal Mus Mem 18:1–238

Robinson GS (1979) Clothes-moths of the *Tinea pellionella* complex: a revision of the world's species (Lepidoptera: Tineidae). Bull British Mus (Nat Hist), Entomology 38: 57–128.

Robinson GS, Nielsen ES (1993) Tineid Genera of Australia. In: Monographs of Australian Lepidoptera, vol 2. CSIRO, Melbourne, 344 pp

Zagulajev AK (1960–1979) Tineidae. In: Fauna USSR. Lepidoptera, 4(3):1–267 (1960); 4(2):1–424 (1964); 4(4):1–126 (1973); 4(6):1–408 (1979). Academie Nauk USSR, [in Russian], St. Petersburg

Furanocoumarins

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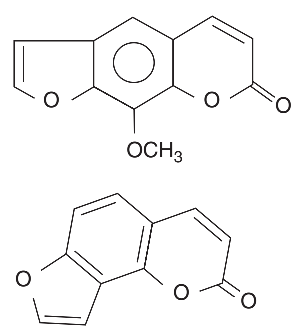
Furanocoumarins (or furocoumarins) are known to exert photodynamic action. Furanocoumarins are of special interest from entomological, medicinal, public health, and environmental viewpoints because of their high photobiological activity. Wavelengths in the near ultraviolet (i.e., UV-A: 320–380 nm) are the most effective spectra, even though furanocoumarins absorb relatively poorly in this region. Although plants containing photosensitizing furanocoumarins have been used by Indian and Egyptian civilizations for more than 3,000 years to treat certain skin disorders, it was only in the middle of the last century (late 1940s) that the photosensitizing and pigment-stimulating agents in these plants were identified. Extensive research on different aspects of furanocoumarins has been conducted since this discovery.

Furanocoumarins are a group of heterocyclic compounds in which the furan ring is fused with coumarin. They arise in nature from two configurations of the basic tricyclic ring structure, e.g., linear (psoralen: e.g., xanthotoxin) and angular (isopsoralen: e.g., angelicin) (Fig. 100). Based on available data, the linear furanocoumarins are more biologically active than their angular analogs. Furthermore, substitutions that increase polarity of the molecules usually decrease the activity. Naturally occurring phototoxins are an integrated part of our environment and they are apparently used by plants as defense mechanisms against herbivores. For instance, the biosynthesis of furanocoumarins and polyacetylenes, which are well established as phytoalexins, are drastically enhanced following plant infection with pathogens.



Furanocoumarins, Figure 100 **Chemical structure of two classes of furanocoumarins: above, linear (e.g., 8-methoxypsoralen, known as 8-MOP or xanthotoxin); below, angular (e.g., angelicin).**

Occurrence in Plants

Photoactive furanocoumarins have been isolated from at least a hundred plant species from eight families, including Apiaceae (Umbelliferae), Rutaceae, Leguminose (Papilionaceae), Moraceae, and Orchidaceae, but find their greatest diversity in the Apiaceae and Rutaceae. The seeds and roots are major sources of furanocoumarins in some of the clinically important plants species that are cultivated solely to obtain these photosensitizers.

Effects of Furanocoumarins

Since the discovery of the photosensitizing and the pigment-stimulating activities of furanocoumarins in 1940, entomological, medicinal and veterinary medicinal aspects have been the focus of different investigations.

Insects

Xanthotoxin, a linear furanocoumarin also known as 8-methoxypsoralen (or 8-MOP), was the first natural phototoxin that was shown to have insecticidal properties in 1978. When this compound was administered at a rate of 0.1% to the larvae of the southern armyworm (*Spodoptera eridania*), a low level of toxicity was observed. The activity was, however, greatly enhanced when the larvae were irradiated with near UV light. It also was shown that the southern armyworm will feed on carrot which does not contain furanocoumarins. It will not, however, feed on parsnip that does contain these compounds. A very low concentration of 8-methoxypsoralen has ovicidal activity against *Drosophila melanogaster* when exposed to light, but much higher concentrations are inactive in darkness.

Studies on insects also have determined how furanocoumarin-tolerant species avoid phototoxicity. There are several mechanisms for the resistance of insects to photosensitizers. While dark coloration due to the deposition of melanin is suggested to govern the resistance of *Papilio machaon* and *Manducta sexta* to phototoxic furanocoumarins, rapid metabolism of these toxins is considered to be the biochemical reason for *Papilio machaon*, *P. polyxenes*, *Depressaria pastinacella* and *Pastinaca sativa* to feed on umbelliferous host plants known to contain furanocoumarins. Nevertheless, the larvae of the furanocoumarin-sensitive fall armyworm (*Spodoptera frugiperda*) which also metabolize linear furanocoumarins by similar pathways, fail to avoid the toxicity due to a slower metabolism.

Domestic Animals

As early as 1946, it was suggested that ingestion of furanocoumarin-containing plants was a significant cause of photosensitization in domestic animals. For example, the furanocoumarin-containing plant spring parsley, *Cymopterus watsonii*, is a serious problem to domestic animals in the western USA, and *Ammi majus* is an important photosensitization source in cattle in the USA. While both cases involve severe blistering, the latter case also may lead to blindness.

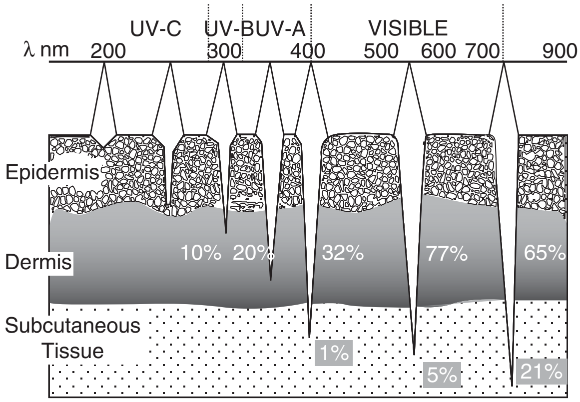
It is likely that most wildlife species have adapted through evolutionary pressures to avoid such plants. Nevertheless, it has been demonstrated that furanocoumarins, upon activation by light, are powerful antimicrobial agents, nematicides, molluscicides, piscicides, and powerful skin photosensitizers against humans and animals.

Photodynamic Therapy

The various photobiological actions exhibited by furanocoumarins have contributed to their extensive range of actual and potential uses in human medicine. Xanthotoxin (8-MOP) plus UV light, known as PUVA therapy, is now the treatment of choice for severe psoriasis. PUVA therapy has also been potentially beneficial for treatment of numerous human disorders including mycosis, atopic dermatisis, herpes simplex and lymphoma. Studies have shown that DNA and RNA viruses, both enveloped and non-enveloped, in nearly all major virus families have been successfully inactivated by psoralen derivatives in tissue culture medium and in blood products such as serum. The only viruses resistant to psoralen inactivation observed to date are picornaviruses. There is evidence to suggest that this resistance is due to the failure of psoralen to penetrate the exceptionally dense coat of this virus. Inactivation of human hepatitis viruses (B and non-A and non-B: i.e., C) by 8-MOP was successful in an in vivo chimpanzee infectivity model (Fig. 101).

Mode of Action

Although furanocoumarins are primarily known for their light-dependent activity, their biological activities in the absence of light, even though moderate, have also been demonstrated. They are, however, of special interest from agricultural, medicinal, public health, and environmental viewpoints for their highly photobiological activity.



Furanocoumarins, Figure 101 Extent of penetration of ultraviolet (UV) and visible light into human skin. (Drawing from the late B.E. Johnson, Department of Dermatology, University of Dundee, Scotland, U.K., courtesy of Springer-Verlag and G. Moreno, R.H. Pottier, T.G. Truscott (eds.), 1988, Photosensitisation: molecular, cellular and medical aspects.)

Wavelengths in the near ultraviolet (320–360 nm) range are the most effective ones, even though the absorption of these compounds in this region is relatively poor.

Psoralens readily pass through membrane structure (e.g., cell wall and virus coats), to photoreact preferentially with nucleic acids. Studies have shown that diadducts and mono-adducts (bound to a single pyrimidine) block nucleic acid replication and transcription. Consequently, the infectious quality of the virus is lot, while the surface and structure of the virus may remain largely unmodified.

At least a major part of the photobiological actions of furanocoumarins results from their intercalation into the double helix of DNA where, upon light activation, they form cyclobutane adducts with pyrimidine bases. Although there is clearly no direct involvement of oxygen in this interaction, which is governed by the Type I reaction, photogeneration of singlet oxygen by furanocoumarins has also been well demonstrated. The latter reaction (Type II) which involves singlet oxygen, may potentially be responsible for enzyme inactivation and membrane disruption.

Risks and Benefits Associated With Furanocoumarins

Photodynamic agents demonstrate a drastic increase in toxicity (usually 2–3 orders of magnitude) in the presence of UV-A or visible light. This is a property which should not be overlooked in assessment of toxicological data for the safety of these compounds. Although in the absence of light the oral LD_{50} for a furanocoumarin [i.e., xanthotoxin (8-MOP)] ranges between 300and 600 mg/kg body weight in rats, an oral dose of only about 1 mg/kg of body weight can be dangerous for humans with as little as 1 h of subsequent sunlight exposure. Phototoxicity symptoms include severe erythema followed by blistering and peeling of the skin. Fair-skinned individuals are much more likely to suffer sunburn and blistering reactions from furanocoumarin exposure than are more pigmented individuals.

The level of furanocoumarins in celery (originally 1 mg/kg) can increase about 100-fold if the celery is stressed or diseased. Many cases of contact photodermatitis have been reported in humans who have had dermal contact with furanocoumarin-containing plants. For example, celery pickers and handlers suffer from periodic outbreaks of celery dermatitis by the appearance of skin rashes on their arms when exposed to diseased celery. The causative agents have been identified as xanthotoxin (8-MOP) and trisoralen, which celery produces in response to "pink rot" infection with *Sclerotina sclerotiorum*.

There is up to 25-fold increase of several photocarcinogenic furanocoumarins (including 8-MOP and psoralen used in PUVA therapy) in the roots of diseased parsnips when compared with those isolated from the roots of healthy plants. In some instances, the amounts are so high that mixed crystals of furanocoumarins can be detected on the surface of parsnip roots by light microscopy. Linear furanocoumarins such as psoralen derivatives, which are widespread in plants of the Umbelliferae family, are potent light-activated carcinogens and mutagens. Skin cancer in animals and probably in humans are known consequences of photosensitization with furanocoumarins. Xanthotoxin (8-MOP), as well as other naturally occurring photosensitizers such as cercosporin, hypericin, polyacetylenes and their thiophenes, may represent a hazard to health as they possess the ability to induce genetic damage and mutations.

Side Effects of Photodynamic Therapy

Patients treated by photodynamic therapy normally suffer from different side effects of phototoxicity, such as nausea, hair loss, erythema, etc. In addition, numerous types of damage at the cellular level have been observed. For example, nuclear aberrations, single-strand breaks, interference with repair processes, DNA-protein cross-links, and injury to cell membrane, mitochondria and the nucleus have been documented.

Naturally occurring photosensitizers, such as 8-MOP, currently used in the treatment of psoriasis (PUVA therapy) also may represent a hazard to health as they possess the ability to induce genetic damage and mutations. Low concentrations of 8-MOP, mediated by UV-A, were sufficient to induce an increase in the frequency of chromosome aberrations in Syrian hamsters. There is no question that major changes occur to both tumor and surrounding normal microvasculature during and following photodynamic therapy. Changes to the endothelium, smooth muscle contraction and increased capillary permeability also have been observed during therapy. Thus, PUVA therapy should be used with caution.

References

Ames BN (1983) Dietary carcinogens and anticarcinogens: oxygen radicals and degenerative diseases. Science 221:1256–1264

Blum HF (1964) Photodynamic action and diseases caused by light. Hafner Publishing Co, New York, NY, 309 pp

Heitz JR, Downum KR (eds) (1987) Light-activated pesticides. ACS Symposium Series 339, Washington, DC, 339 pp

Ivie GW (1978) Toxicological significance of plant furocoumarins. In: KeelerRF, van Kampen KR, James LF (eds) Effects of poisonous plants on livestock. Academic Press, London, UK, pp 475–485

North J, Neyndorff J, Levy JG (1993) Photosensitzers as virucidal agents. J Photochem Photobiol B 17:99–108

Young AR (1990) Photocarcinogenicity of psoralens used in PUVA treatment: present status in mouse and man. J Photochem Photobiol B 6:237–247

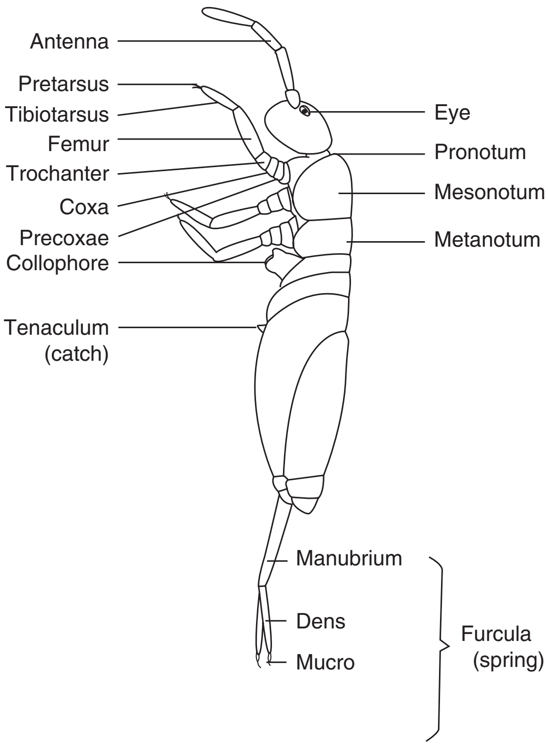
Furcate

Having a forked appearance.

Furcula

A forked structure found beneath the abdomen of springtails (Collembola), attached apically, and used for leaping (Fig. 102).

► Abdomen of Hexapods



Furcula, Figure 102 **Lateral view of a springtail (Collembola).**

Furniture Beetles

An alternative name for beetles of the family Anobiidae, or death-watch beetles. They feed on dry substances such as cereal grains or wood, including furniture.

► Beetles

► Food Habits of Insects

Fused

This term usually is used to indicate structures that were once (in an evolutionary sense) separate, but are now joined, and lack indication of former separation.

Fusiform

This term describes a structure that is widest at the midpoint, and narrowed at both ends.

G

Gahan, Arthur Burton

Arthur Gahan was born into a large farm family in Kansas on December 9, 1880. He attended Kansas State College, graduating in 1903. Then in 1904 he became assistant in the Department of Entomology of Maryland Agricultural College, and received an M.S. from that institution in 1906. He remained there as Assistant Entomologist, becoming interested in "parasitic" Hymenoptera in general and braconid parasitoids of aphids in particular. In 1913 he accepted a position with the U.S. Department of Agriculture, to work as a taxonomist at the U.S. National Museum. There, he worked on various groups of "parasitic" Hymenoptera, but ultimately concentrated on Chalcidoidea and became a leading authority of them and publishing copiously. He married in 1908, was active in civic affairs and the Entomological Society of Washington, becoming its president in 1922. He died on May 23, 1960, and was survived by his wife and two children.

Reference

Mallis A (1971) Arthur Burton Gahan. In: American entomologists. Rutgers University Press, New Brunswick, NJ, pp 373–374

Galápagos Islands Insects: Colonization, Structure, and Evolution

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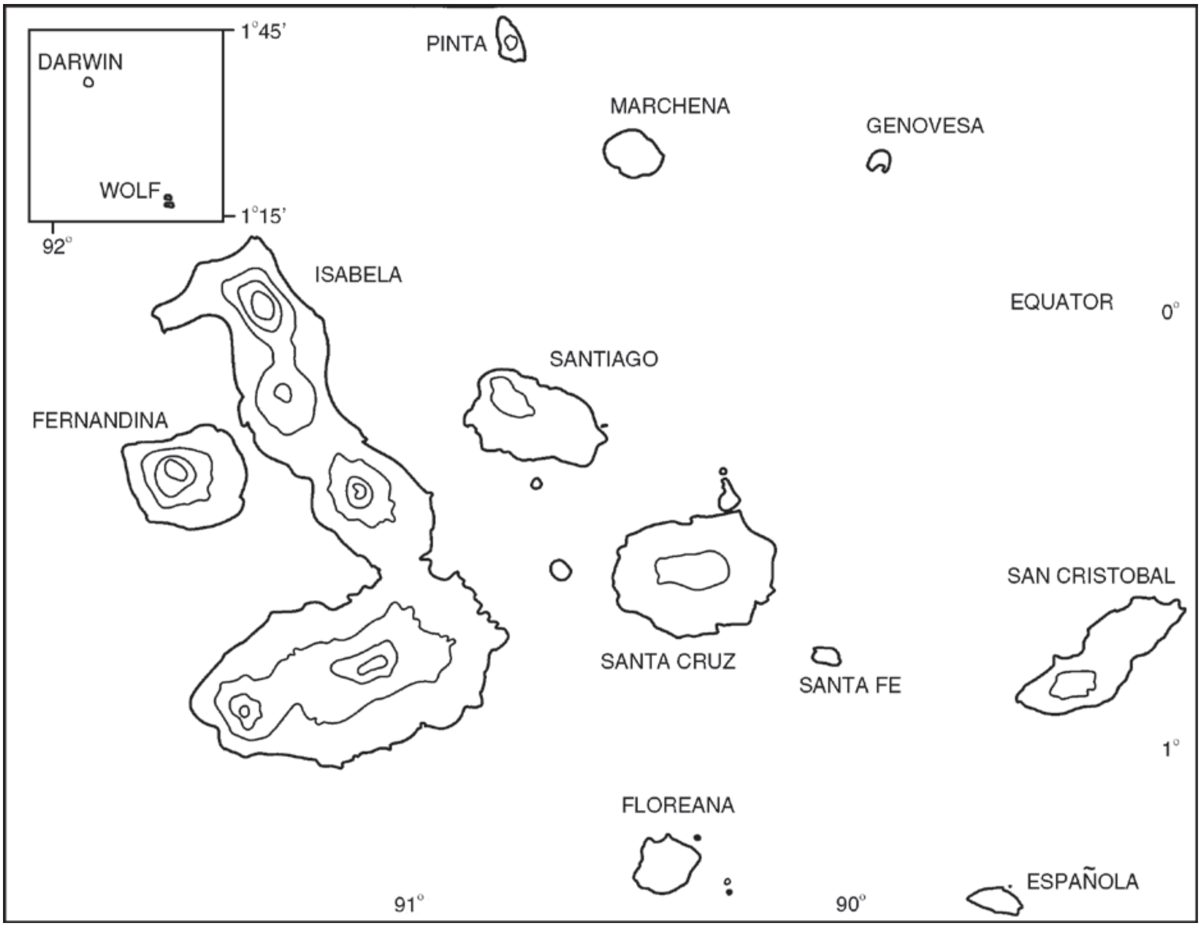
The Galápagos archipelago of Ecuador has an interesting insect fauna that is now rather well known. The archipelago is composed of 19 islands larger than 1 km^2, with a total land area of 7,882 km^2. It is the world's only remaining tropical oceanic archipelago that is little altered by humans. The present islands, 800–1,000 km west of the Pacific coast of Ecuador, have been available for terrestrial colonization for 3–4 million years. The archipelago is a model system for assessing the dynamics of biotic dispersal to, and differentiation on, oceanic islands. They are a natural experiment which has been running in oceanic near-isolation for about 3 Ma. Each island (Fig. 1) is a replicate of an experiment in biotic dispersal, colonization, and differentiation. The present plants and animals can be seen to be a record of the successes in dispersal to the islands, and of the dynamics of their subsequent evolution in isolation. The story has been well (or even exhaustively) reported for many of the larger plants and vertebrates. This story, however, has not been well studied for the vast majority of insects and other terrestrial invertebrates.



Galápagos Islands Insects: Colonization, Structure, and Evolution, Figure 1 **Map of Galápagos Archipelago.**

The insect fauna (Tables 1 and 2) is now known to contain 23 of the world's 31 orders of insects, with at least 255 families, 1,057 genera, and 1,853 species, of which 736+ are endemic, 818+ are indigenous, and 295+ are introduced. Within the beetles (Coleoptera), the islands have 56 families, 297 genera, and 486 species (266 endemics, 110 indigenous, and 110 introduced species). The 376 native beetle species (indigenous and endemics combined) represent a rate of species accumulation of about one every 9,260 years (through successful colonization plus speciation through about 3.5 million years).

Charles Darwin is known to have been a keen collector of insects and especially beetles. However, as he wrote in his 1845 book "Voyage of the Beagle," he was not impressed by the abundance or diversity of the insects of the Galápagos Archipelago. In fact, the entire biota of the Galápagos is generally not very impressive in appearance. But there are a few exceptions and these have received exceptional publicity. Most of the organisms are, however, small or drab when compared with those of the luxuriant tropical forests of mainland South America. This is partly a reflection of the isolation of the islands (800–1,000 km west of the coast of Ecuador), their youth (only 3–4 million years), the difficulty of dispersing to them, their seasonally harsh and semi-arid tropical climate, and the difficulty of establishment by colonizing species.

Galápagos Islands Insects: Colonization, Structure, and Evolution, Table 1 Numbers of native (endemics plus indigenous) genera, species, and single-island endemic beetle diversity, arranged by increasing island size . The larger islands have more genera, more species, more single-island endemics, and more species per genus. These generalizations also occur in the rest of the native insects fauna

Island	Area	Total native	Total native	Single-island species/	
	(km²)	Genera	Species	Endemics	Genus ratio
Caamaño	0.045	9	10	0	1.11
Beagle	0.08	1	1	0	1.0
Campeón	0.095	16	16	0	1.0
Plazas Sur	0.119	17	17	0	1.0
Eden	0.23	8	8	0	1.0
Daphne Major	0.330	3	4	0	1.33
Gardner at Floreana	0.812	7	7	0	1.0
Darwin	1.063	15	15	2	1.0
Bartolomé	1.24	16	17	0	1.06
Tortuga	1.298	3	3	0	1.0
Wolf	1.344	17	17	2	1.0
Seymour	1.838	31	33	0	1.06
Rábida	4.993	46	48	0	1.04
Genovesa	14.10	44	48	2	1.09
Pinzón	18.15	42	44	2	1.05
Santa Fé	24.13	40	48	2	1.20
Baltra	26.19	28	32	0	1.14
Pinta	59.40	76	87	0	1.15
Española	60.48	55	65	4	1.18
Marchena	129.96	56	63	2	1.13
Floreana	172.53	114	141	5	1.24
San Cristóbal	528.09	123	153	17	1.24
Santiago	584.65	119	148	14	1.24
Fernandina	642.48	72	80	1	1.11
Santa Cruz	985.55	186	258	27	1.39
Isabela	4,588.0	158	205	24	1.30

Colonization Processes

How do insects get to oceanic islands? The processes of colonization and any subsequent evolution on islands can seldom be directly observed. Usually, they are deduced from an analysis of the distributional and ecological patterns of the organisms in conjunction with evolutionary and ecological theory.

There are two general groups of hypotheses about processes which place biotas on islands. One of these, the "Continental Drift" process of distribution of ancient biotas, is irrelevant for the Galapágos because of their geological youth and oceanic origin.

Galápagos Islands Insects: Colonization, Structure, and Evolution, Table 2 Summary of numbers of species and native genera of the insect orders of the Galápagos islands. Some orders have a disproportionate number of introduced species, especially on the islands with human settlement. A figure of 1.00 in the column of native species/native genus ratios shows that there has been no speciation in many insect orders after the natural colonization event of a single species in each genus, and comparatively little in the other orders

Order	Introduced Species	Native species	Native Genera	Species/Genus Ratio
Collembola	3	35	22	1.57
Diplura	1	2	2	1.00
Archeognatha	0	1	1	1.00
Thysanura	1	2	2	1.00
Odonata	0	8	7	1.14
Orthoptera	4	29	13	2.23
Mantodea	0	1	1	1.00
Blattodea	11	7	3	2.33
Isoptera	0	4	3	1.33
Dermaptera	4	3	2	1.50
Embioptera	1	1	1	1.00
Zoraptera	0	1	1	1.00
Psocoptera	14	26	22	1.18
Thysanoptera	8	42	42?	1.00?
Hemiptera	118	198	86	2.30
Phthiraptera	8	80?	40?	2.00?
Neuroptera	0	8	5	1.6
Strepsiptera	0	1	1	1.00
Siphonaptera	3	1	1	1.00
Coleoptera	111	378	226	1.67
Lepidoptera	64	±300?	160?	1.88?
Diptera	66	±200?	150?	1.33?
Hymenoptera	46	±250?	160?	1.56?

Thus, all terrestrial colonists have crossed the oceanic water gap by one of four general dispersal mechanisms. The method of dispersal is a property of all the ecological, behavioral, and physiological characteristics of the species and of its mode and frequency of transport opportunity. Colonization is a property of both the life history requirements of the species and the characteristics of the new environment.

Aerial Transport (Actively by Flight and/or Passively by Wind)

This probably accounts for about half of the insects of the Galápagos. The mean body size of Galápagos insects appears to be smaller than for a mainland Ecuadorian fauna (but measurements are available for neither). Darwin first noted the small size of the insect fauna. The smaller body size would support the idea that the majority of the insect colonists were carried as flying individuals by winds. In contrast to its importance for insects, it may seem surprising that wind transport may account for only 9% of natural seed-plant colonizations of the Galápagos.

Marine Transport

A significant component of the total insect fauna probably arrived on the sea surface, either on rafts of vegetation and flotsam or by floating themselves (as pleuston). This may be the most important mode for most of the flightless terrestrial arthropods. For the insects themselves, it is estimated that marine transport may also account for about half of the original colonists. Flightless or poorly flying groups of large-bodied beetles such as weevils and darkling beetles probably used this mode, as did millipedes, centipedes, terrestrial isopods, oribatid mites and others. Bostrichids, cerambycids and various other wood-boring and wood-associated beetles probably arrived by rafting in wood as adults or immatures. Flightless *Gerstaeckeria* weevils may have arrived on rafting pieces of their *Opuntia* cactus host plants.

Several groups of large-bodied wingless beetles such as endemic *Galapaganus* weevils and the three genera of Darwin's darkling beetles (genera of Tenebrionidae containing nine species that were first collected by Darwin: *Stomion*, *Ammophorus*, and *Blapstinus*) are represented by species that occur on more than one island. Such cases are usually within the older eastern and central group of islands. It is logical that these species originated (speciated) on one island and that they have then moved from this to another island, probably after being washed to sea during heavy El Niño rainstorms and floods.

Transport on or in Other Animals

Insect ectoparasites, such as all of the 80 species of Phthiraptera (chewing bird-lice) and the 8 species of Hippoboscidae (louse flies, Diptera), as well as bird ticks, reptile ticks and chigger mites, undoubtedly arrived on their vertebrate hosts. Bird transport has also been important for seed-plants, because it is estimated that 79% of the angiosperms arrived as propagules with birds, either on or in their feathers or in their digestive tracts. Rafting terrestrial mammals and reptiles seem to have carried a few arachnid and insect ectoparasites. And invertebrate colonists themselves have also carried some of their own arthropod parasites. Examples are one strepsipteran (in leafhoppers), several dryinid wasps and some pipunculid flies (in leafhoppers). Among the beetles, there are two examples: one meloid blister beetle (on *Xylocopa* carpenter bees), and two rhipiphorid beetles (in wood-boring beetle larvae) probably arrived as parasitic immatures on or in their host insects. The parasitized bee hosts themselves probably arrived by rafting on floating wood and the hosts of the rhipiphorids in lumber imported for construction of buildings.

Human Mediated Transport

Humans have intentionally introduced many domestic animals and agricultural or horticultural plants to the Galápagos. Some of these have escaped and become feral. But there is only one example of the intentional introduction of an arthropod: the vedalia beetle (Coccinellidae) for the bio-control of the cottony cushion scale (*Icerya purchasi*, Hemiptera), an introduced pest. By 1998 there were at least 292 recognized examples of unintentional introductions of insect species and the number in 2004 was at 450 species of introduced insects. Such species are here called introduced species, but the term "adventive" has also been used for these. The first such introduced insect may have arrived with the first European landings of Bishop Tomas de Berlanga and his party in 1535, as *Dermestes* (dermestid) and *Necrobia* (clerid) beetles and cockroaches. These were all commonly associated with humans and stored products in their sailing ships. Pirates, who used the islands from shortly after the time of their discovery until the early 1700s, and whalers and sealers, from the mid 1700s to mid 1800s, may have brought an alleculid beetle (and other dry-wood insects such as bark-beetles) in logs or firewood from the mainland.

Ships transporting both supplies and tourists have taken insects attracted to ships' lights to and between the islands. The orders with the largest number of introduced species are Coleoptera, Hemiptera, Lepidoptera, and Diptera. Some 111 beetle species are among the more commonly encountered species of insects introduced to date. Not all of the introduced species seem to have become permanently established; some long-horned beetles have not been found since their original collection. The introduced species occur in greatest diversity on the four large islands with permanent human settlements. There is now a program of agricultural quarantine control and inspection of goods and materials coming into the Galápagos in an attempt to limit future introductions of alien arthropods.

Sources of the Colonists

There is limited detailed data on the mainland distributions of either indigenous Galápagos insects or mainland sister species of the endemic species. The data now available seem to indicate that only a few of the Galápagos colonist insects came from southern South America (arid coastal Peru or Chile). Most of the faunal relationships are with the lowland semi-arid and seasonal Neotropics, along the Pacific coast from Mexico to Ecuador. The best phylogenetic and biogeographic analyses show a general biogeographic pattern of a western Neotropical source area and that the Galápagos species are relatively recently derived species.

Stochastic (Random) Processes in Colonization and Distribution

Colonization is seldom strictly predictable or linear even if the islands themselves are relatively linear in age or geography. As an example, one would predict that insect colonization was first to San Cristóbal and Española, which are the oldest and most easterly islands, and that the other islands were colonized sequentially northwestward as stepping stones as they formed through time. Exceptions to these predicted patterns do exist. This shows the lack of absolute predictability in present distributions through the randomness of the processes of either past dispersal, or colonization success, or extinction. For instance, the carabid beetle genera *Platynus* and *Scarites* are on Isabela and San Cristóbal islands, and not on Santa Cruz, which lies between them. The indigenous carabid *Halocoryza acapuliana* Whitehead is known only from small and central Rabida Island.

Neighbor islands are more likely to share endemic species. This is clear in a number of shared beetle species limited to island pairs such as Darwin and Wolf (the tenebrionid *Stomion cribicollis* Van Dyke and the weevil *Galapaganus darwini* Lanteri), and Marchena and Pinta (the tenebrionid *Stomion rugosum* Van Dyke). The isolation of Genovesa is evident in its failure to be colonized by flightless *Ammophorus* beetles and other insect groups. Flightless *Galapaganus* weevils are seemingly absent from Pinta and Marchena. Pinzón is famous for not having the widespread palo santo tree (*Bursera graveolens*), but this island's insects are not well enough known to evaluate a pattern of absence of insect species there.

Randomness is evident in the fact that some colonizations have been across the archipelago (from one side of the archipelago to the other). Molecular data suggest that Pinta Island was colonized by tortoises by oceanic transport from Española, and cladistic analysis suggests the same pattern in flightless *Stomion* beetles.

Structure of the Insect Fauna

An Unbalanced Fauna

Insect representation at the family level in the Galápagos is vastly different from that in the Neotropical fauna. The cause is the inequality of families in their ability to successfully complete both the sequential processes of dispersal and then colonization. When compared to the fauna of the Neotropical continental source area, it is evident that the Galápagos fauna is unbalanced (or disharmonic) and impoverished. This means that the taxonomic composition of the archipelago is significantly different in its makeup and proportions from that of the mainland.

The probable reasons for the absence of many insect families, subfamilies, and tribes are diverse. Difficulties of long-distance over-water dispersal and colonization must lie at the core of the reasons. Long distance dispersal is unlikely for many taxa and the lack of diverse and suitable habitats in the Galápagos is of undoubted importance. The absence of suitable food plants or prey items is involved. The taxa which are present can be viewed as able dispersalists, rugged colonists, and adaptable in acceptance of available microhabitats and food materials.

Trophic Generalists

Colonization is probably easier for trophic generalists (scavengers and predators) than for herbivores which are more likely to be specialist feeders. Island insect faunas in general tend not to be as rich in herbivores as the faunas on continents. In Galápagos beetles there are more trophic generalists (scavengers and predators) than herbivores. However, in Heteropteran bugs, colonization of islands by herbivores seems to be more successful than by predators.

Trophic Specialists

There is little evidence that Galápagos insects have narrow or restricted feeding niches. The few examples are *Gerstaeckeria* weevils which feed only on the tissues of *Opuntia* cactus, and some host specific seed feeding bruchids and scolytids. *Ataenius* scarabs, usually associated with herbivorous mammal dung, feed on the dung of the herbivorous giant tortoises and land iguanas. This may or may not represent a shift to a new food type. Tortoise and land iguana dung appears similar to that of ungulates because it is mostly composed of poorly digested plant materials.

Ecological Escape

Plant or animal colonists on islands may be ecologically "released" through escape from their continental herbivores, parasites, predators, and competitors. Many cases of escape from insect herbivores or predators must exist, but few are recognized. One example is the seed-producing legume plants which have escaped many (but not all) of their seed predator bruchid beetles. The bruchid *Megacerus leucospilus* (Sharp) feeds on the seeds of the widespread beach morning-glory *Ipomoea pes-caprae* in Central America, but the plant seems not to have this seed predator on the Galápagos.

Parthenogenesis

If females of a species can reproduce without the presence of individuals of the male sex, the species is more likely to establish itself as a colonist. Several of the Galápagos insects are known to be parthenogenetic. But there is no apparent evidence that this has been disproportionately important in the colonization of the Galápagos.

Vegetational Zonation and Diversity

Terrestrial communities in the Galápagos are usually characterized according to the elevation-related (precipitation and temperature controlled) zonation of the flora. The archipelago may possess the strongest or most compressed floristic zonation to be found anywhere in the world, passing through its six major vegetation zones in an elevational rise of only about 700 m; the littoral, arid, transition, humid forest, evergreen shrub, and above-treeline fern-sedge ("pampa") zones.

Insect diversity also seems to display some zonation, with fewer species being known from the higher elevations. The arid zone has the largest area in the islands and the most native insect species. The other zones, at higher altitudes, have progressively less area and proportionally fewer species, but sampling has not been equivalent. This probably indicates that the arid zone has been a bigger target for colonization for a longer period of time. The introduced species are more evenly distributed in all zones. This might be a reflection of the more eurytopic (adaptable) nature of the introduced species.

Plants also support diversity in that they provide various structural parts that may be fed upon by feeding specialists. Host-specific plant-feeding insects could be expected to exhibit the same zonation as their hosts, but almost all Galápagos phytophagous insects seem to feed on several species of host plant. Data for genus and family-level host-plant diversity are not available. Host specificity, to be expected in groups which elsewhere are usually monophagous or stenophagous plant-feeders, such as chrysomelids, is slight in Galápagos phytophagous beetles. There is no additional evidence for host specificity in indigenous phytophagous insects other than in *Gerstaeckeria* weevils on *Opuntia* cactus and some bruchids and scolytids. Thus, phytophagous species are in the minority, few are host specific, and none seem to have co-evolved with the endemic vegetation.

Seasonality

Environmental conditions regulate periods of insect activity. Most adult insect species are present or active during the rainy months of January to June. With the arrival of the Galápagos rainy season, insect activity increases and there are large and noteworthy outbreaks of beetles and other insects, which seem to be short-lived. These include *Calosoma* ground beetles, *Camponotus* ants, *Disclisioprocta stellata* Guenée (a geometrid moth), various sphinx moths, and other insects. These mass emergences are best noticed at lights at night and are environmentally triggered, but they also occur annually in coastal mainland Ecuador and seasonal forests elsewhere in Central and South America, so they are not a unique island feature.

Evolutionary Dynamics

Genus Level Endemism

Endemics are taxa limited to the geographic area under discussion. Genera endemic to the Galápagos probably represent an earlier time of colonization and a more prolonged period of isolation. Galápagos endemic genera are proportionally more frequent in the vertebrates and less frequent in the insects. This could mean that vertebrates differentiate at a faster rate or under stronger selective pressures, but more probably is a reflection of the more finely divided subjective criteria for what defines a vertebrate genus. Some endemic insect genera do exist. Among these endemics are some which can be called phylogenetic relicts or paleoendemics and which have no close relatives, such as the eyeless cave staphylinid *Pinostygus* of Isla Santa Cruz, and the *Neoryctes* dynastine scarabs which occur as four species on four islands. Some genera, once thought to be Galápagos endemics, have since been found in mainland Neotropical localities and others may yet be detected.

Species Level Endemism

Most insect colonization has not been followed by much species multiplication; the mean for the native beetle fauna is about 1.35 species per colonizing ancestor. About half the naturally occurring species are endemic, depending on the insect order. These evolved to endemic status following the colonization event of the ancestral species. The factors suppressing speciation in general in the Galápagos (as compared with other archipelagos) seem to be, in probable order of importance: lack of great ecological diversity, closeness to mainland source areas, and geological youth of the islands.

Different groups of organisms need not present equivalent amounts of endemism. This is obviously a result of differences in their vagility and the amount of gene flow between continental and island populations. In beetles, the good dispersers have lower levels of endemism, while poorer dispersers have higher levels. Comparison of the Galápagos and Hawaiian archipelagos shows a much larger mean number of speciation events from a single colonist ancestor in Hawaii. This is probably the result of Hawaii's greater age, area, ecological diversity, and isolation (this is to say that colonist arrival is less frequent, and that genetic dilution of island populations by mainland genomes is also less frequent).

Speciation

Most insect genera in the Galápagos are represented by only a single species. This shows that most colonization of the islands has usually been by only one species in a genus. This pattern was first noted by Darwin. Only a minority of the native insect genera which are present contain more than one species, either through multiple colonization, or species multiplication on the islands. The process of forming several species by allopatric speciation on a single individual island has not been a dominant evolutionary process in Galápagos beetles, while it has been a spectacularly exuberant process in the Hawaiian Archipelago.

Nevertheless, there are several insect genera which have undergone appreciable subspeciation or speciation in the Galápagos but none of these approach the dramatic swarms of species (descended from a single ancestor species) of insects, snails, or birds that have evolved in Hawaii. For instance, while hundreds of species of *Drosophila* occur in Hawaii, there are only 13 species (many cosmopolitan) of in these in Galápagos.

Winged Endemic Species

In the winged insects the most common pattern of distribution is for a species to occur on more than one island. This is easy to understand. It is most likely that these evolved on a single island and then dispersed to other islands, usually by flight.

Loss of Wings

Loss of flight ability is one of the more pronounced phenomena associated with island insects. This is seemingly not a property of island life itself, but of habitat stability and homogeneity. Flightlessness also frequently occurs in insects in desert and semi-arid habitats. This last is the best single characterization of Galápagos environments, and beetles are prime examples. Flightlessness in some South African desert dwelling scarab beetles is a morphological correlate with water conservation capabilities. This may also be true and part of the adaptive strategies of such flightless Galápagos beetles as tenebrionids, carabids, and weevils. Beetle examples of more speciation in less vagile groups are in flightless carabids, weevils, and Darwin's darkling beetles (*Stomion*, *Ammophorus*, and *Blapstinus*). Interestingly, even within flightless genera in the arid lowlands, many species do occur on more than one island, and these are probably evidence of inter-island oceanic transport following the origin of the species on one island.

The single island endemics are usually restricted to either the arid lowlands or the moist uplands (of high islands). Groups that are actively in the process of losing flight ability, such as *Ataenius* and *Neoryctes* scarabs, show discrete polymorphic stages in reduction of hind wings. So, loss of flight ability in Galápagos insects is a significant evolutionary theme. This has not always sponsored a major burst of species multiplication, but it has happened more often in groups that lost their flight ability on the Galápagos as a convergence rather than in groups that arrived already in a flightless condition. There is a parallel in birds: rails have reached many oceanic islands and then convergently experienced a reduction in wings and loss of flight ability.

Speciation and Flightlessness

Flightless terrestrial arthropods would certainly appear to have less dispersal potential than winged ones, and most species proliferation has occurred in the Galápagos beetles that are secondarily wingless. Nine genera of beetles probably colonized in a flightless condition, but only four of these have undergone island multiplication to three or more species. These groups have produced an average of 3.0 species per colonization event. Another 14 genera appear to have become flightless after colonization and these show even more species proliferation, with a mean of 3.6 species per colonization event.

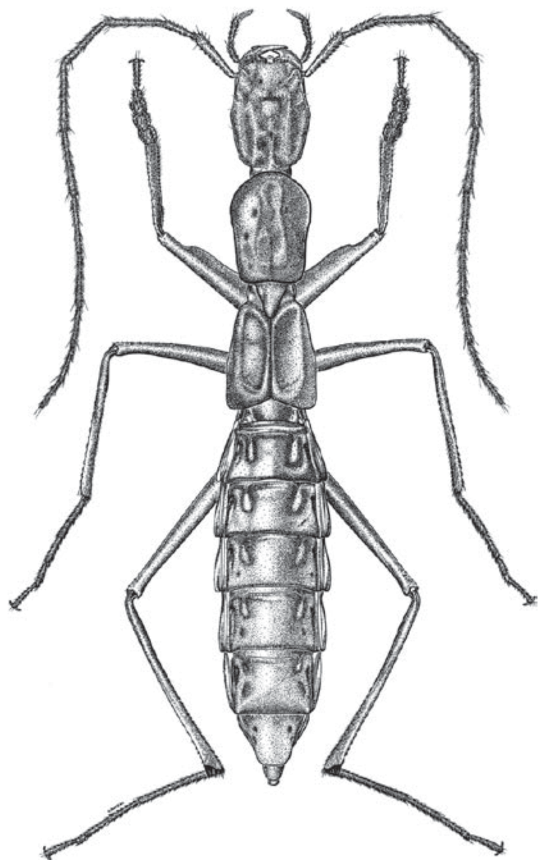
Adaptive Radiation

Adaptive radiation is a common phenomenon on islands. But it is important to note that adaptive radiation is much more than just the simple allopatric species multiplication that follows genetic isolation on separate islands. It is here defined as the set of evolutionary changes which occur in the diversification of a lineage that facilitate the exploitation of new resource types with different morphological or physiological traits. Thus, along with the morphological, physiological, and/or behavioral changes accompanying speciation must also come changes in either or both niche and habitat use. This is what has happened in the famous textbook example of Darwin's finches. Other examples can include the striking adaptive radiation in *Scalesia* trees and shrubs, and perhaps arguably in *Opuntia* cactus. In contrast, the famous giant tortoises and less famous lava lizards have undergone much speciation or subspeciation, but there is little evidence for true adaptive radiation in these examples. Adaptive radiation is probably enhanced by competition for limited resources, as in the case of the finches, especially in times of drought. But, it is difficult to envision intense competition between generalist scavenger or generalist predator insects.

Are the few examples of adaptive radiation indicative of a generalization, or are they exceptions? How many of the monophyletic species swarms in the insects of the archipelago have undergone significant ecological, morphological, or behavioral differentiation that promotes life in a new niche or new habitat? In short, there seem to be very few examples within the insects in general. In the three genera of Darwin's darkling beetles (*Ammophorus*, *Stomion*, *Blapstinus*) there are some cases of congeneric species sympatry and there is some habitat separation between species based on preferences for different substrate types (sand versus volcanic ash), habitat distance from the seacoast, and elevation. Most *Ammophorus* species inhabit the arid zone, but two are restricted to the moist highlands of San Cristóbal and Santa Cruz Islands. The same occurs in *Galapaganus* weevils. Thus, while the Galápagos are famous for having provided a classic example of the process and results of adaptive radiation in Darwin's finches, this is an exception. It is only a very infrequent or arguable result in Galápagos insects.

Subterranean Arthropods

A diverse assemblage of many eyeless arthropods occurs in the extensive systems of caves and rock crevices in the volcanic basalt bedrock of the Galápagos. Some ten species of arthropods such as geophilomorph centipedes, polydesmoid millipedes, soil dwelling earwigs, and darkling and carabid beetles are in eyeless (Fig. 2) genera which must have colonized the Archipelago in an already-eyeless condition. But at least another 23 species of



Galápagos Islands Insects: Colonization, Structure, and Evolution, Figure 2 **The staphylinid beetle *Pinostygus galapagoensis* Campbell and Peck from a lava tube cave on Santa Cruz island. This eyeless and flightless subterranean endemic genus and species has probably changed more from its ancestral colonizing species than any other Galápagos animal. The beetle belongs to a group of visually hunting and flying arboreal predators which live in the canopy of tropical South American rainforests. No other members of its tribe occur in the Galápagos. The body length is about 2.5 cm, and this is the world's largest eyeless-wingless staphylinid beetle.**

eyeless terrestrial arthropods, including seven beetle genera, are in normally eyed groups. These must have lost their eyes after colonizing the islands, and during the process of adapting to soil, litter or subterranean habitats.

Extinction

Extinction through time is a natural process and is to be expected. But extinction caused by human action is different and should be of great concern in the Galápagos. Insect species extinction through human causes is probable, but no documented individual examples are known. Some of the introduced insects, such as *Wasmannia* fire ants and *Polistes* wasps, are preying on or competing with indigenous and endemic insects.

Feral vertebrates have had a two-fold effect on beetles and other insects. (i) The vertebrates have caused the near or complete loss of insect host plants, such as *Opuntia* cactus on most of Floreana and San Cristóbal (eaten by feral goats and donkeys). This has led to the concomitant loss of host-specific insects such as *Gerstaeckaria* weevils. (ii) The vertebrates have also had an effect by being predators, such as mice or rats or pigs, feeding on *Neoryctes* scarab beetles or other large-bodied insects. Despite these examples, there is presently no strong or direct evidence of the actual archipelago-wide extinction of an insect species on the Galápagos through an action ultimately caused by human activity.

Human-caused habitat alteration has had a significant, but unmeasured effect on the native insect populations. The clearing of large areas of *Scalesia* forest for agriculture and pastures and the replacement of large areas of native vegetation by introduced crop plants, grasses and weeds on Floreana, Santa Cruz, San Cristóbal, and Isabela must have had some impact. The importance of all of these introductions and alterations has not been measured or even estimated for the beetles or other insects.

Future Research

Although much is now known about Galápagos insects, there is still much to learn, especially about the life histories and evolutionary relationships of the species and in comparing them with the continental South American insect fauna. The Galápagos National Park Service and Charles Darwin Research

Station invite international research proposals and scientific collaboration with Ecuadorian personnel, students, and researchers. Information on past and present entomology research programs and details for scientific research permit applications can be found at http://www.darwinfoundation.org/terrest/entomology.html Research proposals of an applied and conservation orientation are especially welcome. General collecting without a research purpose is not permitted.

References

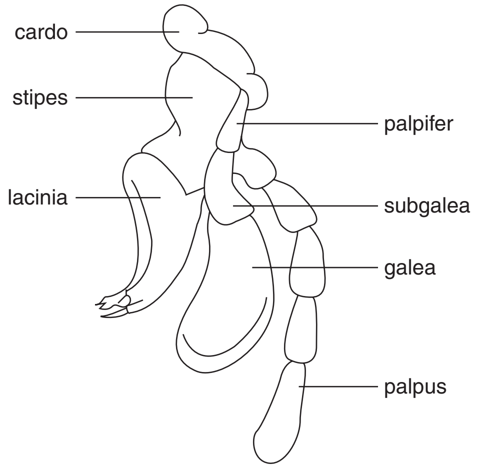
Causton CE, Peck SB, Sinclair BJ, Roque-Albelo L, Hodgson CJ, Landry B (2006) Alien insects: threats and implications for conservation of Galápagos Islands. Ann Entomol Soc Am 99:121–143

Peck SB (2001) Smaller orders of insects of the Galápagos Islands, Ecuador: evolution, ecology, and diversity. Scientific Monograph Series, National Research Council Press, Ottawa, Ontario, Canada, 278 pp

Peck SB (2006) The beetles of the Galápagos Archipelago, Ecuador; evolution, ecology, and diversity (Insecta: Coleoptera). Scientific Monograph Series, National Research Council Press, Ottawa, Ontario, Canada, 313 pp

Galea (pl. galeae)

The outer region of the maxilla, often a lobe (Fig. 3), and sometimes highly modified (Fig. 4) for feeding in Diptera, Lepidoptera and Hymenoptera. It forms the elongate, coiled proboscis in Lepidoptera.



Galea (pl. galeae), Figure 3 External lateral aspect of the left maxilla in an adult grasshopper, showing some major elements.

► Mouthparts of Hexapods

Gall

An abnormal growth on a plant induced by insect or mite feeding, or a plant pathogen.

Gall Formation

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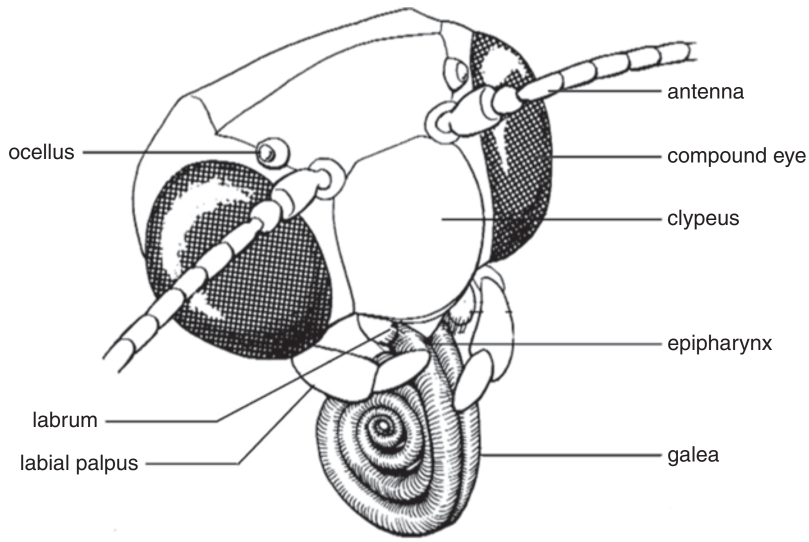
Galls are structures that form as a result of the abnormal growth activities of plants in response to gall-inducing organisms. Most galls are caused by nematodes, insects and mites, while a very small percentage are caused by bacteria, fungi and viruses. There are thousands of species of insects in the world that induce gall formation on the roots, stems, leaves, buds, flowers and fruits of plants in a wide variety of plant families. Insect galls range in complexity from simple outgrowths to more highly differentiated structures such as those typified by many of the cynipid wasp galls. Despite the large numbers and types of insect-induced galls, very little is known regarding the underlying mechanism or mechanisms of insect gall formation. In contrast, the mechanism of crown gall formation by the bacterium *Agrobacterium tumefaciens*, has been well characterized. An understanding of the mechanism of crown gall formation may provide some clues to the mechanism or mechanisms of insect gall formation.

Crown galls form as a result of wound inoculation on many species of plants by the soil dwelling bacterium *Agrobacterium tumefaciens*. Early studies showed that crown gall tissues exhibit autonomous growth and retain their tumorous



Galea (pl. galeae), Figure 4 **The head of a moth (Lepidoptera) showing some components.**

characteristics in the absence of the inducing bacterium. The ability of the bacterium to induce gall formation subsequently has been shown to be encoded by a tumor-inducing (Ti) plasmid that is transferred into the plant tissue. A small fragment (the T-DNA) of the Ti plasmid is integrated into the plant cell genome within the nucleus and is stably maintained and transcribed. It has been shown that the T-DNA contains genes that code for the production of plant hormones, the auxin indole-3-acetic acid (IAA) and for cytokinins. Cytokinins promote cell division in plant cells while auxins play a role in cell enlargement. Both of these hormones also affect tissue differentiation in plants as well as many other processes. Cytokinins have been shown to be produced by additional species of gall forming bacteria including *Erwinia herbicola* pv. *gysophilae*, *Pseudomonas savastonoi* and *Rhodococcus fascians*. A linear plasmid with a cytokinin synthesis gene has been found in *R. fascians*, a bacterium that induces leafy galls.

While an understanding of the mechanism of crown gall formation may provide some clues to the mechanism of insect gall formation, it should be noted that insect galls have some important differences compared to crown galls. Unlike crown galls, insect galls are organized structures, often with very complex morphologies. In addition, early studies have shown that unlike crown galls, insect-induced galls do not exhibit the autonomous growth that is characteristic of crown galls. Gall growth does not continue indefinitely once the gall-inducing insect is no longer present. The physical presence of the insect within the gall tissue is another unique factor that may play a role in the mechanism of insect gall formation, but the role of mechanical tissue disruption in the process of insect-induced gall formation has not been well studied. Instead, studies have focused on the role of chemicals in insect-induced gall formation.

Studies of Insect Extracts and Secretions

A number of studies have been undertaken to test insect extracts and secretions for gall inducing chemicals. Larvae of *Mikiola fagi*, a midge that forms leaf galls (Fig. 5) on the European beech (*Fagus sylvatica*), have been tested to determine if they secrete cecidogenetic (gall-forming) chemicals. When the larvae were placed on a lanolin

Gall Formation, Figure 5 **Leaf gall caused by *Mikiola fagi* on the European beech (*Fagus sylvatica*).**

Gall Formation, Figure 6 **The eastern spruce gall caused by *Adelges abietes* on Norway spruce (*Picea excelsa*).**

paste on leaves of beech and when a paste that larvae had previously been on, was repeatedly applied to leaves, changes involving cell division and cell elongation resulted, but galls did not form.

Studies of the eastern spruce gall on Norway spruce (*Picea excelsa*) have provided evidence for the presence of cecidogenetic activity associated with the salivary glands of the gall-forming adelgid *Adelges abietes*. The characteristic needle swelling associated with the early stages of gall formation (Fig. 6) has been mimicked by injecting spruce buds with a solution containing macerated adelgid salivary glands.

The willow leaf gall, caused by *Pontania pacifica*, is initiated by the accessory gland secretions of the ovipositing female sawfly while further development of the gall is dependent on the presence and activity of the larvae. When gland sacs were placed in developing galls from which larvae had been removed, galls continued to grow. If the glandular material was repeatedly injected over a period of several days, the galls continued to develop to normal size. Extracts of young *Pontania* larvae and extracts of female accessory glands were able to promote the continued growth of galls from which the larvae had been removed. Mixtures of chemicals were tested to see if they played a role in willow leaf gall formation. Rapid and sustained growth of galls was obtained with a periodic injection of a mixture containing a synthetic cytokinin kinetin, a naturally occurring auxin indole-3-acetic acid and adenine.

While the examples noted above provide evidence for gall-inducing factors associated with extracts and secretions, the specific cecidogenetic chemicals have not yet been identified. In addition, while there is evidence for cecidogenetic properties associated with glandular extracts and secretions, no one has been able to mimic the entire process of gall formation with an extract or secretion. This is not surprising given the difficulties associated with attempting to simulate the continual release of a gall-inducing stimulus from the precise location where the insect is normally active within the plant tissue.

Studies of Auxin and Cytokinin Involvement in Insect Gall Formation

Given the importance of plant hormones in plant development as well as in the mechanism of crown gall formation, a number of studies have focused on the roles of the plant hormones auxins and cytokinins in insect gall formation.

There were some early reports that applications of auxins to plant tissues resulted in structures similar to galls, while others reported failure in their attempts to induce galls with auxin. Applications of auxins to plant tissues have not resulted in the formation of structures that exhibited the complexity and the degree of hyperplasia of insect galls. Extracts of the saliva of gall-inducing aphid species have provided evidence for the presence of the auxin indole-3-acetic acid (IAA) and some have concluded that IAA was the active cecidogenetic factor in the aphid species studied. However, it was not determined whether the aphids produced the auxin, or whether they accumulated it from the plant tissue.

IAA has been detected and analyzed in other galls and gall formers. Oak apple galls caused by *Cynips quercusfolii* on *Quercus robur* and *Quercus sessiliflora* were shown to contain twice as much auxin activity as normal leaf tissues, while *Pinus edulis* needles with galls induced by larvae of the midge *Janetiella* sp. near *J. coloradensis* were found to contain 3.7 times higher concentrations of auxin bioactivity compared to needles lacking galls on a fresh tissue weight basis, and 17 times more auxin activity per needle. IAA was detected in *Cynips quercusfolii*, but was not detected in the larvae of the midge *Janetiella* sp. near *J. coloradensis*. In a study of the goldenrod ball gall induced by larvae of the dipteran *Eurosta solidaginis*, the gall-forming larvae were shown to contain high levels of IAA with detection by gas chromatography-mass spectrometry (GCMS). Concentrations of IAA in the gall tissues were higher than in the stem tissues on a weight per stem length basis, but not on a weight per weight basis.

Some studies have shown high levels of cytokinins in gall tissues. Levels of four cytokinins were shown to be higher in developing galls induced by *Pontania proxima* compared to levels in leaf tissue. Levels of the cytokinin isopentenyladenosine were shown to be much higher in hackberry (*Celtis occidentalis*) gall tissues than in control leaf tissues. However, others have not found higher levels of cytokinins in gall tissues compared to normal tissues. Levels of cytokinin bioactivity found in galls formed by *Mikiola fagi* were not elevated when compared to healthy leaves, while cytokinin concentrations in gall tissues formed by a chalcid wasp on *Erythrina latissima* were lower than those in surrounding leaf tissues. Levels of four cytokinins were shown to be higher on a weight per stem length basis in goldenrod ball galls compared to normal stem tissues, but were not higher on a weight per weight basis.

Studies have also shown evidence for cytokinins associated with gall-inducing insects. Cytokinins have been detected in the oriental chestnut gall wasp (*Dryocosmus kuriphilus*) and in the larvae of a chalcid wasp that forms leaf galls on *E. latissima*. The high concentration of cytokinins in the larvae of the chalcid wasp could be responsible for nutrient mobilization by the larvae within the galls, and may also be responsible for the fact that galls containing larvae remain as green islands on senescing leaves, while those without larvae, senesce rapidly. Four different cytokinins have been detected by GCMS in the larvae of *Eurosta solidaginis*, the dipteran responsible for the formation of goldenrod ball galls (Fig. 7). The cytokinin isopentenyladenine was shown to be present at much higher concentrations in first instar larvae than in normal stem tissues. In contrast, in a study of willow galls induced by *Pontania pacifica*, growth promotion was found to be associated with two unidentified adenine derivatives in the female accessory glands of the sawfly, but no significant cytokinin bioactivity of gland extracts was detected.

In summary, studies have provided evidence for yet-to-be-identified gall-inducing factors associated with extracts and secretions of gall-inducing insects. In addition, there have been numerous reports of the presence of plant hormones in gall-inducing insects and gall tissues with detection not only by bioassay, but also by sophisticated state-of-the-art techniques. However, it remains to be seen whether gall-inducing insects have the ability to synthesize plant hormones such as auxins and/or

Gall Formation, Figure 7 **The goldenrod ball gall caused by *Eurosta solidaginis* on *Solidago altissima*.**

cytokinins, whether the gall-formers induce synthesis of the hormones in the surrounding plant tissue, or whether the hormones that have been detected in the gall-formers have just been accumulated from the plant tissue. The high levels that have been found in some species of gall-inducing insects are suggestive of synthetic capabilities. Despite the evidence for plant hormones in galls and gall-inducing insects, the specific role of plant hormones in the development of insect galls has not been determined. Given the important role that auxins and cytokinins play in normal developmental processes in plants as well as their well- characterized role in crown gall formation, it seems likely that they play an important role in insect gall development as well. As the evidence for the involvement of auxins and cytokinins in insect gall formation is more convincing for some of the gall systems that have been studied than for others, it is most probably the case that other yet-to-be-determined cecidogenetic agents will be identified as playing important roles in the mechanism of gall formation for certain types of insect galls.

► Gall Midges (Diptera: Cecidomyiidae)
► Gall wasps (Hymenoptera: Cynipidae)

References

Boysen JP (1948) Formation of galls by *Mikiola fagi*. Physiol Plant 1:95–108

Leitch IJ (1994) Induction and development of the bean gall caused by *Pontania proxima*. In: Williams MAJ (ed) Plant galls: organisms, interactions, populations. Clarendon Press, Oxford, UK, pp 283–300

Mani J (1964) Ecology of plant galls. Junk, The Hague, The Netherlands, 434 pp

Mapes CC, Davies PJ (2001) Indole-3-acetic acid and ball gall development on *Solidago altissima*. New Phytol 151:195–202

McCalla DR, Genthe M, Hovanitz W (1962) Chemical nature of an insect gall growth-factor. Plant Physiol 37:98–103

Plumb GH (1953) The formation and development of the Norway Spruce gall caused by *Adelges abietes* L. Connecticut Agric Exp Station Bull 557:2–77

Van Staden J, Davey JE (1978) Endogenous cytokinins in the laminae and galls of *Erythrina latissima* leaves. Bot Gaz 139:36–41

Gall Midges (Diptera: Cecidomyiidae)

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Cecidomyiidae are one of the largest families in the order Diptera, with more than 5,700 described species and many more undescribed and unknown species worldwide. The family belongs to the suborder Nematocera, and its closest relatives within it are the fungus-feeding gnats in the families Sciaridae and Mycetophilidae (in the broad sense). According to fossils from the Jurassic period, the family is at least 150 million years old, but has apparently experienced explosive speciation during the Cretaceous, with the appearance of flowering plants. Cecidomyiidae have a cosmopolitan distribution, although only the faunas of Europe and North America are fairly well known. This situation makes it impossible to estimate the actual number of species in the family. The common name "gall midges" refers to the gall-inducing habit of most species, which constitute the largest group of gall-inducing organisms. However, the family also contains many species that are fungus-feeders, predators, or feed on plants without inducing galls.

Classification

The Cecidomyiidae are divided into four subfamilies:

The Catotrichinae constitute the oldest subfamily and are considered ancestral to all other subfamilies. This group contains one genus (*Catotricha*) and seven species, which are known from the Holarctic region and from Australia.

The Lestremiinae are a diverse group of about 630 species that is ancestral to the remaining two subfamilies. Although many genera and species in this group are common and widespread, it is still largely unknown, and dozens of species belonging to it are yet to be described from the

Holarctic and the Australasian regions. Faunas of other parts of the world are poorly known. Lestremiinae are fungus or detritus feeders, and their larvae are found in decaying organic matter.

The Porricondylinae constitute a diverse, paraphyletic group of 635 species that are similar in habits to the Lestremiinae. A few species are consistently found in association with plants, such as in already infested fruit or in conifer cones, but are assumed to feed on decaying organic matter in these niches. Several species are known as fossils from the upper and lower Cretaceous. The subfamily is poorly known outside the Palearctic region, and relationships among its tribes are unclear.

The Cecidomyiinae are the youngest, largest, and most diverse subfamily of gall midges, with more than 4,400 described species worldwide. This is a monophyletic group that includes all the plant-feeding species in the family, as well as several unrelated groups of fungus feeders and predators. The Cecidomyiinae are divided into four supertribes: the species-poor Stomatosematidi and Brachineuridi, whose biology is largely unknown, and the very large and biologically diverse Cecidomyiidi and Lasiopteridi.

Morphology

Adult gall midges are tiny, fragile flies, usually 2–5 mm in length. Most species are inconspicuously colored, but some groups have color patterns, especially black and white, resulting from dense covering of scales and hairs. The head is made up largely of compound eyes that often touch at the vertex. The antennae usually number 12 flagellomeres, but their number vary among groups and sometimes also within the same species and even the same individual. Male flagellomeres are often composed of a large node and a long narrow neck, whereas female flagellomeres are mostly cylindrical with much shorter necks. Males of many species have two nodes on each flagellomere, each bearing sensory setae and circumfila – sensory hairs that girdle the flagellomere and sometimes form very long loops. Male antennae of some groups in the family resemble those of the female. Mouthparts are usually greatly reduced and are only capable of liquid consumption; the adults of most plant-feeding species may not feed at all. The wing is usually transparent and has greatly reduced venation in most groups, with only 2–5 long veins, and long hairs along its margin. The legs are usually long and slender and comprise five tarsomeres. In the subfamilies Porricondylinae and Cecidomyiinae, the first tarsomere is considerably shorter than the second, and legs are easily broken beyond it. Tarsal claws are variably shaped, some with 1–2 additional teeth at their base. The ovipositor varies in length and is usually retracted inside the abdomen. Different groups have developed various modifications of the ovipositor, including conspicuous setation, or needle-like or sword-like parts to aid in oviposition. The male genitalia include gonopods that clasp the female during mating.

Larvae pass through three instars. They are legless and have a greatly reduced head capsule with no eyes, very short antennae, and mouthparts that are suited for piercing and sucking liquids. They are often bright yellow, orange, or red, but they may also be white, depending on the species. The third instar larva usually has a spatula, a dark, sclerotized structure on the ventral side of the prothorax, which is unique to the Cecidomyiidae. The spatula, which varies in shape and size among species, is used for digging in the soil or cutting through plant tissue, but many taxa have lost it altogether. Pupae may have diagnostic characters on their head and abdomen in the form of horns and spines that aid in cutting through plant material prior to adult emergence.

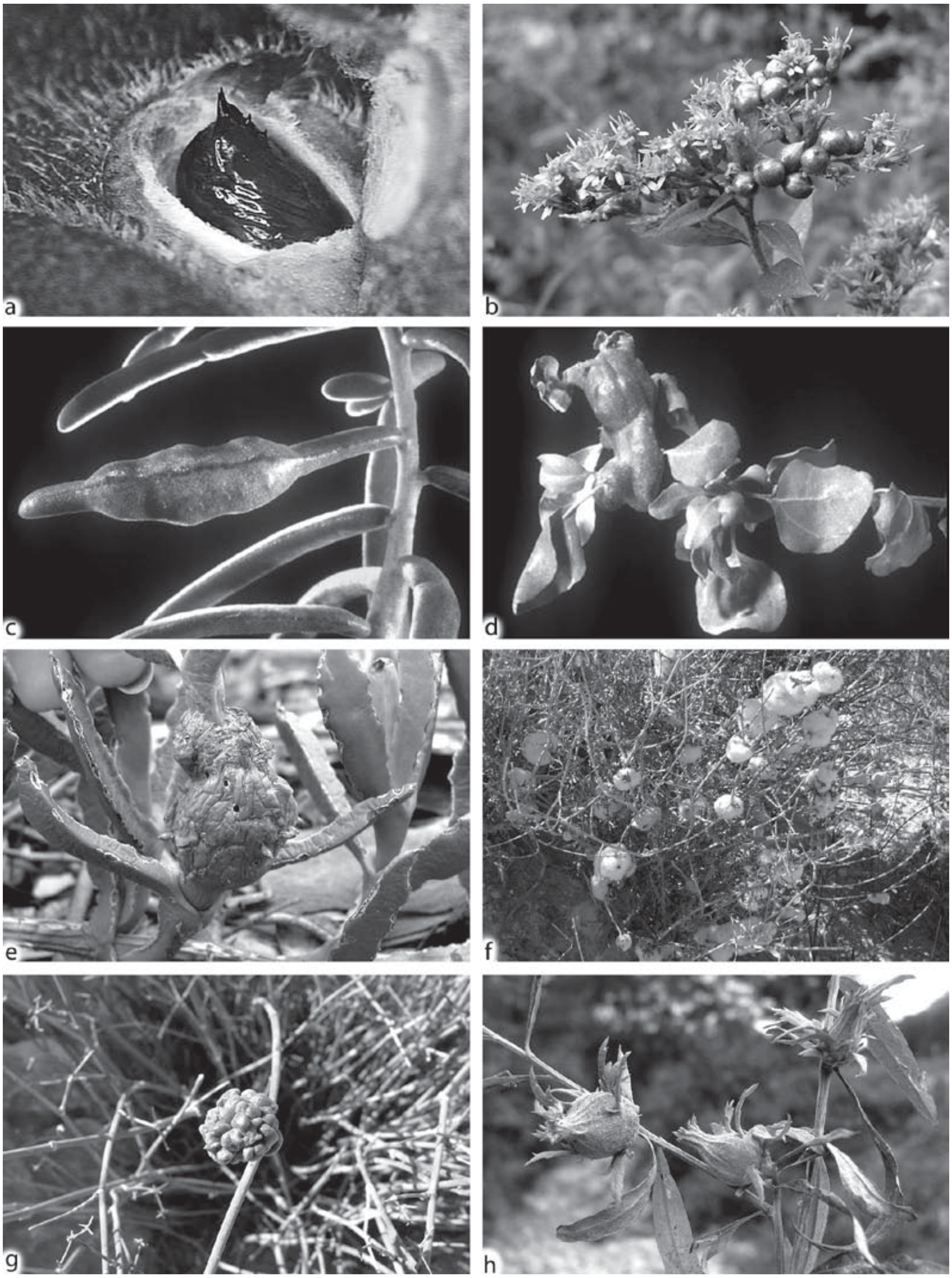
Biology

The gall-inducing guild within the Cecidomyiidae has received more attention than any other group in the family due to the large number of species and the remarkable diversity of host plants, gall structures, and life-history strategies exhibited by its members (Fig. 8). Roughly 70% of the known species in the family are gall inducers, most of which are monophagous (restricted to a single host), or oligophagous (feeding on a few related plant species). A few species are known to use a larger number of hosts that belong to several different families, either simultaneously or at different stages of their life cycle. Gall midges are found on hundreds of plant families all over the world, but certain families, such as the Asteraceae, Chenopodiaceae, Fabaceae, and Salicaceae, support especially high numbers of species. Galls range from simple leaf swellings, leaf curls, and unopened flowers to complex stem and bud galls that may comprise from one to many larval chambers and vary in the extent of tissue differentiation. Galls may be tiny or very conspicuous, green to bright red, hairy or smooth, and they may resemble the original structure of the affected plant organ or greatly deviate from it. The only other group of gall inducers exhibiting similar diversity in gall shapes and forms is the gall wasps (Cynipidae), but these are less species-rich and, as a group, are associated with much fewer plant taxa.

Although plant-feeding is by far the most common strategy in the family, feeding habits among cecidomyiid larvae are extremely diverse. Larvae of all Catotrichinae, Lestremiinae, and Porricondylinae, as well as some of the Cecidomyiinae, feed on fungi or decaying organic matter, while all plant feeders and predators belong to the Cecidomyiinae. Some species feed on or in plants without gall induction, or develop as inquilines, invading galls of other arthropods and feeding on gall tissues at the expense of the gall inducer. Inquilinism has evolved independently many times in the family, and while some genera are entirely or mostly composed of inquilinous species, others include both gall-inducers and inquilines. Predatory larvae occur in many unrelated groups within the Cecidomyiinae and are either specialists or generalists that feed on various arthropods, particularly Homoptera and mites. Certain groups within the subfamily are secondarily associated with symbiotic fungi that develop in their galls (e.g., many species in the tribes Asphondyliini and Lasiopterini), but larvae in these galls seem to feed on plant tissues rather than on the fungus, and the nature of this association is still unclear.

The life cycle of phytophagous gall midges is closely associated with that of their host plants. Species that are associated with trees are usually univoltine, whereas those that are associated with shrubs and herbaceous plants are often bivoltine or multivoltine, since these plants may continuously offer tissues that are suitable for galling. Females usually emerge from the pupae with their eggs fully mature and mate directly or after some courtship with males that wait for them on the host plant or on the ground. Sex ratios among emerging adults are often skewed towards females, and females of some species produce strictly unisexual (all male or all female) progeny throughout their lifetime, a phenomenon known as monogeny. While all Cecidomyiidae reproduce sexually, a few species in the Porricondylinae that feed on fungi may also reproduce by paedogenesis, a much shortened and simplified parthenogenetic life cycle during which larvae or pupae give rise to daughter larvae. This situation has evolved at least twice in the family and seems to be regulated by the availability of food; when food becomes scarce the population switches to normal, sexual reproduction through the development of adults.

Mated females cease to attract males and immediately engage in host seeking for oviposition. In most phytophagous species, the eggs are laid on the surface of plants or in between their scales or leaves. Some species in the tribe Asphondyliini have evolved a piercing ovipositor and insert the eggs directly into plant tissues. Whether eggs are laid individually or in batches is a species-specific trait, as is the morphogenesis of the resulting gall and its final shape and structure. Larval feeding cause modification of plant tissues around them to produce the gall, which often



Gall Midges (Diptera: Cecidomyiidae), Figure 8 **Representative galls induced by gall midges (Diptera: Cecidomyiidae).** ***Top left*****, leaf gall on** ***Solidago altissima*** **cut open to show a pupa of** ***Asphondylia solidaginis*****;** ***top right*****, flower galls on** ***Solidago rugosa*** **induced by** ***Schizomyia racemicola*****;** ***second row left*****, leaf gall on** ***Suaeda monoica*** **induced by** ***Stefaniola siliqua*****;** ***second row right*****; stem gall on** ***Atriplex halimus*** **induced by** ***Stefaniella atriplicis*****;** ***third row left*****, stem gall on** ***Carpobrotus acinaciformis*** **induced by** ***Asphondylia*** **sp.;** ***third row right*****, bud galls on** ***Artemisia sieberi*** **induced by** ***Rhopalomyia navasi*****;** ***bottom row left*****, stem gall on** ***Deverra tortuosa*** **induced by** ***Paraschizomyia buboniae*****;** ***bottom row right*****, bud galls on** ***Artemisia princeps*** **induced by** ***Rhopalomyia longitubifex*****.**

reaches its final size when the larvae are still first instars. Both the physical and the chemical stimulation applied by the larvae are necessary for gall induction, and galls will cease to develop if the larvae are killed. Mature larvae either pupate in the gall or drop to the ground and pupate in the soil, depending on the species, and in some multivoltine species also on the time of year. Larvae of many species, especially in temperate areas, enter diapause in the soil or inside the plant for a certain part of the year until suitable plant tissues become available again. In multivoltine species, larvae of the last generation, and/or a certain proportion of the larvae in each generation, may enter diapause until the following year, and in some species dormancy may last several years.

Economic Importance

Many gall midges are pests of agricultural and food crops, ornamental plants, and forest trees. One of the most serious pests in the family is the Hessian fly, *Mayetiola destructor* (Say), whose larvae feed in the stems of wheat, and kill the plants or severely reduce their productivity. This species was introduced from Europe to North America during the Revolutionary War, presumably in Hessian soldiers' mattresses that contained infested wheat stems. Another serious European pest that was introduced into North America is the sorghum midge, *Contarinia sorghicola* (Coquillet), one of the most important pests of grains in the world, whose larvae feed in seeds and hinder their development. Gall midges from the genus *Orseolia* that develop in buds and stems of rice plants are serious pests of this crop in Asia and Africa. Control of pest species may be achieved by using natural enemies or chemicals, but control has been most efficient with the use of resistant plant strains and modifications of management practices.

Certain predatory gall midges are considered beneficial because they prey on agricultural pests. *Aphidoletes aphidimyza* (Rondani), for example, is a biological control agent that is available commercially against numerous aphid pests. Adults of this species efficiently locate aphid infestations where females lay their eggs, and individual larvae may each consume dozens of aphids throughout their lifetime. Some phytophagous gall midges are successfully used as biological control agents of invasive weeds, although their impact is often too weak when not combined with other agents. Successful weed control projects involving cecidomyiid agents include the bud galler *Spurgia esulae* Gagné against leafy spurge in North America, and the flower-galling *Dasineura dielsi* Rübsaamen against the Australian wattle *Acacia cyclops* in South Africa.

References

Barnes HF (1946–1956) Gall midges of economic importance, vols 1–7. Crosby Lockwood and Son, London

Gagné RJ (1989) The plant-feeding gall midges of North America. Cornell University Press, Ithaca, NY

Gagné RJ (1994) The gall midges of the Neotropical Region. Cornell University Press, Ithaca, NY

Gagné RJ (2004) A catalog of the Cecidomyiidae (Diptera) of the World. Mem Ent Soc Wash 25:1–408

Harris KM (1966) Gall midge genera of economic importance (Diptera, Cecidomyiidae) Part 1: Introduction and subfamily Cecidomyiinae; supertribe Cecidomyiidi. Trans R Entomol Soc London 118:313–358

Yukawa J, Rohfritsch O (2005) Biology and ecology of gall inducing Cecidomyiidae (Diptera). In: Raman A, Schaefer CW, Withers TM (eds) Biology, ecology, and evolution of gall-inducing arthropods. Science Publishers, Inc., Enfield, New Hampshire, pp 273–304

Gall Moths (Lepidoptera: Cecidosidae)

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Gall moths, family Cecidosidae, total only seven species, with five species from southern South

America and two from South Africa. The family is in the superfamily Incurvarioidea, in the section Incurvariina, of division Monotrysia, infraorder Heteroneura. Adults small (7– 26 mm wingspan), with rough head scaling; haustellum reduced, scaled; labial palpi short; maxillary palpi vestigial, 1- segmented. Maculation is somber, usually without spots but often with iridescence. Adults are probably diurnal. Larvae are gall makers on *Schinus* (Anacradiaceae) in Argentina.

References

Becker VO (1977) The taxonomic position of the Cecidosidae Brèthes (Lepidoptera). Polskie Pismo Entomologiczne 47:79–86

Parra LE (1998) A redescription of *Cecidoses argentinana* (Cecidosidae) and its early stages, with comments on its taxonomic position. Nota Lepidopterologica 21:206–214

Wille J (1926) *Cecidoses eremita* Curt., und ihre Galle an *Schinus dependens* Ortega. Zeitschrift für Morpholgie und Ökolologie der Tiere 7:1–101

Gall Wasps (Hymenoptera: Cynipidae)

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The Cynipoidea [Hymenoptera: Apocrita (Parasitica)] superfamily contains plant-feeding (phytophagous) and parasitic wasp species, but is best known for the gall wasps (family Cynipidae). The superfamily includes about 3,000 described species. The number of families within the Cynipoidea is a matter of debate. Some researchers subdivide the group into six families: Cynipidae, Ibaliidae, Liopteridae, Figitidae, Charipidae, and Eucoilidae. Others use different classifications, including four families (Cynipidae, Ibaliidae, Figitidae, and Himalocynipidae), or five families (Austrocynipidae, Ibaliidae, Liopteridae, Cynipidae, and Figitidae).

Order: Hymenoptera
Suborder: Apocrita (Parasitica)
Superfamily: Cynipoidea
Family: Cynipidae

In general, cynipids are either gall-makers or inquilines in galls made by other species. About 1,360 species have been described, but it is estimated that 3,000–6,000 species actually exist. Gall-making cynipids (Cynipinae) are similar to true parasitoids in that they inject a kind of venom with their eggs into plant tissue. A gall forms because of the plant's response to the wasp's egg laying, presence of the egg, and/or feeding stimulation by the larva. Plant cells are usually modified and enlarged, the plant tissue surrounds the egg or larva, and the gall protects and provides nutritive cells for the gall-maker. Inquilines (e.g., Synerginae) cannot make their own galls on plants. Females lay eggs into other galls, and their larvae feed on gall tissue, sometimes changing the normal shape or size of the gall.

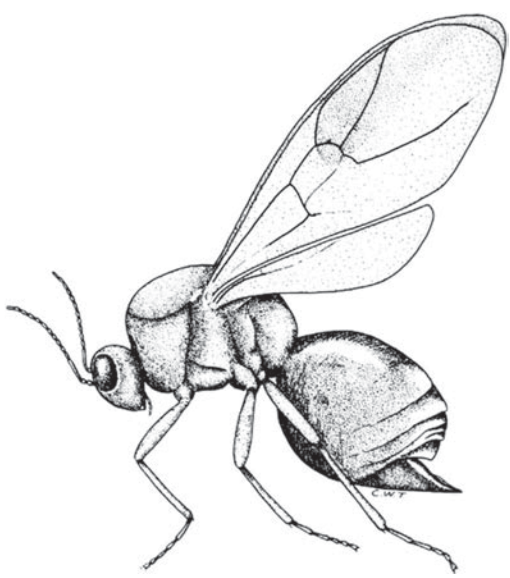
Gall Diversity

Cynipid galls come in a wide variety of forms, the shape and complexity being determined by the species of gall wasp that feeds within. Commonly attacked structures include catkins, seeds, flowers, petioles, branches, stems, and roots, but most galls occur on leaves and buds. The galls that cynipids make are generally described as blister, bud, bullet, oak apple, roly-poly, rosette, twig or stem galls. More than one gall species may also occupy a leaf or other structure. Some galls are single-chambered (monothalamous) and contain only one gall-maker, and others are multi-chambered (polythalamous) and contain many gall-makers. Those plants most often infested by cynipids are in the families Rosaceae, Asteraceae, Salicaceae, and Fagaceae. Oaks (Fagaceae: *Quercus* spp.), however, support the greatest diversity of gall-makers in North America, numbering at least 717 cynipid species.

Biology

Cynipid adults are small (1–6 mm), hard-bodied insects, with compressed abdomen, reduced wing venation, and simple, filiform antennae (Fig. 9). Most are drab-colored (e.g., black, brown, dark red, amber, or straw yellow), and may be either dull or shiny, but never metallic. Antennae of females are usually 13-segmented and males have 14 or 15 segments with the third often elongated and bent. The larvae are about 1-4 mm long, white, lack legs, and have distinct head and chewing mouthparts. Each larva develops within a discrete chamber of a gall, even when multiple gall-maker larvae develop in the same, polythalamous gall. Larvae apparently feed continuously, but do not produce fecal matter until pupation. Pupation always occurs in the gall, wherever the gall is located (e.g., on the plant or in the litter layer). Adults usually chew a circular hole upon exiting the gall.

The life cycle of many cynipids is complex, and involves heterogeny or alternation of generations. As such, a bisexual generation (both males and females) alternates with a unisexual generation (all females). The female generation reproduces by parthenogenesis, and the unfertilized eggs develop into sexual offspring. Because of the haplo-diploid genetics of wasps, all males can develop from unfertilized eggs. However, females result from the replication of chromosomes inside an unfertilized egg' s nucleus. The wasps of the two generations often look morphologically different and may attack the same or different plant structures and make very different galls. As a result, the insects of both generations have occasionally been falsely described as separate species.



Gall Wasps (Hymenoptera: Cynipidae), Figure 9
Adult *Diplolepis rosae*, which develops in the mossy rose gall.

Gall Inhabitants

Galls are good nutrient sources, and can be inhabited by other insects that feed on gall tissues or use the gall for shelter. Some of these insects can kill some or all of the gall-making larvae, either directly or indirectly by competition for resources. In addition to inquilines (e.g., *Synergus* spp. and *Ceroptres* spp. in oak galls), other insects feed opportunistically on gall tissue, including clearwing borers, longhorned beetles, metallic wood-boring beetles, weevils, gall midges, and others. Some of these opportunistic insects may have broad host ranges and also be pests on other plant species (e.g., dogwood borer). Some additional arthropods live externally on gall surfaces (e.g., mites, collembola), or in old, dry galls (e.g., ants). Natural enemies, especially parasitoid complexes, also inhabit galls and increase gall-maker mortality.

Abundance and Distribution

Populations of cynipids are sometimes greater on certain plants within a species than others, and several reasons why this occurs have been proposed. One possibility involves the adult female' s choice of ovipositional sites and her ability to distinguish between host plants or structures that vary in size, nutritional quality, or defensive capability. Because her offspring are embedded in plant tissue, her "choices" determine where eggs and subsequent offspring are dispersed. Especially important for those species that oviposit into buds before leaf flush is synchrony between insect hatch or emergence and plant budburst or leaf and shoot elongation. However, the plant' s genotype and ability to form a gall may still limit its use as a host for gall-makers. Thus, an egg may be laid into a bud, but the plant may not react to the stimulus to make a gall. In addition, because cynipids have limited sexual reproduction and dispersal ability, genetic variation within the population may be reduced, resulting in less adaptation to a variety of hosts and greater specialization on isolated host plants.

Economic Importance

Some galls and gall-makers are beneficial, and are used in biological control programs for weeds. And, historically, those galls containing tannic acid (e.g., oak galls) were used to make inks and dyes, and to tan leather.

Although galling insects are usually not considered pests, certain species can reach outbreak levels and cause either physical or aesthetic damage to high-value plants. Galling insects have been known to reduce photosynthesis and acorn production, discolor foliage, cause defoliation, branch dieback, and plant death. For example, the jumping oak gall wasp, *Neuroterus saltatorius* (Edwards) attacks Garry oak (*Q. garryana* Douglas) in the western United States and Canada, and causes severe and chronic mid-summer leaf scorching and partial defoliation. The rough oak bulletgall wasp, *Disholcaspis quercusmamma* (Walsh), forms galls on bur oak (*Q. macrocarpa* Michaux) and swamp white oak (*Q. bicolor* Willd) that disfigure trees and produce a sticky exudate, which attracts stinging insects. Other galls may host inquilines that are pests of other plants. In addition, aesthetic disfigurement can be enough to prevent the sale of infested nursery stock. At present, little information exists on the effective management of galling insect pests; pruning is labor-intensive and insecticide use may disrupt the natural enemy population, potentially leading to additional outbreaks.

References

Abrahamson WG, Weis AE (1987) Nutritional ecology of arthropod gall makers. In: Slansky F Jr., Rodriguez JG (eds) Nutritional ecology of insects, mites, spiders, and related invertebrates. Wiley, New York, NY, pp 235–258

Askew RR (1984) The biology of gall wasps. In: Ananthakrishnan TN (ed) Biology of gall insects. Edward Arnold, Baltimore, MD, pp 223–271

Rohfritsch O (1992) Patterns in gall development. In: Shorthouse JD, Rohfritsch O (eds) Biology of insect-induced galls. Oxford, New York, pp 60–86

Ronquist F (1999) Phylogeny, classification and evolution of the Cynipoidea. Zoologica Scripta 28:139–164

Wiebes-Rijks AA, Shorthouse JD (1992) Ecological relationships of insects inhabiting cynipid galls. In: Shorthouse JD, Rohfritsch O (eds) Biology of insect-induced galls. Oxford, New York, pp 238–257

Gamagrass Leafhopper, *Dalbulus quinquenotatus* Delong & Nault (Hemiptera: Cicadellidae)

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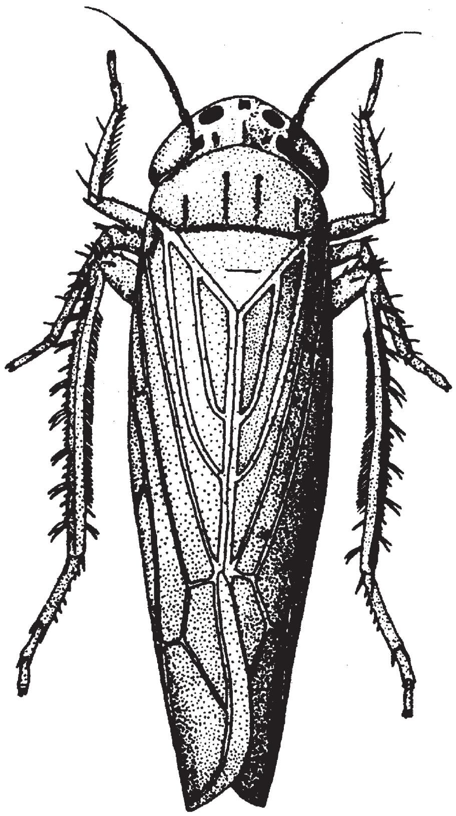
The gamagrass leafhopper is a small (length 3.0–4.3 mm) deltocephaline, brownish orange in color, with five black spots on the head (Fig. 10). This species is found at low elevations (125–1,975 m) and occurs in central and southern Mexico and in Costa Rica.

Its developmental time from egg to adult eclosion is about 34 days at 24°C. Nymphs begin hatching on day 12 and peak nymphal abundance is reached on day 16. Generations develop continuously through the year on perennial gamagrasses (*Tripsacum* spp.).

This leafhopper has particular behavioral and ecological importance because it is among the few leafhopper species tended by ants. Unlike its non-tended congeners, *D. quinquenotatus* responds to

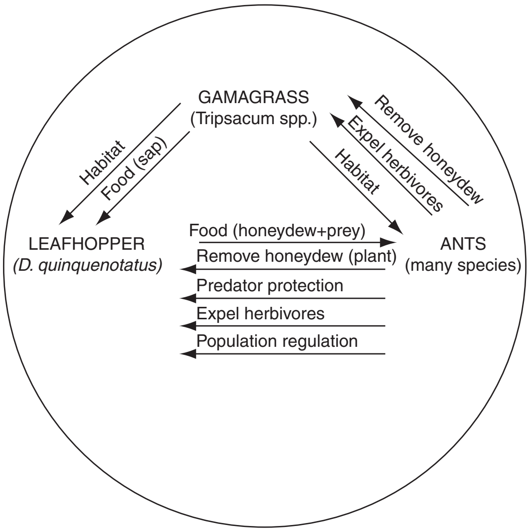


Gamagrass Leafhopper *Dalbulus quinquenotatus* Delong & Nault (Hemiptera: Cicadellidae), Figure 10 *Dalbulus quinquenotatus*.

stroking of the abdomen by ants' antennae by excreting and holding honeydew droplets until droplets are removed by ants. *Dalbulus quinquenotatus* excretes three to six times the volume of honeydew as do non-tended species. Moreover, droplets of *D. quinquenotatus* are about 23% larger in diameter and are excreted two to four times more frequently than its non-tended sister species. Nymphs and adults are sedentary and gregarious. They aggregate within leaves at the bases of *Tripsacum* spp. Sedentary and gregarious behaviors are typical in other hemipterans tended by ants such as aphids (Aphididae), treehoppers (Membracidae), and scales (Coccidae), but rare in leafhoppers. Because it has been broadly investigated, the gamagrass leafhopper can serve as model in the study of other hoppers tended by ants in the tropical and temperate regions.

The gamagrass leafhopper is tended by 18 ant species from four different subfamilies; however, the two most commonly associated ant species are *Brachymyrmex obscurior* Forel and *Solenopsis geminata* (F.). Other insects also inhabit the leaves at the bases of *Tripsacum* spp. where *D. quinquenotatus* is tended by ants. These include the decomposers *Coproporus* sp. (Staphylinidae), *Carpophilus* sp. (Nitidulidae), and *Haptoncus* sp. (Nitidulidae). These taxa occur during the wet season, and of these *Carpophilus* sp. is the most abundant. This species feeds mainly on the fermenting fluid of plants. The source of fermentation in this case is the carbohydrate contained in the honeydew excreted by *D. quinquenotatus*.

The mutualistic association (Fig. 11) between *D. quinquenotatus* and ants occurs because both receive benefits. The gamagrass offers habitat and food in the form of sap for the leafhopper most of the time, except at the end of the dry season, when gamagrass populations dry up. The sap is transformed by the leafhopper into honeydew and prey. The honeydew provides water, sugars, amino acids, lipids, and vitamins to ants. Moreover, ants consume some nymphs and adults thereby obtaining



Gamagrass Leafhopper *Dalbulus quinquenotatus* Delong & Nault (Hemiptera: Cicadellidae), Figure 11 Beneficial effects of the *D. quinquenotatus*- ants-gamagrass relationship.

protein and reducing the leafhopper population. Ants remove the honeydew produced by the gamagrass leafhopper. This leafhopper oviposits its eggs in clusters on the upper surface of midribs of basal leaves; therefore, removal of honeydew by ants reduces the death of leafhopper eggs by suffocation from accumulated honeydew and the formation of sooty mold on host leaves. Also, when the honeydew is removed the sooty mold is eliminated, facilitating plant photosynthesis. Ants protect *D. quinquenotatus* from arthropod predators such as spiders and nabids (Nabidae). Predators not only are expelled by ants when they try to approach *D. quinquenotatus*, but also are captured and transported to the ant nest and presumably used as food. Ants tending *D. quinquenotatus* also expel the related leafhoppers *D. gelbus* and *D. guzmani* that inhabit the canopy of *Tripsacum* spp. Adults of these two species respond readily to mechanical stimuli and avoid capture and predation by ants, especially on large gamagrasses.

The mutualistic association between *D. quinquenotatus* and ants on gamagrasses is affected by biotic and abiotic factors. Under greenhouse conditions, diet influences the response of ants to population of *D. quinquenotatus*. When ants are denied food, they prey upon and extinguish populations of *D. quinquenotatus*, but when supplied with prey (dead yellowjackets), large numbers of ants tend leafhopper populations that grow in size. Few ants tend leafhoppers when supplied with insect prey and honey. In natural conditions ants exploit other food resources to replace *D. quinquenotatus* honeydew during the driest months, when *D. quinquenotatus* populations are lower. That resource is nectar produced in extrafloral nectaries by the plants *Acacia pennatula*, *Leucaena esculenta*, *Lobelia laxiflora*, and *Lysilona* sp. that grow in the gamagrass community. In the wet season, when the host plants contain abundant green foliage, *D. quinquenotatus* and ants are most abundant on *Tripsacum* spp. The gamagrass populations, which grow in open areas in patches alongside herbaceous plants, shrubs, and trees, tend to be maintained in an early state of succession because of frequently occurring fires during the dry winter months in Mexico. Burned gamagrass populations are colonized better than unburned gamagrasses by the gamagrass leafhopper and tending ants. Five months after fire, the mutualistic association is higher in burned than unburned gamagrass populations. Populations of leafhopper adults and ants are equal on gamagrass plants given extra doses of phosphorous, nitrogen, or potassium. This suggests that the mutualistic association between ants and gamagrass leafhoppers is not affected by plant nutrients.

References

Larsen KJ, Heady SE, Nault LR (1992) Influence of ants (Hymenoptera: Formicidae) on honeydew excretion and escape behaviors in a myrmecophile, *Dalbulus quinquenotatus* (Homoptera: Cicadellidae), and its congeners. J Insect Behav 5:109–122

Larsen KJ, Vega FE, Moya-Raygoza G Nault LR (1991) Ants (Hymenoptera: Formicidae) associated with the leafhopper *Dalbulus quinquenotatus* (Homoptera: Cicadellidae) on gamagrasses in Mexico. Ann Entomol Soc Am 84:498–501

Moya-Raygoza G (1995) Fire effects on insect associated with the gamagrass *Tripsacum dactyloides* in Mexico. Ann Entomol Soc Am 88:434–440

Moya-Raygoza G, Nault LR (2000) Obligatory mutualism between *Dalbulus quinquenotatus*. (Homoptera: Cicadellidae) and attendant ants. Ann Entomol Soc Am 93:929–940

Moya-Raygoza G, Larsen KJ (2001) Temporal resource switching by ants between honeydew produced by the fivespotted gamagrass leafhopper (*Dalbulus quinquenotatus*) and nectar produced by plants with extrafloral nectaries. Am Midl Nat 146:311–320

Triplehorn BW, Nault LR (1985) Phylogenetic classification of the genus *Dalbulus* (Homoptera: Cicadellidae), and notes on the phylogeny of the Macrostelini. Ann Entomol Soc Am 78:291–315

Gallinipper

This name is sometimes applied to any large mosquito, but it is more correctly applied to *Psorophora* *ciliata*, a large and ferocious mosquito inhabiting most of the New World. Apparently it is America's largest mosquito. It is distinguished not only by its large size and painful bite, but by its hairy or shaggy legs. Interestingly, an American warship was named Gallinipper. It was part of a "mosquito fleet," a group of small boats, equipped with both sails and oars, which operated from Florida and patrolled the Caribbean in pursuit of pirates in the 1820s.

Gamete

A germ or reproductive cell, i.e., the sperm and ovum or egg.

Gamma Taxonomy

Study of the evolution and biology of taxa.

► Alpha Taxonomy
► Beta Taxonomy

Ganglbauer, Ludwig

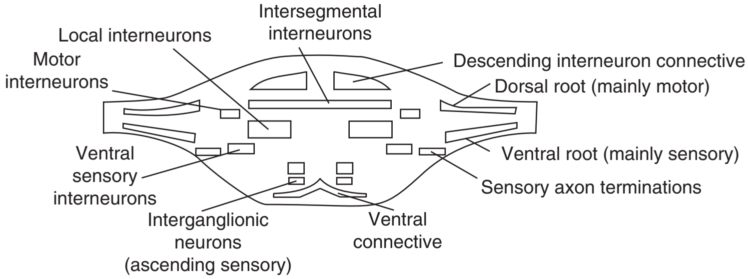
Ludwig Ganglbauer was born in Vienna on October 1, 1856. By the age of six, he had become interested in plants and beetles. He was educated at the Schottengymnasium in Vienna, obtained a teaching diploma in zoology and botany from Universität Wien, and taught for a few years at a high school. He accepted a position at the Wiener Hofmuseum (which later was renamed Naturhistorisches Museum) and by 1881 had begun publishing on the taxonomy of Coleoptera. These early publications gained him acclaim, and in 1898 he was named Kustos in the zoology department, in 1904 head of the zoology department, and in 1906 director. In 1881 he became one of the founders of the journal Wiener Entomologische Zeitung, and served as one of the editors for three years. His major work, a four-volume book "Die Käfer von Mitteleuropa" (1892–1905), was unfinished because of his early death, in Vienna on June 5, 1912. The published volumes are still widely used.

Reference

Herman LH (2001) Ganglbauer, Ludwig. Bull Am Mus Nat Hist 265:68–69

Ganglion (pl. ganglia)

A mass of nervous tissue, and the basic functional unit of the central nervous system. Many insects have three thoracic ganglia (the pro-, meso-, and metathoracic ganglia) in the thoracic region, though in others the meso- and metathoracic ganglia are fused. Each thoracic ganglion (Fig. 12) sends motor axons to the leg muscles of its respective segment, and receives input from sensor receptors in the legs. The meso- and metathoracic ganglia innervate the wing muscles. Ganglia also are found in the abdominal segments, though fusion of ganglia occurs here also. Nearly all ganglia support nerves carrying



Ganglion (pl. ganglia), Figure 12 **Diagram showing the position of nervous tracts within a ventral ganglion.**

both sensory and motor neurons laterally in the insect's body.

Garden Symphylan, *Scutigerella immaculata* (Newport) (Symphyla: Scutigerellidae)

► Potato Pests and their Management
► Symphylans

Gaster

The swollen, terminal abdominal segments of Hymenoptera; the region behind the constriction or pedicel.
► Abdomen of Hexapods

Gasteruptiidae

A family of wasps (order Hymenoptera).
► Wasps, Ants, Bees, and Sawflies

Gastric Caecum (pl. gastric caeca)

Bladder-like extensions of the midgut that function in food absorption.
► Alimentary Canal and Digestion

Gause's Principle

The principle that no two competing organisms can coexist in a stable environment without one species replacing the other. If seemingly equivalent species do co-exist, this implies that there are differences in their niches.

Gelastocoridae

A family of bugs (order Hemiptera). They sometimes are called toad bugs.
► Bugs

Gelechiidae

A family of moths (order Lepidoptera). They commonly are known as twirler moths.
► Twirler Moths
► Butterflies and Moths

Gel Electrophoresis

The separation of molecules on the basis of size and electrical charge.

Gena

The side of the head (Fig. 13) beneath the compound eyes. The "cheek."
► Head of Hexapods

Gene Amplification

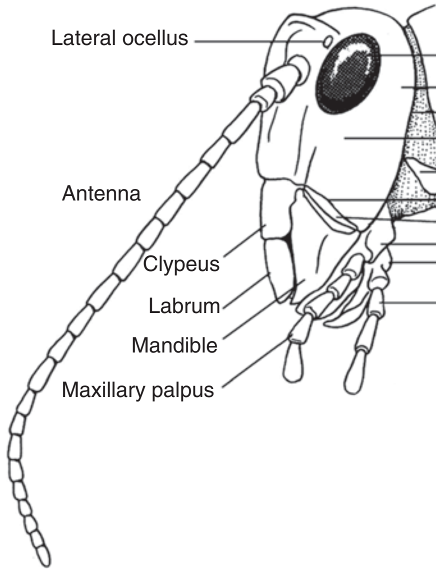
The production of multiple copies of genes in order to increase the rate of expression of a gene. Numerous genes are amplified in the developing oocyte of the mothers ovaries, providing for rapid translation of the genetic message into proteins for rapid embryonic development.

Gene Cloning

Insertion of a fragment of DNA containing a gene into a cloning vector and subsequent propagation of the recombinant DNA molecule in a host organism. Recently, cloning of a DNA fragment by the polymerase chain reaction has simplified the technology.

Gene Duplication

The duplication of a DNA segment coding for a gene; gene duplication produces two identical



Gena, Figure 13 Side view of the head of an adult grasshopper, showing some major elements.

copies which may retain their original function allowing the organism to produce larger amounts of a specific protein. Alternatively, one of the gene copies may be lost by mutation and become a pseudogene or a duplicated gene can evolve to perform a different task.

Gene Expression

The process by which the information carried by a gene is made available to the organism through transcription and translation.

Gene Flow

The movement of genes within and among populations as a result of cross fertilization.

Gene Gun

A method of propelling microscopic particles coated with DNA into cells, tissues, and organelles to produce transformation of the recipients.

Gene Library

A collection of recombinant clones derived from genomic DNA or from the cDNA transcript of an mRNA preparation. A complete genetic library is sufficiently large to have a high probability of containing every gene in the genome.

Gene Regulation

The mechanisms that determine the level and timing of gene expression.

General-Use Pesticide

This terminology was developed by the US Environmental Protection Agency to describe pesticides that are considered to be sufficiently safe that they can be used by the public without special training. Pesticides in this class can be purchased and used without license or permit. In contrast, more toxic or hazardous material are classified as "restricted-use pesticides" and can be purchased and used only by persons who are certified by the appropriate regulatory agency in the state in which they work.

► Insecticides
► Regulations Affecting Use of Pesticides

Generalist

An insect that occupies a broad niche, or consumes a wide range of food.

Generation

The length of time from any given life stage to the same stage in its offspring, though it is usually considered to be egg to egg or adult to adult.

Genetic Modification of *Drosophila* by *P* Elements

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It became possible to genetically modify *Drosophila melanogaster* using recombinant DNA methods in 1982 when *P* elements (described below) were identified and genetically altered to serve as mechanisms (vectors) for inserting genes into the nuclear genome of *Drosophila*. The use of *P*-element vectors provides a powerful tool that has modernized *Drosophila* genetics and made it possible to study the role of many genes important in development and behavior. In addition, the *P*-element system has served as a model for scientists wanting to genetically modify other insects for use in pest management programs (Transgenic Insects).

P Elements are Disposable Elements

P elements are transposable (movable) elements that have been harnessed as a tool for genetically modifying the fruitfly *Drosophila melanogaster* in a consistent manner. Transposable elements are independent genetic elements that can move within and between genomes; some call them selfish genetic elements. The development of *P* elements as tools (vectors) for inserting genes into *D. melanogaster* has revolutionized research on this important model insect, allowing fundamental studies of development and evolution.

Intact *P* elements are 2,907 bp long and encode a single polypeptide that has transposase (an enzyme that facilitates the movement of the element from one chromosome to another) activity. There are four exons (DNA sequences that are transcribed into protein, numbered from 0 to 3) flanked by inverted repeats 31 bp long. The presence of intact inverted repeats is required if the *P* element is to transpose (move).

Multiple copies of *P* elements (30–60) are dispersed throughout the genome of certain strains (called P) of *D. melanogaster*, but are not active because transposition is suppressed by factors in the *P* cytotype. Many *P* elements in *D. melanogaster*, and other *Drosophila* species, have some sequences deleted (are mutated), which also makes them incapable of transposing.

Movements of *P* elements cause mutations by inactivating genes, altering rates of transcription, or developmental- or tissue-specific gene expression. *P*-element movements can break chromosomes and cause chromosome rearrangements and germ cell (oocyte or sperm) death. Transposition of *P* elements in somatic cells reduces the life span of *D. melanogaster* males, as well as reducing fitness, mating activity and locomotion.

Hybrid Dysgenesis

P elements initiate a syndrome called hybrid dysgenesis in *D. melanogaster*. Hybrid dysgenesis occurs when males from a strain that contains *P* elements (P males) are mated with females lacking P (M females). Their progeny have high rates of mutation, chromosomal abnormalities and, sometimes, are completely sterile. These abnormalities are caused by movement of *P* elements in the chromosomes of the ovaries or testes. The reciprocal cross does not generate hybrid dysgenesis because the P female' s cytotype suppresses movement of the *P* elements.

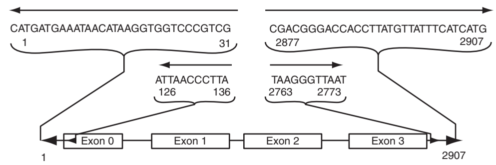
P Element Structure Varies

Many *P* elements in the *Drosophila* genome are defective. Some have internal deletions and are unable to produce their own transposase but, if they retain their 31 bp terminal repeats, they can move if supplied with transposase by intact *P* elements. *P* elements with defective 31 bp terminal repeats are unable to move because these repeats are the site of action of the transposase enzyme and important in movement and insertion of the elements into the chromosomes.

Transposition Method

P elements move from site to site in the genome (jump) by a "cut and paste" method. When a *P* jumps, it leaves behind a double-stranded gap in the DNA. The gap is repaired by using a matching sequence as a template. This matching sequence can occur on the sister chromatid or elsewhere in the genome. If the transposition occurs in an individual that is heterozygous for the *P* insertion, and the matching site on the homologous chromosome is used as the template for DNA replication and repair, there can be a precise loss of the *P* element sequence in the original site. There is no net loss in the genome because the *P* element has simply changed locations.

If a *P* jumps after the chromosomes have duplicated, but before the cell divides, one of the sister chromatids will still have a *P* in its original position. In this situation, the homologous *P* may serve as the template for filling in the (Fig. 14) hole left when the *P* moved to a new position elsewhere in the genome. Under these circumstances, the number of *P* elements in the genome is increased by one. The *P* element is replaced in its original site



Genetic Modification of *Drosophila* by *P* Elements, Figure 14 ***P*-element vector diagram.**

by gap repair and now is present in a new site in the genome, as well.

The cut and paste mechanism of transposition implies that *P* elements don' t have to confer an advantage on the organism to invade and persist in the genome. In fact, a mathematical simulation model indicates that *P* elements can become fixed in populations even when fitness is reduced by 50% and many laboratory studies have shown that colonies can change from M to P strains relatively rapidly.

The location of the *P*-element in the chromosome is important in determining the frequency of transposition. Although transposition is more-or-less at random, P-element vectors containing specific gene sequences-show some specificity by frequently inserting near the parent gene (which is called homing). *P* elements also tend to insert into upstream promoter regions of genes.

How Did *P* Elements Invade *D. melanogaster*?

P elements are relatively new to *D. melanogaster* populations. Surveys indicate laboratory strains of *D. melanogaster* collected before 1950 lack *P* elements, but most colonies collected from the wild within approximately the past 50 years have *P* elements. By contrast, *P* elements are relatively common in many other species of *Drosophila*. Surveys indicate that very closely-related, full sized and potentially active *P* elements are in *D. willistoni*, *D. guanche*, *D. bifasciata* and *Scaptomyza pallida*. *P* elements have been found in other dipteran families, including Opomizydae and Trixoscelididae. Inactive *P* elements were found in the sheep blowfly *Lucilia cuprina* (Calliphoridae) and the housefly *Musca domestica* (Muscidae). The presence of *P* elements in families other than Drosophilidae suggests that *P* elements may be more widely distributed than currently thought.

Phylogenetic analyses of DNA sequences from *P* elements in 17 *Drosophila* species in the *melanogaster* species group show that sequences from the *P* element family fall into distinct subfamilies or clades which are characteristic for particular species subgroups. These clades indicate that vertical transmission of *P* elements has occurred, but in some cases the P phylogeny is not congruent with the species phylogeny. More than one subfamily of *P* elements may exist within a group, with DNA sequences differing by as much as 36%, suggesting that horizontal transfer (movement between species) has occurred. In fact, horizontal transfer may be essential to the long-term survival of transposable elements.

P elements invaded *D. melanogaster* within the past 50 years. The donor species that provided a *P* element to *D. melanogaster* is thought to be in the willistoni group, which is not closely related to *D. melanogaster*. Because these species diverged from each other about 60 million years ago, there should have been sufficient time for considerable sequence divergence in the *P* elements if they had been present in both genomes prior to divergence (and transmitted vertically). However, DNA sequences of the *P* elements from *melanogaster* and *willistoni* are nearly identical, supporting the hypothesis of horizontal transfer. It is thought that the invasion of *D. melanogaster* by *P* occurred after *D. melanogaster* was introduced into the Americas.

Two mechanisms have been proposed to explain how the *P* element could have infected *D. melanogaster*. One involves horizontal transfer and the other involves interspecific crosses. Both *D. melanogaster* and *D. willistoni* now overlap in their geographical ranges in Florida and in Central and South America, but they apparently are unable to interbreed. Horizontal transfer could have been effected by a viral, bacterial, fungal, protozoan, spiroplasmal, mycoplasmal, or a small arthropod vector (perhaps a hymenopteran parasitoid or predatory mites). One candidate for horizontal vector may be the mite *Proctolaelaps regalis*. *P. regalis* is associated with both *Drosophila* species; it has been found in laboratory colonies and in the field associated with fallen or rotting fruit, which is the natural habitat for *Drosophila*. Laboratory observations indicate that *P. regalis* feeds on fly eggs and can make rapid thrusts of its mouth parts into a series of adjacent eggs. This brief feeding on multiple hosts might allow it to pick up DNA from one egg and inject it into another. Mites from colonies of *Drosophila* with *P* elements in their genome were analyzed with several molecular methods that indicated the mites carried both *P* element and *Drosophila* ribosomal DNA sequences. Mites isolated from M colonies (which lack *P* elements) lacked *P* sequences.

For the mite *P. regalis* to have transferred *P* elements to *D. melanogaster* from *D. willistoni*, a number of events had to occur in the proper sequence. Females of *D. melanogaster* and *D. willistoni* had to deposit their eggs in close proximity and mites had to feed sequentially on one and then the other, in the correct order. The recipient egg had to be less than 3 h old, the germ line of the recipient embryo had to incorporate a complete copy of the *P*, the transformed individual had to survive to adulthood, and the adult had to reproduce.

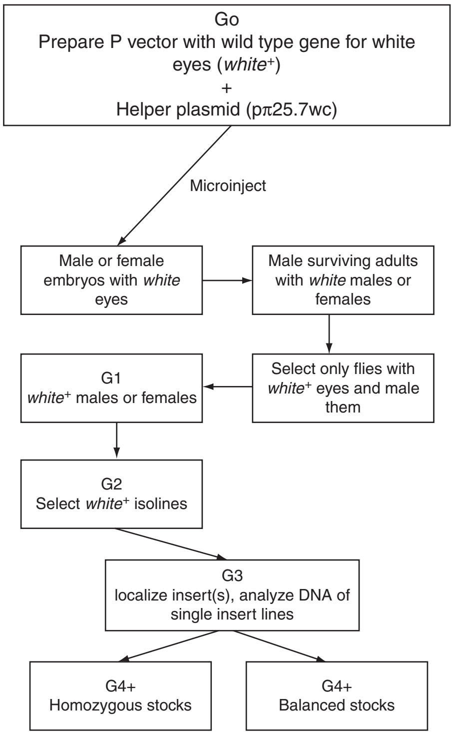
Another potential mechanism for horizontal transfer of *P* involves interspecific crosses. Crosses between the sibling species *D. simulans* and *D. mauritiana* produce sterile males, but fertile females. When F_1 females are backcrossed to males of either species, a few fertile males are produced. Hybridization, although rare, occurs between some *Drosophila* species. Although *D. melanogaster* and *D. willistoni* are unable to cross, interspecific crosses may have allowed the transfer of other types of TEs between *Drosophila* species.

P Element Vectors and Genetic Modification of *D. melanogaster*

P-elements have been genetically engineered to serve as vectors to insert genes into the germ line of *D. melanogaster*. A number of (Fig. 15) different vectors with different genetic characteristics have been produced subsequently.

Isolating pure *Drosophila* lines containing a single *P*-element insertion with a gene(s) of interest requires a sequence of steps over several generations. A *P*-element vector containing the gene(s) of interest inserted into it are microinjected into dechorionated eggs along with a helper plasmid that contains a complete DNA sequence coding for the transposase. The helper vector is unable to insert into *Drosophila* chromosomes by normal transposition methods because it lacks part of one inverted terminal repeat and lacks transposase (the gene of interest is typically inserted into the location of the transposase gene).

Embryos used for injection should be in the preblastoderm (an early embryonic stage prior to the development of the ectoderm, endoderm and mesoderm), when the embryo is still a syncytium



Genetic Modification of *Drosophila* by *P* Elements, Figure 15 Steps in transformation of *D. melanogaster* with a *P*-element vector.

(the nuclei have divided rapidly but cell walls have not formed between them yet). Some of the injected eggs die, but those that survive to produce adults may contain some individuals that contain the introduced gene(s) of interest.

These adults (called G_0) are mated individually to uninjected males or females and their progeny are reared and evaluated to determine if they carry the injected gene, or any injected "marker" genes designed to allow discrimination between genetically modified and unmodified flies. The resulting G_1 progeny will be screened to determine if they carry the gene(s) of interest and the marker genes. Because insertion of the transgenes into the chromosome occurs nearly at random, multiple individual lines of transformed flies will need to be evaluated for fitness and level of expression of the inserted DNA as well as their stability.

Insertion of the genes into germ line chromosomes is enhanced if preblastoderm embryos are microinjected. At that stage, the cleavage nuclei are in asyncytium (lacking nuclear membranes) and exogenous DNA can more easily be inserted into the chromosomes. The preblastoderm embryos are in the process of forming the pole cells (cells that will give rise to the ovaries and testes). Insertion of exogenous DNA into the chromosomes of the germ line results in stable transformation, meaning that the transgenes are likely to be transmitted each generation. If only somatic cells contain the introduced genes, the flies cannot transmit the new trait to their progeny. Such adult flies may exhibit the trait, but are only transiently transformed.

Only a portion of the *P*-element vector inserts into the chromosome. The DNA inserted consists of the *P* sequences contained within the inverted terminal repeats. The plasmid DNA outside the inverted repeats should not insert and is lost during subsequent development.

Once transformed fly lines are obtained, the transgenic fly lines should be stable unless transposase is provided in some manner. Sometimes an experimenter wants to induce movements of the inserted DNA, and secondary transpositions can be induced if transposase is introduced by injecting helper elements containing the transposase gene into preblastoderm embryos.

Transformation success rates vary from experiment to experiment and experimenter to experimenter. Usually, it is important to obtain at least ten lines containing the gene(s) of interest. This may require microinjecting 600 or more embryos, because survival of embryos after microinjection averages 30–70% and, of these, only 50–60% survive to adulthood (G_0). Even after G_0 adults are obtained, damage caused by microinjection may result in early death or sterility in 30–50% of the adults.

Transformation may not take place in all germ line cells in an injected embryo. Usually only a small fraction of the germ line cells of a G_0 individual produces transformed G_1 progeny. Thus, it is important to maximize the recovery of G_1 progeny from each G_0 individual to increase the probability of detecting progeny in which integration of *P* elements occurred. The size of the introduced *P* element is another factor that may influence transformation success; the larger the construct, the less frequent the insertion.

Detailed information on the life history and culture of *Drosophila* are available in a variety of references, as are detailed protocols for transforming *Drosophila* with *P*-element vectors. The protocols provide complete information on the appropriate equipment for microinjection, how to prepare the embryos for injection, align them on slides, desiccate them, and inject them in the region that contains the pole cells. Directions are available for preparing the DNA for injection and for pulling the very fine glass needles required. *P* elements have been engineered to provide an array of vectors with different characteristics and functions.

Uses for *P* Element Vectors

When a *P*-element vector inserts into a nuclear gene, it has been tagged. This allows the researcher to isolate and clone specific genes if the altered gene exhibits an altered phenotype in *D. melanogaster*. This process is called transposon tagging. Genetic engineering with *P*-element vectors in *D. melanogaster* also permit the expression of foreign genes from a variety of organisms.

P-element vectors also can be used to evaluate the effects of position on expression of a transgene by moving stably-inserted transgenes to other sites within the genome. The ability to replace or modify genes in their normal chromosomal locations in *D. melanogaster* is a very valuable genetic tool.

Transformation of Other Insects by *P* Elements

DNA from *D. melanogaster* has been introduced into other species of *Drosophila* with *P*-element vectors. Unfortunately, efforts to use *P*-element vectors to transform arthropod species outside the genus *Drosophila* have failed and research has shifted to the use of other types of transposable element vectors for this purpose. See the entry on Transgenic Arthropods for additional information on this topic.

Evolution of Resistance to *P* Elements

The spread of *P* elements throughout populations of *D. melanogaster* during the past 50 years has been remarkable, particularly since intact *P* elements can induce a variety of severe disadvantages in individuals in newly invaded populations. If *P* elements invade a small population, that population usually goes extinct. If evolution of repression systems (resistance to transposition) fail to occur quickly enough, larger populations also can go extinct.

In fact, several types of *P* repressor systems (resistance mechanisms) have been identified; they either are transmitted cytoplasmically (maternally inherited) or through the nuclear genome, in which case the transmission is biparental. The repressor systems have been classified as P, M′ or Q.

P fly strains have a strong maternally inherited system called P cytotype. P cytotype is mediated by a protein produced by differential splicing of the transcript of the complete element. When P females are crossed to a strong P line, less than 10% of the ovaries in their progeny become dysgenic, indicating that P strains strongly repress hybrid dysgenesis. By contrast, if P males are crossed to M females, more than 90% of the ovaries in their progeny are dysgenic. M′ strains contain repressor elements of P, as well. Transposition repression in M′ strains is due to the KP element. M′ strains display intermediate levels of repression of dysgenesis when crossed to P males. Both males and females from M′ strains are able to pass the repressing factor to their progeny. Q strains can strongly repress transposition and also display a low induction of transposition. Some Q strains show a maternal mode of inheritance of repression while others have biparental mode of inheritance. It thought that a repressor (SR) results from a deletion in the *P* element. The SR repressor cannot produce functional transposase but can produce the repressor protein and a novel protein, both of which may be involved in Q type repression.

Evolution of P, Q and M′ repression systems was evaluated during two surveys of *D. melanogaster* populations conducted along a 2,900 km cline along the eastern coast of Australia. The first survey was conducted in 1983 and the second in 1993. In 1983, P populations were found in the north, Q populations at central locations, and M′ populations in the south. After 10 years, Q and M′ populations had increased their range at the expense of P lines. The surveyors speculated that the P and M′ mechanisms of repression may be early, emergency responses to the harmful effects of transposition by *P*. The surviving *D. melanogaster* populations then may have the opportunity to evolve a superior mechanism to improve fitness by acquiring the biparentally transmitted Q repression system.

In many species of *Drosophila*, in which *P* elements have been present for a longer time than in *D. melanogaster*, no complete functional *P* elements have been found. Instead, many populations contain mutated elements which might encode repressor activity. These results reinforce the notion that active transposition of *P* is highly detrimental to species of *Drosophila* in the wild.

Using *P* Elements to Drive Genes into Populations

The interest in using transposable elements, such as *P*, as drivers for inserting engineered genes into natural populations for insect pest control has led to some computer simulation and empirical studies using *D. melanogaster* as a model system. Several different computer simulations suggest that transposable elements may be used successfully to drive specific genes into pest populations, including populations with different sizes, reproductive rates, density dependence and transposition frequency. Typically an equilibrium was reached quickly (usually within 50 generations), especially if 5 or 10% of the population carried the transposable element. However, if the "sweep" of elements does not occur rapidly, resistance mechanisms might develop that could reduce the effectiveness of the pest management program.

References

Ashburner M (1989) *Drosophila*. A laboratory handbook. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, New York

Carareto CMA, Kim W, Wojciechowski MF, Grady PO, Prokchorova AV, Silva JC, Kidwell MG (1997) Testing transposable elements as genetic drive mechanisms using *Drosophila P* element constructs as a model system. Genetica 101:13–33

Engels WR (1997) Invasions of P elements. Genetics 145:11–15

Fujioka MJ, Jaynes B, Bejsovec A, Weir M (2000) Production of transgenic *Drosophila*. In: Tuan RS, Lo CW (eds) Methods in molecular biology, vol 126: Developmental

biology protocols, vol 2. Humana Press, Totowa, NJ, pp 353–363
Houck MA, Clark JB, Peterson KR, Kidwell MG (1991) Possible horizontal transfer of *Drosophila* genes by the mite *Proctolaelaps regalis*. Science 253:1125–1129
Hoy MA (2003) Insect molecular genetics, 2nd edn. Academic Press, San Diego, CA
Karess RE (1987) P element mediated germline transformation of *Drosophila*. In: Glover DM (ed) DNA cloning, vol 2. A practical approach. IRL Press, Oxford, UK, pp 121–141
Roberts DB (ed) (1986) *Drosophila*. A practical approach. IRL Press, Oxford, UK

Genetic Code

The rules that determine which triplet of nucleotides code for which amino acid during translation. There are more than 20 different amino acids and four bases (adenine, thymine, cytosine and guanine). There are 64 potential combinations of the four bases in triplets (4 × 4 × 4). A doublet code would only be able to code for 16 (4 × 4) amino acids. Since only 20 amino acids exist, there is redundancy in the system so that some amino acids are coded for by two or more different triplets (codons).

Genetic Control

A method of pest control that uses strains of insects with genetic mutations rendering them sterile or disadvantaged. When released into the natural populations of the target insect, the sterile insects mate with wild insects and produce sterile or disadvantaged offspring.

Genetic Distance

A measure of the evolutionary divergence of different populations of a species, as indicated by the number of allelic substitutions that have occurred per locus in the two populations. The most widely used measure of genetic distance is that of Nei (1972), $D = -\ln(I)$.

Genetic Engineering

The deliberate modification of genes by man. Also called gene splicing, gene manipulation, recombinant DNA technology.

Genetic Linkage

Genes are located together on the same chromosome.

Genetic Marker

An allele whose phenotype is recognized and which can be used to monitor the inheritance of its gene during genetic crosses between organisms with different alleles.

Genetic Sexing

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Genetic sexing refers to the methodologies enabling the separation of large numbers of insects according to sex (e.g., the separation or killing of females so that an all male population is produced). It is especially relevant for the Sterile Insect Technique (SIT) which is used to control or eradicate key insect pests by introducing genetic sterility into the target population. The primary active agent in the SIT is the sterile male, although in practice, both sexes have been released. A role for the sterile female in the SIT was sometimes debated, but direct evidence shows that females do not contribute significantly to the sterility induced in the wild population. In fact, releasing both sexes together at the high overflooding ratios required for the SIT to be effective leads to assortative mating among the released flies and, consequently, dilutes their effectiveness.

Genetic sexing can be achieved by utilizing natural differences between males and females (e.g., the time of emergence of tsetse flies, or the size of the pupae of certain Lepidoptera and mosquitoes). If such differences do not exist, then specific strains have to be developed using classical Mendelian genetic techniques. Two independent genetic modifications are required, the induction of a mutation that can be used as a selectable marker (e.g., affecting pupal color, or temperature dependent viability), and a chromosome re-arrangement (reciprocal Y-autosome translocation) that links the selectable marker to the male-determining Y chromosome. The most advanced and operational genetic sexing strains (GSS) are available for the Mediterranean fruit fly, *Ceratitis capitata* (medfly). In this species, two mutations, white pupae (*wp*) and a temperature sensitive lethal (*tsl*), are used either to separate the sexes at the pupal stage using optical sorting machines, or to kill the females at the embryo stage by incubating the eggs at slightly elevated temperatures. Both mutations are found on chromosome 5. In the males of a GSS, the wild type alleles of these selectable markers, wp^+ and tsl^+, are linked to the Y chromosome.

Structure of GSS Based on the Selectable Markers *wp* and *tsl*

The structure of this Y-autosome translocation determines the stability of the GSS over time. Genetic recombination in the male between the selectable marker and the translocation breakpoint, leads to a reversal of the male and female phenotypes. Over several generations, such recombinants can accumulate and the GSS reverts to a standard bi-sexual strain. By choosing translocations where the selectable marker and the breakpoint are close together, and by incorporating recombination suppressors (inversions), GSS can be generated that are stable enough for large scale rearing as required for the SIT. The inclusion of a Filter Rearing System greatly increases the useful life of a GSS in mass rearing factories. The structure of the translocation also determines the rearing efficiency. Ideally, the sterility linked to such chromosome re-arrangements occurs as early as possible with minimal affect on the rearing process/quality. The choice of the most appropriate selectable marker influences the cost effectiveness and the accuracy of the sexing procedure. The *tsl*-based strains currently in use in most medfly facilities allow females to be killed with an accuracy of 99.5% even at production levels of over 500 million males per week, and only inexpensive equipment (a water bath) is needed.

For the application of the SIT, the use of GSS offers the following advantages:

- Sterility is introduced more efficiently into the target population. Data show that 3 to 4 times more sterility can be induced if only sterile males are released.
- Production, handling and release costs are reduced. Only the active agents, the males, in the SIT have to be dealt with.
- Monitoring costs, in combination with female specific traps, are reduced, as only wild females are trapped and not sterile males.
- The males can be aged before release without mating, and as a consequence, they are released closer to sexual maturity.
- Sterile stings by females are eliminated, and SIT can be used for control as well as eradication.

GSS for the medfly are now used in most of the mass rearing facilities worldwide. In 2001, the overall production capacity was 1,400 million males per week. Research is ongoing to generate improved GSS (e.g., by introducing a marker for the discrimination of wild and released flies). In the future, it may be possible to use genetic transformation techniques to produce GSS for SIT programs. In addition, efforts have begun to construct GSS for other key pest species such as the screwworm fly.

► Sterile Insect Technique

References

Fisher K, Caceres C (2000) A filter rearing system for mass reared medfly. In: Tan KH (ed) Area-wide control of fruit flies and other insect pests. Joint Proceedings of the 1998 International Conference on Area-wide Control of Insect Pests and of the Fifth International Symposium on Fruit Flies of Economic Importance. Penang, Malaysia, pp 543–550

Franz G, Gencheva E, Kerremans Ph (1994) Improved stability of sex-separation strains for the Mediterranean fruit fly, *Ceratitis capitata*. Genome 37:72–82

Knipling EF (1959) The sterile male method of population control. Science 130:902–904

McInnis DO, Tam SYT, Grace C, Miyashita D (1994) Population suppression and sterility rates induced by variable sex ratio, sterile insect releases of *Ceratitis capitata* (Diptera: Tephritidae) in Hawaii. Ann Entomol Soc Am 87:231–240

Rendon P, McInnis DO, Lance DL, Stewart J (2000) Comparison of medfly male-only and bisexual releases in large scale field trials. In: Tan KH (ed) Area-wide control of fruit flies and other insect pests. Joint Proceedings of the 1998 International Conference on Area-wide Control of Insect Pests and of the Fifth International Symposium on Fruit Flies of Economic Importance. Penang, Malaysia, pp 517–525

Robinson AS, Franz G, Fisher K (1999) Genetic sexing strains in the medfly, *Ceratitis capitata*: development, mass rearing and field application. Trends Entomol 2:81–104

Genetic Transformation

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Genetic transformation is a process that involves the introduction and expression of foreign genes in a host organism. This expression can result from the extrachromosomal, or episomal, presence of genes in nuclei that may persist if the introduced DNA has a mechanism for replication. Extrachromosomal expression, however, is most often transient as the DNA becomes diluted with cell division. Expression also can result from the integration of foreign DNA into somatic chromosomes that can persist through the lifetime of the organism, but not be inherited. Alternatively, foreign genes may be stably inherited if incorporated into the genome of the germ-line, known as germ-line transformation. This is the most common type of genetic transformation in insects.

Transient or somatic transformation can be achieved in several ways, and most often is used for testing promoter regulatory sequences. Most simply, DNA, usually in the form of circular plasmid molecules, is introduced into tissue by microinjection, biolistic bombardment, or electroporation. The DNA within those plasmids that is taken up into nuclei usually are subject to transcription similar to chromosomal DNA. DNA also can be integrated into viral vectors that may persist extrachromosomally or integrate into somatic chromosomes, and this presents an effective means of transient gene expression. Viral vectors for this purpose include densoviruses, subgenomic Sindbis virus, and pantropic Moloney murine leukemia virus (MoMLV). Transient expression in a foreign host also is possible by gene expression from bacterial symbionts in what is called "paratransgenesis." This may be inheritable if the genes of interest are stably incorporated into the symbiont, and if the symbiont population is inherited. Examples of paratransgenesis include the expression of foreign genes in the bug, *Rhodnius prolixis*, via the bacterial symbiont *Rhodococcus rhodnii*, and the potential for foreign gene expression in *Wolbachia*.

Germ-line transformation that is stable and inheritable most commonly is achieved using transposable element, or transposon, based vector systems. This was first developed for *Drosophila melanogaster* using the *P* element transposon discovered in the same species. The *P* element belongs to a class of transposons that transpose in a precise or nearly precise fashion by using a DNA intermediate. These elements share general structural features including inverted terminal repeat sequences that surround a transcriptional unit that encodes a transposase enzyme. Transposases act at or near the terminal sequences to catalyze the transposition process that includes excision of the entire element from one chromosomal site and insertion into another site. All of the transposons currently in use for germ-line transformation belong to this general class of elements, and are used in a binary vector-transposase helper system. In this system the transposon vector plasmid includes the inverted terminal repeat sequences and subterminal sequences required for mobility that surround a selectable marker gene and other sequences of interest. The transposase gene within the vector is either deleted or made defective, and vector transposition depends upon a separate helper plasmid that includes the complete transposase gene but not the terminal sequences necessary for integration. Thus, when transiently expressed in the germ cells, the helper transposase can catalyze chromosomal integration of the vector, but is lost in subsequent cell divisions allowing the vector integration to remain stable.

Currently, the two transposon systems developed for *Drosophila melanogaster* transformation, based on the *P* and *hobo* elements, do not function or are highly inefficient in other insect species. Four other transposon systems, discovered in other *Drosophila* species or other insects, function in a wide range of insects including *Drosophila*. These include the *Hermes* element from *Musca domestica*, the *mariner* Mos1 element from *Drosophila mauritiana*, *Minos* from *Drosophila hydei*, and *piggyBac* from *Trichoplusia ni*. Together, these systems currently have been used for germ-line transformation of more than 20 species within the Diptera, Lepidoptera, Coleoptera, and most recently, the Hymenoptera.

A critical component of transformation is the use of selectable marker systems used to identify transformed, or transgenic, individuals. Eye color markers are used routinely in *Drosophila*, and similar markers were used in the first transformation of tephritid fruit flies and mosquitoes. This was possible owing to the existence of mutant eye color strains and their wild type alleles cloned as recombinant DNA. Vectors carrying the wild type marker gene integrated into a mutant host strain allow transformed insects to be identified by visible detection of their wild type eye-color phenotype. Later transformations in species not amenable to such "mutant rescue" selections relied on the use of dominant-acting visible marker genes. These include the green fluorescent protein (GFP) from the jellyfish, *Aequora victoria*, and variants of this gene that emit blue (BFP), yellow (YFP), and cyan (CYP) light under epifluorescence optics. The most recent fluorescent protein in use is the DsRed fluorescent protein from the coral *Discosoma striata*. Chemical and drug-resistance genes also have been used as dominant-acting selections, but these often have proven to be unreliable owing to natural resistance mechanisms resulting in the selection of non-transformed individuals.

In addition to the initial selection of transformant insects by marker detection or selection, transformation must be verified by molecular tests that include DNA Southern hybridization, DNA sequencing of the chromosomal integration site, and chromosomal in situ hybridization. These tests confirm chromosomal integration, determine the number of integrations, and assess whether integration has occurred by a transposon-mediated process. The latter confirmation is possible since most transposons duplicate their insertion site sequence, with some transposons integrating solely into a defined nucleotide sequence such as TA or TTAA. In some instances vectors integrate by a random or fortuitous recombination event resulting in integration of the entire vector plasmid, and often in a rearranged fashion. Such integrations can be useful, but may be problematic since rearrangements can disrupt genes within the vector, and in some cases the selection marker may remain intact while other genes of interest become nonfunctional. The potential for vector integration by recombination exists for all insect species, but thus far it is most prevalent in mosquitoes.

Transgenic insects have a wide potential of uses for basic biological analysis and practical application for pest and beneficial species. Transposon-mediated germ-line transformation is especially useful for insertional mutagenesis for functional genomics analysis. Transposon vectors are mutagenic since they can disrupt gene function as a result of chromosomal insertion. Genes and regulatory sequences of interest that are interrupted in this way can be identified by a mutant phenotype or reporter gene expression, and isolated by probing for or amplifying the transposon vector sequences. Numerous genes and genetic pathways involved in development and behavior have been investigated in this way in *Drosophila*, and the availability of transformation vectors for nondrosophilid species now makes the use of these methods, and sophisticated genetic analysis, possible for a wide range of insects.

In addition to further investigating insect genetics and biology by functional genomics studies, strategies also are being modeled and tested in *Drosophila* for the use of transgenic insects for biological control. The first of these will improve existing programs such as the sterile insect technique (SIT) by creating strains that are genetically marked, and allow for genetic-sexing (due to female lethality) or male sterility. Sexing and male sterility should occur in response to a conditional or suppressible gene expression system so that the strain could breed normally under permissive conditions. Of considerable interest is the possibility for new strategies for biocontrol, also based on conditional systems integrated into transgenic strains, that result in the death of the released insects and their offspring in response to changes in diet or environmental conditions. The most common strategies at present include those utilizing a lethal gene expression system that is suppressed by the antibiotic tetracycline, or its analogs, which can be provided in diet but is not present in the field. Other strategies include use of temperature sensitive lethal genes that result in death of host insects at elevated field temperatures, but where strains can survive at lower laboratory rearing temperatures.

The greatest challenge for the effective use of transgenic insects in such highly promising strategies will be the comprehensive ecological risk assessment necessary for the field release of such strains. Transposons that are used as vectors are naturally mobile genetic elements, and many have become distributed among insects and other species by horizontal transfer. Thus, a primary concern for their use in practical application will be the potential for vector movement into unintended host organisms. Vector mobilization or instability also will have serious consequences relating to the effectiveness of the transgenic strain, since the desired traits will be lost with the vector. These concerns for vector stability are diminished by use of vectors that are defective, so that they can be mobilized only by an exogenous source of transposase, or helper plasmid, such as that used for the transformation event. While the helper transposase should not persist in the host, the same or related transposon system may exist in the host or a symbiont or infectious organism resulting in mobilization, or instability, of the vector. Methods to more thoroughly evaluate vector stability, and the creation of new vectors that cannot be re-mobilized, will be our greatest challenge for the effective use of genetic transformation techniques to control pests and improve beneficial insect species.

References

Atkinson PW, Pinkerton AC, Brochta DAO (2001) Genetic transformation systems in insects. Annu Rev Entomol 46:317–346

Handler AM (2000) An introduction to the history and methodology of insect gene transfer. In: Handler AM, James AA (eds) Insect transgenesis: methods and applications. CRC Press, Boca Raton, FL, pp 3–26

Handler AM (2001) A current perspective on insect gene transfer. Insect Biochem Mol Biol 31:111–128

Handler AM, James AA (2000) Insect transgenesis: methods and applications. CRC Press, Boca Raton, FL

O' Brochta DA, Atkinson PW (1996) Transposable elements and gene transformation in non-drosophilids. Insect Biochem Mol Biol 26:739–753

Gene Transfer

The movement of a gene or group of genes from a donor to a recipient.

Gengidae

A family of bugs (order Hemiptera, suborder Fulgoromorpha). All members of the suborder are referred to as planthoppers.

► Bugs

Geniculate

Elbowed or abruptly bent. When used with antennae it is equivalent to elbowed antennae.

Genitalia

The modified abdominal segments used in copulation and release of sperm or eggs.

Genome

The total complement of DNA in an organism. The total genetic composition of the chromosomes.

Genomes of Insects

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The total complement of DNA in an insect is the genome. Nuclear genomes in insects consist of the chromosomes, consisting of DNA and proteins. The nuclear genome is the largest contributor of genetic information within an insect. However, mitochondria, which are organelles in the cytoplasm, also are components of the genome. Mitochondria are derived from bacteria that became essential symbionts of eukaryotic organisms and contain a number of genes essential to the insect. Finally, in addition to the nucleus and mitochondria, many insects contain intracellular and extracellular microorganisms that provide essential services to the insect. Symbionts may be bacteria, viruses, fungi or spiroplasmas that live in or on their insect hosts. Many insect symbionts are unable to survive outside their host and many insects cannot survive without the services of their symbionts. Thus, insects contain genetic information from several sources.

Nuclear Genome Size and Content

The nuclear genome is the most important and largest source of genetic information in the insect. However, the nuclear genome size in arthropods seems to bear little relationship to the complexity of arthropod morphology or to the number of genes encoded. Nuclear genome size varies widely among insects, with up to 250-fold differences in C values known. C stands for constant or characteristic and denotes the fact that the DNA content (size) of the haploid nuclear genome is fairly constant within a species.

C values vary widely among insect species. Size is usually measured in picograms (pg) of DNA or in kilobases (kb) of DNA sequence. For example, the locust *Schistocerca gregaria* has a C value of 9,300,000 kb, 52-fold more than that of the fruitfly *Drosophila melanogaster* yet it is unlikely that the locust is more complex genetically. Likewise, nuclear DNA content varies by five-fold among tenebrionid beetle species.

Genome size also can vary within insect species; diploid cells in the mosquito *Aedes albopictus* contain 0.18–6 pg of DNA and C values vary by three-fold (0.62–1.6 pg) among different populations. The amount of DNA in insect cells is difficult to measure because many tissues are polyploid (containing more than the normal two copies of each chromosome), with different tissues having different degrees of ploidy.

DNA consists of four types of nucleotides containing the bases guanine (G), cytosine (C), thymine (T) and adenine (A). The base ratios in insect DNA are lower than those found in vertebrates, with guanine + cytosine bases (G + C) comprising from 32 to 42% of the DNA bases, compared to 45% for vertebrates. If DNA base composition were random, 50% of arthropod DNA would be G + C.

Sequencing Nuclear Genomes

The entire nuclear genomes of several model species, including humans, the mouse, the fruitfly *Drosophila melanogaster* and the nematode *Caenorhabditis elegans*, have been sequenced in an effort to understand the evolution of genes and genome function. To make the immense amounts of DNA sequence data available to scientists, databanks for depositing the sequences are expanding rapidly. There are three major database sites on the world wide web: the DNA Data Bank of Japan (DDBJ), the European Molecular Biology Laboratory Nucleotide Sequence Data Library (EMBL) and the GenBank Genetic Sequence Data Bank (GenBank). Subsets of the databases also have been organized. For example, there is a database of mitochondrial DNA sequences, a eukaryotic promoter database, a database of restriction enzymes, a database for intron sequences and a database for homeodomains.

The nuclear genome of only one insect, *Drosophila melanogaster*, had been sequenced completely by the date of this writing (2002). The genomes of other species may be sequenced in the future when costs for sequencing decline. The *D. melanogaster* genome contains approximately 180 megabases (Mb or million bases) of DNA located on four chromosomes. A third of the DNA is noncoding heterochromatin, meaning that it does not code for a protein. Heterochromatin typically is found in the centromeres, telomeres and other regions of the chromosomes that do not contain functional genes. Heterochromatin was named this because it stains differently than euchromatin, which is DNA that contains coding sequences. The 120 Mb of coding DNA is on the two large autosomes and the X chromosome; the fourth chromosome is mostly heterochromatin, with only about 1 Mb of coding DNA.

Prior to the start of the *Drosophila* Genome Project, approximately 3,800 different *D. melanogaster* genes had been mapped and many had been associated cytogenetically with one of the 5,000 bands visible on stained polytene salivary gland chromosomes. Approximately 3,000 transcription units (DNA sequences that are transcribed into messenger RNA) had been placed on the cytogenetic map by localizing the DNA on specific polytene chromosomes by a molecular process called *in situ* hybridization. Nearly 10% of the total, 1,300 genes, already had been cloned and sequenced by individual laboratories.

The Genome Project initially was controversial because some feared that it would take funding away from individual research projects, would cost too much, and take too long. Despite this controversy, a *Drosophila* Genome Project was initiated as a collaborative effort among academic and government scientists with public funding. Later, a commercial company (Celera) initiated its own *Drosophila* Genome Project using a different approach.

The actual sequencing of the *Drosophila* genome by Celera began in May 1999. By late fall of 1999, sequencing was completed and multiple computers had assembled the DNA sequences in order! This amazingly rapid conclusion to the project was facilitated by the availability of the sequences produced by the public consortium. The genome sequences were published in the journal Science in March of 2000 and the project represents a major scientific milestone. The entire *Drosophila* sequence is available in GenBank and at FlyBase on the worldwide web. FlyBase is a database of genetic and molecular information and includes information on genes, alleles (variations of genes), phenotypes, transposons (movable genetic elements present in the genome), clones, stock lists, the locations of *Drosophila* workers, and bibliographic references (Table 3).

Several unexpected results were found in the *Drosophila* genome. Early analyses of the *Drosophila* genome suggest that there are only 13,600 genes, which is slightly fewer than the number found in the nematode *Caenorhabditis elegans*. This number (13,600) is far fewer than the 30,000 originally estimated for *D. melanogaster*. However, *Drosophila* has a relatively large number of overlapping genes, so additions eventually may be made to the total.

Immediately after obtaining the *D. melanogaster*-genome sequences, a comparison was made to the genomes of *C. elegans* and the yeast *S. cerevisiae* in the context of cellular, developmental and evolutionary processes. These comparisons indicated there are many genes left to be studied in *Drosophila*.

Analysis of the *Drosophila* sequences also indicated this insect is surprisingly relevant to the study of genes and metabolic pathways involved in tumor formation and development in humans. Many of the well-studied signal pathways in tumor development in humans are conserved between flies and humans: at least 76 *Drosophila* genes are-homologs to mammalian cancer genes and are under intensive study. Furthermore, 178 (62%) of the 287 known human disease genes can be found in *Drosophila*, including genes causing neurological problems (Alzheimer' s disease, Huntington' s disease, Duchenne muscular dystrophy, juvenile-onset Parkinson' s disease). In addition, analysis of the *D. melanogaster* genome may prove useful in the study of renal, cardiovascular, metabolic and immune diseases, malformation syndromes, and cancer. The *D. melanogaster* genome represents a treasure trove of information that can be mined for years to come.

Chromosome Systems in Arthropods

Many insects are diploid (2n) in their somatic cells and haploid (n) in their gametes (eggs or sperm). Diploidy means that each chromosome type is represented twice. Diploid insects undergo meiosis prior to producing haploid eggs and sperm.

Some insect groups are parthenogenetic (females are able to reproduce without mating) and may be polyploid. Species in the Orthoptera (Blaberidae, Tettigoniidae), Hemiptera (Coccidae Delphacidae), Embioptera (Oligotomidae), Lepidoptera (Psychidae), Diptera (Chamaemyiidae, Chironomidae, Psychodidae, Simuliidae), Coleoptera (Ptinidae, Chrysomelidae, Curculionidae), and Hymenoptera (Diprionidae, Apidae) may be parthenogenetic. Polyploid insects usually are 3n or 4n, but exceptions include curculionid weevil species that are 5n and 6n. Parthenogenesis has not been found in the Diplura, Protura, Odonata, Plecoptera, Dermaptera, Grylloblattodea, Zoraptera, Megaloptera, Mecoptera and Siphonaptera, although it is not clear that species in these groups have been examined carefully for this attribute.

Parthenogenesis

Parthenogenesis is reproduction in which progeny are produced by unfertilized females. The mechanisms involved in parthenogenesis are diverse but can be divided into three major types: arrhenotoky, thelytoky, deuterotoky. Deuterotoky involves the development of unfertilized eggs into either males or females, and at least one insect, a mayfly, is reported to exhibit facultative deuterotoky. In the more common arrhenotoky, insects are haplo-diploid, with males developing from unfertilized eggs and females developing from fertilized eggs. The entire order Hymenoptera and many species in the Hemiptera, Thysanoptera, and Coleoptera are arrhenotokous. When the male of a species is haploid, its germ line nuclei contain half the number of chromosomes present in the corresponding diploid nuclei of the female and meiosis is modified so that the sperm remain haploid and do not undergo the typical reductional division.

Insects that exhibit thelytoky have females only. Thelytoky has arisen repeatedly in evolution and consists of several types. Thelytoky can be induced experimentally in a number of ways. In some cases of thelytoky, eggs only develop after penetration by a sperm (pseudogamy or gynogenesis), but the sperm nucleus degenerates without fusing with the egg nucleus so that the sperm makes no genetic contribution to the embryo. The sperm may be derived from the testis or ovotestis of a hermaphrodite or from a male of a different, but closely related, species.

Thelytoky may be the sole mode of reproduction in a species or it may alternate with sexual reproduction in regular manner (cyclical thelytoky). Cyclical thelytoky is found in aphids, gall wasps and some cecidomyiids. In species that reproduce by cyclical thelytoky, genetic recombination is possible. In species with complete thelytoky, there is no way in which mutations that have occurred in two unrelated individuals can be combined in a third. Thelytokous reproduction can be induced in the eggs of many insect species by pricking the egg, or by exposing it to chemical agents or heat. In a number of normally bisexual insects, a few eggs deposited by virgin females can hatch spontaneously; the incidence of such egg hatch can be increased by artificial selection. The capacity for artificial parthenogenesis, induced thelytoky, or facultative thelytoky indicates that some capacity for parthenogenesis is probably present in all eggs. Thelytokous species or thelytokous populations of bisexual species have been found in the Diptera, Hymenoptera, Lepidoptera, Orthoptera and Coleoptera.

In the Hemiptera, both arrhenotoky and thelytoky occur, but even more complex genetic systems are found. For example, in mealybugs (Pseudococcidae), both males and females develop from fertilized eggs but, in the embryos that develop into males, the paternally derived chromosomes become heterochromatic (stain differently with a dye), are genetically inactive and not transmitted to male progeny. This genetic system has been called parahaploidy. Some method of chromosome imprinting is probably involved to ensure that the paternally derived chromosomes are eliminated in parahaploidy and not the maternally derived ones.

Endopolyploidy in Arthropods

Cells within insects may contain the typical diploid (2n) number of chromosomes or may contain multiples of the haploid (n) number. The discussion of chromosome number (ploidy) is confusing because, in most insects, some of the somatic tissues exhibit high levels of endopolyploidy (multiple copies, greater than 2n, of chromosomes may be present in some cells) while other cells may be diploid.

For example, haploid male honeybees (which have one copy of each chromosome in their testes cells) have about the same amount of DNA as diploid females (which are 2n in the ovaries) in some of their other tissues. This increase in chromosome number occurs because nuclei in some of the tissues of the male undergo repeated cell divisions so that equal amounts of DNA are present compared to the diploid (2n) females. In some cases, haploid insect males exhibit higher levels of endopolyploidy than the females of the same species.

Polyploidy of all cells in the body occurs when the chromosome number in an organism increases over the usual diploid (2n) amount, usually by duplicating the number of chromosomes to 3n or 4n. Thus, polyploidy can occur in all cells of an insect or in just some tissues (endopolyploidy). A few insects are polyploid in all tissues, but many have polyploid tissues. For example, the diploid blood cells of the silkworm *Bombyx mori* contain 1 pg of DNA per blood cell, but a polyploid silk gland cell, which is metabolically much more active, in the same individual contains 170,000 pg of DNA. DNA content within cells also varies with developmental stage. At metamorphosis, the amount of DNA in *B. mori* declines by 81% after adults emerge from the pupal stage, which is probably due to histolysis of the polyploid larval silk glands and other polyploid cells that are not needed by the adult moth.

Noncoding DNA

DNA in the nuclear genome can be coding or noncoding. Coding DNA sequences code for enzymes (proteins that facilitate metabolic processes) and structural proteins. Coding DNA is transcribed into messenger RNA and then translated into proteins. In addition, the coding DNA is transcribed and the resulting RNA is used directly (without translation into a protein) as transfer RNAs or ribosomal RNAs.

Noncoding DNA does not code for any known product, although it may have a function or functions. Noncoding DNA can constitute 30% to more than 90% of the insect nuclear genome. Noncoding DNA has been called junk or parasitic or selfish. There are several hypotheses to explain its persistence in nuclear genomes. One suggests that the noncoding DNA performs essential functions, such as regulating gene expression. A second hypothesis is that the noncoding DNA is maintained because it is linked physically to functional genes; the excess DNA is not eliminated because it does not affect fitness of the organism. A third hypothesis suggests that noncoding DNA is a functionless parasite that accumulates and is actively maintained by selection. A fourth hypothesis is that noncoding DNA has a structural function, perhaps for compartmentalizing genes within the nucleus, or for maintaining a structural organization (nucleoskeleton) within the nucleus. The lack of correlation between genome size, complexity and gene number remains a puzzle. Unless the noncoding DNA has a function, it should constitute a load upon the insect and be lost over evolutionary time.

Much of the noncoding heterochromatic DNA in insects is repetitive DNA, DNA sequences that are repeated several times to millions of times. Repetitive DNA is found in heterochromatin near centromeres (regions of the chromosomes to which spindle fibers attach so that chromosomes can be distributed to the daughter cells during mitosis or meiosis), telomeres (the ends of chromosomes) and other heterochromatic regions. Some repetitive DNA sequences are repeated 100 to 10,000 times and include genes that code for ribosomal RNA and transfer RNA.

Species vary in the amount of repetitive DNA in their genome. For example, *Drosophila melanogaster* has about 30% of its genome as heterochromatic DNA, but about 60% of the genome of *Drosophila nasutoides* is repetitive DNA. Aphids have small amounts of repetitive DNA, and scientists have speculated that this reduced amount of repetitive DNA could be associated with a faster development time.

Satellite DNA is a type of highly repetitive DNA that differs sufficiently in its base composition from the majority of DNA in an insect that it separates out as one or more distinct bands when DNA is isolated by centrifugation with cesium chloride. Satellite DNA is rich in either A + T or in G + C sequences, and is found in long tandem arrays within the heterochromatic regions of chromosomes.

Even within an insect family, genome organization can vary. Total DNA in the genome of four mosquito species (*Anopheles quadrimaculatus*, *Culex pipiens*, *Aedes albopictus* and *A. triseriatus*) varies from 0.19 to 0.90 pg with the amount of repetitive elements varying from 0.01 to 0.15 pg. Generally, the amounts of repetitive DNA increase linearly with genome size in these mosquitoes. Intraspecific variation in the amount of highly repetitive DNA was found in *A. albopictus* colonies and may be due to differences in the number or type of transposable elements. Transposable elements are independent DNA or RNA elements that can move from one site to another in the genome and between genomes. The amounts of repetitive DNA in mosquitoes varies from 20% in *An. quadrimaculatus* to 84% in *A. triseriatus*. Because genome organization of relatively few insect species has been studied, it is difficult to determine the significance of these patterns.

Mitochondria

In addition to the nuclear genome, insects contain mitochondria in the cytoplasm. Mitochondrial chromosomes are circular, supercoiled, double-stranded DNA molecules. The mitochondrial chromosome of *Drosophila* contains approximately 18.5 kb of DNA and each mitochondrion contains several copies of the chromosome. Mitochondrial genes in insects lack introns (segments of DNA in the middle of coding regions that are normally removed prior to translation into proteins) and intergenic regions (noncoding regions between coding regions) are small or absent. The ribosomes found in the mitochondria are smaller than the ribosomes in the cytoplasm. Mitochondria contain distinctive ribosomes, transfer RNAs, and aminoacyl-tRNA synthetases. Mitochondria have their own genetic code that differs slightly from the universal genetic code.

The complete sequences of a number of insect mitochondria are known, which allows comparisons of the organization and evolution of insect mitochondrial genomes. These complete mitochondrial genome sequences can be found in GenBank. One of the first mitochondria to be completely sequences was that of *Drosophila yakuba* which was found to have 37 genes: 2 are ribosomal RNA genes, 22 are transfer RNA genes, and 13 are protein genes that code for subunits of enzymes functioning in electron transport or ATP synthesis. Partial DNA sequences of mitochondria have been obtained from many insects and also can be found in GenBank (Table 3).

Mitochondrial DNA is thought to be inherited only through the mother (in the oocyte) and males are not expected to transmit mitochondria to their progeny via the sperm. However, two studies have shown incomplete maternal inheritance of mitochondrial DNA occurs in *Drosophila simulans*. Most eggs and somatic cells contain hundreds or thousands of mitochondria, so a new mutation can result in a situation in which two or more mitochondrial genotypes coexist within an individual (heteroplasmy). Heteroplasmy, however, is apparently a transitory state. Thus, the majority of individuals are effectively haploid with regard to the number of types of mitochondria transmitted to the next generation.

Mitochondrial DNA evolves faster than single copy nuclear DNA because mitochondria are relatively inefficient in repairing errors during DNA replication or after DNA damage. In Hawaiian *Drosophila*, mitochondrial DNA appears to evolve about three times faster than coding sequences in nuclear DNA. Because mitochondrial DNA does not code for proteins involved directly in its own replication, transcription or translation, it often contains a large number of mutations.

Mitochondrial DNA has been extensively used for systematics or population genetic studies. Genes can be amplified easily from mitochondria by the polymerase chain reaction (PCR) because there are multiple copies in each cell. Mitochondria are easier to purify than a specific segment of nuclear DNA.

Transposable Elements

Every genome probably contains several types of transposable elements. Transposable elements are genetic elements that can move from one site to another in the genome. Transposable elements have been divided into two classes, those that transpose with an RNA intermediate and those that transpose as DNA. Transposable elements have been found in the genomes of most organisms, including humans, bacteria, frogs, mice, maize, nematodes, protozoans and insects. An

Genomes of Insects, Table 3 **Some relevant world wide web sites that provide information on insect genomes**

The Interactive Fly is at: sdb.bio.purdue.edu/fly/aimain/1aahome.htm
FlyBase is at: flybase.bio.indiana.edu
Drosophila Virtual Library is at: ceolas.org/fly/
The SWISS-PROT protein sequence database is available at: http://www.expasy.ch/sprot/http://www.expasy.ch//sprot/ and http://www.ebi.ac.uk/swissprot/
The Protein Information Resource is available at: http://pir.georgetown.edu http: pir.georgetown.edu and http://www.mips.biochem.mpg.de

organism may contain multiple types of transposable elements. Most of them may be inactive because they have been mutated or suppressed by the host.

Highly mutated transposable elements probably are the source of much of the noncoding repetitive DNA. There are numerous types of transposable elements in insects. The ubiquity of transposable elements in the genomes of organisms has raised a number of unanswered questions about their evolutionary effects. Examples are still being discovered in which new transposable elements are in the process of invading and spreading within insect populations.

Symbionts of Arthropods

As noted above, mitochondria are derived from a microbial intracellular symbiont that became dependent upon its host cell early in the evolution of eukaryotes (organisms with a defined nucleus and cytoplasm). The relationship between mitochondria and the eukaryotic cell is now mutualistic and obligatory. Other organisms (viruses, bacteria, rickettsia, spirochaetes) also may have long evolutionary relationships with arthropods. Some are gut symbionts, while others are associated with the salivary glands and reproductive tracts. Some relationships are obligatory, others are not.

For additional details about the relationship between microbial genomes (contained within symbionts) and the insect genome.

► Symbionts of Arthropods

References

Hoy MA (2003) Insect molecular genetics, 2nd edn. Academic Press, San Diego, CA

Gray MW, Burger G, Lang BF (1999) Mitochondrial evolution. Science 283:1476–1481

Henikoff S (2000) Heterochromatin function in complex genomes. Biochimica et Biophysica Acta 1470:1–8

Mount DW (2001) Bioinformatics. Sequence and genome analysis. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY

Otto SP, Whitton J (2000) Polyploid incidence and evolution. Annu Rev Genet 34:401–437

Wagner RP, Maguire MP, Stallings RL (1993) Chromosomes: A synthesis. Wiley-Liss, New York, NY

White MJD (1973) Animal cytology and evolution, 3rd edn. Cambridge University Press, Cambridge, UK

Genomics

The study of genome data. The complete DNA sequences of organisms such as the human, mouse, rat, zebrafish, *D. melanogaster*, *C. elegans* and *Arabidopsis thaliana* can provide a plethora of information on entire families of genes and pathways of interacting proteins.

► Proteomics
► Structural Genomics
► Functional Genomics

Genotype

The genetic makeup of an individual (contrast with phenotype).

Genus (pl. genera)

The principal subdivision of a family. A group of species that are similar in appearance and appear to have a common ancestry.

Geographic Information System (GIS)

A management system for data associated with precise locations.

Geological Time

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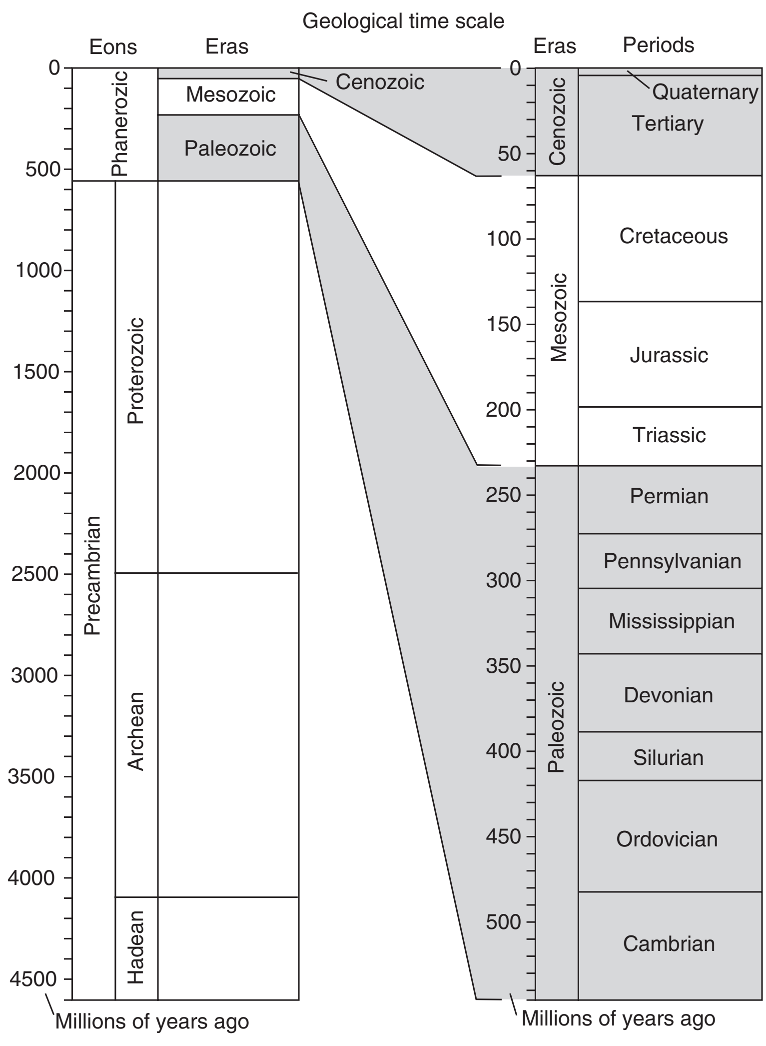
The time line that describes the history of the earth has been divided into large blocks of time, but each large block is normally subdivided, and subdivided again, for convenience (Fig. 16). The generally accepted divisions are eon, era, period, epoch, and age. The names given the block of time often have historical significance, and may be associated with occurrence of different fossils. For example, the Phanerozoic eon also consists of three major divisions: the Cenozoic, the Mesozoic, and the Paleozoic eras. The "zoic" part of the word comes from the root "zoo," meaning animal. "Cen" means recent, "Meso" means middle, and "Paleo" means ancient. These divisions reflect major changes in the composition of ancient faunas, with each era associated with domination by a particular group of animals. The Cenozoic has sometimes been called the "Age of Mammals," the Mesozoic, the "Age of Dinosaurs," and the Paleozoic the "Age of Fishes." This is not entirely accurate, though there is some basis for these designations. Also, unlike most time lines, the time is expressed not only by date, but from the present. Thus, periods or events are commonly described in millions of years ago (mya). Different spans of time on the geological time scale are usually delimited by major geological or paleontological events, such as mass extinctions. For example, the end of the



Geological Time, Figure 16 A graphical depiction of the geological history of earth (adapted from the Geological Society of America).

Cretaceous period of the Mesozoic era is marked by the demise of the dinosaurs and of many marine species.

The oldest known meteorites and lunar rocks are about 4.5 billion years old, but the oldest portions of Earth currently known are 3.8 billion years old. Sometime during the first 800 million or so years of its history, the surface of the Earth changed from liquid to solid. Once solid rock formed on the Earth, its geological history began. This most likely happened to 3.8–4 billion years ago, but firm evidence is lacking. The oldest time period, the Hadean eon, is not a geological period *per se*. No rocks on the Earth are this old, except for meteorites. During the Hadean time, the Solar System was forming, probably within a large cloud of gas and dust around the sun. The Archean eon was marked by formation of land masses as the earth's crust cooled and plates began to form. The atmosphere was hostile to life as we know it today, consisting mostly of methane, ammonia, and other toxic gases. The only life known from this early period are bacteria and bacteria-like archaea, commencing about 3.5 billion years ago. Things got interesting only in the Proterozoic eon, when life became more plentiful and the first more advanced life (eukaryotic) forms began to appear and oxygen began to accumulate. Eukaryotic life forms, including some animals, began to appear perhaps as long ago as one billion years ago, but certainly by 500 mya.

The Paleozoic era was interesting because well-preserved fossils document this period. The seas were dominated by trilobites, brachiopods, corals, echinoderms, mollusks, and others, and toward the end of this period life appeared on land. On land, the cycads, primitive conifers, and ferns were abundant. The Mesozoic saw the radiation and disappearance of dinosaurs, mammals appeared, while more advanced land plants such as ginkgos, ferns, more modern conifers, and eventually the angiosperms began to appear.

The Cenozoic, the most recent era, is divided into two main sub-divisions: the quaternary and the tertiary periods. Most of the Cenozoic is the Tertiary, from 65 million years ago to 1.8 million years ago. The Quaternary includes only the last 1.8 million years. The Cenozoic is particularly interesting to biologists because most of the life forms we see today developed in this period. It has been called the "age of insects" due to the development of great diversity, but could also be known as the age of flowering plants, birds, etc.; most of the flora and fauna we see today evolved during this period. The last 10,000 years (the Holocene) is sometimes known as the "age of man" and is also the time period since the last major ice age. The time period before the Holocene, the Pleistocene, is interesting because though much of the recent flora and fauna is the same as today, some interesting and now extinct megafauna were present, including mastodons, mammoths, saber-toothed cats, and giant ground sloths. The human species, *Homo sapiens*, also expanded during this time period, and as mentioned previously, there was a significant ice age period.

From an entomological perspective, the Phanerozoic eon (Table 4) was an exciting time. Arthropods ventured onto land during the Paleozoic, perhaps 400 mya, though the Silurian entomofauna consisted of primitive myriapods and arachnids. Fossil hexapods have been recovered from the Devonian, most notably springtails from chert. Insects proliferated rapidly during the remainder of the Paleozoic and thereafter. Interestingly, during the Mississippian (also called the Early Carboniferous) we have no fossil evidence of insects, whereas in the Pennsylvanian (also called late Carboniferous) we have numerous records of early (mostly now extinct) insect groups (e.g., protodonata and protorthopterans from deposits in France). At the close of the Paleozoic, the Permian period, the environment of earth was undergoing significant change, most notably a less tropical climate. Numerous insects from many deposits around the world document over a dozen orders of insects, including the occurrence of "giant" insects.

Geological Time, Table 4 Important time periods of the Phanerozoic eon (543 million years ago to present)

Cenozoic era (65 mya to today)	Quaternary period (1.8 mya to today)
	Holocene Epoch (10,000 years to today)
	Pleistocene Epoch (1.8 mya to 10,000 yrs)
	Tertiary Period (65 to 1.8 mya)
	Pliocene Epoch (5.3 to 1.8 mya)
	Miocene Epoch (23.8 to 5.3 mya)
	Oligocene Epoch (33.7 to 23.8 mya)
	Eocene Epoch (54.8 to 33.7 mya)
	Paleocene Epoch (65 to 54.8 mya)
Mesozoic Era (248 to 65 mya)	Cretaceous Period (144 to 65 mya)
	Jurassic Period (206 to 144 mya)
	Triassic Period (248 to 206 mya)
Paleozoic Era (543 to 248 mya)	Permian Period (290 to 248 mya)
	Carboniferous Period (354 to 290 mya)
	Pennsylvanian Epoch (323 to 290 mya)
	Mississippian Epoch (354 to 323 mya)
	Devonian Period (417 to 354 mya)
	Silurian Period (443 to 417 mya)
	Ordovician Period (490 to 443 mya)
	Cambrian Period (543 to 490 mya)
	Tommotian Epoch (530 to 527 mya)

The Triassic period of the Mesozoic era saw a warming of the earth, and fossil deposits document the occurrence of early insects such as Blattaria and some Orthoptera, Coleoptera, Odonata, Plecoptera, Neuroptera and Grylloblattodea. Transition into the Jurassic was not abrupt for insects, and the fossil record documents few marked changes, but increased radiation.

The Cretaceous period is notable for the radiation of angiosperms that took place. Because many insects are intimately associated with plants through phytophagy and pollination, they were profoundly affected by the availability of these new resources. Many of the modern taxa became established during this period, though more modern taxa such as some Diptera and Lepidoptera radiated later, in the Cenozoic. One very noteworthy feature of the Cretaceous is the great availability of amber. The spread of resin-producing trees through this period and into the Tertiary provided an excellent preservation medium for insects. Thousands of species and perhaps 30 orders have been recovered from amber deposits around the world. As insects transitioned from the Cretaceous to the Cenozoic era, the earth witnessed the appearance of "modern" insect groups such as termites, scale insects, fleas, lice, batbugs, flies, bees, and ants.

► Fossil Record of Insects
► Amber Insects: DNA Preserved?

Reference

Grimaldi D, Engel MS (2005) Evolution of the insects. Cambridge University Press, Cambridge, United Kingdom. 755 pp

Geometer Moths (Lepidoptera: Geometridae)

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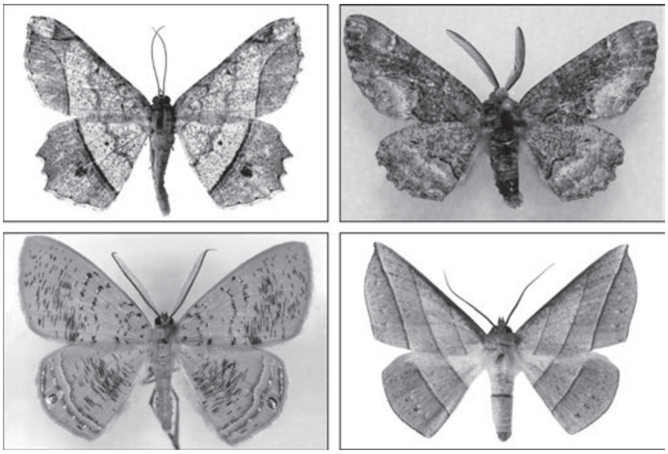
Geometer moths, family Geometridae, also called inch worms, are the second largest family of Lepidoptea, with about 21,150 described species from all faunal regions; the actual fauna probably exceeds 26,500 species. The major biodiversity is in the Neotropics, with over 6,500 species described, and the Indo-Australian region with about 6,670 species. The family is in the superfamily Geometroidea, in the section Cossina, subsection Bombycina, of the division Ditrysia. The family is divided into eight subfamilies (recent past classifications mainly used only 6 subfamilies): Archiearinae, Oenochrominae, Orthostixinae, Ennominae, Desmobathrinae, Geometrinae, Sterrhinae, and Larentiinae. There are a very large number of tribal names used and much study and consolidation of overlapping groups is still needed in order to sort out all the valid tribes among the different faunal regions. Adults small to large (8–120 mm) (most range 20–45 mm), with head scaling normal; haustellum naked; labial palpi upcurved; maxillary palpi small, 1 to 2-segmented; antennae various but mostly filiform (males usually with thicker antennae then females). Wings triangular, usually with somewhat pointed forewings (sometimes rounded), but sometimes emarginate or with falcate apex; hindwings more rounded in most species (rarely tailed); a number of genera have brachypterous or apterous females (Fig. 17). Body usually slender and delicate, but robust in some genera. Maculation extremely varied, but most species with somber hues of brown or gray; occasionally green (especially among Geometrinae) or very colorful among many tropical genera (especially in Ennominae). Adults mostly nocturnal, but also some crepuscular and diurnal groups. Larvae mostly leaf feeders, typically moving in looping fashion due to reductions in proleg numbers, and many remain motionless when disturbed and resemble small sticks or twigs. Some larvae deposit debris on their bodies to camouflage even further (Geometrinae); also known are attacking predaceous larvae (*Semiothisa* sp.) in Hawaii. Host plants include most all plant families. Some major defoliating pests are known in this family.



Geometer Moths (Lepidoptera: Geometridae), Figure 17 **Examples of geometer moths (Geometridae): *top left*, (subfamily Ennominae), *Macaria monticolaria* (Leech) from Taiwan; *top right*, *Nacophora quernaria* (J. E. Smith) from Florida, USA; *bottom row left*, *Palyas auriferaria* (Hulst) from Florida, USA; *bottom row right* (subfamily Oenochrominae), *Sarcinodes aequilinearis* (Walker) from Taiwan.**

References

Hausmann A (2001) The geometrid moths of Europe, vol 1. Introduction: Archiearinae, Orthostixinae, Desmobathrinae, Alsophilinae, Geometrinae. Apollo Books, Stenstrup, p 282 (8 pl)

Holloway JD (1993–1997) Geometridae. In: The moths of Borneo. Pt 9–11. Malayan Nature Society, Kuala Lumpur, (Malayan Nature Journal 45:1–309, 85 + 19 pl. (1993); 49:147–326, 26 + 12 pl. (1996); 51:1–242, 90 + 12 pl (1997))

Janse AJT (1932) Family Geometridae. In: The moths of South Africa, Transvaal Museum, Pretoria, 1:90–376, pl. 15

McGuffin WC, Bolte KB (1967–1990) Guide to the Geometridae of Canada (Lepidoptera). Mem Ent Soc Can 50:1–67 (1967); 86:1–159 (1972); 101:1–191 (1977); 117:1–153 (1981); 138:1–182 (1987); 151:1–252 [Bolte] (1990)

Scoble MJ (1999) Geometrid moths of the world: a catalogue. CSIRO, Collingwood, 1400 pp

Seitz A (ed) (1912–1954) Familie: Geometridae. In: Die Gross-Schmetterlinge der Erde, Kernen, Stuttgart, 4:1–479, pl. 1–25 (1912–1916); 4(suppl.):1–766, pl. 1–53 (1934–1954); 12:1–356, pl. 1–50 (1920–41); 12:1–144, pl. 1–17 (1932–38); 16:1–160, pl. 1–18 (1930–38)

Wang H-Y (1997–1998) Geometer moths of Taiwan and its allied species from the neighboring countries, 2 vol. Taiwan Museum, Taipei

Xue D, Zhu H, Chu H (1999) Fauna Sinica. 15. Lepidoptera: Geometridae, Larentiinae. Science Press, Beijing, 1063 pp, pl. 25

Geometridae

A family of moths (order Lepidoptera). They commonly are known as measuring worm moths or geometer moths.

► Geometer Moths
► Butterflies and Moths

Geophilous

This term, which literally means "ground-loving" is applied to organisms that live on the soil, or favor this habitat.

Georeference

Reference to the location on the earth' s surface based on latitude and longitude coordinates.

Geotaxis

Taxis response with respect to gravity.

Geotrupidae

A family of beetles (order Coleoptera). They commonly are known as earth- boring dung beetles.

► Beetles

Geridae

A family of bugs (order Hemiptera). They sometimes are called water striders.

► Bugs

German Cockroach, *Blattella germanica* (Linnaeus) (Blattodea: Blattelidae)

Blattella germanica is one of the most important nuisance species of cockroaches.

► Cockroaches
► Urban IPM
► School IPM

Germar, Ernst Friedrich

Ernst Germar was born in Germany on November 3, 1786. At 21 he moved to Leipzig and bought Hübner' s insect collection. In 1810 he obtained a doctorate in philosophy from Universität Halle. That was the year when the first part of his (1810–1812) work "Dissertatio sistens Bombycum species…" was published. In 1911, he traveled to Dalmatia, resulting in a (1817) book "Reise nach Dalmatien." In 1813 he founded an entomological journal "Magazin der Entomologie" which ran for six years, was interrupted, and resumed publication in 1839–1845, at which time it was merged into "Linnaea Entomologica." He married

Wilhelmine Keferstein in 1815. In 1817, he was appointed (at first without tenure) professor of mineralogy in Universität Halle. His other great entomological works were (1817–1847) “Fauna insectorum europae” and (1824) “Insectorum species novae…” He died in July 1853.

Reference

Newman E (1854) The president' s address. Trans Entomol Soc London (2) 2:149–150

Germarium

An area at the tip of the ovarioles (in females) or sperm follicles (in males) where egg or sperm formation is initiated.

Germ Band

During the blastoderm stage of embryogenesis a region of thickened cells called the germ band forms on the ventral side and elongates. Eventually in differentiates and invaginates.

► Embryogenesis

Ghilarov, Mercury Sergeevich

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M.S. Ghilarov was born on February 22, 1912, in Kiev (Russian Empire, now the capital of the Ukraine). He was educated at the State University of Kiev (1929–1933) where he specialized in entomology. After graduation from the University, he worked as an entomologist in the Ukrainian Station of Plant Protection. In 1936 he accepted the position of the senior scientific worker in the State Research Institute of Rubber-bearing Plants in Moscow. He studied ecology of soil insects and influence of soil conditions on the fauna of pests in arable soils. In 1938 he obtained a Ph.D. degree. His further scientific interests turned into studies of general problems of insect adaptations to soil environment. In 1944 he moved to the Institute of Evolutionary Morphology, USSR Academy of Sciences (now the Institute of Ecology and Evolution, Russian Academy of Sciences) in Moscow where he remained until the end of his life. In the 1940s he developed the concept of the evolutionary role of soil as an intermediate environment in the course of transition of animals from the aquatic to terrestrial life. For this work he gained the degree of Doctor of Biological Sciences. His monograph “The specificity of soil as insect habitat and its role in insect evolution” (1949) served as the theoretical basis of soil zoology, the modern branch of soil natural history. In 1956 he founded the Laboratory of Soil Zoology in the Institute, and in the 1950–1960s he organized the broad comparative study of soil entomofauna in different regions of the Northern Palearctic. He found that the ranges of a number of soil-dwelling insects coincide with the particular types of the soil (“Zoological method of the soil diagnostics,” 1965). He headed the taxonomic study of soil insects and mites which were resulted in “Key of soil-dwelling insect larvae” (1964), and “Key of soil-dwelling mites” (Sarcoptiformes, 1975; Mesostigmata, 1977; Trombidiformes, 1978). He published more than 500 scientific papers devoted to various aspects of entomology. From 1973 he was the President of the USSR Entomological Society. In 1974 he was elected as a member of the USSR Academy of Sciences and in 1975 he was appointed the Academician-Secretary of the Division of General Biology of the Academy. Beginning in 1978 he also headed the Department of Invertebrate Zoology in the State University of Moscow. He was engaged in a broad range of international activities. He was a member (starting in 1956) and the Vice-president (1967) of the Permanent Committee of International Entomological Congresses, and from 1976–1982 he was the vice-president of the International Union of Biological Sciences. His scientific awards include three USSR State Prizes (1951, 1967, 1980), the Philippo Sylvestry Golden Medal (1965), the Gustav Kraatz Medal of the German Agricultural Academy (1966), a medal of the International Committee on the entomofauna of Middle Europe (1975), a medal of the Zoological Society of France (1976), a medal of the German Academy "Leopoldina" (1977), the I. Mechnikov Golden Medal of the USSR Academy of Sciences (1978) and honorary memberships in entomological societies and academies of sciences of a number of countries. He passed away in Moscow, USSR, on March 6, 1985.

Reference

Polyakova NB, Orlova TA (1990) Mercury Sergeevich Ghilarov. Bibliography of the USSR Scientists. Ser. Biological, Zoology, 1. Moscow, "Nauka" (in Russian).

Ghost Moths (Lepidoptera: Hepialidae)

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Ghost moths (sometimes also called swifts), family Hepialidae, comprise about 496 species and occur in all faunal regions, although most species are in the ancient refugia regions of Australia, South Africa and Chile. The family is the main component of the superfamily Hepialoidea, in the infraorder Exoporia. Adults small to very large (20–250 mm wingspan), with head roughened; haustellum absent or vestigial and no mandibles are evident; labial palpi small and 2- or 3-segmented; maxillary palpi are minute and 1 to 5-segmented; antennae are very short. Maculation is usually dull with light (Fig. 18) spotting, but can include some green or gold iridescent markings or other light spots or bands. The

Ghost Moths (Lepidoptera: Hepialidae), Figure 18 **Example of ghost moths (Hepialidae), *Zelotypia stacyi* Scott from Australia.**

hindwings tend to be large and overall the adults have large bodies. Adults are typically crepuscular or nocturnal, but a few are diurnally active. Larvae feed as borers on roots, trunks or under bark of trees, various bushes, or grasses, or even leaf litter. A few species are considered pests in Europe, Asia and Australia. This family has the record for egg deposition by a single female, of about 50,000 eggs, which are scattered over potential Host plants during flight. A few are economic. The largest species are the Australian *Zelotypia stacyi* Scott and the Amazonian *Trichophassus giganteus* (Herrich–Schäffer).

References

Buser H, Huber W, Joos R (2000) Hepialidae – Wurzelbohrer. In: Schmetterlinge und ihre Lebensräume: Arten – Gefährdung – Schutz. Schweiz und angrenzenden Gebiete, 3:61–96, pl. 1–2. Pro Natura-Schweizerische Bund fuer Naturschutz, Basel

Dugdale JS (1994) Hepialidae. In: Fauna of New Zealand 30:1–161

Nielsen ES, Robinson GS (1983) Ghost moths of southern South America (Lepidoptera: Hepialidae). Entomonographia 4:1–192

Nielsen ES, Robinson GS, Wagner DL (2000) Ghost-moths of the world: a global inventory and bibliography of the *Exoporia* (Mnesarchaeoidea and Hepialoidea) (Lepidoptera). J Nat Hist 34:823–878

Tindale NB (1932–1958) Revision of the ghost moths (Lepidoptera Homoneura, Family Hepialidae). Records of the South Australian Museum (Adelaide), 4:497–536 (1932); 5:13–43 (1933); 5:275–332 (1935); 7:15–46, pl. 5–7 (1941); 7:151–168, pl. 9–11 (1942); 11:307–344, pl. 26–32 (1955); 13:157–197, pl. 16–23 (1958)

Giant Axons

Very large neurons running through the abdominal ganglia of insects, and connecting by electrical rather than chemical synapses. Giant axons promote the rapid transmission of impulses.

Giant Coccids

Some members of the family Margarodidae, superfamily Coccoidae (order Hemiptera).

► Bugs

Giant Butterfly Moths (Lepidoptera: Castniidae)

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Giant butterfly moths, family Castniidae, total 170 known species, mostly Neotropical but with some species also in the Indo-Australian region; likely world total may exceed 180 species. Three subfamilies are known, with the more unusual groups being from Australia and Southeast Asia: Synemoninae, Neocastniinae, and Castniinae. The family is its own monobasic superfamily, Castnioidea, in the section Cossina, subsection Cossina, of the division Ditrysia. Adults medium to large size (24–190 mm wingspan), with head smooth scaled and eyes large; haustellum naked (rarely vestigial); labial palpi often with distal segment erect; maxillary palpi 2 to 4-segmented; antennae clubbed. Body robust. Wings quadratic and broad (Fig. 19); hindwings rounded. Maculation variable but often dark browns with lighter bands or other markings; often colorful with variously colored patches and markings, especially on the hindwings. Adults diurnal or crepuscular. Larvae are borers of monocot plants, including grasses (Gramineae), Cyperaceae, Bromeliaceae, Marantaceae, Musaceae, and Palmae, among others.

Giant Butterfly Moths (Lepidoptera: Castniidae), Figure 19 Example of giant butterfly moths (Castniidae), *Castnia licus* Fabricius from Peru.

A few are economic on banana plants, various palms, and sugarcane. One palm pest from Argentina has become established in southern Spain in recent years.

References

Dalla Torre KW von (1913) Castniidae: subfamily Castniinae, Neocastniinae, Pemphigostolinae. In: Lepidopterorum catalogus, 15:1–28. W. Junk, Berlin

Houlbert C (1918) Révision monographique de la sous-famille des Castniinae. In: Études de Lépidoptèrologie comparée, 15:5–730, pl. 587–612. C. Oberthür, Rennes

Miller JY (1972–1980) Studies in the Castniidae. Bull Allyn Mus 6:1–13 (1972); 60:1–15 (1980)

Seitz A (ed) (1911–1926) Familie: Castniidae. In Die Gross-Schmetterlinge der Erde. Teil 10. Die indo-australischen Spinner und Schwärmer, 6:5–19, pl. 1–8 (1913); 10:1–4, pl. 1, 9 (1911); 14:15–18, pl. 1 (1926). A. Kernen, Stuttgart: [also English and French editions]

Westwood JO (1877) A monograph of the lepidopterous genus *Castnia* and some allied genera. Trans Linn Soc Lon 2-Zool 1:155–207, pl. 28–33

Giant Hooktip Moths (Lepidoptera: Cyclidiidae)

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Giant hooktip moths, family Cyclidiidae, are a small family of 14 described species, all Oriental plus one species in the southern Palearctic. The family is in the superfamily Drepanoidea, in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults medium to large size (56–85 mm wingspan), with head scaling normal; maxillary palpi small, 3-segmented; antennae serrate or filiform; body slender. Wings broad and triangular, with somewhat acute forewing apex; hindwings rounded (Fig. 20). Maculation mostly pale with gray striae or other markings; dark spot on hindwings in some species, otherwise similar to forewings. Adults are nocturnal. Larvae are leaf feeders. Host plants recorded so far only in Alangiaceae.

References

Holloway JD (1998) Subfamily Cyclidiinae. In: The moths of Borneo. Malayan Nature Society, Kuala Lumpur, (Malayan Nature Journal 52), 8:70–72, pl. 6

Inoue H (1962) Lepidoptera: Cyclidiidae, Drepanidae. In: Insecta Japonica. Hokuryukan, Tokyo (2)1:1–54, pl. 3

Warren W (1922) Subfamilie: Cyclidiinae. In: Seitz A (ed) Die Gross-Schmetter linge der Erde. 10. Die indo-australischen Spinner und Schwärmerpl 48. Kernen, Stuttgart, Germany, pp 444–446

Giant Lacewings

Members of the family Polystoechotidae (order Neuroptera).

► Lacewings, Antlions, and Mantidflies

Giant Lappet Moths (Lepidoptera: Eupterotidae)

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Giant lappet moths, family Eupterotidae, total 325 species worldwide (except the Nearctic), but most are Oriental (238 sp.); only four species are recorded in the Neotropics. Three subfamilies are recognized: Janinae (in Africa), Eupterotinae, and Panacelinae (in Australia). Some specialists now include Hibrildinae (plus Tissanginae) in Eupterotidae. The family is in the superfamily Bombycoidea (series Bombyciformes), in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults small to large (23–140 mm wingspan), with head scaling roughened; haustellum (Fig. 21) absent (rarely vestigial); maxillary palpi absent; antennae bipectinate (sometimes tripectinate or serrate); body robust. Wings mostly broad and rounded. Maculation varies but mostly shades of brown or gray with few markings. Adults are nocturnal. Larvae are leaf feeders, usually with many secondary setae. Host plants among numerous different plants, including Acanthaceae, Boraginaceae, Gramineae, Leguminosae, Myrtaceae, Pinaceae, and Rubiaceae, among others. Few species are economic (e.g., rice or forest pests).

Giant Hooktip Moths (Lepidoptera: Cyclidiidae), Figure 20 Example of giant hooktip moths (Cyclidiidae), *Cyclidia substigmaria* (Hübner) from Taiwan.

Giant Lappet Moths (Lepidoptera: Eupterotidae), Figure 21 Example of giant lappet moths (Eupterotidae), *Palirisa cervina* (Moore) from Taiwan.

References

Aurivillius POC (1901) On the Ethiopian genera of the family Striphnopterygidae. Kongliga Svenska Vetenskaps-Akademiens Handlingar (4) 27 (7):1–33, 5 pl

Griveaud P (1961) Insectes. Lépidoptères Eupterotidae et Attacidae. In: Faune de Madagascar, 14:1–64, 12 pl. Tananarive-Tsimbazaza: Tananarive Inst. Sci

Holloway JD (1987) Family Eupterotidae. In: The moths of Borneo. Malayan Nature Society, Kaula Lumpur, (Malayan Nature Journal, 41), 3:61–73, pl. 7–8

Seitz A (ed) (1911–1928) Familie: Eupterotidae. In Die Gross-Schmetterlinge der Erde 2:185–188, pl. 29–30 (1911); 6: 629, pl. 86 (1928); 10: 417–432, pl. 31, 37, 56–57 (1922); 14: 293–311, pl. 42–47 (1927). Kernen, Stuttgart, Germany

Giant Leaf Katydids

A subfamily of katydids (Phyllophorinae) in the order Orthoptera: Tettigoniidae.

► Grasshoppers, Katydids and Crickets
► Katydids

Giant Mealybugs

Members of the family Putoidae, superfamily Coccoidae (order Hemiptera).

► Bugs
► Scale Insects and Mealybugs

Giant Northern Australia Termite

A termite species, and family of termites called Mastotermitidae.

► Termites

Giant Silkworm Moths

Some members of the family Saturniidae (order Lepidoptera).

► Emperor Moths
► Butterflies and Moths

Giant Stoneflies

Members of the stonefly family Pteronarcidae (order Plecoptera).

► Stoneflies

Giant Water Bugs (Hemiptera: Prosorrhyncha Belostomatidae)

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These aquatic insects are also known as giant fish killers, electric light bugs, and toe biters. They are predators of insects and other small organisms up to the size of tadpoles, small water birds or even fish, and occasionally are known to inflict injury to humans. In humans, a belostomatid bite produces a painful burning sensation that lasts several hours.

Morphology

Belostomatidae are large-sized (up to about 110 mm), ovoid to elongate aquatic bugs. They are brownish, dorsoventrally flattened while ventrally convex. The head extends triangularly in front of the large eyes. They have a stout syringe-like rostrum or beak, which is the result of the pair of mandibles and the two pairs of maxillae evolved in long piercing stylets. The beak is three segmented. A pair of short, 4-segmented antennae are concealed in grooves beneath the head. Segments 2 and 3 have lateral projections. Belostomatidae possess a pair of large compound eyes, but lack ocelli. The head does not overlap the pronotum. The front wings are in the form of hemelytra, with a sclerotized basal region (corium) and a membranous apical region (membrane) with reticulate venation. The hind wings are completely membranous.

The front legs usually are raptorial. They are at least dexterous, as in the genus *Limnogeton*, but in most cases they act as a vice-like grip. Very dense short setae on the under surface of most front leg segments help the insect grasp. Front femora are expanded to contain a powerful musculature that allows the tibia and tarsi to seize the prey. Except in the case of *Limnogeton*, the middle and hind legs are paddle-shaped, and well suited for swimming. They are flattened and broadened, and doubled-fringed with long, fine setae that increase the effective swimming surface. The tarsi may be 2-, 3- or more rarely 1-segmented. There may be a single claw, slightly or greatly reduced, or paired claws, like in the front legs of Horvathiniinae. A metathoracic scent gland system (MSGS) has been reported only in Lethocerinae. In nymphs, the dorsal abdominal scent glands are not functional.

In the apex of the abdomen (tergum 8), the Belostomatidae have a pair of retractable, strap-like appendages that allow snorkeling while the insect is under water. These special respiratory structures are the most distinctive feature of the group. Belostomatidae also are provided with static sense organs, associated with spiracles 2–7.

Giant Water Bugs (Hemiptera: Prosorrhyncha Belostomatidae), Figure 22 Adult giant waterbug, *Lethocerus* sp. (photo courtesy of Dave Almquist, University of Florida).

Taxonomy

Belostomatidae, as Belostomida, were recognized as a group by Leach in 1815. This family presently is arranged in three subfamilies: Lethocerinae, Horvathiniinae and Belostomatinae. Currently, 11 genera and approximately 150 species are recognized. The antennal and spiracular characteristics are most often used to identify subfamilies.

The Lethocerinae are 37–150 mm in length. Formerly it contained a single genus, *Lethocerus*, that was recently divided into three genera: *Benacus*, with a single species *B. griseus*; *Kirkaldyia* also with a single species *K. deyrolli*; and *Lethocerus* with the remaining 22 species. *Lethocerus maximus* (Fig. 22) is the largest true bug and is among the largest insects. Males of Lethocerinae perform emergent-brooding, attending clutches glued to vegetation at the shore.

The Belostomatinae are between 9 and 70 mm in length. They are found worldwide, and contain most of the genera of Belostomatidae, and about a hundred species. *Belostoma*, with approximately 60 species, is the most species-rich genus. Other quite species-rich genera are *Diplonychus* (approximately 6 species), *Abedus* (10 species) and *Apassus* (17 species), while *Sphaerodema*, *Hydrocyrius* and *Limnogeton*, among others, comprise very few species each. *Limnogeton*, with its unspecialized legs and its diet restricted to water-snails, is the most primitive genus. *Poissonia* and *Weberiella*, two monospecific genera, are poorly known. Belostomatinae males perform back-brooding.

Horvathiniinae, which measure 25–30 mm in length, are the least known belostomatid subfamily. In the unique genus *Horvathinia*, nine species were described, but recent revision (2005) left only two species: *H. pelocoroides* and *H. lenti*. Generally, only specimens attracted to light are known. However, recently two adults were collected for the first time in their natural habitat, but nymphs have never been observed. The real position of

Horvathiniinae is uncertain. Egg color is as in Lethocerinae, and the eggs are buried as in Nepidae (water scorpions), but those eggs lack the respiratory horn-like structures typically found in water scorpions.

Biology

Giant water bugs live in many freshwater environments. In Japan, rice fields have been reported to function as alternative wetlands for many aquatic insects, including belostomatids. Overwintering occurs in the mud at the bottom of the rice field. Giant water bugs in the subfamily Lethocerinae inhabit ponds, lakes and slow waters of streams and rivers. Belostomatinae prefer lentic waters, from small puddles to margins of large lakes. *Horvathinia pelocoroides* (Horvathiniinae) has been captured in the province of Corrientes, Argentina, in a permanent shallow pond of about 1 ha surface and 2.1 m depth; during the rainy season, the water level is high enough to drain into a stream. The pond was densely filled with floating hydrophytes dominated by water hyacinth, *Eicchornia crassipes*, and water lettuce, *Pistia stratiotes*. Other belostomatids shared the habitat with *H. pelocorides*. Other fauna, including tadpoles and snails were reported to live in the area. Belostomatids are quite easily reared, so their biology has been extensively studied in laboratory trials.

Belostomatids are good flyers, and this ability is needed to escape (migrate) from drying ponds or streams, or due to shortage of prey. Migration may be related to the lunar cycle, as is the case in *Diplonychus rusticus* or *Lethocerus* sp. (in the latter case, during the full moon). Heavy rains also induce flight activity (called “rainfall response behavior”), primarily as an adaptation to migrate to breeding sites. However, the rainfall response behavior also ameliorates the risk of extinction due to flash floods. For *Abedus aberti*, there is a report that a torrential rainfall threshold of 8.0 min caused one-third of the adults to abandon a rapidly flowing stream; immatures respond more slowly to the flooding cue, usually requiring about 30 min of torrential rainfall. In this species, flash flood mortality normally causes less than 15% mortality because they can perceive danger through rainfall rate, while for most freshwater invertebrates exposed to such flooding the mortality may be more than 90%. Belostomatids are good swimmers, but in the case of *Limnogeton* and in Horvathiniinae, they are less efficient than the rest of the group. Positive phototropism (attraction to light, especially to mercury vapor lamps) of giant water bugs is the basis for their common name “electric light bugs.” Such lights interfere with their normal nighttime navigation as they normally navigate using star light.

Giant water bugs are carnivorous, and either ambush or actively pursue and capture the prey (foraging). They attack moving prey, but not still or immobile objects. Once grasped by the front legs with lightning speed, the prey is pierced with the robust rostrum. The bug then injects venomous saliva containing proteases, hyaluronidases, phospholipases, hemolythic enzymes and heart-stopping neurotoxins. This mixture, similar to that in snake venom, easily subdues (paralyzes and kills) the prey. As a result, the prey’s tissues are liquefied by external digestion, and the bug sucks out that liquid using a cybarial pump. Once grasped, the prey is never released, however it struggles to escape from the predator. The size of prey tends to match that of the predatory bug. The smallest belostomatids prey on water snails, which seems to be an ancient trait of the group. Increasing size allows them to prey on crustaceans, dragonfly nymphs, vertebrate larvae, small fish, and even frogs, salamanders, water-birds, larger fish, and snakes. Except for *Limnogeton*, a specialist in water-snails, the rest of the Belostomatidae have a diversified diet, always including vertebrates. It is hypothesized that the ancestral snail consumption, which requires quite precise movements and tight grasping, is a pre-adaptive trait (a trait evolved for one function but later co-opted for another) that allows the insect to handle more demanding prey such as vertebrates. Some species catch more prey than they can eat, a hoarding behavior. Cannibalism is sometimes reported.

Although living in water, belostomatids need to breath air. Breathing is mediated by the special abdominal airstraps, which are protruded to the surface while lying motionless in the water. They transmit the air to the subhemelytral airstore by a channel, formed by the setae, which converge mesioventrally. Air finally passes to the tracheal system mainly through the dorsal first abdominal spiracle. In nymphs, respiration occurs from the airstore on the ventral surface of the abdomen, and cuticular breathing also plays a key role.

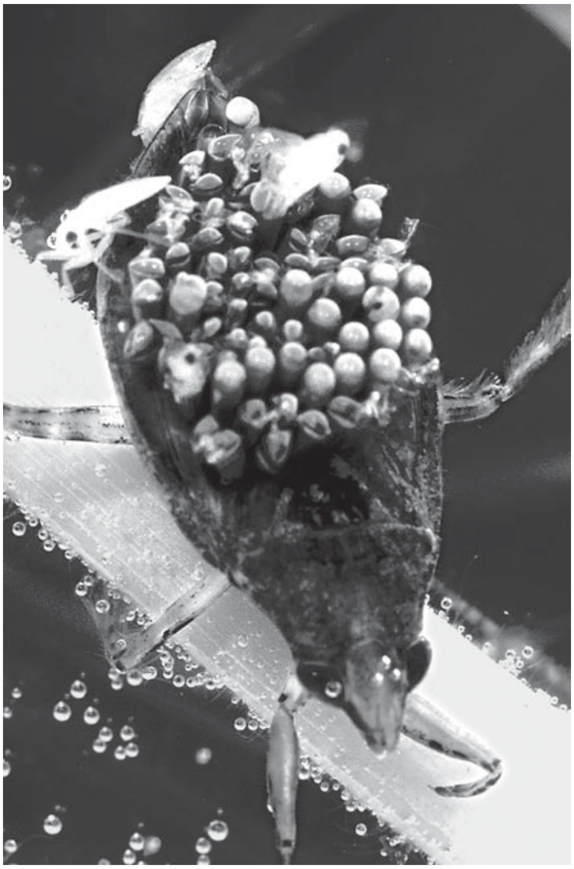
Defensive behavior is well developed in this group. The first reaction to a threat is the motion of the front legs as if to grasp the aggressor. Also, a foul-smelling liquid may be ejected from the anus for more than a meter. In Lethocerinae, the metathoracic scent gland does not play any defensive role, but seems to be essential in marking the trail to the clutch laid on the shore vegetation. The odor of the metathoracic gland does not prevent *Lethocerus* specimens from being eaten by humans in several parts of Asia.

Reproductive behavior of giant water bugs is unique among insects, as paternal care is the rule in most of them. Lethocerinae are emergent-brooders, while Belostomatinae are back-brooders. Only Horvathiniinae seem not to perform brood-caring, and eggs are half-buried in small groups in the wet sand of the shore. When paternal care occurs, a reversal of the typical sexual competition occurs, as the females fight for mates. Most probably, the big size of Belostomatidae, a primary trait, promoted ancillary selection of paternal care. Hatching occurs one or two weeks after egg laying, and nymphal development occurs in one or two months, requiring five molts.

Natural Enemies

Predation of eggs of *Belostoma* by water scorpions, *Notonecta*, has been reported. Also, young nymphs of *Kirkaldyia* are preyed upon by the water scorpions *Laccotrephes*, *Notonecta*, and *Ranatra*, the giant water bug *Appasus*, and dragonflies of the family Aeschnidae.

Belostomatids such as *Belostoma* (Fig. 23) may serve as hosts of ectosymbiont platyhelminths such as *Temnocephala*. Also, *Bodo* kinetoplastid flagellates were isolated from the hindgut of *Lethocerus indicus*. Some belostomatid species have been reported as intermediate hosts for metacercariae of digenetic trematodes; this is the case for several *Belostoma* spp. that are parasitized by the trematode *Stomylotrema* in Brazil and Argentina. Trematode metacercariae lodge in the abdominal cavity of both male and female bugs.



Giant Water Bugs (Hemiptera: Prosorrhyncha Belostomatidae), Figure 23 **Male giant waterbug, *Belastoma* sp., bearing eggs and young (photo courtesy of Doug Tallamy, University of Delaware).**

Distribution

Although distributed worldwide, Belostomatidae are most diverse in the tropics. Lethocerinae have a pantropical distribution, with a few temperate representatives. *Benachus* lives in North America and the Caribbean regions, *Kirkaldyia* is distributed in East and Southeast Asia, and *Lethocerus* is a cosmopolitan genus. Belostomatinae genera differ in their distribution. For example, *Belostoma* is known from the Americas, while *Abedus* is restricted to the southwestern USA and to Central America. *Diplonychus* lives in Asia, India, China, and probably Malaysia. *Appasus* lives in Africa and Asia, *Hydrocyrius* is present in Saudi Arabia, Africa and Madagascar, and *Limnogeton* is found exclusively in Africa. Horvathiniinae have been recorded in Central and South America (northeastern Argentina, Uruguay, Paraguay, Bolivia and southeastern Brazil).

Ecological and Economic Significance

Belostomatids play a key role in freshwater ecosystems, where they perform as intermediate-stage predators in the food chain. Their control over invertebrate populations is greater in the absence of fish. *Belostoma* and *Lethocerus* species, among others, may be efficient controllers of freshwater snail populations. As a consequence, they may play a useful role in preventing human and veterinary schistosomiasis, as snails are an intermediate host. *Lethocerus* may be of concern in fisheries, as it may prey on specimens up to 20 cm long. Mosquito and/or chironomid larvae and/or pupae are actively preyed upon, and controlled to some extent, by *Belostoma*, *Diplonychus*, *Spherodema* and *Lethocerus* species. However, pesticide treatments targeted at mosquito larvae, or other biocide treatments for agricultural purposes, may poison water and prove harmful to giant water bugs. *Kirkaldyia deyrolli* is reported to be a threatened-vulnerable species in the Read Data Book of Japan, most probably due to water pollution. Interestingly, *Bacillus* sp. spread to control larval mosquitoes may remain in belotomatid feces and dead bodies, acting as a mosquito-killing microbe repository.

Relative to humans, the main role of these insects is as a food source in several Asian countries where adults of *Lethocerus* are considered a delicacy, and are eaten both fresh and cooked. In Southeast Asia, some species are highly valued for extraction of a very expensive essence from the essence-producing glands. The "essence" is a sex-pheromone, and is produced by males to attract females. It is used by humans in cooking (dipping sauce).

Belostomatids may also be a nuisance because they are attracted to lights, especially when attracted to lighted pools where they might bite swimmers. The role of some giant water bugs as second intermediate hosts of digenetic trematodes may result in medical importance of giant water bugs in some regions. Thus, like many insects, belostomatids display several behaviors that could result in them being classified as either useful or harmful insects.

Evolution

In past times, giant water bugs likely took advantage of shallow waters teeming with small vertebrates or invertebrate larvae, an empty niche unavailable to large predatory fish, which need deeper water. The individuals best adapted to feed on larger prey succeeded over the predators taking smaller prey, in a feed-back cycle whose only limit was egg size and embryo nutrition. Thus, it appears that large body size, a primary trait under natural selection because it allows feeding on bigger prey, has shifted the evolution of Belostomatidae to their current large body size.

► Parental Care in Heteroptera
► Bugs (Hemiptera)

References

Ichikawa N (1988) Male brooding behaviour of the giant water bug *Lethocerus deyrolli* Vuillefroy (Hemiptera: Belostomatidae). J Ethol 6:121–127

Lauck DR, Menke A (1961) The higher classification of Belostomatidae (Hemiptera). Ann Entomol Soc Am 54:644–657

McGavin GC (1993) Bugs of the world. Blandford, London, UK, 192 pp

Miller NCE (1971) The biology of the Heteroptera, 2nd edn. E.W. Classey, Hampton, UK, 106 pp

Perez Goodwyn PJ (2006) Taxonomic revision of the subfamily Lethocerinae (Heteroptera: Belostomatidae). Suttgarter Beitrage fuer Naturkiunde A695:1–71

Schaefer CW, Panizzi AR (Eds) (2000) Heteroptera of economic importance. CRC Press, Boca Raton, FL, 828 pp

Schnack JA, Estévez AL (2005) On the taxonomic status of the genus *Horvathinia* Montandon (Hemiptera: Belsotomatidae). Zootaxa 1016:21–27

Schnack JA, Estévez AL, Armúa de Reyes C (2006) Laguna Don Blanco, Argentina: first record of *Horvathinia* (Hemiptera: Belostomatidae) as a wetland dweller. Entomol News 117:197–202

Schuh RT, Slater JA (1995) True bugs of the world (Hemiptera: Heteroptera). Classification and natural history. Cornell University Press, Ithaca, NY

Smith RL (2004) Evolution of paternal care in the giant water bugs (Heteroptera: Belostomatidae). In: Choe JC, Crespi BJ (eds) The evolution of social behavior in insects and arachnids. Cambridge University Press, NY, pp 116–149

Gill

A respiratory structure found in immature aquatic insects, through which they obtain dissolved oxygen. Gills take various forms, and are found at various locations.

Girault, Alexandre Arsène

Alexandre Girault was born in the state of Maryland, USA, on January 9, 1884. He earned a B.S. degree from Virginia Polytechnic Institute in 1903, and then in 1904 became employed by the U.S. Department of Agriculture. During that employment he worked as an applied entomologist on the plum curculio, Colorado potato beetle, and lesser peach borer. In 1908 he moved to Illinois as assistant to the State entomologist and then as assistant in entomology at the University of Illinois. There he worked on insects of stored products, the Colorado potato beetle, and Cimex bed bugs. In 1911, he moved to Australia, as entomologist to the Bureau of Sugar Experiment Stations in Queensland. There, he worked on taxonomy of "parasitic" Hymenoptera. He also studied thrips. Three years later, he returned to the USA to work again for the U.S. Department of Agriculture, but this time in Washington, DC, on the classification of Chalcidoidea. He moved back to Australia in 1917, this time as assistant entomologist to the Queensland Department of Agriculture and Stock. His major work was a monograph (1912–1915) "Australian Hymenoptera Chalcidoidea" of over 900 pages. Many others of his over 300 papers were small notes, some of them badly printed on a small press of his own, and distributed to few institutions and hymenopterists, thus not readily available. He died in Brisbane, Australia, on May 2, 1941.

References

Mallis A (1971) Alexandre Arsene Girault, In: American entomologists. Rutgers University Press, New Brunswick, New Jersey, pp 376–377

Muesebeck CFW (1942) Alexander Arsene Girault. Ann Entomol Soc Am 35:122–123

Gizzard

This term is rarely used in entomology, but applies to a pouch-like structure at the juncture of the crop and stomach. This organ is used for filtering and grinding of food and usually is called the proventriculus.

► Alimentary Canal and Digestion

Glabrous

► Smooth and without hairs

Gladiators (Mantophasmatodea)

In 2002, German researchers announced the discovery of a new insect order, Mantophasmatodea. The order name is based on the names of their close relatives, the Mantodea (praying mantids) and the Phasmatodea (walking sticks). This was a significant find because a new order had not been discovered since 1915. Indeed, it remains to be seen whether the entomological community accepts the report that this is a new order. It has been a controversial topic since the initial discovery. Some have argued that Mantophasmatodea is a sister group of Grylloblattodea, and that they should be treated as suborders in the order Notoptera. Further, two of the three families were relegated to subfamily status in this system, and the insects were named "rock crawlers," whereas the members of the sister taxon, were called "ice crawlers."

Characteristics

Mantophasmatodea was first found in the Brandenberg Mountains of Namibia in southwestern Africa (since then they have been found widely in the western regions of South Africa, and in Tanzania). They were found at the base of grass clumps growing in rock crevices. In most respects these insects resemble stick insects (Phasmatodea), but have characteristics of praying mantids (Mantodea), and some unique attributes. Superficially, they resemble immature mantids, which are wingless like gladiators, but the gladiators lack the well-developed raptorial front legs of mantids. They differ from stick insects in that the head is hypognathous (pointing downward), the first thoracic segment is the largest, the first and second pairs of legs are raptorial, and the insects are carnivorous. Unlike mantids, the second pair of legs is used in feeding. The thorax appears to be armored, hence the name "gladiators." They are also known as "heelwalkers" because they tend to elevate their tarsi when walking.

Gladiator insects are hemimetabolous, like other orthopteroids. The antennae are long and filiform, the head hypognathous. The thoracic segments decrease in size from anterior to posterior. The femora of the first and second pairs of legs are broadened and armed with spines. The tarsi have five segments. There is slight sexual dimorphism. In males, the subgenital plate has a median projection. The cerci are one-segmented, prominent and clasping. In females, the ovipositor projects markedly beyond the short subgenital lobe. The female abdomen is widest in the middle, whereas in the male it is widest apically. Males are smaller than females. All insects are apterous. They generally are under one cm in length. They are brown or green, and may be uniform or mottled in color, often with a dorsal stripe or stripes. Polymorphism is common.

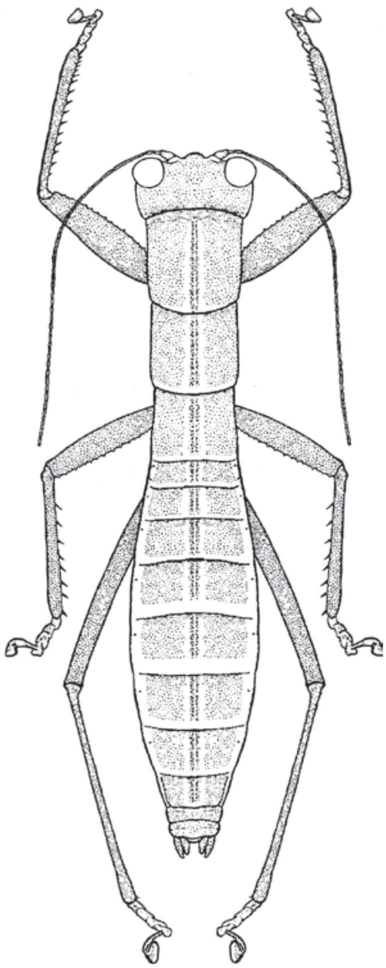
Biology

The eggs of gladiators hatch after the seasonal rains commence, with the nymphs developing during the wet months and the adults maturing at the end of the rainy season. The adults mate, lay eggs and die within two weeks. Mating can be protracted, lasting for 1–3 days. The eggs persist through the arid period in an egg pod in the soil. The pod is composed of sand granules glued together with an exudate. Each pod contains about 12 eggs, and females (Fig. 24) produce several pods.

Gladiators feed on small insects such as flies and bark lice. They may be nocturnal or diurnal. They frequent low vegetation such as tufts of grass. Apparently they communicate vibrationally, as they have been observed taping their abdomen on the substrate.

Taxonomy

The order presently consists of three or more families, several genera (some have yet to be placed in families) and perhaps 12 species. One genus, *Raptophasma*, is known from Baltic amber, dating back



Gladiators (Mantophasmatodea), Figure 24 **Female *Austrophasma* sp. (Mantophasmatodea: Austrophasmatidae) (adapted from Klass et al. 2003).**

about 45 million years. These extinct insects differ from the modern forms in lacking the spines on the femora and tibiae of the first and second sets of legs.

Order Mantophasmatodea
- Family Tanzaniophasmatidae
- Family Mantophasmatidae
- Family Austrophasmatidae

References

Arillo A, Engel MS (2006) Rock crawlers in Baltic amber (Notoptera: Mantophasmatodea). Am Mus Novit 3539:1–10

Klass KD, Zomporo O, Kristensen NP, Adis J (2002) Mantophasmatodea: a new insect order with extant members in the Afrotropics. Science 296:1456–1459

Klass KD, Picker MD, Damgaard J, van Noort S, Tojo K (2003) The taxonomy, genitalic morphology, and phylogenetic relationships of southern African Mantophasmatodea (Insecta). Entomologische Abhandlungen 61:3–67

Glaphyridae

A family of beetles (order Coleoptera). They commonly are known as glaphyrid scarab beetles.

► Beetles

Glaresid Beetles

Members of the family Glaresidae (order Coleoptera).

► Beetles

Glaresidae

A family of beetles (order Coleoptera). They commonly are known as glaresid beetles.

► Beetles

Glassy-Winged Sharpshooter, *Homalodisca vitripennis* (Hemiptera: Cicadellidae)

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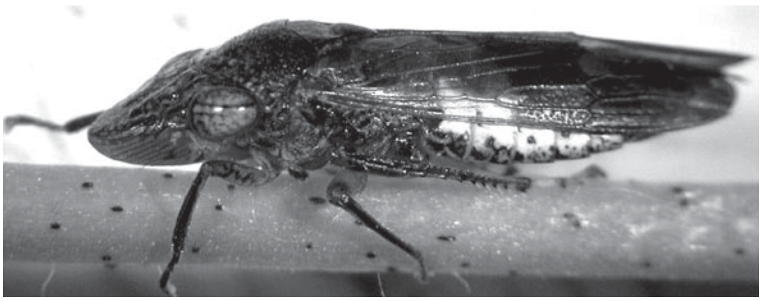
The glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar) feeds on xylem fluid and is damaging to crops and ornamentals through the transmission of *Xylella fastidiosa*, a bacterium that causes phony peach disease, Pierce's disease in grapes, and leaf scorch in almond, plum, elm and oak. In Brazil, a strain of *X. fastidiosa* causes citrus variegated chlorosis, but the current geographic range of the strain does not overlap that of

H. vitripennis. *Homalodisca vitripennis* is native to the southeastern United States, and in the late 1980s or early 1990s spread from Texas to southern California, where Pierce's disease caused $30 million in damage to California vineyards from 1994 to 2000. In California, *H. vitripennis* is a more important vector than the native species because it spreads the disease further into vineyards from surrounding vegetation. Furthermore, in the southeastern United States only muscadine grapes are grown successfully, because only the muscadine varieties are resistant to Pierce's disease. The range of *H. vitripennis* is restricted to areas with mild winters. However, *H. vitripennis* has been accidentally introduced to Hawaii, Tahiti, and Easter Island, Chile. Also, climatological models predict that *H. vitripennis* and *X. fastidiosa* could become established in Central and South America, southern Europe and Asia, Africa, Australia, and northern California.

The "sharpshooter" name refers to leafhoppers in the tribes Proconiini and Cicadellini (Hemiptera: Cicadellidae), and the name has two possible derivations. One reason for the name sharpshooter is the tiny "bullet holes" in branches and stems that are caused by the piercing-sucking behavior. In addition, adults and nymphs quickly move to the opposite side of a branch when startled, and this behavior is similar to the way a military sniper moves to the far side of a tree to avoid detection. The Proconiini tribe comprises 350 species in 56 genera, including *H. vitripennis*, and the range of the tribe includes the Americas and Tahiti.

Homalodisca vitripennis adults (Fig. 25) are generally light brown with black and red wings, and are 11–13 mm in length. Adults usually align head to tail with their heads facing down when feeding, and feed on a wide range of host plants (>100 species), including hardwoods, softwoods, fruit trees, herbaceous crops, and grasses. Some preferred hosts include plum, holly, crape myrtle, citrus, grape and sunflower.

Feeding on xylem may limit the number of competitive interactions *H. vitripennis* encounters, as few insects feed on xylem fluid and there is little or no degradation of xylem quality with insect feeding. In addition, xylem fluid has little or no chemical defensive compounds, which may enable *H. vitripennis* to feed on such a broad host range. However, there are some disadvantages associated with xylem feeding, and *H. vitripennis* has developed some important adaptations to feeding on xylem fluid. To overcome the strong negative pressure associated with xylem tissue, *H. vitripennis* uses a large cibarial pump in the anterior portion of the head to extract the xylem fluid. Furthermore, xylem fluid is approximately 99% water, so a portion of the gut and the Malpighian tubules form a filter chamber that is designed to extract most of the water from the ingested xylem fluid. This process allows nutrients to be absorbed from a more concentrated solution. In addition, *H. vitripennis* feeds for long periods in order to



Glassy-Winged Sharpshooter, *Homalodisca vitripennis* (Hemiptera: Cicadellidae), Figure 25 Adult of glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar).

gain adequate nutrients. Hourly consumption of xylem is often 10–100 times greater than the dry body weight of the individual, so they must produce large amounts of waste. *Homalodisca vitripennis* has become a pest to the tourist industry in Tahiti due to the dense populations of adults and nymphs and the "rain" they excrete that falls on tourists. *Homalodisca vitripennis* excreta consist of a dilute mixture of water and ammonia, which is much less physiologically expensive than urea or uric acid. Most animals do not use ammonia as a waste product, due to the chemical's toxic nature, but *H. vitripennis* waste products are too dilute to cause ammonia poisoning.

Glassy-winged sharpshooters have adapted high assimilation efficiency (about 99%) of amino acids, organic acids and sugars. This assimilation may be due in part to two species of endosymbiotic bacteria that live in the cytosol of *H. vitripennis* cells and aid in attaining the adequate nutritional requirements. Each species of bacteria complements the nutritional advantages of the other and is passed by females to offspring from generation to generation. One species, *Baumania cicadellinicola*, is related to endosymbionts of aphids, tsetse flies, and ants, but is a more primitive species and synthesizes most vitamins and cofactors. The other species, *Sulcia muelleri*, produces many of the essential amino acids that are not abundant in xylem fluid.

Adults often fly from plant to plant, sampling xylem fluid to find optimal hosts and adjust feeding rates to correlate with xylem nutrition. Flight behavior usually consists of short flights from plant to plant and *H. vitripennis* generally flies 2–3 m high, depending on the height of the surrounding vegetation. Dispersal rates vary with available host plants and seasonal conditions, but a single *H. vitripennis* can travel up to 100 m in a matter of minutes. Daily foraging usually occurs between 10 am and 2 pm, during peak xylem flow and this behavior allows adults to attain the best sample of a host in order to make a decision to stay and feed or move on. In addition, *H. vitripennis* may feed on different plants at different times of the day to correlate feeding with maximum xylem flow in the plants. Foraging adults and nymphs are attracted to the color yellow, which may resemble new growth occurring in host plants. *Homalodisca vitripennis* also uses plant volatiles to locate host plants, but olfactory cues appear to be secondary to visual stimuli. Adults do not appear to use pheromones as aggregation cues or to locate mates.

When mating occurs, females line up head to tail on branches, while males fly from branch to branch looking for aggregations of females. Once the male selects a branch to land on, it walks down the branch in a spiral formation and looks for an accepting mate. If the female is not ready to mate, she will stick her legs and abdomen in the air and block off any potential suitors. Mating occurs in the morning or evening, and females deposit eggs at night. Eggs are inserted under the leaf epidermis on the underside of the leaf in groups of 3–28, although eggs are occasionally deposited in fruits or herbaceous stems. A single female can lay up to 1,000 eggs, and eggs hatch approximately 7 days after oviposition. Nymphs are gray and develop through five instars, usually lasting about two months.

Nymphs have different nutritional preferences than adults. Adults prefer to feed on xylem fluid that is high in amides (glutamine and asparagine), and nymphs prefer to feed on xylem fluid with a more balanced spectrum of amino acids. In addition, adults can feed on stems with thicker epidermis than nymphs, due to the adult's thicker proboscis. Pubescent leaves and stems also deter nymphs from feeding, as first and second instars often feed on xylem in leaf veins, and have difficulty reaching the plant through the trichomes. Often eggs are laid on hosts that are acceptable to adults but do not support the development of nymphs, so the nymphs must disperse to find new hosts. However, nymphs have developed excellent dispersal abilities, and third and fifth instars can jump up to 68 and 79 cm, respectively. In addition, nymphs can traverse up to 10 m across a grassy field in three days, and neonates survive an average of 84 h without a host plant.

Nymphs and adults cover themselves in a light coating of lipid-protein molecules called brochosomes, which are produced by special cells in the Malpighian tubules. *Homalodisca vitripennis* secrete brochosomes from the hindgut after each molt and spread them over the integument with their hind legs. In addition, adult females often have conspicuous, white spots of brochosomes on their wings. Females cover their egg masses with these brochosomes by using their hind legs to brush the powdery substance from the forewing patch to the egg mass. All Cicadellidae species cover their integument with brochosomes, but only Proconiini species cover egg masses as well. The structure of brochosomes varies between species, and brochosomes that cover egg masses are structurally different than those that cover the integument. Brochosomes have repellant properties and probably aid adults, nymphs and eggs in the repellency of water and sticky substances, as well as protect against infections. In addition, brochosomes on egg masses may inhibit parasitism by egg parasitoids. Brochosomes may also protect against desiccation and UV light in some instances, as well as aid in thermoregulation.

In northern Florida and southern Georgia there are one or two generations per year. The first generation emerges from eggs laid by overwintered adults in forest edges, and migrates as adults to summer hosts and cropping systems in late May. The second generation migrates back to the forest in August and September, where they spend the winter in reproductive diapause and feed only during warm spells. There are two or three generations per year in California, with the highest oviposition periods in early spring and mid to late summer. During winter months in California adults actively feed on citrus, but do not reproduce. The close proximity of vineyards to these citrus orchards often increases the ease of movement between winter and spring hosts, and can increase the spread of *H. vitripennis* and Pierce's disease into vineyards.

Late in the summer in their native range most *H. vitripennis* eggs are parasitized by mymarid (Hymenoptera: Mymaridae) parasitoids. These parasitoids include *Anagrus stethynioides* and several *Gonatocerus* species, most of which have been evaluated and/or used as biological control agents in California as part of a Pierce's disease management program. The most common parasitoids in the native range are *G. ashmeadi*, *G. triguttatus*, *G. morrilli*, and *G. fasciatus*. Eggs are susceptible to the different parasitoid species at different stages, but generally eggs older than 6 days are not susceptible. Once parasitized, eggs turn black as the parasitoid develops, and eventually the parasitoid chews a distinctive, circular exit hole and emerges. Parasitism often reaches close to 100% in the southeastern United States, but in California parasitism rates rarely exceed 19%. In addition to high mortality from parasitism, *H. vitripennis* populations suffer predation from several generalist predators, including spiders, anoles, dragonflies, and birds.

An entomopathogenic fungus, *Hirsutella homalodiscae*, often infects nymphs and adults, and is most common in mid to late summer. Infected *H. vitripennis* can be recognized by the fuzzy, white fungus growing on the exoskeleton. The generalist fungus *Beauveria bassiana* also infects *H. vitripennis*, but infection rates vary by strain and are generally low. Strains from natural populations in the southeastern United States and Texas are more efficient than commercially available strains. In addition, there are several chemical controls available that have strong effects on *H. vitripennis* nymphs and adults, but low effects on associated egg parasitoids.

The main focus in the control of *H. vitripennis* populations is on limiting the geographic spread of *H. vitripennis*. If *H. vitripennis* populations spread to the north from southern California, the damage to central California vineyards could be devastating. In addition, limiting the international spread is very important to the economic stability of vineyards in Europe and Australia and to the control of citrus variegated chlorosis in South America. The most important method to contain *H. vitripennis* is through the monitoring of horticultural shipments. This is a daunting task, due to the wide range of food and oviposition hosts used by

H. vitripennis. However, if this monitoring is not conducted there could be worldwide consequences.

► Bugs (Hemiptera)
► Leafhoppers (Hemiptera: Cicadellidae)
► Transmission of *Xylella fastidiosa* Bacteria by Xylem-Feeding Insects
► Management of Insect-Vectored Pathogens of Plants
► Transmission of Plant Diseases by Insects
► Citrus Pests and Their Management
► Small Fruit Pests and Their Management

References

Purcell AH, Hopkins DL (1996) Fastidious xylem-limited bacterial plant pathogens. Annu Rev Phytopathol 34:131–151

Redak RA, Purcell AH, Lopes JRS, Blua MJ, Mizell RF, Andersen PC (2004) The biology of xylem fluid-feeding insect vectors of *Xylella fastidiosa* and their relation to disease epidemiology. Annu Rev Entomol 49:243–270

Turner WF, Pollard HN (1959) Life histories and behavior of five insect vectors of phony peach disease. USDA Tech Bull 1188:1–27

Glial Cell

A cell surrounding the axon, soma, and other portions of a neuron. Glial cells provide structural and nutritive support, and protect the nerve cell from outside chemical and ionic influences.

► Nervous System

Global Positioning System (GPS)

Georeferences based on transmission received from a network of satellites.

Globular Springtails

A family of springtails (Sminthuridae) in the order Collembola.

► Springtails

Glory Moths (Lepidoptera: Endromidae)

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Glory moths, family Endromidae, are a monobasic family of four species, with *Endromis* (one sp.) from Europe, *Dalailama* (one sp.) from Tibet, and *Mirina* (two sp.) from Central Asia. There are two subfamilies: Endrominae and Mirininae. The family is in the superfamily Bombycoidea (series Saturniiformes), in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults medium size (29–74 mm wingspan), with head vertex rough-scaled; haustellum absent (or vestigial); labial palpi short, dropping (2 to 3-segmented); maxillary palpi vestigial; antennae bipectinate; body robust with very long hair-like setae. Wings broadly rounded with somewhat acute apex; hindwings rounded. Maculation dark orange brown, with various white spots and darker striae, or lighter and spotted (Fig. 26). Adult males are diurnal but females are nocturnal. Larvae are leaf feeders. Host plants recorded in Betulaceae, Caprifoliaceae, Salicaceae, Tiliaceae, and Ulmaceae.

References

Freina J, de J, Witt TJ (1987) Familie Endromidae Boisduval 1828. In: Die Bombyces und Sphinges der Westpalaearktis, Forschung & Wissenschaft Verlag, Munich, 1:328–329, pl. 24

Jost B, Schmid J, Wymann H-P (2000) Endromidae – Frühlingsspinner. In: Schmetterlinge und ihre Lebensräume: Arten – Gefährdung – Schutz. Schweiz und angrenzenden Gebiete, Pro Natura-Schweizerische Bund fuer Naturschutz, Basel, 3:362–366, pl. 19

Rougeot PC (1971) Endromidae. In: Les Bombycoides (Lepidoptera – Bombycoidea) de ′ Europe et du Basin Méditerranéen. In: Faune de l′ Europe et du Basin Méditerranéen, Masson, Paris, 5:131–140

Seitz A (1911) Familie: Endromidae. In: Seitz A (ed) Die Gross-Schmetterlinge der Erde. 2. Die palaearktischen Spinner und Schwärmer, pl. 35. A. Kernen, Stuttgart, pp 193–194

Zolotuhin VV, Witt TJ (2000) The Mirinidae of Vietnam (Lepidoptera). Entomofauna 11 (suppl.):13–24

Glossa (pl. glossae)

The median lobes on the labium.

► Mouthparts of Hexapods

Glossinidae

A family of flies (order Diptera). They commonly are known as tsetse flies.

► Flies

Glossosomatidae

A family of caddisflies (order Trichoptera). They commonly are known as saddle-case makers.

► Caddisflies

Glossy

Said of a surface having the ability to reflect light. A measurable quality. The antonym is matte. Contrast with LUMINESCENT. Many authors fail to distinguish between these conditions, and erroneously write "shining" or "shiny."

Glory Moths (Lepidoptera: Endromidae), **Figure 26** **Example of glory moths (Endromidae),** ***Endromis versicolora*** **(Linnaeus) from Germany.**

Glover Scale, *Lepidosaphes gloveri* (Packard) (Hemiptera: Diaspidae)

Lepidosaphes gloveri is an important pest of trees and shrubs.

► Citrus Pests and their Management

► Scale Insects and Mealybugs

Glover, Townend

Townend Glover was born in Rio de Janeiro on February 20, 1813. His parents were English, and it to was Leeds, England, that Townend was sent on his mother's death when he was only six weeks old. He became interested in natural history and enjoyed drawing. He was left an inheritance by his father, and this became available to him at the age of 21. He traveled to visit Munich, studied painting, and visited other European cities before returning to Leeds. His paintings, perhaps because he was shortsighted, were meticulous in detail. In 1836 he sailed for the USA to visit relatives, and traveled widely, especially in the South. In 1838 he moved to the state of New York, married in 1840, spent his time on natural history in the widest sense, and in 1846 bought his father-in-law's country estate. In 1854 he joined the "Bureau of Agriculture" which had just been established in the U.S. Patent Office; his job was to collect information about insects. In 1856–1857 he was sent to British Guiana and Venezuela to collect new planting stock of sugarcane for Louisiana. Next, he worked on insect pests of citrus in Florida. He also studied plant diseases, soils, birds, mammals, reptiles, Indian mounds, and even human nature. In 1859 he resigned from the Patent Office and joined the faculty of the Maryland Agricultural College. In 1862 a new U.S. Department of Agriculture was established, independent of the Patent Office, and Glover was appointed United States Entomologist to it. He became a one-man Department of Agriculture, occupied with projects far

Glover, Townend, Figure 27 **Townend Glover.**

broader than entomology. He recommended fumigation of insect-infested shipments from abroad, a clairvoyant policy which has never been followed totally and adequately. He also was occupied with the biological collections of the (Fig. 27) Department of Agriculture. Ill and with failed vision, he resigned in 1878 and went to live in Baltimore with his adopted daughter. The copper plates that he assembled (273 of them) of his drawings of insects were never used to illustrate a major text on entomology but eventually, after his retirement, were bought by the U.S. Government Committee of Agriculture. He was succeeded as U.S. Entomologist by Charles Riley, another Englishman. He died in Baltimore on September 7, 1883, survived by his wife and adopted daughter.

Reference

Mallis A (1971) Townend Glover. In: American entomologists. Rutgers University Press, New Brunswick, New Jersey, pp 61–69

Glowworms

Although this term is sometimes applied to any insect that produces light, it is more correctly applied to *Arachnocampa* spp. (Diptera: Keroplatidae). These insects live in New Zealand and Australia, often in caves or other dark shelters. The best known are *A. luminosa* of New Zealand, and *A. richardsae*, *A. flava* and *A. tasmaniensis* of Australia. The larvae have organs that produce blue-green light. The light is used to attract prey, which are then ensnared in vertical silk threads coated with sticky mucous material that the larvae dangle from the ceiling of the cave or shelter. They are most frequent along streams, and suffer if exposed to low humidity.

Elsewhere, other light-producing flies include *Keroplates sesioides* in Sweden, *K. testaceus* in Germany, *K. nipponicus* in Japan, and *Orelia fultoni* in the Appalachian Mountains of the USA. Several relatives of these insects produce long sticky threads for prey capture but are not luminescent. Fireflies or lightningbugs (Coleoptera: Lampyridae) are sometimes called glowworms, but it is best not to apply this term to lampyrids.

Glowworms produce about 130 spherical eggs that measure about 0.75 mm in diameter. They hatch in 1–3 weeks depending on temperature. The larvae construct a hollow, tubular nest of silk and mucus, release sticky threads and begin light production. There are five instars, with the larva attaining a length of about 30–40 cm in about nine months. This is the only stage that feeds. The pupa is suspended by two silk strands, and in some species the pupal stage is luminescent. Pupation requires about two weeks. Upon emergence, the adults are quite different in appearance, the female being much larger and heavier. The adults live briefly, not more than one week, and the adult males are more active fliers. The adult females of some species luminance intermittently. Mating occurs upon emergence and females mate only once. Females, being poor fliers, tend to lay their eggs near where they emerged.

Glowworms are not selective in their feeding behavior, taking anything that is captured on their sticky threads.

References

Baker CH, Merritt DJ (2003) Life cycle of an Australian glow-worm *Arachnocampa flava* Harrison (Diptera: Keroplatidae: Arachnocampinae). Aust Entomol 30:45–55

Meyer-Rochow VB (2007) Glowworms: a review of *Arachnocampa* spp. and kin. Luminescence 22:251–265

Glycogen

A polysaccharide found in insects that is one of the two most common carbohydrate stored reserves (the other is trehalose) for insect flight. It occurs principally in the glycogen, fat body, and gut tissues. Glucose is released for metabolism from glycogen. Glucose usually is transported by the hemolymph as trehalose.

GLP

An acronym for "Good Laboratory Practice," representing internationally recognized, sound standards of conduct and procedures. The objective of GLP is to ensure the generation of high quality and reliable test data. In entomology, GLP is usually reference to the context of pesticide assessment, but has broad application to laboratory-based science, and has a corresponding protocol for field research, "Good Field Practice" (GFP).

Glyphipterigidae

A family of moths (order Lepidoptera). They commonly are known as sedge moths.

► Sedge Moths
► Butterflies
► Moths

Gmelin, Johann Friedrich

Johann Gmelin was born in Tübingen, Germany, in 1748, the son of a professor of medicine. In 1768, at the age of 20, he took a three-year journey through Holland, England, and Austria. In 1771, he became an untenured professor of medicine at Universität Tübingen, and three years later a tenured professor at Universität Göttingen. His (1787) treatise "Abhandlung über die Wurmtroknis," which described effects of *Ips typographus*, was a major contribution for forest entomology. He contributed pages 1517–2224 to the 13th edition (1790) of Linné' s "Systema naturae…" He died in 1804 at the age of 56.

Reference

Schwertfeger F (1973)Forest entomology. In: Smith RF, Mittler TE, Smith CN (eds) History of Entomology. Annual Reviews Inc, Palo Alto, CA, pp 361–386

Gnat Bugs

Members of the family Enicocephalidae (order Hemiptera).

► Bugs

Gnotobiotic Culture

Culture of insects when all the species (usually of microorganisms) are known.

Goat Moths

Some members of the family Cossidae (order Lepidoptera).

► Carpenterworm Moths
► Butterflies and Moths

Goblet Cells

Goblet-shaped cells found in the midgut of some insects. They house a proton ATPase pump that pumps hydrogen into the goblet cavity. Potassium is exchanged for hydrogen in the goblet cells, a process that creates transmembrane voltages, creates a high midgut pH, and aids in absorption of amino acids released in digestion.

Goblets

Small, round structures located on the spiracular plate of ticks.

Gobryidae

A family of flies (order Diptera).

► Flies

Goeldi, Emil (Emilio) August

Emil Goeldi was born in Ennetbühl im Obertoggenburg, Switzerland, on August 28, 1859. His schooling was in Switzerland until in 1882 he entered Universität Jena in Germany and studied zoology and anatomy. After he was awarded a doctoral degree, he was offered three job possibilities overseas, and of these he chose to become a professor in Rio de Janeiro. There, he worked in the Museu Nacional under the auspices of Brazil's emperor, Dom Pedro II. When a republic was proclaimed in 1889, he lost his job and went to live in the montane Colonia Alpina of Serra dos Órgãos. Later, the new Brazilian government offered him the job of founding a new museum at the mouth of the Amazon, so in 1894 he traveled to Belém, and in a few years had built a large institution, the Museu Paraense. He began two scientific journals, the Boletím and the Memórias of that museum which became known, even in his lifetime, as Museu Goeldi. His first name is usually written in Brazil as Emilio, in keeping with Portuguese spelling. He collected extensively and published numerous papers on various animal groups. Some of those works were on insects, including Coleoptera and Diptera (a major work on the mosquitoes of the state of Pará). In 1907 he returned to Switzerland to teach at Universität Bern. He published (1913) a book on medical zoology, "Die sanitarischpathologische Bedeutung der Insekten und Verwandten Gliedertiere, namentlich als Krankheits-Erreger und Krankheits Ubertrager" drawing upon his experiences in Brazil. He died in Zurich on July 5, 1917.

References

Anon. (2002) Emil August Goeldi. Available at http://www.macalester.edu/environmentalstudies/ARLab/; HypogeanFishes/biogoeldi.hrm. Accessed August 2002

Papavero N (1973) Emil Goeldi. In: Essays on the history of Neotropical dipterology, with special reference to collectors (1750–1905). vol 2, Museu de Zoologia, São Paulo. pp 374

Gold Moths (Lepidoptera: Axiidae)

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Gold moths, family Axiidae, are a very small family of only six Palearctic species in the Mediterranean region, mostly in the genus *Axia*. The family is in the superfamily Drepanoidea, in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults medium size (23–30 mm wingspan), with head scaling normal; labial palpi slightly porrect but very short; maxillary palpi vestigial; antennae bipectinate. Wings elongated and triangular, with relatively acute forewing apex; hindwings triangular and rounded (Fig. 28). Maculation mostly shades of brown to pink, but with at least one bright iridescent mark (often golden color); hindwings unicolorous. Adults nocturnal. Larvae are leaf feeders. Host plants all are in Euphorbiaceae.

Gold Moths (Lepidoptera: Axiidae), Figure 28
Example of gold moths (Axiidae), *Axia theresiae schelhornae* Amsel from Iran.

References

Chrétien P (1916) Observations sur la *Cimelia margarita*, Hb. In: études de Lépidoptèrologie Comparée, 12:37–65, pl. A–D, 502

Freina, JJ de, Witt TJ (1987) Familie Axiidae Rebel 1919. In: Die Bombyces und Sphinges der Westpalaearktis, Forschung & Wissenschaft Verlag, Munich, 1:298–302, pl. 23

Marten W (1937–1938) Zur Kenntnis der Axiidae. Entomologische Rundschau 54:306–308, 408–412, 493–497, 511–515, 534–536, 543–548, 576–579 (1937); 55:15–17, 21–23, 46–48, 61–66 (1938)

Rebel H (1923) *Axia (Cimelia) margarita* Hb. und eine neue Lepidopterenfamilie: Axiidae. Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien 69 (Lepid.):111–114

Reisser H (1933–1934) Beitrag zur Kenntnis der Axiidae (Lep. Heteroc.). Die Biologie der *Axia (Cimelia) napoleona* Schaw. nebst übersetzung der Chrétienschen Arbe1it über *Cimelia margarita* Hbn. Internationalen Entomologische Zeitschrift, 27:357–364, 381–387 (1933), 433–437, 473–479, 485–489, pl. 1–4 (1934)

Gomphidae

A family of dragonflies (order Odonata). They commonly are known as clubtails.

► Dragonflies and Damselflies

Gonad

The basic component of the reproductive system, possessed by both males (testes) and females (ovaries).

Gondwanaland Moths (Lepidoptera: Palaephatidae)

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Gondwanaland moths, family Palaephatidae, total only 31 known species, with 28 from Chile and Argentina and three from Australia. The family forms a monobasic superfamily, Palaephatoidea, in the section Nepticulina, of the division Monotrysia, infraorder Heteroneura. Adults small to medium (8–36 mm wingspan), with head roughened; haustellum is average length and naked (unscaled); labial palpi short and porrect, and 3-segmented; maxillary palpi 5-segmented (rarely 4-segmented and short), long and folded; antennae rather short. Wing venation is heteroneurous, with frenulate wing coupling, and usually with somewhat falcate forewing tips. Maculation is variable, usually with various spots; without large fringes (Fig. 29). Adults are thought to be diurnally active. Biologies are little known and the single known species has larvae that tie twigs together on its host plants (Verbenaceae and Proteaceae).

Gondwanaland Moths (Lepidoptera: Palaephatidae), Figure 29 **Example of Gondwanaland moths (Palaephatidae), *Azaleodes micronipha* Turner from Australia.**

References

Davis DR (1986) A new family of Monotrysian moths from Austral South America (Lepidoptera: Palaephatidae), with a phylogenetic review of the Monotrysia. Smithsonian Contrib Zool 434:1–202

Nielsen ES (1987) The recently discovered primitive (non-ditrysian) family Palaephatidae (Lepidoptera) in Australia. Invertebr Taxonomy 1:201–229

Parra LE, Ibarra-Vidal H (1994) Descripcion de los estados inmaduros y notas biologicos sobre *Metaphatus ochraceus* (Lepidoptera: Palaephatidae), defoliador del notro (Embothrium coccineum). Revista Chilena de Entomologia 21:77–84

Gonopod

An appendage of the genital segment modified for copulation, insemination or oviposition.

Gonopore

The external opening of the ejaculatory duct (in males) or oviduct (in females).

Gorgas, William Crawford

William Gorgas was born on October 3, 1854, near Mobile, Alabama. The son of General Josiah Gorgas, William graduated from the University of the South in 1875. General Josiah Gorgas was an officer in the Confederacy during the American Civil War, so it is perhaps not surprising that William was denied entrance to the premier American military college, the United States Military Academy at West Point, New York. William was determined to have a military career, a prestigious career in earlier days, so he entered the military by way of a medical degree. In 1880 he entered the U.S. Army Medical Corps as an assistant surgeon.

William Gorgas' life was fairly average for about two decades after entering the military. However, he was stricken by yellow fever early in his career, and thereafter he was immune, so was frequently drafted for service wherever yellow fever was a problem. Yellow fever was an enigma at that time, and its appearance, impact, and the inability to control the disease were quite puzzling. Gorgas was dispatched to Cuba during the Spanish-American War, in 1898, when yellow fever was seriously affecting American troops. The prevailing approach for the management of the disease at that time was fire, and the village and hospital to which Gorgas was assigned were torched in September of that year.

In 1898, Gorgas was made chief surgeon of Havana, Cuba, and he followed the generally accepted methods of yellow fever management, relying primarily on sanitation and isolation. However, it was not until the Cuban doctor Carlos Finlay, the English scientist Ronald Ross, and the U.S. Army doctor Major Walter Reed identified the *Aedes aegypti* mosquito as the vector of yellow fever that truly effective practices of management could be implemented. Prior to this time, yellow fever was thought to be transmitted from person to person via personal belongings or merchandise on which the organism was carried, and attempts to prove that mosquitoes could transmit the disease had been futile. Indeed, the earliest attempts to clean up Havana were unsuccessful because although the sanitation efforts cleaned up the water and debris, the relevant vector was favored by clean water and so prospered. However, once all mosquito breeding sites in the city of Havana were eliminated by either preventing mosquitoes from accessing water, or by oiling the surface of water where mosquitoes were likely to breed, yellow fever was effectively suppressed. Thus, Gorgas came to believe that environmental sanitation, and particularly mosquito management, could be used to reduce or eliminate yellow fever.

At the turn of the century, the development of the Panama Canal was in progress. The French were stymied in their efforts to complete the project due to yellow fever and malaria, losing 20,000 lives in an eight year effort to construct the canal. Ironically, the U.S. government seemed similarly inclined to ignore taking adequate measures to prevent workers from contracting the disease. The Canal Commission considered health measures to be extravagant expenditures, but as disease extracted a lethal toll on workers, Gorgas' ideas on sanitation received a better reception. He promoted the draining of swamps in Panama, thereby mitigating malaria and yellow fever and greatly prolonging the life of workers involved in the construction project. Even after conditions improved, Gorgas' enemies were quite effective in discrediting him and his mosquito control policies, and it took the intervention of President Theodore Roosevelt to assure that his procedures would be implemented. Even then, the U.S. military attacked Gorgas' sanitary service. Gorgas prevailed, however, and made the Panamanian cities of Panama and Colon as safe as any city in the United States.

In 1914, based on his successes in Panama, Gorgas was appointed Surgeon General in the U.S. Army. He retired in 1918, but was commissioned to investigate the yellow fever situation in western Africa. Unfortunately, he experienced a stroke in 1920, and died a month later in London on July 4, 1920.

William Gorgas is remembered as the person whose sanitation skills allowed construction of the Panama Canal, a monumental achievement. His achievements at managing yellow fever in Havana are overshadowed by the Panamanian successes, but even the Cuban successes would accord him considerable recognition.

► History and Insects
► Yellow Fever
► Malaria
► Reed, Walter

References

Gibson JM (1950) Physician to the world: the life of General William C. Gorgas. Duke University Press, Durham, NC, 315 pp

Litsios S (2001) William Crawford Gorgas (1954–1920). Persp Biol Med 44:368–378

Gossamer-Winged Butterflies (Lepidoptera: Lycaenidae)

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Gossamer-winged butterflies, family Lycaenidae (including blues, coppers, elfins, hairstreaks, and harvesters), total about 5,955 species worldwide; the actual fauna probably exceeds 7,000 species. About 1,125 species are Neotropical. The family is in the superfamily Papilionoidea (series Papilioniformes), in the section Cossina, subsection Bombycina, of the division Ditrysia. Most of the relictual groups are Southeast Asian and African, such as the subfamilies Lipteninae, Poritiinae, Liphyrinae, Miletinae, and Curetinae. The family has eight subfamilies: those just noted, plus Lycaeninae, Theclinae, and Polyommatinae. North temperate species are only found in the latter three subfamilies. Some specialists include Riodinidae as another lycaenid subfamily, and also reduce the subfamily number to five (including the Riodininae), thus the classification is still in flux. Adults small to medium size (6 to 92 mm wingspan) (most average 20 to 39 mm), with body usually slender (rarely robust). Wings mostly rounded, but some with acute forewing apex; hindwings sometimes with tails (usually very narrow tails) (Fig. 30). Maculation varied but often with blues, greens or other bright colors, and with iridescence or lustrous shine, and often without many dorsal spots (more spotting usually on ventral sides of both wings); hindwings often with color spots near tails at the tornal corner of the wing margin (so-called "false heads"); and fringes short but often white or lustrous. Adults diurnal, but a few of the relict genera possibly crepuscular or only in dark forests. Larvae mostly somewhat slug-like, with tubercles and short setae; head usually retractable into thorax. Larvae feed as leaf feeders (some on other plant parts), but many are myrmecophilous and some even are carnivorous on ant larvae or hemipterans (especially Liphyrinae and Miletinae).

Gossamer-Winged Butterflies (Lepidoptera: Lycaenidae), Figure 30 **Example of gossamer-winged butterflies (Lycaenidae), *Hypaurotis crysalus* (W. H. Edwards) from New Mexico, USA.**

Some of the relict groups feed on lichens (Lipteninae). Host plants are in a wide variety of plant families, particularly Fagaceae and Leguminosae. A few economic species are known.

References

Clark GC, Dickson CGC (1971) Life histories of the South African lycaenid butterflies. Capetown. 272 pp, pl. 125

Eliot JN (1973) The higher classification of the Lycaenidae (Lepidoptera): a tentative arrangement. Bull Br Mus Nat Hist Entomol 28:371–505, pl. 6

Huang SMY (1943) The Chinese Lycaenidae. Notes Entomologicae Chinois 10:67–213

New TR (1993) Conservation biology of Lycaenidae (Butterflies). IUCN, Gland, S173 pp

Pleisch E, Sonderegger P (eds) (1987) Lycaenidae – Bläulinge. In Schmetterlinge und ihre Lebensräume: Arten – Gefährdung – Schutz. Schweiz und angrenzenden Gebiete, Pro Natura-Schweizerische Bund fuer Naturschutz., Basel, 1:319–402, pl. 21–25

Seitz A (ed) (1908–1931) Familie: Lycaenidae. In: Die Gross-Schmetterlinge der Erde A. Kernen, Stuttgart, 1:257–328, pl. 72–83 (1908–1909); 1(suppl.):239–306, 351–353, 817–832, pl. 15–16 (1930–1931); 5:739–832, 1043–1046, pl. 144–159 (1919–1924); 13:297–504, pl. 63–74 (1914–25)

Stempffer H (1967) The genera of the African Lycaenidae (Lepidoptera: Rhopalocera). Bull Br Mus Nat Hist Entomol Suppl 10:1–322, pl 1

Gracillariidae

A family of moths (order Lepidoptera). They commonly are known as leafminer moths or leaf blotch miners.

► Leafminer Moths
► Butterflies and Moths

Gradual Metamorphosis

This is a type of incomplete metamorphosis (hemimetabolous development) found in some aquatic insects (Odonata, Ephemeroptera, Plecoptera). Unlike insects displaying the typical form of incomplete metamorphosis, in which the immature and adult stages are substantially the same in body form (differing principally in the presence of fully formed wings among the adults), immature and adult stages of these aquatic insects differ slightly to significantly in appearance as compared to their adults. However, they lack a pupal stage, which is characteristic of insects with complete metamorphosis (holometabolous development). Because these insects depart from the typical pattern of hemimetabolous development, they sometimes are said to have gradual metamorphosis or paurometabolous development. Consistent with this differentiation, the immature are sometimes called naiads rather than nymphs (contrast with incomplete metamorphosis, complete metamorphosis).

► Metamorphosis

Graham, Marcus William Robert De Vere

Marcus Graham was born in the county of Durham, England, on March 25, 1915. As a boy, he became intrigued with natural history. At the start of World War II, he enlisted in the British army, and served in India from 1942 to the end of

1945. But he had begun to publish entomological papers in 1941. At the end of 1945, he entered Trinity College, Dublin, and graduated in 1950 with a B.A. degree and a B.Sc. degree. In Dublin, he studied the taxonomy of Braconidae, then turned to Chalcidoidea. He was soon appointed to the post of curator of the insect collections of the Hope Department of Entomology, Oxford University. He married in 1953. In 1955, he was awarded the degree of D.Phil. from Oxford University. He taught, took part in administration, and conducted taxonomic research on Hymenoptera until his retirement in 1981. His research was meticulous, he solved many puzzles resulting from inadequate descriptions by early taxonomists of Hymenoptera, and became the foremost authority on European Chalcidoidea. He produced major contributions on the European Pteromalidae, Tetrastichinae (Eulophidae), Encyrtidae, and Myrmaridae. He described 60 genera and 475 species of Hymenoptera. Apart from insect taxonomy and botany, he was interested in Romance languages and medieval literature, painting, and naval history. After retirement, he continued to work (his total production was some 200 papers) and was working on a revision of the genus *Torymus* (Torymidae) when he died, on March 27, 1995. He was survived by his wife, Nora, and son.

Reference

Bouček Z, Noyes JS (1997) Marcus William Robert de Vere Graham (1915–1995) [with a bibliography]. Entomol Mon Mag 133:83–93

Grain Beetles

Several beetles are important pests of stored grain.

► Stored Grain and Flour Insects

Grain Borers

Several beetles in the family Bostrichidae are important grain pests.

► Stored Grain and Flour Insects

Grain Weevils

Several weevils are serious pests of stored grain.

► Stored Grain and Flour Insects

Gramineous Lepidopteran Stem Borders in Africa

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Cereals, especially maize and sorghum, are the most important field crops grown in Africa by commercial and small-scale farmers. Sugar cane is also an important cash crop in many countries on the continent. Although maize and sorghum are grown primarily for human consumption, surpluses are used as fodder for livestock. Among the insect pests found attacking these crops in Africa, lepidopteran stem borers are by far the most injurious.

Given their great economic importance, an enormous amount of literature has accumulated during the past century. The aim of the following sections is to briefly summarize the current state of knowledge on these stem borer pests of cereals. Special attention is given to *Busseola fusca* and *Chilo partellus*, which are the principal borer pests of maize and grain sorghum in Africa, and to *Chilo sacchariphagus*, a serious pest of sugar cane on the Indian Ocean islands, which has recently invaded Mozambique.

Distribution of Major Stem Borers of Maize, Sorghum, Rice and Pearl Millet

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Lepidopteran cereal stem borers in Africa typically occur as complexes of species, with notable regional variation in their distributions. The noctuids *Busseola fusca* Fuller and *Sesamia calamistis* Hampson, and the pyralid *Eldana saccharina* (Walker), are present throughout most of sub-Saharan Africa, but there are important regional differences in the ecozones they inhabit, and their pest status. In eastern and southern Africa, *B. fusca* is a major pest of maize and sorghum at medium and high elevations (greater than 1,000 m), while in West Africa, it is considered to be important from sea level to 2,000 m. *Sesamia calamistis* generally is not a major pest in eastern and southern Africa, whereas in West Africa, this species is one of the most damaging to maize, sorghum and rice. *Eldana saccharina* is primarily a pest of sugar cane in South Africa, while in West Africa, *E. saccharina* is a major pest of maize, and attacks sugar cane to a lesser degree. In some areas of East Africa, *E. saccharina* attacks maize, but tends to arrive late in the season when the crop is less susceptible to yield loss.

Other important stem borers have more limited distributions. *Coniesta ignefusalis* (Hampson) (Crambidae) is the dominant stem borer of pearl millet in the Sahelian region of West Africa, but only a minor pest in other crops and other regions. It also has been recorded from Sudan, Ethiopia and Angola, and thus probably has a fairly wide distribution. *Chilo orichalcociliellus* (Strand) occurs in eastern Africa, mainly in lowland coastal zones, where it once was considered to be a major pest of maize and sorghum. However, recent studies suggest that densities of *C. orichalcociliellus* have decreased due to competition with *Chilo partellus*, an invasive Asian borer. *Chilo partellus* is thought to have arrived in eastern Africa in the early part of the twentieth century, and has since spread to all countries in the eastern and southern parts of the continent. It seems likely that its distribution will continue to expand westward. *C. partellus* is generally the most damaging stem borer of maize and sorghum at elevations below about 1,000 m in eastern and southern Africa. *Sesamia cretica* Lederer, which occurs in Somalia, Sudan, Egypt, and Ethiopia, and *S. nonagrioides botanephaga* Lefebvre, which is found in both East and West Africa, are both important locally. *Chilo aleniellus* (Strand) has been reported as an important pest of maize in Ivory Coast. In addition to stem borers, there are several lepidopteran cob borers in Africa, one of which, *Mussidia nigrivenella* Ragonot (Pyralidae), is an important pest in West Africa. This species is discussed in a later section. The important stem borers of maize, sorghum and millet are listed below (Table 5), along with an approximation of their relative importance in different regions.

Information on rice stem borers is primarily from West Africa, and the Indian Ocean Islands, as these are the areas where rice is an important food crop. *Chilo zacconius* Bleszynski is considered to be the most important stem borer of rice throughout West Africa. *Maliarpha separatella* and *S. calamistis* also are of economic importance in the region. *M. separatella* is the only rice borer that has a widespread distribution in sub-Saharan Africa, and also occurs in the Comoro Islands and Madagascar. Other stem borers in rice in West Africa include *Scirpophaga* spp., *Chilo diffusilineus* (de Joannis), and *S. nonagrioïdes botanephaga* Lefebvre. Additionally, *Chilo aleniellus* (Strand) is mentioned as a rice stem borer in Ivory Coast.

Distribution and Pest Status of African Sugarcane Stem Borers

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Many subsistence farmers throughout tropical and subtropical Africa grow sugar cane for chewing

Gramineous Lepidopteran Stem Borders in Africa, Table 5 Important stem borers of maize, sorghum and millet in sub-Saharan Africa

	Area of Africa			
Family/species	**South**	**East**	**West**	**Central**
Noctuidae				
Busseola fusca	+++	+++	++	+++
Sesamia calamistis	+	+	+++	++
Sesamia cretica		+++[a]		
Sesamia nonagrioides botanephaga			++[b]	
Crambidae				
Chilo partellus	+++	+++		
Chilo orichalcociliellus		++[c]		
Chilo aleniellus			+[d]	
Coniesta ignefusalis			+++(millet only)	
Pyralidae				
Eldana saccharina	(only sugar cane)	+	+++	++

[a]Only in Northeast Africa (Sudan, Somalia, Eygpt)
[b]Only reported as important in Ghana
[c]Only in coastal East Africa
[d]Only in Ghana, Ivory Coast

purposes. Commercial sugar cane production, however, has an interesting history in Africa. Many countries had very strong industries in the early 1900s, which collapsed during various civil wars and for other reasons through the years. Some of these countries now are rehabilitating their industries. A few still have very strong industries, which have withstood the vagaries of time. This section deals only with the commercial sugar industries known to occur in Africa, as it is only from reports and papers emanating from these that pest records are known. Also, for the purposes of this section, Africa is divided into southern, eastern, northern and western regions. The countries known to have, or have had, viable sugar cane industries in southern Africa include South Africa, Swaziland, Zimbabwe, Malawi, Mozambique and Zambia. In east Africa, they are Tanzania, Kenya, Uganda and Ethiopia. In north Africa, these are limited to Egypt, the Sudan and possibly Libya. West African countries producing, or known to have produced, sugar on a commercial scale include Sierra Leone, Ivory Coast, Burkino Faso, Ghana, Nigeria, Cameroon, Gabon, Mali, Senegal, Guinea Bissau and, more recently, Angola.

In Africa, only lepidopteran larvae have been recorded as borers of sugar cane. These can attack the youngest shoots, causing dead hearts, through to the most mature sugar cane stalks. In severe infestations, the rootstock of ratooning sugar cane can harbor developing larvae, which can severely affect the regrowth of the crop. In addition, larvae of some species of Lepidoptera develop in the whole stalk when the cane is mature, others only in the top third, and still others in the bottom third. In different parts of Africa, the same species may develop in the bottom third of mature sugar cane plants, while in other parts, they may develop in the top third of the stalk.

Oviposition by different species of Lepidoptera attacking sugar cane also may vary. Some species prefer to oviposit on the green leaves of sugar cane, either on the abaxial and/or adaxial surfaces of leaf blades, and in sugar cane from one month old to maturity, which may be up to 24 or 30 months old. Other species oviposit in cryptic positions, in older sugar cane behind dead leaf sheaths, in folded dead leaf blades, or even in decaying dead leaf material around the bases of mature sugar cane stalks.

Until 1992, fourteen species of Lepidoptera had been recorded as attacking sugar cane in Africa. The majority of these are indigenous to the African continent. In 1999, a fifteenth species, *Chilo sacchariphagus* (Bojer) (Pyralidae), was confirmed as attacking sugar cane in Mozambique. This is the first record of an exotic lepidopteran establishing on sugar cane in economic proportions in Africa. Prior to this, the only other exotic reported to occasionally attack African sugar cane has been *Chilo partellus* (Swinhoe) (Crambidae).

Most of the boring lepidopteran pests of sugar cane belong to the families Crambidae, Pyralidae, and Noctuidae, and a ranking, in 1994, of these species (using the number of citations in Review of Applied Entomology, 1972 to 1992 to each on sugar cane) has revealed that only four are regarded as major pests in Africa. These are *Eldana saccharina* Walker (Pyralidae), *Chilo agamemnon* Bleszynski (Crambidae), *Sesamia cretica* Lederer and *S. calamistis* Hampson (both Noctuidae) (Table 6). More recently, *Busseola fusca* (Fuller) has been recorded occasionally from sugar cane in West Africa. The following table outlines the distribution of the stem borers regarded as major pests in African sugar cane, and their severity in south, east, north and west Africa.

Eldana saccharina is by far the most injurious stalk boring pest in Africa. It is also one of the few attacking mature (or older) sugar cane stalks. In southern Africa is has been the subject of much research in plant resistance, biological control, insecticide and cultural means in attempts to control it. In southern and coastal eastern Africa, it attacks the lower portion of sugar cane stalks. However, in the Kenyan and Ugandan industries around Lakes Victoria and Albert, respectively, and in West Africa, it attacks the upper third of mature stalks. In many of the more tropical countries, sugar cane is cut at too early a stage for *E. saccharina* to become a pest, although if the cane is not harvested at this early age for some reason, then this borer can affect it seriously.

Chilo agamemnon has received much attention in Egypt, where it is classed as an internode borer, thus attacking the more mature cane stalks. However, it also attacks young plants, causing dead hearts. Researchers in Egypt are working on plant resistance, as well as inoculative biological control using egg parasitoids.

The *Sesamia* species are generally pests of young cane, causing dead hearts. By the time the sugar cane is mature though, these borers have been brought under control by parasitoids, and thus do not become major pests.

Gramineous Lepidopteran Stem Borders in Africa, Table 6 The distribution of stem borers regarded as the major pests of sugar cane in Africa, and a rating of their pest status (+++ = Major Pest; ++ = Occasionally a Pest; + = Present in Low Numbers)

	Area of Africa			
Species	South	East	North	West
Eldana saccharina	+++ Generally[a]+	++ Generally[b]+	+	+
Sesamia cretica			++	
Chilo agamemnon		+	++	
Sesamia calamistis	+	+		+

[a]Only in South Africa and Zimbabwe
[b]Only in Western Uganda

Pest Status of *Mussidia nigrivenella* Ragonot, a Cob-borer of Maize in Western Africa

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In West Africa, five borer species are commonly found feeding in maize cobs, but *Mussidia nigrivenella* Ragonot (Lepidoptera: Pyralidae) is by far the most important across all zones. Grain yield losses are relatively low and range from 2 to 25%. Percentage of grain infected by the toxic fungus *Aspergillus flavus* as well as mean aflatoxin content of samples, however, increases exponentially with grain damage. Cob damage by *M. nigrivenella* also promotes the infestation of storage beetles such as *Sitophilus zeamais* Motschulsky, *Carpophilus* spp. and *Cathartus quadricollis* Guérin. Furthermore, damaged cobs cannot be sold as green maize, an important source of cash in the vicinity of centers of population. Thus, in addition to the direct damage, *M. nigrivenella* induces indirect qualitative and quantitative losses in the field and store.

Mussidia nigrivenella is highly polyphagous, and is found on 20 plant species from 11 different plant families, among them cotton, *Phaseolus* bean and cover-crops such as the velvet and Jack-bean. In West Africa, no parasitoids were ever obtained from annual crops, and most alternate host plants. The solitary chalcidid pupal parasitoid, *Antrocephalus crassipes* Masi, was the predominant species with highest and stable parasitism on *Gardenia* spp.

Mussidia nigrivenella has never been described from annual crops in eastern Africa, but according to some anecdotal reports is found on wild host plants. This opens the opportunity of the novel association biological control or expanding the geographic range of a natural enemy species.

Displacement of Native Stem Borers by *Chilo partellus*

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The invasive stem borer, *Chilo partellus*, has proved to be a highly competitive colonizer in many of the areas it has invaded in eastern and southern Africa, often becoming the most injurious stem borer, and displacing native species. In coastal Kenya, there is evidence that *C. partellus* has partially displaced the indigenous borer, *Chilo orichalcociliellus*. Whether the displacement of *C. orichalcociliellus* will proceed toward complete extirpation in the southern coastal area of Kenya seems unlikely. Recent sampling has shown that *C. orichalcociliellus* continues to persist, and laboratory studies have found that *C. orichalcociliellus* was able to complete development in two native grasses in which *C. partellus* could not develop. This difference in niche breadths of the two species may account for the continued occurrence of the native species. Additionally, a parasitoid of *C. partellus* from Asia, *Cotesia flavipes* (Cameron), has been introduced and established in several countries in Africa. Evidence from coastal Kenya suggests that the introduction of *C. flavipes* has resulted in a marked population decrease of *C. partellus*, but that populations of two native borers, *C. orichalcociliellus* and *Sesamia calamistis*, have slightly increased.

In addition to the work in coastal Kenya, there is evidence of displacement of native stem borers in two other areas in Africa. In the Eastern Province of Kenya, work conducted in the 1980s found that *C. partellus* was present, but less abundant than *Busseola fusca*. However, in the same area in the late 1990s, *B. fusca* was rare and *C. partellus* was dominant. Similarly, in the Highveld region of South Africa, *C. partellus* has partially displaced *B. fusca*.

Several factors may be responsible for the competitive superiority of *C. partellus* over the native stem borers. Various studies have shown that *C. partellus* completes a generation in less time than *C. orichalcociliellus*. As fecundities of both species are similar, the shorter generation time is likely to lead to higher population levels, which may give the alien species a numerical advantage. A more rapid diapause termination compared to both *C. orichalcociliellus* and *B. fusca* has also been shown, which may allow *C. partellus* females to colonize host plants before the two native species, which would be particularly important if the native species avoid previously infested plants.

Damage and Pest Status

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Feeding and tunneling by stem borers can result in serious damage and crop losses. Damage is caused by the larvae, which at first feed on the young leaf funnels at the growing point and then later by tunneling into the stems. Apart from leaf damage, growing points may be killed, leading to stunting and deadhearts or to early senescence of plants. Stem tunneling may cause lodging, but also secondary and insidious effects, such as interference with translocation of metabolites and nutrients, resulting in malformation and loss of grain. There can also be a sharp increase in the incidence of stalk rot. Feeding in ears has been associated with fungal infection and elevated levels of mycotoxins.

Busseola Fusca

In South Africa, crop loss assessments in cereal crops from *B. fusca* attack ranged from 10 to 100%. Although much of this was due to leaf damage in maize, the most severe loss was from stem-boring activity. In Lesotho, seasonal variation in maize yields due to *B. fusca* ranged from 0.4 to 37%.

In Tanzania, 40–100% of the sorghum crop can become infested with *B. fusca*. Together with Kenya, loss of about 12% maize yield for every 10% of plants infested with B. fusca has been documented. In Ethiopia, movement of *B. fusca* larvae into the base of the sorghum panicle resulted in undersized panicles and a 15% yield reduction. In Burundi, using insecticides and exclusion cages, 30–50% of the maize harvest was shown to be lost to *B. fusca*.

In the Northern Guinea savanna of Nigeria, where *B. fusca* is the dominant stem borer, 49% loss of sorghum was reported. Comparative yields on 22 farmers' sorghum fields in Nigeria, sprayed and unsprayed with insecticide, showed a 21% mean loss in yield due to this borer. Losses to *B. fusca* in sorghum crops in Nigeria are very much dependent on the time of initial infestation. Thus, sorghum infested prior to the booting stage suffered the greatest yield losses. The proportion of internodes bored in the lower part of the stalks had a more consistent negative correlation with harvested grain than did the proportion of stalks tunneled. A recent study in Cameroon showed that stem borers, primarily *B. fusca*, were responsible for a 9 g loss in sorghum yield per plant per borer. There was also an 11% crop loss through deadheart.

Chilo Spp

The estimated yield losses in maize and sorghum in South Africa due to *C. partellus* exceeded 50%. A negative correlation between the level of *C. partellus* infestation and yield has been demonstrated. Comparative trials in separate and mixed stem borer populations, using artificial infestation techniques, indicated that *C. partellus* was more injurious to sorghum than *B. fusca*. More damage also was caused by *C. partellus* to long-season sorghum cultivars, mainly due to their longer exposure to stem borer attack while in the susceptible pre-flowering stage.

In Mozambique, the third generation of *C. partellus*, the most important stem borer occurring in the country, was reported to infest 87% of cobs of late planted maize and to cause 70% loss of grain. Infestations of up to 100% of the crop, with considerable yield losses, were recorded in the Maputo and Gaza Provinces and in the Limpopo Valley, in southern Mozambique.

In Zimbabwe, *C. partellus* caused sorghum yields to drop by 50–60%, while in maize up to 70% damage was reported from the fields of resource-poor farmers. However, in the commercial farming areas, where insecticides are routinely applied, maize damage was less than 30%.

In Kenya, 18% loss of maize was attributed to *C. partellus* and *C. orichalcociliellus*, while 88% loss of sorghum crop to *C. partellus* was reported. Heavy stalk damage to maize, and up to 80% of the sorghum harvest, was lost to the latter borer on 20-day-old crops. *Chilo partellus* infestations caused insignificant crop loss when 60-day-old plants became infested. Similar observations were reported from Uganda.

Sesamia spp

In Ghana, a positive relationship between the number of *Sesamia* sp. larvae and the extent of damage to maize stalks, and a negative relationship between damage to maize stems and maize yields were demonstrated. The calculated losses caused by *Sesamia* sp. to maize in the rain forest, coastal, derived and Guinea ecological zones were 27, 15, 18 and 14%, respectively. Chemical control of stem borers in sorghum in the Southern Guinea savanna of Nigeria, where *S. calamistis* predominates, increased yields by 16–19%.

Eldana Saccharina

In West Africa, natural infestations by *E. saccharina* decreased maize yields by 16, 15 and 28%, respectively, in the dry season and the first and second rainy seasons. Infested maize plots had significantly lower grain weight, indicating that *E. saccharina* damage to the stems affected grain filling.

In Burundi, insecticides and exclusion cage trials indicated diminished maize yields of 12–15% by *E. saccharina*. Curiously, in southern Africa, *E. saccharina* is not known as a pest of either maize or sorghum, but is a serious pest of sugar cane.

Stem Borer–Fungal Interactions

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Both fungi and insects possess chitin-based exteriors. Also, both are heterotrophic, i.e., acquire nutrients by feeding on other organisms. It is at this nutritional interface where fungi and insects often intersect, giving rise to many different types of insect-fungus relationships, which can be neutral, mutually beneficial, exploitative, or antagonistic. Some relationships are merely opportunistic, while others are co-evolved and have become obligatory. Direct mycophagy, or fungivory, occurs when insects preferentially select fungi as a food source. Alternatively, many fungi require insects as a food source and become pathogens. Insects that feed on plants often encounter fungi that either live within the plant as endophytes or in association with plant tissues, resulting in an indirect effect on insect fitness. Often, insects are the vehicle by which fungi gain ingress into a plant or disperse throughout a habitat.

Fusarium verticillioides is an endophyte of wild and cultivated grasses. It produces mycotoxins such as fumonisin, which promotes esophageal cancer in humans and leucoencephalomalacia in horses. The fungus may attack at all growth stages of the plant and move from seed to stem into the cob. Similarly, variants of *F. moniliforme* have been found to produce the compound beauvericin, which was originally isolated from the entomopathogenic fungus *Beauveria bassiana*. In a survey in southern Benin, *F. verticillioides* was the most common endophytic fungus inhabiting maize stalks. Incidence was higher in plants damaged by insect pests, and was cultured from stems of 71–80% of plants damaged by stem borers. It was found that ovipositing adult lepidopteran stem and cob borers such as *E. saccharina*, *S. calamistis* and *Mussidia nigrivenella* not only preferred infected plants, but that offspring had higher survival and fecundity. This relationship is completely mutualistic because the insects feeding on infected plants may also vector the fungus from soil to plant and from plant to plant. Furthermore, lepidopteran pests feeding in the ear produce exit holes before pupating, which then are used as entry holes by storage beetles, which may be grain or fungal feeders. They, in turn, vector the mycotoxic fungus *Aspergillus flavus*, which has been shown to be suppressive to *S. calamistis*, *E. saccharina* and *C. partellus*; *M. nigrivenella*, on the other hand, was not sensitive to aflatoxin or *A. flavus* in the diet, which makes it a perfect vector; thus, aflatoxin content in grain increase exponentially with grain damage caused by *M. nigrivenella* or resulting increased beetle infestations. Control programs at the International Institute of Tropical Agriculture in Nigeria aim at both the fungi and the insects, and include biological control (e.g., *Trichoderma* sp.) and seed treatment against *F. verticillioides*, cultural control (sorting of infected ears), host plant resistance, competitive niche displacement (the use of atoxigenic, competitive races) against *A. flavus,* and host plant resistance, biological control and habitat management against stem and ear borers.

Larval Diapause

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Many cereal stem borers undergo a resting period toward the end of the cropping season in response to cold and/or dry conditions. The resting period is spent as mature larvae within dry crop residues and stubble in the fields.

In the elevated regions of southern Africa, *B. fusca* and *C. partellus* pass winter (May to September), which is the cold dry season, in diapause in the lower portions of the dry stalks of their host plants, where they are well protected from adverse climatic conditions. In West Africa, *B. fusca* also enters a prolonged diapause during the dry season, which takes up to six months to complete. With the start of the rains, the larvae pupate within the stems and 10–12 days later emerge as adult moths.

While *B. fusca* diapauses throughout its distribution range in Africa, the larvae of *C. partellus* do not undergo diapause in the warmer low-lying South African provinces of Kwazulu-Natal and Mpumalanga, Swaziland and southern Mozambique. Likewise, while *C. partellus* is known to diapause in the dry season in India and on several islands off the coast of Africa, non-diapausing larval populations occur along the coast of Kenya. In periods between cropping seasons, some *C. partellus* larvae enter diapause within maize stubble, whereas other larvae remain actively feeding on alternative host plants, such as Napier grass growing in the proximity of the cultivated areas.

Thus, in coastal regions where there is an abundance of host plants and where the climate remains favorable, *C. partellus* normally exhibits continuous development. Whereas inland, on the upland plateau, which experiences a long dry or cold season, larvae enter a diapause. Similarly, *C. ignefusalis* in West Africa exhibits a facultative diapause within dry millet stems.

In the interior of Kenya, the larvae of *C. partellus* and *C. orichalcociliellus*, together with *S. calamistis*, enter diapause for several months in the dry season. However, *S. calamistis* was reported not to enter diapause in Uganda nor in Nigeria.

An increase in carbohydrates and a decrease in protein and water content of the host plant are the principal factors inducing diapause in *B. fusca*. Drying out of the host plant, and a general deterioration in the nutritive environment, were found to induce diapause in *C. partellus* larvae, even when climatic conditions remained favorable for development. Diapause also could be "artificially" induced in non-diapausing larvae by introducing them into aging maize stems.

During diapause, larvae of *B. fusca* and *C. partellus* both showed a progressive decrease in weight and an increase of up to seven additional molts. The longer the larvae remained in diapause, the smaller the resultant moths became. Such female moths showed impaired ovarian development with fewer oocytes, and also laid fewer eggs. After eight months in diapause, the emerging moths weighed about half as much and produced half as many eggs as those moths emerging from non-diapausing larvae.

Diapausing larvae of *B. fusca* collected in South Africa in the field during winter emerged as moths in mid-October, regardless of the date of collection and the length of time they were kept at 21°C and 60% RH in the laboratory. However, larvae of *C. partellus* collected during April to June from the field emerged in November, while those collected in July emerged as moths in October. Those collected in August emerged in September. Regardless of collection date, *C. partellus* started to emerge from diapause earlier and the emergence period of the moths was up to twice as long as that found for *B. fusca*. In the field, *C. partellus* moths emerged from diapause in the second half of August and continued doing so until the first week of November, emergence thus lasting a total of 12 weeks. In contrast, *B. fusca* only pupated during October to November.

B. fusca hence had an obligatory larval diapause, whereas *C. partellus* had a facultative diapause. These differences in the pattern of moth emergence following diapause explain the distinct annual generations occurring in *B. fusca* and the continuous overlapping generations of *C. partellus* observed in South Africa.

Conditions of continuous moisture during the long rainy season in Kenya played a significant role in the termination of diapause in *B. fusca*. However, rainfall alone did not appear to be the main cause. Contact with free water was of more significance in breaking diapause than water uptake. In Ethiopia, as well as in the Ivory Coast, provision of water played an important role in promoting pupation during post-diapause dormancy of *B. fusca*. Any delay in wetting of larvae after diapause, and access to water early in diapause, had an adverse effect on the larvae. The key factor enabling diapausing *B. fusca* larvae to survive adverse conditions appears to be efficient water conservation.

A combination of temperature and photoperiod also played an important role in termination of diapause of *B. fusca* in South Africa. Water was important in stimulating morphogenesis following larval diapause. Long days accelerated termination of diapause in *C. partellus*, but under a 16 h daylight regime, termination of diapause was faster than under constant illumination. In contrast, temperature, relative humidity and day length did not affect diapause of *C. partellus* and *C. orichalcociliellus* larvae in Kenya.

It appears that *C. partellus* larvae collected in South Africa at 25°38′ latitude are more affected by day length than Kenyan borer populations located near the equator. It has been suggested that the right combination of day length and temperature could be used for breaking diapause in order to rear large numbers of larvae for experimental use in plant resistance trials. Simpler and cheaper facilities could hence be used for maintaining continuous laboratory cultures of these stem borers.

Pest Management

Use of Synthetic Sex Pheromones

Pheromone-baited traps are useful devices for monitoring stem borer moth populations. Trap catches of male moths provide useful information for quantifying moth abundance and for alerting and timing of spray applications. From the advances made in the identification and the use of sex pheromones in stem borer monitoring, it was concluded that trapping alone was unlikely to provide effective control; mating disruption was a more likely control option. Synthetic pheromone blends for *Chilo suppressalis*, *C. sacchariphagus*, *C. indicus*, *C. auricilius* and *C. zacconius* have been shown to be attractive to male moths in the field. Sex pheromones for *B. fusca*, *C. partellus*, *S. calamistis*, *S. cretica*, *S. nonagrioides* and *Coniesta ignefusalis* have been identified and are now commercially available.

Several years of monitoring *B. fusca* moths in South Africa with the aid of sex pheromone traps have revealed that the first flight of moths, emerging from overwintering larvae, peaked about mid-November. A second, larger flight then occurred in the latter half of February, while a third flight peaked around mid-April. No moths were trapped during winter (June to September). In the field, larval peaks of *B. fusca* lagged from 4 to 6 weeks behind the corresponding moth flight peaks. Omni-directional traps were found to be superior to delta traps for quantitative and qualitative estimation of *B. fusca* moth populations. More research into trap design and the correlation between trap catches and subsequent field infestations are required before trapping of *C. partellus* moths can be used in predicting economic threshold levels.

A slow-release pheromone formulation produced high levels of mating disruption in *B. fusca* when applied at 40 g a.i. per hectare at 250–500 release points per hectare. This effect persisted for at least 18 weeks and, based on release rate studies, was predicted to last for six months. In field trials in Kenya, some reduction in damage levels was observed, suggesting that mating disruption had indeed occurred.

Cultural Control

Cultural control is probably still the most relevant and economical method of stem borer control available to farmers in Africa. Other control methods are less practical. For example, pesticides often are unavailable or are too expensive for resource-poor farmers. Resistant cultivars are likewise not easily available, nor can biological control of stem borers be completely relied upon.

Cultural control is amongst the oldest, traditional, farming practice known. It is considered the first line of defense against stem borer pests and includes methods such as removal and destruction of old crop residues, intercropping, crop rotation, manipulation of planting dates and use of different tillage methods. The latter three cultural practices are of particular importance and can directly benefit crop yields. Though many of these cultural practices are very labor intensive, they do have the advantage of having minimal environmental impact and also can be readily implemented without extra capital investment.

However, adequate knowledge of stem borer biology and phenology, together with a close working relationship with the crop through all its growth stages, are essential for the development of efficient cultural control strategies. The differences found in the behavior of *E. saccharina* in South Africa and in East Africa affords an example of the importance of pest knowledge in making the right control decision. In South Africa, larvae of *E. saccharina* mainly infest the lower part of sugar cane stalks and farmers therefore cut off the tops of the cane, which are simply left lying as crop residues in cane fields. In contrast, the same larvae in East Africa largely occur in the upper cane, and any tops of plants left as residues would therefore provide a further source of infection and exacerbate the carry-over of the pest population.

Although cultural control options for stem borer management appear promising and offer relief, many African farmers have not adopted them. Cultural control is still severely constrained by a lack of management capability of farmers, especially in areas where agricultural extension services are inadequate.

Managing Crop Residues

Crop residues are especially important for the carry-over of stem borer larval populations from one growing season to the next. In Nigeria, larvae of *B. fusca*, *E. saccharina* and *S. calamistis* were found in crop residues below the soil surface, and higher incidences of these borers always occurred in no-tillage plots. In Kenya, *C. orichalcociliellus*, *C. partellus*, *E. saccharina* and *S. calamistis* were observed in stalks after harvest. In Ethiopia, a considerable proportion of *B. fusca* larvae survived in the stubble. In Uganda, untreated crop residues often were used to mulch the next crop. Under these conditions, moths emerging from the previous crop constantly reinfest newly planted crops.

An effective control option would thus be to reduce the first generation moth populations by destroying the bulk of the mature larvae overwintering in the old stalks. Plowing, in order to bury the maize stubble, proved an effective measure for controlling *B. fusca* infestations as far back as the 1920s in South Africa.

In Zimbabwe, it was observed that *B. fusca* moths experienced difficulty in emerging through 5 cm of soil and that deep burial under 10–15 cm of soil could totally prevent moth emergence. Deep plowing tillage in South Africa, where large areas are under maize or sorghum and where densities of up to 226,000 borer larvae per hectare have been estimated, is thus a viable control option for *B. fusca* and *C. partellus*.

Slashing of maize and sorghum stubble to expose overwintering larvae to the elements and natural enemies destroyed 70% of *C. partellus* and *B. fusca* populations, while additional plowing and disking destroyed a further 24% of the pest population in sorghum and 19% in maize.

However, for these cultural control measures to be really effective, the close cooperation of all farmers in a particular region is required because moths emerging from untreated fields will readily infest neighboring crops. Currently, this cultural control strategy is no longer so widely practiced in South Africa, owing to the advent of minimum tillage and to the importance of providing winter grazing on old maize fields for beef cattle.

In rural Africa, farmers often use the dry stalks of maize, sorghum and millet as building construction material in their houses and fences, in contour terracing and for use as stakes. Stalks also are kept for fuel and for use as bedding for livestock. Farmers often stack the dry stalks in the field, where they are kept until the start of the rainy season, thus creating ideal reservoirs of stem borer infection. To solve this problem, early cutting of stalks and horizontal placement on the soil surface have been recommended. This was found to cause 97% mortality of stem borers in maize and 100% in sorghum in Ethiopia. This practice also has reduced the residual population of borers in uncut millet stems from 16% to 3%. The high levels of mortality of *C. partellus*, *C. orichalcociliellus* and *S. calamistis* larvae observed in horizontally placed stalks was ascribed to the combined effects of radiant heating and high temperatures on the thermal tolerance of borer larvae. On the other hand, in Nigeria, the control of *S. calamistis*, *B. fusca*, *C. ignefusalis* and *E. saccharina*, through removal of maize stalks and stubble after harvest, did not reduce stem-borer populations significantly, apparently because of immigration of moths into the crop.

Control of *B. fusca* and *C. partellus* by burning old stalks and other crop residues after harvest also has been recommended. For example, almost complete eradication of *C. partellus* was achieved on maize and sorghum in Tanzania after setting fire to old crop residues. However, in Nigeria where the majority of farmers make use of their old sorghum stalks and do not normally burn them after harvest, a partial burn when the leaves were dry and the stalks still green gave up to 95% control of *C. partellus* larvae. The heat generated from burning the leaves apparently killed the larvae inside their tunnels. At the same time this cured the stalks, which not only improved their strength for building purposes, but also made them more resistant to termite attack. On the other hand, crop residues are the only organic matter that is added to the soil on many small scale cultivations in Africa. Burning of old crop residues can thus deprive the soil of organic matter and also result in increased soil degradation due to wind and water erosion.

Manipulation of Sowing Dates and Plant Densities

Planting crops when the pest is least abundant ensures that the more susceptible early growth stages escape becoming infested. In Kenya, an attempt to legislate this principle was made for controlling *B. fusca* on maize during the 1920s and 1930s. The aim was to restrict maize plantings to the February to May period, a time when moth infestations were normally low. Unfortunately, there is no available information on the efficacy of these measures, and the last attempt at implementing such legislation was in 1937–1938, after which it fell into disuse.

In West and Central Africa, early planting has been found to reduce *B. fusca* and *S. calamistis* infestations. Reports of increased stem borer damage to late maize plantings, as compared to early plantings, have come from Benin, Cameroon, Ghana, Nigeria, Burundi and Zaire. In some areas of West Africa, farmers also do not plant maize during the second rainy season because of the risk of severe infestation. This also influenced the borer populations found in the rain forest zone, where alternative wild host plants in the dry season are scarce.

Early planting of cereals also is practiced in the semi-arid tropics, where rainfall is variable and unpredictable. Late sowing, however, is also unpopular because of poor yields, even in the absence of stem borer damage.

On the Highveld region of South Africa, the second generation of *B. fusca* in mid-summer is larger and causes more damage than the first spring generation. The best control strategy is hence to plant early in the season. Similar conditions apply to Lesotho, Zimbabwe and Ethiopia, where second generation larvae caused crop losses of 23–100% as compared to 0–23% by first generation larvae.

At lower elevations in South Africa, it is recommended that sorghum be planted after mid-October to avoid infestation from the first moth peak of *C. partellus*. In Tanzania, it was shown that maize planted early in the season was more liable to severe infestation by *B. fusca* than later maize plantings. In Malawi, planting date also influenced pest levels of *B. fusca* and *C. partellus* on sorghum. However, the choice of optimum sowing date also depended on the sorghum cultivar planted. In contrast, in the Sahelian region, manipulating the planting dates of millet was not an effective option against infestation by *C. ignefusalis*.

Sowing density may also affect crop growth and thereby influence pest population levels. The behavior of the pest in its search for food or for oviposition sites may well be adversely affected by plant density. Young *C. partellus* larvae need to migrate from their hatching site to the leaf funnels or to reach adjacent plants within their immediate vicinity. During this critical migration period, up to 100% mortality of the first instar larvae may occur. The lowest incidence of deadheart was caused by *B. fusca* at low plant densities of sorghum in South Africa and from maize in Nigeria. Conversely, a reduction in row width increased the number of stem borer larvae infesting adjacent crop rows through migration, and this in turn resulted in greater crop damage. *B. fusca* larvae can migrate up to a distance of 2.4 m from their eclosion site. At the standard 90 cm inter-row planting distance used in commercial maize production in South Africa, lateral transmission over ±4 rows of maize is thus possible.

Rather than reducing plant densities within individual rows, wider row spacings also have been used in the Ivory Coast in an attempt to reduce *B. fusca* and *E. saccharina* damage to maize. However, studies on *C. partellus* in maize and on *C. ignefusalis* in millet, planted at different crop densities, showed no significant differences in stem borer incidence.

In subsistence farming systems in Africa, where farmers normally intercrop cereals with other crops, and where lack of water is an overriding constraint, manipulation of sowing dates and plant densities is not always possible. Farmers generally must plow and plant after the first rains have fallen, rendering some of these cultural control alternatives impractical.

Fertilizers

Providing fertilizer to cereal crops has been shown to increase stem borer infestation and survival of borer larvae. For example, damage to rice by *Maliarpha separatella* in Nigeria increased with fertilizer application, while sorghum plants with no fertilizer supplied were less preferred for oviposition by *C. partellus* moths in South Africa. However, no such differences were observed in similar oviposition behavior trials with *B. fusca*. However, in South Africa, where *E. saccharina* is a problem on sugar cane, a reduction in nitrogen fertilizer rates from 50 kg to 30 kg per hectare proved beneficial.

Increased survival of *S. calamistis* larvae and accelerated larval development occur with increased nitrogen content of maize resulting from fertilizer treatment. It also was suggested that addition of fertilizer might stimulate additional annual generations of stem borers.

Although nitrogen fertilizer enhanced borer development, it also had a positive effect of increasing host plant tolerance to borer attack. Yield losses decreased linearly from 20% with no fertilizer, to 11% with 120 kg nitrogen added per hectare. It also has been reported that timing of nitrogen fertilizer application influenced the incidence of *C. ignefusalis* on millet. The suggestion has been made that by manipulating the timing and quantity of nitrogen fertilizer, a compromise between using low fertilizer levels to dampen stem borer infestation, and high fertilizer levels to stimulate better yields, might be achievable.

Intercropping and Habitat Management

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Small-scale farmers in Africa practice intercropping or mixed cropping to reduce risk of crop failure, attain higher yields, and improve soil fertility. Although no studies have shown that farmers grow specific intercrops to reduce insect pests, some of these practices also lead to suppression of cereal stem borer populations. Studies in Kenya have concentrated both on the practice of intercropping cowpea with maize and sorghum, and on the ways in which these systems could be adopted by small-scale farmers in the region. Most studies on intercropping have shown a reduction in the incidence of stem borers. Maize/cassava intercropping systems in Nigeria were found to reduce by half larval numbers of stem borer populations. Unfortunately, many of these intercropping studies did not seek to determine the underlying mechanisms behind the effect of intercropping on stem borer populations. Intercropping maize with cowpea was an effective way of reducing damage caused by *C. partellus*, because 30% of *C. partellus* oviposition was on cowpea.

Planting an outer encircling row of a highly preferred host to act as a trap plant is a useful diversionary tactic to control stem borers. Napier grass, *Pennisetum purpureum*, and Sudan grass, *Sorghum vulgare sudanense,* common fodder plants in Africa, are reported to provide natural control of stem borers by acting as trap plants. Although the stem borers oviposit heavily on the attractive Napier grass, only very few larvae are able to complete their life cycles. In on-farm trials in Kenya, planting Napier grass around maize fields has been shown to significantly increase crop yields by reducing the stem borer population in maize. Sudan grass provided natural control of stem borers by acting as a trap plant, and as a reservoir for its natural enemies.

A recent study from Kenya has reported the effectiveness of intercropping maize with a non-host grass, *Melinis minutiflora*. In field trials, *M. minutiflora* showed no colonization by stem borers, and when used as an intercrop with maize, significantly reduced stem borer infestation in the main crop. A significant increase in parasitism of stem borers by the larval parasitoid *Cotesia sesamiae* was also observed. Volatile agents produced by *M. minutiflora* repelled stem borers but attracted *C. sesamiae*. Female *C. sesamiae* were attracted to (E)-4,8-dimethyl-1,3,7-nonatriene, one of the volatile components released by intact molasses grass. While serving as an effective cover crop, *M. minutiflora* at the same time provides good fodder for livestock. The grass is now being tested in on-farm trials in Kenya to control stem borers on maize.

For the control of stem borers in resource-poor maize farming systems in eastern Africa, "push-pull" or stimulo-deterrent diversionary tactics have been developed. These strategies involve combined intercropping and trap crops. Stem borers are trapped on highly susceptible trap plants (pull) and are driven away from the maize crop by repellent intercrops (push). The plants that are used as trap or repellent plants in a push-pull strategy are Napier grass, Sudan grass, *M. minutiflora* and silverleaf desmodium, *Desmodium uncinatum*. Napier grass and Sudan grass are used as trap plants, whereas *M. minutiflora* and silverleaf desmodium repel ovipositing stem borers. All four plants are of economic importance to farmers in eastern Africa as livestock fodder.

Before making decisions on the use of intercrops and trap plants for stem borer control, it would be important to assess economic impact as well as the biological effects. The economic gain from the use of intercrops usually depends on the balance between a lowered cost of stem borers control and the increased cost of maintaining an intercropped field, along with any decrease in yield of the main crop from greater plant competition. Net profit can be increased if the intercrop favorably changes the balance between income and costs.

Host Plant Resistance

Host plant resistance as an approach to pest management in gramineous crops confers many advantages. Resistant crop varieties provide an inherent control that involves no environmental problems, and are generally compatible with other insect control methods. Major emphasis on the host plant resistance work in Africa has been on screening maize and sorghum crops against *Chilo partellus* and *Busseola fusca*. Attempts have been made to understand the nature of *C. partellus* and *B. fusca* resistance in maize and sorghum. A general association between plant phenology and resistance to stem borers has been established. A wide range of mechanisms are involved in *C. partellus* and *B. fusca* resistance in maize and sorghum, including non-preference for oviposition, reduced larval settling, reduced larval feeding and food utilization, and reduced larval survival and development. The cause of ovipositional antixenosis mechanism in maize against *C. partellus* was found to be a high number of trichomes on the lower leaf surface.

Information on the mode of inheritance and the number of genes involved in the resistance of plants to particular insect species, although not essential for breeding plants, has great practical significance for identifying donors for resistance, developing isogenic lines, and breeding broad-based resistant varieties. In maize and sorghum, resistance to *C. partellus*, measured in terms of leaf-feeding, deadhearts and stem-tunneling, is polygenic. Polygenic resistance is moderate, but more stable and longer lasting than monogenic or oligogenic resistance. In sorghum, an additive gene effect was important in the inheritance of *C. partellus* resistance.

Efforts are underway in Africa to identify sources of stem borer resistance in cereal crops, but high levels of resistance have not been found. Crop varieties resistant to one stem borer species are not necessarily resistant to others. Therefore, it is important that sources with multiple resistance to stem borers are selected for breeding for durable resistance. During the last two decades, several national and international programs have been attempting to incorporate resistance to *C. partellus* into a good agronomic background of maize and sorghum, and many genotypes are already in national yield trials. Resistant lines/hybrids with good general combining ability have been identified. Several hybrid sorghums bred in South Africa exhibited tolerance to stem borer damage, and therefore suffered low yield losses.

Introduction of Biological Control of *Chilo partellus* in Africa

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Because *C. partellus* is an exotic stem borer in Africa, there have been several attempts to introduce exotic parasitoids for its control. The first was in East Africa, where eight species of parasitoids, mostly from India, were released from 1968 to 1972 by the Commonwealth Institute of Biological Control. There were no reports of establishment. In South Africa, there were a series of introductions of 11 parasitoids from various locations from 1980 to 1993, but again, none established.

In 1993, a program was initiated in Kenya to introduce the gregarious larval endoparasitoid, *Cotesia flavipes*, from Pakistan for biological control of *C. partellus*. Releases were made in 1993 at three locations in the southern coastal area of Kenya, and the parasitoid was recovered during the season of release from *C. partellus* and two native stem borers, *C. orichalcociliellus* and *S. calamistis*. *Cotesia flavipes* was released at a fourth site in coastal Kenya during the non-cropping season of 1994 in an area where the vegetation was dominated by a wild grass, *Sorghum arundinaceum* (Desv.) Stapf. Recoveries in the wild habitat, and in a nearby maize field during the following cropping season, indicated that the parasitoid could sustain its population during the dry season in wild grasses and then colonize maize fields during cropping seasons.

Other than recoveries at the wild sorghum site, only one stem borer parasitized by *C. flavipes* was found in 1994, despite intensive sampling. In 1995 and 1996, a few recoveries were made, but parasitism was low. In 1997, the number of recoveries increased dramatically and parasitism at 30 sites averaged about 6%. Parasitism continued to increase during the next two years with average parasitism of about 13% at 67 sites in 1999.

Surveys in other maize growing areas of Kenya in the mid to late 1990s showed that *C. flavipes* was present in the Eastern Province and in the area bordering Lake Victoria in western Kenya. In the Eastern Province, which borders the Coast Province, *C. flavipes* was found in low densities in 1996 and then released at three sites in 1997. Parasitism during the season following the releases was about 14%. Parasitism in western Kenya did not increase to the levels observed in coastal Kenya or the Eastern Province, which may be due to the composition of the stem borer complex. In western Kenya, four stem borers are common: *C. partellus*, *S. calamistis*, *B. fusca* and *E. saccharina*. All of these are attractive and acceptable hosts for *C. flavipes*, but two of them, *B. fusca* and *E. saccharina*, are not suitable for its development. The presence of acceptable, but unsuitable, hosts in an area appears to act as a sink which depresses population growth of *C. flavipes*.

The impact of *C. flavipes* on stem borer populations in coastal Kenya was recently investigated. A host-parasitoid model was used to estimate the stem borer density with and without the parasitoid. A reduction of 1.1 to 1.6 stem borers/plant, equivalent to a 32–55% decrease in the stem borer density, was shown. As there is not yet any evidence that the *C. flavipes* density has reached an equilibrium, it may continue to increase and provide greater suppression of stem borers in the future.

In addition to the work in Kenya, *C. flavipes* was found in northwestern Tanzania in 1995. Based on surveys conducted prior to 1994, and on electrophoretic evidence, it was concluded that the most likely explanation was that *C. flavipes* moved into Tanzania from Kenya. Likewise, surveys in 1999 and 2000 revealed that *C. flavipes* had moved into Ethiopia.

Releases of *C. flavipes* have now been made in several other countries including Mozambique, Uganda, Somalia, Malawi, Zambia, Zanzibar and Zimbabwe. Establishment has been confirmed in Mozambique, Uganda, Malawi and Zanzibar. In Uganda, *C. flavipes* was found to be the most common larval parasitoid of stem borers one year after its release.

Biological Control of *Chilo saccharriphagus* on the Indian Ocean Islands and Africa

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Over 150 years ago, *C. sacchariphagus* was introduced from Java to the Indian Ocean islands of

Mauritius, Réunion and Madagascar in cane cuttings. The biology of this insect is similar to that of other sugarcane borers like *Eldana saccharina* in Africa or *Diatraea saccharalis* in the Americas. Damage is caused by the larvae, which penetrate into the stalk internodes where they feed until pupation. In terms of economic losses, damage results in a significant lowering of cane tonnage and, to a lesser extent, in a loss of sugar due to the inversion of saccharose, and to impurities in the juice. On a susceptible variety, the loss in cane weight is estimated to range from 10 to 30 tons per hectare, depending on the growing conditions. This pest has been increasing in some cane producing areas of the island due to the adoption of new varieties, and since 1994 it has been the subject of research to devise an integrated control program. Recent results from field experiments suggest new strategies for minimizing borer attack using predators, parasitoids and varietal resistance.

Biological Control Attempts: Lessons from the Past

In the Indian Ocean islands, attempts to control *C. sacchariphagus* with exotic parasitoids started in the 1940s. However, variable results were obtained. In Mauritius and Réunion, introduction and large scale releases of parasitoids, mainly originating from India, did not control *C. sacchariphagus*, despite the successful establishment of species like *Trichogramma chilonis* Ishii and *Cotesia flavipes* in sugar cane fields. In Réunion, several attempts at biological control in the 1970s by introducing and releasing tachinid flies also failed to control the pest.

Paradoxically, during the years of mass-releases, there were few ecological studies on *C. sacchariphagus* and its indigenous parasitoids and predators. Moreover, no accurate information was available concerning the parasitization rate of borer eggs by *Trichogramma* spp. and other egg parasitoids. However, in Réunion, Mauritius and Madagascar, natural parasitism of *C. sacchariphagus* eggs was generally high and ranged from 80 to 90%.

The Imoprtance of Predation by Ants

Predation of *C. sacchariphagus* eggs in Réunion was assessed on sugar cane fields in 1996–1997 by placing fresh eggs on the top leaves through the cane cycle. In two experiments conducted at different localities, 70–100% of the eggs were attacked by ants when sugar cane was six months old. The level of predation remained very high until the harvesting period (12 months). Trap catches and regular observations in the plots revealed that *Pheidole megacephala* F. (Hymenoptera: Formicidae) was the major predatory species.

However, predation by ants on eggs interfered with a major parasitoid, *Trichogramma* sp. Observations of parasitized eggs in clutches spared by the ants indicated that the ants destroyed the eggs whether they were parasitized or not. Despite this, natural control of the stem borer is a reality in sugar cane fields, and efforts should be focused on conserving natural enemies. This can be done by ceasing certain cultural practices such as burning at harvest, which is totally incompatible with the conservation of predatory insects.

Revised Biological Control with the Use of Trichogramma sp

A new biological control program using *Trichogramma* spp. is currently being implemented in Réunion Island. This program encompasses different steps, from field and lab research to technology transfer. It includes the choice of suitable species and the selection of strains to improve field performance (higher fecundity, survivorship and more efficient parasitism). One of the most important steps was to identify the *Trichogramma* strains and set up different studies on biology and population dynamics. Morphological and molecular characterization of numerous strains collected form different sites around the island led to the identification of *Trichogramma chilonis* Ishii. This species, previously named *T. australicum*, probably originated from Southeast Asia, the native home of *C. sacchariphagus*. All biotypes identified were evaluated for parasitism and the most suitable one will be mass-reared for inundative releases in the field. Further studies on population dynamics of *T. chilonis* are currently being conducted on a susceptible cane variety. The main objective of this study is to investigate the response of *T. chilonis* to different densities of *C. sacchariphagus* eggs. This information is essential to determine the ability of *T. chilonis* to control the borer in the field.

The technology for mass rearing of *Galleria* moths to produce high quality *Trichogramma* has been transferred to an organization in Réunion, which has many contacts with farmers. The method will be improved for eventual mass-releases. Nevertheless, small scale production of *Trichogramma* will allow the testing of different factors linked to the methods of release, quantity of *Trichogramma* per hectare, time of releases, packaging of the parasitoids, and indicators to assess efficacy of the releases. These practical studies will be conducted in partnership with farmers.

Predation by ants, as mentioned previously, also should be considered in the timing of *Trichogramma* releases. Therefore, to ensure the highest efficiency, these releases should be conducted during the period when predation is low and sporadic, which is also the egg laying period for *C. sacchariphagus*. After this period and until maturity of the cane, predation should assure the destruction of most of the borer eggs.

C. sacchapriphagus in Mozambique: a Threat to the South African Sugar Industry

In 1998, the presence of *C. sacchariphagus* in sugar cane in Mozambique was confirmed. Prior to that, its presence was suspected and was mentioned in various unpublished reports as early as the 1970s. Subsequent to its positive identification, a biological control program has been initiated with the collaboration of the sugar estate management. An ichneumonid pupal parasitoid, *Xanthopimpla stemmator*, which is a parasitoid of *C. sacchariphagus* in Sri Lanka, and which had been introduced and established in Mauritius and Réunion, was chosen as the first biocontrol candidate.

Methods to detect the presence of *C. sacchariphagus* in the South African sugar industry are already organized. During the last two years, a series of insect pheromones traps have been in operation in strategic locations along the border of South Africa with Mozambique. However, traps cannot detect the presence of borers in sugar cane stalks transported across the border. It is suspected that the first introduction of this pest into the Indian Ocean islands and Mozambique was made in this way. Presently, the risk of invasion of *C. sacchariphagus* is high for countries that have a common border with Mozambique (particularly Zimbabwe and Tanzania). Continued vigilance along the common borders will minimize the possibility of the importation of infested sugar cane stalks. Appropriate control measures can be applied immediately should an infestation in sugar cane farms be detected.

References

Goebel FR, Fernandez E, Bègue JM, Tibère R, Alauzet C (2000) Predation and varietal resistance as important components of integrated protection of sugarcane stemborer *Chilo sacchariphagus* (Bojer) (Lepidoptera: Pyralidae) in Réunion. In: Allsopp PG, Suasa-ard W (eds) Sugarcane pest management in the new millennium. International Society of Sugar Cane Technologists, Brisbane, Australia, pp 51–56

Kfir R, Overholt WA, Khan ZR, Polaszek A (2002) Biology and management of economically important lepidopteran cereal stem borers in Africa. Annu Rev Entomol 47:701–731

Polaszek A (1998) African cereal stem borers: economic importance, taxonomy, natural enemies and control. CABI, Wallingford, UK, 530 pp

Schulthess F, Cardwell KF, Gounou S (2002) The effect of endophytic *Fusarium verticillioides* on infestation of two maize varieties by lepidopterous stemborers and coleopteran grain feeders. Phytopathology 92:120–128

Sétamou M, Schulthess F, Poehling H-M, Borgemeister C (2000) Monitoring and modeling of field infestation and damage by the maize ear borer *Mussidia nigrivenella* Ragonot (Lepidoptera Pyralidae) in Benin, West Africa. J Econ Entomol 93:650–657

Williams JR, Metcalfe JR, Mungomery RW, Mathes R (1969) Pests of sugar cane. Elsevier Publishing Company, Amsterdam, The Netherlands

Graminivory

Eating or feeding on grasses (the plant family Graminae or Poaceae). Arthropods that feed on grasses are said to be graminivorous or graminivores. Grasses are sometimes said not to be particularly well defended biochemically against insect feeding, depending instead on silicification, lignification, trichomes, and a basal meristem for defense against herbivory. However, secondary plant compounds are also abundant in grasses.

References

Redak RA (1987) Forage quality: secondary chemistry of grasses. In: Capinera JL (ed) Integrated pest management on rangeland. A shortgrass prairie perspective. Westview Press, Boulder, CO, pp 38–55

Rittenhouse LR, Roath LR (1987) Forage quality: primary chemistry of grasses. In: Capinera JL (ed) Integrated pest management on rangeland. A shortgrass prairie perspective. Westview Press, Boulder, CO, pp 25–37

Granary Weevil, *Sitophilus granarius* (Linnaeus) (Coleoptera: Curculionidae)

This is an important pest of Stored grain.

► Stored Grain and Flour Insects

Granivory

Seed feeding. Such arthropods are said to be granivorous or granivores. This is distinct from graminivorous (graminivores), or grass feeding, though animals that feed on grass seeds can be said to be both granivorous and graminivorous.

► Food Habits of Insects
► Phytophagy
► Herbivory

Granular Formulation

A dry formulation of pesticides that is substantially larger and heavier than dust, and applied with a granule applicator, not a duster.

Granule

The individual particles that are used in a granular formulation of pesticide.

Granulocyte

A type of hemocyte that is important in encapsulation of foreign objects found in the hemolymph.

► Hemocytes of Insects: their Morphology and Function

Granulosis

A disease of certain insects caused by granulosis virus (granulovirus) and characterized by the presence of minute granular inclusions in infected cells.

► Granulovirus

Granulovirus

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There are an increasing number of problems associated with the use of chemical pesticides, including emergence of resistant insects, elimination of non-target insects, and environmental contamination. Thus, the need for alternative biological insecticides that are cost-effective and environmentally safe is greater than ever. As a result, interest in microbial insecticides is increasing. Microbiological pathogens include various species of bacteria, fungi, nematodes, and viruses. The best-known example of a microbiological insecticide, which is used in large scale against agriculture and forest pests, is the bacterium, *Bacillus thuringiensis* (commercially known as Bt).

Viruses comprise another important class of insect pathogens that are being considered as good alternative biological insecticides due to their specificity for insect hosts. At least eight families of insect viruses are known, but the viruses most commonly used as viral bioinsecticides are those from Baculoviridae family.

Baculoviruses are a group of viruses that are specific to arthropods. Unlike other insect viruses, no morphologically similar counterpart to baculoviruses has been detected in vertebrates. Baculoviruses are characterized by the presence of a large protein matrix or occlusion body which encase the viral particles. Baculoviruses are classified in two genera: the nucleopolyhedroviruses (NPVs), and the granuloviruses (GVs). Safety testing of non-target organisms including mammals, fish, and birds has shown baculoviruses to have a very limited host range and to be safe to non-target organisms. Of the insect viruses, only baculoviruses have been recommended for field use.

Although baculoviruses have been isolated from different orders of insects, they have been used mostly to control pest species from the orders Lepidoptera, Hymenoptera, and Coleoptera. Overall, the most successful examples of baculovirus usage can be found in forestry. For instance, in the U.S.A. and Canada, baculoviruses have been used successfully in large-scale against the Douglas fir tussock moth (*Orgyia pseudosugata*), pine sawfly (*Neodiprion sertifer*), red headed sawfly (*Neodiprion lecontei*) and gypsy moth (*Lymantria dispar*).

Granulovirus Infection (Granulosis)

Granulovirus (GV) infection, known as granulosis, was first detected by Paillot, in 1926, in the larvae of *Pieris brassicae* (the large white butterfly). At that time he called this disease pseudograsserie. Later he described a similar disease in *Agrotis segetum* (a cutworm). In 1947, Steinhaus rediscovered the disease in *Peridroma saucia* (variegated cutworm), and he called the disease granulosis because he observed some tiny granules in affected tissues when observed with light microscopy. In 1948, a similar disease in *Choristoneura muriana* (pine shoot roller) was described by Bergold. Bergold was the first to demonstrate the viral nature of granulosis with electron microscopy; he described the virus as rod-shaped particles.

Infection begins when larvae ingest the occlusion body. Several days after infection, larvae begin to display unusual characteristics such as sluggishness, loss of appetite, followed by color change from the light brown to pink or white. For example, *Choristoneura fumiferana* (spruce budworm) and *Pieris rapae* larvae become pink, and *Cydia pomonella* (codling moth) larvae become white in very late stages of infection. The organ of the insect that is principally affected is the fat body, but virus also replicates in other tissues such as the epidermis, hemocytes, tracheal matrix cells, and Malpighian tubules.

The high pathogenicity of GVs toward different insect pests of agricultural crops and forests make this group of viruses a very attractive candidate to be used as biological insecticides. Since the 1950s, different GVs have been used as a biological insecticide in different parts of the world. One of the first countries to use GVs against *Hadena sordida* and *Trichoplusia ni* was the former Soviet Union. In Canada, GVs are mostly used in forestry against spruce budworm (*C. fumiferana*), and fir budworm (*C. muriana*). In the U.S.A., GVs have been used against *Cydia pomonella* (codling moth) and *Plodia interpunctella* (Indian meal moth).

General Aspects of Granulovirus

GVs are rod-shaped enveloped virions that contain one molecule of circular (super coiled) double stranded DNA. Nucleocapsids, which consist of proteinaceous capsid and DNA-protein core, are relatively large, 200–450 nm long and 30–100 nm in diameter. Nucleocapsids are cylindrical structures in which subunits of capsid are assembled in rings stacked one on top of another. Each turn of the helix consist of 12 copies of the capsid protein. The two ends of the nucleocapsid are different in shape and have been described as "nipple and claw." One end (nipple end) has the appearance of stacked rings of decreasing diameter.

GVs produce two different phenotypes, termed budded virions and occlusion-derived virions. Distinct viral structures are visible in thin sections of infected tissue. These two phenotypes are produced at different times and locations in the infected larvae. Budded virions are produced in the late phase of the infection cycle, when nucleocapsids bud from the surface of infected cells. Occlusion-derived virions, on the other hand, are produced very late in infection; they become enveloped and subsequently occluded within an occlusion body within the infected cell. Enveloped nucleocapsids are individually encased in occlusion bodies. Occlusion body is a protein matrix, termed granulin, which protect the viral DNA against the UV radiation of sunlight. Each phenotype has different functional roles. Occlusion-derived virion is the phenotype that is released in the environment after the death of the infected insect, it has a great infectious potential toward other susceptible insects.

Molecular Biology of Granulovirus

Genome

Granuloviruses have large genomes (80–180 kbp) that have the potential to encode about 100 genes. On the contrary, other viruses with big genomes like poxvirus that carry an extensive array of enzyme which are essential for early gene transcription, granuloviruses (like other baculoviruses) carry no virion-associated proteins that are essential for virus early gene transcription on their genome. The genome of granuloviruses is composed almost entirely of unique DNA sequence, though several small repeated sequences known as homologous regions are known in the DNA. The homologous regions have roles as enhancers for early genes, and also as origin of DNA replication. The activation property of an early gene known as *ie*-1 is enhanced when the genes are linked to homologous region sequences.

Open reading frames (ORFs) are located on either strand of the DNA. Most ORFs are separated by 2–200 bps of DNA rich in A + T. There are also some overlapping ORFs in granulovirus genome, usually termination codon UAA overlaps with the primary polyadenylation signal AAUAAA. Some promoters are located within the neighboring ORFs.

Frequently, transcripts of one gene initiate within, into, or through neighboring ORFs. Beside partial clustering of genes which have assigned roles in early gene regulation (e.g., *ie*-1, *ie*-2, and pe-38), genes in the genome of granulovirus, like other baculoviruses, do not appear to be clustered. Genes encoding structural proteins are distributed throughout the genome with no obvious pattern to the location.

Structural Proteins

Granulin is the major protein in SDS-polyacrylamide gel electrophoresis (SDS-PAGE). Studies on alkaline solubilized granulin of different GVs show that matrix protein of GVs has a molecular weight equal to approximately 30 kDa. Analysis of the nucleotide and amino acid composition of granulin in different GVs show a high degree of similarity. Amino acid sequence analysis of granulin in different granuloviruses showed conserved amino acid residues, which is likely due to "evolutionary memory," which maintains the secondary structure of granulin in all GVs.

The presence of 12–20 proteins has been shown in enveloped nucleocapsids of different GVs by SDS-PAGE analysis. Molecular weight of these polypeptides ranges from 12 to 160 kDa.

Cycle of GV Infection in Susceptible Insects

The infection cycle of granulovirus has two distinct phases: primary and secondary cycle.

Primary Cycle of Infection

The primary phase of infection is initiated by ingestion of virus by larvae, followed by dissolution of granulin (matrix protein of occlusion body) in the midgut of the insect, and liberation of the enveloped nucleocapsids. Granulin dissolved due to the alkaline environment of the insect' s midgut. Occlusion-derived virion infectivity is boosted by a protein present in occlusion body, termed Enhancin, which is a proteolytic compound with structural and functional characteristics of metaloproteases. Enhancin seems to have a direct effect on degradation of the peritrophic membrane in insect midgut.

Enveloped nucleocapsids attach to the surface of microvilli of columnar cells, and nucleocapsids enter the cytoplasm of cells following fusion of the viral envelope with plasma membrane. Nucleocapsids move toward the nucleus of the cell by polymerizing the actin filaments and release their DNA into the nucleus.

Replication and transcription of viral DNA take place in the nucleus of infected cells, and progeny nucleocapsids are formed in the nucleus of columnar cells. Nucleocapsids acquire their envelope by budding through the modified plasma membrane. This modification is due to the transportation of virus-made proteins into the plasma membrane of the infected cells. The primary phase of infection terminates when these enveloped nucleocapsids, known as budded virion phenotype, are released from infected cells. Budded virions are potentially infectious for tissues within the hemocoel. The mechanism by which the budded virion traverses the basal lamina of the midgut epithelium is not completely known. Some researchers suggest this possibility that budded virions may directly traverse the basal lamina of the midgut epithelium during budding. There is also another possibility that budded virions may use the tracheal system as a conduit to cross the basal lamina of the midgut epithelium.

Secondary Cycle of Infection

The secondary phase of granulovirus infection is different from the primary phase in several ways: (i) budded virions enter these cells by a receptor-mediated endocytosis in contrast to the occlusion-derived virion, which enter by fusion, (ii) more cells are infected, (iii) the yield of progeny virus per cell is much higher, (iv) progeny nucleocapsid acquire envelope inside the cell (instead of budding through the plasma membrane), (v) enveloped nucleocapsids encased inside the proteinaceous matrix, and (vi) the occluded progeny (termed occlusion-derived virion phenotype)are released upon cell lysis.

Viral entry by endocytosis is a process that usually consist of six steps: (i) virion attachment to a receptor on the surface of host cell, (ii) invagination of host plasma membrane in the viral attachment site, (iii) formation of a vesicle containing the enveloped virion (endosom), (iv) acidification of the endosom, (v) fusion of the viral envelope and endosomal membrane, and (vi) release of the nucleocapsid into the cytoplasm.

Following the release of nucleocapsid into the cytoplasm, they are transported toward the nucleus. Studies that concentrate on the mechanism of the transportation in NPVs showed that actin cables might play a major role in this movement. These studies also suggest that a structural protein in the nucleocapsid triggers the polymerization of actin cables. After nucleocapsid reach the nucleus, viral DNA is directly released into the nucleus through the nuclear pores. It seems that a phosporylated capsid protein (P78/83), which is localized at one end of the nucleocapsid, plays a role in the interaction of nucleocapsid and nuclear pores. The mechanism of uncoating of DNA in another baculovirus genus, NPVs, is different than GVs. Nucleocapsids of NPVs enter host cell nuclei and uncoat within the nucleus.

Upon uncoating of granulovirus DNA in the nucleus, early genes are transcribed by a host RNA polymerase. Early viral products are mostly regulatory proteins that activate transcription from other early genes. The transition from early to late phase is characterized by inhibition of host transcription and replication of viral DNA. Replication of viral DNA seems to be a crucial step prior to late phase transcription. Late genes are transcribed by a viral RNA polymerase. At least 18 baculovirus genes have been shown to control the late gene expression; these genes are identified as late expression factors genes (*lef* genes). All structural proteins are expressed in late and very late gene expression.

Nucleocapsid assembly begins after synthesis of late proteins. Electron microscopy studies demonstrate that initially a virogenic stroma appears within nuclei, and empty capsids assemble within this stroma. These capsids then fill with DNA. A basic DNA binding protein in the capsid (P7/12) may play a role in packaging of viral DNA. This protein has similarity to cellular protamines, the basic proteins that substitute for histones in the packaging of DNA within the sperm of many species. Both proteins (i) are rich in arginine residues which lead to a high basic charge, (ii) have the ability bind zinc (Zn^{+2}), and (iii) are a substrate for kinase activity.

After the process of packaging viral DNA, nucleocapsids are ready for envelopment followed by occlusion. The mechanism for envelopment is not known, but some researchers suggest that budding through the nuclear membrane fragments is a possible way for envelopment. The very late phase of infection starts by hyperexpression of very late genes such as granulin (the occlusion body protein). Granulin crystallizes around the enveloped nucleocapsids and encases the virions. Following the occlusion process, an envelope-like structure (calyx) covers the occlusion body.

At the final stage of granulovirus infection, cells become packed with occluded virions that cause cell lysis and liberation of virus into the hemocoelum followed by death of the insect.

Use of Baculovirus against Lepidoptera

Baculoviruses have been used to control different lepidopterous pests in agriculture and forestry. Historically, the first attempt to use viruses as a bioinsecticide date back to 1892. In this year, a baculovirus was used to control *Lymantria monacha* population in pine forests in Germany. The United States was the first country in North America to use a baculovirus against *Lymantria dispar*.

There is no record of large scale use of baculoviruses in agriculture in United States before the late 1940s. In this year, aerial application of NPV against *C. eurytheme* (alfalfa caterpillar) were attempted in California. The use of *Helicoverpa zea* NPV in the 1970s showed promising results in soybean and maize agriculture. Between 1975 and 1980, over one million hectares were treated by HzNPV. Introduction of synthetic pyrethroids in the early 1980s decrease the use of HzNPV, but the emergence of a worldwide resistance against pyrethroids during the 1990s promoted the use of the HzNPV. In 1996, HzNPVwere again used in large scale in the cotton industry in the United States. Currently, China is one of the countries that use HzNPV and *H. armigera* NPV in cotton industry. Annually, 100,000 ha of cotton fields in China is treated by HaNPV. Thailand and Vietnam are two other countries, among others, that use HaNPV on a large scale.

One of the best examples of using baculovirus in fruit crops is the use of a granulovirus against *Cydia pomonella* (codling moth: a pest of apples, pears and walnuts). *Cydia pomonella* granulovirus (CpGV) demonstrates a high pathogenicity against the larva and kills the insect very quickly. Field tests with CpGV in North America demonstrated that CpGV is a highly virulent and selective control agent against codling moth. CpGV is currently in use in different European countries. France, Switzerland, Germany, and Russia are the major consumers.

Records of using baculoviruses in forestry show that the following insects were the most important Lepidopera that were subjected to applications of baculoviruses: *C. fumiferana* (spruce budworm), *C. occidentalis* (western spruce budworm), *C. pinus* (jackpine budworm), *L. dispar* (gypsy moth) and *O. pseudotsugata* (Douglas-fir tussock moth). A NPV for *O. pseudotsugata* was registered and used in United States in 1976. This virus has been used during the last three decades in different parts of the United States and Canada. *Lymantria dispar* NPV is another baculovirus that has been used widely since its registration in 1978.

The first baculovirus used against spruce budworm was CfMNPV. The most important problem related to CfMNPV is its low pathogenicity. The other baculovirus that has a great potential to be used as a microbiological insecticide against spruce budworm is *C. fumiferana* granulovirus (ChfuGV).

A Case Study: Use of *Choristoneura fumiferana* Granulovirus (ChfuGV) in Canada

In eastern North America, spruce budworm is considered the most destructive insect of coniferous trees. The spruce budworm is a huge economic threat to vast forest areas (60 million ha) in Canada and eastern United States. The Maritime Provinces (New Brunswick, Nova Scotia, Newfoundland), Quebec, Ontario, and the Great Lake states are the areas that are affected by spruce budworm outbreaks most extensively. Spruce budworm larvae feed on a number of conifers, but balsam fir (*Abies balsamea* [L.] Mill.), and white spruce (*Picea glauca* [Moench] Voss) are the major hosts in eastern North America. Species occasionally attacked include black spruce (*Picea mariana* [Mill.] B.S.P.), red spruce (*Picea rubens* Sarg.), eastern hemlock (*Tsuga canadensis* [L.] Carr.), tamarack (*Larixlaricina* [Du Roi] K. Koch), and white pine (*Pinus strobus* L.).

In Quebec, Canada the outbreak of *C. fumiferana* usually affects huge forest areas. For example, the infested area in 1999 was estimated more than 23,000 hectares. This figure was twice as large as the infested area in 1998. Defoliation, inhibition of seed production, cone mortality, root mortality and tree mortality are the most important impacts of spruce budworm on trees. Defoliation caused by spruce budworm decreases the growth rates of trees; this decline can last several years. When outbreaks occur, the affected trees usually die after three to four years of heavy defoliation, and most of the trees die between six and ten years after the first attack. Even when the spruce budworm population returns to its endemic level, the damaged trees continue to die.

Chemical insecticides were the most common method of protecting spruce-fir forests from spruce budworm from 1927 up to the 1970s. DDT and Phosphophamidon were used mostly during the period from 1944 to 1970. In the 1970s and 1980s organophosphates and carbamates replaced DDT. Most of these compounds are toxic to humans and other warm-blooded animals. The concern about finding an alternative for chemicals started during the 1960s and among the candidates were biological insecticides. Also, as insects continue to gain resistance to chemical pesticides, industrial interest in commercial development of biological pesticides increases.

Natural predators, parasites, competitors and pathogenic microorganisms like fungi, bacteria and viruses have been used as biological agents. In eastern Canada *Bacillus thuringiensis* var. *kurstaki* (Btk) is used in insect control programs against spruce budworm. No major resistance against Btk in natural population of spruce budworm has been reported. However, laboratory results demonstrated that several insect species are able to develop resistance against the Btk toxin. The risk of appearance of resistance against Btk obligates the researchers to quest for new alternatives.

ChfuGV has been isolated from infected spruce budworm in several part of eastern Canada. This virus is considered a very attractive and powerful candidate to be used instead of, or along with, Btk in the case of the emergence of resistant spruce budworm larvae.

Laboratory bioassays with ChfuGV demonstrated its high pathogenicity for spruce budworm population ($LD_{50} = 5.72 \times 10^5$ viruses/larvae). The development and implementation of ChfuGV as a microbial insecticide were carried out during a pilot project on 100 ha of forests in Quebec, Canada. The results of these field experiments demonstrated that two weeks after treatment with ChfuGV a considerable reduction (40%) of defoliation was observed in treated areas as compared to control areas. Also, the number of *C. fumiferana* larvae was reduced by over 35% in treated areas. One of the most interesting results, from an economical perspective, is that when ChfuGV was used in a lower rate volume applied per ha, the same level of protection was observed.

Production of Granulovirus-based Insecticides

Currently, most granuloviruses are produced in vivo. The reason is due either to the absence of cell lines for some granuloviruses, or low yield of virus production for the others. One of the most important drawbacks concerning the in vitro production is that the viruses often lose infectivity after several passages through cell culture. The most important aspect of the virus production process is: (i) choice of the host. (ii) rearing conditions. (iii) virus purification. (iv) formulation.

Usually, a natural virus host is the best choice in virus production, but in the cases that the natural host is not suitable for laboratory rearing, and alternative hosts must be considered. The following cases are examples of unsuitable hosts: (i) when the natural host has a special dietary requirement, or (ii) when long obligatory diapause is required.

Temperature and humidity are the most important aspects in insect rearing. The other key factor for in vivo virus production is the number of larvae per each diet container and the size of container. The use of large containers is not recommended for species with a cannibalistic nature.

Formulation of granulovirus-based insecticides is a very important part in production. For large-scale applications, different aspects such as storage stability and UV protection must be considered in order to have a stable and high quality product. The formulation also must provide good residual activity in field. The formulation must not contain any additive with negative effects on virus activity.

Standardization and Quantification of Granulovirus-based Insecticides

One of the most important requirements for the production and use of GVs is the availability of bioassays. With bioassays, GV producers can determine the potency and virulence of an industrial product or preparation. On the other hand, bioassays can be also used: (i) to determine the biological activity of GVs for different insect species, (ii) to determine the relative biological activity of several viruses against one or more insect hosts.

Bioassays ensure the activity of the product prior to field use. In each bioassay there are some facts that should be respected to ensure the quality of the bioassay: (i) the purity of the virus preparation should be established by electron microscopy or other analytical procedures, (ii) presence of contaminating micro organisms such as bacteria and mycets should be checked, (iii) the assay must be reproducible for the same strain of insect species under similar conditions. Different methods of bioassays, such as bioassays by injection, bioassay by contaminated leaf disks, and finally bioassays by contaminated artificial diet have been suggested by different workers.

Injection methods have been used for establishment of activity of non-occluded virus obtained from alkaline-dissolved granules (granule: a complete granuloviral particle contain nucleocapsid, envelope and occlusion body). This method is very tedious and time consuming, but the primary advantages of this type of assay are (i) the amount of inoculums per insect is known, and (ii) the time of the beginning of infection is known.

Another time consuming method of bioassay is using leaf disks contaminated by with known quantities of GV preparation. Bioassays using contaminated artificial diets are the most commonly used assays for many insect viruses including GVs. In this method, known quantities of GVs are incorporated into, or layered on, the surface of artificial diets, which allows the evaluation of the LC_{50}. There are two very important advantages related to this method: (i) early stages of insect larvae, which are generally the most susceptible to viral infection, can be used in large numbers, (ii) insect handling is minimized since the stay in the same container throughout the bioassay. The disadvantage of this method is that the dose of the virus ingested by each insect is not known. There are always problems that could arise in different types of bioassays, but these problems can be avoided if certain precautions are taken.

Methods of Application of Granuloviruss-based Insecticides

An effective application should distribute virus to the insect' s feeding sites in a way that the probability of acquiring a lethal dose of virus is maximized. Granuloviruses, like most other baculoviruses, are applied by spraying the viral product to the target site. Ground application is mostly used for agricultural crops, but aerial application is the common method in forestry. There also are other application techniques that have been demonstrated, such as release of infected insects, though these have some limitations.

The Future of Granulovirus

Baculoviruses and among them granulovirus, can be considered to be major elements in biological control programs in the next 10 years. On the other hand, considering the fact that a great deal of effort has been directed toward the development of recombinant baculoviruses, it also is probable that recombinant viral insecticides will be used on a large scale against insects pests of forests and crops in near future. The most important issue concerning the use of genetically modified baculoviruses is the safety issue. Therefore, to be safe, it is important to prepare comprehensive risk assessment protocols for genetically modified baculoviruses.

References

Tanada Y, Hess RT (1991) Baculoviridae, granulosis viruses. In: Adams JR, Bonami JR (eds) Atlas of invertebrate viruses. CRC Press, Inc., Boca Raton, FL, pp 227–257

Summers MD (1977) Baculoviruses. In: Maramorosch K (ed) The atlas of insect and plant viruses. Academic Press, New York, NY, pp 3–28

Bonning BC, Hammock BD (1996) Development of recombinant baculoviruses for insect control. Annu Rev Entomol 41:191–210

Cory JS, Hails RS (1997) The ecology and biosafety of baculoviruses. Curr Opin Biotechnol 8:323–327

Miller LK (1996) Insect viruses. In: Fields BN (eds) Fields virology, vol 1, 3rd edn. Lippincott-Raven Publishers New York, NY, pp 533–585

Grape Berry Moth, *Endopiza viteana* Clemens (Lepidoptera: Tortricidae)

Endopiza viteana is an important grape pest.

► Small Fruit Pests and their Management

Grape Leafhopper, *Erythroneura* sp. (Hemiptera: Cicadellidae)

Several species of *Erythroneura* are pests of grapes.
► Small Fruit Pests and their Management

Grape Phylloxera, *Daktulosphaira vitifoliae* (Fitch) (Hemiptera: Aphidoidea: Phylloxeridae)

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Grape phylloxera is a primitive aphid that feeds and develops on grapevines (*Vitis* species). It is notorious for the damage it caused to viticulture first in France, then globally as it was introduced and spread into vineyards in nearly every grape-growing region of the world in the middle to latter part of the nineteenth century. Its native range is North America east of the Rocky Mountains, the southwestern USA, and well into Mexico and Central America to as far south as Venezuela. Grape phylloxera has had a checkered nomenclatural history, and the genus names *Pemphigus*, *Rhizaphis*, *Peritymbia*, *Viteus*, and *Daktulosphaira* as well as *Phylloxera* have been applied to it. For many years, *Phylloxera* was the most commonly applied name so the common name and Latin genus name were one and the same. This name was subsiding from use after 1952, however, and Russell cleared up the nomenclatural mess more than thirty years ago. However, there is no phylogenetic hypothesis for the Phylloxeridae so nothing is known about the relationship of *D. vitifoliae* to the approximately 41 described species of *Phylloxera* and it may still turn out, once such a hypothesis is in hand, that erecting a new genus for grape phylloxera was unjustified. There is an unfortunate prevalence in both entomological and viticultural circles to use the name phylloxera as the common name. Because a large number of other species in the family have this as their Latin name, it is desirable to specify "grape" phylloxera when discussing this insect.

Life Cycle and Biology

Grape phylloxera is a gall forming insect (as are the majority of species in the Phylloxeridae) causing galls on leaves and young roots on native vines and on hardened roots of susceptible cultivars. It has been stated that grape phylloxera may form galls on vine tendrils, but this is not true under natural conditions. Its host range appears to be restricted to about six to eight (depending on taxonomic concepts) of the some 20 or so *Vitis* species in the Americas and a number of cultivars, most notably the wine grape *V. vinifera* L. The distribution of grape phylloxera in Mexico and Central America is uncertain at this time. On leaves, pouch galls are formed that completely enclose the gall-former and her eggs. Galls on young roots (typically called nodosities) have a characteristic hook shape as cells distal to the insect feeding site become hypertrophied. The gall-former may be partially hidden in the elbow of the hook, but is otherwise exposed. Galls on hardened roots (tuberosities) appear as bumps on the surface of the root, with the gall-former and her eggs exposed on the surface. There is currently no evidence to suggest that the mechanism of gall induction differs on the three different plant organs or tissue types attacked; the different morphology is due to the different substrates galled (i.e., a pouch gall cannot form on a cylindrical and hardened root).

The life cycle differs in the native range and under most vineyard conditions and these will be discussed separately:

Native Range

As with the majority of Aphidoidea, grape phylloxera is a cyclic parthenogen in its native range. That is, one to multiple generations pass by apomictic parthenogenesis followed by a single generation of sexual reproduction each year. Sexually produced eggs are cold-resistant and are the overwintering stage. Individuals hatching in the spring from these zygotic eggs are called fundatrices. As first instar crawlers, fundatrices initiate galls on newly forming leaves in which they will mature in 2–3 weeks, laying upwards of 300 eggs as adults. Galls can only form on the newly expanding leaves. Fundatrices and all subsequent gall mothers (gallicolae) generally do not leave their gall after gall initiation. As eggs hatch, the crawlers leave the galls and move up the shoots to newly forming leaves where they in turn make their galls. A variable number of generations may pass this way. New leaf growth tends to slow or cease as summer progresses, meaning there is no longer any leaf resource for grape phylloxera. In the southwestern USA, and perhaps Mexico and Central America, it appears that this is when sexual forms (sexuales) are induced and overwintering eggs produced, ending the life cycle. There is evidence that gallicolae will sometimes secondarily occupy already-formed galls. There are no winged forms (alatae). In eastern North America the life cycle is prolonged by crawlers moving to the roots where they (called radicicolae) form galls on new, unhardened rootlets. Analogous to host alternation in aphids, it is here that alatae are produced that ascend into the canopy to lay a small number of male and female eggs. Induction of alatae may be influenced by density dependence, deterioration of the resource, or temperature. The neotenic sexual morphs have no mouthparts and live only a few days. Following mating these females lay a single zygotic egg each. It is often said that the overwintering eggs are laid in crevices in the bark on the trunks of vines but there have been too few observations to convincingly say how these eggs are distributed.

Vineyards

Vineyards in the eastern part of North America appear to be attacked by the local populations of grape phylloxera, and the life cycle on these cultivated vines does not differ. Elsewhere, except in cases where rootstocks are allowed to sucker or grow from cut down vines, the life cycle has been modified by elimination of the leaf galling phase, and with it production of sexual forms. Overwintering occurs as first or second instars. There is now good evidence that most populations of grape phylloxera, in vineyards of Australia and California at least, reproduce only asexually. Alate individuals are common, however, and have been observed at various times of the year. Apparently they are either infertile, their eggs are inviable, or sexuales do not survive to adulthood. Both nodosities and tuberosities are formed, with some cultivars resistant to tuberosity formation but susceptible to nodosity formation.

Dispersal of grape phylloxera occurs by flight of alatae and by blowing of crawlers by wind, and may also occur by windblown or water-carried galled leaves that harbor eggs or live individuals. In vineyards, all stages could be moved by agricultural equipment and activities.

Damage and Management

There are no data directly relevant to how damaging grape phylloxera is to wild grapevines and what effect on fitness, if any, is incurred. It has commonly been assumed that these vines are tolerant, but this is not likely to be strictly true because extensive galling must divert resources away from seed production. More study of this plant-insect interaction on wild grapevines is needed and would aid in understanding the evolution of resistance in grapevines.

In vineyards, damage is most severe when tuberosities are formed, vines being able to withstand the damage from nodosity formation. Tuberosities tend to occlude the vascular system, and a heavy infestation high up in the root system will effectively remove a substantial proportion of the translocation to and from the root system. This effect is exacerbated significantly by entrance of fungal pathogens through the cracked surface of the galled portion of the roots, resulting in necrosis and loss of root area. Ultimately, attacked vines die.

Management tactics have varied over the years and have included spraying of copper bisulphide in the early days to more modern insecticides (especially against leaf galling forms), and even flooding vineyards. The cryptic and protected habitat of root galling individuals makes use of conventional insecticides problematic. Systemic insecticides have found some use, but have not been widely applied. The use of natural enemies has not been thoroughly explored. Because fungal pathogens play an important role in damage, efforts are underway to control these. Finally, grape phylloxera has been effectively excluded from some wine regions in Australia by enforcing strict quarantine measures.

The only effective and durable management tactic has been the development and use of host plant resistance. Resistant cultivars have been developed directly from vine collections from the native range or, more often, from breeding programs, often leading to complex hybrids. The dominant *Vitis* species that have been used in these breeding programs have been *V. riparia*, *V. rupestris*, and *V. berlandieri*. Once developed, these cultivars are used as rootstocks for scions of the wine grape, *V. vinifera* L. The mechanisms of resistance are not well understood but there is evidence for antixenosis (insect avoidance), antibiosis (death or poor development of the insect) as well as tolerance (plant can suffer large numbers of herbivores without succumbing). Phenolic compounds may play a role in inhibiting development, and a hardened periderm beneath the feeding site has been observed, which would inhibit gall formation and isolate the insect from its nourishment.

Host plant resistance has been an effective strategy for managing grape phylloxera since it was introduced in the late 1800s, with only a few examples of failure. A notable example of a failure of what was previously considered to be a resistant rootstock is that of the rootstock AXR#1 in California in the 1980s. This rootstock was widely planted in California vineyards in the 1960s and 1970s but began declining under grape phylloxera attack in the 1980s, leading to large scale replanting to other rootstocks and massive economic outlays. It is likely, however, that this rootstock was never sufficiently resistant to grape phylloxera under California conditions, and the failure of resistance in this case may be more a failure of implementation than a failure of resistance.

References

Corrie AM, Crozier RH, Van Heeswijck R, Hoffmann AA (2002) Clonal reproduction and population genetic structure of grape phylloxera, *Daktulosphaira vitifoliae* in Australia. Heredity 88:203–211

Downie DA (2002) Locating the sources of an invasive pest using a mtDNA gene genealogy. Mol Ecol 11:2013–2026

Downie DA, Granett J, Fisher JR (2000) Distribution and abundance of leaf galling grape phylloxera and *Vitis* species in the central and eastern United States. Environ Entomol 29:979–986

Granett J, Walker MA, Kocsis L, Omer AD (2001) Biology and management of grape phylloxera. Annu Rev Entomol 46:387–412

Moore MO (1991) Classification and systematics of eastern North American *Vitis* north of Mexico. Sida 14:339–367

Lin H, Walker MA, Hu R, Granett J (2006) New simple sequence repeat loci for the study of grape phylloxera (*Daktulosphaira vitifoliae*) genetics and host adaptation. Am J Enol Vitic 57:33–40

Omer AD, Granett J, De Benedictis JA, Walker MA (1995) Effects of fungal root infections on the vigor of grapevines infested by root-feeding grape phylloxera. Vitis 34:165–170

Russell L (1974) *Daktulosphaira vitifoliae*, the correct name for the grape phylloxeran (Hemiptera: Homoptera: Phylloxeridae). J Wash Acad Sci 64:303–308

Grape Root Borer, *Vitacea polistiformes* (Harris) (Lepidoptera: Sesiidae)

Vitacea polistiformes is one of the most important grape pests in eastern North America.

► Small Fruit Pests and their Management

Grapevine Leafhopper Complex (Hemiptera: Cicadellidae) in Cyprus

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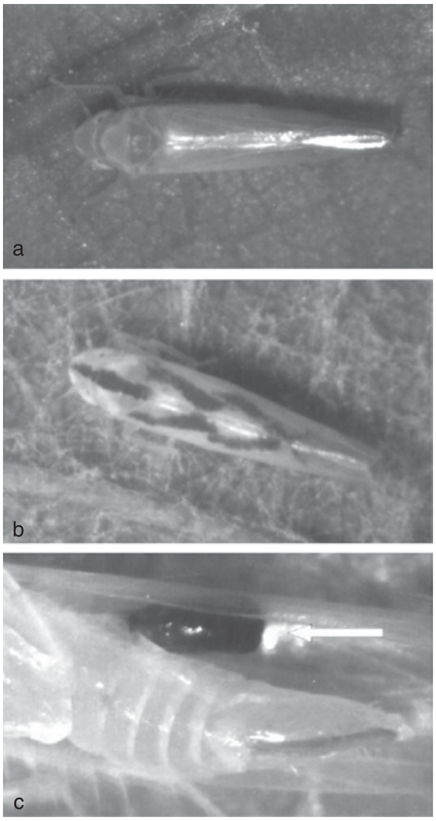
Various species of leafhoppers attack grapevines throughout the world. In Cyprus, the grapevine leafhopper complex consists of three species that have been identified by C.A.B. International Institute of Entomology (London) as *Zygina rhamni* (Ferrari), *Jacobiasca lybica* (Bergevin & Zanon), and *Asymmetrasca decedens* (Paoli). Assessment of population density through D-vac samples and insect counts directly on the plants showed an overall prevalence of *Zygina* over the other two. *Zygina* and *Jacobiasca* prevailed in areas with drier microclimatic conditions (Avdhimou and Pakhna) where the overall relevant populations were 52% and 45%, respectively. At Phassouri, though, a much less drier area, 45% of the leafhopper population was *Asymmetrasca*. This pest prevailed from April to early August and then its populations dropped significantly as it moved to other host-plants. Minor differences have so far been found in the within-plant distribution of the two principal species. At low population levels, these cicadellids had the tendency to live on different leaves, but at higher populations they could also be found on a same leaf, almost exclusively on the lower leaf surface. More insects were found on the basal than on the apical half of the vines.

The adult females lay their eggs singly in the epidermal tissue of the leaves and appear like tiny bean-shaped blisters. The young leafhoppers that emerge (nymphs), and the adults, are found almost exclusively on the lower leaf surface. They feed by sucking out the sap from the leaf cells or veins causing discoloration, deformation and in cases of heavy infestation, drying and shedding of leaves. Although *Zygina* is more widespread, it is not so harmful to the plants because it sucks the sap from the leaf cells, causing only leaf discoloration. The other two leafhopper species are more harmful because they suck the sap from the leaf veins, causing leaf deformation and drying. Yellow sticky trap catches showed increased populations of *Zygina* only from the end of July to the end of November, while those of *Jacobiasca* followed the same trend with about a three-week delay. Considering this population behavior, and the insect count on the grapevine leaves that were much lower than those reported as economically significant elsewhere, the pest status of the leafhopper complex was questionable.

Adults of *Z. rhamni* overwinter on *Rubus* sp. and *Sarcopoterium spinosum* (L.) Spach. They present a reddish pigmentation on their head and front wings, which in grapevines with poor growth starts appearing gradually from mid-August onwards, while in those with rich and tender growth, 15 days later. This gradual change of adult pigmentation is completed generally by mid-November. Adult migration to the winter quarters may start as early as September with a gradual infestation of *Rubus*, which is an evergreen bush. *Sarcopoterium* is available for infestation from around mid-November. This cicadellid develops (Fig. 31) one generation on these plants in early spring, and then it moves to grapevines where it stays for as long as there are green leaves, developing a maximum of 4 more generations.

Jacobiasca lybica overwinters as adult on *Rubus*, and then it develops only on grapevines, completing a maximum of six generations per year. *Asymmetrasca decedens* overwinters on citrus and on several weeds without interrupting its development, although it slows down because of the lower temperatures. In spring it moves to several vegetables and to grapevines where it prevails until the end of July. It then develops on various vegetables until winter, completing a maximum of eight generations per year.

Aphelopus orphanidesi Olmi (Hymenoptera Dryinidae), a new species, was the only parasite of *Z. rhamni* found so far in Cyprus. Adult females oviposit in the body of the leafhopper nymphs



Grapevine Leafhopper Complex (Hemiptera: Cicadellidae) in Cyprus, Figure 31 ***Zygina rhamni*: (a) adult of summer generations, (b) adult of overwintering generation, (c) adult female parasitized by *Aphelopus orphanidesi*.**

only and larval development extends in the adult stage of the host. The older nymphal stages seem to be preferred. Adult leafhoppers exposed to parasitoid females have never been attacked. The parasitoid female grasps the cicadellid nymph with her mandibles, holds it in position with her legs, and oviposits in its body. Parasitized leafhoppers, noticed by the unaided eye only at the adult stage, bear a sac on either side of the fore parts of the cicadellid gaster in a dorso-lateral position under the wings that contains the parasitoid larva. No leafhopper nymphs have been found to carry any larval sac of the parasitoid. On the overwintering leafhoppers, the sac darkens gradually as the parasitoid larva grows, and becomes shining black. It then becomes white after the larva abandons it. On adults reared in the laboratory at 25°C and in the field during the summer, the sac remains white throughout the entire larval development. Upon completion of its development, the parasitic larva leaves its moribund host, and drops to the soil where it becomes pupa and then adult.

The parasitoid completes five generations in one year. Emergence of adult parasitoids from the overwintering generation occurs in March and coincides with the appearance of first generation host nymphs, which are available for parasitization. Adults of the following parasitoid generations appear in May, July, August, and September. Parasitization rates are relatively high (75%) only on the overwintering leafhopper generation. In this generation, oviposition starts from September, but parasitized leafhoppers are noticed by the unaided eye from January onwards.

References

Jensen FL, Flaherty DL (1982) Grape leafhopper. In: Grape pest management. Division of Agricultural Sciences, Publication No. 4105. University of California, Davis, CA, pp 98–110

Olmi M, Orphanides GM (1994) A new species of the genus *Aphelopus* from Cyprus (Hymenoptera Dryinidae). Bolletino del Museo Regionale di Scienze Naturali di Torino 12:407–412

Orphanides G (1995) Bioecology and biological control of the leafhopper complex on grapevines. In review for 1994, Agricultural Research Institute, Ministry of Agriculture. Natural Resources and the Environment, Nicosia, Cyprus, pp 33

Orphanides G (1996) Biological control of the grapevine leafhopper, *Zygina rhamni* (Ferrari). In review for 1995, Agricultural Research Institute, Natural Resources and the Environment, Nicosia, Cyprus, pp 37

Grass

A plant with narrow leaves containing parallel veins. A monocotyledonous plant. A common name for plants in the family Graminae (contrast with broadleaf plant).

Grass Flies

Members of the family Chloropidae (order Diptera).

► Flies

Grasshopper and Locust Pests in Africa

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Africa has an exceedingly rich fauna of Orthoptera, including several families and well over 1,000 species, that could be considered to be grasshoppers or locusts. In Africa (also in Asia, Australia, and South and Central America), some grasshoppers are called "locusts." This term is applied to species of grasshoppers that display phase polymorphism. Phase polymorphism is largely a behavioral change between different states: gregarious and solitary forms, with intermediate forms called "transiens." During the gregarious phase, which is induced by high densities, locusts tend to disperse long distances in groups (during the nymphal stage the groups are called bands, during the adult stage they are called swarms). These same species are not very dispersive, nor gregarious, during the solitary phase. Physical changes in appearance may also occur during the change in phase, and of course physiological changes underlie the behavioral and morphological shifts. Transition between the solitary and gregarious phase takes more than one generation. In contrast, grasshoppers tend not to disperse long distances, tend not to aggregate during dispersal, and their appearance remains about the same regardless of density conditions. Thus, "grasshoppers" do not display phase change. Africa suffers from both grasshopper and locust infestations, but is best known for locust problems. The Arabic phrase for locusts translates to "teeth of the wind," providing some indication of the severity of the problem. As is the case elsewhere in the world, most of the orthopteran pests are in the family Acrididae, but other families of the order Orthoptera, particularly Pyrgomorphidae, are present as pests.

Locusts and grasshoppers sometimes, but not always, conform to the "typical" phase pattern suggested by the common name of these insects. As expected, when comparing the gregarious and solitary phases of desert locust, *Schistocerca gregaria* (Forskål), and migratory locust, *Locusta migratoria migratorioides* (Reiche & Fairmaire), the different phases can be quite distinctive. The behavior, coloration and size differ markedly between the gregarious and solitary phases. A common measure of the gregarious phase is the ratio of wing length to the width of the head; the gregarious phase has relatively longer wings. However, in some other species such as the Moroccan locust, *Dociastaurus maroccanus* (Thunberg), there is little or no change in color, though the relative size of body parts does change. The Senegalese grasshopper, despite not being called a locust, displays some morphological differences between the swarming and non-swarming populations, including longer wings. Thus, it is a good idea not to dwell on the common name of orthopterans, but to look critically at the biology of species individually. Other species are more typically grasshopper-like. Africa has a few spectacular species of "locusts" that command most of the attention and notoriety (as is largely the case in Australia), but some regions also suffer from a large assemblage of grasshoppers (as is largely the case in North America). Some of the more important species are shown in Table 7 and Fig. 32.

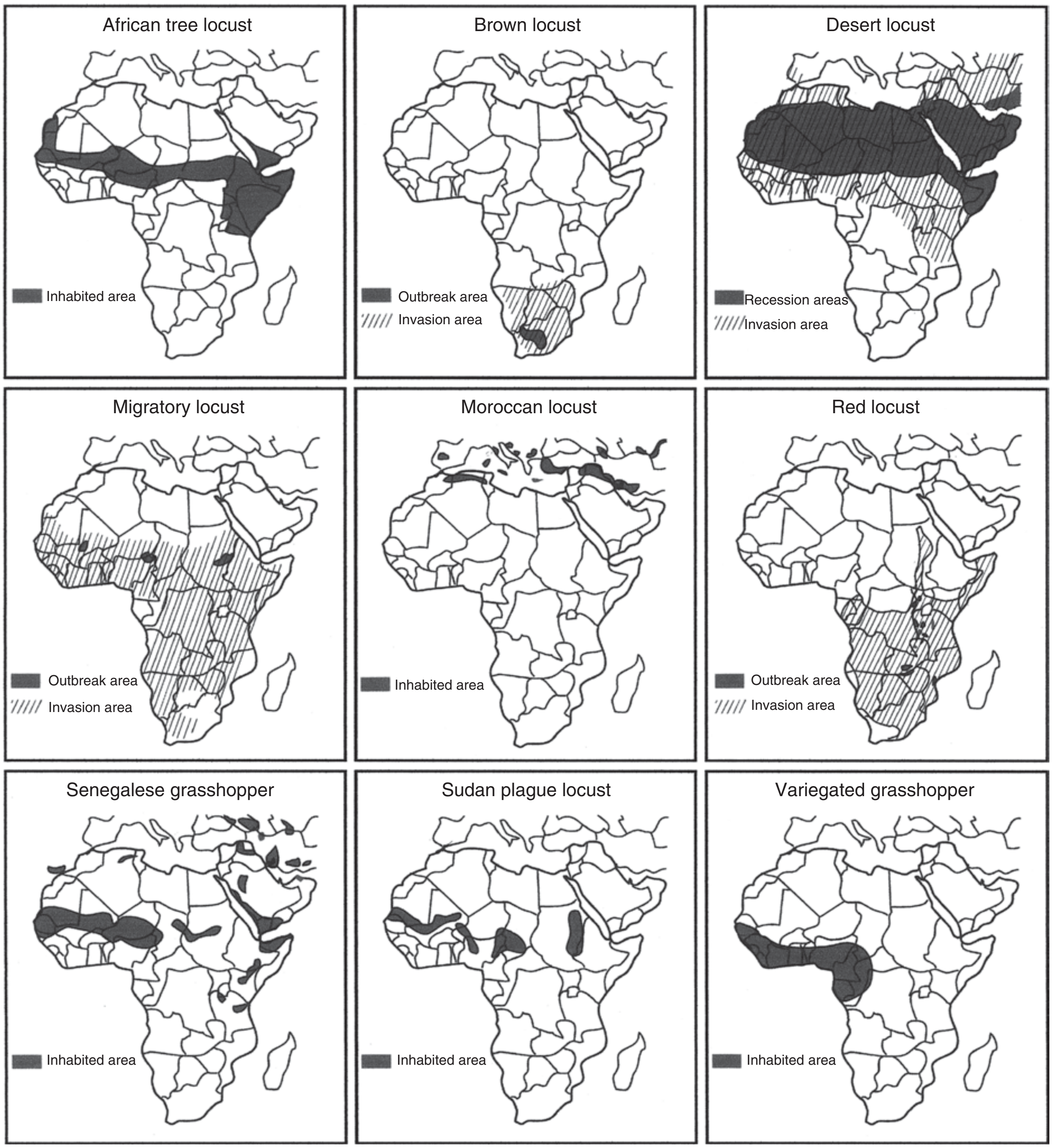
In Africa, and generally elsewhere in the world, grasshopper and locust populations in arid regions tend to grow in response to increased rainfall, and increased availability of host plants brought about by the precipitation. Annually, favorable habitats result from the belt of rain that

Grasshopper and Locust Pests in Africa, Table 7 Examples of serious and less serious locust and grasshopper pests in Africa, and regions of Africa where they are abundant

Pest status	Scientific name	Common name	Region
Serious	*Schistocera gregaria* (Forskål)	Desert locust	N, E, W
	Locusta migratoria migratorioides (Reiche & Fairmaire)	Migratory locust	N, S, W
	Nomadacris septemfasciata (Serville)	Red locust	S, E, W
	Locustana pardalina (Walker)	Brown locust	S
	Dociostaurus maroccanus (Thunberg)	Moroccan locust	N
	Anacridium melanorhodon Walker	Tree locust	E
	Oedaleus senegalensis (Krauss)	Senegalese grasshopper	N, W
	Aiolopus simulatrix (Walker)	Sudan plague locust	E, W
	Zonocerus variegatus (Linnaeus)	Variegated grasshopper	W
Less serious	*Hieroglyphus daganensis* Krauss	Rice grasshopper	E, W
	Kraussaria angulifera (Krauss)		N, E, W
	Cataloipus fuscocoeruleipes Sjöstedt		E, W
	Cataloipus cymbiferus (Krauss)		N, S, W
	Kraussella amabile (Krauss)		
	Diabolocatantopx axillaris (Thunberg)		N, W
	Ornithacris turbida cavroisi (Finot)	Bird locust	W
	Pyrgomorpha spp.		
	Acorypha glaucopsis (Walker)		E, W
	Acanthacris ruficornis (Fabricius)		W
	Zonocerus elegans (Thunberg)		S
	Catanops spp.		
	Eyprepocnemis plorans (Charpentier)	Bersim grasshopper	N, E, W

N, S, E, and W indicate northern, southern, eastern and western Africa, respectively

follows the movement of the intertropical convergence, the pattern of prevailing winds that sweeps southward toward the equator from the northern hemisphere, and northward to the equator from the southern hemisphere. Higher than normal levels of precipitation in the arid regions tends to result in population upsurges, but population decrease can be brought about by losses due to dispersal, competition for food, reduction in food due to decrease in precipitation, and the actions of



Grasshopper and Locust Pests in Africa, Figure 32 **The distribution of some important grasshoppers and locusts in Africa. The regularly inhabited areas are dark-shaded. For the dispersive species, the areas inhabited occasionally (during periods of outbreak) are shown as cross-hatched.**

natural enemies. However, as is often the case in biology, not always does this simple pattern of seasonal rainfall leading to population increase occur. This is due partly to the vagaries of weather, which are quite complex, and regionally and temporally subject to variation. Also, the different grasshopper and locust species have evolved different survival strategies. Species like the desert locust, especially when in the gregarious phase, are capable of long distance dispersal, and contrary to expectations, may seemingly disperse against the prevailing winds or disperse to areas where rainfall has not recently occurred.

Temperature is as important as rainfall and food in governing grasshopper and locust populations. Temperature affects nearly all biological activities, and when grasshoppers are outside their relatively narrow optimal temperature zone, they do not thrive. Optimal body temperature for most species is 35–42°C. To some degree, grasshoppers can modify their internal temperatures by changing their behavior, a process called thermoregulation. By basking in the sun, they can raise their body temperature by several degrees, and by moving into the shade or elevating themselves away from the hot soil surface, they can reduce their temperature. However, they remain substantially at the mercy of ambient weather conditions. In northernmost and southernmost Africa, weather is predictably limiting during the cool periods of the year. However, even in the warmer regions, temperature can be limiting, and grasshoppers engage in basking behavior and suffer metabolically during periods of heavy cloud cover or rain.

Desert Locust, *Schistocera gregaria* (Forskål)

Not only is desert locust a devastating pest in Africa, but worldwide it is the most dangerous locust species. It has the capacity to produce very large, long-lasting, and dispersive swarms. This insect is graminivorous, but during outbreaks it feeds on a large number of plants, including all the important grain crops, cotton, and fruit of the region. It occurs in a persistent form within a large area of northern Africa, Saudi Arabia, and east to India. Only small areas of this area of persistence, called a recession area, typically produce the locusts leading to swarms that spread more widely, to regions called invasion areas. Even portions of Europe and the former Soviet Union are invaded on occasion, and invasion of over 60 nations in the area has been recorded. Within the recession area are sites where locusts feed, breed and become gregarious; these can be called outbreak areas. These outbreak areas are characterized by having sandy or silty soils and being in arid or semi-arid regions. They are not always the same sites, however, because rainfall and vegetation are prerequisites to population increase.

Rainfall is required for oviposition, and females produce 20–100 eggs per pod, and two to three pods per female. On average, the solitary form produces about 95 eggs in the first pod, the gregarious form about 75. Subsequent pods have fewer eggs. The eggs complete their development in 11–75 days, fastest at about 32–34°C. The ensuing nymphs develop in about 38 days (range of 20–66 days), undergoing five instars. The molt to the adult is called fledging, and the young adult a fledgling. The adults require weeks to months to mature reproductively, but once mature persist for only about 30 days. Once they are ready to oviposit, they have only a few days to find a suitable site. Eggs do not undergo diapause. One to three generations are completed per year, depending on conditions.

Crowding for more than one generation is required for development of fully gregarious characteristics. Reduction in plant material within the outbreak sites sometimes forces the insects into closer proximity and stimulates gregarization. Alternately, repeated rains can produce several generations in the same area, allowing population increase and crowding. Sometimes partially gregarized populations move to another site that fosters further gregarization. Hoppers spend most of the day marching, and then roost at night on vegetation. Much of the feeding occurs while roosting. Once hoppers reach the adult stage, they are soon capable of flight, but do not always do so. Solitary locusts fly at night, gregarious locusts during the day. During swarms, locusts can fly for up to 17 hr per day, and travel for 5,000 km during their lifetime. Breeding can occur in the winter months in the Somali peninsula and along the Red Sea, some of the Saharan summer breeding areas and southeast Africa, and some of Pakistan and India.

Migratory Locust, *Locusta migratoria migratorioides* (Reiche & Fairmaire)

There are several named subspecies of migratory locust found in the eastern hemisphere. In Africa, the *migratorioides* subspecies is by far the dominant race. Migratory locust traditionally has been more of an issue in the southern half of Africa. It occurs in varied habitats, including dunes with open tussock vegetation, man-made habitat including fallow fields, and flooded areas. Its areas of outbreak normally are limited to small areas just south of the Sahara Desert where grass plains flood during summer rains, providing ample food. In more recent times, migratory locust has benefited from the expansion of irrigated agriculture in the Sahara region, and northern Africa is now realizing migratory locust problems. It is graminivorous. Migratory locust has two to four generations per year, and females produce one to five egg pods with up to 65 eggs per pod. Eggs normally hatch in 10–50 days, but sometimes persist for up to 100 days. There are five to seven instars, requiring a total of 21–40 days. The adults remain immature for 10–14 days, but persist for up to 70 days.

Unlike most locusts and grasshoppers, migratory locust lacks a stage that can tolerate long periods in unfavorable conditions. They must breed continuously or they die out. On the other hand, favorable conditions allow them to increase in number rapidly. The locusts migrate from the flood plains to the surrounding Sahelian areas where they oviposit, but then migrate back to the flood plain and reproduce further. The offspring of this generation again migrate to the Sahel, and return, as did their parents, to the flood plains.

Red Locust, *Nomadacris septemfasciata* (Serville)

Red locust occurs widely in southern Africa during periods of swarming, but the areas of outbreak are limited to several small regions along the Rift Valley in eastern Africa. Outbreak areas are wet lowland regions dominated by grasses and characterized by extreme conditions of flooding and drought. The outbreak areas comprise only 1/1,000 of the invasion area. This locust has only one generation per year, and eggs complete their development in 30 days. The female deposits about 100 eggs in each pod (more in the solitary form), with up to five pods produced per female at 10–15 day intervals. Six to seven instars are completed in about 60–70 days. The pre-reproductive adults persist through the dry season in regions called retention areas; these are principally in eastern Zimbabwe, southern Malawi, southwest Uganda, and northern Tanzania. They persist in this stage for over eight to nine months, and then at the start of the rainy season they mature and lay eggs, but adults live for only about a month. Eggs are deposited in areas of bare soil or sparse vegetation.

Young hoppers initially remain clumped in family groups, then disperse and re-group in about the second or third instar. The tendency to concentrate is highest in dense vegetation. About the third instar, nymphs begin to form into hopper bands. They shelter at night beneath vegetation and then climb upward to bask in the sun in the morning. As ambient temperatures reach 23°C the nymphs commence feeding and disperse, only to reassemble into bands for evening roosting. This species is graminivorous, and there always seems to be plenty of grass in the outbreak areas, so formation of swarms cannot be ascribed to lack of food. Swarms persist for long periods within their favored habitats, but when they disperse to other areas that are less favorable for reproduction the population declines.

Brown Locust, *Locustana pardalina* (Walker)

Brown locust occurs only in southern Africa, and its outbreak area is found in the southernmost part of the continent. Like most locusts, its preferred habitat is semi-arid and desert. It is graminivorous, feeding on grain crops and pastures. There are two to four generations per year. The female deposits four to five egg pods with about 40 eggs per pod at 7–8 day intervals. Oviposition occurs in dry soil but eggs require moisture to hatch. They can persist for up to 15 months without rain. These locusts tend to oviposit communally. Some eggs display delayed hatch of 1–3 months, even though they may be in the same pod as eggs hatching quickly. The rapidly developing eggs require only about 10 days to develop, and hatch when 10 mm or more of precipitation occurs. The nymphal stage has 4–5 instars, and requires 20–40 days to develop. Solitary hoppers complete development in as few as 20 days whereas gregarious hoppers tend to require 40 days, and transient forms intermediate in development time. The adults are short-lived, persisting for 2–3 weeks in the pre-reproductive stage and then 1–2 months in the reproductive stage.

Moroccan Locust, *Dociostaurus maroccanus* (Thunberg)

Moroccan locust occurs throughout the Mediterranean region on semi-arid steppe and semi-arid desert with grasses, particularly *Poa bulbosa*. It is found in northern Africa in Morocco, Algeria, and Tunisia, but is also found in southern Europe and east to Iran and central Asia in a discontinuous pattern. Formerly a minor pest, it has assumed greater importance due to destruction of forests and overgrazing, which provide additional habitat for this insect. This graminivorous species thrives in regions with winter rains and untilled soil for oviposition. Tilled soil is unsuitable, but fallow or abandoned crop land becomes suitable again. Moroccan locust has only one generation per year, and persists during the dry season, about nine months, in the egg stage. The female produces 2–5 pods, each containing 20–30 eggs. Pods tend to be grouped in clusters of 5–6 pods with several such clusters in a one meter square area. The nymphs have fives instars, and develop in 30–45 days. They form narrow bands when marching, often only 2 m deep, but a single band may extend for several km. Bands usually march during the day, but sometimes extend into the night. The adult persists for 2–4 months. The adult is gregarious, but not migratory.

Tree Locust, *Anacridium melanorhodon* (Walker)

Tree locust generally is considered to be inconsequential except in Sudan, where it defoliates *Acacia senegal*, the tree used to produce gum arabic. It feeds preferentially on trees, and is found in the Sahelian region, south of the Sahara desert, from coast to coast. Despite this preference for *Acacia*, there are reports of it attacking fruit trees, cotton, tobacco, and millet. Outbreaks occur in semi-arid areas, within natural thickets of *Acacia* spp. Normally, a single generation occurs annually, sometimes a second. Egg pods contain about 150 eggs per pod, and the eggs require 1–2 months before hatching. The nymphs undergo 5–8 instars and complete their development in 2–3 months. Immatures are found throughout the dry season, and adulthood is attained with the onset of rains (usually May-June). Oviposition begins in June-July, and young hoppers appear in August-October. Despite numerous attempts to differentiate between swarming and non-swarming populations on the basis of morphometrics, there is little difference to be found. Swarms and bands, when they occur, are relatively small. Both adults and immature forms tend to roost high in trees during the day, descending and feeding at night or early in the morning. They also fly at night.

Senegalese Grasshopper, *Oedaleus senegalensis* (Krauss)

The Senegalese grasshopper is graminivorous, and is associated with sandy soils and open steppe vegetation, predominately grasses. Found mostly in Sahelian central Africa, its distribution also extends to North Africa, the Arabian peninsula, and beyond into southwest Asia. It occurs principally in lightly wooded or open savanna, and steppe or ephemeral prairies with sandy soil. It often is associated with *Aristada pallida*, a perennial tussock grass, and *Cenchrus biflorus*, an annual grass. This species has 2–4 generations per year, and the female produces 1–2 pods with only 20–30 eggs. Eggs are deposited in moist, sandy soil. The eggs resist desiccation, and enter a period of quiescence if adequate moisture is not available. Eggs laid after late August enter obligatory diapause, which can continue for two or more years if adequate moisture is not available. The young hoppers develop quickly, progressing through fives instars in 17–20 days. The interval between hatch and first oviposition is about 35 days. The adults can live for 1–4 months. Like some other grasshoppers, this species shows some of the characteristics of locusts, displaying changes in morphology, marching by hoppers, limited swarming by adults, and long distance migration. Flight occurs mostly at night.

Sudan Plague Locust, *Aiolopus simulatrix* (Walker)

Sudan plague locust occurs in a broad band across Central Africa, and also in Asia. It is most abundant, and damaging, in the Nile Valley of Sudan. It is graminivorous and has two generations per year. Breeding begins soon after the start of rains. The female produces 2–3 pods containing 20–30 eggs per pod, which require less than a month for development. The nymphs undergo five instars, and complete their development in less than a month. The adults are long-lived, persisting for 6–9 months. Adults disperse when they are unable to find suitable breeding sites, which are normally the clay soils of flood plains.

The first generation adults migrate north, where the second generation is produced. In turn, the adults from the second generation migrate southward. Flight occurs at night. Second generation adults survive the dry season hidden deeply within the cracks in the parched soil. As temperatures and humidity rise, signaling the beginning of the rainy season, the adults emerge from the soil cracks, but return during the heat of the day. The populations inhabiting the Nile Valley, which is oriented north and south, generally have higher densities than other inhabited areas, which are smaller and not so oriented. The north-south orientation of the Nile Valley allows the locusts to remain within suitable habitat during their migrations, resulting in lower mortality.

Variegated Grasshopper, *Zonocerus variegatus* (Linnaeus)

Variegated grasshopper is found in west-central Africa. Unlike most African grasshopper and locust pests, it is found in humid and sub-humid area, inhabiting openings in the forest zone. It occupies both natural clearings and deforested, cultivated areas. This species has only one generation per year. In the mid-March to May period, females produce 2–3 pods, each containing 50–60 eggs. Egg pods tend to be clustered, often in groups of hundreds or thousands. The eggs enter diapause, and require 6–7 months for development. Hatch occurs in October or November. The nymphs require a fairly long time, 75–90 days, to undergo 5–6 instars. The nymphs tend to remain clustered into dense groups, and emit foul-smelling liquids from the first abdominal segment. They disperse relative short distances.

The adults emerge in February and persist for 60–90 days. They are dimorphic for wing length, and the long-winged forms are capable of short flights. This species is also unusual in that it prefers broadleaf plants rather than grasses.

It damages herbs, flowers, citrus, and coffee. To a lesser extent it feeds on banana, cassava, and cotton. They are most abundant, and damaging, in the dry season.

Damage

Most of the African grasshopper and locust pests feed on grasses, and it is the cultivated grasses, the grain crops, that are most damaged. The grain seedlings and immature seed heads are most susceptible to damage. Although rangeland grasses are injured, they usually recover quickly, unlike crops. However, many rangelands, particularly in the Sahel region, are being overgrazed by livestock. The additional loss of forage to locusts on such rangelands can have long-term implications for the health of this ecosystem.

Damage to both crops and rangeland is often greatest along the margins of deserts. However, when locusts swarm they can affect crops nearly anywhere. Insect damage, when taken on a regional or national basis, often seems relatively insignificant, or difficult to justify when compared to the costs of pest suppression. However, to an individual farmer or pastoralist, the losses can be devastating, and sometimes fairly large regions suffer severe losses simultaneously. Particularly in Africa, the losses caused by grasshoppers and locusts are not easily rectified due to poor infrastructure for reallocation of food, poor communication, or political turmoil. Thus, locust and grasshopper problems can have surprisingly severe consequences, and suppression programs can provide significant benefit.

The severity of the issue in Africa can be seen by examining Table 8, which shows the frequency and distribution of locust and grasshopper problems in northern Africa and adjacent areas of the Middle East for the 20-year period of 1963–1982. This example shows only countries experiencing large-scale problems that resulted in organized suppression campaigns, not smaller or localized problems. Nevertheless, the scale of the problem is apparent, and in each year there was need for organized suppression in at least one country. Also, it is apparent that some countries experienced locust or grasshopper problems almost annually, whereas for others it was an infrequent issue. Lastly, an element of area-wide population increase and decrease is evident, with many countries experiencing problems nearly simultaneously, and then release from locust and grasshopper problems at about the same time.

Management

Technologies for population assessment have improved, eliminating some of the element of surprise from locust and grasshopper outbreaks. Weather monitoring and modeling are often very useful for forecasting the potential for problems, and vegetation can be assessed with remote sensing technology. However, insect populations are normally confirmed by ground survey personnel via site visits, although swarming populations are sometimes monitored by observers in aircraft. The most important benefit of newer (remote) assessment technologies is that ground survey personnel are able to focus their visits and insect sampling to areas and times where they are likely to detect the pests. This improved efficiency translates into considerable financial savings. The locust outbreak areas are often targeted for more intensive monitoring and control efforts because costs are greatly reduced by treating pests while they are confined to these relatively small areas.

Although it is possible to recommend cultural and physical management techniques to help suppress grasshoppers and locusts, implementation is often difficult. Over the last 50 years, chemical insecticides have proven to be the management technique of choice, and a considerable amount of effort has been dedicated to improving the application techniques or otherwise affecting the killing power of the insecticides. Generally, application of liquid, residual insecticides to plants, by use of both ground application equipment and aircraft,

Grasshopper and Locust Pests in Africa, Table 8 North African and Middle Eastern countries in which large-scale locust/grasshopper suppression occurred during the 20 year period of 1963–1982 and the total number of years the suppression programs were instituted

COUNTRY	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	No. years
Somalia					•	•				•	•			•		•				•	7
Djibouti						•					•					•				•	4
Ethiopia	•		•	•	•	•	•		•	•	•	•			•	•	•				13
Sudan		•		•	•	•	•		•	•	•	•	•	•	•	•	•	•	•	•	17
Saudi Arabia		•	•		•	•	•		•	•	•	•	•	•	•	•	•	•	•	•	17
Yemen AR			•		•	•	•		•	•	•	•	•	•	•	•				•	13
PDR Yemen					•	•	•		•	•	•	•	•	•		•				•	11
Egypt					•	•	•	•			•							•			6
Oman														•							1
U.A.E.				•										•	•						3
Kuwait														•							1
Jordan						•															1
Nigeria						•															1
Niger					•	•	•	•				•	•	•	•	•		•	•		11
Mali				•	•	•	•	•	•			•		•	•			•	•		11
Chad				•	•																2
Mauritania			•	•		•	•	•				•	•						•		8
Western Sahara						•		•													2
Morocco						•	•		•			•	•	•							6
Algeria					•	•	•	•					•	•				•	•		8
Libya		•		•						•	•	•	•	•	•	•	•		•	•	12
No. of countries doing control in any year	1	3	4	7	11	16	11	6	7	7	9	10	9	13	8	9	4	6	7	7	

has been effective. On a much more restricted scale, poison bait applications have been used, especially for the treatment of bands of the gregarious, wingless stages of locusts. More recently, flying swarms have been sprayed with insecticides, or even better, swarms that have alighted. For both ground and air application of liquid insecticides, ultra low volume (ULV) techniques are preferred because mixing and dilution with water is unnecessary, and applicators can spray more land area with each load of insecticide.

Bioinsecticides have recently been developed as an alternative to chemical insecticides. In particular, identification of a relatively fast-acting fungal pathogen, *Metarhizium anisopliae* var. *acridum* (formerly known as *M. flavoviridae*), and the formulation of this in oil, have greatly improved the ability to implement non-chemical suppression. Other bioinsecticides, such as *Beauveria bassiana* and *Nosema locustae*, have proven to be less efficacious, as has the botanical insecticide neem. Insect growth regulators have been shown to disrupt the development of grasshoppers, but this requires that the product be applied to the immature stages, and will not protect against winged swarms.

► Grasshoppers, Katydids and Crickets (Orthoptera)
► Diseases of Grasshoppers
► Grasshoppers and Locusts as Agricultural Pests
► Grasshopper and Locust Pests in Australia
► Grasshopper Pests in North America
► Grasshoppers of the Argentine Pampas
► Desert Locust Plagues

References

Anon (1982) The locust and grasshopper agricultural manual. Center for Overseas Pest Research, London, UK, 690 pp

Farrow RA (1990) Flight and migration in acridoids. In: Chapman RF, Joern A (eds) Biology of grasshoppers. Wiley, New York, NY, pp 227–314

Goettel MS, Johnson DL (1997) Microbial control of grasshoppers and locusts. Mem Ent Soc Can 171, 400 pp

Lecoq M, Welp H, Zelazny B (2005) Locust literature. ISPI-CIRAD. Available at http://ispi-lit.cirad.fr Accessed August 2007

Lomer CJ, Prior C (1992) Biological control of locusts and grasshoppers. CAB International, Wallingford, UK, 394 pp

Grasshopper and Locust Pests in Australia

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In Australia (also in Asia, Africa, and South and Central America), some grasshoppers (Orthoptera: Acrididae) are called "locusts." This designation is applied to species of grasshoppers that display phase change. Phase change is largely a behavioral change between different states, gregarious and solitary forms. During the gregarious phase, which is induced by high densities, locusts tend to disperse long distances as groups (during the nymphal stage, the aggregations are called bands, during the adult stage, they are called swarms). These same species are not very dispersive or gregarious during the solitary phase. Physical changes in appearance may also occur during the change in phase, and of course physiological changes underlie the behavioral and morphological shifts. Transition between the solitary and gregarious phase takes more than one generation. In contrast, grasshoppers tend not to disperse long distances, tend not to aggregate during dispersal, and their appearance remains about the same regardless of density conditions. Thus, "grasshoppers" do not display phase change.

The distinction between grasshoppers and locusts is not clear-cut. At low densities, locusts are not gregarious, nor highly dispersive, but they are still called locusts. Some species that occasionally form aggregations, even forming bands, are called grasshoppers, not locusts, because they do not disperse long distances. In Australia, migratory locusts have all the features associated with phase change: change in body shape and color, and formation of dense swarms during dispersal. The Australian plague locust displays a tendency to become gregarious and to swarm, but lacks a change in appearance during the transition between phases. The spur-throated locust rarely forms bands, though it does form swarms. The small plague grasshopper forms aggregations, but does not undergo long distance dispersal in swarms. So the "locusts" of Australia display a wide range of behaviors, from very locust-like to not so typically locust-like.

Australia is known for frequent and severe problems with locusts, but grasshoppers also are implicated. The severity of the problem is due principally to the fact that Australia is largely an arid country (about 80% is arid or semi-arid), and in this environment not only do grasshoppers tend to thrive, but the effects of their herbivory are amplified by the sparse grass and other herbage available to livestock in this climate. During periods of drought, forage plants are especially valuable, and vital for livestock grazing; thus, conflict with humans is inevitable. However, the relationship of grasshoppers with moisture is not simple. In the more arid, ephemeral grasslands, high levels of summer moisture provide an abundance of food, allowing grasshoppers to maximize their reproductive potential and build to high numbers, usually over three to four generations. As the vegetation dries, the grasshoppers disperse (migrate) until they find areas with green vegetation.

In regions with more rainfall during the summer breeding season (formerly forested but cleared by humans for grazing or crops), however, biotic factors that suppress grasshopper numbers are more effective during wet seasons, so population outbreaks are associated with drought. In some areas, clearing of forest, expansion of improved pasture, and the introduction of irrigation have created environments conducive to grasshopper outbreaks. In these areas, species not formerly causing problems have emerged as pests.

Pest Species of Grasshoppers in Australia

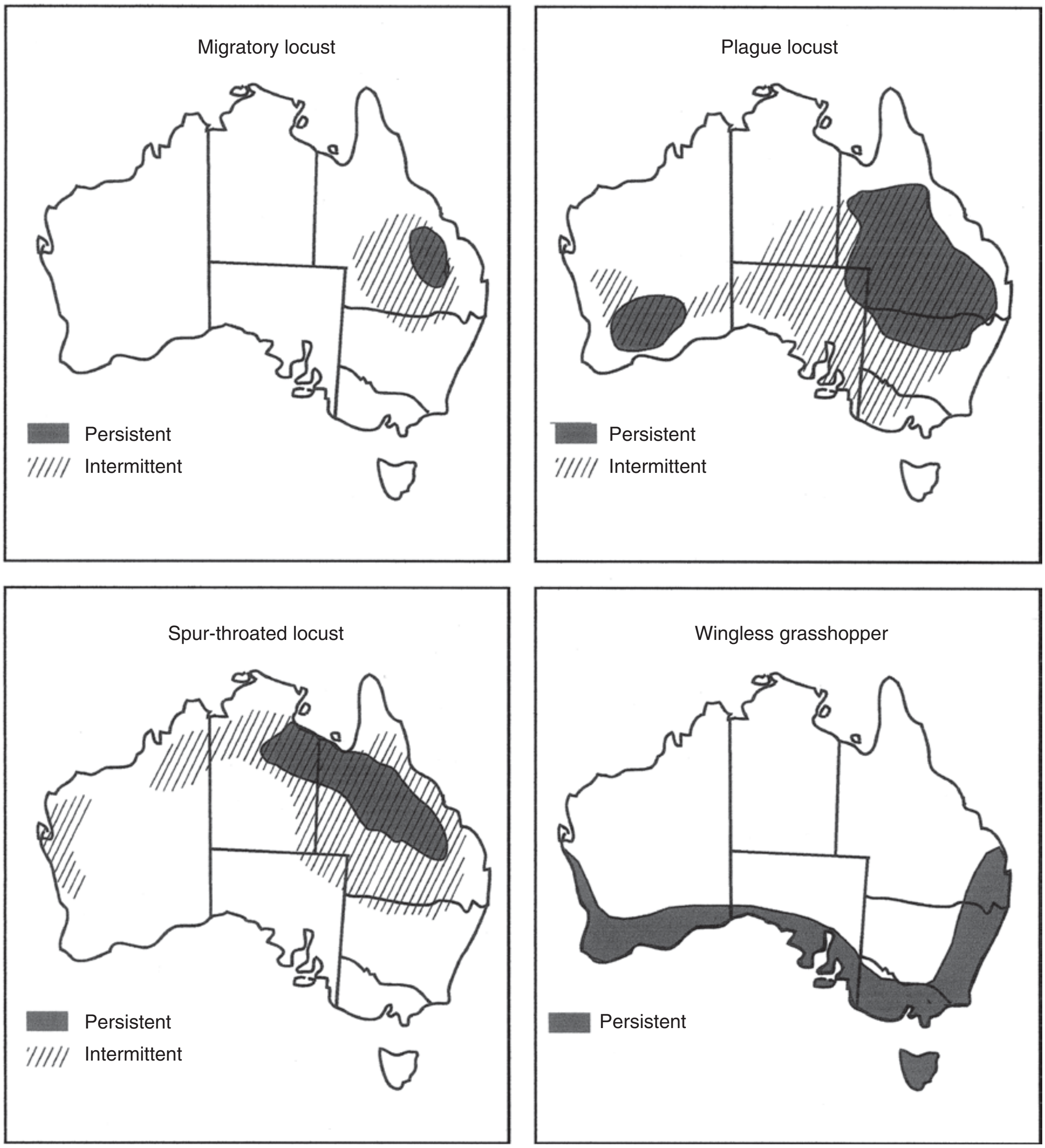
Despite that fact that about 275 species of grasshoppers are known from Australia, only a few are serious pests, and most are indigenous to Australia. However, most of the damage is caused by only four species: Australian plague locust, *Chortoicetes terminifera* (Walker); spur-throated locust, *Austracris guttulosa* (Walker); migratory locust, *Locusta migratoria migratorioides* (Reiche & Fairmaire), and wingless grasshopper, *Phaulacridium vittatum* (Sjöstedt), and of these, two are rather widespread in Southeast Asia (Fig. 33). The important species are given in (Table 9).

Spur-throated locust and migratory locusts sometimes cause severe damage on a localized basis, but the frequency of this is low. Wingless grasshopper has emerged as a chronic pest of improved pastures in southeastern Australia. Small plague grasshopper was formerly a serious pest in Australia during the 1930s and 1940s on cereal crops grown in southern and western Australia, but has diminished in importance. Giant grasshopper is pestiferous only occasionally, and this species is limited to northern and eastern Australia. Yellow-winged locust feeds only on grasses, and though irregularly important, seems to be favored by drought.

Australian Plague Locust, *Chortoicetes terminifera* (Walker)

The Australian plague locust is the most important grasshopper pest in Australia due to the high frequency of outbreaks and the widespread nature of the problem. For example, during the period of 1976–2001, Australian plague locust required control in eastern Australia in 18 of the 27 years. The number of generations ranges from one per year in arid, interior regions, to three per year in the more favorable regions of eastern Australia. Outbreaks normally originate in the arid zone of southeastern Australia, and to a lesser degree southwestern Australia, but they can disperse into adjacent but much larger areas during periods of outbreak.

Australian plague locust normally inhabits areas containing Mitchell grass, *Astrebla* spp., species that remain green for several months after rain, thus providing a relatively constant



Grasshopper and Locust Pests in Australia, Figure 33 **The distribution of some important grasshoppers and locusts in Australia. The regularly inhabited areas are dark-shaded. For the dispersive species, the areas inhabited occasionally (during periods of outbreak) are shown as cross-hatched.**

food supply. If multiple rainfall events occur, populations build rapidly, and migrate if rain does not continue. The direction of dispersal is determined by the pattern of weather; in eastern Australia, those moving in southerly or easterly directions pose a serious threat to crops. Long-distance dispersal occurs when nighttime temperatures (above 25°C) are warm, and strong winds are present at high altitudes. These locusts typically remain airborne for 8–9 h, descending

Grasshopper and Locust Pests in Australia, Table 9 **The most important grasshopper pests in Australia**

Scientific name	Common name	Occurrence
Chortoicetes terminifera (Walker)	Australian plague locust	Semi-arid interior of Australia
Austracris guttulosa (Walker)	Spur-throated locust	Northern and northeastern Australia, and elsewhere in Southeast Asia; adapted to seasonally dry regions
Locusta migratoria migratorioides (Reiche & Fairmaire)	Migratory locust	Adapted to continuous moist tropical and subtropical conditions, especially coastal regions of northern and eastern Australia, but widespread in the Pacific Region
Phaulacridium vittatum (Sjöstedt)	Wingless grasshopper	Moist uplands of temperate regions of Australia
Austroicetes cruciata (Saussure)	Small plague grasshopper	Limited to southern fringe of arid zone in Australia
Gastrimargus musicus (Fabricius)	Yellow-winged locust	Moist subcoastal regions of Australia
Valanga irregularis (Walker)	Giant grasshopper	Eastern Australia
Oedaleus australis Saussure	Eastern plague locust	Eastern interior Australia
Aiolopus thalassinus Fabricius	Clearwinged grasshopper	Coastal and subcoastal eastern Australia
Praxibulus spp.	Yellow-bellied grasshoppers	Southeastern Australia
Fipurga crassa Sjöstedt	Dimorphic grasshopper	Southeastern Australia
Urnesia guttulosa Walker	Salt and pepper grasshopper	Semi-arid interior of Australia

at daybreak. Emigrants may breed successfully and continue the outbreak, but Australian plague locust outbreaks typically dissipate within a few generations. Thus, its notoriety is based more on the frequency of occurrence than the length of the plague. Sometimes migration proves to be deadly for locusts, as their dispersal is largely determined by strong winds associated with weather fronts or low pressure systems. Low pressure is often indicative of rain, which works to the advantage of insects requiring green grass for breeding, but sometimes locusts are deposited in lakes or the ocean, causing massive mortality. Also, though it is less evident, the progeny of some migratory locusts return from the invaded areas to their regions of persistence, helping to re-establish the potential for new outbreaks.

In the south, the cool winters inhibit development and no egg laying occurs for about three months. Egg deposition typically occurs in hard, packed soil or stony areas. In the warmer north, the interruption in reproduction is shorter. Irrespective of location, however, at the start of the spring the majority of the population is usually in the egg stage, and some diapause occurs. This locust has five or six nymphal instars after hatching, which requires (in total) 3–5 weeks. Males of Australian plague locust measure about 25–30 mm long, females 30–42 mm. Adults of this species are distinguished from other common locusts by the presence of a dark spot at the tip of the hind wing. The adult requires only about 2 weeks to mature, and then deposit eggs. Eggs are deposited in the soil at a depth of 6–8 cm. If the weather is favorable and no diapause occurs, eggs can hatch in as little as 2 weeks. Females deposit two to three egg pods, each containing about 50 eggs. Often females lay large numbers of pods in the same area (egg beds), probably because soil moisture conditions are appropriate. If the rainfall is concentrated into a brief period (typically summer, but winter in some locations) the population is limited to a single generation, but if rainfall continues (e.g., spring and autumn), up to four generations may occur. It is these multiple generations per year that can result in rapid population increase and development of a plague.

Spur-Throated Locust, *Austracris guttulosa* (Walker)

This tropical species occurs widely in Australia and nearby islands, north to the Philippines. Unlike most of Australia's locust and grasshoppers, which survive the inclement periods in the egg stage, this species undergoes reproductive diapause. Thus, it fails to reproduce during the dry season, but commences egg production with the onset of the monsoons in the spring. Additional rain is needed for good egg and nymph survival. As noted previously, the egg stage does not undergo diapause and requires warm conditions in order to develop. A period of quiescence is possible, however, and egg hatch can be delayed for a month if moisture is absent.

This species is distinguished by the presence of a large spine between the front legs, and its large size. Males are 55–65 mm in length, females 70–80 mm long. This species lays up to 160 eggs in a pod, and up to five pods within its life span. It does not favor oviposition in egg beds, though barren areas are favored. Areas along roadways and irrigation ditches often are favored oviposition sites. Eggs require 18–30 days to hatch. Nymphs can be found at high densities, but they do not form marching bands. Duration of the nymphal stage is 1–2 months. There are 6–8 instars. The adults mature at the end of summer. Only one generation develops per year.

Outbreaks of spur-throated locust are infrequent, and initially are quite confined in area. Population dynamics are not well understood, but abnormally high summer rainfall is thought to precede population increases. If vegetation becomes dry, adults are more likely to migrate. After spending the dry winter months in a rather sedentary manner, roosting in trees or other tall vegetation, the adults become active in the spring and may disperse and expand the outbreaks. The populations cannot thrive without wet conditions, however, so except during outbreaks it is largely confined to the wet northern regions. Grasses are the principal host during the early instars. As summer habitats dry up, swarms disperse to winter habitats, which are woodlands and cultivated crops. Because the adult stage persists through the winter until mid summer, it can easily damage a wide range of winter crops (wheat, barley, millet) and summer crops (sunflower, soybean, cotton, sorghum), and others. The adults tend to feed during the day, and roost in trees at night.

Control of this species is directed at the adult stage, which is sedentary in winter and therefore easy to assess and treat with insecticides. Once the adults disperse, egg laying is scattered, so treatment of nymphs is difficult.

Migratory Locust, *Locusta migratoria migratorioides* (Reiche & Fairmaire)

Widely distributed in the Australasian region, this is a diapause-free insect that inhabits the mild, mostly coastal and subcoastal regions of Australia, and cannot survive the colder regions of southern Australia. Two (in temperate areas) to four (in tropical areas) generations are produced per year. They are primarily grass feeders, attacking grass pastures and grass crops such as sugarcane, sorghum, maize, and wheat.

This large, heavy-bodied species measures about 45–55 mm in length for males, and 55–65 mm for females. Females commonly oviposit in groups, resulting in "egg beds" that contain numerous egg pods. A pod contains about 50–60 eggs, with females producing 3–5 pods. Eggs require 11–15 days to hatch. There are about six instars, and this insect requires approximately 30 days to attain maturity.

Changes in weather precipitate outbreaks of this species, resulting in gregarization. Increases in winter rainfall and decreases in summer rain are the normal triggers. However, forest removal and pasture improvement has fostered winter breeding in some areas, and provided good sites for oviposition. It was not until the extensive clearing of native vegetation of the central highlands of Queensland that migratory locust became a pest, as pastures and crops have become important food resources.

Migratory locust is less dispersive than many other locusts, and nighttime flights are lacking, so development of outbreaks proceeds slowly. The swarms are unusually cohesive, however, and characterized by a low, tumbling or rolling progression. Once the swarms leave habitat suitable for breeding, they collapse. Duration of outbreaks is 10–20 generations over 4–5 years, which is longer than some other locusts but shorter than exhibited by the same species in Africa and the Philippines (7–13 years). A wide range of crops are damaged by migratory locust, and damage can be quite severe, but due to the limited dispersiveness it tends to be a regional concern rather than a national problem.

Control of migratory locust is feasible if properly timed because, during the period of gregarization, the populations are confined to relatively small areas. If detected during the period of gregarization, suppression with chemical insecticides, using aerial or ground application technology, is quite efficient and economical.

Wingless Grasshopper, *Phaulacridium vittatum* (Sjöstedt)

Wingless grasshopper is actually a species complex, consisting of *Phaulacridium crassum* Key (though much less important and confined to southwestern Australia) in addition to *P. vittatum*, though the presence of *P. crassum* is often overlooked. It is found in the cooler, temperate areas of Australia. Wingless grasshopper has only one generation per year. Eggs are deposited in the fall, undergo diapause and hatch in the spring. Egg pods contain only about 12 eggs per pod, considerably less than the aforementioned locusts, which usually produce pods of 50 or more eggs. However, they may produce 12–16 pods. There are five instars during the summer months.

Males of wingless grasshopper are about 8–12 mm in length; females are 12–18 long. Despite the name given these grasshoppers, wingless grasshopper is short-winged under most pasture conditions and often long-winged in woodland and garden conditions.

Wingless grasshopper problems were not known in Australia until about 1935, and were not recorded as a severe problem until 1979, but are increasing in severity. This grasshopper normally feeds on broadleaf plants in woodlands and pastures, and though present, is not common in natural woodlands, probably due to shortage of suitable food. With European settlement came land clearing and introduction of grazing animals that depleted the native grasses. Accidentally introduced and deliberately introduced broadleaf plants soon replaced native grasses; the broadleaf plants proved to be very suitable food for wingless grasshoppers. However, it was not until about 1945, when subterranean clover (a winter-active plant) was planted into pastureland, and fertilized, that wingless grasshopper became a regular problem. Addition of other legumes (perennial clover in southeastern Australia and alfalfa [lucerne] in southwestern Australia) during the summer exacerbated the grasshopper problem by providing a continuous suitable food supply. It also attacks crops such as sunflowers, sweet corn, potatoes, grapes, ornamentals, and trees. Movement of these grasshoppers is unlike that of most locusts. The dispersing assemblages are described as streaming, and as formation of loose bands. They occur when food is depleted, which often is associated with hot weather.

The continuous availability of food predisposes improved pastures to wingless grasshopper problems, but outbreaks also involve drought, overgrazing, and insect parasitic nematodes. When droughts occur, the carrying capacity of pastures is exceeded, and overgrazing occurs. Overgrazing, and opening of the canopy, initially favors grasshopper survival, and drought inhibits mermithid nematodes (*Amphimermis acridiorum*, *Agamermis catadecaudata*, *Mermis quirindiensis*, *Hexamermis* spp.) from parasitizing wingless grasshoppers. When rainfall again increases, the activity of the nematodes increases correspondingly, resulting in grasshopper suppression.

Wingless grasshoppers can be managed if continuous vegetative cover is maintained, particularly an increase in grasses at the expense of legumes. Natural enemies, particularly mermithid nematodes, are important and favored by good vegetative cover and high moisture. Reforestation, especially of ridge lines where grasshopper survival is favored, will reduce grasshopper numbers. Overgrazing should be avoided.

Management Strategies

Many of Australia's locust problems result from changes in precipitation, and there is little to be done about weather other than careful weather monitoring. However, it is imperative to understand how different species respond to precipitation, and to be alert for impending problems. Population monitoring can be difficult when dealing with swarming insects, as it is easy to overlook mobile swarms until they move to cultivated areas. Once increasing populations are detected, it is advisable to decrease the threat of economic loss from migrating swarms by eliminating the problem before it fully develops. This usually requires decreasing the pest population by 50% in each generation, even when the pests are limited to waste areas and not immediately threatening. This is a departure from past practices, when populations were treated primarily when they moved into crop or pasture areas. The reasoning behind not treating locusts until the threat was imminent was that many swarms would collapse due to changes in weather without ever doing damage to crops. However, to allow the populations to develop unimpeded meant that the resultant populations could be quite large and difficult to control. Locust and grasshoppers are treated with liquid insecticides by air and ground; poison baits also are used, especially for wingless grasshopper. As noted above, some species become problems following changes in land management, mostly land clearing for crops or replacing grasses with more susceptible plants. Thus, some problems can be alleviated by wise land use.

► Grasshoppers, Katydids and Crickets (Orthoptera)
► Diseases of Grasshoppers
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► Grasshopper and Locust Pests in Africa
► Grasshopper Pests in North America
► Grasshoppers of the Argentine Pampas

References

Anon (1982) The locust and grasshopper agricultural manual. Center for Overseas Pest Research, London, UK, 690 pp

Baker GL (1993) Locusts and grasshoppers of the Australian region. The field guides to the most serious locust and grasshopper pests of the world. D9E. The Orthopterists' Society, 66 pp

Deveson ED, Walker PW (2005) Not a one-way trip: historical distribution data for Australian plague locusts support frequent seasonal exchange migrations. J Orthoptera Res 14:91–105

Hunter DM, Strong K, Spurgin PA (1998) Management of populations of the spurthroated locusts, *Austracris guttulosa* (Walker) and migratory locust, *Locusta migratoria* (L.) (Orthoptera: Acrididae), in eastern Australia during 1996 and 1997. J Orthoptera Res 7:173–178

Hunter DM, Walker PW, Elder RJ (2001) Adaptations of locusts and grasshoppers to the low and variable rainfall of Australia. J Orthoptera Res 10:347–351

Rentz DCF, Lewis RC, Su YN, Upton MS (2003) A guide to Australian grasshoppers and locusts. Natural History Publications, Sabah, Malaysia, 419 pp

Grasshopper Pests in North America

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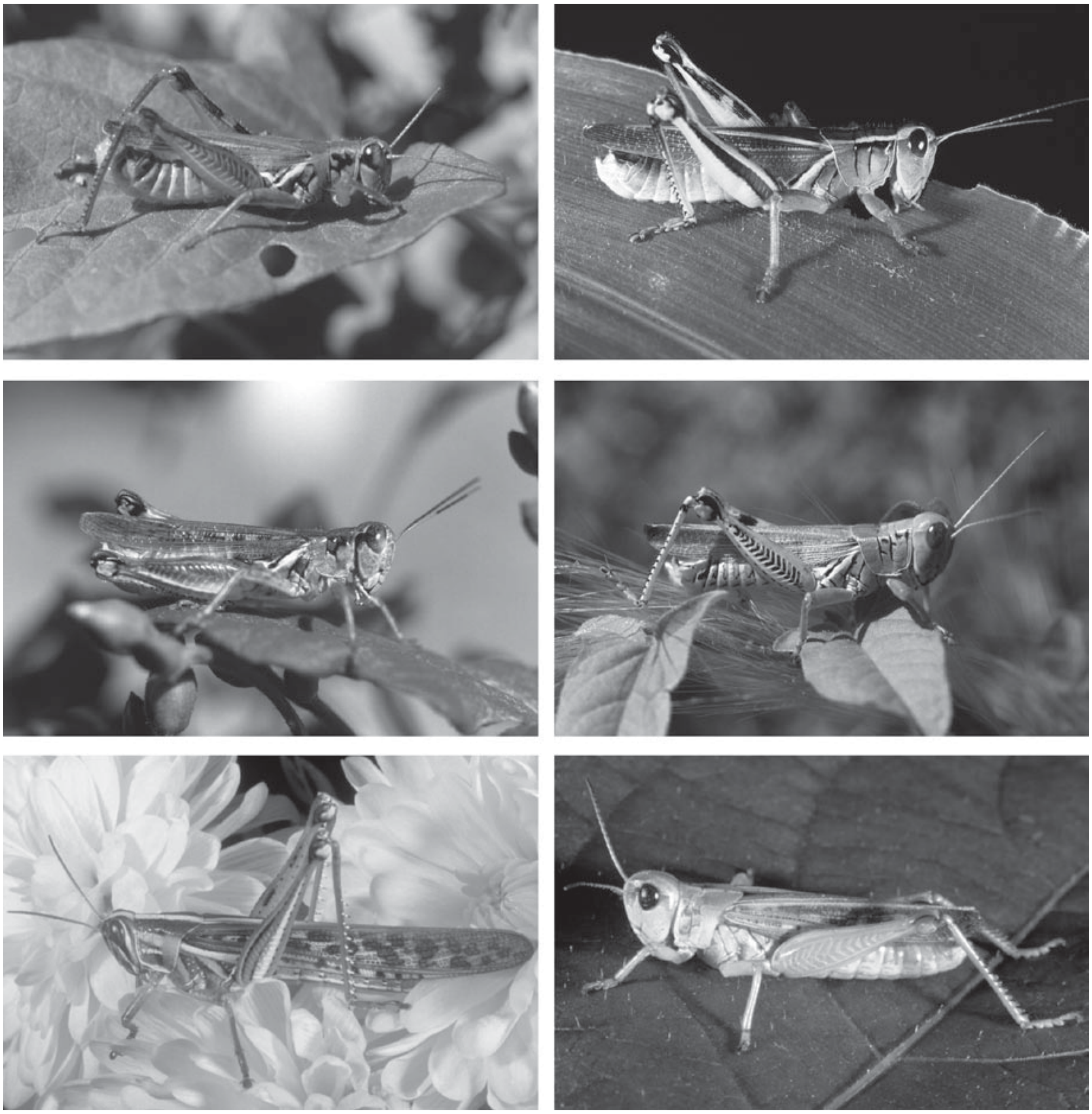
In North America, there is not much effort to label grasshopper species as "locusts," as is done elsewhere in the world, though the Central American locust, *Schistocerca piceifrons* (Walker), occurring in Mexico and southward into South America, is a notable exception. At least one additional species (*Melanoplus sanguinipes* [Fabricius]), perhaps others, would qualify as locusts using the standards of orthopterists elsewhere (see "Grasshopper and locust pests in Australia" for discussion of this topic). Also, the crop-damaging shieldback katydids or long-horned grasshoppers (Orthoptera: Tettigoniidae) are often called crickets, but functionally affect crops and rangeland like grasshoppers, or maybe even locusts, so they are mentioned below even though they are technically neither grasshoppers nor crickets. With few exceptions, North American grasshoppers considered to be pests are in the order Orthoptera and family Acrididae; the exceptions are lubber grasshoppers (Romaleidae) and the aforementioned tettigoniids.

Grasshoppers attack nearly all grain, forage, field, fruit, and vegetable crops. Ornamental plant crops are also damaged in both nurseries and the landscape when grasshoppers are especially abundant, but less often than other crops due to their common location in or near urban and suburban areas, away from habitats conducive to grasshopper outbreaks. Rangeland is the natural habitat of an immense assemblage of grasshoppers, and more than any cultivated crop, it is affected by grasshoppers. Sometimes the grasshoppers cause injury when the plants are quite small and easily defoliated, or stressed by lack of precipitation. However, mature or nearly mature crops are commonly damaged when grasshoppers enter crops along the field margins, feeding on the foliar or reproductive structures. Unhindered, they may eventually spread over the entire field. On rangeland, grasshoppers are often found throughout the environment, though the elements of the species assemblage vary according to topographic and host plant characteristics.

Ragged leaf tissue or complete defoliation of plants along field margins is suggestive of grasshopper problems. Normally the grasshoppers are readily visible, though the adults of some species sometimes disperse to distant areas with good cover, re-invading the crop daily.

Identity of Crop-Feeding Grasshoppers (Families Acrididae, Romaleidae, Tettigoniidae)

Melanoplus spp. (family Acrididae) grasshoppers are the most important grasshopper pests of crops in North America. The principal pests in North America are two-striped grasshopper, *Melanoplus bivittatus* (Say); differential grasshopper, *M. differentialis* (Thomas); red-legged grasshopper, *M. femurrubrum* (De Geer); and migratory grasshopper, *M. sanguinipes* (Fabricius) (Fig. 34). In northernmost states of the United States and the Prairie Provinces of Canada, Packard's grasshopper, *M. packardi* Scudder, can be locally important, as can other species including some band-winged species, particularly the clear-winged grasshopper, *Camnula pellucida* (Scudder). In southeastern North America, eastern lubber grasshopper, *Romalea microptera* (Beauvois) (family Romaleidae) and American grasshopper, *Schistocerca americana* (Drury) (Acrididae) are locally important. In Mexico and Central America, the Central American locust, *Schistocerca piceifrons* Walker displays locust-like behavior. Overall, migratory grasshopper is the most damaging species, and though not usually called a "locust," nonetheless it is a strong flier and has gregarious tendencies. Other species can surpass the abundance of *M. sanguinipes* locally, and others display gregarious and dispersive tendencies, but none compare on a regional basis to this widespread grasshopper. In the mountain and intermountain areas of western North America, certain shieldbacked katydids (family



Grasshopper Pests in North America, Figure 34 **Some common crop-feeding grasshoppers: *upper left* – red-legged grasshopper, *M. femurrubrum* (De Geer); *upper right* – two-striped grasshopper, *M. bivittatus* (Say); *center left* – migratory grasshopper, *Melanoplus sanguinipes* (Fabricius); *center right* – differential grasshopper, *M. differentialis* (Thomas); *lower left* – American grasshopper, *Schistocerca americana* Drury; *lower right*, clear-winged grasshopper, *Camnula pellucida* (Scudder) (photos by J.L. Capinera).**

Tettigoniidae) are grasshopper- or locust-like, though flightless. The most important is Mormon cricket, *Anabrus simplex* Haldeman, but sometimes coulee cricket, *Peranabrus scabricolis* (Thomas) is abundant enough to be damaging to crops.

Life Cycle of Crop-Feeding Grasshoppers

Most grasshoppers pass the winter in the egg stage and have a single generation per year, but in southern areas *M. sanguinipes* and *S. americana* may have additional generations, and *S. piceifrons* has two generations. Grasshoppers typically hatch from eggs in the spring or early summer. The species differ slightly in the timing of their hatch, and the hatching is not synchronous, so different stages may be found throughout the summer. Grasshoppers usually molt five or six times and require about 5–6 weeks to reach maturity. About two weeks later they commence egg laying, and continue to deposit eggs, in clusters called pods, containing 20–100 eggs per pod until they are killed by cold weather. Eggs, which are deposited in the soil, are not normally affected by weather, but are susceptible to damage by tillage and certain predatory insects. When the young grasshoppers hatch in the spring they are susceptible to inclement weather (low temperatures and rainfall). Throughout their lives, grasshoppers are attacked by parasitic insects, diseases, and insect and vertebrate predators. These natural enemies can suppress grasshoppers locally, but often only after the grasshoppers attain very high and damaging densities. Plants differ greatly in suitability for grasshopper survival and growth. In general, these pests prefer broad-leaf plants, not grasses, but the cultivated grains, especially wheat and corn, are highly attractive and suitable for grasshopper survival.

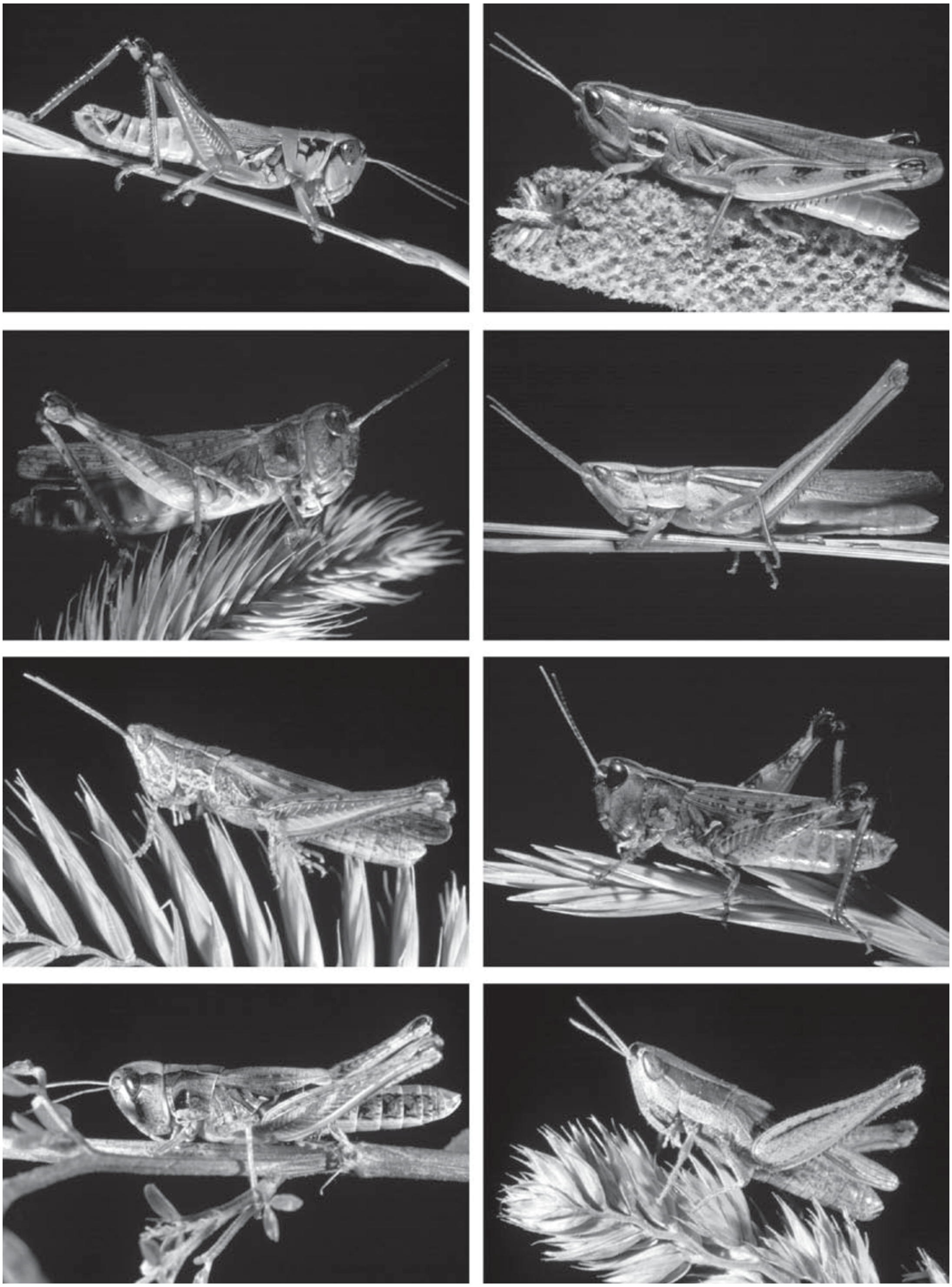
Management of Crop-Feeding Grasshoppers

The need for management is most directly related to grasshopper density. As a general rule, when grasshopper densities are 15 or more per square yard (18 per square meter) within a grain field or more than 40 per square yard (48 per square meter) along field borders, economic damage will ensue. With densities of 8–14 per square yard (10–17 per square meter) within a field, or 20–40 per square yard (24–48 per square meter) along field borders, the crop is at risk. These lower densities can prove damaging when the grasshoppers are more mature (larger), the crop is young, or the crop is stressed by lack of soil moisture. Thus, for winter wheat culture (the crop is planted in the late summer, becomes dormant in the winter, and completes its growth in the spring), the lower thresholds for treatment are used because the grasshoppers are mature in the autumn when the wheat is young.

Grasshopper problems most often originate outside the crop field (though planting into wheat stubble or fields that were previously weedy can be exceptions), so treatment of weedy or waste areas (sometimes rangeland) surrounding a field with an insecticide can be an effective approach to prevent invasion of the crop (Fig. 36). Liquid formulations of contact insecticides are usually used for this approach. Alternatively, treatment of the crop margin (about 150 feet [47 m] of the border areas) will kill most grasshoppers as they disperse into a crop. Fast-acting contact insecticides applied to foliage or soil, contact insecticides applied to wheat bran bait, and systemic insecticides applied to the foliage or seed are some approaches used to deliver toxicants to grasshoppers. In some areas, farmers commonly plant higher densities of grains along the field margins if they anticipate grasshopper problems, to allow for some crop loss.

Identity of Rangeland Grasshoppers

Rangeland occurs mostly in arid and semi-arid regions, which corresponds roughly with the western half of the United States and Canada. This habitat consists of grasses and broadleaf plants (forbs), and sometimes shrubs, but not usually trees. The North American grasshoppers affecting rangeland sometimes are the same as those affecting crops, particularly *Melanoplus sanguinipes*, and to a lesser degree *Camnula pellucida* and *Anabus simplex*, which can be abundant and damaging in both environments. Most often, however, the abundant species on rangeland are not the same as those affecting crops (Fig. 35), even when irrigated crops are surrounded by rangeland, providing good opportunity for rangeland species to disperse into crops. Often when the crop-feeding



Grasshopper Pests in North America, Figure 35 Some common rangeland grasshoppers: *upper left – Phoetaliotes nebrascensis* Thomas; *upper right – Amphitornus coloradus* Thomas; *second row, left – Aulocara elliotti* Thomas; *second row, right – Mermiria bivittata* Serville; *third row, left – Cordillacris occipitalis* Thomas; *third row, right – Ageneotettix deorum* Scudder; *bottom left – Aeropedellus clavatus* (Thomas); *bottom right – Opeia obscura* Thomas (photos by J.L. Capinera).

Grasshopper Pests in North America, Figure 36 **Damage to the edge of a winter wheat field caused by grasshoppers. Grasshoppers dispersed from the residue of a previous weedy wheat crop (designated "a"), to the margin of a young wheat crop, where they destroyed the seedlings (location "b"). The undamaged wheat is in the foreground (location "c").**

species are present on rangeland, it is due to disturbance and growth of weedy vegetation instead of native grasses or forbs. Floral disturbance can occur following overgrazing, excessive trampling of the soil (a common occurrence around livestock water tanks), or other factors such as outbreaks of white grubs (Coleoptera: Scarabaeidae) which kill the grasses, allowing weeds to invade. The species most commonly associated with rangeland damage are listed in the table.

North America has a surprisingly rich fauna on rangeland, with a large number of species contributing to "grasshopper" population outbreaks (Table 10). About 375 species of grasshoppers are found inhabiting North American rangeland. About a third are considered to be pests, but nearly all the rest are innocuous, either due to their dietary habits or their lack of abundance. Most outbreaks on rangeland consist of an assemblage of species, with the species varying from place to place, and some peaking early in the outbreak cycle, and others later. Another interesting aspect of rangeland grasshopper problems is that some species have proven to be destructive at one time or another, only to fade into oblivion for many years (e.g., high plains grasshopper, *Dissosteira longipennis* Thomas).

Interestingly, not all rangeland-dwelling grasshoppers are pests. Many species do not feed on grasses or other important livestock food (the "grass" hopper designation, like many common names, is not entirely accurate). More importantly, some species feed selectively on rangeland plants that are considered to be toxic to livestock (e.g., *Hesperotettix viridis* [Scudder] on snakeweed, *Gutierrezia sarothrae* and *microcephala*) or competitors for moisture or light with more nutritious species (e.g., *Hypochlora alba* Dodge on sagebrush, *Artemisia* spp.). Even *Anabrus simplex*, long viewed as a scourge of farmers and ranchers in the Rocky Mountain region, has been shown to be relatively innocuous on rangeland under normal conditions. It avoids grasses, except for seed heads, preferring to feed on flowers and foliage of low-value broadleaf weeds. Only under severe drought conditions, when there is almost no forage available for livestock, is this insect a pest of rangeland.

Life Cycle of Rangeland Grasshoppers

The biology of rangeland grasshoppers and crop-feeding grasshoppers is, in most cases, about the same. However, a few rangeland species overwinter as nymphs, and in southernmost areas adults are sometimes found in the winter. Natural enemies are more important in the survival of rangeland grasshoppers because insecticides are rarely used, and therefore beneficial insects are more abundant. Tillage is not normally practiced on

Grasshopper Pests in North America, Table 10 Grasshoppers commonly damaging to rangeland in North America

Family	Subfamily	Scientific name
Acrididae	Melanoplinae	*Melanoplus sanguinipes* Fabricius
		Melanoplus infantilis Scudder
		Melanoplus devastator Scudder
		Melanoplus occidentalis Thomas
		Oedaleonotus enigma Scudder
		Phoetaliotes nebrascensis Thomas
	Gomphocerinae	*Aulocara elliotti* Thomas
		Aulocara femoratum Scudder
		Ageneotettix deorum Scudder
		Aeropedellus clavatus (Thomas)
		Amphitornus coloradus Thomas
		Phlibostroma quadrimaculatum Thomas
		Opeia obscura Thomas
		Cordillacris occipitalis Thomas
		Mermiria bivittata Serville
		Chorthippus curtipennis Harris
		Psoelessa delicatula Scudder
		Eritettix simplex Scudder
	Oedopodinae	*Camnula pellucida* Scudder
		Trachyrhachys kiowa Thomas
		Dissosteira longipennis Thomas
		Dissosteira spurcata Saussure
		Encoptolophus costalis (Scudder)
		Metator pardalinus Saussure
		Trimerotropis pallidipennis Burmeister
Tettigoniidae	Tettigoniinae	*Anabrus simplex* Haldeman

rangeland, so there is less soil disturbance that might result in destruction of egg pods. In contrast to crop environments, egg pods in rangeland are less likely to be concentrated along field margins, as often occurs with crops that have weedy margins along fences and irrigation ditches, which are favored by grasshoppers for oviposition.

A notable aspect of rangeland grasshopper biology is the relatively synchronous increase or decrease in abundance of different species in the grasshopper species assemblage. Population cycles are related to weather, host plant abundance, and natural enemy abundance. Generally, hot and dry weather are responsible for increase in population density in northern areas, where grasshoppers are limited by inadequate daily warmth during the summer days, or a short summer season. In southern regions, however, warmth is not so limiting, and the lack of abundant nutritious vegetation is more constraining, so rainfall during the spring (which determines the availability of host plants) is a controlling variable.

Grasshoppers need to control their body temperature if they are to feed, develop, and reproduce optimally. Patches of bare soil allow grasshoppers a site to elevate their body temperatures by basking in the sunshine, and so many species thrive where the vegetation density is low enough to allow basking. However, if there is too much vegetation-free space they cannot meet their nutritional needs. Thus, there are trade-offs between not enough and too much vegetation, and this is made more complex by the differing dietary needs (different host preferences and amount of vegetation required) of different species of grasshoppers. Competition for the most suitable food resources is more frequent and important than generally acknowledged. Many observers fail to recognize that grasshopper populations can be under nutritional stress when there is still relatively abundant vegetation on rangeland because it may be difficult to discern that the most favored plant species have already been consumed.

Rangeland differs greatly in suitability for plants and grasshoppers. Precipitation is the major determinant of plant species occurrence and in plant size, but temperature effects, due both to altitude and latitude, are important. The dominant species of grasses, and their biomass, change with location. For example, the dominant grasses are various *Adropogon*, *Agropyron*, *Stipa*, *Panicum*, and *Calamovilfa* spp. in the eastern areas of the Great Plains of North America, but are replaced by *Bouteloua* and *Stipa* spp., *Koleria scoparius*, and *Agropyron smithii* centrally, and *Bouteloua gracilis*, *Agropyron smithii*, and *Buchloe dactyloides* in more western regions. There is also a general decrease in the average height of vegetation as one moves from east to west in the Plains region, so these regions are denoted as tallgrass, mixedgrass and shortgrass regions, respectively. In the intermountain region, bunchgrasses such as *Agropyron spicatum* and *Bromus* spp. predominate. As noted in the table, species from three subfamilies, Melanoplinae, Gomphocerinae, and Oedopodinae, are important rangeland grasshoppers. Generally, members of each subfamily occur together, but the proportion in each subfamily is not constant among different localities. Though tallgrass and mixedgrass environments are dominated by grasshoppers in the subfamily Melanoplinae (spurthroated grasshoppers), shortgrass sites are dominated by grasshoppers in the subfamily Gomphocerinae (stridulating slantfaced grasshoppers).

Management of Rangeland Grasshoppers

The principal challenges confronting rangeland grasshopper management are the extensive areas to be managed, and the low value of the forage. Both factors limit the amount of money that can be expended per unit area, and preclude using anything but the most economic pest suppression measures in most instances.

Insecticides are generally used for suppression of grasshoppers, and usually area-wide campaigns are instituted with the help of government agencies because when a problem develops, it normally occurs over a large geographic area. Large, specially equipped aircraft often are used to treat large land areas with liquid insecticide, and sometimes ultra low volume (ULV) insecticides are applied because they are applied undiluted and at very low application rates, which means that more land area can be treated between refills of the spray tanks. This reduces time and labor costs considerably. A common alternative to liquid insecticide application is to apply insecticide-treated bran bait using aircraft. This has the advantage of being more selective, because although many species of grasshoppers will feed on bait and perish, many other insects are unaffected.

When initiating grasshopper suppression on rangeland, the common biological considerations are the grasshopper species involved, their density, and the stage of development. Not all grasshoppers are damaging, and some are quite a lot more damaging than others. A density of 10–15 grasshoppers per square yard (12–18 per square meter) is normally needed to justify treatment (hopefully adjusted for the species involved). Not all grasshoppers hatch synchronously, and applications are timed to allow for all, or at least most, of the hoppers to hatch and thus come into contact with the insecticide. Waiting too long, however, is counterproductive because they will have already consumed a significant amount of livestock forage.

Grasshopper suppression operational considerations are as important as biological considerations in determining the feasibility of area-wide grasshopper suppression. Operational considerations usually involve population sampling to delineate areas that need treatment over an extensive area, including areas that are "sensitive" and cannot be treated; obtaining and scheduling the aircraft and toxicants; organizing ranchers to obtain funds and permission for treatment; and establishing a mechanism of effective mapping, communication, and rancher and public information, including news releases.

Livestock grazing pressure is often suggested as an element that affects grasshopper abundance. Historically, overgrazing by livestock disrupted the native flora, especially in the eastern regions of the Great Plains, allowing invasion of weeds more suitable for grasshoppers. Also, grazing can result in more barren soil, which is attractive to grasshoppers for thermoregulation and oviposition. Thus, grasshopper problems are sometimes attributed to overstocking of livestock. While overgrazing should be avoided for several reasons, including the ability to cause grasshopper problems under certain conditions, some rangeland can tolerate quite a lot of grazing pressure, and even benefit from grazing by livestock. Extensive research has demonstrated a positive correlation between vegetation abundance and grasshopper abundance in the arid regions of the Great Plains where vegetation is shorter or less abundant, and grasshoppers tend to be food-limited. As noted previously, these areas are dominated by gomphocerine species, whereas other areas have proportionally more melanoplines and oedopodines. Where gomphocerine grasshoppers predominate, moderate or heavy grazing can reduce the abundance of grasshoppers relative to ungrazed or lightly grazed areas.

► Grasshoppers, Katydids and Crickets (Orthoptera)
► Diseases of Grasshoppers
► Grasshoppers and Locusts as Agricultural Pests
► Grasshopper and Locust Pests in Africa
► Grasshopper and Locust Pests in Australia
► Grasshoppers of the Argentine Pampas
► Migratory Grasshopper
► Red-Legged Grasshopper
► Two-Striped Grasshopper
► Differential Grasshopper
► American Grasshopper
► Mormon Cricket

References

Capinera JL (ed) (1987) Integrated pest management on rangeland; a shortgrass prairie perspective. Westview Press, Boulder, CO, 426 pp

Capinera JL, Scott RD, Walker TJ (2004) Field guide to grasshoppers, katydids, and crickets of the United States. Cornell University Press, Ithaca, NY, 249 pp

Cunningham GL, Sampson MW (1996) Grasshopper integrated pest management user handbook. USDA, APHIS Tech Bull 1809

Gangwere SK, Muralirangan MC, Muralirangan M (eds) (1997) The bionomics of grasshoppers, katydids and their kin. CAB International, Wallingford, UK, 529 pp

Pfadt RE (2002) Field guide to western grasshoppers, 3rd edn. Wyoming Agricultural Experiment Station Bulletin 912. University of Wyoming, Agricultural Experiment Station, Laramie, WY, 288 pp

Vickery VR, Kevan DKMcE (1985) The insects and arachnids of Canada. Part 14. The grasshoppers, crickets and related insects of Canada and adjacent regions. Agriculture Canada Biosystematics Research Institute Publication 1777, 918 pp

Grasshoppers

The suborder Caelifera of the order Orthoptera.

► Grasshoppers, Katydids and Crickets

Grasshoppers and Locusts as Agricultural Pests

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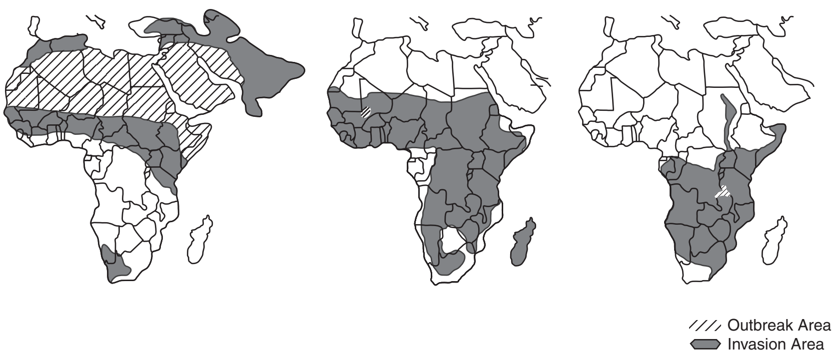
Orthoptera represent a large insect order with a worldwide distribution. Taxa in the superfamily Acridoidea are commonly either called grasshoppers or locusts. This division separates insects that readily aggregate in persistent bands or swarms in response to increases in intra-specific density ("locusts") from those that show no such change in behavior ("grasshoppers").

Economically, socially and historically, locusts and grasshoppers are one of the most destructive pests. This century alone, there have been eight major plagues of the desert locust *Schistocerca gregaria* Forskål. Agricultural production across 29 million km^2 in Africa and south-western Asia is threatened during plague periods.

Although the desert locust is probably the most infamous of all acridoid pests, a suite of other locust and grasshopper species and species assemblages cause more frequent and cumulatively far more significant damage (Fig. 37) throughout Africa, Australia, the middle East and parts of Asia and North and South America. In Southern Africa, the Brown Locust, *Locustana pardalina* Walker, has necessitated frequent widespread control measures over the last 45 years. In central and southern Africa, the Red locust, *Nomadacris septemfasciata* Serville; in Sudan, the tree locust, *Anacridium melanorhodon* Walker; in Madagascar, the migratory locust, *Locusta migratoria migratoriodes* Reiche and Fairmaire; and in semi-arid territories around the Mediterranean, the Moroccan locust, *Dociostaurus maroccanus* Thunburg, all require regular control measures to prevent the formation of migratory swarms. Although less mobile, grasshoppers such as *Melanoplus sanguinipes* Fabricius within North America, and *Phaulacridium vittatumeastern* Sjöstedt within Australian grasslands also require frequent control measures. Grasshopper complexes within the semi-arid African Sahelian belt such as *Aiolopus simulatrix* Walker, *Kraussaria angulifera* Krauss, *Acrotylus* spp. and *Oedaleus senegalensis* Krauss, as well as those from the more humid West Africa zone, notably *Hieroglyphus daganensis* Krauss and *Zonocerus variegatus* L., represent a continuing threat to the food security of many rural communities. Even today, locusts and grasshopper outbreaks cause problems in every major continent of the world.



Grasshoppers and Locusts as Agricultural Pests, Figure 37 Outbreak and invasion areas of some African locusts. The locusts tend to persist in the outbreak areas, and when conditions for reproduction are favorable the locusts multiply and spread to invasion areas. Desert locust, *Schistocerca gregaria* (*left map*), has a relatively large area of persistent habitation, consisting of most of northern Africa and the Arabian Peninsula, whereas African migratory locust, *Locusta migratoria migratorioides* (*center map*), and red locust, *Nomadacris septemfasciata* (*right map*) have small areas of origin in northwest and south central Africa, respectively.

Grasshopper and Locust Control

The task of combating locust and grasshopper plagues usually falls to the national crop protection services in cooperation with regional control organizations such as the Desert Locust Control Organisation for Eastern Africa (DLCO-EA). In recent years, this challenge has largely relied on the application of synthetic chemical insecticides applied as baits or dusts, and more recently and more commonly, sprayed as ultra low volume (ULV) oil formulations. The adoption of recent environmental monitoring technologies means the breeding habitats of some migratory locusts and grasshoppers can be monitored using satellite imagery as well as aerial and ground surveys. Prevention of upsurges by early intervention is now normally the preferred approach. Modeling and recent improvements in forecasting have helped some governments, donors, researchers and locust officers predict potential outbreak periods and contain the problem of outbreaks at the source level. For example, the goal of the FAO's Emergency Prevention System (EMPRES) for Transboundary Animals and Plant Pests and Diseases is to minimize the risk of locust plagues emanating from the central region of the desert locust distribution area through timely, environmentally sound interventions. However, in many rural areas, such as the Sahel, where access to pesticides is limited, traditional methods such as using smoke to repel arriving swarms or driving migrating hopper bands (immature locusts) into steep-sided ditches from which they cannot escape continue to be employed.

Chemical Control

Locust and grasshopper control has evolved since the middle of the twentieth century. Until the 1970s, most control operations used persistent organochlorine insecticides, with dieldrin favored for desert locust control due to its effectiveness at low doses and in barrier sprays. There is circumstantial evidence supporting the effectiveness of such insecticides in suppressing plagues, with the period 1930 to 1960 representing the longest known interplague period for the desert locust. Dieldrin, however, is now banned in most countries due to environmental damage, negative effects on human and animal health and legislation originating in the USA concerning the stockpiling of toxic wastes. The use of carbamate and organophosphorous such as bendiocarb, malathion and fenitrothion began in the 80s, and more recently pyrethroid insecticide compounds such as deltamethrin have been used. However, although these products have a lower mammalian toxicity (most insecticides currently used for locust control are classified as "moderately hazardous" to human health based on acute oral and dermal toxicity studies in rats) their reduced persistence makes them less effective than dieldrin, and repeated applications are often necessary to achieve the same level of control. This is of particular importance in recession (permanent sites of locust breeding) areas where the requirements for repeat applications have resulted in increased control costs and amounts of pesticides used. Most recently, the phenylpyrazole compound fipronil has been promoted as a significant break-through in locust control, since it is effective and persistent at low doses. Fipronil was largely used in the half-million hectares treated against migratory locusts in Madagascar in recent years.

The most recent desert locust upsurge (1986–1989) and a simultaneous grasshopper outbreak in the West African Sahel triggered a massive emergency response from the international community. The problem was again countered by large-scale spraying of swarms as well as feeding and breeding sites. Nearly 14 million hectares in Africa alone were sprayed for locusts while additional millions of hectares were sprayed in the Sahel for grasshopper control. Total donor assistance was approximately $250 million (U.S. dollars) and total costs including contributions from afflicted countries exceeded $295 million (U.S. dollars). However, the value of recent desert locust control campaigns has been called into question. While crop losses caused by swarms during plague conditions may be high (national pre-harvest losses due to grasshoppers in the Sahel have been estimated at 30% or more), overall yields may not be affected, as plague years are normally rainy and thus associated with better than average harvests.

As well as concerns over economic viability, the environmental and human health consequences of large-scale control campaigns using synthetic broad-spectrum insecticides in sensitive ecological areas (often representing breeding sources for many migratory acridid pests) has come under increasing scrutiny. For example, at the recommended rates for locusts and grasshoppers, fenitrothion is near the threshold where it can cause immediate death among birds. Chlorpyriphos and pyrethroids may reduce the biodiversity of honeybees, spiders and aquatic insects. Fipronil is highly toxic to certain birds, fish, terrestrial and freshwater invertebrates. Human exposure to pesticides during control operations can present problems during handling, or as a result of spray drift from operations, especially where protective clothing is not available or there is an unwillingness to wear it under hot field conditions. Local residents and nomadic pastoralists may also be affected directly through spray drift or through contamination of livestock, water or foodstocks.

Biological Control

There are numerous reports of natural enemies of grasshoppers and locusts. The principle groups consist of vertebrate and invertebrate predators which attack eggs, nymphs and adult insect, as well as insect parasitoids, parasitic nematodes and pathogens. In addition to natural control, recent research has led to the development of biopesticides based on entomopathogenic fungi.

Most locusts and grasshopper predators are generalists, and will attack a range of species, rather than any single host. Both nymphs and adults are attacked by various arthropods such as scorpions, spiders and solifugids and predaceous insects like asilid flies, sphecid wasps, ants, mantids and ant lions, and also by many species of lizards, snakes and birds. Eggs are also attacked by larvae of bombyliid flies and various Coleoptera, chiefly tenebrionid larvae. Additionally, a number of naturally occurring diseases also suppress locust and grasshopper populations worldwide, including descriptions of spectacular epizootics by the *Entomophaga grylli* complex of fungal pathogens. There are, however, relatively few in-depth studies on the impact of grasshopper and locust natural enemies, especially for tropical species.

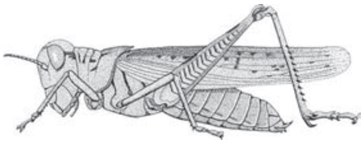
Although they merit conservation, indigenous natural enemies are often killed by nonselective chemical insecticides. This aspect, plus the concerns over the human health consequences of large-scale applications of chemical pesticides during recent locust campaigns, has led to recommendations by the World Bank and others to place locust and grasshopper control within the context of integrated pest management (IPM) programs. This has increased pressures to introduce biological control.

Although arthropod predators and parasitoids may hasten the end of plagues, apart from possibly controlling static grasshopper populations they cannot be manipulated, and migratory pests such as the desert locust are poor targets for classical biological control. However, pathogens can be manipulated for use as biological pesticides. Many locusts and grasshoppers are migratory pests and have characteristics amenable for control with microbial agents, (i) feeding and breeding take place outside the crop, often in conservation areas where high natural mortality can be expected to occur; (ii) as there is often public funding for control, high environmental values are involved in the purchasing decisions.

The major pathogen groups that have received interest as biological control agents of locusts and grasshoppers are bacteria, protozoa, entomopox viruses and fungi. The characteristics needed for a good agent include cheap and easy production, toxicological safety, host specificity and (given the existence of highly developed application technology) the ability to be formulated and applied using currently available equipment. Commercial formulations of entomophilic nematodes are available, but their high cost and water requirements during application and infection restrict their use in most regions against locusts and grasshoppers.

The use of entomopathogenic bacteria against locusts and grasshoppers has received some attention. The non-sporeforming *Serratia marcescens* Bizio and *Pseudomonas aeruginosa* (Schroeter) Migula have high pathogenicity in laboratory cultures. However, disappointing field results and concerns over mammalian safety have precluded further investigation. Though it has a well-developed production technology, efforts to find strains of *Bacillus thuringiensis* that produce endotoxins with pathogenicity against locusts or grasshoppers have not yet been successful. Various protozoa are known to infect locusts or grasshoppers. Among the Microsporidia (Phylum Microspora), *Nosema locusta* Canning has received the most attention, possibly due to its easy and efficient in vivo production characteristics. *N. locusta* has been the subject of a number of inundative field trials against grasshoppers where its spores are typically incorporated into bait carriers. However, the release of such pathogens generally only causes modest reductions. Nevertheless, because *N. locusta* may reduce the rates of host development, fecundity and feeding, it is considered by some to be a candidate for long-term population suppression and low impact maintenance in IPM strategies. *N. locusta* is registered for grasshopper control within conservation rangeland areas in the USA.

The use of entomopox viruses (EPVs) against locusts and grasshoppers is also receiving attention. The most extensively studied is the rangeland grasshopper *Melanoplus sanguinipes* (Fig. 38) virus (MsEPV), which is considered to have some potential as a biocontrol agent on Canadian rangelands. However, field studies demonstrating effective control are limited and restrictions to their production *in vitro* and ability to be formulated in spray carriers suggest that using EPVs against locusts and grasshoppers currently



Grasshoppers and Locusts as Agricultural Pests, Figure 38 **Migratory grasshopper, *Melanoplus sanguinipes* (Fabricius), an American grasshopper with locust-like dispersive behavior. (artwork, J. Mottern)**

remains unlikely. Further investigations into the infectivity of the baculoviruses, such as the nuclear polyhedrosis viruses (NPVs), which have better production characteristics, may open up new opportunities.

Among pathogens, the entomopathogenic fungi are the easiest to be manipulated as biopesticides. They have the advantage over other pathogens because they are able to infect through the insect cuticle, thus avoiding the necessity of providing bait. Spores (conidia) of fungal pathogens are also lipophilic, favoring their formulation in the oil-based carriers that are typically applied as a low volume spray in locust and grasshopper control campaigns.

Over 700 species of fungi from approximately 90 genera are pathogenic to insects; however, only the deuteromycetes *Metarhizium* spp. and *Beauveria* spp. (class Hyphomycetes) currently fulfill the criteria required for a successful inundative biological control agent. The entomophthoralean fungi, in particular members of the *Entomophaga grylli* (Fres.) Batko species complex, represent a group of obligate pathogens found in most areas of the world that have frequently been recorded decimating populations following epizootics. Although species in the *E. grylli* complex have been used successfully in some classical biocontrol introductions in the USA, difficulties with host specificity and *in vitro* mass production limit their application for inundative release.

Recent research programs have developed the fungal pathogen *Metarhizium anisopliae* var. acridum for the control of locusts and grasshoppers in Africa and Australia, and *Beauveria bassiana* for grasshopper control in Canada. Currently the development of microbial-based pesticides follows the same procedures of testing and registration as the chemical ones. Ongoing technological research in these programs has resulted in significant advances in the *in vitro* production, storage and formulation characteristics of such pathogens and recently has been the focus of commercial scale efforts to produce available mycopesticide products. Accordingly, applied using conventional spraying equipment at rates of 0.5–5 l per hectare, mycopesticides have proven at least as effective as chemical insecticides against locusts and grasshoppers in a variety of ecological zones.

► Grasshoppers, Katydids and Crickets
► Diseases of Grasshoppers and Locusts
► Desert Locust Plagues

References

Carruthers RI, Onsager JA (1993) Perspective on the use of exotic natural enemies for biological control of pest grasshoppers (Orthoptera: Acrididae). Environ Entomol 22:885–903

Chapman RF, Joern A (1990) Biology of grasshoppers. Wiley, New York, NY

Goettel MS, Johnson DL (eds) (1997) Microbial control of grasshoppers and locusts. Mem Ent Soc Can 171, 400 pp

Joern A, Gaines SB (1990) Population dynamics and regulation in grasshoppers. pp. 415–460 in Chapman RF, Joern A (eds) Biology of grasshoppers. Wiley, New York, NY

Lomer CJ, Bateman RP, Johnson DL, Langewald J, Thomas MB (2001) Biological control of locusts and grasshoppers. Annu Rev Entomol 46:667–702

Grasshoppers, Katydids and Crickets (Orthoptera)

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Members of the order Orthoptera are found at nearly all latitudes, though they are primarily tropical insects as judged by species diversity, which is greatest in warm areas. Most are known for their well-developed hind legs and jumping abilities, but many are noteworthy because they "sing," particularly at night. Orthopterans, or at least the grasshoppers and locusts, are often considered synonymous with "plagues" due to the devastating damage they inflict during periods of abundance.

Orthopterans are usually medium-sized to large insects. Not surprising for a large taxon, the wing condition varies considerably. They may be apterous (wingless), micropterous (short-winged and incapable of flight), or macropterous (long-winged and capable of flight). When bearing wings, which is the usual condition, they usually bear two pairs, and sometimes are capable of very strong flight. The name Orthoptera means "straight-winged" and refers to the thickened front wings or tegmina. The front wings bear numerous veins, and function more for protection than as an aid for flight. The front wings often are pigmented with a color or pattern that provides camouflage. Sometimes the front wings are quite broad and modified to resemble leaves. The hind wings usually are broader, folded like a fan, and though sometimes brightly colored, often are unpigmented. The wings, even if short, are often involved in sound production. Species inhabiting open desert and grasslands tend to be strong fliers, those inhabiting woodlands, islands and mountaintops tend to be flightless. In a few taxa, the second pair of wings is absent. In several groups, including many crickets, katydids and pygmy grasshoppers, the front wings are shorter than the hind wings.

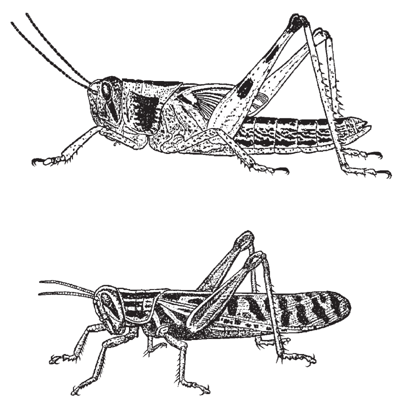
Orthopterans possess chewing mouthparts. Their eyes are large, and ocelli are usually present and three in number. The antennae usually are narrow, but vary in length: short in suborder Caelifera and long in suborder Ensifera. The thorax is large, and the saddle-shaped pronotum bears large lateral lobes that serve as the sides of the thorax. The legs are long. The hind legs are most often enlarged, especially the hind femora, and allow the insects to jump when alarmed. The tarsi have 1–4 segments and normally end with a pair of claws. Contrary to popular belief, normal locomotion is by walking, not jumping. Sometimes the front legs are enlarged, either for digging or for prey capture. The abdomen consists of about 11 segments and usually is free of notable structures other than the cerci and the ovipositor. Tympana, or hearing organs, are commonly present in these insects. In the suborder Caelifera, they are located on the side of the first abdominal segment. In the suborder Ensifera, they are found on the front tibiae.

Orthopterans display gradual metamorphosis. After hatching from the egg, the immature stage (nymph) feeds and grows, molting four or more times before reaching the adult stage. The number of molts varies considerably among taxa, and is commonly 4 or 5 in grasshoppers, but generally more than 10 in crickets. As in all exopterygote (wings developing externally) insects, the nymphs greatly resemble the adults, both in appearance and in mode of life. There is an exception, however. Grasshoppers and katydids hatching in the soil actually have a pronymphal stage preceding the first instar. This initial form is called the vermiform (worm-like) larva, and consists of the young nymph encased in a cuticular covering. The vermiform larva wriggles through the soil to the surface, and then the nymph escapes the covering, beginning its above-ground existence as a young hopper. The vermiform stage is not counted in the instar numbering system because it is just the first instar within a sheath.

Nymphs and adults can be difficult to distinguish (Fig. 39). The principal differences in appearance are the imperfectly developed wings and genitalia of nymphs. Nymphs have external wings pads that enlarge with each molt. Their shape is useful for determining the instar. In Acrididae, Tettigoniidae and Gryllidae, the wing pads initially point downward, but part-way through nymphal development, the orientation switches and the wing pads point upward or backward. With wingless or short-winged species, distinguishing the instar is more difficult. At maturity, the males court the females (rarely the roles are reversed) and copulate. In the suborder Caelifera, the male deposits the sperm internally. In the suborder Ensifera, the males of some taxa attach a spermatophore (packet containing sperm) externally at the female' s genital opening, whereas others display the internal sperm deposition system. In both cases, the female stores sperm until oviposition (egg deposition), when fertilization occurs.

Insects with gradual metamorphosis have the ability to regenerate lost limbs. If a grasshopper loses an antenna or leg as a young nymph, the missing appendage is regrown, in part, at the next molt. If the damage occurs early enough in the development of the insect, the lost appendages may be completely regenerated. These insects also shed limbs readily, a process called autonomy. If a leg is grasped by a predator or caught in a spider web, the leg may be shed, allowing the insect to escape.

The order Orthoptera is usually divided into two suborders: Caelifera and Ensifera. The suborder Caelifera consists of the grasshoppers and locusts (including the deceptively named pygmy



Grasshoppers, Katydids and Crickets (Orthoptera), Figure 39 Typical nymphal and adult stages of a grasshopper, *Schistocerca americana* (Thomas). Note that they are similar in body form, with the primary distinguishing factor the abbreviated wings of the nymph (*top*). Shown is the sixth instar, which bears the largest wings prior to the molt to the adult. Unfortunately, many grasshopper species possess such abbreviated wings as adults, making age determination difficult. Some possess both short-winged and long-winged forms. A few species show no development of wings. (images from United States Department of Agriculture).

mole "crickets," which are now recognized to be derived from grasshoppers, not crickets). The suborder Ensifera consists of the katydids and crickets (including the true crickets, mole crickets, camel crickets and Jerusalem crickets). There are many easily-recognizable groups within the order, and there is little dispute about most of these divisions and their phylogenetic relationships. However, there is considerable disagreement over the placement of the groups within the taxonomic hierarchy, i.e., whether or not they should be regarded as superfamilies, families or subfamilies. There are more than 25,000 species of Orthoptera in the world and, depending on the author of the classification system, up to about 35 families within the order.

Suborder Caelifera

The Caelifera usually have enlarged hind femora, short antennae, and tarsi with three or fewer segments. The antennae are normally threadlike, sometimes flattened, and occasionally enlarged at the tip. Tympana are often present, and are located on the sides of the first abdominal segment. Wing length is variable, but the cerci and the ovipositor are always short. Most species are diurnal, and phytophagous. Some primitive caeliferans, such as Eumastacidae, Tetrigidae and Tridactylidae, feed on more primitive plants, such as ferns and algae. Some Caelifera species inhabit areas of bare soil, many are associated specifically with grasses or broadleaf plants, while others dwell in trees. Visual and acoustic displays are part of the mating ritual of many species, and one or both sexes may produce sound. Sound production usually results from rubbing the hind legs against the front wings (called stridulation), although some groups stridulate by rubbing the front wings against the hind wings. Wing snapping in flight (called crepitation) also can occur. Eggs are normally deposited in the soil in clusters, and usually within a protective foamy structure called an egg pod. Univoltine and multivoltine species occur, with a tendency for greater multivoltinism in the warmer latitudes.

Following is one possible classification system for Caelifera, which basically follows Otte' s Orthoptera Species File. Subfamilies are not given in the following list except in the case of Acrididae, the largest and most important family.

Suborder: Caelifera
- Superfamily: Acridoidea
  - Family: Acrididae
    - Subfamily: Acridinae
    - Subfamily: Calliptaminae
    - Subfamily: Catantopinae
    - Subfamily: Conophyminae
    - Subfamily: Coptacridinae
    - Subfamily: Cyrtacanthacridinae
    - Subfamily: Dericorythinae
    - Subfamily: Egnatiinae
    - Subfamily: Eremogryllinae
    - Subfamily: Euryphyminae
    - Subfamily: Eyprepocnemidinae
    - Subfamily: Gomphocerinae
    - Subfamily: Hemiacridinae
    - Subfamily: Illapeliinae
    - Subfamily: Lithidiinae
    - Subfamily: Melanoplinae
    - Subfamily: Oedopodinae
    - Subfamily: Ommatolampinae
    - Subfamily: Oxyinae
    - Subfamily: Podisminae
    - Subfamily: Proctolabinae
    - Subfamily: Rhytidochrotinae
    - Subfamily: Spathosterninae
    - Subfamily: Teratodinae
    - Subfamily: Tropidopolinae
    - Subfamily: Trybliophorinae
  - Family: Charilaidae
  - Family: Lathiceridae
  - Family: Lentulidae
  - Family: Ommexechidae
  - Family: Pamphagidae
  - Family: Pauliniidae
  - Family: Pyrgomorphidae
  - Family: Romaleidae
  - Family: Tristiridae
- Superfamily: Eumastacoidea
  - Family: Eumastacidae

Family: Proscopiidae
Superfamily: Pneumoroidea
Family: Pneumoridae
Family: Tanaoceridae
Family: Xyronotidae
Superfamily: Trigonopterygoidea
Family: Trigonopterygidae
Superfamily: Tetrigoidea
Family: Tetrigidae
Superfamily: Tridactyloidea
Family: Cylindrachetidae
Family: Regiatidae
Family: Ripipterygidae
Family: Tridactylidae

Following is information on some of the important families and subfamilies within the suborder Caelifera:

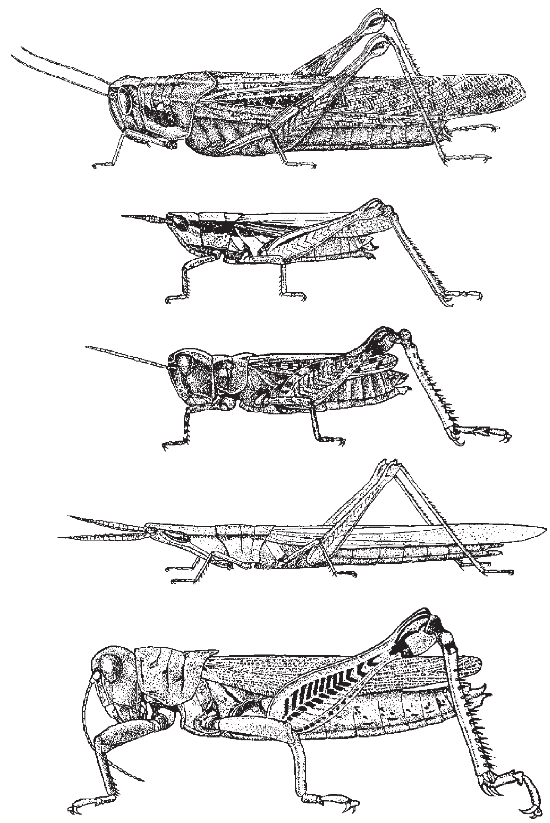
Family Acrididae

This is the largest family of the Orthoptera, and consists of the "true" grasshoppers and locusts. It is not uncommon to see other approaches to the classification of this family. The acridids are small to large in size, and stout to slender in general appearance. Their color is variable, but green and brown are common. The antennae and the pronotum are elongate and distinct. The legs are long, the hind legs are especially long and the femora is stout. The wings are variable in length, but often long. Acridids possess tympana, and sometimes produce sound. They are found in nearly all habitats. They are generally phytophagous, but vary in specificity. Eggs are deposited within pods in the soil; pods may contain three to 200 eggs, depending on the species.

Some subfamilies, such as Catantopinae, Gomphocerinae, Melanoplinae and Oedopodinae, are large and contain 500 or more species. Other subfamilies possess as few as one to five species. Some subfamilies are quite limited geographically and are found only on a single continent. Other taxa are found across Africa, Europe, Asia and Australia, or even more broadly (though they are absent from Antarctica).

Subfamily Acridinae (Silent Slantfaced Grasshoppers)

Grasshoppers in this subfamily have a slanted face and flattened, sword-shaped antennae (Fig. 40). Acridines lack a spine (the prosternal spine) between the front legs. The hind wings are colorless or nearly so. Acridinae are very similar in appearance to the



Grasshoppers, Katydids and Crickets (Orthoptera), Figure 40 Representative grasshoppers in the family Acrididae (*top to bottom*): a birdwing grasshopper, *Schistocerca nitens* Thunberg (subfamily Cyrtacanthacridinae); stridulating slantfaced grasshoppers, *Opeia obscura* (Thomas), *Psoloessa texana* (Scudder), and *Achurum sumichrasti* Saussure (subfamily Gomphocerinae); a New World spurthroated grasshopper, *Melanoplus differentialis* Thomas (subfamily Melanoplinae). (images from Arizona Agricultural Experiment Station).

stridulating slantfaced grasshoppers (subfamily Gomphocerinae), but as the common name suggests, members of this subfamily lack stridulatory pegs on the hind femora of males and thus do not produce sound. This subfamily is most abundant in Africa and Eurasia, though it occurs widely. Over 400 species are known.

Subfamily Calliptamine

These small to medium-sized grasshoppers are fairly typical in most respects, but the males are distinguished by their large, forceps-like cerci. The antennae are threadlike. The face is vertical or curved, but not strongly angled. The wing length is variable. Tympana are present, though sound production is limited to mandibular stridulation. They occur in Europe, Africa and Southeast Asia. About 100 species are known.

Subfamily Catantopinae (Old World Spurthroated Grasshoppers)

These typical-appearing grasshoppers vary considerably in size, and in wing structure. Their antennae are threadlike. The tympana generally are present though sound production is unknown. A prosternal spine is present. They greatly resemble Melanoplinae, and are separated mostly on the basis of geography. Cantantopines occur in Europe, Asia and Africa. Over 1,000 species are known.

Subfamily Cyrtacanthacridinae

The treatment of this subfamily varies greatly among authors. Sometimes the subfamily name Cyrtacanthacridinae is used to include a great number of genera and species. Here, it is restricted to about 75 genera, the most important of which is *Schistocerca*, the birdwing grasshoppers.

These grasshoppers bear a prosternal spine ventrally between the front legs (on the prosternum). The antennae usually are threadlike. The head is not especially large in size, and these grasshoppers do not appear to be especially heavy-bodied. In most genera, the head has a vertical orientation. These grasshoppers generally have long wings. The genus *Schistocerca* contains especially long-winged, strong fliers. Cyrtacanthacridine grasshoppers do not make sounds during flight; nor do they stridulate.

The habitat preferences of these grasshoppers are highly variable. Dietary habits also vary, but generally these insects are polyphagous. This group contains many important pests. Many of the grasshoppers are called "locusts" because of the swarming behavior found in this group. These grasshoppers are found throughout the world, but the greatest diversity occurs in Africa. In *Schistocerca*, however, the greatest diversity is in Central and South America.

Subfamily Eyprepocnemidinae

These insects are fairly typical in appearance, and variable in size. The antennal shape also varies. They possess a prosternal spine. The wing length is variable. The typana are present, though sound production is limited to mandibular stridulation. These insects are found principally in Africa, but also in southern Europe and Southeast Asia. About 175 species are known.

Subfamily Gomphocerinae (Stridulating Slantfaced Grasshoppers)

Grasshoppers in this subfamily tend to have slender bodies and long, slender legs. Their heads are elongate and often cone-shaped, usually with a highly slanted face. The hindwings are not colorful. Gomphocerines often have relatively short wings, rendering them incapable of sustained flight. When disturbed, these grasshoppers leap and use their wings, but their wings often do little more than increase the distance jumped. They do not make sounds during flight. This does not mean that these grasshoppers are silent. They can stridulate by rubbing the inner surface of the hind femur on the edges of the forewing while resting. Because the males of this subfamily usually have a row of stridulatory pegs on the inner surface of the hind femora, they are also known as toothlegged grasshoppers.

The habitat of gomphocerines tends to be tall grasses in open fields. The form and color of many species allows them to blend in with stems and blades of grass, making them difficult to detect until they move. Most species feed predominantly on grasses. They are found throughout the world, and species number nearly 1,000.

Subfamily Melanoplinae (New World Spurthroated Grasshoppers)

These grasshoppers bear a prosternal spine, the basis for their common name. For this reason, they are often grouped into the Cyrtacanthacridinae. The antennae usually are threadlike. The head is not especially large, and they do not appear to be especially heavy-bodied. In most genera, the head has a vertical orientation. The wing length is variable. Melanoplines do not make sounds during flight; nor do they stridulate. The habitat of these grasshoppers is highly variable. Thus, their dietary habits vary. This group contains many important crop and pasture pests. During periods of drought, they often attain high densities and cause considerable damage. They are found in North, Central and South America. Over 600 species are known.

Subfamily Oedipodinae (Bandwinged Grasshoppers)

The bandwinged grasshoppers are usually heavy bodied, and bear enlarged hind legs. The head of these grasshoppers often appears enlarged and broadly rounded. The orientation of the face is nearly vertical. Bandwinged grasshoppers lack a spine between the front legs. The bandwinged grasshoppers tend to be gray or brown in color, and often are mottled with darker spots. The forewings frequently bear distinct or indistinct transverse bands. The bandwinged grasshoppers usually bear bright colors, but this may not be obvious. The hindwings are often yellow, orange, or reddish basally, with a broad black band crossing near the center of the wing. The colorful hindwings are hidden by the front wings except when in flight. The males produce sound in flight.

The oedipodine grasshoppers normally are associated with open, sunny areas, and particularly with bare soil where their coloration provides excellent camouflage. About 800 species are known throughout the world.

Subfamily Oxyinae

These are small to medium-sized grasshoppers, and their body has a smooth integument. They do not stridulate, and they lack tympana. The wing length is variable. The antennae are threadlike. An interesting characteristic of these grasshoppers is that the hind tibiae usually are expanded distally, which is thought to be an adaptation for swimming. The female' s ovipositor valves are serrate or spined. Oxyinids are found in Africa, Europe, Southeast Asia and Australia, but are most abundant in humid, tropical habitats, especially wet environments. About 175 species are known.

Family Eumastacidae

This is one of the more primitive forms of grasshoppers, and they are sometimes referred to as monkey grasshoppers. The common name is derived from their agility when moving through vegetation. They tend to be small to medium in size. These insects lack tympana. They may bear wings, or be wingless. The legs, when the insect is at rest, are often held away from the body. The tarsi are three-segmented. The antennae usually are variable in shape, unusually short, and often bear a small tubercle on an apical segment, called the antennal organ. They lack a prosternal spine. These are tropical insects, and are absent from Europe and northern Asia. In North America, they are found only in the warm-weather Southwest. They feed on ferns, algae and gymnosperms. Most of the approximately 750 known species occur in the Old World.

Family Pamphagidae

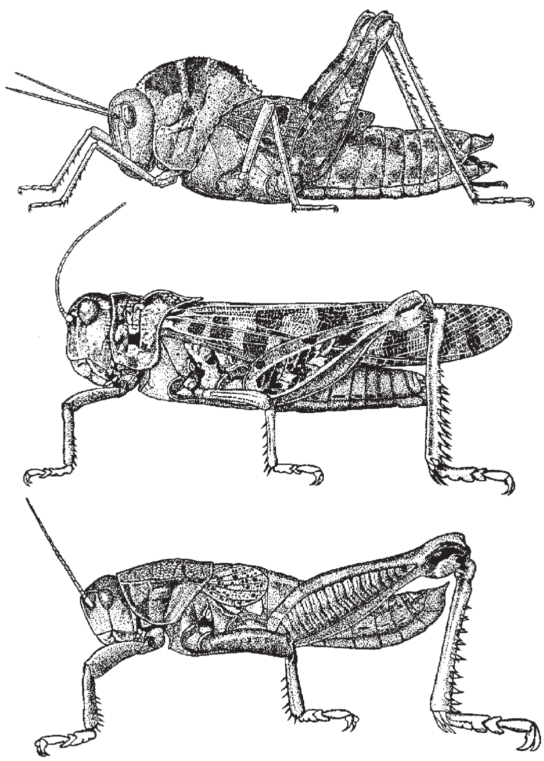
Generally medium or large in size, these grasshoppers possess a prosternal spine or elevated process. The pronotum is often elevated, sometimes forming a distinct crest. The wing development is variable. The tympana are either present or absent, and stridulation occurs. These grasshoppers often are cryptically colored, allowing them to blend with rocky soil and sand. These grasshoppers are found in Africa, southern Europe and Asia. Over 300 species are known.

Family Pyrgomorphidae

These insects have a conical head, usually with a very slanted face. They have a relatively soft body and weak integument. The antennae are threadlike or flattened. A prosternal spine or elevated process on the prosternum is present. Often brightly colored, they also excrete body fluids from between the first and second abdominal segments that provides a form of chemical protection that is variously repellent or poisonous. Wing length varies in this group. These grasshoppers usually are associated with grass vegetation in tropical and subtropical areas. They are known mostly from eastern Africa, Southeast Asia, Australia, and Central and northern South America – basically everywhere except North America. Over 400 species are known in this family.

Family Romaleidae

This group, also known as lubber grasshoppers, is sometimes considered to be a subfamily of Acrididae. It is distinguished, in part, by having a spine on both the inner and outer surface at the tip of the hind tibiae. Other grasshoppers (Fig. 41) may have moveable spurs, which resemble spines, but lubbers also have immovable spines at this location. Lubber grasshoppers also bear a prosternal spine. Lubber grasshoppers often are large, robust, colorful and usually bear short wings. The name "lubber" is derived from the heavy-bodied appearance and clumsy behavior of these insects. The shape of the



Grasshoppers, Katydids and Crickets (Orthoptera), Figure 41 Representative grasshoppers in the family Acrididae (*top to bottom*): bandwinged grasshopper, *Tropidolophus formosus* (Say) and *Xanthippus corallipes* Haldeman (subfamily Oedipodinae). Representative grasshopper in the family Romaleidae: a lubber grasshopper, *Brachystola magna* Girard. (images from Arizona Agricultural Experiment Station).

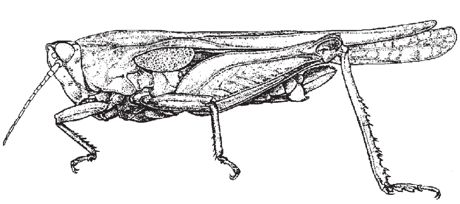
head, though variable, is usually broadly rounded. The hind femora are enlarged. When disturbed, lubber grasshoppers may hiss and spread their wings. The males also may use their wings to stridulate. The forewings and hindwings sometimes are brightly colored. The lubber grasshoppers are found in North, Central and South America, with their abundance greater in the southern latitudes. About 500 species of Romaleidae are known.

Family Tanoceridae

These grasshoppers, known also as desert long-horned grasshoppers, are medium in size and wingless. The threadlike antennae are relatively long in males and shorter in females. They are nocturnal, and are not often found by collectors. They are known only in the southwestern region of North America. Only four species from this family have been described thus far.

Family Tetrigidae

The pygmy grasshoppers (Fig. 42) are also known as groundhoppers and grouse grasshoppers. They are distinguished by their small size, usually 6–16 mm in length; their dull, cryptic coloration, usually brownish gray, gray, or black or mottled, but never green; their prominent eyes; and especially their greatly elongated pronotum, which often extends backward to the tip of the abdomen and ends in a sharp point. The antennae are relatively short. They may be long- or short-winged, or wingless. Like other grasshoppers, their hind femora are enlarged. Both sexes stridulate, and mating is a very brief process. They apparently feed on algae and possibly other organic matter in the soil. They often are found in marshy areas and at the margins of water, or in moss covered habitats. Some can descend into water, carrying an air bubble with them. They deposit loose clusters of eggs in wet soil. They tend to live in small groups in a more or less gregarious condition. They are difficult to collect unless special effort is made to sweep close to the soil. In some environments, they may be common. Tetrigids are found throughout the world, but they are most abundant in Southeast Asia. About 1,200 species are known.



Grasshoppers, Katydids and Crickets (Orthoptera), Figure 42 Representative of the family Tetrigidae: (*top*) a pygmy grasshopper, *Tetrix subulata* (Linnaeus).

Family Tridactylidae

These very small insects, usually measuring only 4–10 mm in length, are grasshoppers despite their common name: pygmy mole crickets. The antennae are relatively short, as with acridid grasshoppers. However, they possess some unusual features that differentiate them from other grasshoppers. They resemble mole crickets because they have front legs that are adapted for digging in soil and an arched pronotum. The tip of the abdomen bears a set of bristly appendages that resemble cerci, so they appear to have two sets of cerci. The hind tarsi possess plates that help them move on water, an important feature because they frequent the sandy edges of streams and ponds. They are quite good at walking on the water surface. Their diet consists mostly of organic material such as algae, possibly fungi, nematodes and bacteria, often ingested along with sand particles. Tridactylids are found throughout the world, but seem to flourish in tropical and subtropical locations. Nearly 200 species are known.

Suborder Ensifera

The ensiferans, like the caeliferans, are jumping insects. However, their legs tend to be longer, and the hind femora less enlarged, than the caeliferans. Their most distinctive feature is their long, threadlike antennae, which normally exceed the length of the body. The tarsi are three or four-segmented. The tympana, when present, are located on the front tibiae. Stridulation is common, and normally is caused by rubbing one front wing against the other. Sometimes the wings are slightly elevated when singing, but this behavior varies among taxa. Females bear a long sword-shaped or cylindrical ovipositor. The wing length is variable, but often even the long-winged species are weak fliers. Most species are nocturnal, and dietary habits vary from carnivory to phytophagy, but omnivory is common. Ensiferans often are associated with thick vegetation, and are most common in mesic areas. The superfamily Tettigonioidae, in particular, frequent vegetation almost exclusively. The Gryllacridoidea and Grylloidea, in contrast, often seek shelter in crevices, tunnels beneath the soil, or tree holes. Acoustic displays are an important part of the mating ritual of many species. Eggs are deposited singly, though several may be laid at the same location. Unlike grasshoppers, katydids and crickets do not produce egg pods. Some crickets and katydids deposit eggs on or in vegetation, others in soil.

Following is one possible classification system for Ensifera, based on that found in Otte's Orthoptera Species File. Subfamilies are not given, except in the case of the Tettigoniidae and Gryllidae, the most important groups.

- Suborder: Ensifera
  - Superfamily: Tettigonioidea
    - Family: Haglidae
    - Family: Tettigoniidae
      - Subfamily: Austrosaginae
      - Subfamily: Bradyporinae
      - Subfamily: Conocephalinae
      - Subfamily: Hetrodinae
      - Subfamily: Lipotactinae
      - Subfamily: Listroscelidinae
      - Subfamily: Meconematinae
      - Subfamily: Microtettigoniinae
      - Subfamily: Phaneropterinae
      - Subfamily: Phasmodinae
      - Subfamily: Phyllophorinae
      - Subfamily: Pseudophyllinae
      - Subfamily: Saginae
      - Subfamily: Tettigoniinae
      - Subfamily: Tympanophrinae
      - Subfamily: Zaprochilinae
    - Family: Prophalangopsidae
  - Superfamily: Gryllacridoidea
    - Family: Gryllacrididae
    - Family: Cooloolidae
    - Family: Anostostomatidae
    - Family: Stenopelmatidae
    - Family: Schizodactylidae
    - Family: Rhaphidophoridae
  - Superfamily: Grylloidea
    - Family: Gryllidae
      - Subfamily: Brachytrupinae
      - Subfamily: Cachoplistinae
      - Subfamily: Eneopterinae
      - Subfamily: Euscyrtinae
      - Subfamily: Gryllinae
      - Subfamily: Gryllomiminae
      - Subfamily: Itarinae
      - Subfamily: Malgasiinae
      - Subfamily: Nemobiinae
      - Subfamily: Oecanthinae
      - Subfamily: Pentacentrinae
      - Subfamily: Podoscirtinae
      - Subfamily: Pteroplistinae
      - Subfamily: Sclerogryllinae
      - Subfamily: Trigonidiinae
    - Family: Gryllotalpidae
    - Family: Mogoplistidae
    - Family: Myrmecophilidae

Following is information on some of the important families and subfamilies within the suborder Ensifera.

Family Anostostomatidae

This unusual group is known as king crickets and wetas. They are large, stout, and have oversized heads. Nearly all are wingless, but a few have fully formed wings. The mandibles and hind legs are sometimes enlarged. they are nocturnal. King crickets seem to be omnivores, though wetas are herbivores. To deter avian and reptilian predation, wetas raise their hind legs, exposing long spines. However, hiding below-ground is the principal defense. Wetas possess large tympana on their front legs. wetas and king crickets stridulate, though their sound production is a relatively primitive, intermediate stage in the evolution of acoustic signaling. They also transmit vibratory signals through their substrate. Tree wetas, but not king crickets, maintain harems of females and possess enormous mandibles that they use for fighting with competing males, whereas giant weta males freely compete for females without aggression. The king crickets and wetas occur in a variety of habitats. About 40 king crickets are known from southern africa, and 60 from australia and New Zealand. Wetas occur in Australia and New Zealand. Wetas are at risk of extinction because they are relatively defenseless against imported animals such as rats.

Family Cooloolidae

The cooloolids are called cooloola monsters due to their unusual appearance. These insects, though considered to be ensiferans, have short (10-segmented) antennae. They possess a large abdomen, and relatively short legs and with a muscular, hump-backed appearance. They resemble king crickets and wetas (Anastostomatidae) and to a lesser degree Jerusalem crickets (Stenopelmatidae). These are not leaping insects. Also, they do not tunnel, rather, living below ground where they "swim" through sandy soil. This very small (three species) and unusual family is known only in Australia.

Family Gryllacrididae

Some gryllacridids are known as leaf-rolling crickets, but not all species exhibit this behavior. They produce silk from glands in their mouthparts, and use it to tie leaves. The leaf rolls provide daytime shelters, but some species inhabit burrows in soil. The common name raspy crickets has also been suggested. This name stems from a raspy sound produced during defense. These are robust crickets, and can be fairly large, attaining 15 cm in length. They may be winged or wingless. The antennae are as long as or longer than the body. They are distinguished by the lateral lobes of the tarsi, and the presence of pegs on the inner surface of the hind femora that rub against the abdomen. They are not as long-legged as the cave and camel crickets (Rhaphidophoridae), and are soft bodied as compared to the king crickets and wetas (Anastostomatidae). This group is not well known, but all are thought to be nocturnal. They occupy varied habitats, and their dietary habits include herbivory, omnivory and carnivory. They are found widely in southern Africa, southwestern Asia, Australia, the Pacific region and South America. Few species are known from the northern hemisphere. Over 600 species are known around the world.

Family Gryllidae

Most crickets are compact and large-headed insects. Their antennae are long, usually reaching the tip of the abdomen or beyond. The forewings, when fully formed, are relatively broad, and flattened over the abdomen. Many species are wingless or short-winged. The front wings may be shorter than the hind wings, and in males, may function principally as acoustic devices. Many species can only be recognized by their calling behavior. Some species are mute. Tympana are found on the front tibiae. The ovipositor is long, thin and tubular. The body color is dull, usually pale, brownish or black. Long cerci are found near the tip of the abdomen and are similar in both sexes. Gryllids are often considered to be omnivorous, which is largely true, though individual species vary from herbivorous to nearly carnivorous. About 3,000 species occur in this large family.

Subfamily Eneopterinae (Bush Crickets)

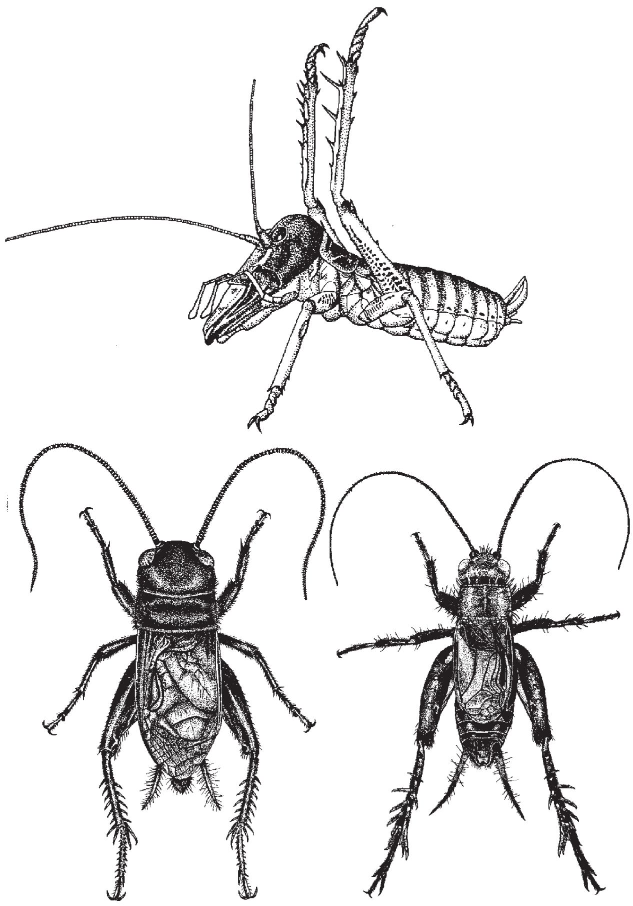
The bush crickets are medium sized and slender. The body usually has a fine covering of hairs. They frequent vegetation rather than soil. About 200 species are known from this subfamily.

Subfamily Gryllinae (Field Crickets)

These common crickets (Fig. 43) are similar to the ground crickets (Nemobiinae), but usually are medium in size rather than small. They tend to be heavy-bodied and brown or black in color. Their wing length varies considerably. They can call during the day and night, and tend to dwell belowground. Many species are similar morphologically and are distinguished by their calling behavior. They are omnivorous. About 500 species are known and are distributed widely in the world. A few species are considered to be crop pests.

Subfamily Nemobiinae (Ground Crickets)

The ground crickets tend to be small, and often bear a sparse covering of hairs. Tympana are present on the front tibiae. The wing length is variable. They often are uniformly brown, which



Grasshoppers, Katydids and Crickets (Orthoptera), Figure 43 **Representative of the family Anostostomatidae (*top*) a weta, *Hemideina crassidens* (Blanchard) (image from Larry Field); the family Gryllidae: (*bottom left*) a field cricket, *Gryllus veletis* (Alexander and Bigelow) (subfamily Gryllinae); and (*bottom right*) a ground cricket, *Allonemobius griseus* E.M. Walker (subfamily Nemobiinae) (images from Lyman Entomological Museum).**

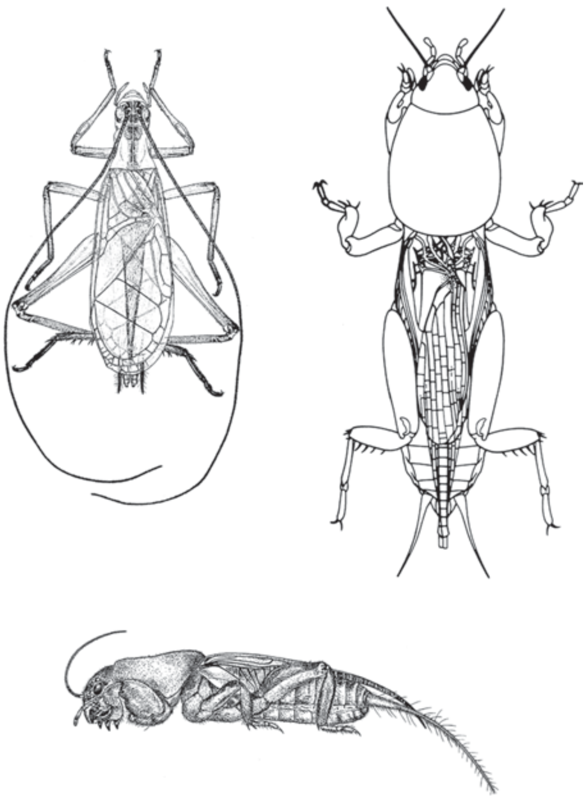
allows them to blend in well with their terrestrial environment. These insects can be quite numerous in pastures and woodlands, and can be active during the daylight hours. They are omnivorous. About 200 species are known around the world.

Subfamily Oecanthinae (Tree Crickets)

The tree crickets (Fig. 44) are slender and pale colored, often greenish or whitish. The males tend to have broad front wings. Most are quite vocal. They inhabit trees, shrubs and weedy fields. Some cause injury to trees and shrubs by depositing their eggs within twigs. Tree crickets tend to be predatory. They are found throughout the world, but are most numerous in Africa and South America. About 175 species occur in this subfamily.

Subfamily Trigoniinae (Sword-Tail Crickets)

These insects tend to be small, and pale in color. The wing length is variable, though the wings can be quite long when present. Tympana are present. Sword-tail crickets often are found in vegetation adjacent to water, and do not normally frequent the soil surface. About 275 species are known throughout the world.



Grasshoppers, Katydids and Crickets (Orthoptera), Figure 44 Representative of the family Gryllidae, (*top left*) a tree cricket, *Oecanthus nigricornis* (subfamily Oecanthinae); the family Gryllotalpidae, (*top right*) a mole cricket, *Scapteriscus* sp.; and (*bottom*) a mole cricket, *Neocurtilla hexadactyla* (images Lyman Entomological Musuem except *Scapteriscus* from Florida Division of Plant Industry).

Family Gryllotalpidae

Among the most easily distinguished orthopterans, the mole crickets bear wide forelegs modified for digging. Both the femora and tibiae are flattened, with the tibiae bearing enlarged teeth or "dactyls." The hind legs are not markedly enlarged. The antennae are shorter and thicker than in many ensiferans. The oval pronotum is disproportionately large and sturdy. They are often, but not always, long-winged. The ovipositor is not apparent. These insects dwell below-ground during the day, often emerging in the evening to sing or eat. They sing from specially constructed acoustical chambers, constructed in the soil, that expand as they open to the outside like the end of a trumpet. This design serves to amplify their call. Some species are mute. Mole crickets create deep permanent burrows, but also superficial foraging tunnels. The eggs are deposited in special egg chambers within the burrows. Their dietary habits range from carnivorous to phytophagous, but some are important vegetable and pasture pests. Three species of *Scapteriscus* from South America were accidentally introduced into southeastern North America and have caused considerable damage. Less than 100 species are known from this family.

Family Mogopistinae

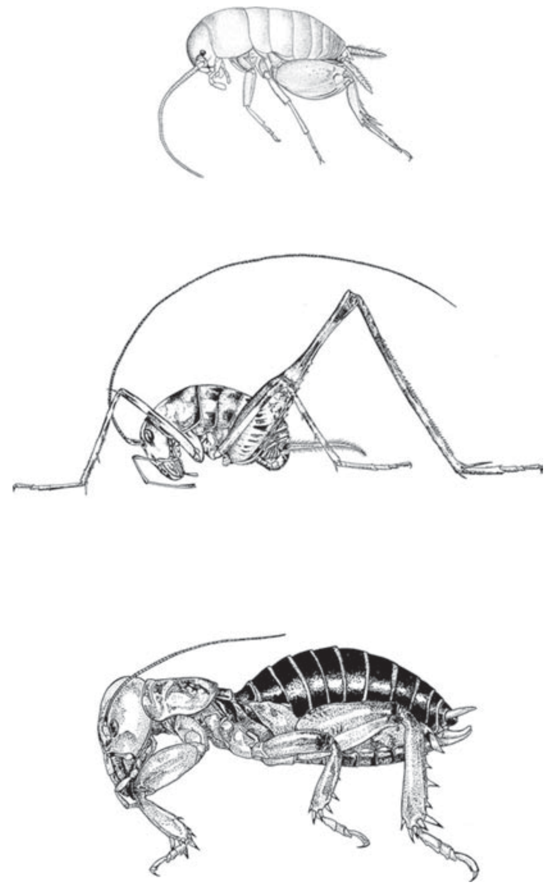
These insects are called scaly crickets. Resembling silverfish, these small crickets tend to be short-winged, flat and slender. Their name is derived from the presence of translucent scales covering most of their body. They are mostly tropical in distribution and seem to favor areas near water. Over 350 species are known.

Family Myrmecophilidae

This is a small family of very small, wingless, oval and flattened crickets that inhabit ant nests. They cannot live independently from the ants. The eyes are reduced, though the cerci are pronounced. The tympana are lacking. The ovipositor is shortened and stout. The hind femora are broad. These unusual insects feed on secretions produced by ants. Apparently, they are taken to be ants by their hosts. Some species are parthenogenetic. Only about 50 species are known.

Family Rhaphidophoridae

The camel crickets (Fig. 45) are similar to the Tettigoniidae, but wingless. They bear long, thread-like antennae, usually longer than in Tettigoniidae. Their legs also are quite long. The pronotum is smoothly rounded and lacks ridges. Unlike most of their close relatives, they do not have a hearing organ on the front tibia. They are not usually considered to be singers, though some are capable of making some sounds, and some species have stridulatory pegs. Because they lack wings, it is difficult to distinguish adults from nymphs except by the developing ovipositor, or fully developed male genitalia. They are dull colored insects, usually some shade of brown or gray. Camel crickets are nocturnal. About 250 species are known around the world.



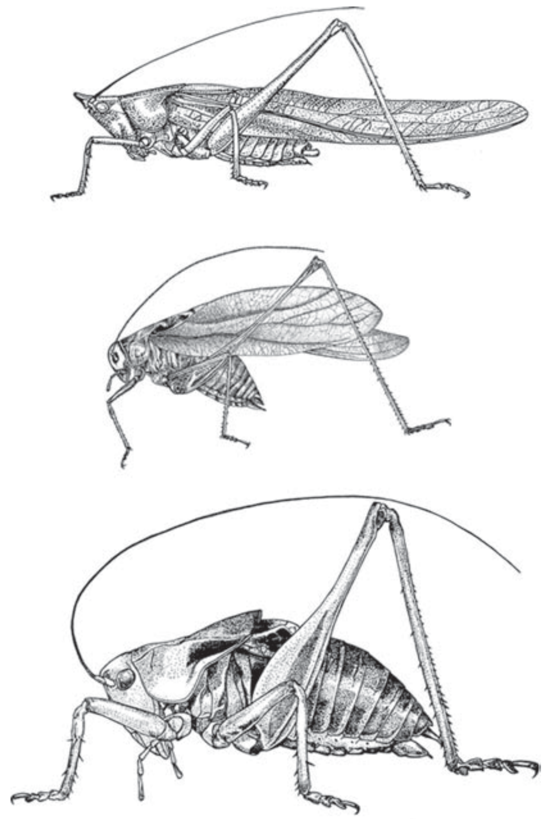
Grasshoppers, Katydids and Crickets (Orthoptera), Figure 45 **Representatives of the family Myrmecophilidae, (*top*) an ant nest-inhabiting cricket, *Myrmecophilus oregonensis* Bruner; the family Rhaphidophoridae, (*center*) a camel cricket, *Tachycines asynamorus* Adelung; and the family Stenopelmatidae, (*bottom*) a Jerusalem cricket, *Stenopelmatus fuscus* Haldeman (images from Lyman Entomological Museum).**

Family Stenopelmatidae

This group consists of cricket-like insects known as Jerusalem crickets. They are flightless, nocturnal and infrequently encountered. Thus, they are poorly known. Jerusalem crickets are large, somewhat hump-backed, with large heads resembling anastostomatids. Their legs bear stout spines. They have large mandibles and bite readily. When disturbed, Jerusalem crickets will flip onto their backs, exposing their mandibles in a defensive posture. They seem to be omnivores, and they benefit from animal protein. Most occupy arid western North America, often resting below-ground or beneath objects, but surfacing at night to feed. In Central America, however, some inhabit rotting logs and stumps. Jerusalem crickets can be large, some species weighing as much as 8 g, but others weigh less than 1 g. They transmit vibratory signals through the substrate. The males are sometimes eaten by the females after copulating. At least 80 species are known to occur in North America, but most are undescribed.

Family Tettigoniidae

This is a large and important family that is variously known as katydids in North America and Australia, or bush crickets in other English-speaking areas. These species tend to be medium-sized or large in size, often 35–50 mm in length. The antennae are longer than the body. These insects bear tympana on the front tibiae. The pronotum only rarely bears a ridge. A large, sword-shaped ovipositor is usually present in the females. Although some katydids oviposit in soil, they also deposit eggs in leaf tissue, stem tissue and even bark crevices. Some oviposit flattened, overlapping eggs like roof shingles on leaf and stem tissue. A small number construct "nests" of chewed plant material and mud. Katydids (Fig. 46) are usually green or brown in color, and though some species are active during the day, most are largely nocturnal. The males stridulate freely, and in many environments, these insects are an important element of night-time sounds. They are largely phytophagous, but are also omnivorous and a few feed on other insects. They prefer proteinaceous food, and even the phytophagous species often select blossoms and fruit for their higher protein content. The males tend to produce a large edible spermatophylax, a structure containing the spermatophore. The spermatophylax is passed on to the female as a nuptial gift, and is also a means of providing a protein supplement to the female when she is producing eggs. Tettigoniids are found throughout the world, and number nearly 400 species.



Grasshoppers, Katydids and Crickets (Orthoptera), Figure 46 Representatives of the family Tettigoniidae: (*top*) a coneheaded katydid, *Neoconocephalus ensiger* (Harris) (subfamily Conocephalinae); (*center*) a false katydid, *Amblycorypha oblongifolia* (De Geer) (subfamily Phanopterinae); and (*bottom*) a shield-backed katydid, *Atlanticus monticola* Davis (subfamily Tettigoniinae) (images from Lyman Entomological Museum).

Subfamily Conocephalinae (Meadow and Coneheaded Katydids)

These katydids are small to medium in size. They are long, thin insects and some have a conical head. The ovipositor may be long and sword-shaped. The antennae are long. They are green or brown, blending well with vegetation. The preferred habitat is short or tall grasses and broadleaf plants, normally in fields and swamps, but sometimes in forests. They sing mostly at night, and are found throughout most of the world. Nearly 1,000 species are known. One tribe, the copiphorini, is sometimes treated as a subfamily.

Subfamily Meconematinae (Quiet-Calling Katydids)

These are small, diurnal insects. They are found in Africa, Europe and northern Asia. Over 400 species are known in the subfamily.

Subfamily Phaneropterinae (False Katydids)

This group of katydids is distinguished by the absence of spines on the prosternum and by the wing length; the hind wings are longer than the front wings. These insects are noted songsters, and they vocalize late in the day and during the evening. They normally are brown, but pink forms are known. About 2,000 species are known.

Subfamily Phyllophorinae (Giant Leaf Katydids)

These leaf feeders are the largest of the tettigonids. Their wing spans attain 25 cm. They bear a very heavy pronotum, and the males have lost the ability to stridulate using the tegmina. There are about 70 known species, all from Australia and nearby areas.

Subfamily Pseudophyllinae (True Katydids)

These are broad-winged insects that commonly inhabit trees and shrubs. The subfamily is quite diverse in the tropics of both the New World and the Old World, and different species often mimic different natural elements of their habitat such as leaves and bark. About 1,000 species are known.

Subfamily Saginae (Stick Katydids)

These flightless insects occur in Africa, Europe and Asia. One species, of European origin, has established in North America. This flightless species, *Saga pedo*, reproduces parthenogenetically, a rare occurrence among katydids. Sagines are predators, and quite aggressive about grasping prey with their spined forelegs. About 50 species are known.

Subfamily Tettigoniinae (Shield-Backed Katydids)

Many large, ground-dwelling, flightless species are found in this subfamily. They tend to be shortwinged, and are sometimes dark in color, often brown or black. Other species in this same subfamily are long-winged and good fliers. They occupy a diversity of habitats. Some, such as the Mormon cricket, *Anabrus simplex* Haldeman, are crop pests in western North America. Omnivory and carnivory are common in this group. Nearly 900 species are known from this group. They are found throughout the world.

Evolution of Orthoptera

The evolution of Orthoptera can be traced back to the Protorthoptera of the Upper Carboniferous-Permian period some 300 million years ago. The

Protorthoptera gave rise to several primitive groups that eventually gave rise to the ancestors of the most recent orthopteroid orders. The order Orthoptera probably underwent an early split to give rise to the two major lines of evolution now recognized as Caelifera and Ensifera. Ensifera is considered to be more primitive than Caelifera.

The orthopterans are closely related to the mantids, walkingsticks, cockroaches and rock crawlers. They are less closely related to earwigs, webspinners and termites. Collectively, these taxa are referred to as the orthopteroid orders. All are thought to be descended from a common neopteran ancestor that predated the Protorthoptera.

Not everyone agrees with this interpretation, however. It is also possible that Caelifera and Ensifera evolved independently from different protorthoperan ancestors. It has even been suggested that the Orthoptera could be an artificial group (Caelifera plus Ensifera) that appears united mostly because they have enlarged hind legs for leaping. Consider that although the orthopterans produce sound, the two suborders differ in how they produce and hear sound. However, most available evidence, and most orthopterists, support the idea of a single order.

Natural Enemies of Orthoptera

There are numerous natural enemies of orthopterans, and the same types of natural enemies generally affect the several taxa of Orthoptera. However, the relative importance of the natural enemies varies among orthopterans, among different periods of the orthopteran population cycle, in different regions of the world, according to the weather and according to the soil type.

Natural enemies of orthopterans include predators (which kill and eat their prey), parasitoids (parasitic insects that develop in or on the host orthopteran and kill the host only when the parasite reaches maturity), and pathogens (microbial diseases that kill the host after the host' s nutrients are exhausted).

Important egg predators include bee flies (Diptera: Bombyliidae), ground beetles (Coleoptera: Carabidae) and blister beetles (Coleoptera: Meloidae). Nymphs and adults are captured and eaten by spiders, birds, small mammals and rodents, ants (Hymenoptera: Formicidae), sphecids (Hymenoptera: Sphecidae) and robber flies (Diptera: Assilidae). Among the important parasitoids of nymphs and adults are blow flies (Diptera: Calliphoridae), sarcophagids (Diptera: Sarcophagidae), nemestrinids (Diptera: Nemestrinidae) and tachinids (Diptera: Tachinidae). Mites (Acari) are commonly found clinging to orthopterans, and some feed on the blood of their host. Although mites weaken their host, they are not thought to be important mortality agents. Pathogens affect all stages of orthopteran development, and among the most important are nematodes, fungi, viruses and microsporidians. Nematodes and fungi are readily affected by soil and weather conditions, so their occurrence is inconsistent. However, these pathogens can have dramatic effects on orthopteran populations when conditions favor their virulence. Viruses and microsproridians are found widely, though they often are not especially virulent. The impact of pathogens is often overlooked relative to predators and parasitoids because their effect may be expressed as a shortening of the life span or as a reduction in reproduction, rather than in direct mortality.

The importance of natural enemies is difficult to measure, and the action of these beneficial organisms may come too late in a population outbreak to prevent damage. Sometimes they may interfere with one another, as when robber flies capture insect parasitoids as well as grasshoppers, or when fungal diseases kill a host insect prematurely, causing the death of the parasitoid contained in the host orthopteran. Nevertheless, there are many striking examples of natural enemies suppressing orthopteran populations. Examples of natural enemy effects include: parasitism of grasshoppers by the nematode *Mermis nigrescens* killed 71% of *Melanoplus femurrubrum* grasshoppers in Michigan, USA; mermithids infected 69% of

Locusta migratoria in wet areas of Papua New Guinea, but only 15% in dry areas; 30–70% of field crickets were infected with microsporidians in Michigan, USA; grasshoppers comprised 94% of the diet of the robber fly *Proctacanthus milbertii*, a generalist predator, in studies conducted in Montana, USA, and this fly consumed about 25% of all hoppers present; birds ate about 27% of adult grasshoppers during the summer in Nebraska, USA; over 200 species of birds in Nebraska feed on grasshoppers, and during the summer months, the average bird's stomach contains at least 25 grasshoppers at any time; parasitism of *Zonocerus* locusts exceeded 40% by a calliphorid in Africa; and the combined effects of natural enemies accounted for about 50% mortality in desert locust, *Schistocerca gregaria*, populations in Africa.

Importance of Orthoptera to Humans

Grasshoppers, katydids, crickets and other orthopterans vary considerably in their importance to humans. In some societies, grasshoppers are a minor source of food, and katydids and crickets are kept as pets for their acoustical abilities. However, these beneficial aspects are minor compared to their destructive attributes. Grasshoppers are widely recognized to be serious pests of arid-land or prairie agriculture, and to a lesser degree, in mesic areas. Katydids, crickets and allied insects usually have minor effects on agriculture, though a few species are quite damaging. Grasshoppers, katydids and sometimes other orthopterans consume considerable amounts of foliage during their nymphal development, and also as adults. Occasionally, other insect activities such as tunneling (by mole crickets) or oviposition (by tree crickets) may be the basis for injury. Pasture, forage, grain, vegetable, and even fruit and ornamental crops can be affected. Historically, grasshoppers and locusts have been very disruptive to civilizations in Africa, the Middle East, India, China and North America. However, Australia, Europe and South America also have witnessed serious problems, so, virtually no area of the globe is immune to attack by grasshoppers. However, except in areas where access to technology and funds are limited, the tools are now available to manage these pests and to prevent them from excessive destruction.

Abnormally high densities of grasshoppers are called outbreaks or plagues. Regardless of the terminology applied, the phenomenon occurs throughout the world, and its origin is invariably related to food and weather. Grasshoppers that tend to attain high densities periodically, especially those that tend to become gregarious and move together as groups or swarms, are sometimes called locusts. Locusts do not really differ from grasshoppers, other than displaying a greater degree of gregarious behavior. Even species known as locusts periodically experience periods when they are not numerous, not gregarious, and do not cause much injury.

Grasshoppers require warm and sunny conditions for optimal growth and reproduction. Warmth alone seems to be inadequate, and grasshoppers often bask in the sun to raise their body temperatures. Thus, drought stimulates grasshopper population increase, apparently because there is less rainfall and cloudy weather to interfere with grasshopper activity. A single season of such weather is not adequate to stimulate massive population increase; rather, 2–3 years of drought usually precede grasshopper plagues. Warm winter temperatures also seem to be beneficial, because less mortality occurs by overwintering nymphs and adults. This scenario explains outbreaks that occur in temperate climates, where food is not limited, but heat may be inadequate. However, it does not explain all grasshopper outbreaks.

Food is a necessary prerequisite for grasshopper success, and optimal weather alone, in the absence of adequate food supply, will prove insufficient for rapid grasshopper population growth. For outbreaks or plagues to occur, both requisites must be satisfied. Thus, some precipitation must be present at the appropriate time to stimulate plant growth, but an over-abundance results in too much cloud cover. In tropical or subtropical climates, especially warm but arid regions, precipitation is an important stimulus that increases grasshopper breeding and causes outbreaks to develop.

Management of Orthoptera Pests

The ideal way to manage orthopteran pests is to manage the environment to prevent them from attaining pest status. One example of how this can be accomplished is with weed management in fallow fields, and along roadsides and irrigation ditches. Luxurious growth of weedy vegetation often favors the survival of grasshoppers, which then can spread to adjacent crops. If this land is instead tilled or planted with short grass, fewer grasshoppers will breed there and the damage potential is greatly reduced. Unfortunately, many environments cannot be manipulated easily, and when weather or other factors favor population increase, a suppressive action must be initiated. Another example of how problems can be prevented is by introducing natural enemies of grasshoppers that have invaded a new area, and have therefore left their natural enemies behind. The introduction of a parasitic fly, *Ormia depleta*, and an entomopathogenic nematode, *Steinernema scapterisci*, for the suppression of *Scapteriscus* mole crickets in Florida, illustrates how this method can be applied effectively to invaders. However, most orthopteran pests are native, and there is little opportunity to identify natural enemies from elsewhere.

Biological suppression of orthopteran populations is difficult to achieve once they have attained damaging levels. Natural enemies sometimes eventually build to high enough levels to help decrease pest abundance. For example, wild birds will sometimes switch their feeding to take advantage of an abundance of grasshoppers, but this is effective only on a local scale, not a regional scale. Domestic fowl, especially turkeys, readily consume vast quantities of grasshoppers, and can be used for small-scale suppression. There also are grasshopper disease agents that are under investigation, and even some that are sold commercially, but so far, none has been shown to provide adequate suppression. Entomopathogenic nematodes are used for mole cricket suppression in some environments. Biological control remains a promising area for research, and the search continues for more effective products, but thus far, there are few practical options. For some people, neem products are attractive. Neem products are botanical derivatives that, when applied to plants, act as a feeding deterrent, reducing damage. Also, if applied to grasshopper nymphs, neem can act as a growth regulator, disrupting the normal growth and development, and sometimes resulting in the death or sterilization of grasshoppers. Although neem products are chemicals, many people take comfort in knowing that they are derived from plants, and are therefore somewhat "natural." Like many natural controls, effectiveness is not always consistent.

In some situations, physical barriers can provide some protection from damage. It is possible to screen or cover valuable plants with netting, floating row cover, or similar material to deny grasshoppers access to susceptible plants. This is suitable for small gardens, and is even applied commercially for ornamental plant production, wherein shade houses are sealed tightly to deny access to orthopterans. The potential for this approach is limited in scale due to the cost. For flightless species such as lubber grasshoppers or Mormon crickets, physical barriers such as a ditch with steep sides, or a short metal or plastic "wall," can prove to be effective impediments to grasshopper dispersal. If such a wall is contemplated, however, consider that orthopterans have sharp claws and can ascend vertical surfaces with amazing agility, so the top of a barrier should end in a 45 degree angle, forcing the insects to fall back.

As mentioned above, cultural management of crop- and pasture-land can sometimes be used to manipulate orthopteran abundance. The habitats most favorable for grasshopper population growth and survival are open, sunny habitats containing mixed, early to mid-successional plants. Land with trees providing moderate to deep shade rarely produce large numbers of grasshoppers. Also, land that is kept mowed, either mechanically or by livestock grazing, tends not to produce grasshoppers unless grass pasture-land is damaged by overgrazing and broadleaf weeds invade.

If natural enemies and cultural manipulations have failed to keep orthopteran pests in check, chemical insecticides are most often used to prevent excessive damage. Chemical insecticides can be applied in liquid form, by application directly to the grasshoppers, or to the plants they will walk or feed upon. Insecticides can also be applied to food bait, usually bran flakes, and distributed in the pest's environment. If insecticides are to be used, it is advisable to apply the chemicals when the pests are young. Small insects are much easier to kill than large ones, and grasshoppers and crickets are notoriously difficult to kill under any conditions. Also, because the grasshoppers usually develop in surrounding vegetation, it is usually best to take the "battle" there, and apply insecticides to the young grasshoppers before they disperse into crops and cause damage.

► Grasshoppers of the Argentine Pampas
► African Pine-Feeding Grasshopper
► Diseases of Grasshoppers and Locusts
► Grasshoppers and Locusts as Agricultural Pests
► Desert Locust Plagues
► *Rhammatocercus schistocercoides*
► Weta
► Katydids
► Jerusalem Crickets

References

Chapman RF, Joem A (eds) (1990) Biology of grasshoppers. Wiley, New York, NY

Field LH (ed) (2001) The biology of wetas, king crickets, and their allies. CABI Publishing, Wallingford, UK

Gwynne DT (2001) Katydids and bush-crickets. Reproductive behavior and evolution of the Tettigoniidae. Cornell University Press, Ithaca, NY

Huber F, Moore TE, Loher W (eds) (1989) Cricket behavior and neurobiology. Cornell University Press, Ithaca, NY

Otte D (1981/1984) The North American grasshoppers, vol 1, 2. Harvard University Press, Cambridge, MA

Otte D (1995) Orthoptera species file, vol 1–7. The Academy of Natural Sciences of Philadelphia, Philadelphia, PA. Available at http://viceroy.eeb.uconn.edu/Orthoptera

Uvarov B (1966/1977) Grasshoppers and locusts. A handbook of general acridology, vol 1, 2. Cambridge University Press, London, UK

Grasshoppers of the Argentine Pampas

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The Pampas, which occupies the Province of Buenos Aires and parts of the Provinces of Entre Ríos, Santa Fe, Córdoba, La Pampa and San Luis, are temperate subhumid grasslands. Mesothermic grasses dominate in this region of mild climate with mean annual temperature ranging from 10 to 20°C, and annual rainfall between 400 and 1600 mm. There is a general decrease southwestward in annual precipitation, soil organic matter and grassland productivity.

The landscape has been altered markedly during the last century due to agricultural and grazing activities, and pristine grasslands have been drastically modified. Most of the land has been converted to cropland, mainly soybean, corn, sunflower and wheat.

Among the most important native herbivores are grasshoppers, which are a recurrent pest of the agro ecosystems of this area. These insects may cause, in some years, forage and crop losses of considerable magnitude.

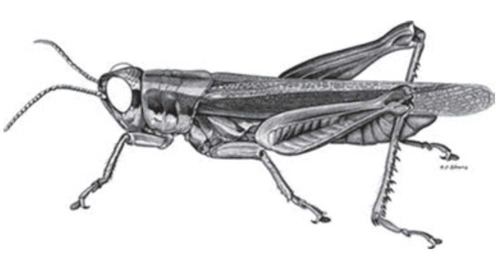
The Pampas and the Great Plains of North America have some ecological similarities in grasshopper fauna. However, species richness and diversity are higher in the US grasslands, while the Pampas have a greater diversity of higher acridid taxa, three families (Acrididae, Romaleidae and Ommexechidae) and nine subfamilies (Melanoplinae, Gomphocerinae, Copiocerinae, Leptysminae, Cyrtacanthacridinae, Acridinae, Romaleinae, Ommexechinae and Aucacrinae)

Grasshoppers of the Argentine Pampas, Table 11 **Grasshopper species composition of the argentine pampas**

Acrididae		Romaleidae
Acridinae	**Melanoplinae**	**Romaleinae**
Allotruxalis strigata (Bruner)	*Atrachelacris gramineus* G.Tos	*Diponthus argentinus* Pictet & Saus
Covasacris albitarsis Liebermann	*Baeacris punctulatus* (Thumberg)	*Elaeochlora viridicata* Serville
Laplatacris dispar Rehn	*Baeacris pseudopunctulatus* Ronderos	*Xyleus laevipes* Stål
Parorphula graminea Bruner	*Dichroplus conspersus* Bruner	*Zoniopoda omnicolor* Bruner
Copiocerinae	*Dichroplus elongatus* (G.Tos)	*Zoniopoda tarsata* Serville
Aleuas linneatus Stål	*Dichroplus maculipennis* (Blanchard)	
Aleuas viticolis Stål	*Dichroplus obscurus* Bruner	
Leptysminae	*Dichroplus patruelis* Stål	
Leptysma argentina Bruner	*Dichroplus pratensis* Bruner	
Gomphocerinae	*Dichroplus schulzi* Bruner	
Amblytropidia australis Bruner	*Dichroplus vittatus* Bruner	
Borellia brunneri (Rehn)	*Leiotettix pulcher* (Rehn)	
Euplectrotettix ferrugineus Bruner	*Neopedies brunneri* G.Tos	
Orphulella punctata De Geer	*Ronderosia bergii* (Stål)	
Rhammatocerus pictus Bruner	*Ronderosia forcipatus* (Rehn)	
Scyllina signatipennis Blanchard	*Scotussa cliens* Stål	
Scyllina variabilis Bruner	*Scotussa daguerrei* Liebermann	
Sinipta dalmani Stål	*Scotussa lemniscata* (Stål)	
Staurorhectus longicornis G.Tos		

versus two families (Acrididae and Romaleidae) and six subfamilies (Oedipodinae, Melanoplinae, Gomphocerinae, Acridinae, Cyrtacanthacridinae and Romaleinae). The Melanoplinae is the main subfamily in both regions and the genus *Melanoplus* of North American is considered to be the ecological equivalent to the South American genus *Dichroplus* (Table 11).

There exists a large-scale association between grasshopper and plant communities along the Pampas. Indeed, assemblages may differ in density, dominance, and species composition because of differences in vegetation and climatic conditions. Total species richness is thirty nine, ranging from four to sixteen at different sites. *Dichroplus pratensis* and *D. elongatus* (Fig. 47) are clearly the most common and widely distributed species in this region. Both are polyphagous species, eating grasses and forbs. Eggs hatch in November and, after passing through 5 nymphal instars, reach the adult stage in January. They have an obligatory embryonic diapause and one generation a year.



Grasshoppers of the Argentine Pampas, Figure 47
***Dichroplus elongatus* G. Tos. Another species of this genus, *D. maculipennis*, one of the most harmful species of this area thirty years ago, has exhibited very low populations during the last decade.**

In relation to damage, a population of *D. pratensis* with a peak of 22.19 individual/m^2 may cause a forage loss of approximately 274.32 kg/ha.

Another species of this genus, *D. maculipennis*, one of the most harmful species of this area thirty years ago, has exhibited very low populations duringthe last decade.

Other common species are *Laplatacris dispar*, *Amblytropidia australis*, and *Scotussa lemniscata* in the humid northeastern grasslands. The central grasslands are dominated by *D. pratensis*, *D. elongates*, *Staurorhectus longicornis*, *Leiotettix pulcher* and *D. vittatus*. *Borellia brunneri*, *Covasacris albitarsis* and *S. lemniscata* are common in the southeastern habitats. Grasshopper assemblages of the xeric western grasslands are dominated by *D. pratensis* and *Neopedies brunneri*, and among common species are *Rhammatocerus pictus*, *S. longicornis*, *D. vittatus* and the Romaleidae *Zoniopoda tarsata*.

Most species in the Pampas are rare. Some are registered every year from most sites, but in low numbers (e.g., *Baeacris punctulatus*), whereas others are found in many years but only in some sites (e.g., *Xyleus laevipes* and *Z. omnicolor*).

At present, the only control measure against these insects is the use of chemical pesticides. The microsporidian pathogen *Nosema locustae* Canning was introduced between 1978 and 1982 to control pest grasshoppers, and became established in some areas. However, no surveys to evaluate the effectiveness as a biological control agent has been conducted. Only one native microsporidian pathogen, *Perezia dichroplusae* Lange, is currently known in argentine grasshoppers. Other pathogens, like the amoeba *Malameba locustae* King & Taylor (Protozoa: Rhizopoda), the virus *Entomopox* (Poxviridae: Entomopoxvirinae) and the fungus *Entomophaga grylli* (Fresenius) (Zygomycetes: Entomophtorales) also are recorded.

References

Cigliano MM, de Wysiecki ML, Lange C (2000) Grasshopper (Orthoptera, Acrididae) species diversity in the Pampas, Argentina. Diver Distrib 6:81–91

de Wysiecki ML, Sánchez NE (1992) Dieta y remoción de forraje de *Dichroplus pratensis* (Orthoptera: Acrididae) en un pastizal natural de la provincia de La Pampa, Argentina. Ecología Austral 2:19–27

Lange CE (1998) Patógenos asociados a tucuras (Orthoptera: Acrididoideae) en las provincias de Buenos Aires y La Pampa. Monografía 16. Comisión de Investigaciones Científicas de la provincia de Buenos Aires

Sánchez NE, de Wysiecki ML (1990) Quantitative evaluation of feeding activity of the grasshopper *Dichroplus pratensis* Bruner (Orthoptera: Acrididae) in a natural grassland of La Pampa, Argentina. Environ Entomol 19:1392–1395

Soriano A (1992) Río de La Plata Grasslands. In: Coupland RT (ed) Natural grasslands. Introduction and western hemisphere. Ecosystems of the World, 8. Elsevier, Amsterdam, The Netherlands, pp. 367–407

Grassi, Giovanni Battista

Giovanni Grassi (Fig. 48) was born in the province of Como, Italy, on March 27, 1854. He was educated at the universities of Pavia and Messina (Italy) and Heidelberg and Würzburg (Germany). In 1883 he was appointed professor of zoology, anatomy, and comparative zoology at Università di Catania, and in 1895 he was appointed to a similar position at Università di Roma. His works began on intestinal worms, proceeded to Protozoa (especially of termites), continued with flies (1883, "Malefizi delle mosche") as vectors of eggs of nematodes and spores of fungi, on embryology of the honey bee, morphology and phylogeny of arthropods, the biology of termites, the transmission of malaria by *Anopheles* mosquitoes, the life history of *Phlebotomus*, on the grapevine pest *Phylloxera*, and on chaetognaths, marine eels, and development of the vertebral column. In 1908 he was made a member of the Italian senate. In 1884–1889 he studied Thysanura, *Scolopendrella*, and *Koenema mirabilis*, the last being an arachnid that he discovered. For his collaborative work with Sandias on termites, and for his studies of muraenoid eels, he was awarded the Darwin gold medal of The Royal Society. In 1898–1900, he concentrated on malaria, finding that all Italian species of *Anopheles* can transmit *Plasmodium*, and that *Plasmodium* is the same parasite that Ross described under the name

Grassi, Giovanni Battista, Figure 48 **Giovanni Batista.**

Proteosoma (1900, Studi di uno zoologo sulla malaria). He continued his studies of malaria in 1917, continued to publish, but died on May 5, 1925.

Reference

Wyatt AK (1926) Obituary. Entomological News 37:126–128

Grass Miner Moths (Lepidoptera: Elachistidae)

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Grass miner moths, family Elachistidae, comprise about 723 species worldwide, but most are Palearctic (472 sp.), and many are in the genus *Elachista*. Two subfamilies are used, or only tribes: Perittiinae and Elachistinae. The family is part of the superfamily Gelechioidea in the section Tineina, subsection Tineina, of the division Ditrysia. Adults small (5–23 mm wingspan), with head smooth-scaled; haustellum scaled; labial palpi upcurved but sometimes porrect; maxillary palpi minute, 1 to 2-segmented. Wings narrow and lanceolate, with reduced venation, but with large hindwing fringes (Fig. 49). Maculation often white with various markings or bands, or darker, sometimes with iridescence. Adults are often crespuscular or nocturnal, but some are diurnal. Larvae are leafminers (sometimes gregarious) or stem miners, especially on grasses (Gramineae) and related plant groups like Juncaceae and Cyperaceae, but other plant families are also utilized.

Grass Miner Moths (Lepidoptera: Elachistidae), Figure 49 **Example of grass miner moths (Elachistidae), *Biselachista cucullata* (Braun) from Florida, USA.**

References

Braun AF (1948) Elachistidae of North America (Microlepidoptera). Mem Am Entomol Soc 13:1–110, pl. 26
Kaila L (1996–1999) A revision of the Nearctic Elachistidae s.l. (Lepidoptera, Elachistidae). Entomologica Scandinavica 27:217–238 (1996); Acta Zoologica Fennica 206:1–93 (1997), 211:1–235 (1999)
Keila L (1999) Phylogeny and classification of the Elachistidae s.s. (Lepidoptera: Gelechioidea). Syst Entomol 24:139–169
Traugott-Olsen E (1995–1996) Phylogeny of the Elachistinae s.str. (Lepidoptera, Elachistidae). SHILAP Revista de Lepidopterologia 23:153–180, 257–290, 417–449 (1995); 24:129–149 (1996)
Traugott-Olsen E, Nielsen ES (1977) The Elachistidae (Lepidoptera) of Fennoscandia and Denmark. In: Fauna Entomologica Scandinavica, 6:1–299. Scandinavian Science Press, Klampenborg

Grass Moths

Some members of the family Pyralidae (order Lepidoptera) also known as snout moths.

► Snout Moths
► Butterflies and Moths

Gravenhorst, Johan Ludwig Christian

Johan Ludwig Gravenhorst was born in Braunschweig [Brunswick], Germany, on November 14, 1777. He was educated at the Katharinen Gymnasium in Braunschweig. Despite an early interest in natural history, he decided on a career in law, and entered Universität Helmstadt to study law. However, in 1790 he entered Universität Göttingen to study zoology, mineralogy, and botany. In 1801 he returned to Helmstadt and defended his dissertation "Conspectus historiae entomologiae" and was awarded the title of "Doctor philosophiae et magister liberalium artium." Then he returned to Braunschweig and spent all his time on entomology. His first major publication (1802) was "Coleoptera Microptera Brunsvicensia," after which he journeyed to Paris to study insect collections, and meet entomologists. On return to Braunschweig, he bought entomological collections, became a "Privatdocent" at Universität Göttingen, and published (1906) "Monographia Coleopterorum Micropterorum," which expanded his recognition among entomologists. He worked on an expanded edition of this work until Erichson' s (1840) "Genera et species Staphylinorum" made it redundant. In 1810 he accepted a position of professor of natural history and second director of the botanical garden at Frankfurt an der Oder. In 1811, this university was transferred to Breslau (now Wroclaw in Poland), and Gravenhorst followed. In 1814 he sold his insect collection to the university in return for a guaranteed annual income transferable to his widow, and he founded the zoological museum there. He began to work on Ichneumonidae (Hymenoptera) on which he published intensively to 1829. In 1830 he travelled to Prague, Vienna, and Trieste to study marine animals, on which he published. He was a member of at least 21 natural history societies in Germany, France, Italy and England. He died in Breslau on January 17, 1857, after a very lengthy illness.

Reference

Herman LH (2001) Gravenhorst, Johan Ludwig Christian. Bull Am Mus Nat Hist 265:70–71

Gravid

This refers to a female that is full of eggs, or is ready to deposit her eggs.

Gray Mold of Grapes

This is a serious fungal disease of grape.

► Transmission of Plant Diseases by Insects

Graybacks

A family of dragonflies in the order Odonata: Petaluridae.

► Dragonflies and Damselflies

Greater Date Moth, *Arenipses sabella* Hmps. (Lepidoptera: Pyralidae)

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The importance of the greater date moth as a date pest seems to be increasing. It is known from India, Iran, Iraq, Saudi Arabia, Oman, Egypt and Algeria.

Description

The adult greater date moth is 18–22 mm long, with a wing span of 33–35 mm in males and 40–42 mm in females. They are light brown to yellowish. The head and thorax are light brown and the abdomen is silvery white, the front wings are brownish to yellowish with black scales and the hind wings are light brown. The eggs generally are laid singly, but also have been observed in clusters. They are creamy-white in color and spherical in shape. The larvae of the greater date moth are 28–35 mm in length and are dark pink in color. The pupae are elongated, about 18 mm in length, and are light brown.

Behavior

The adult greater date moths are nocturnal, but attracted to artificial light. They hide in the inner side of the bases of the palm petioles during the daytime. The larvae are also nocturnal at high temperatures, but have been seen active during the daytime at moderate temperatures. The hiding places of the larvae are at the inner bases of the split spathes, between the base of strands, in the inner base of the palm petioles. The larvae are quite mobile and can hide easily when threatened.

Biology and Damage

The biology of this pest is not well understood. The adults are active most of the year in warm areas and are not seen in the winter months in cold areas. The pest spends the winter in the larval stage in coccons under the fibers of the tree cabbage (head of the tree). The number of generations per year is uncertain, but there are at least two generations per year. In February in warm areas, larvae feed on the inner base of the petioles. The females lay eggs on the external tips of the unopened spathes, on strands and on fruit clusters. Hatched larvae feed on the tips of unopened spathes, which become black because of the clustering of black frass and silken threads. The larvae penetrate the sheath of the unopened spathes and feed on the strand mainly on tips. The tips of the strands become light gray to silver in color and devoid of flowers. When the spathes open, the larvae may remove the flowers and young fruits from the strands. The larvae also feed on the base of the main axis of the fruit cluster and make longitudinal tunnels and holes, both filled with black frass, coarse silks and plant fragments. The larvae feed in September on the ripened fruits. The infested dates become filled with black frass tied by silks. The infested dates may be inadvertently harvested and transferred to stores where consumers unfortunately encounter the larvae and adults.

Control

No definitive studies have been done to control this pest. The adult greater date moths were observed to be attracted to light traps with high rates of attracting from March to May. Pruning of the palm fronds may eliminate the hiding places of the larvae and adults. The current general practices to control this pest are dusting the cabbage of the tree with organophosphorus or pyrethriod insecticides in the autumn after harvesting, and dusting the strands and the bases of the fruit clusters with an insecticide at the time of pollination. If the problem persists, sprays also should be applied on the young fruits. No active and promising natural enemies have been recorded for this pest. The pheromone of this pest has not yet been identified, therefore, it is important that new research focus on this aspect.

References

Talhouk N (1984) The most common agricultural pests in Saudi Arabia. Ministry of Agriculture and Water, Riyadh, Saudi Arabia, 121 pp (In Arabic)

Hussain A (1974) Pests of date palm trees and dates in Iraq. University of Bagdad, Ministry of Higher Education and Scientific Reasearch, Iraq, 190 pp. (In Arabic)

Talhouk A (1969) Insects and mites injurious to crop in Middle Eastern countries. Verlag Paul Parey Hamburch, 239 pp

Hammad SM, Kadous AA (1989) Studies on the biology and ecology of date palm pests in the eastern province. Research Grants Program, Technical Report No. 25. KACST, Riyadh, Saudi Arabia, 142 pp

Greater Fritillaries or Silverspots, *Speyeria* [=*Argynnis*] (Lepidoptera: Nymphalidae)

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Speyeria scudder (Nymphalidae: Heliconiinae: Argynnini), commonly known as greater fritillaries or silverspots, are medium to large butterflies (wingspans of 40–90 mm) that represent conspicuous members of North American Lepidoptera. The genus was named in honor of a German entomologist, Adolph Speyer, who specialized in butterfly studies. The origin of the common name "fritillaries" is obscure, and one explanation is that these butterflies resemble the lily genus *Fritillaria*. Typically orange and black or brown in color, most are recognized by distinctive black spots and bars on the dorsal wing surface and silvery or cream-colored spots located on the ventral surface of the hind wings.

Speyeria fritillaries are restricted to North America (absent in southeastern regions of the United States and all but northern Mexico), although morphologically similar genera exist in other temperate parts of the world and together may be considered the temperate-zone counterpart to tropical Heliconiini (i.e., passion-vine butterflies). Long included in the Old World genus *Argynnis* Fabricius, they differ from their Eurasian relatives primarily in genitalic structure and were thus considered generically distinct from *Argynnis* by dos Passos and Grey; all North American taxa named since that time have been described within *Speyeria*. Recent workers, however, have treated *Speyeria* as a subgenus of the primarily Palearctic *Argynnis* fritillaries.

Speyeria species and associated geographical forms have been collected and examined in great detail in the past and continue to be a target for professional and amateur butterfly enthusiasts. The early works on *Speyeria* listed over 100 "species" names, but subsequent workers realized that most of these "species" were no more than geographical forms or races associated with a few polytypic species. Since then, several additional subspecies have been described, three subspecies have been elevated to full species status, and some taxon names have been declared synonyms.

Speyeria is presently comprised of 16 species Table 12), and according to some authors, over 100 subspecific, geographical forms. *Speyeria cybele* (Fabricius), *S. aphrodite* (Fabricius), *S. idalia* (Drury), and *S. atlantis* (Edwards) occur east of the Mississippi River, each with distributions or subspecies occurring in western North America, while *S. diana* (Cramer) is restricted to the eastern United States (in Appalachian and Ozark Mountain ecosystems). The remaining species occur in the western regions of North America, some as far north as Alaska. All but three *Speyeria* species are extremely variable [exceptions include *S. diana*, *S. idalia*, and *S. edwardsii* (Reakirt)], with the western North American species, in particular, fragmenting into numerous geographic forms that are often clinally joined with considerable intergradation occurring.

Species and subspecies determinations are made primarily using wing patterns, wing coloration, and geographical location; because of this, specific and subspecific identification is difficult in many taxa due to subtle pattern (Fig. 50) and color variations. Generally, adult morphological variation between species and subspecies is based on overall size, varying degrees of sexual dimorphism, and the wings. Important wing characteristics found dorsally are ground color, intensity of black markings, degree of dark basal suffusion, prominence of marginal band, and thickness of veins on the wings. Ventrally the important characteristics are the general ground color of the discal area on the hindwings, the size, shape, color and position of spots on the hindwings, and color and width of the submarginal band between the two outer rows of spots on the hindwings (Fig. 52).

Life History

Adults frequent open fields, moist meadows, and open woodlands near streams, or are restricted

Greater Fritillaries or Silverspots, *Speyeria* [=*Argynnis*] (Lepidoptera: Nymphalidae), Table 12 The known species of Fritillary butterflies

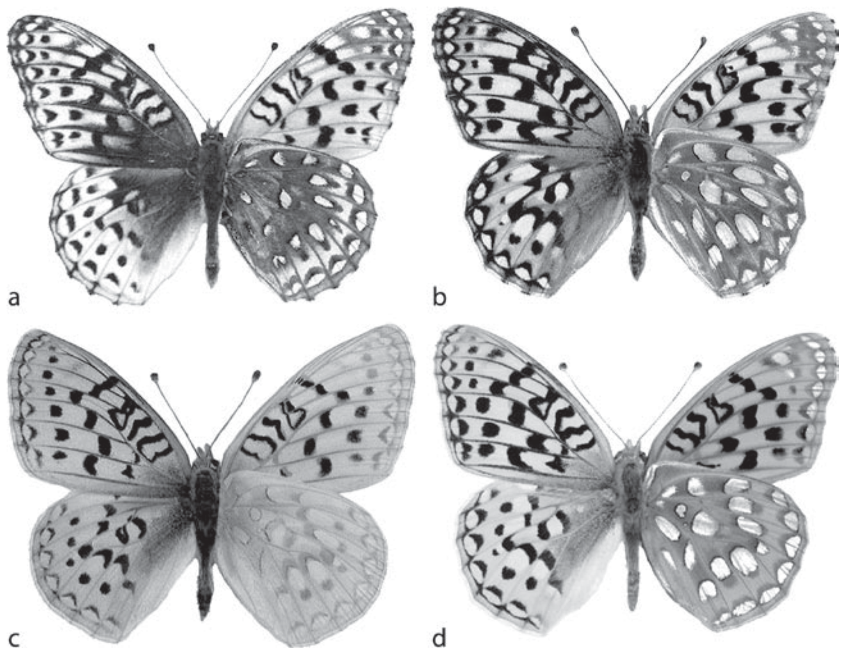
Speyeria species and associated common names
Speyeria diana (Cramer) – Diana Fritillary, Great Smokies Fritillary
Speyeria cybele (Fabricius) – Cybele Fritillary, Great Spangled Fritillary
Speyeria aphrodite (Fabricius) – Aphrodite Fritillary
Speyeria idalia (Drury) – Regal Fritillary, Eastern Regal Fritillary, Prairie Regal Fritillary
Speyeria nokomis (Edwards) – Nokomis Fritillary, Western Seep Fritillary
Speyeria edwardsii (Reakirt) – Edward's Fritillary
Speyeria coronis (Behr) – Coronis Fritillary
Speyeria carolae (dos Passos and Grey) – Carol's Fritillary
Speyeria zerene (Boisduval) – Zerene Fritillary
Speyeria callippe (Boisduval) – Callippe Fritillary
Speyeria egleis (Behr) – Egleis Fritillary, Great Basin Fritillary
Speyeria adiaste (Edwards) – Unsilvered Fritillary
Speyeria atlantis (Edwards) – Atlantis Fritillary
Speyeria hesperis (Edwards) – Hesperis Fritillary, Western Fritillary
Speyeria hydaspe (Boisduval) – Hydaspe Fritillary
Speyeria mormonia (Boisduval) – Mormon Fritillary

to coastal dunes, tallgrass prairies, or mountains. During the summer months they may be abundant in forest clearings, by roadsides, and along flower rich slopes and meadows in mountainous regions. *Speyeria* often prefer tall nectar sources such as thistles, wild asters, sunflowers, penstemons, mint, and dogbane. Males are often found congregating in large numbers at seeps and roadside puddles. Adults are strong fliers and can fly many kms, especially in late summer. They are rather long lived (several weeks to 2–3 months from May-September) and all members of the genus are univoltine.

Adult males typically emerge a week before females and patrol for potential mates. Courtship is rather elaborate, and pheromone cues from both sexes may be a reproductive barrier between species. *Speyeria* adults (Fig. 51) bear scent scales that lie along the veins on the upper side of the wings. Males pursue females, draw their forewings forward, and flick the closed wings slightly open in quick bursts. Each burst of two to five flicks lasts less than a second, wafting pheromones up to the female's antennae. The tips of the abdomens of male Argynnini (including *Speyeria*) contain paired glands normally hidden in the abdomen that aid in courtship. Courting males keep their forewings in a forward position and open and close them near the resting female to waft pheromones. Unreceptive females will flutter their wings to reject males.

Fritillaries are fecund butterflies, with some species laying over 2,000 eggs. Females delay egg-laying until late summer and usually oviposit rather haphazardly near their host plants rather than carefully placing them on the plant as most butterflies do. They are known to deposit eggs on twigs, leaves, stones and other debris. Eggs bear a tannish, camouflage coloration and are slightly rounded, tapering toward the apex. They are highly sculptured and likely adapted to withstand considerable environmental pressures including submergence, frost, and ground dwelling predators and microbes.

Larvae usually pass through six instars, overwintering as first instars and breaking diapause to complete development the following season. They are generally secretive and feed primarily at night, returning to hiding places under host leaves or



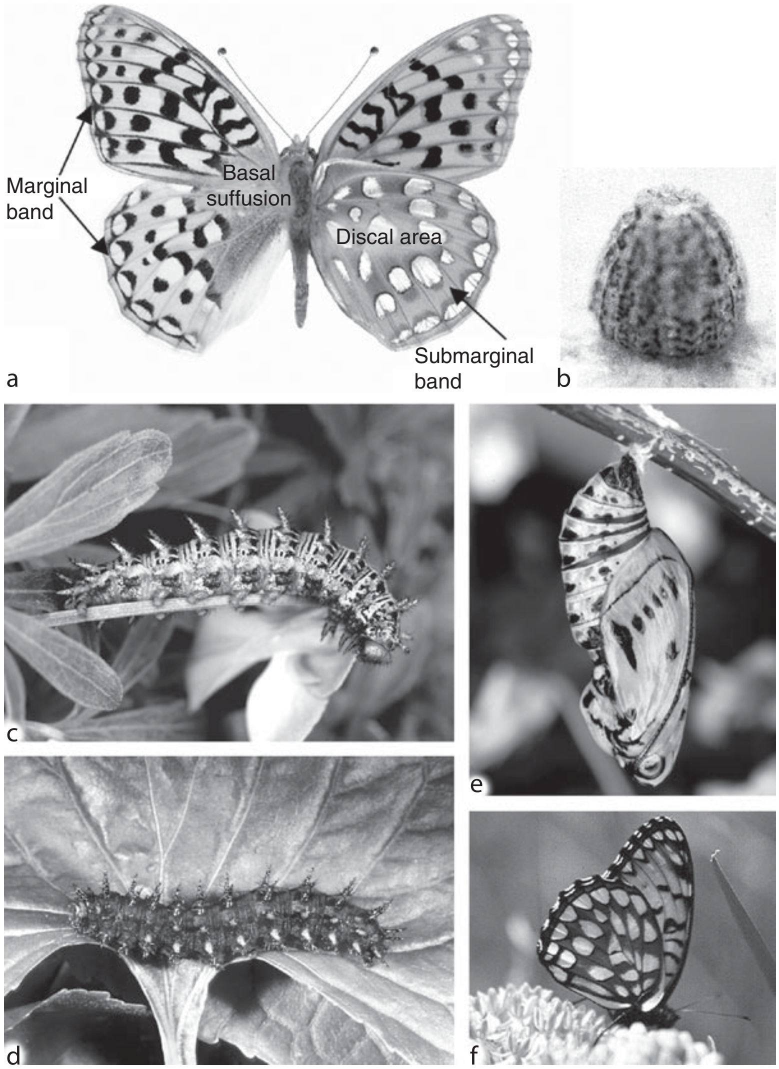
Greater Fritillaries or Silverspots, *Speyeria* [=*Argynnis*] (Lepidoptera: Nymphalidae), Figure 50 **Dorsal (*left*) and ventral (*right*) wing patterning of some *Speyeria* species: (a) *Speyeria hesperis* (New Mexico); (b) *Speyeria callippe* (Nevada); (c) *Speyeria mormonia* (Nevada); (d) *Speyeria zerene* (Nevada) (images by James C. Dunford).**

nearby vegetation during the day. Most species are black with lighter markings and bear three rows of branching spines on either side of the body. Some species exhibit spots of red/orange or other colors. Larvae feed on various violet species (*Viola*), and in laboratory conditions they are known to feed on every American violet species tested. *Viola* species range widely across temperate habitats of the Northern Hemisphere and into higher elevations of mountain systems towards the equator. *Speyeria* pupae are generally tan or brown with a few markings and hang freely from the cremastral end.

Speyeria individuals likely gain protection from potential predators in a variety of ways. *Speyeria diana* females (Fig. 52) are sexually dimorphic from *S. diana* males and, unlike the typical orange and black patterning of most *Speyeria* species, have been implicated in a Batesian mimicry complex with the distasteful, similarly colored pipevine swallowtail butterfly. In some *Speyeria* species, an eversible gland, capable of producing an unpleasant odor, is located on the dorsum of the female abdomen. Larvae also bear a gland located ventrally just behind the head that is likely used for defense against predators. Other avoidance measures during the larval stages include taking refuge under leaves during the day and feeding at night. First instars will also often hibernate inside grass stems. Eggs in some species may also contain phytochemicals used to deter potential predators.

Conservation

A few *Speyeria* species have been declining over the past 200 years and have been listed as either federally/state endangered or threatened [e.g., *S. idalia*, *S. diana*, *S. zerene hippolyta* (Edwards)]. *Speyeria* and their larval host plants (*Viola*) are among the best indicator organisms of native, undisturbed ecological communities in North America. They are also among the first organisms to be eliminated from such communities as a result of human-caused disturbances.



Greater Fritillaries or Silverspots, *Speyeria* [=*Argynnis*] (Lepidoptera: Nymphalidae), Figure 51 ***Speyeria*** **(a) general wing features; (b) *Speyeria idalia* egg; (c) *Speyeria idalia* larva; (d) *Speyeria aphrodite* larva; (e) *Speyeria idalia* pupa; (f) *Speyeria idalia* (Regal Fritillary) nectaring on butterflyweed (Wisconsin) (images b-e by David L. Wagner; images a and f by James C. Dunford).**

Speyeria idalia populations have been extirpated in much of the northeastern United States and have declined precipitously in other parts of its range. They inhabit native tallgrass prairies in the Midwest, an ecosystem that is shrinking due to development and agricultural activities. *Speyeria diana* disappeared from southeastern Virginia in about 1951 and is considered uncommon or extirpated in many other parts of its range. Historical populations in the Midwest and the Virginia Piedmont were extirpated in the 1800s, and most occurrence records (except in the Appalachians and Ozarks) are more than 50 years old. Coastal subspecies, such as the Oregon Silverspot (*S. z. hippolyta*), have been federally listed and depend on vanishing salt-spray meadows along the Oregon coast. Research on *Speyeria* butterflies continues to focus on various conservation and management measures required to maintain and protect threatened or endangered species.

Greater Fritillaries or Silverspots, Speyeria [=Argynnis] (Lepidoptera: Nymphalidae), Figure 52 *Speyeria diana* (a) male and (b) female (Tennessee). In each image, the left side is the dorsal wing surfaces and right side is the ventral wing surfaces (images by James C. Dunford).

References

Dos Passos CF, Grey LP (1945) A genitalic survey of Argynninae (Lepidoptera, Nymphalidae). Am Mus Novit 1296:1–29

Ferris CD (1989) Supplement to: a catalogue/checklist of the butterflies of America north of Mexico. Mem Lep Soc No 3, 103 pp

Hammond PC, McCorkle DV (1984) The decline and extinction of *Speyeria* populations resulting from human environmental disturbances (Nymphalidae: Argynninae). J Res Lepidoptera 22:217–224

Holland WJ (1931) The butterfly book. Doubleday, Doran and Co., Garden City, NY, 382 pp

Moeck AH (1957) Geographic variability in *Speyeria*: Comments, records and description of a new subspecies (Nymphalidae). Milwaukee Entomological Society Special Publication, 48 pp

Opler PA, Warren AD (2005) Lepidoptera of North America. 4. Scientific Names List for Butterfly Species of North America, North of Mexico. Contributions of the C.P. Gillette Museum of Arthropod Diversity, Colorado State University, Fort Collins, Colorado. 83 pp

Scott JA (1986)The butterflies of North America: a natural history and field guide. Stanford University Press, Stanford, CA.

Simonsen TJ (2006) Fritillary phylogeny, classification, and larval hostplants: reconstructed mainly on the basis of male and female genitalic morphology (Lepidoptera: Nymphalidae: Argynnini). Biol J Linn Soc 89:627–673

Greenbottle Flies

Members of the family Calliphoridae (order Diptera).

► Flies

Greenbug, *Schizaphis graminum* (Rondoni) (Hempitera: Aphididae)

Greenbug is an important aphid pest of grass crops.

► Wheat Pests and their Management

Green-Eyed Skimmers

A family of dragonflies in the order Odonata: Corduliidae.

► Dragonflies and Damselflies

Green Flies

Members of the family Aphididae (order Hemiptera).

► Bugs

Greenheads

Some members of the family Tabanidae (order Diptera).

► Flies

Greenhouse Whitefly, *Trialeurodes vaporariorum* (Westwood) (Hemiptera: Aleyrodidae)

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Greenhouse whitefly is found widely around the world, including most of the temperate and subtropical regions of North America, South America, Europe, Central Asia and India, northern and eastern Africa, New Zealand and southern Australia. It does not thrive in most tropical locations, and occurs in colder regions only by virtue of its ability to survive winter in greenhouses. It often overwinters only in such protected locations, but in mild-winter areas it survives outdoors throughout the year. The origin of this species is not certain, but is thought to be Mexico or the southwestern United States.

Life History

The development period from egg to adult requires about 25–30 days at 21°C, and 22–25 days at 24°C. Thus, because the preoviposition period of adults also is short, less than two days above 20°C, a complete life cycle is possible within a month. Greenhouse whitefly can live for months, and oviposition time can exceed the development time of immatures; this results in overlapping generations. Optimal relative humidity is 75–80%. The developmental threshold for all stages is about 8.5°C.

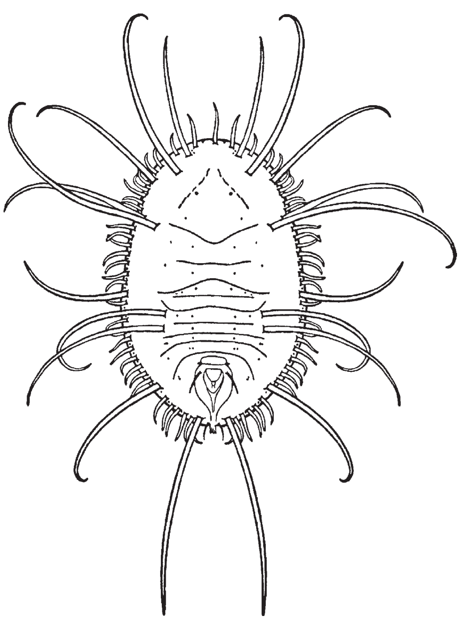
Eggs are oval in shape, and suspended from the leaf by a short, narrow stalk. The eggs initially are green in color and dusted with white powdery wax, but turn brown or black as they mature. The eggs are about 0.24 mm long and 0.07 mm wide. Eggs are deposited on the youngest plant tissue, usually on the underside of leaves in an incomplete circular pattern. Up to 15 eggs may be deposited in a circle measuring about 1.5 mm in diameter. This pattern results from the female moving in a circle while she remains with her mouthparts inserted into the plant. This pattern is less likely on plants with a high density of trichomes because plant hairs interfere with the oviposition behavior. Duration of the eggs stage is often 10–12 days, but eggs may persist for over 100 days under cool conditions. When cultured at 18, 22.5, and 27°C, egg development requires an average of 15, 9.8, and 7.6 days, respectively. Maximum fecundity varies according to temperature; optimal temperature is 20–25°C regardless of host plant. When feeding on eggplant, greenhouse whitefly produces over 500 eggs, on cucumber and tomato about 175–200 eggs.

The newly hatched whitefly nymph is flattened, oval in outline, and bears functional legs and antennae. The perimeter is equipped with waxy filaments. The first instar measures about 0.3 mm in length. It is translucent, usually appearing to be pale green in color but with red eyes. After crawling one cm or so from the egg, it settles to feed and molt. Development in the first instar requires 6.5, 4.2, and 2.9 days, respectively, when cultured at 18, 22.5, and 27°C. The second and

Greenhouse Whitefly, *Trialeurodes vaporariorum* (Westwood) (Hemiptera: Aleyrodidae), Figure 53 **Adult of greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood).**

third nymphal stages are similar in form and larger in size, though the legs and antennae become reduced and nonfunctional. They measure about 0.38 and 0.52 mm in length, respectively. Duration of the second instar requires about 4.3, 3.2, and 1.9 days whereas third instars require 4.5, 3.2, and 2.5 days, respectively, when cultured at 18, 22.5, and 27°C. The fourth nymphal stage, which is usually called the "pupa," differs in appearance from the preceding stages. The fourth instar measures about 0.75 mm in length, is thicker and more opaque in appearance, and is equipped with long waxy filaments. The pupal stage actually consists of the fourth nymphal instar period, which is a period of feeding, plus the period of pupation, which is a time of transformation to the adult stage. Thus, pupation occurs within the cuticle of the fourth instar. Duration of the fourth instar period and pupal period are 8.7 and 5.9, 5.9 and 4.0, and 4.5 and 2.8 days, respectively, at 18, 22.5, and 27°C.

The form of the pupa is used to distinguish among whitefly species (Fig. 54), and can be used to separate greenhouse whitefly from the similar-appearing *Bemisia* spp. Greenhouse whitefly is straight-sided when viewed laterally, ovoid, and lacks a distinct groove near the anal end of the body. In contrast, the *Bemisia* spp. are oblique-sided, irregularly oval, and possess a distinct groove in the anal region.



Greenhouse Whitefly, *Trialeurodes vaporariorum* (Westwood) (Hemiptera: Aleyrodidae), Figure 54 **Pupa of greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood).**

Individuals of greenhouse whitefly which develop on lightly or moderately pubescent leaves tend to be relatively large and to have four pairs of well developed dorsal waxy filaments. In contrast, whiteflies developing on densely pubescent leaves tend to be smaller, and to bear more that four pairs of dorsal filaments. These morphological variations are not entirely consistent, and have led to considerable taxonomic confusion.

Adults (Fig. 53), are small, measuring 1.0–2.0 mm long. They are white in color, with the color derived from the presence of white waxy or mealy material, and have reddish eyes. They bear four wings, with the hind wings nearly as long as the forewings. The antennae are evident. In general form, viewed from above, this insect is triangular in shape because the distal portions of the wings are wider than the basal sections. The wings are held horizontally when at rest; this characteristic is useful for distinguishing this species from the similar-appearing *Bemisia* spp. whiteflies, which hold their wings angled or roof-like when at rest. Mating may occur repeatedly, though females can also produce eggs without mating.

This species has a very wide host range, with over 300 species recorded as hosts. However, some hosts are more suitable. Vegetable plants often serving as good hosts are bean, cantaloupe, cucumber, lettuce, squash, tomato, eggplant, and occasionally cabbage, sweet potato, pepper, and potato. Among greenhouse-grown vegetables, the most common hosts are tomato, eggplant, and cucumber. Many ornamental plants serve as good hosts, including ageratum, aster, chrysanthemum, coleus, gardenia, gerbera, lantana, poinsettia, salvia, verbena, zinnia and many others.

Natural enemies of greenhouse whitefly are numerous, but few are consistently effective, especially under greenhouse conditions. Greenhouse whitefly is attacked by the common predators of small insects, including minute pirate bugs (Hemiptera: Anthocoridae), some plant bugs (Hemiptera: Miridae), green lacewings (Neuroptera: Chrysopidae), brown lacewings (Neuroptera: Hemerobiidae), and ladybirds (Coleoptera: Coccinellidae). Parasitic wasps attacking greenhouse whitefly are largely confined to the family Aphelinidae, but many species are involved and they vary regionally. Some of the important parasitoids are *Encarsia formosa* Gahan, *Aleurodophilus pergandiella* (Howard), *Eretmocerus haldemani* Howard, *Prospaltella transvena* Timberlake, and *Aphidencyrtus aphidivorus* (Mayr). Although these agents exercise considerable control on whitefly populations in weedy areas or on crops where insecticide use is minimal or absent, they do not survive well in the presence of most insecticides. *Encarsia formosa* has been used successfully under greenhouse conditions, and to a lesser extent field conditions, to affect biological suppression.

The pathogens of greenhouse whitefly are principally fungi, particularly *Aschersonia aleyrodis*, *Paecilomyces fumosoroseus*, and *Verticillium lecanii*. All occur naturally and can cause epizootics in greenhouses and fields, and also have been promoted for use in greenhouses as bioinsecticides. *Aschersonia* is specific to whiteflies, *Verticillium* has a moderately wide host range, and *Paecilomyces* has a broad host range. For optimal development of disease, high humidity is required. *Aschersonia* is spread principally by rainfall, so often fares poorly in greenhouse environments.

Damage

Adult and nymphal whiteflies use their piercing-sucking mouthparts to feed on the phloem of host plants. This results in direct damage, resulting in localized spotting, yellowing, or leaf drop. Under heavy feeding pressure, wilting and severe growth reduction may occur. Whiteflies also secrete large amounts of sugary honeydew, which coats the plants with sticky material, and must be removed from fruit before it is marketed. The honeydew also provides a substrate for growth of sooty mold, a black fungus that interferes with the photosynthesis and transpiration of plants.

Greenhouse whitefly is, as the common name suggests, primarily a pest in greenhouses, and is a serious limitation to the production of vegetables grown in such structures. However, it can also be a field pest, often in warmer climates but also in cool climates when seedlings contaminated with whiteflies are transplanted into the field.

Greenhouse whitefly is capable of transmitting viruses to plants, but is not considered to be a serious vector, particularly relative to the *Bemisia* spp. However, greenhouse whitefly transmits beet pseudo-yellow virus to cucumber in greenhouse culture.

Management

Although whitefly nymphs and adults can be detected readily by visual examination of foliage, most monitoring systems take advantage of the attraction of adults to yellow, and use yellow sticky traps to capture flying insects. Sticky cards or ribbons are suspended at about the height of the crop for optimal monitoring. Traps must be placed close to plants or close to the ground or population densities will be underestimated. Traps should be dispersed widely because whitefly distribution is not uniform within a crop. Whitefly flight peaks at about noon, but under greenhouse conditions is independent of temperature if the basal flight temperature of 16–17°C is exceeded.

Applications of insecticides are often made to minimize the effects of whitefly feeding on crops in greenhouses. Greenhouse whitefly feeds on the lower surface of foliage and is sessile throughout most of its life, habits that minimize contact with insecticides, and resulting in frequent applications and effectiveness mostly against the adult stage. In greenhouse culture, application intervals of only 4–5 days are common, and systemic insecticides are often used to increase the likelihood of insect contact with toxins. Thus, whitefly resistance to nearly all classes of insecticides is known, and rotation of insecticide classes is encouraged. Mixtures of insecticides are often used, which is indicative of high levels of resistance among whiteflies to insecticides. Field populations of greenhouse whitefly invariably are derived from greenhouse populations, and possess similar resistance to many insecticides. Applications of petroleum oils and biological control agents help to avoid difficulties with insecticide resistance.

Some insecticidal materials can be integrated into biologically based whitefly management systems. Selective materials that affect only adult and nymphal whiteflies, insect growth regulators, and insecticidal soaps are somewhat compatible with parasitoids and can be used when parasitoids are failing.

Few cultural practices are available, but disruption of the whitefly population with host-free periods is important. Continuous culture of plants allows whiteflies to move from older to younger plants. Similarly, weeds may allow whiteflies to bridge crop-free periods, and should be eliminated. Culture of plants over white reflective mulch also reduces whitefly densities. Yellow sticky traps can be hung in greenhouses to capture adult whiteflies, thereby reducing whitefly density.

Seasonal inoculative release of the parasitoid *Encarsia formosa* Gahan into crops infested with greenhouse whitefly has been used extensively for suppression of whiteflies on greenhouse-grown vegetable crops. Excellent suppression of whiteflies is attainable, but on host plants such as cucumber and eggplant, which are very favorable for whitefly reproduction and have hairy leaves that interfere with parasitoid searching, frequent releases must be made. Alternatively, cucumber varieties with reduced trichome density have been developed, and which favor parasitism. Another critical factor is temperature, because low greenhouse temperatures are more suitable for whitefly activity than parasitoid activity. Daytime temperatures of about 24°C seem to be optimal; temperatures of 18°C or less suppress parasitoid searching. A cold-tolerant *Encarsia* strain that is active at 13–17°C has also been used to overcome this temperature problem. Interference from pesticides can markedly affect parasitoid survival, so other pests such as mites must be managed biologically also. Lastly, release rates are important because if too many parasitoids are released the host whiteflies are driven nearly to extinction, leading to disappearance of the parasitoids; this is most likely to occur in small greenhouses. Alternatively, parasitoid releases can be made throughout the season, irrespective of whitefly presence. Although the protocols and technologies for whitefly management using *E. formosa* have been perfected for use in greenhouses, management under outdoor conditions awaits further research.

The fungus *Verticillium lecanii* is sometimes used commercially in Europe for whitefly and thrips suppression in greenhouses, though its success is strongly affected by humidity. Where humidity can be raised to a high level, epizootics can be induced in 1–2 weeks. Both young and adult stages are susceptible to infection.

References

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, CA, 729 pp

van Roermund HJW, van Lenteren JC (1992) The parasite-host relationship between *Encarsia formosa* (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae) XXXIV. Life history parameters of the greenhouse whitefly, *Trialeurodes vaporariorum* as a function of host plant and temperature. Wageningen Agricultural University Papers 92–93,Wageningen, The Natherlands, 147 pp

Green June Beetle, *Cotnius nitida* (Linnaeus) (Coleoptera: Scarabaeidae)

► Turfgrass Insects and their Management

Green Lacewings

Members of the family Chrysopidae (order Neuroptera).

► Lacewings, Antlions, and Mantidflies

Green Muscardine

A mycosis of various larval, pupal, and adult insects, caused by the fungus *Metarrhizium*.

► Muscardine

Green Peach Aphid, *Myzus persicae* (Sulzer) (Hemiptera: Aphididae)

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Green peach aphid is found throughout the world, including both tropics and temperate latitudes. It is considered to be a pest nearly everywhere, often due to its ability to transmit plant viruses. In addition to attacking plants in the field, green peach aphid readily infests vegetables and ornamental plants grown in greenhouses. This allows high levels of survival in areas with inclement weather, and favors ready transport on plant material. When young plants are infested in the greenhouse and then transplanted into the field, fields will not only be inoculated with aphids but insecticide resistance may be introduced. These aphids are also reported to be transported long distances by wind and storms.

Life History

The life cycle varies considerably, depending on the presence of cold winters. Development can be rapid, often 10–12 days for a complete generation, and with over 20 annual generations reported in mild climates. Where suitable host plants cannot persist, the aphid overwinters in the egg stage. In the spring, soon after the plant breaks dormancy and begins to grow, the eggs hatch and the nymphs feed on flowers, young foliage, and stems. After several generation on *Prunus* spp., dispersants from overwintering hosts deposit nymphs on summer hosts. In cold climates, adults return to *Prunus* spp. in the autumn, where mating occurs, and eggs are deposited. All generations except the autumn generation culminating in egg production are parthenogenetic.

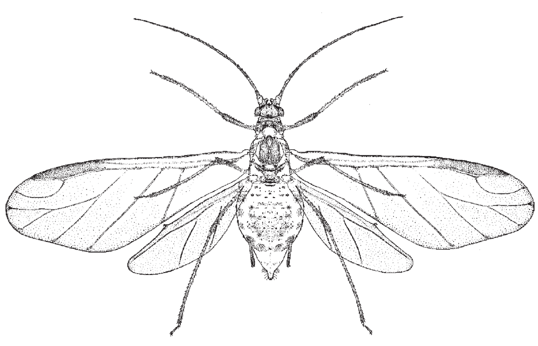
Eggs are deposited on *Prunus* spp. trees. The eggs measure about 0.6 mm long and 0.3 mm wide, and are elliptical in shape. Eggs initially are yellow or green, but soon turn black. Mortality in the egg stage sometimes is quite high.

Nymphs initially are greenish, but soon turn yellowish, greatly resembling viviparous adults. There may be four instars in this aphid, with the duration of each averaging 2.0, 2.1, 2.3, and 2.0 days, respectively. Alternatively, five instars also have been reported, with a mean development time of 2.4, 1.8, 2.0, 2.1, and 0.7 days, respectively. Parthenogenetic females give birth to offspring 6–17 days after birth, with an average age of 10.8 days at first birth. The length of reproduction varies considerably, but averages 14.8 days. The average length of life is about 23 days under caged conditions where predators are excluded. The daily rate of reproduction averages 1.6 nymphs per female, with about 75 offspring produced. The maximum number of generations occurring annually is 20–21, depending on the year.

Up to eight generations may occur on *Prunus*, but as aphid densities increase winged forms are produced, which then disperse to summer hosts. Winged (alate) aphids have a black head and thorax, and a yellowish green abdomen with a large dark patch dorsally. They measure 1.8–2.1 mm in length. Winged green peach aphids seemingly attempt to colonize nearly all plants available. They often deposit a few young and then again take flight. This highly dispersive nature contributes significantly to their effectiveness as vectors of plant viruses.

The offspring of the dispersants from the overwintering hosts are wingless, and each produce 30–80 young. The wingless (apterous) aphids are yellowish or greenish in color. They measure about 1.7–2.0 mm in long. A medial and lateral green stripes may be present. The cornicles are moderately long, unevenly swollen along their length, and match the body in color. The appendages are pale. The rate of reproduction is positively correlated with temperature, with the developmental threshold estimated to be about 4.3°C. As aphid densities increase or plant condition deteriorates, winged forms are again produced to aid dispersal. The nymphs that give rise to winged females may be pinkish. The dispersants typically produce about 20 offspring, which are always wingless. This cycle is repeated throughout the period of favorable weather.

In the autumn, in response to change in day length or temperature, winged male and female aphids are produced which disperse in search of *Prunus* (Fig. 55). Timing is important, as foliage on the *Prunus* hosts is physiologically optimal as leaves begin to senesce. Females arrive first, and give birth to wingless (apterous) egg-laying forms (oviparae). Males are attracted to oviparae by a pheromone, capable of mating with several females, and eggs are produced. The oviparous female deposits 4–13 eggs, usually in crevices in and near buds of *Prunus* spp. The oviparous female is 1.5–2.0 mm long, and pinkish.



Green Peach Aphid, *Myzus persicae* (Sulzer) (Hemiptera: Aphididae), Figure 55 Adult of green peach aphid, *Myzus persicae* (Sulzer).

Parthenogenic reproduction is favored in the many parts of the world where continuous production of crops provides suitable host plants throughout the year, or where weather allows survival on natural (noncrop) hosts. The average temperature necessary for survival of active forms of green peach aphid is estimated at 4–10°C. Plants in the families Cruciferae and Chenopodiaceae, both crops and weeds, readily support aphids through the winter months.

Green peach aphid feeds on hundreds of host plants in over 40 plant families. However, it is only the viviparous summer stages that feed so widely; the oviparous winter stages are much more restrictive in their diet choice. In temperate latitudes the primary or overwintering hosts are trees of the genus *Prunus*, particularly peach and peach hybrids, but also apricot and plum. During the summer months the aphids abandon their woody hosts for secondary or herbaceous hosts, including ornamental, vegetable and field crops. Crops differ in their susceptibility to green peach aphid, but it is actively growing plants, or the youngest plant tissue, that most often harbors large aphid populations. In warmer climates the aphids do not seek out overwintering hosts, but persist as active nymphs and adults on hardy crops and weeds.

Broadleaf weeds can be very suitable host plants for green peach aphid, thereby creating pest problems in nearby crops. Common and widespread weeds such as field bindweed, *Convolvulus arvensis*; lambsquarters, *Chenopodium album*; and redroot pigweed, *Amaranthus retroflexus*, are often cited as important aphid hosts, and plant viruses may be acquired from these hosts.

Natural Enemies

Hundreds of natural enemies have been recorded, principally ladybirds (Coleoptera: Coccinellidae), flower flies (Diptera: Syrphidae), lacewings (Neuroptera: mainly Chrysopidae), parasitic wasps (Hymenoptera: Braconidae), and entomopathogenic fungi (mainly Entomophthorales). Most are general predators, moving freely among green peach aphid, other aphids, and even other insects. Quantitative data generally are lacking for the influence of most natural enemies. Weather also reportedly contributes to significant change in aphid numbers, including direct mortality, but this also is poorly documented.

The ephemeral nature of aphid infestation in many crops is believed to prevent the beneficial organisms from consistently locating the aphids and reproducing in a timely manner. Nevertheless, anyone who has frequently observed green peach aphid at high densities probably has observed sudden population decreases following the appearance of ladybirds, wasp parasitoids, or entomopathogenic fungi such as *Erynia neoaphidis*. Unfortunately, the disease epizootic often occurs too late to keep aphids from attaining high numbers. Various studies that selectively excluded or killed beneficial organisms have demonstrated the explosive reproductive potential of these aphids in the absence of biological control agents, thus demonstrating their value in reducing damage potential. In greenhouse crops, where environmental conditions and predator, parasitoid, and pathogen densities can be manipulated, biological suppression can be effective and consistent.

Damage

Green peach aphids can attain very high densities on young plant tissue, causing water stress, wilting, and reduced growth rate of the plant. Prolonged aphid infestation can cause appreciable reduction in yield of root crops and foliage crops. Contamination of harvestable plant material with aphids, or with aphid honeydew, also causes loss. Where mild winters allow good overwintering survival of green peach aphid on spinach, crop value is affected by insect presence. Blemishes to the plant tissue, usually in the form of yellow spots, may result from aphid feeding. Leaf distortions are not common except on the primary host. Contamination of vegetables by aphids sometimes presents quarantine problems and fumigation techniques have been developed that kill the insects without causing harm to the vegetables.

The major damage caused by green peach aphid is through transmission of plant viruses. Indeed, this aphid is considered by many to be the most important vector of plant viruses throughout the world. Nymphs and adults are equally capable of virus transmission, but adults, by virtue of being so mobile, probably have greater opportunity for transmission. Both persistent viruses, which move through the feeding secretions of the aphid, and non-persistent viruses, which are only temporary contaminants of aphid mouthparts, are effectively transmitted. Over 100 viruses are transmitted by this species. Some of the particularly damaging diseases include potato leafroll virus and potato virus Y to Solanaceae, beet western yellows and beet yellows viruses to Chenopodiaceae, lettuce mosaic virus to Compositae, cauliflower mosaic and turnip mosaic viruses to Cruciferae, and cucumber mosaic and watermelon mosaic viruses to Cucurbitaceae. A discoloration in potato tubers, called net necrosis, occurs in some potato varieties following transmission of potato leafroll.

Management

Day-degree models using a developmental threshold of 4°C can be used to predict various phenological events such as egg hatch and immigration of alate aphids. Yellow traps, particularly water pan traps, are commonly used for population monitoring.

Despite the numerous options potentially available, many crop producers are dependent on insecticides for suppression of green peach aphid abundance. Systemic insecticide applications are especially popular at planting time, most of which provide long-lasting protection against aphid population buildup during the critical and susceptible early stages of plant growth, and some of which provide protection for months.

Green peach aphid is able to develop at lower temperatures than its parasitoids, so the wasps are beneficial only in benign climates or where temperature can be controlled, as in some greenhouses. Indeed, there has been considerable success using parasitoids, the entomopathogenic fungus *Verticillium lecanii*, and the predatory midge *Aphidoletes aphidimyza* (Diptera: Cecidomyiidae) for greenhouse-grown vegetables in Europe.

The overwintering behavior of green peach aphid, which in many areas is restricted to *Prunus* or other relatively restricted sites, has fostered research on techniques to reduce aphid abundance and disease transmission to other crops, by either removing the overwintering site or by eliminating the aphids before they disperse. Destruction of peach and apricot trees, and treatment of trees with dormant oil and insecticide, have been used effectively to disrupt aphid population increase. Similarly, vegetable and flower plants grown in greenhouses during the winter months have been shown to be an excellent source of infestation during the following spring, and incidence of leafroll in potatoes can be directly related to the abundance of aphids in home gardens. Inspection of garden centers and treatment of seedlings found infested with aphids can be important elements of the overall potato leafroll reduction effort. As is usually the case with aphids, green peach aphid populations tend to be higher when plants are fertilized liberally with nitrogen fertilizers.

Because some of the virus diseases transmitted by green peach aphid are persistent viruses, which typically require considerable time for acquisition and transmission, insecticides can be effective in preventing disease spread in some crops. For example, potato leafroll virus is transmitted within the potato crop principally by wingless aphids moving from plant to plant. Infected seed potatoes are the principal source of leafroll in most potato crops, so planting disease-free seed is obviously an important step in minimizing the incidence of the disease. Insecticides may not keep winged aphids from alighting in a crop and quickly transmitting non-persistent virus, but they can certainly prevent the secondary spread of virus within a crop by colonizing aphids. However, insecticide resistance is a severe problem in many areas. Application of mineral oil and use of aluminum or white plastic mulch reduces virus transmission. Aphids that are not effectively repelled by reflective mulch seem to thrive on mulched crops and exhibit high rates of reproduction. Therefore, even in mulched crops some aphid control is necessary.

References

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, CA, 729 pp

van Emden HF (1966) Studies on the relations of insect and host plant. III. A comparison of the reproduction of *Brevicoryne brassicae* and *Myzus persicae* (Hemiptera: Aphididae) on Brussels sprout plants supplied with different rates of nitrogen and potassium. Entomologia Experimentalis et Applicata 9:444–460

van Emden HF, Eastop VF, Hughes RD, Way MJ (1969) The ecology of *Myzus persicae*. Annu Rev Entomol 14:197–270

Green Stoneflies

Members of the stonefly family Chloroperlidae (order Plecoptera).

► Stoneflies

Green Vegetable Bug

This is *Nezara viridula* (Linnaeus) (Hemiptera: Pentatomidae), and is also known as southern green stink bug. The latter name is based on its distribution in the USA, but it now occurs on most continents.

► Southern Green Stink Bug

Gregarines of Insects

The subclass Gregarinasina currently encompasses about 220 genera and 1,500 named species. The modern day gregarines are a monophyletic group associated with invertebrates, including various polychaetes (marine worms), oligochaetes (earthworms), and arthropods. The majority of the gregarines have been described from insect hosts, including a wide variety of aquatic insects and many coleopterans. Normally, these organisms are capable of infecting a certain group of hosts without the involvement of a vector or secondary host. It is likely that the current list of gregarine species represents only a small percentage of the gregarines existing in nature. Gregarines display a high degree of host specificity, and may be restricted to a particular tissue (or site) of a specific life stage of a single insect species. However, certain neogregarines (*Mattesia* spp.) have been experimentally transmitted to insects of different orders. In many cases, insects may harbor a gregarine complex. Gregarines, lacking the virulence of other insect disease agents and not possessing a vertebrate counterpart, have not received much attention from pathologists during the past several decades.

Morphologically, the gregarines produce mature gamonts which have the conoid structure modified into an epimerite or mucron. The epimerite, often containing attachment hooks, mediates gregarine attachment to the host cell. This anucleated segment, separated from the main cell by a septum, often is lost when the gamont detaches from the host cell. The mucron, unlike the epimerite, lacks the septal structure. Gregarines are divided into four major groups: the Archigregarines, Blastogregarines, septate Eugregarines, and Neogregarines. The primitive archigregarines and blastogregarines are parasites of the digestive tracts of marine worms and annelids. The life cycle of these latter gregarines includes three schizogonies: merogony, gametogony, and sporogony.

The Eugregarine group, believed to arise from an ancestral archigregarine, contains the vast majority of the described gregarines (1,300 species). Most eugregarines that are detrimental to the host insect are found within the genus *Ascogregarina*. The life cycle of the eugregarines, unlike the archigregarines or neogregarines, lacks the merogony phase. Host insects ingest the dormant oocyst stage that is activated to release infectious sporozoites that exit through the polar canals. Excystation is a pH-sensitive event and, therefore, may be regulated by the pH gradient existing in the insect's digestive tract. Excysted sporozoites (4–8 per oocyst) migrate to the midgut epithelium and undergo both intracellular and extracellular growth phases. Upon attaching to the midgut epithelia, sporozoites differentiate and produce either epimerite (septate gregarine) or mucron (aseptate gregarines) attachment structures. These cells, referred to as trophozoites or gamonts (Fig. 56), may penetrate the midgut or remain attached to the microvillar surface. Individual gamonts undergo extensive growth, reaching a size that may be measured in millimeters. Normally, the fully mature detached gamont is the stage that is detected in infected insects. Mature gamonts detach themselves from the midgut and pair off in the lumen, forming a prenuptial association known as syzygy. A membrane is formed around the paired gamonts, forming the gametocysts that are expelled in feces. Within the gametocyst one of the gamonts produces microgametes and the second gamont develops macrogametes. Alternatively, both gamonts may produce isogametes. The gametes fuse, producing a diploid zygote that undergoes successive meiotic and mitotic divisions, resulting in a thick-walled oocyst filled with haploid sporozoites.

Gregarines of Insects, Figure 56 **Light micrograph of septate gamonts of *Gregarina blatteria* attached to cockroach midgut surface.**

Eugregarines lacking the merogonic cycle are unable to multiply and spread within host insects. The number of gamonts found in the host is a direct reflection of the number of sporozoites released from the ingested oocysts. The impact of gregarines inhabiting the digestive tract is often negligible; damaged host cells are replaced without a noticeable impact on the host insect. For example, the mealworm *Tenebrio molitor* is host to *Gregarina polymorpha*, and can harbor up to 6,000 gamonts in its digestive tract without any pathological effect. In certain cases, these organisms are considered commensals. However, in other cases, the presence of these gregarines results in a measurable impact on the host. Large numbers of gregarines often damage the gut barrier and allow opportunistic microbes to invade and kill the host. This is especially true for the coelomic gregarines that penetrate the midgut and develop in the hemocoel. Normally, the impact of these organisms is subtle and cannot be measured simply in terms of insect mortality. For example, *Ascogregarina barretti* does not kill infected *Aedes triseriatus*, but results in the production of short winged adults. Similarly, under appropriate environmental conditions, infection by the aseptate gregarine *Ascogregarina culicis* alters the developmental kinetics and reduces the survival fitness of the host mosquito *Aedes aegypti*. A second aseptate gregarine, *Ascogregarina chagasi*, has been reported to cause population declines in laboratory colonies of the dipteran *Lutzomyia longipalpus*.

The order Neogregarinida includes the neogregarines characterized by their additional merogonic life stage. Neogregarines are found commonly in members in the orders Lepidoptera, Coleoptera, Hemiptera, Diptera, and Orthoptera and include the well-studied genus *Mattesia*. Neogregarines are transmitted orally and display a high level of host specificity. These gregarines usually are smaller than the eugregarines and possess a nonsegmented body plan. The oocyst stage of neogregarines is ingested and the digestive fluids act on polar caps (plugs), allowing for the release of the infectious sporozoites. The sporozoite penetrates the midgut and invades the fat body. Within this tissue, the sporozoites develop and give rise to micronucleate meronts. These meronts grow, producing multinucleate cells that measure 20–30 μm in length, and contain 30–200 nuclei. The nuclei move to the peripheral region and bud from the meront, releasing motile, elongate merozoites. These motile merozoites, released from infected cells, infect other healthy cells, spreading the infection through the target tissue(s). The merozoites, after undergoing one or more cycles, eventually undergo macronuclear merogony. The exocellular budded macronuclear merozoites round up and transform into gamonts, thus initiating the sexual phase. The gametocytes form pairs that synthesize an envelope and transform into the gametocyst. The gamonts within the cyst each produce a set of gametes that fuse to form the zygote. The zygotes develop a spore wall forming the oocyst. The zygote undergoes division, producing a set of sporozoites within the oocyst or spore.

The best-studied genus of insect neogregarines is *Mattesia*. The species *M. grandis*, pathogenic to the cotton boll weevil, *Anthonomous grandis*, has been examined as a microbial control agent. Under insectary conditions, *M. grandis* was found to cause epizootics and to decimate laboratory colonies. In the mid-1960s, this pathogen was mass-produced in host weevils. Spores harvested from infected adults were bait formulated and tested against weevil populations. Field-cage experiments demonstrated that spores delivered as baits could infect weevils. The high cost of production and erratic field performance has limited subsequent interest in this pathogen.

References

Cook TJP, Janovy J Jr, Clopton RE (2001) Epimerite-host epithelium relationships among eugregarines parasitizing the damselflies *Enallagma civile* and *Ischnura verticalis*. J Parasitol 87:988–996

Levine ND (1988) The protozoan phylum Apicomplexa, vol 1. CRC Press, Boca Raton, FL.

Schrevel J, Caigneaux E, Gros D, Philippe M (1983) The three cortical membranes of the gregarines. I. Ultrastructural organization of *Gregarina blaberae*. J Cell Sci 61:151–174

Siegel JP, Novak RJ, Maddox J (1992) Effects of *Ascogregarina barretti* (Engregarinida: Lecudinidae) infection on *Aedes triseriatus* (Diptera: Culicidae) in Illinois. J Med Entomol 6:968–973

Sulaiman I (1992) Infectivity and pathogenicity of *Ascogregarina culicis* (Eugregarinida: Lecudinidae) to *Aedes aegypti* (Diptera: Culicidae). J Med Entomol 29:1–4

Gregarious Behavior

The tendency of organisms to stay in groups.

Gregarious Behavior in Insects

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Many insects spend time in a group of conspecifics at some point during their lives. Insect groups can form passively, for example, through the common use of feeding, mating, oviposition, basking or shelter sites. Alternatively, insect aggregations may arise through the detection and active movement toward conspecifics or their associated cues. Cues used to detect the presence of conspecifics can be tactile, visual, auditory, olfactory or pheromonal, and may act alone or in combination.

Gregarious behavior is commonly associated with social insects that live in communal colonies (see Sociality of Insects), but it is also widespread among the non-social insects considered here. In these cases, insect groups of various sizes form under a myriad of conditions and are often interchangeably referred to as aggregations, associations, clumps and other such terms. Importantly, gregariousness is not limited solely to insects, but rather is widespread throughout the animal kingdom (e.g., fish schools and bird flocks). As such, the study of group living and its population level consequences are active areas of behavioral, ecological and evolutionary research. Entomological studies have played important roles in all of these disciplines.

In general terms, insect groups are considered as associations among multiple conspecifics at some point in space and time. Although a precise definition of groups and their respective sizes that might be appropriate for all non-social insects is lacking, this omission is largely irrelevant to the study of gregariousness. The conditions under which insects aggregate, the developmental stages during which aggregation occurs, as well as the physiological and behavioral mechanisms that underlie their formation have all been found to vary among and even within species (Fig. 57).

The evolution and maintenance of gregariousness necessarily requires the benefits of group formation to outweigh the corresponding costs in terms of individual fitness consequences. Empirical and theoretical studies investigating the benefits of grouping have historically outnumbered those concerned with measuring its costs. Even more rare are integrative empirical studies that have attempted to examine both the costs and benefits of gregariousness within single species. Comparative phylogenetic analyses that seek to examine the evolutionary relationships between gregariousness and other ecological, morphological and behavioral traits are similarly rare, but have provided important insights and will likely increase as phylogenetic frameworks become available for a variety of different insect lineages.

Some of the many examples of the costs and benefits of gregariousness in insects are provided below. When considering these examples, it is important to keep in mind that they are by no means mutually exclusive. Multiple benefits, as well as costs, may be at play and those benefits that initially favor the evolution of gregariousness need not be the same ones responsible for its maintenance. Indeed, a broad consensus has emerged that no single factor likely serves as a general explanation for the evolution and maintenance of gregarious behavior, or the lack thereof, among insect species.

Gregarious Behavior in Insects, Figure 57 **A dense aggregation of *Doratifera casta* caterpillars. *Doratifera casta* expresses ontogenetic variation in gregariousness. Larvae are gregarious during the early instars, but become solitary in later stages. Gregariousness confers at least two advantages during early stages of development, facilitation of feeding and functioning as part of an aposematic anti-predator strategy. Their subsequent switch to a solitary lifestyle suggests that these advantages disappear or are outweighed by costs associated with intraspecific competition during the final instars. (Photo by Dieter Hochuli.)**

Benefits of Gregarious Behavior

Mate Finding

Many insects that are otherwise solitary-living form groups during the process of finding a mate. In acoustically signalling insects such as crickets and some grasshoppers, males can be attracted to the calls of conspecific males, resulting in local aggregations. Males in these groups often have a higher probability of securing a mate than their solitary counterparts. Among desert clicker grasshoppers, *Ligurotettix coquilletti*, which tend to aggregate in this manner, males selectively chose the highest quality food plants from which to call. Thus, a male's call may also serve as an indicator of host plant quality to females. Insects in a variety of orders also form leks in which males aggregate and display to attract mates. Females visit these sites only to mate and typically gain no other resources. The advantage to females afforded by leks appears to be the choice of a large number of potential mates and the opportunity to simultaneously assess the quality of multiple males. The advantage to males of participating in leks is less clear, but is likely related to the prediction that the rates of female visiting and mating should increase with lek size, thereby increasing the average number of matings per male participant in the lek.

Facilitation of Feeding

Gregarious insects are often able to obtain food resources that they would otherwise be unable to consume as solitary individuals. Nymphs of the two-spotted stinkbug, *Perillus bioculatus*, feed together on caterpillars and beetle larvae. Older and larger nymphs are better able to overcome prey defenses than are the smaller and younger nymphs that often join them in feeding. Older nymphs likely benefit from the assistance provided by younger nymphs in subduing larger prey, whereas the younger nymphs gain access to otherwise unobtainable prey items.

Among herbivorous insects, there are many examples in which individuals in larger groups develop at an increased rate compared to smaller groups or lone individuals. Grouped larvae of the neotropical nymphalid *Chlosyne janais* achieve this benefit either by inducing a nutrient sink in the damaged leaf or by overcoming an induced defensive response on the part of their host plant. In the eucalyptus-feeding beetle *Chrysophtharta agricola*, neonate survivorship increases with group size because feeding sites on tough leaves initiated by larvae with larger mandibles provide smaller individuals with access to feeding sites. Milkweed bugs, *Oncopeltus fasciata*, feed on seedpods and also survive better in larger groups. In this case, the joint secretion of lytic enzymes by multiple individuals facilitates the ingestion of nutrients from the seeds within the pod.

Microhabitat Modification

Insect aggregations can serve to buffer group members from harsh environmental conditions. Aggregations of *Blattella germanica* cockroach nymphs enable group members to better survive under dry conditions. The diffusion fields of water vapor overlap among group members and reduce individual evaporative water loss to the air. Anti-desiccant effects have also been observed in aggregations of other insects such as woodlice, stinkbugs and beetles. Clustering of eggs by ovipositing females similarly functions to prevent water loss by reducing the amount of exposed surface area. Importantly, this strategy of egg clustering may serve as one of the principle mechanisms underlying the initial formation of many larval insect groups.

Grouping has also been shown to play an important role in thermoregulation. Higher body temperatures in grouped versus solitary caterpillars have been observed in a number of different lepidopterans. These higher temperatures result in faster growth rates and reduced development times that in turn can reduce the risk of exposure to predators, parasitoids or pathogens, and possibly allow the insects to outpace a decline in host plant quality. Some gregarious insects even build structures within which their microhabitat is modified. For example, temperatures inside the tent shelters constructed by eastern tent caterpillars, *Malacosoma americanum*, have been shown to be higher than outside air temperatures.

Protection from Natural Enemies

By far the most commonly invoked benefit of gregarious behavior is protection from natural enemies such as predators and parasitoids. The notion that individual attack risk declines as group size increases has been widely referred to as the "selfish herd" effect. In other words, the reduction in attack risk provides individuals with a selfish motive to join a group. However, a number of different underlying mechanisms, both passive and active, may be responsible for conferring protection to individual group members. Similarly, as evidenced by the other benefits described above, instances in which the improved survivorship of insects in groups was assumed to be due to protection from natural enemies may actually have been due to other unrecognized benefits of group living.

The simplest scenario for protection in a group is a dilution effect in which the risk of attack to an individual group member is inversely proportional to the size of the group. However, few if any insects rely solely on a dilution effect for protection. They often also have some means of active defense such as early detection, evasion, chemical defense and warning coloration (aposematism).

Groups of sea-skaters, *Halobates robustus*, detect and respond to predators from a greater distance than do solitary individuals. Once a predator attack has been initiated, insects in dense groups will often flee in erratic patterns that are assumed to either startle or confuse predators, or reduce the predictability of prey locations.

Given that individual predators have an upper limit to the number of prey they can consume, sufficiently high numbers of insects in aggregations may effectively swamp or satiate local predators and confer the benefit of reduced predation on surviving group members. Predator swamping has been proposed for mass emerging insects such as mayflies and periodical cicadas, and likely operates during outbreak periods in insects such as locusts (e.g., *Schistocerca* spp.) and Mormon crickets (*Anabrus simplex*) that exhibit widely fluctuating local population dynamics.

Many gregarious insects are also aposematic. These insects utilize conspicuous warning coloration as a signal to potential predators that they are deterrent or unpalatable by virtue of possessing some form of defense, usually chemical. The relationship between insect gregariousness and the evolution of both unpalatability and warning coloration has been the source of long running debate. Theoretical and empirical evidence suggest that grouping can facilitate the evolution of chemical defenses, as well as enhance predator learning of warning coloration. Based on this, it has been hypothesized that gregariousness initially promotes the evolution of unpalatability, followed by the evolution of conspicuous warning coloration. Despite the seeming logic behind this argument, a series of phylogenetic analyses using lepidopteran larvae suggest a different polarity for the evolution of these traits. These analyses indicate that gregariousness has repeatedly evolved after, rather than before, unpalatability and warning coloration. Thus, although it seems likely that defenses have evolved prior to warning coloration and gregariousness, the precise polarity of events could feasibly vary among taxa depending on the specific ecological circumstances. Additional phylogenetic analyses in other insect lineages will be critical in resolving this issue.

Costs of Gregarious Behavior

Intraspecific Competition

One of the most obvious and widely documented costs of gregariousness is intraspecific competition. As more individuals share a limited resource, the amount available per individual decreases. Food, mates, and sites for shelter, basking or oviposition can all be limiting resources. Some insects such as bark beetle larvae may deplete their food sources and die before reaching the more mobile adult stage. In others such as aphids, the effects of competition may be less severe but still result in restricted access to nutrients, smaller adult size and reduced fecundity. Perhaps the most extreme form of intraspecific competition is cannibalism, the threat of which can be particularly severe among larval forms of insects that feed in enclosed environments such seeds, fruit, stems, and stored products. Cannibalism can also serve as an important mechanism by which individual insects redress nutritional imbalances brought on by increased competition for resources at high population densities.

Pathogen Transmission

Another clear cost of living in a group is the increased risk of becoming infected with a pathogen or parasite. An increased probability of fungal pathogen infection among group members has been shown in a variety of insects such as aphids, cicadas, caterpillars, and beetle larvae. Both pathogens and parasites can be spread by direct contact with infected individuals as well as their excrement and saliva. Alternatively, propagules from infected individuals may be rapidly dispersed locally among group members through the air or across the substrate surface where they can be secondarily encountered. Some insects have evolved an elegant solution to the increased risk of pathogen infection in crowds by incurring the metabolic cost associated with pathogen resistance only under high population density conditions. This form of density-dependent pathogen resistance or prophylaxis has been demonstrated across insect orders in taxa such as *Tenebrio molitor* beetles, *Spodoptera exempta* caterpillars, and *Schistocerca gregaria* locusts.

Increased Conspicuousness to Predators

A group of insects should simultaneously be more apparent to predators and more worthwhile as a source of potential food than solitary prey. The cost of increased conspicuousness in a group should be even greater for aposematic insects that are themselves conspicuously colored. That so many gregarious insects exist in the first place suggests that this cost is routinely surmounted by at least one of the benefits described above. In addition to providing a larger visual stimulus to predators, aggregations may also result in the local concentration of other cues used by natural enemies to find insect prey. Predators and parasitoids can locate their prey directly by orientation toward cues such as aggregation pheromones or the sound of calling males, as well as indirectly through cues such as volatile compounds emanating from frass or plant tissues exposed by feeding damage.

Physiological Costs

Among insects that use aggregation pheromones for group formation, pheromone production necessarily involves a metabolic cost. For example, these costs may range from minimal when pheromones are by-products of existing metabolic pathways and structures as they appear to be in *Phylotretta cruciferae* flea beetles, to more substantial when pheromone production requires the development and maintenance of specialized glands or organs as in the triatomine bugs. Furthermore, aggregation pheromone production has been shown in some beetles to be regulated and can be reduced under crowded conditions. However, it is not yet known if this facultative response serves to reduce metabolic costs or is perhaps an adaptation that reduces some other cost associated with crowding.

Population Level Consequences of Gregarious Behavior

Gregariousness not only affects the performance and survivorship of individual insects, but can also have important population level consequences. The expression of gregarious behavior can interact with other ecological processes to influence a species' population dynamics, dispersal or migration, and spatial distribution patterns. Gregarious behavior in insects can sometimes lead to devastating consequences for humans, as evidenced by its central role in the biology of two major pest species, the desert locust, *Schistocerca gregaria*, and the Mormon cricket, *Anabrus simplex*.

The Desert Locust

Under outbreak conditions, locusts form huge groups in which millions of insects can travel en masse on the ground in migratory bands as juveniles and in the air as characteristic swarms of flying adults. Unlike other grasshoppers, locusts can express an extreme form of density-dependent phenotypic plasticity known as "phase polyphenism." Individuals reared under low population densities (the harmless, non-migratory "solitarious" phase) differ markedly in behavior, physiology, color and morphology from locusts reared under crowded conditions during outbreaks (the migratory swarming "gregarious" phase) (Fig. 58). A shift to the expression of gregarious behavior at high population density is central to the process of locust phase change. This form of behavioral phenotypic

Gregarious Behavior in Insects, Figure 58 **Gregarious behavior in locusts is environmentally determined and mediated by changes in local population density. Examples of the alternative density-dependent phenotypes of final instar desert locust nymphs, *Schistocerca gregaria*, are pictured. The non-migratory and cryptic "solitarious" phase produced at low population density is on the left. The migratory and aposematic "gregarious" phase induced by high population density is on the right. (Photo by Greg Sword.)**

plasticity suggests that natural selection has favored, within the same individual, the ability to lead a solitary lifestyle when it is advantageous at low population densities, as well as the ability to take advantage of gregariousness under high population density conditions.

At the heart of locust swarm formation and migration is the shift from the shy, cryptic behavior of solitarious phase locusts, which are relatively sedentary and avoid one another, to the highly active behavior and tendency to aggregate typical of gregarious phase insects. Nymphs of the desert locust, *Schistocerca gregaria*, can become behaviorally gregarious after just 1 h of crowding. This behavioral transition to gregariousness is soon followed by changes in other traits. One such change is a shift in feeding behavior in which the newly crowded insects become willing to feed on noxious plants that cause the locusts to be toxic to their predators. In turn, these behavioral changes are followed at the next nymphal molt by a density-dependent change in coloration from crypsis to warning coloration that enables the nymphs to advertise their recently acquired unpalatability to predators. Predator learning and subsequent avoidance of aposematic gregarious phase locust nymphs can reduce the per capita predation risk and facilitate additional population growth.

In addition to functioning as part of an aposematic anti-predator strategy, gregariousness in desert locusts also interacts with local habitat structure resulting in some habitats being more likely than others to generate locust swarms. Individual locusts are more likely to come in contact with each other and change into the migratory gregarious phase when the resources they utilize, such as host plants or roosting sites, are distributed in an aggregated as opposed to dispersed manner. As more and more locusts become gregarious, they also become locally concentrated, and once a critical population density is reached, mass migration is triggered. Recent evidence suggests that mass movement among juvenile locusts in migratory bands is mechanistically linked to the risk of cannibalism in high-density groups, a process first identified in Mormon crickets and described below.

The Mormon Cricket

Mormon crickets are flightless tettigoniids from western North America that also form huge migratory bands during outbreaks. Although Mormon cricket and locust migratory bands share many similar characteristics, Mormon crickets do not appear to express the density-dependent phase changes in gregariousness or other traits as do locusts. Thus, the phenomenon of migratory band formation (Fig. 59) and movement appears to have convergently evolved in these two groups via different underlying behavioral mechanisms.

Mormon crickets constitute a unique model system in which understanding the costs and benefits of gregariousness has provided a unifying framework that explains both how and why inter-individual interactions can lead to landscape-scale mass movement. In terms of benefits, a radiotelemetry-based mark recapture study revealed that migratory bands form as part of an anti-predator strategy. Individual band members are much less likely to be killed by predators than are insects that have been separated from the group. As predicted, once migratory bands have formed, individual band members are subject to increased intraspecifc competition for nutritional resources. Individual crickets within migratory bands have been shown to be deprived of specific nutritional resources, namely protein and salt. When provided with augmented dietary protein, individual crickets spent less time walking, a response that was not

Gregarious Behavior in Insects, Figure 59 **A migratory band of Mormon crickets, *Anabrus simplex*, crossing a dirt road in NE Utah, USA. Migratory bands can contain millions of insects that walk up to 2 km/day. Gregariousness confers protection from predators. However, band members suffer from intraspecific competition and must keep moving to encounter new nutritional resources as well as to avoid being cannibalized by other hungry insects in the band. (Photo by Greg Sword.)**

found when crickets had ample carbohydrate. Thus, group movement results in part from locomotion induced by protein deprivation and should act to increase the probability that individual band members will encounter new resources and redress their nutritional imbalances.

An additional cost of group formation is that Mormon crickets are notoriously cannibalistic. Their propensity to cannibalize is a function of the extent to which they are nutritionally deprived. Given that Mormon crickets are walking packages of protein and salt, the insects themselves are often the most abundant source of these nutrients in the habitat. As a result, individuals within the band that fail to move risk being attacked and cannibalized by nutritionally deprived insects approaching from the rear. Thus, the mass movement of individuals in migratory bands is a forced march driven by cannibalism due to individuals responding to their endogenous nutritional state. The fact that migratory bands are maintained as cohesive groups despite these conditions suggests that the risk of predation upon leaving the band must outweigh the combined costs of intraspecific competition for resources and cannibalism.

► Cycloalexy
► Sociality of Insects
► Aposematism
► Phase Polymorphism in Locusts
► Phase Polyphenism in Insects
► Juvenile Hormone

References

Hunter AF (2000) Gregariousness and repellent defenses in the survival of phytophagous insects. Oikos 91:213–224

Krause J, Ruxton GD (2002) Living in groups. Oxford University Press, Oxford, UK

Prokopy RJ, Roitberg BD (2001) Joining and avoidance behavior in nonsocial insects. Annu Rev Entomol 46:631–665

Reader T, Hochuli DF (2003) Understanding gregariousness in a larval Lepidopteran: the roles of host plant, predation, and microclimate. Ecol Entomol 28:729–737

Ruxton G, Sherratt T (2006) Aggregation, defense and warning signals: the evolutionary relationship. Proc R Soc London B Biol Sci 273:2417–2424

Simpson SJ, Sword GA (2007) Phase polyphenism in locusts: mechanisms, population consequences, adaptive significance and evolution. In: Whitman D, Ananthakrishnan T (eds) Phenotypic plasticity of insects: mechanisms and consequences Science Publishers, Inc., Plymouth, pp 93-135

Simpson SJ, Sword GA, Lorch PD, Couzin ID (2006) Cannibal crickets on a forced march for protein and salt. Proc Natl Acad Sci USA 103:4152–4156

Vulinec K (1990) Collective security: aggregation by insects as a defense. In: Evans DL, Schmidt JO (eds) Insect defenses: adaptive mechanisms and strategies of prey and predators. State University of New York Press, Albany, NY, pp 251–288

Wertheim B, Van Baalen EJA, Dicke M, Vet LEM (2005) Pheromone-mediated aggregation in nonsocial arthropods: an evolutionary ecological perspective. Annu Rev Entomol 50:321–346

Gregarious Parasitoid

Parasitoids than can co-exist with others of the same species within the body of a host insect.

Gressitt, Judson Linsley

Judson Linsley Gressitt was born in Tokyo in 1914 to an American family. He grew up in Tokyo and was educated at an American school. On finishing school, he traveled alone at age 18 to Taiwan and collected insects in much of the island, including the highest mountains. His first degrees were in entomology at the University of California, after which he accepted a position at Lingnan University in Guangzhou, China. He continued fieldwork, and he married Margaret Kriete. The family was interned in 1941–1943 by Japanese forces in China. After the war, Lin returned to Berkeley and earned a doctorate in entomology. Then he returned to Lingnan University as Associate Professor until 1951. In 1949 the family was interned again, this time by Chinese forces as the Chinese revolution raged and the Korean War was imminent. His involvement with Pacific entomology and especially with the Bernice

P. Bishop Museum in Honolulu followed. In 1955, he began an association with New Guinea, which led in 1961 to establishment of what is now the Wau Ecology Institute. His research interests covered biogeographic and ecological questions in plants, vertebrates, and invertebrates. His particular taxonomic interests were in the beetle families Cerambycidae and Chrysomelidae. But his work included many other projects such as insect disease carriers, Antarctic entomology, transoceanic dispersal, and insect conservation. He was editor of four serial publications. He and his wife, Margaret, died in an air crash in China on April 26, 1982.

Reference

Holloway JD (1982) Dr J Linsley Gressitt, 1914–1982. Antenna 6: 285

Grid Mapping

Mapping the locations of pests in a field using coordinates.

Gripopterygidae

A family of stoneflies (order Plecoptera).

► Stoneflies

Grooming

Cleaning of the body using the mouthparts or legs. In solitary insects, it is a self-cleaning process, but in social insects individuals groom one another.

Grote, Augustus Radcliffe

Augustus Grote (Fig. 60) was born in Liverpool, England on February 7, 1841, of a Welsh mother and German father who moved with him to a farm in New York when he was seven. As a schoolboy he spent much time collecting insects. His hopes of attending Harvard University were dashed when his father's investments failed and the family was left in straitened circumstances. He did, however, receive an A.M. degree from Lafayette College, Pennsylvania, after studies in Europe. In Alabama in the early 1870s, he studied the cottonworm, *Alabama argillacea*, eventually publishing five papers on it. On the death of his wife in 1873, he moved to Buffalo, New York, and worked as museum director. He was publisher of the Bulletin of the Buffalo Society of Natural History and of a short-lived journal called "The North American Entomologist." He wrote many articles on Lepidoptera, and produced with Coleman Robinson "A synonymical catalog of North American Sphingidae, with notes and descriptions" and a "List of the Lepidoptera of North America." In 1884 he moved to Germany, first to Bremen and then to Hildesheim, but continued writing for North American journals. For the last nine years of his life, he was honorary assistant at the Roemer Museum in Hildesheim, in which city he died on September 12, 1903. His large insect collection was offered

Grote, Augustus Radcliffe, Figure 60 **Augustus Grote.**

for sale in the USA, but when there were no buyers it was sold to the British Museum (Natural History).

Reference

Mallis A (1971) Augustus Radcliffe Grote. pp. 304–308 in American entomologists. Rutgers University Press, New Brunswick, New Jersey. 549 pp.

Ground Beetle (Coleoptera: Carabidae) Feeding Ecology

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The Carabidae, or ground beetles, represent approximately 40,000 described species found throughout the world, with most species present in the tropics. There are nearly 2,700 described species in Europe and over 2,000 species in North America. Detailed biological descriptions are available for fewer than 100 species (mostly western European species). Many carabids are easily recognized at the family level. Adults are well-proportioned beetles with pronounced mandibles and palps, long slender legs, striate elytra, and sets of punctures with tactile setae. Many possess an antenna-cleaning organ and mostly pubescent antennae. Many are dark colored, shiny or dull. Some have bright or metallic colors and some are pubescent.

Although carabids possess an easy-to-recognize general body form, they have undergone morphological adaptations to suit the habitat in which they are found. Such modifications have permitted running, burrowing in soil and sand, living under tree bark, climbing plants, and swimming in water. Consequently, some species are found in very unique places. For example, some inhabit the edges of ice glaciers, others live in caves, others along stream banks. Others are found in woodlands, or are found in deserts. Most species reside on the ground (epigeic), but some species are plant-dwelling (arboreal) during the adult stage. Others live in self-constructed tunnels in sand or fine soil.

Based upon research in Britain (in Europe), carabid genera are found typically in certain habitats: species of *Bembidion* are common amongst vegetation alongside rivers and lakes; species of *Acupalpus*, *Agonum*, *Stenolophus*, and smaller-sized *Pterostichus* are present in litter on the soil surface in marshy (fresh water) habitats. The genera *Dicheirotrichus*, *Dyschirius*, and *Pogonus* are found in salt marshes. Larger-bodied genera such as *Calathus*, *Carabus*, *Harpalus*, *Nebria*, or *Pterostichus* can be found in rough grass, or in gardens. In drier habitats, especially exposed to sun, *Amara*, *Badister*, some *Harpalus* and *Notiophilus* can be found. The location of the preferred habitat (and microhabitat) can be influenced by season, temperature and humidity extremes, life history pattern, competitors, and food availability.

General Feeding Ecology

Feeding Preferences

Carabid beetles can be categorized as carnivores, herbivores, or omnivores. A recent survey of 1,290 literature references indicated that 775 species were partially or exclusively carnivorous, 85 species were exclusively herbivorous, and 206 species were omnivorous. Some carnivorous species opportunistically feed on a diversity of prey. For example, the diet of numerous species in the genera *Agonum*, *Calathus*, *Chlaenius*, *Poecilus*, or *Pterostichus* is most often dependent on the season and availability of specific prey. Other carnivorous species are more selective. Some oligophagous species such as those in the genera *Cychrus* and *Scaphinotus* are predators of snails and slugs. Others in the genus *Calosoma* prey upon caterpillars. Species of *Loricera* and *Notiophilus* are predators of springtails (Collembola). Species in the genus *Promecognathus* specialize upon millipedes. Some species are parasitoids in the larval stage, but are predators in the adult stage. For example, the larvae of *Lebia* spp. are ectoparasitoids of pupae of leaf beetles (Chrysomelidae), whereas the adults attack egg and larval stages. The larvae of *Brachinus* spp. (bombardier beetles) are ectoparasitoids of pupae of water scavenger beetles (Hydrophilidae) and whirligig beetles (Gyrinidae).

Herbivorous carabids may consume plant seeds, ripe fruit, and foliage. *Zabrus* adults and larvae consume ripe grains and sprouting leaves of cereal plants. Many *Harpalus* and *Amara* adults feed on germinating weed seeds. The diet of the larvae, however, is unknown for the majority of species. Several *Harpalus* species collect and cache seeds of grasses in burrows.

Omnivorous carabids are apparently opportunists that feed upon the food items most readily available in their immediate habitat. Many carabid species are likely omnivorous. In fact, predominantly carnivorous species probably consume pollen, fungi, and other plant materials during periods of prey shortage to avoid starvation.

Searching for Food

Carabid beetles are known to search actively for food by means of random search, vision, or chemical cues. Most adults rely on random search, in which the beetle contacts the prey with its mouthparts, antennae, or setae on some body part or appendage. This strategy is common to nocturnal species. Very little is known about the searching behavior of carabid larvae. Presumably, the larvae of most nocturnal species rely on random search and then physical contact with prey. Some carabid larvae do not actively search for prey. Instead, they deploy an ambush strategy. They remain concealed inside burrows or tunnels and only attack prey that come too close to their burrows. This strategy is typical of tiger beetle larvae (tribe Cicindelini; e.g., *Amblycheila*, *Cicindela*, *Megacephala*, and *Omus*).

Diurnal species rely upon short-range vision to locate prey. For example, *Notiophilus biguttatus* adults and larvae feed extensively on springtails (Collembola). Adults are aided by their large compound eyes to hunt their prey. This predator may intensify its search for prey in relation to light intensity. Greater light intensity usually results in an increased search rate. The *N. biguttatus* larvae rely more on physical contact for detection of prey.

Several carabids respond to the odor of their prey to facilitate detection. Adults of *Pterostichus melanarius* and *Harpalus rufipes* were attracted to an aphid alarm substance released by aphids under attack by predators, such as ladybird beetles. In contrast, *Nebria brevicollis* adults were attracted to the odor of live springtails, but not to aphid alarm substance. Note that *P. melanarius* was also attracted to the odor of live aphids, but the other two species were not. Larvae of *N. biguttatus* are guided by chemical cues to the aggregation sites of springtails. Reliance upon chemical cues from prey (or hosts in the case of parasitoids searching for concealed prey) is probably more widespread than currently reported.

Although most carabids search for prey on the ground, some species seek prey on plants. *Calleida*, *Cymindis*, *Dromius*, *Lebia*, *Parena*, *Pinacodera*, and *Plochionus* adults have been found foraging on plants during the day. More than 30% of tropical carabid species (e.g., *Agra*, *Lebia*) forage on plants. Adults of a few species of *Agonum*, *Amara*, *Chlaenius*, *Harpalus*, and *Pterostichus* are occasionally found foraging on plants. Both adults and larvae of *Calosoma sycophanta* (and other species of *Calosoma*) forage for prey on the trunks of forest trees.

Prey Capture

Once prey is located, some species lunge toward it with their mandibles agape. Most adult carabids use their well-developed mandibles to subdue and kill prey. Morphological and behavioral adaptations can be involved in capturing prey, particularly for the species with specialized feeding habits. *Cychrus caraboides* and *Carabus violaceous* successfully subdue slugs (gastropods) by biting them at specific locations on the body, which may paralyze prey. This could prevent the production and secretion of mucus by the slugs, a mechanism of defense against predation.

Species that specialize on snails are not deterred by the shell. Some *Cychrus* and *Scaphinotus* adults readily capture and consume large-sized snails by inserting their slender, elongate head and prothorax into the opening, then proceed to kill and consume the prey. *Cychrus* larvae crawl inside the shell and feed, in spite of the mucus secretions of the prey. Some generalists such as *Pterostichus* species can crush shells with their mandibles. Shell thickness could influence the vulnerability of snails to attack from generalist carabids.

Prey capture behavior has been described for several species that hunt springtails. Adults and larvae of *N. biguttatus* rely on vision to capture elusive springtails. Prey capture occurs when the predator rapidly lunges toward the springtail and grasps it within the mandibles. Adults of *Loricera pilicornis* capture springtails at night. Physical contact, rather than sight, is a prerequisite to prey capture. Adults lunge toward prey during the attack and bring their antennae together to entrap the springtail. Long, strong setae on the antennae enclose the prey and draw it toward the gaping mandibles. The prey capture behavior of *L. pilicornis* larvae differs from that of adults. Although prey are located by physical contact, the larvae do not lunge toward prey. Instead, larvae turn in the direction of contact while opening their mouthparts. The setae on the maxillae and an adhesive secretion coating the proximal end of each maxilla function to entrap the prey. The springtail is ultimately grasped by the mandibles.

Digestion

The adults of most carabids ingest and digest prey fragments, after mastication, with little or no extra-intestinal (i.e., pre-oral) digestion. The mandibles are used for crushing or tearing off fragments of food, which then are ingested. Enzymes involved in digestion are copious once food enters the foregut. In contrast, the adults of other species, particularly in tribes Carabini (e.g., *Calosoma*, *Carabus*), Cicindelini (e.g., *Cicindela*, *Omus*), and Cychrini (e.g., *Cychrus*, *Scaphinotus*, *Sphaeroderus*) masticate their prey only to lubricate it and extract the fluid contents from it. Extra-intestinal digestion commences after adults discharge a fluid from their buccal cavity (mouth) onto the prey or prey fragments. This fluid contains enzymes (proteases, carboxylases, amylases, etc.) that liquefy tissues. These enzymes are synthesized in the midgut, but are stored in the crop, from whence they are regurgitated onto the food prior to feeding. Only very fine particles and liquefied remains of prey are ingested. Digestion proceeds within the foregut, including the crop. Absorption of nutrients occurs primarily in the midgut. As far as is known, carabid larvae digest their food extra-intestinally. Once liquified food is ingested, the digestion process continues in the foregut, with absorption occurring primarily in the midgut. Carabid larvae that are ectoparasitoids (e.g., *Brachinus*, *Graphipterus*, *Lebia*) may rely almost exclusively on extra-intestinal digestion of host tissues.

Applied Feeding Ecology

Predation of Aphids and Leafhoppers

In sugar beet fields, carabid adults (especially *Pterostichus dorsalis*) were capable of reducing aphid (*Aphis fabae*) population densities in field cages. Carabids, even when at relatively low densities, were able to locate low density populations of aphids.

The impact of carabids and wolf spiders (Class Arachnida, Order Araneae, Lycosidae) on leafhopper (Cicadellidae) and aphid populations was assessed in maize fields. The abundance of both predator groups was manipulated by removing or adding individuals within field enclosures during mid-season and end-of-season. Although the impact of carabid predation could not be differentiated from spider predation, the combined action of both predator groups reduced populations of leafhoppers. In addition, the combined predators were capable of reducing aphid populations during mid-season.

Research in cereal fields indicated that the rate at which aphids (*Sitobion avenae*) dropped from plants to escape predators on the plants was critical to the efficacy of carabid predation on the ground. Carabids intercepted many aphids before they could climb back up on the plants. The effect of generalist predators functioning in-concert to impact aphid populations was investigated in experiments deploying carabids and lady beetles (Coccinellidae) in alfalfa fields. Positive predator-predator interactions occurred between the lady beetle *Coccinella septempunctata*, and the carabid *Harpalus pensylvanicus*. In laboratory arenas and in field cages, both predators fed on pea aphids, *Acyrthosiphon pisum*. Predation rates were greater than expected for the combined action of both predators. Thus, synergism occurred as *C. septempunctata* foraged on plants and *H. pensylvanicus* foraged at the base of the plants.

Predation of Flies

Predation of gall midge (Cecidomyiidae) larvae on the soil surface was found to be considerable, since polyphagous predators were responsible for 43–58% reduction of wheat gall midges (*Contarinia tritici*). Predation caused an 81% decrease in adult emergence of the midge Sitodiplosis mossellana. Feeding bioassays in the laboratory indicated that the carabids *P. melanarius* and *Platynus dorsalis* were primarily responsible for the decline of *S. mossellana* populations.

Carabid predation of the cabbage root fly (*Delia radicum*) and other anthomyiid species has been examined. Carabids (especially *Bembidion lampros* and *Trechus quadristriatus*) caused approximately 30% mortality of *D. radicum* by predation of eggs and first instar larvae in the soil. In a greenhouse experiment, a predator density of two *Bembidion tetracolum* adults per plant prevented an infestation of *D. radicum* in the spring season. Carabid predation caused an 82% reduction of the pest population, when *D. radicum* eggs were exposed on the soil surface. But, other carabid species (*B. tetracolum*) had difficulty locating eggs that were buried just beneath the surface.

Bembidion quadrimaculatum adults located onion maggot (*Delia antiqua*) eggs that were buried 1 cm deep in the soil. Up to 25 eggs were consumed daily under laboratory conditions and onion maggot numbers were reduced by up to 57% in field cages. Another study investigated the impact of predation on *D. antiqua* pupae exposed on the soil surface in corn fields. Carabid beetle abundance was manipulated so that the rate of removal of pupae from field exclosures (excluding vertebrates but not invertebrates) was determined during the growing season. Significantly more onion maggot pupae were removed from the cages that excluded vertebrates than from the cages that excluded both vertebrates and invertebrates. Carabid abundance correlated positively with predation rates. Feeding trials in the laboratory indicated that the four most abundant carabids (*Pterostichus* and *Poecilus* species) in corn fields readily consumed *D. antiqua* pupae.

Predation of Beetles

Carabids can be significant predators of the Colorado potato beetle *Leptinotarsa decemlineata* (Chrysomelidae), a pest of cultivated potato. In Bavaria (Germany), predation of larvae by *Carabus* spp. reduced the yield damage from this pest by approximately 33% in experimental plots compared to infested control plots that did not contain *Carabus* adults. *Carabus* consumed from 8 to 10 *L. decemlineata* larvae (third and fourth instars) per day in the laboratory.

In the United States, *Lebia grandis* larvae are confirmed ectoparasitoids and adults are specialist predators of *L. decemlineata* on cultivated potato. In the late 1930s, several years after the inadvertent introduction of *L. decemlineata* into

France, *L. grandis* was imported from the United States and a mass rearing program was initiated. The rearing technique was capable of generating large quantities of *L. grandis*, but was too labor intensive. Released adults had little demonstrable impact on *L. decemlineata* populations and failed to become established in France.

Carabid predation of weevils (Curculionidae) was documented. One study revealed that 28% of *Sitona hispidulus* eggs were removed by carabids when placed in experimental cages in alfalfa fields. Of the carabid species tested, *Amara aenea* was the most efficient predator. Carabid predation resulted in greater than 30% reduction of larvae and overwintering adults of *Sitona lineatus* in field beans. *Bembidion properans* adults consumed *S. lineatus* eggs and young larvae.

Predation of the rape blossom beetle, *Meligethes aeneus* (Nitidulidae) by the carabid *Clivina fossor* was documented. In a two-week period *C. fossor* adults consumed 65% of *M. aeneus* larvae and pupae that had been introduced into an arena containing soil at a depth of 6–7 cm. Another investigation indicated that *M. aeneus* experienced a 39% population decline, perhaps, during the time that mature larvae had left the crop plants (rape) and wandered on the soil surface, prior to pupation. Predation by polyphagous predators was thought to be responsible for the decline of the pest population. Research is ongoing to determine the contribution of different species to the mortality of *Meligethes* spp.

Predation of Moths

In the early 1900s, *Calosoma sycophanta* was introduced into northeastern United States to control the gypsy moth *Lymantria dispar* (Lymantriidae), an inadvertently introduced pest of forest and shade trees. The beetle is well-established in most areas where gypsy moth is distributed, and is an important arthropod natural enemy of larval and pupal stages. Adult C. sycophanta are long-lived (2–4 yr) and even a low density of beetles can have considerable impact on L. dispar populations. A single *C. sycophanta* larva can kill more than 50 late instar *L. dispar* larvae during a two-week time span, whereas, an adult can kill an average of 150 late instar larvae. Unfortunately, this carabid has a slow numerical response to pest population densities and has not been able to prevent gypsy moth outbreaks.

In apple orchards, carabids are important predators of codling moth, *Cydia pomonella* (Tortricidae), a worldwide pest of pome fruit, including apple. Carabids can forage on the ground during the season when mature larvae are wandering on the soil surface before pupation in leaf litter or under loose tree bark. Several carabid species from an apple orchard in Canada gave positive serological reactions to antiserum against *C. pomonella* larvae. *Pterosticus* species consumed *C. pomonella* mature larvae in experimental arenas in the laboratory. In the field, tethered mature larvae were located and then killed by carabids; 60% predation by carabids per night was estimated during the first generation of codling moth in the spring in an apple orchard in northern California, USA. *Pterostichus californicus*, *Pterostichus cursitor*, and *Pterostichus lustrans* dominated the carabid assemblage in an unsprayed orchard in northern California.

Maize plants suffered significantly less damage from armyworms *Pseudaletia unipuncta* (Noctuidae) when ground-foraging predators were included in experimental arenas rather than excluded from arenas. Carabid predation of armyworms was thought to be responsible for the reduction. *Pterostichus chalcites*, *Pterostichus lucublandus*, and *Scarites subterraneus* adults readily consumed second and fourth instar *P. unipuncta* larvae in the laboratory.

A laboratory and field investigation assessed the impact of carabid predation on diamondback moth *Plutella xylostella* (Yponomeutidae) larvae on seedling cabbage plants in Japan. The highest consumption rate (of 24 carabid species tested) was 23 larvae (fourth instars) per day by *Chlaenius* *posticalis* adults. Note that *C. posticalis* and *Chlaenius micans* larvae consumed approximately 92 and 191 early fourth instar *P. xylostella* larvae, respectively.

Conclusion

Despite their generally accepted role as natural enemies, detailed information on the feeding ecology of carabids is not available for many species. More research is needed to clarify the trophic relations of carabid larvae. Carabids appear to affect the populations of some crop pests. Carabids may have their greatest impact when operating in concurrence with other natural enemies.

References

Chaboussou F (1939) Contribution à l' étude biologique de *Lebia grandis* Hentz, prédateur américain du Doryphore. Annales des épiphyties et de Phytogénétique 5:387–433

Digweed SC (1993) Selection of terrestrial gastropod prey by Cychrine and Pterostichine ground beetles (Coleoptera: Carabidae). Can Entomol 125:463–472

Hagen KS, Mills NJ, Gordh G, McMurtry JA (1999) Terrestrial arthropod predators of insect and mite pests. In: Bellows TS, Fisher TW (eds) Handbook of biological control: principles and applications of biological control. Academic Press, San Diego, CA, pp 383–503

Hengeveld R (1980) Polyphagy, oligophagy and food specialization in ground beetles (Coleoptera, Carabidae). Neth J Zool 30:564–584

Kromp B (1999) Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. Agric Ecosyst Environ 74:187–228

Lang A, Filser J, Henschel JR (1999) Predation by ground beetles and wolf spiders on herbivorous insects in a maize crop. Agric, Ecosyst Environ 72:189–199

Larochelle A (1990) The food of carabid beetles (Coleoptera: Carabidae, incl. Cicindelinae). Association des Entomologistes Amateurs du Québec. Fabreries, Suppl 5:1–132

Losey JE, Denno RF (1998) Positive predator-predator interactions: enhanced predation rates and synergistic suppression of aphid populations. Ecology 79:2143–2152

Lovei GL, Sunderland KD (1996) Ecology and behavior of ground beetles. Annu Rev Entomol 41:231–256

Luff ML (1991) Carabidae. In: Cooter J (ed) A coleopterist' s handbook, 3rd edn. The Amateur Entomologist' s Society, Middlesex, UK, pp 69–72

Menalled FD, Lee JC, Landis DA (1999) Manipulating carabid beetle abundance alters prey removal rates in corn fields. BioControl 43:441–456

Stork NE (ed) (1990) The role of ground beetles in ecological and environmental studies. Intercept, Andover, UK

Suenega H, Hamamura T (1998) Laboratory evaluation of carabid beetles (Coleoptera: Carabidae) as predators of diamondback moth (Lepidoptera: Plutellidae) larvae. Environ Entomol 27:767–772

Thiele HU (1977) Carabid beetles in their environments: a study on habitat selection by adaptations in physiology and behaviour. Springer-Verlag, Berlin, Germany

Ground Beetle (Coleoptera: Carabidae) Taxonomy

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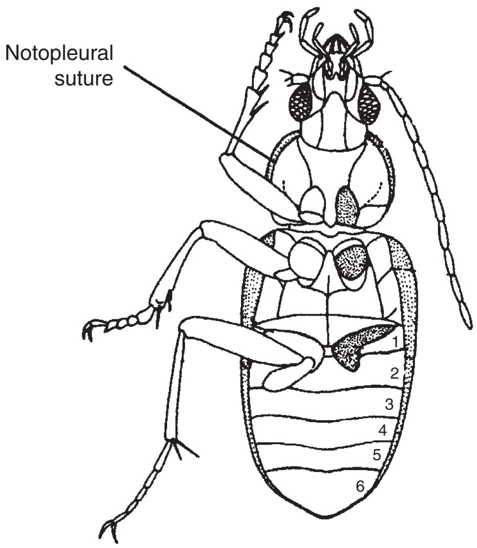
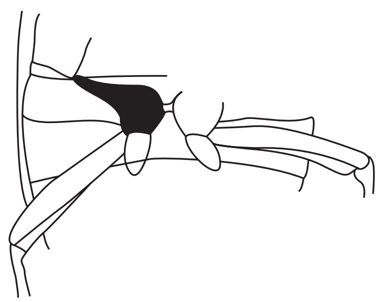
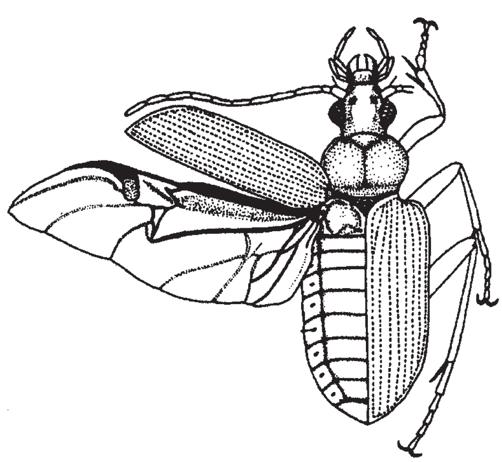
There are approximately 110 families of beetles found worldwide. The order Coleoptera is subdivided into two major sub-orders, Adephaga and Polyphaga. Polyphaga contains most beetle species. Ground beetles are placed in the sub-order Adephaga. This sub-order contains relatively few families of beetles, most families belonging to the much larger sub-order Polyphaga. As now defined, Adephaga contains the families Gyrinidae, Haliplidae, Trachypachidae, Noteridae, Amphizoidae, Dytiscidae, Hygrobiidae, and Carabidae. Adult Adephaga are separated from all other beetle families by the presence of a visible notopleural suture on the prothorax; six visible abdominal sterna; with the first 3 segments fused and divided by hind coxae (Figs. 61–64). Many species are capable of flight and possess fully developed flight wings. Ground beetles range in size from less than 1 mm to more than 60 mm in length. Most ground beetles are uniformly dark in color, but some species are brightly colored (especially tropical species). Carabids occur throughout the world, and may be found from sea level to altitudes of above 5,000 m in the Himalayas. Although there is diversity of form among carabid tribes (Figs. 65–74), the large number of species in



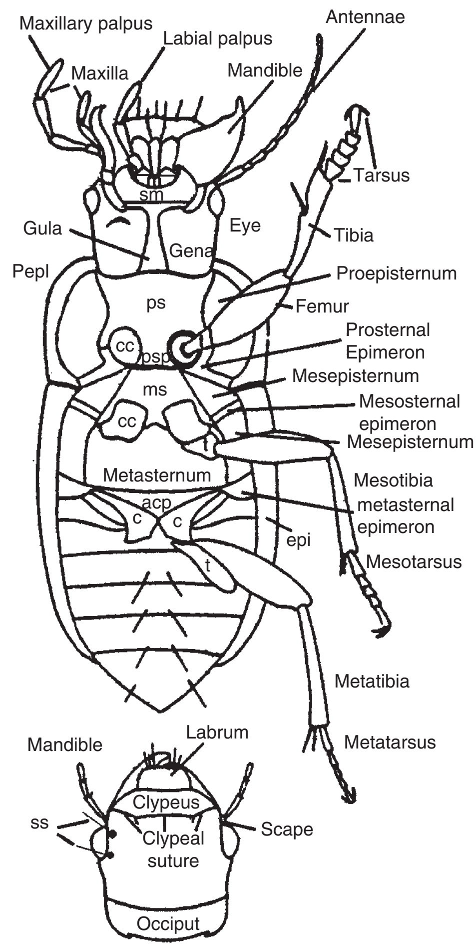
Ground Beetle (Coleoptera: Carabidae) Taxonomy, Figure 61 Ventral view of adult ground beetle.



Ground Beetle (Coleoptera: Carabidae) Taxonomy, Figure 62 Hind coxa (shaded) fused to and dividing sternite 1.

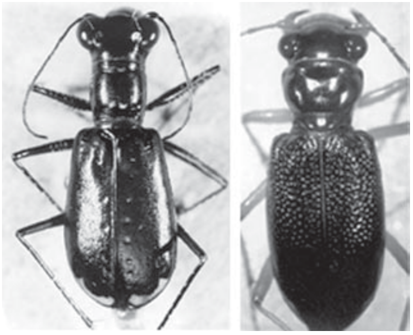


Ground Beetle (Coleoptera: Carabidae) Taxonomy, Figure 63 Dorsal view of ground beetle adult, showing exposed flight wing.

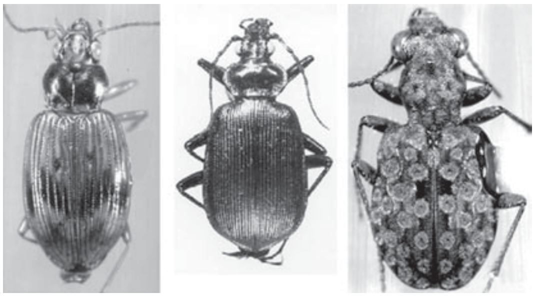


Ground Beetle (Coleoptera: Carabidae) Taxonomy, Figure 64 Ventral view of a ground beetle showing major sclerites, followed by dorsal view of head. Abbreviations: ps = prosternum; psp = prosternal process; cc = coxal cavity; c = coxa; t = trochanter; epl = epipleuron; pepl = proepipleuron; ss = supraorbital setae; acp = anterior coxal process.

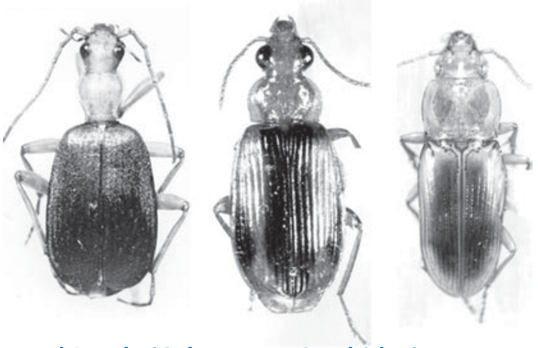
some genera makes separation of specimens difficult at the species level. In spite of the abundant number of species, the tribal classification is fairly well established. Because there are no rules for assignment of categories above the species level, grouping of taxa above tribes is very much unsettled, and vary according to author and region. What follows here is a current arrangement of the higher taxa of ground beetles with representative illustrations of adults of several tribes.



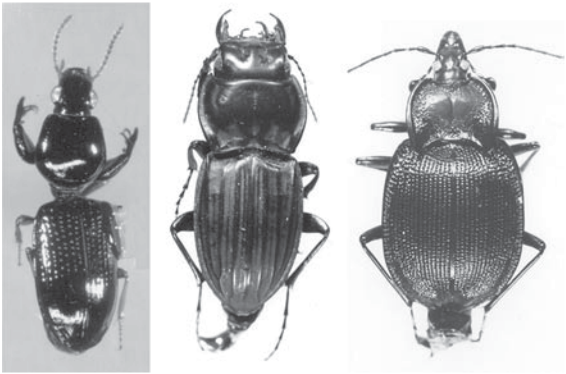
Ground Beetle (Coleoptera: Carabidae) Taxonomy, Figure 65 Representative figures of ground beetle tribes: tiger beetles, (*left*) Cicindelini, *Cicindela*; (*right*) Megacephalini (*Megacephala*).



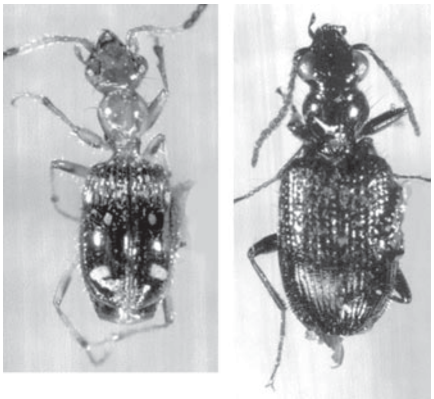
Ground Beetle (Coleoptera: Carabidae) Taxonomy, Figure 66 Representative figures of ground beetle tribes: (*left*) Bembidiini, *Bembidion*; (*middle*) Carabini, *Calosoma*; (*right*) Elaphrini, *Elaphrus*.



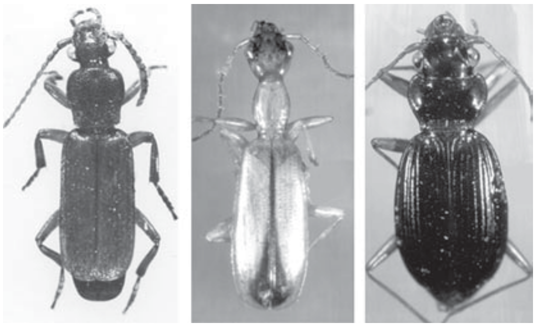
Ground Beetle (Coleoptera: Carabidae) Taxonomy, Figure 67 Representative figures of ground beetle tribes: (*left*) Brachinini, *Brachinus*; (*middle*) Lebiini, *Plochionus*; (*right*) Pogonini, *Diplochaetus*.



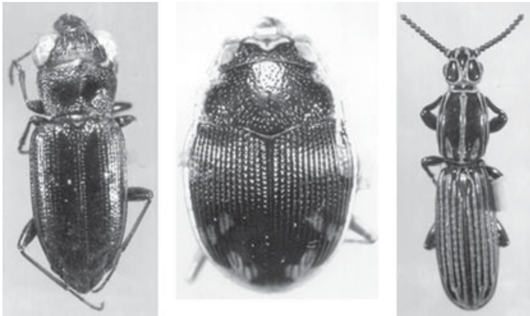
Ground Beetle (Coleoptera: Carabidae) Taxonomy, Figure 68 Representative figures of ground beetle tribes: (*left*) Dyschirini, *Dyschirius*; (*middle*) Scaritini, *Pasimachus*; (*right*) Cychrini, *Scaphinotus*.



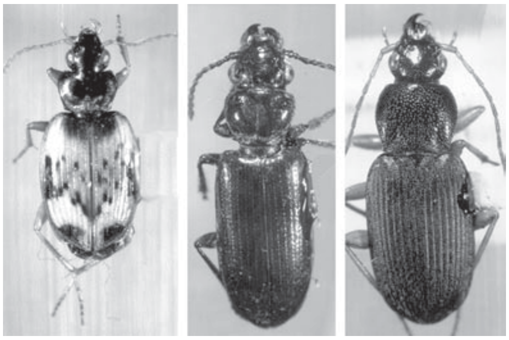
Ground Beetle (Coleoptera: Carabidae) Taxonomy, Figure 69 Representative figures of ground beetle tribes: (*left*) Lachnophorini, *Calybe*; (*right*) Lachnophorini, *Euphorticus*.



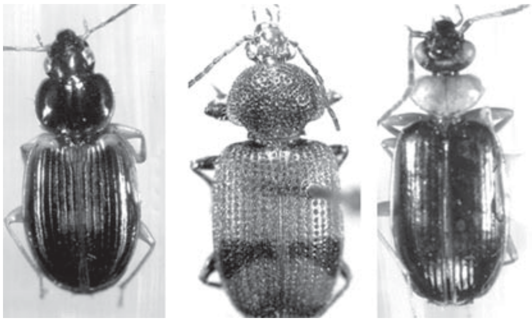
Ground Beetle (Coleoptera: Carabidae) Taxonomy, Figure 70 Representative figures of ground beetle tribes: (*left*) Helluonini, *Helluomorphoides*; (*middle*) Ctenodactylini, *Leptotrachelus*; (*right*) Nebriini, *Nebria*.



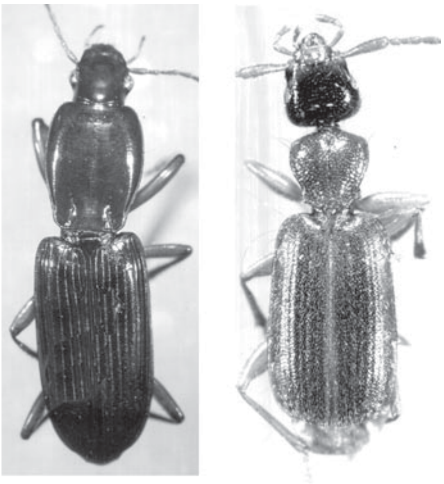
Ground Beetle (Coleoptera: Carabidae) Taxonomy, Figure 71 Representative figures of ground beetle tribes: (*left*) Notiophilini, *Notiophilus*; (*middle*) Omophronini, *Omophron*; (*right*) Rhysodini, *Omoglymmius*.



Ground Beetle (Coleoptera: Carabidae) Taxonomy, Figure 72 Representative figures of ground beetle tribes: (*left*) Cyclosomini, *Tetragonoderus*; (*middle*) Psydrini, *Nomius*; (*right*) Chlaeniini, *Chlaenius*.



Ground Beetle (Coleoptera: Carabidae) Taxonomy, Figure 73 Representative figures of ground beetle tribes: (*left*) Platynini, *Olisthopus*; (*middle*) Panagaeini, *Panagaeus*; (*right*) Pentagonicini, *Pentagonica*.



Ground Beetle (Coleoptera: Carabidae) Taxonomy, Figure 74 Representative figures of ground beetle tribes: (*left*) Harpalini, *Stenomorphus*; (*right*) Zuphiini, *Zuphium*.

Identification of ground beetles includes analysis of external morphological characters, and frequently comparison of genitalic structures. The latter requires dissection of specimens and is used less commonly than external morphological characters. Species definitions for ground beetles are varied, dependent upon the group and diagnostic characters defined by that group' s expert.

Literature dealing with the identification of ground beetle species is voluminous. Maddison (1995) listed the world higher classification of ground beetles. His classification differed somewhat from Ball and Bousquet (2001), who presented a comprehensive outline of higher classification of the Nearctic ground beetles based on the classification scheme of Lawrence and Newton (1995). In their classification scheme the wrinkled bark beetles are treated as the family Rhysodidae. Madison (1995) cited disagreement over placement of several Adephaga families, namely the tiger beetles (family Cicindelidae or supertribe Cicindelitae) and the wrinkled bark beetles (family Rhysodidae or tribe Rhysodini). I follow the classification scheme of Lawrence and Newton (1995) here. Tribes are listed in phylogenetic order (according to degree of relatedness) beginning with what are considered the most primitive groups.

The following abbreviations are used in the listing of ground beetle taxa (f = family; s.f. = subfamily; t = tribe; ** = with representatives in North America). Approximate distributions are listed for those taxa that are sufficiently well known and defined.

Family: Carabidae
- Subfamily: Paussinae
  - Tribe: Metriini ** – 2 species restricted to western North America
  - Tribe: Ozaenini ** – Pantropical, occurring in Oriental, Afrotropical, Australian, and Neotropical regions
  - Tribe: Paussini – myrmecophilous, restricted to tropics in southern Hemisphere
- Subfamily: Gehringiinae
  - Tribe: Gehringiini** – a single Pacific Northwest species in North America
- Subfamily: Nebriinae
  - Tribe: Notiophilini** – Palearctic, Oriental, Nearctic, Neotropical regions
  - Tribe: Notiokasini – Neotropical
  - Tribe: Pelophilini** – Arctic and subarctic regions
  - Tribe: Opisthini** – Nearctic and China, India, Bhutan, Nepal, and Taiwan
  - Tribe: Nebriini** – Holarctic and north Oriental
- Subfamily: Carabinae –
  - Tribe: Carabini** – worldwide distribution
  - Tribe: Ceroglossini – Chile
  - Tribe: Pamborini – Australia
  - Tribe: Cychrini** – Holarctic, and China, Tibet, and Sikkim, Himalaya
- Subfamily: Cicindelinae (tiger beetles)
  - Tribe: Omini** – western US
  - Tribe: Collyridini – Pantropical
  - Tribe: Megacephalini** – Nearctic, Palearctic
  - Tribe: Ctenostomatini – Neotropical
  - Tribe: Manticorini – South Africa
  - Tribe: Cicindelini** – worldwide
- Subfamily: Loricerinae –
  - Tribe: Loricerini** – Holarctic – Oriental regions
- Subfamily: Omophroninae – found in all major zoogeographical regions except Australia
  - Tribe: Omophronini**
- Subfamily: Elaphrini – Holarctic
  - Tribe: Cicindini – Kuwait
  - Tribe: Elaphrini** – Holarctic
  - Tribe: Migadopini – Chile
  - Tribe: Amarotypini – distribution uncertain
- Subfamily: Promecognathinae –
  - Tribe: Promecognathini** – Nearctic and South Africa
- Subfamily: Scaritini – all major zoogeographical regions
  - Tribe: Siagonini – Palearctic
  - Tribe: Hiletini – Peru, tropical Africa, Southeast Asia, Indonesia
  - Tribe: Clivinini** – all major zoogeographical regions
  - Tribe: Scaritini** – all major zoogeographical regions
- Subfamily: Rhysodinae – worldwide
  - Tribe: Rhysodini** – wrinkled bark beetles, sometimes placed in family Rhysodidae
- Subfamily: Trechinae – worldwide, mostly in temperate regions
  - Tribe: Psydrini** – Holarctic and Australia
  - Tribe: Melaenini – South India
  - Tribe: Cymbionotini – South India
  - Tribe: Broscini** – temperature portions of all major zoogeographical regions
  - Tribe: Apotomini – South India
  - Tribe: Trechini** – worldwide distribution
  - Tribe: Zolini – Chile
  - Tribe: Pogonini** – all zoogeographical regions
  - Tribe: Bembidiini** – all zoogeographical regions
  - Tribe: Patrobini** – Oriental, Palearctic, and Nearctic regions
  - Tribe: Amblytelini – Australia
- Subfamily: Harpalinae
  - Tribe: Pterostichini** – all major regions
  - Tribe: Morionini** – Nearctic and pantropical regions
  - Tribe: Cnemalobini – Argentina
  - Tribe: Catapieseini – Neotropics
  - Tribe: Platynini** – all major zoogeographical regions
  - Tribe: Zabrini** – Holarctic, Oriental, Ethiopian, and Neotropical regions
  - Tribe: Bascanini – sub-Saharan Africa

Tribe: Peleciini – Neotropics, Oriental, Africotropical regions
Tribe: Cuneipectini – western Australia
Tribe: Chaetogenyini – distribution uncertain
Tribe: Licinini** – all major zoogeographical regions
Tribe: Oodini** – all major zoogeographical regions
Tribe: Panagaeini** – Nearctic, Neotropics
Tribe: Chlaeniini** – worldwide
Tribe: Harpalini** – all major zoogeographical regions
Tribe: Dryptini** – all major zoogeographical regions
Tribe: Zuphiini** – all major zoogeographical regions
Tribe: Galeritini** – Pantropical, Holarctic
Tribe: Physocrotaphini – distribution uncertain
Tribe: Anthiini – eastern Hemisphere tropics
Tribe: Helluonini** – most zoogeographic region
Tribe: Idiomorphini – India
Tribe: Orthogoniini – eastern Hemisphere
Tribe: Hexagoniini – Afrotropical, Oriental regions
Tribe: Ctenodactylini** – Neotropical
Tribe: Amorphomerini – distribution uncertain
Tribe: Lachnophorini** – Western hemisphere
Tribe: Pentagonicini** – all major zoogeographical regions
Tribe: Odacanthini** – all major zoogeographical regions
Tribe: Calophaenini – distribution uncertain
Tribe: Perigonini** – Pantropical
Tribe: Graphipterini – Afrotropical
Tribe: Cyclosomini** – primarily tropical, Oriental, Afrotropical, Neotropical
Tribe: Masoreini – Afrotropical
Tribe: Lebiini** – all major zoogeographical regions
Subfamily: Pseudomorphinae
Tribe: Pseudomorphini** – Nearctic, Neotropical, and Australian regions
Subfamily: Brachininae (bombardier beetles) – all major zoogeographical regions
Tribe: Crepidogastrini – eastern Hemisphere
Tribe: Brachinini** – all major zoogeographical regions, largely tropical

References

Ball GE, Bousquet Y (2001) 6. Carabidae Latreille, 1810. In: Arnett RH Jr, Thomas MC (eds) American beetles, vol 1. Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia. CRC Press, Boca Raton, FL, pp 32–132

Ball GE, Casale A, Vigna Taglianti A (eds) (1998) Phylogeny and classification of Caraboidea (Coleoptera: Adephaga). Torino, Italy. Atti Museo Regionale di Scienze Naturali, 543 pp

Erwin TL, Ball GE, Whitehead DR, Halpern AL (eds) (1979) Carabid beetles: their evolution, natural history, and classification. Dr. W. Junk, The Hague, The Netherlands, 644 pp

Lawrence JF, Newton AF Jr (1995) Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). In: Pakaluk J, Slipinski SA (eds) Biology, phylogeny, and classification of Coleoptera: Papers celebrating the 80th birthday of Roy A. Crowson. Museum I Instytut Zoologii PAN, Warsaw, Poland, pp 779–1006

Maddison DR (1995) Carabidae. Ground beetles and tiger beetles. Available at http://www.tolweb.org/Carabidae/8895

Ground Beetles

Members of the family Carabidae (order Coleoptera).

► Ground Beetle Taxonomy
► Ground Beetle Feeding Ecology
► Beetles

Ground Crickets

A subfamily of crickets (Nemobiinae) in the order Orthoptera: Gryllidae.

► Grasshoppers, Katydids and Crickets

Ground Pearls

Some members of the family Margarodidae, superfamily Coccoidae (order Hemiptera).

► Bugs
► Turfgrass Insects and their Management

Group Predation

Hunting and retrieving of prey by groups of cooperating individuals. Among insects, this is well developed in ants.

Group Selection

An evolutionary process functioning through the effects of different numbers of descendents left by groups rather than by individuals.

Grouse Locusts

A family of grasshoppers Tetrigidae) in the order Orthoptera.

► Grasshoppers, Katydids and Crickets

Grub

A thick-bodied larva with well-developed head and thoracic legs, but without abdominal prolegs. At rest, the body is curved, and often is described as C-shaped. A scarabaeiform larva (Scarabaeidae). This term also is sometimes applied to larval wasps (Hymenoptera).

► Beetles

► Scarab Beetles

► Hymenoptera

Gryllacrididae

A family of crickets (order Orthoptera). They commonly are known as leaf-rolling crickets.

► Grasshoppers, Katydids and Crickets

Gryllacridoids

Certain members (suborder Ensifera, superfamily Gryllacridoidae) of the order Orthoptera.

► Grasshoppers, Katydids and Crickets

Gryllidae

A family of crickets (order Orthoptera). They commonly are known as crickets.

► Grasshoppers, Katydids and Crickets

Grylloblattodea

An order of insects. They commonly are known as rock crawlers.

► Rock Crawlers

Gryllotalpidae

A family of crickets (order Orthoptera). They commonly are known as mole crickets.

► Grasshoppers, Katydids and Crickets

Gryropidae

A family of chewing lice (order Phthiraptera). They sometimes are called guinea pig lice.

► Chewing and Sucking Lice

Guenée, Achille

Achille Guenée was born in Chartres, France, on January 1, 1809. He began to study Lepidoptera as a boy. His first university education was at Chartres, and then he studied law in Paris. Of a wealthy family, he married and had a son and two daughters, of whom the son died young. He lived at his country residence at Châteaudun for the remainder of his life and contributed 63 papers on Lepidoptera. A major contribution was his six volumes in the series "Suites à Buffon" [a supplement to Buffon's series on "Histoire naturelle"], "Spécies général des lepidoptères" (1852–1857). Another was "Essai sur une nouvelle classification des microlepidoptères" (1845), a major classificatory work. He died at Châteaudun on December 30, 1880.

Reference

Essig EO (1931) Guenée, Achille. In: A history of entomology. The Macmillan Company, New York, NY, pp 640–642

Guérin-Méneville, Félix Edouard

Félix Guérin-Méneville was born in Toulon, France, on October 12, 1799, named Félix Edouard Guérin. He produced taxonomic works on most orders of insects, but later wrote on applied entomology, including sericulture and pests of grapevines. In 1836 he changed his surname to Guérin-Méneville. In 1831 he founded and edited "Magasin de Zoologie," and when it was merged with "Revue Zoologique" in 1849 as "Revue et Magasin de Zoologie," he continued as editor until 1873. His own output of publications was over 400, of which his encyclopedic "Iconographie de règne animal de G. Cuvier" in seven volumes brought him the most recognition. France's "Legion d'Honneur" was the most prestigious of his many awards. He died in Paris on January 26, 1874.

Reference

Herman LH (2001) Guérin-[Méneville], Félix Edouard. Bulletin of the American Museum of Natural History 265:72–73.

Guest

Among social insects, this term is used to indicate a social symbiont.

Guild

A group of species that exploits the same resource in a similar manner. Examples of a guild are the various insects that are responsible for decomposition of cow dung, or the various insects that attack the flower head of sunflower.

Guinea Pig Lice

Members of the family Gryropidae (order Phthiraptera).

► Chewing and Sucking Lice

Gula

A sclerite found centrally beneath the head, in the position of the "throat." It also is called the gular plate.

Gundlach, Johannes (Juan) Christopher

Johannes Gundlach was born in Marburg, Germany, on July 17, 1810. His father, a university professor there, died young, leaving his widow and their five children with inadequate income. Johannes became interested in natural history, and began to collect birds by shooting them in preparation for taxidermy. An early accident with a gun left him with an injured palate and nose, and loss of his senses of smell and taste. His mother wanted him to study religion, and he began to do so, but he obtained a job as conservator of the university museum and put aside his religious training to study zoology. He obtained free tuition as son of a faculty member, a master of arts degree in 1837, and a doctorate in philosophy in 1838. He was offered accommodation in Surinam by a friend who was a military doctor there, and began to seek funding for his trip, the funds to be repaid by the sale of specimens collected. While organizing this funding, he spent six months studying specimens in the zoological museum at Frankfurt am Main, southern Germany. His sea voyage to Surinam took him first to Cuba, where he spent from Christmas 1838 through early January 1839 collecting before learning that his friend in Surinam had died. Johannes decided to remain in Cuba and to repay his loan with specimens collected in Cuba. He received much hospitality in Cuba from landowners, even to the extent in 1846 of establishing a museum of his collections at a farm called "El Refugio" near to Cárdenas. This museum received thousands of visitors. In 1864 the collection was moved to a building on the farm of the Cárdenas family. He collected in all parts of Cuba with enthusiasts and sponsors or alone. The Cuban insurrection against Spanish rule began in 1868 and made fieldwork dangerous because of roving bands of rebels and Spanish soldiers, so Johannes collected intensively on the Cárdenas farm and made three visits to Puerto Rico, in 1873, 1875–1876, and 1881. His hosts, the Cárdenas family, had meanwhile encountered great financial difficulty. In 1892, after approval from Spain, Johannes sold his collections to the Instituto de Segunda Enseñanza de la Habana ("Institute of Havana"), and gave all the proceeds to the Cárdenas family. However, the transaction also allowed a small salary as curator to Johannes. The collections were installed in Havana in 1895, and Johannes (known in Cuba as Juan) died on March 17, 1896. He published on numerous aspects of Cuban and Puerto Rican zoology. His major works on insects were (1881, 1886, 1891) "Contribución a la entomología cubana" in three volumes, and (1887, 1891, 1893) "Apuntes para la fauna puerto-riqueña" (a series published in Anales de la Sociedad Española de Historia Natural, of which the parts in volumes 16, 20 and 22 of that journal concern insects). He never married, lived very frugally, and dedicated his life to Cuban zoology.

Reference

Ramsden CT (1915) Juan Gundlach [with bibliography]. Entomol News 26:241–260

Gustatory

This is used to describe features related to the sense of taste such as gustatory sensilla or gustatory behavior.

Gut pH

The pH of the insect gut is variable, and has significant influence on the actions of enzymes secreted in the midgut, and solubility of the food. Different enzymes function optimally at different pH levels. Though the gut tends to be slightly acidic in most species (about pH 4–6), the gut pH is related to host plant chemistry. Insects that feed on trees, which typically possess high levels of tannins, have higher pH levels, around 8.6, apparently because this reduces the effects of ingested tannins. The hindgut regions of insects ingesting cellulose, such as termites and crickets, tend to be acidic due to anaerobic fermentation of glucose derived from cellulose digestion.

► Alimentary Canal and Digestion

Gyllenhal, Leonhard

Leonhard Gyllenhal was born in Algusthorp, Sweden, on December 3, 1752. At the age of 17 he entered the University of Uppsala, and studied natural history with Linnaeus, being influenced by the latter to specialize in entomology. However, after three years he entered the Swedish army and served for 27 years. Upon retirement as a major from the army, he met Gustav Paykull and helped the latter with his "Fauna svecica" (1798–1800), and collaborated with Carl Johann Schönherr in production of the latter' s "Synonymia insectorum" (1806, 1808). Only then did he start his own work, "Insecta Svecica," of which four volumes were published (1810–1827) on Coleoptera. In the 1830s he also contributed heavily to Schönherr's "Genera et species curculionidum" He died on May 13, 1840, in Hoeberg, Sweden.

Reference

Herman LH (2001) Gyllenhal, Leonhard. Bull Am Mus Nat Hist 265:73–74

Gynandromorph

An individual that contains structural characteristics of both sexes, often with one sex on one side and the other sex on the other side. This is an abnormal condition in insects, occurring infrequently.

Gyne

A female of the reproductive caste in social Hymenoptera. It is applied to potential or actual queens of ants, bees and wasps.

Gynopara (pl. gynoparae)

In aphids, viviparous females that are produced on the secondary host in the autumn, and then fly to the primary host to produce new females that mate and deposit eggs.

► Aphids

Gypsy Moth, *Lymantria dispar* Linnaeus (Lepidoptera: Lymantriidae)

WAYNE BREWER
Auburn University, Auburn, AL, USA

Gypsy Moth, *Lymantria dispar* Linnaeus (Lepidoptera: Lymantriidae), Figure 75 Etienne Leopold Trouvelot, a French naturalist who accidentally introduced gypsy moth into the field at Medford, Massachusetts, in 1869 (courtesy of USDA).

The gypsy moth, *Lymantria dispar* L., is recognized as one of the most serious insect defoliators of North American forests and urban landscapes. Since its introduction, the gypsy moth has spread to all or part of 17 states and the District of Columbia. Yearly defoliation often reaches into the millions of acres, and the costs of damage and control run into tens of millions of dollars. The moth is a native of Europe and Asia where it is a sporadic pest. It was introduced into the U.S. in 1869 by a French naturalist, Etienne Leopold Trouvelot (Fig. 75), who brought the moths to his home in Medford, Massachusetts. He apparently intended to cross them with other moths to create a prolific and hardy strain of silkworms. The experiment failed, the moths escaped and spread to the surrounding area.

The first outbreaks of the gypsy moth began in Trouvelot's neighborhood about 10 years after their introduction and, in 1890, the State and Federal Government began attempts to eradicate the moth. These efforts ultimately failed and the gypsy moth has continued to spread since that time. Currently established populations occur throughout the northeastern U.S. and the moth is spreading south and west across the U.S. The moth often "hitchhikes" to new areas on the camper trailers and motor homes of northern residents vacationing in uninfested areas. The result is that every year isolated populations are discovered beyond the contiguous range of the gypsy moth, but these are usually eradicated or disappear without intervention. However, it is inevitable that the gypsy moth will continue to expand its range in the future.

Biology

The gypsy moth (Fig. 76) has one generation per year. The adults emerge in midsummer, usually in July but variations occur depending on local or regional conditions. Although winged, the females cannot fly and usually remain near the pupal case from which they emerged. Soon after emerging, the females release a sex pheromone that attracts the males, which do fly; they mate and she begins to lay eggs. The females normally produce one egg mass in which the number of eggs may range from fewer than 100 to over 1,000. The eggs are covered by a dense coating of hairs that are sloughed from the abdomen of the female as she oviposits. It is thought that these hairs provide a form of insulation that helps protect them from low temperatures. Gypsy moths overwinter in the egg stage which lasts 8–9 months. The following spring, the eggs hatch and the larvae emerge. The date of larval emergence is strongly influenced by temperature. Larval feeding continues through four instars with the last instar doing most of the damage to foliage. It has been estimated that a single larva consumes about one square meter of foliage during its development. Pupation occurs about eight weeks after egg hatch. The pupae are usually located in cryptic locations such as cracks or crevices of the bark, in the leaf litter, or in other protected places. This stage lasts about two weeks and then adults emerge to continue the cycle.

Gypsy Moth, *Lymantria dispar* Linnaeus (Lepidoptera: Lymantriidae), Figure 76 Some stages of the gypsy moth life cycle: *top*, a mature larva; *center*, female moths (adults) with egg masses protruding from beneath; *bottom*, a male moth (adult photos courtesy of John Ghent, U.S. Forest Service).

Dispersal

The newly hatched, small and hairy larvae move to the tops of trees and feed on new foliage. Some may be blown by the wind to new locations. The long larval hairs of the early instars and the strands of silk they produce from special glands in their heads are conducive to this type of transport. This "ballooning" is a major means of natural dispersal. However, most long distance spread to new locations occurs as result of the transport of infested items by humans. The larvae may pupate, or females may lay egg masses, on almost any object left outside. These include campers, mobile homes, packing crates, pallets and other items. If infested items are moved to a new location, a new infestation may become established.

Hosts

The gypsy moth is known to feed on the foliage of over 300 species of trees and shrubs with species of oaks ranked among the most preferred hosts. Oaks are common in much of the forested and urban areas of the U.S. and their wide distribution will be a major factor in the ultimate distribution of the moth. Where oaks are less common, however, the gypsy moth has maintained populations on other tree species including aspen and other hardwoods. A few species, including tulip poplar and dogwood, appear to be immune to feeding and other species, especially conifers, are not acceptable to very young gypsy moth larvae, but older instars feed readily on them.

Damage

When the gypsy moth first moves into a new area, tree mortality is often extensive. Species of oaks, especially white and chestnut oaks, appear to be most susceptible with mortality often exceeding 50 %. The effects of repeated defoliation can be very serious. Coniferous trees often die after a single defoliation. Deciduous trees can withstand one or two defoliations but the mortality level rises sharply after the third. Other stresses, such as drought or poor site conditions, may increase the risk of mortality. Much tree mortality is actually caused by pathogens or insects, such as wood borers that attack and kill weakened trees. In areas where the gypsy moth has existed for some time, such as New England, the moth is more notorious as a nuisance rather than for killing large numbers of trees. This may be a result of gypsy moth populations eventually coming under control by natural enemies, or the change in forest composition due to favored hosts being killed and the remaining trees being less suitable as sources of nutrition.

Nuisance Factors

At low population levels, gypsy moth larvae remain inactive and secluded in resting places during the day, but when populations are high, their behavior changes dramatically. Larvae in dense populations become hyperactive during the day. Infested areas are literally crawling with larvae as they move incessantly up and down trees and travel along the ground. These larvae are attracted to and climb any object in their path including trees, telephone poles, cars and people. They are not harmful, but the presence and activity of such large numbers of these larvae create a nuisance. In addition, when outbreaks occur, many larvae die from various mortality factors. The unpleasant odor of decaying larvae is often evident throughout the defoliated area. Outdoor activities, such as picnics and barbeques, are often disrupted by larvae, or their frass (excrement) dropping from infested trees onto patios, decks and picnic tables.

Natural Enemies

Various biological control agents have been collected from Asia and Europe and introduced into infested areas of the U.S. over the last 100 years. These include over 20 insect parasitoids and predators that are natural enemies of the gypsy moth. Small mammals, like the white-footed mouse, and other rodents such as shrews, are perhaps the most important gypsy moth predators, especially at low population densities. Birds are also known to prey on gypsy moths, but do not seem to cause any substantial reduction in moth populations. A nucleopolyhedrosis virus usually causes the collapse of outbreak populations, and recently an entomopathogenic fungus species has caused considerable mortality of gypsy moth populations in North America.

Control

In addition to the introduction of natural enemies, several million acres of forest land have been aerially sprayed with pesticides over the last 20 years to suppress gypsy moth populations. Though some areas are treated by private companies under contract with land owners, most areas are sprayed under joint programs of state governments and the USDA Forest Service. The USDA, state and local governments also jointly participate in programs to identify and eradicate new gypsy moth populations in currently uninfested areas. These survey programs involve the use of small triangular-shaped traps baited with a synthesized female sex pheromone. In addition, the USDA Forest Service, working with state and federal cooperators, began a Gypsy Moth Slow the Spread (STS) project in 1999. The project covers the 1,200 mile gypsy moth frontier from North Carolina through the Upper Peninsula of Michigan. The project goal is to use novel integrated pest management strategies to reduce the rate of moth spread.

References

Campbell RW (1975) The gypsy moth and its natural enemies. U.S. Department of Agriculture, Washington, DC, Agriculture Information Bulletin 381

Doane CC, McManus ML (1981) The gypsy moth: research toward integrated pest management. U.S. Department of Agriculture, Washington, DC, Forest Service Bulletin 1584

McManus ML, Zerillo RT (1979) The gypsy moth: an illustrated biography. U.S. Department of Agriculture, Washington, DC, Home and Garden Bulletin 225

Smith HR, Lautenschlager RA (1978) Predators of the gypsy moth. U.S. Department of Agriculture, Washington, DC, Agriculture Handbook 434

Talerico RL (1978) Major hardwood defoliators of the eastern United States. U.S. Department of Agriculture, Washington, DC, Home and Garden Bulletins 223 and 224

Gyrinidae

A family of beetles (order Coleoptera). They commonly are known as whirligig beetles.

► Beetles

Gyropidae

A family of chewing lice (order Mallophaga). They sometimes are called guinea pig lice.

► Chewing Lice

H

Habitat

The place where an organism dwells. This is a less inclusive term than "niche."

Habitat Diversity

The range of habitats present in an area. Because insects often have preferred habitats, there usually is a strong correlation between habitat and insect diversity.

Habituation

Failure to elicit normal response after repeated stimuli. Often the organism gradually decreases it response to the stimulus, and the organism may not respond even after the stimulus is discontinued for a protracted period. All insects are thought to be capable of habituation to some stimuli, and it is considered to be the simplest form of learning.

► Associative Learning
► Latent Learning
► Insight Learning
► Learning in Insects

Haddow, Alexander John

Alex Haddow was born in Scotland in December 1912, and as a boy showed intense interest in insects. His first degree was in zoology, from Glasgow University in 1934. He took another 4 years to complete an M.D. degree. Next, he studied at the London School of Tropical Medicine for a diploma in tropical medicine. In 1941 he traveled to Kenya and studied biting cycles of mosquitoes under conditions of a 24-h continuous catch, developing and standardizing methods for collecting and analyzing the data. Other work in Africa was on the epidemiology of yellow fever, and it involved collecting and sampling from monkeys. After 24 years in Africa, he returned to Britain in 1965, to become Administrative Dean of the Faculty of Medicine at Glasgow University. His honors include election to the fellowship of The Royal Society as well as the Royal Society of Edinburgh. He died in Glasgow on December 26, 1978, survived by his wife, Peggy, and two sons.

Reference

Gillett JD (1979) Alexander John Haddow 1912–1978. Antenna 3:54

Haematomyzidae

A family of chewing lice (order Phthiraptera).

► Chewing and Sucking Lice

Haematopinidae

A family of sucking lice (order Phthiraptera). They sometimes are called ungulate lice.

► Chewing and Sucking Lice

Hagen, Hermann August

Hermann Hagen (Fig. 1) was born in Königsberg (now Kaliningrad), then in German East Prussia (now in Russia), on May 30, 1817. He was educated at Universität Königsberg, and became a physician in that city. He studied extant insects (Odonata, Neuroptera, Isoptera, Psocoptera, Plecoptera, and Trichoptera) and fossil insects. Some of his major works were "Monographie der Termiten" (1855–1860) and "Bibliotheca Entomologica" (1862–1863) [for a subsequent bibliography of the world's entomological literature, see: Horn, Walther]. In 1867 he was invited to the USA to take charge of the entomological section of the Museum of Comparative Zoology at Harvard University in Massachusetts. He accepted, organized and built that collection, and greatly influenced taxonomic entomologists in the USA. In 1890–1891 he was afflicted with paralysis and influenza, and died in Massachusetts in 1893.

Hagen, Hermann August, Figure 1 **Hermann Hagen.**

References

Essig EO (1931) Hagen, Hermann August. In: A history of entomology. Macmillan, New York, NY, pp 643–646

Mallis A (1971) Hermann August Hagen. In: American entomologists. Rutgers University Press, New Brunswick, NJ, pp 119–126

Hagen, Kenneth Sverre

Ken Hagen was born in the state of California, USA, on November 26, 1919. He displayed an early interest in insects and formed a collection. He earned a B.S. degree from the University of California at Berkeley in 1943. After service in the U.S. navy in World War II (landings at Normandy and Okinawa), he returned to the graduate school of the same institution, earning degrees of M.S. in 1948 and Ph.D. in 1952. While he was a graduate student he worked as a technician, but after his Ph.D. he was hired as junior entomologist in the Division of Biological Control, of the University of California's Agricultural Experiment Station at Albany. He became entomologist in 1965 and professor of entomology in 1969. His areas of research interest included the behavior of coccinellids, highlighted in a (1970) article in National Geographic called "The high-flying ladybug." He was the leader of projects that resulted in introduction of 25 species of biocontrol agents against 17 economically important pests. He had a pioneering role in the nutrition of biocontrol agents, with proof in the field that manipulative techniques using artificial nutrition could work. He authored more than 160 scientific publications and received numerous awards. He was also a gifted teacher. He died on January 10, 1997, survived by his wife, Maxine, and one son.

References

Caltagirone LE, Dahlsten DL, Garcia R (1997) Kenneth Sverre Hagen, Entomological sciences: Berkeley. Available at http://sunsite.berkeley.edu:2020/dynaweb/teiproj/uchist/inmemoriam/inmemoriam1997. Accessed Aug 2002

Hahn, Carl Wilhelm

Carl Hahn was born on December 16, 1786, and lived mainly in Nürnberg (Nuremberg), Germany. He studied the spiders of his country, which he described and illustrated in two major works, "Monographie der Spinnen" and "Die Arachniden". His premature death in 1836 interrupted publication of the latter, of which he completed only two volumes. It was then completed, in a further 14 volumes, by C. L. Koch between 1836 and 1849.

Reference

Bonnet P (1945) Bibliographia Araneorum 1:32

Hair Pencil

Clusters of long setae on the body of certain insect (particularly male Lepidoptera and some Neuroptera). They occur on various parts of the body, but usually on the abdomen. They are associated with exocrine glands, and usually used during courtship to disperse sex pheromones. This term is synonymous with "brush organ."

Hair Plate

A sensor structure found at the leg joints and at other limb articulations. They respond to touch, bending and joint flexing by emitting nervous stimuli, and adapt slowly. They allow the insect to know the orientation of the head and appendages. A more complex version of the hair plate is the chordotonal sensillum.

Hairstreaks

Some members of the family Lycaenidae (order Lepidoptera).

► Gossamer Winged Butterflies
► Butterflies and Moths

Hairy Chinch Bug, *Blissus leucopterus hirtus* Montandon (Hempitera: Lygaeidae)

Hairy chinch bug is an increasingly important pest of turfgrass.

► Turfgrass Insects and their Management

Hairy Fungus Beetles

Members of the family Mycetophagidae (order Coleoptera).

► Beetles

Hale Carpenter, Geoffrey Douglas

Geoffrey Hale Carpenter was born in Eton College, England, on October 26, 1882. His undergraduate studies were at Oxford University, and then in 1908 he qualified in medicine and took a D.M. degree in 1913. But by 1911, interested in tropical medicine and natural history, he was studying the bionomics of *Glossina palpalis* and its relation to sleeping sickness in Uganda. His research was published in reports of The Royal Society in 1912, 1913, and 1919. In Uganda, too, he studied mimicry in butterflies, and through rearing experiments solved problems of relationships. He viewed mimicry among butterflies as a result of natural selection by predatory birds, mammals, and reptiles. His butterfly studies are published mainly in journals of the Royal Entomological Society. In 1933 he was appointed Hope Professor at Oxford University, succeeding Sir Edward Poulton. He retired in 1948 and died in Oxford on January 30, 1953.

Reference

Riley ND, Hale Carpenter GD (1953) Entomologist 86:155–156

Half Life

The period of time required for a pesticide to lose half of its original effectiveness or toxicity.

Halictidae

A family of bees (order Hymenoptera, superfamily Apoidae).

► Wasps, Ants, Bees and Sawflies

Halictophagidae

A family of insects in the order Strepsiptera.

► Stylopids

Haliday, Alexander Henry

Alexander Haliday (Fig. 2) was born in Belfast in 1807. At the age of 15, he entered Trinity College, Dublin, remaining there 5 years and obtaining an M.A. degree. Next, he studied law, and apparently was successful, although it is not clear that he ever practiced this profession. Returning to the north of Ireland, he devoted his time to the study of literature and natural history. He was appointed High Sheriff of the county of Antrim in 1843, a political position rather than one in law-enforcement. Beginning in 1828, he published a long series of papers on the Irish insect fauna, especially Diptera. He also published extensively on Chalcidoidea and other "parasitic" Hymenoptera, and on Thysanoptera. Due to poor health, he emigrated to Lucca, Italy, about 1860. There, he continued collecting insects and helped to found the Società Entomologica Italiana. He died on July 12, 1870.

Haliday, Alexander Henry, Figure 2 Alexander Haliday.

Reference

Anonymous (1870) Alexander Henry Haliday. Entomologist's Monthly Magazine 7:91

Halimococcidae

A family of insects in the superfamily Coccoidae (order Hemiptera).

► Bugs

Haliplidae

A family of beetles (order Coleoptera). They commonly are known as crawling water beetles. Beetles

Haltere

(pl., halteres) The vestigial, modified hind wings of Diptera that function as balancing organs.

Hamophthiriidae

A family of sucking lice (order Phthiraptera).

► Chewing and Sucking Lice

Hamulus

(pl., hamuli) Hook-shaped hairs on the leading edge of the hind wing in Hymenoptera that unite the fore- and hind wings.

► Wings of Insects

Handling Time

The time a predator spends pursuing, subduing, and consuming prey (a meal).

Handlirsch, Anton

Anton Handlirsch was born in Vienna on January 20, 1865. He studied pharmacy, and in 1883 received a master's degree in that subject. Then, he became scientific helper, assistant (1892), adjunct custodian (1899), second-class custodian (1906), first-class custodian (1918) and director (1922) of the Naturhistorisches Hofmuseum of Vienna. His earliest entomological work was on Hymenoptera, reaching a climax (1887–1894) with a monograph of wasps related to *Bembex* and *Nysson*. He took charge of Hemiptera at the museum, purchased the Signoret collection for it, and wrote a monograph on Phymatidae (1897). Next, he turned his attention to fossil insects. His (1906–1908) book "Die fossilen Insekten und die Phylogenie der rezenten Formen" enumerated or described all known fossil insects. It included a new classification with discussion. In his contributions to Schroeder's (1925) "Handbuch der Entomologie" and Kükenthal's (1926–1935) "Handbuch der Zoologie," he modified the classification. He also published about 100 other titles. He died in Vienna on August 28, 1935.

Reference

Calvert PP (1936) Obituary. Entomological News 47:168–169

Handsome Fungus Beetles

Members of the family Endomychidae (order Coleoptera).

► Beetles

Hangingflies

Members of the family Bittacidae (order Mecoptera).

► Scorpionflies

Hansen, Viktor

Viktor Hansen was born in Copenhagen on August 29, 1889. In 1907 he entered the Metropolitanskolen and in 1913 obtained his law degree. He worked in the Justitsministeriet from 1915, became a superior judge in 1941, and worked in that capacity until he retired in 1959. However, he began to collect beetles as a teenager, and in 1905 joined the Entomologisk Forening [entomological society]. His first paper was published in 1907 in Entomologiske Mededelser. His lifetime total was more than 100 papers on the Danish beetle fauna. His major production was 23 volumes on beetles in the series Danmarks Fauna. For this, he was awarded an honorary doctoral degree from Københavns Universitet in 1950, and medals from entomological societies in Denmark and Sweden, and from a natural history society in Denmark. He died on March 6, 1974.

Reference

Herman LH (2001) Hansen, Viktor. Bull Am Mus Nat Hist 265:75

Haplodiploidy

A type of parthenogenetic reproduction in which males are produced from unfertilized eggs and are haploid, while the females are diploid. In Hymenoptera, females can control the release of sperm, and regulate the sex ratio of offspring.

Haploid

Cells or organisms that contain a single copy of each chromosome.

Hardy-Weinberg Equilibrium

An equilibrium of genotypes achieved in populations of infinite size in which there is no migration, selection, or mutation after at least one generation of panmictic mating. With two alleles, *A* and *a*, of frequency *p* and *q*, the Hardy-Weinberg equilibrium frequencies of the genotypes *AA*, *Aa* and *aa* are p^2, $2pq$ and q^2, respectively.

Harlequin Bug

► Crucifer Pests and their management

Harlequin Bug, *Murgantia histrionica* (Hahn) (Hemiptera: Pentatomidae)

JOHN L. CAPINERA
University of Florida, Gainesville, FL, USA

Indigenous to Mexico and Central America, harlequin bug has dispersed north into the United States. Its appearance in Texas, USA, in 1864 coincided with the occurrence of Union troops during the American Civil War, and in parts of the South earned it the name "Sherman-bug" after the northern General Sherman, and "Lincolnite" after President Abraham Lincoln. It rapidly spread throughout the southern states, and eventually reached northern locales such as Colorado, Iowa, southern Michigan, Pennsylvania, and Massachusetts. It is considered to be a serious pest only in southern states, however, and is not regarded as a problem in California. It has also dispersed to the Hawaiian Islands.

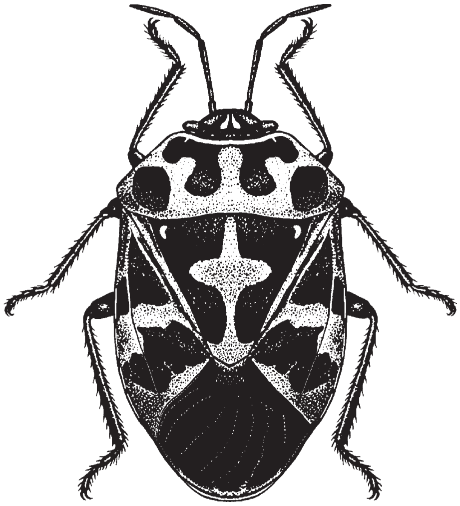
Life History

Harlequin bug breeds continuously in the southern portions of its range. During mild winters all stages have been observed as far north as Virginia. In colder climates only the adults survive the winter in sheltered locations. They seek shelter in and near fields, among overwintering crop plants, and in other organic debris such as dead leaves and bunches of grass. Two or three generations per year seem to be normal, but there appears to be four generations in south Texas.

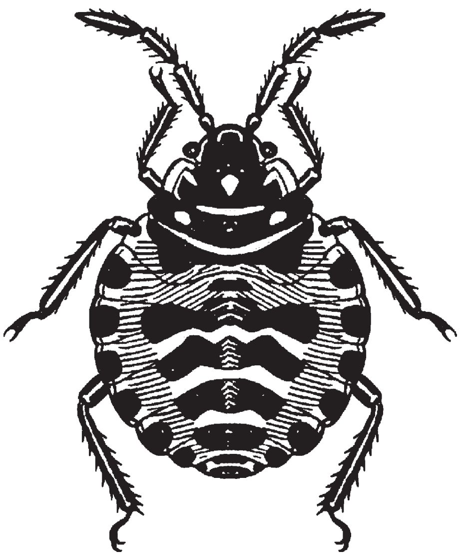
Adults begin depositing eggs about 2 weeks after becoming active in the spring. Eggs are deposited beneath leaves, usually in clusters of 12 arranged in two rows of six, at intervals of 5–6 days. As the female nears the end of her life, the egg batches get slightly smaller and the egg arrangement less regular. The eggs are barrel-shaped, and measure about 1.30–1.38 mm long and 0.90–0.92 mm in diameter. They are light gray or pale yellow in color, and generally are circled by two black bands. They may also bear small black dots or spots, and the top has a semicircular black marking. The average number of eggs is reported to be 115 per female. Egg deposition may occur over a period of 40–80 days. Eggs hatch in about 4–5 days during warm weather, while 15–20 days may be required during cool weather.

Upon hatching, young nymphs stay clustered near the old eggs for 1 or 2 days. The newly hatched nymphs are pale green with black markings, but soon become brightly colored: black or blue, with red and yellow or orange markings. Reportedly there are six instars in Texas, and nymphal development can be completed in as little as 30 days. There, average development times are 3.4, 3.2, 4.7, 4.7, 7.0, and 4.3 days, respectively, for the six instars developing under summer conditions. Under spring conditions, development times were increased by about 30%. Studies in Virginia suggest only five instars, however, and a development time requirement of 40–60 days during the summer, and slightly longer, perhaps 70 days, during cool weather.

The adults usually live about 60 days, but may live considerably longer during the winter. They measure about 8.0–11.5 mm in length. The adults are brightly colored, similar to the large nymphs, principally black and yellow or black and red. The color pattern varies (Figs. 3 and 4), with the spring and summer bugs being more brightly colored



Harlequin Bug, *Murgantia histrionica* (Hahn) (Hemiptera: Pentatomidae), Figure 3 **Adult of harlequin bug, *Murgantia histrionica* (Hahn).**



Harlequin Bug, *Murgantia histrionica* (Hahn) (Hemiptera: Pentatomidae), Figure 4 **Third instar of harlequin bug, *Murgantia histrionica* (Hahn).**

than the overwintering insects. As with many stink bugs, harlequin bugs produce a disagreeable odor if disturbed, and birds avoid eating them.

Harlequin bug is principally a pest of crucifers, attacking broccoli, Brussels sprout, cabbage, cauliflower, Chinese cabbage, collard, kale, kohlrabi, mustard, radish, rutabaga, turnip, and watercress. Harlequin bug is reported to be especially fond of horseradish. In the southernmost states, crucifers do not thrive during the summer months, and the bugs are forced onto other plants. Thus, they are sometimes found feeding on asparagus, beans, okra, squash, tomato and many other vegetables, but this is usually due to lack of normal food. Harlequin bug feeds readily on cruciferous weeds such as wild mustard, *Brassica* spp.; shepherds purse, *Capsella bursa-pastoris*; and pepperweed, *Lepidium* spp.; and related mustard oil-containing plants such as members of the family Capparaceae. Other weeds common in crops, such as pigweed, *Amaranthus* spp., and lambsquarter, *Chenopodium album*, are also fed upon, and reproduction occurs on these plants.

Harlequin bug appears to be relatively free of natural enemies, other than for egg parasites and general predators. The egg parasitoids are *Oencyryus johnsoni* (Howard) (Hymenoptera: Encyrtidae), *Trissolcus murgantiae* Ashmead, and *T. podisi* Ashmead (both Hymenoptera: Scelionidae). The species that is best known is *O. johnsoni*, which has been reported frequently from harlequin bug eggs, and has caused up to 50% mortality during a harlequin bug outbreak in Virginia. This parasite is widely distributed, and apparently has other hosts. It attacks eggs in all stages of embryonic development, and prevents the eggs from hatching. However, *O. johnsoni* is not the only effective parasite, as *T. murgantiae* was observed to parasitize 45% of harlequin bug eggs in North Carolina, at locations where *O. johnsoni* parasitized only 30% of eggs. Because of its effectiveness, *T. murgantiae* was introduced into California.

Damage

The piercing-sucking feeding behavior of this insect results in white blotches at the site of feeding. Wilting, deformity, and plant death may occur if insects are abundant. Mild winters are said to favor survival, and subsequent damage. Once considered the most serious crucifer pest in the south, this insect has been relegated to minor status in commercial production and persists mostly as a home-garden pest.

Management

Insecticides are applied to the foliage for suppression of harlequin bug. Harlequin bug can be difficult to control with insecticides; targeting the young bugs and thorough coverage are recommended. Soap applied alone or in combination with rotenone has provided good control.

Trap crops, usually consisting of early-planted mustard, rape, or kale are sometimes recommended to divert the overwintering bugs from the principal crop. Such trap crops must be sprayed or destroyed, however, or the adults will soon move to the main crop. Destruction of crop residues, on which the insect may overwinter in the north or oversummer in the south, is an important cultural practice to alleviate harlequin bug damage.

Susceptibility to damage varies among crucifer crops. Mustard and Chinese cabbage are quite susceptible; turnip, kale, rutabaga, and some radishes are intermediate; and cauliflower, cabbage, broccoli, collard, Brussels sprout, kohlrabi, and most radish varieties are fairly resistant. Cabbages are the most resistant crop, but considerable variation among cultivars is evident.

► Crucifer Pests and their Management
► Vegetable Pests and their Management, Stink Bugs (Hemiptera: Pentatomidae) Emphasizing Economic Importance

References

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, 729 pp
White WH, Brannon LW (1939) The harlequin bug and its control. USDA Farmer's Bulletin 1712, 10 pp

Harris, Thaddeus William

Thaddeus Harris (Fig. 5) was born in Massachusetts on November 12, 1795. He obtained a first degree from Harvard University in 1815 and then a medical degree in 1820, after which he practiced medicine and married. In 1823 he published his first entomological paper. In 1831 he published a catalogue of insects and became librarian at Harvard University. Teaching of courses in natural history and entomology followed. His 1841 "Report on insects injurious to vegetation" became a classic and was reprinted several times. He also published some descriptions of new species of insects that were of economic importance. He died in Massachusetts on January 16, 1856.

References

Essig EO (1931) Harris, Thaddeus William. In: A history of entomology. Macmillan, New York, NY, pp 651–653
Mallis A (1971) Thaddeus William Harris. In: American entomologists. Rutgers University Press, New Brunswick, NJ, pp 25–33

Harvester Ants

Ant species that store seeds in their nests. This behavior occurs in many ant taxa, including some that are not closely related.

► Harvester Ants, *Pogonomyrmex*

Harris, Thaddeus William, Figure 5 **Thaddeus Harris.**

Harvester Ants, *Pogonomyrmex* Mayr (Hymenoptera: Formicidae)

THOMAS O. CRIST
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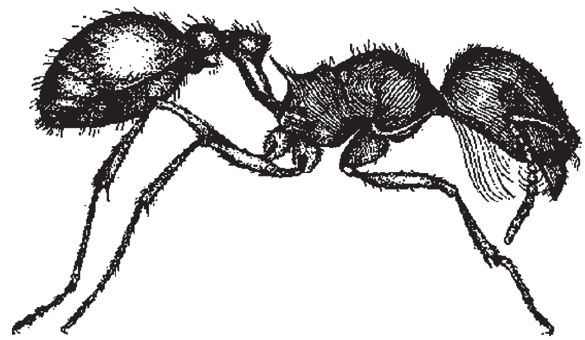
Harvester ants are so named because they collect and store seeds in their nests for later consumption. The seed-harvesting habits of ants are noted in several historical accounts and are the subject of numerous scientific studies. Over 150 species of seed-harvesting ants occur worldwide. In the New World, harvester ants comprise 60 species belonging to two closely related genera, *Pogonomyrmex* Mayr ("bearded ant") and *Ephebomyrmex* Wheeler ("youthful ant"). The beard, or psammophore, refers to the tuft of hairs that extend below the head on the workers of nearly all 45 species of *Pogonomyrmex*. This distinctive trait corresponds to the ground-nesting habits of harvester ants because the psammophore is used to move particles of soil. Some harvester ants build large mounds or craters of soil and gravel on the soil surface while others have more inconspicuous nests under rocks.

Most *Pogonomyrmex* occur in deserts and grasslands where seeds are abundant, but a few species are found in forest and montane environments. Harvester ants (Fig. 6) range throughout South America, portions of Central America and the Caribbean, and virtually all of western North America and the southeastern Coastal Plain. The geographic ranges of most species, however, are found within southwestern North America and northern South America, the latter of which is likely the evolutionary origin of *Pogonomyrmex*.

The mating behavior and life cycle is generally similar among *Pogonomyrmex* species. During spring or summer, ant colonies produce numerous winged males and females ("alates") that are reproductively viable and larger than the sterile workers. Alate flight activity is synchronous among colonies, usually occurring in the late morning on 2 or 3 days following a significant rainfall. Mating flights can occur several times a year, but are usually restricted to a 2 or 3-week period. After leaving the nest, alates



Harvester Ants, *Pogonomyrmex* Mayr (Hymenoptera: Formicidae), Figure 6 A worker harvester ant. The genus *Pogonomyrmex* is named after the prominent beard (the psammophore) on the lower side of the head. Drawing is by Ruth Ann DeNicola, published in Cole, A. C., Jr. (1968) *Pogonomyrmex* harvester ants: a study of the genus in North America. Reproduced with permission from The University of Tennessee Press, Knoxville, Tennessee.

aggregate on hills or cliffs and in the uppermost portions of shrubs, trees, or structures such as fence posts, windmills, or buildings. Males often "lek" (form mating aggregations) together in groups of 5–20 individuals, and females are attracted to male aggregations by a pheromone. Females typically mate with several males, a behavior that results in genetically variable workers after the queen begins reproduction. In some species, such as *P. badius* (the Florida harvester ant), lekking does not occur and males fly to another nest to mate with females, or mating might take place between males and females of the same colony, which can result in inbreeding and a loss of genetic variability over time.

After mating, the fertilized female sheds her wings and begins excavating a nest in the soil. Most "foundress queens" die before successfully establishing a colony. The queen must carry out all of the worker tasks – foraging, nest maintenance, and brood care – for 2 or 3 weeks until her first brood matures into adult workers. The mortality of young colonies continues to be high until the next year when the size of the worker population may increase substantially. *Pogonomyrmex* colonies have variable numbers of workers: *P. laticeps* and *P. magnacanthus* have only 50–250, whereas *P. rugosus* (the rough harvester ant) and *P. barbatus* (the red harvester ant) may boast up to 15,000. Most species have a worker force of 500–5,000 ants. Two species, the slavemaking *P. anergismus* and *P. colei*, have no workers at all; instead, they live in the nests of *P. rugosus* or *P. barbatus* and enslave workers to raise reproductive males and females for them. It appears that all *Pogonomyrmex* species are monogynous (have one queen) during the life of a colony, which may persist for 10–50 years in some species such as *P. occidentalis* (the western harvester ant) and *P. owyheei* [*salinus*] (the Owyhee harvester ant).

Workers perform a variety of tasks. Nest workers take care of the queen and developing larvae and pupae. They also create and maintain a variety of nest chambers for seed storage, brood development and discarded refuse. Storage chambers are connected by networks of tunnels, which may extend 2–3 m vertically below ground in some species. The queen and workers usually overwinter more than a meter below ground in colder climates. Worker tasks vary according to the age of the worker and the needs of the colony. After emerging from pupae, ants work mostly within the nest. Then, as workers get older, they shift to exterior maintenance of the nest, and finally to patrolling, scouting, or foraging, which may entail venturing up to 20 m from the nest in some species. Workers also switch tasks according to the needs of the colony. For example, if a nest is damaged by heavy rain, foraging workers might switch to nest maintenance. Similarly, a nest intruder may elicit an alarm pheromone that rapidly employs a substantial number of workers to defend the nest. Harvester ants are well-equipped for nest defense, as the workers of many species will deliver a painful sting.

A number of scientific studies have examined the foraging and seed-harvesting behavior of *Pogonomyrmex* ants. Foraging workers search for seeds in an individualistic manner, specializing on particular seed species or locations near the nest. Although this is the primary foraging strategy in some species (e.g., *P. desertorum*, *P. maricopa*, and *P. californicus*, the California harvester ant), several harvester ants also show group foraging tactics. These involve the use of permanent pathways (trunk trails) that orient workers to different foraging areas, and pheromone trails that chemically recruit workers to areas of high-food density (e.g., *P. rugosus*, *P. barbatus*, and *P. occidentalis*). Recruitment pheromones are volatile compounds that dissipate rapidly if workers do not reinforce them by laying additional pheromones along the recruitment trail. Ants usually harvest <10% of the total seeds available in their foraging areas, but they often remove a much larger fraction of the seed species they prefer – grasses and small-seeded forbs – and consequently, influence the types of plants that are found near nests. A significant part of the harvester ant diet is arthropods, especially in some species found at higher elevations (e.g., *P. montanus* and *P. mayri*). A variety of other materials are also returned to the nest by workers, including twigs, leaves, flowers and feces.

Several vertebrates and arthropods prey on harvester ants. Most commonly, these are birds, lizards and spiders. Horned lizards (*Phrynosoma* spp.) are specialist predators of harvester ants and have evolved a resistance to the toxic compounds in the venom delivered by the sting of worker ants. Predation by horned lizards can substantially reduce the number of workers in a nest. Ants respond to lizard predation by reducing their foraging activity, or closing their nests entirely. The storage of seeds in harvester ant nests is thought to provide a food source when foraging activity is decreased in response to predation. Other seed-eating animals, such as kangaroo rats (*Dipodomys* spp.), may also compete with harvester ants for food.

The large nest size and colony longevity of many *Pogonomyrmex* species have important consequences to soils and plants. Ants change the physical and chemical characteristics of soil by increasing the porosity, organic matter and nutrient levels. The alteration of nest soils and the removal of plants and seeds by ants result in different plant species near nests compared to surrounding areas. Therefore, in deserts and grasslands where colony densities are high, harvester ants influence plant species diversity and composition. Recently, however, the native *Pogonomyrmex* ants have been displaced in several areas by more aggressive, invasive species such as the red imported fire ant (*Solenopsis invicta*), or the Argentine ant (*Linepithema humile*). A loss of harvester ants from these ecosystems may have several consequences to the constituent soils, plants and animals.

The biology and behavior of *Pogonomyrmex* ants continues to fascinate scientists and amateurs alike. Most studies of harvester ants are from relatively few of the 60 species; future investigations of lesser-known species will further our understanding of these remarkable insects.

► Ants

References

Cole AC Jr, (1968) *Pogonomyrmex* harvester ants: a study of the genus in North America. University of Tennessee Press, Knoxville, Tennessee

Gordon DM (1995). The development of organization in an ant colony. Am Sci 83:50–57

Hölldobler B, Wilson EO (1990) The ants. The Belknap Press of Harvard University Press, Cambridge, MA

MacKay WP (1990) The biology and economic impact of *Pogonomyrmex* ants. In: Vander Meer RK, Jaffe K, Cedeno A (eds) Applied myrmecology: a world perspective, Westview Press, Boulder, Colorado, pp 533–542

MacMahon JA, Mull JF, Crist TO (2000) Harvester ants (*Pogonomyrmex* spp.): their community and ecosystem influences. Ann Rev Ecol Syst 31:265–291

Taber SW (1998) The world of the harvester ants. Texas A&M University Press, College Station, Texas

Harvesters

Some members of the family Lycaenidae (order Lepidoptera).

► Gossamer-Winged Butterflies
► Butterflies and Moths

Hatch, Melville Harrison

Melville Hatch was born in Detroit, Michigan, USA, on November 25, 1898. An early interest in biology led to his seeking and obtaining a university education in the subject, culminating in a Ph.D. from the University of Michigan in 1925. He became a teaching assistant at the University of Michigan in 1926, then an instructor at the University of Minnesota, and next an assistant professor at the University of Washington. Promotions followed, and he became professor in 1941 and chairman of the Zoology Department, and Curator of Entomology at the university's Burke Museum in 1962. He retired from teaching in 1969. Meanwhile he had begun to write and publish his greatest work, "The beetles of the Pacific Northwest," which appeared in five volumes, the last in 1971. His other publications numbered more than 170, and he served as editor of "The Biologist" from 1959 through 1967. His Coleoptera collection was moved to the University of Oregon after he had ceased to work on it. He died near Seattle, Washington, on January 19, 1988.

References

Becker EC (1993) Melville H. Hatch (1898–1988). Coleopterists Bull 147:112

Herman LH (2001) Hatch, Melville Harrison. Bull Am Mus Nat Hist 265:75–76

Haustellate

This term is used to refer to mouthparts that are formed for sucking, or piercing and sucking.

► Mouthparts of Hexapods

Haustellum

The portion of the mouth through which liquid food is imbibed.

► Mouthparts of Hexapods

Hawk Lice

Members of the family Laemobothriide (order Phthiraptera).

► Chewing and Sucking Lice

Hawk Moths (Lepidoptera: Sphingidae)

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Hawk moths, family Sphingidae (also called sphinx moths, bee moths and hummingbird moths), total 1,230 species worldwide. Tropical regions of the New World, Africa and Asia have the most biodiversity. There are three subfamilies: Smerinthinae, Sphinginae, and Macroglossinae (sometimes only two subfamilies are used). The family comprises the monobasic superfamily Sphingoidea, in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults (Fig. 7) medium size to very large (23–200 mm wingspan), with head vertex scaling mostly normal but sometimes roughened; haustellum usually very long, to 30 cm (rarely vestigial); labial palpi mostly upcurved (sometimes porrect), with small third segment; maxillary palpi small; antennae mostly clavate or lamellate and thickened; body very robust (sometimes with longer hair-like setae); some genera with long needle-like spines on hind tibiae (e.g., *Oxyambulyx* species from Southeast Asia). Wings elongated and usually with acute apex; hindwings usually elongated but basally rounded, and much smaller than forewings. Maculation varied but many with shades of brown and gray, often with few markings, but also very colorful species; some with hyaline wings and mimicking wasps. Adults nocturnal or crepuscular but some a diurnal. Larvae are leaf feeders, usually with a posterior tail-like scolus; many larvae extremely large. Host plants recorded in numerous plant families. A few are economic. Among the largest species in the family are females of *Clanis titan* Rothschild & Jordan, of Southeast Asia, and *Coequosa triangularis* Donovan, of Australia, both also with massive bodies, while the smallest is *Sphingonaepiopsis obscurus* Mabille, from Madagascar.

Hawk Moths (Lepidoptera: Sphingidae), Figure 7 **Example of hawk moths (Sphingidae), *Callambulyx rubricosa* (Walker) from Indonesia.**

References

D'Abrera B (1986) Sphingidae mundi: hawk moths of the world. E. W. Classey, Farringdon, 226 pp
Hodges RW (1971) Sphingoidea. In: Dominick RB, et al. (eds) The moths of America north of Mexico, including Greenland. Fasc. 21. E. W. Classey and R. B. D. Publishers, London, 158 pp, 14 pl
Kitching IJ, Cadiou JM (2000) Hawkmoths of the world: an annotated and illustrated revisionary checklist (Lepidoptera: Sphingidae). Cornell University Press, Ithaca, 226 pp, 8 pl
Pinhey ECG (1962) Hawk moths of Central and Southern Africa. Longmans, Salisbury, 139 pp, 17 pl
Pittaway AR (1993) Hawk moths of the western palaearctic. E. W. Classey, London, 256 pp
Seitz A (1911–1934) Familie: Sphingidae. In: Die Gross-Schmetterlinge der Erde, 2:229–273, pl 36–43 (1911–12); 2(suppl): 137–166, 286, pl 12–13 (1932–34); 6:839–900, pl 90–98 (1931); 10: 23–576, pl 56, 60–68 (1928–29); 14:353–386, pl 61–67 (1927–28). A. Kernen, Stuttgart

Hazelnut and Walnut Twig Borer, *Oberea linearis* L. (Coleoptera: Cerambycidae)

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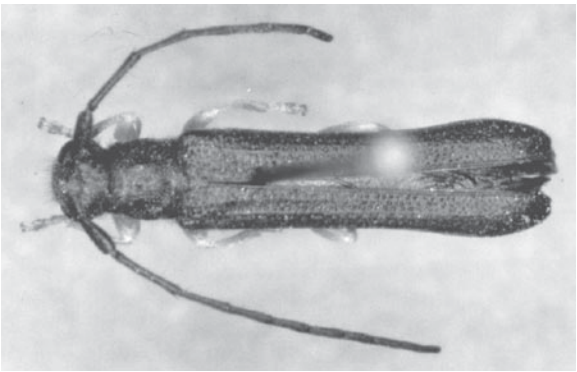
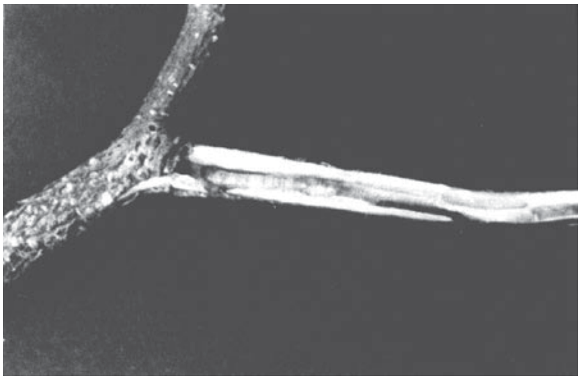
The adult (Fig. 8) of this hazelnut and walnut twig borer is long and slender, measuring 11–16 mm long and 2 mm wide. The body is black and the legs yellowish. The antennae do not reach the tip of the elytra. The pronotum and the elytra are covered



Hazelnut and Walnut Twig Borer, *Oberea linearis* L. (Coleoptera: Cerambycidae), Figure 8 *Oberea linearis* adult.



Hazelnut and Walnut Twig Borer, *Oberea linearis* L. (Coleoptera: Cerambycidae), Figure 9 *Oberea linearis* larva in its gallery in a hazelnut twig.

by fine dark brown hairs. The larva (Fig. 9) is apodous, yellowish or light brown with a brown prothoracic shield, and has the characteristic form of cerambycid larvae. Its final length is 20–25 mm.

On hazelnut, in southern and central Europe, *Oberea linearis* completes one generation every 2 years, whereas in colder regions one in every 3 years. There is a report that on walnut, in Greece, it completes one generation per year, but this needs confirmation. On hazelnut, this borer spends the first winter as a relatively young larva and the second winter as a fully-grown larva at the end of its gallery in a twig. It pupates in spring. The female lays an egg in a slit she gnaws in the bark of a shoot, 10–15 cm from its tip. The first-instar larva bores a gallery which is first semicircular and perpendicular to the longitudinal axis of the shoot. This causes the ultimate death of the apical part of the shoot which often breaks off. Subsequently, the gallery goes deeper, and is directed towards the base of the shoot. The larval excrement is pushed out through small holes the larva opens along its gallery. After its first overwintering, the larva continues boring its gallery during spring and summer of the second year, reaches full growth in autumn and overwinters. On hazelnut, the larval gallery reaches 40–60 cm the first year and is directed towards the base, whereas in the second year it is directed towards the apex of the twig.

On walnut, in southern Europe, according to Anagnostopoulos, the adults emerge from the twigs in May or early June. After feeding on new growth for a few days and mating, the female lays an egg on the bark of a shoot a few cm from the tip, or on the pedicel of a fruit. She prefers shoots bearing fruits, and shoots not very turgid. If the shoot is turgid, the female gnaws a semicircular to circular groove in the bark. This weakens the shoot and seems to favor the development and survival of the young larva. When the egg is deposited on the fruit pedicel, the gallery is bored first in the pedicel, then extended in the shoot. Sometimes the gallery goes to the mesocarp of the walnut. On walnut, galleries are shorter than on hazelnut. Galleries in the fruit pedicels cause early drying and early drop of walnuts, while galleries in the shoots cause the death of the eroded part of the shoot and of the fruits it bears. Therefore, on walnut, there may be loss of fruits, loss of dormant floral buds, and of some parts of the foliage. The damage may be serious if the insect's population density is high. In hazelnuts, the damage is limited to shoots and twigs and usually is not such as to justify control measures. Yet, even on hazelnut economic damage may occur under excessive population densities of the insect.

On hazelnut, the best method of control is the removal and destruction of infested dry twigs from late autumn to early spring, before the adults come out of them. Another measure is spraying with an organic contact insecticide of long residual action when the period the adults come out in spring. On walnut, where cutting off infested twigs is usually not practical because of the height of the trees, insecticidal sprays are usually recommended. Sprays applied against the codling moth may suffice. Where pruning is feasible, Anagnostopoulos recommends that it be done in July, to prevent further injury, or in spring, when new growth has started and infested twigs having no leaves can easily be distinguished.

References

Balachowsky AS (1962) Entomologie Appliquée a l' Agriculture. Tome I, vol 1. Masson et Cie, Paris, France

Paillot A (1933) Un cerambycide parasite de noyers, *Oberea linearis*. Ann Epiphyties 19:369–379

Tzanakakis ME, Katsoyannos BI (1998) Insects of fruit trees and grapevines. Agrotypos, Athens, Greece (in Greek)

Head

The anterior body region bearing the eyes, antennae (Figs. 10 and 11) and mouthparts.

► Head of Hexapods

Head Lice, *Pediculus humanus capitus* DeGeer (Phthiraptera: Pediculidae)

Head lice are a continuing pest problem for humans, especially children.

► Human Lice
► School IPM

Head of Hexapods

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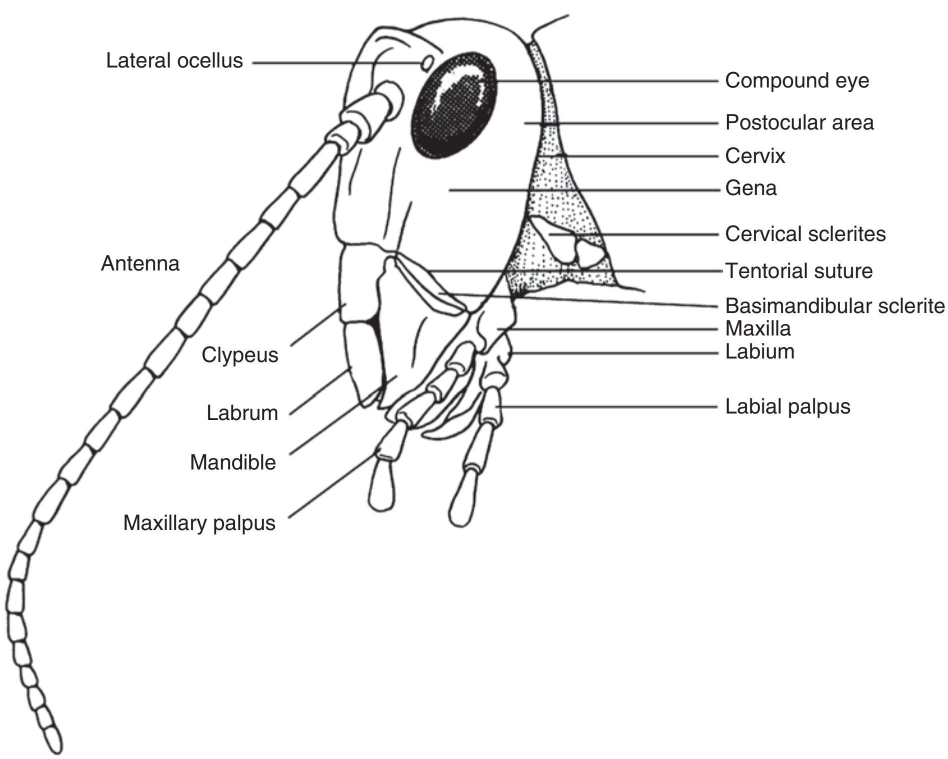
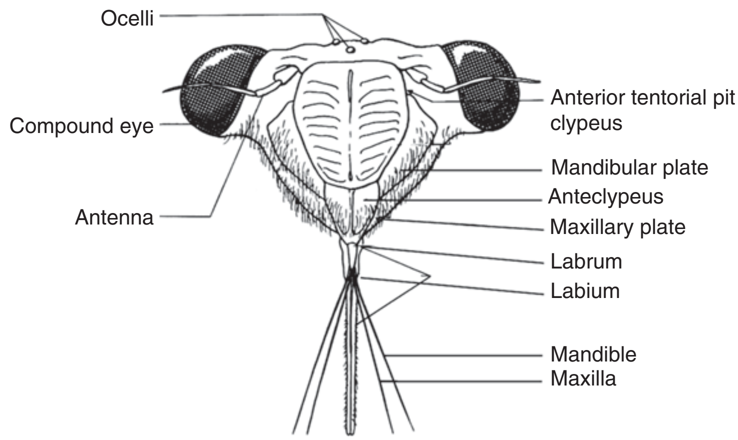
In the insects, the head is the tagma in the cephalic or anterior position. Structures related to two vital functions are situated in this tagma: feeding (mouthparts) and sensory function (organs like the antennae and visual organs: two compound eyes in the lateral position and three ocelli). The



Head, Figure 10 **Side view of the head of an adult grasshopper, showing some major elements.**



Head, Figure 11 **Anterior aspect of the head and mouthparts of a cicada (Hemiptera).**

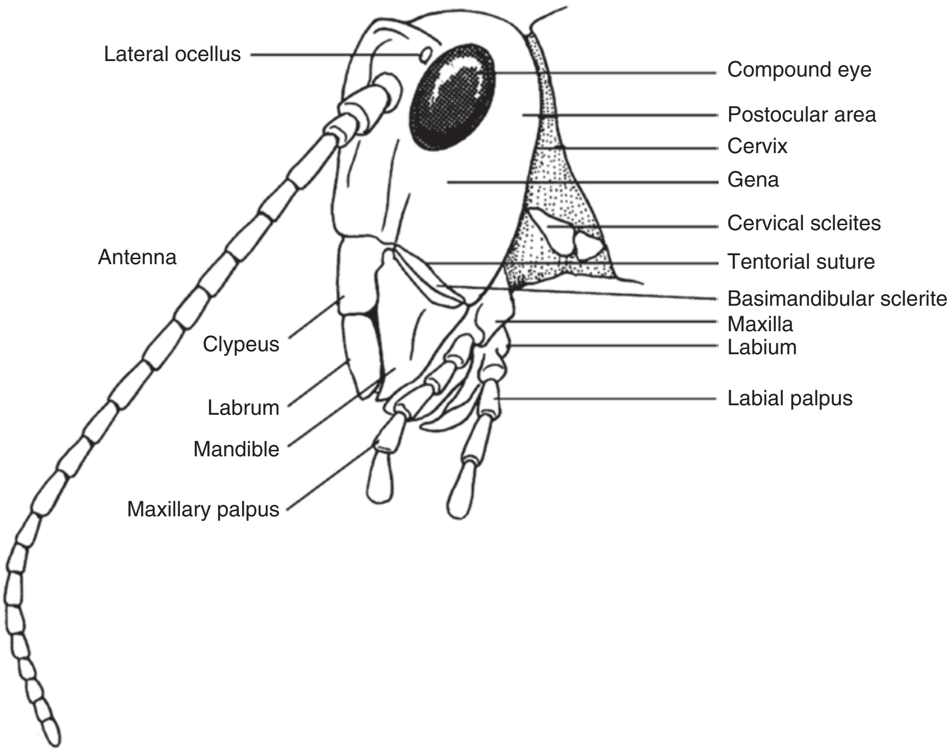
insertion of the antennae in the head capsule (Figs. 12 and 14) can vary from the median frontal area to a more or less ventral position. The compound eyes are situated laterally and generally occupy an ample surface area. The ocelli are situated between the compound eyes, arranged like an isosceles triangle; of the three, the most anterior (median position) seems to be conserved like a well-differentiated lens, while the two posterior ones (lateral position) tend to be reduced or modified, as occurs in some genera of Hymenoptera.

The foramen magnum (Fig. 13) is found in the posterior part of the head, connecting the head and the thorax, and on its ventral border is situated the oral cavity, from which the mouthparts articulate. It is formed by the acron and the preantennal segment (some consider one labral segment), the antennal segment, the intercalary or premandibular segment (some consider a postantennal fused to the antennal segment), the mandibular segment, the maxillary segment, and the labial segment. Externally, this segmentation is not visible due to the existence of the head capsule, formed by the strong sclerotization of the integument. However, this scelerotization is not homogeneous, being differentiated into sutures and grooves that separate sclerites. Among these sutures are found the epistomal or frontoclypeal that unites the anterior tentorial pits and separates the labroclypeal (preoral) region from the frontal region (postoral); likewise, it separates the frons from the clypeus. The clypeus is separated from the labrum by the labroclypeal suture. In certain species the clypeus is differentiated into an anteclypeus and a postclypeus.

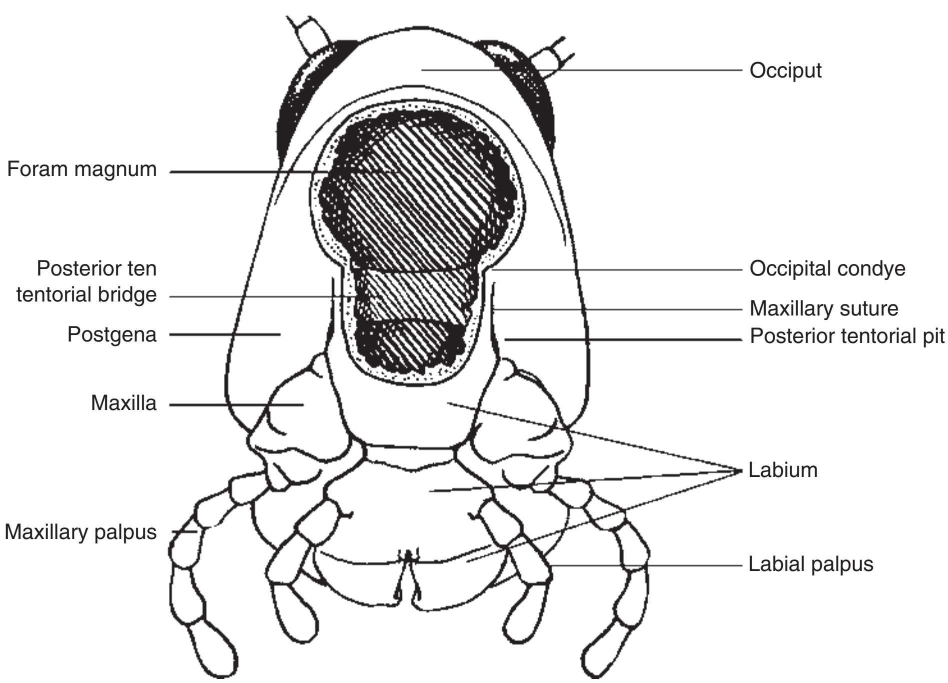
The posterior limit of the frons (Fig. 14) is marked by the branches of the epicranial suture (in the form of a Y). This suture represents the ecdysial line of the preimaginal stages, and its trajectory can vary; thus, postfrontal sutures appear (delimiting a postfrons) situated externally at the antennal sockets, and frontal sutures that are internal to those sockets (delimiting the frons). Both sutures can coexist, or only one of them may be present. This generalized arrangement of sclerites and sutures may exhibit numerous modifications, depending on the group of insects in question.

The odd branch of the epicranial suture, known as the coronal suture, separates two parietal sclerites that constitute the laterodorsal regions of the head capsule. The most dorsal zone is called the vertex (Figs. 14 and 15). Each parietal sclerite continues ventrally, forming the postocular area and the gena (areas situated ventrally and posteriorly to the compound eye).

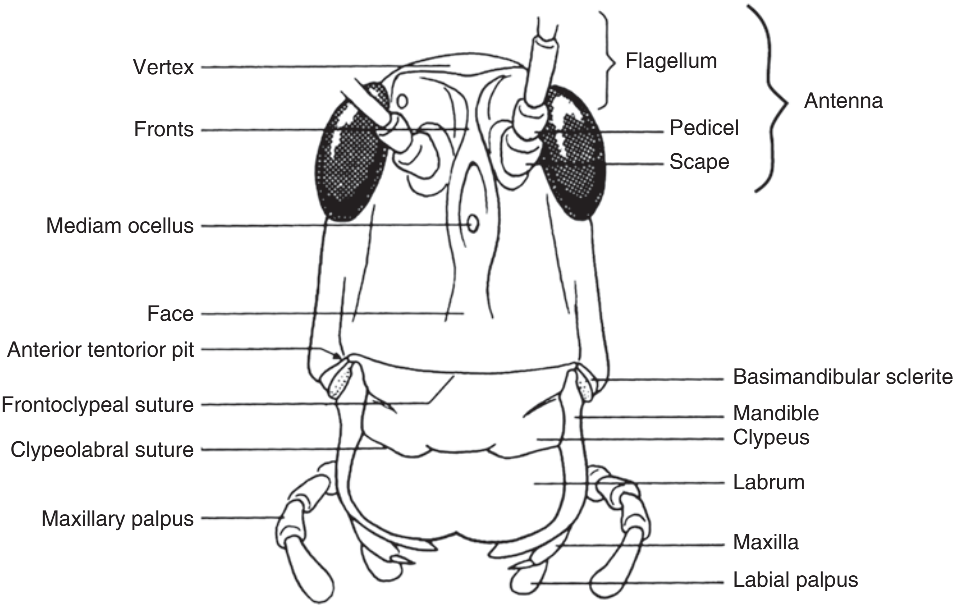
Two transverse sutures are generally differentiated in the posterior part of the head capsule: the occipital and the postoccipital, between which are found the occiput (dorsal) and the postgenae



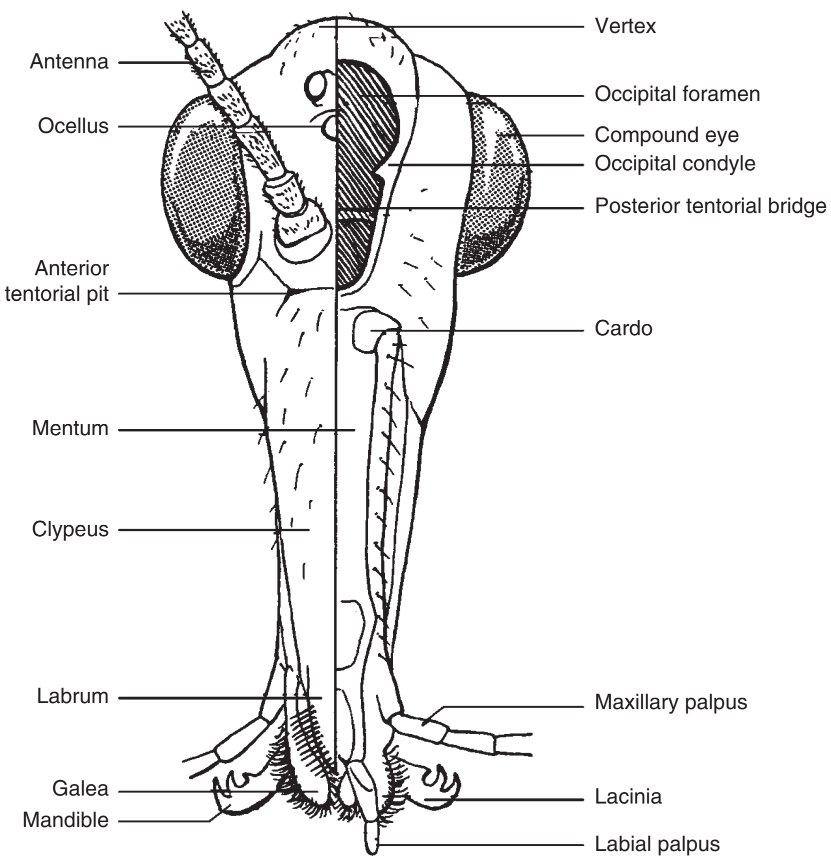
Head of Hexapods, Figure 12 **Side view of grasshopper head (Orthoptera: Romaleidae).**



Head of Hexapods, Figure 13 **Rear view of grasshopper head (Orthoptera: Romaleidae).**



Head of Hexapods, Figure 14 **Front view of grasshopper head (Orthoptera: Romaleidae).**



Head of Hexapods, Figure 15 **Front (*left half*) and rear (*right half*) view of scorpionfly head (Mecoptera).**

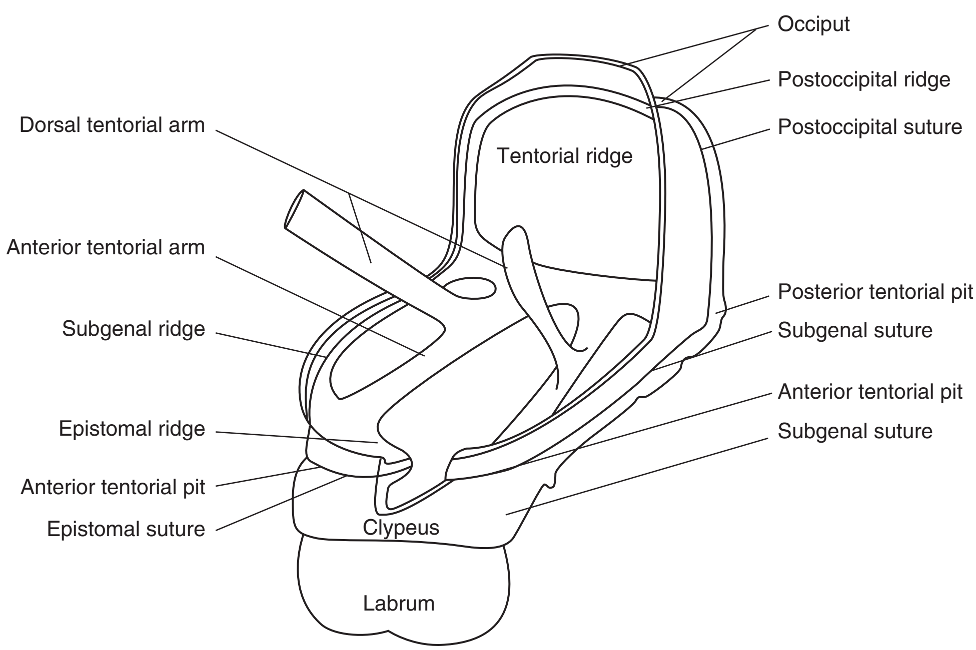
(lateral). The postocciput forms the posterior margin of the cranium by way of a narrow band posterior to the postoccipital suture.

The subgenal suture separates the gena and postgena from a well sclerotized band in the ventral position, the subgena. The subgenal suture consists of two parts, an anterior (pleurostomal suture) and a posterior (hypostomal suture), which delimit the pleurostoma (in which are found the mandibular articulations) and the hypostoma (where the maxilla articulates). The joining of the pleurostoma and hypostoma forms the subgena. Certain authors utilize the term epicranium to denote what together is formed by the occiput (posterior), vertex (dorsal), frontoclypeus (anterior) and genae (lateral).

Internally, the head has some endoskeletal structures, the occipital phragma and the tentorium. The occipital phragma corresponds to an internal ridge or phragma of the postoccipital suture. This phragma normally is formed by a pair of laterodorsal plates, in which the gnathal muscles and the prothoracic motor muscles of the head are inserted. The tentorium is a complex structure that has two fundamental functions; it serves as the area of muscular insertion and reinforces the head capsule. The number and type of muscles that are inserted into the tentorium varies depending on the hexapod group. In primitive groups of hexapods like the Machilidae it consists of three parts, the anterior and posterior tentoria and the tentorial-neck plate.

In the Pterygota, the tentorium is an odd structure (Fig. 16) formed by the tentorial body, from which are differentiated three pairs of extensions, one pair in the anterior position (anterior arms or pretentorium), another posterior (posterior arms or metatentorium) and a third dorsal (dorsal arms or supratentorium). Anterior and posterior arms result from anterior invaginations (pretentorinae) and posterior invaginations (metatentorinae), respectively. They are apodemal structures. These invaginations constitute important morphological reference points. The pair of dorsal arms is directed toward the antennal region. Their union with the cuticle is through naturally fibrous connective structures. Those dorsal arms constitute evaginations of the anterior arms.

Two types of head capsules are distinguished, depending on whether the mouthparts are positioned externally (ectotrophous or ectognathous) or



Head of Hexapods, Figure 16 **Internal structures of the insect cranium (after Snodgrass).**

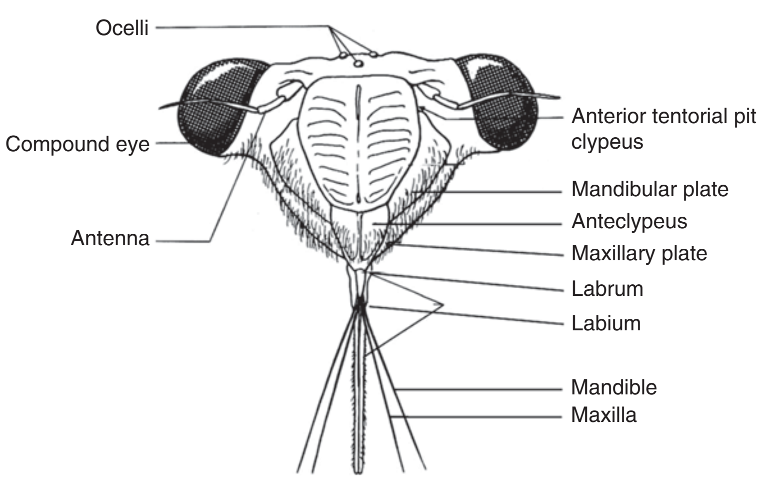
internally (entotrophous or entognathous). These terms can also be applied to the mouthparts themselves. In the first case, both the mouthparts and their articulations with the head are visible externally. In the case of the entognathous insects, the mouthparts are withdrawn into the head, in internal cavities, and are not visible externally when the insect is at rest. Clear examples of this type of head capsule are found in Collembola, Protura and Diplura, and to a lesser extent in Thysanoptera (Fig. 20), Phthiraptera (Anoplura) and some Hemiptera (Fig. 17).

If we consider the position of the oral cavity and consequently of the mouthparts with respect to the cephalocaudal axis, three fundamental types of head capsules (Fig. 21) are distinguished: orthognathous or hypognathous; prognathous; and opisthognathous or opisthorhynchous (these names can also be applied to the mouthparts).

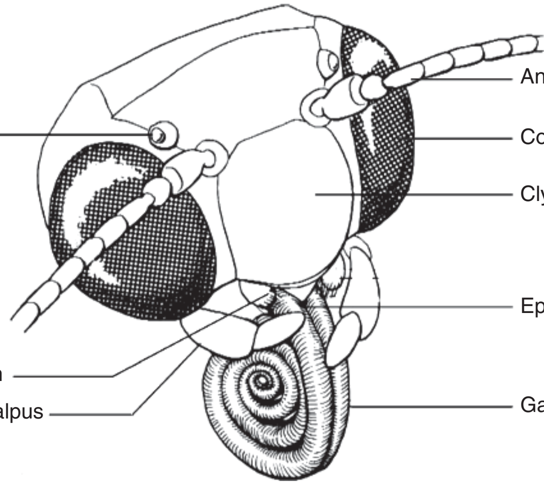
In the orthognathous or hypognathous condition, the mouthparts are situated more or less perpendicular to the cephalocaudal axis. This model is differentiated in phytophagous insects that feed on solid particles and in some predators. In the prognathous condition the oral cavity is situated in the anterior ventral part of the head, and the mouthparts are directed forward. Modifications of certain parts of the head capsule result, such as a tendency to incorporate the clypeus into the frons, a shortening of the occipital areas, and a lengthening of the structures that form the ventral closure of the head. The prognathous condition is represented in many hexapod orders, being considered a primitive condition (for example, Embiidina, Isoptera and Dermaptera) or secondarily acquired (larvae of Neuroptera, mining caterpillars and certain beetle larvae). The prognathous condition is characterized by the predatory species, whose adults actively hunt their prey. The condition is also found in some larval forms (particularly in Coleoptera) that use their mandibles for burrowing.

The opisthognathous condition is characterized by the oral cavity being (Fig. 17) situated in the posterior ventral part of the head and the mouthparts directed toward the back, being held at rest between the anterior legs (Hemiptera).

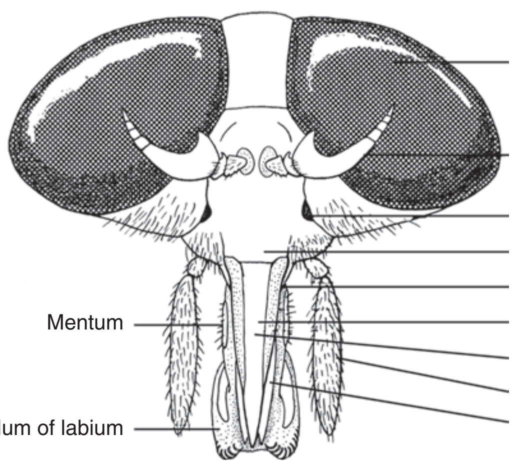
There exists a tendency for the ventral closure of the head to be differentiated into two types of head or cranial capsules: open and closed. In the first case, the foramen magnum is bordered ventrally by the proximal margin of the submentum, having the metatentorinae in the inferior extremes of the occipital suture, near the foramen magnum. Nevertheless, the most frequent case is where the labium is separated from the foramen magnum by a more or less wide, sclerotized band. This band can be situated anteriorly to the metatentorinae,



Head of Hexapods, Figure 17 **Front view of cicada head (Hemiptera: Cicadidae).**



Head of Hexapods, Figure 18 **Dorsolateral view of a moth head (Lepidoptera).**



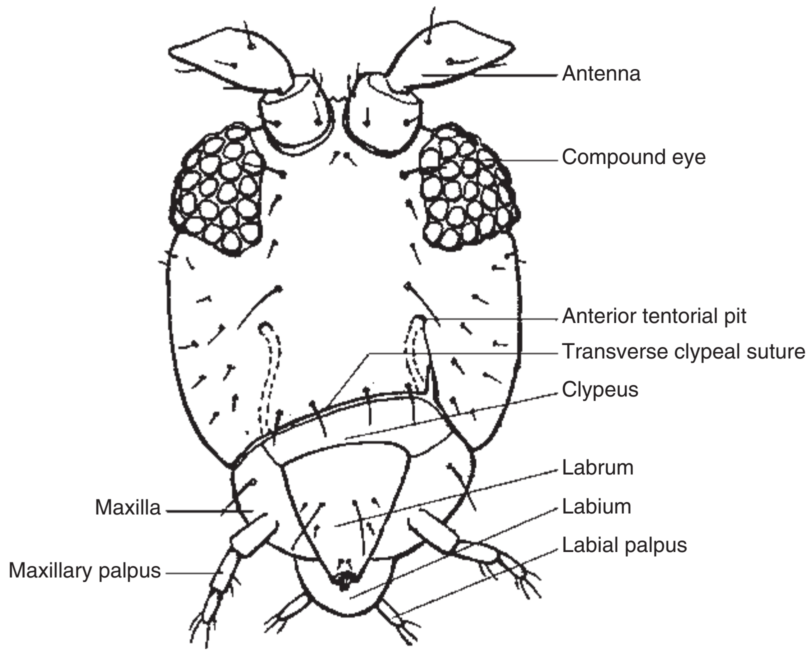
Head of Hexapods, Figure 19 **Front view of a horse fly head (Diptera: Tabanidae).**

forming the hypostomal or postgenal bridge, or it can be posterior to the metatentorinae, forming the gula. These sclerotized formations can occupy a great part of the ventral zone of the head, with the consequent displacement of the mouthparts (Fig. 21) toward the front. The prognathous condition discussed earlier originated in this manner.

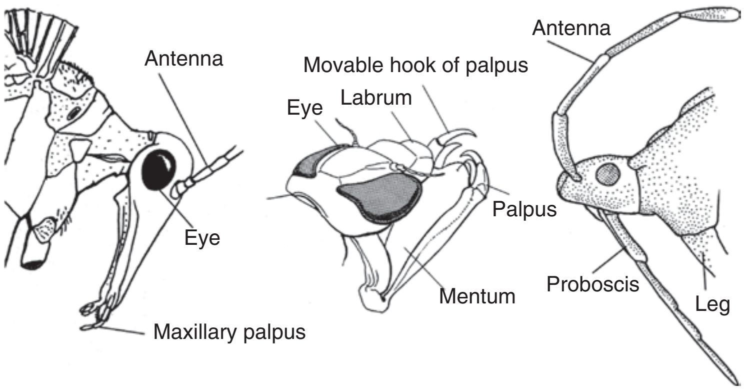
The hypostomal bridge is formed by the union of two lobes that are of mixed origin (each one is formed beginning from the hypostoma and the postgena). Clear examples of this bridge exist in advanced Hymenoptera and Diptera.

The gula constitutes a sclerotized zone that prolongs the submentum behind the metatentorinae, which are advanced, and it is separated from the postgenae by the gular sutures. The origin of the gula is disputable, and although it probably pertains to what is called labial, some attribute its origin starting from the neck and including the prothoracic region. Clear examples of the presence of the gula are found in certain beetles.

► Antennae of Hexapods
► Mouthparts of Hexapods



Head of Hexapods, Figure 20 **Front view of a thrips head (Thysanoptera).**



Head of Hexapods, Figure 21 **Comparison of mouthpart orientation: hypognathous (*left*), prognathous (*center*), and opisthognathous (*right*).**

References

Bitsch J (1973) Morphologie de la tête des insects. Partie Générale. In: Grassé PP (Dir.) Traité de Zoologie, VIII(I) 19:3–100

Bitsch J (1994) The morphological groundplan of Hexapoda: critical review of recent concepts. Ann Soc Entomol France 30:103–129

Borror DJ, Triplehorn CA, Johnson NF (1989) An introduction to the study of insects. Saunders College Publishing, Philadelphia, Pennsylvania

Gillot C (1995) Entomology, 2nd edn. Plenum Press, New York, NY

Imms AD (1957) A general textbook of entomology, 9th edn. Methuen, London, UK

Manton SM (1977) The Arthropoda. Habits, functional morphology and evolution. Clarendon Press, Oxford, UK

Matsuda R (1965) Morphology and evolution of the insect head. Mem Am Entomol Inst 4:1–334

Nauman ID (ed) (1994) Systematic and applied entomology. An introduction. Melbourne University Press, Melbourne, Australia

Quéinnec E (2001) Insights into arthropod head evolution. Two heads in one: the end of the "endless dispute?" Ann Soc Entomol France 37:51–70

Richards OW, Davies RG (1977) Imms' general textbook of entomology, 10th edn. Chapman and Hall, London, UK

Snodgrass RE (1951) Comparative studies on the head of mandibulate arthropods. Comstock Publishing, Ithaca, New York
Snodgrass RE (1952) A textbook of arthropod anatomy. Comstock Publishing, Ithaca, New York
Steinmann H, Zombori LM (1981) An atlas of insect morphology. Akademiai Kiado, Budapest, Hungary

Heart

Also known as the dorsal vessel (Figs. 22 and 23), it is a muscular tube extending dorsally through the abdomen of the insect which pushes blood (hemolymph) forward into the aorta and to the head.

Hebridae

A family of bugs (order Hemiptera). They sometimes are called velvet water bugs.

► Bugs

Hedylidae

A family of moths (order Lepidoptera) also known as American butterfly moths.

► American Butterfly Moths
► Butterflies and Moths

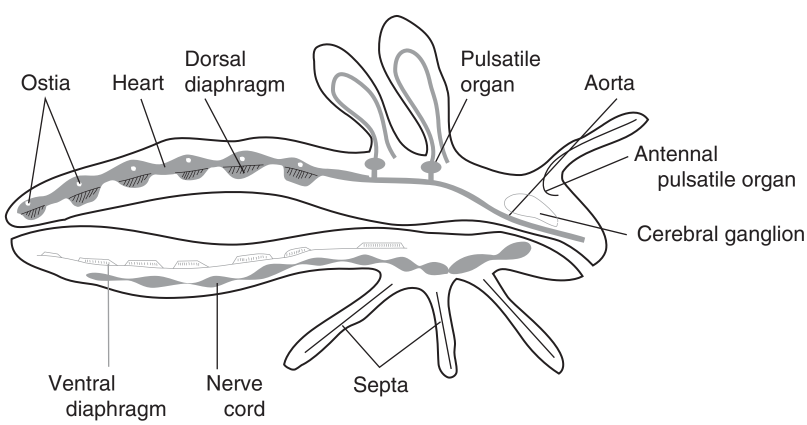
Heel Flies

Members of the family Oestridae (order Diptera).

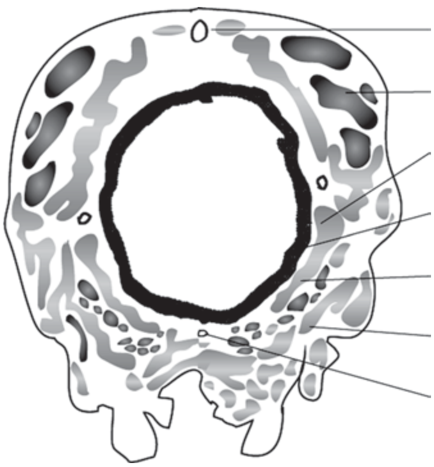
► Flies (Diptera)
► Myiasis

Heer, Oswald

Oswald Heer was born in Matt, a mountain village in Switzerland, on August 31, 1809. His interest in natural history was aroused there. In 1828, he went to Universität Halle in Germany to study theology (his father was a priest) and there met several renowned naturalists. He was ordained in St. Gallen, Switzerland, but also pursued natural history. In 1832, he obtained the post of curator of the Escher-Zollikofer natural history collection in Zurich. Two years later he became docent of botany and zoology of Universität Zurich, and in 1835 professor of botany there. His work on paleobotany and paleozoology was perhaps his most notable research contribution. Nevertheless, his multi-part "Fauna Coleopterorum Helvetica" was seminal for Swiss



Heart, Figure 22 **Diagram of the components of the insect circulatory system; hemolymph moves through the heart and aorta to the head, filtering back through the body cavity and back into the heart via the ostia. Pulsatile organs assist in moving hemolymph through the appendages, especially the wings. (adapted from Chapman, The insects: structure and function).**



Heart, Figure 23 **Cross section of caterpillar larva showing the location of the heart (adapted from Chapman, The insects: structure and function).**

entomology, and is still consulted. He died on September 27, 1883, in Lausanne.

Reference

Herman LH (2001) Heer, Oswald. Bull Am Mus Nat Hist 265:76–77

Heleomyzidae

A family of flies (order Diptera). They commonly are known as heleomyzid flies.

► Flies

Helgrammite

The aquatic larvae of corydalids (Megaloptera: Corydalidae).

► Alderflies and Dobsonflies

Helicopsychidae

A family of caddisflies (order Trichoptera).

► Caddisflies

Helicosporidium

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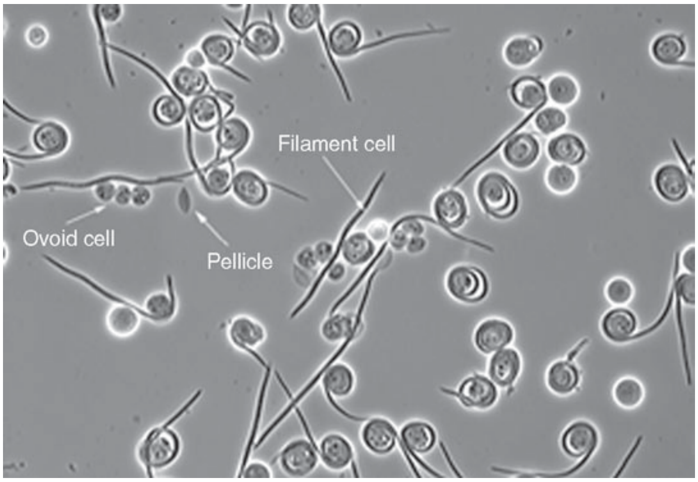
To date, there is only one named species of Helicosporidia: *Helicosporidium parasiticum*. It was initially described and named by Keilin in 1921, who detected this protist in larvae of *Dasyhelea obscura* Winnertz (Diptera: Ceratopogonidae) collected in England. He examined the new parasite thoroughly and attempted to infer its life history from his observations. He described a vegetative growth characterized by very active multiplications of helicosporidial cells inside the body cavity of the host, and noticed that these "schizogonic multiplications" were followed by the formation of what he called spores. Keilin noted that the spores are very easily recognized; they consist of the assembly, inside an external membrane, of three ovoid cells (named by Keilin "sporozoites") and one peripheral, spiral, filamentous cell. These features, especially the highly characteristic filamentous cell, have since remained the principal diagnostic for identification of a *Helicosporidium* sp. Keilin was able to describe and characterize structurally the new genus *Helicosporidium*, and the new species *H. parasiticum*. He also was able to present a hypothetical life cycle of this protist based on his microscopy observations. He suggested that the spores (or cysts) break open in the host hemocoel, releasing the filamentous cell and the three "sporozoites," which he proposed are the infective forms of *H. parasiticum* (Fig. 24). Keilin believed that *H. parasiticum* belonged to the Protozoa, and compared this isolate with members of various clades: Cnidiosporidia (which, at that time, included Microsporidia such as *Nosema bombicis*), Haplosporidia, Serumsporidia, and Mycetozoa. He concluded that the genus *Helicosporidium* differed markedly not only from all these groups, but also from all the protists known at that time. He finally proposed that *Helicosporidium* "forms a new group, which may be temporarily be included in the group of the Sporozoa."



***Helicosporidium*, Figure 24** **Light micrograph of dehisced *Helicosporidium* sp. cysts. Following rupture of the pellicle, one filamentous cell and three ovoid cells are released from each cyst.**

Following the discovery of another isolate of *Helicosporidium parasiticum* in a larva of *Hepialis pallens* (Lepidoptera: Hepialidae), another taxonomic position was proposed for the group Helicosporidia. Based on observation of this new isolate as well as the original specimen described by Keilin, Weiser claimed that the Helicosporidia are best placed among the lower Fungi. He argued that the spore characteristics are much too different from what is found in Protozoa, but are similar in some aspects to primitive Fungi, such as insect pathogens of the genus *Monosporella*, classified as Nematosporoideae inside the Saccharomycetaceae (primitive Ascomycetes).

In the early 1970s, *Helicosporidium parasiticum* was isolated from larvae and adults of the beetle *Carpophilus mutilatus* (Coleoptera: Nitidulidae). This isolate was infectious per os to 18 species of arthropods, including three orders of insects (Lepidoptera, Coleoptera, Diptera) and one family of mites. In contrast, species of Orthoptera, Hymenoptera, and Diptera were not susceptible to this isolate. The spores (cysts) present in the host artificial diet were ingested and released the three round cells and the filamentous cells in the host midgut. After 24 h, helicosporidial cells appeared in the host hemolymph and grew vegetatively. The vegetative growth is characterized by cell division that occurs within a pellicle. After division, the pellicle ruptures and releases the daughter cells (4 or 8). Empty pellicles and daughter cells eventually fill the entire host hemocoel. Daughter cells then develop into spores, in which the filamentous cell differentiates and encircles the three round cells. Additional studies reported the presence of *Helicosporidium* sp. in new host species such as crustaceans, mites, collembolans, and trematodes.

In 1999, a *Helicosporidium* sp. was discovered in larvae of the black fly *Simulium jonesi* Stone & Snoddy (Diptera: Simuliidae). This isolate was demonstrated to grow under both in vitro and in vivo conditions. In vivo, the ingested helicosporidial cysts dehisced and released the three ovoid cells and the filamentous cells. The filamentous cells attached to the peritrophic membrane and penetrated the midgut epithelium initiating infection. The in vitro growth of *Helicosporidium* sp. was reminiscent of that reported for unicellular, achlorophytic algae belonging to the genus *Prototheca*. Both the genera *Helicosporidium* and *Prototheca* are characterized by a vegetative growth that consists of cell divisions inside a membrane. Four, eight, or sixteen daughter cells are produced inside this pellicle and eventually are released. Such cell divisions result in the accumulation of both round daughter cells and empty pellicles. The suggestion that *Helicosporidium* was related to algae has been confirmed by molecular analysis. The 18S, 26S, 5.8S regions of the *Helicosporidium* ribosomal DNA, as well as some partial sequences of the actin and tubulin genes, were sequenced. Comparative analyses of these nucleotide sequences were performed in order to evaluate the position of *Helicosporidium* sp. within the phylogeny of eukaryotes. All trees depicted *Helicosporidium* sp. as a green alga (Chlorophyta), and as sister taxon to the genus *Prototheca* (class Trebouxiophyceae). This association always was supported by significant bootstrap values. On the basis of this phylogenetic analysis, *Helicosporidium* sp. is clearly neither a protozoan nor a fungus, but represents the first described algal invertebrate pathogen.

References

Boucias DG, Becnel JJ, White SE, Bott M (2001) In vivo and in vitro development of the protist *Helicosporidium* sp. J Eukaryotic Microbiol 48:460–470

Kellen WR, Lindegren JE (1974) Life cycle of *Helicosporidium parasiticum* in the navelworm *Paramyelois transitella*. J Invertebr Pathol 23:202–208

Tartar A, Boucias DG, Adams BJ, Becnel JJ (2002) Phylogenetic analysis identifies the invertebrate pathogen *Helicosporidium* sp. as a green alga (Chlorophyta). Int J Syst Evol Microbiol 52:273–279

Heliodinidae

A family of moths (order Lepidoptera). They commonly are known as sun moths.

► Sun Moths
► Butterflies and Moths

Heliomyzid Flies

Members of the family Heliomyzidae (order Diptera).

► Flies

Heliozelidae

A family of moths (order Lepidoptera). They commonly are known as shield bearer moths.

► Shield Bearer Moths
► Butterflies and Moths

Heloridae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Helosciomyzidae

A family of flies (order Diptera).

► Flies

Helotrephidae

A family of bugs (order Hemiptera).

► Bugs

Hematophagous

(haematophagous) Insects that feed on blood.

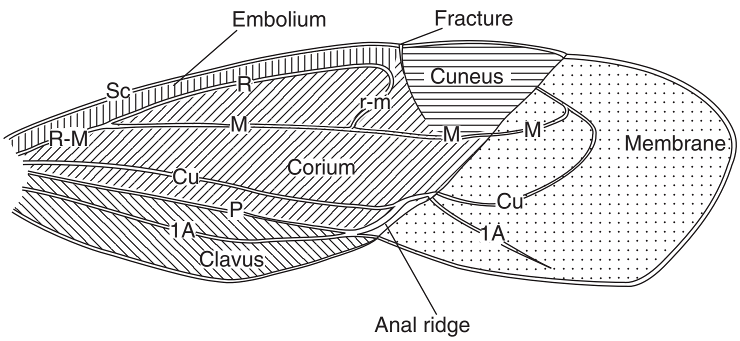
Hematophagy

(haematophagy) Feeding on blood. Usually this refers to arthropods that bite to obtain blood, but secondary hematophagy also is possible, wherein arthropods feed at a bleeding wound, with the wound accidental or inflicted by another organism.

Hemelytron (pl. hemelytra)

The front wing of insects in which the basal portion in thickened and the distal portion membranous (Fig. 25), usually Hemiptera.

► Wings of Insects



Hemelytron (pl. hemelytra), Figure 25 **Front wing of a bug (Hemiptera: suborder Heteroptera), thickened basally and membranous distally.**

Hemerobiidae

A family of insects in the order Neuroptera. They commonly are known as brown lacewings.

► Lacewings, Antlions and Mantidflies

Hemipsocidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice or Psocids

Hemiptera

An order of insects. Many of these insects are called bugs, or true bugs, but this is a very diverse assemblage, and includes leafhoppers, treehoppers, cicada, scales, aphids, whiteflies, and many others. Hemiptera is sometimes treated as two orders: Hemiptera and Homoptera.

► Bugs

Hemimetabolous Development

Insects having incomplete metamorphosis, or a gradual change in body form with each molt, and wings developing externally. A subset of insects (Odonata, Ephermeroptera, Plecoptera) with a modified form of hemimetabolous development are said to have paurometabolous development. The hemimetabolous insects (including paurometabolous insects) lack the pupal stage that is found among insects with holometabolous development. The immature forms of hemimetabolous insects are called nymphs, though some entomologists call all immature insects larvae, regardless of developmental pattern. (contrast with holometabolous development)

► Metamorphosis
► Complete Metamorphosis
► Incomplete Metamorphosis

Hemocoel

(haemocoel) The hemolymph (blood)- filled body cavity of arthropods.

Hemocoelic Insemination

Female bed bugs (Hemiptera: Cimicidae) are inseminated by the male's needle-like penis, which can be inserted in many locations in the female's body, because the sperm migrate through the hemolymph to the ovary. This process may provide additional nutrients to the female, but certainly other insects do this in less traumatic ways. This process is also called "traumatic insemination."

► Bed Bugs

Hemocytes of Insects: Their Morphology and Function

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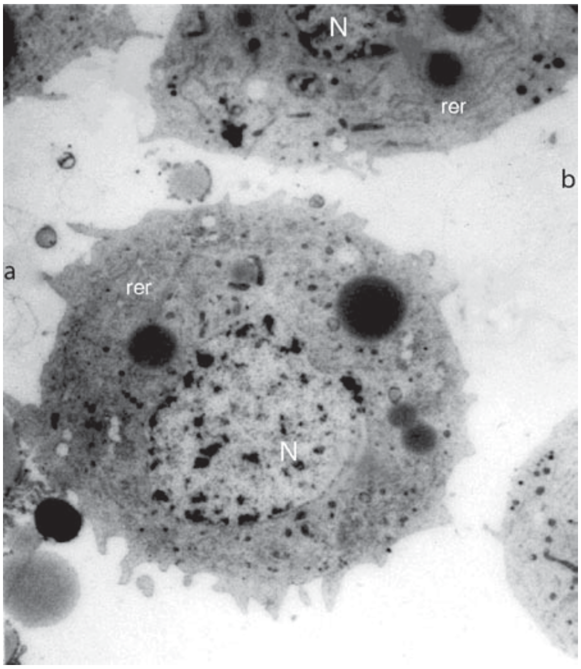
Hemocytes are blood cells that circulate in a clear fluid, the plasma, within the hemocele (body cavity) of insects. The hemocytes, plasma, and dissolved inorganic and organic molecules constitute the hemolymph. Nutrients, nitrogenous waste products, hormones, and a variety of other substances also are transported in the hemolymph for distribution to various tissues. In most insect larvae, the hemocytes are produced within hematopoietic (hemopoietic) organs (blood cell producing factories) where they replicate and differentiate. The number and types of hemocytes vary with insect species, developmental stage, and physiological state. In general, total hemocyte count (the number of hemocytes per unit volume) increases throughout larval development, reaching a maximum at each larval ecydsis but probably not during pupal/adult ecdysis. Qualitative and quantitative fluctuations in hemocyte populations also may be influenced by endocrine events as well as by wounding and microbial and parasitic infections.

The classification of insect hemocytes has been based primarily on the morphology of cells observed under the light and electron microscopes. While all hemocyte types described to date do not occur in all insects, the six recognized and most common types are: adipohemocytes, granulocytes, oenocytoids, plasmatocytes, prohemocytes, and spherule cells. Adipohemocytes vary in size and are ovoid with well-defined lipid droplets and granular cytoplasm with rough endoplasmic reticula (RER) and Golgi complexes, indicative of synthetic and secretory functions. Granulocytes vary in size and shape and have a small nucleus: cytoplasm ratio and small, uniform acidophilic cytoplasmic inclusions. Their cytoplasm is richly supplied with an elaborate network of RER, Golgi vesicles and other organelles. In studies of the encapsulation process in Lepidoptera, granulocytes were determined to attach to, and release their contents (degranulate) on, the surface of a foreign object during the initial phase of capsule formation, and to release cytokines that recruit plasmatocytes (Fig. 26) to the site. The innermost cells of the capsule then flatten and develop desmosomes that hold the cells together. Gap-junctions develop between cells of the external and internal layers of the capsule, providing an intercellular pathway presumably for nutrients, hormones, and probably cytokines for intercellular signaling, and for other factors needed to maintain the integrity of the capsule. Granulocytes are presumed to arise from plasmatocytes, and their



Hemocytes of Insects: Their Morphology and Function, Figure 26 Transmission electron micrograph of a spherical (discoid) plasmatocyte (a) from the third instar of the Caribbean fruit fly, *Anastrepha suspensa* (Diptera: Tephritidae). Three populations of discoid plasmatocytes occur in *A. suspensa*, ranging from 10–25 μm in diameter. (b) Portion of a lamellocyte showing rough endoplasmic reticula (RER). Lamellocytes are 15–20 μm long and 6–10 μm wide. N = nucleus. (Micrograph by P.O. Lawrence.)

population ranges from 30 to 65% of the total hemocyte count. Some authors consider cystocytes (also called coagulocytes) to be a small form of granulocytes because they are presumed to participate in the coagulation process. Like granulocytes, cystocytes have acidic cytoplasmic inclusions and a small nucleus. Because their cell cytoplasm is translucent, cystocytes sometimes are called hyaline cells. To date, cystocytes have not been identified in lepidopterans, dipterans or hymenopterans.

Oenocytoids are large (18–38 μm in diameter), sometimes with two eccentric nuclei and an acidophilic cytoplasm. They have numerous microtubules and few synthetic organelles. They also exhibit endogenous phenoloxidase activity and are presumed to participate in the process of melanization (melanosis), often associated with wound healing and encapsulation. Plasmatocytes usually represent more than 28% of the total hemocyte population in most insects. They are pleiomorphic, varying in size and shape from round (discoid), to spindle-shaped (lamellocytes) and have a single nucleus that occupies about 40–50% of the granular, basophilic cytoplasm. They possess RER and Golgi organelles, indicative of a synthetic function. They are motile and phagocytic, with lysosomal vesicles, and are the primary line of defense in the insects' cellular response to microbial infection. Indeed, they release substances that induce degranulation of the granular hemocytes during the final stage of encapsulation. They also participate in other defense-related processes such as nodulation and, along with cystocytes, in plasma coagulation. Podocytesare considered by some authors to either arise from, or be a form of, plasmatocyte. Prohemocytes are thought to be the smallest blood cells. They are round with a large nucleus:cytoplasm ratio, and basophilic, but are devoid of synthetic organelles (e.g., endoplasmic reticula, etc). They undergo mitosis, presumably giving rise to prohemocytes, plasmatocytes, and probably to granulocytes. Thus, they are considered the hemocyte stem cells. Spherulocytes (spherule cells) are ovoid and usually are larger than prohemocytes, but smaller than some plasmatocytes. In some cases, spherulocytes represent about 4% of the total hemocyte population. Their cytoplasm appears to contain large acidophilic inclusions. Other hemocytes such as podocytes and vermiform cells could be forms of plasmatocytes, but neither their origins nor specific functions are known.

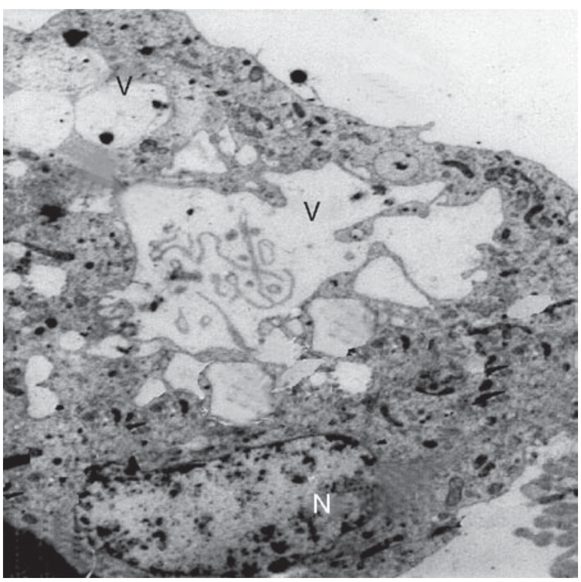
Larval dipterans have hemocytes (e.g., prohemocytes, plasmatocytes, and oenocytoids) similar to some found in other insects. However, they are thought to lack true granulocytes and spherule cells. Indeed, some authors consider previously described "spherule cells" and "granulocytes" of some Diptera (e.g., *Calliphora erythrocephala*) to be plasmatocytes and thrombocytoids, respectively. True spherule cells are thought to be absent in dipterans while thrombocytoids, crystal cells, and vacuolated cells are presumed to be unique to dipterans, although they do not occur in all species.

Crystal cells, unique to drosophilids, are 10–12.2 μm with a nucleus of 3.5–5 μm in diameter and comprise 5–10% of the total hemocyte count. They characteristically have large cytoplasmic paracrystalline inclusions that are presumed to contain tyrosine, a substrate of phenol oxidase. Consequently, upon disruption, these cells release their contents, causing melanosis which is important in wound healing and other defense responses. Since oenocytoids of other dipterans, and indeed other insects, are known to have endogenous phenol oxidase activity and are involved in wound healing, it is likely that the crystal cells of *Drosophila* are at least analogous, if not homologous to them.

Thrombocytoids are round cells with numerous invaginations of the plasma membrane that penetrate deep into the cytoplasm close to the nucleus. Based on in vitro studies, thrombocytoids are presumed to phagocytose bacteria, and to participate in encapsulation and wound healing. They disintegrate within the hemolymph to give rise to cytoplasmic fragments and naked nuclei. Thrombocytoids are absent from *Drosophila* sp.

and culicid mosquitoes, but occur in calliphorids and tipulids.

Vacuolated cells (Fig. 27) are 14–23 μm in diameter and are characterized by extensive vacuolation of the cytoplasm, presumably the result of invaginations of the cell membrane. Numerous free ribosomes, RER, Golgi bodies, and mitochondria are dispersed throughout the cytoplasm. Vacuolated cells are <20% of the total hemocyte count. These cells are presumed to be unique to the Diptera, although do not occur in all species. They have been reported from larval sciarids, the fruit fly *Anastrepha suspensa*, and from mutant *Drosophila melanogaster* that have a lethal malignant blood neoplasm (lmbn) (i.e., melanotic tumors of the hemocytes). These tumerous blood cells [l(2)mbn] when cultured in vitro, readily differentiate into hemocyte morphotypes that correspond to plasmatocytes, lamellocytes, podocytes, and vacuolated cells of the wild type (normal) larvae. Lamellocytoids (apparent homologs of the lamellocytes in vivo) were transformed to vacuolated-like cells in vitro upon treatment with the insect molting hormone 20-hydroxyecdysone (20-OHE). Interestingly, the combined application of juvenile hormone III (the predominant juvenile hormone found in dipterans) and related JH agonists, along with 20-OHE, counteracted the effects of 20-OHE alone. Given the respective roles of JH and 20-OHE in the maintenance of larval characteristics and induction of metamorphosis, it is likely that the incidence of vacuolated cells in dipterans may be influenced by hormonal and/or related developmental events, as is apparently the case with certain other hemocytes.



Hemocytes of Insects: Their Morphology and Function, Figure 27 **Transmission electron micrograph of a portion of a vacuolated hemocyte from the third instar of the Caribbean fruit fly, *Anastrepha suspensa*. These vacuolated cells are 25–30 μm in diameter (compared to 14–23 μm in other dipterans). N = nucleus, V = vacuoles. (Micrograph by P.O. Lawrence.)**

The behavior and function of hemocytes are influenced by the release of humoral factors such as cytokines, cell adhesion molecules, lectins, and agglutinins that mediate intercellular communication. The receptors for these factors have not been fully characterized, and neither is their distribution among the different hemocytes.

Overall, it appears that certain hemocytes, such as the plasmatocytes, have similar morphology and ultrastructure across the various insect families. Indeed, techniques have been used to establish criteria that facilitate interspecies comparisons and classification of some hemocytes. These include the use of electron microscopy, the development of monoclonal antibodies for specific hemocytes, and histochemistry. Nevertheless, additional approaches are needed to identify unique characteristics of hemocyte types and facilitate meaningful interspecies and within species comparisons. The plasticity in hemocyte morphology as a result of normal ontogeny, stage specific factors, and hormonal or environmental events demands additional approaches to provide insights into hemocyte identity within and between species and families. Likely technologies include differential display, microarrays and glycobiology.

► Hemolymph

References

Brehelin M, Zachary D (1986) Insect haemocytes: a new classification to rule out the controversy. In: Brehelin M (ed) Immunity in invertebrates. Springer-Verlag, Berlin, Germany, pp 36–48

Caveney S, Berdan R (1982) Selectivity in junctional coupling between cells of insect tissues. In: King RC, Akai H (eds) Insect ultrastructure. Plenum Press, New York, NY, pp 434–465

Ratcliffe N (1993) Cellular defense responses of insects: unresolved problems. In: Beckage NE, Thompson SN, Federici BA (eds) Parasites and pathogens of insects, vol 1: Parasites. Academic Press, San Diego, CA, pp 267–304

Shrestha R, Gateff E (1986) Ultrastructure and cytochemistry of the tumorous blood cells in the mutant lethal(3) malignant blood neoplasm of *Drosophila melanogaster.* J Invertebr Pathol 48:1–12

Strand M, Pech L (1995) Immunological basis for compatibility in parasitoid-host relationships. Ann Rev Entomol 40:31–56

Hemolymph

(haemolymph) The fluid filling the hemocoel and dorsal vessel (Fig. 28). The blood cells, or hemocytes, are considered to be part of the hemolymph. The insect's "blood." The hemolymph has several important functions, including the transport of nutrients to cells and tissues; the transport of hormones, waste products and water; the transport of body heat away from organs generating the heat, or the localization of heat in tissues such as thoracic muscles where heat is needed; it serves as a reservoir of nutrients, enzymes and fluids; it functions as a sink for carbon dioxide; it serves as a lubricant and hydraulic fluid for the maintenance of body shape and the expansion of wings; the hemocytes attack invading organisms and foreign substances.

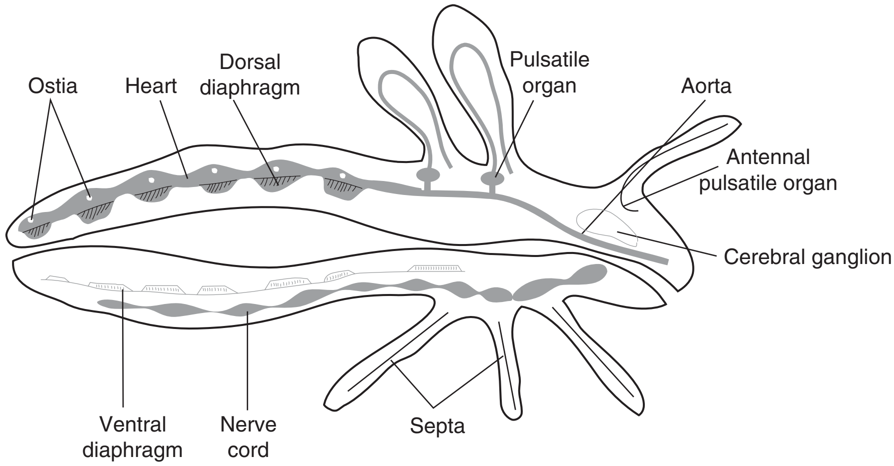
Hemolytic Anemia

(haemolytic anemia) A shortage of red blood cells due to their destruction. This sometimes occurs in the case of envenomization by brown recluse spider.

Hemophagous

Blood feeding. This term is used to describe biting flies, fleas, mites, ticks and mites. Many blood-feeding arthropods vector diseases.

► Vector Capability of Blood Sucking Arthropods: A Forecasting Matrix



Hemolymph, Figure 28 **Diagram of the components of the insect circulatory system; hemolymph moves through the heart and aorta to the head, filtering back through the body cavity and back into the heart via the ostia. Pulsatile organs assist in moving hemolymph through the appendages, especially the wings. (adapted from Chapman, The insects: structure and function).**

Henicocoridae

A family of bugs (order Hemiptera, suborder Pentamorpha).

► Bugs

Henneguy, Louis Félix

Félix Henneguy was born in Paris on March 18, 1850. He studied medicine, was an assistant in physiology in Montpellier (1871–1875) and earned a doctorate in medicine there. He moved to Paris in 1881 and became a preparator in comparative embryology at the Collège de France. He earned a doctorate in science in 1888. In 1900 he became a professor of comparative embryology. In 1907 he was elected member of the Academie de Médecine, and in 1908 of the Academie des Sciences. His other interest, in entomology, led to his (1904) book "Les insectes" which emphasizes morphology and embryology. He also contributed some shorter entomological papers. He died on January 28, 1928.

Reference

Howard LO (1928) Obituary. Entomol News 39:136

Hennig, Willi

Willi Hennig was born in Durhennersdorf, Germany, on April 20, 1913. As a youth, he collected beetles and butterflies, was interested in birds and reptiles, started a herbarium, and liked to visit the zoological museum in Dresden. In 1932, he entered Universität Leipzig to study zoology, botany and geology. He graduated in 1936, having written a thesis on the copulatory organ of cyclorraphous Diptera, and also having published eight papers. He trained briefly at the zoological museum in Dresden, then went to the Deutsche Entomologische Institut in January 1937. By 1939 he had published some 41 papers, most of them on flies. But, in the spring of 1939, he was drafted into the German army, in which he served as infantryman and was wounded. Next, he was sent by the German army to northern Italy, to work in malaria control. Captured by British troops, he continued to work in malaria control. Before he was sent home to Germany, he drafted a manuscript under the title "Grundzüge einer Theorie der phylogenetischen Systematik." Even during the war he published, including about his work in malaria control. After returning to Germany, he spent some months in several cities, including 13 months at Universität Leipzig, until in April 1947 he was able to return to the Deutsche Entomologische Institut in Berlin. He continued to work on his manuscript on larval forms of Diptera, which eventually was published (beginning in 1948, in three volumes) as "Die Larvenformen der Dipteren." He worked some more on his "Grundzüge einer Theorie…" and then published it in 1950. Numerous other publications followed, but then the government of East Germany in 1961 built a wall across the city of Berlin. Hennig could no longer travel from his home in West Berlin to the institute in East Berlin. Instead of emigrating to what was then the communist country of East Germany, he resigned from his job, and taught for 2 years at the Technische Universität in Berlin. Then, he moved with his family to Ludwigsburg (West Germany) in 1963. He resumed an earlier interest in fossil insects, and published (1964–1972) 17 papers on Diptera from Baltic amber and three on fossils from Lebanese amber. The insight this gave him resulted in his (1969) book "Die Stammesgeschichte der Insekten," translated (1981) to English as "Insect phylogeny." Meanwhile, his "Grundzuge…" had been translated to English as (1966) "Phylogenetic systematics," whose translation and concomitant editing did not please Willi. A German edition, truer to its author' s intent, was published (1982) as "Phylogenetische Systematik." He continued working on taxonomic revisions of flies of the palearctic region, and published works on the families Muscidae (1955–1964) and Anthomyiidae (1966–1976) in Lindner's multivolume work "Die Fliegen der palaearktischen Region," which were his 13th and 14th contributions to this work. He was appointed associate professor at Universität Tübingen in 1970, and gave lectures there, and he was co-editor of the journal Zeitschrift für Morphologie der Tiere/Zoomorphologie. In his last year, he was working on a revised edition of "Die Larvenformen der Dipteren." He had a very important influence on biology as a whole because of his phylogenetic theory, even taking into account his dissatisfaction at its translation into English. He died on November 4, 1976, survived by his always-supportive wife and their three sons.

References

Kuhne WG (1978) Willi Hennig 1913–1976: Die Schaffung einer Wissenschaftstheorie. Entomol Germanica 4:374–376

Schlee D (1978) In Memoriam Willi Hennig 1913–1976. Eine biographische Skizze. Entomol Germanica 4:377–391

Hepialidae

A family of moths (order Lepidoptera). They commonly are known as ghost moths and swifts.

► Ghost Moths
► Butterflies and Moths

Heptageniidae

A family of mayflies (order Ephemeroptera).

► Mayflies

Heptapsogastridae

A family of chewing lice (order Phthiraptera).

► Chewing and Sucking Lice

Herbaceous Vegetation

Plants with soft, not woody, stems that die back annually. (contrast with woody vegetation)

Herbicide

A pesticide used to control weeds.

Herbivore

Animal that consumes plant tissue. A phytophage. (contrast with carnivore)

Herbivory

Feeding by insects on plant parts (= phytophagy, though herbivory can be more narrowly defined as feeding on herbage [grass and other low-growing plants, not trees]). Such animals are said to be herbivorous or herbivores.

► Phytophagy
► Food Habits of Insects
► Allelochemicals
► Plant Secondary Compounds and Phytophagous Insects
► Graminivory
► Granivory
► Folivory

Herman, Ottó

GEORGE HANGAY
Narrabeen, NSW, Australia

Ottó Herman was born on June 26, 1835 at Reznóbánya, in Zólyom Shire, Hungary. He was introduced to natural sciences, especially the study of birds, at an early age, as his father was a medical practitioner and keen amateur ornithologist. However, the 1848 Hungarian Revolution and freedom fight against the Austrian Empire interrupted young Ottó's formal studies. Probably he wasn't the best of students anyway, because shortly after the revolution, his father decided that scholastic life wasn't the way for his son, who continued his career as a locksmith's apprentice. Later he went to

Vienna and enrolled in the polytechnic college, but upon the death of his father, once again he discontinued his formal studies. This didn't mean that his interest in natural history dwindled, rather the contrary, he begun to educate himself by autodidactic methods and soon built up a reputation as an outstanding naturalist, versed in many aspects of zoology, botany and ethnography. In 1875 he was appointed as assistant curator of the Hungarian National Museum's zoological collections. By then he was immersed in the research of spiders, and between 1876 and 1879 he published his major entomological work: "The Spider Fauna of Hungary," in three volumes. In 1877 he founded a journal entitled "Natural History Notebooks" (Természetrajzi Füzetek). He remained the editor of this journal for 10 years, during which it became one of the most popular scientific publications of the country. In 1888 he embarked on a North European and Sub-Arctic expedition, following the route of migratory birds. He passed away on December 27, 1914. Ottó Herman produced eminent works in a number of scientific disciplines. Beside entomology, he explored the bird and fish fauna of Hungary, conducted ethnographical studies, directed palaeontologic and historical excavations, and initiated the establishment of nature reserves and the protection of the natural environment. He produced 14 books and a great number of scientific articles. He is regarded as one of the most outstanding pioneers of natural history studies in Hungary.

References

Balázs D (ed) (1993) Magyar utazók lexikona. Panoráma. Budapest, Hungary

Lambrecht K (1920) Herman Ottó. Az utolsó magyar polihisztor élete és kora. Budapest, Hungary

Hermaphrodite

An individual bearing the features or characteristics of both sexes. Although common among some invertebrates, hermaphroditism does not occur in insects.

Hermatobatidae

A family of bugs (order Hemiptera). They also are known as coral treaders.

► Bugs

Herrich-Schäffer, Gottlieb August

Gottlieb Herrich-Schäffer, son of a medical doctor, was born in Regensburg, Germany, on December 17, 1799. He was influenced in his early interest in natural history by his great uncle. By 1817 he had formed a collection of Lepidoptera and other insects. In 1818 he entered Universität Würzburg, and obtained a medical degree in 1821. However, he used his holidays to travel to Erlangen in 1919, to Heidelberg in 1820, to Berlin in 1821, and to Munich in 1822 to further his entomological interests with time spent in the field. In 1824 he began practicing as a medical doctor in public service and, at the retirement of his father from such service in Regensburg, he returned there in 1828 to take the vacant position. He occupied this position until his retirement in 1856. In 1832 he befriended C.L. Koch, who was a forestry official for the Regensburg region (and entomologist), learned to engrave, and provided 960 engraved plates for a supplement to Panzer's "Faunae insectorum germaniae initia." He continued Hübner's "Sammlung europäischer Schmetterlinge." In 1835 he published the first part of his own "Nomenclator entomologicus." In 1843 he published the first part of his greatest work, "Systematische Bearbeitung der Schmetterlinge von Europa," with Geyer as its illustrator, completed in 1856 in six volumes. Other works followed, including works on exotic species such as "Die Schmetterlinge der Insel Cuba." He used to lead insect-collecting expeditions composed of family members and friends in the countryside surrounding Regensburg. He died in Regensburg on April 14, 1874, leaving a son and four daughters.

Reference

Hofmann O (1874) Necrolog. EntomolZtg (Stettin) 35:277–284

Hesperiidae

A family of butterflies (order Lepidoptera). They commonly are known as skipper butterflies.

► Skipper Butterflies
► Butterflies and Moths

Hesperinidae

A family of flies (order Diptera).

► Flies

Hessian Fly, *Mayetiola destructor* (Say) (Diptera: Cecidomyiidae)

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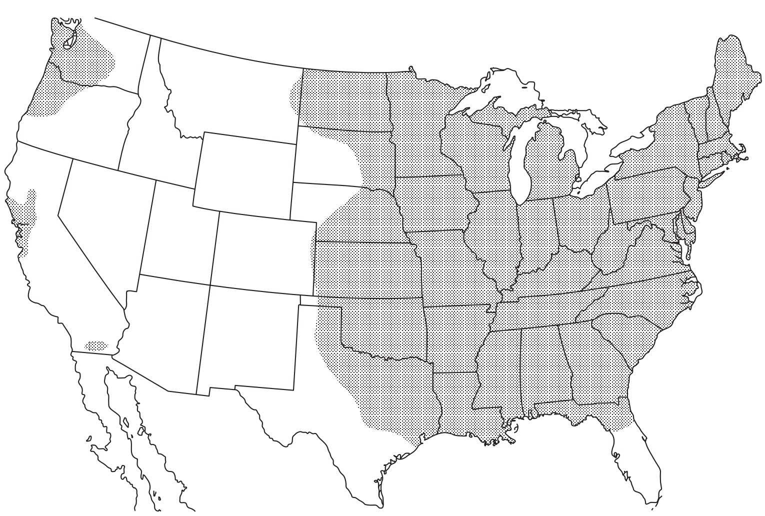
The Hessian fly, *Mayetiola destructor*, is a destructive pest of wheat and occurs in most wheat-growing areas of the United States (Fig. 29) and most other production areas of the world. It is thought to be endemic to the southern Caucasus and southwest Asia, the center of origin of the genus *Triticum* L., and to have dispersed to Europe, North Africa and North America. While chiefly injurious to wheat, at times it causes some damage to barley, rye and triticale. It also can be found on wild grasses such as *Agropyron repens* (L.), *Elmus virginicus* L., *Hordeum pusillum* Nutt., and *Aegilops* sp., which may serve as hosts when wheat is not available. The insect received its common name from Americans when it was found infesting wheat on Long Island, New York, in 1779, and it was believed Hessian mercenaries serving with Lord Howe's army 3 years earlier had brought the pest from Europe in bedding straw.



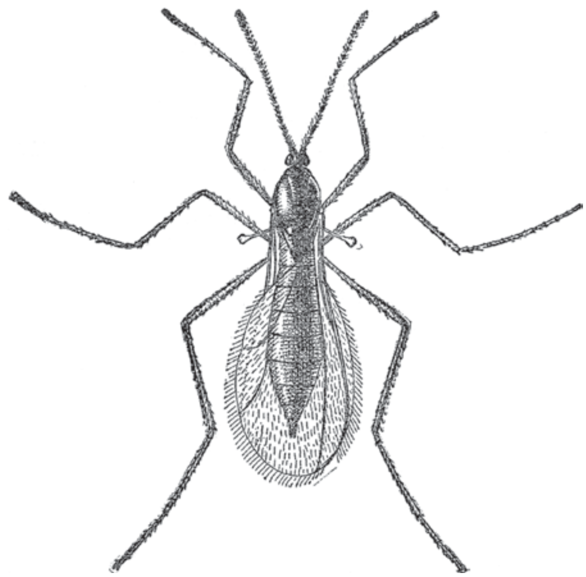
Hessian Fly, *Mayetiola destructor* (Say) (Diptera: Cecidomyiidae), Figure 29 Distribution of the Hessian fly within the United States. (from Foster, J. E., P. L. Taylor, and J. E. Araya. 1986. The Hessian fly. Department of Entomology Agricultural Experiment Station Bulletin 502, Purdue University, West Lafayette, Indiana.)

Interestingly, the insect was not reported in England until 1886. It has been recorded in Russia from 1847 onward, especially in the Ukraine, and has been recognized as a serious pest of wheat in Morocco, Algeria and Tunisia since the early 1900s.

Life History

As with other flies, development in the Hessian fly has four life stages: egg, larva, pupa and adult. Adults are small dark to black midges about 3 mm long and live for 2–3 days after they emerge. Females emit a sex pheromone to attract males with mating taking place soon after emergence. As in other members of the Cecidomyiidae, individual Hessian fly females generally produce all male or all female progenies, with the sex of a progeny determined by the female. Shortly after mating, females begin to deposit eggs in the grooves along the veins on the upper surface of the leaves of wheat. The eggs are glistening-red, cylindrical and about 0.5 mm long. They hatch in 3–7 days depending on temperature, and the larvae crawl down the leaves to feed near the crown in seedlings or at the nodes during culm elongation. First-instar larvae also are red but begin to turn white within a few days. Second-instar larvae are white, cylindrical and about 4 mm long when mature. The cuticle of the mature larva hardens and turns a dark brown forming a puparium, which is commonly called a "flaxseed" because it resembles the seed of flax. Pupation occurs within the puparium.

In northern winter wheat areas, there are typically two generations a year. In the fall, adults (Fig. 30) that emerge from infested wheat stubble infest volunteer wheat or early fall-seeded fields. Larvae in the fall generation are found in the leaf sheath at, or near, the crown. With the onset of cold weather, the mature larva forms a protective puparium in which it over-winters. In the spring, these larvae pupate within the puparium and adults emerge and infest wheat plants about the time they begin to joint. Larvae in the spring generation are found above the nodes (frequently the second node) under the leaf sheaths. Larvae pass the summer within the puparia in dry wheat stubble. In late summer or fall, the larvae pupate and adults emerge to infest volunteer or early-seeded wheat. In southern winter wheat areas, supplementary broods can develop either before or after the main fall generation, or after the main spring generation. In Canada and the northern spring wheat areas of the United States, only one annual spring generation occurs.



Hessian Fly, *Mayetiola destructor* (Say) (Diptera: Cecidomyiidae), Figure 30 **Hessian fly: adult female. (from Webster, F. M. 1915. The Hessian fly. USDA Farmers' Bulletin 640 – author's illustration.)**

Injury to Wheat

Damage in wheat is due entirely to feeding by larvae. In fall infestations, larval feeding results in stunting (Fig. 31) and development of a dark green color in infested primary culms or tillers and can lead to the death of seedling plants. In spring infestations, larval feeding prevents normal elongation of internodes, transport of nutrients to developing grain and results in lodging at the nodes. The mouthparts of larvae are highly specialized mandibles that are thought to inject salivary secretions into the plant. These secretions are believed to contain enzymes that inhibit plant growth, increase the permeability of cell membranes, and soften cell walls.

Hessian Fly, *Mayetiola destructor* (Say) (Diptera: Cecidomyiidae), Figure 31 **Fall-infested wheat seedling showing typical stunting. A non-infested tiller is shown on the left for comparison. (from Foster, J. E., P. L. Taylor, and J. E. Araya. 1986. The Hessian fly. Department of Entomology Agricultural Experiment Station Bulletin 502, Purdue University, West Lafayette, Indiana – illustrator G. Safranski.)**

While economic threshold levels have not been established for Hessian fly infestations, evaluation of injury and loss of winter wheat grain yield indicates significant damage occurs when fall infestations exceed 5–8% of tillers, or when spring infestations exceed 13–20% of stems. When 10% of tillers are infested in the fall or 20% of stems in the spring, grain yield loss is estimated at about 250 kg/ha. Historically, the Hessian fly has caused losses estimated at $100 million in a single year. Recently, losses in Georgia were estimated at $4 million in 1986, and at $28 million in 1989. Damage from Hessian fly also has been reported in other southern states; in Texas, losses estimated at $5 million were reported in 1984.

Control

Because many biotic and abiotic factors regulate the abundance of the Hessian fly, when and where economic infestations may occur is not easily predictable. Thus, control measures for Hessian fly are primarily preventive rather than remedial. Prevention of infestation is achieved through (i) planting resistant wheat varieties, (ii) delaying seeding of winter wheat to escape fall infestation, (iii) destruction of volunteer wheat. The use of resistant varieties is the most economically and environmentally sound method of control, and has been employed for the past 50 years. Insecticides are seldom used for control of Hessian fly. Once larvae have entered the leaf sheath, a systemic insecticide is required, and research has demonstrated that resistant wheat varieties are as effective in controlling damage as application of systemic insecticide at seeding. If resistant varieties are not seeded, infestations can be reduced by cultural practices (i.e., delayed planting and destruction of volunteer wheat). In much of the United States cultural practices are effective in reducing infestations in winter wheat. However, in the southern United States, delayed planting is not as effective as it is in northern winter wheat areas because oviposition and development of larvae can occur throughout the winter.

Hessian fly Resistance in Wheat

Resistance to Hessian fly has been identified in common and durum wheat, wild wheat and rye. Resistance in these sources is expressed as larval antibiosis; larvae die within 3 days and do not injure the wheat. Resistance generally is controlled by single genes that are partially to completely dominant. To date, twenty-nine major genes controlling Hessian fly resistance in wheat, designated *H1* through *H29*, have been described. Other genetic factors for resistance are those derived from Kawvale and Marquillo wheat. The genetic control of resistance in Kawvale has not been determined. Several recessive genes might control the resistance in Marquillo. However, recent work has suggested the resistance is controlled by a temperature-sensitive, partially dominant gene designated *H18*. The molecular/biochemical basis of resistance in wheat to the Hessian fly has not been determined for any gene. However, cytological studies support the hypothesis that a hypersensitive reaction is the phenotypic basis of resistance in the Hessian fly/wheat interaction and involves "recognition" of an avirulence gene product or process.

Hessian fly Biotypes

The existence of life types or "biotypes" of Hessian fly, capable of infesting resistant wheat, has been known for many years. These biotypes describe populations that vary in host-adapted alleles. Virulence, the ability of Hessian fly larvae to survive on and stunt plants, is controlled by recessive genes at single loci and operates on a gene-for-gene basis with resistance. Presently, sixteen defined biotypes, Great Plains (GP) and A through O, have been identified in field populations by their reaction in a differential set of four wheat genes for resistance *H3*, *H5*, *H6* and *H7/8*. The Great Plains Biotype is avirulent with respect to each of these genes for resistance, while Biotype L is virulent on each of these genes.

Management and durability of resistance

The development of virulent biotypes of the Hessian fly capable of surviving on and stunting formerly resistant wheat is the greatest threat to the durability of resistance. Several factors in the biology of the Hessian fly can affect the development of virulent biotypes. Dispersal by adults is limited; adults are short-lived (2–3 days) and oviposition by females begins one to three hours after mating, limiting time spent in dispersal. These factors restrict local gene flow, which can increase the probability of recessive mutations for virulence becoming homozygous in a population. In opposition to this are the observations that virulent larvae can affect the expression of resistance in wheat and allow avirulent larvae that co-infest to survive. Survival of avirulent larvae would reduce selection pressure for virulence in populations and slow the increase in frequency of virulence alleles associated with selection from resistant cultivars.

The deployment strategy implemented also can affect the durability of resistance genes to Hessian fly in wheat. A sequential release program has been utilized to date. Under this regime, a single gene is released in cultivars and used until it begins to lose effectiveness in the field (generally 6–10 years), at which time new biotype specific resistance genes are released. Another strategy is to stack or pyramid multiple resistance genes. This strategy has not been utilized to date because of a lack of suitable markers to monitor incorporation of multiple resistance genes; however, the development of molecular markers will allow implementation of this strategy.

► Wheat Pests and their Management

References

Buntin GD (1999) Hessian fly (Diptera: Cecidomyiidae) injury and loss of winter wheat grain yield and quality. J Econ Entomol 92:1190–1197

Cartwright WB, Jones ET (1953) The Hessian fly and how losses from it can be avoided. USDA Farmers' Bulletin 1627

Gallun RL (1977) Genetic basis of Hessian fly epidemics. Ann NY Acad Sci 287:223–229

Grover PB, Shukle RH, Foster JE (1989) Interactions of Hessian fly (Diptera: Cecidomyiidae) biotypes on resistant wheat. Environ Entomol 18:687–690

Painter RH (1951) Insect resistance in crop plants. Macmillan, New York, NY, 520 pp

Ratcliffe RH, Hatchett JH (1997) Biology and genetics of the Hessian fly and resistance in wheat. In: Bondari K (ed) New development in entomology. Research signpost. Scientific Information Guild, Trivanduram, India, pp 47–56

Ratcliffe RH, Cambron SE, Flanders KL, Bosque-Perez NA, Clement SL, Ohm HW (2000) Biotype composition of Hessian fly (Diptera: Cecidomyiidae) populations from the southeastern, midwestern, and northwestern United States and virulence to resistance genes in wheat. J Econ Entomol 93:1319–1328

Heterobathmiidae

A family of moths (order Lepidoptera). They commonly are known as Valdivian archaic moths.

► Valdivian Archaic Moths

► Butterflies and Moths

Heteroceridae

A family of beetles (order Coleoptera). They commonly are known as variegated mud-loving beetles.

► Beetles

Heteroecious Life Cycle

A life cycle where there is alternation of host plants by insects (generally aphids) through the season. In species with this type of life cycle, typically the autumn, winter and spring are spent on a woody (primary) host plant and summer is spent on an unrelated herbaceous (secondary) plant. (contrast with autoecious life cycle)

► Aphids

Heterogamy

Alternation of bisexual and parthenogenetic reproduction.

Heterogastridae

A family of bugs (order Hemiptera, suborder Pentamorpha).

► Bugs

Heterogynaidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Heterogynidae

A family of moths (order Lepidoptera) also known as Mediterranean burnet moths.

► Mediterranean Burnet Moths

► Butterflies and Moths

Heteronemiidae

A family of walkingsticks (order Phasmatodea). They commonly are known as common walkingsticks.

► Walkingsticks and Leaf Insects

Heteroptera

Sometimes considered to be suborder of Hemiptera, containing the "true bugs."

► Bugs

Heterosis

Also known as hybrid vigor.

Heterotroph

An organism that obtains energy and other materials by eating other organisms. (contrast with autotroph)

Heterothripidae

A family of thrips (order Thysanoptera).

► Thrips

Heterozygosity

Having a pair of dissimilar alleles at a locus; a measure of genetic variation in a population estimated by a single locus or an average over several loci.

Heterozygous

A diploid cell or organism that contains two different alleles of a particular gene.

Hewitt, Charles Gordon

Charles G. Hewitt was born near Macclesfield, England, on February 23, 1885. He obtained a B.Sc. from Manchester University in 1902, a M.Sc. in 1903, and then worked at that university as a lecturer until 1909, when he received a D.Sc. degree and emigrated to Canada. His move to Canada was well timed, as the position of Dominion Entomologist was vacant. Hewitt had demonstrated considerable potential while in England, and despite considerable misgivings about his level of experience, he was named Dominion Entomologist of Canada in 1909, and served in this capacity until 1916. Along they way, he played a key role in passage of the "Destructive Insect and Pest Act" of 1910, which allowed Hewitt to add staff in the form of inspectors and field officers, and to establish entomological field stations at nine points from coast to coast. He also published an important treatise on "House flies and how they spread disease" in 1912, and "The house fly, *Musca domestica* Linn." in 1914, and served as an officer in several scientific societies. His position was enlarged to "Dominion Entomologist and Consulting Zoologist of Canada" in 1916, and he continued in this capacity until 1920. His interests and expertise extended well beyond insects, and he also was active in natural history and ornithology organizations. He died prematurely at Ottawa, Canada, on February 29, 1920. In 1921, his book titled "Conservation of the wild life of Canada" was published posthumously, which proved to be his most renowned contribution to science. Most importantly, during his brief tenure Hewitt had developed economic entomology from a small division to an important branch of the Department of Agriculture.

Hexapoda

A superclass in the phylum Arthropoda containing animals with three major body segments and three pairs of walking legs. Hexapoda consists of the class Insecta, the insects, and the class Entognatha, the collembolans, diplurans, and proturans.

Hibernaculum

An overwintering retreat in which an early-instar larva retreats or diapauses during the winter. It is usually made of silk, but may consist of other materials as well.

Hilarimorphid Flies

Members of the family Hilarimorphidae (order Diptera).

► Flies

Hilarimorphidae

A family of flies (order Diptera). They commonly are known as hilarimorphid flies.

► Flies

Hilltopping

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When you are small, locating a potential mate can be a challenge. Insects employ many strategies of mate finding, from swarms to individual territories to specific landmark mating strategies. Landmark mating strategies involve species setting up mating aggregations over any conspicuous marker. This can range from a rock to a tuft of grass, a road, a stream course, a canyon, a bog, an emergent tree (taller than the others) or a hilltop. Although this article focuses on the latter, this phenomenon is essentially a continuum. The difference between simple landmarks and hilltops is that simple landmarks typically support only a single species. However, emergent trees in rainforests are likely immensely important for landmark mating species. Unfortunately, few data are available on this. Hilltops are significant landmarks in that they support many species, often hundreds or in rare cases even thousands. Hilltops range from massive rocky mountain tops over 4,000 m high to small hummocks in flat country. These hummocks can function as full-fledged hilltops, particularly if they have some conspicuous landmark on top. A small rise of land in an otherwise flat area in Western Australia exemplifies this (Fig. 32); a shelter at the top of the rise serves as a major hilltopping site for many species and families of flies, wasps and butterflies.

Arguably the best hilltop (most diverse) anywhere in the world is in Queensland, Australia. Mount Moffatt (1,097 m, 25°03’35” S, 148°02’38” E) is a distinctive, conical hilltop, rising about 350 m above the surrounding land (Fig. 32). It is somewhat of a mystery what makes one hilltop better than another. Despite this, Mount Moffatt gives us some clues.

The height above the surrounding land is not too intimidating to exclude many species, while the hilltop is distinctive and visible for large distances. The summit is focused and not very large (about 100 m by 20 m), is variably vegetated (with a rocky open north end, and shaded south end) and the habitat around the hilltop is excellent (in Carnarvon National Park). Further, no other high points compete for hilltopping insects within a several kilometer radius. Hilltops covered entirely by tall trees may also be important but it is difficult for entomologists to access these habitats.

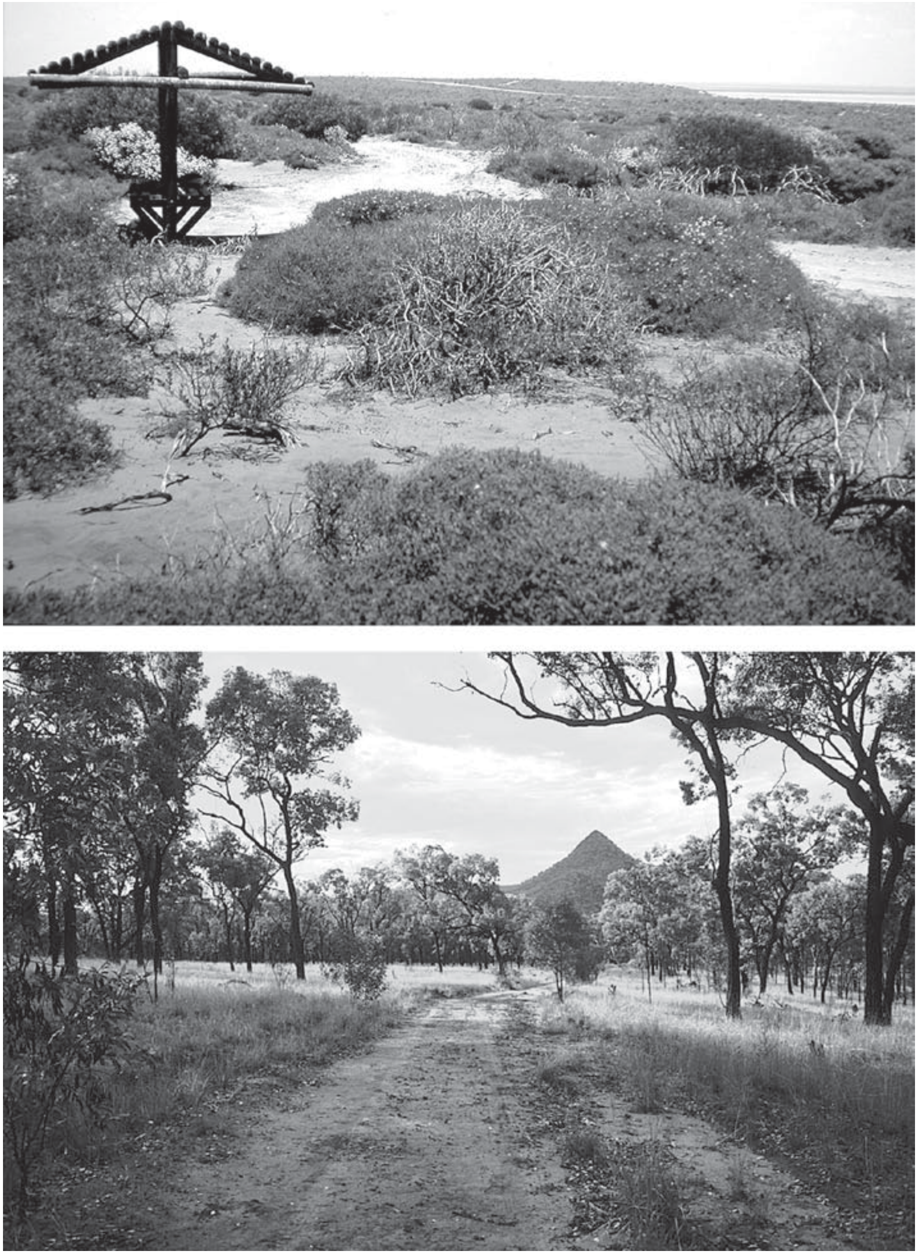
The diversity of insects using Mount Moffatt as an aggregation site almost certainly numbers well over 1,000 species. Over the course of 3 days between October 10 and 13, 2002 (early in the austral spring), three entomologists collected 104 species of hilltopping Tachinidae (Diptera) on Mount Moffatt. Based on this, there are almost certainly over 200 species of this family alone using Mount Moffatt as a hilltopping aggregation site. Pipunculidae (Diptera) diversity is also high on Moffatt and exceeds 50 species (Fig. 33). No other groups have been inventoried, but other abundant and diverse groups using Mount Moffatt include: Diptera: Anthomyiidae, Bombyliidae, Calliphoridae, Muscidae, Pipunculidae, Sarcophagidae, Syrphidae, Tabanidae and Tachinidae; Hymenoptera: Ichneumonidae; and Lepidoptera: Nymphalidae. More information on hilltopping taxa is included below.

Hilltopping Taxa

The dominant orders of insects represented on hilltops are Diptera, Hymenoptera, and Lepidoptera. Within Diptera, the following families have been found to have hilltopping species: Acroceridae, Agromyzidae, Anthomyiidae, Anthomyzidae, Apioceridae, Athericidae, Bibionidae, Bombyliidae, Calliphoridae, Conopidae, Culicidae, Empididae s.l., Fanniidae, Ironomyiidae, Lonchaeidae, Muscidae, Mydidae, Nemestrinidae, Oestridae, Pelecorhynchidae, Phoridae, Pipunculidae, Platypezidae, Rhagionidae, Sarcophagidae, Scenopinidae, Sepsidae, Simuliidae, Sphaeroceridae, Stratiomyidae, Syrphidae, Tabanidae, Tachinidae, and Therevidae (Fig. 33). Most work on hilltopping of Lepidoptera has focused on butterflies in the following families: Hesperiidae, Lycaenidae, Nymphalidae, Papilionidae, and Pieridae. Within Hymenoptera, all families of sawflies appear to hilltop. Braconidae, Formicidae, Ichneumonidae and some Sphecidae are also important components of the hilltopping diversity.

Definition of Hilltopping

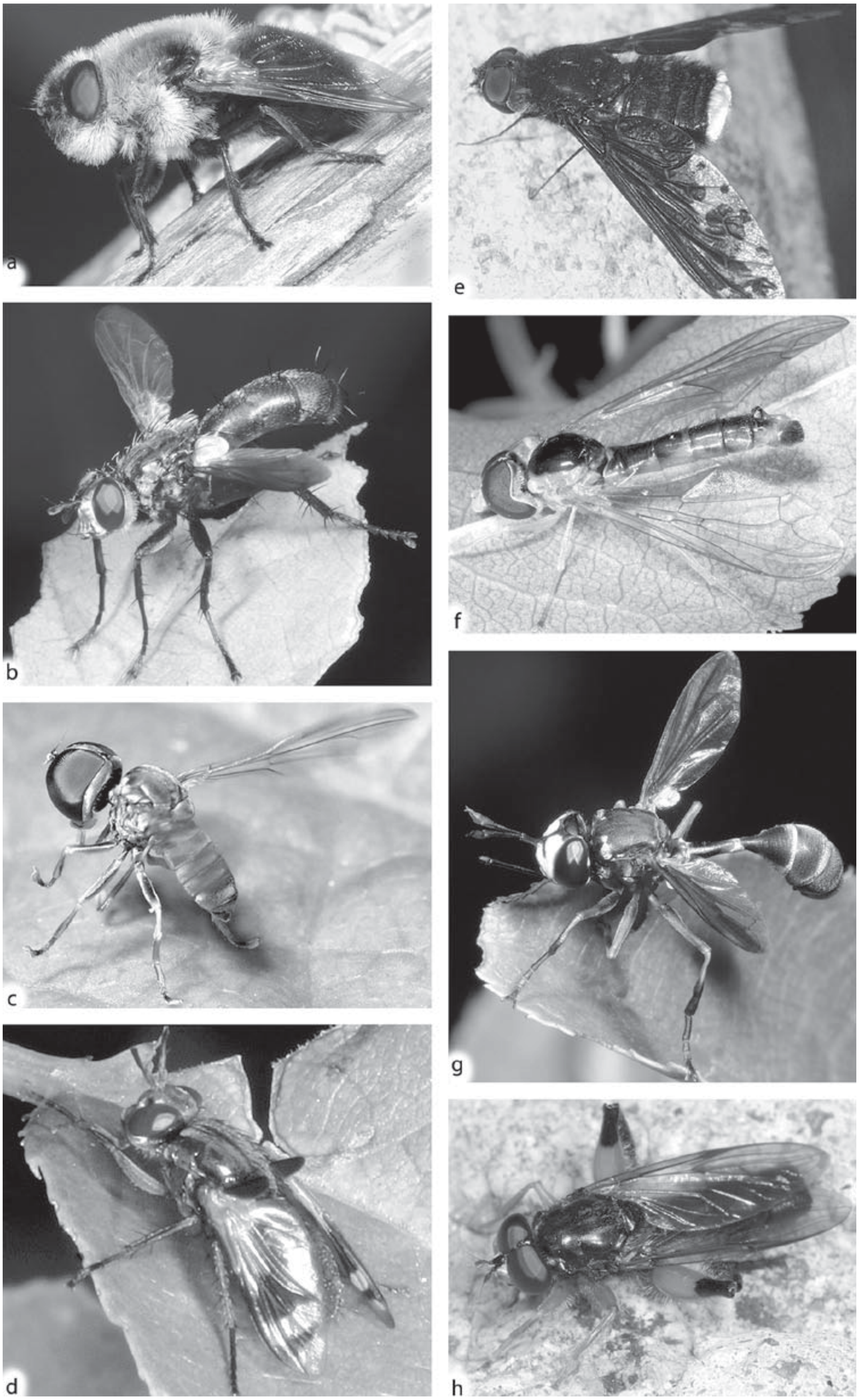
Hilltopping is a phenomenon apparently restricted to insects in which males and virgin or multiple-mating females instinctively seek a topographic summit to mate. Larval foodplants or hosts are typically not present on the hilltop and may be a



Hilltopping, Figure 32 (*above*) **A shelter at the top of a small rise of land in an otherwise flat area in Western Australia serves as a major hilltopping site for many species and families of flies, wasps and butterflies (Denham, Western Australia (25°54′33″ S, 113°31′54″ E). (*below*) Arguably the best hilltop in the world is Mount Moffatt in Queensland, Australia (1,097 m, 25°03′35″ S, 148°02′38″ E). This distinctive, conical hilltop, rising about 350 m above the surrounding land is a model hilltop in terms of shape, vegetation and proximity to other hilltops.**

considerable distance away. Hilltopping is a widespread mating system among insects and is focused on groups that are rare, parasitic, predaceous on ephemeral prey, or whose larval foodplants are scattered or rare. Mate-finding is difficult under these conditions.

Note that some species that form behavioral aggregations do so at hilltops (e.g. *Forficula lurida*



Hilltopping, Figure 33 **(Continued)**

Fischer (Dermaptera) and some species of Coccinellidae (Coleoptera)). This prelude to communal hibernation is not considered hilltopping as defined here as in such cases sex ratios are typically 1:1 and no mating or feeding activity typically occurs.

Hilltopping Behavior

General

Typically, there is a very high proportion of male insects on hilltops. This is explained by the persistence of males in such areas (see below) and the brief visits by females. Arriving females typically quickly select a mate and leave the summit. Once they have mated, males return to the summit while mated females typically never return. Males often select bare or open areas from which they can see approaching females best.

Studies of butterflies reared and released in different sites suggest that hilltopping species are genetically programmed to seek out hilltops. Once there, many species seem to be similarly predisposed to seek out very specific places on the hilltop or otherwise partition the hilltop by their behaviors. For example, three similar species of *Chalcosyrphus* (Diptera, Syrphidae) occur on a hilltop in Rigaud, Quebec, Canada (45°27'59" N, 74°19'35" W). These species partition the hilltop by their different behaviours. *Chalcosyrphus plesia* (Curran) hovers low over rocks near the summit, *C. curvaria* (Curran) typically sits on rocks around the summit and *C. vecors* (Osten Sacken) perches on the leaves of Serviceberry (*Amalanchier* sp.) or Red Oak (*Quercus rubra*) near the summit.

Hilltopping, Figure 33 **Collage of hilltopping flies (Insecta, Diptera): (a) *Cephenemyia phobifer* (Clark) (Oestridae). Voucher #CNCD144 (Canadian National Collection of Insects-CNC, Ottawa). This rarely observed fly is common on Mount Rigaud (Quebec, Canada) where this photo was taken. Bot flies are often found on hilltops despite being found rarely elsewhere (unless they are reared from their hosts). (b) *Cylindromyia* sp. (Tachinidae). Voucher #CNCD354. Tachinidae form a major component of most hilltopping insects. This species is common on Mount Rigaud. (c) *Eudorylas* sp. (Pipunculidae). Voucher in University of Guelph Insect Collection (no unique number) (photo by S.A. Marshall). Big-headed flies are often abundant on hilltops. (d) *Euthera tentatrix* Loew (Tachinidae). Voucher in CNC (no unique number). This attractive little fly is rarely collected away from hilltops such as Mount Rigaud (where this one was photographed). (e) *Anthrax maculatus* Macquart, (Bombyliidae). Voucher in University of Queensland Insect Collection (no unique number). Common on hilltops in Eastern Australia. This specimen was photographed on Mount Wellington in Tasmania. (f) *Nephrocerus acanthostylus* Skevington (Pipunculidae). Voucher #JSS16983 (in CNC). This enigmatic genus of big-headed flies is rarely collected anywhere. Mount Rigaud has hosted three of the six Nearctic species, including the specimen in the photo. Two additional species have been found at a nearby hilltop in Gatineau. This illustrates how effective hilltop collecting can be to survey many groups of insects, particularly parasitoids such as Conopidae, Pipunculidae and Tachinidae. (g) *Physocephala marginata* (Say) (Conopidae). Voucher #CNCD347. This is another family of flies that can often be found most readily on hilltops. Photograph taken on Mount Rigaud. (h) *Chalcosyrphus curvaria* (Curran) (Insecta, Diptera, Syrphidae) is one of three closely related flower fly species that partition hilltops in northeastern North America by subtle choices in habitat and differences in behavior. *Chalcosyrphus curvaria* (Curran) typically sits on rocks around the summit as in this photo taken at Mount Rigaud, Quebec, Canada (45°27'59" N, 74°19'35" W). *Chalcosyrphus plesia* (Curran) hovers low over nearby rocks and *C. vecors* (Osten Sacken) perches on the leaves of serviceberry (*Amalanchier* sp.) and red oak (*Quercus rubra*) in the same vicinity near the summit.**

Effectiveness of Hilltopping for Males Seeking Mates

In theory, if virgin females move randomly upslope, males patrolling or perching near the summit should have a higher probability of mating success than those dispersed throughout the vegetation below. In years of low population density it should be adaptive if both sexes tend to move uphill toward landmarks. However, in years of high population density the numerous males that find their way to the ridge would compete heavily for a few females since most would be mated on their uphill flight. Thus the smaller the population, the lower the chance of virgin females encountering males before reaching the hilltop and the more adaptive the behavior becomes for the males that join the hilltopping aggregation.

Measuring the adaptive advantage of hilltopping is difficult as males on summits likely face considerable additional pressures. The energy allocated to hilltopping is likely higher than that required by individuals remaining off the summit. Predation rates may also be higher as many predatory insects and birds take advantage of the abundance of prey on hilltops. For example, aerial foraging birds such as swifts and swallows clearly focus on hilltop feeding and many large predatory insects, such as dragonflies (Odonata, Anisoptera) and robber flies (Diptera, Asilidae), also congregate there to feed. However, given that this may be the only way for some insects to find a mate, it is clearly beneficial and has been adopted by a wide variety of insects.

Evidence for Hilltopping

Mark-recapture studies, particularly using butterflies, have garnered considerable evidence supporting a hilltopping strategy as defined here. In one study, about half of the unmated, reared females released 610 m (117 vertical meters) away from a summit, were found on the hilltop within 1 day. Mated females did not go to the summit. In fact, an abnormally high percentage of female butterflies collected on the summit were virgin when compared to those captured elsewhere. The percent virginity for non-hilltop sites was mostly under 10% in contrast to 35–97% of females at the summit which were virgin upon arrival. The apparent scarcity of females at hilltops was due to inconspicuousness of mating pairs and due to the fact that virgins stayed only long enough to mate and non-virgins rarely approached the summit. When arriving at or released on summit, males strongly adhered to it. After copulating, females showed little response to topography.

Mark-release of males of the butterfly *Papilio zelicaon* Lucas away from the hilltop resulted in about 33% returning from varying distances (similar to the rate of recovery of specimens released directly on the hilltop). These males returned from multiple directions and one returned from five km away and flew into a wind to return. When transported further away, they would go to another closer hill; however, there is some evidence that they prefer their own hill when two are similar distances apart (even though both are used by the species). The return speed for four *P. zelicaon* recaptured the same day varied from 14 (no wind) to 42 (strong wind at right angle to motion) meters per minute.

In one study, butterflies were found to fly toward the highest point available. Uphill movement was directed by two cues, the highest location within a distance of 50 m, and the immediate slopes available to the butterfly. This suggests that the highest landmark available in an area is likely to be used for hilltopping, but this is clearly not always the case. For example, in an area of high rocky hills in Tasmania, Australia, the best (most diverse) hilltop was a partly vegetated hill that was hundreds of meters lower than the many surrounding hills (Donaghy's Hill, 42°11'52" S, 145°55'55" E). More work is clearly needed to understand how insects choose specific hilltops and navigate to these summits.

Differences in behavior between males and virgin females have been hypothesized to represent asymmetry in the mate-searching strategy between genders. This may improve the mate-searching algorithm by increasing an insect's chances of meeting the opposite sex of another of its species along the way. In butterfly studies, virgin females were found to perform little searching for males when not on summits whereas males searched for conspecifics everywhere.

Timing and Weather

Hilltopping activity is highest in the morning on sunny, warm days with relatively little wind. Peak flight times are clearly correlated with temperature and humidity. Early morning activity (before 8 am) is marked in very hot, dry climates. Even in moderate climates, the intensity and diversity of hilltoppers declines rapidly after mid-day. A resurgence of activity occurs in some species in the evening although most species do not appear to have daily bimodal activity patterns. Crepuscular and nocturnal species such as *Ormia* (Diptera, Tachinidae) and many moths (Lepidoptera) start to appear at dusk and some may fly all night. Very little research has been conducted on nocturnal hilltopping species. One note describes the observations of someone carrying a lantern up a mountain. No moths were observed except at the very summit where hundreds of moths of many species were sitting everywhere. These insects were there when the observer arrived and were not attracted to his light. This clearly illustrates the unexplored potential of studying nocturnal hilltopping patterns.

The effect of clouds on insect behavior is extremely pronounced on hilltops. Thousands of insects can be flying one minute in the sun, producing a loud hum, when suddenly with the passing of a cloud over the sun, the insects land and the humming stops. As the cloud passes, it is as if the entire hill erupts at once as everything takes to the air simultaneously. The effect of wind and reduced temperature are similar but not as dramatic because of the slower shifts. As wind speed increases, activity moves to the leeward side of the hilltop and remains focused there until the wind reaches too high a speed and all activity ceases.

Some species are active throughout the entire period of peak activity while others have clear arrival and departure times throughout the day. Research on the diversity of hilltopping taxa thus necessitates long hours over many days. Individual species abundance, particularly of parasitoids, also varies considerably from year to year. Studies that span several years may give a much more representative picture of diversity at a particular summit.

Distances Covered

A few mark-recapture studies have attempted to determine how far hilltopping individuals travel. Much remains to be learned here, but it appears that some species travel considerable distances to suitable hilltops. Two species of ants, *Formica subnuda* Emery and *Leptothorax muscorum* (Nylander), captured at a hilltop in British Columbia, Canada returned (even against or across the wind) from distances up to 760 m away (the farthest tested). Over 20% of the winged ants released returned to the hilltop from 760 m away.

Minimum distances traveled by hilltopping butterflies from the nearest areas of their foodplants were several thousand vertical feet for *Papilio indra kaibabensis* in Arizona and 1,700 vertical meters for *Pieris callidice* in France.

It is presumed that once animals initiate a hilltopping movement they may persistently fly upwards and cover distances of several kilometers or even tens of kilometers. This remains to be tested.

Site Tenacity

A substantial number of hilltopping males remain for periods of time on a summit on a given day. There is some evidence that some males of some species may spend their entire lives at a particular summit. Mark-release and re-sighting studies have shown that males remain at aggregation sites for life and that there is a shifting of territories from day to day. Roosting males of several species have been found at or near the summit of hills, also supporting the notion that they stay there all of their lives once they have arrived. One marked *Papilio zelicaon* male was seen on a summit on eight different days over a 20-day period. The longest period recorded for an individual was 29 days of one *P. zelicaon* specimen.

Despite the discovery that male insects of some species spend most of their lives on a particular hilltop, it seems unlikely that most species are this sedentary in their behaviors. At night, during hot parts of the day, and on days with poor weather, few diurnal insects can be found anywhere near the summit. Most presumably leave during these times to feed or take shelter somewhere below.

Multiple day site fidelity has been demonstrated in many studies but the reduction in returns over several days always appears to be steep. The fact that even successful territory holders rarely spend more than a single day at a site suggests that males rapidly deplete their energy reserves, experience a very high rate of mortality and/or regularly disperse to different landmark sites. A sex ratio of 2:1 in favor of males reported for *Cuterebra approxima* is hypothesized to offset high male mortality at aggregation sites.

One study conducted more than 20 years after the initial study found individuals of *Cuterebra austeni* occupying the same landmark site. This species used the same perching areas for over two decades. Other unpublished research on tachinid flies has found that this is the case for hundreds of species. This supports the notion that these behaviors are hardwired by instincts that have evolved over millennia.

Survey of Hilltopping Insects

Capture of hilltopping insects typically requires a focused effort at hand netting. This can be difficult because of the high degree of habitat partitioning shown by the species. Three systematists concurrently focusing on Diptera collecting on Mount Moffatt had surprisingly little overlap in 3 days of collecting Tachinidae. This is presumably due to the different search strategies employed by these dipterists. To sample the diversity of a particular group, an effort should thus be made to vary the collecting technique. Trapping is typically ineffective, at least for males. Malaise and pan traps positioned on hilltops catch a very unrepresentative sample of the species present. Presumably this is because males are focused on the task of finding a mate and are not moving far from their chosen sites. Females tend to be picked up in these Malaise traps, likely because they are commuting through the area more than males. Sugaring (spraying a mixture of artificial honeydew (honey, Coca-Cola™ and water) on the leaves of plants) is sometimes effective at attracting the attention of parasitoid flies on hilltops.

Conservation

The contribution of hilltopping to genetic mixing between populations may be of great ecological importance. These aggregation sites may be crucial to the maintenance of populations of many species and their identification could aid in attempts to protect threatened populations. Conversely, efforts to eradicate pests made sparse by control measures could be focused on hilltops but the potential effects on other species would have to be evaluated before attempting such measures.

Very little effort has been focused on conservation of hilltops, even in parks. Microwave towers and other communication devices are often installed even in protected areas on hilltops. Critical evaluation of these sites is needed before their development proceeds. The loss of any hilltop could endanger a particular, or even numerous, species. The loss of a significant hilltop such as Mount Moffatt that supports over 1,000 species of hilltopping insects could have tremendous impacts on the insect fauna of an area.

Integrated pest management often explores habitat matrices available in agricultural settings with the intention of increasing habitat for beneficial insects; however, these strategies have not explored the importance of hilltops. Given the critical importance of this mating strategy to many parasitoid insects, more attention should be given to these structures in the future.

References

Alcock J (1987) Leks and hilltopping in insects. J Nat Hist 21:319–328
Alcock J, Gwynne DT (1991) Evolution of insect mating systems: the impact of individual selectionist thinking. In Bailey WJ, Ridsdill-Smith R (eds) Reproductive behaviour of insects: individuals and populations. Chapman and Hall, London, UK, 356 pp
Alcock J, Smith AP (1995) Landmark-defense and scramble competition mating systems in two Australian tachinid flies (Diptera). J Kansas Entomol Soc 68:85–94
Alcock J, Kemp DJ (2004) Long-term stability in the mating system of the bot fly *Cuterebra austeni* (Cuterebridae). J Insect Behav 17:273–280
Baughman JF, Murphy DD, Ehrlich PR (1988) Population structure of a hilltopping butterfly. Oecologia 75:593–600
Beall G (1953) Congregation of butterflies at hilltops. Lepid News 7:41–43
Britton DR, New TR, Jelinek A (1995) Rare Lepidoptera at Mount Piper, Victoria – The role of a threatened butterfly community in advancing the understanding of insect conservation. J Lepid Soc 49:97–113
Dodson G, Yeates D (1990) The mating system of a bee fly (Diptera: Bombyliidae). II. Factors affecting male territorial and mating success. J Insect Behav 3:619–636
Downes JA (1969) The swarming and mating flight of Diptera. Ann Rev Entomol 14:271–298
Ehrlich PR, Wheye D (1986) "Nonadaptive" hilltopping behavior in male checkerspot butterflies (*Euphydryas editha*). Am Nat 127:477–483
McAlpine JF, Munroe DD (1968) Swarming of lonchaeid flies and other insects, with descriptions of four new species of Lonchaeidae (Diptera). Can Entomol 100:1154–1178
Merz B (2000) Hilltopping von Dipteren in der alpinen Stufe [Hilltopping of Diptera at alpine levels]. Entomol Basiliensia 22:297–302
O'Hara JE, Skevington JH, Hansen DE (2004) A reappraisal of tachinid diversity in Carnarvon N.P., Australia, and estimation of the size of the Australian Tachinidae fauna. Tachinid Times 17:5–8
Pe'er G, Saltz D, Thulke HH, Motro U (2004) Response to topography in a hilltopping butterfly and implications for modeling nonrandom dispersal. Anim Behav 68:825–839
Poulton EB (1904) A possible explanation of insect swarms on mountain-tops. Trans Entomol Soc Lond 1904:23–26
Scott JA (1968) Hilltopping as a mating mechanism to aid the survival of low density species. J Res Lepid 7:191–204
Shields O (1967) Hilltopping. J Res Lepid 6:69–178
Wood DM (1987) Tachinidae. In: McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR, Wood DM (eds) Manual of nearctic Diptera. Agriculture Canada Monograph no 28, Research Branch, Agriculture Canada, Ottawa, Canada, pp 1193–1269
Yeates D, Dodson G (1990) The mating system of a bee fly (Diptera: Bombyliidae). I. Non-resource-based hilltop territoriality and a resource-based alternative. J Insect Behav 3:603–617

Himantopteridae

A family of moths (order Lepidoptera). They also are known as long-tailed burnet moths.

► Butterflies and Moths

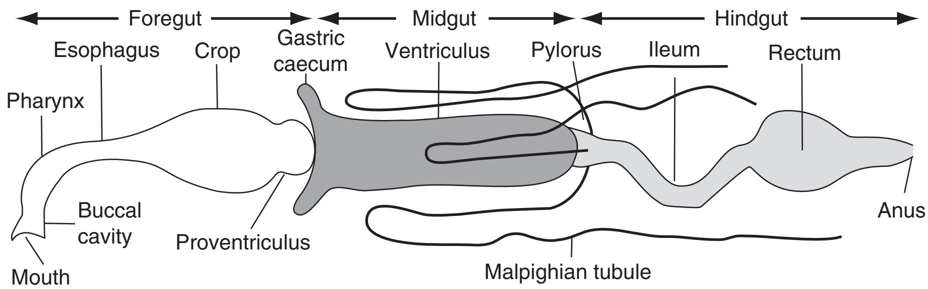
Hindgut

The third or posterior section of the gut. The hindgut receives products from the midgut at the juncture of the Malpighian tubules, and consists of the ileum and/or colon, and the rectum (Fig. 34). The waste products exit the hindgut from the anus.

► Alimentary System
► Alimentary Canal and Digestion

Hinton, Howard Everest

Howard Hinton was born August 24, 1912, in Mexico of American parents, but attended high school and university in Berkeley, California. Then he entered Cambridge University in 1934 to study for a Ph.D. Between 1939 and 1949 he worked as a taxonomist in the Department of Entomology of the British Museum (Natural History) in London. He published copiously, including a 350-page work (1945) "A monograph of the beetles associated with stored products." In 1945 he moved to Bristol University as Reader in Entomology, later being given a professorial chair and then becoming head of the Zoology Department. He was elected a fellow of The Royal Society in 1961 and was president of the



Hindgut, Figure 34 Generalized insect alimentary system (adapted from Chapman, The insects: structure and function).

Royal Entomological Society of London in 1969–1970. His research covered many areas of insect anatomy, physiology, biochemistry and behavior. But he found time to publish (1967) "Mongooses; their natural history and behavior" and to found and edit two journals: "Journal of Insect Physiology" and "Insect Biochemistry." He died in Bristol on August 2, 1977. The 3-volume book "Biology of insect eggs" on which he had been working just before his death was published in 1981.

References

Anon (1977) H. E. Hinton. Antenna 1:33
Rothschild M (1978) Howard Hinton – the pharate adult. Antenna 2:34–36

Hippoboscidae

A family of flies (order Diptera). They commonly are known as louse flies or keds.

► Flies

Hirsutella

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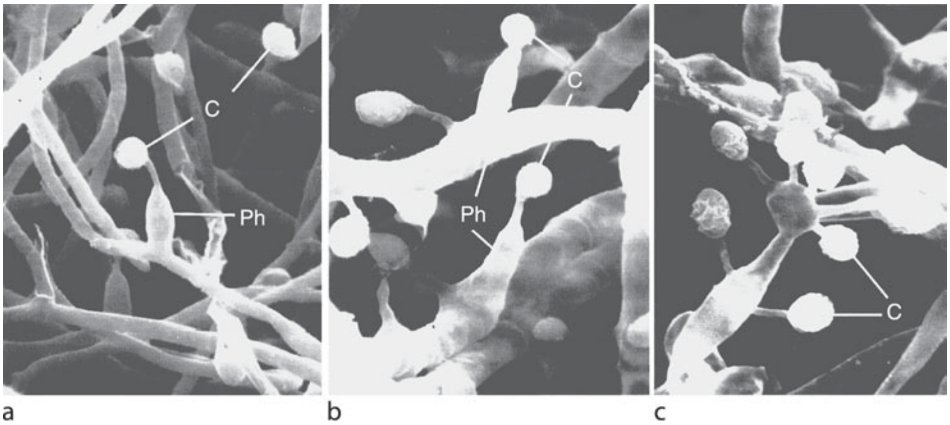
The genus *Hirsutella* infects a number of different types of insects as well as mites and nematodes. Most of the species (about 50) that infect insects produce synnemata, i.e., structures composed of a compact group of erect conidiophores. The most common species, *H. thompsonii*, is pleomorphic and has been separated into three morphologically distinct groups. *Hirsutella thompsonii* variety synnematosa occurs in the tropics, whereas varieties *vinacea* and *thompsonii* occur in subtropical and temperate zones, respectively. All three varieties can produce conidiogenous structures that are solitary, proliferating phialides that generate one or more globose, verrucose (warty) conidia, or polyblastic conidia that generate subglobose to ellipsoidal conidia with smooth walls. In addition, variety *vinacea* produces vinaceous (purple) colonies on agar, and variety *thompsonii* characteristically produces gray-green colonies in culture. Under *in vitro* conditions (Ridell mounts), different *H. thompsonii* isolates have shown extensive variation in the length of the phialide, the length of interval between phialides, the rate of linear growth along substrate, and in the relative degree of mycelial branching.

The *in vivo* life cycle of *H. thompsonii* in host mites takes only 60–72 h. The conidia invade hosts (e.g., mites) through the integument. It should be noted that these short-lived conidia germinate within minutes after being placed in water. Additionally, these propagules, unlike the hydrophobic conidia of many Hyphomycetes, are hydrophilic, and they possess a mucus coat that facilitates adhesion to the mite cuticle. It is presumed that these conidia produce penetrant germ tubes that gain ingress through the



Hirsutella, Figure 35 **Scanning electron micrograph of the conidiophores of *Hirsutella thompsonii* (A), and (B) represent phialides producing solitary conidia, and (C) phialides producing polybastic conidia.**

cuticle. Internalized hyphae break up and form round, multinucleate chlamydospores, which then germinate and produce aerial mycelia with conidiophores; initially, the mycelia may emerge only through oral, anal, or genital openings. These observations suggest that the pathogens may be ingested and grow out from the gut lumen. *In vivo*-produced phialides (Fig. 35) are solitary and arise from mites attached to plant substrates. Conidiogenesis occurs within 9–24 h after host death and requires at least 98% relative humidity (RH) and optimal temperatures (about 25–30°C). In hot, humid weather, *H. thompsonii* can cause spectacular natural epizootics among mite populations (citrus rust, blueberry, coconut, tomato mites, etc.) and is considered to be a key natural enemy of various mite pests.

In vitro, this fungus displays a simple growth cycle. Conidia germinate and produce the mycelial phase that gives rise to conidiophores and/or chlamydospores. Shake flask cultures of several strains of *H. thompsonii* var. *thompsonii* (strain HTF-87, HtF JAB) produce toxic metabolites including the protein toxins, Hirsutellin A (HtA) and B (HtB) and the phomalactones, 6-(1-propenyl)-5,6-dihydro-5-hydroxypyran-2-one. The gene encoding for HtA (GenBank U86836) has been cloned and sequenced. This gene codes for a precursor of 164 aa which includes a 34 aa leader sequence that contains both a signal and a pro-sequence. This monomeric cationic protein undergoes post-translational modification, producing a mature 130 aa HtA toxin which has a calculated M_r=14,159 and pI = 9.21. HtA has been reported to possess consensus sequences similar to those found in various microbial exocellular ribonucleases. Crude filtrates of mycelial cultures containing HtA were found to be toxic to wax moth, *Galleria mellonella*, larvae and *Drosophila melanogaster* (Meigen) adults via injection and per os applications, respectively. In addition, culture filtrates were active against the citrus rust mite, *Phyllocoptruta oleivora*, and the common two-spotted spider mite, *Tetranychus urticae* (order Prostigmata).

References

Chandler D, Davidson G, Pell JK, Ball BV, Shaw K, Suderland KD (2000) Fungal biocontrol of Acari. Biocontrol Sci Technol 10:357–384

Jaffee BA (2000) Augmentation of soil with the nematophagous fungi *Hirsutella rhossiliensis* and *Arthrobotrys haptyla*. Phytopathology 90:498–504

Mazet I, Vey A (1995) Hirsutellin A, a toxic protein produced in vitro by *Hirsutella thompsonii*. Microbiology 141: 1343–1348

McCoy CW (1996) Pathogens of eriophyid mites. In: Lindquist EE, Sabelis MW, Bruin J (eds) Eriophyid mites: their biology, natural enemies, and control. Elsevier, Dordrecht, The Netherlands, pp 481– 490

Samson RA, McCoy CW, O' Donnell KL (1980) Taxonomy of the acarine parasite *Hirsutella thompsonii*. Mycologia 72:359–377

Hister Beetles

Members of the family Histeridae (order Coleoptera).

► Beetles

Histeridae

A family of beetles (order Coleoptera). They commonly are known as predaceous diving beetles.

► Beetles

Histopathology

A study of abnormal microscopic changes in the tissue structure of an organism.

History and Insects

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It is impossible to list the number of times insects affected the course of history, mostly because historians and physicians, during much of our history, were not aware that many of the diseases that caused such loss of human life were transmitted by insects. Even today, medical scientists speculate over the identity and causes of the "plagues" that devastated armies and civilian populations in our early history. While scientists feel confident in attributing some of these plagues to specific diseases, many of which are vectored by insects, they cannot be certain.

America, the French and Yellow Fever

In 1803, Thomas Jefferson, president of the United States, negotiated one of the greatest land deals in history. He did so by buying from the French Emperor Napoleon a vast tract of land known as Louisiana for the then great sum of $15 million. This transaction is forever remembered in history as the Louisiana Purchase. At that time, control of the city of New Orleans was strategically important to the growing United States, as the nation that controlled New Orleans controlled the Mississippi River. The United States desperately needed control of the Mississippi so that western farmers could ship their grain, hogs, cattle and other produce to market by flatboats that floated down the river.

Early in Jefferson's first administration the Spanish, who then controlled Louisiana, had closed the port at New Orleans to the United States' western settlers and caused them great hardship. Jefferson knew he needed to secure for his country a quick and dependable way to transport bulky goods to market cheaply. But France was then the most powerful country in the world, and there was no hope of forcing any privileges from it.

So, in 1802, Jefferson sent James Monroe to France with an offer to buy New Orleans, and if possible West Florida, for $2 million. Napoleon countered with an offer to sell all of Louisiana for $15 million. Jefferson accepted, doubled the size of the United States, and ensured that there would eventually be just one nation spanning the center of the North American continent. History books teach us that Napoleon's primary reason for selling Louisiana was that he needed the money to pay for his new war against Great Britain, but this is incorrect. The real reason Napoleon sold Louisiana had to do with mosquitoes.

In January 1802, a flotilla of French transports carrying 35,000 soldiers commanded by Captain-General Victor-Emmanuel Charles Leclerc, escorted by 62 warships, arrived at the island of Hispaniola in the Greater Antilles. (Today it is divided into the Republic of Haiti in the west and the Dominican Republic in the east.) The mission of the force was to reestablish direct control over the colony of Saint Domingue (now Haiti and then one of the richest colonies in the world) as the colony's leaders were behaving as if it were an independent republic. The former black slaves put up a spirited and well-led defense, but they also had help. By July, more than 10,000 French troops were dead, mostly due to yellow fever, a disease transmitted by mosquitoes. Leclerc himself died of the fever. His successor requested another 35,000 troops as reinforcements. Estimates vary as to the number of French troops Napoleon sent to the island, but the best recent study suggests that the total exceeded 60,000 men and women. By November, only 7,000 starving, sickly troops remained. Four-fifths of the French had died of yellow fever, including 18 generals. By mid-March 1803, France was once again at war with Great Britain. With his need for troops to fight the British in Europe, and with little hope of victory over yellow fever, Napoleon decided that he could not maintain a strong military force in the Americas. He abandoned his idea to secure Saint Domingue and to reestablish French power on the North American continent. On April 30, 1803, he completed the accords that sold Louisiana to the United States.

Yellow Fever and the Transatlantic Slave Trade

The victory of yellow fever, and the mosquitoes that transmitted it, over the French had far greater consequences. The collapse of French power in the West Indies, as their other Caribbean colonies fell to Britain, negated the argument British slave holders had that abolishing slavery would not diminish the transatlantic slave trade, but only turn it over to the French. In 1807 Britain outlawed slavery for its own flag vessels. During the late Napoleonic Wars, Britain began boarding the ships of other nations and freeing slaves. By the early 1820s, the British had set their sights on slavery's abolition around the world. Due to their efforts, the transatlantic slave trade came to an end. With the importation of inexpensive slaves at an end, the value of slaves in the southern United States grew, and they became important enough economic assets that their owners would eventually resort to war to protect them. Additionally, in 1818, the restored French monarchy under Louis XVIII considered an attempt to recover Haiti for France by force. Survivors of the Leclerc expedition, relating their experiences with yellow fever, helped talk the French government out of it and possibly prevented a war between France and the United States.

James Monroe, president of the United States from 1817 to 1825, introduced the Monroe Doctrine (although it was not called that until 20 years after his death) in December 1823. The Monroe Doctrine basically stated that the United States would resist any attempts of "colonization by any European Powers" in the Western Hemisphere. When the French later seized control of the Mexican government during the American Civil War of the early 1860s, the United States was too deeply committed to interfere. However, immediately at the end of that conflict a large American army was sent to the Texas-Mexican border. The French understood the gesture and withdrew their economic and military support of the government, which soon fell. A French-American War in the Western Hemisphere during the nineteenth century would have been a real possibility, if France had maintained colonies there as Spain did. In the late 1890s American public opinion was directed against Spain's remaining colonies in the New World, and in 1898 The Spanish-American War took place.

Insects, Greece, Rome and the Mongols

More than once a powerful army or nation was defeated or reduced in stature due to insect-vectored diseases. For example, many suggest that Alexander the Great's death was most likely due to malaria, which is transmitted by mosquitoes. When Alexander died, his driving force died with him and his empire broke up. Who knows what might have happened had Alexander lived, to expand his empire and establish a dynasty that would have maintained that empire?

Malaria both hurt and aided the ancient Romans, who dedicated a temple honoring the fever goddess. They prayed for mercy from the mysterious illness that appeared every summer and made life and travel dangerous. That illness was malaria, and it both helped and harmed the Romans. Occasionally barbarian hordes would descend on mighty Rome during its times of ebbing power, only to find themselves dying more rapidly from malaria than from the famous Roman short sword. Visigoths, Vandals, Ostrogoths and Huns would temporarily seize control of the Italian countryside but, lacking immunity to the local strain of malaria, would soon die by the thousands. As the poet Godfrey of Viterbo wrote in 1167, "When unable to defend herself by the sword,/Rome could defend herself by means of the fever".

Rome's legions also suffered when they ventured into newly conquered areas. Perhaps one reason the Roman Empire built Hadrian's Wall in northern England was to keep out the strain of malaria that killed half of an 80,000-man army that tried to conquer Scotland. During the Dark and Middle Ages, malaria strains to which the soldiers weren't immune decimated entire invading armies. Death from mosquito-transmitted malaria has even been suggested as one of the reasons the Mongols decided not to continue their invasion of Western Europe after their subjection of much of Russia and the Balkans. Their raids deep into Western Europe brought back slaves and loot, but part of that loot was death to many of the raiders from the European strains of malaria.

Great epidemics are recorded throughout history as either having laid waste to great empires or saving them from invading armies. The oldest recorded epidemic occurred during the Second Peloponnesian War in Greece. Large armies camped in Attica, and refugees crowded the cities. Diseases spread, but which diseases were involved isn't certain. The choices seem to be typhus, bubonic and pneumonic plague, and smallpox, with typhus having the most supporters. Typhus is transmitted by both fleas and human lice, and has been associated with war for so long that it is also known as "war fever." In any case, Athens was defeated and the Golden Age of Greece came to a close.

Bubonic Plague

Diseases, especially bubonic plague transmitted by fleas, also helped bring about the decline of the still strong Eastern Roman Empire. Edward Gibbon, in his "The Decline and Fall of the Roman Empire," states that "during 3 months, five and at length ten thousand persons died each day at Constantinople; and many cities of the East were left vacant, and that in several districts of Italy the harvest and vintage withered on the ground." Thus did insects and disease cooperate with wars and political corruption to finally bring the Roman Empire to its knees. The Roman administrators died, and their talents died with them. Barbarians laid waste to civilization and its trappings, and the Dark Ages settled over much of Europe.

William McNeill, in "Plagues and Peoples," states that bubonic plague epidemics occurred in the eastern Mediterranean region several times during the late Roman empire. Outbreaks of this disease were a major factor in preventing Justinian, emperor of the Byzantine empire, from finding the required resources needed to restore imperial unity to the region. Furthermore, flea-transmitted bubonic plague significantly contributed to the failure of the Byzantine and Persian empires to offer effective resistance to the Moslem armies that swarmed out of Arabia in the middle of the seventh century.

In China, the first descriptions of the bubonic plague date from the year 610, or two generations after its first appearance in the eastern Mediterranean. A series of devastating epidemics began in 762, and the records relate that entire provinces lost 50% or more of their populations. These catastrophes resulted in a weakening of the existing Chinese empire, major revolts and an influx of barbarian influence. China took hundreds of years to regain pre-plague population levels.

Diseases were even used as an early method of biological warfare that often spread far beyond the battlefield and had consequences beyond the immediate goals of the armies that used them. In 1347, when the Mongols used catapults to hurl decaying corpses of plague victims over the walls of Kaffa, a city they were besieging on the shores of the Crimea, they had no idea that the end result would be a complete transformation of European social, educational, religious and political infrastructures. The bodies carried with them what we know today as the Black Death, a bacterium that causes plague in both its bubonic and pneumonic forms. It is initially spread by fleas, then by fleas and airborne bacteria after an epidemic starts. The Black Death, or Black Plague, was one of the major calamities in history. In Europe alone, it caused 25–75 million deaths in <40 years, depending on the authority quoted. Most revised estimates place the total closer to the lower estimate than the higher.

As Genoese traders fled Kaffa and sailed to Sicily, they carried with them rats and fleas that carried the plague. When ships docked at Messina, most aboard were dead or dying. Soon local inhabitants also began to die from the plague. Other ships carried the Black Death to Italy, where the results were the same. Tens of thousands died in the major cities, and many smaller towns and villages lost all their inhabitants. By the spring of 1349 the Black Death had reached as far as Ireland, and in 1350 it passed through Scandinavia. Along its way, it caused moral, religious and political disintegration, as well as cruelty. For example, in many European countries, thousands of Jews were accused of poisoning the wells, tortured and killed.

In Europe, there were four major bubonic plague epidemics in the fourteenth century, with the last three having significantly declining death rates as the population developed immunity. When the first onslaught of the plague was over, one out of every three Europeans was dead. This was the reason the Black Death had such an effect on Europe at that time. Imagine a society in which one out of every three workers, craftsmen, teachers, religious and political leaders, and others died in such a short period. With people believing that they were soon to die, law and order broke down in many areas and chaos reigned for a time. The very fabric of society was torn apart. The Black Death established a dividing line between the central Middle Ages, with medieval culture in full bloom and at its greatest strength, and the later Middle Ages. The later period was one of a significantly reduced population which required hundreds of years to attain its pre-Black Death density.

The Black Death Changes Europe

The Black Death is often credited with bringing an end to the feudal system in Europe. However, that system was already in decline, although the Black Death hastened its end. Strong city states and nations were already emerging, but that process was drawn out as a result of the Black Death. Urban populations recovered quickly, in some cases within a few years, as peasants left the countryside for better opportunities in the cities. As the other three epidemics occurred, city dwellers (many of them former peasants) died, only to be replaced by more peasants who left the land. But the Black Death killed many in rural areas, and this left large areas of farmland without sufficient workers. With a decreased work force, local lords either lost wealth and influence or simply went bankrupt, if they didn't die of the plague themselves. By the fifteenth century, feudalism was in the past. The surviving workers demanded and received higher wages and more rights, and many historians believe that this new sense of freedom and self-worth led to the Peasants' Revolt of 1381.

This severe population loss is considered the main or sole reason for the rise of a monetary economy and increased technological development. When debtors died, their creditors could not collect as the debtors' families quite often died with them. This helped create a monetary economy as it allowed immediate payment for many goods or services. Surprisingly, so many deaths also led to a better standard of living. Fewer people meant a decreased demand for goods. This led to price reductions, which allowed people, now earning higher wages, to purchase items they could not have afforded before. In addition, the local lords, with more land to care for than their work force allowed, sold off parcels to peasants and townspeople who never dreamed they would have a chance to own property. The middle class grew in size and influence. All this happened because fleas were busily transmitting the plague.

The fourteenth century was not a good time for Europe, as it had problems before the arrival of the Black Death. The economy was in decline. The rise of the Mongol and Ottoman empires disrupted important trade routes, and areas of Europe with seafaring economies were already experiencing some economic depression. In the interior of Europe, the overall climate was changing, and the cooler and wetter weather resulted in lower crop yields even as the population increased. By the early 1300s, some parts of Europe were already experiencing famines. Plus, it didn't help that The Hundred Years' War (1337–1453) added war to plague and famine. In fact, if the Black Plague had a beneficial effect, it was that the four epidemics produced periods of peace in The Hundred Years' War.

While the breakdown of class relationships due to the effects of the Black Death led to a massive restructuring of society, it also had a lasting effect on art, literature and religious thought. Certain professions suffered a higher mortality rate from the Black Death, especially those whose duties required them to administer to the sick, such as doctors and clergy. When the priests died and no one could hear confession, people learned that they could live without the church forgiving their sins. The Black Death is a particularly gruesome disease, and it caused despair throughout Christianity. First, people wondered if they had angered God, and many looked to the church for guidance. Then they wondered why His chosen servants in the church were not able to do something to mitigate the disease and why so many of the clerics died from it. This caused the Catholic church to lose much of its prestige, breaking down blind allegiance to that church and setting the stage for the Protestant Reformation.

Education of the elite suffered as universities and schools, usually located in urban areas, were closed or even abandoned. Up to that time, most books had been written in either Latin or Greek, which required rigorous study to learn. But the Black Death killed many educators and left students uneducated or undereducated in Latin and Greek. This led to a temporary decline in universities and a long-term decline in the knowledge of classical languages. The result was a drastic change in the entire educational system as new professors and students used the language of the region instead of Latin or Greek. As a consequence, authors wrote books directly in, and scholars translated directly to, the vernacular. Without the need to learn Latin or Greek, more of the common people could achieve some level of education.

Due to the death of so many priests and monks, scribes were authorized to make copies of manuscripts. This not only greatly increased the number of people copying manuscripts and books produced, but it also decreased the price of those books. During this time the printing press was invented, which allowed for faster and cheaper duplication of books. Books, and the knowledge they contained, were no longer the domain of the wealthy.

The Black Death even became a part of our literature. A common children's nursery rhyme of that time survives to this day: Ring a-round the rosy/Pocket full of posies/Ashes, ashes!/We all fall down! (Ring a-round the rosy – use your rosary beads to implore God's help. A pocket full of posies – posies were used to hide the odor of rotting bodies which was also thought to cause the plague, so doctors used posies to protect themselves from infected plague patients. Ashes,

ashes – the church sanctioned burning the dead when burying them became too time consuming. We all fall down – dead.) In Shakespeare's "Romeo and Juliet," a friar is sent to inform Romeo that Juliet's apparent suicide was a fake. When the friar stops to help a family infected with the plague, he is boarded up in the house with them by their frightened neighbors. When the friar finally emerges, he is too late to reach Romeo to tell him the truth, and both lovers kill themselves over the other's apparent and real suicides.

After the four great epidemics in Europe, the Black Death returned often, but usually only for a short time and even then in smaller areas. However, Spain suffered three major outbreaks of plague during the end of the sixteenth and in the middle seventeenth centuries. More than half a million died in the first outbreak and probably as many in the next two. Together the three epidemics count as one of the significant factors contributing to Spain's decline in economic and political power.

As time passed, people learned how to deal with the plague, and the mortality rate decreased sharply as the population gained immunity. One way people avoided the plague was to leave the infected area if they could afford it. During the last big outbreak in Europe, which occurred in London in 1665, one university professor did just that and retired to his home in the country. This was fortunate as it gave him time to compose his thoughts concerning some theories he held. It was during this unscheduled vacation that Isaac Newton worked out the mathematics for his theory of gravity. Popular history tells us that Newton developed the theory of gravity because an apple dropped on his head. We see now that it was because of a flea.

Although the Black Death finally left Europe in peace, it continued to plague other areas. Egypt also experienced a major outbreak of the plague at the same time it first ravaged Europe, in 1347–1349. Approximately a third of the population died at that time, and smaller outbreaks continued to plague that region over the centuries. During the fourteenth century many areas of China experienced the plague, and records indicate that up to "two thirds of the population" died. During the nineteenth century, most of the Ottoman governors and administrators in the Turkish-occupied Balkans lived in the cities and towns where disease, especially bubonic plague, was common. As they died they were replaced by more administrators from Turkey, who also did not have an immunity to local strains of malaria and other diseases. Meanwhile, the local Christian populations, most of whom lived in the rural areas and did not convert to Islam, grew in size as the numbers of Turks declined. Eventually the Christian populations revolted, and Ottoman rule was overthrown in the Balkans.

Just because Europe was no longer ravaged by the Black Death did not mean that it was free from the effects of other insect-transmitted diseases. For example, in 1643, Charles I of England had to give up his attempt to seize London during the English Civil War because typhus ravaged his army, and he missed his chance to quell Parliament's revolt. Typhus was originally transmitted from rats to humans by fleas, but later was most frequently spread by body lice. But the Class Insecta does not play favorites and Charles got his revenge, years after being beheaded, when Oliver Cromwell died from malaria in 1658. However, at least one historian presents the case that Oliver Cromwell was actually poisoned by his enemies, who used his illness from malaria to disguise his murder. Even if true, a mosquito still contributed to Cromwell's death by assisting in the coverup of the crime.

Insects and Armies

Diseases have always been closely associated with large gatherings of armed men and have influenced the outcomes of wars and invasions many times. Even the greatest of military commanders were often helpless against disease-transmitting insects. For example, early in his career, insects dealt Napoleon a defeat in his Syrian campaign in the Middle

East as he boldly attacked into what is now Israel and Palestine, striking northeast from Egypt. Many of his troops fell ill from bubonic plague, transmitted by fleas. While total casualties to the plague were not excessive, the mortality rate was almost 92%. The morale of Napoleon's soldiers suffered greatly, and some even committed suicide when they contracted symptoms.

But even Napoleon eventually learned how to use insects to win battles. When England landed 25,000 troops on the Dutch island of Walcheren during a campaign in the Netherlands, Napoleon relied on malaria-transmitting mosquitoes to defeat this threat to his flank. Of course, at that time, neither he nor anyone else knew that mosquitoes were responsible for spreading malaria. The malaria was there and that was all that mattered.

Napoleon in Russia

Napoleon, defeated in the West Indies by the mosquito and in the Middle East by the flea, suffered another stunning setback due to an insect – the human body louse. When he assembled his armies for the invasion of Russia in June 1812, they numbered almost a half million men as they left their staging centers in Germany and Italy. As the armies converged and moved through Poland, many of the soldiers appropriated the insect-infested hovels of the peasants. Sleeping on the straw mats, the soldiers were infested with the body lice living there, many of which were carrying typhus. Countless thousands were left in makeshift hospitals or by the wayside and never made it to Russia. By August 25, Napoleon's main army had lost 105,000 men out of an original 265,000. By September, typhus, the prominent disease, and dysentery had ravaged Napoleon's armies and some corps were only half their original size. In October, when the French entered Moscow, Napoleon's armies totaled only 100,000 men, an 80% reduction in strength. By November, pneumonia had joined typhus and dysentery in ravaging the Grand Army. For example, by December only 20 men remained in the Third Army Corps commanded by Marshal Ney. When the Grand Army completed its retreat from Russia, it could muster only about 7,000–10,000 men fit for duty. This was not the last of Napoleon's problems with diseases. In 1814 he raised another army of 500,000 men only to see it reduced to 170,000 by the Battle of Waterloo. Of the 330,000 casualties, two-thirds were caused by disease, mostly typhus.

The Mexican War of 1847

But insects also could help an army win great victories on the field of battle even without causing significant casualties to the opposing force. During the Mexican War of 1847, General Winfield Scott, the commander of a small American army, led his forces to victory after victory over much larger Mexican forces, which were often in highly defensive positions. He did this because mosquitoes forced him to take risks. In March of that year, the American army under Scott's command seized Vera Cruz on the Mexican coast. Scott knew that he had to move into the interior without waiting for reinforcements, as the malaria season was soon to begin. In this case, moving into the interior also meant gaining considerable altitude and leaving the mosquito-infested coast behind. Another general might have waited for reinforcements and watched his army die from malaria. But Scott chose to do otherwise, leaving his supply line hanging in the air, and the result was a brilliant military campaign.

The Crimean War

The lice and typhus that helped defeat Napoleon remained a problem in later wars. During the Crimean War of the late 1850s, the Allies and the opposing Russians were sometimes suffering 12,000 casualties a month from diseases, mostly typhus, which occurred in two major outbreaks. During the war, the French suffered 200,000 casualties out of an army of 309,000. Only 50,000 of the casualties were from wounds received in battle; the other 150,000 were hospitalized by disease. Many of these men were sent to the hospitals because they were infected with typhus but then died from other diseases, like cholera, that they contracted in the filthy hospitals. These terrible deaths continued until Florence Nightingale arrived, reorganized the Allied military hospitals and reduced the death rate from 45 to 2%. It is unknown to the author how many casualties the Russians suffered from typhus.

The American Civil War

Lice played no favorites during the American Civil War, as they infested Federal and Confederate soldiers alike. The armies of both sides were heavily infested as soldiers often wore and slept in the same clothes for months. Fortunately, the lice did not have a typhus reservoir to draw upon as they fed on Blue and Grey combatants. Although two-thirds of the 622,000 military deaths during the American Civil War were caused by disease, typhus was not a significant cause. According to medical records, only about 820 deaths were attributed to typhus. Instead, lice were just an irritant that the soldiers learned to live with. Federals called the lice "greybacks," a name they also used for the Confederates. And both sides helped pass the time in camp by playing a gambling game with lice. Soldiers placed a tin plate issued for meals over a candle. As the flame heated the center to the point where it was just uncomfortable for lice, but not deadly, the men would place bets and release several lice in the center of the plate. The first to scramble over the edge won money, coffee, tobacco or fewer hours on guard duty for its recent host. Today, Civil War reenactors often joke that the true test of authenticity in a reenactor is when he does not have to buy his lice from the sutlers (period merchants), but grows his own.

Dysentery was probably the major non-combat killer of American Civil War soldiers. Of the approximately 410,000 deaths due to disease, it is estimated that 40,000–100,000 died from dysentery. Dysentery is caused by unclean conditions, and the American Civil War armies were just as unclean as any mass army at that time. People, even medical personnel, had little awareness of the good effects a little sanitation would bring. Latrines were ignored just as often as they were used. Consider the filth that an army of 75,000–150,000 men, along with tens of thousands of horses and mules, creates daily. One month after General Sherman captured Savannah he began to ask the government to give him another mission so he could move his troops from their bivouacs, which were beginning to accumulate filth. He knew what disease could do to what was then one of the finest fighting armies in the world. After a while he stopped just asking and began to beg. Eventually, the government allowed him to move his armies north into the Carolinas. Dysentery was such a constant companion to the Civil War soldiers that today's reenactors sometimes tell spectators their unit is so authentic that when they camp they assign a man to defecate upstream from where they draw their drinking water. Other armies in other wars also fought battles against General Dysentery, and the combined casualty lists were enormous.

Certainly humans can spread filth, but filth-feeding flies are also a great help. Civil War letters and diaries are filled with tales of soldiers who fought the flies more often than they fought the enemy. With sanitary conditions in a poor state, and open kitchens as the rule, flies who fed on filth one minute might be feeding on the armies' rations the next. The flies also fed on the dead soldiers and their horses and mules. During the American Civil War, as with many wars, General Dysentery had an aide-de-camp, and his name was Colonel Fly.

Filth-feeding flies weren't the only members of that insect order that helped make life miserable for the Federals and Confederates (Fig. 36). An examination of medical records revealed that during the American Civil War over 1.3 million

History and Insects, Figure 36 **Confederate soldiers from the American Civil War cover themselves with sand to avoid mosquitoes (courtesy of the Florida State Archives).**

cases of malaria, and 10,000 deaths from that disease, were reported just in the Union Army. While medical records for the Confederates are nowhere near complete, it is known that in the first 2 years of the war alone, more than one-seventh of all cases of sickness reported by Confederates stationed east of the Mississippi River were due to malaria. Mosquito-transmitted malaria even helped stop one of the first attempts by Union forces to capture Vicksburg.

Many Civil War historians maintain that the Confederacy lost the Civil War in the West, and not in the campaigns in Virginia. The loss of Vicksburg was the beginning of the end for the Confederacy, and an early victory there would have hastened the end of the war. A shorter war, without the horrendous casualties suffered in mid-1864 and later, might have resulted in a more lenient attitude toward the South after the war. This in turn might have helped avoid so many of the problems the United States endured over the next 100 years, problems created by a harsh Reconstruction that the winners forced on the South. An early victory might also have left President Lincoln alive at the end of the war. Only he had the political influence to counter the political clique known as the Black Republicans, who dictated policy after the Civil War. We know from his writings that Lincoln intended to be very lenient toward those who had fought against the Federal government. What the history of the United States might have been had he lived is something we can dream of only wistfully.

World War I

Lice may have played a role in allowing the Allies to eventually win World War I. As a result of the early battles of the war, when the Austrians invaded Serbia and were eventually driven out, northern Serbia was devastated. Then typhus began to appear in the Serbian armies in November 1914. There were fewer than 400 doctors in the country, most of whom caught the disease, and 126 died. The country was in ruins: it had almost no experienced nurses, relatively few hospitals for the flow of wounded, inadequate prisoner-of-war camps and appalling sanitary conditions. In early 1915, a typhus epidemic flared up that outpaced any other recorded typhus epidemic. By April, new cases numbered in the thousands per day. The mortality rate among infected patients rose from 20% early in the disease outbreak, to 60–70% at the height of the epidemic. Hans Zinsser reports, in his book "Rats, Lice and History," that 150,000 people died in 6 months, Austrian prisoners included. Although Germany mobilized and went to the aid of Austria on the Serbian front, there was no troop movement. With the Serbian armies smitten by disease, the Austrian and German armies stayed put. The last thing their high commands wanted was a typhus epidemic destroying their armies. For almost 6 months, the front was quiet. This delayed the timetable for the German-Austrian advance all along the Eastern Front, kept the Russians in the war longer and may possibly have saved the Middle East for Britain.

During World War II, the Germans would transfer units swiftly between the Western and Eastern fronts, as necessity demanded. However, during World War I this was not done. For some reason, although lice were just as common in the trenches of the Western Front as they were on the Eastern Front, typhus wasn't. The battlegrounds of France and Belgium never experienced the typhus epidemics of the Eastern Front. As a result, German and Austrian units were transferred only after they had undergone a lengthy delousing program. Generals Louse and Typhus robbed the Germans and Austrians of the military advantage of interior lines during World War I.

The Russian Revolution

During the period after the Russian Revolution, from 1917 through 1923, one Russian scientist estimated that there were 30 million cases of typhus, resulting in 3 million deaths, in European Russia alone. How this might have affected the political turmoil of this period, when Reds and Whites were locked in battle for ownership of Mother Russia, is unknown, but interesting to speculate about. Even Lenin is supposed to have said, "Either socialism will defeat the louse, or the louse will defeat socialism."

Lice

Lice have been our constant companions for most of history. Only in recent times have many come to believe that just the poor and uneducated are infected. In Sweden during the Middle Ages, the mayor of Hurdenburg was even chosen by a louse. The eligible elders sat around a table with a louse in the center and spread their beards. The one whose beard the louse climbed into was mayor for the next year. Thomas Becket, the murdered Archbishop of Canterbury, suffered even further distress after his death. As he was laid out for viewing in all his woolen clothes, his body cooled and the parasites began to depart. As one chronicler reports, "The vermin boiled over like water in a simmering cauldron, and the onlookers burst into alternate weeping and laughter." Lice have even entered our literature. For example, one of Scottish poet Robert Burns' more famous works is entitled, "To A Louse, On Seeing One On A Lady's Bonnet At Church."

And for all those who wondered why for centuries Europeans insisted on shaving off their hair only to cover their heads with elaborate wigs, I give you this simple answer – head lice. (Actually, head lice were probably only part of the reason for wearing wigs.) Unfortunately, while an interesting attempt at cultural control, because you could wash or change most wigs easier than hair, the fad quickly gained a life of its own. Some wigs were so elaborate that upper-class women had to sleep sitting up in bed to prevent destroying what a hairdresser had spent hours creating. Eventually people lost track of why wigs were initially worn, and the wigs were just as infested with head lice as hair once was. In addition to lice there is one report of a mouse family setting up housekeeping in one lady's elaborate hairpiece. And at least one noblewoman actually had a bird's nest woven into her wig. Eventually wigs were slowly replaced by powdered hair. I' m not sure why this fashion came about (cheaper than wigs?), but the white powder (usually flour) might have served as a mechanical control for lice.

Mosquitoes

During the Spanish-American War of 1898, the United States suffered far more casualties from malaria and yellow fever, transmitted by mosquitoes, than it did fighting the Spanish. These casualties occurred just as often in the camps around Tampa, Florida, as they did in Cuba, Puerto Rico and the Philippines. Approximately 80% of the American soldiers in Cuba came down with yellow fever. Fortunately, the death rate, while high, was nothing like that suffered by the French in Hispaniola at the beginning of the eighteenth century.

Both before and after the Spanish-American War, mosquitoes played a major role in preventing the successful completion of the Panama Canal, first by a French corporation, then by the Americans. During these attempts, thousands of workers died, and tens of thousands of investors lost more than $3 billion in the French attempt alone, an extremely large sum at the time. It was only after medical scientists realized that malaria and yellow fever were transmitted by mosquitoes and ordered that housing conditions be improved (with screening) and containers of standing water (in which the mosquito larvae developed) be emptied or destroyed that the workers stopped dying like flies.

The French seemed to have a continual problem with disease-transmitting mosquitoes. During World War I, a French general in Macedonia told his government that he had to disobey his orders to attack as his army was in the hospital with malaria. Fortunately for him, his German opponents were telling the same thing to their government.

The American military would have other encounters with malaria transmitted by mosquitoes. During World War II, American forces in the southwest Pacific and southeast Asia suffered 500,000 cases of malaria. General Douglas MacArthur once complained that two-thirds of his army was either suffering from malaria or recovering from it and therefore useless to the war effort. It was only when he consulted with a malaria-prevention team, and then commanded that their efforts be given much higher priority, that the tide of battle against malaria turned and the Army could then concentrate on defeating the Japanese. The Allies also had a secret weapon that came into use during 1943 – DDT. Used in all theaters of war, in bases far behind the lines and in newly liberated cities and towns, DDT was instrumental in reducing louse-borne disease and malaria. And during the Viet Nam War, the author remembers regularly forming up his Marine Corps platoon and walking the line with a Navy corpsman to ensure every marine swallowed his malaria prevention tablet.

Tsetse Fly

Outside of Africa, most people encounter tsetse fly only when reading about the African adventures of European explorers of the nineteenth century. But for inhabitants of sub-Saharan Africa, tsetse fly is much more than an interesting insect from the history books. Nearly 100 years ago, the tsetse was identified as the vector of sleeping sickness, a deadly disease that still has a stranglehold on a vast area larger than the United States. Tsetse fly, and the disease it transmits, is the reason why the ungulate herds of the African savanna have survived to the present day. This is because, without modern prophylaxis, livestock cannot live in regions where the tsetse fly flourishes, and significant human losses occur as well. As a result, economic development or exploitation of this region, although attempted many times by African and European concerns, was never successful. The tsetse fly has even been viewed as a beneficial insect in that it protected central Africa and the huge ungulate herds from those rapacious European governments of the nineteenth century that were busy looting the resources of the rest of the world. According to the World Heath Organization, human sleeping sickness threatens more than 60 million people in 36 countries. Without treatment, the disease is fatal. In the last century, there have been three major epidemics of sleeping sickness in Africa. The last one began in 1970 and is still in progress as of 2002. The tsetse fly may have protected central Africa from exploitation, but it had help from other flies. Even before venturing into central Africa, European powers had difficulty penetrating the wall created by malaria- and yellow fever-transmitting mosquitoes.

In cattle, sleeping sickness is called Nagana, and it is found in an area over 6 million square miles (or 10 million square kilometers) in Africa. It affects an estimated 46 million cattle in Africa alone and causes 3 million cattle deaths annually. Ninety percent of Africa's livestock consists of herds in small villages where maintaining healthy animals can be the difference between subsistence misery and a tolerable life for herders and their families. Other species have also suffered indirectly from this disease. Just in the country of Zimbabwe alone, more than 2,900 tons of DDT have been used in an attempt to control the tsetse fly. The effects of DDT on many vertebrate and beneficial insect species are too well-known to mention here. Fortunately, scientists developed new baiting methods that resulted in a dramatic decrease in pesticide use.

Black Flies

River blindness, or onchocerciasis, made parts of Africa and Latin America virtually unlivable. This disease, caused by a filarial worm, is transmitted by black flies. The worms migrate from the initial infection under the surface of the skin throughout the body and eventually to the surface of the eye, causing intolerable itching and scarring that results in a progressive loss of vision. Fortunately, medical science has developed treatments that are extremely effective. Recently completed multinational control programs coordinated by the World Health Organization have effectively eliminated this disease from large parts of West and Central Africa. This has been accomplished by temporarily (for about 20 years) eliminating the immature vectors from the breeding sites in rivers with insecticides, while at the same time therapeutically controlling the disease in humans. New programs are being mounted with the hope of continuing these exciting successes.

Mosquitoes, Disease and Society

Mosquito-transmitted malaria and yellow fever have also influenced economic and social conditions. To appreciate this you must first understand how the mosquitoes acquire and then transmit the diseases. You have probably been wondering, while reading this article, how these diseases can cause severe casualties among invading armies but leave the local residents still standing. Here is a very simplified explanation of a complex process. There are many strains of malaria and yellow fever, each of which is endemic to a region. When children are born in a region they are usually infected with the local strain. In children, the diseases may produce mild reactions, often confined to flulike symptoms. In many cases, their parents are not even aware the children have been infected. Sadly, this is not true for all children, as will be related later. Children who survive infection by the local strains may acquire partial immunity to those strains. However, as people travel to a different region, they encounter different strains to which they may not be immune. If they are adults, the new strains now infecting them can be life-threatening.

A female mosquito must first bite an infected person to acquire the disease. After a short period for the disease organism to complete the next portion of its life cycle, the female mosquito is now ready to pass it on to another person the next time it feeds. Many of the more common mosquitoes that transmit malaria and yellow fever have relatively short flight ranges, often less than a mile.

Therefore, a female mosquito that acquires the disease organism from an infected person will not normally travel great distances to spread that strain to new areas hundreds or thousands of miles away. (Unfortunately, modern methods of transportation have helped mosquitoes and disease strains to overcome these natural barriers.) It is especially important to know that the mosquitoes that transmit malaria and yellow fever are either dawn and dusk feeders and/or night feeders. If you are new to an area where malaria or yellow fever is common but take care to protect yourself from dusk to dawn from biting mosquitoes, then the chances of becoming infected with and dying from the local strains of malaria or yellow fever are greatly decreased. However, there are also at least two species of yellow fever-transmitting mosquitoes that also feed during daylight hours.

One of the lessons learned in Panama was that an area could be created that was relatively free of mosquito-borne infections. This area could then be inhabited by foreign troops, workers, administrators and their families. The French began to advocate separate communities for natives and Europeans. British medical scientists endorsed this concept by insisting that only natives carried the disease organisms in their blood. As a result, representatives of these governments in many colonies issued regulations against Europeans socializing or living near local populations. Some called this segregation, others called it apartheid. In some countries it eventually took on a social meaning of its own that was no longer related to disease transmission.

After the American Civil War, the southern states were devastated and needed capital investment to return the region to its former prosperity. Unfortunately, for most regions in the South, capital investment never arrived in the amounts necessary. As a result, the southern states would not achieve economic parity with most northern states until well into the twentieth century. One of the reasons for the lack of capital investment was very simple. The listlessness associated with malaria-infected workers, as well as the ever-present threats of malaria and yellow fever epidemics, kept many northern and European investors from risking their capital in the South. Workers infected with malaria may not have died, but the recurring illness contributed to a significant amount of missed work days and reduced productivity even when at work. It was estimated that one-third of all work missed by southern railroad workers was due to malaria. Other sectors of the economy also reported reduced productivity during those months when malaria was most pronounced.

The Continuing Effects of Insects on Society

Plagues, famine, social upheaval and conflict, and the insects that cause them, are easy to write about. Not as easy to understand and weigh are the everyday situations we live with that are also influenced or caused by insects. Numerous insect species continue to have a direct or indirect effect on the world economy. Here are a very few examples.

First, there is their entertainment value. Just as with our ancestors, insects are a part of our literature. Locust swarms, as depicted in Pearl Buck's "The Good Earth" which was also made into a very good movie, are still very much a threat for farmers in many regions of the world. "Leiningen Versus The Ants," an excellent fictional short story of one man's battle against army ants, has been adapted for many movies and TV dramas. Japanese film-makers used immense caterpillars and moths to destroy Tokyo many times. The 1950s saw Hollywood produce many films in which insects were threats to humanity, the author's personal favorite being "Them," a movie about giant ants. Even the least threatening of insects have been used to frighten theatergoers. For example, in "Damnation Alley," hordes of Madagascar hissing cockroaches were supposed to have eaten the entire population of Salt Lake City. The different ways in which insects have been featured in articles, books, films and TV shows is beyond counting. Aside from being entertaining, all of these have provided jobs and revenue to the countless people who wrote, directed or otherwise worked on them. And probably the world's shortest poem is even about an insect. Ogden Nash, the poet laureate of Maryland until his death in 1971, wrote "Fleas," which consists entirely of Adam/Had'm.

In a more serious vein, screwworms, the maggots of some fly species, feed on the flesh of living mammals. In the early part of the twentieth century, these pests cost the United States and Central American cattle industries millions of dollars in losses each year. A major effort using sterile flies has eliminated the primary screwworm from the United States all the way to southern Panama, where a barrier is maintained by quarantine and sterile fly releases to prevent reinfestation from South America. In 1996, the benefits to the various cattle industries were estimated at: USA – $796 million, Mexico – $292 million, Central America – $77.9 million. Before the primary screwworm threat was eliminated from these regions, many pet owners accepted that their dogs and cats would only live with them for a few years. Superficial cuts suffered by these cherished family members often resulted in a screwworm infestation, and the pets would wander off to die.

The urban pest-control industry in the United States provides hundreds of thousands of jobs and annually generates more than $5 billion in income. Termites alone are responsible for more than $1 billion in damage each year. The amount of wood used to replace such damage is considerable. Its harvest often generates bad feelings between the timber industry and environmentalists. Not only are millions of dollars spent on lawsuits by and against the timber industry, but the amounts spent on termiticides and new termite-proof construction practices take their toll on our economy.

In the United States, the major reason for most urban children missing school is asthma. And the major cause of asthma for these children is an allergic reaction to airborne cockroach feces and body parts. The social cost of these missed school days cannot be measured.

The urban pest-control industry formerly was the primary industry responsible for flea control in the United States. This is no longer true as the veterinary industry now markets several systemic insecticides to pet owners to the tune of more than $250 million dollars a year. This does not include the amount spent to prevent or cure heartworm, another mosquito-transmitted disease in dogs and cats.

And let us not forget the red imported fire ant (RIFA), which has become such a costly nuisance in the southern United States. As this ant expanded its range in the middle of the last century, the United States spent more than $270 million in an attempt to destroy it with airborne application of insecticides. That did not work, and it killed a lot of the native ant species and allowed the most aggressive RIFA to move into the vacant niches. Meanwhile, we continue to spend huge amounts every year in an attempt to control RIFA, which has an economic impact on the ornamental, agricultural and livestock industries, as well as others. In 2002, Congress funded a 5-year, multimillion dollar program to demonstrate RIFA management in pastures. Fruit pickers demand extra wages to work in infested citrus groves. And the amount spent by homeowners on RIFA insecticides, much of it wasted as they do not understand how to apply the baits properly, can only be guessed at.

Visit any hardware/garden store or supermarket and count the number of products specifically designed to control or manage insects. Scan any garden or home catalog to see the numerous products, many of which work and others of which do not, for eliminating insects from your home, garden or life. While many people believe that these problems and products cost our economy more than they benefit it, other people believe that they create even more jobs and strengthen the economy. Insecticides allow us to feed billions, but they also generate a cost to human health and the environment. And these problems are worldwide in scope. Whether you are growing corn in the American Midwest or tomatoes in a backyard in Italy, your insect problems are similar to farmers in Central Africa fighting whiteflies on cassava or rice farmers in the Philippines trying to control leafminers.

Of course, we now live in the twenty-first century, and we expect that the great insect-caused plagues of the past will not occur again because we have the technology to control them. Tell that to the government of Brazil, which employs 50,000 people to go into neighborhoods and empty out water-filled containers that serve as breeding areas for disease-vectoring mosquitoes. During late 2001 and early 2002 in Brazil, one out of every 10 workers just in the Brazilian state of Rio de Janeiro missed work due to being ill with dengue fever, another mosquito-borne disease. The region's association of merchants estimated that 30% of workers had contracted the disease. Dengue fever is characterized by severe headache, pain behind the eyes, high fever, backache, pain in the joints and a severe rash, with convalescence that may require several weeks.

Four strains of dengue virus have been identified, each of which produces lifelong immunity against the infecting virus. However, exposure to infection by a second strain of dengue virus in an already immune individual may result in a more severe form of dengue known as dengue hemorrhagic fever (DHF), with accompanying dengue shock syndrome. Death is then common, particularly when the Type 2 virus infects children who had previously been infected with another strain. Increased incidence of DHF has been experienced in the Western Hemisphere in the last 20 years, with outbreaks occurring in the Caribbean region. About 205,000 cases of dengue fever were reported annually in Brazil before the recent 2001–2002 season. In 1998, an epidemic in that country caused 540,000 cases. Worldwide, dengue is one of the most important arthropod-transmitted human viral diseases, and about 50 million 100 million cases of DHF are reported annually. On many Caribbean islands, residents are forbidden to have bird baths in their yards, and government employees perform the same function as those in Brazil, searching for and emptying water containers on private property. Although it has not experienced a dengue epidemic in decades, Florida began surveillance for dengue fever in 2002 and by October had reported nine confirmed and nine probable cases, all incurred from outside the United States. Texas occasionally reports cases of dengue fever. Currently, there is no vaccine available for dengue.

Malaria is also a major problem in Brazil, with 600,000 cases reported annually. Worldwide, 10% of the world's population suffers from malaria, and this mosquito-transmitted disease continues to kill up to 3 million people every year, including one child every 30 sec (another authority estimates one child every 12 sec). Today, malaria is so uncommon in most industrialized countries that people think it is a tropical disease. This is not true. Malaria was once common even in Scandinavia, and, as previously stated, malaria played a role in defeating the Roman invasion of Scotland and the Mongol invasion of western Europe. On the North American continent the Missouri and Mississippi watersheds were once major reservoirs for the disease, as was Canada. Malaria epidemics were once common on the East Coast, and Staten Island in New York only experienced heavy development when extensive draining of marshes occurred after 1900. Today, improvements in housing (screening, air conditioning, etc.) in many countries make the severe malaria epidemics of the past unlikely. However, the malaria virus strains and their vectors continue to evolve, and scientists are concerned that the newer, hardier breeds will one day make us pay greatly for thinking that it "can't happen again."

Encephalitis viruses are spread by mosquitoes. Eastern equine encephalitis (EEE) is the most lethal of the mosquito-borne encephalitides. Originally isolated from horses, this virus can also infect humans. The profitable race-horse industry can suffer large losses with just the death of a few highly-valued animals. However, when humans contract the disease, the cost is far worse. Older victims usually die, and Florida lost several elderly adults in 2001, when mosquito populations were low. When children are infected the cost is particularly high, not even counting the suffering among families. It is estimated that survivors of EEE each cost society $2.8 million in health care costs, long-term care and lost productivity.

The West Nile virus, which surfaced in New York in 1999, moved more quickly across the United States than many scientists estimated. By late-2002, it was present in more than 40 states. Yet with all the publicity surrounding this new disease to the North American continent, most people have still not changed their cultural behavior. Perhaps because, unlike dengue and malaria, not enough people are dying from it. Parents still take their children for walks at dusk, mostly shirtless, in areas where West Nile and other mosquito-transmitted diseases have been confirmed. Bird baths are a popular item in many backyards and are seldom emptied and the water changed. Other water-filled containers, mostly trash, are commonly found in yards and lots and serve as breeding grounds for untold billions of mosquitoes. At least two primary mosquito vectors of yellow fever and dengue fever breed in these containers, and both feed during daylight hours. One, the Asian tiger mosquito, is an introduced species that is now firmly established in the southern United States and is increasing its range.

Will Americans change their cultural habits only when many of them are sick and dying as the result of mosquito-transmitted diseases? Probably not. In South and Central America, and on many Caribbean islands, where governments often have more forceful methods of ensuring citizen cooperation, many residents still are strong believers in the right of property and resist government intrusion into their yards. As a result, people still die. The World Health Organization reports that worldwide there are still 2.5–3 million deaths a year from malaria, after decades and billions of dollars spent on educational outreach. And do not think that West Nile virus is a worst-scenario disease. There are other mosquito-transmitted diseases in other regions of the world that are just waiting for the opportunity to immigrate to North America, Europe and other continents.

For example, the Indian subcontinent, like the rest of Asia, has never experienced a yellow fever epidemic. What might happen if yellow fever were to be unleashed on this huge population that has no immunity to the disease? Andrew Spielman and Michael D'Antonio in "Mosquito," an excellent book detailing the natural history of this group, state that "If yellow fever broke out in India, for example, where vector mosquitoes and their human hosts are exceptionally abundant, the loss of human life would be cataclysmic." If you believe this to be an exaggeration, then consider that in the first half of the twentieth century, India had an average of 75 million people infected with malaria at any given time and that the death rate from malaria was 800,000 a year.

Mosquitoes are such a scourge in India that they sometimes can accomplish what modern armies cannot. During mid-2002, swarms of malaria-bearing mosquitoes along India's border with Bhutan were able to drive guerilla insurgents from their jungle hideouts in search of medical treatment. The mosquitoes accomplished something that Indian security forces have been unable to do for years.

Based on the above, it might seem that humanity would be better off if all insects were eliminated. Fortunately, entomologists, as well as scientists in many other disciplines, and a growing number of politicians realize that this is not the case. With well over a million identified species of insects, only a few hundred species are listed as serious pests of humans and their crops, animals and structures. A few thousand more species can be considered minor pests. But all the rest are considered directly or indirectly beneficial to humans. Just in the United States alone, insects annually pollinate more than $15 billion worth of fruit and vegetables. This does not include insects that pollinate flowering ornamentals which bring so much joy to our lives and provide employment in a huge industry. Plus, the insects themselves are responsible for destroying a thousand times more pest insects than we are able to with our feeble "advanced technologies." As a result, governments, universities and private concerns are expanding their funding for research and implementation of cultural and biological control techniques that are successfully managing insect and other pest populations. Without insects and other arthropods killing other insects and pollinating plants, the human species probably would have died out, either through disease or lack of food, even before leaving the trees.

The next time you swat at a mosquito, or flea, or other pest, try to remember that its ancestors did more to change human history than anything your ancestors ever did. For only when we recognize the tremendous influences insects have had on the history of our civilization can we begin to appreciate the adjustments in human behavior that will be necessary to live acceptably with them in the future.

References

Bray RS (1996) Armies of pestilence: the impact of disease on history. Barnes and Noble Books, New York, NY

McNeill WH (1998) Plagues and peoples. Doubleday, New York, NY

Miller GL (1997) Historical natural history: insects and the Civil War. Am Entomol 43:227–245

Peterson RKD (1995) Insects, disease, and military history: the Napoleonic campaigns and historical perception. Am Entomol 41:147–160

Spielman A, Antonio MD (2001) Mosquito: a natural history of our most persistent and deadly foe. Hyperion, New York, NY

History of Biological Control of Wheat Stem Sawflies (Hymenoptera: Cephidae)

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Wheat stem sawflies (Hymenoptera: Cephidae) are important pests of wheat and other grain crops in the northern hemisphere. The egg, larval, and pupal stages are spent inside the wheat stem, while the adult is mobile but short-lived. Sawfly larvae feed inside the stem and the damage they cause reduces the number and weight of the kernels. The sawfly larva also cuts the stem at the base of the plant as it constructs a pupation chamber. The weakened stem breaks and the grain lodges or falls to the ground, adding to yield losses and making harvesting difficult. Yield losses of more than 20% have been reported for different sawfly species from North America, Europe, North Africa and Asia. The value of these losses may reach $100 million annually.

Management of wheat stem sawflies has focused on three strategies: the development of resistant wheat cultivars, relying primarily on solid-stems as a resistance mechanism; various tillage operations to destroy larvae and/or pupae in the wheat stubble; and biological control. Pesticides are generally ineffective because the larvae are hidden within the stem and are too costly for a relatively low value crop such as wheat. Efforts to develop solid-stemmed wheat cultivars began in the 1930s. The first solid-stemmed cultivar was released in 1946, and more than 20 cultivars have been released since then. Unfortunately the performance of these cultivars has been variable, and yields in the absence of sawflies are lower than hollow-stemmed cultivars. Tillage, either in the spring or fall, has also been somewhat successful in reducing sawfly populations but has important limitations. Tillage requires an additional field operation, increasing wheat production costs and reducing profitability, and can also increase soil erosion rates. The third strategy used to manage sawflies is biological control using exotic parasitoids. Three cephids, *Cephus cinctus*, *C. pygmaeus*, and *Trachelus tabidus*, have been targets of biological control programs in Canada and the USA. These efforts have been extensive, though only partially successful. The remainder of this section reviews previous biological control efforts against these pests, beginning with the biology of sawfly natural enemies (the parasites, predators and pathogens that attack these pests).

Sawfly Natural Enemies

The most important sawfly natural enemies are parasitic Hymenoptera. A small number of pathogens and predators are known to attack sawflies but have relatively little impact on sawfly population dynamics compared to parasitoids. More than 40 parasitoids are reported to attack sawflies, though little is known about most species; fewer than ten have a significant impact on sawfly populations. Many species attack other hosts found in grasses or other parasitoids (these are then called hyperparasitoids). The most important primary parasitoids of grass-feeding sawflies are in the Braconidae, Ichneumonidae, and Eulophidae families. Before discussing sawfly biological control programs, it is important to understand the biology and ecology of the key natural enemies.

Several species of braconid attack sawflies in different regions of the world. All of these braconids are larval ectoparasitoids, living and feeding on the outside of the host larva's body. The most important are *Bracon cephi* and *Bracon lissogaster* that attack *Cephus cinctus*, and *Bracon terebella* and *Heterospilus cephi* that attack *Cephus pygmaeus*. In general, braconid parasitoids have more impact on sawfly populations in the New World than in the Old World. This may be due to the absence of ichneumonid parasitoids in North America. In other parts of the world, ichneumonids dominate sawfly parasitoid complexes. Parasitism levels by braconids range from 20 to more than 90% of available hosts in North America, while in Europe and the Mediterranean region a considerably lower percentage, often <5%, of hosts are parasitized. The biology of the braconids is similar among species. Females locate sawfly larvae inside the stems from the vibrations produced by the feeding larva. She inserts the ovipositor and paralyzes the larva before laying one or more eggs. Eggs hatch within a few days and the braconid larvae begin feeding on the sawfly larva. Depending on the braconid species, more than one parasitoid may develop on a host larva. The braconid larvae consume the entire host except for the head capsule and epidermis. Larval development is completed in 2–3 weeks, and the parasitoid larva usually overwinters in the stem of the host plant. There may be one or two generations per year.

More than ten species of *Ichneumonidae* attack sawflies, though most are rare or are present at very low levels. The most important are species of *Collyria*. This group is egg-larval endoparasitoids, meaning they live and feed from inside the body of the host. In Europe, *Collyria coxator* is the dominant primary parasitoid of the European wheat stem sawfly (*Cephus pygmaeus*). Parasitism levels of 20–76% have been reported from England, Belgium, France, Switzerland, Germany, Russia, and Bulgaria. *Collyria coxator* females locate and oviposit into sawfly eggs inside the plant stem. Up to eight *Collyria* eggs and/or larvae have been found within a single sawfly (known as superparasitism), though it is not known whether these eggs are from the same or different females. Despite the presence of more than one *Collyria* larva, only a single adult parasitoid will emerge from a parasitized sawfly larva. Unlike the braconid parasitoids, *Collyria* does not paralyze the sawfly larva. The parasitized sawfly larva continues to feed within the stem throughout the season, and moves to the base of the plant and cuts the stem in a manner similar to an unparasitized sawfly larva. The *Collyria* larva remains within the host body until spring when it emerges and pupates. The adult then chews through the plugged end of the stub and emerges prior to the emergence of the unparasitized sawfly adults.

The third and least common group of primary parasitoids are several species of Eulophidae. The impact of these species is very low, and only two species (*Pediobius* spp.) have been studied in any detail. These two are found throughout the northern hemisphere, and are internal larval parasitoids. In addition to attacking sawfly larvae, they also attack other phytophagous Hymenoptera and Diptera found in grass stems. Parasitism of more than 50% of sawfly larvae in grasses has been observed, while in wheat, parasitism levels rarely exceed 5%. The reasons for the low attack rate in wheat are unknown.

Previous Biological Control Programs

Cephus cinctus was the first sawfly targeted for biological control. This work was initiated in Canada, and used parasitoids collected in the United Kingdom. Three parasitoids were selected for introduction into Canada, two from England (*Collyria coxator* and *Pediobius nigritarsus*), and one from the eastern United States (*Heterospilus cephi*). The three species were not collected from *C. cinctus* but rather from the related sawfly species, *Cephus pygmaeus*. From 1930 to 1938, when the program was discontinued due to the onset of World War II, more than 450,000 *C. coxator* and 120,000 *P. nigritarsus* individuals were released at sites in Saskatchewan and Alberta. Relatively few *H. cephi* adults were released, approximately 1,500, at one site in Alberta, and in only 1 year. None of the three released parasitoids became permanently established, though recoveries of *C. coxator* were made up to 2 years after release, with parasitism up to 9% at some sites.

A second biological control attempt against *Cephus cinctus* was undertaken in the western USA between 1952 and 1955. This program also used parasitoids obtained from *C. pygmaeus*, but this time collections were made in France instead of England. The predominant parasitoid collected was again the ichneumonid *Collyria coxator*, which parasitized 25–90% of the *C. pygmaeus* hosts. A second parasitoid, *Bracon terebella*, was also collected. Parasitized *C. pygmaeus* cocoons were collected and shipped to Moorestown, New Jersey, where they were held for adult emergence. After emerging, parasitoid adults were flown to release sites in Montana and North Dakota. Nearly 40,000 *C. coxator* and 3200 *Bracon terebella* were released over 4 years. Release sites were sampled for 6 years beginning in 1953. No recoveries were made of *B. terebella* in either Montana or North Dakota. Low numbers of *C. coxator* were recovered at some sites, but never more than 2 years after release. The last recovery was in 1957.

The third and smallest biological control program against *Cephus cinctus* began in the late 1950s, when it was recognized that parasitoids collected from England and France might be poorly adapted to climatic conditions in western North America. Parasitoids were collected, again from the related host *C. pygmaeus*, in the Ukraine, the Caucasus region of Russia, and from Sweden. As in the two previous attempts, the most common parasitoid collected was *Collyria coxator*. However, in laboratory studies, *Collyria coxator* suffered high mortality in *C. cinctus*. Nonetheless, a small quantity (119) of *Collyria coxator* from the Ukraine was released in Alberta. There is no report of establishment.

The biological control efforts directed at *Cephus cinctus* are examples of an approach that has been called "new associations" or neoclassical biological control. This approach utilizes natural enemies from a different but closely related species to the target host. The target host and natural enemy thus form a new association, and according to the theory, establish a lower equilibrium population level for the target host. In this instance, four parasitoid species, *Collyria coxator*, *Pediobius nigritarsus*, *Bracon terebella* and *Heterospilus cephi*, were released against *C. cinctus* in North America. Despite a sustained effort, particularly for *Collyria coxator*, none of these species was successfully established. The lack of establishment was likely due to the use of poorly adapted parasitoids. The parasitoids were collected from a different sawfly species and the locations where they were collected, predominantly England and France, are climatically and agronomically very different from the North American Great Plains. Host suitability studies conducted early in the program could have saved considerable time and effort by identifying the lack of compatibility between the target host and the natural enemies. In hindsight, these studies could have avoided the needless release of an inappropriate parasitoid.

In contrast to the program for *Cephus cinctus*, biological control of *C. pygmaeus* was very successful. These efforts, carried out from 1935 to 1938 in the USA and 1937–1940 in Canada, resulted in the successful establishment of a parasitoid and a reduction in sawfly population levels. Because both *C. pygmaeus* and *T. tabidus* were attacked in Europe by many of the same parasitoid species, the release program in the US was intended to address both pest species (*Trachelus tabidus* has not been reported from Canada). These programs utilized *Collyria coxator* which Canada had arranged to obtain from England for use against *Cephus cinctus* in the western Prairie Provinces (described above). More than 28,000 *C. coxator* adults were released in the US, and more than 24,000 *C. coxator* females were released in Canada. *Collyria coxator* was successfully established in both the US and Canada, and based on the levels of parasitism observed in the field, it appears to play an important role in regulating *C. pygmaeus* populations. By the mid-1980s, *C. coxator* parasitized up to 80% of *C. pygmaeus* larvae in the field.

This program is an example of classical biological control, where an introduced pest is controlled by collecting natural enemies from the target pest's area of origin, and releasing them into the new habitat. Once established, the introduced natural enemies can lower the target pest's population to sub- economic levels.

Summary

Wheat stem sawflies are important pests of wheat in the northern hemisphere, particularly in North America. Host plant resistance and cultural control strategies offer partial control, though both have significant drawbacks. Attempts at biological control using exotic parasitoids have been variably successful. For *Cephus pygmaeus* and *Trachelus tabidus* in eastern North America, an ichneumonid parasitoid (*Collyria coxator*) was successfully established and contributes to reduced population levels now observed in these two sawflies. In contrast, biological control for *Cephus cintus* has been attempted unsuccessfully three times. Several factors may have contributed to the lack of establishment of natural enemies in the western US and Canada. A key factor may have been that the parasitoids selected for release were collected from a different sawfly host and perhaps they were unable to complete development in this new host. A second problem may have been that the parasitoids were not adapted to the colder, drier climate they were released into. The release protocol may also have contributed to the lack of establishment. Adults were transported across the country (Canada or the US) and released immediately into the field. This may have resulted in injury or death to the adult parasitoids due to shipping and handling, and poor timing and/or synchronization between C. cinctus populations and the parasitoids.

References

Beirne BP (1972) The biological control attempt against the European wheat stem sawfly, *Cephus pygmaeus*. (Hymenoptera: Cephidae), in Ontario. Can Entomol 104:987–990

Filipy FL, Burbutis PP, Fuester RW (1985) Biological control of the European wheat stem sawfly in Delaware (Hymenoptera: Cephidae). Environ Entomol 14:665–668

Morrill WL, Kushnak GD, Gabor JW (1998) Parasitism of the wheat stem sawfly (Hymenoptera: Cephidae) in Montana. Biol Control 12:159–163

Salt G (1931) Parasites of the wheat stem sawfly, *Cephus pygmaeus*. Linnaeus, in England. Bull Entomol Res 22:479–545

Shanower TG, Hoelmer KA (2002) Wheat stem sawfly biological control: past and future. J Agr Urban Entomol 21:197–221

Smith RW (1959) Status in Ontario of *Collyria calcitrator* (Grav.) (Hymenoptera: Ichneumonidae) and of *Pediobius beneficus* (Gahan) (Hymenoptera: Eulophidae) as parasites of the European wheat stem sawfly *Cephus pygmaeus* (L.) (Hymenoptera: Cephidae). Can Entomol 91:697–700

Streams FA, Coles LW (1965) Wheat stem sawfly parasites, *Collyria calcitrator* and *Pediobius nigritarsis*, in eastern United States. J Econ Entomol 58:303–306

Hobby, Bertram Maurice

Maurice Hobby was born in Southampton, England, on October 23, 1905. As a schoolboy living in Southampton, he developed an early interest in insects and lived close enough to the New Forest that frequent collecting trips there were possible. In 1925 he became a student at Oxford University, gaining his first degree in zoology in 1929. As a graduate student at Oxford, he worked on "Predaceous insects and their prey," and gained a D.Phil. degree in 1934, whereupon he was awarded a Junior Research Fellowship and, the following year, was appointed assistant to the chairman of the entomology department (the Hope Department of Entomology). Other positions and promotions followed at Oxford University, until he retired in 1972. But, in 1938 he was appointed examiner to the Oxford Delegacy of Local Examinations, and later a delegate of that organization, as well later still as a Delegate of Oxford University Department for External Studies. Thus, he served as a teacher and tutor within the university and outside it. His research was mainly on predatory insects, especially Asilidae and Empididae, and included analyses of insect diets and taxonomy. In 1932, while still a student, he took part in an Oxford University expedition to Sarawak, bringing back large collections of insects, which were described in part by him and in part by others. In 1937, he married Marcia Prestidge and, the same year, joined the editorial board of the Entomologist's Monthly Magazine. He and Marcia had a 45-year association with the editing of that journal, and it was in this capacity that they had contact with so many entomologist authors. He was the editor, and a very patient one; she handled much of the correspondence. He was a member of entomological societies, president of the Society for British Entomology in 1937, elected an honorary fellow of the Royal Entomological Society of London in 1982, and elected a fellow of the Linnean Society in 1948, became a fellow of the Zoological Society of London, and was secretary of The Entomological Club (an exclusive organization) and secretary of the Ashmolean Natural History Society. His ability at swimming led not only to his participation in swimming and water polo teams but as Examiner for the Royal Life-Saving Society, Treasurer of the Oxford University Swimming Club, and President of the Oxfordshire Swimming Association. He also represented Oxford University as a chess player. He died at his home in Oxford on July 19, 1983, survived by Marcia and their one son.

References

Rivers C (1984) Dr Bertram Maurice Hobby, 1905–1983. Antenna 8:17

Smith KGV et al (1983) Dr. Bertram Maurice Hobby, 1905–1983. Entomologist's Monthly Magazine 119:179–191

Hocking, Brian

Brian Hocking was born in London on September 22, 1914. With a bachelor's degree and supportive wife, Jocelyn, he served as an entomologist in the Indian army in World War II. In 1946, he was appointed a faculty member of the Department of Entomology, University of Alberta, and eventually became professor and head. His interests were in insect flight, behavior, migration, and physiology, especially of Diptera of medical importance, the diseases transmitted by biting flies, and he studied the biting flies of Churchill, Manitoba, and means of their control. He published 110 papers and supervised research of 30 graduate students. He was president of the Entomological Society of Alberta in 1967, and was awarded the Gold Medal of the Entomological Society of Canada in 1973. He died on May 23, 1974.

Reference

Riegert PW (1989) Entomologists of Alberta. Entomological Society of Canada, Ottawa, 56 pp

Hodotermitidae

A family of termites (order Isoptera). They commonly are known as Old World harvester termites.

► Termites

Holarctic Realm (Nearctic and Palearctic Realms)

The holarctic realm is a large zoogeographic region encompassing most of North America, Europe, and northern Asia. It often is subdivided into the Nearctic realm (North America south to central Mexico) and Palearctic realm (Europe and Asia except for Southeast Asia), but the faunas are really quite similar, and characterized by such fauna as vireos, wood warblers, deer, bison and wolves.

► Zoogeographic Realms

Holcopogonidae

A family of moths (order Lepidoptera).

► Butterflies and Moths

Holdfast

A structure that functions to attach an insect to a substrate (e.g., the anal tube of some beetle larvae).

Holidic Diet

A chemically defined diet. A diet in which all the components added to the diet are precisely known. There may be chemical reactions that occur after mixing, however, that change the nature of the diet. This type of diet is important for determining the effects of various nutrients on insect biology. (contrast with meridic and oligidic diets)

Holland, William Jacob

William Holland was born in Bethany, Jamaica, on August 16, 1848, and his parents returned with him to the USA in 1851. His father, a pastor of the Moravian church, was very interested in natural history and brought collected items to Ohio, USA, from Jamaica. In 1858 the family moved again, to North Carolina, and in 1863, during the American Civil War, to Pennsylvania. In 1867 he completed studies at Moravian College, and in 1869 entered Amherst College, Massachusetts, and studied chemistry, physics, geology, astronomy, paleontology, and philosophy. After graduation he became a school principal. However, in 1871 he entered Princeton Theological Seminary at his father's request, in preparation for a church ministry. In 1874 he became pastor of a church in Pittsburgh, Pennsylvania, and worked in this position until 1891, when he became Chancellor of the Western University of Pennsylvania. While still occupying the last position, he also became in 1898 Director of the Carnegie Museum (in Pittsburgh). His great entomological contributions were his (1898) "The butterfly book…" and (1903) "The moth book…" which were affordable illustrated works on the butterflies and moths of the USA and Canada. His research was on the Lepidoptera of equatorial Africa and of Central and South America. His collection was rich in lepidopterous specimens from those places, Asia, and the USA. His interests extended also to fossil reptiles. He died on December 13, 1932.

References

Holland WJ (1929) Biographical sketch. In: Gunder JD (ed) The Carnegie Museum, Pittsburgh, Pennsylvania. Entomological News 40:205–217, p. 210–217

Mallis A (1971) William Jacob Holland. In: American entomologists. Rutgers University Press, New Brunswick, NJ, pp 308–315

Holocyclic Life Cycle

A life cycle in which a viviparous parthenogenetic female produces live nymphs without mating during some time of the year, but cyclically produces males and females that mate and produce eggs. (contrast with anholocyclic life cycle)

Holometabolous Development

A type of development, also known as complete or complex metamorphosis, characterized by the occurrence of the egg, larval, pupal, and adult stages during the life cycle. This is considered to be a more evolutionarily advanced form of development than hemimetabolous development (incomplete or simple metamorphosis).

► Metamorphosis
► Hemimetabolous Development

Holoptic

A term used to describe flies in which the compound eyes meet dorsally.

Holotype

The original specimen from which a new species description is created. Also referred to as the "type" specimen.

Homeostasis

Stability or steady state in an ecological community or in physiological functions.

Homeothermic

An organism capable of maintaining a relatively constant body temperature, usually elevated above the ambient temperature. Although some insects are capable of limited temperature regulation, they are poikilotherms, not homeotherms.

► Poikilothermic

Homeotic Gene

Genes that determine the identification and sequence of segments during embryonic development in insects.

Homeotic Genes in Coleoptera

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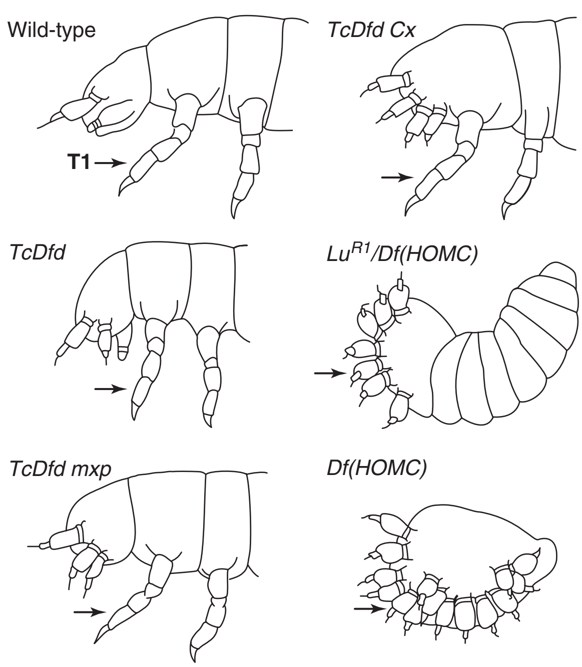
Ever since W. Bateson coined the term "homeotic" in the late nineteenth century to describe arthropod and vertebrate variants in which one body part is transformed into the likeness of another, scientists have been intrigued by the underlying implication that single genes may have large effects on the morphological development of individual segments. Indeed, during the last half-century, eight homeotic genes located in two clusters (Antennapedia Complex = ANTC and Bithorax Complex = BXC) have been identified by genetic and molecular analysis in the fruit fly *Drosophila melanogaster*. These genes encode structurally similar transcription factors that regulate many other genes to control regional identity along the anterior-to-posterior axis during embryogenesis in arthropods and virtually all other animals. A. Sokoloff and others described several homeotic mutants in the beetle, *Tribolium castaneum*, as early as 1960 in the *Tribolium* Information Bulletin. In 1987, R. Beeman determined that, similar to homeotic mutations in flies, *Tribolium* homeotic mutations display colinearity in that their order on the chromosome reflects the order of their functional domains along the anterior-to-posterior axis of the insect. In addition, he demonstrated that they are located in a single homeotic complex (HOMC) rather than in two separate clusters, as in flies. This information allowed M. Akam and others to infer the ancestral state of the homeotic complex (single and contiguous) by comparing insect and vertebrate "Hox" genes.

Genetic and molecular analyses have been exploited to elucidate the structure and function of homeotic genes in *Tribolium*. The evolutionary counterparts (orthologs) of all eight *Drosophila* homeotic genes have been cloned and characterized. In addition, the region of the *Tribolium* HOMC corresponding to the *Drosophila* ANTC has been sequenced. The expression patterns of the *Tribolium* homeotic genes are similar to those of their *Drosophila* orthologs. The genetic tractability of *Tribolium* makes it the most useful non-Drosophilid arthropod for the study of homeotic genes. Mutations in all but one of the *Tribolium* homeotic genes are now available, and comparison of mutant phenotypes between *Tribolium* and *Drosophila* orthologs has yielded several important insights into how homeotic gene function may have evolved in these two insect lineages. Many phenotypic differences may reflect the highly derived morphology of *Drosophila* larvae, which has internalized head structures and no external limbs.

Perhaps the most striking case of functional difference is that of the *Tribolium* gene, *maxillopedia* (mxp), and its *Drosophila* counterpart, proboscipedia (pb). In *Drosophila*, *pb* specifies the identity of the adult maxillary and labial appendages. In *pb* mutants, maxillary appendages are abnormal, while labial appendages are transformed to legs. However, *pb* has no apparent embryonic function, because larvae lacking *pb* function are completely normal. In beetles, *mxp* is required for proper maxillary and labial appendage identity in both larvae and adults. In individuals completely lacking *mxp* function, the maxillary and labial palps are transformed to legs. Individuals with reduced mxp function survive to adulthood and show the transformation of the adult maxillary and labial palps to legs. These observations suggest that an ancestral *pb* gene may have had an embryonic function that was lost along the lineage leading to *Drosophila*, and subsequent analysis of pb orthologs in other insects supports this conclusion.

Mutations in the *Drosophila Deformed* (*Dfd*) gene cause abnormal head development in both embryos and adults (Fig. 37), but do not produce homeotic transformations. In *Tribolium*, embryos lacking function of the corresponding gene, *Tribolium castaneum Deformed* (*TcDfd*), the mandibles are transformed to antennae and the endite lobes of the maxillary appendages are missing. This phenotype suggests that an ancestral *Dfd* gene had a homeotic function.

The embryonic phenotype of *Drosophila Sex combs reduced* (*Scr*) mutants is somewhat controversial. The first thoracic segment (T1) is unambiguously transformed toward second thoracic segment (T2) identity, but the effect on the



Homeotic Genes in Coleoptera, Figure 37 **Mutations caused by expression of homeotic genes.**

labial segment has been interpreted as either a transformation to maxillary identity, or merely a loss of labial identity. In adults, weak Scr alleles cause T1 to T2, as well as labial to maxillary, transformations. In *Tribolium*, the embryonic mutant phenotype of *Cephalothorax* (*Cx*) (the ortholog of *Scr*) is quite different from that of Scr. In larvae completely lacking *Cx*, the labial appendages are transformed to antennae, and there is no segmental groove between the T1 segment and the head, such that the T1 segment is cephalized.

Drosophila mutants lacking *Antennapedia* (*Antp*) function die as larvae and display transformations of all three thoracic segments toward more anterior segments. The posterior portion of T1 is transformed toward posterior labial identity, and T2 and the anterior portion of T3 are transformed toward T1. During adult development, patches of T2 leg tissue that lack *Antp* function are transformed toward antennal identity. However, in *Tribolium* larvae lacking function of prothoraxless (the *Antp* ortholog), all three legs are transformed to antennae.

Null mutants of *Drosophila Ultrabithorax* (*Ubx*) affect segments in the posterior thorax and the anterior abdomen. One notable effect is the appearance of a rudimentary thoracic limb (Keilin's organ) on the first abdominal segment (A1) of *Ubx* mutant larvae. Further studies have demonstrated that *Ubx* normally represses expression of *Distalless* (*Dll*) in this segment, and thus prevents Keilin's organ formation. In contrast, during embryonic development in *Tribolium*, a pair of modified appendages, called pleuropodia, transiently appears on A1. *Ultrathorax* (*Utx*), the *Tribolium* ortholog of *Ubx*, and *Dll* are co-expressed in the pleuropodia. In mutants lacking Utx, the pleuropodia are transformed toward legs. Thus, in *Tribolium*, *Utx* modifies appendage identity rather than repressing appendage formation.

The *Drosophila abdominal-A* (*abd-A*) gene is expressed throughout most of the abdomen, but *abd-A* mutations cause only the anterior abdominal segments to be transformed. In contrast, *Tribolium* mutants lacking function of *Abdominal* (*A*) (the beetle ortholog of *abd-A*) develop appendages with mixed leg/pleuropodia identity on A1–A8. Thus, the Tribolium *abd-A* ortholog (A) is responsible for the limbless abdomen in Tribolium.

The *Drosophila Abdominal-B* (*Abd-B*) gene specifies the identity of the posterior abdomen and the post-abdomen. These functions are performed by two protein isoforms, M (expressed in the posterior abdomen) and R (expressed in the post-abdomen). In *Tribolium*, expression of the *Abd-B* ortholog is limited to the post-abdomen, and mutant effects are confined to this region as well. Thus, the Tribolium ortholog seems to lack the M function. This restriction of the Abd-B domain also accounts for the expanded region affected by *A* mutants.

An overarching theme of the *Tribolium* homeotic mutant phenotypes is that removal of all homeotic genes from a segment results in the transformation of the appendages on that segment to antennae (diagrammed in the accompanying figure, first thoracic appendage indicated by arrow). This is dramatically demonstrated by a deficiency mutation, (*Df*(*HOMC*)), that deletes most of the *Tribolium* homeotic genes (*TcDfd* through *A*). Embryos homozygous for Df(HOMC) have antennae on every segment from anterior head through posterior abdomen. Another deficiency, (Lu^{R1}), which removes all HOMC genes except *A* and the *Abd-B* ortholog, as well as genes outside the HOMC, has been identified. Although, individuals homozygous for Lu^{R1} die early in embryogenesis, embryos carrying one copy of *Df*(*HOMC*) and one copy of Lu^{R1} survive to hatching. These larvae have normal abdomens, but they also have antennae on all thoracic and head segments. These results suggest that the default appendage state in the absence of homeotic genes is antenna, and that the presence of homeotic genes is required to specify other appendage types, either directly or indirectly.

In *Drosophila*, artificially induced expression of most homeotic genes transforms antennae toward legs. This transformation is apparently caused by repression of *homothorax* (*hth*), a gene required for antennal development. In the absence of *hth* and homeotic gene expression, the antennae are transformed toward legs. Thus, it appears that homeotic gene repression of *hth* causes transformation of antenna to leg by uncovering an even lower default state of appendage identity. Limited data from *Drosophila* suggest that homeotic genes also may repress antennal development within their normal expression domains. The phenotypes of the *Tribolium* homeotic mutants demonstrate that this is a conserved, global property of homeotic genes in insects, and that these genes have dual roles: the specification of regional identity and the repression of antennal identity.

References

Akam M (1989) Hox and HOM: homologous gene clusters in insects and vertebrates. Cell 57:347–349

Beeman RW (1987) A homoeotic gene cluster in the red flour beetle. Nature 327:247–249

Beeman RW, Stuart JJ, Brown SJ, Denell RE (1993) Structure and function of the homeotic gene complex (HOM-C) in the beetle, *Tribolium castaneum*. BioEssays 15:439–444

Beeman RW, Stuart JJ, Haas MS, Denell RE (1989) Genetic analysis of the homeotic gene complex (HOM-C) in the beetle *Tribolium castaneum*. Dev Biol 133:196–209

Brown SJ, Shippy TD, Beeman RW, Denell RE (2002) *Tribolium* Hox genes repress antennal development in the gnathos and trunk. Mol Phylogenet Evol 24:384–387

Denell RE, Brown SJ, Brown RW (1996) Evolution of the organization and function of insect homeotic complexes. Semin Cell Dev Biol 7:527–538

Homologous Chromosomes

Two or more identical chromosomes.

Homologous Genes

Two genes from different organisms and therefore of different sequence that code for the same gene product.

Homology

Homology has been defined as "having a common evolutionary origin," but also is often used to mean "possessing similarity or being matched." At the genetic level, it means that organisms have two or more gene products in common.

Homoplasy

The resemblance of organisms due to convergent evolution or parallelism, rather than to common ancestry.

Homoptera

Sometimes considered to be a suborder of Hemiptera, containing the aphids, whiteflies, scale insects, leafhoppers, and many other small insects with piercing-sucking mouthparts.

► Bugs

Homotomidae

A family of bugs (order Hemiptera, superfamily Psylloidea).

► Bugs

Homozygous

Diploid cells or organisms that contain two identical alleles of a particular gene.

Honey Bee, *Apis mellifera* (Hymenoptera: Apidae)

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The genus *Apis* in the family Apidae consists of at least nine species. This genus is distinguished from other bee genera by a combination of eusocial behavior, construction of vertical sheets of beeswax comb, communication and recruiting by a dance language, and a barbed stinger in the worker bee. Unlike some other bees, *Apis* species do not construct material to surround their nests.

The honey bee kept by most beekeepers, *Apis mellifera* L., is native to Europe, Africa and Asia west of the Caspian Sea. Approximately 20 subspecies are distributed across this very large range. The other *Apis* species are all native to southern and eastern Asia. *Apis cerana*, the species most closely related to *A. mellifera*, is also managed by beekeepers in China and other Asian countries.

Anatomy

The honey bee conforms to the general Hymenopteran morphology. The mandibles are developed for biting and chewing, and the proboscis for sucking liquids. Like nearly all apids, *Apis* species are adapted to collect and consume nectar and pollen from flowering plants. Branched hairs facilitate pollen collection and the pollination of plants they visit.

The queen bee is the primary reproductive female. Glands that produce pheromones are in the mandibles, tergites, rectum and tarsi. Her abdomen is noticeably enlarged when actively laying eggs, as her ovaries fill most of her abdomen. She can extend a curved, unbarbed stinger from the tip of her abdomen.

The drone is designed entirely for reproduction. He is easily recognized by his robust thorax and abdomen, and large compound eyes which touch each other dorsally and cover most his head. Most of the abdominal cavity is filled with the reproductive organs.

The worker bee is a female derived from the queen form. She is usually sterile, although she has several small ovarioles in each ovary. A few individuals in a typical colony are inclined to become "laying" workers with developed ovaries.

The worker is enabled in her many tasks by several modifications. Many of the youngest workers become nurse bees, with enlarged hypopharyngeal, salivary and mandibular glands which secrete food for larvae and the adult queen. Eight wax glands in the underside of the abdomen are activated when the colony needs to build comb. The crop is large enough for the bee to carry nearly its own weight in nectar or honey. A segment of each hind tarsus, concave and fringed with hairs, holds the pollen loads of returning forager bees. These are corbiculae, or pollen baskets. A straight, barbed stinger at the tip of the abdomen is used against intruders, including worker bees from other hives. The barbs keep it embedded in a large intruder. When the stinging bee breaks away from the intruding animal, she leaves the venom sac attached to the stinger where it continues to pulse and inject venom. The venom contains a potent mix of proteins and peptides.

Life History

The egg, larval and pupal stages of each bee are spent inside of a beeswax cell. The cells are built by worker bees according to the needs of the colony. In this way, the workers direct much of colony growth and reproduction (Fig. 38).

Honey Bee, *Apis mellifera* (Hymenoptera: Apidae), Figure 38 **Comb with adult bees, brood cells and stored honey.**

The queen cell begins as an inverted, thimble-shaped cup. Nurse worker bees add a glandular secretion, royal jelly, to the cup as the larva grows inside of the queen cell. Worker bees extend the cell walls as the larva grows. Soon the cell takes on a peanut shape, hanging down across the face of comb. The highly nutritious royal jelly allows the queen to reach adulthood only 16 days after being laid as an egg. Within a week or two of emerging from the cell, the queen takes a mating flight, returns to the hive, and begins to lay eggs. In the course of one or several flights, she will mate with 15–20 drones. After mating, her ovaries will enlarge greatly. She may lay as many as 2,000 eggs daily during late spring. In temperate climates she will cease oviposition during winter. The queen rarely lives more than 2 years. When she begins to fail due to age or disease, the workers rear a replacement queen, a process called supersedure.

Drone cells are hexagonal and horizontal, usually built along the bottom and edges of the comb. Drone larvae are fed a mix of glandular secretions and honey. The drone emerges as an adult after 24 days of development. He is fertile and prepared for mating flights within several weeks of adult life. He may fly a kilometer or more to a drone congregation area where he may mate on the wing with a young queen. If he is successful in mating, he then falls away from the queen, leaving his genitalia inside of her, and dies soon afterward. In temperate climates, any drones that survive until autumn are evicted from their hive by worker bees and die soon afterward.

Most of the cells in the hive are worker cells. They are hexagonal and horizontal like drone cells, but smaller. Worker larvae, like drones, consume glandular secretions and honey. A worker bee takes 21 days to mature in the cell, and emerges as an adult. She then takes on a complex series of tasks that collectively maintain the colony. A worker lives 1 or 2 months during the very active period of spring and summer. Workers winter with their queen in a quiet cluster in temperate regions.

As a highly eusocial insect, the honey bee is always colonial. The colony will overwinter with as few as 10,000 workers and a single queen. Colony population grows rapidly in spring, often to over 50,000 workers, several thousand drones and a queen. Colony fission, or swarming, is normal in spring. One or more queens are reared in preparation for this event. The original queen leaves the hive with a fraction of the colony's workers and drones to found a new nest. A daughter queen remains and inherits her mother's hive. One or two afterswarms may leave with other daughter queens and part of the remaining colony population.

In many regions, honey hoarding ends in early summer. Late summer and autumn are spent in reduced foraging, nest maintenance and winter preparations. In a cold winter, brood rearing and foraging will cease. The colony clusters tightly to conserve heat. A healthy, populous colony with sufficient stored honey will survive until spring, when it begins again to forage and rear brood.

One honey bee subspecies from southern Africa, *A. mellifera scutellata*, was brought to Brazil in 1956 and was later released. It reproduced and spread rapidly, as it is well adapted to the New World tropics. Over the following four decades *A. m. scutellata* displaced most of the European race bees from northern Argentina through Mexico, except where beekeepers maintained European stock. In the United States it is now established in many southern states. This African, or Africanized, bee is undesirable in most countries because of its extreme tendency to sting, swarm and abscond. However, it is a much better honey producer in the tropical countries such as Brazil, where beekeepers have learned to manage it effectively.

Another subspecies, *A. m. capensis*, is notable for its ability to produce females from unfertilized eggs. By this trait the colony can create a new queen long after its original queen has disappeared. This bee is native to a small area of South Africa. However, it has recently begun to colonize the region further north where it interbreeds with, and replaces, the colonies of *A. m. scutellata* kept by South African beekeepers. *Apis mellifera capensis* is a poor honey producer, and very difficult to exclude from hives. This bee has created a crisis in South African beekeeping.

Behavior and Physiology

During the first days of adult life, the worker bee cleans cells. Care for larvae follows, including the production of glandular secretions. Some workers will secrete beeswax, build comb, circulate air through the hive by fanning their wings, ripen honey, guard the hive entrance, and attend the queen according to the needs of the colony. The oldest bees forage for nectar, pollen and water. This progression creates a division of labor based on the ages of worker bees in the colony: age polyethism. The transition is regulated in part by juvenile hormone secreted by the corpora allata.

The honey bee colony has sophisticated mechanisms which allow it to respond appropriately to needs and opportunities. One is the flexibility in the workers' division of labor. The proportion of the workers in a colony which attend to a task changes quickly when need arises. The number of nurses, beeswax producers, guard bees, water collectors, or foragers increases if more larvae are reared, new comb must be constructed, enemies threaten, the hive overheats, or flora become available, respectively.

Another mechanism is the communication of floral food sources among foragers. A fraction of the forager bees are scouts, searching for new nectar and pollen sources. Successful scouts communicate the direction, distance and quality of food sources to other foragers inside the hive. A waggle dance in a figure-8 pattern gives this information. Direction is given by the angle of the dance on the comb, distance by the duration of the waggling, and quality by its vigor. Recruit workers that attend the dance are then able to find the flora, even kilometers from the hive.

The discovery and assessment of potential nest sites by scout bees is comparable to the cooperative search for forage. This occurs soon after a swarm has left its original hive. Individual bees search for cavities and assess them according to size, location, dryness and other criteria. These scouts communicate the location and desirability of each site to the others, by waggle dancing on the surface of the swarm. This assessment and communication behavior is analogous to that for food sources.

The queen bee's presence in the colony and her condition are communicated to the workers by pheromones. These pheromones inhibit the construction of queen cells and ovarian development in workers. On a queen's mating flight, they attract drones.

Worker bee pheromones play critical roles in colony life. One comes from the Nasanov gland at the dorsal tip of the abdomen. Workers release volatile chemicals from this gland to draw others to a particular site. When a colony must aggregate at a new nest site, or unite after a disruptive event, workers releasing Nasanov pheromone attract the other colony members. A second pheromone is a volatile mix at the stinger. When a stinger embeds in a hive intruder and breaks free of the stinging worker bee, the sting pheromone is released. This encourages other bees to sting near the same spot. By this chemical communication, a quick and painful defense is mounted against the intruder. Also, worker and queen bees produce pheromones that allow them to identify kin and nestmates.

The brood is also a source of pheromone that inhibits the development of worker ovaries and stimulates workers to forage. Beeswax stimulates foraging, apparently due to volatile chemicals in the wax secreted by the workers' wax glands.

Honey bees, like all eusocial insects, share food by passing it directly from one individual to another. This process, trophallaxis, involves the entire colony. Trophallaxis informs all colony members of the availability of food and allows the efficient transfer of food to storage cells or to those individuals that most require it.

The temperature of the colony is carefully regulated. During cold weather, the bees coalesce into a ball with their branched hairs interwoven. By rapidly contracting their flight muscles the workers generate enough heat to maintain the core of the cluster at around 35°C. In hot weather, water foragers place droplets of water on the cell walls of the comb. Other workers perch at the hive entrance and inside the hive where they pull air through the hive by fanning their wings. This evaporative cooling keeps the hive at the critical 35°C.

Honey and pollen hoarding is behavior adaptive for long periods without forage, especially winters in cold climates. Honey is made from nectar gathered from the nectaries of many types of flowering plants. A foraging worker bee carries the nectar from the flower to another worker waiting in the hive, which in turn deposits the nectar in a wax cell. Other workers then ripen the nectar into honey by adding enzymes and evaporating much of the water by fanning their wings to circulate air through the hive. Ripe honey contains glucose, fructose, approximately 18% water, a small amount of hydrogen peroxide, and is slightly acidic. Microbes will not grow in ripe honey. Small amounts of minerals, amino acids and other nutrients vary in honey according to the floral source. Pollen is also stored in wax cells, with honey and glandular secretions added.

Honey is primarily an energy source for adult bees. Pollen contains protein, vitamins, lipids and minerals to support brood rearing and the queen when she is laying eggs. Pollen is not directly consumed by larvae and the queen, however. Nurse bees feed glandular secretions to them after digesting large amounts of pollen.

Genetics and Breeding

Like all hymenopterans and some insects of other orders, honey bees are haplodiploid. Females have two sets of 16 chromosomes, while drones have one set. When the queen is about to lay an egg she may apply a bit of semen from that stored in her spermatheca, as the egg passes through her reproductive tract. This egg is thereby fertilized, and in most cases becomes diploid and a female. Alternatively, the queen may withhold semen from the egg. It is then laid as a male, retaining its haploidy. The development of individuals, in this case males, from unfertilized eggs, is termed parthenogenesis.

The queen's ability to control the sex of her offspring is critical to social life. The rearing of drones, which are unable to perform the tasks necessary to colony maintenance, is relegated to mating season.

Honey bees differ from many hymenopterans in their sex determination mechanism. A single locus controls the sex of the individual bee. A diploid bee that is heterozygous at this "sex locus" is female. A haploid bee has only one allele at the locus and hence develops as a male, or drone. Most populations of honey bee colonies include many alleles for this locus. Consequently, most fertilized eggs will be heterozygous and female. However, some fraction of the diploids will be homozygous, depending on the number of alleles in the population and the degree of inbreeding. These individuals become "diploid drones." They are routinely cannibalized as very young larvae shortly after they hatch.

The queen bee's habit of mating far from her hive and with many drones has important implications for the colony. It promotes outbreeding and ensures that most of her diploid offspring will be heterozygous at the sex locus, hence female. Also, multiple mating creates multiple subfamilies of workers within the colony. Worker bees with the same queen mother and drone father share 75% of their genes by common descent. Workers from the same mother and different fathers share only 25% of their genes by common descent. These relationships are the basis of cooperation and rivalry among colony members. Much of our understanding of insect sociality is derived from the genetic systems of honey bees and other social Hymenopterans.

Honey bee breeding has been fairly successful in many respects. Bees can be bred for gentle behavior, disease and mite resistance, honey production, pollen hoarding and color. However, breeding is complicated by two factors. One is the bees' habit of mating in flight, far from the hive. Attempts to control mating within an enclosed structure or on isolated islands have been unpractical or unsuccessful. Complete control over breeding relies on instrumental insemination. This technique works well, but is laborious when practiced for a large scale operation. The second factor is the production of diploid drones as lines are inbred to select for a desired trait. Inbred colonies with queens producing many diploid drone larvae suffer badly. A closed breeding population must be maintained carefully to retain sufficient sex alleles.

The honey bee genome was sequenced in 2004. This allows close inspection of the bee's traits and also illuminates comparisons with other species.

► Apiculture
► Bees
► Pollination and Flower Visitation
► African Honey Bee
► Cape Honey Bee

References

Rinderer T (ed) (1986) Bee genetics and breeding. Academic Press, New York, NY
Ruttner F (1988) Biogeography and taxonomy of honeybees. Springer Verlag, New York, NY
Seeley TD (1985) Honey bee ecology: a study of adaptation in social life. Princeton University Press, Princeton, NJ
Snodgrass RE (1956) Anatomy of the honey bee. Cornell University Press, Ithaca, NY
Winston ML (1987) The biology of the honey bee. Harvard University Press, Cambridge, MA

Honey Bees

Members of the family Apidae (order Hymenoptera, superfamily Apoidae).

► Bees
► Wasps, Ants, Bees and Sawflies
► Apiculture (Beekeeping)
► Pollination an Flower Visitation

Honey Bee Sexuality: An Historical Perspective

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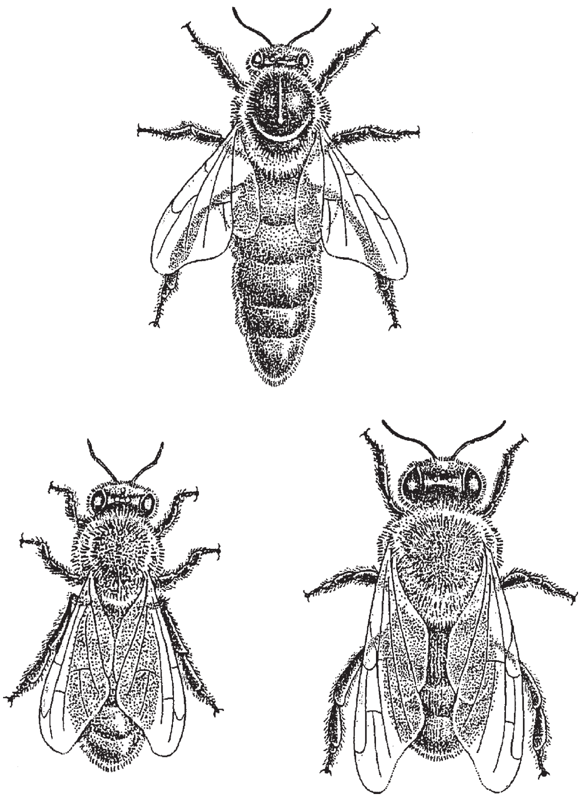
Before honey bees (*Apis mellifera* L. and other *Apis* species) were domesticated, honey was gathered from wild hives. Rock painting dating from 8,000 to 15,000 years ago depict a fascinating history of this process. The earliest recorded hives, which signify domestication, are about 5,000 years old, and are seen in paintings and drawings on tombs and other monuments in Egypt. However, the traditional hives of Iran and Turkey may provide a clue to the question of the origin of the hives that were depicted in Ancient Egypt.

Despite a long history of beekeeping, the first report on the sexuality of the queen honey bee is relatively new. Although Aristotle (384–322 B.C.) noted that some authorities referred to the large ruler bee as the hive's mother, he found the hypothesis unlikely, as "nature only arms males." Because the hive's ruler has a sting, Aristotle concluded that it must be the king and the defenseless drones were, therefore, the females (Fig. 39). Although erroneous, Aristotle's word was taken as virtual law for the next 1,800 years.

It was not until 1609 that Charles Butler (an English beekeeper) in his famous book titled "The Feminine Monarchie," challenged the idea of king bees. Thereafter, in 1670, a Dutch scientist (Jan Swammerdam) proved this hypothesis through dissection, accompanied by his full anatomical drawings of queen, drone and worker. He died in 1680, but his work was not published until 1737–1738.

"The Feminine Monarchie" consists of over 230 pages in ten chapters. The introductory chapter (Cap. I.), titled "Of the nature and properties of Bees, and of their Queene," contains information on the benefits and behavior of honey bees in general and a description of the Queen bee in particular.

"*Among all the creatures which our bountifull GOD hath [has] made for the use and service of man, in respect of (1) great profit with small cost (2) of their ubiquity or beeing [being] in al [all] countries, and (3) of their continual labour and consenting order, the Bees are most to be admired. For first with the provision of a hive and some little care and attendance, which need be no hinderance to other busines [business], but rather a delightful recreatio*



Honeybee Sexuality: An Historical Perspective, Figure 39 **Three castes of adult honey bees: *above*, the queen; *below left*, the worker, and *below right*, the drone.**

amid the same, they bring in store of sweete delicates most holesome both for meate and medicine…

"For their order it is such that they may wel [well] be said to have a comon wealth, since al that they do is in como [community] without any privat [private]… They work for al, they watch for al, they fight for al. In their private quarrels when they are from the hive or common treasury howsoever you use them they wil not resist it by any meanes they can get away. Their dwelling and diet are common to al alike: they have like commo [common] care both of their wealth and young ones. And al this under the government of one Monarch, of whom above al things they have a principal care & respect, loving, reverencing, and obeying her in al things.

"If she goe [goes] forth to solace [rescue] her selfe (as sometime she wil) many of them attend upon her, garding her person before and behind; they which come forth before her ever now & the returning, and looking back, and making with all and extraordinarie noise, as if they spake [speak] the language of the knight. Marshalls men, & so away they fly together, and anon [immediately] in like manner they attend her back againe [again]. This I may say because I have seene [seen] it: although the Philosopher be of another minde [mind].

"If by hir [her] voice she bid them goe [go], they swarme [swarm]; if being abroad she dislike the weather, or lighting place, they quickly returne [return] home again; while she cheereth [cheers] thé [them] to battaile [battle] they fight; when she is silent they cease, while she is well, they are cheerfull about their worke [work], if she droope [droops], they faint also; if she dy [dies], they will never after prosper, but thenceforth languish till they bee [be] dead too.

"If they have many Princes, as when two fly away with one swarme, or when two swarmes are hived to gether [together]: they strike one of them presently, and sometime they bring her down that evening to the matle [battle?], where you may find hir covered with a little heape [heap] of Bees, otherwise the next day they carie [carry] her forth either dead or deadly wounded. Likewise if the olde [old] Queene [Queen] bring forth many Princes (as she may have six or seaven [seven], yea sometime halfe [half] a skore or more which superfluitie [superfluity] nature affordeth [affords] for more suretie [security], in case some miscarrie [miscarry]) then lest [in order to avoid] the multitude of rulers should distract the unstable commons into factions, within two daies [days] after the last swarme, you shall finde [find] them that remained, dead before the hive. I have taken eight of thé [them] up [above-mentioned] together brought out of one hive, when two were already gon [gone] forth with the swarmes.……

"The Queene-bee is a Bee of a comely and stately shape, browne [brown] of colour as other Bees, but that her belly is more bright: she is longer thé [than] honi-bee [honey-bee], by one third part, that is almost an inch long: she is also bigger then [than] a honi-bee [i.e., the Worker] but not so big as a drone, although somewhat longer: hir head

proportionable, but that it is more roud [round] thé [than] the little Bees, by reason hir fanges [fangs] be shorter; hir tonge [tongue] not halfe so long as the little Bees: for whereas they gather with one nectar, with the other ambrosia, shee [she] hath no need to use either, beeing to bee [be] maintained, as other Princes, by the labor of hir subicects [subjects]; hir wings of the same size with a smal [small] Bee, & therefore in respect of hir long body, they seeme [seem] very short, for they reach but to the middle of hir nether [lower] part: hir legges [legs], proportionable, and of the colour of hir belly, but hir two hinlegges more yellowe: hir nether part so long, and halfe so long as hir upper part, more picked thé [than] smale Bees, and without such three whitish ringes [rings] as other Bees have at the three partitions: the speere [spear] she hath is but little, and not halfe so long as the other bees: which, like a kings sword, is borne rather for shewe [show] and authoritie [authority], then [than] for any other use: For it belongeth [belongs] to her subiects as well as to fight for her, as to provide for her."

The year 1609 A.D. (i.e., the date of publication of "The Feminine Monarchie") is considered by some to mark the beginning of our knowledge about the sexuality of the ruler of the hive (the Queen). However, the first person to understand the sex of the queen probably was Luis Méndez de Torres in Spain who published a book in 1586 titled "*Tractado breve de la cultivacion y cura de las colmenas*." In this book, he stated clearly that the leader bee in the hive laid the eggs, from which all workers, drones and future queens developed. In addition to de Torres, the knowledge of several Persian scientists about the queen bee may be traced back to a much earlier period.

Ikhawân-ul-Safâ (or The Brethren of Purity), who flourished in A.D. 950–1000 at Basra, composed a series of tracts in Arabic language known as the "Epistles of the Brethren of Purity," (also reported as "Epistles of the Brethren of Sincerity") in the latter half of the tenth century (A.D. 950–1000). The authors of these series were six encyclopaedists, with at least three of them from Persia. Among their work, the "Dispute Between Man and the Animals" is of zoological interest. The following citation from this work refers to the sexuality of the ruler of the hive:

"*There, the king of the hasharât [insects], Ja'sub [i.e., the bee queen], rules over the wasps, the flies, the bugs, the mosquitoes, the dung beetles, the spanish flies, the butterflies and moths and over the locusts, i.e., over all small animals which fly by wings, have no feathers, no bones, no soft hair and no fur.*"

The above statement, which uses the Arabic word of *Ja'sub* [the bee queen], clearly refers to the sexuality of the hive ruler. It is also the first attempt to define an insect. After about three centuries, al-Qazwini (the author of "*Ajâ' ib al-Makhluqât*," composed in A.D. 1263) clearly speaks of the role of the king of honey bees (the queen) in the production of a new king. Despite this report, the sexuality of the queen as well as the definition of the insect were overlooked by other scholars for a long time. While the sexuality of the "King" remained unnamed until publication of "The Feminine Monarchie" by Charles Butler in 1609 A.D. (or the publication of the book of Luis Méndez de Torres in 1586 A.D.), the definition of insect was ignored until the seventeenth century.

Some citations from al-Qazwini (1263) follow:

"*Honeybee is a nice, pleasant animal with fine body structures…*"

"*A king has been established to give orders. He has inherited his honour from his ancestors, since it is the king who produces again a new king.*"

"*The king is twice as large as the others and leads the work…*"

Although the word "King" used in the former sentences may indicate the ignorance of al-Qazwini about the sexuality of the "Queen," the second phrase (i.e., "since it is the king who produces again a new king"), leaves no doubt on the awareness of this author about the sex of the "Queen."

References

Abivardi C (2001) Iranian entomology – an introduction, 2 vols. Springer Verlag, Heidelberg, Germany, 1033 pp

Butler C (1609) The feminine monarchie: a treatise concerning bees, and the due ordering of them wherein the truth, found out by experience and diligent observation, discovereth the idle and fond conceipts, which many have written anent this subject. Joseph Barnes, Oxford (Facsimile reprinted by De Capo Press, Amsterdam 1969), not paginated
Crane E (1983) The archaeology of beekeeping. Duckworth, London, UK, 360 pp
Crane E (1985) World perspectives in apiculture. International Bee Research Association, London, UK, 184 pp
Gould JL, Gould CG (1995) The honey bee. Scientific American Library, New York, NY, 239 pp

Honeydew

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Honeydew is the liquid excrement produced by certain insects in the order Hemiptera that feed on the phloem of plants. It is an often highly concentrated, sugary fluid mixed with some nitrogenous compounds. Honeydew is primarily produced by aphids, certain "soft scales," mealybugs, whiteflies, some leafhoppers and some treehoppers. Honeydew is sometimes used to describe the sugary-rich materials exuded from certain plant structures and some insect galls.

The sugars found in honeydew are a complex of simple plant-derived sugars (e.g., glucose, fructose) and more complex sugars (e.g., melezitose) that have usually been derived by the insect using enzymes. Various nitrogenous materials are found in honeydew that primarily reflect plant products of the host plant, but also includes waste products of the insect. Nitrogenous materials may occur in concentrations typically ranging 1–2% in honeydew.

Excreted honeydew is sometimes described as "dripping sap" or "ghost rain," particularly when it drops from shade trees. Some honeydew-producing insects may excrete several times their weight per day. It is sticky and can foul surfaces where it lands, producing significant nuisance problems. Surfaces on which honeydew persists also allow growth of sooty mold fungi.

The high sugar content of honeydew may also attract wasps and bees. This can create nuisance problems with these insects aggregating as they forage on shade trees, shrubs and ornamental plants. However, honeydew is sometimes a valued resource for honey bees, particularly in Europe where honey dew-derived honey may be described as "forest honey," usually collected when normal nectar sources are limited and honeydew-producing insects are common.

Honeydew and other exudates of phloem-feeding hemipterans have also been used as sweet materials in the human diet, sometimes described as manna. The most notable description of this material is from the Biblical chapter Exodus, and likely involved a honeydew-producing local scale insect (*Trabutina mannipara*) associated with tamarisk.

Honey Pot

A container constructed from cerumen by stingless bees and bumblebees and used to store honey.

Hood

A structure found in soft ticks that projects over, and covers, the mouthparts.

Hoogstraal, Harry

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Harry Hoogstraal was born on February 24, 1917 in Chicago, Illinois. As a young man he and his sister Catherine were taken by their mother to the Chicago Natural History Museum on Lake Shore Drive to attend Saturday morning lectures for children on natural history. Mrs. Hoogstraal then convinced museum administrators to allow Harry to listen also to Saturday afternoon lectures for adults. Here they were exposed to fascinating adventures by speakers such as Admiral Byrd and makers of wildlife films, and Harry was allowed into the research area of the museum. This exposure kindled a passion for natural history that Harry maintained for the rest of his life.

He went on to receive the B.A. degree from the University of Illinois and, while working on a M.S. degree from the same university, conducted four expeditions (1938–41) exploring the distribution of animals and plants (first on reptiles and amphibians) and later with the late Robert Traub and Kenneth L. Knight (fellow student) collecting invertebrates, mammals and birds. During the second year, the brakes failed on a truck that Harry was driving on June 20, 1940, while on a remote mountain road in the Sierra Madre mountains, in the central highlands of Mexico. Harry was caught beneath the truck's frame when it rolled, while his associates in the back were thrown clear. His back was broken and he suffered other injuries and was taken to the hospital in Mexico City where physicians predicted he would never walk again. However, two physicians from the University of Chicago were visiting and they just happened to have a new sulfa drug, sulfonilimide, that had been recently developed. He was treated with this drug, making him one of the first persons to receive it.

After receiving the M.S. degree in 1942 he joined the U.S. Army and worked on mosquito taxonomy in New Guinea and in the Philippines. During wartime he developed plans for a Philippine expedition with Donald Heyneman, Floyd Werner and Philippine colleagues by convincing the herpetologist, Karl Schmidt, Curator of Zoology, Field Museum to join with the Philippine National Museum in conducting a faunal survey.

Later, in 1948–49, he conducted surveys in East Africa and Madagascar under the U.S. Navy and the University of California African expedition and became head of the Sudan sub-unit of Naval Medical Research Unit #3, where he conducted host-parasite studies in the equatorial province of the Sudan. This resulted in his 1,099 page monograph on the "Ticks of the Sudan" (1956), which continues to be cited today. In 1950 he became Head of the Medical Zoology Department at NAMRU #3 in Cairo, a post that he held until his death. He received the Ph.D. from the London School of Hygiene and Tropical Medicine in 1959, with the D.Sc. from the same institution in 1971. He also received a doctorate (honoris causa) in 1978 from Ain Shams University, Cairo and an honorary D.Sc. from the University of Khartoum in 1983.

Starting in the late 1940s, Harry pursued the study of ticks with a single-minded dedication, producing over 500 research papers, an 8-volume bibliography of ticks and tick-borne diseases, and over 1,750 translations of Russian and Chinese articles. Harry was interested in ticks on a world-wide basis, not just in Africa, and few scientists outside of Russia or China could read these languages. When Madam Pospelova-Shtrom published her paper on a new *Argas* tick from a vulture in Turkmenia (former USSR) (previously known as the fowl tick, *Argas persicus*), Harry made the translation (T89) available to anyone working on ticks. He would routinely send his publications to anyone interested in ticks, as well as copies of his bibliography, and he cooperated with Rocky Mountain Laboratory scientists in Montana (USA) as well as tick authorities in England, and in South Africa. He and Makram Kaiser then reviewed the *Argas persicus* problem by re-examining as many ticks as possible from museums and collections that had previously been misidentified as *persicus*, resulting in several new species being described such as *Argas arboreus* from heron and cattle egret rookeries in Cairo, *Argas africolumbae* from swallows in South and East Africa, *A. zumpti* from a vulture in South Africa, and *A. walkerae* from domestic poultry in southern Africa. In the Americas, persicus were also re-examined as it was originally believed this tick occurred world-wide between 40° N and 40° S latitude. Glen Kohls and C. Clifford then reported *A. sanchezi* in southwestern USA and Mexico, *A. radiatus* in central and southern USA, and *A. miniatus* in Panama and South America; all had previously been misidentified as *persicus*.

Harry was considered a workaholic and slept only short periods at night. However, this restlessness was forced upon him due to the truck accident in Mexico that left him in considerable pain. Another reason for Harry's tremendous productivity was that he took full advantage of postal services (before e-mail) to persuade anyone working in tropical countries to send him ticks they had collected. He also kept up-to-date with his correspondence (150–200 letters/week), which often kept three or four secretaries working full time to keep up with him. Harry would have the ticks sent to him identified and catalogued, or refer them to Kaiser in Cairo or Clifford and Keirans (in Montana), and then correspond with the collector regarding their identification, often requesting more material. For example, Dr. Alex Fain (Belgium) sent Harry males and larva of an argasid tick from fruit bats that were collected in Zaire (1956) but Harry needed the other tick stages so when the late Dr. Robert Usinger, on sabbatical leave from University of California was planning a trip to Africa to collect cimicid Heteroptera, Harry asked him to look for more material of this tick; subsequently, Usinger collected females and nymphs that turned out to be a new species, *Ornithodoros* (now *Carios*) *faini*, from roosts of *Rousettus* fruit bats in the Congo. Usinger sent a sample of the live ticks to Harry in pouch-mail from Zaire and hand carried another sample to Cairo to ensure their survival for rearing purposes so that all of the stages (larva, nymph, male, female) could be described and illustrated in the published manuscript. Harry, as well as his colleagues in Montana, didn't wish to describe new species of ticks based on only one of the stages. When a particular tick was collected it would be catalogued and compared with closely related material that was often laboratory reared. Previously, tick workers had described ticks based on finding one sex (the male, for example) and confusion could later result when other stages were collected. Harry would not describe a species based on only a single specimen.

Harry also did not believe in what he called "tampering with present concepts of tick genera," something done in present day with the discovery of RNA/DNA and molecular studies. He believed that phylogenetic trends among ticks, especially in the genus *Argas*, were lucidly demonstrated on a subgeneric level.

A portion of the ticks collected would always be preserved and portion "ground up" by his associates in Cairo or at the Rocky Mountain Laboratory (Montana, USA) and tested for arbo-viruses. This was undertaken before the tick arbo-viral activities of the U.S. Public Health Service were phased out.

Robin Rice (Hawaii) was an individual Harry recruited to collect ticks for him on Peruvian cliffs, in the Galapagos of South America, in coastal Texas of the USA, and in southeastern Kenya of East Africa. Some of the African material that Rice collected remains undescribed to this day, as more material was needed by Harry before publication to be sure that they were new species. This author (E.R.E) accompanied Harry to an escarpment south of Nairobi near Lake Kwenia to search for argasid ticks of the Griffon vulture (1975). There we examined the massive thorn-stick nests of the red-billed buffalo weaver in Baobab trees (Kiboko Range Research Station) for a tick previously collected there by Rice and tentatively known as *A. bubalornis*; it remains undescribed.

His enormous tick collection was combined with the Rocky Mountain Laboratory collection and his material is currently housed at the U.S. National Tick Collection, currently on loan with Georgia Southern University in Statesboro.

Harry was a complex man, having many interests, including sculpture and culture of cacti. He died in his sleep in Cairo on his 69th birthday, on February 24, 1986.

References

Heyneman D (1985) Presidential address. Introduction of President Hoogstraal. In: 60th Annual Meeting of the

American Society of Parasitologists, Athens, Georgia, pp 685–686
Keirans JE (1986) Harry Hoogstraal (1917–1986). J Med Entomol 23:342–343
Linsley EG, Gressitt JL (1972) Robert Leslie Usinger: autobiography of an entomologist. In: Memoirs of Pacific Coast Entomological Society, San Francisco, CA, pp 223–224
Yunker CE, Keirans JE (1998) Makram N. Kaiser 1930–1996. Exp Appl Acarol 22:61–62

Hooktip Moths (Lepidoptera: Drepanidae)

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Hooktip moths, family Drepanidae, comprise 812 species worldwide, but predominately Oriental (647 sp.); none are known for the Neotropics and only a few are in the Nearctic; the actual fauna probably exceeds 950 species. Three subfamilies are known: Drepaninae, Oretinae, and Nidarinae (the latter only from Madagascar). The family is in the superfamily Drepanoidea, in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults small to medium size (18–66 mm wingspan), with head scaling normal; haustellum small or absent in some species; maxillary palpi vestigial; antennae bipectinate to filiform; body sometimes somewhat robust. Wings broadly triangular, usually with the forewings falcate; hindwings mostly rounded (Fig. 40). Maculation mostly shades of brown to yellow with various markings, sometimes more colorful, or hyaline to white with tan bands. Adults nocturnal. Larvae are leaf feeders. Host plants include a variety of plants in Anacardiaceae, Betulaceae, Caprifoliaceae, Fagaceae, Myrtaceae, Rosaceae, Theaceae, and others. A few are economic.

Hooktip Moths (Lepidoptera: Drepanidae), Figure 40 Example of hooktip moths (Drepanidae), *Tridrepana flava* (Moore) from Taiwan.

References

Bryner R (1997) Drepanidae – Sichelflügler. In: Schmetterlinge und ihre Lebensräume: Arten-Gefährdung-Schutz. Schweiz und angrenzenden Gebiete, 2:447–476, pl 11. Pro Natura-Schweizerische Bund fuer Naturschutz, Basel
Holloway JD (1998) Family Drepanidae. In: The moths of Borneo, Malayan Nature Society (Malayan Nature Journal, 52), Kuala Lumpur, Malaysia, 8:17–70, pl 1–4, 6, 8
Seitz A (ed.) 1911–33. Familie: Drepanidae. In: Die Gross-Schmetterlinge der Erde, 2:195–206, pl 22–23, 30, 48 (1911); 2 (suppl):167–170, pl 10 (1932–33) 6:631–633, pl 86 (1928); 10:443–490, pl 48–51 (1922–23); 14:287–292, pl 41 (1927). A Kernen, Stuttgart
Watson A (1965) A revision of the Ethiopian Drepanidae (Lepidoptera). Bull Brit Mus (Nat Hist), Entomol 1–178 (Suppl 3): 18 pl
Watson A (1968) The taxonomy of the Drepanidae represented in China, with an account of their world distribution (Lepidoptera: Drepanidae). Bull Brit Mus (Nat Hist), Entomol 1–151 (Suppl 12):, 14 pl
Wilkinson C (1972) The Drepanidae of Nepal (Lepidoptera). Khumbu Himal 4:157–332

Hope, Frederick William

Frederick Hope was born in London on January 3, 1797. In 1817 he entered Oxford University, and graduated in 1820 with a B.A. degree in classics, and in 1823 obtained an M.A. The intent was that he should enter the church, and he was presented with a curacy in the county of Shropshire, but his health did not allow this to continue. While he was an undergraduate, he became fascinated with the natural sciences and spent much time studying geology and entomology. After leaving Shropshire, he returned to London and,ww later aided by Ellen Meredith, the wife he married in 1835, began to collect natural history objects into his own private museum. He built his collections not just by his own collecting, but by purchase, gifts and exchange, such that he acquired materials from Britain and abroad. He travelled in France, Germany, Holland and Switzerland in the 1830s. He was elected fellow of The Royal Society in 1834. He was one of the founder members of the Entomological Society of London in 1833, and served as president in 1835–1836, 1839–1840, and 1845–1846. He also published mainly taxonomic works on insects, especially Coleoptera, and many in the pages of the journals of the Entomological Society of London. These works included descriptions of some of the insects collected by Charles Darwin. In 1855, Oxford University began to build a new museum to house scientific collections, and Frederick Hope's collections and personal library were promised to that museum by deed of gift, with the stipulation that a conservator of his collections should be appointed by the university. Thus, the position of Hope Professor of Zoology was created, and this position was held first by J. O. Westwood. Frederick Hope died on April 15, 1862. A few entomologists (faculty, technicians, and graduate students) associated with the Hope Professor of Zoology (Entomology) remained housed with the Hope Entomological Collections and Hope Library in the University Museum, as the Hope Department of Entomology, until 1978. Then, the name Hope Department of Entomology disappeared, merged into Oxford University's Zoology Department. The title of Hope Professor of Zoology (Entomology) disappeared in 1995. But, the name "Hope Entomological Collections" still persists for the insect collections housed in the University Museum, and a curator and assistant curator are responsible for them. The lecture room of the University Museum, on Saturday June 30, 1860, was scheduled to be the site of the now-famous debate between Thomas Henry Huxley, a staunch supporter of Darwin, and Samuel Wilberforce, Bishop of Oxford and creationist. Wilberforce "begged to know, was it through his [Huxley's] grandfather or grandmother that he claimed descent from a monkey." Huxley replied that he would not be ashamed to have a monkey as an ancestor, but he would be "ashamed to be connected to a man who used great gifts to obscure the truth." It would be expected that Hope and Westwood would have been present at that meeting of the British Association. Their reactions were not recorded. Neither had accepted Darwin's theory, although both had been correspondents of his, and both described species that he collected during the voyage of the Beagle.

References

Irvine W (1959) Apes, angels, and Victorians. Meridian, Oxford, OH, 399 pp

Smith AZ (1986) A history of the Hope entomological collections in the University museum, Oxford, with lists of archives and collections. Clarendon Press, Oxford, xiii 1/2 172 pp

Hopkins, Andrew Delmar

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A. D. Hopkins, a pioneering entomologist, is generally considered the "father of forest entomology in North America." He was born in Harrison County, Virginia (now Jackson County, West Virginia) on August 20, 1857. Though he never received much formal education, Hopkins showed an interest in natural history at an early age, spending many hours collecting and studying rocks, plants, and animal life in the rural West Virginia landscape where he grew up. His formal education ended at age 17, though he would receive an honorary doctoral degree in 1893. As a matter of fact, Hopkins appears to have had a relatively low opinion of formal education, and espoused the opinion that "college is a place where pebbles are polished and diamonds dimmed." His lack of formal training certainly did not prevent him from becoming an eminent scientist and ushering in the discipline of forest entomology in the United States.

Hopkins was deeply involved in the agricultural activities of West Virginia, and organized one of the first farmer's cooperatives in the state, the Farmers' Institute Society. He was an accomplished agriculturalist himself, developing a superior strain of timothy hay through plant breeding, and introducing purebred sheep and cattle to the area. Through his activities with the Society, he became acquainted with Dr. John Myers, the first director of the West Virginia Agricultural Experiment Station. In 1889 Hopkins wrote Dr. Myers, volunteering to be the entomologist for the Station, but was politely rebuffed due to his lack of formal training. Not one to be easily discouraged, Hopkins wrote back, offering to work on a trial basis for $1.00 a day. Dr. Myers offered him the job on trial for 3 months at $50.00 per month. Hopkins officially began work on March 1, 1890.

Hopkins early research projects (Fig. 41) involved a large bark beetle outbreak in the pine and spruce forests of eastern West Virginia, and Hessian fly as a pest of wheat. His seminal work on the Hessian fly showed that delayed planting could control the fly, and he produced appropriate planting dates for West Virginia and much of the United States as well. This work was the foundation for a lifelong interest in bioclimatics, the study of the relationships among life, climate, and the seasons.

Hopkins' discovery of a massive bark beetle outbreak in the pine and spruce forests of Randolph County and his subsequent investigations of this group of insects launched his career as a forest entomologist, and marked the beginning of forest entomology as a distinct discipline in the U.S. It was for this work that Hopkins would receive his honorary Ph.D. degree in 1893 from West Virginia University. After extensive sampling, Hopkins concluded that the southern pine beetle, *Dendroctonus frontalis*, was the major cause of tree mortality. Hopkins initiated an early forest entomology importation biological control program, importing the clerid beetle *Thanasimus formicarius* from Germany for release against the beetles. However, there was no evidence that the clerids became established, and the bark beetle epidemic subsided following a severe winter in 1893–94. Interestingly, Hopkins and his clerid release received credit for ending the bark beetle epidemic, even though Hopkins emphatically denied that the clerids had become established.

Hopkins, Andrew Delmar, Figure 41 **Andrew D. Hopkins, the Father of American Forest Entomology.**

During his 12 years with the Experiment Station, Hopkins published scientific papers and bulletins at a prodigious rate. In addition to his papers on the southern pine beetle outbreak, his most important forest entomology works included the "Catalog of West Virginia Scolytidae (Bark Beetles) and Their Enemies" and "Catalog of West Virginia Forest and Shade Tree Insects." As an indicator of Hopkins' productivity, during a single year with the Experiment Station he described 196 new species and six genera of insects, and this was primarily background work for his studies of insect biology and pest control. In addition to his research work, Hopkins duties included answering hundreds of extension-type questions from citizens on a wide variety of entomological subjects.

Hopkins expertise in forest entomology was recognized by the U.S. Department of Agriculture, and Gifford Pinchot, head of the Division of Forestry, hired him to conduct special investigations of insect problems in forests of the western U.S. Hopkins had traveled through parts of the far west in 1899, and made observations on stand characteristics of ponderosa pines that became the basis for a risk rating system for this species. In barely over 2 months, Hopkins correctly identified and detailed most of the important forest insect problems of the far west. In October 1901, he was sent to the Black Hills region of South Dakota to investigate bark beetle problems there. Though he was in the Black Hills for only 4 days, Hopkins collected an incredible amount of information on the mountain pine beetle, *Dendroctonus ponderosae*, which he published in a bulletin only 3 months later.

In 1902, Hopkins took a position with the U.S. Department of Agriculture Bureau of Entomology in Washington, D. C., initially working under the famous entomologist C. V. Riley. Within 2 years, however, he was named head of the Division of Forest Insects, a position he would hold for 21 years until his retirement in 1923. Among those who worked under his direction during this period were F. C. Craighead, H. E. Burke, J. M. Miller, F. P. Keen, and W. F. Fiske, a virtual "Who's Who" of forest entomologists in the early twentieth century.

Characteristically, Hopkins remained quite active after his retirement from the Bureau of Entomology. He quickly resumed pursuit of his lifelong interests in plant breeding and bioclimatics. One well-known product of this research is Hopkins' Bioclimatic Law, which states that elevational decrease in temperature is mirrored in latitudinal decrease in temperature as one moves away from the equator. His Wood County, West Virginia farm was designated a special field station of the Department of Agriculture, "The Kanawha Farms Intercontinental Base Station for Bioclimatic Research." Hopkins was married in 1880 to Adelia Butcher, and they had four children, including W.B. Hopkins, who became a well-known petroleum engineer and was listed in "Who's Who in American Men of Science." A. D. Hopkins died in 1948, truly one of the outstanding scientists of his time.

References

Berisford CW (1991) Andrew Delmar Hopkins – a West Virginia pioneer in entomology, vol 14. West Virginia University Agricultural and Forestry Experiment Station, Morgantown, West Virginia, pp 20–26

Furniss MM (1997) American forest entomology comes on stage: bark beetle depredations in the Black Hills forest reserve, 1897–1907. Am Entomol 43:40–47

Johnson MM (1930) A half century with a West Virginia scientist. West Virginia Rev November:47, 65

Hopperburn

A plant disease caused by toxicogenic secretions associated with feeding, usually by leafhoppers (Hemiptera: Cicadellidae), hence the common name.

Hoplopleuridae

A family of sucking lice (order Phthiraptera).

► Chewing and sucking lice

H-Organ

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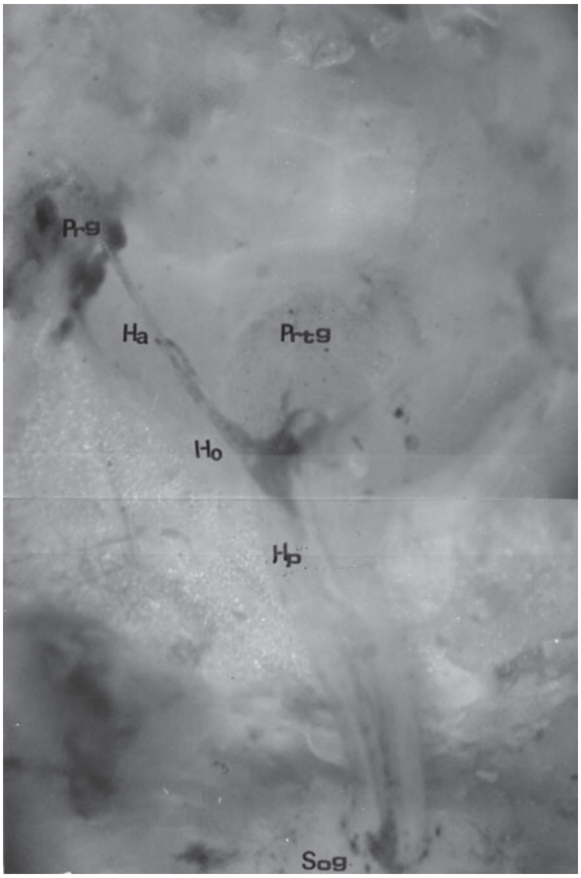
H-organ is a neurohaemal organ associated with the perisympathetic organs of the ventral nerve cord. The H-organ was first discovered in 1986 in various Lepidopteran species and later was studied in some Orthopterans. It is named the H-organ due to its shape, resembling the letter H. It is located in the prothoracic region between the subesophageal ganglion and prothoracic ganglion. It is approximately three times smaller than a single prothoracic gland. It extends across the narrow cervical region and is exposed to good hemolymph flow. The organ consists of three parts: anterior arms, posterior arms and a central region. The anterior arms stretch out laterally toward the prothoracic glands and consist of two types of nerve fibers. The posterior arms are composed of nerve axons extending backward and to the lateral arms. The central part of the organ is connected with the prothoracic ganglion via median nerves. The organ includes abundant nerve fibers, invaginated neurilemma, neurosecretory products and irregularly distributed glial cells. The H-organ is very similar to the regular metameric perisympathetic organs. However, the organ has a very complex structure, differing from other regular perisympathetic organs in its appearance, and consisting of two fused perisympathetic organs. The first belongs to the subesophageal ganglion attached from its rear, and the second is in the frontal part of the prothoracic ganglion. The most complicated part appears in the middle region. In this branching area between the anterior arms, transverse nerve of the H-organ (Fig. 42) and the posterior arms, an organ that seems like the corpus cardiacum was found. The H-organ receives neurosecretory product from both subesophageal and prothoracic ganglia.



H-Organ, Figure 42 **The H-organ in the prothoracic region of an insect: Prg = prothoracic gland; Ha = anterior arm of the H-organ; Ho = H-organ; Hp = posterior arm of the H-organ; Prtg = prothoracic ganglion; Sog = subesophageal ganglion.**

The H-organ often shows species-specific variations in its shape. Within the order Lepidoptera, in *Pieris brassicae* and some other members of the family Pieridae and Nymphalidae, the organ is almost rectangular or square. In *Actias selene* and several other members of the family Saturniidae, it shows a tracheolized structure projecting from the prothoracic ganglion where posterior arms seem absent. In *Barathra brassicae* and *Noctua pronuba* (Noctuidae) it has rather narrow anterior and posterior arms and a more compact central region. In this case, the anterior arms are well developed so that the organ provides neurosecretory products and neurosecretory axons to the prothoracic glands. Studies in some Orthopteran species show that both *Locusta migratoria* and *Acrida bicolor* have a triangular shaped H-organ composed of a central body with its extensions connected to the subesophageal ganglion by two thick bundles of nerve fibers, and by a single thick connection to the prothoracic ganglion. The organ is connected to the prothoracic glands at the laterals by its anterior arms.

Together with other perisympathetic organs, as a translucent and poorly visible structure, the H-organ is important in insect development and it is the main source of innervation and neurosecretory material for the prothoracic glands, which secrete ecdysone, a hormone that stimulates larval molts and metamorphosis in insects. It has direct neurosecretory connections with the prothoracic gland and the prothoracic spiracle, and may control metabolism in the prothoracic gland. The H-organ shows more-or-less a continuous growth without apparent cyclic changes. This acyclic growth and other nervous characteristics of the H-organ suggest that the physiological nature of the H-organ be predominantly of a nervous rather than glandular character.

The H-organ is well developed in all instars. During metamorphosis, the H-organ starts to retreat gradually, and disappears during adult development. The middle part of the H-organ appears to be hypertrophied during the molting periods, containing material in the form of clusters or droplets, and then atrophied during interecdysis. Histofluorescence studies indicate the presence of catecholamines and indolealkylamines, and some other neurosecretory products that are azocarminophilic in their nature. These are found in the lateral parts of the H-organ surrounding the central region, a region called the corpus prothoracale. The lateral branching area with the corpus prothoracale is richly supplied with trachease, indicating a high metabolic activity in this region of the organ. Although the function of the H-organ is not yet clear, it has been suggested that the central region of the organ with the corpus prothoracale is the most important neurohaemal area among the whole ventral nerve cord among the studied insect species.

References

Abou-Halawa S, Slama K (1986) A neurohaemal organ in the prothorax of Lepidoptera. Acta Entomol Bohemoslovaca 83:241–252

Abou-Halawa S (1987) The H-organ and innervation of the prothoracic glands in *Galleria mellonella* (Pyralidae, Lepidoptera). Vestn Cesk Spolegnosti Zool 51:81–84

Abou-Halawa S (1987) Detailed morphological studies on the H-organ in the larvae of *Galleria mellonella* (Pyralidae, Lepidoptera). I. The anatomy of the organ. Vestn Cesk Spolegnosti Zool 51:161–167

Abou-Halawa S (1987) Detailed morphological studies on the H-organ in the larvae of *Galleria mellonella* (Pyralidae, Lepidoptera). II. The histological structure of the H-organ. Vestn Cesk Spolegnosti Zool 51:241–245

Bhargava S, Slama K (1987) Growth of the prothoracic H-organ in larvae of *Galleria*. J Insect Physiol 33:55–57

Mutun S, Ober A (1998) The localization and structure of a neurohaemal H-organ in *Acrida bicolor* (Thunberg) and *Locusta migratoria* (Linneaus) (Orthoptera). Turk J Zool 22:41–44

Horizontal Gene Transfer

The transfer of genetic information from one species to another.

Horizontal Transmission

This is movement of a pathogen among members of a species within the same generation, or within the same season. In contrast, transmission of a pathogen between members of an arthropod species by movement from parent to progeny (transovarial or transovum transmission) or between instars within a generation (trans-stadial transmission) is called vertical transmission.

Hormoligosis

Subharmful quantities (low, sublethal exposure rates) of stress agents (e.g., temperature, radiation, minor injuries, chemicals) can be stimulatory to organisms in a stressful environment. In entomology, this usually is seen in the increased development rate of insects or mites, or increased reproduction, following exposure to insecticides and reared under suboptimal conditions. It is derived from the Greek words "hormo" (to excite) and "oligo" (minute quantities). Hormoligosis is sometimes used to explain population resurgence of insects and mites following insecticide treatment. It is important to separate direct physiological (horm oligotic) effects from indirect effects related to the destruction of natural enemies by low doses of pesticides; either can cause increases in abundance. Also, the response of insects to such stressors may be delayed.

References

Luckey TD (1968) Insecticide hormoligosis. J Econ Entomol 61:7–12

Cohen E (2006) Pesticide-mediated homeostatic modulation in arthropods. Pest Biochem Physiol 85:21–27

Hormone

A chemical produced internally by one organ and conveyed, usually by means of the hemolymph, to another organ, where it can trigger physiological, morphological and behavioral changes.

► Adipokinetic and Hypertrehalosemic Neurohormones
► Ecdysteroids, Endocrine Regulation of Insect Reproduction
► Juvenile Hormone
► Metamorphosis
► Prothoracicotropic Hormone

Horned Powder-Post Beetles

Members of the family Bostrichidae (order Coleoptera).

► Beetles

Hornets

Members of the family Vespidae (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Horn Fly, *Haematobia irritans* (L.) (Diptera: Muscidae)

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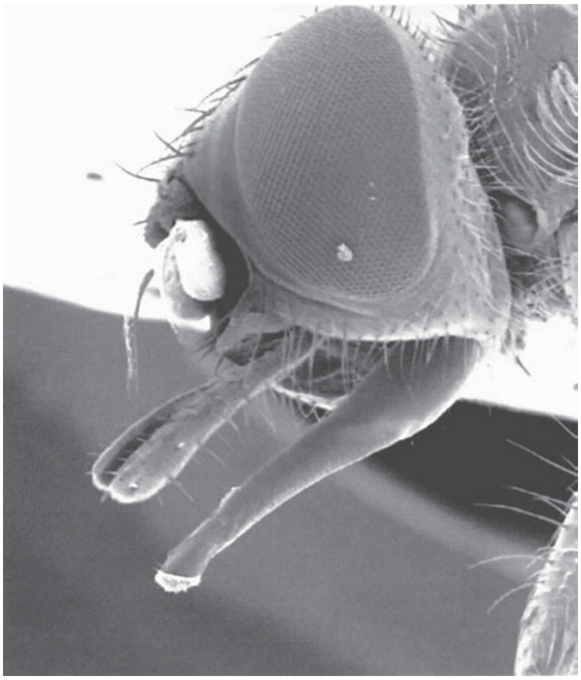
The horn fly is a significant pest of cattle throughout much of the world. The fly occurs throughout Europe, Asia and North Africa, and was accidentally introduced to North America in the 1880s. It was first reported in Canada in the early 1890s. It colonized most of the continent, and had reached Venezuela by the 1930s. Horn fly arrived in Brazil in the mid 1980s and has spread through much of the cattle -producing areas of South America.

The adult horn fly lives in close association with cattle. The fly is about 5 mm long; gray, with four dark stripes on the top of the thorax. The wings are broad and held in a V-shape at rest (Fig. 43). The eyes are large and red, widely spaced in the females and close together in the males. The mouthparts are similar to the stable fly's with a heavily sclerotized labium that forms the sheath of the proboscis (Fig. 44). The food canal is formed by the labrum-epipharynx and the hypopharynx forms the salivary canal. The labium ends in a pair of labella that bear sharp teeth used for cutting the host's skin. The maxillae are greatly reduced and only the maxillary palps are visible at the proximal end of the proboscis. The maxillary palps are longer than half the length of the proboscis.

Horn Fly, *Haematobia irritans* (L.) (Diptera: Muscidae), Figure 43 **Horn fly, *Haematobia irritans*.**



Horn Fly, *Haematobia irritans* (L.) (Diptera: Muscidae), Figure 44 Head and mouthparts of horn fly.

The adult flies spend most of their lives in close contact with cattle. Adults are most abundant on bulls, followed by steers, cows and calves. The adults are quite mobile and the distribution of flies on the cattle body will change markedly during the day as adults move from the backs and sides of the animals to the belly. The proportion of flies on the belly shows a distinct seasonal trend, and is highest in late summer and lowest in the spring and fall. This movement may be in response to increasing numbers on an animal, environmental fluctuations, increasing proportion of gravid females in the population, and the presence of lesions along the belly. Both sexes feed on cattle by cutting the skin with the labellar teeth and ingesting the resulting blood and tissue. Flies can ingest from 11 to 21 mg of blood per day. The irritation resulting from feeding activity of a relatively few flies (12–25 flies per animal) is believed to be responsible for an immediate decline in animal productivity associated with behavioral changes that reduce forage utilization and feed efficiency. Horn fly infestations of yearling cattle have been responsible for 18% reduction in weight gains. When fly numbers exceed 200 flies per animal, cattle will undergo physiological changes that result in further reductions in productivity that increases with fly numbers. Horn fly infestations on cows can indirectly reduce weaning weights of calves by reducing milk production by the cow. Every 100 flies per cow can reduce calf weaning weights by 8%, with reported decreases ranging from 3 to 16%.

Female horn flies use ingested blood for egg production. Females feed for 2–3 days before oviposition, and lay from 8 to 13 eggs per day. Eggs are laid every 1–2 days until death. As females become gravid, they move to the rear and underside of the cattle, and leave to lay eggs on the undersides of newly deposited cattle manure. Although female may live a maximum of 21 days, the average female lifespan is generally <1 week. Females could lay 100–200 eggs if they reach the maximum lifespan, but few do. On average, a female will contribute 20–25 eggs to the next generation.

The eggs are 1.2 mm in length and reddish-brown in color. Eggs hatch within a day and the first instar larvae enter the pat. Larvae feed on bacteria within the manure and pass through three instars. The third-instar larvae are easily identified. These are typical maggots with a reduced head and an anteriorly tapering body. The posterior spiracles have a characteristic pattern with a button located on the inside margin surrounded by three sinuous slits. Larval survival is influenced by chemical factors such as manure pH, nitrogen content, and moisture; physical factors such as temperature; and biotic factors such as predation. Larvae survive best in feces from animals feeding on forage compared with those fed concentrated or grain-based diets, hence the greater occurrence of this pest in pasture or rangeland systems. The larval stage is completed in 1–2 weeks depending on temperature. Larval development requires 9 days at 20°C and 4 days at 30°C.

The pupal stage is formed beneath the pat (feces). Pupae weight about 6 mg and develop within a reddish brown puparium formed by the last larval skin. The duration of the pupal stage is strongly influenced by temperature, requiring about 12 days at 20°C and 5 days at 30°C. The pupal stage occupies about 55% of the total immature developmental time. Pupae can be attacked and killed by a variety of hymenopterous parasitoids. When pupal development is complete, the adults emerge, find a host, mate and continue the life cycle.

The entire life cycle is completed in 2–4 weeks under field conditions. Reproduction is continuous, and there are several overlapping generations. The number of generations per season increases with warmer climates. In northern areas, there may be 3–5 generations per year, and 5–8 generations per year in southern regions. Populations generally show a major peak in mid-summer in northern areas, and may show spring and fall peaks in southern climates.

In the fall, environmental cues trigger the production of diapausing pupae, the overwintering stage. The increasing proportion of diapausing pupae produced in the fall results in reduced recruitment to the adult stage and adult populations decline. Earlier research suggested that diapause is induced by declining photoperiods acting on female flies causing them to produce eggs that are predisposed to enter diapause when they reach the pupal stage, and that temperatures to which the immatures are exposed mediate the proportion of pupae that enter diapause. More recent work has indicated that diapause occurs in response to reduced temperatures experienced by the larvae during a diapause-sensitive period and that maternal influences play little role in diapause induction.

The diapause sensitive period begins when immatures have completed 10% of their development to the adult stage, and ends when 82% of the immature developmental period is completed. The incidence of diapause increases as temperatures decline and a greater number of days are spent in the diapause sensitive period. In warmer climates, temperatures may not be low enough for diapause to occur, and generations may occur the entire year. Temperatures experienced during the diapause sensitive period are correlated with overwintering success. Overwintering survival is low when temperatures average <10°C during the diapause sensitive period, and greater when temperatures range from 10 to 23°C. Diapause is not induced at temperatures above 23°C. Once diapause is induced, overwintering survival is relatively uninfluenced by ambient temperatures. The diapausing pupae can survive extended periods of exposure to −5°C, and temperatures below the pats rarely drop below −10°C, even when air temperatures reach −30°C.

Diapause is terminated gradually throughout the winter, and post-diapause development begins in the spring when temperatures increase. The rate of completion of post-diapause development is temperature-dependant and adults emerge during a 3–4 week period in the spring. Flies colonize cattle, and begin the life cycle again. The flies that emerge in the spring are produced during a 3–6 week window the previous fall.

Most methods for controlling horn flies are oriented towards treating cattle, as this is the commodity that is affected. The population of adult flies is in constant association with cattle, and is a convenient target. Immature stages are typically not targeted for control as these are protected within the manure pat and are dispersed throughout the pasture. Chemical control options are most frequently used and may be applied to the cattle in several ways. Direct applications, in the form of sprays or pour-ons can be used when the animals are gathered. These will provide 1–2 weeks control of the adults, but after this period cattle can be re-colonized by newly emerged adults that were in the immature stages when the treatment was applied. Reapplication requires gathering the animals for treatment, and this may not always be practical. Self-application devices can be placed in the field so that cattle will receive a dose of insecticide when they contact the application device. These devices must be placed in areas such as watering sites or salt licks where they cattle will contact them, and are most effective in forced-use situations. The most common method for controlling horn flies is the use of insecticide-impregnated ear tags. These tags are applied in the spring before cattle are turned out to pasture, and release insecticides over the animals' bodies for the entire fly season. Initially, these provided season-long control, but horn flies quickly developed resistance to the commonly used chemicals. Use of ear tags should be managed to delay the development of resistance. This can be accomplished by applying tags to all animals, removing tags at the end of the season, using tags containing different classes of chemicals in successive seasons, and alternating tag use with other application methods. Relatively few non-insecticidal options are available for horn fly control. Various traps have been designed to remove the adult flies from cattle when cattle walk through the trap. These can be effective, especially when used in situations such as dairies where cattle must walk through the trap routinely.

References

Lysyk TJ (1991) Use of life history parameters to improve a rearing method for horn fly, *Haematobia irritans irritans* (L.) (Diptera: Muscidae) on bovine hosts. Can Entomol 123:1199–1207

Lysyk TJ (1992) Simulating development of immature horn flies, *Haematobia irritans irritans* (L.) (Diptera: Muscidae), in Alberta. Can Entomol 124:841–851

Lysyk TJ (1999) Effect of temperature on time to eclosion and spring emergence of post-diapausing horn flies (Diptera: Muscidae). Environ Entomol 28:387–397

Lysyk TJ, Moon RD (1994) Diapause induction in the horn fly (Diptera: Muscidae). Can Entomol 126:949–959

Lysyk TJ, Moon RD (2001) Diapause recruitment and survival of overwintering *Haematobia irritans* (Diptera: Muscidae). Environ Entomol 30:1090–1097

McLintock J, Depner KR (1954) A review of the life-history and habits of the horn fly, *Siphona irritans* (L.) (Diptera: Muscidae). Can Entomol 84:20–33

Horn, George Henry

George Horn was born in Philadelphia on April 7, 1840. He was interested in entomology and other areas of natural history by the time he completed high school. He entered the University of Pennsylvania, and obtained a medical degree in 1861. In the American Civil War he served as surgeon to the infantry of the California Volunteers in 1862–1866. This allowed him to collect insects in California, Arizona, and New Mexico. Then he returned to Philadelphia and excelled in obstetrics. But he was elected president of the American Entomological Society in 1866 and, because he was unmarried, was able to devote all his spare time to the study of beetles. He obtained greater fame in entomology than in medicine, publishing 265 papers, and describing 154 genera and 1,682 species. His entomological papers included syntheses of genera and higher taxa, and several of them stood for about a century before being bettered. He was closely associated with the American Philosophical Society and was awarded honorary memberships in several entomological societies. He died on November 24, 1897, nearly a year after suffering a debilitating stroke. His collections are now in the Museum of Comparative Zoology of Harvard University.

References

Calvert PP (1898) A biographical notice of George Henry Horn. Trans Am Entomol Soc 25:i–xxiv

Henshaw S (1989) The entomological writings of George Henry Horn. Trans Am Entomol Soc 25:xxv–xxii

Herman LH (2001) Horn, George Henry. Bull Am Mus Nat Hist 265:80–81

Horn, Hermann Wilhelm Walther

Walther Horn was born in Berlin on October 19, 1871. By the age of eight he already was building an insect collection. In the late summer of 1889 he made the acquaintance of Gustav Kraatz, who influenced his entomological training. In 1891 he and his schoolfriend Hans Roeschke published an entomological paper, a monograph of palearctic tiger beetles, the first for either of them. Following his father's wishes, he studied medicine, obtained his medical degree in 1893, and took his medical practitioner's examination in 1895. By this time he had published 39 entomological papers, and in 1896 took his first foreign collecting trip, to Italy, Tunisia, Algeria, Portugal, and France, lasting 9 months. In 1899, he took his second trip, to Ceylon and India, lasting 8 months. His third trip came in 1902, to South, Central, and North America. In 1904, he was appointed by Gustav Kraatz to the position of director of the entomological museum that Kraatz had founded. In a private house in Berlin, it was first called Deutsche Entomologische National museum and in 1920 was renamed Deutsche Entomologische Institut. Walther served in the German army during World War I, and was posted to the eastern front. Inflation in Germany after the war caused great financial difficulties for the institute which, like some in Britain and the USA, was privately financed [compare with the American Entomological Institute]. In 1922, Walther arranged the institute's affiliation with the Kaiser Wilhelm Gesellschaft zur Förderung der Wissenschaften ["Kaiser Wilhelm association for the advancement of sciences"] which made funding more secure, at least until circumstances changed again. In 1934, the institute was made part of a national institute for systematic and applied entomology. Walther's taxonomic contributions were almost entirely on tiger beetles (Carabidae: Cicindelinae), on which he published 284 papers. His was the work on tiger beetles in "Genera insectorum" (1908–1915), and in "Coleopterorum catalogus" (1926). He nevertheless published 51 papers on insect studies, 19 on museum studies, and six bibliographies. His (1935–1937) work "ű ber entomologische Sammlungen, Entomologen und Entomo-Museologie" (on entomological collections, entomologists, and entomological museum methods), together with a work coauthored with Schenkling (1928–1929) "Index literaturae entomologicae" (index to the entomological literature) were and still are of worldwide importance to entomologists. They are still of worldwide importance because although computerized bibliographies exist to the literature from some time (variously) after 1970, the older literature is not thus computerized, so Horn's works are invaluable. With such interest in bibliographies, he built the institute's entomological library to be the best in continental Europe. He died on July 10, 1939.

Reference

Korschefsky R (1939) Dr. Walther Horn. Entomol Blätter 35:177–184

Horntails

Members of the family Siricidae (order Hymenoptera, suborder Symphyta).

► Wasps, Ants, Bees and Sawflies

Hornworm

A caterpillar of the order Lepidoptera, family Sphingidae, normally bearing a large, pointed spine– like structure on the last abdominal segment.

► Hawk Moths
► Butterflies and Moths

Horse Flies

Members of the family Tabanidae (order Diptera).

► Horse Flies and Deer Flies
► Flies

Horse Flies and Deer Flies (Diptera: Tabanidae)

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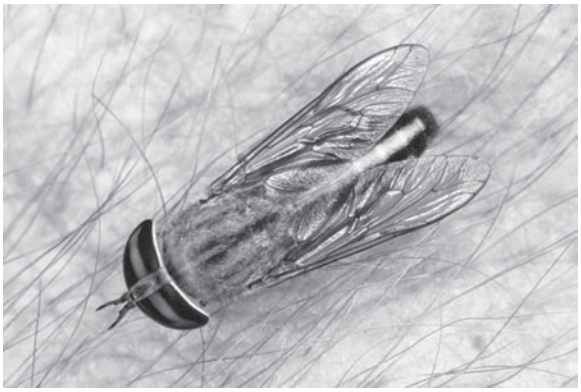
The family Tabanidae is primarily composed of two fairly large groups of biting flies known collectively as horse flies and deer flies. They occur worldwide and are represented by 4,300 species and subspecies from 137 genera. Generally, the wings of deer flies possess a vertical dark band from the mid-line of the wing down to the margin, while wings of horse flies can be entirely dark, mottled, or completely clear. Horse fly wings never possess a vertical band down the mid-line of the wing. Members of this family have large eyes; the females are dioptic (eyes widely separated) and the males are holoptic (eyes contiguous). Adult size range varies tremendously. Some deer flies, *Chrysops* sp., are as small as 6 mm, while some of the larger horse flies, *Tabanus* sp., can be up to 25 mm in length (Fig. 46).

Horse Flies and Deer Flies (Diptera: Tabanidae), Figure 45 **Adult deer fly, showing the vertical dark band of wing (photo, J. Castner, University of Florida).**

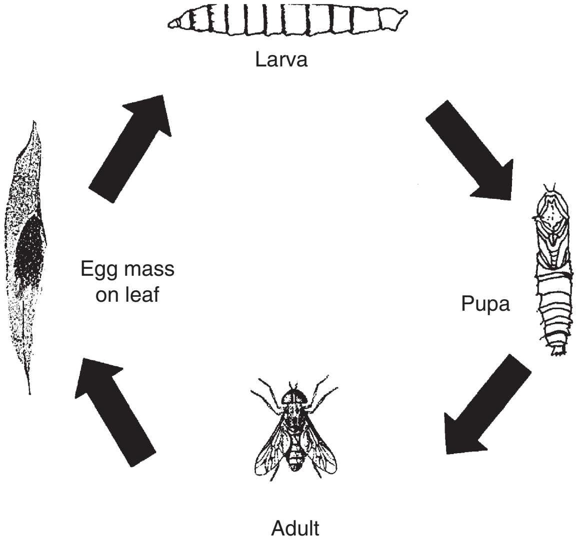


Horse Flies and Deer Flies (Diptera: Tabanidae), Figure 46 **Adult horse fly (photo, J. Castner, University of Florida).**

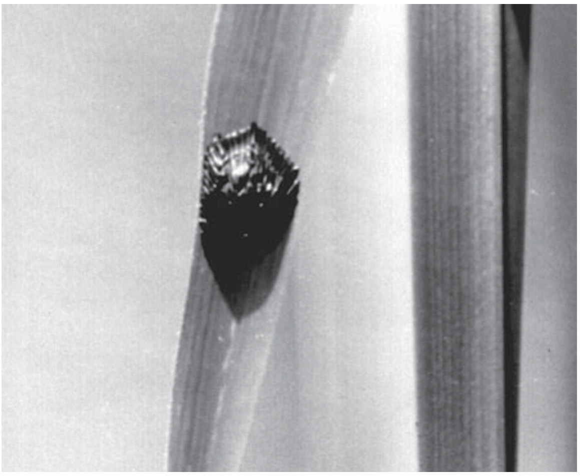
Only females feed on blood to mature their eggs, while both sexes feed on nectar sources that provide carbohydrates. Males cannot bite because they lack mandibles. Blood-seeking adults can be severe pests of humans as well as animals.

Tabanids go through complete metamorphosis, i.e., egg, larva, pupa and adult (Fig. 47). Generally, the eggs are deposited in layers on vegetation or other objects hanging over the water (Fig. 48). The eggs range in size from 1.0 to 2.5 mm and vary in number from about 100–1,000 depending on the species. After oviposition, the female will deposit a waterproof secretion that covers the eggs to prevent desiccation and parasitization by wasps. Once the egg shells harden, they will turn black and sometimes appear as "tar spots" on vegetation. The eggs hatch in 5–12 days.

Newly hatched larvae will drop immediately into the water and burrow into the mud to feed upon organic matter. Developmental habitats for most horse flies and deer flies are primarily aquatic to semi-aquatic. However, some species of horse fly larvae can develop in open pastures or rotted logs (Fig. 46).



Horse Flies and Deer Flies (Diptera: Tabanidae), Figure 47 **Generalized life cycle of Tabanidae. (Source, redrawn and reproduced from Harwood and James, and University of Florida).**



Horse Flies and Deer Flies (Diptera: Tabanidae), Figure 48 **Egg mass of *Hybomitra lasiophthalma* (source, J. V. Freeman).**

The larvae are cylindrical and tapered at one end. The number of larval instars (stages) and duration are profoundly influenced by weather conditions. Several tabanid species have been reported to be predators of a variety of invertebrates including insect larvae, crustaceans, snails and earthworms. Sometimes even small vertebrates can be preyed upon, such as the unique case of the predatory capture of adult, newly emerged spadefoot toads, *Scaphiopus multipicatus*, by horse fly larvae, *Tabanus punctifer*, on an Arizona mudflat.

In most temperate climates, tabanids usually have one generation per year. In more southern regions, a few species may have two generations per year. But there are exceptions, for some species take 2 or 3 years to complete development.

Tabanid bites usually cause mild irritation in most humans. But some deerfly species (*Chrysops* sp. and a closely related species *Diachlorus ferrugatus*) have been reported to cause allergic reactions that, in extreme cases, can result in hospitalization. Allergic reactions occur as the body reacts to the anticoagulant injected into the feeding wound by the female fly in order to stop blood from clotting and facilitate the uptake of blood from the host.

Horse flies and deer flies have been incriminated in the transmission of a number of protozoan, helminthic, bacterial and viral organisms that cause human and/or animal disease. Some pathogenic microorganisms, such as the protozoans *Trypanosoma theileri* and *Haemoproteus metchnikovi*, require the adult fly as a multiplication source in their life cycle in order to infect animals.

Most disease causing organisms are transmitted by the contaminated mouthparts of the fly. Several species of horse flies (*Tabanus* sp.) have been incriminated in the transmission of *Trypanosoma evansi* in Africa, southern Asia and Central and South America. This protozoan is frequently fatal to horses, camels and dogs, although it appears to be non-pathogenic to cattle and buffaloes.

Certain species of deerflies from the genus *Chrysops* can transmit the African eye worm, *Loa loa,* to humans. Members of the genus Tabanus have been implicated in transmitting the rickettsial agent that causes anaplasmosis (*Anaplasma marginale*) in cattle. In the southern U.S., a few species of *Tabanus* have been found to transmit a viral infection in horses referred to as equine infectious anemia. Transmission occurs by the interrupted feeding of horse flies, via their contaminated mouthparts, between infected and non-infected horses. *Francisella tularensis*, the bacterial agent of tularemia, is sometimes transmitted to man by a few species of *Chrysops*. Tularemia primarily appears during summer months and occurs in the Northern Hemisphere between latitudes 30° and 71°.

Control

Currently, there are no effective long-term methods to control horse fly and deer fly populations. Over the years, a variety of non-toxic traps (often supplemented by a carbon dioxide source as an attractant) have been developed, but most have proven suitable only for sampling populations.

Because tabanids are attracted to movement, it is possible to lure and trap them with suspended dark spherical objects such as black beach balls coated with an adhesive. Many tabanids are collected by this method, but it remains to be proven whether or not they actually reduce local populations. Box traps are another method (Fig. 49) that have been used for a number of years to reduce greenhead adults, *T. nigrovittatus*, in the salt marshes around Cape Cod, Massachusetts.

Larval control, through habitat modification of wetlands or direct application of insecticides to developmental sites, is not an option because of state and federal regulatory issues. Insecticide application against adult horse flies or deer flies has met with only limited success.

Control of horse flies and deer flies on cattle, horses and other animals primarily consists of direct application of over-the-counter insecticides labeled for such use. However, the effectiveness of the insecticide to kill tabanids resting on the hair coat can be reduced by the animal's grooming behavior as well as environmental factors, e.g., rain and/or sunlight. Repellents for humans or animals do not offer more than brief relief, at best, from biting annoyance. Efficacy is often dependent upon the number of horse flies/deer flies in the immediate area that are seeking a blood meal.

Horse Flies and Deer Flies (Diptera: Tabanidae), Figure 49 **Box trap for collecting horse flies on salt marshes of Cape Cod, Massachusetts (source, J. E. Cilek).**

References

Jackson R, Nowicki S, Aneshansley DJ, Eisner T (1983) Predatory capture of toads by fly larvae. Science 222:515–516

McKeever S, French FE (1997) Fascinating beautiful blood feeders, deer flies and horse flies, the Tabanidae. Am Entomol 43:217–226

Mullen GR, Durden LA (eds) (2002) Medical and veterinary entomology. Academic Press, New York, NY, 720 pp

Horsehair Worms (Nematomorpha)

A phylum of insect-parasitic invertebrates known as nematomorphs, Gordian worms, and hair snakes, the Nematomopha are named after the tendency of these worms to be long and thin, resembling the hairs of horses. Also, these invertebrates are commonly found in water sources where livestock such as horses drink. In most cases this is due to the tendency of common hosts such as grasshoppers to leap into water troughs and then be unable to escape. The horsehair worms contained within the bodies of the grasshoppers then emerge and swim around in the water

► Nematomorphs (Nematomorpha: Gordioida: Several Families)

Horsfall, William R

William Horsfall was born in the state of Missouri on January 11, 1908. He received a bachelor's degree in 1928 from the University of Arkansas, and a master's degree the following year from Kansas State University. Then he entered Cornell University as a graduate student, and received a Ph.D. in entomology in 1933. His employment as a teacher and researcher began at Cornell, continued at the University of Arkansas, then South Dakota State University and finally, beginning in 1947, at the University of Illinois at Urbana-Champaign. But World War II interrupted his academic work. He served in the South Pacific as commander of a U.S. military malaria survey unit for 3 years. At the University of Illinois in 1947–1976, he published five books (including, in 1955, "Mosquitoes. Their bionomics and relation to disease" and in 1962. "Medical entomology. Arthropods and human disease") and 140 scientific papers, taught medical entomology and insect bionomics, and won a citation for outstanding teaching. His research was on the bionomics of meloids, grasshoppers, chinch bugs, bean weevils, scarabs, and mosquitoes. He was an elected fellow of the American Association for the Advancement of Science. He received awards of merit from the American Mosquito Control Association, the Zoological Society of Finland, the Entomological Society of America, and the Illinois Mosquito Control Association. After retirement, he continued to work as a consultant and to publish. He died in Illinois on November 18, 1998, survived by his wife, Annie Laurie.

Reference

Berenbaum MR (1999) William R. Horsfall. Am Entomol 45:61–62

Horticultural Oil

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Oils have long been used for their insecticidal properties, including application of oil to plants to kill plant-feeding species. Most oils used for insect control are petroleum products, and are also known as mineral oils. However, oils are also derived from plants, and usually referred to as vegetable oils. Historically, the greatest use of oils was a winter application to twigs and trunks of fruit trees and ornamental plants, and this product is called dormant oil. However, more highly refined, lighter-weight oils have become available for use during the growing season, and these are called summer oils. Both mineral and vegetable oils, properly refined and applied, can be used for winter or summer applications.

Dormant Oils

The use of dormant oils was popular because it addressed some difficult insect control problems, mostly involving aphid and caterpillar eggs, mites (both adults and eggs), and scale insects (usually eggs). Also, the treatments could be made during a relatively slow season (winter) when there was not much else that could be done to fruit and ornamental crops (except perhaps for pruning). Application of dormant oil to trees and shrubs before bud swelling and bud break poses little risk of injury to the plant, and yet kills many insects and mites. Both eggs and active forms of small arthropods are susceptible to oil because the oil apparently inhibits air exchange, often by clogging the air passages (spiracles) through which arthropods breathe. Dormant oils are relatively heavy-weight products, and often contain aromatic compounds such as sulfur that can cause toxicity to vegetation, hence the timing of application to avoid active growth by the plant. Heavy oils evaporate slowly, which is a good characteristic for insect control, but which can be damaging to plants. Dormant oils are normally mixed with an emulsifying agent that allows the oil to mix with water and be dispersed uniformly. Upon mixing, the oil solution typically turns white due to actions of the emulsifying agent; this is the basis for one of the names applied to dormant oil spray, "white oil." Oil is normally diluted to about 2% of the spray mixture. Oils are not applied before winter hardening has occurred, if the weather is below freezing, or if the plants are beginning to grow. Some plants are sensitive to oil, so the product label should be consulted for precautions.

Summer Oils

Summer oils are lighter in weight, less contaminated with residues that may prove phytotoxic, and useful for many more plants than are dormant oil sprays. They are also called superior, supreme or ultra-refined oils. Summer oil is often applied to control aphids, whiteflies, leafhoppers, thrips, mealybugs, mites, and the early stages of many other insects, usually at concentrations of 1–4%. Damage can occur when too much oil is applied, the plants are under water stress (inadequate soil moisture), the temperature is high (32°C or 90°F), or the humidity it too high (the oil cannot evaporate). Vegetation with hairy leaves (dense trichomes) may be more prone to damage because more oil is held on the leaf. It is advisable to test a few leaves if you are uncertain about the safety of application, and wait a few days to see if damage occurs. Summer oils are not selective, and will kill most small insects, including beneficial species. However, once they are dry they are no longer toxic, so relative to traditional insecticides they are relatively non-toxic to beneficial insects. Also, they tend to impart a shine or sheen to treated plants, so they are popular because they improve the appearance of ornamental species.

Stylet Oils

Lightweight oils also are sometimes recommended for disruption of plant virus transmission by insects such as aphids; such formulations are called stylet oils. The oil interferes with transmission of virus on the stylets of the insects. Such viruses are the non-persistent types. Persistent viruses, which are harbored within the insect, are not affected by stylet oils.

Vegetable Oils

Vegetable oils do not really originate with vegetables. The common sources are oil seed crops such as soybean, canola and cottonseed. Other sources include neem seed, sesame seed, rosemary, and other plants. Like petroleum-based oils, they can cause phytotoxicity. Neem seed is well known as a source of azadirachtin, a growth regulator-based insecticide and feeding deterrent. However, some neem products contain mostly neem oil and are relatively free of azadirachtin.

Phytotoxicity

Among the plants that are known to be sensitive to oil are:

Azalea, *Rhododendron* spp.
Beech, *Fagus* spp.
Black walnut, *Juglans nigra*
Douglas-fir, *Pseudotsuga* spp.
Hickory, *Carya* spp.
Japanese holly, *Ilex crenata*
Juniper, *Juniperus*
Cedar, *Cedrus* spp.
Maple, *Acer* spp.
Redbud, *Cercis* spp.
Smoke tree, *Cotinus coggygria*
Spruce, *Picea* spp.

Also, neem oil is reported to affect several plants, including:

Impatiens, *Impatiens* spp.
Fuchsia, *Fuchsia* spp.
Some roses, *Rosa* spp.
Olive, *Olea europaea*
Some carnations, *Dianthus caryophyllus*

As noted previously, if there is uncertainty about phytotoxicity of an oil product to a crop, it is better to test and watch for several days for toxic effects rather than treat an entire tree or crop with a product of unknown phytotoxicity. If phytotoxicity is not a problem, then oils are a great pest control technique to consider for small arthropods. Oils are relatively harmless to everything except small arthropods and some aquatic insects, and of course some plants.

► Neem

Horticultural Oil

Petroleum or botanical oil that is used to control pests on plant.

Host

An organism that provides food and/or shelter for another organism. In entomology, it also is the insect that supports a parasitoid or pathogen.

Host Feeding

A behavior displayed by a parasitoid when the adults feed on insects that normally are used for larval development.

Host Location in Parasitic Wasps

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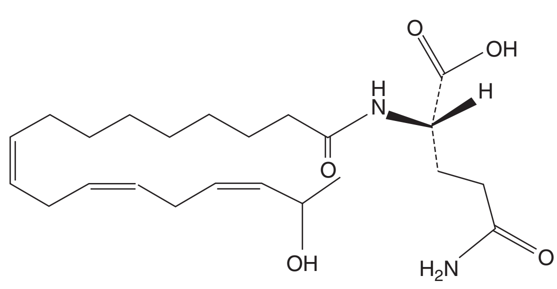
Generally, three steps are recognized in host location and acceptance by parasitic insects (parasitoids) which reproduce by oviposition on or in the bodies of other insects. First, parasitoids must locate the proper habitat in which their host is found. Second, within the habitat they must find the proper microhabitat. Within that microhabitat, they must locate the host itself, and decide whether or not to accept it (i.e., whether or not to oviposit), generally using cues obtained from physical contact with the host.

Most studies have focused on the last two stages, orientation toward the microhabitat and host location within the microhabitat. Microhabitat location has been examined using laboratory equipment such as wind tunnels and olfactometers – branched tubes in which an insect is required to make a decision leading to one of two or more odor sources. A few have determined specific compounds to which antennal sensilla are sensitive, using a combination of a gas chromatograph and electroantennogram (EAG). The chromatograph separates volatile complexes into constituent compounds, and the signal as each compound comes into contact with the insect's antenna is recorded.

As a result of these studies we can draw several general conclusions about parasitoid odor discrimination and learning. First, biochemical analysis (using chromatography to separate individual compounds) shows that feeding by herbivorous insects on their host plants induces systemic production of specific volatile compounds that are not induced by artificial damage alone. Most commonly found are the two homoterpenes 4,8-dimethyl-1,3(*E*),7-nonatriene and 4,8,12-trimethyl-1,3(*E*),7(*E*),11-tridecataene. These have been found to be produced by several species of herbivore-infested plants from agricultural systems, including lima bean, apple, cucumber, corn, and cotton. These compounds are induced during feeding (at least by beet armyworm caterpillars) by a compound that was isolated from their saliva, *N*(17– hydroxylinolenoyl)-L-glutamine, known as volicitin (Fig. 50).



Host Location in Parasitic Wasps, Figure 50 **Volicitin, a compound in the saliva of beet armyworm larvae, that induces production of volatiles attractive to wasps. (After Alborn, H. T., T. H. Jones, G. S. Stenhagen, and J. H. Tumlinson. 2000. Identification and synthesis of volicitin and related components from beet armyworm oral secretions. Journal of Chemical Ecology 26: 203–220.)**

Parasitoids, in general, seem to be able to exploit these specific induced compounds to more accurately locate their hosts. They orient upwind preferentially to plants damaged by herbivores, over artificially damaged and undamaged plants. Parasitoids also learn odors, which increases their foraging efficiency. They are more responsive and more accurate in host location when a host is associated with an odor that a parasitoid has encountered before in the presence of a host. This is true not only of plant odors, but is extendible to novel, artificial odors such as vanilla and chocolate.

Because a reduction in herbivore feeding is beneficial to plants, it has been suggested that systemic odor production by plants may have evolved to exploit odor-orientation abilities of the natural enemies of herbivores; in effect, plants are "calling" wasps to come and attack the insects feeding upon them. Several authors, however, have also pointed out that such an effect could also be explained by wound response. For example, damage accompanied by the presence of insect saliva could make a plant more susceptible to infection by a pathogen, and the systemically released compounds are antipathogenic. Research to this point has not ruled out either of the explanations, which are not mutually exclusive.

Significantly less is known about the use of visual cues by foraging female parasitoids. Most parasitoids studied are wasps, and wasps are believed to rely more on odor for orientation, as they usually have long antennae and small eyes. Research indicates, however, that parasitic wasps orient to, and learn preferentially, certain colors and patterns associated with hosts. For example, wasps may show a preference for a pattern of feeding damage on a leaf that is unique to its host. Parasitoids attacking frugivorous (fruit-feeding) species may only be attracted to colors similar to those of the fruits which its host infests. Within the range of a meter or two, visual cues are likely more useful than odors, which might not be as easily traceable in turbulent air currents.

We lack information about the host-locating abilities of most parasitoids in their natural environments, especially at the level of habitat location. A few studies that have examined microhabitat location in the field, however, have reinforced findings in the laboratory. But the mechanism by which a parasitoid flying through a forest locates a small egg cluster or first-instar larva under a leaf, for example, remains a mystery.

► Tritrophic Interactions
► Arthropod-associated Plant Effectors (AAPEs): Elicitors and Suppressors of Crop Defense

References

Alborn T, Turlings TCJ, Jones TH, Stenhagen G, Loughrin JH, Tumlinson JH (1997) An elicitor of plant volatiles from beet armyworm oral secretion. Science 276:945–949

Dicke M (1994) Local and systemic production of volatile herbivore-induced terpenoids: their role in plant-carnivore mutualism. J Plant Physiol 143:465–472

Turlings TCJ, Tumlinson JH, Lewis WJ (1990) Exploitation of herbivore-induced plant odors by host seeking parasitic wasps. Science 250:1251–1253

Vet LEM, Dicke M (1992) Ecology of infochemical use by natural enemies in a tritrophic context. Ann Rev Entomol 37:141–172

Wackers FL, Lewis WJ (1999) A comparison of color-, shape- and pattern-learning by the hymenopteran parasitoid *Microplitis croceipes*. J Comp Physiol A Sensory Neural Behav Physiol 184:387–393

Host Plant Resistance

Any host plant-related factor that disrupts the host selection process or causes the plant to be less suitable for insect growth, survival or reproduction than is normal among plants.

► Plant Resistance to Insects

Host Plant Selection by Insects

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Host plant selection by insects is often divided into "host plant finding" and "host plant acceptance." While the two are easy to separate conceptually, in practice, they are really part of a continuum of three, rather than two, inextricably bonded links. However, the central link of host plant finding, thought previously to be governed by volatile chemicals, has, until now, proved intractable to scientific experimentation. Thus, the focus here is on host plant selection by insects associated with cruciferous plants as, since the classical work of Verschaffelt in 1910, most theoretical studies on herbaceous plants have used the interaction between insects and cruciferous plants as their test system. Such a selection is logical, as cruciferous (Cruciferae) vegetable and oilseed crops are of high economic importance and are now cultivated on large farms in most parts of the world. In addition, cruciferous plants are ideal for biological studies, as their chemistry is well understood and they support pest species from a wide range of insect orders.

Many researchers have shown that the numbers of pest insects found on cruciferous crop plants are reduced considerably when the background of the crop is allowed to become weedy, when the crop is intercropped with another plant species, or when the crop is undersown with a living mulch. Obviously, if placing non-host plants in the vicinity of host plants reduces the numbers of insects that actually find their host plants, then this could provide a clue as to how insects find their host plants. It has been suggested that when the background of crop plants growing in bare soil is made more diverse by allowing other non-host plant species to grow in the inter-row spaces, that the additional diversity "disrupts" insects from selecting otherwise acceptable host plants. Such disruption is considered to be mediated through the non-host plants providing (i) physical obstruction, (ii) visual camouflage, (iii) masking of host plant odors, (iv) repellent chemicals, or through (v) the non-host plants altering the physiology of the host plants. Two other suggestions, named by Root (1973) as the "Resource Concentration Hypothesis" and the "Enemies Hypothesis," have also been used to explain why fewer phytophagous insects are found on host plants growing in diverse backgrounds than on similar plants growing in bare soil.

A discussion of the seven hypotheses put forward to date is presented here, followed by a description of a theory based on "appropriate/inappropriate" landings, which the authors believe is the key, or "missing link," to host plant selection by phytophagous insects. Finally, the new theory will be used (i) to discuss the type of information required to make intercropping, undersowing and companion planting more successful, (ii) to suggest how insect biotypes could develop, and (iii) to describe why wild host plants are not decimated by pest insects.

Description and Discussion of the Seven Earlier Hypotheses

Physical Obstruction

This hypothesis was used to describe those situations in which the host plants were, in effect, hidden physically by using larger or taller non-host plants. For example, tall maize plants were used to protect bean plants from pest infestations. Tall plants were considered to be effective because they obstructed the movement of the pest insect within the cropping system.

It could be argued that there is an element of physical obstruction when clover disrupts host plant finding by pest insects of brassica crops as, to have maximum impact, the foliage of the clover has to surround much of the host plant. Although clover growing in such close proximity to the host plant will obviously obstruct the searching insects, no suggestions have been made as to how this mechanism might operate.

However, a mechanism relying solely on physical obstruction is not supported by recent findings in which clover plants were desiccated so that they retained the same architecture as the living plants and differed only in color, being brown rather than green. When the cabbage root fly (*Delia radicum*), the diamondback moth (*Plutella xylostella*) and the large white butterfly (*Pieris brassicae*), were presented with host plants surrounded by desiccated (brown) clover, the number of eggs laid did not differ from the numbers laid on host plants presented in bare soil. Hence, the physical presence of the clover was not sufficient on its own to reduce the numbers of eggs laid, a reduction occurred only when the surrounding clover was green.

Visual Camouflage

This hypothesis was based on the two types of visual stimuli that induce low-flying insects to land on plants. The first is a directed response to the color of the plant, which, in most cases, means green, and the second is an optomotor response in which landing is provoked by plants "looming up" along the path of the flying insect. Anything that competes with such stimuli, such as other green plants, or raising the height of the overall background with weeds so that the distance over which the host plant can be separated from the background is foreshortened, helps to visually camouflage the host plants. This makes the host plants less "apparent" among the foliage of the non-host plants.

Although many authors showed clearly that aphids, whiteflies and certain Lepidoptera preferred plants that stood out against a background of bare soil, no attempts were made to determine how such a mechanism might operate.

Masking of Host Plant Odors

The release of "odor-masking" substances into the air by non-host plant species is considered to confer some protection to the associated host plants. Although this "associational resistance" seems a plausible hypothesis, few data have been collected during the last 25 years to support it.

The possibility that the odor of the host plant could be masked by that of the non-host plant now seems much less likely, though not impossible. For example, host plant selection by the cabbage root fly was disrupted when its host plants were surrounded by a range of different plants including the weeds fat-hen (*Chenopodium album*), fumitory (*Fumaria officinalis*) and spurrey (*Spergula arvensis*); and cultivated plants such as pea (*Pisum sativum*), onion (*Allium cepa*), carrot (*Daucus carota*), rye-grass (*Lolium perenne*), or clover (*Trifolium*). As each of these non-host plants has a different odor profile, it seems highly improbable that they would all be capable of preventing an adapted specialist insect from finding its host plants. Furthermore, observations made in wind tunnels revealed that brassica plants growing in clover were approached by cabbage root flies as readily as brassica plants growing in bare soil, indicating that the odors from the clover did not mask those of the flies' host plants. More striking, however, was that the same disruptive effect could be produced by surrounding the host plants with plant models made from green cardboard, or simply with sheets of green paper, neither of which were releasing plant chemicals. It seems that once the characteristic host plant chemicals stimulate the insects to land, the disruption is caused simply by providing the insects with a greater number of green surfaces on which to land.

Repellent Chemicals

It is implicit in this hypothesis that the odors given off by the non-host plants are sufficiently strong to actually repel the searching insects. It was suggested that the diamondback moth could be repelled from cabbages by intercropping the cabbages with tomatoes (*Lycopersicon esculenta*) and that the highly odorous ragweed (*Ambrosia artemisifolia*) could be used to repel the cabbage flea beetle (*Phyllotreta cruciferae*) from crops of collard (*Brassica oleracea* var. *acephala*). Such suggestions were made to describe why pest insect numbers were different in the two situations. They were not based on scientific experimentation. Whether or not true deterrency is a mechanism still needs to be proven. Deterrency usually involves highly aromatic plants that often have to be crushed and tested in small, confined spaces in the laboratory to show that they are actually capable of repelling pest insects. As such tests are far from natural, the validity of using such data during the synthesis of new behavioral mechanisms is questionable. In reality, no experimental evidence has been produced during the last 15 years to support the hypothesis that plants produced effective levels of chemical repellents.

Plants chosen for their odorous nature, such as French marigolds (*Tagetes patula*), failed to deter the carrot fly (*Psila rosae*) when used as the intercrop in carrots. In addition, oviposition by the diamondback moth was similar on Brussels sprouts (*Brassica oleracea* var. *gemmifera*) plants intercropped with plants of sage (*Salvia officinalis* L.) and thyme (*Thymus vulgaris* L.), two plant species selected for their pungent odors. Extracts of the essential oils of sage and thyme were shown to reduce oviposition by the diamondback moth, but the effect resulted from contact stimuli and not from repellent volatile stimuli. Doubtless, many contact chemicals play a major role during host plant acceptance, but as these come into play only after an insect has landed, they are included only in the second part of this review, which is concerned with host plant acceptance.

Altering the Profiles of the Host Plant Odors

While this seems a novel mechanism, it relies upon the host plants' inability to metabolize certain chemicals they take up from the soil, so that such chemicals, in effect, change the subsequent physiology of the plant. Many claims are made that African marigolds (*Tagetes* spp.) planted between rows of crop plants reduce pest numbers. It is clear from the earlier discussions that this is unlikely to be a direct effect of the odors of the African marigolds repelling the colonizing insects. However, it is well known that species of African marigolds release large amounts of root exudates, which can be taken up by adjacent plants. It is possible, therefore, that any host plant growing in an intercrop could be affected directly by chemicals taken up through its roots rather than by having its odor masked.

To test whether the uptake of such chemicals was responsible for the differences in plant colonization, several batches of the host plants were left in their pots throughout the test periods. As the effects of the clover were still evident, and often within minutes of starting an experiment, a generic mechanism based on the non-host plants (here, clover) causing physiological changes in the host plants cannot be supported.

The Resource Concentration Hypothesis

The last two hypotheses are the ones quoted most frequently. Both were derived from one study in which Root monitored insect distribution during three field seasons in pure stands of collard plants and in single rows of collard plants bounded on each side by diverse meadow vegetation.

The "Resource Concentration Hypothesis" states that phytophagous insects are more likely to find and remain on host plants that are growing in dense or nearly pure stands. Phytophagous insects that arrive in a clump of host plants, by whatever means, and find conditions suitable, will tend to remain in the area. This "arresting effect" of host patches will depend upon several factors such as the size and the purity of the plant stand and the type of host plant required by the phytophagous insect. In many cases, this accumulation of specialist insects on a concentrated resource (here, cultivated *Brassica* plants) will be sufficient to increase the numbers of phytophagous insects in that locality. Again, this hypothesis describes simply the effect of changes in the purity of a host plant stand on insect numbers and does not include any attempt to develop a general theory to describe how phytophagous insects select their host plants.

The Enemies Hypothesis

Contrary to five of the earlier hypotheses, which claim that the differences are due to the direct effects of the diverse backgrounds on the behavior of the pest insects, this hypothesis, like hypothesis 5 (altering the profiles of the host plant odors), proposes that the effects are indirect. In essence, this hypothesis proposes that lower numbers of phytophagous insects are found in complex environments because predators and parasitoids are more effective in such situations. Thus, outbreaks of phytophagous insects are checked early by the higher numbers of enemies that can be supported by the diverse resources available in complex environments. Unfortunately, Root found that the effectiveness of the "enemies" did not differ significantly between collards grown as pure stands and those grown in single rows among diverse meadow vegetation. Nevertheless, Root pursued this "enemies hypothesis" by discussing sets of data collected mainly in England. His own, more extensive data, however, indicated clearly that the diversity of both predators and parasitoids was higher in the pure stands, probably because more prey/host species were also present in that habitat. Consequently, he concluded that factors other than natural enemies were responsible for much of the differences in insect numbers recorded between simple and diverse habitats. Although Root himself discounted the "enemies hypothesis," many subsequent scientists have championed the cause of predators, often on the flimsiest of evidence, or without collecting the data necessary to support their claims.

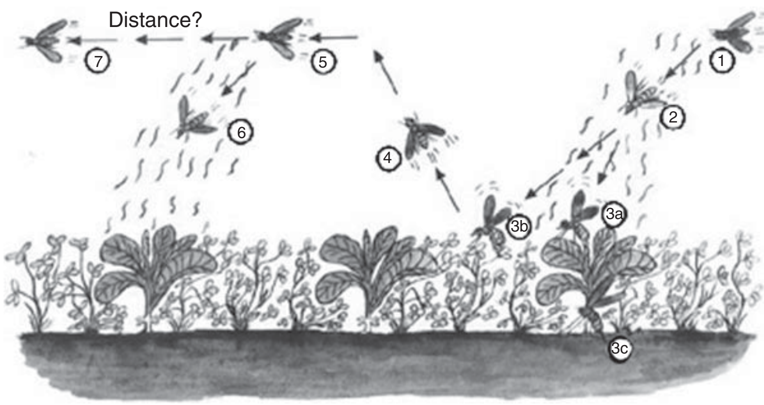
Conclusions From Recent Work

Although authors have indicated that diverse backgrounds can affect host plant selection in the seven ways described above, it is hard, from the results presented in recent publications, to refute the more simplistic view that one mechanism is operating against all species. Recent work published by Finch and Collier (2000) included experiments on the cabbage moth (*Mamestra brassicae*), the diamondback moth, the garden pebble moth (*Evergestis forficalis*), the small white butterfly (*Pieris rapae*), the large white butterfly, the cabbage aphid, the cabbage root fly and the mustard beetle (*Phaedon cochleariae*). Despite these eight test species being from four insect orders, the ability of each of them to find host plants was affected adversely, though to differing degrees, when their host plants were surrounded by clover. It appeared that differences in the initial rates of colonization were the factor that regulated the numbers of phytophagous insects found on host plants growing in bare soil or clover, as differences between the two situations were often apparent within minutes of starting an experiment.

Description and Discussion of the New Theory

Unfortunately, no one has yet developed any of the earlier hypotheses into a robust general theory, they are still only hypotheses. Hence, we have generated our own theory from detailed studies of insect behavior.

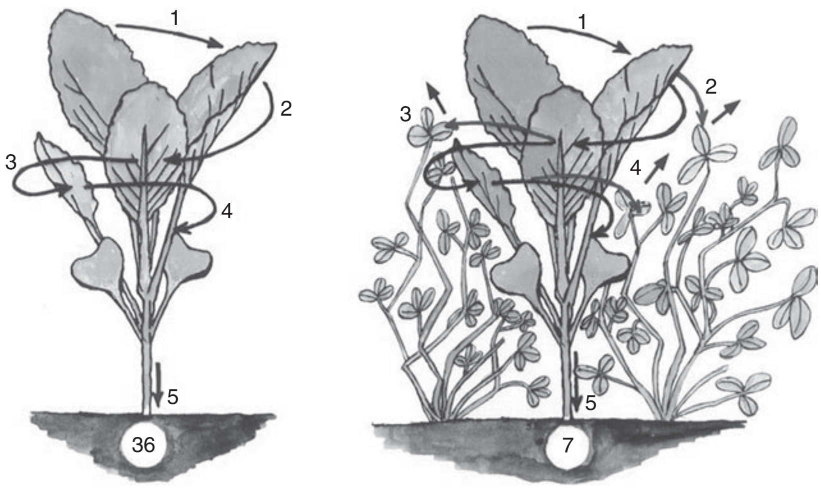
Instead of the seven hypotheses described previously, we believe that a mechanism that we have described as "appropriate/inappropriate landings" is the central link in host plant selection by insects. In the overall system, the new theory of host plant selection can be divided into a chain of actions involving just three links. In the first link (Link 1; Fig. 51), volatile chemicals emanating from plants indicate to flying, receptive insects (action 1) that they are passing over suitable host plants. Once the odor of the host plant in the air becomes sufficiently concentrated, it induces the insect to land (2). In this way, the volatile chemicals bring the insects into the close vicinity of the host plants. However, during the last few milliseconds, when the insects are only a short (often <1 m) distance away from the plant, instead of maintaining their directed response to



Host Plant Selection by Insects, Figure 51 **Schematic diagram to illustrate how diverse backgrounds, here represented by clover (*Trifolium* spp.), influence host plant finding by the cabbage root fly. Numbers represent insect actions 1–7 (see text).**

volatile stimuli, phytophagous insects switch to a directed response to green objects, which, in most cases, means to plant leaves. It is logical that vision takes over at this stage, as most flying animals use vision to "pin-point" a suitable object on which to land. Therefore, insects that fly over plants growing in bare soil will be stimulated to land on host plants, the only green objects available to them (3a), as most phytophagous insects avoid landing on brown surfaces, such as soil. When host plants are growing in bare soil, most landings will be what we have classed as "appropriate," and so, the host plants will, in effect, "concentrate" the insects. In contrast, insects flying over host plants surrounded by clover land in proportion to the relative areas occupied by leaves of the host and non-host (3b) plants, as specialist phytophagous insects do not discriminate between the two when both are green. Hence, any landings made on the non-host plant (3b) are classed as "inappropriate." The amount of time the insects spend on the leaves of the non-host plants before taking off again (4) is governed by whether the insects receive acceptable or antagonistic stimuli through their tarsal receptors. Once the insects are again airborne, if they are stimulated to land after flying only a relatively short distance, they could land on a host plant (5, 7). In all situations, however, the plant on which the insect first lands, even if it is a "host plant," may not stimulate the insect sufficiently to cause it to remain on the plant, and the overall process will be repeated. If this represented the complete system, then under "no-choice" situations in the field, it would just be a matter of time before the numbers of eggs laid on host plants growing in diverse backgrounds were similar to those laid on host plants (3c) growing in bare soil. However, this does not occur, as there is a second phase to host plant finding.

This second phase can be illustrated (Fig. 52) most clearly by data collected from a detailed study of the cabbage root fly. Before accepting a host plant as a suitable site for oviposition, receptive female cabbage root flies make, on average, four spiral flights before laying eggs beside the plant. Hence, the insects stand a much greater chance of "losing" the host plant in a diverse background as, on average, they repeat the initial appropriate/inappropriate landing procedure an additional three times. Observations under laboratory conditions showed that for every 100 females that landed on a brassica plant surrounded by bare soil, 36 received sufficient stimulation from the plant to be induced to lay eggs. In contrast, only seven out of 100 females that landed on host plants surrounded by clover managed to lay eggs. Fewer flies managed to lay eggs in this

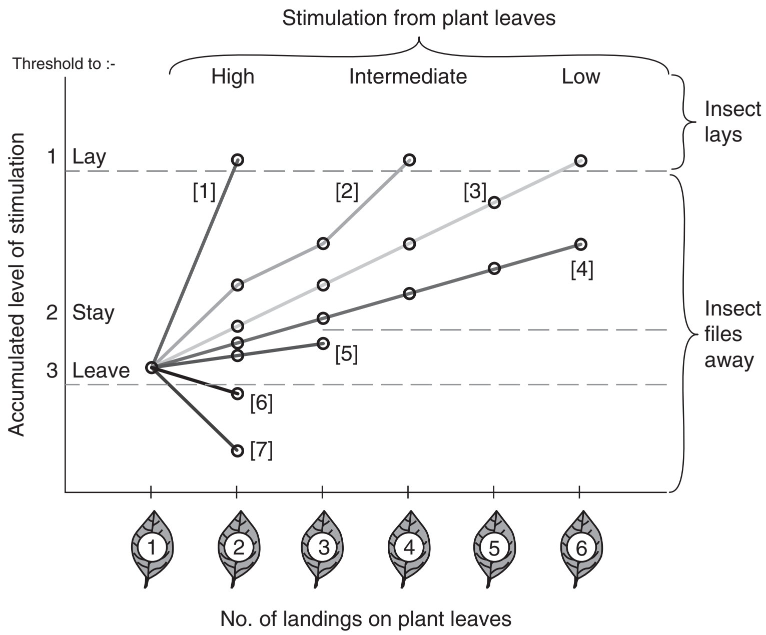


Host Plant Selection by Insects, Figure 52 **Schematic diagram to illustrate how diverse backgrounds, here represented by clover (*Trifolium* spp.), influence host plant acceptance by the cabbage root fly. Numbers represent the four (mean no.) leaf-to-leaf flights made by the fly to ascertain whether the plant is a suitable site to lay its eggs.**

situation, because following each short spiral flight, a proportion of the flies landed on the leaves of the surrounding clover plants. This failure to re-contact a leaf of a host plant after any spiral flight prevented the females from accumulating, within the allotted time, sufficient stimulation from the host plant to be induced to lay eggs. Hence, the barrier that this fly faces when its host plants are grown in diverse backgrounds is not chemical nor mechanical, but behavioral, simply because during the innate series of spiral flights, the fly must continue to accumulate more positive host plant stimuli each time it lands.

The amount of stimulation the female picks up on each landing is crucial, and this is where the phase of host plant finding (Link 2) becomes truly integrated with host plant acceptance (Link 3). In essence, the complete system really involves finding and refinding the host plant. Obviously, the insect can re-find the host plant quite easily in bare soil situations, but not as easily when the plant is growing in a diverse background of other plants. The schematic representation shown in the final figure indicates that the female cabbage root fly may only have to visit two leaves of a highly stimulating plant [1] compared to six leaves on a poorly-stimulating plant [3] before finding it an acceptable site to oviposit. Other insects, however, may accumulate sufficient stimuli to keep them searching [4], but not sufficient stimuli to induce oviposition and so will fly away. A similar outcome results when insects visit several leaves but do not manage to accumulate sufficient stimuli in the allotted time to be induced to stay [5]. Two other variations occur when the insects land initially on a stimulating leaf, but subsequently on a non-stimulating leaf. It does not matter whether this leaf is from a host [6] or a non-host plant [7], as anything that interrupts (Fig. 53) the rate of accumulation of positive stimuli causes the insect both to abort its attempt to lay and to move elsewhere. In addition, interspecific competition may also become important. At any stage during the host plant selection process, many of the new immigrants may not remain on otherwise acceptable plants if those plants are colonized already by certain, but not all, of the other insect species present in the pest complex.

The physiological status of the insect, which depends partly on its age and also on how long it has been deprived of a suitable oviposition site, also has to be superimposed upon this already



Host Plant Selection by Insects, Figure 53 **The number of leaf landings a cabbage root fly may have to make before accepting a plant as a suitable site for oviposition or deciding to fly elsewhere. The numbers in [] represent seven possible variations in the pattern of insect behavior.**

complex system. With time, phytophagous insects tend to become less discriminating in their choice of oviposition sites. The condition of the plant is also extremely important, as some cruciferous plant species are more highly preferred than others, and during their phase of exponential growth, many individual plants become highly stimulating to insects. However, even when the insect and the plant are both in the appropriate physiological state, it counts for nothing the moment the insect makes a wrong choice and alights on any green object other than a leaf of a host plant. This, however, is tempered by the fact that when the host plant is highly stimulating, the insect has to visit fewer leaves and so has less chance of making an inappropriate landing. In addition, the highly stimulating plants invariably induce the individual insects to lay more eggs. Detailed descriptions of the multitude of other factors involved during host plant acceptance can be found in many of the papers published in 1999 in the proceedings of the Tenth International Symposium on Insect-Plant Relationships.

Although the other seven test species mentioned earlier have not been studied in detail, records of the movements of the small white butterfly in the field showed that it always made contact with several leaves, interspersed with short flights, before laying an egg. Although the original author concluded that this butterfly needed some flight time to get the next egg ready, these short flights could also represent a behavioral repertoire similar to that of the cabbage root fly. It seems likely, therefore, that the relative differences in the effects that diverse backgrounds have on host plant selection by the test species may simply reflect the numbers of contacts/re-contacts the insect has to make to accumulate sufficient positive stimuli to lay eggs. Results from recent experiments indicated that the diamondback moth was the species affected least by diverse backgrounds. It raises the question of whether the diamondback moth has become such a major pest of cruciferous crops simply because it has a limited behavioral repertoire prior to oviposition, and so, lays eggs on more or less the first host plant leaf it encounters.

General Discussion

The "appropriate/inappropriate landing" theory (Fig. 53) can be used to explain why certain aspects of host plant finding by phytophagous insects, supposedly regulated by volatile plant chemicals, proved intractable to scientific experimentation in the past.

Compared to our simple theory of host plant finding, other theories invoke complex processes involving volatile chemicals to guide phytophagous insects to their host plants. For example, it is known that the odorous environment of a given insect is a shifting maze of overlapping active spaces. Therefore, it was suggested that it is in this shifting maze that the insect must find the active space containing those few signals that will lead it to its host plant. However, in the open air, it is turbulence rather than diffusion that determines the distribution of odorous molecules, and there is nearly always a prevailing wind to blow the odorous molecules away from the plant. Registering directional cues from odorous molecules is even more complicated for flying insects, as the movement of the air relative to the insect depends on the insect's own activity, and the wind direction has to be determined by the insect in the absence of fixed markers.

The evidence that volatile chemicals are the main regulatory stimuli in the central link of host plant finding is weak, as the maximum distance recorded for insect orientation to host plant volatiles in the field is only a few meters. In wind tunnel experiments, cabbage root flies flew upwind to a cruciferous plant odor released at 2.5 g/day, a rate similar to that dispensed from field traps. This rate of release is at least 105 times higher than the amount of chemical released from a healthy cruciferous plant. Although the flies moved upwind in response to this odor, $<10\%$ of the flights lasted more than 0.5 m. While the shortness of such flights was described as unexpected, it would not have been unexpected had the chemicals involved been regarded as arrestants rather than attractants. Similarly, with insect traps releasing large amounts of chemical to provide directional cues in the field, many insects miss the trap and subsequently fail to enter, suggesting again that stimuli other than volatile chemicals take over once the insect nears the source of the odor. The current mechanism seems much more robust than one based on volatile chemicals, as the sooner an insect lands, the sooner it is freed from the plethora of problems it faces while still in the air.

The "appropriate/inappropriate landing" theory works equally well for generalist feeders, where the decision of whether to stay is determined primarily by the chemicals the insect detects via its contact chemoreceptors once it has landed on a leaf. However, it should be remembered that if an insect that is considered to be a "generalist" has been stimulated to land by volatile chemicals released from a specific plant species, the insect may continue its search for such a plant rather than choosing the first acceptable plant it encounters.

Finally, the "appropriate/inappropriate landing" theory appears to apply equally well to nocturnal insects, as oviposition by the diamondback moth and the cabbage moth was not disrupted when their host plants were surrounded by brown clover. Although both of these moth species are considered to be nocturnal, much of their oviposition activity is concentrated at, or shortly before, dusk. The above results indicate that during this period, both species of moth appeared to be able to discriminate between green and brown objects.

From a crop protection standpoint, the more non-host plants removed from any crop area, the greater chance an insect has of finding a host plant. Hence, current cultural methods are exacerbating pest control problems, as "bare soil" cultivation ensures that crop plants are exposed to the maximum pest insect attack possible in any given locality.

Future Work

If the theory based on "appropriate/inappropriate landing" is accepted, it raises searching questions regarding several aspects of entomological research.

In the first instance, we have expressed considerable doubts about whether host plant volatile chemicals on their own are capable of guiding phytophagous insects to their host plants. Most of the detailed experiments with host plant volatile chemicals have been done by releasing plant odors from a point source sited at one end of a wind-tunnel, introducing responsive insects and then recording whether the insects move upwind to the source of the odor. Results from this approach have been disappointing. Often, the only way to obtain data is to place a visual stimulus, normally a green object, alongside the site where the volatile chemical is being released.

If, as the "appropriate/inappropriate landing" theory suggests, it is only the number of green objects surrounding a host plant that reduces colonization by pest insects, then it should not be too difficult in the future to quantify the type and number of plants needed for the diverse background to reduce pest insect numbers in any given crop. If several plant types proved appropriate for a given cultivated crop, it would then simply be a case of choosing the one that caused the least reduction in yield to the harvested product.

There is also a need to obtain a better understanding of "companion planting" a practice used frequently by organic growers. Recent data show that there is no scientific evidence proving that the odors from highly aromatic plants can actually deter pest insects. This, therefore, brings into question how these aromatic plants produce their effects. A survey of the literature should help to show whether such systems are effective only when the companion plants possess relatively large amounts of foliage when compared to the crop plants. If this idea can be substantiated, the differences recorded may simply be a reflection of appropriate/inappropriate landings, and, again, have little to do with volatile chemicals, no matter how pungent the plant odors might appear to the researcher.

Apart from its impact in practical pest control situations, the "appropriate/inappropriate landing" theory helps also to explain why wild host plants growing among other plants in natural vegetation are rarely decimated by pest insects. However, some insects that are considered to be pest species do develop on wild-host plants. The question then, is do such insects prefer to remain on the wild host plants in subsequent generations, a situation that could give rise to biotypes? The answer to this question is of considerable practical importance. Future work is required to determine what proportion of any given pest population develops on wild-host plants, and whether such insects readily switch back to the cultivated crop plants. If they do not, then it should be possible to control certain pest insects by isolating new crops from earlier infestations.

Additional work is required also to determine whether appropriate/inappropriate landings influence the overall distribution of the parasitoids of the pest species. It is well documented that such insects use both host plant chemicals and kairomones to locate their host insects. Research in the 1940s in which cabbage plants infested with the larvae of the small white butterfly were placed in bare soil crop fields and in hedgerows, showed clearly that one specific parasitoid, *Apanteles rubecula*, was also affected adversely when the plants on which its host insects were feeding were placed into a diverse background. Further work is needed on other parasitoids to determine whether this is a general phenomenon. If it is, then the suggestions of some researchers that diverse backgrounds have adverse effects on pest insects and no effect on their parasitoids warrant further study.

Similarly, with respect to the "Enemies Hypothesis," it should not be too difficult to show whether predation is higher on infested plants surrounded by non-host plants, than on similarly infested plants surrounded by bare soil.

As much of the aforementioned work has been based on detailed information on the cabbage root fly, work is needed to determine the detailed activity of each of the other pest species. It appears that diverse backgrounds may have a greater effect on the cabbage root fly than on the diamondback moth simply because, before acquiring sufficient stimulus to oviposit, the cabbage root fly repeats the sequence of host plant finding four times, but the diamondback moth only once. It would be difficult to prove that once the cabbage root fly starts one of its spiral flights it is again stimulated to land (arrested) by volatile chemicals, as the distances between taking-off and landing again are extremely short. However, olfaction is considered to be used by phytophagous caterpillars in choosing their feeding sites, so the intervention of olfactory stimuli again at this stage cannot be ruled out.

The hypothesis of "appropriate/inappropriate landings" does appear to provide a robust description of host plant selection by insects under a wide range of different conditions. It shows how elements of all the earlier hypotheses can be incorporated into the overall system, and in particular, how the lack of detailed research on insect behavior, and in particular, on visual stimuli, has led to many of the current anomalies. Apart from the future work proposed, it will be interesting to determine whether the same theory regulates host plant selection by specialist insects found associated with plant families other than the Cruciferae. While we believe the simplicity of our theory makes it all-embracing, only time will tell whether our optimism is justified.

References

Altieri MA (1994) Biodiversity and pest management in agroecosystems. Haworth Press, New York, NY, 185 pp

Anon (1999) In Menken SBJ, Minks AK Schoonhoven LM (eds), Simpson S, Mordue (Luntz) AJ, Hardie J (guest eds), Proceedings of the tenth international symposium on insect-plant relationships. Entomol Exp Appl 91:265 pp

Finch S, Collier RH (2000) Host plant selection by insects – a theory based on "appropriate/inappropriate landings" by pest insects of cruciferous plants. Entomol Exp Appl 96:91–102

Kennedy JS (1978) The concepts of olfactory "arrestment" and "attraction". Physiol Entomol 3:91–98

Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). Ecol Monograph 43:95–124

Schoonhoven LM, Jermy T, van Loon JJA (1998) Insect-plant biology – from physiology to evolution. Chapman & Hall, London, UK, 409 pp

Thorsteinson AJ (1960) Host selection in phytophagous insects. Ann Rev Entomol 5:193–218

Host Specific

An organism that is monophagous, feeding only on a certain host.

Host Specificity

The degree of specificity of an animal preying on hosts. Levels of host specificity include monophagous, stenophagous or oligophagous, and polyphagous.

Host Specificity of Weed-Feeding Insects

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The understanding of evolutionary processes is necessary when considering biological diversity and the relationships existing between insects and plants. The major forces in structuring the populations of phytophagous insects act vertically through trophic levels (e.g., from natural enemies of phytophages to phytophages, and from these to host plants), rather than horizontally through interspecific competition. Therefore, due to the selection pressure by phytophagous insects, plants evolved – and sometimes co-evolved with them – interspecific negative or positive interactions. These are expressed by a gradient of interactions. At one end of the spectrum, negative interactions are seen in defense mechanisms; at the other end of the spectrum, positive interactions can be seen in obligate mutualistic interactions. Both are a result of reciprocal, repeated intimate adaptations and counteradaptations. This is exemplified in phototoxic plants, which developed very effective defense mechanisms, and in entomophilous plants, which conversely are extremely specialized and could not even survive without a given species of insect.

Adaptations of Insects to Plants, and of Plants to Insects

The adaptations in insect-plant relationships involve behavioral, phenological, physiological, morphological and biochemical traits of phytophages and plants, which ultimately determine the success and fitness of species. The attack by herbivores induces production of allelochemicals in plants. In turn, the selection pressure driven by plant resistance, especially through allelochemicals, results in patterns of specialized insect natural enemies, whose success is enhanced by the reduced competition for food that they encounter once they overcome plant defenses. These evolutionary adaptations especially involve the feeding and oviposition habits of phytophagous insects, leading to a high level of specialization for their host plants, and also defense mechanisms that allowed them to be resistant. Resistance is expressed as being non-palatable, repellent, digestion-inhibiting, or toxic to other species of insects. Besides toxic chemicals, plant defenses also include physical (morphological) structures, and low levels of available nitrogen, or water/nitrogen ratios. On the other hand, insects develop specific morphological, biochemical and behavioral adaptations, and synchronize their life histories with their hosts.

Host Selection

The ability of specialist weed-feeding insects to identify, locate and select the proper host as breeding substrate, is critical to the performance and survivability of a given species of insect. All phytophagous insects show some degree of selectivity for their food-plants, and possess a definite host range. The host selection behavior includes a specific sequence of activities and responses to environmental cues, principally orientation, feeding and/or oviposition. Adults usually must choose the right host for oviposition, thus facilitating the development of immature stages, which often have limited mobility. Nevertheless, also immature stages of insects are capable of displaying host selection behavior. For oviposition, adults may not only choose the host plant species, but also a suitable individual plant, the most favorable geographical area, the site, the habitat, plant density, and the size and the part of the plant. Even subtle factors such as the degree of protection from biotic or abiotic damage to eggs, the correct micro-environmental conditions for the development of eggs and immatures, and the nutritional status of the food supply affect host selection. The spatial pattern of the host plant can affect oviposition behavior, and plant shape can modify its attractiveness to insects. Adults also regulate their oviposition behavior in terms of the number of eggs oviposited per plant, and in some cases will avoid oviposition on plants where other eggs have already been laid. This behavior facilitates a regular distribution of eggs on the plants, and regulates the effect of insect feeding on the host plants. In some species, adults are deterred from laying eggs if the plant has already been fed upon by other insects.

The selection of a suitable species of plant by phytophagous insects is guided by a combination of physical and chemical stimuli. The sensorial selection of the host plant by insects involves the senses of smell, sight, touch, taste and other forms of contact chemoreception, and may be facilitated by activity and behavioral patterns typical for a given species of insect (e.g., pattern of flight). Plant-produced volatile semiochemicals such as kairomones and allomones, as well as nonvolatile secondary chemicals and interactions with microorganisms, play a major role in determining insect behavior. The sense of smell is highly developed in insects, and the olfactory signal is usually the main indicator of an appropriate host, often complemented by visual elements. Leaf surface contact cues are then important in the host selection process. Insects also respond to the hardness of tissue, which is usually associated with lessened feeding. In general, the balance between phagostimulatory and deterrent compounds contained in the ingested plant tissues determines the acceptance or rejection of the plant by polyphagous insects. In contrast, for monophagous and many oligophagous species, the perception of a single, specific, chemical, or group of chemicals of the plant seems to trigger feeding. A complex of factors and interactions may ultimately cause the association of the herbivore with the target plant. The characteristics of the plant causing it to be unsuitable for insects are described as "xenobiosis" (also called antibiosis); the subset of plant characteristics that cause an insect not to accept a prospective host plant are described as "antixenosis" (nonpreference).

Learning

Experience may play a role also in the host selection process, although differences seem to exist between polyphagous and oligophagous insects. It is necessary to consider the importance of the physiological conditions of plants and insects, abiotic factors, presence of other plants species and other biotic factors, as these can greatly influence the behavior of the insect during the host selection process, and largely modify the host range that the insect has under standard conditions.

Plant Defenses

The great genetic plasticity and biological diversity in insects is amply seen in their specialization on the most diverse species of host plants. This is clearly shown also by insects that attack weeds. The species of weed-feeding insects have a wide array of relationships with their food-hosts and several mechanisms to overcome plant resistance to attack. Most phytophagous insects are relatively specific for their hosts, and generalists represent a minority. However, it is possible to distinguish different levels of specificity, in a continuum of patterns of resource use, ranging from species that are strictly monophagous, to polyphagous species. The degree of specificity varies, with exceptions, among orders of insects, but also among lower taxonomical levels, including species and even sub-specific entities. The host range depends on characteristics intrinsic and extrinsic to a species of insect. In the first category fall all the biological, biochemical and ecological characteristics of the weed-feeding insect and its responses to environmental stimuli, whilst in the second category fall the characteristics related to the life history, phenology and physiology of the species of plant considered. For instance, because of the life history of the plant considered, a species of insect may not be present at the time of the year when the plant, or plant part, is susceptible of being attacked. The fact that narrow host specificity is prevalent among phytophagous insects means that most of them developed mechanisms allowing to overcome hurdles to phytophagy in the food web represented by the defensive evolutionary barriers of plants. Land and aquatic plants, including weeds, show a great biochemical diversity, growth forms, leaf shapes and seasonal phenologies, and the reciprocal (coevolutionary) influences between these diverse forms of plants and insects, led to the specificity of weed-feeding insects for their hosts. This was achieved in various ways by specialized insects. They alternatively developed the ability to (i) detoxify and metabolize xenobiotic compounds contained in the tissues of the host plant; (ii) sequester toxic secondary plant metabolites; (iii) rapidly excrete the toxicants ingested; or (iv) attack poisonous plants without ingesting an overdose of the toxic allelochemicals, as a result of behavioral defenses. On the whole, specialists are more efficient in the use of resources and better competitors than generalists. Specialized monophagous and oligophagous insects, rather than polyphagous insects, have the major effect in the regulation of the abundance of their host plants.

Weed-Feeding Insects

Host specific weed-feeding insects can be used as beneficial organisms in programs for the biological control of weeds, as an alternative to chemical herbicides, or other forms of control. Therefore, they may be a component of integrated pest management programs and in some cases may represent the best, if not the only effective solution to control exotic weeds introduced in a new geographical area. This is the case in particular for rangeland weeds, and weeds that represent an environmental problem, for example in protected areas and where the area infested is very large. Nevertheless, biological control can be successfully applied also against weeds infesting crops. This form of control offers many important advantages, being effective, selective, environmentally sound, self-perpetuating and cost-effective, especially in the long term. Information about the host range of a weed-feeding insect is essential for organisms that have prospective use as biological control agents. It is necessary that, in addition to being effective in controlling the target plant, it does not harm other plants such as agricultural crops, ornamental plants, or plants of ecological value. Therefore, studies must be conducted to be able to predict the effectiveness of the biological control agent, and to determine which plants are likely to be attacked in the region where the insect should be released. Several approaches were considered to study the level of specialization of a candidate agent in order to define its host range and in general these methods include tests on (i) species of plants taxonomically related to the target plant for biological control; (ii) plants attacked by other species of insects related to the candidate agent; (iii) cultivated plants of economic importance in the region of release; (iv) threatened, endangered, or other native plants of ecological value present in the area of release; (v) plant species with an increasing phylogenetic distance from the target plant; and (vi) unrelated plants with biochemical, or morphological characteristics in common with the target plant. The evaluation of the safety and future performance of candidate biological agents in the release environment depends on a complex of biotic and abiotic factors and has to be considered for each specific situation. In order to assess the degree of specificity of a species of insect, studies can be conducted in the laboratory and in the field on the test plant species. The ability of the insect to feed, produce fertile eggs and oviposit on the test plants is verified. Also, the ability to complete its development under no-choice and multiple-choice conditions is studied. Once this information is available, studies on the following generations can show if the test plant affects their biology, and if there are variations in fertility, or other key biological traits. Studies conducted in the field will complement the information obtained in the laboratory and will help to define the true host range of the insect. Depending on the nature of the weed problem, it may be necessary to use organisms with various degrees of specialization for their hosts, ranging from highly specific (e.g., attacking exclusively a variety of the weed species), to less specific insects. In-depth studies on the life history of these insects are also required, since often these weed-feeding insects being considered as candidate agents for biological control are new to science, and even when they are not new species, their biology is usually very poorly known. Due to intraspecific variability among insects, host range studies should include a sufficiently large sample of insects to be representative of that species, and it is preferable that they are conducted on precise, geographically distinct populations. The biology, habits, degree of host specificity and, if necessary, genetics of populations of different origin are compared.

► Foreign Exploration for Insect that Feed on Weeds
► Biological Control of Weeds
► Arthropod-associated Plant Effectors (AAPEs): Elicitors and Effectors of Crop Defense

References

Ananthakrishnan TN, Raman A (eds) (1988) Dynamics of insect–plant interactions. Oxford & IBH Publishing Co, New Delhi, India

Barbosa P, Letorneau DK (eds) (1988) Novel aspects of insect–plant interactions. Wiley, New York, NY

Dettner K, Bauer G, Völkl W (eds) (1997) Vertical food web interactions: evolutionary patterns and driving forces. Springer, Berlin, Germany
Hunter MD, Ohgushi T, Price PW (eds) (1992) Effects of resource distribution on animal–plant interactions. Academic Press, San Diego, CA
Jolivet P (1998) Interrelationship between insects and plants. CRC Press, Boca Raton, FL

House Dust Mite

Several species of mites in the family Pyroglyphidae are considered to be dust mites.

► Mites

House Fly, *Musca domestica* L. (Diptera: Muscidae)

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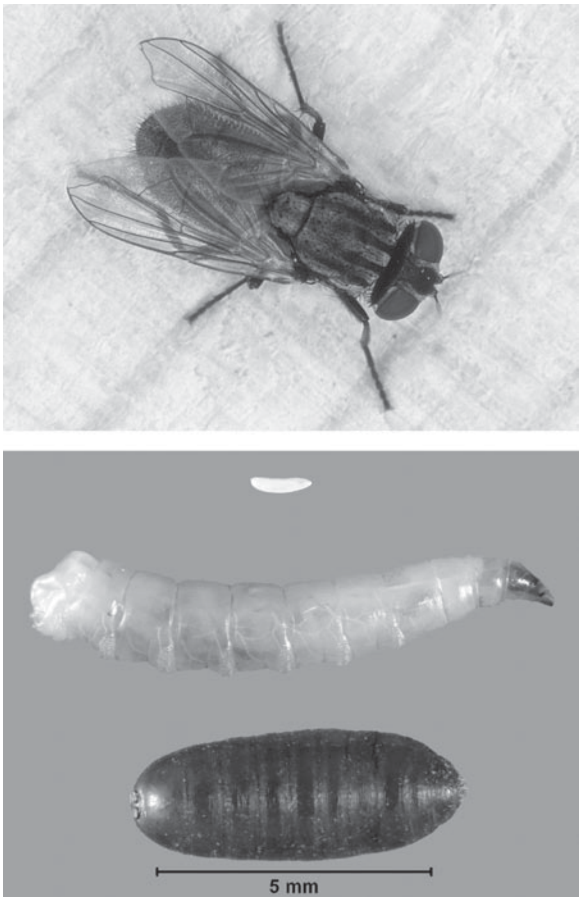
This common fly originated on the steppes of central Asia, but now occurs on all inhabited continents, in all climates from tropical to temperate, and in a variety of environments ranging from rural to urban. It is commonly associated with animal feces, but has adapted well to feeding on garbage, so it is abundant almost anywhere people live. It is the most common fly to invade homes, and often is the dominant species around livestock and poultry. Despite its inability to bite, it is both a nuisance and a public health problem.

Life History

The life cycle of the house fly may be completed in as little as 6 days, but under suboptimal conditions may require up to 2 months. It breeds continuously in warm climates such as in the tropics and subtropics, producing more than 20 generations annually. Even in more temperate areas they commonly undergo ten generations. In cooler areas they overwinter as larvae or pupae, but adults perish when exposed to cold. In heated areas in cold climates, however, they breed throughout the winter months if the adults have access to food and larvae to suitable developmental media.

The cylindrical-oval eggs (Fig. 54) are white, and 1.0–1.2 mm long. Eggs typically are laid in clusters, often numbering 75–150 eggs per cluster. A female normally deposits 2–6 clusters of eggs during her life span. Maximum egg production occurs at intermediate temperatures, 25–30°C. Often, several flies will deposit their eggs in close proximity, leading to large masses of larvae and pupae. Eggs must remain moist or they will not hatch. Egg hatch usually occurs within 8–20 h. Due to its rapid development time and high reproductive capacity, the house fly has the capacity to increase in abundance rapidly. Indeed, scientists impressed with its reproductive capacity have calculated that, lacking mortality, a single pair of flies could grow to a population of 191,010,000,000,000,000,000 in only 5 months, enough to cover the entire earth in a layer of flies several meters deep!

The larvae are creamy white, cylindrical, legless, and taper to a point at the head. The head of larval house flies, like most maggots, have dark mouth hooks. There are three larval instars. The optimal temperature for larval development is 35–38°C, though larval survival is greatest at 17–32°C. Larvae complete their development in 4–13 days at optimal temperatures, but require 14–30 days at temperatures of 12–17°C. The moisture level of the food affects larval survival, and 50–70% moisture content favors survival, though some survival can occur at almost any moisture level. Nutrient-rich substrates such as animal manure provide an excellent developmental substrate. Very little manure is needed for larval development, and sand or soil containing small amounts of degraded manure allows for successful belowground development. At maturity, larvae are 7–12 mm long, and prefer to disperse to a dry location to pupate.



House Fly, *Musca domestica* L. (Diptera: Muscidae), Figure 54 House fly stages of development: *above*, adult; *below* (top to bottom), egg, larva and pupa. Note that the eggs are normally deposited in clusters. (Upper photo by Jim Castner, lower by Lyle Buss, both of the University of Florida).

The mature larva pupates within the cuticle of the last larval instar (this structure is called the puparium), though the shape of the pupa is quite different from the larva, being bluntly rounded at both ends. It is about 8 mm long. The color of the pupa changes from yellowish, to reddish brown, to dark brown or black over the course of the pupal stage. Pupae complete their development in 2–6 days at 32–37°C, but require 17–27 days at about 14°C.

The adult is about 4–7.5 mm long. The female is typically larger, and can be distinguished from the male by the relatively wide space between the eyes (in males, the eyes almost touch). The dull, grayish fly bears four narrow dark stripes on the thorax. The abdomen may be gray, but often is yellowish, and has a narrow dark line dorsally. The wings are transparent except for the dark veins. They have sponging mouthparts, which allows them to lap up liquid food. Thus, they cannot bite animals and humans. Flies regurgitate readily, secreting saliva onto solid foods so it can be liquefied and ingested. Adults may live up to 2 months, but more typically live 2–3 weeks. Without food, they survive only 2–3 days. Longevity is enhanced by availability of suitable food, especially sugar. Access to animal manure does not lengthen adult life and they live longer at cooler temperatures. They require food before they will copulate, and copulation is completed in as few as 2 min or as long as 15 min. Oviposition commences 4–20 days after copulation. Female flies need access to suitable food (protein) to allow them to produce eggs, and manure alone is not adequate. They prefer sunlight, and are active fliers during warm days. They are inactive at night, and commonly can be seen perching on the ceilings of barns or other shelters. Lacking buildings on which to perch, flies rest on trees, poles, wires, and other elevated objects. If adequate food and oviposition sites are available, emerging flies generally remain in the area. Lacking these conditions, however, flies will easily disperse a kilometer or more in search of food.

According to a study conducted in Texas, USA, breeding site suitability (in descending order), was horse manure, human excrement, cow manure, fermenting vegetable, and kitchen waste. However, another study found that structures containing swine, horse, sheep, cattle, and poultry varied in fly abundance, with swine facilities containing the most and poultry the least. Fruit and vegetable cull piles, partially incinerated garbage, and incompletely composted manure also are highly favored sites for breeding.

Damage

House flies are mechanical vectors of animal and human pathogens, particularly enteric diseases. At times, they have been found contaminated with viruses, bacteria, fungi, protozoa, and nematodes. These microbial organisms adhere to their tarsi, legs, mouthparts, and elsewhere as the flies move about their environment, and then these microbes can be relocated when the flies move to new food sources. Of particular concern is their movement from animal or human feces to food that will be eaten uncooked by humans. Also, when consumed by flies, some pathogens can be harbored in the mouthparts or alimentary canal for several days, and then be transmitted when flies defecate or regurgitate. In situations where plumbing is lacking, such as open latrines, serious health problems can develop, especially if there are outdoor food markets, hospitals, or slaughter houses nearby. Among the pathogens commonly transmitted by house flies are *Salmonella, Shigella, Campylobacter, Escherichia, Enterococcus, Chlamydia*, and many other species that cause illness. These flies are most commonly linked to outbreaks of diarrhea and shigellosis, but also are implicated in transmission of food poisoning, typhoid fever, dysentery, tuberculosis, anthrax, ophthalmia, and parasitic worms.

In addition to disease transmission, house flies can be a severe nuisance. These flies alight on and near people where they can be an irritant, especially for people who cannot wave them away, such as infants and the asleep or infirm. If left undisturbed, the flies may feed on the secretions of the mouth, nose and eyes. When human habitations are in close proximity to animal production facilities, the flies emanating from such operations usually prove to be a point of contention, sometimes resulting in legal actions.

Management

Tolerance of flies depends greatly on circumstances. In sensitive environments such as food preparation and packing facilities, restaurants, and hospitals, even small numbers of flies cannot be tolerated. In the context of livestock or poultry production, however, some flies are inevitable. Serious problems occur when cities or suburban development occur near poultry production facilities, as residents usually will not tolerate the large numbers of flies emanating from such facilities.

Fly populations are commonly monitored directly using sticky tapes or ribbons, or baited traps, to capture flies. Densities are also assessed indirectly using spot cards to assess the number vomit or fecal spots. Traps can be baited with molasses, sugar, fruit or meat, and often are used in combination with a device that captures the attracted flies. The sex pheromone (Z)-9-tricosene also functions as an aggregation pheromone, and is called muscalure. Muscalure is formulated with sugar as a commercially-available fly bait for local population suppression, as well as an enhancement for population monitoring.

Ultraviolet light traps can be used to assess population levels, but also serve as a non-chemical control technique that can be used indoors in both agricultural and non-agricultural areas. They normally function by electrocuting flies that enter the trap, though those used in restaurants typically have a sticky panel. Flies do not orient to traps from a great distance, so several are normally needed for them to be effective. Placement should include within 4–8 m of entryways, and within 1.5 m of the floor, to take advantage of fly flight behavior. They should be operated continuously, although they are most effective when the room lights are off.

The most important approach for fly management is sanitation. Flies should be deprived of suitable oviposition sites, and larval environments should be eliminated or made too dry for high levels of survival to occur. To accomplish this, removal of fecal material, agricultural refuse, spilled feed, soiled animal bedding, and food wastes should occur at least twice per week. Around homes and businesses, screening or covering of windows, doors or air doors, and trash containers proves useful in denying access of flies to breeding sites. Packaging household trash in plastic bags, and burying trash under at least 15 cm of soil and in sanitary landfills also helps to eliminate breeding. Trash cans and dumpsters should have tight-fitting lids; failing this, slow release fumigant insecticide dispensers are sometimes installed on the inside of the lids to reduce fly survival.

In agricultural areas, manure can be scattered over fields so that it quickly dries and becomes unsuitable for egg and larval survival. Composting of manure can be effective if the compost is properly maintained, including regular turning. Manure can also be liquefied and stored in lagoons anaerobically, though at some point the solids need to be separated. Manure can also be treated with an insecticide, though this method is highly discouraged as it interferes with biological control of flies, often resulting in a rebound of the fly population. More commonly, insecticides (especially insect growth regulators) can be fed to livestock, and residual insecticide in the manure inhibits fly breeding. In animal facilities, insecticides are often applied to the favored resting places of adults, or bait stations established to poison adults with either solid or liquid formulations. Continuous exposure of flies to insecticides has led to development of insecticide resistance to many insecticides.

Natural biological suppression of the house fly results primarily from the actions of certain chalcidoid wasps (Hymenoptera: Pteromalidae), of which many species have been associated with house fly around the world. Among the more important are *Muscidifurax* and *Sphalangia* spp. Ichneumonids and other parasitoids, as well as some predatory insects (especially histerids [Coleoptera: Histeridae] and staphylinids [Coleoptera: Staphylinidae]), also contribute to fly mortality, but under optimal fly breeding conditions the house fly quickly builds to high numbers. Augmentative biological control using insectary-reared parasitoids has been quite successful in some dairies, feedlots and poultry house situations. The species most often released for biological suppression in North America are *Muscidifurax raptor* Girault and Saunders, *M. raptorellus* Kogan and Legner, *Spalangia endius* Walker, and *S. nigroaenea* Curtis. These different species function better under different conditions, some performing better under cooler or warmer conditions, others parasitizing flies near the surface or deeper in the pupation medium.

References

Barnard DR, Geden CJ (1993) Influence of larval density and temperature in poultry manure on development of the house fly (Diptera: Muscidae). Environ Entomol 22:971–977

Bishoff FC, Dove WE, Parman DC (1915) Notes on certain points of economic importance in the biology of the house fly. J Econ Entomol 8:54–71

Hogsette JA (1996) Development of house flies (Diptera: Muscidae) in sand containing various amounts of manure solids and moisture. J Econ Entomol 89:940–945

Howard LO, Bishopp FC (1925) The house fly and how to suppress it. USDA Farmers' Bulletin 1408, 18pp

Lysyk TJ (1991) Effects of temperature, food, and sucrose feeding on longevity of the house fly (Diptera: Muscidae). Environ Entomol 20:1176–1180

Hedges SA (ed) (2004) The Mallis handbook of pest control, 9th edn. GIE Media, Cleveland. 1396 pp

Seymour RC, Campbell JB (1993) Predators and parasitoids of house flies and stable flies (Diptera: Muscidae) in cattle confinements in west central Nebraska. Environ Entomol 22:212–219

Hover Flies

Members of the family Syrphidae (order Diptera).

► Flies

Howard, Leland Ossian

Leland Howard was born in Illinois on June 11, 1857, but moved with his parents to New York state when he was young, and it was in the vicinity of the town of Ithaca that he grew up. His interests in natural history were encouraged by his parents. However, when he entered Cornell University, it was to study civil engineering at the insistence of his mother, who by then was a widow. Leland transferred to the natural sciences without telling his mother, studied botany, geology, and chemistry, and worked in the laboratory of Henry Comstock. He graduated in 1877, and the following summer was contacted by Charles Riley to persuade him to go to Washington, DC, and work for the U.S. Department of Agriculture. The offer was accepted, and Howard moved there and worked on numerous projects in applied entomology, including brown-tail moth, gypsy moth, European corn borer, Japanese beetle, and scale insects, and taxonomy of Hymenoptera including Ichneumonidae, Braconidae, Chalcididae, and Prototrupoidea. He received an M.S. degree from Cornell University for his thesis "The morphology of Chalcididae." He and Riley were among the founders of the Entomological Society of Washington in 1884. He married in 1886. In 1894 after the resignation of Riley, Leland Howard was appointed Division Chief in his place. Books followed, such as (1901) "Mosquitoes, how they live, how they are classified, and how they may be destroyed," (1901) "The insect book," (1911) "The housefly – disease carrier," (1912–1917) with Dyar and Knab as coauthors "The mosquitoes of North and Central America and the West Indies," (1930) "A history of applied entomology," (1931) "The insect menace," and (1933) "Fighting the insects: the story of an entomologist." Awards followed in the form of honorary doctoral degrees from Georgetown, Pittsburgh, California, Toronto, and Rutgers universities, as well as an honorary M.D. degree from Georgetown University. In 1894 he became president of the American Association of Economic Entomologists, and in 1898 permanent secretary of the American Association for the Advancement of Science. He retired in 1927 and died on May 1, 1950, perhaps the most respected entomologist in American history.

Reference

Mallis A (1971) Leland Ossian Howard. In: American entomologists. Rutgers University Press, New Brunswick, NJ, pp 79–86

Hübner, Jacob

Jacob Hübner was born in Augsburg, Germany, on June 20, 1761. His early life seems unrecorded. His great works were (1786–1790) "Beiträge zur Geschichte europäischer Schmetterlinge," (1793) "Sammlung äuserlesener Vogel und Schmetterlinge," (1805–1824) "Sammlung europäischer Schmetterlinge," (1806–1818) "Geschichte europäischer Schmetterlinge," and (1806–1824) "Sammlung exotische Schmetterlinge," (1806) "Tentamen determinationis, digestionis atque denominationis singularum stirpium Lepidopterorum…," and (1816) "Verzeichniss bekannter Schmetterlinge." All of the works deal with Lepidoptera (the second also with birds). Some of the works are magnificently illustrated with copper plates, making identification easy. The (1806–1824) "Sammlung exotische Schmetterlinge" deals with exotic species of Lepidoptera [meaning those that occur abroad] and includes several North American species, some of which are pests. The (1806) "Tentamen" was a work distributed to just a few entomologists, in which the author tried to fix scientific names, whose validity was subsequently hotly debated. He died in Augsburg on September 13, 1826. This man was the world's first great lepidopterist.

References

Essig EO (1931) Hübner, Jacob, p. 664–667 in A history of entomology. Macmillan, New York, 1029 pp
Freyer CF (1861) Erinnerung an Jacob Hübner aus Augsburg. Stettiner Entom Ztng 22:297–299

Huffaker, Carl Barton

Carl Huffaker was born in the state of Kentucky, USA, on September 30, 1914. His B.S. (1938) and M.S. (1939) degrees were from the University of Kentucky, with a Ph.D. from Ohio State University in 1942. His career began as medical entomologist with the U.S. Health and Sanitation Division of Inter-American Affairs, in Colombia, Haiti, and the Dominican Republic. He was recruited in 1946 by the Division of Biological Control of the University of California, stationed in Berkeley, and remained in Berkeley for the rest of his career. His work emphasized the biological control of weeds, and a major one was control of *Hypericum perforatum* (perforated St. Johnswort, or Klamath weed) in the Pacific coastal states of the USA. He published over 200 papers. In 1970–1983 he was director of the University of California's International Center of Integrated and Biological Control. He was co-leader (with Paul DeBach) of the Integrated Pest Management Project, sponsored by the U.S. Department of Agriculture, U.S. Environmental Protection Agency, and National Science Foundation, involving scientists from 18 universities. This project was so much associated with his leadership that it was widely known as "The Huffaker Project." He served as president of the Entomological Society of America and was elected to the National Academy of Sciences. He died on October 10, 1995, after a prolonged illness, and was survived by his wife and four children.

Reference

Caltagirone L, Dahlsten D, Garcia R, Gutierrez A, Hagen K, Sylvester E (1995) Carl Barton Huffaker, Department of Entomology and Parasitology, Berkeley. Available at http://sunsite.berkeley.edu:2020/dynaweb/teiproj/uchist/inmemoriam/inmemoriam 1995 Accessed Aug 2002

Human Botfly, *Dermatobia hominis* (Linneaus, Jr.) (Diptera: Oestridae)

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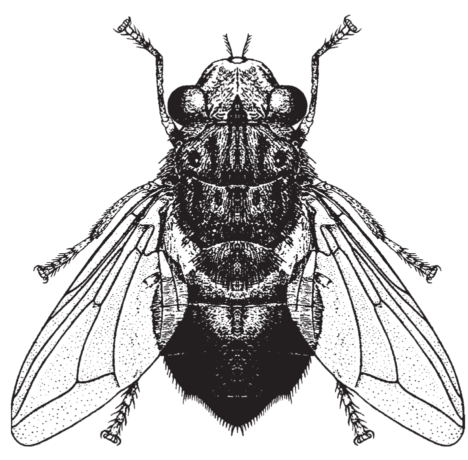
This large (approximately 12 mm) metallic blue fly is also known as tropical warble fly, human warble fly, and torsalo. The fly occurs in Mexico, Central and South America from approximately 25°N to 32°S latitude. The fly, which does not feed, is found primarily along the margins of forested areas. It affects livestock, pests and other mammals in addition to humans. On occasion birds are affected, and young livestock in Central and South America can be so heavily infested that they are killed by this fly. The life cycle is unusual, as the adult female botfly (Fig. 55) lays its white eggs on day-flying flies, particularly mosquitoes, usually of the genus *Psorophora*. The mosquito then inadvertently transports the eggs of the botfly to distant vertebrate hosts. The female lays 14–200 eggs on the ventral surface of the transport insect, usually mosquitoes, but sometimes ticks serve as hosts. The eggs are 1 mm in length. When the egg-bearing transport insect feeds on a warm-blooded host, the heat stimulates the *Dermatobia* eggs to hatch, the larva emerges and bores into the skin. They usually penetrate at the feeding site of the mosquito, but also can penetrate unbroken skin at the hair pore. This botfly has also been known to lay eggs on wet laundry. When a person puts on the egg-infested clothes, the larvae emerge from the eggs and bore into the skin. Within the skin, the larva grows, molts, and forms a cyst, boil or warble. In humans, lesions develop mainly in



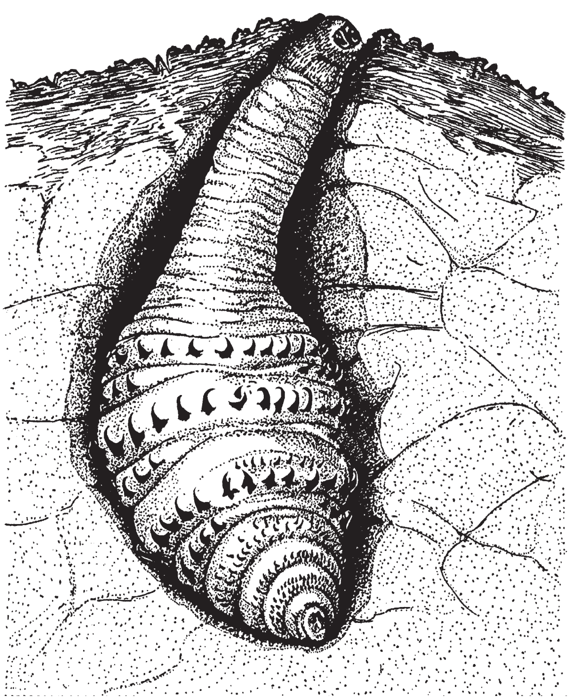
Human Botfly, *Dermatobia hominis* (Linneaus, Jr.) (Diptera: Oestridae), Figure 55 Adult female human botfly, *Dermatobia hominis* (adapted from James 1947).

the hands, wrists, ankles, neck, face and head, but occasionally also in the brain. Several larvae can inhabit the host simultaneously, and they normally stay close to the site of entry, using the entry pore as a breathing site. The inflamed pocket may itch, larval movement is painful, and eventually discharge emanates from the swelling. Larval development time is about 1–4 months. Though not generally considered life-threatening, it can be fatal to very young children (<5 years of age). The adult lifespan is brief, usually only a few days.

Treatment of humans usually involves exercising pressure on or around the lesion, resulting in expulsion. This may not be effective, however, and excision follow by treatment to prevent secondary infection may be preferable. Secondary infection is common.

The larva has twelve body segments. The first segment has mouthparts with hooks. Most of the body segments have spines. The larva pushes its posterior spiracles through the aperture in the skin to maintain a hole open to the external air. After several weeks the mature larva (Fig. 56) emerges during the night or early morning, and drops to the ground to pupate. The larval period lasts approximately 40 days. The last larval skin serves as a shell for the pupa. The pupal period lasts from 14 to 24 days, and then the adult emerges. The emerging females mate and seek a transport insect.

Management includes using mosquito repellents on the skin and clothing, and mosquito netting around beds. This benefits not only human botfly management, but helps prevent mosquito-vectored diseases such as dengue, yellow fever, and malaria.



Human Botfly, *Dermatobia hominis* (Linneaus, Jr.) (Diptera: Oestridae), Figure 56 **Mature larva of human botfly, *Dermatobia hominis*, shown infesting its host, with the posterior spiracles protruding from a hole in the host's skin (adapted from Craig and Faust 1940).**

References

Bates M (1943) Mosquitoes as vectors of *Dermatobia* in eastern Colombia. Ann Entomol Soc Am 36:21–24

Banegas AD, Mourier H, Graham OH (1967) Laboratory colonization of *Dermatobia hominis* (Diptera: Cuterebridae). Ann Entomol Soc Am 60:511–514

Catts EP (1982) Biology of New World bot flies: Cuterebridae. Ann Rev Entomol 27:313–318

Guimarães JH, Papavero N (1966) A tentative annotated bibliography of *Dermatobia hominis* (Linnaeus Jr. 1781) (Diptera, Cuterebridae). Arquivos de Zoologia do Estado de São Paulo 14:223–294

Koone HD, Banegas AD (1959) Biology and control of *Dermatobia hominis* (L. Jr.) in Honduras. J Kansas Entomol Soc 32:100–108

Rosen IJ, Neuberger N (1977) Myiasis *Dermatobia hominis* Linn: report of a case and review of literature. Cutis 19:63–66

Sancho E (1988) *Dermatobia*, the neotropical warble fly. Parasitol Today 4:242–246

Human Lice

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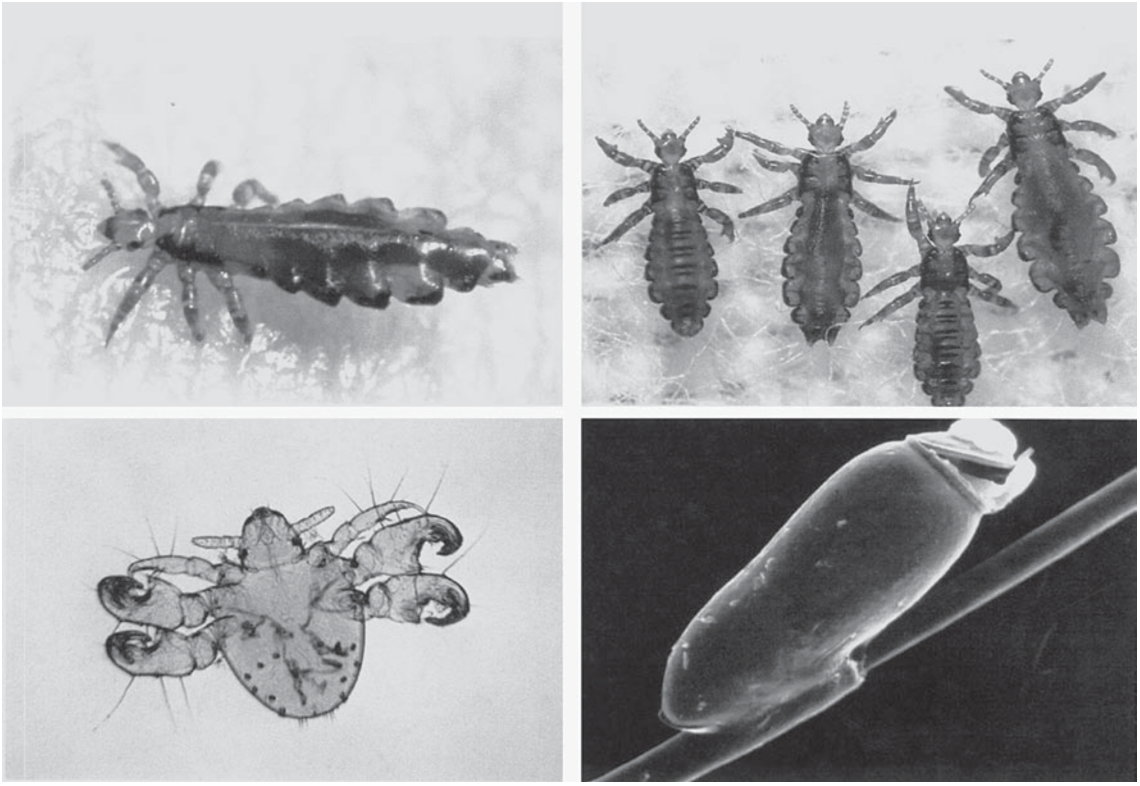
Lice are wingless, six-legged, bloodsucking insects that belong to the order Siphunculata (also called Anoplura, or combined with the chewing lice and called Phthiraptera). There are nearly 4,000 species of lice recognized, although only 560 species suck blood and feed on mammals. Lice are very host specific; therefore, human lice cannot be transmitted between mammals. There are only three species of lice that infest humans: *Pediculus humanus humanus*, the body or "clothing" louse; *Pediculus humanus capitis*, the head louse; and *Phthirus* (or *Pthirus*) *pubis*, the pubic or "crab" louse (Fig. 57).

Biology

Lice are hemimetabolic, meaning that they do not go through a complete metamorphosis like mosquitoes or fleas. After a 7–12 day incubation period, nymphs are hatched from eggs or "nits." Almost immediately, the nymph must feed on a human host to avoid death from starvation and dehydration.

Nymphs resemble miniature adults and undergo three nymphal instars before maturation. Several feedings occur between each molt of the chitinous exoskeleton. When feeding, the body structure of the louse is capable of expanding by one third of its body weight per meal. Crab and head lice feed regularly every 4–6 h, although the body louse can survive several days without a blood meal.

It is not until the 3rd and final molt that the sex is determined. It is more difficult to identify the gender of *P(h)thirus* than *Pediculus*. Within 2 days of maturation, the female will feed several times, copulate, and begin laying eggs. The female head louse lays an average of 3–6 eggs per day, with crab lice laying fewer and body lice laying more. The female louse attaches nits to hairs



Human Lice, Figure 57 **Human lice. *Upper left*: adult female head louse with blood meal; *upper right*: alternating male and female head lice (male-female-male-female); *lower left*: nymph of crab louse; *lower right*: scanning electron micrograph of head louse egg (nit).**

(or ibers in the case of body lice) by secreting a glue that hardens on contact with air.

In each species, females are usually 20% larger than males, with longer, wider, and rounder bodies. Only males have dark brown stripes on their back. Only females, however, have an invaginated V-shape located on the posterior end of their body, in order to deposit eggs on the hair shaft or cloth fiber. The average life span of a louse is 30–42 days.

Habitat and Epidemiology

Pediculus humanus

The body louse does not live on the body, but in clothing or bedding, and only travels to the host to feed. Nits are laid on cloth fibers, particularly in the seams and collars. Although people associate all lice with poor hygiene, only body lice infestations are due to lack of cleanliness. Infestations are common in individuals who are unable to change or wash their clothing. Frequently, these people are forced to live in crowded, unsanitary environments, such as those exposed to war, natural disaster, refugee status, or homelessness.

Pediculus capitis

Head lice are 25% smaller than body lice, but otherwise are identical in appearance. Head lice live on the scalp, preferring a clean, healthy head. Nits are usually laid close to the scalp for warmth, although in tropical climates, they can be found anywhere on the hair shaft. The female louse deposits nits on the hair shaft with a biological adhesive for which there is no known solvent. Hair debris such as gel, spray, and dandruff, are often mistaken for nits. However, hair residue slides easily off the hair, whereas nits are firmly cemented to the hair shaft. Head lice infestations are most common in children aged 3–11 due to their frequent head to head contact during play. Other close contacts, such as family members, teachers and day care workers, may also become infested. Head lice transmission can also occur by sharing of brushes, combs, hats, helmets, and other headgear and hair accessories.

P(h)thirus pubis

Crab lice are not discriminatory in host choice, and are found in all levels of society and various ethnic groups. Crab lice are typically located in the pubic and perianal areas, but can be also found on any hairy part of the body. Secondary sites of infestation commonly include beards, mustaches, scalp, eyebrows, eyelashes, and axillae. Transmission generally occurs by sexual contact, although crab lice can also be transmitted by infested towels and bedding. It is not uncommon to find crab lice with their craws caught in the fiber loops of a towel recently used by an infested individual. Fomite transmission occurs more commonly than originally thought because adult crab lice are viable off the host for at least 36 h.

Disease Transmission

Pediculus humanus

Disease transmission is not caused by the bite of the louse, but by infected fecal pellets that can be scratched into the bite site or by an abrasion in the skin. The body louse is known to transmit the following diseases: epidemic typhus (caused by *Rickettsia prowazekii*), murine typhus (caused by *Rickettsia typhii*, trench fever (caused by *Bartonella quintana*), and relapsing fever (caused by *Borrelia recurrentis*).

Pediculus capitis and *P(h)thirus pubis*

Head and crab lice are known to mechanically transmit group A *Streptococcus pyogenes* and *Staphylococcus aureus*. Head and crab lice have not yet been investigated as transmitters of blood borne diseases.

Treatment

Pediculus humanus

Treatment of body lice includes washing clothing and bedding in hot water and then drying in a hot cycle (65°C, 149°F). Drug therapies, such as permethrin or malathion dusting powders, are effective treatment methods in instances of mass infestation. In individual cases, prescription permethrin 5% topical cream or oral ivermectin are recommended treatments.

Pediculus capitis

Treatments for head lice include lindane, malathion, permethrin or natural pyrethrin products. Lindane products demonstrate resistance and may have harmful toxicity effects to the central nervous system (CNS). Over-the-counter treatment with 1% permethrin or natural pyrethrin products can be used, but resistance has been reported in the United States and other countries. Currently, the most effective treatments for head lice include prescription malathion lotion, oral ivermectin (off-label), certain products with anise oil and alcohol, and nit combs as adjunct therapy.

P(h)thirus pubis

Although head lice products may be used in treating crab lice, 5% permethrin cream (prescription treatment for scabies) or oral ivermectin are the most effective treatments. Medication should be applied to all hairy areas of the body, including the scalp.

Phthiriasis palpebrarum

Topical treatments should not be used around the eye area. Vaseline is an effective treatment for crab lice of the eyelashes, as it suffocates lice and eggs and lubricates the lashes, making nit removal easier and is non-toxic.

► Chewing and Sucking Lice
► School IPM

References

Alexander JO (1984) Arthropods and human skin. Springer-Verlag, Berlin, Germany

Andrews M (1976) The life that lives on man. Taplinger, New York, NY

Burgess I (1995) Human lice and their management. Adv Parasitol 36:271–342

Chosidow O (2000) Scabies and pediculosis. Lancet 355:819–826

Meinking TL, Taplin D (1995) Infestations. In: Schachner LA, Hansen RC (eds) Pediatric dermatology, 2nd edn. Churchill Livingstone, New York, NY, pp 1347–1392

Meinking TL (1999) Infestations. Curr Prob Dermatol 11:75–118

Mumcuoglu KY, Hemingway J, Miller J, Ioffe-Uspensky I, Klaus S, Ben-Ishai F, Galun R (1995) Permethrin resistance in the head louse *Pediculus humanus capitis* from Israel. Med Vet Entomol 9:427–432

Humeral

Pertaining to the "shoulder" (near the point of attachment of the wing) of the insect, or located in the anterior basal portion of the wing.

Humeral Angle

The angle of the base of the costal margin of the wing, near the point of attachment.

► Wings of Insects

Humeral Cross Vein

The cross vein extending between the costa and the subcosta near the base of the wing.

► Wings of Insects

Hummingbird Lice

Members of the family Ricinide (order Phthiraptera).

► Chewing and Sucking Lice

Hummingbird Moths

Some members of the family Sphingidae (order Lepidoptera).

► Hawk Moths
► Butterflies and Moths

Humpbacked Flies

Members of the family Phoridae (order Diptera).

► Flies

Human Lymphatic Filariasis (Elephantiasis)

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Human lymphatic filariasis (elephantiasis) is a debilitating and deforming disease caused by infection with parasitic round worms belonging to the phylum Nematoda, order Spirurida, superfamily Filarioidea, and family Filariidae, genera *Wuchereria* and *Brugia*, species *W. bancrofti* and species *B. malayi* and *B. timori*. Humans are the final and exclusive host of *W. bancrofti*. *Brugia malayi*, in addition to infecting humans, has other strains that infect some feline and/or monkey species, but the life-cycles in humans and in these other animals generally remain epidemiologically distinct. These parasites complete their development in two host types, the human (the final and definitive host) or other vertebrates, and the mosquito (the intermediate host). The disease spreads from person to person by the bites of infected mosquitoes.

Approximately 120 million people are infected in at least 80 countries of the world throughout the tropics or subtropics (41 North latitude to 31 South latitude), that include South America, Cuba, Puerto Rico, West Indies, Africa, Spain, Turkey, Asia, Australia, and many South Pacific Islands. It is estimated that one billion (20% of the world's population) are at risk of acquiring infection. Ninety percent of these infections are caused by *W. bancrofti*. The remaining 10% of infections caused by *B. malayi* are restricted to southeast Asia, including India, Thailand, Vietnam, southern China, and the south Pacific islands, and by *B. timori* in the Lesser Sunda Islands of eastern Indonesia.

Both *W. bancrofti* and *B. malayi* have four types based on the density of microfilariae in the peripheral circulation: nocturnally periodic, nocturnally subperiodic, diurnally subperiodic and diurnally periodic. Nocturnally periodic type of *W. bancrofti* is generally found in the slum areas of cities (urban type) and rural areas (rural type). A nocturnally subperiodic type is found in Thailand and Vietnam. The diurnally subperiodic type is rural and found in the eastern Pacific islands and the diurnally periodic type of *B. malayi* is mostly found in areas with irrigated rice fields.

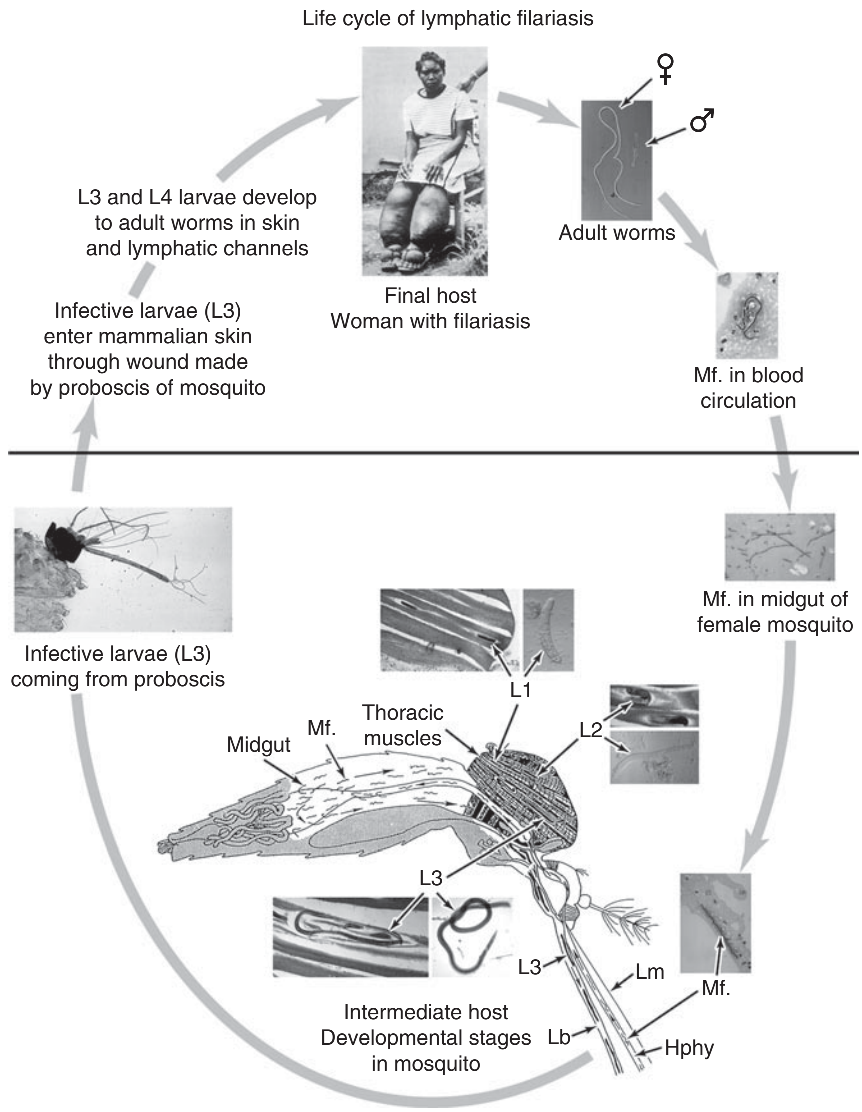
The adult worms that cause the disease live for 7–10 years in the victim's lymph vessels, near to and in lymph nodes. Adult females are long and slender (*W. bancrofti* – 6–10 cm long and 300 μm wide, *B. malayi* – 48 mm long, and *B. timori* – 40 mm long) with a smooth cuticle and bluntly rounded ends. The head is slightly swollen and bears two circles of well-defined papillae. The mouth is small; a buccal cavity is lacking. Males are much smaller (mean length for *W. bancrofti* – 40 mm, *B. malayi* – 18 mm, and *B. timori* – 15 μm) with a fingerlike tail. The vulva of the female is near the level of the middle of the esophagus. Adult females, after mating, produce microfilariae (mean length for *W. bancrofti* – 290 μm, *B. malayi* – 222 μm and *B. timori* – 310 μm) which are found in the blood and peripheral circulation. In endemic areas, in the nocturnally periodic type, the level of microfilariae in the peripheral circulation of humans is controlled by a circadian periodicity or 24 h light-dark cycle, that is, the numbers of microfilariae in the peripheral circulation show a marked peak during the night. In the day time the microfilariae move mainly to the pulmonary capillaries and very few are found in the peripheral circulation. The appearance of large numbers of microfilariae in the peripheral circulation at night coincides with the biting activity of the local mosquito vector. In the nocturnally subperiodic, diurnally subperiodic and diurnally periodic types, microfilariae can be found in the peripheral circulation at all hours of day and night. The microfilariae do not develop further in humans, but only in susceptible species of mosquitoes.

Development of microfilariae to the L_3 or infective larval stage in mosquitoes is identical in all three species (Fig. 58). In mosquitoes, ingested microfilariae in the blood meal do not multiply but grow to the L_3 stage after two molts with 2 weeks. Within a day after the microfilariae are ingested, they shed their sheath and penetrate the midgut wall, move in to the hemocoel, then migrate to the thoracic muscles and lodge themselves intracellularly. The slender active microfilaria transforms to the short thick inactive sausage-stage or L_1 larva within the next 2–4 days. The L_1 larva has a cuticle which forms a conspicuous tail, characteristic of this stage. In the genus *Brugia* one to two nuclei are present in the tail. Five to six days after being ingested as microfilariae, the L_1 larva molts to the L_2 stage. The L_2 larva grows rapidly and has a thin cuticle which can be seen at the caudal end as a short tail. There are one or two papillae at the caudal end. During the second molt the larva sheds its cuticle and becomes the infective L_3 larva. The L_3 larva grows further in length but not in width, moving actively to the hemocoel of the mosquito, first towards the abdomen and later to the head and proboscis. The caudal end of *W. bancrofti* is characterized by having three teat-like papillae of equal size, whereas in the *Brugia*, the central papilla is the most prominent. The duration of larval development in mosquito vectors is affected by the ambient temperature; generally, the warmer it is the more rapid the development. It usually takes 10–14 days for *W. bancrofti* to reach the infective stage, and 7–10 days for *Brugia* species.

When the now infective mosquito bites a human, some or all the infective larvae escape from the proboscis onto the skin and actively enter the wound made by the mosquito. The L_3 larvae move to the lymphatic system and start to develop and molt to the L_4 stage followed by the L_5 or young adults and finally to the mature male and female worms. After fertilization, the female worms produce microfilariae, which find their way from the lymphatic system to the blood circulation. The pre-patent period from the entrance of L_3 when the mosquito bites the human to the appearance of microfilariae in the peripheral blood, is about 3–4 months for *Brugia* sp. and about 8–9 months for *W. bancrofti*.

The intermediate hosts (mosquitoes belonging to the genera *Aedes*, *Culex*, *Anopheles*, and *Mansonia* – about 77 species) become infected when they take an infective blood meal from an infected definitive host (man). Urban *W. bancrofti* with noctural periodicity is transmitted mainly by *Culex quinquefasciatus* in tropical regions, by *Culex pipiens pallens* in China and Japan, and *Culex pipiens molestus* in the eastern Mediterranean. Rural *W. bancrofti* that is nocturnally subperiodic over most of its range is mainly transmitted by several species of *Anopheles* in the western Pacific islands and Africa, occasionally *Aedes* spp. in eastern Pacific islands, and rarely by *Mansonia uniformis* in Sri Lanka. The diurnally subperiodic type is transmitted predominantly by several species of *Aedes,* and the nocturnally subperiodic type by the mosquitoes of the *Aedes niveus* group. The nocturnally periodic type of *B. malayi* is transmitted in certain regions by *Mansonia* spp. and in other regions by *Anopheles barbirostris* or *An. campestris* in Indonesia and Malaysia. *Aedes togoi* is a vector in coastal parts of the Republic of Korea, and parts of southern China. The nocturnally subperiodic type of *B. malayi* is transmitted by *Mansonia* spp. *B. timori* is transmitted by *Anopheles barbirostris*.

Clinical course of lymphatic filariasis in humans can be divided into three distinct stages, asymptomatic, acute and chronic, generally progressing in that order. The asymptomatic stage is characterized by the presence of microfilariae in the peripheral blood, although there are no clinical manifestations of filariasis. The acute symptomatic



Human Lymphatic Filariasis (Elephantiasis), Figure 58 **Life cycle of lymphatic filariasis. Stages of filarial worm in human: L_3 = third stage larvae and L_4 = fourth stage larvae. Stages of filarial larvae in the mosquito: mf = microfilariae, L_1 = first stage larvae (sausage stage), L_2 = second stage larvae, and L_3 = third stage larvae. Larval stages L_1 to L_3 are shown both as normal larvae and in histological sections. Lm = labium, Lb = labrum, and Hphy = hypopharynx.**

stage is characterized by recurrent attacks of fever associated with inflammation of the lymph nodes (lymphadenitis) and lymph vessels (lymphangitis). In bancroftian filariasis recurrent attacks of fever associated with lymphadenitis are less frequently seen than in brugian filariasis. In addition to the lymph nodes in the inguinal, axillary and epitrochlear regions, the lymphatic system of the male genitalia is frequently affected. Typically, each attack of fever and lymphadenitis lasts for several days or weeks and usually subsides spontaneously following bed-rest. The chronic signs of filariasis do not develop usually before the age of 15 years and only a small portion of the community is affected. During the chronic stage microfilariae are usually absent from the blood.

In bancroftian filariasis, the occurrence of the major chronic signs are accumulation of serous fluid in the body cavity (hydrocele), appearance of microfilariae in urine (chyluria), swelling of body parts (lymphodema) and hardening and thickening of the skin of swollen body parts (elephantiasis), which may differ from one area to another. The most common are hydrocele and swelling of the testis, followed by elephantiasis of the entire lower limb, the entire arm, the vulva, and the breast, in descending order of frequency. In brugian filariasis, the leg below the knee or the arm below the elbow are characteristically affected. Genital involvement has not been reported for brugian filariasis.

The worms in the lymphatic system cause tissue changes which restrict normal flow of lymph and result in swelling, fibrosis and eventually secondary infections in the affected tissues. The lower extremities and groin are the parts most likely to be affected. In its severest form, lymphatic filariasis causes elephantiasis, or dramatic swelling of limbs (usually the leg) and genitals (usually the scrotum). These conditions have a devastating effect on the quality of life of those affected, impacting them not only physically, but also emotionally and economically.

Human lymphatic filariasis is a disease which develops over several years and is localized in communities. Individuals can be treated with albendazole plus either diethylcarbamazine (DEC) or ivermectin (Mectizan®), which have been shown to be effective in removing microfilariae from the blood for a full year after treatment and slowly killing the adult stage of the parasite. Recently, the World Health Organization has adopted the policy of a Global Program to Eliminate Lymphatic Filariasis by 2020. The strategy for such a program is based on two concepts: first, to interrupt transmission of infection and second, to alleviate the suffering of infected individuals through management of the disease. The first concept includes treatment of each individual in the community with a single dose of either of the two-drug combinations, albendazole and DEC or albendazole and ivermectin, once a year for several years and to implement vector control practices in each infected community. The second concept is to alleviate the suffering caused by the disease by educating the community about the programs to raise awareness in affected patients. This would promote the benefits of intensive local hygiene, vector control and possible improvement, both in the damage that has already occurred, and in preventing the debilitating and painful, acute episodes of inflammation.

References

Anon (1987) Control of lymphatic filariasis. A manual for health personnel. World Health Organization, Geneva, Switzerland, 89 pp

Anonymous (1992) Lymphatic filariasis: the disease and its control. Fifth report of the WHO Expert Committee on Filariasis. WHO Technical Report Series No. 821. World Health Organization, Geneva, Switzerland

Anonymous (1999) Lymphatic filariasis. WHO information fact sheet. World Health Organization, Geneva, Switzerland, 3 pp

Anonymous (1999) Global program to eliminate lymphatic filariasis. An informal report from WHO/CDS/CPE/CEE/Fil. World Health Organization, Geneva, Switzerland

Sasa M (1976) Human filariasis. University of Tokyo Press, Tokyo, Japan

Human Scabies

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Scabies is a skin condition, also known as “7 year itch” or “Norwegian itch,” produced by almost invisible parasitic mites commonly referred to as “itch mites,” *Sarcoptes scabiei* (DeGeer).

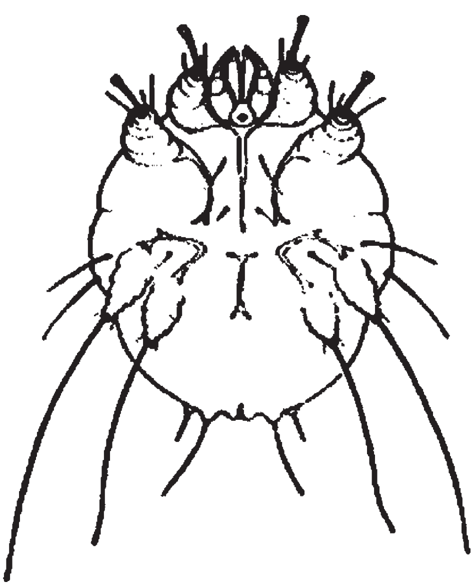
There are several varieties of itch mites that can be distinguished only by the host they attack. Dog, pig, horse and human itch mites are known to exist. Though it is possible for people to be infested with non-human species, usually little to no adverse effect is produced.

Biology

Itch mite nymphs and adults are whitish in color and have eight short, pointed legs equipped with suction devices on the two front pairs and long hairs on the remaining hind legs (Fig. 59). The life cycle of the human itch mite consists of the egg, six-legged larval, eight-legged nymphal and adult stages. The period from egg to mature adult takes 10–14 days at body temperature. Itch mites seldom survive more than a few hours off the host.

Injury and Spread

Mature female mites are responsible for the majority of the skin irritation caused by tunneling in the upper skin layer. Eggs are deposited in these tunnels that extend over one inch in length at 2–3 day intervals over a 2-month period. Once the eggs hatch in 3–8 days, emerging larvae exit the tunnels and remain on or near the skin surface until they reach adult stage. During this time, male mites move about the surface where it is thought they mate with females. These newly fertilized female mites are highly active and are thought to be the contagious stage. Itch mites are primarily transmitted through close personal contact, though bed linens and clothing may serve as secondary sources.



Human Scabies, Figure 59 The human itch mite, *Sarcoptes scabiei* (actual size about the size of this period ".").

Signs, Symptoms and Diagnosis

Red patches of skin on various regions of the body characterize scabies. The most common infested areas include: wrists, elbows, breasts, penis, bends of the knees, between the fingers, and between the buttocks. Sometimes the actual raised tunnels or bumps produced by the mites can be seen. Tunneling mites may release toxic substances that produce severe itching. Often, constant itching causes the individual to become pale and haggard from loss of sleep. Scratching to relieve itching frequently leads to secondary bacterial infections that may become more serious than actual scabies. Widespread allergic reactions also may occur due to the mite presence.

First-time infestations often cause no immediate itching, although sensitivity normally occurs after 1 month. Thereafter, subsequent infestations result in reactions within the first 24 h. Infestations producing these symptoms typically involve less than 12 adult mites. Diagnosis is best made by applying mineral oil to the affected skin surface where tunnels occur, scraping the skin with a scalpel, and examining for the mites under a microscope.

Control

Recognize signs and symptoms of a possible infestation and attempt to recover mites for identification.

Inspect all individuals coming in contact with infested person(s).

Treat all infested persons with one of the recommended miticides listed in the following treatment section. Prophylactic treatment of non-infested persons should be avoided unless screening programs are not effectively suppressing an outbreak.

Isolate infested person(s) for 24 h after treatment has been applied.

Machine wash bed linens, clothing and all other possible contaminated articles in hot (130°F) water and soap, or tightly seal non-washables in plastic bags for 2 weeks.

Treatment

Ointments containing 5% permethrin cream (Elimite®), benzyl benzoate, malathion (Derbac-M®), crotamiton (Eurox®), tetraethylthiuram monosulfide (Tetmosol®), sulfur, thiabendazole, or 1% lindane (Kwell®) are the most widely recommended medications for itch mite control. These products are available only through a physician by prescription and should be applied strictly according to labeled and/or prescribed directions.

► Mites

References

American Academy of Dermatology (1999) Available at http://www.aad.org/education/students/parainfest.htm Accessed January 2008

Benenson AS (ed) (1990) Scabies. Control of communicable diseases in man, 15th edn. American Public Health Association, Washington, DC, pp 385–388

Centers for Disease Control and Prevention (1999) Parasitic diseases. Scabies. http://www.cdc.gov/ncidod/dpd/parasites/scabies/default.htm

Indian and Inuit Health Committee, Canadian Pediatric Society (1994) Scabies management. Can J Paediatr 1:152–155

Greene A (1996) What is the appropriate medication to use for scabies? Available at http://www.drgreene.com/961118.html

Hungerford, Herbert Barker

Herbert Hungerford was born in Kansas on August 30, 1885. He grew up on a farm and trained as a teacher, becoming teacher, principal, and superintendent of schools between 1904 and 1909. Having married in 1905, he entered the University of Kansas in 1909 and obtained a bachelor's degree in 1911. He immediately became a member of the university faculty, and in 1924 was appointed head of the Department of Entomology and State Entomologist. His research interest was the taxonomy, ecology and behavior of water bugs, especially Corixidae and Notonectidae. He built a large collection of aquatic and semiaquatic Hemiptera on which he continued working after retirement in 1956. In 1936, he was elected president of the Entomological Society of America and in 1953 of the Society of Systematic Zoology. He died on May 13, 1963.

References

Mallis A (1971) Herbert Barker Hungerford, In: American entomologists. Rutgers University Press, New Brunswick, NJ, pp 236–238

Woodruff LC (1963) Obituary of Herbert Barker Hungerford. J Kansas Entomol Soc 36:197–199

Hunting Billbug, *Sphenophorus venatus vestitus* Chittenden (Coleoptera: Curculionidae)

This billbug has become a serious problem for some turfgrasses.

► Turfgrass Insects and their Management

Hyaline

Transparent, colorless, or glass-like.

Hyblaeidae

A family of moths (order Lepidoptera). They commonly are known as teak moths.

► Teak Moths
► Butterflies and Moths

Hybosorid Scarab Beetles

Members of the family Hybosoridae (order Coleoptera).

► Beetles

Hybosoridae

A family of beetles (order Coleoptera). They commonly are known as hybosorid scarab beetles.

► Beetles

Hybothiridae

A family of sucking lice (order Phthiraptera).

► Chewing and Sucking Lice

Hybrid Vigor

Increased vigor resulting from the crossbreeding of two genetic lines (races, strains). The offspring of such crossbreeding are more virgorous than either parent.

Hydraenidae

A family of beetles (order Coleoptera). They commonly are known as minute moss beetles.

► Beetles

Hydrobiosidae

A family of caddisflies (order Trichoptera). They commonly are known as microcaddisflies.

► Caddisflies

Hydrometridae

A family of bugs (order Hemiptera). They sometimes are called water measurers or marsh treaders.

► Bugs

Hydrophilidae

A family of beetles (order Coleoptera). They commonly are known as water scavenger beetles.

► Beetles

Hydropsychidae

A family of caddisflies (order Trichoptera). They commonly are known as net-spinning caddisflies.

► Caddisflies

Hydropyle

Hydropyles are structures that allow the uptake of water, and are found on some eggs. Water is absorbed when the embryo is rapidly growing, and the egg enlarges in size. The eggs of most aquatic insects absorb water, but terrestrial insects that deposit their eggs where moisture may occur (e.g., grasshopper eggs in soil) also may have eggs that enlarge. The hydropyle is formed interiorly from the serosal layer, but may be visible externally by an extension of the chorion.

► Eggs of Insects

Hydroscaphidae

A family of beetles (order Coleoptera). They commonly are known as skiff beetles.

► Beetles

Hydrostatic Skeleton

Maintenance of body form in soft-bodied insects such as caterpillars by muscles exerting pressure on the fluid-filled body.

Hygrokinesis

A kinesis response with respect to moisture.

Hygrotaxis

A taxis response with respect to moisture.

Hymenopodidae

A family of praying mantids (Mantodea).

► Praying Mantids

Hymenoptera

An order of insects. They commonly are known as wasps, ants, bees and sawflies.

► Wasps, Ants, Bees and Sawflies

Hyocephalidae

A family of bugs (order Hemiptera, suborder Pentamorpha).

► Bugs

Hypericin

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Hypericin, well known for its photodynamic action, is an aromatic polycyclic compound (a highly condensed quinone) mainly synthesized by plants of the genus *Hypericum* (family Hypericaceae). A survey covering 200 species within the family Hypericaceae, revealed that ca. 60% of these plants contained Hypericin. It is usually confined to certain species of the genus *Hypericum*, e.g., the St. John's worts, a common pasture weed throughout the world. While this compound is found in the leaves, stem and flowers of *Hypericum perforatum*, it occurs only in multicellular trichomes of the calyx of *H. hirsutum*.

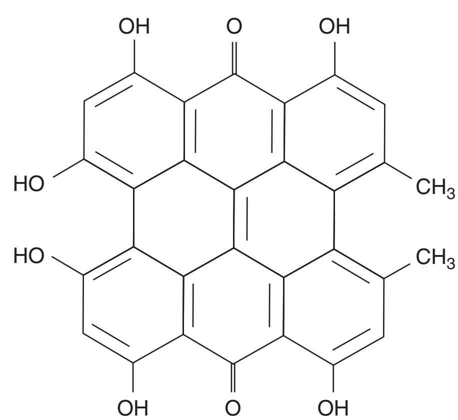
Hypericin (Fig. 60) and its derivatives have also been recorded from other sources. Hypericin has been found in the chromophore of the photoreceptor of *Stenor coeruleus* (a blue-green ciliate) and in the integument of an Australian insect (*Nipaecoccus aurilanatus*). Fagopyrin (a derivative of hypericin) is found in buckwheat (*Fagopyrum esculentum*). In addition, pencilliopsin, which can be oxidized and irradiated to form hypericin, has been isolated from a mold (*Penicilliopsis clavariaeformis*).

Biological Activity

Effects on Insects

Although photodynamic reactions are generally not species specific, the phototoxicity of hypericin is known in only a few systems. Its phototoxicity toward grazing animals, antiviral activity against HIV-1, and insecticidal effect on Aedes mosquito larvae have been reported.

It is well established that the active wavelengths in hypericin toxicity are greater than 500 nm. For larvae of the sphingid *Manduca sexta*, the LD_{50} of purified hypericin was 16 μg/g larval initial fresh weight in constant light (22 W/m^2), but reduced irradiance resulted in decreased mortality. Sublethal applications of



Hypericin, Figure 60 **Structure of hypericin ($C_{30}H_{16}O_8$). an aromatic polycyclic compound mainly synthesized by plants of the genus *Hypericum* (family Hypericaceae).**

hypericin retarded larval growth (body fresh weight) in a dose-dependent manner. While the phototoxic effect was lost when larvae were maintained in darkness for more than 8 h before irradiation, the potential for light-dependent mortality was retained if larvae were starved before irradiation.

Interestingly, several insects with different lifestyles have been reported to overcome the phototoxic effects of hypericin by appropriate behavioral and biochemical strategies: (i) by avoiding light, (ii) by feeding on the plant parts lacking hypericin, or (iii) by decomposing hypericin. Studies on the behavioral and biochemical adaptations of generalist and specialist herbivorous insects feeding on *Hypericum perforatum* (Guttiferae) have revealed that the generalists *Tettigonia viridissima* L., *Ruspolia nitidula* Scopoli, and *Conocephalus discolor* Thunberg preferentially fed on the part of the leaf lacking the phototoxic, hypericin-laden dark glands. In contrast, the specialists *Galeruca tanaceti* L., *Chrysolina geminata* Paykull, and *Cloantha perspicillaris* Boisduval showed no discriminatory feeding pattern but exhibited a negative phototaxis that is presumed to be an efficient strategy to overcome the light-induced toxicity of hypericin.

Another mechanism of defense for insects feeding on phototoxic plants may be the presence of antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), glutathione peroxidase (GPOX), and glutathione reductase (GR). The activities of these enzymes were examined in the larvae of three lepidoptera: *Ostrinia nubilalis*, *Manduca sexta*, and *Anaitis plagiata*. The highest levels of antioxidant enzyme activity were found in *A. plagiata*, a specialist feeder on *Hypericum perforatum*, a plant which contains high levels of the phototoxin hypericin. Larvae of *A. plagiata* that were fed leaf discs treated with hypericin exhibited a short-term, concentration-dependent decline in enzyme activity. Longer term studies with *A. plagiata* fed either the phototoxic *H. perforatum*, or the closely related but non-phototoxic *H. calycinum*, resulted in increased CAT and GR activity in the larvae that were fed the phototoxic plant whereas SOD activity was not significantly different. These results suggest that CAT and GR may be inducible defenses against phototoxins.

Similar results also have been reported for other generalist and specialist herbivorous insects feeding on *Hypericum perforatum* (Guttiferae). The specialist insects had lower constitutive activities of two antioxidant enzymes, glutathione S-transferase and glutathione reductase, than the generalists. Both enzymes are considered to be biochemical adaptations used by phytophagous insects to attenuate the oxidative stress caused by photosensitization.

Medicinal Use and Potential

H. perforatum is presently a source for the preparation of several herbal drugs. There is increasing interest in use of the herbal preparation St. John's wort (*Hypericum perforatum*). Hypericin, the major active ingredient, has many psychoactive properties. The herbal preparation is sold as a nutritional supplement and is recommended for numerous conditions, including depression, anxiety, insomnia and inflammation.

Hypericin, and the structurally related quinone, pseudohypericin, have also been described as having potent antiviral effects, in that they could inhibit both retroviral replication in cell culture and could also control the symptoms of retovirus-induced disease in mice. It has been shown to have impressive light-mediated antiviral activities against different viruses including human immunodeficiency virus type 1 (HIV-1).

Strategies have been studied using hypericin to inactivate enveloped viruses in red blood cell concentrates. Photodynamically induced virus inactivation appears promising in preventing transmission of enveloped virus infections in transfusible blood products. The results of studies on the practical potential of hypericin as a photosensitizer to inactivate key enveloped viruses in packed red blood cell concentrates (PRC) are promising. Also, hypericin induces differentiation and apoptosis in neoplastic cells and exerts phototoxic effects on two cancer cell lines: (i) PC-3, a prostatic adenocarcinoma non-responsive to androgen therapy and (ii) LNCaP, a lymphonodal metastasis of prostate carcinoma responsive to androgen therapy. The results suggest that photodynamic therapy with hypericin could be an alternative approach to the treatment of prostatic tumors, and could be beneficial in tumors that are non-responsive to androgen therapy.

Effects on Domestic Animals

Recently, it has been found that the photosensitization of grazing animals following the ingestion of certain *Hypericum* species is due to the presence of hypericin. This disease which is known as hypericism (or "bighead" in sheep) is manifested by skin irritation and inflammation. It is most commonly caused by the ingestion of *H. perforatum*.

Hypericin must be ingested by mammals to result in hypericism. Unlike the furanocoumarins, it does not appear to be absorbed through the outer layer of the epidermis. After ingestion of the plants, animals remain sensitive to sunlight for a week or more. Skin irritation and inflammation is most severe in regions of unpigmented skin devoid of hair (e.g., the mouth, nose and ears). Other effects are central nervous system disturbances and increase in body temperature. It is, however, rarely fatal and does not appear to deter grazing animals. Nevertheless, sunlight-associated hyperthermia is a consistent and rapidly developing clinical sign in sheep intoxicated by St. John's wort.

Mode of Action

Many secondary plant compounds are capable of photoactivation, resulting in the production of toxic oxygen. Early studies on mammals have shown that the photosensitizing action of hypericin requires both visible light and oxygen. Hypericin promotes Type II photodynamic reactions. Hypericin is known to generate singlet oxygen, and possibly other reactive species, in the presence of light (650–700 nm). It is thought that such photoproducts inactivate viruses by damaging the membrane, since non-enveloped viruses appear to be resistant to hypericin.

References

Aucoin RR, Philogene BJR, Arnason JT (1991) Antioxidant enzymes as biochemical defenses against phototoxin-induced oxidative stress in three species of herbivorous Lepidoptera. Archi Insect Biochem Physiol 16:139–152

Colasanti A, Kisslinger A, Liuzzi R, Quarto M, Riccio P, Roberti G, Tramontano D, Villani F (2000). Hypericin photosensitization of tumor and metastatic cell lines of human prostate. J Photochem Photobiol B Biol 54:103–107

Guillet G, Podeszfinski C, Regnault-Roger C, Arnason JT, Philogene BJR (2000) Behavioral and biochemical adaptations of generalist and specialist herbivorous insects feeding on *Hypericum perforatum* (Guttiferae). Environ Entomol 29:135–139

Jacobson JM, Feinman L, Liebes L, Ostrow N, Koslowski V, Tobia A, Cabana BE, Lee D, Spritzler J, Prince AM (2001) Pharmacokinetics, safety, and antiviral effects of hypericin, a derivative of St. John's wort plant, in patients with chronic hepatitis C virus infection. Antimicrob Agents Chemother 45:517–524

Samuels R, Knox P (1989) Insecticidal activity of hypericin towards *Manduca sexta* larvae. J Chem Ecol 15:855–862

Hypermetamorphosis

A type of development in which there is more than one distinct form of the larval stage. For example, in the Meloidae, young larvae must locate a food source, but older larvae remain and feed on that source; thus, the long-legged, mobile young larvae are replaced by sessile older larvae with shorter, less functional legs.

Hyperparasitoid

An insect parasitoid that parasitizes another parasitoid. A secondary parasitoid.

Hyperplasia

An increase in the number of functional units of an organ (organelles, cells, tissues), excluding tumor formation.

Hypertely

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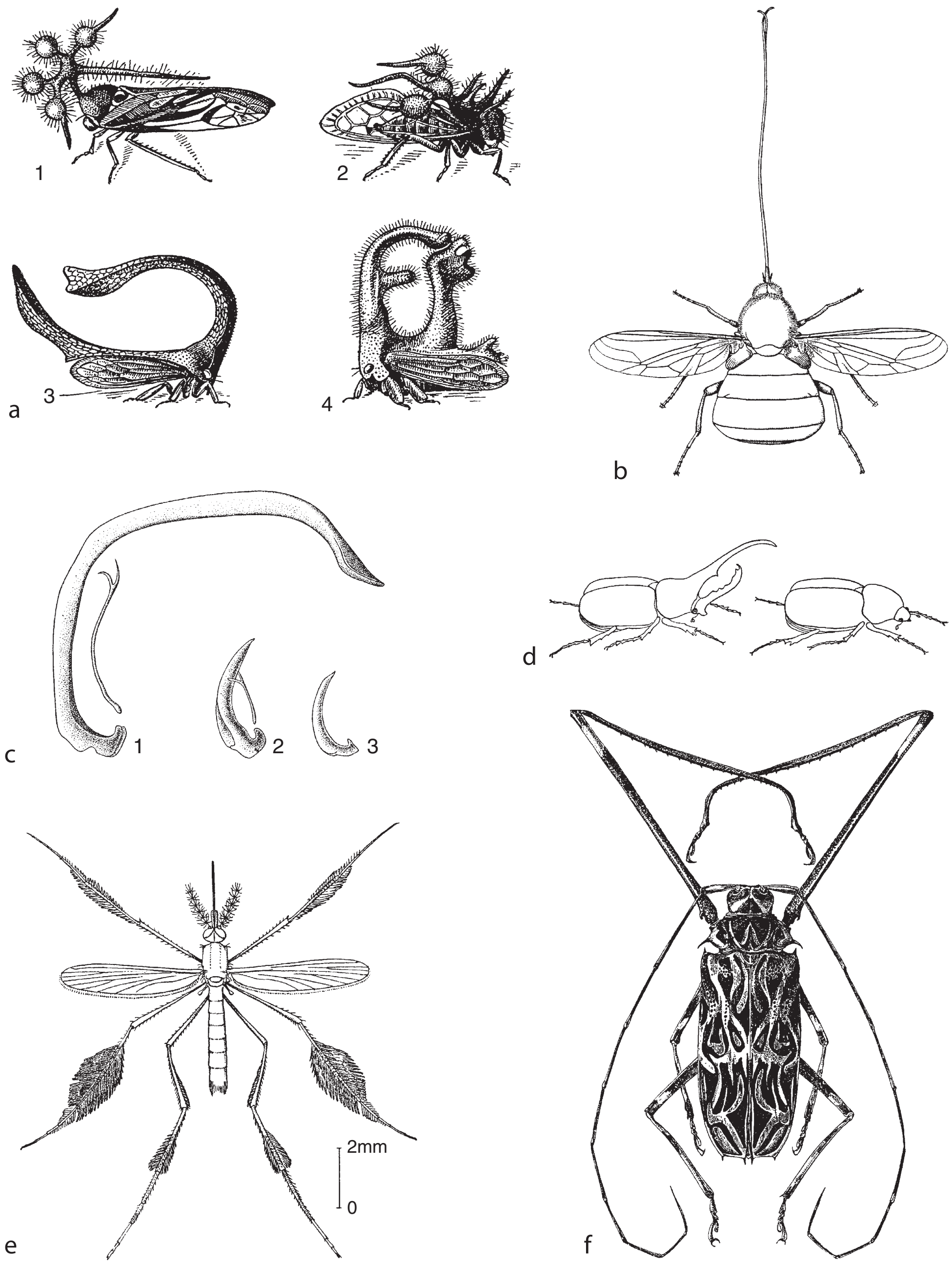
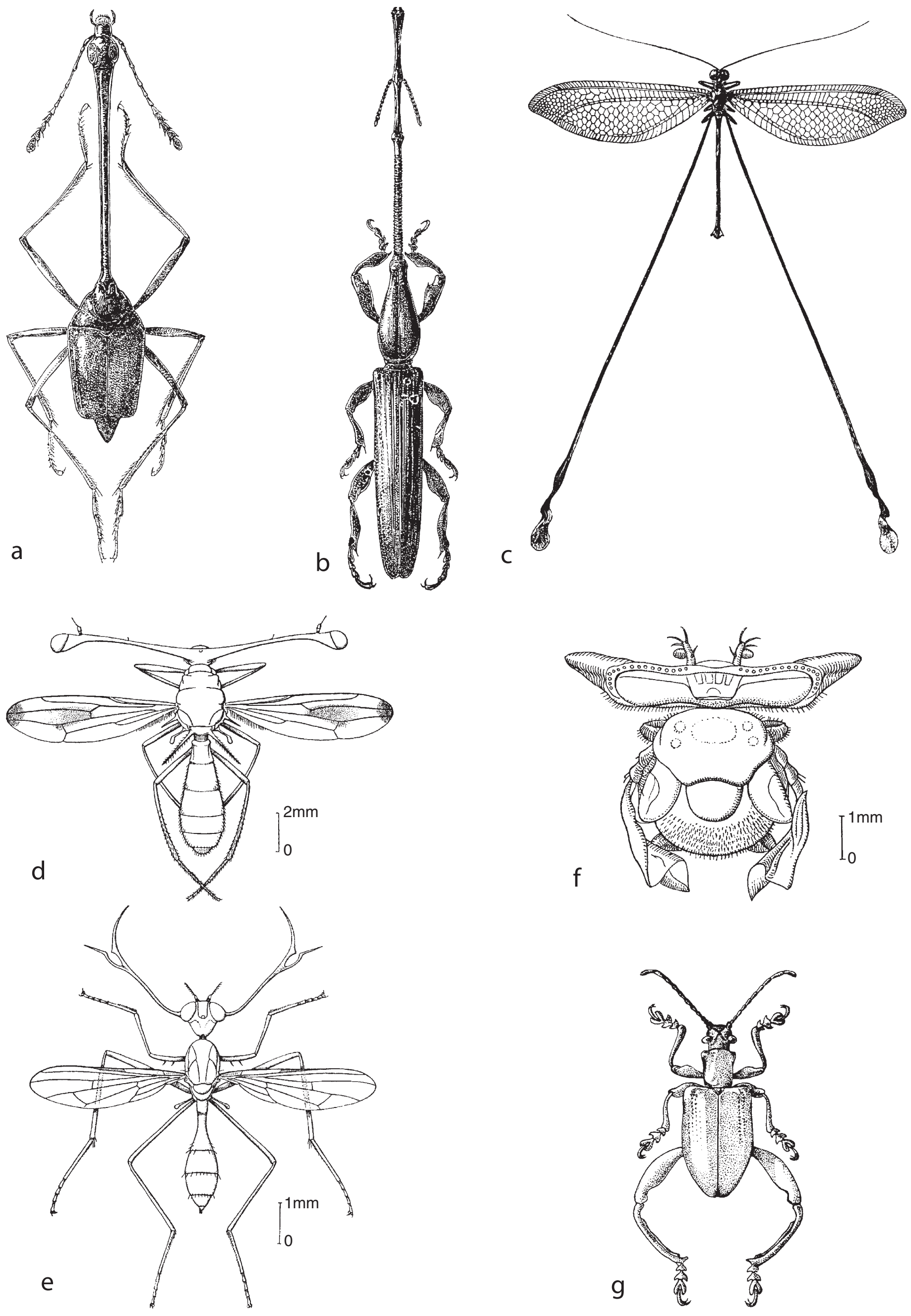
The concept of hypertely, a non-Darwinian concept, has been mainly developed by Lucien Cuénot and René Jeannel in France, though originally advanced by certain stubborn lamarckists of the middle of the last century. It can be defined as an excessive development of certain organs, in size and complexity, mostly among males, and was attributed to orthogenesis. The theory of orthogenesis was an alternative to Darwinian natural selection, and at one time found support in the USA and Germany, especially among palaeontologists and developmental biologists. Orthogenesis can be defined as evolutionary change proceeding consistently in one direction, resulting from a tendency to accumulate similar mutations in successive generations rather than by natural selection. Thus, the purported result of hypertely was the development of certain organs (horns, tusks, legs, antlers, etc.) up to the extent of a certain monstrosity.

Such a concept is very much debatable and may be explained as the result of a normal Darwinian selection and just part of natural biodiversity. Such organs are often useful or at least harmless, and the best proof of it is that the animals endowed with them survive, multiply and do not seem to be ill at ease with them. Beetle horns help the males when fighting over access to females, long legs of Sagrines help them, when mating, and also to clutch on the stems, thoracic extensions among the Membracidae or certain Curculionidae can help in camouflage and, in all cases, the insects survive well and reproduce. The extreme flattening of the *Mormolyce* (Carabidae) in Indonesia allow them to hide under loose pieces of bark during the day, and similarly the aberrant tenebrionid *Cossyphus* can easily slide under the bark of *Acacia* trees in the Sudan. *Hololepta plana* (Histeridae) lives under the loose bark of felled trees; it is so flattened that its height is only a small fraction of its width. Of course many beetles are flattened, but this is an adaptation to their habitat. Mimicry and camouflage are not hypertely, and may provide protection for the animal against his predators. It has been demonstrated recently that pronotal horns help some beetles during ecdysis, at least among *Onthophagus* (Scarabaeidae), which means that allometry or differential growing is not just a meaningless developmental process. An apparently non-adaptive organ is often an organ not functionally well understood, or at least an organ that was adaptive before some change occurred in the environment (Figs. 61 and 62).

Hypertely can be defined as "beyond the bounds of the useful." Some dictionaries give the following definition: "excessive development of certain organs, in size and complexity, among certain species, mostly among males." The horns of the Scarabaeidae and the mandibles of the Lucanidae might sometimes appear excessive, but they help in defense, and during the fight among males the winner is often the most well equipped with such a horn. The thoracic prolongations of the Membracidae can seem a bit odd, but they serve as camouflage. The long thoracic horn of the *Cranopoeus* (Curculionidae) mimics the seeds of the host tree. The excessive development of certain organs (antennae, legs) of cavernicolous (cave-dwelling) insects compensate for the loss of eyes. The pseudophysogastry (artificial swelling of the abdomen, not connected with ovary development) of some cavernicolous insects is more difficult to interpret, but it increases the isolation of the abdomen against cold or humidity. Pseudophysogastry is known also among termiticolous (living in association with termites) insects, also living in a close and isolated world. The long rostrum of the Brentidae help in digging their tunnels. The enormous legs of certain weevils such as



Hypertely, Figure 61 Some cases of hypertely (a) Hemiptera: Membracidae. 1: *Bocydium*; 2: *Cyphonia;* 3 and 4: *Spongophorus*. Tropical America; (b) *Lasia nigritarsis* Blanchard (Diptera: Oncididae). Male. Tropical America; (c) Aedeagus of various Monoxia (Coleoptera: Chrysomelidae: Galerucinae). USA. 1: *Monoxia puncticollis* Say; 2: *Monoxia debilis* LeConte; 3: *Monoxia sordida* LeConte; (d) *Dynastes hercules* (L.) (Coleoptera: Scarabeidae: Dynastinae). Male and female. Tropical America; (e) *Sebethes longipes* Fabricius (Diptera: Culicidae). Male. Tropical America; (f) *Acrocinus longimanus* L. (Coleoptera: Cerambycidae). French Guyana (c, after Jolivet, 1957–59; f, after Grassé, 1949; a, b, e, after Grassé, 1951; d, after Paulian, 1935).



Hypertely, Figure 62 **Some additional cases of hypertely (a) *Diatelium* sp. (Coleoptera: Scaphididae). Male; (b) *Rhyticephalus brevicornis* Chevrolat (Coleoptera: Brentidae); (c) *Nemopistha imperatrix* Westwood (Planipennes). Equatorial Africa; (d) *Diopsis tenuipes* Westwood (Diptera: Diopsidae). Tropical Africa; (e) *Phytalmia cervicornis* Gerstacker (Diptera:Phytalmiidae). Male. New Guinea; (f) *Asyntona tetyroides* Walker (Diptera: Platystomidae). Malaysia; (g) *Sagra femorata* Drury (Coleoptera: Chrysomelidae: Sagrinae). Thailand (figs. a and b, after Paulian, 1988; c, after Cuénot and Tétry, 1951; d, e, f, after Grassé, 1951; g, after Jolivet and Verma, 2002).**

neotropical Cerambycidae (*Acrocinus*), Malagasy eumolpines (*Arsoa*; Chrysomelidae) and the big femora of the sagrines (Chrysomelidae), are used for holding on to the stems or mating. The sternal horn of certain *Doryphora* (Chrysomelidae) is used as a weapon in fighting between males. It is also evident that sensorial dimples on the abdomen of many beetles have their usefulness in detection of humidity or mates. Examples are many of those organs which appear excessively developed, but they are not functionally meaningless.

For Darwinists, the concept of hypertely is a mistake of interpretation, because although the character may look functionless, it is not without its functional significance. The phenomenon seems coherent and related to some function such as sexual selection, mimicry, self defense, clutching, lodging, etc. Some French zoologists such as Jeannel, Cuénot, and Grassé could, in the past, see hypertely as the result of extreme orthogenesis. Cases of hypertely were suggested to include the bent tusks of the mammoths, the bent canines of the babirussa, the teeth of the *Machairodus* or *Smilodon*, the antlers of the Irish deer, the horns of the Tithanotherians, the sword of the saw fish (*Pristis*) and the swordfish (*Xiphias*), the long spines of certain urchins (Cidarids), the dermic armor of the Stegosaurians, the complex septa of certain Ammonites, the thoracic expansions of the Membracidae, the horns of the Scarabeids, the mandibles of the Lucanids, the foliaceous expansions of the legs of certain Hemiptera or Diptera, the reduced hind wings of the Nemopteridae, and even the long legs of the Tipulidae. However, these seemingly unusual structures can be explained. For example, the long legs of those Diptera prevent them from getting captured on spider webs when they dance rhythmically, and the mandibles of the Lucanidae and the horns of the Scarabeidae help them when fighting (and those organs have some other functions too, recently decrypted). Some beetles have a very elongated body, but this form is useful for digging and living in tunnels. Others, as the *Cychrus* (Carabidae) have the head and pronotum elongated and narrow, but this is an adaptation used to penetrate snail shells. The long proboscis of certain Diptera or moths are needed to penetrate some deep flowers. All those modifications of the morphology seem to be functional specializations, not meaningless exaggerations.

All modern authors see in the so-called hypertely of the carabeid horns a case of allometry, sometimes under the influence of hormones or food. Individuals are able to express different morphologies in response to environmental conditions during their development. Recently, it was suggested that pronotal horns among *Onthophagus* are crucial during ecdysis of the larval head capsule during the larval-to-pupal molt. This function in molting seem unrelated with fighting and defense, but all criteria are positive and useful for the insect.

Additional examples of exaggeration include organs used in reproduction; often, the male genitalia of certain beetles are very big, while other species of the same genus have a normal aedeagus. That is the case among the galerucines of the genus *Monoxia* (Chrysomelidae), where only one species, *Monoxia puncticollis*, has an enormous intromittent organ, but its body size is not much bigger than the body of other species with a normal aedeagus. The mating is done and successful with the female of *M. puncticollis*, which probably has some kind of adaptation. There is also the case of *Hydrochus interruptus* (Hydrophylidae), an aquatic beetle, which is provided with so complex an aedeagus that some entomologists have doubted its real sexual function. Very often, the beetles or other insects are gifted with so complicated aedeagi that one wonders how they work. But such aedeagi function, and the insect reproduces normally. Also, sometimes the spermatozoa are enormous. This is the case of many Alticinae (Chrysomelidae) or the *Drosophila* flies (Drosophilidae), for instance. However, it appears that, in the case of the Alticinae, the role of the long sperm is in forming a vaginal plug. It seems also that the males of *Drosophila* which have developed those long spermatozoa have an increased chance to fertilize the eggs successfully.

As far as we can see, the concept of hypertely is obsolete. All those so-called exaggerated morphologies have a function and the animals survive, multiply and they do not seem to suffer from those "monstrosities." As a rule, handicapped specimens are eliminated and only the fit ones survive. A non-adaptative organ is an organ not understood. So-called hypertelic insects are just part of the biodiversity, having evolved through selection.

References

Carayon J (1977) Insémination extra-génitale traumatique. Traité de Zoologie, Masson publ., Paris 8 (5A):351–390

Cuénot L, Tétry A (1951) L'Evolution Biologique. Masson, Paris, 592 pp

Eberhard DJ (1985) Sexual selection and animal genitalia. Harvard University Press, Cambridge, MA, 244 pp

Emlen DJ, Nijhout HF (2000) The development and evolution of exaggerated morphologies in insects. Ann Rev Entomol 45:661–708

Gould SJ (1977) Ever since Darwin. Reflexions in Natural History. Penguin Books, Harmondsworth, England, 285 pp

Grassé PP (1949) (1951) Traité de Zoologie. Anatomie, Systématique, Biologie. Insectes. IX & X (1 & 1). Masson, Paris, 1117 + 1949 pp

Jolivet P (2004) Inverted copulation. In: Capinera J (ed) Encyclopedia of entomology, vol 2. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 1208–1212

Moczek AP, Cruickshank TE, Shelby A (2006) When ontogeny reveals what phylogeny hides: gain and loss of horns during development and evolution of horned beetles. Evolution 60:2329–2341

Moczek AP, Emlen DJ (2000) Male horn dimorphism in the scarab beetle, *Onthophagus taurus*: do alternative reproductive tactics favour alternative phenotypes? Anim Behav 59:459–466

Paulian R (1935) Le polymorphisme des mâles de Coléoptères. Hermann, Paris, 35 pp

Virkki N, Bruck T (1994) Unusually large sperm cells in Alticinae: their formation and transportation in male genitalia system and their evolution. In: Jolivet P, Cox ML, Petitpierre E (eds) Novel aspects of the biology of Chrysomelidae, Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 371–381

Hypertrehalosemic Hormone (Hth)

A peptide hormone important in the regulation of carbohydrate metabolism.

Hypertrophy

An increase in the size of the functional units of an organ (organelles, cells, tissues), excluding tumor formation.

Hypha (pl., hyphae)

A strand of the threadlike mycelial tissue of fungi.

Hypochthonellidae

A family of bugs (order Hemiptera, suborder Fulgoromorpha). All members of the suborder are referred to as planthoppers.

Hypodermosis in Deer

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Hypodermosis is a common myiasis produced by flies of the genus *Hypoderma* (Diptera: Oestridae), affecting a wide variety of hosts, but specially important in domestic animals like cattle and goats. It is spread over almost all the northern hemisphere, and these flies produce serious economic losses in hosts, especially in herds reared for meat and dairy production. Little research has been directed, however, at wild and semi-wild animals such as deer. Nonetheless, existing studies have pointed out just how serious this infestation may be in these hosts, because widespread parasitosis currently affects deer in numerous Palaearctic countries. The situation is truly worrying, due to the high degree of prevalence and intensity of parasite infestation.

Effects of Hypodermosis

Little is known about the infestation of deer, and few studies have discussed the influence of environmental factors on the biology of flies and their resulting distribution. At the same time, the pathogenicity of larvae for host deer remains unknown. Although it is patently clear that, in deer, this disease should be classed as critical, since it affects:

Deer Health

The *Hypoderma* life cycle in deer is still not well known, but due to the similarities with cattle myiasis, it is thought to have an internal migratory cycle that affects the health of the host. There is a decrease in meat production, retarded growth and reduction in skin quality (Fig. 63).

Rural Development in Poor Areas

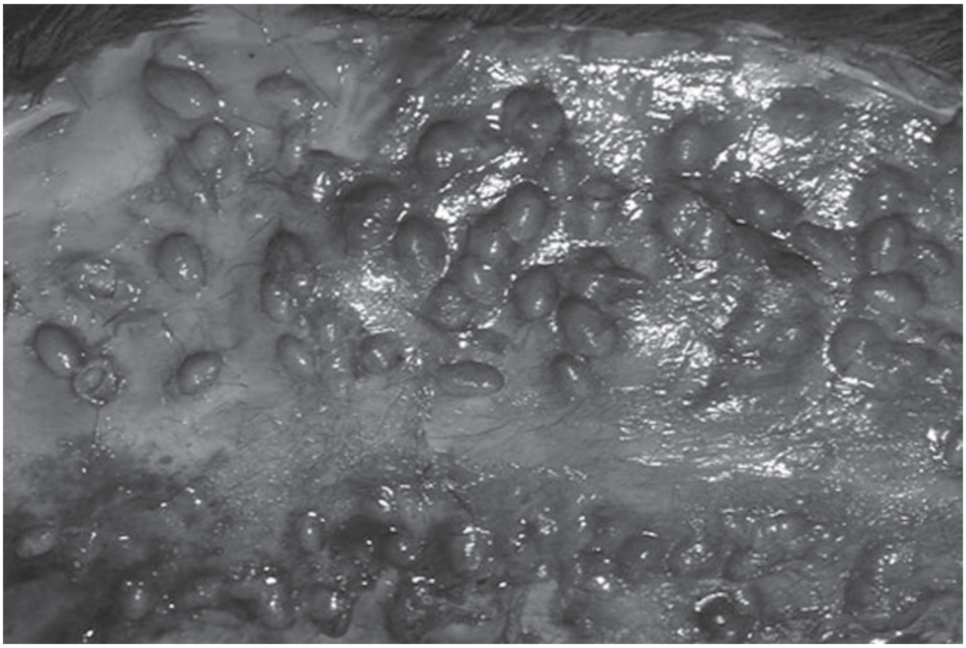
Deer hypodermosis affects the economic development of many poor areas due to repercussions on the hunting-based economy. In social terms, hunting is a developing force in depressed areas, where it provides a major source of income through the employment of local labor.

Deer Farming

This is a growing farming activity, and venison offers an alternative to beef, pork and lamb.

Species and Hosts of *Hypoderma* spp.

Several *Hypoderma* species are found in deer, but the three main parasites are *H. diana*, *H. actaeon* and *H. tarandi*. *H. diana* is euryxenic and affects, in addition to red deer (*Cervus elaphus*), a range of other hosts including roe deer (*Capreolus capreolus*), fallow deer (*Dama dama*), elk (*Alces alces*)



Hypodermosis in Deer, Figure 63 Myiasis in deer caused by *Hypoderma*.

and reindeer (*Rangifer rangifer*), and lives in a great diversity of ecosystems.

Host specificity is strong in *H. actaeon* and *H. capreolus*, as the former only affects red deer and the latter roe deer.

Morphological differentiation between *H. diana* and *H. actaeon* is made according to the pattern of spine morphology and morphology of spiracular plates.

H. (*Oedemagena*) *tarandi* shows greater specificity, affecting only *R. rangifer*, and is found within the subarctic region.

Biology

Biology of deer-infesting *Hypoderma* spp. is still a relatively unknown aspect of myiasis. Some particulars are important in deer hypodermosis. For example, *H. diana* is present in a great variety of habitats, and also of hosts, and this departs from the principle of host specificity of warble flies, maintained by a complicated equilibrium with its host by means of internal regulatory systems. It is spread throughout Europe and Asia, from 30° to 60° north, and lives in several different ecological zones such as mixed, deciduous and coniferous forests, wooded steppes and wetlands, overlapping the territory of its hosts and adapted to the wide variety of ecosystems in which live the parasite's hosts.

Flight and oviposition of female flies are conditioned by air temperature and ambient light, so they are most active at midday. In contrast, their endogenous cycle has yet to be fully described, although some authors claim that they arrive at the dorsal area via the spinal canal, exhibiting a cycle similar to that of *H. bovis*. Resistance and susceptibility to infection has to be studied, as previous studies have demonstrated that the extent of parasitism and prevalence are higher in younger animals, possibly due to a measure of resistance built up through repeated contact with the parasite.

Pupation is highly influenced by the nature of the land, pupae being more viable when produced in areas where there is at least some grass. This viability decreases depending on to what extent the land freezes or frosts over.

Hypoderma tarandi is more specific and is found in just one host (*R. rangifer*); it has thus adapted itself to live in the same habitat as its host, usually subarctic regions. Its biology has been studied in great detail due to the importance of the reindeer in cold northern countries. Two different habitat are occupied by these flies, one of wooded regions, and other of wide open or mountainous areas with plentiful water courses. Usually only the female approaches the host; the male rarely does so, and is usually found in sunny, rocky areas. The flight range of females is absolutely astonishing, as they can fly as far as 600–900 km. Males, however, tend to fly for shorter distances and times, although they may achieve a radius of 400 km.

The degree of parasitism in male deer is usually higher than in females and castrated animals; thus, resistance to this disease is greater in females than in males. Prevalence is higher in herds which did not move to new pastures after calving than in those continually changing their grazing grounds. When deer are led to new pastures, the number of infested animals and the degree of parasitism drops substantially.

Hypoderma actaeon is confined to one host, red deer (*Cervus elaphus*), and it seems to be restricted to Europe. Little is known about the biology of this parasite, but it has been observed that yearling hosts are more parasitized than older ones, and it suggests the development of resistance by repeated contact with the parasite. The internal life cycle of *H. actaeon* lasts up to 9 months, as subcutaneous stages are found from September to May, with the presence of first instar larvae for a period of 2–3 months, and then the second (L2) and third (L3) instars.

Chronobiology

The seasonal dynamics of *H. diana* adapted to central European countries are as follows: larva migration and growth take place in the host until April, pupation lasts for 26–33 days, and flying is observed in May and June. In eastern countries (Czech Republic), L1 larvae develop from November to March, L2 from December to April, and L3 from January to June. Flies have been observed from April to June. By contrast, in southern European countries such as Spain, this cycle is brought forward by 2–2.5 months. L1 may be observed September to December, L2 October to January, and L3 onwards of December.

Hypoderma tarandi, owing to its northern ecology, does not develop until later, beginning in October and with L3 appearing June to July; flying takes place between June and September.

Chronobiology of *H. actaeon* is similar to that described to *H. diana*, with L1 larvae developing in September to November, second instar larvae from September to December and L3 from December to May.

Prevalence

Hypoderma diana is widely distributed throughout Europe, and cases of parasite infestation as high as 100% have been reported, such as those recorded in Russia. In Bulgaria, parasitism ranges from 48 to 66%, whereas in Spain there is a mean of 90%.

The other important species in red deer is *H. actaeon*, which reach very high levels of prevalence in southern and central Spain, ranging from 44 to 92%, with a mean intensity of parasitization of near 40 larvae per animal (1–317).

The extent of parasitism with regard to the number of larvae per animal varies greatly in *H. diana* and *H. actaeon*. In Spain, values ranging from 1 to 400 larvae per animal have been recorded, where over half of the animals contained more than 50 larvae. In the former Czechoslovakia, cases have been reported of up to 300 larvae per animal, in Germany 300–500 larvae, in Bulgaria up to 150 larvae, and in France up to 200. *H. tarandi* has also reached levels of 99.9%.

Other Negative Effects of Hypodermosis

It has been shown that *H. diana* can infest other hosts in addition to deer. In the United Kingdom, cases have been reported of sheep living near deer-populated forests being affected. Cases of ophthalmomyiasis produced by *H. tarandi* have been described in children, in dogs and in horses, and always in the vicinity of deer-populated areas.

The cost of the damage caused by *Hypoderma* spp. is difficult to calculate although, as occurs in bovines, losses are incurred both in reduced meat yield and in depreciation of skins and horns/antlers.

Control

It is never easy to develop strategies for the control of disease in wild and semi-wild animals, and deer are no exception. Any such controls also must be based on a total respect for the environment, since the quality of their surroundings plays an important role in the welfare of not only deer but all wild animals living on the same biotope.

It should be borne in mind that ecological or "organic" meat such as venison, supplied to a gourmet market, must satisfy sophisticated organoleptic criteria and its quality must never suffer. Thus, the use of medicaments and pharmacological substances has to be strictly controlled in order not to affect meat quality.

There are only a few studies about the treatment of warble flies in deer, but we can assume that the same drugs used in other species should be useful in deer, i.e., some organophosporous, avermectines and milbemicynes.

Handling practices may be modified through a knowledge of the parasite cycle and ecology. Animals could enjoy greater protection by being herded into corrals, or at least into the shelter of shaded areas to reduce the risk of infestation when adult flies are active.

In domesticated animals or semi-domesticated animals living on the range, such as reindeer, the rate of infestation may be reduced when, after giving birth, the herd migrates to fresh pastures or is led to new pastures away from those frequented during the muddy season. The aim is to distance the deer from the pupae and flies. These measures are not particularly effective, however, so greater control of parasitism will still depend on pharmacological treatment.

For free-range deer, and only when they cannot be captured for the administration of treatment, food may be supplemented with oral forms of antiparasite preparations. The problem arises, however, in choosing a suitable vehicle for the anti-parasitic treatment, because it cannot be freely distributed around the environment due to the danger of its being consumed by other animals. Neither could the ingested volume be controlled. Experimental trials with rafoxanide and ivermectin in the daily salt pellets required by the animals' diet have yielded promising results.

Farm-raised animals are obviously easier to control, and a program of preventative medicine may be applied, with regular treatment in accordance with the local chronobiology of *Hypoderma*.

► Flies

► Veterinary Pests and Their Management

References

Colwell DD, Martínez-Moreno FJ, Martínez-Moreno A, Hernández-Rodríguez S, De La Fuente López, C, Alunda JM, Hall MJR (1998) Comparative scanning electron microscopy of third instar *Hypoderma* spp. Med Vet Entomol 12:181–186

Martinez-Moreno FJ, Navarrete I, Hernandez-Rodriguez S (1995) Deer hypodermosis in the south of Spain. In: Tarry DW, Pithan K, Webster K (eds) Improvements in the control methods for warble fly in farm livestock. E.C., Luxembourg, Luxembourg, pp 115–124

Minar J (1982) A contribution to the knowledge of distribution and ecology of botflies (Oestridae) and warble flies (Hypodermatidae) in the cervids. Folia Facultatis Scientiarum Naturalium Universitatis Purkynianae Brunensis, Biologia 23:87–92

San Miguel JM, Álvarez G, Luzón M (2001) Hypodermosis of red deer in Spain. J Wildlife Dis 37:342–346

Zumpt F (1965) Myasis in man and animals of the old world. Butterworths, London, UK

Hypogaeic

Living primarily underground, or at least beneath a layer of material on the soil surface. (contrast with epigaeic)

Hypogastruridae

A family of springtails (order Collembola). They commonly are known as elongate-bodied springtails.

► Springtails

Hypognathous

An insect that has the head pointing forward and the mouth pointing downward. It is also known as orthognathous. This is considered to be the ancestral condition for insects.

► Mouthparts of Arthropods

Hypopharynx

A tongue-like structure in the buccal cavity on the upper surface of the labium.

Hypostomal Bridge

The portion of the head capsule that closes off the ventral area of the foramen magnum, near the base of the labrum.

► Head of Hexapods

Hypostome

In ticks, this is a denticle-bearing ventral structure occurring parallel to, and between, the palpi.

Hypsypterygidae

A family of bugs (order Hemiptera).

► Bugs

Hystrichopsyllidae

A family of fleas (order Siphonaptera). They sometimes are known as rodent fleas.

► Fleas

I

Ibaliidae

A family of wasps (order Hymenoptera).
► Wasps, Ants, Bees and Sawflies

Ichneumonid Wasps

Members of the family Ichneumonidae (order Hymenoptera).
► Wasps, Ants, Bees and Sawflies

Ichneumonidae

A family of wasps (order Hymenoptera).
► Wasps, Ants, Bees and Sawflies

Ichthybotidae

A family of mayflies (order Ephemeroptera).
► Mayflies

Identification of Insects

Usually the first question that comes up when someone encounters an insect is: "What is it?" Answering this question can be a difficult or simple process. It can be difficult because insects are incredibly diverse, with nearly one million described species. On the other hand, within a 300 km radius there may be only about 15,000 species (fewer in cooler climates, more in tropical areas). So it is possible for a person to have a reasonable grasp of the local fauna, especially the more common or distinctive species.

In the process of identification, one common mistake is to consult an illustrated book of national or international scope, particularly one that treats the entire class of insects, matching pictures with specimens. Though this can work with the most common insects, it usually is doomed to failure. There are entirely too many insects, and too many are similar in appearance (differing only in minute detail) for this approach to be very successful. Greater success can be attained with books of regional scope, or books that treat smaller groups. Thus, "Grasshoppers of the United Kingdom," "Butterflies of Costa Rica," or "Plant bugs of the Prairie Provinces" will prove to be more useful than more general treatments. In the hands of specialists who have reasonable grasp of the diversity, or in the case of specialty publications that are comprehensive in treatment, picture books are useful. However, in most cases, accurate determination of insects requires the use of diagnostic aids called "keys."

Insect Keys

Keys are arrangements of taxa, with similar taxa (usually based on external morphology, or appearance) clustered together. Thus, insects with wings

Identification Key to the Classes of Adult Arthropoda

P.M. Choate

Insects represent one **Class** of animals within the **Phylum *Arthropoda***. If you do not immediately recognize an insect you may need to identify some arthropods to first determine if they are in fact insects before proceeding further.

Biologists have adopted the use of *dichotomous keys* to identify organisms. Starting at couplet 1, decide which of the first 2 choices best fits the organism you are trying to identify. Proceed by going to the couplet indicated at the end of your choice. By process of elimination you will arrive at an identification. Compare your results with pictures and notes in this handout and in your books to see if you have arrived at a likely identification. If you are satisfied with your result, proceed to the next key that you wish to use and follow the same process. As you move from **Class** to **Order** to **Family** and perhaps to **Genus** and **Species** you will notice that choices may become more difficult. This is due to the details necessary to separate these categories. Since this key is designed to help you recognize insects, and to also recognize Arthropods that might be confused with insects, we will start with an obvious and surefire couplet, #1. There are many insects which do not appear to have wings or actually lack wings. However, many have easily observable and functional wings which immediately identify the creature as an insect.

1. With 1-2 pair of obvious, visible, usually transparent wings (**Fig. 1**). (*If it's not a bird or a bat then it is an insect*) .... **Insecta**

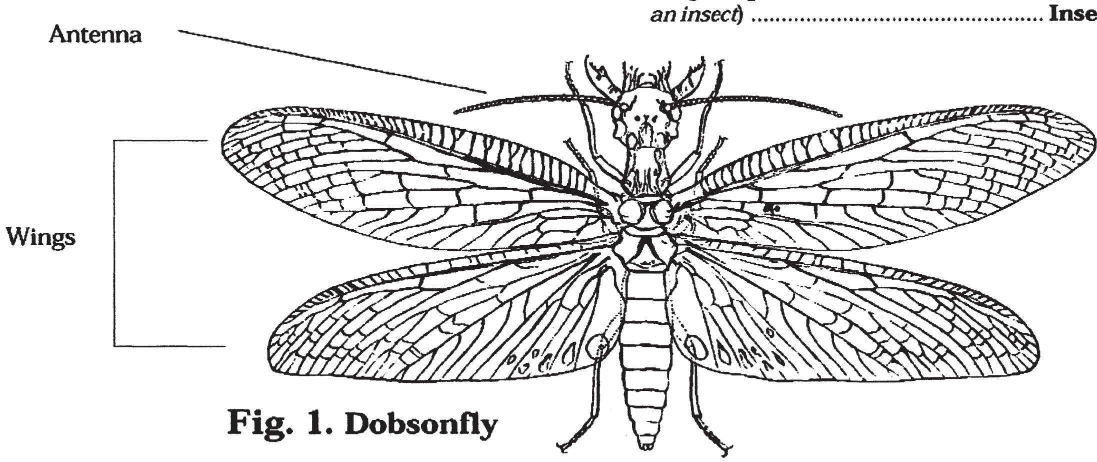


Fig. 1. Dobsonfly

- Without obvious wings 2

2. With 1 or 2 pairs of antennae ("segmented feelers") of various shapes (see **Figs. 1, 3-5**) inserted on front of head, usually between the eyes. Antennae may be inconspicuous, hidden beneath head when viewed from above, or small and more bristle-like than typical segmented structure. ***Note***: some non-insects carry their front legs or modified mouthparts (pedipalps, **Fig. 2**) in a manner resembling antennae 3

- Lacking segmented antennae and always lacking any suggestion of wings. 8

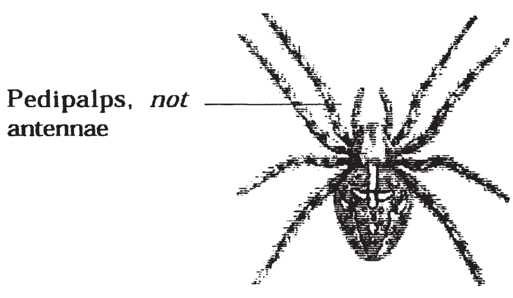


Fig. 2. Spider

3. With 2 pairs of antennae (one pair may be smaller than the other; *2nd pair is vestigial in terrestrial Isopoda* (pillbugs, **sowbugs**); body usually with 2 distinct regions (**Figs. 3-4**), **cephalothorax** and

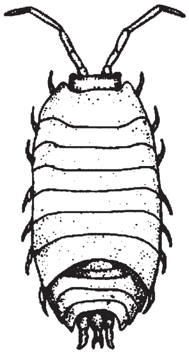


Fig. 3. sowbug

abdomen; variable number of legs on cephalothorax, abdomen with or without appendages which when present are not leg-like; (amphipods, sowbugs, lobsters, crayfish) .... **Crustacea**

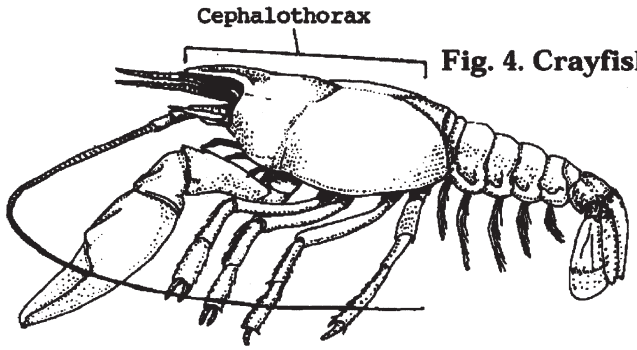


Fig. 4. Crayfish

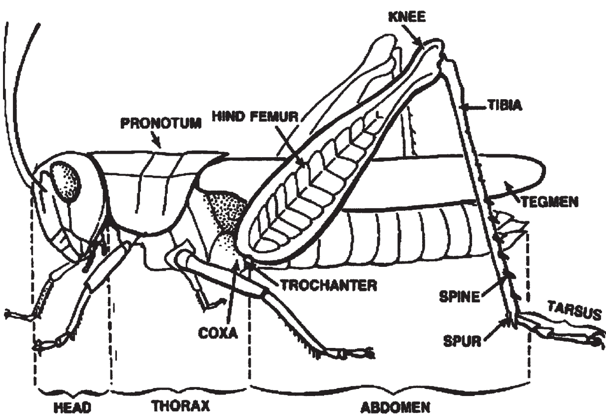


Fig. 5. Grasshopper

- **Always** with **only 1 pair** of antennae; body regions and numbers of legs variable; appendages not biramous 4

4. With only 3 pairs of legs and often with 1-2 pairs of wings; 3 body regions (**Fig. 5**). Abdomen without segmented legs but may have appendages; body shape variable .... **Insecta**
- With 9 or more pairs of legs (**Figs. 6-7**) which are on most segments posterior to head; head distinct; wings absent; body elongate and wormlike 5

5. Legs evenly spaced along body, usually 1 pair of legs per segment 6
- Legs arranged in pairs, 2 pair per segment (**Fig. 6**) (millipedes) .... **Diplopoda**

6. Body flattened, with 15 or more pairs of legs; size variable but usually longer than 25mm. (**Fig. 7a**) (centipedes) .... **Chilopoda**
- Body cylindrical; *minute* forms with 9-12 pairs of legs 7

7. Antennae branched (**Fig. 7b**); 9 pairs of legs ....
.... **Pauropoda**
- Antennae not branched; 10-12 pairs of legs (**Fig. 7c**) ..
.... **Symphyla**

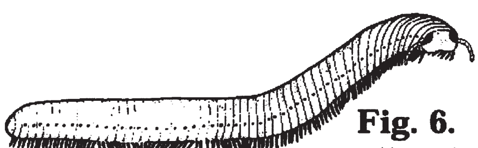


Fig. 6. Millipede

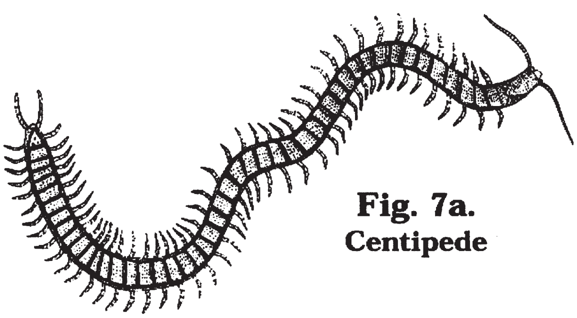
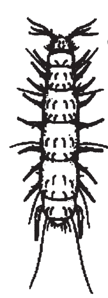
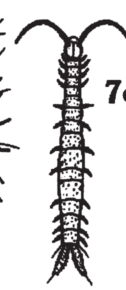


Fig. 7a. Centipede

7b. Pauropod





7c. Symphylan

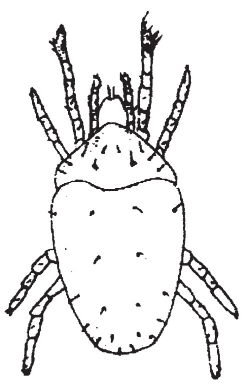
7d. Horseshoe crab

8. Usually 7 pairs of appendages, 5 pairs of legs; *marine organisms only*; abdomen rudimentary .... **Pycnogonida**
- Six (rarely fewer) pairs of appendages, with 4 (-5) pairs of legs; abdomen well developed 9

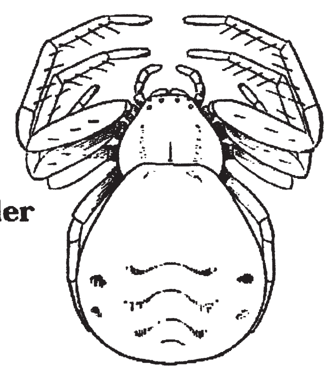
9. Large marine forms up to 460mm in length; body oval, covered with hard shell; long spinelike tail present. (Horseshoe crabs. **Fig. 7d**) .... **Xiphosura**
- Smaller forms, less than 75mm in length; body without hard shell and without spinelike tail; *See below*. (spiders, ticks, mites, whip scorpions, windscorpions, scorpions) .... **Arachnida**

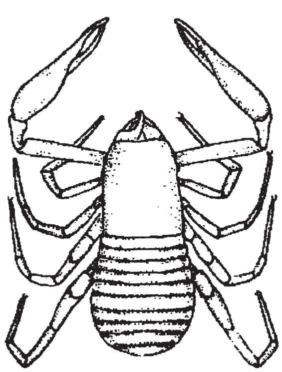
Some Arachnids

Mite



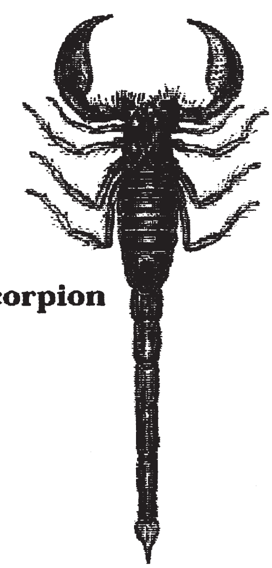
Crab Spider

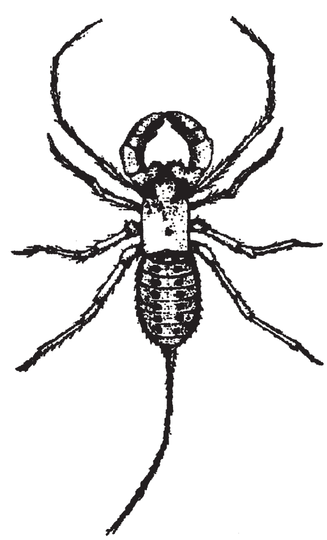




Pseudoscorpion

Scorpion





Vinegaroon

Key to the Orders of Insects Normally Found in Insect Collections

P.M. Choate

Once you have determined that the organism you have before you is an insect you may wish to further identify it. This means that you may have to use additional keys to determine the Order of that specimen. Some insects will be immediately recognized as insects but you may not be familiar with the oder to which it belongs. The key that follows will help you determine many of the more commonly encountered orders of insects. Not all insects will be able to be determined here. If you decide that your specimen may not be included here, use the reference books. These should permit identification of any specimen you happen upon.

Once you have determined the Order, the next step is to determine the Family within that order to which the insect belongs. This may mean an increase in complexity for you, and will usually require additional knowledge about specific types of structures and the variation that exists within these structures. Once the family of an insect has been determined you are left to hunt for literature that will permit identification to genus and species. Not only may this prove difficult, it may prove impossible. Not all insects are discussed or are identifiable to species. Literature may be scattered, outdated, or non-existent. You may have to call upon specialists for help. This is a normal part of the identification process. For our purposes here we will concentrate upon keys that should help you arrive at an Order level identification, and within a few of these Orders, some of the more commonly encountered families.

The following key to orders begins with a couplet that asks you to determine whether or not the insect has wings. This may be a confusing beginning for you. Many insects have flight wings which are hidden beneath another set of modified wings called elytra. Elytra are wings which act as protection and covering for the flight wings of beetles. At first glance there is little to indicate to you that these insects have wings. To further confuse the issue there are many beetles that lack flight wings, and whose elytra are fused to form a solid cover. Similar modifications may occur in such diverse groups as grasshoppers and the true bugs.

A similar point of confusion may be the determination of presence or absence of antennae. Antennae come in a variety of sizes and shapes . Dead insects may have antennae hidden or broken. If antennae are not apparent check to see if attachment "sockets" are visible on the insect's head in front of and beneath the eyes.

These two characters (antennae and wings) are mentioned here to emphasize the point that it is almost impossible to generalize about the characteristics that make up an insect order. There are many exceptions. With this in mind, proceed to identify specimens, using your book and examples here to help arrive at your final determination. When you have finished you should go to a museum or reference collection and compare your results. With practice you may find that the identification of insects will become a challenging avocation.

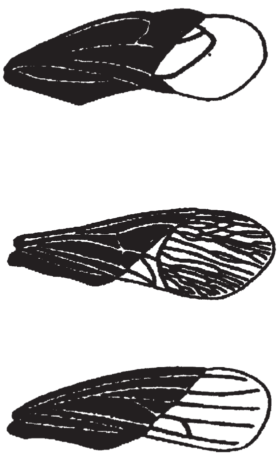


Fig. 8. Hemelytra

Fig. 9. Tegmen

1. Wings present (wings may be hidden under external elytra (p. 10-11), hemelytra (Fig. 8), or tegmina (Fig. 9) such that "wings" do not appear to be present) 22
— Wings absent or reduced to small pads; many abdominal segments visible from above 2

2. Antennae absent; body slender and whitish in color. Very small (Fig. 10) (1mm.) .... **Protura**
— Antennae present (may be difficult to see) 3

3. Usually with forked spring (furcula - Fig. 11)on abdomen. Size small, 2-4mm. Always lacking apical abdominal cerci. If furcula absent, size and body shape are characteristic of order .. **Collembola**

Fig. 10. Protura

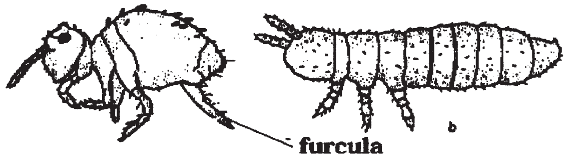


Fig. 11. Collembola

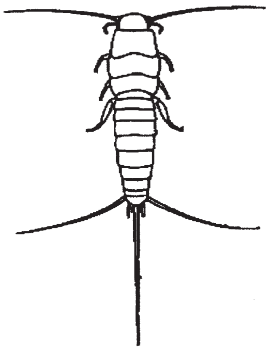


Fig. 13. Thysanura

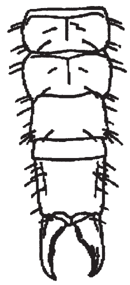


Fig. 12. Diplura

Fig. 14. Homoptera

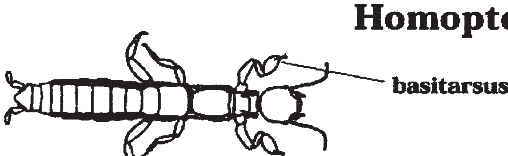


Fig. 15. Embiidina

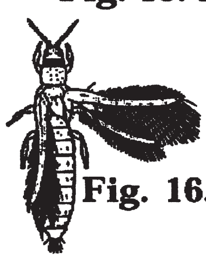


Fig. 16. Thysanoptera

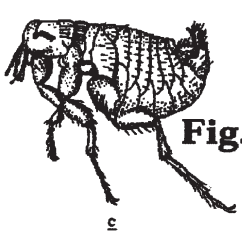


Fig. 17. Siphonaptera

— Furcula always absent. Body size larger, shape various 4

4. Apex of abdomen with long cerci (Fig. 13) and lacking ventral abdominal styliform appendages, or if ventral styliform appendages present, cerci are short 5
— Cerci short or lacking; abdominal styliform appendages always absent 6

5. Apex of abdomen with 3 filamentous cerci (silverfish) .... **Thysanura**
— Apex of abdomen with 2 cerci, either forceps-like (Fig. 12) or short and segmented .... **Diplura**

6. Large unsegmented forceps-like structures at apex of abdomen(earwigs) .... **Dermaptera**
— Cerci (when present) neither forceps-like nor unsegmented 7

7. Large insects, usually > 25mm in length; antennae frequently very long and slender 8
— Small insects, usually < 12mm in length 9

8. 4-segmented tarsi .... **Orthoptera**
— 5-segmented tarsi .... **Phasmida**

9. Tube-like structures (cornicles) (Fig. 14)protruding posteriorly from 4th to last abdominal segment; *OR* body covered with waxy filaments or a scale .... **Homoptera**
— Cornicles absent *AND* no scale or waxy filaments covering body 10

10. Abdomen constricted to narrow waist where it joins thorax (bees, wasps, ants, sawflies) .... **Hymenoptera**
— Abdomen not constricted into narrow waist 11

11. Front legs with enlarged first segment (Fig. 15) (basitarsus), which is modified for production of silk (webspinners) .... **Embiidina**
— First tarsal segment not enlarged 12

12. Mouthparts (rasping-sucking) contained in a short, cone-like beak; wings when present often with fringe of hairs (Fig. 16); size <3mm; abdomen often pointed at apex (thrips) .. **Thysanoptera**
— Mouthparts other than rasping-sucking; may be in form of elongate beak which extends ventrally and posteriorly beneath head; 13

13. Body flattened laterally, with numerous backward-projecting spines and bristles; legs long, with greatly enlarged coxae modified for jumping (fleas) (Fig. 17) .... **Siphonaptera**
— Body not flattened laterally; may have hairs or spines but these are not backwards projecting; if legs are modified for jumping, femora are enlarged 14

Fig. 18. Hemiptera

Fig. 19. Isoptera

Fig. 20. Mecoptera

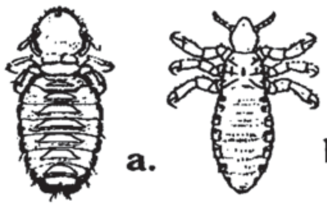


Fig. 21

Fig. 22. Ephemeroptera

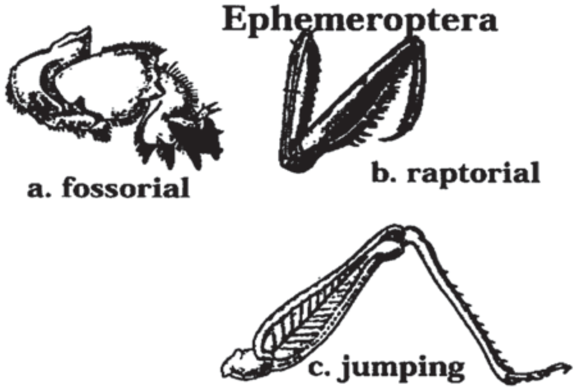


Fig. 23. Orthoptera leg types

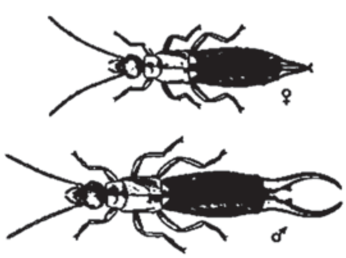


Fig. 24. Dermaptera

14. Mouthparts elongated into piercing-sucking beak 15
— Mouthparts not elongated into long piercing beak; head may be prolonged 16

15. Antennae hidden in grooves in head .... **Diptera**
— Antennae long and easily seen (Fig. 18)**Heteroptera**

16. Body covered with dense hair .... **Lepidoptera**
— Body lacking dense hair 17

17. Antennae moniliform (segments beadlike); short cerci present (Fig. 19)(termites) .... **Isoptera**
— Antennae not moniliform; cerci absent 18

18. Antennae long and slender 19
— Antennae short 20

19. Head prolonged and beak-like (Fig. 20); males of some species have scorpion-like abdomen (scorpionflies) .... **Mecoptera**
— Head not prolonged and beak-like .... **Psocoptera**

20. Tarsi with 4-5 segments .... **Diptera**
— Tarsi with 1-3 segment (lice) - **Phthiraptera** 21

21. Chewing mouthparts; head usually broader than long (Fig. 21a) .... **Mallophaga**
— Piercing-sucking mouthparts retracted into head; head usually longer than broad; legs greatly enlarged for grasping (body lice)(Fig. 21b) .... **Anoplura**

22. Abdomen with large unsegmented forceps-like cerci (Fig. 24) .... **Dermaptera**
— Cerci appearing segmented when present, not forceps-like, or absent 23

23. Cerci filamentous, longer than last 3 abdominal segments combined 24
— Cerci shorter than last 3 abdominal segments combined, not filamentous, or totally absent 28

24. Wings folded upright and parallel to body length; antennae setaceous (Fig. 22. mayflies) .... **Ephemeroptera**
— Wings various but not held upright above body; antennae elongate and filiform 25

25. Front pair of legs shaped differently than mid and hind pair, modified for digging (Fig. 23a) (fossorial) or grasping (Fig. 23b) (raptorial) .... **Orthoptera**
— Front pair of legs similiar to middle pair 26

26. Hind pairs of legs enlarged for jumping (Fig. 23c) .... **Orthoptera**
— Hind pair of legs similar to middle pair 27

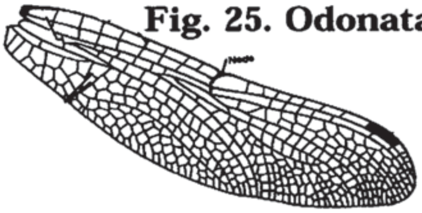


Fig. 25. Odonata wing

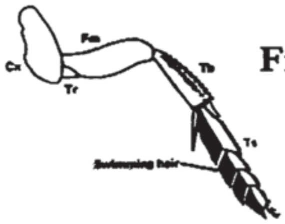


Fig. 26. Aquatic Hemiptera

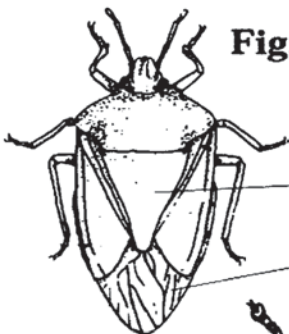
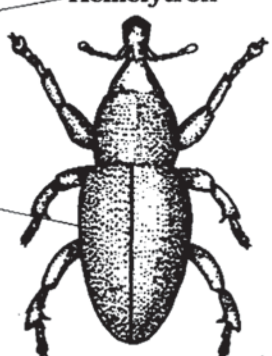


Fig. 27. Hemiptera



28. Coleoptera

Fig. 29. Orthoptera

Fig. 30. Lepidoptera

27. Tarsi 3-segmented; cerci long or short, not forceps-like; many segmented .... **Plecoptera**
— Tarsi variable (4-5 segments). Includes large, bulky insects, frequently with well developed wings. 31

28. Cerci present, shorter than last 3 abdominal segments combined 29
— Cerci absent (do not be confused by genitalia) 33

29. Small, delicate insects; wings transparent, uniform shape and size 30
— Body shape varied; wings in form of elytra, tegmina, or hemelytra 31

30. Front basitarsi (1st tarsomere) enlarged and dilated to form a webspinning organ .... **Embiidina**
— Front basitarsi not enlarged and dilated, appearing of normal proportions (termites) .... **Isoptera**

31. Tarsi 4-segmented .... **Orthoptera**
— Tarsi 5 segmented 32

32. Prothorax much longer than mesothorax; front legs modified for grasping .... **Mantodea**
— Prothorax not greatly lengthened; front legs not modified for grasping .... **Blattaria**

33. Large insects with 2 pairs of wings; wings usually transparent, each wing with an anterior node (Fig. 25)or notch (dragonflies, damselflies) .... **Odonata**
— Wings variable but lacking anterior node 34

34. One pair of wings; halteres present .... **Diptera**
— Two pairs of wings; halteres absent 35

35. Mouthparts in the form of a piercing-sucking, elongate beak which is mostly held beneath and behind the head; palpi absent 36
— Mouthparts other than above; palpi present 38

36. Hind leg without tarsal claws; adapted for swimming (Fig. 26) .... **Heteroptera**
— Hind leg with tarsal claws 37

37. Beak arises from anterior part of head; forewings usually as hemelytra (Fig. 27) .... **Hemiptera**
— Beak appears to originate from between front pair of legs; forewings of uniform texture .... **Homoptera**

38. Rasping-sucking mouthparts in form of cone-like beak; wings fringed with long hairs .... **Thysanoptera**
— Not as above 39

39. Front pair of wings hardened, of different texture than rear flight wings 40


Fig. 18. Hemiptera


Fig. 19. Isoptera


Fig. 20. Mecoptera

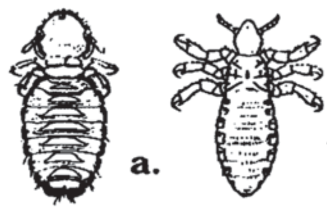


Fig. 21 a. b.


Fig. 22. Ephemeroptera

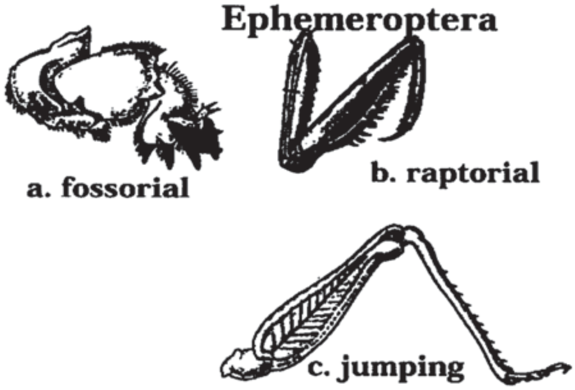

a. fossorial b. raptorial c. jumping

Fig. 23. Orthoptera leg types

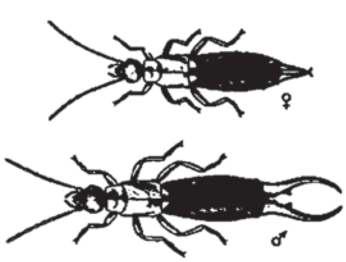


Fig. 24. Dermaptera

14. Mouthparts elongated into piercing-sucking beak 15
— Mouthparts not elongated into long piercing beak; head may be prolonged 16

15. Antennae hidden in grooves in head .... **Diptera**
— Antennae long and easily seen (Fig. 18)**Heteroptera**

16. Body covered with dense hair ....**Lepidoptera**
— Body lacking dense hair 17

17. Antennae moniliform (segments beadlike); short cerci present (Fig. 19)(termites) .... **Isoptera**
— Antennae not moniliform; cerci absent 18

18. Antennae long and slender 19
— Antennae short 20

19. Head prolonged and beak-like (Fig. 20); males of some species have scorpion-like abdomen (scorpionflies) ....**Mecoptera**
— Head not prolonged and beak-like .... **Psocoptera**

20. Tarsi with 4-5 segments .... **Diptera**
— Tarsi with 1-3 segment (lice) - **Phthiraptera** 21

21. Chewing mouthparts; head usually broader than long (Fig. 21a) .... **Mallophaga**
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— Cerci appearing segmented when present, not forceps-like, or absent 23

23. Cerci filamentous, longer than last 3 abdominal segments combined 24
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24. Wings folded upright and parallel to body length; antennae setaceous (Fig. 22. mayflies) .... **Ephemeroptera**
— Wings various but not held upright above body; antennae elongate and filiform 25

25. Front pair of legs shaped differently than mid and hind pair, modified for digging (Fig. 23a) (fossorial) or grasping (Fig. 23b) (raptorial) .... **Orthoptera**
— Front pair of legs similiar to middle pair 26

26. Hind pairs of legs enlarged for jumping (Fig. 23c) .... **Orthoptera**
— Hind pair of legs similar to middle pair 27

Fig. 31. Neuroptera, including Megaloptera

Fig. 32. Hymenoptera

Fig. 33. Psocoptera

— Front wings not thickened or hardened to form cover for flight wings 41

40. Front pair of wings thickened and usually hard, without crossveins, meeting along midline (meson) of the body to form elytra (Fig. 28); many forms with elytra shortened, exposing one or more abdominal segment from above (beetles); hind legs usually not modified for jumping .... **Coleoptera**

— Front pair of wings with obvious crossveins and veins (Fig. 29, tegmen), overlapping one another at least partially; hind legs often enlarged for jumping (grasshoppers, crickets, Katydids) .... **Orthoptera**

41. Front basitarsi (1st segment) enlarged to form silk-producing glands (Fig. 15) (webspinners) .... **Embiidina**

— Front basitarsi not any more enlarged than remaining segments 42

42. All wings equal in size; (termites) .... **Isoptera**

— Hind wings usually smaller than front pair of wings; 43

43. Mouthparts in the form of a coiled siphon (Fig. 30); wings and body usually covered with scales (butterflies and moths) .... **Lepidoptera**

— Mouthparts not in the form of a coiled siphon; body scales absent or few in number, restricted to wings and wing veins 44

44. Many crossveins in wings (Fig. 31), particularly at anterior edge; if few crossveins, wings covered with waxy coating and insect very small .... **Neuroptera**

— Few crossveins in wings; body and wings lacking waxy coating 45

45. Mouth reduced, vestigial; only palpi obvious; hairs often present on wings (caddisflies) .... **Trichoptera**

— Mouthparts not reduced or vestigial; chewing or chewing-lapping types 46

46. Chewing mouthparts elongated into a beaklike structure. Some males with scorpion-like abdomen (scorpion flies) .... **Mecoptera**

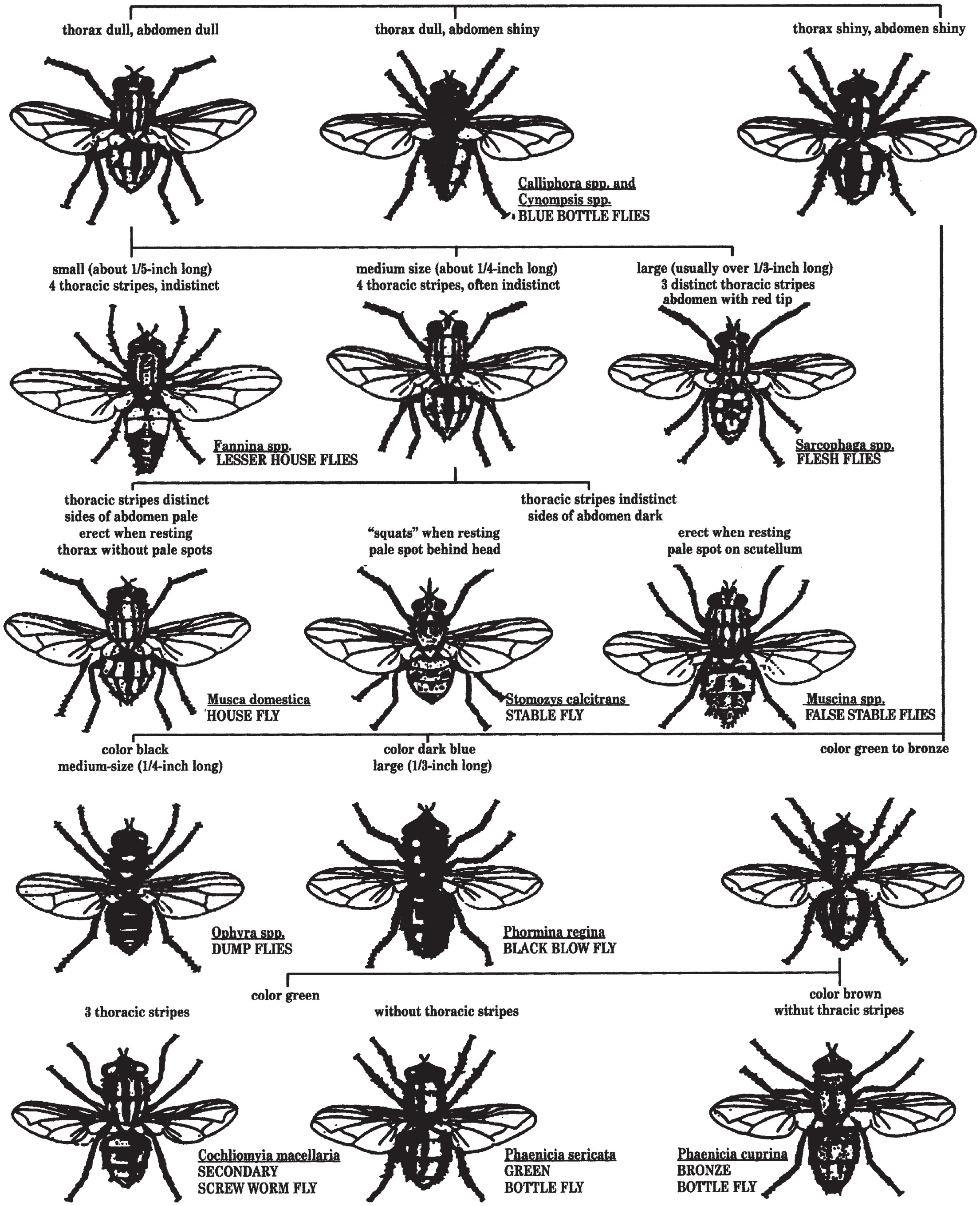
— Chewing mouthparts not elongated into beak; or with chewing-lapping mouthparts 47

47. Tarsi 4- or 5-segmented; wings folded flat over body (Fig. 32) (bees, wasps, ants, sawflies) .... **Hymenoptera**

— Tarsi 2- or 3-segmented; wings folded roof-like over body (Fig. 33) (treelice, booklice) .... **Psocoptera**

Domestic Flies: Pictorial Key to Comon Species

Harold George Scott and Margery R. Borom



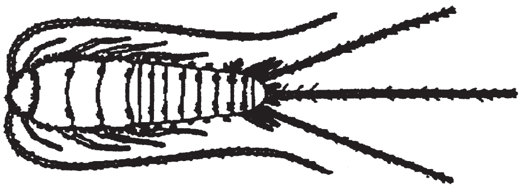
U.S. DEPARTMENT OF HEALTH, EDUCATION, AND WELFARE
PUBLIC HEALTH SERVICE, Communicable Disease Center, Training Branch, Atlanta, Georgia - 1962

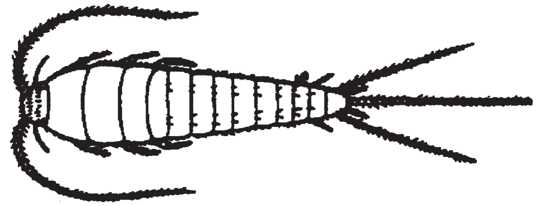
Silverfish Pictorial Key to Domestic Species

Chester J. Stojanovich and Harold George Scott

setae in tufts
color brown

setae single

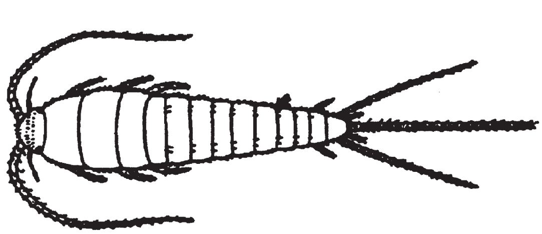


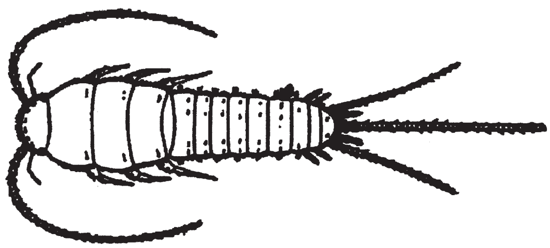


Thermobia domestica
FIREBRAT

without setal combs
color silver

with setal combs

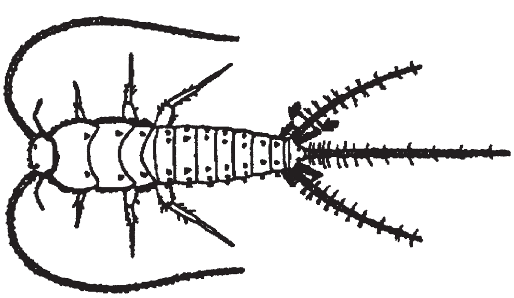


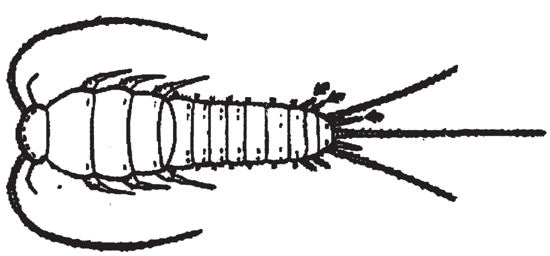


Lepisma saccharina
COMMON SILVERFISH

2 pairs of styli
color gray

3 pairs of styli
color brown





Ctenolepisma urbana
GIANT SILVERFISH
***Ctenolepisma longicauda* of some authors**

Ctenolepisma quadriseriata
FOUR-LINED SILVERFISH

U.S. DEPARTMENT OF HEALTH, EDUCATION, AND WELFARE
PUBLIC HEALTH SERVICE, Communicable Disease Center, Training Branch, Atlanta, Georgia - 1962

may be in one cluster, wingless in another. Then within one of these clusters, some other character such as antenna length is used to segregate individuals further: those with wings and long antennae in one cluster, those with wings and short antennae in another. Extended far enough, this process can lead to species-level determinations. Keys usually require the user to make a choice between only two characters at a time: so-called "dichotomous keys." However, it is also possible to have keys where the user is asked to pick among several groups of characters simultaneously. The choices are usually numbered (e.g., 1 and 1′, 2 and 2′, etc.), and the user is referred to various sections of the key by number.

Keys tend to be of two general types: "phylogenetic keys" or "artificial keys." Phylogenetic keys group together taxa with the same evolutionary history. Sometimes it is hard to see their common relationships based on external morphology. Thus, it is commonplace to group together taxa that simply share similar morphologies, regardless of phylogeny, creating a so-called artificial key. A combination of both approaches also is feasible.

In almost all cases, keys begin with a large taxon (e.g., arthropods or insects), and work down to smaller and smaller groups. Often insect keys segregate orders, and then there are separate keys for each order that separate families, then other keys to distinguish among the genera in the families, and then finally keys to species, which sometimes are integrated with keys to the genera. A common, but incorrect, assumption is that order or family keys are easier to use than species keys. The opposite is true. Keys to larger taxa must accommodate a great deal of variation, and sometimes it is difficult to find unifying characteristics.

Keys are often based primarily or exclusively on text: written description of a contrasting character or characters is used to distinguish among specimens. Illustrated keys have a major advantage in that they graphically display the characters of interest. It is much easier to understand differences among contrasting characters when they are illustrated. It also helps to have the key graphically displayed in a flow-chart arrangement. This gives the user better opportunity to see at a glance where the key is headed, and to easily work backward if diagnosis proves difficult. A few pointers on use of keys follow:

- Do not attempt to skip through a key, or to take short-cuts. Start at the beginning and work through the key methodically.
- Read the descriptions *carefully*; a large percentage of errors are caused by careless reading, or by the user not understanding the meaning of the words. Terminology may differ between taxa, so if you are not familiar with a taxon it is advisable to look up the exact meaning of terms. Illustrations are immensely helpful.
- You will be asked to make a series of decisions, usually making the "best" choice among two options. Your specimen should fit one of the two choices; if not, perhaps you made an incorrect decision earlier in the key.
- If more than one character is provided for you to examine, the first character is usually the most important. The others are secondary, or apply only in part.
- It is helpful to examine more than one specimen. It may be difficult to see a key character on certain individuals, or there may be sexual differences in the degree of expression.
- When you arrive at a final destination, do not automatically accept it. Always seek a more complete description of the organism to ascertain that the specimen seems to match.

Examples of Keys

Accompanying this section are some examples of North American keys to the classes of adult arthropods, to the orders of insects normally found in insect collections, and to some small groups of insects that are a nuisance or of public health concern. They illustrate some of the common types of keys used by entomologists, and demonstrate the value of illustrations. Note, however, that these are simply examples, and that they treat the names of certain taxa differently than treated elsewhere in this encyclopedia. Included in the reference section are some additional widely used sources of keys to insect orders and families. Each book contains numerous citations to other keys. Unfortunately, in most cases the scope is primarily North America.

References

Arnett RA Jr (2000) American insects. A handbook of the insects of North America, 2nd edn. CRC Press, Boca Raton, FL, 1003 pp

Borror DJ, Triplehorn CA, Johnson NF (1989) An introduction to the study of insects, 6th edn. Saunders College Publishing, Fort Worth, 875 pp

Stehr FW (1987) Immature insects, vol 1. Kendall/Hunt Publishing, Dubuque, Iowa, 754 pp

Stehr FW (1991) Immature insects, vol 2. Kendall/Hunt Publishing, Dubuque, Iowa. 974 pp

Idiobiont

Parasitoids that immobilize or paralyze their hosts after oviposition, preventing further development. The larvae of these parasitoids normally develop externally, as ectoparasitoids.

Idiostolidae

A family of bugs (order Hemiptera, suborder Pentamorpha).

► Bugs

Ihering, Hermann Von

Hermann von Ihering was born in Kiel, Germany, on October 9, 1850. At the age of 18, he accompanied his father to Vienna. In 1870, during the Franco-Prussian war, he enlisted in a regiment of musketeers, served as medical assistant, then studied medicine in Berlin and Göttingen and obtained medical degrees. In 1876, he obtained a Ph.D. degree in zoology. In 1880, he moved to Brazil, and in 1893 was appointed director of the Museu Paulista. His research interests were in zoogeography and in South American social insects. For example, he published on the foundation of new colonies and fungus-gardens by leaf-cutting ants. In 1924 he returned to Germany and was appointed honorary professor of paleontology at Universität Giessen and published (1927) "Die Geschichte des Atlantischen Ozeans." He died in Büdingen, Germany, on February 24, 1930. His son, Rodolpho (1883–1939), also was an entomologist.

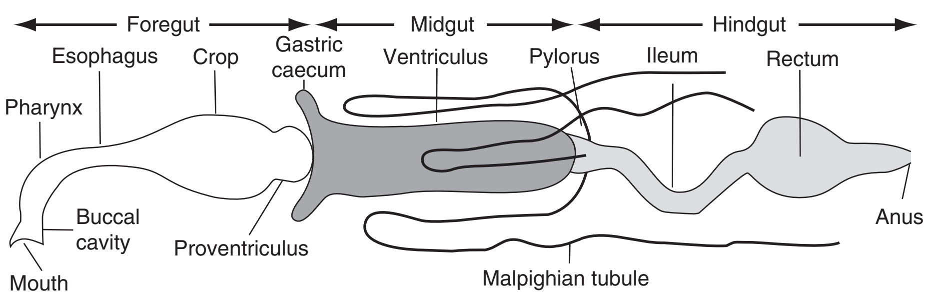
Reference

Anonymous (1930) Todesfälle. Mitteilungen der Deutschen Entomologischen Gesellschaft 1:34

Ileum

The anterior portion of the hindgut, preceding the colon (if present) and rectum (Fig. 1).

► Alimentary System
► Alimentary Canal and Digestion



Ileum, Figure 1 **Generalized insect alimentary system (adapted from Chapman, The insects: structure and function).**

Imaginal Disc

A group of cells set off during embryonic development that are activated upon transformation to the adult stage, and develop into adult characters.

► Metamorphosis

Imago (pl. imagoes)

The adult or reproductive stage of an insect.

Immaculate

This describes objects lacking spot or dark markings.

Imma Moths (Lepidoptera: Immidae)

JOHN B. HEPPNER
Florida State Collection of Arthropods,
Gainesville, FL, USA

Imma moths, family Immidae, comprise 246 species, all tropical, and mostly Indo-Australian and South Pacific, mostly in the genus *Imma*; actual fauna likely exceeds 450 species. The family is the only family of the superfamily Immoidea in the section Tineina, subsection Tineina, of the division Ditrysia. Adults small to medium size (14–42) mm wingspan), with head smooth-scaled; haustellum naked; labial palpi upcurved and often prominent, with long second segment; maxillary palpi minute, 1–2-segmented. Forewings often somewhat rounded on the termens (Fig. 2). Maculation varies, but mostly shades of brown or gray, with various markings or bands, or more colorful; sometimes with translucent hindwings. Adults are diurnal, but some may be crepuscular. Larvae are leaf feeders, but only three species have biological data. Host plants are in Myrtaceae, Podocarpaceae, and Violaceae.

Imma Moths (Lepidoptera: Immidae), Figure 2
Example of imma moths (Immidae), *Imma homocrossa* Meyrick from Malaysia.

References

Clarke JFG (1969) Imma Walker. In: Clarke JFG (ed) Glyphipterygidae [sic], Catalogue of the type specimens of Microlepidoptera in the British Museum (Natural History) described by Edwards Meyrick, 6. British Museum (Natural History), London, pp 100–167

Clarke JFG (1986) Family Immidae. In: Pyralidae and Microlepidoptera of the Marque sas Archipelago. Smithsonian contrib Zool 416, pp 318–334

Common IFB (1990) Superfamily Immoidea. In: Common IFB (ed), Moths of Australia, Melbourne University Press, Melbourne, pp 310–312

Heppner JB (1982) Review of the family Immidae with a world checklist (Lepidoptera: Immoidea). Entomography 1:257–279

Meyrick E (1906) On the genus *Imma*, Walk. (=*Tortricomorpha*, Feld.). Trans Entomol Soc Lond 169–206

Immature

The feeding stage of insects after birth but before adulthood, including both larvae and nymphs.

Immidae

A family of moths (order Lepidoptera) also known as imma moths.

► Imma Moths

► Butterflies and Moths

Immigrant

An organism that was accidentally introduced. An immigrant is an organism that is not native to an area (it is adventive), and has arrived as the result of hitch-hiking (traveling) or by its own means of dispersal (usually by flight or rafting). Immigrants are often called "invaders" or "invasives," though their invasive properties vary considerably once they have arrived.

► Invasive Species

Immiscible

Liquids that cannot mix to form a homogeneous solution.

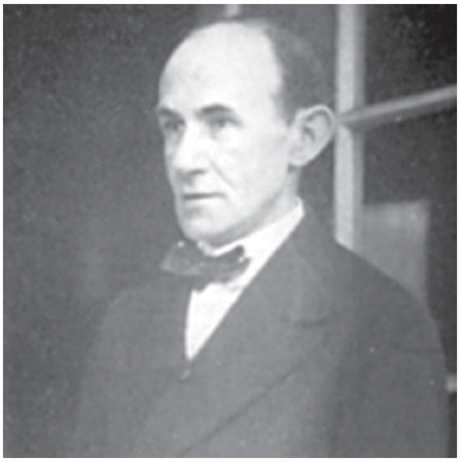
Immigration

Entry of organisms into a population from elsewhere (contrast with emigration).

► Invasive Insects

Imms, Augustus Daniel

Augustus Imms was born on August 24, 1880. He was educated at the University of Birmingham and then obtained a B.Sc. from London University. Next, he entered Cambridge University, from which he obtained a B.A. degree, and then a D.Sc. in 1907. In 1907 he became the first professor of biology in the University of Allahabad and later forest entomologist to the Indian government. He returned to England in 1913, and was appointed reader in agricultural entomology in the University of Manchester. He



Imms, Augustus Daniel, Figure 3 **Augustus Imms.**

worked at Rothamsted Experimental Station from 1918. In 1931, he was appointed head of the new Entomology Department of Cambridge University, where he remained until his retirement in 1945. Some of his research was on termites, and he wrote a book (1925) "Social behavior in insects." At Manchester and then at Cambridge, his teaching responsibilities were important. Two of his books, (1925) "A general textbook of entomology," and (1947) "Insect natural history" were aimed at students. The first of these, through its numerous editions, has been the primary textbook of entomology used in Britain and British Commonwealth countries by generations of students. He was elected a fellow of The Royal Society in 1929. In 1936–1937, he served as president of the Royal Entomological Society of London. He died on April 3, 1949 (Fig. 3).

Reference

Wigglesworth VB (1949) The president's remarks. Proceedings of the Royal Entomological Society of London (C) 14:64–66

Immunity

Immune response is defined as that response made by the immune system when invaded by foreign substances or by microorganisms. Invertebrate organisms, including insects, possess immune capability, but it is dissimilar to vertebrate immunity. Vertebrate immune response can be anticipatory, meaning that once a vertebrate animal acquires an infection, it is unlikely to develop this same infection again. This is due to the fact that protein molecules called antibodies or immunoglobulins, which are highly specific for the immunostimulatory molecules produced by the agent that caused the initial infection, can be rapidly generated by memory cells. Memory cells are lymphocytes (white blood cells) that do not actively engage in making a response to a foreign antigen during the primary challenge, but which react readily upon re-exposure of the animal to the same antigen.

Invertebrates lack the lymphocytes necessary to produce the antibodies needed for immunological memory and subsequent anticipatory immune response. It has been suggested that invertebrates do not require such complex immune defense mechanisms. For instance, the invertebrate body plan is less complicated than that of vertebrates. Insects are r-strategists and have a much higher reproductive potential than vertebrate species. Even if a large percentage of an invertebrate population is killed by disease, there are still enough surviving individuals for repopulation. Additionally, the life span of most invertebrates is relatively short, so that the production of immunological memory is not necessary and may even be excessive. The invertebrate intrahemocoelic cellular and humoral defense mechanisms form the innate or natural immune system, an immediate defense response that acts on microbes that breach the highly resistant insect cuticle.

Imported Cabbageworm *Pieris (Artogeia) rapae* (L.) (Lepidoptera: Pieridae)

This is one of the most abundant white butterflies in the temperate areas of the world. It feeds on cruciferous plants, including vegetable crops such as cabbage.

► Crucifer Pests and Their Management
► Cabbageworm

Import Permit

An official document that authorizes importation of a commodity in accordance with specified phytosanitary requirements.

► Regulatory Entomology

Incense-Cedar Wood Wasps

Members of the family Anaxyelidae (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Incidence

(of a disease) The number of new cases of a particular disease within a given period of time, in a population being studied.

Incipient Species

Consistent variation from the "normal" in appearance, physiology or behavior in a species that might lead to reproductive isolation and speciation.

Inclusion Body

A polyhedral structure which, in insect viruses, normally contains virions. They are also called polyhedral inclusion bodies (PIBs). Inclusion bodies are the product of occluded viruses.

Incomplete Metamorphosis

A type of metamorphosis characterized by slight changes in body form during the developmental period, and the presence of the egg, nymphal and adult stages. The pupal stage is lacking. This is also known as simple metamorphosis or hemimetabolous development. Some of the aquatic insects displaying incomplete development (Odonata, Ephemeroptera, Plecoptera) differ in the degree of difference between the mature and immature stages, and so are sometimes said to have gradual metamorphosis or paurometabolous development.

► Metamorphosis
► Complete Metamorphosis
► Gradual Metamorphosis

Incubation Period

The period in which the embryo develops within the egg before hatching (eclosion). In epidemiology, however, it refers to the period between when organisms are infected with a disease, and the appearance of the disease.

Incurvariidae

A family of moths (order Lepidoptera). They commonly are known as leafcutter moths.

► Leafcutter Moths
► Butterflies and Moths

Index of Similarity

The ratio of the number of species found in each of two communities to the total number of species that are found in both.

Indian Meal Moth *Plodia interpunctella* Guenée (Lepidoptera: Pyralidae)

This grain-feeding insect attacks stored grain products throughout the world.

► Stored Grain and Flour Insects

Indicator Species

A species that can be used as an assessment or indicator of the general condition of a habitat, community or ecosystem. This is also called a sentinel species.

Indifferent Species

Species that occur in may different types of communities, and thus are not useful for characterizing a community.

Indigenous

Normally found within the region, at least within recorded history.

► Invasive Insects

Indirect Flight Muscles

Muscles that power wing movement by changing the shape of the elastic thorax. Among the indirect muscles are the dorsal longitudinal muscles that arch the tergum and depress the wings, and the dorsoventral and oblique dorsal muscles that flatten the tergum and elevate the wings.

Indirect Pests

Pests that inflict damage by attacking a portion of the plant that is not harvested (often the roots, stems, or foliage), and weaken the plant, reducing overall yield.

Induced Food Preference

A tendency of insects to prefer food that they have fed upon previously, even though capable of eating other foods.

Induction

In insect ecology, the display of induced food preference. In insect pathology, the activation of an occult pathogen, leading to progressive infection and disease.

Industrial Melanism

The predominance of darker forms of some Lepidoptera resulting from natural selection (reduced predation) in areas with severe air pollution. A form of crypsis.

Infection

The introduction or entry of a pathogenic microorganism into a susceptible host, resulting in the presence of the microorganism within the body of the host, whether or not this causes detectable pathologic effects.

Infectivity

The quality of being infective; the ability to produce infection.

Infestation

The presence of a number of pests in a field, on plants, or in the soil.

Inflorescence

The flowering part of a plant. The flower.

Innate Capacity for Increase

(r_{max}) A measure of the rate of increase of a population under controlled conditions. Normally this is the maximum rate of reproduction possible under laboratory conditions without the effects of naturally occurring mortality due to disease, predation, etc.

Innate Immunity

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Innate immune systems, although lacking the highly evolved antibody-producing mechanisms, are complex and involve gene families involved in signal detection, signal transduction, signal modulation, and stimulus response. For example, recent transcriptional profiling has revealed that over 500 genes are altered in *Drosophila* challenged by septic injury. The pathways and component gene products associated with the innate immune response observed initially in *Drosophila* have homologues in other insects (*Apis*, *Anopheles*) that have been subjected to genome-wide sequencing efforts. Interestingly, the innate immune pathways, excluding the insect phenoloxidase melanization and encapsulation components, are remarkably similar to those found in the innate systems of mammals. For example, immune response in insects depends upon several different activities that interact to form a well-coordinated immune system. These different activities include cellular defense reactions such as phagocytosis, nodulation, and encapsulation, as well as proteolytic cascades including, most notably, the prophenoloxidase (melanization) cascade and the coagulation cascade, which has actually been better described in other invertebrates, e.g., the horseshoe crab (*Limulus*). Insects produce an array of antimicrobial substances, which are usually low molecular weight, cationic peptides. The vertebrate innate system, likewise, consists of a complex of cellular defense reactions (phagocytosis, granuloma formation) and activities associated with the so-called complement proteolytic cascade systems and with various antimicrobial factors.

The immunocytes that function in the innate response include the neutrophils and macrophages found in vertebrates, and the granulocytes and plasmatocytes that occur in insects. Several other types of immunocompetent hemocytes have been described in some insect species (e.g., lamellocytes from *Drosophila*) and non-insect invertebrates. These cells are generally analogous with respect to phagocytic activities and even have similar morphological characteristics. Invertebrate hemocytes, like the leukocytes, often contain numerous granules, which can be sites of synthesis and/or storage of substances needed in the killing and digestion of ingested microorganisms, for enzymes used in cascade reactions, and for sequestering humoral antimicrobial peptides or AMPs. However, even though the invertebrates lack true lymphocytes, their immunocytes are more comparable to the lymphocyte-like natural killer cells (NKCs) found in vertebrates than to the neutrophils and macrophages. NKCs are cytotoxic cells that kill certain kinds of tumor cells and virus-infected cells. NKCs do not need the same types of receptors (e.g., immunoglobulin receptors) used by other types of lymphocytes (B and T lymphocytes) in order to carry out their activities. Instead, they have a more primitive recognition system that identifies self and then reacts against any material that is nonself. NKCs have been found in some invertebrates and thus may represent a vertebrate remnant of invertebrate immunocytes that operate by self-recognition. Some of the receptors that function in this type of response are carbohydrate-type binding molecules, termed lectins, which are common in both invertebrates and vertebrates. The NKC lectins constitute a unique superfamily of integral membrane proteins that inhibit as well as activate cell function.

After nonself material has been recognized, it can become attached to the receptors on the membranes of immunocompetent blood cells and then eliminated from circulation via phagocytosis. Phagocytosis (from the Greek *phagein* meaning to eat) is a process that is carried out not only by the immune reactive cells in higher animals, but also by organisms such as protozoans (e.g., *Amoeba proteus*), which ingest foreign material for nutritional purposes as well as for self-defense. With respect to immune activities, nonself particles that become attached to phagocytic immunocytes are endocytosed. These particles are taken into the host cell usually by way of membrane-bound phagosomes; and are killed by mechanisms such as enzymatic degradation or by the effects of toxic reactive oxygen and/or nitrogen intermediates. Not all microorganisms are susceptible to the destructive processes that occur within the phagolysosomes; some survive and replicate as intracellular parasites. Intracellular parasitism blood cells provide infective propagules an effective means to avoid further encounters with immune system activities and to be disseminated throughout the host.

Phagocytic hemocytes can function individually, or they can be recruited to sites of infection where, in insects, they may aggregate around the invading microorganisms to form nodules and/or capsules; these structures are comparable to the granulomas, i.e., aggregates of leukocytes, found in vertebrate systems. Recruitment molecules that stimulate the movement of blood cells to infection sites have been identified in both vertebrates and invertebrates. The chemokines, including the chemotactic cytokines and cytokine-type signaling molecules are present in some invertebrates. In insects, molecules belonging to the eicosanoid group of signaling moieties have been reported to function in the nodulation process; eicosanoids include the well-known prostaglandins described in vertebrates.

Pattern-Recognition Receptors of Nonself

The recognition and attachment events that initiate cellular defense response in innate systems are regulated by humoral and by membrane-bound molecules (receptors) that discriminate self versus nonself by a process known as pattern recognition. Pattern-recognition proteins (PRPs) are able to distinguish the highly conserved characteristics (pathogen recognition molecular patterns, PAMPS) that are unique to pathogens and are not usually found on the cells of other types of organisms, including self. These patterns can be displayed on microbial surfaces in the form of peptidoglycan molecules in the case of bacteria, or as mannose, galactose, or β-1,3-glucan residues in the case of fungi. Such components, since they commonly occur on surfaces of a variety of different microorganisms, enable complementary pattern recognition molecules to identify a broad spectrum of potential pathogens. Many insect pathogens produce modified surface that either lacks or camouflages PAMPs thus mimicking self surface epitopes.

In vertebrates, pattern recognition molecules serve as a primary defense line during the lag time required for antibody production to take place. They are acute phase reactants and are rapidly induced upon challenge. Lectins constitute a widespread group of pattern recognition molecules in vertebrates and in invertebrates. In both systems, the occurrence of C-type (i.e., calcium-dependent) lectins has been especially well documented. In vertebrates, this lectin group is best exemplified by the mammalian serum mannose-binding protein (MBP) and the macrophage mannose receptor. The C-type lectins in invertebrates, including insects, have sequences similar to those of the vertebrate lectins such as MBP. Lectins and other types of pattern recognition molecules serve as opsonins, so that the microorganisms that they coat become better targets for immunoreactive blood cells (see cell defense systems). Pattern recognition molecules bound to their respective ligands, often in an opsonic capacity, activate other components (the complement pathways in vertebrates) in the innate system.

Non-lectin pattern recognition molecules that bind to peptidoglycans, and β-1,3-glucans play multifunctional roles in both cellular and humoral defense responses. For example, the peptidoglycan recognition proteins (PGRPs) described initially as extracellular sensor of bacterial infection is now recognized as a family of PRPs. In *Drosophila*, two isoforms exist, the short version that functions as a co-receptor in the recognition of diaminopimelic acid-type peptidoglycans and the long version that functions at an intracellular level in defense of potential intracellular bacterial pathogens. A second subgroup, the catalytic PGRPs produced by the midgut cleave glycans off the peptidoglycan structure reducing their immunostimulatory ability thus preventing diet borne innocuous peptidoglycan from initiating an immune response. Another subgroup would include the secreted PGRPs that degrade peptidoglycan structure and either directly destroys the bacterial invader or clears bacterial cell wall debris from the insect. A second group of non-lectin pattern recognition molecules would be the gram-negative binding proteins (GNBPs). Certain GNBPs interact with PGRPS in the activation of the Toll in response to gram positive bacteria. These GNBPs may contain glucanase-like domain can detect fungal β-1,3-glucans and/or effect the agglutination of fungal cells (Table 1).

Signaling Pathways

At present, there are several major signaling pathways used to activate the host cellular response to microbial infection. The NF-κB pathways Toll and Imd activate the transcription of antimicrobial peptides (AMPs). Mutations in these pathways increase the susceptiblilty of insects to infection. The insect Toll, described initially in *Drosophila*, is activated when a cocktail of PGRPs and GNBPs interact with lysine-type peptidoglycan (gram positive bacteria) or β-1,3-glucans. The resulting complex induces serine proteases that cleaves and activates membrane-bound Spaetzle. This active protein binds to the transmembrane receptor Toll, triggering an intracellular serine kinase cascade. This leads to the phosphorylation and degradation of the inhibitor κB protein Cactus. Removal of Cactus activates of the NF-κB proteins DIF and Dorsal that are translocated into the nucleus to activate the transcription of the insect AMPs and prophenoloxidase activators. The meso-diaminopimelic acid peptidoglycans associated with gram-negative bacteria and with *Bacillus* spp. elicit the Imd pathway. Different membrane-bound PGRPs recognizing monomeric and polymeric peptidoglycan fragments stimulate the Imd pathway, activating a protease cascade that activates the

Innate Immunity, Table 1 Granular contents of vertebrate and invertebrate immunocytes[a]

Vertebrate cells		Invertebrate cells
Neutrophils	**Macrophages**	
Primary (azurophilic granules)		
Myeloperoxidase	Collagenase	Acid phosphatase
Acid phosphatase	Elastase	Esterase
Glucosaminidase	Plasminogen activator	β-glucuronidase
5′-Nucleotidase	Arginase	Lysozyme
α-Mannosidase	Tissue procoagulant	Cationic peptides
Arylsulfatase	Lysozyme	Lectins and hemagglutinins
α-Fucosidase	Complement proteins	Prophenoloxidases and associated
Esterase	Interferons	Factors (e.g., proPO activating enzyme, 76 kDa adhesion protein from crayfish)
Cathepsin	Interleukins	Coagulation factors
Elastase	Tumor necrosis factors (TNF)	LPS – binding protein
Histonase	Growth factors	β-1, 3 glucan-binding protein
Phospholipase A	Apolipoprotein E	(Silkworm)
Cationic proteins	Platelet activating factor	Acid mucopolysaccharides
Defensins	Oxygen metabolites	TNF, ACTH (adenocorticotropin)[b]
Glycosaminoglycans	Nitric oxide	ECM components[c]
Chondroitin sulfate	Fibronectin	
Heparin sulfate		
Lysozyme		
Secondary and tertiary granules		
Alkaline phosphatase		
Histaminase		
Collagenase		
Vitamin B_{12}-binding protein		
Laminin receptor		
C3bi receptor		
FMLP		
Lactoferrin		
Cytochrome b245		
Flavoproteins		
Lysozyme		
Tetranectin		
Gelatinase		

[a]Represents only a partial list of granule contents
[b]Localized in hemocytes, but not definitively in granules of *Calliphora* (fly) (See Franchini et al. (1996))
[c]Indicated by cross-reactivity of monoclonal antibodies to both basement membranes and hemocyte granules, e.g., in beet armyworm and other insects

NF-κB protein Relish that up-regulates transcription of AMPs and melanization components.

In addition to the Toll and Imd pathways, various insects possess components of the Jun N-terminal Kinase (JNK) pathway and JAK/STAT signal pathways. The JNK, an important pathway in the morphogenesis of imaginal discs, plays an important role in wound healing and in cell program death or apoptosis. The JAK/STAT or Hopscotch (Hop) signaling pathway, initially associated with embryonic segmentation, has been associated with immune response of both *Anopheles* and *Drosophila*. The Hop pathway in the fat body is triggered by the hemocyte produced cytokine Upd3, a 65 kDa glycoprotein. The Upd3 binds to the transmembrane receptor dome that stimulates Hop to phosphorylate the transcriptional activator the STAT 92E protein. The Hop pathway controls the expression of both TEP1 and the Turandot (Tot) proteins in fat body. In mosquitoes, the TEP1 is believed to act as an opsonin promoting phagocytosis of nonself. Removal of TEP by RNAi reduced phagocytosis of bacteria in mosquitoes. The Tot proteins, although not antimicrobial, appear to be involved in protection and repair of damaged tissues. In *Drosophila*, this pathway has been implicated in lamellocyte differentiation and hemocyte proliferation, events important to both phagocytosis and encapsulation.

Antimicrobial Response

Since the early 1900s, insects have been reported to respond to microbial challenge and to produce soluble components having potent antibacterial activity. In the late 1950s, heat-stable antibacterial components were detected in several lepidopteran hosts that had been challenged with microbial antigens. This research demonstrated that the tolerance of these immunized insects to a second bacterial challenge was correlated with the titer of the heat-stable antibacterial component. Pioneering work by H. Boman and associates at Stockholm University during the late 1970s to early 1980s using the diapausing pupae of the giant silkworm (*Hylaphora cecropia*) as a model provided details on the biochemistry of insect humoral response. Hemocoelic challenge with non-pathogenic viable bacteria induced these pupae to produce antibacterial activity within 10 h post-injection. These diapausing pupae, having an intrinsic low metabolic activity, allowed Boman's team to selectively radiolabel the induced antimicrobial components. Using various biochemical methods, the major antibacterial components produced by *H. cecropia* pupae have been isolated and characterized.

In several respects, the insect humoral response has been compared to the acute phase response of vertebrates. Wounding or septic injury induces many insects to rapidly synthesize a complex of antimicrobial proteins/peptides that may act on a range of bacteria and/or fungi. Hultmark describes eight classes of AMPs including lysozyme, defensins, cercropins, diptercins, attacins, drosocins, Metchnikowins, and drosomycins. The synthesis of these antimicrobial components, detected in various host tissues within hours after being induced, protects the host animal against rapidly dividing microbes. It should be noted that insects produce a family of AMPs that are regulated by multiple overlapping pathways. In many insects, the levels of antimicrobial activity are maintained at inhibitory levels for several days. The majority of antimicrobial proteins found in insects are small peptides (about 10 kDa) that act in a stoichiometric fashion on the microbial membranes.

Lysozyme

The lysozymes from the wax moth *Galleria mellonella* and silkworm *Bombyx mori* represent the first antibacterial proteins to be purified from insects. Insect lysozyme, unlike other antimicrobial proteins, acts catalytically and digests the cell walls of certain gram positive bacteria. In several cases, lysozyme acts as a synergist with the smaller cationic peptides. The outer membrane of gram negative bacteria usually serves as an effective barrier against lysozyme attack. This enzyme digests the glucosidic bond between *N*-acetylglucosamine and *N*-acetylmuramic acid of the peptidoglycan layer. Additionally, certain insect lysozymes possess potent chitinolytic activity. Lysozyme synthesized in various tissues may possess a multifunctional role in different insects. In certain cyclorrhaphous flies, this enzyme is produced constitutively by the midgut tissue and assists in the digestion of ingested bacteria. The insect midgut lysozymes are active at an acidic pH, possess a high chitinolytic activity, and are functionally similar to the stomach lysozymes of vertebrates.

These enzymes are relatively small (about 15 kDa), heat stable, basic proteins and are very easy to detect and extract from insect tissues. Tissue homogenates may be acidified, heat-treated (boiled for 2 min), and centrifuged to remove large molecular weight proteins. The lysozyme may be readily extracted from the supernatants using cation exchange chromatography. During purification, lysozyme activity may be assayed against a cell wall preparation of the gram positive *Micrococcus lysodeiktus*. Lysozyme digests the cell wall, causing a decrease in the turbidity of the substrate that may be measured spectrophotometrically at 570 nm. Lysozyme may be detected in both normal and immunized insects. Many insects produce multiple forms of lysozyme that possess distinct isoelectric points and pH optima. The lysozyme genes of *D. melanogaster* exist as a multiple gene family, lack introns, and are not induced by bacterial challenge. In other insects, low levels of lysozyme are detected as a normal component of the hemolymph. The hemolymph lysozyme of *Manduca sexta* larvae has been reported to have played a key role in initiating and sustaining the humoral defense response. This enzyme digests the bacterial cell wall and releases peptidoglycan fragments which act as elicitors of the humoral response. The fat body is triggered by these elicitors (inducers) to synthesize and to secrete high titers (mg/ml) of both lysozyme and other antibacterial peptides into the insect hemolymph.

Antibiotic Peptides

The antibiotic peptide group, containing members with 50 amino acids (aa) or less, may be divided into the linear peptides and the cyclic peptides that contain one or more disulfide bridges. The hydrophobic domains allow these peptides to interact with the lipid bilayer of microbial membranes. Secondly, the majority of antibiotic peptides contain multiple arginine and/or lysine residues that confer a basic net charge to these cationic peptides. These peptides act stoichiometrically, inserting into and disrupting the microbial cell membrane. Although capable of killing many different species of prokaryotes, many antibiotic peptides have little or no effect on eukaryotic cells. In part, this specificity reflects the preferential binding of these cationic peptides to the anionic phospholipids contained within outer layers of bacterial cells. The presence of high levels of cholesterol in eukaryotic cell membranes has been reported to neutralize the effects of certain amphipathic peptides. In most insects, the synthesis of these peptides is induced when certain microbial elicitors (e.g., lipopolysaccharides, mannans, peptidoglycans) bind to cell membrane receptor domains. Induction results in the synthesis of a family of these antibiotic peptides that act in concert against a spectrum of potentially pathogenic microorganisms.

Many of the methods used to detect and to isolate insect antimicrobial peptides were established by H. Boman (University of Stockholm). His research group found that *H. cecropia* pupae and *Drosophila* larvae challenged with either live or killed bacteria or preparations of bacterial wall components generate a potent humoral response. Large insects such as lepidopteran larvae may be injected directly with a bacterial suspension, whereas smaller insects such as fruit fly larvae may be pricked with pins coated with elicitor preparations. At various time intervals post-challenge, either hemolymph or whole insects can be sampled for subsequent processing. Typically, hemolymph or tissue is homogenized in an acidified buffer containing appropriate protease inhibitors. These mixtures may then be heat-treated and centrifuged to precipitate large molecular proteins. The relative levels of antimicrobial activity may be monitored using growth inhibition assays. Target microbes, placed in broth or incorporated in solid media, are assayed against test suspensions. For example, to measure activity against gram negative bacteria, the *E. coli* K12 strain D-31 is used routinely as the detector organism. Bacteria are incorporated into solid media and test suspensions applied to wells cut in the agar surface. The diameters of the resulting inhibition zones are measured and compared to those produced by commercially available synthetic antibacterial peptides. Alternatively, detector bacteria may be placed in broth and amended with various dilutions of the test preparations. Growth inhibition, measured spectrophotometrically as a reduction in turbidity, may be used to calculate the minimum inhibitory concentration (MIC). It should be noted that certain insect antibacterial peptides/proteins may act in a synergistic fashion. For instance, the cell membrane-disrupting action of many peptides is known to increase the activity of lysozyme against gram negative bacteria. Therefore, the high antimicrobial activity detected in crude preparations may be dramatically reduced as the cofactors are subjected to chromatographic fractionation.

Linear Peptides (Cecropins)

The cecropins, initially described in the early 1980s from fruit flies and silkmoths, have since been detected in various vertebrates. These antibiotics consist of a linear chain of 35–37 amino acids organized into three regions: a strongly basic N-terminus, a long hydrophobic stretch at the C-terminus, and a middle hinge region containing proline and/or glycine. Structurally, these peptides form two α-helices connected by the middle hinge region. Various insect cecropins isolated from lepidopteran and dipteran host insects have been sequenced and their cDNA cloned. Structurally distinct forms of cecropins, produced by the same or different insects, possess distinct antibiotic activities against different bacteria. Cecropins are usually highly active against gram negative bacteria, active against selected gram positive bacteria, and inactive against most eukaryotic cells. In addition to insects, cecropins have been detected in vertebrates, e.g., cecropin P1 in porcine intestine. Unlike the insect cecropins, the P1 molecule contains an amphipathic α-helical structure through the entire sequence.

The cecropins secreted from insect cells recognize and bind to target microbial cells. The incubation of liposomes, comprised of acidic phospholipids, with sarcotoxin resulted in a dose-dependent release of entrapped glucose molecules demonstrating that cationic peptides can bind to acidic phospholipids and permeabilize the lipid layer. Amending liposome preparations with cholesterol repressed the cecropin activity. Further studies suggested that at a high dosage, cecropins aggregated on the bacterial membrane to produce ion channels. Cecropins at physiologically active levels bind to the outer membrane as monomers and then diffuse into the wall to reach the target inner membrane. As monomers, the active cecropins possessing a 12–15 aa α-helix have an estimated length of 20 Å, which is too short to span the 30 Å membrane lipid bilayer. Rather than producing ion channels, cecropins apparently cause a rapid lysis of bacterial cells acting in a detergent-like fashion to disrupt the bacterial membrane.

In addition to cecropins, animals produce a number of other linear antibiotic peptides with amphipathic α-helical conformations. For example, the honey bee *Apis mellifera* synthesizes a venom peptide, mellitin (26 aa), that possesses α-helical structures at both C- and N-termini. Mellitin is one of the most powerful cell lytic agents and is active against both prokaryotic and eukaryotic cells. This peptide is constitutively produced by the secretory cells of the venom duct as promellitin (70 aa) which is later activated by proteolytic cleavage. Hybrid molecules containing the

N-terminal sequences of mellitin and cecropin A have been synthesized and found to possess enhanced antibacterial activities. In addition to honey bees, several adult dipterans have been reported to constitutively secrete cecropin-type antibiotics from their reproductive organs. The ceratotoxins, 3 kDa antibacterial peptides, are specifically synthesized by the female accessory gland of the medfly *Ceratitis capitata*. These peptides, like mellitin, possess potent activity against gram negative and gram positive bacteria and possess a strong hemolytic response. Although related structurally to cecropins, ceratotoxin synthesis is stimulated by mating and not by septic wounding. The ceratotoxin gene codes for a 71 aa proceratotoxin which is activated by a dipeptidase. It has been proposed that this peptide, detected on the egg surface, protects the developing embryo from microbial attack. A second sex-specific antibiotic peptide, the 3 kDa andropin, has been found to be synthesized in the male ejaculatory duct of *D. melanogaster*. Andropin synthesis, unaffected by bacterial challenge, is induced by mating and is believed to inhibit bacterial infections in the reproductive tract.

Disulfide-Linked Peptides

These peptides, unlike the linear peptides, possess a β-sheet structure and contain one or more intramolecular disulfide bonds. The defensins are presently the most diverse and best-studied disulfide-linked antibiotic peptides. Pioneering research on defensins was conducted by immunologists studying the cationic peptides associated with the azurophilic granules of vertebrate neutrophils. Insect defensins, initially described in the dipterans *Phormia terranovae* and *Sarcophaga peregrina* are structurally similar to the defensins isolated from vertebrate phagocytic cells. The insect defensins contain about 40 aa residues, including six cysteines which produce the characteristic three intramolecular disulfide bridges. Insects in the orders Diptera, Hymenoptera, Coleoptera, Odonata, Trichoptera, and Hemiptera have been reported to produce defensins. Members within the order Lepidoptera, characterized by possessing inducible lysozyme genes, have not been found to produce defensins. Structurally, insect defensins possess an N-terminal flexible loop, a central amphipathic α-helix, and a C-terminal anti-parallel β-sheet. The *S. peregrina* defensin, termed sapecin, was isolated from the culture media of embryonic cell lines of *S. perigrina*. This peptide, constitutively produced by the cell line, inhibits gram positive bacteria more effectively than gram negative bacteria. Sapecin has a high affinity to cardiolipin, a major phospholipid of certain gram positive bacteria. Gram negative bacteria contain less cardiolipin and possess the outer LPS layer believed to serve as a barrier for certain cationic antibacterial substances. The second well-characterized insect defensin group was isolated from *P. terranovae* larvae which had been challenged by pricking insects with needles coated with the gram negative *Enterobacter cloaca*. Analysis of the *P. terranovae* defensins A and B demonstrated that their structures, which differ by a single amino acid, are highly homologous to the well-characterized vertebrate defensins. Various other defensin molecules have been detected in many other insects, including mosquitoes, honey bees, and hemipterans. In all cases, the insect defensins possessing a well-defined α-helix may be readily distinguished from the vertebrate defensins, which consist of only β-sheets. The vertebrate and insect defensins have been reported to form voltage-dependent ion channels in bacterial membranes. Vertebrate defensins are known to sequentially permeabilize the outer and inner bacterial membranes. Vertebrate defensins, existing as dimers, bind to the membranes via electrostatic interactions and produce a barrel stave aggregate, forming an ion channel. The *P. terranovae* defensin, like the vertebrate defensin, induces the formation of ion channels in assayed bacterial membranes. These channels, also produced by defensin treatment of liposomes, can be opened and closed by manipulation of the membrane potential.

Proline-Rich Peptides

These small (2 kDa), linear peptides contain high levels of proline residues. The first insect proline-rich antibacterial peptide, drosocin, was isolated from bacterially challenged *D. melanogaster*. Drosocin is *O*-glycosylated and possesses an *N*-acetylgalactosamine-galactose derivative on the threonine residue. Synthetic drosocin, lacking the sugar residue, possessed reduced antibacterial activity against target gram negative bacteria. Metchnikowin, also described from *Drosophila*, is a 26 kDa proline-rich inducible peptide that targets gram positive rather than gram negative bacteria and is also antifungal. Metchnikowin is expressed in fat body, and there is some sequence similarity to another proline-rich peptide, abaecin, from honey bees. Additional *O*-glycosylated proline-rich peptides have been detected in the hemipteran *Pyrrhocoris apterus*. This peptide, termed pyrrhocoricin, is highly active against selected gram negative bacteria. Unlike the previously discussed cationic peptides that are hydrophobic, the presence of the polar sugar residue confers a hydrophilic property to these proline-rich peptides. In general, the glycosylated antibiotic peptides act more slowly than the hydrophobic peptides. Sequence analysis has shown that pyrrhocoricins are somewhat homologous to the N-terminus of the glycine-rich peptides (see following section). The apidaecins, major components of the honey bee antibacterial repertoire, are small, non-glycosylated, proline-rich peptides.

Glycine-Rich Peptides

Various inducible proteins such as attacins (20 kDa) and sarcotoxins (24 kDa), and peptides such as coleoptericins (8 kDa), diptericins (9 kDa), and hymenoptaecins (10 kDa) can be included within this heterogeneous group. All of these antibiotic peptides/proteins contain a high percentage of glycine residues (12–22%). The attacins, named for the saturnid tribe *attacini*, were first isolated from *H. cecropia*. A total of six attacins, four cationic and two anionic isoforms, have been characterized in the hemolymph extracted from bacterially challenged *Cecropia* pupae. The different attacin isoforms are produced by differential post-translational modifications of two parental proattacin sequences. Attacins, unlike the smaller cationic peptides, are bacteriostatic and possess only limited activity against selected gram negative bacteria that are actively growing. Southern blot hybridizations of the radiolabeled attacin probe and digested *B. mori* genomic DNA suggest that *B. mori*, like *H. cecropia*, contains a multi-gene attacin family. Sequence analysis of the *B. mori* gene demonstrated extensive homology to the *Cecropia* attacins, and an attacin from *Trichoplusia ni* also shows significant homology to these peptides at both the nucleotide and peptide levels. In addition, the *B. mori* gene exhibits sequence similarity to the sarcotoxin II family. The sarcotoxins II (A-D), isolated from challenged *Sarcophaga peregrina* larvae, are large (24 kDa) glycine-rich peptides. The glycine-rich domain of sarcotoxins extends over 60 residues from the C-amidated terminus. *Sarcophaga peregrina* larvae may also be induced to synthesize a glycine-rich 8 kDa diptericin.

Diptericins were detected initially in bacteria-challenged *P. terranovae* and were characterized as cationic antibacterial peptides possessing an N-terminal proline-rich region and a C-terminal glycine-rich region. Some consider diptericins as chimeric molecules containing components of both the proline-rich and glycine-rich antibacterial peptides. The *P. terranovae* diptericin A possesses potent bactericidal activity against smooth strains of selected gram negative bacteria. Detailed chemical analysis of various isoforms of diptericin A demonstrated that this peptide is *O*-glycosylated at threonine residues located at both the proline-rich and glycine-rich domains. Septic wounding of larvae, pupae, and adult fruit flies induced the synthesis of diptericin transcripts within 2 h post-inoculation. In addition, both early pupae and adult stages displayed low levels of constitutive expression. Recently, a 133 residue glycine-rich peptide has been characterized from *P. apterus*, termed hemiptericin, which displays some homology to the glycine-rich domain of diptericin and is active against certain gram negative bacteria.

In addition to the glycine-rich antibacterial peptides, several members within this heterogenous group possess potent antifungal activity. The cationic antifungal peptide AFP is constitutively produced by *S. peregrina* larva. This peptide, possessing 67 amino acids, contains high levels of glycine (31%), histidine (20%), and glutamine (18%) residues. Bioassays have demonstrated that this peptide binds to the yeast *Candida albicans* through electrostatic interaction and disturbs the osmotic integrity of treated cells. Peptides related to AFP have been isolated from several coleopteran hosts. The peptide tenecin 3, extracted from the naïve meal worm *Tenebrio molitor*, possesses 78 aa of which 80% are glycine, histidine, and glutamine residues. Tenecin 3 at concentrations of 10 µg/ml inhibits the growth of the dimorphic vertebrate mycopathogens *Candida albicans* and *Cryptococcus neoformans*. A third antifungal peptide, referred to as drosomycin, has been detected in wounded, septic *Drosophila*. Unlike tenecin 3 and AFP, drosomycin is cysteine-rich and does not contain high levels of glycine, histidine, and glutamine. Structural characterization of drosomycin has demonstrated significant homology to the cysteine-rich plant antifungal peptides found in seeds of the Brassicaceae.

Genetics and Biosynthesis of Antibacterial Peptides and Proteins

Transcription of the antibacterial genes is induced by treating insect cells or whole insects with various elicitors such as bacterial LPS, phorbol myristate acetate (PMA), live and killed bacterial cells, etc. Sequencing regions upstream of the open reading frames of antibacterial genes has revealed the presence of cis-regulatory sequences resembling the κβ-binding motif that serves as the binding site for the transcription activators (see signal pathways). The κβ -binding motif has been found to be associated with genes coding for acute phase proteins, cytokinins, immunoreceptors, transcription factors, and in genes of certain DNA viruses.

The insect antibiotic protein and peptides are products of m-RNA transcripts translated on the insect ribosome. In most cases, the translation products are preproproteins and require additional processing for both secretion and activation events. Many preproproteins consist of three domains: a signal sequence, prosequence, and mature peptide. Within a particular peptide group extensive homology exists in the primary and secondary structure of the mature peptides. However, the N-terminal signal sequence may vary extensively among peptides extracted from different insect hosts. The signal sequence, usually comprised of ~20 aa, guides the translation product into the endoplasmic reticulum for further processing and transport to either intracellular or exocellular locations. The antibiotic peptides may undergo various post-translational modifications within the insect cell. The cecropins and certain glycine-rich peptides undergo a C-terminal amidation. Various defensins such as drosocin, pyrrohocoricin, and certain diptericins undergo *O*-glycosylation in the endoplasmic reticulum. These peptides are decorated with sugar moieties covalently linked to defined threonine residues. The basic and acid preproattacins may be proteolytically cleaved at a terminal tetrapeptide site of the mature peptide and/or have an N-terminal pyroglutamate residue formed. The result of these post-translational modifications is the production of six isoforms of attacins. Activation of the antimicrobial peptides involves proteolytic removal of the prosequence. For example, the preprocecropins contain 62–64 aa of which the signal peptide comprises the initial 22 aa of the N- terminus. The adjacent proline or alanine dipeptide (prosequence) is selectively removed by a dipeptidylaminopeptidase. Similarly, the 29 aa prosequence of the attacins is removed in the Golgi compartment by a dipeptidase recognizing the arg-arg motif.

In conclusion, the humoral antimicrobial peptides and proteins produced in insects play a significant role in their defense against invading pathogens, especially during the early phases of infection. Similarly, in vertebrates, such components often serve as acute phase molecules that function to protect an organism prior to activation of the more complex adaptive (antibody) response. These vertebrate antimicrobial proteins (e.g., lysozymes) and peptides (defensins) are structurally similar to those in invertebrates, so that the invertebrate homologues most likely represent evolutionary prototypes. Evidence that *H. cecropia* antibacterial genes have κβ-binding site transcription activators further confirms that innate immunity in higher animals is directly related to the defense response mechanisms displayed in more primitive organisms (Table 2).

Cellular Defense Systems

The major cellular defense systems in insects involve specific classes of mobile hemocytes found in the hemocoel. Morphological heterogeneity within a population of these cells due to variations in age or physiological state has led workers to assign more than 70 different names to the blood cells collected from insects. Insect hemocytes can be placed into six different categories: prohemocytes (stem cells), granulocytes, plasmatocytes, spherulocytes, adipohemocytes, and oenocytoids. The morphology of these cells varies considerably among the orders of insects and even among the different genera, and morphological changes also occur as the cells

Innate Immunity, Table 2 Different groups of antimicrobial peptides and proteins produced by various insect and vertebrate hosts

Peptide group	General structure	Host animal	Target microbe
Linear peptide without cysteine			
Cercropins A, B bacteria (35–39 aa)	Two α helical domains connected with hinge c-amidated	Lepidoptera, pig small intestine	Diptera gram negative
Magainins (23 aa)	Amphipathic α helix	Frog skin	Gram positive and negative bacteria, fungi, protozoa
Ceratotoxin	Helical	*Ceratitis capitata* females	Bacteria
Andropins (32 aa)	Two helices	*Drosophilia* males	Bacteria
Linear peptides and proteins with high proportion of a amino acid(s)			
Apidaecins (18 aa)	Proline, arginine rich	Honeybees	Gram negative bacteria
Drosocin (19 aa)	Proline rich, glycosylated	*Drosophila*	Gram negative bacteria
Bac (43, 59 aa)	Proline, arginine rich	Bovine neutrophils	Gram negative bacteria, antiviral
PRPs (39 aa)	Proline, arginine rich	Pig intestine	Gram negative bacteria
Acid attacin (20 kDa)	Glycine rich protein two G-domains	*H. cecropia*	Gram negative bacteria
Sarcotoxin IIA (24 kDa)	Glycine-rich protein C-animated, two g-and one P-domain	Fleshfly *Sarcophaga*	Gram negative bacteria
Diptericin (9 kDa)	Glycine and proline C-amidated, one G and one P-domain	Fleshfly *Phormia*	Gram negative bacteria
Peptides with A single disulfide bond			

Innate Immunity, Table 2 Different groups of antimicrobial peptides and proteins produced by various insect and vertebrate hosts (Continued)

Peptide group	General structure	Host animal	Target microbe
Bactenecin (12 aa)	4 Arginine residues	Bovine neutrophils	Bacteria (neuronal cells)
Brevinin (34 aa)		Frog skin	Bacteria
Peptides with two or more disulfide bonds			
α-Defensins	3 Disulfide bridges, pore formers	Vertebrate phagocytic and mucosal cells	Bacteria, fungi
β-Defensins (38–42 aa)	3 Disulfide bonds	Bovine neutrophils	Bacteria
Insect defensins	3 Disulfide bonds inducible peptides	Species within six insect orders	Gram positive bacteria
Protegrins (16–18 aa)	2 Disulfide bonds	Pigs leukocytes	Bacteria
Tachyplesins (17–18 aa)	2 Disulfide bonds	Granules of horseshoe crab hemocytes	Bacteria
Androctonin (25 aa)	2 Disulfide bonds	Scorpion hemolymph	Bacteria, fungi
Buthin (34 aa)	3 Disulfide bonds	Scorpion hemolymph	Bacteria

For additional data see Boman, 1995

mature. There are a number of synonyms for granulocytes, including coagulocytes, cystocytes and amoebocytes, among others. In *Drosophila*, plasmatocytes involved in encapsulation have been named lamellocytes, and the crystal cells in these insects may be the equivalent of the oenocytoids described in other genera. Markers (e.g., lectins, monoclonal antibodies) for specific cell surface ligands have been used to distinguish different types of hemocytes in some insects.

It is generally agreed that hemocytes from the granulocyte (GR) and plasmatocyte (PL) classes perform most of the cell defense activities. In some insects, the GRs are the predominant immunocompetent cells, whereas in others, the PLs carry out most of the immunological activities. The number of immunocompetent cells can fluctuate, most notably during morphogenesis and aging of insects. As in the case of the mobile phagocytes (polymorphs and macrophages) in vertebrates, the GRs, PLs, and other types of insect hemocytes associate with various tissues either as loose aggregates of cells or as distinct, well-defined organs. These reservoirs of sessile hemocytes function as phagocytic organs and/or as hemopoietic organs, i.e., as sites for the formation of new blood cells.

The granulocyte is the most common type of blood cell found among arthropods and is considered to be the primitive cell form from which other classes of hemocytes evolved. As suggested by their name, these cells are distinguished by the presence of numerous cytoplasmic granules. Insect granulocytes are generally spherical or oval and vary in size. The granules also differ in size and in shape and can be electron-dense or electron-lucent. Numerous ribosomes and polysomes, Golgi bodies, endoplasmic reticulum, lysosomes, and microtubules also are found in the GR cytoplasm. The nucleus varies in size and is usually centrally located. The plasmatocytes are polymorphic and are round, amoeboid, spindle, or leaf-shaped. The cytoplasm may contain electron-dense granules and, as in the GRs, is rich in organelles, ribosomes, and microtubules.

The Phagocytic Process

Phagocytosis consists of several discrete steps which include chemotaxis, activation of receptors on the phagocyte plasma membrane, attachment of the microorganism to the membrane receptors, and engulfment by extensions of the phagocyte (pseudopodia) so that the microbe becomes encased in a vacuole, i.e., a phagosome. Events which follow the formation of the phagosome usually result in the killing and digestion of invading microorganisms. Chemotaxis in invertebrates in several respects parallel those pathways operating in the vertebrate system. For example, hemocytes from some invertebrates (e.g., the oyster or the clam) are attracted only to live bacterial (*E. coli*) cells, thus demonstrating that migration of the blood cells is induced by chemo-attractants that are secreted by the microbial cells. Mollusc hemocytes have been found to migrate to *N*-formylmethionyl peptides, the bacterial metabolites that are chemotactic for vertebrate neutrophils. Among this group of peptides, formyl-methionyl-leucyl-phenylalanine (fMLF) is the strongest attractant for neutrophils. It also affects migration of the clam hemocytes and is chemokinetic, thus affecting speed and/or turning maneuvers for randomly moving *Mytilus edulis* (mollusk) hemocytes. As in vertebrates, microorganisms other than bacteria have been observed to be chemotactic for invertebrate hemocytes. Invertebrate phagocytes are comparable to those of vertebrates in that they require a functional cytoskeleton in order to be mobile. Toxic fungal metabolites, such as cyclic peptides, are known to inhibit chemotactic and chemokinetic response.

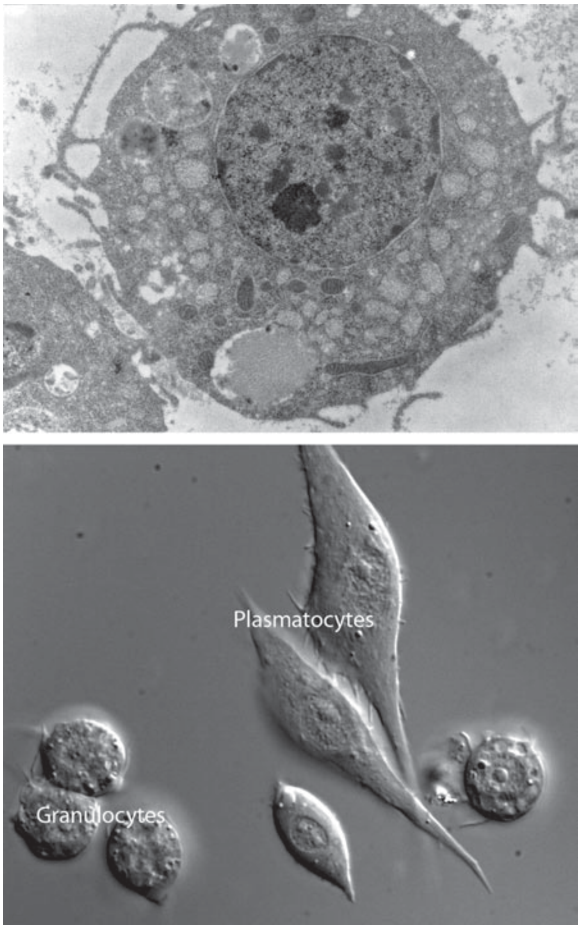
In insects and other invertebrates, the aggregation of hemocytes around infectious propagules (i.e., nodulation, encapsulation), as in the generation of granulomas in vertebrates, requires intervention by chemotactic factors. The cytokines and neuropeptides and the activities of eicasonoid-type signaling molecules are likely involved in the nodulation and phenoloxidase cascade in some insects. There are chemo-attractants released during activation of the cascade that facilitate hemocyte recruitment. Prophenoloxidase and phenoloxidase form a complex with the IL-1-like molecules in *Manduca*. When phenoloxidase is deposited on foreign material subsequent to activation of the ProPO cascade, the IL-1 molecules become localized and, as a result, other chemo-attractants as well as hemocytes are directed to an infection site.

Cell Surface Receptors and Ligands

The attachment step in the phagocytic process involves the binding of microbial cells to phagocytic cell surfaces. Divalent cations are required for phagocytosis and may be involved in the initiation of binding via electrostatic forces as well as in the receptor-mediated consolidation of attachment which follows. Lectin-mediated attachment, which involves the interaction between microbial surface oligosaccharides and receptors with lectin or lectin-like properties is often calcium-dependent. Phagocytosis resulting from lectin-carbohydrate attachment mechanisms is termed lectinophagocytosis. This process does not require opsonization of microorganisms prior to attachment to phagocyte surfaces. Opsonization involves the coating of foreign particles by host serum components (e.g., humoral lectins, immunoglobulins, or complement) so that they become better targets for phagocytic cells. Opsonin-mediated phagocytosis is called opsonophagocytosis, and this process, since it often requires the presence of IgG or complement, is probably more advanced in evolutionary terms than non-opsonin-mediated mechanisms such as lectinophagocytosis.

In invertebrates, the physicochemical aspects of attachment have been characterized quite extensively, often with respect to surface charges on foreign particles that are targeted for encapsulation by insect hemocytes. However, very little is known about the specific plasma membrane receptors that mediate microbial attachment to invertebrate phagocytes, especially as compared to the information available on vertebrate leukocyte receptor biology. The binding patterns of monoclonal antibodies produced against insect hemocytes suggest that certain epitope binding sites function in recognition of and attachment to microorganisms. In the waxmoth *Galleria mellonella*, monoclonal antibodies bound to a 90 kDa protein antigen on granulocytes reduced the phagocytic ability of these hemocytes. A number of studies have utilized both exogenous (plant) and purified endogenous lectins with different sugar specificities to probe the surface distribution of specific carbohydrate residues on invertebrate hemocytes. These lectin binding sites represent glycosolated protein and lipoprotein receptor molecules that function during non-opsonin-mediated lectinophagocytosis or during opsonophagocytosis of microbes coated with exogenous lectins. In some insects, hemocyte lectin binding patterns correlate to the immune capabilities of these cells. For example, binding patterns of wheat germ agglutinin (WGA)-FITC conjugates to *Aedes* or *Drosophila* hemocytes coincide with immunocompetence, but it is not known if the WGA-binding epitopes are the same as those that recognize and attach to surface components on parasitic organisms. In other insects, lectin binding sites visualized on hemocyte surfaces appear to represent functional microbial recognition and attachment sites. For example, a galactose-specific lectin purified from *Spodoptera exigua* (beet armyworm) hemolymph specifically labels a plasma membrane component(s) only on granulocyte-type hemocytes. Granulocytes, in turn, are the only hemocytes involved in recognition, attachment, and phagocytosis of certain fungal cells. Most importantly, these fungal cells must be opsonized with the lectin in order to elicit cellular response. Granulocytes from *S. exigua* also are labeled by some exogenous plant lectins, and these too enhance binding if used to coat selected target particles (Fig. 4).

Lectins are integral components of the invertebrate hemocyte membranes. These lectins function as pattern recognition molecules during



Innate Immunity, Figure 4 Granulocytes: (*above*) Transmission electron micrograph of a granulocyte. The cell contains a centrally located nucleus and is characterized by the presence of a number of morphologically diverse granules. (*below*) Differential interference contrast micrograph of insect hemolymph showing round granulocytes and spindle-shaped plasmatocytes containing an elongate nucleus and numerous mitochondria.

non-opsonin-mediated phagocytosis and thus are comparable to mannose receptors and to integrin receptors that have lectin domains in vertebrates. There are integral hemocyte membrane receptors that cannot be classified as lectins which mediate phagocytic activities in invertebrates. These include adhesion molecules comparable to the integrins which, in vertebrates, have dual functions in cell-cell adhesion and in nonself recognition. In *Drosophila*, a 68 kDa membrane protein (croquemort) expressed in embryonic macrophages is a member of the CD36 type superfamily of membrane receptors which, in vertebrates, serves in both cell adhesion and in nonself recognition.

A second membrane receptor expressed in embryonic hemocytes from *Drosophila* is a scavenger-type molecule referred to as DSR-C1 (*Drosophila* scavenger receptor, class C). Class A and B scavenger receptors (SR-A and SR-B) have been identified in vertebrate systems. Mammalian SR-A is macrophage-specific and binds to a wide variety of polyanionic ligands. DSR-C1 has similar binding specificities, but its protein sequence differs from the SR-A and SR-B sequences. The insect receptor is a multidomain protein having the polyspecificity necessary for the self versus nonself discrimination mechanisms that operate during innate immune response in both vertebrates and invertebrates. Scavenger receptors therefore function in the recognition and phagocytosis of a variety of different microorganisms as well as in the clearance of damaged or dead self tissues and cells, and as adhesion molecules during development, where they interact with other cells or with ECM-type components.

Immunoglobulin-like Molecules and Humoral Lectins in Insects

Pathogens invading invertebrate organisms often require opsonization before they can be recognized by specific receptors on phagocytic cells. In insects, there are several different classes of molecules which are opsonic. These include humoral lectins, lectin-like agglutinin molecules, and products of the prophenoloxidase (proPO) cascade system. The multifunctional proPO cascade is comparable to the vertebrate complement system in a number of ways. Both systems generate opsonic intermediates that assist in the initial recognition and attachment phases of phagocytosis.

The insect humoral as well as those from other invertebrates function in ways not necessarily related to host defense. These include activities associated with metamorphosis, such as the scavenging and removal of cells and tissue fragments during molting and at pupation. In addition, they aid in regulating tissue growth and differentiation, act as cell-to-cell adhesion molecules, and as transport or storage molecules for sugars. With respect to immune defense, invertebrate humoral lectins can function as opsonins and as agglutinins, causing the formation of clumps of microbial cells (e.g., bacteria) or parasites (trypanosomes), both of which can be more easily phagocytosed or encapsulated than individual cells. A lectin (M13) from *Manduca* initiates hemocyte coagulation. Since coagulation and the proPO cascade are interactive processes, humoral lectins and proPO components must also be interactive, functioning interdependently rather than as separate entities in the immune defense system. It has been reported that insect lectins have binding sites other than those for their specific carbohydrates, and that these alternative sites are involved in the activation of the proPO cascade. For example, several lectins from *Blaberus discoidalis* (cockroach) serum have been observed to activate the proPO system, even in the presence of carbohydrates for which they have a known affinity. Thus, insect lectins may activate proPO in much the same manner that MBP stimulates the complement system in mammals. In addition, the *B. discoidalis* lectins may regulate the proPO cascade by affecting serine protease and/or protease inhibitor activities along the chain. The initial regulatory step involves the binding of the lectin(s) to specific glycoprotein receptors on hemocyte membranes. Evidence from earlier studies already has shown that these (i.e., sugar residues specific for the *B. discoidalis* lectins) are displayed on the hemocyte membranes. The relationship between the proPO system and humoral lectins is probably less complicated in some other insects. For example, it is reported that hemagglutinin(s) in the hemocoels of *Anopheles quadrimaculatus* binds to carbohydrates on the surfaces of *Brugia malayi* filarial parasites. The coated filarial parasites are then recognized as nonself, resulting in activation of the proPO cascade. The nonself display is due to the bound hemagglutinin moieties presenting a configuration different from the unbound, endogenous form.

Hemolin has been isolated from the hemolymph of the moth *Hyalophora cecropia* and the tobacco hornworm *Manduca sexta*. It is a 48 kDa protein made up of four C2-type Ig domains; C2 domains are present in many cell adhesion molecules and may best represent the prototypical Ig domains. Hemolin is closely related to the other insect IgSF molecules, i.e., amalgam, fasciclin II, and to the neural cell adhesion protein neuroglian, with which it shares approximately 38% homology. Hemolin is present in low levels in naïve insects, and these levels increase significantly upon challenge with gram negative or gram positive bacteria or with bacterial cell wall components. The protein is encoded by a single gene and is synthesized in the fat body and hemocytes. Induction is rapid, with increases in levels of hemolin mRNA appearing in the fat body within 1 h after injection of bacteria. Thus far, hemolin is the only invertebrate IgSF member found that can be up-regulated and released upon infection. Hemolin has been observed to bind to fat body, Malpighian tubules, and hemocyte surfaces; thus, it may serve to recruit hemocytes to these tissues much like the cell adhesion molecules that regulate leukocyte adhesion to endothelial cells and ECM components during inflammation in vertebrates (e.g., selectins).

With respect to its role in the insect immune system, hemolin binds to hemocyte membranes, thus preventing hemocyte aggregation and adhesion of these cells to other surfaces. Hemolin may trigger the release of sessile immunocompetent hemocytes into the hemocoel during infection and/or prevent excessive formation of hemocytes into nodules so that these aggregates do not become large enough to deplete the supply of circulating hemocytes or to interfere with circulation. In addition, hemolin binds to bacterial (e.g., *E. coli*) surfaces; this association is mediated by a specific molecule on the microbial surface. Hemolin is not bactericidal, but functions as an opsonin so that when it coats the bacteria, it makes them better targets for hemocytes participating in cellular immune response. Opsonization is, of course, a major function of antibody-type IgSF members in vertebrates. Hemolin stimulates the phagocytosis via a pathway that involves protein kinase C activation and protein tyrosine phosphorylation, which indicates that its role in phagocytosis is as a signal transduction molecule. This function may be a result of the structural relatedness of hemolin to the IgSF cell adhesion factors, which can also participate in intracellular signaling processes. So far, no variability has been observed in the invertebrate IgSF members. In vertebrates, sequence variability resulting from the rearrangement of genes coding for antibodies is a hallmark of adaptive immunity.

Among the insects, the most thoroughly described humoral lectin is *Sarcophaga* lectin from the larvae of the fleshfly *Sarcophaga peregrina*. This lectin has dual functions, operating both in immune defense and developmental processes. As mentioned above, the *Sarcophaga* lectin is a C-type lectin, specific for galactose. The native molecule (190 kDa) consists of two α and two β subunits, with molecular weights of 32 and 30 kDa, respectively. Synthesis occurs in the fat body, and both subunits are derived from the same gene. Lectin secretion into the hemolymph occurs upon injury to the body wall, indicating that protein synthesis is induced under conditions that stimulate defense activities. Other insect lectins share similarities with the well-characterized *Sarcophaga* lectin system. For example, a lectin from pupal hemolymph of the Chinese oak silk moth *Antheraea pernyi* also has dual functions, serving both in developmental and in immune defense capacities.

Fungal cell wall β-1,3 glucans and bacterial LPS are involved in activating the expression of lectin genes as well as the previously discussed AMPs. The promoter regions of the several insect opsonin genes (lectins, hemolin) have NF-κβ-like binding sequences. Many insect lectins have multiple binding specificities and thus have the potential to opsonize the surfaces of cells from a broad range of microorganisms, as compared to lectins with limited specificity. As opsonins, humoral lectins and agglutinins from insects are somewhat comparable to vertebrate immunoglobulins. Although the lectins may not be synthesized in the blood cells, as in the case of Ig production in B lymphocytes, they can be synthesized at other sites such as fat body, then sequestered from the hemolymph into the hemocytes and stored in granules. Alternatively, it has been reported that some lectins, such as those from *Bombyx* and *Leucophaea* are synthesized in the hemocytes. In any event, when the lectins are released from the hemocytes, they serve as opsonins, binding to carbohydrate moieties on either microbial cell surfaces or hemocyte plasma membranes.

The galactose-specific lectin from the larval beet army worm *Spodoptera exigua* is synthesized in the fat body and, as evidenced by immunocytochemical localization, is stored in the granular hemocytes. This lectin can be visualized on the granulocyte surface, and there is strong evidence suggesting that it is closely associated with cytoskeletal elements (e.g., actin) in the granulocytes either directly as a plasma membrane receptor or indirectly if bound to another membrane receptor as an opsonin. The cytoskeleton is an essential part of the phagocytic process. As a hemocyte opsonin or a receptor, the beet armyworm lectin remains evenly distributed over the granuloctye surface at cold temperatures or in the presence of cytoskeletal inhibitors such as cytochalasin. However, at normal temperatures, the membrane lectin is highly mobile and aggregates, via cytoskeletal activity, at coated pits, where it is rapidly endocytosed. This lectin is a microbial opsonin binding to galactose residues on the surfaces of some microorganisms and mediating their attachment to granulocytes at significantly higher rates than those of non-opsonized target cells.

In addition to the beet armyworm lectin, several other humoral lectins from insects, including those from *Melanoplus differentialis* (grasshopper), *Locusta migratoria*, and *Periplaneta*, have been shown to have opsonic properties. The 30 kDa lectin from *Periplaneta americana* recognizes 2-keto-3-deoxyoctonate in bacterial LPS. This protein, as well as the 28 kDa LPS-binding protein from this insect, participates in the clearing of bacteria from abdominal cavities. It is speculated that a peptidoglycan-binding protein from *Bombyx* serves as an opsonin for gram positive bacteria. The attachment of such opsonized cells to specific receptors on immunocompetent hemocytes likely stimulates the proPO cascade. Thus, LPS and β-1,3 glucan-binding molecules, some of which may be lectin or lectin-like proteins, could constitute a functional link between the humoral opsonins and the proPO cascade. For example, a β-1,3 glucan-specific lectin on *Galleria mellonella* (wax moth) plasmatocyte membranes may trigger proPO activities as it binds to soluble β-1,3 glucans in the hemolymph or to these components on fungal cell wall surfaces. It is important to mention that the proPO pathway, no matter how it is activated, can generate additional opsonins, which allows for further recognition of nonself material. In addition to producing opsonins, the proPO system plays a major role in a number of other invertebrate immune defense activities.

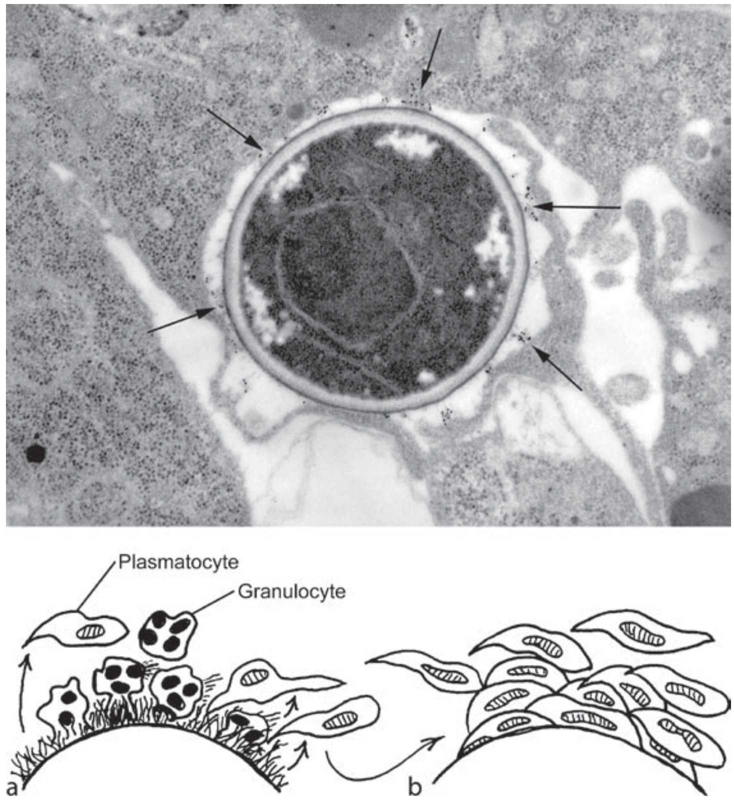
Prophenoloxidase (proPo) Cascade Systems

Phenoloxidases, the enzymes involved in production of melanin pigments, are widespread among microorganisms, plants, and animals. In arthropods, melanin is formed during hardening and darkening of the cuticle and in response to cuticular wounding and invasion of foreign matter into the hemocoel. Phenoloxidases occur as inactive precursors, termed the prophenoloxidases. Prophenoloxidases are activated by a proteolytic cascade system referred to as the proPO-system. Activation of the cascade produces melanin and stimulates cellular defense activities including hemocyte attachment, spreading and degranulation, phagocytosis, nodule formation and encapsulation, and hemocyte locomotion. The cascade is activated by microbial cell wall components such as bacterial LPS and peptidoglycans as well as the fungal β-1,3-glucans. Insect hemolymph prophenoloxidases share many similarities. The cDNA clone for *Manduca* proPO encodes for a 80 kDa polypeptide, and *Bombyx* and *Galleria* proPOs also have subunits in this molecular weight range. The amino acid compositions of the proPOs from the latter two insects are very similar, and a monospecific antibody against the *Galleria* protein cross-reacts with *Manduca* proPO. The proPO from *Bombyx* has been localized in the oenocytoids and plasmatocytes, but not in granulocytes. The cDNAs of this enzyme lack signal peptide sequences, thus indicating that mature proPO is stored in hemocytes. Prophenoloxidase is synthesized in hemocytes, and then released into the hemolymph when insects are challenged (e.g., bled).

Proteins that bind to the microbial cell wall elicitors of proPO have been isolated from the plasma of both insects and crustaceans. A 62 kDa and a 90 kDa β-1,3-glucan binding proteins (BGBP) have been isolated from *B. mori* and from *B. craniifer* plasma, respectively, The silkworm BGBP has been localized in granules, of both granulocytes and spherulocytes, but not in other hemocyte types, fat body, or integument BGBPs appear to be highly specific for glucans with β-1,3-glycosidic linkages; they do not bind to other carbohydrates such as mannans and cellulose. BGBPs from both insects and crustaceans enhance β-1,3-glucan activation of the proPO system. In insects, it has been suggested that the serine protease enzymes are activated when β-1,3-glucans bind to BGBPs due to conformational changes in the BGBPs. It also has been proposed that the BGBP-β-1,3-glucan complexes bind to specific receptors on granulocyte (e.g., *B. mori*) membranes, causing degranulation and release of more BGBP stored in the granules. This newly released protein then concentrates around invading fungal cells and triggers the proPO cascade in the hemolymph. When the cascade is triggered, other molecules, including opsonins and chemokinetic factors, are produced and stimulate additional defense-related activities such as phagocytosis and encapsulation (Fig. 5).

ProPO systems are normally triggered when specific elicitor molecules are present. However, if extensive lysis of hemocytes containing proPO components occurs, there are inhibitory molecules in the plasma that prevent the cascade process. These include protease inhibitors such as the trypsin inhibitors found in the hemolymph of some insects. Significantly, both the proPO cascade in insects are analogous to the vertebrate complement pathways not only with respect to the protease inhibitory functions but in other ways as well. These systems activated lectins or lectin-like molecules binding to microbial cell wall components and involve the limited proteolytic activities of serine-type proteases that are regulated by enzyme inhibitors.

Although the complement-like activities generated during the proPO cascade contribute significantly to immune defense in invertebrates, the melanin produced as an end-product of the cascade is also important. Phenoloxidase, the enzyme which catalyzes the synthesis of melanin, self-aggregates and associates with other plasma macromolecules (e.g., proteins) and with surface molecules on foreign particles such as microbial cell wall polysaccharides. Phenoloxidase oxidizes phenolic substrates (e.g., tyrosine) to generate intermediate quinones which then form the melanins. Thus, when phenoloxidase is deposited on microbial surfaces it can produce melanotic capsules capable of physically restraining growth and movement of the microorganisms and of isolating them from host tissues. In addition, both the quinones and melanin can be toxic to microorganisms. Studies also have shown that the phenoloxidase-activated melanization reaction in *Heliothis virescens* (tobacco budworm) larval hemolymph is the basis for the antiviral activity observed in this serum. The hemolymph has no antiviral activity when phenoloxidase activity is inhibited by the addition of phenylthiourea, which acts by combining with copper in the enzyme.



Innate Immunity, Figure 5 **Phagocytosis and encapsulation: (*above*) Transmission electron micrograph showing phagocytic uptake of a blastospore of the fungus *Paecilomyces farinosus* by granulocytes. The fungal cells were first opsonized with the galactose-specific lectin purified from the insect; this coating was then visualized by labeling with a lectin-specific monoclonal antibody followed by an anti-IgG-gold secondary antibody (see *arrows*). The lectin-antibody complex becomes detached from the fungal surface and is endocytosed by the phagocytic hemocyte via a coated pit mechanism. (*below*) Diagrammatic representation of the formation of a cellular capsule around a pathogen invading a host insect. When the pathogen enters the insect hemocoel, the granulocytes discharge their contents onto its surface. The discharged contents include factors that recruit other cells such as plasmatocytes to the microbe, and these cells may then aggregate to form the capsule. The hemocytes deposited directly on the surface of the pathogen become tightly appressed, whereas the more distal cells are loosely aggregated and can even separate from the capsule.**

Cellular Encapsulation

Cellular encapsulation occurs in arthropods when a foreign object is too large to be phagocytosed and thus becomes surrounded by one or more layers of hemocytes. This process is less specific than humoral encapsulation in that it is provoked by a wider variety of organic and inorganic substances. Tissue grafts, parasitoid eggs, various bacteria, fungi, protozoans, nematodes, filarial worms, glass, nylon, plastic resins, gold colloids, and paraffin, among other things, have been reported to elicit cellular encapsulation. Initially, it was believed that elicitation of cellular encapsulation in insects depends upon physicochemical properties, especially the charge on the surfaces of foreign objects. Therefore, since the basement membranes of insect (self) tissues do not stimulate hemocyte response and are negatively charged, it was generally accepted that only positively charged foreign objects would be interpreted as nonself and encapsulated. However, in some insects encapsulation of negatively charged particles does occur. For example, even though *Schistocera* (locust) hemocytes do not respond to negatively charged Sepharose beads, *Periplaneta* (cockroach) hemocytes encapsulate these beads as well as those with positively charged and neutral surfaces. In the soybean looper *Pseudoplusia includens* larvae, both negatively charged and positively charged particles are encapsulated. The rate of encapsulation of negatively charged Sephadex beads is slower than that for positively charged Dowex beads but, after 24 h, most beads from both of these types are encapsulated. Interestingly, in this insect only a small percentage of DEAE Sepharose beads, which are positively charged, are encapsulated even after 24 h. Thus, although physicochemical properties do mediate the rapid response of hemocytes to some particles (the Dowex beads), other particles (e.g., the negatively charged Sephadex beads) may require surface modification for hemocyte recognition.

The humoral encapsulation promotion factors that coat foreign objects are homologous to certain basement membrane (ECM) proteins. Sepharose beads coated with Arginine-Glycine-Aspartate (RGD) peptide fragments are encapsulated within 3 h after injection into *Pseudoplusia* larvae, whereas those coated with RGE (E = glutamic acid, the negative control) are not encapsulated until 24 h later. In addition, encapsulation of the RGD beads is inhibited only by soluble RGD. RGD-containing proteins, present in vertebrate ECM components such as laminin, serve as cell recognition adhesion sites for integrin-type receptors on membranes of cells that bind to the ECM. It is likely that capsule formation by plasmatocytes in *Pseudoplusia* is an RGD-dependent cell adhesion mechanism. ECM-like RGD-containing proteins may be released from granular hemocytes and coat foreign particles that are recognized by integrin-like receptors on the plasmatocyte membranes. Results from several studies show that ECM-type proteins are synthesized in and released from insect hemocytes. Monoclonal antibodies to hemocyte antigens in *Periplaneta* cross-react with basement membranes (ECM) of tissues lining the hemocoel and, in *Locusta*, the same antibodies that bind to basement membranes also bind to hemocyte components.

In *Pseudoplusia*, the integrin-like receptors of plasmatocytes that bind to RGD fragments on foreign particles are likely to be in an activated state, in contrast to the inactivated receptors on hemocytes from non-challenged larvae. Switching between active and inactive states explains why hemocytes do not bind to RGD molecules displayed on the basement membranes lining the hemocoel. Insect hemocytes adhere to damaged areas on basement membranes or to abnormally developing tissues, thus indicating that trauma such as wounding activates the RGD receptors, or that changes in the self-arrangement of matrix components allows hemocytes to bind by an alternative receptor mechanism. Interestingly, completed cellular capsules in some insects have an outer coating that is similar to basement membranes in ultrastructure and in staining properties. Coated capsules from one insect (*Periplaneta*), when washed and transferred to hemocoels of allogeneic or xenogeneic (*Schistocerca*) recipients, will not elicit further encapsulation, demonstrating that once a capsule is completely formed, it is interpreted as self and is no longer subject to defense processes.

Capsule formation requires the active recruitment of encapsulating hemocytes to foreign objects. In vertebrates, recruitment of phagocytes (e.g., macrophages) and the formation of granulomas around parasitic organisms are regulated by the cytokines released by the activated T-cells. There are probably similar substances that are responsible for elicitation of hemocytes during capsule formation in invertebrates. These factors attract additional granulocytes and/or other types of hemocytes (plasmatocytes, lamellocytes), which interact with surface components on the nonself and with each other to form capsules. As mentioned earlier, components of the proPO system could function as signaling molecules to promote encapsulation. Recently, a 400 kDa complex consisting in part of prophenoloxidase, phenoloxidase, and an interleukin 1 (cytokine-like signal molecule) was isolated from *Manduca* hemolymph. Likewise, proPO cascade factors such as the 76 kDa protein (peroxinectin) from crayfish and the 90 kDa protein from *Blaberus*, when released from granular cells upon activation, play roles in signaling. These components, as well as other cascade molecules, may also be opsonic, coating foreign particles so that recruited hemocytes can recognize and bind to them. In some insects the initial recognition, opsonization, and recruitment processes appear to be a passive phase of encapsulation. This initial phase proceeds even during metabolic inhibition, whereas a second phase, the consolidation of hemocytes around target objects, is active and cannot take place under inhibitory conditions (e.g., low temperatures). In addition, the phases in capsule formation can be morphologically as well as physiologically distinct from one another. For example, in the hemocoel of *Anopheles* mosquitoes, humoral encapsulation of microfilariae begins as early as 10 min after a blood meal, followed by cellular encapsulation within 2 h. After 24–48 h, the melanized humoral capsules become surrounded by a single layer of two or three plasmatocytes; these completed capsules isolate and destroy the microfilariae. The formation of a melanized humoral capsule before initiation of the cellular encapsulation phase confirms that components of the proPO system deposited on foreign particles serve as hemocytic recruitment and/or adhesion factors during organization of the cellular layer(s).

In many insects the encapsulation response results in the production of a multilayered structure. In addition, the total encapsulation process may not always occur in well-defined non-cellular and cellular phases. For example, in *Galleria mellonella* larvae implanted with nerve tissue from *Schistocerca*, granulocytes making contact with the transplants immediately discharge their contents onto the nonself surfaces. After 20 min, plasmatocytes, elicited by the material from the lysed granulocytes, attach to the transplants at sites of lysis. The plasmatocytes then form a multilayered sheath. Alternatively, *Periplaneta* challenged with tissue implants, produces a capsule composed of three distinct regions of granulocyte. The inner cellular region next to the debris layer (lysed granulocytes) exhibits up to seven layers of necrotic hemocytes which, in the completed capsule, forms a continuous syncytium-like giant cell mass with no delineating plasma membranes. The second region of the cellular capsule consists of 10–12 layers of flattened, necrotic cells which are not as compressed as those in the first layer and which have intact plasma membranes. Cells near the periphery of this region show less degradation than cells nearer to the transplant. The third and outer region of the capsule consists of three or four layers of loosely aggregated, normal hemocytes. There is little melanization of capsule products in this system. Likewise, in beetle (*Diabrotica*) larvae, capsules are composed of three layers of hemocytes overlaying an inner layer of material from cells that have lysed onto the target (e.g., nematode) surfaces. Unlike the encapsulation process in *Periplaneta*, however, this layer becomes melanized, then is covered by a layer of necrotic, pigmented hemocytes. The middle layer consists of extremely flattened hemocytes, and the third, outer region is composed of a layer of loosely attached hemocytes. Syncytia do not form in these capsules.

Cellular capsule formation varies depending upon the host insect and the nature of the foreign object to be encapsulated. It is suggested that the surfaces eliciting capsule formation stimulate hemocytes to different degrees, and that the degree of stimulation can determine the number of cells recruited to a target surface and the thickness of the resulting capsule. Also, factors (e.g., cytokine-type molecules) which regulate the activities of the elicitors (other cytokines) released during hemocytic stimulation serve to control the number of recruited cells. A hemocyte aggregation inhibitor protein (HAIP) from *Manduca* hemolymph modulate the adhesive properties of hemocytes and thus act as regulatory factors during encapsulation. Capsule formation is a physically self-limiting process. When the innermost layers of the capsule containing the recruitment factors become covered by other layers of hemocytes, the factors no longer diffuse to the outer regions of the capsule to recruit more cells. This stimulus gradient from the center to the periphery of the capsule results in a loose aggregation of the hemocytes in the outer region. Some of these cells detach from the capsule surface and return to circulation in the hemolymph.

The association between melanization and encapsulation varies. If melanization occurs, it begins during the early phases of capsule formation, as described above in *Anopheles* and *Diabrotica*. Melanization begins on the surface of the foreign object where hemocyte lysis products are deposited, and it sometimes expands from this inner region to the middle and outer capsule layers. Cross-linking of proteins occurs during melanization, and these interactions can function to strengthen and harden the capsule. It is believed that in some *Drosophila* larvae, darkening of capsules around parasitoid eggs is due to hemocyte necrosis rather than to melanin deposits in the outer layers. Melanization occurs only during the early stages of capsule formation, i.e., during opsonization of the egg surface and activation and recruitment of hemocytes. The toxic effects (e.g., synthesis of free radicals) of melanin production on the egg surface kill the parasitoid embryo and cause necrosis of the insect hemocytes.

There are instances in which phenoloxidase activity and melanization are not involved in encapsulation as illustrated in *Drosophila melanogaster*. The prophenoloxidases necessary for melanin formation are released onto the parasitoid (*Leptopilina boulardi*) egg surfaces from crystal cells that are hemocytes with paracrystalline inclusions containing the prophenoloxidases. Mutant *D. melanogaster* larvae possessing disfunctional crystal cells utilize lamellocytes to recognize and encapsidate nonself. Unlike the capsules in normal larvae, those in the mutants do not darken or harden. Lamellocytes have sticky surfaces and can mediate cell-to-cell adhesion without the input of the opsonic components of the proPO system. In other experiments designed to evaluate the role of prophenoloxidases during encapsulation, it was found that *S. gregaria* hemocytes, which normally fail to encapsulate uncoated, negatively charged beads, still do not respond to these particles even if they are precoated with a lysate known to contain activated phenoloxidase. In summary, a central, well-defined role for proPO cascade and melanization reactions in the immune encapsulation process in insects has not yet been characterized (Table 3).

Nodulation

Nodulation is a defense reaction in arthropods that occurs in response to the invasion of the hemocoel by large numbers of particles that cannot be removed by phagocytosis alone. Nodules can form around various types of abiotic and biotic materials, including ink and dye particles, red blood cells, bacteria, fungi, and protozoans. In addition, soluble molecules such as endotoxins from bacterial cell walls and β-1,3-glucans from fungal walls can stimulate nodule production. Nodulation, which involves the trapping and isolation of foreign particles within hemocytic aggregates, may be compared to granuloma or giant cell formation by macrophages in vertebrate systems. Nodules and cellular capsules can form simultaneously in an insect and are often difficult to distinguish from one another.

A detailed study of the nodulation process has been carried out in *Galleria mellonella* and *Pieris brassicae* larvae challenged with various bacteria. In *G. mellonella*, the process takes place in two phases. The first phase begins 1 min after injection. Granulocytes contact bacteria and degranulate so that both the cells and other reactive hemocytes become trapped in a mass of coagulum. These aggregates then attach to

Innate Immunity, Table 3 Selected insect hemolymph lectins[a] and lectin-like hemagglutinins

Source insect	Carbohydrate specificity	Probable function(s), if proposed
Anopheles quadrimaculatus[b]	Gluconic acid, galacturonic acid, glucosamine, mannosamine, NeuNAc*	Bind to carbohydrates on sheaths of microfilarial parasites, resulting in activation of proPO cascade
Antheraea pernyi	Gal, GalNAc	Immune defense, development and morphogenesis
Anticarsia gemmatalis	Gal, Lac, fucose, NeuNAc	Immune defense
Blaberus discoidalis[b]	Glc, man, GlcNAc, β-1, 3-glucan	proPO activation
Bombyx mori (Hemocytin, C-type lectin)	D-man, GalNAc, D-maltose	Immune defense, LPS binding, metamorphosis, scavenging, coagulation
Extatasoma tiaratum	Gal, Lac, α-MeGal, GalNAc, raffinose	Opsonin
Hyalphora cecropia[b]	Gal, GalNAc	
Hyphantria cunea	Gal	LPS binding C-type lectin
Leptinotarsa decemlineata	Heparin, mucin, hexosamines	
Leucophaea maderae[b]		
Locusta migratoria	α-Gal pyranosides, fucose	Opsonin
Manduca sexta (immunolectin-2)	Gal	LPS binding C-type lectin
Melanoplus differentialis	Gal, Glc	Opsonin
Periplanta americana (30 kDa lectin)	2-keto-3-deoxyoctonate	Opsonin, proPO activation
Rhodnius prolixus[b]	GalNAc, Gal, α-MeMan	Immune defense
Sarcophaga peregrina	Gal, Lac	Metamorphosis, scavenging, opsonin, activation of immune defense
Schistocerca gregaria	Sucrose, fetuin, l-Rhamnose	Immune defense
Spodoptera exigua	Gal, Lac	Opsonin

[a]Represents a partial list of insect humoral lectins
[b]Indicates the presence of multiple lectins or hemagglutinins
*Carbohydrate abbreviations: GalNAc = N-acetyl-D-galatosamine; NeuNAc = N-acetyl neuraminic acid; GlcNac = N-acetyl-D-glucosamine; Gal = galactose; Lac = lactose; Glc = glucose; man = mannose; α-MeGal = α-methyl galactose; α-MeMan = α-methyl mannose

various tissues such as fat body or Malpighian tubules. By 1 h post-injection melanization begins within the aggregates, and the mass of cells becomes compacted. At 1–6 h, the second phase begins with the attachment of plasmatocytes to the melanized aggregate. Plasmatocytes form a multicellular sheath with an inner region of flattened, degenerating cells, a middle region of extremely flattened cells with well-defined cell junctions (desmosomes) and numerous microtubules, and an outer region of recently attached plasmatocytes. Thus, after 24 h, the bacteria are surrounded by a central area of melanized, necrotic hemocytes enclosed in a plasmatocyte sheath. In other insects, such as the beetle *Tenebrio molitor*, attaching plasmatocytes contain bacteria.

The extent of nodule formation varies depending upon the insect and/or the nature of the foreign substance introduced into the hemocoel. In both *Schistocerca gregaria* and *Periplaneta americana*, large nodules (>100 μm in diameter) form in response to the presence of fungal spores, whereas medium to small (<40 μm) nodules form in the presence of soluble molecules such as LPS. Nodulation is not always effective in eliminating potentially pathogenic organisms and in preventing infection. In *G. mellonella*, nodules are formed around pathogenic *Bacillus cereus*. However, *B. cereus* overcomes this defense mechanism either by the active escape of vegetative cells (e.g., by digestion of nodule components) or by the germination of endospores, which allows the bacteria to break out of the nodule. Hyphae of some entomopathogenic fungi, which often elicit nodulation, can elongate, break free from the hemocyte aggregates, and establish successful infections. Pathogenic microbes may not elicit nodule formation in host insects. For example, nodule production does not occur in *G. mellonella* or *P. brassicae* injected with pathogenic *Staphylococcus aureus* bacteria or in *Lymantria dispar* (gypsy moth) larvae challenged with highly virulent *Xenorhabdus luminescens* bacteria; however, nodules do form in this insect in response to the non-pathogenic bacteria (*Bacillus subtilis*). Likewise, there is rapid nodule development around non-pathogenic *Candida albicans* yeast cells injected into *Spodoptera exigua* (beet armyworm) larvae, but yeast-like hyphal bodies of the fungal pathogen *Nomuraea rileyi* do not elicit any immune response. *Trypanosoma cruzi*, which is not pathogenic to the vector reduviid *Rhodnius prolixus*, is rapidly cleared from this insect via nodule formation, but hemocyte aggregation is delayed in response to pathogenic *T. rangeli* cells.

The destruction of microorganisms trapped in nodules may be due to the toxins (e.g., quinones) generated during melanization. Activities of the proPO cascade preceding melanin production appear to be closely linked to nodule formation. For example, it has been shown that in locusts, soluble LPS which can elicit a high degree of nodulation also induces greater levels of phenoloxidase activity in whole blood homogenates than does LPS from a different bacterium which elicits little or no nodule formation. In addition, it has been suggested that in *Ceratitis capitata* (medfly) larvae, nodulation in response to the introduction of *E. coli* results from binding of a hemocyte protein to the bacteria, forming complexes which cross-link to hemocytes via quinone intermediates. ProPO components also may be involved in recruitment of hemocytes to nodule forming sites, as during hemocytic recruitment in the cellular encapsulation process (see previous section). During nodulation in *G. mellonella*, active recruitment of hemocytes most likely occurs during the second stage when the plasmatocytes aggregate to form the outer sheath. Plasmatocytes require stimulation by chemotactic factors that may be released by granulocytes in order to be attracted to the central region of the nodule. In addition to the proPO components mentioned above, chemotactic factors may include cytokine-type molecules as well as biogenic amines and eicosanoids.

Biogenic amines and eicosanoids are known to mediate immune response in mammals. Amines (neurohormones), which in mammals elevate cAMP levels, have been found in insect hemolymph, and amine-sensitive receptors have been identified in some insect hemocytes. Two amines, octopamine and 5-hydroxytriptamine (5-HT), have been shown to increase the survival of cockroaches (*P. americana*) challenged with *S. aureus* by enhancing phagocytic and nodulation activities. Eicosanoids are autocrine signaling molecules which enable cells to send signals to other identical cells or to themselves. They function in cell-to-cell communication during development and, in mature mammals, function in platelet aggregation as well as pain and inflammatory response mechanisms. Eicosanoids are fatty acid derivatives found in all mammalian tissues, and recently they have been identified in some insects (e.g., *M. sexta*). They are synthesized from precursors, mainly arachidonic acid, that are cleaved from plasma membrane phospholipids by phospholipases, such as the PLA_2 identified from *Manduca* hemocytes and *Bombyx* fat body. Phospholipases, including PLA_2, have been found in various pathogens (bacteria, protozoans, fungi), where they may function as virulence factors since they have the potential to damage host cells and tissuues. In mammals, eicosanoids are continuously synthesized, released from the cell, and then broken down by enzymes in the extracellular fluid. There are four major classes of eicosanoids synthesized via one of two specific biosynthetic pathways. In insects, it has been found that nodule formation in response to bacterial infection is strongly reduced in larvae when eicosanoid synthesis is inhibited. Such inhibition can be effected by injecting test insects with the phospholipase A_2 inhibitor dexamethasone or with specific cyclooxygenase or lipoxygenase inhibitors. Therefore, since nodulation is affected by inhibiting eicosanoid production at various stages along its biosynthetic pathway, it is likely that several different kinds of these signaling molecules are involved in the numerous steps leading to complete nodule formation.

Clotting

Although the active recruitment of cells may not be necessary during the first stage of nodulation in *G. mellonella*, another mechanism within the immune defense system, clotting, is important at this time. The formation of sticky coagulum upon activation of the granulocytes (degranulation) traps foreign particles. Clotting is important in wound sealing in insects and in other invertebrates. As mentioned earlier (see proPO section) clotting or coagulation can result from a cascade-type reaction, as described in detail for the mechanism that occurs in *Limulus*. However, a cascade system has not yet been fully described in insects.

Clotting in insects has been characterized as pattern II-type coagulation. In this process, long strings form between the hemocytes and develop into a dense mesh which traps hemocytes and insoluble hemolymph components. The long strings develop from material extruded from granules in the hemocytes. True clots are composed of a hemocyte-derived component and a plasma coagulogen, which cross-links with the hemocyte coagulogen. Evidence for the involvement of two factors in clot formation comes from studies on *Locusta migratoria* and *Leucophaea maderae* (cockroach) showing that plasma without hemocytes will not clot. Although the material from the hemocytes can gel in the absence of the plasma coagulogen, this gel differs from a clot formed by both coagulogens. The hemocyte gel is dissolved with urea and a reducing agent (DTT), whereas the clot resists this treatment.

The most likely plasma coagulogen is lipophorin, which functions in adsorption and transport of lipids as well as in clotting. Lipophorins, major components in hemolymph, are lipoproteins consisting of 30–50% lipid and 1–4% carbohydrate. The carbohydrates, usually mannose and glucosamine, are associated with the apoprotein portion of the molecule, which in turn consists of two subunits of about 250 and 80 kDa. Lipophorins from different insect orders are similar. They are synthesized in the fat body along with other hemolymph proteins. The hemocyte coagulogen is present in granules of granular-type hemocytes (granulocytes, plasmatocytes, coagulocytes). The gel formed by this coagulogen is not only sensitive to DTT, but also to proteolytic enzymes. Therefore, it must consist of at least a protein backbone with disulfide bridges and, since most hemocyte granules contain carbohydrates, it could be a glycoprotein. The hemocyte coagulogen ages within 30 min of its release from the cells and loses its clotting ability very rapidly.

In order to form a true clot, the two coagulogens must interact. They may form separate networks that interweave, but it is more likely that they form an intermolecular connection since true clots are insoluble in DTT. Antibodies to the hemocyte coagulogen inhibit binding of the gel to the plasma coagulogen. The mechanism of an intermolecular interaction in clot formation requires divalent cations (Ca^{++}), since chelating agents inhibit clotting. This strongly implies that the cross-linking of the coagulogens involves the catalytic activities of Ca^{++}-dependent enzymes (e.g., transglutaminase). It is known also that hydroxylamine inhibits clotting of the two *Leucophaea* factors, thus suggesting that as in vertebrate and crustacean systems, amino groups participate in cross-linking. In other words, interaction may occur via cross-links between free amino groups of the plasma coagulogen molecule and the hemocyte coagulogen. The acceptor residue on the hemocyte coagulogen may be similar to vertebrate fibrin or to some type of collagen moiety. In addition, it is possible that the role of lipids on the plasma coagulogen molecule (i.e., lipophorin) is to interact with hydrophobic entities of the hemocyte coagulogen molecule, thus establishing affinity between the two factors.

Many components function in the insect clotting system, but most have not been identified or well-characterized. One protein from *Manduca* hemolymph, scolexin, which appears to be involved in coagulation, has been described in detail. Scolexin is an immune protein with lectin-like properties that is induced by bacterial challenge but is not bactericidal. It concentrates in the coagulum in nodules that form around injected bacteria and thus is assumed to play a role in clotting. Scolexin is synthesized, in part, in the epidermis. It is structured from two 36 kDa subunits that have the same N-terminus. The subunits form two different charge isomers, scolexins 1 and 2, and scolexin 2 is glycosylated. The protein is larval-specific, and its synthesis declines during the fifth instar.

Phagocytosis of Nonself

For over 30 years, the most widely accepted mechanism of phagocytosis in vertebrates has been the zipper mechanism. In this model, phagocytosis of one foreign particle does not initiate the nonspecific uptake of other particles in the vicinity of the phagocyte. Instead, particles become specifically bound via their surface ligands to receptors on the phagocyte plasma membrane. Thus, as long as the entire particle is covered with the appropriate ligand (e.g., an opsonin), the receptors on the phagocyte pseudopodia sequentially bind or zipper to the ligand molecules until the entire particle is engulfed. If the target is unevenly covered with ligand moieties, then pseudopodial extension around it stops at the surface region lacking these moieties. This zipper mechanism model represents the phagocytic process that occurs when opsonized fungal cells are taken up by *S. exigua* hemocytes in monolayer experiments. The purified lectin from larval hemolymph, the ligand, bound to the walls of the fungal cells, can be visualized by TEM using gold particles. The lectin-gold conjugate binds to galactose residues in a fibrous coat on the fungal surface, then the granulocyte receptor attaches to this lectin complex. These complexes are sequestered from the pseudopodia into coated pits located along the granulocyte plasma membrane. The coated pits then form into vesicles and move via cytoskeletal activity into the cytoplasm. Actin is heavily concentrated in the pseudopodia and is likely to function not only in the formation of these structures, but also in the sequestering of the lectin complexes to the coated pits. Microtubules are more prevalent in the non-extended areas of the phagocyte and are often associated with coated pits and vesicles and sometimes with endocytosed fungal cells. In a successful phagocytic event, the pseudopodia fuse at their tips so that they completely encircle the target particle. This results in the formation of a vacuole, the phagolysosome.

The *S. exigua* phagocytic process is comparable to the zipper model that was proposed as a result of studies on vertebrates using lymphocytes coated with IgG (ligand) molecules. The lymphocytes capped the IgG, which was labeled with peroxidase, onto one small region of the plasma membrane, leaving the rest of the cell surface void of ligand molecules. Thus, the pseudopodia of the phagocytes (macrophages) could not completely surround the target lymphocytes since the IgG was not distributed evenly. The macrophage attached to the lymphocyte only at the small area where the ligand was capped. Likewise, in the insect system, fungal cells unevenly coated with the lectin are not completely engulfed by the granulocyte pseudopodia. As in the case with vertebrate cells, the coated pits and vesicles on *S. exigua* granulocytes become filled with the ligand complex, i.e., the lectin-gold complex and fibrous fungal cell wall material that has detached during sequestering.

After complete engulfment of pathogenic microorganisms by host phagocytes, the phagosome goes through a maturation process. In vertebrates, and undoubtedly in invertebrates as well, this process involves an inward (endocytosis) and outward (exocytosis) movement of various components to and from the phagosome. Maturation of phagosomes is a modification of the endocytic system that functions during pinocytosis of soluble molecules and small particles.

Receptor-mediated endocytosis has been described best in vertebrates using LDL (low density lipoprotein) as the internalized ligand. This trafficking system can be used as a model to explain the movement and processing of the *S. exigua* lectin-cell wall complex that detaches from the fungal surface and enters the granulocytes in coated pits and vesicles. These structures are so named because they are coated with clathrin, a protein that forms basket-like lattices that function in vesicle budding. Clathrin is shed from the coated vesicles before they fuse with the early endosomes. Early endosomes are acidic and separate the ligand-receptor complexes so that the receptors can be recycled back to the plasma membrane and the ligand can be carried to lysosomes. Late endosomes, which constitute an intermediate step in the trafficking process, are more acidic than early endosomes and contain lysosomal hydrolases which have been transported from the Golgi apparatus. Late endosomes actually mature into lysosomes as they reach a more acidic pH due to further fusion with Golgi-derived vesicles containing a battery of acid hydrolases.

The processing of large particles in phagosomes consists of a pathway similar to that of LDL. Phagosomal components move into the early endosomes, and molecules from the endosomes and primary lysosomes move into phagosomes. This transport of materials both into and out of the phagosome results in the formation of a phagolysosome able to fuse with secondary lysosomes (acidic late endosomes). In some cases, primary lysosomes can be identified with specific granules observed in some immunocytes, such as vertebrate neutrophils and invertebrate granulocytes. Acid hydrolases have been localized in granules in some invertebrate immunocytes, but lysosomal functions are limited to a certain group(s) of these structures. The endolysosomal pathway proposed for granular cells in this organism is very similar to the vertebrate model except that the early endosomal or prelysosomal stage may be represented by multivesicular bodies (MVBs), which also are common in some insect (*S. exigua*, *G. mellonella*) phagocytes. Granules containing acid hydrolases (primary lysosomes) also fuse with MVBs, which then mature into late MVBs capable of fusing with Golgi vesicles containing more hydrolases. Granules also can fuse with the plasma membrane to release lysozymes into the serum.

Killing of Engulfed Microorganisms

Killing of the microorganisms trapped in phagolysosomes often results from the activities of the acid hydrolases introduced into the vacuole by fusion with endosomes, granules, and Golgi vesicles. These enzymes also are necessary to digest the microbial cells even if they must be killed by another mechanism. For example, in order to kill gram positive bacteria, lysozyme hydrolyses the cross-links of peptidoglycan molecules. However, gram negative bacteria are more resistant to this enzyme because they have an additional LPS component on the outer surface. Therefore, killing these cells may require an alternative mechanism. Killing of pathogens via enzymatic activity is grouped among the oxygen-independent killing mechanisms. The acidification of the phagolysosome may be severe enough to kill some pathogens. This drop in pH occurs not only because of the presence of acid hydrolases, but also because of the production of protons by microorganisms and the active transport of hydrogen ions. Other oxygen-independent killing systems can include deprivation of iron necessary for bacterial growth. Vertebrate neutrophil granules release lactoferrin, which absorbs iron and therefore kills some bacteria. A vitamin B_{12}-binding protein also can be released from some granules, and the cationic peptides such as defensins described in relation to humoral immunity in insects are common in vertebrates as well. Defensins, in fact, may constitute up to 50% of the protein in vertebrate neutrophil granules. Serine proteases, found in both vertebrates and invertebrates, can kill a variety of different pathogens, and enzymes such as gelatinases, elastases, and collagenases also exhibit defensive activities. In addition, bacterial permeability-increasing proteins, some of which may be cationic peptides, function in all types of host organisms.

Oxygen-dependent killing mechanisms have been described for both vertebrate neutrophils and insect hemocytes. Toxic reactive oxygen intermediates (ROIs), including superoxide anions and H_2O_2, are produced during phagocytosis via a respiratory burst pathway that is stimulated by substances such as LPS, β-1,3-glucans and cytokines. In addition, the granule protein lactoferrin can be involved in limiting the formation of hydroxyl radicals that occurs in the presence of iron (Fe^{3+}). A reduction in hydroxyl radicals is believed to allow the killing of microbial cells without the concurrent destruction of host tissues. Superoxide anion generation has been detected in several invertebrates, including some insects. Relatively little is known about oxygen-dependent microbial killing mechanisms in insects. Superoxide anions have been detected in several lepidopterans (*T. ni*, *B. mori*, *Pseudaletia separata*), and there is evidence that lipophorin is involved in production of these molecules. The presence of superoxide in *P. separata* and *B. mori* hemolymph is due to the result of a process involving at least two factors. These factors have been purified from *B. mori* sera and include a low molecular weight (<5 kDa) moiety (LMF) and a high molecular weight (>100 kDa) component (HMF) which has been identified as lipophorin. A mixture of these two purified components caused a reduction of NBT which would be inhibited specifically by superoxide dismutase. It is speculated that the LMF is a substrate discharging electrons and that the lipophorin (HMF) acts as an enzyme, mediating the transfer of electrons to O_2 to form O_2^-. Reactive nitrogen intermediates (RNIs) such as nitric oxide (NO) also act as a signaling/messenger molecule and/or as a toxic antimicrobial agent. Nitric oxide synthetase (NOS) has been detected in *B. mori* fat body and Malpighian tubules, but not in hemocytes. The fat body NOS is induced by LPS, whereas Malpighian enzyme levels correlate to the life cycle and may be hormonally regulated. The expression of Malpighian NOS at the late stage of the fifth instar occurs in synchrony with increases in the activity of the *B. mori* lectin, hemocytin. Thus, both components could be significantly involved in metamorphosis and/or defense reactions.

The residual molecules produced during killing and degradation of microorganisms in phagolysosomes are usually discharged from the cells. For example, in *S. exigua*, the gold particles linked to the opsonizing lectin on blastospore cell walls cannot be degraded and are subsequently observed outside of the granulocytes several hours after the initiation of phagocytosis. In another experiment using *B. mori* hemocytes *in vitro*, it was found that LPS is released into the medium shortly after the phagocytosis of *E. coli* cells. It is assumed that the bacteria taken up by the granular cells are digested in the phagolysosomes and that the LPS residue is then excreted. More importantly, the increased levels of LPS, and perhaps other molecules released as a result of phagocytosis and degradation, strongly induce gene expression of cecropin B. This is reminiscent of the antigen-presentation process in vertebrates which serves to induce further immune response.

Microbial Evasion of Cellular Immune Response

The strategies used by various microorganisms to overcome host defense mechanisms have been described throughout the textbook. Such strategies are notable because they are included among the basic concepts of pathogenicity, and the ability of a microorganism to bypass immune response contributes to or represents the major determinant that confers pathogenicity. Cellular immune response can be avoided, depending upon the microorganism, at any of the steps along the phagocytic pathway (chemotaxis → phagolysosomal killing). Inhibition of immunocyte chemotaxis can result from the effects of bacterial (e.g., streptolysins, *Clostridium perfringens*) toxins or fungal (cytochalasins, destruxins) toxins. Other inhibitors act by interfering with the chemotaxins that stimulate phagocyte migration.

The basic physicochemical properties of both the host and pathogen cell surfaces affect defense responses during the attachment step of phagocytosis. The nature and magnitude of the surface charge on a microorganism, for example, often determines whether or not immunocyte attachment occurs (see Encapsulation section). A more specific evasion strategy is molecular mimicry, in which the parasite produces surface molecules that mimic those on host cell surfaces. The pathogen is perceived as self rather than nonself so that phagocytes do not respond. Hyphal bodies of the hyphomycete *Nomuraea rileyi* avoid *S. exigua* granulocyte attachment via molecular mimicry. Mimicry also may be a result of molecular disguise, in which the mimicking molecules expressed by the pathogen are actually encoded by genes acquired at some time from the host. For example, *Metarhizium anisopliae*, the hyphal bodies produce a collagenous coat that masks the antigenic surface epitopes. This strategy could prove to be relatively widespread once more information from molecular studies on insect pathogens becomes more available.

Another evasion method is antigenic variation. This is well-described among the trypanosomes infecting vertebrate hosts, although it is not the only evasion strategy used by this organism. In this case, the parasites display variant surface glycoproteins (VSGs). There is a sequential variation in surface coats so that even though the initial group of infecting parasites is eliminated by antibody response, parasites with variants produced later with new antigen are not recognized. Although invertebrates do not have antigen/antibody systems (adaptive immune response), variations in pathogen cell surface epitopes during the infection process occur and affect evasion of host defense. For example, *Beauveria bassiana* blastospores are phagocytosed rapidly by *S. exigua* hemocytes due to binding of the insect lectin to galactose on the fungal cell walls. However, the blastospores are not killed in the granulocytes; they survive and replicate as intracellular pathogens. When they emerge from the phagocytes, they possess little or no cell wall material and therefore have no lectin binding sites. These cells are not recognized and rapidly shift to an invasive hyphal form. In addition to a lack of lectin binding sites, it is possible that the emerging blastospores further evade granulocyte response via mimicry, since antibodies against *S. exigua* hemocytes strongly cross-react with fungal surface epitopes. Protoplasts from some Entomophthorales, like the intracellularly produced *B. bassiana* blastospores, also are able to evade insect immune response. In contrast, their walled forms elicit strong defense activities. This is due to the presence of cell wall β-1,3-glucans that stimulate the phenoloxidase cascade. Likewise, the nature of microbial cell surface components determines the effectiveness of vertebrate complement pathways.

Invertebrate phagocytes, especially those of insects, react rapidly to fungal hyphae, while showing little or no response to blastospore or yeast-like forms. This is probably due to the presence of hyphal β-1,3-glucans that activate proPO components in the same manner as for the Entomophthorales. In invertebrates, production of specific defense molecules such as the mollusk defense molecule can be down-regulated or suppressed by parasite activities. Such inhibition can occur before the microbe is engulfed and/or within the phagosome. Some yeasts are known to resist phagolysosomal digestion in vertebrate cells, and within these specialized environments, they can produce novel proteins. Some of the proteins include heat shock proteins that could interfere with the activities of host proteins (e.g., enzymes) by controlling their conformation. In addition, the levels of host-degradative components could be down-regulated in the presence of the pathogen. Such mechanisms may be involved in the *B. bassiana* – *S. exigua* system, thus enabling the blastospores to survive as intracellular parasites within the host granulocytes.

The ability of *B. bassiana* hyphae as well as hyphae from other fungi to overcome the rapid nodulation or encapsulation response elicited in many insects is due to a different mechanism than that used by the intracellularly parasitic blastospores. The hyphal cells must overcome the toxins (e.g., melanin) resulting from proPO activation and must have the mechanical strength to grow out from host cell aggregates that form the nodules or capsules. The size of these aggregates may be self-limiting (see Encapsulation) or may simply depend on the number of available hemocytes. Parasites other than fungi can escape from nodules (e.g., the microsporidian *Vairimorpha plodiae* infecting *G. mellonella* larvae). This response is advantageous to the pathogen because the nodules circulate in the hemolymph and spread the infection throughout the insect.

Returning to microbial survival strategies within the phagosome, some of the specific mechanisms by which intracellular pathogens can evade host oxygen-dependent killing have already been described. More generally, intracellular bacteria can produce catalase and/or superoxide dismutase to detoxify H_2O_2 and O_2^-, respectively. Little information is available as to how invertebrate pathogens can escape phagolysosomal activities. It is likely that similar mechanisms are used by both types of organisms. For example, *Bacillus cereus* can evade cockroach (*Leucophaea maderae*) cellular immune response by producing cytolytic phospholipase C to disrupt hemocyte membranes. In addition, molecules such as the annexins that are likely involved in membrane fusions along the endocytic pathway have been identified from invertebrates, including the insect *Drosophila*.

Summary

It is obvious that even though the immune system in insects lacks the intricate adaptive component present in the vertebrate system, it is nevertheless a complex mechanism. Insect defense against microorganisms can involve an array of different molecules, many of which must interact with each other in order to be functional. Many aspects of invertebrate immunity are not well understood, especially in comparison to vertebrate systems. For example, in insects little is known about coagulation and whether or not it is a multi-step cascade process as reported for other invertebrates. The possible function of lectins in insect defense is also not well defined and insect resistance to viral pathogens is just beginning to be characterized. There is no doubt that further research is needed in this field. It is essential to understand host-pathogen interactions for the purpose of developing bioinsecticides, as well as for defining the steps leading to the evolution of immunity in higher animals.

► Hemocytes of Insects: Their Morphology and Function

References

Agaisse H, Perrimon N (2004) The roles of JAK/STAT signaling in *Drosophila* immune responses. Immunol Rev 198:72–82

Boman HG, Faye I, Hofsten PV, Kockum K, Lee J-Y, Xanthopoulos KGZ, Bennnich H, Engstrom A, Merrifield BR, Andreu D (1986) Antibacterial immune proteins in insects – a review of some current perspectives. In: Brehelin M (ed), Immunity in invertebrates. Springer, New York, NY, pp 63–72

Evans JD, Aronstein K, Chen YP, Hetru C, Imler J-L, Jiang H, Kanost M, Thompson GJ, Zou Z, Hultmark D (2006) Immune pathways and defence mechanisms in honey bees *Apis mellifera*. Insect Mol Biol 15:645–656
Gotz P, Boman H (1985) Insect immunity. In: Kerkut GA, Gilbert LI (eds) Comprehensive insect physiology, biochemistry and pharmacology. Pergamon Press, New York, NY, pp 453–485
Gupta AP (ed) (1991) Immunology of insects and other arthropods. CRC Press, Boca Raton, FL, 508 pp
Hultmark D (2003) *Drosophila* immunity: paths and patterns. Curr Opin Immunol 15:12–19
Lemaitre B (2004) The road to toll. Nat Rev/Immunology 4:521–527
Marchalonis JJ, Schluter SF (1990) On the relevance of invertebrate recognition and defense mechanisms to the emergence of the immune response of vertebrates. Scand J Immunol 32:13–20
Pinheiro VB, Ellar DJ (2006) How to kill a mocking bug? Cell Microbiol 8:545–557
Ratcliffe N, Rowley AF (1979) Role of hemocytes in defense against biological agents. In: Gupta AP (ed) Insect hemocytes, development, forms, functions, and techniques. Cambridge University Press, New York, NY, pp 331–414

Inocelliid Snakeflies

Some members of the family Inocelliidae (order Raphidioptera).

► Snakeflies

Inocelliidae

A family of insects in the order Raphidioptera. They commonly are known as inocelliid snakeflies.

► Snakeflies

Inoculative Biological Control

Release of a biological control agent into an area where it does not occur, with the intent of establishing the population.

► Classical Biological Control

Inoculum

A small number of pests or pathogens that can lead to a greater abundance, and subsequent damage.

Inorganic

Not containing the element carbon. Usually derived from naturally occurring minerals.

Inorganic Insecticide

A category of insecticides that lack carbon, being instead of mineral origin. Typically they are crystalline, and applied as dusts or baits. Examples include cryolite, diatomaceous earth, borate, silica, and sodium fluoride. These materials vary from moderately toxic to quite toxic, and tend to be quite persistent. Their use is fairly restricted.

► Insecticides

Inornate

In ticks, this refers to the absence of a color pattern on the scutum.

Inquilines and Cleptoparasites

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Inquilines are arthropods that live in structures created by other arthropods, such as galls, burrows or nests. Generally, they are considered to do so without interfering in an important way with their hosts, or they may scavenge for a living without significantly harming their hosts. In some cases, especially in the case of social insects, inquilines may be parasitic and consume their host's food resources. When insects steal food and pillage nests of other species they are usually called cleptoparasites. Social insects such as ants and termites typically have many inquiline inhabitants of their nests, but it is not always apparent whether or not the inquilines are cleptoparasites. Many inquilines (particularly ants) are very closely related to their host organism.

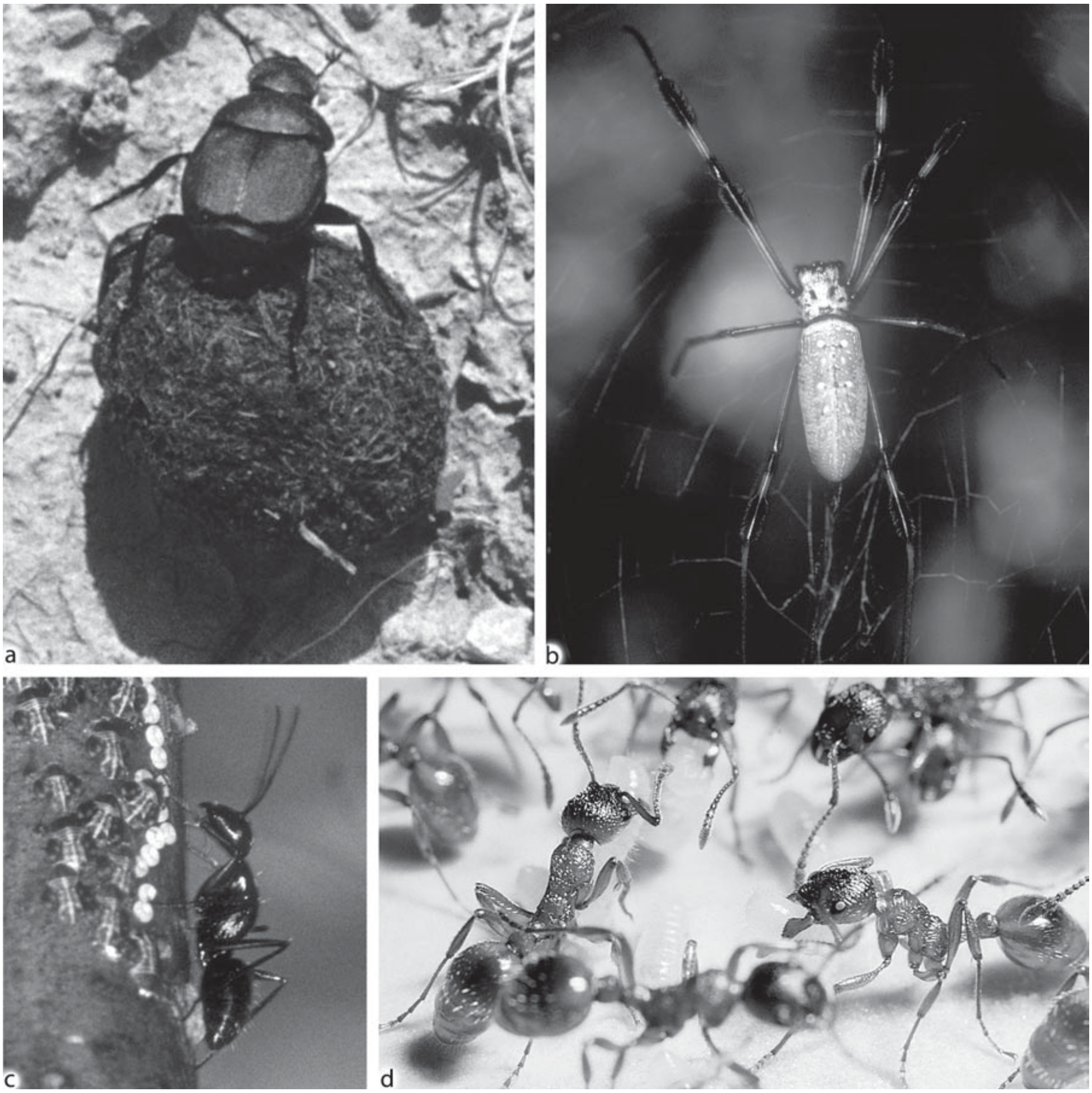
Scarab beetles are known for rolling balls of dung, which they bury deep underground in burrows, and which serve as a food resource for their immatures (grubs). When they roll their dung balls, small flies (various families) are attracted. These flies show remarkable dependence on the scarabs in their life cycle. The adult flies are attracted to a scarab beetle's burrow, lay their eggs in the dung ball, and escape before the beetle seals the hole. The fly larvae share the provisions with the grubs, but do not negatively affect the host. Without the new generation of dung beetles developing successfully, newly developed flies would not be able to dig their way out of the sealed burrows. In this case, the host does not suffer from the activities of the inquiline (Fig. 6).

Some spiders simply hide in or near the predators' homes and steal or snack on their prey without directly harming the predators. For example, a minute droplet spider, *Argyrodes* sp., lives in webs of the large golden orb weaver spider, *Nephila* sp. It hides until the much larger *Nephila* has subdued a prey, and then sneaks up and shares the meal. *Argyrodes* relies on speed for defense, as well as its ability to travel through the web without moving it.

Among other insects that steal food from spiders are milichiid flies that often sip blood from stinkbugs caught in the spider webs. Scorpionflies have been observed to feed on sphinx moth caterpillars that fell victim to spiders. Some mirids also inhabit the webs of a subsocial spider *Anelosimus studiosus* (Hentz) in Florida, where they scavenge on dead insects. Recently it was discovered that the same spider gives a home to caterpillars of the pyralid moth *Tallula watsoni* Barnes and McDunnough, which are never found outside of spider webs. Spiders do not attack the caterpillars, probably because these caterpillars have developed some sort of chemical camouflage as well as the ability to remain motionless and not set off the vibration of the web. In Florida, the caterpillars simply feed on the vegetation that happens to be incorporated into the spider web, but in the Neotropics there is a noctuid moth caterpillar (*Neopalthis madates* Druce) that scavenges on the dead insects caught in the webs.

Inquiline associates of ants are especially well studied, and display varying levels of host exploitation. In the Neotropics, predacious silverfish and wasps follow raiding army ants, looking for easy prey. There are also species that infiltrate the ants' nests and eat their brood or food. Pausid beetles produce secretion in their huge balloon-like antennae. The ants bite into the balloons and suck up this nectar while the beetles consume their brood. Blue butterflies (Lycaenidae), induce ants to feed and care for their young by secreting pheromones that mimic those produced by the ant brood; the ants actually carry the caterpillars into their own nests. The caterpillars also produce a sweet, nutritious fluid much liked by the ants. In exchange, they benefit from frost and fire-proof housing in the ant nests and are protected from predators and parasitoids. Like pausid beetles, they also frequently feed on the ant larvae.

Commonly known as cuckoo wasps, the hymenopteran family Chrysididae is a very large group of over 3,000 described species. They often have sculptured metallic bodies, so they are also known as jewel wasps, gold wasps, or emerald wasps. They are typically associated with solitary bee and wasp species. Cuckoo wasps lay their eggs into the nest of these other hymenopterans, sometimes puncturing the mud wall of the nest with the ovipositor, or chewing a hole in it to gain access. After ovipositing in the cell of its host, cuckoo wasps seal the hole, and leave its offspring to kill the host wasp larva and to complete its development on a stockpile of food meant for raising the host's offspring. Some cuckoo wasps enter the nest of its host at the moment when the provisions are brought in, laying their eggs on the food (various paralyzed insects or spiders) in plain site of the host.



Inquilines and Cleptoparasites, Figure 6 **Some examples of inquilinines and cleptoparasites: (a) Dung balls created by dung beetles as a larval food substrate often provide food for other insects. (b) A tiny droplet spider *Argyrodes* sp., lives in webs of the large golden orb weaver spider, *Nephila* sp. It hides until the big *Nephila* has subdued a prey and then sneaks up and shares the meal. *Argyrodes* relies on speed for defense as well as its ability to move in the web without moving it. (c) An ant guarding lycaenid eggs. (d) Many species of ants host caterpillars of Blue butterflies in their colonies. Larvae of the European lycaenid, *Maculinea arion*, are carried by *Myrmica rubra* ants into the nest, where it feeds on ants' brood in exchange for sweet secretions.**

The cuckoo wasps can roll up like an armadillo into an impenetrable ball, which saves them from possible attack by the host. Some cuckoo wasps do not accept the "loot" until they have won it in a contest. Larvae of the cuckoo wasp *Praestochrysis lusca* Fabricius, for example, do not touch the stockpiled food of their hosts unless a battle with the host larva occurs. If the combat (the outcome of which is never certain) does not take place, the cuckoo wasp larva starves to death – apparently the battle with the host larva triggers feeding behavior.

The sarcophagid fly *Miltogramma germari* Meigen depends on *Bembex* digger wasps to obtain a suitable host (a paralyzed caterpillar) and also a suitable habitat. The sarcophagid stalks the *Bembex* while it digs a hole in the ground – the site for a nest where the caterpillar will be buried together with the *Bembex*'s egg. While the wasp digs, there are numerous opportunities for the fly to lay its own eggs on the caterpillar, but it waits until the very last moment. Only as the wasp disappears into the hole dragging the caterpillar along does the fly deposit live larvae on the edge of the hole. The wasp emerges from the hole and covers the entrance with dirt; the fly larvae are the first to fall in. The hole is sealed and so is the fate of the wasp's offspring – the fly larvae will feed on the caterpillar, consuming the wasp egg in the process. Obviously, this is a case of parasitism; the host wasp suffers and the fly benefits.

References

Deyrup M, Kraus J, Eisner T (2004) A Florida caterpillar and other arthropods inhabiting the webs of a subsocial spider (Lepidoptera: Pyralidae; Araneida: Theridiidae). Fla Entomol 87:554–558

Hölldobler B, Wilson EO (1990) The ants. The Belknap Press of Harvard University Press, Cambridge, MA

Insecta

The class of organisms containing insects. It is sometimes called Hexapoda, though Hexapoda is more often is considered to be a superclass containing class Insecta and class Entognatha. Insecta is one of the most important classes within the phylum Arthropoda, and the largest class of animals. Estimates of insect diversity range from 1.4 million to over 5 million species, but less than 1 million have been described.

► Classification
► Phylum
► Orders

Insect Growth Regulator

A hormone-like substance (hormone analog) naturally produced by plants, or produced synthetically by chemists, that affects the normal growth of insects.

► Ecdysone Agonists
► Ecdysteroids
► Juvenile Hormone
► Insecticides

Insecticide

A pesticide applied to manage insect populations.

► Insecticides
► Acaricides
► Miticides

Insecticide Application: The Dose Transfer Process

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In the broadest sense, the application of pesticides involves the transfer of a toxicant from the manufacturer to the target organism. This is the dose transfer process, which can be broken down into several major events. However, difficulties at any step can result in a loss of biological activity, excessive environmental contamination or both.

The dose transfer process is a roadmap for the events that take place in delivering a toxicant to a target organism. In field agriculture, a small quantity of toxicant must be spread over a large area (acres or hectares). On a smaller scale, the same process is used for home garden and turf application. However, many steps in the dose transfer process are reduced when traps are used (e.g., cockroach and ant control in houses), or when the toxicant is used as a barrier (e.g., treated lumber for insect and fungus control). Each step in the dose transfer process is unique for each toxicant, its formulation, its intended use and the environment where it will be used. A general outline of the steps in the dose transfer process that emphasizes their interrelatedness is presented here. While most applicable to water-dispersed toxicants applied to field crops via atomization through a small orifice, the discussion could be applied to most pest control activities with some judicious modification (Fig. 7).

The act of formulation is the addition of chemicals other than the toxicant or diluent to the overall sprayed product. These chemicals are collectively called "adjuvants." The manufacturer of the toxicant, distributors of the toxicant, and persons involved in applying the toxicant determine the formulation that is applied to the field. While the applicator is not usually thought of as a formulation chemist, he is altering the physicochemical properties of the toxicant-diluent mixture when adjuvants are added. Usually the objectives of adding adjuvants are: (i) consumer usability; (ii) dispersal in diluent; (iii) retention by foliage; (iv) reduced redistribution through the drift of small droplets in the air, or the washing off of the toxicant from rainfall; (v) improved biological activity, including improved pick-up of the toxicant by the insects and redistribution to the chemically active site in the insects; and (vi) correction of existing problems like the presence of specific ions in the water used for the diluent.

This description of the dose transfer process focuses on the application of toxicants with water as a diluent. The second most common diluent is oil. As oil is different from water, the following discussion may not always apply to applications with oil as the diluent.

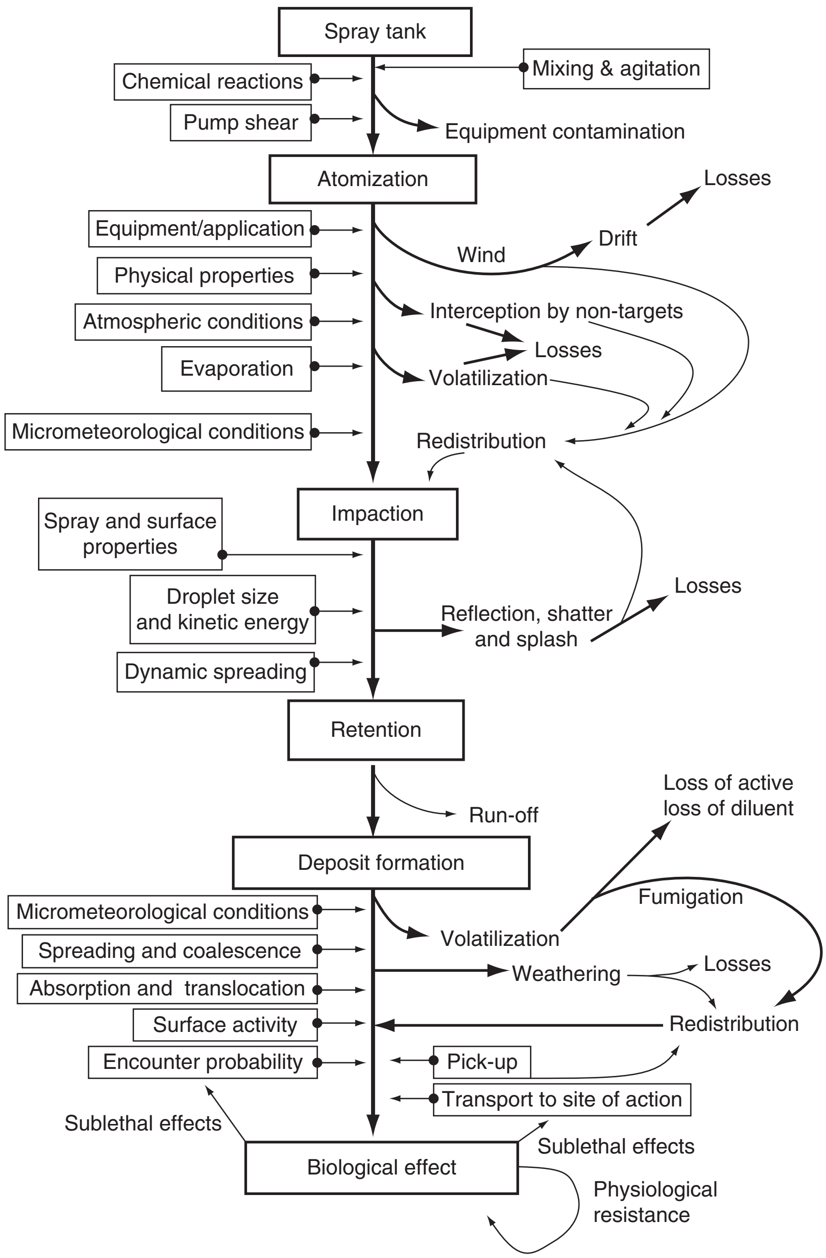
Consumer Usability

Consumer usability does not fit in the dose transfer process because it is strictly a human use and safety issue. A colorless, odorless toxicant can be made less hazardous by including an odiferous adjuvant (= stenching agent) in the formulation. Other issues include ease of removal from the container, or increase the shelf life of the product. While addressing these issues may result in formulation changes that affect toxicant efficacy, the goal is not related to the manipulation of toxicant functioning. Therefore, consumer usability is not listed as part of the dose transfer process.

Spray Tank

Dispersal is first affected by the chemistry of the different formulation components interacting with each other and the diluent. Water is a common diluent for high volume applications (100 gallons per acre). Many pesticides are hydrophobic (repel water). Therefore, additional chemicals are needed to keep the toxicant suspended in the diluent. This is done with chemicals that promote the formation of an emulsion (emulsifiers), or that promote the formation of a suspension (antiflocculating agents). These approaches lead to the formation of two important classes of pesticide formulation: "Emulsifiable Concentrates (EC)" and' suspension Concentrates (SC)'.

Following the addition of chemicals (toxicant(s), formulation components and adjuvants) to the spray tank, the initial goal is to distribute these chemicals uniformly throughout the diluent. This can be achieved through agitation of the carrier liquid and the addition of dispersing agents. However, vigorous agitation is not always



Insecticide Application: The Dose Transfer Process, Figure 7 Flow diagram representing application of liquid pesticide.

a guarantee of proper mixing. Interactions between the types of agitation (e.g., paddle mixing, recirculating pumps) and the shape of the spray tank can leave areas of relative calm where formulation components or toxicants can separate or settle out of solution. Where agitation is provided by recirculation through a centrifugal pump, the heat and friction from the pump may promote chemical reactions that alter the expected behavior of the atomized spray. An example of this would be the addition of long chain polymers for drift control. The mechanical action of the pump breaks the long chains, thereby reducing their effect on the atomization properties of the liquid. Dispersing agents that can be added include emulsifiers (surfactants used to mix oil and water), buffers (solubility is sometimes pH dependent), and anti-flocculants (keeping small particles suspended in water).

Atomization

In some way, the toxicant must be distributed over the target area. While other methods are used (e.g., dusting, painting), a common approach is to atomize a liquid containing the toxicant and distribute the resulting droplets over the target area. This can be done in several ways, among them are: (i) hydraulically forcing fluid through a small orifice (hydraulic sprayers); (ii) use a high speed air stream (mist blowers); (iii) placing liquid on a rapidly spinning disk or cage (Controlled Droplet Applicators [CDA] like spinning disks and rotary cage atomizers); (iv) using a hot and rapidly moving air stream (thermal foggers); (v) electrohydrodynamically (Figs. 12 and 13). The general process whereby the bulk liquid is broken up into millions of small droplets is similar for all these application strategies.

In hydraulic sprayers, the most common approach to atomization, a liquid is forced through a small orifice under pressure. At pressures close to atmospheric pressure, the liquid flows out of the orifice as a stream because surface tension forces exceed the energy from internal and external sources. Increasing pressure will increase the internal turbulence in fluid flow and increase the velocity of the liquid exiting the orifice relative to the surrounding air. Low-pressure application pressures are 15–40 psi. At some point below these pressures, sufficient energy is imparted to the liquid stream to cause it to disintegrate into small droplets, and increasing pressure results in smaller droplet sizes. Most hydraulic atomizers exhibit three modes of liquid sheet disintegration: rim disintegration, perforated sheet disintegration, and wavy-sheet disintegration. Rim disintegration is droplet formation from a thickened rim at the leading edge of the liquid sheet (usually occurring in high viscosity and high surface tension liquids). Perforated sheet disintegration takes place in holes that develop in the sheet. Wavy sheet disintegration takes place due to oscillations that tear off droplets at the leading edge of the sheet (Fig. 14). In all three cases, ligaments form and disintegrate to produce droplets. However, droplets produced from rim disintegration tend to be larger. Wavy sheet disintegration produces a highly variable range of droplet sizes. Thus, the relative contribution of the different modes of liquid sheet disintegration will determine the size range of droplets produced and the abundance of droplets of a particular size within this range. Droplet sizes within the spray cloud are determined by the thickness of the liquid sheet from which the droplet originates, with larger droplets being produced by thicker sheets. The droplet size range in the spray cloud is also dependent on the velocity of the sheet relative to the surrounding air, and the liquid properties of the atomized fluid (e.g., viscosity, surface tension). Other processes involving high pressures can also atomize a fluid. However, all of them ultimately rely on the Rayleigh mechanism, so named because Lord Rayleigh postulated the breakup of a liquid stream first by ligament formation, then by ligament disintegration into droplets.

The large droplets produced by primary atomization may undergo further disintegration. In still air, the surface tension of the liquid will create spherical droplets because a sphere minimizes the strain within the droplet. It also minimizes the surface area exposed to the air. However, the velocity of the droplets creates air turbulence, and the process of atomization produces a vacuum that also creates turbulence. Also, the droplet is elongated while attached to the ligament, and relaxation of this deformation following detachment from the ligament produces additional stresses. If these forces exceed the surface tension, the droplet will disintegrate by one of three processes described by the shape of the parent droplet prior to breakup: lenticular deformation, cigar-shaped deformation, or bulgy deformation. The breakup of droplets is termed secondary atomization.

Droplet diameters range in size from under 1 μm (1/1,000 mm) to over 1 mm depending on the process used to form them. For field application of pesticides with a low-pressure (15–40 psi) hydraulic nozzle, a typical droplet size range is from 50 to 1,000 μm in diameter. Some high-pressure (2,500 psi) hydraulic sprayers used in greenhouses have a droplet size range of 1–300 μm in diameter. These ranges would be typical for water, but small quantities of adjuvants (e.g., surfactants or polymers) can change these ranges significantly'. Surfactants' are *sur*face *act*ive *agents*.

Measurement

The output of atomization devices needs to be measured to maintain proper functioning of the equipment and to develop new methods for improving the pesticide application process. Methods of evaluating the output from nozzles can be categorized as quantitative and qualitative. Quantitative measures are most useful for equipment maintenance. These approaches include measuring the output of individual nozzles with a bucket to check for plugged or damaged nozzles. At a finer resolution, smaller containers, or a sheet of corrugated roofing material could be used to measure the fluid deposited over a specific area. This approach would also detect plugged nozzles, but would also detect proper alignment of the nozzles along the boom. While these measures improve the uniformity of toxicant distribution over a field by aiding in equipment calibration, they are not designed to provide sufficient detail for evaluating coverage of individual plants (or leaves) within that field.

Devices for measuring atomization characteristics of nozzles are categorized as mechanical, electrical and optical. Furthermore, the techniques are grouped as intrusive and non-intrusive. An example of an intrusive mechanical approach would be to use several vials placed in different parts of the spray cloud. One then measures the liquid collected per vial over some time interval, much like what is done for equipment evaluation. This provides some measure of uniformity across the spray cloud for individual nozzles, and can also be used to measure output from several interacting nozzles. However, describing the spray cloud in terms of droplet sizes, numbers and velocities provides a better picture of the output of a specific nozzle. The factors to consider when selecting a technique for measuring spray cloud parameters include the effects of spatial sampling versus temporal sampling (factors like equipment cost are not considered here). Spatial sampling describes the droplets that pass through a specific volume in an instant in time. Methods for spatial sampling include high-speed photography and laser holography. Temporal sampling measures droplet sizes that pass through a specific volume over some time interval. Methods for temporal sampling include collection techniques and optical instruments. One collection technique is droplet freezing by injecting liquid nitrogen into the spray cloud. Balls of ice drop into a collection pan and are subsequently sieved. The mass collected in each sieve is divided by the average diameter between the next largest sieve and the current sieve and the numbers of droplets collected can then be estimated. These types of collection techniques are not usually used for assessing agricultural sprays. Spatial drop size data may be converted to temporal data by multiplying the size-specific droplet velocities by the droplet sizes. Temporal sampling has been suggested as the most appropriate method for agricultural uses. Optical instruments for sampling spray clouds include the Malvern particle sizer and the Phase Doppler Particle Analyzer (PDPA). The Malvern is a nonintrusive technique for measuring droplet sizes. The device is based upon a Fraunhofer diffraction of a laser beam. The PDPA is another nonintrusive approach based on work by Bachalo. However, it measures droplet velocity, and then estimates the numbers and sizes of droplets that passed through the probe volume while it was measuring other droplets. The PDPA uses a beam splitter to create two in-phase beams of coherent light. The point where these beams cross is the area that is measured. Droplet sizes are based on the interference fringe pattern as detected by three successive independent sensors. Droplet size is estimated based on the phase shift of droplets as each sensor detects their fringe pattern.

Characterization

Characterizing the spray cloud is done with descriptive statistics and mathematical models for which parameters are estimated based on measurements. At present, the most common model is the Rosin-Rammler droplet size distribution function that was based upon work done by these authors for describing particle sizes in powders, or a modified version of this model based on work by Rizk and Lefebvre. The advantage of using a model is that droplets that were not measured (for whatever reason) can be included in the calculation of descriptive statistics. However, regardless of the approach used, the data need to be summarized for comparative purposes and to provide concise inputs for studying the effects of atomization on retention and biological effect. Variables include droplet surface area, droplet diameters, droplet volumes and droplet velocities. These variables can then be described using the mean, median, or mode. Additionally, some description of the dispersion of the data around these values is often useful. These measurements can apply to the entire cloud, but typically scans are made along one axis of the spray cloud. For a flat fan nozzle, the z-axis is parallel to the flow out of the orifice with the origin at the center of the orifice; the x-axis is perpendicular to the z-axis and oriented along the major axis if droplet dispersion in the x-y plane forms an ellipse. This can be broken down further by taking point measurements at discrete intervals throughout the x-y plane at one or more points along the z-axis. However, it is not clear how these measures of spray quality can be used to predict toxicant retention on plant surfaces, or ultimately, the biological effects of the application.

Post-atomization

Following atomization, droplets must travel through the atmosphere to arrive at their target. Two forces act to alter droplet sizes arriving at the plant surface: evaporation and friction with the atmosphere. Evaporation changes the droplet size, and for any evaporation rate, the change will be greater in smaller droplets than in larger droplets; i.e., the smaller droplets will get smaller more quickly than will the larger droplets. In some cases, the aqueous component may completely evaporate, leaving only non-volatile formulation components. Friction with the atmosphere is important because smaller droplets loose velocity more quickly than larger droplets, and the terminal velocity of smaller droplets is much lower than for larger droplets. Consequently, small droplets do not travel as far nor penetrate as deeply into the crop canopy. However, small droplets can be entrained in the air turbulence formed by the wake of a passing larger droplet (Table 4).

In the application of pesticides, one cause of toxicant loss is the drift of small droplets away from the field. Drift may occur when the wind speed “up” (away from the crop canopy) exceeds the terminal velocity of the droplet. Under such conditions, the droplet will not fall onto the crop, and any lateral wind has the potential to move the droplet outside the field boundaries. Given sufficient wind, even the largest droplets will become susceptible to drift. While drift is a loss of toxicant out of the field, some wind-generated turbulence can aid deposition by moving drift-prone droplets into the plant canopy.

In application, a common height above the crop canopy is 18 inches (0.46 μm). Thus, a 10 μm diameter droplet will probably evaporate before the droplet reaches the canopy if the air is still, and as droplet size decreases, the droplet becomes more susceptible to drift because it will take it longer to travel the remaining distance to the target surface. Thus, some wind is beneficial because the small droplets are moved into the plant canopy, which prevents these droplets from becoming driftable.

Insecticide Application: The Dose Transfer Process, Table 4 **Terminal velocities of droplets of water falling through still air**

Droplet diameter (μm)	Droplet volume (μl)	Terminal velocity (m/s) [mph]	Extinction time (s)[1]	Time to fall 18″ (0.46 m) in s
10	5.24×10^{-7}	0.003 [0.007]	0.568	152.4
50	6.54×10^{-5}	0.072 [0.161]	14.205	6.4
100	0.00052	0.253 [0.566]	56.818	1.8
500	0.06545	2.051 [4.588]	1420.455	0.2
1000	0.52360	3.869 [8.655]	5681.818	0.1

[1]Extinction time is estimated based on 20°C ambient temperature, 80% relative humidity, and a temperature difference of 2.2°C between wet and dry bulb thermometers

It should be noted that atomized droplets are not in still air, and are often traveling faster than their terminal velocities near the nozzle. Droplets then slow down to their terminal velocity due to friction. Also, because the bulk liquid is, on average, traveling into the crop canopy, there is considerable air movement into the crop canopy, especially with high volume (934.6–9346 l per hectare = 100–1,000 U.S. gallons per acre) application strategies. Thus, the values in the table should not be used too literally. While it might be nice to provide more accurate values, such calculations are difficult (may be impossible) due to the number of variables that must be accounted for both in terms of the physico-chemical nature of the sprayed liquid and the external environment.

Many adjuvants added to tank mixtures modify one or more atomization parameters. Such adjuvants include anti-evaporants, spreaders and drift reduction agents. Anti-evaporants retard water loss, thereby increasing the life expectancy of droplets. Anti-evaporants have the greatest effect on smaller droplets. Anti-evaporants may retard water loss by forming a film, or they may be hygroscopic. Spreaders are surfactants. By lowering surface tension, the liquid has less cohesion and breaks apart more readily. Drift-reduction agents are usually polymers. The addition of a polymer increases the viscosity of the liquid, thereby increasing droplet size and reducing the proportion of smaller droplets in the spray cloud. The addition of surfactants and drift control agents may also change the atomization characteristics of the liquid.

Much of the above discussion on atomization is based on the atomization of pure water, or water and a water-soluble formulation. Additional problems arise when the toxicant is dissolved in oil (as in emulsifiable concentrate [EC] formulations) or is left as discrete particles that are suspended in water (as in suspension concentrate [SC] formulations). As an example, consider the SC formulation. During atomization, droplets with diameters less than the particle size of the formulation cannot have any toxicant (assuming the toxicant is completely insoluble, or nonfunctional if particles are damaged as is the case with the application of an insect pathogen). On the other hand, particles will carry some water with them and some particles will group together to form larger droplets. Consequently, the presence of particles will decrease the numbers of droplets with diameters less than the particle size of the formulation. The distribution function for the numbers of particles based on the size of the droplets will determine the toxicant distribution over the treated surface, and this distribution will influence the biological effect.

Following atomization, the droplets must travel to the plant canopy. They have a velocity vector along the z-axis, and a radial component away from the z-axis is also present in most droplets. Furthermore, the traveling speed of the nozzle over the crop canopy will add a velocity vector that is almost parallel to the y-axis (the exact orientation being determined by the orientation of the nozzle axes on the spray boom). Turbulence from wind passing over the crop canopy and turbulence from the spray boom moving over the field will change the velocity vector of droplets before they impact the plant surface.

The air flow at the plant surface is essentially stationary. The depth of this stationary layer is determined by leaf surface topology. Wind velocity increases gradually until it reaches the current wind speed above the crop. The transition zone between the stationary air and the current wind speed is termed a boundary layer. The boundary layer has no specific dimensions except those defined by the researcher. The direction of air flow in the boundary layer changes from the current wind direction to become almost parallel to the leaf surface (laminar boundary layer). The depth of the laminar boundary layer increases with distance from the leading edge of the leaf. However, temperature gradients, leaf topology and turbulent air flow within the crop limit the size of the laminar boundary layer.

Air flow above the crop canopy is usually turbulent due to interactions between the air mass above the crop and the irregularities within the crop. Furthermore, heating of the ground and crop surface creates convective cells that also contribute to air turbulence above the crop. If temperature gradients are small and the surface is fairly regular (same species, same height, etc…), then the average velocity will increase logarithmically with the height above the canopy until it reaches the wind speed. The depth of the boundary layer above the crop where the air velocity is increasing to the wind speed is a function of the distance traveled over the crop. This is similar to what happens at the leaf-air interface, but the mathematical relationships differ considerably.

The air flow over the crop and over surfaces in the crop canopy are important because droplets must pass through these layers before they impact the plant surface. Droplets that eventually impact a leaf surface must pass through a turbulent layer of air above and within the crop canopy, and then pass through a boundary layer close to the leaf surface where the air movement is laminar and parallel to the leaf surface. Small droplets (usually less than 100 μm diameter) may be carried in the air currents in the laminar boundary layer unless they have sufficient energy to penetrate this layer. These droplets may then deposit on the underside of the leaf if the turbulence at the leeward edge is sufficient, or they are carried somewhere else. Droplets with insufficient energy to reach the crop may end up drifting to other locations and may become health or environmental hazards. Even if such hazards are not present, such losses represent lost revenue to the farmer because the toxicant is no longer in a location for effective management of pest problems in the field.

Impaction and Retention

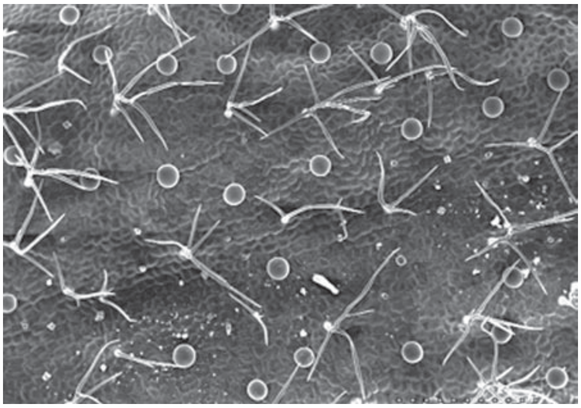
Three physical properties of liquids that are important in relating atomization characteristics to retention on plant surfaces are: (i) equilibrium surface tension; (ii) dynamic surface tension; (iii) viscosity. Equilibrium surface tension is caused by the cohesive molecular attraction between molecules in the liquid, and molecules at the surface that have one or more sides exposed to the air. Liquids minimize this exposure by keeping the surface area to a minimum, which means that droplets in air will form spheres. Molecules at the surface tend to be more tightly packed and are arranged more regularly than those in the bulk liquid. Equilibrium surface tension is the energy required to expand the surface area of a liquid at rest. When a liquid is moving, the molecules at the surface are less ordered and more similar to the molecules in the bulk liquid. For water, it takes about 40 milliseconds for the surface film to become stable. This period of adjustment is characterized by declining surface tension. Because the surface tension is constantly changing during this period, it is termed dynamic surface tension. Viscosity is a function of the cohesive forces between molecules, but it also depends on molecular shape. Viscosity is a mea-sure of how readily molecules pass one another. High viscosity may be due to high cohesion between molecules, or because molecules become entangled with one another.

Once the spray cloud reaches the plant canopy, the foliage acts as a filter that removes droplets from the air column. The leaves and stems fill an area through which the droplets will pass aided or hindered by their original velocity following atomization, gravity, friction with the atmosphere, and air turbulence. As foliage density increases, the degree of penetration into the canopy will decrease. Furthermore, spray deposits will be greater on surfaces directly facing the nozzle. Usually this is the upper (adaxial) leaf surface, though bent leaves and the flexing of leaves due to air turbulence may result in specific examples where the abaxial surface receives more toxicant. As a general rule, larger droplets will penetrate the plant canopy more effectively than smaller droplets, but smaller droplets have a greater potential to deposit on the bottoms of leaves. The reason is that small droplets are entrained in the laminar air flow around the leaf and are subsequently deposited on the abaxial surface by the turbulent air flow at the edges of the leaf. This results in a common abaxial leaf surface deposit pattern of more droplets occurring at the edge relative to more central abaxial leaf areas.

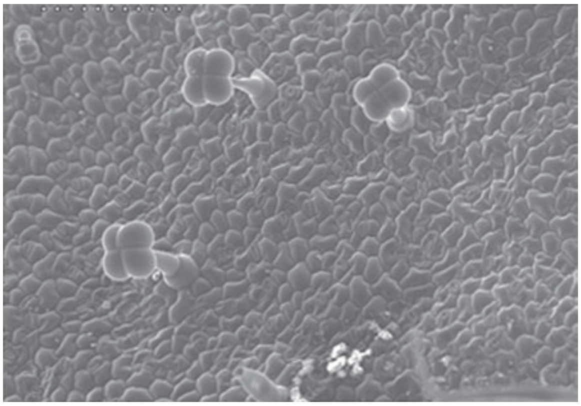
Impaction occurs when the droplet has penetrated the boundary layers around the leaf and hits the leaf surface. Droplet deformation occurs upon impact with any surface (leaf, leaf hairs, stems, soil, etc.). Droplets spread upon impact, where the degree of spread is a function of the energy of impact balancing with the cohesive forces within the droplet. If the energy of impact is too great, the droplet will shatter into several smaller droplets. If the droplet does not shatter, it will deform into a torus. Dynamic surface tension will pull the torus back into a sphere and the droplet will rebound if it has not adhered to the plant surface. The impact of a droplet upon a surface, its deformation and subsequent rebound (if that occurs) takes about 1 millisecond.

A plant surface consists of several elements important to the retention of droplets. The physical topology of the leaf is defined by the shape of the leaf, folding or bending of the leaf surface, leaf hairs, stomata, the presence of specialized tissues like veins or glands and the shape of the individual cells within these tissues and how they fit together. Leaf shape determines how far air currents travel from the windward to the leeward sides of the leaf. Leaf hairs may increase retention of droplets, but may also prevent droplets from touching the leaf cuticle. Stomata provide a direct route through which insecticides may enter, but only if the surface tension is low enough to reduce the contact angle below the wall angle of the stomata. While this may be desirable for systemic insecticides, it may reduce the biologically available dose for other insecticides. Veins provide channels that may reduce the liquid carrying capacity of the leaf by providing routes along which liquid flows. The spaces between cells also are recessed relative to the intracellular areas. Liquid often becomes trapped in these areas, thereby promoting retention (Figs. 8-10).

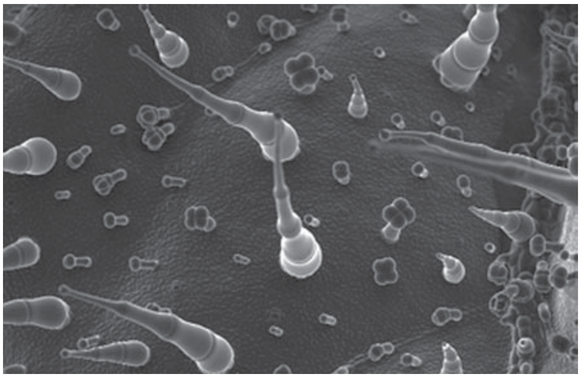
The physico-chemical property of the plant cuticle also plays a role in retention. Plant cuticles are a thin continuous covering that may be from less than 0.1 to 10 μm thick depending on the species and the location on the plant. The outermost two layers are an epicuticular wax layer that blends into the cuticular wax layer. These layers are attached to the cell wall by a matrix of cutin (a cross-linked polymer of hydroxylated fatty acids) and carbohydrate fibers. Below the cell wall is the cell membrane. The physical characteristics of the epicuticular waxes provide the first barrier to retention. The physical structure of this layer is often crystalline, as plates, tubes, rods, or other shapes. These shapes rise above the cuticular waxes and repel water by their physical structure. The epicuticular waxes are mostly composed of long



Insecticide Application: The Dose Transfer Process, Figure 8 The adaxial surface of a rosemary leaf. The circular objects are glands. The leaf has a little bit of dirt that has splashed onto the leaf surface (Courtesy of Molecular and Cellular Imaging Center, The Ohio State University).



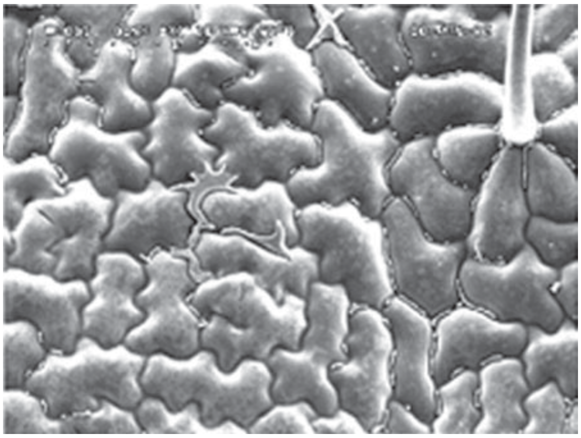
Insecticide Application: The Dose Transfer Process, Figure 9 The adaxial surface of a tomato leaf. The 4-lobed glands are on stalks (Courtesy of Molecular and Cellular Imaging Center, The Ohio State University).



Insecticide Application: The Dose Transfer Process, Figure 10 Glands and hairs on the adaxial surface of a young tomato leaf. Glands may be four-lobed or simple (Courtesy of Molecular and Cellular Imaging Center, The Ohio State University).

chain (often C_{26} or C_{28}), even numbered, primary alcohols, acetates, aldehydes and fatty acids. Additionally, this layer has odd-numbered (usually C_{29} or C_{31}) alkanes. Additional components are present, though in lesser amounts, and the exact composition is species-specific as modified based on abiotic conditions (e.g., temperature, humidity, light). Thus, the problem for pesticides is to stick to the plant surface. However, contact insecticides cannot stick too well to the plant surface because they must adhere to the insect cuticle. Systemic insecticides also present a special problem because they must pass through these cuticular layers and then be transported in the phloem/xylem. Penetration rates through the cuticle will be dependent on the molecular size of the toxicant, and the path length through the cuticle. Because the cuticle is partly composed of cutin and other long chain organic molecules, toxicants must move around these molecules to penetrate the cuticle. Therefore, the path length is greater than the liner thickness of the cuticle.

Given the physical and chemical composition of the cuticle, the impacting droplet will remain on the surface if the kinetic energy of the droplet is less than the adhesive forces keeping it on the plant surface. If the droplet has wetted the plant surface upon impaction, some portion of the droplet will remain. Droplets with considerable kinetic energy that have adhered to the plant surface may shatter, giving rise to one or more smaller droplets. Droplets that hit a pre-wetted surface may also provide enough energy to produce one or more smaller droplets. These droplets may impact other plant surfaces, or be lost from the crop. The likelihood that droplets will rebound from a surface or shatter upon impact can be modified with the appropriate selection of stickers, polymers and surfactants. The selection of product must balance drift, impaction and retention. While these products will influence the final distribution of the toxicant, the toxicant distribution will also influence the biological effect of the application. However, in many cases, there is a period of time between the retention of the liquid on the plant surface and the time when the insect encounters the toxicant. During this time, several dynamic events take place that influence toxicant distribution as encountered by the target (or non-target) insect.



Insecticide Application: The Dose Transfer Process, Figure 11 **Roundup Ultra sprayed on the adaxial surface of a cotton leaf. The deposit has filled in the gaps between cells (Courtesy of Molecular and Cellular Imaging Center, The Ohio State University).**

Redistribution and Deposit Formation

Once the liquid spray has settled on the leaf, the deposit finishes spreading over the leaf. The maximum spread is related to the viscosity, surface tension and chemistry of the liquid along with the chemical and physical structure of the plant surface. However, the rate of spread will be inversely proportional to time. Thus, in some cases, droplets will not achieve their maximum dimensions because they do not achieve equilibrium before evaporation reduces the liquid volume. Alternatively, some sprays will contain lipophylic components that may continue to spread through the cuticular wax layers until a steady state has been reached. While it is easy to see an oil spread on waxy plant surfaces, the spread of the lipophylic components is not necessarily representative of the spread of the toxicant (Fig. 11).

Droplet size interacts with evaporation to change concentrations within the droplet. Small droplets with a dilute surfactant solution may have insufficient surfactant to wet the leaf surface. Such droplets will evaporate, and the final microscopic piece of formulation and toxicant will be easily dislodged from the surface. Larger droplets of the same solution will maintain a large contact angle with the plant surface until the surfactant concentration reduces surface tension to the point where the surface is wetted.

Under some conditions, the leaf surface could be viewed as a thin layer chromatography plate, and the formulation components as solvents for the toxicant. If the toxicant is nearly insoluble in the formulation, then most of the toxicant will remain wherever it was deposited following atomization. However, if the toxicant is soluble, it will flow over the cuticle with the bulk liquid, and then be carried some distance further as the solvent moves through the cuticular waxes.

The final shape of the deposit after spreading and evaporation have finished is highly variable, and subject to the physico-chemical parameters already discussed. On a flat leaf surface, droplets can form deposits that look like atolls (a ring of small islands located near the outer edges of the droplet), archipelagoes (irregular islands randomly located within the boundaries of the old droplet), mountains (a hill where the formulation components went out of solution, usually near the center of the old droplet), solid films that may or may not cover underlying features of the cuticle, and various other shapes.

Degradation

During these processes, and throughout the life of the toxicant, the toxicant will degrade. Degradation is a combination of a large number of forces that can be classified as chemical or physical. The two most common chemical actions are hydrolysis and photolysis. Hydrolysis is the addition of water to the toxicant molecule. This usually splits the toxicant into two inactive molecules. Photolysis is the action of sunlight hitting the toxicant and breaking it. Within the plant (for systemic toxicants), and within the insect, enzymatic degradation will become more important, but the toxicant has not yet entered the insect or the plant. Physical degradation of the deposit is an abiotic process whereby the toxicant is physically removed from the plant surface. Rain is a common source of physical degradation, but heavy dew or fog can also act in the same manner. For water-soluble toxicants, dew can also redistribute the toxicant over the leaf by rewetting deposits. Wind and wind-blown sand can provide mechanical abrasion to remove surface deposits. While not commonly considered, gutation (exudation of water from leaves due to water pressure from the roots) could also provide sufficient leaf surface water to redistribute toxicants.

The physical forces in toxicant degradation can also act to redistribute the toxicant within the plant canopy. For example, rain may pick up some portion of the toxicant on a leaf surface and move it to the leaf axil, or along the stem. Water that does not fall off the plant will then evaporate creating a new deposit.

Toxicant Acquisition and Biological Result

Following deposition on the plant (or other) surface, the toxicant must be acquired by the insect in sufficient amounts to produce the desired result. Complicating factors include growth of the insect because the lethal dose is determined in part by insect biomass.

Consider a caterpillar feeding on a leaf treated with sufficient toxicant to kill the larva if the larva consumes the entire deposit. If the toxicant is spread uniformly over the entire leaf surface (as might happen if sufficient surfactant is added), then the larva must consume the entire leaf before acquiring a lethal dose. During this time, the larva is exposed to sub-lethal doses, and exposure to sub-lethal doses is one factor that can lead to insecticide failure. Furthermore, the entire leaf has been eaten, so the level of plant damage is high. One solution is to increase the dose of toxicant, but for every doubling of the dose, the savings is only half of the leaf eaten by the larva at the next lower dose; i.e., double the dose from the previous example, save half the leaf, quadruple the dose save three-quarters of the leaf, and so forth. An alternate solution is to concentrate the toxicant into a single deposit. In this case, the larva will (on average) eat only half the leaf. However, in this case there is no benefit to increasing the dose unless there is an accompanying increase in the size of the deposit. This is because the biological response is driven entirely by the probability that the larva will encounter the dose. The benefit is that for a minimal dose, more of the plant is saved and there is no exposure to sub-lethal doses. Obviously, "real" applications produce deposit structures somewhere between these two extremes.

Deposit structure is defined as the distribution of toxicant over a surface. It can be relatively uniform, absolutely uniform, or heterogeneous. Relative uniformity is scale specific, i.e., uniform at 1 cm or greater scales; for example, the ink distribution in a picture in the newspaper. Absolute uniformity is scale independent (at least down to the sub-micrometer level); for example, the distribution of silicon over a computer microchip. Thus, absolute uniformity implies relative uniformity, but the reverse is not true. This is important in application technology because one measure of uniformity is coverage, where the goal of some applications is 100% coverage. 100% coverage may be uniform over a hectare or a whole plant, but is seldom uniform over every leaf on that plant. Absolute uniformity thus implies 100% coverage, but the reverse is not true. Other ways of viewing absolute uniformity is that all toxicant molecules have the greatest possible distance between them over the treated area. Deposit structure can also be heterogeneous. While there are many texts describing heterogeneity in different fields of research, there is no currently accepted measure for heterogeneity in pesticide application.

Two examples will suffice to demonstrate how insect behavior interacts with heterogeneous deposit structures to influence the biological result:

1. If the deposit applied to the leaf surface is sufficient to kill the larva, and the deposit is large enough so that it takes two bites for the larva to ingest the entire deposit, then the way in which the larva feeds will determine the survival time of the larva and the amount of damage to the leaf. At the extremes, a larva could start in one place and feed until all the food was consumed (called "chompers"), or a larva could take one bite, move, take another bite, move, and so forth (called "nibblers"). With chompers, the larva is most likely to consume the entire deposit once it has encountered it. Thus, on average, the larva will eat just slightly more than half the leaf before it dies. With nibblers, it is unlikely that the larva will eat the second part of the deposit in the bite following acquisition of the first part. Depending on how the larva moves, it may eat half the leaf before encountering the deposit for the first time, and then eat half of the remaining leaf before encountering the deposit again. Thus, the feeding behavior of individuals interacts with heterogeneous toxicant distributions to influence the biological result.
2. If three lethal doses of toxicant are applied as three deposits and three larvae are allowed to feed on the leaf, the result is dependent on whether feeding is sequential or simultaneous. If feeding is sequential, then the first larva will eat 1/2*1/3 of the leaf, the second will eat 1/2*((1–1/2*1/3)/2), and the third will eat half of what is left – thus, 37/48ths (a bit over 3/4) of the leaf will be eaten. If all three larvae feed sequentially, then each larva will feed on its 1/3 of the leaf and consume half of that before encountering a deposit – thus, half the leaf will be eaten. Of course, there are many assumptions necessary to make this simple model work. A few of these are: larvae do not interact, larvae are not cannibalistic, deposits are far apart, larvae die upon consuming the deposit, contact with a deposit does not elicit a behavioral response in the larvae, and the toxicant is only acquired through feeding. Obviously, few larvae interact with toxicants in this way. However, modeling more complex systems can be done by judicious modification to the simplified model.

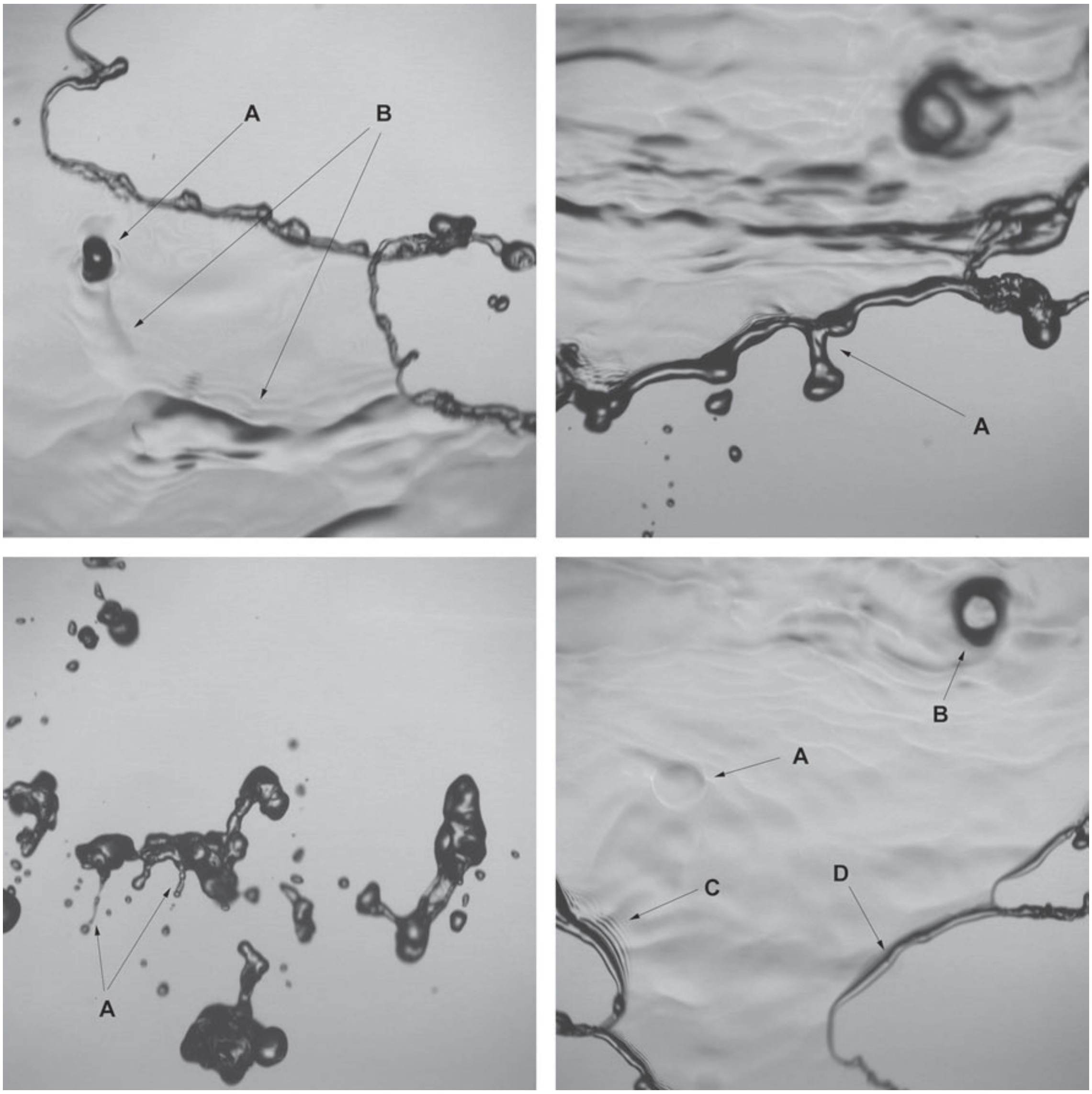
This approach identifies expected results based on one (or a few) larvae interacting with very well defined deposits. However, many toxicants do not behave in this way (consider a toxicant which acts through inhalation). Furthermore, it requires a careful set of experiments to identify "lethal dose" and care must be taken because the definition of "lethal dose" will change based on how the insect encounters the toxicant. If the toxicant is uniformly distributed, the lethal dose may be quite high because the insect has time to metabolize the toxicant and it can grow. If the toxicant is concentrated, the effect of metabolism is minimized, but the insect will have a variable length of time to grow depending on how long it takes before the toxicant is encountered. An alternative approach is to model the system based only on the characteristics of the droplets used to create deposits on the leaf surface.

In an atomized spray, the total quantity of toxicant applied to a leaf is related to the number of droplets that are retained by the leaf, the diameter of those droplets (volume = 4/3 π (droplet radius)^3), and the concentration of toxicant within each droplet. In an ideal world, all droplets can be considered to have the same toxicant concentration (uneven tank mixing and evaporation rates may change this under actual conditions, but that adds additional complications). Clearly in this

Insecticide Application: The Dose Transfer Process, Figure 12 **The DRAMM Coldfogger sprayer for greenhouse pest management. The sprayer delivers a fine mist under high pressure.**

system, if the toxicant load on the leaf remains constant, then a change in toxicant concentration must be compensated for by changes in droplet number, droplet size, or both factors. While still a novel approach, recent experiments suggest that the optimal distribution of toxicant is a balancing act between these factors. Thus, smaller droplets increase efficacy up to a point. This point is reached when the accompanying increases in droplet number provide excessive uniformity, or when accompanying increases in concentration no longer have any effect. Increases in concentration may not have an effect if they do not result in additional toxicant transferred to the target, or (especially with herbicides) the toxicant produces localized damage that restricts further acquisition of toxicant. Likewise, increases in concentration (as with ULV application relative to high volume applications) will improve efficacy until accompanying changes in droplet size or droplet number change the encounter probabilities and thereby

Insecticide Application: The Dose Transfer Process, Figure 13 **The Electrostatic Spraying Systems Inc. EPS-5 sprayer. The sprayer delivers a fine mist that is electrically charged and forced into the canopy by compressed air.**



Insecticide Application: The Dose Transfer Process, Figure 14 **Wavy sheet disintegration. Each picture is a 9.4 mm² area of the disintegrating liquid sheet produced by a Spraying Systems AI110015 nozzle. Pictures taken with an Oxford Lasers Visisizer. *Upper left*: Sheet disintegration (a) hole formation, (b) waves in the sheet. *Upper right*: Ligament formation, (a) ligament between sheet edge and forming droplet. *Lower left*: Secondary droplet disintegration (a) ligaments and droplets developing from larger unstable droplets. *Lower right*: Disintegration from holes in the sheet also produces droplets, (a) a developing hole that has not yet perforated the sheet (b) a hole in the sheet, (c) shock waves at the edge of the sheet, (d) thickened edge (Photos by Timothy Ebert and James Hacker and courtesy of Laboratory for Pest Control Application Technology).**

reduce toxicant efficacy. By extension, reducing the numbers of droplets will increase toxicity up to the point where reductions in efficacy from suboptimal values of droplet size and toxicant concentration overcome further benefits from using fewer droplets (Fig. 13).

The four variables (dose, droplet number, droplet size and toxicant concentration) define much of the dispersion of toxicant over a leaf surface. If the method of application ensures that the number, size and location of droplets impacting the leaf is random (and toxicant concentration is uniform), then this would be sufficient to define the toxicant distribution over the leaf. However, the distribution of droplet sizes is not uniform within the spray pattern in the x-y plane. Also, large droplets create a wake that can capture smaller droplets. Further, droplet spread, evaporation, and the coalescence of droplets are not independent of droplet size (Fig. 14). It is, therefore, possible that the models predicting toxicant effects would be improved by including some measure of dispersion. Defining the proper measure of dispersion is still being researched.

This discussion may make the dose transfer process appear like a very ordered set of linear steps that result in a biological result. However, the process is not entirely linear. A droplet that shatters on impact may hit the ground and be lost, or it may impact the underside of another leaf. If the target insect typically lives on abaxial leaf surfaces, this may improve efficacy. A deposit may be encountered by a non-target insect and moved to another part of the leaf where it may be more (or less) effective. If the deposit contained insufficient toxicant to kill the insect, it could produce a behavioral change in the insect. This behavioral change would then influence the probability of further contact. Also, while it is important to understand how toxicant distributions influence the fate of individual targets, the effect this has on populations should not be ignored. For example, if sublethal doses are common for the population, expect the population to become less susceptible to the toxicant. Sensitive individuals are selected against, and resistant individuals survive to breed the next generation.

This discussion on the dose transfer process is focused on insects and insecticides. However, much of it is important to other pesticides. Most of the material about deposition on surfaces came from research on herbicides, but will also apply to fungicides. The description of the biological effect is specific to insecticides, but with judicious modification, will also apply to some herbicides and systemic fungicides. Because the driving force in many systemic products is a function of the area of contact between the toxicant and the plant surface along with the concentration gradient of the toxicant, there is clearly a tradeoff between increasing the contact area (larger droplets and higher application volume) and increasing the toxicant concentration in the spray tank to achieve a greater concentration gradient. While it is possible to have both of these factors increase by increasing the quantity of toxicant applied, such an approach is environmentally unfriendly and not an economically viable option for farmers.

The importance of insect behavior should not be underestimated. Behavior reflects toxin apparency, mode of action, and insect response to sublethal doses. The interaction between these behavioral responses and heterogeneously distributed toxins and physiological mechanisms of tolerance may influence the evolution of insecticide resistance.

► Insecticides
► Acaricides
► Insecticide Formulations

References

Bailey AG (1988) Electrostatic spraying of liquids. Research Studies Press Ltd., Somerset, United Kingdom, 197 pp

Davies JT, Rideal EK (1963) Interfacial phenomena. Academic Press, New York, NY, 480 pp

Ebert TA, Taylor RAJ, Downer RA, Hall FR (1999) Deposit structure and efficacy of pesticide application 1: interactions between deposit size, toxicant concentration and deposit number. Pestic Sci 55:783–792

Hall FR, Menn JJ (1999) Biopesticides use and delivery. Humana Press, Totowa, NJ, 626 pp

Hartley GS, Graham-Bryce IJ (1980) Physical principles of pesticide behaviour, vol 1. Academic Press, New York, NY, 1007 pp. (in two volumes: 1–518 in vol 1 and 519–1007 in vol 2)

Kirkwood RC (1999) Recent developments in our understanding of the plant cuticle as a barrier to the foliar uptake of pesticides. Pestic Sci 55:69–77

Lefebvre AH (1989) Atomization and sprays. Hemisphere Publishing Corp., New York, NY, 421 pp
Matthews GA (1999) Application of pesticides to crops. Imperial College Press, London, United Kingdom, 325 pp
Schonherr J, Baur P (1994) Modelling penetration of plant cuticles by crop protection agents and effects of adjuvants on their rates of penetration. Pestic Sci 42:185–208

Insecticide Bioassay

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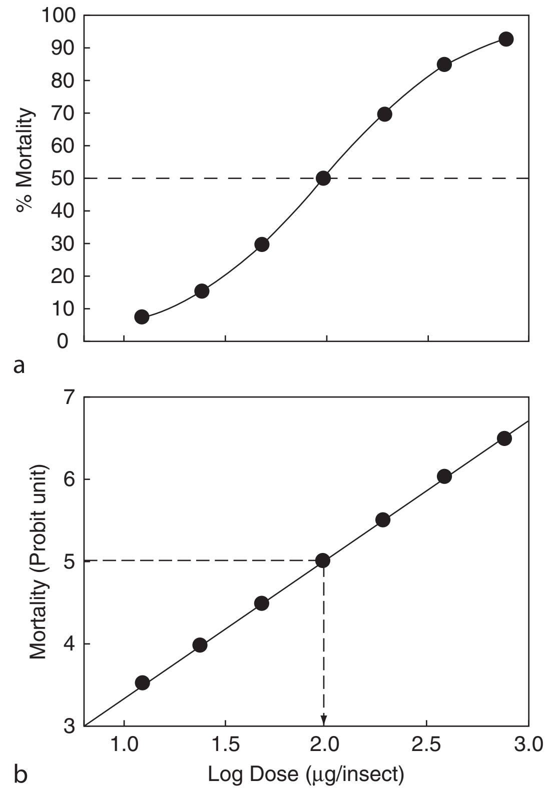
Insecticide bioassay refers to any quantitative procedure used to determine the relationship between the amount (i.e., dose or concentration) of an insecticide administered and the magnitude of response in a living organism. If the toxic effect (e.g., death) indeed results from the action of an insecticide, there must be a positive correlation between an appropriate range of the insecticide dose administered and the magnitude of the effect. Such a relationship is known as the dose-response relationship and is fundamentally important in insecticide bioassay (Fig. 15).

Insecticide bioassay with insects or other arthropods often is used to estimate the median lethal dose (LD_{50}) or concentration (LC_{50}) and its associated 95% confidence intervals (95% CI) from a dose-response model. The LD_{50} or LC_{50} is the dose or concentration of an insecticide required to kill 50% of a given population or strain under the specified conditions. These statistics are adopted as the benchmarks to express the toxicity level of an insecticide because the medians tend to be more consistent and to have narrower confidence intervals than lower or higher percentiles in dose-response models.

Insecticide bioassay also may be used to estimate the median lethal time (LT_{50}) which is the time required to kill 50% of a test population or strain with a fixed dose or concentration of an insecticide. For insecticides with a knockdown activity, such as many pyrethroid insecticides, the median knockdown dose (KD_{50}) or concentration (KC_{50}), or median knockdown time (KT_{50}) may be determined by a bioassay. In some instances, the toxicity of an insecticide is measured as sublethal effects (e.g., effects on growth, reproduction, etc.) instead of mortality or knockdown. In such



Insecticide Bioassay, Figure 15 **Two graphic representations of the dose-response relationship. a) When the extent of any particular response (e.g., % mortality) is plotted against log dose, a characteristic S-shaped curve is obtained.**
(b) When % mortality in the y axis is converted to probit units, the dose-response relationship becomes linear. In the log-probit analysis, the antilogarithm of the log dose corresponding to the probit unit of 5, which represents 50% mortality, is the LD_{50} value for the insecticide tested.

cases, the term median effective dose (ED_{50}) or concentration (EC_{50}) may be used to express the toxicity level of the insecticide.

A number of standard techniques are available for insecticide bioassay. The most commonly used techniques include topical application, residual or surface contact, immersion, and feeding bioassays. For example, the LD_{50} or LC_{50} value for an insecticide can be estimated by exposing insects to several different doses (or concentrations) of the insecticide for a certain length of time under specified conditions. Insects treated with the insecticide solvent often are used as a control. Insect mortality data are then recorded and subjected to an appropriate statistical analysis (Table 5).

Based on the concepts of the dose-response relationship, the dose-response data can be analyzed for the LD_{50}, LC_{50} or other toxicity parameters. For example, in the log-probit analysis for the LD_{50}, the doses of an insecticide are transformed into the logarithm scale and the % mortality at each given dose into the probit unit. The transformation of the % mortality data into probit unit allows the conversion of a typical S-shaped curve into a straight line. The antilogarithm of the log dose corresponding to the probit of 5 (i.e., 50% mortality) is taken as the LD_{50}. All the calculations for the LD_{50} value and its associated statistics (e.g., 95% confidence intervals, Chi-square, etc.) can be simultaneously performed using a computer program.

Representative Procedure of Insecticide Residual Contact Bioassay For Aphids (from Gao and Zhu, 2000).

- Pre-determine the insecticide concentration range that results in appropriately 10 and 90% mortality for the lowest and highest concentrations, respectively.
- Prepare at least five concentrations of the insecticide in an appropriate solvent (e.g., acetone).
- Label four 8-ml glass vials for each concentration and the control with the name and concentration of the insecticide.
- Pipet 0.25-ml aliquots of the solvent (for control) and each insecticide solution into each set of vials, beginning with the lowest concentration.
- Load the dosed vials onto a rotator and rotate the vials in a fume hood for 3 min or until acetone is completely evaporated.
- Place 20 apterous adult aphids in each vial with a fine brush and loosely cover the vial with a cap.
- Assess aphid mortality after they are maintained at an appropriate temperature (e.g., 25°C) for a specific time period (e.g., 24 h) in a growth chamber.
- Calculate the LC_{50} value and its related statistical parameters using the log-probit analysis procedure.

Insecticide Bioassay, Table 5 **Insecticide bioassay techniques commonly used for insects**

Technique	Description of Technique	Data Expected
Topical application	Individual insects are directly treated with a known dose of an insecticide via a microapplicator or microsyringe	LD_{50}, KD_{50}, ED_{50}, LT_{50}, or KT_{50}
Residual contact	Groups of insects or individual insects are exposed to a dry residue of an insecticide on natural (e.g., leaf) or artificial (e.g., glass) substrates	LC_{50}, KC_{50}, EC_{50}, LT_{50}, or KT_{50}
Immersion	Groups of insects or individual insects are dipped in insecticide solutions of known concentration	LC_{50}, KC_{50}, EC_{50}, LT_{50}, or KT_{50}
Feeding	Groups of insects or individual insects are reared on a diet containing an insecticide of known concentration	LC_{50}, KC_{50}, EC_{50}, LT_{50}, or KT_{50}

Because the toxicity of an insecticide is related to the size of the organism exposed, the body weight units (milligram, gram, kilogram, etc.) of the test organism should be taken into consideration when the toxicity level is expressed. For example, the oral LD_{50} value of parathion for rats is 2 mg of parathion per kilogram of the rat's body weight (i.e., $LD_{50} = 2$ mg/kg). For insects, researchers sometimes use slightly different units for LD_{50}. One of the commonly used units is μg/insect. In this case, the toxicity level of an insecticide is expressed based on the unit of an insect rather than the unit of the insect body weight. Because substantial differences exist among different ages, developmental stages, and genders of an organism due to their different body size and metabolic capability, the age and developmental stage of the test organism must be clearly specified. In addition, the purity of the insecticide, the solvent used to prepare the insecticide solution, the method and time of insecticide exposure, and the temperature and sometimes humidity must also be specified in an insecticide bioassay.

► Insecticides
► Acaricides

References

Busvine JR (1980) Recommended methods for measurement of pest resistance to pesticides. FAO Plant Production Protection Paper No. 21. FAO, Rome, Italy, 132 pp

French-Constant RH, Roush RT (1990) Resistance detection and documentation: the relative roles of pesticidal and biochemical assays. In: Roush RT, Tabashnik BE (eds) Pesticide resistance in arthropods. Chapman and Hall, New York, NY, pp 4–38

Gao J-R, Zhu KY (2000) Comparative toxicity of selected organophosphate insecticides against resistant and susceptible clones of the greenbug, *Schizaphis graminum* (Homoptera: Aphididae). J Agric Food Chem 48:4717–4722

Newman MC (1998) Fundamentals of ecotoxicology. Ann Arbor Press, Chelsea, MI, 402 pp

Robertson JL, Preisler HK (1992) Pesticide bioassays with arthropods. CRC, Boca Raton, FL, 127 pp

Tomlin C (2000) The pesticide manual, 12th edn. British Crop Protection Council and the Royal Society of Chemistry, Farnham, Surrey, United Kingdom, 1250 pp

Insecticide Formulation

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An insecticidal chemical synthesized by a manufacturer or laboratory prior to its further processing is known as technical grade compound. Technical grade insecticides often have high purity (e.g., greater than 95%). The essential component of a technical grade insecticide is the active ingredient (A.I.) that exerts toxic actions on an organism. However, technical grade insecticides are seldom used directly for pest control because their chemical and physical properties often are not suitable for commercial use. Therefore, technical grade insecticides should be brought into more appropriate forms (i.e., formulations) for their application, either as sprays, powders, granules, fumigants, baits, seed dressings, or other types of formulations.

The process of insecticide formulation involves the use of various methods to improve the properties of an insecticidal compound for storage, handling, application, efficacy, or safety. Typically, insecticides are formulated by mixing the active ingredients and auxiliary materials. Most auxiliary materials (Table 6) are inert; they serve strictly as carriers for active ingredients and have no direct effect on pests. However, other auxiliary materials, including synergists, surfactants (wetting agents, spreaders, emulsifiers, and dispersing agents), foam suppressants, and stickers, have important properties and functions. These auxiliary materials are commonly known as formulation adjuvants.

Main purposes of insecticide formulation

- Minimization of hazards to human s, animals, non-target organisms, and environment
- Maintenance of chemical and physical stability of formulations during storage, application and post-application periods (e.g., stability to heat, oxidation, water-hydrolysis, sunlight, and various forms of chemical deterioration)

- Application of a relatively small amount of the A.I. uniformly on a target to achieve the desired biological effect (efficacy) at the lowest cost
- Application of insecticides with ease and with readily available equipment
- Enhancement of the compatibility of the insecticide with other pesticides

The active ingredients of most insecticides are not very soluble in water, but are fairly soluble in lipophilic organic solvents such as petroleum and xylene. If an insecticide active ingredient is dissolved in an organic solvent and then diluted with water, the organic layer will quickly separate out from the water. This problem can be solved by adding an emulsifier, which is a surface active agent, to the insecticide solution in a formulation process. The emulsifier will allow the insecticide to form a stable emulsion of small globules on mixture with water in the spray tank. Thus, the insecticide emulsion can be sprayed easily onto the crop. Generally, the term formulation is reserved for commercial preparations of insecticide before they are sold. Final dilution of a formulated insecticide is not considered the process of formulation (Table 6).

Formulated insecticides are the final physical state that may be sold under the formulator's designated brand names. Because one insecticide active ingredient may be formulated into several different formulations for different applications, the same active ingredient may have several different formulations under different brand names. In 1997, approximately 20,700 formulations, representing 891 registered active ingredients of pesticides (insecticides, herbicides, fungicides, and others), were sold in the United States.

Many different types of insecticide formulations are currently available (Table 7). Choosing the most appropriate formulation for a particular pest management project is critical to effective and safe uses of insecticides. The most important question to ask in choosing an insecticide formulation is whether or not the product is labeled for the insect and crop or circumstance for which application is intended. In the United States, the State Agricultural Experiment Stations and Cooperative Extension Services are excellent sources for recommending the most appropriate insecticides and formulations for particular pest management problems.

Common factors to be considered in choosing an insecticide formulation (from Higley et al., 1989)

- Pesticide regulation: Whether or not the product is labeled for the insect pest and crop or circumstance for which application is intended.
- Type of environment: Some formulations may be more suitable for certain environmental settings (agricultural, urban, aquatic, etc.).
- Plant, animal, or surface to be protected: Some formulations may be phytotoxic, absorbed by the animal, or may pit and mar surfaces.
- Availability and suitability of application machinery: Some formulations require constant agitation or specialized equipment.

Insecticide Formulation, Table 6 Types of commonly used insecticide formulation adjuvants

Adjuvant	Properties and function
Surfactants	Affect properties that depend on surface tension, namely dispersability, emulsifiability, wetting and spreading of liquids
Spray modifiers	Modify the spray solution in the tank on the way to the target or on the target itself, such as spreaders and stickers that enable active ingredients to be retained on treated surfaces for a longer period
Utility modifiers	Widen the range of conditions under which a given pesticide formulation is useful, such as buffering agents and antifoam agents
Synergists	Are relatively nontoxic themselves, but capable of enhancing the toxicity of an active ingredient when mixed or used sequentially

Insecticide Formulation, Table 7 Common insecticide formulations and their characteristics

Formulation	Characteristics
Aerosol (A)	An active ingredient is dissolved in an oil solvent (or liquid carbon dioxide) and propellant. The insecticide is applied as a gas-propelled spray through a fine opening into closed or confined areas
Bait (B)	An active ingredient is mixed with an edible or attractive substance
Dust (D)	An active ingredient is mixed with a dry inert diluent (e.g., talc, clay). The formulated insecticide can be suspended easily in air
Emulsifiable concentrate (EC)	An active ingredient is dissolved in an oil-based solvent (toluene) and mixed with an emulsifying agent which permits the formulation to mix with water to form an emulsion
Flowable (F or L)	An active ingredient is wet-milled with a clay diluent and water to produce a gel-like material that can be measured as a liquid and mixed with water to form a suspension for spraying
Fumigant (F)	A volatile liquid or solid insecticide acts as a poisonous gas that is used in confined areas
Granular (G)	A liquid insecticide is applied to coarse particles (20–80 mesh) of a porous inorganic material such as clay or organic material such as macerated walnut shells or oat bran
Microencapsulation	An insecticide (either liquid or dry) is encapsulated in permeable microscopic spheres or capsules to permit the release of the insecticide at a slow or consistent rate
Soluble powder (SP)	An active ingredient is mixed with a finely-ground inert solid. The formulated insecticide can be dissolved completely in water or other liquid to form a true solution
Solution (S)	A concentrated liquid insecticide formulation may be used directly or mixed with water to form a true solution
Ultra low volume (ULV)	An insecticide concentrate can be sprayed undiluted at 0.6–4.7 l per hectare as finely dispersed droplets
Wettable powder (WP or W)	An active ingredient is mixed with an appropriate inert solid (e.g., talc, diatomaceous earth) and a wetting agent which permits the powder to mix with water to form a suspension

- Hazard of drift or run-off: Some formulations have greater hazard of drift or run-off than others. Proximity to sensitive areas and the likelihood of wind or rain should be considered.
- Safety to applicator and non-target animals: Insecticide exposure to an applicator and non-target animals can be significantly reduced by choosing an appropriate formulation.
- Habits or growth patterns of the pest: Some formulations may be more suitable to control pests in certain habits or at certain developmental stages.
- Cost: The price, efficacy and application of different formulations of the same insecticide may affect overall cost.

► Insecticides, Acaricides

References

Aspelin AL, Grube AH (1999) Pesticides industry sales and usage: 1996 and 1997 market estimates (733-R-99–001).

Office of Prevention, Pesticides and Toxic Substances, U.S. Environmental Protection Agency, Washington, DC, 39 pp
Cremlyn RJ (1991) Agrochemicals: preparation and mode of action. Wiley, New York, 396 pp
Foy CL, Pritchard DW (1996) Pesticide formulation and adjuvant technology. CRC Press, Boca Raton, FL, 384 pp
Higley LG, Karr LL, Pedigo LP (1989) Manual of entomology and pest management. Macmillan Publishing Company, New York, NY, 282 pp
Ware GW (2000) The pesticide book, 5th edn. Thomson Publications, Fresno, CA, 418 pp

Insecticide Resistance

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Insecticide resistance refers to the insecticide-selected inheritable ability of an insect or other arthropod population to withstand the exposure to a dose of an insecticide that would kill the majority of a normal (susceptible) population of the same species. Insects and other arthropods acquire resistance to natural, synthetic or bioengineered insecticides through various genetic alterations. Insecticide resistance is known to occur in target species for virtually all insecticide classes.

In contrast to resistance, insecticide tolerance is a natural tendency and is not a result of forced change in the genetic makeup of a population. Therefore, tolerance is often known as natural resistance. Many factors can lead to tolerance to insecticides in an insect. For example, old larvae of many lepidopteran insects are more tolerant to many insecticides than young larvae of the same species due to substantial differences in body size, cuticle thickness, and detoxification ability. Such differences should be identified as tolerance or natural resistance rather than true insecticide resistance.

Insecticide resistance was first found in the San Jose scale, *Quadraspidiotus perniciosus* (Comstock) to lime sulfur in 1908 in the state of Washington. There were only a few reported cases of insecticide and acaricide resistance before the introduction and widespread use of synthetic pesticides in the late 1940s. Currently, however, at least 540 insect and other arthropod species have been documented to have strains or populations resistant to one or more insecticides or acaricides. Insecticide resistance has become the limiting factor in managing many agriculturally and medically important pests worldwide.

Possible consequences of developing insecticide resistance in agricultural pests (based on Forgash, 1984)

- Loss of many formerly efficacious insecticides
- Significant losses and even complete failures of crops due to the increased difficulties in pest management
- Increase in production costs because of the need for higher dosages and more frequent applications of insecticides, or for new insecticides that are often more expensive
- Secondary pest outbreaks or pest resurgence because of the ecological disruption of the density relationships between the pest and beneficial species
- Increase the hazards of added insecticide burdens to non-targets and the environment
- Socioeconomic disruptions in agricultural communities because of the change of cultivation to escape from resistance scenarios

Development of insecticide resistance in insect populations can be explained by the selection principle of evolution. The alleles (genes) that can confer resistance to insecticides probably already exist in a given population due to polymorphism or gene mutation. When an insecticide is applied, the susceptible individuals are killed, leaving behind only those with the resistance alleles. Resistant individuals continue to reproduce and pass their resistance traits to the next generation. Thus, as more generations are exposed to the same insecticide, a larger proportion of the population becomes resistant to the insecticide. Eventually, the whole population may become resistant to the insecticide. Although the selection pressure of insecticides is a key factor leading to the development of resistance in an organism, many other factors also can influence the development and stability of insecticide resistance.

Major factors affecting development and stability of insecticide resistance

- Availability of resistance-conferring allele(s) in a given population
- Degree of dominance of the resistance-conferring allele(s)
- Degree of selection pressure by an insecticide within the population
- Persistence of the insecticides
- Relationship of an insecticide to earlier used insecticides (e.g., chemical nature, mode of action, etc.)
- Number of generations per year for the organism
- Mode of reproduction (sexual vs. asexual, fecundity, etc.)
- Population size
- Mobility of the organism (e.g., migration)

Both the chemistry of insecticides and the biology of arthropods are very diverse, but the number of mechanisms conferring insecticide resistance is relatively small. All known mechanisms can be generally classified into five types including behavioral avoidance, reduced penetration, sequestration, metabolic detoxification, and reduced sensitivity of target sites. Some mechanisms may be more common and important than others in conferring insecticide resistance in a given arthropod species.

Known mechanisms of insecticide resistance in arthropods

- Behavioral avoidance of exposure to insecticides in an organism (less well studied)
- Reduced penetration of insecticides through insect cuticle
- Sequestration of insecticide molecules by binding proteins or enzymes (e.g., esterases)
- Increased metabolic detoxification by various enzymes: Cytochrome P450 polysubstrate monooxygenases, carboxylesterases (e.g., malathion-specific carboxylesterases), phosphotriesterases, glutathione *S*-transferases
- Reduced sensitivity of insecticide target-sites: Acetylcholinesterase for organophosphates and carbamates, voltage-gated sodium channels for DDT and pyrethroids, γγ -aminobutyric acid (GABA) receptors for cyclodienes, binding receptors for the *Bacillus thuringiensis* toxins

An insecticide resistant population may show cross-resistance to several closely related insecticides (e.g., organophosphates) because of a common detoxification pathway or a change in susceptibility to common biochemical or physiological lesions. A resistant population also may show multiple-resistance to several unrelated insecticides with different modes of action and different detoxification pathways. Multiple-resistance often is caused by multiple resistance mechanisms and results from selection with different insecticides.

Because the development of insecticide resistance is a natural response of a pest population to selection by insecticides, resistance will remain an ongoing dilemma as long as insecticides are used in pest management programs. On the other hand, the use of insecticides will continue to be an indispensable component of pest management systems for the foreseeable future. Therefore, resistance management is a critical issue in any pest management program involving the use of either conventional chemical insecticides or transgenic plants containing toxin genes from other organisms such as the bacterium *Bacillus thuringiensis* (Bt). Every effort should be made to promote the long-term effectiveness of both currently available and newly developed insecticides.

References

Clark JM, Yamaguchi I (2002) Scope and status of pesticide resistance. In: Clark JM, Yamaguchi I (eds) Agrochemical resistance: extent, mechanism, and detection. American Chemical Society, Washington, DC, pp 1–22

Forgash AJ (1984) History, evolution, and consequences of insecticide resistance. Pestic Biochem Physiol 22:178–186

Melander AL (1914) Can insects become resistant to sprays? J Econ Entomol 7:167

Soderlund DM (1997) Molecular mechanisms of insecticide resistance. In: Sjut V, Butters JA, Sjut V (eds), Molecular mechanisms of resistance to agrochemicals (Chemistry of plant protection, 13). Springer, Berlin, Germany, pp 21–56

Ware GW (2000) The pesticide book, 5th edn. Thomson Publications, Fresno, CA, 418 pp

Zhu KY (2002) Resistance management. In: Pimentel D (ed) Encyclopedia of pest management. Marcel Dekker, New York, NY, pp 705–707

Insecticides

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Pesticides, chemical substances used to kill pests, may be more specifically categorized by the group of organisms they are designed to control. For example, herbicides are used to kill plants, rodenticides are used to kill rodents, and insecticides are used to kill insects. Herbicides are the leading type of pesticide, in terms of both user expenditures and volumes used. Annual pesticide use expenditures in the United States totaled $11.3 billion in 1995 with agriculture accounting for more than two thirds. About 1 billion pounds of active ingredient of pesticides are used annually in the USA. These chemicals are steeped in controversy. They are disparaged by environmentalists and lauded by many in the agricultural and public health communities. Despite how you may feel personally about pesticides, their use has undeniably improved the quality of life of human beings by increasing agricultural yields to levels that have maintained pace with an exponential human growth rate and improved public health by reducing or eliminating insect disease vectors. The following sections provide a brief overview of pesticide characteristics such as classification, mode of action, relative toxicity, and use. For more specific information on pesticides, the reader is referred to several authoritative references cited at the end of this article.

Definitions

Knowledge of a small number of definitions will be beneficial in understanding a discussion on pesticides and their characteristics. Most of these definitions can be found in the Federal Insecticide Fungicide and Rodenticide Act (FIFRA) which was first passed in 1947 (7 U.S.C. s/s 136 et seq. [http://www.epa.gov/pesticides/fifra.htm]) and later revised to the Federal Environmental Pesticide Control Act (FEPCA) in 1972. The primary focus of FIFRA was to provide federal control of pesticide distribution, sale, and use. The environmental protection agency (EPA) was given authority under FIFRA to study the consequences of pesticide usage and to require users to register when purchasing pesticides. The law also requires users to take exams for certification as pesticide applicators. All pesticides used in the U.S. must be licensed by the EPA (equivalent agencies in other countries regulate pesticide use). The Food and Drug Administration (FDA) is responsible for enforcing pesticide tolerances for humans. Listed below are some important terms necessary for the discussion of pesticides. An extended dictionary of terms can be found at the URL http://pmep.cce.cornell.edu/facts-slides-self/dictionary.html.

Pesticide

Any substance or mixture of substances intended for preventing, destroying, repelling, or mitigating any pest; any substance or mixture of substances intended for use as a plant regulator, defoliant, or desiccant.

Pest

Any insect, rodent, nematode, fungus, weed, or any other form of terrestrial or aquatic plant or animal life or virus, bacteria, or other micro-organism (except viruses, bacteria, or other micro-organisms on or in living man or other living animals) which the Administrator declares to be a pest under section 25(c).

Active Ingredient

In the case of a pesticide other than a plant regulator, defoliant, or desiccant, or nitrogen stabilizer, an ingredient which will prevent, destroy, repel, or mitigate any pest; in the case of a plant regulator, an ingredient which, through physiological action, will accelerate or retard the rate of growth or rate of maturation or otherwise alter the behavior of ornamental or crop plants or the product thereof; in the case of a defoliant, an ingredient which will cause the leaves or foliage to drop from a plant; in the case of a desiccant, an ingredient which will artificially accelerate the drying of plant tissue; and in the case of a nitrogen stabilizer, an ingredient which will prevent or hinder the process of nitrification, denitrification, ammonia volatilization, or urease production through action affecting soil bacteria.

MSDS (Material Safety Data Sheet)

Data sheet required to accompany all restricted use pesticides. Contains information on toxicity, reactivity and fire hazards, emergency information, health information, personal protection information and waste disposal instructions.

Lethal Dose Value

The LD value is associated with a subscripted numeral (e.g., LD_{50}). This is the quantity of active ingredient (expressed as milligrams of active ingredient per kilogram of body weight [mg/kg]) required to kill a specified proportion of a sample population. For example, the oral LD_{50} of malathion in the rat is 5,500 mg/kg. Therefore, at a dose of 5,500 mg/kg, malathion would be expected to kill 50% of the same species of rats by oral treatment. This value provides a method for comparing toxicities among and between species and for developing acceptable minimal exposure levels for humans.

Exposure Type

The method used to expose an organism to an active ingredient, including oral, inhalation and dermal. In addition, the exposure method may be conducted by acute treatment (one large single dose), subacute (several small doses over time), or chronic (small consistent doses over the course of an organism's lifetime).

Formulation

A mixture of active and inert ingredients that make a pesticide available for practical use.

Restricted Use Pesticide

A pesticide that can only be applied by EPA-certified applicators because of their inherent toxicity or potential hazard to the environment.

Mode of Action

The biochemical and/or physiological methods by which a toxicant functions.

Insecticide Toxicity Categories

FIFRA required that the toxicity of every insecticide appear on its label. A classification system was developed that placed an insecticide in one of four categories based on toxicity. Category I insecticides have an oral LD_{50} of up to 50 mg/kg and are labeled with the hazard indicator "Danger-Poison." Category II insecticides have an oral LD_{50} between 50 and 500 mg/kg and are labeled with the hazard indicator "Warning." Category III insecticides have an oral LD_{50} between 500 and 5,000 mg/kg and are labeled with the hazard indicator "Caution." Category IV insecticides have an oral LD_{50} greater than 5,000 mg/kg and are labeled with the hazard indicator "Caution."

Pesticide Nomenclature

There are currently about 875 active ingredients registered for use in the USA as federally restricted pesticides. Literally thousands of formulations are manufactured from these basic chemicals for use in urban, agricultural and other specialized environments. To avoid confusion among the different forms of pesticides, a standardized method of nomenclature has been established. There are four names a pesticide can be assigned: the manufacturer's identification number, the common name, the formulation name, and the chemical name. Hydramethylnon will be used to illustrate these different names. When the manufacturer assesses an active ingredient for activity as a pesticide, it is assigned an identification number for obvious reasons. Using our example, hydramethylnon was assigned the number AC 217,300 (AC is for American Cyanamid). Once the manufacturer is satisfied with the performance of an experimental pesticide, a common name is assigned to the active ingredient by the professional society most closely associated with the chemical's use. AC 217,300 was developed as an insecticide, therefore, the Entomological Society of America assigned the common name hydramethylnon to the active ingredient. Formulation manufacturers are now able to use hydramethylnon to produce a number of formulations for use, perhaps, in different areas and against different insect pests. The formulated products are identified by trade names. Several examples of trade names for formulated hydramethylnon include Amdro (fire ant bait), Combat (cockroach bait), and Maxforce (cockroach bait). The final name is the chemical name which is assigned according to IUPAC (International Union of Pure and Applied Chemists) rules. The chemical name for hydramethylnon is tetrahydro-5,5-dimethyl-2(1H)-pyrimidinoine (3-(4-(trifluoromethyl)phenyl)-1-(2-(4-(trifluoromethyl)phenyl)ethenyl)-propenylidene) hydrazone.

Formulations

A formulated insecticide is a mixture of active and inert ingredients that permit practical use of an insecticide. The active ingredient alone is rarely used in its raw form. Formulation processing improves active ingredient properties of storage, handling, application, effectiveness, and safety. Most restricted use insecticide formulations must be diluted before being used. Conversely, most general use insecticides (those applied without specialized training) are diluted and ready to apply. For example, Raid Ant and Roach spray is sold in a ready to use form. Insecticide formulations are listed, described and general characteristics provided below. Traditionally, each formulation type is abbreviated (shown in parentheses). In agriculture and urban settings, most insecticides (more than 75%) are applied as water-based sprays. However, it must be realized that most insecticide active ingredients are not water soluble; therefore, to apply as a water spray, surfactants must be added to facilitate dispersion in water. Obviously the goal of insecticide formulating is to make the product more efficacious against the target pest. An array of chemicals, called adjuvants, may be included in an insecticide formulation to achieve this goal. Surfactants are adjuvants that disperse an insoluble insecticide in water. These may be anionic (e.g., sodium lauryl sulfate), cationic (e.g., lauryl trimethyl ammonium chloride), or nonionic (e.g., glycol monolaurate). In addition, surfactants lower the surface tension of water which provides more coverage by aqueous solutions on leaf surfaces. Synergists are also important adjuvants added to insecticide formulations. Alone, synergists are non-toxic, but when mixed with certain insecticides greatly increase their toxicity. Synergists achieve this by inhibiting the metabolic enzymes that detoxify the insecticide. Synergists are most widely used in combination with pyrethrins and pyrethroids, especially in the urban environment. The most common synergists are methylene dioxyphenyl compounds (e.g., piperonyl butoxide and sesamex). Other adjuvants include foam suppressants, penetrants, and pH buffers.

Emulsifiable Concentrates (EC)

Concentrated oil solutions of the technical grade material containing an emulsifier (surfactant). The emulsifier is a detergent-like material that surrounds the hydrophobic insecticide active ingredient creating microscopically small oil droplets in water to form an emulsion. The appearance of a prepared EC is milky. The toxicant content in an EC generally ranges from 25% to 50% w/v. Because ECs contain organic solvents they may burn foliage. ECs are applied as liquid sprays.

Water-Miscible Liquids (Includes Water-Soluble Concentrates [WSC], Liquids [L], Soluble Concentrates [SC], and Solutions [S])

The technical material is provided in a water or alcohol base that is diluted in water. The active ingredients are generally water or alcohol miscible. These formulations are applied similarly to ECs. Most of these formulations are restricted use. These formulations are applied as liquid sprays.

Water-Soluble Powders (SP)

The technical material is water soluble and provided as a powder or solid. A small amount of surfactant may be added to facilitate mixing. These can be very toxic to handle because the active ingredient is not diluted in any way. Thus, they are often manufactured in water soluble bags that are simply dropped into a spray tank with water. After dissolution, the insecticide is ready to be sprayed. SPs are applied as liquid sprays.

Wettable Powders (WP)

In WPs the technical material is adsorbed onto a dust particle. In addition, wetting agents are added to facilitate dispersal. The powder is added to water and sprayed as a suspension of particles in water. This formulation requires constant agitation to keep the particles suspended. It is generally packaged at a concentration of 50–75% active ingredient. WPs are abrasive to spray equipment and do not burn foliage because they do not contain an organic solvent as ECs do. WPs are applied as liquid sprays.

Oil Solutions

Oil solutions are most often the ready-to-use household and garden insecticide sprays. The active ingredient is dissolved in some type of oil or organic solvent. Oils may be further diluted in kerosene or diesel fuel. Oil solutions are applied as liquid sprays.

Flowables (F)

This formulation was created for insecticides that were not soluble in water or oil. Therefore, the technical material is wet-milled with a clay diluent and water, leaving the pesticide-diluent mixture finely-ground but wet. This thick and creamy "pudding" mixes well with water and can be sprayed. However, constant agitation is required as with the WPs. Flowables are applied as liquid sprays.

Ultralow-Volume (ULV)

Technical material dissolved in a very low volume of solvent. Applied without dilution by special aerial or ground equipment that limits the volume applied (0.5 pints to 0.5 gallons per acre). ULVs are applied as a liquid spray.

Dusts (D)

An active ingredient with an inert clay diluent (such as pyrophyllite). Dusts are distinguished from granulars by size. Dusts will pass through a 60 mesh screen. Drift is a major disadvantage of using dusts. Dusts are applied as a dry formulation.

Granular (G)

Small pellets formed from inert clays sprayed with a toxicant-containing solution to give the desired content. Granulars range from 2% to 25% active ingredient. Granulars are applied as a dry formulation.

Aerosols

A common formulation used by homeowners. Aerosols are comprised of technical material solubilized in a volatile, petroleum solvent which has been pressurized (by a propellant gas). When the petroleum solvent is atomized, it evaporates quickly, leaving micro droplets of toxicant suspended in the air. Little to no residual activity is provided by aerosols. Aerosols are a liquid formulation.

Fumigants

The active ingredient of a fumigant either sublimates or boils at standard temperature and pressure. For example, moth balls and moth crystals, naphthalene and paradichlorobenzene, respectively, are solids that sublimate slowly at room temperature. Other fumigants have extremely low boiling points and are kept as liquids under high pressure. Pressurized fumigants are primarily used for drywood termite control, nematode control, and stored product insect control. Fumigants are applied as a gas.

Baits

This formulation has seen renewed interest in recent years because they use a very small quantity of insecticide and specifically target the pest of interest. Baits are comprised of an active ingredient incorporated into a food matrix that is palatable to the target insect pest.

Controlled-Release (CR)

This formulation is based on the incorporation of a volatile insecticide into a (usually) polymer matrix. By several mechanisms, including degradation or diffusion, a steady release of insecticide occurs. Controlled release formulations may be liquids or solids that are released as a gas.

Insecticides

Insecticides can be classified or grouped by their chemical structure, mode of entry into the insect, toxicity, or mode of action. The most common method of classification employed by insecticide toxicologists is chemical structure. By this method, insecticides with a similar chemical framework or motif are grouped together. As this is the most widely accepted method of discussing insecticides, it will be employed here. Pesticides have been used since at least 1,200 B.C.; however, the following discussion will focus on modern synthetic organic insecticides debuting after World War II. Some mention of botanical insecticides will also be included as these plant-derived chemicals often serve as models for synthetic organic insecticides. The characteristics, mode of action, toxicity, uses, examples and peculiarities of each insecticide chemical class will be described.

Organochlorines

Dichlorodiphenyltrichloroethane (DDT) Group

Examples of this group include DDT, DDD, TDE, Dicofol, and Methoxychlor. These insecticides are effective against a wide range of insect pests, most notably the mosquito. In fact, Paul MÜller won the Nobel prize in 1948 for discovering the insecticidal properties of DDT. These insecticides are environmentally persistent (DDT has a half life of 10 years), have a low vapor pressure, low water solubility, moderate stability to sunlight and low mammalian toxicity (toxicity category II to III). They are also lipophilic and metabolically stable which results in bioaccumulation (Fig. 16).

Interestingly, these insecticides exhibit a negative temperature coefficient of toxicity. In other words, they become more toxic at lower temperatures. DDT was banned from use in the United States in 1973. The target site for this group is the voltage-gated sodium channel, a neuron protein involved in the propagation of nerve impulses. It is believed that these chemicals act as a wedge that hold the channels in the open position thus preventing repolarization and resulting in constant stimulation of the nerve.

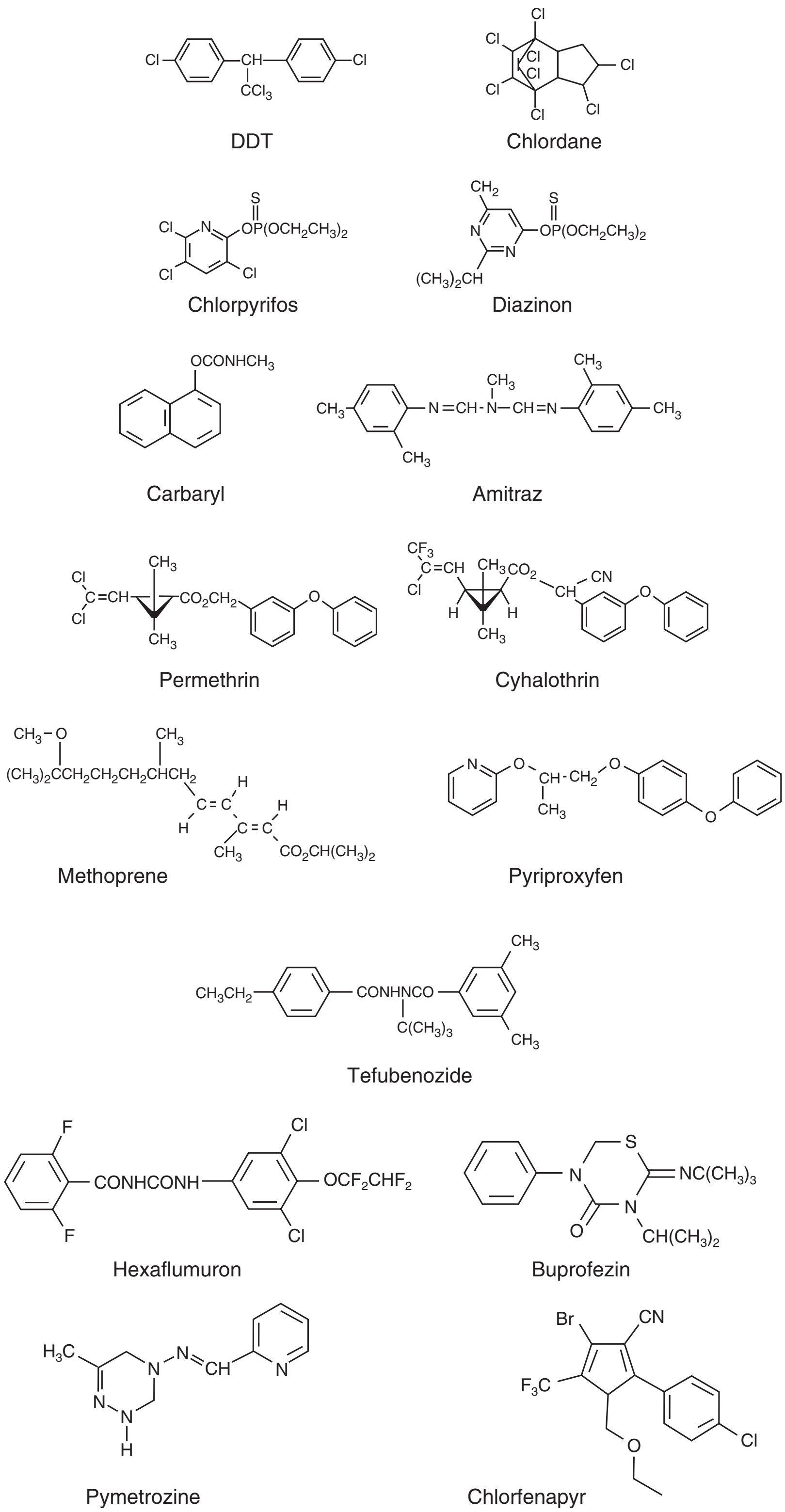
Chlorinated Cyclics

Examples of this group include Lindane, Aldrin, Dieldrin, Endrin, Isodrin, Chlordane, Mirex, Heptachlor, Chlordecone, and Endosulfan. These insecticides were used widely in urban settings, most notably for termite (Chlordane, Aldrin, Heptachlor) and imported fire ant (Mirex) control. Also, because they were stable in soil and against ultraviolet light, they were used against soil inhabiting insects in agriculture. Most of these insecticides were banned from agricultural use in the USA between 1975 and 1980. Mirex was banned for use in the USA in 1977 and chlordane in 1988. This group is persistent, lipophilic and has a low vapor pressure (10^{-6}–10^{-7} mmHg). Lindane is still available for use in the USA on avocados, pecans, Christmas trees, commercial ornamentals, structural treatments, and dog dusts. Many of these insecticides are metabolically activated (i.e., are made more toxic *in vivo*) by an epoxidation reaction catalyzed by cytochromes P450. The mode of action of cyclodienes was only recently elucidated. These insecticides are gamma-aminobutyric acid (GABA) receptor antagonists. Although environmentally persistent, acute toxicity of organochlorines is generally low to moderate (toxicity category II–III).

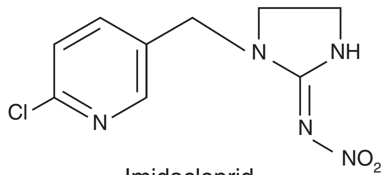
Organophosphates

Derived from phosphoric acid, this is the most toxic group of insecticides (toxicity category I to II). This large group of insecticides replaced the organochlorines and includes Malathion, Parathion, Dimethoate, Dicrotophos, Disulfoton, Monocrotophos, Trichlorfon, TEPP, Acephate, Methamidophos, Diazinon, Azinphosmethyl, and Chlorpyrifos among others. Organophosphates are unstable, susceptible to hydrolytic and oxidative detoxification, moderately to considerably water soluble and have a vapor pressure in the range of 10^{-3}–10^{-5} mmHg. The insecticidal activity of organophosphates was discovered in Germany during World War II while studying the nerve gases Sarin, Soman, and Tabun, which are also phosphoric acid derivatives. Organophosphate insecticides are anticholinesterases. They bind, with tenacious affinity, to acetylcholinesterase (AChE), a crucial enzyme found in the synaptic cleft between neurons or neuromuscular junctions. AChE normally hydrolyses the neurotransmitter acetylcholine released from the presynaptic neuron. However, organophosphate insecticides inhibit this enzyme preventing normal hydrolysis of acetylcholine and resulting in constant post-synaptic depolarization (stimulation). Many orga-nophosphate insecticides are activated (made more toxic) *in vivo*. Phosphorothioate (P = S) is oxidized to an oxon (P = O) form by cytochromes P450 making the insecticide bind even more tightly to acetylcholinesterase.

Although organophosphorus insecticides are all derived from phosphoric acid, there are 6 different subclasses depending on the molecular composition about the phosphate nucleus.



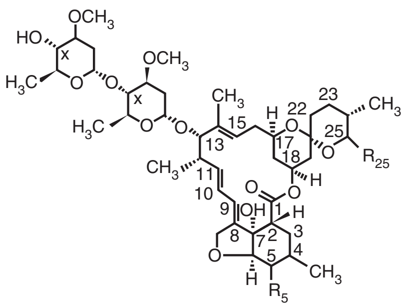
Insecticides, Figure 16 **Representative molecular structures of each insecticide class.**



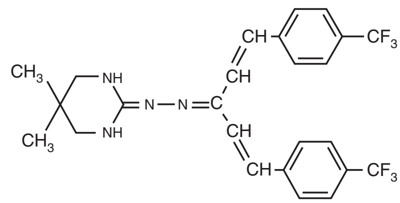
Imidacloprid

$F_3C-CF_2-CF_2-CF_2-CF_2-CF_2-CF_2-CF_2-S(=O)_2-NH-CH_2-CH_3$

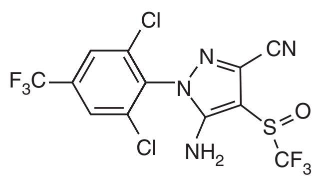
Sulfuramid



Avermectin (base structure)



Hydramethylnon



Fipronil

Insecticides, Figure 16 (Continued).

These subclasses include phosphate, phosphonate, phosphorothioate, phosphorothiolate, phosphorodithioate, and phosphoramidate. Organophosphate insecticides have seen wide use in agricultural, silvicultural, and urban insect control. However, because of their acute toxicity, much of this insecticide class is being banned from use, especially in the urban environment.

Carbamates

Introduced by the Geigy Chemical Company in 1951, carbamates are derivatives of carbamic acid (CO_2NH_3). As with the organophosphates, these insecticides are also anticholinesterases. They are biodegradable, moderately volatile (vapor pressure between 10^{-4} and 10^{-6} mmHg), moderately soluble in water, and susceptible to hydrolysis. Some of the more common carbamates include Propoxur, Bendiocarb, Carbaryl, Methomyl, Carbofuran, Aldicarb, and Thiodicarb. These insecticides exhibit toxicities that range from class I (e.g., Methomyl) to III. Carbaryl, introduced in 1956, has been used more than any other carbamate because of its low mammalian toxicity (Oral LD_{50} 307 mg/kg) and broad spectrum of insect control.

Formamidines

This is a small group of pesticides with insecticidal, acaracidal and ovacidal activities. The only formamidine currently in use in the USA is Amitraz. Chlordimeform was found to be carcinogenic and banned from use in the USA in 1988. Formamidine insecticides are octopaminergic agonists, so they interfere the normal activity of biogenic amines.

Because octopamine is an important neurotransmitter, formamadine interference results in behavior modification. For example, it causes loss of appetite and feeding, alters mating behavior, and detachment of ticks from the host. They also have been shown to synergize pyrethroid insecticide toxicity by modifying binding cooperativity in neural proteins. Toxicity category ranges from II to III.

Pyrethroids

Pyrethroids are synthetic chemicals modeled after the botanical insecticide pyrethrum, an organic extract of *Chrysanthemum cinerariaefolium* (Compositae) flower heads. The active principle of pyrethrum is pyrethrins, esters formed by the combination of acid (mono- and di-chrysanthemic acids) and alcohol (pyrethrelone, cinerolone, and jasmolone) components. Although pyrethrins exhibit good insecticidal activity, they were very labile. Therefore, synthetic versions were produced to improve their stability. Pyrethroids may be further categorized based into Type I and Type II groups. These refer to the types of neurological tremors produced and is loosely associated with the presence of a cyano (-CN) moiety at the alpha carbon position. Pyrethroids are widely used broad spectrum insecticides including Permethrin, Resme-thrin, Tetramethrin, Allethrin, Bifenthrin, Cypermethrin, Fenvalerate, Deltamethrin, Tralomethrin, Fluvalinate, Fenpropathrin, Cyhalothrin, and Esfenvalerate. Pyrethroids exhibit stereoisomerism (geometric, enantiomeric), low water solubility and vapor pressure (10^{-6} to 10^{-7} mmHg), negative temperature coefficient of toxicity (the alpha-cyano pyrethroids may exhibit a slightly negative or positive temperature coefficient of toxicity) and stability without persistence (bioaccumulation). They are susceptible to hydrolysis. Pyrethroids represent one of the first steps toward a precision targeting approach to pest control because they are more toxic to insects than mammals. This moderate level of specificity has resulted in extensive use of pye-throid insecticides. Unfortunately, pyrethroids are extremely toxic to fish, so care must be exercised when applications take place near water. Pyrethroids target the voltage-gated sodium channel of the nervous system and result in uncontrolled nerve excitation, as do the DDT insecticides. However, the specific binding site on the voltage-gated sodium channel is different from the DDT group.

Insect Growth Regulators

This group is comprised of a diverse group of chemical compounds with varying molecular structures. However, they are grouped together here because they all affect insect growth in some manner. Note that these chemicals are comparatively new tools used in insect control. Interestingly, these chemicals illustrate the evolution of insect control methods which are becoming more specific for the target species which reduces environmental impact and improves efficacy.

Juvenoids

Compounds that mimic the juvenile hormone of insects include Methoprene and Hydroprene. These juvenoids keep the insect in its immature form which prevents the production of future generations and often results in death from conflicting hormonal messages during ecdysis to the adult stage. Fenoxycarb (a carbamic acid derivative without anticholinesterase activity) and Pyriproxyfen also are juvenoids, however, unlike Methoprene and Hydroprene do not resemble the structure of juvenile hormone. All of these compounds act as juvenile hormone agonists (mimics).

Ecdysone Agonists

These chemicals mimic the action of the insect hormone ecdysone and thus induce premature molting. Rohm and Haas have developed several ecdysone agonists including Tebufenozide and RH-5849. These are substituted dibenzoyl hydrazine compounds.

Chitin Synthesis Inhibitors (CSI)

The final group of insect growth regulators include the chitin synthesis inhibitors. These include benzoylphenyl ureas (Diflubenzuron, Chlorflurazuron, Teflubenzuron, Hexaflumuron, and Novaluron) and buprofezin. These CSIs inhibit chitin formation thereby causing abnormal cuticular formation and abortive molting. Benzoylphenyl ureas have become important components of subterranean termite control in the US. They also have found utility in veterinary and agricultural areas.

Pyridine Azomethines

The only example of this new insecticide group is Pymetrozine (GCA 215,994). Pymetrozine is anticipated to be an important component of IPM programs against sucking insect pests because it exhibits a high degree of selectivity, low mammalian toxicity, and safety to birds, fish and nontarget arthropods. The target site for this insecticide is not currently known; however, it causes an immediate and irreversible cessation of feeding after exposure. The mode of action is due to a blockage of stylet penetration.

Chloronicotinyls

This group was initially developed during the 1970s (heterocyclic nitromethylenes), but recent chemical optimizations have resulted in the highly active insecticide, Imidacloprid. Other modifications resulting in insecticidal chloronicotinyls include Nitenpyram and Acetamiprid. The group has broad applicability as many insect species are susceptible. Imidicloprid is translocated making it ideal for use against sucking insects. It has also been shown to be quite effective as a termiticide. Imidicloprid has been shown to displace alpha-bungarotoxin, a specific ligand of the nicotinic acetylcholine receptor (nAChR) which demonstrates that it acts directly on this receptor. Indeed, electrophysiological experiments have shown that Imidacloprid depolarizes the cell membranes of insect cholinergic motor neurons. Furthermore, Imidacloprid does activate vertebrate nAChRs, however, the effect is more than 1,000-fold weaker than the action on insects. Therefore, it appears as if Imidacloprid is insect selective.

Inhibitors of Cellular Respiration

A number of relatively new insecticide classes that target cellular respiration are available. These insecticides exhibit a novel mode of action by inhibiting oxidative phosphorylation through several mechanisms. Many are proinsecticides (i.e., they require metabolic activation for toxicity).

Pyrroles

The inspiration for development of this group originated in dioxapyrrolomycin, a fermentation product of *Streptomyces fumanus* isolated in 1985 by American Cyanamid's Medical Research Division. Unfortunately, the mammalian toxicity of this compound was quite high which precluded its use in the insecticide market. However, after extensive chemical manipulation based on a fundamental understanding of oxidative phosphorylation, an insecticidal chemical was produced with acceptable vertebrate toxicity. CL 303,630 (Chlorfenapyr) was the result. This insecticide uncouples oxidative phosphorylation by disrupting the proton gradient across the inner mitochrondrial membrane impairing ATP production. Interestingly, Chlorfenapyr is a proinsecticide requiring oxidative N-dealkylation for toxicity. Chlorfenapyr is active against a wide array of insects and is being marketed for use in agricultural and urban environments.

Amidinohydrazones

This insecticide class is represented by Hydramethylnon. Hydramethylnon is primarily used in baits (e.g., against fire ants, pest ants, and cockroaches). It is an extremely effective insecticide with low mammalian toxicity (toxicity category III). This insecticide is a potent inhibitor of electron transport, specifically ubiquinone cytochrome c reductase (complex III). Interestingly, Hydramethylnon has been used against the German cockroach, *Blattella germanica*, for nearly two decades, however, no resistance has been observed to date.

Halogenated Alkyl Sulphonamides

Represented by a single insecticide, Sulfluramid, this compound acts as a protonophore disrupting the proton gradient generated by the electron transport system, thus inhibiting ATP production via oxidative phosphorylation. As is Chlorfenapyr, Sulfluramid is a proinsecticide that requires oxidative *N*-dealkylation for toxicity. It is primarily used in ant and cockroach baits.

Sulfluryl Fluoride

Sulfluryl fluoride is a fumigant used primarily for the treatment of drywood termites. This is not an organic insecticide, however, it is included here because of its importance in termite control. Known by the trade name Vikane, sulfluryl fluoride disrupts substrate level and oxidative phosphorylation by inhibiting aconitase in the tricarboxylic acid cycle and enolase in the glycolytic cycle.

Additional Inhibitors of Cellular Respiration

Several additional insecticidal compounds that inhibit cellular respiration have been identified and investigated. However, they are in varying stages of development and not currently available for use in the US. These include: (i) Diafenthiruon, a thiourea that is activated *in vivo* to its carbodiimide product which blocks the coupling site and mitochondrial F_0/F_1 ATPase activity; and (ii) Fenazaquin, a quinazoline that uncouples oxidative phosphorylation by inhibiting complex I of the electron transport chain. The only other insecticide known to inhibit complex I is Rotenone, a botanical insecticide.

Avermectins

Avermectins are a series of homologous macrocyclic lactone natural products (termed A_{1a}, A_{1b}, A_{2a}, A_{2b}, B_{1a}, B_{1b}, B_{2a}, and B_{2b}) derived from the soil microorganism *Streptomyces avermitilis*. The B_{1a} and B_{1b} homologues are very potent against mites and certain insect species. These compounds act as chloride channel agonists (GABAergic channels) as do the cyclodienes. Primarily used as an acaracide, avermectins have also been used in fire ant baits and against several leafminers.

Phenylpyrazoles

Represented by Fipronil, the phenylpyrazoles are also GABA-gated chloride channel antagonists. Other phenylpyrazoles exhibit herbicidal activity. Based on synergist data from some insect species (e.g., German cockroach), fipronil may be activated *in vivo*. This insecticide is effective against a wide array of insects and appears to be an extremely effective termiticide.

Miscellaneous/Botanicals

Insecticidal chemicals derived from plants (botanicals) also serve as an important source of insecticides. Numerous botanicals are available with diverse modes of action which are discussed elsewhere in this reference. Although botanical insecticides are "natural," often they are extremely toxic and should be handled with great care.

Other insecticides used currently include *Bacillus thuringiensis* (Bt), the active component of which (delta-endotoxin) is now heterologously expressed in numerous crop plants, inorganic insecticides (e.g., boric acid, cryolite [Na_3AlF_6]), fumigants (e.g., para-dichlorobenzene, methyl bromide), and soaps. Many of these additional insecticides are described elsewhere in this reference or can be found in the following references.

Toxicity

Insecticide toxicity is dependent upon the class, formulation, mode of action and mode of entry of a chemical into an organism, and may be assessed or quantified in many different ways. For example, an insecticide's toxicity can be measured based on its carcinogenicity, dermal effects, inhalation effects, reproductive effects, acute toxicity, subchronic and chronic effects and genetic effects. Each group of insecticides will exhibit unique characteristics, and although the toxicity will vary considerably among and between insecticide groups, they must all be handled with great care (Table 10).

► Acaricides or Miticides
► Detoxification Mechanisms in Insects
► Insecticide Application: The Dose Transfer Process
►Insecticide Bioassay
►Insecticide Resistance
►Insecticide Toxicity
►Synergism
►Pesticide Hormoligosis
►Botanical Insecticides
►Food-Based Poisoned Baits for Insect Control

Insecticides, Table 10 **Comparative toxicity ratings of some common insecticides by insecticide class**

Active ingredient	Insecticide class	Toxicity category	LD_{50} (mg/kg, oral rat)
DDT	Organochlorine	II	113
Methoxychlor	Organochlorine	IV	6,000
Parathion	Organophosphate	I	2
Malathion	Organophosphate	IV	5,500
Chlorpyrifos	Organophosphate	II	96–270
Methomyl	Carbamate	I	17
Carbaryl	Carbamate	II	246
Amitraz	Formamidine	III	650
Permethrin	Pyrethroid	II–III	430–4,000
Cypermethrin	Pyrethroid	II	250
Fenvalerate	Pyrethroid	II	451
Pyriproxyfen	IGR (Juvenoid)	IV	>5,000
Methoprene	IGR (Juvenoid)	IV	>34,600
Tebufenozide	IGR (Ecdysone Agonist)	IV	>5,000
Diflubenzuron	IGR (Chitin Synthesis Inhibitor)	III	>4,640
Buprofezin	IGR (Chitin Synthesis Inhibitor)	III	2,198
Pymetrozine	Pyridine Azomethine	IV	5,820
Imidacloprid	Chloronicotinyl	II	450
Hydramethylnon	Amidinohydrazone	IV	>5,000

References

Hopkins WL (1996) Global insecticide directory. William Hopkins Agricultural Chemical Information Services, Indianapolis, IN

Matsumura F (1985) Toxicology of insecticides. Plenum Press, New York, NY

Meister RT (2002) Farm chemical handbook. Meister Publishing Company, Willoughby, OH

Reigart JR, Roberts JR (1999) Recognition and management of pesticide poisonings (EPA 735-R-98–003). U.S. Environmental Protection Agency, Washington, DC

Ware GW (1989) The pesticide book. Thomas Publications, Fresno, CA

Insecticide Toxicity

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Toxicity refers to the innate capacity of a chemical to be poisonous to living organisms. Virtually every known chemical has the potential to produce toxic effects (e.g., injury or death) if the chemical is administered to an organism at a sufficient dose. If a chemical indeed exerts its toxicity on an organism, there must be two key features associated with the toxicity as determined by an appropriate bioassay. First, there is an observable and well-defined end effect resulting directly from the action of a toxic chemical. For example, the death of insects exposed to an insecticide is an observable and well-defined end effect. Secondly, the toxic effect must be dose-dependent. Within an appropriate dose range, the toxic effect must be positively correlated with the dose. Such a relationship, commonly known as the dose-response relationship, is the most fundamental and important feature of toxicity.

Insecticide toxicity can be either acute or chronic. Acute toxicity refers to injury or death after a short and often intense exposure of an organism to an insecticide. In laboratory toxicity testing, the duration of an acute exposure to an insecticide generally ranges from several to 48 h. For example, a single dose or exposure of an insecticide to insects and other arthropods for 24 h is most commonly used to evaluate the acute toxicity of the insecticide. In contrast, chronic toxicity refers to adverse effects after prolonged or repeated exposures of an organism to low doses of an insecticide. Chronic toxicity is commonly determined beyond 96 h, and usually after several weeks to several months of exposure. In vertebrates, for example, observable end effects for chronic toxicity of an insecticide may include development of tumors or cancer, reproductive problems, damage to the nervous system, damage or degeneration of internal organs such as the liver, allergic sensitization, etc.

Acute toxicity of an insecticide is commonly expressed as the median lethal dose (LD_{50}), concentration (LC_{50}) or time (LT_{50}). The LD_{50}, LC_{50}, and LT_{50} refer to the dose, concentration, or time, respectively, required to kill 50% of the population of the test organism under stated conditions. In the cases in which the rate of knockdown of the test organism is a more important criterion than the rate of killing for the toxicity of an insecticide, the median knockdown dose (KD_{50}), concentration (KC_{50}), or time (KT_{50}) is used. In some instances, the toxicity of an insecticide is measured as developmental and reproductive toxicity, mutagenicity and other effects rather than the mortality or knockdown caused by the insecticide. In such cases, the median effective dose (ED_{50}) or concentration (EC_{50}) is commonly used.

Because the toxicity of an insecticide is related to the developmental stage, body size, gender and species of the organism exposed, the species (and strain), developmental stage, and sex of the test organism are often specified and the body weight units (milligram, gram, kilogram, etc.) used to express the toxicity level of an insecticide. For example, the LD_{50} value of cypermethrin for third-instar larvae of the fall armyworm (*Spodoptera frugiperda*) is 0.46 μg/g determined by a 48-h topical bioassay. That is, if the larvae are topically applied with cypermethrin at the dose of 0.46 μg/g of the larval body weight, 50% of test larvae will die in 48 h. Obviously, the smaller the LD_{50} value is, the greater the toxicity is for an

Insecticide Toxicity, Table 8 Representative toxicities of two pyrethroid insecticides to larval and adult fall armyworm (*Spodoptera frugiperda*) and black cutworm (*Agrotis ipsilon*) (Lepidoptera: Noctuidae)

Insect	Stage/sex	Cypermethrin LD_{50} (95% CI), µg/g	Permethrin LD_{50} (95% CI), µg/g
Fall armyworm	Third instar	0.46 (0.33–0.59)	0.71 (0.58–0.87)
	Male	0.95 (0.75–1.19)	1.20 (0.92–1.54)
	Female	1.28 (0.63–1.72)	1.85 (1.46–2.27)
Black cutworm	Third instar	0.48 (0.26–0.64)	0.35 (0.05–0.62)
	Male	2.26 (1.83–2.82)	2.52 (2.01–3.18)
	Female	1.74 (1.37–2.23)	0.99 (0.81–1.20)

Data adapted from Usmani and Knowles (2001). The Ld_{50} values were determined based on 48-h topical bioassays

Insecticide Toxicity, Table 9 Classification of toxicity and examples of insecticide toxicity to rats (from Tomlin, 2000)

Toxicity class (LD_{50} range, mg/kg)	Name of insecticide	Oral LD_{50} (mg/kg)
Supertoxic (<5)	Parathion	2
Extremely toxic (5–50)	Carbofuran	8
Very toxic (50–500)	Chlorpyrifos	135–163
Moderately toxic (500–5,000)	Malathion	1,375–2,800
Slightly toxic (5,000–15,000)	Fenoxycarb	>10,000
Practically non-toxic (>15,000)	Methoprene	>34,600

insecticide, or the more susceptible the insect is to an insecticide. Researchers sometimes use slightly different LD_{50} units for insects. One of the commonly used units is 1/4g/insect, which is expressed based on the unit of an insect rather than the unit of the insect body weight (Table 8).

Based on the LD_{50}, LC_{50} or other toxicity values determined using a standard animal species such as rats, insecticides can be classified into six categories from supertoxic to practically non-toxic. Although there are considerable differences in response to an insecticide among different animal species, toxicity data determined using a vertebrate species (e.g., rats, mice and rabbits) generally serve as good references for other vertebrates such as humans. Therefore, the mammalian toxicity data can be very useful in helping establish the guidelines for safe handling, storage, and application of insecticides (Table 9).

► Insecticides
► Acaricides

References

Crosby DG (1998) Environmental toxicology and chemistry. Oxford University Press, New York, NY, 336 pp

Eaton DL, Klaassen CD (2001) Principles of toxicology. In: Klaassen CD (ed), Cassarett and Doull's toxicology: the basic science of poisons 6th edn. McGraw-Hill, New York, NY, pp 11–34

Newman MC (1998) Fundamentals of ecotoxicology. Ann Arbor Press, Chelsea, MI. 402 pp

Tomlin C (2000) The pesticide manual, 12th edn. British Crop Protection Council and the Royal Society of Chemistry, Farnham, Surrey, United Kingdom. 1,250 pp

Usmani KA, Knowles CO (2001) Toxicity of pyrethroids and effect of synergists to larval and adult *Helicoverpa zea*, *Spodoptera frugiperda*, and *Agrotis ipsilon* (Lepidoptera: Noctuidae). J Econ Entomol 94:868–873

Ware GW (2000) The pesticide book, 5th edn. Thomson Publications, Fresno, CA, 418 pp

Insectivore

An animal that feeds on insects. An entomophage.

Insectivorous Plants

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For all the popular enthusiasm for insectivorous (carnivorous) plants and the general assumption that insects are the victims, there is little knowledge of the victims. This article provides a brief background to distribution, diversity, and trapping methods of insectivorous plants, and it attempts to associate the entomological knowledge for each genus. Lack of entomological information below under the name of any plant genus simply means that the author found none, or at least none obtained from the field. (The ability of these plants to digest insects such as fruit flies provided to them in cultivation tells little about their diet in nature.) Carnivorous fungi are not discussed in this article.

In general, plants absorb nitrogen and phosphorus from the soil through their roots. Insectivorous plants, however, absorb nitrogen and phosphorus from their animal prey through their leaves specially modified as traps. Thus, at simplest, insectivorous plants trap animals and absorb nutrients from the trapped prey.

However, some botanists have codified this process and they claim that to be insectivorous, a plant should have:

- A method of attracting animal prey
- A method of trapping animal prey
- A method of killing animal prey
- A method of digesting animal prey and taking up nitrogen (and phosphorus)

Not all insectivorous plants listed as such by botanists pass all these tests. In particular, many have not yet been shown to secrete digestive enzymes or take up nitrogen through their leaves. Conversely, the account below shows that some plants obtain nutrients from trapped prey by variant mechanisms. The principal types of traps used by plants to capture insects are discussed elsewhere (see Carnivorous Plants).

Nepenthaceae: *Nepenthes*

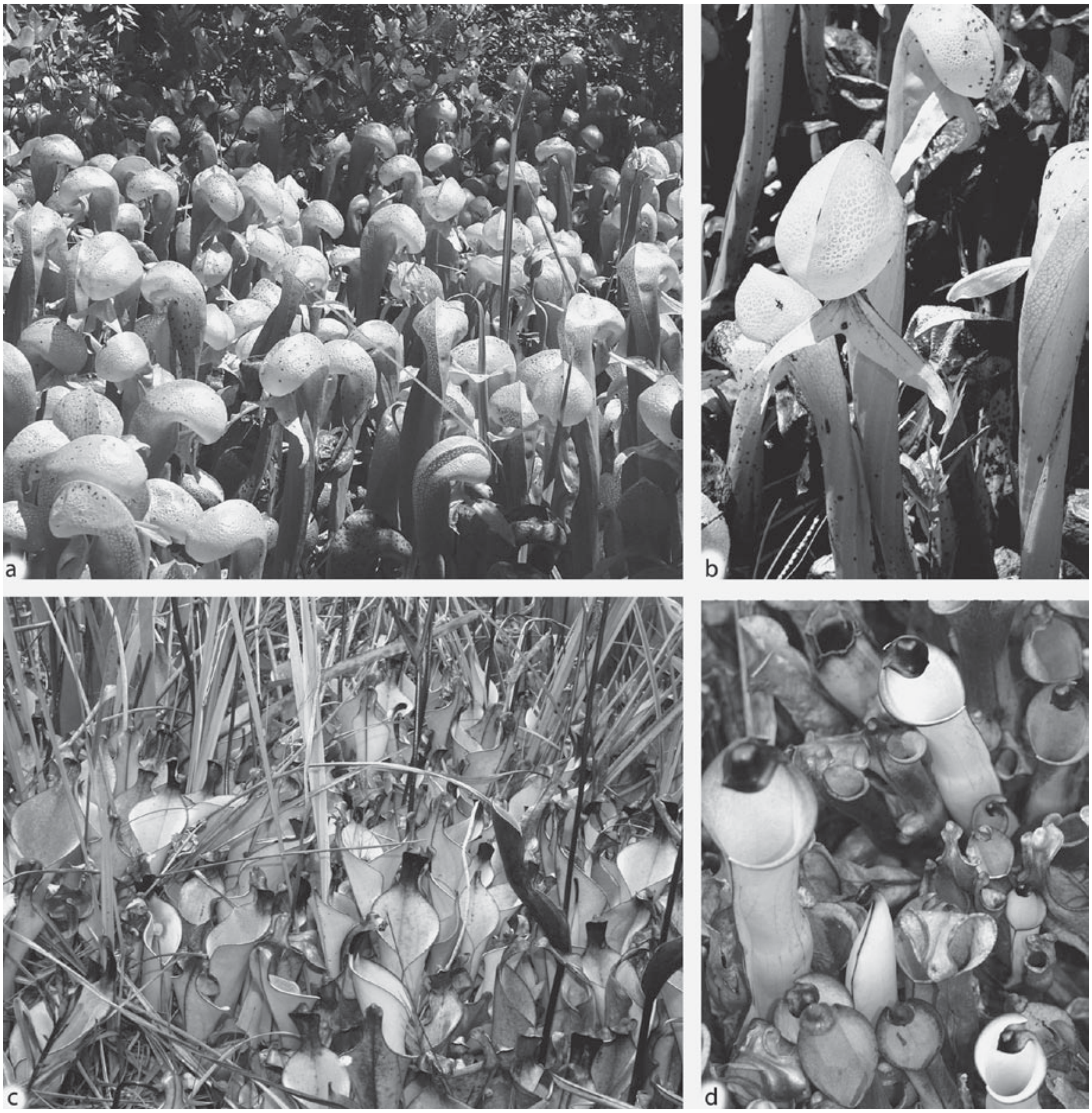
Ninety species of *Nepenthes* are known from northern Australia, New Guinea, Indonesia, Southeast Asia, Sri Lanka., the Seychelles, and Madagascar. They exist from sea level to 3,500 m depending upon species, in humid habitats, for the most part in full tropical sun. Each plant when young and short-stemmed develops a rosette of leaves, all of which form round-bottomed, cup-shaped pitchers resting on the ground. In some species the plant then grows as a climbing vine and develops aerial pitchers with slender, curved bases. The pitchers are modified leaf-tips, each with a cap which may or may not be large enough to exclude some rainfall. They are green or suffused with red and vary in shape between species, the largest capable of holding 1,000 ml of liquid in *N. rajah* Hook f. The rim (peristome) of the pitcher has radial ridges of overlapping epidermal cells and is wettable by rain or nectar so that adhesive pads of insect tarsal claws "hydroplane" on it whereas insect claws slip due to surface topography. Nectaries of the pitcher (the plant has others) are on the underside of the lid and between the teeth of the peristome at its inner edge. Insects attracted to the nectar may slip over the peristome into the pitcher. The upper walls of the pitcher are very smooth and slippery due to a waxy coating. In the depths of the pitcher is a zone of absorptive cells producing phosphatase and (in some species) protease. The pitcher is generally part-filled with fluid which is partially the product of secretory cells and partially water. Ants are well-represented among the prey. (Although most *Nepenthes* grow in full sun, *N. ampullaria* Jack grows in forests and obtains up to 35% of its nitrogen from trapped leaf litter rather than from prey. It has evolved to use leaf litter in parallel to epiphytic bromeliads.) Cleptobionts (which steal the trapped prey) are represented by spiders, sarcophagid and calliphorid flies, a mycetophilid fly, and the necrophagous caterpillar of *Eublemma radda* Swinhoe (Lepidoptera: Noctuidae).

Pollination may be by nocturnal insects but these remain unstudied. *Nepenthes* pitchers provide phytotelmata for a wide array of insects including larvae of mosquitoes and midges which have been reasonably well-studied in a few localities. Larvae of the leafminer *Phyllocnistis nepenthae* Hering (Lepidoptera: Gracillariidae) are attacked by a parasitoid, *Coprodiplosis syringopais* Hering (Diptera: Cecidomyiidae), in Sumatra.

Sarraceniaceae: *Darlingtonia*, *Heliamphora*, and *Sarracenia*

Darlingtonia is represented by a single species, *D. californica* Torrey, native to northwestern California and southwestern Oregon (Fig. 17). Its typical habitats are cool and moist with fresh water and have 0–40% shade from other plants. It reproduces asexually by means of woody stolons, and sexually by means of a flower borne on a tall scape. Immature plants produce small tubular leaves, but mature plants produce leaves shaped like pitchers. The pitchers are green, mottled above with red and variously suffused with red. Each pitcher is hooded, and distal to its opening hangs an appendage shaped like a fishtail. In the hood of the pitcher are transparent cells forming a window (fenestration). The dome of the hood with its fishtail appendage has earned the plant the name of cobra lily for a fancied resemblance to the erect head of a cobra with tongue represented by the fishtail appendage. The pitcher may grow to about 1 m in height and it widens with height. Inside it, at the upper levels are downward-pointing hairs, but the surface below is smooth. Glands on the reverse of the fishtail appendage secrete a sweet-smelling nectar which attracts various flying insects to the vicinity of the opening to the pitcher. Similar glands also are present around the opening, on a structure that has been termed a nectar roll. Insects that then move to leave by following the light shining through the fenestration hit against the hood of the pitcher and fall within it to the liquid contained inside, where they drown. All attempts to demonstrate production of digestive enzymes have failed. Nevertheless, bacterial decomposition of trapped prey occurs within the pitchers. The prey is said to consist of various flies, wasps, and beetles. The pitchers provide phytotelmata within which various invertebrates, notably the immature stages of *Metriocnemus edwardsi* Jones (Diptera: Chironomidae), develop.

Heliamphora is currently represented by 15 species, and perhaps more will be discovered, all of them native to the Guiana Highlands. This geologically ancient area is the sandstone mesas of southern French Guiana, Suriname, Guyana, Venezuela, the far north of Brazil, and adjacent areas of lower altitude. Roraima, on the border of Guyana and Venezuela is an example, and Auyán tepui in Venezuela is another (tepui, plural tepuis, is an Amerindian word adopted into Spanish meaning mesa or flat-topped mountain). They grow on top of these high tepuis at 1,800–2,800 m, and some in surrounding areas at altitudes as low as 600 m. Their typical habitat is a cool seepage bog with high humidity. The plants develop along a branching rhizome (as does *Darlingtonia*), all the leaves form pitchers, and the flower is borne on a scape 20–50 cm tall. Hybridization occurs readily as in *Sarracenia* (below). Most grow in full sunlight, although some (at lower altitudes) grow among other vegetation and may tolerate up to about 20% shade. Each plant forms a rosette of 3–10 leaves. Leaves of young plants are tubular (as in *Darlingtonia*) and up to about 12 cm long. Leaves of mature plants are upright and cylindrical and may reach 1.5 m in height, although some have been reported to reach a height of 4 m. Pitchers are not necessarily plain green, but may be variously suffused with red, or even may be deep dark red, almost black. Each pitcher (unlike other pitcher plants) has a vertical slit to drain off excess water so that it does not become overly full. Each pitcher of most species has a small apical growth ("nectar spoon") having nectar glands. The inner surface of the pitcher is waxy and,



Insectivorous Plants, Figure 17 **Examples of insectivorous plants in the family Sarraceniaceae: (a, b) *Darlingtonia californica*; (c, d) *Heliamphora heterodoxa* (photos by Bruce Holst, Marie Selby Botanical Gardens).**

in most species, has downward-pointing hairs. The method of prey digestion is not understood. Pitchers at least of some species serve also as phytotelmata, having a fauna including larvae of some mosquito species.

Sarracenia is represented by eight to ten species. They are distributed in an arc from eastern Texas via northern Florida to North Carolina. But one of them, *S. purpurea* L., has a wider distribution, occurring also in the northern USA from Lake Superior eastward, and even more widely in Canada, from northeastern British Columbia to Newfoundland. There also are many hybrids. The typical habitat is acidic freshwater bogs in full sun. As in *Darlingtonia* and *Heliamphora*, a branching rhizome produces first a

15–70 cm tall flower scape and then a rosette of leaves. Four species produce simple leaves, but they and all others produce pitcher-shaped leaves, and each mature pitcher has a lid that excludes rain. The lid is in the same position as the nectar spoon of *Heliamphora*. Leaves of newly germinated plants are more or less simple tubes. Pitchers are not necessarily plain green, but may be variously mottled with yellow, red or white. Dependent upon species, the pitchers may be tall, widening with height, or pipe-shaped and horizontal in *S. psittacina* Michaux, in all instances exceeded in height by the flower scape. Nectar glands are concentrated around the rim of the opening, or form a trail leading ground-dwelling insects such as ants to climb the pitcher, and also inside the pitcher beneath the lid. In *S. minor* Walter and *S. purpurea* L., however, the pitcher is hooded, and areoles in the hood function like the window of the hood of *Darlingtonia*, to misdirect exiting insects. The upper part of the interior of the pitcher is smooth and slippery, but below are downward-pointing hairs, and below that are embedded digestive glands. Phosphatase and protease are secreted by *S. purpurea* L., but the enzymes of other species are little-studied. Prey lists have been compiled for *S. purpurea* in Ontario and North Carolina, for *S. flava* L. in North Carolina, and to some extent for *S. rubra*, all showing that ants are a major prey item. Ants also form a major prey item for *S. minor* in Florida. Larvae of *Exyra* spp. (Lepidoptera: Noctuidae) feed on the leaves, with those of *E. semicrocea* (Guenée) reported as making two thirds of the pitchers of *S. minor* non-functional in Florida. An aphid, *Macrosiphum jeanae* Robinson, was reported as feeding on *S. purpurea* in Manitoba, but not yet detected elsewhere. One species, *S. purpurea*, is perhaps the best-studied phytotelm plant anywhere and harbors larvae of *Wyeomyia smithi* (Coquillett) (Diptera: Culicidae), *Metriocnemus knabi* Coquillett (Diptera: Chironomidae) and other arthropods. Sarcophagid larvae of the genera *Fletcherimyia* and *Sarcophaga* inhabit pitchers of *S. purpurea* and some other species and perhaps concentrate their feeding as cleptobionts on the prey trapped by the pitchers. Pollination of *Sarracenia* flowers by wild bees, Halictidae and Melittidae for the smaller-flowered species, and queens of *Bombus* spp. (Apidae) for the larger-flowered species, has been noted.

Cephalotaceae: *Cephalotus*

Cephalotus has only one species, *C. follicularis* Labillardière, which dwells in peaty swamps in southwestern Australia. It has leaves of two forms: normal leaves and pitchers. Each pitcher (much as in *Nepenthes*, and about 3–5 cm long) is fitted with a lid, and a group of them sits on the ground surface around the base of the tall flower scape. The peristome resembles that of *Nepenthes*. Within each pitcher are down-pointing spines which prevent trapped insects (mainly ants) from escaping. It produces a phosphatase. Larvae of a fly, *Badisis ambulans* McAlpine (Diptera: Micropezidae), live within the pitchers, feed on the plant's prey, and leave the pitcher to pupate.

Bromeliaceae: *Brocchinia* and *Catopsis*

First detection of an insectivorous bromeliad (*Catopsis berteroniana* Schult. (f.) Mez) was by University of Florida entomology graduate student Durland Fish, outlined in his 1976 dissertation. Three years later, the observations and hypothesis were explained again by botanist D.B. Ward and Durland Fish in a book on Florida's rare and endangered plants. The hypothesis was that a white ultraviolet-reflecting powder produced by the green or yellow-green leaves camouflages the plants from insect vision (they are not distinguishable from open sky), causing insects to crash into them. Insects hitting the plants may then tumble into the tank (a rosette of leaves forms a water-impounding tank) and are unable to escape because of the coating of slippery white powder. The insects eventually drown and are decomposed by autolysis. The normal method of water and nitrogen uptake by epiphytic bromeliads of the subfamily Tillandsioideae is through foliar trichomes which may be especially aggregated on the surfaces near the leaf bases (within the water-impounding axils of those species that form tanks). This plant grows in some places on telephone lines, clearly dependent for nutrients on minerals absorbed through its leaves and with roots serving only as holdfasts. Therefore, these plants do not need digestive enzymes to avail themselves of the nitrogen provided by the corpses of drowned insects. Yet the carnivory of *C. berteroniana* has been criticized irrationally on grounds that "digestive enzymes have not been demonstrated." That *C. berteroniana* does indeed trap insects was confirmed experimentally by J. H. Frank and G. F. O'Meara, published in 1984. Clearly, *C. berteroniana* is insectivorous because it traps insect prey and obtains nutrients from them by autolysis and uptake through trichomes.

In 1984 came designation as insectivorous of the South American *Brocchinia reducta* Baker, and later of the very similar *B. hechtioides* Mez. Both of these plants grow in the southern uplands of Venezuela and Guyana with adjacent extreme northern Brazil. Their trapping of insects, however, has not yet been confirmed experimentally. Like *C. berteroniana*, they produce a slippery white powder from yellow-green leaves which was stated to attract insect prey. This explanation is questionable because ultraviolet light is an attractant for some nocturnal insects, but ultraviolet lamps do not attract insects in daylight hours, and the white powder of *Brocchinia* and *Catopsis* must reflect ultraviolet only when it is present (during daylight). *Brocchinia* belongs to the subfamily Pitcairnioideae, in which plants are terrestrial, their roots absorb nutrients, and their propensity to absorb nutrients through their leaves is slight. Thus, to be insectivorous, *B. reducta* must (unlike *C. berteroniana*) not only be demonstrated to secrete digestive enzymes but also be able to take up the nutrients through its leaves.

Additional phenomena in Bromeliaceae bear investigation. For example, unopened flower pods of a species of *Vriesea* in Venezuela secrete a copious mucilage that traps tiny flying insects. This species is illustrated and named as *V. platynema* Gaudichaud in a book about Venezuelan bromeliads, but Elton Leme (Rio de Janeiro) has suggested that it does not belong to that species and probably is *V. oleosa* Leme.

Byblidaceae: *Byblis*

Byblis, with six species, is the only included genus in this family. The species are distributed in Western Australia and Northern Australia, with one, *B. liniflora* (Salisb.) extending also to New Guinea. They have bilaterally symmetrical flowers, and mucilage-secretory cells on the leaves. Only some of them, *B. filifolia* (Planchon) and *B. gigantea* (Lindl.), are believed to secrete phosphatases. They have a remarkable relationship with *Setocoris bybliphilus* China and Carvalho (Hemiptera: Miridae) in that these long-legged, agile bugs roam the leaf surfaces of the plant sucking body fluids from trapped insects. The plants are believed to benefit nutritionally from the excreta of the bugs.

Roridulaceae: *Roridula*

Roridula has two shrubby species in Cape Province of South Africa, *R. dentata* L. and *R. gorgonias* Planchon. They have stalked glands secreting a sticky resin, and they produce a phosphatase. With *R. dentata* is associated a mirid bug, *Pameridea marlothi* Poppius, and with *R. gorgonias* is associated *P. roridulae* Reuter. These bugs roam the plant surfaces sucking the body fluids of the trapped prey just as do *Setocoris* spp. on *Byblis* and *Drosera* in Australia. Urea in the excreta of the bugs is absorbed by the plant.

Dioncophyllaceae: *Triphyophyllum*

Triphyophyllum peltatum (Hutchinson and Dalziel) Airy Shaw is a climbing vine (liana) native to moist West African forests. It produces leaves of three types, one type borne on short shoots, having a reduced lamina, and appearing almost cylindrical. Such leaves are produced before the height of the rainy season, perhaps when suitable prey insects are most abundant. The entire surface of this type of leaf bears large, stalked glands producing mucilage and involved with trapping and digestion of prey. Phosphatase and protease have been detected. The Coleoptera, Isoptera, Hymenoptera, and Diptera trapped may be mainly species with crepuscular or nocturnal activity. The plant has been termed a "part-time carnivore" because the trapping leaves persist only briefly.

Drosophyllaceae: *Drosophyllum*

Drosophyllum has a single species, *D. lusitanicum* (L.) Link, in southern Portugal, extreme southern Spain and adjacent northern Morocco. It is a shrub, growing up to 1.6 m tall and has elongate leaves, each with a deep furrow on the upper side. Leaves have sessile digestive glands and stalked mucilage-secreting glands. They secrete a phosphatase and a protease.

Droseraceae: *Aldrovanda*, *Dionaea*, and *Drosera*

Drosera (sundew) has 152 species distributed in tropical and temperate regions throughout the world (Fig. 18). Many species are confined to freshwater bogs, but some species occupy drier soils. Its flowers are borne on a tall flower spike. The upper surface of each leaf is covered with stalked glands that function as tentacles, those toward the margin of the leaf being longest. The tentacles secrete a sticky mucilage. When a prey insect lands on the leaf surface, it becomes stuck in the mucilage, tentacles wrap toward it, and (at least in species with broader leaves) the closest leaf edge rolls upward. Proteases and phosphatases have been detected and they digest the prey. As in *Byblis*, two Australian species of *Setocoris* are associated in the same way with *Drosera*. They are *S. droserae* (China) and *S. russelli* (China). Larvae of the plume moth *Buckleria parvula* (Barnes and Lindsey), which feeds on several *Drosera* spp. in Florida, are attacked by a parasitoid, *Cotesia* sp. (Hymenoptera: Braconidae). The food pyramid thus has a wasp at its top, a caterpillar at the next level below, an insectivorous plant below that, the insect prey of the plant below that, and the food of the prey insects at a still lower level, so has at least five steps, matching those of *Phyllocnistis nepenthae* in *Nepenthes*.

Dionaea muscipula J. Ellis (Venus flytrap) is the only species of this genus and is native to freshwater bogs in the coastal plains of the Carolinas of the USA. It has an even taller flower spike than does *Drosera*, but a very different trapping mechanism. Leaf margins are provided with spines which mesh together when the leaves fold along their central vein. The leaves are triggered to fold by contact of insects with leaf hairs, and they fold rapidly in about 0.5 s to enclose any insect resting on the abaxial surface. Each leaf can fold and unfold about seven times during its life, but the mechanism is not yet fully understood. All leaves are of the same form. Leaves produce a phosphatase and a protease to digest the prey (Fig. 19).

Aldrovanda vesiculosa L. is the only known species of this genus, and is widely distributed in the Old World including Australia. It is an aquatic plant, floating just below the water surface of freshwater pools and having short flower scapes. A slender stem bears whorls of eight leaves, each leaf broadening to its apex and culminating in four or six long spines and a snap-trap operating rather like those of *Dionaea*. A phosphatase has been detected. The whorls of leaves resulted in its being named waterwheel plant.

Insectivorous Plants, Figure 18 **Examples of insectivorous plants in the family Droseraceae: (a) *Drosera intermedia*; (b) *Drosera capensis* (photos credits: (a) Jay Hupp; (b) Lyle Buss, both University of Florida).**

Lentibulariaceae: *Genlisea*, *Pinguicula*, and *Utricularia*

Genlisea has 20 species, known from Africa, Madagascar, and South America. Some of its species have been shown to secrete digestive enzymes. The plants are aquatic and lack roots. The emersed foliage leaves have chlorophyll, but the submersed leaves lack chlorophyll and appear like threadlike leaves except that they bear bladders (utricles, 1–4 mm long) proximal to the deeply forked apices of these submersed leaves. Distal to the utricle, each submersed leaf is a hollow tube which divides to form two helical ducts. A phosphatase is secreted. Protozoa are the prey. The flower is borne on a tall scape.

Pinguicula (butterwort) has 79 species, known from Asia, Europe, North America, and South America. The plants are terrestrial but in wet (freshwater) locations, typically in full sun. A rosette of yellow-green leaves grows from a short stem, the leaves lying flat on the ground and looking and feeling soft and greasy due to secretion of mucilage. Flowers are borne on tall scapes. The leaves form sticky traps for numerous small insects. When a prey item is trapped, the closest leaf edge curls partially upward as if to protect the catch. A phosphatase and a protease are secreted.

Utricularia (bladderwort) has about 220 species known from temperate and tropical areas throughout the world. Plants once attributed to the genera *Biovularia* and *Polypompholyx* are now considered to belong to *Utricularia*. Phosphatases are produced by at least 27 species. The habitat of some is in wet mosses, and two are epiphytic, one of these seemingly restricted to the tanks of bromeliads. Most are aquatic in freshwater ponds and, lacking roots, they float. Their trapping mechanisms are tiny bladders (utricles), ranging from 0.5 to 10 mm depending upon species. Bladders arise from the stolons as well as the leaves of the plant. Trigger hairs in many but not

Insectivorous Plants, Figure 19 **Example of insectivorous plant in the family Droseraceae: (a, b) *Dionaea muscipula* (note tall flower spike in "a") (photos credits: (a) Lyle buss; (b) Jay Hupp, both University of Florida).**

all species of *Utricularia* trip the inwardly opening door of the trap. The hinged door opens rapidly, accompanied by a dilation of the thin wall of the bladder to produce negative water pressure and suck in the victim with inflowing water. Traps that are sprung without catching prey may be reset within 15 min. Otherwise, digestion of the prey proceeds. A phosphatase and a protease are secreted. The size of the bladders obviously limits the size of the prey, which may typically be minute Anomopoda (Crustacea), but some trap tiny aquatic insect larvae including those of mosquitoes. Experimental evidence from Canada has revealed reduced numbers of mosquito larvae in ponds with *Utricularia* than in ponds without. Even tiny anuran tadpoles have been trapped within bladders of some species, such as young tadpoles of *Bufo marinus* L. in Australia. The flower is borne on a tall scape (Fig. 20).

Conclusion

All insects die somewhere, and recycled nutrients from their bodies are generally available for uptake by plants. Some insect bodies are recycled in the form of excreta of their predators. So, insectivorous plants have evolved to gain an improved supply of these nutrients. They have done it by trapping insects and other small animals and, in some way, by being able to absorb the nutrients from the bodies of their prey.

Most insectivorous plants are dicotyledons, but one monocotyledonous plant family (Bromeliaceae) has two genera (*Brocchinia* and *Catopsis*) each with one or two insectivorous species among others that are not insectivorous. Those few species are the exceptions among the bromeliads, a family of about 2,500 known species. Their diet in their nutrient-poor habitats is supplemented by insectivorory.

Insectivorous Plants, Figure 20 **Example of insectivorous plant in the family Lentibulariaceae: (a) *Utricularia quelchii*; (b) *Utricularia jamesoniana* (photos by Bruce Holst, Marie Selby Botanical Gardens).**

Insectivorous Plants, Figure 21 **Other insectivorous plants: (a)** ***Catopsis berteroniana*** **(family Bromeliaceae) (photo by Howard Frank); (b)** ***Pinguicula lutea*** **(family Lentibulariaceae) (photo by Jay Hupp); (c)** ***Nepenthes*** **sp. (family Nepenthaceae) (photo by Diane Davidson).**

Dicotyledons provide most of the approximately 500 known species of insectivorous plants. All species of most of the families named above are insectivorous, and those that have not been demonstrated as such are assumed to be so, rightly or wrongly. Many of these plants secrete digestive enzymes but, in some, no digestive enzymes have been demonstrated. Nor has a method of nutrient uptake through the leaves been demonstrated in all of them. However, some (*Byblis*, *Roridula*) can absorb nutrients from the excreta of cleptiobiont bugs, and some (*Darlingtonia*, some *Sarracenia*) can wait until trapped insects and the pitchers that contain

Insectivorous Plants, Figure 22 **Examples of insectivorous plants in the family Sarraceniaceae: (a, b) *Sarracenia* hybrid; (c) *Sarracenia rubra*; (d) *Sarracenia leucophylla*; (e) *Sarracenia flava* (photo credits: (a, b) Lyle Buss; (c, d, e) Jay Hupp).**

Insectivorous Plants, Table 11 Cleptobionts are animals that steal the animal prey trapped by insectivorous (carnivorous) plants. Note that many other insect species living in insectivorous plants that form phytotelmata may participate at some level in consumption of trapped prey or their breakdown products. Those listed here are viewed as primary cleptobionts specialized to their host plants and specialized to consuming the trapped prey

Cleptobiont	Plant	Geographical area
Aranea: Thomisidae		
Misumenops nepenthicola	*Nepenthes* spp.	Indonesia, Malaysia
Misumenops thienemanni	*Nepenthes tobaica*	Sumatra (Indonesia)
Diptera: Mycetophilidae		
Xenoplatyura beaveri	*Nepenthes ampullaria*	Malaysia
Diptera: Micropezidae		
Badisis ambulans	*Cephalotus follicularis*	Australia
Diptera: Calliphoridae		
Nepenthomyia malayana	*Nepenthes ampullaria*	Penang (Malaysia)
Wilhelmina nepenthicola	*Nepenthes ampullaria, N. rafflesiana*	Borneo, Sumatra
Diptera: Sarcophagidae		
Fletcherimyia abdita	*Sarracenia* spp.	Southern USA
Fletcherimyia celarata	*Sarracenia leucophylla*	Southern USA
Fletcherimyia fletcheri	*Sarracenia purpurea*	Canada, northeastern USA
Fletherimyia folkertsi	*Sarracenia rosea*	Alabama, Florida (USA)
Fletcherimyia jonesi	*Sarracenia flava, S. minor*	Southern USA
Fletcherimyia oreophilae	*Sarracenia oreophila*	Alabama (USA)
Fletcherimyia papei	*Sarracenia rubra*	Southern USA
Sarcophaga papuensis	*Nepenthes mirabilis*	Queensland (Australia)
Sarcophaga sarraceniae	*Sarracenia* spp.	Southern USA northward to eastern Canada
Sarcophaga urceola	*Nepenthes albomarginata*	Penang (Malaysia)
Hemiptera: Miridae		
Pameridea marlothi	*Roridula dentata*	Southern South Africa
Pameridea roridulae	*Roridula gorgonias*	Southern South Africa
Setocoris bybliphilus	*Byblis spp.*	Australia
Setocoris droserae	*Drosera* spp.	Australia
Setocoris russelli	*Drosera* spp.	Australia
Lepidoptera: Noctuidae		
Eublemma radda	*Nepenthes* spp.	Borneo, etc.

them decompose and return nutrients to the soil surrounding the plants; the same objective is reached by all these mechanisms.

Insects have the following relationships with insectivorous plants:

- Pollinators. Flowers of insectivorous plants (except *Nepenthes*, *Byblis* and *Roridula*, and except *Aldrovanda*, which does not trap winged insects) seem to be borne on tall flower stalks that are well away from the trapping mechanism,

Insectivorous Plants, Table 12 Phytophages are animals that eat insectivorous plants. Listed below are only specialist phytophages, those that are believed to eat nothing but the plant specified

Phytophage	Plant	Geographical area
Hemiptera: Aphididae		
Aphis droserae Takahashi	*Drosera* sp.	China, Taiwan
Macrosiphum jeanae Robinson	*Sarracenia purpurea*	Manitoba (Canada)
Lepidoptera: Gracillariidae		
Phyllocnistis nepenthae Hering	*Nepenthes* sp.	Sumatra (Indonesia)
Lepidoptera: Noctuidae		
Exyra fax (Grote) [= *rolandiana* (Grote)]	*Sarracenia purpurea*	Central to eastern Canada, eastern USA
Exyra ridingsii (Riley)	*Sarracenia flava*	Southeastern USA
Exyra semicrocea (Guenée)	*Sarracenia* spp.	Southeastern USA
Lepidoptera: Pterophoridae		
Buckleria brasilia Gielis	*Drosera* spp.	Brazil
Buckleria paludum (Zeller) [= *paludicola* Fletcher]	*Drosera* spp.	Palearctic and southern Asia
Buckleria parvula (Barnes and Lindsey)	*Drosera* spp.	Florida, Alabama (USA)

as if to shield insect pollinators from becoming prey. Pollinators of *Sarracenia* species are various bees, with *Bombus* spp. queens pollinating the larger plants. Almost nothing is known of pollination in other insectivorous plants, and the dearth of observations of pollinating insects has even led to suggestions that spiders may pollinate *Darlingtonia* (Fig. 21).

- Prey. Extensive lists of prey trapped by *Sarracenia flava*, *S. purpurea*, *S. rubra* (Fig. 22), *Nepenthes mirabilis* and *N. reinwardtiana* have been published. From these it can be seen that insects trapped seem to represent much of the diversity of the prey. Ants are well-represented among the prey. Information on prey of *Drosera* suggests that the bulk of their prey is nematocerous Diptera, but in some localities and times Collembola may outrank Diptera.
- Cleptobionts (Table 11). These are insects and other organisms that obtain their food directly from the trapped prey of insectivorous plants. In those insectivorous plants that also are phytotelmata, such as pitcher plants, the breakdown of trapped prey is the basic food resource of a web of denizens, includin0.g insects (see Phytotelmata).
- Phytophages (Table 12). These are insects, and perhaps other organisms, that specialize in feeding on insectivorous plants. Other species may eat insectivorous plants as part of their diet.

► Carnivorous Plants
► Carnivory and Symbiosis in the Purple Pitcher Plant
► Bromeliad Fauna
► Phytotelmata
► Plume Moths

References

Beaver RA (1983) The communities living in *Nepenthes* pitcher plants: fauna and food webs. In: Frank, JH Lounibos LP (eds) Phytotelmata: terrestrial plants as hosts for aquatic insect communities. Plexus, Marlton, NJ, pp 129–159

Botanical Society of America (2007) Carnivorous plants online. Available at http://www.botany.org/Carnivorous_Plants/index.php

Erber D (1979) Untersuchungen zur Biozönose und Nekrozönose in Kannenpflanzen auf Sumatra. Archiv für Hydrobiologie 87:37–48

Frank JH, O'Meara GF (1984) The bromeliad *Catopsis berteroniana* traps terrestrial arthropods but harbors *Wyeomyia* larvae. Fla Entomol 67:418–424

Juniper BE, Robins RJ, Joel DM (1989) The carnivorous plants. Academic Press, London, 353 pp

Judd WW (1959) Studies of the Byron Bog in southwestern Ontario. X. Inquilines and victims of the pitcher, *Sarracenia purpurea* L. Can Entomol 91:171–180

Lloyd FE (1942) The carnivorous plants. Chronica Botanica, Waltham, Massachusetts [reprinted 1976 by Dover Books, London]. 368 pp

Ward DB, Fish D (1979) Powdery *Catopsis* In: Ward DB (ed) Rare and endangered biota of Florida, vol 5, Plants. University Presses of Florida, Gainesville, FL, pp 74–75

Wray DL, Brimley CS (1943) The insect inquilines and victims of pitcher-plants in North Carolina. Ann Entomol Soc Am 36:128–137

Insectoverdin

This is a common green pigment of insects produced by a mixture of blue and yellow compounds. The blue is usually mesobiliverdin, and the yellow is a carotenoid. The normal green coloration of insects results from a blending of blue and yellow pigments, and variance in green coloration observed in some species may be due to lack or excess of the blue or yellow pigments.

Insects as Aphrodisiacs

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Throughout history, humans have used insects and their products as aphrodisiacs to produce physiological effects, real or imagined. Insects were used in various ways, including entomophagy, external applications of insect preparations, and as symbolic charms. Spanish fly, or the chemical cantharidin produced by meloids, is the most famous insect aphrodisiac, yet many insect species (or their products) in several orders have been used as sexual aids.

People around the world have consumed insects in hopes of curing sexual maladies and influencing their sexuality. Some of the supposed benefits were pleasure enhancement, genital enlargement, increasing attractiveness, love, sexual desire, fertility, semen quantity/quality, penile turgidity and erections, soothing scrotal irritation, and prevention of amenorrhea, groin buboes, male weakness, impotence, nocturnal emissions, and premature ejaculation. Insects in multiple orders were consumed in hopes of attaining these benefits, including: Blattodea, Coleoptera, Hemiptera, Hymenoptera, Isoptera, Lepidoptera, Mantodae, Neuroptera, Odonata, and Orthoptera. The underlying reason(s) for associating a given insect with a particular amorous effect is often unclear, but can relate to its behavior, chemical composition, or physical attributes. One example of the latter is the belief that eating queen termites enhances human reproduction, because these insects are prolific egg producers.

Insect products were also applied externally in an attempt to cure ailments or alter genitalia. Ash from hornets' or wasps' nests was mixed with water or wine and applied to the penis for sexual stimulation, erectile dysfunction, and plentiful sperm production. People would also topically apply formic acid or dried ants in oil, which caused dermal irritation and thus sexual arousal. The "*Kama Sutra of Vitsayayana*," a classic in erotic literature, talks at length about aphrodisiacs, including how men could cause permanent lingam (penis) enlargement by undergoing a 10-day process that involved rubbing oil and bristles from specific arboreal insects on their phalluses.

Other insects have a symbolic role, including cicadas and butterflies, which are associated with love charms and represent love and marital satisfaction due to their singing and beauty. Egyptians used a ritual involving scarabs bound with colored threads to gain sexual mastery, while Europeans analyzed ladybird beetles' flight paths to discover potential lovers.

One of the most widely used aphrodisiacs is honey, either pure, mixed with other ingredients, or as mead. One common practice was ingesting various honey mixtures with numerous ingredient variations, including almonds, pine pollen, onion seeds, plant juices, fruit, radishes, resins, frankincense, oil, spices (pepper, saffron), drugs (cannabis, opium) and animal products (lizards, bird eggs, ass or camel milk, and dove blood). Other practices involved applying the honey directly to the body, either for sexual excitation or submissiveness, or genital enlargement for both men and women. To increase penis size, a man would rub honey and ginger or spit a mixture of chewed cubeb berries (Piperaceae: *Piper cubeba* L.), honey, and pepper onto the distal end of his member.

But perhaps the most famous insect aphrodisiac is Spanish fly. The name "Spanish fly" (in older literature, "Spanish flies" or "cantharides") is a misnomer. It refers to blister beetles and/or cantharidin, a crystalline substance synthesized solely by meloids, including *Lytta vesicatoria* L. (Coleoptera: Meloidae), a species commonly found in Spain. Meloids biosynthesize and sequester cantharidin, which they subsequently use to deter predators (Figs. 23 and 24).

Historically, Spanish fly was prescribed for a multitude of human and animal medical conditions, and despite its toxicity, has been employed in diverse amorous exploits over the centuries, including sexual coercion, orgies, and sexual blackmail. Spanish fly was ingested in several forms, including pills, desserts (cookies, laced candies, chocolates, and cakes), sweetmeats, liquor epispasticus, folklore remedies, and live and roasted blister beetles. Concoctions of Spanish fly were often mixed with other ingredients, including honey, spices (cloves, cubeb peppers, nutmeg, cinnamon and saffron), nuts or seeds (acorns, almonds, and sesame seeds), butter, and cannabis (Table 13).

Cantharidin was first isolated in 1812 from *Lytta vesicatoria*, and despite its reputation as a medical wonder and putative sexual stimulant, Spanish fly is highly toxic and can be deadly. Contemporary examples of cantharidin poisoning abound, both intentional and accidental. The latter commonly involve ignorance of the inherent danger of ingesting Spanish fly or blister beetles, although poisonings are not always fatal. Applied topically, cantharidin is a strong irritant that readily enters and affects the epidermis, causing redness, intense burning, and blisters. Ingestion results in mucous membrane corrosion, blisters and hemorrhage, epithelial cell alterations, dysphagia, nausea, dysuria, bladder lesions, hematuria, severe colic, intestinal inflammation and pain, and vaginal and rectal bleeding. Multiple organs and physiological systems can be affected, including the skin, heart, kidneys, intestines, liver, spleen, lungs, genitals and central nervous system. Extremely serious conditions include renal failure, intravascular coagulation, internal hemorrhage, seizures, spontaneous abortion, pulmonary collapse, myocardial degeneration, cardiac disturbance, coma and death.

Insects as Aphrodisiacs, Figure 23 **Photograph of "Spanish Flies, Cantharis." Crude drug form, donated to the Smithsonian Institution in 1881 by Schieffelin and Co. National Museum of American History object catalog #50,590; Smithsonian photo negative #74–1947.**

Insects as Aphrodisiacs, Figure 24 **Mating *Meloe niger* Kirby (Coleoptera: Meloidae). (Picture by R. Akre, Washington State University.)**

Given the long list of adverse effects associated with cantharidin, why did people believe Spanish fly was an aphrodisiac? Because cantharidin irritates the urogenital tract, tingling and burning sensations are felt in the genitalia, and due to blood vessel dilation, the penis and labia engorge with blood. Because it made people more aware of their genitals, it was thought to build erotic passion and cause sexual excitement. Occasionally Spanish fly caused persistent erections, although this condition, termed priapism, usually is not associated with sexual pleasure, can require surgical correction, and if left untreated can damage the organ's vascular tissues.

Due to their history, diversity, and varied biological activities, insect aphrodisiacs (notably cantharidin) have appealed to humans on several levels. They encompass a plethora of materials, concoctions, techniques, and ideas, with effects ranging from innocuous to deadly. However, although insect aphrodisiacs have outstanding reputations, these claims have not been validated, while the harmful effects of Spanish fly, or cantharidin, have been well documented.

► Blister Beetles
► Costs and Benefits of Insects

References

Carrel JE, Eisner T (1974) Cantharidin: potent feeding deterrent to insects. Science 183:755–757
Prischmann DA, Sheppard CA (2003) Insects as aphrodisiacs, with emphasis on Spanish fly. Am Entomol 48:10–21

Insight Learning

This form of learning requires reasoning, which involves analyzing past experiences from which deductions are made. This level of learning is

Insects as Aphrodisiacs, Table 13 Historical uses of insects for sexual purposes

Insect Order/Family	Region Used/ Consumed	Historical Sexual Use
Blattodea (cockroaches)	China	Enhance fertility, prevent sterility
Coleoptera (beetles)		
Buprestidae (metallic wood-boring beetles)	China	Increase sexual desire and attractiveness, invoke love
Carabidae (ground beetles)	China	Invoke love between couples
Coccinellidae (ladybird beetles)	Europe	Discover mate(s)
Dytiscidae (predaceous diving beetles)	Malay, Singapore	Aphrodisiac
Elateridae (click beetles)	China	Increase sexual desire and attractiveness, invoke love
Meloidae (blister beetles)	Worldwide	Aphrodisiac, sexual stimulant, used in orgies, sexual blackmail, cure impotence, persistent erections
Scarabaeidae (scarab beetles)	Egypt	Obtain sexual prowess
Tenebrionidae (darkling beetles)	Malaysia	Aphrodisiac
Hemiptera (true bugs)		
Belostomatidae (giant water bugs)	Malay, Singapore	Aphrodisiac
Cimicidae (bedbugs)	Morocco	Love potion
Pentatomidae (stink bugs)	China	Erection stimulator
Reduviidae (assassin bugs)	Mexico	Aphrodisiac
Cicadidae (cicadas)	China	Symbol of love and bliss, increase semen production and fertility, aphrodisiac, impotence cure
Coccidae (scales)	China	Sexual malady cure
Hymenoptera (bees, wasps, etc.)		
Apidae (bees: honey, mead, royal jelly)	Worldwide	Aphrodisiac, increase sexual vigor, become more attractive, increase female subjugation, enlarge male and female genitalia, benefit sperm (male potency), increase sexual pleasure, premature ejaculation, confer fertility
Formicidae (ants)	Italy	Sexual stimulant, love potion
Vespidae (wasps, hornets)	China	Increase sexual stimulation and vigor, impotence cure, increase sperm count
Isoptera (termites)	India	Aphrodisiac, rejuvenation
Lepidoptera (moths, butterflies)	North America, China	Love charm, symbol of love and bliss
Bombycidae (silkworms)	China	Stimulate erections, prevent ejaculation, enhance semen, extend intercourse, ease scrotal itching, benefit women
Sphingidae (hawk moths)	China	Aphrodisiac, cause large erections, increase male fertility and semen

Insects as Aphrodisiacs, Table 13 **Historical uses of insects for sexual purposes (Continued)**

Insect Order/Family	Region Used/ Consumed	Historical Sexual Use
Mantidae (mantids)	China	Prevent premature ejaculation, nocturnal emission and impotence
Neuroptera (lacewings, etc.)		
Myrmeleontidae (antlions)		Make married couples attracted to each other
Odonata (damsel- and dragon flies)		
Anisoptera (dragonflies)	China	Stimulate erections, prevented ejaculation
Orthoptera (crickets, grasshoppers)		
Acrididae (locusts)	China	Increase sexual desire and attractiveness, invoke love
Tettigoniidae (katydids)	China	Sex drive stimulator

unknown in insects, although some have suggested that tool use displayed by some insects may be indicative of insight learning.

► Habituation
► Associative Learning
► Latent Learning
► Learning in Insects

Inspection

From a regulatory perspective, this is the official visual examination of plants, plant products, or other regulated articles to determine if pests are present, and/or to determine compliance with phytosanitary regulations. The individual who performs the inspection according to standard regulatory procedures is the inspector.

► Regulatory Entomology

Instar

The insect (larva or nymph) between molts. Instars are referred to by number: the first instar is the stage between after hatching and before the first molt, the second instar occurs after the first larval (nymphal) molt but before the second, etc. Technically, the pupal stage (if present) is an instar, though it is not numbered like the others, and is simply referred to as the pupa. This term often is confused with 'stadium,' a term restricted to the time interval of an instar.

► Stadium, Metamorphosis

Instinct

Behavior performed without the benefit of previous experience or learning from other members of the species. Unlearned stereotypic behavior.

Integrated Pest Management (IPM)

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Integrated pest management (IPM) refers to coordinated systems for managing pest populations that use preventive and suppressive control tactics, which are unified by surveillance to assess hazard for injury and to determine whether curative action is needed. Technically, IPM programs can be developed for any pest, including insects and mites, plant pathogens, weeds, vertebrate pests, etc., and IPM programs on specific commodities can involve complexes of several types of pests. The nature of IPM is perceived differently among individuals that are dependant on or are affected by pest control technologies, including pest control professionals, growers, environmentalists, government officials, and the general public. Conceptually, many people believe that IPM avoids reliance on pesticides and promotes preventive control tactics that restrain pest populations, but are not detrimental to non-target animals or the environment. In many practical circumstances, however, IPM programs must rely heavily on judicious use and management of pesticides, especially in circumstances where tolerance of pests or injury is low. Most people would agree that IPM involves strategic blending of multiple pest control procedures. IPM programs are highly specialized and adapted to individual needs on many commodities that have various fixed and variable constraints on the type of control tactic that can be used at a particular time. Regulatory controls (pesticide laws, government subsidies, etc.) and societal concerns (non-acceptance of pest presence or damage and anxiety about effect on health of pesticide residues and transgenic insecticidal crops) have tremendous effect on decisions for IPM tactics that are used on certain commodities. Strategic planning for IPM is based on knowing details of pest biology and cumulative risk for injury to a commodity, and an awareness of the costs and effectiveness of control methods that can be practically applied in a coordinated management program.

IPM includes both prevention and suppression philosophies of pest management. The objective of prevention is to restrain pest populations from producing appreciable injury to commodities, whereas the goal of suppression is to exterminate pest infestations. There are many preventive control methods that can be used in IPM programs. Use of pesticides or some form of direct physical destruction (e.g., burning, freezing, or crushing) are methods used for suppression of pest infestations that threaten immediate and severe damage to a commodity. Surveillance of pests or having knowledge based on past histories that a high probability exists for pest infestations is a central element of IPM. Surveillance involves accurate identification and effective sampling or scouting of pests and observing symptoms of injury on a commodity. The information from pest monitoring is used to determine when action thresholds (pest populations or injury levels that equal or exceed the cost of pest suppression) requiring remediation have been reached.

Preventive control tactics used in IPM programs include:

Cultural Control

The use of any commodity production or use method with some consideration for IPM. Cultural control practices either avoid developing high hazard environments for pest problems or produce conditions that are detrimental to pests. There are numerous cultural control practices used in IPM programs, examples include sanitation of infested materials, selecting pest tolerant or resistant crops or cultivars (including pesticidal transgenic plants), manipulating planting and harvesting dates to avoid pest populations, etc.

Biological Control

The manipulation of natural enemies (parasitoids, predators, and pathogens) to control pests. The manipulation of biological control agents for IPM is done either naturally by manipulating commodity environments to conserve or enhance existing populations of natural enemies or it is accomplished artificially by rearing or mass-producing natural enemies for introduction or application in pest environments.

Mechanical Control

The direct application of lethal physical forces to pests including heating, freezing, suffocation, irradiation, crushing, chopping, etc., or the use of devices or packaging that prevent access of pests to commodities.

Chemical Control with Enticements or Deterrents

The use of attractants, feeding stimulants, repellents, and antifeedants to manipulate pest behavior for control.

Chemical Control with Pesticides

The use of formulated substances that kill pests by physiological intoxication or by inducing lethal pathogenic infections.

Regulatory Control

Participation by IPM personnel in governmental programs that govern pest management activities such as quarantine and area wide eradication projects and by abiding by laws created to protect or indemnify individuals that are impacted by IPM actions. Regulatory control also includes following use requirements prescribed by manufacturers of pesticides and transgenic crops.

The design and implementation of IPM programs using preventive or suppressive strategies requires an awareness of resident pest hazard on a commodity, which is influenced by numerous factors that may fluctuate in diverse locations at different times. Pest hazard can be high, normal, or low, and knowledge of all three possible conditions is important in making IPM decisions. For example, a preventive control tactic that lowers pest hazard by direct lethal impact, such as fall tillage in cornfields for burial of pest-infested debris, is considered a cultural control tactic for IPM. On the other hand, having knowledge that late planting of the crop has high hazard for pest problems is also a form of cultural control, because alternative tactics such as early planting can be considered as a preventive tactic. Pest hazard of a commodity involves both its vulnerability to pests and its loss in value from injury. Vulnerability involves susceptibility of the commodity and the prevalence and aggressiveness of pests for producing injury. Commodity value relationships influence pest hazard by dictating the amount of injury the commodity can bear under pest presence before real value is lost and how much can be spent for IPM. Value relationships include costs of production, commodity unit value, and economic tolerance of the commodity for the presence of pests or injury. Commodity value relationships with pests are used to develop action (economic) thresholds. In IPM practice, much of preventive control is initially based on assessment of hazard for pest problems on a commodity and surveillance is used to determine when suppression is warranted.

► Economic Injury Level and Economic Threshold Concepts in Pest Management
►Cultural Control of Insects
►Regulatory Entomology
►Plant Resistance to Insects
►Microbial Control of Insects
►Natural Enemies Important in Biological Control

References

All JN (2002) Integration of tactics In: Pimentel D (ed) Encyclopedia of pest management. Marcel Dekker, New York, NY, pp 416–419

Barfield CS, Swisher ME (1994) Historical context and internationalization of IPM. Food Rev Int 10:215–267

Kogan M (1998) Integrated pest management: historical perspectives and contemporary developments. Ann Rev Entomol 43:243–270

Pedigo LP (1999) Entomology and pest management, 3rd edn. Prentice-Hall, Englewood Cliffs, NJ, 691 pp

Stern VM, Smith RF, van den Bosch R, Hagen KS (1959) The integrated control concept. Hilgardia 29:81–101

Integument

The outer covering or cuticle of an insect, plus the epidermal cells that secrete the cuticle. The integument functions in locomotion, feeding, excretion, protection from desiccation, breathing, and many other important functions. Many of the characteristics that make insects unique among animals are attributable to the integument.

► Cuticle
► Epidermis
► Integument: Structure and Function

Integument: Structure and Function

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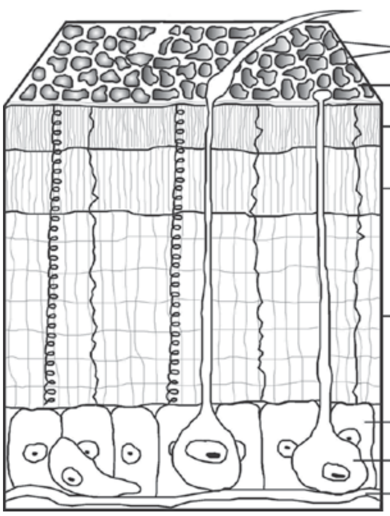
The integument is composed of the cuticle and the underlying epidermal cells that secrete the cuticle. The cuticle serves as the exoskeleton of the insect, the site for muscle attachment, the first line of defense from fungi, bacteria, predators and parasites, and environmental chemicals, including pesticides. The integument functions in locomotion, breathing and respiration, feeding, excretion, protection from desiccation, behavior, osmoregulation, water control, and as a food reserve. The many roles played by the integumentary covering of insects are in part reflected in the complexity of its structure and chemistry, and in the special ways it is adapted to function in the ecology of its owner.

Despite many species-specific features, there are certain common features in the integument. There is always a single layer of epidermal cells lying immediately beneath the cuticle. These cells secrete the new cuticle at molting, and in some insects at least, continue to secrete cuticle even in the adult. In all insects there is a thin layer of cuticle with special properties called the epicuticle at the surface of the insect, and beneath this there is additional cuticle that can sometimes be divided into several layers depending primarily upon the degree of sclerotization or cross-linking of the molecules of protein and chitin.

The cuticular part of the integument is composed of several layers, including epicuticle, exocuticle, endocuticle, and an epidermal cell layer. There is always an epicuticle layer and the epidermal cell layer, but the exocuticle and endocuticle may be greatly reduced or absent in particular parts of the cuticle of the same or different insects. Often there are additional cuticle layers within one or more of the three principal layers as evidenced by electron density in cross sections viewed in the transmission electron microscope. The epidermal cells secrete the overlying cuticle, the lipids (waxes), cement, and often many additional chemical components that occur on or in the cuticle layers. When a new cuticle is secreted at molting, the cuticle below the epicuticle layer is first called procuticle, because it is not sclerotized into the distinct layers noted above. Such sclerotization occurs, however, soon after the cuticle is secreted (Fig. 25).

Epicuticle

Epicuticle is the outermost part of the integument in contact with the environment. Because it is so thin (from 1 to 4 μm in thickness), the detailed chemical structure of the epicuticle has been difficult to discern, but it is known to contain



Integument: Structure and Function, Figure 25 A generalized diagram of the layers of the cuticle.

sclerotized proteins impregnated with lipoproteins, lipids, waxes, cement, and minor amounts of various minerals and other chemical components. It does not contain chitin, a major structural carbohydrate in other parts of the cuticle. The proteins and some of the lipids appear to be covalently linked, and the proteins are tanned or sclerotized by phenolic compounds and their oxidized products, quinones. Sclerotization gives the epicuticle strength, hardness, and low water permeability. Reduced permeability to water is also provided by lipids and the cement layer on the surface.

Because the epicuticle bears the surface sculpturing of insects, its gross appearance is highly variable in different species. It does, however, contain one common layer in all insects, the cuticulin layer. Cuticulin is a very thin layer of protein about 0.0075 μm thick, which is the typical thickness of an animal cell membrane. It is impregnated with lipids, some of which may be covalently bound to proteins as lipoproteins. Cuticulin is the first layer of new cuticle to be secreted in preparation for a molt, and new procuticle is secreted beneath it. There may be additional layers in the epicuticle, such as an inner cuticulin layer similar in composition to cuticulin. If present it is usually thicker than the cuticulin layer and may be up to 1 μm thick. In some insects numerous layers interior to cuticulin can be differentiated as layers of greater or less electron density with transmission electron microscopy.

Cement, often described as a shellac-like substance at the air interface of the cuticle, is secreted by specialized epidermal cells called dermal glands and transported to the surface of the epicuticle. A traditional view is that the cement layer is the outermost layer on the cuticle, with a lipid layer just beneath the cement. Probably in some insects this view is valid, but in the caterpillar *Calpodes ethlius* the cement layer is not continuous, but is broken by patches of lipids, called “wax blooms,” at the surface. It seems likely in many insects that a mosaic patchwork of cement and lipid exists at the surface of the epicuticle. Other insects are known that have much or even all the body covered with lipid at the surface. Despite the thin nature of the epicuticle, it nevertheless is extremely important to surface pattern and features, to permeability of the cuticle, and it represents a limitation on expansion of the cuticle in immature insects, necessitating molting during growth.

Exocuticle

The exocuticle, containing chitin and protein, lies just beneath the epicuticle. It is highly sclerotized and is therefore hard and rigid. Lamellae or layers within the exocuticle may refract light in such a way to produce structural colors in some insects. Many of the iridescent greens and blues of insects are structural colors due to refracted light rather than to pigments. The thickness of the exocuticle is variable and species specific. Adult insects generally have a thicker and more sclerotized exocuticle than larval insects. In particular, the thorax in flying insects has heavily sclerotized exocuticle to support the strong flight muscles. Many larvae have a soft flexible cuticle with little or no exocuticle. Exceptions exist; there are larval insects with hard sclerotized exocuticle, and soft-bodied adults with little or no exocuticle.

The greater the degree of sclerotization, the harder the cuticle. The content of chitin does not control hardness of the cuticle, but sclerotization does. Because of the sclerotization, little or none of the exocuticle is digested by molting fluid, and it is shed, along with the epicuticle, at molting.

Mesocuticle

Some insects have a layer of less highly sclerotized cuticle between the exo- and endocuticle called mesocuticle. It also contains chitin and protein. Mesocuticle is distinguished on the basis of the degree of sclerotization and by its red staining reaction with acid fuchsin in Mallory’s triple stain.

Endocuticle

The endocuticle is soft, flexible cuticle containing both chitin and proteins. It has little sclerotization, which is why it is soft and flexible. Stabilization of the proteins and chitin in the endocuticle occurs through some covalent bonds, hydrogen bonds, and probably occasional quinone cross-links. Generally soft-bodied insects have relatively thick endocuticle, which remains flexible and soft, and thin or no exocuticle. There is, however, always an epicuticle layer at the body surface of soft-bodied insects.

Pore Canals and Wax Channels

Pore canals are passageways from 0.1 μm to 0.15 μm diameter extending from the epidermal cells through the endo- and exocuticle. Larger canals are often flattened, ribbon-like, and may be twisted or straight. The pore canals transport lipids and cement, and sometimes additional chemical components. Formation of the pore canals has not been entirely resolved. Some research has suggested that the passageways are the result of cytoplasmic extensions of the epidermal cells present during cuticle secretion. Usually after a new cuticle has been secreted, the cell extensions are withdrawn leaving the open canals. Some workers who have studied cuticle formation do not accept this mode of formation because cell extensions are not always evident even during new cuticle secretion, but no competing alternative idea has been advanced. The pore canals can be very numerous; for example, as many as $1.2 \times 10^6/mm^2$ in some cockroaches, or as few as $15{,}000/mm^2$ (about 50–70 per epidermal cell) in a sarcophagid (a flesh fly) larva.

Pore canals terminate at the junction of the epicuticle; they do not penetrate epicuticle. There are, however, passageways through the epicuticle called wax channels (about 0.006 μm–0.013 μm in diameter) that are 10–20 times smaller than pore canals. Wax channels stain with osmium tetroxide, a stain for unsaturated lipids, and this is taken as evidence that the channels continue the transport of lipids, and probably other materials, to the surface. There is no evidence of a 1:1 correspondence of pore canals to wax channels at the junction of the exo- and epicuticle. Chemicals passing up through the pore canals probably diffuse out of the pore canals laterally to some extent all along their length, and also at the epicuticular interface, and thus impregnate the entire cuticle. Some of the lipids find their way to the surface of the insect, where they provide waterproofing, and perhaps other ecological and behavioral functions.

Epidermal Cells

The cells underlying the cuticle are arranged in a single layer. They usually are called simply the epidermal cells, but sometimes referred to as the cuticular epithelium and the hypodermis. All epidermal cells probably secrete chitin and proteins, and some may secrete lipids, although the cells that secrete lipids have not been easy to always identify. Cement may be secreted by specially modified glandular epidermal cells. There frequently are specialized glandular cells in the cell layer, either in small groups or as scattered isolated glandular cells, that secrete special products. For example, the sex pheromone in most female Lepidoptera is secreted by a small patch of tall, columnar epidermal cells located beneath the cuticle of the ventral intersegmental membrane in the 8–9th segment of the abdomen.

Epidermal cells are separated from the circulating hemolymph by a basement membrane or basal lamina, a layer of poorly defined chemical composition, but with pores large enough to permit larger hemolymph proteins and other molecules to pass from the hemolymph into the epidermal cells. Small tracer particles of gold or ferritin pass from the hemolymph through the basement membrane, but larger particles are stopped on the hemolymph side. Hemidesmosomes hold the basement membrane to the epidermal cells. The origin of the basement membrane is not defined for most insects; some evidence supports secretion by hemocytes, while the desmosomal attachments to epidermal cells suggest that the epidermal cells themselves secrete it. Tracheae, tracheoles and nerves pass through the basement membrane to reach the epidermal cells.

The basal membrane of epidermal cells may be smooth or may contain many and deep infoldings, depending upon function and stage in which the insect exists. The basal cell membrane may change in appearance, and undoubtedly in function, as the insect develops, and there are marked changes in preparation for and during a molt.

In the intermolt period epidermal cells typically have a regular polygonal outline and form a sheet of cells beneath the cuticle. Contiguous epidermal cells often are held together by various types of junctional contacts. The same types of cell-to-cell contacts occur in many other cells as well. The junctional contacts not only hold cells together, but help prevent movement of molecules that might otherwise squeeze between adjacent cells. The cell-to-cell contacts help reduce outward loss of water and inward penetration of chemicals the insect might encounter in the environment. Septate desmosomes are close together and numerous, like stitches, between the lateral faces of cells, particularly toward the apical (cuticular) surface, and likely play an important role in preventing inward and outward movement of materials between the cells. Gap junctions also occur in this region. Depending upon cell function and physiological condition of the insect, there may be sinuses with varying width from time to time between adjacent cells, with cells being held together mainly at basal and apical surfaces. Cationic ferritin does not penetrate these spaces.

Under the influence of hormones, and in preparation for a molt, epidermal cells generally change shape to become more columnar. They begin to divide by mitosis, and move or expand into new space, and sometimes new shapes, that will become the body outline of the next instar as they secrete the new cuticle.

Epidermal cells secrete cuticle at the apical face, and a typical cell has a series of ridges or knobby projections on its apical face where the fibers of chitin are secreted. These projections have been called plasma membrane plaques. They may be involved in transport of precursors for chitin synthesis and/or assembly of chitin fibers. At the initiation of new cuticle synthesis prior to molting, cuticulin, the first new cuticular layer secreted, begins to form on these knobby plaques. There also may be long microvilli on the apical face which may transfer lipids to be passed to the cuticular surface.

Epidermal cells have extensive rough endoplasmic reticulum (RER) where protein synthesis occurs, and areas of smooth endoplasmic reticulum (SER) for lipid synthesis. Cell nuclei are often polyploid, with multiple nucleoli. During development, nucleoli enlarge and develop multiple lobes, when there is evidence of new synthesis of RNA and ribosomes. The Golgi complex is prominent in epidermal cells, and probably serves several functions including the following: (i) processing of secretory substances necessary to synthesize cuticle, (ii) production of material for the plasma membrane of the cell, (iii) packaging of cellular components in isolation envelopes for later autophagy, and (iv) processing and packaging of lysozymes needed for autophagy and heterophagy.

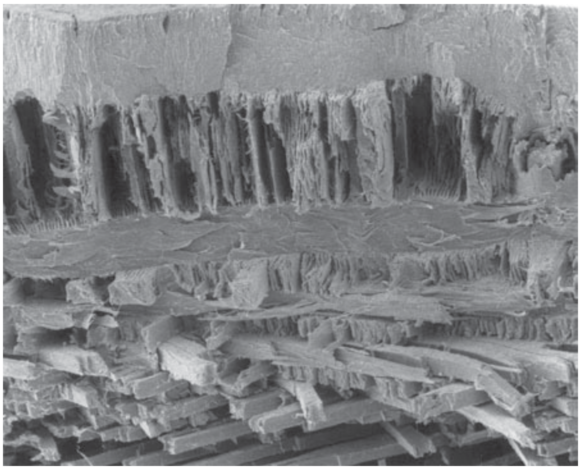
Epidermal cells are involved in wound repair, and can move from an area of undamaged cells into an area of damaged or destroyed cells. Cells at the leading edge spread over the wound until they cover it and establish contact with another epidermal cell. The population of cells in the peripheral zone around a wound is temporarily reduced as cells migrate toward the wound area, but cell divisions soon repopulate the area.

Oenocytes are large, prominent cells scattered among the epidermal cells, and also clustered at spiracles, near origin of larger tracheae, and scattered among fat body cells. Oenocytes present among the epidermal cells are considered a type of epidermal cell, but as noted, some are located outside the epidermal layer. Oenocytes are differentiated from epidermal tissues during embryogenesis, as well as later in development. These cells are usually large, polyploid, and always have extensive tubular smooth endoplasmic reticulum and well developed plasma membrane reticular system. Their function is not very clear, but their morphology suggests lipid secretion and lipid metabolism.

Cuticle is secreted as thin lamellae or sheets, like sheets of paper stacked on top of each other. The rods or crystallites of chitin are embedded in the protein matrix of a sheet and provide strengthening, in much the same way as that provided by steel rods (reinforcement bars, commonly called "rebar" in the construction industry) embedded in concrete columns and walls. Adjacent sheets of cuticle are stabilized by quinone tanning agents and by hydrogen bonds between chitin rods in adjacent cuticle sheets when the rods are near the surface of each sheet. It is still uncertain whether quinone tanning agents directly link chitin rods to protein.

In successive sheets of cuticle the chitin rods often are shifted slightly in orientation relative to the sheet above it (the older sheet), and this gives rise to bouligand helicoids in thin transmission electron micrographs sections. One structural model is that chitin rods are embedded parallel to each other in the protein matrix in a plane or sheet of cuticle only a few nm thick. In each successive sheet of cuticle the model suggests that rods are reoriented slightly through a small angle relative to rods in the plane lying above. The shift in orientation of the chitin rods produces a helicoid pattern when oblique sections are cut through the cuticle. When the rotation has passed through 180°, the result is a lamella of cuticle (Fig. 26).

Cross sections and freeze-fracture of insect cuticles often show a "plywood-like" arrangement. The "plywood" arrangement has been explained as a sandwich arrangement in which there is a very thin lamella of cuticle holding together two layers of cuticle of many sheets in which rods do not shift, but run parallel to each other through many successive sheets. Based upon the principle that manufactured plywood sheets are designed in this way for added strength, one can assume that similar strength is imparted to cuticle with this arrangement.



Integument: Structure and Function, Figure 26 Plywood-like arrangements of layers of the cuticle in the thorax of the palm weevil, *Rhynchophorus cruentatus* (photo courtesy of Robin Giblin-Davis, University of Florida).

References

Giraud-Guille MM, Bouligand Y (1986) Chitin-protein molecular organization in arthropods. In: Muzzarelli R, Jeuniaux Ch, Gooday GW (eds) Chitin in nature and technology. Plenum Press, New York, NY, pp 29–35

Hadley NF (1984) Cuticle: ecological significance. In: Bereiter-Harn J, Matoltsy AG, Sylvia Richards K (eds) Biology of the integument. 1. Invertebrates. Springer-Verlag, New York, NY, pp 685–693

Hopkins TL, Kramer KJ (1992) Insect cuticle sclerotization. Ann Rev Entomol 37:273–302

Locke M (1984) Epidermal cells. In: Bereiter-Harn J, Matoltsy AG, Sylvia Richards K (eds) Biology of the integument 1. Invertebrates. Springer-Verlag, New York, NY, pp 502–522

Intercalary Vein

An added or supplementary wing vein; it varies in appearance among different taxa.

► Wings of Insects

Intercropping

The culture of two (or more) crops simultaneously in the same field.

► Polyculture

Interference Competition

Competition for resources wherein one individual or species acquires greater access to necessary resources. The "winner" of the competition is not necessarily ensured adequate resources, only a greater probability of acquiring sufficient food. It also is known as contest competition.

Intergenic Region

The noncoding region between segments of DNA that code for genes (i.e., introns).

Internal Anatomy of Insects

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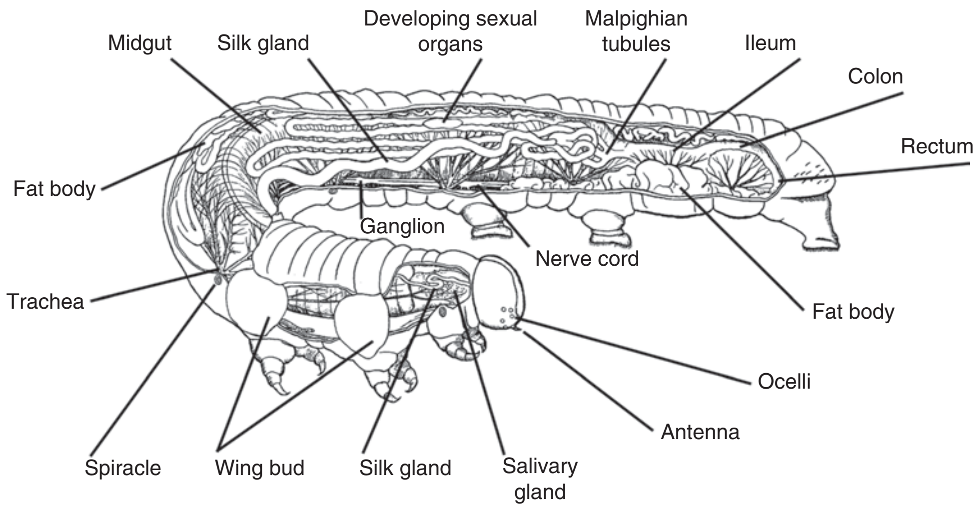
The insect body is a slightly to pronounced elongate, cylindrical structure. Its shape is determined by the integument and associated muscles. As is the case with the wide variation in external appearance among taxa, there is considerable variation in internal structure. The same basic systems are normally present in all insects, of course, but their expression varies with their behavior and ecology. Similarly, the systems found in the immature and adult stages may be quite similar in some insects or quite different in others, depending not only on the development of reproductive structures in adults but also on the feeding ecology on the insects. There are several important internal systems that together provide many of the unique characteristics that make an insect different from most other animals (Fig. 27).

Muscular System

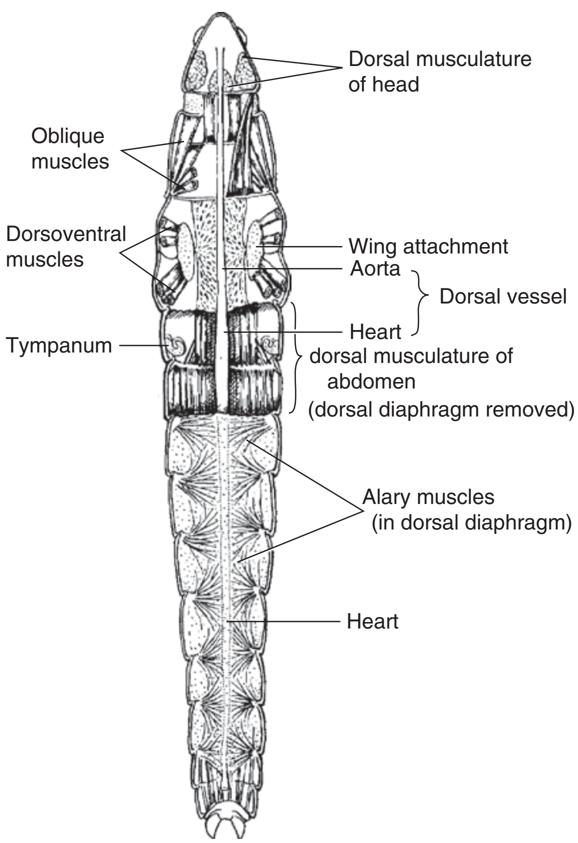
Muscles are found throughout the insect body, though they are most pronounced in the head (for ingestion) and thorax (for locomotion). The muscles are pale in color and striated, forming flat or strap-like bundles. The naming system of muscles is confusing, and tends to be named in some cases for the function they perform, but in other cases based on their point of attachment to the integument. Skeletal muscles tend to be segmented in concert with body segments, the most important of which are the cephalic, thoracic (including flight) and abdominal muscles. They are anchored to various points of the integument, including internal extensions of the integument. The cephalic muscles control the activities of the head, such as moving the head, moving the mouthparts, and moving the antennae. The thoracic muscles control the legs and wings. The wing muscles may act directly on the wing (so-called direct flight muscles) or indirectly (so-called indirect flight muscles. The indirect flight muscles are of two principal types: the dorsoventral and the longitudinal. The alternately deform the shape of the integument, which in turn provides energy to help power the wings. The indirect muscles usually are more important for flight. The abdominal muscles connect abdominal segments and serve to bend and contract the abdomen. In addition, there are visceral muscles associated with such organ systems as the gut, heart, and gonads. They may encircle the organs, or run longitudinally, but they are small muscles and not well tracheated (Fig. 28).

Fat Body

The fat or adipose tissue is found widely in the body, and consists principally of lipids, glycogen



Internal Anatomy of Insects, Figure 27 **Caterpillar with integument partially removed to expose the internal anatomy (modified from Essig 1942).**



Internal Anatomy of Insects, Figure 28 **Dorsal view of a grasshopper showing principal elements of the circulatory and muscular systems.**

and protein. It is not simply a storage area for energy, however, and sometimes assumes other functions. Usually it is whitish or yellowish in color, and forms irregular masses or lobes. It is especially pronounced in immature forms of insects.

Digestive System

The digestive system (also called alimentary system or alimentary canal) extends the length of the body from the mouth to the anus. In general, is consists of a straight tube, though there are various points where it may be dilated, convoluted, or branched.

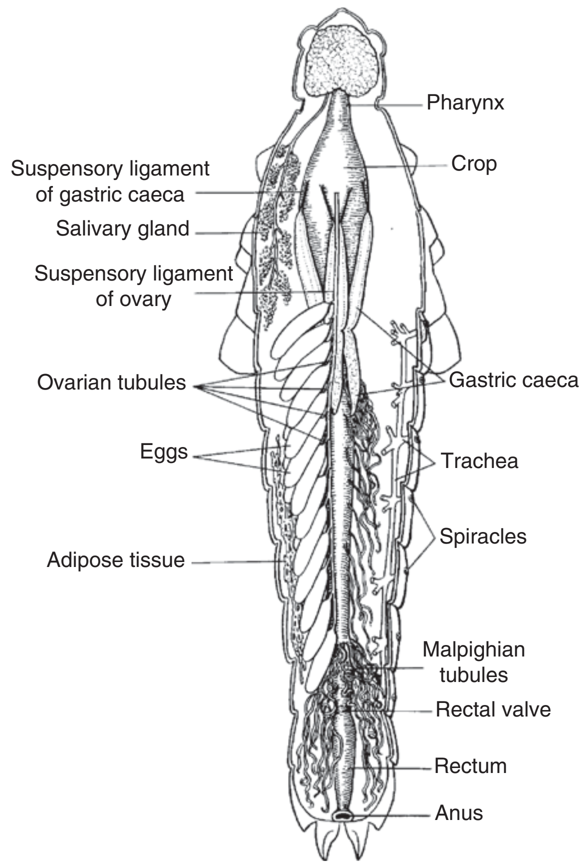
This system begins at the mouth or buccal cavity, and salivary glands often provide enzymes and lubricants at this point. Generally, the alimentary system is said to consist of three parts: the foregut, midgut, and hindgut. Sometimes the buccal cavity is considered to be part of the foregut. The foregut (also known as the stomodeum) also consists of the pharynx, esophagus, crop, proventriculus, and esophageal valve. This section serves mostly to transport, store, and sometimes filter the ingested food, which then enters the midgut (ventriculus). The midgut is the' stomach' of insects, and is the principal site of digestion. It may possess gastric caeca, bladder-like pouches that increase the surface area of the midgut. The posterior region, or hindgut, consists of an anterior portion of intestine, or ileum, followed by the posterior intestine, or colon. The anterior and posterior regions of the intestine are not always differentiated. The beginning of the hindgut is marked by the attachment of Malpighian tubules. The hindgut terminates with a chamber called a rectum, which regulates movement of waste materials into the anus (Fig. 29).

Circulatory System

The circulatory system of insects is usually but a single dorsal vessel. It extends from the posterior region forward to the head, and consists of two principal components, a pumping organ or heartposteriorly, and a large vessel for transport, or aorta anteriorly. The blood, or hemolymph, circulates freely in the spaces between the organs. However, diaphragms in various parts of the body also serve to direct the flow of blood, and blood flows through veins of the wings. In some insects, accessory pulsatory organs occur. These sac-like structures function independently of the heart, and assure that blood flows into the appendages.

Respiratory (Ventilatory) System

Exchange of gases in insects is accomplished through a system of trachea (large vessels) and tracheoles (small vessels). It is analagous to a system of arteries, veins, and capillaries, with air (rather than blood) provided to the organs, tissues and cells of the body. The trachea take on a silvery appearance when filled with air. The trachea open to the outside of the body through opening called

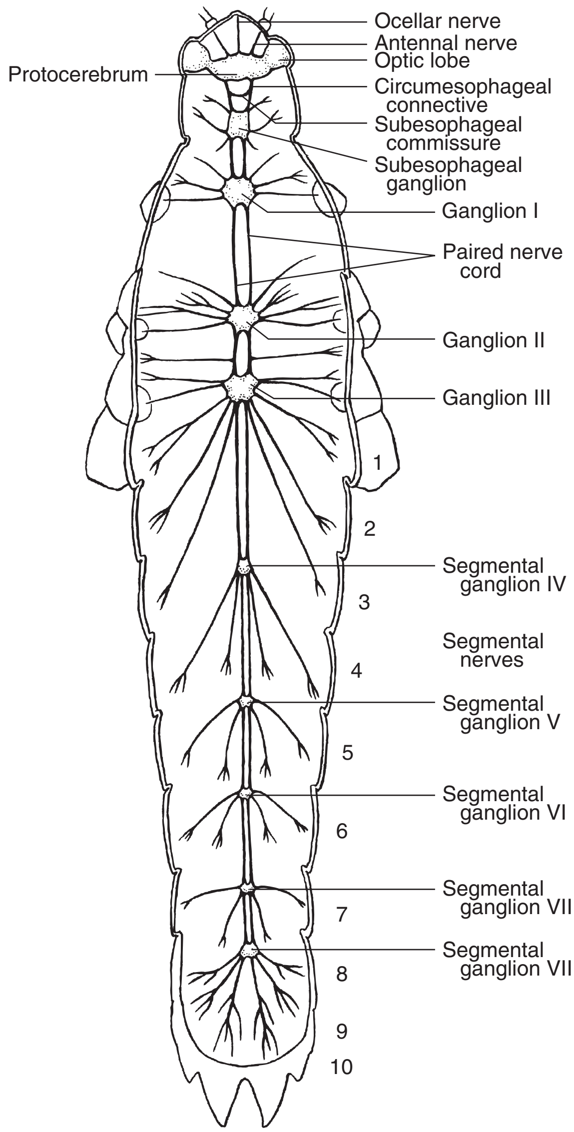


Internal Anatomy of Insects, Figure 29 Dorsal view of a grasshopper showing principal elements of the digestive, respiratory and female reproductive systems.

spiracles. The spiracles are arrayed laterally along the thorax and abdomen. Although traditionally considered to be a passive system, air sacs occur in many insects. Air sacs are dilations of the trachea, and constitute a significant air reservoir. Pressure on the air sacs helps to move air through the ventilatory system. In aquatic insects, the exchange of gases may occur in tracheal gills that occur in the normal positions of the spiracles, or from the sides of the body or associated with the rectum. Sometimes gas exchange is cutaneous.

Nervous System

The central nervous system of insects is located ventrally along the length of the body. It consists of a series of ganglia (often one per segment) that are connected by a double nerve cord. Nerves also radiate to all regions of the body, though each ganglion tends to serve principally the functions of the segment in which it is found. In the head, enlarged ganglia form the brain and subesophageal ganglion. The nerves connect to the sense organs, and though there are many types of sense organs in insects, the compound eyes and antennae are most important (Fig. 30).



Internal Anatomy of Insects, Figure 30 Dorsal view of a grasshopper showing principal elements of the nervous system.

Glandular Systems

There are many important secretions from various glands in the insect body. Exocrine glands release chemical to the outside, whereas endocrine glands release chemicals internally. Among the important exocrine glands are the salivary glands, silk glands, poison glands, odor glands, wax glands. Salivary glands are located in the head and thorax and empty into the region of the mouth. Sometimes the salivary glands are very large. Silk glands similarly can be quite large, depending on the silk production of the insects. Silk glands produce fibrous protein material, which is often used to construct cocoons. Normally, silk is released from the labium, but in some insects the tarsi or anus is involved. Poison glands sometimes produce secretions associated with setae, such as the venom found in caterpillars with stinging hairs or spines. Some secretions are sticky and aid in insect adhesion. Poison glands also may be found in association with the ovipositor or sting, and are modified accessory reproductive glands. Odor glands are quite variable. Those associated with glandular scales on wings of butterflies are quite small, whereas those associated with the osmeteria of swallowtail caterpillars, and the stink glands of stink bugs are larger. Many glands have a defensive function. Wax glands are found commonly in Hemiptera and bees. Wax secretion range from a powdery covering to large and complex body coverings.

Among the endocrine glands are the corpora allata, corpora cardiaca and the prothoracic glands. Corpora allata are small exocrine glands associated with the brain, and produce juvenile hormone. Corpora cardiaca are small organs associated with the brain that store and release prothoraciotropic hormone (PTTH) that activates the prothoracic glands. The prothoracic glands are found in the thorax of insects and secrete molting hormone (ecdysone) or a closely related ecdysteroid.

Reproductive System

The reproductive system of insects is quite variable among species, but unlike most other systems, also differs markedly between the sexes. The male reproductive system consists of paired tested composed of testicular follicles, paired vasa defferentia, a seminal vesicle, a media ejaculatory duct, and accessory glands that open into the genitalia. Sperm are produced in the testicular follicles, travel down the vas deferens to the seminal vesicle where they are stored, and then released, often is association with a secretion of the accessory glands. The female reproductive system consists of paired ovaries composed of ovarioles, paired oviducts, a common oviduct and vagina, accessory glands, spermatheca, sometimes a bursa copulatrix, and an ovipositor. The eggs are produced in the ovarioles, travel down a paired oviduct to the common oviduct, where they are may be fertilized by sperm that has been stored in the spermatheca.

► Alimentary Canal and Digestion
► Endocrine Regulation of Insect Reproduction
► Locomotion and Muscles
► Nervous System
► Oogenesis
► Tracheal System and Respiratory Gas Exchange

Interneurons

Nerves that are located entirely within the central nervous system and transmit messages to other interneurons or to motor neurons.

Interspecific Competition

Competition between members of different species. (contrast with intraspecific competition)

Interstitial

Situated between two segments.

Intertidal Dwarf Bugs

Members of the family Omaniidae (order Hemiptera).

► Bugs

Intima

The cuticular lining of the foregut, hindgut, and trachea (but not the midgut).

Intraspecific Competition

Competition between members of the same species. (contrast with interspecific competition)

Intrinsic Rate of Increase

(r) The maximum rate of population growth, estimated as the birth rate less the mortality rate. The net increase in population size.

Introduced

An organism that is native elsewhere, but was deliberately moved by people to the area specified. This term is often incorrectly applied to organisms that invaded.

► Invasive Insects

Introgression

The incorporation of genes of one species into the gene pool of another. If the ranges of two species overlap and fertile hybrids are produced, they will tend to backcross with the more abundant species.

Intron

A region of eukaryotic DNA coding for RNA that is later removed during RNA splicing. The final RNA product does not contain the intron segments.

Inundative Biological Control

The release of large numbers of a biological control agent relative to the target organism, with no expectation of permanent establishment.

Invader

An organism that has arrived in an area from elsewhere. Other terms for invader are nonindigenous, non native, and adventive.

Invasion Area

An area invaded by insects (usually locusts) during a period of outbreak, though this area typically does not support the invaders.

Invasive Species

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Invasion of new territories by insects and related organisms has always been a major source of pest problems. Indeed, in most areas of the world the principal pests are invaders from another area, usually another continent. This is not to say that invaders cannot be local or regional pests. For example, agricultural pests commonly move from native flora or weeds to crops, and can be considered invaders of the crop. Likewise, biting insects often disperse short distances from undisturbed natural areas to places inhabited by people or livestock. Sometimes highly dispersive pests fly thousands of kilometers each year to invade areas where they cannot survive the winter. However, this article focuses on nonindigenous (adventive, alien) invaders, which are considered to be pests that have moved a considerable distance, rather than locally, to permanently establish populations where they have not occurred previously.

Some Terminology

Terminology related to invasiveness is not always used consistently. Following is some clarification of terminology:

Invasive. Having a tendency to spread, or population increase resulting from immigration. Invading (adventive) organisms differ in their invasive potential, but have a tendency to be more invasive if they find a particularly suitable habitat or are free of the suppressive agents occurring in their home environment. However, naturally occurring (precinctive) organisms can also become invasive, as might occur when habitat is altered, making it more suitable for the precinctive organism.

Indigenous. An organism is present, occurs naturally, and evolved in this location. Indigenous = "native." The opposite of indigenous is "nonindigenous," and although "adventive" is a preferable term relative to nonindigenous, the latter is used widely because it is unambiguous.

Precinctive. An organism is indigenous/native, but only found in a certain area. It is also possible for an organism to be indigenous but not precinctive, as it may be found widely. The term "endemic" is sometimes used in place of precinctive, but it has other meanings so should not be used with respect to distribution.

Adventive. An organism that came from elsewhere. Adventive = not native, or nonindigenous, or alien. Adventive organisms may be introduced or immigrants.

Introduced. An organism not native to an area but that has arrived as a result of purposeful introduction. Introduced species sometimes are quite invasive and escape beyond the region or purpose of their release, so this must be guarded against.

Immigrant. "Accidentally introduced." An immigrant is an organism that is not native to an area (it is adventive), and has arrived as the result of hitchhiking (traveling) or by its own means of dispersal (usually by flight or rafting). Immigrants are often called "invaders" or "invasives," though their invasive properties vary considerably once they have arrived.

Why Invasive Species Are So Abundant

As mentioned previously, the major pests throughout the world often are nonindigenous species. When nonindigenous species invade new areas they sometimes cause great damage simply because they are new, and management procedures have not been formulated or communicated. Once effective techniques have been developed and implemented, the nonindigenous species may join the ranks of most indigenous pests as occasional problems. But in some cases, nonindigenous pests attain and maintain unusually high levels of abundance, relative to their place of origin, and continuously inflict considerable damage. In a few cases, such pests are abundant everywhere they invade, and *also* in their place of origin. The exact reason for the unusual abundance of nonindigenous species usually is not certain, but several explanations have been suggested, including:

Enemy Release

This is the explanation most often given to explain unusual abundance of invaders. In this scenario, the invader leaves behind its natural enemies, which may be parasitoids, predators, pathogens, and even vertebrates. The best evidence for this explanation being valid is the spectacular success of some classical biological control programs once natural enemies have been introduced into territory newly invaded by a pest. Likewise, the failure of some biological control programs to achieve success can be used to argue that the absence of such biotic agents are not the only reason invaders are so successful. However, biological control programs never achieve complete transplant of natural enemies. Only the seemingly most important natural enemies are introduced, leaving behind most of the nonspecific arthropod predators and vertebrate predators, and usually most of the insect pathogens. From this perspective, it is amazing that natural enemy relocation (classical biological control) works as well as it does.

Competitive Advantage

A nonindigenous invader would not necessarily be expected to out-compete indigenous species for resources, but it sometimes happens that indigenous species are displaced by invaders with higher rates of reproduction, better survival rates, or other fitness factors that lead to increases in their abundance. In other cases, not all niches are occupied, so in some instances it is exceedingly easy for invading species to take up residence without significant competition. For species that are serious pests nearly everywhere they occur, superior fitness is a logical explanation for their abundance.

Novelty

Invaders may be taxonomically unrelated or functionally distinct from indigenous species or, as mentioned previously, may occupy vacant niches. This may not only allow ready establishment due to limited competition, but may account for a dearth of natural enemies that might adopt the invader as a resource. It commonly requires several generations or years for indigenous parasitoids and pathogens to develop strains that can effectively kill new (nonindigenous) hosts. Thus, the novelty (newness) of the invader may account for initial success in the newly invaded environment.

Preadaptation

Invaders may be uniquely adapted for a particular resource or environment. Crop plants may be especially suitable for exploitation because crops usually are bred for horticultural attributes, but usually not antiherbivore traits. In fact, many efforts to improve horticultural characteristics weaken the natural antiherbivore defenses of plants. Even if the fitness of a host has not been diminished by artificial selection, once an insect parasite adapts to the host it has a very large resource base available to it. So long as the adapted herbivore is able to track its resource in time and space, it can readily exploit the host population. Evidence for the importance of preadaptation can be seen in the redistribution of crop pests around the world; the same important (well-adapted and damaging) species tend to follow the movement of crops to new environments. Preadaptation also applies to weather and climate, because insects perform better in certain environments than in others. Upon attaining the most favorable environment, their populations are most likely to display explosive growth.

Pathways of Dispersal

Natural dispersal of pests (dispersal without assistance of human activities) is frequent, and the natural range of most insects was established by natural dispersal long before humans were navigating the globe. Even remote locations such as the Hawaiian Islands and the Galapagos Islands had a modestly rich insect fauna before the arrival of humans. Rafting on floating debris, hitchhiking on birds, and direct flight are the likely modes of transport, of course, with rafting probably most important. However, since regular movement by humans to these remote locations began about 300 years ago, the fauna has changed considerably, and of course the pathways have changed through the use of ships and aircraft. Species richness in Hawaii has increased immensely with the addition of about 2,300 invaders to the approximately 3,750 indigenous species, and in the Galapagos by the addition of 295 nonindigenous species to the 1,550 indigenous species. At these island locations, nearly all of the increase in species richness is due to the inadvertent (but sometimes deliberate) movement of hitchhiking (traveling) arthropods. This is not to say that natural dispersal over such long distances is not possible. The relocation of large numbers of desert locusts, *Schistocerca gregaria* (Forskall), to the Caribbean and northern South America from Africa with the assistance of weather fronts in 1988 stands out as an example of how natural, long-distance transport remains possible. And although the dispersing *S. gregaria* did not establish successfully in the western hemisphere during this dispersal episode, the ancestors of the numerous *Schistocerca* species inhabiting the western hemisphere are believed to have originated from a similar episode thousands of years ago.

Human-assisted dispersal now is the principal means by which nonindigenous insects gain access to new territory. Sometimes relocation of nonindigenous species is deliberate. European honey bee, *Apis mellifera* L., for example, has likely been relocated to everywhere that humans exist, except for polar regions. Other examples of deliberate relocation include silkworm, *Bombyx mori* L., for silk production, and the many predators and parasites that attack plant pests of crops grown in greenhouses. Nowadays, these arthropod relocations are usually accompanied by appropriate regulatory oversight, and there is minimal risk of ecological and economic problems.

Accidental dispersal of insects is much more likely to result in problems. In earlier times, dispersal of nonindigenous insects was often associated with sailing ships, or more specifically, with disposal of ballast carried in sailing ships. The unloading of ships' ballast on the seashore of ports often resulted in inoculation with nonindigenous organisms. Ballast is weight needed to stabilize sailing ships so that they do not tip excessively.

The traditional ballast for sailing ship in the 1600s–1800s was stones, gravel, and rubble. Local ordinances in ports forbade the dumping of ballast in the water (where it would soon clog the harbor), so it was unloaded on the shore. Many arthropods, molluscs, and nonindigenous plants were introduced to port cities via ballast. Many spread from these sites of introduction, but often the only records are from these ballast heaps, and they did not disperse more broadly, eventually disappearing. Interestingly, ships traveling from Europe to North America often contained human passengers or refined goods, which did not constitute a great deal of weight, hence the need for ballast. However, on the return journey, the cargo consisted of heavy, raw materials such as lumber, hides, grains and tobacco, so ballast was not needed. This perhaps explains the overwhelming movement of pests from Europe to North America, and the relatively slight movement from North America to Europe. During this period of time, straw was often used for packing and for animal forage, serving to provide a convenient mode of inoculation of organisms associated with straw.

As sailing ships were replaced by steam-powered ships, the importance of ballast as a source of inocula was diminished because steam ships were less susceptible to tipping, and changes in technology allowed liquid ballast to be used. However, the proliferation of steamships in the late 1800s and early 1900s was coincidentally accompanied by a strong interest in botanical gardens, and the introduction of new plants for food and forage crops with the aim of improving agriculture. Travel by steam-powered ships was more reliable and often faster than by wind-powered vessels, so shipments of plants (and their hitchhiking arthropod pests) were more likely to arrive at their destination alive. Thus, accidental transport of insects increased rather than decreased.

This time period was also accompanied by the proliferation of canals and railroads. Thus, not only was it more likely for pests to traverse the world's oceans, but upon introduction to new territory the pests were quickly moved far inland from the ports by canal boats and railroad cars. Thus, the inland environments as well as the coastal environments were inoculated with nonindigenous organisms.

In the latter half of the 1900s, the movement of products by sea in sealed containers became dominant, and travel by air became commonplace not only for people, but for expensive and perishable goods such as flowers and fruit. This allowed short-lived organisms easier access to new environments. Also, the nature of ballast had changed, and liquid (seawater or riverwater) rather than solid ballast predominated. Thus, marine and freshwater invertebrates, algae, and perhaps vascular plants became important items of concern, and arthropods were less likely to be associated with ballast. However, arthropods remained important as contaminants of sea containers, perishable goods and other agricultural commodities, and of contaminants of handbags carried by the ever-increasing numbers of tourists. Infestation of wood used to construct shipping crates also became an issue as tree-infesting pests were moved around the world, and ants proved especially adept at entering shipping containers and being relocated with the ever-increasing international commerce. The table below shows some recent data on infestation frequency of commercial shipments arriving in the USA from Mexico, and demonstrates that most types of cargo shipments have the potential to be contaminated with insects (Table 14).

A less-important but notable method of introduction of invasive nonindigenous organisms is contamination of military equipment. Within the context of war, concern about contamination or equipment and material by pests is replaced by concerns about safety and success of the military operation. Thus, in the wake of major conflicts of the twentieth century there was some relocation of pests. But even during relatively peaceful times, movement of military equipment is a potentially important source of pest inoculum.

By way of example, the following table highlights some of the pathways of invasion of Japan by immigrant insects (Table 15).

Invasive Species, Table 14 Insect interceptions associated with transport of cargo from Mexico to the USA during the period 1997–2001 (adapted from Work et al. 2005. Biological Invasions 7: 323–332)

Type of Transport	Type of Cargo	Number Containers Inspected	Number Insect Interceptions
Maritime	Empty container	606	0
	Nonagricultural	883	0
	Nonrefrigerated containers	6459	125
	Refrigerated containers	2578	208
Air	Agricultural	4150	142
	Nonagricultural	1266	2
Land	Low-risk agriculture	4902	5
	Empty container	2407	0
	Nonagricultural	1019	0
	Agricultural	5093	77

Invasive Species, Table 15 Probable pathways of introduction of insects accidentally introduced into Japan during 1917–1999

Probable pathways	Number of species
Flight (air currents, typhoons, etc.)	4
Plant material (nursery stock, bulbs, etc.)	52
Military transportation	10
Hay (dried fodder)	9
Fruits and vegetables	8
Grain	8
Hitchhiking (traveling)	3
Wood and packing materials	2
Cut flowers	1
Seeds	1
TOTAL	98

Adapted from Kiritani, Yamamura (2003) Exotic insects and their pathways for invasion. In: Ruiz GM, Carlton JT Invasive Species, pp 44–67

Ecological and Taxonomic Patterns of Dispersal

In addition to the shift in the method of transport of nonindigenous organisms, the nature of the pests being relocated has also changed with time. In North America, many of the pests initially introduced were stored products pests. This was a period of relatively slow transport, however, when perishable goods did not survive the many months at sea necessary for long distance travel, so long-lasting stored grains and legume seed were disproportionately used as food for sailors and transported to support colonists who were struggling to establish new economies. As the rate of transport was enhanced, vegetable and fruit pests were moved around the globe, as such foodstuffs survived the weeks of transport from location to location. More recently, ornamental plants are being moved with greater frequency, and the pest complex has changed again. Often it is propagative materials that are being moved from low-labor cost areas to higher labor cost areas in an effort to reduce the overall labor costs associated with ornamental plant production. Also, cut flowers are commonly produced in relatively small areas favored by climate or labor costs, and then redistributed around the world. Homogenization of ornamental plant pests, especially greenhouse-grown plant pests, seems inevitable.

The taxonomic shift is as significant as the ecological changes among North American invaders. Early in the settlement of North America, beetles (Coleoptera) were the dominant invaders. By the late 1800s, however, Lepidoptera (moths) and Hemiptera/suborder Stenorrhyncha (aphids, whiteflies, scales, and mealybugs) assumed dominance. In the 1900s, Hymenoptera (principally ants) became quite important.

The continents of origin for arthropods successfully invading the USA (except for Alaska and Hawaii) are shown in (Fig. 30). Perhaps it is not surprising that the majority of immigrant arthropods originated in Europe, because early colonization of North America was by Europeans, there remain strong cultural and economic ties with Europe, and the climates and flora are similar. However, due to the proximity and presence of a land bridge between North and South America, we might expect a higher rate of invasion of North America from Central and South America. But the tropical fauna of Central and northern South America are not well adapted to temperate North America, and temperate South America has reversed seasons from North America, which likely impedes movement and establishment. This pattern is seen elsewhere in the world. For example, the acquisition by remote Australia of European fauna is likely due to similar circumstances.

In Japan, a similar but slightly different pattern of introduction emerged. There, the island nation was largely protected from invasive pests until about 1868 when the national isolation policy ceased. Immediately thereafter, new fruit tree varieties were imported, and scale insects and mealybugs were introduced along with nursery stock. Following the cessation of World War II in 1945, massive quantities of grain were imported to compensate for food shortages caused by the war. Not surprisingly, the grain insects that earlier had been moved around the world were finally introduced to Japan. Then, during the 1960s to the mid-1980s, a number of weevils were introduced that affected food crops, ornamental trees, and turf. Finally, at the close of the 20th century, Japan saw the accidental introduction of the many greenhouse pests that were being redistributed elsewhere in the world, including thrips, whiteflies, mealybugs, leaf miners, and aphids. Not surprisingly, the principal arthropods associated with nursery stock and other propagative materials were aphids, thrips, whiteflies and mites; the contaminants of cut flowers were aphids, thrips and mites; the contaminants of fruits and vegetables were fruit flies, weevils and leaf beetles; the contaminants of grain and other seeds were bean weevils and khapra beetles; and the contaminants of wood were bark beetles, longhorn beetles and other wood borers. The following table shows how the pests of greenhouses elsewhere in the world have also become the pests of Japanese greenhouses (Table 16).

In many respects, the accidental movement of molluscs (slugs and snails) is similar to that of arthropods. Homogenization of the world's mollusc fauna is occurring rapidly. In earlier times, deliberate introductions of snails (e.g., European land snails for escargot) for human consumption was unimpeded, but this has been largely curtailed. However, the aquarium trade has resulted in relocation of many snails as "pets" or as contaminants of aquatic plants, much to the detriment of aquatic communities in some areas. Also, in an effort to curtail the problems of snail damage to plants, some predatory snails have been moved to new locations. Examples include the rosy predator snail, *Euglandina rosea* (Férrusac), which has been introduced for control of giant African snail, *Achatina fulica* Bowdich, and likewise decollate snail, *Rumina decollata* (L.), for brown garden snail, *Helix aspera* Müller. Unfortunately, in some cases these imported predators have affected native snails as well as their intended targets. Similarly, in an effort to control aquatic weeds such as water lettuce, *Pistia stratiotes*, herbivorous snails have been released in some

Invasive Species, Table 16 Comparison of greenhouse pest fauna among Japan, Europe, and the USA

Species	Japan	Europe	USA
Thrips			
Frankliniella occidentalis	P*	P*	P
Frankliniella intonsa	P	P	P
Thrips palmi	P*	P*	P*
Thrips simplex	P*	P*	P*
Whiteflies			
Trialeurodes vaporariorum	P*	P*	P
Bemisia argentifolii	P*	P*	P
Leafminers			
Liriomyza trifolii	P*	P*	P
Liriomyza bryoniae	P*	P	A
Liriomyza huidobrensis	A	P*	P
Aphids			
Aphis gossypii	P*	P	P*
Myzus persicae	P	P*	P*
Mites			
Tetranychus urticae	P	P	P
Aculops lycopersici	P*	P*	P*
Weevils			
Otiorhynchus sulcatus	P*	P	P*

P, indicates presence; A, indicates absence; *, indicates invader Adapted from Kiritani, Yamamura (2003) Exotic insects and their pathways for invasion. In: Ruiz GM, Carlton JT Invasive Species, pp 44–67

tropical locations, only to have the snails serve as vectors of human schistosomes.

Despite these examples of deliberate and misguided relocations of molluscs, accidental relocation remains the principal means by which nonindigenous molluscs move around the world. The principal pathways of introduction are the same as for arthropods, the contamination of horticultural and agricultural products, soil, military equipment, and shipping containers. In the USA, plants for propagation and cut flowers are the principal source of detected mollusc entry, followed by crates of roofing and household tiles, attachment to sea containers, and finally by association with agricultural products.

Mollusc contamination is particularly threatening because many species are hermaphroditic, and capable of self-fertilization, which means that even introduction of a single individual can lead to successful inoculation. Even those that require sperm storage, however, often can store sperm for over a year, and snails are capable of surviving for months without moisture. Water ballast has significant potential to move snails between fresh water ports, a route not usually considered to be associated with invading arthropods.

Establishment and Spread

Accidental introduction is usually determined by human activities. Hand luggage is often cited as a pathway of introduction, and indeed, many travelers naïvely or deliberately bring fresh produce (mostly fruits and vegetables) into new areas, and sometimes these are infested with pests. Even smuggling of wildlife or pets is risky, because ticks and other parasites have been introduced with such unlikely hosts as tortoises and snakes. Although some pests probably are introduced in this manner (large fruit flies [Diptera: Tephritidae] are perhaps the most likely to accompany smuggled fruit and vegetables from tropical areas) the legal international shipment of propagative plant materials also is a principal route of entry for most pests, with contamination of wood crates or natural packing material also an increasing problem. The following table illustrates the frequency of infestation of baggage and cargo detected upon entering the USA during the period of 1984–2000, and demonstrates how commodities vary with respect to the occurrence of infestation (Table 17).

Certain patterns of introduction of immigrant insects, or potential introduction, usually emerge when the history of invasion is studied.

For example, 70% of the interceptions of immigrants in the USA are made at only three ports: Miami, New York, and Los Angeles. In Miami, the vast majority of detections originate in Central America, whereas in New York, Europe and China predominate as sources, and in Los Angeles most interceptions originate in China, Thailand and Central America. The table below shows the top sources of invading insect detections found on plant material intended for propagation that was imported in recent times. These data show that the sources of pests do not necessarily reflect trade with the "top" trading partners of the USA; rather, they reflect the unique circumstances of the plant propagation trade, and point out the need to fully understand the unique pathways of international trade (Table 18).

The increase in the "free trade" movement throughout most of the world in recent years has resulted in vast increases in material moving by truck, boats and aircraft. Only a small proportion of the material crossing international boundaries is inspected, and even then it is difficult to critically examine many commodities. In New Zealand, for example, 20% of sea containers are inspected, and in the period of 1999–2000, 24.8% of the containers were found to be contaminated and require quarantine action. Unfortunately, the incidence of contamination by pests has been increasing steadily since 1993–1994, when only 6.4% of the containers held pests. In contrast, only 1–2% of shipments to the USA are inspected, despite the fact that 10.4% of the aircraft arriving at Miami International Airport in 1998–1999 contained insects. Aircraft from Central American countries had a higher incidence of infestation, 23%. These

Invasive Species, Table 17 Numbers of nonindigenous pests intercepted in cargo and baggage upon inspection when entering USA, 1984–2000

Commodity	Insects	Mites	Molluscs
Cargo			
Bulbs	591	3	8
Cut flowers	79,934	424	1716
Cuttings	4860	1090	800
Fruit	37,680	485	130
Plant parts	50,154	2043	1670
Seed	1526	0	9
Soil	39		10
Wood products	6960	1	295
Not applicable	9069	10	4661
Total	190,813	4056	9299
Baggage			
Bulbs	371	3	10
Cut flowers	21,900	187	61
Cuttings	4905	50	48
Fruit	195,707	963	65
Plant parts	88,395	300	374
Seed	26,509	5	17
Soil	156	0	13
Wood products	196	0	1
Not applicable	3469	41	1048
Total	341,608	1549	1637

Adapted from McCullough et al. (2006). Biol Invasions 8:611–630

Invasive Species, Table 18 Arthropod interceptions on plant material intended for propagation in USA (top 12 countries for 1990–1999) (after National Research Council. 2002.)

Origin	Number of Interceptions
Costa Rica	4723
Guatemala	1456
Mexico	1193
Netherlands	902
Honduras	886
Thailand	770
China	588
Singapore	498
Japan	339
Belize	232
South Africa	217
Dominican Republic	200

alarmingly high levels of infestation clearly indicate that insects are routinely transported in commercial cargo, and that inadequate efforts are being made to prevent such transport. Shippers and retailers of imported products often are unwilling or unable to curtail contamination, which is best handled by prevention before shipment, not inspection after shipment.

Establishment of pests in a new environment is related to several factors, including:

Frequency of Inoculation

Some pests are a greater hazard because they more frequently are transported to new environments. Pests that are more cryptic, that infest perishable produce which must be transported with little delay, or that infest material that is imported in high volume are more likely to be transported.

Climatic Suitability of the New Environment

Transport of insects between like climates is most likely to result in successful establishment of the immigrant. Thus, movement of insects between Europe and North America has a higher potential for successful inoculation of a new pest than transport between North America and South America, because in the former case the seasons are the same, whereas in the latter case the opposite seasons prevail. Related to this is the fact that benign climates are more likely suitable for insect invaders than are severe climates.

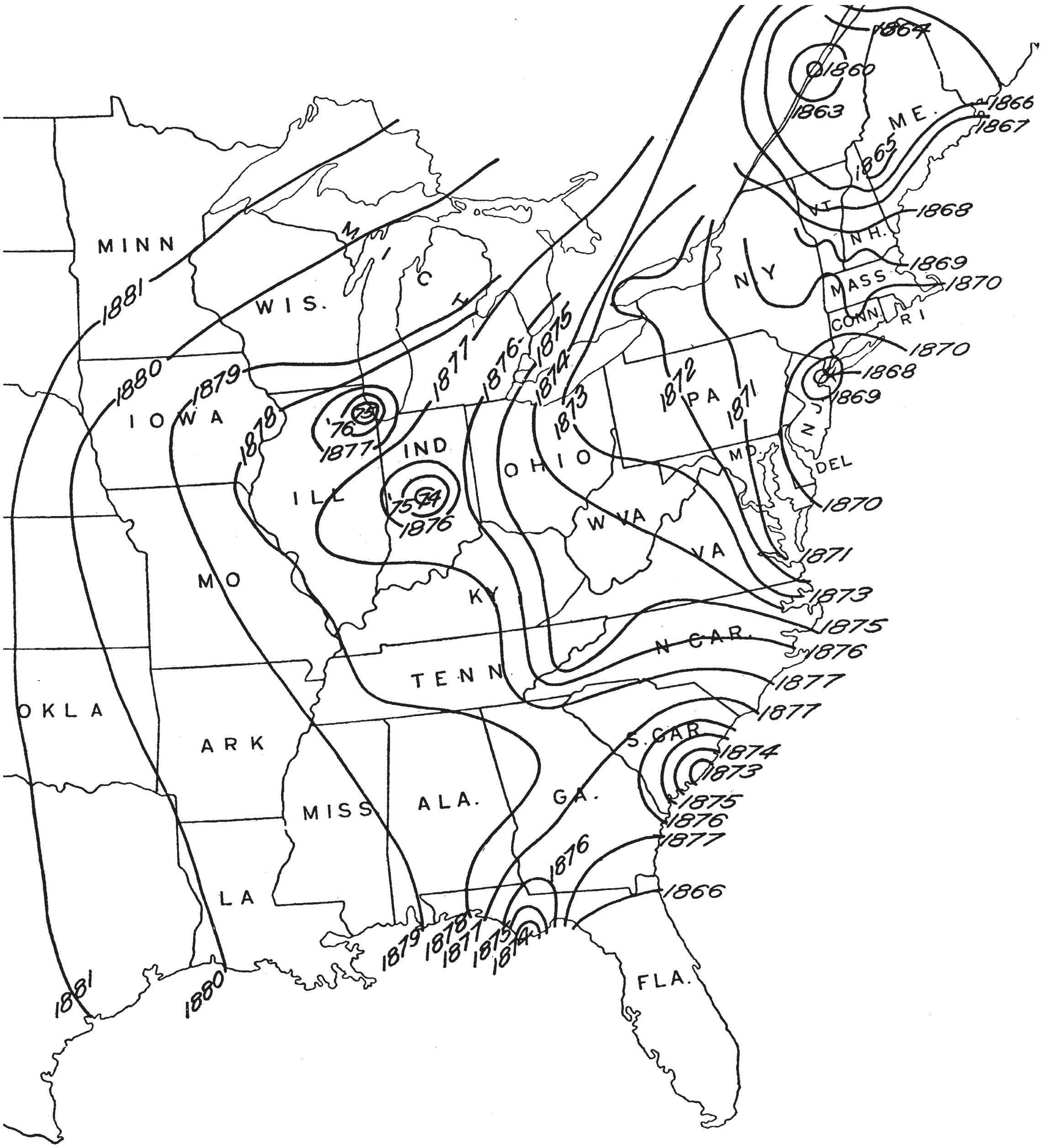
Biological Characteristics of the New Environment

The availability of suitable hosts is critical for successful establishment of invaders. Insects with a narrow host range are more at risk of not arriving in a location where a suitable host is present, but even insects with a broad host range have some hosts that are much more suitable for survival. In fact, insects that are preadapted (that have coevolved) have an extraordinarily high rate of success in tracking their host plants as they are moved around the world. The likelihood of an invading organism establishing successfully is positively related to the size of the area (e.g., number of hectares under cultivation) supporting a suitable host. Disturbed habitats, and habitats with few competing species, also are favorable for establishment of invaders.

Biological Characteristics of the Potential Invaders

Certain biological characteristics predispose insects to establish successfully. Invaders that are small enough to escape detection, that have good powers of flight, that reproduce parthenogenetically, that have a high rate of reproduction, and that are preadapted for the new environment (both host environment and weather) have an above average chance of establishment. The likelihood of establishment also increases when the invader arrives with a large founding population.

The actual pattern of invasion varies with the nature of the introduction, the environment into which the invader is introduced, and the biological characteristics of the invading organism. The accompanying map of the eastern USA (Fig. 31) shows the invasion of this area by imported cabbageworm/small white cabbage butterfly, *Pieris rapae* (L.) (Lepidoptera: Pieridae), and serves to illustrate several points about invaders. *Pieris rapae* was first found in North America at Montreal, Canada (top, right portion of the map), about 1860. After this primary invasion event, it spread by natural means in all directions, but in some cases it apparently was assisted in its dispersal by movement of material. Thus, in a secondary invasion event it was detected in the area of New York City in 1868, before it occurred in surrounding areas. Likewise, it was introduced to Charleston, South Carolina, about 1873 before the adjacent



Invasive Species, Figure 31 **The pattern of invasion of *Pieris rapae* in eastern North America following its introduction about 1860 (from F.H. Chittenden. 1916. *USDA Farmers' Bulletin* 766. 14 pp.).**

areas were infested, etc. It is not surprising that port cities would be points of introduction (including the inland, lake port of Chicago, Illinois, in 1875). The inoculation of central Indiana in 1874 before the surrounding areas were infested could be due to movement of infested produce to this area, an unusual weather event depositing winged adults, or an artifact of early detection.

Weather can play a significant role in assisting dispersal, but climate often sets boundaries on long-term establishment. In the case of *P. rapae*, the entire region has been infested with this adaptable species. In contrast, there are many examples where climate limits distribution of immigrant species in this same area, such as imported red fire ant, *Solenopsis invicta* Buren

(Hymenoptera: Formicidae), which occurs only in the southern region of USA, north to Tennessee, whereas Japanese beetle, *Popillia japonica* Newman (Coleoptera: Scarabaeidae) occurs in the northern region of USA, south to Georgia. The occurrence of host plants limits the distribution of species with a narrow host range, but usually the plant host range exceeds that of the arthropod herbivore range.

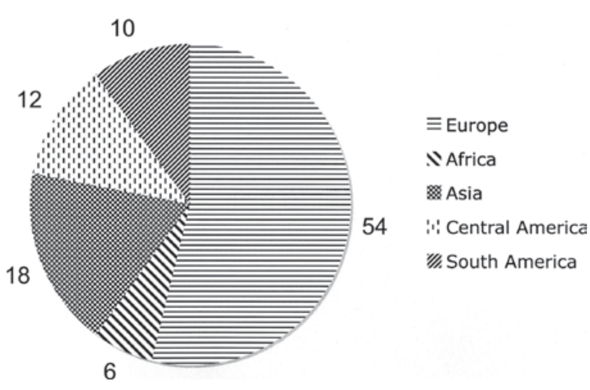
Latency

The period of time between the introduction of nonindigenous species and their detection has been called the latent period. It is usually impossible to pinpoint the exact time that an alien invader arrives, though sometimes it can be deduced with a degree of accuracy. One exception to this generalization is the accidental release of gypsy moth, *Lymantria dispar* L. in Medford, Massachusetts, in 1869. In this case the date was known precisely, but because the city administration did not care, nothing was done until this species became abundant and damaging 20 years later, in 1889. This might be viewed as a surprisingly long period for such a potentially damaging insect to be latent and unnoticed. However, it is not uncommon for gypsy moth to be at a low level of abundance for 10 or more years, only to suddenly increase in abundance, presumably due to some shift in weather.

In Japan, an analysis of the latent period showed a range of from 0.5 to 80 years of latency, and a mean of 11.8 years. However, the mean value is inordinately affected by a few "statistical outliers." In fact, most species (25 of the 35 species) had a much shorter period of latency, and of this group, the latent period was only 3.8 years. Extremely damaging species, and perhaps species that affect certain crops, are more likely to be detected earlier. Thus, because greenhouse crops tend to be high value and inspected regularly, we would expect pests of such crops to be noticed soon after invasion. On the other hand, tree pests that inflicted little damage might go undetected for a considerable period. Often, the likelihood of detection is a function of morphology or behavior; things that look strikingly different or behave differently are apt to be noticed (Fig. 32).

The latent period for detection of invaders is almost never known precisely, but in most cases it is a considerable period of time. Thus, there is a good possibility that new invaders will have time to establish and spread, making eradication difficult or impossible. Most countries make efforts to prevent establishment of potential invaders not only by inspection of incoming materials, but also by trapping at ports and other routes of entry. The period of latency makes it unlikely that immigrants will be detected in a timely manner.

Often there is a population outbreak displayed by immigrants following establishment and adaptation. The outbreak (and the lack of sizable populations during latency) is likely due to genetic shifts in the invading organisms as they adapt to new hosts and new weather, or as they await opportunity to arrive in an optimal environment. Once conditions are suitable, and especially if natural enemies of the pests have been left behind, populations can increase. Often they attain alarmingly high numbers, but then subside. Subsidence may be due to a shift of indigenous natural enemies to new hosts, a shift in the genetics of the host, induced resistance in the hosts, change in



Invasive Species, Figure 32 **The sources of arthropods establishing in the USA (modified from R. I. Sailer. 1978.).**

weather, or a change in the management practices of people in the affected area.

Impacts

The economic effects of nonindigenous arthropods are difficult to assess accurately. In the case of crops and livestock, it is possible to estimate the costs of pesticides used for their protection, and to add to this the loss experienced by the commodity even in the presence of pesticide use. However, such data are notoriously unreliable. Even more problematic are aesthetic costs (e.g., damage to the appearance of lawns and gardens) and environmental effects (e.g., water quality, habitat degradation, loss of wildlife). Sometimes the calculations used to generate such figures use imperfect methodology, though often out of necessity. For example, one might partition the total economic losses due to insects into the proportions caused by indigenous species and nonindigenous species. However, would one make that partition based on the proportions of indigenous and nonindigenous species in the pest species assemblage? This approach has been used, but it likely underestimates the impacts of nonindigenous species, which often account for disproportionately large amounts of damage. For example, of the total crop losses attributable to arthropods in Hawaii, Florida, and California, the proportions due to nonindigenous species are estimated to be 98, >90, and 67%, respectively, whereas the proportions of nonindigenous arthropod pests in these locations are only 34, 7.5 and 2%, respectively.

Some estimates of loss caused by nonindigenous pests in several countries are found in Table 19. For comparison purposes, losses are partitioned into "agricultural" losses to crops, pastures and forests, and into environmental losses to the nonagricultural environment. Also, arthropod-caused losses are contrasted with losses due to weeds, vertebrates, and plant pathogens. Although these data may be imperfect, they clearly demonstrate how costly nonindigenous pests are to societies throughout the world.

The redistribution of arthropods around the world has been occurring for many years, and in some respects is continuing unabated. The pattern of establishment of immigrant arthropods in Florida, USA, is shown in Fig. 33, and demonstrates the high degree of year-to-year variation in invasion (or detection). It also shows that there is not much of an increase, if any, in the rate of invasion. The same pattern is occurring in California, USA. On the other hand, there is growing concern about invasive pests throughout the world, so how can we reconcile the increase in concern with the apparent steady rates of invasion? There are several possible explanations, including:

High-Profile Pests

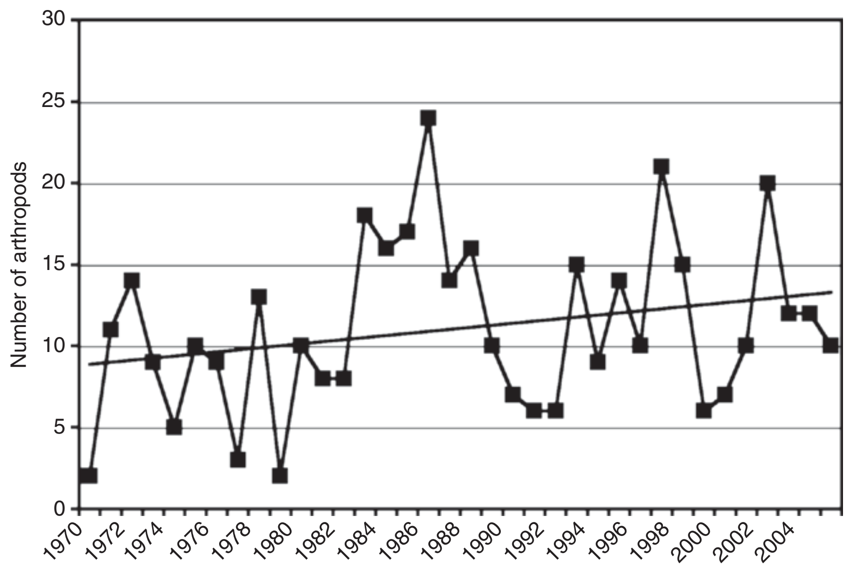
In recent years there have been some especially high-profile invasions that severely affected crop production in agricultural areas, but also some that affected inhabitants of cities and elsewhere, including the health of humans. Thus, more people have become aware of the problem.

Cumulative Effects

Although the rate of invasion may not be increasing, the number of immigrant species continues to increase, and the total impact grows ever larger. Although the impacts of some nonindigenous pests are neutralized by highly effective, low-cost methods such as biological control, in most cases they remain a problem requiring continued vigilance and economic cost (Fig. 34).

Increased Environmental Awareness

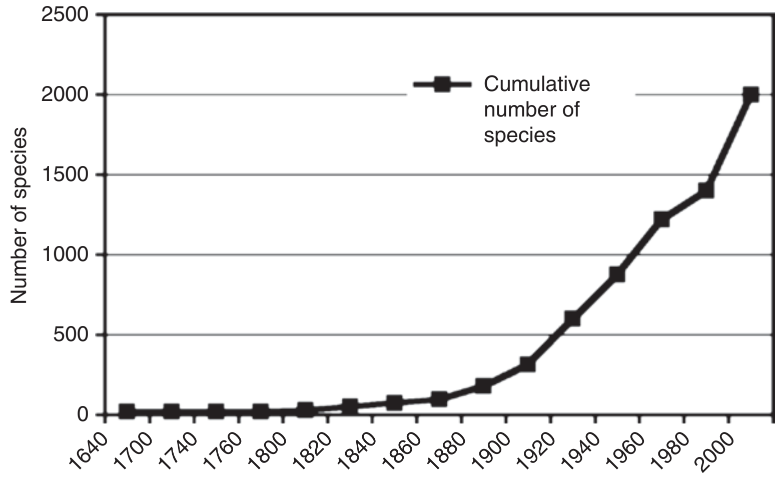
Over most of the globe, there is increasing concern about the quality of the natural environment. As human populations continue to grow, we see decreases in water quality, increases in soil erosion, more deforestation, depletion of



Invasive Species, Figure 33 **Frequency of establishment of nonindigenous arthropod species in Florida, USA, from 1970 to 2005 (M.C. Thomas. Unpublished. Florida Department of Agriculture, Division of Plant Industry.).**

Invasive Species, Table 19 **Economic losses (US $ billions per year) attributable to different groups of nonindigenous pests, and the location of impact, in the United States, United Kingdom, Australia, South Africa, India, and Brazil. "–" indicates that data are not available (adapted from Poinar et al. 2002. Economic and environmental threats of alien plant, animal, and microbe invasions. pp. 307–329 in D. Poinar [Ed.]).**

Pest and Location	USA	UK	Australia	South Africa	India	Brazil
Weeds						
Crops	27.9	1.4	1.8	1.5	37.8	17.0
Pastures	6.0	–	0.6	–	0.92	7.52
Environment	0.148	–	–	0.09	–	–
Vertebrates						
Crops	1.0	1.2	0.2	–	–	–
Environment	39.2	5.5	5.8	2.7	25.0	4.0
Arthropods						
Crops	15.9	0.96	0.94	1.0	16.8	8.5
Forests	2.1	–	–	–	–	–
Environment	2.14	–	0.23	–	–	–
Plant pathogens						
Crops	23.5	2.0	2.7	1.8	35.5	17.1
Forests	2.1	–	–	–	–	–
Total	119.9	11.1	12.3	7.1	116.0	54.1



Invasive Species, Figure 34 The cumulative number of nonindigenous arthropod species that have established in the USA, excluding Hawaii and Alaska, since colonization (modified and updated from R. I. Sailer. 1978.).

energy reserves, reduction in marine fish populations due to over-fishing, and global warming. Perhaps we have become more sensitive to the problem of invasive species because it is just another manifestation of natural resource mismanagement.

Risk Assessment and Quarantines

Quarantine procedures commonly eliminate the likelihood of pest relocation by banning the movement of potentially infested products or by requiring product treatment to eliminate the threat of pest movement. Though effective, this interferes with international commerce. Indeed, the risk of pest infestation has been used, at times, as a trade barrier to reduce competition covertly. Sociopolitical issues increasingly dictate that quarantines not be used to interfere with trade, necessitating better risk assessment, reducing the risk that pests will enter the stream of commerce, improving early pest detection, and developing more efficient pest elimination techniques.

Risk assessment necessitates determining which pests could be imported, the likelihood of importation, and the consequences of importation. Several systems have been designed for determining the probability that a pest will become invasive. The assessments are fundamentally qualitative, but by assigning ratings to a series of pest biological characteristics (e.g., reproductive potential, dispersal abilities, host preferences, etc.), characteristics of pest "opportunity" (e.g., likelihood that pests will hitchhike, likelihood that pests will evade detection), and consequences of introduction (e.g., economic or environmental impact), it is possible to categorize risk in an objective fashion. It appears that the best predictor of a pest's invasiveness and potential for damage is its record elsewhere, but particularly in similar climatic areas. Although there are no scientific principles that conclusively identify invasive potential, the opinions of experts who have first-hand knowledge are extremely valuable, even though "data" may be lacking.

Modern quarantine procedures often have several layers of defense designed to mitigate the threat of invasion. In addition to conducting a careful risk assessment, which can be used to identify the likely pathways of inoculation and provide focus for efforts to prevent introduction of pests, quarantine procedures may include:

Production Management Techniques

Commodities should be cultured in a manner that reduces the likelihood of infestation with pests of quarantine importance. This usually requires use of insecticides to eliminate pests, but also could include production of commodities in pest-free areas, use of pest-resistant hosts, etc.

Pre-border Clearance

Overseas inspection of commodities and certification of "pest-free" status as they are packaged for international shipment is sometimes an option, eliminating the need for inspection at the port of entry. The advantages of obtaining pre-clearance include the reduction in backlog at ports of entry and eliminating delay of entry (this can be very important for highly perishable commodities), and the elimination of the need to discard/destroy infested commodities after the expense of transport has been incurred.

Disinfestation

Commodities that are infested or might be infested can often be disinfested in transit by use of cold storage, heat treatment, or controlled atmospheres that will kill the pests without harming the commodities. Alternatively, chemical fumigation with insecticides can be used.

Border Treatments

Efficient detection is the most important quarantine protocol when commodities have arrived at an international (sometimes intranational) border. Detection of small or cryptic pests, or pests occurring at a low incidence, may be nearly impossible. Detection is enhanced by knowing which pests are likely to be hitchhiking, and the exact origin of the commodities. There can be significant differences in infestation rates among geographic regions, and times of the year when pests are likely to be hitchhiking. Even the practices of individual producers and shippers can influence the level of infestation. If pests are present, disinfestation with fumigants or other techniques may be mandated. If this is not possible, commodities may be returned to the country of origin, or destroyed.

Restricted Distribution of Commodities

In large countries with varying environmental conditions, the threat of nonindigenous pest introduction and establishment may be limited to only a portion of the area within its political boundaries. Thus, risk can be mitigated by restricting importation and distribution of commodities that might be infested to areas where the pest cannot survive.

Eradication

Inevitably, some pests are detected in a new location, and a reproducing population may be established by the time of detection. Again, efficient detection is the best defense against this occurring, but if it does occur, host destruction and chemical treatment with insecticides are the commonest approaches to eliminate the pests. For pests where sterility techniques (e.g., release of sterile males for some tephritid fruit flies) or effective trapping (e.g., oriental fruit fly, *Bactrocera dorsalis* [Hendel]) exist, these approaches may be more effective. However, alternatives to insecticides and host destruction usually exist only for pests that have been well studied.

Risk Mitigation for Avocado: An Example

An excellent example of risk mitigation involves the quarantine protocol allowing importation of avocados from Mexico to the USA. Avocados in Mexico are infested with fruit flies not found in USA, so for many years the importation of this fruit was prohibited. The quarantine protocol developed for Mexican avocados consists of several mitigation procedures, including:

Field Survey

Growing areas must demonstrate absence of flies.

Trapping

Traps in production and packing areas must remain fly-free.

Sanitation

Fallen and over-ripe fruit must be collected and destroyed to minimize fly breeding.

Host Resistance

Haas avocado, the variety produced commercially in California (the principal avocado production region in USA) is not susceptible to infestation.

Post-harvest Safeguards

Packing houses must be screened and have double-door entrances to minimize threat of infestation after harvest. Fruit must be inspected at the packing house.

Phenology

Avocados can be harvested and shipped only during the winter months.

Port of Arrival Inspection

Upon arriving in the USA, fruit must undergo further inspection.

Limited Distribution

Distribution of Mexican avocados is limited to the northeastern USA, where there is no avocado production and the weather would be inhospitable to any flies that emerge.

In many cases, invasion of nonindigenous pests is detected only after they become well established, and eradication is not possible because they have spread over an area that is too large to treat effectively or safely. In this case, the pest's impact is reduced by implementing new pest management programs. Self-sustaining programs such as introduction of biological control organisms are desirable, but not always possible. Education and improvement of management techniques in the invaded area is often possible, though such efforts require additional effort and expense.

► Pest Risk Analysis (Assessment)

References

Capinera JL (2002) North American vegetable pests: the pattern of invasion. Am Entomol 48:20–39

Frank H (2002) Pathways of arrival. In: Invasive arthropods in agriculture. Problems and solutions. Hallman G, Schwalbe C (eds), Science Publishers, Enfield, NH, USA, pp 71–86

McCullough DG, Work TT, Cavey JF, Liebhold AM, Marshall D (2006) Interceptions of nonindigenous plant pests at US ports of entry and border crossings over a 17-year period. Biol Invasions 8:611–630

National Research Council (2002) Predicting invasion of nonindigenous plants and plant pests. National Academy Press, Washington, DC, 194 pp

Pimentel D (ed) (2002) Biological invasions. Economic and environmental costs of alien plant animal, and microbe species. CRC Press, Boca Raton, FL, 369 pp

Ruiz GM, Carlton JT (eds) (2003) Invasive species. Vectors and management strategies. Island Press, Washington, DC, 518 pp

Sailer RI (1978) Our immigrant insect fauna. Bull Entomol Soc Am 24:3–11

Work TT, McCullough DG, Cavey JF, Komsa R (2005) Arrival rate of nonindigenous insect species into the United States through foreign trade. Biol Invasions 7:323–332

Invasive

An organism that is expanding its range, or has a history of expansion.

► Invasive Insects

Inversion

Alteration of the sequence of a DNA molecule by removal of a segment followed by its reinsertion in the opposite orientation.

Invertebrates

Animals lacking an internal skeleton or "backbone," including such animals as insects, mites, and worms.

Inverted Copulation

PIERRE JOLIVET
Paris, France

There are extremely rare cases among insects, and possibly among some mites, where females possess a specialized extensible intromittent organ, that collects the male's spermatophore or the male sperm. The cases are known among certain Lepidoptera: Nymphalidae (*Argynnis*) and Lycaenidae (*Plebejus*) and Coleoptera: Scirtidae or Helodidae (*Cyphon*). It could exist among certain Acari: Canestriniidae, but the fact has to be confirmed. However, the whole concept needs further investigation, and in certain cases (Lycaenidae) other interpretations are to be considered. In all cases, anyhow, the female lightly penetrates the male. In some cases, the female seems to capture and aspirate the spermatophore or the semen and actively collect it from the male genitalia. The extensive organs of certain Lepidoptera families seem to have evolved independently and convergently and are divergent in shape if not in function. It is evident that a reevaluation of the structure and of its functioning is necessary.

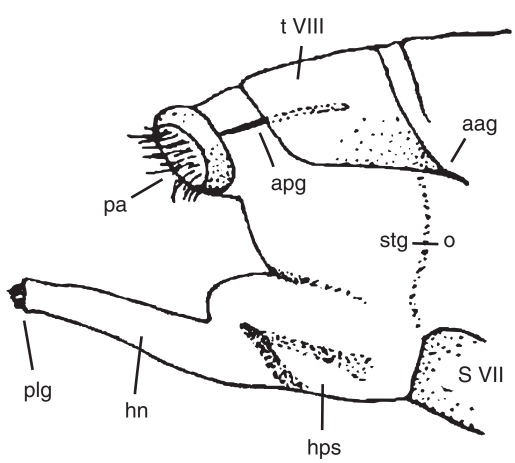
Lepidoptera

Female erection exists only among two families of Lepidoptera, Nymphalidae and Lycaenidae, and only among some genera and species. The only problem is, what is the function of those erections? The structures seem convergent, but completely different anatomically. It is also evident that those organs are extremely fragile and have escaped the attention of most of the authors. The organs are almost transparent. We can see this strange "inverted copulation" only if we capture a male and a female in copula, if the couple does not separate in the net or in the cyanide killing jar, and if we can clear the preparation for the microscope.

In *Argynnis paphia* (L.) (Nymphalidae), André Bayard was lucky enough to obtain a slide with both individuals, male and female, remaining in copula. This coupling, so easy to obtain in rearing cages with Heterocera, was once believed to be impossible to get in captivity for Rhopalocera. Actually, we can get it easily in mosquitoes, bees, and butterflies by manipulating the male and bringing the male abdomen into contact with the female extremity. Among many insects, artificial mating is currently used, and cutting the male head facilitates the operation.

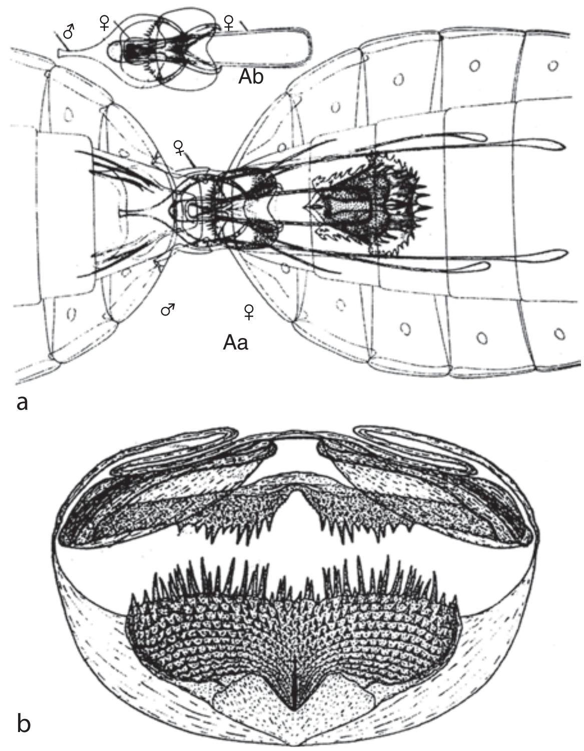
After removal of the left valve in an *Argynnis paphia* male, Bayard showed the strange mating procedures of that butterfly. In the male, the penis seems somewhat modified. The penis here is a massive asymmetric organ, laterally compressed and partly covered with strong spines set sideways. In the female, there exists an enigmatic organ, partly membranous, partly sclerotized, looking when at rest like an accordion in a rosette. It has been called a "clitoris," a "horn of plenty," and a "cornucopia." Mating among these insects seems to be a reversing of the normal relationships between male and female parts. The female enters in erection. In prolongation of the ostium bursae, this cornucopia is transformed into vulvar prolapsus. The inferior grooves of that organ give it a certain rigidity which transforms it into an accordion. This organ pumps the liquid semen from the spermatophore. This prolapsus, when resting, is folded upon itself but enters into erection when acting. In the male, the penis does not seem to move, but the male uncus folds down at its basal part and its terminal hook and crest catch the female prolapsus to direct the opening towards the ductus ejaculatorius. The adjustment of this female organ, extending toward the male during mating, is done through the hooks which grab the cornucopia. Thus, the female penetrates the male in a system which can look extravagant but works perfectly. The origin of the system is difficult to understand due to the fact that the evolution of the structure is not known among the genus *Argynnis* and relatives (Fig. 35).

Bayard describes analogous structures among other species of European *Argynnis*, including *A. pandora* (Denis and SchiffermÜller) and possibly similar facts exist among many or all (including Asian) species of the genus *Argynnis*. The interpretation of the bursa copulatrix remains to be restudied. Artificial mating must be conducted among other species of the genus to study the evolution of this strange morphology (Fig. 36).

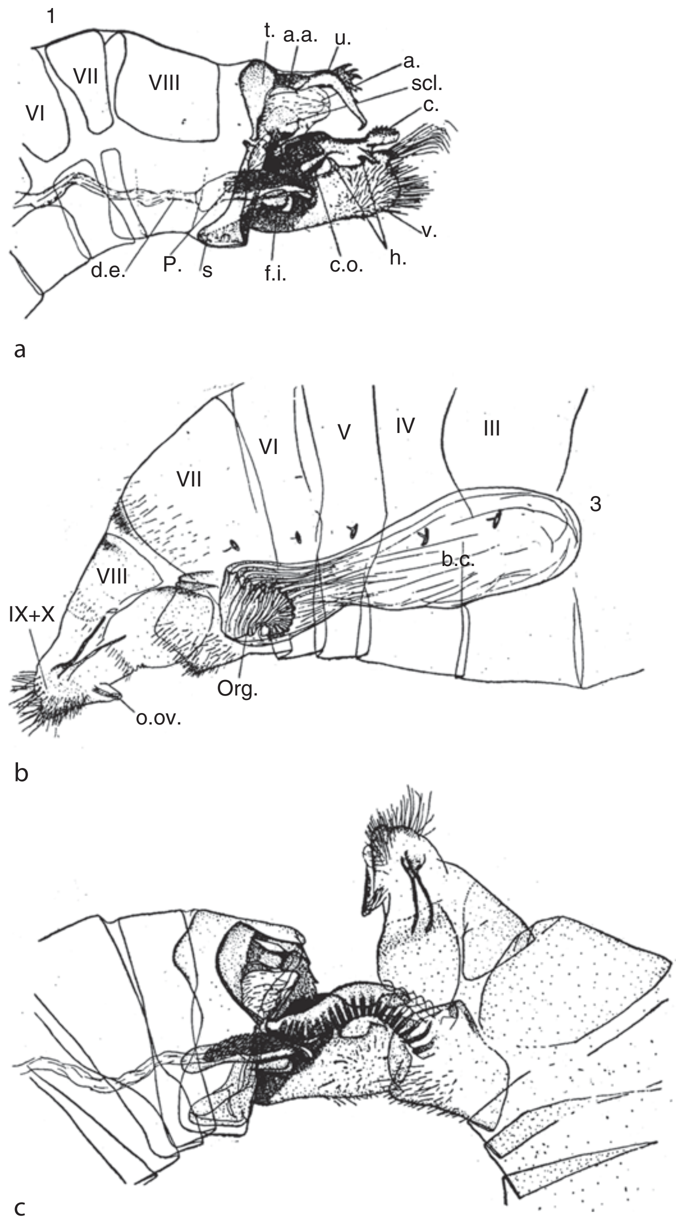


Inverted Copulation, Figure 35 **Evaginated terminalia of a plebejine (Lepidoptera: Lycaenidae). t VIII, eighth tergite; agg, left anterior apophyse; apg, left posterior apophyse; pa, anal papilla; stg, stigmate; s VII, seventh sternite; hps, hypostema; hn, henia; plg, genital plate (after Séguy, 1967.).**

Chapman described what seems to be a similar female erection among the *Plebejus* Klug (Lycaenidae, Polyommatini, Plebejini). According to the author, this phenomenon seems limited to the Plebejini. It is really an erection made with organs different from that of *Argynnis*. The female prolapsus is made of two parts: hypostema and henia. A henia is a distal, membranous, tubular part of an erectile everting apparatus by means of which ostium bursae can be extruded to contact the male in copula. An hypostema is the proximal sclerotized part of an erectile everting apparatus. Chapman gives his explanation without showing an illustration of the mating between the sexes. Several hooks maintain a contact of both female and male organs during



Inverted Copulation, Figure 36 **(a) Mating in *Cyphon kongsbergensis* (Scirtidae or Helodidae). The prehensor is in part inside the male abdomen (Ab). Diagram of the male-female interrelationships during mating. (b) Prehensor acting like a trap in *Cyphon coarctatus* Paykull (female) (after Nyholm, 1969.).**



Inverted Copulation, Figure 37 (a) Genital armature of *Argynnis paphia* (Linné), VI, VII, VIII, sixth, seventh and eighth abdominal segment; t, tegumen; a.a., angular appendix; u, uncus; a, anus; scl, sclerotized rackets; C, cercina; v, right valve, the left valve being removed; h, harpe; c.o., crista obliqua; f.i., inferior fultura; s, saccus; p, penis; d.e., ductus ejaculatorius. (b) Genital armature of *Argynnis paphia* (Linné) ♀, III to VIII, third to eighth abdominal segment; IX + X, last visible segment of the abdomen with its external apophyses; o.ov., ostrium oviductus; org., cornucopia; b.c., bursa copulatrix. (c) Diagram of the mating of *A. paphia* (Linné), according to a slide (after Bayard, 1945.).

the mating. Another interpretation of the evaginated henia would be that of a titillator organ and not a sperm pumping organ. The only way to settle this matter is to see a slide showing the sexes in copula. What is surprising is that in *A. artaxerces*, as in other species, the henia seems terminated by an enigmatic sclerotized genital plate. However, certainly this organ penetrates the male parts and it is difficult to see a titillator in this structure.

Probably, female erection exists elsewhere and has not yet be found. So complex and diverse are these structures that slides are necessary to visualize correctly the matching of the sexes in nature (Fig. 37).

Coleoptera

Among Scirtidae (Helodidae or Cyphonidae) with aquatic larvae, females possess a complex mating apparatus with a kind of forceps at the extremity, which acts as a jaw to receive the spermatophore from the male. This odd organ is found among certain species of the genera *Cyphon*, *Hydrocyphon* and related. However, it remains an exception.

Among Helodidae (Scirtidae), the male genital parts do not seem to penetrate much into the female parts. There exists, at the extremity of the female genitalia, an apparatus, the prehensor, made of two multidentate jaws, evoking a shark mouth. Nyholm distinguishes at the base of the female genital chamber two kinds of prehensors: the bimellater and the konfuser. This prehensor seems to seize the extremity of the spermatophore and to pull it into the vagina, then softening it and liberating the spermatozoa. Does the female organ really penetrate the male? It remains strongly probable. Although Nyholm's drawings are really difficult to interpret, others also have noted that because of the undifferentiated structure of the internal sac, mating was abnormal in the genus *Cyphon*, and that it remained possible that the female ovipositor was penetrating the male in the large median orifice.

Conclusion

More research is needed to clarify the previous examples where the female seems to penetrate the male during the mating to pump the spermatozoa. Other interpretations are possible, but this is the explanation suggested by most entomologists. Moths are easy to mate in the laboratory, but for butterflies artificial copulation is needed. Such observations are necessary among *Argynnis* and Plebejini and probably among other butterflies to interpret correctly this aberrant behavior and the exact mechanism used. At least, there are very peculiar anatomical designs. Mite behavior has also to be reexamined to see if such interpretations are sometimes possible.

References

Bayard A (1944) Observations sur l' accouplement de *Dryas paphia* (L.). Bulletin Société Entomologique de France 49:92–94

Chapman Th (1916) On the pairing of the plebeid blue butterflies. Trans Entomol Soc Lond 64:156–179

Jolivet P (1999) "Women's Lib." chez les insectes ou quand le sexe faible devient le sexe fort (Col. Scirtidae, Lep. Nymphalidae & Lycaenidae). L' Entomologiste, Paris 55:1037–1122

Klausnitzer B (1983) Beetles. Exeter Books, New York, NY, 214 pp

Nyholm T (1972) Zur Morphologie und Funktion des Helodiden-Aedaeagus (Col.) Entomologia Scandanavica 3:81–119

In Vitro

In the "test tube," or other artificial environment; outside a living organism (contrast with *in vivo*).

In Vivo

In the living organism (contrast with *in vitro*).

IPM

An abbreviation for integrated pest management.

► Integrated Pest Management
► School IPM

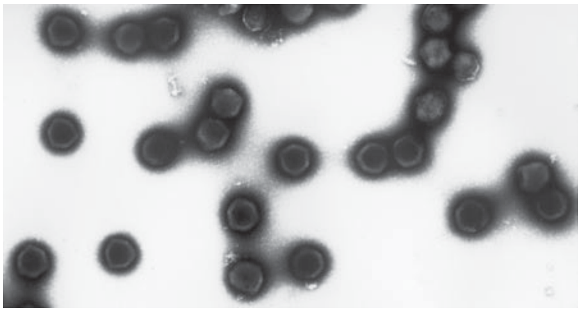
Iridescent Virus Disease

A disease of Diptera, Lepidoptera, and Coleoptera, caused by large icosahedral viruses that impart an iridescent color to host tissue; also known as iridovirus.

Iridoviruses

The iridoviruses produce large icosahedal particles (130–330 nm) which encapsidate a single dsDNA (150–350 kbp). Certain iridoviruses contain an outer envelope, whereas others appear non-enveloped. Various invertebrates, including crustaceans, annelids, nematodes and insects, are known to support iridovirus infections. To date, more than 30 insect iridoviruses have been detected in species of the orders Diptera, Lepidoptera, Coleoptera, Hymenoptera, Orthoptera and Hemiptera. Four genera are recognized: the *Ranavirus* (frog iridovirus), *Iridovirus* (small invertebrate iridoviruses), *Chloroviridovirus* (large mosquito iridovirus), and *Lymphocystisvirus* (fish iridovirus). Comparative restriction endonuclease digests and Southern blot analyses assign members of the genus *Iridovirus* into three subgroups: the *Polyiridoviruses*, *Oligoiridoviruses* and the *Crustaceoiridoviruses* (isopod). Individual iridoviruses have been assigned sequential numbers within a particular group. For example, the iridescent viruses from the cranefly *Tipula paludosa* and the beetle *Tenebrio molitor* have been assigned the types 1 and 29 within the serogroup IV.

Historically, the *Tipula* iridescent virus (TIV or Serotype IV1) was one of the initial models used to examine virus ultrastructure. The two-directional shadowing method, involving coating virus particles at two different oblique angles with metal vapors, demonstrated the icosahedral design of the iridovirus particle (Fig. 38). Structural elements of iridoviruses can be observed in partially disrupted ($CHCl_3$-treated) particles negatively stained with potassium phosphotungstate.



Iridoviruses, Figure 38 Transmission electron micrograph of a negative-stained preparation of icosahedral-shaped iridovirus.

The iridoviruses possess the characteristic 2, 3, and fivefold rotation axes of an icosahedron and consist of 12 pentagons and 20 triangles composed of 1,472 subunits. SDS-PAGE showed that purified iridoviruses contain a major structural protein (MSP, 50–55 kDa) which comprises over 40% of the virion mass as well as over 25 other structural peptides having M_r values ranging from 10 to 230 kDa. In addition to structural proteins, iridoviruses contain various enzymes, including an RNA polymerase, deoxyribonuclease, protein kinase, alkaline protease, phosphorylase, and an ATPase. The nucleocapsid may be surrounded by a viral unit membrane. The lipid composition of this membrane, comprising 4–9% of the virion, is characterized by an abundance of phospholipid and diglycerides.

The iridovirus genome consists of a linear single copy dsDNA molecule ranging in size from 150 to 280 kbp. These linear molecules are terminally redundant with up to 40% of the genome containing repetitive sequence elements. DNA molecules prepared by the Kleinschmidt method revealed linear dsDNA and a small number of circular dsDNA molecules. Tandem exonuclease and restriction endonuclease digestion of iridovirus DNA produced a decrease in amounts of all DNA fragments, suggesting that the genome is circularly permuted. The iridoviruses, which possess characteristics of the T-4 bacteriophage, are the only eukaryotic viruses possessing both terminal redundancy and circular permutation in their

DNA. Screening cloned restriction fragments or the dsDNA by plasmid rescue methods have identified the origin of replication at six sites on the *Chilo* iridescent virus (CIV) genome.

Unlike many DNA viruses, the extracted iridescent DNA is non-infectious when transfected into host cells. Certain insect iridoviruses replicate and produce plaques in insect cell culture. Interestingly, UV-irradiated virus causes the non-genetic reactivation of purified DNA, resulting in cell infection. Evidently, the inner membrane components of the virus particle possess potent biological activity and are capable of selectively switching off host cell biosynthetic events (phosphorylation of host ribosomal proteins and disruption of polyribosomes) and stimulating the transcription of the immediate-early genes of the viral genome.

Acute (patent) infections of host insects by iridoviruses usually result in an iridescent symptom. The coloration is caused by paracrystalline arrays of particles in infected tissues which create Bragg reflections of light. Patent infections result in the production of high numbers of progeny virus, which may comprise more than 25% of the insect body weight. In these cases, the iridovirus undergoes extensive replication in both mesodermal and epidermal tissues. Patently infected insects eventually will die or be cannibalized by conspecifics. The route of transmission of iridoviruses is unclear. Oral ingestion, wound-entry, transovarial transmission, contamination of egg chorion, and entry through spiracles are routes that have been suggested to operate in natural host populations. Under laboratory conditions, feeding healthy insects large quantities of virus results in low infection rates, whereas hemocoelic injection causes significantly higher infection levels.

Historically, surveys of host populations have demonstrated that the frequency of iridoviruses is very low. In most cases the presence of the iridescent symptom has been the chief diagnostic tool and may have caused the underestimation of iridovirus levels. Population samples consisting of more than a million larval blackfly (*Simulium*) contained only 12 individuals exhibiting acute iridovirus symptoms. However, injection of homogenates of apparently healthy-looking blackfly larvae into the permissive larvae of the wax moth, *Galleria mellonella*, revealed that about 40% of the sampled blackflies supported covert iridovirus infections. Utilizing primers designed from the MSP gene, a series of amplification using the polymerase chain reactions (PCR) method were conducted on DNA samples extracted from simuliid larvae. The frequency of PCR-positive larvae was found to vary between 17% and 37%, confirming the chronic nature of iridoviruses. Restriction endonuclease digests of the blackfly iridoviruses amplified in *G. mellonella* larvae produced extensive polymorphisms, suggesting a complex of iridoviruses in these insect populations.

References

Anthony DW, Comps M (1991) Iridoviridae. In: Adams JR, Bonami JR (eds) Atlas of invertebrate viruses. CRC Press, Boca Raton, FL, pp 55–86

Kelly DC (1985) Insect iridescent viruses. Curr Top Microbiol Immunol 116:23–35

Williams, T (1996) The iridoviruses. Adv Virus Res 46:345–412

Williams T, Cory J (1994) Proposals for a new classification of iridescent viruses. J Gen Virol 75:1291–1301

Ironclad Beetles

Members of the family Zopheridae (order Coleoptera).

► Beetles

Ironomyiidae

A family of flies (order Diptera).

► Flies

Ischnopsyllidae

A family of fleas (order Siphonaptera). They sometimes are called bat fleas.

► Fleas

Island Biogeography

The study of species distribution and community composition, on islands or in island-like environments.

Iso-Amyl Acetate

A sting gland alarm pheromone of *Apis* bees. Release of this compound releases attack behavior by bees.

Isonychiidae

A family of mayflies (order Ephemeroptera).
► Mayflies

Isoptera

An order of insects. They commonly are known as termites.
► Termites

Isotomidae

A family of springtails in the order Collembola. They commonly are known as smooth springtails.
► Springtails

Isozyme

An isomer of an enzyme. Various structurally related forms of the same enzyme having the same function but differing from each other in chemical or immunological characteristics.

Issidae

A family of insects in the superfamily Fulgoroidae (order Hemiptera). They sometimes are called planthoppers.
► Bugs

Iteroparous

This term is used to describe insects that are long-lived as adults, and that deposit their eggs singly or in small batches throughout the adult stage. It is used mostly in the description of mosquito biology.
► Semelparous

Ithonidae

A family of insects in the order Neuroptera.
► Lacewings, Antlions and Mantidflies

Ithycerid Beetles

Members of the family Ithycridae (order Coleoptera).
► Beetles

Ithyceridae

A family of beetles (order Coleoptera). They commonly are known as ithycerid beetles.
► Beetles

J

Jacquelin Du Val, Pierre Nicolas Camille

Camille du Val was born at Prades, southwestern France, on July 28, 1828. A sickly child from the age of five, he had no distractions from study and work, and was a brilliant scholar. He travelled to Paris in 1849 to study medicine, and there met some young entomologists, including Laboulbène who helped him join the Société Entomologique de France. This changed his career plans. His first entomological publication was in 1850. His first major entomological paper, a masterly work, was on European species of the genus *Bembidion* (Carabidae) in 1852. This resulted in Guérin Méneville charging him with writing the section on Coleoptera for Sagra's "Histoire physique, politique et naturelle de l' Ile de Cuba. Animaux articulés, insectes, coléoptères," pp 1–136 (1856), pp 137–326 (1857). He published other papers in the Annales de la Société Entomologique de France. A tireless worker, he dreamed of a general work on European beetles. This began as "Genera des coléoptères" in 1857; he managed two more volumes, and Fairmaire achieved its volume 4 in 1868. Equally, the journal that he founded, "Glanures entomologiques," achieved its first two volumes in 1860, but was not continued. His death softened by the presence of his family, he died on July 5, 1862. He left a valuable collection of European beetles, classified according his work "Genera des coléoptères."

Reference

Migneaux J (1862) Notice necrologique sur Jaquelin du Val (Camille). Annales de la Société Entomologique de France 2(4):617–619

Japanese Beetle, *Popillia japonica* Newman (Coleoptera: Scarabaeidae)

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The Japanese beetle, *Popillia japonica* Newman, is the most widespread and destructive pest of turf and landscape plants in the eastern United States. Adults feed on the leaves, flowers, or fruits of nearly 300 species of wild or cultivated plants including trees and shrubs, garden plants, fruits, and crops such as corn and soybeans. The soil-dwelling larvae, or grubs, consume roots of turf and pasture grasses, vegetables, nursery seedlings, and field crops. Hundreds of millions of dollars are spent each year for managing the beetles and grubs, and for state and federal regulatory efforts aimed at limiting the beetle's rate of spread within the United States and elsewhere.

Japanese beetles were first found in North America in 1916, near Riverton, New Jersey. The manner by which the species was inadvertently transported from its native Japan is not known;

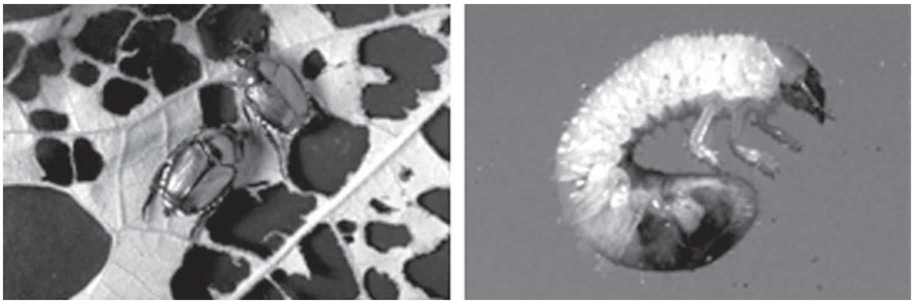
however, the grubs may have arrived in soil about the roots of nursery plants. It is considered a minor pest in Japan, where much of the terrain is unsuitable for larval development, and because natural enemies keep it in check. The eastern United States, however, provided a favorable climate, many adult food plants, lush grassland habitat for the grubs and, at that time, no host-specific natural enemies. Populations rapidly increased and spread. By 2001, the beetle was established in all states east of the Mississippi River except for Florida, and in parts of Arkansas, Iowa, Kansas, Minnesota, Missouri, Nebraska, Oklahoma, Texas, and Wisconsin. It also has spread into southern Ontario and Quebec, Canada. Isolated infestations that were found in California, Idaho, Oregon, Nevada, and Washington probably originated from beetles that were accidentally transported in commerce. Eradication and quarantine efforts have so far prevented establishment in western states.

Japanese beetles belong to the family Scarabaeidae, subfamily Rutelinae. Adults are broadly oval, 8–11 mm long and 5–7 mm wide. The body is metallic green, with coppery-brown elytra that do not quite reach the tip of the abdomen. Each side of the abdomen has five patches of white hairs, and there is another pair of white tufts on the dorsal surface of the last abdominal segment. Females usually are slightly larger than males. The sexes can be distinguished by slight differences in the tibia of the foreleg. The female tibia ends in an elongate, spatula-shaped spur, used for digging. This spur is shorter and more pointed in males.

Larvae are typical scarabaeiform grubs: C-shaped (Fig. 1), whitish to grayish, with three pairs of jointed thoracic legs, a yellow-brown head capsule, and chewing mouthparts. Neonate grubs are about 1.5 mm long; full-sized third instars are about 32 mm long. The ventral side of the last abdominal segment bears a scattering of rather long brown hooked spines, as well as many yellowish hairs at the sides and end. Medially, two rows of shorter straight spines are arranged in the form of a truncated "V." This pattern distinguishes Japanese beetle larvae from other common scarabs. The end of the abdomen appears dark because of ingested soil and food.

Japanese beetles have a 1-year life cycle throughout most of the species' range. In most areas, the beetles begin to emerge in early to mid-June, and adult activity extends into August. Virgin females emit a potent sex pheromone. Early in the seasonal flight period, males fly over stands of grass in search of mates, and jostling clusters of a dozen or more males may accumulate around a single emerging female. Females also re-mate on food plants between bouts of egg-laying.

The beetles typically feed from the upper surface of leaves, leaving only a lace-like skeleton of veins. They also feed on the petals of certain flowers (e.g., roses, hibiscus), as well as developing fruits and berries. Where the beetle is abundant, preferred hosts such as grape, sassafras, and linden may be completely defoliated. Host plants growing



Japanese Beetle, *Popillia japonica* Newman (Coleoptera: Scarabaeidae), Figure 1 ***Left*: Japanese beetles with characteristic feeding damage. *Right*: Japanese beetle grub.**

in sunny locations are preferred. Usually the beetles begin to feed on foliage near the top of a plant, regardless of its height. They tend to aggregate on shoots or plants that have been damaged by other Japanese beetles. This phenomenon results from both sexes being attracted to blends of aromatic volatile compounds released from beetle-damaged leaves.

Despite the beetles' broad host range, some plant species are rarely or never fed upon. Closely-related cultivars within plant species also may differ in susceptibility. The beetles' dietary preferences are probably determined, in large measure, by deterrent or toxic secondary plant compounds. Some plants, e.g., geranium (*Pelargonium × hortorum*), are palatable to the beetles but cause paralysis or other toxic effects when eaten.

After feeding, females fly to a suitable site in which to lay eggs. Areas with moist, loamy soil covered with turf or pasture grasses are preferred. Eggs are deposited in small clutches (1–4 eggs), mostly in the upper 8 cm of soil. The cycle of feeding and oviposition is repeated every few days. A female beetle may live for 30–45 days, during which she may deposit 40–60 eggs.

Eggs are pearly-white, and about 1.5 mm long. They are ovoid at first, becoming more spherical as they absorb moisture from the soil. Eggs hatch in about 2 weeks, usually by early to mid-August, and the grubs feed on fine roots and organic matter, mainly in the upper 5 cm of soil. When grubs are numerous, the root system of turf grasses may be completely severed, such that the turf wilts and dies, and can be pulled from the soil like loose carpet. Most grubs are third instars by late September. They feed until about the time of first frost, and then burrow deeper (about 15–30 cm) to overwinter. They begin to move back up into the root zone in early spring when soil temperatures warm to about 50°C. They feed for another 4–6 weeks, then go slightly deeper and form an earthen cell in which to pupate. The first adults begin emerging a few weeks later.

Skunks, raccoons, moles, shrews, and birds dig in infested areas to forage on the grubs. Indigenous predatory insects, including ants and ground beetles, consume the eggs and young larvae. Birds, toads, fish, and other insectivores eat the adults. From 1920 to 1933, entomologists searched for natural enemies of the Japanese beetle and other closely-related scarabs in Asia, mainly Japan and Korea. Numerous species of predaceous and parasitic insects were imported and released in the hope that biological control could be attained. Only a few of these became established in the eastern United States. The most widely-distributed are *Tiphia vernalis*, a tiphiid wasp whose larvae are ectoparasitoids of the grubs, and *Istocheta aldrichi*, a tachinid fly that parasitizes the adults. Japanese beetle grubs are susceptible to parasitic nematodes (e.g., *Steinernema* and *Heterorhabditis* spp.), as well as several lethal microbial pathogens, especially the milky disease bacterium *Paenobacillus popilliae*.

► Small Fruit Pests and Their Management
► Turfgrass Insects and Their Management

References

Fleming WE (1968) Biological control of the Japanese beetle. U.S. Department of Agriculture Technical Bulletin 1383
Fleming WE (1972) Biology of the Japanese beetle. U.S. Department of Agriculture Technical Bulletin 1449
Loughrin JH, Potter DA, Hamilton-Kemp TR, Byers ME (1996) Role of feeding-induced plant odors in aggregative behavior of the Japanese beetle. Environ Entomol 25:1188–1191
Potter DA, Held DW (2002) Biology and management of the Japanese beetle. Annu Rev Entomol 47:175–205
Vittum PJ, Villani MG, Tashiro H (1999) Turfgrass insects of the United States and Canada, 2nd edn. Cornell University Press, Ithaca, New York.

Japanese Encephalitis

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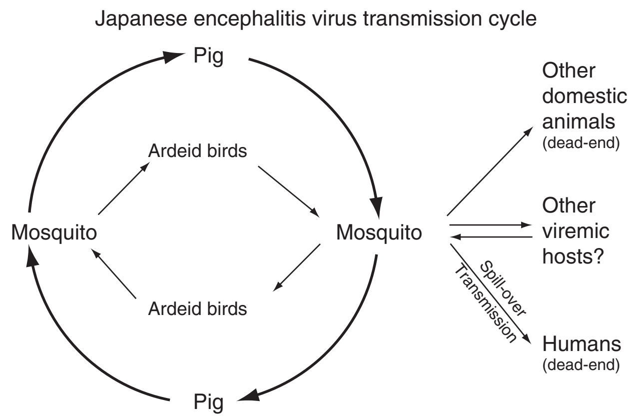
Japanese encephalitis is the most important cause of epidemic encephalitis in the world. Japanese encephalitis is a mosquito-borne viral infection of the nerve cells (neurons) of the brain. Fever, headache, vomiting, depressed mental status, coma and death characterize the disease. The immune systems of most infected humans are able to destroy the virus, but between one in 100 to one in 500 people develop symptoms of the disease. Approximately 3 billion people (60% of the world's population) live in Japanese encephalitis endemic areas, and roughly 50,000 clinical cases are reported each year. Approximately 20% of clinical cases succumb to the disease, and 20–50% of the survivors suffer from temporary or permanent physical and mental disability. The virus, known as the Japanese encephalitis virus is transmitted from host to host by mosquitoes across much of tropical and temperate Asia. It was first isolated in Japan in 1935 (hence the name of both the virus and the disease). Japanese encephalitis outbreaks have been reported from Bangladesh, India, Nepal and Sri Lanka in South Asia, through most countries of Southeast Asia, to China, Japan, Korea, Taiwan and southeastern Siberia in the east. Until recently, Japanese encephalitis did not appear to extend east of Bali in Indonesia, but in 1995 outbreaks of the disease occurred in the Torres Strait islands of Australia near the border with Papua New Guinea. Over the past decade, case rates have been the highest (3–5 cases per 100,000 people per year) in countries like China, Laos, Nepal, Sri Lanka, Thailand and Vietnam, and the lowest (0.1–0.2 cases per 100,000) in countries like Indonesia and Japan.

Japanese encephalitis belongs to a group of viruses commonly known as arboviruses because they are carried (transmitted) by arthropods (jointed-legged invertebrates such as insects, ticks, etc.). It is classified under the *Flavivirus* genus within the family Flaviviridae, and is related to other encephalitis-causing viruses like Murray Valley Encephalitis virus, Saint Louis Encephalitis virus, tick-borne encephalitis virus, and West Nile virus. The virus enters the body of a mosquito via the blood when it feeds on an infected host. The virus particles proliferate inside the mosquito, migrate to the salivary glands, and are expelled with the saliva when the mosquito feeds again. This process can take 7–14 days, depending on ambient temperature. Mosquitoes of the genus *Culex* are the primary vectors (carriers) of Japanese encephalitis virus. The most important vector throughout much of Asia is *Culex tritaeniorhynchus*. Other species are more locally important: *Culex vishnui* in India, Taiwan and Thailand; *Culex gelidus* in Indonesia, Sri Lanka, Thailand and Vietnam; *Culex fuscocephala* in Malaysia, Sri Lanka, Thailand and Taiwan; *Culex annulus* in Taiwan. Also, these mosquito species (especially *Culex tritaeniorhynchus* and *Culex vishnui*) are associated with rice land ecosystems because they breed prolifically in rice fields. Thus, rural rice ecosystems are the major areas where virus transmission occurs.

The virus transmission cycle (Fig. 2) in nature is not well understood, but is thought to involve wild birds, bird-feeding (ornithophilic) mosquitoes, and possibly other susceptible vertebrate hosts. Birds belonging to the Family Ardeidae (egrets, herons, storks, etc.), are believed to be the most important hosts of the virus in nature, and migratory birds are especially important in virus dispersal. Pigs (and in some instances ardeid birds) are the major vertebrate hosts involved in the peridomestic Japanese encephalitis transmission cycle. These animals are extremely susceptible to the virus, develop high levels of virus in their blood and can pass it on to blood-feeding mosquitoes. Thus, pigs are known as "amplifying hosts" for Japanese encephalitis. However, the virus does not adversely affect the health of pigs except in the case of pregnant sows that tend to abort their fetuses as a result of virus infection. Other domestic animals (goats, sheep, cattle, buffalo, chickens, etc.) are known to get infected and show antibodies to Japanese encephalitis virus in their blood. However, it is generally accepted that they do not develop a sufficiently high viremia (blood virus level) long enough for significant transmission to mosquitoes. They are thus known as "dead-end" hosts because they are not involved in the onward transmission of the virus. The "dead-end" domestic animals, too, do not generally show any ill effects



Japanese Encephalitis, Figure 2 **Virus transmission cycle of Japanese encephalitis.**

from virus infection, with the exception of horses that can develop fatal encephalitis. Humans also are dead-end hosts, but as with horses, humans can develop severe illness as a result of virus infection.

The Japanese encephalitis vector mosquito species are primarily zoophilic (i.e., prefer to feed on animals rather than humans), so the main cycle of virus transmission is known as a zoonotic cycle involving mosquitoes and susceptible wild or domestic hosts. Transmission to humans occurs when mosquito abundance reaches such a high level that infected mosquitoes encounter and feed on humans. This is known as "spill-over" transmission. Outbreaks of Japanese encephalitis occur when there is a convergence over time and space of the virus, amplifying hosts and vector mosquitoes. This often occurs in the rainy season in tropical countries or in the spring in more temperate areas when vector mosquito densities increase dramatically. Irrigated rice lands also are prone to Japanese encephalitis outbreaks associated with the increased vector abundance resulting from releases of irrigation water for cultivation. Rearing pigs in irrigated rice lands is especially dangerous, because it brings the amplifier host into a human-occupied environment where there is intense vector breeding. Pigs have a high reproductive rate and are bred almost exclusively for the food industry, so there is a rapid turn-over of these animals – typically they are slaughtered at 6–9 months of age. Thus, newly bred uninfected swine hosts are always available for Japanese encephalitis virus amplification in areas where extensive pig husbandry is practiced.

Measures used to control the transmission of Japanese encephalitis include the control of mosquito breeding in rice fields through proper water management, mosquito-proofing pig sties, personal protection measures against mosquito bites, and immunization of both humans and swine.

References

Hanna JN, Ritchie SA, Phillips DA, Shield J, Bailey MC, Mackenzie JS, Poidinger M, McCall BJ, Mills PJ (1996) An outbreak of Japanese encephalitis in the Torres Strait, Australia, 1995. Med J Aust 165:256–260. Available at http://www.mja.com.au/public/issues/sep2/hanna/hanna.html Accessed 6 March 2008

Hoke CH, Gingrich JB (1994) Japanese encephalitis. In: Beran GW, Steele JH (eds) Handbook of zoonoses. Section B: Viral, 2nd edn. CRC Press, Boca Raton, Florida, pp 59–69

Japanese Encephalitis Facts. Available at http://www.astdhpphe.org/infect/jpenceph.html

Japanese Encephalitis-Health Information for International Travel, 2001–2002. Available at http://www.cdc.gov/travel/yellowBookCh4-japaneseEncephalitis.aspx#375 Accessed 6 March 2008

Japygidae

A family of diplurans (order Diplura).

► Diplurans

Jeannel, René

René Jeannel was born in 1879. Son and grandson of medical doctors, he was interested in insects since childhood, but studied medicine in Paris. He decided to work on a degree in science followed by doctoral studies at the Sorbonne. Some invertebrates that he had collected in a cave in southwestern France (described in part in 1905 in his second entomological paper) drew the attention of Emil Racovitza, who began to include René in 1905 in a huge project to explore the zoology of the subterranean world. His doctoral thesis in medicine (surgery) was published in 1907. From 1908 to 1912 he worked alongside Racovitza at the Arago laboratory. In 1912 he moved to the entomology laboratory of the Muséum National d'Histoire Naturelle, and worked there until 1914, the outbreak of World War I. In 1919–1920 he worked in the faculty of sciences at Toulouse, France, but in 1920 was appointed professor at the university of Cluj in Romania. In 1927 he returned to France as professor at the Muséum National d'Histoire Naturelle and director of the museum's vivarium. His overseas explorations were with Charles Alluaud in 1912–1913 to eastern Africa, with Arambourg and Chappuis in 1932–1933 to eastern Africa, and on the voyage of the Bougainville to the subantarctic Kerguelen and Crozet islands in 1938. He also explored caves in the eastern USA in August-September 1928 following the International Congress of Entomology in Ithaca, New York. His interests were in systematics and speleology, with a strong component of biogeography. He quickly recognized the importance of Wegener's theory of plate tectonics. His taxonomic interests were in the families Carabidae and Catopidae (now called Leiodidae), and Pselaphidae (subsequently reclassified as subfamily Pselaphinae of Staphylinidae). A long series of publications recounted cave explorations and discoveries, and dozens of these were published in a numbered series called "Biospeologica" in the pages of the journal Archives de Zoologie Expérimentale et Générale. His works on the taxonomic groups of his interests were of worldwide scope, including, for example, studies of all three in southern South America, published in volume 1 of "Biologie de l' Amérique australe" (1962). His huge output of publications was a model for colleagues and students alike. Married and with children and grandchildren, he died on February 20, 1965.

Reference

Delamare Deboutteville C, Paulian R (1966) Le professeur René Jeannel [avec bibliographie]. Annales de la Société Entomologique de France (Nouvelle série) 2:3–37

Jerusalem Crickets (Orthoptera: Stenopelmatidae)

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Four extant New World genera, herein collectively referred to as Jerusalem crickets, comprise the subfamily Stenopelmatinae, family Stenopelmatidae in the order Orthoptera. These genera are *Stenopelmatus* (with 33 described species), *Ammopelmatus* (2), *Viscainopelmatus* (1), and *Stenopelmatopterus* (3). Species are frequently distinguished by a combination of subtle morphological characters present only in adults, karyotype number, geographical distribution, calling-drum patterns, and mitochondrial DNA (mtDNA) profiles.

The Entomological Society of America's common name directory lists "Jerusalem cricket" as applicable only to *Stenopelmatus fuscus*, a species restricted to northern New Mexico and adjoining northeastern Arizona. Unfortunately, this name has been applied by various authors to many species ranging from the California Pacific coast north into Canada, east to the Great Plains, and south into Mexico. Because of such taxonomic confusion and general physical similarities between species, we have decided to call all individuals of the subfamily "Jerusalem crickets" until Weissman's revisionary studies are completed.

Jerusalem crickets are distributed (Fig. 3a) in the western half of the U.S. and throughout Mexico and Central America. Though 17 species are described from the United States and Canada, we estimate that three times that many species are undescribed. Similarly impressive biodiversity occurs in Mexico and Central America where 19 species are named and dozens of taxa are unnamed. Two described species have no locality data. The three heaviest insect species, on average, in California are undescribed Jerusalem crickets that easily reach about 7.5 cm in length and weigh up to 13 g.

Origin of Common Name

In the United States, stenopelmatids are called sand crickets, stone crickets, potato bugs, skull insects, and most commonly Jerusalem crickets. The last name is preferred since using it would eliminate confusion with any other insect group. "Jerusalem cricket" appears to be derived from jargon of young boys of the nineteenth century. The epithet "Jerusalem" was commonly used as a swear word by any young lad who was suddenly startled or surprised by a natural phenomenon. Additionally Berrey and van den Bark's 1953 *American Thesaurus of Slang* lists both "Jerusalem!" and "cricket!" as expletives. Thus, R. Doutt envisioned a rural boy in the western United States turning over a rock and in surprise shouting, "Jerusalem! What a cricket."

In various parts of Mexico, Jerusalem crickets are called niña de la tierra (child of the earth) or cara de la niña (face of the child). They are universally, and mistakenly, thought to be poisonous.

Determination of the Adult Stage

Females: Adult females are distinguished by a darkened (at least at the tips and on the ventral surfaces), sclerotized ovipositor (Fig. 3b), the four components of which develop progressively with each molt.

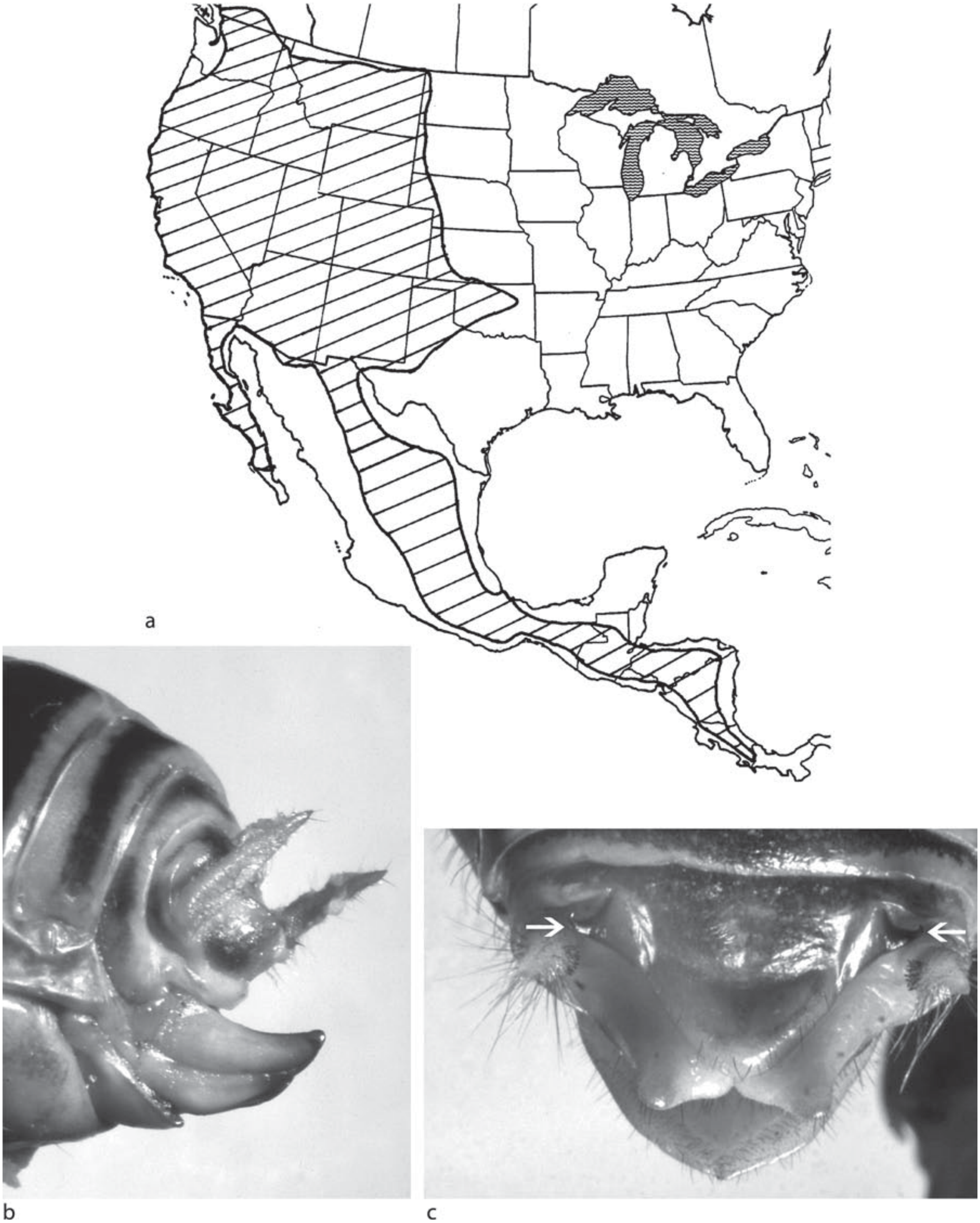
Males: Adult males have two fully developed, black, sclerotized, incurved hooks located medial to each cercus (Fig. 3c). These hooks develop gradually with each molt starting from tiny ridges barely visible in early instars. The hooks are used in mating and their importance is discussed later.

Karyotype

Jerusalem crickets have the typical orthopteran male XO/female XX sex determination system. Analysis by N. Ueshima shows that two Jerusalem cricket species have 19 chromosomes in the male and three species have 21. Another 150 individuals, probably representing some 80–90 species, have been karyotyped, and the 25 karyotype number was found twice as often as the 23 number.

Life Cycle

Most Jerusalem cricket species require 1¾ years from egg hatch to maturity (molt to adult), although some individuals in populations at high elevations and/or northern latitudes, with their shorter growing season, may require an extra year. Individuals of most species become adult in midsummer, with members of some California species maturing a month or two later. There is no obvious protandry, wherein males mature before females. Adult males disappear in the field before adult females, apparently due to a combination of



Jerusalem Crickets (Orthoptera: Stenopelmatidae), Figure 3 **Characteristics of Jerusalem crickets: (a) distribution (*stippled area*) of the Jerusalem crickets in North and Central America; (b) adult female Jerusalem crickets are characterized by a pointed, sclerotized, dark ovipositor; (c) adult male Jerusalem crickets are characterized by completely formed hooks (*arrows*).**

shorter life span (as documented in laboratory specimens) and sexual cannibalism (see below). At least two southern California species have a summer adult aestivation period where they are physically active but do not drum and are sexually unreceptive.

Eggs apparently are laid underground soon after mating, as indicated by the fall appearance of tiny nymphs. It is unknown if eggs have any dormancy period since Weissman has never been able to get females to oviposit in the laboratory, nor has he collected egg clutches in the field. Jerusalem crickets probably have from 9 to 12 molts before becoming adult, but since all individuals quickly eat their cast skins, such determination is imprecise. There is no evidence of prenatal care.

Adult females live from 6 to 12 months in the laboratory. Adult males live about half as long as females.

Ecology

Within the United States, Canada, Baja California, Mexico, and northern mainland Mexico, various Jerusalem cricket species live in most available habitats from oak savannah, grassland, chaparral, coastal and inland sand dunes to above the tree line. These species are generalists and a laboratory diet of organic romaine lettuce (for water), and dry cat and rabbit food, along with uncooked old-fashioned oats, is adequate for rearing. Many sand dune inhabiting species are endemics restricted to that particular dune system. Jerusalem crickets are absent from both salt and fresh water habitats, and desert areas of high alkalinity or salinity.

Once south of the United States-mainland Mexico border, and throughout their distribution as far south as southern Costa Rica, most Jerusalem cricket species are associated with some combination of high elevation, cool and moist, cloud forest type environment. The largest group is characterized by tens of species, most undescribed, where individuals readily hop upwards to 10 cm. These fast moving, good climbing, "spiny" and thin-legged individuals, occasionally with wing pads or completely developed wings, all appear to be active obligate predators. These species seek daytime refuge in downed forest trees (where they may eat co-inhabiting beetle larvae), possibly ascending at night into vertical trees to hunt live arthropods. They are most easily captured by tearing apart such downed, rotting trees, using a pickax or similar tools during daylight. The wetter and cooler the weather, the higher the rate of successful discovery.

Jerusalem crickets are large morsels of food and are eaten by many nocturnal predators, including foxes, skunks, bats, opossums, various owl species, various rodents, tropical vipers, and scorpions. Because of such risks, Jerusalem crickets employ several defensive strategies: they are largely nocturnal in activity; frequently flip on their backs with strong mandibles (which can draw human blood) agape when disturbed; employ abdominal-femoral defense stridulation; can kick with long, sharp, hind leg tibial spines; and some taxa have an offensive-smelling anal discharge. They are parasitized by tachinid flies (Diptera: Tachinidae), hairworms (Nematomorpha), and mermithid (Nematoda: Mermithidae) worms.

Different Jerusalem cricket species are rarely microsympatric, two species having been found together at only 30 localities (out of thousands) involving 20 different species-pairs. They may be commensals in *Pogonomyrmex* harvester ant nests in the southwestern United States.

Drumming and Communication

Jerusalem crickets are generally nocturnal and largely subterranean, thus limiting the effectiveness of visual and olfactory communication. They also do not fly, in spite of several species having fully developed hind wings. Jerusalem crickets have no auditory tympana to detect airborne sounds, nor does any species have wings with a sound producing apparatus. Information on location, distance, and sometimes sex, is exchanged via ground transmission of impulses produced by the abdomen (and sometimes the thorax-abdomen unit) striking the substrate (drumming), producing a percussion wave. These ground impulses are detected by other Jerusalem crickets through their subgenual organs, which are located in the proximal tibiae of all six legs and are the most vibration-sensitive organs in any insect group. Subgenual organs also respond to high intensity airborne sounds. Both sexes of all species drum spontaneously, sometimes producing sounds audible at 20 m.

There are four types of drumming. "Calling" drums are, in many cases, species-specific and spontaneously made by isolated adult males and females. This drumming is as valuable a taxonomic character as the species-specific calling songs of field crickets and katydids because it appears to serve in uniting the sexes. These drums vary in complexity among species and range from a series of single strikes at rates of 0.5–15 drums per second, to groupings of strikes with rates approaching 40 drums per second (Fig. 4b). In several species, the male and female drum differently (Fig. 4a) thus permitting long range sex determination. Calling-song drumming rates in Jerusalem crickets vary linearly with temperature. Those species with fast rates increase their drumming speed more for a given temperature rise than does a slower drumming species. While drumming speed appears to be unrelated to body size, it may be related to substrate consistency and/or density: sand-dune-inhabiting taxa all drum relatively slowly.

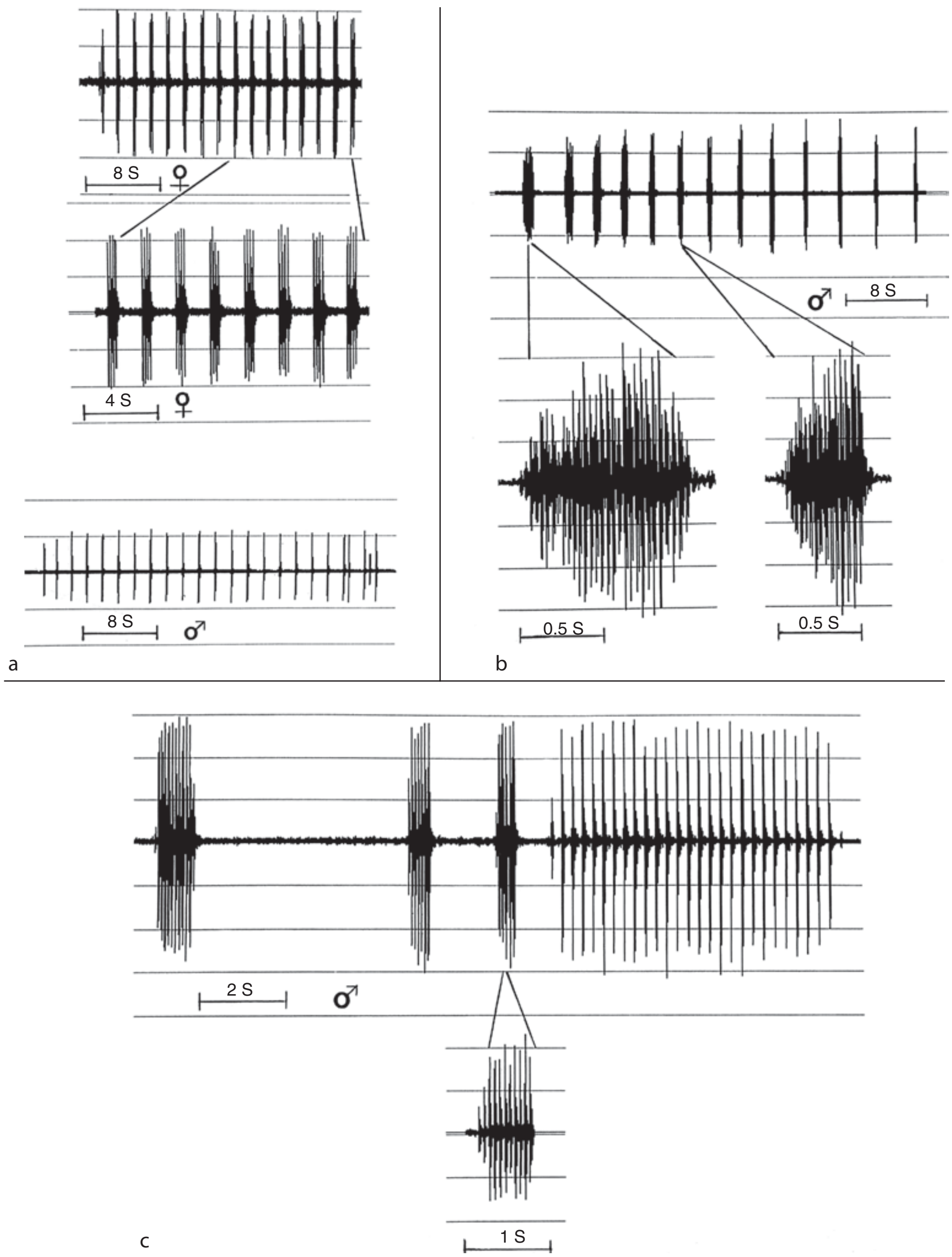
Presumptive "sex clarification" drums are produced by adult males of certain species. These are a series (Fig. 4c) of fast, very loud, non-species-specific drums produced when these males detect their calling drum. Sex clarification drums occur only in species where the male and female have the same calling drum, and one sex cannot tell who they are answering. In the field, this answering strategy should enable males to conserve energy and avoid possible injury or predation by not searching for other males. Sex clarification drums are unknown from any of the eight species where males and females drum differently, since each sex can identify the other sex by drum.

"Courtship" drums are frequently made by males (and less commonly by females) when two adults of either sex are within 6 cm of each other. This drumming consists of short series of barely audible, non-species-specific abdominal strikes or tremulations (where the abdomen does not make surface contact) at a rate of two to four per second.

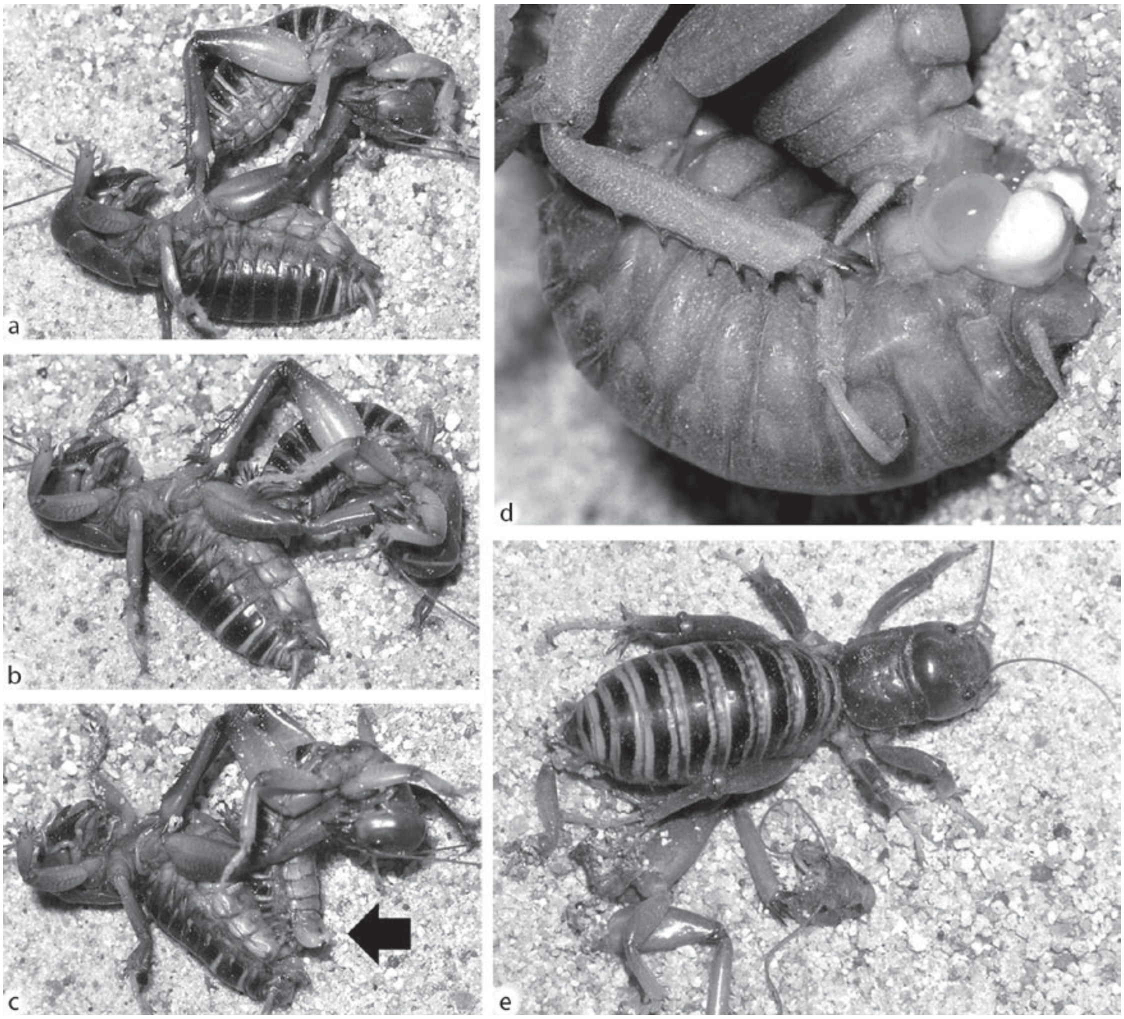
"Nymphal" drums are known from at least 25 species. They have the same pattern as the adult species-specific calling drum, but are produced less frequently, are usually of shorter duration, and are rarely heard during more than one instar. These subadult Jerusalem crickets do duet with other nymphs and adults, although the function of such drumming is unknown.

Mating

Jerusalem cricket orientation during mating appears to be unique among orthopteroid insects, if not among all insects. The male initiates the process by rolling on his side. Once the female is also on her side, the male assumes a lateral position beside her but facing in the opposite direction (Fig. 5a). He bites one of her hind tibiae (doing no damage), positions his hind tarsi near her coxae, and curls his abdomen (Fig. 5b) between his hind legs and her hind legs toward her subgenital plate, a maneuver that often requires several minutes of adjustments. As the male's telescoping abdomen nears the female's subgenital plate, he positions his hooks underneath a terminal ventral plate. This provides the necessary anchor as he everts his phallic lobes (Fig. 5c) and makes contact with her subgenital plate area. Immediately upon contact, a bilobed ampulla containing sperm is passed to the female and the everted phallic lobes then empty and deposit a sticky bilobed spermaphylax lateral to each ampulla lobe (Fig. 5d). The complete structure takes 10–20 s to transfer and weighs from 3 to 7.5% of the male's body weight. The spermatophore is not eaten by the female.



Jerusalem Crickets (Orthoptera: Stenopelmatidae), Figure 4 **Calling song (a) of southern California Jerusalem cricket species where female and male drum differently: female song (*top, middle*) composed of five trills (four drums per trill) in 8.5 seconds at 18°C male song (*lower*) composed of 10 single drums in 16 seconds at 20°C; (b) calling song of central California Jerusalem cricket species consists of grouping of strikes (trills), the drumming rate within a trill approaching 40 times per second at 20°C. This is the fastest drumming Jerusalem cricket; (c) three series of sex clarification drum in a Nevada Jerusalem cricket were followed by a calling song drum, all at 20°C. Sex clarification drum rate around 15 per second; calling drum rate around 4 per second.**



Jerusalem Crickets (Orthoptera: Stenopelmatidae), Figure 5 **The mating ritual: (a) early mating stage in central California Jerusalem cricket species. Male (*top*) is biting female's right hind tibia while facing in opposite direction; (b) male (*top*) is biting female's right hind tibia while positioning his hind legs and starting to curl his abdomen; (c) male (*top*) curling his abdomen between female's hind legs toward her subgenital plate and setting his hooks. Note his everted phallic lobes (*arrow*); (d) mating finished. Male (*top*) has passed spermatophore composed of whitish bilobed ampulla and clear bilobed spermatophylax. Note tip of ovipositor visible between ampulla lobes; (e) female has consumed male after mating.**

In both nature and the laboratory, some 10% of matings end with the male permitting the female to eat him alive. In these first described cases of male-complicit postcoital sexual cannibalism, the male remained motionless while the female consumed him (Fig. 5e). As both males and females can and will mate repeatedly, the function of this behavior is unknown.

Systematics

A. Vandergast has examined the evolutionary patterns of acoustic signaling and karyotype number changes within the context of molecular phylogeny in the North American Jerusalem crickets. These phylogenies are highly concordant with major song characteristics and geographic regions. Specifically, she found that species producing single drums group in a well supported monophyletic clade. Additionally, single drum species that produce a sex clarification drum (see Fig. 4c) also fall out together. Species with groupings of strikes are restricted to the Pacific coast states of California, Oregon and Washington, usually within 100 km of the coast. Lastly, those seven undescribed species from southern California and Baja California, Mexico, where males and females drum differently, also form a well-supported monophyletic lineage. When karyotype numbers were integrated into the molecular phylogeny, she found evidence for at least five independent fusion events leading to loss of chromosomes, and potentially one fission event (2N = 19 to 2N = 21) throughout this group's evolutionary history.

Endangered Species

Because several Jerusalem cricket species have very limited geographical distributions, especially those endemic to small coastal and inland sand dune systems, coupled with all species being flightless, care will be necessary to protect these vulnerable taxa. The importance of limited Jerusalem cricket vagility is underscored by our genetic study of a widespread southern California Jerusalem cricket species. We showed that less than 100 years, or 50 generations, was sufficient to display patterns of genetic divergence between populations correlated with contemporary urbanization. In other words, urban development and roads disrupt gene flow and quickly cause isolated populations of Jerusalem crickets to genetically diverge from their neighbors.

► Grasshoppers
► Katydids and Crickets

References

Poinar G Jr, Weissman DB (2004) Hairworm and nematode infections of North American Jerusalem crickets, field crickets, and katydids (Orthoptera: Stenopelmatidae, Gryllidae and Tettigoniidae). J Orthoptera Res 13:143–147

Vandergast AG, Bohonak A, Weissman DB, Fisher RN (2007) Understanding the genetic effects of recent habitat fragmentation in the context of evolutionary history: phylogeography and landscape genetics of a southern California endemic Jerusalem cricket (Orthoptera: Stenopelmatidae: *Stenopelmatus*). Mol Ecol 16:977–992

Weissman DB (2001) North and Central America Jerusalem crickets (Orthoptera: Stenopelmatidae): taxonomy, distribution, life cycle, ecology and related biology of the American species. In: Field LH (ed) The biology of wetas, king crickets and their allies. CAB International, New York, pp 57–72

Weissman DB (2001) Communication and reproductive behaviour in North American Jerusalem crickets (*Stenopelmatus*) (Orthoptera: Stenopelmatidae). In: Field LH (ed) The biology of wetas, king crickets and their allies. CAB International, New York, pp 351–375

Weissman DB (2005) Jerusalem! Cricket? (Orthoptera: Stenopelmatidae: *Stenopelmatus*); origins of a common name. Am Entomol 51:138–139

Jewel Beetles

Another name for metallic wood-boring beetles or buprestids (Coleoptera: Buprestidae).

► Beetles

Jewel Bugs

Another name for shield-backed bugs or scutellerids (Hemiptera: Scutelleridae).

► Bugs

Jewel Wasp, *Nasonia vitripennis* (Walker) (Hymenoptera: Pteromalidae)

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Loyola College in Maryland, Baltimore, MD, USA

Nasonia (=*Mormoniella*) *vitripennis* is a gregarious, ectoparasitic wasp that attacks pupae and pharate adults from several families of the higher Diptera, particularly representatives of Calliphoridae and Sarcophagidae. Formerly a monophyletic genus, *Nasonia* is now represented by three species: *N. vitripennis* which appears to be cosmopolitan in distribution; *N. longicornis*, a species found predominantly in western North America; and *N. giraulti*, which ranges from the Mississippi river to the east coast of the United States. *N. vitripennis* has served as invaluable research tool to investigate topics associated with genetics, reproductive behavior, ecology, photoperiodism, host-parasite relationships, sex ratio theory, venom systems, and biological control. Recently, the entire genome of *N. vitripennis* has been sequenced, making it the first parasitoid to be selected for such studies and increasing its use as a model organism for several lines of research. It is considered an important natural enemy of filth flies inhabiting confined livestock facilities and associated with human habitation. Currently, this parasitoid is used as a biological control agent in poultry facilities and confined feedlots, however, its efficacy at reducing fly populations is considered questionable at best.

During host attack, the female parasitoid examines the host puparium through a series of stereotypic behaviors, and, if the fly is accepted, then drills a hole through the host puparium. The female wasp will insert her ovipositor through the newly created hole to probe the pupal surface, and then she plunges the distal third of the ovipositor into fly tissues. Prior to oviposition, the wasp always injects venom into the host, an event that appears to be capable of killing some fly hosts within 24 h. The parasitoid's eggs are then deposited on the surface of the host's body, but within the hardened puparium surrounding the fly pupa. The number of eggs laid is dependent on the host species and size of the host, as well as on the physiological condition of the host. The wasp eggs hatch 24–36 h later. Depending on host species, larval development (four instars) is completed within 5–7 days at 25°C. Larval feeding initially consists of piercing the pupal integument with mandibles so that feeding on host fluids dominates the first two instars. Upon molting to the third instar, larvae switch to tissue feeding, during which time the developing offspring consume all or nearly the entire fly host. Pupal development occurs within the puparium as well and typically requires an additional 4 days before adult eclosion ends the duration of the wasp's lifecycle within the host puparium.

Males eclose approximately 24 h before the females within the puparium. These males will chew an exit hole through the host puparium that will later be enlarged by the females as they make their escape. The males have reduced wings that prevent their dispersal from the site of eclosion. Upon emerging from the host, females are immediately courted by males, typically who are siblings, resulting in intense local mate competition. Mated females then disperse from the emergent site, attracted to the odors emitted from fly-infested decaying animal carcasses.

The sexes are clearly dimorphic. Females are dark in appearance with a metallic hue, which is perhaps why the species is often referred to as the "jewel" wasp. The abdomen is black while the thorax and head are a dark blue. Most of the appendages (legs, ovipositor, pedicel of antennae) are brown in color with the exception of the coxa. Wild type eye color is black with traces of deep red, although many mutant eye colors have also been observed. The female body is much larger than the male. Adult females range from 1.8 to 2.5 mm from head to abdominal tip, with most of the variation in size being attributed to host quality.

Males are substantially smaller than the females; most never reach more than 1.5 mm in length and can be stunted in size dramatically with crowding on hosts or during superparasitism. The color of the males is also more brilliant than the female. Adult males appear metallic green on the dorsal surfaces of the head and thorax, while the abdomen is all black. The legs are light brown, as are the scape and pedicel of the antennae. Males possess two pairs of reduced wings (brachypterous) that are functional but not capable of flight.

In temperate regions, *N. vitripennis* overwinters by entering a facultative larval diapause. Short-day photoperiods, sustained changes in thermoperiod, and host deprivation have all been examined as possible diapause-inducing cues. Interestingly, diapause in sarcophagid fly hosts typically begins 3–4 weeks before that of the wasp. After females interpret environmental tokens for diapause, they lay their last clutch of the season on diapausing hosts. The developing wasp larvae apparently consume the host's cryoprotectants as means to increase cold tolerance during larval diapause. The diapausing host puparia have also been enhanced for winter dormancy, which serves as added protection for the diapausing parasitoids.

Reproduction in this species entails a haploid-diploid mechanism of sex determination with parthenogenesis accounting for the production of males. Courtship between males and females amounts to not much more than males ambushing siblings as they exit host puparia. A successful male typically remains mounted on the female for several minutes before dismounting or being removed by a competing male. Females normally mate only once and store sperm in a spermathecae. Ovulation has been speculated to be directed by the female, as has sperm release from the spermathecae. Fertilized eggs are diploid and develop into daughters. In contrast, males develop from unfertilized eggs and consequently are haploid. Recent genetic studies have also uncovered a relatively common occurrence of diploid males and a more rare condition of haploid females. On favored hosts, such as large sarcophagids and calliphorids, broods will have a characteristic female-biased sex ratio of 3:1. This ratio becomes increasingly more male-biased as the quality of the host declines.

Injection of venom into the fly host seems to be central to the success of *N. vitripennis* in parasitizing a host and in producing viable progeny. Envenomation induces a developmental arrest in most fly hosts that is sustained until host death. During the halt in fly development, a series of biochemical changes in host intermediary metabolism occurs that appear to be associated with parasitoid larval growth. This is preceded by an inhibition of the host cellular immune responses, thereby permitting feeding on host fluids by both adult females and their developing offspring. Eventually, visible signs of tissue necrosis are evident, which is first restricted locally to the site of ovipositor insertion, but then gradually spreads throughout the fly. This generally signals the end of the parasitic relationship because the fly has become nutritionally unsuitable for developing larvae of *N. vitripennis*.

Nasonia vitripennis has served as a test subject for numerous genetic studies due to its mechanism of sex determination (haploid-diploid), small genome (five chromosomes), ease in rearing and handling, and availability of linkage maps for each chromosome. Several types of mutants of *N. vitripennis* are available to investigate inheritance of traits such as eye color, body color, eye shape, and fecundity. Additional comparative molecular genetic data is accumulating for all three species comprising *Nasonia*. Adding to the interest in this wasp is the presence of cytoplasmic bacteria (*Wolbachia* spp.) that may alter sex ratios by inducing hypercondensation of maternally derived chromosomes and contribute to speciation by evoking mating incompatibility.

Few parasites and no predators, at least that specifically target *N. vitripennis*, have been reported. At least one species of microsporidia has been found to be parasitic in this wasp, but the occurrence of the protozoan is not widespread as is evident for other genera of ectoparasitic pteromalids. In fact, only a few strains of *N. vitripennis* from specific geographical locations (e.g., upstate New York, central Florida) display microsporidian infections. When infected, females show a reduced fecundity that continues to decline over time. Spores apparently can be passed into the host either through venom injection or transovumly.

Predatory activity toward *N. vitripennis* seems to be by generalists. Predators of fly pupae, if unable to distinguish between parasitized and unparasitized flies, may consume wasp larvae in various stages of development. This would be especially easy to do since the larvae are feeding on the pupal surface. Such predation, however, has not been documented and would be expected to occur infrequently since the fly pupae are typically buried 2 or more centimeters below the soil surface.

Allospecific competition occurs regularly when *N. vitripennis* utilizes muscoid fly pupae. Several species of ectoparasitic pteromalids can be found searching for fly hosts in areas associated with livestock rearing. In some instances, adult females of other species will enter into confrontation with *N. vitripennis* for fly hosts. Battles are not fierce and usually amount to pushing and shoving with antennae. The frequency of confrontation apparently increases when available hosts are limited. In contrast, allospecific competition among larvae during multiparasitism is not only fierce, but deadly. Solitary wasp species tend to have cannibalistic larvae that will attempt to consume any competitors. *Nasonia vitripennis* does not avoid laying eggs on hosts previously parasitized by these solitary species. The apparent strategy employed to combat the cannibalistic larva is gregariousness. Females of *N. vitripennis* lay very large clutches on the parasitized hosts, and though many are consumed, several larvae reach adulthood. The sex ratios of such broods also tend to be male-biased.

References

Edwards RL (1954) The host-finding and oviposition behavior of *Mormoniella vitripennis* (Walker) (Hym., Pteromalidae), a parasite of muscoid flies. Behavior 7:88–112

Ratcliffe NA, King PE (1969) Morphological, ultrastructural, histochemical, and electrophoretic studies on the venom system of *Nasonia vitripennis* Walker (Hymenoptera: Pteromalidae). J Morphol 127:177–204

Rivers DB, Ruggiero L, Yoder JA (1999) Venom from *Nasonia vitripennis*: a model for understanding the role of venom during parasitism by ectoparasitoids. Trends Entomol 2:1–17

Werren JH (1980) Sex ratio adaptations to local mate competition in a parasitic wasp. Science 208:1157–1159

Whiting AR (1967) The biology of the parasitic wasp *Mormoniella vitripennis* (=*Nasonia brevicornis*) (Walker). Q Rev Biol 42:333–406

Johannsen, Oskar Augustus

Oskar Johannsen was born in the state of Iowa on May 14, 1870, the son of Danish immigrants. He obtained only an elementary school education before dropping out of school. However, when his older brother decided to go to college, Oskar decided to go too. So, he spent the summer of 1890 studying in order to pass the entrance examination to the University of Illinois, was admitted, and gained a B.S. degree in architectural engineering in 1894. He worked for the next 5 years as a draftsman for a Chicago company. Oskar had wanted to study insects at college, but was persuaded by his father to study engineering instead, as a more reliable way of making a living. In 1899 he was offered and accepted a teaching position at the Civil Engineering College at Cornell University. This provided an income while allowing him to study the biological sciences, in which he obtained an M.A. in 1902 and a Ph.D. in 1904. In 1909 he accepted a position at the University of Maine as professor and entomologist in the Extension Division. In 1912 he returned to Cornell University and was successively professor of biology and professor of entomology until he retired in 1936. He married Harriette Fuller in 1896, and they had three children. With special interests in aquatic Diptera (Chironomidae and Mycetophilidae), he published more than a hundred scientific papers and was coauthor of three books, "Medical entomology" (with W. A. Riley), "Histological techniques" (with B. F. Kingsbury), and "Embryology of insects and myriapods" (with F. H. Butt). He was American representative on the permanent executive committee of the International Congresses of Entomology, president of the Entomological Society of America in 1937, and a member of several other scientific societies. English was his native language, but he learned to speak and read German and Danish, and to read Dutch, Norwegian, Swedish, and some of the Romance languages. He died at Ithaca, New York, on November 7, 1961.

Reference

Crook DJ (1973) Oskar Augustus Johannsen 14 May 1870 – 7 November 1961. Entomol News 84:101–102

Johnston's Organ

A large, complex chordotonal organ found at the pedicel (basal segment) of the antenna. It responds to antennal movement, wing beat frequency, gravity, detection of ripples in water, and sometimes sound.

Joppeicidae

A family of bugs (order Hemiptera).

► Bugs

Jordan, Heinrich Ernst Karl

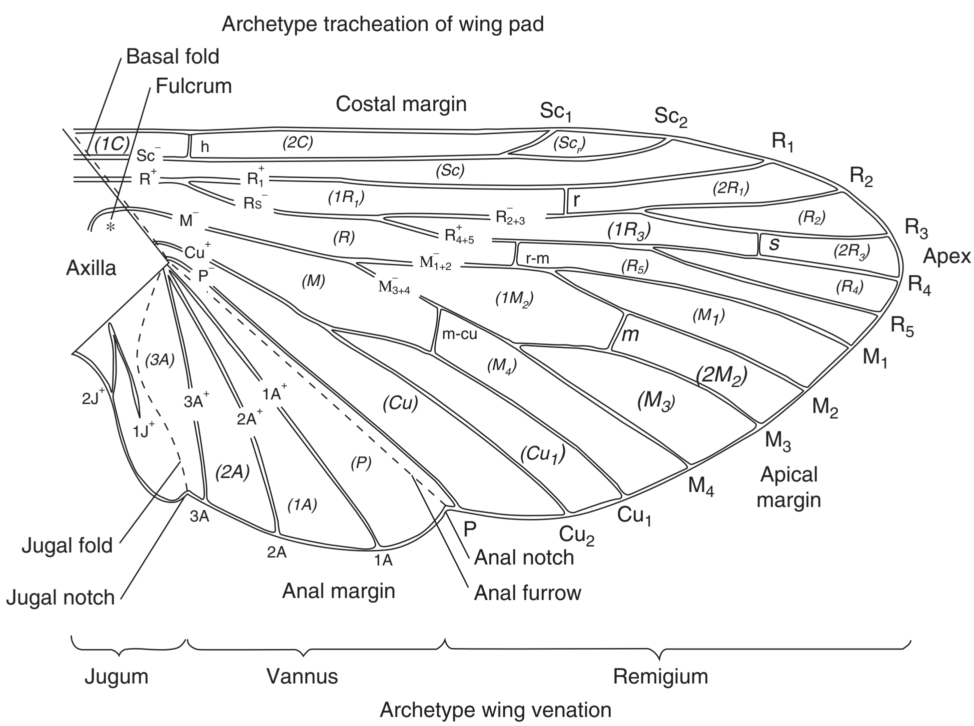
Karl Jordan was born in Almstedt, Hanover, Germany, on December 7, 1861. He obtained a doctoral degree from Universität Göttingen in 1885. In 1892, he became curator of the entomological department of the Tring Park Museum, Hertfordshire, England, the private collection of the "entomological" branch of the Rothschild family, of which the brothers Lionel Walter Rothschild (Baron Rothschild) (1868–1937) published on butterflies, and Nathaniel Charles Rothschild (1877–1923) on fleas. Karl, a full-time professional, published copiously on beetles (especially Anthribidae), butterflies, and fleas. He was president of the Royal Entomological Society of London in 1929–1930, and in 1932 was elected a fellow of The Royal Society. The Rothschilds claimed to be hobbyists, yet published very substantial scientific contributions. Karl died on January 12, 1959.

Reference

Richards OW (1959) The president's remarks. Proc R Entomol Soc Lond C 23:71–74

Jugal Lobe

A well developed basal lobe at the base of the forewing in some Lepidoptera and Trichoptera that overlaps the hindwing and serves as a wing



Jugal Lobe, Figure 6 **Hypothetical ancestral pattern of wing venation.**

coupling mechanism during flight. In others, the jugal lobe is modest. It is also called the jugum (Fig. 6).
► Wings of Insects

Jugal Veins

Small veins found in the jugal lobe.
► Wings of Insects

Juglar-Horned Beetles

Members of the family Prostomidae (order Coleoptera).
► Beetles

Jugum

A lobe at the base of the front wing in some Lepidoptera and Trichoptera, and also known as the jugal lobe.
► Wings of Insects

Jumping Spiders (Class Arachnida, Order Araneae, Family Salticidae)

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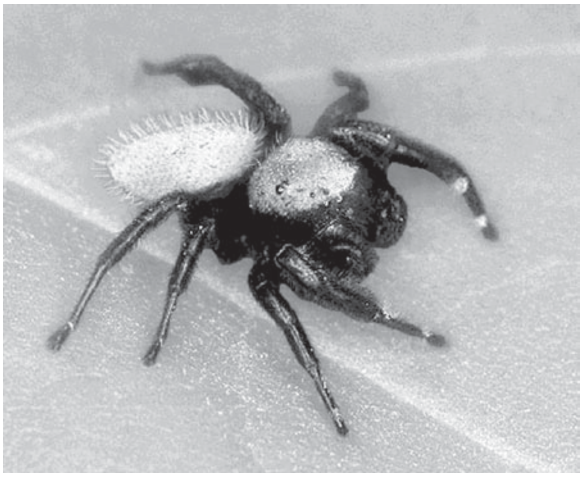
The jumping spiders (Salticidae) comprise the largest known spider family worldwide. Over 5,000 species are known, and this family makes up roughly 10% of the order Araneae. Over 300 species are known from North America north of Mexico, and many more occur in the tropics. Although primarily a tropical family, the Salticidae is known to occur from Canada and northern Europe in the north to Terra del Fuego and New Zealand in the south. They have been collected on Mt. Everest and also below sea level in the Salton Sink of California. They were among the first colonists on Krakatoa in the Malay Archipelago after the eruption in 1883 (one of the largest volcanic eruptions in recorded history) and they have been discovered in intertidal zones in Malaysia. Thus, they are among the most successful of spiders and among those most commonly encountered.

The members of this family (Figs. 7–9) are characterized by having a box-like cephalothorax, eyes in three to four rows, anterior median eyes highly enlarged, and a tendency to progress by leaping. They vary in size from about 1 to 25 mm in length, with most around 3–10 mm. The anterior median eyes of jumping spiders have been shown to be among the best in the invertebrates, second only to the cephalopod eyes in visual acuity. They differ from cephalopod and vertebrate eyes in that the lens is a fixed part of the cuticle and the cone-shaped retina is moved by a set of muscles to scan the environment. The eyes have a relatively large focal length to aperture ratio, which allows for better focus without the need for a lens that is perfectly curved. It is thought that these spiders probably evolved from clubionoid or philodromoid-like ancestors, although the exact ancestry is very difficult to establish at present.

Jumping Spiders (Class Arachnida, Order Araneae, Family Salticidae), Figure 7 ***Eris militaris*** **male from Oklahoma. Photo by D. Richman.**



Jumping Spiders (Class Arachnida, Order Araneae, Family Salticidae), Figure 8 ***Phidippus apacheanus*** **male from New Mexico. Photo by D. Richman.**

Jumping Spiders (Class Arachnida, Order Araneae, Family Salticidae), Figure 9 ***Salticus austinensis*** **female from Oklahoma. Photo by D. Richman.**

The acute visual abilities of jumping spiders allow for a highly varied and complex behavioral repertoire. Studies on jumping spider behavior have shown them to be able to remember prey location, even after losing sight of the prey, and to experiment with prey-catching strategies so as to develop a workable methodology. Their high visual acuity also invests them with the ability to have complex intraspecific interactions, including visual courtship displays and agonistic behaviors. In addition, some of the jumping spiders resemble ants, velvet ants, or beetles, and often behave much like the organism they resemble. Some ant mimics have been shown to be Batesian mimics, being themselves good to eat and not especially venomous (although they can bite). Salticid ant mimics do not normally feed on ants, at least those that have been studied; thus, they appear not to be aggressive (Peckhamian) mimics. There are ant-feeding jumping spiders, but these tend to be not especially ant-like.

Courtship in jumping spiders is primarily visual (although most species employ other methods as well, such as inaudible sounds) and can be quite complex. Male spiders are often (but not always) highly ornamented. Several arachnologists have studied salticid courtship, beginning with George and Elizabeth Peckham at Milwaukee, Wisconsin, in the 1890s and continuing through Jocelyn Crane at Rancho Grande, Venezuela, in the 1940s. Robert R. Jackson and his associates in New Zealand, and in other parts of the Southern Hemisphere, have continued this work to the present day. In many ways, jumping spiders function much like birds in male displays, with the ornate males of many species performing elaborate stepping movements and displaying brightly colored scales and tufts, as well as front leg fringes and knobs and/or spikes on other legs. For example, *Habronattus hallani* not only raises its front legs during courtship to display the metallic pink scales on the underside of the femora, but makes short sideways runs ending in a vertical jump which flashes the metallic scales on the underside of the second pair of legs as well. The minute *Neonella vinnula* (1.8 mm as adults) males vibrate their entire bodies in courtship, while *Habrocestum pulex* goes through a mutual spiral dance, with the female rotating around the displaying male. Males of *Hentzia palmarum* rock their bodies back and forth while twisting their abdomens to the right or left.

Male-male agonistic displays have been less studied, but are almost as varied. In agonistic display, *H. palmarum* performs a mutual zigzag rocking dance with abdomen twisted and chelicerae extended. These displays usually result in an attempt to bite the opposing male. The “losing” male then backs away and runs. Smaller males may attack, but often will retreat before initiating or joining in a display. Similar biting attempts have been observed in *Anasaitis canosa*, but only in approximately equal-sized opponents. Usually smaller males retreat after perceiving the presence of the larger male, apparently gauging its size by sight. For some reason, agonistic displays seem to be rare or even non-existent in certain genera, such as *Habronattus*, with males often only casting cursory glances at other males.

Courtship can also involve other cues, such as stridulation (some *Phidippus* and *Habronattus*), tactile stimulation, and semiochemicals (pheromones). It is probable that cryptic species such as *Menemerus bivittatus* and *Platycryptus undatus* may depend more on these chemical cues, like the wolf spiders in the family Lycosidae. Male lycosids can be stimulated to display by the presence of female silk, but at least some male salticids do not even seem to notice female silk strands. *Menemerus bivittatus*, a cosmotropical tramp species, has been shown to recognize female silk and to spend time palpating it, apparently picking up chemical signals. It does not, however, initiate courtship unless it sees a female. However, many (if not most) salticid males can recognize and enter the silken sacs of penultimate females and mate with them after their molt. This activity probably involves both sight, and chemical and tactile stimuli. Why salticids evolved such a varied methodology in courtship is a mystery, but perhaps this courtship versatility allowed them more chances to reproduce.

Prey capture is another area in which salticids are especially adept. Usually, prey capture involves the sighting of a moving insect or other arthropod, followed by a stalk and final capture jump. *Phidippus*, for example, is an excellent hunter who can use landmarks to find prey items that have been lost from sight. They can occasionally grab web-building spiders from their webs. The Australian *Portia fimbriata*, a medium to large jumping spider belonging to a genus with members also found in South Africa and Sri Lanka, is quite versatile in its approach to prey capture, taking both insects and spiders, but preferring the latter. With spiders, *Portia fimbriata* will experiment until something works. It will use web vibrations on web-building spiders or even perform fake courtship to individuals of different species of jumping spiders. *Portia*, which looks like a piece of lint with eyes, usually wins at this game.

Obviously, jumping spiders are highly versatile in their behavioral repertoire and are excellent subjects for studies of behavior, ecology and evolution. However, their simplified genital structure often make species determination difficult and the sexual dimorphism found in many species has resulted in a number of one-sex descriptions and often complex synonymies. Thus, there is a definite need for more systematic studies to correct the errors and to apply new methods to phylogeny. Such studies will undoubtedly turn up many undescribed species, especially in the tropics, as well as to add to our understanding of the relationships within the family and of the family's relationship to other spiders. Jumping spiders are extremely complex organisms and at times difficult to research, but are always fascinating.

References

Foelix R (1996) Biology of spiders, 2nd edn. Oxford University Press, Oxford

Forster L (1982) Visual communication in jumping spiders (Salticidae). In: Witt PN, Rovner JS (eds) Spider communication: mechanisms and ecological significance. Princeton University Press, NJ, USA, pp 161–212

Jackson RR (1982) The behavior of communicating in jumping spiders (Salticidae). In: Witt PN, Rovner JS (eds) Spider communication: mechanisms and ecological significance. Princeton University Press, NJ, USA, pp 213–247

Richman DB, Cutler B (1978) A list of the jumping spiders (Araneae: Salticidae) of the United States and Canada. Peckhamia 1(5):82–109

Richman DB, Jackson RR (1992) A review of the ethology of jumping spiders (Araneae, Salticidae). Bull Br Arachnol Soc 9:33–37

Richman DB, Cutler B, Edwards GB (2005) Salticidae. In: Ubick D et al. (eds) Spiders of North America. American Arachnological Society, College Park, MD, USA, pp 205–216

June Beetles, *Phyllophaga* spp. (Coleoptera: Scarabaeidae: Melolonthinae: Melolonthini)

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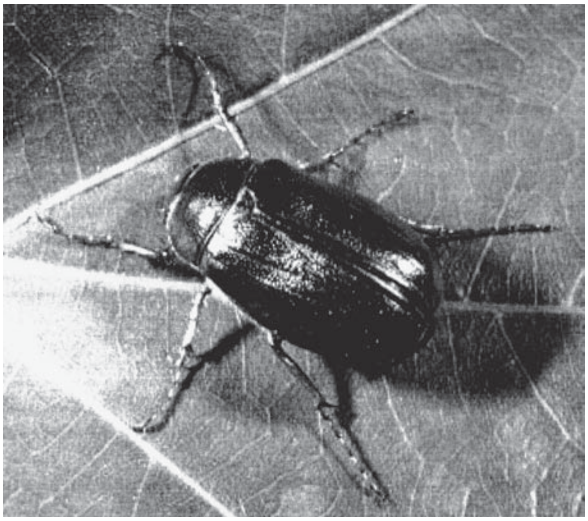
June beetles, also known as May beetles, are stout-bodied, brownish, plant-feeding scarabs belonging to the genus *Phyllophaga* (formerly *Lachnosterna*). They occur in both the Old and New Worlds. Throughout the continental United States and Canada about 200 species are known, many of which are found in the eastern and north-central United States. Some species are localized within a particular geographic region whereas others may be more widely distributed. June beetles also occur in South and Central America, the West Indies, eastern and southern Asia, and the islands of the Pacific and Indian Oceans.

Adult June beetles have a cylindrical or oblong body shape (Fig. 10), with different species ranging from 7 to 25 mm in length. Body color ranges from tan, to mahogany, to dark chocolate brown. The metasternum is covered with dense hair. The beetles have lamellate antennae ending in a three-segmented club that is longer in males than in females. The elytra of some species are pubescent, whereas in others they are nearly smooth. Species with a spring reproductive flight are referred to as May beetles, whereas those with summer flights are often collectively called June beetles or "June bugs." Despite these common names, beetle flight of either group can begin or end outside of those months.

The larvae are typical scarab grubs; cream-colored, C-shaped when feeding or at rest (Fig. 11), with a brown head capsule, chewing mouthparts, and three pairs of jointed legs. Full-sized larvae are 25–38 mm long. The hind part of the abdomen is typically dark because of ingested food and soil. The raster, an area of bare spaces and spines on the ventral surface of the last abdominal segment, bears two parallel rows of short spines in a pattern that resembles a zipper.



June Beetles, *Phyllophaga* spp. (Coleoptera: Scarabaeidae: Melolonthinae: Melolonthini), Figure 10 Adult June beetle or "June bug."

June Beetles, *Phyllophaga* spp. (Coleoptera: Scarabaeidae: Melolonthinae: Melolonthini), Figure 11 Larva of June beetle; these often are called "grubs."

Most June beetles feed on the leaves of deciduous trees such as oak, hickory, walnut, and elm. When the beetles are abundant, trees may be stripped of their young leaves in spring. Adults of some species feed on herbaceous plants, or on gymnosperms (conifers and their close relatives). Most June beetles are polyphagous, feeding on as many as 70 plant species, so several species of *Phyllophaga* may be present together on a particular plant. The larvae, called white grubs, develop in the soil where they feed on roots of turf and pasture grasses, young nursery plantings, corn, small grains, potatoes, strawberries, and other agricultural crops. Although some species can be quite destructive, most are not considered to be significant pests.

Adults typically are active from April to June. The beetles emerge after sundown and fly to the tops of trees to feed, returning to the soil or protected sites before dawn. They are clumsy fliers and often are attracted to outdoor lights. Collections at lights consist primarily of males. Mating occurs only at night, either on the surface of turf or pasture, in the soil, or on host plants. Males are attracted by a female-produced sex pheromone. Once mated, females fly to turf, pastures, or agricultural fields and burrow down 5–18 cm to lay eggs. Oviposition can occur during the day or night. Eggs are pearly-white, about 2.5 mm long, and typically laid singly in earthen cells. Newly laid eggs appear elliptical, becoming more spherical as the embryo develops. Each female lays 20–50 eggs in her lifetime. Hatching occurs in about 3 weeks and the young grubs begin feeding on fine roots and organic matter within the upper 5 cm of soil.

Most June beetles have 2- or 3-year life cycles, although a few species have cycles lasting 1 or 4 years. There are three larval instars. Because of overlapping generations and presence of more than one species, several sizes of June beetle grubs may be found together at a given site. Larvae of species with 2-year cycles typically overwinter as second instars. They resume feeding in early spring, molting again in April or May. Third instars attain their full size by summer's end. Pupation occurs underground, in an earthen cell. Most species reach the adult stage by late autumn, but the beetles remain underground until the following spring. Grubs of species with 3-year cycles feed throughout the first two summers, hibernating twice and pupating midway through the third summer. Their adults are usually fully formed by autumn, but do not emerge from the soil until spring.

June beetle grubs are susceptible to entomopathogenic nematodes and various microbial pathogens including fungi (e.g., *Metarhizium anisopliae*) and specific strains of milky disease bacteria, *Paenibacillus popilliae*. Night-active flies in the genus *Pyrgota* (Diptera: Pyrgotidae) parasitize the adults, whereas several species of wasps in the family Tiphiidae are ectoparasitoids of the larvae. Mites are often found on adults and larvae; however, they are probably just phoretic and harmless to their hosts. Predatory insects (e.g., ants, carabids) feed on the eggs and young larvae. The grubs also attract vertebrate predators including insectivorous birds, skunks, raccoons, moles, and armadillos.

In the past, farmers were advised to clean June beetles out of heavily infested fields by pasturing the land with hogs, which would root out and eat the grubs. Management, when necessary, is now accomplished with soil insecticides, or through crop rotation. Control actions can be timed by monitoring adult activity using black light traps. Adults, too, can be controlled with insecticides, but defoliation may continue due to reinfestation of previously treated plants.

► Beetles

References

Bøving AG (1942) A classification of larvae and adults of the genus *Phyllophaga* (Coleoptera: Scarabaeidae). Memoirs of the Entomological Society of Washington No. 2

Forschler BT, Gardner WA (1990) A review of the scientific literature on the biology and distribution of the genus *Phyllophaga* (Coleoptera: Scarabaeidae) in the southeastern United States. J Entomol Sci 25:628–651

Luginbill P, Painter HR (1953) May beetles of the United States and Canada. United States Department of Agriculture Technical Bulletin 1060

Ritcher PO (1966) White grubs and their allies. Oregon State University Press, Corvallis, Oregon

Vittum PJ, Villani MG, Tashiro H (1999) Turfgrass insects of the United States and Canada, 2nd edn. Cornell University Press, Ithaca, New York

Jumping Genes

Genes that move within the genome, usually because they are associated with transposable elements.

Jurassic Period

A geological period of the Mesozoic era extending from about 213 to 170 million years ago.

Juvenile

The immature form of a nematode. The stages between the egg and adult form.

Juvenile Hormone

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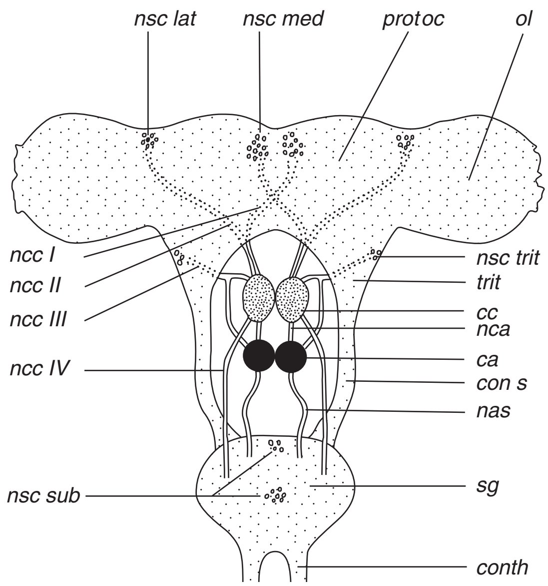
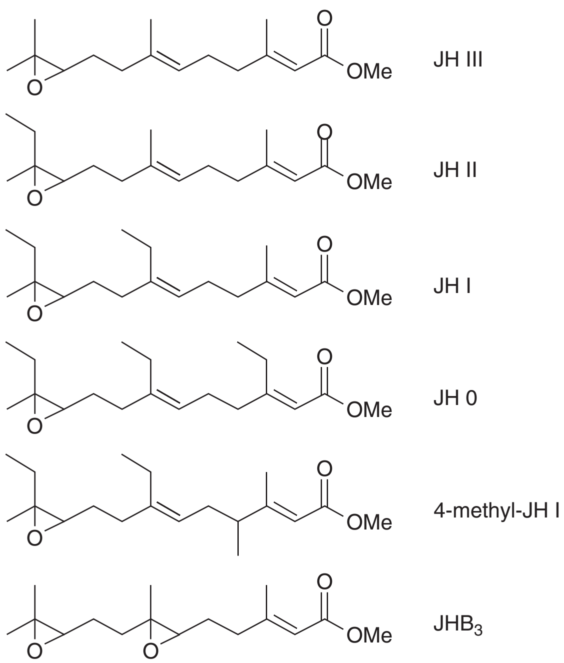
Evidence for the existence of a blood-borne factor that influenced or modified the molting process was provided for the first time by Wigglesworth in the 1930s. His innovative experiments on the blood-sucking bug, *Rhodnius prolixus*, pointed to the corpora allata (CA) which are small (usually) paired glands found in close association with the corpora cardiaca, posterior to the insect brain (Fig. 12), as the source of this factor, later termed "juvenile hormone" (JH) due to its status quo action on the molt. In 1956, Williams isolated, from abdomens of *Hyalophora cecropia* male moths, an oil displaying juvenile hormone activity; however, it took an additional 10 years before the chemical structure of a natural juvenile hormone was successfully determined (JH I, by Röller and co-workers).

Juvenile hormones make up a group of lipophilic sesquiterpenes produced by the CA and released to the hemolymph. Six different forms (Fig. 13) of juvenile hormone have been identified so far from insect tissue and hemolymph. All known juvenile hormones are methyl esters of epoxyfarnesoic acid or of one of its homologs (i.e., with one or several methyl and/or ethyl side chains). JH III, the simplest and most ubiquitous one, is the only juvenile hormone found in the majority of insects. In the Lepidoptera, however, five juvenile hormones have been described, including JH III and the homologous JH 0, JH I, JH II, and 4-methyl-JH I. In addition, the CA of cyclorrhaphous Diptera secrete both JH III and a bis-epoxide form of this hormone (JHB_3).



Juvenile Hormone, Figure 12 Schematic representation of the head components of the neuroendocrine system in a Lepidoptera larva, showing the position of the corpora allata relative to the corpora cardiaca, the brain and the suboesophageal ganglion, as well as the nervous connections among these entities. *ca*, corpora allata; *cc*, corpora cardiaca, *con s*, suboesophageal connectives, *con th*, thoracic connectives, *nas*, nervus allatosuboesophagealis, *nca*, nervus corporis allati, *ncc* I–IV, nervi corporis cardiaci, *nsc lat*, neurosecretory cells (nsc) of the lateral part of protocerebrum, *nsc med*, nsc of the pars intercerebralis protocerebri, *nsc sub*, nsc of the suboesophageal ganglion, *nsc trit*, nsc of the tritocerebrum, *ol*, optic lobe, *protoc*, protocerebrum, *sg*, suboesophageal ganglion, *trit*, tritocerebrum (from Sláma K, Romaňuk M, Šorm F (1974) Insect hormones and bioanalogues. Springer-Verlag, New York).



Juvenile Hormone, Figure 13 Chemical structure of the six known juvenile hormones; *Me*, methyl.

Biosynthesis of juvenile hormone proceeds through the mevalonate pathway – the end product of which is cholesterol in most other animals – and thus uses acetyl-CoA as the principal building block. In the case of juvenile hormones with ethyl side chains, one unit of propionyl-CoA, derived from valine and isoleucine, substitutes for one of the three acetyl-CoA units that make up mevalonate, thus leading to the formation of homomevalonate. Condensation of three isoprene units by farnesyl diphosphate synthase results in the formation of the juvenile hormone backbone (i.e., farnesyl diphosphate or one of its homologs). This diphosphate is then sequentially converted to an alcohol and an acid, followed by the formation of a methyl ester and epoxidation.

One of the most intensively studied functions of juvenile hormone is its juvenilizing effect during larval development, whereby high levels of the hormone during larval molts modify the type of cuticle secreted at a molt, thus maintaining the insect in a juvenile state. Consequently, the juvenile hormone titer is maintained at a relatively high level during most of the larval period until the final instar, at which time it drops precipitously, allowing the subsequently released ecdysteroids to induce the larval-pupal or nymphal-adult transformation. With the exception of a rise in its levels during the prepupal stage (at least in some Lepidoptera), the juvenile hormone titer usually remains low until adult emergence when the CA are reactivated.

In adult females of most insects, juvenile hormone induces vitellogenin synthesis in the fat body as well as its uptake by developing oocytes, making it an absolute requirement for egg maturation. In these insects, titers are observed to fluctuate as a function of the various phases of the ovarian cycle. Sex pheromone production and sexual receptivity, the expression of which is often coordinated with the ovarian cycle, are regulated by juvenile hormone in many species of insects. In males, juvenile hormone may be necessary to promote the production of accessory sex gland secretions and to control courtship behavior. Other processes that juvenile hormone has been shown to govern in some adults include migration, polyphenism, caste differentiation and reproductive diapause.

The principal factors regulating the level of juvenile hormone in insect hemolymph are the rate of hormone synthesis by the CA and its degradation in the hemolymph and tissues. These glands do not store juvenile hormone, but they release the hormone into the blood as soon as it is produced. The biosynthetic activity of the CA is controlled chiefly by neuropeptides that either stimulate (allatotropins), or inhibit (allatostatins, allatinhibins) juvenile hormone production. These neuropeptides are produced by neurosecretory cells and are delivered to the CA via neural connections to the brain. Juvenile hormone biosynthesis may also be modulated by factors released in the hemolymph by organs or tissues that are anatomically distant from the CA (e.g., ovary, neurosecretory cells in the ventral nerve cord, etc.).

Catabolism significantly affects the hemolymph titer of juvenile hormone at certain stages of insect development. In this respect, juvenile hormone esterase (JHE) is instrumental in the critical lowering of juvenile hormone titers during the final instar of lepidopteran insects. The same enzyme may also play an important role in juvenile hormone titer regulation following mating in adult females of certain lepidopteran species. Within tissues, an epoxide hydrolase (JHEH) plays a significant role in the degradation of juvenile hormone.

Experimental evidence suggests that juvenile hormone can modulate gene transcription in insects (e.g., induction: transcription of the JHE gene; suppression: transcription of the *Broad Complex* gene), implying that it likely binds to an intracellular receptor in a fashion similar to that described for steroid hormones, including ecdysone. To date, although several hemolymph juvenile hormone carrier proteins have been identified, few cytosolic or nuclear juvenile hormone binding proteins have been isolated, and their role as a juvenile hormone receptor has either been questioned or remains unconfirmed. Some of the effects attributed to juvenile hormone, including the induction of vitellogenin uptake by developing oocytes through the juvenile hormone-dependent formation of openings between follicular cells (patency), appear to result from the interaction of juvenile hormone with a cell-surface receptor, in a manner similar to that described for peptide hormones. Clearly, thus far, juvenile hormone does not fit any single pre-established receptor-ligand model and may well have pleiotropic effects in a given cell mediated by different receptors.

The disruption of juvenile hormone functions in insects has long been viewed as a promising strategy for the development of environmentally safe, insect-specific pest control products. Williams was the first to suggest the use of juvenile hormone or juvenile hormone-like compounds as a means of controlling insect pests, reasoning that an artificial increase in the levels of juvenile hormone at times when such levels are normally low would result in a fatal disruption of insect development. Various compounds, collectively referred to as juvenile hormone analogs (JHAs) or "juvenoids" have, indeed, been developed for this purpose, and a few have enjoyed commercial success for the control of insects whose pest status is restricted to the adult stage (e.g., mosquitoes). These insecticides, however, do not usually provide adequate control of crop and forest pests that feed as larvae, because death usually is not immediate and larvae continue to feed and cause damage, dying only near the end of larval life or at metamorphosis. For this reason, current research efforts are aimed at finding ways of artificially *lowering* juvenile hormone titers, or antagonizing juvenile hormone function at the receptor level; if successful, such strategies would result in the precocious (and fatal) induction of metamorphosis in the larva and in the inhibition of reproduction in the adult.

► Endocrine Regulation of Insect Reproduction
► Reproduction
► Metamorphosis
► Diapause
► Corpus Allatum
► Howard Schneiderman
► Carroll Williams
► Vincent Wigglesworth

References

Riddiford LM (1994) Cellular and molecular actions of juvenile hormone. I. General considerations and premetamorphic actions. Adv Insect Physiol 24:213–274

Schooley DA, Baker FC (1985) Juvenile hormone biosynthesis. In: Kerkut GA, Gilbert LI (eds) Comprehensive insect physiology, biochemistry and pharmacology, vol 7. Pergamon Press, Oxford, UK, pp 363–389

Tobe SS, Feyereisen R (1983) Juvenile hormone biosynthesis: regulation and assay. In: Downer RGH, Laufer H (eds) Endocrinology of insects. Alan R. Liss, New York, NY, pp 161–178

Tobe SS, Stay B (1985) Structure and regulation of the corpus allatum. Adv Insect Physiol 18:305–432

Wyatt GR, Davey KG (1996) Cellular and molecular actions of juvenile hormone. II. Roles of juvenile hormone in adult insects. Adv Insect Physiol 26:1–155

Juvenoid

Chemicals that act as growth regulators, mimicking juvenile hormone. Ingestion or topical exposure can result in disruption of the normal endocrine functions, including prolongation of the immature stage, induction of supernumerary instars, and loss of fertility. Juvenoids are juvenile hormone analogs, most of which are synthetic, and which are applied as fairly selective insecticides. Plants also produce juvenile hormone-like compounds, however.

K

Kairomone

A chemical produced by one species that is perceived by another species, and benefits the perceiver. Kairomones are a type of semiochemical.

► Chemical Ecology

Kala-Azar

A form of visceral leishmaniasis caused by *Leishmania donovani*. In humans it causes enlargement of the spleen and liver, and can be fatal. It is vectored by sandflies (Dipera: Psychodidae).

► Leishmaniasis

Kalotermitidae

A family of termites (order Isoptera).

► Termites

Kaolin

A white clay or crushed rock derived from feldspar that, when applied to foliage, often reduces insect feeding.

Kaolin-Based Particle Films for Arthropod Control

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At the beginning of the twentieth century, the few pesticides that were available were applied as spray solutions using steam or gas driven spray gun systems. The high labor inputs involved in spraying orchards and other crops by handgun and the use of large volumes of water motivated researchers to investigate dust applications that used mineral particles as insecticidal carriers. Dust applications gained favor over liquid sprays in the 1920s because of the speed of dust operations, economy in labor, good plant coverage, and comparable insect control with liquid sprays. In the 1930s, researchers discovered that certain inert minerals themselves were toxic agents to insects. The primary mechanisms that inert minerals acted upon insects as summarized in 1939 were (i) ingestion of the dust into the digestive system, (ii) desiccation, (iii) chemical reaction with the body wall of the insect, and (iv) direct mechanical abrasive action. Interest in mineral particles for insect control continued through the 1960s but had little impact on the agricultural industry. Control of insects with inert dusts transitioned from minerals to synthetic compounds like silica aerogels and fumed silicas by 1970. These synthetic dusts were believed to have the greatest potential for the pest control needs of the grain industry; however, inexpensive chemical fumigants became widely used instead. Much of the research on mineral particles after 1970 was limited to pesticide formulations where mineral particles were used as carriers for synthetic insecticides and microbial agents, and in the use of minerals for sunburn control. Certain minerals such as diatomaceous earth (e.g., Celite®, Cryacide®) for insect control, wettable sulfur for plant disease control, and hydrated lime for sunburn prevention are still utilized to a varying degree in tree fruit and grape production.

Development of Particle Film Technology

Mineral particle research and development continued to advance since the 1970s in the paint and plastics industry where particles were being engineered with specific sizes, shapes, and light reflective properties for paper, paint, cosmetic, and plastic products. Congress mandated the United States Department of Agriculture (USDA), Agricultural Research Service (ARS) to develop reduced risk alternatives to chemical pesticides in 1985 as part of the Low Input Sustainable Agriculture (LISA) program; this motivated many researchers to investigate new ideas to control plant pests in an economically sustainable and environmentally safe manner. Particle film technology was conceived by ARS scientists in the mid-1990s as an alternative to chemical pesticides. This technology was based on coating plant parts with mineral films that met the following properties: (i) chemically inert mineral particle, (ii) particle diameter <2 μm, (iii) formulated to spread and create a uniform film, (iv) forms a porous film that does not interfere with gas exchange between the leaf and atmosphere, (v) transmits photosynthetically active radiation (PAR) but excludes ultraviolet (UV) and infrared (IR) radiation to some degree, (vi) alters insect behavior on the plant, and (vii) can be removed from harvested commodities. Various minerals and their properties were investigated but many contained the respirable human carcinogen crystalline silica (SiO_2), and did not transmit sunlight; thus, crystalline silica would adversely affect plant photosynthesis. In 1996, ARS researchers partnered with industry to focused on a novel class of particles based on kaolin, a white, non-porous, non-swelling, non-abrasive, fine grained, plate-like, aluminosilicate mineral ($Al_4Si_4O_{10}(OH)_8$) that easily disperses in water and is chemically inert over a wide pH range. Coating grade kaolin is >90% pure and has a high brightness quality of >85% and is capable of transmitting sunlight. The chemical and physical properties plus the availability of engineered kaolin particles that were heat treated, shaped and sized made this mineral an ideal candidate for study. The term "particle film technology" was coined by the group for the research that led to the development of a multifunctional mineral product capable of controlling many insects pests, certain diseases and improved plant health.

Particle film technology was originally based on kaolin particles made hydrophobic by a silicone coating. Hydrophobic kaolin, M-96–018, (BASF, Research Triangle Park, North Carolina, USA; formerly Engelhard Corporation, Iselin, New Jersey, USA) was initially applied as a dust using various hand-operated dusters or modified sand-blasters for large scale studies because the hydrophobic material could not be mixed and delivered in water. However, the drift associated with dusting operations, plus lack of adhesion to the plant, made M-96–018 dust applications impractical. In 1998, the first particle film formulations were registered with the U.S. Environmental Protection Agency (EPA) under the names M-96–018 and M-97–009 Kaolin. M-96–018 was soon formulated by using a methanol (MEOH)-water system where M-96–018 could be pre-slurried with

99% MEOH (11.3 kg or 25 lbs M-96–018 + 18.0 L or 4 gal MEOH premixed then added to 436 L or 96 gal water) and delivered as a spray to trees. During field tests, it was determined that this formulation was too expensive for practical use, and handling and transportation of 99% MEOH presented logistical and safety problems. Laboratory and field studies determined that formulations based on hydrophilic kaolin particles (M-97–009) plus a spreader sticker were just as effective as M-96–018 hydrophobic kaolin dusts or aqueous sprays in controlling insects and diseases. As a result, the development of M-96–018 was dropped in favor of M-97–009.

Advantages to using hydrophilic M-97–009 kaolin formulations were (i) ease of mixing, (ii) more economical, (iii) compatible with other materials for tank-mixes, and (iv) formulation flexibility to alter spreading and rain fastness. M-97–009 + M03 became commercially available in 1999 under the name Surround® (BASF, Research Triangle Park, North Carolina; formerly Engelhard Corporation, Iselin, New Jersey) and in most cases was applied at 25 lbs kaolin plus 1 pt spreader-sticker in 96 gal water. In 1999, a new formulation of M-97–009 was registered with the U.S. EPA under the name Surround™ WP that had the spreader-sticker system incorporated into the particles as a single packaged system that could be added directly to water. This formulation became available in 2000 and is the main formulation currently in use.

The historical safety record of kaolin in the paint and plastics industry, including a series of health and toxicity tests for EPA registrations, has been used to support the approval of Surround™ products for organic crop production.

Action of Particle Films on Arthropods

Two basic actions of mineral particles against insects have been well addressed in the literature. Minerals (diatomaceous earth, fumed silica) that are abrasive or absorptive to the insect's cuticular waxes can be used for control of insects, mainly stored grain pests. Minerals that were white and reflective to sunlight (calcium carbonate) could potentially be applied as whitewashes to the soil as reflective mulches to repel aphid pests. Although these concepts were sound, these materials had little impact on the arthropod pest control industry, although calcium carbonates have been widely used for sunburn protection in fruit production. Particle film technology diverged from all other mineral-based insecticides in concept where the effects on insect behavior and on plant health were recognized. A major advancement in this technology was in formulation chemistry that enabled kaolin particles to be mixed with water, applied through conventional pesticide sprayers, forming a porous film, and producing a film that could resist rain and wind, yet be easily removed after harvest.

Particle films act on the insect's processes of locating and accepting plants as hosts for feeding and reproduction which are dictated through the senses of touch, taste, sight, and smell. During the process of locating and accepting hosts, the four senses interact to produce both positive and negative cues, the sum of which provokes a positive or negative behavior in insects. Plant tissues coated with white particle films are altered visually and tactilely to insects. Particle films also may alter the taste or smell of the host plant. Choice and no-choice laboratory bioassays on various insects revealed that the primary mechanism of action was repellence of adults from treated foliage, resulting in reduced feeding and oviposition. Repellency is only used tentatively as a mechanism since it has not yet been demonstrated if insects orient away from particle films before film contact (repellence) versus after film contact, which is more appropriately termed a deterrent. Other mechanisms include (i) reduced survival of adults or immature insects (larvae) when born into the particle film coated leaf environment, (ii) reduced mating success of adult Lepidoptera exposed to particle films, (iii) impeded movement/host finding ability within plant canopies,

(iv) camouflage of the host by turning the plant foliage white with the particle film, and (v) impedance of the insect's ability to grasp the plant. Most of the effects particle films have on insects result from particle attachment to the insect's various body parts (Fig. 1). The underlying mechanisms of this technology make it unlikely that insects would develop resistance.

Particle Film Applications for Arthropod Pest Control

Applications of particle films, M-96–018, M-97–009, Surround™ and Surround™ WP for pest control are typically made at 3–6% solids in water (w:w). Particle film solutions can be applied by any type of boom, orchard blast, or hand sprayers and can be applied aerially. Research on film weather ability and functionality on insects have concluded that 3% are as effective as 6% solutions under most circumstances. There are usually at least three applications made 7–14 days apart for control of foliar pests. In certain circumstances, such as dormant applications, only 1–2 applications of 6% solutions are needed for pear psylla control in pear. Applications are typically made to near "run-off" or "drip," and are considered a "dilute application" where 200 gallons/acre (1850 L/ha) are applied to mature fruit trees 8 m in height.

The principal use for particle films is for control of pear psylla, *Cacopsylla pyricola* Foerster, in pear in the USA and (Fig. 2) Europe. Dormant applications of Surround™ WP and Surround™ CF have been used on nearly 100% of the pear acreage in northern Washington over the past several years. Particle films are effective against many key orders of arthropod pests affecting crops

Kaolin-Based Particle Films for Arthropod Control, Figure 1 **SEM of a two-spotted spider mite, *Tetranychus urticae* Koch., that was exposed to a M-96–018 particle film treated apple leaf for 10 minutes. Inset is a 10 μm diameter circle to indicate scale of particle coverage.**

Kaolin-Based Particle Films for Arthropod Control, Figure 2 **Particle film, Surround WP, dormant timing application to pear to prevent infestations of pear psylla near Wenatchee, Washington, USA.**

including hemipterans, coleopterans, lepidopterans, dipterans, rust mites, and eriophyid mites. Examples of other uses are for leafhoppers and sharpshooter control in grapes, plum curculio, *Conotrachelus nenuphar* (Herbst), in apple and plum, and olive fruit fly, *Bactrocera oleae* L., in olive. Particle films are not effective against tetranychid mites and San Jose scale, *Quadraspidiotur perniciosus* (Comstock), in tree fruits. These pests are generally controlled by natural predators and parasites and the particle film is thought to reduce the efficacy of these beneficial organisms. Research continues to expand, with over 25 research papers on the effects of particle films on insects on various crops. Most of the research focuses on crops where particle film residues are either not a concern and are processed with the fruit (e.g., wine grapes, fruits for juices) or are removed in packhouse operations where fruits are washed, brushed, waxed and bagged (e.g., apples, pears, citrus) for the fresh fruit and vegetable market.

Multi-Functionality of Particle Films

Initial studies into particle film technology discovered that plants directly benefited from the film's properties, including film porosity, which allowed gas exchange between the leaf and atmosphere, and the ability of the film to transmit photosynthetically active radiation (PAR) yet exclude ultraviolet (UV) and infrared (IR) radiation to a significant degree. Whole-tree photosynthesis, water use efficiency, yield, size, and quality of apples were compared for the kaolin, Surround™ WP, and calcium carbonate. Only the kaolin formulation increased photosynthesis over the untreated control although water use efficiency was reduced through increases in stomatal conductance associated with reduced leaf temperature. Calcium carbonate, despite its white color, produced none of these effects and reflected more PAR from the tree canopy than processed kaolin.

Increases in plant photosynthesis from kaolin-based particle film treatments can lead to favorable effects on plant productivity. Yield and fruit size increases have been noted in apple, pear, cotton, and citrus. In addition, cooling of the tree canopy through the reflectance of IR can improve fruit color in apple and pear, but these results are variety dependent.

Numerous studies throughout the world have supported the consistent ability of a kaolin particle film to reduce sunburn. Reflectance of IR and UV in conjunction with significant reductions in plant surface temperatures reduce solar injury. The impact of particle film technology as a sunburn prevention agent in agriculture is essentially equal to the pesticidal uses of particle film. Surround™ WP is currently used to prevent sunburn and heat stress in apple, pear, citrus, walnut, banana, cantaloupe, and tomato.

Particle films have many other applications where the properties of the films can be altered by particle physics and formulation chemistry. These potential uses include sprayable reflective mulches, herbicides, frost prevention, and in pesticide delivery.

► Visual Attractants and Repellents in IPM
► Host Plant Selection by Insects
► Diatomaceous Earth
► Pear Psylla

References

Glenn DM, Puterka GJ, Van der Zwet T, Byers RE, Feldhake C (1999) Hydrophobic particle films: a new paradigm for suppression of arthropod pests and plant diseases. J Econ Entomol 92:759–771

Glenn DM, Puterka GJ (2005) Particle film technology: A new tool for agriculture. Hortic Rev 31:1–45

Puterka GJ, Glenn DM, Pluta RC (2005) Action of particle films on the biology and behavior of pear psylla (Homoptera: Psyllidae). J Econ Entomol 98:2079–2088

Puterka GJ, Glenn DM, Sekutowski DG (2000) Method for protecting surfaces from arthropod infestation, U.S. Patent No. 6,027,740

Puterka GJ, Glenn DM, Sekutowski DG, Unruh TR, Jones SK (2000) Progress toward liquid formulations of particle films for insect and disease control in pear. Environ Entomol 29:329–339

Puterka GJ, Reinke M, Luvisi D, Ciomperik MA, Bartels D, Wendel L, Glenn DM (2003) Particle film, Surround WP, effects on glassy-winged sharpshooter behavior and its utility as a barrier to sharpshooter infestations in grape. Online. Plant Health Progress doi:10.1094/PHP-2003–0321–01-RS

Kaszab, Zoltán

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Zoltán Kaszab was born on the September 23, 1915 at Farmos, in Pest- Pilis- Solt- Kiskun Shire in Hungary. Even as a child, he was deeply interested in animals, especially insects. He completed his tertiary education at the University of Science in Budapest, where he was awarded a doctoral degree in zoology, geology and mineralogy. After university he gained employment with Professor Endre Dudich in the Institut of Zoological Taxonomy and eventually joined the staff at the Hungarian Natural History Museum in Budapest. In 1955 he became the chief curator of the zoological collections and from 1970 until 1985 he was the principal director of the museum. Kaszab was an extremely hard worker, totally committed to entomology, specifically to the Tenebrionidae and Meloidae (Coleoptera). He researched the tenebrionid beetles of Bíró's vast New Guinean collection and published the results. In a relatively short time he became a world expert of these aforementioned beetle families. From 1963 until 1968 he dedicated most of his time and energy to the zoological exploration of Mongolia. During this period he undertook six collecting expeditions, mostly on his own, and collected 486,342 specimens, mainly insects. More than 200 workers from the international scientific community participated in the research of this singular collection. By the mid 1980s nearly 500 papers (approximately 7,000 pages in total) were produced, including 60 new genera and 1,600 new species. Zoltán Kaszab appeared to be physically strong, yet he had a weak heart. In 1963, just before his first Mongolian expedition, he overcame a very serious illness and survived a major heart operation. His health improved somewhat and he could work harder than anyone around him. In the mid-eighties his health declined and he had to resign from his directorial post in order to devote himself completely to his beetle studies. On the April 4, 1986 he passed away. Zoltán Kaszab's achievements in entomology are unparalleled amongst the Hungarian entomologists. He described 2,800 new species and published 397 scientific papers, totalling approximately 10,000 pages.

References

Matskási I (1987) In memoriam Dr. Zoltán Kaszab (1915–1986). Annales Historico-Naturales Nationalis Hungarici, Tomus 79. Budapest, Hungary

Papp CS (1986) In memoriam Zoltán Kaszab (1915–1986). Entomography, vol 4

Katydids (Orthoptera: Tettigoniidae)

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Katydids belong to a family of ensiferan orthopterans with over 6, 000 described species and found in a variety of habitats on all continents except Antarctica. Most taxonomic schemes recognize katydids (called bush-crickets in Europe) as a family, Tettigoniidae. Katydids are typically large insects of several centimeters in length. They share with most other Ensifera – a suborder that includes Grylloidea, the true crickets, Rhaphidophoridae, the camel crickets, and Anostostomatidae, the weta – nocturnal activity, long antennae, a long blade-like ovipositor, tibial tympana, and a complex spermatophore that has a spermatophylax serving as a food gift for the female. There are about 17 subfamilies although this scheme is likely to be revised with further phylogenetic study. A formal phylogenetic analysis of the family is currently lacking. The earliest fossil tettigoniids are Permian.

Katydids are best known for the distinct male sounds produced by tegminal (forewing) stridulation and used to attract mates. In many species the tegmina are leaf-like, allowing daytime crypsis in the vegetation habitat. Other species have short tegmina, a robust cricket-like appearance, and inhabit low vegetation, occasionally moving over the ground. The use of vegetation as a retreat during daylight contrasts with most other ensiferans that use burrows or crevices. Features that distinguish katydids from other ensiferans, and indicate that the family is a natural (monophyletic) group, include: four tarsal segments, left-over right tegminal stridulation, and certain DNA sequences. Grylloidea, the second most diverse ensiferan subgroup, also show tegminal stridulation but with the opposite tegminal overlap to that of katydids. Also, in contrast to other ensiferan subgroups, most species of true crickets and katydids have an egg-to-adult life cycle that is completed within one year.

As in other Ensifera, many katydids lay their eggs in soil. However, many others oviposit into leaves, bark and other plant parts, or paste their flattened eggs like overlapped shingles onto leaves. There is a diversity of development patterns typically involving diapause, the temporary cessation of development during favorable conditions in order to survive future severe periods such as winter. Eggs of some species diapause through just one winter, whereas in others several winters may be required to continue development to the adult stage. Depending on the species, there are four to nine instars. A few tropical species show an unusual change during development. For example, the small larvae of *Macroxiphus sumatranus* (Conocephalinae) mimic ants both in structure and movement whereas the adult insect is brightly colored and aposematic.

Some katydids are herbivorous, others carnivorous, but most species are omnivores. A few species have specialized diets such as pollen (the Australian Zaprochilinae). The list of natural enemies of tettigoniids includes predators such as bats that orient to the calls of males. Sphecid wasps (some of which are katydid specialists) use paralyzed katydids as food provisions for their fossorial larvae. Katydid killers also include parasitoids such as ormiine flies (Tachinidae) that larviposit on males after being attracted to their calls, and the thread-like horsehair worms (phylum Nematomorpha) and mermithid nematodes that can virtually fill the body cavity of their hosts. Important parasites include endoparasitic microsporidians and gregarine protozoans. Ectoparasites include mites, stick ticks (ceratopogonid flies) and strepsipterans. Katydid defenses against natural enemies include camouflage with some tropical katydids showing remarkable mimicry to leaves. A few species have chemical defenses including reflex bleeding in which blood squirts can be aimed at predators.

Although most katydids live a mainly solitary existence, a few show gregarious habits which can lead to economic damage. For example aggregations of ovipositing false-leaf katydids (Pseudophyllinae: *Pterophylla*) can damage forest trees. A few species at very high densities show coordinated group behavior. This is best known in the locust-like swarms of flying cone-headed katydids (Conocephalinae: *Ruspolia*) in Africa and, in particular, the massive migrations of bands of North American Mormon crickets, a flightless shield-backed katydid (Tettigoniinae: *Anabrus simplex*). Band-forming populations contrast with other populations of Mormon crickets that are quite solitary in their behavior. Bands form in the early instars and by the adult stage can form huge aggregations several hundred meters wide and kilometers long that show highly directed migrations. Such bands can devastate agricultural crops. Individuals in bands experience a much reduced risk of predation but need to move continuously to avoid cannibalism by conspecifics. Cannibalism reflects intense competition within the band for protein and salt.

Male katydids stridulate by moving a scraper on the top of the right tegmen over a file on the underside of the left tegmen. Stridulatory calling is found in virtually all species and functions mainly to attract females. Calling song can mediate female choice of males and in a few species can serve as a barrier to matings between species. In most species the male song is a series of noisy (broad spectrum of sound frequencies) buzzes, zips or clicks. More musical (narrow spectrum) sounds are produced by many neotropical species, some of which are ultrasonic. Although pairing in most species is accomplished when the female is attracted to the male call, in a few species, including many Phaneropterinae, females answer males with their own call and males move to these sounds. Individuals hear sounds using a complex system of foretibial tympana connected to specialized thoracic tracheae and paired thoracic spiracles. The acoustical systems of katydids have been studied extensively and have been model systems for neurophysiological, behavioral and evolutionary studies.

Copulation typically follows the female mounting the male and the mated pair assuming a position in which the male is curled behind the female. The end of the spermatophore is inserted into the female's genital chamber. The exterior sperm ampullae and attached spermatophylax of the spermatophore comprise up to 40% of the male's weight (Fig. 3).

Katydids (Orthoptera: Tettigoniidae), Figure 3 Photograph: Mormon crickets, the shield-backed katydid *Anabrus simplex*. The female in the foreground has just mated and has a spermatophylax meal attached to her abdomen. The male is in the background. His short singing wings protrude from beneath the pronotal shield.

The need for protein in katydids in band-forming Mormon crickets, and katydids in which food supplies can be limited, underlies extreme variation in sexual selection and mating behavior observed in these species. Starvation decreases male mating (spermatophore producing) frequency but increases the propensity of hungry females to mate as they seek spermatophore meals. This leads to sexual competition among females that is not seen in populations with adequate food. Experimental manipulations of proteinaceous food in these species have supported a central tenet of sexual selection theory that relative investment of the sexes in offspring controls sexual differences in both mate choice and sexual competition.

► Grasshoppers, Katydids, and Crickets (Orthoptera)
► Mormon Cricket
► Cannibalism
► Gregarious Behavior in Insects
► Sexual Selection
► Acoustic Communication in Insects

References

Bailey WJ, Rentz DCF (eds) (1990) The Tettigoniidae: biology, systematics and evolution. Crawford House, Bathurst, Australia, 395 pp

Capinera JL, Scott RD, Walker TJ (2004) Field guide to grasshoppers, katydids, and crickets of the United States. Cornell University Press, Ithaca, NY, 280 pp

Gwynne DT (2001) Katydids and bush-crickets: reproductive behavior and evolution of the Tettigoniidae. Cornell University Press, Ithaca, NY, 400 pp

Ragge DR, Reynolds WJ (1998) The songs of the grasshoppers and crickets of western Europe. Harley Books, Colchester, UK, 600 pp

Kaufmann Effect

The developmental response of insects to temperature is usually determined by exposing different groups of them to various constant temperatures. The relationship between environmental temperature and insect development rate over most of the range between the highest and lowest tolerable temperatures is usually linear, with higher temperatures promoting (up to a point) higher rates of development. However, some nonoptimal temperatures may cause either a retardation or acceleration of development rates; this deviation from what is expected (non-linearity) shows up when insects are exposed to alternating temperatures. The difference between development predicted by linear models, and the development observed under variable temperature conditions (or predicted by nonlinear models) was first observed by O. Kaufmann in 1932, and so is called the "Kaufmann effect" or the "rate summation effect."

► Phenology Models for Pest Management

References

Petavy G, David JR, Gilbert P, Moreteau B (2001) Viability and rate of development at different temperatures in *Drosophila*: a comparison of constant and alternating thermal regimes. J Therm Biol 26:29–39

Worner SP (1992) Performance of phenological models under variable temperature regimes: consequences of the Kaufmann or rate summation effect. Environ Entomol 21:689–699

Kauri Moths (Lepidoptera: Agathiphagidae)

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Kauri moths, family Agathiphagidae, have only two known species, one each from Queensland and Fiji. The family comprises the monobasic superfamily Agathiphagoidea and the only representative of the suborder Aglossata. Adults small (9–14 mm wingspan), with head vertex rough-scaled; with rudimentary chewing mouthparts (haustellum absent); short labial palpi, 3-segmented; maxillary palpi 5-segmented and folded. Maculation somewhat similar to Micropterigidae but mostly gray with fine speckling spots. Adults are diurnally active. Larvae are seed-borers of kauri pines (*Agathis*, Araucariaceae) of the South Pacific and are modified for this kind of feeding. Thus, they appear much more elongated and different from larvae of Micropterigidae.

References

Common IFB (1973) A new family of Dacnonypha (Lepidoptera) based on three new species from southern Australia, with notes on the Agathiphagidae. J Aust Entomol Soc 12:11–23

Dumbleton LF (1952) A new genus of seed-infesting micropterygid moths. Pac Sci 6:17–29

Kristensen NP (1967) Erection of a new family in the lepidopterous suborder Dacnonypha. Entomlogiske Meddelelser 35:341–345

Kristensen NP (1984) The male genitalia of *Agathiphaga* (Lepidoptera, Agathiphagidae) and the lepidopteran ground plan. Entomologica Scandinavica 15:151–178

Upton MS (1997) A twelve-year larval diapause in the Queensland kauri moth, *Agathiphaga queenslandensis* Dumbleton (Lepidoptera: Agathiphagidae). Entomologist 116:142–143

Ked

A louse fly; a member of the fly family Hippoboscidae.

► Flies

Keel

The crest or raised ridge running along the dorsal midline of cockroach oothecae; the median carina (a dorsal raised ridge) on the pronotum of a grasshopper.

Kellogg, Vernon Lyman

Vernon Kellogg was born December 1, 1867, in Emporia, Kansas, USA. He received his B.S. and M.S. degrees from the University of Kansas in 1889 and 1892, respectively. He also was awarded the LL.D. degree from the University of California in 1919 and from Brown University in 1920. He was awarded a Sc.D. from Oberlin College in 1922. Kellogg worked at the University of Kansas as an assistant professor of entomology, and then at Stanford university as an assistant professor, associate professor, and professor. He was a successful teacher of entomology. His areas of expertise were morphology, genetics, and behavior. Kellogg authored several general zoology and evolution texts, and also an economic entomology and zoology book (co-authored with R.W. Doane). Despite a successful career as an educator, Kellogg is best known for his humanitarian work. During World War I, he worked U.S. Food Administration and other relief groups in Europe in the aftermath of the war. He was decorated by several European governments for his humanitarian efforts. He was also instrumental in forming the National Research Council in the USA, an agency that links government and science. He died August 8, 1937.

References

Essig EO (1931) A history of entomology. The Macmillan Company, New York, NY, 1029 pp
Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Kennedy, John S

John Kennedy was born May 15, 1912, in Pennsylvania, USA, but spent most of his early life in London, England. He attended University College, London and then attained a M.S. with G. S. Frankel followed by a Ph.D. in 1938 at the Imperial Institute of Entomology in Birmingham. He studied locusts and mosquito behavior before joining V. B. Wigglesworth at the Unit of Insect Physiology in Cambridge. The unit was dissolved in 1967 but Kennedy moved to Imperial College and started a new physiology research unit. Kennedy was known for his research on many facets of insect behavior, including animal orientation, insect migration, and insect flight. He was a leader in separating behavioral research from anthropomorphic interpretation, an unfortunate result of the influence of Konrad Lorenz and research on "higher" animals. This crusade won him few friends initially, but his disciplined, clear-thinking approach won out and he eventually received considerable acclaim, honors and awards. He died on February 4, 1993, at Oxford, England.

Reference

Brady J (1993) Professor J. S. Kennedy, F.R.S., (1912–1993). Antenna 17:105–107

Kermesidae

A family of insects in the superfamily Coccoidae (order Hemiptera). They sometimes are called gall-like coccids.

► Bugs
► Scale Insects and Mealybugs

Keroplatidae

A family of flies (order Diptera).

► Flies

Kershaw, John Crampton Wilkinson

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John Kershaw was born in Broughton, Nottinghamshire, England, in 1871, and was known as a scholar as early as age 10. His father, George S. Kershaw, was Vicar of Broughton in Nottingham. Very little is known of John's early life but his two younger brothers were also interested in entomology. Colonel Sidney H. Kershaw collected butterflies and moths wherever he was stationed and G. Bertram Kershaw collected them in England, so the family was interested in Lepidoptera.

John grew up during the latter part of the nineteenth century when the need of a college education was not an absolute necessity to work in natural history; however, his lack of it may have influenced success in later life. The coleopterist David Sharp, who was most liberal in giving assistance and encouragement to young persons planning to visit other countries, may have influenced him, as many entomologists as well as zoologists went to Sharp at the Cambridge museum in search of information about suitable equipment and the most profitable method of work. He was surely influenced by Edward B. Poulton, Hope professor of Zoology at the University of Oxford, who collected a wide variety of natural history objects. Kershaw's robber flies collected in Macao are listed in Poulton's pioneering work on *Predaceous insects and their prey* (Transactions of the Entomological Society of London, 1906) and Kershaw and Frederick Muir are listed in several of the *Hope Reports* (Oxford University) for their contributions in entomology in Macao, South China, over several years. He was certainly influenced by his long-lived friend, Dr. Robert C. L. Perkins, with whom he collected *Odynerus* vespid wasps in Hawaii later in 1912.

In 1898, at the age of 28, John Kershaw was in China where he studied natural history. He met the ornithologist and Englishman Frederick W. Styan (a tea merchant in Shanghai) who influenced him to study birds. Kershaw observed and collected them along the South China coast before Hong Kong became established. At that time, the Portuguese enclave of Macao was occupied by the English and other Europeans exploring or doing business in China. John Kershaw occupied one of the beautiful colonial type residences at 19 Praie Grande in Macao on the outer harbor as early as 1900, and used the rooftop of his home to rear the insects he studied.

When the exploratory entomologist Frederick A. G. Muir came to China via Macao in 1906–1907, they collaborated in Hawaiian Sugar Planter Association activities. Kershaw had recently published, and was becoming well known for his book on the *Butterflies of Hong Kong* (1906), the first to be published on South China Lepidoptera. Kershaw probably gained insight on insect parasitoids from his friend, as Muir was looking for biological control agents that could be introduced into Hawaii to control a leafhopper. Biological control had been criticized by economic entomologists, and Muir set out to prove that it would work in Hawaii. The sugar cane weevil, *Rhabdocnemis obscura* (Boisduval), was also affecting sugar production in the islands and Muir was looking for a biological control agent to control it. John Kershaw possessed local experience collecting insects that was not found among others in Macao. He had collected Hemiptera that were sent to G. W. Kirkaldy in Honolulu. This had resulted in several papers they published together until Kirkaldy's untimely death in 1900. Kirkaldy had named a cicada after Kershaw that the latter found in Macao; it remains known as *Balinta kershawi* Kirkaldy. John Kershaw also traveled with Muir to the How-lik Monastery area in the Guangdong province of China, collecting insects that were housed in the former Hawaiian Sugar Planters insect collection (currently in the Bernice P. Bishop Museum, Honolulu).

After collecting in the How-lik area among fine forest trees in virgin forest (in what is now known as the Dinghushan Biosphere Reserve) in search of cane leafhopper parasites, they began to search in other areas of Southeast Asia. In November 1908, they both traveled to Indonesia to look for parasites of the sugar cane weevil in west Ceram (The Moluccas). Although unable to locate parasitized cane borers, their time was still profitable with the discovery of a new velvet worm (Onychophora), a species of *Peripatus* known today as *Paraperipatus ceramensis* (Muir and Kershaw). This invertebrate was earlier believed to be a "missing link" between the Annelids and the arthropods, and they worked out the developmental biology in this animal.

In a later trip to Papua New Guinea in 1909, Muir discovered a tachinid fly, *Lixophaga sphenophori* (Villeneuve) that was affecting populations of the sugar cane weevil and he tried to import it into Hawaii, but failed to bring in enough live material for propagation and release in the fields. John Kershaw was sought from Macao to help him in this endeavor. John had developed exceptional skill in keeping insects alive. For example, he had reared several species of butterfly including the rare lycaenid *Miletus chinensis* C. Felder, and the ant-attended larva of the long-banded silverline, *Spindasis lohita* (Horsfield), in preparation for his book on Hong Kong butterflies. He was also successful in culturing an asilid fly (*Promachus* sp.), the pentatomids *Erthesina fullo* (Thunberg) and *Chrysocoris stollii* (Wolff), a predaceous pyrrhocorid bug *Dindymus sanquineus* (Fabricius), the fulgorid *Fulgora candeleria* (L.), and even a rare primitive grasshopper of the genus *Eumastax*, now known as *Erianthus versicolor* Brunner van Wattenwyl in the family Eumastacidae.

In 1910 Kershaw left Macao and traveled to Mossman in Queensland of northern Australia to establish a rearing colony of *L. sphenophori* at the Mossman central sugar mill. The flies had been collected originally in lowland Papua New Guinea, and work at the mill was pre-arranged by Muir. Kershaw then approximated the natural conditions of the fly by designing very large cages over 2 m in height (screen covered and topped with leafy materials to supply shade during sun-lit periods of the day) and he filled them with sugar cane stalks and placed the cages a foot above the ground on posts to avoid predation by ants. The smaller sized cages used earlier had evidently lacked enough space to allow the pre-nuptial flight necessary for mating behavior in the tachinid flies because although the smaller cages only produced 10 parasitoid puparia, the new large cages produced 300 puparia. Using a relay station in the Fiji islands, Muir brought live larvae and pupae in sugar cane stalks into the state during the latter part of 1910, and Kershaw arrived later with additional stock. Their actions insured that enough parasitoids reached Hawaii's plantations to save the sugar industry from appreciable loss. Without Kershaw's mass rearing skills, this fly would not have been successfully reared and the cane-beetle effectively controlled in Hawaii.

Kershaw was a member of the Hawaiian Entomological Society, a Fellow of the Entomological Society of London, a fellow of the Zoological Society of London, and also a Fellow of the Entomological Society of Belgium. He resigned as assistant entomologist with the Hawaiian Sugar Planters Association in 1912 taking a position in Trinidad, West Indies, working on economic control of the froghopper *Tomaspis* sp. (Hemiptera) of sugar cane. After completing this contract, he returned to England and, following the war, wrote a natural history book with the local historian Charles G. Harper on the *Downs and the Sea, wildlife and scenery in Surrey, Sussex & Kent*, published by C. Palmer, London, in 1923. He then retired as an entomologist/zoologist. He passed away in Whiffen's cottage, Kent County, England, on the August 26, 1959 at age 79.

If not acknowledged as the father of natural history in South China, Kershaw should at least be remembered as the "Father of Entomology in Macao." In addition to the aforementioned accomplishments and abilities, he was skilled in insect embryology, writing on egg development in

Siphanta acuta (Walker), a flatid hemipteran (common at higher elevations in Hawaii), and on *Pristhesancus papuensis*, a New Guinea reduviid. Also, he was an early pioneer in the study of web-spinning Embioptera, and one of the first persons to study egg development in *Antipaluria urichi* (de Saussure) in Trinidad. A skilled craftsman, he was an excellent illustrator in all of his publications. This is particularly apparent in his excellent drawings on the anatomy of the fulgorid homopteran, *F. candeleria*, once believed to possess a snout with luminous qualities and commonly found on trunks of lychee and longan trees in South China.

References

Easton ER (1999) John Kershaw – Something old and something rare: the work of one of South China's earliest naturalists. Porcupine, Newsletter of Ecology and Biodiversity, University of Hong Kong, vol 20, p 28

Kershaw JC, Kirkaldy GW (1910) A memoir on the anatomy and life history of the homopteran insect, *Pyrops candeleria* (or candle-fly). Zoologische Jahrbücher. Abteilung für Systematik, Geographic and Biologie 29:108–124

Kershaw JC (1907) The life history of *Spindasis lohita* Horst. Trans Entomol Soc Lon 55:245–248

Kershaw JC (1914) Development of an Embiid. J R Microsc Soc 34:24–27

Muir F, Kershaw JC (1909) *Peripatus ceramensis* n. sp. Q J Microsc Sci 53:737–740

Muir F, Kershaw JC (1912) Development of the mouthparts in the homoptera with observations on the embryo of *Siphanta*. Psyche 19:77–89

Steinheimer FD, Easton ER, Lewthwaite RW (2003) Rediscovery of John Crampton W. Kershaw's birds from Macau including his record of small *Niltava*. Bull Br Ornithol Club123:220–227

Kerriidae

A family of insects in the superfamily Coccoidea (order Hemiptera). They sometimes are called lac insects or lac scales.

► Bugs
► Scale Insects and Mealybugs
► Shellac
► Costs and Benefits of Insects

Kevan, Douglas Keith Mcewan

Keith Kevan was born at Helsinki, Finland, in 1920, but spent most of his early years near Edinburgh, Scotland. He attended Edinburgh University and graduated with first class honors in 1941. He then attended Imperial College, Trinidad for a two-year course in tropical agriculture, and afterwards worked in Kenya with the Kenya Department of Agriculture. He returned to England in 1947 to head the Zoology Section of the University of Nottingham, where he worked on soil fauna but also developed a strong interest in orthopteroids. Kevan relocated to Canada in 1957 to head the Entomology Department at McGill University in Quebec, where he served as chairman from 1957 to 1971. Kevan was an accomplished entomologist as well as an effective administrator. He became one of the world's foremost authorities on grasshoppers, and the undisputed authority on the family Pyrgomorphidae. He also was interested in Neuroptera, and published on cultural entomology and ethnoentomology. He authored several books including "Soil animals" (1962), and several monographs on grasshoppers and locusts. In addition, he authored over 400 technical articles. Kevan served as president, and was named a fellow of the Entomological Society of Canada, as well as receiving many other honors. He also played a key role in initiating the biological survey of insects of Canada. Kevan died in 1991.

References

Vickery VR (1991) Douglas Keith McEwan Kevan. Am Entomol 37:253–254

Vickery VR (1992) Douglas Keith McEwan Kevan (1920–1991). Antenna 16:4–6

Key Factor

The factor most responsible for changes in population trends. In life table studies, key factor analysis is used to identify population regulating mechanisms.

► Life Table

Key Pests

The pests that have the greatest potential to affect the profitability of the crop.

Keystone Species

A species that has a particularly great influence on an ecosystem and, if removed from the system, its loss has a significant effect on the entire ecosystem, especially its other inhabitants.

Khapra Beetle, *Trogoderma granarium* Everts (Coleoptera: Dermestidae)

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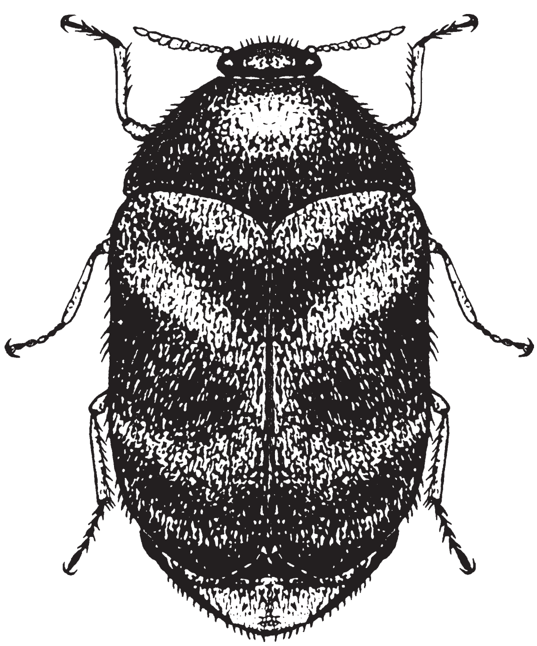
A very serious pest of stored grain, khapra beetle has been the target of many successful eradication efforts in regions of the world where it does not naturally occur. Generally, it thrives in warm dry regions. It is found in northern and central Africa, the Middle East, and east through India to Myanmar. It is generally absent from Europe, though there are a few localized infestations. Presently it is absent from the western hemisphere, Australia, and New Zealand.

The life cycle can be as short as 35 days at about 34°C, but is nearly 150 days long when reared at 10°C. As many as 12 generations are reported annually in India. The adults are short-lived, seldom living more that 10–12 days. Mating occurs immediately at high temperatures but may require several days at cooler temperatures.

After a short pre-oviposition period, females (Fig. 4) deposit up to100 eggs, but mean fecundity is about 35 eggs. The eggs are cylindrical, with one end rather pointed and bearing spine-like projections, but the other end rounded. Normally they measure about 0.7 mm long and 0.25 mm wide. They are translucent white, but yellowish or reddish marks develop on the chorion. The eggs hatch in 3–14 days, depending on temperature.

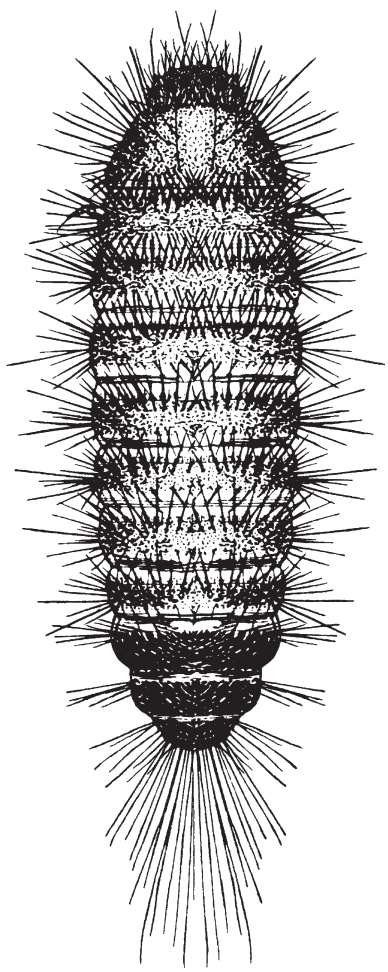
The larvae are yellowish brown or brown, and bear numerous long hairs on the dorsal surface. Younger larvae bear a "brush" of long hair on the ninth abdominal segment that projects like a "tail," and although this look tends to diminish as the larvae grow older, the tuft of hairs remains prominent. The larval period can be completed in 15 days, but when faced with starvation the larvae can persist for 13 months, and with limited food can survive for up to six years! Males typically undergo four instars, females five, though this varies considerably. Larvae attain a length of about 5 mm. Young larvae feed on cracked grain kernels as such food is not protected



Khapra Beetle, *Trogoderma granarium* Everts (Coleoptera: Dermestidae), Figure 4 **Adult Khapra beetle, *Trogoderma granarium*.**

by a seed coat, but larger larvae attack the intact kernel. Larvae (Fig. 5) are usually found feeding on the surface of infested material, but can penetrate several centimeters in search of food. Cast skins also are commonly found on the surface of grain containing infestations. Some larvae are able to undergo diapause when exposed to unfavorable temperature, humidity and crowding, but others lack the capacity for diapause.

When they are ready to pupate, larvae crawl into crevices. Pupation occurs within the last larval exuvium, and typically lasts 3–5 days. Pupae measure about 5 mm long, and are light brown, and bear a medial ridge of long hairs dorsally.



Khapra Beetle, *Trogoderma granarium* Everts (Coleoptera: Dermestidae), Figure 5 **Larva of Khapra beetle, *Trogoderma granarium*.**

The emerging adults are small, only 1.8–3.8 mm long. They are oblong-oval in shape, and females are larger than males. They are yellowish brown to reddish brown, with the pronotum usually darker than the elytra, and indistinct reddish brown marks on the elytra. The males are distinguished from other male *Trogoderma* by an antennal club of five or fewer segments; females by an antennal club of three or fewer segments. The adults can produce eggs without having to drink or eat after emerging. Adults reportedly do not fly.

Several natural enemies are known, including predatory Hemiptera and mites, parasitic wasps, and diseases. Biological suppression is not practiced.

Damage

This species attacks such vital staples as wheat, barley, rice, millet, sesame, corn (maize), sorghum, and peanut. Feeding reduces grain to a powdery mass, reducing weight and grade of the grain. The larvae chew through grain sacks as well, weakening the fibers and resulting in tears. They are favored by hot, dry conditions and cannot compete with other species under moist conditions.

Management

Hygiene is an important element of management, and it is useful to remove old grain, avoid spillage, and fill cracks and crevices. Treatment of grain storage facilities with residual contact insecticides deters infestation, and fumigants are used to disinfest grain. The diapausing larvae are fairly resistant to fumigants, so protracted fumigation is advised. On-farm grain storage in India often used neem seed powder mixed in with the grain. Heat treatment also can be effective. Traps for detecting infestation use both food and sex pheromones as bait.

► Stored Grain and Flour Insects

References

Banks HJ (1977) Distribution and establishment of *Trogoderma granarium* Everts (Coleoptera: Dermestidae): climatic and other influences. J Stored Prod Res 13:183–202

CABI and EPPO (1997) *Trogoderma graminarium*. In: Quarantine pests for Europe, 2nd edn. CABI International, Wallingford, UK, pp 554–559

Hadaway AB (1956) The biology of the dermestid beetles *Trogoderma granarium* Everts and *Trogoderma versicolor* Creutz. Bull Entomol Res 46:781–796

Kiesenwetter, Ernst August Hellmuth Von

The noted Saxon entomologist E. A. H. von Kiesenwetter was born at Dresden, Germany, on November 5, 1820. He studied law at the University of Leipzig until 1843, and rose to prominence in the Ministry of the Interior. He began taking collecting trips, and publishing entomological articles, in the 1840s. Though known principally as a coleopterist, Kiesenwetter also published on other orders. His principal contribution, other than the numerous papers he authored, was to author much of the Coleoptera section of the "Naturgeschichte der Insecten Deutschlands." He died on March 18, 1880, at Dresden, Germany.

References

Anon (1880) Obituaries, E. A. Hellmuth von Kiesenwetter. Entomol Mon Mag 16:280

Herman LH (2001) Kiesenwetter, Ernst August Hellmuth von. Bull Am Mus Nat Hist 265:85–86

King Crickets and Wetas

A family of crickets (Anostostomatidae) in the order Orthoptera.

► Grasshoppers, Katydids and Crickets
► Weta

Kinnaridae

A family of insects in the superfamily Fulgoroidae (order Hemiptera). They sometimes are called planthoppers.

► Bugs

Kin Selection

A theory put forth by W. D. Hamilton (1964) that states that an altruistic act by close relatives is favored because it increases the inclusive fitness of the individual performing the social act. Inclusive fitness is the fitness of the individual as well as his effects on the fitness of any genetically related neighbors. The theory is that alleles change in frequency in a population due to the effects on the reproduction of relatives of the individual in which the trait is expressed rather than on the reproductive success of the individual. A mutation that affects the behavior of a sterile worker bee, even though detrimental to her, could increase the fitness of the worker if her behavior increased the likelihood that a close relative would reproduce. Kin selection could explain the evolution of sociality, which appears to have developed as many as eleven times in the order Hymenoptera.

Kinesis (pl., kineses)

A class of orientation behavior characterized by undirected movements in which the frequency of turning (klinokinesis) or speed of movement (orthokinesis) is related to the intensity of the stimulation. A change in the rate of movement in response to an environmental condition, with the direction of the movement random and unrelated to the stimulus. Often, if conditions are favorable, organisms remain quiescent, moving to another location if conditions are not favorable. Types of kineses include: chemokinesis, stereokinesis, photokinesis, and hygrokinesis (contrast with taxis).

Kirby, William

William Kirby was born in September 1759 at Witnesham Hall, Suffolk, England. Kirby is known as the "father of British entomology." He was educated for the clergy, and graduated from Caius College, Cambridge, in 1781. Kirby successfully conducted his ministry, but also studied insects. His first publication was a monograph on British bees, published in 1802. He also established the Order Strepsiptera. He was a fellow and honorary member of numerous scientific societies. Kirby met William Spence when he was 48 years old, and co-authored, with Spence, the first popular entomology work on insects published in English: "An introduction to entomology," which was published in four volumes between 1816 and 1826. It remained the most important work on insects published in English for over 100 years, and was published in seven editions. The significance of his work is easy to underestimate because we now take for granted that entomology is a legitimate pursuit, whereas until Kirby and Smith authored their book, the common notion was that anyone interested in insects was not entirely sane. He died at Barham, near Ipswich, England, on July 4, 1850.

References

Essig EO (1931) A history of entomology. The Macmillan Company, New York, NY, 1029 pp
Morris FJA (1915) The centenary of Kirby and Spence's "An introduction to entomology." Can Entomol 47:384–386

Kissing Bugs (Hemiptera: Reduviidae: Triatominae)

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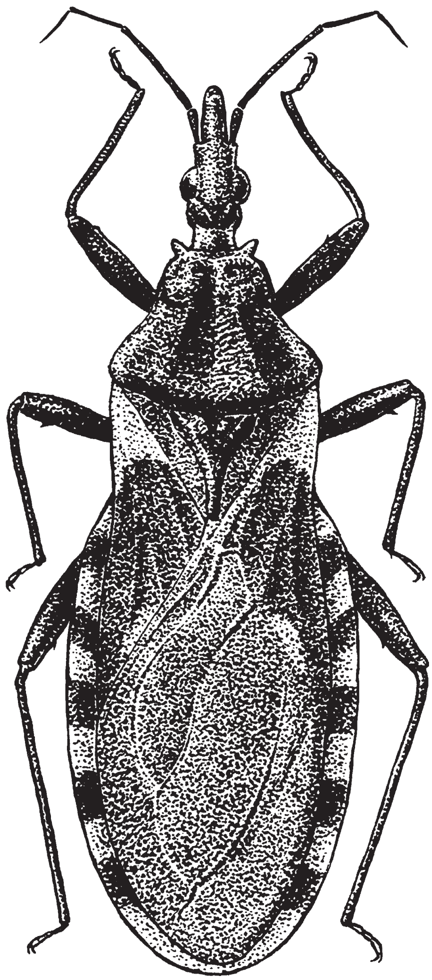
Kissing bugs of this subfamily are also known as conenoses, Mexican bed bug (Fig. 6), barbeiro, chipo, vichua, pito and other names in Latin America. The head of triatomine bugs is more or less cone-shaped, the sturdy proboscis can be thrust forward or repose beneath the head, and the prothorax is well developed. The antennae are four or five-segmented. They fly readily. These insects are obligate blood feeders. Many species are vectors of the trypanosome *Trypanosoma cruzi*, the etiologic agent of Chagas disease, or American trypanosomiasis. Kissing bugs become infective by imbibing blood from an infected vertebrate host. The parasite develops in the gut of the triatomine and the infective trypomastigotes pass out in the feces. When the infective feces are rubbed into the bite site, skin, or mucous membranes, transmission occurs. Another mode of transmission is through blood transfusion. In vertebrates other than humans, infection may occur by ingestion of the infected bug. The bite of kissing bugs is often painless, a useful adaptation for feeding on vertebrates, but some are capable of inflicting a painful bite. Humans vary in their sensitivity to bites. Some bitten individuals are hypersensitive and may suffer an anaphylactic reaction. Kissing bugs are chiefly nocturnal, and on humans they prefer to feed on exposed skin, such as the face, particularly the upper lip, arms and legs.

Many species of kissing bugs transmit *Trypanosoma cruzi*, but *Triatoma infestans* (Klug), *T. maculata* (Erichson), *T. dimidiata* (Latreille), *Panstongylus megisus* (Burmeister) and *Rhodnius prolixus* (Stål) are common vectors. Humans suffering from infection often exhibit a swelling of the eyelid and face, a symptom known as "the sign of Romaña." Infection can last many years, and affect the heart.

Some species principally inhabit the soil surface, though others frequent trees or other habitats. Natural hosts are generally woodrats or other animals; humans are accidental. The woodrat builds nest of available plant materials, and these nests are favored by triatomes. Kissing bugs will also feed on domestic pets and wild animals that may occur near human habitation.

The development of the kissing bug requires five to eight nymphal instars, which may last



Kissing Bugs (Hemiptera: Reduviidae: Triatominae), Figure 6 **A representative kissing bug, *Triatoma sanguisuga* (LeConte), also known as the "Mexican bed bug."**

from three months to a few years. The length of the nymphal instars depends upon the quantity of the blood meals. The nymphs and adults require blood meals usually of vertebrate animals. The amount of blood ingested varies from approximately 6 mg to over 275 mg. Females are ready to mate shortly after the final molt. The female may oviposit 1–3 weeks after copulation. There is considerable variation in the number of eggs deposited. The eggs are shiny and smooth. Eggs, which are often barrel-shaped, may possess a fringed cap. They are deposited singly or in small clusters, and deposited in the same habitats as occupied by adults. The eggs hatch in 8–30 days.

In addition to transmission of Chagas disease, bugs can also cause anaphylactic reactions. Hypersensitivity follows repeated bites. Patients develop nausea and diarrhea, welts and rashes, edema, and itching.

► Chagas Disease or American Trypanosomiasis
► Assassin Bugs
► Kissing Bugs and Others (Hempitera: Reduviidae)
► Chagas
► Carlos Justiniano Ribeiro

References

Ryckman RE (1979) Host reactions to bug bites (Hemiptera, Homoptera): a literature review and annotated bibliography, pt 1. Calif Vector Views 26:1–24

Ryckman RE, Bentley DG (1979) Host reactions to bug bites (Hemiptera, Homoptera): a literature review and annotated bibliography, pt 2. Calif Vector Views 26:25–49

Ryckman RE, Casdin MA (1976) The Triatominae of western North America, a checklist and bibliography. Calif Vector Views 23:35–52

Tonn RJ (1988) Review of recent publications on the ecology, biology and control of vectors of Chagas' Disease. Revista Argentina de Microbiologia 20:4–24

Usinger RL (1944) The Triatominae of North and Central America and the West Indies and their public health significance. Public Health Bull 288:1–81

Klee, Waldemar

G. Waldemar Klee was born in 1853 in Copenhagen, Denmark. He was educated in agriculture in Denmark, but moved to the USA at the age of 19 and worked for the University of California. For many years he studied the biology and management of fruit pests, and was appointed Inspector of Fruit Pests by the California State Board of Horticulture in 1886. Klee received parasitoids of cottony cushion scale from Australia and liberated them in San Mateo County in 1888, initiating the first biological control effort directed at this serious pest. He died in 1891 in Santa Cruz, California, USA.

Reference

Essig EO 1931. A history of entomology. The Macmillan Company, New York, NY, 1029 pp

Knipling, Edward Fred

Edward Knipling was born at Port Lavaca, Texas, USA on March 20, 1909. He graduated from Texas A&M University (B.S. 1930) and Iowa State University (Ph.D. 1947) before joining the United States Department of Agriculture for a 43-year career with that agency. He led the Orlando, Florida, laboratory that developed DDT and other insecticides and repellents to protect American troops during World War II from disease- spreading insects. He also led the Insects Affecting Livestock, Man, Households, and Stored Products Division in Washington, DC, and led the Entomology Division. Knipling is credited with developing the sterile insect technique, and also the use of mathematical models for pest suppression based on the sterile insect technique. This technique has been used successfully to eradicate screwworm fly, Mediterranean fruit fly, tsetse fly, melon fly, and other pests throughout the world. He published over 225 technical articles during his career, including an insightful but oft-overlooked book "Principles of insect parasitism analyzed from new perspectives: practical implications for regulating insect populations by biological means" (1992). He was a member of the prestigious National Academy of Sciences and received numerous honors and awards. He died on March 17, 2000 in Arlington, Virginia.

► Sterile Insect Technique

Reference

Suszikiw J (2000) Edward F. Knipling. Am Entomol 46:269–270

Knockdown

Incapacitation of an insect following exposure to a sublethal dose. Following such exposure, insects may recover due to metabolic detoxification of the pesticide, or perish. In assessing the response of insects to insecticides, knockdown is usually assessed separately (at about 1 h post-treatment) from mortality (often at 24 h post-treatment).

Koch's Postulates

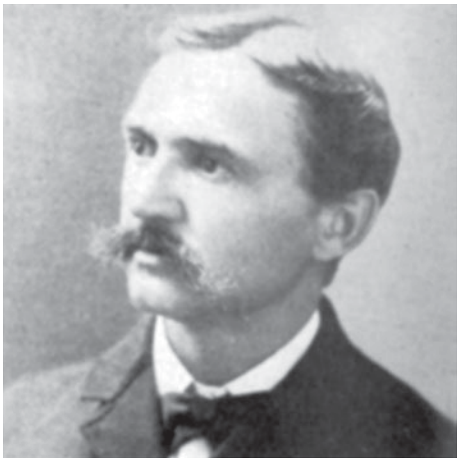
Criteria proposed by Koch that are commonly used for establishing the pathogenicity of a microorganism: the microorganism must by consistently associated with the disease; the microorganism can be isolated and grown in culture; and when the microorganism is injected into a healthy host, disease is expressed.

Koinobiont

Parasitoids that do not immediately impair their hosts upon oviposition, and host development continues. These are typically endoparasitoids.

Koebele, Albert

Albert Koebele was born in 1852 at Waldkirch, Germany. When he moved to the United States is not certain, but he became a citizen in 1880. His abilities so impressed C. V. Riley that Riley appointed him to the US Department of Agriculture in 1881 and assigned him to work on cotton pests in Florida and Georgia. In 1885 he transferred to California to work on fruit pests. He was sent to Australia in 1888, where he sent a parasitic fly, *Cryptochetum iceryae* (Williston), and a ladybird beetle, *Rodolia cardinalis* (Mulsant), to California. The ladybeetle was a very successful biological control agent, gaining him recognition for saving the citrus industry from cottony cushion scale. On a later trip to the region he also traveled to New Zealand where he introduced some ladybirds from California into New Zealand, and several additional ladybirds into California. His success earned him the ire of some collaborators who were jealous of his recognition, and he resigned from USDA in 1893 to (Fig. 7) join the Hawaii Board of Agriculture and Forestry. There, he continued introductions from Southeast Asia, Australia, Japan, and Mexico. In 1903 he joined the staff of the Experiment Station of the Hawaiian Sugar Planters Association. Koebele suffered from illness (probably malaria) contracted while living in the tropics, and he returned to Germany in 1908 to recuperate. During World War I he suffered considerable hardship and attempts were made to move him back to California. However, Koebele never regained his health, despite his move to Germany, and he was found to be too feeble to be transported. He died in Waldkirch, Germany, his home town, on December 28, 1924.



Koebele, Albert, Figure 7 **Albert Koebele.**

References

Essig EO (1931) A history of entomology. The Macmillan Company, New York, NY, 1,029 pp

Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, USA, 549 pp

Kraatz, Ernst Gustav

Ernst Kraatz was born in Berlin, Germany, on March 13, 1831. He began collecting insects at an early age, and published his first paper at the age of 18. From 1850 to 1853 Kraatz studied law at the Universities of Heidelberg and Bonn, but had no real interest in this field, so he moved to the University of Berlin and obtained a Ph.D. in 1856. He was active in German entomological societies, and founded the Deutsche Entomologische Gesellschaft, and served as its president for 25 years. He also was the primary force behind establishment of the Deutsche Entomologisches Nationalmuseum. Kraatz was a very prominent coleopterist, and published nearly 1400 papers. He described hundreds of species. Late in life he lost his eyesight. Kraatz died in Berlin on November 2, 1909.

Reference

Herman LH (2001) Kraatz, Ernst Gustav. Bull Am Mus Nat Hist 265:90–92

Kring, James Burton

Jim Kring was born on May 25, 1921, at Monett, Missouri. He graduated from Rockhurst College and received both the M.S. and Ph.D. degrees from Kansas State University. After serving in the military during World War II, Kring became an instructor at Kansas State, then moved to the Connecticut Agricultural Experiment Station, where he worked from 1951 to 1977. In 1977, he became head of the

Department of Entomology at the University of Massachusetts, and later acting Dean of the College of Food and Natural Resources. He retired in 1981 and moved to Florida, but continued to conduct research in conjunction with the University of Florida's Gulf Coast Research and Education Center at Bradenton, Florida. Kring had diverse interests of both basic and applied nature, but he is remembered for his pioneering work in aphid ecology. Kring, along with V. Moericke of Germany and J. S. Kennedy of England, elucidated the changing host selection behaviors of dispersing aphids, namely a positive response to sunlight when dispersing, and a negative response to sunlight and a positive response to plant pigments when alighting. He was the first to demonstrate that aphids could be managed through visual disruption of their host-seeking behavior, which he accomplished by application of reflective mulch to the soil surrounding plants. Subsequently, this practice has been shown to be both effective for reducing aphid and whitefly infestation rates and plant virus infection, and economic for high-value crops such as vegetables. Thus, the practice has been widely adopted in some production areas. An author of over 100 papers, Kring was also very involved in professional society affairs. He served as president of the Connecticut Entomological Society, the president of the eastern branch of the Entomological Society of America, and president of the Entomological Society of America. He received several other honors from this society. He died at Anna Maria, Florida, on October 29, 1990.

Reference

Cardé R, Prokopy R, Doane C (1991) James B. Kring. Am Entomol 37:59

K-Strategists

Species with life history characteristics making them well suited for population stability and stable environments ("K" is an expression of carrying capacity of the environment). K-selected species represent an extreme on a continuum of life history characteristics, with r-selected species at the other end of the continuum. K-selected species can also be said to conform to the "competitive strategy" (Table 1).

Kyasanur Forest Disease

This tick-borne virus disease is found in southern Asia.

► Ticks

K-Strategists, Table 1 **A comparison of the characteristics of r-selected and K-selected species**

	r-selected	K-selected
Habitat type	Unstable, not permanent	More stable
Reproduction	Rapid under favorable conditions; many offspring produced	Usually slower; fewer offspring produced
Development	Rapid; often multivoltine	Slower; often univoltine
Mortality	Often density independent and catastrophic	Often density dependent and more gradual
Population size	Extremely variable in time	Less variable in time
Dispersal capacity & mode	High and random	Lower and oriented
Brood care	Absent	Sometimes present
Body size	Often quite small	Often larger
Competition	Variable, but often low	Often very keen
Ultimate effect	High productivity	Efficient use of resources

L

Labellum

The mouth of certain Diptera, consisting of a ridged lip at the end of the proboscis. This term also is used to describe the extension of the labrum covering the base of the rostrum in Coleoptera and Hemiptera, and a lobe at the apex of the glossa in honey bees.

► Mouthparts of Hexapods

Labial Glands

Glands opening at the base of the labium that secrete saliva to aid digestion. Sometimes they also produce silk.

Labial Palpi

Short (one- to four-segmented) sensory appendages on the insect labium.

► Mouthparts of Hexapods

Labiduridae

A family of earwigs (order Dermaptera). They sometimes are called striped earwigs.

► Earwigs

Labiidae

A family of earwigs (order Dermaptera). They sometimes are called little earwigs.

► Earwigs

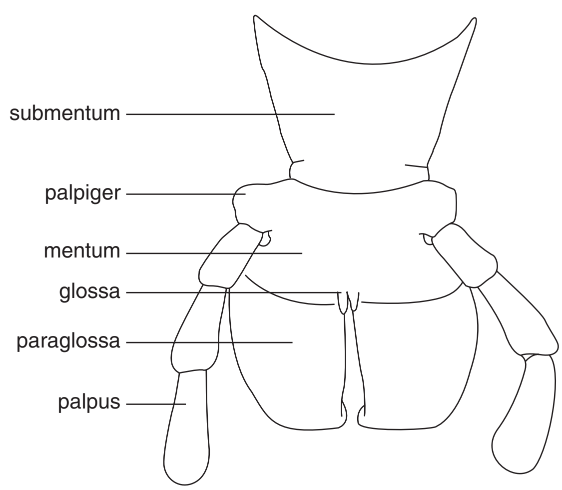
Labium

A structure that forms the floor of the mouth. The lower lip (Fig. 1).

► Mouthparts of Hexapods

Laboubeniales

The Laboubeniomycetes (Ascomycota) contains the order Laboubeniales with the greatest number of ectoparasitic species (more than 1,300). However, in some instances, parasitization by selected numbers of the Laboubeniales may result in pathological symptoms in host insects. These fungi most commonly infect Coleoptera but can be



Labium, Figure 1 **External aspect of the labium in an adult grasshopper, showing some major elements.**

found among other insect orders, usually on the adult stage, and also in mites and millipedes. They may attack only one sex of an insect and may even be site-specific, developing only on certain areas of the cuticle. Their association with arthropod hosts is obligate (essential) for completion of a life cycle.

The Laboubeniales may appear as hair-like structures on the cuticle surface. Careful examination of these structures reveals a thallus, consisting of a receptacle and its appendages. The thallus, as recently described for *Hesperomyces virescens*, arises from ascospores that contact and attach to the host (ladybird beetle) cuticle. The receptacle is attached to the host cuticle by a basal cell called the foot. Antheridia (male gametangia) arising from the receptacle produce non-motile spermatia. Trichogynes (the female receptive hyphae) are borne on young perithecia also located on receptacles. There are no known anamorphs so that infection and thallus development on the cuticle must originate from the sexually produced ascospores. In a few cases, haustoria may grow from the foot and penetrate the cuticle and the underlying hemocoel, as reported for *H. virescens*, to obtain nutrients. Narrow branches of these invasive haustoria (rhizomycelia) may destroy fat body and muscle, thus causing symptoms of severe disease. Premature death may result or basic functions such as egg production and feeding may be affected.

References

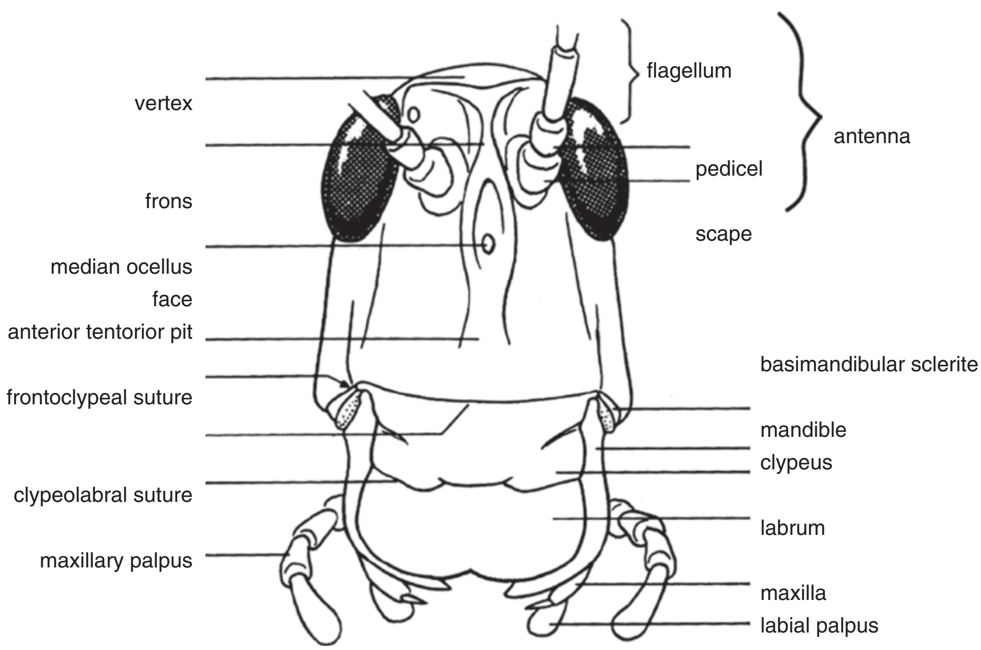
Tavares II (1979) The laboubeniales and their arthropod hosts. In: Batra LR (ed) Insect-fungus symbiosis: nutrition, mutualism, and commensalism. Allanheld, Osmum, Montclair, NJ, pp 229–258

Weir A, Beakes GW (1996) Correlative light- and scanning electron microscope studies on the developmental morphology of *Hesperomyces virescens*. Mycologia 88:677–693

Labrum

A structure that forms the roof of the mouth. The upper lip (Fig. 2).

► Mouthparts of Hexapods



Labrum, Figure 2 **Front view of the head of an adult grasshopper, showing some major elements.**

Lace Bugs (Hemiptera: Tingidae)

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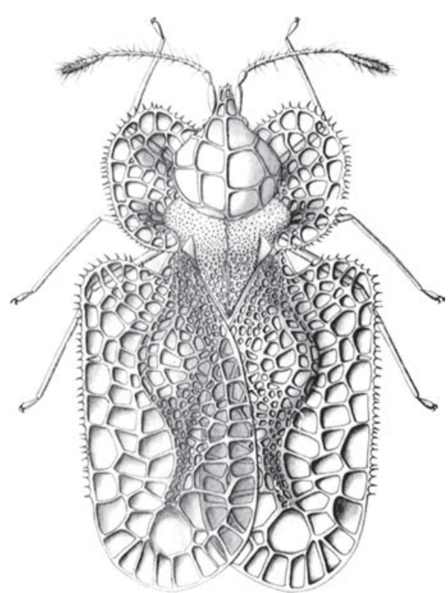
Tingids are commonly called lace bugs because the pronotum and forewings have delicate and intricate reticulations resembling lace. Lace bugs can be confused with the Piesmatidae or ash-gray lace bugs, which also have forewings that are somewhat lace-like or reticulated. However, the lack of ocelli in the Tingidae distinguishes them from the Piesmatidae. All tingids are phytophagous and generally are host specific. Some species can be very destructive to plants, some of economic importance.

The Tingidae are distributed worldwide. The family is comprised of approximately 2,000 species placed in three subfamilies. The Cantacaderinae occur mainly in the Southern Hemisphere, the Tinginae are represented throughout the tropical and temperate zones, and the Vianaidinae are a small Neotropical group. The Tinginae comprise the majority of the lace bugs within the family, including some 220 genera out of approximately 250 genera. The higher level classification is:

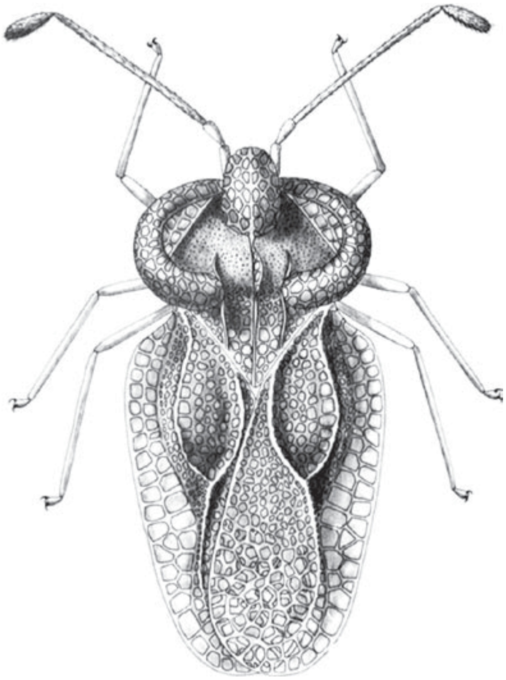
Order: Hemiptera
- Suborder: Heteroptera
  - Superfamily: Tingoidea
    - Family: Tingidae
      - Subfamily: Cantacaderinae
      - Subfamily: Tinginae
      - Subfamily: Vianaidinae

Diagnosis

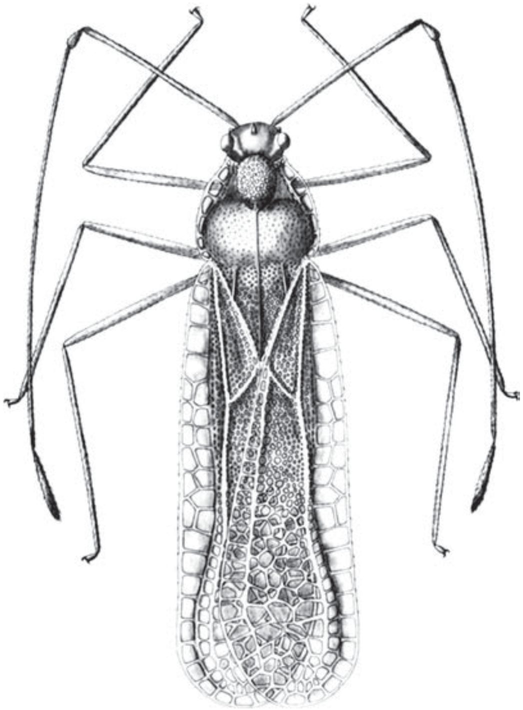
Tingids are very small insects, approximately 2–10 mm in length. Their coloration is generally cryptic, ranging from white or yellowish to brown and black. Their general appearance is somewhat flattened dorso-ventrally, and it can vary from quadrate or broadly oval to narrow and slender. Dorsally, they look like fancy lace, the pronotum and forewings having a network of multiple cells or areolae (Figs. 3–7). Many species have very wide wings and their head can be concealed or partially obscured under a hood-like projection from the pronotum. Many others have very narrow wings and very small pronotal hoods or no hoods at all. The pronotum can have extremely diverse structures, from low carinae to globose hoods, bump-like projections, and foliaceous overgrowths. Lace bugs have no ocelli. The antennae are four- segmented, with the third antennomere being the longest. The head can possess spine-like, finger-like, or tubercle-like projections, or it can be completely devoid of such projections. The hemelytra, which are the first pair of wings, are translucent or transparent in many species. Some species have brachypterous forms, meaning that the wings are reduced in some degree, sometimes exposing one or two posterior abdominal segments. The rostrum or beak is elongate with four segments. In repose, it rests in a rostral groove, which has margins that are delimited by foliaceous and areolate carinae. Their legs are generally thin and elongate with the tarsi divided to form two tarsomeres.



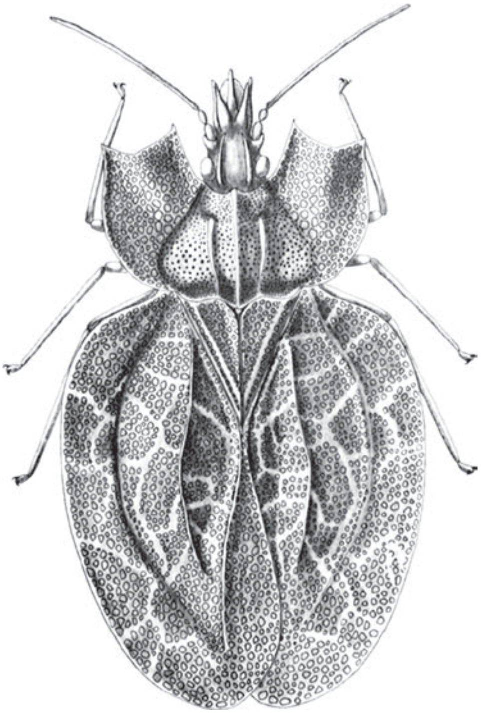
Lace Bugs (Hemiptera: Tingidae), Figure 3
***Corythucha* sp. lace bug.**



Lace Bugs (Hemiptera: Tingidae), Figure 4
***Calotingis* sp. lace bug.**



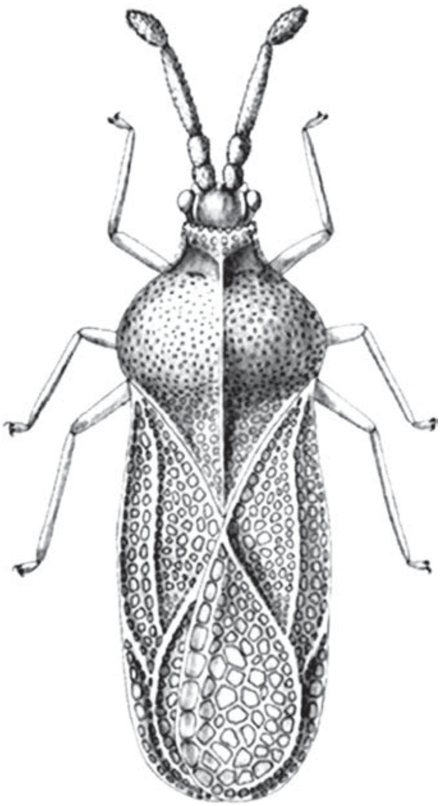
Lace Bugs (Hemiptera: Tingidae), Figure 6
***Macrotingis* sp. lace bug.**



Lace Bugs (Hemiptera: Tingidae), Figure 5
***Phatnoma* sp. lace bug.**

Biology

Most species of lace bugs live on the underside of leaves, but a few can live on the upper and lower parts of stems (*Melanorhopala froeschneri* Henry and Wheeler, *Physatocheila plexa* (Say)) or even on the upper parts of roots (*Coleopterodes*). Species of two Old World genera, *Copium* and *Paracopium* are gall-makers on the flowers of their host plants. Adults and nymphs alike feed on the sap of the host plant by piercing the epidermis. Although each tingid species is usually somewhat host specific, lace bugs collectively feed on a diverse array of plants. They complete their whole life cycle on the same host plant species and on the same part of the plant. Most species of lace bugs are gregarious, and some have shown parental care. Tingids generally have one or two generations a year, although some species have multiple generations. Most species of lace bugs over-winter



Lace Bugs (Hemiptera: Tingidae), Figure 7
***Leptoypha* sp. lace bug.**

as adults, but a few over-winter as eggs (*Stephanitis*) and some as nymphs (*Acalypta*). Lace bugs can lay their eggs deeply into the plant tissues or set them on the abaxial surface of a leaf. They are hemimetabolous or, in other words, have incomplete metamorphosis, in which the immature stages (nymphs) are similar to the adult stage, with the exception of smaller size and the absence of fully developed wings and genitalia. Wings appear as small pads in the second or third instar (nymphal stage) and increase in size with each moult. Most species have five instars before reaching the adult stage, although a few species have four instars (for example, *Stephanitis rhododendri* Horvath). The nymphs' general appearance can be flat with a great number of needle-like spines covering the dorsal surface, or it can be smooth. In some species, the spines seem to produce secretions that afford protection against predators.

Economic importance

Although not all tingid species are of economic importance, some are serious pests. Lace bugs are capable of causing great damage to their host plants during seasonal outbreaks. The piercing of the plant's epidermis can cause extensive tissue damage that diminishes photosynthesis. As a result, especially when high numbers of nymphs and adults are present, chlorosis (yellowing of the plant parts) occurs due to chlorophyll reduction, and as a consequence, the plant loses vigor.

A good number of tingids are common pests of forest trees, agricultural crops, fruit trees, and ornamentals. Some examples are as follows: *Gargaphia tiliae* (Walsh), the basswood lace bug, is a common pest of *Tilia americana* L., a forest and ornamental tree in North America; *Corythucha gossypii* (Fabricius), the cotton lace bug, is an important pest of beans and cotton from the southern United States to northern South America; *C. cydoniae* (Fitch), the hawthorn lace bug, attacks many species of wild and ornamental woody rosaceous plants in North America; *C. mcelfreshi* Drake, the peach lace bug, causes constant defoliation which greatly affects fruit production in some areas of Mexico; *C. ciliata* (Say), the sycamore lace bug, is a very common lace bug that feeds on *Platanus occidentalis* L., the common sycamore tree in North America, and on its ornamental hybrid *P.* x *acerifolia* Ait., the London plane tree; *Stephanitis pyri* (Fabricius), a polyphagous pest in Europe and the Middle East, feeds primarily on a variety of trees and shrubs, including rose, elm, oak, poplar, cherry, etc.; *Habrochila ghesquierei* Schouteden is an important pest of coffee from eastern Africa; and *Stephanitis pyrioides* (Scott), the azalea lace bug, probably a native of Japan, has become an important pest of ornamental azaleas almost anywhere azaleas are grown.

Some species of lace bugs have been considered for the biological control of noxious weeds. The lantana lace bug, *Teleonemia scrupulosa* Stål, feeds on the invasive weed *Lantana* spp. *Oncochila simplex* (Herrich-Schaeffer) is a possible control for leafy spurge *(Euphorbia* spp.) in the U.S.A. *Dictyla* *echii* (Schrank) has been considered for the control of viper's bugloss, *Echium plantagineum* L., an invasive weed of pastures.

► Bugs (Hemiptera)

References

Blatchley WS (1926) Heteroptera or true bugs of eastern North America, with especial references to the faunas of Indiana and Florida. Nature Publishing Co, Indianapolis, IN, 1116 pp

Drake CJ, Davis NT (1960) The morphology, phylogeny, and higher classification of the family Tingidae, including the description of a new genus and species of the subfamily Vianaidinae (Hemiptera: Heteroptera). Entomol Am 39 (ns):1–100

Drake CJ, Ruhoff FA (1965) Lacebugs of the world: a catalog (Hemiptera: Tingidae). U.S. National Museum Bulletin 243, 634 pp

Schaefer CW, Panizzi AR (2000) Heteroptera of economic importance. CRC Press, Boca Raton, FL, 828 pp

Schuh RT, Slater JA (1995) True bugs of the world (Hemiptera: Heteroptera): classification and natural history. Comstock Publishing Associates, A division of Cornell University Press, Ithaca, NY, 336 pp

Slater JA, Baranowsky RM (1978) How to know the true bugs (Hemiptera: Heteroptera). Pictured Key Nature Series. Wm. C. Brown Co. Publishers, Dubuque, Iowa, 256 pp

Lacewings, Antlions and Mantispids (Neuroptera)

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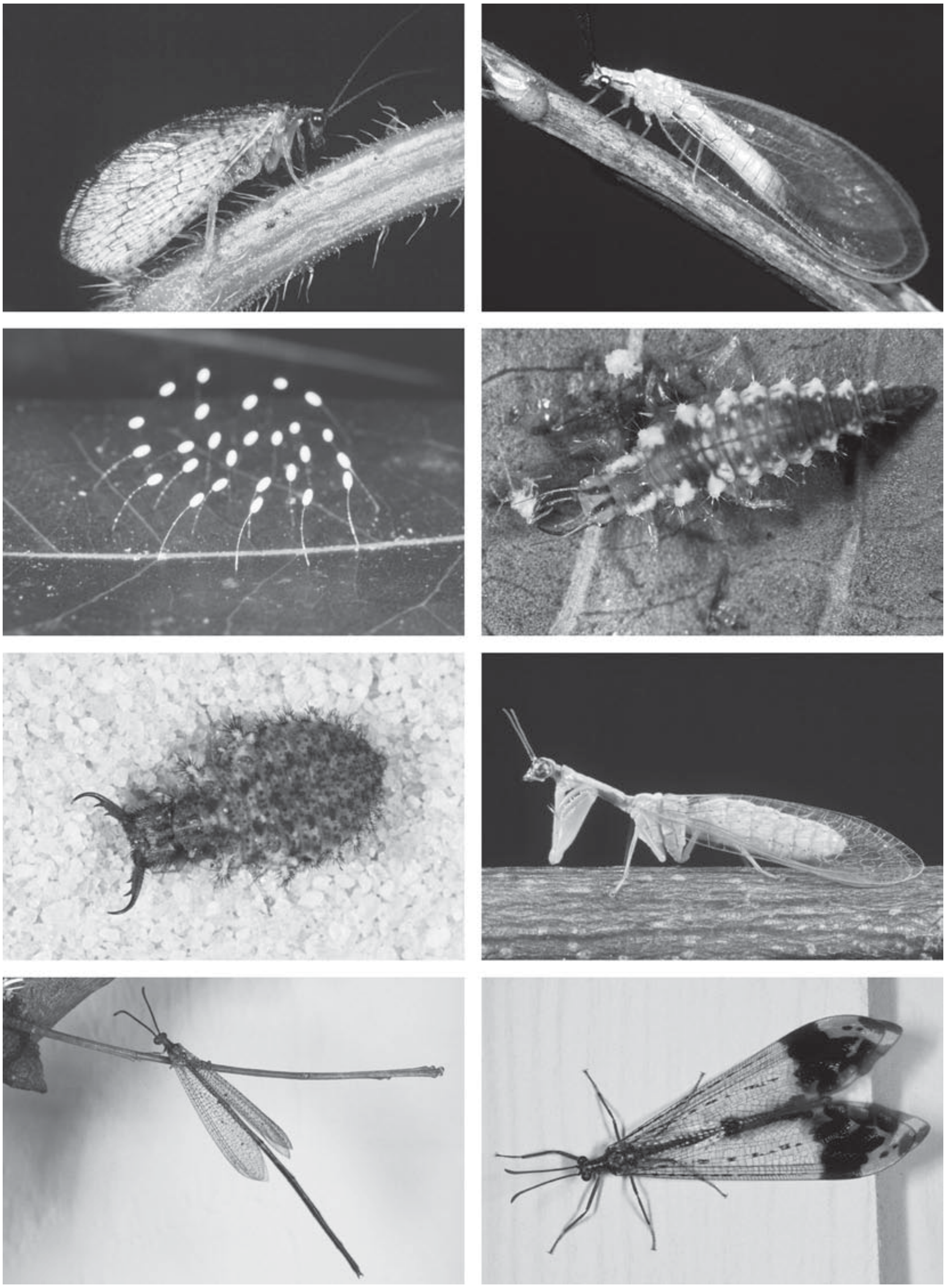
This is the largest order of the Neuropterida which also includes snakeflies, alderflies and dobsonflies and contains about 5,000 described species. Until the recent split of the order Neuroptera into three orders, the true Neuroptera were also called Planipennia. Seventeen extant families are recognized which include minute insects with a forewing length of about 2 mm (Coniopterygidae) to very large insects with forewing lengths of 70 mm or more (Myrmeleontidae). Most species are moderate-sized insects. They are holometabolous insects in which the families have been grouped by the shape of the larval mandibles. They are short and stout in Ithonidae and Polystoechoetidae (which have subterranean larvae), elongate but straight in the Osmylidae, Sisyridae, Nevrorthidae, Dilaridae, Berothidae and Mantispidae, curved without teeth in the Chrysopidae, Nemopteridae and Hemerobiidae and curved with teeth in the Psychopsidae, Nymphidae, Nemopteridae, Ascalaphidae and Myrmeleontidae. The mandibles of the Coniopterygidae appear to be highly modified which contributes to their phylogenetic isolation from other families. The adults are conservative morphologically with chewing mouthparts, five segmented tarsi and two pairs of wings which have dissimilar venation. Venation is usually dense (Fig. 8) and complete but can be very reduced, especially in small species. The larvae are unique in that the mandible is grooved to receive part of the modified maxilla to form a sucking "jaw." Also, the digestive tube is strange in that the midgut does not empty into the hindgut until the adult emerges from the pupa and deposits a meconium pellet. This is made easier by the fact that food is always taken in liquid form as the larva injects digestive enzymes into the prey to liquefy the tissue. However, they can pass urine. The Malpighian tubules (usually eight in number) are adapted to produce silk which is manipulated by the anal spinneret to construct the silken cocoon. The carnivorous larvae are terrestrial except for the aquatic Sisyridae and some Osmylidae.

The Neuroptera were clearly distinct by the Permian, with extant families (Chrysopidae, Coniopterygidae, Nymphidae, Psychopsidae) present in the Triassac Period. Schlüter (1986) recognized an additional 14 families existing in the Mesozoic Era which are now extinct. Although the primitive Neuroptera flourished during the Mesozoic Era, they now appear to be dying out with many families represented by only a few species. Polystoechotidae are now restricted to the Western Hemisphere and are represented by only four species in three genera. The Neurorthidae with about 10 species is



Lacewings, Antlions and Mantispids (Neuroptera), Figure 8 **Some common Neuropterans: *top left*, brown lacewing (Hemerobiidae); *top right*, green lacewing (Chrysopidae); *second row left*, eggs of green lacewings; *second row right*, larva of green lacewing; *third row left*, antlion larva (Myrmeleontidae); *third row right*, mantispid (Mantispidae); *bottom left and right*, antlion adults (upper photos by Jim Castner, lower photos by Lyle Buss).**

found only in the Old World, the Rapismatidae with 16 species limited to the Oriental Region, the Nymphidae with about 25 species restricted to Australia and New Guinea and the Ithonidae with about 17 species limited to Australia and North America. The Nemopteridae and Osmylidae are now absent from North America but both families are represented in the Florissant shales of Colorado (Miocene). The other 10 families have representatives on all continents but even the most speciose families, Chrysopidae and Myrmeleontidae, have only about 1,700 species each.

- Coniopterygoidea
  - Coniopterygidae
- Ithonoidea
  - Ithonidae
  - Rapismatidae
  - Polystoechotidae
- Osmyloidea
  - Dilaridae
  - Neurorthidae
  - Osmylidae
  - Sisyridae
- Mantispoidea
  - Berothidae
  - Mantispidae
- Hemerobioidea
  - Chrysopidae
  - Hemerobiidae
- Myrmeleontoidea
  - Ascalaphidae
  - Myrmeleontidae
  - Nemopteridae
  - Nymphidae
  - Psychopsidae

The family Coniopterygidae contains the pygmies of the order with the forewing length ranging between 2 and 6 mm and are called dusty wings. Although considered rare for many years because of their size, they often are among the most abundant Neuroptera in many habitats, living on trees and shrubs although the aberrant Brucheiserinae evidently live under stones. The body, wings, and legs often are coated with white or grey wax secreted by hypodermal glands. The antenna has 15–62 segments with the flagellar segments moniliform, often with scale-like hairs in distinct whorls in the males. The wings are held roof-like over the body. The hindwing usually is smaller than the forewing, sometimes greatly reduced, and the venation is highly reduced. There are never more than two basal costal crossveins, the forewing Sc is forked distally and the posterior branch resembles the distal part of R1; radial sector separating from R1 near middle of wing, often forked and the posterior branch sometimes resembling the distal part of medial vein. The tarsus is distinctive in the order although similar to those of the Sialidae in having the fourth segment modified (flattened and bilobed). The abdomen lacks the spiracle on the eighth segment which is apomorphic and distinctive among the Neuroptera. The genera usually are separated by wing venation, whereas examination of the male genitalia usually is required to identify the species. The larvae are active predators, often feeding on mites, but they also feed on other small, soft-bodied insects in their environment. They have a large head but the mouthparts are mostly concealed and consist of a short labial palpus with the apical segment expanded, short, straight and pointed styles. The eyes consist of 4–5 stemmata. There are about 490 described species in about 30 genera in three subfamilies and is the fourth most speciose family in the order. The aberrant Brucheiseridae are found in arid areas of Argentina and Chile and consist only of the genus *Brucheiser* with several species. These apparently are flightless insects with highly sclerotized, reticulate wing venation. Their biology is unknown. The Aleuropteryginae is mostly cosmopolitan although the genera are not. They possess peculiar and unique structures on the abdomen called plicaturae. These are paired organs which are strongly folded and placed on an oblong, somewhat membranous area. Their function is unknown. Also, the wing venation differs from the other subfamilies in having two radio-medial crossveins in the middle of the wing. The larvae have the mouthparts projecting from beneath the labrum and the antenna is about as long as the labial palpus. There are about 14 genera classified in three tribes. The most common are *Aleuropteryx* (Holarctic), *Neoconis* (Neotropics) and *Spiloconis* (Australia). The Coniopteryginae have two speciose, cosmopolitan genera, *Coniopteryx* Curtis and *Semidalis* Enderlein (except Australia). The members of this subfamily lack plicaturae and have only one radio-medial crossvein. Often the males have scale-like setae on the antennae and a few species have a hook on the frons. This subfamily is the most commonly collected and of great biological control interest since many species live on economic crops such as citrus. The vast majority of coniopterygids fly at dawn or dusk, fluttering slowly between plants where they lay eggs. Many species are specific to certain types of plants like junipers.

The family Ithonidae is similar in appearance to the Rapismatidae but are whitish to brownish in coloration and commonly live in arid regions. They hold their wings relatively flat over the back which is unusual in the order and resemble dull hepialid moths both in appearance and in flight, which has led to the common name "moth lacewings" for this family. The forewing ranges from about 15 to 30 mm. Three monotypic genera occur in the southwestern United States (*Oliarces* Banks), in Mexico (*Narodona* Navás) and in Honduras (*Adamsiana* Penny). Elsewhere, they are found only in Australia (about 24 species in *Ithone* Newman, *Megalithone* Riek and *Varnia* Walker). Ngymata (slightly domed, bare areas on the wing) are found in this family and are of unknown function; similar structures are found in other families of Neuroptera, as well as Trichoptera, Megaloptera and Mecoptera. Claims have been made that the subterranean larvae are predacious on Scarabaeidae grubs but this has not been clearly established. Some species of ithonids (*Ithone*, *Megalithone* and *Oliarces*) have been observed swarming in vast numbers for short periods of time. In most cases, the swarming sites have been detected first by the presence of many frenzied birds which have a feast when these fat, hapless insects are swarming. The adults can run fairly quickly and lay their eggs in the sand by means of a "sand plough."

The family Polystoechotidae is another family of robust sized insects and superficially similar to the Ithonidae and Rapismatidae. The forewing ranges from 15 to 40 mm. There are only four species known in three genera. The genus *Polystoechotes* Burmeister has one species in Chile and another in North America. The genus *Platystoechotes* Carpenter is limited to the Sierra Nevada of California and Oregon where it may be associated with *Libocedrus* (incense cedar). The third genus, *Fontecilla* Navás, lives in arid zones in central Chile. Little is known of the biology of this family although the larva has been described. They are subterranean but claims that they feed on plant roots are unsubstantiated. *Polystoechotes punctatus* (F.) was once commonly distributed through the northern half of the United States. The reason why this species is now restricted to the southwestern United States south to Central America is unknown. Apparently this species is attracted to smoke and all the species are attracted to light.

The family Rapismatidae is found in the Oriental region. These large, sturdy lacewings with complex venation are usually greenish to yellowish in coloration and live in mountainous areas. The forewing ranges from about 20 to 36 mm. There are about 20 species, all in the genus *Raspisma* McLachlan. These insects are relatively rare in collections and little is known about their biology.

The family Osmylidae is a relatively large family of lacewings with about 170 species in about 20 genera. The classification is suspect with eight subfamilies recognized based on simplistic wing venational characters. They are found on most continents except North America. The species are moderate sized insects (forewing 15–30 mm long). Nearly all the species have three ocelli and usually two wing nygmata (sometimes faint) which helps define the family. Also, there is a small stylus at the end of gonapophyses laterales of the female. Most of the species have semi-aquatic larvae which have the jaws elongate and straight or slightly curved. The larvae have long legs and lack gills. The Porisminae is composed of one very brightly colored species from southeastern Australia. Apparently the larvae live under bark of

Eucalyptus. The adults are distinguished by having numerous subcostal crossveins. The Kempyninae contains some of the largest species and is found in southern temperate South America, New Zealand and Australia. The Spilosmylinae is the largest and most diverse group found only in the Old World. Many species have an embossed forewing spot on the posterior margin. *Spilosmylus* has 35 species known from New Guinea. The Stenosmylinae is another disjunct group with species in South America and Australia. The Osmylinae is a Palaearctic subfamily with one well known species in Western Europe. The Protosmylinae (Oriental region), Eidoporisminae (one species from Australia) and the enigmatic Gumillinae (two anomalous species with long antennae from Mexico but are probably Mexican Chrysopidae) complete the survey of this family.

The family Dilaridae consists of small delicate lacewings (forewing length 4–15 mm) and are easily distinguished in the male by the plumose antenna and in the female by the well developed ovipositor. The known larvae are elongate and live in burrows in wood, probably feeding on beetle larvae. There are 67 described species in two subfamilies which are nearly exclusive geographically. The Dilarinae are found only in the Old World (except Australia), and the Nallachiinae are found only in the New World except for recently discovered species in South Africa and India.

The family Sisyridae is a small family with about 30 species in four genera. *Sisyra* Burmeister is cosmopolitan and the large genus *Climacia* McLachlan is found only in the Western Hemisphere. Two other genera exist but are of doubtful validity and with few species in the Old World. These are small insects (forewing length 4–10 mm). The female has the terminalia elongated into an ovipositor like structure. The wings have relatively few crossveins and there are small thickenings (trichosors) on the posterior margin of the distal half of the wings. They are most easily confused with the Hemerobiidae. The larvae are aquatic and feed on freshwater sponges and probably Bryozoa. The larval jaws are the longest in the order, apparently adapted for sucking out the contents of sponges. They are called Spongilla-flies for this reason. They are the only truly aquatic insects in the order with the larvae bearing external gills in the second and third instars. The larvae leave the water to pupate, usually constructing a distinctive double cocoon with a mesh-like covering. The adults are predacious on insect eggs and small insects.

The family Neurorthidae used to be included in the Sisyridae until the terrestrial larvae were discovered and found to be greatly different morphologically. This small family of delicate lacewings (forewing length 6–10 mm) consists of only 10 species found in Europe and North Africa (*Neurorthus*), Asia (*Nipponeurothus*) and Australia (*Austroneurothus*). There is some data suggesting that this family is not closely related to other families of the order.

The family Berothidae, or beaded lacewings, is another family (about 110 species) of small (forewing length 6–15 mm), delicate lacewings occurring on all continents (except Antarctica). Many species have falcate wings and some species have scale-like setae on the wings and sometimes on the body (*Lomamyia* Banks). There are trichosors present on the wing margins. The family is difficult to define and usually keys out at the end of the family key on venational characters. There are four distinct subfamilies. The Rhachiberothinae are found only in southern Africa and have the forelegs raptorial. There are two genera. The Cyrenoberothinae contains one monotypic genus from Chile (*Cyrenoberotha* Adams and MacLeod) and one monotypic genus from southern Africa (*Manselliberotha* Aspöck and Aspöck). Nothing is known of their biology. The adults have the face elongated below the eyes. The Nosybinae contains but one genus, *Nosybus* Navás, known only from Africa. The wings are rounded and have small venational differences from the Berothinae. The Berothinae is the largest subfamily with about 24 genera in all continents. The life cycle of the North American genus, *Lomamyia* Banks, has been described. The larvae live in termite burrows. In one species the first instar waves its abdomen at a termite releasing an "allomone" which paralyzes the termite in a few minutes. Later instars can produce enough gas to immobilize up to six termites per shot.

The family Mantispidae, containing about 350 described species, are easily recognized by having raptorial forelegs and thus can be confused only with the subfamily Rhachiberothinae of the Berothidae in the Neuroptera. The larvae are hypermetamorphic, being very active triungulins in the first instar, and becoming inactive scarabaeiform larvae in subsequent instars. Adults of the same species can vary greatly in size since most species are parasitic on spiders. The forewing can vary between 5 and 30 mm. The pronotum is sometimes many times longer than wide and, in contrast to the snakeflies, the legs originate near the anterior margin. There are four subfamilies. The Drepanicinae is found in Chile and Australia and contains the largest species of the family, *Drepanicus gayi*, from Chile which is green and somewhat leaf-like. The genera *Ditaxis* McLachlan and *Theristria* Gerstaecker are found only in Australia; the latter is the most diverse mantispid genus in Australia. The biology of this subfamily is unknown. The Calomantispinae is a small subfamily with only two genera, *Nolima* Navás (North America) and *Calomantispa* Banks (Australia). The larvae of *Nolima* may be generalist predators. The Symphrasinae is a New World subfamily containing three genera, *Anchieta* Navás, *Plega* Navás, and *Trichoscelia* Westwood. The latter genus has been reared out of larval cells of *Polybia* (Vespidae). The larvae of *Plega* appear to be generalist predators with prey records including the pupae of Noctuidae and Scarabaeidae and the cells of a leaf-cutting bee (*Megachile*). Many of the species of Anchieta resemble bees. This subfamily has a well developed ovipositor and possess other characters which isolate it especially from the largest subfamily, Mantispinae. All of the Mantispidae are "parasites" of spider egg sacs. The triungulins either board the female spider until she makes her egg sac or directly searches for the egg sac without phoretic behavior. This varies between species. Some species of Mantispinae resemble vespoid wasps such as *Cimaciella* Enderlein in North America and *Euclimacia* Enderlein in the Oriental region. These mantispids show considerable variation in color pattern throughout their ranges probably in relation to the variation of the wasp models. Adults are active predators and usually are found in trees and shrubs. They are attracted to light. The genus *Mantispa* Illiger was once thought to be widespread but apparently is paraphyletic and absent in the New World and Australia. The present number of genera is about 30 but some other genera appear to be undescribed (Fig. 8).

The Chrysopidae is probably the largest family of the Neuroptera with more than 1,300 described species in 75 genera and three extant subfamilies. Although called green lacewings, there are many species which are brownish in coloration, especially species that rest on rocks during the day. Also, the greenish color of museum specimens often fades in a few years. The adults lack microtrichia on the wing membrane found in most families of Neuroptera. Nearly all the species possess a tympanal organ on the ventral base of the radial vein. One function of this auditory organ is to detect bat echo-locating sounds, that once identified, will signal the adults to fold their wings and drop to the ground. This family contains the most significant biological control agents in the order, and species of *Chrysoperla* Steinmann are sold worldwide for biological control. The larvae are active predators living on plants and feed on diverse, soft-bodied insects, especially aphids. The most plesiomorphic subfamily appears to be the Nothochrysinae with about 20 species in seven genera found in Australia (*Dictyochrysa* Esben-Petersen, *Triplochrysa* Kimmins), Europe (*Hypochrysa* Hagen, *Nothochrysa* McLachlan), Africa (*Kimochrysa* Tjeder, *Pamochrysa* Tjeder), and North America (*Nothochrysa* McLachlan, *Pimachrysa* Adams). These are mostly robust and moderate sized insects, often dark brown in color and lack the tympanal organ. They seem to live in forests of ancient trees (such as Gymnosperms). The Apochrysopinae contain the giants of the family (forewing length 18–34 mm) and represent a small group with about 25 species in 12 genera. Like the Nothochrysopinae, the genera are limited in distribution such as to Australia (two genera), South America (four genera), Africa (two genera) and Asia (four genera). They appear to prefer the dark areas of dense forests. The Chrysopinae are by far the largest subfamily with more than a 1,000 species in nearly 70 genera. Many genera are now cosmopolitan partly because species of *Chrysopa* Leach, *Ceraeochrysa* Adams, and *Chrysoperla* Steinmann have been released and established in diverse regions of the world. The adults of some of these genera (i.e., *Chrysoperla*) feed on honeydew and employ extracellular symbiotic yeasts to aid in digestion. Many genera (i.e., *Ceraeochrysa*, *Leucochrysa* McLachlan) have trash bearing larvae. Special species communication occurs in the family. Some adults (i.e., *Chrysoperla*) move the abdomen rapidly, transmitting by way of the legs to the substrate a vibration (tremulation), and in the genus *Meleoma* Fitch stridulation is accomplished by moving the hind femur against abdominal sternites. The larvae have long, strong, curved mandibles (no teeth) similar to those of the Hemerobiidae and can be distinguished by the presence of the trumpet like empodium between the tarsal claws. Nearly all species lay their eggs on stalks, either separate stalks or stalks stuck together at the base, which may help to keep emerging larvae from eating each other.

The Hemerobiidae consists of about 500 species in 28 genera and 10 subfamilies. Nearly all species are yellow to dark brown in color but there are a few green species. The species can be distinguished from those of other families by the presence of at least two apparent radial sectors except for the monotypic genus *Adelphohemerobius* Oswald from Chile. The family appears most closely related to the Chrysopidae but differs notably from that family in possessing microtrichia on the wing membrane. Many species are relatively small (forewing length 4–10 mm) but a few species attain 18 mm in wing length. The biology of the family seems similar among the different genera and are similar to those of the Chrysopidae. Larvae of Hemerobiidae lack the trumpet-shaped empodium in instars 2 and 3 but have similar shaped "jaws" which are curved and without teeth. This family is important in biological control with most of the larvae being active predators on mostly soft bodied insects and mites on plants. Several genera are cosmopolitan or very widespread (i.e., *Hemerobius* L, *Micromus* Rambur, *Notiobiella* Banks, *Sympherobius* Banks, *Wesmaelius* Krüger) whereas most are restricted to one biogeographical realm (eight genera restricted to South America; five genera to Australia). This family demonstrates an unusual amount of wing reduction with flightless species of *Micromus* in Hawaii and of *Conchopterella* on the Juan Fernandez Islands. *Psectra diptera* Burmeister has forms with only one pair of functional wings.

The Psychopsidae, or "silky lacewings" contains 26 species in five genera and two subfamilies. The Zygophlebiinae is restricted to southern Africa and contains three genera (*Silveira* Navás, *Cabralis* Navás and *Zygophlebius* Navás). *Balmes* Navás (Oriental region) and *Psychopsis* Handlirsch (Australian) belong to the Psychopsinae. These are moderately large lacewings with broad wings and dense venation (forewing length 10–35 mm). Biology and larval stages are poorly known. *Cabralis gloriosus* Navás is a mostly white species which flutters around in fairly dense and spiny vegetation. *Silveira* contains four relatively small species living mostly in arid zones.

The Nymphidae are found only in Australia and New Guinea. There are about 25 species in eight genera. The Myiodactylinae contain very broad winged lacewings which lack tibial spurs whereas the Nymphinae contains more narrow winged lacewings with short tibial spurs; *Nymphes myrmeleonoides* Leach resembles some antlions and owlflies in overall appearance but have filamentous antennae. The larvae have strongly curved mandibles, usually with one tooth. There are two types of larvae known. Those of the Myiodactylinae (*Myiodactylus* Brauer; *Osmylops* Banks) are strongly flattened and presumably relatively immobile as in most Ascalaphidae. The larvae of *Nymphes* are more antlion-like, being narrower and searching for prey among litter and vegetation.

The Myrmeleontidae currently have the most described species (about 1,700) in the order with 188 extant genera, 15 tribes and three subfamilies. They are found on all continents but are most abundant in xeric areas since the larvae live in sand or loose soil. The adults are small to large (forewing 10–75 mm) with characteristic wing venation with an elongate cell under the stigma, and the male of many groups has a special gland at the base of the forewing ("pilula axillaris"). Antlions are closely related to the Ascalaphidae but lack the elongate, clubbed antennae of that family The larvae are distinguished from other Neuroptera larvae in having the hind tarsal claws much larger than those of the other legs which is an adaptation for burrowing. Studies have shown that the larvae have preferred habitats and some live under the protection of rock overhangs or in tree holes or animal burrows, but the majority live in open sand. Some prefer coarser sand than others, and members of the tribe Myrmeleontini construct pitfall traps, whereas most others do not. Exceptions occur in the Brachynemurini (i.e., *Scotoleon pallidus*), Nesoleontini (*Cueta* Navás) and Myrmecaelurini (*Isoleon* Esben-Petersen; *Myrmecaelurus* Costa); these larvae construct a double structured pitfall trap (funnel shaped pitfall below which is a tubular extension) in hard pan soils. Members of *Callistoleon* Banks (Myrmeleontini) have side furrows to the pitfall trap. There are three extant subfamilies. Palparinae contains the giants of the family with the fore wing length reaching 75 mm. All live in the Old World (except Australia) except for a small group (Dimarini) in South America. One member of the Dimarini, *Millerleon pretiosus* Banks, has larvae that live in extreme desert conditions and can survive in the larval stage for more than 5 years and can exist many months without feeding. The palparine larvae have enlarged setae distally called fossoria which enable the bulky larvae to dig more efficiently. They have been observed to capture ground resting grasshoppers. The Stilbopteryginae is a small subfamily of large antlions with short, knobbed antennae (similar to *Albardia* of the Ascalaphidae) restricted to Australia (two genera). The Myrmeleontinae contains more than 90% of the genera and species in about eight tribes. The Nemoleontini is the largest tribe, found on all continents, and most genera have similar biologies. However, a few genera (i.e., *Navasoleon* Banks) have larvae that live on bare rock surfaces. These larvae can remain motionless for weeks. Species of *Gatzara* of the tribe Dendroleontini, also live on bare rock surface and cover themselves with green lichens for camouflage. Most known larvae of the Dendroleontini have a debris carrying bunch of setae on the metascutum which apparently lures prey. All larvae of the tribe Myrmeleontini and a few genera of the tribe Acanthaclisini move only backwards. Perhaps the most striking species of antlion, *Pseudimares iris* Kimmins of the monospecific tribe Pseudimarini is large, with a large eyespot on the hindwing and has been collected only twice from southern Iran. All the larvae and nearly all the adults are predacious on other insects. A few adults apparently feed on pollen. Most adults are nocturnal but there are a few day-flying species, such as the butterfly-like species of *Pamexis* Hagen from South Africa and *Maracandula* Currie from Mexico.

The owlflies, or Ascalaphidae, contain mostly fast flying insects that resemble dragonflies. Adults are moderate to large in size (forewing length 15–60 mm), robust and usually very pilose with huge compound eyes which suggested the common name. There are about 500 species in about 80 genera and three subfamilies on all continents (except Antarctica). They are mostly crepuscular aerial predators and sometimes swarm in flight. Nearly all species have elongate antennae which are clubbed somewhat like butterflies except for the monotypic subfamily Albardiinae with short antennae that exists in Brazil. The Ascalaphinae is the largest group and is unique in having the eyes divided by a transverse sulcus. This subfamily contains the day-flying and colorful *Libelloides* Schäffer of Europe. The females of the most common New World genus of this subfamily, *Ululodes* Hagen, lay sterile eggs (repagula) coated with ant repellent material at least on the basal side of a string of eggs for protection. The third subfamily, Haplogleniinae, is worldwide. The males of some species of this subfamily (i.e., *Haploglenius*) have an apparent startle display in which a hinged flap covering the pronotum is suddenly lifted to expose a contrasting cream or white patch. The taxonomy of this family is difficult and the only worldwide treatment is by Van der Weele (1908), but much general information is found in Tjeder (1992).

The Nemopteridae are among the most distinctive looking of the Neuroptera with the hindwings often extremely narrowed. The larvae have strongly curved mandibles but lack teeth. The Crocinae have the hindwing threadlike whereas the Nemopterinae have the hindwing broadened distally. The head is often greatly prolonged ventrally similar to the Mecoptera and is a modification for feeding in flowers. The family is found in most continents except in North America. Most species are nocturnal but some are diurnal and very colorful, such as in the genus *Nemoptera* Latreille found in Europe. The Crocinae are mostly nocturnal with species usually very limited in distribution and are often in xeric areas. They flutter around at night and are attracted to white flowers. The crocine larva often has the prothorax greatly lengthened and are among the only Neuroptera to live peacefully together in groups of 30 or more, often in sand and small rocks under rock overhangs. These alert larvae have been seen to escape predators (and a shovel) en masse like a herd. The larvae of Nemopterinae appear more diverse and usually burrow into the sand head first in contrast to the antlions. Some genera (i.e., *Stenorrhachus* McLachlan) have larvae that live relatively deep under the sand and lack ocelli. In that genus, the females are wingless. *Palmipenna* Tjeder contains day-flying species in which the hindwing is greatly broadened, evidently reducing attacks by robber flies.

References

Brooks SJ, Barnard PC (1990) The green lacewings of the world: a generic review (Neuroptera: Chrysopidae). Bulletin of the British Museum of Natural History (Entomology) 59:117–286

Meinander M (1972) A revision of the family Coniopterygidae (Planipennia). Acta Zoologica Fennica 136:1–357

New TR (1989) Planipennia/lacewings. In: Handbuch der zoologie 4. Gruyter, Berlin, Germany, pp 1–129

Oswald JD (1993) Phylogeny, taxonomy and biogeography of extant silky lacewings (Insecta: Neuroptera: Psychopsidae). Mem Am Entomol Soc 40:1–65

Tjeder B (1992) The ascalaphidae of the afrotropical region (Neuroptera). Entomol Scand (Suppl) 41:3–169

Van der Weele HW (1908) Ascalaphiden. Collections zoologiques du baron edm. De Selys Longchamps. Catalogue systematique et Descriptif. Fascicle:1–326

Lachesillidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice and Psocids

Lacinia

(pl., laciniae) The inner lobe of the maxilla. It is modified in various ways, and in some flies it forms a flat, blade-like structure for piercing.

► Mouthparts of Hexapods

Lackey Moths

Some members of the family Lasiocampidae (order Lepidoptera).

► Lappet Moths
► Butterflies and Moths

Lacquers and Dyes From Insects

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The use of wild organisms as sources of decorative and protective substances has ancient origins, with recorded instances dating as far back as 6,000 years ago in the use of indigo dyes from plants (*Indigofera tinctoria*, Leguminosae) in

China, or pre-Columbian use of scale-insect lacquer (*Llaveia axin,* Margarodidae) in the Mayan civilization of Mesoamerica. While this article deals primarily with insects, it is important to note that natural lacquers, dyes and various types of varnishes have been obtained from a broad range of organisms. Molluscs, for instance, are the ancient source of royal purple dye (from whelks, *Murex brandaris*, Muricidae) and the indelible sepia-brown ink obtained from cephalopods (octopuses, squid, etc.) in the genus *Sepia*. This substance is so durable that extracts from fossil cuttlefish have yielded perfectly viable ink. Plants are the most diverse source of dyes, and also provide raw material for the famous lacquer art of the Orient, which uses sap from a relative of sumac trees (*Toxicodendron verniciflua*, Anacardiaceae).

In the insect world, only a few species, concentrated in the superfamily Coccoidea (Hemiptera) or scale insects, historically have been the source of pigments and artistic and protective finishes. This does not include the use of butterfly wings as decorative materials, or metallic flies, wasps and beetles as ornaments (either dead or as living jewels tethered to a lapel!). Such decorative value stems from structural characteristics in the wing scales or the cuticle which cause various reflection patterns of light, distinct from internal chemical pigments used for dyes.

This article deals primarily with pigments and finishes derived from insects, but other sources are mentioned insofar as they are used together, or for the sake of comparing key characteristics. Basic physical and chemical characteristics of dyes and lacquers are discussed in order to provide working definitions and basic concepts.

Some Basic Terminology of Dyes and Finishes

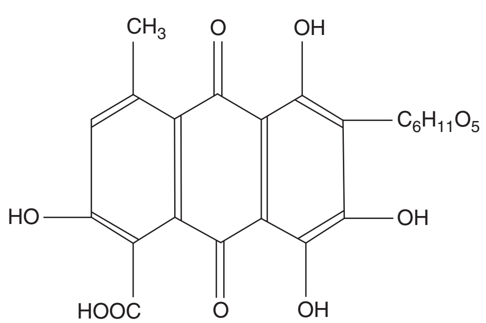
The terms dye and pigment are often used interchangeably, though traditionally dyes were considered of plant origin while pigments were derived from minerals, earths and ground rocks. Usually, a dye is made up of pigments in solution (often in water) which binds to a substrate, such as cloth or leather, in such a way that the color change in the substrate is permanent and difficult to remove. The chemistry of dyeing is still not completely known, though the presence and arrangement of double bonds, C=C, C=O, C=N, and N=N in the dye molecules are important in the production of color. For example, the pigment in cochineal insects, carminic acid, results from the condensation of three benzene rings and contains several such double bonds. To improve the fastness of the dye, substances called mordants are added to the dye and are known to form chemical bridges between the substrate and the pigment, which remain stable after the solvent has evaporated. Salts of various metals are common mordants.

Varnishes and lacquers are also terms used without clear distinctions for liquids or pastes which dry to form durable, protective and decorative semitransparent films when applied to various substrates. A useful distinction is that varnishes produce the desired finish with as little as a single coat, while lacquers are the result of many, sometimes hundreds, of thin coats applied over time to produce the final finish. The process by which the substance converts from a paste or liquid to a dry film also varies, and can include simple evaporation of a solvent, the chemical linking of repeating units into polymers or a combination of the two. Both varnish and plant-derived lacquer consist of resins mixed with essential oils (volatile and fragrant), but varnishes are artificial mixtures while lacquer comes from naturally existing combinations.

Resins are substances found as natural polymers, usually dissolved in ethanol for application, and include the sap of *Toxicodendron verniciflua* used for oriental lacquer, shellac from Indian lac insects (*Kerria lacca*, Kerriidae) as well as many other plant products like water-absorbing gums. Waxes and drying oils are a final group of substances used in producing lacquer finishes, resulting from the presence of reactive double bonds which take up oxygen when exposed to air, and which form extensive polymers linked through the oxygen atoms between the original chains of fatty acids. Linseed oil is a well-known drying oil, which produces a simple but not highly durable finish on furniture, for example.

Production and Use of Insect Dyes and Lacquers

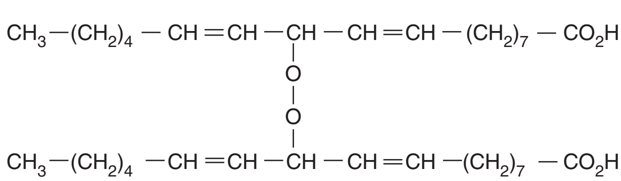
Probably the best known colorant from insects is cochineal dye (Figs. 9 and 10), obtained from the body contents of cochineal scales, *Dactylopius coccus* (Dactylopiidae) which yields a bright red color used in textiles, food, drugs, etc. Pre-Columbian Maya and Aztec cultures used the dye for wood, feathers, cloth and as writing ink for codices. The vermilion pigment is concentrated in the female fat body and is thought to repel ants and parasites. Like all scale insects, cochineal exhibits dramatic sexual dimorphism, with wingless females developing through several nymphal instars on the prickly-pear cactus host plants (*Opuntia* spp.).



Lacquers and Dyes From Insects, Figure 9
Structure of carminic acid, an anthraquinone dye obtained from cochineal insects (*Dactylopius coccus*).

They are readily recognized on *Opuntia* by the stringy white wax masses they produce. The males, which are indistinguishable from females in the early instars, form pseudopupae and emerge as two-winged adults resembling small flies.

The adult females are brushed off the cactus pads, dried and then stored, traded or processed to obtain pure dye. The crimson color is obtained by "reconstituting" the dry bodies (known as "grana" in Spanish) in boiling water to extract the pigment, then precipitating, filtering and drying to a powder. Cultivated from Mexico to Peru by indigenous cultures since before the Spanish conquest, these insects are generally considered native to Mexico and Central America. However, some evidence suggests that they originated in South America and were then traded northward. The cochineal insects found in Mexico and Central America show a long history of domestication and dependence on human protection, along with propagation of the host plants, while production of dye in Peru by ancient Quechua Indians was based on wild *Dactylopius*. Cochineal first became a product for export to Spain and other parts of Europe in the sixteenth century (Table 1). Initially, this new dye was rejected by the traditional textile industry which used a different insect, Mediterranean-grown *Kermes* spp., as a source of dye. But the intense red quality and relative cost advantages of cochineal soon served to expand its market, rendering it an extremely important product in the Spanish colonial economy of the eighteenth and nineteenth centuries. This was particularly so for Central America, which did not enjoy the great wealth of precious metals found in South America or Mexico but was richly endowed in biological resources. The other great agricultural export of



Lacquers and Dyes From Insects, Figure 10 **Formation of a lacquer polymer by uptake of oxygen at double-bond sites, crosslinking individual fatty acid chains through a peroxide bridge.**

Lacquers and Dyes From Insects, Table 1 Characteristics of some natural dyes and lacquers from insects, plants and molluscs

Common/ scientific name	Product obtained	Chemical nature	Sites and history of production
Cochineal insect (*Dactylopius coccus;* Hemiptera: Coccoidea: Dactylopiidae)	Bright red dye from dried bodies of adult females	Applied in solution (often water) to impart permanent color by binding to cloth, leather, wood, etc. To become fast, most dyes require the use of a chemical which binds the due to the substrate, called a mordant. Tannins from insect-induced oak galls are a mordant used since antiquity. Salts of several metals, since as tin, aluminum, iron and chromium, are also well known mordants	Pre-Columbian Central America, major export to Europe between sixteenth and nineteenth centuries, renewed value today as natural dyestuff
Kermes insect *(Kermes illcis* and *K. vermillo;* Hemiptera: Coccoidea: Kermesidae)	Bright red dye, carmine, from dried bodies of adult females		Mediterranean region, the medieval standard red due since 1700 B.C., displaced by cochineal beginning in the sixteenth century
Indigo plant *(Indigofera tinctoria, I. suffruticosa, I. guatimalensis, I. thibaudiana*; Fabaceae)	Blue indigo dye from leaves and stems, obtained by fermentation, then drying to a powder; oxidation in contact with air produces indigotin, the blue color.		Originally from India, *I. tinctoria* was traded widely as of 450 B.C. *I. suffruticosa* and others in genus became a major export from colonial Central America; displaced by cochineal in nineteenth century
Mediterranean (*Murex brandaris*), Central American and Mexican (*Purpura patula*) mollusc or whelk (Muricidae)	Purple dye from mucous glands, the original "royal" or Tyrian purple of Greek, Roman and Phoenician societies		Costly to produce, "royal purple" was traded in the Mediterranean and associated with high rank and wealth; pre-Columbian use for dying cotton fibers on both coasts of Central America and Mexico
Lac insect (*Kerria lacca*, Hemiptera: Coccoidea: Kerriidae)	Natural shellac secreted as a protective shell by female scales, harvested in flakes from a wide variety of host plants.	Resin flakes commonly dissolved in ethanol. Resins are naturally occurring terpene polymers often in mixtures with essential oils, insoluble in water, contrast with varnishes which are man-made mixtures of resins and boiled oils	Known from India since at least 250 A.D. Non-toxic finish used widely on wood furniture and floors, in pharmaceuticals as a coating for pills, applied as a stiffener for hats, as a glossy coating for candy and fruits, as glue for boding glass and metal, and many other uses

Lacquers and Dyes From Insects, Table 1 Characteristics of some natural dyes and lacquers from insects, plants and molluscs (Continued)

Common/ scientific name	Product obtained	Chemical nature	Sites and history of production
Niij (Guatemala) or Aje (Mexico) insect (*Llaveia axin;* Hemiptera: Coccoidea: Margarodidae)	Lacquer used on gourds, wood, ceramic, leather, from the fat body of the adult females, harvested prior to egg production; used also as skin ointment	The fat, which resembles a soft wax, is a mixture of triacylglycerols and free fatty acids; when rubbed onto the substrate, with various pigments. It polymerizes into a durable and decorative film	Cultivated and traded in pre-Columbian Mexico and Central America; now produced only in Uruapan, Mexico and Rabinal, Guatemala, but offers potential as a natural finish for new markets
Lacquer or "varnish" tree (*Toxicodendron vernicifluum;* Anacardiaceae)	Japanese and Chinese lacquer from a milky tree sap	Natural resin; urushiol is the main component, together with a gum and glycoprotein, which undergo oxidative polimerization; hundreds of coats are often applied to achieve the finished lacquer	Developed in China before the Christian era; perfected by the Japanese during Ming Dynasty (1368–1644 A.D.). Lacquerware was at one time restricted to high classes and production was regulated by the state. Currently produced as fine finish and art form.

the Central American colonies was indigo dye, which had been the mainstay of the local economy during the 17th and 18th centuries. Cochineal production surpassed indigo in the 1800s, but then the advent of synthetic aniline dyes around 1860 caused the virtual demise of both products. Interestingly, this decline indirectly stimulated the development of the budding coffee industry in Guatemala and other countries. Currently, the demand for non-toxic red dyes has created new markets for cochineal. Peru is now the world's main producer, and Mexico and Central America are also returning to an ancient ethnoentomological crop.

With regard to insects used for lacquer, two species are of particular interest: lac insects, *Kerria lacca* (Kerriidae), of Asian origin, and the giant margarodid scale insects, *Llaveia axin* (Margarodidae), native to Mexico and Central America, where they are commonly known as "aje" and "niij," respectively (Table 1). While most scale insects are only a few millimeters in size, adult niij females reach a total body length of 2.5 cm and can weigh over 0.5 g (Figs. 11 and 12). The substances produced by these insects and used for lacquer are entirely different, as shellac from *K. lacca* is an external body secretion which encloses the female insect and her eggs in a resinous mass, whereas niij wax is the internal body fat of the adult females. However, both yield a fine, smooth and durable finish for woodwork, ceramic, metal and many other substrates (Fig. 13).

The production of lac insects is an ancient tradition in India, and consists of harvesting the amber-colored resin secretion and eliminating insect and plant remains from the crude "sticklac" to yield clean flakes of shellac. The host plants of lac insects span a wide range of families, including Anacardiaceae, Dipterocarpaceae, Euphorbiaceae, Leguminosae, Moraceae and several others. The purification process is rather complex, and includes dissolving the raw resin or sticklac in a base, such as sodium hydroxide, and bleaching with sodium hypochlorite. Dilute acid is used to precipitate the

Lacquers and Dyes From Insects, Figure 11 **Sexual dimorphism of scale insects, shown here in niij insects (*Llaveia axin*). Adult females are sac-like and wingless, while males possess a single pair of wings and resemble small flies.**

Lacquers and Dyes From Insects, Figure 12 **Raw body fat from an adult niij female, normally used for egg production; extracted by artisans to yield a fine lacquering substance.**

resin in curds like cottage cheese; these are then dried to form dry flakes which can be stored or dissolved in ethanol for use in finishing wood, etc (Figs. 11–13).

Niij insects, on the other hand, are one of the least known sources of artistic and protective lacquer. Adult females are harvested from the host plants (primarily *Jatropha* spp., Euphorbiaceae;

Lacquers and Dyes From Insects, Figure 13 **Traditional black lacquer on rattles and piggy banks made from gourds and finished with niij wax combined with fine soot, then etched to reveal natural pale gourd color.**

Spondias spp., Anacardiaceae; and *Acacia* spp., Leguminosae), boiled and then mashed through fine cloth to produce a crude aqueous extract. The product used for lacquering is the body fat, which is found as a thick liquid in the living females and accounts for about 30% of total body weight. After prolonged beating of the extract, fat globules separate from the other components and coalesce into bright yellow globs of a soft, paste-like material. These are washed thoroughly with water, shaped into patties or cylinders roughly 0.5 kg in weight and are then ready to use or store. The soft fat, with physical properties similar to cocoa butter, can be rubbed onto a substrate alone or in combination with powdered pigments to produce a permanent film. Traditional uses in Guatemala combine black (fine powdered soot) with red (paste from the seeds of anatto, *Bixa orellana*, Bixaceae) on the surface of gourds. Etching into the finished surface to reveal the pale gourd color then produces many intricate patterns and figures. The fat alone provides a durable, satiny finish on pottery, ceramic, leather and metal and is resistant to abrasion, water and heat. In the Uruapan art of Mexico, various figures are scraped out from the initial lacquer layers on wooden plates or furniture and filled in with a different color to produce highly complex inlays.

Niij fat is solid at ambient temperature which makes it similar to many waxes. Chemically, the fatty acid chains that make up its main tryacylglycerol components contain many reactive double bonds. In contact with air, oxygen is taken up at these sites and forms links to neighboring chains, thus forming a polymer film. In this sense, niij "wax" shares the properties of drying oils, such as linseed oil, with which it can be mixed to extend and dilute the insect fat. Chía oil is another plant-derived lacquering substance used in the Mexican community of Olinalá in combination with various pigments, but without the use of insect products.

Like cochineal, niij insects show an old history of domestication and human protection, which has probably influenced the geographic distribution of the species. Cultivation practices for niij insects involve storing the cottony egg masses in covered gourds during the dry season, which protects them against severe egg predation by coccinellid beetles. With the beginning of the rainy season, newly hatched insects are set out at the base of the host plants to initiate a new generation which feed in dense aggregations (Fig. 14) on the host plants. Traditionally, insect rearing takes place on fence rows rather than dedicated plots of agricultural land. However, the high value of niij "wax" relative to other agricultural products that share its arid tropical habitat provides an opportunity for a novel type of agroforestry production. Like cochineal, niij lacquer has suffered a decline in production (although it was never as important in economic terms), but offers great promise as a decorative and protective finish to substitute synthetic and often toxic industrial products.

Lacquers and Dyes From Insects, Figure 14 Dense population of adult niij females on *Jatropha curcas* host tree. The insects are harvested prior to oviposition in order to extract the body fat.

In conclusion, synthetic products have displaced many of the original uses of natural substances, but the current emphasis on non-toxic finishes and dyes, and the premiums often associated with natural products, are providing opportunities to rediscover and improve the production of insect and plant-based compounds. Not only are these of interest for their particular protective or esthetic qualities, but they can also contribute to biodiversity conservation through agroforestry productions systems in native habitats.

References

Heil C (1995) The pre-Columbian lacquer of West Mexico. Neara J 30:32–39 (includes descriptions of oriental lacquer as well)

Hogue CL (1993) Latin American insects and entomology. University of California Press, Berkeley, CA, 536 pp

Jenkins KD (1970) The fat-yielding coccid, *Llaveia*, a monophlebine of the Margarodidae. Pan-Pac Entomol 46:79–81

Kosztarab M (1987) Everything unique or unusual about scale insects (Homptera: Coccoidea). Bull Entomol Soc Am 33:215–220

Simpson BB, Conner Ogorzaly M (2001) Economic botany, plants in our world, 3rd edn. McGraw-Hill, New York, NY, 529 pp

La Crosse Encephalitis

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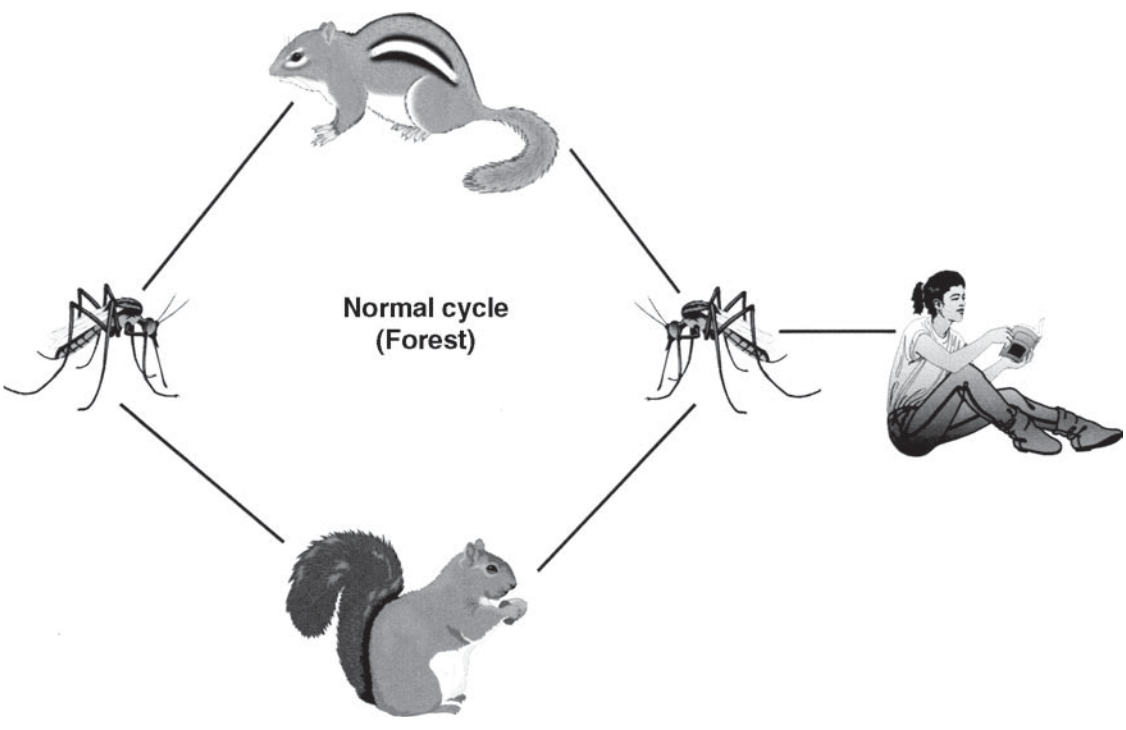
La Crosse encephalitis is a relatively rare viral disease that is spread by infected mosquitoes. The disease affects the central nervous system and can be serious and even lethal in rare instances. It is named for the city of La Crosse, Wisconsin, where it was first identified in 1963. Since then, La Crosse encephalitis has been identified in several Midwestern and Mid-Atlantic states. On average, 73 cases per year are reported to the Centers for Disease Control (CDC), with the majority being from children under 16 years of age. It is suspected that La Crosse encephalitis has a higher incidence and wider distribution in the eastern United States, but is not reported because the virus is often not identified, and because symptoms are often mild and medical attention is not sought.

The La Crosse encephalitis organism is an arbovirus (arthropod borne virus) of the family Bunyaviridae. It is normally cycled between the treehole mosquito *Ochlerotatus triseriatus* and vertebrate hosts (chipmunks and squirrels) in forest habitats throughout the range of the disease. *O. triseriatus* is a daytime biting mosquito that normally inhabits tree holes, but can also develop in other water-holding containers such as discarded tires, cans, etc. Recently, eggs of the Asian tiger mosquito, *Aedes albopictus*, infected with the La Crosse encephalitis virus have been collected in North Carolina and Tennessee. The virus can be maintained during the winter by transmission in mosquito eggs. An infected female lays eggs that carry the virus and eventually develop into infected adults. This process, where the virus is passed from mother to offspring, is called transovarial transmission.

The Virus Transmission Cycle

In a normal cycle, the virus is transmitted to the vertebrate host through the bite of an infected mosquito (Fig. 15). In the host, the virus replicates and increases in abundance rapidly (a process known as amplification). When sufficiently abundant, the virus can then be passed on to other mosquitoes when they feed on the infected vertebrate host. Infected chipmunks and squirrels do not show signs or symptoms of disease. Although not part of the normal cycle of the disease, humans can also contract the disease by the bite of an infected mosquito. However, humans are "dead end hosts," meaning that an infected human cannot transmit the virus to uninfected mosquitoes because sufficient amplification of the virus does not occur in humans.



La Crosse Encephalitis, Figure 15 **Transmission cycle of La Crosse encephalitis.**

Additionally, the virus is not transmitted from human to human.

Symptomology and Treatment

As the name implies, the disease can cause inflammation of the brain which interferes with brain and spinal cord functions. Initial symptoms of La Crosse encephalitis infection include fever, headache, nausea, vomiting and lethargy. More severe symptoms usually occur in children under 16 and include seizures, coma, paralysis and neurological after effects. The death rate for clinical cases of La Crosse encephalitis is about 1%. Many pediatric cases that present La Crosse encephalitis symptoms are screened for herpes or other viral diseases, but are not specifically tested for presence of the La Crosse encephalitis virus. Many of these cases are reported as "aseptic meningitis" or "unknown viral encephalitis".

Diagnosis of the disease is confirmed by the presence of clinical symptoms and a fourfold rise in serum antibody and specific immunoglobulin M antibody capture in cerebral-spinal fluid (CSF) or serum; and/or by isolation of the virus or detection of the viral antigen in blood, CSF, or brain tissue. Serological test for the virus may be negative early in the course of the infection. New diagnostic techniques such as enzyme-linked immunosorbent assay (ELISA) may now be used soon after infection (they do not require a fourfold increase in titer). The use of monoclonal antibodies has also helped to standardize the testing protocols and have increased our ability to quickly identify viral agents. Viral agents can now also be rapidly identified by polymerase chain reaction techniques, but use of these is still not widespread in clinical settings.

There is no specific treatment for La Crosse encephalitis. No anti-viral drugs are available at this time, and antibiotics are not effective against viruses. Patients with the disease are given supportive treatment for the symptoms, particularly headaches, fever and seizures.

Preventing Infection

Risk of contracting La Crosse encephalitis is highest in children younger than 16 years, in people residing in or near woodlands that harbor the treehole mosquito, in people who maintain water-holding containers in their residences, and in those involved in outdoor activities where *O. triseriatus* is present. Prevention of the disease involves protection against the bite of infected mosquitoes. Personal measures include the use of repellents containing DEET, and the use of protective clothing (long sleeved shirts and long pants) when exposed to mosquitoes. Effective local mosquito control measures can also decrease disease risk by lowering mosquito populations, and thus decreasing the probability of mosquito-human encounters, and possibly, the transmission of the disease among wild populations of mosquitoes and vertebrate hosts. Mosquito control includes the use of appropriate pesticides and cleanup of water- holding containers that may offer breeding sites for *O. triseriatus*. Some mosquito control agencies also fill tree holes where *O. triseriatus* may develop with sand or cement.

References

McJunkin JE, Khan RR, Tsai TF (1998) California La Crosse encephalitis. Infect Dis Clin North Am 12:83–98

McJunkin JE, de los Reyes EC, Irazuzta JE, Caceres MJ, Khan RR, Minnich LL, Fu KD, Lovett GD, Tsai T, Thompson A (2001) La Crosse encephalitis in children. New Engl J Med 344:801–807

Rust RS, Thompson WH, Matthews CG, Beaty BJ, Chun RW (1999) La Crosse and other forms of California encephalitis. J Child Neurol 14:1–14

Lac Scales

Members of the family Kerriidae, superfamily Coccoidae (order Hemiptera).

► Scale Insects and Mealybugs
► Lacquers and Dyes From Insects
► Costs and Benefits Of Insects
► Shellac

Lacturidae

A family of moths (order Lepidoptera). They commonly are known as tropical burnet moths.

► Tropical Burnet Moths
► Butterflies and Moths

Ladybird Beetles (Coccinellidae: Coleoptera)

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"Ladybird" is a name that has been used in England for more than 600 years for the European beetle *Coccinella septempunctata* L. As knowledge about insects increased, the name ladybird became extended to all its relatives, members of the beetle family Coccinellidae. Of course these insects are not birds, but butterflies are not flies, nor are dragonflies, stoneflies, mayflies, and fireflies, which all are true common names in folklore, not invented names. The lady for whom they were named was "the Virgin Mary," and common names in other European languages have the same association (the German name Marienkafer translates to "Marybeetle" or ladybeetle). Prose and poetry mention ladybird, perhaps the most familiar in English being the children's rhyme:

"Ladybird, ladybird, fly away home,
Your house is on fire, your children all gone…"

In the U.S.A., the name ladybird was popularly Americanized to ladybug, although these insects are beetles (Coleoptera), not bugs (Hemiptera). Then, the Entomological Society of America decreed that the official name in the USA should be "ladybird beetle." Elsewhere in English-speaking countries it is still ladybird. Now the word ladybird applies to a whole family of beetles, Coccinellidae or ladybirds, not just *Coccinella septempunctata*. There are many species of ladybirds (almost 6,000 now known worldwide). The number of bird species known worldwide is somewhat more than 9,000. Regrettably, newspaper writers are prone to writing about "the ladybird" and erroneously referring to species of ladybirds as "varieties," although few or none of them would write about "the bird" and consider that bird species (from auks through eagles to hummingbirds), are "varieties." Many ladybird species are considered beneficial to humans because they eat phytophagous insects ("pests of plants," often called "plant pests"), but not all eat pests of plants, and a few are themselves pests.

Classification

Coccinellidae are a family of beetles belonging to the superfamily Cucujoidea, which in turn belongs to the series Cucujiformia within the suborder Polyphaga of the beetles (Coleoptera). Their relatives within the Cucujoidea are the Endomychidae (handsome fungus beetles) and Corylophidae (minute fungus beetles). The classification of lady beetles is:

- Order Coleoptera
  - Suborder Polyphaga
    - Series Cucujiformia
      - Superfamily Cucujoidea
        - Family Coccinellidae

The internal classification of the family into tribes and subfamilies is not settled because there are competing systems, none of them clearly correct. In this article, mention of species is grouped according to the food of adults and larvae, an ecological rather than phylogenetic grouping. When subfamilies and tribes are mentioned, it must be understood that these classifications are not universally accepted.

More than 480 species are currently reported to occur in America north of Mexico, just 44 in the British Isles, and 600 in Australia. Most of the

480+ in America north of Mexico are considered to be native, and others to be adventive (having arrived from somewhere else and established feral populations). Among the adventive species, some were introduced (introduced deliberately), and others are immigrants (having arrived by any means except deliberate introduction).

Description

Ladybird adults are oval, range in length from about 1 mm to over 10 mm depending upon species, and have wings. Females on average are larger than males. Adults of some species are brightly colored. Their mandibles are used for chewing. Adult ladybirds are able to reflex-bleed from the tibio-femoral articulations (leg joints). The blood (hemolymph) is repellent by having a repulsive smell as well as containing (in some species) various alkaloid toxins (adaline, coccinelline, exochomine, hippodamine, etc.). The hemolymph is yellow and its repellency and toxicity are believed to be a defense mechanism against predators. Some people have claimed that the bright (red on black, or black on red) colors of some adult ladybirds are aposematic, which is to say that the colors warn would-be predators that the beetles are distasteful or toxic.

The immature stages (eggs, larvae, and pupae) also contain the toxins that their adults have. Toxins are said to be produced by dorsal glands in the larvae. Eggs are elongate-ovoidal, and in just a few species are protected by secretions of the adult female. Cannibalism of eggs, larvae and pupae is common, especially when prey is scarce. Larvae are mobile, and in some species (for example of *Scymnus* and *Cryptolaemus*) are protected by waxy secretions. Pupae are unprotected by a cocoon (some other beetles pupate in a cocoon) but larvae may wander some distance from feeding sites (where they may be at risk from cannibalism) before pupating.

Life Cycle and Behavior

Ladybird eggs are laid in clusters by at least most aphid-eating species and singly by at least most scale-insect-eating species. Eggs produce larvae that undergo four instars before pupating, metamorphosing, and giving rise to adults. One scale-eating ladybird is reported to have only three instars. Ladybirds may have one or, more typical of warmer climates, several generations each year, and reproduction is slowed or halted by cooler winter weather, when adults may hibernate. In hot, dry climates, ladybirds may aestivate (become inactive) during the hottest months.

Ladybirds that feed on aphids develop faster, age faster, move faster, typically are larger, and lay their eggs in clusters. Those that feed on scale insects develop more slowly, live longer, move more slowly, typically are smaller, and lay their eggs singly.

Food

Pest Species – Feeding on Plants

Adults and larvae of the subfamily Epilachninae feed on plants. Some 500 species are known worldwide. In America north of Mexico, this subfamily is represented only by *Epilachna borealis* (Fabricius) and *E. varivestis* Mulsant. *Epilachna borealis*, the squash beetle, feeds on members of the squash family (Cucurbitaceae). *Epilachna varivestis*, the Mexican bean beetle, feeds on members of the bean family (Leguminosae). Mexican bean beetle is native to southern Mexico, but it is an immigrant to the USA, first detected in the west in 1849. Now, its distribution is from Costa Rica north through Mexico to the Rocky Mountain states of the USA, and with a separated eastern population which extends southward to northern Florida. In the eastern USA, it has been controlled efficiently by annual releases of the parasitoid wasp *Pediobius foveolatus* (Crawford) (Eulophidae). This wasp was initially imported from India, where it attacks *Henosepilachna sparsa* (Herbst), which likewise belongs to Epilachninae. *Epilachna philippinensis* Dieke, a pest of solanaceous crop plants in the Philippines, has been the object of a biological control program by *Pediobius epilachnae* (Rohwer), native to parts of the Philippines.

Innocuous Species – Feeding on Mildews

Ladybirds of the tribe Halyziini (until recently called Psylloborini, of the subfamily Coccinellinae) feed on fungal growths (mildews, Ascomycetes: Erysiphales) on the leaves of plants. Their greatest species diversity is in the tropics, with only six species in America north of Mexico. One of them is the West Indian *Psyllobora nana* Mulsant which has invaded the extreme south of Florida. In the neotropics, the coccinellid genus *Neocalvia* feeds on larvae of Halyziini.

Predatory Species – Feeding on Mites

Adults and larvae of the tribe Stethorini (of the subfamily Scymninae) feed on tetranychid mites. The tribe is distributed worldwide, and has only one genus. There are five species in America north of Mexico. An example is *Stethorus utilis* (Horn), a minute ladybird which is distributed in the coastal plains of the southeastern states from North Carolina south through Florida and west through Texas. Another is *S. punctillum* Weise, a European species that was reported in 1950 as detected in Ontario and Massachusetts.

Predatory Species – Feeding on Whiteflies

Four species in America north of Mexico appear to be more-or-less specialized predators of whiteflies. They are *Delphastus catalinae* (Horn), *D. pallidus* (LeConte), and *D. pusillus* (LeConte) (tribe Serangiini), and *Nephaspis oculatus* (Blatchley) (tribe Scymnini). The first and probably the fourth seem to be immigrant species from the Neotropical region. The others (*D. pallidus* and *D. pusillus*) are considered to be native. After *D. pusillus* was found to be a very useful biological control agent against sweetpotato whitefly (*Bemisia tabaci* (Gennadius)) including the "form" that later was named silverleaf whitefly (*Bemisia argentifolii* Bellows and Perring), "it" was exported from Florida to California and made available commercially and used in other parts of the USA. Somehow this resulted in commercial biological control companies selling *D. catalinae* under the name *D. pusillus*.

Predatory Species – Feeding on Cottonycushion Scale

Cottonycushion scale (*Icerya purchasi* Maskell), native to Australia, belongs to the family Margarodidae (commonly called "ground pearls," although this name hardly fits this species) in the superfamily Coccoidea (scale insects). It is a major pest of citrus, and an important pest of several other trees and shrubs including *Acacia*, *Casuarina*, and *Pittosporum*. After its arrival in California, presumably as a contaminant of imported plants, it threatened to ruin California's citrus industry in the late 1800s. It was controlled by importation, release, and establishment (as classical biological control agents) of *Rodolia cardinalis* (Mulsant) and a parasitoid fly, *Cryptochetum iceryae* (Williston). When cottonycushion scale became a problem in many other countries, *R. cardinalis* was the biological control agent of choice, so stock of it has been shipped to other continents and countries.

Predatory Species – Feeding on Mealybugs

Mealybugs are the homopterous family Pseudococcidae, which includes some notable pests of plants. *Cryptolaemus montrouzieri* Mulsant, a ladybird native to Australia, is a notable predator of mealybugs. It was introduced into California first in 1891, and some time later from California into Florida. It has been marketed commercially as a control agent for mealybugs and is often effective, but has one unfortunate characteristic: its larvae produce waxy filaments making them look to the uninitiated like their mealybug prey. Many owners of plants have sprayed the larvae with chemicals in the mistaken belief that they are pests. This misidentification must be overcome by education. *Cryptolaemus montrouzieri* does not confine its attentions to mealybugs, and also eats soft scales (Coccidae) and armored scales (Diaspididae). Such a catholic diet is normal for a long list of ladybirds, so that their diet cannot neatly be pigeonholed as armored scales or soft scales or mealybugs – they may eat some prey in all of these families, and a few of the larger ones may even eat an aphid from time to time. For that reason, many genera and species are placed below under "Feeding on Scale Insects."

Predatory Species – Feeding on Armored Scale Insects

Some species appear to feed largely or entirely on armored scale insects (Diaspididae). Examples include *Microweisea coccidivora* (Ashmead), *M. misella* (LeConte), and *M. ovalis* (LeConte) of the tribe Microweiseini, *Zilus horni* Gordon, *Z. eleutherae* Casey, and *Z. subtropicus* (Casey) of the tribe Scymnillini, and *Cryptognatha nodiceps* Marshall of the tribe Cryptognathini. One of these, *Cryptognatha nodiceps*, is not native to America north of Mexico, having been imported in the 1930s, released, and established as a classical biological control agent for coconut scale (*Aspidiotus destructor* Signoret).

Predatory Species – Feeding on Scale Insects

A large trophic group has scale insects as its prey, meaning members of the superfamily Coccoidea (the scale insects). This superfamily includes various related families, notably Coccidae (soft scales), Diaspididae (armored scales), Pseudococcidae (mealybugs), Dactylopiidae (cochineal scales), Kermesidae (gall-like scales), Eriococcidae (felt scales), Cerococcidae (ornate pit scales), and Asterolecaniidae (pit scales). Examples of ladybird genera belonging to this group are: *Decadomius*, *Diomus*, *Nephus*, and *Scymnus* (all in tribe Scymnini), *Brachiacantha*, *Hyperaspidius*, and *Hyperaspis* (all in tribe Hyperaspini), *Axion*, *Chilocorus*, *Curinus*, and *Exochomus* (all in tribe Chilocorini), *Rhyzobius* (tribe Coccidulini), and *Azya* (tribe Azyini). It is not yet clear how, or whether, they divide up the scale insects between them, because reliable prey records are too incomplete. However, there is at least some level of prey specialization in these (and the three aforementioned groups) that feed on scale insects, which seems not to be the case for the next-discussed trophic group (those that feed on aphids). *Brachiacantha* has a curious life history in that its larvae so far as is known feed on scale insects within ant nests.

Rhyzobius lophanthae (Blaisdell) was introduced to California from Australia in 1892 to control scale insects, and somehow later made its way to Florida (there is no record of an early introduction into Florida). *Chilocorus circumdatus* (Schoenherr) [other writers give the author name as Gyllenhal] is native to southeastern Asia and is adventive in Australia; it was imported from Australia to the U.S.A. and was released in Florida in 1996 against citrus snow scale, *Unaspis citri*, and is established. *Azya orbigera* Mulsant is an immigrant from the Neotropical region. *Decadomius bahamicus* (Casey) is an immigrant from the Caribbean or the Bahamas or Bermuda. *Diomus roseicollis* Mulsant is an immigrant from Cuba.

Predatory Species – Feeding on Aphids

Adults and larvae of many species (the tribe Coccinellini) probably feed primarily on aphids. Amomg many others, they include *Coccinella* *novemnotata* Herbst, *C. septempunctata* L., *Coelophora inaequalis* (F.), *Coleomegilla maculata* DeGeer, *Cycloneda munda* (Say), *Cycloneda sanguinea* (L.), *Harmonia axyridis* Pallas, *Harmonia dimidiata* (Fabricius), *Hippodamia convergens* Guérin-Méneville, *Mulsantina picta* (Randall), *Naemia seriata* (Melsheimer), *Neoharmonia venusta* (Melsheimer). Although *Olla v-nigrum* Casey feeds on some aphid species, it has been shown to be an important predator of psyllids (Figs. 16 and 17).

Four of these, *C. septempunctata* (from Europe), *C. inaequalis* (from Australia), *H. dimidiata* (from China), and *H. axyridis* (from Japan) were introduced into North America, although there is some doubt that the presence of *C. septempunctata* and *H. axyridis* is due to introduction; their presence may be due to immigration, albeit as hitchhikers aboard ships.

Two of these genera, *Coleomegilla* and *Mulsantina*, include adelgids (Adelgidae), which are closely related to aphids, in their diet. Further, *Coleomegilla* also includes pollen whereas *Mulsantina* also includes scale insects in the broad sense.

Alternative Food

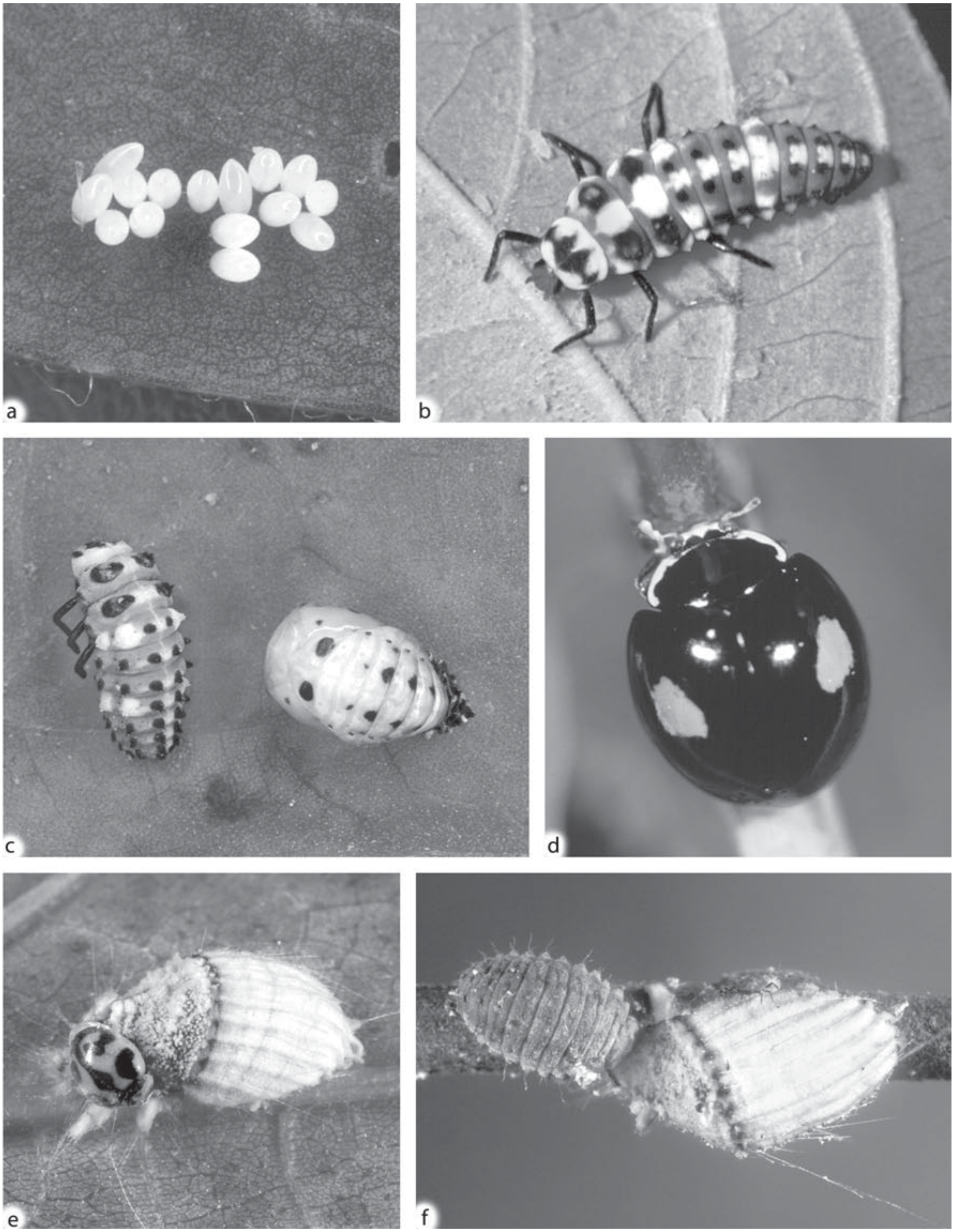
Ladybird larvae and adults may supplement their normal prey in times of scarcity with other types of food. They consume flower nectar, water and honeydew – the sugary excretion of piercing-sucking insects such as aphids and whiteflies – or pollen. Many plant species also contain organelles in locations on the plant other than the flower – termed extrafloral nectaries – that produce a nutrient-laden secretion. While it was first thought that extrafloral nectaries were used by the plant for excretion, it is well substantiated that most plants actually use the extrafloral nectaries to attract predators and parasites for protection from their herbivores. Over 2,000 species of plants in 64 families have extrafloral nectaries. Extrafloral nectaries may be located on leaf laminae, petioles, rachids, bracts, stipules, pedicels, fruit, etc. Ladybirds often use the secretions from extrafloral nectaries in their diet and are just some of the many beneficial insects that use extrafloral nectary secretions.

Natural Enemies

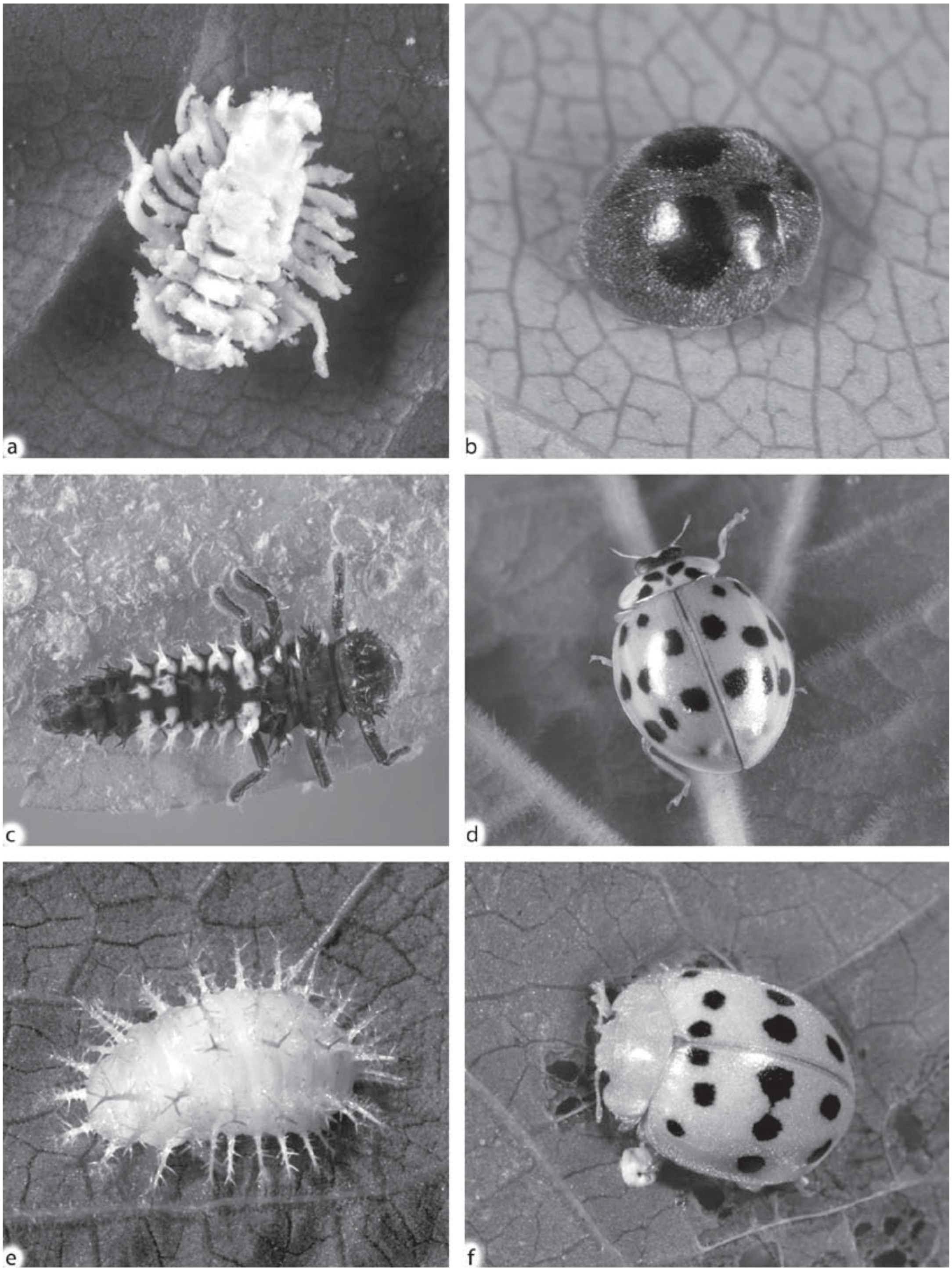
All insects have predators, parasites/parasitoids, and/or pathogens. Ladybirds are not exempt. Larvae of *Epilachna borealis* and *E. varivestis* are attacked by a North American tachinid fly (*Aplomyiopsis epilachnae* (Aldrich)) which specializes in the genus *Epilachna*. Larvae of *E. varivestis* also are attacked by an introduced eulophid wasp (*Pediobius foveolatus*, see above). Another native tachinid fly, *Hyalmyodes triangulifer* (Loew), is less specialized, attacking larvae not only of *Epilachna varivestis*, but also of *Coleomegilla maculata*, several weevils, and a pterophorid moth. Perhaps the best known of the parasitoids of ladybirds is the braconid wasp *Perilitus coccinellae* (Schrank). It attacks adult ladybirds and to a lesser extent larvae and pupae of *Coccinella septempunctata*, *Coleomegilla maculata*, and several other species. Microsporidial diseases include *Nosema hippodamiae* Lipa and Steinhaus, *N. tracheophila* Cali and Briggs, and *N. coccinellae* Lipa (Fig. 18).

Use of Ladybirds in Biological Control

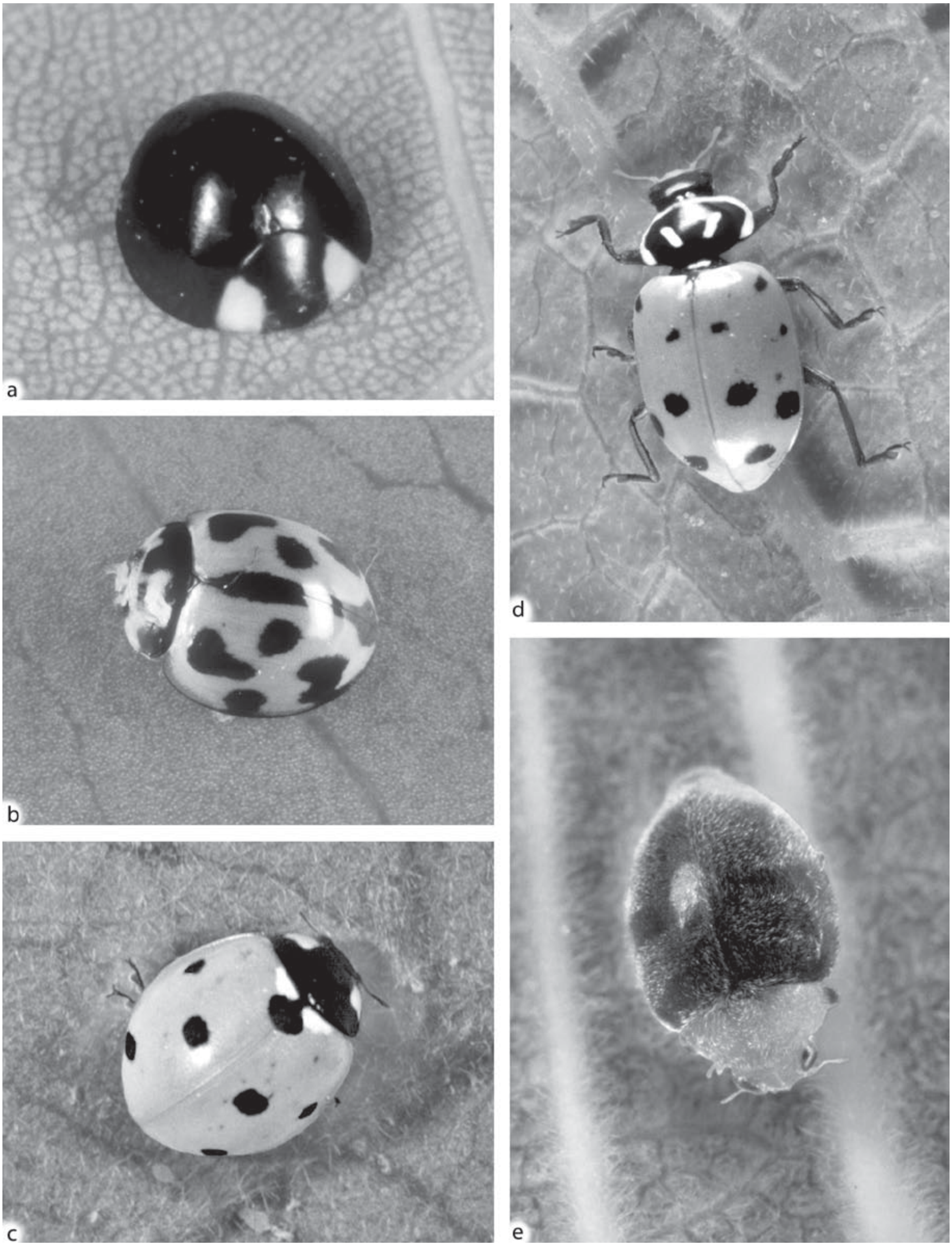
Most species of ladybirds are considered beneficial because they are predators of Hemiptera: Sternorrhyncha or Acarina, many of which are considered to be pests. These predatory ladybirds contribute to the regulation of populations of their prey, and in some situations contribute a high level of regulation. When ladybirds naturally contribute a high level of control of pests, or in combination with other predators and/or parasitoids and diseases contribute a high level of population regulation of pests, people may benefit. That is to



Ladybird Beetles (Coccinellidae: Coleoptera), Figure 16 **Ladybird beetles: *Olla v-nigrum* eggs (a), larva (b), prepupa (c, *left*) and pupa (c, *right*), and adult (d). This species is dimorphic in the adult stage and also occurs as an orange beetle with small black spots. Vedalia beetle, *Rodolia cardinalis*: adult (e) and larva (f) feeding on cottony cushion scale. This beetle saved the California citrus industry from destruction by cottony cushion scale.**



Ladybird Beetles (Coccinellidae: Coleoptera), Figure 17 **Larvae and adults of some ladybird beetles: *Azya orbigera* larva (a) and adult (b). This species is typical of those that produce waxy secretions in the larval stage. The multicolored Asian ladybird beetle, *Harmonia axyridis*, larva (c) and adult (d). This species, though predatory, has become a serious nuisance due to its habit of aggregating in buildings during the winter. Mexican bean beetle, *Epilachna varivestis*, larva (e) and adult (f). This species is one of only a small number of phytophagous ladybird beetle species.**



Ladybird Beetles (Coccinellidae: Coleoptera), Figure 18 **Some typical adult ladybird beetles: *Curinus coeruleus* (a), *Coleophora inaequalis* (b), *Coccinella septempunctata* (c), *Hippodamia convergens* (d), and *Cryptolaemus montrouzieri* (e).**

say that gardeners, growers and farmers may benefit, at no cost, because they have no or negligible pest problems.

Sometimes, gardeners mistake the ladybird larvae for pests and spray chemical pesticides that kill them (this is much less of a problem with growers and farmers because they have more experience). The result is increased problems from real pests. The answer is a constant educational effort to inform people about ladybirds and what their larvae look like. This effort cannot end, because people knowing nothing about ladybird life cycles are born each minute.

One type of biological control is thus called manipulative biological control (of which a subset is conservation biological control). The objectives are simply to capitalize on the ladybirds (or other beneficial organisms) that already are present, to make conditions as favorable as possible for them (manipulation), and especially to avoid spraying chemicals (insecticides, fungicides, or herbicides) that will harm them (conservation).

A second type of biological control is augmentative biological control. This begins with the recognition that ladybirds in a given pest situation are present but too few to do the job required, and buying more from a commercial producer to release to augment those already present. A risk is that if adult ladybirds are released, many of them may fly away. But, if ladybird larvae are released, they have the option of eating the pest with which they are presented, or starving – they cannot fly away. Obviously, this requires matching the pest to a purchased ladybird species that will eat that pest (see above for species options). The rub here is that the number of purchased ladybirds needed for a given pest situation may not have been worked out in detail – it demands a huge amount of practical experience to tie down the details for at least hundreds of situations. Documentation of this experience is progressing very slowly.

A third type of biological control is classical or inoculative biological control. Here, some individuals of a ladybird (or other) species that is not already present are released in the hope that they will establish a population and eventually control the pest that is of concern. Classical biological control typically applies to a situation in which a new pest has invaded, and researchers (from a university, or a national or state department of agriculture) import and release a ladybird (or other kind of organism) that is believed to control the pest elsewhere. Typically, the imported ladybird (or other organism) becomes established or does not become established; if it becomes established, it may or may not control the pest in this new situation. Typically, the foregoing things are done under the name of "research," and either are cost-free to gardeners, growers and farmers (especially if done by state or federal departments of agriculture) or, if done by university researchers, then gardeners, growers and farmers are asked to contribute toward a grant that will pay for the cost of importation and research on the biological control agent (but subsequently, after it has become established, there are no further costs). The archetypical example is control of cottonycushion scale of citrus by the introduced ladybird *Rodolia cardinalis*. Although chemical pesticides of the time were failing to control it, and although it threatened to ruin California's citrus industry, nobody was willing to invest funds in biological control research. Nevertheless, biological control research was "bootlegged" onto other operations by dedicated researchers, was astoundingly successful, and saved California's (and later Florida's) citrus industry from ruin: there was no subsequent need to use chemicals against this pest, thus saving billions of dollars as against a trivial expenditure (about $1,500 at the time, for foreign travel).

Glasshouses (greenhouses) provide a habitat for plants and pests and biological control agents that differs from outdoor habitats. Typically, culture begins with initiation of a crop of plants that has no pests (or seems to have none). But then pests somehow show up, and there are no ladybirds (or other organisms) to control them. The situation is very much like that of classical biological control, and ladybirds (and/or other beneficial organisms) released into the greenhouses may control the pests and eliminate need to use chemical pesticides. Here, the question is not about funding new research into a new pest, but into buying the right numbers of ladybirds (or other organisms) of the appropriate species to control a pest that has already been researched. For many such situations, ladybirds (or other organisms) can be purchased from commercial supply houses to control the pest(s).

Commercial Availability

The following is a partial species list of commercially available ladybirds posted on the California Department of Food and Agriculture's website, which can be accessed to provide information about commercial suppliers in Canada, Mexico and the USA in 1997 (it is not up-to-date). The URL (http://www.cdpr.ca.gov/docs/ipminov/bensuppl.htm) still works.

Coleomegilla maculata – a predator of aphids.

Cryptolaemus montrouzieri – a predator of mealybugs.

Delphastus pusillus – a predator of whiteflies.

Harmonia axyridis – a predator of aphids.

Hippodamia convergens – a predator of aphids. Some suppliers do not rear the beetles but collect overwintering adults from the mountains of eastern California; these overwintering adult beetles (i) may be heavily parasitized and many may die, and (ii) may be programmed at the end of the winter to end the hibernation by flying west, which may do you no good if they all take to flight and leave your property.

Rhyzobius lophanthae – a predator of scale insects.

Rhyzobius ventralis – this name is listed in error, it should be called *Rhyzobius forestieri* (Mulsant).

Stethorus picipes – a predator of tetranychid mites; this name is listed in error, it should be called *Stethorus punctum picipes* Casey, a subspecies of *Stethorus punctum* (LeConte).

Stethorus punctillum – a predator of tetranychid mites.

Commercial suppliers of biocontrol agents in Australia are listed by the Association of Beneficial Arthropod Manufacturers (ABA: http://www.gc.goodbugs.org.au), and some of these suppliers sell ladybirds. Commercial suppliers of biocontrol agents in Europe (and some other countries around the world) are listed by the International Biocontrol Manufacturers Association (IBMA: http://www.ibma.ch), and some of the listed companies sell ladybirds. Commercial suppliers belonging to the Association of Natural Biocontrol Producers, a North American Organization, are listed (ANBP http://www.anbp.org). By examining the individual sites of these companies, you may determine what ladybird species are available and, from the websites of some of these companies, some of the characteristics of the species available.

There is yet no website listing insect cultures available worldwide for purchase, with a list of suppliers for each species. Insect Production Services, Natural Resources Canada, is beginning to compile such a list (http://www.insect.gflc.cfs.nrcan.gc.ca).

However, just because a biocontrol agent such as a ladybird species (or subspecies), is available somewhere in the world for purchase, does not necessarily mean you will be able to obtain it. Your own national (and perhaps provincial or state) department of agriculture (or some other government agency) may regulate importations. It is most probable that you will only be able to import species (and subspecies) that already exist in your area. For example, all shipments of living insects into Florida are required to have permits from the Florida Department of Agriculture and Consumer Services, Division of Plant Industry; in general, a permit will be supplied for importation of species (and subspecies) that already occur in Florida. It is the vendors who are required to obtain the permits for commercial shipments. Furthermore, no reputable producer is likely to ship living ladybirds to you unless there is a rapid commercial shipper. Stated policies of some international shippers (e.g., Federal Express, DHL, UPS) say that they will not accept consignments of living animals (including insects) for reasons that they do not explain. The lesson is that you should buy from a local supplier wherever possible.

Despite all the difficulties in purchase and shipment, some biocontrol producers can provide you with a good product rapidly. Please see the website of the Belgian producer Biobest (http://www.Biobest.be), which also has websites in other countries (at least Canada, France, Greece, and Spain) as an example of how it can work. That company provides you an online description of the product and what it can do.

Four ladybird species (*Coleomegilla maculata*, *Cryptolaemus montrouzieri*, *Harmonia axyridis*, and *Hippodamia convergens*) have been reared on purely artificial diets, thus promising to reduce labor costs and thus the price of commercially available ladybirds. Diets for others may now be available or under development.

The Downside of Ladybirds

The great success of the imported *Rodolia cardinalis* in controlling cottonycushion scale in California and then in various countries around the world led to great enthusiasm among growers to attempt importation of additional ladybirds to control a long list of pests of plants. Many of these additional ladybirds failed to establish where they were introduced. Others became established but did not provide the required level of control. Relatively few achieved the required level of control. One of the reasons for success of *R. cardinalis* was its high level of specialization to cottonycushion scale – it would control that pest effectively, but no others.

Growers of many crops encounter pest aphids. Ladybirds that prey on aphids are widely distributed, and native ladybirds are often recruited to aphid infestations on crop plants in North America and elsewhere. Perhaps it was a sense of lack of effectiveness of native ladybirds in rapid and complete control of aphid infestations that led to attempts to import additional aphid-feeding ladybird species into North America. At all events, considerable effort was made by USDA entomologists (in collaboration with state and university entomologists) to import the Eurasian *Coccinella septempunctata* and the Asian *Harmonia axyridis* to eat more aphids than were consumed by native ladybirds. Whether those efforts succeeded or whether those two ladybird species arrived as immigrants is unclear, but eventually both species became established and spread widely. They proved to be more successful than native ladybirds at controlling aphids in general, and their populations grew and spread. Perhaps if this had happened in the 19th century the success would have been welcomed. But, by the late twentieth century, it was their side-effects that received publicity – there is some evidence that in some places native ladybird populations have declined because of the efficiency of the introduced ladybirds in killing aphids and thus denying food to the native ladybirds. It is undeniable that adult *H. axyridis* may hibernate in some places (loosely constructed houses, railway electrical boxes, etc.) where they are not welcome. It matters little that houses and railway electrical boxes should and could have simple physical screens to exclude insects (building codes in the southern U.S.A. require screening of houses against mosquitoes) because the public has become incensed against *H. axyridis*. The era of importation of generalist biological control agents has ended (even, for example, those that feed on many aphid species but no other prey may no longer be welcome), and only specialists may in future be permitted.

References

Dixon AFG (2000) Insect predator-prey dynamics: ladybird beetles and biological control. Cambridge University Press, New York, NY

Gordon RD (1985) The Coccinellidae (Coleoptera) of America north of Mexico. J New York Entomol Soc 93:352–599

Hodek I, Honěk A (1996) Ecology of Coccinellidae. Kluwer Academic Publishers, Dordrecht, The Netherlands, 464 pp
Kuznetsov VN (1997) Lady beetles of the Russian Far East. Center for Systematic Entomology, Gainesville, FL (Memoir No. 1)
Vandenberg NJ (2000) Coccinellidae Latreille 1807. In: Arnett RH, Thomas MC, Skelley PE, Frank JH (eds) American beetles, vol 2. CRC Press, Boca Raton, FL, pp 371–389

Laemobothriidae

A family of chewing lice (order Phthiraptera). They sometimes are called hawk lice.

► Chewing and Sucking Lice

Laemophloeidae

A family of beetles (order Coleoptera). They commonly are known as lined flat bark beetles.

► Beetles

Lagenidium giganteum

Lagenidium giganteum (Lagenidiales) is the best-known entomopathogen belonging to the class Oomycetes. It has been described as a facultative parasite; it infects and kills available insect hosts, but also is capable of surviving saprophytically. *Lagenidium giganteum* most often infects young mosquito larvae; only occasionally does it infect older larvae and pupae. In addition, infection also has been reported to occur in certain species of gnats and biting midges. The infective propagules are asexually produced biflagellate zoospores that migrate upward and concentrate at the surface of the water to contact surface-breathing mosquito larvae. Once contact is made, the zoospores recognize and attach to the insect cuticle. Zoospores may attach over the entire larval surface or may concentrate in the head region (e.g., in the buccal cavity). After encystment and attachment, the zoospores (cysts) form delicate germ tubes that penetrate the cuticle. Mechanical and enzymatic disruption of the cuticle and underlying tissues produced by apical growth of the fungal germ tube promotes the penetration of *L. giganteum* into host larvae. Successful infection by *L. giganteum* is host-specific in terms of the ability of a particular strain of the fungus to bypass the defensive reactions exhibited by challenged host larvae. Mycelia eventually fill the body cavity, and this extensive vegetative growth results in the starvation of the insect. At this time, septation of the mycelia occurs, and the resulting segments may become asexual sporangia or male and female gametangia. Zoosporogenesis takes place in the asexual sporangia. In *L. giganteum*, the sporangia produce exit tubes that pass through the host cuticle and form bubble-like vesicles. The sporangial protoplast moves through an exit tube into a vesicle; the protoplast then divides into individual zoospores, which are released into the water when the vesicle ruptures. The free-swimming, wall-less zoospores, which do not represent a resistant or resting stage of the fungus, must contact host larvae within several hours in order to initiate another infection cycle. The male and female gametangia (i.e., antheridia and oogonia, respectively) may form from segments of the same mycelium or from segments of contiguous mycelia. The antheridium forms a fertilization tube that attaches to the oogonium, and the contents of the antheridium move into the oogonium. Plasmogamy (fusion of the sex cells) and karyogamy (fusion of the nuclei) occur in the oogonia, and the zygotes resulting from these fusion events form into thick-walled oospores. Oospores represent the dormant, resting spore stage of *L. giganteum*, and their existence insures survival of the fungus during environmental extremes (drought, cold temperatures). Under proper conditions, oospores germinate, and the fungus may then grow saprophytically, or the germinating oospores may act as zoosporangia, releasing infective zoospores.

Lagenidium giganteum is a sterol auxotroph that requires exogenous sterols for both zoosporogenesis and oosporogenesis, but not for vegetative growth. Oospores of *L. giganteum* are resistant to environmental extremes and can be stored indefinitely at room temperature. In vitro, oospores may be produced in yeast extract-basal media supplemented sterols, unsaturated fatty acids; calcium, and magnesium. Sterols such as cholesterol also regulate the cellular uptake of unsaturated fatty acids. Unsaturated fatty acids increase bilayer fluidity when they become incorporated into plasma membranes and, as in the case of sterols, may affect adenylate cyclase activity by changing membrane fluidity. In addition, there is an increase in oospore viability if the unsaturated fatty acids are added as triacylglycerols, which can function as storage products in dormant cells such as oospores. Calcium is required during all stages of oospore formation from induction to spore maturation. At antheridial induction, calcium interacts with the regulatory cyclic nucleotides, and it may be involved in membrane phase transitions during gametangial fusion.

Lag Phase

A phase in the typical growth cycle of a population when there is no growth, typically between the introduction of an organism and the period of exponential growth.

Lamarck, Jean-Baptiste

Jean-Baptiste Pierre Antoine de Monet, Chevalier de Lamarck, was born near the village of Bazentin-le-Petit on August 1, 1744. After study at a Jesuit seminary, military service, and work as a bank clerk, he began to study medicine and botany. He earned great recognition for his book "Flore Française," published in 1778. During the French Revolution he called for a reorganization of the Jardin du Roi, where he worked, and when it was implemented he was appointed a professor of the natural history of insects and worms, a subject about which he knew nothing. This was a period when few naturalists considered invertebrates worthy of study. In fact, the word "invertebrates" did not exist at the time, so Lamarck coined it to describe his responsibilities! Lamarck published a series of books on invertebrate zoology and paleontology. Publication of "Histoire naturelle des animaux sans vertèbres" in 1815 and 1822 greatly advanced the classification of invertebrates. However, his work never became popular, and in particular his theories on evolution brought him considerable criticism. "Lamarckism" is now used in a derogatory sense to refer to the discredited theory that acquired traits can be inherited. However, Lamarck's beliefs were actually more complex, and not so out of step with what became known as Darwinism. Lamarck believed that environmental change affects organisms so that they change their behavior. Altered behavior leads to greater or lesser use of a structure or organ; use would cause it to be enhanced over several generations; disuse would cause it to disappear. The concept that use or disuse would cause structures to enlarge or shrink was called the "first law" in Lamarck's book "Philosophie zoologique" published in 1809. His "second law" stated that changes were heritable. The result of his first and second laws is that organisms change and adapt to their environment. So although the mechanism proposed by Lamarck to explain evolution is different than Darwin's, the outcome is about the same. Thus, Lamarck should be credited with advancing the concept of evolution, though Darwin should be justifiably credited with the stronger mechanistic argument and the stronger set of supporting data. He died on December 28, 1829.

References

Jackson RT (1905) Professor Packard's "Lamarck, his life and work". Psyche 12:36–38

Waggoner BM (1996) Jean-Baptiste Lamarck (1744–1829). Available at http://www.ucmp.berkeley.edu/history/lamarck.html. Accessed 4 April 2008

Lamella

A thin plate or leaf-like process.

Lamellate

With flattened, plate-like structures. This is usually used to describe antennae with flattened structures at the tip.

► Antennae of Hexapods

Lampyridae

A family of beetles (order Coleoptera). They commonly are known as lightningbugs or fireflies.

► Beetles

Lanceolate

A structure that is spear-shaped, with a pointed tip.

► Antennae of Hexapods

Lance-Wing Moths (Lepidoptera: Pterolonchidae)

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Lance-wing moths, family Pterolonchidae, total only 11 species, mostly Mediterranean, with two in South Africa. The family is part of the superfamily Gelechioidea in the section Tineina, subsection Tineina, of the division Ditrysia. Adults small (24–27 mm wingspan), with head smooth-scaled; haustellum absent; labial palpi porrect; maxillary palpi absent. Wings elongated. Maculation mostly light shades of brown or mostly white. Adults may be mostly crepuscular. Larvae are root borers as far as is known. Only recorded host plants are in Compositae.

References

Campobasso GR, Sobhian L, Knutson AC, Pastorino, Dunn PH (1994) Biology of *Pterolonche inspersa* (Lep.: Pterolonchidae), a biological control agent for Centaurea diffusa and *C. maculosa* in the United States. Entomophaga 39:377–384

Heppner JB (1997) Immature stages of the Mediterranean knapweed borer, *Pterolonche inspersa* (Lepidoptera: Pterolonchidae). Holarctic Lepidoptera 4:63–66

Minet J (1988) Quelques caractères pré-imaginaux permettant de maintenir les Pterolonchidae au sein des Gelechioidea (Lepidoptera: Ditrysia). Annals de la Société Entomologique de France (n.s) 24:375–376

Vives-Moreno A (1984) *Pterolonche gozmaniella* Vives nov. sp., nueva especie de la familia Pterolonchidae Meyrick, 1918, para la fauna de España. SHILAP Revista de Lepidopterologia 12:195–197

Languriidae

A family of beetles (order Coleoptera). They commonly are known as lizard beetles.

► Beetles

Lappet Moths (Lepidoptera: Lasiocampidae)

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Lappet moths, family Lasiocampidae (also called tent caterpillars), include 2,130 species worldwide, with the most in Africa (790 sp.). Subfamilies remain unclear and need more study, but five are now recognized: Chondrosteginae (African), Chionopsychinae (African), Poecilocampinae (Palearctic), Macromphalinae (New World), and

Lasiocampinae. The family is in the superfamily Bombycoidea (series Bombyciformes), in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults small to very large (19–172 mm wingspan), with head vertex rough-scaled; haustellum absent (rarely vestigial); labial palpi short, upcurved or somewhat porrect; maxillary palpi absent (rarely vestigial); antennae bipectinate; body robust and usually with very long hair-like setae. Wings broadly triangular and usually rounded, but sometimes with forewing apex somewhat acute; hindwings rounded; some with micropterous females. Maculation mostly somber browns or grays, with various markings, but can be more colorful with pink spotting or completely bright green or yellow, for example, or white with black spotting. Adults mostly nocturnal but some males are diurnal. Larvae are leaf feeders, sometimes communally in silken tent-like webbings. Larvae typically have many lateral secondary hair-like setae that cover the prolegs when on the host leaf. Host plants are various, with many records in Betulaceae, Compositae, Fagaceae, Gramineae, Lauraceae, Leguminosae, Myrtaceae, Rosaceae, Salicaceae, and Tiliaceae, among others. Some species are economic as tree defoliators (Fig. 19).

Lappet Moths (Lepidoptera: Lasiocampidae), Figure 19 Example of lappet moths (Lasiocampidae), *Lasiocampa quercus* (Linnaeus) from Italy.

References

Fitzgerald TD (1995) The tent caterpillars. Cornell University Press, Ithaca, 303 pp, 2 pl

Franclemont JG (1973) Lasiocampidae. In: Dominick RB (eds) The moths of America north of Mexico including Greenland, Fasc. 20.1. Bombycoidea. E.W. Classey, London, 86 pp, 11 pl [part]

Holloway JD (1987) Family Lasiocampidae. In: The moths of Borneo, Malayan Nature Society (Malayan Nature Journal, 41), Kuala Lumpur, pp 311–361, pl 1–6

Jost B, Schmid J, Wymann HP (2000) Lasiocampidae–Glucken, Wollraupenspinner. In: Schmetterlinge und ihre Lebensräume: Arten–Gefährdung-Schutz. Schweiz und angrenzenden Gebiete 3:263–350, pl 11–15, Basel

Seitz A (ed) (1911–1934) Familie: Lasiocampidae. In: Die Gross-Schmetterlinge der Erde, 2:147–180, pl 24–30 (1911); 2(suppl):109–125 (1932), 284–285, pl 9–10 (1934); 6:565–628, pl 75–86 (1927–28); 10:391–415, pl 32–35, 46 (1921–22); 14: 205–281, pl 29–40 (1927). A. Kernen, Stuttgart

Large Cabbage White Butterfly, *Pieris brasicae* (Linnaeus) (Lepidoptera: Pieridae)

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This species occurs widely in Europe, east to India and southwestern China, and in North Africa, but is not yet found in North America, unlike the similar cabbageworm or small cabbage white, *Pieris rapae* (Linnaeus). Large cabbage white was accidentally introduced to Chile, in South America, in 1971, and to South Africa in 1994.

Life history

The number of generations per year depends on day length. In the northernmost regions it displays only one generation, but four generations are common in central Europe and six generations may occur in northern Africa. It is highly dispersive, regularly migrating from continental Europe to the United Kingdom, often in mixed swarms with other pierids such as *Pieris rapae* (Linnaeus) and *P. napi* (Linnaeus).

Adults lay cone-shaped eggs bearing sharp vertical ridges. They are yellow, about 1.2–1.4 mm high, and resemble the eggs of *P. rapae* but are laid in groups of 20–50 instead of singly or in pairs as in *P. rapae*. The eggs may be deposited beneath or on the upper surface of the leaves, but the former position is favored. The eggs hatch in 3–13 days, depending on temperature.

Upon hatching, young larvae consume the egg chorion before consuming foliage. The young, pale green larvae remain clustered together, though they soon acquire a mottled blue-green appearance. Larvae remain gregarious until nearing their maturity. Usually there are 3 instars (though up to 5 has been reported), and mature larvae wander considerable distances before pupating. Mature larvae are 25–40 mm long, yellowish brown, with black spots and yellow longitudinal stripes. The larva is densely clothed with hairs. About 30 days are normally required for larval development.

Typical pupation sites include crop plants, weeds, fence posts, stone walls and other protected areas above the soil. In preparation for pupation, the larvae attach themselves by a supporting silken girdle and posterior hooks; the anterior end faces upward. The chrysalis is 20–24 mm long, 5–6 mm wide, and gray-green to yellow-brown but marked with small black and yellow spots. It bears lateral ridges and a dorsal ridge, and several blunt spikes on the abdomen. Pupation requires 7–60 days, depending on temperature. The butterfly, after it escapes from the pupal case, climbs and expands its wings to dry.

The adult is a white butterfly with a wingspan of about 63 mm in males, and 70 mm in females. The forewings have black tips, and the hindwing has a small amount of black at the front margin. Dorsally, the female, but not the male, also bears two prominent black spots and a black dash on the forewing. The ventral surface of the wings is usually pale yellow. The adults favor sunny areas containing flowers, and are most active in hot weather. Adults mate 1–4 days after emergence. The male butterfly of *P. brassicae* can be distinguished from *P. rapae* by the presence of one dark spot on the forewing of *P. rapae*.

The natural enemies of cabbage white butterfly are numerous, but perhaps most important are a baculovirus and the parasitoid *Cotesia (Apanteles) glomerata* (L.) (Hymenoptera: Braconidae). *Trichogramma* sp. (Hymenoptera: Trichogrammatidae) has been reared from eggs, but normally is not a very important mortality factor. General predators such as ground beetles (Coleoptera: Carabidae) and birds also can be locally important.

Damage

This species feeds predominantly on cruciferous species, but adults are attracted to mustard oil glycosides so other plants containing these chemicals also are attacked. Crops damaged include broccoli, Brussels sprouts, cabbage, cauliflower, horseradish, kohlrabi, mustard, rape, radish, rutabaga, sarson, toria and turnip. Many weeds are affected, including shepherd's purse, *Capsella bursa-pastoris*, flixweed, *Descurainia sophia*, hoary cress, *Cardiaria draba*, and many others. It is a defoliator, and because it is a fairly large insect, it can cause impressive levels of defoliation when present. However, damage tends to be limited to margins of fields.

Management

Large cabbage white now is much less damaging in Europe than formerly, possibly due to better weed management and better insecticides. The principal concern is that due to its dispersive nature, large numbers of butterflies may suddenly appear in some areas, suddenly triggering the need to control them. Normally, a single application of insecticide to foliage provides season-long protection to vegetables; field crops are usually not treated. The bacterial insecticide *Bacillus thuringiensis* is effective if applied to young larvae, though use generally requires more frequent application. For small-scale cultivation, netting may be used to cover the crop and prevent oviposition.

► Cabbageworm
► *Pieris rapae* (Linnaeus) (Lepidoptera: Pieridae)
► Vegetable Pests and Their Management

References

Feltwell J (1982) Large white butterfly. The biology, biochemistry and physiology of *Pieris brassicae* (Linnaeus), vol 18. W. Junk, The Hague, The Netherlands

Harvey JA (2006) Development of the herbivore *Pieris rapae* and its endoparasitoid *Cotesia rubecula* on crucifers of field edges. J Appl Entomol 130(9–10):465–470

Hochberg ME (1991) Intra-host interactions between a braconid endoparasitoid, *Apanteles glomeratus*, and a baculovirus for larvae of *Pieris brassicae*. J Anim Ecol 60:51–63

McKinlay RG (1992) Vegetable crop pests. CRC Press, Boca Raton, FL, 406 pp

Large Caddisflies

Members of the family Phryganeidae (order Trichoptera).

► Caddisflies

Large-Legged Thrips

Members of the family Merothripidae (order Thysanoptera).

► Thrips

Large Milkweed Bug, *Oncopeltus fasciatus* (Hemiptera: Lygaeidae)

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The large milkweed bug, scientific name *Oncopeltus fasciatus* (Dallas), is the most common of the five known species of this genus in the U.S. There are at least 24 species of *Oncopeltus* worldwide and these may all be called milkweed bugs because they feed on milkweed plants. Although all the bugs look quite similar, there are some differences in the color patterns. *Oncopeltus fasciatus* is found from the east coast to California, north to Massachusetts and south to Florida and Texas. Related species are found wherever species of milkweed grow. Asclepiadaceae is the very large family of milkweed species. *Oncopeltus fasciatus* (Dallas) has also been found on live oak in Florida, on the foliage of willow and flowers of goldenrod in Indiana, on the flowers of avocado in Texas, on oleander in Florida and on *Apocynum* in Missouri. The reports do not indicate whether the insects were actually feeding on the plants. In the laboratory, the bugs were tested on the following, but none would go through their life cycles on them: black walnuts, English walnuts, pecans, Brazil nuts, almonds, seeds of *Helianthus*, seeds of *Arachis hypogaea*, raisins, whole kidney beans, rolled oats, cantaloupe seeds, wheat, bluegrass, parsley, gelatin, cabbage, hamburger, peanut butter, fresh string beans and coconut. The bugs have been successfully reared through their life cycles in the laboratory on watermelon seeds that had the coats cracked, raw or blanched peanuts, sunflower seeds, pumpkin seeds and squash seeds. After several generations, milkweed bug strains became adapted to sunflower seeds, cashews and almonds. Survival and reproduction were poor for several generations until the insects became adapted. The sunflower seeds produced the best results in terms of survival and reproduction, but the results were never on a par with the results obtained from feeding them on milkweed seeds. Even after several years of generations fed on sunflower seeds, the bugs seem to still prefer milkweed seeds in choice tests.

The bugs are easy to rear in the lab on milkweed seeds and water. It is quite labor intensive to collect a year's supply of milkweed seeds in the fall when the seeds are ripe, and a number of attempts have been made to develop a chemically defined diet, but these attempts have not been very successful. Milkweed pods and seeds can be kept in a dry condition in a freezer, or at room temperature for years and still be adequate food for rearing the bugs.

Although a few laboratory studies have shown that adult milkweed bugs can live for short periods of time under freezing conditions, it is generally agreed that these bugs survive the winter only in warm climates. It is thought that all instars die in the fall in northern areas and that new insects migrate up from the south in the spring or summer because, in some states, they have not been seen until July. The large milkweed bug was found to be a migratory insect principally from laboratory studies using tethered insects to determine how long they could fly. The evidence does seem to be rather strong and there is no other explanation as to why they are never found over-wintering in the midwestern and northern states. The adult female large milkweed bug undergoes a reproductive diapause before it enters its migratory phase.

The large milkweed bug is described as a hemimetabolous insect that has five immature stages and the adult stage. The immature stages look very much alike except for size. Wing pads appear in the third instar and increase in size in the fourth and fifth instars. The adults have two pairs of fully developed wings in *O. fasciatus*. The temperature and the amount of available food affect the rate of growth and the size of the insects, but, in general, the adult female is about three-quarters of an inch long and is bigger than the male. At 29.5°C in one experiment, the egg stage lasted 4 days, the five immature stages lasted 5.8, 5.9, 6.1, 4.5 and 6.8 days, respectively. There is considerable variation in the life history of the bugs reported in the literature. There is great variability in the length of the adult stage, but many adults live for 2 months. The longest life span seen in the literature was 24.7 weeks for virgin females. Higher temperatures, longer photoperiods and lower densities of the insect increase their reproduction and also their mortality. As long as there are milkweed seeds available and the temperatures are not very cold, milkweed bugs will go through a series of life cycles and all stages of the bug may be seen at the same time on the plants.

The preferred food of the milkweed bug in the field seems to be *Asclepias syriaca* and some of the reasons given for the preference are that this species has a relatively large number of pods and the plants grow in clumps or groups. Some of the clumps can be very large and include hundreds of plants. Because the immature large milkweed bugs cannot fly, the adult female has to lay her eggs where there will be abundant food for the offspring. The eggs are usually laid in clumps of 30 or so on the undersides of the leaves, on the unopened pods, or on the fluff of the opened pod. The sucking mouth parts of *O. fasciatus* are fairly long compared to the size of the insect, but the mouth parts of the young stages cannot penetrate the seed pod to reach the seeds inside. The young insects can feed on the leaves and green pods, but they seem to prefer the ripe, brown seeds when they are available. When feeding on the ripe, brown, hard seeds, the insects build a short sheath or tube that can be seen on the surface of the seed. Some scientists theorize that this serves as a support or a guide for the stylets (mouth parts). The functional mouth of the milkweed bug and its relatives is made up of a pair of elongated maxillae and a pair of elongated mandibles. The maxillae form the inner members of this stylet bundle, and each maxilla has two deep grooves that are opposite the grooves of the other maxilla, and thus, two canals or tubes are formed. Saliva is pumped down one tube and fluids are sucked up through the other tube. There are barbs on the tips of the mandibles that aid in the penetration of foods. When feeding on ripe seeds, the insects eject their salivary secretions into the seeds and then suck up the digested or dissolved seed material. In this way, they completely remove all edible parts of the seed and leave nothing but the seed coat.

A number of species in the milkweed family and the closely related family, Apocynaceae, have been shown to contain cardenolides (digitalis-like, toxic compounds). Cardenolides are specific inhibitors of Na, K-ATPase activity, and, therefore, are toxic to many vertebrates and invertebrates. The milkweed bug (and probably other insects that feed on these two families of plants) sequesters the ingested cardenolides into the dorso-lateral space fluid by an energy-dependent physical process. The Na, K-ATPase activity of the milkweed bug is highly resistant to cardenolides, and the bug can tolerate high doses of cardenolide that would be lethal for vertebrates and many other invertebrates. The presence of the cardenolides in the milkweed bugs protect them from predation by many vertebrates and invertebrates. The predators learn that the milkweed bugs are toxic for them and they do not prey on them. There are many red and black insects (the colors of the milkweed bugs) who benefit from mimicking the colors of the toxic milkweed bugs. The cardenolides cause some birds to vomit, which is a quick way to determine the susceptibility of birds and other animals to cardenolides. Some investigators have shown that milkweed bugs feed preferentially on milkweed species that have higher levels of cardenolides, and that seed cardenolide content was a good parameter for the growth efficiency of *O. fasciatus*.

The large milkweed bug has been used extensively as a research insect because of the ease with which it can be reared. Some of the research has shown that the large milkweed bug is somewhat different from the majority of insects. One of these differences is that makisterone A is the major molting hormone of *O. fasciatus*. Ecdysone and 20-hydroxyecdysone are the principal molting hormones in most other insects that have been studied. Because insects cannot synthesize cholesterol, they must use precursor molecules to make the molting hormones. Campesterol has been suggested as the precursor for the synthesis of makisterone A. Precocenes are compounds derived from the plant, *Ageratum houstonianum*, and they have been shown to destroy the corpora allata of insects, principally in the Order Hemiptera. The corpora allata are the site of juvenile hormone synthesis, and the inactivation of the corpora allata in the younger large milkweed bug instars resulted in precocious metamorphosis to a small adult, inhibition of oogenesis in females and inhibition of long-term (migratory) flight in both males and females. The effects of precocene can be counteracted by an appropriate application of juvenile hormone.

The large milkweed bug midgut is made up of four subdivisions, and the residues of nymphal meals seem to be retained in the third region until after the molt to the adult when the residues are voided. The fourth region does not have a complete lumen until the adult ecdysis (molt).

The ovaries of Hemiptera are different from other insects. In the Hemiptera, each ovariole has a region of nutritive cells at the anterior end of a string of oocytes. Therefore, there is a nutritive tube that carries nutrients from the nutritive cells to the developing oocytes. This is called a telotrophic ovary.

Variations on the typical or normal appearance of *O. fasciatus* have appeared spontaneously in different laboratory strains around the world. A gynandromorph appeared in Oslo, and a white strain or a partially white strain has appeared in several different labs in the U.S. Interspecific hybridizations of *O. fasciatus* have been found rather frequently in nature, and, in some cases, hybrid individuals have been collected. The authors concluded that both pre- and post-mating isolating mechanisms work to prevent introgressive hybridization. In general, there is a gradual change in color in captive milkweed bugs, which is much less dramatic than in the preceding examples. However, the gradual change (often a lightening of the orange-red color) should be remembered because it might indicate that other changes occur in the bugs with prolonged cultivation. These changes are different in different laboratories; therefore, it might be wise to obtain insects from various laboratories when doing any type of research on milkweed bugs.

l-amino acids are by far the most common amino acids in animals. *O. fasciatus* has d-alanine in its hemolymph. This isomer must be produced during intermediary metabolism because it is not present in the milkweed plant. An antibacterial agent, active against *Staphylococcus aureus* and one strain of *Bacillus subtilis*, has been found in the hemolymph of the fifth instar. The formula of this compound was determined to be $C_{13}H_{14}O_3$, and it was suggested to have a three-ring structure. The hemolymph of the fifth instar also contains an agglutinating factor for human erythrocytes. However, its activity was lost after 45 min at room temperature.

O. fasciatus is a natural host for three species of trypanosomatids: *Leptomonas oncopelti*, *Phytomonas elmassiani* and *Crithidia oncopelti*. *Leptomonas oncopelti* has been found in various parts of the digestive tract and in the salivary glands. Binary fission switches to budding in the midgut of the bug. The flagellates do not appear in the rectum until adulthood. The flagellates form a "carpet" attached to the cuticular intima of the rectal glands of adults. Because the milkweed plant dies back every fall, and there is no continuity of latex tubules in the roots, the flagellates have no way of overwintering in the plants and, therefore, the plants have to be reinfected every year. Reinfection is probably done by *O. fasciatus*. The flagellates pass from bug to bug, probably by fecal contamination.

Photoperiod affects several aspects of the large milkweed bug's life. Mating and feeding activities reached the maximum levels at the end of the light phase. Long photoperiods produced higher levels of mating and feeding than did short photoperiods.

Large milkweed bugs have a very characteristic odor, which is readily picked up when handling the bugs. This odor probably comes from the accessory gland of the metathoracic scent apparatus in the adult. The odor is probably not a defensive secretion. The dorsal scent glands of the larvae do not function in the adult.

References

Chaplin SJ (1980) An energetic analysis of host plant selection by the large milkweed bug, *Oncopeltus fasciatus*. Oecologia (Berlin) 46:254–261

Feir D (1974) *Oncopeltus fasciatus*: a research animal. Annu Rev Entomol 19:81–96

Jones GL, Mei JV, Yin CM (1986) Meridic diet for *Oncopeltus fasciatus* (Heteroptera: Lygaeidae) and its utilization in evaluating an insect growth regulator. J Econ Entomol 79:323–328

Masner P, Bowers WS, Kalin M, Muhle T (1979) Effect of precocene II on the regulation of development and reproduction in the bug, *Oncopeltus fasciatus*. Gen Comp Endocrinol 37:156–166

Scudder GGE, Duffey SS (1972) Cardiac glycosides in the *Lygaeinae* (Hemiptera: Lygaeidae). Can J Zool 50:35–42

Larger Grain Borer, *Prostephanus truncatus* (Coleoptera: Bostrichidae)

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As are most other beetles in the family of Bostrichids, the larger grain borer, *Prostephanus truncatus* (Horn), is a wood-boring beetle. It is native to Central American and Mexican forests and has long been known to occasionally attack stored commodities such as maize and cassava, sporadically causing serious damage in small-scale farmers' stores. However, the beetle attracted much greater public and scientific interest after its serendipitous introduction into Africa in the late 1970s and early 1980s. The beetle was first observed by farmers in the Tabora region of Central Tanzania. This new pest caused tremendous damage to their maize harvest, and because of the resemblance of the flattened head of the beetle to commonly used trucks in East Africa, farmers called it "scania beetle." Later, the pest was identified as *P. truncatus*, which was probably introduced to Tanzania through maize imports from Mexico that had not been properly fumigated. A second independent introduction of *P. truncatus* happened around 1984, when the pest was first recorded in the greater Lomé area, the capital of the small west African state of Togo. From these two focal points of introduction, the beetle has spread, to date, to a total number of 17 African countries, thus covering a great part of the maize-producing region of sub-Saharan Africa. In some of these countries, *P. truncatus* has become the most serious pest of farm-stored maize, sometimes causing losses of up to 30 to 40% of the harvested commodity.

Biology, Ecology and Damage Potential

The larger grain borer attacks a whole variety of stored commodities besides the various tree species that are their natural host plants. However, the greatest damage is inflicted to farm-stored maize and cassava, though it is a more serious pest of maize than of cassava. Infestations often commence in the field when the adult beetles bore into the maize cobs prior to harvest. Female *P. truncatus* usually lay up to eight eggs in clutches in maize grains, and their offspring develop within the grains, feeding on the starchy-rich endosperm of the maize kernels. However, the greatest damage is caused by the tunneling behavior of the adult beetles that often turn the maize into flour. The enormous amount of frass caused by the feeding pattern of the adults is often the first and most conspicuous sign of a *P. truncatus* infestation. Larger grain borer attacks cause greater damage when the maize is stored on the cobs than as shelled grain, unlike the two other important pests of post-harvest maize in Africa, the maize weevil *Sitophilus zeamays* Motschulsky (Coleoptera: Curculionidae), and the Angoumois grain moth *Sitotroga cerealella* (Olivier) (Lepidoptera: Gelechiidae). Moreover, *P. truncatus* can thrive on maize even when the moisture content of the grain drops below a level of 10%, the threshold for most of the other pests attacking stored maize. In southern Togo, maize losses after an average storage period of 6 months increased from 11% prior to the introduction of *P. truncatus*, to more than 35%. In areas with high incidence of *P. truncatus* in Tanzania, up to 34% losses of maize have been observed after three months of on-farm storage. When male *P. truncatus* locate a suitable breeding substrate like maize where there are no females present, they produce a pheromone that is highly attractive to individuals of both sexes. Once the females have been guided to these sites, the males cease pheromone production. However, beetles feeding and reproducing on maize or other suitable food substrates are no longer receptive to the pheromone. Thus, the pheromone is of paramount importance for the host-finding behavior of the beetles. In the late 1980s, the chemical composition of the pheromone was identified. The pheromone was subsequently synthesized, and is currently commercially available. It is primarily used for monitoring purposes, particularly to document the spread of infestation of *P. truncatus* throughout sub-Saharan Africa. Larger grain borer adults are rather poor flyers. Pheromone trap data revealed that the beetles only fly during short periods at dusk and at dawn. Thus, the spread of the beetle in Africa is mainly due to movement of infested commodities, i.e., within and between countries trading maize and cassava.

Conventional Control Strategies

After its first detection in Tanzania, campaigns were launched in the early 1980s to eradicate the beetle from the African continent. Prostephanus truncatus is highly susceptible to synthetic pyrethroid insecticides like permethrin and deltamethrin, and also to fumigants like phosphine and methyl bromide, (though the latter is now banned in many African countries). However, since the beetle not only attacks stored commodities, but also breeds in natural forest habitats, these eradication efforts were not successful. Yet, binary insecticide programs, consisting of a synthetic pyrethroid for control of *P. truncatus* and an organophosphorus insecticide for control of other storage pests like *S. cerealella*, were successfully implemented in many affected East African countries. However, the adoption rate of such a chemical control strategy was much lower in West Africa, mainly due to socio-economic constraints on behalf of the farmers, and logistical difficulties in the distribution of the insecticides.

Classical Biological Control

As an exotic outbreak pest in Africa that caused spectacular damage in its new area of distribution but was of considerably lower economic importance in its area of origin in Mexico and Central America, *P. truncatus* was considered to be a prime candidate for a classical biological control program. Hence, in the mid 1980s, intensive surveys were carried out in Mexico and several countries of Central America to identify efficient natural enemies of *P. truncatus*. However, the natural enemy complex of *P. truncatus* turned out to be rather poor in diversity. Several hymenopteran parasitoids, mainly pteromalids, were found to be associated with *P. truncatus*. Yet, all of these parasitoids were of cosmopolitan distribution, already existed in Africa, had a very broad host range, and showed no clear host preference for *P. truncatus*. Therefore, they were not considered for importation into Africa. The only specialized natural enemy that was identified during these surveys was the predator *Teretrius* (formerly *Teretriosoma*) *nigrescens* (Lewis) (Coleoptera: Histeridae). A close association between *P. truncatus* and *T. nigrescens* had already been observed prior to the introduction of the larger grain borer into Africa. During the subsequent search for natural enemies of *P. truncatus* in Mexico and Central America, the predator was always found in grain stores that were infested by the larger grain borer. Moreover, once the synthetic pheromone of *P. truncatus* became available, consistently high by-catches of *T. nigrescens* were recorded in pheromone traps located both in areas with agricultural production as well as in forests. Later, studies revealed that the predator uses the pheromone of *P. truncatus* as a kairomone to locate its prey. Electro-antennograms then showed that *T. nigrescens* reacts as sensitively to the pheromone as *P. truncatus* itself. In a large series of laboratory experiments by British and German researchers, *T. nigrescens* was able to fully suppress *P. truncatus* populations at a predator:prey ratio of 1:10. Both the adults and the larvae of *T. nigrescens* feed on the eggs and the larval stages of *P. truncatus*, though the larvae are far more voracious than the adult beetles. Adult *T. nigrescens* are strong flyers, long-lived with a longevity exceeding 20 months, and can survive extended periods of starvation (more than 60 days). Based on these findings, the predator was considered for importation into Africa. However, prior to the release, concerns were expressed about the potential ecological risks associated with a wide spread deployment of *T. nigrescens* in Africa. Histerids are, in general, oligo- to polyphagous predators. Therefore, prior to the release, the prey behavior of *T. nigrescens* was investigated in laboratory experiments. Results of these studies showed that *T. nigrescens* readily preys on other insects, mainly other coleopteran and lepidopteran larvae that occur in the maize storage environment, but it strongly prefers *P. truncatus* as prey in a choice situation. A post-release prey composition study, using electrophoretic gut content analysis techniques, showed that *T. nigrescens* clearly prefers *P. truncatus* as prey. The predator was first released in 1991 in southern Togo, and three years later in Ghana and Kenya. Between 1992 and 1997, a long-term impact assessment study was conducted in southern Togo and the neighboring Republic of Benin. Data from pheromone traps, as well as from large-scale storage experiments and surveys of farmers' maize stores showed a rapid spread of the predator, with substantially decreased trap catches of *P. truncatus*, as well as significantly reduced infestation levels and post-harvest losses of maize, particularly in the south of Togo and Benin. In Kenya, where the predator had been released in a bush land region dominated by forests, long-term pheromone trapping revealed a substantial decline in trap catches of *P. truncatus*. Thus, *T. nigrescens* is capable of controlling *P. truncatus* both in the maize store environment, as well as in its native forest habitat. To date, the predator has been released in eight African countries and several impact assessment studies are ongoing. This is the first case where classical biological control has been rather successfully used against a post-harvest pest.

► Stored Grain and Flour Insects

References

Borgemeister C, Djossou F, Adda C, Schneider H, Djomamou B, Azoma K, Markham RH (1997) Establishment, spread and impact of *Teretriosoma nigrescens* Lewis (Coleoptera: Histeridae), an exotic predator of the larger grain borer *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae), in south-western Benin. Environ Entomol 26:1405–1415

Hodges RJ (1994) Recent advances in the biology and control of *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae). In: Highley E, Wright EJ, Banks HJ, Champ BR (eds), pp 929–934, Proceedings of the 6th international working conference on stored-product protection, 17–23 April 1994, Canberra, Australia

Markham RH, Wright VF, Rios Ibarra RM (1991) A selective review of research on *Prostephanus truncatus* (Col.: Bostrichidae) with an annotated and updated bibliography. Ceiba 32:1–90

Rees DP (1985) Life history of *Teretriosoma nigrescens* Lewis (Coleoptera: Histeridae) and its ability to suppress populations of *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae). J Stored Prod Res 21:115–118

Scholz D, Borgemeister C, Meikle WG, Markham RH, Poehling HM (1997) Infestation of maize by *Prostephanus truncatus* initiated by male-produced pheromone. Entomol Exp Appl 83:53–61

Largidae

A family of bugs (order Hemiptera).

► Bugs

Larva

(pl., larvae) The growing stage of an insect (usually an insect with complete metamorphosis). The feeding stage between the egg and pupal stages. The immature stages of mites also are called larvae. Larval insects usually bear little resemblance to the adult stage, and often feed on different items.

Larvicide

An insecticide used to control the larvae of insects. This term is often used to describe the insecticides used for suppression of mosquito larvae (contrast with adulticide).

Larviform

Shaped like a larva.

Larviporous

A method of reproduction, especially in flies, wherein the eggs hatch within the female's body, and the larvae are deposited. In some cases the larvae obtain nutrition from the female, and pupate almost immediately upon being deposited.

Lasiocampidae

A family of moths (order Lepidoptera). They commonly are known as tent caterpillars, lappet, or lackey moths.

► Lappet Moths
► Butterflies and Moths

Lasiochilidae

A family of bugs (order Hemiptera).

► Bugs

Latent Infection

An inapparent infection in which the pathogen is still present in a "dormant" or noninfective phase, and in which a certain pathogen-host equilibrium is established.

Latent Learning

This form of learning, also called exploratory learning, involves the ability to recognize and remember landmarks. Social insects use landmarks as a means of finding their way back to their nest after they leave to forage for food.

► Habituation
► Associative Learning
► Insight Learning

Lateral Oviduct

A tube of the female reproductive system that connects the ovaries to the common oviduct, through which eggs pass prior to fertilization (Fig. 20).

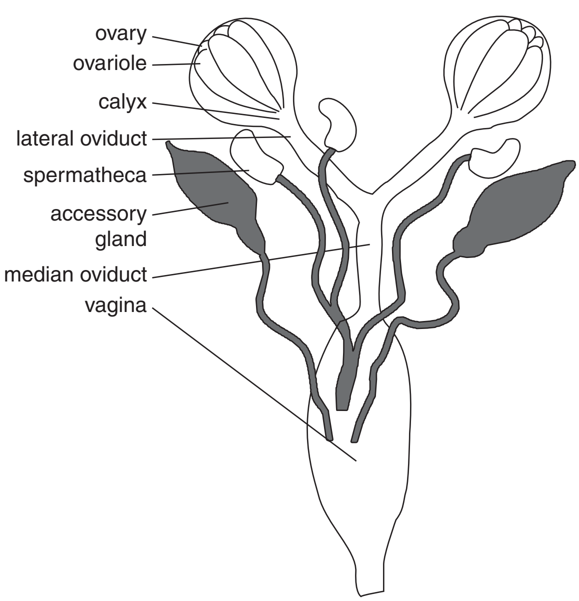
Lathridiidae

A family of beetles (order Coleoptera). They commonly are known as minute brown scavenger beetles.

► Beetles

Latreille, Pierre André

Pierre Latreille was born on November 29, 1762 at Brive, in the province of Limousin, France. An illegitimate child of the baron d'Espargnac, he was abandoned by his mother at a church in Brive. His biological father eventually made financial arrangements for his son's education,



Lateral Oviduct, Figure 20 **Diagram of female reproductive system, as found in *Rhagoletis* (Diptera) (adapted from Chapman, The insects: structure and function).**

and he was educated at the Collège des Doctrinaires at Brive and the Collège du Cardinal Lemoine at Paris. He also was awarded a Master of Arts from the Paris University in 1780, entered a seminary and was made a Deacon in 1786. He likely was made a priest, though there is no record of this, and he was acting vicar at Lostanges in October 1789. At this time he became interested in entomology, living on the income that his father, the général baron d'Espargnac, had established for him. However, the French Revolution would cause him to be imprisoned, and sentenced to death or deportation. His interest in insects was recognized while he was in prison, and a sympathetic official terminated Latreille's sentence. He remained in prison until 1794, however, and he gave up the priesthood and became a teacher. In 1796, encouraged by Fabricius, he published the "Précis des caractères génériques des insectes." This innovative treatise created the concept of insect families. In 1798 he received an appointment at the Muséum, where he worked closely with Lamarck. In 1814 he was named a member of the Académie des Sciences, and he entered a very productive stage of his life, but he remained very poor. He often assisted others in their natural history publications, though he also published his own work. In Cuvier's "Règne Animal" (1829) Latreille laid down the taxonomy of the entire Arthropoda. Eventually he replaced Lamarck as the dominant scientist of the institute. In 1830 he was awarded a new chair at the Muséum. Thus, he received recognition only late in life, despite a legacy of innovative contributions and decades of toil. Latreille is remembered primarily as a taxonomist, though he made important contributions in other areas. He introduced new methodologies and examined an enormous number of taxa. He believed in basing taxonomic groupings on the natural order: assembling species into genera, then into families, etc. Indeed, he was most interested in establishing genera, and named hundreds of new genera. Latreille also had profound impact on zoological nomenclature, emphasizing the principle of

Latreille, Pierre André, Figure 21 **Pierre Latreille.**

priority, insisting that families be named after an included genus, and emphasizing the concept of type species of a genus. Latreille was interested in morphology, and created several new terms. Interestingly, he considered field work most important, and was particularly interested in behavior. He sometimes incorporated behavioral characteristics into his taxonomic treatments. Though Latreille's achievements were often overshadowed by better-known scientists of the era, he eventually became known as the foremost entomologist of his time, and has even been called the "prince of entomology." He died at Paris on February 6, 1833 (Fig. 21).

References

Dupuis, Claude (1974) Pierre André Latreille (1762–1833): the foremost entomologist of his time. Annu Rev Entomol 19:1–13

Herman LH (2001) Latreille, Pierre Andre. Bull Am Mus Nat Hist 265:94–96

Lauxaniid Flies

Members of the family Lauxaniidae (order Diptera).

► Flies

Lauxaniidae

A family of flies (order Diptera). They commonly are known as lauxaniid flies.

► Flies

LC_{50}

An abbreviation for lethal concentration, with the subscript denoting a proportion of the population tested. LC_{50} is the concentration of a substance that kills half of the test organisms.

LD_{50}

An abbreviation for lethal dose, with the subscript denoting a proportion of the population tested. LD_{50} is the dose of a substance that kills half of the test organisms

Lea, Arthur Mills

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Arthur Mills Lea was born on August 10, 1868 in Sydney, Australia. He began collecting beetles at an early age. During his frequent visits to the Australian Museum where he was assisted and encouraged by Sir William J. Macleay and George Masters. He enrolled in night school to learn Latin and that was the only supplementary education he received, as his family could not afford to give him more. At the age of 15 he began work with an accountant firm in Sydney and remained in this employment for 6 years, during which he pursued entomology as a hobby, winning prizes for his excellent insect collection and drawings of insects. He also taught himself French and German in order to understand entomological articles published in those languages. In 1891 he was appointed as entomologist's assistant in the New South Wales Department of Agriculture in Sydney and later became Entomologist in the Western Australian Department of Agriculture. In 1899 he took up the position of Government Entomologist in Tasmania. In little more than ten years Lea has built the largest collection of Tasmanian Coleoptera (most of this collection is now in the South Australian Museum, Adelaide) and established himself as a recognized authority in applied entomology and biological control. In 1910 he became Museum Entomologist in the South Australian Museum. He worked for this museum until his untimely death on February 29, 1932. During his 21 years in the South Australian Museum more than a million specimens were added to its collections. Arthur Lea was undoubtedly the most productive Australian Coleopterist. He described and named 5,432 species new to science and published a staggering number of works. He had an exuberant personality and gave inspiration to many of his colleagues and students.

Reference

Zimmermann EC (1993) Australian weevils, vol 3. CSIRO, East Melbourne, pp 622–648

Lea, H. Arnold

Arnold Lea was born on November 13, 1907, and was raised in Transvaal, South Africa. He was educated at the University of Pretoria, and in 1930 joined the Division of Entomology in Pretoria, the start of a 42-year career with the South African Department of Agriculture. South Africa experienced severe plagues of locusts beginning in 1932, and Lea joined a newly organized Locust Research Institute. His first task was to improve insecticidal control of red locusts, using improved bait formulations of sodium arsenite. Later he worked on identification of breeding areas and disruption of incipient locust outbreaks. With the onset of World War II, his area of responsibility was changed to North Africa and he developed desert locust campaigns, based on distribution of BHC-treated bait, to help protect the food supply of the area. Returning to civilian life in 1946, he again tackled the sodium arsenite bait problem because ranchers were increasingly reluctant to use this toxic material, which often killed livestock. He enlisted use of BHC against brown locusts beginning in 1947. Lea was responsible for effective emergency locust suppression campaigns, but he also found time for a disciplined, scientific approach to understanding the locust problem. Throughout his career, he studied locust forecasting, population dynamics, and phase transformation. A principal product of his investigations was "Locust control and research in southern Africa" (1972), and he is widely acknowledged as being one of the eminent locust researchers. Lea was fellow of several scientific societies and served as president of the Entomological Society of Southern Africa, and editor of its journal. He died at Pretoria, South Africa on August 25, 1989.

Reference

Brown D (1991) Lea HAF (1907–1989) Antenna 15:61–66

Leaching

The movement of pesticides through the soil, assisted by water.

Leaf Beetles (Coleoptera: Chrysomelidae)

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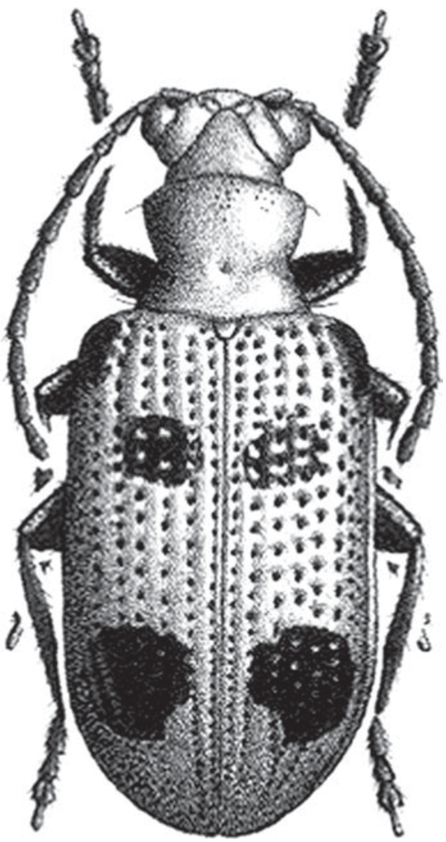
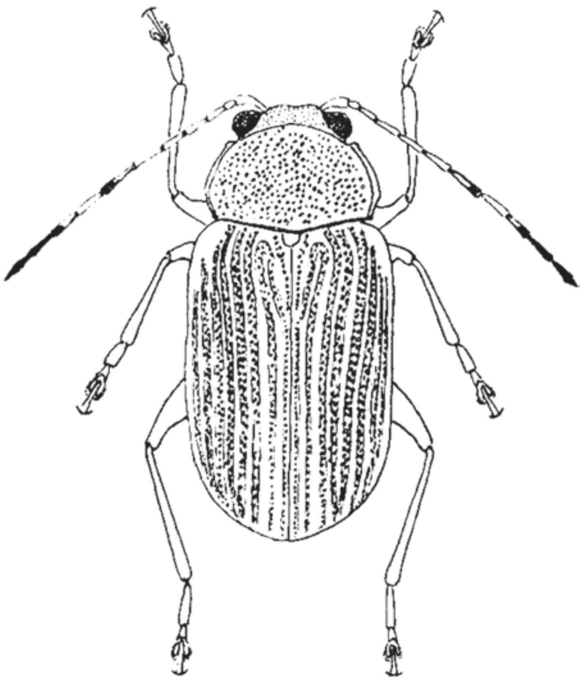
The Chrysomelidae, or leaf beetles, are the third largest family in the Coleoptera, with 37,000 described species and possibly as many as 60,000 when estimates of undescribed species are included. Only the Curculionidae and Staphylinidae are larger families. As the common name implies, Chrysomelidae are intimately associated with plants, although specific associations are known for only a small minority of the species. Chrysomelid adults are small to medium-sized beetles, often brightly colored, boldly patterned, or metallic. Some species are covered with hairs or scales. Most species are ovate or elongate-ovate, but body shape can vary from elongate to almost spherical (Figs. 22–26).

Classification

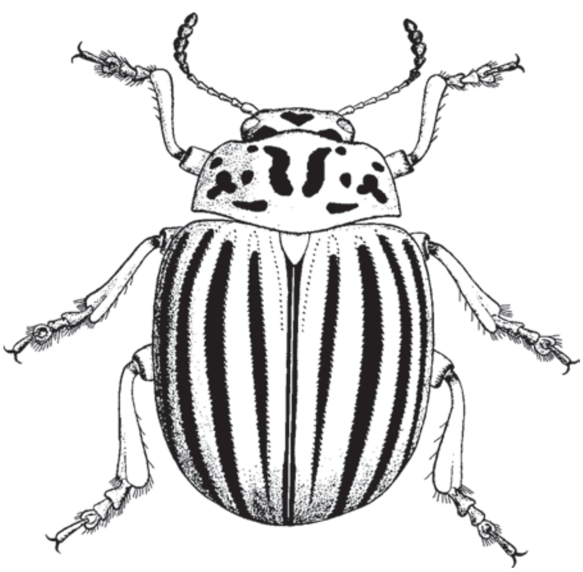
Chrysomelidae belong to the infraorder Phytophaga of suborder Polyphaga within the order Coleoptera



Leaf Beetles (Coleoptera: Chrysomelidae, Figure 22 Criocerinae: ***Neolema sexpunctata*** **(Olivier).**

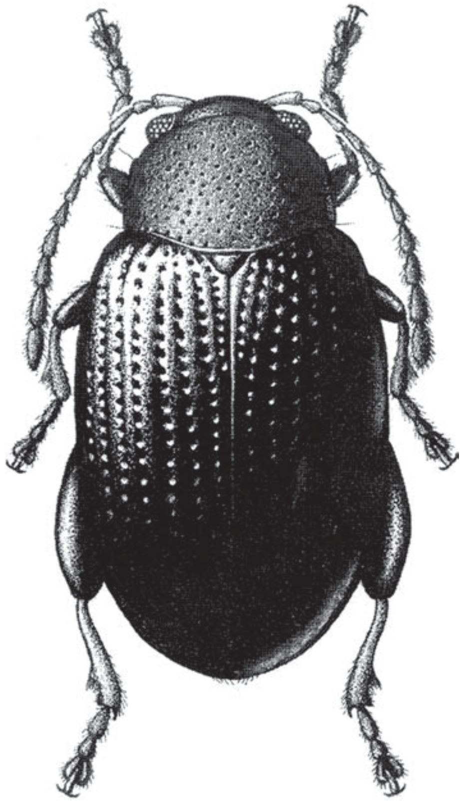


Leaf Beetles (Coleoptera: Chrysomelidae, Figure 23 Eumolpinae: ***Colaspis louisianae*** **(Blake).**

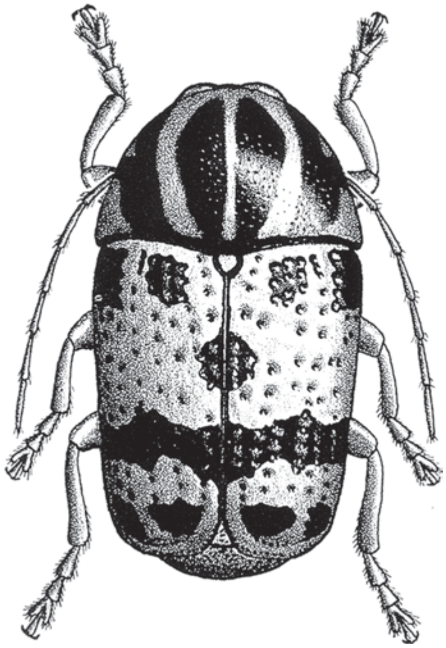


Leaf Beetles (Coleoptera: Chrysomelidae, Figure 24 Chrysomelinae: ***Leptinotarsa decimlineata*** **(Say).**

(beetles). The Phytophaga are characterized by crytopentamerous tarsi, in which the fourth tarsal segment is greatly reduced (sometimes entirely absent) and largely hidden by the third segment. The



Leaf Beetles (Coleoptera: Chrysomelidae, Figure 25
Galerucinae: *Chaetocnema pulicaria* (Melsh).



Leaf Beetles (Coleoptera: Chrysomelidae, Figure 26
Cryptocephalinae: *Cryptocephalus maccus* (White).

Phytophaga contain the superfamily Chrysomeloidea, which includes the Chrysomelidae, and the superfamily Curculionoidea (weevils and their allies). The Chrysomelidae are one of two major families in the Chrysomeloidea (the other being the Cerambycidae) and are distinguished by having antennae not partially surrounded by the eyes, and by the presence of a basal hood on the median lobe of the male genitalia.

Although the major groups within the Chrysomelidae have been generally recognized, the taxonomic ranks and boundaries of these groups continue to be actively debated. Recent phylogenetic analyses have resulted in the removal of several small problematic groups from the Chrysomelidae to other families, and some realignments and changes of the traditional subfamily classification. In the United States, the following subfamilies occur.

Bruchinae

Until recently classified as a separate family, bruchids, or seed beetles, are now regarded as a subfamily of the Chrysomelidae, closely related to the Old World and Neotropical Sagrinae. Seed beetles are distinguished by their robust bodies, elongate heads, and enlarged hind legs. Larvae feed within seeds of legumes and other plants.

Donaciinae

Adults in this subfamily somewhat resemble lepturine cerambycids in body shape. The head and pronotum are narrower than the width of the elytra at the base, and the general color is bronze or sometimes dark metallic. The family is aquatic in the larval stage and adults are found on emergent aquatic plants such as waterlilies or arrowheads. The underside of the adult is densely covered with hydrofuge hairs, and the hind femora often bear small teeth. This subfamily is world-wide except South America; in the Western Hemisphere representatives occur only as far south as Costa Rica.

Criocerinae

Adults of this subfamily are generally brightly colored and all have a characteristic constriction across the pronotum. As in the preceding family, the head and pronotum are narrower than the basal width of the elytra, and the head has deep frontal grooves forming an “X” on the facial area (Fig. 22). Larvae feed openly on plants, covering themselves with their own feces for protection. Native North American species feed for the most part on plants of the families Solanaceae or Commelinaceae and cause little economic harm. However, three introduced species have become pests. One, the cereal leaf beetle (*Oulema melanopus* (L.)) is a serious pest of grain, and two species of *Crioceris* feed on asparagus.

Hispinae

This subfamily has recently been expanded to include the tortoise beetles (Cassidini). The nominate tribe, Hispini, contains elongate beetles, frequently with the elytra very strongly punctate and costate. Members of the tribe Cassidini, on the other hand, are very broadly ovate to hemispherical, with margins of the pronotum and elytra explanate. In many species the head is concealed under the front margin of the pronotum. Many adult cassidines have striking gold or other metallic colors on the dorsal surface which in some species can be turned on or off by the animal. Becauce these colors reside in the living tissues, they unfortunately disappear in pinned specimens. Although ‘typical’ hispines and cassidines have contrasting shapes, intermediate species occur and are not uncommon in tropical areas. All Hispinae have mouthparts that appear crowded into a constricted opening in the head capsule, and all have four-segmented tarsi, in which the reduced fourth segment found in the rest of the Chrysomelidae has been completely lost. Larvae of the Hispini are leaf miners or, in a widespread Neotropical tribe, specialists in the unrolling terminal leaf of large monocots such as Heliconia; cassidine larvae are open feeders on many plants and cover their bodies with fecal shields for protection. In some tropical cassidine genera, maternal care of larvae has been observed.

Chrysomelinae

The Chrysomelinae include some of the largest species of Chrysomelidae. As adults, most are robust oval to hemispherical beetles. The third tarsal segment is entire or at most weakly bilobed (it is strongly bilobed in some Eumolpinae that resemble chrysomelines), and a membrane between the clypeus and labrum is present. A more subjective but quite reliable method of separating chrysomelines from other robust Chrysomelidae is that, viewed from above, the head capsule of most Chrysomelinae appears rectangular with the eyes set diagonally at the anterior corners. Many chrysomeline adults have striking color patterns or bright metallic colors. Adults of Neotropical Doryphora, Platyphora and Metastyla have a prominent horn arising from the ventral surface between the middle and hind legs. Species of Doryphora are among the largest known Chrysomelidae. Adults of the New Guinea genus Promechus are large, elongate and bear a close resemblance to large Buprestidae. Larvae of Chrysomelinae are open feeders on leaves and many are chemically protected. The Colorado potato beetle, (*Leptinotarsa decemlineata* (Say)), one of the most destructive insect pests in the world (Fig. 24), belongs to this subfamily.

Galerucinae

This subfamily is characterized by antennae set close together between the compound eyes, antennal calli above the insertions, and the pronotum often narrower than the base of the elytra but without the transverse constriction found in the Criocerinae. This is the largest subfamily in the Chrysomelidae, the more so since the formerly independent Alticini (flea beetles) are now included in this subfamily. Although most species from the two major tribes Galerucini (rootworms) and Alticini can readily be distinguished by the size of the posterior femur (greatly enlarged in the flea beetles), many intermediate forms exist and a recent phylogenetic analysis indicates that the Galerucini is paraphyletic with respect to the Alticini. Adult galerucines display feeding behaviors ranging from narrow oligophagy to polyphagy. Larvae are mostly subterranean root feeders, but some open leaf feeders occur in both the Galerucini and Alticini. While most species are of no economic significance, several Galerucini species in the subtribe Diabroticina are extremely serious pests of corn and beans. Control of the corn rootworms (*Diabrotica* spp.) is the one of the costliest insect pest problems in North America.

Eumolpinae

This group, which reaches its greatest diversity in South America, is the second largest subfamily in the Chrysomelidae. Adults range from large to very small, most are broadly oval with glossy dark or metallic colors. Recent phylogenetic studies have placed the formerly independent Synetini and Megascelidini within the Eumolpinae. Although the body shape found in these tribes (slender and elongate) is not typical for the subfamily, intermediate genera exist and genitalic characters strongly support their inclusion in the Eumolpinae. Larval eumolpines apparently are all root feeders; the biology is known for only a few species. Adults are leaf or pollen feeders and tend to be oligophagous or polyphagous. Some appear to specialize on young leaves. In North America, a few species are intermittent pests of strawberries and sweet potatoes, and other species cause occasional short-term damage to corn, grapes, and other crops.

Lamprosomatinae

This small subfamily is worldwide with most of its diversity in the American tropics. Only one species, *Oomorphus floridanus* Horn, occurs in North America and it is limited to the tip of the Florida Peninsula. Adults are small and oval to almost spherical, with legs and antennae that can retract into groves on the lower body surface. The upper surfaces are always smooth and shiny. Adults feed on leaves of various trees and known larvae feed on the young bark of trees, living in cone-shaped cases constructed of fecal matter and wood particles.

Cryptocephalinae

Members of this subfamily are characterized by a compact body, the second to fourth abdominal sterna narrowed medially, and the pygidium exposed. The subfamily contains three tribes until recently considered separate subfamilies: Cryptocephalini, Clytrini, and Chlamisini. Larvae of all species are case-bearers. Cryptocephalini larvae are found in leaf litter and detritus, on which they are thought to feed. Many larvae of Clytrini are found in association with ants, although it is not known whether this trait holds true for the majority of the tribe. Larvae of Chlamisini feed on leaves alongside the adults. Adult Chlamisini are noteworthy for the extreme rugosity of their dorsal surfaces, giving many species the appearance of pieces of caterpillar frass. While the effectiveness of this mimicry on birds and lizards has not been tested, there are documented instances of entomologists being fooled by the resemblance.

Chrysomelidae and Pest Management

Relatively little research has been done on natural enemies of pest Chrysomelidae. Before the era of modern pesticides, several natural enemies of the Colorado potato beetle had been identified and their effectiveness as control agents was beginning to be investigated. The introduction of synthetic pesticides following World War II put an end to this line of research, since it was assumed that the new miracle chemicals would eliminate the need for alternate forms of control. Now, after decades of attempts at chemical control, the Colorado potato beetle has evolved a complex, multifaceted spectrum of resistances virtually unmatched in any other insect. Not surprisingly, there are the beginnings of renewed interest in the natural enemies of this pest.

While the economic damage inflicted by the corn rootworm complex and the Colorado potato beetle are among the best known effects of the Chrysomelidae, this family also has its positive aspects as a source of biological control agents of weeds. One of the success stories of classical biological control is the use of two species of the chrysomeline genus *Chrysolina* to control the Klamath weed in the western United States. Another success story has been the importation of the alligator weed flea beetle from Argentina. Alligator weed is an aquatic plant accidentally introduced from South America into the Southeastern United States. The weed was highly invasive in fresh water bodies, and its uncontrolled growth choked lakes and rivers. Once the flea beetle was introduced, its feeding reduced alligator weed to a relatively rare species in the U.S. More recently, Palearctic *Apthona* flea beetles have been introduced into western rangelands to control leafy spurge, and several European Galerucini have been introduced in an attempt to control purple loosestrife in northeastern United States. Invasion by weeds is a continuing and growing problem (e.g., tropical soda apple in Florida and Melastomataceae in Hawaii), and Chrysomelidae are now routinely investigated as potential control agents of these emerging weed problems.

References

Casagrande RA (1987) The Colorado potato beetle: 125 years of mismanagement. Bull Entomol Soc Ame 33: 142–150

Graham F Jr (1984) The dragon hunters. Dutton, New York, New York. 333 + xii pp

Jolivet P (1997) Biologie des Coléoptères Chrysomélides. Sociéte Nouvelle des Éditions Boubée, Paris, France. 279 pp

Konstantinov A, Vandenberg N (1996) Handbook of Palearctic Flea Beetles (Coleoptera Chrysomelidae: Alticinae). Cont Entomol Int 1:237–439

Lingafelter SW, Konstantinov AS (1999) The monophyly and relative rank of alticine and galerucine leaf beetles: a cladistic analysis using morphological characters (Coleoptera: Chrysomelidae). Entomologica Scandinavica 30:397–416

Reid CAM (1995) A cladistic analysis of subfamilial relationships in the Chrysomelidae sensu lato (Chrysomeloidea). In: Pakaluk J, Slipinski SA (eds) Biology, phylogeny, and classification of Coleoptera: papers celebrating the 80th birthday of Roy A Crowson. Muzeum i Instytut Zoologiii PAN, Warsaw, Poland pp. 559–631

Riley EG, Clark SM, Flowers RW, Gilbert AJ (2002) Family 124. Chrysomelidae. In Arnett RH, Thomas MC (eds) American Beetles, Vol. 2. CRC Press, Boca Raton, Florida, pp. 617–691

Leaf Blotch Miners

Members of the family Gracillariidae (order Lepidoptera).

► Leafminer Moths
► Butterflies and Moths

Leafcutter Moths (Lepidoptera: Incurvariidae)

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Florida State Collection of Arthropods,
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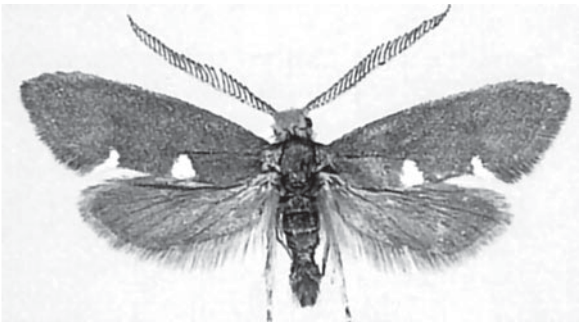
Leafcutter moths, family Incurvariidae, total about 116 species from all regions, but most are



Leafcutter Moths (Lepidoptera: Incurvariidae), Figure 27 Example of leafcutter moths (Incurvariidae), *Incurvaria masculella* (Denis and Schiffermüller) from Italy.

Palearctic (64 sp.), divided into two subfamilies, Incurvariinae and Crinopteryginae. The family is in the superfamily Incurvarioidea, in the section Incurvariina, of division Monotrysia, infraorder Heteroneura. Adults small (7–18 mm wingspan), with roughened head; haustellum reduced, scaled; labial palpi upcurved; maxillary palpi 5-segmented and folded. Maculation usually is somber, with large spots or bands and some iridescence. Adults are mostly diurnal in shaded habitats. Larvae are leafminers at first, then switch to leaf skeletonizing on a variety of host plants; some are casebearers or shoot borers (Fig. 27).

References

Nielsen ES (1981) A taxonomic revision of the species of *Alloclemensia* n. gen. (Lepidoptera: Incurvariidae s. str.). Entomol Scand 12:271–294

Nielsen ES (1982) Incurvariidae and Prodoxidae (Lepidoptera: Incurvarioidea) from the Himalayan area. Insecta Matsumurana 26:187–200

Nielsen ES, Davis DR (1981) A revision of the Neotropical Incurvariidae s. str., with the description of two new genera and two new species (Lepidoptera: Incurvariidae). Steenstrupia 7:25–57

Scoble MJ (1980) A new incurvariine leaf-miner from South Africa with comments on structure, life-history, phylogeny, and the binomial system of nomenclature (Lepidoptera: Incurvariidae). J Entomol Soc S Afr 43:77–88

Wojtusiak J (1976) Incurvariidae. In: Klucze do Oznaczania Owadów Polski. 27. Motyle–Lepidoptera 94:1–60. Polskie Towardzystwo Entomologiczne (in Polish)

Leaf-Cutting Ants (Formicidae: Myrmicinae: Attini)

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All ant species in the tribe Attini (Formicidae: Myrmicinae) cultivate a symbiotic fungus (Basidomycete: Lepiotacae) in order to feed their brood. The most conspicuous members of this tribe are undoubtedly the leaf-cutter ants from the genera *Atta*, *Acromyrmex* and *Trachymyrmex*. These ants cut leaves, which they prepare by removing surface waxes that normally harbor fungicides, before feeding their symbiotic fungus with it. The fungus helps to detoxify the leaves by degrading the insecticides which are normally found inside the leaves. The larvae feed basically on the fungus, whereas workers feed also on sugary plant sap flowing from the leaves while they are being cut. These ants build subterranean nests in which they grow their fungus which also needs a symbiotic bacterium in order to prosper. The workers regulate nest conditions so as to maintain humidity, temperature and carbon dioxide concentrations between narrow ranges. Workers avoid contaminations from other fungi and bacteria thanks to antibiotic secretions from their metapleural glands and the action of the symbiotic bacterium. The filamentous bacterium (Actinomycete) of the genus *Streptomyces* produces antibiotics specifically targeted to suppress the growth of the specialized garden-parasite *Escovopsis*. The symbiotic fungus is known only to occur in association with Attini ants. The lower Attini, which are not considered to be leaf-cutting ants, feed their fungus flowers, fruit pulp, dead insects, and animal excrements.

The Colony

The leaf-cutting ant colony is normally monogynic, that is, it contains a single queen. A few cases of polygynic colonies (2–6 queens) have been reported, but this certainly is not the norm for these ants. The colony is formed by different individuals and each type of individuals is called a caste. The leaf-cutting ant colony contains normally only female individuals of at least two different castes, the queen and the workers. Just before the beginning of the tropical rain season, the colony produces winged individuals, fertile males and females which wait inside the nest for their nuptial flight after the first rains. All these types of individuals or castes are found in their different life stages such as eggs, larvae, nymphs and adults in a single colony. The architecture of the subterranean nest is characteristic for each species. Workers also have behavioral castes. Young workers are more often engaged in caring for the fungus whereas older workers forage or engage in dumping rubbish and dead ants. The different components of a typical colony are:

The Queen

Most mature leaf-cutting ant colonies have a single fertile queen, i.e., they are monogynic. The queen is the fertile female individual, inseminated during the nuptial flight by various males, in charge of laying eggs. The eggs might have been fertilized by a male spermatozoon or not. In the first case, they will produce females; in the second, they produce males. Depending on the amount of food the larvae of females receive (and may be on hormones provided by the colony), they will become either virgin queens, ready to start a nuptial flight and eventually a new colony, or sterile worker ants.

The Workers

Workers are sterile female ants. A single *Atta* colony has workers of different sizes – they are polymorphic – whereas those from *Acromyrmex* and *Trachymyrmex* colonies are monomorphic, i.e., they are all approximately the same size. Polymorphism among workers from *Atta* species is continuous, that is, sizes of workers vary from just above a millimeter to over 2 cm in length. The smallest workers are found mostly inside the nest, caring for the fungus and larvae, whereas the bigger ones engage in foraging, leaf cutting, and transport of leaf fragments to the nest. *Atta* colonies have a special soldier caste, formed by very large workers with strong mandibles, which make them have big heads with small brains.

Winged Sexual Individuals

The sexually active individuals are born with transparent wings that allow them to engage in the nuptial flight, at the beginning of the rain season, where they copulate. Males die shortly after a single copulation. Once the winged female is inseminated, she lands on the ground, sheds her wings, looks for an appropriate sandy spot, and starts digging her initial nest. Often winged individuals are found inside the nest. These are virgin males or a queen that failed to swarm or will do so in the future. Virgin females in addition have much smaller gasters compared to their physogastric mothers. Males have much smaller heads than females. Males show little activity and their main role is transferring their sperm to the female's spermatheca.

The Super-Organism

In a given leaf-cutter ant colony we generally find only a single queen and her daughters, the workers. Thus, a colony is a family unit. The coordination between the members of a colony-family is so tight that some authors consider the colony to be a superorganism. That is, each individual acts to optimize the adaptive value of the colony rather than itself. The queen dedicates herself to produce eggs, the gut of the larvae and that of workers works like a communal digestive system, the foragers work as the movable extremities of the colony providing the required food, and the glandular secretions of all individuals mingle so as to produce a characteristic colony odor. Thus, the colony has properties that are known to characterize an organism. This is especially true when we look at the systems regulating the temperature and humidity of the nest.

The Uninvited Guests

A leaf-cutting ant colony hosts a number of other animals. They range from invertebrate ectoparasites to vertebrates such as snakes, lizards and birds. They normally feed on the brood and/or use the nest as shelter. Reptiles especially profit from the nice temperature in a leaf-cutting ant nest, which is suitable for their eggs. That is certainly the case with the snake *Elapomorphus lemniscatus* (family Boidae) which is a frequent visitor of *Acromyrmex* nests. Once inside the nest, the reptile houses in a fungus chamber, eats the ant's larvae, and exits the nest only when searching for a mate. Beetles, spiders, isopods, flies, collembolans, mites and other arthropods are known to live inside the ants' nest. A large number of these ectoparasites live in the refuse chamber where they feed on dead ants and other refuse of the colony.

The Nest

Atta Nests

The nests of the ants from the genus *Atta* are among the largest and more complex known among insects. A typical nest may occupy a subterranean space of 20 m in diameter and 5 m in depth. It consists of interconnected galleries leading to chambers where ants cultivate their symbiotic fungi. Other galleries lead to the surface and are used to regulate the flux of fresh air so as to maintain the temperature, carbon dioxide concentration and humidity constantly at the optimum inside the nest. A large chamber is used to dispose of the colony's waste which consists mainly of dead fungus and dead ants. This chamber produces heat and carbon dioxide that allows for a better regulation of the colony's climate. Other galleries lead deep into the soil for access to the ground water. Galleries leading to the surface end beneath an earth mound with a crater, allowing the exit and entrance of workers. These mounds work as chimneys, helping to regulating the flux of fresh air and stopping running water from flooding the nest after torrential rains. Often workers seal the nest entrances with dry leaves and earth, especially when fighting other colonies. Some underground galleries lead up to 200 m from the nest to the colony's foraging areas. Each *Atta* species builds nests with its own characteristics. For example, *Atta colombica* has no refuse chamber but throws its rubbish outside the nest. The form of the mounds with craters depends on the soil's texture. The depth of the nest is also dependent on soil conditions; for example, nests are shallower in more humid areas.

The Nests of *Acromyrmex* and *Trachymyrmex*

Nests of *Acromyrmex* species have variable architecture, depending on the species that builds it. *Acromyrmex landolti* builds nests with a single vertical gallery with nest chambers connected on the sides of the gallery. The vertical gallery can go as deep as 3–4 m. *Acromyrmex octospinosus* builds more superficial subterranean nests with many chambers and galleries connected in all directions. *Acromyrmex coronatus* sometimes builds superficial nests under accumulated dry leaves. These nests are often found in caves of dead tree trunks. Nests of *Trachymyrmex* species are less elaborate. They are subterranean but normally close to the surface and rather small compared to those of *Acromyrmex* and *Atta* (Figs. 28 and 29).

The Life Cycle

Reproduction

Leaf-cutting ants reproduce sexually, with copulation occurring during the nuptial flight. Normally a virgin queen mates with several males. Nuptial flight occurs at the beginning of the rainy season. After the first heavy rain, thousands of winged individuals start flying from all affected nests in an area. They fly

Leaf-Cutting Ants (Formicidae: Myrmicinae: Attini), Figure 28 **Nest of *Atta laevigata*.**

Leaf-Cutting Ants (Formicidae: Myrmicinae: Attini), Figure 29 ***Acromyrmex landolti*** **(drawing by Eduardo Perez).**

normally in the early evening and concentrate in a given space several meters above the ground. As males die shortly after mating, dead bodies of males that have copulated rain to the ground, just under the visible swarm. Once successfully inseminated, the new queen flies to the ground, sheds her wings and starts looking for an appropriate site to excavate a nest. Queens also reproduce asexually; non-fertilized eggs will produce haploid males (as are all hymenoptera, these ants are haplodiploid).

The Birth of a Colony

Once the recently fertilized queen has found an adequate site (often next to a small tree), she starts digging using her mandibles to remove earth. She digs a small gallery about 15 cm long leading to a small chamber about 7 cm wide. After digging is completed, she seals the nest entrance. In the chamber she lays some unfertilized eggs upon which she deposits the mycelium of the fungus she has taken from her mother's nest, stored in a cavity in her mouth. If available, roots are also used as a substrate for the fungus. Then she lays her first fertilized eggs. The first larvae that emerge are fed with special unfertile "trophic" eggs produced by the queen. Eventually small "nanitic" workers emerge. During that period, the queen survives on her fat reserves and by metabolizing her wing muscles, now useless. Once the first nanitic workers emerge, they open the nest entrance and start foraging for leaves, flowers, insect droppings, seeds, etc., to feed the fungus. After this initial phase, larger workers emerge capable of cutting fresh leaves.

The Life Cycle of a Worker

Leaf-cutting ants have four phases in their life cycle: egg, larvae, nymph and adult. The white larvae feed mainly on the symbiotic fungus. They have very little mobility. After several molts, the larvae initiate its metamorphosis without spinning a cocoon and eventually emerges as an adult worker. The amount of food ingested during the larval stage will determine the final size of the worker, as adult workers stop growing. Young workers have a lightly pigmented soft cuticle, whereas older ones are darker. Adult workers have different nutritional requirements than larvae do; they feed mainly on plant sap because their protein requirement is less than that of the larvae, which mainly feed on the fungus.

The Life Cycle of a Colony

The colony starts with the birth of the first nanitic workers. During the first few years, the colony grows continuously in number of workers and in the space occupied by the nest. During that period, workers forage every day, except when it is raining copiously, and feed their fungus, which occupies ever more chambers which must be prepared by the workers. When the colony reaches maturity (4–6 years after being initiated by the queen for *Atta*, and less for *Acromyrmex* and *Trachymyrmex*), the colony produces winged individuals that accumulate in the nest until the initiation of the next rainy season, when they will leave the nest for their nuptial flight. We know little of how the leaf cutter ant colony produces winged females instead of workers, or how the queen decides to fertilize an egg with sperm, producing female offspring, or lay unfertilized eggs that will produce males. It is likely that these ants use hormones for this purpose, as bees do, but little is known for leaf-cutting ants. After a few nuptial flights, the colony is left without winged individuals and with few workers. The colony then has the whole year to again build its workforce, forage for food to grow its fungus, and eventually produce a new batch of individuals capable of sexual reproduction. This cycle is repeated until the old queen dies, which may take several decades.

Communication

Pheromones

The most common communication system between workers of leaf-cutting ants consists of volatile chemicals or odors called pheromones. These ants produce their pheromones through a series of exocrine glands located in different parts of their body. Each of these glands produces a specific secretion composed of a mix of chemicals which are used to communicate information between workers. These multicomponent pheromones are perceived through the insect's antennae. Some pheromones are detected only upon contact of the antenna with the substrate containing the pheromone; these are called contact pheromones. For example, larval recognition in leaf-cutting ants seems to be achieved using contact pheromones that are located on the cuticle of the larvae.

Alarm Pheromones

Leaf-cutting ant workers produce an alarm pheromone in their mandibular glands. This pheromone is composed of highly volatile compounds that disperse rapidly in the air and alarm nestmates up to distances of 60 cm. This same pheromone helps workers and soldiers to orientate to the source or location that caused the alarm, thus helping to coordinate cooperation in defense. This coordination can be very fast and effective when fighting other ant colonies or when deterring an intruder. The compounds of this pheromone are absorbed on the cuticle of these insects, thanks to the cuticular hydrocarbons that cover the insect's surface. There, the alarm pheromone serves as an individual recognition signal, helping ants to differentiate between nestmates and intruders.

Recruitment Pheromone

Another well studied pheromone is the recruitment or trail pheromone. This pheromone is produced in the poison gland located in the gaster. Workers lay trails using this pheromone when returning from a palatable food source. The less volatile compounds in the pheromone serve as orientation cues, whereas the more volatile ones regulate the amount of new workers recruited to the trail, which in turn will depend on the quality and quantity of food to which they are recruited. Some of the compounds of this pheromone, isolated from leaf-cutting ant species, are 4-metyl-2-pyrrol-carboxilate for *Atta laevigata*, *Atta cephalotes*, *Acromyrmex octospinosus*, and 3-ethyl-2,5-dimethyl-pyrazine for *Atta sexdens rubropilosa* and *Acromyrmex niger*.

Territorial Pheromones

These are used to mark the colony's territory using a secretion from the Dufour's gland. Workers on territories marked by their colony are more aggressive and fight longer, whereas workers over territories of a foreign colony try to escape. During ant wars, many small workers swarm outside their nest to mark the surroundings of their nest entrance and the battlefield, whereas larger workers engage in combat. These combats can last weeks if the food source they are defending is especially scarce or attractive. This pheromone helps achieve the harmonious cohabitation of neighboring colonies of similar size, which seems to be the norm in nature.

Individual Recognition

Leaf-cutting ant workers recognize their nestmates and differentiate them from foreign ants, even if they are of the same species. They achieve this by detecting odors absorbed on the cuticle. These odors mainly come from the mandibular alarm pheromone. This system allows them to recognize individuals even at a distance, and is also used to recognize nestmates from different parts of the nest.

Other Pheromones

Other pheromones are less well known. The queen is recognized as such by pheromones, and so are the larvae. Leaf fragments are marked using the Dufour's gland, probably to ascertain the colony's property and to help detect it when workers drop it from the trees. Other communication systems remain to be discovered.

Visual Communication

Although known from other ants, nothing is known for leaf-cutter ants.

Communication by Sound

Leaf-cutter ants have a stridulatory apparatus between the gaster and the second petiole. This apparatus consists of a stridulated cuticular surface on the dorsal part of the gaster and a cuticular tooth extruding from the petiole that serves as a bow producing vibrations when gliding over the stridulated surface. The ants produce rhythmic ultrasounds with this apparatus by vibrating and elevating their gaster. The sound is barely perceived by some humans. The ants use this sound to guide workers toward branches on trees that need leaf-cutters. They also stridulate when buried, guiding workers to dig in their direction. The sound is transmitted over solid substrate and is perceived thanks to special receptors at the end of their legs.

Trophalaxis and Antennal Contacts

Workers exchange liquids through their mouthparts. They do this after contacting the other ant with their antennae. We do not know what information they are transmitting with these behaviors but they might transmit information about the quality of food.

Foraging

Leaf-cutting ants have especially sophisticated foraging behaviors. They use trunk trails that they maintain free of leaves and obstacles, facilitating their movement from the nest to the foraging areas. From this trunk trail, smaller trails lead to the plants they harvest. Scout ants use the same trail system but eventually leave it to explore new terrain. When finding a palatable food source, they return to the nearest trunk trail, leaving trail pheromone behind. Foragers might cut a leaf fragment and carry it through the trail system to the nest. Alternatively, they might do it in stages; some workers cut the leaves and let them drop from the tree, or just carry the leaves to the nearest junction, where other workers collect the leaf fragments and carry them to the nest entrance, where still other workers remove the superficial waxes from the leaves and carry the clean leaves inside the nest, where other workers cut them into fine pieces to feed the fungus. Very small or minima workers are often seen climbing on leaf fragments that are carried by larger workers. The minima help fend off flies from the family Phoridae and other parasites that attempt to attack the carrying worker or enter the nest via the leaf fragment. Older workers remove dry leaves, dead ants and dry fungus from the nest chambers and drop it in the refuse pile.

The Decision Making System

The colony has to coordinate its efforts in order to forage efficiently. Not all ants are required at the same place at the same time. Specifically, in the case of recruitment to food, leaf-cutting ants use a decision making system that is different from that used by all other ants studied and which resembles the system used by termites. It works as follows: a scout discovering food will return to the nest or the trunk trail while laying a pheromone trail. The concentration of pheromone on the trail will depend on the quality of the food. Workers encountering this trail, according to their motivation for food, will follow the new trail. On their way back, they will reinforce the pheromone trail but in such a way that the total concentration of pheromone is roughly constant. They will not just add their pheromone onto that of others (as done by *Solenopsis geminata*, for example), but will restrain from adding pheromone if enough of it is already on the trail. In this way, the concentration of pheromone on the trail will not depend on the amount of ants laying trails or returning from the food source but only on the quality of the food. This system allows leaf-cutters to recruit to various different food sites at the same time.

Orientation

Foraging scouts need to find their way back to the nest. They achieve this by integrating various keys or environmental signals when foraging and homing. We know that they can use polarized light, visual cues, spatial memory, olfactory cues and tactile cues. They might possibly also use gravitational cues and the earth's magnetic field. Each species seems to have its own hierarchy in which these cues are used in actual orientation in the field.

Defense

Organisms need to defend themselves against predators and parasites in order to increase their odds for survival. Leaf-cutter ants possess no functional sting but they do secrete a toxic fluid from their anal region which they deposit onto enemy combatant ants. This secretion dries or polymerizes quickly, helping to immobilize the affected worker. It also seems to contain neurotoxic substances and volatiles that attract other ants. Large workers and soldiers also use their mandibles to cut wounds on molesting vertebrates and then add irritant secretions to the wounds. The mandibles can cut appendages from invertebrate enemies or even cut them into pieces. Another form of defense is using cryptic behavior, including cessation of all movement until the danger has passed. This behavior is often used by lone foraging scouts. The thick, hard cuticle and the spines over the thorax help the insect to avoid being eaten by predators such as lizards, birds and spiders. In addition, the secretion of the metapleural gland is spread all over the body of these insects, helping to fend off fungi, bacteria and other potential illness-causing agents. The main predators of these ants are spiders, armadillos and anteaters, which feed copiously on them.

Ecology

Leaf-cutting ants are only found in the neotropics. They might have an important effect on plant growth, on occasion achieving pest status. Densities of up to 60 adult *Atta* nests per hectare, or hundreds to thousands of *Acromyrmex* nests per hectare, can cause serious harm to plantations and crops. On the other hand, the large accumulation of organic material inside the nest, once the queen and the colony die, makes it a formidable substrate for plant growth. In nutrient poor savannas, old collapsed *Atta* nests are colonized by trees and shrubs, forming forested islands. It is the occasional status as agricultural and forestry pests that has made leaf-cutters most famous. Leaf-cutters with the highest economic importance as pests are all *Atta* species and some *Acromyrmex* species. An adult *Atta laevigata* colony, for example, may cut an average of 5 kg of plant material each day. They target especially young plant tissue, which can be especially damaging to the plants. Estimates of the economic damage caused in the Americas by these ants are close to a hundred billion US dollars per year (Figs. 30 and 31).

Control of Leaf-Cutting Ants

There are three basic methods for reducing the populations of these pest ants: (i) Stopping the ants from accessing the plant. Asphalt or other sticky greases painted at the base of tree trunks, plastic or rubber rings that retard ants from reaching the plants, or water barriers that deter the access of these ants are useful ways of dealing with this pest. (ii) Direct control, killing the ants with insecticides. For large nests this might be difficult and expensive. Fogging and powder pumps may help to get the insecticide inside a nest. (iii) Indirect control, using poisoned but attractive baits, is the most efficient way known to manage large areas with this pest. Attractants (such as citrus pulp) mixed with slow acting insecticides, allow the foragers to carry the poison into the nest so that it is distributed to all chambers by the workers before it starts killing the insects.

References

Cameron R, Currie CR, Scott JA, Summerbell RC, Malloch D (1999) Fungus-growing ants use antibiotic-producing bacteria to control garden parasites. Nature 398:701–704

Cedeño A (1984) La ecología de los bachacos. Fondo Editorial Acta Cientifica Venezolana, Caracas

Chapela IH, Rehner SA, Schultz TR, Mueller UG (1994) Evolutionary history of the symbiosis between fungus-growing ants and their fungi. Science 266:1691–1694

Herman HR (1982) Social insects, vol 4. Academic Press, New York, NY, 385 pp

Hernandez JV, Lopez H, Jaffe K (2001) Nestmate recognition signals of the ant *Atta laevigata*. J Insect Physiol 48:287–295

Jaffe K (1984) Negentropy and the evolution of chemical mass recruitment in ants. J Theor Biol 106:587–604

Jaffe K (1987) The evolution of agonistic communication systems in ants. Exp suppl 54:295–311

Jaffe K, Howse PE (1979) The mass recruitment system of the leaf-cutting ant *Atta cephalotes*. Anim Behav 27:930–939

Jaffe K, Villegas G, Colmenares O, Puche H, Zabala N, Alvarez M, Navarro JG, Pino E (1985) Two different decision making systems in ants. Behavior 92:9–21

Mayhe A, Jaffe K (1998) On the biogeography of the Attini. Ecotropicos 11:45–54

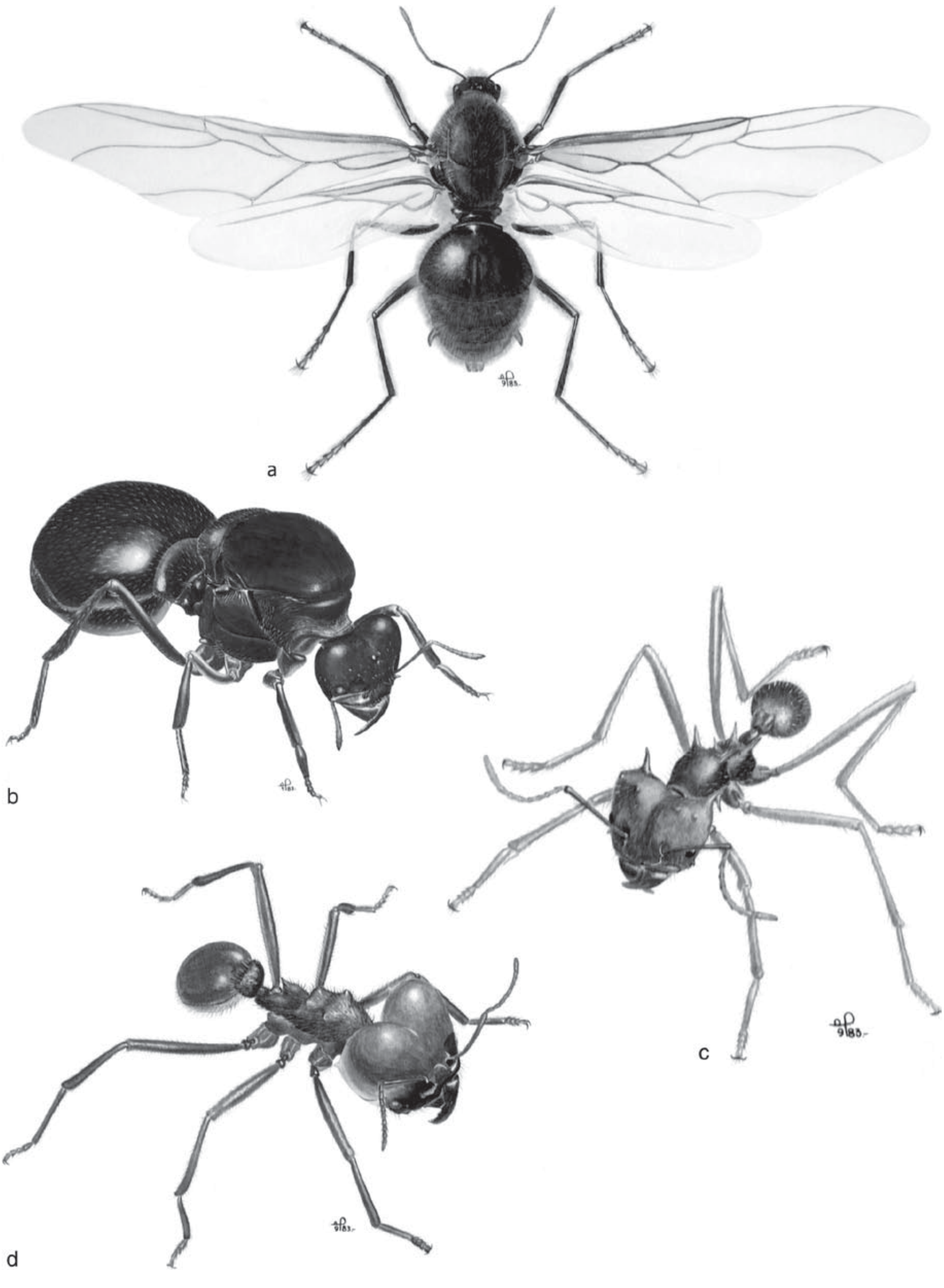
Vilela E, Jaffe K, Howse PE (1987) Orientation in leaf-cutting ants. Anim Behav 35:1443–1453

Weber N (1972) The gardening ants. American Philosophical Society, Philadelphia, 142 pp

Wheeler WM (1965) Ants: their structure, development and behaviour, 4th edn. Columbia University Press, New York, NY, 663 pp

Whitehouse M, Jaffe K (1996) The ant wars: combat strategies, territoriality and nest defense in the leaf-cutting ant *Atta laevigata*. Anim Behav 51:1207–1217

Wilson EO (1971) The insect societies. Belknap Press, Harvard University, Cambridge, MA, 548 pp



Leaf-Cutting Ants (Formicidae: Myrmicinae: Attini), Figure 30 ***Atta laevigata*****: (a) male, (b) queen, (c) worker, (d) soldier (drawings by Eduardo Perez).**

Leaf-Cutting Ants (Formicidae: Myrmicinae: Attini), Figure 31 ***Atta cephalotes*** **transporting vegetation (photo by Scott Bauer, USDA).**

Leaf-Footed Bugs

Members of the family Coreidae (order Hemiptera).
► Bugs

Leafhoppers (Hemiptera: Cicadellidae)

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Leafhopper adults and nymphs are active, jumping insects recognized by their piercing-sucking mouthparts and by the presence of four rows of enlarged, spinelike setae on their hind tibiae.

Order: Hemiptera
Infraorder: Cicadomorpha
Superfamily: Membracoidea
Family: Cicadellidae

Cicadellidae, the largest family of hemimetabolous insects and one of the largest families of plant-feeding insects, comprises nearly 25,000 described species and over 3,200 genera. their great diversity may be due to a combination of their long (ca. 125 million years) evolutionary history, their association with a wide variety of flowering plants, and their success at occupying a broad range of habitats and climates. Their closest living relatives are the treehoppers and related families (Membracidae, Aetalionidae and Melizoderidae), and the relict southern hemisphere family Myerslopiidae. More distant relatives include the other two superfamilies of infraorder Cicadomorpha: Cercopoidea – the spittlebugs or froghoppers; and Cicadoidea – the cidadas.

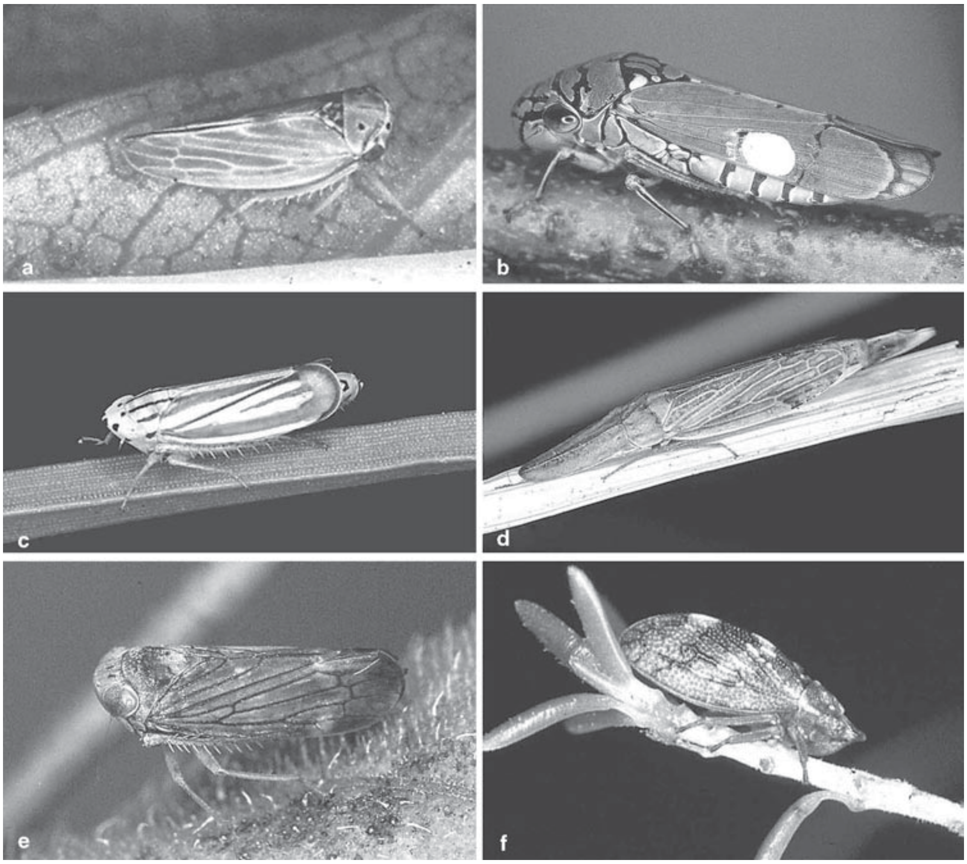
Leafhoppers occur in terrestrial habitats worldwide, wherever vascular plants are found. They are most diverse and abundant in the tropics; however, temperate grasslands, savannas and forests also harbor diverse leafhopper faunas and a few species inhabit high elevations and latitudes. A few generalist species occur worldwide and utilize dozens of plant species as hosts, but most species are associated with particular host plants and/or habitats and have relatively small geographic ranges. The oldest fossil Cicadellidae are known from the lower Cretaceous Period.

External Morphology

Adult leafhoppers range from 2 to 30 mm in length and are usually somewhat cylindrical or wedge-shaped. Less commonly, species may be strongly flattened dorso-ventrally, greatly elongated, or globular in appearance. They differ from their close relatives, the treehoppers, because they lack a posteriorly produced pronotum and because (with a few exceptions) the setae of their hind tibia are enlarged and spinelike. Most leafhopper species are brown or green but many, particularly in the subfamilies Cicadellinae and Typhlocybinae, are strikingly marked with various color patterns. As in planthoppers (Fulgoromorpha), the head of leafhoppers is highly variable in shape, ranging from short to elongate, from round to strongly flattened, and sometimes bears spines or other ornamentation (Fig. 32). The median ocellus is absent and the position of the two lateral ocelli, when present, is also highly variable and is one of the main features used to distinguish subfamilies. Other important differences among the major lineages are found in the wing venation, the arrangement of setae on the legs and the male and female genitalia. Although some leafhopper species are easily recognized by their distinctive shapes and color patterns, many groups contain species that closely resemble one another and are difficult to distinguish. In many genera, the most reliable morphological features for distinguishing species are the male genitalia.

Life History and Habits

Details of the life cycle vary from species to species. In general, the female inserts several eggs into the living tissue of the host plant. The eggs either remain dormant for a period ranging from a month to over a year, or they develop and hatch within a few weeks. The young, known as nymphs, feed on plant sap by inserting their beaks into the vascular or parenchyma tissues of the host plant and go through a series of five molts, reaching the adult stage after a period of several weeks. Adult males and females seek each other out for mating, locating each other through vibrational signals made by sound producing organs at the base of the abdomen called tymbals. Leafhopper songs are



Leafhoppers (Hemiptera: Cicadellidae), Figure 32 **Leafhoppers (Cicadellidae): (a)** ***Agalliopsis novella*** **(Say); (b)** ***Oncometopia alpha*** **Fowler (the white patch on the forewing is a deposit of brochosomes); (c)** ***Commelus comma*** **(Van Duzee); (d)** ***Attenuipyga platyrhyncha*** **(Osborn); (e)** ***Jikradia olitoria*** **(Say); (f)** ***Ulopa reticulata*** **(Fabricius). (Photos by C. H. Dietrich.)**

transmitted through the substrate and, in most cases, are too faint to be heard by human ears without special amplifying equipment.

As implied by their name, most leafhoppers are strong jumpers as both adults and immatures. The adults of most species are also strong fliers, but many species, particularly in arid environments, have the wings reduced or absent and are incapable of sustained flight. Most species are solitary as nymphs and adults, but a few species are gregarious and ant-mutualistic. Some of these, in turn, exhibit parental care (presocial) behavior-females guard their eggs and remain with the nymphs throughout their development. Another interesting aspect of leafhopper behavior is a phenomenon known as anointing, in which the leafhopper collects a special fluid secretion from the anus and spreads this secretion over the body using the legs. When the secretion dries, a residue of minute spherical granules called brochosomes remains and provides a hydrophobic coating to the integument. Brochosomes are produced in a specialized glandular segment of the Malpighian tubules. In the leafhopper tribe Proconiini, females of several genera store large globs of brochosomes on the forewings and use their hind legs to scrape the brochosomes onto their egg masses after oviposition.

Predators and Parasites

Leafhoppers are attacked by a wide variety of predators, including birds, lizards, spiders, assassin bugs, robber flies and syrphid flies. Mymarid and trichogrammatid wasps parasitize the eggs; dryinid wasps, pipunculid flies, strepsipterans and epipyropid moths parasitize the nymphs and the adults.

Economic Importance

Several leafhopper species are important agricultural pests, injuring plants either directly through feeding, or indirectly through the transmission of plant pathogens. Among the most important are the aster leafhopper (*Macrosteles quadrilineatus* (Forbes)), the African maize leafhopper (*Cicadulina mbila* (Naude)), the potato leafhopper (*Empoasca fabae* Harris), the beet leafhopper (*Neoaliturus tenellus* (Baker)), the corn leafhopper (*Dalbulus* spp.), the green rice leafhopper (*Nephotettix* spp.), the glassy-winged sharpshooter (*Homalodisca coagulata* (Say)), and various grape leafhoppers (*Erythroneura* spp.).

Control Measures

Control of injurious leafhopper populations is most often accomplished by using conventional contact insecticides. However, use of resistant plant varieties and cultural control (e.g., removal of crop debris used in overwintering) is effective for some species. The potential for biological control using entomopathogenic fungi or parasitoids is a topic of active research.

References

Evans JW (1966) The leafhoppers and froghoppers of Australia and New Zealand (Homoptera: Cicadelloidea and Cercopoidea). Mem Aust Mus 12:1–347

Nault LR, Rodriguez JG (eds) (1985) The leafhoppers and planthoppers. Wiley and Sons, New York, NY, 500 pp

Oman PW (1949) The Nearctic leafhoppers-a generic classification and check list. Mem Entomol Soc Wash 3:1–253

Oman PW, Knight WJ, Nielson MW (1990) Leafhoppers (Cicadellidae): a bibliography, generic check-list, and index to the world literature 1956–1985. CAB International, Institute of Entomology, Wallingford, UK

Leaf Insects

Members of an order of insects (order Phasmatodea).

► Walkingsticks and Leaf Insects

Leafcutting Bees

Members of the family Megachilidae (order Hymenoptera, superfamily Apoidae).

► Bees
► Wasps, Ants, Bees and Sawflies

Leaf-Miner Flies (Diptera: Agromyzidae)

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The Agromyzidae, also known as leaf-miner flies, is a large family of phytophagous flies. The family contains approximately 2,860 described species occurring from the tropics to the high arctic, although the majority of known species live in temperate areas of the Northern Hemisphere. There are still many more species of agromyzids to be discovered; as many as half the actual number of species may not yet be described.

Biology and Economic Importance

Larvae of all species of Agromyzidae are internal plant feeders. Although they are best known as leaf-miners, many species feed inside other plant parts such as stems, roots, seeds and flowers, while a few species are gall inducers. There are about a hundred species of particular economic importance that may cause damage to cultivated crops and ornamental plants (see examples in Table 2). The degree of damage inflicted on plants may depend on the part of the plant being attacked, the plant's growth stage at the time of infestation and more importantly, the size of the agromyzid population on the plant. Under normal conditions, agromyzids are naturally controlled by a large complex of hymenopteran parasitoids, keeping agromyzid populations below the economic threshold. Unfortunately, this natural balance has often been disrupted by the use of insecticides. This is because the agromyzids often have higher resistance to chemicals than the parasitoids.

When present in large numbers, leaf-miners may affect the general health of the plant by reducing its photosynthetic capacity. They also cause aesthetic damage due to their highly visible feeding traces, reducing the commercial value of ornamental plants. For those commercially grown plants, the presence of only a few agromyzid leaf-mines is often enough to make a plant unmarketable. Stem-borers also cause considerable damage by affecting the vascular system of the plant, disturbing water and nutrient supplies. This is especially injurious when the larval feeding occurs in young plants or seedlings.

Although most of the damage to plants is caused by the agromyzid larvae, the adult females may also injure plants by inserting their well-sclerotized ovipositor into the plant tissues (Fig. 33a). This is primarily for egg-laying purposes, but the females use these scars also as feeding sites, sucking plant sap through the punctures. These punctures increase the risk of infection of the plant by fungi and bacteria.

Some agromyzid species feed on noxious and invasive plants, and are regularly considered as potential natural control agents for those plants. Unfortunately, many attempts at biological weed control using agromyzids have so far failed or encountered problems (Table 3).

Host Plants

Agromyzidae have colonized a wide range of host plants including primitive lineages such as horsetails and ferns, but more importantly, over 160 families of flowering plants, including some economically important ones such as the Poaceae (rice, wheat, corn, barley, etc.), Fabaceae (beans, peas, soybeans, lentils, etc.), Solanaceae (potatoes, tomatoes, pepper, etc.) and Asteraceae

Leaf-Miner Flies (Diptera: Agromyzidae), Table 2 Examples of some important agromyzid pest species

Species	Host plants	Larval habits	Localities
Ophiomyia simplex– Asparagus miner	Asparagus (*Asparagus officinalis*)	Root and stem miner	Western Europe, North America
Ophiomyia phaseoli– Bean fly	Various species in family Fabaceae including snapbeans (*Phaseolus vulgaris*), soybeans (*Glycine max*), cowpeas (*Vigna unguiculata*), garden pea (*Pisum sativum*)	First instar larva as leaf-miner. Older larva bores into the stem. May also mine towards the roots in seedlings or highly infested plants	Southern Asia (China, India, Indonesia), Hawaii, Australia, East Africa
Melanagromyza obtusa– Pigeon pea pod fly	Various species in family Fabaceae, especially pigeon peas (*Cajanus indicus*)	Eggs laid inside pods. Larvae are seed feeders	Southeast Asia, Papua New Guinea. Also recorded in Neotropical region (Guadeloupe)
Agromyza frontella– Alfalfa blotch leafminer	Fabaceae: Alfalfa (*Medicago sativa*) other species of *Medicago*. Also *Melilotus* spp.	Leaf-miner	Europe, Afghanistan, Israel, North America
Liriomyza sativae– Vegetable leafminer	Polyphagous. Nine plant families including Cucurbitaceae (cantaloupe, cucumber, squash), Fabaceae (pigeon pea, alfalfa, lima bean and others), Solanaceae (pepper, tomato, egg-plant, potato), also ornamentals (e.g., *Chrysanthemum*)	Leaf-miner	Cosmopolitan
Liriiomyza trifolii– American serpentine leaf miner	Highly polyphagous. Approximately 400 host species known from 25 families. Attack various cultivated crops such as onions, beans, potatoes, tomatoes, celery, ornamentals (e.g., *Chrysanthemum*)	Leaf-miner	Cosmopolitan. Spread around the world mainly with cut flowers. Restricted to greenhouse in temperate regions
Liriomyza huidobrensis– Pea leafminer	Polyphagous. Known from 14 plant families. Attack various cultivated crops such as beets, peas, beans, lettuce, onions, tomatoes, potatoes. Also some ornamental plants	Primarily leaf-miner. May feed occasionally on outer surface of young pods	Central and South America. Expected in all tropical and subtropical regions of Europe, Asia and Africa. Restricted to greenhouse in temperate regions. So far absent from North America (previous records represent cryptic species *Liriomyza langei*)

Leaf-Miner Flies (Diptera: Agromyzidae), Table 2 Examples of some important agromyzid pest species (Continued)

Species	Host plants	Larval habits	Localities
Chromatomyia horticola– Garden pea leafminer	Highly polyphagous. Known from 35 plant families, including many cultivated plants (onions, peas, cabbages, alfalfa), and ornamentals	Leaf-miner	Europe, Africa and Asia

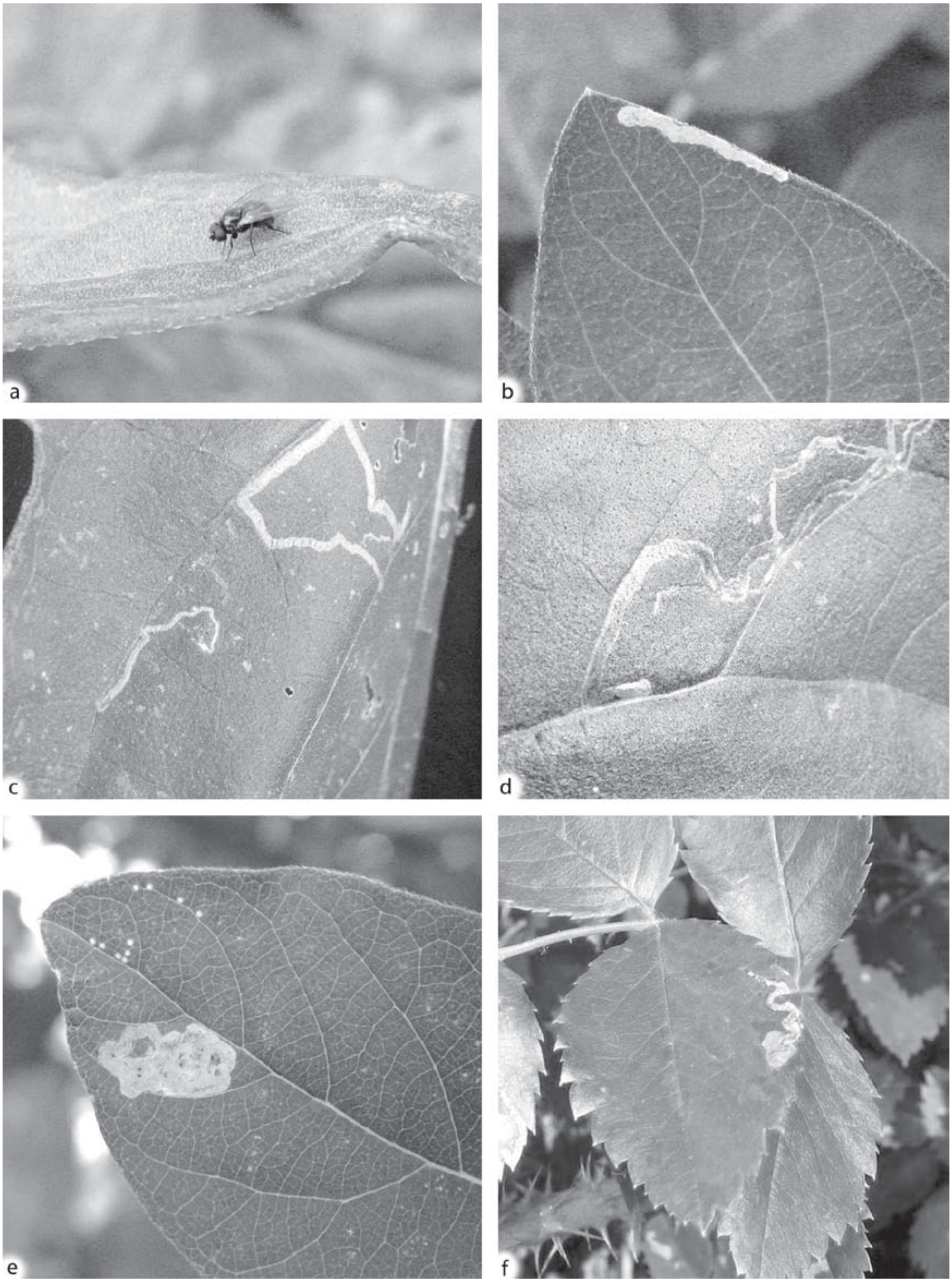
(lettuces, artichokes, chrysanthemums, etc.). There are no species of Agromyzidae that are known on mosses and very few species have been reared from gymnosperms: one record is from Tropicomyia atomella, an agromyzid species that forms leaf mines on Gnetum sp. in Malaysia and further records consist of feeding channels in wood of gymnosperms that are possibly caused by agromyzid larvae. The host plants are known for approximately 50% of the described agromyzid species. Most agromyzid species show a high degree of host specificity. These are known to feed on plants from a single genus (monophagous) or from multiple genera in the same family (oligophagous). Only a few species (<10%) are truly polyphagous and feed on a number of unrelated families. These include some of the most serious agromyzid pests worldwide. At the generic level, some agromyzids have a narrow range of host plants. For example, species in the genus *Cerodontha* are only known from four plant families (Poaceae, Cyperaceae, Iridaceae and Juncaceae) while species in the genus *Liriomyza* are known from 76 different families, showing the widest range of host plants of all agromyzids.

Leaf Mines

The mines formed by agromyzids can be of different forms such as linear (larva tunnels in a straight line), serpentine (linear winding mines) or blotch-like (larva forming a broad patch) (Figs. 33 and 34). In some cases the first instar larva forms a linear or serpentine mine and later instars form a blotch mine. These feeding patterns are species-specific and often helpful in the identification of Agromyzidae. Most species feed in the upper surface of the leaf, in the palisade parenchyma, or less often immediately beneath the leaf epidermis. Others feed on the lower surface of the leaf, in the spongy parenchyma. The part of the leaf where the mine is formed is also helpful in the identification of the agromyzid. Some species feed along the margin of the leaf, while others stay along the midrib or along a strong lateral vein. Other than the mine itself, the arrangement of the frass inside the mine is also characteristic. The frass may be in the form of small pellets or short strips, and these may be widely separated, interconnected, deposited alternately on each side of the mine, or in some cases the frass is excreted only at the very end of the mine.

Life History

After choosing the host plant, an adult female lays a single egg into the plant tissue at the appropriate oviposition site. The number of eggs laid by females varies considerably (e.g., the female of *Agromyza frontella* may lay between 25 and 294 eggs during her lifetime). After a few days, the larva emerges and starts feeding on the plant tissues, causing a mine or sometimes a gall. Larval feeding may last from a few days to several



Leaf-Miner Flies (Diptera: Agromyzidae), Figure 33 **Agromyzid leaf miner and characteristic mines: (a) Female Agromyzidae inserting ovipositor in a leaf of *Rudbeckia* sp.; (b) Linear leaf mine on *Lonicera* sp.; (c) Serpentine leaf mines; (d) Serpentine leaf mine with larva visible; (e) Blotch mine on *Lonicera* sp.; (f) Serpentine-blotch mine on *Rosa* sp.**

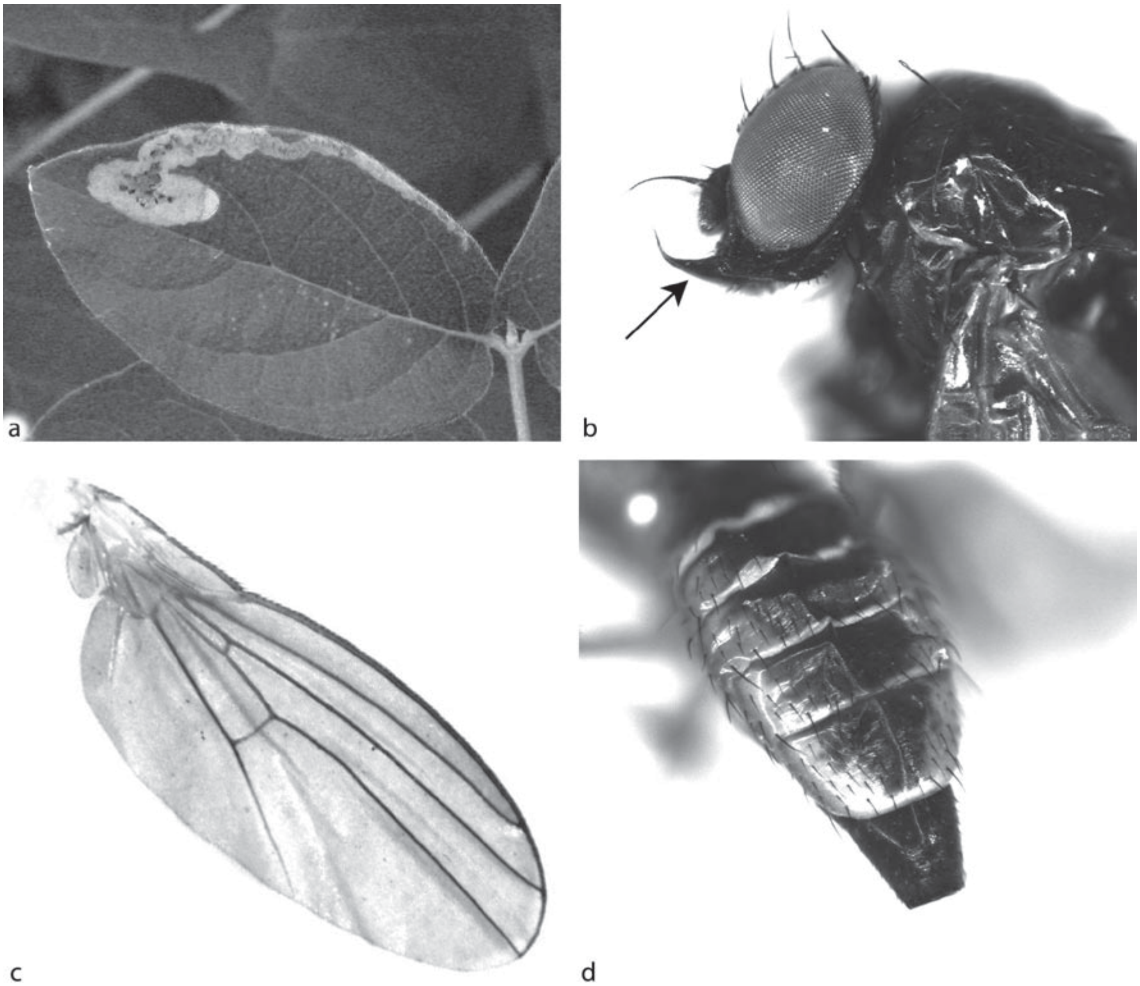
Leaf-Miner Flies (Diptera: Agromyzidae), Table 3 Examples of Agromyzidae that have been used or considered as potential biological control agents of invasive plant species

Species	Host plant	Larval habit	Distribution	Problems
Ophiomyia lantanae	*Lantana* spp.	Seed feeder	Southern United States, Caribbean, Central and South America. Introduced (deliberately or with its host plant) in many other regions, including Hawaii, Australia, India, Hong Kong, Kenya, South Africa, Malaysia	Seed embryo often not affected. Do not reduce significantly the spread of lantana
Ophiomyia strigalis	*Striga* spp.	Stem and root miner	East Africa	Flies attack mainly mature plant, having little effect on seed production
Napomyza lateralis	Many species in family Asteraceae, including, *Matricaria* (scentless chamomile). Also plants in the family Linaceae and Fabaceae	Leaf and stem miner. Also found in flower heads	Europe, Middle Asia, North America	Considered as possible control agent for scentless chamomile in Canada, but host range and behavior of this fly may suggest the presence of cryptic species. Further studies are required
Phytomyza orobanchia	*Orobanche* spp.	Seed and fruit feeder	Palaearctic region, Ethiopia. Deliberately introduced in Chile	Efficiency of the fly reduced by parasitoids. Often requires mass release of agromyzid species to insure success. Control of *Orobanche* was successful in many regions

months. Larvae of species having many generations a year develop more rapidly than univoltine species. In most cases, when the third larval instar reaches maturity it cuts a semi-circular exit slit and drops to the ground for pupation. But for most seed feeders, stem borers, and a few leaf-miners pupation takes place within the plant, at the feeding site (Figs. 33 and 34).

Diagnosis and Classification

The Agromyzidae are minute to small-sized flies, generally from 2–4 mm in wing length (but extremes range from 0.9 mm to 6.5 mm). They are often yellow and/or black, brown or grey, a few have some metallic greenish, bluish or coppery coloration (e.g., genus *Melanagromyza*). Most have clear wings, but



Leaf-Miner Flies (Diptera: Agromyzidae), Figure 34 Leaf mines and leaf miner characteristics: (a) Linear-blotch mine on *Lonicera* sp.; (b) Vibrissal fasciculus (*arrow*) of male *Ophiomyia*; (c) Wing of the agromyzid *Cerodontha dorsalis*; (d) Oviscape of female agromyzid *C. dorsalis*.

they may be patterned or infuscated in a few tropical species. Agromyzidae are generally divided into two subfamilies: Agromyzinae and Phytomyzinae. These can be differentiated by the wing venation. The combination of the following characters are used to recognize the family: vibrissa well developed, some males (genus *Ophiomyia*) have a vibrissal fasciculus; fronto-orbital and ocellar bristles strong; postocellar bristles divergent; fronto-orbital setulae in one or more rows, usually reclinate, but sometimes proclinate, upright or absent; dorsocentral bristles varying from 2 to 5; acrostichal bristles may be present (in up to 10 rows) or absent; wings with costal break present near the end of R_1, humeral break absent; Sc incomplete distally or reaching C as a linear fold (subfamily Phytomyzinae), or Sc complete and fusing with R_1 (subfamily Agromyzinae) before reaching costa; CuA_2 and A_1 present, forming a small cell *cup*; A_1 does not reach wing margin; abdomen tapering, composed of six visible segments; females with abdominal segment 7 modified into a large conical nonretractile oviscape (Fig. 34d).

► Leafminers
► Flies
► American Serpentine Leafminer
► Pea Leafminer
► Vegetable Leafminer

References

Dempewolf M (2004) Arthropods of economic importance – Agromyzidae (CD-ROM). ETI, University of Amsterdam, Amsterdam. Available at http://ip30.eti.uva.nl/bis/agromyzidae.php (accessed 25 March 2008)
Spencer KA (1973) Agromyzidae (Diptera) of economic importance. Series entomologica, vol 9. W. Junk, The Hague, The Netherlands
Spencer KA (1987) Agromyzidae. In: McAlpine JF et al (eds) Manual of nearctic diptera, vol 2. Monograph No. 28, Research Branch, Agriculture Canada, pp 869–879
Spencer KA (1990) Host specialization in the World Agromyzidae (Diptera). Series Entomologica, vol 45. Kluwer Academic Publishers, Dordrecht, The Netherlands
Spencer KA, Stegmaier CE (1973) Agromyzidae of Florida with a supplement on species from the Caribbean. Arthropods Fla Neighboring Land Areas 7:1–205

Leafminer Moths (Lepidoptera: Gracillariidae)

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Leafminer moths, family Gracillariidae, comprise the major leafmining family of Lepidoptera, with about 1,740 species from all regions. The actual world total probably exceeds 6,000 species. There are three subfamilies: Gracillariinae, Lithocolletinae, and Phyllocnistinae. The family is part of the superfamily Tineoidea, in the section Tineina, subsection Tineina, of the division Ditrysia. Adults minute to small (4–25 mm wingspan), mostly with roughened head scaling, but some with smooth heads (Phyllocnistinae); haustellum naked; maxillary palpi porrect, 4-segmented (sometimes reduced). Maculation various but often colorful or strongly marked with contrasting spots or lines, and many with metallic-iridescence (especially Phyllocnistinae); venation reduced (especially on hindwing) and with long hindwing fringes. Adults are active diurnally. Larvae are usually leafminers but change form in later instars (hypermetamorphism) from sap feeders with reduced legs, to later instars with a 3-proleg pair larval form, which is unique among the Microlepidoptera. Later instars sometimes feed externally as leaf skeletonizers. The leaf mines have various forms, from blotch mines to elaborate serpentine mines, often unique to particular genera (serpentine mines are typical for Phyllocnistinae). Host plants include a great number of plant families. A few species are of economic importance, such as the citrus leafminer (*Phyllocnistis citrella*).

References

Davis DR, Deschka G (2001) Biology and systematics of the North American *Phyllonorycter* leafminers on Salicaceae, with a synoptic catalog of the Palearctic species (Lepidoptera: Gracillariidae). Smithson Contrib Zool 614:1–89
Deschka G (1982) Nearktische *Phyllonorycter* Huebner, 1822 (Lepidoptera, Lithocolletidae). Entomofauna 3:243–270
Hering EM (1951) Biology of the leaf miners. W. Junk, The Hague, The Netherlands, 420 pp, 2 pl
Kumata T (1982) A taxonomic revision of the *Gracillaria* group (Lepidoptera: Gracillariidae) occurring in Japan. Insecta Matsumurana (n.s) 26:1–186
Kuznetsov VI (1981) Fam Gracillariidae (Lithocolletidae). In: Identification keys to insects of European Russia. 4 (Lepidoptera) 2:149–311, Academie Nauk USSR, St Petersburg
Vari L (1961) Lithocolletidae. In: South African lepidoptera, vol 1. Transvaal Museum Memoirs 12, 1–238, 23 pl

Leafminers

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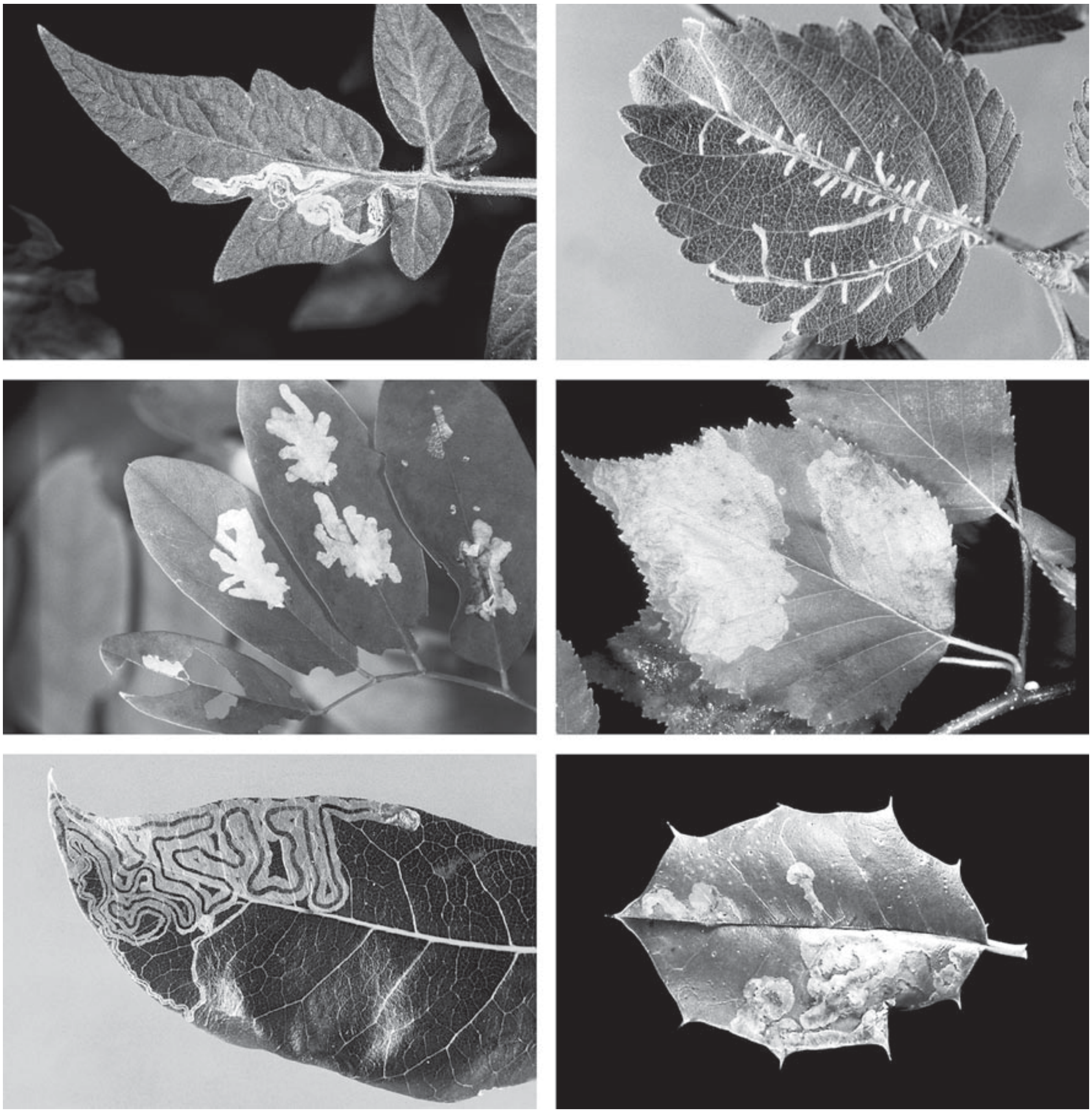
For at least part of their lives, several insects develop while chewing between the surfaces of leaves and needles. These include species found in several families of four insect orders notably including Diptera (Agromyzidae, Anthomyiidae), Coleoptera (Chrysomelidae), Lepidoptera (Gracillariidae, Gelechiidae, Yponomeutidae, Tortricidae, Elachistidae) and Hymenoptera (Tenthredinidae). Species that tunnel internally into the needles of conifers are called needleminers. Most needleminers in North America are Lepidoptera in the families Tortricidae and Gelechiidae. In some cases, insects tunnel beneath the surface of the stem or fruit tissue in a leafminer fashion, but such insects are usually just called "miners" to indicate that they do not inhabit true leaf tissue.

Leafminers are sometimes classified by the pattern of the mine that they create (Fig. 35). Serpentine leaf mines wind snake-like across the leaf, gradually increasing in diameter as the insect develops. Blotch leaf mines are irregularly rounded and often filled with frass. One subgroup of these are the tentiform leafminers that produce blotch-type mines that bulge upon drying to



Leafminers, Figure 35 **Leaf mines caused by leafmining insects. Top left is a serpentine mine caused by the American serpentine leafminer (Diptera). Top right is a linear mine (insect unknown). Middle left is a digitate mine caused by a caterpillar (Lepidoptera) affecting locust. Middle right is a blotch mine caused by the birch leafminer (Hymenoptera). Bottom left is a rather long winding mine caused by the citrus leafminer (Lepidoptera). Bottom right is a blotch mine caused by the holly leafminer. (Birch leafminer photo by J. L. Capinera, University of Florida; others by J. L. Castner, University of Florida.)**

curve upward somewhat like a tent. Digitate leaf mines spread from the center like rays of a flower or fingers on a hand. Linear mines, which are not common, are relatively straight. Mines of all types are often restricted by larger leaf veins, at least during the early life of the insect. Some leaf miners can move to other leaves when they exhaust their food resources.

Some insects may develop entirely as leaf or needleminers, pupating within the galleries that they form, and ultimately, emerging as adult insects. Other insects, notably many Lepidoptera, feed in a leafmining habit during early instars and later have a more generalized defoliating habit. The spruce budworms (*Choristoneura* spp.), are important North American forest insects that develop in this manner. Others may mine leaves during early instars then later emerge from the mines to feed externally. Subsequently, the foliage may be tied together with silk and the later- stage caterpillars will feed in a leafroller manner. Alternately, the larvae of some moths that produce tentiform mines originally develop on the exterior of the leaf then subsequently act as leafminers in later growth stages.

► Leaf-miners Flies

Leafrollers

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Leafroller is a term given to insects that, during their larval development, use silk to tie together the leaves of various plants. The term is limited to insects that are not gregarious and that individually produce a structure of folded, enclosed leaves on which they feed. The common name intergrades with insects of similar habit, including leaftiers and certain webworms. During very high populations, structures produced by leafminers may coalesce and resemble the more elaborate silken structures that are produced by gregarious, tent-making Arctiidae and Lasiocampidae. All leafrollers are in the order Lepidoptera with the great majority found in the family Tortricidae. Leafrolling caterpillars are also present in other families including the Gracillaridae, Crambidae, Galacticidae and Hesperiidae. Economically important species in North America include the fruittree leafroller, *Archips argyrospila* (Walker), the obliquebanded leafroller, *Choristoneura rosaceana* (Harris), the orange tortrix, *Argyrotaenia citrana* (Fernald), the bean leafroller, *Urbanus proteus* (Linnaeus), the larger canna leafroller, *Calpodes ethlius* (Stoll), and many others. (Fig. 36).

Leafroller Moths (Lepidoptera: Tortricidae)

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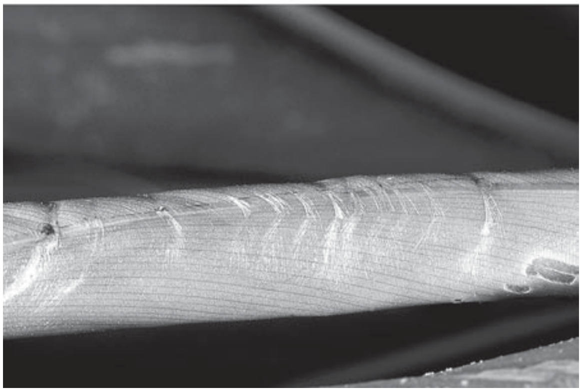
Leafroller moths, family Tortricidae, are a large family of 8,945 described species from all faunal regions; the actual fauna likely will exceed 12,000 species. Three subfamilies are known: Tortricinae, Chlidanotinae, and Olethreutinae. The family is its own monobasic superfamily, Tortricoidea, in the section Cossina, subsection Cossina, of the division Ditrysia. Adults small (rarely medium sized) (7–60 mm wingspan), with head rough-scaled (rarely smooth-scaled); haustellum naked; labial palpi usually porrect (sometimes upcurved); maxillary palpi usually 4-segmented (rarely minute). Body relatively robust. Wings elongated, but often rather truncated distally, or somewhat pointed (rarely irregular margined); hindwings usually more rounded or somewhat blunt pointed (Fig. 37). Maculation highly variable and sometimes very colorful, with metallic-iridescent markings (especially in diurnal species), but usually subdued shades of brown and gray, with various spots, lines, or other markings; hindwings often pale and unicolorous, or



Leafroller, Figure 36 **Leaf rolling by caterpillars in the family Hesperiidae. Above are two small leaf rolls made by the bean leafroller. These caterpillars cut a section of the leaf and then fold the edge of the leaf over to make increasingly large rolls as they mature. Below is a leaf roll constructed by the larger canna leafroller. In this case, the leafroller simply webs together the leaf before it unfurls, forming a large tubular structure within which it feeds. (Bean leafroller photo by J. L. Castner; canna leafroller photo by J. L. Capinera; both from University of Florida.)**

dark. Adults mostly nocturnal or crepuscular, but some are diurnal. Larvae mostly leafrollers, but some are borers (advanced groups in this family, rather than more typically being the primitive forms) in various plant parts, including stems, branches, flowers, and seeds; a rare few are leaf litter feeders. Most species are restricted to certain host plants, but innumerable

Leafroller Moths (Lepidoptera: Tortricidae), Figure 37 **Example of leafroller moths (Tortricidae), Olethreutes osmundava (Fernald) from Florida.**

plant families have recorded host plants. Many species are economic.

References

Bentinck GA, Diakonoff AN (1968) De Nederlandse bladrollers (Tortricidae). Monographieën van de Nederlandsche Entomologische Vereeniging 3:1–201, 99 pl

Clarke JFG (1958–1963) Torricidae. In: Catalogue of the type specimens of microlepidoptera in the British museum (natural history) described by Edward Meyrick, 3:1–600 (1958); 4:1–521 (1963) "part." British Museum (Natural History), London

Diakonoff AN (1973) The south Asiatic Olethreutini (Lepidoptera, Tortricidae). In: Zoologische Monographieën, 14 pl, Rijksmuseum, Leiden, pp 11–699

Geest van der LPS, Evenhuis HH (eds) (1991) Tortricid pests: their biology, natural enemies and control. In: World crop pests, vol 5. Elsevier, Amsterdam, 808 pp

Heinrich C (1923) Revision of the North American moths of the subfamily Eucosminae of the family Olethreutidae. Bull U S Nat Mus 123:1–298, 59 pl

Heinrich C (1926) Revision of the North American moths of the subfamilies Laspeyresiinae and Olethreutinae. Bull U S Nat Mus 132:1–216, 76 pl

Leaf-Rolling Crickets

A family of crickets (Gryllacrididae) in the order Orthoptera.

► Grasshoppers, Katydids and Crickets

Leaf-Rolling Sawflies

Some members of the family Pamphiliidae (order Hymenoptera, suborder Symphyta).

► Wasps, Ants, Bees and Sawflies

Leaf-Rolling Weevils

Members of the family Attelabidae (order Coleoptera).

► Beetles

Learning in Insects

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Learning encroaches upon virtually every aspect of the natural history of an insect. Where it has been investigated in insects, it has typically been found. Most of what is known about learning in insects comes from studies on the social Hymenoptera. For example, honeybees, *Apis mellifera*, have been shown to learn to use both flower color and shape as a way to increase their foraging efficiency for nectar and pollen, and foraging workers of the desert ant, *Cataglyphis fortis*, have been shown to associate directional information with landmarks. More recently, as researchers turn their attention to other insects, particularly phytophagous ones, the wider occurrence of the phenomenon is being appreciated. For instance, numerous studies have demonstrated that learning in grasshoppers is a mechanism that is commonly used to help regulate the intake of important macro- and micronutrients. However, the small size of insect brains and central nervous systems may place a limit on what and how much they can learn. Variation in learning ability also exists among individual insects, and those that are good learners may be at an adaptive advantage over those that are poor learners. However, conclusively demonstrating that learning in insects has an adaptive advantage that translates into increased individual fitness can be difficult.

What is Learning and How Does an Animal Learn?

Most people probably have a vague notion of what learning is, but an unambiguous definition is often hard to provide. Interestingly, even among scientists that study learning, an all-encompassing definition seems to be elusive. Therefore, the following is a broad description of what constitutes learning.

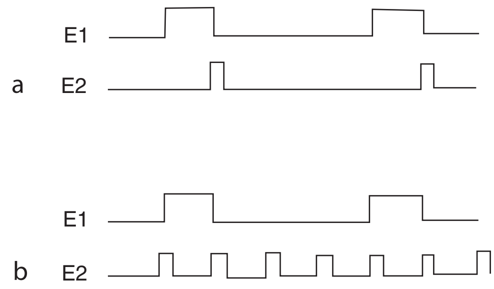
In general, learning involves attention, concentration and effort. However, specifying that learning has taken place requires that at least one of the following is occurring. One, an animal changes its behavior in a repeatable manner as a result of experience. Usually, the repeatability of a behavior is determined by statistical analyses on the results collected from a properly designed learning experiment. Two, with experience, a behavior gradually changes. Typically, the concept of a "learning-curve" is invoked here. Three, an observed change in behavior that was the result of a previous experience diminishes as that experience becomes less frequent. More simply put, in the absence of experience, it must be demonstrated that an animal forgets what was learned. In some cases, a new or traumatic experience may alter, or even purge altogether, a previously learned behavior.

It is worth noting that one prominent author, Thorpe (1963), defined learning as "…that process which manifests itself by adaptive change in individual behavior as the result of experience." Some, especially contemporary biologists, have objected to the use of "adaptive change" since it implies that learning has evolved under the action of natural selection and that it has some definable function, which is not always the case. For example, some larval lepidopteran species, after they have become accustomed to feeding on a particular host-plant (a phenomenon called food imprinting), will die from starvation rather than feed on a different host-plant species.

If, however, "adaptive" is taken to mean that animals generally learn to do what is sensible (e.g., turn toward, not away from, a rewarding stimuli), then the above definition becomes less controversial.

There are a number of different forms of learning, but conditioned, or associative learning, is probably the most thoroughly studied. An example using the common housefly, *Musca domestica*, in a laboratory demonstrates how conditioned learning works. First, a fly is secured to a vertical rod, using a specially designed harness, so that it faces forward and has its legs hanging at its sides. Next, one of its tarsi is brought into contact with either salt or water. This does not cause extension of the proboscis (feeding). Directly following this, the fly is presented with a droplet of sugar water, which causes its proboscis to extend. After this sequence of events had been repeated a number of times, the fly will start to extend its proboscis as soon as its tarsi comes in contact with the salt or water. This suggests that the fly has learned that the salt or the water, both previously neutral stimuli, predicts the arrival of the sugar water. In the above example, the formation of the learned association occurred by way of three steps. First, an unconditioned stimulus (US), the sugar water, triggered an unconditioned response (UCR), the proboscis extension. Next, the pairing of the unconditioned stimulus with a conditioned stimulus (CS), the salt or the water, led to an association forming between the US and CS. Finally, the US (the salt or the water) itself a conditioned response (CR) triggers the proboscis extension. Diagrammatically, the nature of this relationship can be expressed by Figure 38.

It is important to note, however, the CS will only become associated with the US if two criteria are met. First, there must be a positive correlation between the two stimuli. Second, the conditioned stimulus must have a certain intensity and duration. In the case of the fly, both criteria are met because the salt or the water always came into contact with one of the tarsi prior to the presentation of the sugar solution, and the salt or the water is readily "felt" and distinguished from other forms of "background noise".



Learning in Insects, Figure 38 Different patterns of correlation between two stimuli. In (a) the stimuli E2 occurs during, or shortly after, E1 and an association is formed. In (b) E2 is equally likely to occur when E1 is present or absent, so no association is formed.

A second form of associative learning is operant conditioning (also called instrumental or trial-and-error learning). This form of learning is distinguished from associative learning because it is characterized as "learning to do," rather than "learning to recognize." In operant learning, an animal learns to optimize a novel behavior through repetition and practice. Documented examples of operant learning in insects is rare, but is certainly the case when a honeybee becomes more efficient at collecting pollen after repeated visits to the same flower type.

Finally, it is worth discussing two other forms of non-associative learning that seem to share a relationship: sensitization and habituation. Sensitization is a short-term response that is the result of a sudden and intense stimulus. For instance, when a caterpillar is touched with a probe, its immediate reaction is to curl into a ball. However, if it is repeatedly touched in the absence of any significant event, its reaction to the probe begins to wane. This reduction in the level of behavior to the same stimulus over time is called habituation.

What do Insects Learn?

If learning permeates every aspect of life, then insects should be able to learn about locating and securing food and mates, caring for their offspring, escaping and defending themselves from natural enemies and navigating to and from their homes. However, the extent to which they are able to do this will depend on two things. The first is their ability to pay attention to what is happening in their immediate vicinity. Like other animals, insects gather information using their various senses, which include seeing, hearing, touching, smelling and tasting. The second is their ability to access the importance of any novel events. Usually, importance is measured by noting what happens shortly before or after a sequence of events has occurred. For example, a fly that has recently been attacked by a predator (or attacked with a fly swatter) will be acutely aware of any stimuli that are in any way similar to those it experienced immediately prior to the attack.

The easiest type of learning in insects to study relates to food acquisition, and both associative and non-associative examples have been identified. However, the degree to which an insect learns useful information about its food largely depends on the breadth of its diet. In general, learning tied to food acquisition is potentially more useful for an insect that feeds on a wide range of foods than for one that feeds on a single food, or food type, over its lifetime. For instance, associative learning seems to be a regularly employed mechanism used by honeybees when foraging for nectar. In most situations, the nectar is the unconditioned stimulus and some aspect of the flower, be it odor, color or shape, is the conditioned stimulus. Experiments investigating the strength of different floral characteristics as conditioned stimuli for honeybees suggest that there is a hierarchical structure, where odor>color>shape. Other pollinators, including bumblebees and butterflies, also show the ability to rapidly learn to associate flower colors and shapes with the presence of food rewards. Among foliage feeding insects (e.g., grasshoppers), learned associations between odors and major essential nutrients, and between particular color/light intensity cues and high-quality food, have been documented. However, there are examples of specialist insects learning, particularly among parasitoids and specialist butterflies that require specific hosts for their offspring. For example, *Microplitis croceipes*, a specialist parasitic wasp, uses plant volatiles released from the plant following feeding by caterpillars, which are hosts of the parasitic wasp. Its response to these volatiles is not, however, innate. Rather, an association of the plant volatile (the CS), as a result of damage to the plant following feeding by its caterpillar host (the US), is learned after a few successful oviposition events.

Learned associations between a neutral stimulus and a bad feeding experience are particularly valuable for insects because they provide a reliable and rapid mechanism for avoiding foods that contain toxins or unsuitable nutrients. However, examples of learned aversions to foods by insects are rare. Part of this may be because aversion learning tends to occur only in generalist herbivores, as feeding in specialist insects is driven by innate behavior. Additionally, demonstrating learned aversions in insects in the field can be difficult, so a laboratory approach is often required. Nonetheless, examples of learned aversions in insects do exist, particularly among generalist grasshoppers. For instance, two laboratory experiments have revealed that the generalist grasshopper *Schistocerca americana*, uses aversion learning to regulate the intake of an unsuitable dietary nutrient that cannot be tasted. In an initial experiment, grasshoppers were allowed to feed on spinach, which contains the unsuitable nutrient. After they finished eating, the unsuitable nutrient, or a closely related suitable one, was injected with a syringe directly into their hemolymph (blood). They were then allowed to take a second meal. Interestingly, those injected with the unsuitable nutrients took significantly shorter second meals on spinach (on average 3 sec) than those receiving the suitable nutrient (on average 90 seconds), suggesting that the unsuitable nutrient was detected post-ingestively, and that learning was occurring centrally rather than peripherally. The second experiment, using artificial foods with manipulated nutrient profiles and added flavors, indicated that the grasshoppers were learning to associate the taste of the food with the presence of the unsuitable nutrient. This example, plus others that show grasshoppers develop aversion responses to foods after being injected with various toxins, suggest that aversion learning may have an important role in the maintenance of dietary mixing.

In addition to securing food, insects must also find and choose mates. Although it is generally assumed that mate location and acquisition is innate and unresponsive to change through experience, the behavior of male apple maggot flies, *Rhagoletis pomonella*, seems to suggest otherwise. The males spend time on host fruit (either apples or hawthorns) waiting for females to arrive so they can mate. Research has shown that prior positive experience with females on one of the two host fruits influences the time a male will spend on the two fruits. That male insects may learn to assess the characteristics of females has also been suggested. For example, males of sacrophagous *Drosophila* learn to distinguish between females in particular physiological states, and the male *Lasioglossum* bees have been shown to learn characteristics of individual females. Where parental care is practiced, insects also must be able to recognize their offspring and feed them accordingly. For species of digger wasps that provide food to several burrows at once, evaluating food demands on an individual basis can be important because offspring may be at different developmental stages (newly hatched to nearly pupating). To assess food requirements, a mother will visit each burrow before setting off to gather food and, over the course of the day, will provide the appropriate amount of food to each burrow. However, experimental manipulation of the larva belonging to one species of digger wasp showed that there is considerable inflexibility in this system. When the larva in the burrows were exchanged following the female's morning inspection, the amount of food that the mother provided to each larvae upon returning to each burrow was shown to be based not on the current occupant, but on the individual that had been in the burrow during the morning inspection period.

Learning to escape from danger (specifically predators) would also be highly beneficial for insects, but when danger is sufficiently predictable and can be recognized innately, the use of sign stimuli should be favored over associative learning. Because of this, examples of learning to avoid danger are rare. Some butterfly larvae have an innate response to the sound of hunting wasps, and quite a few moths are able to counteract the echolocation used by bats. Also, in the laboratory, bees have been shown to associate sound with impending shock, but within a more natural situation, no examples of learning to associate sounds with danger are documented. The limited resolution of the insect compound eye greatly hinders visually based learning of danger, and no evidence exists to suggest that shapes associated with danger can be learned. At least one example of olfactory-based learning of danger is known. In a laboratory experiment, *Drosophila* maggots, using associative conditioning, learned to avoid electrical shocks associated with an odor.

Some insects have homes (either localized like a nest, or diffused like a home-range) and learning may aid in navigating to, from and around their homes. Most insects use innate mechanisms when navigating through their home territories, but the role of learning appears to be an important factor in calibrating their movements. Bees, for instance, appear to learn the direction of the sun's movements (left to right or visa versa) before they begin their foraging, and their memory seems to be irreversible. Learning related to navigation in bees is thought to depend on two alternative systems. If large, unambiguous landmarks are visible, the sun's course relative to these objects is memorized. If large objects are not available, the sun's rate of movement over the previous 40 minutes is measured and that value is used to calculate the change in the solar azimuth. Among experienced bees, large and unambiguous landmarks may be used in preference to celestial cues.

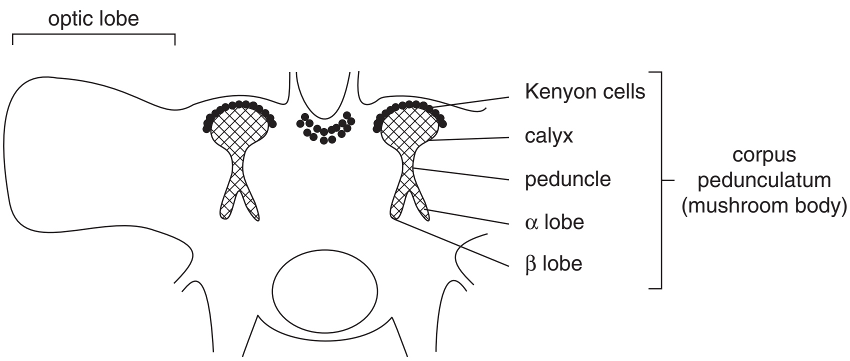
When Should Insects Learn?

In general, insects should learn in situations where the information necessary for guiding behavior is highly predictable, or too complex for innate responses to handle. That innate responses should be favored over learning makes sense because learned information is not as efficient and as reliable as innate information. It is also true that learning takes time, and mistakes (particularly during the initial stages of learning) are inevitable. Interestingly, learning is most favored in environments that are described as being "predictably unpredictable." This concept is best understood by viewing predictability along a continuum, with 0 being completely unpredictable and 1 being completely predictable. Using feeding as an example, specialist insects live in a predictable world because they only feed on a single plant species over their lifetime (a predictability value near 1). As a result, they will have no need to learn about their food since it is always the same. Likewise, at the other end of the scale, a generalist insect that feeds on a wide range of foods, but that never encounters the same food twice (a predictability value near 0), would never have the opportunity to learn since its experience would never be repeatable. This latter situation is unlikely to occur, and, for most generalist insects, remembering a bad experience with a toxic plant would be beneficial. However, if the plant on which the bad experience occurs is rare, there is limited opportunity to reinforce the learning experience. Where unsuitable foods occur with regularity, the combination of learning and sampling foods before taking large meals is one way in which highly mobile, generalist insects can increase the speed with which foraging decisions are made. However, learning related to food acquisition is probably only practiced in highly mobile insects that are in the latter stages of larval development or in the adult stage. Among generalist grasshoppers, for instance, learning may not be important during the first few instars because they are likely to spend the majority of their early life feeding on only a small number of plants.

What Constrains Learning?

The brain is the central processing center of information for all animals, including insects, and is responsible for transmitting signals that coordinate all behaviors (Fig. 39). However, the small size of the insect brain may place a great constraint on learning ability. The brain of an insect is split into three main regions (the protocerebrum, deutocerebrum and tritocerebrum) and it is generally thought that learning abilities in insects are in some way related to the size of a region of cells called the mushroom bodies, or corpora pedunculata. These bodies are given their name based on the shape of the five identifiable cell types. The uppermost region of these bodies consists of a flattened cap of neuropiles, called Kenyon cells. Below it lies the calyx, which has a peduncle running from it that eventually splits into two or three lobes, which are designated α, β and γ. The mushroom bodies, which occur at the sides of the pars intercerebralis in the protocerebrum, are small in the Collembola, Heteroptera, Diptera and Odonata, are largest in the social insects (where most examples of learning are documented), and are of intermediate size in Coleoptera, Orthoptera, Blattodea, Lepidoptera and sawflies. Researchers have shown that changes take place in the mushroom bodies with age and experience, but perhaps more interestingly experiments with *Drosophila* and *Apis* indicate that mushroom bodies also increase with experience, and are involved in associative learning (Fig. 39).

A second constraint on learning relates to the idea that intelligence is modular and that some associations formed between stimuli are more readily learned than others. For instance, experiments with rats show that illness following a meal is more easily associated with the taste and/or smell of the food that caused the illness than is a burst of light or a loud noise given at the time of the meal. This type of constraint may arise because taste and olfactory systems are intimately intertwined with digestion, whereas hearing and vision are not. That such constraints on learning occur makes sense because, evolutionarily, perceptual systems that respond to the most ecologically relevant stimuli in a rapid and reliable manner should be favored.



Learning in Insects, Figure 39 **The insect brain is divided into three main regions: the protocerebrum, deutocerebrum and tritocerebrum. The mushroom bodies, found in the protocerebrum, are thought to be a primary region of the insect brain associated with learning. This body consists of the Kenyon cells, calyx, peduncle and two or three lobes running from the peduncle. It has been suggested that the size of the mushroom bodies (specifically the number of neuropiles found in this region of the brain) is positively correlated with learning abilities.**

Can Learning Evolve?

If learning is to evolve in insects in an adaptive manner it supposes that genetic-based variation in learning exists, and differences in learning are associated with differences in fitness. Clearly, insect populations show genetic variations, and in *Drosophila* and *Phormia* flies, existing genetic variations within strains have been used to analyze the physiology of learning. Variation in learning has also been documented in honeybees and it has been shown to be heritable. In phytophagous insects, however, little information on genetically based variation in learning exists. Since documented cases of variation in learning are rare, it is not surprising that so little is known about the extent to which such differences translate into differences in fitness. One study has suggested that learning in generalist grasshoppers translates into higher growth rates, but this study only explored performance over a single instar. Because evolutionary fitness is defined as the ability of an individual/s offspring to survive and reproduce, there are significant logistical problems associated with demonstrating a fitness enhancement associated with learning. Clearly, more work in this field is needed, and a larger number of taxa need to be examined before any conclusive judgments can be made on the evolution of insect learning.

Conclusions

Learning in insects probably occurs with a greater frequency than is appreciated. Of the two main types of learning normally recognized, associative learning is probably easier to document, but operant learning (e.g., learning to handle food, to negotiate different types of substrates, etc.) probably occurs with greater regularity and is likely to take place over the entire life of an insect. Much remains to be discovered about insect learning, particularly the neural-basis of learning and the extent to which learning in insects evolves, but new technologies and methodologies are generating rapid advances. As model systems to explore learning, insects offer many great advantages, and their potential for contributing to a greater understanding of the mechanisms animals use to aid in learning provides a rich opportunity for future research.

► Learning in Insects: Neurochemistry and Localization of Brain Function

References

Bernays EA (2001) Neural limitations in phytophagous insects: implications for diet breadth and evolution of host affiliation. Annu Rev Entomol 46:703–272

Manning A, Dawkins MS (1998) An introduction to animal behaviour. Cambridge University Press, Cambridge, UK

Papaj DR, Lewis AC (1993) Insect learning: ecological and evolutionary perspectives. Chapman and Hall, London, UK

Papaj DR, Prokopy RJ (1989) Ecological and evolutionary aspects of learning in phytophagous insects. Annu Rev Entomol 34:315–350

Shettleworth SJ (1998) Cognition, evolution and behavior. Oxford University Press, Oxford, UK

Learning in Insects: Neurochemistry and Localization of Brain Function

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Research studies conducted over the last decade on the cellular and molecular mechanisms associated with learning (behavioral plasticity) have led to several generalizations: (i) learning involves changes in neural pathways that are correlated with alterations in synaptic efficacy; (ii) training procedures result in changes in membrane currents; (iii) learning involves second messenger systems; and (iv) behavioral plasticity is associated with changes in macromolecular synthesis within the central nervous system (CNS). These macromolecules include RNA and protein. Proposed cellular mechanisms for learning include reverberating circuits, modification of dendritic processes and synapses, voltage-dependent membrane channels and use-dependent modification of neural pathways. Although these ideas have been applied to both the vertebrate and invertebrate CNS, invertebrate models are particularly well suited for this type of analysis owing to their relative simplicity in contrast with vertebrate systems.

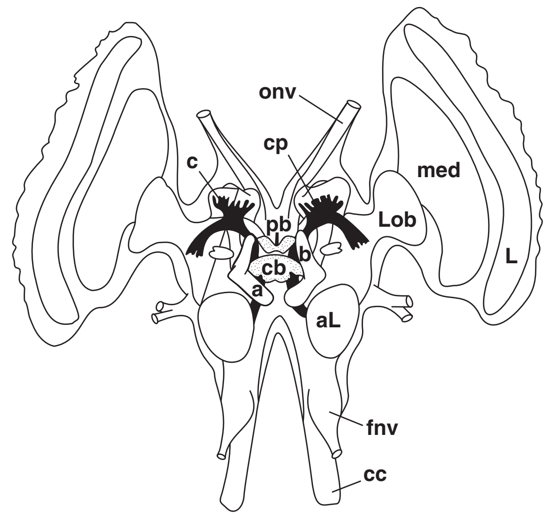
Invertebrates that have been used in studies on the cellular and neurochemical basis of learning and memory include gastropod molluscs, decapod crustaceans, theraphosid spiders and insects. Specific neurochemical changes that accompany learning include an increase in RNA and protein synthesis, a decrease in cholinesterase activity and changes in biogenic amines and amino acids. These neurochemical events have also been used to identify specific anatomical loci within the arthropod brain (cerebral ganglion) that have been implicated in the mediation of the learning process.

Inhibition of protein synthesis within the CNS was found to impair learning in vertebrates as well as orthopteran and coleopteran insects and theraphosid spiders. It was also found to impair the innate phototactic behavior of tenebrionid and passalid beetles suggesting that even rigid (closed) behavioral programs are dependent upon ongoing neurochemical events.

This elucidation of the neurochemical correlates of learning and memory in arthropods has occurred in conjunction with advances in behavioral ecology and neuroethology. The importance of learning in many diverse animal groups has been widely discussed. The ability of an organism to modify its behavioral response to varying environmental conditions is often essential to survival and can increase overall fitness. Learning encompasses adaptive changes in individual behavior that increase survival capacity and occur as the result of previous experience.

Insects and other arthropods have traditionally been viewed as creatures of instinct characterized by relatively rigid, stereotyped behavioral patterns. Nevertheless, although the behavioral repertoires of many insects are endowed with a rigidity of structure characteristic of Tinbergen's concept of Fixed Action Patterns (FAPs), there have been many studies demonstrating behavioral plasticity in insects and other arthropods. Furthermore, environmental parameters can influence the neuroarchitecture of specific brain regions in insects. The number of neuronal fibers in the brain of adult *Drosophila melanogaster* varies according to age, sex, early experience and olfactory conditioning.

Traditional categories of learning such as habituation, avoidance learning, trial-and-error learning, association and latent learning, and classical conditioning have been demonstrated in insects. The capacity for correcting behavior, imprinting and olfactory conditioning have been reported as well. More recently, investigators have been primarily concerned with the adaptive significance of learning. The contributions of behavioral ecologists and neuroethologists have made it clear that any analysis concerning the adaptive significance of behavior must take into account: (i) the evolutionary history of the behavior; (ii) processes related to the development and/or modification (learning) of the behavior under present conditions; and (iii) the environmental setting in which the behavior occurs. The ability of an organism to learn can also be used to obtain answers to questions concerning how the organism perceives its world, the role of CNS integration in the learning process (molecular mechanisms of learning), and what specific regions of the CNS are involved in the consolidation and storage of experiential information (localization of brain function). This contribution summarizes some of the recent work concerning the neurochemical correlates of learning and localization of brain function in insects.



Learning in Insects: Neurochemistry and Localization of Brain Function, Figure 40
Diagrammatic representation of a frontal view of the insect brain. aL, antennal lobe; a, alpha lobe of corpora penduculata; b, beta lobe of corpora pedunculata; cb, central body; cp, corpora pedunculata; c, calyx; fnv, frontal nerve; cc, circumesophageal connective; L, lamina of optic lobe; Lob, lobula of optic lobe; med, medulla of optic lobe; onv, ocellar nerve; pb, protocerebral bridge.

Learning and Development: Brain RNA Synthesis and the Retention of Learning Through Metamorphosis in Holometabolous Insects

The insect brain (cerebral ganglion) (Fig. 40) is divided into three major anatomical divisions: protocerebrum, deutocerebrum and tritocerebrum. The tritocerebrum innervates the muscles and sensory organs of the mouthparts. The deutocerebrum innervates the antennae which contain a rich array of chemo- and mechano-receptors. The protocerebrum innervates the optic lobes of the compound eyes and the ocellar nerves, and also contains several major ganglionic centers including the protocerebral bridge, central body and the corpora pedunculata (mushroom bodies) (Fig. 40).

Insects exhibiting complete metamorphosis (Holometabola) are characterized by distinct egg, larval, pupal and adult life cycle stages. During pupation, some larval tissues and organ systems undergo an extensive breakdown and are eventually reorganized to form the adult animal. As a result, holometabolous insects provide an excellent model for an analysis of the effects of development and CNS reorganization on learning and memory. The degree to which a behavioral response learned during the larval stage is retained by adults can be used to assess the extent of CNS reorganization during development.

The retention of an associative learning task following metamorphosis was reported for the locust (Hemimetabola), *Locusta migratoria*.

However, the degree of CNS reorganization exhibited by hemimetabolous insects does not compare with that exhibited by the Holometabola. However, because relatively few species of holometabolous insects have been studied, the degree of CNS reorganization during pupation may vary widely between species, depending on specific life history characteristics.

Research has been conducted on the retention of learning through metamorphosis in the holometabolous darkling beetles, *Tenebrio molitor* and *Tenebrio obscurus*, using a more complex spatial learning task (complex maze). These studies were also interested in studying neurochemical events (brain RNA synthesis) associated with learning. The maze consisted of a start chamber, goal chamber and six blind alleys. Only older larvae (<10 mm) were used for learning experiments. Adults were tested in the maze within 24 h of eclosion without regard to sex. Because the larval and adult stages of this insect are negatively phototactic, a fluorescent lamp placed directly over the maze served as an aversive stimulus. Larval insects were randomly assigned to an experimental group (L group) that was subjected to learning trials and a control group (no exposure to the maze). The number of blind-alley errors (BAE) was recorded for each trial as the insect progressed through the maze. The goal chamber was opaque and allowed the insect to avoid the aversive light stimulus. Mean number of BAE were recorded for trained larvae (L), adults previously trained as larvae (PTA), and adult controls (CA) which had no previous larval training.

The results indicated that T. obscurus larvae and adults are capable of learning a relatively complex maze. There was a significant improvement in performance over the 7-day training period for all test groups. For larvae, BAE decreased from a mean of 132.4 ± 21.8 S.D. (day 1) to 17.1 ± 4.9 (day 7). Over a similar 7-day training period, mean BAE decreased from 51.6 ± 11.2 to 7.3 ± 3.2 for PTA insects. However, adults with no previous maze training as larvae (CA), exhibited a mean of 90.5 ± 10.1 BAE on day 1 which decreased to 11.2 by day 7. This represents a significantly higher number of errors than the 51.6 BAE shown by adults previously trained as larvae and clearly demonstrates the retention of maze learning through metamorphosis in this species.

These findings strongly suggest that those specific brain regions associated with the consolidation and storage of experiential information do not undergo an extensive reorganization during pupation in *T. obscurus*. Previous studies on insects have identified the corpora pedunculata (mushroom bodies) and protocerebral bridge of the protocerebrum as playing an important role in complex behaviors including learning and memory. Future studies should include a detailed histological analysis of brain morphology throughout metamorphosis to ascertain the extent of reorganization of these and other brain regions.

Neurochemical Correlates of Learning and Memory in Insects and Localization of Brain Function

It is well known that specific neurochemical changes within the brain accompany the learning process in both vertebrates and invertebrates. Changes in the concentrations of amino acids, proteins, neurotransmitters and RNA have been shown to accompany learning and memory. An analysis of these neurochemical changes will result in a more complete picture of the molecular mechanisms underlying behavioral plasticity. In addition, such neurochemical events can be used to identify specific brain regions involved in the consolidation and storage of information within the CNS.

Neurochemical correlates of learning have been identified in insects and other arthropods. It has also been suggested that biochemical changes in RNA, proteins, neurotransmitters and amino acids may cause changes in the structural (number of synaptic connections, degree of dendritic branching) and functional (dynamics of gated channels and neurotransmitter release, postsynaptic thresholds) properties of neurons that participate in a learned response, thereby rendering such neurons more effective in later trials.

With respect to insects, studies on the cockroach (*Periplaneta*) indicated that leg-position learning (learning to flex the leg to avoid electric shock) was associated with an increase in protein synthesis and a decrease in cholinesterase activity in the CNS. Several ninhydrin-positive neuropeptides were identified from whole-brain extracts of a mantid, *Stagmatoptera biocellata* trained to attack a moving object. These compounds were not found in brains from non-trained controls or from insects that had been subjected to similar handling procedures. This strongly suggests that the neurochemical changes observed in trained insects were the result of learning procedures and not merely stress. Alterations in brain peptides have also been associated with ontogenetic changes in learning and memory in praying mantids. It was also demonstrated that arginine enhanced memory consolidation in mantids. Additional studies reported a correlation between biogenic amine concentrations (catecholamines such as norepinephrine, octopamine, dopamine) and conditioned responses to olfactory cues in honeybees (*Apis mellifera*). These findings are consistent with previous work showing that pools of amino acids and amines enhance acquisition and memory formation when injected into vertebrates.

Studies on a cricket, *Pteronemobius* sp. reported a significant change in the concentrations of urea, alanine, histidine, glutamine, cysteine and arginine in whole-brain extracts from animals trained in a simple Y-maze. Since alanine, arginine and urea are all related to the urea cycle, it appears that this metabolic pathway plays an important role in memory consolidation. Further studies showed that injections of alanine, arginine and glutamine blocked anoxic retrograde amnesia and enhanced memory formation. More recent studies have demonstrated a significant increase in hemolymph levels of taurine, urea, threonine, histidine and gamma-amino-butyric acid (GABA) following an aversive conditioning task. These findings are consistent with biochemical models of learning and memory in which information entering the CNS results in morphological and functional alterations at synapses.

Neurochemical events have also been associated with leg-position, shock-avoidance learning in a number of arthropod species. Through the use of H^3-labeled uridine (for RNA) and amino acids (for proteins), a significant increase in brain RNA and protein synthesis was found to accompany avoidance learning in a grasshopper, *Schistocerca americana*. Furthermore, these macromolecular changes were restricted to the corpora pedunculata and protocerebral bridge of the protocerebrum. No significant changes in RNA and protein were found in the deutocerebrum, tritocerebrum or other major ganglionic centers of the protocerebrum including the central body. These results indicate that learning experiments can be used to determine specific brain regions involved in the learning process (localization of brain function). Using similar procedures, a significant increase in RNA and protein synthesis were found to accompany learning in the protocerebral bridge and central body of the mud crab, *Eurypanopeus depressus* (Decapoda), and a theraphosid spider, *Aphonopelma chalcodes* (Orthognatha). In addition to RNA and protein, changes in neurotransmitter (catecholamine) levels were found to accompany olfactory conditioning in the honeybee, *Apis mellifera*.

Similar neurochemical correlates of learning have been reported for the hunting behavior of a spider wasp, *Pepsis formosa*. Nectivorous adult female wasps selectively hunt large, fossorial tarantula spiders (host species) which provide a food source for their carnivorous larvae. The hunting behavior of these wasps can be divided into several distinct sequential acts. The wasp locates an active host burrow while walking rapidly over the surface of the ground utilizing visual and olfactory cues. Once a burrow occupied by a tarantula has been located, the wasp enters the burrow, forces the spider to the surface and begins to explore the surface of the spider's body with its antennae. The wasp then moves a short distance away and cleans its antennae using its mouthparts. During this time, the spider makes no attempt to escape or move back into its burrow. The wasp then returns to the host and again explores the spider with its antennae. This is followed by a rapid movement whereby the wasp positions itself beneath the body of the host. The wasp grasps the hindlegs of the spider with its mandibles and inserts its stinger into the thoracic ganglion of the host causing rapid paralysis. The paralyzed spider is then dragged into its burrow and a single fertilized egg is deposited on its abdomen. The wasp then seals the entrance to the burrow and initiates a search for another host. Each of its eggs must be provided with another host spider. Upon hatching, the wasp larva feeds on the paralyzed host and completes its larval development.

This hunting sequence has traditionally been considered a classic example of instinctive behavior characterized by rigid, stereotyped behavioral acts. However, recent studies have shown that previous encounter experience can improve hunting behavior. Naive female wasps encountering a host for the first time require a mean of 251.7 min to complete the entire hunting sequence (from the initial approach through closure of the burrow). After eight encounters with spiders, the time required was reduced to 159.6 min. This significant improvement in performance associated with increasing number of encounters indicates that experience (learning) can modify hunting behavior and contribute to the overall fitness of these spider wasps. In terms of energy budgets and optimal foraging theory, time spent in locating a required resource is rendered unavailable for other important activities such as mating and reproduction in addition to increasing exposure to potential predators. By decreasing the time spent on hunting, *P. formosa* can minimize its foraging costs and thereby increase fitness.

It has also been shown that improvement in hunting behavior was accompanied by changes in brain chemistry. Increasing encounter experience resulted in a significant increase in protocerebral RNA and protein synthesis as compared to control wasps exposed to the same rearing and handling conditions but without any encounters with a spider. This difference reflects neurochemical events within the CNS attributable to the learning process and not merely to stress or a general increase in motor activity. Control wasps were allowed to fly, feed and explore a host-free encounter chamber on a daily basis. They were also within the same size and age range as wasps used in the encounter trials. The only consistent difference between these two groups was the encounter experience with host spiders. This represented the first demonstration of changes in brain neurochemistry associated with a naturally-occurring behavior consisting of sequential acts.

The importance of macromolecular events in learning and memory consolidation is also supported by experiments in which the animal was treated with a protein synthesis inhibitor prior to training. Injection of cycloheximide (CXM) has been shown to impair the learning process in crustaceans, spiders, grasshoppers, and mantids, as well as in reptiles and mammals.

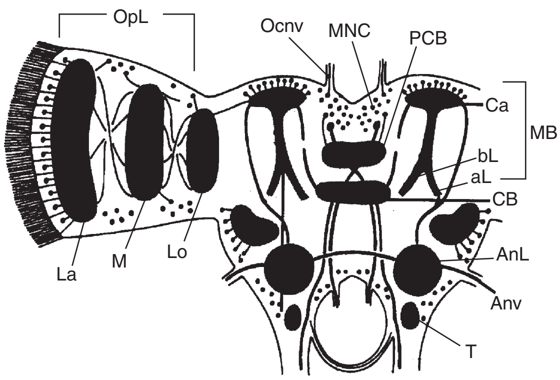
It should also be mentioned that macromolecular synthesis appears to play an important role in the expression of innate behavior as well. A fundamental question that has been asked metaphorically but never tested experimentally, concerns the functional relationship (if any) between instinct and the retrieval of learned information. Molecular mechanisms that could serve as models for the storage of information within the CNS should also be involved in learning and instinctive behavior and thus have access to the genome. It is well known that neurons are characterized by significantly higher rates of RNA synthesis than are other somatic cell types. RNA is essential to the expression of gene function. Regulatory molecules such as cyclic AMP, calmodulin and other second messengers, as well as some hormones, are known to activate genes. It has been suggested that environmental and behavioral factors could also activate genes. Behavioral events, either learned or instinctive, could trigger conformational changes in neuronal proteins through differential gene activation. Studies have been conducted on the effects of protein synthesis inhibition on the innate negative phototactic responses of the beetles *T. molitor* and *Popilius disjunctus*. Injection of CXM resulted in a pronounced impairment in the ability of *T. molitor* larvae to burrow into a cereal bran substrate to avoid an aversive light stimulus. Only 27% of the larvae treated with CXM exhibited burrowing with a mean burrowing time of 219 sec. One hundred percent of the non-treated controls burrowed with a mean time of 51 sec. All CXM-treated insects moved freely across the surface of the grain indicating that CXM did not impair normal motility. There was also no apparent deleterious effect of CXM on developmental processes; CXM-treated larvae and non-treated controls both completed pupation and emerged as functional adults. Cycloheximide treatment had a similar effect on the time required by *P. disjunctus* adults to traverse a runway to avoid light.

It is interesting to note that changes in CNS amino acids and biogenic amines have been found to accompany ontogenetic behavioral changes (age polytheism) in a number of insects and other arthropods. One of the most intriguing questions in neuroscience pertains to the relationship between brain chemistry and behavior. Neurotransmitters and comodulators have been implicated in a variety of ontogenetic behavioral changes in honeybee workers (*A. mellifera*) including shifts in discrimination between olfactory cues and the onset of guarding behavior. Brain dopamine (DA) levels were significantly higher in forager honeybees than in nurses or food storers. Similarly, amino acids and biogenic amines have been implicated in age polytheism in a carpenter ant *Camponotus floridanus*. A significant increase in the concentration of 5-hydroxytryptamine (5-HT, serotonin) has been reported in the brain of a solpugid, *Eremobates palpisetulosus* (Arthropoda, Arachnida, Solpugida) between the first and second nymphal instars. Dopamine levels increased significantly after the second nymphal instar. No changes were observed for octopamine (OA) throughout postembryonic development, and *N*-acetyldopamine (NADA) concentrations were found to decrease. Thus, lower DA and 5-HT concentrations were associated with those developmental stages characterized by low levels of locomotor activity and the absence of aggressive behavior between nymphal conspecifics. Agonistic interactions between siblings and other conspecifics first appeared in second-instar nymphs and are correlated with increasing concentrations of 5-HT and DA in the brain. It is also during this developmental stage that solpugid nymphs begin to burrow and actively hunt for food. The neurotransmitter acetylcholine as well as acetylcholinesterase levels also increased between the first and second nymphal instars.

Learning, Experience, and Brain Morphology

A link between macromolecules associated with learning, early experience, and specific cells (neurons) within the insect brain has been established in a number of insects including fruit flies (*Drosophila melanogaster*), honeybees (*Apis mellifera*), and several species of ants. The mushroom bodies (MB), also known as the corpora pedunculata, have been identified as an important brain region mediating complex behavior in insects. The neurons of the MB are called Kenyon cells (KC). To a lesser extent, other areas of the insect brain implicated in the learning process include the antennal lobes, the central body, and protocerebral bridge. This is not surprising since the MB represent convergence sites for chemosensory, visual, and mechanosensory pathways in the insect brain (Fig. 41).

The MB in *Drosophila* are bilateral clusters comprising about 2,500 cells which send their dendrites into a centrally located neuropil receiving neural inputs from the antennal lobes and central body. The MB consist of a calyx and two lobes (alpha and beta).



Learning in Insects: Neurochemistry and Localization of Brain Function, Figure 41 **Frontal view of insect brain. aL, alpha lobe of mushroom body; bL, beta lobe of mushroom body; AnL, antennal lobe; Anv, antennal nerve; Ca, calyx of mushroom body; CB, central body; La, lamina of optic lobe; Lo, lobula of optic lobe; M, medulla of optic lobe; MB, mushroom body – corpora pedunculata; MNC, median neurosecretory cells; Ocnv, ocellar nerve; OpL, optic lobe; PCB, protocerebral bridge; T, tritocerebrum.**

Evidence suggesting the involvement of the MB in olfactory learning was first observed in fruit flies. Localized cooling of these brain structures within 8 minutes after olfactory/reward training produces a type of retrograde amnesia. In addition, mutant flies with defective MB exhibit defective learning capacity.

The MB of honeybees, each consisting of about 170,000 cells, have been shown to change morphologically as the result of experience and training. There is a significant, age-dependent increase in the volume of the neuropil which is further enhanced following the first foraging flights by workers. The volume of the MB is significantly larger in nurses and foragers as compared to newly emerged bees.

In the ant *Camponotus floridanus*, the volume of the MB and neuropil increases by almost 50% between the time of pupation and 10 months of age. This increase in volume is associated with the increase in behavioral complexity associated with brood care and foraging. This increase in volume has been attributed to the growth of cellular axons and dendrites rather than an actual increase in the number of cells.

Summary

The present neuropharmacological evidence from invertebrates and vertebrates strongly suggests that the consolidation, storage and retrieval of experiential information within the CNS is dependent on macromolecular events involving second messengers, neurotransmitters, amino acids, proteins and RNA. It also seems that training procedures exert an effect on RNA and protein synthesis mediated by changes in neuronal transmission properties resulting from activation of neural circuits involved in the learning process. Environmental stimuli can alter steady-state levels of messenger RNA molecules encoding neurotransmitters resulting in changes affecting neuronal, synaptic and dendritic connections over time. The processing of experiential information alters electrogenic events causing changes in membrane depolarization and ultimately in the expression of specific neurotransmitter genes.

In animals exposed to learning trials, postsynaptic membrane changes within well-defined neural systems associated with learning appear to be involved in encoding the learned response for later recall. Specific ionic currents across neuronal membranes undergo changes that can last for variable periods of time following training procedures. For example, it is known from the study of invertebrate and vertebrate neural systems that intracellular calcium increases during acquisition accompanied by a concomitant decrease in potassium that persists for days after conditioning. This increase in calcium facilitates calmodulin-dependent phosphorylation of proteins involved in the regulation of specific gated ion channels. This may form the basis of a biophysical/biochemical memory trace. There is also evidence that conditioning causes an increase

in the excitability of dendritic membranes caused by a voltage-dependent Ca^{2+} current responsible for excitatory postsynaptic potentials (EPSPs) at synapses of neural pathway(s) involved in the learned response. This may lead to the formation of activated sets of neurons involved in the mediation of a learned response. A particular association could then activate specific neuronal convergence sites on the dendritic membranes of those neurons thereby enhancing recall.

The evidence supports the assumption that specific neuronal electrogenic events associated with learning and memory cause intracellular metabolic changes resulting in alterations in macromolecular synthesis. The synthesis of specific proteins could stabilize the changed cellular metabolism in its new state. This intracellular change could result in the release of molecules affecting the membrane's permeability characteristics and postsynaptic thresholds. In addition, the numerous studies demonstrating changes in RNA and protein concentrations in specific brain regions that accompany learning indicate that these macromolecular events are involved in acquisition and the consolidation of memory. See also: Learning in Insects, Nervous System.

References

Davis RL (1993) Mushroom bodies and *Drosophila* learning. Neuron 11:1–14

Hammer M, Menzel R (1998) Multiple sites of association odor learning as revealed by local microinjections of octopamine in honeybees. Learn Mem 5:146–156

Menzel R, Muller U (1996) Learning and memory in honeybees: from behavior to neural substrates. Annu Rev Neurosci 19:379–404

Punzo F (1996) Localization of brain function and neurochemical events associated with learning in insects. Rec Trends Comp Biochem Physiol 2:9–16

Punzo F (2000) An experimental analysis of maze learning in the wolf spider, *Trochosa parthenus* (Araneae: Lycosidae). Fla Sci 63:155–159

Tully T, Preat T, Boynton SC, del Vecchio M (1994) Genetic dissection of consolidated memory in *Drosophila*. Cell 79:35–47

Leatherjackets

Larvae of craneflies (Diptera: Tipulidae), especially *Tipula* spp., sometimes damage crops such as potatoes and small grains.

► Potato Pests and Their Management

Lecanicillium

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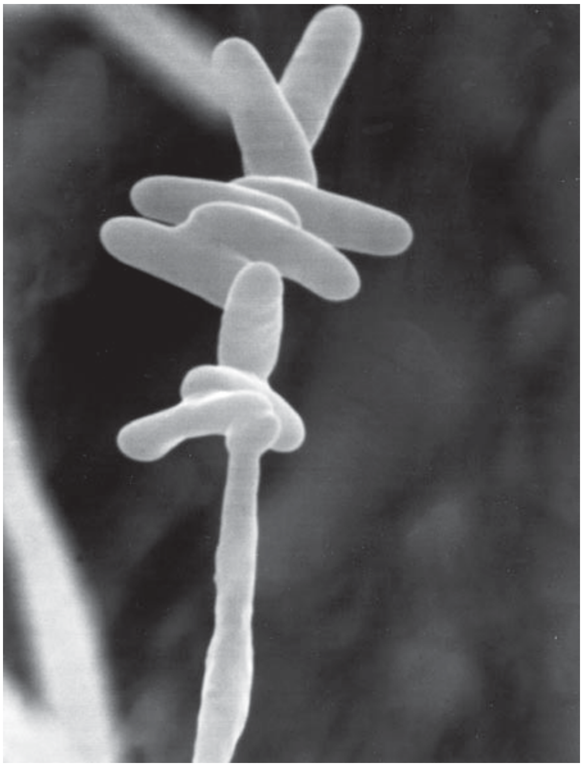
This is a newly formed genus within the family Clavipitacae (Hyocreales) that contains many of the entomopathogenic species that were once placed in the genus *Verticillium*. This genus contains 17 anamorph species that are closely related to the teleomorphs in the *Cordyceps* and *Torrubiella* groups. Members have been distinguished from *Verticillium* by their frequent formation of octahedral crystals in culture, entomogenous or fungicolous habit, phialides discrete and aculeate, conidia accumulating at phialide tips, mostly single-celled conidia (Fig. 42). Historically, the best-known entomopathogenic species, *V. lecanii*, known to contain strains that infect whiteflies, aphids, scales, thrips and grasshoppers, has been split into segregate species. The type species *Lecanicillium lecanii* (Zimmerman) Gams and Zane = *Verticillium lecanii* (Zim.). Viegas is restricted to those strains that infect scale insects in the tropical and subtropical habitats. Several other strains developed previously as *V. lecanii*-based microbial controls for greenhouse insect pests have been given new names. For example, the whitefly biocontrol Mycotrol is now considered to be *L. muscarium*, whereas the long-spore strains, such as the one developed into the Vertalac formulations, are contained within *L. longisporum*.

Different species of *Lecanicillium* have been used in greenhouses for whiteflies and aphids. The whitefly strain has not proven to be as efficient a control agent as the aphid strain, perhaps because whiteflies are sessile, so the fungus is not dispersed



Lecanicillium, Figure 42 **Scanning electron micrograph of *L. muscarium* conidia. Note how the conidia are stuck together in clusters.**

as easily from one insect to another as in the case of mobile aphids. *Aschersonia aleyrodis*, another Deuteromycete, has been suggested to be a better control agent of greenhouse pests than *L. muscarium*. For example, *A. aleyrodis* appears to be more virulent to whiteflies, and the spores survive on host plant leaves longer than those of *L. muscarium*. *Lecanicillium muscarium* conidia are relatively unstable and must be stored frozen or at 4°C. Multiple passaging of the fungus on mycological media does not seem to cause attenuation, but can alter colonial morphology and growth rates, which indirectly affect the use of the fungus in biocontrol programs. Interestingly, certain species of *Lecanicillium* display a broad spectrum of activity. For example, various strains of *L. longisporum* have been shown to be infectious to a spectrum of aphids including species of *Aphis*, *Macrosiphum*, and *Myzus* as well as being antagonistic to powdery mildews. Application of such a fungus may play a dual biocontrol role causing a lethal mycosis in the insect pest and in preventing plant disease.

References

Hall RA (1981) The fungus *Verticillium lecanii* as a microbial insecticide against aphids and scales. In: Burges HD (ed) Microbial control of pests and plant diseases. Academic Press, London, UK, pp 483–498

Heale JB (1988) The potential impact of fungal genetics and molecular biology on biological control, with particular reference to entomopathogens. In: Burge MN (ed) Fungi in biological control systems. Manchester University Press, Manchester, UK, pp 211–234

Kim J, Goettel MS, Gillespie DR (2006) Potential of *Lecanicillium* species for dual microbial control of aphids and the cucumber powdery mildew fungus, *Sphaerotheca fuliginea*. Biol Control 40:327–332

Verhaar MA, Hijwegen T, Zadoks JC (1996) Glasshouse experiments on biocontrol of cucumber powdery mildew (*Sphaerotheca fuligines*) by the mycoparasites *Verticillium lecanii* and *Sporothrix rugulosa*. Biol Control 6:353–360

Zare R, Gams W (2001) A revision of *Verticillium* section *Prostrata*. IV. The genera *Lecanicillium* and *Simplicillium*. Nova Hedwigia 73:1–50

Lecanodiaspididae

A family of insects in the superfamily Coccoidae (order Hemiptera). They sometimes are called false pit scales.

► Bugs

Lecithoceridae

A family of moths (order Lepidoptera). They commonly are known as tropical longhorned moths.

► Tropical Longhorned Moths
► Butterflies and Moths

Leconte, John Lawrence

J. L. LeConte was born May 13, 1825, in New York, New York, USA. He came to be known as the greatest coleopterist in North America. His education was typical for the period, a time when study of natural history was not popular. However, John LeConte's father had a passionate interest in beetles, and young John was introduced to entomology at an early age. In fact, they later would publish together. LeConte graduated from Mount St. Mary's College in 1842 and from the New York College of Physicians and Surgeons in 1848. In 1852 the LeContes moved to Philadelphia. John traveled extensively in North America, Europe, and North Africa, and served as a surgeon in the American Civil War (Fig. 43). At one point John sent 10,000 beetles in alcohol from his collections near San Francisco, and his father mounted them and made notes on the important characteristics of each. From 1878 to 1883 he served as assistant inspector of the United States Mint in Philadelphia. LeConte introduced a high degree of precision in the description of insects, establishing new standards for taxonomy. He published 184 papers, including some monumental works, including "Classification of Coleoptera of North America" (with G. H. Horn, in 1883). At the time of his death, he had described about one-half of the beetle fauna of North America, approximately 6,000 species. LeConte was a member of all the leading entomological societies and served as president of the Entomological Club of the American Association for the Advancement of Science, the forerunner of the American Association of Economic Entomologists. He died in Philadelphia, Pennsylvania, on November 15, 1883.

Leconte, John Lawrence, Figure 43 **John L. LeConte.**

References

Essig EO (1931) A history of entomology. The Macmillan Company, New York, NY, 1,029 pp

Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Leech, Hugh Bosdin

Hugh Leech was born in British Columbia, Canada, on May 10, 1910. His interest in entomology, especially beetles, began early, and his first paper was published in 1930. His employment at the Canadian Forest Entomology Laboratory in Vernon in 1930–1947 was interspersed with university studies. He attended the University of British Columbia, from which he received a B.Sc. degree in agriculture in 1933, and then the University of California at Berkeley, receiving the degree of M.Sc. in 1938. In 1936, he married Frances Quail, and eventually they had a daughter and three sons. In 1947 he took his family to California, having accepted a position as Assistant Curator in the Entomology Department of the California Academy of Sciences. He served for a time as editor of the Pan-Pacific Entomologist. His collecting expeditions, curation of specimens, promotion, and publications progressed until, at his retirement in 1975, he had almost 250 publications, and was recognized as a leading authority on water beetles. His contributions on water beetles of western North America are especially valuable. After retirement, with the status of Curator Emeritus, he indulged a passion for gardening. He died on November 8, 1990 in California.

References

Kavanaugh DH, Arnaud PH (1991) Hugh Bosdin Leech-a curator's curator with a bibliography. Pan-Pac Entomol 57:1–42

Leech RE (1991) Hugh Bosdin Leech (1910–1990). Coleopt Bull 45:95–96

Lefroy, Harold Maxwell

Harold Lefroy was born on January 20, 1877, at Itchel Manor, Crondal, Hamsphire, England. He graduated from King's College, Cambridge, in 1898 and served as entomologist to the Imperial Department of Agriculture for the West Indies from 1899 to 1903. He then served as Imperial Entomologist for India from 1903 to 1912. After his service in India he moved to the Imperial College of Science and Technology in England, where he remained until his death except for some service with the military in the Middle East and Australia. Lefroy (Fig. 44) was interested in both systematic and applied entomology. He made major contributions to human health through improved sanitation, and published major works based on his time in India: "Indian insect pests" (1906), "Indian insect life" (1910), and "Manual of entomology" (1923). His activities at Imperial College were controversial. Lefroy enjoyed popularizing entomology, including publishing popular accounts for newspapers and appearing on the radio - activities that were frowned upon by his more conservative colleagues. His success at saving the roof of an important historical building from the ravages of wood-boring beetles with a fumigant insecticide paved the way for new approaches to wood preservation. He went on to protect many more buildings and eventually founded a company to market his products. Unfortunately, he did not live to see the full success of his company, and died prematurely on October 24, 1925, while experimenting with new fumigant gases.

Lefroy, Harold Maxwell, Figure 44 Harold Lefroy.

References

Bateman PLG (1979) The imperial entomologist. Antenna 2:5

Felt EP (1925) Harold Maxwell Lefroy. J Econ Entomol 18:848–849

Legs of Hexapods

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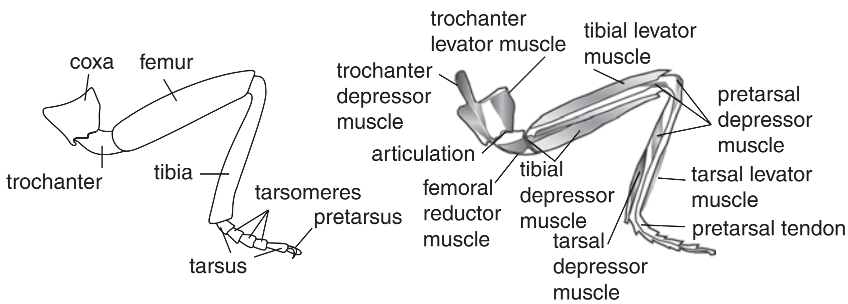
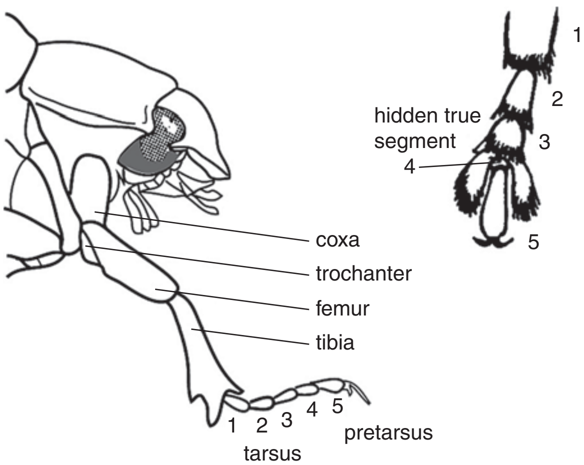
Despite the controversies that currently exist about the origin of the legs of the hexapods, and of the arthropods in general, the majority of authorities consider that the legs exhibit common morphological characteristics, and that their development is controlled by similar genetic mechanisms. Thus, the uniramous legs of the hexapods probably are derived from biramous appendages similar to those found in certain present-day groups of crustaceans.

Hexapods have three pairs of legs, situated in each one of the thoracic segments, from which comes the name of the group. There are certain exceptions, like the apodous larval forms and some adults with a specialized life form (e.g., adaptation to parasitism).

The locomotor appendage, basically adapted to walking on the ground, is formed by one branch with two parts: one basal or protopodite and the other distal or telopodite. The protopodite is formed by just one segment named the coxa, while the telopodite comprises five segments (Figs. 45 and 46) that, from the basal to the apical part, are named trochanter, femur, tibia, tarsus and pretarsus. The segments are joined by means of monocondylic and dicondylic articulations, differentiating extrinsic



Legs of Hexapods, Figure 45 **Basic leg components (*left*) and musculature (*right*).**



Legs of Hexapods, Figure 46 **Leg of a beetle (Coleoptera: Scarabaeidae) showing tarsal components.**

musculature and, in each one of the segments, intrinsic musculature.

The coxa generally has a globular shape. In its basal region is a submarginal suture named the basicostal suture, which internally corresponds to a crest called the basicosta. That suture separates a basal sclerite (basicoxite) that bears coxal cavities in which are articulated the condyles of the pleuron. In some orders, the basicostal suture has the form of "U" or of "V" on the posterior surface, delimiting an enlarged sclerite called a meron. In Thysanura, three points of articulation with the coxa (anterior, median, and posterior) are generally distinguished. In Pterygota the posterior point of articulation disappears due to development of the pleural crest, and the median condyle becomes the posterior. In certain insects, a longitudinal suture named the coxal suture can be distinguished over the external surface of the coxa, passing between the basicoxite and the anterior articulation of the trochanter. This suture corresponds internally to a reinforcement crest.

The trochanter is generally a small segment that articulates with the coxa through a horizontal hinge, which permits only movements in the vertical direction. It may be subdivided in two, as in Odonata, or be fused to the femur, as occurs in the last two pairs of legs of Strepsiptera. The articulation with the femur varies according to the group. In the majority of insects, the femur is the most robust segment; its greater or lesser development is related to its function, such as in the jumping insects in which it is very well developed to accommodate strong musculature.

The tibia is generally a narrow segment and the longest one, displaying a dicondylic articulation with the femur that enables it to carry out movements in a vertical plane and to fold back on the internal surface of the femur itself. The basal part of the tibia forms what is called the articular head and is known commonly as the knee, while in the distal part it bears one to many spurs.

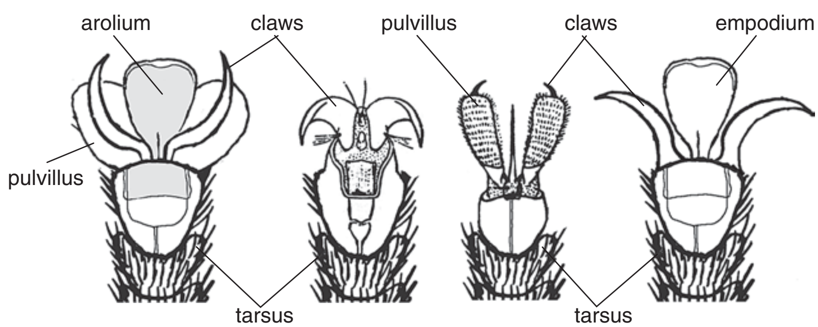
With regard to the tarsal-pretarsal region, two clads are distinguished in the hexapods; on one hand, Protura, Diplura and Collembola, with undivided tarsi (fused with the tibia in Collembola) that end in just one claw; on the other hand, the rest of the hexapods (the insects), with the tarsi subdivided basically in 3–5 tarsomeres that terminate in two pretarsal claws.

The tarsomeres do not exhibit intrinsic musculature, being articles and not true segments, although for practical purposes a few authorities use the name "subsegments." The whole tarsus is traversed by a tendon that is joined to the flexor muscle of the pretarsus, whose fibers originate in the tibia and, at times, in the femur. Although some authorities consider that the basal tarsomere (basitarsus) is a true segment that is named eutarsus, the majority think that convincing arguments do not exist to consider it in that way. It has already been noted that the number of tarsomeres can vary in distinct groups of hexapods; thus, in Archeognatha and Thysanura (Zygentoma) three tarsomeres exist. In Pterygota the number varies according to the group, with one tarsomere (nymphs of Ephemeroptera, and holometabolous larvae), with three (Odonata, Plecoptera, Embidiina; and Orthoptera, Acridoidea and Gryllidae), or with a variable number of one to three (Hemiptera). Pentamerous tarsi exist in the majority of Pterygota. There are special characteristics of the tarsomeres including the development of structures that support the insect in walking, such as the euplantulae (pad-like formations without hairs, situated on one or more tarsomeres) and the plantar lobes (special adhesive spiny formations).

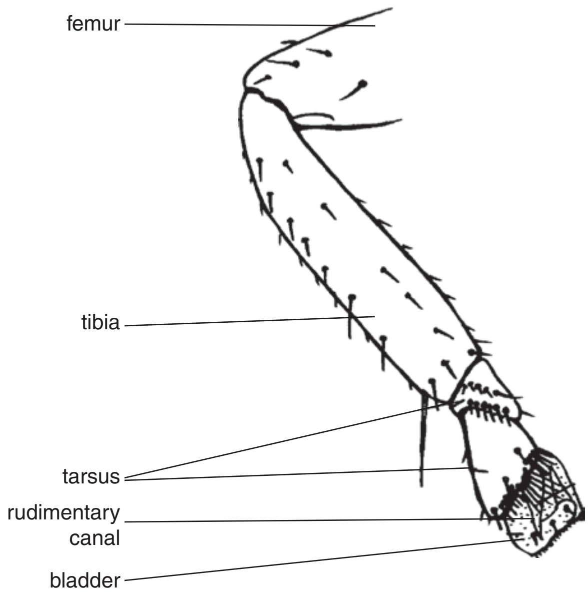
As a general norm, in the entognathous apterygotes, in the fossil group of the Monura and in the larvae of certain pterygotes, the existence of a single tarsomere is associated with the existence of a single pretarsal claw, while in the Ectognatha (Archaeognatha, Thysanura, and generalized Pterygota) the presence of three or five tarsomeres carries with it the existence of two claws (Fig. 47). In some apterygotes like Japygidae and many Thysanura, there is a third, a middle one, which at times is not obvious.

The pretarsal segment (post-tarsus of some authors) constitutes the apical part of the leg. It is formed by a complete annulus plus the unguiform structures in entognathous hexapods, while normally in the ectognathous insects two ventral sclerites are differentiated, the planta and the unguitractor plate, in which is inserted the tendon of the flexor muscle, which permits the movement of the two claws. There are also different structures in the pretarsus that enable the insects to join with the substrate over which they move, whether through the claws or by the development of structures like suction cups that let them grasp smooth surfaces such as glass (Fig. 48). Among these structures are the auxiliae (auxiliary sclerites of some authors), sclerites situated ventrally in the base of the claws. The pulvilli are smooth or setaceous membranous lobes situated ventrally to the claws and above the auxiliae, which take part in the movements of the pulvilli themselves. The empodium is a median process situated between the pulvilli, in the form of a spine or lobe, which is joined to the unguitractor plate. The arolium is a hollow and membranous lobe (at times partially sclerotized) in the median position. The arolium is morphologically and ultrastructurally different from the empodium.

As indicated in the section dedicated to the hexapod thorax, this tagma is basically dedicated to the locomotory functions, which are carried out



Legs of Hexapods, Figure 47 **Some variation among tarsal claws (*left to right*): Diptera: Tabanidae; Hemiptera: Cicadidae; Diptera: Asilidae; Blattodea: Blattidae.**



Legs of Hexapods, Figure 48 **Leg of a thrips (Thysanoptera) lacking tarsal claws.**

through the wings (see the corresponding chapter) and the legs. The locomotory function of the legs is developed in a different manner, taking into account, in the first place, if the environment in which a particular insect lives is aquatic or terrestrial and, in this last case, if the legs serve to walk or to jump. Moreover, whether it is an aquatic or terrestrial environment, the legs can be adapted to different functions than the original locomotory ones. All of that is translated into morphological modifications of the legs, with the following standing out among the most important:

Swimming Legs

The adaptation to the aquatic environment of different groups of insects carries with it a series of morphological modifications, which generally affect the posterior legs. The tibiae and tarsi are flattened and are bordered by long hairs that permit the legs to swim in a rowing manner and at times can be used as a rudder. Characteristic examples exist in the families of aquatic Coleoptera and Hemiptera. Less important modifications are found in hemipterans that live on top of the water (*Gerris, Hydrometra*) and that affect only the apex of the leg, over which are developed moisture-proof hairs that enable these insects to "skate" on the surface film of the water.

Running and Jumping Legs

The prior description of the segments corresponds to one typical for the running leg. The greatest velocity of running is usually related to a predatory behavior (e.g., Coleoptera: Carabidae, Cicindellinae). On the contrary, prey species should escape from their predators; one of the forms most commonly utilized in insects is the jumping form through the posterior legs, the insects being called for that reason jumpers. In these legs, the femora are particularly thick and long, since they accommodate a strong extensor musculature in the tibiae. They are longer than those in the anterior pairs of legs. The jump is produced by the rapid stretching of the femur-tibia complex. This type of leg is typical of groups like Orthoptera and Halticinae (Coleoptera: Chrysomelidae).

Digging Legs

The anterior legs of certain insects are usually adapted to dig, displaying different morphological modifications. Thus, in Coleoptera, Scarabeidae the tibiae are flattened and toothed, having the tarsus reduced. In species of *Gryllotalpa* (Orthoptera: Gryllotalpidae) with a subterranean life, the tibia and tarsus form a robust blade with strong teeth to make galleries. In the case of the nymphs of Cicadidae that also have a subterranean life, the femora are more robust and toothed apically, while the tibiae are thin; in this way, the nymphs can remove the earth to find the roots of plants that they eat.

Raptorial Legs

They are developed in species with predatory habits. In the most generalized model, the first pair of legs experiences modifications that enable them to act as a pincer to capture the prey. In the case of Mantida, the femur and the tibia are covered with strong spines on their opposite surfaces, which upon joining form a strong chela where the prey remain trapped. In Hymenoptera, Dryinidae the pincer is formed by the elongation of one of the pretarsal claws and the extension of the fifth tarsomere; both structures can be toothed.

Other Functions

In the adults of Odonata, the legs do not serve to walk, but rather the anterior legs are directed forward and serve to capture the prey in flight and to affix to the substrate when at rest. In the males they serve, in addition, to grasp the females during mating, and in certain cases, during oviposition.

In Orthoptera, Ensifera the anterior legs have crevices containing communication devices, the tympanic organs. In contrast, in many Orthoptera, Caelifera, structures for the production of sound are found above the internal surface of the femora. In the case of Siphunculata, the adaptations for ectoparasitism include modifications in the legs to grasp the hairs or feathers of the hosts.

In some species of aquatic coleopterans like that of the genus *Dytiscus*, the males have the first three tarsomeres flattened in the anterior legs, whose surface forms a structure that bears lines of small cuticular suction cups, except two of greater size situated in the first tarsomere. This structure serves to grasp the females during mating and, on occasion, to grasp prey.

The Hymenoptera can display on the anterior tarsi a structure called the "cleaning organ," consisting of the spatulated spur of the tibia and the contiguous notch (bordered with bristles) of the metatarsus. These form a zone through which the insect passes the antennae repeatedly and, at times, the mouthparts and even the last pairs of legs. The females of predatory wasps (e.g., Hymenoptera: Spheciformes) can use the legs to transport the prey to the nest. The bees (*Apis*) and bumblebees (*Bombus*) have the third pair of tibiae grooved in their external surface and bordered with long bristles, forming the corbicula that they use to transport pollen.

References

Beutel RG, Gorb SN (2001) Ultrastructure of attachment specializations of hexapods (Arthropoda): evolutionary patterns inferred from a revised ordinal phylogeny. J Zoolog Syst Evol Res 39:177–207

Bitsch J (2001) The hexapod appendage: basic structure, development and origin. Annales de la Societé Entomologique de France (NS) 37:175–193

Manton SM (1977) The Arthropoda. Habits, functional morphology and evolution. Clarendon Press, Oxford, UK

Matsuda R (1970) Morphology and evolution of the insect thorax. Mem Entomol Soc Can 76:1–431

Snodgrass RE (1935) Principles of insect morphology. McGraw Hill, New York, NY

Leiodidae

A family of beetles (order Coleoptera). They commonly are known as round fungus beetles.

► Beetles

Leishmaniasis

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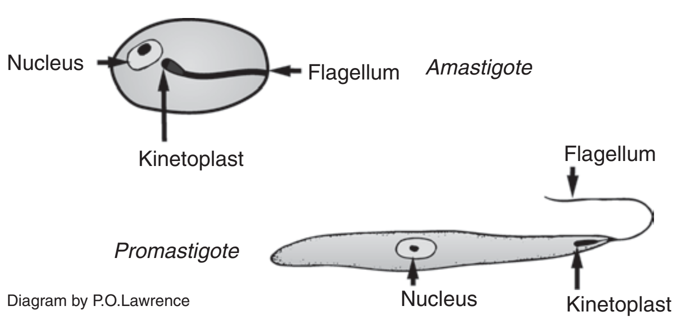
The World Health Organization (WHO) currently estimates that there are 1.5–2 million new cases of leishmaniasis each year and a total of 12 million cases worldwide. With ongoing epidemics of leishmaniasis in high conflict areas like Afghanistan and Somalia, and the recent discovery of a focus of infections in hunting dogs in North America, it should be of no surprise if there is an increase in *Leishmania* infections, in a manner consistent with other emerging infections. Leishmaniasis is caused by the eukaryotic parasites, *Leishmania* sp., of the order Kinetoplastida, which exist in two morphological forms (Fig. 49). The flagellated promastigote or insect form that develops in the sandfly vector (*Lutzomyia* sp. and *Phlebotomus* sp.) is deposited in the human or animal host during a blood meal. Soon after, promastigotes infect cells (primarily macrophages) that are recruited to the vector-feeding site. Within macrophages, *Leishmania* parasites reside in vacuoles wherein they transform into aflagellated amastigotes, the replicative form of the parasite in the animal host. For largely undetermined reasons, some *Leishmania* species in infected macrophages remain at the infection site where the interactions of recruited inflammatory cells, activated cells and parasites result in cutaneous lesions. Alternatively, some *Leishmania*-infected cells are transported to the viscera (spleen, liver and bone marrow). There too, inflammatory cells are recruited to sites of amastigote propagation where they form visceral lesions. Leishmaniasis manifests as a disease spectrum such that infected persons can develop self-limiting cutaneous lesions, disseminated cutaneous lesions that exhibit minimal tendency to self-cure, grossly disfiguring mucocutateneous lesions, or lethal visceral disease. A noted trend in leishmaniasis disease presentations has been a tendency for visceral symptoms to be associated with multiple parasite species, even those that are known to mostly cause cutaneous symptoms. Such was the case with the American service personnel whose manifestations of "Gulf War Syndrome" was the result of "viscerotropic" *L. tropica* infections. *L. tropica* infections are most often associated with cutaneous infections.

It should be expected that several factors, in addition to the parasite species and strain, determine the site of parasite propagation and disease severity. Recent studies have illustrated that the vector too plays an important role in determining the establishment of organisms and maybe even disease severity. During a blood meal, the sandfly vector releases molecules (vector saliva) in the host to facilitate feeding. The magnitude of the host's response to the vector saliva components can determine the fate of transmitted organisms. In naïve hosts, where the response to vector saliva is minimal or absent, vector saliva components apparently disarm initial host responses and thus permit transmitted organisms to establish themselves within those hosts. This latter observation might explain the high incidence of leishmaniasis in children and travelers or migrants through endemic areas. It is also noteworthy that in experimental visceral leishmaniasis, addition of saliva appears to be requisite for the establishment of infections.

The Immune Response and Consideration of Drug Therapy

Another worrisome trend in leishmaniasis is the "reactivation" and/or exacerbation of leishmaniasis as a result of co-infection with human immunodeficiency virus (HIV). In one study from Spain, leishmaniasis in 40 out of 40 patients co-infected with HIV was found to have resulted from reactivation of a previous *Leishmania* infection. The observations in immunocompromised hosts



Leishmaniasis, Figure 49 **Promastigote and amastigote forms of *Leishmania* sp.**

highlights the critical role of the cell mediated immune response, specifically CD4+ T cells in the control of leishmaniasis. It is widely accepted that the production of interferon-gamma (IFNγ) and interleukin 12 (IL12) as well as other T_H1 cytokines are the primary immune mediators of parasite control. In contrast, reduced production of these T_H1 cytokines, as appears to be the case in experimental infections with *L. mexicana* complex parasites or the production of IL4, IL10, transforming growth factor (TGF-β) and other T_H2 cytokines enables or promotes progressive Leishmania infections. Based on the current understanding of immunity to leishmaniasis, it is plausible to expect that vaccination strategies, which elicit protective T cell responses against *Leishmania* sp., would be effective at limiting leishmaniasis in the future. At present, therapeutic control of leishmaniasis is achieved with pentavalent antimonials (sodium stibogluconate [pentostam by GlaxoSmithKline] and meglumine antimonate). The use of these drugs in *Leishmania*-endemic areas, however, is limited by the fact that pentavalent antimonials need to be administered parenterally and preferably under controlled clinical conditions. Recent reports of the spread of *Leishmania* strains that are resistant to these drugs in *Leishmania*-endemic regions will increasingly limit their usefulness. In light of this reality, the new drug, miltefosine, which can be administered orally, would be a welcome addition to treatment options.

Mechanisms that Promote Parasite Persistence

A significant proportion of *Leishmania* infections exhibit a minimal tendency to self cure. From a review of the literature, there is evidence that two major mechanisms might contribute to the parasite's capacity to persist in the infected host. These are: (i) infection of macrophages by certain parasites results in the production of cytokines that inhibit the elaboration of and response to protective host responses, which consequently permits parasite growth and persistence; (ii) infected cells minimally present endogenously synthesized parasite antigens to CD4+ T cells. The result is that there is minimal T cell activation in response to infected cells. This assures parasite propagation and persistence. These mechanisms are discussed further below. It should be expected, however, that other factors such as host genetics, and the health status of the individual also would determine the extent of the host's capacity to control infections.

Induction of Inhibitory Host Responses

A well-documented feature of visceral leishmaniasis is that infected hosts have measurable levels of IFNγ in their serum. In addition, their peripheral blood mononuclear cells (PBMC) can produce IFNγ in response to parasite antigen. Similar observations also have been made in experimental studies of visceral leishmaniasis. Since these subjects have ongoing infections, it can be concluded that although IFNγ is an important mediator of parasite control, its presence is not sufficient to ensure control. In contrast, the production of IL10, IL4 and TGFβ appear to exert a greater effect on the host's capacity to control *Leishmania* infections. Experimental infections in $IL10^{-/-}$ animals and transgenic animals have confirmed the role of these cytokines in parasite persistence. It is presumed that these inhibitory cytokines function by suppressing T cell activation or the response of cells to leishmanicidal T cell products such as IFNγ.

In light of these findings, it has become of interest to determine what factors result in the production of immune inhibitory cytokines in leishmaniasis. There is some evidence that the differential engagement of phagocytic molecules on the surface of the macrophage by the parasite during infection might result in differential cytokine production. Following from the observation that *Leishmania* amastigotes that are recovered from tissue are opsonized with antibody, it was shown that engagement of macrophage Fc receptors by these opsonized parasites induced the production of IL10. Production of IL10 by macrophages then would block the leishmanicidal effects of IFNγ and thus promote parasite persistence. At the initiation of *Leishmania* infections, vector saliva that is released into the feeding site contains molecules that suppress the host response in addition to potent vasodilatory activities. The suppressive effects of such vector saliva components can be overcome by inducing a specific host response to them. Such an approach has been shown to limit the establishment of *Leishmania* infections.

Immune Evasion by Limitation of Infected Cell Recognition

In infections with *L. amazonensis*, there is increasing evidence that the host's responses to the pathogen are low or minimal. Many patients don't mount a Montenegro skin (delayed type hypersensitivity reaction to *Leishmania* antigens) test response. In addition, PBMC's from *L. amazonensis* patients exhibit lower recall responses *in vitro* to parasite antigens, as compared to recall responses of patients infected with other *Leishmanias*. Complementary observations have been made in experimental infections of C57BL/10 mice. These mice are resistant to *L. major* infections but they develop progressive *L. amazonensis* infections. C57BL/10 mice don't mount either a T_H1 response or a T_H2 type response of much significance, when infected with *L. amazonensis*. Further, neither the addition of IFNγ or IL12, nor the absence of IL4 or IL10 in knockout animals (lacking the genes that encode for these cytokines) significantly alters the course of *L. amazonensis* infections in most mouse strains tested. Paradoxically, it has been shown that CD4+ T cells are required for the establishment of *L. amazonensis* infections, presumably because the products of T cell activation results in cell recruitment to the eventual lesion site.

The absence of a significant T helper cell response in *L. amazonensis* infection might be explained by observations that have shown that amastigote-infected macrophages minimally present endogenously synthesized parasite antigens to CD4+ T cells. Those studies showed that while promastigote-infected macrophages could present parasite antigen transiently to parasite antigen-specific CD4+ T cells, amastigote infected macrophages were unable to activate the same antigen-specific CD4+ T cells. The effects of the parasite on antigen presentation were shown to be limited to parasite molecules in the parasitophorous vacuole, since parasite molecules fed exogenously could be presented by infected macrophages. Neither the reduced expression of MHC class II or accessory molecules could account for the phenomenon. The mechanism that underlies this process is not known presently. However, it is known that parasitophorous vacuoles that harbor parasites of the *L. mexicana* complex (*L. amazonesis*, *L. pifanoi* and *L. mexicana*) can selectively acquire particles ingested by the infected macrophage. Zymosan particles and live *Listeria* that are ingested by the macrophage, enter the Leishmania parasitophorous vacuole, in contrast to latex beads and antibody-opsonized *Listeria* that are excluded from entry into these vacuoles. In light of these observations of parasitophorous vacuole selectivity, it has been suggested that vesicles that play a role in antigen processing might similarly be excluded by the parasite.

The capacity of parasites to either limit CD4+ T cell recognition of infected cells or inhibit the response to T cell effector molecules is an evasion strategy that ensures parasite persistence. Studies that elucidate the mechanisms that underlie these processes should prove valuable in the design of new strategies to limit leishmaniasis.

References

Kamhawi S, Belkaid Y, Modi G, Rowton E, Sacks D (2000) Protection against cutaneous leishmaniasis resulting from bites of uninfected sand flies. Science 290:1351–1354

Morales MA, Cruz I, Rubio JM, Chicharro C, Canavate C, Laguna F, Alvar J (2002) Relapses versus reinfections in patients coinfected with *Leishmania infantum* and

human immunodeficiency virus type 1. J Infect Dis 185:1533–1537
Reed SG (1999) TGF-beta in infections and infectious diseases. Microbes Infect 1:1313–1325
Jones DE, Ackermann MR, Wille U, Hunter CA, Scott P (2002) Early enhanced Th1 response after *Leishmania amazonensis* infection of C57BL/6 interleukin-10-deficient mice does not lead to resolution of infection. Infect Immunol 70:2151–2158
Kane MM, Mosser DM (2001) The role of IL-10 in promoting disease progression in leishmaniasis. J Immunol 166:1141–1147
Silveira FT, Lainson R, Shaw JJ, De Souza AA, Ishikawa EA, Braga RR (1991) Cutaneous leishmaniasis due to *Leishmania (Leishmania) amazonensis* in Amazonian Brazil, and the significance of a negative Montenegro skin-test in human infections. Trans R Soc Trop Med Hyg 85:735–738
Silveira FT, Blackwell JM, Ishikawa EA, Braga R, Shaw JJ, Quinnell RJ, Soong L, Kima P, McMahon-Pratt D, Black GF, Shaw MA (1998) T cell responses to crude and defined leishmanial antigens in patients from the lower Amazon region of Brazil infected with different species of *Leishmania* of the subgenera *Leishmania* and *Viannia*. Parasite Immunol 20:19–26
Kima PE, Soong L, Chicharro C, Ruddle NH, McMahon-Pratt D (1996) *Leishmania*-infected macrophages sequester endogenously synthesized parasite antigens from presentation to CD4 + T cells. Eur J Immunol 26:3163–3169

Lek

A courtship site where males gather and display, competing for females.

Lemoniidae

A family of moths (order Lepidoptera) also known as autumn silkworm moths.

► Autumn Silkworm Moths
► Butterflies and Moths

Leng, Charles William

Charles Leng was born at Staten Island, New York, on April 6, 1859. As a child he collected insects and at the age of 16 joined the Brooklyn Entomological Society. He graduated from Brooklyn Collegiate and Polytechnic Institute as an engineer, and commenced work with his father's company. However, he remained interested in entomology. He coauthored, with W. S. Blatchley, "The Rhynchophora or weevils of northeastern North America," a monumental undertaking that includes descriptions of 1,800 species. He also published the "Catalogue of the Coleoptera, north of Mexico" (1920), with supplements in 1927 and 1933. His "Catalogue" became an essential tool for all coleopterists. Leng died at Staten Island on January 24, 1941.

Reference

Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Lentic Community

A community of organisms in standing or slow-moving water such as lakes, as opposed to those dwelling in fast moving water (lotic communities).

Leopard Moths

Some members of the family Cossidae (order Lepidoptera).

► Carpenterworm Moths
► Butterflies and Moths

Lepeletier, Amédée Louis Michel

A. L. M. LePeletier, Comte (count) de Saint-Fargeau, was born at Paris on October 9, 1770. He was educated in the seminaries of Paris, and seemed destined for an ecclesiastic life. However, the French Revolution of 1789 disrupted his life, as it did for most French nobility. Also, LePeletier discovered that his principal interest was natural history, including botany and entomology.

He became particularly interested in Hymenoptera, and devoted his efforts to understanding the social behavior of these insects. He promoted a system of classification for Hymenoptera based on sociality, not recognizing that sociality had evolved independently several times in this group. He was prominent among the entomologists of the time, and assisted in the preparation of "Dictionnaire des insectes de l' encyclopédie méthodique," published in 1825, and he authored "Monographia Tenthredinetarum" in 1823. He died on August 23, 1845.

Reference

Audinet-Serville M (1846) Notice nécrologique sur M. le comte LePelletier de Saint-Fargeau. Annales de la Société Entomologique de France 4:193–200

Lepidopsocidae

A family of psocids (order Psocoptera).
► Bark-Lice, Book-Lice or Psocids

Lepidoptera

An order of insects. They commonly are known as butterflies and moths.
► Butterflies and Moths
► Butterflies
► Moths

Lepidostomatidae

A family of caddisflies (order Trichoptera).
► Caddisflies

Lepidotrichidae

A family of silverfish (order Zygentoma).
► Silverfish

Lepismatidae

A family of silverfish (order Zygentoma).
► Silverfish

Leptohyphidae

A family of mayflies (order Ephemeroptera).
► Mayflies

Leptophlebiidae

A family of mayflies (order Ephemeroptera).
► Mayflies

Leptopodidae

A family of bugs (order Hemiptera). They sometimes are called spiny shore bugs.
► Bugs

Leptopsyllidae

A family of fleas (order Siphonaptera). They sometimes are called scaled fleas.
► Fleas

Leptotoceridae

A family of caddisflies (order Trichoptera).
► Caddisflies

Lerp

A protective covering formed from fecal and wax exudates produced by immature psyllids.

Lerp Insects

Some members of the family Psyllidae (order Hemiptera).
► Bugs

Lesion

A localized area of damage or infection, usually discolored or deformed.

Lesser Date Moth, *Batrachedra amydraula* Meyrick (Lepidoptera: Cosmopterygidae)

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The lesser date moth is a serious pest infesting flowers and immature fruits of the date palm, *Phoenix dactylifera*. The lesser date moth occurs over a large area in Asia from Bangladesh to western Saudi Arabia and Yemen, and most areas of North Africa.

Description

The adult moths have a wing span of 10–14 mm. The front wings are lanceolate with brownish scales. The hind wings are narrow, light grey and long-fringed. The eggs are small, light yellow and are laid singly on the flowers and immature fruits. The larvae, when full grown, are about 10–12 mm long. The head and the prothorax are light brown while the rest of the body is translucent white. The prolegs are on the abdominal segments 3–4 and on the last. Pupae are slender, long and light-brown in color.

Life Cycle

The lesser date moth has three generations annually. The longevity of the first and second generations is about a month. The first generation is called the flower generation because its larvae mainly attack the inflorescences, while the second generation is called the young fruit generation. The fully grown larvae of the third generation pass the winter protected in a cocoon that is spun in the inner base of fronds (petiole) and other tissues of a palm tree. Adults usually emerge by mid-April. Females lay eggs singly on the flowers, on which the young larvae feed. Larval feeding causes about 20% of the damage to the inflorescences. Moths of the second generation appear in early May and lay eggs singly on young fruit strands. Pupation takes place in early June and adults of the third generation emerge by mid-June. The eggs of the third generation are laid singly on the young fruits. The fully grown larvae of the third generation leave the fruit and go into dormancy throughout the remaining summer, fall and winter. In late March or early April of the following year, they pupate and emerge as moths of the first generation.

Economic Importance

The damage by this pest can cause up to 80% fruit loss. The importance of this pest varies from one year to another. It causes more damage in the internal oases than in the coastal ones. Each larva may attack and damage up to five fruits. A larva seldom feeds on more than a third of the fruit before it seeks another one. The damaged fruit becomes dry, brown in color, and half the size of a healthy one. Larvae egress by a hole bored close to the attachment at the perianth. Frass and silk can be seen protruding from the holes. Injured fruits usually fall, although the stout webbing spun by the larvae attaches some of the fruits to the strands or to other fruits.

Control

There are no biocontrol studies of this pest. However, larvae are parasitized by hymenopterous species at a low rate of parasitism. *Bacillus thuringiensis*, however, showed rather promising results. Chemical control is not effective unless insecticide is applied early in the season at the time of pollination, preferably using a pyrethroid to dust the fruit fronds. A spray may be needed 2–3 weeks following pollination. Aerial application achieves good results in Saudi Arabia, but scale insect populations can increase due to the death of its natural enemies.

References

Al-Fahdawey TM (1988) Effectiveness residues and temperature coefficient of permethrin insecticide when applied to control the lesser date moth *Batrachedra amydraula* Meyrick (Lepidoptera: Cosmopterygidae) and figmoth *Ephestia cautella* (Walker). Masters Thesis. Baghdad University, Baghdad, Iraq, 70 pp (In Arabic, summary in English)

El-Bashir S, El-Makaleh S (1983) Control of the lesser date moth *Batrachedra amydraula* Meyrick in the Tihama region of the Yemen Arab Republic. Proceedings of the 1st Symposium on the Date Palm in Saudi Arabia, pp 418–422

Talkhouk AS (1977) *Batracheder amydraula*. In: Kranz J, Schmutter H, Koch W (eds) Diseases, pests and weeds in tropical crops. Verlage Paul Parey, Berlin, Germany

Talhouk AS (1991) On the management of the date palm and its arthropod enemies in the Arabian Peninsula. J Appl Entomol 111:514–520

Lesser Grain Borer, *Rhyzopertha dominica* (L.) (Coleoptera: Bostrichidae)

This is one of the most damaging pests of grain.

► Stored Grain and Flour Insects

Lesser Mealworm, *Aphitobius diaperinus* Panzer (Coleoptera: Tenebrionidae)

This is the smallest of the mealworms commonly found infesting grain.

► Stored Grain and Flour Insects

Lestidae

A family of damselflies (order Odonata). They commonly are known as spread-winged damselflies.

► Dragonflies And Damselflies

Lestobiosis

A parasitic relationship wherein a small species lives within the nest walls of a larger species, and enters the nest to raid food stores or to prey on brood.

Lestoniidae

A family of bugs (order Hemiptera, suborder Pentamorpha).

► Bugs

Lethal Yellowing of Coconut Palms

This planthopper-vectored disease affects several types of palms.

► Transmission of Plant Diseases by Insects

Lettuce Root Aphid, *Pemphigus bursarius* (Linnaeus) (Hemiptera: Aphididae)

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This species is likely of European origin, but is now found widely around the world, including the Middle East, Central Asia, Siberia, North and South Africa, Australia, and North America. It thrives in temperate environments.

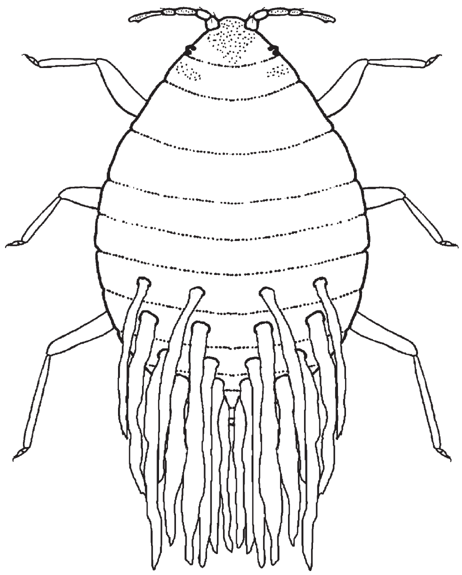
Life History

Lettuce root aphid normally overwinters in the egg stage on poplar trees, *Populus* spp., hatching in early spring. The females hatching from these eggs are large, rotund, and highly fecund. They reproduce parthenogenetically, and after two generations on poplar, winged forms (alatae) disperse to summer hosts. Dispersal of alatae usually occurs in early summer, and on summer hosts the aphids produce about three generations of parthenogenetic wingless aphids (apterae). Beginning in late summer, winged aphids are again produced, with dispersants migrating to the overwintering hosts. On poplar, small non-feeding male and egg-producing female aphids are produced, mating occurs, and eggs are produced. However, some aphids can also remain on lettuce or weed roots throughout the winter, colonizing nearby plants in the spring.

The egg is elongate oval in shape, initially greenish white but eventually orange in color, and enveloped in slender strands of waxy material. The egg measures about 0.48 mm long and 0.23 mm wide. Eggs are deposited in cracks and crevices of poplar bark at various heights on the tree to a height of at least 9 m.

Nymphs infesting foliage are green in color, and initially are found within poplar leaf petiole galls caused by feeding of the first generation adult. The nymphs have five instars, and may require 50–60 days in the spring to complete their development. Nymphs also are present on summer hosts, where development time is much shorter, and where they respond to increasing density and declining host quality by producing winged progeny that disperse to poplar trees. Nymphs on roots of summer hosts are not green; rather, they are light gray and covered with bluish wax. Nymphs are not capable of burrowing through soil, but they move freely through cracks on the soil, and over the surface of the soil, sometimes moving from plant to plant in this manner. Nymphs of all instars can overwinter belowground on summer hosts, often occurring at depths of 10–20 cm.

Adults of this species lack elongate cornicles; cornicles are porelike or absent. Adults possess relatively short antennae and legs. The adult female resulting from overwintering eggs is enveloped in bluish white wax. It is greenish in (Fig. 50) color, with dark appendages, and measures 2.0–2.2 mm in length. The feeding of this adult induces formation of a gall on the leaf petiole of poplar. The gall measures 6–18 mm in diameter and can eventually contain about 100 aphids or more. Adults emerging from the gall are winged (alate), disperse



Lettuce Root Aphid, *Pemphigus bursarius* (Linnaeus) (Hemiptera: Aphididae), Figure 50
Adult female lettuce root aphid, *Pemphigus bursarius* (Linnaeus).

to summer hosts, and immediately begin reproduction. The new females produce 15–25 nymphs within the first hour, which give rise to wingless (apterous) adults. Wingless adult females produced during the remainder of the year are oval in shape, yellowish white, and measure 1.6–2.5 mm in length. The short antennae are grayish to dark in color, the head black. The dorsal surface of the body bears six longitudinal rows of circular wax glands which produce waxy threads over the body. The entire aphid also is dusted with a fine white powder. The population of aphids peaks in August, at which time some nymphs move close to the surface and molt into winged adults. Winged adult females (alatae) are gray, green, or brownish in color, with darker head, antennae, thorax and markings on the abdomen. The wing veins are dusky brown. The alatae also produce a waxy secretion, and are 1.7–2.2 mm long. The reproductive forms produced late in the season on poplar are orange and lack functional mouthparts. The sexual forms are quite small, the males measuring 0.65 and the females 0.75 mm long. The abdominal cavity of the female is filled with a single egg that is deposited in a bark crevice.

The primary, or winter, host of lettuce root aphid is poplar, *Populus* spp. The Lombardy poplar, *Populus nigra* var. *italica* is the most common host, but other varieties of *P. nigra* and of *P. deltoides* also are recorded as hosts. The secondary, or summer hosts of lettuce root aphid are normally plants in the family Compositae such as wild lettuce, *Lactuca seriola*; sow thistle, *Sonchus arvensis*; and dandelion, *Taraxacum officinale*. Plants from other families such as redroot pigweed, *Amaranthus retroflexus* (Amaranthacea); shepherdspurse, *Capsella bursa-pastoris* (Cruciferae); lambsquarter, *Chenopodium album* (Chenopodiacea); and white campion, *Lychnis alba* (Caryophilaceae), have been reported to support small populations of these aphids, but these records are suspect. Lettuce is the principal crop affected, but chicory and endive are also infested.

Several natural enemies are known, but the natural enemy complex varies considerably depending upon the host plant and location of the aphids on the host. It is difficult for large predators to gain access to aphids feeding within intact galls, but galls are sometimes damaged by birds, and small predators can gain entry through the gall exit hole. The pirate bugs *Anthocorus* spp. (Hemiptera: Anthocoridae), the flower flies *Syrphus ribesii* (L.) and *Metasyrphus musculus* (Say) (both Diptera: Syrphidae), the chaemaemyiid *Leucopis pemphigae* Malloch (Diptera: Chamaemyiidae), and the lacewings *Hemerobius* and *Chrysopa* spp. (Neuroptera: Hemerobiidae and Chrysopidae) feed on aphids within galls. Aphids on the surface of poplar leaves and lettuce leaves also are subject to predation by such insects as lacewings, *Chrysopa* sp.; spined assassin bug, *Sinea diadema* (Fabricius) (Hemiptera: Reduviidae); the damsel bug *Nabis ferus* (Linnaeus) (Hemiptera: Nabidae); and such ladybird beetles as *Adalia* sp., *Coccinella* spp., *Coleomegilla maculata* (De Geer), and *Hippodamia* spp. (all Coleoptera: Coccinellidae). Aphids feeding on roots are less exposed to predation, but *Thaumatomyia glabra* (Meigen), *T. bistriata* (Meigen) (both Diptera: Chloropidae), *Sphaerophoria menthastri* (Linnaeus) (Diptera: Diptera: Syrphidae), rove beetles (Coleoptera: Staphylinidae), and ground beetles (Coleoptera: Carabidae) have been recorded feeding on these aphids. Fungal disease readily infects aphids belowground, and protozoa and a nematode were occasionally observed.

Damage

Feeding on lettuce by lettuce root aphid results in wilting, yellowing and stunting of leaves. Rootlets may turn brown and die, and roots will be covered with masses of bluish white, woolly material if aphids are present. Heavy infestations can cause softening and collapse of the lettuce head, and death of the plant.

Management

Insecticides may be applied to the soil for protection of lettuce varieties that are susceptible to root aphid attack. Contact and systemic materials, liquid and granular formulations, and planting-time as well as side dressed applications can be made, but effectiveness varies among products, and most insecticides work better as a preventative.

Destruction of old lettuce plants, particularly root stumps, and alternate hosts is often recommended to reduce the likelihood that aphids will be present when future crops are planted. Although the practice of sanitation always has considerable merit, it is most effective if soil temperatures are warm. This is due to the fact that at cool temperatures lettuce root aphids can survive for months without food. Also, the presence of Lombardy poplars near lettuce fields is detrimental to aphid management, and though planting of Lombardy poplars in lettuce production areas should be avoided, few advocate destruction of these short-lived trees if they already exist.

Soil water management can be important in minimizing aphid damage. Adequate and even levels of soil moisture promote rapid growth of lettuce, enabling the plants to mature quickly and escape the eventual population increase of the aphids. Plants also are more tolerant of injury if they are provided with adequate moisture. Constant soil moisture also limits cracking of the soil, limiting access to the roots by aphids and interplant movement.

Lettuce varieties differ considerably in their susceptibility to damage, with some commercial romaine (cos) and crisphead varieties displaying some resistance.

References

Alleyne EH, Morrison FO (1978) Vertical distribution of overwintering soil apterae of the lettuce root aphid, *Pemphigus bursarius* (L.) in Quebec. Ann Entomol Soc Quebec 23:155–157

Alleyne EH, Morrison FO (1978) Resistance of lettuce varieties to attacks by the root apterae of *Pemphigus bursarius* (L). Ann Entomol Soc Quebec 23:158–167

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, CA, 729 pp

Dunn JA (1959) The survival in soil of apterae of the lettuce root aphid, *Pemphigus bursarius* (L.). Ann Appl Biol 47:766–771

Dunn JA (1959) The biology of lettuce root aphid. Ann Appl Biol 47:475–491

Leucospidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees, and Sawflies

Leuctridae

A family of stoneflies (order Plecoptera). They sometimes are called rolled-wing stoneflies.

► Stoneflies

Libellulidae

A family of dragonflies (order Odonata). They commonly are known as common skimmers.

► Dragonflies and Damselflies

Libytheidae

A family of moths (order Lepidoptera). They commonly are known as snout butterflies.

► Snout Butterflies
► Butterflies and Moths

Lice

A group of ectoparasitic insects affecting mammals and birds. Considered here to be a single order (Phthiraptera), sometimes it is divided into two orders, Mallophaga (chewing lice) and Siphunculata (sucking lice).

► Chewing Lice and Sucking Lice

Life Cycle

The complete sequence of changes undergone by an organism during its life, often expressed as hatching of the eggs through the immature and adult stages of development, to hatching of the eggs produced by the insects developing from the first eggs.

Life History

An organism's lifetime pattern of growth, behavior, and ecology.

Life Table

A system of assessing population growth through tabulation of reproduction and survival within and among generations, and a method of recording age-specific survival. This approach usually analyzes the fate of a cohort – a group of individuals born at the same time. Females are the focus of life table analyses due to their reproductive potential, and the analysis partitions the life history of the insect into convenient stages, often the egg, young larva, older larva, pupa, and adult. The sex ratio of adults is also considered. An

Life Table, Table 4 **A typical life table (adapted from Harcourt's studies of imported cabbageworm)**

X	lx	dxF	Dx	100 qx	Sx
Eggs	658	Infertility	8	1.2	0.99
Young larvae	650	Rainfall & other	328	50.5	0.50
Older larvae	322	Virus	219	68.0	
		Rainfall & other	7	2.2	
		A. glomeratus	1	0.3	
		Total	227	70.5	0.29
Pupae	95	*P. vulgaris*	12	12.7	
		P. puparum	16	16.8	
		Other	1	1.0	
		Total	29	30.5	0.69
Adults	66	Sex (50.5% female)	–.07	–1.0	1.01

accounting of the mortality rate at each stage, and the factor(s) responsible, are the key elements of the analyses. The life history elements recorded, and the standard method of notation, are:

x – the age interval at which the sample was taken
lx – the number surviving at the beginning of the stage noted in the x column
dx – the number dying in the age interval stated in the x column
*dx*F – the mortality factor responsible for dx
100 *qx* – percentage mortality
Sx – survival rate within x

Generation survival is a product of survival in the individual life stages. survivorship among cohorts is often assessed using "key-factory analysis," which evaluates the relative contributions of various mortality factors to generation survival. The individual mortality factors that are most correlated with (Table 4) intergenerational survival are called "key factors." Key factors are those that determine population trends, and often determine whether insect populations will grow or decline.

References

Begon M, Mortimer M (1981) Population ecology. A unified study of animals and plants. Blackwell Scientific, London, 200 pp
Harcourt DG (1966) Major factors in survival of the immature stages of *Pieris rapae* (L). Can Entomol 98:653–662
Varley GC, Gradwell GR (1970) Recent advances in insect population dynamics. Annu Rev Entomol 15:1–24

Lightningbugs

Members of the family Lampyridae (order Coleoptera). These are also known as fireflies.

► Beetles
► Fireflies
► Fireflies: Control of Flashing
► Glowworms

Lignicolous

Referring to organisms that dwell within wood, usually tree-feeding species.

Ligula

The central or terminal portion of the labium, often formed from the merger of two lobes. It is sometimes used in a manner synonymous with "glossa" or "tongue."

► Mouthparts of Hexapods

Limacodidae

A family of moths (order Lepidoptera). They commonly are known as slug caterpillars.

► Slug Caterpillar Moths
► Butterflies and Moths

Limiting Factors Concept

The concept of limiting factors holds that there are a number of individual factors that limit insect population size, and if any one of these is in short supply (or over-supply), population size will be limited. Examples of limiting factors include food, space, temperature, predators, parasitoids, and disease agents.

Limnephidae

A family of caddisflies (order Trichoptera). They commonly are known as northern caddisflies.

► Caddisflies

Limnichidae

A family of beetles (order Coleoptera). They commonly are known as minute marsh-loving beetles.

► Beetles

Limoniidae

A family of flies (order Diptera).

► Flies

Lindroth, Carl H

Carl Lindroth was a Swedish naturalist, and was born on September 8, 1905. As a child, Lindroth was interested in natural history, and frequently visited the Natural History Museum in Gothenburg. He commenced with beetle collecting in the 1920s. He was educated at the University of Uppsala, where he received a doctoral degree in 1931. He worked for many years at Lund University, in Lund, Sweden. Lindroth is known for his contributions to our knowledge of carabid beetles of northern Europe ("Die fennoskandischen Carabidae," published from 1945 to 1948), but more particularly to historical biogeography emphasizing the distribution of European and North American carabids. He examined critically the routes of introduction of European fauna into North America in both recent times and the late Pleistocene. He began some important field work in 1949 with visits to Newfoundland, and by the early 1950s had discerned the true identities of the carabid fauna of Newfoundland, Nova Scotia and Labrador. His 1957 treatise "The faunal connections between Europe and North America" identified the species shared between western Europe and North America, but he then continued to study the entire carabid fauna of Canada and Alaska, which was published in a 6-volume series, "The ground beetles of Canada and Alaska" (1961–1969). Lindroth discovered that over 40% of the carabid species shared between Europe and North America owe their introduction to humans, but also that ancient trans-Atlantic land bridges were important in connecting the Palearctic and Nearctic. He emphasized the significance of isolation in the evolution of brachyptery, and identified probable refugia during the ice ages. He also wrote about zoogeography in other regions of the world. His lasting contributions include a secure nomenclature for the northern carabids, identification of many new species, and the highest standards of descriptions and illustrations. Lindroth died on February 23, 1979.

References

Ball GE (1981) Carl H. Lindroth: contributions of a Swedish naturalist to systematics and biogeograhy in

North America. Entomologica Scandinavica Suppl 15:17–32
Brinck P (1981) Carl H. Lindroth in the Old World. Entomologica Scandinavica Suppl 15:5–15

Lined Flat Bark Beetles

Members of the family Laemophloeidae (order Coleoptera).

► Beetles

Lingula

A more or less slender tongue or strap-shaped organ.

► Mouthparts of Hexapods

Linnaeus, Carolus (Linné, Carl Von)

Carl Linnaeus was born in Roeshult, Sweden, on May 2, 1707. Carl disappointed his father, a Lutheran minister, by displaying no interest in the priesthood. His parents were pleased when he entered the University of Lund in 1727 to study medicine, but after only a year he transferred to the University of Uppsala. There he studied botany, which was part of the medical curriculum. He then went to The Netherlands in 1735 and completed his degree in medicine at the University of Harderwijk, and immediately enrolled for additional studies at the University of Leiden. That same year he published his first edition of the classification of living things, his "Systema Naturae." He returned to Sweden in 1738, where he worked as a medical doctor until employed by the University of Uppsala in 1740. Linnaeus was known principally as a naturalist and botanist, but he had profound effects on entomology. He established the binomial system of nomenclature, which made possible the modern classification of insects and other organisms. Thus, he is rightly known as the "father of biological systematics and nomenclature." He also developed the wing vein-based system for separation of orders, and established the chronological starting point for the naming of insects. Linnaeus traveled extensively in Europe, but also received specimens from other countries, so many of the common species from all over the world were named by him. Linnaeus' publication "Systema Naturae," 10th edition (1758) is considered the starting point for naming of insects. All names pre-dating this publication are considered invalid. His scientific works were written in Latin, with his author name as Carolus Linnaeus. In 1761 he was ennobled, and subsequently was known as Carl von Linné. He died in Uppsala, Sweden, on June 10, 1778.

References

Essig EO (1931) A history of entomology. The Macmillan Company, New York, NY, 1,029 pp
Herman LH (2001) Linné (Linnaeus), Carl. Bull Am Mus Nat Hist 265:99–100
Waggoner BM (1996) Carl Linnaeus (1707–1778). Available at http://www.ucmp.berkeley.edu/history/linnaeus.html Accessed August 2002

Linognathidae

A family of sucking lice (order Phthiraptera). They sometimes are called pale lice.

► Chewing and Sucking Lice

Linsley, Earle Gorton

Earle Linsley was born at Oakland, California, on May 1, 1910. As a child he became interested in insects, and attended the University of California at Berkeley. There he received all his degrees in entomology, with the Ph.D. awarded in 1938. His doctoral dissertation was on the Cerambycidae of California, and he worked on this subject throughout his career, culminating in a publication on the Cerambycidae of North America in 1997. Linsley became known as one of the world's leading authorities on this group. He also worked on the classification of solitary bees. Linsley joined the faculty of the University of California in 1939, chaired the Department from 1951 to 1959, and served as dean from 1960 until his retirement. During his productive career he published over 400 articles and books, named several hundred species or subspecies, and named 132 genera. Among his major publications were "Principles and methods of systematic zoology" (1953), which was co-authored with E. Mayr and J. A. Chemsak, and the 9-volume "The Cerambycidae of North America," in which Chemsak also participated. Linsley received numerous awards and honors, served as editor of "The Pan-Pacific Entomologist," and was president of both the Pacific Coast Entomological Society and the Entomological Society of America. He died at Oakland, California, on March 8, 2000.

Reference

Chemsak JA (2000) Earle Gorton Linsley. Am Entomol 46:270–271

Liopteriidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees, and Sawflies

Lipases

Lipid digesting enzymes secreted by the midgut, releasing fatty acids and gylcerol from triacylglycerols, the principal source of fat eaten by insects.

Liposcelidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice or Psocids

Literature and Insects

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Insects enliven literature in many ways. Even authors who typically ignore the natural world mention insects now and then. Jane Austen (1775–1817) is a good example of such a writer. In *Sense and Sensibility*, Austen's character Marianne reports she has been told in the East Indies, "the mosquitoes are troublesome."

The attachment of writers to insects seems to be as old as the existence of writers. Two early nineteenth century entomologists, William Kirby and William Spence, highlighted the link. Kirby and Spence saw students of insects in Virgil, Shakespeare and (Edmund) Spenser. In their 1812–1826 series about insects, compiled as the *Introduction to Entomology*, they quoted poets who reminded them of "the connection between natural science and agriculture, and the arts." In fact, the work of Kirby and Spence attracted many of the best known naturalists to insects. Among them was Charles Darwin, who cited the importance of the work by Kirby and Spence in hooking him, or at least, reinforcing his pre-existing curiosity.

By 1842, Robert Patterson, then the treasurer of the Natural History Society of Belfast, had published a detailed analysis titled, *Natural History of the Insects Mentioned in Shakespeare's Plays*. Title aside, his scrutiny of the literary uses made of insects extends well beyond Shakespeare. Moreover, Patterson, pointed out that many others, including writers, were already aware of the phenomenon of insects beguiling literary authors. He cited the label that the eighteenth century author and lexicographer, Samuel Johnson, also known as Dr. Johnson, applied to Shakespeare. It was, "the Poet of Nature."

In the early twentieth century, Harriette Wilbur (1919), and W. R. Walton (1922), took separate looks at the insects that pervade English poetry. Walton focuses on English works dated from Chaucer (1340–1400) forward. He identified

25 references to insects, belonging to six orders, in Chaucer's work.

Indeed, there may be no richer territory for finding insects in literature than in poetry. Walton suggested the reason when he wrote, "your true poet must of necessity ever be a naturalist in the broader sense." The tome, *Destructive and Useful Insects*, by Metcalf and Metcalf (1993 edition), includes an outline note that, "Insects have served as subject matter for hundreds of poems." No doubt the estimate of "hundreds" is low, but the point is made. W. John Tennent (2001), recently noted that he is compiling a compendium of insects in poetry, and in all likelihood the list will grow to the thousands, or more. Dependent upon allusions and the activities of the ancient gods to strengthen their metaphors and similes, writers would inevitably be drawn to the natural world, even if they were simply reading other writers and not wandering outdoors.

More than 2,500 years ago, Aesop launched many allegories built on the ways of insects. Among them are "Ant and the Grasshopper," which suggests a long-term reward for toiling instead of having fun, and "Bee and Jupiter," which illustrates that the empowerment rendered by a sting can also be a liability.

Psyche personified the soul to the late Greeks, even as she stirred Aphrodite's wrath and besotted Eros. Aristotle (384–322 B.C.), an early naturalist as well as a philosopher, assigned the name Psyche to butterflies.

Some mention of insects was made probably because the creatures annoyed writers so. Walton points to Edmund Spenser (1552–1599) as one that seemed to have a low tolerance for flies, and noted the *Faerie Queen*, had, "no less than eight references," to the disturbances they cause, from buzzing to filling chambers. From Austen to Spenser, it is not surprising that dipterans get attention. A writer need not look for flies. They make their presence known by alighting, biting or swarming. They are most often nuisances.

Yet even early writers that were living among flies and fleas, wonderfully nurtured by the dirty and crowded streets of pre-industrial London, found time to make careful observations of animal and plant interactions of a happier sort. Shakespeare's (1564–1616), play *The Tempest*, offers many acute insights into the cycles of the natural world, serving as an early, poetic treatise on ecology. It also includes some often cited and lovely lines about, "Where the bee sucks, there suck I/In a cowslip's bell I lie;... Merrily, merrily shall I live now/Under the blossom that hangs on the bough."

Entomologist, Writer, or A Little of Both?

In some cases, the boundary between the entomologist and the writer blurs. Novelist and poet Vladimir Nabokov (1899–1977), perhaps best known for *Lolita*, was also a serious student of butterflies. Smithsonian Institution entomologist Harrison Gray Dyar, who died in 1929, and is known for his biometric studies of immature insects, also wrote short fiction.

Contemporary author Margaret Atwood is the daughter of an entomologist, and insects often wriggle into her fiction. The father of Sylvia Plath (1932–1963), Otto Plath, was a Harvard University-based entomologist. Sylvia Plath committed suicide in a London dwelling once occupied by William Butler Yeats (1865–1939), a poet that had a great affinity for insects.

Yeats's poem, *Long-Legged Fly*, captures the essence of the movement of a water strider (Gerridae) on a stream. (His fly appellation probably derives from a Latin moniker applied to water striders, *tippula*, long before they had English common names.) French novelist Gustave Flaubert (1821–1880), also fretted about what to call striders, and settled on "long-legged insects."

Flaubert sought the help of correspondent and friend George Sand (1804–1876) in sorting out a lyrical name for what he described at one juncture as, "troublesome creatures," vexing to him because he did not like the sound of their available names. And, ultimately, he did not include striders in the novel for which they were destined. Correspondence between Flaubert and Sand indicate the former had no love of natural world, but the latter did.

Sand wrote of taking time for "botanizing" with her son, Maurice, whose entomological leanings were quite serious. Maurice produced a gilded volume, *Le Monde des Papillons*, published by Rothschild, in 1867.

Yet, one need not reach beyond a shelf of works by living writers to find insects. Mosquitoes, flies, crickets, locusts, wasps and bees get mentioned in Vikram Seth's *A Suitable Boy*, (1993). Even Hana, the lovesick caregiver in Michael Ondaatje's *The English Patient*, (1993), has time to notice the way, "bluebottles stumble in the air." Calliphorids wend their way into a great deal of fiction and poetry, probably because of their luster and ubiquity.

Read enough of a favorite author, and insects will emerge from the text in more instances than not, for two reasons. One, even the most reclusive writers sometimes cast a cursory look at nature and eventually see insects and write about them, or read writers that have done. Two, ideas and images are fortified by the introduction of insects, either as literal entities, or as figures of speech.

Significance

Entomologists and writers share common ground, and sometimes exploit it in a similar way. A search for solace sends both groups into the field, or into a book, seeking the same returns, comfort, context and common sense. Entomologists are more likely to quantify their experiences with insects than writers are, but to some extent, entomologists also allow themselves to make qualitative, or impressionistic judgments.

Insects make their way into prose and poetry through allegory, metaphor, simile, or simply by becoming central to the point of a story. Certainly, in some of the best-known tales involving insects, there are multiple uses in play.

A fly, or fly-man, takes a central role in Franz Kafka's (1883–1924), *The Metamorphosis*. The scarab beetle that is "The Gold-Bug" of Edgar Allan Poe (1809–1849), serves as a cipher and the key to a fortune. The eponymous heroine of A. S. Byatt's novella, *Morpho eugenia*, (1992), conceals as many secrets as any butterfly, and leaves the reader guessing throughout her transformation and amazed at its outcome.

Kafka, Poe and Byatt are just some of the many authors who have not been content to draw on insects for imagery alone. The authors also demonstrate knowledge of natural history and biology that is quite refined. Kafka taps the ancient mystery of complex life cycles, and anticipates DNA manipulation. Poe shows that mythology and beauty are melded in the ancient fascination with scarabs.

The history of exploration always plays itself out. The man that pursues Byatt's Morpho is a naturalist with a fondness for butterflies, freshly returned from the Amazon, where all serious nineteenth century naturalists trekked. Moreover, the man confronts a choice all naturalists make between comfort (the field) and context (the home).

C. P. Snow (1905–1980), wrote *The Two Cultures and the Revolution*, in part, as a lament over the gulf between the sciences and the humanities. Yet, thanks to the exceedingly large number of links between writers and entomologists, there are stepping-stones across the gap, making the reach across the divide so contiguous as to make Snow blush and reconsider.

Strong Images

When insects enter the picture, every stroke a writer makes seems to become stronger. For example, the most mundane and intangible thing, a rumor, can be made visible. Consider a simile Vikram Seth uses in *A Suitable Boy*. He wrote, "For every fact or imagined fact that appeared in print, there were ten rumors that hovered about like wasps over a rotting mango."

Or, focus on the nexus of beauty and horror, which is eternally in flux, and nevertheless can be portrayed. In *The Yachts*, William Carlos Williams (1883–1953), considered the way the ocean, when riled, can ravage sail bearing boats, and sink them, "pitilessly/mothlike in mists."

Thanks to insects, the reasoned, patterned ways of the world can be retold simply. Emily Dickinson (1830–1886) wrote, "To make a prairie it takes a clover and one bee."

Many writers transcribe their observations of the natural world in verse. In *The Sick Rose*, William Blake (1757–1827), speculated, "The invisible worm/that flies in the night/in the howling storm/has found out the bed."

Other writers try to sort out their place in the world by comparing natural entities. In *The Dancer* Philip Larkin (1922–1985), wonders, "Butterfly/Or falling leaf, Which ought I to imitate/In my dancing?"

Flaubert and Yeats are just two of the many writers captivated by water striders. Henry Wadsworth Longfellow (1807–1882), wrote in *Hiawatha* that, "Insects glistened in the sunshine, Insects skated on the water." In the same poem, "The mosquito, sang his war song." Walton (1922), saw the reference as prophetic, given it was published in 1855 and the role of mosquitoes as vectors for malarial parasites had not yet been established.

Trends

Over time, writers and entomologists have moved in roughly the same direction in the level of attention they give to the details of insect life. While the showiest, most common or most pestiferous insects got noticed early on, as time permitted a more leisurely approach to things, there has been a progression in literature that matches the one in science.

In general, there has been a trend away from observing more highly derived insects to observing less highly derived ones and from familiar to cryptic, nuisance to joy (or harbinger), destructive to helpful, and described to named. The shift in perspective was first cited by Walton (1922). As interest in the importance of insects in literature grows, the possible evolution in the precision of observation, or level of engagement, will be tested.

The change to more defining names is an easy trajectory to document. But, in certain instances, the correlation may reveal more about the author than the period of time. Yeats, who tapped insects in at least eight orders for his poems, also named tortoiseshell butterflies (*Nymphalis* sp.) and the peacock butterfly (*Inachis io*). As it happens, Yeats collected insects enthusiastically in his youth and anticipated at least once in writing that he would become an entomologist. He was also so fascinated by Alfred Russel Wallace, and he considered an homage to him.

There are other trends worth investigating as well. Across the centuries, simile has given way to metaphor, basic similitude to complex allegory, and comparative notes to central themes. To illustrate, and give a mention to arachnids, which also garner considerable interest from writers, look to *Mr. Edwards and the Spider*, by Robert Lowell (1917–1977). When Lowell, "saw the spiders marching through the air," he also saw a metaphor for humans without a purpose.

Finally, the reflection of insects in literature seems to mirror settings that are the major population centers. Thus, urban insects have lost some favor to rural ones, just as imaginary insects have been supplanted by real ones. The contemporary Irish poet Seamus Heaney describes a flirtation with the natural world that did not end well. In *Death of a Naturalist* (1966), he describes a, "flax-dam festered" where, "…bluebottles/Wove a strong gauze of sound around the smell."

A Full Circle

Sorting out the direction of influence when insects, entomologists and writers are linked is never easy, and is really just beginning to get the serious scholarship the subject area deserves. Almost every author has something to say about insects. In *Seven Pillars of Wisdom* (1926), T. E. Lawrence

(1888–1935), wrote that only, "bodily exhaustion," from marching across the Arab peninsula in hot sun was responsible for, "proofing me against the onslaught of lice and fleas."

The epigraph, a popular tool for nonfiction writers, entomologists among them, illustrates the ring writers and insects and entomologists tend to form. Choose a book of essays by any of the best known twentieth century entomologists from Howard Evans to E.O. Wilson, and see how skillfully the authors mined the rich territory of literature for nuggets.

An outstanding example of the integrative technique of the epigraph exists in *Wings in the Meadow* (1967). Author and amateur entomologist Jo Brewer taps Shakespeare, Lorenzo de Medici, Alfred Lord Tennyson, Walt Whitman, and others to find the perfect words to introduce and encapsulate the chapters on the life cycle of the monarch.

Alfred Russel Wallace's (1823–1913), influence on Yeats has already been mentioned. Wallace wrote in *My Life* (1905), his autobiography, about his father's fondness for the work of the poet William Cowper (1731–1800). His father read Cowper's work to him, which may have helped cement Wallace's interest in nature.

Cowper not only wrote about nature, he translated poems written by or credited to his schoolmaster Vincent Bourne, a scholar who wrote in Latin. Many of the poems, including *The Silk Worm*, provide good, basic descriptions of metamorphosis. He also did translations from Greek verses, such as *Of the Grasshopper*, which, interestingly, portrays the singing grasshopper as one that heralds spring. The match between the orthopteran and vernal days may signal the generic use of the name "grasshopper," and not a fondness for the humming.

There is much satire among Cowper's original verses, and, to be sure, much nature. On both counts, it is easy to understand why Cowper's work appealed to Wallace, a social critic as well as a preeminent naturalist.

Although this is very much an introductory word on the topic of insects in literature, and one heavily biased toward work written or available in English, someone must have the last word. The American satirical poet Thomas Hood (1799–1845), gets it. Hood nicely envisioned what the world would be like for entomologists and writers without insects. It would be like November, which Hood described in a poem titled, "*No*," for, among other absences, "No shade, no shine, no butterflies, no bees."

References

Calabrese DM (1994) The entomologist in William Butler Yeats. Antenna 18:201–204

Kirby W, Spence W (1812–1826) (1878 edition). Introduction to entomology or elements of the natural history of insects. Longmans, Green, and Co., London, UK, 607 pp

Patterson R (1842) Natural history of the insects mentioned in Shakespeare's plays. A. K. Newman & Co., London, UK, 270 pp

Tennent JW (2001) The poetry bug. Antenna 25:159–165

Walton WR (1922) The entomology of English poetry. Proc Entomol Soc Wash 24:159–203

Wilbur H (1919) The entomology of the poets. Am Cathol Q Rev 45:566–587

Litter

The uppermost layer of accumulated organic matter of the soil surface. Litter is mostly senescent leaf tissue material, and provides a rich source of food for decomposing fauna and flora. The arthropods associated with decomposition are mostly mesofauna, though large insects sometimes occur.

► Decomposer Insects

Little Bear Moths (Lepidoptera: Brachodidae)

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Little bear moths, family Brachodidae, comprise 140 species, most being Old World tropical, particularly Indo-Australian; the family was formerly

Little Bear Moths (Lepidoptera: Brachodidae), Figure 51 Example of little bear moths (Brachodidae), *Nigilgia limata* (Diakonoff) from Taiwan.

known as Atychiidae. Some species are Neotropical but none are known from North America. There are three subfamilies: Pseudocossinae (only two species from Madagascar), Brachodinae, and Phycodinae. The family is in the superfamily Sesioidea in the section Tineina, subsection Sesiina, of the division Ditrysia. Adults (Fig. 51) small to medium size (8–42 mm wingspan), with head usually rough scaled, but smooth heads in Phycodinae; haustellum naked; labial palpi usually porrect (sometimes upcurved); maxillary palpi 1 to 3-segmented; antennae usually thickened and often bipectinate. Forewings elongated and rounded on termens but hindwings often much enlarged and subtriangular. Bodies often robust; in one Neotropical genus the head is greatly reduced (*Hoplophractis*). Maculation very varied, but either subdued and darker, or colorful and with metallic-iridescent scaling; hindwings either mostly white or dark. Adults are diurnal. Larvae are root feeders of grasses (in the European *Brachodes*, Brachodinae), using silken tubes, or borers in palm trunks and leaf stems, or other plants; some are leaftiers (Phycodinae). Host plants are in Gramineae, and also Bromeliaceae, Melistomaceae, Moraceae, and Palmae. Few are economic on palms.

References

Buszko J, Sliwinski Z (1978) Atychiidae. In: Klucze do Oznaczania Owadów Polski. 27. Motyle-Lepidoptera, Polskie Towardzystwo Entomologiczne 11:18–24 (In Polish)

Diakonoff AN (1986) Glyphipterigidae auctorum sensu lato. (Glyphipterygidae sensu Meyrick, 1913). In: Amsel HG, et al (eds) Microlepidoptera palaearctica, 7. Karlsruhe: G. Braun. 2 pts, 436 pp, pl. 175 [includes Brachodidae]

Heppner JB (1981) Family Brachodidae, new status. In: Heppner JB, Duckworth WD Classification of the superfamily Sesioidea (Lepidoptera: Ditrysia), 8–15. Smithsonian Contrib Zool 314:1–144

Kallies A (1998) A contribution to the knowledge of the Oriental and Australian Brachodidae (Lepidoptera, Sesioidea). Tinea 15:312–337

*Kallies A (2000) The Brachodidae of Sumatra (Lepidoptera, Sesioidea). In: Heterocera Sumatrana, Heterocera Sumatrana Society, Göttingen, 15:97–107

Little Earwigs

Members of the earwig family Labiidae (order Dermaptera).

► Earwigs

Littoral Zone

A zone at the edge of a lake or ocean which is periodically immersed in water.

Lizard Beetles

Members of the family Languriidae (order Coleoptera).

► Beetles

Lock and Key Hypothesis

Closely related insect species often have varied genitalia. The lock and key hypothesis purports that this complex anatomy is maintained to provide reproductive isolation through physical barriers to copulation.

Locomotion and Muscles

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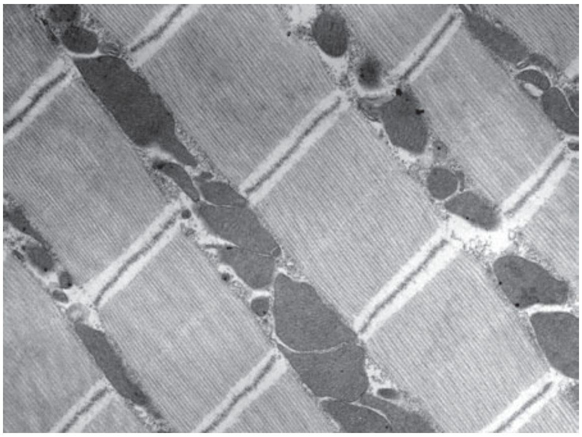
The capacity for movement is one of the most fundamental properties of animals. All insects are capable of locomotion at some stage in their life, including walking, running, swimming, crawling, or flying. Insects were the first animals to evolve flight, and today only insects, birds, and bats fly by flapping their wings. Insects evolved as wingless creatures about 400 million years ago but sometime between 300 and 400 million years ago insects with primitive extensions of cuticle from the thorax, presumably the beginning of wings, appeared in the fossil record. Several theories as to how insect wings might have evolved have been advanced, but none is universally supported. Flight no doubt gave insects a vast advantage over other terrestrial arthropods by allowing them to search widely for patchy food resources, escape predators, seek food, shelter, mates, find oviposition sites, and migrate in search of new habitats to escape limited food supply or other unfavorable environmental conditions. Locomotion has been highly important in the evolution of insects.

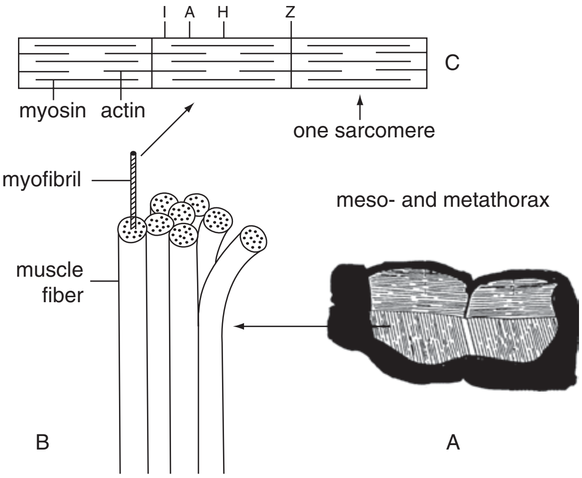
Movement in the animal kingdom is possible because of a series of linear protein molecules that shorten or contract when the appropriate chemical and physical conditions exist. These proteins will shorten when suspended in a cell-free buffer in a test tube, but of course in animals they are organized into a highly complex array in cells or fibers that form muscles. Although muscle proteins can shorten, they cannot lengthen by themselves. They must be stretched to their original length by an antagonistically arranged muscle or, in some cases, by the natural elasticity of a physical structure such as the insect cuticle. Antagonistic muscles are common in the appendages of insects and nearly all other animals. When an insect leg flexes (bends) because of contraction of one set of muscles, another set must contract to extend the leg, which then stretches the flexor muscles to their original length. Tymbal muscles that pull the thin cuticle of a cicada's sound-producing tymbal inward until it clicks into a new position are not arranged antagonistically, but when the muscle stops shortening, the elastic cuticle snaps back into its original position and stretches the muscle. Rapid repetition of tymbal muscle contraction followed by the elastic pull of the cuticle creates the high-pitched trilling sound we hear when cicadas call. Thus, in addition to enabling simple locomotion, contractile proteins created opportunities for insects (and other animals, too) to evolve chewing, digging, singing, oviposition, movements of the alimentary canal that aid digestion, and many complex behavioral displays of wing, antennal, and body movements during courtship displays and mating. The subject dealt with here, however, is limited to locomotion made possible by legs and wings and their associated muscles.

Skeletal Muscle Structure and Physiology

The skeletal muscles that enable leg and wing function are composed of relatively long muscle fibers composed of cells whose cell boundaries are no longer distinct. Still evident, however, are the nuclei from these cells, so muscle fibers appear to be multinucleate. In muscles of the alimentary canal, individual cells are short, cell boundaries are distinct, and the cells are uninucleate. Muscles are usually divided into broad categories such as skeletal-, flight-, heart-, alary- (associated with the heart), and gut muscles based on location within the body, structure, and function. Regardless of the type of muscle, the contracting units are called sarcomeres and each sarcomere is composed of several proteins including actin and myosin. The energy for muscle contraction is supplied by mitochondria. In flight muscles the mitochondria are abundant, and so large and irregularly shaped that they were first called sarcosomes, i.e., muscle bodies, because it was not certain that they should be considered the same as the much smaller mitochondria of many other cells (Fig. 52). After extensive physiological and biochemical research, sarcosomes were shown to have all the functions of other mitochondria. All mitochondria function aerobically, and oxygen is supplied to the large mitochondria of insect muscles by tracheoles that terminate only a few micrometers away from the mitochondria, after the tracheoles have indented the muscle cell membrane like a finger pushed against a soft balloon. Such tracheoles are called "intracellular tracheoles" although they are not really inside the muscle cell membrane. All insect muscle (and skeletal muscle of other animals) has a striated appearance in microscopic sections and the generally the striations or bands of adjacent myofibrils are aligned side by side (Figs. 53). The various bands or striations were designated by letters of the alphabet long before much was known about the chemical or physiological nature of the bands. Thus, there are A, H, I, M and Z bands. Z bands set (Figs. 52 and 53) the boundary of a sarcomere, and the other bands occur within the sarcomere. A skeletal muscle is composed of thousands of sarcomeres arranged end to end. A sarcomere typically is 2–3 μ m long in a muscle at rest, but longer sarcomeres occur in some very slow contracting muscles. Since the sarcomere is the contractile unit, the distance between Z bands decreases upon shortening. Shortening requires some finite time, and there is some relationship



Locomotion and Muscles, Figure 52 **A transmission electron microscope view of flight muscle showing periodic Z bands as dark lines across the muscle fibers and large sarcosomes (mitochondria) between the muscle fibers (photo courtesy of Jimmy Becnel and Alexandra Shapiro).**



Locomotion and Muscles, Figure 53 **Drawings to illustrate the subunits of muscle. (a) The large dorsal longitudinal and dorsoventral muscles in the meso- and metathorax that change the shape of the thorax and cause the down stroke and upstroke, respectively, of the wings; (b) Individual muscle fibers, with muscle fibrils (myofibrils) represented as black dots at the cut end of fibers, with one myofibril drawn as an illustration; (c) Three repeating sarcomere units among the thousands that occur along the length of a myofibril. Each sarcomere contains the linear proteins actin and myosin, as well as other proteins important in muscle function. I, A, H, and Z refer to the banding pattern that can usually be seen in muscle.**

between the length of sarcomeres and the speed of contraction. It is known now that the Z line is a plate-like sheet of protein to which actin and some other muscle proteins are attached. Actin filaments are about 5 nm in diameter, and extend from the Z line to about two-thirds to nearly the mid-point of a sarcomere. Myosin filaments, about 20 nm in diameter, lie between the actin filaments, across the middle of the sarcomere, but usually do not extend to the Z line. The various overlapping regions of myosin and actin filaments give muscle in thin histological sections its banded or striated appearance as light passes through regions of different density. The A band appears dark because light must pass through the overlapping regions of actin and myosin filaments, while the H zone in the middle of the sarcomere and the I band near the Z line transmit more light because those regions contain only myosin or actin filaments, respectively. The M line across the middle of the H zone is created by cross-links between myosin filaments that help hold the myosin filaments in place. The zones are of variable length in different muscles, depending upon the degree of overlapping of filaments. The width of the H zone bears some relationship to how much the sarcomere (and thus the whole muscle) will shorten upon stimulation and how fast it can accomplish its shortening. Muscles with very narrow H and I zones, such as fibrillar muscles that cause the wing movements in Diptera and Hymenoptera, shorten only a small amount upon contraction (2–3%), while some muscles may shorten much more. Each skeletal muscle is composed of multiple numbers of muscle fibers, although there may be only a few individual fibers in very small muscles. Muscle fibers can be separated into myofibrils, which are long linear arrays of sarcomeres containing actin, myosin, and other important proteins necessary for muscle function.

At the biochemical and molecular level the physiology and biochemistry of muscle contraction appears to be the same in insects as in other organisms. The sliding filament theory in which actin and myosin filaments slide over each other, drawing Z bands closer together, and thus shortening the entire muscle, adequately explains insect muscle contraction.

Muscle Attachments to the Exoskeleton

Skeletal and wing muscles are anchored to a relatively non-moveable part of the exoskeleton, and this anchor point is called the origin of the muscle. The other end of the muscle, called the insertion, is attached to a moveable part of the body, such as a wing hinge, an appendage, or a movable part of the exoskeleton. Skeletal muscle and wing muscles usually are anchored to the epicuticle layer of the exoskeleton. Recall that a single layer of epidermal cells lies just beneath the cuticle, so a skeletal muscle must attach first to the basal side of the epidermal cell. Recent research indicates that a protein encoded by the *dumpy* gene acts as the cement to attach the muscle cell membrane to the epidermal cell membrane. Bundles of intracellular microtubules arise at the muscle-epidermal cell contact point, extend through the epidermal cell to the apical membrane surface where they are cemented by dumpy protein to chitinous fibers called tonofibrillae in the cuticle. Tonofibrillae pass through the cuticle and anchor upon the epicuticle. Thus, although muscle cells do not themselves pass into the cuticle, they are nevertheless anchored to the epicuticle, the hard outer shell of the cuticle that provides a strong anchor for powerful muscles that power wing movements and jumping, running, swimming and digging legs. Tonofibrillae are very resistant to the action of molting fluid, and allow muscles to remain attached to the exoskeleton after apolysis and secretion of new cuticle begins. This is beneficial to many molting insects because apolysis occurs in some insects hours or even days before ecdysis, and movement during the interval between apolysis and ecdysis may be critical to feeding and predator escape. The final loosening of the tonofibrillae has not been elucidated, but once they detach, reattachment to the new epicuticle occurs rapidly. The old cuticle then is shed, and most insects rest quietly for some minutes or hours immediately after molting until the new cuticle has hardened, and can act as a strong support for the skeletal muscles.

Neural Control of Muscles

Because of the small size of insects, only a few neurons can be allocated to control each muscle. Muscles of very small insects are, of course, also small, and a muscle that moves a leg may be composed of only a few muscle fibers in some insects. Only two stimulatory neurons, commonly described as the slow neuron and the fast neuron, serve skeletal and other muscles in many cases. Large muscles, such as the jumping leg muscles in a large grasshopper or locust, may receive 4 or 5, or rarely a few more, stimulatory nerves. Both fast and slow axons break into a number of arborizations at the muscle surface and make multiple contacts with the muscle fiber. These multiple contacts ensure that the neural stimulus is rapidly communicated to the entire length of the muscle fiber. This is called multiterminal innervation, and it is common in invertebrates, but represents a major difference in muscle innervation between invertebrates and vertebrates. In vertebrates, a neuronal branch makes only one contact with a muscle fiber, and the muscle fiber itself conducts the electrical stimulus along its length. Although insect muscle fibers can be made to conduct an electrical stimulus like vertebrate fibers under certain experimental conditions, they seem not to do so in the living insect. Hence, the evolution of the multiple nerve contacts ensures that the neural stimulus is rapidly communicated to the entire muscle.

The fast axon sends multiple terminals to all or most of the muscle fibers in locust jumping leg muscle, but the slow axon makes junctional contacts with only 30–40% of the muscle fibers. This arrangement allows the locust (and similar insects) to make a maximal response (a jump) when the fast axon carries the nerve impulse to all the jumping muscle fibers, and a slower, graded walking response when the slow axon carries the nerve impulse. The routing of the nerve impulse through the fast or slow axon is controlled in the central nervous system of the insect. A third type of neuron, one that produces an inhibitory response, has been found in the jumping leg muscles of several insects. The overall effects of these three potential types of neurons feeding a muscle may be additive, and we might represent the fast and slow axons with a plus sign (+), and the inhibitory one with a minus sign (−). If the central nervous system of the insect specified some intermediate action between "jump" and "walk," it is conceivable that it might send 5 plus signals (+++++) and two minus signals (− −); the overall effect achieved in the muscle is a graded contraction, neither maximal response nor the slowest response. It may be worthwhile to point out that inhibitory nerve action is considered to be important, indeed necessary, in all higher nervous systems.

The stimulatory transmitter chemical released from fast and slow nerve junctions with the muscle fiber is the amino acid L-glutamic acid. At inhibitory junctions it is gamma amino butyric acid (GABA). Although vertebrates use GABA as an inhibitory transmitter, they use acetylcholine as the stimulatory transmitter at neuromuscular junctions in skeletal muscles. Insects also use acetylcholine as a stimulatory transmitter at nerve to nerve contacts within the central nervous system (CNS). Thus, organophosphate insecticides, which inhibit the enzyme acetylcholinesterase, are quite toxic to both insects and vertebrates, but the principal site of action in insects is within the CNS, while in vertebrates toxic action occurs at both CNS and skeletal muscle sites.

Insect Flight

Perhaps the most important act of locomotion that an insect makes is flight. Unlike birds, the muscles that flap the wings do not attach directly to the wing structure, except in a few groups of insects to be described later. In most insects the large wing muscles actually pull upon the thoracic wall and change the shape of the thorax, and thereby cause the up and down movement of the wings. The thorax, although heavily sclerotized to withstand the pull of the flight musculature, is not composed of one large sheet of cuticle, but rather consists of plates that come together at definite suture lines. The whole is flexible enough for some change in shape with the contraction of muscles inserting upon it. The wings are attached to the thorax by a number of small, hard sclerites, the wing hinges, at the junction where the top of the thorax, the tergum, laps over the side and meets the pleuron or side plate. The wings pivot up and down over a heavily sclerotized finger-like fulcrum of cuticle, the pleural process, that is part of the pleuron. Thus, the wings function much like a seesaw, except that the fulcrum is very close to one end, the junction point of the wings with the thorax. As every collector of insects knows, the wings of insects are only in a stable position when positioned either up or down. The horizontal position of the wings of butterflies and moths preserved in an insect collection can be achieved only by pinning the wings in this position until the thorax dries.

The wing down stroke in the majority of insects is produced by contraction of dorsal longitudinal muscles in response to a volley of nerve impulses. The dorsal longitudinal muscles do not attach directly to the wing hinges, but their origin and insertion are on the hard cuticular processes at the anterior and posterior, respectively, of each of the meso- and metathoracic segments. When they contract, they arch the tergum and slightly lift the attachment base of the wings at the tergopleural junction. The dorsal longitudinal muscles work against the elasticity of the thorax and the resistance of the air beneath the wings. Arching of the thorax causes the wings to begin to move downward, approaching the unstable horizontal position, and with continued contraction of the dorsal longitudinal muscles they suddenly pivot releases the dorsal longitudinal muscles from most of the load against which they were acting, and they stop contracting. It is a general characteristic of all muscle that there must be a load to work against or contraction ceases.

If now the dorsoventral muscles receive a volley of nerve impulses, they begin to contract. These dorsoventral muscles cause the upstroke of the wings in all insects. These powerful muscles have their origin or anchor on the heavily sclerotized ventral thoracic cuticle. They insert on the tergum, the top plate of the thorax. When they contract, they pull on the tergum and reduce the arching of the thorax that was caused by the dorsal longitudinal muscles. The wings now start to move upward, reach the unstable horizontal position, and suddenly pivot into the up position. This reduces the load on the dorsoventral muscles and they cease to shorten, but decreasing the arching of the thorax stretches the dorsal longitudinal muscles back to their original length. A sudden stretch acts on muscle (all muscle) like a nerve stimulus, and can cause the muscle to contract provided the muscle is still in an active biochemical state. Thus, the antagonistic sets of muscles, the dorsal longitudinal and the dorsoventral muscles, alternately contract against the resistance of the wings moving through the air. As one set contracts, it stretches the other set, inducing a subsequent contraction in that set. When the wings pivot up or down, the load or resistance of the wings against the air is released for one set of muscles and introduced to the other set. These wing muscles are capable of making several contractions in this antagonistic harness mechanism to one volley of nerve impulses to each set. This enables some insects to beat the wings at a rate of several hundred times per second - for example, 180 beats per second for honeybees, about 180 for a *Drosophila* fly, 150 for a housefly, and as many as 800 to more than 900 in a very small *Chironomus* species of fly. The important point is that these small insects with small wings must beat the wings very fast in order to produce enough lift to stay in the air. The smaller the wing surface, in general, the faster the wings must beat to generate sufficient lift for flight. Insects with much larger wings, such as a swallowtail butterfly

(5 beats per second) and the desert locust (17 beats per second) can get enough lift from the larger wings without beating them so fast. The evolution of this ability to beat the wings several hundred times per second depends upon successful operation of several anatomical and physiological factors: (i) the anatomical arrangement of the antagonistic wing muscles, (ii) the unstable horizontal position of the wings, (iii) the pleural process over which they pivot, (iv) the way the wings are hinged to the thorax, (v) the short distance over which both sets of muscles must contract to produce wing movement (shortening of the muscle by about 2% of its length is sufficient to produce a down stroke or upstroke), (vi) the elasticity of the thorax, and (vii) persistence of the biochemically active state of the muscle for about one second following a nerve impulse. A control center in the thorax sends out periodic nerve impulses to each set of muscles to keep a flight rhythm going.

The muscles enabling several hundred wing beats per second are called asynchronous muscles because they are not dependent upon a nerve impulse for each contraction. They also are called fibrillar muscles because the muscle fibrils that make up a fiber are so large and are loosely packed into the muscle fiber with thousands of very large, irregularly shaped mitochondria lying between muscle fibrils. These mitochondria, of course, supply the vast amount of energy needed for the rapid wing beats. Asynchronous wing muscles are found in the fast flying insects and smaller insects; achieving multiple muscle contractions for each nerve impulse enables fast flight and flight with a small wing airfoil.

Most slow flying insects beat the wings much slower than 100 times per second, and the muscles that cause the wing movements must get a nerve impulse for each contraction. These muscles are called synchronous muscles, because their contraction is synchronized with the rate of nerve firing. The muscles that move the wings are still the dorsal longitudinal muscle set and the dorsoventral set of muscles. Nerves that innervate the muscles are not able to carry repeated nerve transmissions faster than about 100 nerve impulses per second, a rate that allows only 10 ms for the repolarization interval in a neuron. There are important morphological and physiological differences in the structure of the synchronous muscles that make it more difficult for them to maintain the biochemically active state as long as the asynchronous muscles do after a nerve stimulus. The active state in synchronous muscles disappears so quickly, that a stretch is not a sufficient stimulus for them to contract again as in asynchronous muscles.

Flight in Dragonflies, Damselflies, and a Few Other Groups of Insects

The Odonata, representatives of an early group to evolve, and a few other groups of insects, depart from the description above about how wing down stroke occurs. In these few groups, the down stroke of the wings is produced by the basalar and subalar muscles that are attached directly to the wing hinges. The basalar muscles insert on the anterior part of one of the principal wing hinges, and contraction pulls the wings downward, with the leading edge twisted downward. This downward twisting of the leading edge of the wing during the down stroke is common in all insects and is called pronation of the wing. The subalars insert on the main wing hinge at the base of the wing posterior to the pleural wing process, also pull the posterior edge of the wing downward, with some twisting of the trailing edge. In dragonflies and damselflies, the basalar and subalar muscles are large, powerful muscles that have to act on the very short end of the lever to pivot the relatively long wings over the pleural wing process against the resistance of the air. They are anchored to parts of the heavily sclerotized ventral and pleural cuticle. The upstroke in odonates and all other insects is produced by the dorsoventral muscles that reduce the natural arching of the thorax, as described above.

Control of Pitch and Twisting of Wings

In addition to flapping the wings, insects control pitch and orientation of the wings with respect to the plane of the body. The principal muscles involved in controlling wing pitch and twisting in most insects are the basalar and subalar muscles that attach directly to the wing hinge sclerites. In most insects these muscles are not strong enough to pull the wings downward in rapid flapping flight, but they can change the pitch of the wings. During downward movement, the leading edge of the wing pronates or tips downward as the basalar muscles contract. During the upstroke, contraction of the subalars pull the posterior edge of the wing downward (supinates the wing), again tipping the leading edge of the wing upward. These changes in shape and angle of attack of the wings are important in generating lift forces.

In Diptera and Hymenoptera, the tergum of the thorax is divided by the scutal cleft into two plates, the scutum and the scutellum. Sclerites at the posterior of the wing base join to the posterior plate, the scutellum. When the scutellum is pulled slightly forward by the contraction of the dorsal longitudinal muscles, the wing tilts slightly forward, or pronates, as it pivots down over the pleural process. Relaxation of the dorsal longitudinal muscles at the end of the down stroke allows the tergal plates to move further apart, and the wing tilts slightly backward (supinates) as it is forced upward by the contraction of the dorsoventral muscles. The wing tip describes a figure eight during flight.

Lift Produced by the Motion of the Wings

In order to stay in flight, insects like airplanes have to have enough lift beneath the wings to overcome body weight. Contrary to the flight of fixed-wing aircraft operating under steady-state conditions, insect flight is characterized by unsteady-state conditions in which there are brief high lift forces followed by lower lift forces, or even negative lift conditions. One example of unsteady-state lift conditions occurs in very small chalcid wasps and has been described as a "clap" and "fling" wing motion. In this small insect the wings "clap together" at the top of the upstroke, and then twisting motions controlled by some of the small muscles inserting on the wing hinges fling the wings apart at the start of the down stroke. The flinging motion sets up air movements that increase the lift force of the down stroke, and may aid very small insects to generate enough lift for flight in spite of having tiny wings. Larger insects may also utilize discontinuous lift forces. For example, some workers have measured large, transient lift forces 15–20 times the body weight of tethered dragonflies, with time-averaged lift values equal to 2–3 times body weight created by the turbulent flow of air generated by the independent movement of the front and rear wings.

Tethered tobacco hornworm moths (*Manduca sexta*) generate unsteady lift forces during the down-stroke of the wings equal to at about 1.5 times the body weight. Coincident with the lift forces generated by the down stroke movement, intense leading-edge vortices of low pressure air above the wings are created by the pronation of the wing (tilting downward of the leading edge) during the down-stroke. The vortices form first over the leading edge of the wing, move out towards the wing tips, and finally extend behind the insect in a ring of turbulent air. These low pressure vortices increase the lift of the down stroke. The high angle of attack of the wing, a condition that rapidly creates stalling in a fixed wing aircraft, creates the vortices. This condition of dynamic or delayed stall can be tolerated in an insect for the brief interval of one down stroke (an interval of only a few milliseconds) or upstroke, at the end of which the stall conditions are eliminated as the wings stop and change direction. Measurements have shown that energy input to mechanical output is about 3% in a katydid singing muscle to as high as 10% in flight muscles of *Drosophila hydei* fruitflies. Flight clearly is a very energy-demanding activity.

Walking and Jumping

Walking and jumping depend upon muscles in the legs. In walking or running, insects must coordinate six legs. Like many other repetitive, rhythmical actions, walking is controlled by a motor program – a coordinated set of nerve impulses that repeats over and over as long as walking or running continues. In the American cockroach, *Periplaneta americana* L., two neural control centers are localized in each of the pro-, meso-, and metathoracic segmental ganglion. One center in each ganglion controls the leg on one side of the body. A small number of master command neurons provides control over the individual centers and ensures that legs are coordinated in movement. Neurons from the control centers go to the flexor muscles that bend a leg and swing it forward for the next step, while others supply the extensor muscles that straighten the leg and allow the tarsi to make contact with the substrate on which the cockroach is walking. Both positive and negative feedback loops in the neural circuitry are coordinated so as to allow inhibition of one set of muscles (say the extensors) while the other set (the flexors, for example) is stimulated. Similar neural motor programs allow humans to walk and swing the arms without any conscious thought; fortunately so, because if one does think about the process, it becomes much harder to do.

The ability of some insects to jump many times their body length and height might suggest that insect muscles are stronger than vertebrate muscles. Actual measurements of the force developed per unit cross sectional area for insect muscles reveal about the same force per unit cross sectional area as for other animals. It is anatomical arrangement of muscles and appendages, as well as physiology and lever systems, which enable some insects to jump so far. For example, the main muscle in the femur of the jumping (metathoracic) leg of a grasshopper or locust is composed of many short muscle fibers that insert on the cuticular apodeme extending the length of the femur. The muscle fibers are anchored to the epicuticle of the femur. Upon contraction, each muscle fiber shortens very little and pulls only slightly off the perpendicular to the long axis of the femur. The many muscle fibers along the length of the long femur exert large force rapidly upon the tendon that straightens the leg and propels the locust into the air in a jump. Furthermore, the long femur and tibia of the metathoracic leg (which is much longer than either of the pro- or mesothoracic legs) give the locust something of a "pole-vaulting" advantage, similar to a human who uses a long pole as an extension of the arms during pole vaulting.

Very massive muscles, with fibers that shorten only a small percentage of the muscle length, enable fleas to make extraordinary jumps. Although not all fleas are equipped for major jumping activity, those that do jump have an extraordinarily large coxa, in contrast to most insects. Inside the coxa is a large muscle with fibers that are anchored to the thorax. The coxal muscle fibers insert on the femur, which also is large and long. Overall, the jumping leg is about 80% of the length of the body of a cat flea, and contains large muscles inserting on the tibia. In preparation for a jump, a flea utilizes a cocking mechanism in which the femur is pulled up to overlap the large coxa. In this cocked position both coxa and femur are perpendicular to the body axis and to the substrate. The cocking action compresses an arch of resilin, a rubber-like protein, in the pleural arch near where the coxa is attached to the thorax. In addition, the cocking action clamps the three thoracic segments together by engaging a "catch" mechanisms between the three thoracic segments. The flea holds the sternum of the mesothorax tightly against the metathorax, and this allows the large muscles involved in raising the femur and locking the catches to relax, resisting tiring and reducing energy requirements. In this crouched position, a flea is poised for its leap with trochanter and tibiotarsal joint and most of the tarsi resting on the substrate. The flea propels itself into the air by relaxing the levator muscle holding the femur in the perpendicular position and relaxing the ventral longitudinal muscles holding the catches in the cocked position. The compressed resilin, like a compressed spring, forcefully drives the trochanter against the substrate to provide the initial leverage off the substrate. Powerful muscles extend the joint between the trochanter and the femur, and extend the leg providing further thrust as the terminal tarsal segments and tarsal claws press against the substrate. The long jumping legs aid the leap.

References

Dudley R (2000) The biomechanics of insect flight: form, function, evolution. Princeton University Press, Princeton, NJ, 476 pp

Kingsolver JG, Koehl MAR (1994) Selective factors in the evolution of insect wings. Annu Rev Entomol 39:425–451

Marden JH, Kramer MG (1994) Surface-skimming stoneflies: a possible intermediate stage in insect flight evolution. Science 266:427–430

Nation JL (2002) Insect physiology and biochemistry. CRC Press, Boca Raton, FL, 485 pp

Rothschild M, Schlein Y, Parker K, Neville C, Sternberg S (1988) The flying leap of the flea. Sci Am 229:92–100

Locus (pl. loci)

The position of a gene on a chromosome.

Locust Borer, *Megacyllene robiniae* (Forster) (Coleoptera: Cerambycidae)

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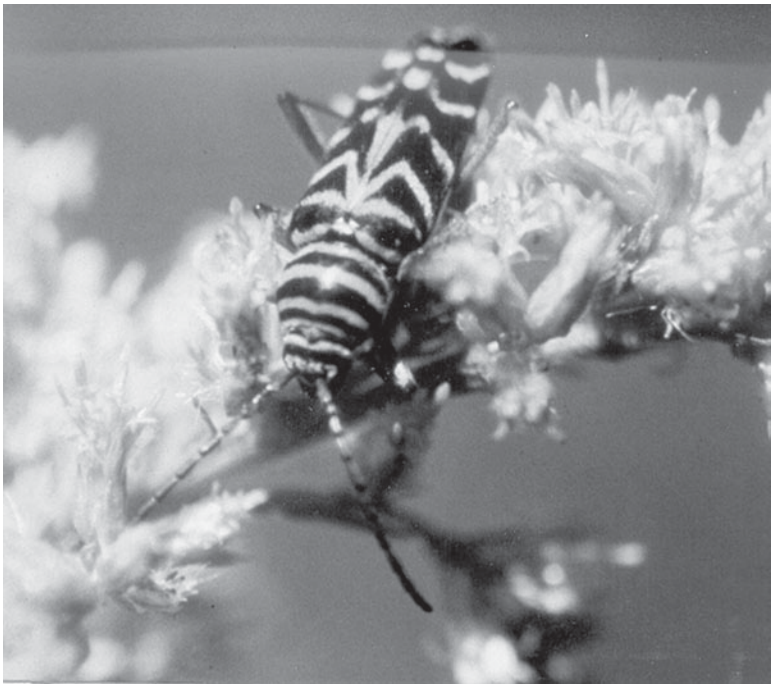
The locust borer, *Megacyllene robiniae* Forster inflicts severe damage upon its host, the black locust tree, *Robinia pseudoacacia* L. Damage is encountered as the larva develops, tunneling first in sapwood and then in heartwood, in the host. The locust borer is monophagous, capable of developing on only one host, the black locust tree. Whereas the usual habit of longhorned beetles is to enter and destroy trees already weakened or dead, the locust borer invades only living trees, which are not normally killed, but suffer structural weakening and deformity, depending upon the numbers of borer tunnels in the trunks. The locust borer retains another habit of adults of the Cerambycidae; that of feeding on flowers. In this case, it feeds on goldenrod (*Solidago* spp.). Locust borer adults feed on (Fig. 54) pollen of goldenrod blossoms during August and September, where they are easily collected, and are frequent representatives in insect collections. As they occur on the goldenrod, intermingling with yellowjackets, wasps, and bees, they exhibit classic Batesian mimicry, with color patterns resembling the stinging hymenopterans, which may ward off predators.

Host, Range, and Impact

Aside from pollen-feeding by adults on bright summer flowers, the locust borer's main host is a valuable tree, native to the eastern United States. Researchers have determined that the original range of black locust was restricted to the Appalachian mountains form Pennsylvania to Georgia, and to portions of Arkansas and eastern Oklahoma. Best growth of black locust is reportedly the west slopes of the Allegheny ridge, in the mid-Atlantic region, and quality of growth recedes with distance eastward and westward from the ridge feature. However, humans expanded its range, beginning early in American history, because of certain properties of its wood, i.e., hardness, strength, and resistance to rotting. In addition, it is in the family Leguminosae, and has nitrogen-fixing properties. Thus, it survives when planted under adverse conditions, such as the exposed mineral soils from coal strip-mining, and depleted soils, where other species fail. Ecologically, it is termed a "pioneer" species, with thin crown allowing much light to the forest floor, being first to occupy openings and fringes, and later giving way to other tree species with thicker



Locust Borer, *Megacyllene robiniae* (Forster) (Coleoptera: Cerambycidae), Figure 54 Locust borer adult on goldenrod.

crowns. Farmers value it highly for posts, planks and structural material; shipwrights sought it for their trade. In New England, a local strain was named "shipmast locust" because of its straightness, height, and clearness of bole. The available trees were quickly cut, but the search was on for other sources of so-called "shipmast" locust. It was soon recognized that the supply of locusts with superior bole form was limited, but stands of reasonable quality could be found, and their seeds transported by settlers westward, northward, and across the seas. It now is common in the Pacific northwest, into British Columbia, and up the Atlantic seacoast to Nova Scotia, where it is seen planted along roadsides. It is now reported to be one of the most planted tree species in the world. The locust borer followed its host to its new areas in North America, but not in Europe, which is free of the insect and its damage.

The effect of the locust borer on the black locust tree is sustained and intense in most of its native localities. The larval tunnels typically start with a cavity, advance toward stem center through sapwood and into heartwood, and loop back in opposite direction 5–8 cm. Tunnels, with diameters of 5–8 mm, may heal over at their surfaces, but not in the inner wood, where they remain for the life of the tree. Numbers of tunnels per tree therefore accumulate with time, and vary in number per unit of trunk length. Among foresters and producers, the price per 6 ft (2 m) post is affected if more than 7 borer mines are present. Many trunk lengths sustain far more borer attacks than tolerable, and are deemed unacceptable. Where black locust is planted for coal strip-mine revegetation, devastating borer damage often renders the crop a loss for products, but the tree's ability to survive, fix nitrogen, and provide cover for other species keeps it in an important element in land reclamation; it survives where other species die.

Life Cycle

The locust borer is univoltine, having one generation per year. Adults are present from early

July until late September or early October, but disappear with onset of heavy frosts. They aggregate on blossoms of goldenrod, where they mate, and also feed on pollen from the flowers. Experiments have indicated they are not dependent on goldenrod pollen for survival, though it is normally present in the gut. They have been observed on other yellow flowers such as sunflowers, and in the absence of the goldenrod would probably feed on pollen from other species, but they nonetheless frequent the yellow goldenrod, which is usually found near black locust groves, and whose flowering period parallels the presence of locust borer adults. They may use the various goldenrod species, but the greatest numbers are found on the prominent *S. altissima* L. They are strong flyers, and fly back and forth from goldenrod to locust trees. Once on the trunks, females search out crevices on outer bark for egg deposition. Eggs are deposited singly, and hatch in about 10 days. The newly-hatched larvae then bore into the outer bark, where they overwinter. In milder seasons, some excavation at the cambium layer may occur in fall. In spring, the young larvae resume feeding activity, first (Fig. 55) hollowing out a cavity, then proceeding to tunnel inward toward stem center. Tunneling activity proceeds from May through most of June, at which time the fully-grown larvae pupate, behind a plug of shavings. The pupal stage lasts about 8–12 days. Prior to pupation, the larvae push excavated material back to the cavity and out to the trunk surface. The white boring dust, usually wet with sap, can be useful in finding active attacks. Because the new adult must exit through its larval tunnel, a proper-sized opening to exterior must be

Locust Borer, *Megacyllene robiniae* (Forster) (Coleoptera: Cerambycidae), Figure 55 **Locust borer larval tunnel, 3 to 4 yrs old, with wound surface healed over (*left*); locust boring dust on trunk, from active larval tunnels (*right*).**

maintained. In healthy trees, energy is expended to repair and seal over the wound entrances, which may be closed by the time of adult emergence, requiring that the adult chew its way out or die within the tunnel. Only a small percentage of those which have successfully pupated fail to exit the tunnels. With the onset of July, adults are again seen in the field, to begin the life cycle anew.

Control/Suppression

Although the tools are available, none of the artificial control measures against the locust borer are recommended. Researchers have experimented with a variety of approaches, including contact pesticides applied to tree surfaces, and systemic insecticides which can be absorbed within stem tissue. The dispersal of locust trees throughout the regional landscape renders most poisoning efforts costly, plus environmentally unacceptable. Parasites and predators have only slight effect, although ichneumonid wasps, garden spiders, woodpeckers, and others have been observed. The most commonly-suggested approach to damage reduction is to encourage growth of black locust on better sites, combined with sanitation removal of heavily-attacked trees. Some older trees, even on average or good sites, become weakened through aging, breakage, fungal attack, and similar causes, and assume the characteristics of "brood" trees for the locust borer. Managers normally seek out and remove such trees, promoting healthier growth, and conduct thinnings to avoid excessive crowding and establish desired stand composition. Unfortunately, some circumstances contribute to the problem, such as occur when black locust is planted for reclamation on stressed sites. In this situation, tree health and vigor are compromised, and borer populations increase. Better sites, and healthier trees, incur fewer borer tunnels. Deep soils with limestone outcrop may be seen supporting black locusts with improved stem form and reduced borer damage. An exaggerated view of the effect of site may be seen where heavily attacked black locusts occur on mineral soils of coal strip-mined lands, directly adjacent to lightly-attacked locusts on undisturbed soils nearby.

Ecological Overview

Tropically, the locust borer may be viewed as a consumer in reasonable balance with its host, in that its invasions do not result in (immediate) host mortality. Actual long-term damage varies with vulnerability of individual trees, and is influenced by many factors. Wound entrances become feeding sites for a group of organisms, including nitidulid beetles, dipterans, nematodes, mites, and others. The subcortical cavities at wound entrances shelter the sap-feeding guild, and many of these organisms, particularly mites, nematodes, and others, may be dispersed as winged borers depart the tunnels. The cavity organisms appear to progress with little effect on the borer larva or the tree. However, the sap-feeding organisms may also feed upon, and disperse, the fungus, *Fomes rimosus* (Berk.), which is present in the wood tissue of a vast percentage of black locust trees. The role of the fungus in relation to the locust tree and the borer is poorly known, but the fungus may be observed to cause a yellow heart rot in living tissue throughout the range of the tree, and perennial hard woody conks on the trunk surfaces of badly infected trees. The fungus likely reduces the tree's ability to overcome the invading borer larvae, and the hyphae and spores probably serve as food for the larvae within the tunnels. The locust borer is also labeled a disperser of *F. rimosus*, which infects a vast percentage of living black locust trees (it is also reported from mesquite, but from few if any others). The fungus, though an invader of living tree, also performs the essential function of decomposition of dead material on the forest floor. Other factors should also be mentioned. With their pollen feeding habit, locust borer adults perform cross-pollination in the forest ecosystem, an activity of increasing importance, due to loss of many native pollinating insects. In the present day of stressed environments, pest suppression tactics must be considered in terms of ecological impacts, as well as economic ones, and a balance must be sought which is not too costly to either.

References

Galford JR (1977) Evidence for a pheromone in the locust borer. U.S. Forest Service Research Note NE-240, 3 pp
Hall RC (1937) Growth and yield in shipmast locust on Long Island and its relative resistance to locust borer injury. J Forestry 35:721–727
Harman DM, Harman AL (1990) Height distribution of locust borer attacks (Coleoptera: Cerambycidae) in black locust. Environ Entomol 19:501–504
McCann JM, Harman DM (1990) Influence of intrastand position of black locust trees on attack rate of the locust borer (Coleoptera: Cerambycidae). Ann Entomol Soc Am 83:705–711
Wollerman EH (1969) Continuous laboratory culture of the locust borer, *Megacyllene robiniae*. Ann Entomol Soc Am 62:647–649

Lodging

Toppling of crop plants, often in association with wind or rain, but ultimately due to destruction of roots by insects.

Loew, Hermann

Herman Loew was born in Weissenfels, Germany, on July 19, 1807. He is considered to be the "father of dipterology." He graduated from the University of Halle later and taught natural history, philosophy, and math at that institution as well as other schools and as a private tutor. He received recognition for publication of his "Horae anatomicae," a treatise on anatomy, particularly genial anatomy. Though participating in only one major international expedition, to the Orient, it proved to be a very important and productive trip. He described over 1,300 exotic species from this expedition. Over the course of his life, he described another 2,700 European species. In addition to his scientific studies, Loew was active in politics, serving in the parliament in Frankfurt. He became frustrated by politics, however, and in 1850 returned to teaching, which he continued until 1868. He then devoted his time to entomological research until 1873, when he returned to politics, accepting a seat in the Berlin legislature. Loew suffered a stroke in 1876, and though experiencing partial recovery, died April 21, 1879.

References

Essig EO (1931) A history of entomology. The Macmillan Company, New York, 1029 pp
Papavero N (1971, 1973) Essays on the history of Neotropical Dipterology with special reference to collectors (1750–1905). Museu de Zoologia, Universidade de São Paulo, São Paulo

Logistic Growth

Population growth in which the growth rate initially is exponential, but as the ideal circumstances deteriorate due to competition for resources and the impact of natural enemies, the rate of population increase decreases. The curve describing this relationship (number of individuals and time) is S-shaped.

Logistic Model

A type of optimum growth model in which the growth is predicted from the overall function of population growth without specific consideration of specific elements such as mortality and recruitment.

Log-Normal Distribution

A frequency distribution of species abundances in which the log number of individuals represented in a sample is plotted on the X-axis, and the number of species is plotted on the Y-axis.

Loiasis

A disease cause by infection with *Loa loa*. These filarial worms develop in tabanid flies (Diptera: Tabanidae) and are passed to vertebrates when the flies feed on blood. It occurs only in forested areas of central Africa. The human form is vectored by *Chrysops silacea* and *C. dimidiata* deer flies. Another form occurs in monkeys. Years may pass before infection is evident. Diagnosis is accomplished by finding microfilariae in the blood. The worms are sizeable, with females attaining a length of up to 70 mm. They migrate under the skin, inducing inflammations called "Calabar swellings." The swellings, often on the wrists and ankles, are due to an immune response to the filariae. The filariae can also be seen in the cornea and conjunctiva of the eye, hence the term "eye worms." They may migrate to the brain as well, inducing encephalitis.

Lonchaeid Flies

Members of the family Lonchaeidae (order Diptera).

► Flies

Lonchaeidae

A family of flies (order Diptera). They commonly are known as lonchaeid flies.

► Flies

Lonchopteridae

A family of flies (order Diptera). They commonly are known as spear-winged flies.

► Flies

Lone Star Tick, *Amblyomma americanum* Linnaeus (Acari: Ixodidae)

This species inhabits mesic environments in eastern North America.

► Ticks

Longhorned Beetles

Members of the family Cerambycidae (order Coleoptera).

► Beetles
► Longicorn, Longhorned or Round-headed Beetles

Longhorned Fairy Moths (Lepidoptera: Adelidae)

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Longhorned fairy moths, family Adelidae, comprise 295 species worldwide, but most are Palearctic (143 sp.); actual fauna probably exceeds 400 species. The family is in the superfamily Incurvarioidea, in the section Incurvariina, of division Monotrysia, infraorder Heteroneura. There are two subfamilies: Nematopogoninae and Adelinae. Adults minute to small (4–29 mm wingspan), with head very rough-scaled and with large eyes; haustellum reduced, scaled; labial palpi upcurved (sometimes strongly scaled); maxillary palpi 2 to 3-segmented (rarely 4 to 5-segmented); antennae extremely long (often 2× wing lengths) in males (Fig. 56), but of average length in females, although often thickened in both sexes toward bases. Maculation is often very colorful, with iridescent markings, and with wings rather elongated. Adults are usually diurnal but a few are crepuscular. Larvae are leafminers, but in later instars change to casebearers. Host plants include a number of different plant families.

Longhorned Fairy Moths (Lepidoptera: Adelidae), Figure 56 Example of longhorned fairy moths (Adelidae), *Nemophora polychorda* (Meyrick) from Taiwan.

References

*Janse AJT (1945) Adelidae. In: Janse AJT (ed) The moths of South Africa. Transvaal Museum, Pretoria, 4(2):79–150, pl. 19

Küppers PV (1980) Untersuchungen zur taxonomie und phylogenie der westpaläarktischen Adelinae (Lepidoptera: Adelidae). Wissenschaftliche Beiträge Karlsruhe 7:1–497, pl. 12

Nielsen ES (1980) A cladistic analysis of the Holarctic genera of adelid moths (Lepidoptera: Incurvaroidea [sic]). Entomologica Scandinavica 11:161–178

Powell JA (1969) A synopsis of Nearctic adelid moths, with descriptions of new species (Incurvariidae). J Lep Soc 23:211–240

Wojtusiak J (1972) Adelidae. In Klucze do Oznaczania Owadów Polski. 27. Motyle-Lepidoptera. Polskie Towardzystwo Entomologiczne 9:1–52 (In Polish)

Longhorned Grasshoppers

This term is sometimes applied to the katydids in the order Orthoptera: Tettigoniidae.

► Grasshoppers, Katydids and Crickets

Longicorn, Longhorned, or Round-Headed Beetles (Coleoptera: Cerambycidae)

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The family Cerambycidae belongs to the suborder Polyphaga of the order Coleoptera. Classification of higher taxa such as subfamilies is still controversial but the most recent treatment (Lawrence and Newton 1995) is considered here.

Order: Coleoptera
Suborder: Polyphaga
Superfamily: Chrysomeloidea
Family: Cerambycidae

Thirteen subfamilies are included in the Cerambycidae: Vesperinae, Oxypeltinae, Disteniinae, Anoplodermatinae, Philinae, Paradrinae, Prioninae, Spondylidinae, Apatophyseinae, Necydalinae, Lepturinae, Cerambycinae, and Lamiinae. Lamiinae and Cerambycinae are the most speciose subfamilies.

External Morphology

Cerambycid adults range from 3 to 85 mm in length. Color varies greatly from very bright to dark gray or black. They are usually elongate and cylindrical with long antennae inserted on frontal prominences (Fig. 57). Antennae have 11 segments. Eyes are usually emarginated, surrounding the antennal insertions. Tarsi of most longicorn beetles appear 4-segmented with the third segment bilobed, but are actually 5-segmented with the fourth segment small and concealed in the notch of the third and not easy to see. Sexual dimorphism is most commonly reflected in greater ratio of antennal length vs. body length in male than in female.

The larvae are elongate, cylindrical and almost legless, and usually whitish or cream in color. The anterior end of the body is rounded. Therefore, they are called round-headed borers, to distinguish them from flat-headed borers (larvae of Buprestidae), whose anterior end of body is broadened and flattened.

Biodiversity and Life Cycle

Cerambycidae are one of the largest beetle families in the world, with over 35,000 described species in

Longicorn, Longhorned, or Round-Headed Beetles (Coleoptera: Cerambycidae), Figure 57 ***Epithora dorsalis*** **adult.**

about 4,000 genera worldwide. Its species are distributed in all biogeographic regions including Palaearctic, Oriental, Afrotropical, Australian, Neotropical, and Nearctic. However, the distribution pattern varies at subfamily level. For example, Cerambycinae, Lamiinae and Prioninae occur in all regions, but Lepturinae, Aseminae and Disteniinae are naturally absent from Australian region. More than 50% of cerambycid species are found in the tropics.

Eggs are usually laid in, or on, larval host plants and hatch in 6–25 days depending on species and temperature. Neonate larvae in the vast majority of species immediately bore into the hosts and make tunnels. Those of a few species start feeding on roots. Tunnels made by longicorn larvae are usually more or less circular in cross section and go straight for a short distance before turning. Length of the larval stage varies greatly depending on species and climates, being from 2 months to 3 years. They usually pupate in pupal cells inside the host plants (most) or in the soil (some). The adult, after eclosion, may remain in the pupal cell for days, or even months, before emergence from the host. Many longicorns do not hibernate, as their feeding stages are in quite stable environments (inside plant hosts or in the soil). In species with a lifecycle longer than a year, larvae may continue to feed all year round, but reduce feeding rate during cold months. Cerambycids can overwinter as larvae, pupae or adults.

Habitats and Food

Longicorn beetles occur almost anywhere the higher plants exist. Larvae of most species are borers, feeding on solid tissues of living, dying, dead or rotten plants. Most species are woodborers, such as *Anoplophora*, *Monochamus*, and *Phoracantha*; some are herbaceous plant feeders such as *Tetraopes*, *Phytoecia*, and *Paraglenea*; and a few are root feeders such as *Prionus* and *Dorysthenes*. Most woodborer (Fig. 58) species feed on subcortical tissues, at least initially. They may later burrow further into sapwood and even hardwood to continue feeding. Herbaceous feeders usually bore in host stems. Root feeders may bore in the roots, hollowing out and killing the roots of the host plants, or live in the soil and feed on the roots of grass and other small annual or perennial plants.

Each species has its range of host plants. In general, species feeding on dead or rotten plants have a very wide host range. Some of these species may be able to develop on wood of many plant families of both coniferous and nonconiferous origin (for example, most species from Parandrinae, Prioninae, Lepturinae, and some primitive Cerambycinae and Lamiinae). Most others are limited to families of either gymnosperm or angiosperm hosts (for example, Spondylinae, Aseminae and less specialized Cerambycinae are largely limited to gymnosperms while most Lamiinae and

Longicorn, Longhorned, or Round-Headed Beetles (Coleoptera: Cerambycidae), Figure 58 ***Oemona hirta*** **larva.**

Cerambycinae are restricted to angiosperms). Living or healthy plant feeders have much narrower host range, and dying or sickly plant feeders fall in between. Living plant attackers employ different strategies to consume the hosts. They may destroy the heartwood of a tree or branch but allow the living tissue to remain alive, such as *Pyrotrichus vitticollis*, or make tunnels in the (Figs. 58 and 59) cambium and heartwood in turn to avoid killing the host, such as *Oemona hirta*. The larvae of many living plant-feeders will die if the hosts are cut before they mature, such as *Saperda* and *Goes*. The host range of living- and stressed plant-feeders is usually quite stable in their natural and native habitats. However, these beetles can shift and expand their host range to attack introduced plant species, or once they are introduced to a new habitat they may attack plants there and establish new beetle-plant relationship. Furthermore, closely related longicorn species are usually sympatric with quite different host plants, but closely related allopatric species usually have identical or closely related host plants.

Longicorn, Longhorned, or Round-Headed Beetles (Coleoptera: Cerambycidae), Figure 59 **Citrus twigs damaged by *O. hirta*.**

Adults are free-living insects. All subfamilies have both diurnal and nocturnal species in adult stage. Adults of most species from Lamiinae, Paradrinae, Prioninae, Spondylidinae, and Aseminae are nocturnal while those of most species from Cerambycinae, Lepturinae, and Necydalinae are diurnal. Most nocturnal species are attracted to light. Diurnal species are usually bright in color and their eyes are finely faceted while nocturnal ones are usually dark in color and have coarsely faceted eyes. Most species can fly and some are flightless. Most flyers fly at dusk or night, but flower visitors are usually active during the day and are faster flyers.

Although some longicorn adults appear to require little or no food, most species need some feeding for egg maturation and oviposition. They feed on foliage, tender bark, shoots, flowers (including stamens, pollen and nectar), roots, coniferous cone, seeping sap or even fungi. Lack of feeding in the adult stage appears to be common among root and dead-wood feeders in larval stage. Adult feeding behavior usually plays an important role in sex location in longicorns. Adult feeding is usually insignificant to plants, but flower visitors help pollinations through feeding and other activities.

Host Finding and Selection

Location and selection of hosts for oviposition by adult longicorns are critical because the larvae are usually incapable of moving between hosts. Chemical cues appear to play an important role in host finding and selection by longicorn beetles. There is a definite succession of species which visit felled or wind-broken logs; the species which arrive a day or so after felling are quite different from those which appear a week or two later. Obviously the chemical changes in the logs have a selective effect on the beetles. For example, *Monochamus* species are attracted by pine terpenoids and ethanol; some *Phoracantha* species are attracted to newly felled or heavily stressed eucalyptus trees; and some *Arhopalus* species are attracted to newly burned pine forest for oviposition.

Baits for attraction of longicorn beetles exhibit similar selectivity in different stages of fermentation. Fermenting baits have been used as a means of attracting adults, as have natural sites of oozing saps. American entomologists reported the attraction of watermelon rinds of different fermenting stages to *Dendrobias* and *Eustromula* adults. Beers can also attract some cerambycid adults in the field.

Reproduction

Adults of longicorn beetles can usually live for weeks and a few can live for up to 8 months after emergence from larval hosts. During this time, main activities of adults are for reproduction. Males of a given species usually emerge earlier than the females and play the active role in mate location.

Sex pheromones are reported in many longicorn beetle species, but long-range sex pheromones appear to be associated only with a few species that do not feed in the adult stage. Most sex pheromones are operative either in short distance (~1 m), such as in the root-feeding *Migdolus fryanus* and the vine-boring *Xylotrechus pyrrhoderus*, or in contact, such as in the wood-boring *Anoplophora chinensis* and *Nadezhdiella cantori*. In some species such as *Phytoecia rufiventris*, no evidence of any kind of sex pheromones is found. Because long-range sex pheromones are not involved in mate location in most cerambycid species, other mechanisms must have evolved to bring both sexes together for mating, which may take place on the larval or adult hosts.

If both sexes visit the larval host for feeding, then mate location, mating and oviposition usually also occur on the same host. During their presence on the host, they may make a series of brief matings at intervals, with mating and oviposition taking place in turns, such as *Oemona hirta* and *Monochamus scutellatus*. In some species, however, mating and oviposition are two clear-cut phases and after mating the female oviposits either alone or with the attendance of her mate, such as *Anoplophora chinensis*. In many diurnal and flower visiting species (mainly in Lepturinae and diurnal Cerambycinae), mate location and mating occur on flowers of plants, either the same as or different from the larval hosts. Both males and females visit the flowers for feeding and sex. Females leave for the larval host for oviposition after mating, such as *Strangalia davidi* and *Zorion guttigerum*. Oozing saps from plants also bring sexes together in the species whose adults feed on oozing saps, such as *Dendorbias mandibularis*. When sex ratio is male-biased, male-male competition is common. They usually show strong territorial defense and/or mate-guarding behavior. In general, larger males are advantaged in fighting, but the size-dependent advantage may or may not translate into mating success.

Lamiine adults usually prepare the oviposition sites using mandibles, and lay eggs in slits cut by mandibles. Some genera from this subfamily even girdle the plants before making oviposition slits. For example, the parent beetles of *Oncideres* and their relatives completely girdle twigs and branches and then lay eggs beyond the girdle, thus providing freshly killed tissue in which their larvae can develop. Species of *Phytoecia* also girdle the twigs or shoots, but they lay eggs slightly below the girdled point and neonate larvae bore away from the killed part of the twigs or shoots. Most adults of other subfamilies lay eggs exclusively with the aid of the ovipositor. They deposit eggs on the bark or outer surface of the host such as *Spondylis*, in bark cracks or under bark scales such as most species that use the ovipositor only, in cracks and crevices in wood such as *Arhopalus* and *Hylotrupes*, in holes in plants made by other insects such as some lepturines and prionines, or in the soil such as many prionines.

Associations with Other Arthropods

Many arthropods are associated with longicorn beetles. Some of the most spectacular associations among arthropods occur between longicorns and mites. Many species of mites use longicorn beetles as vehicles for dispersal, and this phenomenon has been termed phoresy. Mites in longicorn larval galleries disperse with adult beetles to new, suitable habitats. In return, the longicorn may benefit as the mites they carry may help clean their larval galleries by feeding on fungi, nematodes and debris that may be harmful to the beetle larvae. In this way, commensalism or mutualism may be established. There is also the possibility that this might evolve further so that the mites become parasitic or even parasitoidal on longicorns.

Many insect parasites and predators are associated with longicorns. Ichneumonidae and Braconidae are among the most important parasitoids of longicorn larvae. Encyrtidae parasitize eggs. Clerid beetles prey on both eggs and larvae. There are also reports of longicorn parasites and predators in the orders Diptera and Hemiptera.

Economic and Ecological Importance

Cerambycidae are of high ecological and economic importance. They are responsible for the damage to forests, ornamental trees and tree crops. Heavy attacks usually occur in dense monoculture, and stressed/dying trees (such as fire damage, water stress, and lack of light due to high density). The genera *Monochamus* (on pines) and *Phoracantha* (on eucalyptus) contain some of the most important forest pests in the world. *Megacyllene robiniae* (on black locust), *Saperda tridenta* (on elm) and *A. glabripennis* (on poplar and willow) are among the most important pests of ornamental plants. Pests on tree crops seem more localized. For example, *A. chinensis* and *N. cantori* are important pests on citrus in Asia, and *S. candida* is an important pest on apple in North America.

Some longicorn species are candidates for the biological control of weeds by killing healthy weedy plants. For example, *Moneilema* spp. were used to control weedy cacti. Finally, most longicorn species feed on dead plants and are significant for renewal of forests by decomposing dead and sickly trees into humus.

►Beetles

References

Duffy EAJ (1963) A monograph of the immature stages of Australasian timber beetles (Cerambycidae). British Museum (Natural History), London, UK

Duffy EAJ (1968) A monograph of the immature stages of oriental timber beetles (Cerambycidae). British Museum (Natural History), London, UK
Hanks LM (1999) Influence of the larval host plant on reproductive strategies of cerambycid beetles. Annu Rev Entomol 44:483–505
Lawrence JH, Newton AF (1995) Families and subfamilies of Coleoptera (with selected genera, notes, references and data pm family-group names). In: Pakaluk L, Slipinski SA (eds) Biology, phylogeny, and classification of Coleoptera. Museum I Instytut Zoologii PAN, Warsaw, Poland, pp 779–1006
Linsley EG (1961) The Cerambyidae of North America, pt 1. Univ Calif Publ Entomol 18:1–135

Longitudinal Veins

The principal wing veins, normally extending lengthwise through the wings (contrast with cross veins).

► Wings of Insects

Long-Legged Flies (Diptera: Dolichopodidae)

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The family Dolichopodidae is one of five major lineages within the superfamily Empidoidea of the infraorder Muscomorpha. The other four empidoid families that are currently recognized are the Empididae, Atelestidae, Hybotidae and Brachystomatidae. The Dolichopodidae are generally divided into 17 subfamilies (see classification below), including the recently added basal subfamilies Microphorinae and Parathalassiinae. This expanded concept of the family is referred to as Dolichopodidae *s.lat*. The other 15 subfamilies exclusive of Microphorinae and Parathalassiinae are referred to as Dolichopodidae *s.str*., which is equivalent to the traditional concept of the family.

Subper family: Empidoidea
- Family: Dolichopodidae *s.lat.*
  - Subfamily: Microphorinae
  - Subfamily: Parathalassiinae
- Family: Dolichopodidae *s.str.*
  - Subfamily: Achalcinae
  - Subfamily: Babindellinae
  - Subfamily: Diaphorinae
  - Subfamily: Dolichopodinae
  - Subfamily: Enliniinae
  - Subfamily: Hydrophorinae
  - Subfamily: Medeterinae
  - Subfamily: Neurigoninae
  - Subfamily: Plagioneurinae
  - Subfamily: Rhaphiinae
  - Subfamily: Sciapodinae
  - Subfamily: Stolidosomatinae
  - Subfamily: Sympycninae
  - Subfamily: Xanthochlorinae

Distinguishing Characters and Relationships

The Dolichopodidae *s.lat*., including the very species rich Dolichopodidae *s.str.* and the much smaller subfamilies Microphorinae and Parathalassiinae, are clearly a monophyletic lineage that is characterized by the following features: wing with vein Rs originating at or near the level of crossvein h, shortened basal cells (less than half the length of cell dm) with crossvein r-m in the basal fourth of the wing; male terminalia rotated and lateroflexed forward below the preceding abdominal segments with the pregenital segments partially twisted or rotated, and several characters of the male genitalia.

The Microphorinae and Parathalassiinae comprise the basal dolichopodids and are small (1–3 mm) non-metallic, greyish to dark colored flies, usually with wing cell dm emitting three branches. The Parathalassiinae forms a monophyletic group with the Dolichopodidae *s.str*. supported by several features of the wing venation, mouthparts and thorax. The Dolichopodidae *s.str*. are a well-supported monophyletic group and are readily separated from the Microphorinae, Parathalassiinae and the remaining Empidoidea by the combination of a metallic or yellow body color, and the generally narrow wings with the costal vein ending at M_1, vein Sc very short and ending in vein R_1, cell dm emitting two veins (instead of three), and cells bm and dm fused.

It has been hypothesized that the Dolichopodidae *s.str*. descended from marine coastal inhabitants, and that the common ancestor of the parathalassiines (which are almost exclusively marine littoral) and the Dolichopodidae *s.str*. invaded the sea coast from the ancestral terrestrial habitat of the microphorines. It has been further suggested that marine littoral habitats are still occupied by a basal grade of the Dolichopodidae *s. str*., which have traditionally been placed in the subfamily Hydrophorinae. The remaining Dolichopodidae *s.str*. abandoned the marine habitat in favor of a return to terrestrial and freshwater habitats, assuming independent reinvasions of the sea coast by several species in various subgroups. At present, phylogenetic relationships between subfamilies and between genera are not very clear, although some subfamilies like the Dolichopodinae and Sciapodinae seem more cohesive than others.

Fossil Record

Dolichopodids are well represented in the fossil record. Most dolichopodid fossils are amber inclusions which is unsurprising given that many groups of this family are associated with tree trunks and thus prone to becoming stuck in resins and fossilized. The earliest known representatives of the Dolichopodidae *s.lat*. (i.e., the microphorine genera *Microphorites* and *Avenaphora*) first appeared in Lebanese amber from the Lower Cretaceous (120–135 mya). The Dolichopodidae *s.str*. have also been reported from Lebanese amber (i.e., *Sympycnites primaevus*); however, the dating of this fossil is in question and is suspected to be from Baltic amber (40 mya). The earliest parathalassiines were found in Siberian amber from the Upper Cretaceous. The oldest definitive representative of Dolichopodidae *s.str*. is *Prosystenus zherikhini* in amber of Sakhalin Island, Far East Russia, from the Paleocene. Dolichopodids are very abundant in Baltic (Eocene/Oligocene) and Dominican (Miocene) ambers. The majority of fossil species of Dolichopodidae *s.str*. have been described from Baltic amber and assigned to extant genera. However, recent studies indicate that the majority of Baltic amber species cannot be included in extant genera based on synapomorphies and require separate fossil genera, suggesting that most recent genera of Dolichopodidae *s.str*. did not appear until after the Eocene/Oligocene.

Morphology

Adults (Figs. 60 and 61a–e) range from 0.8 to 9.0 mm in length. Most dolichopodids are metallic green, bronze to blue in body color, whereas some genera often feature yellow (*Achalcus*, *Neurigona*, *Xanthina*, *Xanthochlorus*), or – sometimes dull – brown to black, or greyish colors (*Aphrosylus*, *Micromorphus*, *Medetera*, *Microphor*, *Parathalassius*). Eyes are large and occupy most of the head, but are rarely holoptic on the frons (males of *Diaphorus*, *Microphor*, *Schistostoma*) or nearly continuous on the face (*Chrysotus*, *Allohercostomus*). The antenna is usually inserted rather high on the head and consists of a scape, pedicel, postpedicel (1st flagellomere) and arista-like stylus that usually consists of two articles (one article in Parathalassiinae and in some males with modified antennae). The stylus is basidorsal to apical, and the shape of the scape, pedicel and postpedicel is highly variable. In some genera the antenna is subject to strong sexual dimorphism which is mostly reflected in the shape and size of the antennal segments (e.g., arista-like stylus with terminal flag or binodate, postpedicel multilobate), but sometimes also in their color (Achalcinae). Palps are flat, usually with fine pubescence and one or more distinct apical bristles. In some genera, males possess palps that are greatly enlarged or elongated, silvery white or brilliantly metallic which are employed during courtship. The proboscis is equipped with a pair of flexible labellar lobes, each of which has six variously sclerotized narrow pseudotracheae on its inner surface. In *Melanderia*, these lobes are highly sclerotized and mandibuliform. The Dolichopodidae *s.str*. possess stout and sharply pointed epipharyngeal blades presumably utilized in tearing the bodies of their prey, and an elongated epipharyngeal apodeme that projects vertically into the head.

In most dolichopodid flies, the chaetotaxy of the scutum (thorax) is well differentiated and usually includes biserial acrostichal setae medially (sometimes uniserial or absent), a row of dorsocentral bristles laterad of the acrostichals, a row comprising one presutural, one sutural, two postsutural supraalar, and one postalar bristles laterally flanking the dorsocentrals, and one postpronotal, two posthumeral and two notopleural bristles near the lateral margin of the scutum. The chaetotaxy of the microphorine scutum is usually less differentiated than that of other dolichopodids, and in some species, the acrostichal and dorsocentral bristles are pluriserial and uniformly distributed over the scutum. The scutellum always has a strong medial pair of marginal bristles, and usually an outer pair of smaller bristles (absent, e.g., in some *Medetera* species groups). The proepisternum also bears one or more bristles, but the pleuron is usually devoid of bristles and hairs except in some genera (e.g., *Dolichopus*, *Ethiromyia*, *Gymnopternus*, *Thambemyia*, *Hydatostega*, *Syntormon*). Wings are mostly narrow but can be rather broad (*Diaphorus*, *Enlinia*). In general, the wing venation is reduced and most species entirely lack vein M_2, except for the Microphorinae, most Parathalassiinae, most Sciapodinae and some *Dolichopus* (with M_2 represented as a stub). In most species, vein M_1 is straight, gently curved, or distinctly bent towards R_{4+5}, whereas it is interrupted in *Asyndetus* and *Cryptophleps*, or divergent from R_{4+5} in Enliniinae and most Achalcinae. Two crossveins are present in the Dolichopodidae *s.str*., with the basal r-m very short and dm-cu usually situated in the centre or the apical half of the wing and connected to M_{1+2}. In most Microphorinae and Parathalassiinae an additional basal crossvein is present (bm-cu) and crossvein dm-cu is connected to the base of M_2. Micropterous (*Emperoptera*, some *Schoenophilus*), stenopterous (*Papallacta*) and apterous dolichopodids (*Apterachalcus*) occur, and males of the genus *Erebomyia* display directional asymmetry, with the left wing larger and of a different shape than the right wing.

The abdomen can be quite long and slender (*Neurigona*, Sciapodinae) or strongly shortened (*Hydrophorus*). Most females have five well-developed setose segments with the apical segments largely bare and retracted into segment 5, whereas others (e.g., some Microphorinae and Parathalassiinae) have the apical segments retracted into segment 6. Females of *Xanthochlorus* are unusual, with eight setose abdominal segments. Tergite 10 of females is usually partially or completely divided medially with each side bearing one to six stout spines arranged in a row. In some dolichopodids (e.g., *Microphor*, Neurigoninae, some Medeterinae, some Sciapodinae, *Xanthochlorus*), however, these spines are not developed. The female cerci are usually situated laterally and are partly or entirely divided into a longer, well-sclerotized dorsal lobe and smaller ventral lobe. The female terminalia of some genera are highly modified. In *Thrypticus*, the eighth segment and proctiger are fused into a strongly sclerotized lanceolate ovipositor. In the Taiwanese genus *Alishanimyia* the terminalia are greatly enlarged forming a rounded sclerotized cavity, the function of which is unknown.

The number of setose segments (at least tergites) varies from five to seven in males. The male hypopygium is either largely enclosed in an invagination formed by the sixth, and more rarely also the fifth abdominal sternite (many Sympycninae), free but sessile (many Hydrophorinae, Rhaphiinae) or pedunculate (Dolichopodinae, Medeterinae, Sciapodinae). In the pedunculate condition segment 7 is modified into a peduncle or external arm that supports the genital capsule. Segment 7 can be quite short to greatly elongated. The hypopygium itself is highly variable in structure and includes very important diagnostic features essential for identification.

The Dolichopodidae are best known for their legs which are usually long and slender (hence the common name of the family) and, in males, subject to an apparently endless variation in shape and vestiture. These specific ornamentations or Male Secondary Sexual Characters (MSSC) involve peculiarities in pubescence and chaetotaxy, and/or elongation, compression or deformation of tarsi, tibiae or femora. Extreme examples of these MSSCs on legs are found in *Campsicnemus* (e.g., *C. magius*). Although MSSCs are most commonly developed on the legs, they also occur on the head, wings and abdomen of males. Next to the detailed structure of the male hypopygium, these MSSCs are crucial diagnostic characters for identification. Males of a few genera largely lack these special structures (e.g., some *Medetera* species groups, *Micromorphus*), and examination of the male genitalia is usually required for species identification.

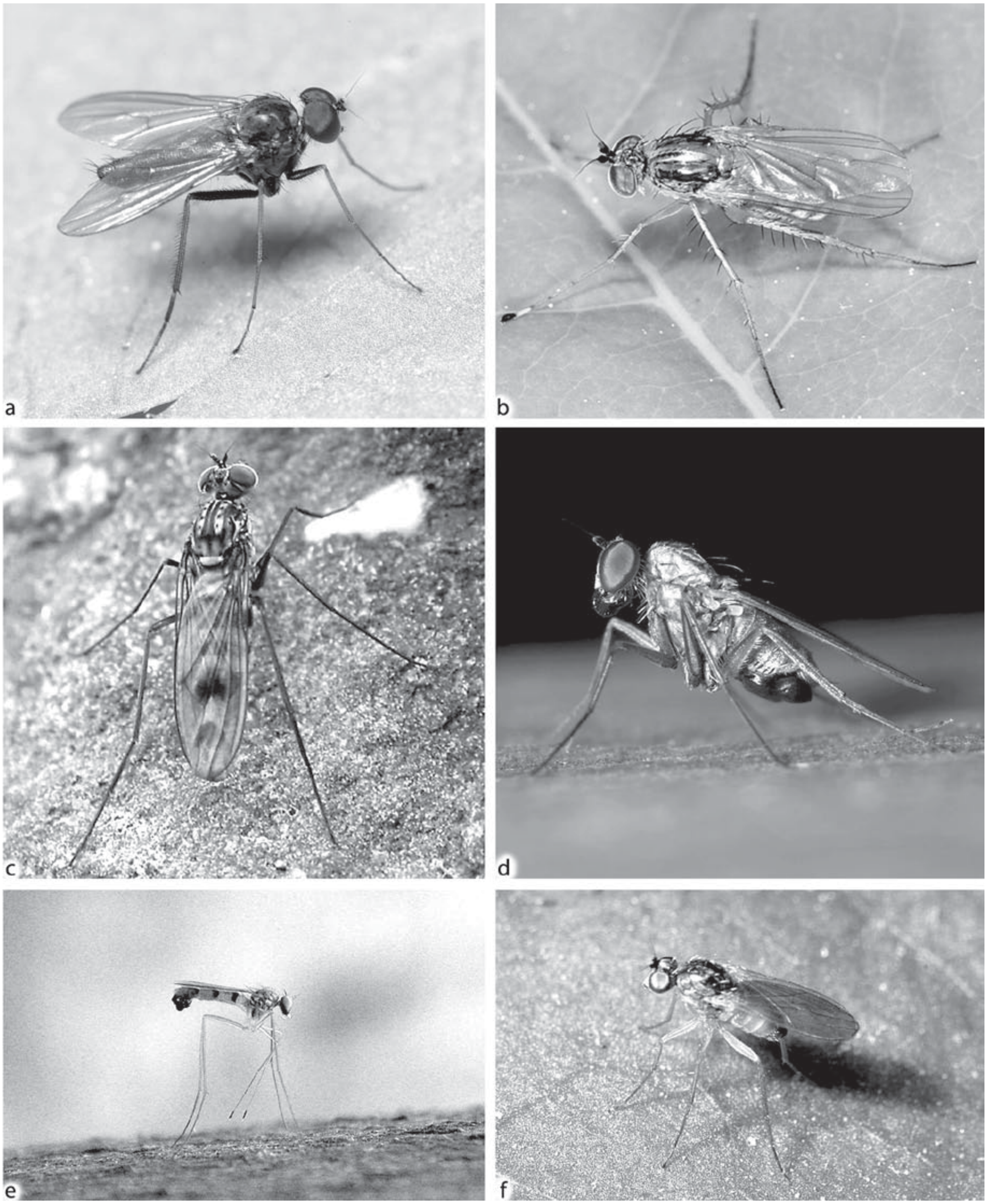
The larvae (Fig. 61f) are whitish cylindrical maggots with a slightly tapering anterior apex. The four-lobed head segment is usually short, lacks external sclerotization and has brown to black internal mouthparts. Each of the seven anterior abdominal segments shows a pair of creeping welts or swellings bearing spicules on its anterior margin, with those on the first segment being sometimes very large and resembling prolegs (*Systenus*). The terminal (12th) segment of the body is truncate and divided posteriorly by a horizontal and vertical furrow, producing four or more lobes that are usually elongate, but can be very short in some species (*Medetera*, *Neurigona*). Each of the dorsal lobes usually bears a posterodorsal spiracle.

Dolichopodid pupae are enclosed in a loose silky cocoon spun by the final instar larva which incorporates debris from the habitat. The pupae possess a pair of large respiratory horns that arise from the dorsal surface of the cephalothorax just behind the eyes. The tips of these horns are projected through a small aperture in the cocoon. The abdominal tergites are usually equipped with transverse rows of spines whereas the anal segment is bluntly rounded or ends in a pair of stout spines.

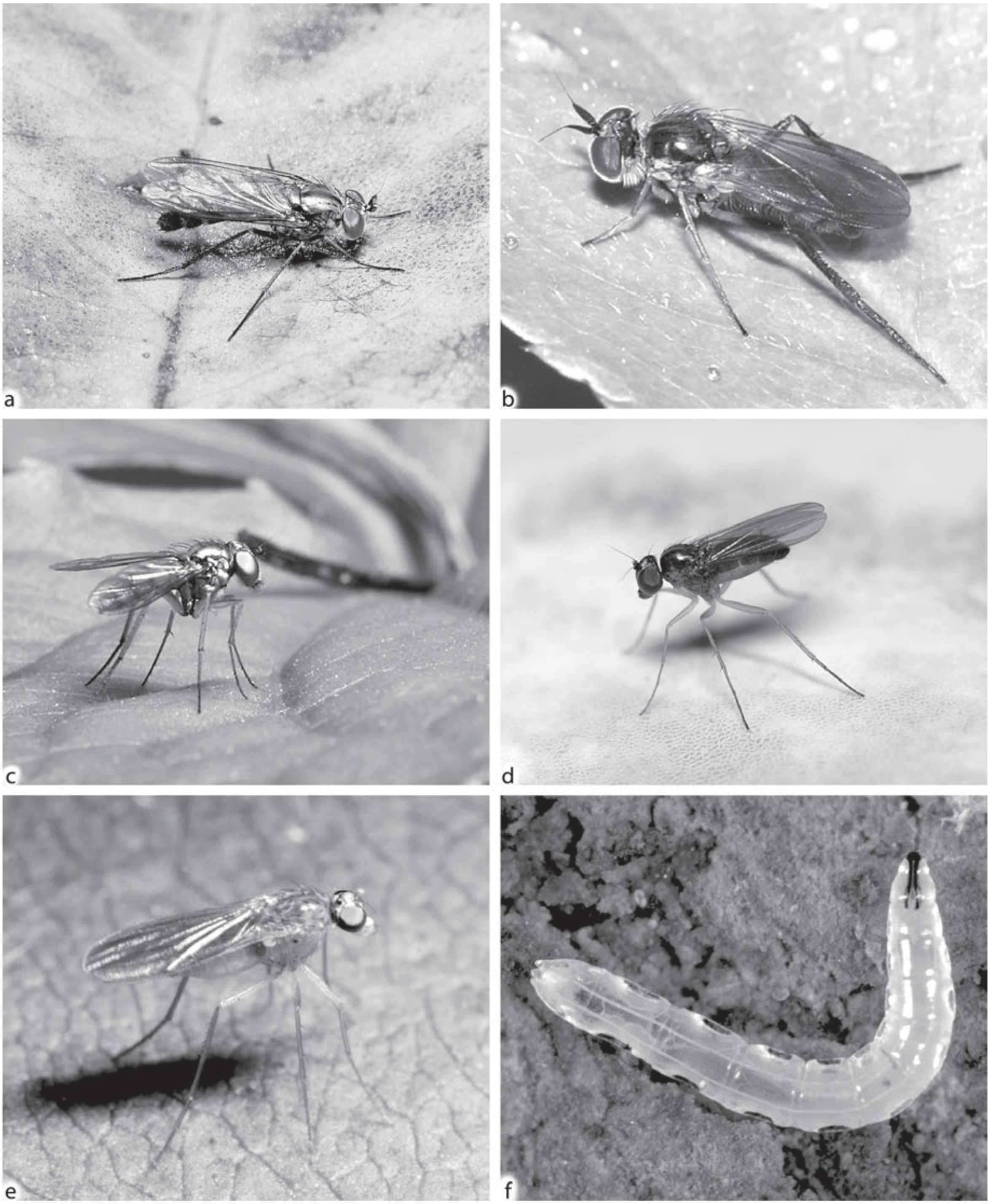
Diversity, Ecology and Distribution

With about 6,900 species in more than 220 genera worldwide, the Dolichopodidae represent over 5% of all described fly species, preceded only by the Tipulidae (approximately 11%) and Tachinidae (approximately 7%). Over one thousand species have been recorded in each zoogeographical region, except for the Afrotropical realm with about 700 species. These numbers, however, cannot be considered a reliable reflection of the real extant biodiversity: while certain areas in the Palaearctic and Nearctic regions have been sampled thoroughly, this is hardly the case for the tropics where the number of described species is likely only a fraction of the real diversity.

Long-legged flies occupy all semi-aquatic and terrestrial habitats in every zoogeographical realm, even on small islands amid the Pacific. Most species seem to prefer fairly humid to very humid habitats. They are most diverse and abundant in mangroves, salt marshes, reed marshes and swamps, humid deciduous forests and rainforests, humid heathlands and peat moors, and on banks of streams and stagnant water bodies. Drier habitats like coastal dunes and dry grasslands are characterized by lower diversities with only some xerophilous genera (*Chrysotus*, *Medetera*, *Sciapus*) being well represented. Most adult Dolichopodidae (Figs. 60 and 61a–e) are usually found on broad-leaved vegetation of low shrubs and trees and on humid or muddy soils, whereas others are confined to vertical structures like tree trunks, rock surfaces or fences. Larvae (Fig. 61f) occur in mud, damp soil, leaf litter, moss, algal mats, decaying seaweed, under bark and within plant tissues. Pupae have been found under bark of trees (*Medetera*) and in the muddy soil of riparian habitats (*Tachytrechus*). A number of microhabitats house a specialized dolichopodid fauna. Rotholes and sapruns on deciduous trees are inhabited by larvae of *Systenus* in all realms, and by *Australachalcus melanotrichus* and some *Hercostomus* species in the Palaearctic Region. Springs and waterfalls with water falling on, or seeping over, rocks show typical



Long-Legged Flies (Diptera: Dolichopodidae), Figure 60 **Some examples of long-legged flies: (a) *Diaphorus* sp. (Diaphorinae) (Nearctic) (photo by Steve Marshall); (b) *Dolichopus* sp. (Dolichopodinae) (Nearctic) (photo by Tom Murray); (c) *Liancalus genualis* (Hydrophorinae) (Nearctic) (photo by Steve Shaw); (d) *Medetera jacula* (Medeterinae) (Palaearctic) (photo by Janne Sinkkonen); (e) *Neurigona quadrifasciata* (Neurigoninae) (Palaearctic) (photo by Diederik D'hert); (f) *Chrysotimus* sp. (Peloropeodinae) (Neotropics) (photo by Steve Marshall).**



Long-Legged Flies (Diptera: Dolichopodidae), Figure 61 **Some additional examples of long-legged flies: (a) *Plagioneurus univittatus* (Plagioneurinae) (New World) (photo by Steve Marshall); (b) *Rhaphium* sp. (Rhaphiinae) (Nearctic) (photo by Tom Murray); (c) *Condylostylus* sp. (Sciapodinae) (Nearctic) (photo by Garrett Bailey); (d) *Sympycnus* sp. (Sympycninae) (Neotropics) (photo by Steve Marshall); (e) *Xanthochlorus helvinus* (Xanthochlorinae) (Nearctic) (photo by Steve Marshall); (f) larva of *Medetera* sp. (Medeterinae) (Palaearctic) (photo by Beat Becker).**

hygropetric faunas with Hydrophorinae present in all realms. In contrast, other taxa associated with these hygropetric habitats differ between realms, with *Hercostomus* being more prominent in the Palaearctic Region, *Gymnopternus* in the Nearctic Region and Enliniinae in the Neotropical Region.

At present, ecological data on the habitat affinity of most dolichopodids is entirely lacking. Only the western European fauna has been fairly well documented in this respect. In what follows, distribution and ecology of the subfamilies are discussed primarily on the basis of the currently available data.

The Microphorinae are a small subfamily that includes the genera *Microphor* and *Schistostoma*. *Microphor* is primarily Holarctic, but also includes one species from Tasmania. Species of this genus occur in lowland shrubby habitats and forests. *Schistostoma* is known from the Holarctic and Afrotropical regions and is found in warm sandy habitats, and on dry river banks with sand and gravel.

The subfamily Parathalassiinae includes a relatively small group of dolichopodids that are primarily associated with sea coasts, with the exception of some *Microphorella* species known from inland sand and gravel river banks, or associated with mist of waterfalls. Parathalassiines are known from all realms.

At present, the strongly hygrophilous Achalcinae only account for about 1% of dolichopodid diversity with hotspots in the Neotropics and New Zealand. In the northern hemisphere, *Achalcus* prefers marshland habitats with a well developed vegetation layer, whereas *Australachalcus* species breed in rotholes of deciduous trees. The endemic Neotropical genus *Xanthina* is most diverse at low altitudes in contrast to *Achalcus*, *Australachalcus* and a number of yet undescribed genera.

The Babindellinae are endemic to the tropical and subtropical closed forests of Australia. The subfamily comprises two species in the genus *Babindella*.

The Diaphorinae are a diverse subfamily (approximately 12% of world fauna) with *Chrysotus*, *Diaphorus*, *Asyndetus* and *Argyra* as dominant genera. *Chrysotus* and *Diaphorus* are among the most species rich dolichopodid genera in the tropics with the former remarkably diverse in the Neotropics. They are both active on the soil and in the vegetation in dry to very wet places. *Asyndetus* is riparian with some species inhabiting crab holes. Many species of the primarily Holarctic genus *Argyra* are readily recognized by the silvery white pruinosity of the thorax and abdomen, which produces silver flashes while flying swiftly along forest paths and streams.

The Dolichopodinae are by far the most species rich subfamily in the Dolichopodidae *s.str*. with approximately 26% of the world fauna. The genus *Dolichopus*, which occurs in the Holarctic, Afrotropical, Oriental and Australasian regions, and also on the Hawaiian Islands, encompasses over 8% of all dolichopodid species. Other species rich genera include *Hercostomus*, *Tachytrechus*, *Gymnopternus*, *Paraclius* and *Pelastoneurus*. Although Dolichopodinae are found in very different habitats, ranging from salt marshes to humid forests, most species prefer humid conditions. *Tachytrechus* is often encountered on sandy beaches and on rocks in pools and along rivers, and like *Paraclius* and *Pelastoneurus*, is most diverse in the Neotropics.

The Enliniinae are a subfamily of microdolichopodid flies (most species less than 1.0 mm in length) that is endemic to the New World. Enliniines account for more than 1.4% of the world fauna but remain largely unstudied outside Mexico. They are mainly found at river runoffs or small waterfalls, hovering along wet vertical rock surfaces. They are sometimes very abundant in these habitats, with several species hovering together.

The subfamily Hydrophorinae includes approximately 8% of described species which are among the most hygrophilous dolichopodids. Many hydrophorines show strong habitat affinities. Some genera are restricted to rocky seashores (*Aphrosylus*, *Thambemyia*), whereas others prefer sandy to muddy beaches (*Thinophilus*, *Machaerium*), or mountain seeps (e.g., *Eucoryphus*, *Sphyrotarsus*). Species of the dominant genus *Hydrophorus* occur on beaches and along stagnant and running water, where they skate on the water surface in search of mates and prey.

The majority of Medeterinae (e.g., *Corindia*, *Medetera*, *Systenus*) are arboreal and usually encountered on tree trunks and other vertical surfaces. With over 300 species mostly described from the Palaearctic Region, *Medetera* is one of the largest genera in the family. This genus also appears to be very diverse in the Neotropics, but remains largely unstudied in this region. The larvae of many *Medetera* species live in the galleries of bark beetles (Curculionidae: Scolytinae) and are predaceous on the developing beetles. *Systenus* larvae develop in rotholes and sap runs of deciduous trees. The larvae of *Thrypticus* are unique among dolichopodids as leafminers in monocots. The Medeterinae represent approx. 8% of all described dolichopodid species.

The Neurigoninae are a rather small subfamily including approximately 3% of described species. Adults are typically slender, and long-legged. Neurigonines are most diverse in the Neotropical Region, and like many Medeterinae, are often encountered on tree trunks.

The Peloropeodinae are a small subfamily (approximately 3% of described species) comprised of several genera that were previously placed in Sympycninae. Its status as a separate subfamily remains in question. *Chrysotimus*, *Nepalomyia*, *Peloropeodes* and *Micromorphus* are the most species rich genera. *Chrysotimus* occurs in the canopy of deciduous trees, *Nepalomyia* is often found in dark, cool sites with running water, whereas *Peloropeodes* and *Micromorphus* are distinctly soil-dwelling.

The subfamily Plagioneurinae includes a single distinctive species, *Plagioneurus univittatus*, that is endemic to, but rather widespread in the New World.

About 94% of the species in the subfamily Rhaphiinae (approximately 3% of described species) belong to *Rhaphium* and *Nematoproctus* which are primarily Holarctic genera, with only few species in adjacent zoogeographical realms. Species of both genera show distinct sexual dimorphism. Many of the more than 180 *Rhaphium* species are among the first dolichopodid flies to appear in the spring and prefer very wet conditions, usually with open water.

The Sciapodinae account for about 19% of all described species and have been studied in greater detail than any other subfamily in the past two decades. Sciapodines are among the largest and most conspicuous dolichopodids in the tropics, and are frequently found sun-basking in the higher herb vegetation or the lower tree canopy. The widespread genera *Amblypsilopus*, *Condylostylus* and *Chrysosoma* include more than 200 species each. *Amblypsilopus* is most diverse in Australasia whereas most *Condylostylus* species are found in the Neotropics. Most species of *Chrysosoma* have been recorded from Afrotropical, Oriental and Australasian realms. *Sciapus* is primarily Palaearctic and comprises about 60 species with rather diverse habitat affinities. Some are stenotopic forest species that occur on tree trunks, whereas others prefer dry sandy habitats where they are found at soil surface level.

Most of the 29 species of the Stolidosomatinae are endemic to the Neotropics with a few species known from the Nearctic. *Stolidosoma* is found on tree trunks and on broad-leaved vegetation in rainforests.

The subfamily Sympycninae includes about 14% of the described species of the Dolichopodidae. Among the 40 described sympycnine genera, *Sympycnus*, *Campsicnemus*, *Teuchophorus* and *Syntormon* are the most species rich. *Sympycnus* and *Syntormon* are known from all realms, whereas *Campsicnemus* and *Teuchophorus* have not been recorded from the Neotropics. *Teuchophorus* is most diverse in the Oriental (Southeast Asia) and Australasian realms (New Guinea), whereas *Campsicnemus* has undergone a phenomenal radiation on the Hawaiian Islands similar to *Drosophila*, with nearly 160 or 70% of the world's species. Most Sympycninae are distinctly hygrophilous and occur in very wet places, from salt marshes to peat moors and high altitude mountain habitats. *Campsicnemus* is soil-dwelling and has been seen skating on water surfaces. Unlike most of the other Dolichopodidae, some *Sympycnus* species are considered dark-preferent.

The subfamily Xanthochlorinae includes the single genus *Xanthochlorus*, with one Nearctic species and 11 species in the Old World. The western Palaearctic species seem to prefer dry deciduous forests.

Feeding Ecology and Economic Importance

Both adults and larvae are predatory, with the exception of *Thrypticus* larvae which are phytophagous (see above). Adults seem to be generalists that feed on any suitable prey available. Soft-bodied arthropods such as mites, springtails, aphids, thrips, and the larvae and adults of Diptera are the most frequently recorded prey items. Predation by dolichopodids has also been recorded on annelids, cladocerans, amphipods, small myriapods, odonate eggs, termites, psocopterans, beetle larvae, early instar caterpillars, dead and wounded arthropods and amphibian embryos. Females of *Microphor* are known to be kleptoparasitic, feeding on insect prey in spider webs. The prey of dolichopodids is usually seized and held by the labella, cut open by the epipharyngeal blades and its liquid and liquefied contents sucked out. Honeydew is also used as a food source. Some Palaearctic species of *Hercostomus* (*H. germanus*, *H. chaerophylli*, *H. nigripennis*) and *Ortochile* appear to feed on nectar and pollen of flowers and possess elongated mouthparts.

Dolichopodids are important natural enemies of pests in a variety of habitats. Dolichopodid species with the greatest potential as biological control agents belong to the genus *Medetera*. Larvae of most *Medetera* species feed on developing bark beetles in their galleries under the bark. Adult *Medetera* use tree volatiles and/or pheromones released by the beetles to locate infested trees and oviposition sites. Predation on bark beetles by *Medetera aldrichii* has been investigated in detail in the Nearctic Region. Several Neotropical species of *Thrypticus* have been reared from the petioles and stems of water hyacinth (*Eichhornia crassipes*). As such, they have potential as biocontrol agents of this New World aquatic plant which is an invasive weed in the waterways of Africa, Asia and Australia. Several genera of Dolichopodidae have also been reported as predators of mosquito larvae.

Conservation

The Ko'Olau Spurwing Long-legged Fly (*Emperoptera mirabilis*, previously in *Campsicnemus*) from Hawaii is the only dolichopodid species that is currently included in the IUCN Red list of threatened species. This micropterous fly was discovered on a single occasion in 1900, but has not been seen since, and is currently regarded as extinct.

At present, little attention has been given to the conservation status of dolichopodids. However, during recent years Red Data Books (RDB) on the Dolichopodidae of Flanders (northern Belgium), Germany and Great Britain have been published. These RDBs, which are also available for water beetles, water bugs, butterflies, dragonflies, ground beetles and spiders, prove to be valuable tools for site quality assessment. Recent studies indicate that dolichopodids have very specific habitat requirements and appear to react quickly to environmental alterations. As more detailed ecological data become available and more revisionary studies are completed, dolichopodids show potential to be used as bioindicators for site quality assessment and conservation programs outside Europe.

► Flies

References

Bickel DJ (1994) The Australian Sciapodinae (Diptera: Dolichopodidae), with a review of the Oriental and Australasian faunas, and a world conspectus of the subfamily. Rec Austr Mus Suppl 21:1–394

Brooks SE (2005) Higher classification and phylogeny of Dolichopodidae. Available at www.nadsdiptera.org /Doid/ Doliclass/Doliclass.htm Accessed on April 24, 2007
Brooks SE (2005) Systematics and phylogeny of Dolichopodinae (Diptera: Dolichopodidae). Zootaxa 857:1–158
Chvála M (1983) The Empidoidea (Diptera) of Fennoscandia and Denmark. II. General Part. The Families Hybotidae, Atelestidae and Microphoridae. Fauna Entomologica Scandinavica 12:1–279
Grichanov IY (1999) A check list of genera of the family Dolichopodidae (Diptera). Studia dipterologica 6(2):327–332
Grimaldi D, Cumming J (1999) Brachyceran Diptera in Cretaceous ambers and Mesozoic diversification of the Eremoneura. Bull Am Mus Nat Hist 239:1–124
Pollet MAA (2000) A documented red list of the dolichopodid flies (Diptera: Dolichopodidae) of Flanders. Commun Instit Nat Conserv 8:1–190 (In Dutch with English summary)
Pollet MAA (2004) Dolichopodidae. In: Pape T (ed) Fauna Europaea: Diptera, Brachycera. Fauna Europaea version 1.1. Available at http://www.fauneur.org Accessed on December 16, 2004
Pollet MAA, Brooks SE, Cumming JM (2004) Catalog of the Dolichopodidae (Diptera) of America north of Mexico. Bull Am Mus Nat Hist 283:1–114
Pollet M, Grootaert P (1999) Dolichopodidae (Diptera): poorly known but excellent agents for site quality assessment and nature conservation. Proc Exper & Appl Entomol., N.E.V. Amsterdam 10:63–68
Robinson H, Vockeroth JR (1981) 48. Dolichopodidae. In: McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR, Wood DM (eds) Manual of Nearctic Diptera. vol 1. Agriculture Canada Monograph 27. Biosystematics Research Institute, Ottawa, Canada, pp 625–639
Sinclair BJ, Cumming JM (2006) The morphology, higher-level phylogeny and classification of the Empidoidea (Diptera). Zootaxa 1180:1–172
Ulrich H (2003) How recent are the Empidoidea of Baltic amber? Studia Dipterologica 10:321–327
Ulrich H (2004) Phylogenetic considerations about an early colonization of the sea coasts by Dolichopodidae (Diptera). Studia Dipterologica 11(1):233–243
Ulrich H (2004) Predation by adult Dolichopodidae (Diptera): a review of literature with an annotated prey-predator list. Studia Dipterologica 11(2):369–403

Long-Lipped Beetles

Members of the family Telegeusidae (order Coleoptera).

► Beetles

Long-Tailed Burnet Moths (Lepidoptera: Himantopteridae)

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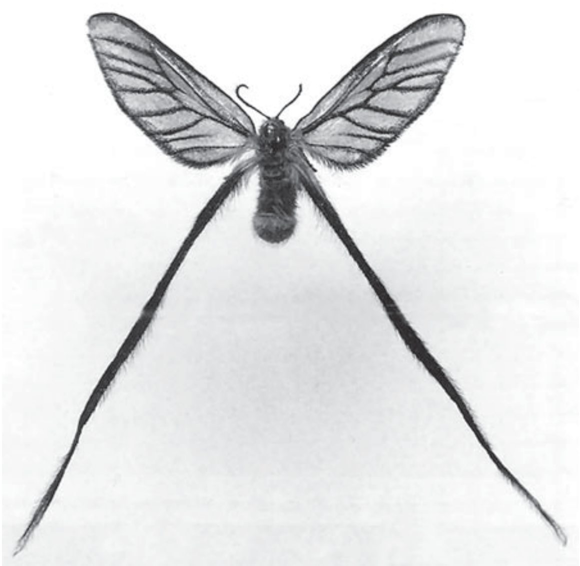
Long-tailed burnet moths, family Himantopteridae, include 56 species from Africa and tropical Asia; formerly included in Zygaenidae. The family is in the superfamily Sesioidea in the section Tineina, subsection Sesiina, of the division Ditrysia. Adults small to medium size (16–42 mm wingspan), with head scaling average; haustellum naked; labial palpi upcurved; maxillary palpi 1 to 2-segmented; antennae mostly bipectinate. Wings triangular; hindwings with extremely long tails (Fig. 62). Maculation usually colorful, with spots on the hindwing broader basal area; tails usually darker. Adults are diurnal but few are known biologically. Larvae are leaf skeletonizers, often communal; sometimes massing in the 1,000s as they move down the host trunk before pupating in soil; slug-like, with concealed head. Known host plants are in Dipterocarpaceae.



Long-Tailed Burnet Moths (Lepidoptera: Himantopteridae), Figure 62 **Example of long-tailed burnet moths (Himantopteridae), *Himantopterus fuscinervis* Wesmael from Malaysia.**

References

Barlow HS, Carter DJ (1996) A breeding record for *Himantopterus fuscinervis* Wesmael (Lepidoptera, Hymantopteridae [sic]). Malayan Nat J 50:27–32
Hering EM (1937) Synopsis der Himantopterinae (Lep. Zygaen.). Revue Zoologique et Botanique Africain 29:237–254
Heynderyckx J (1999) *Himantopterus fuscinervis* Wesmael (Lepidoptera Himantopteridae). Lambillionea 99:217–218
Kishida Y, Inomata T (1992) A new species of the himantopterid genus, *Himantopterus* from Borneo (Lepidoptera). Tyô to Ga 44:49–51

Long-Toed Water Beetles

Members of the family Dryopidae (order Coleoptera).
► Beetles

Looper

A caterpillar of the order Lepidoptera, family Noctuidae, subfamily Plusiinae (but sometimes others, especially the measuringworms, family Geometridae) that move with a pronounced looping motion. Such caterpillars are lacking most of the abdominal prolegs, and move by bringing the remaining prolegs (two to three pairs), located near the tip of the abdomen, up to the true legs before moving the anterior part of the body forward. (contrast with semilooper)

Lophocoronidae

A family of moths (order Lepidoptera). They also are known as Australian archaic sun moths.
► Australian Archaic Sun Moths
► Butterflies and Moths

Lophopidae

A family of bugs (order Hemiptera, suborder Fulgoromorpha). All members of the suborder are referred to as planthoppers.
► Bugs

Lorguin, Pierre Joseph Michel

Pierre Lorguin was born in Valenvicennes, France, on July 2, 1787. He graduated from the University of Douay and pursued a career in law. He was very successful, but with the outbreak of the French Revolution in 1848 he moved to Algiers. In 1850, Lorguin moved to California in response to discovery of gold in 1849. His family joined him in California in 1852, and he remained there until 1859. Lorguin collected Lepidoptera for J.A. Boisduval and contributed greatly to the California Academy of Science. In fact, nearly all of the Lepidoptera described by Boisduval from California were collected by Lorguin. In addition to California, he collected in the Philippine Islands, China, and in Southeast Asia. After contracting a disease he returned to France in 1865 where he died in Paris on February 8, 1873.

Reference

Essig EO (1931) A history of entomology. The Macmillan Company, New York, 1029 pp

Lotic Community

A community of organisms dwelling in fast-moving water, such as rivers, as opposed to those dwelling in standing or slow moving water (lentic communities).

Louping Ill

Louping ill is a tick-transmitted viral disease affecting mammals and birds, but particularly sheep, in Great Britain.
► Ticks

Louse

The singular form of lice, these are ectoparasites of warm-blooded vertebrates. Often the lice, order

Phthiraptera, have been treated as two groups, chewing and sucking lice, which reflects major differences in their feeding behavior. However, they have common origins.

► Chewing and Sucking Lice
► Human Lice

Louse Flies

Members of the family Hippoboscidae (order Diptera).

► Flies

Lovebug, *Plecia nearctica* Hardy (Diptera: Bibionidae)

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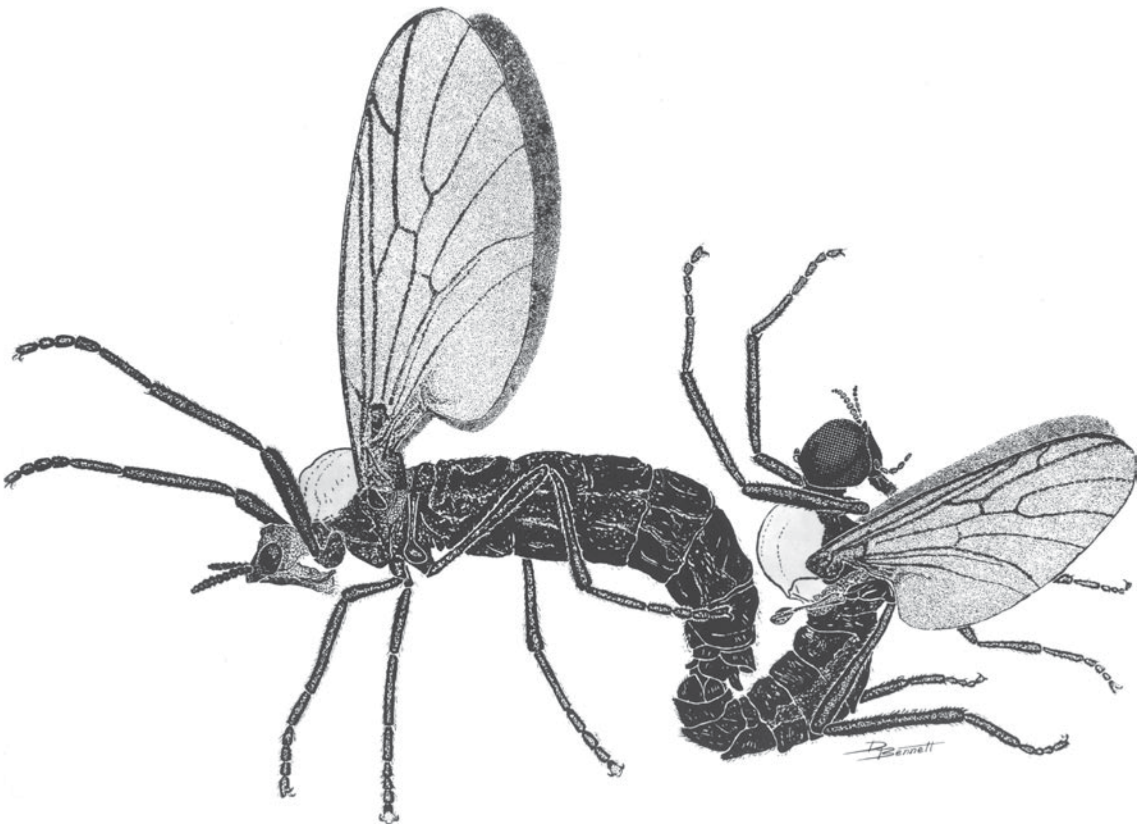
The lovebug is a seasonally abundant member of a generally unnoticed family of small flies related to gnats and mosquitoes. The males are about 6–7 mm and the females 6–9 mm in length, both entirely black except for red on the dorsum of their thorax. Other common names for this insect include March flies, double-headed bugs, honeymoon flies, and united bugs. Lovebugs characteristically appear in great abundance along the Gulf Coast of the USA as male-female pairs for only a few weeks every April-May and August-September. Although their range extends over a broad area, including south into Central America, their abundance varies greatly from place to place and from season to season. During the spring and autumn peak flight periods they can reach outbreak levels in some areas and yet be almost absent in others. Lovebugs are a nuisance pest, as opposed to destructive or dangerous, in areas where they accumulate in large numbers.

Lovebug Description and Biology

Lovebugs can be identified superficially as swarms of little black flies, each bearing a red thorax, that fly as pairs of males and females in tandem. Members of some related families contain pests of agriculture and vectors of pathogens that cause human and animal diseases (e.g., sand flies [Psychodidae], mosquitoes [Culicidae], biting midges [Ceratopogonidae], black flies [Simuliidae], fungus gnats [Mycetophilidae] and gall midges [Cecidomyiidae]) but bibionids are relatively harmless. Bibionids have antennae with seven to 12 segments and ocelli (simple eyes) on their heads. Their wings each have an undivided medial cell, a costal vein that ends at or before the wing tip, a large anal area and two basal cells. All members of the genus *Plecia* have an upper branch to the radial sector vein of the wing. The only two species of this genus in the U.S., *P. nearctica* and *P. americana* Hardy, are very similar in appearance. Males of both species are (Fig. 63) considerably smaller than females and have much larger compound eyes; *P. nearctica* males weigh 6–10 mg and females 15–25 mg. Both species and sexes have red dorsal thoraxes but *P. nearctica* has completely black pleura (sides of thorax) and a head with an oral margin distinctly extended forward. In contrast, the thorax of *P. americana* is almost completely red and rarely slightly brownish black on the metathoracic pleura (sides of third thoracic segment). The oral margin of the head does not extend forward but is evenly convex.

Other members of the family Bibionidae might be confused with the lovebug, particularly *Dilophus sayi* Hardy (= *Dilophus orbatus* Osten Sacken, = *Philia orbata* (Osten Sacken). However, *D. sayi* is clearly smaller than the *Plecia* species, completely black, much less abundant, and does not congregate noticeably on highways. Females are larger than males and have smoky brown rather than clear wings. The reproductive behavior of *D. sayi* is similar to that of the lovebug and in both species males and females can mate more than once. Unlike lovebugs, however, *D. sayi* adults do not disperse in pairs, instead males remain in the emergence areas while the females seek suitable oviposition sites. Females of *D. sayi* deposit 100–300 eggs that hatch in about 20 days. Under

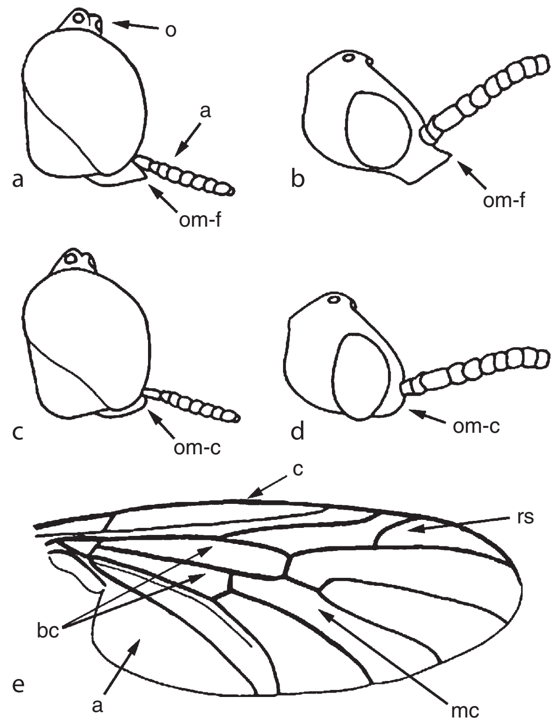


Lovebug, *Plecia nearctica* Hardy (Diptera: Bibionidae), Figure 63 **Pair of mating lovebugs with larger female on left. Note the elongated female rostrum (snout-like prolongation of the head) and large circular male eyes (drawing by Dwight Bennett).**

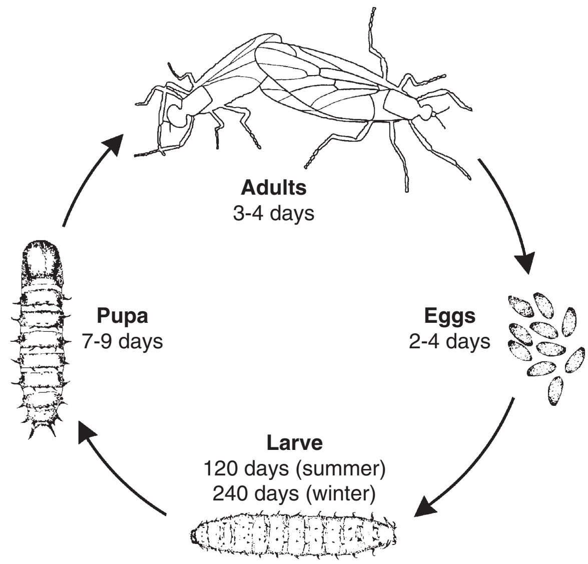
laboratory conditions, females live for about 72 hours, whereas males survive for about 92. Adults of this species are periodically considered a nuisance pest in the southern USA from South Carolina to Florida and across the Gulf States into Texas, and also in California.

Although the lovebug has two distinct generations per year over much of its range, adults can be found during most months. Higher temperatures cause adult populations to peak slightly earlier in the southern areas of the state. As in all other flies, lovebugs exhibit complete metamorphosis, having egg, larva, pupa and adult stages. An individual female deposits an average of 350 eggs under (Fig. 64) decaying vegetation in a grassy or weedy area with adequate moisture. Conditions must not be too wet or dry, although the larvae soon emerge and can move short distances to locate the best habitats. Larvae develop more rapidly at higher temperatures, so the summer generation is shorter than the one in the winter. The larvae feed on decomposing leaves and grass until they pupate. The pupal stage lasts 7–9 days. In nature, the adults live just long enough to mate, feed, disperse and deposit a batch of eggs, about 3–4 days.

Lovebug reproductive behavior occurs within three general activity periods during the day. The first period (8 A.M.–2 P.M.) begins with the insects moving up onto the plants and feeding on nectar. Lovebug flight is initiated when the air temperature reaches about 20°C and illumination is 1500–2000 ft-c. Males and females that coupled and mated late during the previous day fly into the air to disperse. Unmated males and females first couple and mate before dispersing. Mating begins



Lovebug, *Plecia nearctica* Hardy (Diptera: Bibionidae), Figure 64 **Taxonomic characters to distinguish *P. nearctica* from *P. americana*. Head of *Plecia nearctica* male (a) and female (b), head of *P. americana*, male (c) and female (d): ocelli (*o*), antenna (*a*), oral margin- forward (*om-f*), and oral margin- convex (*om-c*). Wing of *P. nearctica* (e): costa (*c*), radial sector (*rs*), medial cell (*mc*), anal cell (*a*), and basal cells (*bc*) (from Thompson 1975).**



Lovebug, *Plecia nearctica* Hardy (Diptera: Bibionidae), Figure 65 **Lovebug life cycle with the approximate duration and size of each stage (not drawn exactly to scale, adult pair 15.2 mm head to head). Drawings of the eggs, larva and pupa are from *P. plagiata* (Wiedemann) (Pinto 2002). In Florida, the lovebug has two generations each year, emerging as adults in April-May (winter generation, 240 days) and August-September (summer generation, 120 days).**

when swarms of 40 or more males form above the emergence sites, oscillating up and down rhythmically more than 6 m above the ground, even on windy days. These swarms last 10–30 min and end with the males eventually landing to rest or feed. Swarming peaks at 10–11 A.M. and again at 6–8 P.M. Larger males prefer positions at the bottom of a swarm. Individual females fly into a swarm and are grasped almost immediately by a male, after which the pair lands on vegetation to mate. Males prefer larger and heavier females, often grasping them before they fly into swarms or displacing attached males. In this competition for (Fig. 65) females, larger males are able to displace smaller ones about 20% of the time but success diminishes if the original male has been attached for a long time. Even if undisturbed, however, males and females often will disengage and mate a second time. After coupling, the male faces the opposite direction from the female within 1.5–10 min and the pair begins copulating. Insemination involves discharging the contents of the spermatophore into the spermatheca of the female.

During the second activity period (2–5 P.M.), single males and females are considerably less mobile but pairs continue to disperse. As in the morning, males swarm and grasp incoming females during the third period (5–8 P.M.) but at this point the pairs remain on vegetation throughout the night. Pairs that have been dispersing during the day also settle on vegetation when illumination falls below the 1500–2000 ft-c threshold, even though the temperature remains above 20°C. Lovebugs do not fly during the night. After a pair disperses, the male perishes and the female deposits as many as 600 eggs under decaying leaves or grass before also dying. Groups of about 300 larvae have been found on or near the surface of the soil among the roots of grasses.

Lovebug Myths

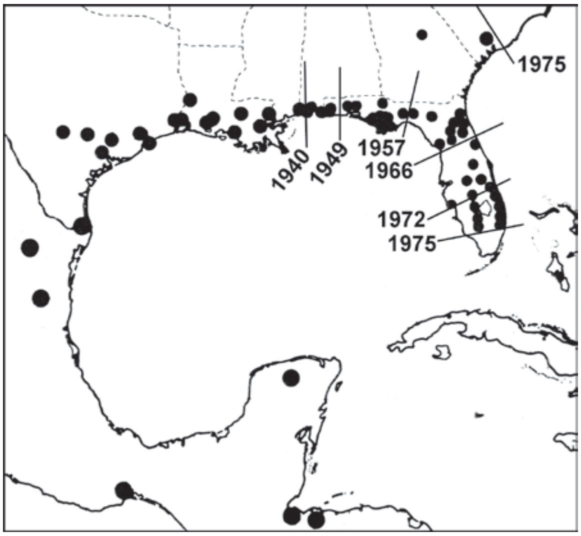
The invasion of the USA by the lovebug prompted development of much erroneous information about the origin and behavior of this species. This problem is exacerbated by the lack of research on this nuisance species. Following are some of the most common myths:

Lovebugs Escaped After University of Florida Researchers Brought Them Into Florida

Lovebugs are not native to most of the southern United States. Since 1940, *P. nearctica* has extended its range from Mississippi and Louisiana across the Gulf States, reaching Florida in 1949. In the late 1960s, it became established entirely across north Florida. During the 1970s, explosive populations occurred progressively southward nearly to the end of peninsular Florida and northward into South Carolina. Its movement may have been accelerated by prevailing winds, vehicle (Fig. 66) traffic, sod transport, increased habitat along highways and expansion of pastures - but not by university researchers.

University of Florida Researchers Genetically Engineered Lovebugs to Kill Mosquitoes

Lovebugs are small, slow herbivorous insects that feed on the pollen and nectar found in flowers. Thus, they lack the mandibles (jaws), grasping legs,



Lovebug, *Plecia nearctica* Hardy (Diptera: Bibionidae), Figure 66 **Pattern of migration of *Plecia nearctica* from Central America to the southeastern U.S. (from Buschman 1976).**

speed and other characteristics of predatory insects, such as dragonflies. Lovebugs are active during the day, whereas most mosquitoes are crepuscular (active at twilight) or nocturnal, and they are only adults for a few weeks each year. For these and many other reasons, the lovebug would be a poor candidate to genetically engineer as a mosquito predator, even if it were possible.

Lovebugs are Attracted to Automobiles

After mating, lovebugs disperse as coupled pairs, presumably flying in search of nectar on which to feed and suitable oviposition sites. Mated females are attracted to sandy sites with adequate moisture, dead leaves, grass clippings, cow manure and other decomposing organic debris. Lovebugs are attracted to anethole, an essential oil found in plants that also attracts bees. Female lovebugs are also attracted to UV-irradiated aldehydes, a major component of automobile exhaust fumes. They may confuse these chemicals with the odors emitted from decaying organic matter at typical oviposition sites. Heat has also been shown to attract lovebugs and contribute to their abundance on highways. Additionally, lovebugs seem to collect on light-colored buildings, especially when freshly painted. Many kinds of flies are attracted to light-colored and shiny surfaces, although the physiological or behavioral mechanisms are unknown. Thus, lovebugs apparently accumulate in relatively warm, humid, sunny areas with chemicals in the atmosphere that mimic feeding and oviposition sites.

Dispersing Lovebugs Move Great Distances and are Attracted to Homes

Lovebug pairs are not strong fliers, so tend to remain within a few hundred meters of emergence sites when there is little or no wind. They are able to move across the wind when it is 8–12 kph and search for sources of nectar and suitable oviposition sites. Stronger winds blow them as high as 450 m in the air and concentrate them against downwind objects. Coupled females initiate and control flight but males assist if they are able to obtain food. Locations within 30–50 km can have quite different levels of lovebug emergence and dispersal and this variable distribution can lead to naturally occurring “hotspots” in different places from year to year. Lovebugs are most abundant in moist grassy habitats. People who live near these habitats, or are exposed to winds that deposit the insects at their homes, can perceive erroneously that they are attracting these pests.

Lovebugs Mate the Entire Time They are Coupled

The general pattern of mating in lovebugs begins with males forming swarms above emergence areas each day in the morning and afternoon. Females emerge from the soil later than males, crawl on to vegetation, and fly into the swarms. A male may grasp a female before or after she flies into a swarm. In either case, the pair couples on vegetation and the male transfers sperm to the female. Sperm transfer requires an average of 12.5 hours but the pair usually remains coupled for several days during which they feed and disperse. The male ejects a depleted spermatophore after separating from the female and both sexes may mate again. Pairs formed during the morning hours begin dispersal flights, whereas those that couple in the evening remain in place on vegetation until taking flight the following day.

The Body Fluids of Lovebugs are Acidic and Immediately Dissolve Automobile Paint

When numerous lovebugs are smashed on the front of a vehicle, the contents of their bodies, especially eggs, coat the painted surface. No permanent damage is caused, however, if the surface is cleaned before the coating is baked by the sun for several days. Lovebugs are about neutral, with a pH of 6.5, but become acidic at 4.25 within 24 h. Yet, automobile paint may not be damaged after being coated with macerated lovebugs and held in a humid indoor environment for 21 days. A lovebug-coated surface exposed to the sun for an extended period of time, however, may be damaged by the insects and their removal. The front of a vehicle can be protected by coating it with wax and removing the lovebugs within 24 h.

Lovebugs Have no Significant Natural Enemies

No parasites have emerged from lovebug larvae or adults held in the laboratory and few cases of predation have been observed in nature over the years. Apparently lovebugs adults are avoided by red imported fire ants, *Solenopsis invicta* Buren and most other predators but periodically are eaten by spiders, dragonflies and birds. They have aposematic coloration that implies defensive mimicry but have not been chemically analyzed or tested as food for predators. Beekeepers report anecdotally that honeybees do not visit flowers infested with lovebugs. Fungal pathogens have been identified, six from larvae and one from adults, that could limit lovebug populations. These fungi include the well-known insect pathogenic genera, *Metarhizium*, *Beauveria* and *Conidiobolus*. Although not yet studied, lovebug eggs may be subject to predation or parasitism.

Insecticides are Effective in Controlling Lovebugs

Insecticides available to the public for controlling houseflies, mosquitoes and other flies will also kill adult lovebugs. However, there are risks associated with using these products around humans and pets, and the lovebugs will likely reinvade almost immediately. Other insects are often misidentified as being lovebugs, some of which are innocuous or beneficial and therefore should not be killed. It is important to preserve lady beetles, lacewings, honeybees and other insects that help to protect or pollinate plants. Thus, insecticides are expensive, potentially harmful and of no value in controlling lovebugs. It is best to avoid lovebugs if they become a nuisance during their brief appearances each year.

Lovebugs and People

It is possible but usually not necessary to avoid lovebugs and the problems they cause. Unlike some of their close relatives, lovebugs do not bite, sting or transmit diseases, and are not poisonous. Lovebugs are only active in the daylight and are much less mobile during the early and late daytime hours. Typically, the pairs fly across the wind during their dispersal flights and are blown against obstacles, especially vehicles traveling at high speeds. Their remains can be removed from surfaces easily if not left to bake in the sun. Lovebugs are poor fliers that can be kept out of a building by creating positive pressure with an air-conditioning fan. If a few lovebugs enter, a vacuum cleaner can be used to remove them. Screens can be added to windows and doors, particularly on the prevailing windward side of a building, and placed over decks and swimming pools. A fan can be used outside near work or recreational areas to keep lovebugs away. Due to their abundance and mobility, lovebugs cannot be controlled effectively with poisons or repellents.

People consider the lovebug to be among the peskiest alien invasive species to become established in the Gulf States. On the contrary, these potentially annoying flies are actually beneficial as larvae because they help to decompose dead plant material. People would also appreciate esthetic aspects of the adults, if these insects were not such a nuisance. Like migratory birds, lovebugs signal changes in the seasons from spring to summer and again from summer to fall. Moreover, if they were larger, people could easily see and admire their delicate features, particularly the big round eyes of the males. Wilhelm Rudolph Wiedemann named the genus *Plecia* for the lovebug and its relatives in 1828, so his concept for the term may never be known. A reasonable guess, however, is that he applied the Greek verb "pleo" intending to mean "to sail." Lovebugs sail from flower to flower much like butterflies, and in smaller numbers they could be perceived as beautiful. They have become less abundant over the past 30 years and people living in the Gulf States are beginning to accept them as a normal part of nature. However, newcomers tend to be intolerant of lovebugs until they learn that these pests are not dangerous. Because lovebug populations tend to rebound unpredictably, it is fortunate that these creatures create only minor inconveniences rather than threaten human health and the environment.

References

Buschman LL (1976) Invasion of Florida by the "Lovebug" *Plecia nearctica* (Diptera: Bibionidae). Fla Entomol 59:191–194

Cherry R, Raid R (2000) Seasonal flight of *Plecia nearctica* (Diptera: Bibionidae) in southern Florida. Fla Entomol 83:94–96

Hardy DE (1966) Family Bibionidae. In: A catalog of the Diptera of the Americas south of the United States. Departmento de Zoologia, Secretaria da Agricultura, Sao Paulo. vol 18, pp 1–20
Hetrick LA (1970) Biology of the "love-bug," *Plecia nearctica* (Diptera: Bibionidae). Fla Entomol 53:23–26
Leppla NC, Carlysle TC, Guy RH (1975) Reproductive systems and the mechanics of copulation in *Plecia nearctica* Hardy (Diptera: Bibionidae). J Ins Morphol Embryol 4:299–306
Leppla NC, Sharp JL, Turner WK, Hamilton EW, Bennett DR (1974) Rhythmic activity of *Plecia nearctica*. Environ Entomol 2:323–326
Thompson FC (1975) "Lovebugs," a review of the nearctic species of *Plecia* Wiedemann (Diptera: Bibionidae). USDA, Cooperative Economic Insect Report 25:87–91
Thornhill R (1976) Reproductive behavior of the lovebug, *Plecia nearctica* (Diptera: Bibionidae). Ann Entomol Soc Am 69:843–847

Lower Subterranean Termites

Members of the termite family Rhinotermitidae.

► Termites

Loxoscelism

An ailment caused by the bite of the brown recluse spider, *Loxosceles reclusa*. The spider occurs in south-central and southeast USA. It is not an aggressive spider, but when it inflicts a wound it sometimes causes persistent gangrenous necrosis, resulting in significant tissue destruction.

► Spiders

Lubber Grasshoppers

A family of grasshoppers (Romaleidae) in the order Orthoptera.

► Grasshoppers, Katydids and Crickets
► Eastern Lubber Grasshopper

Lucanidae

A family of beetles (order Coleoptera). They commonly are known as stag beetles.

► Beetles

Lugger, Otto

Otto Lugger was born at Hagen, Westphalia, Germany, on September 16, 1844. In 1865, after service in the military, he and his family moved to the United States. Initially he worked as an engineer, surveying the Great Lakes region. He always was interested in entomology, however, and became acquainted with C. V. Riley. When Riley became state entomologist of Missouri, he appointed Lugger to be his assistant. There he labored for several years, but in 1875 moved to Maryland to serve as curator of the Maryland Academy of Sciences. In 1885 he was appointed to the Division of Entomology of the United States Department of Agriculture, and in 1888 was appointed entomologist to the Minnesota Agricultural Experiment Station. The first challenge he faced in Minnesota was invasion of the area by the Rocky Mountain locust, but with the governor's backing the insects were destroyed and damage averted. Lugger published numerous articles on economic entomology, but also a detailed series on the insects of Minnesota. This important series of publications was unfortunately interrupted by his death on May 21, 1910.

Reference

Howard LO (1901) Otto Lugger. Entomol News 12:222–224

Luminescent

Producing light.

►Fireflies
►Fireflies: Control of Flashing
►Glowworms

Lutrochidae

A family of beetles (order Coleoptera). They commonly are known as robust marsh-loving beetles.

► Beetles

Lycaenidae

A family of butterflies (order Lepidoptera). They commonly are known as gossamer-winged butterflies, coppers, elfins, hairstreaks, blues, and harvesters.

► Gossamer-Winged Butterflies
► Butterflies and Moths

Lycidae

A family of beetles (order Coleoptera). They commonly are known as net-winged beetles.

► Beetles

Lyctocoridae

A family of bugs (order Hemiptera).

► Bugs

Lygaeidae

A family of bugs (order Hemiptera). They sometimes are called seed bugs.

► Bugs

Lygistorrhinidae

A family of flies (order Diptera).

► Flies

Lygus Bugs, *Lygus* spp. (Hemiptera: Miridae)

Bugs in the genus *Lygus* can be serious pests of plants, especially affecting blossoms and fruit.

► Potato Pests and their Management

Lymantriidae

A family of moths (order Lepidoptera). They commonly are known as tussock moths.

► Tussock Moths
► Butterflies and Moths

Lyme Borreliosis

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Lyme borreliosis and the clinical syndrome, Lyme disease, are currently epidemic throughout much of the northern hemisphere and are reported sporadically world-wide. Lyme disease is the most frequently reported vector-borne infection in the United States. This tick-borne bacterial zoonosis is maintained in rodent populations by hard ticks of the subgenus *Ixodes*. Human cases resulting from infection with the gram-negative spirochete, *Borrelia burgdorferi s.l.,* are largely a consequence of human encroachment into areas where the enzootic cycle is naturally maintained. The ticks that transmit this spirochete are largely opportunistic and will feed on a wide variety of hosts including mammals, birds and reptiles.

Clinical Manifestation

Clinical Lyme disease is remarkably variable, especially in the manifestations of chronic syndromes. Onset of "flu-like" symptoms occurs after a one to three week incubation period following transmission via tick bite. These symptoms are generally characterized by headache, fever, lymphadenopathy, myalgias, arthralgias, sore throat and stiffneck. Less frequent symptoms are malaise, fatigue, nausea and vomiting. Approximately 60–80% of people also exhibit a circular rash at the bite site, called erythema migrans (EM). The EM lesion generally expands in size and clears in the center giving the characteristic "bullseye" appearance. In addition, atypical or multiple lesions may appear away from the bite site. Without treatment, the EM and flu-like symptoms will resolve in several days or weeks. In some patients the disease appears to be self-limiting and no further symptoms appear. In other patients, chronic syndromes may start to appear within weeks or months. Chronic syndromes may range from mild to severe, involving neurologic, cardiac or arthritic manifestations. Treatment of early disease with 2–3 weeks of oral antibiotics (most commonly doxycycline or amoxicillin) will usually prevent onset of chronic symptoms. Treatment of chronic manifestations is much more complicated and controversial, and may involve multiple organ systems.

Etiology

Borrelia burgdorferi s.l. is a member of the Family Spriochaetaceae. These bacteria are Gram-negative, flagellated microaerophiles and have the typical helical shape of spirochetes. Considerable genetic variation is recognized in these spirochetes and has resulted in the recognition of at least three species in North America (*B. burgdorferi s.s.*, *B. bissettii*, *B. andersoni*), 5 species recognized in Europe (*B. burgdorferi s.s.*, *B. afzelii*, *B. garinii*, *B. lusitaniae*, *B. valaisiana*) and six species recognized in Asia (*B. japonica*, *B. turdae*, *B. afzelii*, *B. garinii*, *B. valaisiana*, *B. sinica*). In addition, application of a variety of molecular techniques is revealing that a considerable amount of genetic variation also occurs at the microgeographic scale. The high polymorphism of many of the protein encoding genes evaluated in these studies is not surprising in terms of the pathogen's ability to evade host immune response. In fact, differential correlation of variant genotypes with clinical Lyme disease may assist in the explanation for the broad variability in clinical manifestations of this disease.

In culture (in BSK growth media), these bacteria replicate by binary fission with a doubling time of 18–26 h at 33°C. However, pathogenicity appears to be lost during multiple passages and prolonged cultivation. It is hypothesized that this phenomenon is attributable to alterations or loss of plasmids known to contain genes that encode outer envelope proteins. In contrast to the logarithmic growth rate in culture, growth in the vector tick appears programmed. Following ingestion of the bacteria in a bloodmeal, spirochetes quickly multiply, adhere to the tick midgut wall and become dormant. The tick then completes digestion of the bloodmeal and molts to the next life stage (i.e., larva to nymph or nymph to adult). Maintenance of infection throughout this process is referred to as transstadial transmission. Dormant spirochetes become active soon after initiation of the next bloodmeal. The active bacteria traverse the midgut wall, enter the hemocoel and can be visualized near the salivary glands within 48 hours. Due to this feeding initiated activation step, the process of transmission is slow. Laboratory experiments have illustrated that transmission of the spirochete from infected tick to host does not occur within the first 48 hours of feeding following attachment.

Vectors, Hosts and Ecology

As is the case with many vector-borne diseases with a broad geographic distribution, the tick and vertebrate species involved in the maintenance of *B. burgdorferi s.l.* in enzootic cycles are geographically dependent. For example, *Ixodes scapularis* is the primary vector in the eastern United States, *I. pacificus* in the western US, and *I. ricinus* and *I. persulcatus* serve as the primary vectors in Europe and Asia, respectively. Despite this variability, these enzootic cycles exist nearly worldwide, even where clinical Lyme disease does not occur. The stability of these enzootic cycles is attributable to several ecological and biological factors. The primary factor responsible for the distribution of Lyme disease is the presence of a competent vector.

All recognized vectors of *B. burgdorferi s.l.* to humans are 3-host ticks. The significance of this observation is that all these ticks spend the majority of their existence off-host and exposed to environmental factors. Therefore, distributions of the vectors involved in the transmission *B. burgdorferi s.l.* have ecological limitations, which may include humidity, vegetative cover and/or soil composition. Ixodid, or hard ticks, have four life stages, the egg, larva, nymph and adult, with each stage other than the egg requiring a single blood meal before molting to the next stage. Sexual differentiation, in terms of morphology and behavior, only occurs in the adult stage. Females will take an enormous blood meal to produce a single batch of eggs. In the northeastern United States, this entire life cycle is generally completed in 2 years. In cooler climates, the life cycle may be extended, and in warmer climates the entire life cycle may be completed in as little as one year. The temporal distribution of these life stages is important in the intensity and maintenance of *B. burgdorferi* in an enzootic cycle. Larval ticks are rarely infective, with transovarial transmission rates (from female tick to her eggs) less than 1% in most vector species. Nymphal *Ixodes* ticks (1.0–1.5 mm long), having had the opportunity to become exposed to the spirochete during the first feeding as larvae, are widely considered to be responsible for the majority of human transmission. Their small size allows them to attach to the host and feed without being noticed for the 48 hours required for transmission. In addition, larval and nymphal (immature) *Ixodes* have the preference for the same hosts. In endemic regions in the United States, nymphal Ixodes may have infection rates of 40% or higher and precede larval ticks in the spring and early summer. This temporal stagger allows the small mammal hosts to be infected with *B. burgdorferi* from the nymphal ticks, and in turn become infective to the larval ticks that will subsequently feed. Adult ticks, although having had twice the opportunity to become infected as nymphal ticks, are relatively large and easily seen and felt by human hosts. Therefore, adult *Ixodes* are often discovered and removed from a human host within the first few hours of feeding and although capable, are rarely implicated in *Borrelia* transmission.

Where competent vectors are distributed, animal hosts play an enormous role in the intensity of transmission to man. Animal hosts tend to serve as either source of infection or as amplifying hosts resulting in high tick densities. Rodents (primarily *Peromyscus* in North America) become infected with *B. burgdorferi s.l.* while serving as hosts for ticks that have become infected from an earlier blood meal taken from an infective host. There is no evidence for animal-to-animal or tick-to-tick transmission. Infected rodents become important in the exacerbation of infection as they may support life-long infections of the pathogen and may therefore serve as the source of infection, or reservoir, for several generations of ticks. These small mammals however, usually only serve as hosts for the immature stages of the ticks. As adults, most tick species within the subgenus *Ixodes* will seek medium to large mammals as hosts. In eastern North America, white-tailed deer are notoriously involved in the maintenance of Lyme disease as each of these large mammals may serve as a host for hundreds if not thousands of female ticks, each of which will produce 3,000–6,000 eggs. Although egg batches and the resulting immature ticks may incur significant amounts of mortality due to desiccation, exposure or predation, if hosts are available tick populations have a tendency to explode. Host reduction or exclusion, primarily of deer, has been shown to significantly reduce tick densities within control areas.

Emergence, Expansion and Control of Lyme Disease

Lyme disease is recognized as an emerging disease, in particular with relation to range expansion. In the United States, this expansion is primarily recognized in the upper Midwest where the geographic range of the vector, *I. scapularis*, appears to be growing. This phenomenon is probably due, at least in part, to the transport of ticks on highly mobile hosts such as deer and birds. These ticks are rapidly relocated to new suitable habitats where they found populations that locally expand. Improved diagnosis and increased recognition of the clinical manifestations of this disease also contribute to the growing number of cases reported.

Control of Lyme disease is perhaps most effective at the level of the individual, by reducing exposure and evading tick bite. This is accomplished by either avoiding seasonal tick habitats or by following personal protection practices such as wearing long sleeves and pants, tucking pants into boots, and the use of acaricides and repellents, such as pyrethroid-based products that are readily available. Frequent tick checks and careful removal of attached ticks, to be kept for identification should symptoms occur, are appropriate preventative practices for individuals living or traveling through endemic regions. Timely treatment is salient to the prevention of chronic manifestations. Some success with area control has been illustrated with the use of barrier acaricides and host (i.e., deer) exclusion. Acaricide-treated bedding material for rodents has also proven effective at reducing ectoparasite loads on these hosts, theoretically reducing vector densities within control areas. In addition to vector reduction strategies, both canine and human vaccines are currently available. However, these prophylactics are still new and controversial, as the actual cause of the chronic syndromes associated with Lyme disease remain elusive. Although there is no human mortality directly associated with Lyme disease, the debilitation and loss of productivity associated with the chronic manifestations can be significant and deserve further scientific investigation.

References

CDC Lyme Disease Home Page. Available at http://www.cdc.gov/ncidod/dvbid/lyme/index.htm Accessed on January 1, 2002

Parola P, Raoult D (2001) Ticks and tickborne bacterial diseases in humans: an emerging infectious threat. Clin Infect Dis 32:97–928

Sonenshine DE (1993) Biology of ticks, vol 2. Oxford University Press, New York, NY, 465 pp

Lyme Disease

► Lyme Borreliosis

Lymexylidae

A family of beetles (order Coleoptera). They commonly are known as ship-timber beetles.

► Beetles

Lyonetiidae

A family of moths (order Lepidoptera). They commonly are known as lyonet moths.

► Lyonet Moths
► Butterflies and Moths

Lyonet Moths (Lepidoptera: Lyonetiidae)

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Lyonet moths, family Lyonetiidae, total 264 species, mostly Holarctic; actual fauna probably exceeds 600 species. There are three subfamilies: Cemiostominae, Lyonetiinae, and Bedelliinae. The family is part of the superfamily Yponomeutoidea in the section Tineina, subsection Tineina, of the division Ditrysia. Adults are minute to small (4–12 mm wingspan), with head roughened; haustellum naked; labial palpi short, slightly porrect; maxillary palpi 1-segmented (rarely vestigial); antennae with eye-caps. Wings elongated and hindwings linear with long fringes. Maculation typically white with a black, silvery or golden tornal spot. Adults mostly crepuscular and nocturnal. Larvae are blotch leafminers; rarely mining stems. Many plant groups are recorded as hosts. A few species are economic. The family and nominate genus Lyonetia are named after the French entomologist, Pierre Lyonet (1706–1789).

References

*Buszko J (1981) Lyonetiidae. In: Klucze do Oznaczania Owadów Polski. 27. Motyle-Lepidoptera. Polskie Towardzystwo Entomologiczne 27:42–58 (In Polish)

Emmet AM (1985) Lyonetiidae. In: Heath J, Emmet AM (eds) The moths and butterflies of Great Britain and Ireland. Harley Bks., Colchester, UK, 2:212–239, pl. 9–10

Kuroko H (1964) Revisional studies on the family Lyonetiidae of Japan (Lepidoptera). Esakia 4:1–61, pl. 1–17

Mey W (1994) Taxonomische bearbeitung der westpaläarktischen arten der gattung Leucoptera Hübner, [1825], s.l. (Lepidoptera, Lyonetiidae). Deutsche Entomologische Zeitschrift (n.s.)41:173–234

Real P (1966) Famille des Lyonetiidae. In: AS Balachowsky (ed) Traité d' Entomologie Appliquée à l' Agriculture Paris, 2:256–273

Lysis

The process of disinte grating a cell, which involves rupturing the membrane, breaking up the cell wall.

M

Machadorythidae

A family of mayflies (order Ephemeroptera).

► Mayflies

Machaerotidae

A family of bugs (order Hemiptera, suborder Cicadomorpha).

► Bugs

Machilidae

A family of bristletails (order Archeognatha).

► Bristletails

Mackenzie Globular Springtails

A family of springtails (Mackenziellidae) in the order Collembola.

► Springtails

Mackenziellidae

A family of springtails in the order Collembola. They also are known as Mackenzie globular springtails.

► Springtails

Macleay (Sir) William John

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William John Macleay was born on June 13, 1820, in Wick, Scotland. His parents died early and he had to discontinue his medical studies at Edinburgh University, and in 1839 he migrated to Australia. He accompanied his cousin, William Sharp Macleay (a son of Alexander Macleay, the founder of the greatest Australian natural history collection at the time, which later became known as the Macleay Collection and consequently the Macleay Museum). For about 16 years he lived in the rural Murrumbidge area of New South Wales, chiefly as a pastoralist and woolgrower. His interest in natural history was evident from an early age and he collected insects, many of which he described later on as new species. He also assisted his cousin in various curatorial tasks at the Macleay Collection, then housed in Elizabeth Bay House, in Sydney's Elizabeth Bay. When William Sharp Macleay died in 1865, the collection was entrusted to the care of William John, who left the Murrumbidge property and moved into Elizabeth Bay House. By then he took a very active part in politics, eventually serving seven successive parliaments over a period of 20 years. However, his main interest was natural history and within that entomology with coleopterology the focus. He became the main patron and benefactor of science of his time, amounting to about 100,000 pounds (a very large sum at that time), mainly spent on expanding and curating the collections, which contained more than a million specimens. In 1874 he and his friends laid the foundations of the Linnean Society of New South Wales. Several collectors hired by him worked the field, channeling a constant stream of specimens to the collections. George Masters was appointed as Curator, although Macleay himself described most species new to science. In 1875, he purchased the barque "Chevert" and organized a major expedition to New Guinea. In 1889 he was knighted, and two years later, on December 7, 1891 he passed away.

References

Fletcher JJ (1893) The Macleay memorial volume. Linnean Society of New South Wales, Sydney, pp 7–51

Musgrave A (1930) The history of Australian entomological research. Aust Zool 6:189–203

Macquart, Pierre Justin Marie

P. J. M. Macquart was born at Hazebrouck, France, in 1776. Much of the family was interested in natural history, so it is not surprising that Macquart became interested in insects. He served in the military starting at the age of 21, visiting Germany, Switzerland, and Austria, which provided an opportunity to collect specimens and books. Upon his return home in 1798 he devoted himself to his studies, and came to know the great French entomologist Latreille. He came to specialize in Diptera, publishing "Diptères du nord de la France" (1828–1833). He then was invited by Latreille to participate in a group effort, with Macquart handling the Diptera, which became known as "Histoire naturelle des Insectes Diptères." (1834, 1935). Macquart acquired the holdings of Meigen, and tackled the job of describing all the new species acquired by French naturalists from around the globe. In this monumental effort, he described 1,800 new species. He continued to publish updates of his work until his death in 1855.

Reference

Papavero N (1971, 1973) Essays on the history of Neotropical Dipterology with special reference to collectors (1750–1905). Museu de Zoologia, Universidade de São Paulo, São Paulo

Macrofauna

A term used to describe the larger of the soil invertebrates, usually in the body width size range of 2–20 mm. (contrast with microfauna and megafauna)

Macropsyllidae

A family of fleas (order Siphonaptera).

► Fleas

Macropterous

Having long wings. (contrast with brachypterous)

Macroveliidae

A family of bugs (order Hemiptera).

► Bugs

Maculate

This describes an object that is marked with irregular spots.

Maggot

An elongate, legless larva that lacks a well-developed head. This term usually is reserved for larvae of flies (Diptera).

► Flies

Maggot Therapy

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Maggot therapy, or maggot debridement therapy, is the medicinal use (biotherapy) of live fly larvae (maggots) for cleaning non-healing wounds and osteomyelitis (bone infection). Maggots debride, or clean, wounds by eating necrotic (dead) tissue. They secrete therapeutic chemicals such as ammonia and calcium carbonate, which disinfect wounds and promote healing. Only larvae that eat dead tissue (usually calliphorids from the genus *Lucilia*) can be used for medicinal purposes (Table 1). Obviously they must display no invasive behavior to living tissue.

For centuries, maggots have been used to help heal wounds. Historically, it has been military surgeons who noticed the benefits of maggot-infested wounds. One of Napoleon's surgeons noticed that maggots consumed only putrefying tissue and that they seemed to promote wound healing. The surgeon, Baron Dominic Larrey, stated that "during the progress of suppuration, the patients were only troubled by worms or larvae of the blue flies common in Syria although these insects were troublesome, they expedited the healing of the wounds by shortening the work of nature, and causing the sloughs to fall off." During the American Civil War, military surgeon W. W. Keen noted that "maggots were very common in summer – the resulting maggots were certainly disgusting but so far as I ever observed they did no harm." J. F. Zacharias of Cumberland, Maryland, USAMD, a surgeon for the Confederate Army, wrote, "I first used maggots to remove the decayed tissue in hospital gangrene and with eminent satisfaction. In a single day they would clean a wound much better than any agents we had at our command".

Maggot Therapy, Table 1 The species of flies used in maggot therapy (adapted from Sherman et al. 2000)

Family	Species
Calliphoridae	*Calliphora vicina*
	Chrysomya rufifacies
	Lucilia caesar
	Lucilia cuprina
	Lucilia illustris
	Lucilia sericata
	Phormia regina
	Protophormia terraenovae
Sarcophagidae	*Wohlfahrtia nuba*
Muscidae	*Musca domestica*

During World War I, soldiers with compound femur fractures and abdominal wounds, with the best of medical care, had only a 75% chance of survival. Those that had maggots in their wounds were more likely to survive. William Baer, an orthopedic surgeon at Johns Hopkins University, was the first physician in the USA to promote maggot therapy. His research and results were published posthumously by his colleagues in the *Journal of Bone and Joint Surgery* in 1931. By 1932, approximately 300 hospitals in Canada and the US were using maggot therapy to heal deep tissue wounds. Hospitals stopped using maggots in the 1940s as better antibiotics became available.

Though still useful, maggot therapy has been marginalized by the medical community, as has use of leaches and some other medical procedures, but occasionally these approaches remain very useful. Renewed interest in maggot therapy has been generated in response to an increase of chronic wound infections that are resistant to antibiotics. Chronic wound infection is a problem that costs billions of dollars worldwide. Wound tissue provides a perfect environment for proliferation of bacteria. Wound infection is compounded by the widespread occurrence of antibiotic-resistant "superbugs." Maggots secrete antibacterial activity against a range of these superbugs which include Gram-positive *Staphylococcus aureus*, both methicillin-resistant *S. aureus* (MRSA), and methicillin-sensitive *S. aureus* (MSSA), and *S. pyogenes*. Additionally, larval secretory products can withstand lyophilization (freeze drying) and long-term storage. These secretions may be a potential source of antibiotic-like compounds for treatment of MRSA.

Before use, medicinal maggots are sterilized internally and externally. Eggs from adult flies are sterilized in solutions containing formalin or mercuric chloride, alcohol, hydrochloric acid, dilute sodium hypochlorite or prolonged immersion in hydrogen peroxide. Hatched larvae are placed on a sterile food source and are ready to be used medicinally after two days of growth. Sterile maggots are placed on wounds within a cage-like structure or a sealed pouch for 2–4 days. The maggots are removed and new ones are applied as needed. Most patients, after an initial period of adjustment (as would be expected), adapt well to the presence of maggots.

Maggot therapy is generally limited to non-acute external wounds that have failed conventional treatment. Treatment is protracted, so if the ailment is life threatening, surgery is normally recommended rather than maggot therapy. Medicinal maggots provide three forms of benefit: debridement or elimination of dead tissue, disinfection of the wound by elimination of microbes, and promotion of wound healing. Elimination of necrotic tissue is easy to imagine, but the antimicrobial maggot exudates are more important in eliminating infection and in promoting wound repair. The species that have been used in maggot therapy are shown in Table 1. Interestingly, the species most commonly used, *Lucilia sericata*, is a pest to the sheep industry in some regions of the world. *Lucilia cuprina* must be used with care as it has a tendency to cause myiasis.

The actual application of maggots to a wound is rather simple. Prior to application, a hole matching the shape and size of the wound is cut out of a hydrocolloid pad, which prevents wound drainage from further contamination of surrounding healthy skin. Next, Dacron® chiffon is placed over the hole in the hydrocolloid pad, which creates a cage-like structure that prevents the maggots from crawling away. The dressing is further covered with a layer of gauze, which absorbs necrotic drainage from the wound. Sterile maggots, at a density of approximately 5–8 per cm^2, are placed on the wound for one 48 h cycle per week.

According the BioTherapeutics Education and Research Foundation, current use of maggots for wound therapy involves approximately 3,000 doctors, clinics and hospitals in over 20 countries, including Germany, Britain, Israel, Australia and Japan. In 2004, "medical maggots" were approved by the FDA as a medical device; however, only a single laboratory in California has been approved for production and distribution of medicinal maggots in the USA.

References

Baer WS (1931) The treatment of chronic osteomyelitis with the maggot (larva of the blow fly). Am J Bone Joint Surg 13:438–475

Kerridge A, Sappin-Scott H, Stevens JR (2005) Antibacterial properties of larval secretions of the blowfly, *Lucilia sericata*. Med Vet Entomol 19:333–337

Nigam Y, Bexfield A, Thomas S, Ratcliffe NS (2006) Maggot therapy: the science and implication of CAM, Part I – History and bacterial resistance. Evid based Complement Alternat Med 3:303–308

Sherman RA, Hall MJR, Thomas S (2000) Medicinal maggots: an ancient remedy for some contemporary afflictions. Annu Rev Entomol 45:55–81

Sherman RA, Pechter EA (1988) Maggot therapy: a review of the therapeutic applications of fly larvae in human medicine, especially for treating osteomyelitis. Med Vet Entomol 2:225–230

Mahogany Pests and Their Management

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Mahoganies are the source of an exceptionally valuable cabinet wood, and are widely considered the most economically important tropical timber trees in the world. Thus, the insects that attack mahoganies are of considerable economic importance. True mahoganies include three species of

Swietenia (family Meliaceae) that are native to the American Tropics. These are West Indies mahogany (*S. mahagoni* Jacquin), Honduras, or big-leaf, mahogany (*S. macrophylla* King), and Pacific mahogany (*S. humilis* Zuccarini).

West Indies mahogany is native to the Greater Antilles except Puerto Rico, with its native range extending north of the tropics proper to southern Florida and some islands of the Bahamas. Exploitation of West Indies mahogany began early in the European colonial period, especially in Cuba, Hispaniola, and Jamaica, and by the twentieth century the species was greatly depleted from natural areas by excessive logging. It remains a popular shade tree in urban areas of southern Florida, the Antilles, Bermuda, and other areas with a tropical climate, and potentially could be restored as a plantation or forest tree.

By the twentieth century, mahogany logging had largely shifted to Honduras mahogany, which is native to mainland Tropical America. This species occurs in lowland humid regions from about 23°N latitude on the Atlantic side of Mexico though Central and South America to about 18°S latitude in Bolivia. Currently, Honduras mahogany is the commercial source of almost all mahogany wood. It is being severely depleted in many areas, and research and conservation are greatly needed to conserve this species. Pacific mahogany is distributed in a narrow zone along the relatively dry Pacific.

Khaya is a genus closely related to *Swietenia* with about seven species distributed in Africa. These species are collectively known as African mahoganies. There are many similarities between *Swietenia* and *Khaya* in structure, utilization, and ecology including relationships with insects.

The family Meliaceae contains several additional genera and species of large tropical timber trees, notably *Cedrela* spp., known as cedros or tropical-cedars, an important local wood source throughout Tropical America, and *Toona* spp., which is widely distributed in Australia and East Asia. Some of these are hosts of the same or similar insects that attack mahoganies.

Hypsipyla spp. (Lepidoptera: Pyralidae: Phycitinae)

The most important pests of mahoganies are moths in the genus *Hypsipyla* (Lepidoptera: Pyralidae: Phycitinae), whose larvae bore into the shoots and seed capsules of mahoganies and their relatives. The genus includes one species in Tropical America and several in the tropics of the Eastern Hemisphere. The American species, *Hypsipyla grandella* (Zeller), is known as the mahogany shoot borer. It is considered the most important pest of mahoganies in the Americas because its damage can reduce growth in height and cause distorted growth of the main stem. Damage by this shoot borer is a major impediment to establishing and growing mahoganies in plantations. It is also a serious pest of mahoganies grown in nurseries for use as ornamentals. *Hypsipyla grandella* is distributed in southern Florida, the West Indies, northern Mexico southward through Central America, and South America except Chile. This distribution coincides with that of its host plant species, i.e., mahoganies and other tropical meliaceous trees.

Hypsipyla robusta (Moore) plays a similar role as an important shoot borer of African mahoganies and other meliaceous trees in the tropics of the Eastern Hemisphere. The distribution of *H. robusta* was formerly reported as extending from Africa to Tropical Asia, Australia, and some Pacific islands, but *H. robusta* as currently understood is a species complex and its taxonomy is being resolved. *Hypsipyla robusta* and perhaps other species of this complex have been variously referred to as the toona fruit and shoot borer, cedar tip moth, cedar shoot caterpillar, and also in some countries as the mahogany shoot borer. *Hypsipyla grandella* and *H. robusta* have been the subject of considerable research. Since the various species of *Hypsipyla* are very similar insects in appearance, biology, economic impact, and in the approaches to managing them as pests, this discussion will focus on *H. grandella*, which is the better known of the two species (Fig. 1).

The adults of *H. grandella* are grayish–brown in color with a wingspan measuring about 23–45 mm.

Mahogany Pests and Their Management, Figure 1 **Mahogany insects: (a) The larva of the mahogany shoot borer, *Hypsipyla grandella*; (b) A shoot of West Indies mahogany, *Swietenia mahagoni*, damaged by the mahogany shoot borer, *Hypsipyla grandella*; (c) A seed capsule of West Indies mahogany, *Swietenia mahagoni*, with boring damage of the mahogany shoot borer, *Hypsipyla grandella*; (d) The mahogany webworm, *Macalla thyrsisalis*; (e) The abaxial surface of a leaflet with the larva of the mahogany leaf miner, *Phyllocnistis meliacella* within the mine; (f) Leaf mines of the mahogany leaf miner, *Phyllocnistis meliacella*, in leaflets of West Indies mahogany, *Swietenia mahagoni* (photos by F.W. Howard).**

They are nocturnal and oviposit during the early morning hours on leaf scars, new shoots, leaf veins and fruits (seed capsules). The eggs hatch in several days. Recently emerged first instar larvae may begin feeding on the surfaces of the leaves or other plant parts, then bore into new shoots or seed capsules. The total development time including the larval, prepupal, and pupal stages, is usually one to two months and may be extended if the larvae undergo diapause.

Larvae that bore in shoots produce a tunnel of several centimeters in length and expel frass from the tunnel entrance as a reddish–brown mass which becomes intertwined with the insect's silk. The hollowed out portion of the shoot dies and the shoot buckles.

In southern Florida, where the rainy season usually begins in May or June, and the flush of West Indies mahogany takes place from April to June, *H. grandella* attacks shoots from early spring to mid-summer, with pronounced peaks in May. Population surges in spring, i.e., at the beginning of the rainy season, also have been observed in some studies in the tropics. But generally in the tropics, *H. grandella* is active all year with high shoot borer activity typically coinciding with flushes of mahoganies subsequent to periods of high rainfall.

Hypsipyla grandella also attacks seed capsules of mahoganies and cedros, penetrating between the valves of the capsules when they have dehisced. There they bore into seeds and hollow them out, after which they bore into the core of capsules. The pupal stage takes place inside the hollowed portions of the twig or seed capsule, or in the leaf litter or soil beneath host trees.

Damage. Mahogany trees are susceptible to attack beginning when they reach a height of about 0.5 m. The shoot borers may attack both the terminals of side branches and the leader (central terminal). Boring of the leader causes the more serious damage to the form of the tree, because this breaks apical dominance, resulting in excessive side-branching, and more importantly, in the replacement of the leader with one or more lateral branches and thus the formation of a crooked main stem. Small trees whose terminal shoots are attacked repeatedly in successive years become extremely deformed. Because attacks ultimately result in a reduction in the number and length of straight, clear logs, *H. grandella is* a major pest of mahoganies, cedros, and some other meliaceous tropical trees grown as timber. Mahogany shoot borer attack reduces the grade and thus the monetary value of young mahoganies grown in nurseries for use as shade trees, their chief use in southern Florida and urban areas in various tropical countries.

Damage to seeds by *H. grandella* has usually been regarded as unimportant or second in importance to the damage to the shoots, as seeds are thought to be produced abundantly enough to compensate for losses to the shoot borer. However, in a study in southern Florida, *H. grandella* attacked up to 100% of the seed capsules of West Indies mahogany trees and consumed 50–96% of the seeds per capsule. During the same period, only 14–22% of new shoots on the same trees were attacked. The impact of this insect on regeneration should be investigated further, especially in natural areas and managed plantations.

Management. Considerable research has been conducted to develop methods of managing *Hypsipyla* shoot borers. This insect is notoriously difficult to control, primarily because although some methods reduce the pest population considerably, even light populations can cause significant damage. In fact, destruction of the leader, which is the most critical damage, is caused by a single larva.

A review of published information on chemical control of *Hypsipyla* spp. shoot borers reported that after more than eight decades of research in 23 tropical countries there is still no reliable, cost-effective, and environmentally sound chemical control method available to prevent economic damage by these insects. However, chemical control of these pests might be appropriate in nursery situations.

About 40 species of insects have been identified as natural enemies of *H. grandella* in the Americas. As a natural enemy complex, they undoubtedly are important in regulating populations of this insect, but their effect is generally insufficient to prevent economic damage.

Mahoganies growing at low densities in mixed forests are generally less frequently attacked by *H. grandella* than mahoganies in pure plantations. This and other ecological principles have been applied in silvicultural techniques to reduce shoot borer damage, with varying degrees of success.

In testing different provenances of mahoganies and cedros, less damage has been seen in some selections. Research to identify genetic strains of these trees that are resistant or that can overcome shoot borer attack has progressed well.

An international workshop on *Hypsipyla* shoot borers held in 1996 (online at http://aciar.gov.au/web.nsf/doc/JFRN-5J472Q), in which 36 papers were presented, concluded that the strategies most promising for management of these pests involved identification and use of resistant genotypes, and silvicultural methods, viz., growing mahogany and cedro trees in mixed rather than pure stands and under an established canopy. It was also emphasized that vigorous growth of young trees should be promoted by cultural methods in the nursery and in young plantations. Chemical control was seen as a tool for temporarily reducing shoot borer populations in limited areas.

In addition to *Hypsipyla* species, several other insect species that are specific feeders on mahoganies and close relatives sometimes cause significant damage. In the Americas, these include a defoliator, a leaf miner, a bark weevil, and a scale insect (Fig. 2).

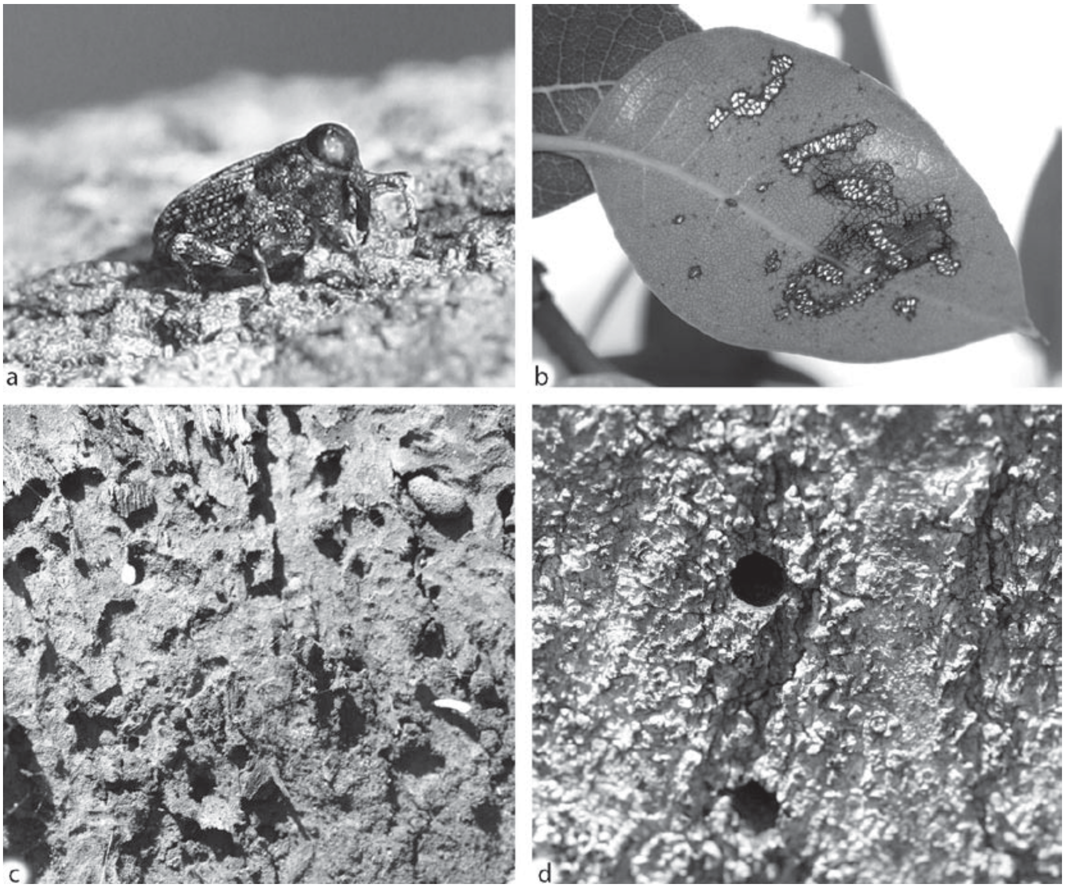
Mahogany Webworm, *Macalla thyrsisalis* Walker (Lepidoptera: Pyralidae: Epipaschiinae)

The mahogany webworm is a defoliator of mahoganies reported from throughout most of the range of mahoganies in the Americas. Nearly all records in Tropical America are based on trap catches of the adult, with no data on the larva and its hosts. It has not been reported as a pest except in southern Florida, and the biology of this species has been studied only in that locality.

The adult is a small gray–brown moth with whitish hindwings. They are probably nocturnal. Their peak flight period is in late winter or early spring prior to the annual flush of mahoganies. The eggs have not been observed in nature, and possibly are eaten by the recently hatched larvae, as is known in many Lepidoptera. The larva has a vivid yellow ground-color and lateral bands that consist of three narrow black stripes alternating with two white stripes. Each larva spins a web to pull several leaves together, and remains partially hidden in the resulting leaf cluster, consuming laminar tissue from the margins of leaflets inward, leaving the midveins intact. The larval stage is completed in about 10 days, and multiple generations may be produced during the spring season, so that by mid-spring webworm populations may consist of larvae in early and late instars. As with the mahogany shoot borer, their presence on their host trees coincides with the period of spring flush and leaf expansion of mahogany. The webworm larvae feed on young leaves before they have matured and hardened off. Dense populations of these caterpillars may entirely strip a tree of foliage.

In southern Florida, several years of annual spring outbreaks of mahogany webworms have alternated with periods of years in which populations are diminished, but there has been no long-term monitoring to record the patterns of outbreaks. Possibly, outbreak cycles of mahogany webworm are related to cycles of their parasitoid populations. In southern Florida and presumably throughout its native range, the mahogany webworm is under natural control. A fly, *Lespesia* n. sp. (Diptera: Tachinidae) and two species of wasps, *Habrobracon* sp. and *Apanteles* sp. (Hymenoptera: Braconidae), are parasitoids of mahogany webworm in southern Florida.

When parasitoids and other natural control factors fail to adequately control mahogany webworms, landscape or nursery managers may resort to chemical control. In the interest of discovering a safe treatment with minimal negative environmental effects, a study was conducted involving foliar applications of a neem product. It was



Mahogany Pests and Their Management, Figure 2 **More mahogany insects: (a) The mahogany bark weevil, *Copturus floridanus*, resting on bark of the West Indies mahogany, *Swietenia mahagoni*; (b) A leaflet of West Indies mahogany, *Swietenia mahagoni*, with feeding damage of the adult mahogany bark weevil, *Copturus floridanus*; (c) Galleries of the mahogany bark weevil, *Copturus floridanus*, beneath the bark of West Indies mahogany, *Swietenia mahagoni*. A cocoon is at upper right in photograph; (d) Exit holes of the mahogany bark weevil, *Copturus floridanus*, in the bark of West Indies mahogany, *Swietenia mahagoni* (photos by F. W. Howard).**

determined that the product acted as an antifeedant against this pest, and when applied early in the development of an infestation, it prevented mahogany webworm attack on the treated trees.

Mahogany Leafminer, *Phyllocnistis meliacella* Becker (Lepidoptera: Gracillariidae)

The mahogany leafminer attacks foliage of Honduras and West Indies mahogany, cedro, and probably some other meliaceous trees. It was described from specimens from Honduras mahogany in Costa Rica, and during certain years is common on West Indies mahogany in southern Florida. More recently this species was listed as an insect on cedro in Tamaulipas, Mexico. Although not reported elsewhere, it is probably widely distributed throughout the range of mahoganies in the Americas, but seldom noticed. In fact, an unidentified leaf mine identical to that of *P. meliacella* is visible in a photo of leaves of *Cedrela odorata* in Venezuela in a paper on mahogany shoot borer published 12 years prior to the publication of the taxonomic description of *P. meliacella*.

The adult of the mahogany leafminer is a minute white moth about 2 mm long from the apex of the head to the folded-back wings. The apodous, wormlike, white larva consumes leaf mesophyll, creating a winding gallery in the leaflet (mahoganies leaves are compound, with 5–7 leaflets) that eventually terminates in the leaflet margin, which the larva rolls. Pupation takes place within the rolled margin. Several hymenopterous species are parasitoids of the mahogany leafminer in Florida.

The mahogany leafminer is generally considered a minor pest at most, and has received little study. In observations in a research planting in Florida during spring 1993, which was a year when mahogany leafminer damage was relatively extensive, 62% of the leaves of young West Indies mahoganies had at least one leaf mine made by this insect, and 8.8–12.4% of the leaflets were mined. The amount of leaf tissue consumed by one larva is undoubtedly very small, but mined leaflets become distorted and stunted and may be shed early. Nevertheless, the effects on tree vigor of mahogany leafminer damage, even when populations are high, are presumably negligible. In a test of a neem product to control mahogany shoot borer, the treatment suppressed shoot borer attack and also acted as a preventative against mahogany leaf miner damage, but treatments applied specifically to control the leafminer would probably seldom be economically justifiable.

Mahogany Bark Weevil, *Copturus floridanus* (Fall) (Coleoptera: Curculionidae)

The mahogany bark weevil is reported in the Bahamas, Cuba, and southern Florida. The adult weevils are about 4–6 mm long and 3 mm in width, and dark grey–brown, with patches of fine whitish speckling on the elytra. Their coloring and texture blend well with the bark of mahogany, upon which they rest for long periods during the day, flying quickly when disturbed. They are often seen feeding on the leaf lamina, leaving closely grouped small feeding holes, which eventually become surrounded by brown necrotic leaf tissue. The females bore similarly small holes through the bark to the cambium, then turn around and oviposit in them.

The larva is small, apodous, ivory colored, and has the typical c-shape of weevil larvae. They feed in the cambium of mahoganies, producing winding galleries, and construct a cell in which they pupate. Development is completed in three to six months. Adults and larvae are present all year in Florida.

The feeding damage of the adult weevils on the leaves of a mahogany tree serves as an indicator that the mahogany bark weevil adults are present in the area, but does not necessarily imply that the same tree is infested with bark beetle larvae. A mahogany bark beetle infestation may result in the formation of drops of a reddish–brown resinous exudate on the bark, although these may be a result of almost any kind of injury to mahogany stems. The presence of round exit holes of about 3 mm in diameter in the bark is a stronger indicator that a tree is infested with the larvae. The holes indicate that weevils have completed development in the tree and it can ordinarily be assumed that additional weevils are still in the larval stage beneath the bark. In Florida, mature mahogany bark weevils are commonly seen in low numbers on the bark of mahoganies in plantings where there is no visible borer damage to mahogany trees except for exit holes in or near dead branches. Extensive damage to the main stem appears to occur mostly on stressed trees, as when trees are severely damaged by hurricanes or growing under excessively wet conditions. Mahogany saplings transplanted during drought periods are said to be highly susceptible to attack. Thus, like stem borers in general, the mahogany bark weevil is regarded as a secondary pest which can be managed by horticultural or silvicultural techniques.

West Indies Mahogany Scale, *Conchaspis cordiae* Mamet (Hemiptera: Conchaspididae)

Mahoganies tend to be relatively free of scale insects, but West Indies mahoganies were recently found to be highly infested with West Indies mahogany scale, over a broad area of southern Florida, where this scale insect was apparently accidentally introduced. This species, which is in the small and relatively unstudied tropical scale insect family Conchaspididae, is native to several islands of the Caribbean, where it is apparently under natural control factors. In Florida, 5–8% of scale coverings of *C. cordiae* had parasitoid exit holes, and a parasitoid, *Marietta* sp., was reared from this scale insect.

Although this scale insect has been reported on mahoganies, *Cordia* sp. and seagrape (*Coccoloba uvifera* L.) in its native range, it has been observed only on mahoganies in Florida, and shows a strong preference for West Indies mahogany as compared to Honduras mahogany and *Khaya nyasica* (Stapf.). Heavy infestations occur on twigs and branches of up to about 6 cm in diameter, but no more than light infestations have been seen on larger branches and main stems. Although it has become widely disseminated in southeastern Florida, it has not yet caused serious damage to mahoganies.

Other Insects

In addition to the above insects, which are specific to mahoganies and their close relatives, some insect pests of mahoganies are polyphagous species whose host ranges include mahoganies. These include various species of ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) that bore the twigs or main stems, and species of Scarabaeidae whose adult beetles feed on the leaves.

Although mahoganies are acknowledged as the most important tropical timber trees in the world and there has been much interest in their genetics and breeding, there is almost nothing known concerning their pollination, except for results of some observations in southern Florida indicating that the pollen of West Indies mahogany is adapted to entomophily, and various species of thrips (Thysanoptera) are abundant in mahogany flowers and apparently transfer the pollen between flowers. No other insects have been implicated as potential pollinators of mahoganies in southern Florida. However, southern Florida is where the West Indies mahogany is isolated at the northern extreme of its natural range, and can be considered a recent arrival in the context of geological time. Possibly, within the principal range of mahoganies in the tropics, pollination of mahoganies is accomplished by other insects. That there is an effective pollination system present in Florida is evident in that mahoganies here are typically highly productive of fruits, i.e., seed capsules.

Research on insects associated with mahoganies has focused almost entirely on *Hypsipyla* spp., with far less attention to the other pests noted in this discussion. In the natural habitats of mahoganies, there are undoubtedly many additional species of insects associated with them that have not been studied.

References

Floyd RB, Hauxwell C (2001) *Hypsipyla* shoot borers in Meliaceae. In: Floyd RB, Hauxwell C (eds) International Workshop on *Hypsipyla* Shoot Borers in Meliaceae, ACIAR Proceedings No. 97, 20–23 August 1996

Howard FW, Nakahara S, Williams DS (1995) Thysanoptera as apparent pollinators of West Indies mahogany, *Swietenia mahagoni* (Meliaceae). Ann Sci Forest 52:283–286

Howard FW, Hodges GS, Gates M (2006) First report of *Conchaspis cordiae* (Hemiptera: Conchaspididae) in Florida and the United States. Fla Entomol 80:102–104

Lamb FB (1966) Mahogany of tropical America. Its ecology and management. University of Michigan Press, Ann Arbor, Michigan

Lugo AE, Alayaon M, Figeroa JC (2002) Big-leaf mahogany: genetics, ecology, and management. Springer, Berlin Heidelberg New York

Mayhew JE, Newton AC (1998) The silviculture of mahogany. CABI Publications, Wallingford, United Kingdom

Wylie FR (2001) Control of *Hypsipyla* spp. shoot borers with chemical pesticides: a review. Pp. 109–115 In: Floyd RB, Hauxwell C (eds), International Workshop on *Hypsipyla* Shoot Borers in Meliaceae, ACIAR Proceedings No. 97, 20–23 August 1996

Maindroniide

A family of silverfish (order Zygentoma).

► Silverfish

Maize (Corn) Pests and Their Management

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In some English speaking countries, principally USA, Canada and Australia, maize is known as corn. Maize, *Zea mays*, is one of the world's most important cereal grains. More maize is produced than wheat or rice, though because much of the maize is fed to livestock or used for industrial purposes, more people are directly dependent on these other grains. Nevertheless, maize is a tremendously important crop, particularly in the Americas, China, and parts of Africa.

Maize was domesticated in Mesoamerica, probably in Mexico, sometime between 7,500 and 12,000 years ago. Its origin is obscure, but seems to be derived from a small-seeded wild *Z. mays* subspecies known as teotsinte. Small teosinte-like cobs have been found in caves that date back to about 2750 B.C., but later, beginning about 1500 B.C., this grain began to be dispersed widely in the Americas. It became a staple of the indigenous peoples not only in Mesoamerica, but also in North and South America and the Caribbean. When Europeans (starting with Christopher Columbus) made contact with the Americas they quickly recognized the value of maize, and it became introduced to many areas of the world, where it is grown in all but the coldest and driest regions. In 2002, for example, over 70 countries harvested at least 100,000 ha of maize. The major maize producers (2005 data) were USA, China, Brazil, Mexico, Argentina, and Indonesia, which accounted for 40.5, 18.9, 5.0, 3.0, 2.9, and 2.2% of the world's production, respectively. Thus, though some maize is grown almost everywhere, most of the production is concentrated in a few countries. Note that a considerable amount of maize is grown in southern Europe, but it is easy to underestimate its significance in this region because many small countries are involved in its production.

Maize is a productive plant, and is rich in many of the nutrients needed by humans and livestock. However, alone it does not provide completely balanced nutrition. Early Americans supplemented their maize consumption with beans, fish, meat, and other grains to obtain a complete range of amino acids. They also liberated the niacin found in maize through the addition of wood ash or lime. Failure to take the steps to provide balanced nutrition in maize-dependent diets results in severe nutrient deficiency.

Maize is a tall grass, and some varieties surpass 7 m in height. Male flowers are found at the apex of the stem, in a structure called the "tassel." Pollen from the tassel falls or blows to the "silk," which are elongated stigmas that protrude from the female inflorescence, or "ear." Once on the silk, the pollen produce pollen tubes that grows the length of the silk, resulting in pollination. Pollination results in expansion of the individual fruits or "kernels" on the ear. They are attached to a pithy core called a "cob," and generally occur in rows. Ears usually contain 200–400 kernels. Different varieties produce varying sizes and numbers of ears and kernels, and kernels with differing properties, allowing the grain to be used for several purposes. Maize has long been used to feed livestock (as grain corn which uses the kernels, or silage corn which also uses the stalk and foliage), as corn flour for baking, as popcorn, and as a sweet vegetable called "sweet corn." Increasingly, however, it is being used as a source of fructose for sweetening, or fermented and distilled as ethanol for production of liquor or as a gasoline additive.

Maize removes a considerable amount of nutrients from the soil, and is often grown as part of a crop rotation with a soil-replenishing legume crop such as alfalfa or soybean, and with a small grain crop such as wheat or barley. Nitrogen fertilization is normally required. Maize is not tolerant of cold weather, so in temperate areas it is planted after all danger of frost is past. It is tolerant of drought, but must have adequate moisture during the pollination period. Sugar-rich maize varieties harvested as sweet corn are harvested soon after kernel formation, before starch has begun to form. For silage, the maize may be harvested any time before it dries. For grain production, the ears and kernels are allowed to remain on the plant until they are very dry, which is late fall or even winter.

As one would expect of a crop grown on extensive acreage and in most regions of the world, many pests have adapted to the crop. Some of the most important are shown in Table 2.

Although there are numerous pest species, for an overview of the pests and their management, most can be grouped together with similar species based on their feeding behavior. The principal groups are stem borers; rootworms; earworms; armyworms; cutworms; aphid, leafhopper, delphacid plant disease vectors; and mites.

Stem Borers

Stem borers are the most important pests of maize wherever it is grown. Most are in the order Lepidoptera, and usually in the families Noctuidae or

Maize (Corn) Pests and Their Management, Table 2 Some important arthropod pests of maize (corn) and places where they are damaging

Feeding behavior	Primary taxon	Common name	Scientific name	Location
Foliage (leaf), chewing	Lepidoptera	Fall armyworm	*Spodoptera frugiperda*	Americas
		African armyworm	*Spodoptera exempta*	Asia, Africa
		Common armyworm	*Pseudaletia unipuncta*	Asia, Europe, Africa, America
		Maize webworm	*Marasamia trapezalis*	Africa
	Coleoptera	Grey weevils	*Tanymecus* spp.	Asia, Europe
Foliage, piercing-sucking	Hemiptera	Corn leaf aphid	*Rhopalosiphum maidis*	Asia, Europe, Africa, America
		Corn delphacid	*Peregrinus maidis*	Americas
		Corn leafhopper	*Dalbulus maidis*	Americas
		African leafhopper	*Cicadulina* spp.	Africa
		Chinch bug	*Blissus leucopterus*	N. America
	Acarina	Twospotted spider mite	*Tetranychus urticae*	Asia, Europe, Africa, America
		Banks grass mite	*Oligonychus pratensis*	C., N. America
Stalk, chewing	Lepidoptera	European corn borer	*Ostrinia nubilalis*	Asia, Europe, Africa, N. America
		Asian corn borer	*Ostrinia furnacalis*	Asia
		Lesser cornstalk borer	*Elasmopalpus lignosellus*	Americas

Maize (Corn) Pests and Their Management, Table 2 Some important arthropod pests of maize (corn) and places where they are damaging (Continued)

Feeding behavior	Primary taxon	Common name	Scientific name	Location
		Southwestern corn borer	*Diatrea grandsiosella*	N., C. America
		Neotropical corn borer	*Diatrea lineolata*	C., S. America
		Sugarcane borer	*Diatrea saccharalis*	Americas
		Asiatic rice borer	*Chilo suppresalis*	Asia
		Spotted stem borer	*Chilo partellus*	Asia, Africa
		Pink stem borer	*Sesamia cretica*	Africa
		African pink stem borer	*Sesamia calamistis*	Africa
		Mediterranean corn borer	*Sesamia nonagroides*	Europe
		Asiatic pink stem borer	*Sesamia inferens*	Asia
		African maize stalk borer	*Busseola fusca*	Africa
		African sugarcane borer	*Eldana saccharina*	Africa
		Potato stem borer	*Hydraecia micacea*	Asia, Europe, N. America
		Cutworms	Various	Asia, Europe, Africa, Americas
		Termites	*Microtermes* spp.	Africa, Asia
	Diptera	Frit fly	*Oscinella frit*	Europe
		Shoot flies	*Atherigona* spp.	Asia, Africa
	Coleoptera	Epilachna beetle	*Epilachna similis*	Africa
Ear, chewing	Lepidoptera	Corn earworm	*Helicoverpa zea*	Americas
		Corn earworm	*Helicoverpa armigera*	Asia, Africa
		Western bean cutworm	*Loxagrotis albicosta*	N. America
	Diptera	Cornsilk fly	*Euxesta* spp.	Americas
	Coleoptera	Dusky sap beetle	*Carpophilus lugubris*	Americas
Roots, chewing	Coleoptera	Western corn rootworm	*Diabrotica virgifera*	Americas, Europe
		Northern corn rootworm	*Diabrotica barberi*	N. America
		Wireworms	Various	Asia, Africa, Europe, Americas
		White grubs, chafers	*Phyllophaga, Cyclocephala, Melolontha* spp.	Asia, Europe, Americas

Maize (Corn) Pests and Their Management, Table 2 Some important arthropod pests of maize (corn) and places where they are damaging (Continued)

Feeding behavior	Primary taxon	Common name	Scientific name	Location
		Seedcorn beetle	*Stenolophus* spp.	N. America
		Flea beetles	*Chaetocnema* spp.	N. America
	Diptera	Seed fly	*Delia platura*	N. America. Europe, Asia

Pyralidae. Initially they feed on the foliage, but then move into the stems and affect movement of water and nutrients. Fungi, particularly *Fusarium* spp., gain access to the plants through the openings created by borers, leading to various rots and the occurrence of mycotoxins. When they bore into the base of the ear they can cause ear drop. In North America and Europe, the most important stalk borer is European corn borer, though some European countries also suffer from Mediterranean corn borer. Similarly, portions of North and Central America are affected by southwestern corn borer. In South America, the sugarcane borer and the lesser cornstalk borer predominate. In Africa, the African stalk borer and spotted stem borer are most important, but pink stem borer and sugarcane borer also can be important. In Asia, the most important species are Asian corn borer, Asiatic rice borer, Asiatic pink stem borer, and spotted stem borer.

Rootworms

Corn rootworm larvae feed on the roots and base of the stem. They disrupt water and nutrient uptake, and cause plants to lodge (fall over), making harvest difficult. Adults also feed on foliage and silks, sometimes interfering with pollination, but this generally is not very important. Historically, the *Diabrotica* rootworm problem was mostly a North American issue, though causing some damage in Central and South America. However, western corn rootworm was discovered in Yugoslavia in 1992, and has since spread through several countries in Europe. More insecticide is used in North America for suppression of corn rootworms than is used for control of any other insect pest on any crop, and 80% of the insecticides used in North America on corn is directed to corn rootworms, so the effect on Europe of the establishment of western corn rootworm is potentially great. In the USA, other corn rootworm species can inflict damage, but none are as important as western corn rootworm.

Corn Earworms

The corn earworm found in the Americas, *Helicoverpa zea*, can be a extremely damaging insect on sweet corn, though it is of lesser significance on field corn. In the old world, *Helicoverpa armigera* is the corn earworm of importance. These insects feed on both silk and within the ears, with the latter being of importance. Due to their feeding habits, sweet corn has a low tolerance threshold, so a great deal of insecticide is used against these insects during sweet corn production. Damage by these insects also facilitates entry of plant pathogens. These are not the only earworms, of course, but other ear feeders such as western bean cutworm are not nearly as important.

Armyworms

Most armyworms, *Spodoptera* and *Pseudaletia* spp., attack maize at intermediate stages in the growth of the plant, during the whorl stage. They can cause extensive defoliation and occasionally affect the ear. In tropical and subtropical areas of the Americas they can be the most severe problem, and often cause injury annually.

Cutworms

These insects affect mostly the seedling stage, severing the shoot at the soil surface, and often killing the young plant. A large number of noctuids possess this feeding habit, but the most important is black cutworm, *Agrotis ipsilon*. This species overwinters in subtropical areas throughout the world, but disperses to more temperate areas early each spring, causing considerable damage to young corn plantings.

Aphids, Leafhoppers and Delphacids

Alone, aphids (Hemiptera: Aphididae), leafhoppers (Hemiptera: Cicadellidae), and delphacids (Hemiptera: Delphacidae) are not usually very damaging to maize. However, because they can vector plant viruses, they can become quite important. For example, although corn leafhopper, *Dalbulus maidis*, can cause plant wilting due to direct feeding injury, its principal effect is to vector disease such as maize rayado fino virus, maize bushy plant mycoplasma, and corn stunt spiroplasma. Likewise, an African species of Delphacidae, *Peregrinus maidis*, that has become redistributed around the world in tropical and subtropical areas transmits maize mosaic virus and maize stripe virus.

Mites

Mites are severe pests of maize mostly in arid areas or under dry conditions. However, dry land production is common with maize, and mites can become the dominant pest in such situations. Also, under irrigated conditions in dry environments, mite problems develop when the weather is unusually dry or dust is abundant. Along unpaved roadways, for example, the large amounts of dust produced by vehicles can be lethal to predatory insects while mites harbored beneath a layer of silk on the foliage are protected from the desiccating effects of dust. Mites are often resistant to chemical insecticides, and there is risk of their populations flaring up when insecticides are applied against caterpillars or other pests, resulting in the inadvertent destruction of the mite's natural enemies.

Other Pests

Locally, other pests can be quite important due to ecological situations favoring their abundance, or because the crop is especially susceptible. For example, wireworms tend to be more troublesome following rotations of other grasses or when grass weeds are abundant in the previous crops. Moisture conditions can also favor the occurrence of wireworms in low-lying areas of fields; corn wireworm, *Melanotus communis* (Coleoptera: Elateridae), is commonly associated with more moist areas of fields. Grasshopper and locust (Orthoptera: Acrididae) outbreaks can occur intermittently, or occur where weeds or weedy crops are not managed properly, resulting in dispersal of these insects into maize fields and causing extensive damage, especially along the margins of the field.

The high value and low threshold for damage associated with sweet corn can create special conditions favoring the occurrence of pests. Sap beetles such as *Carpophilus lugubris* (Coleoptera: Nitidulidae), and cornsilk fly, *Euxesta* spp. (Diptera: Otididae), are very damaging to sweet corn in some areas, but they are not considered to be pests of grain corn. Even the earworms, which are devastating pests of sweet corn, because consumers are repulsed by the presence of insects or insect parts in their food, have little impact on grain corn production.

Pest Management in Maize

The effect of arthropod pests on corn production is considerable, though quite variable from location to location. Data in Table 3 suggests that the potential level of damage in maize is about 14–17% worldwide. In contrast, the actual level of arthropod-caused losses is about 10–12%. The approximately 5% difference is due to the plant protection efforts of producers. The different areas of the world vary considerably in the effectiveness at protecting maize from damage. Most effective, it seems, are producers in North America and the Near East, which incur only about 6 and 9% loss, respectively. In contrast, areas of Africa and Asia derive little benefit from protection efforts, or make little effort to reduce losses. Virtually all the African countries (also Mexico and Brazil) have high levels of pest pressure (infestation) on maize, whereas most of the rest of the world has moderate levels of infestation.

Maize (Corn) Pests and Their Management, Table 3
Estimated actual and potential losses due to maize pests in the major maize-producing regions of the world (adapted from CABI Crop Protection Compendium, 2002)

	Actual % loss with controls	Potential % loss without controls
Africa	14	17
Eastern	17	18
Western	17	17
Southern	13	16
Northern	9	17
Asia	12	16
Southeast	15	18
South	15	16
East	9	16
Near East	10	14
Americas	11	15
Southern S. America	13	14
Andean	10	14
North America	6	15
Central America	13	14
Europe	9	14

Cultural or environmental management. A number of approaches are used to manage maize pests. Cultural practices such as early planting or harvest, crop rotation, and effective weed suppression can be used to advantage in many cases. For example, rotation of maize with a non-grass crop can usually be used effectively in North America to manage corn rootworm because they overwinter as eggs. Upon hatching in the spring, young corn rootworm larvae will perish if they cannot reach the roots of suitable grass crops such as corn. So simply rotating corn with soybeans was a successful technique for many years, though in recent years a strain of rootworm has begun to evolve that diapauses for two seasons, necessitating a longer crop rotation period or other management approaches. Sometimes growers prefer not to rotate crops, instead growing maize continuously. Under these conditions, some benefit can be acquired by planting the new crop between the rows of the previous crop, rather than in the same location as the previous crop. Moving the crop planting even a few centimeters requires that the rootworm larvae must disperse to find the roots of the young plants, and many die while searching for food.

Insecticides. Insecticides (including bioinsecticides such as *Bacillus thuringinsis*) are a principal approach to avoid loss in maize. In the Americas, where rootworms are a problem, most of the insecticide is applied to the soil to protect roots. The rootworms hatch several weeks after the maize is planted, and if the insecticide is to be applied at planting, this requires the use of a persistent insecticide. Post planting applications are possible, but it is difficult to attain good root protection with post-plant applications, and it is more costly. Lesser amounts of insecticide are sprayed onto foliage to protect against defoliation and ear damage, and only a small amount is expended via seed treatment to protect the seed and young seedling from injury by seed-feeding insects. The insecticide used on maize in North America is estimated at over 50% for rootworm suppression, 11% for the stalk borers (European corn borer and southwestern corn borer), and 12% for corn earworm. In other areas of the world, however, proportionally more insecticide is used as a foliar protectant and seed treatment because soil pests are not as important. About 70% of the insecticide used on maize is used in the Americas, and of the insecticide used in the Americas, about 2/3 is used in North America. This pattern is not surprising considering the preponderance of maize production in North America, and the propensity to maximize yield in corporate-type farming operations. In less well financed or subsistence agriculture, insecticide purchase is a much more difficult option.

Genetically engineered germplasm. The soil bacterium *Bacillus thuringiensis* has long been recognized for its ability to control caterpillars, and in more recent times strains have been identified that affect lower flies (e.g., mosquitoes, blackflies) and beetles. With the advances in genetic engineering, it has proved possible to incorporate components of the *B. thuringiensis* bacterium into plants (usually called transgenic plants), thereby conferring a degree of resistance against lepidopterous insects. In maize, the caterpillar-specific elements of *B. thuringiensis* (cry1Ab gene), which affect stalk borers, have been rather widely deployed via genetically modified maize germplasm. The beetle-specific elements (cry3B1), which are active against rootworms, are less well known but are beginning to gain acceptance, at least in the Americas. When farmers plant maize that is engineered to resist herbivory by Lepidoptera and Coleoptera, they effectively eliminate much of the potential damage that they might incur. Such practices do not eliminate all problems, of course, as there are other taxa that can be damaging. Also, expression of the *Bacillus thuringiensis* toxin is not uniform throughout the plant, and not all pests are affected. Nevertheless, yield gains in the USA are attributable to maize containing *Bacillus thuringiensis* genetic elements (Bt corn) is estimated at 5%. In areas of the world where insecticide use is less prevalent, Bt corn confers higher yield gains, often 10% or more. The detrimental effects of Bt corn are somewhat obvious, principally higher cost of seed and the risk of widespread resistance to Bt. On the other hand, there are certainly economic, health, and environmental benefits associated with decreased use of insecticides in Bt corn. Overall, the benefits of genetically engineered maize will only be known with additional time.

► African Armyworm
► Armyworm
► Black Cutworm
► Corn Delphacid
► Corn Earworm
► Corn Leafhopper
► European Corn Borer
► Gramineous Lepidopteran Stem Borers in Africa
► Northern Corn Rootworm
► Seedcorn Maggot
► Spotted Cucumber Beetle
► Western Corn Rootworm

References

James C (2003) Global review of commercialized transgenic crops: 2002. Feature Bt maize. International service for the acquisition of agri-biotech applications, 182 pp

Steffey K, Rice M, All J, Andow D, Gray M, Van Duyn J (eds) (1999) Handbook of corn insects. Entomological Society of America. Lanham, MA, 174 pp

Major Worker

A subcaste of social insects consisting of especially large workers. In ants, this subcaste is often specialized for defense, and called soldiers. (contrast with media and minor workers)

► Ants

Malacopsyllidea

A family of fleas (order Siphonaptera).

► Fleas

Malaise Trap

An interception trap that captures flying insects, the Malaise trap is tent-like with vertical nets serving as baffles and a sloping canopy that funnels insects upward to a jar or other apparatus for capture. They may be constructed as unidirectional, bidirectional or nondirectional traps.

► Traps for Capturing Insects

Malaria

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Malaria is a debilitating disease caused by an infection of one or more protozoan parasites belonging to the subphylum Sporozoa, family Plasmodiidae, genus *Plasmodium*. These parasites are found in the blood of mammals, birds and reptiles. Human malaria is transmitted by the bite of female anopheline mosquitoes of the genus *Anopheles* (Diptera: Culicidae).

Malaria is a major endemic tropical disease characterized by severe chills and fever, anemia, and splenic enlargement. The disease has a wide geographical range, occurring from the temperate zones to the sub-tropics and tropics. It has been estimated that there are 150–400 million malaria cases a year, with five million deaths.

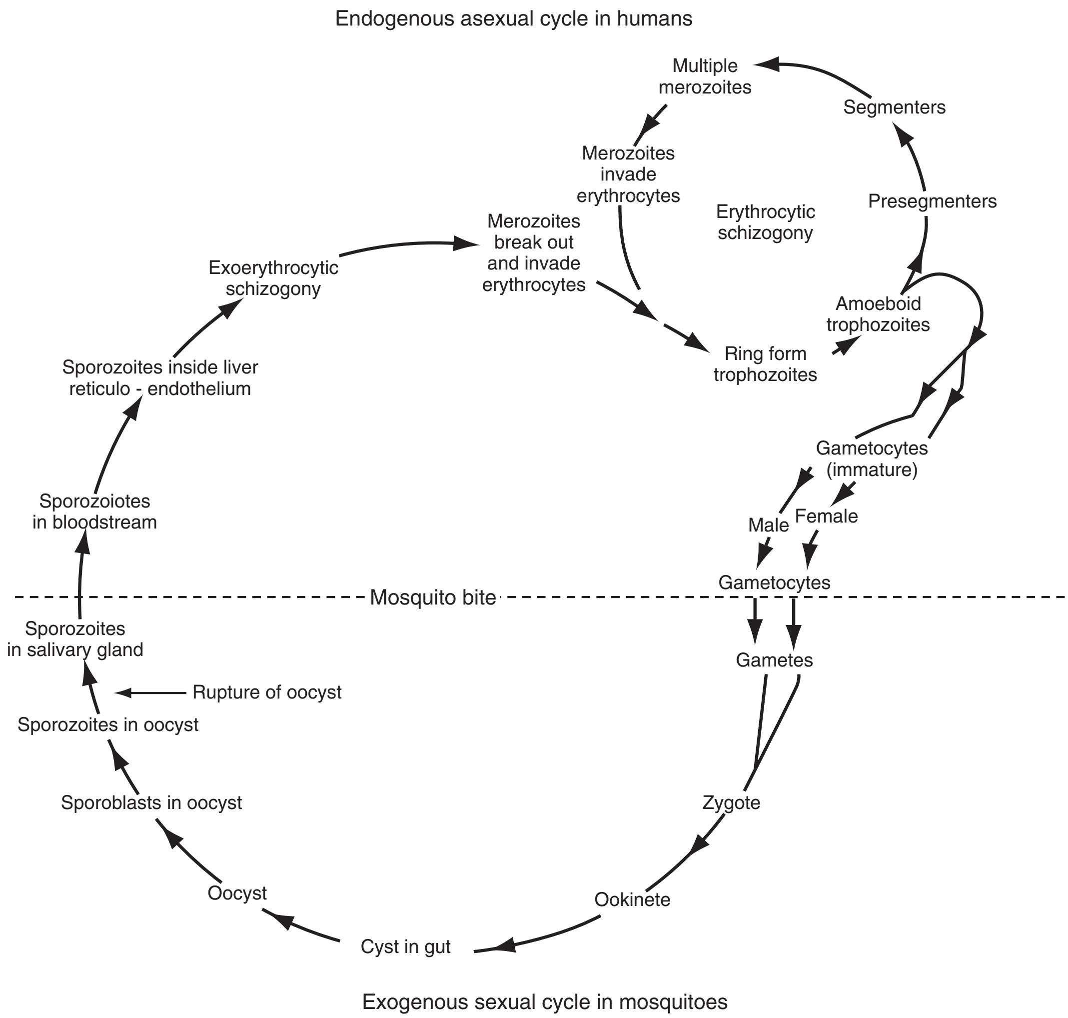
Malaria once was thought to be caused by vapors arising from swampy areas, and thus in the eighteenth century the Italians called it malaria, or bad air. It wasn't until 1880 that Charles Laveran, a French army surgeon, described malaria parasites in the red blood cells of humans. In 1897, Ronald Ross found a form of a malaria parasite in a mosquito. In 1898, Battista Grassi, Amico Bignami and Giuseppe Bastianelli, in Italy, described the malaria cycle in humans and mosquitoes.

Plasmodium undergo two types of multiplication by an endogenous asexual division (erythrocytic schizogony, and exo-erythrocytic schizogony) in the vertebrate host, and an exogenous sexual multiplication (sporogony) in the mosquito host.

The life cycle may start with the ingestion of blood by a female *Anopheles* mosquito from a malarious person (Fig. 3). The female mosquito requires a blood meal for subsistence and for egg production. The ingested blood may contain sexual cells (gametocytes). In the stomach of the mosquito, the male gamete (microgametocyte) exflagellates, producing microgametes which seek out and fertilize the female gamete (macrogamete) to form a globular zygote. Within 18–24 h it becomes elongate and motile, and is known as an oökinete. The oökinete forces its way into the epithelial lining of the stomach wall of the mosquito, and is now called an oöcyst. The mosquito stomach may contain several hundred globular oöcysts. The oöcyst increases in size, and the nuclei divide to form many spindle-shaped motile sporozoites. The oöcyst reaches maturity in 4–15 days, bursts, and liberates thousands of the sporozoites into the body cavity (hemocoel) of the mosquito. Many then migrate to the salivary glands. The mosquito is now infective. Malaria infection is initiated when sporozoites are introduced into the new host following the bite of the infective mosquito.

The sporozoites now enter the parenchymal cells of the liver where they develop and multiply in what is known as pre-erythrocytic schizogony. As the parasite (schizont) divides, it forms many thousands of merozoites. After about 6–16 days, the schizont bursts and releases the merozoites into the tissue and into the blood circulation. The time between the date of infection and the appearance of the parasites in the peripheral blood is known as the pre-patent period.

After a period of growth, the parasite multiplies in the red blood cell by asexual division, called schizogony, in which a mature schizont divides into a number of small merozoites. When the red blood cell bursts, the merozoites are released into the bloodstream. This is the stage that is responsible for the morbidity and mortality associated with malaria. The merozoites then invade fresh red blood cells (erythrocytes) and



Malaria, Figure 3 Life cycle of the malaria parasite, *Plasmodium falciparum* (adapted from Scott and Rice 1966).

grow at the expense of the host cell. A vacuole is formed, surrounded by a thin ring of cytoplasm. A small round or oval nucleus lies within the ring. This stage of the parasite is called the ring form. Within a few hours, the cytoplasm becomes somewhat ameboid and is in the trophozoite stage. After a number of nuclear divisions, the mature schizont may contain 16 merozoites. The blood cell ruptures and the merozoites enter the bloodstream where they may invade new blood corpuscles. This process of erythrocytic schizogony is repeated over and over again. After several generations of merozoites having been produced, sexually differentiated forms or gametocytes are produced. These are taken up when the mosquito bites, and thus the circle is completed.

There are four types of human malaria, *Plasmodium vivax*, *P. falciparum*, *P. malariae* and *P. ovale*. Based on the length of time of the erythrocytic cycle of schizogony or schizogonic periodicity, the species may differ. Thus *P. malariae* is 72 h and is known as quartan malaria. The other species of *Plasmodium* last 48 h, and are called tertian malaria. *P. falciparum* is the most dangerous type of malaria, and is called malignant tertian malaria, and is also the cause of a condition known as blackwater fever. *P. vivax* is known as benign tertian malaria. These names have become obsolete, and the various forms of malaria are now known by their specific name, unitalicized, i.e., vivax malaria.

There are approximately 400 species of *Anopheles* mosquitoes throughout the world. Of these, approximately 75 are considered to be important vectors of malaria. Resting or feeding adult *Anopheles* usually have their abdomen at an oblique angle, compared to other genera of mosquitoes whose abdomen is usually parallel to the resting surface. The palpi of both sexes of *Anopheles* are as long as the proboscis. The eggs are boat-shaped with floats. They are laid on the surface of the water. The larvae that hatch from the eggs do not have a prominent air tube, and have float or palmate hairs on the abdominal segments. The Anopheline larvae lie parallel to the surface of the water, in contrast to Culicine larvae which hang head down from the surface of the water. The aquatic habitats of the larvae may be temporary or permanent, natural or made by humans. Anopheline species vary in their oviposition requirements. Some species may prefer sunlit pools, while others may prefer a shady slow-moving stream. Some species prefer brackish water while others may prefer fresh water along the grassy margins of lakes. Breeding sites inadvertently created by human activity are often troublesome. Roadside ditches, badly maintained irrigation ditches, gem mining pits and other water collecting structures can be the source of large numbers of anophelines. The flight range of adult anopheline mosquitoes is usually about 2 km, though they have been known to be carried by wind for much greater distances.

Over the past half century, vector control and chemotherapy have reduced, and in some cases eradicated, malaria in many countries. Malaria control has been based on a number of measures to prevent mosquitoes from feeding on humans: by environmental control modifications, by residual spraying of habitations to destroy the adult mosquitoes, or larvaciding to destroy the larvae. Chemotherapy has been used to eliminate or control the parasite in humans. Insecticide resistance by the vector mosquito and drug resistance by the parasite has now made malaria control more difficult, and in some countries malaria incidence has increased. In many areas, indoor spraying of residual insecticides is still the main control measure. Malaria vaccine research has been extensive, but to date a truly effective vaccine has yet to be developed. One of the goals of the World Health Organization is to use primary health care as a means to deliver malaria control services, whether it be the use of insecticide treated bed nets, distribution of drugs, or limited vector control.

References

Bruce-Chwatt LJ (1980) Essential malariology. William Heinemann Medical Books Ltd., London, United Kingdom, 354 pp

Garnham PCC (1966) Malaria parasites and other haemosporidia. Blackwell Scientific Publishers, Oxford, United Kingdom, 1114 pp

Harrison G (1978) Mosquitoes, malaria and man. EP Dutton, New York, 314 pp

Kreier JP (ed) (1980) Malaria. Vol. 1: Epidemiology, chemotherapy, morphology, and metabolism. 416 pp. Vol. 2: Pathology, vector studies and culture. 328 pp. Vol. 3: Immunology and immunization. Academic, New York 346 pp

Russell PF, West LS, Manwell RD, MacDonald G (1963) Practical malariology. Oxford University Press, London, United Kingdom, 750 pp

Sachs JD (2002) A new global challenge to control malaria. Science 298:122–123

Shuler AV (1985) Malaria: meeting the global challenge. U.S. Agency for International Development, Washington, 110 pp

Malaya Disease

A lethal disease of larvae of the Indian rhinoceros beetle, *Oryctes rhioceros* (Linnaeus), caused by the Orcytes virus.

► Orcytes Virus
► Other Nudivuruses

Malcidae

A family of bugs (order Hemiptera, suborder Pentamorpha).

► Bugs

Malignant Jaundice

This is a tick-transmitted protozoan disease also known as canine babesiosis.

► Piroplasmosis

Mallis, Arnold

Arnold Mallis was born at New York, New York, USA, on October 15, 1910. He and his family relocated to California in 1927 and he entered the University of Southern California with the intent of becoming a dentist. The Great Depression intervened and Mallis had to leave college to work. He then became interested in natural history and enrolled at Pasadena Junior College and the University of California, Berkeley. He was awarded a B.S. degree in 1934 and an M.S. degree in 1939, both in entomology. Mallis worked for several years as an entomologist with the building and grounds department of the University of California, Los Angeles. During World War II, he worked on malaria control, and from 1945 to 1968 he was employed by Gulf Oil Company, where he worked on screening and formulating insecticides. In 1968 he joined Pennsylvania State University as an extension entomologist, where he worked until he retired in 1975. Mallis is best remembered as the author of "the bible of the structural pest control industry," also known as the "Handbook of pest control" (1945 and subsequent editions). In retrospect, Mallis' varied positions prepared him well for authoring this tome, which treats most of the pests associated with buildings and the immediate environs. It is a remarkably complete and interestingly written treatment of pest control, and anyone who examines it critically is not surprised that it has persisted as the favorite reference manual for the pest control industry for over 50 years. Mallis died on January 16, 1984.

Reference

Snetsinger R (1984) Arnold Mallis 1910–1984. Am Entomol 30:90

Mallophaga

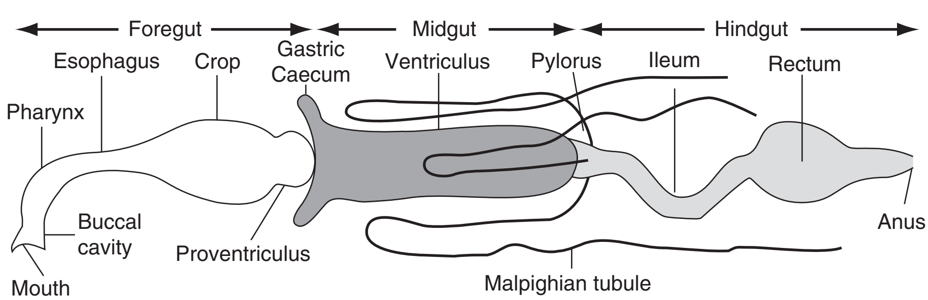
A suborder of wingless ectoparasitic insects commonly called lice, Phthiraptera. It is sometimes treated as an order.

► Chewing and Sucking Lice

Malpighian Tubules

Long slender ducts found in the hemocoel that collect nitrogenous wastes, solutes and water, and terminate at the juncture of the midgut and the hindgut. A key component of the excretory system (Fig. 4).

► Alimentary and Sucking System



Malpighian Tubules, Figure 4 **Generalized insect alimentary system (adapted from Chapman, The insects: structure and function).**

Mammal Chewing Lice

Members of the family Trichodectidae (order Phthiraptera).

► Chewing and Sucking Lice

Mammilla (pl., mammillae)

Elevations found on the integument of *Ornithodoros ticks*.

Management of Insect-Vectored Pathogens of Plants

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Epidemiology of vectored plant pathogens involves the plant, the pathogens, the vectors, and the environment, all interacting in various ways. Often, an understanding is needed of seasonal cycles of host plants, pathogens, and vectors. For example, pathogens and vectors important to an annual crop may have non-crop reservoirs between harvest and re-planting. Vectors may overwinter in the crop, or on alternate host plants. The host range of the pathogen may determine whether inoculum control is feasible or not. Some pathogens are transmitted via plant propagation, and others are not. The epidemiology of vectored plant pathogens often is complex, and an integrated approach to management is needed. Often, no single approach will achieve adequate control. This section is organized according to the concept of integrated pest management, including chemical control, biological control, host plant resistance, cultural control, and regulatory measures. Each of these categories will be considered in terms of the vectors and the pathogens.

Chemical Control

Chemical control of vectors will limit spread of vectored plant pathogens if two conditions are met. First, the vector being controlled must be a colonizer of the crop being treated. Some plant viruses are transmitted by transient flying insects. In these cases, chemical control has a poor record. Second, most of the spread must come from within the treated area (secondary spread). For the most part, insecticides simply prevent the buildup of populations of insects within a treated area. Most pesticides will not kill an immigrant insect before it has a chance to transmit a pathogen. Thus, if there is an infected field nearby with a high population of vectors, pesticide treatment may not be very effective in preventing infection from primary spread. Pesticide treatment has a good track record for control of certain luteovirus diseases such as potato leafroll and barley yellow dwarf, spread by colonizing aphids. Even if the above conditions are met, dependence on chemical control of vectored pathogens in perennial crops may be risky, because a single missed spray application or insecticide failure could result in infection and demise of the crop.

Another variation on chemical control is the use of stylet oil. Certain horticultural oils can reduce transmission of viruses by aphids. This methodology can reduce transmission of pathogens carried by transient insects, something that is not usually possible with standard insecticides. There is also potential for use of insect repellents for vector management. Some work has been done with visual repellents (mulches, paints, colored netting), but little has been done with chemical repellents.

There is no known chemical control of plant viruses, but some fastidious bacteria in perennial tree crops can be controlled with injected antibiotics. Remission of symptoms usually is temporary.

Biological Control

The use of biological control for management of vectored pathogens has a mixed review. Obviously, fewer vectors is better; however, sometimes the economic threshold for vectors is so low that it is not achievable through biological control. Sometimes, the presence of natural enemies evokes scatter responses in vector prey. This can actually cause an increase in pathogen transmission.

Total dependence on biological control for a vectored pathogen in a perennial crop is risky. Biological control inherently fluctuates between high populations of pests and high populations of natural enemies. If pests are not vectors, the crop often can stand temporary high pest populations, but if the main concern is pathogen transmission, the entire crop can be lost if populations fluctuate in favor of the pest. Similarly, often a grower will have to spray for another pest. The pesticide may kill the natural enemies of the vector, resulting in an increase in transmission of the pathogen and destruction of the crop.

Biological control in simpler island ecosystems may have a better chance to work than in more complex settings. For example, the introduction of psyllid parasitoids into RÉunion Island dramatically reduced the transmission of the bacteria that cause citrus greening disease. However, the same parasitoids are present in Viet Nam, and citrus greening disease is a major limiting factor in citrus production there.

Sometimes disruption of existing biological control can result in an increase in transmission of a plant pathogen. Increased spraying for late blight (caused by a fungus) in potatoes was linked to a major increase in numbers of green peach aphids. Evidently, populations had been controlled by an aphid pathogenic fungus that was killed by the fungicide applications for late blight. The result was a big increase in incidence of potato leafroll virus (PLRV), transmitted by the aphids.

Biological control of the pathogen is another option. Usually this is done by means of cross protection - infecting a crop with a mild strain of a pathogen that prevents symptom expression of a more severe strain that may be transmitted by an insect later on. Cross protection has worked very well for control of citrus tristeza virus, an aphid transmitted closterovirus, in several parts of the world.

Host Plant Resistance

The efficacy of plant resistance to vectors depends on the means of resistance and the mode of transmission. Resistance that prevents feeding or repels the insects can prevent transmission of pathogens spread by feeding. If the resistance merely prevents or slows population growth, it cannot prevent primary spread. It can, however, have some effect on secondary spread.

Resistance to the pathogen probably is the most effective means of controlling vectored plant pathogens. If plant resistance to the pathogen is available, it should be the first line of defense. Complications with host plant resistance can occur if the pathogen evolves strains that can break down the resistance. Also, some crops are notoriously difficult to breed due to difficult genetics or longevity.

Resistance to the pathogen may be the only means of management in some cases. An example is sugarcane mosaic virus. Sugar cane is propagated vegetatively, so the virus is propagated with the crop. Once planted, a crop remains in the same field for several years of production, and planting is staggered throughout the production area. Thus, even if clean planting stock could be found, there is no possibility for an area-wide crop-free (and virus-free) period. The virus is transmitted by transient winged aphids, including species that do not necessarily colonize the sugar cane crop, so pesticide application is not effective. Fortunately, there has been success with mosaic resistant cultivars.

Cultural Control

Many of the effective management practices for diseases caused by vectored plant pathogens involve some sort of cultural control such as adjusted planting date, pruning, roguing, and removal of volunteer crop plants and other non-crop reservoir hosts of vectors or pathogens.

Adjusting planting dates can minimize crop exposure to vectored pathogens. In the Pacific Northwest, several vectored pathogens, transmitted by eriophyid mites and aphids, can damage early-planted fall cereals. The mite transmitted viruses are particularly serious because they cause severe yield loss, resulting in total crop failure in some cases. These viruses infect newly seeded winter wheat that is planted near a maturing crop from the previous season, or near infected volunteer grain. These viruses are most troublesome in years when the old crop is slow to mature, and there is overlap between late-maturing cereal crops from the previous season and emergence of newly sown winter wheat. The infective mites are blown from the old crop to the new one. After landing on the new crop, they apparently stay put, because there is little secondary spread in the fall. The mites cannot survive very long off a host plant, so any break in the "green bridge" between old and new crops will prevent infection. As little as 10 days delay in planting can make the difference between crop failure and negligible incidence. Similarly, the aphid-transmitted barley yellow dwarf virus complex largely can be prevented by delay in planting. Other viruses are managed on an area-wide basis by maintaining a crop-free period at some time during the year. For such a policy to work, all growers in the area must cooperate in field clean-up and coordination of planting dates.

Pruning and roguing often are used as a means of management of vectored plant pathogens, especially in perennial crops. The efficacy depends on whether latent infections remain, and if so, whether plants with latent infections are suitable source plants for vectors. In the early stages of an epidemic, there usually will be more plants with latent infections than with visible symptoms. If plants with latent infections can serve as source plants for vectors to acquire the pathogens, and vectors are present, pruning and roguing will not be very effective.

In some cases, pruning actually can eliminate disease. Pierce's disease of grape vines is caused by a xylem limited bacteria called *Xylella fastidiosa*. It moves slowly in the plants. If Pierce's disease is transmitted by small leafhoppers that feed on twigs, winter pruning can eliminate most of the infection. However, if the disease is transmitted by the much larger glassy-winged sharpshooter (*Homalodisca coagulata*), which feeds on larger branches and trunks, pruning is much less effective.

Control of volunteer crop plants may limit or eliminate primary inoculum for newly planted crops. Volunteer potatoes are important sources of virus inoculum in Idaho potato seed production areas. Similarly, volunteer grain can be an important reservoir for aphids and barley yellow dwarf at planting time for winter wheat. The volunteer wheat provides a "green bridge" for the viruses and their vectors between harvest of one crop and emergence of the next one.

Other cultural control measures include elimination of weed hosts of vectors or pathogens, use of reflective mulches and paints to repel vectors, and various protective row covers. Quite a bit of work also has been done on the use of windbreaks and barrier crops to protect susceptible plantings.

Regulatory Measures

Regulatory measures for control of vectored plant pathogens are a very important aspect of management, especially for those pathogens that are transmitted through propagation. Strict sanitation measures for propagative material are common. Other kinds of regulatory measures include crop-free periods, quarantines, and required virus testing.

One of the best ways to prevent vector-borne disease in plants is to keep the disease and the vector out. Many plant diseases and vectors that occur elsewhere in the world do not occur in the United States. Some of these are listed as quarantine or actionable pests/diseases. If they are found at U.S. ports of entry, the shipment is rejected. If a pest or disease has a limited distribution in the U.S., there may be a state quarantine for certain items. For example, if a pest is found in Florida but not in

California, California may reject shipments from Florida that contain the pest.

Production of healthy propagation materials involves regulatory agreements. Potato tubers grown for seed are subject to winter testing for a variety of vector-borne viruses. Standards are much stricter for early generation seed. Citrus trees are propagated vegetatively by grafting, in order to ensure varietal uniformity. Citrus trees used for budwood in Florida are required to be tested for citrus tristeza virus every year. Those found to contain severe strains are no longer allowed to be used for propagation purposes. Lettuce mosaic virus and bean common mosaic virus are transmitted by seed as well as by aphid vectors. Some states have regulations in place requiring that seed used commercially in the state be tested and meet standards for virus incidence.

In warm climates where crops are grown year around, control of diseases caused by vectored pathogens can be particularly challenging. Sometimes an agreement is made to adhere to a crop-free period to break the disease cycle. State regulatory agencies may be involved to ensure that there are consequences for any growers that do not comply.

Other regulations are tailor-made for a given situation. Green peach aphids (*Myzus persicae* (Sulzer)) transmit potato leafroll virus (PLRV), which causes an important disease in potatoes. The aphids overwinter in peach and apricot trees. In the spring, they leave the trees and infest potatoes and other plants. In parts of Idaho where seed potatoes are grown, it is illegal to grow peach and apricot trees. If the trees are found, the state can require their removal. Guy Bishop, University of Idaho, discovered that another source of green peach aphids was greenhouse grown bedding plants. These infested seedlings were purchased by home gardeners, who often also grew potatoes. Frequently, the home grown potatoes either were grown from seed saved from previous years, or from unregistered seed. Thus, the PLRV infection rate in home gardens was high. Bishop found that the closer a seed potato field was to a town with home gardens, the more likely it was that the seed farmer had unacceptably high levels of PLRV. Regulations were made to prevent sale of infested bedding plants. Additionally, the local growers provided home gardeners with clean potato seed tubers. Incidence of PLRV in seed potatoes decreased dramatically in the region after the regulations were implemented.

Integrated Management

Most often control of vectored pathogens of plants will involve an integrated approach. A good example is potato production. Some popular varieties of potatoes develop internal discoloration as a result of infection with PLRV that results in rejection by potato processors. In order to prevent PLRV infection there are regulatory measures to ensure clean propagation material. Additionally, commercial ware potato growers employ scouts to survey for green peach aphids. If numbers reach an economic threshold the crop is treated with insecticide to prevent secondary spread of PLRV. Cultural controls include removal of volunteer potatoes, and in some cases, removal of peach and apricot trees that are overwintering sites for vectors. Department of Agriculture inspectors make the rounds of retail vendors of bedding plants, preventing sale of infested ones. Finally, there is work at the federal and state levels to breed potato varieties that are more tolerant to PLRV infection, but that also retain the taste, baking and processing qualities of the popular susceptible cultivars.

Epidemiology of vectored pathogens affecting crops is a complex and very interesting field of study. Many more puzzles remain to be solved that will make even more effective management a possibility.

References

Hadidi A, Khetarpal RK, Koganezawa H (eds) (1998) Plant virus disease control. APS, St. Paul, Minnesota, 684 pp

Harris KF, Maramorosa K (eds) (1982) Pathogens, vectors, and plant diseases: approaches to control. Academic, New York, 310 pp

Mandible

One of the pair of jaws in insects, attached to the head. The mandibles of insects with biting and chewing mouthparts usually are stout and tooth-like in appearance. Mouthparts of Hexapods.

Mandibular Glands

Paired glands that open near the base of the mandible, these glands have evolved varied functions. They may produce saliva, pheromones, defensive secretions, and have antimicrobial activity.

Mandibulate

Insects that have the mandibles adapted for biting and chewing.

Mandibulate Archaic Moths (Lepidoptera: Micropterigidae)

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Mandibulate archaic moths, family Micropterigidae, comprise 130 sp. known worldwide, in 2 subfamilies: Micropteriginae and Sabatincinae. The actual fauna likely exceeds 175 species. The family is in the monobasic superfamily Micropterigoidea, the only representative group of the most primitive extant Lepidoptera, the suborder Zeugloptera. The family includes small lepidopterans that have retained chewing mouthparts as adults, yet have lepidopteran scales and other adult and larval features that exclude them from Trichoptera. Adults small (5–12 mm wingspan), with very roughened head scales, and prominent five-segmented folded maxillary palpi; labial palpi short, one to three-segmented; haustellum absent (chewing mouthparts). All species are diurnally active as far as is known and most species have some iridescent scales on the forewings. Larvae are small, slug-like in shape, feeding mostly on mosses, liverworts, or detritus, as far as is known.

References

Davis DR (1987) Micropterigidae. In: Stehr FW (ed) Immature insects 1: 341–343, Kendall/Hunt, Dubuque

Issiki ST (1931) On the morphology and systematics of micropterygidae (Lepidoptera Homoneura) of Japan and Formosa, with some considerations on the Australian, European, and North American forms. Proceedings of the zoological society of London 1931:999–1039

Kristensen NP, Nielsen ES (1979) A new subfamily of micropterigid moths from South America. A contribution to the morphology and phylogeny of the Micropterigidae, with a generic catalogue of the family 1931: Zeugloptera. Steenstrupia 5:69–147

Lorenz RE (1961) Biologie und morphologie von *Micropterix calthella* (L). (Lep. Micropterygidae). Deutsche Entomologische Zeitschrift (n.s.) 8:1–23

Tuskes PM, Smith NJ (1984) The life history and behavior of *Epimartyria pardella* (Micropterigidae). J Lepidopterists' Soc 38:40–46

Mange

Mange or scabies is an important skin disease caused by psoroptid and scarcoptid mites.

► Mites

Mango Mealybug, *Rastrococcus invadens* Williams (Hemiptera: Pseudococcidae)

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This is one of many insects that came to the attention of science only after it had been inadvertently transported and established on a new continent, where it became an important pest. To date, most field data concerning this species are therefore from West Africa. In the 1980s, mealybug infestations suddenly devastated mango, but also many ornamental and shade trees, around Lomé, Togo, and Cotonou, Bénin. From there, this new plague rapidly spread along the coast, west to Ghana and Côte d' Ivoire and east to Nigeria. At the turn of the millennium, it had invaded most of West and Central Africa (from Senegal to R. D. Congo). In Benin, for instance, it was observed most often in and around large cities, being less abundant in commercial orchards and even less so on local mango varieties in farmers' fields.

In 1986, it was described as *Rastrococcus invadens* Williams (Hemiptera: Pseudoccocidae) from India, where several cryptic species of Rastrococcus infest mango, a native of this sub-continent. Among them, only *R. invadens* had made it to West and Central Africa; but interestingly, the species is still absent from East Africa. It is also known from all over India, Bangladesh, Malaysia, Sri Lanka, Indonesia, where it seems to be of minor or no economic importance, and it has been intercepted by quarantine authorities in Hawaii.

Morphology and Biology

This is a typical white mealybug. It is covered with waxy dust, oval in shape (3–4 mm length) with no wings, weak legs, and long sucking mouth parts on the ventral side. It has characteristic waxy lateral filaments (anterior up to 6 mm, posterior up to 8 mm long). Females produce up to 200 first instar larvae, which disperse and develop through three nymphal instars, which resemble each other and the adult, except for the size increase. Males are typical winged adults with long caudal filaments and milky wings. They emerge from a characteristic resting stage ("pupa") and are short-lived.

The life cycle (egg to first egg) is completed within one month. The females are long-lived (up to 225 days) and the mealybug reproduces throughout the year. Dispersal is probably mostly through humans, particularly on fruits and cuttings from nurseries. Population densities were usually higher on young than on old leaves and differed markedly between individual mango trees, indicating the importance of plant genotype on mealybug reproduction and survival. Population peaks were irregular, but mostly in the wet season. Population dynamics were highly influenced by the parasitoids introduced in a classical biological control project.

Damage

Wherever *R. invadens* turned up in Africa, it infested a wide variety of trees from many families (over 100 hundred plant species were listed as hosts), being noticeable primarily on shade trees, like *Terminalia catappa*. The abundant honeydew ejected by the mealybug, and the resulting sooty mold and leaf drop, led to wide-spread cutting of ornamental trees and economic damage, mainly on mango and citrus. In the early 1990s, mango production along the Benin and Togo coast was almost completely jeopardized.

Control Options

Wherever this mealybug appeared for the first time, extension services tried to combat it with pesticides. As the mealybug is often hidden in the buds and the large mango trees are difficult to cover, insecticides are generally inefficient. Indigenous natural enemies, like coccinellids, are sometimes abundant, but fail to reduce mealybug populations to acceptable levels.

Mango varieties vary a lot in their susceptibility, but generally it is the wild type mangos ("mangotiers") that are least affected, but also least productive. It is clear that resistant/tolerant varieties alone are not a satisfactory solution. Similarly, cutting infested branches or entire trees gave only temporary relief.

The Solution: Biological Control

Mango, *Mangifera indica* L. (Anacardiaceae) has been cultivated in India for about 4,000 years. It was brought to East Africa in the tenth century A.D. and from there by the Portuguese to West Africa. It was therefore surmised that this new mealybug came from India and that classical biological control, i.e., the transfer of natural enemies that keep this mealybug under control in its original home, could bring the solution. Foreign exploration to find natural enemies was therefore undertaken by CABI Bioscience in Southeast Asia. This led to the discovery of two specific parasitic wasps *Gyranusoidea tebygi* Noyes and *Anagyrus mangicola* Noyes (Hymenoptera, Encyrtidae).

They were shipped to CABI Bioscience in the United Kingdom for quarantine. There, the insects were reared and checked as described for the biological control project against the cassava mealybug. With the necessary import permits and under the umbrella approval of the Inter-African Phytosanitary Council of the Organisation for African Unity, *G. tebygi* was then sent to an FAO-supported GTZ project in Lomé, Togo, and from there to IITA in Cotonou, Bénin, whereas *A. mangicola* was sent directly to IITA. Further studies, mass rearing, and releases followed, first in Togo in 1987 (six releases of *G. tebygi*), and from IITA in another ten countries, from 1988 to 2001 (48 releases/deliveries of *G. tebygi* and 57 releases/deliveries of *A. mangicola*). This was always done on request by the local quarantine authorities and in close collaboration with national scientists.

Laboratory studies revealed that mated females lay their eggs into mealybugs, where a larva develops freely floating in the coelom of the mealybug. The larva pupates in the sausage-shaped dry remains of the mealybug, called a "mummy," from where the adults emerge after a total life cycle of about 2–4 weeks, depending on the host stage attacked. The tiny *G. tebygi* attacks first to third instars, where as the larger A. *mangicola* prefers older instars, including adult mealybugs that cannot be attacked by *G. tebygi*. As a consequence the two wasp species do not strongly compete with each other, but are complementary.

By the end-1990s, *G. tebygi* was established everywhere in Africa where *R. invadens* occurred, having dispersed sometimes long distances from the release sites. *A. mangicola* was more difficult to establish; but is now well represented mainly in large towns. Both species were never found on any other mealybug.

Both parasitoids are attacked by indigenous hyperparasitoids and compete with several species of indigenous coccinellids, which have now become uncommon on mango. As biological control took hold in Africa, the original wide host spectrum collapsed and today (2002) *R. invadens* is confined almost exclusively to mango. Overall, good biological control was achieved, particularly in the more humid areas of West and Central Africa. In the northern savannas, equilibrium might not yet have been reached or this equilibrium might not lead to complete control.

Economic and sociological studies demonstrated that homeowners and farmers are well aware of this biological control and that returns are similar to those found for the biological control project against cassava mealybug, with yearly gains for southern Benin of $50 million and a benefit-cost ratio of $145 for each $1 invested, again for Benin alone.

References

Agounké D, Agricola U, Bokonon-Ganta HA (1988) *Rastrococcus invadens* Williams (Hemiptera: Pseudococcidae), a serious exotic pest of fruit trees and other plants in West Africa. Bull Entomol Res 78:695–702

Bokonon-Ganta A, de Groote H, Neuenschwander P (2002) Socio-economic impact of biological control of mango mealybug in Benin. Agric Ecosyst Environ 93:367–378

Neuenschwander P (1996) Evaluating the efficacy of biological control of three exotic homopteran pests in tropical Africa. Entomophaga 41:405–424

Neuenschwander P, Boavida C, Bokonon-Ganta AH, Gado A, Herren HR (1994) Establishment and spread of *Gyranusoidea tebygi* Noyes and *Anagyrus mangicola* Noyes (Hymenoptera: Encyrtidae), two biological control agents released against the mango mealybug, *Rastrococcus invadens* Williams (Homoptera: Pseudococcidae) in Africa. Biol Control Sci Technol 4:61–69

Williams DJ (1986) Rastrococcus invadens sp. n. (Homoptera Pseudococcidae) introduced from the oriental region to West Africa and causing damage to mango, citrus, and other trees. Bullet Entomol Res 76:695–699

Manicapsocidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice or Psocids

Manitoba Trap

A trap for capturing horse flies and deer flies (Diptera: Tabanidae). It consists of a dark sphere suspended from a tripod, with a canopy suspen-ded above, and topped by a collection apparatus. The flies are attracted to the dark color and movement of the sphere and fly upward where they are directed by the canopy into the collection apparatus, usually a jar. Traps for Capturing Insects.

Mann, William M

William M. Mann was born at Helena, Montana, on July 1, 1886. He was interested in animals beginning in his childhood, and he earned a B.S. degree at Stanford University in 1911, and a Sc.D. at Harvard University in 1915. The latter degree was earned under the guidance of William Morton Wheeler, so it is not surprising that Mann became an authority on ants. He was appointed to the United States Department of Agriculture, where he worked as a specialist on ants, from 1917 to 1925. In 1925 he became director of the National Zoological Park of the Smithsonian Institution, and served in this capacity until his retirement in 1956. In this capacity he traveled over much of the world, and became renowned as a collector of wild animals. He discovered many new species, and was featured many times in National Geographic Magazine. He is remembered as a creative and progressive zoo director, and received many awards from zoological park organizations. He died October 10, 1960, in Washington, DC.

Reference

Snyder TE, Graf JE, Smith MR (1961) William M. Mann, 1886–1960. Proceedings of the Entomological Society of Washington 63: 68–73

Mannerheim, Carl Gustav Von

Carl Gustav von Mannerheim was born on August 10, 1797, near Lemo, Finland. He was born into one of the most distinguished families in Finland and trained to enter government administration. Mannerheim served as a governor of two regions of Finland. Despite his political career, Mannerheim was interested in natural science, particularly entomology. He studied at the University in Turku, Finland, under the noted entomologist C. R. Sahlberg. Mannerheim was a coleopterist who described many beetles from Russian collections, including species taken in Siberia, Alaska, and California. A prolific writer, Mannerheim was a member of many scientific societies. Mannerheim died on October 9, 1854, in Stockholm, Sweden.

References

Essig EO (1931) A history of entomology. The Macmillan Company, New York. 1029 pp

Herman LH (2001) Mannerheim, Carl Gustav von. Bull Am Mus Nat His 265:107–108

Manotidae

A family of flies (order Diptera).

►Flies

Mantidae

A family of praying mantids (Mantodea).

►Praying Mantids

Mantidflies (Neuroptera: Mantispidae)

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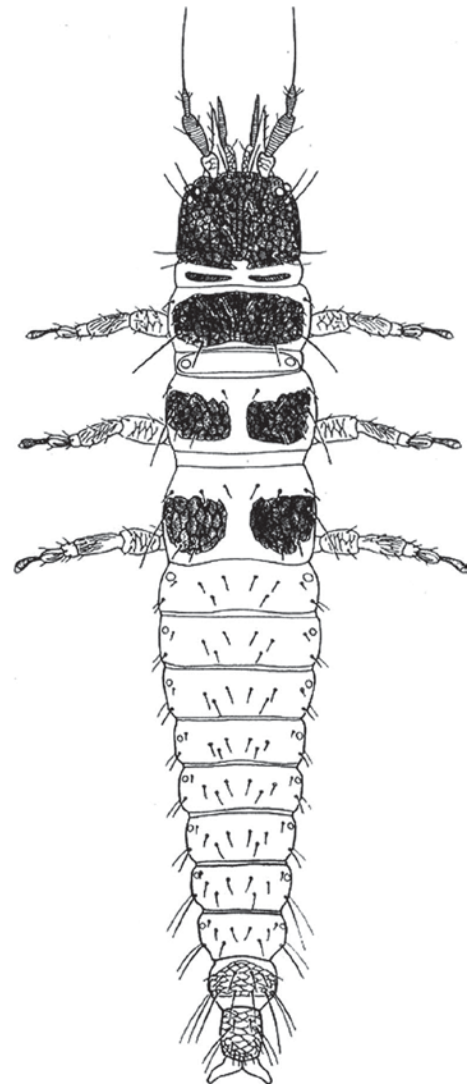
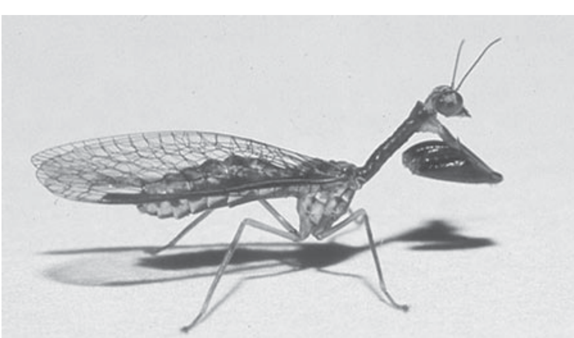
The family Mantispidae belongs to the suborder Planipennia of the order Neuroptera. The group receives its name from the remarkable resemblance of the adults to praying mantids. Like mantids, adult mantispids, or mantidflies as they are sometime called, have an elongate prothorax, a freely movable head with prominent eyes, and raptorial forelegs composed of a lengthened coxa and a spined femur, which fits against the tibia to immobilize prey (Fig. 5). Of course, the two groups are not closely related, instead providing an excellent example of convergent evolution. Unlike the mantids, mantispids have membranous wings, no cerci, and are holometabolous.

Features that mantispids share in the larval stage with other Planipennia include three instars (with the exception of the Coniopterygidae), grooved mandibles and maxillae that fit together to form a piercing/sucking tube, a blind-ended midgut that accumulates wastes that are then voided as a meconial pellet or fluid when the gut becomes complete at maturity, and Malpighian tubules modified for cocoon silk production in the last larval instar (Figs. 6 and 7).

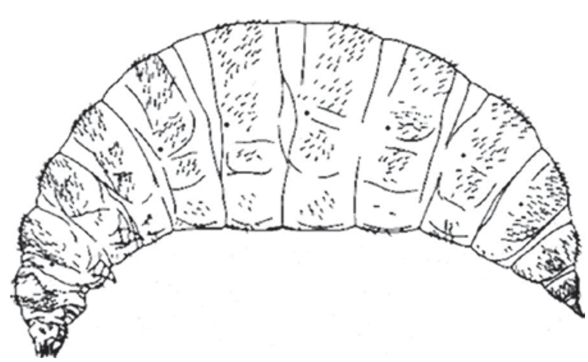
There are four recognized subfamilies: Symphrasinae (*Anchieta, Trichoscelia, Plega*),



Mantidflies (Neuroptera: Mantispidae), Figure 6 ***Mantispa uhleri*** **Banks, unfed first instar.**



Mantidflies (Neuroptera: Mantispidae), Figure 5 ***Mantispa uhleri*** **Banks, adult male.**



Mantidflies (Neuroptera: Mantispidae), Figure 7 ***Mantispa uhleri*** **Banks, mature third instar.**

Drepanicinae (*Drepanicus, Ditaxis, Theristria, Gerstaeckerella*), Calomantispinae (*Calomantispa, Nolima*), and Mantispinae (all other genera).

While adult mantispids are general predators, larval feeding is more specialized. Our knowledge of the developmental biology of the first three subfamilies is sketchy. The larval stages of some members of the Symphrasinae have been linked with immature Hymenoptera, Lepidoptera, Coleoptera, and Diptera. It is possible that larvae of some members of these three subfamilies may simply be generalist predators feeding on a wide variety of sedentary arthropod foods.

In contrast, the biology of the Mantispinae is far better known. Mantispine mantispids develop within the egg sacs of spiders. This association has sometimes been referred to as parasitic, but the feeding ecology of mantispines is more appropriately termed spider-egg predation because the first instar larvae are responsible for finding a source of spider eggs. Adult mantispines lay large clutches of stalked eggs containing from a few hundred to several thousand eggs, depending on the size of the ovipositing female, which can vary greatly. Extreme size variation in both males and females occurs because larvae are locked into their supply and there can be great variation in the quantity of food contained within a spider egg sac. There is no compelling evidence indicating where females lay their eggs. The stalk (produced from the female colleterial gland) on the egg is quite short and it is difficult to see how it could serve as the kind of protective device that longer stalks afford the eggs of Chrysopids. The eggs hatch in about ten days. Newly hatched larvae are campoediform and less than a millimeter in length. They aggregate for unknown reasons around the empty egg cases for a day or so before they disperse. After entering an egg sac, they pierce the eggs with their short, straight, modified mandibles and maxillae and drain the eggs of yolk. There are two subsequent larval instars with a quiescent period of about a day separating the first and second and second and third stadia. The second and third instars are physogastric, with reduced legs that are consistent with their limited need for locomotion. Mantispids have been described as hypermetamorphic, but this is not really true. The three larval instars are not uniquely different from each other and utilize the same basic feeding mechanism. The abdominal tip of the third instar is modified into a spinneret. When all of the eggs within the sac have been consumed, the third instar spins a cocoon with silk from the Malpighian tubules. Pupation occurs within the cocoon. The pharate adult chews its way out both the cocoon and egg sac. Since the egg sac may have been constructed in a constricted area, such as under tree bark, the pharate adult crawls some distance away before undergoing the final ecdysis.

There are two basic strategies for spider egg location by larval mantispids - direct penetration of egg sacs that have already been produced and deposited in the environment versus the boarding of female spiders with entry into the sac occurring during, or closely associated with, its construction. *Mantispa viridis* Walker, a green mantispid common in the southern United States, is an example of an obligate egg sac penetrator. Larvae are attracted to spider silk and adept at burrowing through it but they display no interest in the spiders themselves. Once inside the egg sac, *M. viridis* larvae are tolerant of other larvae and will commence feeding immediately. It is not uncommon in this species for more than one adult to emerge from the same spider egg sac. Although *Mantispa viridis* will enter the egg sacs of a wide variety of spiders, it is particularly adept at entering the sacs of web-building spiders that tend to be relatively immune from attack from spider-boarding mantispids. Spiders utilized by *M. viridis* include the cob-web weaver, *Achearanea tepidariorum*, the orb-builder, *Argiope aurantia*, as well as several species of funnel-web spiders belonging to the genus *Agelenopsis*. *Mantispa viridis* overwinters inside the spider egg sac where cool temperatures arrest its development; it does not seem to have a specific diapausing stage. Thus, severe winter temperature can kill it, which probably explains its more southern distribution.

Climaciella brunnea (Say) is probably the mantispid most familiar to naturalists. Adults are diurnal, often frequent flowers, and are excellent Batesian mimics of *Polistes* wasps. *Climaciella* larvae are obligate spider boarders. First instar larvae exhibit a unique phoretic behavior in which they rear up on caudal suckers and sway back and forth with legs outstretched awaiting a passing spider that they can board. Larvae enter the egg sac as it is being constructed. Larvae are unable to directly penetrate the silk of an egg sac. In fact, if they arrive at the eggs after the eggs have been partially enveloped with silk, they can be spun into the fabric of the sac and become permanently trapped. *Climaciella brunnea* specializes on the egg sacs of wolf spiders of the family Lycosidae, especially the genus *Schizocosa*. Larvae adopt positions around the edge of the spider's carapace. Multiple boardings of more than one larva per spider do occur. Larvae pass the winter aboard the spider. *Mantispa pulchella* Banks is also an obligate spider boarder. In this species, there is always only one larva to each spider; the larva is always found loosely draped over the spider's pedicel. *Mantispa pulchella* specializes on boarding small, foliage-inhabiting spiders, particularly spiders of the family Anyphaenidae.

Some mantispids facultatively utilize either egg location strategy. In the laboratory, first-instar *Mantispa uhleri* Banks will penetrate egg sacs and can also be found extensively in the field aboard a variety of spiders. After penetrating an egg sac, *uhleri* larvae can halt the development of the spider eggs within the sac with an aggressive allomone, although the manner by which the mantispid uses this chemical is not yet known. If more than one larva enters the sac, each larva will attempt to kill the other and refrain from engorging on eggs until they are the only larva left alive in the egg sac. If the sac contains hatching spiderlings, the larva will board one of the spiderlings and attempt to follow the spiderling through to its adult stage. Larvae wrap themselves tightly around the spider's pedicel after they board. Larvae can easily negotiate the spider's molts during which they either remain on the pedicel or enter one of the spider's book-lungs. More than one *M. uhleri* larva may initially board a spider but as the spider progresses through molts, the number of larvae is usually winnowed down to one. Analogous to the behavior within an egg sac, a larva attempts to kill or dislodge any competing larvae on the spider. While aboard the spider, larvae maintain themselves by piercing the spider's cuticle and ingesting blood. Other spider-boarding mantispids probably do this also. Thus, in this phase of its life cycle, *M. uhleri* is actually a spider parasite after all. Larvae will board male as well as female spiders even though only females will provide them with a direct source of spider eggs. This situation is not as "dead end" as it sounds. Larvae of *M. uhleri* will transfer from males to females when they are cannibalized after mating. Larvae of *Mantispa pulchella* and *Climaciella brunnea* will actually make the transfer during copulation by their spider hosts.

The major spider host for *M. uhleri* in the Midwest is the philodromid spider *Philodromus vulgaris* Hentz. Infestation levels on this spider often exceed 50% Selection pressure is so great on this spider that it has evolved an anti-mantispid mechanism. Without any additional feeding, female *P. vulgaris* produce a second, smaller egg sac a few days after the first sac. The two sacs are constructed next to each other and the female guards both sacs. If a mantispid successfully enters the first egg sac, all the eggs within it are consumed. But, the second egg sac escapes predation, at least from mantispids.

References

Brushwein JR, Hoffman KM, Culin JD (1995) Seasonal phenology and overwintering of *Mantispa viridis* Walker (Neuroptera: Mantispidae) in South Carolina. J Entomol Sci 30:112–119

Hoffman KM, Brushwein JR (1989) Species of spiders (Araneae) associated with the immature stages of

Mantispa pulchella (Neuroptera: Mantispidae). J Arachnol 17:7–14
MacLeod EG, Redborg KE (1982) Larval platymantispine mantispids (Neuroptera: Planipennia): possibly a subfamily of generalist predators. Neuroptera Int 2:37–41
Redborg KE, Redborg AH (2000) Resource partitioning of spider hosts (Arachnida, Araneae) by two mantispid species (Neuroptera, Mantispidae) in an Illinois woodland. J Arachnol 28:70–78
Redborg KE (1998) Biology of the Mantispidae. Annu Rev Entomol 43:175–194
Redborg KE, MacLeod EG (1985) The developmental ecology of *Mantispa uhleri* Banks (Neuroptera Mantispidae). Illinois Biological Monographs, 53, p130

Mantids

Members of an order of insects (Mantodea) They also are known as praying mantids.

►Praying Mantids

Mantispidae

A family of insects in the order Neuroptera. They commonly are known as mantidflies. Lacewings

► Antlions and Mantidflies

Mantodea

An order of insects. They commonly are known as praying mantids or mantids. Praying Mantids

Mantoididae

A family of praying mantids (Mantodea).

► Praying Mantids

Mantophasmatidae

A family of gladiators (order Mantophasmatodea).

► Gladiators (Mantophasmatodea)

Many-Plumed Moths (Lepidoptera: Alucitidae)

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Many-plumed moths, family Alucitidae, total about 184 species worldwide. The family is part of the superfamily Copromorphoidea in the section Tineina, subsection Tineina, of the division Ditrysia. Adults small (7–28 mm wingspan), with head smooth-scaled; haustellum naked; labial palpi porrect, mostly with long second segment; maxillary palpi 3–5-segmented (rarely vestigial). Wings with rounded shape (hindwing merges with forewing margin) and all veins as separate wing clefts to near the wing bases, and fringed (at least one Neotropical species has the clefts split only half way in from the termen). Maculation shades of gray, with various bands or spots, but a few with shades of brown or yellow, or white, and both forewings and hindwings with matching or merging patterns. Adults active in deep shade, or may be crepuscular. Larvae are borers or gall makers as far as is known. The few plant records are in Bignoniaceae, Caprifoliaceae, Compositae, Dipsaceae, Labiatae, and Rubiaceae.

References

Buszko J (1977) Alucitidae. In Klucze do Oznaczania Owadów Polski. 27. Motyle-Lepidoptera, 97:1–17. Polskie Towardzystwo Entomologiczne [in Polish]
Heppner JB (2003) Alucitidae of North America (Lepidoptera: Copromorphoidea). Holarctic Lepidoptera (Gainesville), [in prep]
Meyrick E (1910) Lepidoptera Heterocera. Fam. Orneodidae. In Genera Insectorum, 108. P. Wytsman, Brussels. 4 pp, 1 pl.
Scholz A, Jäckh E (1994) Taxonomie und Verbreitung der westpaläarktischen Alucita-Arten (Lepidoptera: Alucitidae (Orneodidae)). Alexanor 18(4):1–64
Sutter R (1990) Beiträge zur Insektenfauna der DDR: Lepidoptera-Alucitidae. Beiträge zur Entomologie 40:113–119

March Flies

Members of the family Bibionidae (order Diptera).
► Flies

Margarodidae

A family of insects in the superfamily Coccoidae (order Hemiptera). They sometimes are called giant coccids or ground pearls.
► Bugs

Marginal Cells

Cells found along the periphery of the wing near the costal margin.
► Wings of Insects

Marginal Vein

A vein found at or near the wing margin.
► Wings of Insects

Marginidae

A family of flies (order Diptera).
► Flies

Marine Bugs

Members of the family Aepophilidae (order Hemiptera).
► Bugs

Marine Insects and the Sea-Skater *Halobates* (Hemiptera: Gerridae)

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Although insects originated in swampy areas some 300 millions years ago, they then moved toward a terrestrial existence, evolving various physiological adaptations which allowed them to become independent of water or damp places, and to achieve dispersal though the air.

Some of the most important adaptations of many insects living on land include the following:

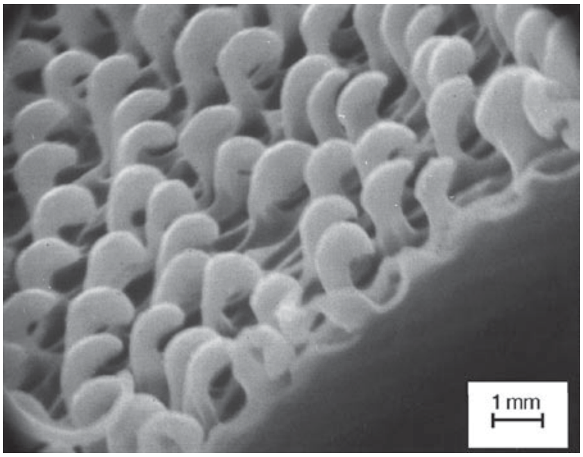
- Hardened, impermeable cuticle often impregnated with lipids to cut down on water loss.
- Tracheal breathing system for efficient distribution of oxygen by diffusion.
- Wings for long-range aerial dispersal.
- Complete metamorphosis, which may allow adults and young to exploit completely different habitats.

Surviving the Marine Environment

In order to return to the sea they have had to solve a number of ecological, physiological as well as physical problems. Some of these problems, e.g., osmotic regulation, they have succeeded in solving, while others, e.g., underwater respiration, are perhaps insurmountable, hence the rarity of insects at sea. Although, several thousand insect species are known to live in various marine environments, the five oceanic *Halobates* species are the only ones known to spend all their lives at sea, but even they are confined to the air-sea interface. Because they do not fly, nor do they normally dive, *Halobates* must face certain challenges in order to live in such an unusual habitat. Some of these challenges are:

- Avoidance of drowning – This is probably the foremost problem they have to solve. Storms at sea can be fierce, and it is highly likely that these tiny insects would then be pushed underwater. They solve this by surrounding their bodies with a layer of tiny hairs that trap air and form an air-bubble around them (Fig. 8). This not only allows them to bob up to the surface rapidly if they are pushed underwater, it also acts as a mechanical gill in that when the oxygen level in the bubble is low, more oxygen diffuses into the bubble from surrounding sea water.

- Solar irradiation – On sunny days, *Halobates* are totally exposed to the tropical sun because there is no shade to be found anywhere in the open ocean. They have, therefore, evolved a sort of sunscreen in the form of a UV-absorbing layer in the cuticle to protect them from radiation damage (Fig. 9). Although the chemical composition of this substance is unknown, it is able to absorb almost all of the UV rays at the potentially damaging wavelength of 280nm, allowing less than 0.01% to pass through the cuticle to reach reproductive and other soft tissues underneath.
- Starvation – Prey animals may be found only sporadically at the sea surface, thus *Halobates* must have the ability to withstand short-term starvation. They do this by storing triglycerides in their fat bodies, which provide a ready energy source.
- Mate location – It is not known how adult *Halobates* find mates of the opposite sex at sea. Even if individuals are brought within meters of one another by winds and waves, it is still necessary for the sexes to come into contact. They may use surface-dispersible pheromones for aggregation or as sex attractants. Although no such chemicals have yet been detected in *Halobates*, they have been demonstrated in a coastal relative, *Trochopus plumbeus* (Veliidae) (Fig. 8).



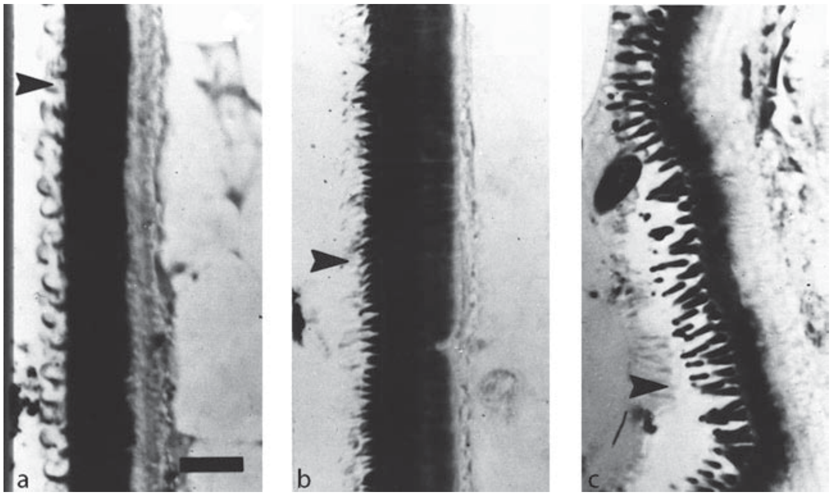
Marine Insects and the Sea-Skater *Halobates* (Hemiptera: Gerridae), Figure 8 **Section of cuticle of *Halobates germanus* showing micro-hairs layer in side view (scale = 1 μm, from Cheng, 1973; Nature 242: 132–133).**

Sea-skaters, *Halobates* spp

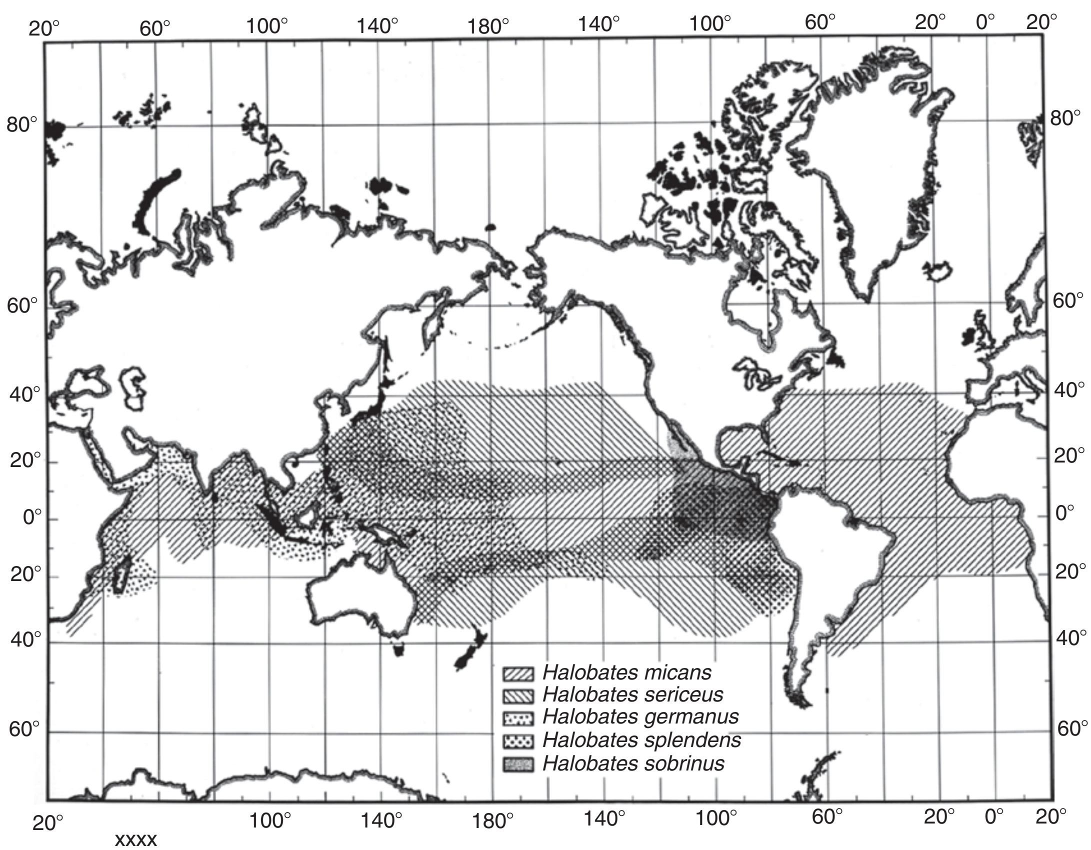
The sea-skater *Halobates* is undoubtedly one of the most remarkable members of the class Insecta. It is the only insect that has succeeded in living in the open sea. It is a member of the Family Gerridae, commonly known as pond-skaters or water striders. The gerrids are some of the most common aquatic bugs in the order Heteroptera and can be found in a great variety of fresh water as well as brackish and marine habitats. The genus *Halobates* is almost exclusively marine. All but one of its known species occur in the sea. Of the 45 described species, only five are found in the open ocean, miles away from land. The others occur near the coast and, under ordinary circumstances, do not venture out to the open ocean (Fig. 10).

Sea-skaters are found only in warm waters where the winter temperature is above 20°C. Coastal species are common around tropical islands fringed with mangroves or other trees, but are normally absent from coral atolls or islands devoid of fringing vegetation. They feed on terrestrial insects that have fallen or are trapped at the sea surface, and carry out their life cycle very much like those of their fresh water cousins. Oceanic *Halobates*, however, have evolved many special adaptations necessary for their survival at sea.

The air-sea interface where these insects live is unique in many ways. This is where the ocean meets the atmosphere, where air-borne particles accumulate when they fall, where nutrients are brought up to the surface from deep water by air bubbles and where various chemical and physical interactions take place. Although scientists have been measuring seawater temperature, salinity, current flow, wind velocity, etc., for decades, almost all of the measurements were taken in a water column. Physical and chemical measurements of the surface film have proved to be more difficult until



Marine Insects and the Sea-Skater *Halobates* (Hemiptera: Gerridae), Figure 9 **UV photomicrography taken at 280 nm of thin sections of *Halobates* cuticle showing dark UV-absorbent layer (from Cheng et al. 1978; Limnology and Oceanography 23:554–556).**



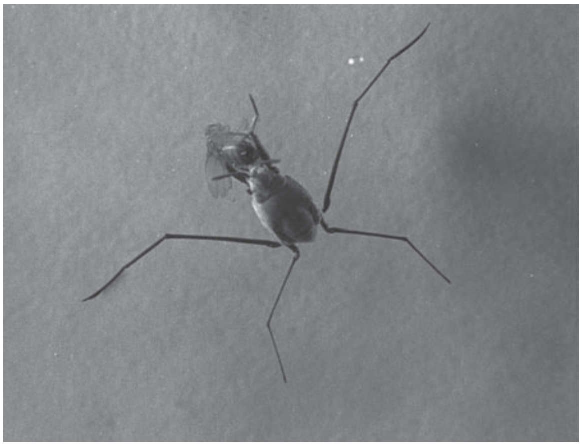
Marine Insects and the Sea-Skater *Halobates* (Hemiptera: Gerridae), Figure 10 **Distribution of five pelagic *Halobates* species (from Cheng 1974; Marine Fisheries review 36:1–7).**

the last 10 years, when special sensing devices were developed. Attempts to correlate the occurrences of oceanic *Halobates* with physical or chemical features of the sea surface are thus still in their infancy. We do, however, know quite a lot about their distributions, biology and special adaptations.

All five pelagic (i.e., open ocean) *Halobates* species occur in the Pacific Ocean, two are found in the Indian Ocean and only one occurs in the Atlantic Ocean. Each species has a rather well defined distribution pattern, but we still do not understand fully what determines such patterns. We do know, however, that these patterns are controlled to a large extent by seawater temperatures and currents.

General Biology

The eggs of oceanic *Halobates* are laid on flotsam: seeds, plastic, wood, mollusk shells, sea bird feathers and even tar lumps. There are five larval stages. The young resemble adults in general morphology although they are smaller. The sexes are not distinguishable until the final larval stage. The general body plan of *Halobates* is similar to those of other gerrids (Fig. 11), but *Halobates* are totally wingless at all stages of their life cycle. Adults measure 5–6 mm in body length and the sexes are easily distinguished by the presence in the males of external genital processes that are characteristic for each species. They are predators, feeding on animals trapped at the sea surface. Adults and older nymphs are also cannibalistic. They are, in turn, preyed upon by sea birds (by far their most important predators), surface-feeding fishes, and occasionally turtles.



Marine Insects and the Sea-Skater *Halobates* (Hemiptera: Gerridae), Figure 11 ***Halobates sericeus*** **female feeding at sea surface.**

References

Cheng L (1973) Marine and freshwater skaters: differences in surface fine structures. Nature 242:132–133

Cheng L (1974) Notes on the ecology of the oceanic insect *Halobates*. Mar Fish Rev 36:1–7

Cheng L (1976) Insects in marine environments. In: Cheng L (ed) Marine insects. North-Holland Publishing Company, Amsterdam, pp 1–4

Cheng L, Douek M, Goring DAI (1978) UV absorption by gerrid cuticles. Limnol Oceanogr 23:554–556

Cheng L (1985) Biology of *Halobates*. Annu Rev Entomol 30:111–135

Cheng L (2003) Marine insects. In: Resh VH, Carde R (eds) Encyclopedia of insects. Academic, San Diego, California, pp 679–682

Herring JL (1961) The genus *Halobates* (Hemiptera: Gerridae). Pac Insects 3:223–305

Cheng L, Frank JH (1993) Marine insects and their reproduction. Oceanography and marine biology Annu Rev 31:479–506

Mariner

A transposable element that has been engineered for transforming insects other than *Drosophila. mariner* elements are widely found in most arthropods and in insect-parasitic nematodes, other nematodes, flatworms, hydras, humans, mouse, rat, Chinese hamster, sheep and cow. *mariner* has been used to transform chicken, zebrafish and a protozoan.

Marker (DNA Marker)

A DNA fragment of known size used to calibrate an electrophoretic gel.

Marker (Genetic)

A trait that can be observed to occur (or not) in an organism. Marker genes include genes conferring resistance to antibiotics, expression of green fluorescent protein, eye color, etc.

Marking Insects for Studying Ecology and Behavior

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Insect ecology and behavior studies often occur in conditions that preclude visual observations. To assess insect dispersal, subterranean habits, feeding, and complex ecological relationships among diversified taxa, efficient markers (synonymous with labels and tags) are useful. An effective and versatile marker should have the following characteristics: easy to apply to large populations, minimal manipulation and trauma to the test insect(s), detectable without destroying or killing the insect sample, persist in the insect or community, and no adverse effects on the physical functions or behavior of the labeled organisms. A number of marking techniques have been used for insect tagging in behavior and ecology studies.

Visually Detected Markers

Visually detected markers include wire ties, paints, dyes, inks, powders, pollen, and spores that are fixed to the insects at least until sampling for tagged insects is completed. These methods, however, commonly suffer limitations. One study evaluated the use of wire ties, paint, and excised legs as markers for ants (*Solenopsis* sp.). The wire ties stayed on, but attaching them was laborious and required anesthetization of the ants. Workers with excised legs were killed by their nestmates, and painted labels were scraped off. In another study, a ground sprayer and an airplane were used to spray cotton fields with a blue enamel paint, and it was estimated that about one-third of the boll weevils received the marker. However, this method was reported as being messy, hard on the spray equipment and the cotton plants, and it had unknown effects on boll weevil behavior.

In one study where fluorescent dye was applied to hornflies, *Haemotobia irritans* L., only 26–60%; of the dye was detected, and the dye was also lethal to the hornflies. Individually applied external labels often inflict trauma upon the insect and are impractical in lieu of other options. Dusts (including pollen) and dyes have been used to label large numbers of insects. Pollen can be used to determine the origin of insects in dispersal studies by passive marking (the insects' natural interaction with flora in the area) but these labels may be lost, are suitable only between molts, and are not reliable for monitoring species with cryptic habits. Therefore, external markers are usually of little value for studying insect behavior over long periods of time, for researching trophallaxis and food webs. Visual labels can affect insect behaviors by abrasion, added mass, altered appearance, and health related side effects. Some researchers have suggested that external visual markers might make labeled insects more visible to predators.

Dyes were ingested by imported fire ants, *Solenopsis invicta* Buren, in an experiment to monitor the intracolony exchange of various foods; however, detection of the label required the destruction of the insects for dye extraction, partitioning and drying before light wavelength absorbance was measured. In another study, imported fire ants were labeled with ingested dyes which were detected visually after the ants were crushed on white paper. Ants have also been dissected in order to detect ingested dyes, however, it is difficult to detect dyes and vital stain indicators in small quantities.

Ingestion of pollen and spores can also be used to mark insects but the labeled insects must be dissected to determine the presence or absence of these markers. In spite of the limitations and assumptions required for many applications of visual markers, a large number of studies, especially on dispersal (mark-recapture studies), have been conducted with varying degrees of success.

Rubidium

Rubidium (Rb) markers can be ingested from labeled artificial diet, tagged solutions sprayed onto host plants, and host plants raised from Rb-treated seeds. For example, pea aphids, *Acyrthosiphon pisum* Harris, have been labeled after feeding on bean, *Phaseolus* sp., plants cultured in Rb-tagged nutrient solutions. Rubidium can be detected using atomic absorption spectroscopy in pea aphids for up to 4 days (77% was eliminated in 2 days) after marking, and for up to 34 days after marking in the adult Mexican bean beetle, *Epilachna varivestris* Mulsant. Unlike most visually detectable markers, ingested Rb can be retained from larval to adult stages as has been demonstrated in the corn earworm, *Heliothis zea* Boddie; tobacco budworm, *Heliothis virescens* F.; fall armyworm, *Spodoptera frugiperda* J. E. Smith; pink bollworm, *Pectinophora gossypiella* Saunders; cabbage looper, *Trichoplusia ni* Hübner; and the imported cabbage worm, *Pieris rapae* L., and other insects with no observed toxic effects. Cabbage looper fecundity, fertility, longevity, mating behavior, and responses to sex pheromones were not influenced by ingested Rb concentrations of as much as 28,000 ppm. Rubidium labels have been useful for studying the dispersal patterns of the flights of various insects, including the corn earworm, fall armyworm, and pink bollworm. Food chains to the primary predator level in crop systems (e.g., cotton and grain sorghum) have been studied using Rb tags. Despite these advantages, researchers have reported equivocal results because of variation and detectable levels of naturally occurring Rb in their samples. Quantification of Rb also requires the physical destruction of samples for the use of atomic absorption spectroscopy or flame emission spectrophotometry.

Radiotracers

A desirable marker (i) provides analogs for biologically essential elements, (ii) does not require the destruction of labeled samples, (iii) persists in readily detectable quantities for longer periods of time, (iv) is easily applied to large numbers of insects with minimal manipulation of the populations, and (v) may permit detection in the field, even when tagged insects are located underground or within plant material. Unlike Rb, radioactive isotopes (radiotracers) provide analogs of biologically essential elements such as P-32, C-14, H-3, I-125, S-35, and Ca-45 that can be applied to study physiological phenomena including reaction rates, metabolic pathways, and the distribution and incorporation of elements or molecular compounds in biological systems. Radioactive analog or non-analog nuclides can also be administered to monitor the behavioral and ecological dynamics of individuals, populations, and biotic communities. The sensitivity of radiation detection exceeds that of most chemical and physical methods. To illustrate, carrier-free tritium at 30 Ci per mmole can be diluted by a factor of 10^{12} without hindering detection. In one study, 200 μ Ci Zn-65 in 20 ml molasses was used to label an entire imported fire ant colony. The tracer was easily detectable in the ants six months after the tagged bait was removed. Radiolabels can be detected while the tagged insect is living or dead, after being ingested by a predator or while the insect is functioning in the environment.

More than 44 different radionuclides have been used in entomological studies. To select a radiotracer for labeling insects, several factors must be considered: (i) the effective half-life of the isotope in the organism, (ii) possible toxic effects to the insect, (iii) the type of radiation emitted, (iv) the energy of the radiation, (v) the form or valence of the radionuclide, and (vi) the ease of handling and detecting the label.

The amount of a radioisotope retained by an insect after administration of a single internalized dose can decrease exponentially through time because of biological elimination and radioactive decay. The time required for the amount of a particular internalized radiotracer to decrease by one-half in a given insect is termed the "effective half-life." Effective half-lives of radiotracers decrease in response to excretion, oviposition, length of exposure to labeled bait, life stage, or caste of the insect, and the nature of the labeled food ingested (e.g., oil, protein, carbohydrate). Radioactivity can, however, be unequivocally detected long after the isotope's effective half-life has elapsed. To minimize loss of radiotracers in individuals over time, isotopes may be delivered to insects in a continuous infusion through a constant supply of radiolabeled food or water, or by using large, but nontoxic, single pulse doses of radionuclides.

A radiolabel might be detrimental to the inoculated system (and researcher) because of the nature of the emitted radiation. The biological hazards of radiation, although negligible in most studies, have been emphasized by the media, thus the decline in radioecology studies after the early 1960s. Radiotracers have received wide application in insect biochemistry and physiology experiments; various isotopes are selectively distributed within insect bodies. Female *Aedes aegypti* L. mosquitoes were twice as radioactive as males. Depending on the isotope, the dose of radionuclide, the type of radiation, the insect species and life stage exposed, and the method of administration, radiation levels that cause toxic effects may differ. Toxicity can also result from a species-dependent overdose of the element itself. Toxic levels of isotopes such as Ca-45, Fe-59, Ag-110, Cd-115, and I-131 in certain insect species have been documented.

White pine weevils, *Pissodes strobi* (Peck), painted with 500 μ Ci Co-60 per individual did not suffer increased mortality for at least two months, whereas in boll weevils, *Anthonomus grandis grandis* Boheman, mortality increased when P-32 concentrations exceeded 9.9 μ Ci per gram of labeled diet. Mortality studies on termites, *Reticulitermes flavipes* Kollar, revealed that although equivalent amounts of Mn-54, Sr-85, and Sr-85 + Co-60 produced lethal effects, Co-60, Cs-137, Sb-125, Mn-54 + Zn-65, Mn-54 + Se-75, Co-60 + Cs-137, and Cs-137 + Se-75 were not toxic to the termites. The wasp *Habrobracon juglandis* Ashmead developed "radioresistance"; P-32-treated adults survived as long or longer than controls. In some cases, sublethal doses of radiation have been shown to reduce insect fecundity. *Habrobracon juglandis* adults fed on less than 50 μ Ci P-32 per gram of labeled food showed no ill-effects, 50–200 μ Ci resulted in decreased (26%) egg production, and 200 μ Ci halted the egg production process. Eggs produced from radiolabeled adults may also show increased mortality and offspring hatched from labeled eggs may be deformed or die soon after eclosion. Boll weevil larvae raised on P-32-labeled diet had reduced longevity, fecundity, and pre-oviposition and oviposition periods compared to adults fed on P-32-labeled diet. On the other hand, radiotracers in other insects, such as the screwworm fly, *Cochliomyia hominivorax* Coquerel, did not affect longevity, fecundity, fertility or egg eclosion. Therefore, the use of a fixed radionuclide dose may be suitable for one species or life stage within the same species, but impractical for another species or intraspecies life stage.

Nuclides that release energy as gamma photons have advantages peculiar to the nature of gamma radiation. Gamma-emitting isotopes produce characteristic spectral emission' signatures' such that confusion between different radionuclides in the same insect or community is eliminated. Additionally, because gamma rays have negligible mass and are highly energetic, gamma-emitting isotopes have been employed to locate cryptic insects through several cm of soil and up to 14 cm of wood.

There are several methods for administering radiotracers to insects. Radiotracers can be applied as components of biologically essential compounds for biochemical research and radiolabeled mosquito sperm has been developed for mating studies. The following methods have been implemented to tag individual insects, populations, or biotic communities.

Dipping and Painting

Dipping insects in radioactive solutions, including I-131, Se-46, Ir-192, and Co-60, has been used to mark individual arthropods such as white pine weevils, and Co-60 dips for labeling boll weevils. The addition of a detergent allowed a P-32-labeled water dip to penetrate the cuticle of the ant *Lasius flavus* F. for a detectable retention time of 10 days. Dipping might not work in some instances, such as when the plum curculio, *Conotrachelus nenuphar* Herbst., was dipped in P-32 solution despite supplementation with wetting and sticking agents. However, P-32-glycerin suspensions painted onto the southern pine beetle, *Dendroctonus frontalis* Zimmermann, enabled the location of the tagged beetles after dispersal by the presence of radiotag on host tree pitch tubes. Southern pine beetle adults were also labeled as they emerged from tree boles painted with P-32. Painted radiolabels, like many visual markers, can be chipped or washed off, and thus might give false indications of radioactivity in the environment.

Disc and Wire Attachments

The movements of various subterranean beetle larvae have been monitored with external attachments labeled with Ra-226, Ta-182, and Co-60. Similarly, Ta-182 wire glued to coccinellid larvae was used to investigate crawling behavior on foliage. Discs and wires glued or tied to the insect exoskeleton or inserted within the insect's body have the disadvantages of some visually detected markers.

Ingestion

Isotopes can be transferred to insects by ingestion of radiolabeled food; in this way, large numbers of marked insects can be reared simultaneously. Tagged sugar and honey solutions, artificial diets, royal jelly, milk, raw meat, and living plants smeared or sprayed with radiotracers have produced desired results in a variety of insects. Labeled wood, blood, and living insect prey have been employed to tag termites, mosquitoes, and mantids, respectively. A more refined radionuclide delivery technique involves rearing insects on plants cultured in radiotagged nutrient solutions or plants injected with radioisotopes. Insect food webs on the thistle, *Cursium undulatum* Nutt., balsam fir, *Abies balsamea* L., and other plants were determined by injecting the plants with P-32. Similarly, P-32 injected into living rats, rabbits, goats, sheep, and hamsters resulted in the tagging of insects including *A. aegypti*, screwworm flies, and Oriental rat fleas, *Xenopsylla cheopis* Rothschild. Food interaction studies have been conducted in the White Oak Lake bed, an area in South Carolina contaminated by Cs-137 and Sr-90 wastes that were subsequently translocated by the terrestrial plant community. Naturally occurring U-238 and Th-232 fission products bismuth-214 and actinium-228 were similarly used in a stream ecosystem.

Water Culture

Large quantities of aquatic insects such as mosquitoes and blackflies have been labeled through adulthood when the larvae were raised in P-32-tagged water. In a large scale application of this technique, Zn-65 was sprayed onto a lake, and P-32 was systematically dripped into a stream to examine the trophic structure of each system.

Trans-life Stage Transmission

Radiotracers can be passed from one life stage of an insect to other life stages, and in a sense, this can be viewed as being a delivery system if an earlier life stage is more effectively tagged for studying a subsequent life stage. This can be accomplished when the initially labeled insect stage obtains the tag by injection, ingestion, or water culture. Grasshoppers, *Melanoplus mexicanus* Sauss and *Camnula pellucida* Scudder, were shown to retain ingested P-32 from nymphs to adults. Similarly, radioisotopes ingested by larvae of imported cabbageworm (Ca-45 and P-32), *Panaxia* sp. and *Arctia caja* L. (S-35), and boll weevil (P-32) were retained to adulthood. Screwworm fly larvae raised on P-32-injected goats and sheep had detectable levels as pupae, adults, and eggs and larvae of the next generation. Examples of insects that had ingested radiotagged food and transferred the label to their eggs include *Habrobracon juglandis*, (Sr-89), the walnut husk fly, *Rhagoletes completa* Cresson, and the velvetbean caterpillar, *Anticarsia gemmatalis* Hübner (P-32). P-32 was transmitted from tobacco budworm adults to eggs to larvae. Larval mosquitoes and blackflies raised in P-32-labeled water cultures retained the tag into adulthood, and egg batches of *Culex pipiens* L. mosquitoes retained P-32 from adults raised as larvae in a labeled water culture.

There are a number of different ways of detecting radioactive decay. The choice of detector depends upon the type of radiation, the physical state of the sample, and where detection will occur (e.g., in the laboratory or the field). The Gieger–Müller tube, liquid scintillation and solid detectors, autoradiography, and portable rate meters have received the greatest application in insect ecology and behavior studies.

Representative insect ecology and ethology radiotracer include population measurements, dispersal and movement, territoriality, feeding behavior (including trophallaxis), vector-parasite relationships, and food chains and webs.

Neutron Activation Analysis

Because of public concern regarding the potentially hazardous effects of ionizing radiation, some scientists have used neutron activation analysis (NAA) as an alternative. Rare earth elements, such as Sm and Dy, are good tracers but are not analogous to biochemically essential elements. Because NAA markers are made radioactive by exposing samples to specific thermal neutron fluxes in a nuclear reactor, the thermal neutron capture cross-section of the nuclide should be large (≥ 0.1 barn). The natural abundance of the stable tracer in the experimental system should be less than 10% of the applied dose to avoid equivocal results such as those encountered with Rb labels. The NAA tracer for insect studies should be selected for a short half-life and readily detected radiations (preferably gamma rays) after the nuclide has been activated. NAA methods provide radio-safety in the environment, a diversity of nuclides from which to choose, and sensitivity of detection. The techniques also permit long-term experiments without decay of the tracer, nondestructive sample analysis such that the same sample can be repeatedly activated and measured, and quantification of the label in each sample based upon the amount of radiation emitted. Drawbacks to NAA techniques include (i) relatively long (≥ 1 d) analyses of the samples, (ii) persistence of the stable tracer in the environment which may render future experiments in the same area unreliable, and (iii) "loss" of the tracer in the experimental system until NAA is performed. The activated nuclide can be detected and quantified using the same diversity of methods available for conventional radiotracers.

Toxicity to the insect may result from stable-activable tracers, but detectable nontoxic levels may be determined by experimentation. Application of these elements to insects has been achieved through ingestion and by exposure to the insect's cuticle. Some plant species, such as white mustard, Brassica hirta Moench, and hairy vetch, *Vicia villosa* Roth., have been shown to translocate Dy and Eu from soil to leaves; thus certain herbivorous insects may be labeled on tagged host plants, and by extension, food webs could be examined using NAA methods.

Rare earth tags have been detected in medically and agriculturally important insects, including the tsetse fly, *Glossina morsitans* Westwood (from Eu-, Dy-, Au-, and Ir-labeled nutrient solutions), and the Mediterranean fruit fly, *Ceratitis* *capitata* Wied. (Mn-labeled nutrient solutions). NAA has been used in some insect ecology and ethology studies, including dispersal of *Drosophila* spp. and effects of vegetative cover on the sizes of imported fire ant territorial areas.

Other activation analysis methods have been conducted with trace elements and compounds such as zirconium oxide, Bi, Pb, cerium oxide, Sn, and Se sprayed on mosquitoes then bombarded with alpha particles in a cyclotron to produce X-ray emissions.

Carbohydrate Profiling

Gas-liquid chromatograph profiles of cuticular lipids extracted from the surface of insects is a form of "passive" marking in that the marker was naturally acquired by the insect during its lifetime. This technique has received limited use, including application for determining differences in age, sex, and geographical origin of screwworm flies. One preliminary study showed that overwintered boll weevils could be distinguished from other individuals, and that geographic origins of boll weevils may be determined with 90% certainty.

Immunoglobulin

Various immunoglobulins (Ig) can be applied to insects and later detected using enzyme-linked immunosorbent assays (ELISA). Applications of this marking method have been few and the primary limitation has been relatively rapid loss of unequivocally detectable levels of the Ig (generally measurable loss occurs within a week). The following examples, however, illustrate how Ig methods can be used in different ways. Convergent lady beetles, *Hippodamia convergens* Guérin–Meneville, were marked and recaptured after as long as 30 d using rabbit Ig, and chicken Ig was 75% effective after 11 d. *Lygus hesperus* Knight were marked for 8 d by submersion in rabbit Ig. *Anaphes iole* Girault, a parasitoid of *Lygus* spp. eggs were marked by feeding them with rabbit Ig-tagged honey solution, and others were marked externally tagged by contact exposure or topical mist. The Ig marker was retained by the parasitoid throughout the entire adult lifespan (<2.5 d) regardless of the application method.

References

DiGregorio D, Kitchings T, Van Voris P (1978) Radionuclide transfer in terrestrial animals. Health Phys 34:3–31

Hagler JR, Cohen AC, Bradley-Dunlop D, Enriquez FJ (1992) New approach to mark insects for feeding and dispersal studies. Environ Entomol 21:20–25

McKibben GH, Robbins JT (1996) Chemical fingerprinting of boll weevils using surface lipid analysis. In: Proceedings of the Beltwide Cotton Conferences. National Cotton Council, Memphis, Tennessee, pp 232–233

Showler AT, Knaus RM, Reagan TE (1988) The versatility of radiotracer methods for studying insect ethology and ecology. Fla Entomol 71:554–580

Showler AT, Knaus RM, Reagan TE (1990) Foraging territories of the imported fire ant as determined by instrumental neutron activation analysis. Insectes Soc 36:235–239

Southwood TRE (1978) Ecological methods. (2nd edn) Chapman and Hall, London

Marking Pheromones

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A marking pheromone is a chemical compound (or mixture of compounds) emitted by an insect that advertises the past or current presence of the insect or its progeny at or in association with a valued resource. The type of resource may be food, an egglaying site, or a site of shelter.

Some kinds of insects foraging for food save valuable time and energy and improve foraging efficiency by following a trail of marking pheromone deposited by conspecifics that have discovered a quality food resource. Other kinds of insects foraging for food or egglaying sites avoid investing time, energy, or progeny at depleted or overcrowded resources by rejecting locales scented with marking pheromone. A few kinds of insects use pheromone to mark territories around nests that serve as sites of shelter.

Marking pheromones may be released from a variety of endocrine or exocrine glands of insects as well as from other structures associated with digestive, reproductive and locomotory systems. Most marking pheromones are non-volatile and can be detected only when touched by antennae, mouthparts, tarsi, or the ovipositor. Some, however, are volatile and can be detected via antennae at distances of several centimeters.

Ants and tent caterpillars are good examples of insects that follow a trail of marking pheromone to enhance food-foraging efficiency. After finding food, fire ant workers and tent caterpillar larvae deposit marking pheromone on their return to the nest. The pheromone signals the discovery of food to conspecifics, which then proceed to follow the trail to its source. The greater the amount or quality of the food, the greater the amount of pheromone deposited. Trail marking ceases when the food supply is exhausted.

Honeybees and bumblebees are good examples of insects that use information from marking pheromone as a cue to cease foraging (at least temporarily) for food at marked sites. Bees may visit a variety of flowers to obtain nectar. When doing so, they temporarily deplete the nectar supply of florets, which may not be renewed for an hour or more. If a bee were to invest time and energy probing for nectar in florets whose supply was not yet renewed, it could jeopardize its ability to acquire a full complement of nectar. Marking pheromone deposited on a floret by a previous forager signals the arriver that the supply of nectar has been exhausted, or at least is not yet fully renewed. Interestingly, honeybees and some species of bumblebees can detect each other's marking pheromone. Moreover, the time required for nectar replenishment appears to correspond closely to the duration of activity of marking pheromone.

Among insects foraging for egglaying sites, hymenopterous parasitoids that oviposit in host eggs, larvae, or pupae, fruit flies (family Tephritidae) that oviposit in the flesh of host fruit, and beetles that oviposit on or in seeds illustrate the role of marking pheromone in preventing overcrowding of larval food resources. Often, the host of a parasitoid, tephritid fly, or seed beetle can support only a single larva to maturity. Pheromone released during or after egg deposition signals occupancy by a conspecific. In a few cases, host-foraging females may be able to detect host occupancy and associated marking pheromone of a close or distant relative.

Sometimes, a host is sufficiently large enough to support several larvae to maturity, though never an unlimited number. In such cases, marking pheromone may allow a female to assess not merely the presence versus the absence of an occupant, but also to assess the level of occupancy, as determined by the amount of pheromone present relative to the size of the host.

Some predatory insects, such as neuropteran lacewing females and coleopteran ladybird females, use marking pheromone as a cue for avoiding overcrowding food resources (particularly colonies of aphids) that will serve as prey for larval progeny. Although aphids may be numerous at the time of predator oviposition, they are unlikely to remain so in the face of the voracious appetites of lacewing and ladybird larvae. Several members of these groups are known to refrain from ovipositing in the presence of conspecific larvae. The most frequently encountered cue indicating larval presence is the marking pheromone associated with the footprints of conspecific larvae.

The physiological and informational state of an insect, along with the state of the environment, may have a strong effect on the degree to which an individual in search of a resource responds to the presence of marking pheromone. If prior experience informs an insect that a desired resource is plentiful in the local habitat, then the insect may almost always respond strongly to marking pheromone and, except in cases of trail-marking pheromone, leave the marked locale and search elsewhere. On the other hand, if prior experience informs the insect that a desired resource is scarce and the insect is highly motivated to acquire the resource, then the insect may respond weakly to the marking pheromone, or even ignore it, and proceed to attempt to use the depleted or occupied resource at hand.

Numerous species of ants deposit marking pheromone in the vicinity of their nests. Such pheromone may serve not only as a home-range marker that circumscribes the territory within which colony members forage, but also may serve as a signal to alien ants from other colonies that the nest itself is occupied.

Some marking pheromones have been exploited for managing pest insects. For example, the European cherry fruit fly, *Rhagoletis cerasi* L., deposits marking pheromone on the surface of host fruit after laying eggs. The pheromone has been identified, synthesized and sprayed on cherry trees in Switzerland to protect cherries against fly oviposition. Formulation with adjuvants helps protect the water-soluble pheromone against the degrading effects of rainfall. It is anticipated that enhanced knowledge of the identity of marking pheromones will be accompanied by the increasing use of such pheromones in pest management.

► Pheromones

References

Fitgerald TD (1995) The tent caterpillars. Cornell University Press, New York

Hölldobler B, Wilson EO (1990) The ants. Belknap, Cambridge

Landolt P, Averill AL (1999) Fruit flies. In: Hardie J, Minks AK (eds) Pheromones of non-lepidopterous insects associated with agricultural plants, CAB International, Oxford, United Kingdom, pp 3–25

Nufio CR, Papaj DR (2001) Host marking behavior in phytophagous insects and parasitoids. Entomol Exp Appl 99:273–293

Prokopy RJ, Roitberg BD (2001) Joining and avoidance behavior in non-social insects. Annu Rev Entomol 46:631–665

Ruzicka Z (2001) Oviposition responses of aphidophagous coccinellids to tracks of ladybird and lacewing larvae. Eur J Entomol 98:183–188

Stout JC, Goulson BD (2001) The use of conspecific and interspecific scent marks by foraging bumblebees and honeybees. Anim Behav 62:183–189

Marlatt, Charles Lester

Charles Marlatt was born in 1863. He attended Kansas State University, where he received a B.S. in 1884 and an M.S. in 1886. He joined the staff at Kansas State in 1887, but in 1889 C. V. Riley hired him to work in Washington, DC, as an assistant entomologist and artist. Riley became first assistant entomologist and assistant chief of the Division of Entomology in 1894, a position he held until 1925. It is largely through Marlatt's persistent efforts that the Plant Quarantine Act of 1912, important legislation that helped curb the unregulated movement of plants (and insects) into the United States, was passed. In 1927 he was named chief of the Bureau of Entomology, a job he held in addition to the position as Chief of the Plant Quarantine and Control Administration. He administered the Plant Quarantine Act until 1929. Marlatt was an authority on both sawflies and scale insects, and in 1900 assumed responsibility for the government's collection of scales. He played an important role in identifying the homeland (northeastern China) of the San Jose scale, and of establishing biological control in the United States through importation of a predator. Under his leadership two successful eradication campaigns were conducted: the Mediterranean fruit fly in Florida and the date scale in California. Marlatt received a number of honors during his career, and served as president of the Entomological Society of Washington and the American Association of Economic Entomologists. He died on March 3, 1954.

Reference

Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Marsh Beetles

Members of the family Scirtidae (order Coleoptera).
► Beetles

Marsh Flies

Members of the family Sciomyziidae (order Diptera).
► Flies

Marsh Treaders

Members of the family Hydrometridae (order Hemiptera).
► Bugs

Marsupial Chewing Lice

Members of the family Boopidae (order Phthiraptera).
► Chewing and Sucking Lice

Marsupial Lice

Members of the family Trimenoponidae (order Phthiraptera).
► Chewing and Sucking Lice

Marx, George

George Marx was born in Hess, Germany, on June 22, 1838. He is known as an illustrator of renown. Marx completed pharmaceutical studies in Germany before moving to the United States in 1860. There, he served in the Union army during the American Civil War. After working as a pharmacist in Philadelphia, Marx accepted a position as a natural history illustrator with the United States Department of Agriculture in 1878. He received a M.D. degree in 1885. In 1889 he was made chief of the Division of Illustrations. Although acknowledged as an expert on spiders and scorpions, he is remembered primarily for his excellent illustrations. He died in Washington, DC, on January 3, 1895.

Reference

Essig EO (1931) A history of entomology. The Macmillan Company, New York. 1029 pp

Masked Chafers, *Cyclocephala spp*. (Coleoptera: Scarabaeidae)

The larvae of these species feed on the roots of turfgrasses.
► Turfgrass Insects and Their Management

Mason Wasps

Members of the family Vespidae (order Hymenoptera).
► Wasps, Ants, Bees and Sawflies

Mass Provisioning

The act of storing all the food required for the development of an immature insect at the time of egg laying. (contrast with progressive provisioning)

Mass Rearing of Natural Enemies

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Mass rearing involves the production of millions of insects, with the objectives of controlling pests and supporting Integrated Pest Management (IPM) programs. Several definitions have been proposed for mass rearing, including:

- Mass rearing is the economic production of millions of beneficial insects, as if in an assembly line, in order to produce the maximum number of fertile females, with the least number of men/hours and space, in the shortest time possible, at low cost;
- Insect production that can accomplish goals at an acceptable cost/benefit ratio, in numbers exceeding from 10 thousand to 1 million times the average productivity of a population of native females;
- Systematic, automated activity conducted in integrated facilities, in order to produce a relatively large supply of insects for distribution.

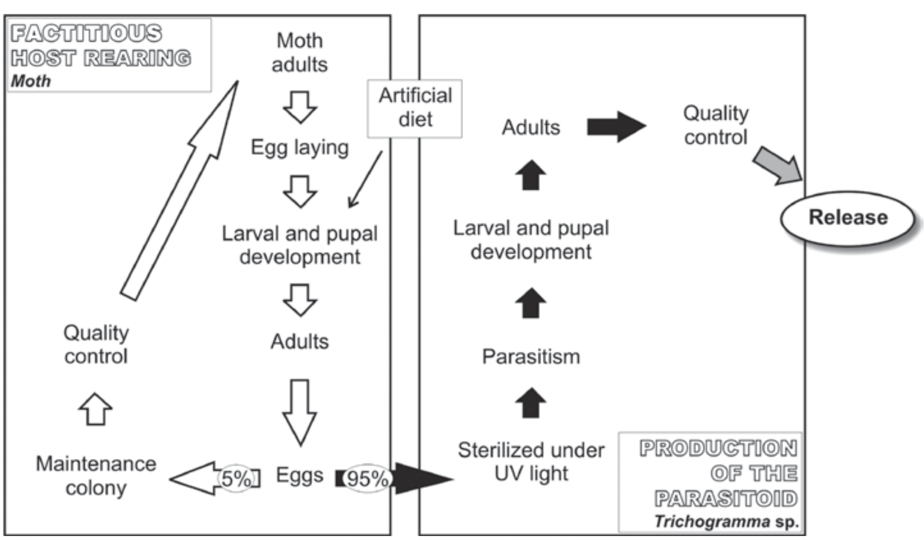
Therefore, mass rearings are truly factories, in which cost is highly important, particularly with respect to labor, since it represents 70–80% of total production cost. To achieve this goal, the personnel involved in rearing must be highly qualified in the field of insect rearing techniques. Often such personnel are not readily available. Consequently, it becomes necessary to automate the process for the production of natural enemies, especially in countries where labor is more costly.

Mass rearings are started from smaller-scale or research rearings (conducted by one or two people), or intermediate-sized rearings, upon which basic research about the target (often an agricultural pest) and the natural enemy (parasitoid or predator) are conducted. Therefore, in order to produce natural enemies, two species have to be reared, the pest and the natural enemy (Figs. 12 and 13). The potential for rearing a large number of natural enemies increased as artificial diets began to be developed since the 1960s, with emphasis on artificial diets for Lepidoptera, Coleoptera, and Diptera.

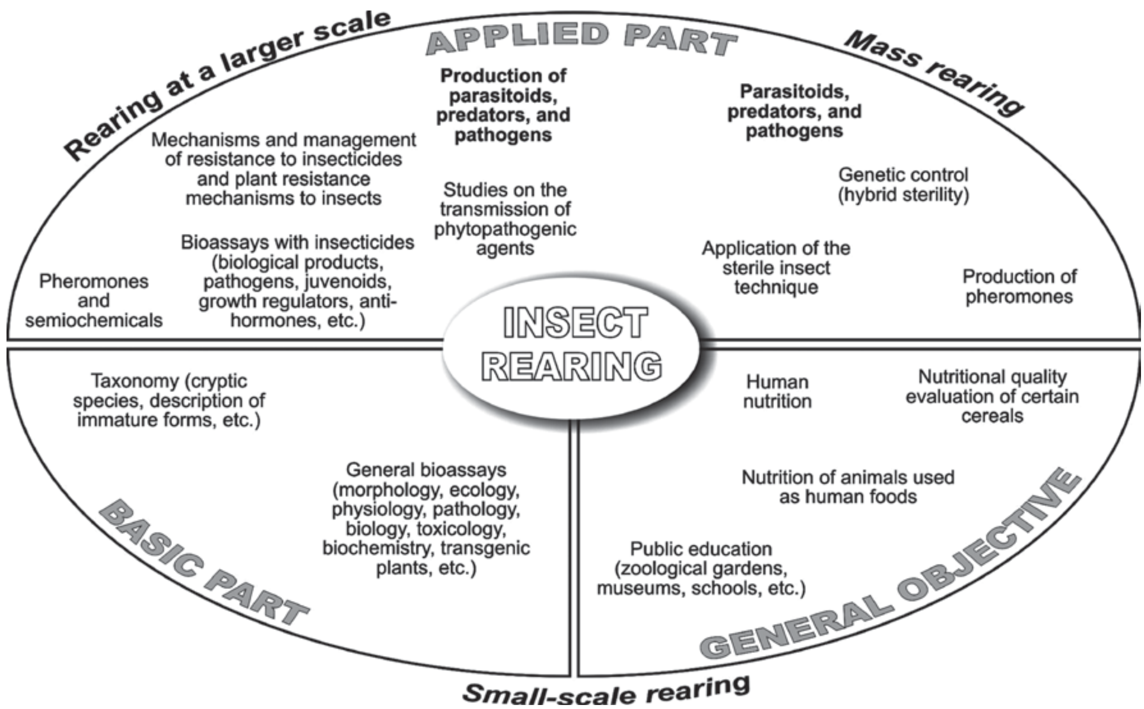
Considering the fundamental approaches to implementing biological control, i.e., introduction (classical biological control), conservation (natural biological control), and multiplication (applied biological control), mass rearings assume greater importance in the latter because, in this case, inundative releases are made with a similar effect as conventional insecticides, because they decrease pest populations more rapidly and are well accepted by growers because of their similarity with conventional agrochemicals.

Although many government-sponsored programs exist worldwide involving mass rearings of fruit flies, boll weevil and the egg parasitoid *Trichogramma* spp., most rearings are commercial. These are companies that sell natural enemies.

Although the first mass production by a private company took place in 1926 (Fillmore Citrus



Mass Rearing of Natural Enemies, Figure 12 **Rearing schematics of *Trichogramma* spp. on a factitious host.**



Mass Rearing of Natural Enemies, Figure 13 **Relationships between insect rearings and various areas of entomology.**

Protective District) in the USA, insect trading was initiated in the 1960s, with ladybugs and mantids sold to control garden and nursery pests. Beginning in the 1980s, the number of companies that supplied insects significantly increased. In 1992, 95 suppliers (twice as many as in 1977) made 106 species available in the market; in 1997, there were 142 suppliers and 130 beneficial insect species for sale. In Europe, there was also a great increase in this type of trade from the 1970s.

A principal impetus to the use of insectary production of natural enemies was the successful use of the predatory mite *Phytoseiulus persimilis* to control mite pests. Today, several natural enemy species, produced by many companies, are available for the grower, especially against protected-cultivation pests. *Encarsia formosa* is the most frequently sold parasitoid on the European continent to control whiteflies in protected cultivations. As a result, today many companies worldwide sell biological control agents packed in a similar manner as agrochemicals at market prices.

In South America, Colombia is the industry leader, with about 20 companies, particularly in the Cauca Valley, a region with a well-developed, technical agriculture. Brazil already has a similar number of companies, with emphasis on the production of *Cotesia flavipes*, which is currently released into 1.7 million ha annually to control *Diatraea saccharalis*, the sugarcane borer. *Trichogramma* spp. is released in about 200,000 ha of sugarcane, corn, and vegetables, while *Trissolcus basalis* is released in about 20,000 ha of soybean to control bugs. India, the Philippines, the Canary Islands, Venezuela, and Chile, among others, are players in this industry. New Zealand and Australia have a tradition in rearing natural enemies. China, Russia, and Cuba, in turn, have government-supported rearings. At present, between 15 and 20 million hectares are treated worldwide with such agents. *Trichogramma* is still the most widely used.

More than 125 natural enemy species are available in the market, with hundreds of producing companies. Currently, a US$50 million annual market exists for biological products; even though this represents 0.5% of the agrochemicals market, this figure is expected to double or triple in the first part of this century.

As the number of insects produced in any rearing increases, problems related to facilities, costs, microorganisms (contaminants), and insect quality control also increase. In addition to a necessity for automation, problems with employees may arise due to allergies, such as those caused by moth handling, in *Trichogramma* rearings, for example.

As previously commented, two insect species have to be reared; this requires basic knowledge about the pest and the natural enemy (biology, ecology, biochemistry, behavior, physiology, nutrition, etc.). Knowledge about temperature requirements (in degree-days) is essential for production planning.

Another problem in mass rearings relates to the fact that the insect will be used during one season of the year only. When it is not being used, it must be stored. These techniques, still incipient, are used with *Trichogramma* by inducing diapause and subsequently stopping it when demand for the insect arises. Liquid nitrogen has also been used to store eggs. Quality of the insects produced is one of the greatest concerns today. Loss of genetic variability in mass-reared insects may lead to the loss of wild-insect traits, preventing laboratory-reared insects from being as competitive as those found in nature. There are two types of processes that may result in genetic deterioration: random and non-random or adaptive processes. Among these deterioration mechanisms, genetic drift (or founder effect), inbreeding, and selection are the most relevant. Therefore, monitoring the production, the process, and the product over successive laboratory generations is essential for the production of laboratory insects that are as competitive as those that occur in nature. The International Organization for Biological Control has already established standards that take into account biological characteristics and molecular analyses, which must be followed up and regulated by law to prevent ethical problems that may discredit the reputation of biological control.

An ideal situation in mass rearing would occur if the insect host could be eliminated and the parasitoid or predator reared on artificial (*in vitro*) diets. Although the Chinese demonstrated *in vitro* advancements to the world in 1982 by rearing *Trichogramma dendrolimi* on artificial diet, the expected developments in this area did not occur, frustrating the scientific community, which had high expectations for this new technology.

Further studies are required, since the diets used today are based on those developed in the 1960s. The search for better diets must include greater knowledge of the nutritional requirements of insects, but also must take into account the technology and equipment used in this food processing industry for large-scale production. More refined bioassays, using microscopic, nanotechnological, molecular, and biochemical and fermentation techniques may provide advancements in this field. More sophisticated bioassays may improve microorganism control in large rearings and elucidate the role of symbionts (*Wolbachia*, *Buchnera*, etc.) in insect nutrition. Together with these, it is essential to foster those that work in the insect-rearing sector, training them at both the undergraduate and graduate levels. The process of using natural-enemy agents to control pests is a cultural as well as an economic process that requires high-quality employees, in order to assure acceptance by agricultural producers.

References

Chambers DL (1977) Quality control in mass rearing. Annu Rev Entomol 22:289–308

Cohen AC (2004) Insect diets: science and technology. CRC, Boca Raton, FL, 324 pp

Etzel LK, Legner EF (1999) Culture and colonization, pp 125–197. In Bellows TS, Fisher TW (eds) Handbook of biological control: principles and applications of biological control. Academic, San Diego, CA, 1,046 pp

Finney GL, Fisher TW (1964) Culture of entomophagous insects and their host, pp 328–355. In: DeBach P,

Schlinger EI (eds) Biological control of insect pests and weeds. Chapman & Hall, London, 844 pp
King EG, Leppla NC (1984) Advances and challenges in insect rearing. USDA-ARS, New Orleans, LA, 306 pp
van Lenteren JC (Ed) (2003) Quality control and production of biological control agents: theory and testing procedures. CABI Publishing, Cambridge, 327 pp
Leppla NC, King EG (1996) The role of parasitoid and predator production in technology transfer of field crop biological control. Entomophaga 41:343–360
Leppla NC, Adams F (1987) Insect mass-rearing technology, principles and applications, 20 pp
Parra JRP, Botelho PSM, Corrêa-Ferreira BS, Bento JMS (2002) Controle biológico no Brasil: parasitóides e predadores. Manole, São Paulo, Brazil, 609 pp
Singh P, Moore RF (eds) (1985) Handbook of insect rearing. Elsevier, Amsterdam, 496 pp

Masters, George

GEORGE HANGAY
Narrabeen, NSW, Australia

George Masters was born in July 1837 in Kent, England. Not much is known of his early years, except that he was a horticulturist and when he migrated to Australia, he lived in Tasmania. Later, the amateur entomologist A.W. Howitt in Melbourne employed him. Consequently, many of the specimens which he collected are now in the Howitt Collection in the Museum of Victoria (Melbourne). In 1864 he became Assistant Curator and Collector of the Australian Museum in Sydney. In 1874 William John Macleay employed him as curator of his zoological collections. Masters remained in this position even after the collections (by then Museum) were transferred to the University of Sydney. He was a very good field worker, not only with insects but also with most vertebrate animals, especially birds. It was said that at time more than half of the natural history specimens in the Australian Museum were of his taking. As Curator of the Macleay Collections he participated in the "Chevert" New Guinea expedition. Apart from his collecting and curating activities, his Coleoptera catalogues are his main contributions to Australian entomology (Catalogue of the described Coleoptera of Australia, 1871–1886; Catalogue of the known Coleoptera of New Guinea, 1888). Later in life he suffered from nervous complaints and his eyesight became very poor. He died in a cab accident on July 23, 1912.

Reference

Lea AM (1929) George Masters. Vic Nat 45:164–167

Mastotermitidae

A family of termites (order Isoptera) presently containing only one species, Giant Northern Australia termite.

► Termites

Maternally Inherited

Characters that are transmitted primarily by cytoplasmic genetic factors, including mitochondria, viruses, etc., derived from the maternal parent. This is also known as cytoplasmic inheritance or extranuclear heredity.

Matheson, Robert

Robert Matheson was born at West River, Nova Scotia, Canada, on December 20, 1881. He received all his degrees in entomology at Cornell University, attaining his Ph.D. in 1911. He worked for South Dakota State University, Nova Scotia Agricultural College, and Cornell as a medical entomologist. His expertise was on mosquitoes and malaria, and he helped in the elimination of malaria from the east-central United States. He trained many students in medical entomology, and published "Handbook of mosquitoes of North America" (1929), "Medical entomology" (1932), and "Entomology for introductory courses" (1944). He died on December 14, 1958, at Princeton, New Jersey.

Reference

Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Mating Disruption

Use of pheromones to interfere with mating and reproduction, resulting in pest population suppression.

Matsumura, Shonen

Shonen Matsumura was born on March 5, 1872, and is considered to be the "father of Japanese entomology." He was interested in insects from an early age, and studied entomology at Sapporo Agricultural College (now Hokkaido University). He was appointed to the faculty there in 1896 and in 1898 published "Nippon Konchugaku" (Entomology of Japan). In 1899 he moved to Europe to advance his knowledge and in 1902 returned to Japan as professor. Much of his work was on Lepidoptera and Hemiptera, but he published on most orders. He authored about 240 papers and 35 books during his career. The illustrated 12-volume "Thousand insects of Japan" published between 1904 and 1921 was especially noteworthy. He also accumulated Japan's largest insect collection. He died on November 7, 1960.

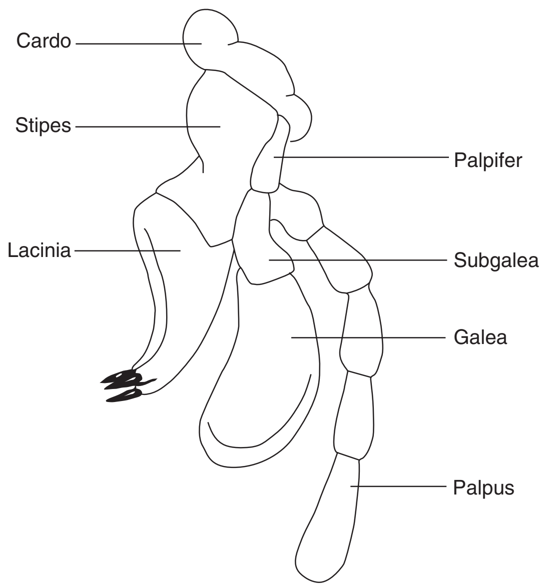
Reference

Herman LH (2001) Matsumura, Shonen. Bullet Am Mus Nat His 265:108–109

Maxilla

A pair of mouthparts located posterior (ventral) to the mandibles, and bearing sensory structures or palpi (Fig. 14).

► Maxillary Palp
► Mouthparts of Hexapods



Maxilla, Figure 14 External lateral aspect of the left maxilla in an adult grasshopper, showing some major elements.

Maxillary Palp (or palpus; pl., maxillary palpi)

A one- to seven-jointed sensory appendage (pair of appendages) on the insect maxilla (Fig. 15).

► Mouthparts of Hexapods

Maximum Parsimony Methods

Taxonomic methods that focus on the character values observed and minimizing the number of changes in character state between species over the tree, making the assumption that there have been approximately constant rates of change. The changes at each node in the tree are inferred to be those that require the least number of changes to give each of the two character states of the immediate descendants.

► Phylogenetics

May Beetles

Members of the subfamily Melolonthinae, family Scarabaeidae (order Coleoptera).

► Beetles
► Turfgrass Insects and their Management

Maxillary Palp (or palpus; pl., maxillary palpi), Figure 15 Front view of the head of an adult grasshopper, showing some major elements.

Mayflies (Ephemeroptera)

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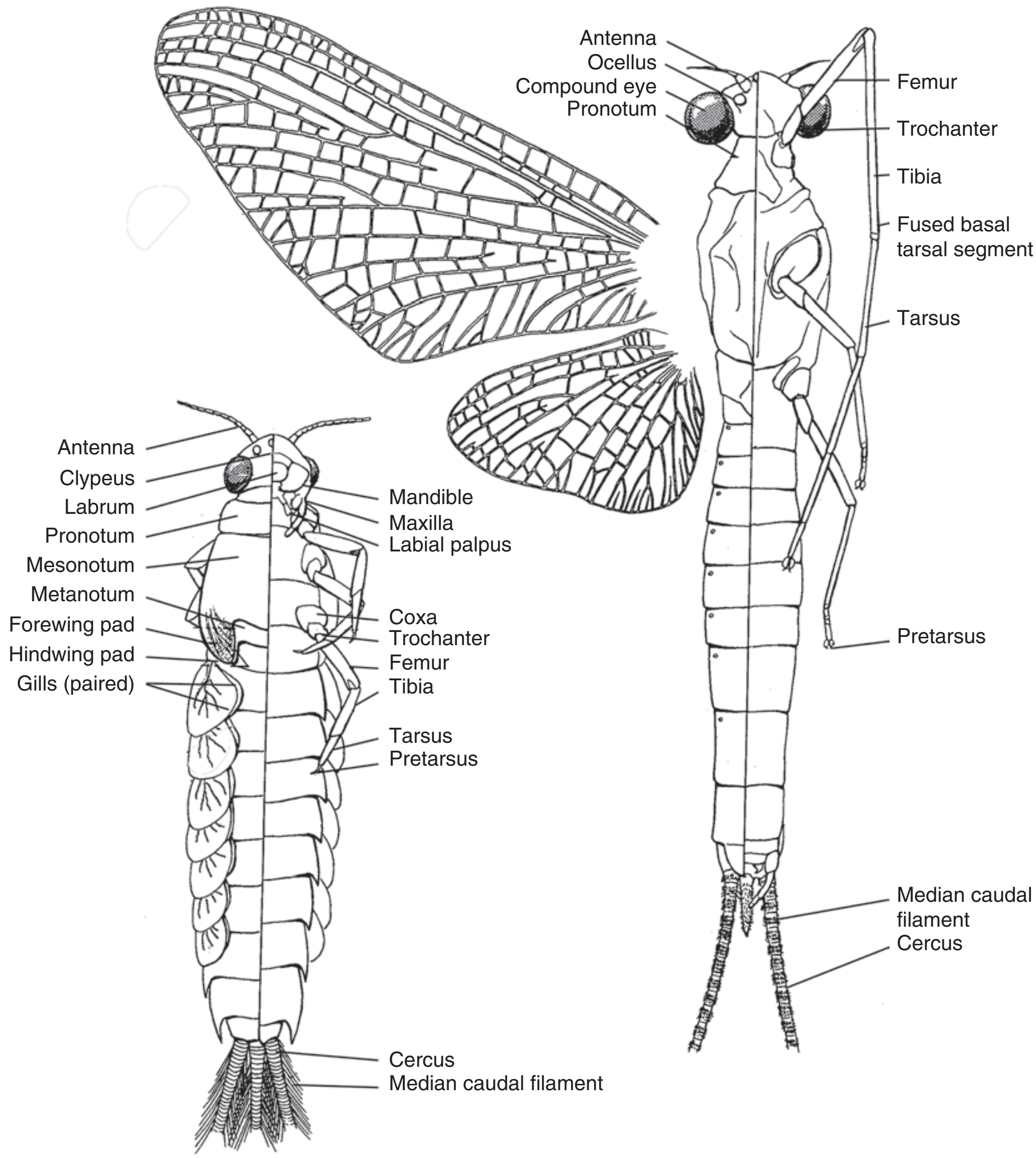
The Ephemeroptera or mayflies, are a primitive order of aquatic insects that, as adults, are easily distinguished by the presence of two pairs of membranous wings, the front wings larger and triangular in shape, with the hind wings much smaller (and sometimes absent). The antennae are bristle-like, and two or three long segmented caudal filaments or "tails" extend at the end of the abdomen. Additionally, adults are usually found at or near bodies of water (Fig. 16).

Most mayfly adults have two winged stages, one termed the subimago and the other the imago. The subimago, the winged stage after the molt from the nymphal stage (many entomologists prefer the term larvae for all immature insects) after a period of time that varies from an hour to days, will molt to the imago or adult stage. The angler or fly fisherman terms the subimago the "dun" and the imago the "spinner." The imago stage is ready to reproduce and disperse, the only biological functions of this stage. Some mayflies remain as a subimago and still can reproduce. In fact some subimagoes have vestigial or nonfunctional legs, and can only fly and mate, then die! Adult mayflies often form enormous nuptial flights, during which mating takes place. Swarming behavior can take place over the water, or sometimes remote from a body of water, and at various times of the day from dawn to dusk, or at night. The eyes of the male imago are modified, apparently for better acuity for aerial mating. Mated females return to the stream or pond to oviposit. Eggs of most mayflies are modified for different aquatic environments, usually with specialized attachment structures.

Mayfly immatures or nymphs can be distinguished from other aquatic insects with hemimetabolous or incomplete metamorphosis by the



Mayflies (Ephemeroptera), Figure 16 Diagram of mayflies: adult (*right*) and immature (*left*). Note that each is divided into dorsal (*left portion*) and ventral (*right portion*) perspectives.

presence of two or three caudal filaments or tails at the end of the abdomen, and usually one claw on each leg (absent in Behningiidae). Additionally, gills are attached to various segments on the side of the abdomen, either as flattened plates or filaments. Gills can also occur on the base of the legs or mouthparts. The body length can range from 2 to almost 35 mm, not including the caudal filaments.

Immature mayflies occur in many different habitats, both lotic (flowing waters, streams, rivers) and lentic (standing waters, ponds, lakes, reservoirs). However, the greatest diversity of mayflies is found in lotic habitats, especially those of higher elevations. Some species of Baetidae can be found in tide pools and alkaline desert pools. Some groups such as members of the family Heptageniidae (flatheaded mayflies) have flattened bodies, and are adapted to cling to instream rocks or other firm substrates in fast-flowing streams, whereas others such as members of the Baetidae (small minnow mayflies), Ameletidae (ameletid minnow mayflies), and Siphlonuridae (primitive minnow mayflies) are well adapted for swimming. Members of the Ephemeridae (common burrower mayflies) are burrowers in soft sediments of lakes, ponds and large rivers.

The higher classification of the Ephemeroptera is in part provisional. Researchers have presented much significant work towards a phylogenetic classification of the order. Currently, about 631 species are recognized from North America in twenty-three families of the forty-one extant families known in the world. A comprehensive index to North American mayfly species is provided at the website http://www.entm.purdue.edu/entomology/research/mayfly/mayfly.html.

Order: Ephemeroptera
- Suborder: Carapacea
  - Family: Baetiscidae
  - Family: Prosopistomatidae
- Suborder: Furcatergalia
  - Family: Austremerellidae
  - Family: Behningiidae
  - Family: Caenidae
  - Family: Dicercomyzidae
  - Family: Ephemerellidae
  - Family: Ephemeridae
  - Family: Ephemerythidae
  - Family: Euthyplociidae
  - Family: Ichthybotidae
  - Family: Leptohyphidae
  - Family: Leptophlebiidae
  - Family: Machadorythidae
  - Family: Melanemerellidae
  - Family: Neoephemeridae
  - Family: Oniscigastridae
  - Family: Palingeniidae
  - Family: Polymitarcyidae
  - Family: Potamanthidae
  - Family: Teloganodidae
  - Family: Tricorythidae
  - Family: Vietnamellidae
- Suborder: Pisciforma
  - Family: Acanthametropodidae
  - Family: Ameletidae
  - Family: Ameletopsidae
  - Family: Ametropodidae
  - Family: Arthropleidae
  - Family: Baetidae
  - Family: Coloburiscidae
  - Family: Dipteromimidae
  - Family: Heptageniidae
  - Family: Isonychiidae
  - Family: Metretopodidae
  - Family: Nesameletidae
  - Family: Oligoneuriidae
  - Family: Pseudironidae
  - Family: Rallidentidae
  - Family: Siphlaenigmatidae
  - Family: Siphlonuridae
  - Family: Siphluriscidae

The majority of mayflies reside in running waters, but unlike another group of aquatic insects, the stoneflies (Plecoptera), they attain maximum diversity in warm lotic habitats. Most mayfly nymphs are collector-gatherers or scrapers. A few species are specialized filter-feeders or carnivores. Shredders are very poorly represented. Most mayflies of temperate regions have a one-year life cycle (univoltine), the vast majority of which is spent as an aquatic nymph. In fact, it is the ephemeral nature of the aerial adult stage that is responsible for the Greek name of the order. Adults live from one hour to several days, depending on weather conditions and the species in question. The gills of mayflies are highly variable. In most species gills are present only on the abdomen. Gills often occur on the first seven abdominal segments, although one or more pairs may be absent, depending on the species. A few species also possess gills on the legs and head. Most mayflies possess three caudal filaments; a few have two caudal filaments. Microhabitat occurrence is reflected more distinctly in the body form of nymphs than in that of any other order. Some species have a fusiform body shape that enables them to move about on the tops of rocks in rapid water, whereas others are flattened dorsoventrally to hug rock surfaces. Other groups construct burrows in the substrate with their mandibles, and use their gills to create respiratory and feeding currents. Yet others are adapted for creeping and climbing among accumulations of organic material, or in silty backwaters, or in plant beds.

A brief synopsis of the more common families is provided.

Family Ameletidae (Ameletid Minnow Mayflies)

The nymphs are usually found in small fast-flowing streams among rocks. Some species are confined to very small brooks, often congregating in pool areas. Nymphs are strong swimmers, but often seek quieter waters. Nymphs are scrapers, using the pectinate comb of spines (the diatom rake) on part of the mouthparts to feed on periphyton or algae. There is usually only one generation per year. Some species of *Ameletus* apparently are parthenogenetic, reproducing without the presence of males.

Family Baetidae (Small Minnow Mayflies)

Nymphs are found in a wide variety of aquatic habitats. They may be the only mayflies present in extreme environments such as high-elevation streams, the sources of springs, or mildly polluted waters. They are considered good swimmers, darting in short spurts from one spot to another. Often they are, in terms of numbers, the most important mayflies of many North American streams. The species of *Baetis* collectively occupy an extremely wide range of flowing water habitats. *Callibaetis* is primarily a standing water genus, some species of which occur in the backwaters or quiet margins of running waters. Most members of the family are collector-gatherers or scrapers. Most of the species found in flowing water habitats apparently have two generations per year, others only one.

Family Caenidae (Small Squaregill Mayflies)

The small nymphs are usually found in standing water, and are often abundant in ponds, lakes and wetlands. They are considered sprawlers in silty bottoms in the zones of rooted vegetation. Nymphs feed usually on decaying plant material. Some species have several generations per year, especially in the more southern areas. *Caenis* is the common genus.

Family Ephemeridae (Common Burrower Mayflies)

Nymphs of this family construct a U-shaped tunnel in bottom sediments with openings at both ends. They use their feathery gills to maintain a current within the burrows for obtaining dissolved oxygen. Additionally, they filter out small particles of organic material brought in by the current. Some species ingest sediments mixed with organic material. The nymphs are often abundant in lakes, ponds, large rivers, and reservoirs. Mass emergence of the large-sized adults, especially in the Mississippi River Valley region, attracts attention, and at times is considered a nuisance. Depending on location, species of common burrowers complete their life cycle in 1–2 years. The two genera, *Ephemera* and *Hexagenia* are widespread throughout North America.

Family Ephemerellidae (Spiny Crawler Mayflies)

Nymphs occur in almost all types of flowing water. Some species occur in steep gradient segments of streams in high elevations to silty microhabitats in lower elevations. Some groups also are found in standing waters of lakes and wetlands. Nymphs crawl about and are well camouflaged. Most species are considered collector-gatherers or scrapers, but some *Drunella* species have been reported to be partially predaceous. Nymphs have the peculiar defensive behavior of raising its three tails in a posture called the "scorpion posture." Most species have one generation per year.

Family Heptageniidae (Flatheaded Mayflies)

Heptageniids are perhaps the most typical of all mayfly families found in flowing water. The nymphs are flattened and generally adapted to life in high-gradient mountain streams. Most species are restricted to running waters; a few also inhabit wave-swept shores of lakes. Species of *Heptagenia* generally occupy warmer and siltier running waters than other genera such as *Epeorus*, and *Rhithrogena* are restricted usually to cool, fast mountain streams. Most heptageniids are scrapers, removing attached microscopic plants and other particles from rock surfaces; a few are collector-gathers and predators. The numerous North American species have one to two generations per year.

Family Isonychiidae (Brushlegged Mayflies)

Nymphs of this family can be abundant in a variety of flowing waters, and especially abundant in shallow riffle reaches of streams of eastern North America. Nymphs are strong swimmers, and use hair fringes on the forelegs for filtering organic particles from the water column. Most species have one generation a year, but in more southern areas they may have two generations per year. The genus *Isonychia* occurs over most of North America, and adults are easily distinguished by their reddish coloration.

Family Leptohyphidae (Little Stout Crawler Mayflies)

Nymphs are often associated with beds of aquatic plants or other habitats where silt accumulates. The opercular gill plates protect the remaining gills from silt deposition. Members of this genus are slow-moving sprawlers that feed on sedimentary organic material. The genus *Tricorythodes* is a common North American genus.

Family Leptophlebiidae (Pronggilled Mayflies)

The poor-swimming nymphs of this family are commonly found in shallow streams of all sizes. Some groups are associated with accumulations of leaves and debris in overflow areas or flood plains. Nymphs of some species are filter-feeders in rapid sections of large silty rivers of western North America, while others feed on accumulated decomposing plant material or scrape algae of various substrates. Nymphs of some species are known for their migratory habits of moving in spring from streams to pools associated with the floodplain. One to two generations per year are common with most species. Emergence of some species occurs as early as February.

Family Siphlonuridae (Primitive Minnow Mayflies)

Nymphs occur both in lotic and lentic habitats, usually associated with accumulations of silt or the presence of vegetation. Nymphs often congregate in pools or overflow areas of streams. Nymphs are good swimmers but prefer quieter areas of streams or edges of pools and ponds. They feed on organic debris, but also engulf small aquatic organisms. Most species have only one generation per year. The genus *Siphlonurus* is widespread throughout North America (Fig. 16).

References

Edmunds GF Jr, Jensen SL, Berner L (1976) The mayflies of North and Central America. University of Minnesota Press, Minneapolis, MN, 330 pp

Jacobus LM, McCafferty WP (2006) Reevaluation of the phylogeny of the Ephemeroptera Infraorder Pannota (Furcatergalia), with adjustments to higher classification. Trans Am Entomol Soc 132:81–90
McCafferty WP (1991) Toward a phylogenetic classification of the Ephemeroptera (Insecta): a commentary on systematics. Ann Entomol Soc Am 84:343–360
McCafferty WP (1996) The Ephemeroptera species of North America and index to their complete nomenclature. Trans Am Entomol Soc 122:1–54
McCafferty WP (2004) Higher classification of the burrowing mayflies (Ephemeroptera: Scapphodonta). Entomol News 115:84–92
McCafferty WP, Wang TQ (2000) Phylogenetic systematics of the major lineages of Pannote Mayflies (Ephemeroptera: Pannota). Trans Am Entomol Soc 126:9–101
Sun L, Sabo A, Meyer MC, Randolph RP, Jacobus LM, McCafferty WP, Ferris VR (2006) Tests of current hypotheses of mayfly (Ephemeroptera) phylogeny using molecular (18x rDNA) data. Ann Entomol Soc Am 99:241–252
Zhou CF, Peters JG (2003) The nymph of *Siphluriscus chinensis* and additional imaginal description: a living mayfly with Jurasssic origins (Siphluriscidae new family: Ephemeroptera). Fla Entomol 86:345–352

McDunnough, James Halliday

James McDunnough was born at Toronto, Canada, on May 10, 1877, and studied music before switching to entomology and becoming an authority on the systematics of Lepidoptera and Ephemeroptera. His zoological education commenced at Kaiser Wilhelm Institute in Berlin, Germany, followed by a M.S. from Queen's University in Kingston, Ontario, Canada, and then back to Kaiser Wilhelm for a doctorate. From 1910 to 1919 he worked as a curator at William Barnes' private museum in Decatur, Illinois. In 1919 he left to head the Division of Systematic Entomology at the Canadian National Collection in Ottawa. He served in this capacity for 28 years, accumulating one of the finest collections in North America. McDunnough published over 200 papers on Lepidoptera, 38 on Ephemeroptera, and several on other orders. Important works include "Check list of the Lepidoptera of Canada and the United States of America," and "Saturniidae of North America." Over the course of his career he named about 1,500 species. McDunnough died at Halifax, Nova Scotia, on February 23, 1962.

Reference

Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

McGlashan, Charles Fayette

Charles McGlashen was born August 12, 1847. After obtaining seminary education in California and Massachusetts he became a high school principal in Placerville, California, and also was an accomplished lawyer, editor, and astronomer. He is also remembered, however, as an ardent amateur entomologist. He contributed numerous specimens to Henry Edwards' Lepidoptera studies and collection and developed an all-glass display case for his moths and butterflies. Interestingly, he also established a butterfly farm at Truckee, California, offered a correspondence course for amateur entomologists, and started a short-lived monthly magazine, "The butterfly farmer." He died in 1931.

Reference

Essig EO (1931) A history of entomology. The Macmillan Company, New York, 1029 pp

McPhail Trap

The McPhail trap is a glass or plastic liquid-containing trap that uses protein solutions as bait. Ammonia given off by the trap is attractive to fruit flies, which enter the trap from below. As they instinctively attempt to move upward, they are restrained from escaping by the solid top.

► Traps for Capturing Insects

Meadow and Coneheaded Grasshoppers

A subfamily (Conocephalinae) of katydids in the order Orthoptera: Tettigoniidae.

► Grasshoppers, Katydids and Crickets

Mealworms

Larvae of the family Tenebrionidae are sometimes called mealworms, and infest grain and grain products.

► Stored Grain and Flour Insects

Mealybugs

Members of the family Pseudococcidae, superfamily Coccoidae (order Hemiptera).

► Scale Insects and Mealybugs
►Bugs

Mean-Variance Model

A model, generally a regression model, which predicts the variance of a sample from an estimate of the sample mean. Such models can characterize dispersion over a large range of population densities and are commonly used in developing sampling plans. Common examples are Taylor's power law and Iwao's patchiness regression.

► Sampling Arthropods

Measuring Worm Moths

Members of the family Geometridae (order Lepidoptera).

► Geometer Moths
► Butterflies and Moths

Mechanical Control

Control techniques that are based on the operation of machinery or manual operations to destroy insects. Examples of mechanical control techniques include vacuum machines and black-light traps.

Mechanical Protection of Humans from Arthropod Attacks and Bites

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In addition to chemical repellents for arthropod vectors or annoyers, human protection from their attacks and bites can be provided by numerous mechanical methods. Mechanical protection is based on the creation of a barrier that prevents the penetration by arthropods to the target humans. Such a barrier can protect either a group of people or an individual person.

Environmental Design

A very simple and effective technique to protect a human locality from malarial mosquitoes is so-called "zooprophylaxis." This technique is based on rational planning of localities. The technique was tested at the end of the 1930s in several areas of the then U.S.S.R. and was later successfully applied in antimalarial campaigns in rural areas with developed animal husbandry. Thus, if a cattle-ranch is located between a mosquito breeding site(s) and a village, mosquitoes flying towards the village attack the cattle and only a few specimens reach the human dwellings. The distance between a large ranch and a village should be from 200–500 m, and between an individual cattle stall and the nearest dwelling, about 25–35 m. To protect a human locality from flies which develop on cattle ranches, it is recommended to separate these two sites by creating a brush and tree belt between them of not less than 100 m in width.

Several measures should be taken to protect dwellings from insect penetration. All windows should be fitted with screens of metal netting. The mesh size to prevent penetration of mosquitoes and most flies is 1.5–2 mm, but in the cases of such small insects as midges or sandflies the mesh should be as fine as 0.75 mm. Also, it is desirable to construct a porch before the entrance into the house, which should be fitted with appropriate screen and the entrance should be closed with a net fixed at the upper jamb and freely hanging down to the floor. Entrances to the animal housing also should be closed with screens.

Protective Clothing and Bed Nets

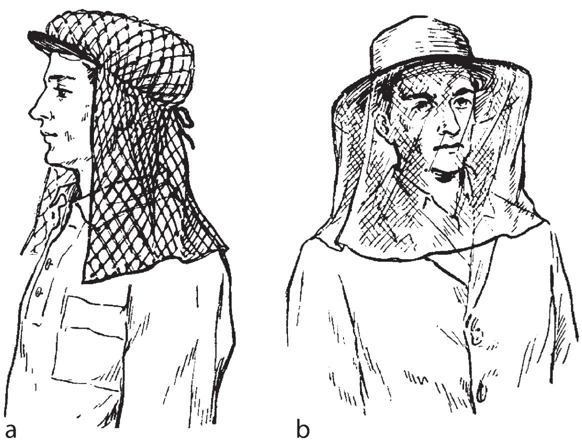
The easiest method of individual protection is proper clothing to create a barrier between attacking arthropods and the human body. In general, the more the human body is covered by clothing, the lower the probability of arthropod bites. A head veil made from a single- or double-layered net (impregnated by repellents, if possible) put over or under a head-dress, as well as a hood on a shirt or a jacket, provide additional protection from insect bites. A veil made from a fine mesh net covering the whole head and tightly fixed to clothing (similar to that used by beekeepers) provides nearly complete protection from insect bites without any necessity of repellents (Fig. 17). There are many things specific to various groups of arthropods that must be taken into account to provide a better barrier between them and the human skin. Blackflies that are active during the day prefer darker clothing rather than lighter fabric when selecting a landing site. To bite, blackflies must penetrate under the clothing and contact the body, using any minute openings for this purpose. Thin and delicate materials only partly protect from bites by horse flies or stable flies, whereas mosquitoes can pierce even fabrics with rough texture using their long proboscis (Fig. 19). For protection of people from night-biting arthropods during sleep, bed nets have been used for many centuries both inside and outside human dwellings. They can be of different shape and made from various materials. If a bed net is properly organized, it may provide nearly complete protection of the person using it. Correct maintenance of the bed net during the day prevents it from being used by mosquitoes as a resting site (Fig. 18). The development of bed nets impregnated with pyrethroid insecticides has supplemented their exclusively protective role by the suppressive effect on mosquito populations and their capacity as malaria vectors. Though the efficacy of impregnated bed nets differs for different mosquito species and in different areas, they have become an important tool in human protection from mosquitoes and malaria. An important factor to remember with nets for both head veils and bed nets is the necessity of good ventilation, a condition not always fulfilled.

Development of pyrethroid resistance in mosquito vectors may threaten the sustainability of impregnated bed nets, though the real impact of this phenomenon on the efficacy of bed nets is controversial. Meanwhile, various combinations of pyrethroid and non-pyrethroid insecticides for impregnation of bed nets have been tested. However, operational difficulties are more critical for effective application of impregnated bed nets, e.g., the necessity for regular retreatment of bed nets to maintain their high efficacy against mosquitoes. Most users do not impregnate their nets in time and properly, and the limited impact of such bed nets on mosquito population decreases the motivation of people to use this technique. This stimulated the development of "long-lasting insecticidal wash-resistant mosquito net" which should maintain its activity for 3–5 years, the average life expectancy of the net.

Arthropod Behavior and Protection

Protection from the bites of ixodid ticks is based on the specificity of their behavior. After adhering to human clothes, ticks usually move upwards, trying to penetrate under the clothes and to contact the body. To make tick penetration onto the body more difficult, people should seal all possible routes for tick penetration under the clothes. Trouser legs should be tucked into boots or socks, the shirt into trousers, and the head should be covered by a hood. Some researchers have recommended making two repellent strips, about 2 cm in width and 5–7 cm from each other, around each trouser leg above the knees. Such strips prevent ticks, most of which adhere to the clothes at a lower level, from moving upwards. Another pair of strips may be made around the collar to protect the head. People at risk of tick attack must regularly carry out self- and/or cross-inspections followed by tick removal. The frequency of such inspections depends on the tick abundance; they should be carried out at least several times per day, but in heavily infested areas, every hour or half hour.

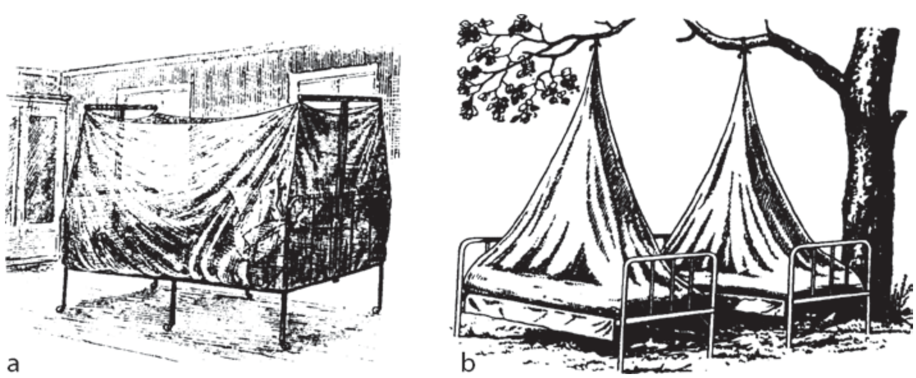
Many areas are populated by both ticks and blood-feeding insects. The necessity of simultaneous protection from both groups of arthropods has always been on the agenda. A protective suit developed by Russian scientists provides mechanical protection from both ticks and insects. Two shirts, which are worn one over the other, are the key part of this suit. The inner shirt is made from a thickened wide-mesh cotton netting, whereas the outer shirt is made from a fine-mesh net material. The outer shirt has elastic cuffs and a hood with an elastic band border. The suit also includes wide trousers with elastic cuffs and a belt, both made from a durable material. A mosquito able to penetrate through the material of the outer shirt cannot reach the human body with its proboscis; the thickness of the fabric of the inner shirt net material is about 2 mm, which is close to the maximal length of the proboscis. Other bloodsucking insects have a shorter proboscis. At the same time, the mesh size of the outer shirt is smaller than the size of the scutum of nymphal ticks. The net shirts made from cotton provide good ventilation so that the suit may be used during hot summer weather even by workers such as lumbermen. Depending on conditions, the suit may be used either for combined protection, or only as an anti-insect or anti-tick device. In the first case, the shirt has no hood but is supplemented by a head net impregnated with repellents. In the second case, only the outer shirt with the hood is used (Fig. 20).



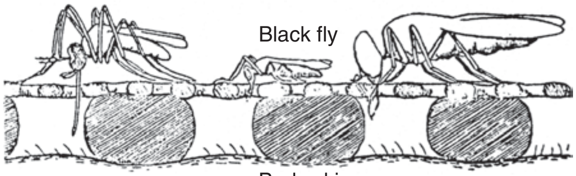
Mechanical Protection of Humans from Arthropod Attacks and Bites, Figure 17 **Head veils of different types: (a) Head is partly protected; (b) Head is completely protected.**

Human Motivation

An important consideration in using different protective techniques is human motivation. The



Mechanical Protection of Humans from Arthropod Attacks and Bites, Figure 18 **Bed nets of different types: (a) Rectangular bed net inside human dwelling; (b) Conical bed nets outside dwelling.**



Mechanical Protection of Humans from Arthropod Attacks and Bites, Figure 19 **Thickness of two net shirts compared with proboscis length of bloodsucking insects from different families.**

Mechanical Protection of Humans from Arthropod Attacks and Bites, Figure 20 **Combined protective suit consisting of two shirts made from net material of different meshes (man shows the inner shirt).**

latter depends to a higher degree on the level of discomfort than on the real danger created by arthropods. In areas where the abundance of bloodsucking insects is enormous, people have willingly applied protective clothes even if the insects are not vectors but just annoyers. On the other hand, even in areas where severe tick-borne diseases are endemic but the tick abundance is moderate, people are reluctant to apply any protective measures creating even minor discomfort. Another aspect concerning human motivation is connected with the purpose for which humans are in areas where they may be attacked and bitten by arthropods. If they work in such an area and have been well instructed, they usually protect themselves properly. However, people at leisure, even when specially instructed, do not like any discomfort and use protective measures rather unwillingly, if at all. In some cases, when people are vaccinated against a disease endemic in the area they are habiting, they believe the use of other protective measures is unnecessary. However, the area may also be endemic for other diseases, which is quite realistic since new cases of mixed infection have been discovered. From all these data presented above, one can see that the problem of human protection from arthropod attacks and bites has two aspects: the development of more efficient and comfortable techniques of protection, as well as the necessity of convincing people to apply them.

► Repellents of Biting Flies
► Mosquitoes
► Ticks

References

Asidi AN, N'Guessan R, Hutchinson RA, Traoré-Lamizana M, Carnevale P, Curtis CF (2004) Experimental hut comparisons of nets treated with carbamate or pyrethroid insecticides, washed or unwashed, against pyrethroid-resistant mosquitoes. Med Vet Entomol 18:134–140

Curtis CF (1992) Personal protection methods against vectors of disease. Rev Med Vet Entomol 80:543–553

Guillet P, N'Guessan R, Darriet F, Traoré-Lamizana M, Chandre F, Carnevale P (2001) Combined pyrethroid and carbamate "two-in-one" treated mosquito nets: field efficacy against pyrethroid-resistant *Anopheles gambiae* and *Culex quinquefasciatus*. Med Vet Entomol 15:105–112

Harwood RF, James MT (1979) Entomology in Human and Animal Health (7th ed). Macmillan Publishing, New York, NY

Marquardt WC (1996) Introduction to arthropods and vectors. In: Beaty BJ, Marquardt WC (Eds) The Biology of Disease Vectors. University Press of Colorado, Niwot, CO, pp 1–24

Sutcliffe JF (2000) Prevention and control of arthropodborne diseases. In: Eldridge BF, Edman JD (Eds) Medical Entomology. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 565–620.
Uspensky I (1999) Ticks as the main target of human tick-borne disease control: Russian practical experience and its lessons. J Vector Ecol 24:40–53

Mechanical Transmission

Transmission of an arthropod transmitted disease wherein the causal organism is transmitted more-or-less incidentally. The disease-causing organism in not well adapted to the vector, does not multiply in the vector, and usually is not consumed. Flies and cockroaches often are implicated in this process.

► Cyclo-Propagative Transmission
► Cyclo-Developmental Transmission
► Propagative Transmission

Meconium

Wastes accumulated during the pupal stage and excreted by the adult insect shortly after emergence.

Mecoptera

An order of insects. They commonly are known as scorpionflies and hangingflies.

► Scorpionflies

Media

The fourth longitudinal wing vein, extending from the base to at least the middle of the wing. It usually is branched, but not with more than four branches.

Media Workers

Among ants with polymorphic worker castes, the intermediate size workers. (contrast with major and minor workers)

Median

Referring to the middle, or near the middle.

► Wings of Insects

Median Furrow

The furrow between the radius and media. In some Hemiptera, the indentation separating the embolium from the remainder of the corium.

► Wings of Insects

Mediocubital

Referring to the media and cubitus veins of the insect wing.

► Wings of Insects

Mediterranean Burnet Moths (Lepidoptera: Heterogynidae)

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Mediterranean burnet moths, family Heterogynidae, include only seven species, with three species from the Mediterranean region of southern Europe and northern Africa (genus *Heterogynis*) and four species from South Africa (genus *Janseola*). The family is in the superfamily Zygaenoidea in the section Tineina, subsection Sesiina, of the division Ditrysia. Adults small (9 to 29 mm wingspan), with head rough-scaled; haustellum absent or vestigial; labial palpi reduced, 3-segmented; maxillary palpi absent; antennae bipectinate. Wings rather rounded. Maculation mostly gray, with similar hindwings. Adults are diurnal, but females are apterous and larviform. Many of the species resemble bagworms and were originally described as Psychidae. Larvae, upon hatching inside the female cocoon, feed on the dead female and then become external leaf feeders. Host plants are in Leguminosae.

References

Dalla Torre KW Von, Strand E (1923) Heterogynidae. In Lepidopterorum Catalogus, 28: 1–14 W Junk Berlin

Daniel F, Dierl W (1966) Zur biologie und anatomie von *Heterogynis penella* (Hbn.) (Lep.) Zoologischer Anzeiger 176: 449–464

Freina JJ de, Witt TJ (1990) Familie Heterogynidae Herrich-Schaffer 1846. In Die Bombyces und Sphinges der Westpalaearktis 2: 74–80 pl. 10 Forschung and Wissenchaft Verlag, Munich

Guenin R (1997) Heterogynidae – Federwidderchen (Mottenspinner) In Schmetterlinge und ihre Lebensräume: Arten - Gefährdung-Schutz. Schweiz und angrenzenden Gebiete, Lebensräume: 309–312 pl. 10. Pro Natura-Schweizerische Bund Fuer Naturschutz Basel

Sukareva IL (1978) Heterogynidae. In Identification keys to the insects of European Russia, 4 Lepidoptera 1: 138–140 Academic Nauk (in Russian) St. Petersburg

Mediterranean Flannel Moths (Lepidoptera: Somabrachyidae)

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Mediterranean flannel moths, family Somabrachyidae, include only five species, with three species from Southern Europe and North Africa (genus *Somabrachys*) and two species from South Africa (genus *Psycharium*). The family is in the superfamily Sesioidea in the section Tineina, subsection Sesiina, of the division Ditrysia. Sometimes the group is included in Megalopygidae. Adults small (18–22 mm wingspan), with head scaling average; haustellum absent; labial palpi absent; maxillary palpi absent; antennae bipectinate. Wings very broadly rounded and body robust. Maculation gray or brown on wing margins, with most of wings hyaline. Adults are diurnal, but females are larviform and wingless (females of the South African species are unknown). Larvae are leaf feeders (eggs laid on leaves, not in the female cocoon), somewhat slug-like, with concealed head. Hosts are grasses (Gramineae) and Compositae.

References

Epstein ME (1996) Somabrachyidae Hampson, 1920, pp 85–86. In Revision and phylogeny of the limacodid-group families, with evolutionary studies on slug caterpillars (Lepidoptera: Zygaenoidea). Smithsonian Contributions to Zoology 582: 1–102

Freina JJ de, Witt TJ 1990. Familie Megalopygidae Herrich-Schäffer 1855 (=Somabrachyidae Hampson 1920). In: Die Bombyces und Sphinges der Westpalaearktis, 2:48–50, pl 6. Forschung & Wissenschaft Verlag, Munich

Geertsema H (1998) Studies on African zygaenoid moths (Lepidoptera: Zygaenoidea) (Somabrachyidae). S Afr J Zool 33:210–225 (1998); Afr Zool 35:251–259 (2000)

Powell H (1911) Notes sur les Somabrachys des environs de Géryville (Sud-Oranais). In Études de Lépidoptéres Comparée, 5: 227–301, pl 84–85, A-D. C. Oberthür, Rennes

Powell H (1916–17) Megalopygidae. In: C. Oberthür, Faune des Lépidoptères de Barbarie (Partie II). In Études de Lépidoptères Comparée, 12: 376–428 (1916); pl. 529–531 (1917). C. Oberthür, Rennes. [all Somabrachyidae]

Mediterranean Flour Moth, "*Ephestia kuhniella Zeller* (Lepidoptera: Pyralidae)"

This is a minor pest of stored grain.

► Stored Grain and Flour Insects

Mediterranean Fruit Fly, *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae)

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The Mediterranean fruit fly (medfly) belongs to the tribe Ceratitidini of the sub-family Dacinae, and is the most well-known of the 65 species of the genus *Ceratitis*. It is highly polyphagous, very widespread (both in tropical and temperate areas), and it is considered one of the most important pests for world fruit production.

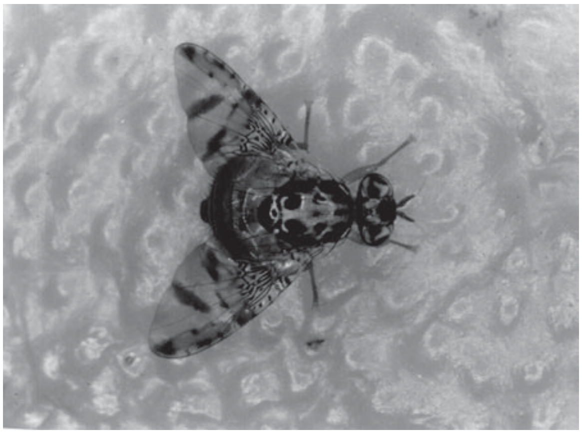
Origin and Geographical Distribution

The Mediterranean fruit fly was first described in 1824 by Wiedemann, when he analyzed a specimen collected aboard a ship in the Indian Ocean that was transporting fruits from Africa. Most of the studies suggest that this insect is native to tropical Africa, originating from areas south of the Sahara desert. This suggestion is supported by recent genetic studies. It is believed that the fly invaded first the Mediterranean basin either by dispersing along the valley of the Nile and then following the Middle East coastline, or by reaching Spain from the North Western coast of Africa and Gibraltar. From Spain, where it was first detected in 1850, it probably dispersed to the New World (Latin America). The fly usually disperses to neighboring orchards by flying. Invasions of new areas are achieved through the national, international and intercontinental transport of infected fruits. In general, suitable areas for the development of medfly lay between 45° north and 45° south geographical latitude. In the Northern Hemisphere, the fly is endemic in areas located below 41° latitude. The fly has been reported in many parts of Africa, in the Middle East, in Western Australia, in most of the Central and South America countries and in islands of the Atlantic, Pacific and Indian Oceans. It has invaded North America many times and is believed to be established in California, USA. In Europe, medfly occurs in all the Mediterranean countries and in Portugal.

Morphology

The adult medfly measures 4–6 mm in length, and 1.2–2 mm in width. It has quite a colorful appearance, owing to the yellow, brown, black, white and whitish stripes on its thorax, abdomen and wings. Compound eyes, which are iridescent royal purple to blue-greenish, occupy most of the head, which is yellowish in color. The antennae have a general brown color and several small black setae. The two base segments of the antennae are red-brown, while the aristae are almost black. The males are easily distinguished from females and from other species of the family by a pair of stalky, cornea like, pointed, black-gray expansions at the apex of the anterior part of their head. The wings (measuring about 4.5 mm in length) are transparent with yellow, brown, and red stripes. In resting or walking adults the wings are semi-open, sloping towards the posterior part of the body resembling a roof. The notum of the thorax is shiny black with discrete whitish stripes, whereas that of the sternum is yellow. The apical half of the scutellum is completely black. The abdomen is orange yellow with two red brown transverse stripes. The ovipositor is 0.9–1.3 mm in length. The legs are yellow red with several rather long, yellow setae on the back part of the tibiae (Fig. 21).

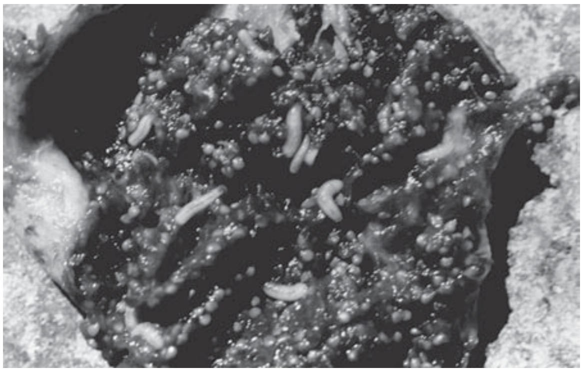
Eggs are oblong, elliptical, glossy white and measure around 0.9–1.1 mm in length and 0.2–0.3 mm in diameter.



Mediterranean Fruit Fly *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae), Figure 21 Mediterranean fruit fly, *Ceratitis capitata*, adult female.

Larvae are white or cream-white, oblong without legs, with the anterior part being narrower than the posterior. There are three instars that can be differentiated from each other by the shape, size and color of their mouthhooks. In general, the first instar measures 0.17–2.2 mm, the second instar 2.3–5 mm and the third 6–10 mm.

The puparium is elliptical barrel-like, and measures 4.4–4.5 mm in length and 2–2.5 mm in diameter. The color depends mostly on the larval food and ranges from almost white to dark brown.



Mediterranean Fruit Fly *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae), Figure 22 **Ripe fig infested by medfly larvae.**

Hosts and Economic Importance

The medfly is the most polyphagous tephritid and infests fruits of plants belonging to more than 67 families. Of the 353 hosts reported (although some lack confirmed field infestation), 40% belong to the families Myrtaceae (6%), Rosaceae (10%), Rutaceae (9%), Sapotaceae (9%), and Solanaceae (6%). Medfly develops in many fruits of tropical, sub-tropical, and temperate fruit trees. In the tropics and sub-tropics, it is a serious pest of coffee (*Coffea arabica*), mango (*Manifera indica*), papaya (*Carica papaya*), avocado (*Persea americana*), guava (*Psidium guajava*), carambola (*Averrhoa carambola*), sweet orange (*Citrus sinensis*), sour orange (*Citrus aurantium*), fig (*Ficus carica*), grapefruit (*Citrus x paradisi*), prickly pear (*Opuntia vulgaris*), loquat (*Eriobotrya japonica*), and oriental persimmon (*Diospyros kaki*). In temperate regions, it also infests stone and pome fruits such as apricot (*Prunus armeniaca*), peach (*Prunus persicae*), apple (*Malus domestica*), pear (*Pyrus communis*) and other fruits (Fig. 22).

Ceratitus capitata is one of the most serious pests worldwide, with infestation levels reaching 100% in some of its hosts. It is a quarantine pest in countries such as the United States of America and Japan. Intensive control programs have been carried out, coordinated by national and international organizations, with the aim of restricting the expansion of the distribution of medfly or of erradicating it from invaded areas.

Biology

Medfly is a multivoltine, non-diapausing species that usually completes between 3 and 7 generations per year. The number of generations is determined mostly by geographic area, climatic conditions (mostly temperature), host species and host availability. In the tropics and subtropics, as well as in the southern Mediterranean areas, this species develops continuously all year round with slower developmental rates in response to low temperatures. However, in the northern Mediterranean coasts only larvae inside infested fruits can survive and maintain the populations throughout winter.

Adults need to feed on carbohydrates and nitrogen after their emergence in order to reach sexual and reproductive maturity. The mating system of this insect is mainly based on receptive female attraction to "calling" males emitting a sex pheromone. Seven to 10 day-old females begin to lay eggs just after mating, in ripe or semi-ripe fruits. They open a small hole a few millimeters deep into the fruit using their ovipositor, and insert a batch of up to nine eggs in the flesh of the fruit. The oviposition sting is only visible in some hosts. Hatching larvae feed on the flesh of the fruits and, after completing their development, they leave the fruits to pupate at a small depth (up to 5 cm) in the ground beneath host trees. The direct damage of the larvae to fruits is usually accompanied, and magnified by, secondary infections of fungi and bacteria. The mean generation time under constant conditions in the laboratory (25°C) is estimated at one to two months depending on the host in which the fly developed. Throughout her life span each female lays from 250 to 1,000 eggs.

Control

The conventional control of *C. capitata* is based on population monitoring using adult traps and the application of bait or cover insecticide sprays. Of the many adult traps used, two are the most acceptable, the McPhail trap with various food baits, and the Jackson trap baited with the male lure trimedlure. A McPhail trap with the food attractants ammonium acetate, putrescine and trimethylamine, loaded in dispensers lacking a month, constitutes a very effective, female-targeted and medfly-selective trapping system that outperforms most of the other trapping systems. Several insecticides, used in cover or bait sprays, have been proved effective to control medfly. For example, malathion is very effective and is less toxic for invertebrates, and has been used extensively in several, large, area-wide control programs (Fig. 23).

Besides chemical control, several other pre-harvest and post-harvest methods have been developed and deployed for controlling medfly. There is also a set of cultural measures effective for the suppression of the fly. The most important of them are fruit bagging, sanitation (destruction of infested fruits), destruction of all wild host over a vast area, or stripping and destroying fruit over a large area. Satisfactory control has been achieved in some cases (mostly under low population densities) by biological control and mass trapping. The sterile insect release technique (SIT) has been used with success, the aim being in most cases the eradication of the fly from an area. More recently, this method has also been used to suppress the pest. There are several cases of successful combination of SIT with other methods such as bait sprays and/or augmentative releases of parasitoids. The control of this pest is most successful on an area-wide basis. Succesful implementation of an area-wide control programme can lead to the establishment of pest free zones within a country and also to the eradication of the pest from a state or country.

Mediterranean Fruit Fly *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae), Figure 23 **Jackson trap.**

In addition to direct control measures, there are other strategies to control this fly. The most important of these are the legislative measures. Very often, strict quarantine regulations are set up to prevent the entry of the fly into an uninfested area. Several markets accept only those fruits and/or vegetables that have undergone a commodity treatment that secures a mortality of at least 99.9968% (Probit 9) that is generally acceptable as zero infestation. The best-known of the commodity treatments is the exposure of the fruits to lethal low or high temperatures, and to fumigant insecticides.

► Citrus Pests and their Management
► Tropical Fruit Pests and their Management
► Fruit Flies (Diptera: Tephritidae)

References

Carey JR (1991) Establishment of the Mediterranean fruit fly in California. Science 253:1369–1373

Katsoyannos BI, Heath RR, Papadopoulos NT, Epsky ND, Hendrichs J (1999) Field evaluation of the Mediterranean fruit fly (Diptera: Tephritidae) female selective

attractants for the use in monitoring, mass trapping and sterile insect technique. J Econ Entomol 92:583–589
Liquido NJ, Shinoda LA, Cunningham RT (1991) Host plants of the Mediterranean fruit fly (Deptera: Tephritidae): an annotated world review. Miscellaneous Publication 77. Entomological Society of America, Lanham, MD
Mitchell AC, Saul SH (1990) Current control methods for the Mediterranean fruit fly, *Ceratitis capitata*, and their application in the USA. Rev Agric Entomol 78:923–940
Papadopoulos NT, Carey JR, Katsoyannos BI, Kouloussis NA (1996) Overwintering of *Ceratitis capitata* (Diptera: Tephritidae) in northern Greece. Ann Entomol Soc Am 89:526–534
Papadopoulos NT, Katsoyannos BI, Carey JR, Kouloussis NA (2001) Seasonal and annual occurrence of the Mediterranean fruit fly (Diptera: Tephritidae) in northern Greece. Ann Entomol Soc Am 94:41–50
White IM, Elson-Harris MM (1992) Fruit flies of economic significance: their identification and bionomics. CAB International, Wallingford

Mediterranean Spotted Fever

Also known as Boutonneuse Fever, this disease is caused by a tick-transmitted *Rickettsia*.

► Ticks

Mediterranean Theileriosis

This is a tick-transmitted disease caused by the protozoan *Theileria annulata*.

► Piroplasmosis

Medocostidae

A family of bugs (order Hemiptera).

► Bugs

Meenoplidae

A family of bugs (order Hemiptera, suborder Fulgoromorpha). All members of the suborder are referred to as planthoppers.

► Bugs

Megachilidae

A family of bees (order Hymenoptera, superfamily Apoidae). They commonly are called leafcutting bees.

► Bees
► Wasps, Ants, Bees and Sawflies

Megafauna

The largest of the animals in an area, often greater than 20 mm body width. (contrast with microfauna and macrofauna)

Megalodontidae

A family of sawflies (order Hymenoptera, suborder Symphyta).

► Wasps, Ants, Bees and Sawflies

Megalopodid Beetles

Members of the family Megalopodidae (order Coleoptera).

► Beetles

Megalopodidae

A family of beetles (order Coleoptera). They commonly are known as megalopodid beetles.

► Beetles

Megaloptera

An order of insects, sometimes considered to part of the order Neuroptera. They commonly are known as alderflies and dobsonflies.

► Alderflies and Dobsonflies

Megalopygidae

A family of moths (order Lepidoptera). They commonly are known as flannel moths.

► Flannel Moths

► Butterflies and Moths

Megalyridae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Megamerinidae

A family of flies (order Diptera).

► Flies

Megapodagrionidae

A family of damselflies (order Odonata).

► Dragonflies and Damselflies

Megarididae

A family of bugs (order Hemiptera, suborder Pentamorpha).

► Bugs

Megaspilidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Meigen, Johann Wilhelm

J. W. Meigen was born at Solingen, Germany on May 3, 1764. He became interested in insects at an early age, but had little opportunity for formal education. By various circumstances, he acquired knowledge of math and French, and eventually gained access to books. Thus, he became qualified to serve as a tutor in 1784, and moved away from home. He made the acquaintance of Mathias Baumhauer, an ardent collector of insects, and became extremely interested in insects. About 1778 he came to realize that Linnaeus had not described everything, and that the Linnean genera were too inclusive. He began a reclassification of Diptera based on wing venation, which eventually was expanded to include other body parts. Meigen taught himself enough Latin to read the works of Fabricius. In 1796 he took a teaching position in Stolberg. Meigen's approach to classification, using many body parts, did not find favor at the time, especially with Fabricius. Due to the political turmoil of the era, Meigen found difficulty with employment, but always maintained his interest in Diptera, and eventually became renowned as a pioneer in dipterology. He published several volumes on Diptera, but also on Lepidoptera. Meigen sold his collection and drawings to P.J.M. Macquart in 1839 and retired. He died July 11, 1845 (Fig. 24).

Meigen, Johann Wilhelm Figure 24 Johann Meigen.

Reference

Steyskal GC (1974) On the life and influence of JW Meigen. Mosq Syst 6:79–87

Meinertellidae

A family of bristletails (order Archeognatha).

► Bristletails

Meiosis

The sequence of events occurring during two cell divisions to convert diploid cells into haploid cells.

Meiotic Drive in Insects

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Mendel's law of segregation proposes that equal numbers of alleles (variants of the same gene) derived from the paternally and maternally-derived chromosomes are distributed to eggs and sperm during meiosis (the reductional division that results in haploid eggs or sperm having only one copy of each type of chromosome). However, this law is sometimes violated due to a phenomenon called meiotic drive. Meiotic drive has been studied in insects and has been proposed to be a future tool for suppressing pest populations.

Meiotic drive alters the equal assortment of chromosomes during meiosis so that certain chromosomes are inherited by the progeny more frequently than expected (greater than 50% of the time). Meiotic drive most frequently is observed affecting sex chromosomes (chromosomes that are different in males and females). In most insects, females are XX and males are XY (or heterogametic, with half the sperm receiving the X and half the Y chromosome) and the ratio of male and female progeny is 1:1. If changes in distribution of the X and Y chromosome occur through meiotic drive, it is detected because more females or males are produced than expected. Whether meiotic drive mechanisms actually affect the sex chromosomes more frequently, or whether meiotic drive is more frequently discovered because it is relatively easy to detect due sex ratio changes, is unknown.

Meiotic drive has been found most often in Diptera, including *Drosophila obscura*, *D. melanica*, *D. tripunctata*, *D. testacea*, *D. melanogaster* and *D. quinaria* groups, mosquitoes (*Aedes* and *Culex*), sciarid flies and stalk-eyed flies (Diopsidae). Whether meiotic drive is common in other insect orders is controversial.

Three examples of sex chromosome meiotic drive are described below, including Segregation Distorter (SD) in *Drosophila*, male drive (MD) in the mosquitoes *Aedes aegypti* and *Culex quinquefasciatus*, and meiotic drive in stalk-eyed flies.

Segregation Distorter (SD) In *Drosophila melanogaster* the SD phenotype is present at low, but stable, frequencies in most field populations. *D. melanogaster* males containing one SD chromosome and one normal (SD^+) chromosome may produce only progeny with the SD chromosome, instead of half with SD and half with SD^+, due to the failure of sperm with the SD^+ chromosome to mature. Segregation distortion occurs because the nuclei of the sperm with the normal SD^+ chromosome fail to condense at sperm maturation. The Enhancer locus of SD, E(SD), is required for the full expression of this type of meiotic drive.

The SD phenotype actually involves two overlapping genes, one called HS2ST and the second called RanGAP. RanGAP is an essential component of a system that transports proteins and RNA molecules into and out of the cell's nucleus. Both HS2ST and RanGAP are present twice on the SD, as opposed to once on the SD^+, chromosome. This tandem duplication is necessary for segregation distortion. Both genes appear normal in the right hand copy, but the

RanGAP gene on the left lacks the last 234 amino acids. It is possible that the truncated RanGAP protein functions incorrectly and is mislocalized within the cell.

Distorter Gene Meiotic drive also has been described in the mosquitoes *Aedes aegypti* and *Culex quinquefasciatus*. In both species, a Y-linked gene results in excess males. Excess males are produced because X chromosomes are broken during meiosis in males. As a result, fewer X than Y chromosomes are transmitted, leading to the production of fewer female embryos. The *Distorter gene* (D) is linked closely to the sex-determining locus m/M and causes the chromosome breakage.

Additional genes are involved in the sex ratio distortion; sensitivity to *Distorter* is controlled by m, the female-determining locus. In some strains, sensitivity is influenced by a second sex-linked gene t. Yet another sex-linked gene A enhances the effect of *Distorter*. *Distorter* has been found in mosquito populations from Africa, America, Australia and Sri Lanka, but resistance to it is widespread.

Female-biased Sex Ratios in Stalk-eyed Flies Extreme female-biased sex ratios are found in two sister stalk-eyed flies, *Cyrtodiopsis dalmanni* and *C. whitei* (Diopsidae), due to a meiotic drive element on the X chromosome. Eye stalks are more exaggerated in males than in females in these species and females prefer to mate with males with a longer eye span. The longer eye stalks may be an indicator that the male either lacks meiotic drive or can suppress the meiotic drive. Thus, females prefer to mate with males with longer eye stalks because it should increase the female's fitness by avoiding a biased sex ratio in her progeny. Apparently, there are both autosomal- and Y-linked genes involved in resistance to the meiotic drive.

Meiotic Drive as a Pest Management Tool?

Meiotic drive operates as an evolutionary force which can cause an increase in the population frequency of the allele or chromosome which is favored in transmission, even if it confers a disadvantage on its carriers. It has been proposed that meiotic drive might be used to introduce new genes (such as cold-sensitive lethal genes, insecticide-susceptibility genes, or behavior-altering genes that would reduce the impact of pest populations on humans) into natural populations as a method to achieve control of pest insects. However, much remains to be learned about the stability of such drive mechanisms and the conditions under which they might function in pest management programs. Furthermore, as noted above, resistance to meiotic drive mechanisms can evolve in some species or populations; such resistance mechanisms, if developed rapidly, could reduce the effectiveness of the drive mechanism in the pest management program.

Hybrid Sterility and Meiotic Drive

It is sometimes possible to cross different insect species, and the progeny sometimes show altered sex ratios, with one sex absent, rare, or sterile. The missing or sterile sex is usually the heterogametic sex (XY). This phenomenon is known as Haldane's Rule. However, Haldane's Rule appears to occur only in taxa with sex chromosome-based meiotic drive, such as the Lepidoptera and Diptera. Haldane's rule may be occurring if suppression of sex ratio distorters is lost in the novel nuclear cytotype of the hybrid.

References

Ashburner M (1989) *Drosophila* a laboratory handbook. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY

Ganetzky B (2000) Tracking down a cheating gene. Am Sci 88:128–135

Jiggins FM, Hurst GDD, Majerus MEN (1999) How common are meiotically driving sex chromosomes in insects? Am Nat 154:481–483

Lyttle TW (1993) Cheaters sometimes prosper: distortion of mendelian segregation by meiotic drive. Trends Genet 9:205–210

Wilkinson GS, Presgraves DC, Grymes L (1998) Male eye span in stalk-eyed flies indicates genetic quality by meiotic drive suppression. Nature 391:276–279
Wood RJ, Newton ME (1991) Sex-ratio distortion caused by meiotic drive in mosquitoes. Am Nat 137:379–391
Wrensch DL, Ebbert MA (eds) (1993) Evolution and diversity of sex ratio in insects and mites. Chapman and Hall, New York, NY

Melander, Axel Leonard

A.L. Melander was born at Chicago, Illinois, USA, on June 3, 1878. He became interested in insects while in high school, and studied with William Morton Wheeler at the University of Chicago and the University of Texas. He received his M.S. in 1902. Melander taught at Washington State University from 1904 to 1926, and was head of the department for 20 years. He completed his Sc.D. at Harvard University in 1914. He left Washington State in 1926 and moved to the City College of New York where he served as professor of biology and head of the department, and retired in 1943. Melander worked on many insect problems, and among his accomplishments was the first documentation of declining effectiveness of an insecticide. He collaborated with C.T. Brues on authorship of "Key to families of North American insects" (1915), and "Classification of insects" (1932). He served as president of the Entomological Society of America in 1938. Melander also accumulated one of the world's largest collections of flies, which is now incorporated in the Smithsonian Institution. Melander died at Riverside, California, on August 14, 1962.

Reference

Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Melandryidae

A family of beetles (order Coleoptera). They commonly are known as false darkling beetles.

► Beetles

Melanothripidae

A family of thrips (order Thysanoptera).

► Thrips

Melissococcus pluton (Bacteria)

The causative agent of European foulbood in honey bees.

► European Foulbrood

Melittidae

A family of bees (order Hymenoptera, superfamily Apoidae).

► Bees
► Wasps, Ants, Bees and Sawflies

Melittin

A protein in bee venom thought to be responsible for the toxic properties.

► Honey Bees

Melittology

The scientific study of bees.

Melittophile

An organism spending at least part of its life in association with bee colonies.

Melizoderidae

A family of bugs (order Hemiptera, suborder Cicadomorpha).

► Bugs
► Leafhoppers

Mellanby, Kenneth

Kenneth Mellanby was born in 1908 and was educated at King's College, Cambridge, England, and the London School of Tropical Medicine, but his studies were interrupted by World War II. At the time, scabies was widespread in the military, and Mellanby deduced that the purported means of spread were erroneous and quickly demonstrated effective control. This work effectively released the equivalent of an additional two divisions of soldiers from the hospital to aid in the war effort. This work also resulted in publication of two books, "Scabies" (1943) and "Human guinea pigs" (1945). After the war he moved to Nigeria to start a college, and in a few years had a program operational. Mellanby returned to England in 1953, worked on various projects, and eventually assumed the position of Head of Entomology at Rothamsted Experimental Station. However, it was not until 1961, when he was appointed Director of the Nature Conservancy's Experimental Station at Monk's Wood did his career again flourish. He quickly assembled the largest research station in Britain devoted to studying conservation of wildlife. Work done here included the effects of pesticides on wildlife, habitat management, monitoring changes in distributional status, and establishment of a records center. Mellanby was the founding editor of the journal "Environmental pollution," and he wrote several books related to environmental causes, including "Pesticides and pollution" (1967), "Farming and pollution" (1991), and "The DDT story" (1992). Mellanby was active in several scientific societies and received numerous honors, including several honorary doctorates. He died in 1993.

Reference

Dempster J (1994) Kenneth Mellanby CBE ScD (1908–1993) Antenna 18:110–112

Mellinidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Meloidae

A family of beetles (order Coleoptera). They commonly are known as blister beetles.

► Blister Beetles
► Beetles

Melon Aphid, *Aphis gossypii* (Hemiptera: Aphididae)

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The melon aphid is a polyphagous species capable of feeding and reproducing on plants in over 90 plant families. There are over 72 crops in over 32 plant families worldwide that require some kind of human intervention for managing this aphid. This aphid is considered a pest in crops produced both in the field and in the greenhouse. Host plant damage includes direct feeding and transmission of plant pathogenic viruses. Reproduction in this aphid is entirely asexual in warmer climates, but includes a sexual phase in colder climates. Aphids of any given clonal line do not have the ability to utilize the entire host range reported for this species. Indirect damage by this aphid may also occur through the production of honeydew. Honeydew is a sugary liquid excreted by aphids to eliminate excess carbon and water. Honeydew coats plant surfaces below the aphid colony. Fungi able to utilize honeydew as a food source then cover the plant surface, thereby reducing the light reaching the chloroplasts.

Systematics and Biology

Common Names

The most popular English common names are the cotton aphid, or the melon aphid. These are the Entomological Society of America approved common names. However, there are at least 40 "common" names which are older, of more regional importance, or not English.

Description

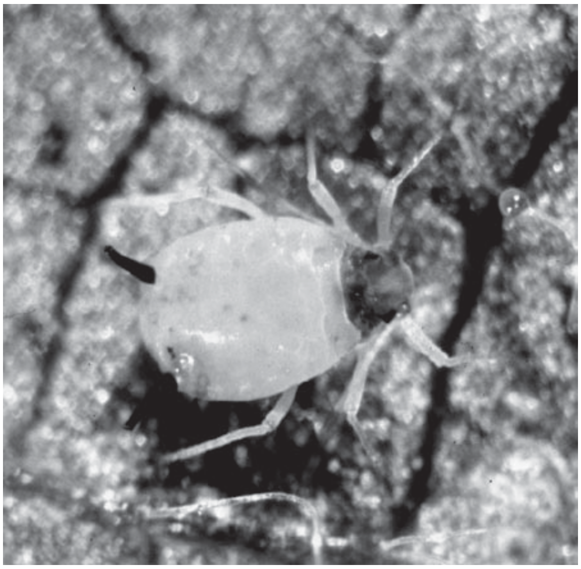
Apterous, mature, viviparous, yellow females can be <0.83 mm long and weigh <5.8 mg, while green females can be over 1.8 mm long and weigh over 66 mg. The body is generally rounded. Antennae have 5–6 segments. Cornicles (also known as siphunculi, and located between the fifth and sixth abdominal tergites) are dark, slightly conicle with the proximal end slightly larger in diameter than the distal end, and the length up to five times the diameter. Cornical length ranges from 0.13 to 0.35 mm. The cauda is pale to dark with two or three pairs of lateral setae.

The following stages have been observed: fundatrix (first parthenogenic generation from fertilized egg), fundatrigeniae (viviparous females on the primary host), alienicola (viviparous females on a secondary host), gynoparae (viviparous females are born on a secondary host and then migrate to the primary host to produce sexual females), oviparous female (egg laying female), alate and apterous male, hibernating viviparae (viviparous female), androparae (viviparous females that exclusively produce males), heteroparae and androgynoparae.

In addition to the specific life stages, this aphid displays considerable variability within clones. Adult individuals may have wings that fail to develop fully and range in size from little stubs to nearly functional. Furthermore, this aphid has a wide range in color variation, from yellow to a "green that is almost black," and individuals can be found anywhere along a gradient within this range. Additionally, some individuals may appear to be part yellow and part green. The yellow (and smaller) form occurs during warmer summer conditions. The green (and larger) form occurs during cooler spring (Fig. 25) and fall temperatures, with uncrowded conditions. Color is not a host race trait because color morphs are able to produce progeny of the other color morph. Host plant also influences aphid color, presumably due to stress – where the yellow form predominates under stressful conditions. The mechanism for color morph development is unknown. Some insecticides can cause a reverse stress response: e.g., LC_{10} doses of sulprofos (an insecticide).

Genetics

2n = 8, with chromosome lengths of about 2.3–3.65, 3.4–5.42, 3.8–6.24, and 5.0–7.64 μm.



Melon Aphid, *Aphis gossypii* (Hemiptera: Aphididae), Figure 25 **Melon aphid (cotton aphid), *Aphis gossypii*.**

Chromosomes are believed to be holokinetic (chromosomes lack a centromere), which could simplify genetic rearrangement and permit more rapid adaptation to new conditions: from adapting to new host plants to developing pesticide resistance.

Host Range and Utilization

The worldwide distribution of *A. gossypii* is partly due to its broad host range and its ability to switch hosts. One study reported *A. gossypii* surviving at least 15 days following transfer from plants in the Scrophulariaceae, Brassicaceae, Asteraceae, Lamiaceae, Rosaceae and Malvaceae to plants in the Asteraceae, Solanaceae, Cucurbitaceae, Liliaceae, Portulacaceae, Commelinaceae and Araceae. The broad host range increases survival under unfavorable conditions (e.g., when the original host plant species is unavailable), and aids in the transfer of viruses from reservoir plants to crop plants.

Reproduction in *A. gossypii* is mostly asexual with either alate (winged) or apterous (wingless) females. In warmer environments, this aphid has an anholocyclic life cycle (reproduction only through parthenogenesis), while in cooler areas, the aphid exhibits either a heteroecious or autoecious holocyclic life cycle. The heteroecious cycle involves a migration from a primary host to a secondary host in the spring and a return to a primary host in the fall for laying eggs. The primary host for the aphid is considered to be the ancestral host upon which the aphid evolved, and therefore, it is where the sexual phases of the life cycle are completed. The primary host for this aphid is unknown because there is the possibility that the aphid has secondarily acquired new "primary" hosts. The ancestral host is probably one of the following: *Citrus* (Rutaceae), *Hibiscus syriacus* L. (Malvaceae), *Rhamnus dahuricus* Pall. (Rhamnaceae), *Celastrus orbiculatus* Thunb. (Celastraceae), *Rubia cordifolia* L. (Rubiaceae), *Catalpa bignonioides* Walter (Bignoniaceae), *Zanthoxylum simulans* Hance (Rutaceae), or *Punica granatum* L. (Lythraceae). Aphids that remain on the primary host for both sexual and parthenogenic reproduction are described as "autoecious".

Population Growth

Population growth is a function of survival, time to reproduction and nymphs produced per day. A recent study examined the stage-specific influence of temperature on the population growth rate for this aphid on cotton. Temperatures examined were from 10 to 35°C. Individual life table parameters were optimized at slightly different temperatures; e.g., total fecundity of 28.3 nymphs per female was highest at 25°C, while development was fastest at 30°C where it took only 4.6 days from birth to time of first reproduction. The development threshold was estimated for the first through fourth instar, and the adult, to be 8.2, 8.0, 7.2, 6.2 and 7.9°C, respectively. Overall, the maximum intrinsic rate of increase (0.386 per day) was achieved at 25°C, which results in a population doubling time of only 1.8 days. While other studies have reported specific values that would lead (if combined) to a faster population growth rate, in total, this is probably close to the upper limit for the population growth rate for this aphid.

Nutrition

The nutritional requirements of aphids are modified due to endosymbionts that produce some nutrients the aphid is unable to make without them. Typically, nutritional quality for aphids is measured by reproductive rate, or growth rate. Diet pH is best between 7.4 and 7.8. Sugars in the diet serve as nutrition and to stimulate feeding. Optimal sucrose concentrations in artificial diets are between 20 and 30%, and diets with other sugars are less suitable, although 20% sucrose with 10% maltose came close to equaling a sucrose-only diet. Experiments on identifying amino acid requirements have shown that cystine and methionine in the diet improve growth rate, but above 30 mg/ml, they are toxic. While not essential, improved growth was observed with tyrosine, phenylalanine and tryptophan in the diet.

Abiotic Environment

One of the most important abiotic factors affecting the life cycle of this aphid is temperature. A lower developmental threshold for this aphid was estimated at 7.34°C on squash. Development thresholds have also been estimated for the aphid on cucumber at 5.8°C from birth to age of first reproduction, but the development threshold for the nymphal stages was 6.9°C. A study of this aphid on speedwell, Veronica persica, estimated a developmental threshold of 10.47°C for the preflight period. An upper limit of survival at 35°C was reported on squash in Saudi Arabia, but the authors pointed out that the aphid survives in okra fields where the daytime temperature exceeds 45°C. Temperature is also thought to be responsible for some strains of *A. gossypii* being holocyclic while others are anholocyclic.

Light intensity and day length are also important abiotic factors in the reproductive capacity of this aphid. Increasing day length increases the intrinsic rate of increase, decreases population doubling time and decreases generation time. However, there is some indication that at 18-h daylengths, population growth rates decline slightly. The effects of light intensity have been studied, but with conflicting results; sometimes light intensity increases reproduction, and sometimes it decreases reproduction. In the field, increased light intensity may decrease reproduction. Reflective mulch can decrease aphid populations, and a suggested mechanism was increased light intensity on abaxial leaf surfaces.

Production of Winged Aphids (Alates)

There are two proposed triggers for production of winged aphids in *A. gossypii*: nutritional factors (physiological stress), and crowding. Aphid-aphid contact has been proposed as a mechanism for triggering alate production, but it is possible that the aphid has a chemical means of identifying the number of neighbors. It is not known if the trigger for production of alates is continuous, discrete, or a combination of the two. As a continuous process, increased numbers of aphids changes plant nutrition and brings about a corresponding change in alate production. However, it would appear that production of alates is partly a discrete process where crowding gets to some threshold level and suddenly alates are produced.

Crowding effects have been conclusively demonstrated for alate production on cotton. One study examined crowding using leaf disks with a single, apterous aphid that was removed following reproduction. The resulting colonies contained from one to seven nymphs. From 52 colonies with one or two nymphs, no alates were produced. From 41 colonies with three or four nymphs, <10% of the colony became alate. However, of 29 colonies with five to seven nymphs, over 30% of the total number of aphids became alate. The observation that colonies with one to two individuals never produce alates has beed reported several times.

Nutritional factors from other sources also play a role in production of alates. One of the more interesting hypotheses is the possible role of aphid-borne plant viruses. The survival of the virus is dependent on having an efficient aphid vector, and the most efficient vector is alate. Therefore, one might expect that a virus would promote conditions favoring alate production in the aphid. Indeed, zucchini plants infected with the zucchini yellow mosaic virus increased alate production in the melon aphid.

The parentage and physiological state of the parent influence production of alates. Starved nymphs from apterous parents resulted in 13% alates versus 0.4% from unstarved nymphs, but the starvation of nymphs from alate parents resulted in no increase in formation of alates. A similar result was also reported for starved parents, where starved, apterous parents produced more alate progeny than well-fed, apterous parents (23% and 2%, respectively), and there was no increase in alate formation by starved, alate parents.

Behavior

Flight

Flight is the beginning of the dispersal or sexual reproductive phase in the life cycle of the melon aphid. It begins with the preflight period (from molt to flight), which lasts from 1 to 70+ hours depending on host plant and temperature. Adult flight activity is most common from about sunrise to early afternoon, with little or no activity after dark. Alates typically fly within 1 m of the ground.

In laboratory colonies, the flight period lasted from 1 to 4 days. Older colonies produced fewer alates that flew for 1 day and more that flew for 2 days. Aphids flew from one to several (about five) times each day, with the first flight always longer than the others. Alates larviposited after flight, and flew again when the number of embryos with pigmented eyes per ovariole decreased. Alates that flew longer had a shorter reproductive period and produced fewer total progeny. Alates that land on previously colonized plants have a decreased probability of larvipositing.

Light

The melon aphid is sensitive to different wavelengths and intensities of light, but the nature of the effect is not clearly understood. Aphids were attracted to Auclair's artificial diet illuminated at 570–595 nm, while diets illuminated at 420–485 nm were repellent. This contradicts other findings where newly molted, alate adults preferred shorter wavelengths down to 357 nm. Adults of mixed age also preferred this short wavelength, though some preference was also shown for wavelengths of 550 nm. Furthermore, there is a stage-dependent response to light, the adults being more sensitive to different wavelengths than the nymphs.

Host Plant

Orientation to host plants begins at 6 h after wing development, but has a maximal response after about 24 h. In addition to the type of host present in a field, the arrangement of hosts within the field is also important. An experiment was done using soybean, dwarf sorghum and tall sorghum planted in monoculture or interplanted. At the sorghum canopy level, landing rates were highest on monocultures of dwarf sorghum, then monocultures of tall sorghum, and lowest in mixed plantings.

Feeding

In one set of experiments, alates were placed on squash, *Cucurbita pepo*, plants and watched under a microscope. Given that probing occurs when aphids pressed their labium to the surface and placed their antennae flush with the body, the aphid took 6–9 min following contact with the plant before probing. However, this is the same time it took newly emerged alates, and may not be characteristic of alates after migration.

Egg Laying

Egg laying on *Hibiscus syriacus* occurred mostly between the leaf scar and the twig near where the buds would emerge in the spring. Some eggs were also laid at the branching point of twigs. However, from the wandering behavior of the oviparous females, it appears that females searched for protected places to lay eggs rather than for specific parts of the plant.

Biotic Interactions

Virus Transmission

The ability of the melon aphid to transmit plant pathogenic viruses increases its ability to damage a wide range of crops. This ability is influenced by the biochemistry of all three participants: plant host, virus and aphid. Some examples are: Citrus Tristeza virus acquisition rates are affected by citrus cultivar. Transmission of the virus is influenced by virus strain, but not by the aphid strain nor the rearing host for the aphid. Cucumber mosaic virus (CMV) transmission is governed by virus RNA strands 1, 2 and 3, but not strand 4. Transmission of CMV is influenced by the previous aphid host, and aphid clones differ in their ability to transmit the virus. The relationship between aphid and virus is very specific in that changes in amino acids 129, 162 and 168 of the coat protein significantly alter the ability of the aphid to transmit the virus. The interaction between this aphid and other plant pathogenic viruses can be equally specific at a biochemical level. While some viruses like CMV have specific locations on the coat protein, which mediate aphid transmission, other viruses produce helper components, which mediate transmission: e.g., *Aphis gossypii* transmission of tobacco etch potyvirus (TEV) and turnip mosaic potyvirus (TuMV).

Mortality

This aphid is an important food resource for many organisms. These include many insect predators (ladybugs: *Coccinella septempunctata* L., *Hippodamia convergens* Guérin-Méneville, *Menochilus sexmaculatus* (Fabricius), *Scymnus louisianae* Chapin; lacewings: *Chrysopa carnea* Stephens, *Chrysoperla rufilabris* (Burmeister), *Chrysopa sinica* Tjeder; hoverflies: *Syrphus* sp.; Hemiptera: *Orius insidiosus* (Say), *Geocoris* spp., *Nabis* spp., *Zelus* spp.), hymenopteran parasitoids (*Trioxys* spp., *Aphelinus* spp., *Lysiphlebus testaceipes* (Cresson), *Aphidius colemani* Viereck, *Lipolexis scutellaris* Mackauer), and some parasitic mites (*Allothrombium ovatum, Allothrombium pulvinum* Ewing). Several fungi are also able to cause aphid mortality (e.g., *Paecilomyces fumosoroseus*, *Neozygites fresenii*, *Cephalosporium lecanii*, *Verticillum lecanii*, *Erynia neoaphidis*, *Beauveria bassiana*), as well as some bacteria. These lists of names are provided as an indication of the melon aphid's importance in the food chain and are far from complete.

This aphid has also been associated with ants, which both protect the aphid and feed off the aphid. The association is opportunistic rather than obligate. The ants, which have been found with this aphid, include: *Camponotus japonicus* Mayr, *Camponotus compressus* Fabricius, *Anoplolepis* spp. and *Solenopsis invicta* Buren, among others.

► Aphids
► Vegetable Pests and their Management
► Citrus Pests and their Management

References

Ebert TA, Cartwright B (1997) Biology and ecology of *Aphis gossypii*. Glover (Homoptera: Aphididae). Southwest Entomol 22:116–153

Miyazaki M (1987) Forms and morphs of aphids. In: Mink AK, Harrewijn P (eds) Aphids: their biology, natural enemies, and control. Elsevier, Amsterdam, The Netherlandspp 27–50

Stoetzel MB, Miller GL (2001) Aerial feeding aphids of corn in the United States with reference to the root-feeding *Aphis maidiradicis* (Homoptera: Aphididae). Fla Entomol 84:83–98

Xia JY, van der Werf W, Rabbinge R (1999) Influence of temperature on bionomics of cotton aphid, *Aphis gossypii*, on cotton. Entomol Exp Appl 90:25–35

Melon Fly, *Bactrocera cucurbitae* (Coquillett) (Diptera: Tephritidae)

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Melon fly is found in the tropical regions of Asia, a portion of east Africa, and on some Pacific islands, including Hawaii, USA. Melon fly has been recovered on several occasions in California, and although it has not become established in the western hemisphere, the tropical and subtropical regions would be suitable habitat.

Life History

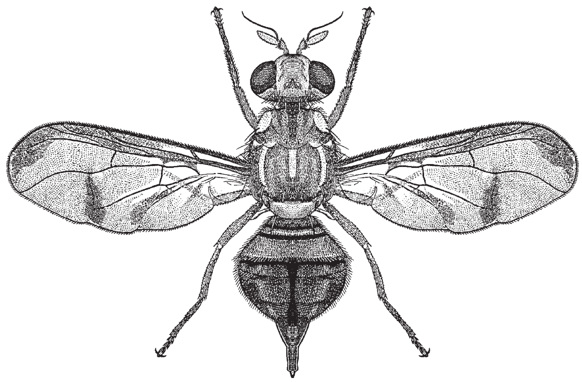
A life cycle can be completed in about 5 weeks in warm climates, but may require 3–4 months in cool climates. The adults (Fig. 26) can survive for months, and will continue to reproduce if fruit is available. In tropical climates such as Hawaii they are present throughout the year. Their abundance is determined mostly by availability of suitable host plant material, but they tend to be most common in summer and autumn.

Females deposit eggs in small batches, usually 5–20 eggs each. Females may produce 800–900 eggs over their life span. The white eggs are about 1.3 mm long and 0.25 mm wide, and are deposited in the fruit or vegetative parts of plants. The lower and upper developmental thresholds for egg development are about 10 and 40°C, respectively. Eggs hatch, on average, in 1.3 days.

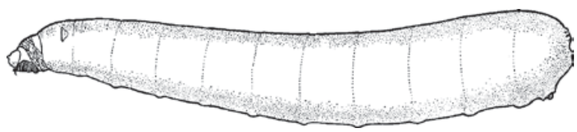
The larvae (Fig. 27) are white, and when they hatch they are about the length of the egg. Larvae immediately begin to grow, and attain a length of about 2.5, 5.5, and 11.0 mm in length during instars 1–3, respectively. The mouth hooks are pale in the first instar, but thereafter are darkened and easily observed. Larvae complete their development in 5–8 days, with instars 1–3 requiring about 1, 1–2, and 2–3 days, respectively, in soft hosts such as papaya. The lower and upper developmental thresholds for larvae are about 12 and 34°C, respectively.

When mature, larvae leave the host, burrow into the soil up to a depth of 10 cm, and pupate. The adults emerge from the tan or yellow-brown puparium after about 10 days (range of 7–14 days), and dig to the soil surface.

Newly emerged adults crawl to a sheltered location where they rest for 2–3 h before taking flight. Adults are yellow or yellow-brown in color, with yellow wings marked with brown bands. They measure about 6–9 mm in length. Dark markings resembling a "T" occur on the abdomen, and two lateral and a medial yellow stripe are found on the thorax. The presence of wing bands and the dark abdominal markings can be used to differentiate melon fly from oriental fruit fly and Mediterranean fruit fly, respectively. The preoviposition period of adults is about 7.4 days, and they are capable of depositing eggs for about 3 months.



Melon Fly, *Bactrocera cucurbitae* (Coquillett) (Diptera: Tephritidae), Figure 26 **Adult of melon fly, *Bactrocera cucurbitae* (Coquillett).**



Melon Fly, *Bactrocera cucurbitae* (Coquillett) (Diptera: Tephritidae), Figure 27 **Mature larva of melon fly, *Bactrocera cucurbitae* (Coquillett).**

Adults spend most of their time associated with the adult host plants, seeking vegetable crops or other prospective larval hosts intermittently for oviposition. Fly activity in crop fields peaks in the afternoon hours. At dusk, males form aggregations called leks, and by making wing vibrations and releasing sex pheromone, attract and copulate with females.

Melon fly prefers such cucurbits as watermelon, cantaloupe, pumpkin, squash, and cucumber, but infests other vegetables including tomato, pepper, green bean, and cowpea. Wild hosts, particularly bitter melon, *Mormordica charantia*, can be important. Passion fruit, papaya, grape, and citrus also are suitable larval hosts, but it is the availability of vegetable crops that generally determines melon fly abundance.

The adult often is found associated with plants that are not larval food sources, but rather provide sustenance for the adults. Honeydew produced by such insects as aphids and scale insects, and secretions of extrafloral nectaries, attract flies to plants such as corn; castor bean, *Ricinus communis*; spiny amaranth, *Amaranthus spinosus*; rattlepod, *Crotolaria incana* and *C. mucronata;* and other cultivated and wild plants.

Extensive research has been conducted around the world to identify effective natural enemies of this serious pest. The wasp *Psytallia fletcheri* (Silvestri) (Hymenoptera: Braconidae), a larval parasitoid, is the most effective biological control agent located. Although *P. fletcheri* is effective at parasitizing melon fly larvae infesting wild cucurbits, it is relatively ineffective in crops. Therefore, its use is limited to reduction of background populations only.

Damage

In the absence of biological or chemical control, melon fly is extremely damaging. Melon fly larvae develop in blossoms, fruits, and some vegetative portions of plants. Among vegetative plant material, newly emerged seedlings and terminal shoots are preferred. Similarly, among fruits, immature fruit is usually selected. Larval feeding also opens the plant tissue to secondary invaders, both microbial and insect. Damage can also occur from egg laying even when larvae cannot survive because oviposition allows entry of microorganisms or causes deformities in the growing fruit. Some differences in damage among cucurbits exists. Seedling and stem damage is more common in watermelon and cantaloupe than in squash, cucumbers, and pumpkin. Blossom damage is serious among all cucurbits except cucumber.

Management

Fruit may be sampled for eggs and larvae, and soil for pupae, but this is not done routinely because of the high labor requirements and expense. A natural chemical constituent of some plants, raspberry ketone, is highly attractive to male melon flies, and a synthetic analog called cue-lure is equally or more attractive; the latter is useful with traps for sampling. Fluorescent yellow sticky traps can also be used to sample adult densities, and odor and visual stimuli are sometimes combined in a single trap design. However, the most widely used trap is the McPhail trap, a liquid-baited trap.

Melon fly adults, unlike many insect pests, do not remain in contact with larval host plants for extended periods of time. Instead, they spend a great deal of time in weedy vegetation surrounding crop fields. A program of treating the surrounding vegetation, rather than the crops, is often recommended. Treatment of border vegetation can be much more effective than treatment of crops. Bait sprays containing insecticide also can be used effectively for adult suppression. Sugar or protein hydrolysate is mixed with various insecticides to produce bait sprays. Insecticide and bait treatments have been combined with mass release of sterile male insects to eradicate melon fly from some Pacific islands. Cue-lure can also be mixed with insecticide to attract and kill flies, but it is only effective against males.

Field sanitation is the most important element of cultural management. High melon fly populations result from continuous availability of larval food, which may be due either to continuous cropping or failure to dispose of crop residues. Destruction of infested or unmarketable vegetables in a timely manner is essential. Trap crops have not been effective at protecting vegetables, probably due to the relatively wide host range and vagility of the insects.

Protective coverings have long been used to deter oviposition by melon fly. Paper bags and newspapers are used to wrap individual fruit in the case of large produce such as cantaloupe and watermelon. This is effective but tedious, and not useful for small-fruited vegetables. Also, it does not protect vines and flower buds. Row covers provide more complete protection, but pollination may be interrupted.

► Fruit Flies (Diptera: Tephritidae)
► Vegetable Pests and their Management

References

Nishida T (1954) Further studies on the treatment of border vegetation for melon fly control. J Econ Entomol 47:226–229
Nishida T (1955) Natural enemies of the melon fly, *Dacus cucurbitae* Coq. in Hawaii. J Econ Entomol 48:171–178
Nishida T, Bess HA (1957) Studies on the ecology and control of the melon fly *Dacus* (*Strumeta*) *cucurbitae* Coquillett (Diptera: Tephritidae). Hawaii Agr Exp Stat Tech Bull 34:44
Vargas RI, Miyashita D, Nishida T (1984) Life history and demographic parameters of three laboratory-reared tephritids (Diptera: Tephritidae). Ann Entomol Soc Am 77:651–656

Melon Thrips, *Thrips palmi* Karny (Thysanoptera: Thripidae)

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Until the mid 1970s, the distribution of melon thrips was limited to Southeast Asia. In recent years it has spread throughout Asia, and to many Pacific Ocean islands, North Africa, Australia, Central and South America, the Caribbean region and southernmost mainland USA (Florida). It has the potential to infest greenhouse crops widely, but under field conditions likely will be limited to tropical and subtropical areas.

Life History

A complete generation may be completed in about 20 days at 30°C, but it is lengthened to 80 days when the insects are cultured at 15°C. Melon thrips are able to multiply during any season that crops are cultivated but are favored by warm weather and suppressed by senescent crops. In southern Florida, they are damaging on both autumn and spring vegetables. In Hawaii, where vegetables are grown during the summer months, they also become numerous during the summer growing season.

Eggs are deposited in leaf tissue, in a slit cut by the female. One end of the egg protrudes slightly. The egg is colorless to pale white in color, and bean-shaped in form. Duration of the egg stage is about 16 days at 15°C, 7.5 days at 26°C, and 4.3 days at 32°C.

The larvae (sometimes called nymphs) resemble the adults in form except for the lack of wings and smaller body size (Figs. 28 and 29). There are two instars during the "larval" period. Larvae feed gregariously, particularly along the leaf midrib and veins, and usually on older leaves. Larval development time is determined principally by the suitability of temperature, but host plant quality also has an influence. Larvae require about 14, 5, and 4 days to complete their development at 15, 26, and 32°C, respectively. At the completion of the larval instars the insect usually descends to the soil or leaf litter where it constructs a small earthen chamber for a pupation site.

There are two instars during the "pupal" period. The prepupal and pupal instars are inactive, nonfeeding stages, although the insect changes slightly in form at each molt. The prepupae and pupae resemble the adults and larvae in form, except that they possess wing pads. The wing pads of the pupae are longer than that of the prepupae. The combined prepupal and pupal development time is about 12, 4, and 3 days at 15, 26, and 32°C, respectively.

Adults are pale yellow or whitish in color, lacking blotches of dark pigmentation but with numerous dark setae on the body. The population is heavily weighted toward females. The slender fringed wings are pale. The hairs or fringe on the anterior edge of the wing are considerably shorter that those on the posterior edge. Adults measure 0.8–1.0 mm in body length, with females averaging slightly larger than males. Unlike the larvae, the adults tend to feed on young growth, and so are found on new leaves. Adult longevity is 10–30 days for females and 7–20 days for males. Development time varies with temperature, with mean values of about 20, 17, and 12 days at 15, 26, and 32°C. Females produce up to about 200 eggs, but average about 50 per female, which they deposit in leaf tissues in an incision made with the ovipositor. Both mated and virgin females deposit eggs.

Damage

Melon thrips is a polyphagous species, but is best known as a pest of Cucurbitaceae and Solanaceae. Among vegetables injured are bean, cabbage, cantaloupe, chili, Chinese cabbage, cowpea, cucumber, bean, eggplant, lettuce, melon, okra, onion, pea, pepper, potato, pumpkin, squash, tomato and watermelon. Other crops infested include avocado, carnation, chrysanthemum, citrus, cotton, hibiscus, mango, peach, plum, soybean, tobacco, and others.

Melon thrips cause severe injury to infested plants. Leaves become yellow, white or brown, and then crinkle and die. Terminal growth may be discolored, stunted, and deformed. Densities from 1 to 10 per cucumber leaf have been considered to be the threshold for economic damage in some Japanese studies. However, studies in Hawaii suggested a damage threshold of 94 thrips per leaf early in the growth of the plant. Feeding usually occurs on foliage, but on pepper, a less suitable host, flowers are preferred to foliage. Because melon thrips prefer foliage, they are reported to be less damaging to cucumber fruit than western flower thrips, *Frankliniella occidentalis* (Pergande). Nevertheless, fruits may also be damaged; scars, deformities, and abortion are reported. In Hawaii, thrips were observed to attain higher densities on cucumber plants infected with watermelon mosaic virus, but it was not determined whether the plants were more attractive to adults or suitable for survival and reproduction.

In addition to direct injury, melon thrips are capable of inflicting indirect injury by transmitting some strains of tomato spotted wilt virus and bud necrosis virus.

Management

To assess population density, nymphs and adults are collected from foliage. Adults tend to move toward young foliage, with nymphs tending to be clustered on foliage inhabited by adults several days earlier. Adults can also be sampled with sticky and water pan traps. Blue and white are attractive colors for thrips, and have been used to trap melon thrips. However, yellow has also been suggested to be an attractive color.

Foliar insecticides are frequently applied for thrips suppression, but at times it has been difficult to attain effective suppression. Various foliar and drench treatments, alone or combined with oil, have achieved some success. The eggs, being in the foliar tissue, and the pupae, which reside in the soil, are relatively insensitive to insecticide application.

Several cultural practices apparently affect melon thrips abundance. Physical barriers such as fine mesh and row cover material can be used to restrict entry by thrips into greenhouses, and to reduce the rate of thrips settling on plants in the field. Organic mulch is thought to interfere with the colonization of crops by winged thrips. Plastic mulch also is reported to limit population growth, but it is uncertain whether this is due to reduced rates of invasion or denial of suitable pupation sites. Crop stubble is not an effective deterrent. The effects of intercropping potato with onion are variable. Although aphid and aphid-borne disease incidence was decreased in such potato plantings, the density of thrips on potatoes was increased. Thus, the benefits of such cropping practices are largely a function of which pests are likely to be most important in an area. Heavy rainfall is thought to decrease thrips numbers. However, there seems to be no evidence that overhead irrigation is an important factor in survival.

Predation is often considered to be important in population regulation, and misuse of insecticides exacerbates thrips problems by killing predators. The predatory mite *Neoseiulus cucumeris* (Oudemans) has been investigated for suppression of melon thrips. Mite density is correlated with thrips density, but within-plant distribution differs among the two species, suggesting that although the mites may increase in numerical abundance they are unlikely to drive the thrips to extinction.

References

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, CA, 729 pp

Castineiras A, Baranowski RM, Glenn H (1996) Temperature response of two strains of *Ceranisus menes* (Hymenoptera: Eulophidae) reared on *Thrips palmi* (Thysanoptera: Thripidae). Fla Entomol 79:13–19

Castineiras A, Baranowski RM, Glenn H (1997) Distribution of *Neoseiulus cucumeris* (Acarina: Phytoseiidae) and its prey, *Thrips palmi* (Thysanoptera: Thripidae), within eggplants in south Florida. Fla Entomol 80:211–217

Castineiras A, Peña JE, Duncan R, Osborne L (1996) Potential of *Beauveria bassiana* and *Paecilomyces fumosoroseus* (Deuteromycotina: Hyphomycetes) as biological control agents of *Thrips palmi* (Thysanoptera: Thripidae). Fla Entomol 79:458–461

Girling DJ (ed) (1992) *Thrips palmi*. A literature survey with an annotated bibliography. International Institute of Biological Control, Silwood Park, Ascot, UK, p 37

Tsai JH, Yue B, Webb SE, Funderburk JE, Hsu HT (1995) Effects of host plant and temperature on growth and reproduction of *Thrips palmi* (Thysanoptera: Thripidae). Environ Entomol 24:1598–1603

Melonworm, *Diaphania hyalinata* Linnaeus (Lepidoptera: Pyralidae)

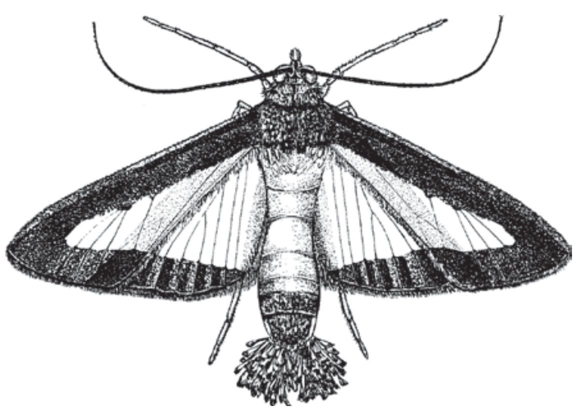
Melonworm is a tropical insect, and occurs throughout most of Central and South America and the Caribbean. It also occurs in some subtropical locations, such as the southernmost United States. Melonworm disperses readily, invading areas where it cannot overwinter, so occurrence in the cooler portions of its range is variable, depending on wind and favorable weather.

Life History

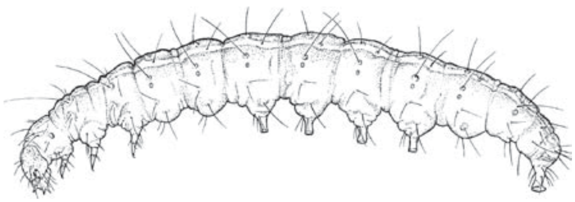
The melonworm can complete its life cycle in about 30 days. It is present throughout the year in warm locations, undergoing numerous generations annually, but has as few as one generation in peripheral, invaded areas.

Melonworm moths (Fig. 28) deposit oval, flattened eggs in small clusters, averaging 2–6 eggs per egg mass. Apparently they are deposited at night on buds, stems, and the underside of leaves. Initially they are white, but soon become yellow in color. They measure about 0.7 mm long and 0.6 mm wide. Hatching occurs after 3–4 days.

There are five instars. Total larval development time is about 14 days, with mean (range) duration the instars about 2.2 (2–3), 2.2 (2–3), 2.0 (1–3), 2.0 (1–3), and 5.0 (3–8) days, respectively. Head capsule widths are about 0.22, 0.37, 0.62, 1.04, and 1.64 mm, respectively. Larvae attain lengths of about 1.5, 2.6, 4.5, 10, and 16 mm in instars 1–5, respectively. Neonate larvae are colorless, but by the second instar larvae assume a pale yellow-green color. They construct a loose silken structure under leaves that serve to shelter them



Melonworm, *Diaphania hyalinata* Linnaeus (Lepidoptera: Pyralidae), Figure 28 Adult melonworm, *Diaphania hyalinata* Linnaeus.



Melonworm, *Diaphania hyalinata* Linnaeus (Lepidoptera: Pyralidae), Figure 29 Mature larva of melonworm, *Diaphania hyalinata* Linnaeus.

during the daylight hours. In the fifth instar, larvae have two subdorsal white stripes extending the length of the body. The stripes fade or disappear just prior to pupation, but they are the most distinctive characteristic of the larvae (Fig. 29).

Prior to pupation, larvae spin a loose cocoon on the host plant, often folding a section of the leaf for added shelter. The melonworm cocoon is much better formed than the cocoon of the co-occurring pickleworm, *Diaphania nitidalis* (Stoll), and the melonworm's preference for green foliage as a pupation site also serves to differentiate these insects. The pupa is 12–15 mm in length, about 3–4 mm in width, and fairly pointed at each end. It is light to dark brown in color. The pupal stage persists for 9–10 days.

The moth's wingspan is about 2.5 cm. The wings are pearly white centrally, and slightly iridescent, but are edged with a broad band of dark brown. Moths frequently display brushy hairpencils at the tip of the abdomen when at rest. Melonworm moths differ from pickleworm in that they remain in the crop during the daylight hours. While they are generally inactive during the day, they will fly short distances when disturbed.

Melonworm is restricted to feeding on cucurbits; both wild and cultivated cucurbits may be attacked. Summer squash and the winter squash species are good hosts. Pumpkin is of variable quality as a host, probably because pumpkins have been bred from several *Cucurbita* species. The *Cucumis* species, cucumber, gherkin, and cantaloupe, are attacked but not preferred. Watermelon is almost never eaten.

Natural enemies of melonworm are nearly the same as those of pickleworm, and the parasitoids attacking pickleworm also attack melonworm: *Apanteles* sp., *Hypomicrogaster diaphaniae* (Muesebeck), *Pristomerus spinator* (Fabricius) (all Hymenoptera: Braconidae), *Casinaria infesta* (Cresson), *Temelucha* sp. (both Hymenoptera: Ichneumonidae), and undetermined trichogrammatids (Hymenoptera: Trichogrammatidae). However, additional species parasitize melonworm, including *Gambrus ultimus* (Cresson), *Agathis texana* (Cresson) (both Hymenoptera: Ichneumonidae) and an undetermined fly (Hymenoptera: Tachinidae). The tachinids known from melonworm are *Nemorilla pyste* (Walker) and *Stomatodexia cothurnata* (Wiedemann). Studies conducted in Puerto Rico reported levels of parasitism reaching 24%. Generalist predators such as *Calosoma* spp. and *Harpalus* (both Coleoptera: Carabidae), the soldier beetle *Chauliognathus pennsylvanicus* DeGeer (Coleoptera: Cantharidae), and the red imported fire ant *Solanopsis invicta* Buren (Hymenoptera: Formicidae) have also been reported to be mortality factors.

Damage

Melonworm feeds principally on leaf tissue, especially if foliage of a favored host plant such as summer or winter squash is available. Usually the leaf veins are left intact, resulting in lace-like plant remains. However, if the available foliage is exhausted, or the plant is a less preferred species such as cantaloupe, then the larva may feed on the surface of the fruit, or even burrow into the fruit. As is the case with pickleworm, growers sometimes refer to these insects as "rindworms" because they cause scars on the surface of melons. In a study of melonworm damage potential to summer squash conducted in south Florida, melonworm caused a 23% yield loss due to foliage damage (indirect loss) and a 9–10% yield reduction due to fruit damage (direct loss).

Historically, melonworm was considered to be a very damaging pest, but because it feeds preferentially on foliage it is easy to control with a variety of insecticides. In tropical areas it often is considered more damaging than pickleworm. In temperate areas, and especially in commercial vegetable production areas, it is treated as only a minor pest. In insecticide-free cucurbit production and in home gardens, melonworm can cause serious damage.

Management

Monitoring the population of moths is difficult. The sex pheromone has been identified but is not available commercially. Moths are not attracted to light traps. Thus, larval populations normally are monitored.

Melonworm is easily suppressed with insecticides. Pollinators, particularly honeybees, are very important in cucurbit production, and insecticide application can interfere with pollination by killing honeybees. If insecticides are to be applied when blossoms are present, it is advisable to use insecticides with little residual activity, and to apply insecticides late in the day, when honeybee activity is minimal. In addition to chemical insecticides, *Bacillus thuringiensis* is commonly recommended for suppression, and this product does not kill bees.

Row covers can be used effectively to exclude melonworm adults. Intercropping of corn and beans with squash was shown to reduce damage by melonworm. Since melonworm prefers squash to most other cucurbits, trap cropping has been suggested, and of course destruction of crop residue which may contain melonworm pupae is recommended. Early plantings, except in tropical areas where melonworm overwinters, often escape serious damage.

References

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, CA, 729 pp

Smith RI (1911) Two important cantaloupe pests. NC Agr Exp Sta Bull 214:101–146

Melsheimer, Frederick Valentine

Frederick Melsheimer was born on September 25, 1749 at Regenborn, in the Duchy of Brunswick, Germany. He attended the University of Helmstadt until 1776 when he was ordained and became a chaplain with a regiment of Hessian dragoons. Soon afterwards he and his regiment were shipped to Quebec, Canada, and captured by American troops during the War of Independence. He remained in the United States after the war, and served as a Lutheran clergyman among the German settlers of Pennsylvania. Melsheimer became a professor of languages at Franklin and Marshall College, and also served as its president. Melsheimer pursued an interest in insects throughout his life, a source of amusement to his parishioners, who considered it an eccentricity. Nevertheless, Melsheimer made the first important collections and wrote the first important entomological work in the United States, "A catalogue of the insects of Pennsylvania" (1806). It remained the only publication available on American insects for 25 years, until Thomas Say's "American Entomology" was published. The "catalogue" considered only beetles, and Melsheimer intended to publish additional tomes to treat other groups, but illness intervened. He died on June 30, 1824. Interestingly, two of Melsheimer's children, John F. and Frederick Ernst, shared their father's interest in insects and were avid collectors, with F.E. Melsheimer gaining prominence as a coleopterist.

Reference

Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Melyridae

A family of beetles (order Coleoptera). They commonly are known as soft-winged flower beetles.

► Beetles

Membracidae

A family of insects in the order Hemiptera. They sometimes are called treehoppers.

► Bugs

► Treehoppers

Membrane

The thin portion of the wing between wing veins. In the case of Hemiptera, the thinner, distal portion of the hemelytron.

Ménétriés, Edouard

Edouard Ménétriés was born at Paris, France, on October 2, 1802. He was employed as conserver of rarities at the Zoological Museum in the Imperial Academy of Sciences, St. Petersburg, Russia. He was an authority on Lepidoptera and Coleoptera. He made extensive collections in Russia, Siberia, Alaska, and California. He died at St. Petersburg on April 10, 1861.

Reference

Essig EO (1931) A history of entomology. Macmillan, New York, 1029 pp

Mengenillidae

A family of insects in the order Strepsiptera.

► Stylopids

Menoponidae

A family of chewing lice (order Phthiraptera). They sometimes are called poultry lice.

► Chewing and Sucking Lice

Mentum

The distal section of the insect labrum, bearing the moveable parts; it is sometimes fused with the submentum (Fig. 30).

► Mouthparts of Hexapods

Meridic Diet

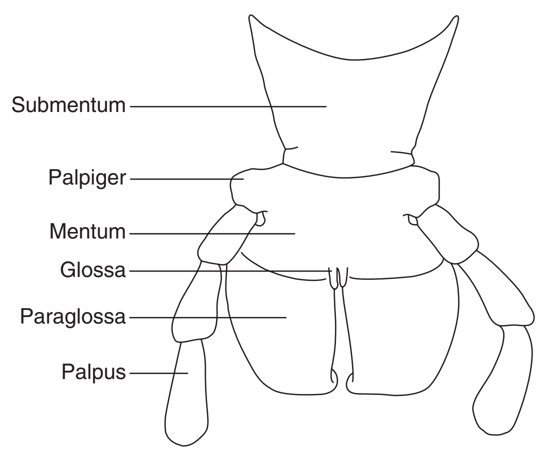
A diet that contains a chemically defined (holidic base), but which also contains one or a few poorly defined substances (e.g., leaf extracts). (contrast with holidic and oligidic diet).

Meristem

The cells capable of division located at the growing point of a plant.

Meroistic Ovaries

Ovaries that have nurse cells associated with the oocytes. (contrast with panoistic ovaries).



Mentum, Figure 30 External aspect of the labium in an adult grasshopper, showing some major elements.

Meropeidae

A family of scorpionflies (order Mecoptera). They commonly are known as earwigflies.
► Scorpionflies

Merothripidae

A family of thrips (order Thysanoptera). They commonly are known as large-legged thrips.
► Thrips

Mesadene (pl., mesadenia)

Accessory glands of mesodermal origin found in the male reproductive system of some insects.
► Accesory Gland

Mesenteron

Another name for the midgut.

Mesepimeron

The epimeron of the mesothorax.

Mesepisternum

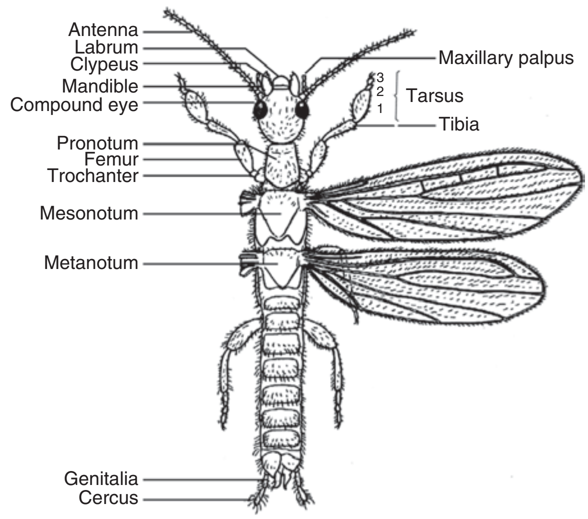
The sternum of the mesothorax or lateral extension of the mesothorax that meet dorsally in a ridge.

Meson

The mid-line of the body; an imaginary line separating the body into right and left halves.

Mesonotum

The upper surface of the second or middle thoracic ring (mesothorax) (Fig. 31).
► Thorax of Hexapods



Mesonotum, Figure 31 Diagram of a webspinner showing the location of the wings relative to the thoracic segments. Note that the front wings are attached to the mesothorax (the upper surface of the mesothorax, or mesonotum, is labeled). The hind wings are attached to the metathorax (seen as metanotum).

Mesopleuron

The lateral surface of the mesothorax.

Mesopsocidae

A family of psocids (order Psocoptera).
► Bark-Lice, Book-Lice or Psocids

Mesoscutellum

The scutellum of the mesothorax; often simply called the scutellum.
► Thorax of Hexapods

Mesothorax

The second or middle thoracic segment. The thoracic segment bearing the middle pair of legs. The thoracic segment bearing the first pair of wings (Fig. 31).
► Thorax of Hexapods

Mesoveliidae

A family of bugs (order Hemiptera). They sometimes are called water treaders.

► Bugs

Messenger RNA (mRNA)

RNA molecules which code for proteins and which are translated on the ribosomes.

Metabolism of Insect Cuticular Lipids

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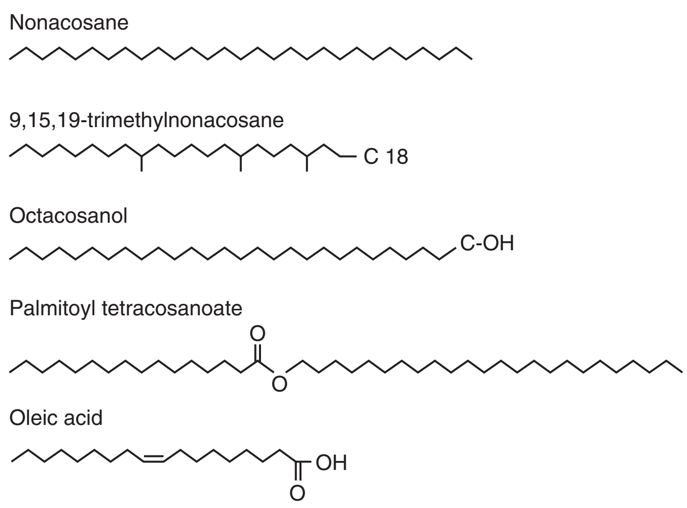
Insect cuticular lipids, also called cuticular waxes, consist of a complex mixture of very long chain compounds with low reactivity and rather high melting point. They provide a variety of functions ranging from water-proofing properties to chemical cues (sexual attractants, deterrents, defensive secretions, kairomones), as well as barrier against microbial or chemical penetration. Among the most usual and major lipid components of the epicuticle are hydrocarbons, fatty alcohols, wax esters, and free fatty acids. They have been reported for more than a hundred species. Minor components include ketones, aldehydes, acetate esters, sterol esters, and less frequently, acylglycerols. Different chain length, branching pattern, substitution, and or unsaturation, determine characteristic blends for different orders, although their relative amounts depend on a variety of internal and external factors: developmental stage, sex, feeding status, reproduction cycle, etc (Fig. 32).

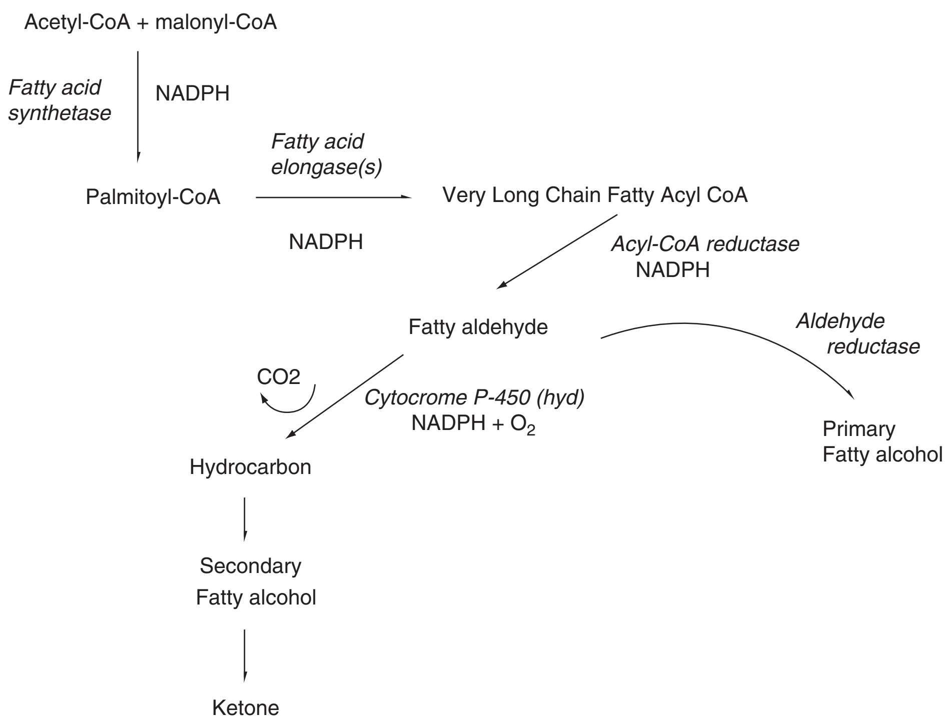
Unique metabolic pathways for the epicuticular lipids have been disclosed in the last 20 years, mostly by Blomquist and co-workers. Depending on the diet, a short chain amino acid, glucose, or fatty acids will be converted to acetate – the building block of two-carbon units – in order to initiate *de novo* straight chain fatty acid biosynthesis which occurs at two different steps. The first one involves condensation with coenzyme A (CoA) to provide acetyl-CoA units, which are then converted to malonyl-CoA by the multienzyme system called acetyl-CoA carboxylase. At the second step, both acetyl-CoA and malonyl-CoA are required for long chain fatty acid synthesis through the multienzyme system of the cytosolic fatty acid synthetase (FAS) from the integument. Reaction will usually proceed until a 16- or 17-carbon fatty acid is released as the end product, remaining as free fatty acid or incorporated into acylglycerols (Fig. 33). Aphids are unusual in this regard, with C14:0 as the major fatty acid due to the presence of an active thioesterase. Exogenous fatty acids of 16 and 18 carbons are incorporated into acylglycerols and phospholipids. Most of the cuticular lipids are biosynthetically related.

One or more malonyl-CoA units might be replaced by methylmalonyl-CoA during fatty acid formation, leading to the formation of methyl-branched fatty acyl precursors. An integumental microsomal FAS is involved in these reactions, as shown in the German cockroach *Blatella germanica*, the housefly *Musca domestica*, and the assassin bug *Triatoma infestans*. Endogenously produced fatty acids serve as primers for microsomal elongation and or desaturation reactions, prior activation as the fatty acyl-CoA derivative by the action of fatty acyl-CoA synthetases, as shown in the cockroaches *B. germanica* and *Periplaneta americana*. There is now overwhelming evidence that insects synthesize hydrocarbons and other cuticular wax components from fatty acids, in a pathway similar to that postulated by Kolattukudy and co-workers in plants in 1976. The reaction occurs through chain elongation by the action of fatty acyl-CoA elongases producing very long chain fatty acyl (VLCFA) moieties that are finally converted to hydrocarbons one carbon shorter, rendering mostly odd-numbered straight chain hydrocarbons.

The major endogenous mono-unsaturated or di-unsaturated fatty acids, rather than newly synthesized unsaturated chains, were suggested



Metabolism of Insect Cuticular Lipids, Figure 32 **Representative straight and methyl-branched insect cuticular lipids.**



Metabolism of Insect Cuticular Lipids, Figure 33 **Biosynthesis of insect cuticular lipids.**

to be the precursor for multi-methylene interrupted alkadiene, and no reports on desaturase activity in the integument are available. Afterwards, chain elongation reactions will proceed as described above. The VLCFA precursors are converted into aldehyde intermediates by a fatty acyl-CoA reductase. Finally, a microsomal cytochrome P-450 type enzyme releases CO_2 to yield odd-chained alkanes. This step was shown in *M. domestica*, the house cricket *Acheta domesticus*, the dampwood termite *Zootermopsis nevadensis*, and *B. germanica*, among others.

Methyl-branched hydrocarbons are abundant in a large number of insect species. They arise through a modification of the straight-chain pathway described above. Methyl branches located on carbon 3 or greater originate from propionate in the form of methylmalonyl-CoA, which replaces one or more malonyl-CoA units during early fatty acid synthesis leading to the formation of internally-branched methyl-alkanes, multiple-methyl-branched alkanes and 3-methylalkanes. An integumental microsomal FAS is the major enzyme responsible for methyl-branched fatty acid formation, whereas the cytosolic integumental FAS shows less activity. Alkanes can then undergo sequential oxidations by cytochrome P-450 oxidation to form secondary alcohols and ketones, as shown by the conversion of 3,11-dimethylnonacosane into 3,11-dimethylnonacosan-2-one, the contact sexual pheromone in *B. germanica*.

Fatty alcohol biosynthesis has been scarcely addressed, but the action of an aldehyde reductase was proposed in *Manduca sexta* for the conversion of the appropriate very long chain aldehyde into the corresponding even-chain primary fatty alcohol. Primary alcohols can then be combined with free fatty acids to form wax esters. Cell fractionation studies have shown that many of the enzyme activities of wax biosynthesis are located in the microsomal fraction. Other than FASs, the wax biosynthetic pathway is composed of various enzyme activities; fatty acid elongase, acyl-CoA reductase, aldehyde reductase and wax synthase. The relative activities of the enzymes determine the chain lengths of the waxes found in the cuticle. However, very little is known about the enzymes of these biosynthetic pathways, the regulation of wax production, and the secretion of wax components onto the surface of the insect.

Methodology

How can these reactions be followed up, the enzymes involved, and metabolite production determined? One of the most powerful and worldwide accepted methodologies is to employ radioactive (labeled) tracer molecules of the same or similar structure than the putative precursor, containing labeled isotopes, usually ^{13}C-, ^{2}H-, ^{3}H-, ^{14}C-or ^{32}P with the label located at specific positions helps to follow the biosynthetic pathways both by *in vivo* and *in vitro* techniques. The most simple *in vivo* experiments are performed by injecting an appropriate fatty acid precursor (i.e., labeled acetate) to a certain number of insects of the target species, following the transport of labeled lipids into the cuticle at selected time intervals. Then, lipids might be washed off from the epicuticular surface (or those from the whole integument by a previous dissection) by solvent extraction. After concentration and preliminary fractionation, information on the total amount and classes of lipids formed is usually obtained employing various kinds of radioactive detectors and methods, i.e., by liquid scintillation counting (LSC) to determine the total amount of metabolites produced in the experimental conditions of an assay, and by radio-thin layer chromatography (radio-TLC) to determine the kind of lipid classes produced. After fractionation, and sometimes derivatization in order to facilitate detector response, radio-high performance liquid chromatography (radio-HPLC) and radio-gas chromatography (radio-GC) are widely used to provide a preliminary identification of the intermediates and end products of the biosynthetic process under study. Final identification and structure assignment require the use of more sophisticated techniques such as capillary gas chromatography-mass spectrometry (CGC/MS), HPLC/MS, and nuclear magnetic resonance (NMR). Enzyme studies might be carried out employing appropriate label tracers and/or by spectrophotometric measurements for preliminary characterization. Studies on enzyme location, purification, cofactors required, kinetic parameters and, regulation are carried out by more complex studies including HPLC purification, molecular mass determination, amino acid sequence, electronic microscopy, immunofluorescent assays, protein purification and characterization in addition to the previously mentioned techniques. Furthermore, if isolation of genes encoding the target enzyme and insertion in an appropriate vector are feasible, the overexpression of such enzyme in an appropriate system can increase the quantity of intermediate precursors, i.e., very long chain fatty acids, and thus increase the substrates available to study wax formation (Figs. 32 and 33).

References

Blomquist GJ, Nelson DR, de Renobales M (1987) Chemistry, biochemistry and physiology of insect cuticular lipids. Arch Insect Biochem Physiol 6:227–265

Blomquist GJ, Tillman-Wall JA, Guo L, Quilici DR, Gu P, Schal C (1993) Hydrocarbon and hydrocarbon derived sex pheromone in insects: Biochemistry and endocrine regulation. In: Stanley-Samuelson DW, Nelson DR (eds) Insect lipids. Chemistry, biochemistry and physiology. University of Nebraska Press, Lincoln, Nebraska, pp 317–351

Juárez MP, Chase J, Blomquist GJ (1992) A microsomal fatty acid synthetase from the integument of *Blatella germanica* synthesizes methyl-branched fatty acids, precursor to hydrocarbons and contact sex pheromone. Arch Biochem Biophys 293:333–341

Buckner JS (1993) Cuticular polar lipids of insects. In: Stanley-Samuelson DW, Nelson DR (eds) Insect lipids. Chemistry, biochemistry and physiology. University of Nebraska Press, Lincoln, Nebraska, pp 227–270

Kolattukudy PE, Croteau R, Buckner JS (1976) Biochemistry of plant waxes. In: Kolattukudy PE (ed) Chemistry and biochemistry of natural waxes. Amsterdam Elsevier North Holland, pp 289–347

Metallic Wood-Boring Beetles

Members of the family Buprestidae (order Coleoptera).

► Beetles

Metallyticidae

A family of praying mantids (Mantodea).

► Praying Mantids

Metalmark Butterflies (Lepidoptera: Riodinidae)

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This is one of the five families of "true" butterflies (in the superfamily Papilionoidea). Recent morphological and molecular evidence, for the first time based on sufficient taxon sampling, indicates the Riodinidae to be the sister group to the Lycaenidae (blues, coppers and hairstreaks). Based on the only confirmed riodinid fossils, of *Napaeina* and *Nymphidiini* species in Dominican amber, the family is at least 25 million years old. The higher classification of the Riodinidae is now relatively well resolved, and the group is currently divided into three subfamilies, twelve tribes and six subtribes, with only one *incertae sedis* section of unplaced riodinine genera still remaining. However, intertribal relationships in the largest subfamily, the Riodininae, are poorly understood.

- Order: Lepidoptera
  - Superfamily: Papilionoidea
    - Family: Riodinidae Grote
      - Subfamily: Nemeobiinae Bates
        - Nemeobiini Bates
        - Zemerini Stichel
        - Abisarini Stichel
      - Subfamily: Euselasiinae Kirby
        - Corrachiini Stichel
        - Euselasiini Kirby
      - Subfamily: Riodininae Grote
        - Mesosemiini Bates
        - Mesosemiina Bates
        - Napaeina Hall
        - Eurybiini Reuter
        - Riodinini Grote
        - Stalachtini Bates
        - Helicopini
        - Symmachiini
        - *incertae sedis* of Harvey
        - Nymphidiini Bates
        - Aricorina Hall & Harvey

Lemoniadina Kirby
Theopeina Clench
Nymphidiina Bates

Morphology

The Riodinidae present perhaps the most kaleidoscopic array of colors, patterns, shapes and sizes of any butterfly family. Many have metallic silver or gold markings, hence their common name of metalmarks. They are generally rather small and range in size from about 12–60 mm. The only distinguishing characteristic of the Riodinidae that is visible to the naked eye is their greatly shortened male forelegs, which are no longer used for walking. Although the Nymphalidae share this character, Riodinidae additionally have a coxa on the male foreleg that extends as a spine-like projection below the trochanter (a character only weakly developed in the two species of Corrachiini, and also quite well developed in various poritiine and curetine lycaenids), trichoid sensilla on the female foretarsal segments that are clustered into single instead of medially divided patches, and no posterior apophyses extending anteriorly from the ovipositor lobes of the female genitalia.

Although their external morphology is comparatively uniform (Fig. 34), the male and female genitalia exhibit a remarkable diversity of form given the relatively small size of the family. The most comprehensive set of drawings of venation, palpi, legs and genitalia is still that of Stichel (1910–1911). Although androconia, specialized male secondary-sexual scales, have historically been thought to be rare in the Riodinidae, especially, for example, compared to the Lycaenidae, a recent comprehensive study found that at least 25% of riodinid species possess a wide morphological array of them. Because the Riodinidae are now known to have abdominal coremata (similar to those of danaine nymphalids), concealed internal and visible external abdominal androconia, genital brush organs and hind leg hairpencils (unique within the Papilionoidea), as well as the more obvious alar organs, the family can reasonably be described as exhibiting among the greatest morphological diversity of androconial organs in the butterflies.

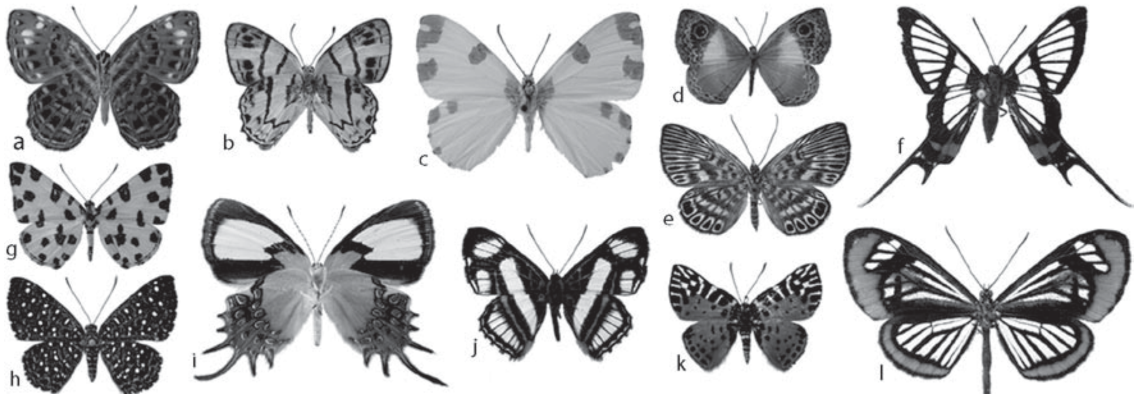
Diversity and Biogeography

The Riodinidae contain about 1,350 species, only a few of which remain undescribed. The family has a worldwide distribution, but it is unique among the butterflies in being almost exclusively confined to a single biogeographic region, the Neotropics, where approximately 95% of the familial diversity occurs. Riodinid diversity peaks in the lowlands of the Amazon basin, where as many as 400 species can be found in a single heterogeneous locality, constituting more than 20% of the local butterfly fauna (including Hesperiidae). Species richness in Central America is roughly half that of Amazonia, and only two dozen species extend northwards into North America. Species richness also tapers off gradually with increasing elevation, and very few species occur above 2,000 m.

On average, riodinids have smaller geographic ranges than their close relatives the lycaenids, and this makes them ideal subjects for biogeographic study. *Detritivora* Hall & Harvey, a genus of small, drab, forest-dwelling riodinines, provides perhaps the most extreme example in the Lepidoptera of a continuously distributed lowland group with highly fragmented species ranges. The *D. cleonus* group is divided into an incredible nineteen parapatrically distributed species across Amazonia, each occupying a variably small area of endemism. A cladogram of these riodinids, superimposed over a map of their distributions, led to the most detailed hypothesis yet of Amazonian area relationships.

Adult Ecology

Riodinids are found in a wide variety of primary and secondary habitats, from dry *Acacia* scrub to pluvial forest, but most are exclusive denizens of



Metalmark Butterflies (Lepidoptera: Riodinidae), Figure 34 **Adult riodinids. A. *Neotaxila thuisto* Hewitson "male" (Nemeobiinae, Nemeobiini). B. *Euselasia labdacus* Stoll (Euselasiinae, Euselasiini). C. *Hermathena candidata* Hewitson (Riodininae, Mesosemiini, Napaeina). D. *Perophthalma lasus* Westwood "male" (Riodininae, Mesosemiini, Mesosemiina). E. *Alesa amesis* Cramer "male" (Riodininae, Eurybiini). F. *Chorinea batesii* Saunders (Riodininae, Riodinini). G. *Baeotis sulphurea* R. Felder (Riodininae, Riodinini). H. *Calydna calamisa* Hewitson "male" (Riodininae, incertae sedis of Harvey). I. *Helicopis gnidus* Fabricius (Riodininae, Helicopini). J. *Synargis fenestrella* Lathy (Riodininae, Nymphidiini.) K. *Symmachia suevia* Hewitson (Riodininae, Symmachiini). L. *Stalachtis phaedusa* Hübner (Riodininae, Stalachtini).**

primary rainforest. Most species are very localized in time and space. Years of observations in an area usually result in finding only one or two places where a particular species occurs and even then the species will most likely only be present for a couple of hours a day, and perhaps only during certain months of the year. It is not surprising then that so many riodinids are very rare in collections. Intergeneric and interspecific differences in male riodinid perching behavior, involving variably sized groups of males resting at characteristic sites and investigating passing butterflies in search of conspecific females, can be explained these differences in the context of premating isolating mechanisms. Such perching behavior, better known in birds, is known as lekking, a word derived from the Swedish verb "leka," meaning "to play." Male riodinids most frequently lek along forest edges, streamsides, and especially on ridgetops and hilltops, where they may use the same patch of vegetation year after year, arriving from the surrounding forest and departing at roughly the same time every day, and always resting on leaves or tree trunks at about the same height above the ground.

Mimicry is perhaps more rampant in the Riodinidae, especially in females, than in any other butterfly family in terms of the diversity of taxa that its species mimic. There are tiger striped riodinids that resemble papilionids, pierids and various nymphalid subfamilies, clear-winged species that seem to mimic ithomiine nymphalids and dioptine and arctiine moths, and gaudy blue, red, orange, or yellow patterned species that seem to be mimicking dioptine, arctiine, geometrid and tortricid moths. Such riodinids also mimic the same flight behavior of the presumed model(s), often even holding the antennae at the same angle. Most of these mimetic relationships are probably Batesian, with moths generally being the unpalatable models, but we know essentially nothing about the palatability of mimetic riodinids.

Like other butterflies, riodinids can be found feeding on flowers, or imbibing nutrients and ions from damp sand or mud (known as puddling). However, carrion is the most frequently recorded food source, both in terms of number of individuals and taxa. This behavior is common elsewhere in butterflies only in certain subfamilies of the Nymphalidae and Lycaenidae. There is also a correlation between food substrate choice and wing area to thoracic volume ratio in male riodinids, with puddlers and carrion feeders having lower such ratios (i.e., relatively larger thoraces for their overall size). These feeding behaviors are believed to supplement nutrient stores from larval feeding to increase reproductive success and provide the necessary nutrients to maintain high metabolic rates during rapid flight.

Immature Stages and Myrmecophily

The early stages of the Riodinidae remain probably the most poorly known of all the butterfly families and only a small fraction of the genera have been reared, making the immatures a fertile field for further study. Riodinid eggs are generally laid singly, but in certain groups, such as the Euselasiinae, they are often laid in clusters, resulting in gregarious groups of often aposematic larvae. Riodinid eggs are remarkably diverse in form compared to those of the Lycaenidae, in anthropomorphic terms resembling crowns, pies, cakes, cones, footballs, automobile tires and more. Those larvae that have symbiotic relationships with ants tend to be smooth, whereas those that are non-myrmecophilous are generally hairy. Riodinid pupae are generally smoothly cylindrical, girdled, and best distinguished from those of other butterflies by their broadly flattened cremaster. Some pupae have spines, others are moth-like cocoons made from the shed larval setae, and those of *Eurybia* Illiger are extraordinary in having an elongate spine-like posterior projection almost as long as the remainder of the pupa to enclose the very long proboscis.

Myrmecophily, or the ability of butterfly caterpillars to form symbioses with ants by providing food secretions in exchange primarily for protection from arthropod predators, is almost entirely confined to the Lycaenidae and Riodinidae. Although this phenomenon is very widespread in the Lycaenidae, only about one quarter of the Riodinidae are myrmecophilous, encompassing the tribes Eurybiini and Nymphidiini. Myrmecophilous larvae possess a suite of "ant-organs" that facilitate their interactions with ants. Tube-like paired tentacle nectary organs (TNOs) on abdominal segment eight, which secrete nutritionally rich droplets to be harvested by ants, are present in both tribes, but a further two "ant-organs" are restricted to the Nymphidiini. Setose paired anterior tentacle organs (ATOs) on thoracic segment three appear to influence ant behavior through the use of semiochemicals, and a pair of stridulatory rod-like appendages on the first thoracic segment, termed vibratory papillae, grate against granulations on the head as it moves in and out to produce an acoustical call that is thought to function in attracting ants. The function of bladder or balloon setae, a corona of inflated setae on the first thoracic segment which also occur in the non-myrmecophilous Helicopini and *incertae sedis* section, is still unclear, but, at least in the Nymphidiini, they may release an ant alarm pheromone analogue, when squeezed by an ant, to confer protection on the caterpillar.

Riodinids are known to feed on over forty families of flowering plants, using leaves, extrafloral nectaries and, more rarely, flower parts, but are of little economic importance. Certain members of the Euselasiinae feed on harvested myrtaceous plants such as guava, and some Napaeina species can be pests on ornamental Neotropical bromeliads and orchids. Aphytophagy, or feeding on non-plant material such as ants or their regurgitations, or on hemipterans and their secretions, is rare in the Lepidoptera and in butterflies also present only in the Lycaenidae (e.g., Liphyrinae, Polyommatinae and Miletinae) and "Riodinidae (Eurybiini and Nymphidiini). Although aphytophagy has only been unequivocally documented for two riodinid species, there is evidence to suggest that this phenomenon is significantly more common in the family.

► Butterflies and Moths

References

Callaghan CJ (1983) A study of isolating mechanisms among Neotropical butterflies of the subfamily Riodininae. J Res Lepid 21:159–176
DeVries PJ (1997) The butterflies of Costa Rica and their natural history, vol 2: Riodinidae. Princeton University Press, Princeton, NJ, 288 pp
Hall JPW, Harvey DJ (2002) A survey of androconial organs in the Riodinidae (Lepidoptera). Zool J Linn Soc 136:171–197
Hall JPW, Harvey DJ (2002) The phylogeography of Amazonia revisited: new evidence from riodinid butterflies. Evolution 56:1489–1497
Hall JPW, Willmott KR (2000) Patterns of feeding behaviour in adult male riodinid butterflies and their relationship to morphology and ecology. Biol J Linn Soc 69:1–23
Stichel HFEJ (1910–1911) Lepidoptera Rhopalocera. Fam. Riodinidae. In: Genera insectorum, vol 112. J. Wytsman, Brussels, Belgium, 452 pp

Metalmark Moths (Lepidoptera: Choreutidae)

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Metalmark moths, family Choreutidae, comprise 418 species worldwide, in three subfamilies (in the past incorrectly included in Glyphipterigidae); actual world fauna probably exceeds 800 species. There are three subfamilies: Millieriinae, Brenthiinae, and Choreutinae. The family is in the superfamily Sesioidea in the section Tineina, subsection Sesiina, of the division Ditrysia. Adults small (7–24 mm wingspan), with head mostly smooth-scaled; haustellum scaled; labial palpi often with a scale tuft on second segment; maxillary palpi 1 to 2-segmented. Forewings somewhat elongate or more triangular (Fig. 35). Maculation variable but usually with brilliant metallic-iridescent spots or marks; sometimes more colorful markings, or subdued in a few species. Hindwings colorful or dark, and often with a light band near termen; sometimes pale. Adults are diurnal; usually near their host plants and tend to hop about on leaves. Larvae mostly leaf skeletonizers, but some are budworms; rarely leafminers (Millieriinae). Cocoons are white and spindle-shaped. Numerous hostplant families are recorded, but many in Compositae and Moraceae. The subfamily Millieriinae and nominate genus *Millieria* are named after the French lepidopterist Pierre Millière (1811–1887).

Metalmark Moths (Lepidoptera: Choreutidae), Figure 35 Example of metalmark moths (Choreutidae), *Saptha beryllitis* (Meyrick) from Taiwan.

References

Arita Y, Diakonoff AN (1979) A survey of the Japanese species of *Anthophila* Haworth and *Eutromula* Froelich and their early stages (Lepidoptera, Choreutidae), with an appendix. Zool Verhandlingen 166:1–42
Diakonoff AN (1986) Glyphipterigidae auctorum sensu lato. (Glyphipterygidae sensu Meyrick, 1913). In Amsel HG et al. (eds) Microlepidoptera Palaearctica, vol 7. G. Braun, Karlsruhe. 2 pts. 436pp, 175 pl
Heppner JB (1981) Family Choreutidae, pp 45–58. In: Heppner JB, Duckworth WD (eds) Classification of the superfamily Sesioidea (Lepidoptera: Ditrysia). Smithson Contrib Zool 314:1–144
Heppner JB (1982) Millieriinae, a new subfamily of Choreutidae, with new taxa from Chile and the United States (Lepidoptera: Sesioidea). Smithson Contrib Zool 370:1–27
Heppner JB (2004) Metalmark moths of North America (Lepidoptera: Choreutidae). Scientific Publishers, Gainesville, FL

Metamorphosis

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Insects are the only invertebrates that fly. The development of a winged form is the culmination of metamorphosis that converts a larva capable only of moving by squirming, crawling or swimming into a flying machine.

Issues of interest in insect metamorphosis include its evolutionary origin, the source of adult structures, hormonal control, and the identity of genes that regulate metamorphosis and code for proteins that form the structures of the different metamorphic stages.

Evolution

Among the orders of insects, patterns of cellular participation in metamorphosis vary from the simplest case, adults only slightly different from larvae, their structures having arisen from the same cells, to the most advanced in which differentiated larval cells in effect commit suicide and are replaced by new cells arising from undifferentiated precursors. By examining insects in different orders we can get an idea of how metamorphosis may have evolved from simple to complex.

A few "primitive" insects do not undergo metamorphosis (are ametabolous) and hence are flightless. Thysanura (silverfish), for example, hatch from the egg looking much like the adult, and only undergo subtle anatomical changes between molts. They never develop wings and continue to molt as sexually mature adults (Fig. 37).

Incomplete metamorphosis (or hemimetabolous development) is found in Blattodea (cockroaches), Orthoptera (grasshoppers), Hemiptera (bugs) and others. Here the larval and adult forms are also similar. After several molts from one larval stage (called instar) to the next, major changes appear at the final molt from larva to adult. These include the development of functional wings, genitalia and internal changes that accompany sexual maturation. These insects have larval wings, which though small and non-functional, are visible as pads on the thorax. Such insects are called exopterygotes because of these external wings.

In insects with complete metamorphosis (holometabolous development), there is a dramatic change in appearance, physiology and behavior between larvae and adults, and a physiologically and morphologically distinct stage, the pupa, has been inserted between the final larval instar and the adult. Available evidence indicates that there was a common ancestor for all of the holometabolous insects. These include the orders, Diptera (flies), Hymenoptera (bees and wasps), Coleoptera (beetles) and Lepidoptera (butterflies and moths). Such holometabolous insects account for about 90% of all insect species. Their success is due presumably to their ability to exploit radically different environmental resources at different stages in their lives.

Morphology and Physiology

The morphological changes in an individual that accompany metamorphosis can be created in one of two ways: First, a single lineage of cells can form larval, then pupal and finally adult structures. Second, change may involve the death of most of the cells of the larva and their replacement by the proliferation and differentiation of clusters of "stem cells". An example of the first type, persistence of cells throughout the life of an insect, is the abdominal epidermis of lepidopteran larvae. Here a single row of epithelial cells secretes first the cuticle of each larval stage, then switches and forms a pupal cuticle, and finally, accompanied by special differentiative cell divisions forms the scales and sockets and background cuticle of the adult.

The second type of change involves groups of cells that contribute little or nothing to larvae, but are used to build the pupa and adult. An example of the second type is seen in wing development. The cells that will contribute to the wings of holometabolous insects are present as imaginal discs in larvae. Imaginal discs are infoldings of the single layer of cells that constitute the surface epithelium. Once formed, they do not contribute to the external structure of the larva but evaginate to the surface at pupation, forming first pupal and then adult cuticle. Insects with such hidden, undifferentiated larval wings are also called endopterygotes, a synonym for holometabolous insects.

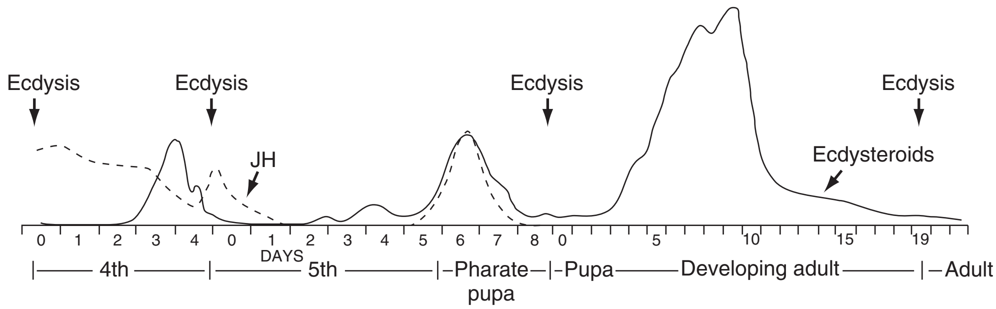
Imaginal discs are found in all holometabola, but arise in various ways. They first appear during late embryonic development of some insects like the higher Diptera, and only shortly before pupation in others like some Coleoptera. In the former case, they are attached to the surface epithelium by a thin stalk; in the latter they are no more than a thickening of the epidermis. In some insects, imaginal discs are only used as the source of a few adult structures, in others there are discs for all of the adult structures. In some cases, a few cells at the base of a larval structure, legs, antennae etc. may proliferate at pupation and be the exclusive source of the corresponding pupal and adult structures. In the *Drosophila* abdomen, there are small clusters of diploid cells, histoblasts that lie amidst the polyploid larval cells. Both types of cells secrete larval and pupal cuticles. Then larval cells die, the histoblasts proliferate and spread to form the adult abdomen.

In addition to the creation of these morphological structures definitive for the pupa and adult, complex changes also occur in the internal organs in the transition from larva to adult. As the food source changes in many cases from leaves to nectar, changes occur in the mouthparts from munching via strong mandibles to sipping via an extensible proboscis. Accompanying these changes in food source are changes in appearance and physiology of the digestive system. Different enzymes are needed to handle different food sources. In lepidopterans, the abdominal prolegs and their muscles, useful in walking, are lost. Flight muscles develop and the nervous system is rewired to accommodate this. Some neurons die; others develop from neuroblasts; while others change their outgrowths, (axons and dendrites) to connect with new targets.

Hormonal Control

There is far less variation in the hormonal control of metamorphosis than in the morphological changes themselves and the cellular events that underlie them. Essentially two classes of hormones (ecdysteroids and juvenoids) are involved, and the same mechanisms of metamorphic controls apply to both hemi- and holo-metabolous insects (Fig. 36). Briefly, ecdysteroids make insects molt. Juvenoids determine what they molt into. When juvenoids are absent at a critical period early in a molt cycle, the cells respond to ecdysteroids by forming the structures of the next metamorphic stage instead of making another larval instar. In this case, unimpeded by juvenoids, ecdysteroids also cause metamorphosis. Final instar hemipteran or lepidopteran larvae that receive an extra dose of juvenoids by injection or by implanting active corpora allata (the glands that make juvenoids) will molt into a giant extra instar larva rather than undergoing a metamorphic molt (to adult in the hemipteran or to pupa in the lepidopteran). If a lepidopteran pupa receives excess juvenoids, it will molt into another pupa, something not seen in nature. This action of juvenoids results in their being recognized as "status quo" hormones, for they direct the repetition of the pattern of syntheses necessary to reform the characteristics of the previous stage.

In the hornworm *Manduca sexta*, when a critical larval size is reached, it has a metamorphic molt. Thus size is in some sense the signal that the time has come for metamorphosis. The signal to undergo metamorphosis causes the corpora allata to cease making juvenoids and other tissues to synthesize enzymes that metabolize and inactive



Metamorphosis, Figure 36 **Diagram of the titers of ecdysteroids and juvenoids (JH) in *Manduca* during the final two larval instars, the pharate pupa, pupa, and developing (pharate) adult. The time at which ecdysis to the next stage occurs is also shown. (Adapted from Riddiford in "Metamorphosis/post-embryonic reprogramming of gene expression in amphibian and insect cells." Reprinted with permission of Cambridge University Press.)**

juvenoids. The mechanism of how size is measured and the nature of the metamorphic signal in other insects remain unknown.

There are exceptions to these findings. *Drosophila* larval tissues, except for the histoblasts, are insensitive to the antimetamorphic actions of juvenoids. Some larvae continue to grow rather than have an extra larval instar in the presence of excess juvenoids, and not all pupae or all pupal tissues can be induced to molt again to a pupa.

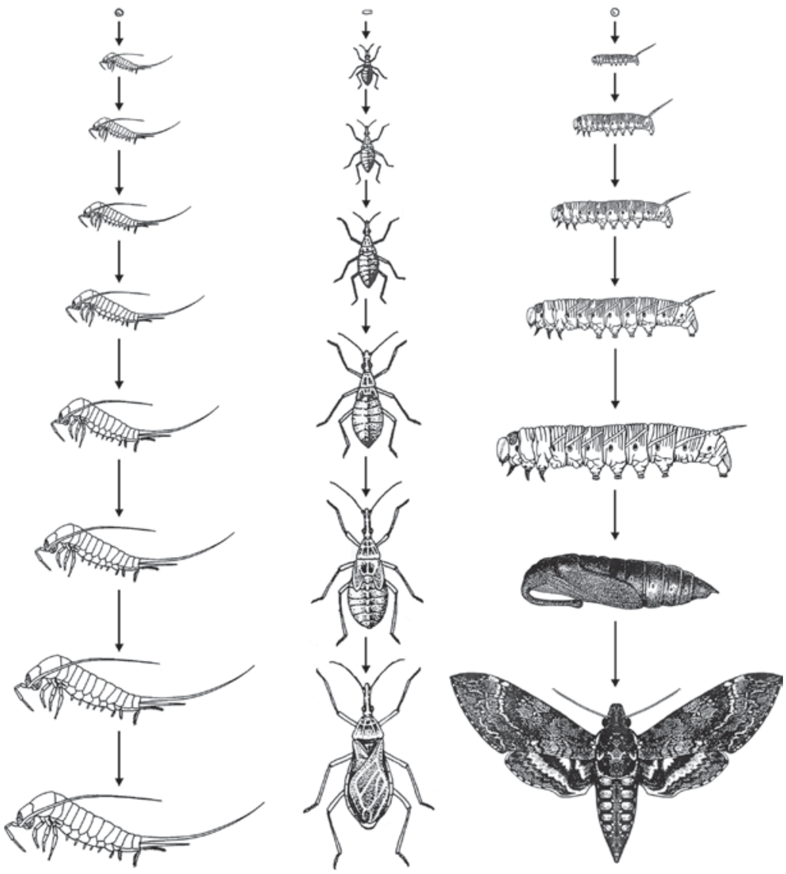
Genes and Metamorphosis

Regulatory Genes

Ecdysteroids initiate a cascade of gene activity that involves both early and late genes. Most of these genes code for transcription factors that activate a series of genes for the proteins that build the structures of the various stages. Thus flies, mosquitoes, beetles and moths have homologous genes that are activated in the same order in response to ecdysteroids, although the culmination of their action is to build very different kinds of insects. One goal has been to identify early ecdysteroid-response genes whose activities differ between larval and metamorphic molts. One such gene, named *broad*, has been found. It was first discovered in *Drosophila* where it is expressed in response to ecdysteroids as they initiate the larval/pupal molt, but it is not expressed at larval/larval molts. A gene with a similar sequence is expressed in *Manduca* larvae in the same manner, at the larva/pupal molt, but not at larval/larval molts. In *Manduca*, juvenoids prevent the activation of broad, in keeping with their status quo action.

Effector Genes

Also of interest are the genes that code for proteins that contribute directly to the form and function of the morphologically distinct metamorphic stages of the holometabolous insects. These can be structural proteins, such as cuticular proteins, or enzymes that participate in physiological activities such as digestion and intermediary metabolism, or even enzymes necessary for the formation of pigments found in different stages. Analyses of cuticular proteins and their genes revealed that quite different structures could be built from the same cuticular components. Thus, the hard structures found in lepidopteran larvae, the head capsule and tubercles, that dot the thorax and abdomen, are composed of the same cuticular proteins that contribute to the hard cuticles of the pupa that cover most of the body surface, the pupal dorsal-fore wing and the abdominal sclerites. The soft cuticles



Metamorphosis, Figure 37 **Three types of development in insects. *Left*, ametabolous development illustrated by *Machlis* (Thysanura). Note that there is little change in external form, and the adults continue to molt. *Center*, hemimetabolous development illustrated by *Rhodnius* (Hemiptera). There are five nymphal (larval) instars, and wing pads are clearly visible in the later ones. Only the adult has functional wings and is capable of reproduction. *Right*, holometabolous development illustrated by the moth *Manduca* (Lepidoptera). Wings in the larva are not visible, as their precursors exist internally as imaginal discs. Both pupae and adults have wings, but they are only functional in the adult. (adapted from H. E. Evans, Insect Biology)**

found across the larval abdomen and in the intersegmental membranes of pupae and adults also share many of the same cuticular proteins. In these cases, the same genes are reused to code for the structural proteins of vastly different morphological structures. The evolution of metamorphosis thus required the development of new morphogenetic signals (architectural plans) affecting the spatial and temporal expression of different genes, so that common structural proteins could be assembled in new ways. Accompanying this was also the appearance of new or modified genes to code for those features that are unique to each metamorphic stage.

It is the complex orchestration of spatial and temporal activities of similar hormones and genes that results in the vast diversity of form and function that is displayed by metamorphosing insects.

► Juvenile Hormone
► Ecdysteroids
► Diapause
► Howard Schneiderman
► Carroll Williams
► Vincent Wigglesworth

References

Nijhout HF (1994) Insect hormones. Princeton University Press, Princeton, NJ, 267 pp

Truman JW, Riddiford LM (2002) Endocrine insights into the evolution of metamorphosis in insects. Ann Rev Entomol 47:467–500

Willis JH (1996) Metamorphosis of the cuticle, its proteins, and their genes. In: Gilbert LI, Atkinson BG, Tata J (eds) Metamorphosis/post-embryonic reprogramming of gene expression in amphibian and insect cells. Academic Press, Orlando, FL, pp 253–282

Zhou X, Riddiford LM (2002) Broad specifies pupal development and mediates the "status quo" action of juvenile hormone on the pupal-adult transformation in *Drosophila* and *Manduca*. Development 129:2259–2269

Metanotum

The upper surface of the third or posterior segment of the thorax (metathorax). In Diptera, it is the oval arched section behind the scutellum.

► Thorax of Hexapods

Metarbelidae

A family of moths (order Lepidoptera) also known as tropical carpenterworm moths.

► Tropical Carpenterworm Moths
► Butterflies and Moths

Metarhizium

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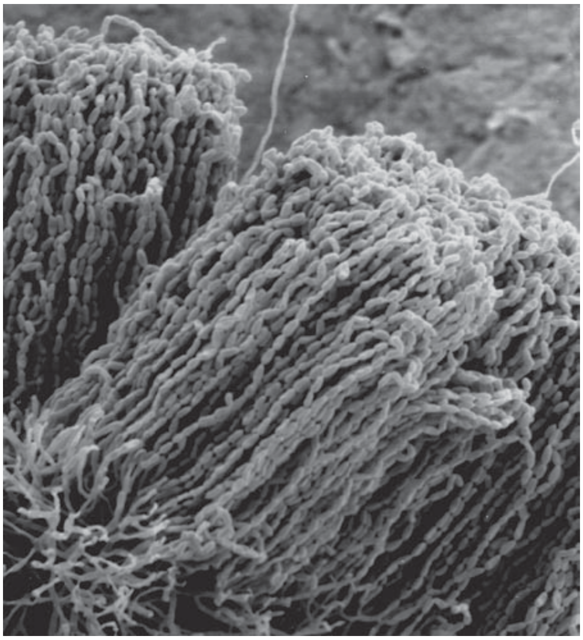
Metarhizium is a haploid, deuteromycetous, insect-pathogenic fungus and a common inhabitant of soil worldwide. At least two species are formally recognized, *Metarhizium anisopliae* and *Metarhizium flavoviride*. Of the two, *M. anisopliae* is by far more common and occurs over a wide range of insect species. However, based on ITS (internally transcribed spacer region of DNA encodings ribosomal RNA) sequence analysis, vegetative compatibility groups, and population genetics analysis, *Metarhizium* may be represented by a large number of species found worldwide. Thus, the taxonomy and systematics of this genus are not fully resolved. Population genetics analysis showed that in nature *Metarhizium* reproduces clonally but also has the potential for recombination. Recombination may occur through a process called parasexuality, a form of mitotic recombination, where vegetatively compatible hyphae fuse and exchange nuclei to form a heterokaryon. The nuclei fuse to produce a diploid homokaryon, the chromosomes recombine, and thereafter the diploid nuclei haploidize. True sexual recombination also may exist; a *Cordyceps* sp. anamorph has been recorded for at least one of the species and ITS analysis suggests that *Cordyceps* is a related Ascomycete.

Microscopically, the conidia are ellipsoidal in shape (8 × 5 μm^2) and are arranged in columns (Fig. 38). It grows on a variety of commercially available agar and conidiates well on potato dextrose agar. Initially, the colonies are white to buff-yellow and turn yellow-green to olivaceous-buff or



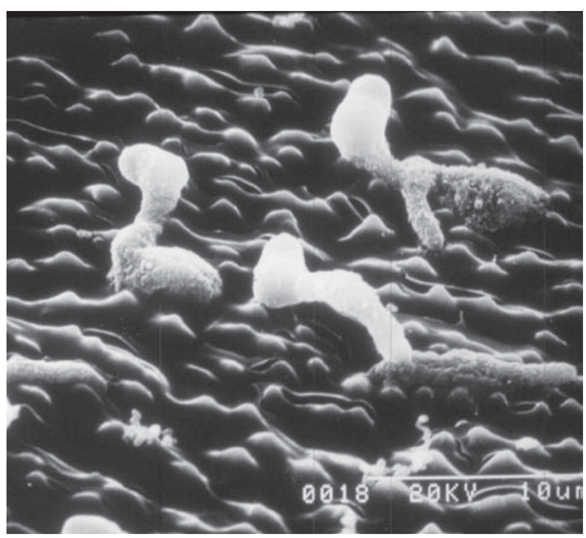
Metarhizium, Figure 38 Scanning electron micrograph of the palisade of conidia produced by *Metarhizium anisopliae*.

dark green when conidia are formed from conidiophores of the mycelia. *Metarhizium* may be selectively isolated from soil on media that contains dodine, chloramphenicol and crystal violet. It also may be isolated from waxworm larvae (*Galleria mellonella*) that have been placed in soil samples in a technique known as the "Galleria bait method".

Metarhizium, the causal agent of the green muscardine disease, is a broad range insect pathogen that frequently infects soil insects. Ecologically, it can best be described as a facultative insect pathogen; it is not an obligate pathogen and grows well on artificial media. Over 200 different insect species are susceptible to infection by *Metarhizium*. One subspecies isolated from Brazil, *M. anisopliae* var. *majus*, shows specificity toward rhinoceros beetle larvae while another from Australia and Mexico, *M. anisopliae* var. *acridum*, shows specificity toward grasshoppers and locusts. However, this level of insect host specificity has not been entirely elucidated with strains from temperate environments. In fact, there is evidence that genotypes of this fungus from temperate areas are associated with different habitats. Generally, *Metarhizium* is isolated more frequently from agricultural or disturbed areas but also can be found in forested habitats. The association of various genotypes of *Metarhizium* with host insect or habitat is still largely unclear.

Of all the insect-pathogenic fungi, *Metarhizium* may be regarded as a model organism for understanding the molecular mechanisms of insect pathogenesis. The infection process includes the following themes: (i) adhesion and germination, (ii) invasion of the host, (iii) dissemination within the host, (iv) role of toxins, (v) avoidance of host immune response, (vi) outgrowth from the host. Like most other insect pathogenic fungi, *Metarhizium* infects the host insect by penetrating the insect cuticle; the fungus need not be ingested. In fact, the potential for infection after ingestion is low since anti-fungal substances may be produced by indigenous microbes in the insect gut. Furthermore, in locusts, food transit time in the insect gut is generally shorter than the time required for germination, and frequent delamination of the peritrophic membrane (approximately every 15 min) restricts fungal attachment to the insect gut.

Infection is initiated when the *Metarhizium* conidium adheres to the insect cuticle. The conidial surfaces are covered by a rodlet, a structural feature composed of "hydrophobin" protein. Since the insect cuticle is hydrophobic, adherence of the conidia to the insect cuticle is achieved through non-specific hydrophobic mechanisms. Once attached to the cuticle, the conidia germinate by utilizing lipids and soluble nutrients found on the insect cuticle (Fig. 39). The germ tube grows for approximately 10–50 μm then differentiates and produces a hold-fast structure on the insect cuticle termed an appressorium, usually within 18 h of infection. From the appressorium, *Metarhizium* hyphae penetrate through the insect cuticle primarily by the action of hydrolytic enzymes. The most important of these enzymes is an extracellular protease termed Pr1. This protease belongs to the subtilisin class of proteases that are homologous to proteinase K from *Tritirachium album* and have a characteristic catalytic amino acid



Metarhizium, Figure 39 Conidia of *Metarhizium anisopliae* germinating on the surface of insect cuticle. Note the appressoria adhered to the cuticle. Under the appressorium, a hyphae penetrates through the cuticle. (Photo courtesy of Dr. R.J. St. Leger, University of Maryland.)

triad of serine, aspartate and histidine. Pr1 is regulated by the presence of carbon and nitrogen. In nutrient rich media, Pr1 is not expressed, but under starvation conditions such as those found on the insect cuticle, Pr1 is expressed in large amounts. Other extracellular enzymes such as trypsin-like proteases, metalloproteases, carboxypeptidases, dipeptidylpeptidases, chitinases and lipases are also implicated in cuticle degradation.

After approximately 48 h, *Metarhizium* transgresses the insect cuticle and enters the insect hemocoel. Since the hemocoel is nutrient rich, Pr1 is not produced. Here, *Metarhizium* differentiates into yeast-like blastospores that proliferate in the liquid insect hemolymph. Many *Metarhizium* isolates produce a toxin called destruxin, a cyclodepsipeptide ionophore that may expedite insect death. *Metarhizium* is confronted with insect immune responses, such as insect blood cells called hemocytes, but can generally outcompete these encounters. *Metarhizium* utilizes the soluble nutrients within the insect and then exits the insect and grows over the cadaver producing conidia. The *Metarhizium* conidia now are able to infect other insects.

There have been many successes using *Metarhizium* to control pest insects. *Metarhizium* is useful especially for control of insects with sucking mouthparts since ingestion is not necessary for infection to take place. Its first documented use was to control wheat cockchafer in Ukraine in 1884, where up to 80% mortality was estimated. *Metarhizium* also has been successfully used to control spittlebugs (Hemiptera: Cercopidae) on sugar cane in Brazil. One of the most interesting applications of *Metarhizium* was to control the larvae of a scarab beetle, *Aphodius tasmanae*, which is a pasture pest in Tasmania. Previously, control of this pest was generally achieved by removing livestock from a pasture and spraying the pasture with chemical insecticides. An economically viable alternative was to apply a bait formulation of *Metarhizium* onto the pasture. At night, the scarab grub would carry the bait to their burrows, where they became infected and died. *Metarhizium flavoviride* has been used to control locusts in Africa where it is formulated with an oil-based emulsion. There are numerous other examples of insect biocontrol using *Metarhizium*.

Mass culture of *M. anisopliae* for biological control has been accomplished using two basic methods: (i) submerged culture, and (ii) surface culture. Submerged culture is much more problematic since *M. anisopliae* produce yeast-like blastospores and/or hyphal fragments when grown in liquid medium. These have little persistence and low infectivity in the field. Submerged culture is most often used in a diphasic system of production. The blastospores and hyphal fragments that are grown in liquid culture are transferred to a surface culture. Surface culture results in the production of aerial conidia. Many inexpensive substrates and culture methods have been used and these generally depend on the availability of substrates in the country of use. In Brazil, *M. anisopliae* has been grown on sterilized rice in polyethylene bags. In the People's Republic of China, conidia are produced on rice, wheat, or ground corn stalks in shallow trays. Unfortunately, *M. anisopliae* is not being extensively used in North America. Problems with public perception, relatively short shelf-life, and longer time for insect kill compared to chemical insecticides have hampered the widespread implementation of *M. anisopliae* as a biocontrol fungus. Nonetheless, many regions, particularly in developing countries, have found that *M. anisopliae* is a viable, locally cultivated and manageable alternative to chemical pesticides for insect control.

References

Bidochka MJ, Kamp AM, Lavender TM, DeKoning J, De Croos JNA, (2001) Habitat association in two genetic groups of the insect-pathogenic fungus *Metarhizium anisopliae*: uncovering cryptic species? Appl Environ Microbiol 67:1335–1342

Bidochka MJ, Kasperski JE, Wild GAM (1998) Distribution and occurrence of deuteromycetous entomopathogenic fungi in temperate and near northern habitats. Can J Bot 76:1198–1204

Driver F, Milner RJ, Trueman JWH (2000) A taxonomic revision of *Metarhizium* based on a phylogenetic analysis of rDNA sequence data. Mycol Res 104:134–150

St Leger RJ, Frank DC, Roberts DW, Staples RC (1992) Molecular cloning and regulatory analysis of the cuticle-degrading protease structural gene from the entomopathogenic fungus *Metarhizium anisopliae*. Eur J Biochem 204:991–1001

Samuels RI, Charnley AK, Reynolds SE (1988) The role of destruxins in the pathogenicity of 3 strains of *Metarhizium anisopliae* for the tobacco hornworm *Manduca sexta*. Mycopathologia 104:51–58

Metatarsus

The basal segment of the tarsus.

► Legs of Hexapods

Metatentorium (pl., metatentoria)

The arm of the tentorium invaginated on the ventral area of the head adjacent to the foramen magnum; the posterior arms of the tentorium.

► Head of Hexapods

Metathorax

The third segment of the thorax, bearing the third pair of legs and (if present) the second pair of wings.

► Thorax of Hexapods

Metcalf, Clell Lee

C. L. Metcalf was born at Lakeville, Ohio, USA, on March 25, 1888. He attended Ohio State University, where he received his B.S. and M.S. degrees in 1911 and 1912, respectively. He received a doctorate from Harvard University in 1919. He held several positions in entomology but had the greatest impact at the University of Illinois, where he served as professor and department head from 1921 to 1947. He was known for his teaching, administrative and research prowess. Among his important publications are "Destructive and useful insects" (with W. P. Flint and later with his son, R. L. Metcalf) (1928) and "Fundamentals of insect life" (1932). "Destructive and useful insects" in its various forms remains the most complete and useful treatment of common insect pests of North America, and formerly was the most widely used text and reference manual for economic entomology courses. Metcalf was president of the Entomological Society of America in 1934. Metcalf died on August 21, 1948.

Reference

Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Metcalf, Zeno Payne

Zeno Metcalf was born at Lakeville, Ohio, in 1885. He received a B.A. degree from Ohio State University in 1908 and a D.Sc. from Harvard University in 1924. He was an instructor at Michigan State University from 1907 to 1908, followed by an appointment with the North Carolina Department of Agriculture from 1908 to 1912, before he joined the faculty at North Carolina State University. He served the balance of his career at North Carolina State, leaving for other universities only for brief periods. Metcalf served as head of the Zoology and Entomology Department from 1912 to 1950, as director of instruction for the School of Agriculture from 1923 to 1944, and as associate dean of the Graduate School from 1943 to 1950. Metcalf had an active professional life in addition to his administrative duties. He was a fellow of the Entomological Society of America and the American Association for the Advancement of Science. He also served as president of the Entomological Society of America, the Ecological Society of America, and the American Microscopical Society, served on the editorial board of four journals, and authored nearly 100 papers and nine books. His most significant publishing accomplishment was completion of 15 volumes of "A catalogue of the Homoptera of the World." At the time of his death, several additional volumes were nearly completed. He died at Raleigh, North Carolina, on January 5, 1956.

Reference

Smith CF (1956) Zeno Payne Metcalf 1886–1956. Ann Entomol Soc Am 49:302

Methodology

The study of methods. Many writers erroneously use the term methodology when they simply mean methods.

Methods for Measuring Crop Losses by Insects

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Measurement of crop losses that occur within a range of pest insect population densities is fundamental for developing pest management programs. The dynamic and complex relationships between herbivore and host are affected by inherent insect fecundity, the phenology of the pest and crop, and the impact of beneficial organisms such as parasitoids, predators and entomopathogens. Assessments of crop losses are further complicated by soil moisture and nutrient availability that affect plants' ability to compensate for insect injury. The major reason for quantifying crop yield and/or quality losses is to estimate the pest population density at which crop loss value equals the cost of applied control. This estimate must be precise enough to be meaningful yet sufficiently robust to be useful over range of dynamic field situations.

Several methods have been used to estimate the relationship between insect population density and plant yield response. These include observing naturally occurring populations, modification of these populations, creating artificial populations, and simulating insect damage. Each of these methods has advantages and disadvantages. Selected examples are presented along with a brief discussion of the advantages and disadvantages of each.

Observation of Natural Populations

The simplest, and one of the most effective, methods of measuring crop loss is to compare yields from individual plants with different population levels or from infested and uninfested plants. In the example that follows, infested and uninfested stems were compared to assess the damage in wheat by two insect species (Table 4). Larvae of the grass sheathminer, *Cerodontha dorsalis* (Loew) (Diptera: Agromyzidae), feed and pupate within tissues of the leaf sheaths that surrounds stems. Larvae of another pest, the wheat jointworm, *Tetramesa tritici* (Fitch) (Hymenoptera: Eurytomidae), feed and

Methods for Measuring Crop Losses by Insects, Table 4 Impact of two species of phytophagous insects on wheat production

Insect infestation	Mean head weight, grams
Jointworm	0.29a
Jointworm (B) sheathminer	0.28a
None (control)	0.95b
One sheathminer	1.28bc
Two sheathminers	1.51c

(Source: Morrill WL (1995) Insect pests of small grains. APS Press, St. Paul, MN) cause galls to form at the stem joints. The interaction of these pests and yields was investigated by evaluation of mature plants were collected from a field. Plant head weights were determined from plants with and without infestations. Each mean is for 200 plants, and means followed by the same letter are not significantly different (P = 0.05).

Jointworms reduced wheat yields by about 70%. However, yields of plants that were infested by sheathminers were higher than yields of uninfested plants. This suggests that sheathminers may have selected the most vigorous plants for oviposition, or oviposition may have occurred when the primary stems were more vulnerable to attack than the lower-yielding tillers that appeared later.

Preferential selection of host plants by phytophagous insects also plays a role in crop loss. For example, ovipositing wheat stem sawflies, *Cephus cinctus* Norton (Hymenoptera: Cephidae), prefer the largest and most productive wheat stems. The resulting larvae bore and feed within host stems, and material cannot move upward in damaged stems to the developing grain. However, there is very little difference in yields of infested and uninfested plants unless plants within size categories are compared (Table 5). In this example, 400 stems were placed in five categorized according to diameters of the upper stem internodes. Mean weights of grain from infested and uninfested stems and the estimated losses within each category were determined, illustrating that actual loss was over 20%.

The advantage of selecting the largest and most suitable host for progeny production was that female progeny were larger, lived longer, and laid more eggs. Also, individuals that developed in the largest stems were more likely to be females due to selective fertilization at the time of oviposition.

Beneficial insects also affect the extent of damage caused by sawfly larvae. Partially grown larvae are attacked by two species of parasitoids (Hymenoptera: Braconidae). If sawfly larvae are paralyzed at the time of attack, plant damage does not continue.

Methods for Measuring Crop Losses by Insects, Table 5 Percent loss of wheat grain caused by wheat stem sawflies within plant size categories

Stem dia. mm	Percent loss
2.2–2.3	14.4
2.3–2.4	26.1
2.4–2.5	24.0
2.5–2.6	17.5
2.6–2.7	22.4
overall mean loss = 20.8	

(Data from Morrill WL et al. (1994) J Econ Entomol 87:1373–1376)

The advantage of working with naturally occurring pest infestations is that this is very close to real field conditions. A disadvantage is that field trials are dependent upon natural populations that occur over a range of densities.

Modification of Existing Populations

Densities of naturally occurring pest populations in crops can be modified and related to the resulting loss levels by applying different rates or types of insecticides. For this example, we will look at a forage legume, sainfoin, *Onobrychis viciifolia* Scop., that is attacked by *Lygus hesperus* Knight (Hemiptera: Miridae) and several other species of plant bugs. The bugs feed on blossoms and developing seeds, thereby significantly reducing seed production (Table 6).

Three rates of insecticides (carbofuran) were applied when sanfoin reached the blossoming stage. Then, insect populations were estimated twice weekly by using a sweep net. Plant bug population densities were lower in the treated plots, and there was a significant increase in seed production.

Another example of the use of insecticides to eliminate or modify pest populations involves the cereal leaf beetle, *Oulema melanopus* (L.) (Coleoptera: Chrysomelidae). Larvae and adults

Methods for Measuring Crop Losses by Insects, Table 6 Pest insect populations and seed production in sainfoin treated with three rates of insecticide

Carbofuran (kg AI/ha)	Mean number of mirids/10 sweeps		Seed yield (kg/ha)	
	6 days	17 days	24 days	
untreated	48.5a	56.5a	69.3a	238.0a
0.28	11.0b	19.0a	77.0a	290.6b
0.56	4.8b	15.0a	78.0a	277.0b
0.84	0.5b	7.5b	47.8a	339.6c

(Source: Morrill WL et al. (1984) J Econ Entomol 77:966–968)

feed on foliage. The impacts on larval feeding on yields in fields were estimated by applying insecticide in test plots. Wheat leaves were collected, and leaf area consumed was measured by using a flat bed scanner. Data showed that a mean of 0.50 eggs per stem resulted in 0.34 fourth instar larvae. These larvae caused 4.0% yield loss, which equaled the cost of material and application with ground equipment.

The advantage to the use of insecticides is that populations can be easily modified (downward) at all stages of crop development. Disadvantages are that many insecticides produce a "fertilizer" effect, especially the organophosphates and can increase yields over an untreated crop due solely to the added input of nutrients from the insecticide. In addition, most chemical pesticides seriously impact natural enemies, thereby making an otherwise natural field situation unrealistic. The composition of resurgent pest populations may differ from untreated populations. This is important because female and nymphs may feed more than male individuals.

Creating Artificial Populations

Barriers can be used to confine pest insects within selected field regions or plants. For example, six densities of larvae of variegated cutworms, *Peridroma saucia* (Hübner) (Lepidoptera: Noctuidae) were placed on alfalfa enclosed with aluminum barriers, and the subsequent foliage yield and quality was determined. This was then related to the cost of treatment and value of foliage lost.

Cages (Fig. 40) can also be used to confine pest insects at predetermined densities. Malayan black bug, *Scotinophara coarctata* (F.) (Heteroptera: Pentatomidae) feeds on rice in Asia. Adults migrate into fields, and damage from toxins and juice removal includes leaf desiccation, "dead heart," and plant mortality. Caged rice plants were infested with 0, l, 2, 4, or 6 bugs per rice panicle, and were permitted to feed for 1, 2, 4, or 6 days. Plant response recorded included number of filled spikelets, number of unfilled spikelets, and weight of grain per panicle. Grain weight was significantly reduced when two bugs fed for six or more days per panicle. Cages can be used to exclude, and thereby protect, plants from expected pest invasions and attack.

An advantage of using artificial populations is that numbers of insects and feeding durations can be managed. On the other hand, cages have the disadvantage of affecting wind, sunlight, and other environmental factors that impact plant growth and yield. Therefore, the experimental design should include caged and uncaged plants (Fig. 40).

Simulated Damage

Plants can be damaged by leaf/flower or fruit removal to simulate insect feeding (Fig. 40). In one example, manual defoliation and feeding by the migratory grasshopper, *Melanoplus sanguinipes* (F.) (Orthoptera: Arididae), were compared for seedling wheat plants. Treatments were 0, 1/3, and 2/3% foliage removal by grasshopper feeding and by manual clipping with a razor blade. Subsequent plant height, tiller production, and plant weights were compared. Results indicate that grasshopper feeding had more of a negative impact on plant growth than artificial defoliation, suggesting that

Methods for Measuring Crop Losses by Insects, Figure 40 **Techniques in crop loss assessment.** ***Top row*, *left*: applying insecticide to small plots of wheat to remove pest insects *top row right*: assessing insect abundance in a sainfoin plot with a sweep net; *middle row*, *left*: cages used to protect rice from dispersal of ricebugs; *middle row*, *right*: cages to enclose ricebugs with rice plants; *bottom row*, *left*: removal of blossoms and pods from cowpea, simulating insect damage; *bottom row*, *right*: visual estimation of insect abundance and damage in field plot.**

grasshopper feeding may impact wound response of wheat seedlings.

Another example involved a trial with larvae of the bean leaf roller, *Urbanus proteus* (L.) (Lepidoptera: Hesperiidae), which feeds on foliage of beans in southeastern United States. Prior to blooming, plants could lose 66% of their foliage before blooming, or 33% during blooming with no measurable impact on yield. Consumption by last (fifth stage) larvae was 83% of the total consumed during larval development. About two larvae survive from one stage to the next. About 4.4 fifth stage or 70 first stage larvae were needed to reduce yields. Similarly, response of soybean to artificial leaf damage was determined by clipping leaves to represent losses from 17 to 76% defoliation. Foliage losses of 67%, when plants were blooming, did not result in yield losses and 17% leaf loss did not affect yields at any stage of the plants phenology. Greatest losses occurred when 67% of the leaf tissue was removed at pod set or when 17% of the leaf area was removed on a continued basis.

There are major disadvantages to using surrogate injury to mimic insect injury. Most insects feed by gradual removal of plant tissue. Studies that employ the simulated injury often use scissors to excise large sections of tissue. Others defoliating/plant part removal work have used manually removing buds, whole leaves, punching holes in leaves by hole punches, or using forceps to remove various plant parts. Thus, plant compensation for damage by artificial means may be quite different from that caused by insects. In addition, the distribution of manually-induced damage in the field may not be the same as the pest insects. Surrogate injury also excludes insect feeding toxins and vectored pathogens. Another disadvantage is the indirect impact on beneficial insects. Infested plants may utilize the phytophagous insects' saliva to produce volatile chemicals that attract parasitoids.

The advantage of using artificial damage is that it provides an overall gross response to damage. The level of damage can be easily manipulated to allow for a range of damage at any stage of plant development.

Natural Enemies and Crop Loss Assessment

Natural enemies such as insect predators, parasitoids, and entomopathogens often are major factors regulating pest insect populations in the field. Thus, because natural enemies influence in pest densities, resulting estimates of crop losses will change depending upon the communities of natural enemies present. This is particularly true when action thresholds are based on pest insect eggs or early instars; insect life stages that are especially susceptible to the action of natural enemies. Unfortunately, there are few studies of crop losses that include the impact of natural enemies on pests and how this may affect crop loss assessment. Therefore, most field sampling strategies used to make treat/no-treat decisions are based only on insect pest density/crop loss relationships.

A sampling scheme to assess crop loss that included the major predators of planthoppers was developed for rice. This scheme was compared to one based a traditional action threshold that did not include predators as a factor. The result was that there was a higher pest threshold when at least five major predators were found in five samples. The two plans were tested over a range of field situations and insect complexes in Philippine rice fields. The sampling plan that included predators as well as pests led to a significant reduction in the number of insecticide applications without compromising yields.

Another example of how natural enemies can affect crop loss estimates and treatment decisions comes from North Sulawesi, Indonesia. The major pest of cabbage is the diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae). Most farmers treat this pest with applications of mixtures of different insecticides at frequent intervals. Field observations revealed populations of diamondback moth with and ensuing outbreak of a disease, *Zoophthora radicans* (Brefeld) Batka, that infects the pest. Collections of diamondback larvae were made and held to determine the incidence of the disease. All of the larvae collected were infected and died of the disease. The field population of the diamondback moth was high enough to cause most farmers to treat with insecticides. However, if farmers understood that the population was dying from the insect disease, all insecticide treatments could have been avoided because little damage resulted.

General

The use of insect-day (ID) can be applied for development of new models. For example, the number of days that the pest insects will feed during the plant's period of susceptibility X number of insects. This can be further modified to "feeding intensity" because the impact of one insect feeding for 10 days (10 ID) can be less than the impact of ten insects feeding for 1 day, also 10 ID.

Pest biology must also be considered. Aphid populations can potentially increase rapidly, but other pests, especially in northern latitudes, have one generation per year. So, pests including army cutworms and grasshoppers cannot increase in number within one growing season. Dispersion of highly mobile pests may require a knowledge of the agricultural landscape.

An understanding of plant phenology is important. Plants may compensate or recover from defoliation that occurs early in the season. For example, the rice whorl maggot, *Hydrellia philippina* Ferino (Diptera: Ephydridae), damages the early seedling stages of rice. Feeding by the maggot inside whorls and on the margins of unopened leaves causes visible damage and rice farmers often apply insecticides that induce outbreaks of other plant feeders such as the brown planthopper, *Nilaparvata lugens* (Stål) (Homoptera: Delphacidae). By scoring damage ranging from 0 to 100% and tagging individual plants, yields were compared at the end of the season. In general, there was no significant difference in yields among plants with different levels of damage. Plants were able to compensate for damage by this early season foliage feeder. This work strongly suggested that insecticide applications to the seedling stage of rice were not needed.

However, the plant cannot compensate for insect feeding directly on the fruit or grain. On the contrary, this feeding damage is often exaggerated as the fruit or grain matures. The type of damage also varies. This includes defoliation, root and stem boring, grain or fruit damage, vectoring of plant diseases, and feeding toxins.

Interaction of pests and plants may be important. Insects may select the most vigorous and therefore the most productive individual plants, thereby maximizing their impact while insuring production of the largest progeny.

In summary, there are a number of methods that can be used to related the population level of the pest insect to plant damage. But all methods have advantages and disadvantages. The most frequently used methods involves natural populations over a range of infestation levels. The use of insecticides to manipulate populations also is common and the use of these two methods will probably suffice in most instances, for determining an acceptable insect pest density/crop loss relationship. All methods, however, must be tested under field conditions in farmers' fields and with current market acceptability. In addition, the use of action levels or thresholds implies that farmers have a viable means of intervention, e.g., they are able to apply an insecticide to reduce the insect population. In developing countries, however, this is not often the case and more long term strategies must be developed (host plant resistance, companion cropping, planting dates, etc.) for sustained suppression of the pest population.

► Sampling Arthropods
► Integrated Pest Management

References

Buntin GD (2001) Techniques for evaluating yield loss from insects. In: Peterson RKD, Higley LG (eds) Biotic stress and yield loss. CRC Press, Boca Raton, FL, pp 23–41

Morrill WL (1984) Wireworms: control, sampling methodology, and effect on wheat yield in Montana. J Georgia Entomol Soc 19:67–71

Onstad DW (1987) Calculation of economic-injury levels and economic thresholds for pest management. J Econ Entomol 80:297–303
Pedigo LP, Hutchins SH, Higley LG (1986) Economic injury levels in theory and practice. Ann Rev Entomol 31:348–368
Shepard BM, Justo HD Jr, Rubia EG, Estano DB (1990) Response of the rice plant to damage by the rice whold maggot *Hydrellia philippina* Ferino (Diptera: Ephydridae). J Plant Protect Trop 7:173–177

Metretopodidae

A family of mayflies (order Ephemeroptera).

► Mayflies

Meyrick, Edward

Edward Meyrick was born at Ramsbury, Wiltshire, United Kingdom, on November 24, 1854. Educated at Marlborough College and Trinity College, Cambridge, he went on to be a schoolmaster for 37 years. The early portion of his career (1877–1886) was spent in Australia and environs, but he served in a similar position in England from 1887 to 1914. Meyrick is well known for his contribution to the Lepidoptera fauna of Australia, New Zealand, the South Pacific Islands, India and Southeast Asia, South Africa, South America, and England. A specialist on the smaller forms of the order, he was a prodigious worker, and described over 20,000 species, many new genera, and several new families. He made major contributions to "Genera insectorum," "Lepidopterorum catalogus," and "A handbook of British Lepidoptera." He also published his own magazine, comprised of over four volumes totaling 2,500 pages, and important books: "Moths and their classification" (1898) and "Moths and their classification, a revised handbook" (1928). Meyrick worked diligently with several zoological, entomological, and natural history societies until he died on March 31, 1938. His immense collection of Lepidoptera was bequeathed to the British Museum.

References

Anon (1938) Edward Meyrick BA, FRS Entomologist 71:121–122
Anon (1938) Edward Meyrick BA, FRS Entomol Monthly Mag 74:136–137

Mexican Bean Beetle, *Epilachna varivestris* Mulsant (Coleoptera: Coccinellidae)

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Mexican bean beetle is native to Mexico and Central America. By the 1800s it was damaging to beans throughout the southwestern United States, wherever beans were cultivated. A major increase in damage followed the accidental transport of Mexican bean beetle to the eastern United States, to northern Alabama about 1918, apparently in shipments of alfalfa hay from Colorado and New Mexico. The beetle, once gaining access to eastern states, spread rapidly to the northeast, and is now found throughout much of the United States and eastern Canada.

Host Plants

Mexican bean beetle develops only on legumes. Other plants are occasionally reported injured. Vegetable crops eaten are cowpea, lima bean, and snap bean, particularly the latter two bean types. Related crops such as faba bean, lentil, and mung bean seem to be immune. Field crops that may be attacked include alfalfa, sweet clover, various dry beans, and soybean. Formerly the field crops other than dry beans were relatively unsuitable and rarely injured. However, starting in the 1970s the eastern, and then midwestern states, began experiencing considerable damage to soybean by Mexican bean beetle. The natural host appears to be tick trefoil, *Desmodium* spp.;

however, in the United States, Mexican bean beetle is almost always found associated with cultivated legumes.

Natural Mortality Factors

Numerous predators, parasitoids, and microbial disease agents of Mexican bean beetle have been identified, but few native natural enemies are considered to be important. Species native to the United States have not adapted to Mexican bean beetle as a host, whereas species imported from Central and South America have failed to establish permanently. A parasitoid from India and Japan, *Pediobius foveolatus* (Crawford) (Hymenoptera: Eulophidae) has been cultured and released in eastern states. Annual release is necessary because the parasitoid is unable to overwinter in the United States. Small gardens, such as those in urban and suburban communities, are most suitable for *Pediobius* release.

Microbial pathogens, especially *Nosema epilachnae* and *N. varivestris* (both Microsporida: Nosematidae), occur in bean beetles. These pathogens are deleterious to Mexican bean beetle; *Nosema epilachnae*, in particular, reduces longevity and fecundity in bean beetles. However, these pathogens also infect the parasitoid *Pediobius foveolatus*. Infection of the parasitoid occurs when the immature stage develops in its host, or when the adult ingests the pathogen.

Although natural enemies may affect bean beetle abundance, weather is also thought to play an important role in population dynamics. Hot, dry weather is thought to be detrimental to survival of all stages, but especially the egg stage. Temperatures above 35–37°C can be lethal.

Life Cycle and Description

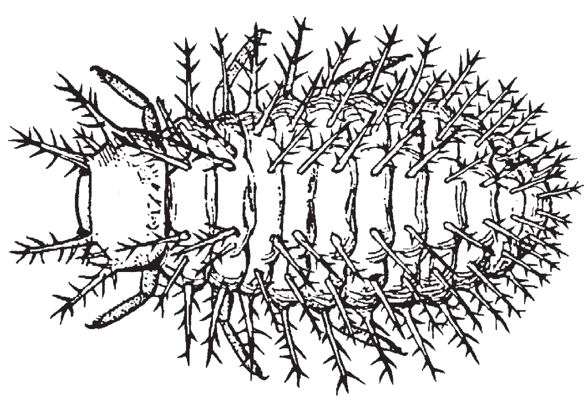
Mexican bean beetle usually exhibits 1–3 generations annually. In the western United States there normally is one complete generation with some individuals reproducing and developing a small second generation. In the southeast, where three generations are more common, a few beetles deposit eggs that form a small fourth generation. Adults are the overwintering stage. A life cycle may be completed in 30–40 days during the summer months, but may require 60 days during cooler weather.

Egg

Eggs are deposited on end in clusters of 40–60 eggs, usually on the underside of leaves. They are elliptical in shape, and measure about 1.3 mm in length and 0.6 mm in width. The eggs generally are yellow in color, but turn orange-yellow prior to hatch. Eggs hatch in 5–14 days, averaging 5.7 days. All females from the first generation deposit eggs, but in South Carolina only 94% of the second and 60% of the third generation beetles reportedly produced eggs as more and more beetles entered reproductive diapause.

Larva

The larvae are yellow in color, and armed with a dense covering of branched spines arrayed in six longitudinal rows (Fig. 41). There are four instars. The mean duration of the instars in a South Carolina study has been reported to be 3.9, 3.6, 3.6,



Mexican Bean Beetle, *Epilachna varivestris* Mulsant (Coleoptera: Coccinellidae), Figure 41 Mexican bean beetle larva, *Epilachna varivestris*.

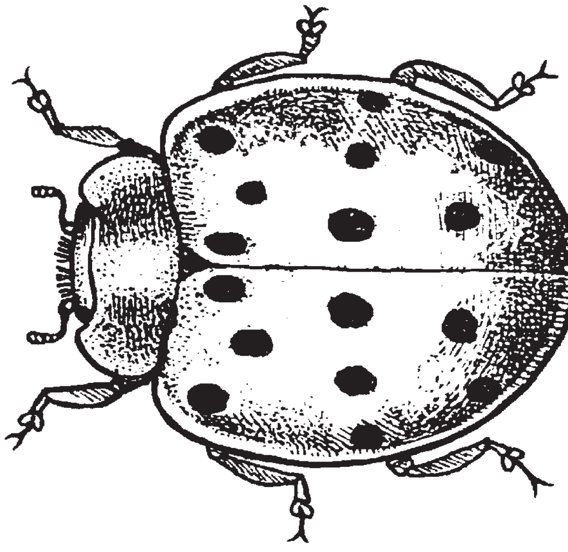
and 3.6 days, respectively. After attaining its full size, about 8 mm in length, the larva attaches its anal end to a substrate, usually the leaf on which it fed, and pupates.

Pupa

During the process of pupation the larval covering, which contains the spines, is pushed back toward the point of attachment to the substrate. Thus, the pupa appears to bear spines, but this is simply remnants of its earlier life, and not firmly attached. Rather, the yellow-orange pupa is quite free from projections. Duration of the pupal stage averages 8.1 days in South Carolina.

Adult

Adults are brightly colored beetles that resemble many beneficial ladybird beetle species. The beetle is hemispherical in shape, and bears 16 black spots. The spots are arranged in 3 rows, with 6 spots in each of the first 2 rows and 4 in the third row; thus, there are 8 on each elytron (Fig. 42). The background color is usually orange or copper, but ranges from yellow when freshly emerged, to reddish brown when old. The beetles normally measure about 6–8 mm in length and 4–6 mm in width, but size varies considerably depending on availability of food. Females commonly produce about 500 eggs, sometimes depositing over 1,200 eggs. Adults overwinter under leaves and other plant debris, and under logs and stones.



Mexican Bean Beetle, *Epilachna varivestris* Mulsant (Coleoptera: Coccinellidae), Figure 42 **Mexican bean beetle adult.**

Damage

Larvae and adults feed principally on leaf tissue, but under high density conditions, and when faced with starvation, they also feed on blossoms, pods, and stems. Bean beetles feed on the lower surface of the foliage, removing small strips of tissue and usually leaving the upper epidermis and veins intact. The upper epidermis soon dies and becomes transparent, leaving characteristic injury consisting of a number of small transparent spots that is reminiscent of a stained-glass window. Entire leaves are quickly reduced to skeletal lace-like remains that have little photosynthetic value and usually dry and die quickly. The larvae are particularly damaging, and a mature larva may consume an entire leaf in a day.

Mexican bean beetle also is capable of plant disease transmission. Larval and adult bean beetles fed on plants infected with cowpea mosaic virus become capable of transmitting the virus to healthy plants for a 2–4 day period

Management

Modern insecticides have relegated Mexican bean beetle to minor status in commercial bean production. They remain a serious problem, however, in home gardens and elsewhere when insecticides are not used. Cultural practices are of limited value. The beetles fly long distances for overwintering, so crop rotation and destruction of overwintering sites is generally not practical. It is a useful practice, however, to destroy bean plants as soon as they have been harvested, as this may disrupt development of many immature insects and inhibit development of additional generations. The principal means of biological suppression of Mexican bean beetle is release of *Pediobius* wasps. However, commercial bean producers rarely consider such an approach, tending to rely instead on chemical insecticides. Some degree of resistance occurs within commercially available cultivars of beans, but this is not completely adequate.

► Vegetable Pests and their Management

References

Auclair JL (1959) Life history, effects of temperature and relative humidity, and distribution of the Mexican bean beetle, *Epilachna varivestris* Mulsant (Coleoptera: Coccinellidae), in Quebec, with a review of the pertinent literature in North America. Ann Entomol Soc Quebec 5:18–43

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, CA, 729 pp

Friend WG, Turner N (1931) The Mexican bean beetle in Connecticut. Conn Agr Exp Stat Bull 332:108

List GM (1921) The Mexican bean beetle. Colorado Agr Exp Stat Bull 271:58

Mexican Fruit Fly, *Anastrepha ludens* (Loew) (Diptera: Tephritidae)

This fruit pest occurs in Mexico and adjacent areas of the USA.

► Citrus Pests and their Management
► Fruit Flies (Tephritidae)

Microbial Control of Insects

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A wide variety of pathogenic organisms (virus, bacteria, protozoa, fungi and nematodes) attack insects and result in reductions in insect numbers within natural ecosystems, agroecosystems, and domestic settings. Natural epizootics of insect disease can result in spectacular declines in insect populations of economic and medical importance. However, dependence upon naturally occurring epizootics for insect control can be risky when economic thresholds might be surpassed, or when plant and animal diseases could be transmitted by the insects before they succumb to disease. Microbial control of insects is the concerted use of insect-specific pathogens and nematodes for the biological control of insects. Microbial pesticides have a number of advantages over conventional chemical pesticides. Although the advantages of microbial pesticides are numerous, some of their characteristics are regarded as disadvantages.

Advantages and Disadvantages of Entomopathogens for Insect Control

Advantages

- specificity to the target organism or to a limited number of host species,
- little or no direct impact upon parasitoids and invertebrate predators,
- harmless to vertebrates and plants,
- no toxic residues,
- little or no environmental pollution,
- little or no development of resistance by the target organism (however, resistance has developed in some target insects to *Bt* and *Bacillus sphaericus*)
- no secondary pest outbreak,
- compatibility with other biological control agents,
- possibility of long-term control,
- ease of application, and
- adaptable to genetic modification through biotechnology.

Disadvantages

- specificity only to target organism,
- strict timing of application for maximal effect,

- long period of lethal infection (i.e., little or no "knock-down" effect),
- inactivation by environmental factors (e.g., ultraviolet light, desiccation, temperature extremes, etc.) and therefore, short field persistence,
- expensive to produce, especially for obligate pathogens, and difficult to formulate,
- short shelf life,
- development of resistance by target organisms, especially to *Bt* and *B. sphaericus*, codling moth granulovirus
- expensive to produce except for niche markets, and
- risks or perceived risks associated with genetically-modified organisms.

Like insect biological control agents (predators and parasitoids), microbial control agents can be employed in classical, conservation and augmentation biological control. Microbial control agents have been used in most settings where insect pests are found including glasshouse and row crops, orchards, ornamentals, range, turf and lawn, stored products, forests, households, aquatic environments, animal waste, and for control of insects of veterinary and medical importance.

In classical biological control using insect pathogens, the disease causing agents are isolated from diseased insects and introduced into an insect population in which they are not currently present. The objective is to establish the pathogen or nematode within the population resulting in recycling within the insect population and providing long term control. Some of the most successful examples of establishment and long term control include the use of the fungus, *Entomophaga maimaiga* against the gypsy moth, *Lymantria dispar*, the *Oryctes* non-occluded virus against the palm rhinoceros beetle, *Oryctes rhinoceros*, the nematode *Deladenus siricidicola* against the woodwasp, *Sirex noctilio* and the fungus *Zoophthora radicans* for control of alfalfa aphid, *Therioaphis trifolii*. Classical biological control using insect pathogens has been most successful in perennial agroecosystems and forests.

Conservation biological control fosters pathogen abundance by reducing harmful influences and enhancing positive ones. This may entail replacing a broad-spectrum fungicide with one with a narrower spectrum of activity, changing the timing of insecticide use to avoid killing host insects while pathogens are developing and increasing within the population, and other practices that enhance the activity of pathogens that are present within the targeted insect population. An excellent example of this strategy is the encouragement of epizootics of the fungal pathogen, *Neozygites gossypii* in populations of the cotton aphid, *Aphis gossypii*.

Augmentative biological control consists of two types of strategies: inoculative and inundative applications. Inoculative control can be used to counteract seasonally repeating problems typical of annual cropping systems, such as the use fungicides, tillage, etc. Insect pathogens can also be introduced earlier in the season than they would normally occur, giving them time to reproduce and suppress pests earlier in the cropping cycle. The most commonly employed augmentative strategy for microbial control agents is inundative application of microbial pesticides. Inundative approaches differ from classical and inoculative strategies in that the activity of the applied pathogens, not necessarily that of secondary inoculum, provides control of the pest insects. Using this strategy, one to several applications of microbial control agents are made for control of the pest insect. Microbial agents that are currently used in commercial products are listed in the following table.

Entomopathogens Commonly Used for Microbial Control

Bacteria

The most widely used insect pathogen for inundative augmentative control is the bacterium, *Bacillus thuringiensis* (*Bt*). It was the development and commercial production of *Bt* that ushered in the practical use of microbial control on a large scale. The larvicidal activity of *Bt* is due to a proteinaceous toxin inclusion that is formed at the time of sporulation which must be eaten by the targeted insect in order to be active. Collectively, the toxins are referred to as delta endotoxins. For detailed information on their chemistry and mode of action see section on *Bacillus thuringiensis* in this volume. Besides relative specificity and efficacy, the other advantages of *Bt* products are that they can be produced by fermentation on a large scale, may be formulated (as wettable powders, granules, flowable concentrates, etc.) for ease of application and enhancement of activity, are applied using conventional equipment and are stable in storage for months or even years depending on storage conditions.

Several varieties of *Bt* have been discovered over the past century that have activity against Lepidoptera, certain families of Diptera and Coleoptera as well as other insects. *Bt* is used to control a wide

Microbial Control of Insects, Table 7 Representative invertebrate pathogens that are currently used in microbial control products

Microbial control agents	Targeted insects
Bacteria	
Bacillus thuringiensis[a]	
Bt kurstaki, Bt aizawai	Several species of Lepidoptera
Bt tenebrionis	Colorado potato beetle
Bt israelensis	Mosquitoes, black flies, fungus gnats
Bacillus sphaericus	Mosquitoes (especially *Culex* spp.)
Paenibacillus popilliae	Japanese beetle
Serratia entomophila	New Zealand grass grub
Fungi	
Lecanicillium (Verticillium) spp.	Aphids, whiteflies, and thrips
Metarhizium anisopliae	Grasshoppers, termites, cockroaches
Beauveria bassiana	Colorado potato beetle, white flies, other insects
Virus	
Nucleopolyhedroviruses[b]	several species of Lepidoptera
Granuloviruses	several species of Lepidoptera
Nematodes[c]	
Steinernema carpocapsae	Numerous insect pests
S. feltiae	Diptera, Lepidoptera, other insect pests
S. riobrave	weevil larvae, Lepidoptera, Orthoptera
S. scapterisci	mole crickets
S. glaseri	scarab larvae
Heterorhabditis bacteriophora	Numerous insect pests
H. megidis	scarab larvae, other insect pests
Phasmarhabditis hermaphrodita	Slugs

[a]representative varieties
[b]numerous species have been developed, see Miller (1997), Hunter-Fujita et al. (1998)
[c]representative species

variety of lepidopteran pests in several row crops, stored foods, orchards and forests. Aerial application for gypsy moth control is one of the larger scale applications of this bacterium against lepidopteran larvae. The beetle active varieties are predominantly used against the Colorado potato beetle, *Leptinotarsa decemlineata*, and certain other Chrysomelidae. The variety *Bt israelensis* is insecticidal for mosquito, black fly, and fungus gnat larvae and certain other nematocerous Diptera. (For further reading on this bacterium for mosquito and black fly control, see Microbial control of medically important insects.) Genes that encode production of *Bt* toxins have been incorporated into varieties of corn, cotton, potatoes and other crop plants. These genetically modified crops provide continuous control of susceptible insects. Various strategies have been proposed or employed to counteract or forestall development of resistance by the targeted pests to the toxins. Public acceptance of *Bt*-transgenic plants is currently a major obstacle to their widespread use as human food.

Other bacteria that are used as microbial control agents against pest insects are *Bacillus sphaericus* (against mosquito larvae), *Paenibacillus popilliae* (against Japanese beetle larvae), and *Serratia entomophila* (against *Costelytra zealandica* [grass grub] in New Zealand). Of these, *B. sphaericus* is second to *Bt* in commercial production and sales. It offers several of the same advantages of *Bt* in terms of ease of production and formulation, application using conventional equipment and good shelf life. It rapidly kills susceptible species within 24 h of ingestion and is more active than *Bti* against certain mosquito species especially in organically enriched habitats. Its two main disadvantages are a narrower host range than *Bti* and the development of very high levels of resistance in certain populations of *Culex quinquefasciatus*, one of the main targeted species.

The success of *P. popilliae* or milky disease as a microbial control agent of Japanese beetle larvae has been variable with substantial long term control reported in certain situations and little or no control reported in others. Spores of *P. popilliae* must be produced in living host larvae or harvested from field collected infected larvae, a distinct disadvantage in terms of large scale production. Properly prepared spore powders can persist for several years. Unlike *Bt* and *B. sphaericus*, infected larvae are not rapidly killed, but slowly develop milky hemolymph and usually die as full grown larvae which serve as source of inoculum for neighboring larvae (Fig. 43).

Viruses

Although there are a huge numbers of viruses that are pathogenic for hundreds of species of

Microbial Control of Insects, Figure 43 **Cabbage looper infected with nucleopolyhedrosis virus, displaying characteristic symptoms including hanging from the prolegs and liquefaction of body contents (photo courtesy of Pat Vail and Darlene Hofmann).**

pest insects, only the baculoviruses have been commercially developed and used on a wide scale. Baculoviruses have been reported with activity against Lepidoptera, Hymenoptera (sawflies), Diptera and a few other arthropods. Most varieties have been isolated from Lepidoptera and are represented by the singly occluded granuloviruses (GV) and multiply occluded nucleopolyhedroviruses (NPV). The GVs and several of the NPVs are specific for one species or closely related group of species. For example, the codling moth GV is highly virulent for codling moth and to a lesser extent related species such as pea moth and the oriental fruit moth, but does not infect most other species in the same family (Tortricidae). The two baculoviruses with the broadest host range are the multiply enveloped NPVs isolated from two noctuids, the alfalfa looper, *Autographa californica* (*Ac*MNPV), and the celery looper, *Syngrapha* (=*Anagrapha*) *falcifera* (*Anfa*MNPV). *Anfa*MNPV has been reported to infect over 31 species of Lepidoptera in ten families. The host range of *Ac*MNPV includes 33 species of Lepidoptera in 12 families. The virulence of both viruses for species in the Noctuidae is especially high. For example, the LC_{50} values for *Anfa* MNPV against *Trichoplusia ni*, *Heliothis virescens*, *Helicoverpa zea* and *Spodoptera exigua* are 0.093, 0.095, 0.147 and 0.327 occlusion bodies/mm^2.

The principal advantages of the baculoviruses are their efficacy, specificity, and production of secondary inoculum (i.e., recycling in host populations). These benefits make them attractive alternatives to broad spectrum insecticides and ideal components of IPM systems due to their lack of untoward effects on beneficial insects including other biological control organisms. The need to produce virus in living cells, either in cell culture or whole insects, increases the cost of virus production. Some of the other drawbacks of using entomopathogenic viruses are their relatively slow action as compared to chemical insecticides, sensitivity to UV light and the need to time applications to coincide with susceptible instars.

Like the bacterial microbial control agents, entomopathogenic viruses must be ingested by the targeted insect in order to be active. This is an important consideration when formulating viruses to facilitate application and protection from UV inactivation; adjuvants that inhibit feeding will reduce efficacy. The use of optical brighteners with baculovirus has markedly improved efficacy against some species of Lepidoptera through their activity on the peritrophic membrane allowing greater contact between virus and the midgut epithelium. Adjuvants that protect the virus from UV inactivation have also improved efficacy, but with an increase in cost.

Some of the baculoviruses have been successfully employed on a large scale for control of agricultural pest insects. For example, the NPV of the velvet bean caterpillar, *Anticarsia gemmatalis*, is currently used to treat approximately one million ha of soybeans in Brazil annually. In many agricultural settings, the cost of entomopathogenic virus will restrict their use to high value niche markets and sensitive areas where chemicals cannot be used.

Fungi

Fungi comprise another large group of microorganisms that have been developed as microbial control agents. A rich diversity of fungi are found causing disease in a wide variety of insects. Because they invade insects via the integument, they are the only effective microbial control agents used for control of sucking insects such as aphids and whiteflies. Viruses, bacteria and protozoa on the other hand must be ingested in order to infect insect hosts. Species of fungi in the order Entomophthorales (subdivision Zygomycotina, class Zygomycetes) are among some of the most virulent and have been responsible for dramatic crashes in insect populations. Their success as natural and classical biological control agents has been mentioned above (e.g., *N. gossypii* and *E. maimaiga*). However, several of the most efficacious Entomophthorales are problematic to manipulate due to difficulty in producing them on artificial media and limited shelf life of infective propagules.

Entomopathogenic species in the Hypocreales (formerly placed in the subdivision Deuteromycotina class Hyphomycetes) are the fungi most commonly used as inundatively applied microbial control agents. These fungi do not have sexual stages, can be produced on artificial media, and are fairly stable in storage (for several months when stored in cool conditions). *Beauveria bassiana*, *Lecanicillium* (*Verticillium*) spp., *Isaria (Paecilomyces) fumosoroseus* and *Metarhizium anisopliae* are commercially produced and have been employed against a wide range of insect species. Most species of fungi require high humidity in order to germinate and infect insect hosts. Environmental manipulation and formulation have been used to improve efficacy and protect spores from deactivation by UV radiation. Although shelf life is somewhat limited relative to bacteria and viruses, refrigeration and formulation have improved the longevity of fungal preparations.

Nematodes

Several families of nematodes parasitize insects. The majority of the research that has been published pertains to the Mermithidae, Steinernematidae, and Heterorhabditidae. The mermithids are obligate parasites of a broad spectrum of insects. One species, *Romanomermis culicivorax* had been commercially produced and used as a biological control agent of mosquito larvae. The necessity of using living hosts for production and a limited shelf life (a few months under refrigeration) has limited the prospects for commercial production of mermithids. On the other hand, they have good potential as classical biological control agents and may persist and recycle in certain habitats in which they have been introduced.

Several species of the Steinernematidae and Heterorhabditidae, collectively referred to as entomopathogenic nematodes, have been grown on artificial media. Infective stages of these families are non-feeding and can be stored for several months, especially under refrigeration. The microbial aspect of steinernematids and heterorhabditids stems from the symbiotic relationship they have with bacteria in the genera *Xenorhabdus* and *Photorhabdus*, respectively. The infective stage of the nematode is the means by which the bacterium gains entry to the insect host. The bacteria facilitate rapid death of the host, digestion of host tissues and the production of antibiotics that provide protection of the host cadaver from invasion by other microbes. The nematodes may actively pursue host insects (cruisers) or wait for hosts to come to them (ambushers). These nematodes have potential for the persistent control of several insect species, especially in soil and cryptic habitats. Their main limitations are prior to invading an insect host. Rapid desiccation severely restricts the window of opportunity for foraging for a host in the absence of sufficient moisture. Some species are limited by temperatures at or below 10°C (*S. carpocapsae*), but there are species that are active at temperatures as low as 5–7°C (*S. kraussei*, *S. feltiae*). Some species have a fairly narrow host range (e.g., *S. scapterisci*) while others attack a wide range of species (e.g., *S. carpocapsae*).

General Considerations

Microbial control agents can be applied using a variety of conventional pesticide application equipment as well as some non-conventional methods. Autodissemination using attractant traps is one of the more innovative approaches. Targeted insects are attracted to traps using pheromones, floral lures and the like and become contaminated with fungi, virus, etc. and disseminate the inoculum to other individuals of their species through direct contact (mating, aggregations) or by dying in larval habitats. The application of microbial control agents using chemagation (application through irrigation systems) in combination with remote sensing also appears to have promise.

Microbial control may provide adequate suppression of insect pests used as a stand alone measure in certain situations or may be integrated into a more complex strategy that includes other biological control agents, environmental modification or manipulation, use of other alternative interventions (such as mating disruption) or the judicious use of conventional pesticides. For example, the use of a chemical pesticide against a specific life stage that is unaffected by the microbial agent, or use of chemical pesticides and a microbial agent in synergistic combination such as the chloronicotinyl insecticide, imidacloprid and the Hypocreales fungus, *Metarhizium anisopliae*.

The comparison of microbial control agents with chemical pesticides is usually made from the perspective of only their efficacy and cost. In addition to efficacy, the advantages of using microbial control agents are numerous including safety for humans and other nontarget organisms, reduction of pesticide residues in food, preservation of other natural enemies and increased biodiversity in managed ecosystems. The selectivity and safety of microbial control agents should facilitate their incorporation into IPM programs where their effects on other natural enemies will be minimal as compared to most presently used chemical pesticides. Increased use of entomopathogens for control of arthropod pests will depend on a variety of factors including improvements in the pathogens related to their efficacy and cost and the perceived benefits of using them relative to conventional chemical pesticides.

References

Burges HD (ed) (1981) Microbial control of pests and plant diseases 1970–1980. Academic Press, London, UK, 949 pp

Gaugler R (2002) Entomopathogenic nematology. CABI Publishing, Wallingford, UK, 402 pp

Grewal PS, Ehlers RU, Shapiro-Ilan DI (eds) (2005) Nematodes as biological control agents. CABI Publishing, Wallingford, Oxon, UK, 480 pp

Hunter-Fujita FR, Entwistle PF, Evans HF, Crook NE (eds) (1998) Insect viruses and pest management. Wiley, Chichester, UK, 632 pp

Lacey LA, Kaya HK (eds) (2007) Field manual of techniques in invertebrate pathology: application and evaluation of pathogens for control of insects and other invertebrate pests, 2nd edn. Springer, Dordrecht, The Netherlands, 868 pp

Lacey LA, Frutos R, Kaya HK, Vail P (2001) Insect pathogens as biological control agents: do they have a future? Biol Control 21:230–248

Miller LK (ed) (1997) The Baculoviruses. Plenum Press, New York, NY, 468 pp

Tanada Y, Kaya HK (1993) Insect pathology. Academic Press, New York, NY, 666 pp

Microbial Control of Medically Important Insects

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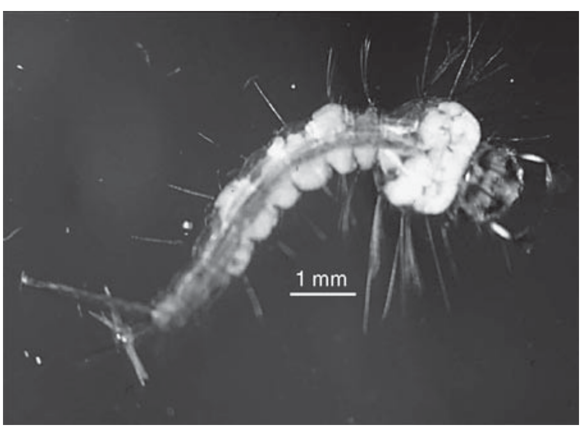
Microbial control of insects of medical and veterinary importance is the use of insect-specific pathogens and nematode parasites for the control of insects that are vectors and pests of humans or domestic animals. Medically important insects include those that suck blood such as mosquitoes (Culicidae), black flies (Simuliidae), and other dipterans, lice (Phthiraptera), fleas (Siphonaptera) and those that do not suck blood but are nevertheless a nuisance (house flies, cockroaches, etc.). Infectious agents of some of the most devastating diseases of humans are transmitted by insects. These include organisms that cause malaria, yellow fever, dengue, several encephalitides (such as West Nile virus), plague, onchocerciasis, typhus, sleeping sickness, and Chagas disease. Domestic and wild animals also suffer from insect transmitted diseases, some of which result in death and/or severe economic losses. Pestiferous insects are also causes for decreased quality of life, weight loss in animals and allergic reactions in humans and domestic animals. The majority of research on microbial control of medically important insects has been conducted on the Diptera, most notably larvae of mosquitoes and black flies. This discussion will focus on microbial control of these two groups.

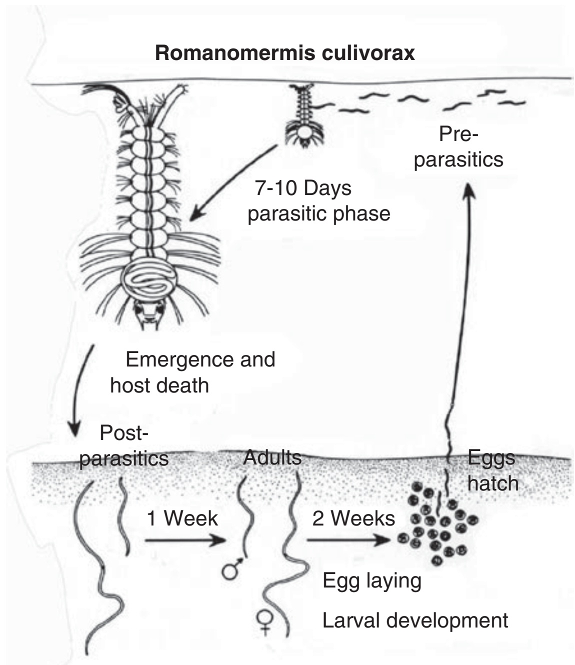
There is a large number of microbial agents (virus, bacteria, fungi, protozoa, rickettsia) and nematodes (Mermithidae and others) reported to infect medically important insects. The most commonly observed in nature are microsporidia [now included in the fungi], other fungi, viruses, and nematodes. Several microsporidia and certain other fungi that infect mosquitoes and black flies include species with complex life cycles, such as *Amblyospora* spp. and *Coelomomyces* spp. that involve intermediate hosts. These requirements and the need to multiply in living hosts decreases their potential as applied microbial control agents. However, their impact as naturally occurring pathogens on populations of medically important insects can be substantial. *Amblyospora* spp. and *Coelomomyces* spp. are particularly common in *Aedes* and *Culex* mosquitoes found worldwide and are a crucial part of a complex of biotic and abiotic factors that impact the dynamics of mosquito populations due to a reduction in the survival, vigor and reproductive success of infected mosquitoes (Fig. 44). Their importance must be viewed not for short-term population reduction but rather for the benefits of long-term abatement as part of an overall management strategy. Some of the other microsporidian pathogens of mosquitoes do not require intermediate hosts. For example, *Edhazardia aedis* is a virulent pathogen of the yellow fever mosquito, *Aedes aegypti* that has good potential as a classical biological control agent. This microsporidian is well adapted to the host mosquito and its container breeding habitats and can persist in *Ae. aegypti* populations through transovarial transmission and spread to additional breeding sites.



Microbial Control of Medically Important Insects, Figure 44 ***Culex salinarius*** **larva infected with** ***Amblyospora salinaria*****.**

Although viruses and mermithid nematodes also require living hosts in order to propagate, certain species have good potential as augmentative and classical biological control agents (see also, Microbial Control of Insects for definitions). The potential of mermithid nematodes has been demonstrated in rice fields and other non-polluted freshwater habitats. An advantage of this group is the potential to become established and recycle in mosquito habitats, but they are less effective in organically enriched and saline habitats. In the case of *Romanomermis culicivorax*, for example, a species that has been studied extensively, the egg stage can be stored in moist sand for use in subsequent microbial control efforts. When flooded with water, stored eggs hatch to produce infective preparasites. These can then be applied to larval habitats with conventional spray equipment. The shelf live of eggs is somewhat curtailed and the cost and logistics of production in living hosts are factors limiting widespread use. A protocol for the application and evaluation of *R. culicivorax* against mosquito larvae in rice fields have been developed. The mermithid nematode *Strelkovimermis spiculatus*, isolated from mosquitoes in Argentina, has a life cycle similar to *R. culicivorax* (Fig. 45). Unlike *R. culicivorax*, *S. spiculatus* has a demonstrated tolerance for high levels of organic pollution and dissolved ions relative to other mermithids and is currently being evaluated for introduction as a biological control agent of mosquitoes, particularly *Culex* spp.

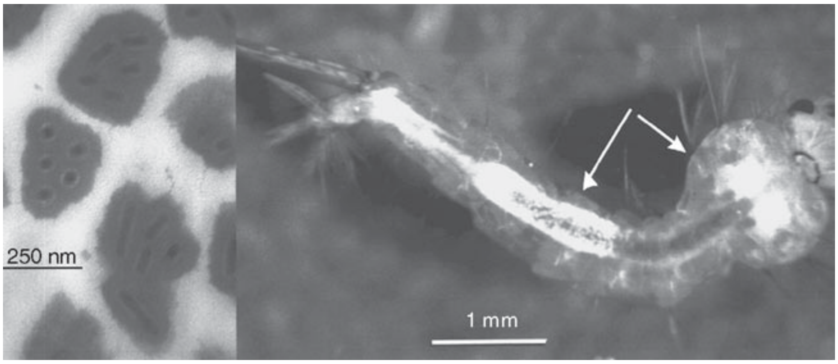
Several insect specific viruses have been reported from mosquitoes and black flies including Deltabaculoviruses, Cypoviruses, Iridoviruses and Densoviruses. Those with the best potential for mosquito control are the Deltabaculoviruses (formerly nucleopolyhedroviruses) within the family Baculoviridae (Becnel, 2007). Deltabaculoviruses (DBVs) have been isolated from thirteen mosquito species within the genera *Aedes*, *Anopheles*, *Culex*, *Ochlerotatus*, *Psorophora*, *Uranotaenia* and *Wyeomia*. Historically, mosquito baculoviruses have been extremely uncommon, difficult to



Microbial Control of Medically Important Insects, Figure 45 **Life cycle of *Romanomermis culicivorax*, an obligate parasite of mosquito larvae (courtesy of Ed Platzer).**

transmit and epizootics in field populations were rarely observed. Recently, a newly discovered DBV, designated CuniDBV, has been discovered that was responsible for repeated and extended epizootics in field populations of *Culex nigripalpus* and *Culex quinquefasciatus* in Florida, USA. CuniDPV infects and destroys the larval midgut (Fig. 46) causing patent infections within 48 h post-inoculation (p.i.) and death 72–96 h p.i. Each of the small globular occlusion bodies measures approximately 400 nm and contains four, sometimes up to eight, singly enveloped virions per occlusion body. While initial attempts to transmit this baculovirus to mosquitoes in the laboratory were unsuccessful, further investigations revealed conclusively that transmission is mediated by divalent cations: magnesium is essential for transmission whereas calcium inhibits virus transmission. This has been an important finding in understanding transmission of baculoviruses in mosquitoes and can explain, in great part, conditions that support epizootics in natural populations of mosquitoes and allow evaluation of CuniNPV as a new microbial control agent.

A multitude of entomopathogenic fungi infect mosquito and black fly larvae and adults. The species *Lagenidium giganteum*, formerly classified with the fungi, has now been placed in the Kingdom Chromista. Compared with mosquitocidal fungi, it has the greatest potential for microbial control. The main advantages of this species



Microbial Control of Medically Important Insects, Figure 46 ***Culex quinquefasciatus* larva infected with nuclepolyhedrosis virus (CuniNPV). White areas of the gastric caeca and posterior midgut (indicated by arrows) are the sites of infection. Inset shows details of viral rods with individual occlusion bodies.**

is that it can be produced on artificial media, has good larvicidal activity against a wide range of mosquito species, and the resting spores have an extremely prolonged shelf life. The infective stage is a short lived zoospore that is formed in vesicles on infected larvae, by mature mycelia in artificial media, or through the germination of resting spores. The zoospores attach to and encyst on the cuticle of mosquito larvae and the subsequent general infection of the larvae results in production of zoospores (secondary inoculum) within 1–7 days of infection depending on environmental conditions and water quality. When grown in artificial media, zoosporogenesis (the production of zoospores) results from nutrient deprivation of mature mycelia (presporangia) from 1–4 week-old cultures. This can be accomplished by diluting mycelial preparations with distilled or deionized water. The application of mature mycelia to larval habitats will result in the production of infective zoospores within hours or days of application depending on conditions. Although resting spores can be stored for extended periods and retain viability, they require 30 or more days of immersion in water before germination begins. The combination of *L. giganteum* mycelia and resting spores could provide a rapid and high level of infection in targeted larvae and a prolonged release of zoospores as new cohorts of larvae begin to hatch. Similarly the combination of larvicidal bacteria and resting spores could provide rapid and continuous control. *Lagenidium giganteum* has become established in several habitats into which it has been introduced providing a certain level of classical biological control in years subsequent to the original introduction. Commercial production of *L. giganteum* has been facilitated by a number of research breakthroughs in the 1980s and 1990s that enabled production of mature mycelia and oospores in artificial media.

By far the most commonly employed pathogens for control of mosquito larvae are *Bacillus thuringiensis* var. *israelensis* (*Bti*) and *Bacillus sphaericus*. *Bti* is also insecticidal for black fly (Simuliidae) larvae. Both bacteria must be ingested in order to be active. The active moieties of each species are proteinaceous toxins that are produced by the bacterium at the time of sporulation. The toxins in *Bti*, found in large parasporal inclusions, are active against a wide range of species in the Culicidae and Simuliidae and certain other families of Nematocera. After ingestion, the toxins are solubilized in the alkaline environment of the midgut and cleaved by enzymes to the active moieties that bind with the epithelial cell membranes. The resultant pore formation in the membranes alters the osmotic balance of the cells, ultimately resulting in rupture of the cells and eventual death of larvae.

In many mosquito abatement programs in North America, Europe and elsewhere, *Bti* is used as the larvicide of choice. In addition to its elevated larvicidal activity, the effects on nontarget organisms, including mosquito predators are minimal to non-existent. Various formulations (liquid, pellets, granules, etc.) and methods of application have enabled a tailored approach to larval control of mosquito larvae in a variety of habitats, including slow release formulations that enable prolonged control in certain smaller habitats. For the most part however, *Bti* has very little residual activity, especially in organically enriched habitats necessitating fairly frequent application when mosquito breeding is continuous.

For control of black fly larvae, *Bti* is a potent larvicide with negligible impact on non-target organisms. As an intervention used in the Onchocerciasis Control Program (OCP), it was responsible for control of *Simulium* vectors of *Onchocerca volvulus*, the causal agent of River Blindness, in an area where the black fly had developed resistance to organophosphate insecticides. It is currently a seasonally implemented control component in the OCP and is used to forestall or avoid the development of insecticide resistance. Because of the nature of black fly habitats (i.e., running water) and the tendency of *Bti* to become rapidly diluted after application, it must be applied at regular intervals in order to control larvae along the course of a river or stream. The distance downstream from the treatment point where control is achieved is referred to as effective carry. As in mosquito habitats, if black fly breeding is continuous, regular applications must be made in order to achieve effective control. The time between applications depends on the developmental cycle of the targeted species.

Bacillus sphaericus functions similarly to *Bti*, but has a narrower host range within the Culicidae and is not active against black fly larvae. Species in the mosquito genera *Psorophora* and *Culex* are highly susceptible to *B. sphaericus* toxins. *Anopheles* and *Mansonia* spp. larvae are also susceptible, but to a lesser extent. *Aedes aegypti* and certain other *Aedes* spp. exhibit little or no susceptibility to this bacterium. One of the main advantages of *B. sphaericus* is greater persistence of larvicidal activity in organically enriched habitats. It has also been reported to recycle within mosquito cadavers and populations under certain conditions. There have been reports in India, Brazil, Thailand and other locations of extremely high levels of resistance to *B. sphaericus* in larvae of *Culex quinquefasciatus*, a common species in organically enriched aquatic habitats.

► Microbial Control of Insects
► Fungal Pathogens of Insects
► Nematode Parasites of Insects
► Amoebae
► Baculoviruses
► Microsporidia
► Individual Taxa

References

Becnel JJ, White SE (2007) Mosquito pathogenic viruses-the last 20 years. In: Floores G (ed) Biorational control of mosquitoes, Bulletin 7. American Mosquito Control Association, Fresno, CA, pp 35–49

Becnel JJ (2007) Current status of deltabaculoviruses, cypoviruses and chloriridoviruses pathogenic for mosquitoes. Virol Sinica 20:117–127

Chapman HC (ed) (1985) Biological control of mosquitoes, Bulletin 6. American Mosquito Control Association, Fresno, CA, 218 pp

Kerwin JL, Petersen EE (1997) Fungi: Oomycetes and Chytridiomycetes. In: Lacey LA (ed) Manual of techniques in insect pathology. Academic Press, London, UK, pp 251–268

Lacey LA (2007) *Bacillus thuringiensis* serovariety *israelensis* and *Bacillus sphaericus* for mosquito control. In: Floore TG (ed) Biorational control of mosquitoes, Bulletin 7. American Mosquito Control Association, Fresno, CA, pp 251–268

Lacey LA, Orr BK (1994) The role of biological control of mosquitoes in integrated vector control. Am J Trop Med Hyg 50 (suppl):97–115

Lacey LA, Merritt RW (2003)The safety of bacterial microbial agents used for black fly and mosquito control in aquatic environments. In: Hokkanen HMT, Hajek AE (eds) Environmental impacts of microbial insecticides: Need and methods for risk assessment. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 151–168

Lacey LA, Undeen AH (1986) Microbial control of black flies and mosquitoes. Ann Rev Entomol31:265–296

Lucarotti CJ, Andreadis TG (1995) Reproductive strategies and adaptations for survival among obligatory microsporidian and fungal parasites of mosquitoes: a comparative analysis of *Amblyospora* and *Coelomomyces*. J Am Mosq Control Assoc 11:111–121

Skovmand O, Kerwin J, Lacey LA (2007) Microbial control of mosquitoes and black flies. In: Lacey LA, Kaya HK (eds) Field manual of techniques in invertebrate pathology: application and evaluation of pathogens for control of insects and other invertebrate pests, 2nd edn. Springer, Dordrecht, The Netherlands, pp 735–750

Microbial Pesticide

Microbial organisms that are applied like chemical pesticides for the suppression of pest abundance. Examples including various bacterial, fungal, viral, and microsporidian pathogens.

► Microbial Control of Insects

Microbiota

The microflora and microfauna of an organism.

Microbivores

Small animal fauna that feed on fungi and other soil flora.

Microcaddisflies

Members of the family Hydrobiosidae (order Trichoptera).

► Caddisflies

Micrococcidae

A family of insects in the superfamily Coccoidae (order Hemiptera).

► Bugs

Microcoryphia

An apterygote order of insects, also called Archeognatha. They commonly are known as bristletails.

► Bristletails

Microdon spp. (Diptera: Syrphidae)

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Ants (Hymenoptera: Formicidae), despite their elaborate social organization, are plagued by a multitude of arthropods that live in their nests, from mites to members of their own family. The majority of these myrmecophilous ("ant loving") arthropods feed upon ant brood, workers, food brought into the colony, or upon other organisms such as fungi which occur in the nest. Some of the most unusual of these myrmecophilous insects are flies of the genus *Microdon* (Diptera: Syrphidae). Unlike most myrmecophiles, behavioral and morphological adaptations to myrmecophily in *Microdon* are found only in the immature stages. Adult *Microdon* are typical syrphid flies that lack the usual adaptations or behavior that would integrate the fly with the habits of the ant. Instead, adult *Microdon* appear to associate with ants only long enough to lay eggs and will be killed and eaten by the ants if they dally too long at that task. In contrast, the slug-like larva are so highly integrated into the nest of their hosts that worker ants will protect them and carry them away from danger as readily as they do their own brood.

There are 31 species of *Microdon* in North America. The adults are about one-half inch long (1.5 cm) and highly variable in appearance between species. The larvae do not have the typical maggot form, and are so atypical in appearance that they were confused with snails and scale insects (Fig. 47), and have been described as such in early literature. Typical of cyclorrhaphous flies (Diptera), *Microdon* exhibits three larval instars, followed by a prepupa and pupa that forms inside the puparium, the hardened integument of the third instar. The larvae, when active, creep through galleries or tunnels of ant nests and are most often found deep within the nest in close proximity to ant brood. For most temperate species of *Microdon*, there appears to be only one generation a year, with the third instar overwintering. Pupation (pupariation) occurs in the early spring about the time ants become active. The integument of the larvae and puparia of most species is

***Microdon* Spp. (Diptera: Syrphidae), Figure 47** **Larvae of *Microdon*. Note the highly sculptured surface. The large protuberance is the posterior spiracle.**

heavily sculpted with a series of fine lateral and connecting ridges, over a strongly convex dorsal surface. In contrast to the larvae, puparia are found most frequently near the drier surface of the nest away from the brood chambers. Presumably this provides the newly emerged adults an opportunity to escape the nest undetected and unscathed. Adults emerge from puparia in the spring and will generally live only 1–2 months.

For many years, the food preference of the larvae was unknown but they were assumed to feed upon either fungi, infrabuccal pellets of ants, or even upon tree sap oozing from gallery wood. It has been determined that many, if not all, species of *Microdon* are actually predators of their hosts, feeding upon ant larvae and pupae. First instars actually will penetrate the cocoon of their host ants to feed upon the enclosed brood. Because of this peculiar relationship, *Microdon* are considered to be "aggressive mimics" of their hosts.

Microdon mimic their hosts physically and chemically. When *Microdon* larvae are disturbed, they will curl longitudinally approximating the shape of an ant cocoon. More importantly, *Microdon* are able to produce chemicals, a variety of large hydrocarbon molecules, that are distributed over their integument. These cuticular hydrocarbons are the same recognition chemicals used by the ants to identify other members of their nest. The type and amount of these molecules produces a colony-specific chemical profile that the *Microdon* are able to almost identically match, chemically integrating them into the host nest. This is truly an example of chemical mimicry. In other words, the *Microdon* larvae are not using cuticular hydrocarbons produced by the ants to camouflage themselves but rather are somehow able to sense the chemical profile of their hosts and produce cuticular hydrocarbons to mimic that profile.

Host range of *Microdon* varies with species. Some species are highly host specific and are found only in nests of one or two species, while others are less specific and can be found in nests of several genera of ants. *Microdon* are found most commonly in nests of *Camponotus* spp. (carpenter ants) and *Formica* spp.

References

Akre RD, Garnett WB, Zack RS (1988) Biology and behavior of *Microdon piperi* in the Pacific Northwest (Diptera: Syrphidae). J Kans Entomol Soc 61:441–452

Garnett WB, Akre RD, Sehlke G (1985) Cocoon mimicry and predation by myrmecophilus Diptera. Fla Entomol 68:615–621

Howard RW, Akre RD, Garnett WB (1990) Chemical mimicry in an obligate predator of carpenter ants (Hymenoptera: Formicidae). Ann Entomol Soc Am 83:607–616

Howard RW, Stanley-Samuelson DW, Akre RD (1990) Biosynthesis and chemical mimicry of cuticular hydrocarbons from an obligate predator, *Microdon albicomatus* Novak (Diptera: Syrphidae) and its ant prey, *Myrmica incompleta* Provancher (Hymenoptera: Formicidae). J Kans Entomol Soc 63:437–443

Microencapsulation

A method of formulating insecticides and other chemicals for controlled release. Microscopic spheres containing the chemical are formed from a polymer with various degrees of cross-linking, thickness of the capsule wall, and sphere size, thereby regulating release rates of the chemicals. This usually produces a longer-lasting method of application, reduced volatility, and lower mammalian toxicity. Sometimes bees are at greater risk, however, due to their tendency to confuse the spheres with pollen grains.

► Insecticides
► Insecticide Formulation

Microfauna

Soil invertebrates in the small size class, usually less than 2 mm in width (contrast with macrofauna and megafauna).

Micromalthidae

A family of beetles (order Coleoptera). They commonly are known as telephone-pole beetles.

► Beetles

Micropezidae

A family of flies (order Diptera). They commonly are known as stilt-legged flies.

► Flies

Microphysidae

A family of bugs (order Hemiptera).

► Bugs

Micropterigidae

A family of moths (order Lepidoptera). They commonly are known as mandibulate archaic moths.

► Mandibulate Archaic Moths

► Butterflies and Moths

Micropterous

The condition in which the wings of the insect are small, and usually non-functional (compare with brachypterous and macropterous).

Micropyle

One or more pores or small holes in the egg chorion through which sperm enter.

Microspines

Minute spines located on various locations of the body of some insects; they usually are visible only under high magnification, and impart a rough feel to the body when they are numerous.

Microsporidae

A family of beetles (order Coleoptera). They commonly are known as minute bog beetles.

► Beetles

Microsporidia (Phylum Microsporida)

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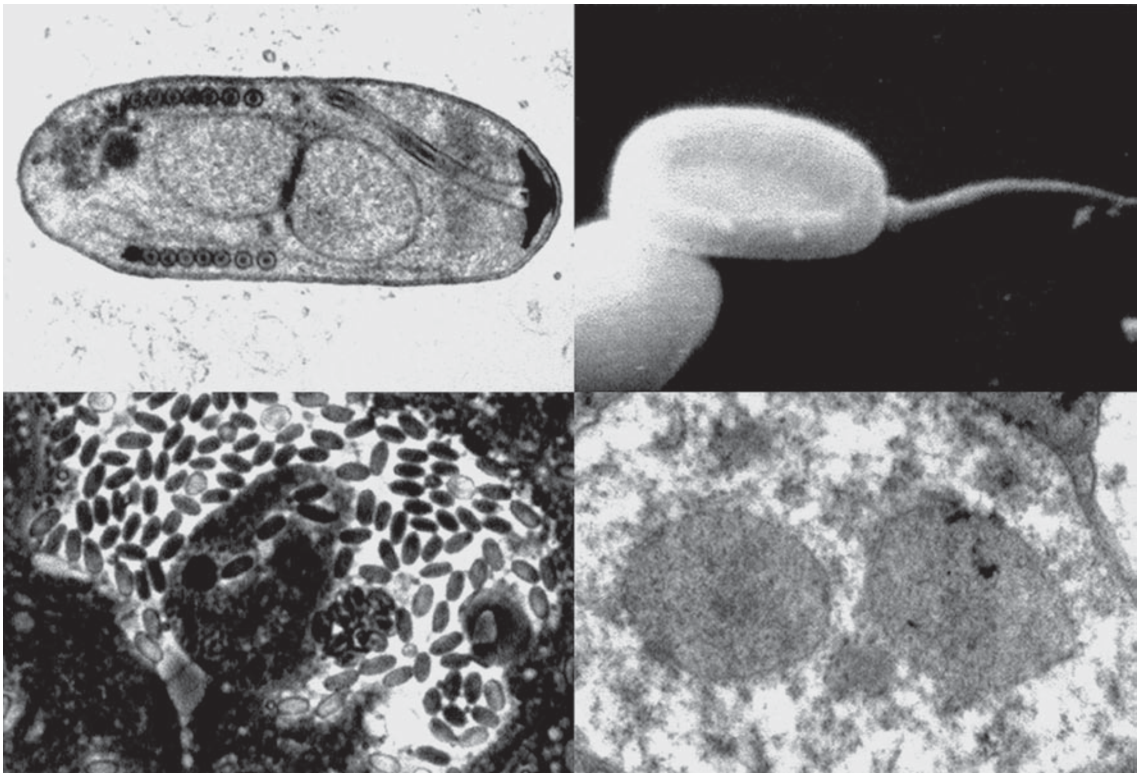
Microsporidia are obligately pathogenic, single-celled, eukaryotic organisms of which nearly 1,000 species have been described, over 700 from insect hosts. Lacking mitochondria, centrioles, peroxisomes and classical Golgi bodies, and possessing a nonmotile amoeba-like vegetative form, microsporidia were considered until recently to be primitive members of the Protozoa. Molecular analyses, however, have determined that the group possesses several gene sequences that suggest a close relationship to the fungi.

The first microsporidium studied was the causal agent of "pebrine disease" of silkworms (*Bombyx mori* L.), a disease that nearly caused the demise of the silk industry in France in the 1860s. Louis Pasteur recognized the infectious nature of the disease and developed a screening technique to rid the industry silkworm colonies of the pathogen. The microsporidium was later described as *Nosema bombycis* Naegli, the type species of the well-known genus *Nosema*.

Microsporidia infect all groups of vertebrate and invertebrate animals, as well as some protozoans, but are particularly common in fish and arthropods. Mammals also host some microsporidian taxa and immune-compromised humans are among the known hosts. Insects, though, comprise the largest group of animals from which microsporidia have been described, probably because of the ease of collecting large numbers of hosts for diagnosis and the impetus to discover biological control agents for insect pests. Some well-studied insect species have been shown to harbor several species of microsporidia. No microsporidia occur as plant pathogens.

Microsporidia from insects are most often and most easily observed in their environmentally resistant infective form, the spore (Fig. 48). Spores are relatively uniform within a species but different species range in size from 1 to 12 μ in length and vary in shape from long oval to round, reniform, spindle-like, or tear-shaped. Species from terrestrial hosts typically possess smooth non-ornamented spores; spores of microsporidia from aquatic hosts such as mosquitoes and black flies may include "wings," mucoid coats, flagella-like appendages, or a patterned surface structure. Spores of all species are discernable as brightly refractive forms under 250–400 x phase contrast light microscopy in crushed host tissues, although aquatic spores, with their typically thinner spore walls may appear more grayish with internal structures somewhat apparent.

Infection by microsporidia occurs either via ingestion of infective environmental spores by a susceptible host, transmission inside or on the surface of eggs oviposited by infected female hosts



Microsporidia (Phylum Microsporidia), Figure 48 **Images of microsporidia. *Top left*, transmission electron micrograph of an environmentally resistant microsporidian spore, approximately 4 μ in length (courtesy J. Maddox and Society of Invertebrate Pathology); *top right*, scanning electron micrograph of germinating spore (courtesy J. Becnel and Society of Invertebrate Pathology); *bottom right*, transmission electron micrograph of vegetative form, approximately 6 μ in diameter (photo by J. Maddox); *bottom left*, light photomicrograph of an insect host midgut epithelial cell cytoplasm filled with spores (photo by L. Solter).**

or, much less frequently, mechanical injection by parasitoids. Very often, a microsporidium is transmitted both orally and via the eggs. The most unique characteristic of microsporidia is the infection mechanism. Along with a single or double nucleus (diplokaryon), cytoplasm and plasma membranes, a polar filament is coiled within the spore. When the spore is activated to germinate by conditions in the gut lumen of the host, the polar filament everts through a disk at its attachment point on the spore and the contents of the spore are emptied into the host gut cell to form a vegetative sporoplasm.

The membrane bound sporoplasm undergoes division in the cytoplasm of the host's gut cells. Some species of microsporidia form a rudimentary autoinfective spore form, which germinates inside the cell and appears to be a mechanism for ensuring that the non-motile pathogen locates the suitable tissues for proliferation and maturation of infective spores. The tissues infected vary for different species of microsporidia; some species pervade all host body tissues and some are limited to one or more specific tissues, such as the midgut or the fat body.

Transmission mechanisms may be determined by the tissues that are targeted. For example, species that infect the gonads, especially of the female hosts, are usually transmitted to the host's offspring. Infective spores from midgut infections may be shed in feces of infected hosts, and silk gland infections may be transmitted by exposure of individual hosts to the silk of infected conspecific individuals. Fat body utilizing species are probably released into the environment when dead larvae decompose. Some microsporidia require an intermediate host for transmission and produce several spore types. For example, the *Amblyospora* spp. in mosquitoes require copepod hosts in the life cycle to produce spores infective in turn to the mosquito hosts.

The effects on hosts of a microsporidian infection vary widely depending on the microsporidian species, initial dosage, mechanism of transmission, host condition, and other factors. Some species are quite virulent, nearly always killing larval hosts prior to or during pupation, but most appear to be chronic pathogens that are more likely to suppress the host populations by lowering fitness of individuals due to decreased adult life span, fecundity and movement, and higher larval mortality in infected offspring. Most microsporidian species seem to have some deleterious effects on the host, but some may be nearly benign.

The epizootiology of microsporidia in host populations also varies greatly but many, if not most, species appear to be strongly host density dependent and can occur in high prevalences, up to 100% of the host population, in high-density host populations. Some species may be maintained in host populations for long periods of time at very low prevalences in stable host populations. There are (Table 8) numerous examples of insect species, both agricultural pests and naturally occurring, that are strongly regulated by the presence of microsporidian pathogens. Two such examples are the European corn borer, *Ostrinia nubilalis*, which is regulated by *Nosema pyrausta* in parts of midwestern North America, and Canadian populations of the spruce budworm, *Choristoneura fumiferana*, which are often strongly suppressed by *Nosema fumiferanae*.

In general, efforts to use microsporidia as microbial insecticides have been unsuccessful. Long-term studies of *Nosema locustae*, the only microsporidium ever registered (U.S. EPA) for use as an insecticide, have shown that it probably functions more effectively as a long-term biological control agent rather than as a "biological insecticide." In general, microsporidia being evaluated for use as biological control agents against insect pests should probably be considered as similar in dynamics and host effects to parasitoids.

One of the most common problems associated with microsporidia are infections in colony insects and arthropods used for research, or in beneficials that are mass produced for biological control projects. As in natural insect populations, symptoms are often subtle and may involve straggling or slow larval development, lowered fecundity, and early larval

Microsporidia (Phylum Microsporidia), Table 8 **Common insect microsporidioses**

Microsporidium	Host	Host common name
Amblyospora spp.	*Aedes* spp. and *Culex* spp.	mosquitoes
Edhazardia aedis	*Aedes aegypti*	yellow fever mosquito
Endoreticulatus schubergi	various Lepidoptera	
Nosema algerae	*Anopheles* spp.	mosquitoes
Nosema apis ("pebrine disease")	*Apis mellifera*	European honey bee
Nosema fumiferanae	*Choristoneura fumiferana*	spruce budworm
Nosema locustae	various spp.	grasshoppers and crickets
Nosema kingi	*Drosophila* spp.	fruit flies
Nosema lymantriae	*Lymantria dispar*	gypsy moth
Nosema pyrausta	*Ostrinia nubilalis*	European corn borer
Nosema tortricis	*Tortrix viridana*	green tortrix
Nosema whitei	*Tribolium* spp.	flour beetles
Octosporea spp.	muscoid and syrphid flies	
Thelohania solenopsis	*Solenopsis invicta*	fire ants
Vairimorpha necatrix	various *Noctuidae*	armyworms and other noctuids

death. Infection can alter experimental results due to changes in host physiology and compromise biological control efforts.

References

Becnel JJ, Andreadis TG (1999) Microsporidia in insects. In: Wittner M, Weiss LM (eds) The microsporidia and microsporidiosis. American Society for Microbiology, Washington, DC, pp 447–501

Boucias DG, Pendland JC (1998) Principles of insect pathology. Kluwer Academic Publishers, Boston, MA, 537 pp

Undeen AH, Vavra J (1997) Research methods for entomopathogenic protozoa. In: Lacey L (ed) Manual of techniques in insect pathology. Academic Press, San Diego, CA, pp 117–151

Bulla LA Jr, Cheng TC (1977) Comparative pathobiology, vol 2: Systematics of microsporidia. Plenum Press, New York, NY, 510 pp

Tanada Y, Kaya HK (1993) Insect pathology. Academic Press, Inc., San Diego, CA, 666 pp

Microsporidiosis

Infection with microsporidia.

Microthoraciidae

A family of sucking lice (order Phthiraptera).

► Chewing and Sucking Lice

Microtrichia

Minute hair-like processes on the wings of certain insects, though sometimes this term is used to describe processes elsewhere.

Middorsal

A term referring to the middle of the upper region or "back" (as opposed to the subdorsal or slightly to the side, or lateral).

Midges

Members of the family Chironomidae (order Diptera).

► Flies

Midges as Human Food

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Cakes made from non-biting midges (Diptera: Chaoboridae) are a traditional food in African communities living along the shores of lakes in the African Rift Valley. Chaoborid swarms above the lakes may stretch over 10–32 miles and contain many millions of insects. They were first described from Lake Nyasa by the famous explorer David Livingstone, and also occur on the Ugandan side of Lake Victoria. The swarming gnats are called "E sami" by local people. It has been reported that the people compressed the flies into cakes that were used in some unknown manner as food. Also noted was the malodor of masses of dead flies that accumulated after the swarms, and the fact that the arrival of huge clouds of these gnats produced outbreaks of nasal catarrh among the white inhabitants.

Gnat cakes are called "kungu cakes" (Fig. 49) in the literature. In the Lake Victoria area, kungu is a term used as a prefix for insect specimens, or product made from insects. A major component of such cakes is a species of fly belonging to the family Chaoboridae, *Chaoborus edulis* Edwards. As the specific name implies, F. W. Edwards knew that this species was edible when he described it. Minor constituents of the cake include chironomid species in the genus *Tanytarsus* and *Cladotanytarsus*. Phylogenetically and anatomically, the Chaoboridae are a Nematoceran family somewhat closer to Culicidae than to Chironomidae. They still bear mouthparts, but not functional ones, and they do not feed as adults, similar to chironomid adults. The male flies have plumose antennae, as do chironomid males.

Midges as Human Food, Figure 49 **Midges as human food: *above*, insect "cakes" prepared from lakeflies; *center*, basket for sweeping flies, Lake Victoria, Kenya; *bottom*, swarm of midges above Lake Victoria (bottom photo by Hanna Nadel).**

The chaoborid larvae are known as phantom midges. They rest close to the bottom of the water body during the daytime, but are active predators during the night. A common North

American species in the same family, *Mochlonyx cinctipes*, swarms in clearings of woods at sunset. The African species, *C. edulis*, undergoes a periodic emergence according to the lunar cycle. Synchronous emergence of adult males and females creates huge swarms and mating takes place above the lake surface. The flying females drop their eggs, packed together in gelatinous masses, into the water and the swarm then moves towards the lakeshore.

These clouds of insects on the Kenyan shore of Lake Victoria can be observed during the long rains. They can be seen at a considerable distance from the shore above the middle of the lake during the early afternoon, and they reach land around sunset or soon thereafter. The edge of the lake at this time becomes an impenetrable column of insects that filled the ears, nostrils and eyes. It is reported that four local fishermen once lost their way inside such a cloud in the middle of the lake and died in a subsequent accident. Adjacent plants may be completely covered with flies, wings touching wings. In many cases, the swarms develop during the early afternoon together with a build-up of dark clouds and, according to local claims, their appearance often precedes a strong thunderstorm.

Flies may be collected by local women; it is possible to fill large plastic bags, many gallons in volume, with flies. "Kungu" (insect) cakes are prepared from the flies. They are similar in size to a commercial hamburger, but are completely black. Although preparation and eating these midge cakes is not a common habit today, it still can be seen along the shore of the Rift Valley Lakes. Traditionally, flies are collected by rotating a basket with a long handle in a manner very similar to that (Fig. 49) of a modern insect sweep net. The simple preservation procedure used is as follows: the accumulated flies are removed from the basket and flattened in the hands as when making chapatti bread; the cakes are then laid on banana leaves on the straw roof of the local houses to dry. This takes 3–4 days when sunny. Cakes are stored in a dry place inside the house before cooking in vegetable or chicken soup, or boiling in water only, and serving with a dip prepared from milk and salt. They are also served fresh as a black cake (not too tasty to an inexperienced western palate, in contrast to termites which are delicious).

Analysis of kungu cake indicates that its water content is 20% and the dry weight includes 58.9% protein and 20.3% fats. The other 20.8% is mainly chitin. This protein is highly digestible (about 73%) for human diet, and nutritious. It may serve as high quality food additive.

► Entomophagy: Human Consumption of Insects

References

Bergeron D, Bushway RJ, Roberts FL (1988) The nutrient composition of an insect flour sample from Lake Victoria, Uganda. J Food Compost Anal 1:371–377

Carr A (1964) Ulendo, travels of a naturalist in and out of Africa. University Press of Florida, Gainesville, FL

Cranston PS (1995) Medical Significance. In: Armitage P, Cranston PS, Pinder LCV (eds) The Chironomidae. Chapman and Hall, London, UK, pp 365–384

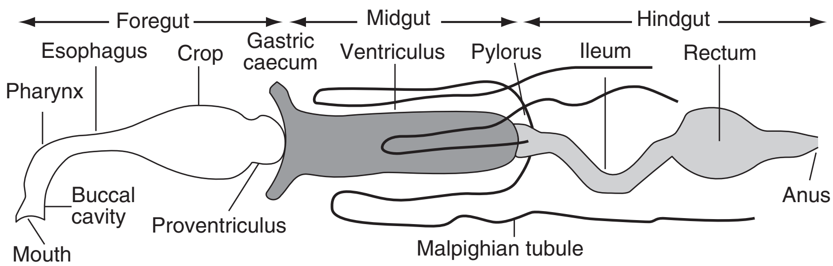
Yashuv A, Ben Shachar R (1967) Breeding and growth of Mugilidae II: feeding experiments under laboratory conditions with *Mugil cephalus*. Bamidgeh 19:50–66 (In Hebrew with English summary)

Midgut

The middle portion of the gut, distinguished as being unprotected by cuticle but lined with a peritrophic membrane. In most insects the midgut is the principal site of digestion and absorption, and the source of digestive (Fig. 50) enzymes. Anatomically, the midgut commences after the proventriculus and terminates at the ileum and juncture of the Malpighian tubules.

► Alimentary System

► Alimentary Canal and Digestion



Midgut, Figure 50 **Generalized insect alimentary system (adapted from Chapman, The insects: structure and function).**

Midgut and Insect Pathogens

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The alimentary canal in insects is the primary location interfacing with their host organisms and other biotic and abiotic factors from the environment. The insect alimentary canal can be divided into three distinct regions, the foregut, midgut and hindgut, based on their embryonic origins, structure and physiological functions. The foregut and hindgut are derived from embryonic ectoderm and are covered by cuticle. The midgut is derived from embryonic mesoderm and does not have the protective cuticle covering. The midgut is the region of the alimentary canal that actively interacts with the gut content from the environment and performs the primary functions of food digestion and subsequent nutrient uptake. In direct contact with the gut contents without protection by cuticle covering, the midgut constantly faces physical, chemical and biological challenges from the environment. It is a primary target and portal of entry for various pathogenic organisms.

Bacterial pathogens primarily target the midgut to gain entry into the hemocoel. Pathogenic bacteria (e.g., *Bacillus thuringiensis* and *B. sphaericus*) commonly produce enzymes or toxins to target and eventually disrupt the midgut epithelium, which enables the bacteria to penetrate through the midgut barrier into the hemocoel for productive infection. The midgut is the primary infection site of the major insect viral pathogens including baculoviruses, cypoviruses and entomopoxviruses. Infection of some viral pathogens in the midgut is limited and the infection in the midgut epithelium is a mode of entry of the viruses into the hemocoel to establish systemic infection (e.g., baculovirus infection and entomopoxvirus infection in lepidopterans). For some viruses, the infection in insects is restricted to the midgut cells (e.g., cypovirus infections in insects). The midgut is not the common portal of entry for fungal pathogens, but fungal infection through the gut may occur in some cases. Protozoan pathogens mostly infect insects through the digestive tract. In addition to microbial pathogens, insect pathogenic nematodes may also enter and penetrate through the midgut as a mode of entry into the hemocoel.

The midgut encounters a variety of microorganisms ingested with dietary materials. In the midgut, insects are equipped with various mechanisms of defense against the pathogens. The midgut peritrophic membrane (PM), alkaline pH in the midgut lumen, digestive enzymes, antimicrobial proteins and other factors contribute to the defense against pathogens. Meanwhile, pathogens have adapted mechanisms to infect insect hosts. The outcomes of midgut-pathogen interactions, which are often multifaceted, critically determine the pathogenesis of the pathogen. The bacterial pathogen *B. thuringiensis* (Bt) produces proteinaceous toxins to target the midgut epithelial cells to break the midgut barrier. The major Bt toxins are known as Cry proteins (crystal proteins) or Cry toxins, which are produced as protoxins in a form of stable crystals in the bacterium. Once ingested by an insect into the midgut, the toxin crystals dissolve in the alkaline pH in the midgut and the dissolved toxin is proteolytically activated by midgut digestive proteinases. The activated Cry toxin then penetrates through the peritrophic membrane and specifically binds to its receptor on the midgut epithelial cells. With involvement of other midgut components, the binding of a Cry toxin to the midgut receptor leads to midgut cell lysis, which enables entry of the bacteria into the hemocoel for infection. The insect pathogenic baculoviruses, cypoviruses and entomopoxviruses are embedded in proteinaceous crystalline inclusions, the viral occlusion bodies, which facilitate survival of the viruses in the environment. In the insect midgut, under the condition of alkaline pH and presence of rich proteinases the occlusion bodies are dissolved and infectious virus particles (virions) are released into the midgut lumen to initiate infection of the midgut cells.

The midgut peritrophic membrane plays an important role in defense against pathogens in general. However, some pathogens have evolved mechanisms to overcome the peritrophic membrane barrier. A unique group of proteases, namely baculovirus enhancins, are produced by some baculoviruses and co-embedded in the viral occlusion bodies. In the midgut, an enhancin is released with the virus particles and specifically degrades the major peritrophic membrane protein, the insect intestinal mucin. The degradation of the intestinal mucin in the peritrophic membrane results in disintegration of the peritrophic membrane structure, leading to permeability of the peritrophic membrane to the virus particles. Similarly, in the infection of malaria parasites in mosquito midgut, the malaria parasite disrupts the peritrophic membrane by secretion of a chitinase to digest the chitin in the peritrophic membrane, enabling the parasite to pass through the peritrophic membrane barrier and reach the midgut cells.

The midgut is in constant contact with various ingested microorganisms, and interactions of the midgut with the microorganisms are complex. The interactions between the midgut and microorganisms critically determine the insect-microbe association to be pathogenic, non-pathogenic or symbiotic.

► Alimentary Canal and Digestion

References

Lehane MJ, Billingsley PF (1996) Biology of the insect midgut. Chapman and Hall, New York, NY, 486 pp

Tanada Y, Kaya H (1993) Insect pathology. Academic Press, San Diego, CA, 666 pp

Wang P, Granados RR (2001) Molecular structure of the peritrophic membrane (PM): identification of potential PM target sites for insect control. Arch Insect Biochem Physiol 47:110–118

Migration

A special form of dispersal in which insects move in a specific direction, and movement is at least partly under the control of the insects, rather than passive (e.g., being blown by wind). Migrants that are arriving are called immigrants, and those that are departing are called emigrants.

Migratory Grasshopper, *Melanoplus sanguinipes* (Fabricius) (Orthoptera: Acrididae)

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This native grasshopper is extremely adaptable, and found throughout most of North America. It is found in every state in the continental United States, and in every province in Canada. It is absent from only the northernmost, coldest regions of

Canada, and from southern Florida and Texas. Its distribution does not extend south into Mexico.

Life History

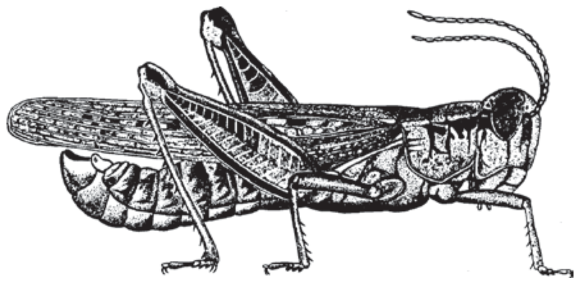
In most areas of its range, migratory grasshopper produces a single generation, and overwinters in the egg stage. However, in southern portions of its range two generations may occur annually. Eggs hatch relatively early, usually beginning in early June but about a week after twostriped grasshopper, *Melanoplus bivittatus* (Say) begins to hatch. Hatching is protracted and may require up to six weeks in an area, resulting in asynchronous development of the population. Early hatching individuals mature early in the summer and have adequate time for reproduction whereas late-hatching individuals are handicapped by the onset of cold weather.

Eggs are yellowish in color, elongate-elliptical and slightly curved in shape. One side is convex and the opposite side concave, causing the eggs to resemble a banana in shape. Eggs measure about 4.5 mm in length and 1.2 mm in width. The eggs are arranged in two columns within a frothy egg pod. Egg pods contain 18–20 eggs per pod, and are buried to a depth of about 35 mm. The pods are curved, about 25 mm in length, and 3–4 mm in diameter. The upper portion contains only froth, allowing ready escape of the nymphs when they hatch. Females can produce 7–10 pods if fed high-quality diets; up to 20 per female is recorded, usually at 2–3 day intervals. Thus, fecundity of about 200 eggs per female is possible. Natural habitats vary greatly in suitability, however, and reproductive potential is sometimes affected. In one study conducted in Montana, for example, females were able to produce only 3–4 egg pods annually. Egg pods are inserted into the soil among the roots of plants. Migratory grasshopper is more likely to deposit pods within crop fields, particularly among wheat stubble, than other common crop-feeding *Melanoplus* spp. Under normal weather conditions about 80% of embryonic development occurs in the autumn before the onset of diapause, with the remainder of development in the spring after a period of cold weather terminates egg diapause.

Nymphs can develop over a range of about 22–27°C, but early instars suffer high mortality at both extremes in temperature. Nymphal development requires about 42, 27, and 23 days when cultured at a constant temperature of 27, 32, and 37°C. Diet also affects development rate. When reared at 30°C, favorable plants such as tansymustard allow complete nymphal development in about 29 days, whereas nymphs developing on less suitable plants such as western wheatgrass require about 42 days. Most field observations suggest that nymphal development requires 35–45 days. Normally there are five instars, though if cultured at low temperatures, six instars is most common.

The nymphs are tan or gray, occasionally greenish, throughout nymphal development. They bear a curved black stripe that extends from behind each eye across the pronotum. The lower edge of the stripe is bordered in white. The outer face of the hind femur is marked with an interrupted black stripe. Body length in instars 1–5 is 4–6, 6–8, 8–11, 11–16, and 16–23 mm, respectively. The number of antennal segments is 12–13, 15–17, 18–20, 21–22, and 22–24 in the corresponding instars.

The adult is a medium-sized species, measuring 20–26 mm in length in males and 20–29 mm in females. They are grayish brown in color, and often tinged with reddish brown. A broad black stripe extends back from the (Fig. 51) eye and about two-thirds of the length of the pronotum. The forewings are grayish brown or brown, usually with a row of brown spots centrally. The hind wings are colorless. The hind femora are not distinctly marked. The hind tibiae are greenish blue or red in color. The cerci of males are broad and flat, turning dorsally at the tip. The subgenital plate is elongate, and bears a notch and groove apically. Females have a preoviposition period of 2–4 weeks. Adults normally



Migratory Grasshopper, *Melanoplus sanguinipes* (Fabricius) (Orthoptera: Acrididae), Figure 51 **Adult male of migratory grasshopper, *Melanoplus sanguinipes* (Fabricius).**

live 60–90 days, though with good food and weather, and living under low density conditions, longevity may be extended considerably. They can mate repeatedly.

Nymphs and adults are affected by daily change in temperature. Activity levels at the soil surface, including feeding, are at their maximum when the air temperature is 18–25°C. This often results in a peak in feeding in late morning, followed by cessation of feeding at mid-day due to excessively hot temperatures, and then perhaps a secondary peak in feeding in the afternoon as temperatures cool. Mass flights by adults take place only if air temperatures are high, often about 29°C, but high densities and light wind also are requisites. When it is hot, grasshoppers tend to climb upward to escape the soil, which is usually considerably warmer than the air temperature. However, they also tend to roost on tall vegetation at night, as this allows them to be warmed by sunlight early in the morning, thus extending their period of activity.

This species accepts a wide range of food plants, and occurs in a wide range of habitats. Relative to the other common crop-feeding *Melanoplus* spp., migratory grasshopper is more tolerant of arid, shortgrass environments. It tends to prefer annual broadleaf plants, but will eat grasses. Dry plant material is an important element of the diet in addition to succulent leaf tissue. Many authors have noted that the population abundance of migratory grasshopper is correlated with the abundance of annual broadleaf plants. Among the preferred plants are dandelion, *Taraxacum officinale*; stinkweed, *Thlaspi arvense*; Johnsongrass, *Sorghum halepense*; Kentucky bluegrass, *Poa pratensis*; shepherdspurse, *Capsella bursa-pastoris*; pepperweed, *Lepidium* spp.; tansymustard, *Descurainia sophia*; western wheatgrass, *Agropyron smithii*; winter mustard, *Sisymbrium irio*; young Russian thistle, *Salsola kali*; and young rabbitbrush, *Chrysothamnus* spp. Among the preferred weeds eaten in North Dakota alfalfa fields are awnless bromegrass, *Bromus inermis*; kochia, *Kochia scoparia*; field sowthistle, *Sonchus arvensis*; field bindweed, *Convolvulus arvensis*; and Russian thistle, *Salsola kali*. On prairie, however, the preferred host plants are Kentucky bluegrass, *Poa pratensis*; leadplant, *Amorpha canescens*; white sage, *Artemisia ludoviciana*; and western ragweed, *Ambrosia psilostachya*.

Migratory grasshopper does not normally infest vegetable crops to a great extent, preferring weedy areas along fences, irrigation ditches, roadsides, and in pastures. However, as favored food plants become over-mature, desiccated, or depleted, grasshoppers will move into vegetable crops. This is especially likely during periods when grasshoppers are extremely abundant. Field crops are more often injured, particularly alfalfa, barley, corn, oat, and wheat. However, as in the case with vegetables, when grasshoppers are numerous they will damage buckwheat, clover, flax, millet, rye, young sorghum, soybean, sugarbeet, timothy, and tobacco. Even fruits such as apple, cherry, currant, grape, peach, plum and strawberry, as well as numerous flowers and shrubs, are attacked during periods of abundance.

Not surprisingly, there is a strong positive relationship between plant preference and grasshopper survival. Among the plants most suitable for nymphal survival were wheat, sunflower, alfalfa, corn and barley, accounting for the reputation of this species as a severe pest in central and western North America. (Alfalfa is an unusual host, however, because although it is quite suitable for large nymphs, it is but a poor source of food for the youngest of the species.) Several broadleaf weeds including dandelion; downy chess, *Bromus tectorum*; tumblemustard, *Sisymbrium altissimum*; slimleaf scurfpea, *Psoralea tenuiflora*; and prickly lettuce, *Lactuca scariola* are quite satisfactory for survival, though not as suitable as the crop plants. Among the least suitable plants are common prairie grasses such as prairie sandgrass, *Triplasis purpurea*; blue grama, *Bouteloua gracilis*; six-weeks fescue, *Festuca octoflora*; needle-and-thread, *Stipa comata*; desert saltgrass, *Distichlis stricta*; green needlegrass, *Stipa viridula*; and Indian ricegrass, *Oryzopsis hymenoides*. Diet also affects fecundity, with favored food such as dandelion resulting in production of a mean value of 3.5 egg pods per female during a 3-week period, whereas grasshoppers fed a mixture of prairie grasses produce only 0.3 pods per female.

Many insects parasitize or eat *Melanoplus* grasshoppers. The most important parasitoids are nymph- and adult-attacking flies (Diptera) in the families Anthomyiidae, Nemestrinidae, Sarcophagidae, and Tachinidae, though egg parasitoids (Hymenoptera: Scelionidae) also cause mortality in grasshopper populations. In Oregon, over 70% of migratory grasshoppers were parasitized by the nemestrinid *Neorhynchocephalus sackenii* (Williston), resulting in reduced longevity and reproduction. Other *Melanoplus* spp. also are affected by this fly, though grasshopper populations on rangeland, not cropland, are usually affected. In a study of migratory grasshopper parasitism conducted in Ontario, the incidence of parasitism reached about 7% by the end of September, with *Blaesoxipha hunteri* (Hough) and *B. atlantis* (Aldrich) (both Diptera: Sarcophagidae) the most effective parasitoids. In Montana, parasitism of migratory grasshopper parasitism was estimated to 15–41%, with anthomyids and sarcophagids accounting for 50 and 35% of the parasitism, respectively.

Among the most important predators are sphecid wasps (Hymenoptera: Sphecidae). Adult sphecids capture and paralyze nymphal and adult grasshoppers, bury them within cells in the soil, and deposit an egg on the surface of the grasshopper. Upon hatching, the larva devours the paralyzed grasshopper. Predatory beetles (Coleoptera) attack the egg, nymphal and adult stages of grasshoppers, and include ground beetles (Carabidae), tiger beetles (Cicindelidae), soldier beetles (Cantharidae), and blister beetles (Meloidae). Blister beetles are most important, though because the grasshopper egg pod is the stage destroyed, their effect is often not appreciated. Several studies conducted during the period 1938–1940 produced an average of 8.8% of egg pods destroyed by blister beetles. Flies also are important predators, particularly robber flies (Asilidae) and bee flies (Bombyliidae). Robber fly larvae and *Gryllus* spp. field crickets (Orthoptera: Gryllidae) occasionally attack egg pods, and robber fly adults routinely attack nymphs and adults of grasshoppers, though other insects also are taken. Robber flies undoubtedly are important predators under rangeland conditions, but predation rates of grasshoppers in cropping systems has not been determined. Also, the propensity of robber flies to capture other predators, such as sarcophagids, significantly reduces their value. Bee fly larvae are predatory on grasshopper eggs and on other insects. In western studies, an average of 6.2% of egg pods were destroyed by bee fly larvae.

Birds are known to be important predators of grasshoppers. They are among the most important sources of food for many avian species due to their large size and abundance. The great abundance of grasshoppers in the spring coincides with the period when most birds are nesting. Birds forage freely on grasshoppers in open areas such as grasslands, with some species consuming 65–150 grasshoppers per day. Although avian predators significantly reduce the abundance of grasshoppers in grasslands, it is less certain that they forage freely in crops.

Microbial pathogens can be quite important mortality agents, especially when weather conditions are suboptimal for grasshoppers, or when grasshoppers are very abundant. The principal microbial pathogens of grasshoppers are fungi, viruses, protozoans, and nematodes and nematomorphs.

The fungus *Entomophthora grylli* causes "summit disease," a behavior wherein grasshoppers ascend vegetation, cling to the uppermost point, and perish. In some areas, particularly near bodies of water, large numbers of dead grasshoppers can be found attached to plants. *Melanoplus* spp. are susceptible to one pathotype of the fungus, and significant grasshopper population decreases have been linked to the incidence of summit disease. Infection normally occurs when nymphs contact spores that are sheltered in the soil. Spores produced in grasshoppers dying from this disease remain in cadavers or soil for protracted periods of time. Attempts to manipulate this pathogen have met with mixed results. This is the only common naturally occurring fungus of grasshoppers.

Several viruses called entomopoxviruses affect grasshoppers. One such virus, *Melanoplus sanguinipes* entomopoxvirus, affects the crop-feeding *Melanoplus* spp. and American grasshopper, *Schistocerca americana* (Drury). The virus disease spreads naturally by cadaver feeding. Infected grasshoppers are pale colored and lethargic, have prolonged developmental periods, and often perish. These diseases are quite rare in the field.

Several types of protozoa are associated with grasshoppers, including amoebae, eugregarines, and neogregarines, but the most important are microsporidia. Species of *Nosema* are most common, and *Nosema locustae* has been developed as a microbial insecticide. *Nosema* spp. affect feeding, development, reproduction and survival, and are transmitted by ingestion. However, they infrequently appear at high levels in natural populations.

Nematodes are important mortality factors of grasshoppers in South America, New Zealand and Australia, but in North America only *Mermis nigrescens*, *Agamermis decaudata*, and *Hexamermis* spp. affect grasshoppers. *Mermis nigrescens* is most important, and is unique in that nematodes crawl from the soil onto vegetation to deposit desiccation-resistant eggs. The eggs hatch when consumed by grasshoppers, and the resulting larvae kill the grasshoppers, return to the soil, and continue the life cycle. These nematodes apparently do not thrive in arid areas, as the adults only emerge during wet periods, and are more common in irrigated croplands than dry rangeland. Sometimes they parasitize up to 70% of grasshoppers in an area. Nematomorphs, commonly called horsehair worms, resemble nematodes but tend to be much longer. They are rare, possibly because part of their life cycle must occur in water, but they attract considerable attention because of their large size.

Migratory grasshopper is greatly influenced by weather. Through most of its range longevity and reproduction are limited by shortage of warm weather. Thus, abnormally warm and dry periods of about 3 years stimulate increase in grasshopper abundance. Warm weather during spring and autumn is particularly important. Cool and cloudy weather in the spring inhibits feeding by young nymphs, and results in high mortality. Also, adults have the potential to be long-lived and highly fecund, but their reproductive effort is normally terminated prematurely by the onset of cold weather. When summers are hot or prolonged, development proceeds faster or longer, resulting in greater egg production. In southern areas grasshoppers are less limited by shortage of warm weather, but more affected by shortages of food. Therefore, occurrence of precipitation early in the season to provide luxurious foliage, especially broadleaf weed vegetation, is an important prerequisite for population increase.

Damage

Migratory grasshopper is a defoliator, often completely removing leafy vegetation and leaving only stem tissue. Sometimes other tissue is eaten; heads of wheat may be clipped, for example. Migratory grasshopper thrives on rangeland that has a high density of broadleaf weeds, so it sometimes moves from grazing land to nearby irrigated crops. In this behavior it differs from some other species, particularly differential grasshopper, *Melanoplus differentialis* (Thomas), and twostriped grasshopper, *M. bivittatus* (Say), which favor the taller undisturbed vegetation usually associated with fences and irrigation ditches, and usually do not develop high numbers on grazing land. Migratory grasshopper is often quite dispersive, and of course this behavior is the basis for the common name. When the grasshoppers are developing at high densities, the weather is abnormally warm, and a light wind is present, swarms of grasshoppers may disperse tens or even hundreds of kilometers and descend without warning to cause immense damage. With the availability of modern insecticides and aircraft for application, such potential disasters can be dealt with quickly and efficiently. When such insecticide and effective application technologies are not available, or where environmentally sensitive land or crops are concerned, grasshopper swarms can be disastrous. This species is the most important grasshopper pest in western North America.

Management

Grasshopper populations are usually assessed by visual observation. A sweepnet is a useful tool to aid in collection, and its use a prerequisite to identification of the species complex. It is important to determine if grasshoppers collected from noncrop areas are crop-feeding species because there are many nonpest grasshoppers that restrict their feeding to grasses or weeds. It is advisable to monitor nearby uncultivated land, particularly weedy areas, in addition to crop plants, due to the tendency of the pest species to invade crops later in the season.

Liquid formulations of insecticides are commonly applied to foliage to protect against damage. Because grasshoppers rarely develop in crops, but instead invade from weedy areas, it is often the edges of crop fields that are most injured. Therefore, application of insecticide to the borders of crop fields is often adequate to protect an entire field. It is even better to apply insecticides to the developing grasshopper populations in weedy areas before they move to crops. This not only minimizes damage to crop plants, but often results in younger grasshoppers being targeted for elimination. Younger grasshoppers are more susceptible to insecticides, with large nymphs and adults sometimes difficult to kill.

Application of insecticide-treated bait is an effective alternative to foliar treatments for *Melanoplus* spp. because these grasshoppers spend considerable time on the soil where they come into contact with baits. Bait formulations are bulky and more difficult to apply than liquid products, so they are less often used, but have the advantage of limiting exposure of crops to insecticide residue and of minimizing mortality of beneficial insects such as predators and parasitoids due to insecticide exposure. Also, the total amount of insecticide active ingredient necessary to obtain control is usually considerably less when applied by bait because the grasshoppers actively seek out and ingest the toxin. Finally, for relatively expensive products that must be ingested to be effective, such as microbial insecticides, baits are the most effective delivery system.

The attractant used most commonly for grasshopper bait is flaky wheat bran, though other products such as rolled oats are sometimes suggested. No additives, other than insecticide (usually 5% active ingredient), are necessary because the wheat bran alone is quite attractive to *Melanoplus* grasshoppers. Other additives such as sawdust, water, vegetable or mineral oil, molasses, amyl acetate, salt, or sugar have been suggested, but provide little or no additional benefit over dry bran. The bait should be broadcast widely to maximize the likelihood of grasshopper contact, and should be applied while grasshoppers are in the late instars because adults ingest less bait.

Elimination of weeds within, and adjacent to, crops is the most important cultural practice, and can have material benefit in preventing damage to crop borders. However, during periods of weather when grasshoppers become numerous they may move long distances and invade crops.

Tillage is an effective practice for destruction of eggs, particularly in migratory grasshopper which is especially likely to deposit eggs among crop plants. Deep tillage and burial are required, shallow tillage having little effect. All the crop-feeding *Melanoplus* species deposit some eggs in crop fields, especially during periods of abundance, but it is fence row, irrigation ditch, field edge, and roadside areas that tend to be the favorite oviposition sites, so tillage is not entirely satisfactory unless other steps are taken to eliminate grasshopper egg pods from these areas that cannot be tilled. Though providing suppressive effects, deep tillage is not consistent with the soil and water management practices in many areas, so may not be a good option.

Row covers, netting, and similar physical barriers can provide protection against grasshoppers. This approach obviously is limited to small plantings, and can interfere with pollination. Also, grasshoppers are capable of chewing through all except metal screening, so this approach does not guarantee complete protection.

The opportunities for biological control are limited. Historically, poultry were found to consume large numbers of grasshoppers and could provide considerable relief if the grasshopper-infested garden was small or moderate in size and the birds were plentiful. This remains a viable option for some people, and turkeys are usually considered most suitable among poultry. The birds may also inflict some direct damage to plants, however, so introduction of poultry is probably most viable when grasshoppers are plentiful and threatening.

The microsporidian pathogen *Nosema locustae* is well studied as a microbial control agent of *Melanoplus* spp. and is available commercially. It is fairly stable, and easily disseminated to grasshoppers on bait. However, its usefulness is severely limited by the long period of time that is required to induce mortality and reduction in feeding and fecundity. Also, the level of mortality induced by consumption of *Nosema* is quite low, often imperceptible. It is best used over very large areas, not just on individual farms, and should be applied at least one year in advance of the development of potentially damaging populations.

Fungi have also been investigated for grasshopper suppression. A grasshopper strain of *Beauveria bassiana* has been effective in some trials, and *Metarhizium anisopliae* var. *acridum* has worked well for grasshopper and locust suppression in Africa and Australia, so it may prove useful for *Melanoplus* spp. Behavioral thermoregulation by grasshoppers, wherein they bask in the sun and raise their body temperatures, is potentially a limiting factor for use of fungi. Basking grasshoppers easily attain temperatures in excess of 35°C; such high temperatures decrease or even prevent disease development in infected grasshoppers. Inconsistent quality control in production of fungi also limits use of these organisms for grasshopper control.

► Grasshopper Pests in North America
► Grasshoppers and Locusts as Agricultural Pests
► Grasshoppers, Katydids and Crickets

References

Capinera JL, Scott RD, Walker TJ (2004) Field guide to the grasshoppers, katydids, and crickets of the United States. Cornell University Press, Ithaca, NY, 249 pp

Parker JR, Newton RC, Shotwell RL (1955) Observations on mass flights and other activities of the migratory grasshopper. USDA Tech Bull 1109, 46 pp

Parker JR (1930) Some effects of temperature and moisture upon *Melanoplus mexicanus* Saussure and *Camnula pellucida* Scudder (Orthoptera). Mont AES Bull 223, 132 pp

Pfadt RE (1949) Food plants as factors in the ecology of the lesser migratory grasshopper, *Melanoplus mexicanus* (Sauss.). Wyoming Agri Exp Stat Bull 290, 51 pp

Pfadt RE (2002) Field guide to common western grasshoppers. Wyoming Agri Exp Stat Bull 912, 288 pp

Shotwell RL (1930) A study of the lesser migratory grasshopper. USDA Tech Bull 190, 34 pp

Milichiid Flies

Members of the family Milichiidae (order Diptera).

► Flies

Milichiidae

A family of flies (order Diptera). They commonly are known as milichiid flies.

► Flies

Milk Gland

Some female flies that give birth to well-developed larvae rather than eggs secrete nourishment for their offspring prior to deposition from a gland called a milk gland. Viviparous insects display such glands, producing little or no yolk, and no chorion. Such insects typically produce few offspring, but the survival rate of progeny is high.

Milkweed Butterflies

Members of the family Nymphalidae, subfamily Danainae (order Lepidoptera).

► Brush-Footed Butterflies

► Butterflies and Moths

Milky Disease of Scarabs

Multiplication of bacteria in scarab beetle larvae, causing turbidity of the hemolymph and a white color in the posterior region of the body. The bacteria usually associated with this disease are *Paenibacillus* (formerly *Bacillus*) *popilliae* and *Paenibacillus lentimorbis*.

► *Paenibacillus*

Miller, David

GEORGE HANGAY
Narrabeen, NSW, Australia

David Miller was born in 1890 in Glasgow and was educated in Edinburgh, Dunedin and Wellington, New Zealand. He had a keen interest in entomology from an early age. From 1916 he was Government Entomologist and in 1926 he joined the Cawthron Institute as Chief Entomologist in Nelson. While holding this position, in 1929 he also became the Director of the Forest Biological Research Station. He held this post until 1932, when he was appointed Assistant Director of the Cawthron Institute. He remained in this position until 1956; however, from 1937 until 1956 he was also the Director of the Entomological Research Station, when he became the Director of the Cawthron Institute. Dr. David Miller was a very active, productive entomologist, who left a great body of work behind. He published many scientific papers, monographs and books. One of his most read works is "Common Ins ects in New Zealand" (1971). He was a leading figure in New Zealand entomology, holding two or more important positions simultaneously in scientific institutions during most of his working life. He passed away in Nelson in 1973 at the age of 83.

Reference

Miller D (1971) Common insects of New Zealand. A.H. and A.W. Reed Ltd., Wellington

Miller Moths

Members of the family Noctuidae (order Lepidoptera).

► Owlet Moths

► Butterflies and Moths

Millipedes (Class Diplopoda)

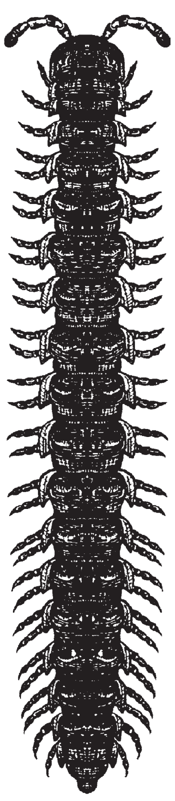
Though the name "millipede" suggests that these animals have 1,000 legs, and although the presence of numerous legs is a characteristic of this group, none have more than 375 pairs, and most have considerably fewer. In differentiating this group from the similar-appearing centipedes and symphylans, the presence of two pairs of legs per body segment is the key character used to identify millipedes.

Classification

The Class Diplopoda is one of six classes in the Subphylum Atelocerata of the Phylum Arthropoda. The other classes in the subphylum are Chilopoda, the centipedes; Pauropoda, the pauropods; Symphyla, the symphylans; Entognatha, the collembolans, proturans, and diplurans; and Insecta, the insects. There are several orders of diplopods, and several arrangements of the taxa have been proposed. These are fairly common arthropods, and as they occasionally are numerous or damaging, they sometimes are confused with insects. More commonly they are confused with centipedes.

Phylum: Arthropoda
- Subphylum: Atelocerata
  - Class: Diplopoda
    - Subclass: Pselophognatha
    - Order: Polyxenida – bristly millipedes
    - Subclass: Chilognatha
    - Order: Glomeridesmida
    - Order: Sphaerotheriida – giant pill millipedes
    - Order: Glomerida – pill millipedes
    - Order: Siphoniulida
    - Order: Platydesmida
    - Order: Siphonophorida
    - Order: Polyzoniida
    - Order: Stemmiulida
    - Order: Callipodida
    - Order: Cordeumatida
    - Order: Julida
    - Order: Spirobolida
    - Order: Spirostreptida
    - Order: Polydesmida – flat-backed millipedes

Millipedes are quite diverse morphologically, though they all consist of a long chain of rather uniform body segments, and lack wings (Fig. 52). Some are rather short, and may be covered with feather or scale-like adornment. Others look greatly like woodlice (pillbugs and sowbugs), and even roll into a ball in the manner of pillbugs. Most, however, are elongate and thin in general body form. There are three basic body regions: the head, which bears a pair of moderately long antennae; the body, consisting of numerous leg-bearing segments, and which normally are rather cylindrical but sometimes bears prominent lateral projections; and the telson, or posterior body segments bearing the anus. The integument is very hard.



Millipedes (Class Diplopoda), Figure 52 Garden millipede, *Oxidus gracilis*.

Life History

Millipedes are poorly known animals, with almost all our information based on studies in northern Europe. The life cycle of millipedes is often long. Many live for a year, but some persist for 2–4 years before attaining maturity. In a *Julus* sp. studied in a temperate environment, oviposition took place in April, with instar 6 to 7 was attained by winter and instars 8 to 9 by the second winter. They overwintered as instars 9–11, then mated and oviposited the following spring, their third year of life, before they perished. Following is a description that is based on the life cycle of a common millipede, *Oxidus gracilis* Koch, a species with a 1-year development time.

Oxidus gracilis is somewhat flattened dorsoventrally, and bears 30 or 31 pairs of legs in males and females, respectively. They generally measure 18.5–22.2 mm in length and 2.0–2.5 mm in width. Initially they are light brown in color but gradually attain a dark brown coloration, and sometimes are bordered with yellow. Adults seem to live for about two months in the spring or summer, and like all millipedes, are intolerant of dry conditions. *Oxidus gracilis* is nocturnal.

The creamy white, yellow or brownish eggs of *Oxidus gracilis* are deposited in the soil, usually in clusters. A glutinous material causes them to adhere to one another. The eggs are nearly spherical in shape, measuring 0.35–0.4 mm in width and about 0.40 mm in length. The female may create a chamber or cell for her eggs. She deposits 50–300 eggs in a cluster, and eggs can be found throughout the summer months. Duration of the egg stage is 9–10 days.

The first instar juvenile millipedes bear only a few segments and three pairs of legs, but body segments, legs, and ocelli are added with each molt. By counting the number of rows of ocelli and adding one, the instar can be estimated for many millipedes. Thus, fourth instar millipedes have three rows of ocelli, fifth instars have four rows, etc. Maturity is often attained after about 10 instars, but some species continue to molt as adults.

In *Oxidus gracilis*, most individuals develop through eight instars before they attain the adult stage. The number of pairs of legs present in the juveniles is about 3, 6, 11, 16, 22, 26, 28, and 30 for instars 1 to 8, respectively. Body length is about 0.5, 1.5, 3.6, 4.1, 4.8, 7.4, 12.4, and 20 mm during the corresponding instars. Development time is 1, 11–18, 13–18, 16–30, 20–38, 28–46, 42–60, during instars 1 to 7, with the final (eighth) instar generally overwintering, though in some cases instar seven overwinters.

Adult millipedes vary considerably in size, often measuring from 10–30 mm in length, but in some species exceeding 100 mm. Their color ranges from whitish to brown and black. The sexes are separate. The external genitalia of adult millipedes are located between the second and third pairs of legs. Some adult millipedes have the ability to molt from a sexually active adult to an intermediate stage that is not functional sexually. Parthenogenesis occurs in some species and some populations, but this is not usual. Millipedes lack a waxy cuticle and are susceptible to desiccation. They have glands, with openings usually located laterally, which secrete chemicals that are toxic and may immobilize predatory arthropods such as spiders and ants.

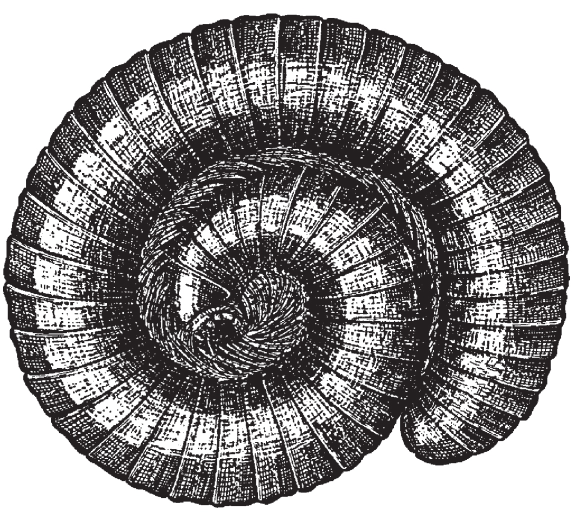
Ecology

Millipedes normally eat dead plant material, usually in the form of leaf litter. However, they occasionally graze on roots and shoots of seedlings, algae, and dead arthropods and molluscs. They are selective in their consumption of leaf litter, preferring some leaves over others. They also tend to wait until leaves have aged, and are partially degraded by bacteria and fungi. Thus, they function principally as decomposers, hastening the break-up of leaf material into smaller pieces, and incorporating the organic matter into the soil. Whether they derive most of their nutritional requirements from the organic substrate or the microorganisms developing on the substrate is uncertain. Millipedes also tend to consume their own feces, and many species fare poorly if deprived of this food source.

Millipedes sometimes are viewed as a severe nuisance as a result of exceptional abundance in an inappropriate location such as in yards, homes, or commercial or food processing facilities. Millipedes can exist in tremendous quantities in the soil and become a problem only when they come to the surface and disperse as a group. This often occurs following abnormally large rainfall events, though hot and dry conditions also are sometimes suspected to be a stimulus for dispersal.

Several species of millipedes are reported to be injurious to plants, or present in high enough numbers to be considered a nuisance. Probably the most important is garden millipede, *Oxidus gracilis* Koch (Diplopoda: Paradoxosomatidae). It apparently was accidentally introduced to most temperate areas of the world from the tropics, probably via transport of specimen plants. In cool areas it is principally a greenhouse pest.

Millipedes produce various foul-smelling fluids (sometimes including hydrogen cyanide) from openings along the sides of their body. Despite the formidable chemical defenses of millipedes (Fig. 53), several natural enemies are known. Small vertebrate predators such as shrews, frogs, and lizards eat millipedes. Invertebrate predators such as scorpions (Arachnida), ground beetles (Coleoptera: Carabidae), and rove beetles (Coleoptera: Staphylinidae) also consume millipedes, though ants are usually deterred. Various disease-causing agents such as fungi, iridoviruses, rickettsia, and protozoa are documented from millipedes, though they seem to be only sporadically effective. Parasitic flies have been reared from millipedes in Europe.



Millipedes (Class Diplopoda), Figure 53 A millipede in a coiled position, a common defensive behavior.

References

Enghoff H (1984) Phylogeny of millipedes–a cladistic analysis. Zeitschrift für Zoologische Systematik und Evolutionsforschung 22:8–16

Hopkin SP, Read HJ (1992) The biology of millipedes. Oxford University Press, Oxford, UK

Kime RD, Golovatch SI (2000) Trends in the ecological strategies and evolution of millipedes (Diplopoda). Biol J Linn Soc 69:333–349

Mimallonidae

A family of moths (order Lepidoptera). They commonly are known as sackbearer moths.

► Sackbearer Moths
► Butterflies and Moths

Mimicry

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Mimicry, broadly defined, is the superficial resemblance of one organism to another organism, usually providing a selective advantage to the mimicker. The term mimicry is used occasionally to describe organisms that mimic inanimate objects in their environment (such as young swallowtail larvae resembling bird droppings and grasshoppers or katydids resembling leaves). However, this phenomenon is also variously labeled as crypsis, camouflage, mimesis or special resemblance, and will not be discussed under the term mimicry.

Many insect species have evolved to mimic other species of insects, and even other groups of organisms, for a variety of reasons. Likewise, some non-insect organisms have evolved to mimic specific insects. The most common type of mimicry is visual, where mimics and their models look very similar to each other. The perceived commonness of this type of mimicry may be elevated somewhat by the visual emphasis of humans, the studiers and cataloguers of nature. However, visual resemblance also can be enhanced by acoustic, olfactory, tactile and behavioral mimicry. The mimicry can be so close that even seasoned entomologists are fooled at first glance.

In the majority of cases, mimicry has evolved in the mimicking species to reduce the likelihood of suffering predation (as is the case in Batesian and Müllerian mimicry). Species that mimic a toxic or unpalatable species experience less predation than those that do not. In many cases, but not all, the toxic or unpalatable species and their mimics have aposematic, or warning, coloration. Aposematic coloration is striking, usually black next to red, yellow or orange, and serves to enhance the learning of distastefulness by predators. Batesian and Müllerian mimicry are effective against predators that are capable of learning and that have good color vision (if the insect is aposematic). Birds, and to a lesser extent, amphibians and lizards, seem to have been the driving force for the evolution of mimicry in insects. The model usually has a true toxin in its body that could kill a predator if the model were consumed in its entirety. However, the model also often contains emetic and bitter chemicals (or the toxin itself may have emetic and bitter properties). Thus, the predator lives another day and associates the regurgitation of the prey item and its bitter taste with a particular morphology or pattern.

In a few cases, insects and other organisms have evolved mimicry so that they become more effective predators (aggressive mimicry) or are better adapted as social inquilines, living in the nests of their host ants (Wasmannian mimicry). In these types of mimicry, the mimics and their models are rarely aposematic.

Batesian Mimicry

This form of mimicry was described in 1862 by Henry W. Bates, an English naturalist studying butterflies in Amazonia, and was later named after him. He noticed remarkable resemblances between palatable pierid butterflies (related to cabbage white butterflies) and unpalatable Ithomiinae butterflies (related to monarch butterflies). The larval host plant of the Ithomiinae butterflies renders them toxic to predators, whereas the diet of the pierid larvae gives them no such protection against predators. He suggested that natural selection had caused the appearance of the palatable pierids to move toward that of the unpalatable Ithomiinae butterflies.

Batesian mimicry, then, is the result of evolutionary convergence in shape, patterning, color, behavior, or smell of an edible mimic toward close resemblance of a less palatable and distantly related model. The predator, after trying to eat a few of the toxic models, learns that an insect with this particular shape, color or smell is toxic and therefore unpalatable. The mimic takes advantage of this predator learning and, in fact, is a parasite on the model species. The model suffers greater predation when it is sympatric with a mimic (sharing the same range) than when it is alone because the encounter of predators with palatable mimics delays the learning process. The predator is also harmed in this system because it learns to avoid a profitable prey item, the mimetic species.

Batesian mimics must evolve very close resemblance to their models so that predators cannot distinguish them. If the mimics become too abundant in the habitat relative to their models, predators may never learn to associate their appearance with distastefulness; thus, both model and mimic suffer increased predation. The models cannot evolve to look too different from their original morphology or they will experience more predation. So, in these situations, it is the mimic that evolves to resemble other toxic model species in the area. The evolution of polymorphisms (many morphs or appearances) is common in Batesian mimics. As one morph becomes too common in a population relative to its model, it is selected against, and other morphs within the population increase in abundance. An extreme example of polymorphism in a Batesian mimic occurs in the African swallowtail species, *Papilio dardanus*. There are thought to be 31 morphs of this species, mimicking several species of danaid butterflies in the genera *Danaus* and *Amauris* throughout their ranges in central and southeastern Africa. The models feed on toxic milkweeds while the mimics are innocuous to predators. Curiously, the males of all *P. dardanus* morphs resemble a typical yellow and black swallowtail and only the females are mimetic.

Batesian mimicry has been studied best among species of butterflies but it is also common in arthropods that mimic bees, wasps or ants – insects that are all equipped with predator-deterring stings. For example, in Honduras, the ant *Camponotus planatus* is mimicked by four species of arthropod: a clubionid spider, a salticid spider, a mirid bug (*Barbariella* sp.), and a praying mantid (*Mantoida maya*). Interestingly, the mimetic mantid nymph resembles the ant model only in the earliest instars when it measures 3–9 mm. When the mantid nymph grows longer than 9 mm, and can no longer pass for an ant, its morphology and color change to mimic a species of vespid wasp common in the area.

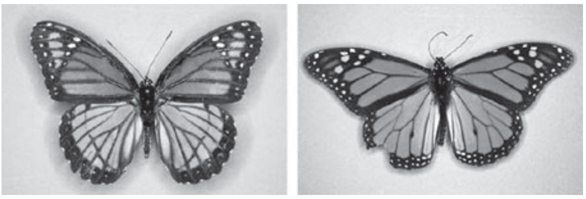
Most examples of Batesian mimicry involve only visual resemblance between models and mimics. However, some insects mimic the sound of their model, in addition to their appearance. For example, a syrphid fly that visually mimics a yellow jacket wasp, also mimics it acoustically, having a wing beat frequency of 147 Hz, which is very similar to the 150 Hz frequency of the wasp. The stridulations of a *Necrophorus* burying beetle that mimics a bumblebee visually have the same frequency as the wing beat of the bumblebee.

Müllerian Mimicry

Henry W. Bates and Fritz Müller, a German naturalist, first noted examples of this type of mimicry in the Neotropics. They wrote independently that many species of unpalatable butterflies resembled each other. In 1879, Müller published a mathematical model that showed that pairs of unpalatable species mutually benefit from resembling each other. Müllerian mimicry, later named for him, is the result of evolutionary convergence in shape, patterning, and color of two, or more, distantly related unpalatable species (Fig. 54). In this type of mimicry, all species benefit from the mimicry because predators need only learn a single appearance and there is less total death among the co-mimetic species than if the predators needed to learn two different patterns. Predators also benefit because they can quickly learn to sight reject unpalatable prey, and avoid wasting time on them.

Müllerian mimicry is common in the tropics of South America. One large mimicry "ring" involves two species of *Heliconius* butterflies and several other more distantly related butterflies and even a day-flying moth. All are toxic due chemicals sequestered from their larval host plants and all resemble each other visually.

The classic example of Müllerian mimicry known from the temperate world is that of the monarch butterfly, *Danaus plexippus*, and the viceroy, *Limnetis archippus*. In this example, adults of the viceroy butterfly are presumed to be palatable mimics of adults of the toxic monarch butterfly whose larvae feed on milkweeds and sequester heart poisons (cardiac glycosides).



Mimicry, Figure 54 The viceroy butterflies (*Limenitis archippus*, left) was long thought to be a palatable Batesian mimic of the toxic monarch butterfly (*Danaus plexippus*, right). Research has indicated that, at least in Florida, the viceroy and the monarch are both unpalatable and are Müllerian co-mimics.

Cardiac glycosides protect monarch butterflies from bird predation. However, this example had to be revised after the 1991 publication of a paper by David Ritland who was a student of Lincoln Brower, one of the pioneers of the study of chemical defense in the monarch butterfly.

Pre-1991, the viceroy butterfly in Florida, whose larvae feed on willow, poplar and other trees, was considered to be a Batesian mimic of the monarch butterfly and the Florida Queen butterfly, *Danaus gilippus berenice*, whose larvae can feed on toxic cardiac glycoside-containing host plants. However, Ritland and Brower found that the viceroy was just as unpalatable to bird predators as was the monarch butterfly. Furthermore, the viceroy was considerably less palatable than the Florida Queen if the larvae of the Queen fed on a host plant that was low in cardiac glycosides. Thus, in this study, the monarch and the viceroy butterflies were actually Müllerian co-mimics and the Florida Queen butterfly was a Batesian mimic of the viceroy and the monarch. Thus, the type of mimicry cannot be ascertained unless the palatability of the species involved is known.

A further issue that complicates our understanding of mimicry complexes is that of automimicry. Researchers have found that the unpalatability of the monarch butterfly varies across a spectrum depending on the larval diet. If a larva feeds on a host plant species with low concentrations of cardiac glycosides, it will develop into an adult that is nontoxic and palatable to bird predators. If a larva feeds on a plant species with high concentration of cardiac glycosides, the butterfly will be toxic and unpalatable. Thus, monarch butterflies with low concentrations of cardiac glycosides are Batesian mimics of monarchs with high concentrations of cardiac glycosides (i.e., automimicry).

Aggressive Mimicry

Aggressive mimicry occurs when one species mimics something that a second species considers desirable. The second species is attracted to the mimic and usually ends up being eaten by the mimic; thus, the mimicry is aggressive in nature. A classic example of behavioral aggressive mimicry occurs in fireflies. It has long been known that male and female fireflies communicate visually by flashing their light organs in a species-specific pattern. Adult female fireflies, usually stationary, flash in response to the flash pattern of flying males. The male locates the female by her flashing and copulation ensues. However, several firefly species in the genus *Photuris* are aggressive mimics of *Photinus* species. The female *Photuris* flashes the female *Photinus*-specific pattern in response to the signaling of the male *Photinus*. The male *Photinus* is lured to the female *Photuris*, expecting a female of his own species, and is then eaten. JE Lloyd has termed these deceptive *Photuris* females "femmes fatales."

An example of aggressive chemical mimicry involves several species of bolas spiders in the genus *Mastophora*. The females in this genus do not spin a web but rather swing a silk thread with a droplet of sticky material at its end (the bolas) at passing insects. The majority of the insects that are caught on the bolas are male moths of a select few species. Chemists determined that the female spiders synthesize the sex attractant pheromone of the females of the moth species that is their predominant prey. Male moths are lured to what they perceive as a virgin female but instead are caught and eaten by the spider.

Wasmannian Mimicry

A final, and very specialized, form of mimicry is Wasmannian mimicry, which occurs in some organisms that live in the nests of ants. E. Wasmann first described this phenomenon in museum specimens of staphylinid beetles. Many species in several genera of staphylinid beetles (e.g., *Wasmannia*, *Myrmeciton*, and *Ecitosius*) live in ant nests and closely resemble ants, having a petiole-like restriction in the abdomen, and an overall slender and dark body. In addition to looking like ants, they produce appeasement substances from glands that calm the ants and allow for their entry into the nests. Wasmann originally thought that the morphology of the staphylinid's body tactilely mimicked the ant's own body and fooled the ant into tolerating its presence. However, because ants rely primarily on chemicals for intraspecific communication, this hypothesis seems less reasonable. It may be that staphylinids that forage outside the nest with their ant hosts may gain protection from potential predators by mimicking the sting-equipped ants.

► Crypsis
► Aposematism
► Myrmecomorphy
► Myrmecophiles

References

Huheey JE (1984) Warning coloration and mimicry. In: Bell WJ, Cardé RT (eds) Chemical ecology of insects. Sinauer Associates, Inc., Sunderland, MA, pp 257–297

Mallet J, Joron M (1999) Evolution of diversity in warning color and mimicry: polymorphisms, shifting balance and speciation. Annu Rev Ecol Syst 30:201–233

Ritland DB (1991) Revising a classic butterfly mimicry scenario: demonstration of Müllerian mimicry between Florida viceroys (*Limenitis archippus floridensis*) and queens (*Danaus gilippus berenice*). Evolution 45:918–934

Sheppard PM (1962) Some aspects of the geography, genetics, and taxonomy of a butterfly. In: Nichols D (ed) Taxonomy and geography. Systematics Association Publication No. 4, Systematics Association, London, UK, pp 135–152

Wickler W (1968) Mimicry in plants and animals. McGraw-Hill, New York, NY, 253 p

Mineral Oil

Horticultural oil that is derived from petroleum.

► Horticultural Oil

Miniature Ghost Moths (Lepidoptera: Palaeosetidae)

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Miniature ghost moths, family Palaeosetidae, are a small family related to Hepialidae, comprising eight species worldwide (five in Assam, Thailand and Taiwan, two in Australia, and one in Colombia). The family is in the superfamily Hepialoidea, in the infraorder Exoporia. Adults are small (12–18mm wingspan), with head roughened; haustellum absent (with no mandibles); labial palpi short and 2 to 3-segmented; axillary palpi absent; antennae are relatively short. Maculation can be rather sparkling, with metallic-iridescent markings on the forewings on a brown or blue base color. Adults are crepuscular or active during the day in dark forested areas, typically near wet moss-covered rock faces. Adults often rest head down under leaves in moist, shaded forest areas near water courses. Biologies remain unknown but larvae of a species from Taiwan have been described and are thought to feed on mosses.

References

Davis DR, Karsholt O, Kristensen NP, Nielsen ES (1995) Revision of the genus *Ogygioses* (Palaeosetidae). Invertebr Taxonomy 9:1231–1263

Heppner JB, Balcázar MA, Wang HY (1995) Larval morphology of *Ogygioses caliginosa* from Taiwan (Lepidopera: Palaeosetidae). Trop Lepidop 6:149–154

Kristensen NP, Kristensen NP (ed) (1999) Lepidoptera, moths and butterflies, vol 1: Evolution, systematics, and biogeography. In Handbuch der Zoologie. Band IV. Arthropoda: Insecta. Teilband. W De Gruyter, Berlin, 35:51–63

Minima

Among ants, a minor worker.

Minor Workers

Among ants, the smallest subcaste of workers (contrast with major and media workers).

► Ants

Minute Bark Beetles

Members of the family Cerylonidae (order Coleoptera).

► Beetles

Minute Black Scavenger Flies

Members of the family Scatopsidae (order Diptera).

► Flies

Minute Bog Beetles

Members of the family Microsporidae (order Coleoptera).

► Beetles

Minute Brown Scavenger Beetles

Members of the family Lathridiidae (order Coleoptera).

► Beetles

Minute Fungus Beetles

Members of the family Corylophidae (order Coleoptera).

► Beetles

Minute Marsh-Loving Beetles

Members of the family Limnichidae (order Coleoptera).

► Beetles

Minute Moss Beetles

Members of the family Hydraenidae (order Coleoptera).

► Beetles

Minute Pirate Bugs (Hemiptera: Anthocoridae)

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Insects in the family Anthocoridae are referred to as minute pirate bugs or flower bugs. Pirate bugs occur worldwide and occupy a variety of natural and disturbed habitats. All but a few species are predaceous, feeding on small soft-bodied arthropods from a variety of taxonomic groups. Pirate bugs contribute to biological control of pest arthropods in a wide variety of habitats, including orchards, row crops, forests, ornamental plants, greenhouses, and granaries.

Classification and Distribution of the Anthocoridae

The family Anthocoridae includes between 500–600 species in 80–100 genera worldwide. The systematic position of the Anthocoridae and close relatives remains somewhat unsettled, and there is a distinct need for additional taxonomic and phylogenetic work. Diversity of Anthocoridae tends to be highest in the tropics and the Holarctic Region. Thorough faunistic studies for some geographic regions are lacking, and estimates of diversity will require revision as these studies are done. Checklists for the North American fauna, including information on distribution, are available in publications by Kelton, Henry, and Maw et al. Citations for these works are provided at the end of this chapter. Keys to many North American species are available in Blatchley and Kelton.

The discussion of classification and distribution to be presented here is based on treatments by Cassis and Gross, Schuh and Štys, Schuh and Slater, Carayon, and Ford (full citations follow at the end of this article). The Anthocoridae are found in the infraorder Cimicomorpha within the suborder Heteroptera ("true bugs"). Classification of the Anthocoridae has seen extensive study and revision since the family was erected in the 1800s, particularly with reference to placement of related families such as the bed bugs (Cimicidae), bat bugs (Polyctenidae), and web lovers (Plokiophilidae), but also with respect to higher level groupings of taxa within the Anthocoridae. Three modern treatments of the pirate bugs allocate genera among seven or eight tribes (Table 9). Carayon, and Cassis and Gross include three subfamilies (Lasiochilinae, Lyctocorinae, Anthocorinae) within the family Anthocoridae. Schuh and Slater elevate the Lasiochilinae and Lyctocorinae to family rank, following the phylogenetic analysis of Schuh and Štys. Four tribes included within the Lyctocorinae by Carayon (i.e., the Almeidini, Cardiastethini, Scolopini, and Xylocorini) are placed in the Anthocorinae by Cassis and Gross, or in the Anthocoridae by Schuh and Slater. Carayon's Cardiastethini is considered a junior synonym of Dufouriellini Van Duzee in both the Schuh and Slater treatment and in the Cassis and Gross treatment, following the assessment of Štys. Péricart used Carayon's classification in his summary and checklist of the Palaearctic Anthocoridae. I follow the Schuh and Slater scheme throughout this article. Because of the close taxonomic affinity among the Lyctocoridae, Lasiochilidae, and Anthocoridae – and because taxonomic rank for these groups is still open to discussion – the present article will not be limited to the Anthocoridae, but will include as necessary reference also to the Lyctocoridae and Lasiochilidae.

Family Anthocoridae – Tribe Almeidini

This is a poorly known group with few described species, known from the Old World tropics, Japan, Nepal, and Australia.

Anthocorini

The Anthocorini is a highly speciose group found primarily in temperate areas. Members of this group include a number of species important in biological control, particularly in orchards and coniferous forests. The most well known of these insects are in the genus *Anthocoris*, which includes over 50 described species found commonly in temperate regions. Species in the Anthocorini feed on phytophagous arthropods primarily in the canopies of deciduous or coniferous trees, or on the foliage of deciduous shrubs.

Blaptostethini

This is a poorly known group of about seven described species known primarily from the Oriental and Pacific regions.

Dufouriellini

The Dufouriellini is a large group of species whose systematic affinities remain somewhat uncertain. The Dufouriellini are well represented in the Neotropical, Australian, and Palaearctic regions. *Cardiastethus* is the most common genus, comprising about 40 described species having a wide distribution.

Oriini

The Oriini contains the geographically widespread and well-known genus *Orius*, having approximately 70 described species. This group has strong representation in the Oriental, Ethiopian, Palaearctic, and Neotropical regions, but is relatively poorly represented in the Nearctic. The Oriini includes a number of species important in biological control of pests on row crops, in greenhouses, and on ornamental plants.

Minute Pirate Bugs (Hemiptera: Anthocoridae), Table 9 Comparison of three classification schemes for the pirate bugs and relatives, including representative genera

Carayon	Cassis and Gross	Schuh and Slater
ANTHOCORINAE	**ANTHOCORINAE**	**ANTHOCORIDAE**
ANTHOCORINI	ALMEIDINI	ALMEIDINI
Acompocoris Reuter	*Almeida*	*Almeida*
Anthocoris Fallén	ANTHOCORINI	ANTHOCORINI
Coccivora McAtee & Malloch	*Acompocoris*	*Acompocoris*
Elatophilus Reuter	*Anthocoris*	*Anthocoris*
Macrotrachelia Reuter	*Coccivora*	*Coccivora*
Temnostethus Fieber	*Elatophilus*	*Elatophilus*
Tetraphleps Fieber	*Macrotrachelia*	*Macrotrachelia*
BLAPTOSTETHINI	*Temnostethus*	*Temnostethus*
Blaptostethus Fieber	*Tetraphleps*	*Tetraphleps*
ORIINI	BLAPTOSTETHINI	BLAPTOSTETHINI
Bilia Distant	*Blaptostethus*	*Blaptostethus*
Macrotracheliella Champion	DUFOURIELLINI	DUFOURIELLINI
Montandoniola Poppius	*Amphiareus*	*Amphiareus*
Orius Wolff	*Brachysteles*	*Brachysteles*
Paratriphleps Champion	*Buchananiella*	*Buchananiella*
Wollastoniella Reuter	*Cardiastethus*	*Cardiastethus*
LASIOCHILINAE	*Dufouriellus*	*Dufouriellus*
Lasiochilus Reuter	ORIINI	ORIINI
LYCTOCORINAE	*Bilia*	*Bilia*
ALMEIDINI	*Macrotracheliella*	*Macrotracheliella*
Almeida Distant	*Montandoniola*	*Montandoniola*
CARDIASTETHINI	*Orius*	*Orius*
Amphiareus Distant	*Paratriphleps*	*Paratriphleps*
Brachysteles Mulsant & Rey	*Wollastoniella*	*Wollastoniella*
Buchananiella Reuter	SCOLOPINI	SCOLOPINI
Cardiastethus Fieber	*Calliodis*	*Calliodis*
Dufouriellus Kirkaldy	*Nidicola*	*Nidicola*
LYCTOCORINI	*Scoloposcelis*	*Scoloposcelis*
Lyctocoris Hahn	XYLOCORINI	XYLOCORINI
SCOLOPINI	*Xylocoris*	*Xylocoris*
Calliodis Reuter	**LASIOCHILINAE**	**LASIOCHILIDAE**
Nidicola Harris & Drake	*Lasiochilus*	*Lasiochilus*
Scoloposcelis Fieber	**LYCTOCORINAE**	**LYCTOCORIDAE**
XYLOCORINI	*Lyctocoris*	*Lyctocoris*
Xylocoris Dufour		

Modification of a table in Cassis and Gross

Scolopini

The Scolopini include at least 13 genera distributed primarily in the Neotropical Region, but with at least some representation in most areas of the world. Species of *Scoloposcelis* are important predators of bark-feeding Coleoptera.

Xylocorini

The Xylocorini occur virtually worldwide, but have heavy representation in the Palaearctic and Nearctic regions. This tribe includes a single genus, *Xylocoris*, having about 40 described species. Species of *Xylocoris* are sources of biological control in stored products, granaries, and beneath the bark of trees. *Xylocoris flavipes* (Reuter) is a geographically widespread species which has been introduced into a number of regions apparently by human commerce.

Family Lasiochilidae

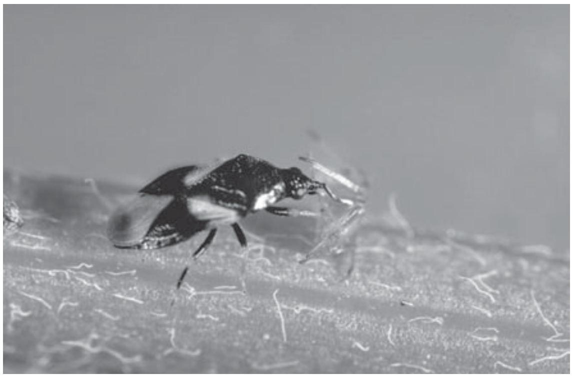
The Lasiochilidae are a poorly studied group with species occurring in most geographic regions, but having the strongest representation in the Neotropical Region and on Pacific islands; the family is virtually absent from the Palaearctic. *Lasiochilus* is composed of approximately 50 described species having a relatively wide distribution. Members of this family are small (3–4 mm), and occur on the ground in litter, under the bark of trees, or on plant surfaces.

Family Lyctocoridae

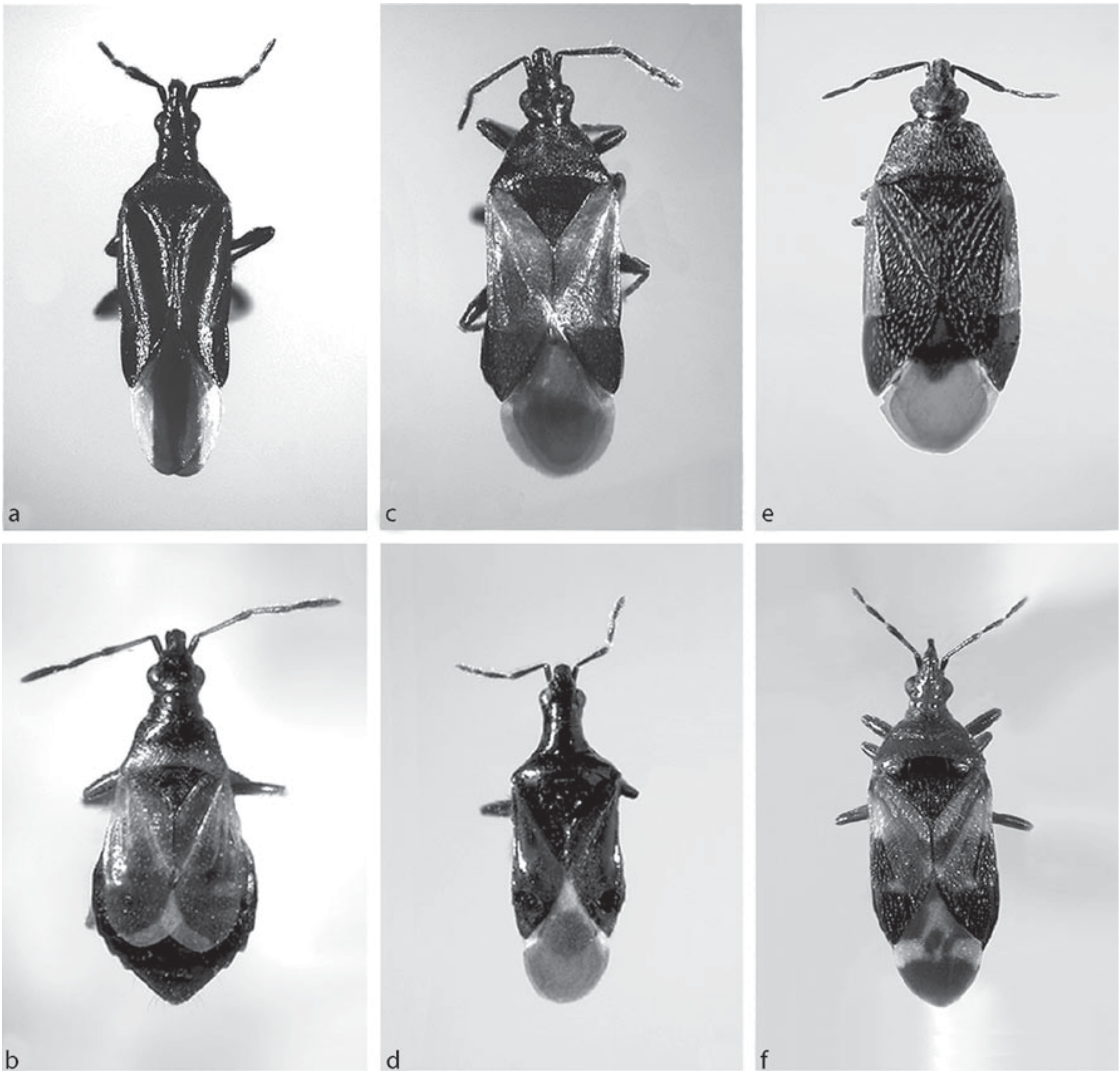
The Lyctocoridae are widely distributed, but with a strong presence in temperate regions. One species, *Lyctocoris campestris* (Fabricius), is essentially cosmopolitan, likely because of unintentional introductions outside of its native range. Members of this family can be found in a number of habitats, including in stored products, in decaying vegetation, beneath bark, and in the nests of birds or mammals.

Morphology

Members of the Anthocoridae are relatively small (1.5–5 mm), having an oval or elongate-oval shape (Figs. 55 and 56). Most are brownish in general coloration. Wing markings or shadings give some species a checkered appearance. The body is generally somewhat flattened, and may be either glabrous or pubescent. The head extends horizontally, with large compound eyes on each side. Paired ocelli are present near the eyes in the adult (ocelli are not present in nymphs). Antennae are four-segmented and inserted anterior of the eyes. Mouthparts are of the piercing-sucking type, in the form of a slender beak or labium. The labium has three visible segments, and may be short or quite long (in some species extending to the end of the abdomen). The labium serves to house the four piercing stylets (paired mandibles and paired maxillae), which collectively form the two channels through which digestive enzymes and the ingested food products are moved. The pronotum is trapezoidal, bearing paired callosities that are



Minute Pirate Bugs (Hemiptera: Anthocoridae), Figure 55 **A common North American pirate bug, *Orius tristicolor* (White) (Oriini) (photograph by Jack Kelly Clark, courtesy of University of California Statewide IPM Program).**



Minute Pirate Bugs (Hemiptera: Anthocoridae), Figure 56 Some Anthocorini and Oriini.
(a) *Macrotrachelia* sp. (possibly *M. nigronitens* (Stål)) (Anthocorini), length approximately 3.3 mm excluding antennae; (b) brachypterous *Anthocoris dimorphicus* Anderson & Kelton (Anthocorini), 2.9 mm; (c) *Elatophilus* sp. (Anthocorini), 3.1 mm; (d) *Macrotracheliella nigra* Parshley (Oriini), 2.4 mm; (e) *Melanocoris nigricornis* Van Duzee (Anthocorini), 3.1 mm; (F) *Anthocoris nemoralis* (Fabricius) (Anthocorini), 3.5 mm.

prominent in some species and inconspicuous in other species. Anthocorids have two pairs of wings: the membranous hind wings, and the thickened forewings (hemelytra) that are characteristic for the true bugs. Most members of the family have fully sized wings, although there are species in some genera (e.g., *Xylocoris*, *Temnostethus*, *Anthocoris*, and *Elatophilus*) that exhibit brachyptery. The forewing has a triangular cuneus, unlike what is found in many other Heteroptera. Genitalia in the male are asymmetrical (discussed below). The ovipositor is well-developed in most species, but is greatly reduced in some taxa (e.g., *Cardiastethus*).

Specimens of Anthocoridae may resemble insects from other families of Heteroptera, including especially members of the Miridae. Morphological characteristics in the Anthocoridae that can be used to separate them from other Heteroptera include: two ocelli; labium with three visible segments; generally an absence of pronounced veins in the hemelytral membrane; presence of a cuneus; and presence of asymmetrical genitalia in males. Insects within the Lasiochilidae, Lyctocoridae, and Anthocoridae may often be very similar in appearance. Placement of specimens in the correct family may require access to faunistic treatments that include keys for identifying genera and species, from which family affiliation can then be derived. Examination of genitalia may be necessary in some cases to confirm or to ascertain family affiliation.

Biology and Life History

Members of the Anthocoridae, Lasiochilidae, and Lyctocoridae are predaceous on small soft-bodied arthropods in a variety of natural or managed habitats. Many species prey upon herbivorous arthropods that attack forbs, shrubs, or trees. Important prey taxa include aphids, psyllids, mites, thrips, scale insects, psocids, and eggs or small larvae of Lepidoptera, Coleoptera, and Diptera. Species of *Orius* are commonly associated with flowers of herbaceous plants, where they feed extensively on thrips and other small arthropods. A number of genera in the Anthocorini (*Melanocoris* Champion, *Tetraphleps*, *Elatophilus*) occur exclusively on coniferous trees, where they feed on aphids and scale insects. Species of *Anthocoris* are common on deciduous trees and shrubs, and prey extensively on psyllids, aphids, and other soft-bodied arthropods. *Scoloposcelis*, *Xylocoris*, and *Lyctocoris* are often found beneath the bark of trees feeding on eggs and larvae of bark beetles. *Xylocoris* and *Lyctocoris* also occur in stored products and granaries, in nests of birds or mammals, in poultry houses, in decaying plant litter, in manure piles, under tree bark, or in ant nests. *Lyctocoris campestris* may occasionally feed on the blood of mammals, including on humans. *Nidicola marginatus* Harris & Drake has been collected from guano beneath roosting bats.

Anthocoridae may often supplement their diets with pollen or plant juices. Species of *Orius* occur commonly in the flowers of herbaceous vegetation, and are known to supplement their diets with pollen. *Orius pallidicornis* (Reuter) appears to have an exclusively plant diet, feeding on pollen from a limited number of species. *Paratriphleps laeviuscula* Champion is a Central and South American species now known to occur in Florida, where it inhabits the flowers of sapodilla (*Manilkara zapota*) and feeds on pollen. Species of *Anthocoris* and *Orius* are known to accumulate systemic insecticides from root-treated plants, due to their habit of ingesting plant juices.

Diet breadth in the Anthocoridae shows a range from highly generalized species to highly specialized species. The generalist species *Anthocoris nemoralis* (Fabricius) has been recorded from over 20 plant genera in Europe and from 13 plant genera in North America, with the latter records occurring only since 1958 following the accidental and intentional introductions of this predator into the Nearctic. *Anthocoris antevolens* White, a widespread North American species, has been recorded from well over 20 plant genera. Species such as *Orius tristicolor* (White) and *Orius insidiosus* (Say) occur on the flowers of a diverse number of plant species, apparently because a primary prey species, the western flower thrips (*Frankliniella occidentalis* (Pergande)), is itself highly generalized. *Lyctocoris campestris* occurs in a variety of habitats, including compost piles, moldy grain, beneath leaf or straw litter, birds nests, mammal burrows, or beneath the bark of trees.

In contrast, many other Anthocoridae show highly restricted diets. Several species of *Anthocoris* reproduce largely or entirely on a few plant species (e.g., *A. gallarumulmi* (De Geer) on elm [*Ulmus*], *A. bakeri* Poppius on manzanita [*Arctostaphylos*], *A. sarothamni* Douglas & Scott on broom [*Cytisus*], *A. dimorphicus* Anderson & Kelton on willow [*Salix*], and *A. visci* Douglas on mistletoe [*Viscum*]). Presumably, the limited host plant range reflects some type of diet specialization (*A. bakeri*, for example, appears to prey extensively on aphids that gall *Arctostaphylos*). Other Anthocoridae are restricted to a few related plant species, and include species of *Melanocoris* (restricted to *Pinus* and *Picea*), *Elatophilus* (restricted to *Pinus*), and *Acompocoris* (*Pinus* and *Picea*). Species of *Elatophilus* often appear to occur in association with scale insects (*Matsucoccus* Cockerell) occurring on *Pinus*; some *Elatophilus* species are attracted to the sex pheromones of *Matsucoccus* scale insects. *Brachysteles parvicornis* (Costa) may feed largely on mites within the Oribatida. Diet breadth in some species may change seasonally. For instance, females of some *Anthocoris* species accumulate on willows (*Salix*) in early spring as the bugs emerge from overwintering sites, and may complete a generation on those hosts before the summer hosts (which can include a number of different plant taxa) are later colonized.

Anthocoridae that occur on plants insert their eggs into plant tissues. Species that attack aphids or scale insects on coniferous trees insert their eggs into the needles, whereas those species that inhabit the foliage of deciduous plants often insert the eggs into leaf tissues. Anthocoridae that occur under bark insert their eggs into the inner surface of the bark, into rotting wood, or into cracks in the bark. Species of *Xylocoris* that inhabit manure piles insert their eggs into cracks in the manure, whereas those species that inhabit straw piles insert their eggs into the decaying straw. In species having a reduced or vestigial ovipositor (e.g., *Cardiastethus*), eggs are deposited on the substrate near prey. Lifetime egg production per female is highly variable even within species, and is probably affected extensively by diet quality. Lifetime estimates of fecundity obtained from laboratory trials are available for *Anthocoris* (70–220 eggs), *Cardiastethus* (35–45 eggs), *Lyctocoris* (95 eggs), *Montandoniola* (50–150 eggs), *Orius* (90–130 eggs), and *Xylocoris* (20–80 eggs).

The pirate bugs have hemimetabolous development, in which the immatures (nymphs) undergo incomplete metamorphosis, and resemble the adults morphologically except in lacking wings, ocelli, and reproductive structures. Nymphs have five instars. Development rates of eggs and nymphs increase with increasing temperature. Anthocoridae in temperate regions overwinter as adults in reproductive diapause. For those species which have been examined, diapause is controlled by photoperiod, with long days prompting reproduction and short days leading to diapause. The critical photoperiod that prompts diapause for a given species may often depend upon latitude. Sex ratios for overwintering adults are often female-biased, and in some Anthocoridae the males appear not to overwinter. Most species of Anthocoridae have two or more generations per year depending upon latitude and elevation. Some species (e.g., *Anthocoris gallarumulmi*) appear to be univoltine throughout their respective geographic ranges.

Reproduction, Mating, and the Paragenital System

The pirate bugs have several reproductive traits and associated structures that differ from most other Heteroptera. Unlike most Heteroptera, the Anthocoridae, Lyctocoridae, and Lasiochilidae (plus some related taxa such as the Cimicidae) have fertilization of the eggs occurring within the vitellarium of the ovaries, rather than in the genital ducts. The anthocorid egg lacks micropyles, and fertilization takes place before the chorion is deposited. Oocyte maturation is inhibited in unmated females. Unfertilized eggs generally degenerate and are resorbed before they reach maturation, and unmated females deposit few or no eggs.

The Anthocoridae and related taxa have evolved a number of unique reproductive structures that are used extensively by taxonomists in developing classification schemes and in defining phylogenetic affinities among higher level taxa (Table 10). In the Anthocoridae and Lyctocoridae, insemination of the female by the male is not done via the usual route through the female genitalia.

Minute Pirate Bugs (Hemiptera: Anthocoridae), Table 10 Comparison of reproductive traits and structures (including the female paragenital system) among Lasiochilidae, Lyctocoridae, and Anthocoridae

	Lasiochilidae	Lyctocoridae	Anthocoridae
1. Insemination	1. intragenital	1. extragenital	1. extragenital
2. Intromittent organ	2. phallus	2. phallus with acus	2. paramere and/or phallus
3. Paragenital system	3. none	3. spermalege	3. spermalege, often in form of copulatory tube(s)
4. Site of copulation	4. female's genital opening (intragenitalic)	4. between segments VII-VIII to right of genital opening	4. variable
5. Sperm storage	5. bursa copulatrix	5. seminal conceptacles	5. seminal conceptacles or spermatic pocket

Rather, insemination occurs outside of the reproductive tract, within the abdominal cavity, and is thus referred to as extragenital insemination. The sperm migrate through the haemocoel or through specialized structures in the female (see below) to the ovaries, and fertilize the developing egg within the vitellarium before deposition of the chorion. It is not clear what evolutionary pressures have led to extragenital insemination in the Anthocoridae or other taxa showing this trait, but it has been suggested that it is a means by which the male circumvents female resistance or bypasses female control of sperm allocation and egg fertilization.

Characteristics of the reproductive system show some similarities and some differences among the Lasiochilidae, Lyctocoridae, and Anthocoridae, and these traits have been used extensively in assessing phylogenetic affinities among these groups. The Lasiochilidae differ from the Anthocoridae and Lyctocoridae in that insemination is of the more typical insect type, occurring within the female's reproductive system (i.e., intragenital insemination), as opposed to the extragenital insemination characteristic of the Anthocoridae and Lyctocoridae. In all three families, the male genitalia are asymmetric. The right paramere is highly reduced or is absent. The intromittent organ in the Lasiochilidae and Lyctocoridae is the phallus. In the Lyctocoridae, the apex of the phallus is sclerotized and in the form of an acus (needle), used to penetrate the abdominal wall of the female for insemination ("traumatic insemination"). For the Anthocoridae, the left paramere or the phallus acts as the intromittent organ. In the Oriini, for example, a portion of the left paramere (the flagellum) is inserted within a specialized female organ (the copulatory tube, as discussed below), and the short membranous phallus slides along the paramere to deposit sperm. The paramere itself may be of quite complex shape in the Oriini, and in fact is used extensively in differentiating species of *Orius* within some difficult species complexes. The Anthocorini exhibit a different strategy. In these species, the paramere is reduced to a relatively simple, sickle-like organ, which is inserted only partially within the copulation site of the female. The male then inflates his long, membranous phallus through the female's copulatory tube to deposit sperm. In the Xylocorini, the left paramere is sharply pointed, and is used to pierce the abdominal wall of the female at the copulation site. Copulation may actually lead to scars that are visible on the surface of the female.

Extragenital insemination in the Anthocoridae and related taxa has led to the evolution in females of structures collectively referred to as the paragenital system (spermalege). These organs are thought to have evolved as a means for the female to reduce costs associated with traumatic insemination, caused by wounding of the cuticle at the copulation site or by the introduction of infections and infectious agents within the haemocoel of the female as the male inseminates her. The spermalege consists of simple to complex structures that act to guide the male's intromittent organ to a specific insemination site (the ectospermalege), and to receive the sperm (the mesospermalege). In some taxa (e.g., the Anthocorini and Oriini), the ectospermalege consists of a specialized copulatory tube, produced as an invagination of the epidermis that opens between sternites VII-VIII on the ventral surface of the female, just lateral of the female's genital opening. The copulatory tube receives the paramere and phallus (as in the Oriini) or phallus (as in the Anthocorini). The distal end of the copulatory tube enters a pouch (spermatic pocket or sperm pouch), which acts to temporarily store the sperm. In the Lyctocoridae, newly deposited sperm collect first in the mesospermalege (a collection of specialized cells at the copulation site), and then migrate through the haemocoel to the sperm storage structures at the base of the ovaries. In the Xylocorini, the mesospermalege may be partially open or completely enclosed. If the mesospermalege is partially open, sperm move from the mesospermalege into the haemocoel, and migrate through the haemocoel to the sperm storage sites at the base of the ovaries. If the mesospermalege is completely enclosed, the structure extends to and connects with the sperm storage structures.

The actual site of copulation in the Anthocoridae and related taxa is highly variable. In the Lasiochilidae, which lacks a paragenital system, insemination takes place within the female's genital tract. In the Lyctocoridae, the male pierces the female on her ventral side between segments VII and VIII, to the right of the female's genitalic opening. Within the Anthocoridae, site of copulation varies among tribes. In the Oriini and Anthocorini, the copulatory tube opens between abdominal segments VII and VIII on the female's ventral side, usually to the left of her genital opening. Female Blaptostethini actually have paired copulatory tubes, located on her ventral side between abdominal segments VII and VIII. In the Xylocorini, the site of copulation in some species is on the dorsal side of the female, towards the anterior end of the abdomen, while in other species copulation takes place on the lateral (right) side of the abdomen.

The spermatheca is reduced to a small vermiform gland having no sperm storage function (Lasiochilidae), or is absent altogether (Lyctocoridae and Anthocoridae). In the Lyctocoridae, sperm travel from the spermalege at the site of insemination through the haemocoel into sperm storage organs (seminal conceptacles) located at the base of the ovaries. In the Anthocoridae, sperm are stored either in the sperm pocket (species having copulatory tubes: Oriini, Anthocorini, Scolopini, Blaptostethini) or in seminal conceptacles (Xylocorini). The seminal conceptacles in the Xylocorini and Lyctocoridae are not homologous, as they derive from different tissues in the two taxa. From the sperm storage organs (sperm pocket or seminal conceptacles), the sperm move to the ovaries through specialized conducting tissues, and fertilize the eggs within the vitellarium.

Economic Importance

The pirate bugs are sources of biological control in annual and perennial crops, in forests, in greenhouse crops, on ornamental plants, and in stored products. Several species of *Anthocoris* are known important sources of biological control in temperate fruit orchards, where they feed extensively on pest psyllids and aphids. Species of *Orius* occur in greenhouses and in a variety of row crops, where they feed on thrips, mites, aphids, and eggs of pest Lepidoptera. These predators may be particularly important natural enemies of flower thrips. *Xylocoris* and *Lyctocoris* attack beetle and moth pests in stored products and granaries. Aphid and scale pests that inhabit the canopies of coniferous trees are attacked by *Elatophilus*, *Tetraphleps*, *Melanocoris*, and *Acompocoris*, whereas bark beetle pests are fed upon beneath bark by species of *Xylocoris*, *Scoloposcelis*, and *Lyctocoris*. Other species are important natural enemies of pests on ornamental plants, including *Montandoniola*, *Macrotrachelia*, and *Macrotracheliella* on ornamental fig (*Ficus*), where they feed on the Cuban laurel thrips (*Gynaikothrips ficorum* (Marchal)). Species reared in insectaries for shipment and release include *Orius insidiosus*, *Orius laevigatus* (Fieber), *Orius majusculus* (Reuter), and *Anthocoris nemoralis*.

The Anthocoridae have been used in a number of classical biological control efforts. Classical biological control is the importation and release of exotic natural enemies for controlling non-indigenous pests. *Anthocoris nemoralis*, a species native to Europe, was released into western North America in the early 1960s to control an introduced psyllid pest of pears (*Cacopsylla pyricola* (Förster)). The predator is now established in British Columbia, Washington, Oregon, and California. Its effectiveness in controlling the psyllid pest of pears, however, is unclear. The North American *Orius insidiosus* has been introduced into Europe and Hawaii for controlling Thysanoptera and Lepido-ptera, and is established in Hawaii. *Montandoniola moraguesi* (Puton) is native to southeast Asia, but has been released in southern California, Texas, Bermuda, and Hawaii to control Cuban laurel thrips. The predator has become established in Bermuda and Hawaii, apparently as a consequence of these introductions. Two species of *Tetraphleps* were introduced into North America from India and Pakistan for control of the balsam woolly aphid (*Adelges piceae* (Ratzeburg)), a non-indigenous pest of various coniferous trees. Apparently neither species became established.

A number of species have become established outside of their native ranges because of accidental introductions or dispersal. Effects of these introductions upon native predators (via competition) and native prey (via predation) are unknown, but are potentially important. There has been speculation, for example, that *Anthocoris nemoralis*, which was introduced intentionally into North America from Europe but which has moved into habitats other than the target pear orchard, may compete with native *Anthocoris* species. Species that associate with stored food products (*Lyctocoris*, *Xylocoris*) have spread dramatically outside of their native ranges, apparently because of human commerce. These and other species of Anthocoridae are regularly intercepted at ports-of-entry on transported flowers, fruits and vegetables, or on other plant materials. As of 1999, it was thought that more than 50% of the anthocorid fauna in Hawaii was non-indigenous, with many of the exotic species arriving because of accidental introductions. *Montandoniola moraguesi*, which has been used extensively in classical biological control efforts against thrips on *Ficus*, is now established in the southeastern United States, apparently because of accidental introduction or natural dispersal. In North America, non-indigenous species that have become established because of apparent accidental introductions or natural dispersal can be found in the genera *Anthocoris*, *Brachysteles*, *Buchananiella*, *Dufouriellus*, *Lyctocoris* (Lyctocoridae), *Montandoniola*, *Orius*, *Temnostethus*, and *Xylocoris*. Effects of these exotic species on North American ecosystems are unknown.

References

Blatchley WS (1926) Heteroptera or true bugs of eastern North America. The Nature Publishing Company, Indianapolis, IN, 1,116 pp

Carayon J (1972) Caractères systématiques et classification des Anthocoridae (Hemipt). Annales de la Société Entomologique de France (N.S.) 8:309–349

Carayon J (1977) Insemination extra-génitale traumatique. In: Grassé P-P (ed) Traité de Zoologie. Anatomie, systématique, biologie. Tome VIII. Insectes. Gamètogenèses, fécondation, métamorphoses. Masson, Paris, France, pp 351–390

Cassis G, Gross GF (1995) Hemiptera. Heteroptera (Coleorrhyncha to Cimicomorpha). In: Houston WWK, Maynard GV (eds) Zoological Catalogue of Australia, vol 27.3A. CSIRO, Melbourne, Australia, 506 pp

Ford LJ (1979) The phylogeny and biogeography of the Cimicoidea (Insecta: Hemiptera). M.S. thesis, University of Connecticut, Storrs, CT, 139 pp

Henry TJ (1988) Family Anthocoridae Fieber, 1837. In: Henry TJ, Froeschner RC (eds) Catalog of the Heteroptera, or true bugs, of Canada and the Continental United States. E.J. Brill, Leiden, The Netherlands, pp. 12–18 (Corrections and additions to the catalog are available. In: Henry TJ, Froeschner RC (1992) Proc Entomol Soc Wash 94:263–272)

Herring JL (1976) Keys to genera of Anthocoridae of America north of Mexico, with description of a new genus (Hemiptera: Heteroptera). The Fla Entomol 59:143–150

Kelton LA (1978) The insects and arachnids of Canada, pt 4. The Anthocoridae of Canada and Alaska. Heteroptera: Anthocoridae. Agriculture Canada Research Publication 1639. Ottawa, ON, Canada, 101 pp

Lattin JD (1999) Bionomics of the Anthocoridae. Annu Rev Entomol 44:207–231

Lattin JD (2000) Minute pirate bugs (Anthocoridae). In: Schaefer CW, Panizzi AR (eds) Heteroptera of economic importance. CRC Press, Boca Raton, FL, pp 607–637

Maw HEL, Foottit RG, Hamilton KGA, Scudder GGE (2000) Checklist of the Hemiptera of Canada and Alaska. NRC Research Press, Ottawa, ON, Canada, 220 pp

Péricart J (1972) Hémiptères. Anthocoridae, Cimicidae, Microphysidae de l'Ouest-Paléarctique. Faune de l'Europe et du Bassin Méditerranéen. Masson et Cie, Paris, France, 402 pp

Péricart J (1996) Family Anthocoridae Fieber, 1836 – Flower bugs, minute pirate bugs. In: Aukema B, Rieger C (eds) Catalogue of the Heteroptera of the Palaearctic Region. The Netherlands Entomological Society, Amsterdam, The Netherlands, pp 108–140

Schuh RT, Štys P (1991) Phylogenetic analysis of cimicomorphan family relationships (Heteroptera). J N Y Entomol Soc 99:298–350

Schuh RT, Slater JA (1995) True bugs of the world (Hemiptera: Heteroptera): Classification and natural history. Cornell University Press, Ithaca, NY, 336 pp

Štys P (1975) Suprageneric nomenclature of Anthocoridae (Heteroptera). Acta Universitatis Carolinae – Biologica 1973:159–162

Minute Tree-Fungus Beetles

Members of the family Ciidae (order Coleoptera).

► Beetles

Miridae

A family of bugs (order Hemiptera). They sometimes are called plant bugs or capsids.

► Plant Bugs
► Bugs

Mite Pests of Crops in Asia

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Acarine pests of agricultural crops include mites in the families Tetranychidae, Tenuipalpidae, Tarsonemidae, Eriophyidae, and Acaridae. Members of all these families are reported to damage various crops in Asia. Among the damaging species are *Amphitetranychus viennensis*, *Eotetranychus cendanai*, *Eo. kankitus*, *Eotetranychus pruni*, *Eotetranychus sexmaculatus*, *Eutetranychus africanus*, *Eu. orientalis*, *Oligonychus coffeae*, *O. litchii*, *O. mangiferus*, *Panonychus citri*, *P. ulmi*, *Petrobia latens*, *Tetranychus cinnabarinus*, *T. fijiensis*, *T. hydrangeae*, *T. kanzawai*, *T. macfarlanei*, *T. piercei*, *T. truncatus*, *T. urticae* (Tetranychidae); *Brevipalpus californicus*, *B. obovatus*, *B. phoenicis*, *Dolichotetranychus floridanus*, *Larvacarus transitans*, *Tenuipalpus pacificus*, *Raoiella indica* (Tenuipalpidae); *Phytonemus pallidus*, *Polyphagotarsonemus latus*, *Steneotarsonemus bancrofti*, *S. spinki* (Tarsonemidae); *Acaphylla theae*, *Acaspina litchii*, *Aceria cajani*, *A. doctersi*, *A. eriobotrya*, *A. litchi*, *A. mangiferae*, *A. sheldoni*, *A. tulipae*, *Aculops lycopersici*, *Aculus schlechtendali*, *Eriophyes litchii*, *Phyllocoptruta oleivora* (Eriophyidae); *Rhizoglyphus echinopus*, *R. robini*, *R. setosus* (Acaridae).

Among them, *Amphitetranychus viennensis*, *T. urticae*, *T. cinnabarinus*, *P. citri*, *P. ulmi*, *O. coffeae*, *B. obovatus*, *B. phoenicis*, *B. californicus*, *Polyphagotarsonemus latus*, *Phytonemus pallidus*, *Phyllocoptruta oleivora*, and *A. tulipae* are worldwide-distributed species and are commonly found from East Asia. These species are important pests of a wide range of crops. Many of them are notorious in having developed resistance to various acaricides. In addition, *T. urticae*, *B. phoenicis*, *B. californicus*, and *A. tulipae* are known to be able to transmit virus diseases of plants. Distribution of *Amphitetranychus viennensis* is limited to the temperate zone or, in subtropical areas, to high elevations with cold climates.

Tetranychus kanzawai is another notorious polyphagous mite pest distributed commonly in

East Asia, but is rarely recorded from other area of the world. *Tetranychus truncatus* is recorded from the Far East and Southeast Asia, and is not considered to be a serious crop pest except in China and Thailand. *Eutetranychus orientalis* has been recorded from most Asian countries, mainly infesting citrus. However, it is not considered an important pest in Japan and Taiwan.

The other mites either are recorded as pests from limited countries, or have a narrow host range. *Petrobia latens* infests wheat, barley, sorghum, grasses, and a few other crops and is known from China, India, Japan, Korea, and Taiwan. *Aceria mangiferae* and *O. mangiferus* mainly infest mango and are recorded only from a few Asian countries, though mango is commonly cultivated in southern Asia. *Eotetranychus kankitus*, *Eo. pruni*, and *Eo. sexmaculatus* damage citrus, apple, and citrus and rubber trees in China, respectively. *Aceria cajani* transmits the sterility mosaic virus disease of pigeon pea in India and neighboring countries. *Aceria doctersi* decreases the oil content of cinnamon (*Cinnamomum zeylanicum*) leaves in Indonesia and Sri Lanka by 18–43%. *Aceria sheldoni* and *Aculops lycopersici* are mainly recorded from west Asia. The former species infests citrus. The latter infests tomato and several other crops of Solanaceae, and may cause serious reductions in yield of tomato. *Aculus schlechtendali* is a pest of apple and pear, and is recorded from Japan, India, Pakistan, and Lebanon. *Eutetranychus africanus* is an important pest of durian, a well-known, peculiar fruit produced in several countries of Southeast Asia. *Eotetranychus cendanai*, *T. hydrangeae*, *T. macfarlanei*, and *T. fijiensis* also are important crop pests in Thailand.

Aceria eriobotrya infests the tip of loquat twigs. *Eriophyes litchii* and *Acaspina litchii* cause leaf erenia to litchee. *Larvacarus transitans* is a serious pest of ber in India. *Dolichotetranychus floridanus* is a pest of pineapple. *Raoiella indica* infests betelnut and coconut. *Steneotarsonemus bancrofti* scars the surface of sugarcane. Infestation of *Oligonychus uruma*, *Schizotetranychus nanjingensis*, and *Aponychus corpuzae* can cause the death of entire bamboo forests.

Rhizoglyphus echinopus, *R. robini*, and *R. setosus* are recorded only from a few Asian countries. The former two species are distributed worldwide, and are infamous in being difficult to control. They may be distributed in more Asia countries than their current distribution record, as may *R. setosus*.

► Mites

References

CABI (2001) Crop protection compendium, 2001 edn. CAB International, Wallingford, UK

Ehara S (1999) Revision of the spider mite family Tetranychidae of Japan (Acari, Prostigmata). Jpn Soc Syst Zool 4:63–141

Ho CC, Lo KC, Chen WH (1997) Spider mite (Acari: Tetranychidae) on various crops in Taiwan. J Agric Res Chin 46:333–346

Kongchuensin M, Charanasri V (1999) Mites injurious to agricultural crops of economic importance in Thailand (abstract). The 4th International symposium on population dynamics of plant-inhabiting mites. May 10–14, 1999, Kyoto, Japan

Wang HF (1981) Acariformes: Tetranychoidea. Econ insect fauna Chin 23:1–150

Mites (Acari)

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Mites belong to the subclass Acari, the largest and most diverse group in the class Chelicera. Because of their small size and secretive lives, much remains to be known about their biology and classification. Mites are distributed worldwide. Some species are of great economic importance as pests of agricultural crops and vectors of important diseases of man, domestic animals and plants.

Evolution and Diversity of Mites

Mites are an ancient group of chelicerates. The earliest known mite fossils are from the Devonian period of geologic time. The fossil record suggests that during the late Mesozoic to early Cenozoic an adaptive radiation of mites occurred with the development of many nonpredatory species. Flowering plants and insects as well as birds and mammals became more widespread during this same period, providing many novel habitats for mites to exploit.

Mites are distributed throughout the world and inhabit almost every ecosystem. They play an important ecological role as inhabitants of the forest floor and soil where they are secondary decomposers of organic matter. Mites are vectors of diseases that affect humans, livestock and crops, and are stored product pests and crop pests.

Mites can be broadly divided into free living and parasitic species. Free living species are by far the most common and are found in all the orders with the exception of the Ixodida (ticks). Ecto and endoparasitic mites attack both vertebrates and invertebrates. Most of endoparasitic species found on vertebrates reside within the respiratory tract. Mites are the most common arthropod ectoparasites of vertebrates, and humans. Species of the human follicle mite *Demodex* are present on most people throughout the world.

Generalized Life History

All mites pass through the same four life stages, egg, larva, nymph and adult, but much variation occurs within the active stages. The most common active stages include a prelarva, larva, protonymph, deutonymph, tritonymph, and adult. A molt occurs between each stage. During the molt, the old cuticle is cast off and replaced by a new one.

The prelarva is the most primitive postembryonic form and commonly remains within the egg. It is usually a nonfeeding quiescent stage. Larvae of most species are six legged. Larvae lack external genital openings and are not well sclerotized. They have few useful taxonomic characteristics. Most larvae are active feeding forms.

Nymphs are eight legged and their body is more sclerotized and has more taxonomic characteristics than larvae, making them easier to identify. The protonymph is the first nymphal instar after the larvae. Protonymphs are usually found in the same type of environment as are other nymphal instars. The protonymph can be either an active or inactive feeding stage depending on the species. The deutonymph is the next nymphal instar. This stage is like the adult in size and design, but often differs in having a less complex sclerotization and setal pattern. The final nymphal instar is a tritonymph. In its absence the deutonymph molts into an adult. The adult forms can be similar (homomorphic) or dissimilar (heteromophic) in one or both sexes, and various male forms (andropolymorphism) are found in a few groups. Molting is rare during the adult stage but occurs in some species.

Classification: The Orders of Mites

There are over 30,000 named species of mites (Table 11) and possibly up to a million unknown species. A list of the major taxa of the Acari follows.

Most scientists divide the Acari into two major groups, the Anactinotrichida and the Actinotrichida. We consider the Anactinotrichida and Actinotrichida superorders, and the major groups within each as orders. Traditionally, the position of the respiratory opening, the stigmata has been used to name the major groups within the two superorders. However, as discussed under the different orders, this system is ambiguous and has mostly been abandoned for a terminology that ends in "–ida." Many of the orders that use the position of the stigmata are now lesser taxa.

Anactinotrichida

"Anactinotrichida" refers to the lack of a birefringent material in cuticular setae. The Anactinotrichida is divided into four orders, the Oplioacarida, Holothyrida, Ixodida, and Gamasida. Some scientists group the Holothyrida, Ixodida and Gamasida as the Parasitiformes and separate out the Oplioacarida

Mites (Acari), Table 11 **Major taxa of the Acari. Numbers in parentheses refer to number of families in the taxon**

Subclass: Acari	Parantennuloidea (2)
Superorder: Anactinotrichida	Heterozerconina
Order: Opilioacarida	Heterozerconidae
Opilioacaridae	Discozerconidae
Order: Holothyridae	Sejina
Holothyridae	Sejidae
Allothyridae	
Neothyridae	Ichthyosomatogasteridae
Order: Ixodida (3)	Uropodellidae
Order: Gamasida	Microgyniina
Cercomegistina	Microgyniidae
Cercomegistidae	Uropodina
Asternoseiidae	Thinozerconoidea
Davacaridae	Polyaspidoidea
Seiodidae	Uropodoidea
Antennophorina	Diarthrophalloidea
Aenictequoidea (4)	Epicriina
Antennophoroidea (1)	Epicriidae
Celaenopsoidea (8)	Zerconina
Fedrizzioidea (4)	Zerconidae
Megisthanoidea (2)	Arctacarina
Arctacaridae	Alicorhagiidae
Parasitina	Proterorhagiidae
Parasitidae	Prostigmata
Pergamasidae	Anystina
Dermanyssina	Anystidae
Rhodacaroidea (3)	Parasitengona (58)
Veigaioidea (1)	Trombidia
Eviphidoidea (5)	
Ascoidea (7)	Calyptostomatoidea
Dermanyssoidea (18)	Erythraeoidea
Superorder Actinotrichida	Trombidioidea
Order Actinedida	Hydrachnidia
Endeostigmata	
Sphaerolichidae	Stygothrombioidea

Mites (Acari), Table 11 **Major taxa of the Acari. Numbers in parentheses refer to number of families in the taxon (Continued)**

Lordalycidae	
Nanorchestidae	Hydryphantoidea
Bimichaeliidae	Eylaioidea
Nematalycidae	Hydrovolzioidea
Proteonematalycidae	Hydrachnoidea
Micropsammidae	Lebertioidea
Oehserchestidae	Hygrobatoidea
Grandjeanicidae	Arrenuroidea
Terpnacaridae	Teneriffidae
Caeculidae	Stigmocheylidae
Adamystidae	Paratydeidae
Eupodina	Order: Oribatida
Bdelloidea (2)	Macrophylina
Halacaroidea (1)	Palaeosomata (6)
Labidostommatidae	
Eupodoidea (5)	Archeonothroidea
Tydeoidea (2–3)	Palaeacaroidea
Eriophyoidea (3)	Ctenacaroidea
Eleutherengona	Enarthronota (13)
Tetranychoidea (5–6)	
Cheyletoidea (8)	Hypochthonoidea
Raphignathoidea (9)	
Pterygosomatoidea (9)	Brachychthonoidea
Pomerantizioidea (1)	
Pseudocheylidae	Atopochthonioidea
Tarsonemina (11)	
Tarsocheyloidea	Heterochthonoidea
Heterocheyloidea	Protoplophoroidea
Pyemotoidea	Parhyposomata (3)
Pygmephoroidea	Parhypochthonioidea
Tarsonemoidea	Mixonomata (10–11)
Phthiracaroidea	Plateremaeoidea
Damaeoidea	
Euphthiracaroidea	Cepheoidea
Lohmannioidea	

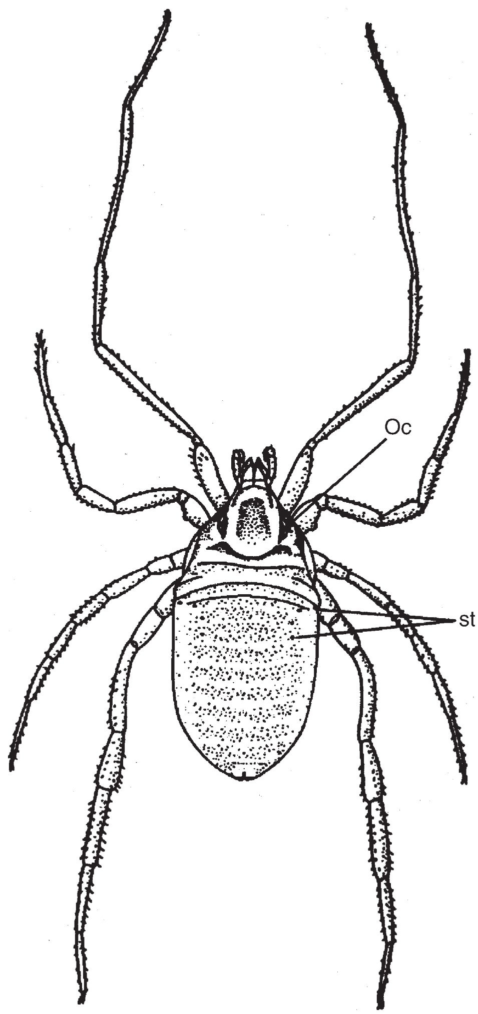
Mites (Acari), Table 11 Major taxa of the Acari. Numbers in parentheses refer to number of families in the taxon (Continued)

Polypterozetoidea	
Eulohmannioidea	
Charassobatoidea	
Perlohmannioidea	Microzetoidea
Amerobelboidea	
Epilohmannioidea	Eremaeoidea
Zetorchestoidea	
Collohmannioidea	Gustavioidea
Nehypochthonioidea	Carabodoidea
Desmonomata (8)	Tectocepheoidea
Crotonioidea	Oppioidea
Hydrozetoidea	
Nanhermannioidea	
Hermannioidea	Ameronothroidea
Brachypylina(>100)	
Pycnonota	Cymbaeremaeoidea
Poronota	
Hermannielloidea	Licneremaeoidea
Neoliodoidea	Oripodoidea
Ceratozetoidea	
Phenopelopoidea	
Oribatelloidea	
Achipterioidea	
Galumnoidea	
Order Acaridida	
Acaridia	
Schizoglyphoidea (1)	
Histiostomatoidea (2)	
Canestrinioidea (2)	
Hemisarcoptoidea (6)	
Glycyphagoidea (7)	
Acaroidea (4)	
Hypoderatoidea (1)	
Psoroptidia	
Pterolichoidea (13)	
Analgoidea (14)	
Sarcoptoidea (14)	

because they appear to be the most primitive mite group. Others group only the Gamasida and the Ixodida as the Parasitiformes (Fig. 57).

Oplioacarida

These are relatively large mites, greater than 1 mm in length, with a leathery cuticle. They resemble the opilones or daddy long-legs. This is the smallest order of mites. One family is recognized,

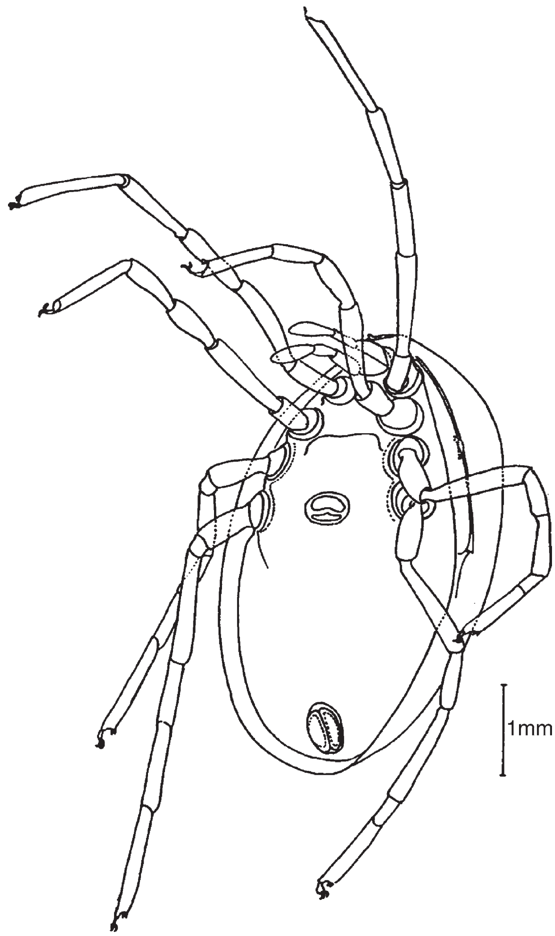


Mites (Acari), Figure 57 Dorsal view of *Opilioacarus segmentatus* (Anactinotrichida, Opilioacarida) *Oc*, ocelli; *st*, stigmata (from Alberti G,Coons LB (1999) The Acari-mites, used with permission of John Wiley and Sons, Inc).

with eight genera and about 20 species. Oplioacarids often have bright pigments distributed in bands across their bodies. The life stages consist of a six-legged quiescent prelarva that molts into a larva. Opiloacarid larvae are unusual in that they have vestiges of the fourth pair of legs. The larva molts into a protonymph, which molts into a deutonymph then a tritonymph which molts into an adult. Adults are unusual in that they may continue to molt. These mites are considered omnivorous, feeding on both small insects and pollen, but they may also be scavengers. Oplioacarids are distributed in Texas in the USA, through South America, the island of Puerto Rico, central Asia through to Africa and southern Europe. They are found especially in semiarid regions where they often are found in the forest litter or dark places such as under rocks, particularly during the day. Oplioacarida are sometimes known as the Notostigmata since they have four pairs of stigmata on the dorsolateral body.

Holothyrida

The Holothyrida have three families, six genera and about 15 species. Holothyrids are found in Australia, New Zealand, islands in the Indian and Pacific Oceans, and the Neotropics. These are large predatory mites that vary in length from about 2–7 mm. The life stages are larva, protonymph, deutonymph, tritonymph and adult. Holothyrids are moderately to heavily sclerotized mites with long legs and an oval body that shows no visible subdivisions. Holothyrids (Fig. 58) are closely related to the Ixodida. They have a sensory area on their first pair of legs that resembles Haller's organ of ixodids. Holothyrids are found under stones or in humus in tropical forests around the world. They may be scavengers that mostly eat solid food such as dead woodlice and amphipods. These mites have been implicated in poisonings of poultry and humans. Holothyrida were previously known as the Tetrastigmata despite the fact that they have only two pair of stigmata.



Mites (Acari), Figure 58 Ventro-lateral view of *Holothyrus coccinella* (Holothyrida) (from Hughes. 1959. Mites or the Acari, used with permission of The Athlone Press).

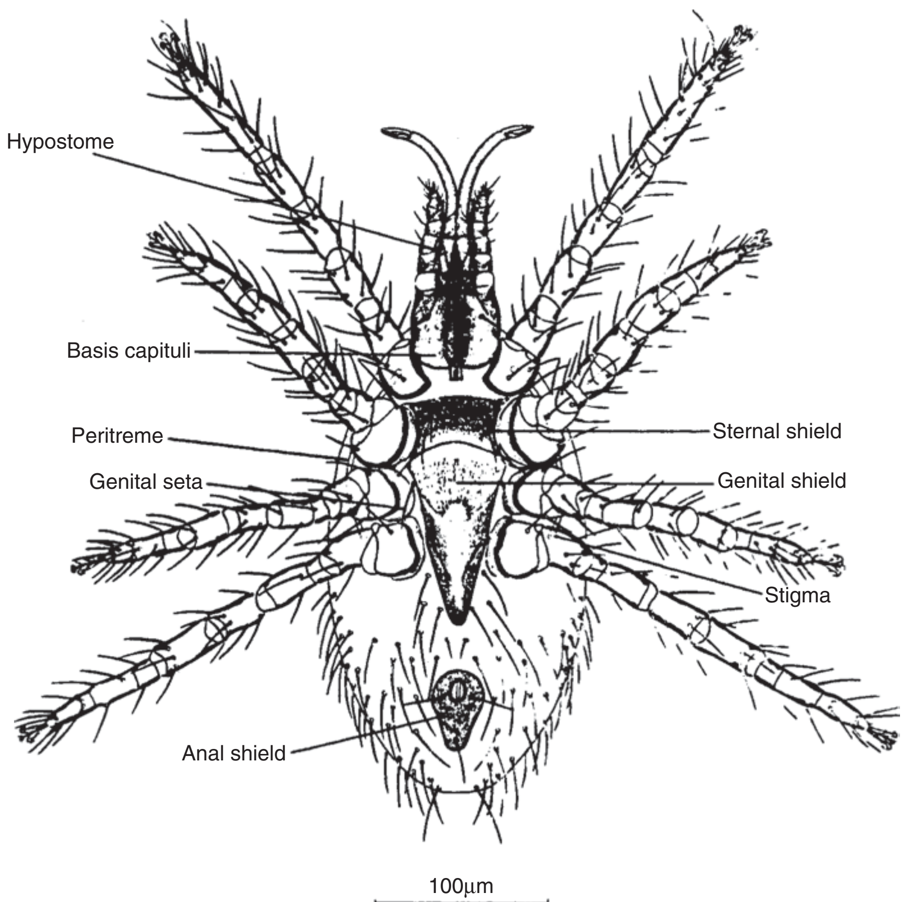
Ixodida

Ixodids or ticks are obligatory blood feeding ectoparasites of vertebrates. Ticks are found worldwide. They are divided into three families, the Argasidae or soft ticks, the Nuttalliellidae with one species, and the Ixodidae or hard ticks. Some 850 species have been described. They transmit serious diseases to humans, livestock and companion animals. Ixodida were previously known as the Metastigmata, however the stigmata are found behind the fourth pair of legs only in the hard ticks while soft ticks have the stigmata between the third and fourth pair of legs. Ticks are covered in a separate entry.

Gamasida

This is the most diverse order and contains the largest number of species in the Anactinotrichida. There are some 77 families divided into 11 subgroups with about 5,000 species. Gamasids are found worldwide in diverse habitats. A typical gamasid life cycle consists of an egg, and four active stages: larva, protonymph, deutonymph and adult. The most common variation on this life cycle is the occurrence of a nonfeeding larval stage and a phoretic stage in the deutonymph. Gamasids range in size from 0.2 to 2.0 mm in length. They are often highly sclerotized with several cuticular shields such as the sternal, genital and anal shields (Fig. 59) that are useful as taxonomic characters as are the positions and number of setae. Setae are hairlike projections of the cuticle and are common on many mites in both superorders. These taxonomic characters are also used throughout the Acari. The Gamasida are still known by some acarologists as the Mesostigmata since they have a pair of stigmata dorsolateral or ventrolateral to the legs.

Most Gamasida are free living predaceous or fungivorous soil-inhabiting mites or are epizoons, attached to the body of arthropods, or commensals with other arthropods. Commensals benefit from a common food supply but do not harm the



Mites (Acari), Figure 59 Ventral view of female tropical poultry mite *Ornithonyssus bursa* (Gamasida, Dermanyssoidea, Macronyssidae) (from Kettle DS (1995) Medical and veterinary entomology, used with permission of CAB International).

other species. Some gamasids are parasites of vertebrates and invertebrates.

The Cercomegistina are made up of four families that are mostly free living mites in litter and humus, but the species of one family are associated with other arthropods. The Antennophorina are divided into six superfamilies with mites that are associated with arthropods, lizards or snakes. The Heterozerconina comprise two families that are commensals or parasites on millipedes, centipedes or snakes. Very little is known about these curious mites. The Sejina contain three families that are associated with other arthropods or found in forest litter or the nests of vertebrates but otherwise their biology is not known. They are distributed worldwide. The little known Microgyniina have a single family found in woody debris in the Holarctic Region.

The Uropodina, with four superfamilies, are found throughout the temperate and tropical zones where they occur mostly in forest litter. Some are seashore dwellers. Species in this group are fungivores, scavengers or predators. Species of Uropodina have phoretic deutonymphs. The Diarthropalloidea, a superfamily of Uropodina, are parasitic on passalid beetles and are distributed in the neotropical and Australian zones. The Epicriina, Zerconina and Arctacarina, each with one family, have similar distributions and habitats. They are found in the northern hemisphere in leaf litter and humus. Their biology is poorly known. The Parasitina contain two families whose species are common in soils and organic debris throughout the world. They are associated with insects or are predators of smaller arthropods and nematodes.

The Dermanyssina, with five superfamilies, have the largest number of species and the most diversity in the Gamasida. This is the only subgroup of Gamasida that contains species of medical and veterinary importance. Parasitic mites of the Dermanyssoidea often have highly modified external morphology and life cycles. The superfamily Rhodacaroidea make up the dominant gamasid predators in tropical soils. The superfamily Veigaioidea contains a single family of predatory mites found in mosses and litter in temperate forests. The superfamily Eviphidoidea are mostly free-living mites found in litter and humus of soils or are associates of other arthropods. This superfamily contains several species of mites that are used as biological control agents. The superfamily Ascoidea are a diverse assemblage of mites. *Phytoseiulus persimilis* (Ascoidea: Phytoseiidae) is used as a biocontrol agent against red spider mites (Tetranychidae) (Fig. 62) in greenhouses. The superfamily Dermanyssoidea includes many economically important parasites as well as predatory species found in nests or in the soil, and contain all gamasid species of medical or veterinary importance. The Dermanyssidae, Macronyssidae, Spinturnicidae, and Histrichonyssidae are parasites that feed on the blood of birds and mammals. The families Halarachnidae and Rhinonyssidae are parasites of the respiratory tracts of birds and mammals. The family Varroidae contains the bee parasite *Varroa destructor* which is further described in the section on "Bee mites."

Actinotrichida

"Actinotrichida" refers to the presence of a birefringent material in cuticular setae. Some workers use the name Acariformes for Actinotrichida. The Actinotrichida contain the largest number of species and has the most morphological and ecological diversity of the two superorders. There are three orders in the Actinotrichida, namely, Actinedida, Oribatida and Acaridida. The last two orders are closely related and are referred to by some workers as Sarcoptiformes.

Actinedida

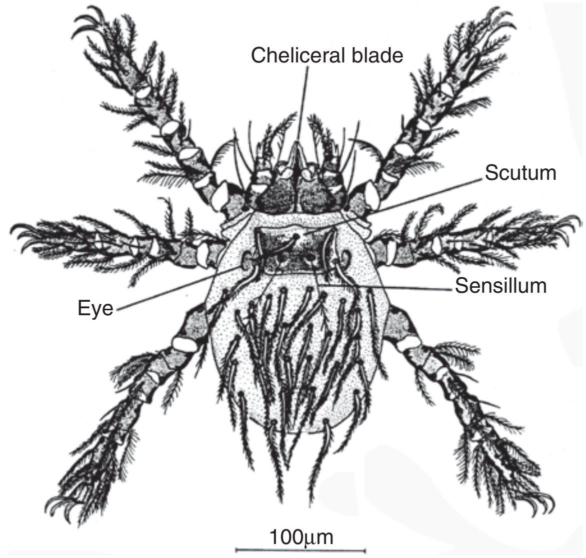
This is the largest order of mites with some 136 families, over 1,100 genera and more than 14,000 species so far described. Unfortunately, the higher classification of this important group is not settled. Actinedids are distributed worldwide in terrestrial, freshwater and marine habitats. They range in size from about 0.1–16 mm. Most Actinedida are soft bodied mites, but heavily sclerotized species occur in some families and there is a wide range of intermediates between the soft-bodied and sclerotized forms. The Actinedida is divided into the Endostigmata and the Prostigmata.

The Endostigmata contain 12 families and is considered to be the most primitive Actinedida. These are small soft bodied free living mites that occur in humus, litter and soil in South Africa. They are believed to be predaceous or microphytophagous.

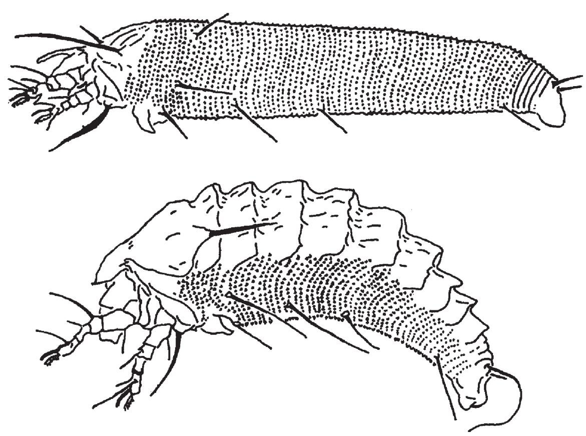
The Prostigmata are divided into three subgroups, the Anystina, Eupodina and Eleutherengona. The Anystina are mostly free-living predators that occur in soil litter, on vegetation and on the seashore. The Parasitengona are a large group of mite species in which most species have a parasitic larva. The Trombidia contain three superfamilies among which are the Trombidioidea with the family Trombiculidae whose larval forms or chiggers are important parasites of terrestrial vertebrates and man (Fig. 60). The other life stages are predators on small invertebrates. The Hydrachnidia contain eight superfamilies. These are freshwater mites, although one family, the Pontarachnidae have secondarily spread into marine habitats.

The Eupodina is the second group and consists mostly of free-living mites. The superfamily Bdelloidea contain the snout mites that prey on other mite species. Some species of snout mites use silk to capture their prey and many spin a cocoon for use during molting. The superfamily Halacaroidea contain marine mites with some freshwater forms. The family Penthaleidae has one species of economic importance, the winter grain mite *Penthaleus major*. The Eriophyoidea (Fig. 61) are plant pests that cause severe damage and can induce gall formation.

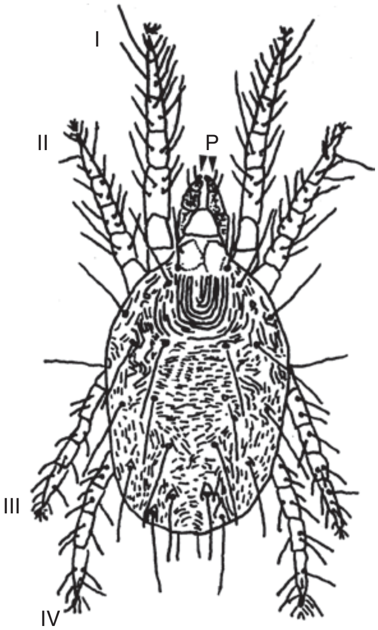
The Eleutherengona are found in various habitats. Spider mites of the superfamily Tetranychoidea are worldwide in distribution. Many species are serious pests of plants. Some produce galls and other types of plant damage (Fig. 62). Some species



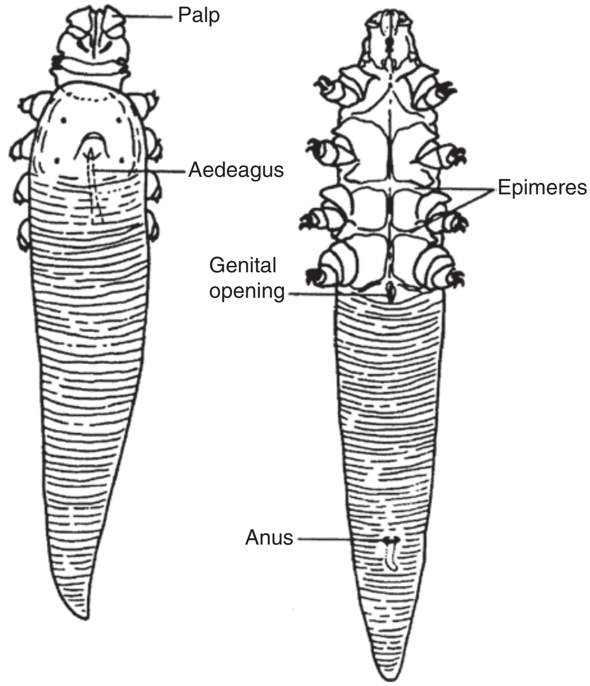
Mites (Acari), Figure 60 **Dorsal view of the larva or chigger of *Leptotrombidium deliense* (Actinedida, Trombidioidea, Trombidiidae), a vector of chigger borne typhus. (from Kettle DS (1995) Medical and veterinary entomology, used with permission of CAB International).**



Mites (Acari), Figure 61 **The two principal body types of Eriophyoidea (Actinedida, Eupodina). *Phytoptus leucothonius* (*top*) with a vermiform body and *Anthocoptes helianthella* (*bottom*) with a fusiform body (redrawn from Lindquist et al. (1996) Eriophyoid mites: their biology, natural enemies, and control, used with permission of Elsevier Science).**



Mites (Acari), Figure 62 **The spider mite *Tetranhychus urticae* (Actinedida, Tetranychoidea). Legs are numbered I, II, III, IV (redrawn from Evans GO, Sheals JG, Macfarlane D (1961) The terrestrial Acari of the British Isles, vol 1. British Museum of Natural History).**

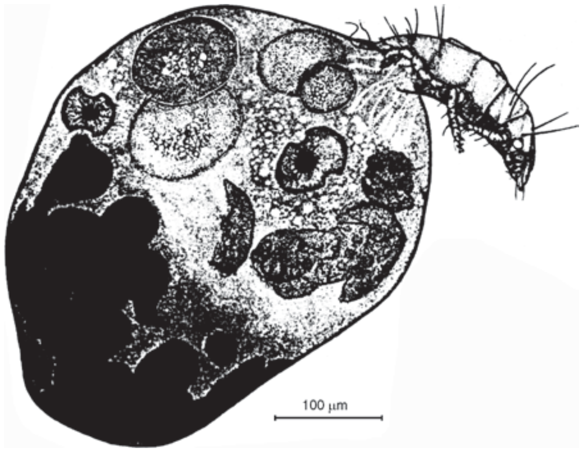


Mites (Acari), Figure 63 **Dorsal view of male (*left*) and female (*right*) *Demodex* (Actinedida, Cheyletoidea, Demodicidae) (from Kettle DS (1995) Medical and veterinary entomology, used with permission of CAB International).**

are the only known mites to transmit plant viruses. An inactive period occurs between each of the final three life stages. During this inactive period, the larva or nymph uses silk to anchor itself to the plant. Spider mites have the capability of rapidly colonizing plants. This ability comes from the large number of generations produced during a given season and not from fecundity. Two heteromorphic females may be produced, the specialized overwintering form, and the typical female form. The superfamily Cheyletoidea are ectoparasites of birds and mammals, and contain the follicle mites. These are further discussed in the section on "skin parasites." Mites of the family Cloacaridae are found in the cloaca of turtles. The superfamily Raphignathoidea contain mostly predaceous mites and species that are pests of plants. The superfamily Pterygosomatoidea contains species that are mostly parasites on other arthropods or on lizards. The superfamily Pomerantizoidea are mostly free living predators in soil litter and humus. The Tarsonemina are small mites from 200 to 600 μm in size. They have unusual life histories and reproductive strategies. Physogastry, a type of reproduction where eggs develop in the female, is found in many parasitic tarsoneminids. In some species, the entire postembryonic development occurs within the female or the eggs transform directly into adults. The physogastric genus (Fig. 64) *Pyemotes* of the family Pyemotidae has a life cycle where all post embryonic development occurs within the body of the female. Some members of the family Pyemotidae are predators of insects of both positive and negative economic importance.

Oribatida

The Oribatida are known as beetle mites (Figs. 65–68) from their outward appearance, or moss mites from their habitats, or box mites from



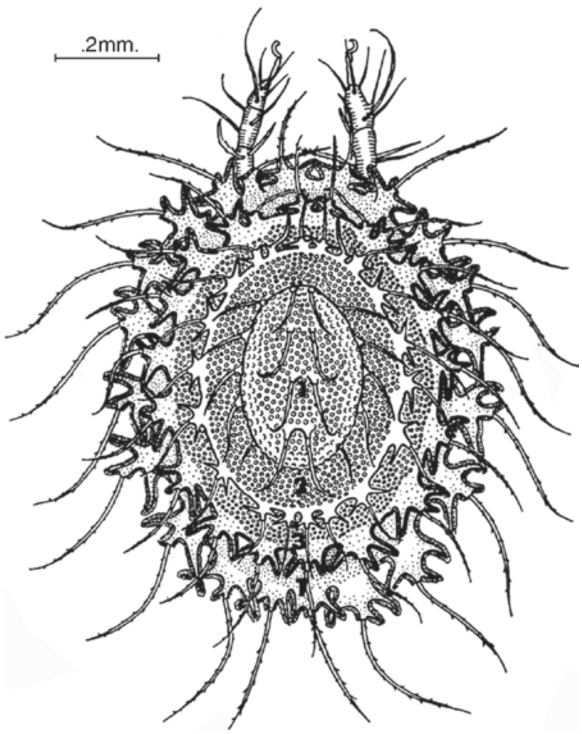
Mites (Acari), Figure 64 Lateral view of a gravid *Pyemotes tritici*. The opisthosoma is the swollen posterior area behind the legs containing eggs and offspring (from Kettle DS (1995) Medical and veterinary entomology, used with permission of CAB International).

Mites (Acari), Figure 65 *Phthiracarus* sp. (Oribatida, Phthiracaroidea), a box mite. When attacked, the mouthparts (gnathosoma) and retracted legs are covered by an operculum-like aspis (arrows), and the lateral body parts are covered by cuticular plates or pteromorphs (arrowheads) (redrawn from Alberti G, Coons LB (1999) The Acari-mites, used with permission of John Wiley and Sons, Inc.).

their ability to (Fig. 65) cover their retracted legs with their body. There are some 150 families, over 1,000 genera, and more than 7,000 described species of Oribatida. The order is divided into the

Mites (Acari), Figure 66 The oribatid *Eupelops torulosus* has a well developed cerotegument or secretion layer (CR) that covers the body surface (S), and movable cuticular plates or pteromorphs that cover lateral body parts (arrowheads) (redrawn from Alberti G, Coons LB (1999) The Acari-mites, used with permission of John Wiley and Sons, Inc.)

Mites (Acari), Figure 67 The oribatid *Heterochthonius gibbus* (Heterochthonioidea, Heterochthoniidae), a beetle-like mite. Note the eyes (arrowheads). The long dorsal setae are able to erect (from Alberti G, Coons LB (1999) The Acari-mites, used with permission of John Wiley and Sons, Inc).



Mites (Acari), Figure 68 **A tritonymph (T) of the oribatid *Cepheus dentatus* (Cepheoidea, Cepheidae) with three scalps on its dorsum, one from each of its previous instars, larva (1), protonymph (2), deuteronymph (3) (relabeled from Hughes TE Mites of the Acari, used with permission of The Athlone Press).**

Macropylina, also known as lower oribatids or Archoribatida, and the Brachyplyina, also known as the higher oribatids or Euoribatida. The Macropylina are divided into five subgroups, and the Brachyplyina are divided into two subgroups. The Oribatida were previously known as the Cryptostigmata but many of these mites completely lack a stigmata or a tracheal system.

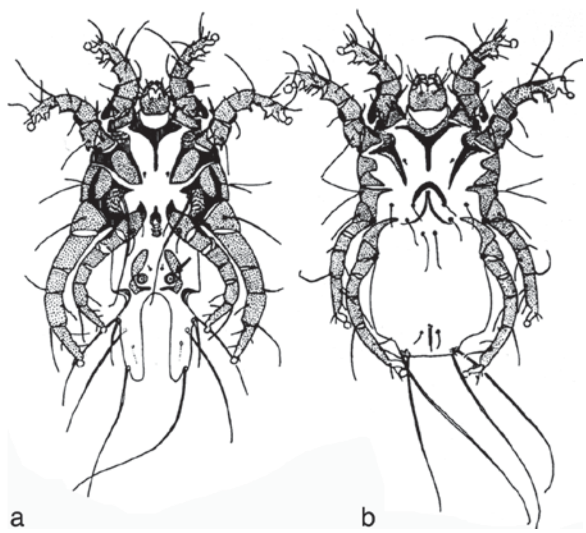
Oribatids are worldwide in distribution. Most range in size 0.3–0.7 mm in size with the smallest 0.15 mm and the largest 1.5 mm in size. Sexual dimorphism is scant or nonexistent. Most oribatids are soil dwellers, but they are also found in moss, humus, lichens, and occasionally on vegetation. A few species are phoretic, usually on beetles. Phoresy is discussed in the section on "Dispersion of mites." Oribatids are slow moving, particulate feeders with mouthparts modified to cut or tear particles up so they can be swallowed. They are saprophagous on decaying higher plant material or microphytophagous on soil microorganisms. The fecal pellet contributes to the soil structure. The oribatids act on the soil system principally by regulating the rate of organic matter decomposition and are considered to be important decomposers. This order is most diverse in the tropics where these mites are the dominant Acari in soils. Some oribatids are intermediate hosts to the sheep tapeworm *Moniezia expansa*. Many species are parthenogenetic, otherwise sperm transfer occurs by stalked spermatophores deposited by a penis. The female picks it up with the genital vestibule. An ovipositor is common. Oribatid mites have a lower fecundity than most other mites.

Acaridida

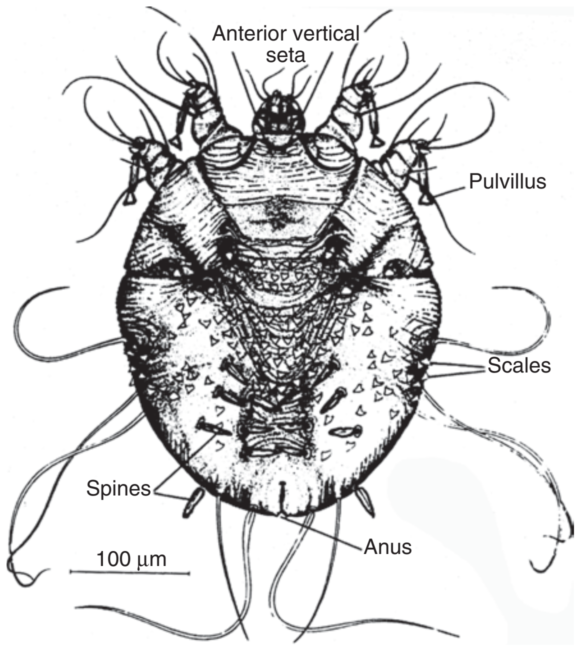
The Acaridida contain some 70 families divided into 800 genera and about 5,000 species. The Acaridida are thought to have evolved within the Oribatida. Acaridids are worldwide in distribution. Sperm transfer occurs by the use of a penis or aedeagus. Sexual dimorphism is common. Most species have a hypopus in the deutonymphal stage. The hypopus is highly modified for survival in marginal conditions and for dispersal by phoresy, or by wind. Acarids include free living species and those that are associated with other animals such as mammals, birds and insects. Parasitic species include skin, hair follicle, or feather parasites of birds and mammals. Others are respiratory parasites of birds and mammals. Most are nonpredatory. Free living species are found in a variety of habitats including decaying organic matter and nests of other animals. The free living forms have evolved some interesting and unusual feeding habits that vary from filter feeding of microorganisms to eating solid food to direct absorption of food material. Many Acaridida have a short generation time which rapidly produces large populations. This allows the exploitation of patchy or ephemeral food resources. Acaridida are weakly sclerotized mites, although sclerotization of the dorsal area occurs to some extent in several species. Acaridida were known as the Astigmata.

The Acaridia are divided into two subgroups, the Acarida and the Psoroptidia. The Acarida contain seven superfamilies. The Schizoglyphoidea are only known from the phoretic deutonymphs collected from a tenebrionid beetle in New Guinea. The Histiostomatidea contain the Anoetidae, the slime mites. Slime mites are filter feeders with a unique gnathosomal structure that strains microorganisms and other food substances. Species of slime mites are found worldwide in liquid or semiliquid habitats where organic matter is undergoing putrefaction. Some slime mites are found in marine environments such as intertidal algal habitats, others occur in the unusual aquatic habitat of pitcher plants. The Guanolichidae are unusual acarids in that they are completely sclerotized in the adult forms. These mites are found in bat guano where they are most likely filter feeders. Canestrinioidea are mostly commensals or parasites found on adult Coleoptera. Most are found under the elytra of beetles where they are thought to feed on exudates, but some occur near the mouthparts of the host from which they obtain food. They are widely distributed except in the Nearctic. The Hemisarcoptoidea occur in a variety of habitats. Most species are associated with wood related habitats. Other habitats of hemisarcoptids include the nests of solitary bees, intertidal zones, and some species live in aquatic or semiaquatic habitats in sap exudates of water-filled tree holes. Mites of the superfamily Glycyphagoidea are mostly associated with mammals, birds, and insects, but some species are pests of stored food products. Most species of the Acaroidea are found in the nests of vertebrates and insects, but some species are found in carrion and dung. The super family Hypoderatoidea are believed to be closest to taxa of the Psoroptidia. Species of Hypoderatoidea are found in the nests of birds and rodents. Often the deutonymphs are subcutaneous or less commonly internal parasites.

The Psoroptidia contain three superfamilies. Mites of the superfamilies Pterolichoidea and Analgoidea are associated with birds. All the Pterolichoidea and part of the Analgoidea constitute the feather mites. Feather mites (Fig. 69) are a large group that are commensals or parasites of birds. They are found on wing, tail feathers or flight feathers. A few are free living in birds nests. In some feather mites with male polymorphism, homeomorphic males have female-like mouthparts and heteromorphic males have strongly aberrant enlarged chelicerae and elongated palpi. Other species of Analgoidea are parasites of the respiratory tract of birds. The superfamily Sarcoptoidea (=Psoroptoidea) contains many economically important mites. Some species cause mange and (Fig. 70) scabies, which are further described in the section on "skin parasites."



Mites (Acari), Figure 69 **Male (a) and female (b) of the feather mite *Euschizalges laglaizeae* (Acaridida, Analgoidea) showing sexual dimorphism. Note the adanal suckers of the male (arrow) (from Kettle DS (1995) Medical and veterinary entomology, 2nd edn, used with permission of CAB International).**



Mites (Acari), Figure 70 Dorsal view of a female scab mite *Sarcoptes scabei* (Acaridida, Sarcoptoidea). Legs III and IV are not visible from the dorsum (from Kettle DS (1995) Medical and veterinary entomology, 2nd edn, used with permission of CAB International).

Dispersion of Mites

Although mites lack the wings of insects, they have other means of dispersal. Crawling short distances is one method. Wind borne dispersal is a common and effective method. In the Tetranychoidea (Actenida: Prostigmata) two methods of becoming airborne occur. Some species use silk threads produced from glands in a form of ballooning. Other species use a dispersal posture to launch themselves into the air.

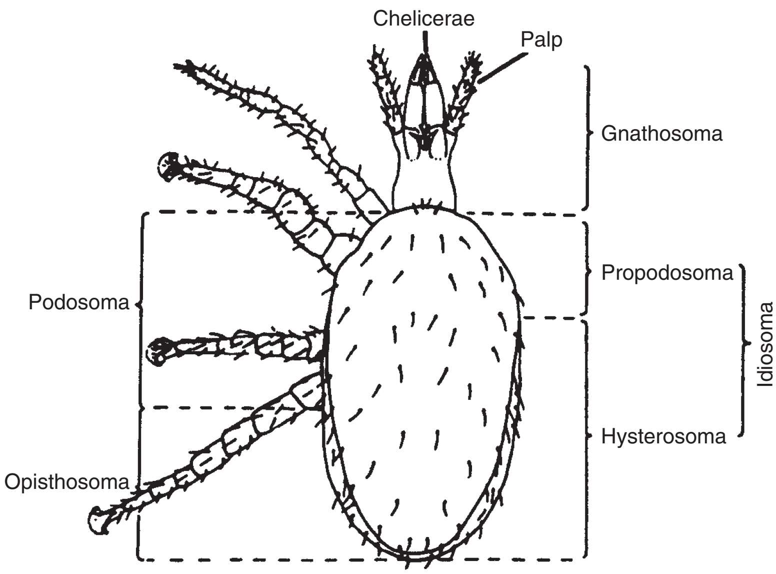
Phoresy, the process where a mite actively seeks out and becomes attached to the outer surface of another animal is an important method of dispersion. Phoretic mites do not feed and ontogenetic development ceases. Phoresy is the most common method of dispersal from one temporary sources of food to another. Phoresy occurs in the Gamasida, the Actinedida, the Oribatida and the Acaridida. Phoretic forms vary from those that resemble the non-phoretic instar to highly specialized forms such as hypopi. *Phoretic hypopi* use claspers or suckers to attach to other animals. Not all attach to animals, some are inert and rely on wind dispersion. The association between phoretics and their hosts ranges from the specific use of a single host species, to the use of a variety of host species. Most phoretic mites are species that can rapidly colonize and exploit temporary habitats. These mites are r-strategists with high rates of reproduction and rapid ontogenetic development. Some associations are not strictly phoretic, i.e., the mites derive nourishment from their hosts. In these mites, the larva is the dispersal form and the other life stages are free-living and usually predatory.

The host is used by ticks and many other parasitic mites for dispersal. This is most effective when the parasitic mite is not host specific, or when the host has a large home range, as is the case of some birds.

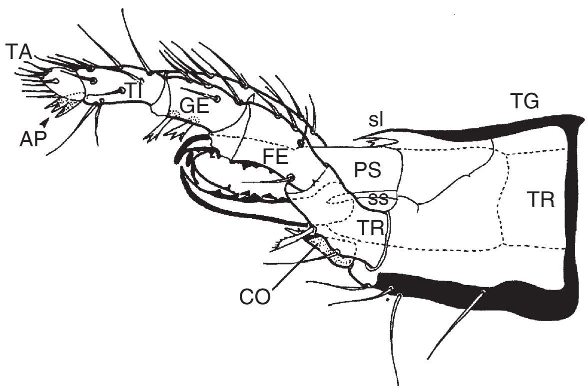
External Anatomy

The body of mites, like all arthropods, can be divided into regions that are based on segments and their appendages. However, mites have little external evidence of segmentation, which makes naming body regions (Fig. 71) difficult. Acarologists have relied on developmental evidence of segmentation during embriogenesis. The most obvious body divisions is the anterior gnathosoma, and the rest of the body, the posterior idiosoma. Another division is the prosoma which constitutes that part of the body that bears the appendages and includes the gnathosoma and the podosoma. Divisions of the idiosoma are discussed below.

The gnathosoma bears the mouthparts. It is not comparable to the head of insects, except that both contain the mouthparts. The gnathosoma (Fig. 72) lacks eyes, antenna, mandibles and does not contain ganglia of the nervous system. The head of insects contains all of these.



Mites (Acari), Figure 71 **Divisions of the body of a mite (from Kettle DS (1995) Medical and veterinary entomology, 2nd edn, used with permission of CAB International).**



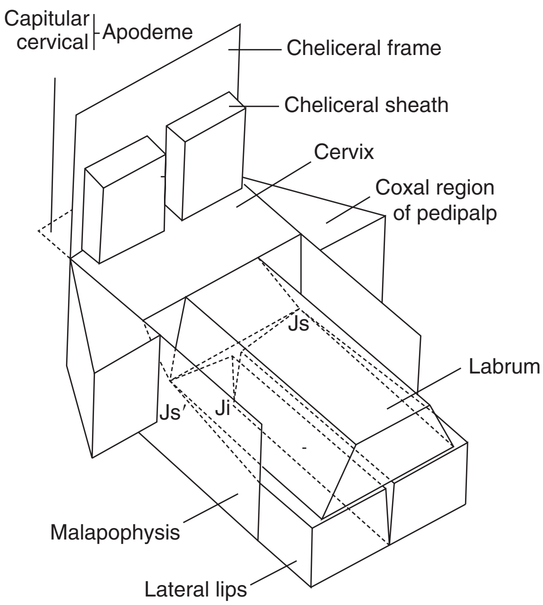
Mites (Acari), Figure 72 **Lateral view of the gnathosoma of a gamasid mite. *AP*, apotele (tined claw); *CO*, corniculus; *FE*, femur; *GE*, genu; *TA*, tarsus; *TI*, tibia; *TG*, tegulum; *TR*, trochanter (of chelicera and palp); *PS*, principal segment of chelicera; *sl*, supracheliceral limbus (gnathotectal process); *ss*, salivary stylus (from Alberti G, Coons LB (1999) The Acari-Mites, used with permission of John Wiley and Sons, Inc).**

The gnathosoma is specialized for sensory perception and food gathering. The adaptations of the gnathosoma to the many types of food used by mites is comparable to the great diversity of mouthparts in insects and has helped make the extensive colonization of diverse habitats by mites possible.

Gnathosoma

The gnathosoma is separated from the idiosoma by a circumcapitular furrow or suture. In many taxa the gnathosoma fits into an anterior cavity formed by the idiosoma, the camerostome.

Because it is composed of several complicated structures in a small space, the gnathosoma is best understood by a diagram of its main components, simplified and drawn in such a way as to emphasize their relationship to one another. The gnathosoma is made up of two components, the cheliceral frame (Fig. 73) and the infracapitulum (=subcapitulum or hypostome). In ticks, the hypostome becomes the toothed device that is used to anchor the parasite to its host. The cheliceral frame, which is part of the integument, serves to anchor the cheliceral sheath. The infracapitulum is located ventral to the chelicerae and bears the palps or pedipalps, labrum and lateral lips. Each palp inserts into the cheliceral frame via the cheliceral sheath which is the coxal region of the chelicerae. The mouth or oral cavity is a space designed to move food into the pharynx and esophagus. The muscular pharynx acts to "suck up" the food. Three structures commonly



Mites (Acari), Figure 73 A diagram that shows the relationships of the main components of a typical gnathosoma. For clarity, only the base of the pedipalps and chelicerae are shown. *Ji*, inferior commissure; *Js*, Js, superior commissures (from Alberti G, Coons LB (1999) The Acari-Mites, used with permission of John Wiley and Sons, Inc).

delineate the mouth: dorsally the labrum, and laterally a pair of lateral lips. A fourth structure, the labium, occurs ventral to the lateral lips, but it is most often reduced or highly modified. The paired malaphophysis lie lateral to the labrum and lateral lips. In some gamasids the malaphophysis have been modified into a corniculus. They may be further modified in other mites. The infracapitulum encloses the mouth and the pharynx.

Chelicerae are movable and function to rip, squeeze, cut, or pierce the wide variety of food utilized by present day mites. Chelicerae often consist of a basal article or trochanter, a principle segment or body which ends with a fixed digit that is heavily sclerotized or hardened, and a movable digit located ventrad of the fixed digit and hinged to the principle segment. The heavy muscles of the chelicerae attach to the trochanter. In this configuration, the chelicerae take the form of a pincer. The chelicerae of the varroa mite *Varroa destructor* have a vestigial fixed digit and a movable digit with two strong teeth that are used to tear the cuticle of the bee to allow the mite to feed on its hemolymph. Chelicerae tend to be elongated in obligate blood feeders of the Dermanyssina and form a channel through which blood can pass into the preoral channel. Chelicerae may be modified for functions other than food gathering. In some gamasida, male chelicerae are modified as gonopods that transfer packages of sperm, the spermatophore, to females.

The palps which were originally sensory appendages used to probe surroundings for the presence of food, remain so in many species. However, in several groups the palps have undergone many modifications: they may be leg-like, as in many gamasids, grasping as in the Cheyletidae and Hydrachnidia, involved in spinning silk in some species of spider mites, reduced to one or two segments in some species of Tarsonemina and Tetranychoidea. Palps may have as many as five segments which are named from proximal to distal: trochanter, femur, genu, tibia, and trochanter.

The gnathosoma has undergone changes for adaptation to the different habitats and type of food used by different mites. One of the most unusual involves the filter feeding slime mites of the Histiostomatoidae (Acaridida, Histiostomatoidea) who inhabit wet, rotting organic material. These mites have modified palps and chelicerae adapted for filter-feeding. The palps have a freely movable flattened distal segment, used to sweep the fluid food suspension towards the anterior part of the infracapitulum. From here particles are raked back into the preoral cavity by means of the specialized non-chelate chelicerae. Other unusual adaptations include the gnathosoma (=capitulum) of ticks and the gnathosoma of *Psoroptes equi*. The former is discussed in the entry on “Ticks,” the latter in the section on “skin parasites.”

Idiosoma

The body proper or idiosoma varies considerably in shape and is closely adapted to the type of habitat occupied by the mite. Common body shapes include a dorso-ventrally flattened body found in unfed hard ticks, a vermiform or fusiform shape, a sac-like body found in gravid Pyemotes, and a box shape. Other shapes such as a laterally flattened body can occur. Sexual dimorphism occurs in some mites.

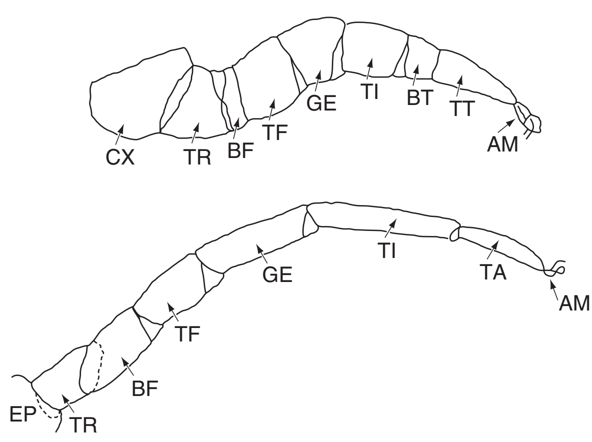
The idiosoma is further divided into the podosoma which contains the four pair of legs, and the opisthosoma which is the rest of the body posterior to the legs. Other divisions of the idiosoma include the propodosoma which contains the first pair of legs, and the hysterosoma which contains the last pair of legs and the rest of the body.

Specialized structures are found on the surface of the idiosoma. The tritosternum is a medioventral structure that extends from the groove separating the gnathosoma from the idiosoma in all orders of Actinotrichida except the Ixodida. In some gamasids it functions to direct prey fluids to the mouth region. A pair of podocephalic channels or canals, which may be open or closed, occur in all Actinotrichida. They usually run from the bases of the first pair of legs to the gnathosoma and carry the products of the coxal glands and other glands. In Opilioararida, these channels run from an area between the first pair of legs to the gnathosoma. No other order of Anactinotrichida has these. Ventral and dorsal sclerotized (hardened) cuticular shields and plates occur on the idiosoma of mites. The shape and location of these are important taxonomic features. A genital opening and an anus are found on the ventral idiosoma. Some mites have a penis (aedeagus). The position of these three structures varies with the species of mite.

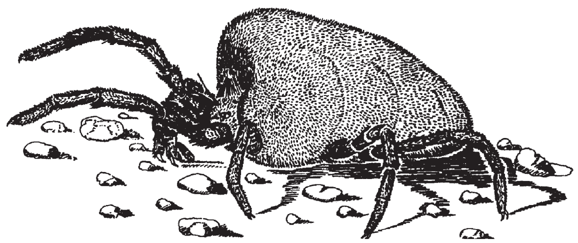
The cuticle of many blood sucking ectoparasitic mites, such as *Echinolaelaps echidninus* and *Dermanyssus gallinae* (Gamasida, Dermanyssoidea, Dermanyssidae) expands during feeding to accommodate large quantities of blood. The most dramatic of these occur in female ixodid ticks that greatly increase their body size during feeding (see the entry on "Ticks"). Some species of oribatids can retract their gnathosoma and legs like a box into an operculum-like device of the cuticle like a box. Others have cuticular plates termed pteromorphs that extend over the lateral body parts and protect them. Some Euroribata carry the dorsal cuticle from a previous molt around as a scalp which may help conceal the mite from predators. Other oribatids stick debris on to their body surface which may have the same function.

Legs

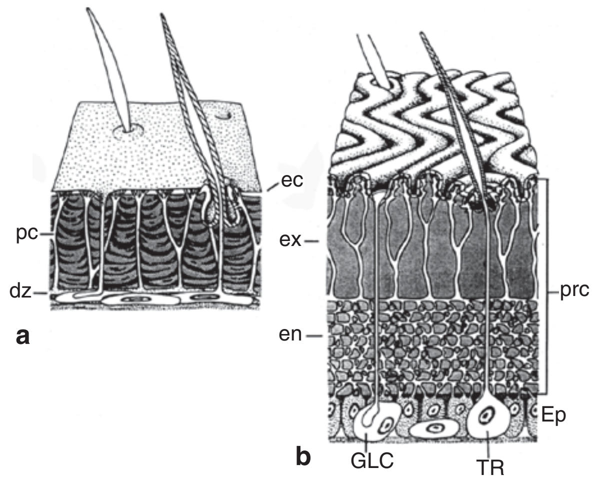
Legs are numbered I through IV from anterior to posterior. Each leg is divided into segments or podomeres which are from proximal to distal: coxa, trochanter, femur, genu, tibia, and tarsus. The distal end of the tarsus forms (Figs. 74 and 75) the terminal part of the leg, the ambulacarum, which bears the claws and a pulvillus



Mites (Acari), Figure 74 Legs of a gamasid (*top*) and an actinedid (*bottom*) mite showing the podomers. *AM*, ambulacrum; *BF*, basifemur (femur I); *BT*, basitarsus; *CX*, coxa; *EP*, epimeron (coxisternum); *GE*, genu: *TA*, tarsus; *TF*, telofemur (femur II); *TI*, tibia; *TR*, trochanter; *TT*, telotarsus (redrawn from Alberti G, Coons LB (1999) The Acari-Mites, used with permission of John Wiley and Sons, Inc.).



Mites (Acari), Figure 75 **A velvet mite, *Trombidium meyeri* (Actinedida, Trombidoidea, Trombidiidae) that uses its first pair of legs as feelers (from Alberti G, Coons LB (1999) The Acari-Mites, used with permission of John Wiley and Sons, Inc).**



Mites (Acari), Figure 76 **Diagram of sclerotized (a) and unsclerotized cuticle (b) of the tick *Boophilus microplus* (Ixodida, Ixodidae). *dz*, deposition zone; *ec*, epicuticle; *en*, endocuticle; *EP*, epidermis; *ex*, exocuticle; *GLC*, dermal gland cell; *pc*, pore canal; *pre*, procuticle; *TR*, trichogen cell (simplified) (from Coons LB, Alberti G (1999) The Acari-Ticks, used with permission of John Wiley and Sons, Inc).**

between the claws which functions as a type of cushion. Secondary divisions, especially with the trochanter and femur can occur. A free movable coxa exists in the Anactinotrichida but not in the Actinotrichida. Many acarologists doubt the presence of a true coxa in the Actinotrichida and therefore use the term epimeron for this leg component. Epimeres are often fused with other components of the ventral idiosoma and are sometimes referred to as a coxisternum. Joints between the body and the legs, between the podomeres, and between the tarsus and the apotele allow movement of the legs. Muscles and tendons run between joints. Muscles, hydrostatic pressure from hemolymph, and bending stresses are used to produce movement of leg segments.

Legs of mites are modified for different types of locomotion, and for special uses such as habitat adaptation, nutritional and sensory functions, and sexual behavior. In general, slow moving mites have stout heavily sclerotized legs, while faster moving mites tend to have long, slender legs. Many Acari have the first legs modified as elaborate sense organs or feelers that are used to touch the soil with their distal parts or are waved in the air in a similar fashion as insect antenna. Often these legs are not used for locomotion. In some soil mites the second pair of legs is much stronger and bears modified setae adapted for digging. Often endoparasitic mites have reduced legs. In some Gamasida, males have specialized leg spurs that grasp the female during sperm transfer. In some Acaridida legs are modified for holding females during copulation. Mites capable of jumping occur in all orders of Actinotrichida. Jumping is associated with modification of the fourth pair of legs.

Many water mites (Hydrachnidia) are fast and elegant swimmers. Their legs have movable, flattened seta that passively erect during the power stroke to increase the thrust and collapse during the recovery movement of the leg to reduce water resistance.

Integument

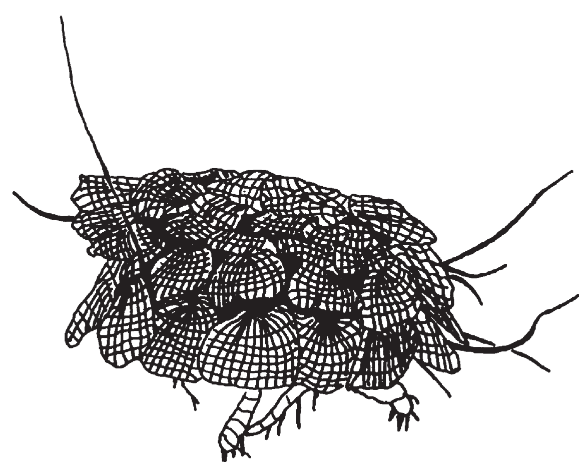
The integument is made up of a non-cellular cuticle and an underlying layer of cells, the epidermis. The epidermis secretes the cuticle (Fig. 76). Interposed between the epidermal cells are trichogen cells that extend into seta and dermal gland cells whose product is released into canals that lead to the surface. The cuticle is shed during molts which allow the mite to grow in size and develop adult characteristics. The cuticle is thrown into projections termed setae. Shapes of setae commonly include but are not limited to simple hair like projections, bipectinate, spine-like, fan-like. Setae may be scarce, or they may completely cover the body of the mite. Some setae have the ability to erect. Setae have different functions. Some are sensory and are further discussed in the section on "Nervous and sensory organs." The number, position and shape of setae are important taxonomic characteristics. Cuticular scales occur in some mites.

The cuticle has many functions. It acts as a barrier to pathogens such as bacteria and pathogenic protozoa and the eggs of insect parasites. It provides protection from mechanical injuries of predators.

The cuticle helps to prevent desiccation through loss of water. Hydrophobic substances in the cuticle prevent excess wetting. The cuticle is involved in gaseous exchange with the atmosphere when the tracheal system is lacking or not well-developed as in all larval mites and in acaridid mites. Cuticular spines and ridges help retain a film of air around the body during flooding. In aquatic species these cuticular modifications are further developed for use in plastron respiration. Regularly spaced surface microstructures or granulations occur on some mites in polar regions. A layer of air trapped by the granulations may facilitate survival by providing a mechanism of cuticular respiration in waterlogged polar soils. This layer of air may also prevent freezing by insulating the mite from direct contact with the ice. The cuticle is a site for muscle attachment. Glands and receptor organs open onto the surface of the cuticle.

A cuticular lining occurs in the fore and hind gut of the digestive system, the tracheae, ducts of many glands, and part of the reproductive system.

The general structure of the acarine cuticle is similar to the cuticle of other arthropods. The cuticle is either sclerotized or unsclerotized. Sclerotization is a process that imparts greater strength by hardening the cuticle. Heavily sclerotized armor plates protect against the attacks of predators (Fig. 77). Unsclerotized (Fig. 76) cuticle is more flexible. The cuticle has two layers, a thicker internal procuticle and a thinner external epicuticle. Chitin is found in the procuticle. In some cases, the procuticle is divided into an inner epicuticle and an outer exocuticle. The epicuticle contains several sublayers depending on the mite species. These are named from the most external: the cement, wax, cuticulin, and dense homogeneous layers. External to the cuticle, two additional layers may be present that are collectively termed the secretion layer or cerotegument. The secretion layer may take the form of distinct granules or other structures which contribute to the appearance of the surface (Fig. 77). Pore canals pass through the procuticle to join structures known as epicuticular canals, wax filaments or wax canals that extend through the epicuticle to the surface. Pore canals have an unknown function, they may allow the exchange of material such as gas, water and lipids between external and internal compartments.

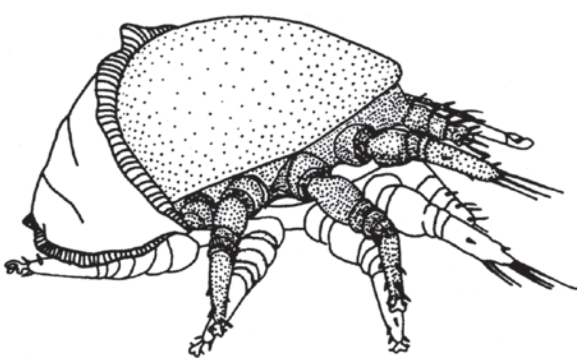


Mites (Acari), Figure 77 Tritonymph of *Conoppia palmicincta* (Oribatida, Cepheoidea, Cepheidae) with fan-shaped setae that completely cover the body (redrawn from Alberti G, Coons LB (1999) The Acari-Mites, used with permission of John Wiley and Sons, Inc).

The cuticle varies considerably in thickness depending on the species of mite and the region of the body. It is a dynamic structure; many of its parts can be modified, or rebuilt or replaced during molting, sclerotization, wound repair or after abrasion of the secretory layers. The impermeable nature of the cuticle is important in preventing desiccation. Mineralization of the procuticle in some Oribatida may further harden the cuticle.

Molting includes apolysis, the separation of the old cuticle from the epidermis and ecdysis, the casting off of the remnants of the old cuticle. In between apolysis and ecdysis, the old separated cuticle, except for (Fig. 78) the epicuticle and secretion layers, is digested and a new cuticle is deposited. Following ecdysis, the new cuticle may be sclerotized or mineralized. The pharate form is the next instar still within the old exuviae. Molting is similar in most mite species. In general, the old cuticle splits along different lines depending on the species of mite, and the new instar leaves the exuvia. Little is known about the hormones involved in the molting of mites.

In some mites there is little or no period of inactivity accompanying apolysis. In others, the instar becomes inactive just before and during apolysis. In general there are no molts after the adult phase except in Prostigmata.



Mites (Acari), Figure 78 Molting in *Uroobovella marginata* (Gamasida, Uropodoidea, Urodinychidae). The old cuticle has split around the anterodorsal border, and the new instar leaves the exuvia (from Alberti G, Coons LB (1999) The Acari-Mites, used with permission of John Wiley and Sons, Inc).

Physiology of Mites

Glands

Mites have endocrine and exocrine glands. Endocrine glands or endocrine organs produce hormones and empty internally while exocrine glands produce a variety of substances and empty onto the surfaces of the mite.

Unlike insects where endocrine organs have been identified and well studied at the cell and molecular level, acarine endocrine organs are classified only by their structure, and thus they are spoken of as putative endocrine glands. These are located mostly around the central nervous system and consist of a retrocerebral organ complex, the lateral organs and paraganglionic plates.

Exocrine glands are described based on their morphological location. Dermal glands are common throughout the Acari. They are small glands located within or just below the epidermis. A duct leads to the cuticular surface. These glands have a variety of functions that include secretion of an allomone, a sex attractant pheromone in ticks and some other mites, and the secretion of a glue in some males of the family Arrenuridae (Hydrachnidia: Arrenuroidea) that is used to attach the female during mating. Arrenuroids are freshwater mites. Other glands are the prosomal glands, lateral glands and anal glands. Two important types of prosomal glands are salivary glands and silk glands. Salivary glands produce digestive enzymes used by the mite to liquefy or predigest their prey and other food prior to swallowing it. In ticks, salivary glands are specialized for osmoregulation. Silk produced by silk glands is used for a variety of functions.

Muscles

All muscles in mites are striated. There are two types of striated muscles, somatic and visceral. Somatic muscles are connected to the integument via specialized attachment complexes. Somatic muscles are divided into three groups: those muscles that move the legs, those that move the gnathosoma and those that move the body proper. Visceral muscles are found around hollow organs such as the digestive system, Malpighian tubules, and parts of the reproductive organs. They are used to move their contents. In many mites a specialized structure, the endosternite, lies within the podosoma. It is analogous to a "floating tendon" and serves as a central suspensory attachment for certain somatic muscles.

Fat Body

The fat body is a diffuse organ that consists of strings of cells, the trophocytes, that are often closely associated with trachea, internal organs and nephrocytes. While a fat body occurs in both superorders, not all mites have a fat body and some develop a fat body only during certain parts of their life cycle. In mated fed female ticks, the fat body under the influence of the hormone ecdysone, undergoes a complete ultrastructural reorganization and produces the female protein vitellogenin, which is secreted into the hemolymph and taken up by developing eggs to become the yolk protein vitellin. Yolk is used as food for the developing embryo.

Circulatory System

Mites have several types of hemocytes that circulate in the hemolymph. Some mites have a pulsating organ or heart, other mites do not. The heart has a specialized striated muscle with an ultrastructure similar to the striated muscle of insect hearts. Hemolymph enters the heart through openings, the ostia, and then is pumped out the anterior end. With or without a heart, circulation is aided by body movements and muscular contraction.

The hemolymph of ticks undergoes coagulation when exposed to air. Mites can recognize self from nonself and can initiate encapsulation of large foreign objects, such as parasite eggs, by hemocytes. Encapsulation is a defense designed to isolate foreign objects. Mites have immune reactions similar to those of insects.

Nephrocytes or pericardocytes are round single cells that are associated with various organs, especially reproductive organs. They function to sequester certain toxic compounds from the hemolymph.

Respiratory System

Mites have three different respiratory mechanisms: gas diffusion through the integument, gas transportation through a tracheal system, and gas exchange through specialized porose areas on the integument. All prelarvae and most larvae respire through their integument. In adults, respiration through the integument is limited to soft bodied forms such as the Acaridida. Respiratory mechanisms in mites must also be adapted to avoid desiccation as well as exchange gasses in these small animals with large surface areas.

A tracheal system is made up of internal tubes that become smaller as they lead to the various organs. Spiral coils inside trachea termed taenadia impart rigidity that keeps them open. Trachea lead to the outside through openings, the stigmata, that are sometimes associated with a peritreme, a canal or gutter-like extension from the spiracles. In some species the peritreme is partially closed. A peritreme usually extends anteriorly or less commonly posteriorly from the stigma. It is thought that peritremes evolved to help keep the spiracles free from blockage. Peritremes are found only in the Holothyrida, Gamasida and Prostigmata. The peritreme and stigma are sometimes surrounded by a prominent sclerotized shield like area of the cuticle, the peritrematal shield. The position of the stigmata, the presence and shape of the peritreme and associated shield are used as taxonomic characteristics.

In mites that live in water, plastron respiration occurs as trapped air in specialized areas of the body. Often a plastron is associated with modifications in a peritreme. Trapped air is also believed to act as a flotation bubble. Porose areas of the integument that are involved in gas exchange occur in some species of Oribatida. They are believed to have originated independently from the respiratory systems of related mites.

Digestive System

Mites utilize a wide variety of food that ranges from solids such as pollen, fungi and tissues of prey to liquids such as vertebrate blood and plant fluids. The range of food habits in free living mites include predaceous (feeding on animals), phytophagous (plant feeding), mycetophagous (feeding on fungi), saprophagous (feeding on dead organic matter), microphagous (feeding on small food pieces), and coprophagous (dung feeding) forms.

The digestive system has three major divisions: a foregut lined with cuticle that extends from the mouth, a midgut that lacks a cuticle, and a hindgut that also has a cuticular lining. The foregut consists of the muscular pharynx and esophagus that passes through the synganglion to enter the midgut. The foregut acts mostly as a conduit of food into the midgut where digestion and absorption of food takes place. Mites partially digest their food before it is taken up into the digestive system using secretions from prosomal glands, especially salivary glands. The meal is taken up in cells that line the midgut, sorted into the lysosomal system of the cell and digested within the lysosomes in a process termed heterophagy. The digested material is then released into the hemolymph. A peritrophic membrane occurs in some mites. The digestive system, especially the midgut, is modified depending on the type of food eaten. Substantial modifications occur in the blood feeding ticks which take in a large meal of blood and in the plant feeding mites which must deal with plant fluids. Microorganisms, which are probably symbiotic, occur in the digestive systems of mites.

Several generalized anatomical types of digestive systems occur in mites. A parasitiform type occurs in the Oplioacarida, Holothyrida, Ixodida, and Gamasida. It is characterized by an esophagus, a small ventriculus with relatively large paired caeca, a short postventricular midgut leading to a short hindgut that in turn leads to an anus. One pair of Malpighian tubules is present except in the Holythrida which have two pair. A trombidiform type of digestive system occurs in most of the Actinedida. It consists of an esophagus that leads to a midgut that is divided into a small ventriculus with large paired caeca. The midgut ends blindly, no postventricular midgut or anus exists. The midgut is closely associated with a dorsomedian excretory organ that opens to the outside via a uropore. A sarcoptiform type of digestive system occurs in the Oribatida and Acaridida. It consists of an esophagus that leads to a midgut that is divided into a ventriculus with small caeca and a postventricular midgut consisting of a colon and postcolon that in turn lead to a hindgut and anus. Malpighian tubules, described in the section on the "Excretory system," are present in some taxa but reduced or absent in others.

Excretory System and Osmoregulation

Excretory organs are involved in the elimination of the end products of nitrogenous metabolism, which in the Acari is guanine and rarely uric acid. Excretory organs include Malpighian tubules and the dorsomedian excretory organ. Osmoregulatory organs regulate water and or ions, and include coxal glands or nephridia, the salivary glands of ixodid ticks, genital papillae, ClaparÈde organs, axillary organs and pregenital capsules.

Malpighian tubules originate in the posterior region of the digestive system and end blindly within the anterior hemocoel. They are present in the Holothyrida, Ixodida, Gamasida and some Acaridida, but are absent in the Actinedida and Oribatida. The ultrastructure of cells in the Malpighian tubules are similar to those of Insecta.

Wastes from the Malpighian tubules pass into the digestive system and are eliminated with the feces.

The dorsomedian excretory organ is found in actinedids and consists of the postventricular midgut and the hindgut which together are modified as an excretory organ. The organ functions in nitrogenous metabolism and osmoregulation. It is most developed in mites that are predators on plants such as the tetranychids. Some mites such as the human follicle mite store metabolic wastes in cells rather than eliminate them.

Coxal glands are derived from the nephridia of annelid arthropod ancestors and are found in both superorders. Coxal glands consist of a thin walled sacculus that faces the hemolymph and a convoluted tubule that leads to an opening to the outside. The sacclus filters the hemolymph, and the convoluted tubule is thought to reabsorb substances including ions from its lumen. Salivary glands are the principal osmoregulatory organs of ixodid ticks during feeding. In addition, they play an important role in preventing dehydration by secreting a compound that takes up water from the air onto the mouthparts. The compound is swallowed or reabsorbed through a specialized cuticular region of the tick.

Genital papillae are commonly found in Actinotrichida where they are considered to be a characteristic feature of this taxon. Genital papillae have different shapes but generally consist of an eversible sac-like structure located anterior to the genital opening. This sac-like structure has an ultrastructure typical of transporting cells. The papillae are protected by two progenital lips. The number of papillae varies or they may be completely lacking. In some species of water mites, multiple papillae may be found on the external surface. Prelarvae and larvae, which lack a progential chamber, have Claparède organs located between the bases of legs I and II which function as osmoregulatory organs. Axillary organs are found on some acaridid mites that inhabit semiaquatic or aquatic environments. These organs are found between the bases of the first and second pairs of legs and have an elevated band of sclerotized porous cuticle. Cells associated with these organs have an ultrastructure typical of transport cells. Axillary organs are probably homologous to ClaparÈde organs. Pregenital capsules occur only in the Opilioacarida where they are found anterior to the genital openings in both sexes. Their function is unknown. Each capsule has an external cover and an evertable sac.

Nervous and Sensory System

The ventral chain of ganglia, which is common in arthropods, is condensed in mites into a mass of nervous tissue termed the synganglion. This is the central nervous system from which sensory and motor nerves originate and extend to parts of the body and organs. A peripheral nervous system is present in some species.

The sensory system includes setiform sensilla sensory hairs and sensory setae which are often grouped as setiform sensilla, nonsetal sensilla, and photoreceptors. Different setiform sensilla function as chemoreceptors, temperature and humidity receptors, and mechanoreceptors. Some setiform sensilla have multiple functions, for example, as both a chemoreceptor and a mechanoreceptor. The ultrastructure of mite sensory receptors is similar to those of insects. A great number of setae are found on most mites, only some of which are known to have a sensory function. The position and pattern of setae is an important taxonomic characteristic.

Sensory setae, like those of insects are classified by their external shape as follows. A peg or cone shaped seta is a sensillum basiconicum, a bristle or spine shaped seta is a sensillum chaeticum, and a seta that has its external portion freely moving in the form of a hair articulated with a base is a sensillum trichodeum.

Nonsetal sensilla function as mechanoreceptors that can sense a variety of stimuli such as gravity, substrate vibrations, sounds and strains within the exoskeleton caused by movements of the mite. Nonsetal sensilla are classified as slit sense organs, cupules, and lyriform fissures. The latter are unlike those of spiders.

Photoreceptors in mites are divided into three types: eyes, secondary light receptors and photosensitive areas. The eyes of mites are simple ocelli that lack facets found in the compound eyes of insects. Typically they have a lens, which is the only cuticular part, and an underlying photoreceptor apparatus. Eyes are located in various places on the prosoma depending on the species of mite. Not all mites have eyes.

Reproductive System

A major reason for the success of mites is their diversity of reproductive strategies. Few common themes occur, but all mites are dioecious, i.e., with separate sexes, and all have internal fertilization. Three modes of reproduction exist in the Acari: diplodiploidy, haplodiploidy and thelytoky.

Mites with diplodiploidy are biparental, parthenogenesis is absent. Sexual reproduction is used to produce offspring. Somatic cells of both sexes are diploid. Diplodiploidy is thought to be the ancestral form of reproduction in mites, and it is the most common mode of reproduction of the Acari. It is found in the Ixodida, the Gamasida, the Actinedida, the Acaridida and the Oribatida. Diplodiploidy is the dominant form of reproduction in the Ixodida and Oribatida.

Parthenogenesis occurs in haplodiploidy and thelytoky. Haplodiploidy produces diploid females and haploid males. Two kinds of haplodiploidy, arrhenotoky or parahaploidy, occur. Arrhenotoky produces diploid females from fertilized eggs while haploid males are produced parthenogenetically. This results in biparental females and uniparental males. Often arrhenotoky produces a female-biased sex ratio. Arrhenotoky is not common in mites, but is found in some Acaridida. Fertilization occurs in parahaploidy, but the paternal set of chromosomes is lost in the diploid male embryo and thus only the maternal set of chromosomes are passed on. Parahaploidy occurs in the Phytoseiidae (Gamasida, Ascoidea). Either sex can develop from unfertilized eggs in deuterotoky. Deuterotoky is not considered to be an independent type of reproduction, but is part of a cyclical type of parthenogenesis. Thelytoky produces females by parthenogenesis. Males are either rare or most commonly absent. It is most common in the Oribatida.

Mites have both indirect and direct sperm transfer. In indirect sperm transfer, the male uses a package of sperm, a spermatophore, that it places on the substrate, and the female transfers the spermatophore to its reproductive opening. In direct sperm transfer, sperm is directly transferred to the genital opening of the female in a spermatophore, or transferred with a penis during copulation. Direct sperm transfer using a spermatophore can occur via the primary genital opening of the female in a process termed tocospermy or via the insemination pore, a secondarily developed genital opening in a process termed porospermy. Insemination pores lead to a complex specialized organ, the sperm access system in the Dermanyssina (Gamasida). Copulation occurs in some mites of the Actinedida and Acaridida.

Economic Importance

Skin Parasites

Skin parasites of vertebrates are found in all Orders of mites except Opiloacarida and Holothyrida. We shall consider only those known to cause pathology in humans and domestic animals. The canary lung mite, *Sternostoma tracheacolum* (Gamasida: Dermanyssoidea: Rhinonyssidae), occurs in the respiratory tract of canaries and can cause illness and even death. This mite is thought to be larviparous. Treatment includes pesticides administered in diets or as aerosols. *Pneumonyssoides caninum* (Gamasida: Dermanyssoidea: Halarachnidae) is usually a benign inhabitant of the sinuses and nasal passages of dogs, but they can cause pathological conditions such as sinusitis. *Pneumonyssus simicoloa* (Gamasida: Dermanyssoidea: Halarachnidae) is found in the lungs of monkeys and baboons. It is tolerated in the natural state, but in captivity can cause a disease with a mortality up to 70%. The tropical rat mite, *Ornithonyssus* (=*Liponyssus*) *bacoti* (Gamasida: Dermanyssoidea: Macronyssidae) is found in tropical and temperate regions worldwide. It is normally a parasite of rats but can bite humans producing a sharp pain and severe itching. Sensitive people can develop a dermitis from the bite.

Several species of skin parasites attack poultry. The tropical fowl mite, *Ornithonyssus bursa* (Gamasida, Dermanyssoidea, Macronyssidae), occurs in tropical and subtropical areas worldwide. It is a common parasite of the English sparrow, *Passer domesticus* and an ectoparasite of poultry. Heavily infested poultry can become listless. Workers associated with poultry are frequently bitten resulting in a slight irritation. The northern fowl mite, *Ornithonyssus sylviarum* (Gamasida, Dermanyssoidea, Macronyssidae), occurs in the north temperate regions, and in New Zealand and Australia. Heavy infestations in poultry can reduce egg production. This mite bites poultry workers and can cause extensive itching. The chicken mite (red chicken mite or roost mite), *Dermanyssus gallinae* (Gamasida, Dermanyssoidea, Dermanyssidae), is worldwide in distribution. It parasitizes domestic poultry, pigeons, starlings and sparrows. The mite attacks at night; during the day it hides in crevices, under floors and in debris where its eggs are laid. Damage to poultry includes less egg production, and weight loss which makes poultry less marketable.

The house mouse mite *Liponyssoides* (=*Allodermanyssus*), *sanguineus* (Gamasida, Dermanyssoidea, Dermanyssidae) transmits the pathogen of rickettsialpox to humans. Both nymphs and adults feed on the blood of a variety of rodents. The mite is a nest dweller and is usually found on its host only when feeding. Rickettsialpox is caused by *Rickettsia akari*, a member of the spotted fever group of rickettsiae. Rickettsialpox is found in many urban areas of the United States, Russia, and Korea. The disease is mild with no recorded fatalities, and has a benign clinical course. Rickettsialpox is characterized by a vesicular rash, a local eschar or tache noire, and a local cutaneous lesion. The eschar, an ulcer covered with a black crust, is a local reaction that occurs at the bite site. The antibiotics tetracycline and chloramphenicol are used as treatments. Prevention includes controlling rodent and mite populations.

Chiggers are larvae of trombiculids (Actinedida: Prostigmata: Trombidioidea: Trombiculidae) that parasitize every major group of terrestrial vertebrates. In humans, chiggers transmit the serious disease chigger-borne typhus. The adults are fungivorous mites that feed within fungal cells using stylettiform chelicerae. The small chelicerae of chiggers are used for penetration of the hosts epidermis and serve as anchors during the attachment of the parasite. A saliva produced by the mite dissolves the integumental layers producing a feeding channel, the stylostome, through which the parasitic larvae takes up predigested material.

Several species of larval trombiculids transmit chigger-borne typhus also known as scrub typhus or tsutsugamushi disease. The causative agent of this disease is *Orientia tsutugamushi*, a member of the typhus group of rickettsiae. Chigger-borne typhus is a zoonosis, humans are only accidental hosts of the pathogen. The disease has four essential components: *Orientia tsutugamushi*, chiggers, rats, and secondary or scrub forms of vegetation. Chigger-borne typhus occurs in Australia, India, Korea, and Japan. *Orientia tsutugamushi* exists as three major antigenic types which has prevented the development of an effective chigger-borne typhus vaccine. Infection with one strain produces long term immunity only to that strain. Other strains can cause another cases of chigger-borne typhus in the same individual. All strains produce a similar disease which manifests itself as chills, fever, and headache after an incubation period of one to three weeks. An eschar followed by a skin rash occurs in less than half of the cases.

Fatal outcomes of chigger-borne typhus ranges from 0 to 50%. The same antibiotics used for rickettsialpox are used to treat chigger-borne typhus.

All species of the genus *Demodex* (Actinedida, Cheyletoidea, Demodicidae) are parasites on mammals and cause demodectic mange or demodecosis which can be serious or of little pathology depending on the host species which include but are not limited to humans, dogs, cats, cattle, hogs, deer, hamsters and various rodents. Transmission is by bodily contact. Two species parasitize humans. These mites are minute, 0.1–0.4 mm long, with an elongated abdomen and eight stubby legs. The follicle mite, *Demodex folliculorum*, lives head down in hair follicles. It is the most widespread parasite of man with a prevalence that approaches 100%. All life stages including eggs may be present in a single follicle. These mites are most common in facial areas, especially oily regions around the eyelids and nose. *Demodex brevis* is found in sebaceous glands. Neither mite causes much pathology. *Demodex canis* causes a more serious pathology in dogs. The demodecosis is either localized or generalized. The latter is a severe form and must be treated or a fatal septicemia can develop. About 10% of cases are of the generalized form.

Many species of the family Pyemotidae (Actinedida: Tarsonemina: Pyemotoidea) are stored product pests and secondarily cause problems with workers. *Pyemotes tritici* which kills its prey with a toxin can cause skin lesions and other problems in humans. The hay itch mite, *Pyemotes ventricosus*, attacks people who come in contact with infected grain or hay.

Mange and scabies are terms often used interchangeably to describe diseases caused by species of mites from the families Psoroptidae and Scarcoptidae of the superfamily Sarcoptoidea (Acaridida). Usually scabies or the scab describes a collective disease, while mange is used to distinguish which mites cause the disease.

Three genera of Psoroptidae, *Psoroptes*, *Choriptes*, and *Otodectes*, are important skin parasites of mammals. These are non-burrowing mites. Psoroptic mange, caused by species of the genus *Psoroptes*, is severe and can sometimes be fatal in cattle and sheep. The family Psoroptidae is worldwide in distribution and is found on many mammalian species. Psoroptic mange is caused by a single cosmopolitan ectoparasitic species, *Psoroptes equi* (Acaridida: Sarcoptoidea: Psoroptidae). This mite has many varieties that are named for their hosts, thus *P. equi* var. *ovis* on sheep, *P. equi* var. *bovis* on cattle, etc. *P. equi* is a very small mite about 0.5 mm in length that spends its entire life on its host. Mites are spread rapidly by the close contact of animals. *Psoroptes equi* is most often found at or near the base of hairs. Mites pierce the host's skin to feed on lymph and tissue fluids which results in an inflammatory response that causes a debilitating dermatitis and mangy or puritic scab formation. The mouthparts of *Psoroptes equi* are adapted to feed on liquefied and semi-liquefied material from abrasions caused by the shearing actions of their mouthparts. The mouthparts form a suctorial cup that serves to direct food into the preoral cavity. Infected animals often have lesions that ooze, and they suffer a great deal of irritation. This irritation often causes the infected animal to scratch against objects to relieve itching which results in further damage to fur and skin. A complete life cycle of *Psoroptes equi* from egg to egg can occur in as little time as 11 days in some hosts, or up to three weeks in others. In sheep and cattle, psoroptic mange is most common in autumn and winter. In the summer the disease enters a latent phase due mostly to shearing or shedding of hair, host nutrition and grooming. Psoroptic mange annually causes millions of dollars in losses in North America.

Chorioptic mange, caused by species of the genus *Chorioptes*, is a less serious disease than psoroptic mange. Chorioptic mange is caused by two species of mites, *Chorioptes bovis* that infests horses, sheep goats, cattle and llamas, and *Chorioptes texanus* that infests goats and cattle. These mites feed on debris on the skin surface and do not burrow. Their mouthparts are modified to scrape the surface of the hosts skin. The mites infest new hosts by contact with uninfected animals.

Parasitic otitis is caused by *Otodectes cynotis* (Acaridida: Sarcoptoidea: Psoroptidae). These mites infest the ears of a wide variety of carnivores. Convulsions can occur in heavily infested dogs and cats.

Sarcoptic mange occurs in a variety of mammalian hosts including man. It is caused by the scab mite *Sarcoptes scabiei* (Acaridida: Sarcoptoidea: Sarcoptidae), which has varieties on different hosts. Scab mites are very small; females are about 0.3–0.5 mm long and 0.2–0.4 mm wide. Males are about 3/4 the size of females. Most scab mites complete their life cycles in 10–14 days. The varieties that infest humans, dogs and hogs are the most studied. Males and females burrow about 1 mm into the skin of the host. Gravid females lay eggs in the burrows. The hexapod larva commonly enters hair follicles where they feed and molt into an octopod protonymph. This stage is followed by a tritonymph and the adult.

The scaly leg mite, *Knemidokoptes* (=*Cnemidocoptes*, = *Knemidocoptes*) *mutans* (Acaridida: Analgoidea: Knemidokoptidae), causes scaly leg disease in domestic poultry. This mite burrows into the skin where it lives and deposits its eggs in channels. The disease presents as a swollen condition in the shank of the bird with deformity and encrustation of shank scales. Mites are easily transmitted from bird to bird by contact. The depluming mite, *Knemidokoptes gallinae* (Acaridida: Analgoidea: Knemidokoptidae), feeds at the base of feathers causing intense itching in the bird which then may pluck its feathers for relief. Mange of parakeets is caused by *Knemidokoptes pilae* (Acaridida: Analgoidea: Knemidokoptidae). *Knemidokoptes jamaicensis* infests canaries. *Epidermoptes bilobatus* (Acaridida: Analgoidea: Epidermoptidae) can cause a scaly skin disease in poultry that can result in weight loss, and is fatal in some birds with heavy infestations.

Two species of mites are internal parasites of poultry. *Cytodites nudus* (Acaridida: Analgoidea: Chytoditidae) is found in the linings of the respiratory tracts of poultry, mostly chickens. *Laminosoptes cysticola* (Acaridida: Analgoidea: Chytoditidae) is found in the tissue of chickens and turkeys where populations can reach in the millions. The condition presents itself as nodules that become calcified on the death of the mite thus reducing the value of the meat. This mite occurs in North and South America, Australia, and Europe.

The Listrophoridae or fur mites are parasites that have evolved specialized structures to attach to the skin and hair of their hosts. The gnathosoma of the fur mite, *Listrophorus leuckarti* (Acaridida: Sarcoptoidea: Listrophoridae), is hidden under a projection that together with the mouthparts and modified legs grasp the hosts hair shaft and provide support to the attached mite. The mite grazes on the hair surface using unmodified chelicerae. The clasping apparatus is closed or opened indirectly by movements of the gnathosoma.

Stored Product Pests

Some species of mites are serious pests of stored products. Many of the stored product pests can also cause a type of dermatitis known as occupational acarine dermatitis. *Lardoglyphus zacheri* (Acaridida: Acaroidea: Acaridae) is a pest of stored meat and *Lardoglyphus konoi* (Acaridida: Acaroidea: Acaridae) is a pest of dried fish. The acarid bulb mites, *Rhizoglyphus echinopus* and *R. callae* (Acaridida: Acaroidea: Acaridae), are pests on ornamental and vegetable bulbs, tubers and the roots of some cultivated crops. *Carpoglyphus lactis* (Acaridida: Acaroidea: Carpoglyphidae) occurs in fruit, dried milk products, flour and other stored food, and honey from hives where this mite lives. *Chortoglyphus arcuatus* (Acaridida: Acaroidea: Chortoglyphidae) is found in stables in hay dust or fodder. The mold mite, *Tyrophagus putrescentiae* (Acaridida: Acaroidea: Acaridae), is found in processed cereals and causes grocer's itch or copra itch which can affect anyone handling infected products. The scaly grain mite, *Suidasia nesbitti* (Acaridida: Acaroidea: Acaridae), causes wheat pollard itch. The dried fruit mite, *Carpoglyphus lactis* (Acaridida: Acaroidea: Carpglyphidae), causes dried fruit dermatitis. The grain mite, *Acarus siro* (=*Tyrophagus farinae*) (Acaridida:

Acaroidea: Acaridae), causes baker's itch. The house mite, *Glycyphagus domesticus* (Acaridida: Glycyphagoidea: Glycyphagidae), and *Lepidoglyphus destructor* (Acaridida: Glycyphagoidea: Glycyphagidae), are common on the walls, furniture and clothing in dwellings where dampness helps the growth of fungi. The former species causes a contact dermatitis described as a form of grocer's itch which occurs mostly in food handlers. *Glycyphagus destructor* (Acaridida: Glycyphagoidea: Glycyphagidae) causes hay itch.

House Dust Mites

Some ten species of mites of the family Pyroglyphidae are common in human dwellings throughout the world where they exist in the dust found on floors, furniture and bedding. The most common house dust mites are the American house dust mite, *Dermatophagoides farinae* (Acaridida: Analgoidea: Pyroglyphidae) the European house dust mite, *D. pteronyssinus* and *Euroglyphus maynei* (Acaridida: Analgoidea: Pyroglyphidae). The European house dust mite and *Euroglyphus maynei* prefer climates with a higher humidity while the American house dust mite occurs in more temperate zones. These mites can produce human allergies especially in susceptible individuals. House dust mites feed on shed human and animal skin. The allergens they produce are in their feces and in their skins shed during molts. Allergic reactions range from asthma and atopic dermatitis to itchy noses and eyes. House dust mites survive best at relative humidities greater than 70% and temperatures from 75 to 80°F. They do not survive well at low relative humidities and higher temperatures. Under the best conditions, their life cycle takes approximately one month from egg to adult.

Pests of Agricultural Crops

The most serious mite pests of agricultural crops are found in two Actinedida superfamilies, the Tetranychoidea and the Eriophyoidea. A comprehensive list of pest species of tetranychids and eriophyoids can be found in the books given in the literature cited section of this article. Here, we will consider only the most economically important species.

There are five families in the Tetranychoidea with over 450 phytophagous species. The most important pests are found in the Tetranychidae or spider mites and the Tenuipalpidae or false spider mites. Many of these are important pests of agricultural crops worldwide. Spider mites can infest every major food crop and many ornamental plants. Their chelicera are modified into whip-like structures which they insert either through or between palisade cells of the plant into the parenchyma which lies below. Here they feed and may inject a toxic saliva. Destructive symptoms include reduction of plant growth, loss of plant vigor, stippling of the tissue at the feeding site and drop off of the leaf and fruits.

The clover mite, *Bryobia praetiosa* (Actinedida: Tetranychoidea: Tetranychidae), infests grasses throughout the world. These mites can overwinter in any stage. In the spring they can occur in large numbers in buildings where they molt and oviposit. The clover mite may be a complex of races that differ somewhat in their life histories and the plants they infest. The brown mite, *B. rubrioculus*, is a pest of pome and stone fruits. However, the brown mite may be a race of the clover mite. The brown wheat mite, *Petrobia latens* (Actinedida: Tetranychoidea: Tetranychidae), the legume mite *Petrobia apicalis*, and *Tetranycopis horridus* (Actinedida: Tetranychoidea: Tetranychidae), a pest of filberts, are serious crop pests. The two-spotted spider mite, *Tetranychus (Tetranychus) urticae*, (Actinedida: Tetranychoidea: Tetranychidae), and *T.* (*Armenychus*) *mcdanieli*, infest deciduous fruit trees. The European red mite, *Panonychus ulmi* (Actinedida: Tetranychoidea: Tetranychidae), attacks deciduous fruit trees in Europe, North America and Japan. In North America, South Africa and Japan, the citrus red mite, *Panonychus citri*, is a serious pest on citrus fruit trees.

The false spider mites (Actinedida: Tetranychoidea: Tenuipalpidae) are most common in subtropical and tropical climates but some species occur in the temperate region. Three genera contain economically important species: *Brevipalpus*, *Tenuipalpus*, and *Cenopalpus*. These mites usually feed on the underside of a leaf. Some species attack grass and occur in leaf sheaths. Some species occur in galls. Three species of *Brevipalpus*, *B. lewisi*, *B. obovatus*, and *B. phoenicis* attack citrus trees in commercial orchards. *Brevipalpus* species also attack ornamentals, grapes, berry crops, orchids and olives. Species of *Tenuipalpus* attack grasses, tea, orchids and other crops. *Cenopalpus lanceolatisetae* and *C. pulcher* attack deciduous fruit trees in North Africa, Asia and Europe.

Members of the superfamily Eriophyoidea (Actinedida: Eupodina), are distributed worldwide. In their northern areas of distribution, some species produce deutogynes that function as overwintering females. Eriophyoids are found mostly on perennial plants. They injure but seldom kill plants. Eriophyoids feed in a similar manner as tetranychids, but eriophyoids are more host specific and produce very different host reactions. These host reactions have resulted in several common names for this group as gall mites, blister mites, bud mites and rust mites. *Catarhinus tricholaenae* (Rhyncaphytopidae) causes leaf rust on corn in Brazil. The peach silver mite, *Aculus comatus* (Eriophyidae), causes leaf spotting or curling. Galls are reactions of the plant to feeding by mites. Several eriophyoid mite species cause galls of different shapes, but all are due to abnormal growth of papillary material of the plant. Galls may be open or closed but all provide an area where mites can feed without pressure from predators and where feeding mites are protected from desiccation. *Eriophyes brachytarsus* (Eriophyidae) attacks California black walnut where it causes either leaf puckering or purse galls. Blisters are formed within the parenchymal leaf tissues by feeding mites. The *Eriophyes pyri* species complex produces blisters on pears, apples, and other pomaceous plants. The citrus bud mite, *Eriophyes sheldoni*, causes deformation in fruit and leaves. Some species of eriophyids can spin silk which may act as a defense against predators. Eriophyid mites also cause plant stunting, shortening of internodes and adventitious twig development or witches broom. Some species of Eriophyidae transmit plant viruses. *Eriophyes tulipae* transmits wheat streak and wheat spot mosaic virus. *Cecidophyopsis ribis* transmits currant reversion, a viral disease of black currants. *Eriophyes ficus* transmits fig mosaic virus. *Eriophyes insidiosus* transmits peach mosaic virus. *Aculus fockeui* transmits latent plum virus.

Bee Mites

Over 100 species of mites are associated with honey bees. Three species are important pests: the varroa mite, *Varroa destructor* (formerly *jacobsoni*) (Gamasida: Dermanyssoidea: Varroidae); and the tropilaelaps mite, *Tropilaelaps clareae* (Gamasida: Dermanyssoidea: Laelapidae); the honey bee tracheal mite, *Acarapis woodi* (Actinedida: Tarsonemoidea: Tarsonemidae).

The varroa mite is considered the major pest of bees. It is found throughout the world with the exception of Australia, New Zealand and Hawaii. It causes varroasis (varroatosis or varrosis). The mite rips open the integument of the bee and feeds on hemolymph. It prefers young bees to older workers. Female mites are phoretic on adult bees. *Varroa destructor* is now considered to be a complex of at least five species. Control has been hard to achieve because chemicals must kill only the mites, and biological methods are often very labor intensive. Both the honey bee tracheal mite and the varroa mite have also been implicated in the spread of bee viruses.

The tropilaelaps mite is found in Asia from Iran south to New Guinea. It has a similar but shorter life cycle to that of the varroa mite. Female mites are phoretic on bees. It is believed that the mites feed only on the soft tissues of brood bees. Tropilaelaps mites can out-compete varroa mites because they have a shorter life cycle, and emerging mites spread by attaching to adult bees. However, both species can coexist because they occupy different niches in the same hive.

The honey bee tracheal mite lives within the tracheae of their hosts and have a foreshorten life cycle with only three stages. In the tracheae, they feed on bee hemolymph. Except for a brief period when searching for a new host, these mites spend their entire life within the tracheae. Females prefer to lay their eggs in the tracheae of younger bees, preferably drones. Infestations cause a cascade of problems from loss of brood area, and smaller bee populations, to lower honey yields. The honey bee tracheal mite is found worldwide except in Denmark, Sweden and Norway, New Zealand and Australia and Hawaii.

Several other species of mites are parasites of wild bees. *Locustacarus buchneri* (Actinedida: Tarsonemoidea: Podapolipidae) is a tracheal parasite of bumble bees of the genus *Bombus*. The female mite overwinters in the trachea of queen bees. In the spring she feeds on hemolymph and lays a moderate clutch of eggs that hatch into non feeding fertile males and motile six legged fertile larviform females. Mating occurs just after hatching and the gravid females go directly to worker bees where they attach inside the tracheal system and molt to an adult female. The adult female is sac like and much larger than males. She has only one pair of legs. In this unusual life cycle, eggs hatch directly into adult or adult like forms.

► Ticks
► Four-legged Mites
► Acaricides or Miticides
► Tracheal Mite
► Varroa Mite

References

Alberti G, Coons LB (1999) The Acarimites. In: Harrison FW, Foelix R (eds) Microscopic anatomy of invertebrates, vol 8C: Chelicerate arthropoda. Wiley-Liss, New York, NY, pp 267–514

Evans GO (1992) Principles of acarology. C.A.B. International, Wallingford, UK, 561 pp

Houck MA (ed) (1994) Mites: ecological and evolutionary analyses of life-history patterns. Chapman and Hall, New York, NY, 357 pp

Helle W, Sabelis MW (eds) (1985) Spider mites. Their biology, natural enemies and control. World crop pests, vol 1A. Elsevier, Amsterdam, The Netherlands, 405 pp

Helle W, Sabelis MW (eds) (1985) Spider mites. Their biology, natural enemies and control. World crop pests, vol 1B. Elsevier, Amsterdam, The Netherlands, 458 pp

Krantz GW (1978) A manual of acarology. Oregon State University Book Stores, Corvallis, Oregon, 509 pp

Lindquist EE, Sabelis MW, Bruin J (1996) Eriophyoid mites: their biology, natural enemies, and control. World crop pests, vol 6. Elsevier, Amsterdam, The Netherlands, 790 pp

Walter DE, Proctor HC (1999) Mites: Ecology, evolution and behaviour. CABI Publishing, New York, NY, 322 pp

Miticide

A pesticide used to control mites. It also is called an acaricide.

► Acaricides and Miticides
► Insecticides

Mitochondrion, (pl., Mitochondria)

An organelle that occurs in the cytoplasm of all eukaryotes, capable of self-replicating. Each mitochondrion is surrounded by a double membrane. The inner membrane is highly invaginated, with projections called cristae that are tubular or lamellar. Mitochrondria are the sites of oxidative phosphorylation which result in the formation of ATP. Mitochondria contain distinctive ribosomes, transfer RNAs, and aminoacyl-tRNA synthetases. Mitochondria depend upon genes within the nucleus of the cells they inhabit for many essential mRNAs. Proteins translated from mRNAs in the cytoplasm are imported into the mitochondrion. Mitochondria are thought to be endosymbionts derived from aerobic bacteria that associated with primitive eukaryotes and have their own circular DNA molecules. The genetic code of mitochondria differs slightly from the universal genetic code. Mitochondria are transferred primarily through the egg, and thus maternally inherited.

Mitosis

The sequence of events that occur during the division of a single cell into two daughter cells.

Mixed Infection

Concurrent infection by two or more pathogenic microorganisms.

M'Lachlan, Robert

Robert M'Lachlan was born near Ongar in Essex, England, on April 10, 1837. He was educated at Ilford and was independently wealthy, allowing him to pursue his interests in botany and entomology. He became a leading British authority on Neuroptera and became the first editor of the British journal "Entomologist's Monthly Magazine." He was a member of many scientific societies, and published monographs on caddisflies and psocids, in addition to Neuroptera. He died in London on May 23, 1904.

Reference

Essig EO (1931) A history of entomology. The Macmillan Company, New York, 1029 pp

Mnesarchaeidae

A family of moths (order Lepidoptera). They also are known as New Zealand primitive moths.

► New Zealand Primitive Moths
► Butterflies and Moths

Mode of Action

The means by which a toxin affects an organism physiologically or metabolically. This term is usually used in concert with discussion of insecticides. Most insecticides are neurotoxins, disrupting normal nervous transmission by affecting either axonic or synaptic transmission. Others are metabolic inhibitors, affecting central cellular metabolic functions such as membrane permeability. Still others are more selective, affecting insect growth or molting.

► Insecticides

Molannidae

A family of caddisflies (order Trichoptera).

► Caddisflies

Molar

The grinding surface of the insect mandibles, often ridged or roughened.

Mole Crickets (Orthoptera: Gryllotalpidae) and Their Biological Control

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Mole crickets are strange creatures, highly adapted for a subterranean existence, including the development of their forelegs for digging. They are currently classified into two tribes, Gryllotalpini and Scapteriscini, although some taxonomists consider these to be subfamilies, Gryllotalpinae and Scapteriscinae. Adult of most species are long-winged and capable of flight, but in some species the adults are brachypterous and flightless. Within some species there are populations having long-winged adults and populations with brachypterous adults. The trochanter of each foreleg bears a long blade. The medial (inner) side of the tibia of each foreleg bears a tympanum (hearing organ). The tibia of each foreleg also bears a line of (in Gryllotalpini) four, or (in Scapteriscini) three or two large, fixed (immobile) dactyls (claws). There also are mobile tarsal dactyls. Each forewing of males bears a harp-shaped cell and a stridulatory file of minute pegs; these structures are used to produce a loud, species-specific song, of about 70 decibels when adequately projected. Adequate projection entails construction of a calling chamber at the mouth of a tunnel in the soil, formed in the shape of a loudspeaker and needing adequate moisture to make it fully functional. Song is projected by males to attract flying females, from sunset onward on humid nights in the flight season. The flight season is that time of year when most flight occurs, and in some species there may be a major flight season in spring and a minor one in autumn. Flying adults are mainly females. Females of at least some Gryllotalpini care for their eggs and the resultant small nymphs, showing a presocial behavior. The number of nymphal instars is variable even within species, ranging perhaps from seven to ten. At all events, the nymphs develop slowly. The number of generations per year may vary even within a species, so the populations of a given species may have as few as one generation every two years at high latitudes, but one annual generation at lower latitudes, or may have one generation per year at higher latitudes, but two at lower latitudes. For the most part, the diet of adults and nymphs is plant material, but in some species the diet has adapted to a major proportion of animal material such as earthworms and some small insects. Adults and nymphs spend most of their lives in the ground, but venture to the surface on warm, humid nights. They form galleries (temporary horizontal tunnels only just below the soil surface) as well as deeper, more permanent tunnels.

More than 90 species of mole crickets have been described, but only a few have been reported as pests. In eastern and southern Asia, some islands of Indonesia and the Philippines, some Pacific islands, and southern Africa, these are species of *Gryllotalpa*. In South America, the West Indies, the southern USA, and eastern Australia, they are species of *Scapteriscus*. Almost all control attempts have been by physical methods or by use of chemical pesticides. There have been few attempts at biological control albeit that some level of population regulation by native natural enemies undoubtedly occurs everywhere.

Five mole cricket species have been the targets of classical biological control programs. In Hawaii an invasive species of *Gryllotalpa* was detected in the late 19th century. Its precise origin and means of arrival seem unreported. However, it is not *G. africana* Palisot de Beauvois as was initially assumed, and it may be *G. orientalis* Burmeister, a species native to southeastern Asia. It was reported to damage sugarcane. There are no native mole crickets in Hawaii. In Puerto Rico, *Scapteriscus didactylus* (Latreille) is of South American origin. Hundreds of years ago it began a gradual range extension northward through the chain of islands of the Lesser Antilles, eventually reaching Puerto Rico and Hispaniola. This range extension most likely was by flight, from island to island. At all events, there is evidence that it had reached Puerto Rico at least as early as the eighteenth century. By the late nineteenth century, it was reported to cause severe damage to sugarcane and many other crops in Puerto Rico. Early reports of its presence in Cuba, Jamaica, and the southeastern USA were incorrect, the result of mistaken identity. Much later, it was detected in New South Wales, Australia, undoubtedly having arrived at least by 1982 as a contaminant of some air cargo or sea cargo. There are no native (pre-Columbian) mole crickets in Puerto Rico. In Florida, three South American *Scapteriscus* spp. arrived at dates between 1899 and 1925, very likely in solid (sand) ballast of ships trading with ports in southern South America. They are *S. abbreviatus* Scudder, *S. borellii* Giglio-Tos, and *S. vicinus* Scudder. They were first noticed as pests of vegetable crops. Later, as they spread and, as turf- and pasture-grasses of foreign origin (bermudagrass and bahiagrass) were imported and grown widely, the three mole crickets caused more and more damage to these grasses. There are no native species of the tribe Scapteriscini in Florida.

Thus, appropriately, classical biological control attempts were made only in new territories that the mole cricket species had invaded. All were attempts to find and import specialist natural enemies, especially from the homelands of the pest species.

Larra (Hymenoptera: Sphecidae) Imported into Hawaii

In 1924, small numbers of two South American *Larra* spp. (Hymenoptera: Sphecidae) were imported. Observation showed that the mole crickets were not suitable hosts for them, which was not surprising because their natural hosts are *Scapteriscus* mole crickets, not *Gryllotalpa*. A few were released and failed to become established. In 1925, *Larra polita* (Smith) ssp. *luzonensis* Rohwer specimens captured in the Philippines were imported into Hawaii, released and became established. It is now believed that the mole cricket attacked by *L. polita* in the Philippines is *G. orientalis*, which is thought to be the natural host of that wasp. The precise effect of the establishment of *L. polita* was not measured. The only evidence of success is lack of subsequent reports of damage caused by mole crickets in Hawaii.

Larra (Hymenoptera: Sphecidae) Imported into Puerto Rico

Puerto Rican entomologists in the 1930s explored northern South America for potential biocontrol agents of their pest mole cricket, *S. didactylus*. In Belém, on the Amazon in Brazil, they encountered *Larra bicolor* (F.) and, after several attempts, finally got it established in their island. They noted heavy use of a nectar-source plant, *Spermacoce verticillata* L. (Rubiaceae), by its adults in Brazil and Puerto Rico. Damage by pest mole crickets seems to have declined dramatically in Puerto Rico since that time, but nobody has measured the effect of *L. bicolor* as a contributor to that decline. It may not have been the only contributor, especially because *Bufo marinus* L. (Amphibia: Bufonidae), a generalist predator of large insects had already been imported by the same Puerto Rican entomologists, and became established. To the extent that *S. didactylus* and two other *Scapteriscus* spp. (*S. abbreviatus* and *S. imitatus* Nickle and Castner) are still at least occasional pests in Puerto Rico (they seem to be constant pests on golf courses), continued effort in their biological control might have been expected. But control attempts after ~1950 reverted to the use of chemical pesticides, and renewed effort in biological control did not occur until the twenty first century.

Larra (Hymenoptera: Sphecidae) Imported into Florida

University of Florida entomologists in the 1940s noted what seemed to have been achieved by importation of *L. bicolor* into Puerto Rico and made feeble attempts to do the same. They were unsuccessful, in part because a war was then in progress and travel was difficult, in part because of the discovery of the chemical chlordane, which seemed at least to their administrators to provide a long-term and inexpensive means of controlling mole crickets, so that there was no need for biological control. Those entomologists were aware of the importance of *Spermacoce verticillata*, and it may have been they who introduced this plant into Florida. The presence of the plant in Florida was not detected by botanists until the 1960s, so the timeline matches. After chlordane was banned by the US EPA in the 1970s, University of Florida entomologists were mandated by the Florida legislature to begin a program that would solve the problem caused by *Scapteriscus* mole crickets. One of their early actions was importation of *L. bicolor* wasps from Puerto Rico, released at sites prepared with plantings of *Spermacoce verticillata*. They were successful at their first attempt in 1981 with a release at Ft. Lauderdale, but unsuccessful with subsequent releases at sites farther north. Regrettably, the *L. bicolor* population near Ft. Lauderdale failed to spread. Worse, its measured effect on the local pest mole cricket population was trivial. Perhaps the reason was because the founding stock was originally from the equator, and was too tropical to spread widely in Florida.

In 1988–1989, University of Florida entomologists imported stock of this same wasp species from a higher altitude, in Bolivia, and released it in northern Florida (Gainesville). The Bolivian stock became established and began to spread and, as of August 2006, has been reported from 28 Florida counties (reports from a few additional counties need confirmation by specimens or photographs). A satellite release at Tifton, Georgia, in 2001, established it there; it has subsequently been reported from Georgia locations 150 miles northeast and >100 miles southwest of Tifton. It has also been encountered in coastal Mississippi; assuming that it spread there from Florida or Georgia, it should be present in coastal Alabama and may possibly spread to coastal Louisiana and Texas. There is no published evaluation of its effect on pest mole crickets anywhere in the USA. A preliminary estimate for two sites in Alachua County is of almost 70% mortality of *Scapteriscus vicinus* in the autumn months of 2000–2001, but verification needs mathematical modeling because there are several wasp generations per one annual mole cricket generation. At all events, *L. bicolor* is a major mortality agent of pest mole crickets in northern Florida, and its population should spread everywhere in Florida where there are pest mole crickets.

Adult female wasps are active during the warmest hours of each day. They search the ground surface for evidence of mole cricket activity, entering mole cricket burrows and chasing the denizens to the surface. There, they grapple with the mole cricket in attempt to sting and paralyze. A sting to the head paralyzes a mole cricket for a few minutes only, during which time the female wasp lays an egg on the underside of the thorax. From the egg hatches a larva (grub) that feeds as an ectoparasitoid (on the outside of the mole cricket). When the grub has killed the mole cricket, it spins a cocoon and pupates in the ground. The duration of the pupal stage is highly variable, lasting many months during the winter in northern Florida, and allowing survival of the population during freezing temperatures. There are more annual generations in tropical areas and fewer generations in more temperate areas, with the pupal stage in diapause acting as the means of surviving winter in places where freezing temperatures occur. The northern limit of occupation by *L. bicolor* in the southeastern USA has not yet been determined, but likely is little more than 31°N.

Ormia depleta (Diptera: Tachinidae) Imported into Florida

Ormia depleta (Wiedemann) larvae parasitize at least some species of *Scaptericus* mole crickets. This fly's distribution includes not only Amazonian Brazil (as was discovered by Puerto Rican entomologists) but also southern Brazil at least as far as 30°S, and at least part of Paraguay. Stock of the fly obtained at 27°S at Piracicaba in the Brazilian state of São Paulo was imported into Florida in several shipments in the late 1980s. Painstakingly reared individually by the thousands on mole cricket hosts, progeny were first released in 1988 near Gainesville (Alachua County) and Bradenton (Manatee County). More releases followed over the next four years in all parts of Florida. By 1994, it was recognized that the stock had occupied all peninsular counties (38 of them) to 29°45' N, but that occupation of the northernmost of these counties was temporary, with a permanent population occurring only south of 28°45' N, and with increase of that area but little to the north each autumn. The established stock of the fly did not overwinter routinely north of about 28°45' N. Southernmost Brazil (Rio Grande do Sul) was then explored for this same fly, and stock was imported from the southernmost locality where it was detected (at 30°S), near Osorio, northeast of Porto Alegre, in 1999. Progeny were reared, and were supplied to collaborators in Georgia, Louisiana, and North Carolina for release, but these collaborators reported no evidence of establishment in their areas. Study of the diapause capabilities of this southern stock was entrusted to two University of Florida PhD students who were to characterize development of the fly at assorted conditions of photoperiod, temperature and humidity, and determine whether diapause can or cannot occur, the idea being to determine whether the fly can survive cold winters in diapause. Neither student succeeded before the fly culture died out, likely due to inbreeding. For the present, we have to conclude that there is no evidence that the fly can diapause in winter, so perhaps there is no hope that it can establish permanent populations in northern Florida and states to the north.

Adult flies are nocturnal and gravid females are phonotactic (use the song of mole crickets to detect hosts). They larviposit, and larvae penetrate the host mole cricket, killing it within ~8 days. Larvae then pupate in the ground for 11–12 days before the new adult generation emerges. Evaluations of mole crickets trapped in pitfall traps in May 1993 and May 1994 in Orange County revealed parasitism of 24–25%. Because parasitized mole crickets die after ~8 days, and because *O. depleta* has several generations each year in contrast to just one for the mole crickets, the mortality inflicted by the fly is likely to be considerable. At all events, the level of control exerted by this fly is now free in central and southern Florida. If funds were made available, it should be possible to further evaluate current effects and to design methods to enhance effects. An effort to import the fly into Puerto Rico in the 1930s was unsuccessful, and the effort has not been repeated.

Steinernema scapterisci (Rhabditida: Steinernematidae) Imported into Florida

Detected by its emergence from dying pitfall-trapped *Scapteriscus* mole crickets in Uruguay in 1995, this nematode was brought to Florida and later described as a new species. Dauer larvae of *S. scapterisci* Nguyen and Smart harbor specialist bacteria of the species *Xenorhabdus innexi* Lengyel et al. When the larvae, lurking in the soil, detect a passing *Scapteriscus* mole cricket, they attempt to enter it through its mouth or spiracles. If they are successful, they break into its body cavity and release the bacteria. The bacteria reproduce inside the insect's body cavity, killing it through septicemia. The nematodes feed within the dying mole cricket, mature, undergo two generations, and release bacterium-carrying dauer larvae back into the soil. This process (from attack to release of offspring into the soil) can be accomplished within ~10 days at warm temperatures, but may perhaps be extended for weeks at cool winter temperatures when pest mole crickets retreat deeply into the soil and activity by mole crickets and nematodes alike is greatly slowed. A further complication is that *Scapteriscus* nymphs are scarcely susceptible to attack by *S. scapterisci*, perhaps because their body apertures (mouth and spiracles) are too small to be penetrated by the dauer larvae. Releases of this nematode, reared within laboratory cultures of mole crickets, were first made in Florida on a very small scale in 1985. They established permanent populations and began to spread.

Development of mass-production methods by industry allowed sales of *Steinernema scapterisci* (several trade names have been used) as a biopesticide. It also allowed experimental applications on a bigger scale than before. These experiences showed that applications are best timed when adult mole crickets (not nymphs) are abundant and active, so in February–April and September–November in central and southern Florida (February is perhaps too early in northern Florida). Applications are effective against *Scapteriscus borellii* and *S. vicinus*. They do not kill as high a percentage of pest mole crickets measured in the short term (days) as do the most effective chemicals. However, applications generally initiate permanent populations that suppress pest mole cricket populations for years in pastures, playing fields, and golf courses. Cost of application in pastures has been greatly reduced by treating one swath (strip) in eight across a pasture, because easily within the space of a year the nematode population spreads throughout the pasture. Such spread is due to transport of nematodes within newly-infected mole crickets. The same transport eventually allows the nematode to occupy distant sites with mole cricket populations.

Steinernema scapterisci (Rhabditida: Steinernematidae) Imported into Puerto Rico

In 2001, under USDA-APHIS permit, *Steinernema scapterisci* was applied at two localities in Puerto Rico, and in subsequent years in three more localities, all in the west of that island. In the laboratory, it was demonstrated to be effective in attacking and killing adult *Scapteriscus didactylus*, but survival of its dauer larvae in some Puerto Rican soils seemed to be poor. Such soils included highly organic sandy soils in which antagonists may have been present. They also included a sandy loam. Such high mortality had not been observed in the sandy soils where survival has been so good in Florida. Nevertheless, the nematode should now be established in Puerto Rico and should gradually spread.

Conclusion for Florida

Classical biological control of *Scapteriscus* mole crickets in north-central Florida has been highly successful due to establishment of three biological control agents from South America, and success is spreading throughout Florida as populations of *Larra bicolor* and *Steinernema scapterisci* spread (*Ormia depleta* may already have spread to its fullest possible extent). The ultimate level of success should be enough to obviate all need for chemical treatment of lawns, playing fields, and pastures to control pest mole crickets. This leaves four situations where classical biological control may need enhancement. The first, in pastures where *Steinernema scapterisci* is not yet present; owners/operators need to be aware of the availability of this nematode, and that it may be applied in swaths (strips) across a mole-cricket-infested pasture, at the level of one treated swath per seven untreated swaths, to achieve distribution throughout the pasture within a few months, a big reduction in cost over complete pasture treatment; they also should be aware of the possibility of planting *Spermacoce verticillata* to enhance *Larra bicolor* presence. The second is organic farms, where owners/operators need to be aware of their ability to buy and apply *Steinernema scapterisci* if it has not already been applied, and to plant *Spermacoce verticillata* or another nectar-source plant to encourage populations of *Larra bicolor* (alternatives to *S. verticillata* are under investigation). The third is regular commercial vegetable farms where owners/operators need to be aware that use of *Steinernema scapterisci* is compatible with use of many if not all chemical insecticides, so they should not be reluctant to buy and apply the nematode because this provides partial control of pest mole crickets indefinitely, at a huge potential cost saving. The fourth is golf courses, most of which have experienced a decline in damage caused by mole crickets. Although this decline is due to the spread of classical biological control agents, the golf course personnel in general have no experience in detection of the presence of any of the three biological control agents, so their assumption has been that they now have wonderful new chemical insecticides that solve their previous problems with mole crickets. A little thought should reveal to them that it is strange that the wonderful new "chemicals" have suppressed mole crickets only, while damage by other insect pests has "increased" dramatically. What of course has happened is that classical biological control has decreased pest mole cricket populations dramatically, and that golf course personnel are left to deal with the previously minor (at least in Florida) problem caused by larvae of Scarabaeidae. Further, mole cricket populations have declined also in pastures, where chemicals are not applied. There is an enormous educational task to be performed – and a new biological control challenge – how to suppress populations of pest scarab larvae, many of which are native.

Conclusion for Other Southeastern States of the USA

Larra bicolor should continue to spread, deliberately helped or not, to the coastal areas of Alabama, Missisippi, Lousiana, and Texas. It is unlikely to spread much to the north of about 31°N. *Ormia depleta* is highly unlikely to spread to northern Florida, and not beyond Florida's borders. *Steinernema scapterisci* may (at least at present) be purchased and applied against pest mole crickets anywhere in the continental USA. Its purchase and application is a good investment if applied in early spring, even if it cannot overwinter. But perhaps it can overwinter, in at least parts of Alabama, Louisiana, Mississippi, North Carolina, South Carolina, and Texas and suppress pest mole crickets for several seasons. It is up to entomologists/nematologists in those states to investigate. At all events, it does overwinter in southern Georgia. If sales of *Steinernema scapterisci* are not sufficient, its producing company is likely to discontinue production. Thus, *now* is the time for trial applications in states north of Florida.

Conclusion for Puerto Rico

Larra bicolor seems to have provided partial suppression of pest mole cricket populations for many decades. *Steinernema scapterisci* should now be established in northwestern Puerto Rico. If so, it should continue to spread. Landowners/managers should familiarize themselves with biological control solutions and urge distributors to import *Steinernema scapterisci* for sale; there should be no bureaucratic impediment to such importation because that nematode already is established. It may be possible to introduce *Ormia depleta*.

Conclusion for Eastern Australia, Islands of the Lesser Antilles, and the Dominican Republic

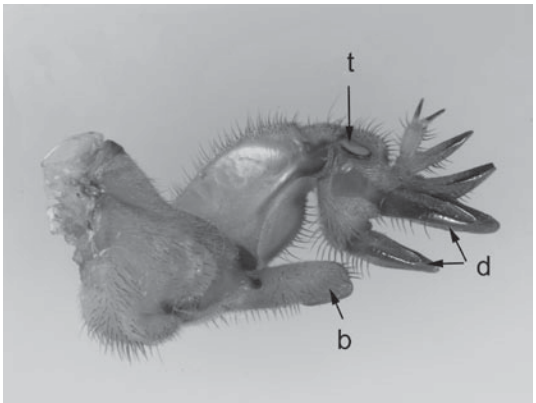
Now is the time to consider whether importation of biological control agents (*Ormia depleta*, *Larra bicolor*, *Steinernema scapterisci*) would be an advantage over current repeated chemical applications against *Scapteriscus didactylus* control. It is not a good idea to delay because the easiest source of these biological agents is Florida, where biological control expertise is winding down with retirements.

Conclusion for South America

Where *Scapteriscus* mole crickets are a problem, for example on golf courses using fresh soils that *Steinernema scapterisci* has not yet reached, application of the nematode is the most immediately viable biological control option. This would now demand the purchase of these nematodes from the only current producer, in North America.

Conclusion for Hawaii

There is no current problem with pest mole crickets. It would be satisfying to identify definitively the one pest species present, which may or



Mole Crickets (Orthoptera: Gryllotalpidae) and Their Biological Control, Figure 79 **Medial (inner) side of left foreleg of *Scapteriscus borellii* Giglio-Tos showing trochantal blade (b), tympanum (t), two fixed dactyls of tibia (d), and movable tarsal dactyls. Photo: Lyle Buss.**

may not be *Gryllotalpa orientalis*, and is not *Gryllotalpa africana* as was assumed for decades.

Conclusion for Africa and Southern Asia Including the Philippines and Indonesia

Taxonomic revision of Asian mole crickets is essential. Decades of "basic" studies of potential biological control agents may be necessary before suitable species for use in any given geographical area are adequately researched. The various biological control agents researched in Florida and Puerto Rico for use against *Scapteriscus* mole crickets are not suitable for use against *Gryllotalpa* mole crickets (Fig. 79).

► Turfgrass Insects of the United States: Biology and Management
► Grasshoppers, Katydids and Crickets
► Mole Crickets and their Biological Control
► Turfgrass Insects and their Management

References

Frank JH, Walker TJ (2006) Permanent control of pest mole crickets (Orthoptera: Gryllotalpidae: *Scapteriscus*) in Florida. Am Entomol 52:138–144

Nguyen KB, Smart GC (1990) *Steinernema scapterisci* n. sp. (Rhabditida: Steinernematidae). J Nematol 22:187–199

Parkman JP, Frank JH, Walker TJ, Schuster DJ (1996) Classical biological control of *Scapteriscus* spp. (Orthoptera: Gryllotalpidae) in Florida. Environ Entomol 25:1415–1420

Vicente NE, Frank JH, Leppla NC (2007) Use of a beneficial nematode against pest mole crickets in Puerto Rico. Proceedings of the Caribbean Food Crops Society 42(2): 180–186

Williams FX (1928) Studies in tropical wasps – their hosts and associates. Hawaiian Sugar Planters' Association Experiment Station. Entomol Ser Bull:191–79 [Note: the adventive mole cricket detected in Hawaii in1896 is in reality probably *Gryllotalpa occidentalis*, and the wasp that was successfully imported as a biological control agent was *Larra polita* (Smith) ssp. *luzonensis* Rohwer]

Wolcott GN (1938) The introduction into Puerto Rico of *Larra americana* Saussure, a specific parasite of the "changa" or Puerto Rican mole cricket, *Scapteriscus vicinus*. J Agric Univ Puerto Rico 22:193–218 [Note: in reality, the wasp is *Larra bicolor* and the mole cricket is *Scapteriscus didactylus*]

Molecular Biology

A term broadly used to describe biology devoted to the molecular nature of the gene and its biochemical reactions such as transcription and translation.

Molecular Diagnosis

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Molecular diagnosis refers to the taxonomic determination of organisms based on molecular criteria. Correct taxonomic determination is critical for entomological applications in many fields, including agriculture, environmental science, biosecurity, and human health. Because a major challenge in taxonomy is the discrimination among closely related forms, diagnosis mainly concerns the identification of organisms at the species level. One example is the case of cryptic species complexes, which are groups of closely related species that are difficult or impossible to distinguish by morphological traits alone. These complexes are known from a wide variety of arthropods and have been well studied in medically and economically important insects. For example, despite a near identity in morphological appearance, several sibling species of mosquitoes are separable with a variety of molecular-based methods. Conversely, molecular systems can be used to establish synonymy between presumed cryptic species. Often, identifying closely related species using traditional taxonomic methods is difficult for non-specialists and requires expert knowledge of the group; molecular identification keys based on targeted DNA sequences can provide a valuable identification system for such groups, as for example for species of thrips in the genus *Scirtothirps*. Molecular diagnosis is a great motivation for recent initiatives in DNA barcoding in which a standard section of DNA, typically part of mitochondrial cytochrome-oxidase I, is used to identify species.

The Species Concept

There has been considerable debate in the literature concerning the most appropriate definition of species. Classically, species are described on the basis of morphological characters, and the common basis for species identification is the presence of one or more fixed or non-overlapping differences. If these differences are both shared and derived, the groups are considered phylogenetic species. However, morphological data alone may be inadequate for defining species boundaries. For example, two species may be sympatric in range (overlapping) or parapatric (abutting), but be so similar in morphology that their specific status goes undetected. Conversely, morphological variation may be so great in one species, that identification of single biological unit is difficult.

Another commonly held view of species is the evolutionary species concept, in which a species represents a single lineage of ancestral-descendant populations that maintains its identity from other lineages and that has its own evolutionary tendencies. This view is similar to the biological species concept, in which species are viewed as a set of interbreeding organisms. While the biological concept of species is a meaningful one for many applications in which a species determination is necessary, biological experiments to assess biological species are not possible for some species.

Tools of molecular biology provide a powerful means to determine whether organisms belong to a single evolutionary lineage or interbreeding unit. Analysis of gene genealogies using coalescent theory can be used to identify single lineages. Individual organisms differ in the DNA sequences that make up their genomes and differentiation between species is based on mutations in the genes that accumulate through time. Because any given allele in an organism derives from an allele in an ancestor, DNA data have the potential to define the genealogies of genes and infer phylogenetic relationships of taxa. Molecular genetic data can also help to understand the nature of biological species, as well as the extent and causes of intra-specific variability, including ecotypes, host races, or phenotypically adapted forms.

Molecular Methods for Diagnosis

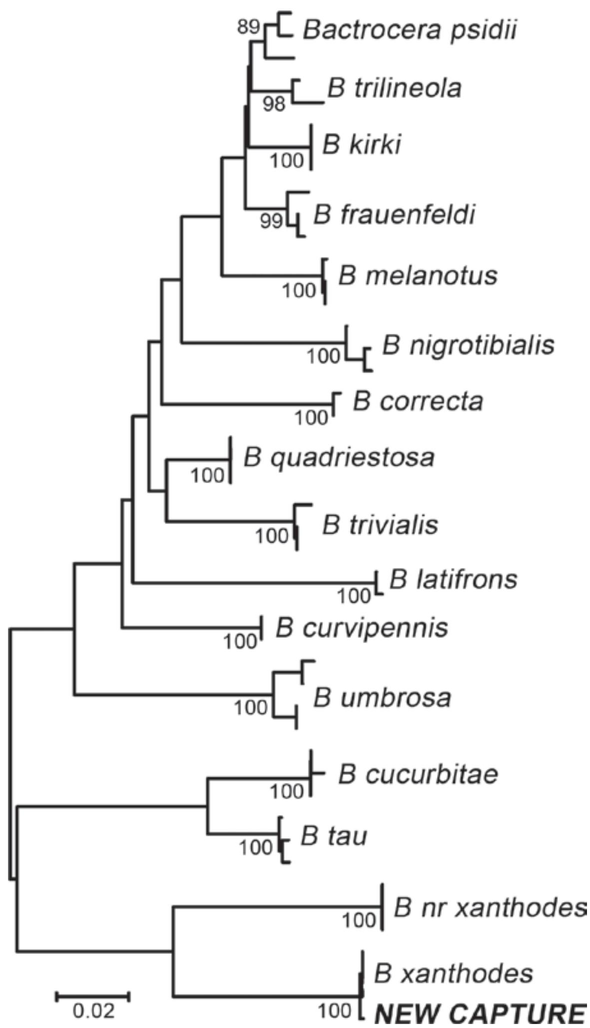
The analysis of DNA is an increasingly important tool in studies of insects, particularly for systematics and population biology. DNA has several significant features that make it especially useful: (i) the genotype rather than the phenotype is assayed; (ii) one or more loci appropriate to a problem can be selected on the basis of evolutionary rate or mode of inheritance, (iii) the methods are applicable to all developmental life stages and both sexes, and (iv) DNA can be prepared from small amounts of tissue and is relatively stable, even in tissues that are not stored cryogenically (deep frozen). One reason for the success of molecular diagnosis is the use of the polymerase chain reaction (PCR) in which specific stretches of DNA are amplified, allowing the development of fast and sensitive molecular techniques. As a result, only a small portion of the insect is needed for molecular diagnosis.

Two major classes of DNA-based approaches are used in taxonomy. The first involves comparison of nucleotide sequences for a particular locus or loci, usually amplified by PCR. The DNA sequence variation can be examined directly following automated DNA sequencing. This is the approach used in DNA barcoding. Sequence variation can also be assessed indirectly by comparing electrophoretically homologous DNA fragments to look for variation in number, size or conformation. In a method termed restriction fragment length polymorphism (RFLP), a PCR product is first generated and then digested to completion with a restriction enzyme to yield a species-specific pattern of bands that can be visualized on a gel. Another powerful technique, allele specific amplification (ASA), is based on the fact that *Thermus aquaticus* (*Taq*) DNA polymerase will only extend primers that are matched to their template DNA and will not extend primers that do not match the template DNA. PCR primers can therefore be designed so that they only match one allele and, providing that the allele is specific to a species, a PCR product will only be generated with the primer matching the genomic DNA of the corresponding species. Other approaches for assessing similarity of sequences are based on the fact that the presence of point mutations of the nucleotide sequence that differ among species will affect the tertiary conformation of the DNA molecule.

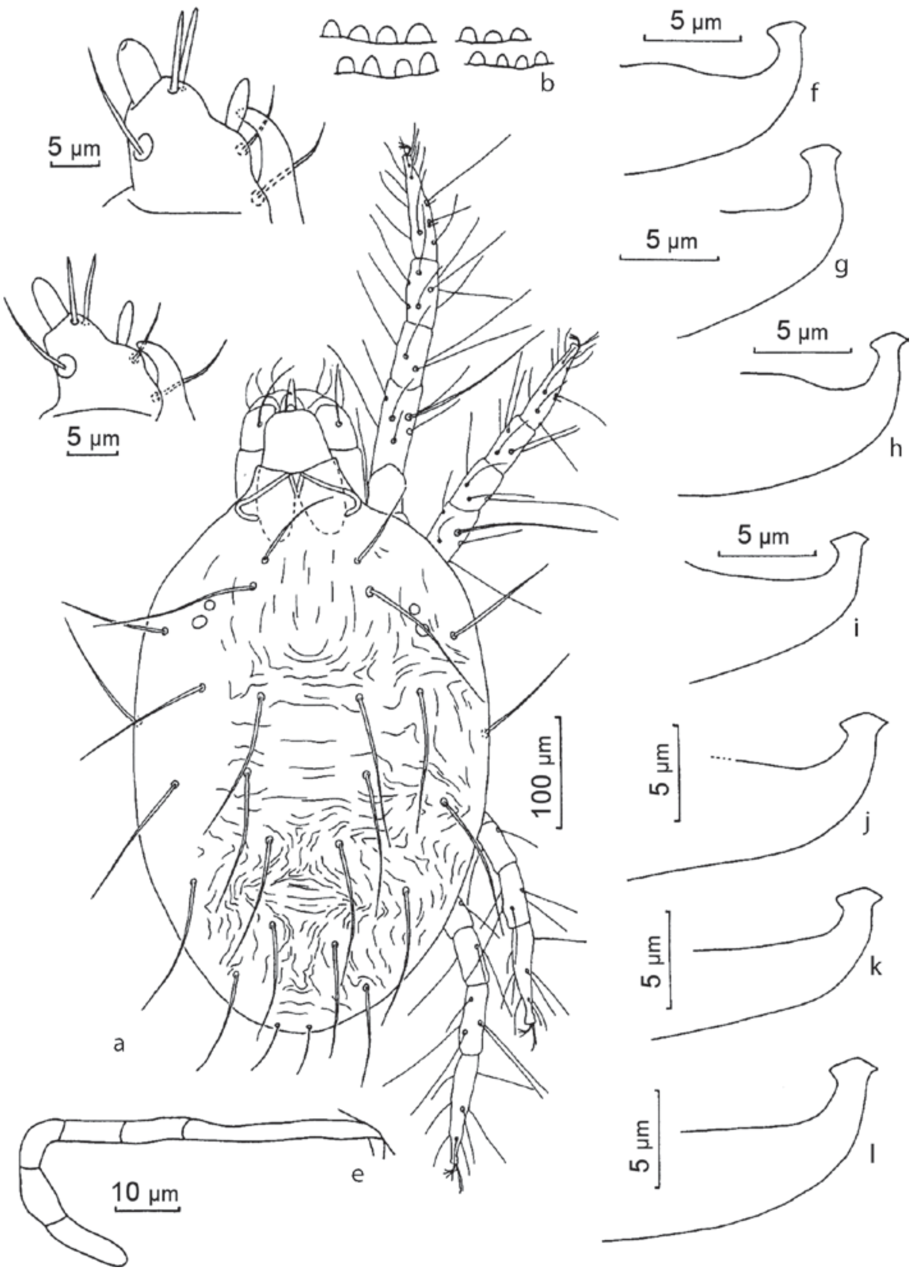
The second class of approaches used in DNA taxonomy is so-called DNA fingerprinting or fragment analysis. Each of these methods simultaneously screens many different DNA regions or fragments, which are thought to be distributed randomly throughout the genome. Although fingerprinting and fragment approaches offer less resolution than nucleotide sequencing in some respects, they are powerful and cost-effective alternatives where large numbers of individuals or large segments of a genome are being screened. In general, these techniques have the great advantage that they can be applied to systems where there is no prior molecular information about particular loci. Multi-locus markers are often detected by annealing primers of arbitrary short sequences during PCR amplification and looking for species-diagnostic bands among the array of randomly amplified fragments, as in the method of randomly amplified polymorphic DNA (RAPDs). More complex and more reliable methods use a combination of restriction enzymes and PCR, as is the case of amplified fragment length polymorphisms (AFLPs). The most widely used markers for population genetics of insects are now microsatellites, which are non-coding sections of repeated small motifs of a few base pairs. Microsatellites are repeatable and can be sufficiently variable for use in many types of population studies including studies of the origins of individuals, population structure, and hybridization. Typically, microsatellite loci must be developed anew for each new species, or set of closely related species.

There is a trade-off between the detailed information that can be obtained by sequencing the DNA at one or a few loci and the more abundant, though less detailed, information that can be obtained through studies of restriction sites, fingerprinting, or microsatellite analysis. For most population genetic analyses the power of a statistical test increases with the number if loci examined. Towards this end, single nucleotide polymorphisms (SNPs) provide the smallest possible (and potentially the greatest number) of genetic loci, but to date studies involving SNPs have only been possible for organisms where there is some prior genomic information that can help to guide the discovery of loci, such as through whole genome sequencing. Initially whole genomes were available only for a select group of model organisms, including species of *Drosophila*, mosquitoes, and the honey bee. However, in the last few years many new projects have made available the genome sequence of more insects and other arthropods (e.g., ticks and spider mites) and the list of these species is continuously increasing. Currently, advances in sequencing technology and bioinformatics are revolutionizing the production of genomic sequence data; accordingly, in the not too distant future whole genomes will be available for a wide spectrum of species.

Selecting the sequence or markers to be analyzed is the first decision to be made in designing any molecular systematic or population genetic study, whether it concerns DNA sequences or fragment variation. In broad terms, choices are made according to evolutionary rate and mode of inheritance. The ribosomal DNA (rDNA) and the mitochondrial DNA (mtDNA) have been the most commonly used genomic regions for systematic studies of animals. The processes governing the evolution and inheritance of mtDNA and rDNA are now well understood and have an impact in their relative performances for systematic inference. For example, the two very closely related but reproductively isolated spider mite species, *Tetranychus urticae* and *T. turkestani* are polyphyletic for mtDNA but monophyletic for rDNA. The influence of life history, mainly haplodiploidy of these species and their female-biased sex-ratio, might explain this apparent contradiction. Another fundamental to establish synonymy between presumed species choice is whether information concerning the phylogeny of the alleles is necessary; some techniques (e.g., RAPDs, AFLPs, microsatellites, SNPs) provide information only on the latter. Recent developments in population genetic theory use information on allele relationships as well as their distribution to combine inferences about population structure and history. However, for species diagnosis, information on allele frequency distributions may suffice.



Molecular Diagnosis, Figure 80 **Identification of a tephritid fruit fly species using DNA barcoding. In this example, fly eggs from an unknown species were found in fruits that were intercepted at the border in New Zealand. Because the eggs of tephritid fruit flies are not possible to identify to species morphologically, similarity in mitochondrial DNA COI was used to match the intercepted eggs (noted as "new capture") with DNA from known voucher specimens. In this example, the unknown species was identified as *Bactrocera xanthodes*. (Data used with permission of Karen Armstrong, Lincoln University, New Zealand; for additional examples, see Clarke et al., 2005.)**



Molecular Diagnosis, Figure 81 The morphological characters classically used to separate *Tetranychus* species are presented for *T. pueraricola*: a = female dorsum; b = lobes on dorsa hysterosomal striae of female (schematic); c = distal palpus segment of female; d = distal palpus segment of male; e = female peritreme; and f–i = aedeagi. Comparison of *T. peuraricola* aedeagi (f–i) with *T. urticae* aedeagi (j–l) illustrates the difficulty in separating the two species by morphological criteria alone. (Data used with permission of Tetsuo Gotoh, Ibaraki University, Japan.)

DNA Barcoding

DNA barcoding is the use of a short DNA sequence from a standardized and agreed-upon position in the genome for molecular diagnosis and identification at the species level. For most animals, including insects, the cytochrome C

Molecular Diagnosis, Figure 82 **Molecular diagnosis of two closely related species of agricultural mite pests, *Tetranychus urticae* and *Tetranychus pueraricola*, which are impossible to separate by morphological criteria. Shown is a PCR-RFLP test in which the second internal transcribed spacer (ITS2) of the ribosomal DNA has been PCR amplified and digested by the restriction enzyme *Rsa*I for the two species. In the figure, *Rsa*I digestion of the PCR-amplified ITS2 derived from the DNA of a single mite clearly shows that *T. urticae* sequence produces 3 fragments (implying 2 recognition sites of the enzyme; lane 2), while the restriction profile of *T. pueraricola* yields only 2 fragments (implying a single recognition site; lane 3). In lane 1 the "100 base pair (bp) ladder" size marker is shown.**

oxidase subunit 1 mitochondrial region (COI) has become the standard barcode region. Because of conserved genetic regions flanking this gene and because it is so abundant within individuals, the COI gene sequence is easily obtained from insects. Within species, COI sequence variability is typically very low, making it useful as a species diagnostic marker. Species are identified based on the similarity of COI sequences to known voucher specimens. However, the widespread use of DNA barcoding has been controversial, particular in its application to systematics. Accordingly, it is now well recognized that additional loci and other sorts of biological data will be necessary for applications in evolutionary and population biology that involve systematics or studies of complex population histories including hybridization (Figs. 80–82).

References

Avise JC (2004) Molecular markers, natural history and evolution, 2nd ed. Chapman and Hall, New York

Behura SK (2006) Molecular marker systems in insects: current trends and future avenues. Mol Ecol 15:3087–3113

Bickford D, Lohman DJ, Sodhi NS, Ng PKL, Meier R, Winkler K, Ingram KK, Das I (2007) Cryptic species as a window on diversity and conservation. Trends Ecol Evol 22:148–155

Caterino MS, Cho S, Sperling FAH (2000) The current state of insect molecular systematics: a thriving tower of Babel. Annu Rev Entomol 45:1–54

Clarke AR, Armstrong KF, Carmichael AE, Milne JR, Raghu S, Roderick GK, Yeates DK (2005) Invasive phytophagous pests arising through a recent tropical evolutionary radiation: the *Bactrocera dorsalis.* complex of fruit flies. Annu Rev Entomol 50:293–319

Excoffier L, Heckel G (2006) Computer programs for population genetics data analysis: a survival guide. Nat Rev Genet 7:745–758

Gomez-Zurita J, Galian J (2005) Current knowledge on genes and genomes of phytophagous beetles (Coleoptera: Chrysomeloidea, Curculionoidea): a review. Eur J Entomol 102:577–597

Gotoh T, Gutierrez J, Navajas M (1998) Molecular comparison of the sibling species *Tetranychus pueraricola.* Ehara & Gotoh and *T. urticae* Koch (Acari: Tetranychidae). Entomol Sci 1:55–57

Krzywinski J, Besansky NJ (2003) Molecular systematics of *Anopheles.*: from subgenera to subpopulations. Annu Rev Entomol 48:111–139

Luikart G, England PR, Tallmon D, Jordan S, Taberlet P (2003) The power and promise of population genomics: from genotyping to genome typing. Nat Rev Genet 4:981–994

Manelm S, Gaggiotti OE, Waples RS (2005) Assignment methods: matching biological questions with appropriate techniques. Trends Ecol Evol 20:136–142
Navajas M, Boursot P (2003) Nuclear ribosomal DNA monophyly *versus*. mitochondrial DNA polyphyly in two closely related mite species: the influence of life history and molecular drive. Proc R Soc Lond B (Suppl) 270:S124–S127
Navajas M, Gutierrez J, Williams M, Gotoh T (2001) Synonymy between two spider mite species, *Tetranychus kanzawai.* and *T. hydrangea*, shown by ribosomal ITS2 sequences and cross-breeding. Bull Entomol Res 91:117–123
Noor MAF, Feder JL (2006) Speciation genetics: evolving approaches. Nat Rev Genet 7:851–861
Robinson GE, Evans JD, Maleszka R, Robertson HM, Weaver DB, Worley K, Gibbs RA, Weinstock GM (2006) Sweetness and light: illuminating the honey bee genome. Insect Mol Biol 15:535–539
Rosenberg NA, Nordborg M (2002) Genealogical trees, coalescent theory and the analysis of genetic polymorphisms. Nat Genet 3:380–390
Rugman-Jones PF, Hoddle MS, Mound LA, Stouthamer R (2006) Molecular identification key for pest species of *Scirtothrips.* (Thysanoptera: Thripidae). J Econ Entomol 99: 1813–1819
Savolainen V, Cowan RS, Vogler AP, Roderick GK, Lane R (2005) Towards writing the encyclopaedia of life: an introduction to DNA barcoding. Philos Trans R Soc Biol Sci 360:1805–1811
Schlötterer C (2004) The evolution of molecular markers–just a matter of fashion? Nat Rev Genet 5:63–69

Molecular Genetics

Genetic studies that focus on the molecular nature of genes and gene expression.

Molecular Phylogeny

An analysis of the relationships of groups of organisms as reflected by the evolutionary history detected in molecules (proteins, DNA).

Molicutes

A class of wall-less microorganisms, surrounded by a membrane, and related to bacteria. They are small, gram-negative, and highly variable in appearance.

Molt

To shed or cast off the outer body covering, a necessary prerequisite to grow and attain the adult stage. The period of molting is a vulnerable stage for insects, as they are susceptible to desiccation and easy prey for predators.

Molting Fluid

An enzyme-rich fluid secreted into the apolysial space by the epidermal cells. The molting fluid consists of proteinases and chitinases that digest the endocuticle during molting. The molting fluid is reabsorbed through the epidermal cells shortly before ecdysis in many insects, though in some insects the new instar apparently swallows the old fluid.

Molting Hormone

A homone regulating molting in insects. Also called ecdysone.

Mompha Moths (Lepidoptera: Momphidae)

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Mompha moths, family Momphidae, total 127 species worldwide, with about half from the Palearctic. The family is part of the superfamily Gelechioidea in the section Tineina, subsection Tineina, of the division Ditrysia. Adults small (8–18 mm wingspan), with head smooth-scaled; haustellum scaled; labial palpi recurved; maxillary palpi small, 3-segmented. Wings elongated and hindwings mostly lanceolate with long fringes (Fig. 83). Maculation often white with golden iridescent markings, or darker with

Mompha Moths (Lepidoptera: Momphidae), **Figure 83** **Example of mompha moths (Momphidae), *Mompha eloisella* (Clemens) from Florida, USA.**

various marks. Adults mostly diurnal or crepuscular. Larvae mostly leafminers, but some are borers in flowers and stems, or gall makers. Hosts are only known in Onagraceae.

References

Bradley JD (1951) A comparative study of four European species, including one new species from Britain, belonging to the genus *Mompha* Huebner, (Lepidoptera: Lavernidae). Entomol Gaz 2:173–182, pl. 5

Hodges RW (1992) Two new species of *Mompha* from California (Lepidoptera: Momphidae). J NY Entomol Soc 100:203–208

Riedl T (1969) Matériaux pour la connaissance des Momphidae paléarctiques (Lepidoptera). Part IX. Revue des Momphidae européenes et compris quelques espéces d'Afrique du Nord et du Proche-Orient. Polsk Pismo Entomol 39:635–919

Riedl T, Popescu-Gorj A (1974) Catalogue of the Momphidae (Lepidoptera-Gelechioidea) from the collections of the Natural History Museum "Grigore Antipa" of Bucharest. Trav Mus Natl Hist Nat Grigore Antipa 14:273–298

Momphidae

A family of moths (order Lepidoptera). They commonly are known as mompha moths.

► Mompha Moths
► Butterflies and Moths

Monarch Butterfly, *Danaus plexippus* L. (Lepidoptera: Danaidae)

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The monarch is one of the world's best-known butterflies. Its distribution is among the widest for any butterfly species. Not only it is found throughout the Americas, including the islands of the West Indies, but it reaches as far as Australia and New Guinea, and occasional individuals migrate to Western Europe.

The monarch butterfly is native to tropical America where populations breed throughout the year. These sedentary populations are different from the migratory North American ones and bear separate names. For example subspecies, *megalippe* Hübner is found in Mexico and Central America and southeastern United States. The southern South American subspecies is called *menippe* Hübner. Several subspecies have also been described from the islands in the Caribbean. None of these geographic races are "pure," with occasional individuals of the migratory subspecies phenotype, *D. plexippus plexippus*, found in all of them. It has even been suggested, yet not proven, that sedentary subspecies might indeed prove to be separate sibling species. Due to the versatility of its weedy host plants – the milkweeds – and its ability to cover large distances, this highly adaptable butterfly occupies a variety of ecological zones, but is found mostly in open sunny areas. In Costa Rica, for example, monarchs fly from sea level up to 2,500 meters in elevation and are particularly common above 1,500 meters.

Though the monarch male has been observed to exhibit a basic kind of courtship behavior, wiggling in its flight while approaching a female, the essence of the mating "ritual" in this species can be described as "rape." Copulation involves the male grasping the female with its legs in flight and bringing the female down from the air to the ground in order to clasp her abdomen with the external genitalia. The white eggs are laid singly on the flowers or the underside of the leaves of one of the many milkweed species, and larval feeding commences immediately upon hatching; there is no diapause stage, except that adults on the overwintering sites go into reproductive diapause. Toxicity of the milkweeds varies and so does toxicity of resulting butterflies, as has been demonstrated through bird-feeding experiments. The striped larvae with two pairs of tentacles (the elongate tubercles, the function of which remains unknown) develop into green, gold-studded pupa within two weeks. The larvae from the Caribbean island of Hispaniola show much wider black stripes than these of the North American population. Differences in length of tentacles and abundance of gold coloration in pupae have also been recorded between the migratory population and one in Jamaica. Overall, though it was one of the earliest butterflies to acquire its scientific name (Linnaeus, 1758), the taxonomy of *Danaus plexippus* remains a widely debated issue.

Monarch Migration

At some time in the relatively recent past, probably during the Pleistocene advances and retreats of great glacial masses across the northern areas of temperate North America, a subset of the North American monarch population began its marvelous annual movements. Its movements represent a true migration, involving a periodic movement from a given area and a return to that area, and likely evolved to exploit dozens of seasonally available milkweed species north of the tropics. Migration apparently is triggered by changes in temperature in an ultimate sense and perhaps changes in photoperiod in a proximate sense. Typically, the monarch populations across the North American continent begin moving in a generally southerly direction starting each fall around September 1. West of the Rocky Mountains, these populations move primarily to about 129 sites along the Pacific coast of California and Baja California. There, they hang in trees such as coastal groves of pine, cypress, redwood, and the introduced Australian eucalyptus trees in clusters or colonies of several hundred to several tens of thousands of individuals from late fall to early spring. Some overwintering colonies have recently been discovered in Saline Valley, north of Death of Valley in the eastern desert areas of California, while other population movements through southern Nevada and Arizona suggest that there are still as yet undiscovered overwintering sites in northern Mexico for these western monarchs.

East of the Rocky Mountains, Canadian and U.S. monarchs move south to the Gulf Coast where the vast majority turn southwest and enter Mexico across the Texas border, flying south by the hundreds of billions. They ascend the Sierra Madre de Oriente into the Central Plateau and eventually end up in the high coniferous forests of the Transverse Neovolcanic Belt of central Mexico, principally within the states of Mexico and Michoacan. The existence of an over-water pathway used by eastern Monarchs has been documented recently. They fly across the Gulf of Mexico between the southwest coast of Louisiana to the northeast coast of Tamaulipas, Mexico, an over-water flight of 400 miles. In addition, some monarchs are known to fly to various points on the northern Florida coast (from which they may still cross the Gulf of Mexico) or to south Florida, from which they may fly to overwinter in Cuba. Most of the eastern monarchs, flying in a south-southwesterly direction, take advantage of southward moving cold fronts. The stored fat allows for only 11 h of wing-flapping flight, or 44 h of cruising flight, but thanks to the frequent tail winds, monarchs use soaring flight that allows for a theoretical transit distance to exceed 1,000 km on their available energy sources without refueling. In actual fact, monarchs feed heavily during migration, and arrive at the overwintering sites with more stored fat than when they started. Migratory monarchs have been observed flying at altitudes as high as 11,000 feet above the land and individuals normally fly 11–12 h, covering 200–400 miles a day. Much of our understanding of the movement rates and migratory pathways followed by the monarchs have been revealed by tagging programs, initiated in 1952 by F.A. Urquhart at the Royal Ontario Museum in Toronto, Canada, and subsequently taken up by hundreds of other workers. The maximum distance traveled by a single tagged monarch is 2,595 miles (from New Brunswick, Canada, to the Cerro Pelon colony in Michoacan).

Once the monarchs arrive at their overwintering sites, they remain largely quiescent for a period of 4.5 months, until late the following March. They may leave the colony area briefly to drink water or nectar but return the same day (often in the same hour or two) to their trees. The overwintering butterflies remain reproductively inactive with the diapause being terminated in late March by the combined influence of temperature and photoperiod onto the monarchs' neuroendocrine system. In the last ten days of March, the Monarchs become increasingly active, mate at the colony site and then take off again for the north. These same individuals who flew south in the fall return in a generally northward direction to recolonize the North American continent for the summer. The adults from the Mexican colonies are known to reach the southern boundary of the United States by early April, lay their eggs, and then die. The eggs are laid on newly leafed out milkweed plants and growth is rapid. The first generation of adults for the new year emerges in late April, flies north through the middle tier of states and lays eggs throughout the area. The second generation of adults emerges by late May or early June and again flies northward. A third and fourth annual generation may emerge by the end of August. At this point, third, fourth and even fifth generation adults of the original northward moving migrants prepare to move south, over a path that they have never followed themselves.

Physiologically, monarchs have to build up fat protein reserves for the migration. However, they arrive on the overwintering sites with even more lipid reserves than they started with; this increase (up to 73% of their dry body weight) is due to heavy feeding on desert flowers as they fly south through the Central Plateau. Adequate lipid energy reserves are essential for passing the winter successfully. Spring monarchs are severely depleted of fat reserves (fat accounts for only 37% of dry weight in March) and they need to feed heavily during their spring northward movement to successfully reach the United States again and reproduce.

The monarch movements represent the world's greatest modern animal migration, involving the movements of at least one billion individual monarchs annually and perhaps as many as three billion in some years. The orientation ability of the monarchs to move nearly 3,000 miles and arrive precisely at a point to which they have never been before (at the end of the fall migration) is only beginning to be understood. A remarkably accurate sun compass mechanism keeps the monarchs on their general bearing. Considerable evidence also exists for orientation by magnetic fields. The Mexican Transvolcanic Range where the largest overwintering colonies exist contains magnetic anomalies a hundred times stronger than other surrounding terrain, due to heavy metallic ore deposits. The presence of magnetic materials in the monarchs' head and thorax has been demonstrated, significantly exceeding magnetite contained in its non-migratory relatives. Scent may be involved in locating the exact trees that their ancestors used the year before. The odor must come from billions of scales and perhaps scent molecules which still remain on the evergreen firs into the fall months, following the spring departure of their predecessors. Almost equally remarkable is the ability of the monarch colony to adjust its exact position on the mountain slope in elevation above sea level, height in tree, and even position on tree trunks and fir boughs daily to compensate for changes in weather, nightly temperature minima, fluctuating insulation values in cloud cover, etc.

Migration of the monarchs is truly one of the natural wonders of the world, a phenomenon equal to none and one that richly deserves preserving for posterity. It impressed the early civilizations: images of monarchs were carved in the ancient stonework at the San Juan Teotihuacan archeological site north of Mexico City more than 1,300 years ago. It continues to impress us now, with monarchs remaining the most popular insect in modern North American cultures.

Conservation Concerns

The greatest threat to the monarch is not the direct destruction of the butterfly species but the destruction of its overwintering habitat sites. Along the California coast, where the species once ranged from Mendocino County southward 650 miles to Baja California, a great many sites have been destroyed or severely altered by development. In Mexico, a number of the high mountain sites (10,000 to over 11,000 foot elevation) are being threatened by logging, firewood gathering, forest thinning by fires, and clearing for agriculture. Forest thinning opens the colony sites to severe winter storm effects, colder temperatures, and restriction of available area to shift the colony site if environmental conditions change. The Mexican government on both federal and state levels has responded with declarations of preserves, parks, and protection for the butterfly. Most of the protection, however, depends on the *ejidos* or associations of local communities that only recently have begun to recognize the economic benefits of ecotourism. monarch colonies today attract hundreds of thousands of visitors annually from throughout Mexico and abroad. Though tourism creates economic incentives for conserving the forest around the colonies, development of permanent trails with concrete steps up the mountains and hundreds of shops and small restaurants also take their toll on the environment.

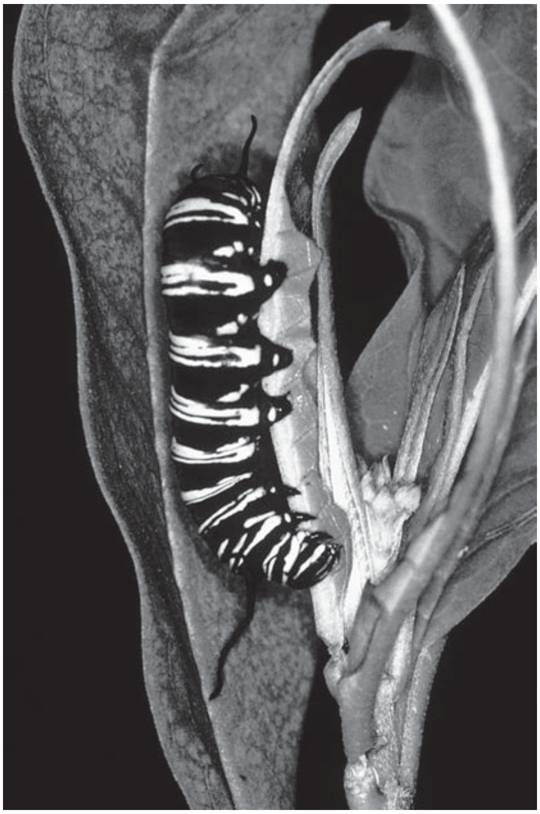
Another, recently emerged concern is tied to genetically engineered crops in the U.S. It appears that the pollen from Lepidoptera pest-resistant corn plants that contain genes of the bacterium *Bacillus thuringiensis* (known as Bt corn), once fallen on the milkweeds adjacent to corn fields and ingested by the monarch caterpillars, causes the death of the latter. Studies are underway to estimate the effect this phenomenon might have on monarch populations. However, it is known that field margins and hedgerows have been the monarchs' breeding grounds in the highly developed environment of the North American Great Plains, and losing this breeding environment might indeed prove to be detrimental for the migratory population.

Monarchs Among Other Butterflies

The Jamaican monarch, *Danaus cleophile* (Godart), is a smaller species found in the highlands of Jamaica and Hispaniola. Remarkably, to date nothing is known about the life history of this colorful, though much less glamorous, butterfly. *Danaus*

Monarch Butterfly, *Danaus Plexippus* L. (Lepidoptera: Danaidae), Figure 84 Aggregations of overwintering monarchs in northern Mexico (photo T. Emmel).

Monarch Butterfly, *Danaus Plexippus* L. (Lepidoptera: Danaidae), Figure 85 **Eggs (*left*), larvae (*middle*), and pupae (*right*) of monarchs in Florida (photo A. Sourakov).**



Monarch Butterfly, *Danaus Plexippus* L. (Lepidoptera: Danaidae), Figure 86 **Mature larva of monarch from Dominican Republic has much darker coloration than this of migratory monarch (photo A. Sourakov).**

Monarch Butterfly, *Danaus Plexippus* L. (Lepidoptera: Danaidae), Figure 87 **Viceroy, *Limenitis archippus*, a Müllerian mimic of monarch, Florida (photo A. Sourakov).**

cleophile is an extremely local and relatively rare island isolate that flies in the montane areas of the islands, ovipositing almost exclusively on *Asclepias nivea*. As far as is known, it is non-migratory. Within the subfamily Danainae, all monarchs belong to the tribe Danaini, subtribe Danaina, genus *Danaus Kluk*. None of the other 11 species in the genus is migratory. However, *Anetia panthrata* (Martyn), a primitive danaeine from Hispaniola, recently has been found to aggregate by the hundreds on pine trees in the highest mountains of Hispaniola.

Almost all danaines, monarchs included, form aggregations of dozens of adult individuals that feed on alkaloid-rich plants such as Boraginiaceae and Fabaceae (Fig. 84). The alkaloids play a role in pheromone production. It also has been suggested that they might contribute to the butterflies being toxic to the predators, though most of this toxicity has been attributed to larvae incorporating the substances called cardenolides from the milkweed host plants (Figs. 85 and 86).

The unpalatability of monarchs and other danaeines accounts for their bright aposematic coloration designed to repel potential predators. Several other butterfly species exhibit coloration similar to that of monarchs, though they are not related to them. Monarchs, being a very common distasteful species, are thought to serve as a model in various mimicry complexes. For example, mimicry between monarchs, queens (*Danaus gilippus* (Cramer)), and viceroys (*Limenitis archippus* (Cramer)) (Fig. 87), is a textbook example of such a mimicry complex. All three of these species are toxic and supposedly combine their efforts to leave an imprint of their wing pattern in the memory of a bird that has the misfortune of tasting them. In the case of the viceroy, which occasionally is eaten by birds, but not to the extent "normal" palatable butterflies are eaten, the toxic compounds must result from toxic substances contained in its host plant, the willow (*Salix* spp.). Such complexes where the model and the mimic are both distasteful are called Müllerian (vs. a Batesian complex, in which only the model is toxic, while the mimic is perfectly palatable).

► Butterflies
► Butterflies and Moths
► Conservation of Insects
► Mimicry

References

Ackery P, Vane-Wright RI (1984) Milkweed butterflies: their cladistics and biology. Cornell University Press, Ithaca, NY, 425 pp

Browser LP (1995) Understanding and misunderstanding the migration of the monarch butterfly (Nymphalidae) in North America 1857–1995. J Lepidopterists Soc 49:304–385

Browser LP (1996) Monarch butterfly orientation: missing pieces of a magnificent puzzle. J Exp Biol 199:93–103

Moniliform

Composed of round or elongate segments and resembling the beads of a necklace. This term usually is used to describe the form of certain antennae.

Monitoring

Careful observation of pest abundance and damage. Pest scouting.

Monkey Grasshoppers

A family of grasshoppers (Eumastacidae) in the order Orthoptera.

► Grasshoppers, Katydids and Crickets

Monoclonal Antibody

A single antibody produced in quantity by cultured hybridoma cell lines.

Monocondylic Articulation or Joint

A joint with a single point of articulation between adjacent segments. Having one condyle.

► Condyle
► Legs

Monocot

A plant with seedlings having a single cotyledon. Most monocots are grasses. (contrast with dicot)

Monoculture

A uniform or homogeneous planting of a crop over a large area.

Monoecious

In botany, having sexual parts of both genders in one individual plant, i.e., hermaphroditic. In entomology, infrequently and confusingly used as a synonym of monophagous – best not used in this sense.

Monogyny

The existence of only a single functional queen in a nest. (contrast with polygyny)

Monomachidae

A family of wasps (order Hymenoptera).
► Wasps, Ants, Bees and Sawflies

Monommidae

A family of beetles (order Coleoptera). They commonly are known as opossum beetles.
► Beetles

Monomorphic

Occurring in only one form.

Monomorphism

Among social insects, the existence of only a single worker subcaste in a colony.

Monophagous

An insect that feeds only on a single species of plant or animal.

Monophyletic

This refers to a group consisting of the ancestral form and all the descendants of that ancestor.
► Phylogenetics

Monophyletic Group

Taxa that are believed to contain all the known descendents of a single stem-species.
► Phylogeny

Monotomidae

A family of beetles (order Coleoptera). They commonly are known as root-eating beetles.
► Beetles

Monotypic

This generally means that a taxon contains only one subdivision. A family, for example, could have only one genus, or a genus could have only one species.

Mordellidae

A family of beetles (order Coleoptera). They commonly are known as tumbling flower beetles.
► Beetles

Morgan, Thomas Hunt

T.H. Morgan was born at Lexington, Kentucky, USA, on September 25, 1866. He received a B.S. degree in 1886 from the University of Kentucky, and a Ph.D. in 1890 from The Johns Hopkins University. He served on the faculty at Bryn Mawr College from 1891 to 1904, at Columbia University from 1904 to 1928, and at the California

Institute of Technology from 1928 to 1945. Morgan initially worked in descriptive embryology, but soon switched to experimental embryology. He then moved to genetics, and worked with *Drosophila*, aphids and phylloxerans. This was an important era, in that he demonstrated that the chromosome theory of sex determination was operable in these complex life cycles. His work with *Drosophila* is perhaps best known, and he discovered exchange between homologous chromosomes, and linkage between sex-linked genes. Morgan's pioneering work laid the groundwork for the chromosome theory of heredity. He also was first and foremost an experimentalist, and had little patience for anything less than scientific evidence. His work largely supported Darwin's theories of evolution. He served as president of the National Academy of Sciences and the American Association for the Advancement of Science, and was a Nobel laureate. He died at Pasadena, California, on December 4, 1945.

References

Muller HJ (1946) Thomas Hunt Morgan 1866–1945. Science 103:550–551

Sturtevant AH (1946) Thomas Hunt Morgan. Am Nat 80:22–23

Moribund

A lethargic or immobile state, usually immediately preceding death.

Mormon Cricket, *Anabrus simplex* Haldeman (Orthoptera: Tettigoniidae)

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Despite its common name, the Mormon cricket is not a cricket, but a katydid. Part of its common name is likely derived from its appearance, which (at high densities) is blackish and nearly wingless, giving it the appearance of a field cricket. The other portion of its common name has its origin in the early history of Utah. Destruction of crickets in 1848 by California gulls, *Larus californicus*, saved the early Mormon settler's grain crops; a fact commemorated by a large statue in Salt Lake City.

Distribution

Mormon cricket is native to western North America. Mormon cricket occurs widely, with a range that includes southern British Columbia to Manitoba in the north, and south to northern California and northern New Mexico. As a persistent pest, however, its range is limited to the Rocky Mountain and Great Basin regions.

Host Plants

Mormon cricket and coulee cricket are often considered to be omnivorous, but despite their wide host range they display some specific preferences until confronted by starvation. Virtually all field crops and vegetable crops can be consumed, but due to the nature of the cropping systems in the areas inhabited by these crickets, alfalfa and wheat are most often injured.

Over 400 species of native grasses, forbs, trees and shrubs are reported to be eaten by Mormon cricket. Most of these records occurred during the arid "dust-bowl" era of the 1930s when cricket densities were extremely high. Thus, they are not typical of cricket feeding behavior. Crickets often feed preferentially on the flowers and seed-heads of plants, ignoring the leaf material. Seed-head consumption is especially pronounced in grasses, though grasses are a minor component of cricket diet. Forbs such as bitterroot, *Lewisia rediviva*; wild onion, *Allium* spp.; arrowleaf balsamroot, *Balsamorhiza sagittata*; wild mustard, *Brassica* spp.; tumblemustard, *Sisymbrium altissimum;* and lupine, *Lupinus* spp.; are preferred by nymphs. In the adult stage, crickets eat mostly big sagebrush, *Artemisia tridentata*. In an analysis of Mormon cricket diet in Colorado, the diet consisted of: 50% forbs, 21% arthropods, 16% fungi, 6% grasses, 5% clubmoss, and 2% grasslike plants.

As suggested from the Colorado dietary analysis, crickets actively prey on other insects, including cicadas, ants, aphids, and beetles if they have the opportunity to catch them. They are quick to consume injured or dead crickets as well, and one of the distinctive characteristics about these crickets is their tendency to stop and feed on comrades that have been crushed on roadways by vehicles. Because the healthy crickets remain on the highways to feed on fallen crickets, they often become crushed also, resulting in long, dark, greasy road slicks consisting of pulverized crickets.

Natural Enemies

Predators are perhaps the best known mortality factor associated with crickets. Gulls are not the only vertebrates attracted to these insects when they become numerous, and among the avian predators most commonly observed feeding on crickets are crows, *Corvus brachyrhynchos brachyrhynchos*; hawks, *Falco* spp. and possibly others; meadowlarks, *Sturnella neglecta*; and blackbirds, various spp. (Wakeland 1959). Mammals such as coyotes, *Canis latrans*; ground squirrels, *Citellus* spp.; and kangaroo rat, *Dipodomys* spp.; also feast on crickets when they are abundant. Also, the wasps *Palmodes laeviventris* (Cresson) and *Tachysphex semirufus* (Cresson) (both Hymenoptera: Sphecidae) capture crickets and feed them to their young. Despite the frequency at which predation is observed, there is little evidence that predators are normally effective at maintaining crickets at low densities, or capable of suppressing crickets during periods of population outbreak.

Parasitism is surprisingly uncommon in cricket populations. Only the egg stage is parasitized with any degree of frequency, and although levels of up to 50% parasitism have been reported, it is usually quite low. The parasitoids responsible for attacking eggs are *Sparaison pilosum* Ashmead (Hymenoptera: Scelionidae) and *Oencyrtus anabrivorus* (Hymenoptera: Encyrtidae).

Pathogens vary greatly in their effect on crickets. The microsporidian *Heterovesicula cowani* (Vairimorpha) can naturally infect substantial proportions of Mormon cricket populations, and causes rapid mortality when young crickets ingest spores. *Heterovesicula* appears to be the most important pathogen of crickets. The nematode *Agamaspirura anabri* (Nematoda) and the horsehair worm *Gordius robustus* (Nematomorpha) have also been observed in crickets. *Gordius* was reported to be quite common in crickets near standing water because part of the horsehair worm's life cycle takes place in water; unfortunately, water is not plentiful in the habitat of these crickets.

Life Cycle and Description

Normally there is one generation per year. Eggs overwinter, with egg hatch occurring in March–May, often while snow remains on the ground. The nymphs are present until June when adults begin to emerge and begin egg production. Adults usually perish by late August, often earlier. The combined nymphal and adult development time requires about 100 days

Egg

The egg is elliptical in shape and measures about 7–8 mm in length and 2.0–2.5 mm in width. Initially brown in color, it soon turns whitish and then gray. Eggs are deposited in the soil singly or in small clusters at a depth of 6–25 mm during the summer, where they remain until spring. Sometimes eggs are deposited around the base of plants, but more often bare soil is favored, including the mounds of ants. Females deposit, on average, about 85 eggs, but up to 160 per female has been observed. Eggs are ready to emerge early in the spring, and begin to hatch when soil temperatures attain about 5°C, a much lower temperature than grasshoppers.

Nymph

Upon hatching from the soil, the nymphs are dark in color, resemble the adults in form, and measure about 6 mm in length. There are seven instars, and by the time they attain the last instar they are about 30 mm in length. The initial instars are black with white along the lateral edge of the posterior end of the pronotum, and the ovipositor of the female is not apparent. As they attain the fourth instar, however, they acquire green, red, purple, or brown color and in the female the ovipositor becomes increasingly obvious. Mean duration of development period of crickets cultured at 21–26°C is 9.5, 7.4, 5.1, 6.5, 5.6, 5.6, and 10.4 days, respectively, for instars 1–7. Thus, the mean total development time of nymphs is estimated at 50 days, though weather significantly affects development rate.

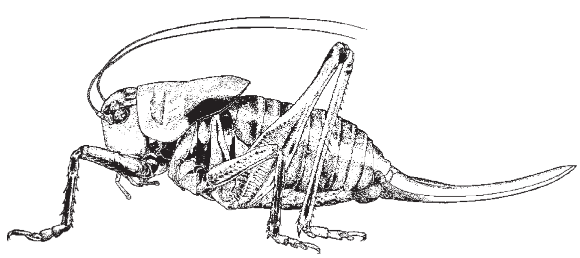
The crickets tend to aggregate, seeking shelter together beneath bushes and debris during inclement weather and at night. Once they reach the third or fourth instar crickets the aggregations begin to move long distances, with huge numbers of crickets coalescing into groups that move in bands. The density of crickets in bands may be 10–30 per square meter. The width of a band is often 300 m or more, but only 10 m deep, with crickets moving in the same direction along the entire width. The crickets all seem to move independently and consistently in the same direction, often at a rate of 1 km per day. There is no indication that they follow one another, and the basis of orientation is unknown.

Adult

The adult is very similar to the mature nymph in form and color but larger, measuring 35–45 mm in length. Also, the sword-shaped ovipositor of the adult female is longer (Fig. 88), and the short wings of the adult male protrude from beneath the pronotum and are used as a stridulatory organ. As is the case with nymphs, the adults will cluster under shelter during the evening and during inclement weather. They will also climb into bushes to escape the hot soil during excessively warm weather. Adults continue to move in bands in the same manner as nymphs, stopping only to eat and oviposit.

Reproduction commences 10–14 days after attaining the adult stage. Males call from perches on vegetation during the morning hours. Females compete for the attention of males, mount the males, and are inseminated. Males are selective in their choice of partners, often choosing the largest female with which to mate. During insemination, the male provides the female, attached to the sac containing sperm, a large proteinaceous mass that protrudes from her genital opening. While the sperm is draining into the female's reproductive system the proteinaceous mass provides a meal for the female.

Mormon cricket exists in solitary and gregarious forms. The aforementioned description applies mostly to the gregarious form, which is the only form causing damage and the only form that has been thoroughly studied. The solitary form occurs at low density between periods of population



Mormon Cricket, *Anabrus Simplex* Haldeman (Orthoptera: Tettigoniidae), Figure 88 Adult female Mormon cricket, *Anabrus simplex*.

outbreak and in areas where crickets do not become numerous. In contrast to the gregarious form, solitary crickets are green in color, and do not aggregate or form bands. Sexual behavior is also reversed, with females choosing among males. This change in mating behavior seems to be related to better nutrition of crickets when they are not at high densities.

Damage

Mormon crickets occur in arid sagebrush rangeland, and generally cause little injury unless they move into irrigated cropland. In earlier times when settlers had to be nearly self-sufficient, vegetable gardens and grain crops were critically important to ranchers, and crop losses caused by Mormon crickets were a significant threat to the existence of western communities. Presently, however, crop production is much less significant in these arid lands, and control technologies have improved markedly, so cricket importance has declined. Crickets remain a threat, however, and when bands of crickets attain lush crop vegetation, they can be devastating.

Management

Sampling

Cricket bands are easily detected when they cross roads, and their presence in an area rarely is a surprise. However, they move rapidly and their course of travel is unpredictable, so when crickets are discovered control efforts are usually directed at the bands before they enter crop-growing areas.

Insecticides

Persistent insecticides are sometimes applied by aircraft to foliage in areas supporting nymphal populations or migrating bands. An alternative is to apply insecticide-treated bait. The preferred bait is flaky wheat bran, and it may be applied dry.

Cultural Practices

In earlier times a common practice to prevent invasion of crop fields by cricket bands was to surround the crop with ditches possessing steep sides; crickets falling into such ditches had great difficulty regaining the soil surface. Similarly, vertical barriers of metal topped by a deflector served to prevent crickets from entering areas surrounded by such "cricket fences."

► Cannibalism
► Gregarious Behavior

References

Capinera JL (2001) Handbook of vegetable pests. Academic, San Diego, 729 pp

Cowan FT (1929) Life history, habits, and control of the Mormon cricket. USDA Tech Bull 161, 28 pp

MacVean CM (1987) Ecology and management of the Mormon cricket, *Anabus simplex* Haldeman. In: Capinera JL (ed). Integrated pest management on rangeland: a shortgrass prairie perspective. Boulder, CO, Westview, pp. 116–136

Wakeland C (1959) Mormon crickets in North America. USDA Tech Bull 1202, 77 pp

Morphogenesis

Growth and change in form during development, either embryonic or post-embryonic development.

Morphology

Study of the form and function of organisms. Many writers erroneously use the term morphology when they simply mean shape, or form, or structure.

► Abdomen of Hexapods

- ► Antennae of Hexapods
- ► Head of Hexapods
- ► Internal Anatomy of Insects
- ► Legs of Hexapods
- ► Mouthparts of Hexapods
- ► Thorax of Hexapods
- ► Wings of Insects

Morphotype

The collection of physical characteristics that provides for the distinct physical appearance of the organism.

Morrison, Herbert Knowles

Herbert Morrison was born in Boston, Massachusetts, USA, on January 24, 1854. He was an individual of great physical strength and endurance, and became a professional insect collector. He specialized in Lepidoptera, traveling widely in the American west and south. He named a number of species of western Lepidoptera, but much of what he collected was named by others. He contracted dysentery on one of his collecting trips, to Key West, Florida, and died on June 15, 1885, at Morgantown, North Carolina.

Reference

Essig EO (1931) A history of entomology. The Macmillan Company, New York. 1029 pp

Morse, Albert Pitts

Albert Morse was born at Sherborn, Massachusetts, USA, on February 10, 1863. His formal education was limited because he was needed to assist with the family's farming operation. He abandoned farming at the age of 23, however, and eventually accepted a position as a zoology assistant at Wellesley College. He served as curator or similar scientific capacity at several institutions, including the Peabody Museum and Carnegie Institution. He also served as a teacher of entomology and zoology. Despite his lack of formal education, Morse became a leading authority on New England Orthoptera, principally Acrididae. He was an associate of S.H. Scudder, also an acridologist. Morse traveled widely and also published on other insect groups, particularly Odonata. Noteworthy publications authored by Morse include "Researches on North American Acrididae" and "Manual of the Orthoptera of New England." He died April 29, 1936.

References

Essig EO (1931) A history of entomology. The Macmillan Company, New York, 1029 pp
Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Mortality Rate

Death rate; the number of deaths per unit population during a given period of time.

Mosquito Larval Feeding Ecology

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Mosquitoes serve as hosts and vectors to a suite of pathogens and parasites such as viruses, bacteria, fungi, nematodes and protists. Because of the number of disease-causing agents that mosquitoes transmit, as well as the magnitude of health problems these diseases cause to humans and livestock worldwide, mosquitoes are medically the most important group of insects. Specifically, in an attempt to lower the incidence of mosquito-borne diseases such as malaria, dengue, yellow fever and most recently West Nile virus, hundreds of millions of dollars have been spent on mosquito surveillance and control. Early observations of insect vector behavior prior to the advent of DDT in the 1920s and 1930s helped formulate control strategies around this period. In fact, because of the availability and effectiveness of synthetic insecticides, and their effective application under a wide range of conditions, the need for vector behavior and ecological studies was reduced. However, the development of insecticide resistance is the primary reason why vector control has moved from broad spectrum, persistent chemicals to more specific biological control agents, e.g., bacterial insecticides such as *Bti* (*Bacillus thuringiensis* var. *israelensis*) and *Bs* (*Bacillus sphaericus*). Because these bacilli species are obligatory stomach toxins in mosquito larvae, their success as particulate larvicides has been enhanced significantly with increased knowledge of larval feeding ecology in terms of where mosquito larvae feed, as well as how and what larvae feed upon, in their environment.

Mosquito Larval Habitats

The ovipositing adult female selects larval mosquito habitats. Female mosquitoes will generally oviposit above, or upon, the water surface of ponds, swamps, lake edges, salt marshes and artificial containers. In addition, oviposition will occur in areas where water is absent (e.g., along the dried edges of temporary pools or other ephemeral puddles, along the inner side of dry tree hole habitats, crab burrows or in phytotelmata). The microhabitats in which larvae feed within these aquatic habitats include (i) at the air-water interface, (ii) within the water column, (iii) along plant root zones, and (iv) on mineral and organic surfaces.

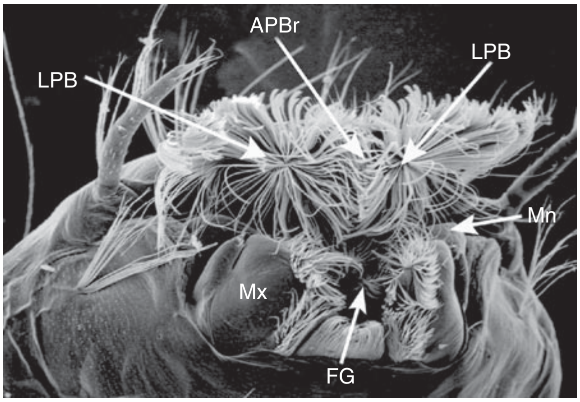
The air-water interface of natural aquatic systems has been defined as a thin zone (less than 1 mm) of the water column and has been classified as the surface microlayer. This interface can be more accurately described as a layer of dissolved substances, particles and microorganisms that accumulate due to simple diffusion, rising bubbles, convection, upwelling from sediments and subsurface water as well as from atmospheric dry fallout. Thus, the surface microlayer becomes an accumulation layer where the concentration of various chemical compounds and microorganisms such as bacteria and algae exceeds that of subsurface water by orders of magnitude. Most *Anopheles* mosquito larvae feed at the surface, presumably because food resources are more abundant at these interfaces.

The subsurface microhabitat within the water column utilized for feeding by mosquito larvae is characterized as the zone below the surface microlayer, and extends to the benthos. Several species of *Culex*, *Culiseta* and *Ochlerotatus* larvae feed in this microhabitat on the suspended particles in the subsurface water column. Mosquito larvae (e.g., *Coquillettidia* and *Mansonia* spp.) that inhabit plant root zones tap into the oxygen source trapped inside the plant using specialized respiratory siphons. Rock pools along tidal zones or riverine systems accumulate water, and consequently provide a type of mineral surface with organic material on which some *Ochlerotatus* spp. can forage.

The distribution and quantity of available food resources largely determine mosquito larval distribution, growth and feeding success. Stress imposed on larvae due to food limitations within microhabitats has shown to have adverse effects on larval survival, developmental rates, adult size and fitness as well as competence as disease vectors.

Mouthpart Morphology and Feeding Modes

Mosquito larvae use different morphological structures and feeding modes (e.g., filtering, suspension feeding, grazing, interfacial feeding or predation) in food acquisition. The larval mouthparts possess specialized setae that are configured into brushes

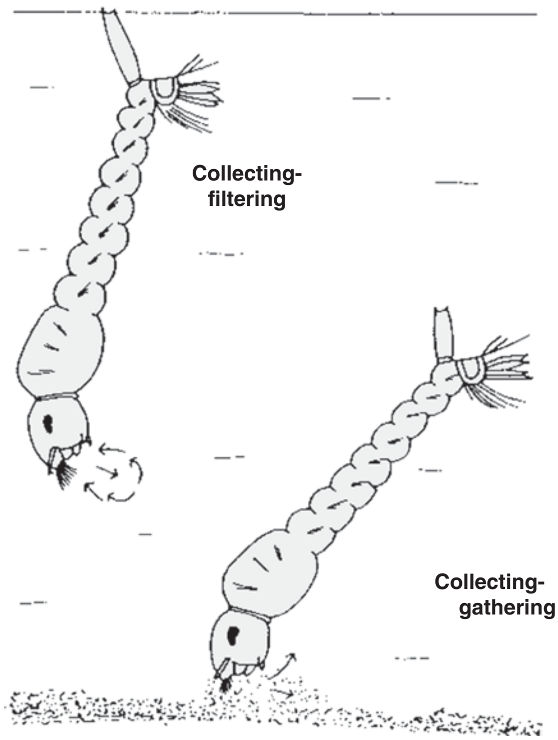


Mosquito Larval Feeding Ecology, Figure 89 **Scanning electron micrograph of the larval head of *Culiseta*. Abbreviations: LPB, lateral palatal brush; APBr, anteromedian palatal brush; Mx, maxilla; Mn, mandible; FG, feeding groove (Photograph by Doug Craig).**

or combs, and commonly referred to as the lateral palatal (or mouth) brushes (LPBs) (Fig. 89). The LPBs move through the water similar to the turning of pages in a book, and generate currents that assist in the removal of suspended food particles from the water surface, and subsurface or benthos. Other mouthpart actions assist with ingestion, chewing, or the formation of the food bolus prior to swallowing. Morphologically, a reduction in the numbers and lengths of LPBs, maxillary brushes and mandibular setae tends to occur in a progression from filter-feeders to predators.

Excluding mosquito larvae predators, the classification of non-predatory mosquito larvae is divided into four behavioral feeding modes: (i) shredding, (ii) collector-filtering, (iii) collector-gathering, and (iv) scraping (Fig. 90). These feeding modes are based on morpho-behavioral adaptations that have evolved to allow mosquito larvae to feed on a wide array of food resources. Nonetheless, because mosquito larvae feed on such diverse food resources, they are likely not restricted to a single feeding mode.

The shredder feeding mode entails chewing or biting-off small fragments of coarse particulate organic material (CPOM size range >1 mm) such as leaves, algae or dead invertebrates. Collecting is



Mosquito Larval Feeding Ecology, Figure 90 **Mosquito larvae displaying collecting feeding modes (After Clements, 1992).**

the feeding mode most commonly observed by mosquito larvae. The collectors are divided into those taxa that filter vs. gather. Filter-feeders or suspension feeders generally remove fine particulate organic material (FPOM size range = 0.45 µm to 1 mm) from the water surface or column. The feeding microhabitat of collector-filterers extends from the air-water interface to feeding in the water column or at plant root zones. Collector-gatherers resuspend food, and remove particles deposited on, or loosely attached to, surfaces by the action of the LPBs. Conversely, those larvae that specialize in the removal of food resources tightly adhered to submerged plants or mineral surfaces are termed scrapers.

Larval Dietary Components

An important determinant of mosquito larval distribution and feeding success is the distribution of larval food resources. Most mosquito larvae are omnivorous, i.e., the major part of their diet consists of microorganisms such as bacteria, algae and protoctistans and particulate organic detritus. Using DNA binding fluorochromatic stains, gut content analyses as well as microhabitat surveys of larval food items have shown that larvae ingest detritus particles, algae, euglenoid protozoans, diatoms, cladocerans and hydrocarina or water mites. However, in terms of overall dietary percentage, bacteria (cocci, rods, spriochetes, and cyanobacteria) have been considered the most important of the microorganisms consumed by mosquito larvae. Several studies have noted that ecological succession and diel periodicity of microorganisms in larval feeding microhabitats directly affects what the larvae ingest through direct availability. The mixed diet of larval mosquitoes provides the necessary proteins, vitamins and fatty acids for growth, development and survival.

► Mosquitoes

References

Clements AN (1992) The biology of mosquitoes. Vol 1. Development, nutrition and reproduction. Chapman Hall Publishers, London, United Kingdom, 509 pp

Laird M (1988) The natural history of larval mosquito habitats. Academic, New York, 555 pp

Merritt RW, Dadd RH, Walker ED (1992) Feeding relationships, natural food, and nutritional relationships of larval mosquitoes. Annu Rev Entomol 37:349–376

Wallace JR (1997) Larval feeding ecology of *Anopheles quadrimaculatus* (Say) and *An. punctipennis* (Say) (Diptera: Culicidae) in southcentral Michigan ponds. Ph.D. Dissertation, Department of Entomology, Michigan State University, East Lansing, Michigan

Mosquito Overwintering Ecology

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To date, there are nearly 3,500 species of mosquitoes (Diptera: Culicidae) identified to science, many of which serve as vectors of disease-causing organisms to humans and animals. Mosquitoes are ubiquitous in their distribution, being found in practically every habitat except permanently frozen areas. Approximately 75% of all mosquitoes are found in the tropics and subtropical areas, and many mosquito-borne illnesses are considered to be more tropical in their distribution (e.g., malaria or dengue fever). However, several diseases are found principally in colder, more temperate climate regimes, including Eastern Equine Encephalitis and La Crosse Encephalitis. Because worldwide travel has increased the potential for new disease introductions (e.g., dengue and West Nile viruses in North America) to more temperate areas of the world, overwintering eco-physiological aspects of mosquito biology have recently become a focal point of epidemiological study.

The survival mechanisms that mosquitoes employ to overwinter are important from both biological and epidemiological perspectives. Early studies were initiated in order to address the mechanisms mosquitoes use to survive adverse winter climates. However, the mechanisms for overwintering by several species are poorly understood. Also, the mechanism of disease overwintering is often not well known. An assemblage of physiological/morphological, ecological and behavioral mechanisms are needed in order to survive cold temperatures.

Life Histories

Mosquitoes exhibit complete or holometabolous metamorphosis. In order to emerge or survive from one season to the next, mosquito life histories have evolved diapausal or hibernation components among all the developmental stages. Many species of spring mosquitoes (e.g., several taxa within the genera *Aedes*, *Ochlerotatus* and *Psorophora* in temperate North America) overwinter in the egg stage. Many of these mosquitoes inhabit either treeholes, vernal pools or other types of transient freshwater habitats. The adult females of these taxa will oviposit in the late spring or early summer along the outer margins of these vernal pools treehole or other container habitats. As water levels diminish, more ovipositional habitats are exposed along these drier margins. These eggs require a dry period and will survive until the following spring despite dry and possibly re-flooded conditions. In other species, e.g., *Ochlerotatus atropalpus* (rock-hole mosquito) it has been observed that females will glue an egg batch to the side of a rock-hole above the waterline for the overwintering generation. It is unknown what this glue-like substance is, or how it is produced. Among mulitivoltine species (i.e., those species with more than one generation per year), morphological differences in egg structure have been observed between diapausing-winter and summer eggs. For example, *Anopheles walkeri* eggs exhibit seasonal differences in that diapausing-winter eggs have larger floats and a reduced exochorion compared to summer eggs.

Because many aquatic systems freeze over for several months during the winter, the larval stage of mosquitoes seems like an unlikely developmental choice in which larvae would overwinter. However, there are several taxa from five genera, *Culiseta*, *Coquilletidia*, *Wyeomyia*, *Orthopodomyia*, and possibly a few *Toxorhynchites* that are found in unique freshwater habitats that overwinter in the larval stage. The larval habitat of these taxa, in most cases, freezes – implying simply that possibly the larvae freeze solid, as is the case of the pitcher-plant mosquito, *Wyeomyia smithii*. With the exception of the *W. smithii*, it is most likely that larvae are not freeze tolerant, and therefore use some microhabitats protected from lethal temperatures.

In temperate climates, overwintering populations of adult mosquitoes include a few taxa from four genera, *Culex*, *Culiseta*, *Anopheles* and *Uranotaenia*. Most studies on overwintering adult mosquitoes have examined those populations distributed in southerly regions or warmer climates of North America. These studies have not examined the mechanisms used by northern populations to survive colder climates. Of most recent interest are those tropical species (e.g., *Aedes albopictus* and *Ochlerotatus japonicus*) that have been introduced to North America that have survived winters in northern latitudes much different from their tropical origins.

Eco-Physiology and Behavior

As stated previously, low temperatures present a suite of ecological and physiological challenges for insect survival. From an ecological perspective, hibernaculum (or place to hibernate) selection may be critical for physiological mechanisms to be effective. In order to escape the formation of ice crystals that freeze cells and/or tissue, insects, and mosquitoes in particular, may opt for protected environments in which to overwinter. These hibernacula should offer protection from significantly colder temperatures, as well as wind and low humidity. Adult mosquitoes tend to be found in two types of overwintering hibernacula: (i) anthropogenic or human-constructed shelters (e.g., houses, garages, barns, culvert pipes, steam tunnels, rabbit hutches, and dog houses), or (ii) natural hibernacula, such as in tree hollows or under bark, and animal burrows. It is possible that other forms of natural hibernacula exist but have not been identified. Two anopheline mosquitoes, *Anopheles quadrimaculatus* and *An. punctipennis*, have been observed in both anthropogenic and natural hibernacula. *Culex pipiens*, or the house mosquito, has been collected from anthropogenic hibernacula. The microclimates of these hibernacula have not been characterized in terms of temperature or relative humidity throughout the hibernation period. Adult mosquitoes do not experience a true diapause in these hibernacula; if temperatures increase enough to allow flight, mosquitoes will move within, or sometimes leave, a hibernaculum during warmer periods.

Generally, in colder climates, female mosquitoes enter the winter season for hibernation or a quiescent period, whereas males typically will copulate and die before winter begins. Female mosquitoes may take a blood meal prior to hibernation, and use this meal for fat production instead of for egg production; this is termed gonotrophic concordance. Movement is limited within hibernacula; however, females have been observed to leave a hibernaculum in search of a blood meal during a warm period of early spring. For many mosquito taxa in temperate climates, ovarian development is essentially arrested during the winter, and resumes again in late spring when females obtain their first blood meal.

Cold hardiness in insects pertains to the capacity of an organism to survive such low temperatures. Two strategies potentially employed by insects to survive winter include freeze avoidance and freeze tolerance. Because cases of freeze tolerant insects are rare, if non-existent, it can be assumed that insects, in general, employ the former of the two strategies. In order to avoid freezing, insects may be able to depress or lower the temperature at which the insect body freezes or when ice crystals begin to form. This is termed supercooling. The capacity for an insect to supercool may be influenced by several factors such as season, life stage, feeding status, thermal acclimation and cryoprotectants (e.g., glycerol or trehalose). In the case of mosquitoes, little information is available for assigning potential disease vectors to either a freeze avoidance or freeze tolerant strategy. To date, one study has shown that *Anopheles quadrimaculatus* and *An. punctipennis* may exhibit a freeze avoidance strategy. It has been shown that *An. quadrimaculatus* will supercool to a temperature of −17°C compared to *An. punctipennis* at −20°C. Lower lethal temperatures for these species were −15°C and −17°C, respectively. Consequently, if *An. punctipennis* can survive colder temperatures, it may have more natural choices in which to overwinter.

► Mosquitoes

References

Bates M (1949) The natural history of mosquitoes. Harper & Row, Publishers, New York, NY, 378 pp

Clements AN (1992) The biology of mosquitoes. Chapman and Hall, New York, NY, 509 pp

Crans WJ, McNelly JR (1997) A classification system for the life cycles of mosquitoes in New Jersey. Proceedings 46th Annual Meeting of the New Jersey Mosquito Extermination Association, pp 148–153

Lee RE, Lee MR, Strong-Gunderson JM (1993) Insect cold-hardiness and ice nucleating active microorganisms including their potential use for biological control. J Insect Physiol 39:1–12

Pratt HD (1959) A new classification of the life histories of North American mosquitoes. Proceedings 84th Annual Meeting of the New Jersey Mosquito Control Association, pp 42–48

Wallace JR, Grimstad PR (2002) A preliminary characterization of the physiological ecology of overwintering *Anopheles* mosquitoes in the Midwestern USA. J Am Mosq Control Assoc 18:126–127

Mosquito Oviposition

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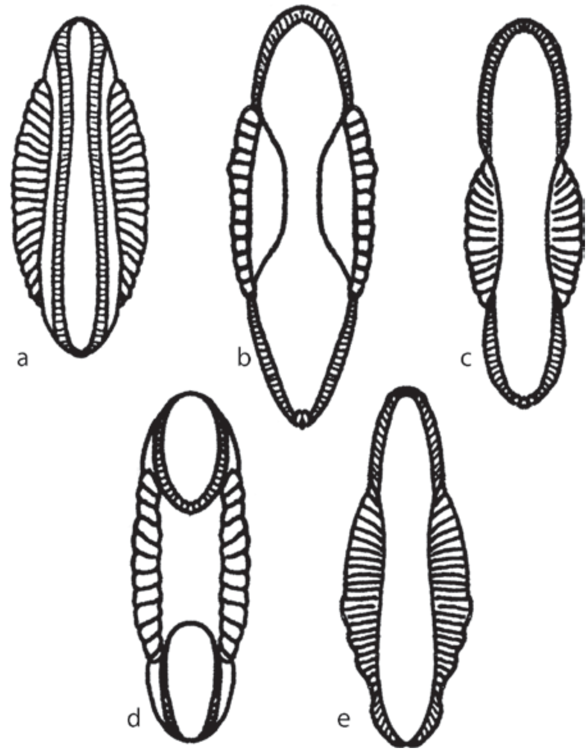
The larval stages of the Culicidae are exclusively aquatic. Therefore, gravid females must seek oviposition sites that are aquatic or will become aquatic in the future. Some of these sites include temporary woodland pools, tree and crab holes, man made containers such as abandoned automobile tires, phytotelmata, moist soil in low lying areas that readily become flooded as well as a great variety of other aquatic environments.

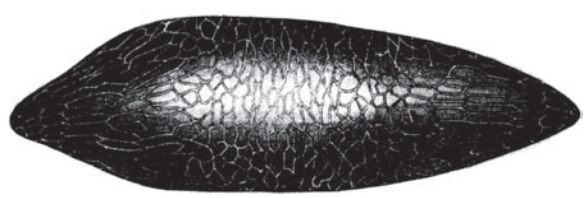
Mosquitoes maximize their reproductive potential by using habitats that are of differing resource richness and this use depends heavily on how quickly batches of eggs are matured by the female. The larvae of mosquitoes are filter feeders, browsers, and predators that utilize the microorganisms and other organic matter present in the water they inhabit. Mosquitoes deposit their eggs either singly or in floating masses that are referred to as “rafts.” The mosquitoes that mature and deposit most or all of their eggs at one time usually do so in the form of rafts or other orderly aggregations above or below the surface of the water. Many of these species tend to use resource-rich environments that have relatively high microbial populations and are rich in organic materials. Pools of foul water or artificial containers containing infusions of plant materials are highly attractive to these mosquitoes. The larvae of these species can often occur in enormous numbers under ideal conditions. Mosquitoes that develop a series of eggs over time usually occur in lower densities and use aquatic habitats that are often not resource rich. These species tend to distribute their eggs over a considerable area and take an appreciable time to deposit an entire clutch.

The gross morphology of mosquito eggs is extremely variable and relate directly to the where and how they are deposited (Figs. 91 and 92). The eggs of *Aedes*, which are often deposited onto soil and are exposed to periods of drying, possess a thick chorion that is resistant to desiccation. The eggs of *Anopheles* are deposited onto the surface of water and remain there until eclosion due to tiny hollow floatation structures referred to as "frill floats." The eggs of *Culex* are deposited on end into an organized floating raft. These eggs have a distinct exo/endo chorionic space that allows water to rise upwards and create an apical droplet on each egg. The apical droplet is hydrophobic and helps in maintaining the correct orientation of tilted eggs and egg-rafts.

Mosquitoes use a variety of olfactory, visual, and tactile cues to locate suitable oviposition sites. Undoubtedly, many species use a combination of these cues that may affect the female's choice of where to deposit eggs (Fig. 93). Because many species of mosquitoes use aquatic habitats that are ephemeral in nature, the rapid detection and subsequent assessment of potential ovisites are essential for successful reproduction. Mosquitoes can readily sense exceedingly small amounts of volatile compounds that are emitted from aquatic habitats by using receptors located on their antenna, mouthparts and or tarsal segments. Over sixty years of studies have generated an enormous data base of some of the volatile compounds that are attractive to dozens of species. Many of these studies involved the use of individuals obtained from laboratory colonies and perhaps might not be considered applicable to understanding the oviposition behavior of



Mosquito Oviposition, Figure 91 **Representative *Anopheles* eggs, showing typical variation of the float among species: (a) *An. gambiae*, (b) *An. walkeri*, (c) *An. maculipennis*, (d) *An. novaguinensis*, (e) *An. pharoensis* (adapted from Mattingly, 1969. Mosquito Systematics Newletter).**



Mosquito Oviposition, Figure 92 **Representative *Aedes* egg: lateral view of *Aedes* (*Aedimorphus*) *domesticus* egg (adapted from Reinert, JF, 1972. Mosquito Systematics).**

Mosquito Oviposition, Figure 93 **Female *Culex pipiens* adding an egg to the egg raft she is about to complete. During the next hour, the white eggs will darken to a color that blends well with the water upon which the raft floats (image courtesy of Richard G. Weber).**

wild populations of mosquitoes, but they do provide important information about the ability of gravid female mosquitoes to detect and respond to a multitude of minute quantities of airborne molecules. The dynamic microbial ecology associated with many temporary aquatic environments often creates an equally dynamic combination of volatiles that provide important cues for gravid female mosquitoes. Additionally, many species of mosquitoes can detect the volatiles associated with presence of life history stages of their own or other species.

Chemoreception of volatile compounds is likely the most important cue for mosquitoes that oviposit at night, and visual cues are important for mosquitoes that are diurnal or crepuscular. Day-flying mosquitoes that use phytotelmata or plant parts that contain water have been shown to discriminate between colors. This visual discrimination could be essential for mosquitoes that use pitcher plants as oviposition sites. Many mosquito species will only deposit their eggs into a particular plant species. The color of the leaves for each species is unique and therefore offers a reliable cue for gravid mosquitoes. Additionally, the color change associated with the senesce of the leaves of pitcher plants could also indicate the quality of the water held within. Studies involving tree-hole inhabiting mosquitoes have determined that darker rather than lighter-hued colors are attractive to gravid females indicating that they can recognize a dark tree hole from other similar aquatic habitats by color.

Many species of mosquitoes in the genus *Aedes* deposit their eggs singly onto soil that is regularly exposed to periods of flooding and drying. Often, this wetting and drying is a prerequisite for successful eclosion of the eggs. Interestingly, one species of *Aedes* found in areas of Africa will often oviposit upon the legs of crabs that inhabit tidal flats. These crabs crawl in and out of the water as part of their normal foraging behavior and can act as phoretic transporters for the mosquito eggs deposited on their shells. The eggs of *Anopheles* are deposited singly on the surface of the water and float until eclosion. Many species of mosquitoes that use tree holes and phytotelmata as oviposition sites tend to deposit their eggs singly due to the limited nutrient resources offered by such sites. The mosquitoes of the genus *Culex* contain the most species that construct floating egg rafts. Other raft-building genera include *Mansonia*, *Coquillettidia*, *Uranotaenia*, *Trichoprosopon*, *Eretmapodites* and *Culesita*. Some species attach their egg rafts to submerged vegetation. Several species of the genus *Armigeres* deposit their eggs into small rafts that are held by the metathoraxic legs of the female until they hatch. Additionally, females of *Trichoprosopon* and *Eretmapodites* display post-ovipositional maternal care in the form of brooding of egg rafts.

For many species of mosquitoes, distinct preoviposition behaviors have been observed and recorded. Often these behaviors are associated with the assessment of potential ovisites and include distinct, observable flight patterns. The larvae of *Toxorhynchites* are predatory on the arthropod inhabitants of tree holes, including the larvae of many species of mosquitoes.

Females of this large species perform an oviposition flight that consists of a series of elliptical loops over the potential ovisite before they drop a single egg from the air. The function of the looping flight has been postulated to be a form of assessment of the volatiles from the site as well as a mechanism to deposit eggs. Many tree holes often have narrow openings that would not allow for easy access to the surface of the water contained within. Additionally, mosquitoes of the genus *Wyeomyia* use the aquatic habitat offered by pitcher plants and drop their eggs into the pitfall trap during an oviposition flight.

The observed preoviposition behaviors of a few species of *Culex* include locating and assessment of potential oviposition sites as well as, distinct behaviors associated with the successful deposition of egg rafts. At dusk, female *Cx. restuans* fly upwind approximately a meter above the ground as they search for the plume of volatiles produced by potential ovisites. After finding a potential ovisite, females perform a bobbing flight over the surface of the water for several minutes. This flight has been termed obstetric dancing and most likely is involved in assessment of the volatiles emitted by the site. Females then land on vertical surfaces near the potential ovisite. During this loitering period, females most likely swallow air into the ventral diverticula. Several minutes later, females land on the surface of the water and then begin to drink. After drinking, females initiate egg rafts between parallel metatarsi onto the surface of the water. Females continue to drink during later stages of egg raft construction. The air swallowing and drinking behaviors are important for the operation of the hydrostatic skeleton and essential for successful oviposition. Future field studies with mosquito species that deposit their eggs at one time in a mass or raft will most likely also display the behaviors of swallowing of air and drinking.

Finally, death stress oviposition has been documented to occur in mosquitoes as well as many other insects. Gravid females that are dying will often release eggs as a strategy to maximize reproduction. Mosquitoes that are dying near or on ovisites can release eggs that could eclose successfully.

► Mosquitoes
► Phytotelmata

References

Allan SA, Kline DL (1998) Larval rearing water and preexisting eggs influence oviposition *Aedes aegypti* and *Ae. albopictus* (Diptera: Culicidae). J Med Entomol 35:943–947

Bates M (1949) The natural history of mosquitoes. MacMillan, New York

Beament J, Corbet SA (1981) Surface properties of *Culex pipiens pipiens* eggs and the behaviour of the female during egg-raft assembly. Physioll Entomol 6:135–148

Bentley MD, Day JF (1989) Chemical ecology and behavioral aspects of mosquito oviposition. Annu Rev Entomol 34:401–421

Christophers SR (1945) Structure of the *Culex* egg and egg raft in relation to function (Diptera). Trans R Entomol Soc Lond 95:25–34

Davis EE, Bowen FM (1994) Sensory physiological basis for attraction in mosquitoes. J Am Mosq Control Assoc 10:316–325

DeCoursey JF, Webster AP (1952) Effect of insecticides and other substances on oviposition by *Aedes sollicitans*. J Econ Entomol:451030–1034

Frank JH (1986) Bromeliads as ovipositional sites for *Wyeomyia* mosquitoes: form and color influence behavior. Fla Entomol 69: 728–742

Goiny H, Van Someren ECC, Heisch RB (1957) The eggs of *Aedes* (*Skusea*) *pembaensis* Theobald discovered on crabs. East Afr Med J 34:1–2

Hinton HE (1981) Biology of insect eggs. Pergamon, Oxford

Hudson BN (1956) The behaviour of the female mosquito in selecting water for oviposition. J Exp Biol 33:478–492

Kennedy JS (1942) On water-finding and oviposition by captive mosquitoes. Bull Entomol Res 32:279–301

Linley JR (1987) Aerial oviposition flight of *Toxorhynchites amboinensis* (Diptera: Culicidae). J Med Entomol 24:637–650

Lounibos LP (1983) Behavioral convergences among fruit-husk mosquitoes. Fla Entomol 66:32–41

Mattingly PF (1969) Mosquito eggs III. Tribe Anophelini. Mosq Syst Newslett 1:41–50

Okazawa T, Miyagi I, Yong HS (1992) Oviposition and eggs of *Armigeres* (*Leicesteria*) *flavus* (Diptera: Culicidae). Jpn J Entomol 60:54–58

Steffan WA, Evenhuis NL (1981) Biology of Toxorhynchites. Annu Rev Entomol 26:159–181

Weber RG, Tipping C (1993) Preoviposition drinking by *Culex restuans* (Diptera: Culicidae). J Insect Behav 6:343–349

Mosquitoes (Diptera: Culicidae)

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The family Culicidae within the order Diptera, the two-winged flies, comprises of approximately 3,500 species of mosquitoes. This family of nematocerous (long-horned primitive flies whose larval head is well developed with laterally moving mandibles) flies is divided into three subfamilies, Toxorhynchitinae, Anophelinae, and Culicinae. There are 37 genera of mosquitoes.

Distribution

Mosquitoes live in humid tropics and subtropics, warm moist climates, temperate and cool zones, everywhere except areas that are permanently frozen.

Metamorphosis

Mosquitoes undergo holometabolous, or complete, metamorphosis, meaning their life cycle includes four distinct forms: eggs, larvae, pupae, and adults. Their eggs require water to hatch. The larvae develop through four instars before they transform into active, non-feeding pupae. The adult's wings, sucking mouthparts, and legs can be seen through the transparent pupal skin. The adult emerges from the pupal skin onto the surface of the water, and then flies to seek carbohydrates and mates. The adults and larvae are anatomically different, reside in different habitats (terrestrial vs. aquatic, respectively), and obtain nutrients from entirely different sources of food.

Morphology and Physiology

Eggs

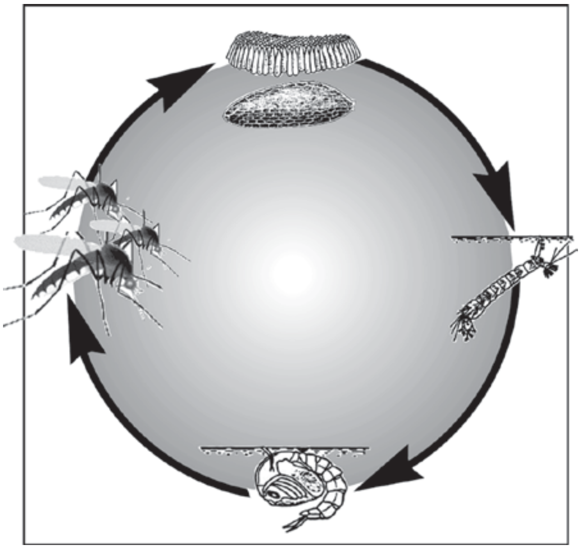
Mosquito eggs have a small pore, the micropyle, at the anterior end for sperm penetration. Females lay approximately 50–500 sculpted eggs on the water surface or in areas that will become flooded. Eggs are soft and white when laid and later darken and become hard. Floodwater mosquitoes lay their eggs on moist soil and are tolerant of dry conditions. Various modifications exist that will allow eggs to float. *Anopheles* eggs are laid singly on the surface of the water. The boat-shaped eggs of most Anophelines possess two air-filled floats on either side; in those that lack floats, the eggs sink if touched. Other mosquitoes lay egg rafts that may contain up to 200 eggs per raft.

Larvae

The larval stage of the mosquito is aquatic. The larvae are legless and spend a majority of time at the surface of the water. However, they can stay submerged for some time. This stage is commonly referred to as "wriggler" or "wiggler," due to the lashing movements of the abdomen that move them forward, backward, or sideways in the water. The only functional respiratory apertures are a pair of dorsal spiracles near the end of the abdomen; lateral spiracles remain closed except during ecdysis. The head can be oval, ovate, or almost rectangular in shape, depending on the genus. The larvae possess slender shafted antennae with spines and tufts of hairs. The eyes are simple lateral eyes with no lenses and are present from the beginning of the larval stage into the adult stage. The large pigmented spots on the side of the larval head are the compound eyes of the adult developing beneath the cuticle of the larva. Larval mosquito mouthparts are composed of lateral brushes which move currents of water toward the head and pectinate hairs that serve as combs for retaining particles filtered from the water. The thorax is oval with no appendages and becomes enlarged during the fourth instar. The abdomen is ten-segmented with the respiratory appendage on the eighth segment. In the Anophelini, the last 5 or 6 abdominal segments bear palmate brushes that aid to suspend the larva from the water surface. These are the only breathing apertures of the larvae. Mosquitoes in the genera *Mansonia* and *Coquillettidia* possess a modified respiratory siphon with spines, hooks, and teeth for insertion into the roots of aquatic plants. The larvae and pupae in these genera remain submerged and obtain oxygen from the plant. Late in the fourth instar, the cuticle is separated from the abdomen and the mosquito develops into a pupa (Fig. 94).

Pupae

The pupal stage of the mosquito is also aquatic. Unlike other holometabolous insects, this stage of



Mosquitoes (Diptera: Culicidae), Figure 94 Mosquito life cycle: above, eggs are deposited singly or in groups; right, the larval stage, which often is found at the surface of water; bottom, the pupal stage; left, the adult or blood-feeding stage.

the mosquito life cycle is very active and is relatively short. The average time spent in the pupal stage is 2–3 days, but varies with species and temperature. The pupa can submerge in their aquatic habitat or move around at the surface. They may remain inactive and passively rise to the surface or actively swim up by abdominal movements assisted by the large tail paddles. Mosquito pupae do not possess functional mouthparts, and, therefore, do not feed during this period; this stage is dependent on the larvae for nutrition.

The head and thorax combine to form a cephalothorax with nothing of the structure of the larval head remaining. Large black compound eyes are located beneath the cuticle. The thorax is approximately the size and shape that it will be during adult life and bears the legs, wings, and respiratory trumpets. The abdomen projects from the cephalothorax and differs from the larvae in the lack of respiratory appendages and the presence of tail fins (paddles). The paddles are located at the end of the abdomen and can increase the motor efficiency of the abdomen. The respiratory organ of the pupae are called "trumpets" and are connected to the anterior ends of the dorsal longitudinal tracheal trunks and project from the thorax with the open ends projecting above the water surface. As with the larvae, the pupae of *Mansonia* and *Coquillettidia* obtain oxygen from the roots of aquatic plants. They remain attached to the aquatic plants until the end of the pupal stage when they detach and float to the water surface for the winged adult to emerge. The appearance of a film of air under the cuticle of the thorax is an indication that the adult is about to emerge from the pupal skin. Prior to emergence, air is drawn forward and begins to form an air bubble at the base of the proboscis that is extended back to the fourth abdominal segment. The pressure from the abdomen ruptures the cuticle where the adult will emerge. When the entire adult body is free from the pupal thorax, the mosquito steps onto the water surface, walks away from the pupal skin and is soon able to fly.

Adults

The adult mosquito is a terrestrial insect possessing one pair of wings. Males and females are distinguishable by the plumose antennae of the male and the circles of short hairs on the female antennae. The bases of the antennae arise close together on the head. The pedicel of the antennae houses Johnston's organ, a sensory structure for sound reception which, in males, is used to recognize conspecific females. The sides of the head are occupied by compound eyes that almost meet dorsally and ventrally. Male mosquitoes feed on carbohydrates for energy; the females also require carbohydrates for flight energy and they consume blood which is necessary for egg development. Species of the *Toxorhynchites* genus do not blood-feed. Autogeny, the ability to lay eggs without a prior bloodmeal, exists in some species.

The adult female mosquito that feeds on blood uses a proboscis, a slender structure composed of seven parts: the labrum, two mandibles, a hypopharynx, two maxillae, and a labium. The labium houses, or encloses, the other six structures of the mouth. The hypopharynx contains the salivary canal and the maxillary stylets are the piercing organs. Once a small blood vessel in the host is encountered, the mandibles are drawn back and blood enters the food canal by suction from the cibarial pump. Saliva is discharged from the hypopharynx while blood is taken into the food canal. The pharyngeal pump, a large bulb-like structure located behind the brain, works with the cibarial pump to keep the blood meal flowing into the stomach. When the bloodmeal is completed, the mosquito pulls out the stylets and once again they are sheathed in the labium. In male mosquitoes, the mandibles and maxillae are reduced and the hypopharynx is not separated from the labium as it is in the female. In nectar feeding females and males of *Toxorhynchites* species, the proboscis is strongly decurved.

A pair of salivary glands located ventrally in the thorax enter the head and open just below the mouth. Salivary glands of the mosquito are made up of three lobes and lie at the sides of the anterior end of the ventriculus and are important in the role of transmission of viruses and other parasites. The salivary glands are the avenue of escape for pathogens from the mosquito to the new host blood. The saliva serves as an anticoagulant, and possibly a food solvent and source of antimicrobial substances.

The mesothorax of the adult mosquito bears one pair of scaled wings. Two halteres, organs that maintain the equilibrium of the mosquito, are present instead of a second pair of wings. Veins and scales on the wings form patterns that are characteristic in species identification. The flight muscles, located in the thorax, make up from 16 to 19% of the total body weight. The rate of wing vibration varies among species, and among males and females within species.

One pair of legs is associated with each of the three thoracic segments of the mosquito. The legs are made up of the coxa, trochanter, femur, tibia, and tarsus. The tarsus is divided into five tarsomeres. The fifth tarsomere has two curved claws, and most species possess a secondary element of the claw, a tooth. The legs bear scales that are used as key characters in identification.

The abdomen is made up of ten segments, the last two being greatly reduced. The last two segments in males are modified to form a genital clasper used in mating. The male genitalia are used in identification of male mosquitoes.

Internal Systems of the Mosquito

Respiratory System

Oxygen is carried to the tissues of the adult and larval mosquitoes in essentially the same manner, through the spiracles to the trachea to the smallest tracheoles which reside in close proximity to the tissues. The respiratory system in mosquito larvae includes a pair of lateral and dorsal tracheal trunks with spiracles that run the length of the insect. The last pair of lateral spiracles on the eighth abdominal segment and the dorsal spiracles on the ninth abdominal segment allows the mosquito larvae to breathe at the water surface. In adult mosquitoes, there are eight pairs of spiracles on the abdomen and two pairs on the thorax.

Circulatory System

The circulatory system of the mosquito is an open system where the blood, or hemolymph, bathes tissues with nutrients, transports waste, and distributes hormones. It does not transport oxygen to tissues. The hemolymph is circulated by a dorsal blood vessel. The structure of the dorsal vessel does not vary considerably between the larval, pupal, and adult stages. The dorsal blood vessel is a muscular tube that extends from the eighth abdominal segment to the head and is divided into the aorta (head and thorax) and the heart (abdomen). Blood is freely discharged into the head and flows backward through the body. Pulsatile organs that help to circulate the hemolymph are located in the bases of the antennae, the adult labium, and possibly in the adult scutellum. The heartbeat runs the length of the dorsal vessel in peristaltic waves. The waves run forward in larvae, and in the pupae and adults may run either forward or backward.

Digestive System

The digestive track (alimentary canal) of the adult mosquito includes the stomodeum (foregut), the mesenteron (midgut), and proctodeum (hindgut). The foregut includes a pharyngeal pump, esophagus, and three diverticula. The largest of the diverticula is a highly elastic ventral crop. Sugars from nectar feeding are hydrolyzed in the crop. The mosquito midgut is essentially a narrow tube where the blood meal passes through to a stomach that retains the blood meal. The function of the midgut is to aid in nutrient absorption, diuresis, and secretion of digestive enzymes. It is the primary organ of digestion of the blood meal. The hindgut includes a pyloric chamber, anterior intestine, and the innervated rectum and anal canal. There are five Malpighian tubules inserted between the midgut and hindgut which hang freely in the body cavity. Water, salts, and excretory products pass from the hemolymph into the Malpighian tubules. These structures aid in excretion and regulation of water and salts.

The foregut of the larval mosquito includes the innervated pharynx which is involved in filtering and swallowing, and the esophagus. The larval midgut consists of cardia, gastric caeca, and the anterior and posterior stomach. As with the adult, the larval hindgut includes the Malpigian tubules, pylorus, anterior intestine, and the rectum and anal canal.

Nervous System

The nervous system consists of a brain, subesophageal ganglion, and ventral ganglia in the abdomen ending in the eighth abdominal segment. The most complex part of the nervous system is located in the head where the primary sense organs are also located. The subesophageal ganglion receives input from the mouthparts. Each of the ventral ganglia provide coordination for the body segment with which they are associated.

Reproductive System

Reproductive organs develop during the larval life. Males mature sexually several hours or days after adult emergence. To be sexually mature, the male antennal fibrillae (long, articulated innervated setae) must be erect and the genitalia must be inverted 180° from their position at emergence. Male genitalia are located on the abdominal segments 8–10, usually bilobed with claspers that hold on to the female. So distinct are they that they are used to identify male mosquitoes to species. Mosquito ovaries contain ovarioles and each ovariole consists of an egg follicle. Females store spermatozoa from the male in organs known as spermathecae. The number of spermathecae varies among mosquito genera: *Anopheles* (1), *Toxorhynchites* (3), most *Culicinae* (3), and some *Aedes* (1). The spermatozoa fertilize the oocytes as they are ovulated.

Mosquito Behavior

Feeding

Feeding during the larval mosquito stage is accomplished through ingestion of particles filtered from the water column or surface, removal and ingestion of surface biofilms, shredding of leaves, and predation of other larvae and insects their own size or smaller. Food is carried to the mouth by currents that are produced with the oral brushes on the larval mouthparts. The larvae provide nutrition for the non-feeding, yet active, stage of the pupa.

In the adult stage, male and female adult mosquitoes feed on sugars from plants and from other insects that feed on plant sugars. This is the only source of nutrition for the males as they do not feed on blood. The females use the sugar meals for energy and the blood meals for egg development.

Sugar meals are obtained from flower nectaries, extrafloral nectaries, rotting fruit, and vegetative parts of plants. An important source of sugar for mosquitoes is honeydew produced by Hemipteran insects. Some females of species of *Malaya* consume fluids that are regurgitated by ants belonging to the genus *Crematogaster*.

Blood is essential for egg development in the female mosquito. The midgut of the adult female mosquito is grossly distended immediately following consumption of a blood meal. Many mosquitoes will imbibe more than their own weight in blood, making it difficult to fly. Their excretory system is able to eliminate over 40% of water and sodium from the blood meal within an hour after consuming the blood. Blood-host preferences vary among species; some females are opportunistic and will feed on a variety of hosts, while some are more discriminating and have a single host preference, or a very narrow range of preferred hosts. Some species exhibit a change in host-feeding as the seasons change. For some species this is explained by host availability, for others, such as *Culex nigripalpus*, the switch is stimulated by rain and humidity.

Oviposition

Egg production is cyclic. At oviposition the eggs are white and soft. After several hours, the eggs darken and harden, and there is some evidence that this is due to sclerotization. Female *Toxorhynchites* lay their oval, barrel shaped eggs individually in flight. Egg rafts are laid by *Culex*, *Culiseta*, and *Uranotaenia* species. *Aedes/ Ochlerotatus* and *Psorophora* eggs are laid singly on surfaces that are moist, not wet, at the time of oviposition. Almost all *Aedes* eggs can withstand desiccation. *Mansonia* species may lay their eggs in rafts on the underside of floating or emergent leaves. *Coquillettidia* egg rafts are laid on the surface of water containing aquatic vegetation, which the larvae and pupae will attach to for the duration of their aquatic life. *Mimomyia* eggs resemble *Anopheles* eggs but do not have the floats attached to the sides. *Ficalbia* eggs are laid on leaves that hang over the water surface. *Wyeomyia* eggs commonly are associated with bromeliads and pitcher plants. *Trichoprosopon digitatum* females hold their egg rafts in their legs until they hatch, and will add eggs they find to their own raft.

Mating

Males and females can come together for mating purposes in several ways: males form swarms and as females approach, the males grab hold of them; males and females gather around their larval habitat or around potential blood meal hosts; or males approach resting females. Once a male obtains a female in flight, he turns around so that the pair is venter-to-venter. Mating is initiated in flight and copulation is completed in seconds in most species. Males of some *Aedes* and *Mansonia* species will make their way to hosts of interest to the blood-seeking female and attempt to mate with the virgin females. *Opifex fuscus* and *Deinocerites cancer* males will approach pupae that are close to emergence and compete for individual pupae. When the adult mosquito begins to emerge from the pupal case, the male forces his way in to make genital contact just prior to emerging. If the pupa is female, copulation will begin. If not, the male will leave. In species that mate when settled rather than during flight, such as *Deinocerites cancer*, copulation can last 45 min or longer. Males of some species of *Wyeomyia*, *Sabethes*, and *Limatus* will locate females by flying up and down the vegetated areas where the females are resting.

Disease Transmission

Mosquitoes are vectors of many pathogens that can cause morbidity and mortality in humans and other animals (see Table 12). The pathogens most often associated with mosquito vectors are arboviruses (arthropod-borne viruses), nematodes, and protozoa. The most studied and well-known mosquito-borne protozoan pathogens belong to the genus *Plasmodium* and cause malaria in humans and birds. Nematodes carried by mosquitoes and passed to humans and dogs during blood-feeding cause human filariasis and dog heartworm disease. There are over 200 known viruses vectored by mosquitoes.

Mosquitoes (Diptera: Culicidae), Table 12 Pathogens that can cause morbidity and mortality in humans and other animals

Pathogen	Disease	Known outbreaks	Hosts with morbidity
Arboviruses			
Togaviruses	Venezuelan equine encephalitis	Central America, South America, North America	Horses
	Eastern equine encephalitis	Central America, South America, North America	Horses, humans
	Western equine encephalitis	South America, North America	Horses, humans
	Highlands-J	North America	Humans
	Chikungunya	Africa, Asia, India, Philippines	Humans
	O' Nyong Nyong	Africa	Humans
	Ross River	Australia, New Guinea, Solomon Islands, South Pacific Islands	Humans
	Sindbis	Africa, Asia, Australia, Czechoslovakia, Russia	Humans
	Barmah Forest	Australia	Humans
Flaviviruses	Yellow fever	Africa, Central America, South America	Humans, monkeys
	St. Louis encephalitis	North America, South America	Humans
	Japanese encephalitis	Australia, Asia	Humans, swine

Mosquitoes (Diptera: Culicidae), Table 12 Pathogens that can cause morbidity and mortality in humans and other animals (Continued)

Pathogen	Disease	Known outbreaks	Hosts with morbidity
	West Nile	Africa, Middle East, North America	Humans, horses, birds
	Wesselsbron disease	Africa	Humans, sheep
	Rocio	Brazil	Humans
	Murray Valley encephalitis	Australia, New Guinea	Humans
	Dengue	Asia, Africa, Polynesia, Micronesia, Caribbean, Central America, South America	Humans
Bunyaviruses	Bunyamwera	Africa	Humans
	Cache Valley	North America	Humans, cattle
	California encephalitis	North America	Humans
	Jamestown Canyon	North America	Humans
	LaCrosse	North America	Humans
	Snowshoe hare	North America	Humans
	Tahyna	Asia, Europe	Humans
	Trivittatus	North America	Humans
	Rift Valley fever	Africa	Humans, sheep, cattle
Rhabdoviruses	Bovine ephemeral fever	Africa, Asia, Australia, Middle East	Cattle
Nematodes			
Wuchereria bancrofti	Filariasis: Bancroftian filariasis	Africa, India, China, Bangladesh, Myanmar, Thailand, Malaysia, Laos, Vietnam, Indonesia, Philippines, Papua New Guinea	Humans
Brugia malayi	Filariasis: Brugian filariasis	China, India, Republic of Korea, Asia	Humans
Brugia timori	Filariasis: Timorian filariasis	Indonesia	Humans
Dirofilaria immitis	Dirofilariasis: Dog heartworm	North America	Canines
Protozoa			
Plasmodium vivax, ovale, malariae, and *falciparum*	Malaria	Africa, Central America, South America, Middle East	Humans

Methods of Control

Management of mosquito populations can be attempted in a number of ways; the use of several methods often is employed in mosquito Integrated Pest Management (IPM) programs. Because mosquitoes have two very different types of habitats during their life cycle, there are two opportunities to apply control techniques: during the aquatic stage and during the terrestrial stage. In the aquatic stage, mosquitoes are more concentrated and less mobile than they are during their terrestrial life, making control in the larval stage more efficient. The major methods of mosquito control include:

- Larviciding – Bacterial products specific for mosquitoes can be applied to the aquatic habitats. Insect growth regulators also are available for control during this stage, as well as some organophosphates. Monomolecular films and some oils are used for control of larvae as well as pupae.
- Adulticiding – Organophosphates, pyrethroids, and natural pyrethrins are available to target flying mosquitoes. These products are applied either by ground fogging units mounted to trucks or by handheld backpack sprayers. Another mode of application is by aerial spraying from airplanes or helicopters.
- Source reduction – This method includes removal of water-holding containers that are not necessary (used tires, cans, bottles, empty buckets, etc.) as well as drainage projects that are more costly and labor intensive and require approval by water and land managers. Impoundment projects have been used to control salt-marsh mosquitoes around coastal areas. These structures are designed to prevent female salt-marsh mosquitoes from laying eggs. This method of control also requires the cooperation and approval of land and water managers as well as mosquito control districts.

References

Clements AN (1992) The biology of mosquitoes. Vol 1. Development, nutrition and reproduction. Chapman and Hall. University Press, Cambridge, Massachusetts

Clements AN (1999) The biology of mosquitoes. Vol 2. Sensory reception and behaviour. Chapman and Hall. University Press, Cambridge, Massachusetts

Eldridge BF, Edman JD (eds.) (2000) Medical entomology. A textbook on public health and veterinary problems caused by arthropods. Kluwer Academic Publishers, Dordrecht

Snodgrass RE (1959) The anatomical life of the mosquito. Smithsonian Miscellaneous Collections, Vol 139, No. 8. Publication 4388. The Smithsonian Institution, Washington, DC

Mosquitoes as Vectors of Viral Pathogens

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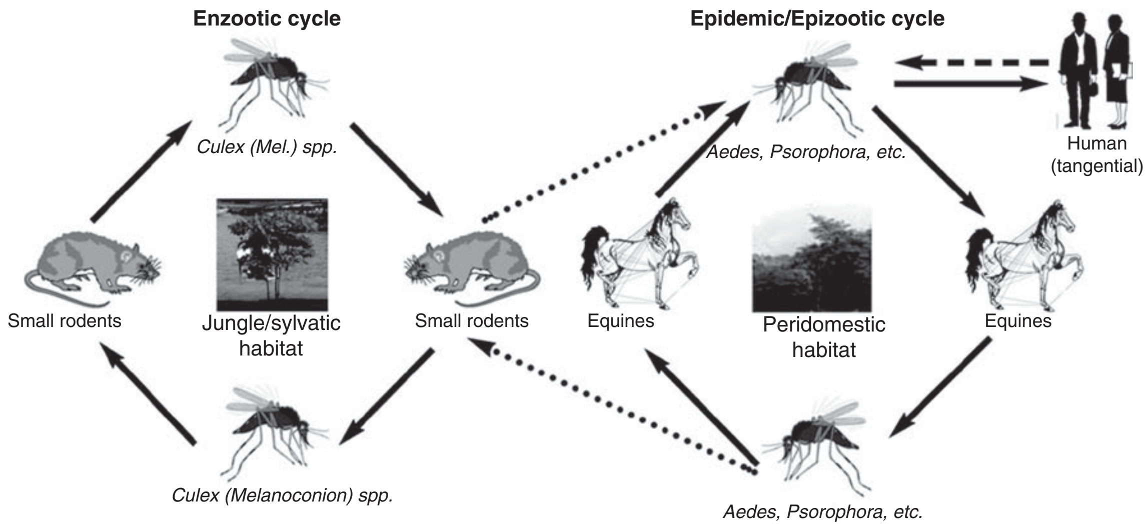
The role of arthropods in the transmission of human and animal disease agents is a significant focus of research for medical entomologists. Insects in the families Culicidae, Psychodidae, Ceratopogonidae, Simuliidae, Glossinidae, Pulicidae, Reduviidae, along with several species of ticks are responsible for the vast majority of vector-borne disease. These insects are capable of transmitting pathogens as diverse as protozoa, helminths, bacteria, and viruses. This section will focus specifically on viruses that are transmitted by mosquitoes, or arboviruses (from arthropod-borne viruses). These viruses are defined by their ability to replicate in, and be transmitted between, both their vertebrate host and their invertebrate vector. It is this unique ability to propagate in dual host systems that differentiates them from other viruses that may be able to be spread only mechanically by insect vectors. However, this characteristic is also likely to be one factor that delineates the natural cycles of these viruses. Here, we describe one half of the natural cycle, how an arbovirus would enter, replicate in, and ultimately be transmitted by a mosquito vector (Fig. 95).

Factors Associated with the Biological Transmission of Arthropod-Borne Viruses

Viruses (Table 13) can be transmitted by an arthropod vector through two distinct mechanisms, mechanical or biological transmission. With mechanical transmission there is no replication of the virus in the insect. This mode of transmission has been demonstrated for a number of viruses with mosquitoes, biting midges



Mosquitoes as Vectors of Viral Pathogens, Figure 95 **Transmission cycles of Venezuelan equine encephalitis virus. Solid arrows indicate known transmission. Hatched arrows indicate possible transmission route.**

Mosquitoes as Vectors of Viral Pathogens, Table 13 **Important mosquito-borne viruses causing human illness**

Virus	Major disease	Invertebrate vector
chikungunya	Febrile/arthralgic illness	*Aedes aegypti*
dengue 1–4	hemorrhagic fever	*Aedes aegypti, Aedes albopictus*
Eastern equine encephalitis	Encephalitis	*Coquilletidia perturbans, Aedes vexans, Culex nigripalpus, Ochlerotatus sollicitans, Culiseta melanura*
Japanese encephalitis	Encephalitis	*Culex univittatus* complex, *Culex tritaeniorhynchus*
LaCrosse	Encephalitis	*Ochlerotatus triseriatus*
Murray Valley encephalitis	Encephalitis	*Culex annulir* ostris
O'nyong nyong	Arthralgic/febrile illness with rash	*Anopheles gambiae, Anopheles funestus*
Rift Valley fever	Febrile illness Hemorrhagic fever, Retinitis	*Culex pipiens* complex, *Aedes* spp.
Ross River	Febrile illness	*Culex annulirostris*
St. Louis encephalitis	Encephalitis	*Culex pipiens* complex, *Culex restuans, Culex nigripalpus*
Venezuelan equine encephalitis	Encephalitis	*Aedes* spp., *Ochlerotatus* spp., *Psoraphora* spp., *Culex* spp.
West Nile	Febrile/encephalitis	*Culex* spp.
yellow fever	Hemorrhagic fever	*Aedes aegypti, Aedes africanus, Aedes simpsoni* complex, *Aedes furcifer, Haemagogus* spp.

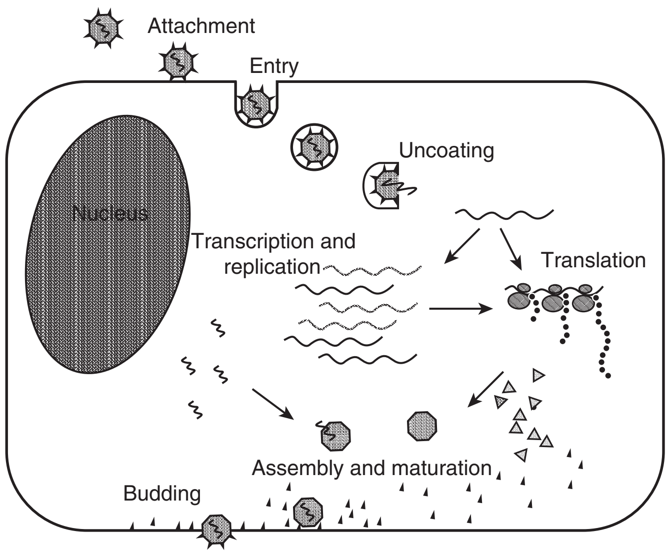
and black flies. One prominent example of a virus transmitted in this manner is myxoma virus that is transmitted mechanically by mosquitoes in Australia. However, with most viruses, mechanical transmission typically only contributes to occasional cases of viral transmission and usually is not involved in the maintenance cycle of arthropod-borne viruses. In contrast, biological transmission, in which virus replication occurs within the arthropod, is the basis for maintaining arboviral transmission cycles and is characterized by a complex interaction between virus and an arthropod vector in which numerous factors combine to determine the efficacy of the virus-vector relationship.

A number of viral and vector factors, both intrinsic and extrinsic, can affect each stage of biological transmission (Fig. 95). The first event in the infection of any arthropod (mosquito) cell is viral binding via specific receptors and entry of virus into the cytoplasm. Once in the cell, the virus must first uncoat, or have the outer proteins removed, to expose the genetic material. The RNA (virtually all arboviruses have an RNA based genome) is then transcribed and translated to produce replication machinery components and structural proteins that will assemble to form new virions. The nonstructural proteins produced from the viral genome combine with cellularly encoded factors to replicate the viral genome. This process results in the production of nascent, full-length genomes that can then be packaged into the assembling viral particles. The new virions complete the maturation and assembly process by release from the cell, typically by budding from the plasma membrane.

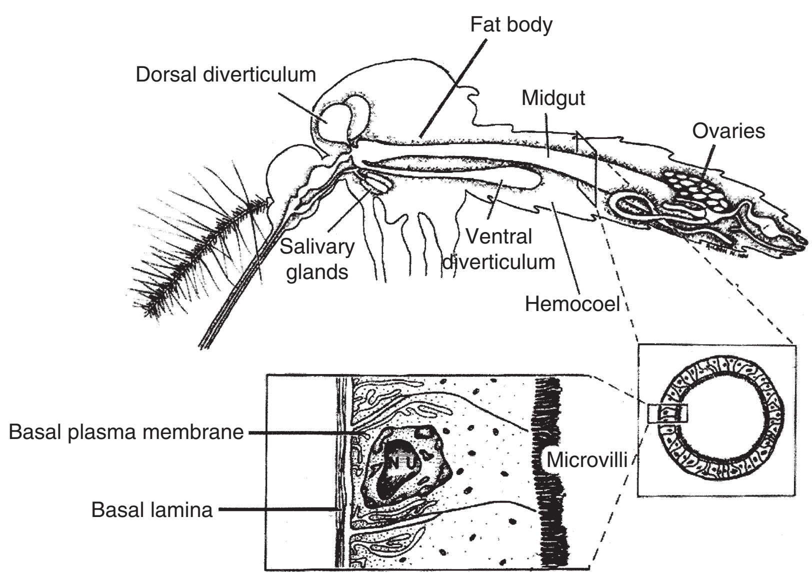
For biological transmission to take place, a number of events must occur including infection of the midgut epithelium, dissemination of virus from the midgut to the hemocoel, infection of salivary glands, and deposition of virus in the apical cavities and ducts of the salivary glands for transmission. This chain of events covers the time frame know as the extrinsic incubation period, or the period between the ingestion of an infectious blood meal and the transmission of an arbovirus. Once the virus enters the mosquito midgut epithelium, it may fail to disseminate from productively infected midgut epithelial cells resulting in an abortive infection. After infection of the midgut, the virus enters the hemocoel of the mosquito, where it infects numerous tissues, especially the fat body, and disseminates to secondary infection sites. The acinar cells of the salivary glands are secondary targets that must be infected if transmission is to subsequently occur. If any of these steps is inhibited, transmission is unlikely to occur in sufficient levels to maintain the virus in nature.

Infection Process

The first stage of biological transmission, infection of the midgut epithelium, has been studied extensively in a number of virus-vector systems. The midgut epithelium is the primary site of the virus replication that must occur if the infection is to be productive. As the virus enters the cells of the midgut and begins the replication process (Fig. 96), the titer of detectable virus drops significantly. This eclipse phase marks the time when replication is occurring within midgut cells but no virus particles have been expelled into the hemocoel of the mosquito. This period typically lasts from 1–4 days depending on the vector species, virus, and extrinsic factors that can affect midgut infection such as larval nutrition and ambient temperature. After the eclipse phase is completed, virus titers in the mosquito multiply by a factor of 1,000 or more within just a few days during a period referred to as the amplification phase. Virus spreads rapidly through the hemocoel of the mosquitoes and infects secondary susceptible target organ systems including the salivary glands, flight muscle, neural tissue, fat body, and ovaries (Fig. 97). The maintenance phase begins when the titer of the virus levels off or decreases presumably due to the mosquito's modulation of the viral infection. Components of the insect immune system including hemocytes and antiviral proteins presumably act to limit the replication of the virus; however, they



Mosquitoes as Vectors of Viral Pathogens, Figure 96 Generalized viral replication strategy.



Mosquitoes as Vectors of Viral Pathogens, Figure 97 Diagram of mosquito anatomy indicating organs important in virus infection, dissemination, and transmission.

do not entirely clear the virus as mosquitoes remain persistently infected.

Abortive Midgut Infections

If the virus fails to enter or replicate in the midgut, the infection is non-productive and the virus will not be transmitted in future blood feeding events. A number of hypotheses have been proposed to explain the refractoriness of a virus for midgut infection. These include: (i) cellular charge/charge distribution differences within the mesenteronal epithelia; (ii) digestive inactivation of virions while within the midgut lumen and, (iii) differential expression of specific receptors on the mesenteronal epithelia of susceptible mosquitoes. The presence of charged ions in an infectious blood meal can significantly alter the midgut infection rate of some mosquitoes for a given virus. However, this phenomenon is not universal and not very well understood. Laboratory experiments have demonstrated midgut surface charge differences among various mosquito species and it is postulated that charged molecules in the blood meal might affect how the virus interacts with specific midgut receptors. The second hypothesis, digestive inactivation of virions in the midgut lumen, may be a result of secretion of the digestive enzymes trypsin and chymotrypsin. Exposure of viral particles to digestive enzymes may result in cleavage of viral surface proteins resulting in either up or down regulation of efficient binding to mosquito cells. The final hypothesis, differential expression of specific midgut receptors is an exceptionally complex issue. The mesenteronal epithelium consists of columnar and squamous epithelial cells with interspersed regenerative cells. The apical side is microvillate and highly invaginated to provide a large surface area from which materials from the lumen can be absorbed. Numerous surface and transmembrane proteins are present in this region to aid in nutrient uptake but it is unclear which of these receptors are used by viruses to bind and enter the midgut cells. Until further studies clearly elucidate the relative importance of various receptor proteins in viral binding, it will remain unclear how critical this component is in the infection process.

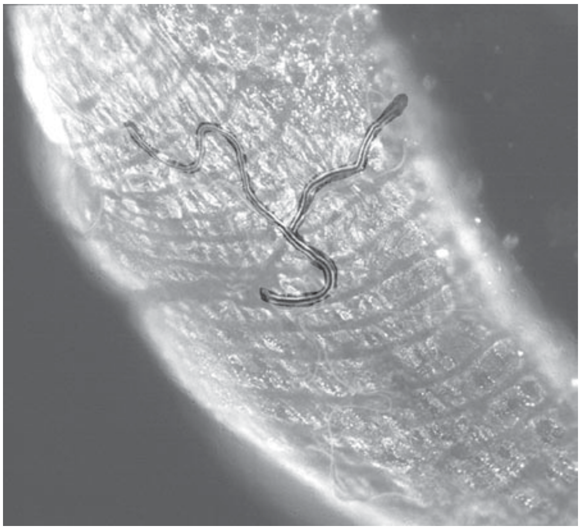
Viral and Vector Genetics Associated with Differences in Midgut Infection

Genetic differences between mosquito vectors can result in drastic differences in vector susceptibility to infection with the same virus. For example, the WR *Culex tarsalis* genetic variant is resistant to infection by western equine encephalitis (WEE) virus, while another genetic variant (WS *Cx. tarsalis*) is extremely susceptible to oral infection with the same WEE viral strain. WEE virus has been shown to infect *Cx. tarsalis* mosquitoes efficiently with bloodmeals containing 3 $\log_{10}$ plaque forming units (PFU)/ml blood ingested, yet fails to infect *Cx. pipiens* at bloodmeal titers in excess of 8 $\log_{10}$ PFU/ml. Furthermore, minimal infection titers differing by as much as 1,000-fold have been identified for geographic strains of *Aedes albopictus*. Viral genetic factors can also play a major role in the infectivity of a given mosquito species. For example, a genetic variant of LaCrosse (LAC) virus demonstrated a reduced ability to productively infect the mesentery of *Aedes triseriatus* mosquitoes (5% infection rate as compared with an 89% rate for wildtype LAC virus). Serial passage of this viral variant in *Ae. triseriatus* regenerated the midgut infectivity to the level of the wildtype virus. Similarly, the development of a monoclonal antibody resistant mutant of a Venezuelan equine encephalitis (VEE) virus vaccine strain resulted in a virus that exhibited reduced infectivity in *Aedes aegypti* mosquitoes. The genetic determinate was mapped to a single amino acid substitution in the E2 glycoprotein, the major antigenic determinant for alphaviruses. This single amino acid alteration within the vaccine strain reduced viral infection of, and dissemination from, the midgut.

Recent advances in molecular virology are allowing researchers to systematically elucidate the viral components of vector specificity. An engineered viral clone based on the genome of Sindbis (SIN) virus is incapable of infecting *Ae. aegypti* mosquitoes orally. However, a distinct Malaysian strain of SIN virus, MRE-16, efficiently infects this mosquito species following oral ingestion. A genetically constructed virus containing the structural genetic components of MRE-16 substituted for the corresponding genes in the parent clone, produced a virus that efficiently infected *Ae. aegypti* orally.

Dissemination from the Midgut

Failure of a virus to infect peripheral tissues after initiation of a productive infection of the midgut epithelium can also result in an aborted infection and lack of transmission. The virus must transverse the mesenteronal epithelium from the apical to basolateral side, exit the cell, and bypass the basal lamina (BL). The thickness of the basal lamina, which can be modulated by factors such as larval nutrition, may be one component in the failure of a virus to reach the mosquito hemocoel. The mechanisms allowing viruses to bypass this potential barrier are not completely understood, particularly since the basal lamina has a size exclusion between 5–8 nm, a pore size significantly smaller than many arboviruses. Interestingly, intrathoracic inoculation of mosquitoes with viruses showing no dissemination from the midgut after per os infections have developed midgut infections, indicating that the virus was capable of bypassing the BL from the basal side. Some evidence has suggested that viral dissemination from the midgut could occur through alternative mechanisms such as pathology to the mesenteron or dissemination from the foregut-midgut junction (Fig. 98).



Mosquitoes as Vectors of Viral Pathogens, Figure 98 ***Ochlerotatus triseriatus*** **midgut infected with LaCrosse virus. Infection occurs in the midgut epithelial cells while longitudinal and circular muscle cells remain uninfected.**

Viral and Mosquito Genetic Basis for Lack of Dissemination

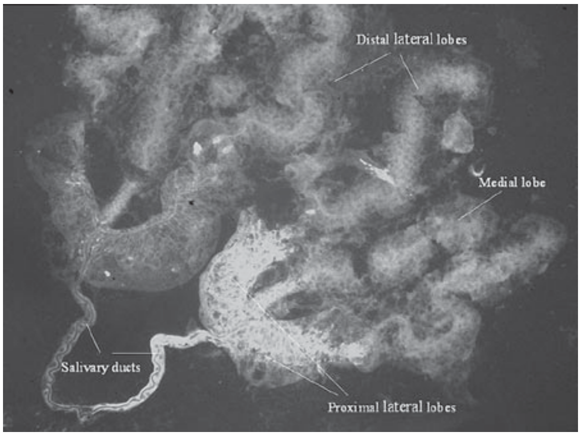
A number of examples of arboviral transmission refractory mosquitoes can be linked to an inability of virus to propagate outside the midgut. For example, failure of yellow fever virus or dengue viruses to move from infected midgut cells to the hemocoel was demonstrated in isofemale lines of *Ae. aegypti* that were resistant to infection. In another example, *Cx. (Melanoconion) taeniopus,* an enzootic VEE mosquito vector, transmits VEE subtype IE viruses efficiently. However, although a closely related alternate subtype of VEE (subtype IAB) infects *Cx. taeniopus* midgut epithelium, the virus fails to invade tissues beyond the mesenteron. The vector genetic determinants that regulate these highly specific interactions are clearly present, but poorly understood.

Viral components are also undoubtedly involved in this inability to escape into the hemocoel of midgut-infected mosquitoes. Reassortant experiments performed with LAC and snowshoe hare (SSH) bunyaviruses, viruses that have a genome consisting of three segments of RNA designated small (S), medium (M), and large (L), have demonstrated that viruses containing the M RNA fragment of SSH with the L and S RNA segments of LAC virus infected the midgut epithelium of *Ae. triseriatus* efficiently; however, these viruses failed to disseminate from the midgut. Reassortants containing the M segment of LAC virus (with the L and S segments from SSH virus) efficiently infected and disseminated from the midguts of *Ae. triseriatus* mosquitoes. Again, while these viral genetic elements can be elucidated, it is less clear how they interact with a given mosquito vector resulting in productive or non-productive interactions.

Recent advances in molecular virology have aided in the process of identifying the viral determinants of vector specificity. The existence of full-length infectious clones of numerous alphaviruses and flaviviruses and the ability to perform site-directed mutagenesis on them are enabling researchers to examine the role of individual genetic elements in binding and replication. Using this approach, chimeric viruses have been generated that contain portions of multiple viral strains. In one example, complete structural protein genes from a virulent VEE strain were introduced into an infectious clone of an avirulent strain that poorly infects an epizootic mosquito species, *Ochlerotatus (Aedes) taeniorhynchus*. This led to the identification of the envelop glycoproteins (E1 and E2) as potential determinants of vector specificity. Further genetic studies identified only three E2 amino acid differences between two VEE viruses exhibiting dramatically different abilities to infect *Oc. taeniorhynchus*. Some combination of these three amino acids was hypothesized to be responsible for extreme differences in the ability to infect the mosquito vector. Site directed mutagenesis of the non-infecting clone to contain all possible combinations of the three amino acids identified a single point mutation that was responsible for vector infectivity. Undoubtedly additional clarification of viral determinants of infectivity will be forthcoming with further advances in molecular arbovirology.

Infection of the Salivary Glands

Viruses that escape the mesenteron and disseminate through the mosquito via the hemolymph must finally infect the salivary glands and replicate in this organ system before transmission can occur. However, many vectors are unable to complete this final step that is often dose and time dependent. Thirty-eight percent of *Cx. tarsalis* infected with low concentrations of WEE virus have been unable to replicate virus in the salivary glands while those receiving higher doses transmit efficiently. *Aedes albopictus* exhibit a similar phenomenon with eastern equine encephalitis (EEE) virus; after fifteen days of extrinsic incubation, only 57% of mosquitoes could transmit by bite, despite the fact that 100% of mosquitoes were positive for infection. Antigenic tests demonstrated that the mosquitoes failing to transmit did not have infected salivary glands (Fig. 99).



Mosquitoes as Vectors of Viral Pathogens, Figure 99 Adult female, *Ochlerotatus triseriatus* salivary glands infected with Sindbis virus (one gland only infected).

If the acinar cells of the salivary glands do become infected, the virus could still fail to be released into the lumen and ducts. Few examples of this phenomenon exist. One example may be *Ae. albopictus* infected with chikungunya (CHIK) virus; this species transmitted CHIK virus less efficiently after longer incubation times even though the salivary glands were still productively infected. The genetic basis for this is completely unclear.

Vertical Transmission of Arboviruses

In addition to mechanical and horizontal biological transmission, arboviruses can be transmitted vertically to naЇve mosquito vectors. A number of viruses have been identified to have been transmitted in this fashion; however, only a few viruses, most notably LAC virus, have been determined to utilize this form of transmission efficiently. Transovarial transmission (TOT) of LAC virus requires that the virus enter the ovaries, infect germ cell lines, persist in the embryonic and larval stages, and survive the enzymatic processing as the larva transitions into the pupal stage. Flaviviruses also have been shown to be transmitted vertically but

Mosquitoes as Vectors of Viral Pathogens, Table 14 Components of vectorial capacity

Viral	Genetic variants that differ in infectivity
Vector	Inherent vector competence – susceptibility to oral infection and efficiency of transmission
Population structure – density, longevity, etc.	
Host preference	
Geographic distribution	
Vertebrate reservoir	Able to develop high titered viremia necessary to infect vectors
Population structure – density, longevity, etc.	
Immune status	
	Overlap in space and time with vectors

through a distinct mechanism. In contrast to LAC virus, many flaviviruses, including yellow fever virus, St. Louis encephalitis virus, West Nile virus, and dengue viruses are transmitted via the micropyle rather than germ cell infection. Again, there is no clear genetic understanding of either process.

Elements of Vectorial Capacity

Vectorial capacity is the combined effect of all of the physiological, ecological, and environmental factors relating vector, host and pathogen that ultimately determine the ability of a given mosquito species to serve as a competent vector for a particular virus (Table 14). This definition encompasses factors other than the biological interaction of virus and vector such as the host preference and longevity of the potential vectors. Intrathoracic infections of multiple mosquito vectors resistant to oral infection reveal that the ability to infect the midgut epithelium appears to be the most critical component of vector competence. However, even an unlikely vector could transmit virus given the correct environmental and ecological conditions. It is significant to note that, because both vector and viral genetics contribute to vectorial capacity, there can be substantial susceptibility variation within a given species of mosquito for a particular virus. Additionally, since environmental factors are involved, this range of susceptibility or refractoriness can vary with the time of year or geographic location. Only a greater understanding of the interactions among the various components to produce a competent system will eventually lead to methods for disease prediction and control.

► Mosquitoes
► individual diseases

References

Guerrant RL, Walker DH, Weller PF (eds) (1999) Tropical infectious diseases: principles, pathogens, and practice. Vols 1 and 2. Churchill Livingstone, Philadelphia, PA, 1644 pp

Hardy JL, Houk EJ, Kramer LD, Reeves WC (1983) Intrinsic factors affecting vector competence of mosquitoes for arboviruses. Annu Rev Entomol 28:229–262

Kettle DS (1990) Medical and veterinary entomology. CAB International, Wallingford, 658 pp

Knipe DM, Howley PM (eds) (2001) Fields virology (4th ed). Vols 1 and 2. Lippincott Williams and Wilkins, Philadelphia, PA, 3200 pp

Monath TP (ed) (1988) The arboviruses: epidemiology and ecology. Vol 1. CRC, Boca Raton, FL, 329 pp

Moss Bugs

Bugs in the family Peloridiidae (order Hemiptera, suborder Pentamorpha).

► Bugs

Moth Flies

Members of the family Psychodidae (order Diptera).

► Flies

Moths (Lepidoptera: Heterocera)

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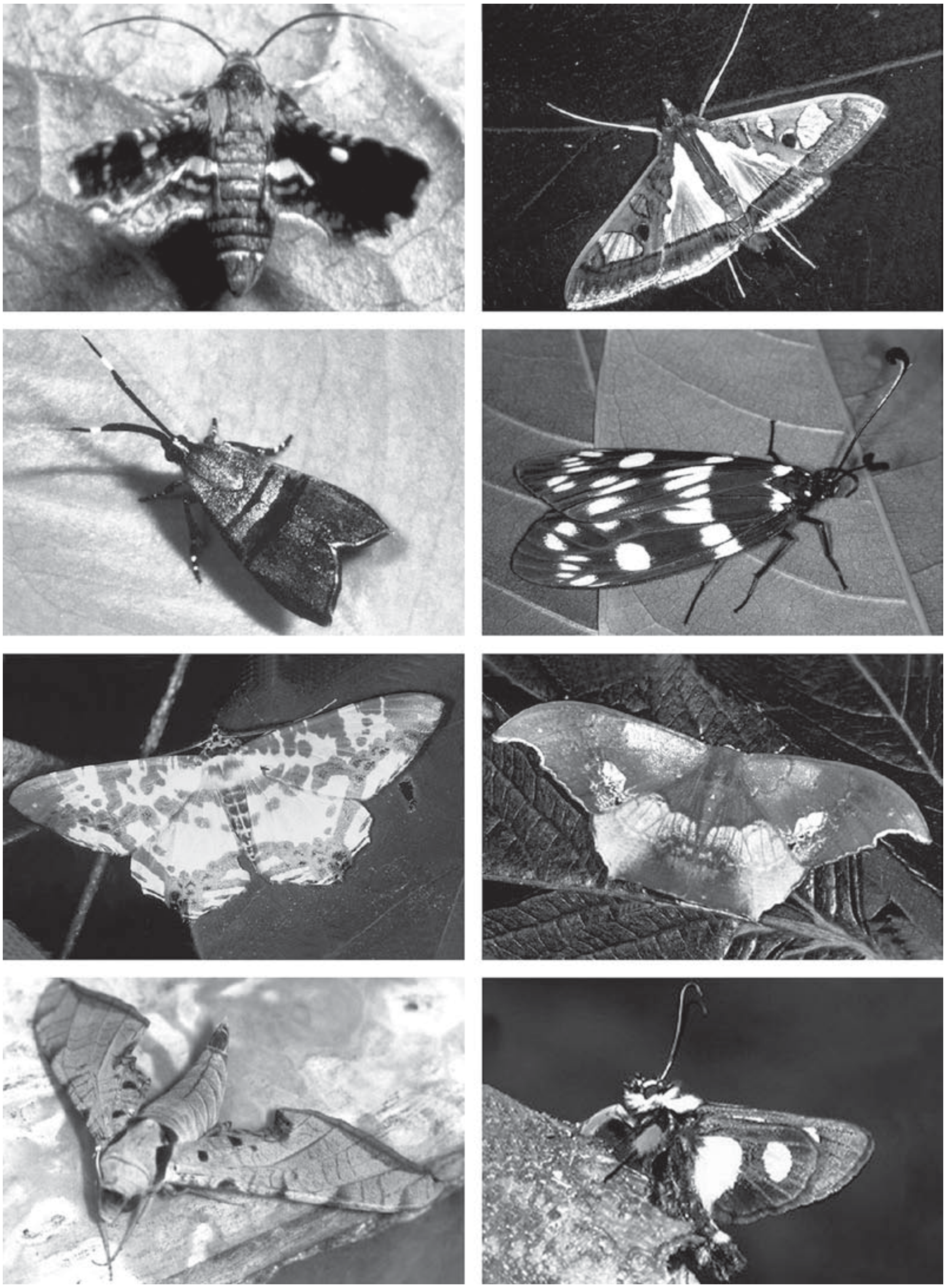
Among the insect order Lepidoptera, moths comprise most of the order worldwide, totaling about 135,700 described species, representing 91% of all lepidopterans (the other 9% are butterflies). There are an estimated additional 100,000 species of moths waiting to be discovered and named, mostly from tropical regions of the world. Although the name Heterocera is not used in modern classification of Lepidoptera, the name can be used to refer to all the moths (Rhopalocera is used as the name for all butterflies). The moth divisions, Macrolepidoptera and Microlepidoptera, likewise have no scientific basis but commonly are used as a convenience in grouping the mostly larger macro-moths versus the mostly more primitive and smaller micro-moths (extraordinary exceptions in size are known for each group).

Of the 125 known families of Lepidoptera, moths comprise 118 families, all but the seven families which involve the butterflies. Some classifications are slightly different, since some specialists split more groups as separate families. Among the moths are found both the most primitive living lepidopterans, the Micropterigidae (mandibulate archaic moths), and what are considered the most advanced, the Noctuidae (owlet moths). Butterflies, while often listed as the most advanced lepidopterans, are placed among the macro-moths after the geometer moths in our modern classification as based on the overall evolutionary development of the Lepidoptera. Butterflies are now thought to be a lineage from ancestors of what remain now as the most primitive of bombycine moths (perhaps resembling Ratardidae and relatives of Southeast Asia), which then evolved to geometer moth ancestors (families Geometridae and Hedylidae) and an alternate lineage that evolved to diurnal lifestyles and modern butterflies.

The main moth families are the Noctuidae (owlet moths), which is the largest family, with a known total of about 26,310 species worldwide, the Geometridae (geometer moths), with about 21,150 species, the Pyralidae (snout moths), with about 16,500 species, the Arctiidae (tiger moths), with 11,155 species, and the Tortricidae (leafroller moths), with 8,945 known species. The other more well known moth families, but with fewer species, are the Saturniidae (emperor moths), Sphingidae (hawk moths), Lymantriidae (tussock moths), Bombycidae (silkworm moths), Lasiocampidae (lappet moths), Notodontidae (prominent moths), Gelechiidae (twirler moths), and Tineidae (fungus moths) (Fig. 100).

Moths are known from all faunal regions and occupy virtually all terrestrial niches on the planet. Many are of economic importance as pests of crops, horticultural plants, or stored products and woolens. Most of the extreme biodiversity known for Lepidoptera is among the moths, from horn-feeding larvae of Tineidae moths in South Africa, to carnivorous hunting inchworms of the Geometridae in Hawaii, to planthopper parasites among the widespread Epipyropidae larvae, among other examples. Most moths, however, are plant feeders, feeding on every possible niche of plants, although the majority are simple leaf feeders.

Adult moths typically have medium-size eyes, a large haustellum (or tongue) which sometimes is scaled, and filiform antennae. There are variations



Moths (Lepidoptera: Heterocera), Figure 100 **Representative moths (Lepidoptera: Heterocera): top left, *Thyris maculata* Harris (Thyrididae) from Maryland, USA (photo J.H.H. Thiele); top right, *Glyphodes bivitralis* Guenée (Pyralidae) from Taiwan (photo C.C. Lin); second row left, *Saptha beryllitis* (Meyrick) (Choreutidae) from Taiwan (photo J.B. Heppner); second row right, *Eterusia aedea* (Clerck) (Zygaenidae) from Taiwan (photo C.C. Lin); third row left, *Vindusara moorei* (Thierry-Mieg) (Geometridae) from Taiwan (photo C.C. Lin); third row right, *Timandromorpha discolor* (Warren) (Geometridae) from Taiwan (photo C.C. Lin); bottom left, *Protambulyx strigilis* (Linnaeus) (Sphingidae) from Ecuador (photo J.B. Heppner); bottom right, *Alypia octomaculata* (Fabricius) (Noctuidae) from Florida, USA (photo M.C. Thomas).**

in many families, where some have large eyes (one family even has split eyes) or very small eyes, and where antennae are clubbed like in butterflies or skippers, or greatly enlarged to being even quadripectinate (many Saturniidae). The most primitive moth families still retain vestigial chewing mouthparts (more well developed in Micropterigidae), and have either no haustellum or only a very small haustellum; some macro-moths also have a reduced or no haustellum, since they do not feed as adults in those species. Moth bodies tend to be covered with more hair-like scales than among butterflies but all kinds of variations are known. Moth adults have various abdominal scent organs (coremata) among some families (e.g., some Arctiidae), and most of the groups in the superfamily Noctuoidea have chordotonal organs in the thorax for hearing (Geometridae, in Geometroidea, have abdominal tympanal organs). Wings include a pair of forewings and a pair of typically smaller hindwings (most primitive moths have hindwings about equal in size to the forewings), and generally the forewings are elongated or triangular in shape and the hindwings are more rounded. Great variety of wing shape, however, is known and many groups have hindwing tails (e.g., some Uraniidae, Zygaenidae, and Saturniidae, among others) or many other irregular wing margins or shapes (e.g., the tropical Himantopteridae have exceedingly long and thin tails that almost are all that remains of the hindwings). Many of the Microlepidoptera have linear wings, especially the hindwings, and very long hair-like scale fringes on the hindwing margins. A number of moth families also have adults that have the wings greatly reduced (brachypterous) or even vestigial (apterous), as for example among some female Geometridae and Lymantriidae. Maculation typically is more somber browns or grays among the moths, but some exceedingly colorful species are known among most families, many with sparkling spots or bands of metallic-iridescent scales.

The caterpillars of moths are commonly encountered, typically with a hard head capsule, three pairs of clawed thoracic legs, and four pairs of abdominal prolegs having crochets (hook-like spines on the base of the prolegs that provide footing when climbing on plants), plus a posterior proleg pair. Specialized feeders have many variations from this standardized form, including the minute flattened leafminers (as in Nepticulidae and Gracillariidae, among others) and the nearly apodous slug caterpillars (superfamilies Zygaenoidea and Cossoidea). Some of the more bizarre caterpillars are found among the Saturniidae and Notodontidae, and among the slug caterpillar groups, while most hawk moth larvae have a horned posterior and a few mimic snake heads. Moth larvae mostly pupate by first making a silken cocoon, or pupate within their leaf mine (e.g., in such families as Nepticulidae and Gracillariidae), or larval shelter (e.g., in such families as Psychidae and Mimallonidae), or in leaf rolls (e.g., as in families Pyralidae and Tortricidae). Hawk moth larvae make an underground pupal cell when ready to pupate. Among other families, there are many other larval life styles and pupation methods, as also adult behavior. However, perhaps as many as 90% of all moths remain unknown biologically, particularly among the tropical species, and this is likewise true for their life histories and behavior.

The largest known moths are among the emperor moths (family Saturniidae), where some of the female atlas moths (genus *Attacus*) of Southeast Asia attain wingspans of up to 300 mm (even to 320 mm if the wings are angled somewhat for maximum distance). Likewise, there are very large hawk moths (family Sphingidae), to 200 mm wingspan, and even among some primitive moths there are large species, as among the ghost moths (family Hepialidae). The largest known moth actually is in the family Noctuidae, where females of the white witch moth (genus *Thysania*) from the Amazon attain wingspans of as much as 305 mm using the standardized wingspan measuring position. The smallest moths are among the pygmy moths (family Nepticulidae), where some wingspans among these leafminers are as little as 2.5 mm. The average for all moths, however, is about 25 mm in wingspan.

References

Barlow HS (1982) An introduction to the moths of South East Asia. Malayan Naturalist Society, Kuala Lumpur, Malaysia, 305 pp, 50 pl
Common IFB (1990) Moths of Australia. Melbourne University Press, Carlton, Australia, 535 pp, 32 pl
Covell CV Jr, (1984) A field guide to the moths of eastern North America. Houghton Mifflin, Boston, MA, 496 pp, 64 pl
Dominick RB, Hodges RW, Dominick T, Edwards CR, Hodges ER (eds) (1971) – The moths of America north of Mexico, including Greenland. Wedge Entomological Foundation, Washington, DC, 27 fasc
Hering EM (1951) Biology of the leaf miners. W. Junk, The Hague, The Netherlands, 420 pp, 2 pl
Holloway JD, Kibby G, Peggie D (2001) The families of Malesian moths and butterflies. E. J. Brill, Leiden, The Netherlands, 455 pp, 8 pl
Inoue H, Sugi S, Kuroko H, Moriuti S, Kawabe A (1982) Moths of Japan. Kodansha, Tokyo, Japan, 2 vol, 392 pl
Krenek V (2000) Small moths of Europe. Cesky Tesín, Czech Rep, 174 pp
Pinhey EGC (1975) Moths of Southern Africa. Tafelberg, Capetown, South Africa, 273 pp, 63 pl
Robinson GS, Tuck KR, Shaffer M (1994) A field guide to the smaller moths of south-east Asia. Malaysian Naturalist Society, Kuala Lumpur, Malaysia, 309 pp, 32 pl
Watson A, Whalley PES (1975) The dictionary of butterflies and moths in color. McGraw Hill, New York, NY, 296 pp, 144 pl
Young M (1997) The natural history of moths. T. & A.D. Poyser, London, United Kingdom, 271 pp, 16 pl

Motile

Active. Able to move freely.

Motor Neurons

Neurons associated with the central nervous system that transmit information to muscles and glands.

Motschulsky, Victor Ivanovich

Victor Motschulsky was born in 1810 in Russia, and became one of the most famous Russian entomologists and greatest coleopterists of his time. He collected extensively from Russia, including Siberia and Russia's (at the time) possessions of Alaska and California. As a colonel in the military, he had unusual access to travel, and took full advantage of his journeys, collecting and studying Coleoptera in Europe, North Africa, and much of North America in addition to the locations previously mentioned. Indeed, it is sometimes stated that his collecting trips were a cover for military intelligence. He also processed enormous amounts of material collected by others. Motschulsky was a strong-illed, independent, and controversial individual. He was possessive, superficial with his descriptions, rough on specimens, and unconventional with his mounting techniques. This led him to clash with other coleopterists of the time, particularly Kraatz. He died June 5, 1871, at Simferopol, Crimea, Russia.

References

Essig EO (1931) A history of entomology. The Macmillan Company, New York, 1029 pp
Herman LH (2001) Motschulsky, Victor Ivanovich. Bull Am Mus Nat Hist 265:110–112

Mountain Midges

Members of the family Deuterophlebiidae (order Diptera).

► Flies

Mountain Pine Beetle, Dendroctonus ponderosae (Coleoptera: Curculionidae, Scolytinae)

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The mountain pine beetle, *Dendroctonus ponderosae* Hopkins, is considered one of the most economically important insect species in coniferous forests of western North America. Adult beetles are capable of successfully reproducing in at least 12 North American species of *Pinus* (Pineacea) from southern British Columbia to northern Baja Mexico. Mountain pine beetle adults attack live trees, and typically must kill the host for successful reproduction. Population outbreaks are most common in a few selected host species, such as lodgepole pine (*P. contorta*), ponderosa pine (*P. ponderosa*), western white pine (*P. monticola*), whitebark pine (*P. albicaulis*), and sugar pine (*P. lambertiana*), which often grow in relatively homogeneous groups over large acreages. Mountain pine beetles typically attack older lodgepole and whitebark pine (e.g., greater than 80 years), while younger ponderosa, western white, and sugar pine can also be attacked. Trees that are stressed by factors such as overcrowding, water, and pathogens are especially vulnerable.

The lifecycle of the mountain pine beetle is highly dependent upon temperature. Commonly, populations are univoltine, although at higher elevations where average temperatures are colder, 2 and sometimes 3 years are required to complete a generation. Adult beetles emerge from host trees and disperse to new hosts in the warm summer months when temperatures are above 15.5°C. Although timing of emergence will vary from year to year depending on beetle development and temperature, peak adult emergence typically occurs within a 2–3 week time span. Rapid and synchronous emergence of the population is essential for mountain pine beetle success in overcoming the resinous defenses of healthy host trees. Adult dispersal involves movement within an infested patch of trees, movement between infested patches of trees, and movement out of the immediate area for initiation of new patches. Long range dispersal to new areas is often aided by wind currents, whereas local dispersal is directed by aggregation pheromones, compounds released when adult beetles attack and feed on new host trees. Monoterpenes, which are major constituents of pine resin, are converted by adult beetles to compounds which, when released, act to aggregate other mountain pine beetles on the tree. Aggregation pheromones enable mountain pine beetles to overcome the defenses of large, vigorous host trees by rapid and highly concentrated attacks. In this manner, mountain pine beetles are functionally able to expand their own food supply. Larger trees require more adults to overcome the tree resin defensives, but also produce a larger number of brood the following generation for continued tree attack. Because a single tree is a finite resource, pheromones are also produced which interrupt the aggregation of adults on a tree. The interruptive aggregation pheromones direct incoming adults to unoccupied portions of the tree under attack, and also to nearby host trees, thereby reducing competition for resources within a single tree. In this manner, during an outbreak, thousands of trees can be attacked and killed in a single year.

Once inside a new host tree, adults mate and eggs are laid individually on each side of galleries excavated vertically in the phloem. Phloem is the inner tissue layer just below the outer bark which translocates carbohydrates up and down the tree. Mountain pine beetle larvae feed horizontally in the phloem, cutting off nutrient translocation, thereby killing the host tree. Larval development rate, which is highly dependent on temperature, dictates the life stages present during the winter. Available evidence indicates that the mountain pine beetle does not diapause, and all larval life stages may be found overwintering under the bark of host trees. The larvae, which are intolerant of freezing temperatures, survive low temperatures by supercooling. Populations in Idaho have been found to survive temperatures as low as −35°C. Mortality due to cold temperatures is usually greatest during the spring and fall months when larvae may not be appropriately acclimated to dramatic swings in temperature. Woodpeckers, clerid beetles (*Enoclerus* spp., *Thanasimus* spp.), and parasitic wasps are also the cause of a small amount of mountain pine beetle mortality, mostly at endemic population levels.

Pupation occurs in the early summer followed by a teneral adult stage during which the new adults feed on a diverse flora of microbial symbionts including fungi (*Ophiostoma* spp.) and yeasts found within the pupal chamber. During this feeding period, the microorganisms are acquired in the mycangia, a specialized structure of the integument. When the adult beetle emerges from the host tree for dispersal to a new tree, the fungi and yeasts are carried inside the mycangia and inoculated into the phloem of the new host. Although the role of *Ophiostoma* spp. in mountain pine beetle population dynamics are not fully understood, at least one species appears to be beneficial to population success, while detrimental effects are attributed to another species. Following maturation feeding in the teneral adult stage, new adults emerge from the dead trees to disperse, attack new live host trees, and begin the cycle again.

Given appropriate weather and stand conditions, populations of mountain pine beetles are capable of attacking and killing hundreds of thousands of trees in a few years. This magnitude of mortality can disrupt forest management plans, recreation, watershed, wildlife, and timber production. In areas of high value, such as forest campgrounds and ski areas, direct control tactics such as insecticides are often used to temporarily reduce mountain pine beetle caused mortality. Synthetic forms of the aggregation pheromone may also be used to concentrate adults in traps or trees which are then removed from the area. Ongoing research is aimed at understanding the role of interruptive aggregation pheromones in mountain pine beetle population dynamics, in the hope that synthetic forms of these compounds may also provide a tool for direct population control. While direct control tactics are useful in small, high value areas, they are not effective or feasible over large areas, and do not alter the habitat and stand conditions that are favorable to mountain pine beetle populations. The optimum approach in areas which have been targeted for management is prevention. Silvicultural practices such as thinning, which decrease the density of host trees, help to maintain vigorous trees and create a less favorable habitat for mountain pine beetle population growth. A mosaic of vegetation types across a landscape, partitioned by age and host and non-host species, may also help to reduce large scale, widespread mortality.

Options for management of mountain pine beetle populations depend on the specific land use objectives. Forested areas targeted for timber production can be silviculturally treated to facilitate reduced susceptibility to mountain pine beetle outbreaks. Many areas designated as wilderness, however, are managed as natural areas and timber harvest is not a major objective. Within these areas the historical role of the mountain pine beetle in forest ecosystems may be emphasized. Mountain pine beetle populations, which are native to western North America, have evolved with their pine hosts and are significant components of healthy, functioning ecosystems. In particular, the mountain pine beetle and fire are considered important disturbance agents favoring the regeneration of lodgepole pine. While tree death is a difficult concept for humans, it is a normal step in the rejuvenation and succession of forest ecosystems, and the mountain pine beetle is an important part of this process.

► Bark Beetles in the Genus *Dendroctonus*

References

Amman GD, Cole WE (1983) Mountain pine beetle dynamics in lodgepole pine forests Part II: Population Dynamics. USDA Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report INT-145

Borden JH, Chong LJ, Lindgren BS (1990) Redundancy in the semiochemical message required to induce attack on lodgepole pines by the mountain pine beetle *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). Can Entom 122:769–777

Logan JA, Bentz BJ (1999) Model analysis of mountain pine beetle (Coleoptera: Scolytidae) seasonality. Environ Entomol 28:924–934

McGregor MD, Amman GD, Schmitz RF, Oakes RD (1987) Partial cutting lodgepole pine stands to reduce losses to the mountain pine beetle. Can J For Resour 17:1234–1239

Raffa KF (1988) The mountain pine beetle in western North America. In: Berryman AA (ed) Dynamics of forest insect populations, patterns, causes and implications. Plenum Press, New York, NY, pp 506–531

Shore TL, Safranyik L (1992) Susceptibility and risk rating systems for the mountain pine beetle in lodgepole pine stands. Forestry Canada, Pacific Forestry Centre, Victoria, Canada

Mouth Beard

In robber flies (Asilidae), the prominent tuft of hairs at the front of the head. This is also called the mystax.

Mouth Cone

A term used to describe the mouthparts arrangement of thrips (Thysanoptera).

► Mouthparts of Hexapods

Mouth Hooks

In larvae of the higher Diptera, the mandible-like feeding structures located at the oral cavity.

Mouthparts of Hexapods

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The hexapods are trignathan, that is to say they present three pairs of buccal appendages, each one of them situated in the corresponding cephalic segment: a pair of mandibles (mandibular segment), a first pair of maxillae (maxillary segment), and a second pair of maxillae that fused, form the labium (labial segment).

Recently, certain authors affirm that the classic point of view, according to which the true capacity of "biting" by the Dicondylia [Thysanura (Zygentoma) plus Pterygota] is functionally correlated to the acquisition of dicondylic mandibles, cannot be maintained, taking into account that the capacity of "biting" transversely is a trait characteristic of the hexapods. Therefore, the division of the mandibles into mono- and dicondylic is not fitting (Koch 2001); because of this, and owing to the great variability existing in the hexapods, this author prefers to treat separately the mandibles of each one of the large groups: Collembola, Protura, Diplura, Archaeognatha, Thysanura and Pterygota.

Despite the opinion of Koch, many authors consider, at least from a practical point of view, the type and number of articulations within the head capsule to separate two fundamental types of mandibles: monocondylic (one articulation) and dicondylic (two articulations). The monocondylic type is characteristic of the majority of Apterygota, although in Collembola, Protura and Diplura an authentic mandibular condyle does not exist as in the case of Archaeognatha. This monocondylic type appears secondarily in entognathous Pterygota, with mouthparts transformed into stylets.

The dicondylic type is typical of the Pterygota, where two mandibular articulations are differentiated, one in the anterior position and another posterior. An intermediate condition exists between the mono- and dicondylic types. In it the mandibles, in addition to the principal articulation (corresponding to the only condyle of Archaeognatha), present a secondary articulation known as the epicondyle. It is situated in the anterior third of the mandibular body and therefore differs from the second articulation of Pterygota, which has a clearly posterior position. This intermediate model is displayed in Thysanura and nymphs of Ephemeroptera.

The morphology of the mandible varies according to the diet and is usually characteristic in each of the hexapod orders. Nevertheless, it basically consists of an incisor zone in the distal or subdistal position and another molar zone situated on the internal mandibular face. The greater or lesser development of these two zones is found in the function of the alimentary behavior. Thus, in predatory species the incisory zone is usually well developed, since it serves to cut and tear the prey. On the contrary, in phytophagous species that consume solid food, the molar zone, which carries out a triturating function, is more developed. The internal face of the mandibles can bear secondary cuticular or tegumentary differentiations: tubercles, keels, spines, and bristles of distinct development and morphology. Additionally, a lobe lacking musculature, called lacinia mobilis or prostheca, is differentiated from this internal face in Diplura and nymphs of Ephemeroptera.

In the majority of Pterygota the musculature related to the mandibles is very profuse, being differentiated into four types of muscles: hypopharyngeal muscles, tentorial-mandibular muscles, zygomatic adductors, and cranial-mandibular muscles. In Pterygota they are generally reduced to two types of muscles, abductors and adductors, although in primitive groups the cranial-mandibular muscles are conserved.

The maxillae are considered more complete appendages than the mandibles. The most generalized model is found in the Thysanura. Modifications of this model are produced that tend to reduce certain structures adapted to different trophic models. The basal part is called the cardo. It is of reduced size, and it articulates from the proximal part of the head capsule in the hypostomal zone of the buccal area. In the apical part, the cardo is joined to the stipes, which is the largest component and forms the maxillary "body". On the stipes, two structures are differentiated apically, the lacinia (internal) and the galea (external). The lacinia is usually well sclerotized and carries out alimentary type functions, while the galea (having little sclerotization) develops functions of a sensory nature.

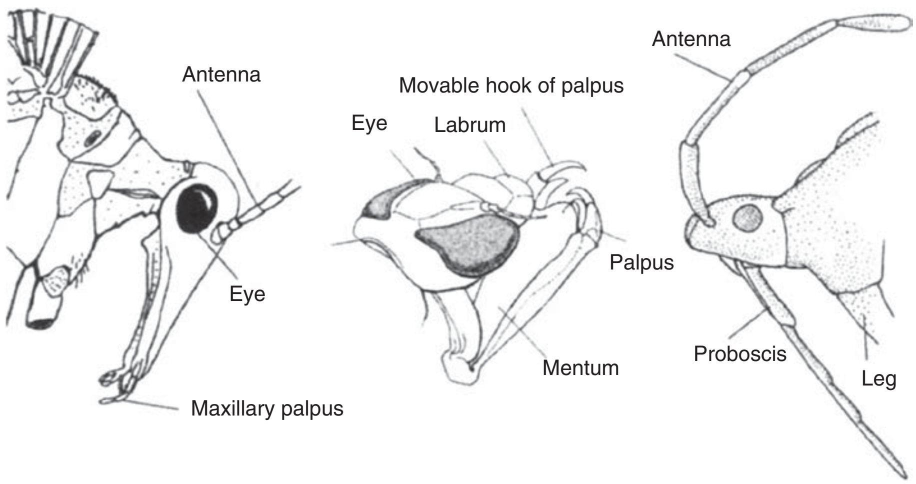
The maxillary palps are inserted in the stipes on a piece named the palpifer or palpiger, and in Hexapoda they exhibit a maximum number of seven segments (Archeognatha), a number that tends to be reduced. In advanced groups of hexapods there is a tendency for the cardo and even all of the maxilla to be incorporated into the ventral face of the cranium, as occurs in larvae of Coleoptera and Diptera. In the basic model of the maxilla two types of related muscles are clearly differentiated: cranial-maxillary muscles and tentorial-maxillary muscles.

During embryonic development a fusion of two maxilla-like structures is produced (second pair of maxillae), from which the labium originates. The number and development of pieces that comprise the labium can vary depending on the hexapod group. In the generalized models two regions are differentiated: the postmentum (basal, united to the oral cavity) and the prementum (distal). There can also be three: submentum, mentum and prementum. Although the majority of authors consider the mentum to be an apical part of the postmentum, in certain cases it is a basal subdivision of the prementum. These regions correspond to a postlabium (postmentum plus mentum) and a prelabium or prementum.

The prementum, which in the most primitive groups is a paired structure, basically carries one pair of palps (lateral position) and four apical pieces, two in the lateral position or external (paraglossae) and two in the median position or internal (glossae). The glossae can be welded to each other or to the paraglossae, forming the alaglossa and totaglossa, respectively. Sometimes the four lobes (glossae and paraglossae) are fused, forming the ligula or tongue. The palpus typically consists of three segments and, like the maxilla, is inserted on a projection named the palpifer.

Various types of muscles related to the labium exist. Those standing out most include the extrinsic muscles of the labium, the extrinsic and intrinsic muscles of the palps, the retractors of the glossae and paraglossae, and the median post-prelabial muscles.

According to their position, various types of mouthparts can be distinguished. Orthognathous or hypognathous mouthparts are situated more or less perpendicularly to the cephalocaudal axis. Prognathous mouthparts are those in which the buccal area is situated in the anteroventral part of the head and the mouthparts are directed toward the front. The opisthognathous type is characterized by displaying the buccal area situated in the posteroventral



Mouthparts of Hexapods, Figure 101 Orientation of insect mouthparts: hypognathous (*left*), prognathous (*center*), and opisthognathous (*right*).

part of the head and the mouthparts directed toward the back, being situated during rest between the anterior legs. These terms are also used to define the head capsules.

Chewing Mouthparts

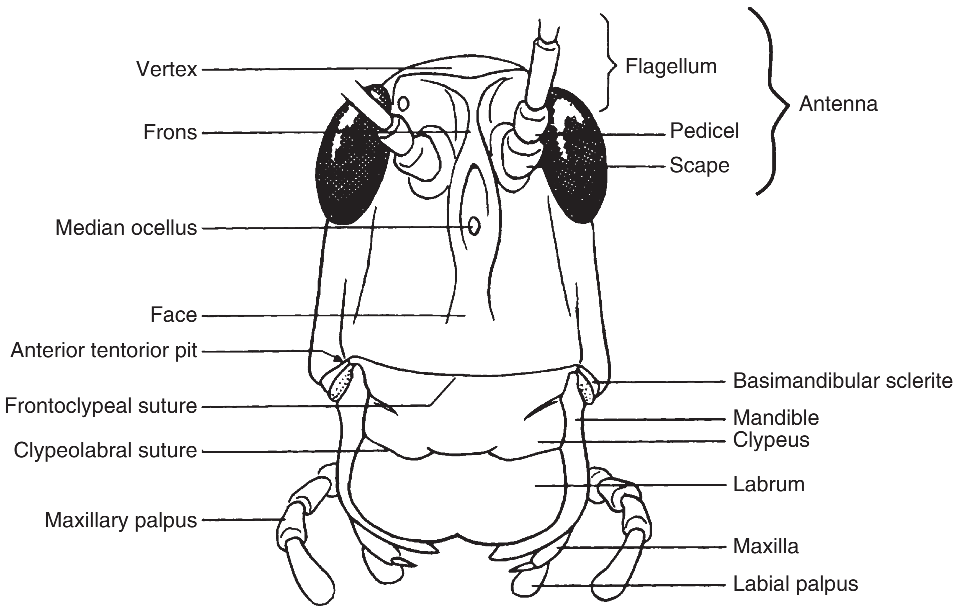
The mouthparts above described correspond to a basic model of chewing mouthparts. However, numerous modifications exist due to the lifestyle and alimentary diet of the insects, resulting in an elevated number of types of mouthparts, although all fit into five types with certain variations in each (Figs. 101–104).

Chewing-Sucking Mouthparts

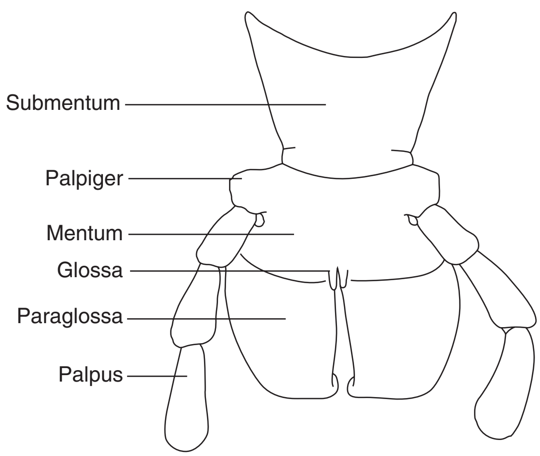
Within the basic chewing mechanism, among the more important modifications are those related to the functions of licking or sucking, as occurs in Hymenoptera. In these cases, the modifications affect the maxillae and the labium, with the mandibles developing functions of work and not of trophic type [for example, in predatory wasps, whose females use the mandibles to construct the nest and transport the prey (Hymenoptera: Spheciformes)]. In the more advanced forms of Hymenoptera, the maxillae and the labium are elongated, giving rise to a sucking and licking proboscis that serves to collect nectar. In this way a maxillolabial organ is differentiated, in which the maxillary stipes have the form of a sheath and surround the base of the labium. The glossae are united, forming a long structure that is the functional part in the collection of nectar and which certain authors call the ligula, the tongue, or the glossa proper. This structure is hollow, and internally it is bathed in circulatory liquid, whose greater or lesser pressure allows its complete extension or its retraction, which is aided by the action of special retractor muscles. When the bee is feeding, the ligula is alternatively extended and retracted, such that the alimentary fluid ascends by capillarity through the central channel of the ligula (Fig. 105).

Piercing-Sucking Mouthparts

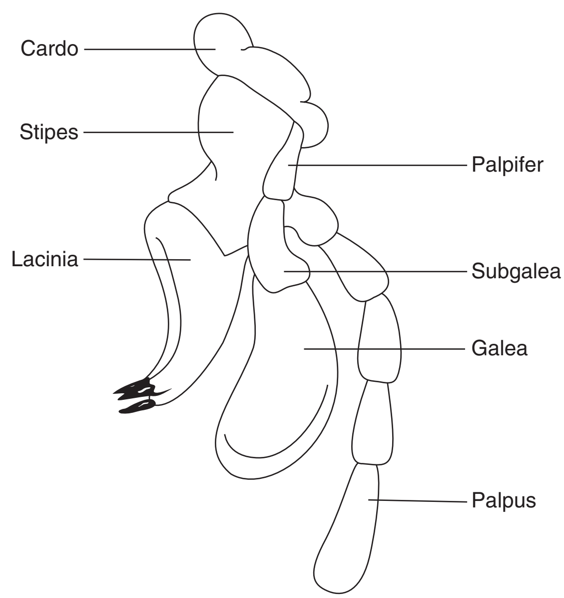
This type of mouthpart is found in hematophagous Hemiptera and Diptera, although morphologically they exhibit differences. In Hemiptera, the mandibles and the maxillae are transformed into more or less chitinized stylets that arise



Mouthparts of Hexapods, Figure 102 **Mouthpart components and their placement in a chewing insect (Orthoptera: Romaleidae).**

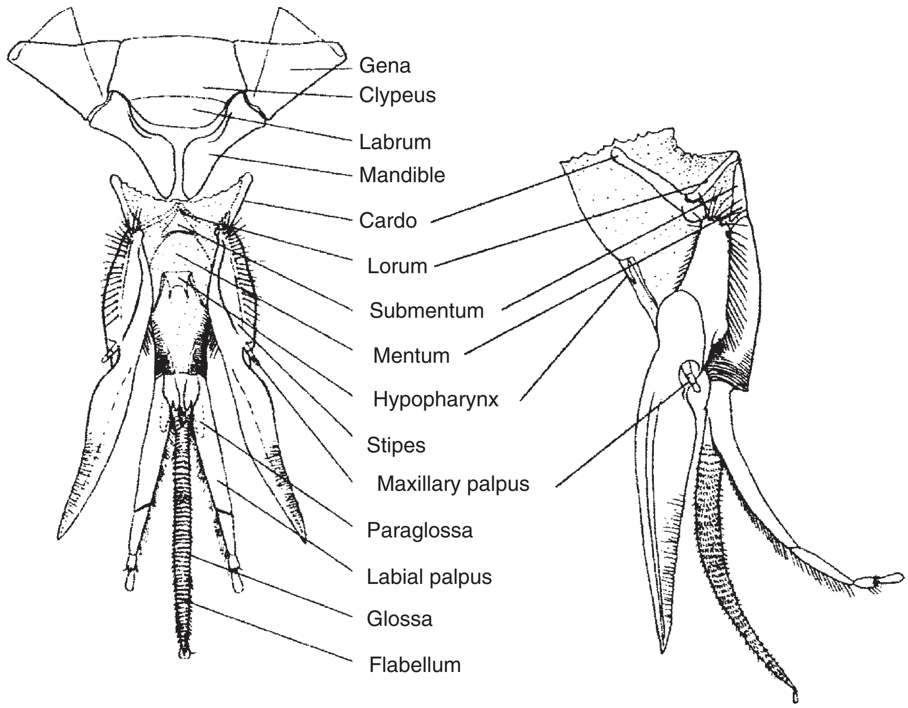


Mouthparts of Hexapods, Figure 103 **Labium of grasshopper (Orthoptera: Romaleidae).**



Mouthparts of Hexapods, Figure 104 **Left maxilla of grasshopper (Orthoptera: Romaleidae).**

separately from a gnathal bag and come near toward the apex, such that the four stylets unite in a fasciculus. The stylets are united along their length, the mandibles being external and the maxillae internal. Internally, these maxillary stylets form two superimposed canals: one dorsal (generally of greater diameter), which is the alimentary canal, and the other ventral through which the saliva flows. The labium is transformed into an elongated structure (with one to four divisions) that forms a sheath protecting the stylets; the labial palps have disappeared. All of the mouthparts together form a "rostrum," which in the resting state is usually directed toward the back



Mouthparts of Hexapods, Figure 105 Front and side view of chewing-sucking mouthparts (Hymenoptera: Apidae).

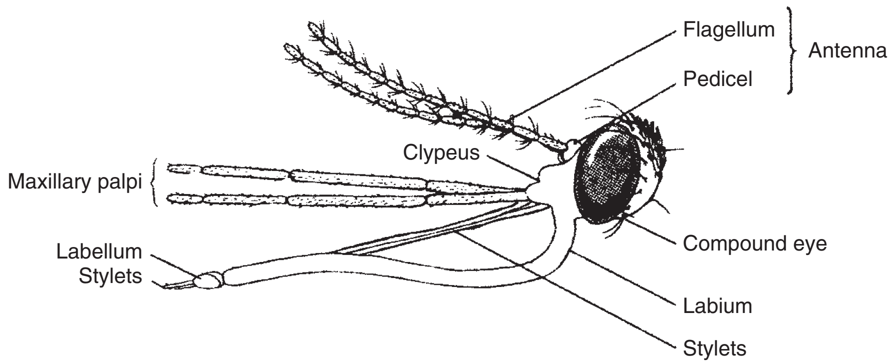
(opisthognathous condition). Although anatomically the hypopharynx does not constitute a mouthpart, in hemipterans its distal part appears as a small lobe between the stylets. In the same way, the labrum (and its ventral epipharyngeal part) are situated in the anterior part (dorsal) of the same mouthpart (Figs. 106–109).

In hematophagous Diptera, piercing-sucking mouthparts are developed, with the mouthparts transformed into stylets, except the palps and labium. In addition, the females exhibit well developed mandibles, contrary to the males, in which they are usually atrophied. Also forming part of the "labial complex" are the labrum, which has a channeled form, and the hypopharynx, which is flattened in the form of a lamella, also channeled, and in whose base runs the salivary canal. Both structures are superimposed and form a canal through which flows the blood collected from the wound produced by the injuring organs (mandibular and maxillary stylets). One variation of this type of mouthparts (named cutting-sucking) is found in Diptera, Tabanidae, in which the mandibles and maxillae are short structures, which are finely toothed apically, and rudimentary labellar structures can be seen (Fig. 110).

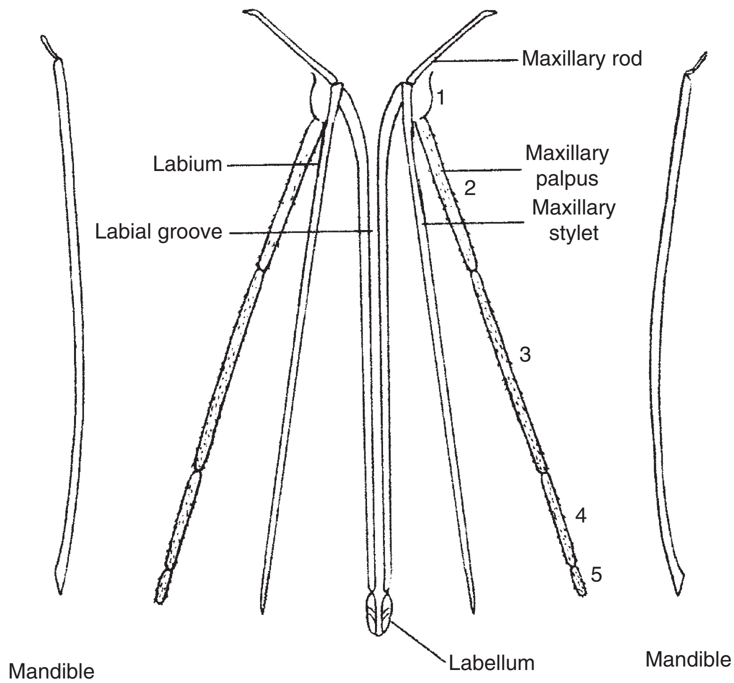
Sucking Mouthparts

This type of mouthpart is seen in Diptera, Cyclorrhapha. All the mouthparts contribute, to a greater or lesser degree, to the formation of a proboscis, whose interpretation is difficult due to the reduction of the maxillae and to the great development of membranous areas. Following the current nomenclature accepted by the majority of authors, this proboscis consists of two morphologically and functionally different zones: one in the basal position, named rostrum or buccal cone, and the other distal, named haustellum, which ends in an oral disc (Fig. 111).

The rostrum morphologically pertains to the head capsule and dorsally carries the palps and a naturally cuticular structure named the fulcrum.



Mouthparts of Hexapods, Figure 106 **Mouthpart components and their placement in a piercing-sucking insect (Diptera: Culicidae).**



Mouthparts of Hexapods, Figure 107 **Components of mosquito mouthparts (Diptera: Culicidae).**

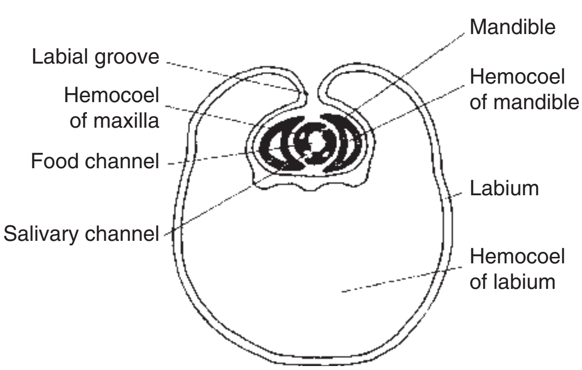
In the base of this fulcrum is situated a small formation in the form of a "U," named the hyoid sclerite, which serves to maintain the lumen of the cibarium.

The haustellum is formed in the dorsal zone (anterior) by the labrum (and its ventral epipharyngeal face) and the hypopharynx, being reinforced in its ventral face (posterior) by the prementum, which articulates with a labial rod like a furca, whose branches form the endoskeleton of the labella (lobes). These labella form an oral disc in their apical part, constituted by a series of canals for taking in fluids, named pseudotracheae. The pseudotracheae maintain their light by a series of incompletely sclerotized and bifurcated rings in their apex, which give them an appearance of tracheae, from which originates their name. The fluid passes through the interbifid spaces, acting as a filter for the solid particles. When the proboscis begins to function, the rostrum is distended by aerial sacs in its base and the haustellum through extensor muscles. In addition, the labella become swollen through the internal pressure from the circulatory liquid. The retraction of the proboscis is carried out by the appropriate muscles.

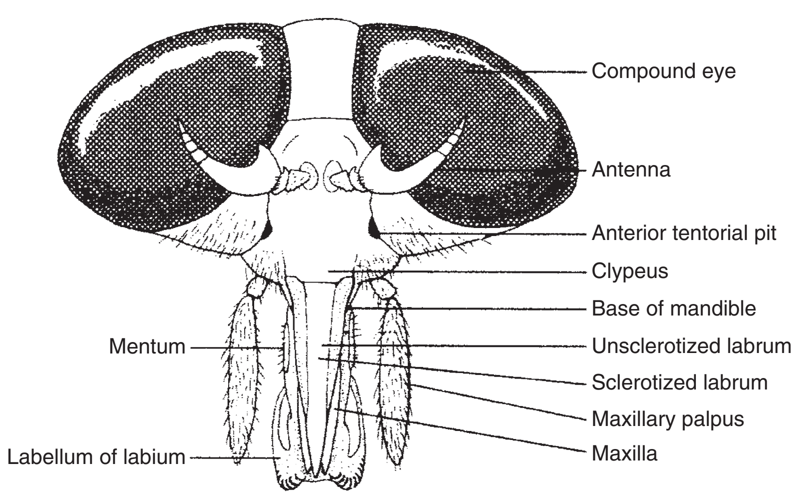
Siphoning-Sucking Mouthparts

This type of mouthpart is seen in Lepidoptera. The mandibles are generally vestigial or non-existent, except that in some families of moths like Tineidae they are evident, although small. The maxillae comprise a basal part (formed by the cardo and stipes) that is incorporated into the head, and one free part formed by the galeae. The apical part of the stipes bears a palpifer prolonged into a generally reduced maxillary palp, except in primitive families like Tineidae in which the palp is well developed and consists of five to six segments. The distal parts of the galeae, which are channeled in their internal side, are united by a system of hooks and spines. A suction tube for feeding named the spiritrompe or haustellum is thus formed. The labium is greatly reduced and is partly membranous, the same occurring with the hypopharynx, which is normally found fused to the internal side of the labium. A nerve, a trachea, and two oblique muscular bundles run internally along the entire length of each half of the proboscis (Fig. 122).

When the proboscis is at rest, it folds back in a spiral below the thorax. This coiling is possible because although normally each part of the spiritrompe is surrounded by incomplete sclerotized rings, among them exist ample membranous zones; in addition, the spiritrompe is very elastic. When the proboscis begins to function, it stretches so that circulatory liquid, whose pressure is regulated by a valve situated in the stipes, penetrates its interior. A wide variation in the length of the spiritrompe exists, reaching the maximum in Sphingidae, in which in some individuals it can measure four times the length of the body.

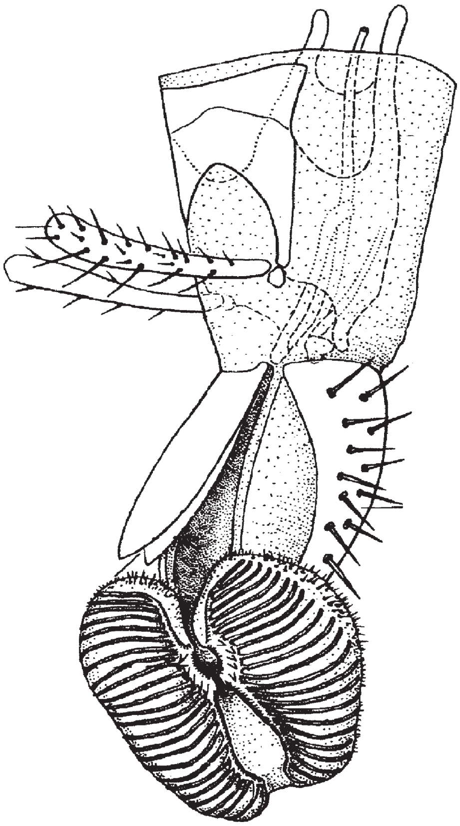


Mouthparts of Hexapods, Figure 108 Cross-section of piercing-sucking mouthparts (Hemiptera: Cicadidae).



Mouthparts of Hexapods, Figure 109 Cutting-sucking mouthparts (Diptera: Tabanidae).

In addition to the basic models of mouthparts mentioned, others exist that are highly specialized to different ways of life, those related to parasitism standing out, such as the case of the mouthparts of Siphunculata and Siphonaptera.



Mouthparts of Hexapods, Figure 110 **Sucking mouthparts (Diptera: Muscidae).**

References

Bitsch J (1973) Morphologie de la tête des insects. Partie Générale. In Grassé, PP (Dir.) Traité de Zoologie VIII (I):3–100

Koch M (2001) Mandibular mechanisms and the evolution of hexapods. Annales de la Societé Entomologique de France (N.S.) 37:129–174

Matsuda R (1965) Morphology and evolution of the insect head. Mem Am Entomol Inst 4:1–334

Quénnec E (2001) Insights into arthropod head evolution. Two heads in one: the end of the "endless dispute"? Ann Soc Entomol Fr 37:51–70

Snodgrass RE (1951) Comparative studies on the head of mandibulate arthropods. Comstock, Ithaca, New York, NY

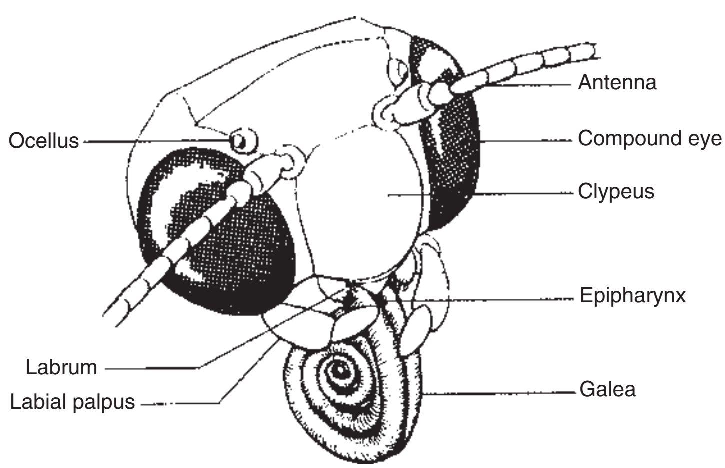
Mud Daubers

Sceliphron spp. (Hymenoptera: Sphecidae) solitary wasps that create mud nests and provision them with spiders as a food supply for their young.

► Wasps, Bees, Ants and Sawflies

Mulch

A layer of material placed on the soil to retard growth of weeds. In commercial crop production plastic is often used, whereas in the home garden organic materials such as leaves, straw, wood chips, and pine needles are often used.



Mouthparts of Hexapods, Figure 111 **Siphoning-sucking mouthparts (Lepidoptera: Sphingidae).**

Müller, Johann Friedrich Theodor

"Fritz" Müller was born at Windischholzhausen, Germany, on March 31, 1822. He entered the University of Berlin in 1841 with the intent of becoming a teacher, received his doctorate in 1844, and commenced teaching in a gymnasium at Erfurt. In 1852, Müller traveled to a German colony in Brazil. Though it was a primitive existence, Müller enjoyed his life in the colony, and again became a teacher, then a public officer, and finally a naturalist with the National Museum of Rio de Janeiro. In 1863 Müller published "Für Darwin," a treatise of support for Charles Darwin's ideas. His studies on insect coloration, published in 1879, became famous and served as the basis for the concept of Müllerian mimicry.

Reference

Papavero N (1971, 1973) Essays on the history of Neotropical Dipterology with special reference to collectors (1750–1905). Museu de Zoologia, Universidade de São Paulo

Müller, Josef

Josef (Giuseppe) Müller was born at Zara, Dalmatia (now Croatia) on April 24, 1880. He obtained a degree in philosophy from Graz University in 1902, and moved to Trieste, Italy. There, Müller joined the Società Adriatica and established an entomological section of the society. He intended, with the cooperation of others, to complete an entomological survey of the area. However, World War I broke out, and Müller was drafted, and he worked on the biology of human lice, a vector of typhus. Müller returned to Trieste after the war, and became conservator and then director of the Trister Naturhistorisches Museum. The museum flourished under his direction, particularly the entomology department. Müller published many encyclopedic works, such as "Catalogo dei Coleotteri della Venezia Giulia" and monographic works on ants, beetles, reptiles, etc. Müller led several expeditions to Ethiopia and the Red Sea. He retired as the director in 1941, but in 1953 published a large work on phytophagous beetles. Müller was an eminent European entomologist during the 1920s and 1930s, and he published 243 papers, mostly on Coleoptera. He died at Trieste on September 21, 1964.

Reference

Herman LH (2001) Müller, Josef. Bull Am Mus Nat Hist 265:112–113

Müllerian Mimicry

Mimicry in which several distasteful organisms share a common appearance. Mutual aposematism.

► Mimicry

Mulluscicide

A pesticide used to kill slugs and snails.

Mulsant, Etienne

Etienne Mulsant was born at Mornant, France, on March 2, 1797. He received his education at colleges in Belley, Roanne, and Tournon. He worked as a curator of the city library in Lyon, and as a professor of natural history at the Lyceum in Lyon, France. He worked at these two posts his entire life, and became a noted coleopterist who is remembered as one of the world's greatest authorities on Coccinellidae. In addition to a monograph on Coccinellidae (in 1866 and 1867), a most important publication was "The natural history of Coleoptera of France" published in 37 parts from 1839 to 1884. His work was meticulous, and this became a standard reference for many years. His publication list totals nearly 250 items. He died at Lyon, France, on November 4, 1880.

References

Essig EO (1931) A history of entomology. The Macmillan Company, New York, 1029 pp
Herman LH (2001) Mulsant, Etienne. Bull Am Mus Nat Hist 265:114

Multifunctional Semiochemicals

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A diversity of factors is undoubtedly correlated with the pronounced success of insects in both terrestrial and aquatic environments. Significantly, in the last several decades, identification of a great variety of natural products (chemical compounds) has resulted in an awareness of the remarkable versatility with which insects use the products of their exocrine glands (external secretions) to manipulate intra- and interrelationships. A multitude of research investigations has demonstrated that insects and related arthropods have converted exocrine products to serve multiple functions in diverse contexts. In addition, it has become clear that exocrine secretions or their individual compounds, which previously had been identified with a single function, often possess several roles which are highly adaptive for their producers. In short, insects may exploit the secretions of a single gland for unrelated diverse roles which can include defense, sexual attraction, and communication.

The multifunctional compounds secreted by insects are termed semiochemicals and primarily include pheromones (communication chemicals) and allomones (defensive chemicals). These compounds, which have been identified in insect species in at least six orders, had previously been assigned single functions, but it is now evident that they possess a variety of unsuspected – and vital – additional functions as chemical regulators of a large diversity of behaviors. Ultimately, this phenomenon has been described as "semiochemical parsimony" as a reflection of the great adaptiveness of insects manipulating their exocrine products in the biological milieu. As will be described subsequently, the ability of insects to exploit a number of habitats is in no small way correlated with the use of external secretions as multifunctional regulators of both intra- and interspecific interactions.

The Parsimonious Activities of Eclectic Alarm Pheromones

Alarm pheromones, which are used by both eusocial and solitary species, are generally produced during traumatic interactions that result in dispersion or defense of the alarm pheromone producers. These pheromones, which are generally produced in much greater quantities than other classes of pheromones, appear to be highly adaptive to function multifunctionally. Because the pheromones are secreted in adversarial confrontations, they possess some of the same properties as defensive allomones, and indeed, are believed to be derived from these widespread defensive products. Alarm pheromones can be visualized as an evolutionary development from defensive compounds, the latter already being programmed for responses to environmental perturbations.

Activity Inhibitors

Some eusocial species have adapted their alarm pheromones to regulate important social activities in a variety of specific contexts. Honey bee workers, *Apis mellifera*, suppress visitations of workers to nectar-depleted flowers by marking these flowers with 2-heptanone, an alarm pheromone produced in the capacious mandibular glands. 2-Heptanone, along with isopentyl acetate (a sting-shaft compound), inhibit the secretion of the worker Nasavov gland, an organ that plays a role in colony fission and swarming. The Nasanov secretion is highly attractive to queens and workers in reproductive swarms but in its absence foreign queens can be rejected.

4-Methyl-3-heptanone, the alarm pheromone of the fungus-growing ant *Atta texana*, can be used to disrupt foraging on well-marked trails in the presence of high concentrations of the alarm pheromone. The ants cut leaf fragments that are normally carried to the nest to generate a fungal food source. Exposure to the alarm pheromone results in the workers dropping their leaves and moving rapidly to the nest. This behavior could be very beneficial if a predator attacked the ants on their crowded foraging trails.

Cryptic Alarm Pheromones in Solitary Insects

Many species of solitary insects, when moving over the ground surface, are exposed to aggressive ants that are capable of rapidly recruiting additional workers for *en masse* attacks. Some species of beetles, cockroaches, and mutillid wasps, as well as non-insect arthropods that have frequent encounters with these formicids, have evolved escape behaviors which are highly adaptive as survival mechanisms. Indeed, it appears that the basis for avoiding attacking ants is identified with the use of cryptic alarm pheromones by these solitary insect species.

4-Methyl-3-heptanone, a characteristic alarm pheromone of aggressive ants in five subfamilies, has been exploited by female mutillid wasps as a disruptive cryptic alarm pheromone that blunts the attacks of the formicids. The wasps are wingless and they undoubtedly encounter foraging ants with some frequency as they move over the ground with great cursorial speed. The wasps secrete copious amounts of the pheromone from cephalic glands and this compound causes an exaggerated alarm response, resulting in dispersion of the ants and rapid avoidance behavior by the mutillids.

Other ketones, regarded as highly stimulatory olfactants, have also been evolved by cockroaches to function as cryptic alarm pheromones. 2-Heptanone, a characteristic alarm pheromone of a variety of dolichoderine ant species, is produced by both cockroaches (*Platyzosteria* spp.) and beetles (*Dyschirus* spp.) and these rapidly moving solitary insects can escape the predatory ants whose attack behavior is severely disrupted by the cryptic pheromone 2-heptanone. 6-Methyl-5-hepten-2-one, another widespread alarm pheromone of dolichoderine ants, is produced by the cockroach *Neostylopyga rhombifolia*, as further testimony of the frequent structural congruency of the cryptic alarm pheromones of solitary insects and their ant predators.

Robbing Agents

A robbing *modus operandi*, predicated on the utilization of idiosyncratic natural products, characterizes the aggressive behavior of a variety of ants and tropical bees. These lifestyles, when analyzed, have been demonstrated to be possible because the chemical agents secreted by these attacking hymenopterans effectively disarm the host species. In all cases in which the disarming chemicals have been identified, they have proven to be alarm pheromones.

Workers of *Lestrimelitta limao*, a stingless bee that constitutes a major raiding species in the Neotropics, subdue other species of stingless bees by secreting copious amounts of mandibular gland secretions on the raided nest. The secretion, dominated by the powerful lemon-smelling compound citral, serves to disorient the host workers while simultaneously attracting additional workers of *L. limao*. Resistance by workers of the host species rapidly ceases and nest plundering is pronounced. Citral proves to be the magic bullet for slaying vulnerable species.

At least two species in the ant genus *Formica* use Dufour's gland constituents to perform slave raids on susceptible species. The attacking workers secrete alkyl acetates from their hypertrophied Dufour's glands and these simple esters function to disarm the host workers, who become disorganized and incapable of organized resistance.

Alarm Pheromones as Trail Pheromones

Multifunctional parsimony characterizes the mandibular gland secretions of a variety of stingless bees in the American tropics. When examined in detail, there is strong evidence that the secretions of these bees are at least trifunctional.

Citral is a major constituent in the mandibular gland secretion of the bee *Trigona subterranea*. This compound, the dominant compound in the exudates, generates well-developed trails when deposited by workers. On the other hand, if the secretion is deposited near the nest, intense alarm activity is released. Pure citral produces the same response. Identical responses were obtained with another *Trigona* species.

Releasers of Digging Behavior

Displacement behavior by some species of ants results when workers undertake digging after exposure to high concentrations of their alarm pheromones. The behavior may be highly adaptive for selected species.

The dolichoderine ant *Conomyrma pyramicus* releases alarm behavior in sister workers with a pygidial gland product, 2-heptanone. Burial of objects treated with high concentrations of this ketone result in workers rapidly burying them. Such behavior effectively removes a highly excitatory and disruptive stimulus from the ground surface.

Another ant species, the myrmicine *Pogonomyrmex badius*, generates an alarm signal with 4-methyl-3-heptanone, a minty compound that is widely distributed in myrmicine species. This alarm pheromone initiates digging behavior in the sandy soil in which these ants nest. Workers may be buried by cave-ins in the sand and their pheromonal signals may be of great importance in signaling their dilemma to other workers.

Antimicrobial Alarm Pheromones

Insect species often develop in environments that are highly suitable for the proliferation of diverse bacterial and fungal microorganisms. Inhibition of pathogenic growth is a *sine qua non* for insect survival in environments that readily support virulent bacteria and fungi. This is particularly true of ground-dwelling ants, bees, and wasps, whose subterranean nests possess the high ambient temperatures and relative humidities favored by microorganisms.

The southern green stink bug, *Nezara viridula*, co-habits plants that contain the fungus *Metarrhizium anisopliae*, a particularly virulent insect pathogen. The alarm pheromones of *N. virudula*, *(E)*-2-hexenal and (*E*)-2-decenal, inhibit spore germination of this entomopathogenic fungus, and this fungistatic activity is critical to maintenance of viable populations of the stink bug.

Several alarm pheromones of ants have been demonstrated to be potently fungistatic. Citral, a monoterpene produced by *Atta* spp., was as active against dermatophytes as some commercial fungicides but was not as active against insect and plant pathogens. Two other characteristic ant alarm pheromones derived from species in the subfamilies Myrmicinae and Dolichoderinae, 4-methyl-3-heptanone and 2-heptanone, were also fungistatic but did not possess the inhibitory activity of the aldehyde citral.

Alarm Pheromones as Attractants

Workers of ants and eusocial species of bees and wasps may mark assailants with alarm pheromones that function to attract additional workers to the labeled individual. This attraction results in forming aggregations around marked adversaries and is highly adaptive in terms of developing a force of combatants. Alarm pheromones have thus been converted to recruitment stimuli whose binary functions – alarm and recruitment – interact effectively to develop group behavior as a first line of defense against adversaries, and prey as well.

Although alarm pheromones may certainly function as traumatic stimuli, these compounds at low concentrations may also be used to promote the formation of both combative and noncombative aggregations. For example, workers of the ant *Camponotus pennsylvanicus* use the hydrocarbon *n*-undecane, a defensive compound, to orient excited workers to sources marked by their major alarm pheromone, formic acid. By contrast, low concentrations of *n*-undecane can produce long-term aggregations of workers. Similarly, low concentrations of 2-heptanone, the alarm pheromone of the dolichoderine ant *Iridomyrmex pruinosus*, label the habitual feeding aggregations of the workers.

While aggregative agents such as *n*-undecane and 2-heptanone are at least bifunctional alarm pheromones, it is certainly recognized that these compounds are, in reality, trifunctional pheromones, as are a wide variety of additional compounds. These pheromones are of great parsimonious use as defensive compounds, in addition to their known roles as aggregative and alarm pheromones. In essence, these semiochemicals clearly possess diverse functions that reflect their adaptive value in the social milieu.

Defensive Allomones as Alarm Pheromones

If the defensive allomones of solitary insects are remarkably eclectic, it is also rather significant that many of these compounds are structurally congruent with the alarm pheromones of eusocial insects. Alarm pheromones are generally secreted in considerably greater quantities than other classes of pheromones, further emphasizing their suitability as defensive allomones. Indeed, defensive allomones and alarm pheromones share many common properties, a fact consistent with the suggestion that the latter were derived from the former. This evolutionary scenario is predicated on a species' preprogrammed behavioral response to a defensive compound to which it already has an adaptive traumatic response.

Ants provide persuasive examples of how compounds demonstrated to be alarm pheromones have been exploited by nonsocial insects as defensive allomones. For example, 6-methyl-5-hepten-2-one, a typical alarm pheromone of dolichoderine ants, is used by cockroaches in the genus *Neostylopyga* as an effective deterrent.

Multifunctional alarm pheromones are widespread in eusocial insects, particularly species of Hymenoptera and Isoptera. In ants and termites, characteristic monoterpenes such as limonene, pinene, citral, citronellal, and 6-methyl-5-hepten-2-one function as effective chemical deterrents and, in addition, releasers of alarm behavior. In ants and bees, 2-heptanone is utilized as an allomone-pheromone, as are 4-methyl-3-heptanone and 3-octanone in many ants.

Sex Pheromones as Parsimonious Agents

A variety of insect species have adapted secretory compounds with clearly established defensive functions that also serve as sex pheromones. In addition to defensive compounds, in some hymenopterous species these sexual pheromones constitute versatile releasers and primers of social behavior that are essential to colonial organization.

Pheromonal Parsimony in the Honey Bee

A mandibular gland product of the queen honey bee, *Apis mellifera*, has been demonstrated to possess a remarkable variety of functions both in the hive and outside the hive. *(E)*-9-oxo-2-decenoic acid (9-ODA), designated as queen substance, is used by the queen as both a releaser (rapid-active behavioral modification) and a primer pheromone (slow acting physiological modification). 9-ODA is distinctive in manifesting pheromonal activity with workers, virgin queens, and drones. In some cases, the pheromonal activity of 9-ODA is synergized by additional compounds in the queen's mandibular gland secretion, and in some cases these synergists are chemically related to 9-ODA.

Queen cell construction is inhibited by the queens' workers in the presence of 9-ODA and, in addition, other mandibular gland constituents including *(E)*-9-hydroxy-2-decenoic acid (9-HDA), an acid related to 9-ODA. Together, these two acids function as primer pheromones that inhibit queen cell construction, but neither acid is active alone. This inhibition is also expressed in workers by immature queens in queen cells. In all cases, the workers must have contact with the queen in order for her primer activity to be expressed.

In addition to inhibiting queen cell construction, 9-ODA possesses another important primer function. This acid, along with 9-HDA and other mandibular gland products of the queen, inhibits ovarian development of workers, provided that they have physical contact with the queen. In addition to these important roles as primer pheromones, the queen also regulates colonial functions by utilizing 9-ODA as a releaser pheromone for both workers and drones. 9-ODA is obviously a powerful mandibular gland product of the queen.

Honey bee queens produce an olfactory attractant for workers, signaling her presence to them. In essence, for worker honey bees this acid is both a powerful olfactant and a tactile stimulant. The versatility of 9-ODA as a chemical releaser of social behavior is demonstrated by its critical roles in the hive and in the exterior.

The formation of retinues, the attraction of workers to the queen in the milieu of the hive, is mediated by 9-ODA. Maximum retinue development occurs in the presence of high concentrations (about 70%) of 9-ODA in conjunction with several other mandibular products of the queen.

Swarming of honey bee colonies is regulated by a potpourri of compounds produced by both the queen and the workers. Swarm formation and movement are regulated by monoterpenes generated in the Nasanov gland secretion of workers. Cavities marked with this secretion are highly attractive to the swarming workers, which attracts other workers for possible nest-site selection. Swarm movement is enhanced by 9-ODA from the queen, which functions as a short-range attractant. By itself, 9-ODA has no swarm-orienting activity.

The parsimonious activity of 9-ODA is further revealed by its activity as a sex pheromone for flying drones in pursuit of queens. Large clusters of drones are attracted to single queens and multiple copulations are characteristic of the mating behavior of queens. Unlike other pheromonal contexts, 9-ODA, by itself, is highly attractive to drones in the aerial milieu.

Several species of Heteroptera (Hemiptera) have been shown to produce sex pheromones in glands clearly identified as defensive organs. Females of the mullein bug, *Campylomma verbasci*, produce sex pheromones in the metathoracic scent glands, characteristic heteropterous defensive organs. (*E*)-crotyl butyrate and butyl butyrate, typical defensive constituents of true bugs, function as highly active sex pheromones for males. In contrast, males of the alydid *Riptortus clavatus* have adapted metathoracic gland constituents to function as sexual attractants for females. Three esters, (*E*)-2-hexenyl-(*E*)-2-hexenoate, (*E*)-2-hexenyl (*Z*)-3-hexenoate, and myristyl isobutyrate, are clearly bifunctional, possessing activities both as sex pheromones and defensive allomones.

Defensive Secretions as Sexual Pheromones

A variety of insects have adapted defensive exudates to function as either female or male sex attractants. Since these sexual secretions still possess their original repellent functions, the evolution of these systems clearly constitutes extreme semiochemical parsimony. The use of characteristic defensive allomones as sex pheromones by species in at least four orders emphasizes the widespread exploitation of insect chemical defenses as sexual communicants.

Both sexes of the staphylinid beetle *Aleochara curtula* produce an effective insect repellent in the hypertrophied tergal gland. The glandular secretion is fortified with 1,4-benzoquinones, hydrocarbons, and aliphatic aldehydes, a formidable mixture of defensive allomones. Three compounds – *(Z)*-4-tridecene, dodecanal, and *(Z)*-5-tetradecenal – are powerful male attractants and release strong copulatory behavior in these insects. A female aphrodisiac sex pheromone from the epicuticular lipids acts synergistically with the tergal gland secretion. On the other hand, high concentrations of the tergal gland secretion function as a repellent for the beetles, the secretion thus acting as a repellent.

The defensive secretion of the grasshopper *Taeniopoda eques* has been adapted to function as a sex pheromone with an important temporal component. The secretion is synthesized in glands surrounding the metathoracic tracheal trunks and is stored in the tracheal lumina. The odoriferous defensive exudate is produced from the third instar on and constitutes the primary deterrent for a variety of vertebrate and invertebrate predators. Significantly, 16–18 days after adult eclosion the female of *T. eques* produces a potent sex pheromone in the tracheal defensive secretion. Sexual synchrony is achieved because the males respond to the sex pheromone about 16 days after adult eclosion.

A Highly Toxic Anhydride with Pronounced Vesicatory Parsimony

Cantharidin, the anhydride of cantharidic acid, is a well-recognized toxin that is only known to be produced by beetles in the families Meloidae and Oedemeridae. Thus, this relatively simple natural product is distinctive in being both a very rare exocrine compound and, in addition, a singular terpene whose toxicological effects are more pathological than any known compound produced by insects.

Beetles in the family Meloidae, the major family producing cantharidin, are frequently referred to as "blister beetles" because of the pronounced lesions that result from dermal contact of these insects with human beings. While cantharidin (or a meloid) can constitute a powerful external vesicant, its pathogenicity upon ingestion can be particularly devastating, usually resulting in the lining of the tongue, throat, and palate peeling away. Internal injuries can rapidly eventuate in death as the corrosive effects of cantharidin are manifested. Unlike most corrosive poisons, the deleterious effects of cantharidin are not instantaneous, and the lag in apparent poisoning is a prelude to detecting the pathological action of the ingested terpene.

Cantharidin is released from the beetles suspended in blood by a process referred to as reflex bleeding. Weakened cuticular areas in the legs "bleed," and accumulated droplets of cantharidin-fortified blood from the stimulated leg can be wiped on adversaries with effective repellent results. This defensive method is not harmful to the beetles unless inordinate amounts of blood are lost as a consequence of extensive reflex bleeding. Clearly, the vesicatory properties of the anhydride make it a powerful vertebrate repellent. On the other hand, cantharidin, topically applied to pigs and humans, effected remission of epidermal cancer. This terpene also is an effective feeding deterrent for insects, and its functional parsimony is further demonstrated by the fact that it is a selective herbicide.

Invasive fungi such as *Trichophyton* and *Microsporum* species are inhibited by cantharidin, and it has been suggested that this anhydride plays an important role in protecting meloid eggs, which are incubated in fungal-rich moist environments. The egg of a meloid beetle is fortified with enough cantharidin to act as a vesicant, a fact that is consistent with its suggested role as a fungicide. Significantly, the cantharidin with which the female treats the eggs is a copulatory bonus, derived from the seminal ejaculate of the male, delivered at copulation. The adult female does not synthesize cantharidin, and the male ejaculatory contribution is not only critical reproductively, in terms of spermatozoa, but defensively as both a predator deterrent and an antifungal agent applied to the eggs as an inhibitor of entomopathogenic fungi.

Multifunctional Venom Alkaloids

Insect venoms are generally endowed with high concentrations of proteins that are often identified with allergic reactions in individuals that have been stung. On the other hand, hymenopterous species in a variety of genera produce venoms that are thoroughly dominated by non-proteinaceous compounds that often possess diverse biological activities. Recent studies have demonstrated that these venomous constituents are often identified with considerable multifunctionality. In essence, their poison gland products have been evolved to demonstrate great parsimony in the biological milieu.

Ants in the genus *Solenopsis* synthesize mixtures of 2,6-dialkylpiperidines, and in general, the venom composition may constitute 95% of these distinctive nitrogenous compounds. The major constituents in these venoms are alkaloids that are related to coniine, the hemlock-derived alkaloid that was drunk by Socrates as an imposed suicide. 2,6-Dialkylpiperidines are found in the venoms of species in several genera and, in the case of species in a single genus such as *Solenopsis*, these alkaloids are qualitatively distinctive. These alkaloids are present as *cis-trans*-mixtures with one or the other isomers invariably predominating. A variety of alkaloids are present due to the fact that the 6-alkyl group on the piperidine ring may be C_9, C_{11}, C_{13}, $C_{13:1}$, C_{15}, $C_{15:1}$, and $C_{17:1}$. In all cases, these alkaloidal venoms are products of ant species in the subfamily Myrmicinae, which includes the aggressive fire ants, whose common name refers to the reaction of humans to the "hot" stings delivered by the workers attacking *en masse*.

Injection of the venom by stinging ant workers results in rapid dermal necrosis, accompanied by the development of pruritic and sterile pustules. These reactions to the venomous alkaloids are also accompanied by considerable algogenicity, as a consequence of the liberation of histamine from mast cells. The alkaloids also have a rapid lytic effect on rabbit erythrocytes, instantly hemolyzing these cells. In addition, the piperidines possess considerable pharmacological activities that further emphasize their parsimonious toxicological functions. These include the inhibition of ATPases, uncoupling of oxidative phosphorylation, reduction of mitochondrial respiration, and blocking of neuromuscular junctions. These activities, directed against vertebrates, demonstrate that these venomous constituents target a considerable variety of biochemical systems in implementing their toxicity. However, the semiochemical parsimony of these cyclic compounds is further demonstrated by their toxic activities against a variety of microorganisms, fungi, and insects.

The alkaloids possess well developed antifungal and antibacterial activities and, in addition, these cyclic compounds are phytotoxic and strongly insecticidal. The antifungal activities of the alkaloids are very adaptive, since the interior of *Solenopsis* colonies is both humid and warm, environmental conditions that are very conducive to the growth of entomopathogenic fungi. Workers treat their larvae with alkaloids, and fire ant queens apply venom to their eggs, and in both cases the antifungal activities of the alkaloids are of great significance.

The insecticidal activities of the alkaloids are quite pronounced, and in the case of termites these venomous constituents are comparable in toxicity to some commercial insecticides. The alkaloids are very repellent to other species of ants; ant-ant competition for resources should strongly favor the piperidine secretors. In addition, the workers can discharge venom through the air by a phenomenon known as gaster flagging, a highly adaptive mechanism for repelling heterospecifics. The diverse pharmacological activities of the *Solenopsis* alkaloids, in combination with the insecticidal and antifungal properties of these cyclic piperidines, further emphasizes the great semiochemical parsimony of these compounds.

► Allelochemicals
► Alarm Pheromones
► Pheromones
► Sex Attractant Pheromones
► Social Insect Pheromones

References

Blum MS (1981) Chemical defenses of arthropods. Academic Press, New York, NY, 232 pp

Blum MS (1996) Semiochemical parsimony in the Arthropoda. Annu Rev Entomol 41:353–374

Buschinger A (1972) Giftdrussensekret als sexual pheromon bei der ameise *Harpagoxenus sublaevis*. 313–314

Koch RB, Dessaiah D, Ahmed K (1977) Effect of piperidines and fire ant venom on ATPase activities from brain homogenate fractions and characterization of Na + -K + ATPase inhibition. Biochem Pharmacol 26:983–985

Schmidt JO, Slessor KN, Winston WL (1993) Roles of Nasanov and queen pheromones in attraction of honeybee swarms. Naturwissenschaften 80:573–575

Multiparasitism

Attack of an insect by two or more species of parasitoids (multiple parasitism).

Multiple Resistance (to pesticides)

The resistance of an organism to a number of different pesticides, requiring different mechanisms of counteracting their effects.

Multivoltine

Having several generations per year.

Mummy

The remains of an aphid whose insides have been consumed by a parasitoid. A dried, shriveled fruit or nut.

Murine Typhus

A rickettsial disease (*Rickettsia typhi*) affecting primarily rats, but sometimes transmitted from rats to humans by fleas and rat lice through their feces. The insects are not affected, and the mortality rate is low in humans less than 50 years old. It is also known as "endemic typhus."

► Lice

Murray Valley Encephalitis

An arbovirus transmitted by mosquitoes and indigenous to Australia and Papua New Guinea. It also is known as Australian encephalitis, and is harbored in wading birds. It is caused by a virus in the family Flaviviridae. It causes fever, nausea, seizure, diarrhea, lethargy and confusion. Most victims do not suffer significant symptomology, but of those that do, severe neurological damage may occur.

► Mosquitoes
► Mosquitoes as Vectors of Viral Pathogens

Musapsocidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice or Psocids

Muscardine

A term used generally in connection with those mycoses of insects in which the fruiting of the pathogenic fungi arise on the exterior of the insect. A number of fungi are capable of causing this condition.

► Fungal Pathogens of Insects

Muscid Flies

Members of the family Muscidae (order Diptera).

► Flies

Muscidae

A family of flies (order Diptera). They commonly are known as muscid flies.

► Flies

Muscoid Larva

A larval body form that is headless, and spindle-shaped or cylindrical and truncate. It occurs in most Diptera.

Mushroom Bodies

Fiber tracts within the protocerebrum, also known as the corpora pendunculata, that are major integrative centers.

► Nervous System

Musk Thistle Suppression Using Weevils for Biological Control

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Musk thistle, *Carduus thoermeri* Weinmann = *Carduus nutans* L. (Campanulatae: Asteraceae) is an invasive Eurasian weed that has become widespread in the contiguous United States. It reproduces by seed and was first reported in the United States in 1953 in Harrisburg, Pennsylvania. Being a highly competitive weed, it has replaced much of the native vegetation in pastures, rangelands, croplands, and along state highways in many parts of the USA and Canada. Its success is due to its prolific seed production, seed longevity, and lack of natural enemies to suppress it. As it spread rapidly in the absence of any native insects capable of suppressing it, the United States Department of Agriculture started a program in search of its natural enemies in Italy in the early 1960s. The Canada Department of Agriculture provided funds for the Commonwealth Institute of Biological Control (now CABI Bioscience) to extend the search across Europe from western France to Austria. As a result of this search, selected insects were imported and screened under quarantine to determine their development and feeding range (host specificity). Two imported weevils that passed the screening tests were subsequently released and have become well established in North America for musk thistle control.

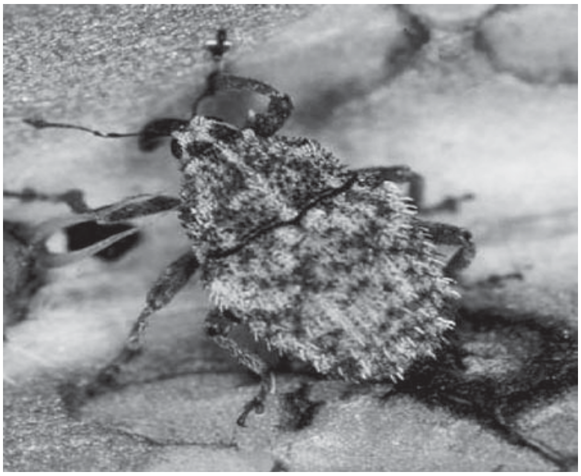
Rhinocyllus conicus Froel (Coleoptera: Curculionidae)

This was the first insect released in North America for musk thistle control. It was collected from the Rhine Valley in France and released in Canada in 1968. In 1969, it was introduced into California, Virginia and Montana, and subsequently relocated to many of the other contiguous states in the United States. This weevil is a native of southern and central Europe, North Africa, and western Asia between latitude 30 and 52 north. The adults are dark brown in color and 10–15 mm long. The adult hibernates in winter and becomes active again in mid to late April. Soon after emerging in spring, the female starts to lay eggs on the bract leaves of thistle heads. Each female lays about 100–200 eggs. The eggs are brown specks 0.5–1 mm in diameter, and hatch in 6–9 days. Newly hatched grubs (larvae) feed through the bracts and into the base of the developing thistle bud. Thus, it is often referred to as the thistle head weevil. Feeding by the weevil grubs prevents the production of viable thistle seeds. Many grubs feed and complete development to the quiescent (pupa) stage in about 6 weeks within a thistle head. It is during this feeding stage that the thistle heads are destroyed and fail to produce the usual number of seeds. The quiescent stage is spent inside the thistle head, where many pupation chambers are formed. Each full-grown grub forms a pupation chamber for its development into a pupa. The quiescent stage lasts for 7–10 days before emergence of the next generation adult weevil. The new adults emerge in July/August and do not stay on the plants for very long. They seek shelter from the summer heat and pass the summer in one place in a state of torpor or inactivity, and then hibernate in the winter to emerge in the spring at the time of thistle elongation. There is usually one generation a year. Once it has become successfully established, this thistle head weevil can suppress musk thistle stands in 5–6 years (Fig. 112).

Trichosirocalus horridus (Panzer) (Coleoptera: Curculionidae)

This was the second weevil released for thistle control in North America. It is native to south and central Europe. Unlike the first weevil, this insect feeds on the crown tissues of thistles in the rosette stage, before plant elongation. This crown or rosette weevil was imported from Rome, Italy, into the USA in 1970–1972 for quarantine tests to determine what type of plants it would feed on. Thirty-five species of plants from seven families, including 12 economically important crop plants were tested. After undergoing 3 years of intensive testing, it was found to feed only on a narrow range of plants and would not be a threat to non-target plants. It was officially approved for field release in Virginia in June 1974. It became established in Virginia in 1977 and has since been relocated to many of the mainland states. This weevil passes the winter in the adult, egg, and grub stages. The adult is about 10 mm long and emerges in late winter and early spring. It lays eggs within the mid-rib on the underside of the leaves, usually in clusters of two or three. The eggs hatch in 10–12 days and the young grubs feed within the mid-rib towards the center growth point of the thistle rosette. The grubs reach the thistle crown in about 7 days and continue feeding within the same place causing localized death of the crown tissues. On completion of feeding in 6–8 weeks, the full-grown grub leaves the plant and changes into the pupa in the soil within a chamber made from soil particles and organic matter. The quiescent (pupa) stage lasts for 12–20 days. The newly emerged weevil is reddish in color, and it changes to dark brown and black with time. The new generation of adults appears in May and June, and goes into heat induced inactivity in July until the fall, when they emerge to feed. Some females begin to lay eggs until the first frost. There is usually one generation per year. Successful suppression of musk thistle by this weevil takes 4–6 years (Fig. 113).

Musk Thistle Suppression Using Weevils for Biological Control, Figure 112 **Thistle head weevil, *Rhinocyllus conicus* adult.**



Musk Thistle Suppression Using Weevils for Biological Control, Figure 113 **Thistle rosette weevil, *Trichosirocalus horridus* adult.**

With the successful field establishment of these two weevils, thistle reductions exceeding 90% of the original density have been achieved in many of the release sites. Because they attack different growth stages of the thistle plant, these two weevils complement each other. Successful biological control of musk thistle is partly due to the good synchronization of plant growth and insect activity. Long term trend lines of musk thistles at sites under study have shown distinct declines in thistle populations despite some occasional spikes due to resurgence of the weed population. Factors that cause resurgence of thistles include: (i) dumping soil with thistle seeds into the site, (ii) exposing soil when trenches are dug in the field, (iii) overgrazing leading to bare patches of soil where thistle seeds can germinate, or (iv) frequent sharp temperature fluctuations during the winter that result in high mortality of the weevils during winter. Also, cool temperatures which favor thistle growth in spring, but inhibit weevil activity, could lessen sustained pressure on the weed. Despite such occurrences that cause temporary resurgence of thistles, the established weevils eventually regain control. Both weevils are highly successful in controlling musk thistle. Their impact is evident after 5 or 6 years of establishment. In places where the weevils multiply rapidly, a dramatic decline in musk thistle is possible after 2 or 3 years. Thistle suppression also is enhanced by planting tall fescue grass in thistle-infested land or pastures in conjunction with the use of weevils. The fescue grass is able to effectively compete against thistles, especially when the latter is weakened by the weevils.

References

Kok LT, Surles WW (1975) Successful biocontrol of musk thistle by an introduced weevil, *Rhinocyllus conicus*. Environ Entomol 4:1025–1027

Kok LT, Ward RH, Grills CC (1975) Biological studies of *Ceuthorhynchidius horridus* (Panzer), an introduced weevil for thistle control. Ann Entomol Soc Am 68:503–505

Kok (1986) Impact of *Trichosirocalus horridus* (Coleoptera: Curculionidae) on *Carduus* thistles in pastures. Crop Prot 5:214–217

Kok LT (1998) Biological control of musk and plumeless thistles. Recent Res Dev Entomol 2:33–45

Sieburth PJ, Kok LT, Lentner M (1983) Factors influencing the effectiveness of *Trichosirocalus horridus* (Coleoptera: Curculionidae) in the control of *Carduus* thistles. Crop Prot 2:143–151

Mutagen

A chemical or physical agent able to induce a mutation in a DNA molecule.

Mutant

An organism expressing the effects of a mutated gene in its phenotype.

Mutation

A change in the nucleotide sequence of a DNA molecule. Mutations can involve duplications, deletions, inversions, translocations, and substitutions.

Mutillidae

A family of wasps (order Hymenoptera). They commonly are known as velvet ants.

► Wasps, Ants, Bees and Sawflies

Mutual Interference

Interference among predators leading to a reduced consumption rate by individual predators.

Mutualism

An association between different types of organisms that benefits both.

Mycangium

In bark beetles, a pocket-shaped receptacle used to carry symbiotic fungi.

Mycelium

The hypha or mass of hyphae that constitutes the body of a fungus.

Mycetocyte

A cell containing intracellular mutualistic and commensalistic microsymbiotes; one of many cells making up the mycetome.

Mycetome

In various invertebrate animals, the structure or organ which houses symbiotes; the cells making up the mycetome and containing the symbiotes are known as mycetocytes.

Mycetophagidae

A family of beetles (order Coleoptera). They commonly are known as hairy fungus beetles.

► Beetles

Mycetophilidae

A family of flies (order Diptera). They commonly are known as fungus gnats.

► Flies
► Fungal Gnats

Mycosis

Any disease caused by the presence of fungi.

Mycotoxin

A toxin produced by fungi.

Mycteridae

A family of beetles (order Coleoptera). They commonly are known as palm beetles.

► Beetles

Mydas Flies

Members of the family Mydidae (order Diptera).

► Flies

Mydidae

A family of flies (order Diptera). They commonly are known as mydas flies.

► Flies

Myerslopiidae

A family of bugs (order Hemiptera, suborder Cicadomorpha).

► Bugs

Myiasis

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This term was first used in 1840 to refer to human diseases originating from dipterous (fly) larvae. More recently, it has been described as the infestation of live vertebrate animals with fly larvae, which, at least for a certain period, feed on the host's dead or living tissue, liquid body substances, or ingested food. Myiasis begins when gravid female flies are attracted by the odors of infested wounds, decaying organic matter, feces, urine, and human food, where they deposit larvae or eggs. There are two principal ways to classify myiasis: entomologically and anatomically.

An Entomological Classification of Myiasis

Myiasis can be classified according to the relationship or level of dependence between the larvae and the host:

Specific or Obligatory Myiasis

This is caused by flies that can develop only on live hosts. Included in this group are members of Oestridae and Sarcophagidae.

Semi-Specific or Facultative Myiasis

This is caused by facultative or opportunistic parasitic flies with larvae that usually develop on decaying organic matter, but with adults that also may deposit their larvae or eggs in live tissues. There are two levels: primary myiasis, wherein the flies are able to initiate myiasis (they attack living tissues) or they can invade living tissue after other species have initiated the myiasis; and secondary and tertiary myiasis, which occurs when the host is nearly dead. Flies in this category include members of Calliphoridae and Phoridae.

Accidental, Pseudomyiasis or False Myiasis

Larvae of these species are normally free-living and non-parasitic, but may be ingested accidentally. This happens when flies deposit eggs on food with pungent odors, eggs hatch, and larvae are ingested. Once ingested, they can pass through the digestive tract without being digested, and cause abnormal digestive reactions in hypersensitive hosts. They also can develop directly in feces or urine-impregnated materials, or badly stored food. Accidental myiasis is usually caused by flies in the family Muscidae. It is important to be able to distinguish these larvae because in sensitive hosts, they can produce digestive disorders, causing symptoms similar to food poisoning. Also, larvae can be found in feces or improperly washed clothing of babies, and produce cases of false parasitism.

An Anatomical Classification of Myiasis

Myiasis also can be classified according to anatomical position, or location, in and on the host.

Dermal or Subdermal Myiasis

In this condition, larvae are found between the epidermis and dermis. Invasion of animal or human skin tissues by the larvae causes tunnels or boils in the dermal layers, and the flies may invade and enlarge existing wounds, or even form wounds themselves. This condition has also been called foruncular, traumatic or cutaneous myiasis. Flies in the families Calliphoridae and Sarcophagidae produce dermal and subdermal myiasis, particularly *Cochliomyia hominivorax*, *Chrysomya bezziana*, *Ch. albiceps*, *Lucilia sericata*, *Calliphora vicina*, *Phormia regina*, *Protophormia terraenovae* and *Wohlfahrtia magnifica*. Also, the fly *Megaselia ruficeps* (Phoridae) is a facultative parasite with larvae that can invade wounds or foul-smelling sores.

Intermedia Anatomical Position Myiasis

Some species of Oestridae cause myiasis of rodents, lagomorphs, and also humans in North

America. Larvae create boil-like swellings on the skin. The most important is *Dermatobia hominis*. It is an important cattle pest in Central and South America, and also affects humans. In Africa, *Cordylobia anthropophaga* (Calliphoridae) causes African foruncular myiasis, a condition very similar to that caused by *Dermatobia hominis* in the western hemisphere, in dogs, other domestic animals, and humans.

Creeping Myiasis

Larvae of Oestridae also can create a condition called creeping myiasis. These are able to move long distances within the host's body, and typically are found in different anatomical positions. The following arrangement has the fly species sorted by site of larval development:

Ocular Myiasis

The eye is invaded by *Oestrus ovis*, *Rhinoestrus purpureus*, *Megaselia scalaria*, *Wolfahrtia magnifica* and *Sarcophaga carnaria*.

Aural Myiasis

The ear is invaded by *O. ovis* and *W. magnifica*.

Nasal Fossae (nostrils), Mouth, Frontal Sinuses Myiasis and Surface of Brain

Flies associated with these tissues are *W. magnifica*, *S. carnaria*, *Calliphora vomitoria*, *O. ovis* and *R. purpureus*, *Cephalopina titillator*.

Urogenital, Anal and Vaginal Myiasis

Flies associated with these tissues are *W. magnifica*, *S. carnaria* and *Sarcophaga haemorrhoidalis*.

Migratory Myiasis

This condition is displayed by *Hypoderma* spp., the larvae of which migrate from oviposition sites by subcutaneous routes and in nerve tissues to the back, where they develop into "warbles" which spoil the host's hide.

Intestinal Myiasis

This is caused by *Gasterophilus* spp. developing in the digestive tract of horses. This condition can be found worldwide.

Atypical Sanguinivorous Myiasis

This unusual condition is caused by the ectoparasitic African fly *Auchmeromyia luteola* (Calliphoridae). Larvae do not live on, or in, the host because the female deposits her eggs on the soil floor of primitive huts. There, larvae suck the blood of sleeping humans. They also feed on burrow-dwelling animals. After feeding, the larva returns to the soil.

Diagnosis

Diagnosis of myiasis is normally based on larval characteristics, though it may be possible to raise the adults. Females deposit eggs (oviparous species) or larvae (larviparous). They may select organic matter for oviposition (accidental parasites) or a wound, mucous membrane or natural body opening (obligate parasites). Larvae immediately begin to feed by burrowing into the tissues (obligate parasites) or in the soil (accidental parasites). When they feed in the tissues, the wounds are enlarged and deepened, resulting in extensive tissue destruction. The larvae lack legs (a), and are pointed at the anterior (head) end, and broader and truncate at the posterior end. The larvae molt twice, resulting in three instars. At the end of the third instar, the mature larva leaves the tissues, falls to the ground, and burrows into the ground to pupate. Flies pupate within the old cuticle of the third instar larva, a structure called a puparium. Adult flies emerge from the puparium, feed and mate, and commence reproducing.

The head of larvae of cyclorraphous flies (infraorder Cyclorrapha, the "higher" flies) is greatly reduced; the antennae, palpi maxillae, and labium are scarcely visible. A cephalopharyngeal skeleton is evident (b) in developing larvae, and sometimes varies among species. It consists of the anterior-most mouth hooks or mandibular sclerite, which articulates with the hypostomal or intermediate sclerite, behind which is the much larger basal or pharyngeal sclerite. In carnivorous species, other small accessory oral sclerites are present (Fig. 114).

For a specific diagnosis, the posterior spiracles, found in the last abdominal segment of the third instar (c), should be used. This segment should be removed with a scalpel under a stereomicroscope. The spiracles should be removed from the cavity, and excess tissue removed. They should be placed on a slide with a drop of water and examined with a light microscope. The following structures should be examined in order to make a correct diagnosis: the ecdysial scar, interspiracular processes, peritremal ring, spiracular plate, and spiracular openings (d) (Fig. 114).

The Taxa Responsible for Myiasis

Following is a list of the principal families, genera, and species of flies known to cause myiasis. After each genus, the tissue of the host affected by the flies is designated as AT/F = alimentary tract/excreted with the feces; BS = blood-sucking; D = dermal layers; HC = head cavities; UO = urogenital organs.

Family Calliphoridae – Blowflies or Bluebottle Flies

Genus *Auchmeromyia* Brauer and Bergenstamm (BS)

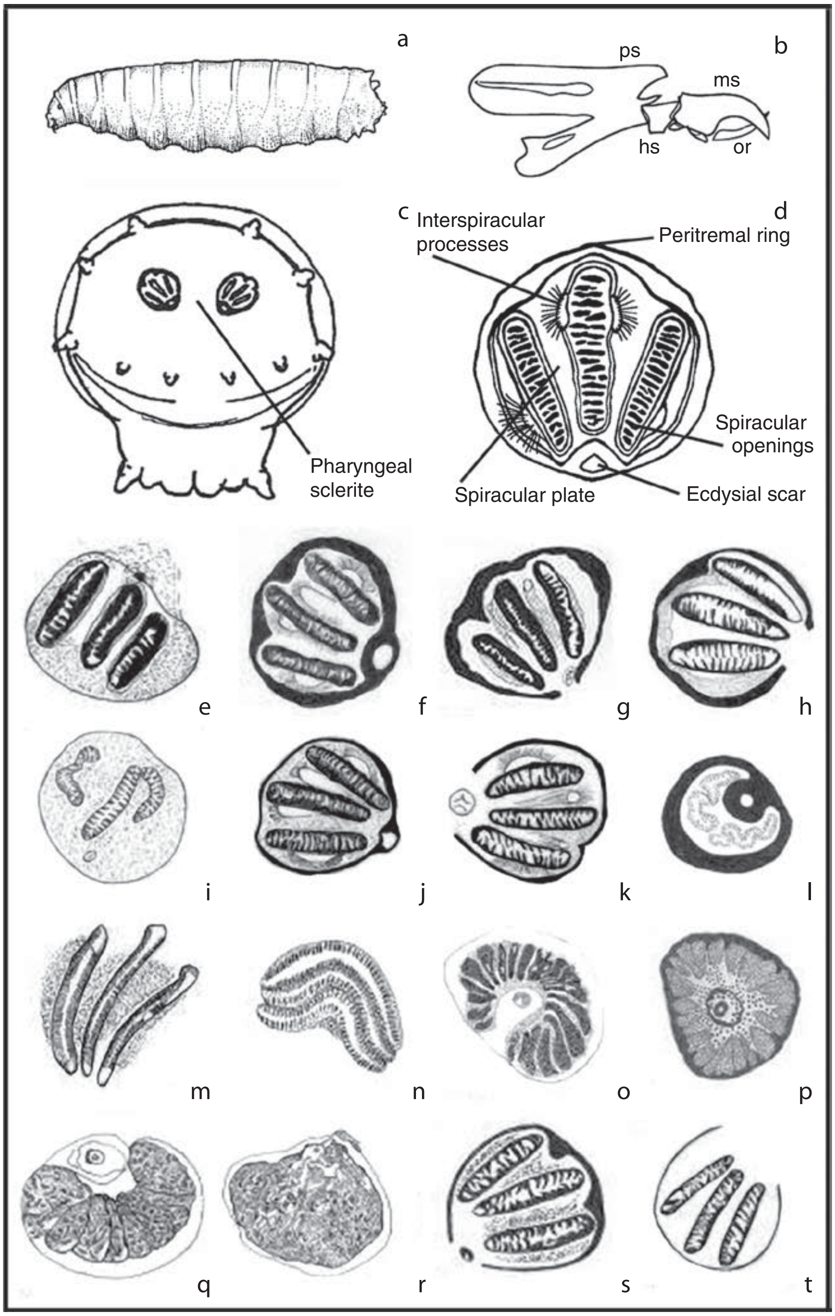
A. bequaerti
A. choerophaga
A. luteola (Congo Floor Maggot)
A. redi

The Auchmeromyia species are African, with *A. bequaerti* and *A. luteola* distributed in the Congo, and *A. redi* present in the Sudan. The adults are 8–13 mm in length, with a yellow-brown or orange body and legs. The distal part of abdomen is black. The diet of the adults appears to be human feces and fermented vegetables. Females also are attracted to wild animal feces. There are three larval stages. All they are blood-sucking. The red ingested blood shines through the body-well. Under normal conditions a meal is taken every night. *Auchmeroyia choerophaga* and *A. redi* do not normally enter human habitations and live in association with wild animals, though *A. luteola* attacks humans. The mature larvae attain a length of 18 mm, with 12 body segments. Laterally, they each bear two or more protuberances with a spine directed posteriorly and a small pit. The ventral portion of the body is flattened. The last body segment bears five pairs of finger-like protuberances. In the posterior spiracle region, the two small perimetral plates are widely separated (e).

Genus *Calliphora* Rob-Desvoidy (Bluebottle Flies) (D; AT/F; UO)

C. albifrontalis
C. augur
C. croceipalpis
C. erythrocepala
C. hilli
C. hortona
C. icela
C. nociva
C. nothocalliphoralis
C. quadrimaculata
C. stygia
C. vicina
C. vomitoria

The *Calliphora* species are cosmopolitan. *Callipora icela* and *C. nothocalliphoralis* are present in New Zealand sheep; *C. nociva*, *C. quadrimaculata* and *C. stygia* are found in Australian sheep. There are certain similarities among the species: *C. albifrontalis*



Myiasis, Figure 114 **Characters used to identify fly larvae causing myiasis: (a) typical maggot, with the anterior end pointed and the posterior end blunt; (b) cephalopharyngeal skeleton (ms, mandibular sclerite; ps, pharyngeal sclerite; hs, hypostomal sclerite; os, oral sclerite); (c) view of the posterior end of a cyclorraphous maggot; (d) close-up of posterior spiracle; (e) spiracle of *Auchmeromyia* sp.; (f) spiracle of *Calliphora* sp.; (g) spiracle of *Chrysomya* sp.; (h) spiracle of *Cochliomyia* sp.; (i) spiracle of *Cordylobia* sp.; (j) spiracle of *Lucillia* sp.; (k) spiracle of *Prophormia* sp.; (l) spiracle of *Musca* sp.; (m) spiracle of *Cuterebra* (*Dermatobia*) sp.; (n) spiracle of *Gasterophilus* sp.; (o) spiracle of *Hypoderma* sp.; (p) spiracle of *Cephalopina* (*Oestrus*) sp.; (q) spiracle of *Pharyngomyia* sp.; (r) spiracle of *Rhinoestrus* sp.; (s) spiracle of *Sarcophaga* sp.; (t) spiracle of *Wohlfahrtia* sp.**

is similar to *C. hilli* and *C. stygia*; *C. augur* is similar to *C. nociva*; *C. croceipalpis* is similar to *C. vicina*; *C. hortena* is similar to *C. quadrimaculata*. The adults are 5–12 mm in length, with a black thorax and legs. The abdomen is a dark metallic blue color. The female's eyes are further separated than that of the male. In both sexes, the buccae are yellow or orange, darkened posteriorly. The females are attracted to decaying matter for oviposition. Most species are oviparous, but some deposit larvae, and others deposit eggs if the weather is cool and larvae during hot months. *Calliphora vicina* may be a primary invader, though *C. vomitoria* is involved only in secondary myiasis. There are three larval instars. The mature larvae are about 19 mm in length, with twelve body segments, and with spinose bands characteristically arranged according to species. The cephaloskeleton bears an accessory oral sclerite. Each posterior spiracle is in a closed peritreme which shows an ecdysial scar and three slits (f).

Genus *Chrysomya* Rob-Desvoidy (Old World Screwworm Fly) (D; AT/F; UO)

C. albiceps
C. bezziana
C. chloropyga
C. inclinata
C. mallochi
C. marginalis
C. megacephala (Oriental Latrine Fly)
C. putoria
C. rufifacies
C. varipes

The *Chrysomya* species are restricted to Europe, Africa, Asia, and the Australian region. *Chrysomya albicens* is present in northern Africa, southern Europe and northwestern India; *C. chloropyga* is an African species; *C. inclinata* is found in Africa; and *C. mallochi* occurs in Australia and New Guinea. *Chrysomya marginalis* is common in human and animal wound myiasis in Kenya and Madagascar; *C. megacephala* is a Chinese, Japanese and Australian species; *C. putoria* was reported in Guinea (Africa); *C. rufifacies* is a species of Australasia and the Orient; and *C. varipes* is an Australian species. *Chrysomya* in the Old World is the ecological equivalent of Cochliomyia in the New World. There are some similarities among species: C. mallochi is similar to *C. megacephala* and *C. putoria* is close to *C. chloropyga* and *C. rufifacies*. The adults are 5–10 mm in length. They possess a metallic green body, with blackish bands in the posterior margin of the abdominal segments, and with reddish-brown to blackish legs. The buccae are partially yellow. *Chrysomya albiceps* is a facultative species, normally laying eggs on carcasses, but the adult can deposit larvae on wounds. It is involved in secondary myiasis of sheep. *Chrysomya bezzina* is an obligate parasite in wounds. Females oviposit on live mammals, in wounds or body orifices (ear, nose or urogenital orifices).

The mature larva is about 18 mm in length, and possesses long processes on the dorsal and lateral sides of the body. The ventral processes are shorter. *Chrysomya albiceps* and *C. rufifacies* have fleshy body projections; those of *C. varipes* are smaller. In the posterior spiracle region the peritremal ring is broadly open (g). The ecdysial scar is present or absent according to species. Larvae hatch and molt twice. Larvae then drop to the ground to pupate. Myiasis has been found in humans, cattle, water-buffalo, sheep, goats, horses, donkeys, dogs, camels and elephants. *Chrysomya chloropyga* is involved in primary and secondary myiasis; *C. inclinata* and *C. marginalis* are common in carrion, but rarely have been found in wound myiasis. *Chrysomya putoria* has been involved in primary and secondary myiasis; *C. putoria* was reported in Guinea in a case of traumatic myiasis. *Chrysomya megacephala* has been found in large numbers around latrines because they breed in feces and other decomposing organic matter. They also are present near slaughter-houses, and open-air meat and fish markets. They can accidentally produce human and animal wound myiasis in Africa. *Chrysomya varipes* is a carrion-breeder, and also is temporarily predatory on other fly larvae.

Genus *Cochliomyia* Townsend (New World Screwworm Flies) (D)

C. americana
C. hominivorax
C. macellaria

This genus is the New World equivalent of the genus *Chrysomyia* in the Old World. *Cochliomyia homnivorax*, formerly found in the United States, Mexico, and northern Africa, it is now restricted to portions of Central and South America. It was eradicated from most of North America and from Africa by continuous release of sterile male flies. *Cochliomyia hominivorax* females lay their eggs on the wounds of humans and animals. In contrast, *C. macellaria* is a secondary invader, and generally is present only in carrion. The posterior spiracle can be seen in (h).

Genus *Cordylobia* Grünberg (African Tumbu Fly) (D)

C. anthropophaga
C. rodhain
C. ruandae

Cordylobia anthropophaga is found in Africa south of the Sahara. It is a myiasis-causing fly similar to *Dermatobia hominis* from the Americas. The adult measures 6–12 mm in length. It is a stout, yellow-brown fly bearing black, undefined bands on the thorax and abdomen. The legs and face are yellow. The mature larva is 13–15 mm in length, with a cephaloskeleton bearing two projecting, hook-shaped labial sclerites. The posterior spiracles consist of three sinuous slits situated on a weakly sclerotized peritreme (i). Larvae cause foruncular (cutaneous) myiasis in dogs, rats and humans. *Cordylobia rodhain* parasitize wild animals and humans. The pupae of *C. ruandae* are found in tree-nests of the rodent *Grammomys dolichurus* (Forest Mouse).

Genus *Lucilia* Rob-Desvoidy (Greenbottle Flies) (D)

L. ampullaceal
L. bufonivor
L. caesar
L. cuprina
L. illustris
L. porphyrin
L. richardsi
L. sericata
L. silvarum

The *Lucilia* species are widespread. *Lucilia caesar* is found in North and South America, Australia and New Zealand. *Lucilia cuprina* is responsible of wound myiasis in South Africa and Australia, and *L. illustris* in North America. *Lucilia porphyrin* has been found in India; *L. richardsi* is common in Great Britain, Finland and France and *L. sericata* occurs in Europe and North America. *Lucilia ampullacea* and *L. illustris* have been confused with *L. caesar*. *Lucilia porphyrin* is similar to *L. ampullacea*, and *L. richardsi* to *L. sericata*. Adults are 5–10 mm in length. The adult fly is metallic-coppery green. Females lay their eggs on carcasses, in neglected, suppurating wounds, and in sheep wool soiled by urine, feces or blood, in which the larvae can complete its development. Other animals affected are horses, cattle and humans. *Lucilia ampullacea*, *L. caesar* and *L. illustris* breed in carrion. The adults are diurnal. Females need a protein-containing meal for the eggs to mature. *Lucilia bufonivora* is an obligatory parasite of amphibians. The mature larva attains a body length of up to 16 mm. The posterior spiracles possess a narrow peritreme which, in fully sclerotized specimens, shows inner tubercles on the upper margin of the posterior cavity approximately equal to the distance between the inner and median ones (j).

Genus *Phormia* Rob-Desvoidy (D)

Ph. regina
Ph. terraenovae

Phormia species occur in the New World. *Phormia regina* is present in the southern United States, whereas *Phormia terraenovae* is common in northern Canada. *Phormia regina* usually breeds in carrion, and possibly can be found in wounds. *Phormia terranovae* is saprophagous, and prefers low temperatures and high altitudes for breeding. The adults possess a black or bluish-green thorax and abdomen.

Genus *Protophormia* Townsend (D)

Pr. terraenovae

Protophormia terranovae is found in the cooler parts of the Holarctic region, and is involved in wound myiasis in Europe and North America. It breeds in carrion or wounds, attacking cattle, sheep and reindeer. *Pr. terranovae* appears in the early sprints. Several samples also have been found in bird's nests, causing myiasis in the nestlings. It has been taken within 550 miles of the North Pole. Adults are 6–11 mm in length. They possess a dark metallic blue, green or black body with black legs. The mature larvae are 17 mm in length. The posterior segment bears fairly pointed tubercles. The posterior spiracle shows a weakly developed ecdysial scar.

Family Muscidae – (Houseflies)

Genus *Musca* Linnaeus (D; AT/F; UO)

M. crassirostris

M. domestica

M. hilli

The distribution of *Musca* species is variable, with *M. domestica* cosmopolitan in distribution, whereas *M. hilli* is found in Australia. *Musca hilli* is similar to *M. domestica*, and they measure 6–9 mm in length. These species are not involved in traumatic myiasis cases. *Musca crassirostris* breeds in cow and horse dung. *Musca domestica* can serve as a mechanical vector of disease, but the larvae feed and molt in decomposing organic matter. *Musca domestica* has a remarkably high reproductive capacity; it is estimated that (in the absence of mortality) a population of 100 eggs hatching on the 1st of May could reach 4,000 trillion specimens on the 30th of September. The larval length is about 12 mm, and the larva is creamy white. The posterior spiracle region has three tortuous slits.

Family Oestridae-(Bot and Warble Flies)

The family Oestridae now is considered to contain a large number of species, including some that formerly comprised the families Cuterebridae, Gasterophilidae and Hypodermatidae; these former families are now considered to be subfamilies.

Genus *Cephalopina* Strand

C. titillator (Camel Nasal Bot Fly)

Cephalopina is a small genus, with only *C. titillator* considered important. It is an obligate parasite, causing nasal myiasis in camels.

Genus *Cuterebra* Clark

The *Cuterebra* species, of which there are many, occur only in North America. In appearance and biology, they are very similar to *Dermatobia*. They are found beneath the skin of rabbits, rodents, cats and dogs, but rarely in humans.

Genus *Dermatobi*a Brauer

D. hominis

Dermatobia species occur in Central and South America. Only *D. hominis* is important. The adult is 15–18 mm in length, with a yellow and black face, black and blue thorax, and metallic blue and violet abdomen. The larvae are found beneath the skin, and produce large swellings. The female uses blood-feeding arthropods, primarily mosquitoes but also ticks, to transfer eggs to the skin of humans and other animals, cattle, dogs, pigs, and cats. The posterior spiracle can be sen in (m).

Genus *Gasterophilus* Leach (Dark-Winged Horse Bot Flies) (D; AT/F)

G. equi

G. flaviceps

G. gedoelsti

G. haemorrhoidalis

G. inermis

G. intestinalis

G. lativentris

G. meridionalis

G. nasalis

G. nigricornis

G. pecorum

G. ternicinetus

G. veterinus

Gasterophilus species originally were restricted to the Palearctic regions, but now can be found on horses in other parts of the world. There are some similarities among the species, with *G. equi* similar to *G. intestinalis*; *G. flaviceps* similar to *G. haemorrhoidalis*; *G. gedoelsti* similar to *G. intestinalis*; *G. lativentris* similar to *G. nigronirmus*; *G. meridionalis* similar to *G. nigronirmus*; *G. nasalis* similar to *G. veterinus*; and *G. ternicinetus* similar to *G. gedoelsti*. The adults are 11–16 mm in length. Males possess a black-brown thorax, and a yellow-brown head and abdomen. The body is covered with yellow hairs, but the thorax shows a transverse band of dark hairs. The female is darker than the male (especially the abdomen). Both sexes have yellow legs. Oviposition occurs in flight. The eggs are attached along the distal half of the hairs.

Eggs are ready to hatch on the fifth day after deposition, though embryonic development depends somewhat on temperature. The larvae penetrate the mouth and the tongue. From time to time larvae make small holes to breathe. Second and third instars are found in the stomach. Mature larvae are excreted with the feces and pupate in the soil. The mature larvae are 16–20 mm in length. They possess rows of spines on each segment, and the shape of the spines varies among species. The region of the posterior spiracles is marked with 12–20 transverse bands, with the number varying among species (n). Larvae can develop only in the alimentary tract of horses, donkeys, zebras and other equids. *Gasterophilus haemorrhoidalis*, *G. inermis*, *G. intestinalis*, *G. nigrocornis*, *G. pecorum* and *G. veterinus* are obligate parasites.

Genus *Hypoderma* Latreille (Heel Warble or Cattle Grub Flies) (D)

H. actaeon
H. bovis
H. capreola
H. diana
H. lineatum

Hypoderma species are found on several continents, including Europe, Africa, Australia and North and South America. Though commonly associated with livestock, *Hypoderma lineatum* has been reported in a wild host, the North American Bison (*Bison bison*). The flies are 13–15 mm in length. They are densely clothed with black and yellow hairs, almost resembling a bumble bee. *Hypoderma actaeon* and *H. capreola* are similar to *G. diana*. *Hypoderma bovis* is an obligate parasite of cattle, equids and humans; *H. diana* is parasite of deer and roedeer, and *H. lineatum* is present in cattle, deer and humans. The flies are active in bright sunshine, calm weather and temperatures in excess of 18°C. Eggs are deposited on the hairs of their hosts.

These large larvae measure 25–30 mm long at maturity, and are yellow-brown. The cephaloskeleton of the larva is strongly reduced, and external mouthhooks are not visible. The posterior spiracles are surrounded by minute spines (o). They are more or less symmetrical and they show a longer and narrower channel in *H. bovis* than in *H. lineatum*, with the inner margins of the channel divergent. Larvae hatch and crawl down the hairs and penetrate the body through an injury of the skin. Larvae migrate below the skin along the nerve, muscle and fat tissues to the skin of the host's back, and there forms small holes in the skin. The larvae molt to the second and third instar, remaining stationary in the slowly enlarging swellings or "warbles." They are a subcutaneous parasite, with the posterior peritremes located near the hole to facilitate obtaining oxygen. From here, the third instar drops to pupate.

Genus *Oestrus* Linnaeus (HC)

O. aureoargentatus
O. caucasicus
O. ovis (Sheep Nasal Bot Fly)
O. variolosus

The *Oestrus* species are found primarily in the Old World: *O. aureoargentatus* and *O. variolosus* are distributed throughout Africa south of the Sahara; and *O. caucasicus* is present in domestic and wild animals of the Caucasus region and Central Asia. However, *O. ovis* is found in all sheep-farming areas of the world.

The adults of *Oestrus* species are 10–12 mm in length. They have a yellow-brown head, with small black tubercles of equal size on the thorax, and yellow legs. They possess yellow-veined wings. The abdomen is marked with black, brown, grey or white, the appearance changing with the light incidence. *Oestrus ovis* is an obligate parasite, affecting the ocular, nasal, and frontal sinuses, and causing maxillary sinus myiasis in sheep and goats. It attacks dogs and man occasionally. In this last case, the larva can be found in the eye, and the syndrome is diagnosed as an acute catarrhal conjunctivitis because the young larva cannot develop. The life cycle is dependent on climatic factors: in West Texas, with its moderate winters, the flies are active during almost all months of the year, except January and February.

The mature larva is about 20 mm in length, and brown with transverse, dorsal blackish bands. The posterior spiracles are circular, with a central ecdysial scar, and without a distinct suture (p).

Genus *Pharyngomyia* Schiner (HC)

Ph. picta

The *Pharyngomyia* species are deer parasites. *Pharyngomyia picta* is an obligate parasite of red deer (*Cervus elaphus*), sika deer (*Cervus nippon*) and in Europe attacks the fallow deer (*Dama dama*), elk (*Alces alces*) and the roe deer (*Capreolus capreolus*). The adult is 13–16 mm long. Its body is densely covered with blackish hairs, and appears black and white, or brown and white, according to the light incidence. The eyes in both sexes are broadly separated. The mature larvae are about 35 mm in length, and have irregular black spots, especially in the posterior part of the body. The posterior spiracles are crescent-shaped, with the inner margins of the sinuate part divergent (q).

Genus *Rhinoestrus* Brauer (Horse Nasal Bot Fly) (HC)

R. antidorciti

R. giraffae

R. hippopotami

R. latifrons

R. nasalis

R. nivarleti

R. phacochoeri

R. purpureus

R. steyni

R. tshernyshevi

R. usbekistanicus

R. vanzyli

The *Rhinoestrus* species vary in their distribution: *R. antidorciti*, *R. steyni* and *R. vanzyli* are present in southwestern Africa; *R. giraffae* occurs in Tanzania (Africa); *R. hippopotami* in Uganda and Zimbabwe (Africa); *R. latifrons* is present in Russia and China; *R. nivarleti* is found in Zimbabwe; *R. phacochoeri* is present in Cameroon (Africa); *R. purpureus* is a palearctic species; *R. tshernyshevi* is present in Central Asia; and *R. usbekistanicus* occurs in East and Central Asia.

These flies are obligate ocular and nasal parasites in bovides and equides. *Rhinoestrus purpureus* is a parasite found in horses and donkey, and their cross-breeds. The female is larviparous. The adults are 8–11 mm long. The eyes in both sexes are widely separated. The abdomen bears glossy black and brown setiferous tubercles. The legs are red and yellow-brown.

The young larvae are undescribed in many species. The mature larvae are about 20 mm in length, with anal bulges bearing spines. The posterior spiracles are open and a little longer than broad (r); the channels lie almost opposite one another in *R. purpureus*.

Family Phoridae – (Scuttle or Humpbacked or Phorid Flies)

Genus *Megaselia* Rondani (D; AT/F)

M. rufipes

M. scalaria

The genus *Megaselia* is important primarily because the larvae of *M. rufipes* produce traumatic myiasis, boils and borrows. *Megaselia scalaria* is a secondary occasional invaders of wounds. These flies are recorded from humans. *Megaselia rufipes* is common in North America and Europe. The mature larva is small, measuring about 4 mm in length. It is small, dirty-white, and slightly flattened. The posterior spiracles are situated on brown, sclerotized tubercles, each with a narrow opening.

Family Sarcophagidae – (Flesh Flies)

Genus *Sarcophaga* Meigen (D; AT/F UO)

S. albiceps

S. argyrostoma

S. carnaria

S. crassipalpis

S. exuberans

S. fertoni

S. froggatti

S. haemorrhoidalis

S. hirtipes

S. misera

S. nodosa
S. peregrina
S. ruficornis
S. striata
S. tibiali

The *Sarcophaga* species are widely distributed: *S. albiceps* occurs in the Hawaiian Islands and New Guinea; *S. argyrostoma* is found in South America, India, Marshall Islands, Hawaii and Yugoslavia (Europe); *S. crassipalpis* is present in South America and Australia; *S. exuberans* and *S. fertoni* are present in the Mediterranean regions; *S. froggatti* is an Australian species; *S. hirtipes* is found in both the Ethiopian and Palearctic regions; *S. misera* is found in the Oriental and Australasian regions and Pacific Islands; *S. nodosa* is present in Zimbabwe; *S. peregrina* is present in the Madagascan and Australasian regions; *S. ruficornis* is present in Indochina; *S. striata* is present in Russia; and *S. tibialis* is present in the Ethiopian and Mediterranean regions. The thorax of the adult typically bears three broad and black longitudinal stripes. The abdomen has a gray and blackish tessellation, a so-called chess-board pattern. The legs are black. The mature larva is densely spinulose. The larval cephaloskeleton has a bifurcated dorsal cornua. The eritremal ring of the posterior spiracles is open (s).

Females of this genus are larviparous, depositing larvae rather than eggs. This species breeds in excrement, carrion and other decomposing organic matter. Adults can be found indoors, and are attracted to freshly deposited stools. The larvae of *S. carnaria* feed in feces, but accidentally can be involved in nose, mouth, anal or vaginal myiasis. Similarly, *S. haemorrhoidalis* larvae breed mainly in feces, but also has been involved in anal and vaginal myiasis.

Genus *Wohlfahrtia* Brauer and Bergenstamm (D; UO)

W. bella
W. magnifica
W. nuba
W. opaca
W. vigil

Wohlfahrtia magnifica is present in the south of Europe, Asia (Russia), and in North Africa. *Wohlfahrtia nuba*, *W. opaca* and *W. vigil* are North American species. Adults are 8–14 mm in length. They are similar to *Sarcophaga* in general appearance, but instead of showing an ill-defined chess-board pattern, the abdomen shows sharply marked black spots. Body is densely grey pollinose. The dark stripes on the thorax are clearly visible. The legs are black. The mature larva is covered with many irregular rows of small dark-pointed backwardly directed spines that are much larger than those of *Sarcophaga*. The posterior spiracles, however, are similar to *Sarcophaga* (t).

Wohlfahrtia magnifica is an obligate parasite of warm-blooded vertebrates. It is a larviparous species. From 150 to 200 larvae are deposited near a wound or body openings of humans or other animals such as sheep, goats, cattle, horses and dogs. Larvae molt twice, then leave the wound of the hosts to drop to the ground, where they pupate. *Wohlfahrtia bella* is an obligate parasite in wounds in sheep, goats and humans; *W. nuba* is a parasite of both living and dead livestock tissues. In the case of *W. opaca* and *W. vigil*, the larvae penetrate the host skin, producing foruncles.

References

Beaver PC, Jung RC, Cupp EW (1986) Parasitología Clínica. Salvat Editores. Barcelona, Spain, 882 pp

Gállego Berenguer, J (1998) Manual de parasitología. Edicions Universitat de Barcelona, Barcelona, Spain, 491 pp

Hall (1991) Screwworm flies as agents of wound myiasis. World Anim Rev. Special 2:6–17

Richards OW, Davies RG (1977) IMMS general textbook of entomology. Vol. 2. Classification and biology. Wiley, New York, NY, 1354 pp

Teskey HJ (1981) Morphology and terminology-larvae. In: MacAlpine JF, Peterson BV, Shewell GE, Teskey GJ, Vockeroth JR, Wood DM (eds) Manual of nearctic Diptera, Vol. 1. Monograph 27. Agriculture Canada Research Branch, Ottawa, Canada, pp 65–88

Zump F (1965) Myiasis in man and animals in the Old World. Butterworths, London, United Kingdom. 267 pp

Mymaridae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Mymarommatidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Myndus crudus Van Duzee (Hemiptera: Cixiidae)

Myndus crudus Van Duzee (Fig. 115) is a planthopper whose adults feed on the foliage of various species of palms. This insect species is the only known vector of lethal yellowing, a highly destructive disease of palms in various countries of the Caribbean Basin region.

This planthopper is distributed on the mainland of Tropical America from northern Brazil to northern Mexico, with its range extending to islands of the western Caribbean region (i.e., Cuba, Jamaica, and the Cayman Islands), but it has not been reported in Hispaniola, Puerto Rico, or other islands of the eastern Caribbean except Trinidad. This distribution pattern in the Caribbean reflects the invasion route of its fauna, i.e., mainland species invaded the westernmost islands from the Yucatan Peninsula, with diminishing numbers of species reaching the easternmost islands. From the south, species crossed the short span to Trinidad, with diminishing numbers reaching islands to the north. *Myndus crudus* is present in southern Florida and is probably present on at least some islands of the Bahamas, since these two political entities are highly similar in climate and other geographical considerations, and border and share flora and fauna with the Caribbean Basin region.

The adult female of *M. crudus* at rest with posteriorly extended wings is about 5 mm long from the vertex of the head to the tip of the wing. The head and body are straw colored. The wings are transparent, with brown veins that have numerous pustules bearing setae. The prominent ovipositor distinguishes the female. The male is slightly smaller and similarly straw-colored, but often paler, with a light green abdomen. Within the geographical range of these planthoppers, they are common on the foliage of many kinds of palms.

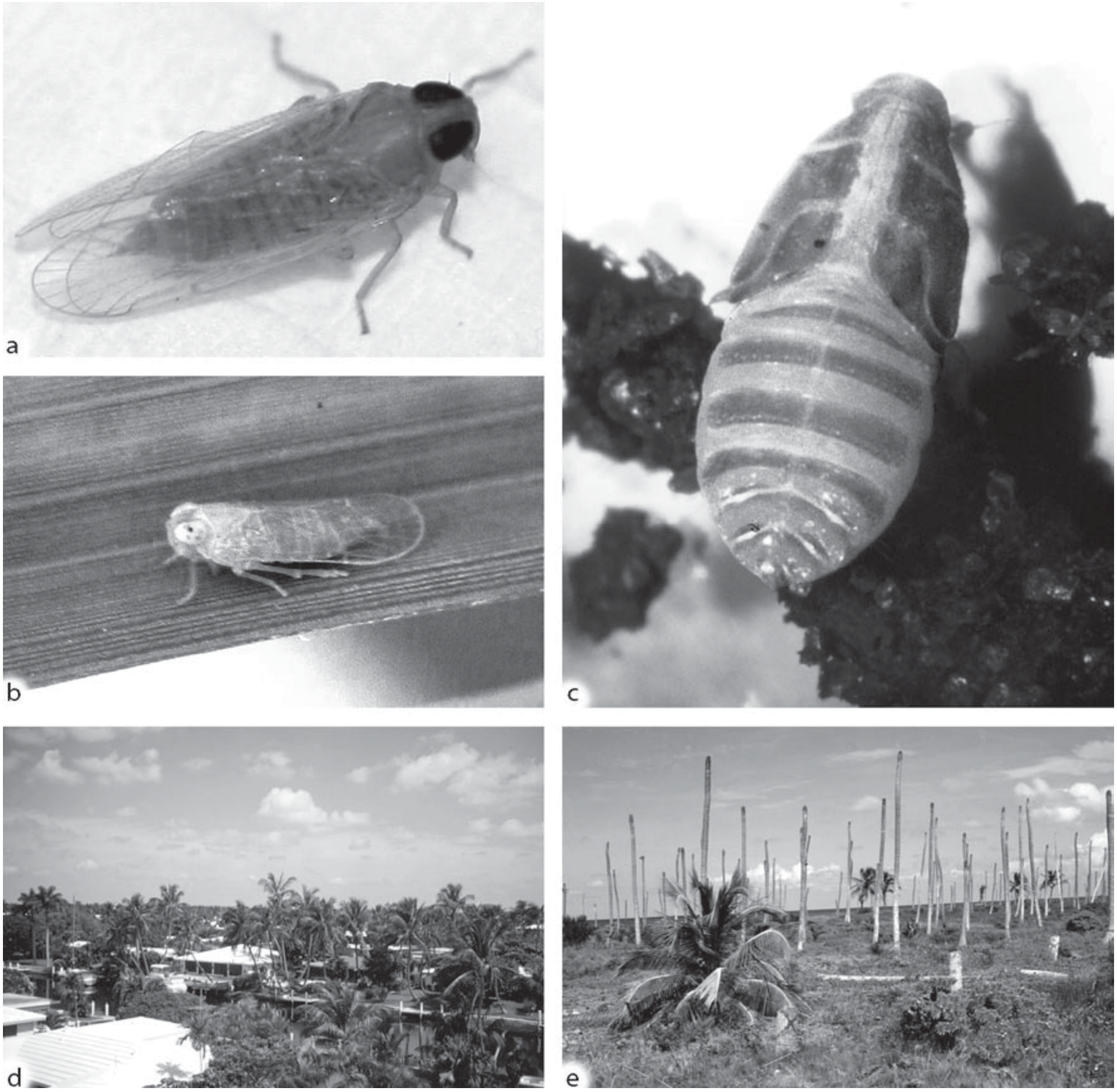
The nymphs feed on the roots of grasses, usually at or near the soil surface. They are tan to grey colored with a reddish blush on the head and legs. The nymphs are covered with a thin, waxy bloom produced by numerous wax glands in the cuticle. The tibiae of the forelegs are flattened, a possible adaptation for digging beneath the soil surface. Guinea grass (*Panicum maximum* Jacquin) and St. Augustine grass (*Stenotaphrum secundatum* (Walter) Kuntz) are two of several grass species that are highly favorable hosts of *M. crudus* nymphs, and both are very common in various localities within the insect's range.

Damage and Economic Importance

Myndus crudus is a vector of lethal yellowing disease of palms. As the name implies, "lethal yellowing" is lethal to nearly all of the palms it infects. The disease is caused by a kind of plant-inhabiting bacterium called a phytoplasma. It is one of the most devastating diseases of palms and has caused serious impacts on the landscape and the agricultural economies of regions that it has invaded.

Lethal yellowing has been known in Cuba, Jamaica, and the Cayman Islands since the 1800s. In the mid-1900s it was first observed in Hispaniola, the Bahamas, and Florida. Florida was the only locality on the mainland of the Americas affected by lethal yellowing until the early 1980s, when it was reported on the Yucatan Peninsula of Mexico. It has since practically eliminated coconut palms from the Caribbean coast of most of southern Mexico and much of Central America. More recently, it has been reported on Nevis in the eastern Caribbean (Fig. 116).

Although it is sometimes suggested that additional species of insects may transmit lethal



Myndus Crudus Van Duzee (Hemiptera: Cixiidae), Figure 115 ***Myndus crudus*** **and damage: (a) female, (b) male, (c) nymph (photo by J.V. DeFilippis), (d) view of Fort Lauderdale, Florida, with initial case of lethal yellowing (center), (e) dead palm trunks in former coconut plantation that was totally destroyed by lethal yellowing, Yucatan State, Mexico.**

yellowing, researchers have found no evidence that any species other than *M. crudus* is a vector of this disease. Transmission experiments have successfully shown this insect to be a vector in Florida, where conditions for conducting this type of experiment were especially favorable, but *M. crudus* is most probably a vector in all countries of Tropical America where lethal yellowing is present. It is also recognized, however, that insect diversity tends to increase relative to decreasing latitude, and indeed there are more species of auchenorrhynchous insects on palms in the tropics than in Florida. Little is known concerning the biology and vector potential of most of these species.

Lethal yellowing has been most intensely studied as a disease of coconut palm because of that species' economic importance. In fact, the coconut palm is considered one of the 20 most important

***Myndus Crudus* Van Duzee (Hemiptera: Cixiidae), Figure 116 Map showing the distribution of lethal yellowing, 2007. Several cases were also reported on the island of Nevis in the Lesser Antilles (not shown on map).**

crop plants in the world, and is a basic element in the agricultural economies of many tropical countries, as well as a source of important products in the world economy. However, lethal yellowing infects and is lethal to at least 35 additional species of palms, including the economically important date palm (*Phoenix dactylifera* L.), as well as many palms that are important as ornamentals or as local sources of food or fiber in tropical countries (Fig. 116).

There are several other diseases of coconut palm in various countries that were formerly thought to be identical to lethal yellowing of the Caribbean, and thus were referred to as lethal yellowing. But as knowledge of phytoplasmas increased in recent decades, lethal yellowing was recognized as a distinct disease of palms in the Caribbean region. Similar diseases of palms, most of which are present in various parts of Africa and Asia, are currently known by other names.

Management

Once *M. crudus* was implicated as a vector of lethal yellowing, interest turned to the possibilities of managing this insect to achieve a corresponding reduction in the spread of lethal yellowing. The prospects for controlling lethal yellowing via biological control of the vector are not promising. As an insect native to the Americas, it is attacked by several natural enemies, but at least in lethal yellowing-affected areas, these do not reduce the populations of this insect sufficiently to significantly reduce the spread of the disease.

Myndus crudus populations can be suppressed by treating palms with insecticides, and there is a slight reduction in the spread of lethal yellowing. But chemical control is not a feasible method of reducing the spread of lethal yellowing over large areas for long periods. Insecticide treatments of palms and grasses have been used as quarantine treatments to attempt to prevent *M. crudus* from being transported to new localities.

Populations of *M. crudus* can be reduced by planting ground covers that do not support development of the immature stages, including various grass species, or legumes such as tropical-kudzu, *Pueraria phaseoloides* (Roxburgh) Bentham, or perennial peanut, *Arachis pintoi* Krapov and W.C. Gregory. The latter legume species are used as ground cover in coconut plantations for soil improvement and erosion control. Where lethal yellowing-resistant palms are planted, the use of leguminous ground covers would reduce the vector population and indirectly the disease pressure on the palms, thus delaying the development of a strain of the pathogen that can overcome the defenses of the resistant palm. This prospective method of managing lethal yellowing has been investigated in experiments in small research systems, but not on farms or other large areas.

Although managing LY indirectly by controlling *M. crudus* has been investigated as mentioned above, virtually all management efforts are focused directly on the disease. A therapeutic treatment involving trunk injections of antibiotics active against phytoplasmas was developed in the 1970s. Although costly, it has been used effectively in preventing the disease in palms in some relatively affluent areas, such as Palm Beach, Florida.

By far the most common management method is the use of resistant palms. Varieties of coconut differ in susceptibility to lethal yellowing, and those that are relatively resistant have been established in large planting programs in lethal yellowing-affected areas. In the remaining 35 susceptible species, distinct varieties have not been distinguished. However, the degree of susceptibility of many species of palms is roughly known from observations in lethal yellowing-affected urban areas, particularly in Florida, where there is an exceptionally high diversity of palms used in landscaping. For example, in urban areas in Florida where lethal yellowing has killed numerous coconut palms, it has also killed many *Adonidia merrillii* (Beccari), while in the same areas a similar palm, *Ptychosperma elegans* (R. Brown) Blume, has not been affected. Landscapers in lethal yellowing-affected areas can select palms that have shown apparent resistance or immunity based on such observations.

References

Howard FW, Moore D, Giblin-Davis R, Abad R (2001) Insects on palms. CABI Publications, Wallingford, United Kingdom, 400 pp

Kramer JP (1979) Taxonomic study of the planthopper genus *Myndus* in the Americas (Homoptera: Fulgoroidea: Cixiidae). Trans Am Entomol Soc 105:301–389

Oropeza C, Howard FW, Ashburner GR (eds) (1995) Lethal yellowing: research and practical aspects. Kluwer Academic Publishers, Dordrecht, The Netherlands, 250 pp

Myofibrils

The fibers that collectively comprise muscles.

Myopsocidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice or Psocids

Myriapods

Classes of Phylum Arthropoda, subphylum Atelocerata (formerly subphylum Myriapoda, the basis for this name) that are insect relatives but possessing many legs. The myriapods consist of the centipedes, millipedes, pauropods and symphylans. There is some question whether this is a natural group.

► Phylum

Myrmecodomatia

Structures found in higher plants that appear to have evolved to serve as dwelling places for ants.

Myrmecolacidae

A family of insects in the order Strepsiptera.

► Stylopids

Myrmecology

The scientific study of ants.

Myrmecomorphy

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Myrmecomorphy, or the morphological and behavioral mimicry of ants, has evolved at least 70 times in the arthropods – 15 times in spiders, at least 10 times in plant bugs, and seven times in staphylinid beetles. More than 2,000 species of myrmecomorphic arthropods have been described thus far, belonging to over 200 genera in 54 families. Myrmecomorphy forms a subset of ant mimicry, which includes all species that resemble ants through convergence in morphological, behavioral, chemical, or textural characters (Fig. 117). The other major group of ant-mimetic species are the myrmecophiles, or those arthropods that associate closely with ants, but do not necessarily resemble them morphologically. Although some are also myrmecomorphic, most myrmecophiles have chemical and/or textural characters that facilitate a close relationship with their ant hosts. Here we describe signal properties of myrmecomorphic arthropods, present their taxonomic distribution, and discuss their adaptive significance.

Signal Properties of Myrmecomorphic Arthropods

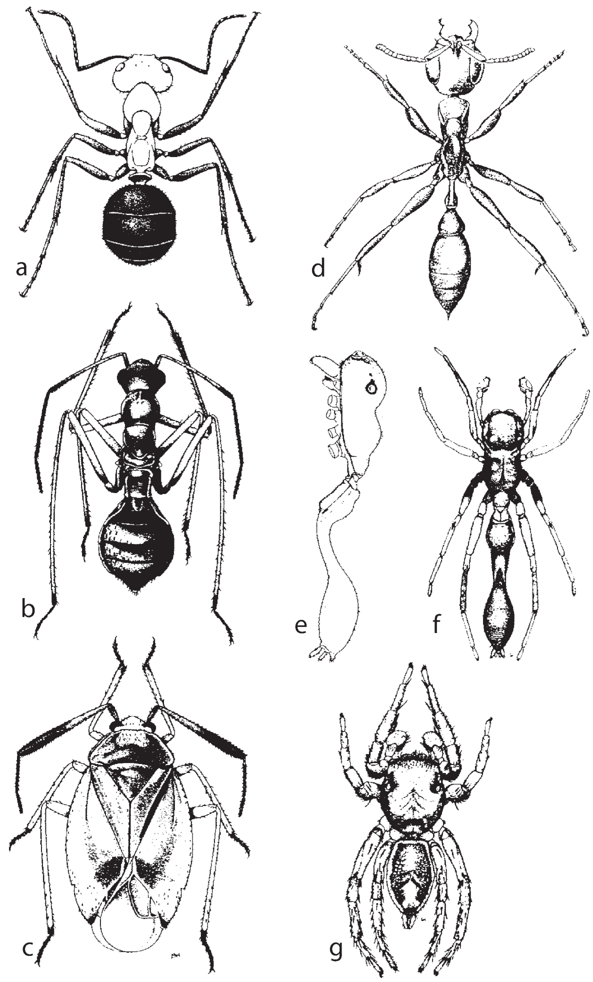
Mimicry can be defined as a system that involves an organism (the mimic) which simulates signal properties of another organism (the model) so that the two are confused by a third organism (the operator) and the mimic gains protection, food, or a mating advantage as a consequence of the confusion. Myrmecomorphic species express a variety of signal properties that enhance their resemblance to ants, involving shape, pattern, texture, color, behavior, and size. In this section, we review how mimicry is achieved for a representative sample of myrmecomorphic spiders and insects, and describe some examples of intraspecific variation.

Spiders

Spiders have a wide variety of body forms, but compared to ants, typically have relatively short, hairy bodies. Ants are generally elongate, have a medially constricted body with a distinct petiole, elbowed antennae, large compound eyes, and typically a shiny integument. Ant-like spiders on the other hand, are relatively elongate, have a medial constriction of the cephalothorax into a head and alitrunk, with a narrowing of the posterior cephalothorax or anterior abdomen to produce a petiole and gaster. Ant-like spiders often use the first or second pair of legs as if they were antennae, have pigmented spots on the cephalothorax that resemble large compound eyes, often have shiny setae or dense mats of reflective hairs to give a shiny illusion, and can have a transparent cuticle to give the illusion of a constriction. Many ant-like spiders match the color of their ant models closely. Populations of the jumping spider *Synemosyna aurantiaca* are color polymorphic, with yellow morphs resembling the ants *Pseudomyrmex flavidulus* and *P. oculatus*, and black morphs resembling *P. gracilis*. Correspondence in the color of individual structures in not uncommon, as in the species-specific mimic *Castianeira memnonia*, in which the yellow terminal segments of the front legs correspond to the bright yellow antennal apices of its otherwise black ant model, *Pachycondyla obscuricornis*. The evolution of ant-like behaviors in myrmecomorphic spiders is not surprising, given that behavior is often identified as the most conspicuous feature of ants. In both clubionid and salticid spiders, the first or second pair of legs are waved around in front of the spider, contacting the substrate in much the same way that ants use their antennae. The antennal illusion is often supplemented by a zigzag running gait, and in jumping spiders, there is a general reluctance to jump. In general, the spiders that are most difficult to distinguish from ants in the field are those that have a combination of morphological and behavioral ant-like features.

Insects

While insects are confronted with many of the same problems as spiders for evolving ant-like form, the possession of a similar body plan requires less profound modification. A major constraint to myrmecomorphy, however, is the one or two pairs of wings found in most adult insects. Consequently, the loss or reduction of wings in the adult is common in ant-like insect species, often accompanied by a constriction of the posterior thorax and/or anterior abdomen. In those species of myrmecomorphic insects that have retained their wings, oblique or transverse pale marks or bands of pale hairs typically interrupt the otherwise darkened forewings, to produce the illusion of a petiole. Still other species, such as alydids and mantids, resemble ants only in the immature form. Compared to many insects, ants have relatively large heads with well developed mandibles. In general, myrmecomorphic insects tend to possess relatively larger heads than their non-mimetic relatives, and the illusion of large mandibles in many ant-like plant bugs is accomplished by enlargement of the ventral region of the head, which also brings the head forward into a more ant-like horizontal position. Many ant-like insects mimic the elbowed antennae of ants through differential pigmentation or enlargement of various antennal segments. Myrmecomorphic insects often display microstructural and color modifications that enhance mimicry, including: (i) silvery, reflective hairs to increase body shine, or when arranged in bands, to act as an interruptive agent; (ii) changes in surface texture corresponding with smooth, roughened, or pitted areas on the ant's body; (iii) thoracic or abdominal spines to mimic those on the alitrunk and petiole of some ants; and (iv) color polymorphisms that match available ant models (Fig. 117).



Myrmecomorphy, Figure 117 Ants (top), myrmecomorphs (mimics; middle), and non-mimetic relatives (bottom). (a) *Formica obscuripes* (Formicidae), western North America. (b) *Coquillettia insignis* (Miridae), western North America. (c) *Pronotocrepis clavicornis* (Miridae), western North America. (d) *Pseudomyrmex tenuis* (Formicidae), Central and South America. (e, f) *Synemosyna aurantiaca* (Salticidae), Trinidad, Brazil. (g) *Habronattus mexicanus* (Salticidae), southern North America, Central America, Caribbean.

As in the spiders, morphological adaptations in ant-like insects are often accompanied by resemblance in behavior. Many staphylinid beetles are difficult to distinguish from their army ant hosts, due to very similar patterns of locomotion.

Regarding the behavior of alydid bugs, Oliveira (1985) remarks, "Nymphs of *Hyalymenus* have a highly differentiated ant-like morphology which is achieved by several structural adaptations. The similarity is greatly enhance by the nymph's ant-like behavior, notably the rapid zig-zag locomotion, the constantly agitated antennae, and the up and down movement of the abdomen (similar to an alarmed ant)".

Transformational Mimicry

Because their ant models are holometabolous, mimic species that develop gradually, like plant bugs and spiders, tend to resemble a range of appropriately sized models, usually representing two or more ant species or genera. This phenomenon is called transformational mimicry, and has been described for mantids, plant bugs, alydid bugs, running spiders and jumping spiders. Species that rely on transformational mimicry are typically genus-specific mimics, presumably because features that provide species-specificity on one life-history stage constrain the evolution of features that promote close correspondence to different ants in other stages.

Sexual Dimorphism

While not common in ant-mimetic systems, sexual dimorphism has been described in several groups of spiders and some Hemiptera/Heteroptera. The adult males of the jumping spider *Zuniga magna* are striking mimics of *Pseudomyrmex gracilis*, while females closely resemble the ponerine *Pachycondyla villosa*. In both cases, the species-specific mimicry involves remarkably accurate structural and color correspondence between model and mimic. Many myrmecomorphic plant bugs are sexually dimorphic; brachypterous or apterous females are among the best morphological mimics of ants, while the macropterous males are comparatively poor pattern mimics.

Taxonomic and Geographic Distribution of Myrmecomorphy

Myrmecomorphy has been identified in nine families of spiders and 45 families of insects, representing 11 different orders. Over 200 spider and insect genera are known to contain myrmecomorphs, and the number of species involved is certainly in the thousands worldwide. Ant-mimicry has arisen at least four times in the spider families Clubionidae and Corinnidae (running spiders), three times in the Salticidae (jumping spiders), and several times each in the Aphantochilidae, Araneidae (orb-weavers) and Theridiidae (comb-foot weavers). In the plant bugs (Heteroptera: Miridae), morphological resemblance to ants has arisen no fewer than ten times, and this family contains the highest diversity of myrmecomorphic species among insects.

Myrmecomorphic arthropods are found in all major regions of the world except Antarctica and the extreme northern Holarctic. The number of species increases toward the tropics, mirroring the pattern observed for other mimetic species, for ants themselves, and for most other plant and animal groups.

Adaptive Significance

The adaptive significance of myrmecomorphy has not been clearly established in most cases. The most common mimetic hypotheses to explain myrmecomorphy are Batesian, Wasmannian, and aggressive mimicry.

Batesian Mimicry

For those ant-like species that do not live with or attack ants, the most widely supported hypothesis for myrmecomorphy is Batesian mimicry. The evolution of Batesian mimicry is presumed to occur within the context of an interactive system involving model, mimic, and a predaceous operator(s). The system has four basic features: (i) certain arthropods (models) are unacceptable to predators and advertise this, (ii) predators (operators) learn about this unacceptability, (iii) generalization in predators takes place allowing acceptable species (mimics) to benefit by resemblance, and (iv) visual discrimination by predators is sufficient to select for increased mimetic resemblance. The behavioral and ecological conditions presumed to favor the evolution of Batesian mimicry include: (i) the model must be an unacceptable prey item to at least some predators, (ii) the mimic must be an acceptable prey item, (iii) the model and mimic must have similar temporal and spatial distributions, (iv) the model must be common relative to the mimic, (vi) the mimic must have signal properties that deceive visually oriented predators within a community of alternate prey, and (vii) predators must be able to learn. Our discussion on the evidence for Batesian mimicry addresses these conditions by describing the qualities of species within selected myrecomorphic systems, and offering observational and experimental evidence of functional Batesian mimicry in the field.

In the best known myrmecomorphic systems, models, mimics and predators tend to possess ecological and behavioral features consistent with a Batesian mimicry hypothesis. Like bees and wasps, ants have features that make them ideal models in Batesian mimicry systems. Ants are among the most common and conspicuous of insects, and workers of many species are aggressive and distasteful. Ants are entirely social, and have alarm pheromones used for common defense against enemies. Therefore, small vertebrate and invertebrate predators must hunt them with caution. Although a variety of small predators attack or specialize on ants, these species are comparatively rare, and typically use special hunting tactics.

Myrmecomorphs that do not attack ants are almost always found in the same microhabitat as their models, but do not associate closely with ants, and often show avoidance reactions to them. Although little quantitative work has been done to estimate population sizes of mimics in relation to their models, observational evidence suggests that ants are almost always more common than co-occurring mimics. Most evidence suggests that free-living myrmecomorphs are relatively palatable – spiders serve as important prey items for birds and lizards, and myrmecomorphs are no exception to this general rule.

The most likely predators that could serve as operators in Batesian mimicry systems are small vertebrate predators such as lizards and birds, and arthropod predators such as jumping spiders and wasps. These predators possess relatively good vision, necessary to select for the detailed structural and behavioral adaptations seen in many myrmecomorphic species. Vertebrate species are also well known to be capable of associative learning, including experimental studies involving mimetic insects. While associative learning has been demonstrated in social insects, similar data on arthropod predators are scanty at best, possibly because of the greater difficulty in choosing meaningful stimuli for arthropods that are solitary, more reclusive than bees and ants, or have unknown feeding habits. Nonetheless, a few studies have demonstrated the capacity for associative learning in arthropod predators, involving wasps, mantids, crab spiders, and assassin bugs.

Some of the most convincing observational evidence that supports Batesian mimicry in ant-like species comes from the existence of a number of remarkably close species-specific correspondences between model and mimic, particularly among the spiders. For example, the running spider *Mazax rettenmeyeri* features a unique ridge of erect hairs along the midline of the cephalothorax, which closely approximates the thoracic keel of its model *Camponotus sericeiventris*. Other characteristics of the mimic, such as color, shape and behavior, accentuate the resemblance between model and mimic. Many other species-specific pairs of model and ant mimic have been described worldwide.

Experimental evidence in support of Batesian mimicry includes feeding trials in which visually oriented predators behave similarly toward model and mimic. For example, in a study on the ant-mimetic plant bug *Coquillettia insignis* in north-eastern Oregon (USA), both the jumping spider *Sassacus papenhoei* and the assassin bug *Sinea diadema* accepted non-mimetic plant bug prey significantly more often than the ant-mimic *Coquillettia insignis*, while their behavior toward the model ant Formica fusca and toward the mimic was indistinguishable. In addition, the assassin bug *Siadema diadema* was able to learn and remember unpleasant experiences with the ant model. While about half of the field-collected specimens of this assassin bug attacked the ant-mimic *Coquillettia insignis*, after close confinement with the ant *Formica fusca*, individual assassin bugs that had previously attacked *C. insiginis* were significantly less likely to do so.

Wasmannian Mimicry

Myrmecophilic arthropods that also possess a body shape or texture that closely resembles their ant models are called Wasmannian mimics. Some observers have argued that the body shape and texture of ant-like rove beetles that associate with army ants evolved as a consequence of selection by the ants themselves. This view is consistent with the general observation that when encountering one another, doryline army ants and other swarm raiding species antennate the petiolar area of their nestmates, and that the same behavior performed by a myrmecomorphic rove beetle allows the mimic to function with the colony as if it were an ant. Yet among the rove beetles that associate with ants (myrmecophiles), most species that do not resemble ants occur entirely within the nest of their hosts, while all known ant-like rove beetles live with legionary ants, spending the majority of their adult lives on the surface, exposed to the full range of visually oriented predators that accompany the foraging raids. Hence, ant-like body form in some rove beetles may have evolved as a consequence of selection by both ants (Wasmannian mimicry) and by visually oriented predators (Batesian mimicry).

Aggressive Mimicry

Ants represent an abundant and conspicuous source of protein for potential predators, and many ant species care for other insect species, from which they extract nutrients. These features attract a considerable diversity of arthropod predators, and among these predators are some of the more remarkable examples of aggressive ant-mimicry. Aggressive mimicry differs from Wasmannian mimicry in that aggressive mimics do not live with their ant models, and typically associate with ants just closely enough to access their resource, either the ants themselves, or their symbiotic associates. Spiders of the genus *Aphantochilus* possess a shiny and granular integument, characters that are thought to facilitate acceptance by their cephalotine ant models, which are their only source of food. The adult crab spider *Amyciaea forticeps* attacks workers of the weaver ant *Oecophylla smaragdina*. Under normal circumstances, the crab spider does not closely resemble the weaver ant. While hunting, however, the spider adopts a behavior in which it looks like a dying or struggling weaver ant, and other workers often come nearer to investigate. The spider then pounces on its prey and quickly withdraws to a more remote location. Myrmecomorphic arthropods may also have evolved ant-like morphology and behavior to gain access to the Hemiptera that some ants tend for honeydew. Several authors have noticed a correlation between the distribution of ant-tended aphids and various species of the ant-like plant bug *Pilophorus*. It is widely believed that myrmecomorphy in *Pilophorus* serves as a temporary illusion, allowing the plant bugs to closely approach and seize their aphid prey.

Mimicry is very common in nature, and occurs in a bewildering array of plant and animal groups. Species that are abundant and ecologically dominant generally make excellent models in mimicry systems, and so it is no surprise that so many myrmecomorphic arthropods have evolved since ants came on the scene some 100 million years ago. Myrmecomorphic species offer abundant opportunities for exploring ecological and evolutionary aspects of mimicry and can lead to a deeper understanding of related fields, such as ant social organization, systematics, and predator-prey relationships.

► Ants
► Mimicry
► Myrmecophiles

References

Edmunds M (1974) Defence in animals. Longman, Essex, United Kingdom, 357 pp

McIver JD, Stonedahl GM (1993) Myrmecomorphy: morphological and behavioral mimicry of ants. Annu Rev Entomol 38:351–379

Oliveira PS (1985) On the mimetic association between nymphs of *Hyalymenus* spp. (Hemiptera: Alydidae) and ants. Zool J Linn Soc 83:371–384

Reiskind J (1970) Multiple mimetic forms in an ant-mimicking clubionid spider. Science 169:587–588

Wickler W (1968) Mimicry in plants and animals. World University Library, London, England, 255 pp

Myrmecophiles

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One of several types of social insect symbionts, myrmecophiles are animals that live with ants for at least part of their life cycle. Other similar symbionts are termitophiles (guests of termites), melittophiles (guests of bees) and sphecophiles (guests of wasps). Of these, myrmecophiles and termitophiles are the most abundant, species-rich and morphologically diverse.

All of these social insect symbionts are thought to be nest parasites. Many previous studies have demonstrated that the guests take food from the hosts and may even prey upon them. Outstanding cases, such as more specialized species, that pass the entirety of their life cycle in the nest, may best illustrate why "nest parasite" is the most commonly cited role of social insect symbionts. Throughout their lifespan, these myrmecophiles receive regurgitations from nurse ants tending the ant larvae, and in the process, drain the resources that would have otherwise gone to the host ant larvae. The larval myrmecophile also preys upon the ant larvae, even in the presence of the nurse ants. Nonetheless, many myrmecophiles may not be solely parasitic on the hosts. More highly adapted species may even provide benefits to their host colonies for at least part of their life cycle, possibly indicating that they are mutualistic with the hosts.

A great number of taxa have evolved myrmecophilous lineages. Mites (Acarina), beetles (chiefly Staphylinoidea), flies (Phoridae) and a few other soil-dwelling insect species have the most myrmecophilous species and are also the most abundant. Myrmecophiles are found living in nests of nearly every species of ant. Colonies that are larger and more persistent at maturity, such as army and driver ants, have more species and individuals of myrmecophiles than smaller mature colonies, such as ponerine and dacetine ants. Additionally, the species found in larger colonies tend to be more specialized than are those living with ants that have smaller, less permanent colonies. Irrespective of the type of colony, the total relative abundance of myrmecophiles is low, often on the order of 1:5,000 ants. Myrmecophiles are found in nearly every area of the nest including the refuse middens, foraging columns, brood chamber and the queen chamber. A single species typically specializes in one of these niches within the nest.

Ecological Categories

Myrmecophilous species generally play one of three consistent roles in the nests of the ants. Symphilic species, the best integrated into the host nest, are species-specific guests who must live with a single species and frequently interact with the host ants. These species usually obtain all food from regurgitations or grooming interactions that they solicit from the hosts. Synoeketes (also called indifferently tolerated guests) are found in ant nests, but do not interact with the host ants. Instead, these guests use the resources that are provided by the nest, such as nest materials, frass, food refuse and other nest detritus. Host ants will attack these species if the myrmecophile is too apparent, forceful, or bothersome. Synecthrans (also called persecuted guests) are only occasionally found with ants and may merely raid the nest for food. This ecological category of myrmecophiles usually does not live within the nest, instead residing in the surrounding litter or soil. Other ant symphiles often classed as myrmecophiles include trophobionts (ant-tended phytophagous insects, usually Hemiptera and Lepidoptera) and ant parasites (mites, phorid flies, or parasitic wasps).

A simpler organizational scheme to help label those species that fall into more than one of the above three categories classifies myrmecophiles as either integrated or non-integrated species. Integrated species are those that play a role in the social life of the colony, including symphiles who occasionally attack the hosts and trophobionts. The roles played by these species can range from procuring food (e.g., trophobionts), to grooming the hosts, and providing what may be psychoactive chemicals (e.g., symphiles). Non-integrated species normally do not interact with the hosts and, instead, use the nest or the ants themselves as an ecological niche to be exploited. This category includes synoeketes, synecthrans and parasites.

Evolutionary Trends

Several trends are consistent with these ecological categories. Obligate, strongly integrated symphiles tend to be host-specific and are found with a single or a few closely related host species. These species are strongly adapted to living in nests of only one particular host species, whereas non-integrated synecthrans are usually not host-specific. They are, instead, found with whatever ant species presents the necessary ecological resources needed by the guest. Most species of myrmecophiles are integrated into the host nest, as this mode of living tends to produce a greater number of species through the processes of resource tracking and coevolution with the host ants. Therefore, as host ants speciate, any well-integrated, species-specific myrmecophile may also speciate and come to specialize on the newly evolved host species. Non-integrated species generally do not have strong parallel evolutionary relationships with their host ants because they generally are not species-specific.

Chemical Communication

Strongly integrated myrmecophiles tend to have a great diversity of adaptations that help to either mimic or crack the communication code of their hosts. These adaptations can include chemical, morphological and behavioral traits. Because they help to break the code, these adaptations often become useful as integrating mechanisms that enable the myrmecophile to enter and become a part of the colony. Non-integrated myrmecophilic species may have, at most, a single, rudimentarily developed integrating mechanism.

Presumably because most communication in the ant colony is done chemically, most well-integrated symphilic myrmecophiles are able to chemically communicate with the host ants. Myrmecophiles both send and receive chemical messages with the host ants. Typically, communications from the host ants to the myrmecophiles are intercepted signals between nestmate ants, rather than pure, interspecific communications. Species that ancestrally possess extensive glandular systems, such as staphylinid beetles of the subfamily Aleocharinae, have evolved prominent structures associated with the glands, such as trichomes and brushes. Complicated processes of chemical exudation have evolved in these species such that some myrmecophilous species use a sequence of three chemicals to first defend against, then appease, and then convince an ant to adopt them and carry them into their nest. These exudates often trigger actions by the ants that mimic the normal brood care behavior of the host ants. Well-integrated, obligate symphiles are frequently able to secrete chemicals that generally resemble the cuticular hydrocarbons of the host. In so doing, they are able to mimic the chemicals that are thought to form the basis of colony odor and nestmate recognition, thereby gaining at least initial entrance to the colony.

Morphological Mimicry

Morphological adaptations can include similar color patterning to the host, development of prominent glandular trichomes and the evolution of specialized body plans. Myrmecoidy, the most unique morphological specialization among myrmecophiles, involves a suite of characteristics including a petiolate abdomen, narrow body, long legs and an expanded basal antennal segment to resemble geniculate antennae. Typically, well-integrated, host-specific symphilic species adopt some aspects of myrmecoidy. In contrast, most synoeketes and synecthrans have either retained their generalized bauplan or have evolved a limuloid, heavily-sclerotized defensive (or trutztypus) form (Fig. 118).

Limuloid species, such as many staphylinid beetles, are characterized by reductions in the appendages and head and development of overlapping, sclerotized body regions so that the insects appear teardrop-shaped. When attacked, species with defensive forms retract their appendages into grooves and feign death until the agitated ant departs. Specializations of the cuticle of the guest so that they resemble their hosts are also common. For example, host-specific phoretic mites have cuticular surfaces that so closely mimic those of their hosts that it is hypothesized that the ants are incapable of detecting the presence of the mites.

Most species of myrmecophiles have not evolved any morphological adaptations, instead retaining the ancestral species bauplan. Morphologically generalized species tend to be either synoeketes or synecthrans, and are rarely well integrated into the colony. These species must instead manipulate the host behavior using either chemical or behavioral specializations.

Myrmecophiles, Figure 118 Myrmecophiles, particularly well-integrated species such as these *Dinardilla mexicana* and *Sceptobius dispar* (Coleoptera: Staphylinidae: Aleocharinae), frequently interact with their host ants. The obligate symphiles require the presence of the hosts to live and are rarely found outside their company.

Behavioral Traits

A myrmecophile may have evolved behavioral traits that allow it to interact peaceably with the host ants. These are found in all types of guests, irrespective of how well integrated they are. Strigilation occurs when the myrmecophile either licks or scrapes the oily secretions from the surface of the ants and serves to acquire what is likely the host odor as well as to provide some food to the guest. Guests often perform a vigorous bout of strigilation when first introduced into a novel nest. This behavior frequently stops the attacks that invariably occur when a myrmecophile first enters a new colony. Behavioral traits such as episodic walking that is similar to that of ants, as well as antennation upon greeting, are frequently manifested in well integrated guests. Whether these traits are selected by the hosts or another species that may be predatory on the guests, such as antbirds, is not clear. It is unlikely that the operator of selection is identical in all cases.

Most research on myrmecophiles conducted at present focuses on Lycaenidae caterpillars, which are trophobionts and are tended by the ants for the honeydew and a diversity of chemical exudates by the caterpillars. The caterpillars are frequently studied within the field of myrmecophily, in part because most species are easily accessible on the branches of a plant. The adult butterflies are not tended nor are they ant associates. The caterpillars are not, strictly speaking, symphiles because they do not live with the ants, but instead are only tended by the hosts. Most of the adaptations of these caterpillars involve chemical cues, including the secretion of many chemicals from a spectacular diversity of specialized exudatory organs. As an example, the caterpillars often produce an alarm pheromone used by the host ants, so that if they are attacked, they signal for help from the host ants.

References

Kistner DH (1979) Social and evolutionary significance of social insect symbionts. In: Matthews RW (ed) Social insects, Vol. I. Academic Press, New York, NY, pp 339–413

Hölldobler B, Wilson EO (1990) The ants. Chapter 13. Harvard University Press, Cambridge, MA

Pierce NE, Braby MF, Heath A, Lohman DJ, Mathew J, Rand DB, Travassos MA (2002) The ecology and evolution of ant association in the Lycaenidae (Lepidoptera). Annu Rev Entomol 47:733–771

Myrmeleontidae

A family of insects in the order Neuroptera. They commonly are known as antlions.

► Lacewings, Antlions and Mantidflies

Mystax

A patch of hair or bristles located above the mouth, especially in robber flies (Diptera: Asilidae). In robber flies it is also called a mouth beard.

Mythicomyiidae

A family of flies (order Diptera).

► Flies

Mythology and Insects

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The study of insects and other arthropods in mythology falls into the realm of cultural entomology. However, in order to approach this subject, it is necessary to understand what mythology is. Quite simply, mythology is the study of myths. One definition of a myth commonly used in everyday conversation is that a myth is something false or imaginary. This definition has nothing to do with mythology. As used in mythology, a myth is a story, presented as having actually occurred in a previous age, explaining the cosmological and supernatural traditions of a people, their gods, heroes, cultural traits, religious beliefs, etc. Mythology is also closely related to religion as exemplified by the saying, “One man’s religion is another man’s mythology.”

Myths in general may be categorized into certain types such as creation myths, emergence myths, etc., and this is also true of many insect myths. For example, the creation of the Milky Way Galaxy by a beetle is explained in a creation myth of the Cochiti tribe of North America. The Negritos of the Malay peninsula have a diving myth in which a beetle dives into mud and brings up earth which become land. The Navajo of North America have an emergence myth in which the origin of the Navajo from the earth is explained in a myth involving several insects. In a fire theft myth, the San of Africa say that fire was stolen by the praying mantis, an insect widely regarded by Africans as sacred. Both bees and ants are totems as the Honey Ancestor and Honey Ant Ancestor respectively in the mythology of Australian aborigines.

Symbols are also closely related to mythology. Myths, spoken or written, are many times extended symbol systems encapsulating religious, philosophical, or psychological beliefs. Of particular interest to zoologists are animal symbols. Well known examples of animal symbols are the magnificent lion for royalty, the bull for masculinity and virility, and the dove for peace. However, although lesser known, many interesting animal symbols also occur among invertebrates, especially insects. For example, the use of ants as symbols for positive traits is widespread throughout various cultures. In many cultures, the humble, hard working ant is a universal symbol of industriousness and organization. The Old Testament states, "Go to the ant you sluggard: consider her ways and be wise," and, "There are four things which are little upon the earth but they are exceedingly wise: the ants are a people not strong, yet they provide their meat in the summer." The bee, also considered to be a rich symbol, is an exemplar of ethical virtues. Among qualities attributed to the bee are diligence, organization, sociability, purity and chastity. The bee was associated with Christianity, the Virgin Mary, and in ancient Greece, with virgin priestesses or *Melissae* who were termed "bees." Also in Greece, the bee was a cult symbol for Artemis, the virgin huntress and goddess of wild nature. In contrast to ants and bees, flies occur as many symbols and almost always with negative connotations. The fly represents feebleness and insignificance, but is also associated with evil gods and corruption. In early European Christian art, flies appear as a universal symbol for torment. Similarly, in Zorastrianism, yazads are major demons including the female Nasu, the demoness of dead matter who is depicted as a fly. The best known mythological figure associating flies with negative symbolism is Beelzebub. A popular title of Beelzebub was "lord of flies" and he is depicted both in human form as a fallen angel and as a demonic-appearing fly. The most famous of all mythological insects is the sacred scarab of ancient Egypt. The sacred scarab, *Scarabaeus sacer* Linn., is a coprophagous scarabaeid found around the perimeter of the Mediterranean. This dung beetle was of great symbolic importance in ancient Egypt. The beetle symbol known as a scarab became a symbol of rebirth after death. Scarabs were found in religious rites, tomb hieroglyphics, as amulets, and large numbers of hand-carved scarabs were buried with the dead. Numerous other insects have also been used for symbols (Figs. 119 and 120).

On a superficial level, myths provide colorful stories of interactions between gods, goddesses, people, and nature. However, beyond providing colorful stories, myths also serve several useful functions. One important function of myths is to explain. How did my people get fire? Why does a zebra have stripes? Why should I be good? Where will I go when I die? Answering questions such as these is the subject matter of

Mythology and Insects, Figure 119 **Ionian coin showing the bee which was a cult symbol for Artemis, the goddess of wild nature.**

Mythology and Insects, Figure 120 **Beelzebub, a demon known as Lord of the flies, is an example of a dipteran being associated with evil.**

myths. Many insect myths explain the origin, morphology, and behavior of different insects. The Tlingit Indians of North America explain the origin of mosquitoes in a story about a blood-sucking, carnivorous giant who fed on humans. This giant is ultimately avenged after his gruesome death by returning to feed on humans in the form of blood-sucking mosquitoes. The reason bees, wasps, and hornets have stingers is explained in a story by the Algonquin Indians of North America. According to this myth, the god Wakonda gave stingers to bees because the bees were industrious, but needed protection. However, since wasps and hornets claimed to be related to bees (which is true), The Great Spirit benevolently endowed them with stinging weapons also.

Besides explaining different facets of insect biology, insect myths also help explain the world in which we live. Why is ancient pottery almost always found broken? The Navajo Indians observed that beetles of the family Rhipiphoridae wander among scattered heaps of broken pottery and carry tiny pots (vestigial wing covers) on their shoulders. They say that these insects are in league with a monster that breaks the pottery of the dead and that it is this beetle that smashes into small fragments the pottery that is found at ancient village sites. On a larger scale, a Cherokee Indian myth tells of how a water beetle dove into a watery Lower World and brought back mud to make earth from which mountains and valleys were formed.

Another function of myths is to provide a basis for social cohesion. A shared mythology is a strong social tie that may be used to justify a social structure such as a religion or government. Myths explaining the common origin of a people provide social cohesion to those people, and insects play important roles in many of these myths. According to South African Khoisan traditions, the first living thing on earth was the tiny praying mantis, and it was he who created the earliest beings, including humans. One of the tribes of Sumatra claims to be descendants of three brothers hatched from eggs laid by a butterfly. In Madagascar, and among the Naga tribes of Manipur, some also trace their ancestry to a butterfly. Among Australian aborigines, insect based totems are found that provide social cohesion by offering group identity and even dictate social restrictions.

A third function of myths is to provide moral order and many animals including insects frequently occur in myths to show how one should lead a moral life. Insects also occur in myths as "enforcers" or punishments to guarantee virtuous behavior. Of the ten plagues, which, according to the Bible, were sent by God to Pharaoh's Egypt at the instigation of Moses and Aaron, three were actually insect plagues, namely lice, flies and locusts. And according to Danish legend the flea was sent to pester mankind as a punishment for laziness. An interesting insect myth with moral overtones is also found in Native American mythology. The Montagnais Indians of eastern Canada believed that the overlord of fish, particularly salmon and cod, was Big Biter (=*Tabanus*

Mythology and Insects, Figure 121 **Enamel plate from Qul' at Sharquat, Iraq, representing an Assyrian noble in a locust prayer before the god Ashur. A swarm of locusts may symbolize the wrath of god or cosmic disorder.**

affinis Kirby). This fly appeared whenever fish were being taken from the water and hovered over the fisherman to see how his subjects were being treated. Occasionally Big Biter would bite the fisherman to remind him that the fish were in his custody and to warn him against wastefulness (Fig. 121).

A fourth important function of myths is to control natural forces. Once one has gods, one can influence them by making sacrifices, offering prayers, or performing rituals. Two interesting examples of insects being used in myths to influence natural forces are found in Indian and Australian mythology. In India, the Dravidians practiced conciliatory control. The custom was to catch a locust, decorate it, revere it, and let it go, which, in turn, would cause the swarm to depart. Native bees were important providers of honey to Australian aborigines. Once the nest was found, the "sugar bag" was eagerly devoured – wax, honey, pupae, dead bees, ants and all. The stick which was used to pry the sugar bag from the tree was thrown into a fire. This simple act allowed the spirits of the bees to return to the heavens where they stay until Mayra, the wind of spring, breathes life into the flowers again. Then the bees return to earth, thus providing more honey for mankind.

The preceding insect myths clearly show that mythology is more than just entertaining stories. Important questions are also the subject matter of mythology. Myths, including many insect myths, help answer fundamental questions about human existence.

References

Capinera JL (1993) Insects in art and religion: the American Southwest. Am Entomol 39:221–229

Cherry R (1985) Sacred scarabs of ancient Egypt. Bull Entomol Soc Am 31:14–16

Kritsky G, Cherry R (2000) Insect mythology. Writers Club Press, New York, NY

Leach M (1984) Funk and Wagnalls standard dictionary of folklore, mythology, and legend. Harper, San Francisco, CA

Myxomatosis

A viral disease of New World rabbits that is transmitted by mosquitoes, blackflies, fleas, lice and mites. It has only mild effects on New World rabbits, but is quite deadly to Old World rabbits. In 1950 it was introduced to Australia to reduce the population of European rabbits that were deliberately but regrettably introduced to Australia, where they had few natural enemies. The rabbits in Australia have caused the extinction of numerous animals and plants, and caused extensive soil erosion due to overgrazing. The virus quickly reduced the population of rabbits from 600 million to 100 million, but the rabbits have developed resistance. Now another virus, rabbit calicivirus, has been introduced to attempt population suppression in Australia. Myxomatosis was also introduced to France, where it spread rapidly throughout Europe, causing significant decreases in rabbit populations, and some of the predators that fed upon them. A vaccine is used in Europe to provide protection of domestic rabbits from the virus.

► Mosquitoes
► Mosquitoes as Vectors of Viral Pathogens

N

Nabidae

A family of bugs (order Hemiptera). They sometimes are called damsel bugs.

► Bugs

Nagana

Also known as animal sleeping sickness or animal trypanosomiasis, this is a disease of animals caused by protozoans in the genus *Trypanosoma*. In humans the same disease is known as African sleeping sickness or human trypanosomiasis. It is transmitted by tsetse flies in Africa.

► Sleeping Sickness or African Trypanosomiasis
► Trypanosomes
► Tsetse Flies

Naiad (pl., naiads)

A name sometimes applied to the nymphs of hemimetabolous insects (also called paurometabolous insects) that inhabit aquatic environments (Odonata, Ephemeroptera, Plecoptera).

► Gradual Metamorphosis

Nairobi Eye

A term used by East African authors for dermatitis linearis, and especially its ocular consequences.

► Dermatitis Linearis

Nairobi Sheep Disease

This tick-borne virus is a serious problem for sheep and goats in eastern Africa.

► Ticks

Nanitic Workers

Among ants, dwarf workers resulting from inadequate nutrition.

Nannochoristidae

A family of insects in the order Mecoptera.

► Scorpionflies

Naphthalene

A hydrocarbon produced from the distillation of coal tar, naphthalene is an aromatic, white, crystalline substance. Naphthalene sublimates at room temperatures. It is sold as an insect repellent in the form of moth balls, moth flakes, or moth blocks, and commonly used to repel clothes moths and dermestid beetles from woolen clothing. In fact, however, it also has insecticidal properties, and is a good fumigant for insect collections. Exposure to fumes should be minimized, however, as there is the possibility of toxicity in humans. A similar aromatic product, paradichlorobenzene, has replaced naphthalene is some cases.

Narrow-Waisted Bark Beetles

Members of the family Salpingidae (order Coleoptera).

► Beetles

Narrow-Winged Damselflies

A family of damselflies in the order Odonata: Coenagrionidae.

► Dragonflies and Damselflies

Nasus

The snout-like organ found in soldiers of some species of Nasutitermitinae, and used to secrete poisonous or sticky secretions at intruders.

Nasute

A type of soldier termite that has a large gland which can expel defensive fluid from the cone-shaped frontal rostrum (nasus).

Natatorial

A term used to describe a structure that is adapted for swimming, and usually applied to legs of aquatic insects.

Native American Culture and Insects

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The role of insects in the culture of the indigenous peoples of North America is, for the most part, poorly documented. This is not entirely surprising, because as Europeans occupied North America, they did not attempt to document or preserve the culture of the native peoples. Generally, any cultures encountered were assumed to be inferior and attempts were made to convert the indigenous peoples to European ways. The indigenous peoples, also called Native Americans, American Indians, or Amerindians, rarely left substantial archeological evidence that would shed light on their way of life. Substantial information regarding insects and culture can be found only in western North America, where native culture remained intact until the middle or late nineteenth century. At this time, the United States government and various museums began to realize the importance of documenting the life of the various rapidly declining western tribes, so ethnologists were dispatched to observe, record and collect information and artifacts. Also, the western portion of North America is generally quite arid. The desert environment greatly enhanced the preservation of archeological artifacts, including caches of food, which provide glimpses of the roles played by insects in the cultures of indigenous peoples. The findings are based primarily on the cultures of western North America, and there is little evidence to support the idea that they are representative of North America as a whole. Also, some aspects of insects in the culture of these peoples is now obsolete, particularly the dietary elements.

The role of insects is best known in the religion or mythology of southwestern tribes, followed by the role of insects as food, in art, and then perhaps, the pharmaceutical uses of insects.

Insects in Mythology

The Navajo perform ritualized ceremonials designed to combat the maladies brought about by violation of taboo or witchcraft, or by contact with dangerous objects. Among the dangerous objects are ants, moths and crickets. An integral part of ceremonials are drypaintings (sandpaintings), which are accompanied by chants. Insects are sometimes portrayed symbolically in the drypaintings (Fig. 4). Dragonflies, for example, are used to symbolize the availability of water. On the other hand, the insects can have a significant role in the mythology. Among the common insects in Navajo mythology are:

Big Fly (Diptera: Tachinidae)

This character is a helper of humans, providing counsel or assistance to the hero of the story. Tachinid flies are associated with this character.

Cornbug (Neuroptera: Chrysopidae)

This character symbolizes reproduction, and is portrayed as either an insect or a girl. Lacewings are associated with this character.

Ants (Hymenoptera: Formicidae)

These insects are common in myths, but not in drypaintings. The images are highly anthropomorphized, or highly stylized. Ants are feared, so it is not surprising that portrayal is limited.

Butterflies (Lepidoptera)

Butterflies symbolize love, temptation and foolishness. Maladies including fainting, frenzy and trembling are attributed to contact with a moth (Fig. 2).

Spiders (Arthropoda: Arachnida)

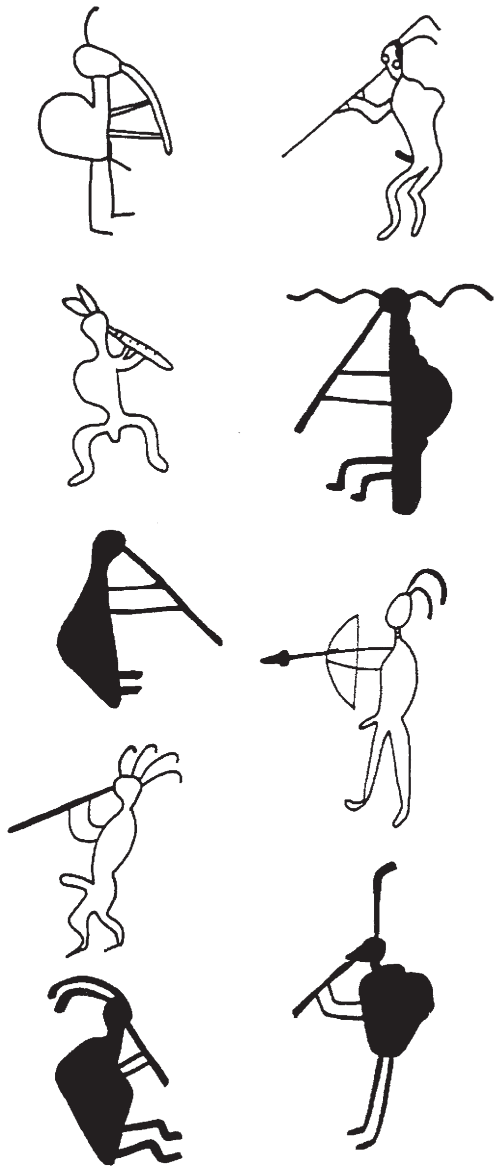
The spider holds a special place in Navajo mythology because spiderwoman is reputed to have taught the Navajo to weave. Traditional weaving contains a small hole in the center of each blanket, mimicking the hole found in the center of the spider web.

Cicada (Hemiptera: Cicadidae)

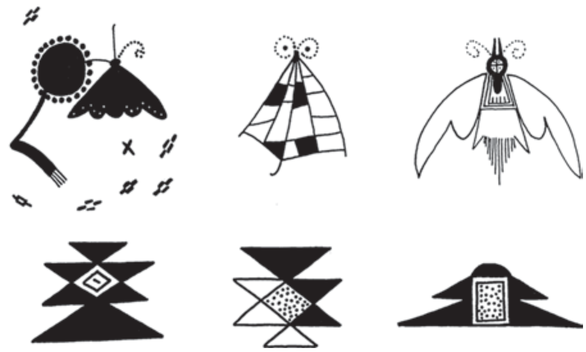
This insect often is portrayed as "humpbacked flute player," a highly anthropomorphic image that symbolizes fertility and reproduction. This character resembles a humpbacked human bearing a flute, and usually bears a pair of antennae and a large penis (Fig. 1).

From an entomological perspective, perhaps the most intriguing aspect of Navajo mythology is the legend of origin or creation, also known as "The Emergence." This myth likely relates the movement of the Navajo's ancestors from Asia, across the Bering Strait, and into the Southwest. Although there are various versions, at least one features insects, or more correctly, "insect-people."

In the Emergence Myth, there are four underworlds beneath the present fifth world. The first world, the site of origin, was inhabited by 12 types of insect-people: dragonflies, red ants, black ants, red beetles, black beetles, white-faced beetles, hard beetles, yellow beetles, dung beetles, bats, cicadas and white cicadas. The inhabitants of the first world committed adultery and quarreled constantly, and were expelled for this reason by a wall of water issued by their gods. Arriving at the second world, which was inhabited by swallow people living in mud houses, the insect people sent out cicadas to explore their new location. Although it was relatively inhospitable, they decided to stay. It was not meant to be, however, for within 24 h they were expelled for sexual misconduct. So they took flight again, led by the cicadas. They entered the third world, also barren, and occupied by grasshopper people who lived in holes in the ground. Again, they were quickly expelled for philandering, and took flight. Upon attaining the fourth world, the cicadas found a fine habitat occupied by people who tended fields, lived in houses, and cut their hair straight in the front. These people (the Pueblos) also accepted the newcomers. The insect-people were gradually transformed into humans, but retained their sinful ways. Again, the gods sent a wall of water to destroy them, but the cicadas helped the people gain access



Native American Culture and Insects, Figure 1
Various images of the humpbacked flute player, a fertility symbol from the southwestern United States.

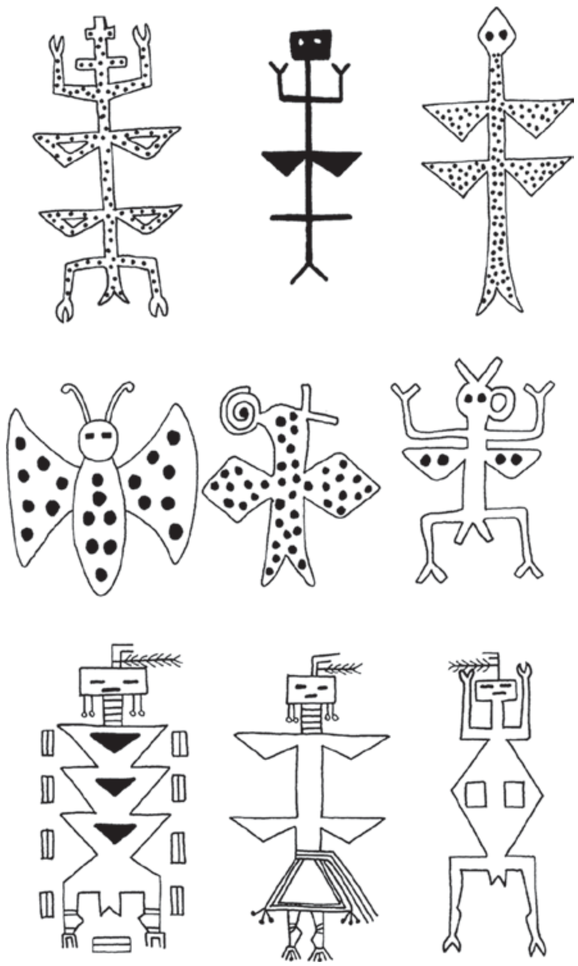


Native American Culture and Insects, Figure 2
Various images of butterflies, ranging from realistic to abstract, produced by Hopi artisans.

Native American Culture and Insects, Figure 3
Insect images from the Mimbres civilization in southern New Mexico. Note that the image at the lower right is a hybrid of a grasshopper and a pronghorn; such hybrids are not uncommon on pottery produced by this group.

to the fifth (present) world, a land ruled by grebes. The cicadas met a challenge posed by the grebes, and gained control of the fifth world for the Navajo.

The Hopi also possess interesting mythology that involves insects. Kachina is the most important ceremonial in the Hopi religious calendar. Kachina are beneficent spirit-beings who accompanied the early Hopi from the underworld, the origin of all peoples. Although the original kachinas were killed by enemies of the Hopi, the Hopi believe that the benefits formerly provided by the kachina can be accrued by wearing kachina costumes. Thus, the kachina serves as a link between the humans and the gods. Kachinas are expected to carry petitions from people, especially from the village elders, to their gods. Among the kachinas present in various ceremonies are bee, wasp, cicada,



Native American Culture and Insects, Figure 4 **Navajo images from drypaintings produced during ceremonial activities.** ***Top row*** **represents dragonflies,** ***center row*** **is butterflies and** ***lower row*** **is flies.**

Native American Culture and Insects, Figure 5 **Hopi kachinas:** ***top left*****, bee;** ***top right*****, butterfly;** ***lower left*****, wasp;** ***lower right*****, cicada.**

butterfly, robber fly, cricket and dragonfly kachinas. Kachinas have specific roles and appear at certain times of the year. Cicada kachina, for example, appears early in the year, presumably as a prayer for the arrival of summer when the real cicada occurs (Fig. 5).

Insects as Food: Entomophagy

There is considerable evidence that insects were regularly a substantial element in the Native American diet, especially during periods of deprivation though this is not presently the case. Most of the evidence comes from the testimony of early explorers traveling through the West, or early European inhabitants, but observations extend into the early twentieth century. Indigenous peoples of the Great Basin region were particularly prone to consume insects, or at least the documentation is better. Archeological evidence is harder to find, probably because insects were ground up into a mealy consistency, a common practice to make the insect food easy to store, so the remnants are easily overlooked. For example, at an archeological site in northern Utah known as the Lakeside Cave, archeologists sifted through 12 m^2 of soil using a standard 1/4-inch mesh screen, but only 28 grasshopper parts were found. This failed to suggest an important role for grasshoppers in the diet of early cave inhabitants. However, when the same soil was sifted with a 1/16-inch mesh screen, the number of grasshopper parts found increased to 8,772. Clearly, this amount of grasshopper debris is more than would occur by accident, and the evidence suggests that pulverized grasshoppers were being consumed or stored within the cave by the human inhabitants. Most likely, such evidence is frequently overlooked because insect fragments are too small to be detected by standard techniques, and anthropologists typically are not trained to consider insects to be a significant dietary element. Further examination of this same cave resulted in the discovery of 500,000 intact grasshoppers cached in the cave, mostly of a single species, *Melanoplus sanguinipes*. This represents a significant investment of energy by the cave inhabitants to collect and store this huge amount of insect matter. It was evidently quite important to these people.

Throughout the world, including present times in some countries, the occurrence of a great abundance of periodically abundant insects sometimes stimulates considerable feeding on the “bonanza” of nutritious and readily available animal food. This can be an important dietary supplement when animal protein and fat is otherwise in short supply. Several types of insects were known to be eaten by the indigenous peoples of western North America, including grasshoppers, Mormon crickets, caterpillars, flies, cicadas, beetles, ants, bees and yellowjackets. Also, insect honeydew and honey were not overlooked as a food source.

Grasshoppers (Orthoptera: Acrididae)

Grasshoppers seem to be one of the favored insect food items, probably due to their great abundance, fairly large size and ease of capture. *Melanoplus*, *Oedaleonotus* and *Schistocerca* grasshoppers are known to have been eaten. Swarming species, such as some *Melanoplus* spp., were easy prey. A common practice of the Northern Paiute was to gather them in the early morning before the grasshoppers became warm and mobile, and to store them in baskets. Alternatively, they were gathered by encirclement with fire and driven into a pit. The Washo boiled them in baskets. Among some California tribes, grasshoppers were sometimes gathered in sacks, placed in a heated trench, and covered with hot stones for 15 min before being eaten. The Northern Paiute ground the grasshoppers into flour after they were roasted, and stored them in buckskin or woven bags. The Northern Shoshoni reportedly only consumed grasshoppers during lean times, though the Eastern Shoshoni consumed them regularly. Instead of grinding, the Eastern Shoshoni placed the grasshoppers between layers of buckskin and pounded them. Southern Paiute, Uintahs, Shivwits, Cahuilla, Utes and others are known to have eaten grasshoppers, sometimes regularly, though some tribes have denied eating insects.

Consumption of grasshoppers was by no means incidental. For example, in 1831, explorers of eastern Colorado encountered a group they called “grasshopper Indians” because they apparently used grasshoppers as their chief item of food, gathering them to produce a meal from which they made mush and bread. Also, a grasshopper hunt by the Northern Shoshoni involved construction of a pit 10–12 feet in diameter and 4–5 feet deep, followed by the herding of grasshoppers from a 4–5 acre area toward the pit. The herders completely surrounded the grasshopper-infested area, gradually driving the insects to the pit. Herding involved beating the ground to induce the grasshoppers to leap forward, and such a “round-up” would frequently result in the hole being filled with grasshoppers. Once captured, the grasshoppers were roasted on sticks, boiled, crushed into a paste, or dried in the sun or before a fire.

The Native Americans were creative in their food preparation. The Utes reportedly crushed service-berries into a jam and mixed in pulverized grasshoppers, producing a kind of "fruit-cake" that was quite tasty. They also produced a mixture of sunflower seeds and grasshoppers; an early type of "trail mix," perhaps.

Mormon Crickets (Orthoptera: Tettigoniidae)

Anabrus simplex, which also is known as the Mormon cricket, the western cricket, and the Rocky Mountain cricket, is a common grasshopper-like insect in the sagebrush-dominated regions of North America. It is not a true cricket, but because it is black, flightless, and the female bears a long ovipositor, it somewhat resembles a cricket. It likely attracted the attention of Native Americans because it is quite large, flightless, gregarious and occasionally, quite numerous. Unlike true crickets, Mormon crickets are active during the day and move synchronously in large aggregations or "bands." It would seem to be relatively easy to drive large numbers of these insects into pits where they could be captured and harvested, but this was not the preferred method of harvest by the Paiute. Rather, the crickets were collected by hand early in the morning when the insects were cold and huddled together in small but dense aggregations. Once captured, they were stored in baskets and then dumped onto hot coals for roasting. Once dry, they were ground into flour and stored in buckskin bags for winter consumption. The Northern, Honey Lake and Surprise Valley Paiute, the Gosiute, Northern and White Knife Shoshoni, Ute, Washo, and some of the California tribes also used this insect for food, and in some cases, it was considered to be an important element of their diet. With these tribes, herding or driving the crickets into trenches or pits was a common method of capture.

The ethnographic and historical literature on the use of Mormon crickets as food is extensive, though archeological evidence is limited to only two sites. The crickets are 56–60% protein and 13–19% fat, so they are highly nutritious. When their large size and large numbers are also considered, it is not surprising that they were often harvested for food.

Caterpillars (Lepidoptera)

Many species of moths and butterflies, principally in the larval stage, were readily consumed. In most cases, it was probably a casual form of consumption, as caterpillars usually were not as numerous as grasshoppers and Mormon crickets in most western environments. However, they are more palatable, lacking the wings, legs and spines that make the orthopterans less appetizing. The two species that seem to have attracted particular attention as food items are pandora moth and whitelined sphinx moth.

Caterpillars of the pandora moth, Coloradia pandora, inhabit several species of pines in the western states. After feeding on pine needles, larvae descend to the ground to pupate. At this time, they are easily captured in trenches dug around the bases of the trees. Alternatively, a smoky fire can be constructed beneath an infested tree because the smoke causes the caterpillars to drop from the tree branches. Both the large caterpillar (up to 60 mm in length) and the pupal stages were popular food items. Sometimes they were barbecued on a stick, boiled, or roasted in hot ashes. Often, they were stored after being roasted. The dried caterpillars and pupae could be preserved for several months or more, and sometimes were used as an ingredient in vegetable "stew," or incorporated into "bread" along with pine nuts and sunflower seeds. One tribe near Lake Mono processed and stored 1.5 tons of caterpillars in the summer of 1920. A single individual could collect 1,000 caterpillars per day, yielding 1,800–2,800 calories per hour. This is an efficient investment of time.

Pandora moth caterpillars were popular food items for several tribes including the Eastern, Western, Owen's Valley and Mono Lake Paiute, the

Central Miwok, Tobatulabal, Yokut, Klamath and Kawaiisu. Indeed, encroachment by the Mono Lake Paiute onto the worm-gathering territory of other tribes nearly caused a war. Pandora moth caterpillars were a popular trading item among tribes. There is excellent historical data on this species as a food resource, but archeological data is limited to trenches dug around trees.

Caterpillars of the whitelined sphinx moth are common in many western habitats, and sporadically are quite abundant in desert areas, especially in the spring months. These caterpillars are large, attaining a length of about 80 mm, and when abundant, occur in dense aggregations. In the process of harvesting, the head of the caterpillar is removed, and the intestines pulled free. The remains of the caterpillars are roasted and eaten fresh, or the caterpillars are roasted until dry and then ground into a meal for storage.

Among the tribes that are whitelined sphinx moth caterpillars were the Southern and Pyramid Lake Paiute, the Western Shoshoni, Western Ute, Cahuilla, Seri, Washo and Navajo.

Shore Flies (Diptera: Ephydridae)

Flies are relatively small insects, and might not be expected to attract the attention of food gatherers. However, what they lack in size they make up for in abundance, sometimes occurring in great numbers and in environments where they are easy to collect. Although crane flies (Diptera: Tipulidae) are reported to be collected from the margins of lakes and consumed during the winter months, their use is poorly documented. However, the consumption of shore flies is well known.

The shore flies *Hydropyrus hians* and *Ephydra gracilis* occur widely in western states; larvae are found in both fresh and salt water bodies. Mono Lake, Owens Lake and Great Salt Lake are prime spots for fly breeding. The larvae may attach themselves to rocks or to other objects on the lake bottoms, or they attach themselves to each other, forming large floating mats. Sometimes hundreds of acres of lake bottom are covered by larvae. At pupation, the flies detach from the substrate, and consequently, the pupae may be driven to shore by storms or winds. The larvae may also be collected, but generally are a small proportion of the insects collected along the shore.

The Mono Lake Paiute dry the flies in the sun and mix them with berries, acorns, grass seeds and other plant products to form a type of bread. They also can be fried. Along the shore of Lake Mono, and presumably elsewhere, hundreds of tons of animal protein and fat were readily available in the form of fly bodies, and there was never any danger of starvation during the winter. In addition to the Mono Lake Shoshoni, other tribes known to collect and consume ephydrid flies include the Paiute, Panamint, and Gosiute Shoshoni, and Pah-Utes. They also were made into cakes and traded to other tribes. Tribes residing by the fly-inhabited lakes often staked out fly collecting territory because the flies were such a regular and important food item, though territorial disputes sometimes erupted among the collectors.

Cicadas (Hemiptera: Cicadidae)

The history of cicada consumption is confused by the historical use of the term "locusts" to describe cicadas. The principal consequence of this is to under-report the consumption of cicadas and to over-report the use of locusts (grasshoppers). Nevertheless, the consumption of cicadas is documented, especially during the cyclical periods of great emergence from the soil. It might be expected that cicadas would be gathered when the nymphs first appear, before transforming into winged adults. However, adult cicadas were easily gathered from bushes in the cool of the morning or early evening when it is not warm enough for the insects to take flight. Cicadas were eaten raw and cooked, often by being thrust onto hot coals long enough to burn off the wings and legs. They also were dried for use in the winter. Among the tribes consuming cicadas are the Gaiute, Northern, and Western Shoshoni, the Pahvant, the Southern and Northern Paiute and the Cahuilla. Cicadas were less important than grasshoppers, Mormon crickets and flies because they appeared in great numbers only irregularly.

Mesquite Beetles (Coleoptera: Bruchidae)

The consumption of mesquite beetles, (*Algarobius* and *Neltumius* spp.), though widespread, must be considered a marginal instance of entomophagy because it is largely inadvertent. Mesquite beetles infest the seeds of honey and screwbean mesquite. Mesquite pods containing seeds are harvested and either used immediately, or coarsely ground and saved for later use. The grinding process does not kill the mesquite beetles and they continue to develop in the bags of stored mesquite seed. In time, the bags become a living mass of beetle larvae interspersed among the seed remnants. The tribes harvesting mesquite seed are not reluctant to consume such infested material, and incorporate the larvae into their "bread." The Southern Paiute, Pima and Cahuilla were observed to engage in the aforementioned practice. Similarly, other tribes followed similar practices with respect to the harvest and consumption of acorns infested with weevils such as *Balaninus uniformis* (Coleoptera: Curculionidae).

Ants (Hymenoptera: Formicidae)

Several species of ants were a component of dishes, and sometimes were the principal component. Ants were collected by digging the nests from soil in the cool of the morning and then sifting the ants from the soil. Ants sometimes were exposed to hot coals to dry them and then ground into flour. Alternatively, they were boiled to prepare a soup. Among the tribes observed to consume ants were the Mono Lake, Northern and Southern Paiute, the Gosiute, Southern, Western, and Wind River Shohone, the Ute and the Cahuilla.

Ants are common in the western states, but are relatively small organisms and not as easily collected in great numbers as shore flies and some other insects. Thus, they probably represent a rather marginal investment of time and energy. Nevertheless, they demonstrate the opportunistic nature of food gathering in this area. Other insects collected opportunistically, but probably not comprising a major element of the diet, included bees and yellowjackets (Hymenoptera) and stoneflies (Plecoptera).

Insects in Art

The Native Americans commonly portrayed animals in their rock carvings, paintings, and sculptures, and at least in the Southwest, insects are a common element. As noted previously, several highly stylized insects are known from Navajo drypaintings. The Hopi also portray insects, but common insects such as butterflies are so stylized that they often are not recognized. Perhaps the most interesting artwork was produced by the Mimbres, an ancient tribe occupying southern New Mexico from about AD150 to AD1450. Their pottery was decorated with many animal subjects, including insects, humans and strange animal–human hybrids. About 12% of the pottery drawing represent insects. Common subjects include grasshoppers, ant lions, caterpillars and dragonflies.

The Medicinal Properties of Insects

There are numerous medicinal properties associated with insects, though most seem to be based on superstition or mythology. Some medicinal properties, and their origins, include:

Cicada (Hemiptera: Cicadidae)

Consumption is considered to be useful for treatment of broken bones, sores, asthma, bronchitis, and contagious diseases such as influenza, measles and smallpox (Navajo).

Crickets (Orthoptera: Gryllidae, Gryllacrididae, and Tettigoniidae)

Crickets are feared, and not handled because they are associated with ghosts (Navajo).

Jerusalem Crickets (Orthoptera: Stenopalmatidae)

These insects are believed to be poisonous, and are useful for the removal of hair, and can produce spots on the skin (Navajo).

Grasshoppers (Orthoptera: Acrididae)

The oral secretion of grasshoppers is considered to be poisonous if eaten (Navajo).

Hornworms (Lepidoptera: Sphingidae)

Hornworms are considered to be poisonous, and can cause nose bleeds. On the other hand, the oral secretion, if mixed with water, is said to be good to counteract the effects of too much smoking (Navajo).

Butterflies and Moths (Lepidoptera)

Butterflies cause vomiting and dysentery, but also can cure vomiting (Papago). Caterpillars taken from ears of corn are fed to children to counteract a stomach ache caused by eating too much corn (Tewa).

Darkling Beetles (Coleoptera: Tenebrionidae)

The secretion of the posterior end of the abdomen, when mixed with water, is applied to insect bites to sooth itching. It is also used as a mouthwash for a sore mouth (Navajo).

Flies (Diptera)

Flies should not be allowed on food because the food will be poisoned and will cause sickness (Navajo).

Bees (Hymenoptera: Apidae)

Bee stings can be treated by the topical application of bee stingers in water, or a mixture of bee stingers, mud, honey and wax. On the other hand, a treatment for the flu is to allow bees to sting the sick person. Also, rubbing the honeycomb on the skin is considered to be good for measles and also for protection against witches. Inhaling ground and burned bees is good for the treatment of smallpox (Navajo). Bees, when heated in a fire, give off a pungent odor useful in reviving an unconscious person (Comanche).

Ants (Hymenoptera: Formicidae)

Ants are greatly feared by the Navajo, and thought to be associated with witchcraft. The consumption of ants is thought to cause kidney or bladder problems (Navajo). Ingested with eagle down, or allowed to sting the stomach, ants can cure bad colds or paralysis (Tubatulabal). Fried ants are rubbed on the legs of children to make them straight and strong (Tewa).

Velvet Ants (Hymenoptera: Mutillidae)

Aqueous extracts of velvet ants are used to treat sores (Navajo).

Wasps (Hymenoptera)

Wasp stings cure rheumatism (Ojibway).

Spiders (Arthropoda: Arachnida)

All spiders are considered to be poisonous (Navajo).

Some of the aforementioned medicinal properties of insects are not surprising. Treatment of bee stings with mud, for example, is common folklore. Bee sting therapy is embraced by many as a curative for various ailments. The prohibition against eating food contaminated by flies also makes sense. Perhaps the most interesting is the belief that the ill effects of smoking can be counteracted by hornworm properties; hornworms, incidentally, are among the most important defoliators of tobacco, and so the association is logical. The Navajo, unlike many of the Great Basin inhabiting tribes, did not regularly consume insects, so it is not surprising that they would hold various beliefs that ingestion was deleterious.

References

Capinera JL (1993) Insects in art and religion: the American Southwest. Am Entomol 39:221–229

Capinera JL (1995) Humpbacked flute player and other entomomorphs of the American Southwest. Am Entomol 41:83–88

Hitchcock SW (1962) Insects and Indians of the Americas. Bull Entomol Soc Am 8:181–187

Sutton MQ (1988) Insects as food: aboriginal entomophagy in the Great Basin. Ballena Press Anthropological Papers 33:1–115. Ballena, Menlo Park, CA

Wyman LC, Bailey FL (1964) Navajo Indian ethnoentomology. University of New Mexico Publications in Anthropology 12:1–158

Natural Control

Maintenance of an insect population at nonoutbreak levels by the natural regulatory factors, including both biotic and abiotic factors. Also known as natural population regulation.

Natural Enemies

Organisms normally killing arthropods that people consider to be pests, without human intervention. Examples of natural enemies include predatory insects or vertebrates, insect parasitoids, and microbial pathogens causing disease (Table 1).

Natural Enemies Important in Biological Control

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All arthropods and weeds have a diverse array of natural enemies. Microorganisms, invertebrates, and vertebrates all affect arthropods. Pathogens (including viruses, bacteria, and fungi) are important natural enemies of insects, mites, and weeds. Many vertebrates (including birds, lizards, fish, and frogs) feed on pest arthropods. Nematodes belonging to several families attack arthropods, with entomopathogenic nematodes in the families Steinernematidae and Heterorhabditidae particularly effective as biological control agents of soil-inhabiting insects.

By far, insects are the most numerous and diverse natural enemies of other insects, with hundreds of thousands of species feeding on other insects. Species in all of the major orders of insects consume other insects, with their feeding specificity ranging from incidental to obligatory. More than 200 families in 15 orders are entomophagous. Entomophagous insects are categorized either as parasitoids or predators.

Parasites or Parasitoids?

Several special terms are used to describe parasitic insects. An insect that develops in or on a single insect host or on the eggs of one host is a parasitic insect. However, the term parasitoid

Natural Enemies Important in Biological Control, Table 1 Some parasitoids and predators of arthropod pests

Parasitoids	
Diptera	
Bombyllidae	Lepidopteran, hymenopteran and coleopteran larvae, Orthoptera eggs
Cryptochetidae	Larvae parasitoids of scale insects
Sarcophagidae (some)	Lepidoptera pupae, locust and spider eggs
Tachinidae	Host range broader than Hymenoptera
Hymenoptera	
Bethyloidea (most)	Lepidoptera and Coleoptera larvae
Chalcidoidea (30+ families), including Mymari-dae, Trichogrammatidae	Coleoptera, Diptera, Hemiptera, Lepidoptera
Aphelinidae, Eupelmidae, Encyrtidae,Pteromalidae, Spalangiidae, Torymidae	
Ichneumonoidea (thousands of species) including Braconidae, Ichneumonidae	Lepidoptera, Coleoptera Diptera, Hemiptera, Hymenoptera
Proctotrupoidea (several families) including Platygasteridae, Scelonidae	Diptera, Hemiptera, Lepidoptera, Hemiptera, Orthoptera
Predators	
Acari	
Anystidae	Tetranychidae, Thysanoptera
Cheyletidae	Tetranychidae, scale insects
Erythraeidae	Tetranychidae, Orthoptera, Thysanoptera, Hemiptera, Lepidoptera, Coleoptera
Hemisarcoptidae	Scale insects; phoretic on coccinellids
Phytoseiidae	Tetranychidae, Eriophyidae, Thysanoptera
Pyemotidae	Lepidoptera, Coleoptera
Stigmaeidae	Tetranychidae, Eriophyidae
Coleoptera	
Cantharidae (many)	Larvae predators of insects
Carabidae	Lepidoptera, misc. insects, snails
Cleridae (most)	Wood-boring Coleoptera, Lepidoptera, Hymenoptera larvae
Cicindelidae	Miscellaneous insects
Coccinellidae	Hemiptera, Lepidoptera, Coleoptera, Acari
Dytiscidae	Aquatic insects
Histeridae	Misc. arthropods in dung, carrion, logs

Natural Enemies Important in Biological Control, Table 1 Some parasitoids and predators of arthropod pests (Continued)

Parasitoids	
Lampyridae	Snails, annelids, Coleoptera adults
Silphidae	Diptera and Lepidoptera larvae, snails
Staphylinidae	Miscellaneous small arthropods
Diptera	
Anthomyiidae (some)	Orthoptera eggs, Misc. insects
Asilidae	Soil insects
Cecidomyiidae	Hemiptera, Thysanoptera, mites
Syrphidae	Hemiptera, Coleoptera, Lepidoptera, Thysanoptera
Hemiptera	
Anthocoridae (*Orius*)	Hemiptera, Lepidoptera, Coleoptera, Thysanoptera, mites
Belostomatidae	Aquatic insects
Corixidae	Mosquito larvae
Gerridae	Mosquitoes
Lygaeidae (*Geocoris*)	Hemiptera, Lepidoptera, mites
Nabidae	Hemiptera, Lepidoptera, mites
Notonectidae	Mosquitoes
Pentatomidae (some)	Lepidoptera, Coleoptera
Reduviidae (some)	Miscellaneous insects
Hymenoptera	
Formicoidea	Miscellaneous insects
Sphecoidea	Orthoptera, Hemiptera, Diptera, Lepidopter
Vespoidea	Lepidoptera and Coleoptera larvae
Mantodea	
Mantidae	Miscellaneous insects
Mecoptera	
Three families	Miscellaneous small insects, mites
Neuroptera	
Chrysopidae	Hemiptera, Lepidoptera eggs and larvae, Thysanoptera, Tetranychidae
Coniopterygoidea	Mites, aphids
Hemerobiidae	Hemiptera, Lepidoptera eggs and larvae, Tetranychidae
Myrmeleontidae	Ants, soil surface insects
Odonata	
Sixteen families	Aquatic insects while immature; flying insects as adults
Thysanoptera	
Three families	Small insects, mites
Nematoda	

Natural Enemies Important in Biological Control, Table 1 Some parasitoids and predators of arthropod pests (Continued)

Parasitoids	
Heterorhabditidae	Lepidoptera, some Coleoptera, Diptera, Orthoptera
Mermithidae	Mosquitoes, miscellaneous other species
Neotylenchidae	Weevils and woodwasps
Steinernematidae	Coleoptera, Diptera, Hemiptera, Hymenoptera, Isoptera, Lepidoptera, Neuroptera, Odonata and Orthoptera

Not all species in each family are predators or parasitoids. Other families and orders have predatory species, but are not included

often is used for parasitic insects because these insects differ sufficiently from true parasites to justify a distinctive term. Parasitoids are distinctive because:

- During development a parasitoid destroys its single host, whereas parasites usually do not kill their host.
- The host is usually of the same taxonomic class (insects), but parasites are not.
- They usually are nearly the same size as their hosts, but parasites usually are smaller.
- They are parasitic as larvae only, with the adults being free-living, but parasites are usually parasitic their entire life cycle.
- During a parasitoid's life cycle, they live on or in a single host, but parasites may have more than one host during different stages in their life cycle.
- Their action resembles that of predators more than that of true parasites in the population dynamics of pests.

Most parasitoids are found in the orders Diptera and Hymenoptera, with hymenopteran parasitoids the most numerous and diverse (Fig. 8). Parasitoids have a complete metamorphosis, including a pupal stage, and have wings that develop internally. Immature stages differ markedly from adults in structure, food needs, and habitat. Many parasitoid females have a preoviposition period when they feed on nectar of flowers, honeydew, or host insects.

Categories of Parasitoids

Parasitoids can be classified based on their mode of attack and type of host. Many females sting and paralyze their hosts prior to depositing an egg. Endoparasitoid females deposit their egg(s) within the host's body. Many endoparasitoids develop within their hosts, but emerge from them to pupate. Others pupate inside their host within a mummy, which is the modified exoskeleton of the host insect. Some endoparasitoid females deposit female eggs in larger hosts and male eggs in smaller hosts; larger hosts produce larger parasitoid females which can live longer and deposit more eggs. Sometimes hosts respond to parasitization with an immune response (called encapsulation).

Encapsulation is an immune response in which host blood cells surround and kill the developing parasitoid. Parasitoid progeny can escape encapsulation by hiding in host tissues that have no immune defenses. Other parasitoids interfere with the host's immune system by injecting substances into the host that influence the physiology of the host. These materials include viruses (polydnaviruses) that grow in cells in the reproductive tract of the parasitoid female and are deposited when the parasitoid female deposits her egg, or chemicals produced in the reproductive tract. Parasitoids may influence the development (by preventing molting) or behavior of their hosts (by causing them to eat more food or to pupate in different sites than normal).

Ectoparasitoids deposit their eggs on the outside of their hosts (usually insect larvae) and the immature parasitoids feed there. Ectoparasitoids often paralyze their hosts with venom before ovipositing to prevent the host from removing the egg. Ectoparasitoids are most commonly found attacking hosts that occur in concealed habitats such as plant stems or seeds. Both ectoparasitoids and endoparasitoids are termed solitary if only one individual develops per host, but some parasitoid species produce several progeny in a single host and are called gregarious. Gregarious parasitoid females apparently can measure the size of their hosts and will deposit more eggs in larger hosts. An extreme example of gregarious development is found in polyembryonic species in which a single egg divides to produce several hundred identical progeny.

Superparasitism occurs when an individual host is attacked by more parasitoids of the same species than can develop successfully. If superparasitism occurs, small adults will emerge or some or all of the progeny will die. Many parasitoids can detect whether hosts have been previously parasitized and will avoid depositing eggs in these hosts.

Multiple parasitism occurs when more than one species of parasitoid attacks the same host. If multiple parasitism occurs, interactions between the immature parasitoids usually results in the death of some or all of the progeny. All stages of host insects are subject to attack. Some parasitoids attack eggs, others larvae, and some pupae; only a few parasitize adults. A particular host may be attacked at different stages by different parasitoid species. Some parasitoid females must feed on hosts to obtain sufficient proteins to deposit their eggs, but such host feeding does not always kill the host. Some parasitoids feed only on nectar or honeydew as adults.

Parasitoids vary in the number of species of host they attack; some attack only one or a few closely-related host species and are considered host specific. Other parasitoids are able to develop in a broad range of hosts and are termed polyphagous. Some parasitoids attack only plant feeding insects, while others specialize in attacking other parasitoids.

Parasitoids that attack and develop within other parasitoids are called hyperparasitoids. Parasitoids that only occasionally attack other parasitoids are called facultative hyperparasitoids. Those that always attack other parasitoids are obligatory hyperparasitoids. Hyperparasitoids may even be attacked by other hyperparasitoids. Hyperparasitoids are potentially detrimental to effective biological control programs, so parasitoids imported for classical biological control must be evaluated in the quarantine facility to determine whether they are potential hyperparasitoids.

Males and females of most parasitoid species develop in a similar manner in the same host, but this is not the case in some genera of aphelinid wasps (Hymenoptera: Aphelinidae). Aphelinid females develop as endoparasitoids of Hemiptera. Males of the same species may develop as endoparasitoids of different hemipteran species, as endoparasitoids of lepidopteran eggs, or as hyperparasitoids of females of its own species.

Another variation on life histories in parasitoids is found in cleptoparasitoids, which require a paralyzed host for their progeny to develop. Because they are unable to paralyze a host, cleptoparasitoids use hosts paralyzed by other parasitoids after eliminating the progeny of the first species. As a result, cleptoparasitoids also are considered undesirable in classical biological control programs.

Adult parasitoids are usually active, flying insects that seek out their hosts in the environment using a variety of cues from the target host and its habitat. Visual, olfactory, and tactile cues are used by parasitoids to find their hosts. When a host is found, the female lays an egg in, on, or near the host. Parasitoid larvae feed on host tissues but may not kill their host until the host has fed and developed to adulthood. Parasitoids pupate in or near the host, and emerging adults mate and disperse to search for hosts or other food sources.

Host finding in parasitoids is complex, and we are still learning how these small insects find their hosts in a complex environment. Long-range chemical attractants have been identified both from plants and insect hosts. Volatile chemical cues produced by the plant or by the insect host as a byproduct of feeding or development are detected by many parasitoids. For example, some parasitoids respond to the volatile sex pheromones produced by their insect host or to odors from the feces of their hosts. Other parasitoids are able to detect damaged foliage by changes in color or shape. Some tachinid parasitoids (Diptera: Tachinidae) are attracted to their cricket or cicada hosts by the sounds they produce. At close range, chemical stimuli also serve to arrest parasitoids so that they initiate an intensive search pattern on substrates where hosts may be present. These chemical cues may be less volatile, are often detected by the parasitoid by contact, and may be found in silk, feces, or exuviae from molting hosts. Both gregarious and solitary parasitoids may produce chemical markers, called oviposition deterrents, that they place on or in their hosts to reduce superparasitism.

Parasitoids (and predators) are capable of associative learning. Previous experience with host/prey insects, and the odors associated with them, may influence what the natural enemy searches for in the environment. The entire host-finding process and the factors that influence it are known for only a few parasitoid species and much of the work was conducted under laboratory conditions. We must learn more about the behavior of parasitoids (and predators) under natural conditions in the environment in order to learn better how to improve their efficacy in pest management programs.

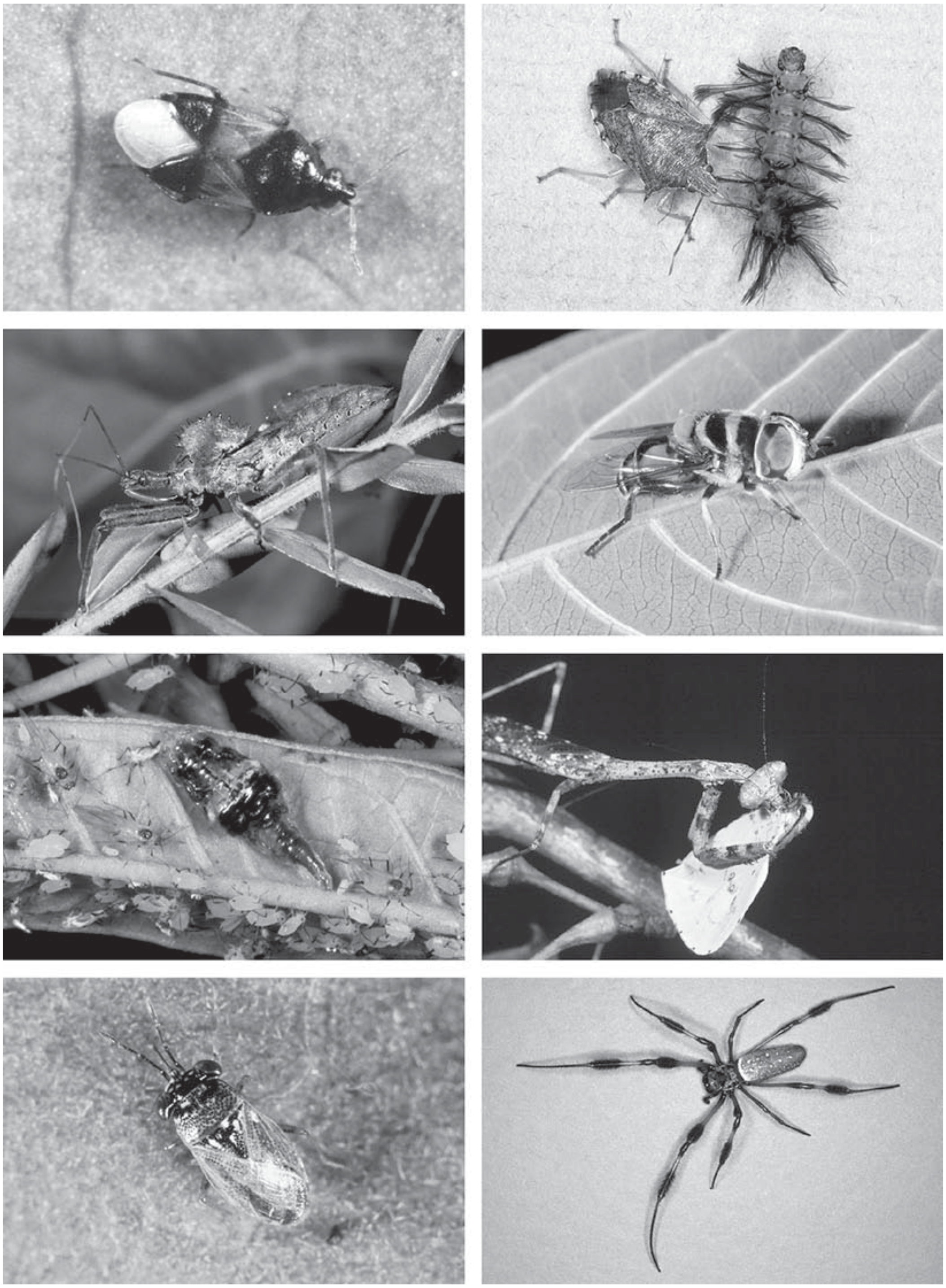
Dipterous parasitoids usually have a 1:1 ratio of males to females, and are diploid. Hymenopterous parasitoids usually have strongly female-biased sex ratios (often two females to one male) and may have a genetic system called arrhenotoky or thelytoky. Thelytoky describes a condition in which all individuals in the population are females (or only a tiny fraction of males are produced). Arrhenotoky produces both male and female progeny; typically male progeny are produced by unfertilized (haploid) eggs and females are produced from fertilized (diploid) eggs. Mated arrhenotokous females often can control the sex ratio of their progeny based on cues from the environment, such as host size, host quality, or crowding. If solitary arrhenotokous parasitoids become inbred, the sex ratio may be altered to produce excess males. Inbreeding by gregarious parasitoids that mate on or near their hosts is probably common, and rarely results in an altered sex ratio. Microbial organisms associated with parasitoids may also alter sex ratios; for example, a bacterium called *Wolbachia* has been found to make populations of arrhenotokous species produce only females (thelytoky). Elimination of the *Wolbachia* by feeding adult parasitoids antibiotics sometimes can restore the normal sex ratio. The life histories, behavior, and genetics of parasitoids are incredibly diverse and we have a great deal left to learn.

Predators

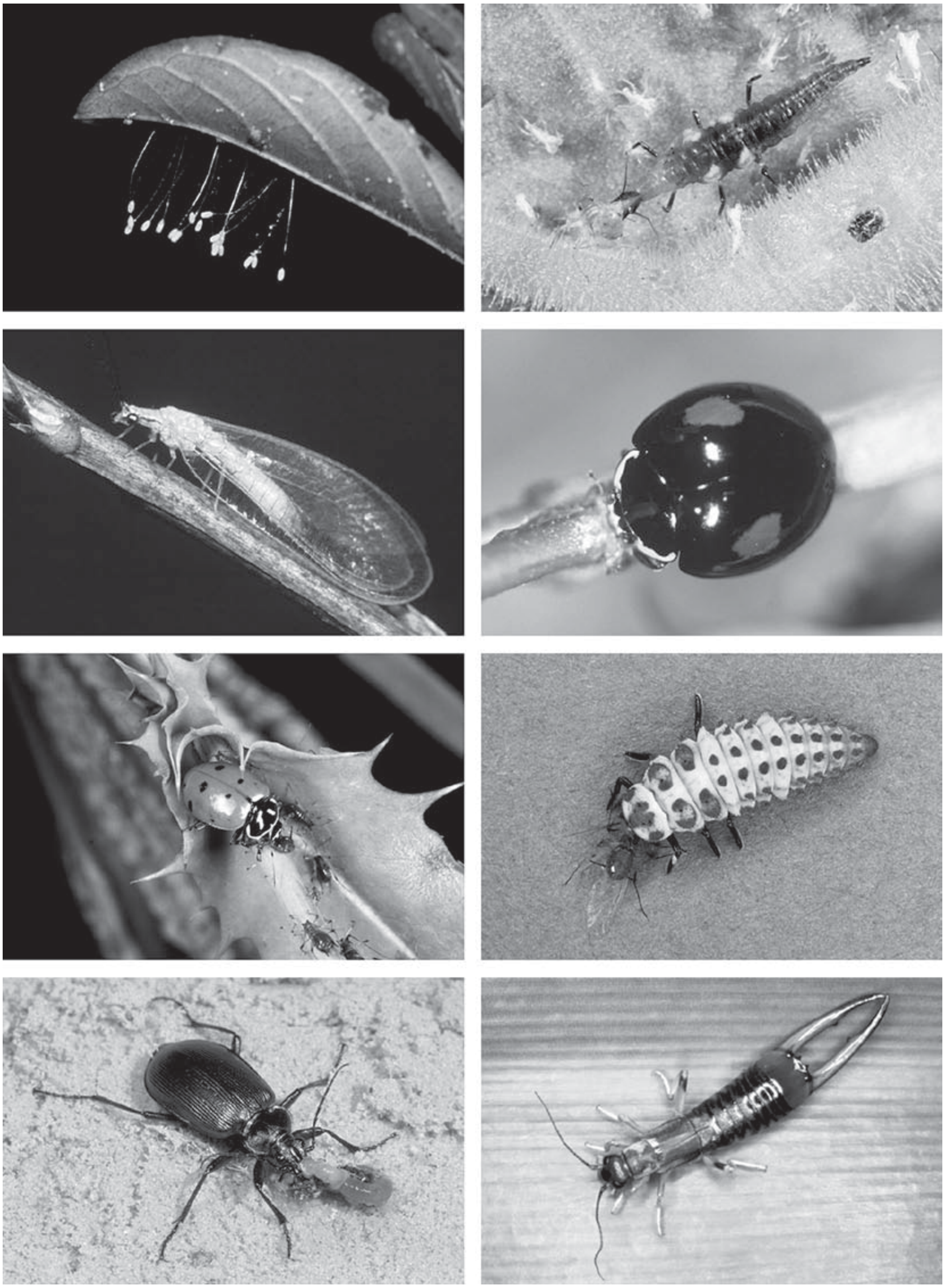
A predatory insect generally is free-living as a larva, kills its prey immediately by direct attack, and requires a number of prey individuals to provide sufficient food for it to develop to adulthood. Some predators can feed, develop, and reproduce on pollen, nectar, or other alternative foods. Others are predators as immatures, but feed on alternative foods as adults. Some are obligatory predators in both the immature and adult stages. Honeydew is an important source of protein for many adult predators in the orders Neuroptera and Diptera (Figs. 6 and 7), influencing their longevity, ability to reproduce, and distribution.

Immature predators typically must find several prey individuals to develop to adults. The searching behavior of predatory larvae and adults is important in understanding predator–prey interactions in biological control. Prey selection by adult predators ranges from highly selective (monophagous or oligophagous) to comparatively broad (polyphagous).

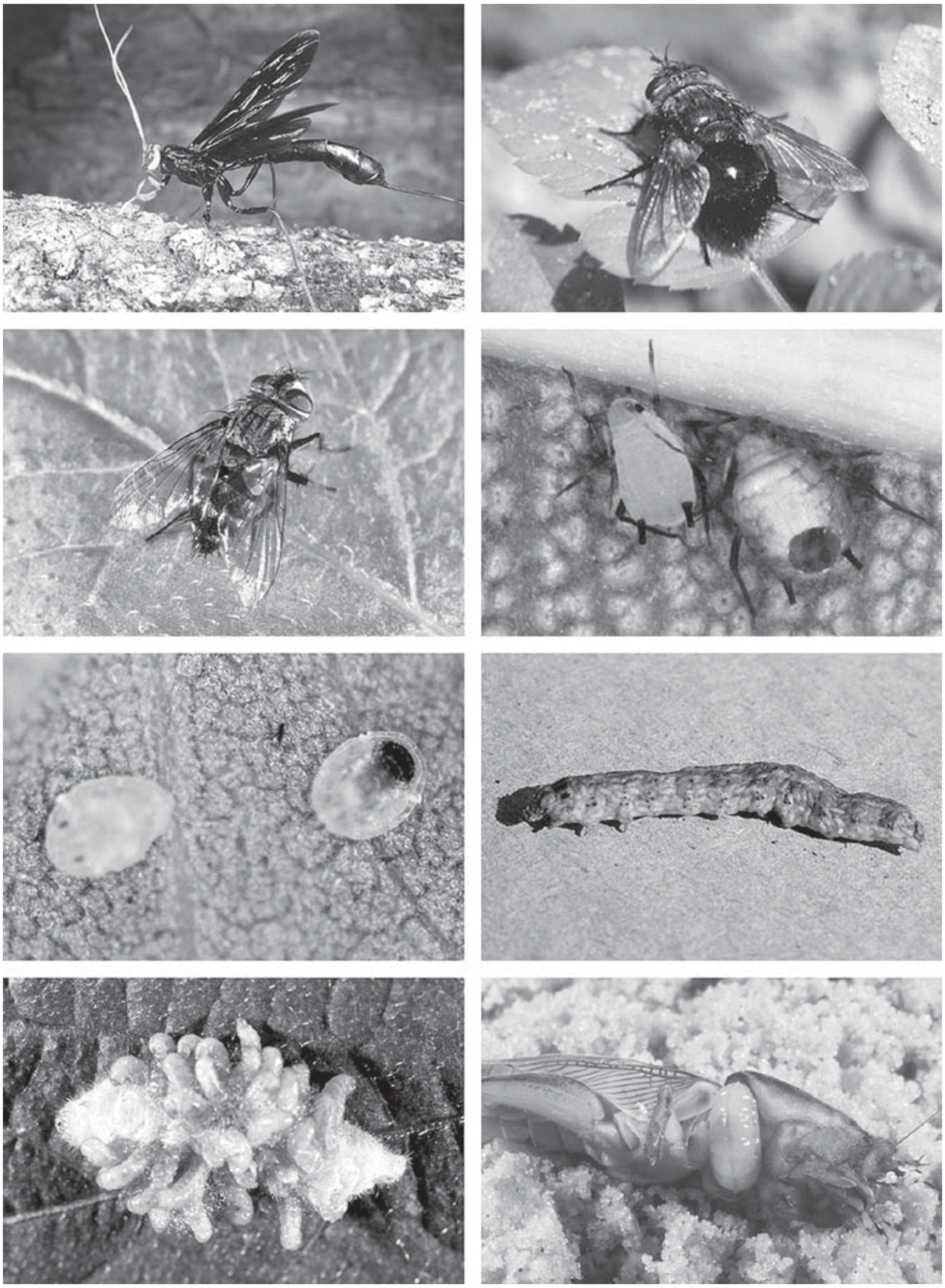
There is considerable debate over the relative importance of generalist versus more-specialized predators in biological control. Monophagous predators feed on one prey species, oligophagous predators feed on several, while polyphagous



Natural Enemies Important in Biological Control, Figure 6 **Some common predatory insects. *Top row, left*: minute pirate bug, *Orius* sp.; *top row, right*: a stink bug, *Alcaeorrhynchus grandis*; *second row, left*: wheel bug, *Arilus cristatus*; *second row, right*: a flower fly, *Palpada* sp.; *third row, left*: a flower fly larva feeding on aphids; *third row, right*: a mantid feeding on a butterfly; *bottom row, left*: bigeyed bug, *Geocoris* sp.; *bottom row, right*: golden silk spider, *Nephila clavipes*. (Photo credits: Palpada, J.L. Capinera; flower fly larva, L. Buss; all others, J.L. Castner.)**



Natural Enemies Important in Biological Control, Figure 7 **Additional predatory insects. *Top row, left*: eggs of green lacewing; *top row, right*: larva of green lacewing; *second row, left*: adult green lacewing; *second row, right*: twicestabbed lady beetle, *Chilocorus stigma*; *third row, left*: convergent lady beetle, *Hippodamia convergens*; *third row, right*: lady beetle larva; *bottom, left*: ground beetle, *Calosoma calidum*; *bottom, right*: an earwig, *Doru* sp. (Photo credits: earwig, J.L. Capinera; all others, J.L. Castner.)**



Natural Enemies Important in Biological Control, Figure 8 **Some parasitic insects. *Top row, left*: yellowheaded ichneumon, *Megarhyssa atrata*; *top row, right*: a tachinid fly, *Archytus* sp.; *second row, left*: a tachinid fly, *Myiopharus doryphorae*; *second row, right*: oleander aphid and aphid mummy showing escape hole from which wasp has emerged; *third row, left*: immature silverleaf whiteflies showing healthy and parasitized (blackened) individuals; *third row, right*: army cutworm larva parasitized by polyembryonic wasp – note the numerous small larvae developing within the cutworm; *bottom, left*: imported cabbage butterfly remains showing pupae of *Cotesia* sp.; *bottom, right*: tawny mole cricket parasitized by the ectoparasitic wasp *Larra bicolor*. (Photo credits: *Myiopharus*, army cutworm, and cabbage butterfly, J.L. Capinera; mole cricket, L. Buss; all others, J.L. Castner.)**

predators may feed on many species. Polyphagous predators may shift to the most abundant prey species, which can stabilize prey populations in a community. If highly mobile, polyphagous predators may be effective in providing control of pests in disturbed environments. Monophagous or oligophagous predators tend to be associated with prey in more stable systems. Eggs of predators are often deposited by females in close proximity to their prey. Predators often use visual and chemical cues to locate plants with prey, and also may use chemical cues produced by prey as cues.

Predatory insects widely recognized in pest management programs primarily are found in the orders Coleoptera, Diptera, Hemiptera, Hymenoptera, and Neuroptera. More than half of all insect predators are beetles.

The Coccinellidae (the ladybeetles or ladybirds) particularly have been studied by biological control workers. Larger species of ladybeetles feed on scale insects, mealybugs, aphids, and whiteflies. Smaller ladybeetles in the genus *Stethorus* are highly effective predators of spider mites. Carabids are usually nocturnal and most abundant in moist environments, and feed on lepidopterous larvae and pupae in the soil or litter. Staphylinid beetles are numerous, yet we know relatively little about them. Most are found in decaying organic matter such as dung and carrion, but one group of species are parasitic on fleas, ants and termites.

Dipteran predators include the Asilidae, Syrphidae, some Cecidomyiidae, and Chamaemyiidae. Some syrphid and cecidomyiid larvae are effective predators of aphids. The Chamaemyiidae are known as predators of aphids, scale insects, and mealybugs.

Among the Hemiptera, some species in the family Lygaeidae are predators, with *Geocoris* species among the best known. The family Anthocoridae includes *Orius* species, which are predators of many small arthropods. A number of aquatic insects are predators of other insects, including the Odonata, Belostomatidae, Dytiscidae, and Notonectidae.

Most Neuroptera are predators, particularly the green and brown lacewings (Chrysopidae and Hemerobiidae). These predators feed on scale insects, aphids, mealybugs, mites, and other small arthropods.

Many of the Hymenoptera are predators, with the ants (Formicoidea) the most important group. Ants may be highly effective predators of insect larvae, pupae, and adults, but they have a negative effect if they interfere with other natural enemies or are direct pests themselves. Other hymenopterous predators include wasps in the Vespidae and Sphecoidea, which provision their nests with insects for their progeny to feed on as they develop.

Other predatory arthropods include the Acari (or mites) and Arachnida (or spiders). Predatory mites in the family Phytoseiidae have been demonstrated to be effective biological control agents of spider mites, thrips, and eriophyid mites in both classical and augmentative biological control. There are at least 30,000 species of spiders, many of which are predators of insects if the environment in which they develop receives few pesticide applications. Predators may be very abundant in numbers of species and individuals in ecosystems that are untreated with pesticides. For example, over 600 species of predators were found in Arkansas cotton fields and over 1,000 were found in alfalfa in California. However, the effect of a particular predator on a specific target pest is difficult to determine because many predators feed on so many different types of prey. As a result, few predators are known to be able to suppress populations of specific pests. Furthermore, many predators are active in the evening or at night, which makes it difficult to measure their effects or observe them.

Pathogens

Pathogens of insects and mites include bacteria, fungi, viruses, and microsporidia (Fig. 9). Pathogens could be used in biological control programs in at least two ways: augmentation (mass rearing and release) and conservation of naturally occurring pathogen populations. We can rely on naturally occurring pathogens to reduce insect and mite populations or we can commercialize effective pathogens and apply them as pesticides.

Microbial pathogens reduce insect and mite populations in natural environments, but relatively few have been developed commercially as microbial pesticides. An exception is the bacterium *Bacillus thuringiensis* (Bt), different strains of which can be applied as sprays to suppress lepidopteran and coleopteran pests. A toxin gene from Bt has been extracted from the bacterium and inserted into a number of agricultural crops; when this protein is produced in the crop plant, insects feeding on the crop are killed (Fig. 9).

Nematodes that Attack Insects

Although approximately 40 families of nematodes are associated with insects, only two families, Steinernematidae and Heterorhabditidae, are used extensively in biological control at this time. Most steinernematid or heterorhabditid nematodes are employed in augmentative releases. These nematodes contain mutualistic bacteria (*Xenorhabdus*) within their guts. Once the nematodes have entered their insect host, the bacteria are released into the hemolymph and multiply to serve as food for the nemotodes. It is the bacteria that kill the insect host in a relatively short time by causing septicemia.

Steinernematid and heterorhabditid nematodes have a simple life cycle, including the egg, four larval stages, and the adult. Both have a third stage larva called the dauer. The dauer is ensheathed in the cuticle of the second larval stage, making it relatively resistant to environmental stresses. The dauer stage is infective and enters the insect through either the mouth, anus, or spiracles. Once within their hosts, the nematodes release *Xenorhabdus*, which multiply and kill the host within 24–48 h. The nematode feeds on the bacterial cells and host tissues, develops to an adult, and reproduces. As bacteria and insect tissues are depleted and the nematodes become crowded, the progeny of the second or third generation develop into dauers, which exit from the dead host. Once out of their dead host, the dauers seek new hosts. If none are found, dauers can survive for weeks to months if the relative humidity is sufficiently high. The behavior of dauers varies from species to species. Some search for hosts on the soil surface, some wait in ambush for insect hosts, while others remain deeper within the soil.

Steinernematids and heterorhabditids have a broad host range under laboratory conditions, particularly when high relatively humidities can be maintained. However, in the field, the effective host range is determined by the nematodes' searching behavior and requirements for high relative humidities. The survival or persistence of dauers is crucial in the effective use of these nematodes for biological control. Applications of dauers to control foliage-feeding insects generally have been unsuccessful because they are not adapted to the environmental conditions found on exposed surfaces; low moisture, sunlight, and high temperatures are lethal.

The soil is the natural habitat for these nematodes, and they have been most effectively used to control soil- or tunnel-inhabiting pest insects. Heterorhabditids have a greater tendency to move down and have superior host-seeking ability compared to steinernematids, making them effective against pests such as Japanese beetle, *Popillia japonica*, and root weevils. Steinernematids show a preference for soil near the surface and may be better adapted to attack pests such as cutworms, which feed at or near the soil surface. Applications of *Steinernema scapterisci* against mole crickets, *Scapteriscus* spp., can be highly effective.

The efficacy of *Steinernema carpocapsae*, a nematode that is commercially produced and sold, has been demonstrated against white grubs (larvae of Scarabaeidae: Coleoptera), which are major pests of turf, pastures, sugarcane and forests, and

Natural Enemies Important in Biological Control, Figure 9 **Some insect diseases. *Top row, left*: acacia whitefly infected with *Aschersonia* fungus; *top row, right*: clover cutworm infected (pale color) with cytoplasmic polyhedrosis virus; *second row, left*: seedcorn maggot infected with *Entomophthora muscae* fungus; *second row, right*: grasshopper infected with *Entomophaga grylli* fungus; *third row, left*: European corn borer infected with *Beauveria bassiana* fungus; *third row, right*: grasshopper infected with *Metarhizium anisopliae*; *bottom, left*: mole cricket infected with *Steinernema scapteriscus* nematodes; *bottom, right*: celery looper infected with baculovirus. (Photo credits: acacia whitefly, L. Buss; all others, J.L. Capinera.)**

against weevils (Curculionidae: Coleoptera), which are pests of pastures, turf and other crops. Both pest groups are difficult to control with chemical pesticides. Commercial firms are selling *Steinernema carpocapsae* for control of the black vine weevil (*Otiorhynchus sulcatus*) in nurseries and cranberry bogs.

Mass production techniques and methods for distributing and applying *S. carpocapsae* are being improved by commercial producers. Steinernematid infective stages can be stored for as long as five years under cold, moist conditions. They can be applied using standard pesticide application equipment with large spray nozzles or with syringes, cotton swab plugs, oil cans, and back pack sprayers. Soils can be treated by applying the nematodes in drip irrigation systems or by drenching. In general, nematode applications have a short-term impact, but a few examples are known in which nematodes have persisted in the soil for long periods.

Heterorhabditis species or other species of *Steinernema*, such as *S. glaseri*, have provided superior control of certain pests. Unfortunately, the development of mass production and application techniques for these other nematode species has lagged. It is likely that when production and storage capabilities improve for species other than *S. carpocapsae*, improved control of other pests will be achieved. Meanwhile, researchers continue to identify new nematode species, more highly-mobile or cold-active strains, and to develop improved application techniques with the goal of providing control of a broader range of insect pests.

► Augmentative Biological Control
► Classical Biological Control
► Conservation Biological Control
► Microbial Control of Insects

References

Askew RR (1971) Parasitic insects. Heinemann, London
Clausen CP (1940) Entomophagous insects. McGraw-Hill, New York, 688 pp
DeBach P (ed) (1964) Biological control of insect pests and weeds. Reinhold, New York
Gaugler R, Kaya HK (eds) (1990) Entomopathogenic nematodes in biological control. CRC, Boca Raton
Huffaker CB, Messenger PS (eds) (1976) Theory and practice of biological control. Academic, New York
Tumlinson JH, Lewis WJ, Vet LEM (1993) How parasitic wasps find their hosts. Sci Am 226:100–106
Waage J, Greathead D (eds) (1986) Insect parasitoids. Academic, London

Natural Enemy Attraction to Plant Volatiles

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Leaves normally release low levels of volatile chemicals. However, when a plant is damaged by herbivorous insects, the emission of volatile organic compounds increases. The chemical composition varies with the herbivorous insect species as well as the plant species. Volatile phytochemicals can serve as airborne semiochemicals, deterring or promoting interactions between plants and insect herbivores. For example, moths (*Heliothis virescens*) are repelled by herbivore induced volatiles released from tobacco plants at night; such odor cues may allow females to avoid oviposition on previously damaged plants. For swallowtail butterflies, volatiles from host plants enhance the effect of contact stimulants, increasing landing rates and oviposition relative to non-host plants. Volatile plant signals may also induce defense responses in neighboring plants. Such semiochemicals that function in communication between and among species are emitted from a diverse group of plants and mediate key processes in the behavior of specific insects.

Plant Volatiles Signal of Beneficial Insects

In addition to the bouquet of compounds that render leaves attractive or disagreeable to herbivores, volatile terpenoids and other compounds emitted from leaves in response to insect damage allow insect parasitoids (such as parasitic wasps) and predators to distinguish between infested and non-infested plants, and thus aid in locating hosts or prey. These phytodistress signals, which result in an active interaction between herbivore-damaged plants and a third trophic level, have been described for several agricultural systems. Examples include lima bean and apple plants, which produce volatiles that attract predatory mites when damaged by spider mites, and corn and cotton plants, which release volatiles that attract hymenopterous parasitoids that attack larvae of several Lepidoptera species. In the case of endoparasitoids, the female injects her eggs when she stings and immature parasitoids develop within the body of the herbivore as it continues to feed on the plant. Once a caterpillar has been stung, its own reproductive cycle is terminated and a new generation of wasps is produced.

Several experiments have shown that natural enemies such as parasitoids make effective use of plant volatile organic compounds to locate the microhabitat of their host. Wind tunnel flight experiments indicate that herbivore odors alone do not provide the required chemical information to allure parasitoids. In contrast, the odors released from herbivore-damaged plants appear to contain critical information that draws parasitoids to air streams spiked with these plant odors in the laboratory and to damaged plants placed among a group of undamaged neighbors in the field. To examine whether systemically released chemicals alone provide sufficient chemical cues to attract parasitic wasps, herbivore-damaged leaves have been removed immediately before flight tests. Wind tunnel experiments showed that systemically released components were detectable at levels sufficient to direct parasitoids to their hosts. In cotton and tobacco field trials using female wasps (*Cardiochiles nigriceps*), the ratio of landings on host (tobacco budworm) damaged versus undamaged plants was high: approximately 95% to 5%, respectively, in systemic or whole-plant volatile emissions. To examine the role of volatile organic compounds in a natural plant system, volatile emissions have been quantified from *Nicotiana attenuata* grown in natural populations during the attack by three species of leaf-feeding herbivores. When volatiles emitted with herbivore damage to the plant were exogenously applied to undamaged plants, three compounds (*cis*-3-hexen-1-ol, linalool, and *cis*-alpha-bergamotene) increased egg predation rates by a generalist predator while linalool and the complete blend decreased Lepidopteran oviposition rates. As a consequence, plants reduced local herbivore populations by more than 90% by releasing volatiles.

Parasitoids Learn the Rewards of Host Odor Cues

Although the volatile organic compounds released by insect herbivore damage are similar among the several plant species studied thus far, the specific blends are quite distinct, varying in both the number of compounds and the actual structures produced. Thus, the task of finding a host is more complicated for the parasitoid when the host feeds on several different plant species. The wasp have overcome this obstacle by developing the ability to learn chemical cues associated with the presence of a host. The odors to which a female wasp is exposed during interactions with her host, familiarize her to particular host location cues. A successful host experience increases the wasp's responsiveness to host-associated chemicals. For example, an oviposition experience on the plant-host complex significantly increase the oriented flight and landing responses of females of the aphid parasitoid *Aphidius ervi* relative to those that are not allowed to sting, but that are exposed to undamaged or host-damaged plants. This points to the importance of the oviposition experience in combination with host-damage plant cues. Interestingly, female wasps can also learn volatile odors associated with food sources and use them to locate necessary food.

Adaptive Advantages of Volatile Emissions for Plants

Parasitoids can and do use plant generated volatile organic compounds in the location of the micro-environment of their host, however the selective pressure for plants to produce these volatile organic compounds is less certain. If increased parasitism results in higher fitness for herbivore-attacked plants, plants that signal parasitoids by the emissions of volatile organic compounds are at a selective advantage. During certain stages of a larva's life cycle, parasitization can result in elevated leaf consumption compared to non-parasitized cohorts, however there are recent examples where parasitism of herbivores provides a clear selective advantage for the plant. In maize seedlings under attack by *Spodoptera littoralis* larvae, parasitization by the endoparasitoid *Cotesia marginiventris* significantly reduced feeding and weight gain in the host larvae. In fact, plants attacked by parasitized larvae suffered less feeding damage and at maturity produced 30% more seed than plants that were attacked by an unparasitized larva. For a member of the mustard family, *Arabidopsis thaliana*, herbivory by unparasitized *Pieris rapae* caterpillars resulted in a decrease in seed production compared to damage by *P. rapae* caterpillars that have been parasitized by a solitary endoparasitoid *Cotesia rubecula*. Interestingly, plants damaged by parasitized larvae did not result in a significant reduction in seed production compared to undamaged plants.

Exploitation of Plant Volatiles in Agriculture

For members of the agricultural community to exploit the release of volatiles from plants as a non-toxic form of pest control will require more research in the area of chemistry genetics and ecology. A simple approach might be to spray plant volatiles directly onto crops or to induce their production using an elicitor such as methyl jasmonate; in fact, tomato fields that have been sprayed with jasmonate have a twofold higher level of parasitism for *Spodoptera exigua* caterpillars by the parasitic wasp *Hyposoter exiguae*. However, if parasitoids are lured to plants that do not contain their host, the learned association between the volatiles released from plants and the availability of host species on plants will be broken and plant volatile organic compounds may lose their attractant powers. Another option is to look for plant varieties that respond more strongly to attack by pests in terms of the speed and/or level of volatiles that are released. Since some of the enzymes involved in volatile biosynthesis are known, plants could be screened and selected for enzymatic activity. Such traits could then be introduced into crops by conventional plant breeding. DNA microarrays are also being employed to determine patterns of gene expression in plants responding to herbivore attack. Such studies may suggest ways of genetically engineering plants to boost their production of volatile chemicals in response to herbivore attack. Studies are also needed to understand how parasitoids and predators interpret the complex cocktail of volatiles; perhaps particular components are more potent than others in their attraction of parasitoids. Even though there are many unanswered questions that need to be addressed before plant volatiles are widely used as an agricultural strategy to protect crops against herbivore pests, this research area has already provided many fascinating new examples championing the adage "the enemy of my enemy is my friend."

References

de Bruxelles GL, Roberts MR (2001) Signals regulating multiple responses to wounding and herbivores. CRC Crit Rev Plant Sci 20:487–521

Hoballah MEF, Turlings TCJ (2001) Experimental evidence that plants under caterpillar attack may benefit from attracting parasitoids. Evol Ecol Res 3:553–565

Kessler A, Baldwin IT (2001) Defensive function of herbivore-induced plant volatile emissions in nature. Science 291:2141–2144

Paré PW, Tumlinson JH (1999) Plant volatiles as a defense against insect herbivores. Plant Physiol 121:325–331

Whitfield J (2001) Making crops cry for help. Nature 410:736–737

Natural Host

A host in which the pathogenic microorganism (or parasite) is commonly found and in which the pathogen can complete its development.

Natural Products Used for Insect Control

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Natural product development has become one of the fastest growing areas of research in the past two decades. Sales of dietary supplements alone (not even including all herbal remedies) increased from $3.3 billion in 1990 to over $20 billion in 2005. According to some reports, between 35% and 50% of the population in the USA uses these products. Given the size of the market, and an increasing interest in all things natural, it is not surprising that commercial products are being developed for a wide range of human and animal uses, including pest control.

The well publicized problems with many of the broad spectrum synthetic pesticides developed in the 1900s have stimulated the scientific and industrial communities to investigate natural materials. Many new journals are essentially devoted to the study of the activity, chemistry and use of natural products. More established journals have added sections for papers that describe the active ingredients or mode-of-action of herbs and other natural products. In addition, internet sites such as the Phytochemical and Ethnobotanical Database (www.ars-grin.gov/duke/) and HerbMed® (http://www.herbmed.org/) offer detailed information on the active ingredients and recent scientific literature on plant species often used in herbal remedies.

The driving force for this expanded effort to find new natural products for pest control is the general belief by the public that natural products offer a safe alternative to synthetic pesticides, and that the natural materials will be less damaging to the environment. However, despite all of the new research effort, most natural products used for insect control are not subject to rigorous testing for safety or efficacy. Many commercially available products are sold in the category of "dietary supplements." Materials sold in this classification are not routinely tested for content, quantity of ingredients, or safety. These materials typically include products that are self-labeled as herbal remedies, aroma therapies, holistic cures, homeopathic treatments, or "New Age" remedies. There are no regulations that provide limitations on the content or amount of ingredients; such decisions are solely at the discretion of the producer. For all of these products, the manufacturer is responsible for making sure that all the dietary ingredients are safe and the contents list is complete. Manufacturers and distributors are not required to register with the Food and Drug Administration (FDA) or get FDA approval before producing or selling dietary supplements. This is in contrast to the categories of "food additives," where FDA review and approval is mandatory, and "pesticides," where the EPA requires extensive testing before considering approval.

Many of the natural product pest control materials available online or in stores incorporate compounds that are listed by the USDA as "Generally Recognized as Safe" (GRAS). These include materials that have a long history of food use (prior to 1958; Code of Federal Regulations 1999) with minimal problems, such as garlic. Unlike many of the more recent herbal control products, the active ingredients in these older materials have often been tested for efficacy and results reported in the scientific literature. However, this does not ensure that any particular preparation or product will function effectively as formulated or advertised by a specific producer.

Unfortunately, many of these products use mixtures of ingredients. While individual materials may have a history of safe use, little scientific information is available on the efficacy or safety of mixtures promoted for insect control. Because some of these products or recipes are used on animals or humans, possible negative interactions with other drugs must be considered. This is particularly problematic in the unregulated areas of the internet where individuals promote recipes and "concoctions" containing multiple plant extracts or components that they believe have value for insect control.

The overwhelming message promoted by the manufacturers, distributors, and advocates of herbal or natural approaches to insect control is that "natural is safe." The literature or web-based descriptions often state that natural materials have been used for many years with no ill effects. In addition, many recipes on the internet describe a history of folk wisdom (from someone's neighbors, cousins, or friends) that provides "proof" of efficacy. Unfortunately, many of the herbal products or recipes for insect control suffer from significant safety problems. In some cases this could lead to potential discomfort for the consumer. For example, a natural repellant such as oil of eucalyptus advertised for use against one insect problem (mosquitoes) can serve as an attractant for another blood-feeding pest (biting midges). However, more serious problems include products or recipes likely to cause contact dermatitis, exposure to carcinogens or mutagens, neurotoxic responses, or even organ failure. As most entomologists are aware, plants contain an exceptional variety of defensive chemical compounds that have evolved to prevent or reduce feeding by animals. Although some of these chemicals can be useful in pest control, many of the plant-derived compounds can be extremely toxic to humans, pets, and the environment if they are used inappropriately.

History of the Use of Natural Products

Prior to the development of synthetic pesticides in the 1940s, people relied on natural materials for pest control. Homer, the Greek poet, described burning sulfur to rid houses of insect pests in about 1000 BC. In AD 70, Pliny the Elder wrote "Natural History," in which he described insect control approaches using the available natural chemicals. The mint known as pennyroyal, *Mentha pulegium* in Europe, was discussed as a particularly effective insect repellant. In fact, the name pulegium is credited to Pliny the Elder, who named the plant for the common practice of spreading it over the floors of houses to control "pulex" or "pulices" (fleas). Similarly, wormwood (*Artimesia absinthium* L. and related species) reportedly repelled insects such as fleas and moths by judicious placement of dried and powdered forms in the house and field. Unfortunately, most of the materials were recommended based on folklore and hearsay, and were later proven to be ineffective. The materials were followed by a succession of compounds such as arsenic, extracts of tobacco (nicotine), lead arsenate, and hydrogen cyanide, which provided good insect control but were dangerous to the applicator and the environment.

By the mid 1800s, some effective botanical materials were in use. Rotenone (most commonly from the roots of the legume *Derris*), nicotine, and pyrethrum (an extract from chrysanthemum) provided some insect suppression. Unfortunately, pyrethrum is unstable in sunlight (and therefore short lived), and rotenone is extremely toxic to fish. Nicotine, in the form of nicotine sulfate, was used into the twentieth century before being banned because of high mammalian toxicity. These materials were followed by other extracts of plants, ryania (from the wood of a Caribbean shrub *Ryania speciosa*) and sabadilla (extracted from lily seeds). While these latter products were useful against certain insects, many key pests were not affected, and the search for better materials continued.

Natural Products in Current Use

Agricultural Uses

Today, natural products with the widest use include four botanical products and a few bacterial and fungal pesticides. The bacterial products have the biggest market share. The most important are those based on the insecticidal bacteria, *Bacillus thuringiensis*. These bacteria, found throughout the world, contain proteins which are toxic to insects but not to mammals. By selecting strains of this bacterium that have particular proteins, entomologists can target some agricultural pests or insects that transmit disease pathogens. One advantage of these materials is that they have minimal impact on beneficial insects. Thus, *B. thuringiensis* products have found a role in integrated pest management programs that rely, at least in part, on the use of predators and parasites for suppression of some insect pests. Some of the proteins from these bacteria have been transferred to corn, soybeans, cotton, and many other plants where they provide insect control. This is one of the relatively few cases where the chemistry of natural products formed the basis for a new control strategy.

The botanical insecticides with the broadest agricultural use for insect suppression include neem (obtained from seeds of the Indian neem tree, *Azadirachta indica*), rotenone, pyrethrum, and essential oils (from several different plants, but particularly mints). Each of these botanical products has a different effect on insects. Neem acts to block the release of hormones important to insect development, and also repels the insect during feeding. Rotenone is a mitochondrial poison that prevents energy production in animals. Pyrethrum is a neurotoxicant that interferes with the movement of signals along neural pathways. Investigations into the chemistry of pyrethrum spurred the development of the pyrethroids, a group of synthetic chemicals that saw widespread use in the past three decades. The toxic action of the essential oils is not entirely understood, but there is evidence for neurotoxic activity. Of these compounds, neem is the only one that is essentially non-toxic to humans. However, all of these materials have extensive histories of safe use.

Medically Important Uses

Although most natural products are applied for agricultural use, some materials are used for insect control on companion animals and humans. For example, linalool is a compound extracted from a variety of plants including lavender (*Lavandula angustifolia*) and basil (*Ocimum* spp.). This chemical can be found in many commercial flea dips for dogs and cats. Recent research suggests that the primary mode of action of linalool is on the nervous system, but toxicity tests suggest there are substantial safety margins that provide suitability for use on mammals.

Another natural product used for medically important pests is the oil of *Melaleuca alterniflora* Cheel (paperbark or tea tree, also several other hybrids and species). This oil has been used for centuries by aboriginal Australians as a traditional remedy for discomfort caused by insect bites, bruises and other ailments. The oil is extracted from leaves and twigs of the plants, and in herbal recipes is frequently combined with other essential oils to control ectoparasitic insects on companion animals and humans. The variation in oil contents in *Melaleuca* species is substantial between geographic regions and within seasons, making chemical analysis of the oil important for standardization of products. There have been several problems reported with the use of *Melaleuca* oil. The most common problematic response is contact dermatitis, with over 30 human cases reported in the scientific literature in the 1990s. This can be caused by the fresh oil, but is enhanced by the formation of degradation products that develop in either open or closed containers. *Melaleuca* oil toxicosis in dogs and cats has been associated with depression, weakness, muscle tremors and lack of coordination.

The compound d-limonene is often extracted with either pressure or steam from the peels of several citrus species, including orange, lemon, mandarin, lime, and grapefruit, and is present in a number of other essential oils. This compound is on the US EPA's GRAS list. This versatile citrus extract has a remarkable variety of uses, including, among others, utility as an industrial degreaser, household cleaning agent, food flavoring, sewage scum remover, and pesticide. As a pesticide, this compound can be found in flea dips for dogs and cats, and pesticides used for indoor pest control. Data on d-limonene are insufficient for the EPA to provide values for an oral assessment, an inhalation assessment or a carcinogenicity assessment. Commercial products available for purchase at stores are usually carefully monitored for appropriate concentrations. However, concentrated products are available on the internet that must be diluted by the consumer. As with many pesticides, inadequate dilution can be problematic. Researchers have described necrotizing dermatitis with sloughing of the skin following exposure to d-limonene. Cats appear to be particularly sensitive, with exposures causing hypersalivation, muscle tremors, ataxia, depression, and hypothermia. Contact dermatitis from d-limonene has also been reported in humans, so some caution may be advisable during application to animals. The internet availability of inexpensive technical grade material, along with the many nebulous recipes offered on the internet, enhance the potential for misuse by consumers.

Conclusions

The potential for the use of natural products for pest control is good. As more research focuses on finding alternatives to the broad-spectrum pesticides developed in the 1900s, the likelihood increases that at least some of these new discoveries will come from natural products. To some degree, this process has already begun; some major agricultural and medical pesticides have recently been developed from biological organisms such as *Streptomyces avermitilis* and *Saccharopolyspora spinosa*. Many countries have recognized the potential of the chemicals held in their native biological organisms, and have developed legislation to protect these resources. However, potential problems with production of the materials, formulation, standardization of the products, and safety testing will slow development and acceptance.

Also, as the interest in organic products increases, the need for natural materials that can achieve organic registrations will increase. Because the costs of natural products that can be produced locally are often less than costs of synthetic products, the economics of use will drive some users to adoption, particularly in developing countries.

Despite the desirable aspects of many natural products, not all such materials are safer than synthetic products. Just because a plant has been used for centuries does not mean it is safe or even desirable. Plants contain many toxins, some of which we can use for pest control purposes. However, some of these toxins can cause significant human or animal health effects, and many deaths have been reported. A great many, if not most, of the compounds in plants used in pest control have not been scientifically evaluated for effectiveness and safety. Nearly any product or substance can be misused. Even relatively benign plant compounds can be dangerous if mixed or prepared incorrectly. Because toxins in plants vary with geography, season, environment, and soil nutrients, one cannot assume that homemade remedies will be consistent in terms of concentrations or effects.

► Botanical Insecticides
► Chinaberry, *Melia azedarac*, A Biopesticidal Tree
► Neem
► Pyrethrum and Persian Insect Powder
► Microbial Control of Insects
► *Bacillus thuringiensis*

References

Isman M (2006) Botanical insecticides, deterrents, and repellents in modern agriculture and an increasingly regulated world. Annu Rev Entomol 51:45–66

Kurtzweil P (1998) An FDA guide to dietary supplements. FDA Consumer Publication No. (FDA) 99-2323

Murphy MS, Wertheimer AI, Mackowiak ED (2007) Dietary supplement use among academic pharmacists. Pharm Pract 5:31–35

Trumble JT (2002) Caveat emptor: safety considerations for natural products used in arthropod control. Am Entomol 48:7–13

USDA (2001) Center for Food Safety & Applied Nutrition "Dietary Supplements," http://www.cfsan.fda.gov/~dms/ds-faq.html

Ware GW (1983) Pesticides Theory and application. Freeman, San Francisco, 308 pp

Natural Selection

Selection among organisms by natural forces, allowing some to survive and others to perish, and with the individuals most fit for the environment surviving and reproducing most successfully while the less fit organisms are eliminated over time.

Naucoridae

A family of bugs (order Hemiptera). They sometimes are called creeping water bugs.

► Bugs

Naupliform Larva

A larval body form found in the minute first instar of *Platygaster* (Hymenoptera), which has branching tails. This term also is applied to free-swimming first instars of other organisms.

Nearctic Realm

The Nearctic realm is a zoogeographic region encompassing most of North America. It often is combined with the Palearctic realm (Europe and Asia except for Southeast Asia), because the faunas are really quite similar, and characterized by such animals as vireos, wood warblers, deer, bison and wolves. When combined, it is known as the Holarctic realm.

► Zoogeographic Realms

Necrophagous

Feeding on dead animals or animal matter.

► Decomposer Insects

Necrosis

Death of tissue, usually accompanied by darkening.

Necrophoresis

Transport of dead colony members away from the colony.

Nectar Guide

A pattern on a flower, perhaps invisible to humans but visible to insects, that guides insects to nectar and pollen.

► Pollination and Flower Visitation

Nectary

A gland in a plant that produces nectar, often associated with the flower, but also sometimes extrafloral.

► Plant Extrafloral Nectaries
► Pollination and Flower Visitation
► Butterfly Gardening

Needham, James George

James Needham was born at Virginia, Illinois, USA, on March 18, 1868. He earned his B.S. and M.S.

degrees from Knox College in Illinois. He also taught at Knox and was offered a scholarship to Cornell University. From 1898 to 1907 Needham was a professor of biology at Lake Forest University in Illinois. He returned to Cornell to teach limnology and biology, and influenced the curriculum at Cornell because of his strong interest in ecology. He served as department chairman from 1914 to 1935. Needham published about 350 papers, many of which were major contributions on the identification, behavior, and ecology of water-inhabiting insects. Some of his important publications were "Aquatic insects of the Adirondacks" (1901), "A monograph of the Plecoptera or stoneflies of America north of Mexico" (with P. W. Claasen) (1925), "The biology of mayflies" (with J. R. Traver and Y-C. Hsu) (1935), and "A manual of the dragonflies of North America (Anisoptera)" (with M. J. Westfall, Jr.) (1955). Needham died at Ithaca, New York, on July 24, 1957.

Reference

Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Neelidae

A family of springtails in the order Collembola. They commonly are known as short-horned springtails.

► Springtails

Neem

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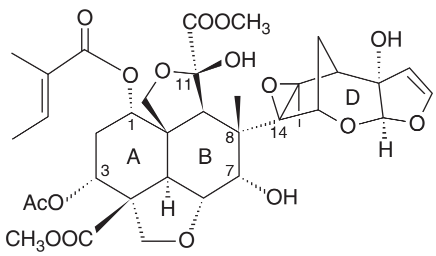
Neem refers to the Indian neem tree, *Azadirachta indica* A. Juss., and products derived from parts of the tree, among the most important being botanical insecticides. The tree is a member of the mahogany (Meliaceae) family with a spreading crown and long pinnate leaves with dentate margins. Though native to the Indian subcontinent, neem has been introduced widely into most tropical and subtropical regions of the world including Africa, Central and South America, the Middle East and Australia. In India neem has a long history of medicinal use (at least 2,000 years), and various extracts of neem leaves and seeds are currently used in soaps and shampoos, toothpaste, antiseptic ointments, male and female contraceptives, and for internal use as a blood purifier and as an antimalarial. Dried leaves have been traditionally used to protect rice, grain and legumes from stored product pests. Western interest in neem as a natural insecticide is attributed to German entomologist Heinrich Schmutterer who noticed neem trees going unscathed during a plague of desert locusts in the Sudan.

For the production of natural insecticides, seeds represent the most important part of the tree. A mature tree can produce upwards of 40 kg of olive-sized fruits, and the seed kernels therein contain a complex mixture of triterpenoid chemicals known as limonoids. By far the most important among these is azadirachtin, a substance with remarkable biological activity against insects, that accounts for much of the total activity seen in crude or refined seed kernel extracts. Azadirachtin was first isolated through bioassay for its potent feeding deterrent activity in locusts, by English chemist David Morgan in the mid-1960s. It remains the most potent antifeedant for locusts yet discovered. Neem seeds typically contain approximately 0.3% azadirachtin by weight, and significantly lesser amounts of other azadirachtin-like substances (Fig. 10).

Subsequent investigation with other insects revealed equally profound physiological actions of azadirachtin (and neem kernel extracts containing this substance) occurring long after ingestion by insects. The most apparent of these is interference with the molting process. Ingestion of microgram quantities of azadirachtin results in failed ecdysis owing to reduced titres of the molting hormone,



Neem, Figure 10 **Chemical structure of azadirachtin.**

ecdysone and juvenile hormone, which retains juvenile characteristics, in the hemolymph. This is not through a direct action of azadirachtin on the prothoracic gland and corpora allata, the sites of hormone synthesis and release, but rather an upstream effect beginning in the central nervous system. Azadirachtin binds with neurosecretory cells in the brain, blocking release of many hormonal neuropeptides, including prothoracicotropic hormone that stimulates the prothoracic gland and corpora allata to synthesize molting hormones. As ecdysteroids and juvenile hormone are involved in reproduction, azadirachtin can also have a chemosterilizing effect in adult insects. Azadirachtin reduces gut motility, possibly accounting for its "anorectic" -like action when administered topically to insects.

Azadirachtin, and neem extracts and preparations containing it, are effective against a broad spectrum of pest species. More than 300 species of insects have been reported to be susceptible. Among the more susceptible pests are foliar-feeding Lepidoptera and Coleoptera. Some filter-feeding larval Diptera are also susceptible. Phloem-feeders (e.g., aphids) and other sucking insects vary widely in susceptibility, a consequence of both innate susceptibility and the availability of azadirachtin in phloem sap or cell cytoplasm for ingestion. Although there are exceptions, neem is rarely effective against subterranean pests or those that bore into plant tissues. Interspecific differences in susceptibility to the behavioral effects of neem (feeding, oviposition deterrence) are far greater than differences in susceptibility to the physiological actions (molt disruption). Also, because azadirachtin has very limited persistence on plant surfaces, neem is not a good choice for crops that are vulnerable to pests for a large portion of the growing season.

Azadirachtin is acclaimed for its systemic action in plants (i.e., ability to translocate throughout treated plants), but this phenomenon does not occur in all plants. As neem/azadirachtin has little contact action and must be ingested to be effective, less risk is posed to natural enemies (parasitoids and predators) or pollinators than that from residual contact insecticides such as pyrethroids. Neem does not appear to deter foraging by pollinating bees, nor are residues from neem-treated crops toxic to bee larvae. Neem is thus considered compatible with biological control as part of integrated pest management programs. A further advantage of neem is that insects seem incapable of developing resistance, at least to the complex chemistry of the seed extract. Laboratory studies have demonstrated that insects are capable of developing resistance to pure azadirachtin, but not to neem extracts containing equivalent amounts of azadirachtin. Also, insects are capable of desensitizing to the feeding deterrent action of azadirachtin when presented alone, but less so to a complex neem extract.

Of perhaps more importance, neem and azadirachtin are essentially non-toxic to vertebrates. Commercial neem insecticides produce no acute oral toxicity in rats at doses as high as 5,000 mg/kg, and they are similarly non-toxic to birds. Acute toxicity of neem insecticides to juvenile rainbow trout is in the parts-per-million range, making them about 20 times less toxic than malathion and 100 times less toxic than pyrethrum, the major botanical insecticide in use at present. Neem also poses little risk of environmental contamination. Like pyrethrum, azadirachtin is rapidly degraded on surfaces by the ultraviolet component of sunlight, and is also rapidly hydrolyzed in water.

Commercial neem insecticides, currently in use in India, the United States and Germany, are based on solvent extracts of neem kernels following removal of oil from the seeds by cold pressing.

Neem oil itself is sold for insect control, but its efficacy, like that of other plant and mineral-based oils, is a consequence of physical actions. The solvent extract of the kernels requires some refinement to enhance the concentration of azadirachtin to around 10% by weight. These technical concentrates are then formulated as emulsifiable con centrate insecticides containing 1–5% azadirachtin as the active ingredient. At present, most of the neem insecticides are based on neem kernel extracts produced in India, but substantial production of neem insecticides in Indonesia, Australia and Brazil is anticipated in the next 5–10 years. Owing to its complex structure, azadirachtin has defied synthesis on even a laboratory scale. However, production of azadirachtin through plant tissue culture appears technically, if not economically feasible in the years to come.

► Insecticides
► Botanical Insecticides

References

Koul O, Dhaliwal GS (2001) Phytochemical biopesticides. Harwood, Amsterdam, 223 pp
National Research Council (1992) Neem. A tree for solving global problems. National Academy Press, Washington, DC, 141 pp
Schmutterer H (ed) (1995) The neem tree-Source of unique products for integrated pest management, medicine, industry and other purposes. VCH, Weinheim, 696 pp
Walter JF (1999) Commercial experience with neem products. In:Hall FR, Menn JJ (eds), Biopesticides. Use and delivery. Humana, Totowa, pp 155–170

Negro Bugs

Members of the family Thyreocoridae (order Hemiptera).

► Bugs

Nematicide

A pesticide that is effective against nematodes.

Nematode

Microscopic roundworms in the class Nematoda. Nematodes may be animal or plant-parasitic, or free living.

Nematode Parasites of Insects

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Nematode parasites of insects (also called entomopathogenic, entomophilic, insecticidal, or entomogenous nematodes) can be found in the orders Aphelenchida, Ascaridida, Mermithida, Oxyurida, Rhabditida, Spirurida and Tylenchida. Phylogenetic relationships reveal that nematodes have established trophic associations with insects numerous times. This finding suggests that nematodes may have a proclivity (exaptation) for negotiating the natural defenses of insects, and that their associations with insects are tremendously fruitful (ecologically and evolutionarily).

Nematode Associations with Insects

Nematodes and insects probably have influenced the shape of each other's evolution from as early as the Devonian (409 million years ago). Over the course of their shared history, nematodes have established many different types of associations with insects.

Facultative Parasitism

Nematodes that are facultative parasites can infect a healthy insect and receive nourishment at the expense of its host, yet retain the ability to complete its life cycle independent of its insect host.

Nematodes in facultative parasitic relationships usually are saprophagous, but when conditions are right, they take advantage of a vulnerable insect. They typically invade and colonize the insect's body cavity, intestine, Malpighian tubules, pharyngeal glands, or tracheal system. Nevertheless, when in the absence of an insect host, they generally can sustain themselves (and complete their life cycle) by feeding on fungi, bacteria, algae, or even higher plants. The nematode orders Rhabditida and Tylenchida have several representative species that are facultative parasites of insects. The damage they do to their hosts can be negligible, but usually the nematode is significantly detrimental to the fitness of the insect. Some of the facultatively parasitic Rhabditida are even lethal to their hosts.

Obligate Parasitism

Obligate nematode parasites of insects typically do not have free-living stages, and cannot complete their life cycle in the absence of their insect host. These nematodes require nourishment from insects, and usually complete their entire life cycle in the same host. The effect of an obligate parasitic nematode on its host can vary widely, from having little effect, to sterilization, to death. Obligate parasites from the families Mermithidae, Tetradonematidae, Allantonematidae, Sphaerulariidae and Entaphelenchidae generally are found in the body cavity of its insect host. Members of the Diplogasteridae, Oxyuridae and Thelastomatidae usually reside in the intestine.

Phoresy

In addition to parasitism, nematodes also can be phoretic, using an insect for transportation. Phoresy is probably the most common form of insect–nematode association and it involves little, if any, damage to the insect. Phoretic nematodes can be found almost anywhere on the body of an insect. They often are recovered from under the elytra of beetles, or coiled around the head, legs or abdomen of flies. However, phoretic nematodes also can be found internally, and may occur in the insect's genital chambers, trachea, head glands or Malpighian tubules. Representatives of the Rhabditida, Diplogasterida, Aphelenchida and Tylenchida are known to have phoretic relationships with insects.

Commensalism and Mutualism

Nematodes may be commensal and remain in contact with their insect host, each feeding on the same resources. Alternatively, they may have a mutualistic arrangement, where both insect and nematode benefit from their association with each other. Little is known of insect–nematode commensalism/mutualism, but few would be surprised to see future work demonstrating that certain nematodes can create optimal habitat for their insect host, and vice versa. For example, many genera of Coleoptera can transport the nematode *Bursaphelenchus xylophilus*, the causal agent of serious disease in pine trees. It just might be that living in a diseased pine tree is advantageous for some of the beetles that transport the plant pathogenic nematode.

Effects of Nematode Parasitism

Insects that are parasitized by nematodes rarely show external signs of infection. Exceptions to this are infections by symbiotic bacteria associated with entomopathogenic nematodes, which can produce color changes in the insect. Upon close inspection, scarring by exposure to numerous nematodes may also be evident. As nematodes grow and develop inside their hosts, they can distend the insect's abdomen, head or thorax. In later stages of their development, mermithid nematodes grow very large and easily can be seen inside or emerging from their hosts without the aid of a microscope.

Some of the common effects of parasitism include disruption of the digestive tract and nutritional uptake that can lead to reductions in host body and muscle size. Similarly, parasitism also can reduce gland production and body fat content. Some nematode species render their hosts infertile.

Many insects exhibit grooming behaviors that make them resistant to infection. Mosquitoes that are more active tend to give nematodes fewer opportunities for infection. However, nematode parasites can influence their host's behavior to favor successful infection or transmission. For example, when the tylenchid nematode *Sphaerularia* parasitizes queen bumblebees (*Bombus* spp.), it alters the foraging behavior of its host. Instead of nesting, the parasitized queen bumblebee flies low to the ground, collecting and digging in and around bumblebee hibernation sites. The bumblebee eventually dies and the nematodes reproduce in a prime location for contacting and infecting a hibernating queen bumblebee.

Evolution of Insect–Nematode Associations

The majority of nematodes associated with insects (Rhabditida, in particular) are not true parasites, but have established only phoretic relationships. These phoretic nematodes usually are referred to as insect "associates." Nematodes in phoretic relationships with insects usually rely on their host to transport them to food resources or improve their chances of finding a mate (or both). Bacterial feeding soil nematodes often are found associated with insect cadavers and incorrectly inferred to be contributing factors to insect pathology. However, it has been proposed that nematode parasitism in some groups may have been initiated by necrogenous nematodes. Early stages in the evolution of insect parasitism may have involved necrogeny (feeding and reproducing on the bacteria of decaying insect cadavers). The association with decaying environments or insect cadavers may have become successively more intimate, as the nematodes began to utilize other saprophagous insects for transportation to new sources of food. Eventually, the nematodes could have changed from being passengers to parasites, invading and feeding on the tissues of their hosts.

Nematodes Associated with Insects

The following is a taxonomic classification of nematodes associated with insects:

- Class Secernentea
  - Order Aphelenchida – insect parasites
  - Order Ascaridida – insect parasites
  - Order Oxyurida – insect associates and parasites
  - Order Rhabditida – insect associates and a few parasites
  - Order Spirurida – blood parasites transmitted by mosquitoes
  - Order Tylenchida – insect parasites
- Class Adenophorea
  - Order Mermithida – insect parasites – obligate parasites

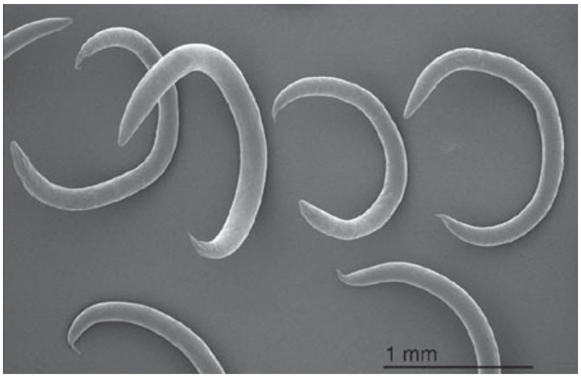
Order Rhabditida

All members of the order Rhabditida feed and breed on bacteria, usually with decaying material, and invade the insect internally. They can be found located in the gut, trachea, head glands, Malpighian tubules and genital chamber, but such opportunistic invasions appear to be merely a way to hitch a ride and to avoid desiccation. They do little damage to their hosts, and exact little or no significant cost. Thus, most rhabditid nematodes associated with insects are phoretic and are not true parasites. Nevertheless, one could expect to find a rhabditid nematode on just about any insect that frequents decaying plant or animal matter.

Notable exceptions to the trend of weak parasitism in the Rhabditida are members of the genera

Steinernema, *Neosteinernema*, and *Heterorhabditis* (Fig. 11). These nematodes have evolved a special parasitic stage that actively enters the hemocoel of its host. They also harbor an extracellular bacterial endosymbiont that, when released into the hemocoel of the insect by the nematode, produces lethal insecticides and other antimicrobial compounds. Because of the broad host range and rapid death of the insect host, the nematode–bacterium complex often is characterized as "entomopathogenic." Recently, this group of nematodes (often abbreviated as EPN for "entomopathogenic nematodes"), has been developed as effective biological control agents against a wide range of insect pests. The number of described species of this group of nematodes is increasing rapidly. For *Steinernema*, two species were described in the 1920s, two in the 1930s, two in the 1950s and 1960s, four in the 1980s, 46 since 1990, and of these 31 since 2000. Currently, more than 67 species of EPN have been reported and they are listed in Table 2.

Several rhabditid nematodes in the family Diplogasteridae have been reported as associates or parasites of different insects. For example, *Mikoletzkya aerivora* has been found in termite heads, where heavy infestations can kill termites. *Mikoletzkya labiata* has been found in the gut of cerambicids, where it ruptures the host's gut wall, enters the hemocoel, and eventually kills its host. *Pristionchus lheritieri* is a facultative parasite of the potato beetle, *Leptinotarsa decemlineata*, with sufficient virulence to regulate some populations and keep them from becoming a greater nuisance to agriculture.



Nematode Parasites of Insects, Figure 11 The entomopathogenic nematode *Heterorhabditis* (females).

Most members of the family Rhabditidae live in decomposing organic material in the soil. *Rhabditis insectivora* (family Rhabditidae) occurs as juveniles and adults in the hemocoel of the antelope beetle, *Dorcus parallelipipedus* (Cerambycidae), and appears to be a facultative parasite. Some nematodes of the genus *Diploscapter* and *Caenorhabditis* have been found to invade the pharyngeal glands of ants, while species of the genus *Parasitorhabditis* have been found in bark beetles where they may be weak parasites. A few other members of the Rhabditidae have been reported to parasitize insects, but in general, this very large group of nematodes is understudied.

Order Spirurida

Nematodes in the order Spirurida are primarily parasites of vertebrates and annelids. However, because insects vector them, they deserve brief mention here. The three species that humans seem most concerned with are *Wuchereria bancrofti*, *Onchocerca volvulus* and *Dirofilaria immitis*. *Wuchereria bancrofti* is the causal agent of debilitating elephantiasis, and it is vectored by several genera of mosquitoes. *Onchocerca volvulus*, vectored by black flies of the genus *Simulium*, causes river blindness. *Dirofilaria immitis* is the dog heartworm. Mosquitoes of several genera, but primarily *Aedes*, vector it. Perhaps fittingly, mermithid nematodes are lethal parasites of mosquitoes and black flies. These nematodes naturally suppress black fly and mosquito populations, and have been used as biological control organisms to reduce the risk of human exposure to parasitic spirurids.

Order Tylenchida

The vast majority of Tylenchid nematodes are plant parasites. These plant parasitic nematodes

Nematode Parasites of Insects, Table 2 Entomopathogenic rhabditid nematodes in the genera *Steinernema*, *Neosteinernema*, and *Heterorhabditis*

Steinernema	***S. diaprepesi***	***S. oregonense***	***S. weiseri***
S. abbasi	*S. eapokense*	*S. pakistanense*	*S. yirgalemense*
S. aciari	*S. feltiae*	*S. puertoricense*	***Neosteinernema***
S. affine	*S. glaseri*	*S. rarum*	*N. longicurvicauda*
S. akhursti	*S. guangdongense*	*S. riobrave*	***Heterorhabditis***
S. anatoliense	*S. hebeiense*	*S. ritteri*	*H. amazonensis*
S. apuliae	*S. hermaphroditum*	*S. robustispiculum*	*H. bacteriophora*
S. arenarium	*S. intermedium*	*S. sangi*	*H. baujardi*
S ashiuense	*S. jollieti*	*S. sasonense*	*H. downesi*
S. asiaticum	*S. karii*	*S. scapterisci*	*H. floridensis*
S. backanense	*S. khoisanum*	*S. scarabaei*	*H. indica*
S. beddingi	*S. kraussei*	*S. siamkayai*	*H. marelatus*
S. bicornutum	*S. litorale*	*S. sichuanense*	*H. megidis*
S. carpocapsae	*S. loci*	*S. silvaticum*	*H. mexicana*
S. caudatum	*S. longicaudum*	*S. tami*	*H. tayseare*
S. ceratophorum	*S. leizhouense*	*S. texanum*	*H. zealandica*
S. cubanum	*S. monticolum*	*S. thanhi*	
S. cumgarense	*S. neocurtillae*	*S. websteri*	

possess a stylet, a hypodermic needle-like structure that is used to puncture cells and tissues of plants. Interestingly, most tylenchid nematodes that have evolved a relationship with insects have retained their stylet, and many other morphological and life history traits. Many appear to have maintained a relationship with a host plant as well.

Tylenchid nematodes parasitize a wide range of Coleoptera, Lepidoptera, Diptera, Hymenoptera, Siphonaptera and Acarina. The life cycle of the nematodes in this order is a bit more complex than most rhabditids. Pre-adult stages leave the host through the genital tract or digestive tract and enter a moist substratum such as egg gallery, frass, bedding, etc., where it molts to the adult stage and then mates. The mated female enters a host and, once in the hemocoel, lays its eggs. The major damage to the host by members of Tylenchida is often sterility from feeding on the reproductive organs or fat bodies. The life cycle often involves an insect host and, sometimes, a closely associated plant.

For example, *Fergusobia* has two hosts as part of its life cycle: a plant parasitic generation in plant galls of *Eucalyptus* and *Syzygium* trees, and the other within the hemocoel of an agromyzid fly (*Fegusonina* spp.). The fly deposits its eggs, which contain juvenile nematodes, in plant tissue. The juvenile nematodes feed, develop, and reproduce inside the resulting gall. When the insect larvae reach the third instar, the pregnant female nematodes enter them and eventually lay eggs. The eggs hatch and migrate to the fly's oviduct to be deposited in fresh plant tissue along with the fly's eggs.

On the other hand, some insect parasitic tylenchids such as *Sphaerularia bombi* have undergone extreme transformations of morphological and life history traits. This parasite of bumblebees (*Bombus* spp.) acquires nourishment by entering its host and everting its uterus, which can absorb nutrients directly from the insect's hemocoel. The everted uterus can grow from 6 to 30 times the length and up to 300 times the volume of the original female's entire body.

Deladenus siricidicola presently is used extensively as a biological agent control against the woodwasp, *Sirex noctilio*, in Australia, New Zealand and Argentina, where it is inoculated into infested trees. *Paraiotonchium autumnale* sterilizes its host, the face fly (*Musca autumnalis*), which is an insect of concern to veterinary entomologists. Another notable tylenchid nematode that parasitizes insects is *Thripinema*, an obligate parasite of thrips.

Order Aphelenchida

Many members of Aphelenchida are associated with insects and several are obligate parasites. The life cycles of insect parasitic aphelenchids are similar to tylenchids. This is not too surprising considering that these two nematode orders are closely related phylogenetically. As with the Tylenchida, Aphelenchida is comprised primarily of plant parasitic and fungal feeding nematodes.

Most insect-associated aphelenchids are ectoparasites. *Bursaphelenchus cocophilus* is the primary cause of red-ring disease of coconut palm, but it is transmitted, at least in part, by the palm weevil, *Rhyncophorous palmarum*. *Vampyronema* and *Noctuidonema* can be found on the abdomens of moths; *Acugutturus* is an ectoparasite of cockroaches. Like little vampires, these nematodes pierce the cuticle of their hosts with their stylets and ingest their hemolymph. However, not all parasitic aphelenchids are ectoparasites. *Schistonchus caprifici* is an endoparasite of the fig pollinator wasp, *Blastophaga psenes*. These nematodes reproduce in the hemocoel of female wasps and are oviposited on the florets of the figs. The nematodes can feed on the florets, but rely on the wasp to transport them to other inflorescences.

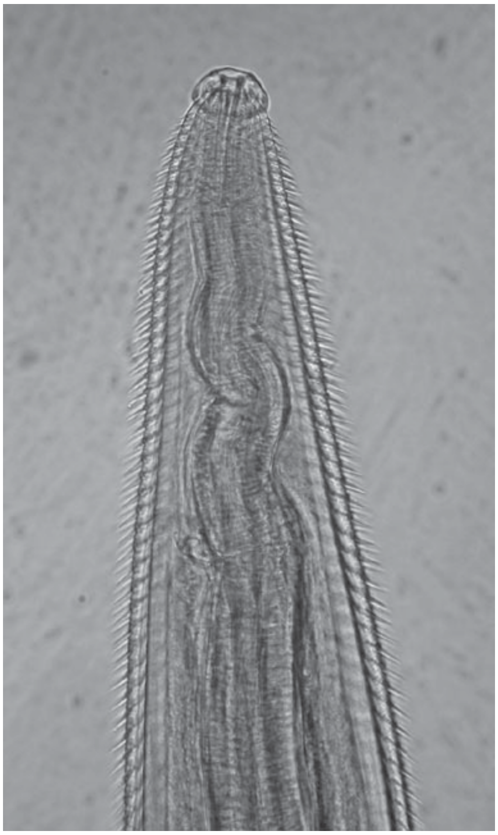
Order Oxyurida

Oxyurid parasites of arthropods appear to be restricted to the Class Diplopoda, the Blattidae and Grylloidea of the Orthoptera, and a few Coleoptera. They inhabit the alimentary tract of their host and feed on the partially digested food and microbes present in the host's gut. Many of these species are unisexual, but when amphimictic, mating and oviposition take place in the intestine of the host. Eggs are passed into the environment where they undergo a developmental period before becoming infective. Hosts become infected when they ingest eggs, which hatch in the host's gut. Hatched nematodes move to the intestine with food boluses where the life cycle is completed. In most cases it is unknown whether intestinal damage is done by the nematode. The northern mole cricket (*Neocurtilla hexadactyla*) is commonly found parasitized by *Pulchrocephala*. Populations of bess beetles (Passalidae) sustain high numbers of *Hystrignathus* while colonies of cockroaches reared in laboratories sometimes become weakened or die, apparently from the effects of nematode parasites such as *Thelastoma*, *Blasticolla*, *Hammerschmidtiella*, or *Leidynema* (Figs. 12 and 13).

Order Mermithida

Mermithid nematodes have been reported to infect virtually all orders of insects. They differ from most insect parasitic nematodes in that they are typically large (up to 405 mm, and usually between 50 and 150 mm long), and, curiously, it is the adult stage that is free-living. They are also unique because they rarely reproduce inside their host. Instead, the larval stages undergo development in their host, while the adults mate outside the host. Most infective mermithid larvae enter their hosts by direct penetration of the cuticle, although some gain entry when their hosts ingest them as eggs, as occurs with *Pheromermis pachysoma*, a wasp parasite, and *Mermis nigrescens*, a parasite of crickets and grasshoppers. Once inside the insect, the developing

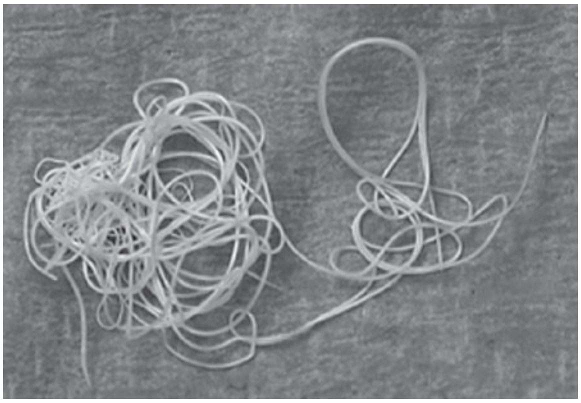
Nematode Parasites of Insects, Figure 12 ***Pulchrocephala*****, an oxyurid parasite of mole crickets.**



Nematode Parasites of Insects, Figure 13 ***Hystrignathus*****, an oxyurid parasite of bess beetles.**

nematodes undergo an amazing transformation, wherein the esophagus atrophies and the gut becomes a giant food storage organ called a "stichosome" or "trophosome." The mouth and lips are lost and the nematode feeds transcuticularly, with nutrients from the host's hemocoel moving directly into the nematode stichosome through its cuticle. The nematodes then grow to an enormous size, occupying much of the host's body cavity. Parasitism frequently results in sterilization, but more commonly in death, as the relatively huge nematodes burst their way out of the insect. After emerging from their host, the juveniles migrate into the soil or water, develop into adult males and females, which copulate and lay eggs (Fig. 14).

Many mermithid nematodes have been employed as biological control agents of arthropod pests. *Romanomermis culicivorax* has been carefully studied for control of mosquitoes, but *Culicimermis*,



Nematode Parasites of Insects, Figure 14 Mermithid nematodes, recently emerged from an insect host.

Empidomermis, *Hydromermis*, *Octomyomermis*, *Perutilimermis* and *Strelkovimermis* also are known to parasitize them. Black flies (Simuliidae) are known hosts of *Gastromermis*, *Hydromermis*, *Isomermis*, *Limnomermis* and *Neomesomermis*. Wasps also are vulnerable to mermithid parasites. *Pheromermis pachysoma* is a parasite of yellowjackets, *Vespula pensylvanica*. Terrestrial mermithids, such as *Mermis*, *Filipjevimemis* and *Agamermis* are quite common, and have been explored for their ability to control beetles, ants and grasshoppers.

► Entomopathogenic Nematodes and Pest Management
► Thrips-Parasitic Nematodes
► Onchocerciasis
► Dirofilariasis

References

Maggenti AR (1981) General nematology. Springer, Berlin Heidelberg New York
Nickle WR (1991) Manual of agricultural nematology. Marcel Dekker, New York
Poinar GO (1975) Entomogenous nematodes: a manual and host list of insect–nematode associations. Brill, Leiden
Siddiqi MR (2000) Tylenchida: parasites of plants and insects. CABI, Wallingford, Oxon
Smart GC, Nguyen KB (1994) Role of entomopathogenic nematodes in biological control. In: Rosen D, Bennett FD, Capinera JL (eds), Pest management in the subtropics: biological control – a Florida perspective. Intercept, Andover, UK, pp 231–252

Nematomorphs (Nematomorpha: Gordioida: Several Families)

A phylum of insect-parasitic invertebrates known as horsehair worms, Gordian worms, and hair snakes, these worm-like invertebrates differ from the similar-appearing nematodes by their symmetrical esophagus and by having gonads that open at the posterior portion of the body through a cloaca in both sexes. In the case of juveniles, the head region of nematomorphs is distinctive because it is barbed. More obviously, nematomorphs are larger (a few cm or larger), more uniformly cylindrical, and tend to be darker in color. The adults are free-living but the immature stages are parasitic. Preparasitic stages are minute and easily ingested. They are found in cockroaches, beetles, mantids, crickets, tettigoniids, grasshoppers, arachnids and crustaceans.

Nematomorphs affecting insects are terrestrial or freshwater, though marine nematomorphs also occur. Those associated with insects are always associated with water. Although perhaps only 250 species exist, they occur commonly in some insects and attract attention. They are commonly confused with mermithid nematodes, so perhaps are under-reported. They are closely related to nematodes (Nematoda).

Few nematomorphs that affect insects have been closely studied, but among this small group are *Chordodes japonensis* in mantids and *Gordius robustus* in Mormon cricket, *Anabrus simplex*. In the case of *C. japonensis*, the eggs and juveniles occur in water and are ingested by aquatic insects such as mayflies, chironomids, and mosquitoes. Mantids become infected by eating infected aquatic insects. In the case of *G. robustus*, the eggs are deposited in water, but are ingested directly by the Mormon crickets as they drink or feed on aquatic plants.

References

Baker GL, Capinera JL (1997) Nematodes and nematomorphs as control agents of grasshoppers and locusts. Mem Entomol Soc Can 171:157–211
Inoue I (1962) Studies on the life history of *Chordodes japonensis*, a species of Gordiacea III. The mode of infection. Annot Zool Jpn 35:12–19

Nemestrinidae

A family of flies (order Diptera). They commonly are known as tangle-veined flies.

► Flies

Neminidae

A family of flies (order Diptera).

► Flies

Nemonychidae

A family of beetles (order Coleoptera). They commonly are known as pine-flower snout beetles.
► Beetles

Nemopteridae

A family of insects in the order Neuroptera.
► Lacewings, Antlions, and Mantidflies

Nemouridae

A family of stoneflies (order Plecoptera). They sometimes are called spring stoneflies.
► Stoneflies

Neoclassical Biological Control

A form of inoculative biological control wherein natural enemies are imported from elsewhere and released to establish permanent biological control of a native pest, which with they have had no prior association (contrast with classical biological control).

Neolinognathidae

A family of sucking lice (order Phthiraptera).
► Chewing and Sucking Lice

Neonate

An insect that has only recently hatched.

Neopetaliidae

A family of dragonflies (order Odonata).
► Dragonflies and Damselflies

Neophemeridae

A family of mayflies (order Ephemeroptera).
► Mayflies

Neopseustidae

A family of moths (order Lepidoptera). They also are known as archaic bell moths.
► Archaic Bell Moths
► Butterflies and Moths

Neopterous

Possessing the ability to fold the wings backward over the abdomen.

Neoteinic

A supplementary reproductive termite.

Neoteny

Sexual maturity in other than the adult stage.

Neotheoridae

A family of moths (order Lepidoptera). They also are known as Amazonian primitive ghost moths.
► Amazonian Primitive Ghost Moths
► Butterflies and Moths

Neotropical Brown Stink Bug, *Euschistus heros* (F.) (Hemiptera: Heteroptera: Pentatomidae)

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This is a Neotropical pentatomid occurring in South America and possibly in Panama. Most reports refer to its distribution in Brazil where it is a major component of the pentatomid-pest complex on soybean. Initially considered a secondary pest, *Euschistus heros* more recently has increased in numbers and may inflict severe damage to soybean (Fig. 15).

Beyond soybean, this insect feeds on several other plants in Brazil, including species of Leguminosae, Solanaceae, Brassicaceae, and Compositae. Even though it is polyphagous and, therefore, able to colonize alternate hosts during the mild winter of northern Paraná state, *E. heros* was found to overwinter underneath dead leaves in this area. This bug is known to accumulate lipids during overwintering that allow survivorship during non-feeding periods, and to break dormancy with the start of favorable weather conditions. During summer, with the availability of the great number of weeds associated with the soybean crop, this bug feeds on some weeds, including the euphorb *Euphorbia heterophylla* and the star bristle, *Acanthospermum hispidum*.

Neotropical Brown Stink Bug, *Euschistus heros* (F.) (Hemiptera: Heteroptera: Pentatomidae), Figure 15 **Neotropical brown stink bug.**

Data on the biology of *E. heros* are relatively scarce due to this species' previous minor importance as a pest of economic crops. However, with its increasing incidence on soybean, its biology on this host and on alternate hosts such as the euphorb *E. heterophylla* has been studied. Depending on the type of food ingested, and whether or not a switch in food from nymph to adult has occurred, reproductive performance of females will vary. In general, females will lay 6–11 egg masses (although it can be as high as 34) during their life spans, with a total of 61–99 eggs per female (but 287 eggs per female have been reported).

Adults are brown, and show lateral expansions of the pronotum (spines) with variable length. During summer, adults show greater length of pronotum spines and are usually dark brown compared to overwintering adults which show pronotum spines smaller and are usually light brown. Eggs are laid in small clusters, and are light yellowish. First and second instars are oval, 1.47–1.72 and 1.81–2.55 mm long, respectively. Third, fourth and fifth instars are also oval, 3.36–3.98, 4.84–5.95 and 6.87–12.08 mm long, respectively.

Euschistus heros feeds on pods of soybeans, and the extent of the damage is related to the stage of seed development. Feeding during early pod and seed development generally results in pod-abscission or abortion of young seeds; during pod-fill, in shriveled and deformed seeds; and during seed maturation, in little deformation of the seed. Feeding activity on soybean will delay leaf maturation, cause foliar retention, and cause development of abnormal leaflets and pods close to the main stem. Transmission of microorganisms also will occur.

Natural enemies include the egg parasitoid *Trissolcus basalis* (Wollaston), *Telenomus mormideae* Lima, *Telenomus* sp., *Trissolcus scuticarinatus* Lima, *Ooencyrtus* sp., and *Neurileya* sp. Adults are parasitized by the encyrtid *Hexacladia smithii* Ashmead and by the tachinids *Trichopoda nitens* (Blanchard) and *Hyalomyodes* sp.

► Stink Bugs
► Hemiptera

References

Panizzi AR (1997) Wild hosts of pentatomids: ecological significance and role in their pest status on crops. Annu Rev Entomol 42:99–122

Panizzi AR, Slansky F Jr (1985) Review of phytophagous pentatomids associated with soybean in the Americas. Fla Entomol 68:184–214

Panizzi AR, Vivan LM (1997) Seasonal abundance of the neotropical brown stink bug, *Euschistus heros* in overwintering sites and the breaking of dormancy. Entomol Exp Appl 82:213–217

Schaefer CW, Panizzi AR (eds) (2000) Heteroptera of economic importance. CRC, Boca Raton, 828 pp

Villas Bôas GL, Panizzi AR (1980) Biologia de *Euschistus heros* (Fabricius, 1798) em soja [*Glycine max* (L.) Merrill]. An Soc Entomol Bras 9:105–113

Neotropical Realm

The zoogeographic region of South and Central America including the Caribbean Islands. It is characterized by having sloths, armadillos, anteaters, tapirs, toucans, and hummingbirds.

► Zoogeographic Realms

Neotropical Soybean Budborer, *Crocidosema aporema* (Walsingham, 1914) (Lepidoptera: Tortricidae)

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The soybean budborer, *Crocidosema aporema*, previously included in the genus *Epinotia* is an oligophagous species of neotropical origin that colonized soybean when this crop was introduced into the new world. In addition to soybean, *C. aporema* feeds on the buds of many other native and cultivated Leguminoseae such as peanut, clover, alfalfa, lotus, melilotus, lupine, broadbean, common bean and others.

Crocidosema aporema is distributed from southern United States throughout Central America to the center of Argentina and Chile. In Argentina, soybean was introduced in the early 1970s and since then the cultivated area has expanded drastically. Accordingly, this insect exhibited a considerable population increase.

As with other herbivorous species related to soybean in the Nearctic and Neotropical regions, *C. aporema* is secondarily associated to this host-plant of oriental origin. As a consequence, its success and relative importance as a soybean pest, among other factors, may depend on the presence and availability of other alternative legume hosts.

Although *C. aporema* is a major soybean pest, larvae perform better when reared on other legumes like broad-bean, common bean and lupine in the laboratory. They reach a higher efficiency of food conversion into biomass and a higher pupal weight, consuming at a lower rate, compared with larvae fed soybean and white sweet-clover. Soybean and white sweet-clover, having a lower water content, are considered sub-optimal host plants because *C. aporema* consumes them at a higher rate, both on a dry and fresh basis.

The life cycle is multivoltine. There are four to five generations per year. At least two generations occur on soybean, and the others on different legumes. Adult activity starts at the end of the spring and lasts until the beginning of the winter. Females start to lay eggs about 2–4 days after emergence and first larvae are detected approximately 2 weeks after adult emergence. Eggs are about 0.6 mm in length and 0.3 mm in width. At hatching they are yellow or light green in color and the chorion is translucent and dotted.

The oviposition behavior of phytophagous insects is crucial in determining the probability of the progeny reaching a suitable feeding site. Although the preferred feeding sites of *C. aporema* larvae in soybean are the buds (the most pubescent part), a greater proportion of its eggs are laid mainly on nodes (a less pubescent part), and secondarily on expanded leaves. This apparent contradiction is explained by the fact that a greater proportion of larvae emerging on nodes reach the buds compared to those emerging on leaves. This behavior maximizes some fitness components like larval survival and growth.

There are five larval instars; the first to the fourth are light yellow or green with a black head, and the fifth instar has a reddish head and a yellow body. A winter diapause occurs during the last larval instar. Before pupation, they turn in a reddish color and spin a cocoon. Larvae feed mainly on vegetative buds and can also bore into stems, floral buds and pods. The damage caused to the buds is easily recognized because larvae attach the leaflets to one another, and persist inside them until they pupate in the soil or in the same leaflets. Pupae are brown reddish. The adult measures 14–17 mm in width when wings are expanded, and sexes can be identified by the distribution patterns of black, bronze and light gray scales of the first pair of wings.

Mean developmental time at 25°C, for the different stages is: 7, 18, 11 and about 20 days for egg, larva, pupa and adult stages, respectively. The maximal adult longevity is 23 days for the male and 21 days for the female and females deposit an average of 119 eggs.

The soybean budborer has many natural enemies. Among predators, the wasp *Polybia scutellaris* (Hymenoptera: Vespidae) shows a positive response to *C. aporema* density, and is distributed such that the proportion of *P. scutellaris* is related to the proportion of prey larvae per plant. This polyphagous predator seems to be an important mortality factor of *C. aporema* larvae and other borers and defoliators of soybean.

Other predators that attack eggs and larvae of *C. aporema* are: *Orius* sp. (Hemiptera: Anthocoridae), *Nabis punctipennis* Blanchard (Hemiptera: Nabidae), *Geocoris* sp. (Hemiptera: Lygaeidae), *Chrysopa* sp. (Neuroptera: Chrysopidae), *Eriopis conexa* Germar (Coleptera: Coccinellidae), *Lebia concina* L., *Venustula* sp., *Calosoma* sp. (Coleoptera: Carabidae) and *Missumenops pallida* (Araneae: Thomisidae).

Several parasitoids are known, principally a wasp egg parasitoid, *Trichogramma brasiliensis* (Ashmead) (Hymenoptera: Trichogrammatidae). Many parasitoids attack larval stages: *Apanteles lesbiae* (Blanchard), *A. piccotrichosus* (Blanchard), *Apanteles* sp. and *Agathis* sp. (Hymenoptera: Braconidae), *Campoletis perdistinctus* (Viereck), *C. grioti* (Blanchard) (Hymenoptera: Ichneumoidae), *Encarsia porteri* (Mercet), (Hymenoptera: Aphelinidae) and *Eucelatoria australis* Townsend (Diptera: Tachinidae).

The soybean budborer *C. aporema* is considered one of the major soybean pests in South America. Current tactics for the control of this insect rely exclusively on chemical applications. However, the particular feeding behavior of the larvae makes chemical control very difficult.

Several ecological studies on population dynamics, demography, plant–herbivore interaction, and herbivore-natural enemies of this pest have been carried out in the Buenos Aires province of Argentina. This knowledge, as well as further studies, should provide the basis for the implementation of alternative control strategies into an IPM program. The understanding of the relationship between the attributes of crop plant, their consumption and utilization, and pest performance is a prerequisite for the development of host plant resistance and cultural control techniques (e.g., trap crops).

Early planting of most suitable host plants might be used as trap crops for attracting and concentrating *C. aporema* populations away from soybean with the purpose of reducing pest immigration to the soybean by appropriately timed insecticide applications to the trap crop. This could become a preventive control strategy, economically and ecologically acceptable and highly compatible with other components of an IPM program for this pest.

References

Correa Ferreira BS (1980) Sampling *Epinotia aporema* on soybean. In: Kogan M, Herzog DC (eds), Sampling methods in soybean entomology. Springer, Berlin Heidelberg New York, pp 372–382

Pereyra PC, Sánchez NE (1998) Effects of different host-plant species on growth, development and feeding of the bud borer *Epinotia aporema* (Lepidoptera: Tortricidae) in La Plata, Argentina. Rev Chil Hist Nat 71:269–276

Rojas GC (1998) Estudio de la interacción entre el barrenador de los brotes *Epinotia aporema* (Walsingham, 1914), el cultivo de soja *Glycine max* (Merrill) y otras leguminosas. Tesis doctoral de la Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Argentina, 186 pp

Sánchez NE, Pereyra PC, Gentile MV (1991) Relación entre las preferencias de oviposición de las hembras y los sitios de alimentación de las larvas del "barrenador del brote" *Epinotia aporema* (Lepidoptera: Tortricidae). Ecol Austral 1:6–10

Sánchez NE, Pereyra PC, Gentile MV (1997) Population parameters of *Epinotia aporema* (Lepidoptera, Tortricidae) on soybean. Rev Soc Entomol Argent 56:151–153

Nepidae

A family of bugs (order Hemiptera). They sometimes are called waterscorpions.

► Bugs

Nepticulidae

A family of moths (order Lepidoptera). They commonly are known as pygmy moths.

► Pygmy Moths
► Butterflies and Moths

Neriidae

A family of flies (order Diptera). They commonly are known as cactus flies.

► Flies

Nervous System

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The nervous system in insects is considered to be based on the ladder type found in the free-living flat worms, annelids, primitive mollusks and primitive crustaceans. This type is found throughout the whole protostomia division of bilateral animals, except nematodes.

Gross Structure

The insect nervous system is divided into three portions: the central, the visceral, and the peripheral sensory nervous systems. Only the first two systems will be addressed.

The central nervous system generally is composed of a cephalic part situated in the head, and a nerve cord extending in the longitudinal midventral line of the body. The cephalic part consists of a brain which lies in the head between the compound eyes, and is connected by two circumesophageal connectives that pass on either side of the mouth and around the esophagus to the subesophageal ganglion which is situated ventrally in the head below the esophagus (in some insects below the pharynx) and above the submentum. Together, they are called the cephalic ganglia. The number of the segmental ganglia making up this part is a subject of controversy. Apparently, each is formed by the coalescence of three primitive ganglia.

The visceral nervous system is directly connected to the brain through many nerves and is closely associated with the process of neurosecretion. It originates from the neuroblasts which move internally along invaginations in the roof of the stomodeum.

The Cephalic Ganglia

The brain consists of three regions: the protocerebrum (forebrain), the deutocerebrum (mesocerebrum, midbrain), and the tritocerebrum (metacerebrum, hindbrain). The ratio of brain volume to the body volume ranges from 1:174 in the honeybee to 1:4,200 in dytiscid beetles. The protocerebrum innervates the eyes and ocelli. Its two optic lobes make up the largest part of the brain in the insects that have well developed visual sense. In the blowfly, half of the total number of the nerve cells of the brain (about 300,000) are in the optic lobes. In Odonata and some diurnal lepidopterans, optic lobes constitute 80% of the brain. The size of the protocerebrum of somewhat large insects such as the cockroach is about one millimeter in diameter (Fig. 16).

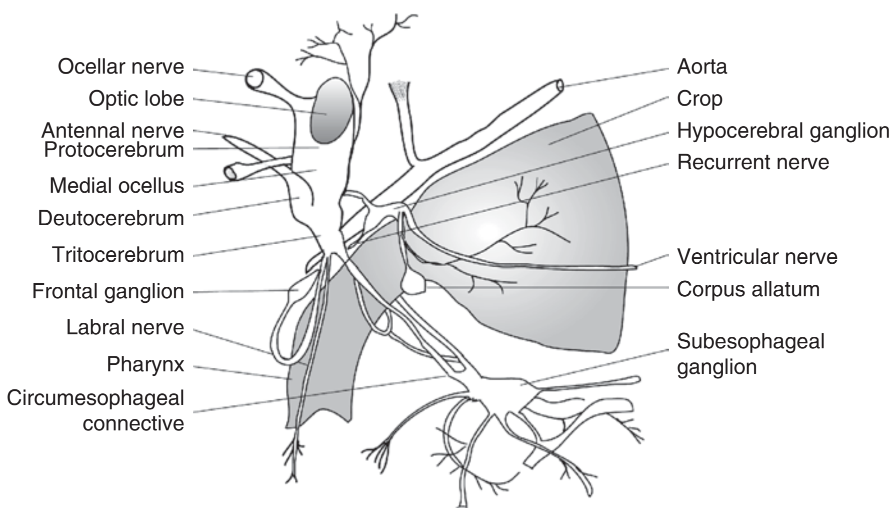
The deutocerebrum is composed of the paired antennal lobes. Development of the deutocerebrum is correlated with antennal senses, as shown in a nocturnal lepidopteran (*Notodonta*) where 13.4% of the brain volume is occupied by the antennal lobes. In contrast, this ratio is only 2.3% in a day-flying lepidopteran (*Pieris*), which is less dependent on antennae for orientation.

The tritocerebrum is composed of two lobes beneath the deutocerebrum, lying above and on both sides of the esophagus. The two lobes of the tritocerebrum are ventrally connected by the postesophageal commissure (postoral) which surrounds the esophagus (there are two commissures in *Locusta*). In some insects, such as Thysanura and the adults of Ephemeroptera, the tritocerebral region is small and its cells are situated partially or totally on the circumesophageal connectives at the sides of the mouth, or, could be rudimentary as in the males of both coccids and some aphids where mouthparts are rudimentary as well. The tritocerebrum innervates the labrum and connects the brain through two connectives to the frontal ganglion and the two circumesophageal connectives, to the visceral nervous system and the subesophageal ganglion respectively. In many insects such as fleas, bees and ants, the circumesophageal connectives are very short, so the subesophageal ganglion and the brain are closely connected to appear as one mass penetrated by the esophagus.

The subesophageal ganglion innervates the salivary glands, both senses and muscles of the mandibles, maxillae, labium and the neck region. It seems to be concerned mainly with feeding because it is rudimentary in the males of coccids and in the males of some species of aphids that do not feed.

The Nerve Cord

The nerve cord is typically double, anteriorly connected with the subesophageal ganglion, and runs along the median line of the floor of the body to the posterior end of the abdomen. This nerve cord connects a chain of ganglia, primitively one ganglion (double in origin) for each primary segment in the embryo. In the post-embryonic stages, the number of ganglia is generally three in the thorax and up to eight in the

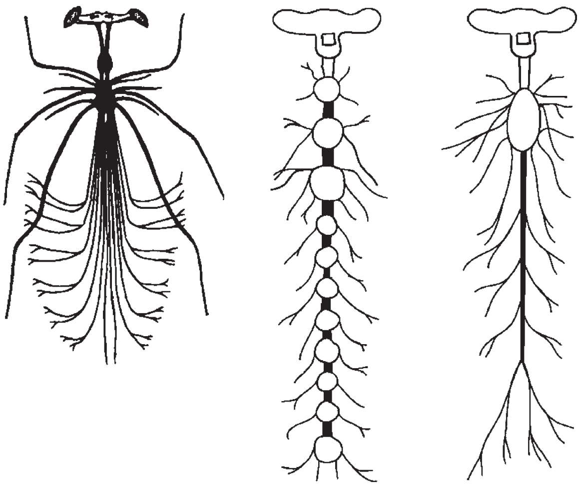


Nervous System, Figure 16 **Diagram of the brain of an insect.**

abdomen, as in the jumping bristletail *Machilis*, and in caterpillars. A wide range of the degrees of fusion and the reduction in the number of ganglia can be seen in the different orders of insects (Fig. 17).

The generalized nerve cord structure is found in Thysanura and Diplura (apterygote insects), and in the primitive orders of pterygota such as Odonata, Isoptera, Dyctioptera and Orthoptera. The last abdominal ganglion is always formed by the fusion of the last abdominal ganglia and innervates the segments behind. The number of abdominal ganglia may differ in the castes of the same species as in the stingless bee *Melipona*, where the queen has four while the worker and the drone possess five abdominal ganglia.

Various types of arrangements of coalescence patterns of ventral ganglia can be found in the different species of insects; abdominal ganglia may be drawn up into the thorax and fuse with the thoracic ganglia as in *Musca*, or move backwards to fuse at the posterior end of the abdomen as in *Coccinella quinquepunctata*. In many semiaquatic hemipterans (*Hydrometra*, *Velia*), all thoracic and abdominal ganglia are fused with the subesophageal ganglion to form one mass located in the thorax.



Nervous System, Figure 17 **The central nervous system in different insects: (a) beetle; (b) cockroach; (c) house fly.**

A segmental ganglion contains 500–3,000 nerve cells. The size of the ganglion is proportional to the function and structure of the segment it serves. Large ganglia, such as the thoracic ones, innervate the appendages of locomotion. The last abdominal ganglion innervates the segments of reproduction.

Embryonic Origin

At an early stage in the embryo, two longitudinal thickenings, called the neural ridges, are formed from the ectoderm along the length of the embryo on either side of the midventral line making a trough which is the neural groove. Certain cells from the inner surfaces of the ridges differentiate. They are distinguishable by their large size, shape and division. These cells are the neuroblasts from which the nervous system originates.

The neuroblasts sink inward arranged in segmental groups representing the anlagen of the ganglionic complex. They remain in their relative positions. Neuroblasts divide and form the nerve cells that are called neurons. Neurons in each body segment are formed from about 60 neuroblasts.

The primitive segmental ganglion (the neuromere) shows a high degree of bilateral symmetry in the distribution of neuroblasts on either side of the embryonic midline. A median sheet-like structure separates the two symmetrical parts of the neuromere. Later on, parallel processes arise from the neurons in each ganglion, forming bundles of fibers that longitudinally extend to make the double nerve cord (the intersegmental connectives) which connects the ganglia. The two parts of each ganglion bind together to constitute one ganglion (Fig. 18).

Histology

The functional cellular elements of the nervous system are the nerve cells (the neurons). Each

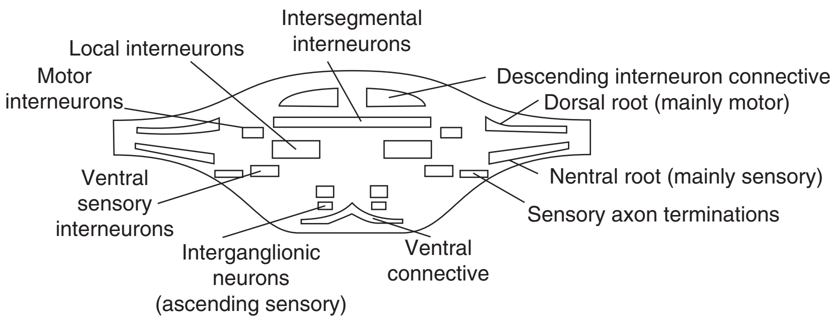
Nervous System, Figure 18 **Major functional centers in the insect brain.**

neuron consists of a cell body (perikaryon, soma, neurocyte) which contains the nucleus, and one or more elongated strands extending from that body. The nerve cells accordingly are either unipolar (monopolar), bipolar, or multipolar when the number of processes arising directly from the perikaryon are one, two, or more respectively. These processes are of fibrous nature (nerve fibers), they are of two sorts; dendrites (dendrons) which are small and specialized to be receptive site in the neuron, and axons (neurites, axis cylinders), which are the longest processes arising from the perikaryon. A neuron has only one axon specialized to conduct nerve impulses for a long distance. In a unipolar neuron, the axon bears a collateral serving as a dendrite for that neuron. Axons have terminal arborization, while dendrites can be branched or unbranched at their ending. Unipolar neurons are the dominant type in insects. Amacrine cells are nerve cells without axons found in special locations.

Based on function, neurons can be classified as sensory, motor, or association (interneuron, internuncial, correlation). Sensory neurons are either bipolar or multipolar with their perikarya located peripherally and on the wall of the digestive system. Their dendrites are associated with sensory structures and their axons, called afferent axons, carry impulses toward the central nervous system. Motor neurons (motoneurons) and association neurons are unipolars whose perikarya are crowded in the outer regions of the ganglia forming a dense cortex (the rind), while the massed processes of these neurons with their branchings and arborizations are in the clear interior portion of the ganglion called the neuropile (Fig. 19).

The neuropile (medullary tissue, punktsubstanz) is also occupied by the intertwined processes of association neurons, which has perikarya in other ganglia. A single association neuron may receive and distribute impulses to several neurons in different ganglia. Axons of the motor neurons are the efferent axons that go from the ganglia to the effectors (muscles, glands).

The core of the ganglion also contains fascicles of passage fibers which are the tracts. The transverse nerve fibers joining two lateral sides of a ganglion are termed commissures. Nerves are parallel bundles of fibers connecting the ganglia with the different body parts. Each nerve fiber grows out of a nerve cell and the core of that fiber



Nervous System, Figure 19 **Diagram showing the position of nervous tracts within a ventral ganglion.**

is an axon. Nerves contain both sensory and motor fibers, but some nerves can consist of either motor or sensory fibers. The connectives between all ganglia of the nervous system are of the same nature as the nerves, but they are mostly formed from the axons of association neurons (Fig. 19).

The Synapses

Nervous conductors are not in direct contact with other nerves or effector cells. They do, however, come to close association at certain regions called synapses where nervous impulses are transferred through a gap or space termed the synaptic cleft, which has a width in the range of 10–25 nm. Transmission of the nerve impulse through the synapses is chemical. Electrical transmission likely occurs as well. A nerve fiber is capable of conducting impulses in both directions from the point of an experimental stimulus. The normal one direction conduction is accomplished by the synapses where impulses can cross in only one direction. Synaptic connections occur in insects within the neuropile.

The Giant Fibers

Giant fibers are enlarged premotor association neurons which run within the ventral nerve cord and are associated with sensory-motor combinations. They extend between the last abdominal and mesothoracic ganglia, from the protocerebrum to the thoracic ganglia, or directly to the thoracic muscles. Their significance is to increase the velocity of conduction where it reaches to 3–7 m/s due to their large diameter (12–45 μm) that can go up to 60 μm compared to less than 5 μm in ordinary fibers. Giant fibers are almost always related to rapid startling responses. There are usually 2–8 giant fibers and they are most studied in Blattodea, Orthoptera, Diptera, and the larvae of dragonflies.

The Neuroglia and Nervous Sheath

The neuroglia or glial cells are non-nervous cells covering all parts of the nervous system and its constituents. These cells fill all the spaces between the nervous elements, forming something similar to a connective tissue. Glial cells located in the rind of the ganglion are intimately associated with the perikaryia, making a cover over the whole surface of each individual one. The membrane of the perikarion invaginates, making a number of thin blind canals which contain the cytoplasm of the glial cells. These structures are called trophospongium (chondriome, intracellular trabeculae). The glial cells that bound the surface of the neuropile send their cytoplasm deeply into the core of the ganglion so that the arborizations of the axons, which form the neuropile, are embedded in that cytoplasm and its membranes.

Each axon is surrounded individually by the membranes of one or several glial cells, also termed Schwann cells, making an investment of one or many overlapping layers around the axon. Many small axons can be enveloped in one glial cell. Loosely wrapped axons in insects are called tunicated, or loosely myelinated. Most of the thin (<0.5 μm) axons are naked, without any cover.

The nervous sheath is a strong outer cover surrounding the ganglia, connectives and nerve trunks. It consists of an inner cellular layer, the perilemma (perineurium) and an outer noncellular layer, the neurilemma (neural lamella, basal lamina). The cells of the perilemma are modified glial cells covering the ganglia. Less modified glial cells are found in regions of perilemma surrounding connectives and large nerves. The neurilemma is apparently secreted by the perilemma. It is composed of an inner, fibrous and thick component of collagen like-fibrils in a matrix of some kind of polysaccharides, and a thin, homogenous part making the outer layer of the sheath. The nerve sheath plays the role of a blood barrier, preventing free exchange of ions with the blood. The nerve sheath and the neuroglia insulates, supports, and nourishes the neurons.

Function of the Central Nervous System

The term "brain" in insects implies no homology to that in vertebrates. An insect deprived of its brain can eat and digest its food if that food is placed in contact with its mouthparts, but the insect is not able to go to that food. The brain seems to be not absolutely necessary for vital processes, but it coordinates the sense organs and the muscles. The subesophageal ganglion may act with the brain for choice of behavior and inhibitory influence on behavioral modes that are not relevant to a given situation.

Insect species differ in their reaction to decapitation. The aquatic beetle *Dytiscus* loses its capability of locomotion upon removal of its head, while headless carabid beetles live and walk for many days. Headless silkmoths live as long as normal ones. However, generalization in this situation does not apply because these moths are short-lived and do not feed. In all insects, the functions of selection, deliberation and control of movements are lost on removal of the head.

Nerve information is processed and integrated in the lobes, centers and tracts inside the brain. The most important of these are the protocerebral bridge which is a tract of axons, the central body which is a neuropile mass, and the corpora pedunculata (mushroom bodies) which consist of unipolar neurons whose perikaryia are arranged in the shape of two circular caps called the calyces, and a dense neuropile forming the stalks of the corpora pedunculata.

The corpora pedunculata are thought to be the centers of learning and memory in insects. Their volume in honeybee workers increases by 20% when they mature. This increase is accomplished through further arborization of neural processes devoted to sensory input. The relative size of the corpora pedunculata may reach 55% of the brain in more intelligent species of insects. The brain index by Alten and Armbruster, which is based on the proportional size of the corpora pedunculata, showed that bumble bees are possibly the most intelligent insects with a brain index of 3.153 for the worker of *Bombus terrestris*. Honeybees ranked the fifth with the brain index being 2.572, 2.526, and 2.455, for the worker, queen and drone, respectively. The brain is concerned with the acquisition of habits. Long-term memory is established in both the head and thoracic ganglia. Memory of the honeybee can be erased by prolonged CO_2 narcosis. Genetically built-in types of functioning is found in the brain and segmental ganglia. However, circadian rhythms are centered in the brain.

Each segmental ganglion possesses almost completely independent sensory and motor centers for the segment or segments with which it is associated, serving primarily as an adjustor for local activities of that part with a very definite and limited control from the brain. There is an anastomosis between the last nerve of a ganglion and the first nerve of the next, in addition to the connections by nerve fibers running in the nerve cord and in the commmissures, through which movements can be coordinated between right and left halves and between neighboring ganglia. In some insects, an isolated thorax can walk. The isolated abdomen of a mated female silkmoth lays eggs as a reflex of rubbing its abdomen, which attempts to lay eggs in the normal way. Even the ganglion of a single isolated thoracic segment of the cockroach can learn to avoid placing its legs in a position where it previously received an electric shock.

Larval Nervous System

Insect larvae generally possess a central nervous system similar to that in primitive insects, where there is a nervous ganglion in each body segment. However, sometimes we find that all ganglia with the nerve cord and the subesophageal ganglion are concentrated in one ganglion, as in the dipteran larvae of the suborder Cyclorrhapha. Larvae of insects having complete metamorphosis undergo reconstruction growth of the nervous system through more or less fusing of its ganglia during its development to reach the adult stage.

Usually most of the larval neurons disintegrate by histolysis during metamorphosis, except the corpora pedunculata, which persist. In Coleoptera, the main regions of the brain persist as well. Ganglionic mother cells, which are not nervous cells, divide and give rise to the neurons of adults. In the first few days of the pupal stage of the sphinx and turnip moths, it was found that clusters of immature neurons and glial cells move from each of the subesophageal and the three thoracic ganglia along the interganglionic connectives to enter the next posterior ganglion.

The Visceral Nervous System

In the adult insect, the visceral nervous system is composed of the frontal ganglion, which is situated in front of the brain and connected to the two sides of the tritocerebrum by the two arching frontal connectives. The recurrent nerve extends from the frontal ganglion backward beneath the brain lying along the dorsal side of the esophagus. It joins the hypocerebral ganglion (occipital, esophageal, anterior visceral) which is lying on the esophagus just behind the brain. Insects differ in having one or two nerves arising from the hypocerebral ganglion and passing backward. Each nerve ends in a ganglion located at the beginning of the midgut. These are the two ingluvial ganglia (ventricular, splanchnic, stomachic), which fuse to form one ganglion if only one nerve arises from the hypocerebral ganglion. The visceral system innervates the foregut, the midgut, the salivary glands, heart and aorta.

The median nerve is considered part of the visceral nervous system. It emerges dorsally from the ventral ganglia and runs posteriorly between the two interganglionic connectives. Two transverse nerves arise from the median nerve in each body segment and innervate the muscles of the spiracles and probably the heart in that segment. Spiracles are controlled by lateral nerves from the ganglion of the nerve cord if the median nerve is lacking, as in bees.

► Embryogenesis

References

Bullock TL, Hordridge AG (1965) Structure and function in the nervous system of invertebrates. Freeman, San Francisco

Chapman RF (1998) The insects: structure and function, 4th edn. Cambridge University Press, Cambridge.

Hanson BS, Anton S (2000) Function and morphology of the antennal lobe: new developments. Annu Rev Entomol 45:203–231

Schmitt JB (1962) The comparative anatomy of the insect nervous system. Annu Rev Entomol 7:137–156

Snodgrass RE (1935) Principles of insect morphology. McGraw-Hill, New York

Nesameletidae

A family of mayflies (order Ephemeroptera).

► Mayflies

Nest Odor

The nests of social insects develop a distinctive and characteristic odor that allows its inhabitants to distinguish that nest from nests of other species, and even other nests of the same species. The nest odor can be dynamic, shifting as one queen is replaced by another.

Nest Parasitism

A relationship among termite species in which one lives in, and on, the carton material forming the nest of the other species.

Net-Spinning Caddisflies

Members of the family Hydropsychidae (order Trichoptera).

► Caddisflies

Net-Winged Beetles

Members of the family Lycidae (order Coleoptera).

► Beetles

Net-Winged Midges

Members of the family Blephariceridae (order Diptera).

► Flies

Neurochaetidae

A family of flies (order Diptera).

► Flies

Neurogenic Flight Muscles

Flight muscles require a nervous impulse for each contraction.

Neurohemal Organ

An organ associated with the nervous system that stores and releases hormones synthesized in nervous tissue.

Neurohormone

Secretions produced in the brain and endocrine glands, released into the hemolymph, and regulating numerous physiological and behavioral functions in insects.

► Endocrine Regulation of Insect Development

Neurological Effects of Insecticides and the Insect Nervous System

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The importance of the nervous system to the functional integrity of insects makes it an extremely sensitive target for the action of poisons. It is by no small coincidence that both nature and the pesticide industry have discovered the best way to poison insects (and other animals) is through the nervous system. Of all the natural poisons known, the most lethal are those that act on the nervous system. Additionally, the vast majority of chemical insecticides in use today act upon the insect central nervous system.

The nervous system achieves the three important functions of sensation, integration and response. *Sensation* is the detection of an organism's environment and gathering of information. *Integration* is the sorting and evaluation of information. *Response* is the coordination of not only motor activity, but also secretory activity, as in the case of the neuroendocrine system.

Structure of the Insect Nervous System

The insect central nervous system consists of a brain situated dorsally in the head and a ventral chain of segmental ganglia. Ganglia are bundles of neurons from which peripheral nerves run to sense organs, muscle systems, internal organs and secretory glands. Ganglia can show a variety of arrangements, ranging from minimally fused segmental arrangements (e.g., *Blattodea*) to highly fused arrangements (e.g., Diptera: *Musca*).

The nervous system is composed of thousands of individual nerve cells, or neurons. Neurons are composed of dendrites, cell bodies (where nuclei are located) and axons. The bodies of neurons are aggregated to form ganglia, while bundles of axons form nerves. Nerve impulses called action potentials are conducted along axons. Nerve impulses can be enhanced or suppressed by regulatory inputs received from dendrites. Most insect neurons are *monopolar*, having only single axonal projections. Some sensory neurons are *bipolar*, while some critical neurons that occur in the brain and stretch receptors are *multipolar* (Figs. 20 and 21).

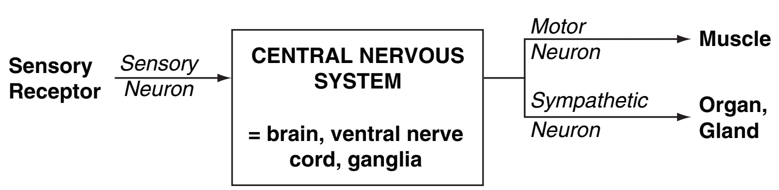
Function of the Nervous System

Information is transmitted through the nervous system both electrically and chemically. Electrical transmission is influenced by the composition of the fluid surrounding a neuron, in particular, its ionic composition. Transmission of electrical impulses along neurons is an "all-or-nothing" process that is mediated by membrane permeability to ions. Transmission of information between neurons across gaps (synapses) is mediated by chemical messengers called neurotransmitters. Neurotransmitters elicit graded post-synaptic potentials that can either be excitatory or inhibitory. The nervous system is not a simple relay system; it simultaneously integrates and sums many inputs from the body. Integration and summation involve both stimulatory and inhibitory effects.

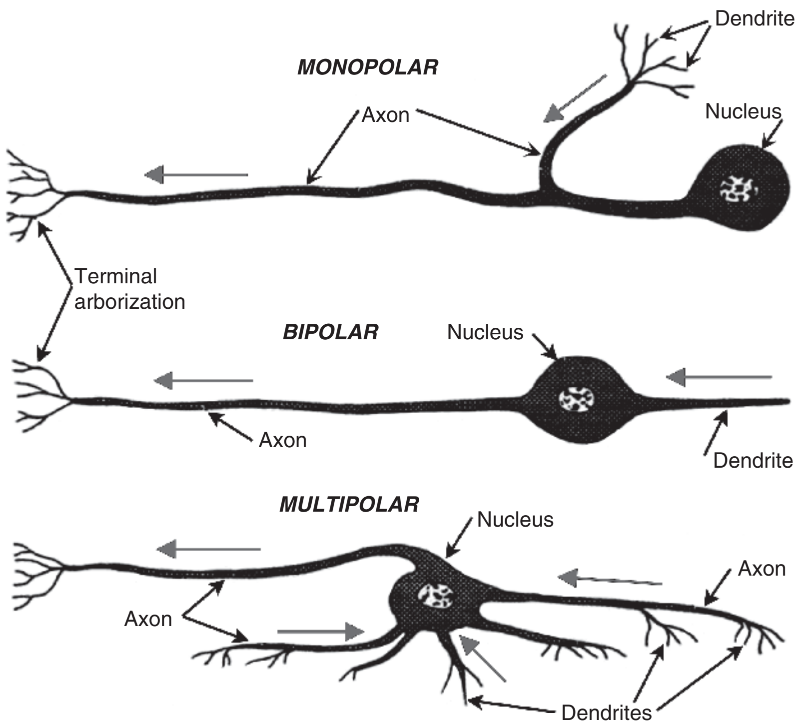
The Resting Potential

The ionic concentrations within an axon differ from those in the adjacent extra-cellular fluid. In particular, sodium (Na^+) and potassium (K^+) ions in a resting neuron are asymmetrically distributed across the cell membrane. Sodium is actively pumped out of the axon so that its concentration is much lower inside than outside. At the same time, potassium is actively pumped into the axon so that its concentration is higher inside than outside. The mechanism that maintains these concentration imbalances is called the sodium–potassium (Na/K) pump. The Na/K pump requires energy from ATP to generate concentration gradients of (internal/external) 450/50 mM for Na^+ and 10/400 mM for K^+.

The difference of Na^+ and K^+ concentrations across the axonal membrane results in a negative charge differential within the axon of about –60 mV relative to the outside. This polarized condition is called the resting or membrane potential. As will be shown later, sodium and chloride play key roles (respectively) in mediating and regulating axonal transmission of electrical impulses. Influx of sodium



Neurological Effects of Insecticides and the Insect Nervous System, Figure 20 **Simplified diagram of the insect nervous system.**



Neurological Effects of Insecticides and the Insect Nervous System, Figure 21 Two types of neurons found in the insect nervous system. Monopolar neurons (*above*) are most common, but multipolar neurons are probably most toxicologically relevant. *Arrows* indicate the direction of impulse movement (modified from Chapman 1983).

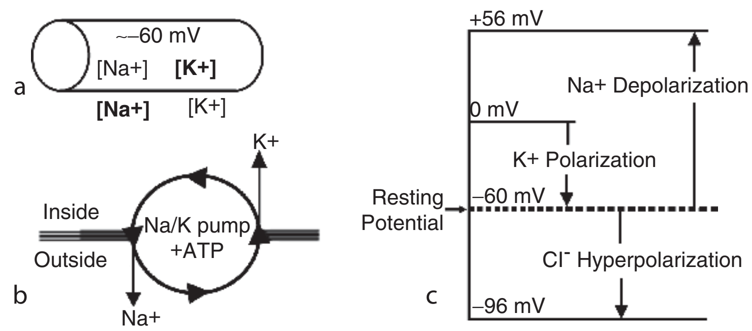
results in depolarization, or a decrease in the charge differential relative to the extracellular environment. The influx of negatively charged chloride ions (Cl^-) results in hyperpolarization relative to the resting potential (Fig. 22).

The Action Potential

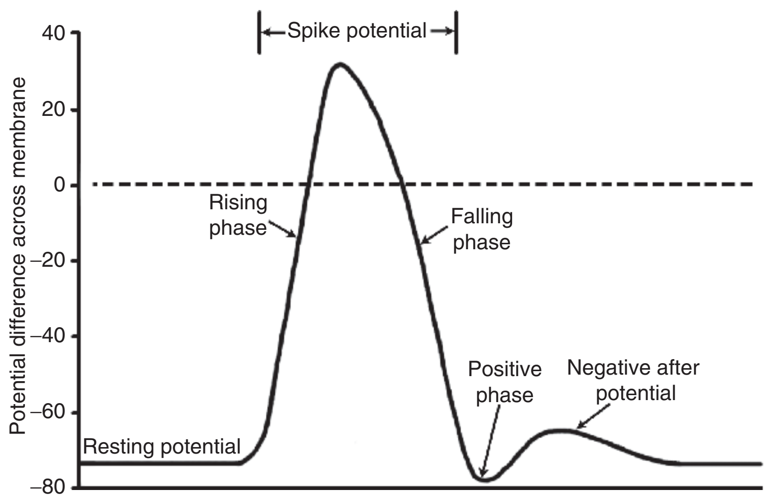
The neuronal action potential is the propagated "all-or-nothing" nerve impulse that is the basis of electrical transmission through the nervous system. This all-or-nothing response of the axonal membrane is a specialized adaptation for transmission of information over distance. The action potential is a traveling zone of depolarization and repolarization that moves along an axon. Action potentials are transient – they are extremely short-lived (<100 ms).

Action potentials are initiated in the spike generating zone, or "axon-hillock," of axons. This initiation is a response to a depolarizing post-synaptic potential (see below). Action potentials are mediated by selective permeability of the axonal membrane to sodium and potassium ions. Selective permeability is mediated by voltage-sensitive Na^+ and K^+ ion channels. When these ion channels open, ions diffuse naturally down their concentration gradients.

Action potentials have four phases that include a rising phase, a falling phase, the positive phase, and the negative after potential. In the rising phase the membrane becomes permeable to Na^+, resulting in Na^+ influx into axon (=depolarization). In the falling phase the membrane becomes permeable to K^+ and impermeable to Na^+, resulting in K^+ efflux out of the axon (=repolarization). In the positive phase, there is a slight overshoot as K^+ permeability terminates. In the final phase, the negative after potential, there is a slight depolarization as the Na/K pump returns the axon to its resting potential (=high interior [K^+]) (Fig. 23).



Neurological Effects of Insecticides and the Insect Nervous System, Figure 22 **Key concepts associated with resting potential: (a) a concentration differential is maintained on either side of the neuronal membrane in the axon, with more sodium outside than inside and more potassium inside than outside; (b) the sodium–potassium differential is maintained by the ATP-dependent Na/K pump; (c) maintenance of the Na/K differential results in an internal charge deficit of about –60 mV relative to the outside. Influx of sodium causes a depolarizing action potential. Influx of Cl^- ions results in a hyperpolarizing inactivation potential.**



Neurological Effects of Insecticides and the Insect Nervous System, Figure 23 **Features of action potentials as determined by electrophysiological measurements from individual neurons (modified from Chapman 1983).**

Synaptic Transmission

Gaps between neurons are called synapses. The two kinds of synapses are electrical and chemical. Chemical synapses are the most toxicologically relevant. The neuron carrying the impulse toward the synapse is called the pre-synaptic neuron. The neuron receiving the signal is called the post- or sub-synaptic neuron.

Neurotransmitters are chemical messengers that cross synapses. These biochemical messengers can be either excitatory or inhibitory. The most important excitatory neurotransmitter is acetylcholine; other relevant excitatory neurotransmitters include octopamine, dopamine and serotonin. The most important inhibitory neurotransmitters are GABA and glutamate. GABA occurs in the insect central nervous system, while glutamate occurs mainly in the peripheral nervous system.

The steps involved in synaptic transmission are outlined in the list below, and shown in the bottom portion of the synaptic transmission concept figure (Fig. 24).

1. An action potential arrives at the axon terminus of the pre-synaptic neuron.
2. Voltage-sensitive calcium channels are activated, resulting in calcium (Ca^{2+}) influx.
3. Ca^{2+} influx triggers neurotransmitter release into the synapse.
4. Neurotransmitter molecules bind their specific receptors on the post-synaptic membrane.
5. An electrical post-synaptic potential is initiated (see next section).

Post-Synaptic Potentials

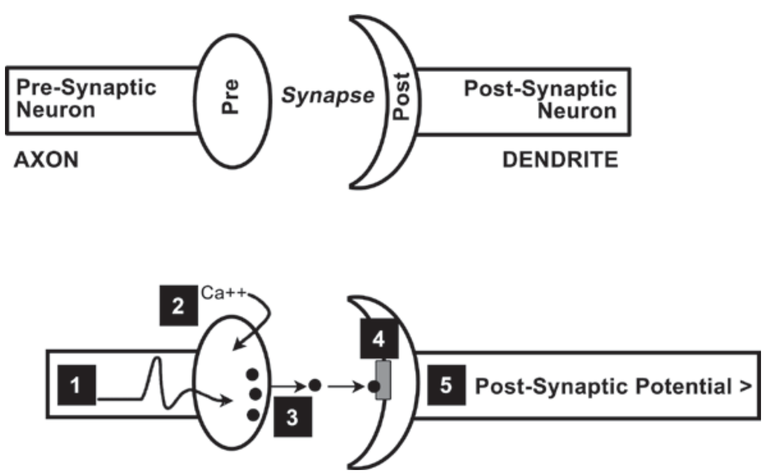
Post-synaptic potentials (PSPs) are electrical transmissions that are initiated in central and peripheral neurons at the post-synapse. Unlike action potentials, which are all-or-nothing and propagated along the entire axon, PSPs are graded, passive and decremental. In other words, the magnitude of a PSP is graded in proportion to the amount of neurotransmitter release, and it is diluted (passive) and diminishing over distance (decremental).

Depending on the neurotransmitter involved, PSPs can be either excitatory or inhibitory. Excitatory neurotransmitters like acetylcholine elicit excitatory PSPs (EPSPs), which are in essence graded action potentials. Inhibitory neurotransmitters like GABA and glutamate elicit inhibitory PSPs (IPSPs), which are quite different from EPSPs. IPSPs are mediated by chloride ion (Cl^-) influx into neurons, which results in axonal hyperpolarization. IPSPs are thusly also referred to as "inactivation potentials."

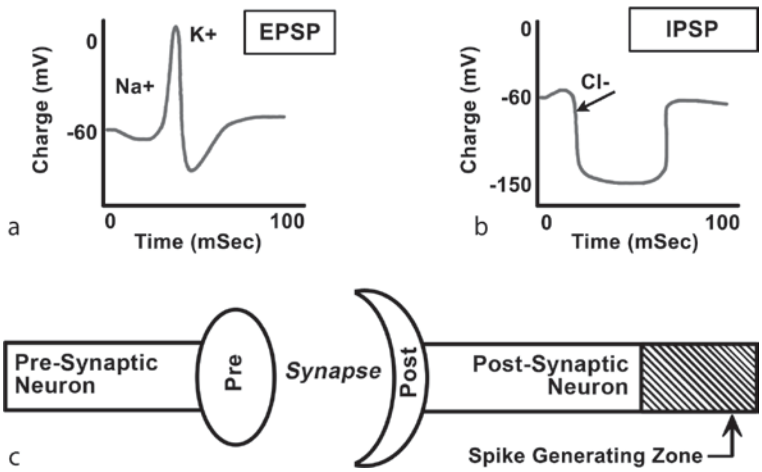
IPSPs counteract or, in other words, cancel EPSPs. However, when an EPSP successfully reaches the axonal spike generating zone at sufficient magnitude, this triggers the formation of an action potential. The frequency of action potential formation is directly proportional to the frequency of EPSPs reaching the spike generating zone (Fig. 25).

Integration and Summation

Most of the time, the nervous system does not act as a simple relay between receptors and response



Neurological Effects of Insecticides and the Insect Nervous System, Figure 24 **Concepts associated with synaptic transmission: (*top*) anatomy of a chemical synapse and relevant terminology; (*bottom*) five major steps involved in synaptic transmission.**



Neurological Effects of Insecticides and the Insect Nervous System, Figure 25 Important concepts associated with post-synaptic potentials (PSPs): (a) PSPs can be excitatory and elicit Na/K-mediated depolarizing EPSPs, or (b) they can be inhibitory and elicit Cl-mediated hyperpolarizing IPSPs; (c) if an EPSP is of sufficient magnitude to reach the axonal spike generating zone, an action potential will be released.

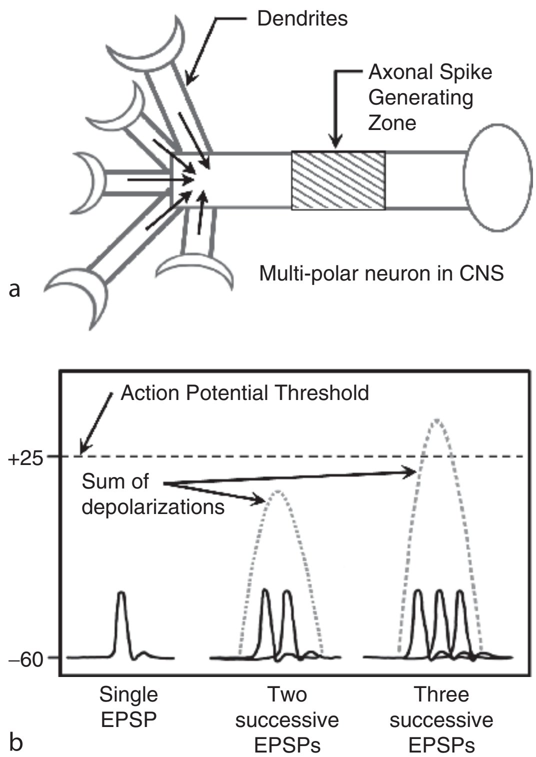
elements. It integrates and sums the activities of different parts of the body so that appropriate behavioral responses and internal regulating changes can be made.

Integration is one important way in which the nervous system can interpret complex inputs coming in from throughout the body. Integration is enabled by morphological features of bipolar and multipolar neurons of the central nervous system. These neurons have multiple dendritic processes that receive inputs from many other neurons. These incoming signals are summed before they reach the axonal spike generating zone. If signals exceed threshold levels, an action potential is generated. Thus, integration enables summation.

Summation is the process by which massive combinations of post-synaptic hyper-polarizations and depolarizations are mathematically interpreted in the central nervous system. In particular, PSPs occurring in rapid succession are summed algebraically in the post-synapse. If their net charge is above threshold at the spike generating zone, this will elicit an action potential. However, a single EPSP or a combination of EPSP and IPSP may not surpass the threshold, and thus, would not elicit action potential formation (Fig. 26).

General Neurological Effects of Insecticides

Insecticide target sites are defined as the specific biochemical or physiological sites within an insect that insecticide molecules interact with to create toxic effects. The physico-chemical properties of insecticides dictate the target sites with which they are capable of interaction. There are several highly relevant neurological target sites that are acted upon by insecticides. The information presented here focuses on target sites of the most prevalent neurotoxic insecticides in use worldwide. In most general terms, there are only two generalized neurological effects of insecticides. However, it is important to note and understand that these effects can be achieved in a diverse number of ways. These general effects include neuroexcitation and neuroinhibition. Neuroexcitation is an increase in neurological activity above baseline levels. At the organismal level, neuroexcitation results in hyperactivity, tremors and rigid paralysis. Neuroinhibition is a decrease in neurological activity below baseline levels. At the organismal level, neuroinhibition results in immobility and flaccid paralysis.



Neurological Effects of Insecticides and the Insect Nervous System, Figure 26 Key concepts associated with integration and summation: (a) A multipolar neuron that receives and integrates signals from multiple dendritic processes. These inputs are summed (added and subtracted) ahead of the axonal spike generating zone; (b) Example of how single and multiple excitatory post-synaptic potentials (EPSPs) are summed. The single EPSP is below threshold and thus, elicits no action potential. The sum of the two successive EPSPs is still below threshold and again results in no action potential. However, the sum of the three successive EPSPs is above threshold, resulting in action potential generation.

Neurological Target Sites and Specific Neurological Effects of Insecticides

The neurological target sites reviewed here include voltage-gated sodium channels, GABA and glutamate-gated chloride channels, the acetylcholinesterase enzyme, and nicotinic acetylcholine receptors. The actions of insecticides at these sites are diverse and range from receptor agonism (binding and stimulating a receptor), to receptor antagonism (binding and blocking a receptor), ion channel modulation (altered gating kinetics), and enzyme inhibition. Table 3 provides an overview of insecticides discussed in the sections that follow, and Table 4 provides a summary of the specific neurological modes of action and effects described in subsequent sections.

Voltage-Gated Sodium Channels

Voltage-gated sodium channels are responsible for the initiation and perpetuation of both action potentials and excitatory post-synaptic potentials, in both central and peripheral neurons. Insecticides that act upon sodium channels include DDT (and related analogs), natural pyrethrins, synthetic pyrethroids, and oxadiazines. Sodium channels are "gated" (i.e., activated and inactivated) at very precise intervals that are dictated by specific physiological properties. DDT, pyrethrins and pyrethroids act by modulating sodium channels, which results in altered gating kinetics. Generally, DDT, pyrethrins and pyrethroids affect sodium channels by causing (i) activation at lower thresholds, and/or (ii) inactivation later than would occur under normal circumstances. The end result is prolonged flow of sodium ions into neurons, which results in neuronal dysfunction from excess neuroexcitation.

The oxadiazine insecticides are a newer class of insecticides that act as sodium channel antagonists. Oxadiazine effects make it appear as if an organism is paralyzed. At the neuronal level, oxadiazine toxicity is the result of sodium current blockage. This effect is in contrast to the gate-modifying sodium channel toxins noted above. Specifically, oxadiazines interact with the sodium channel pore itself, which blocks sodium current flow into neurons.

Neurological Effects of Insecticides and the Insect Nervous System, Table 3 A listing of insecticide classes, their target sites, and some specific insecticides (by common name) that occur in each class

Class	Target site	Insecticides
DDT and analogs	Na^+ Channel	DDT, dicofol, kelthane, methoxychlor, ovex
Pyrethrin	Na^+ Channel	Pyrethrins, chrysanthemum extract
Pyrethroid	Na^+ Channel	Allethrin, cypermethrin, fenvalerate, permethrin, resmethrin, metofluthrin
Oxadiazine	Na^+ Channel	Indoxacarb
Cyclodiene	Cl^- Channel (GABA-gated)	Aldrin, chlordane, dieldrin, endosulfan, endrin, heptachlor, lindane, toxaphene
Phenylpyrazole	Cl^- Channel (GABA-gated)	Fipronil, ethioprole
Avermectin	Cl^- Channel (Glutamate-gated)	Abamectin, doramectin, emamectin-benzoate, ivermectin
Milbemycin	Cl^- Channel (Glutamate-gated)	Milbemycin, moxidectin
Organophosphate	Acetylcholinesterase Enzyme	Azinphos, chlorpyrifos, diazinon, dichlorvos, dimethoate, parathion, fenitrothion, fonofos, malathion, pirmiphos, propetamphos, phorate, temephos, terbufos
Carbamate	Acetylcholinesterase Enzyme	Aldicarb, bendiocarb, carbaryl, carbofuran, carbosulfan, methiocarb, methomyl, propoxur
Nicotine	Nicotinic Acetylcholine Receptor	Nicotine
Nicotinoid	Nicotinic Acetylcholine Receptor	Acetamiprid, clothianidin, dinontefuran, imidacloprid, nitenpyram, nithiazine, thiacloprid, thiamethoxam
Spinosyn	Nicotinic Acetylcholine Receptor	Spinosad, spinetoram

GABA and Glutamate-Gated Chloride Channels

Gamma amino butyric acid (GABA) and glutamate are inhibitory neurotransmitters that elicit the influx of chloride ions into central neurons through chloride channels. Insecticides that are active at chloride channels can produce either neuroexcitation or neuroinhibition, depending on the specific neurotransmitter receptor involved. Early insecticides such as cyclodienes, as well as the newer phenylpyrazoles, function as antagonists at the GABA-gated chloride channel complex. In the case of chloride channels, such antagonism results in a blockage of natural inhibitory chloride currents, leading ultimately to neuroexcitation.

In arthropods, glutamate-gated chloride channels occur at skeletal neuromuscular junctions of both the peripheral and central nervous systems. Avermectin and milbemycin insecticides act as agonists at glutamate-gated chloride channels, and thus they produce effects that are opposite to insecticides that antagonize GABA-gated chloride channels. Because they agonize neuro-muscular chloride channels, avermectins and milbemycins elicit increased chloride current flow into neurons. This increase in chloride current results in intracellular hyperpolarization, and thus neuroinhibition via the cancellation of positively charged excitatory impulses.

Acetylcholinesterase Enzyme

Acetylcholinesterase is an enzyme that occurs in the insect central nervous system; it functions

Neurological Effects of Insecticides and the Insect Nervous System, Table 4 Summary of neurotoxic insecticides, their sites and modes of action, their effects on neurons, and their general effects at the whole organism level

Insecticide class	Target Site	Mode of action	Generalized neurological effect[a]	Whole organism effect[b]
DDT and analogs	Na^+ Channel	Ion Channel Modulation	Neuro-Excitation	Rigid paralysis, uncoordinated movement
Pyrethrins, Type I & II pyrethroids	Na^+ Channel	Ion Channel Modulation	Neuro-Excitation	Rigid paralysis, uncoordinated movement
Oxadiazine	Na^+ Channel	Antagonism	Neuro-Inhibition	Flaccid paralysis, no movement
Cyclodiene	Cl^- Channel (GABA-gated)	Antagonism	Neuro Excitation	Convulsions, rigid paralysis
Phenylpyrazole	Cl^- Channel (GABA- and Glutamate-gated)	Antagonism	Neuro-Excitation	Convulsions, rigid paralysis
Avermectin & Milbemycin	Cl^- Channel (mostly glutamate-gated)	Agonism	Neuro-Inhibition	Flaccid paralysis, no movement
Organophosphate	Acetylcholinesterase Enzyme	Enzyme Inhibition	Neuro-Excitation	Rigid paralysis
Carbamate	Acetylcholinesterase Enzyme	Enzyme Inhibition	Neuro-Excitation	Rigid paralysis
Nicotinoid	Acetylcholine receptor	Agonism	Neuro-Excitation	Rigid paralysis
Spinosyn	Acetylcholine receptor	Agonism	Neuro-Excitation	Rigid paralysis

[a]Effect that would be observed from a nerve recording
[b]Effect that would be observed by watching the whole organism after poisoning

by removing the neurotransmitter acetylcholine from its post-synaptic receptor. The result of this action is the hydrolysis of acetylcholine into acetate and choline, and ultimately, the initiation of action potentials at precise and exact intervals. Organophosphate and carbamate insecticides inhibit the acetylcholinesterase enzyme, which results in prolonged binding of acetylcholine to its post-synaptic receptor. Eventually, this dysfunction leads to the death of an organism from prolonged neuroexcitation.

Organophosphate insecticides are generally very long, and sometimes irreversible, inhibitors of acetylcholinesterase. Carbamate insecticides, alternatively, are fast to act but are reversible acetylcholinesterase inhibitors. Unfortunately, both organophosphates and carbamates have relatively high toxicity to mammals and other non-target organisms, although the carbamates are generally more hazardous because of their greater affinity and speed of acetylcholinesterase inhibition.

Nicotinic Acetylcholine Receptor

Nicotinic acetylcholine receptors occur in post-synaptic membranes of the arthropod central nervous system. These receptors are termed "nicotinic" because they are bound with great affinity by the natural botanical insecticide nicotine. There are also other classes of acetylcholine receptors called muscarinic receptors that are more resistant to the effects of nicotine and which are greatly outnumbered in the insect nervous system by nicotinic receptors. As noted above, the excitatory neurotransmitter acetylcholine functions by binding to the post-synaptic receptor, which causes a local transient influx of sodium ions (EPSP) that ultimately leads to action potential formation. Nicotinic acetylcholine receptors are the target sites for nicotinoid and spinosyn insecticides that are currently in wide-scale use. These insecticides act as neurotoxicants by agonizing nicotinic acetylcholine receptors. The primary toxic symptom associated with these materials is neuroexcitation through prolonged EPSP production.

Conclusions

Structure–function relationships of the insect nervous system are complex and, moreover, there are numerous classifications of the interactions between insecticides and their neurological target sites. In most general terms, there are two basic neurological effects of insecticides: excitation and inhibition. These two general effects, however, can result from a diversity of interactions between the various neurotoxic insecticides and their target sites. Specifically, the four types of interactions here include receptor agonism or antagonism, ion channel modulation, and enzyme inhibition. Even as new types of neurotoxic insecticides with new modes of action are discovered and developed, these general effects will likely remain as the fundamental basis for insecticide-induced neurotoxicity.

► Nervous System of Insects
► Insecticides
► Acaricides or Miticides
► Pesticide Hormoligosis
► Detoxification Mechanisms in Insects
► Pesticide Resistance Management

References

Bloomquist JR (2001) GABA and glutamate receptors as biochemical sites for insecticide action. In: Ishaaya I (ed) Biochemical sites of insecticide action and resistance. Springer, Berlin Heidelberg, New York, pp 17–42

Buckingham SD, Sattelle DB (2005) GABA receptors of insects. In: Gilbert LI, Iatrou K, Gill SS (eds) Comprehensive molecular insect science, vol. 5. Elsevier, Boston, pp 107–142

Chapman RF (1983) The insects: structure and function, 3rd edn. Cambridge University Press, Cambridge, 788 pp

Jeschke EP, Nauen R (2005) Neonicotinoid insecticides. In: Gilbert LI, Iatrou K, Gill SS (eds) Comprehensive molecular insect science, vol. 5 Elsevier, Boston, pp 53–106

Matsumura F (1986) Toxicology of insecticides, 2nd edn. Plenum, New York, 503 pp

Nation JL (2001) Insect physiology and biochemistry. Plenum, Boca Raton, 496 pp

Scharf ME (2003) Neurological effects of insecticides. In: Pimental D (ed) Encyclopedia of pest management. Marcel-Dekker, New York. doi:10.1081/E-EPM 120014765

Silver K, Soderlund DM (2005) Action of pyrazoline-type insecticides at neuronal target sites. Pestic Biochem Physiol 81:136–143

Soderlund DM (2005) Sodium channels. In: Gilbert LI, Iatrou K, Gill SS (eds) Comprehensive molecular insect science, vol. 5. Elsevier, Boston, pp 1–24

Sparks TC, Crouse GD, Durst G (2001) Natural products as insecticides: the biology, biochemistry and quantitative structure activity relationships of spinosyns and spinsoids. Pest Manag Sci 57:896–905

Neuron

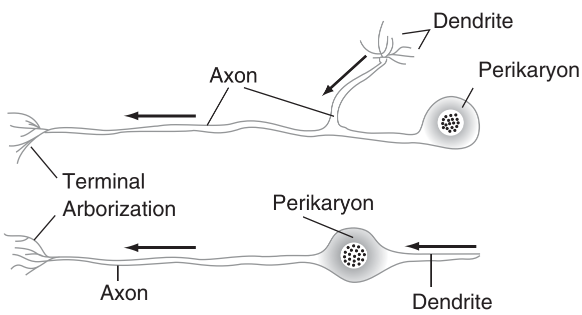
A nerve cell, normally consisting of a cell body or soma, an axon, and dendrites. Types of neurons include sensory neurons, interneurons, and motor neurons (Fig. 27).

► Nervous System

Neuropile

The central region of a ganglion containing synaptic connections between nerves. It is surrounded by a shell of cell bodies (somata or perikarya).

► Nervous System



Neuron, Figure 27 **Diagrams of insect nerve cells showing direction of nervous impulse (adapted from Chapman, The insects: structure and function).**

Neuroptera

An order of insects. They commonly are known as lacewings, ant lions and mantidflies.

► Lacewings, Antlions, and Mantidflies

Neurorthidae

A family of insects in the order Neuroptera.

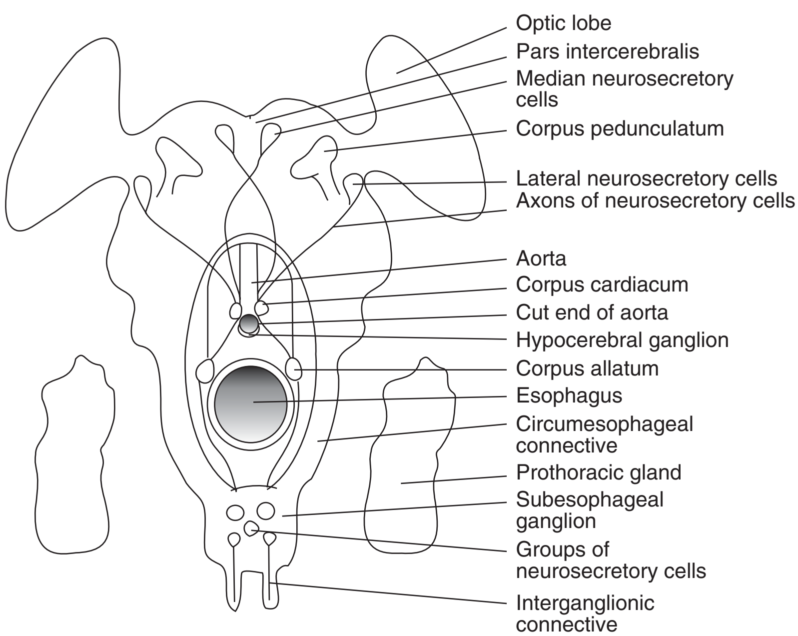
► Lacewings, Antlions, and Mantidflies

Neurosecretory Cell

A cell in the nervous tissue that produces and releases hormones (Fig. 28).

► Prothoracicotropic Hormone

► Regulation of Sex Pheromone Production in Moths



Neurosecretory Cell, Figure 28 **Cross section showing the relationships of the principal endocrine glands and the neurosecretory cells with the brain (adapted from Chapman, The insects: structure and function).**

Neurotoxin

A chemical that affects the nervous system. Neurotoxins may be natural (produced by Hymenoptera or plants, for example) or synthetic (most synthetic insecticides).

► Insecticides
► Insecticide Toxicity
► Venoms and Toxins in Insects

Neurotransmitter

A chemical that is produced by a nerve ending and which enables a nervous impulse to pass over a synapse to stimulate an adjacent nerve cell.

► Nervous System
► Insecticides

Net Primary Production

(NPP) The total energy accumulated by plants during photosynthesis; gross primary production less respiration.

Newell, Wilmon

Wilmon Newell was born at Hull, Iowa, USA, on March 4, 1878. He earned the B.S. and M.S. degrees from Iowa State University in 1897 and 1899, respectively. He served as deputy director of the Iowa State Agricultural Experiment Station in 1898, and then worked at Ohio Agricultural Experiment Station from 1899 to 1902. In 1902 he moved to the Texas Agricultural Experiment Station, and then served as State Entomologist of Georgia in 1903. In 1905 he worked at the Louisiana Agricultural Experiment Station, but he returned to Texas in 1910. Finally, he moved to Florida in 1915, where he spent the remainder of his career. In Florida, he served as Plant Commissioner of the State Plant Board, but in 1921 also was named Dean of the College of Agriculture, Director of the Agricultural Experiment Station, and Director of Agricultural Extension. In 1938, Newell was named Provost for Agriculture at the University of Florida. Newell published on various important subjects during the course of his employment, including apiculture, Argentine ant, cotton insects, scale insects, quarantine, and insect eradication. He had a major role in the eradication of citrus canker from Florida in 1915, and the Mediterranean fruit fly in 1929. Newell died at Gainesville, Florida, on October 25, 1943. The Newell Entomological Society and Newell Hall at the University were named in his honor.

Reference

Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Newman, Edward

LOUIS A. SOMMA, JAMES C. DUNFORD
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Edward Newman was born in Hampstead, England, in 1801 and raised in a Quaker family. During his childhood his parents strongly encouraged him to appreciate and study natural history, a beloved interest that he pursued when he left home for boarding school. In 1817 he returned to his family, then living in Godalming, where he entered the wool trade with his father and continued to work with him for the next 10 years. Throughout that time he continued to pursue his interest in local natural history. He eventually (1832–1850) published his formative observations, mostly on botany, entomology, ornithology and mammalogy, anonymously under the title "Letters of Rusticus" in the *Magazine of Natural History, Entomological Magazine* and *Chamber's Journal*. Many of these observations pioneered the field of economic entomology, a subject that he continued to expound upon in later years in *The Entomologist, The Zoologist*, and *The Field*, until his death in 1876.

In 1826, Newman moved to Deptford, London, and started a rope business. Here he benefited greatly through his contacts with other prominent Victorian naturalists, especially entomologists. He spent little time with the rope trade, and continued studying nature and publishing his observations. In 1837 he abandoned the rope trade out of sheer boredom, and in 1841 became a publisher, specializing in scientific books and journals.

Newman was a tireless, polymathic, and highly opinionated naturalist; a contemporary of Henry W. Bates, Charles Darwin, Edward and Henry Doubleday, Thomas H. Huxley, and Alfred Russel Wallace. Both Darwin and Wallace were among the many prominent researchers who published in his journals. Newman was editor of numerous journals, including *The Field*, the Quaker periodical *Friend*, and those he founded (*The Entomological Magazine, The Entomologist, The Phytologist*, and *The Zoologist*); cofounder and president of the Entomological Society of London (later to become the Royal Entomological Society); and president of the Zoological Society of London. He was passionate about poetry and classic literature, and early in his career seems to have had an obsession with classic language. However, he eventually moved away from excessive use of Latin in his publications and strongly promoted the democratization of scientific knowledge, and in later years championed the use of "readable" and "pure, plain, intelligible English" in scientific publications.

Newman obtained many of his observations by traveling throughout the British Isles, but never truly went abroad. His observations on bird behavior were often obtained from an aviary that he built in his private garden. Newman's journal articles reflected his wide ranging interests, but his most important contributions contain his studies on floral pollination, blackflies (Diptera: Simuliidae), sawflies (Hymenoptera: Symphyta), and British lepidopterans, some of which were published in the serial *Young England* and many of the aforementioned journals.

In addition to his numerous articles containing natural history observations and descriptions of new species of wildlife, especially insects, Newman published an eccentric array of entomological verse and some sharp-witted satire. His eccentric view of nature and idealistic approach to scientific study are evident in his *The Grammar of Entomology* (1835), *A Familiar Introduction to the History of Insects* (1841), and *The Insect Hunters; or, Entomology in Verse* (1858). Newman's books included compendia on British ferns, birds, and insects, some of these going into several editions. His publications were often illustrated with his own woodcuts. It also was not uncommon for Newman to publish under a pseudonym. His opinions and ideas were often controversial, including his efforts to come up with a variety of unique classifications for various animal groups, most notably schemes for endothermic vertebrates, especially birds, based upon physiology. During his career he was awarded society Fellowship titles from The Linnean Society of London, The Zoological Society of London, The Royal Microscopical Society, and the Zoologico-Botanical Society of Vienna. His greatest formal award was an honorary doctorate from Academiæ Cæsareæ Naturæ Curiosorum, the Imperial Academy of Leopold Charles of Austria. Despite Newman's quixotic and sometimes careless efforts, he was a pivotal figure among Victorian naturalists and crucial to the early development of British entomology.

References

Anonymous (1876) Preface. Entomol (London) 9:v–xxiv

Anonymous (1877) Obituary. The Entomologist's Monthly Magazine [Second Series] (London) 1876–1877 13:45–46

Newman E (1835) The grammar of entomology. Frederick Westley and A.H. Davis, London, 304 pp

Newman E (1841) A familiar introduction to the history of insects; being a new and greatly improved edition of

the grammar of entomology. John Van Voort, London, 268 pp
Newman E (1850) Preface. Zool [First Series] (London) 8: v–xvi
Newman E (1853) The insect hunters; or, entomology in verse. Edward Newman, London, 86 pp
Slotten RA (2004) The heretic in Darwin's court. The life of Alfred Russel Wallace. Columbia University Press, New York, 602 pp

Newsom, Leo Dale

Dale Newsom was born at Shongaloo, Louisiana, USA, on February 23, 1915. He attended Louisiana Polytechnic Institute from 1936 to 1938 and received a B.S. in agriculture from Louisiana State University in 1940. He attended Cornell University from 1940 to 1942, and again from 1946 to 1947, serving in the military during the intervening years. Newsom spent his entire professional career at Louisiana State, where he retired as Boyd Professor in 1984. This is the highest professorial rank attainable at Louisiana State, and Newsom was the first agriculturalist to attain this honor. He devoted his career to cotton, soybean, rice, sweet potato, and corn insect research, but in all endeavors he championed interdisciplinary research and the concept of integrated pest management. Early on he was aware of the value of beneficial insects and the hazards of excessive pesticide use, warning of the development of pesticide resistance, pest resurgence, shifts in pest status, and damage to the environment. As an early proponent of the integrated pest management concept, he assumed a leadership role in planning and implementing this new approach to crop protection, and so was asked to serve on numerous federal, state, and professional committees. He also was honored repeatedly by the Entomological Society of America. He died at Magazine, Arkansas, on October 10, 1987.

Reference

Graves JB, Boethel DJ (1988) Leo Dale Newsom 1915–1987. Bull Entomol Soc Am 34:47

New Zealand Primitive Moths (Lepidoptera: Mnesarchaeidae)

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New Zealand primitive moths, family Mnesarchaeidae, are known only from New Zealand. They are another relict family of only six known species. The family forms the monobasic superfamily Mnesarchaeoidea and the basal group of the infraordeer Exoporia. Adults small (5–10 mm wingspan), with head rough-scaled; labial palpi 3-segmented and short; haustellum short and with vestigial mandibles; maxillary palpi short and 3-segmented. Maculation is similar to Eriocraniidae, with purple or golden iridescent scales. Adults are diurnally active in forest clearings and near ferns. Biologies remain unknown.

References

Gibbs GW (1979) Some notes on the biology and status of the Mnesarchaeidae (Lepidoptera). N Z Entomol 7:2–9
Kobayashi Y, Gibbs GW (1995) The early embryonic development of the mnesarchaeid moth, *Mnesarchaea fusilella* Walker (Lepidoptera: Mnesarchaeidae), and its phylogenetic significance. Aust J Zool 43:479–488
Kristensen NP (1968) The skeletal anatomy of the heads of adult Mnesarchaeidae and Neopseustidae (Lep. Dacnonypha). Entomol Medd 36:137–151

Niche

The environmental requirements for an organism to exist. The role or trophic relationship of an organism in an ecosystem.

Niche Differentiation

The tendency of coexisting organisms to differ in their niche requirements.

Niche Overlap

Resource partitioning in which coexisting species share some, but not all, niche parameters.

Nidicolous

Existence by living in a nest. Social insects normally dwell in nests, but other organisms may have symbiotic or parasitic relationships with social insects, and live there too.

Nicoletiidae

A family of silverfish (order Zygentoma).

► Silverfish

Night Blooming Plants and Their Insect Pollinators

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Some insects find warm shelter for the night inside flowers. In exchange, they pollinate the hospitable plants, just as certain bumblebees do with a furry composite flower of *Sussurea* found in the Himalayas. Sometimes, insect visitors looking for nectar are forced to stay overnight inside flowers in spite of their desire; the flower closes, trapping insects temporarily. The flower then showers them with pollen, as some milkweed plants do to mosquitoes.

Many flowers rely on nocturnal animals entirely for pollination, and thus cater their resources specifically to these animals. Fragrances of flowers that bloom at night are among the most pleasant. For instance, the night-blooming ylang-ylang tree in the Philippines produces an extract used in Chanel No. 5 perfume. By producing these scents, plants compete for specialized night pollinators, among which insects are the most common.

The carpenter bee *Xylocopa tenuiscapa* is one of the few nocturnal species of bees. Its activity is unaffected by low nighttime temperatures and it uses moonlight for navigation. In India, these bees are the principal pollinators of the night-blooming tree, *Heterophagma quadriloculare* (Bignoniaceae). Another *Xylocopa* species, *X. tabaniformis*, is known to pollinate the evening primrose, *Oenothera elata*. Organized into spherical heads, small red flowers of the mimosoid tree, *Parkia velutina*, attract *Megalopta* bees which populate the canopy of the Amazonian rainforest after dark. This plant produces no nectar, but bees are after its pollen. Pollination by nocturnal bees is considered (for genus *Parkia*) to be an intermediate stage in evolution from insect pollination by day, to bat pollination by night.

Bees as night pollinators are an exception rather than a rule. Most of the plants that are night bloomers rely on moths in their sex life. Yucca, for example, is completely dependent on the moth *Tegeticula yuccasella*. The moth collects pollen from one yucca flower and forms it into a ball. She then lays her eggs into the ovary of another plant's flower and then places the pollen ball on its stigma. The plant is fertilized this way, insuring that the ovary (and the eggs inside it) will not wither. Larvae that hatch from these eggs eat only a fraction of the seeds. When mature, they chew through the ovary and go into the ground to pupate. The remaining seeds complete their normal development.

Until recently, *Tegeticula yuccasella* was believed to pollinate most yuccas. However, recent studies have revealed that 13 different closely related species of moths are involved in pollinating eight species of yucca found in the United States. These relationships between yucca moths and yuccas highlight the importance of host plant specificity in insect diversification. Similar mutualistic relationships exist between the senita cactus, *Lophocereus schottii*, and a moth which pollinates it, *Upiga virescens*. Both are geographically restricted to the Sonoran Desert. Female moths actively pollinate senita flowers and oviposit onto these flowers. Their larvae feed on developing seeds and fruit, but consume only 25% of immature fruit pollinated by female moth.

The specialization of certain hawkmoths in pollinating particular flowers was predicted by Darwin. In 1862, he wrote that there should be a nocturnal hawkmoth in Madagascar capable of pollinating the night-blooming orchid *Angraecum sesquipedale*, which would require a tongue 10–11 inches in length. The moth was discovered forty years after Darwin made his prediction, when *Xanthopan morgani* predicta with a 12-inch proboscis was described. The adaptation goes beyond the proboscis length of the moth and the flower structure of the orchid. The pollen mass adheres to the moth's head by means of a sticky pad, to which pollen is connected with elastic cord. By the time the pollen is transported by the hawkmoth to another plant, this cord dries up, thus insuring the transfer of pollen. The extraordinary number and diversity of long-spurred Orchidaceae in Madagascar is likely a consequence of unique diversity of long-tongued archaic hawkmoths that has persisted on this isolated island (Fig. 29).

In southeastern Brazil, *Prescottia* orchids are pollinated by pyralid moths. The pollination mechanism is similar to that found in Madagascar: pollen is fixed on the bottom of the insect's proboscis through the pad-like organ (viscidium), and is removed when the insect leaves the flower. A pollen-carrying insect visiting another flower brushes its stigmatic surface and leaves clumps of pollen, thus insuring pollination. South American *Habenaria* orchids are also adapted to pollination by hawkmoths and by settling moths. There, pollen attaches to the pollinator's eyes.

A single pollen "donation" normally accounts for a single pollination, so plants must make sure that the insect messenger takes their precious load to the correct address. In order to achieve that, the fragrances of orchids sometimes mimic moth pheromones (sex attractants). As day-blooming orchids often fool male bees by resembling a female bee in appearance, night-blooming orchids produce trails of pheromone-like chemicals that are followed by moths through the darkness of night until the landing platform of a flower becomes visible. Employment of this chemical deception insures specialization by pollinators and thus precise delivery of the pollen between the plants of the same species (Fig. 30).

Night-blooming plants cannot be considered without mentioning the water lilies. The giant water

Night Blooming Plants and Their Insect Pollinators, Figure 29 **The hawkmoths, which in flight and size can be easily confused with hummingbirds, are among the most important nocturnal pollinators. This species, *Enyo lugubris* Boenninghausen, is found from southern USA to Argentina (photo by Andrei Sourakov).**

Night Blooming Plants and Their Insect Pollinators, Figure 30 **Spiderwort, *Tradescantia virginiana*, is a night blooming plant. Here, the plant is shown during the night with its flowers open. During the day, the flowers remain closed (photo by Andrei Sourakov).**

lily, *Victoria amazonica*, produces leaves capable of supporting a weight of 150 pounds. Its flowers bloom for only two nights, attracting beetles which remain inside the closed flower during the first day, and are released on the second day before the flower sinks. The related water lily species, *Nymphae elegans*, opens its flowers for three successive nights. The stigmata of the first-day flowers secrete fluid which fills the cup surrounding its sex organs. As potential pollen-covered pollinators are attracted and enter the flowers, they land on the vertical, but flexible, inner stamens. These stamens then bend and the insects fall into the stigmatic fluid. The stigmatic fluid washes pollen from the insects and pollination is achieved (Fig. 31).

Pollination is only one aspect of plant–insect interaction that takes place during the night. Some plants release volatiles to repel insects from laying eggs on their leaves. Moths detect these chemical signals produced by a host plant that has already been eaten by caterpillars and avoid laying their eggs on such plants. The signals cause nearby healthy plants to produce insect-repelling compounds. It is one way that plants communicate with each other. All of these interactions result from millions of years of co-evolution between plants and animals. Studies in volatile chemistry, phylogenetics, and historical biogeography are only beginning to illuminate these complex relationships.

Night Blooming Plants and Their Insect Pollinators, Figure 31 **A hawkmoth in flight, feeding at an hibiscus blossom. (Photo by Robert J. Barnas.)**

References

Loewer PH (1993) The evening garden. Macmillan, New York, 256 pp

Nilson LA, Johnson L, Ralison L, Randrianjohany E (1987) Angraegoid orchids and hawkmoths in central Madagascar: specialized pollination systems and generalist foragers. Biotropica 19:310–318

Pellmyr O, James LM (1999) Forty million years of mutualism: evidence for Eocene origin of the yucca–yucca moth association. Proc Natl Acad Sci USA 96:9178–9183

Ninidae

A family of bugs (order Hemiptera, suborder Pentamorpha).

► Bugs

Nitidulidae

A family of beetles (order Coleoptera). They commonly are known as sap beetles.

► Beetles

Noctuid Moths

Members of the family Noctuidae (order Lepidoptera).

► Owlet Moths
► Butterflies and Moths

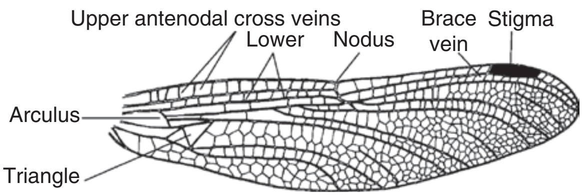
Noctuidae

A family of moths (order Lepidoptera). They commonly are known as noctuid, owlet, miller, or cutworm moths.

► Owlet Moths
► Butterflies and Moths

Nocturnal

Organisms in which the period of activity is night.



Nodus, Figure 32 Front wing of a dragonfly (Odonata).

Nodus

In ants, the small segment(s) between the thorax and the main part of the abdomen. In Odonata, the stout cross vein near the middle of the costal border, joining the costa, the subcosta, and the radius. This also is called the node or nodulus (Fig. 32).

Nogodinidae

A family of bugs (order Hemiptera, suborder Fulgoromorpha). All members of the suborder are referred to as planthoppers.

► Bugs

Nomenclature

The system of names used for organisms, including the process of naming.

► Scientific Name
► Classification

Nomen Conservandum

A scientific name that is technically unacceptable according to the International Commission on Zoological Nomenclature, but which has been preserved by this group.

Nomen Dubium

A questionable name; data are inadequate to justify recognition of this species.

Nomen Inquirendum

A name that requires further investigation; it may seem to lack nomenclatural priority, but should not yet be replaced.

Nomen Novum

A new scientific name.

Nomen Nudum

A scientific name that fails to satisfy the rules of availability according to the Code of Zoological Nomenclature.

Nomen Oblitum

This signifies that the name is old, and has not been used in the literature for at least 50 years.

Nomuraea

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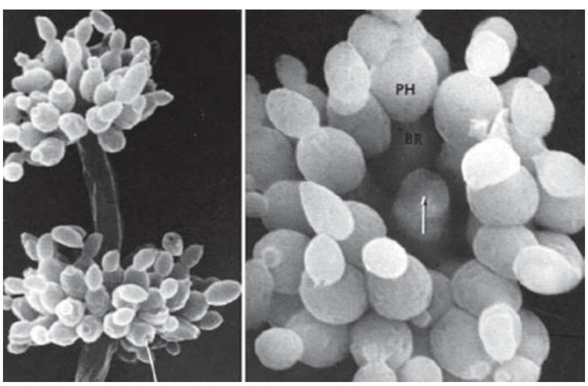
The genus *Nomuraea* (Deuteromycota), a green muscardine fungus, is characterized by the formation of mono- or synnematous conidiophores that bear whorls of phialides. Conidiospores are pale to dark green in mass, aseptate, smooth, round to ovoid or elongate and slightly curved, and are arranged in divergent chains. Two species pathogenic to invertebrates are *Nomuraea rileyi* (Farlow) Samson, a pathogen of lepidopterans, and *N. atypicola* (Yasuda) Samson, a spider pathogen. More recently, two new species, *N. viridulus* and *N. cylindrospora*, were isolated in Taiwan from the black cicada, *Cryptotympana facialis* and brown cicada, *Pomponia linearis*, respectively.

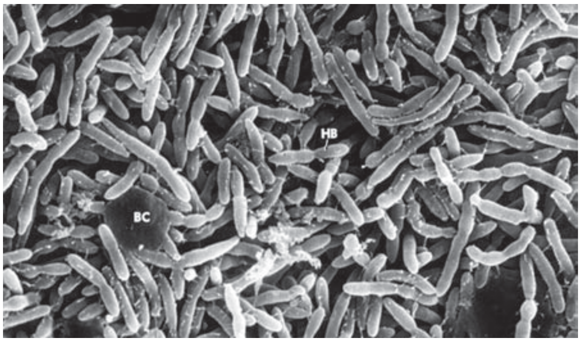
Of the five species of *Nomuraea*, *N. rileyi* is the most common and is documented as the key mortality factor in many noctuid populations. This fungus also has been reported as a potential control agent of the corn earworm, *Helicoverpa zea*, the velvetbean caterpillar, *Anticarsia gemmatalis*, the green cloverworm, *Plathypena scabra*, and the loopers, *Trichoplusia ni* and *Pseudoplusia includens*. *Nomuraea rileyi* is characterized as having septate mycelia with mononematous conidiophores bearing whorls of branches (metulae). These branches bear phialides that form short chains of gray–green, ovoid conidia. *Nomuraea viridulus* and *N. cylindrospora* show obvious similarity, but differ in host specificity, infectious level occurrence, and types of conidia produced. *Nomuraea viridulus* was collected exclusively on black cicada, *Cryptotympana facialis* Walker, with a high infection rate and produced one type of conidia (macroconidia). On the other hand, *N. cylindrospora* infected the brown cicada, *Pomponia linearis*, with very low rate and produced two types of conidia (micro- and macroconidia). *Nomuraea rileyi* isolates are more closely related to *Metarhizium anisopliae* and *M. flavoviride* than to either *N. atypicola* or *N. anemonoides* (Fig. 33).

Nomuraea rileyi undergoes a defined development sequence that involves the production of different cell phenotypes. Caterpillars infected with *N. rileyi* become mummified and covered with a white mycelial mat that produces numerous conidiophores. Conidiogenesis in *N. rileyi*, like most of the entomopathogenic Deuteromycetes, is phialidic. Phialides are specialized cells with one or more open ends from which conidia are produced in basipetal succession so that the apical conidia in a chain are the oldest. The infection cycle is initiated when *N. rileyi* conidia contact a susceptible host cuticle. The fungus infects young larvae, and is not generally infectious to last instar larvae, eggs, pupae or adults. In the field, the hydrophobic conidia are disseminated passively by wind or rain. The hydrophobicity of the deuteromycete conidia, including those of *N. rileyi*, is usually due to the presence of a distinct rodlet layer on the cell wall surface, which can be visualized using carbon–platinum replicas. It is the hydrophobic nature of this outer wall layer that allows *N. rileyi* conidia to attach to insect cuticle. *Nomuraea rileyi* conidia attach to all surface areas of host larvae, although there may be more conidia trapped in regions containing cuticular spines. Germinating *N. rileyi* conidia do not produce specialized appressorial cells but instead secrete extracellular sheath material, which further consolidates attachment of the germ tubes to host cuticle. The amount of sheath produced varies from one isolate to another. Sheath material is detectable on the cell wall surface during conidial swelling just prior to germ tube elongation. As the germ tube begins to emerge and penetrate the larval cuticle, the hydrophobic sheath material may provide a favorable environment for fungal enzyme activity. The hydrolytic activities of enzymes on epicuticular components may provide either nutrients for germ tube formation or appropriate germination signals. Growth of *N. rileyi* germ tubes through the larval cuticle and epidermis toward the hemocoel can require several days, depending upon the insect.



***Nomuraea*, Figure 33 Scanning electron micrograph of whorls of *Nomuraea rileyi* conidiophores bearing newly formed conidiospores.**

Nomuraea rileyi is distinctly dimorphic, and when the germ tubes reach the hemocoel, the fungus switches in a highly synchronous manner from a hyphal mode of growth to a yeast-like hyphal body phase (Fig. 34). This transition is accomplished by budding of the hyphal bodies from hyphal apices into the hemolymph. Hyphae penetrating the hemocoel can become surrounded by insect hemocytes,



Nomuraea, Figure 34 **Scanning electron micrograph of hemolymph sampled from *Nomuraea rileyi* infected *Anticarsia gemmatalis* larva. Note numerous budding hyphal body cells (HB) and the occasional insect blood cell (hemocyte, BC).**

but this immune response is unsuccessful in stopping the mycosis, at least in the insects studied (e.g., *Spodoptera frugiperda*). The *N. rileyi* hyphal bodies exist and replicate in the hemolymph without being subjected to any type of cellular defense reaction such as phagocytosis or encapsulation. Hyphal bodies replicate within the hemocoel by budding and septation. This vegetative growth takes place for as long as 2–3 days after invasion of the hemocoel. When conversion from the yeast-like hyphal body phase to the tissue-invasive mycelial phase is initiated, germ tubes form at the polar ends of the hyphal bodies. Attachment of hyphae to tissues such as fat body may be facilitated by an ECM-binding epitope located on the cell surface coat covering *N. rileyi* mycelial walls. Death of host larvae infected with *N. rileyi* usually occurs 5–7 days after exposure to infectious conidia. Death is probably due to physiological starvation, although there have been several reports of toxin production by the fungus. However, cell-free hemolymph from *N. rileyi* infected larvae is only slightly toxic when injected into naïve *Spodoptera exigua* larvae. In comparison, the hyphomycete *Beauveria bassiana* is known to produce in vivo toxic metabolites that disrupt hemocyte function and kill the larvae at metamorphosis.

Under proper environmental conditions (e.g., high humidity), *N. rileyi* mycelia emerge from the mummified cadavers and produce conidiophores. The aerially produced structures are hydrophobic, and this property provides some protection against environmental stress (e.g., desiccation), at least until the infective conidia become dispersed to new host populations. Conidiogenesis does not take place in *N. rileyi* under unfavorable environmental conditions, i.e., low humidity (<70%) and temperature (<15°C). Instead, several types of resting or overwintering structures form inside larval cadavers and within the extracuticular fungal mats covering them. Thick walled hyphae, chlamydospores, and intrahyphal hyphae form in the mat and sometimes in the cadaver, whereas thin-walled, lipid-filled resting bodies are prevalent in the cadaver. If placed in the proper environment, these resistant cells will resume metabolic activity and produce conidiophores and conidia. Therefore, in the field, these structures contained in larval cadavers in soil or decaying plant material provide a means of survival during dormancy as seasonal changes occur in the environment.

References

Boucias DG, Pendland JC (1991) Attachment of mycopathogens to cuticle. In: Cole GT, Hoch MC (eds), The fungal spore and disease initiation in plants and animals. Plenum, New York, pp 101–127

Boucias D, Stokes C, Suazo A, Funderburk J (2000) AFLP analysis of the entomopathogen *Nomuraea rileyi*. Mycologia 92:638–648

Ignoffo CM (1981) The fungus *Nomuraea rileyi* as a microbial insecticide. In: Burges HD (ed), Microbial control of pests and plant diseases: 1970–1980. Academic, London, pp 513–518

McCoy CW, Samson RA, Boucias DG (1988) Entomogenous fungi. In: Ignoffo C (ed), Microbial insecticides. CRC, Orlando, pp 481–490

Pendland JC, Lopez-Lastra C, Boucias DG (1994) Laminin-binding sites on cell walls of the entomopathogen *Nomuraea rileyi* associated with growth and adherence to host issues. Mycologia 86:327–335

Non-Indigenous

An organism that has arrived in an area from elsewhere. Also known as adventive, non native, and an invader.

Non-Occluded Virus

Those viruses in which the virions are not occluded in a dense protein crystal.

Nonpersistent Virus

A virus carried on the mouthparts of a vector, and usually lost after the insect feeds a few times. A styletborne virus.

Nonpreference

Insect responses to host characteristics that lead away from using the prospective host as food, shelter, or an oviposition site.

North Asian Tick Typhus

This is a bacterial disease that is transmitted by ticks in nothern Asia.

► Ticks

Northern Caddisflies

Members of the family Limnephilidae (order Trichoptera).

► Caddisflies

Northern Corn Rootworm, *Diabrotica barberi* Smith & Lawrence (Coleoptera: Chrysomelidae)

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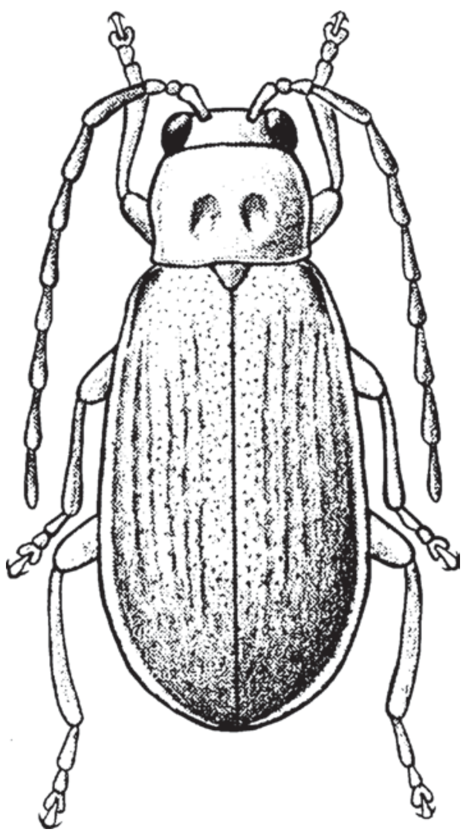
Northern corn rootworm is native to North America. It was first discovered attacking corn in Colorado, in the west-central USA, but has since spread eastward, principally to the corn-growing region in the midwestern states. Range expansion was caused primarily by a change in crop production practices: culture of corn continuously in the same fields. In the United States, northern corn rootworm occurs in the Great Plains region to about North Dakota and Oklahoma, and east to the Atlantic Ocean. As its common name suggests, this insect is largely absent from the south, but is present in Tennessee and the northern regions of Alabama and Georgia. In Canada, northern corn rootworm is found in southern Ontario and Quebec. Northern corn rootworm and western corn rootworm, *Diabrotica virgifera* LeConte, can both be found in the same fields, but western corn rootworm has displaced northern corn rootworm, or at least reduced its abundance, in some areas. Displacement has been attributed to greater insecticide resistance in western corn rootworm, but western corn rootworm also has a much higher reproductive rate than does northern corn rootworm.

Life History

Generally this species displays a single generation per year, with the egg stage overwintering, but sometimes eggs pass through more than one winter before hatch occurs. Eggs hatch in late spring, larvae feed until about June, and adults begin to emerge in July. Development is not very synchronous, so emergence is protracted. The temperature threshold for development of the various stages is 10–11°C. The mean period required for northern corn rootworm to develop from hatching to emergence of the adult is about 100, 47, and 30 days when reared at 15, 21, and 27°C.

The eggs are oval and whitish. Eggs are small, measuring only about 0.6 mm long and 0.4 mm wide. The surface of the eggs, when examined microscopically, are marked with a polygonal (mostly hexagonal) pattern, with each polygon containing small pits. The presence of pits serves to differentiate northern corn rootworm eggs from those of western corn rootworm, which lack pits. Eggs of spotted cucumber beetle, *Diabrotica undecimpunctata* Mannerheim, also contain polygons with pits, but the pits are proportional. Eggs are deposited in the soil, in soil cracks or other breaks in the soil that allow the female to access moist soil. Thus, in irrigated fields the eggs are frequently found in the furrows. The female commonly deposits eggs in loose clusters of 3–10 eggs. Females select corn as an oviposition site over other crops and weeds. Eggs survive temperatures of 4–5°C for brief periods, but survival decreases markedly at −10°C. The temperature threshold for embryonic development is about 11°C. The number of days required for hatch of eggs in the spring is about 21, 32, and 79 days when held at 25, 20, and 15°C, respectively. Duration of egg diapause is somewhat variable, and some members of the population pass through more than one winter before hatching.



Northern Corn Rootworm, *Diabrotica barberi* Smith & Lawrence (Coleoptera: Chrysomelidae), Figure 35 Adult of northern corn rootworm, *Diabrotica barberi* Smith & Lawrence.

The larva is elongate and cylindrical, tapering toward the head (Fig. 36). The body is white, bearing relatively few hairs or spines. The head capsule, and thoracic and anal plates, are yellowish brown. The three pairs of legs are brownish, and terminate in a single claw. The posterior end of the body bears a single retractile extension or tubercle (Fig. 36). Larval development time at variable temperatures is about 47 days. However, larval development requires 73, 32, and 21.5 days at 15, 21, and 27°C, respectively. Mean development time of the three instars was 6.5, 6.5, and 19 days, respectively, at 21°C. Head capsule widths average 0.22, 0.33, and 0.49 mm, respectively, for instars 1–3. Larvae attain a length of about 7 mm at maturity.

Larvae prepare small cells in the soil in preparation for pupation. Pupation often occurs within the upper 5 cm of soil. The pupa is white, except for the reddish brown eyes. It measures about 4.5 mm long and 2.5 mm wide. In general form it resembles the adult except that the wings are reduced in size and twisted ventrally. Also, the pupa bears a pair of hooks at the tip of the abdomen. Duration of the pupal stage is about 27, 12, and 7 days when reared at 15, 21, and 27°C, respectively.

The adults usually are yellowish or yellow–green, and lack the broad black stripes or extensive black pigmentation found on the elytra of western corn rootworm (Fig. 35). However, northern corn rootworm beetles in the northern Great Plains are sometimes striped. Northern corn rootworm beetles generally have yellowish to brownish antennae, tibiae, and tarsi, although in the eastern states they can be blackish. They measure about 6 mm in length. The preoviposition period of beetles is about 14 days, followed by an oviposition period

Northern Corn Rootworm, *Diabrotica barberi* Smith & Lawrence (Coleoptera: Chrysomelidae), Figure 36 Mature larva of northern corn rootworm, *Diabrotica barberi* Smith & Lawrence.

of 40–60 days. Adults can survive for up to nearly 3 months, and produce clutches of 20–30 eggs at about 7-day intervals. Total fecundity averages about 185 eggs per female on a good diet, but considerably less on suboptimal diets. However, if optimal temperatures are also provided, mean fecundity can increase to 274 eggs per female.

Several beneficial organisms have been associated with northern corn rootworm, but they seem to be of little consequence. Predators include ground beetles (Coleoptera: Carabidae), soldier beetles (Coleoptera: Cantharidae), and mites (Acari: Laelaptidae, Rhodacaridae, and Amerosiidae). Probably the most important parasitoid is *Celatoria diabroticae* (Shimer) (Diptera: Tachinidae), a species that also attacks other *Diabrotica* spp., but its relationship with northern corn rootworm is not clearly known. Pathogens such as protozoa, fungi, and bacteria have been isolated from rootworm larvae. The soil-inhabiting fungus *Beauveria bassiana* can cause epizootics in larval populations, but this occurs infrequently.

Northern corn rootworm has a rather restricted host range. Larvae develop only on plants in the family Gramineae. Corn is the only crop regularly attacked by larvae, but development can also occur to a lesser extent on millet, rice, and spelt (a rare type of wheat). Also, some survival occurs on rangeland forage grasses such as foxtail, *Setaria* spp.; wheatgrass, *Agropyron* spp.; weeping lovegrass, *Eragrostis curvula*; and Canada wildrye, *Elymus canadensis*. Adults display a similar pattern of host preference, with corn kernels, corn silk and corn tassel tissue favoring survival and reproduction, although corn leaf tissue is inadequate. Blossoms from goldenrod, *Solidago canadensis*; squash; and sunflower also are suitable. Additionally, adults feed on pollen from plants in the families Gramineae, Compositae, Leguminosae, and Cucurbitaceae.

Damage

Newly hatched larvae feed on the root hairs and outer tissue of roots, but as they increase in size and appetite they burrow into the roots, often consuming them entirely. The root damage can inhibit plant growth, but also reduces the ability of the plant to resist wind, especially when the soil is wet. Plants that topple, or lodge, due to damaged root systems display reduced growth potential. Lodged plants are difficult to harvest. Larval feeding also can allow entrance of Fusarium fungi, resulting in stalk rot. Feeding by adults on corn silks occasionally is enough to interfere with pollination, and beetles sometimes cause direct injury by feeding on the kernels at the tip of the ear. Foliage feeding by adults of this species is rare, though quite common with the related western corn rootworm. Maize chlorotic mottle virus may be transmitted by rootworm beetles. Adult rootworm densities of one per plant or greater suggest damaging larval densities during the next year if corn is planted in the same field.

Management

A great deal of effort has gone into development of improved sampling protocols for rootworms, though the principal concern is the vast acreage of grain corn, rather than the modest acreage of sweet corn. With grain corn, large quantities of insecticide are applied at great expense to a crop with a modest profit margin, so there is ample incentive to improve decision-making relative to insecticide application.

Sampling has been investigated for most rootworm life stages. Egg and larval sampling has been studied extensively, but remains mostly a research protocol due to the high labor requirements. Thus, most field-level sampling involves adult population monitoring, with adult population densities used to predict larval damage during the following year. Visual assessment of adult densities can be made by whole-plant or ear-zone counts, and sequential sampling protocols have been developed. However, traps are usually preferred because they can be left in the field for longer periods and are less affected by beetle movement and short-term weather phenomena. A simple, and therefore popular, trap is the yellow sticky trap. Chemical attractants also have been investigated. Chemical arrestants such as cucurbitacin, lures including sex pheromone, and other chemicals isolated from the Cucurbitaceae such as eugenol, isoeugenol, 2-methoxy-4-propylphenol and cinnamyl alcohol have been found to be successful.

Corn producers generally rely on soil-applied insecticides to protect their crops from larval rootworm damage. Either liquid or granular formulations may be applied to the root zone, and application can be made at planting time or after the corn is partly grown. Where corn is cropped continuously, insecticide resistance and enhanced microbial degradation of insecticides have been noted.

Suppression of adults with foliar insecticides could be made to prevent damage during the subsequent year, but this is rarely done due to the vagility of adults. Adult control is also needed occasionally to protect corn silks and ear tips from injury. There is considerable potential to use insecticide-containing bait to accomplish adult control with greatly reduced insecticide application rates.

Cropping practices can affect corn rootworm biology. Planting synchrony is among the cultural factors affecting corn rootworm populations. Beetles depend on the availability of green silks and pollen, resources that are available only briefly. Delayed planting of crops delays and extends the development of the insect population, and reduces survival, possibly due to deprivation of corn roots to hatching larvae. Thus, late plantings do not require insecticide treatments for this insect, but are likely to be heavily infested in the following year due to attraction of beetles to late-planted corn. Availability of corn flowers is important for adult survival. Beetles tend to disperse to early-flowering corn until it senesces, then disperse to later-flowering fields.

The most important cropping practice is crop rotation, which normally results in destruction of rootworm populations due to the inability of larvae to survive on crops other than corn. Thus, corn routinely is rotated with a non-host such as soybean. This apparently has led to increased incidence of rootworm populations that diapause through two years before hatching, potentially reducing the effectiveness of this practice. As yet, most areas have not experienced a serious problem with 2-year life cycles, and crop rotation remains a preferred management practice.

If corn is to be planted into a field that previously supported corn, tillage and disking will have few effects on the insects. However, planting the new rows of corn between the old rows often is desirable because the eggs often are concentrated at the base of the old corn plants, and young larvae will experience difficulty in dispersing such distances. Application of irrigation water and additional nitrogen helps to offset loss of roots.

References

Capinera JL (2001) Handbook of vegetable pests. Academic, San Diego, 729 pp

Chiang HC (1973) Bionomics of the northern and western corn rootworm. Annu Rev Entomol 18:47–72

Krysan JL, Smith RF, Guss PL (1983) *Diabrotica barberi* (Coleoptera: Chrysomelidae) elevated to species rank based on behavior, habitat choice, morphometrics, and geographical variation in color. Ann Entomol Soc Am 73:123–130

No-See-Ums

Members of the family Ceratopogonidae (order Diptera).

► Flies

Norticolidae

A family of cockroaches (order Blattodea).

► Cockroaches

Nosema apis (Protozoa: Microsporidia)

A microsporidian pathogen of adult honey bees that causes a disease known as Nosema disease.

► Nosema Disease
► Honey Bees
► Apiculture

Nosema locustae (Protozoa: Microsporidia)

Among the protozoan diseases of grasshoppers, a slow-acting species known as *Nosema locustae* was selected for commercial development to provide a biological insecticide for suppression of grasshoppers. This pathogen is found widely, occurring on several continents, and has been shown to infect over 80 species of grasshoppers. To infect a grasshopper, it must be ingested. Spores germinate in the gut and a polar filament is extruded that injects the sporoplasm directly into gut cells. The sporoplasm enters fat body tissue and effectively starves the host of energy reserves.

Production of *Nosema locustae* is accomplished in vivo, normally using *Melanoplus differentialis*, a large species, though *M. bivitattus* is nearly as good. Spores are harvested and incorporated onto wheat bran, an acceptable bait substrate for many species of grasshoppers. The bait can be applied in several ways. However, the results of field applications have been inconsistent, at times seemingly producing high levels of infection and significant population reduction, and at other times producing small or no measurable effects. Infected individuals typically display prolonged development rates. Mortality is maximized by applying *Nosema* to larvae in the third instar, but maximum levels of infection (reducing feeding and reproduction) are obtained by applying *Nosema* later in nymphal development. A significant benefit of *Nosema* application is that it is transmitted transovarially, and may persist for several generations, presumably affecting population numbers over several generations. The reciprocal condition, achieving rapid population reduction, seems not to be achievable unless very high (at non-economic levels) of *Nosema* are applied. However, other *Nosema* spp. (*N. cuneatum* and *N. acridophagous*) perhaps offer greater potential to increase rapid population suppression if culture techniques can be optimized.

Reference

Johnson DL (1997) Nosematidae and other protozoa as agents for control of grasshoppers and locusts: current status and prospects. Mem Entomol Soc Can 171:375–389

Nosemosis

A disease caused by *Nosema* spp. (Protozoa: Microsporidia) affecting honey bees and also called Nosema disease.

► Nosema Disease
► Microsporidia

Nosema Disease

A disease caused by *Nosema apis* (Protozoa: Microsporidia) affects honey bees and is called Nosema disease or Nosemosis. This is the most important disease of adult honey bees, occurring worldwide and probably in all colonies. Because it does not cause dramatic die-offs of the population, however, it sometimes is overlooked as a major cause of hive mortality. *Nosema* resides in the digestive tract of bees, and typically is expressed during periods when the bees are stressed by long confinement, rapid brood increases, nutritional deficiencies and inclement weather. Signs and symptoms of infection are not clear-cut, but often include unhooked wings, distended abdomens, disorientation and paralysis. Examination of the bee's digestive tract can be diagnostic, however, with the hind gut yellow–brown in normal bees and white and distended in *Nosema*-infected bees. Infected bees display diarrhea. This is a debilitating disease, causing reduced longevity of worker bees and a slow reduction in hive population. Workers do not attend to the queen to the same extent as uninfected bees. In the individual bee, certain tissues such as the hypopharangeal gland are affected. Infection occurs when spores are ingested, and eventually the queen becomes infected. Fecal contamination is a major route of transmission.

There are several forms of management, and keeping the hive in good condition is certainly helpful. Antibiotics can be fed to bees occasionally to reduce problems. It is also advisable to reduce the potential for transmission among colonies by sterilizing or fumigating beekeeping equipment.

A related pathogen, *Nosema ceranae*, apparently was formerly associated with the Asian bee, *Apis ceranae* but has moved to *Apis mellifera*. *Nosema ceranae* affects *A. mellifera* bees more dramatically than does *N. apis*, leading to more severe population declines.

► Microsporidia
► Honey Bees
► Apiculture

Reference

Morse RA, Nowogrodzki R (1990) Honey bee pests, predators and diseases, 2nd edn. Cornell University Press, Ithaca, 474 pp

Nosodendrid Beetles

Members of the family Nosodendridae (order Coleoptera).

► Beetles

Nosodendridae

A family of beetles (order Coleoptera). They commonly are known as nosodendrid beetles.

► Beetles

Noteridae

A family of beetles (order Coleoptera). They commonly are known as burrowing water beetles.

► Beetles

Nothybidae

A family of flies (order Diptera).

► Flies

Notodontidae

A family of moths (order Lepidoptera). They commonly are known as prominent moths.

► Prominent Moths
► Butterflies and Moths

Notoligotomidae

A family of web-spinners (order Embiidina).

► Web-Spinners

Notonectidae

A family of bugs (order Hemiptera) They also are known as backswimmers.

► Bugs

Notonemouridae

A family of stoneflies (order Plecoptera).

► Stoneflies

Notopleuron

A small lateral plate adjacent to the mesonotum. The bristles associated with the notopleuron often are diagnostic features for flies (Diptera).

► Thorax of Hexapods

Notoptera

An ordinal name first used by Crampton in 1915, but which was recently suggested as a suitable order name for the sister taxa Mantophasmatodea (gladiators) and Grylloblattodea (rock crawlers), which can be considered to be suborders of Notoptera. The status of gladiators as a separate order will undoubtedly remain controversial for some time, as this order was named only in 2002 and has been little studied thus far.

► Gladiators (Mantophasmatodea)

Reference

Arillo A, Engel MS (2006) Rock crawlers in Baltic amber (Notoptera: Mantophasmatodea). Am Mus Novit 3539:1–10

Notum

A dorsal sclerite on the insect; a tergite.

► Thorax of Hexapods

Nozzle

A mechanism of converting a stream of liquid (pesticide) into droplets, normally in a specific pattern of droplets.

Nuclear Polyhedrosis Virus

A viral disease of insects, mainly the larvae of certain Lepidoptera and Hymenoptera, characterized by the formation of polyhedral inclusion bodies (polyhedra) in the nuclei of the infected cells. A type of baculovirus.

Nucleic Acid

Either of the polymeric molecules DNA or RNA.

Nucleocapsid

The structure compared of the capsid with the enclosed viral nucleic acid; some nucleocapsids are naked, others are enclosed in an envelope.

Nucleolus

A nucleolus is an RNA-rich, spherical body associated with a specific chromosomal segment, the nucleolus organizer. The nucleolus organizer contains the ribosomal RNA genes and the nucleolus is composed of the primary products of these genes, their associated proteins, and a variety of enzymes.

Nucleoside

A chemical consisting of a purine or pyrimidine base attached to a five carbon sugar.

Nucleotide

A chemical consisting of purine or pyrimidine base attached to a five-carbon sugar, with phosphate attached to the sugars.

Nucleus

The membrane-bound structure of a eukaryotic cell containing the DNA organized into chromosomes.

Nulliparous

A female that has not yet given birth or produced eggs; a virgin.

Numerical Response

Population change among predators and parasitoids in response to changes in the availability of food. The presence of more prey increases food availability, nutrition, and the reproductive rate among predators and parasitoids, accounting for increased abundance of predators and parasitoids. (contrast with functional response)

Nuptial

Referring to the time or act of mating or copulation.

Nuptial Flight

The mating flight of a winged queen and male.

Nuptial Gift

A gift (often prey or regurgitated food, but sometimes a nutritious sperm capsule that can be eaten or absorbed) provided to the female insect by the male during courtship or during copulation.

Nurse Cells

Nutritive cells found in association with the developing oocyte in meroistic ovaries.

Nutrient Content of Insects

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Insects are an important food source for both animals and humans, and for that reason, reports of their nutrient composition are found in articles in disciplines ranging from anthropology to zoology. One of the first applications of the nutrient content of insects involves their use as food for humans. Evidence from archeological sites suggests the use of tools by early hominids to dig termites from their mounds. The anthropological literature shows that insects have been, and continue to this day to be, an important human food source. While insects are not routinely eaten in most western societies, in many other cultures, insects continue to be an important source of nutrients. As such, nutritional analysis is commonly performed on insects as a means of helping determine the nutrient intake of certain populations. While a variety of species are commonly eaten, the insects most frequently analyzed include lepidopteran larvae (mostly members of the family Saturniidae), coleopteran larvae, a number of different species of grasshoppers and locusts, and several species of termites. The insects most widely consumed by humans are the larvae from three species of palm weevils (Curculionidae: *Rhynchophorus*). Indigenous people in Africa, South America, Southeast Asia and New Guinea have all developed techniques for mass-producing these larvae, which involves cutting down select species of palms and returning 6–10 weeks later to harvest the larvae from the fallen trees. While insects are sometimes eaten raw, in most cases, insects consumed by humans are processed usually by drying, boiling, frying, or roasting.

Starting in the 1970s, the nutritional value of a number of insect species have been evaluated as potential foodstuff for poultry, or other food-producing animals. Extensive analyses, including feeding trials with rats, poultry and fish, have been published using house fly larvae, *Musca domestica* (L.), silkworm pupae, *Bombyx mori* (L.) and Mormon crickets, *Anabrus simplex* Haldeman. In these studies, the nutritional value of dried insect meals have been evaluated when they were fed as the primary or sole source of dietary protein. These data are especially important as they represent evaluations of insect protein quality based on both amino acid analysis and animal feeding trials. Most of these data have been published in the nutrition and animal science journals.

The large number of insect species and the diversity of the environments they inhabit also means they are an important food source for many terrestrial and aquatic animals. For that reason, the zoological literature contains articles with nutrient analysis of fresh insects to help evaluate the nutrient intake of wild animals. Termites are the insects most frequently studied in this regard, presumably because they are the primary food source for a number of highly specialized mammalian insectivores.

The nutritional content of selected species of cultured insects have also been studied because of their use as food for captive insectivorous reptiles, birds and mammals kept in zoos. The insect species most commonly utilized for these purposes include the house cricket, *Acheta domesticus*, waxworms (larvae of the wax moth *Galleria mellonella* (L.)) and the larvae from two species of beetles in the family Tenebrionidae: yellow mealworm, *Tenebrio molitor* (L.), and superworm, *Zophobas morio* (F.). These analyses are usually performed on raw, whole insects. In an effort to improve the nutrient composition of insects raised as food for zoo animals, the effect of the residual food in the insect's gastrointestinal tract has also been studied. This food can have a substantial impact on the nutrient composition of the insect. For example, the calcium content of fasted house cricket nymphs is about 1,200 mg/kg dry matter, which can be increased to as much as 18,200 mg/kg dry matter when they are fed a high calcium diet.

There are a number of issues to consider in a review of the literature on the subject of insect nutrient composition. The first is combining all the information across a wide range of disciplines. A second issue is that insect nutrient composition is sometimes reported on an as is basis, while other studies report values on a dry weight basis, while amino acids are commonly reported in milligrams of amino acids per gram of protein. Another factor to consider when evaluating insect nutrient composition is the effect of handling, preparing and processing of the insects prior to analysis. Insects prepared for human consumption often have various parts removed, most commonly the wings and the gastrointestinal contents, so results may not be representative of the whole insect. Additionally, insects consumed by humans are often processed in some fashion prior to consumption. Processing methods commonly used include drying, roasting, frying, salting and canning, all of which can have substantial impacts on nutrient composition. Lastly, when evaluating the nutrient composition of raw whole insects, the effect of any residual food in the insect's gastrointestinal tract must be considered.

In order to help facilitate comparisons between different studies, all the data (except moisture) in the tables have been recalculated from the original data to express the information on a dry weight basis. For all tables, a blank indicates the sample was not analyzed for the particular nutrient. If available, information on how the sample was prepared or processed prior to analysis is shown. The information presented does not represent a systematic analysis of insects, but is simply a collection of data available from the literature. As such, it does not adequately represent data for all families, or even different life stages within a single species, so generalizations from these data concerning the nutrient composition of a family or order is unwarranted.

Analysis of insects for moisture, protein, fat, ash and fiber is presentedi n (Table 5). As expected, raw, whole insects generally contain 55–85% moisture. Whole insects with a low moisture content are generally those that also have a high fat content. As expected, insects processed for human consumption generally contain less moisture than raw insects because processing usually involves some type of drying to prolong shelf life.

On a dry weight basis, the nutrient in highest concentration is usually protein, which is not surprising given the protein-rich exoskeleton of insects. Protein contents for raw, whole insects range from 21% for the passalid *Oileus rimator* Traqui larvae, to 80% for adult female gypsy moths, *Lymantria dispar* (L.). Insects processed for human consumption may exhibit an even wider range as the removal of specific parts will affect the overall nutrient composition. For example, the hairs or setae commonly found on many species of lepidopteran larvae, which would be extremely high in protein, are usually removed when the insect is prepared for human consumption.

Fat is the other major component of most insects with raw, whole insects ranging from a low of 2.2% for *Nasuitermes corniger* (Motschulsky) worker termites, to a high of 60% for greater wax moth, *Galleria mellonella* (L.) larvae. Processing of insects for consumption by humans can dramatically affect reported fat contents in two ways. Roasting can remove fat from the insect, thereby decreasing the fat content versus that seen in the raw insect, while frying can increase the insect's fat content. Although there is limited data

Nutrient Content of Insects, Table 5 **Moisture, protein, fat, fiber and ash content of selected insect species**

	Method of preparation	Moisture (%)	Crude protein[a] (%)	Crude fat (%)	Fiber (%)	Ash (%)
Lepidoptera						
Agrotis infusa (larva)	Roasted	49.2	52.7	39.0		5.3
Anaphe panda (larva)	Intestinal contents and hairs removed	73.9	45.6	35.0	6.5[c]	3.7
Anaphe venata (larva)	Dried (without hairs)	6.6	60.0	23.2		3.2
Ascalapha odorata (larva)	Whole raw, not fasted		56.0	15.0	12.0[c]	6.0
Bombyx mori (larva fed artificial diet)	Whole raw, not fasted	82.7	53.8	8.1	6.4b	6.4
Bombyx mori (larva fed mulberry leaves)	Whole raw, not fasted	76.3	64.7	20.8		
Bombyx mori (larva fed mulberry leaves)	Whole raw, intestinal contents removed	69.9	62.7	14.2		
Bombyx mori (pupa)	Whole raw (dried?)	18.9	60.0	37.1		10.6
Callosamia promethea (larva)	Whole raw, freeze-dried	4.5	51.7	10.5	11.3[c]	7.2
Catasticta teutila (larva)	Whole raw, not fasted		60.0	19.0	7.0c	7.0
Conimbrasia belina (larva)	Intestinal contents removed then dried		62.0	16.0	11.4[c]	7.6
Galleria mellonella (larva)	Whole raw, fasted	58.5	34.0	60.0	8.1[b]	1.4
Heliothis zea (larva fed broadbeans)	Whole raw, fasted	77.4		18.2		
Heliothis zea (larva fed artificial diet)	Whole raw, fasted	77.5		30.2		
Hyalophora cecropia (larva)	Whole raw, freeze-dried	2.6	56.2	10.5	15.1[c]	6.1
Imbrasia epimethea (larva)	Smoked and dried	7.0	62.5	13.3		4.0

Nutrient Content of Insects, Table 5 **Moisture, protein, fat, fiber and ash content of selected insect species (Continued)**

	Method of preparation	Moisture (%)	Crude protein[a] (%)	Crude fat (%)	Fiber (%)	Ash (%)
Imbrasia ertli (larva)	Viscera removed then boiled or roasted, dried and salted	9.0	52.9	12.2		15.8
Imbrasia truncata (larva)	Smoked and dried	7.3	64.7	16.4		4.0
Manduca sexta (larva fed artificial diet)	Whole raw, freeze-dried	4.7	61.0	21.7	9.9[c]	7.8
Manduca sexta (larva fed fresh plant material)	Whole raw, freeze-dried	4.7	60.7	17.3	8.8[c]	8.5
Nudaurelia oyemensis (larva)	Smoked and dried	7.0	61.1	12.2		3.8
Porthetria dispar (adult with eggs)	Whole raw, not fasted	68.6	80.0	44.6		8.0
Pseudaletia unipuncta (larva)	Whole raw, freeze-dried	2.0	55.5	15.2	5.1[c]	7.0
Spodoptera eridania (larva)	Whole raw, freeze-dried	4.5	57.3	14.6	7.4[c]	10.3
Spodoptera frugiperda (larva fed artificial diet)	Whole raw, freeze-dried	2.1	59.0	20.6	6.8[c]	5.7
Spodoptera frugiperda (larva fed fresh plant material)	Whole raw, freeze-dried	3.6	59.3	11.7	12.4[c]	11.6
Usta terpsichore (larva)	Viscera removed then boiled or roasted, dried and salted	9.2	48.6	9.5		13.0
Xyleutes redtembacheri (larva)	Whole raw, not fasted		43.0	48.0	6.0[c]	2.0
Coleoptera						
Aplagiognathus spinosus (larva)	Whole raw, not fasted		26.0	36.0	15.0[c]	3.0
Callipogon barbatus (larva)	Whole raw, not fasted		41.0	34.0	23.0[c]	2.0
Oileus rimator (larva)	Whole raw, not fasted		21.0	47.0	13.0[c]	2.0
Passalus punctiger (larva)	Whole raw, not fasted		26.0	44.0	15.0[c]	3.0

Nutrient Content of Insects, Table 5 Moisture, protein, fat, fiber and ash content of selected insect species (Continued)

	Method of preparation	Moisture (%)	Crude protein[a] (%)	Crude fat (%)	Fiber (%)	Ash (%)
Rhyncophorus ferrugineus (larva)	Not reported	70.5	20.7	44.4		
Rhyncophorus palmarum (larva)	Whole raw, not fasted	71.7	25.8	38.5		2.1
Rhyncophorus phoenicis (larva)	Incised, fried in oi	10.8	22.8	46.8		2.7
Scyphophorus acupunctatus (larva)	Whole raw, not fasted		36.0	52.0	6.0[c]	1.0
Tenebrio molitor (adult)	Whole raw, fasted	63.7	65.3	14.9	20.4[b]	3.3
Tenebrio molitor (larva)	Whole raw, fasted	61.9	49.1	35.0	6.6[b]	2.4
Zophobas morio (larva)	Whole raw, fasted	57.9	46.8	42.0	6.3[b]	2.4
Orthoptera						
Acheta domesticus (adult)	Whole raw, fasted	69.2	66.6	22.1	10.2[b]	3.6
Acheta domesticus (nymph)	Whole raw, fasted	77.1	67.2	14.4	9.6[b]	4.8
Blatella germanica (not specified)	Whole raw, not fasted	71.2	78.8	20.0		4.3
Brachytrupes sp.	Fresh, blanched, inedible parts removed	73.3	47.9	21.3	13.5c	9.4
Crytacanthacris tatarica	Fresh, blanched, inedible parts removed	76.7	61.4	14.2	17.2[c]	4.7
Gryllotalpa africana	Fresh, blanched, inedible parts removed	71.2	53.5	21.9	9.7[c]	9.4
Oxya verox	Whole raw, dried	29.8	64.2	2.4		3.4
Oxya yezoensis	Whole raw, not fasted	65.9	74.7	5.7		6.5
Sphenarium histro (nymphs & adults)	Whole raw, not fasted		77.0	4.0	12.0[c]	2.0
Zonocerus sp.	Whole raw, not fasted	62.7	71.8	10.2	6.4[c]	3.2

Nutrient Content of Insects, Table 5 Moisture, protein, fat, fiber and ash content of selected insect species (Continued)

	Method of preparation	Moisture (%)	Crude protein[a] (%)	Crude fat (%)	Fiber (%)	Ash (%)
Isoptera						
Cortaritermes silvestri (worker)	Whole raw, not fasted	77.8	48.6	6.9		8.5
Macrotermes bellicosus (alate)	Dewinged, raw	6.0	34.8	46.1		10.2
Macrotermes subhyalinus (alate)	Dewinged, fried in oil	0.9	38.8	46.5		6.6
Nasutitermes corniger (soldier)	Whole raw, not fasted	69.6	58.0	11.2	34.8[b]	3.7
Nasutitermes corniger (worker)	Whole raw, not fasted	75.3	66.7	2.2	27.1[b]	4.6
Procornitermes araujoi (worker)	Whole raw, not fasted	78.1	33.9	16.1		3.5
Syntermes ditus (worker)	Whole raw, not fasted	79.7	43.2	3.4		17.1
Hymenoptera						
Aphis mellifera (adult female)	Whole raw, not fasted	65.7	60.0	10.6		17.4
Aphis mellifera (adult male)	Whole raw, not fasted	72.4	64.4	10.5		17.8
Aphis mellifera (larva)	Whole raw, not fasted	76.8	40.5	20.3	1.3[b]	3.4
Atta mexicana (reproductive adult)	Whole raw, not fasted		46.0	39.0	11.0[c]	4.0
Oecophylla smaragdina	Fresh, blanched inedible parts removed	74.0	53.5	13.5	6.9[c]	6.5
Oecophylla virescens	Inedible parts removed	78.3	41.0	26.7		6.0
Polybia sp. (adult)	Whole raw, not fasted		63.0	13.0	15.0[c]	6.0
Diptera						
Copestylum ann & Copestylum haggi (larva)	Whole raw, not fasted		37.0	31.0	15.0[c]	8.0
Drosophila melanagaster (adult)	Whole raw, not fasted	67.1	56.3	17.9		5.2
Hermetia illucens (larva)	Dried, ground, not fasted	3.8	47.0	32.6	6.7[c]	8.6

Nutrient Content of Insects, Table 5 Moisture, protein, fat, fiber and ash content of selected insect species (Continued)

	Method of preparation	Moisture (%)	Crude protein[a] (%)	Crude fat (%)	Fiber (%)	Ash (%)
Musca autumnalis (pupa)	Dried, ground, not fasted		51.7	11.4		28.9
Musca domestica (pupa)	Dried, ground, not fasted		61.4	9.3		11.9
Hemiptera						
Acantocephala declivis (nymphs & adults)	Whole raw, not fasted		35.0	45.0	18.0[c]	1.0
Edessa petersii (nymphs & adults)	Whole raw, not fasted		37.0	42.0	18.0[c]	2.0
Euchistus egglestoni (nymphs & adults)	Whole raw, not fasted		35.0	45.0	19.0[c]	1.0
Pachilis gigas (nymphs & adults)	Whole raw, not fasted		64.0	22.5	7.5[c]	3.5
Hoplophorion monograma (nymphs & adults)	Whole raw, not fasted		64.0	14.0	18.0[c]	3.0
Umbonia reclinata (nymphs & adults)	Whole raw, not fasted		29.0	33.0	13.0[c]	11.0

All values (except moisture) on dry weight basis
[a]Crude protein measured as nitrogen × 6.25
[b]Fiber measured as acid detergent fiber
[c]Fiber measured as crude fiber

available, in general, female insects contain more fat than male insects. Data from various species of Lepidoptera suggests that larvae fed artificial diets are higher in fat than those fed fresh plant material. For larvae of the stored product pest, the yellow mealworm, *Tenebrio molitor* (Linnaeus), providing supplemental moisture increased pre-pupal fat content.

As expected, most insects contain only small amounts of ash because they lack the internal calcified skeleton found in most vertebrates. An exception is the puparia of the face fly, *Musca autumnalis* DeGeer. Unlike most insect species where the cuticle consists largely of sclerotized protein, the puparia of the face fly is calcified and so contains 63% ash on a dry weight basis versus 3.7% ash for the puparia of the house fly, *Musca domestica* (L.).

It is frequently reported that soft-bodied insects contain less fiber than those with a hard exoskeleton, but the limited data available and the use of several different techniques to measure fiber prevents a critical evaluation of this assumption. Additionally, the contribution of the gastrointestinal contents can have a marked effect and is likely the reason for the high fiber values seen for many of the insect species. Looking at the data for *Tenebrio molitor*, it does appear that the soft bodied larva has less fiber than the heavily sclerotized adult beetle. The structural similarity between chitin (N-acetyl-D-glucoamine linked by β-1–4 bonds) and cellulose (β-D-glucopyranose linked by β-1–4 bonds) is the reason it is often assumed that the fiber measured in insects consists solely of chitin. Given the physical characteristics of sclerotized proteins and the fact that amino acids have been detected in the acid detergent fiber residue, it seems likely that the fiber (measured as either crude fiber or acid detergent fiber) in fasted insects represents both chitin and sclerotized protein.

As expected, insects contain little calcium and high levels of phosphorus (Table 6). While most wild-caught insects also appear to be low in calcium, in general, the values are somewhat higher than those reported for captive-raised insects. High calcium levels have been reported in only a few species of insects. Insects that have been shown to contain substantial quantities of calcium include stoneflies (1.15% dry matter basis), housefly pupa, *Musca domestica* (0.93% dry matter basis), from larvae raised in poultry manure containing 5.1% calcium, and the previously mentioned *Musca autumnalis* puparia. Presumably, wild living animals feeding primarily on insects obtain sufficient calcium by varying the prey species consumed, eating insects which have consumed a high-calcium diet and by ingesting soil particles adhering to the prey animals. Lastly, the calcium content of wax worms (*Galleria mellonella* larvae), house crickets (*Acheta domesticus*), mealworms (*Tenebrio molitor* larvae) and silkworms (*Bombyx mori* larvae) can all be increased 5- to 20-fold when fed a high calcium diet. This increase in calcium appears to be solely due to the residual food in the gastrointestinal tract with little of the calcium being incorporated into the insect's body (Table 6).

All insects contain high levels of phosphorus, which results in a calcium:phosphorus ratio of less than one. For most monogastric animals, phosphorus from animal sources is virtually 100% available, while plant-based phytate phosphorus is approximately 30% available. The phosphorus in most insects is likely to be readily available as was shown for *Musca autumnalis* puparia with an availability of 92%. Most insects contain substantial levels of the other macro-minerals, magnesium, sodium, potassium and chloride. The very high sodium levels for the three species of lepidopteran larvae (*Imbrasia ertli* Rebel, *Usta Terpsichore* M. & W., and *Conimbrasia belina* Westwood) and for the termite, *Macrotermes subhyalinus* Rambur, is probably a result of salt added during processing.

Most insects appear to be good sources of the trace minerals of iron, zinc, copper, manganese and selenium. For insects prepared for human consumption, some of the elevated levels of iron and copper are likely the result of metal that has leached from the cookware. Mineral composition in general probably largely reflects the food sources of the insect, both that which is present in the gastrointestinal tract and that which is incorporated into the insect's body as a result of the food it consumed. Studies of wild insects show both seasonal variation as well as variations between different populations of the same species living in the same general area. While it is assumed the availability of these trace minerals is good, there are no published studies measuring the availability of trace minerals in insects.

There are a number of published reports on the amino acid composition of insects but recovery (measured as the percent of total nitrogen as amino acids) ranges from approximately 40% to 95%. This could be the result of the presence of large amounts of nitrogen-containing compounds other than amino acids, such as chitin, or methodology problems in the analysis. Because many papers report only a limited number of amino acids (usually those considered essential for humans), it is impossible to calculate recoveries and evaluate the accuracy of the data. In spite of these issues, there are sufficient data to show that insects are a good

Nutrient Content of Insects, Table 6 **Mineral content of selected insect species**

	Ca (mg/kg)	P (mg/kg)	Mg (mg/kg)	K (mg/kg)	Na (mg/kg)	Cl (mg/kg)	Fe (mg/kg)	Zn (mg/kg)	Cu (mg/kg)	Mn (mg/kg)	Se (mg/kg)
Lepidoptera											
Anaphe venata (larva)	400	7,300	500	11,500	300		100	100	10	400	
Bombyx mori (larva fed artificial diet)	1,020	13,700	2,880	18,270	2,750	3,580	95	178	21	25	0.8
Bombyx mori (pupa)	1,950	5,840	2,550				320	284	2	9	
Conimbrasia belina (larva)	1,740	5,430	1,600	10,240	10,320		310	140	9	39	
Galleria mellonella (larva)	590	4,700	760	5,320	400	1,540	50	61	9	3	0.3
Imbrasia epimethea (larva)	2,250	6,660	4,020	12,580	750		130	111	12	58	
Imbrasia ertli (larva)	550	6,000	2,540	12,030	24,170		21		15	34	
Imbrasia truncata (larva)	1,320	8,420	1,920	13,490	1,830		87	111	14	32	
Nudaurelia oyemensis (larva)	1,490	8,710	2,660	11,070	1,400		97	102	12	55	
Usta terpsichore (larva)	3,910	7,650	590	32,580	33,380		390	253	26	67	
Coleoptera											
Phyllophaga rugosa (adult)	430		1,900	11,510	790		170				
Rhyncophorus ferrugineus (larva)	15,630						146				
Rhyncophorus palmarum (larva)	1,000	4,800	3,100	6,800	2,600		34	111	26	18	

Nutrient Content of Insects, Table 6 **Mineral content of selected insect species (Continued)**

	Ca (mg/kg)	P (mg/kg)	Mg (mg/kg)	K (mg/kg)	Na (mg/kg)	Cl (mg/kg)	Fe (mg/kg)	Zn (mg/kg)	Cu (mg/kg)	Mn (mg/kg)	Se (mg/kg)
Rhyncophorus phoenicis (larva)	2,080	3,520	330	22,090	450		147	265	16	8	
Tenebrio molitor (adult)	640	7,630	1,670	9,370	1,740	5,260	60	127	21	11	0.4
Tenebrio molitor (larva)	440	7,480	2,100	8,950	1,410	4,910	54	137	16	14	0.7
Zophobas morio (larva)	420	5,630	1,180	7,510	1,130	3,610	39	73	9	10	0.3
Orthoptera											
Acheta domesticus (adult)	1,320	9,580	1,090	11,270	4,350	7,370	63	218	20	37	0.6
Acheta domesticus (nymph)	1,200	11,000	990	15,370	5,890	9,690	93	297	22	39	0.4
Brachytrupes sp.	3,300	6,120		10,360	2,120		539				
Crytacanthacris tatarica	1,180	6,450		9,330	1,370		128				
Gryllotalpa africana	2,630	8,820		9,300	3,370		1,448				
Isoptera											
Macrotermes bellicosus (alate)	450		280	1,170							

Macrotermes subhyalinus (alate)	400	4,420	4,210	4,810	19,880		76		137	644	
Nasutitermes corniger (soldier)	3,700	2,900	1,500	5,800	600		1,001	164	33	115	0.5
Nasutitermes corniger (worker)	2,000	4,000	1,300	6,100	2,400		394	144	52	32	
Hymenoptera											
Aphis melifera (larva)	590	7,720	910	11,590	550	3,750	56	69	17	3	0.3
Oecophylla smaragdina	1,840	7,920		8,530	2,160		219				
Oecophylla virescens	800	9,360	1,220	9,570	2,700		1,090	169	22	63	
Diptera											
Drosophila melanogaster (adult)	1,400	11,000	1,300				454	147	9	16	
Musca autumnalis (pupa)	24,800	27,400	11,500	5,500	1,800		250	270	15	660	
Musca domestca (pupa)	9,300	14,300		8,800	5,600		465	275	34	370	

source of amino acids and provide good quantities of the essential amino acids. Because some of these amino acids are part of the exoskeleton and may be sclerotized, they may not be readily available when consumed. The only two studies measuring protein digestibility of insect protein in rats reported values of 86% and 89% values, which are only slightly lower than the values reported for other animal protein sources (egg 95%, beef 98%, and casein 99%). Thus, it is likely that overall, the digestibility of insect protein, while slightly lower than that of more traditional animal protein sources such as egg, meat and milk, is higher than that of many vegetable-based proteins (Table 7).

Amino acid analyses from a variety of papers provide no common estimate of the first limiting amino acid for insect protein. While tryptophan is the amino acid most commonly cited as first limiting, all of the amino acids known to be essential for humans have been reported as first limiting. They include histidine, isoleucine, leucine, lysine, total sulfur amino acids (methionine plus cystine), total aromatic amino acids (phenylalanine plus tyrosine), threonine and valine. While it is unlikely that all species of insects would have the same first limiting amino acid, the range of first limiting amino acids reported is difficult to understand, but may be due to the analytical techniques used. Accurate analysis of methionine, cystine and tryptophan requires two separate hydrolysis versus that used for the other amino acids and the low values reported in some papers suggest this was not always done. Another issue confounding the identification of the limiting amino acid is the use of a variety of different standards. Insect amino acid patterns have been compared to World Health Organization recommended patterns for both adults and preschoolers, United Nations Food and Agriculture Organization recommended patterns for pre-school children as well as comparisons to egg protein, or other reference proteins.

In contrast to the variability obtained when calculating the first limiting amino acid, results from feeding studies have been very consistent. When diets containing insect protein from housefly pupae, yellow mealworm larvae, or Mormon crickets were fed to young, growing rats, in all three studies, methionine was shown to be the first limiting amino acid. While methionine was the first limiting amino acid for the growth of rats, when Mormon cricket meal was used as the sole source of dietary protein, no additional response was observed at maintenance, suggesting a different amino acid (not yet identified) was first limiting. As such, insect protein is likely to have a different first limiting amino acid when compared to human standards for either growth or maintenance. The high choline content of most insects also needs to be considered when determining the first limiting amino acid in insects, because high dietary choline levels can reduce the dietary requirement for methionine.

Unlike birds, reptiles, and fish, mammals are ureotelic, excreting urea as an end product of protein metabolism. Arginine is synthesized during this process, which is why the arginine requirement for growing rats is low relative to that for birds or fish. This is why Mormon cricket meal was shown to be co-limiting in the amino acids arginine and methionine when fed to broiler chicks, while only methionine was first limiting when fed to growing rats. As such, the use of insects in poultry or fish diets may require different amino acid supplementation than when used in diets for mammals.

In general, feeding trials using house fly larvae and pupae, face fly pupae, soldier fly larvae, *Hermetia illucens* (L.), Mormon crickets, house crickets, yellow mealworms, and various species of lepidopteran larvae have resulted in good growth of rats, chickens and several species of fish. This suggests that insect protein is readily available with protein quality values similar to, or slightly higher than, that of fish meal or soybean meal. However, in five separate studies, (three that used silkworm pupal meal) dried insect meals have produced poor results. In most of these studies, the poor growth appears to be a result of low food consumption. These results may be due to the presence of oxidized fats. Because dried insect

Nutrient Content of Insects, Table 7 **Crude protein and amino acid content of selected insect species**

	Crude protein (%)	Ala (%)	Arg (%)	Asp (%)	Glu (%)	Gly (%)	His (%)	Ile (%)	Leu (%)	Lys (%)	Met (%)	Cys (%)	Phe (%)	Tyr (%)	Pro (%)	Ser (%)	Thr (%)	Trp (%)	Val (%)
Lepidoptera																			
Ascalapha odorata (larva)	56.0	3.75	3.75	4.87	6.38	2.86	1.57	2.30	3.86	3.53	1.29	1.18	5.32	2.46	4.09	3.25	2.24	0.22	2.69
Bombyx mori (larva fed artificial diet)	53.8	2.40	2.23	3.53	5.35	3.21	1.39	1.73	2.83	2.51	0.71	0.46	1.53	1.68	1.82	1.94	1.65	0.38	2.17
Bombyx mori (pupa)	60.0	3.30	4.08	6.54	8.94	2.76	1.50	3.42	4.98	4.50	2.76	0.84	3.06	3.24	2.40	2.82	3.24	0.54	3.36
Galleria mellonella (larva)	58.5	2.27	1.71	3.23	4.70	1.78	0.80	1.52	2.99	1.90	0.53	0.27	1.28	2.12	2.29	2.53	1.42	0.29	1.64
Imbrasia epimethea (larva)	62.5		4.14				1.23	1.79	5.06	4.64	1.40	1.17	4.06	4.69			3.00	1.00	6.37
Imbrasia ertli (larva)	52.9							1.90	1.94	2.08	0.84	0.71	0.92	0.70			2.14	0.43	2.22
Imbrasia truncate (larva)	64.7		3.59				1.13	1.57	4.73	5.10	1.44	1.07	4.02	4.95			3.03	1.07	6.60
Nudaurelia oyemensis (larva)	61.1		3.88				1.11	1.56	5.05	4.87	1.44	1.20	3.58	4.62			2.72	0.98	5.86

Nutrient Content of Insects, Table 7 **Crude protein and amino acid content of selected insect species (Continued)**

	Crude protein (%)	Ala (%)	Arg (%)	Asp (%)	Glu (%)	Gly (%)	His (%)	Ile (%)	Leu (%)	Lys (%)	Met (%)	Cys (%)	Phe (%)	Tyr (%)	Pro (%)	Ser (%)	Thr (%)	Trp (%)	Val (%)
Xyleutes redtembacheri (larva)	43.0	2.80	2.58	4.60	4.52	2.37	0.69	2.19	3.40	2.11	0.90	0.56	4.00	2.28	2.54	2.67	2.02	0.26	2.62
Coleoptera																			
Callipogon barbatus (larva)	41.0	3.28	2.42	3.73	4.22	3.77	0.90	2.38	4.10	2.34	0.82	0.82	1.93	1.72	2.54	1.52	1.64	0.29	2.87
Rhyncophorus palmarum (larva)	25.8	1.37	1.62	2.29	3.09	1.04	1.02	0.75	1.62	1.72	0.27	0.23	0.73	0.97	1.12	1.33	1.15	0.25	0.81
Rhyncophorus phoenicis (larva)	22.8							1.77	1.34	1.46	0.27	0.24	0.75	0.31			0.65	0.12	1.25
Scyphophorus acupunctatus (larva)	36.0	2.34	1.58	3.28	5.65	2.20	0.54	1.73	2.81	1.98	0.72	0.79	1.66	2.30	1.94	2.38	1.44	0.29	2.23
Tenebrio molitor (adult)	65.3	4.99	2.81	4.57	6.28	5.51	1.87	2.84	5.40	2.89	0.83	0.44	1.71	2.18	4.13	2.70	2.23	0.72	4.13
Tenebrio molitor (larva)	49.1	4.04	2.55	3.99	5.54	2.73	1.55	2.47	5.22	2.68	0.63	0.42	1.73	3.60	3.41	2.52	2.02	0.39	2.89

Zophobas morio (larva)	46.8	3.40	2.28	3.75	5.75	2.26	1.43	2.21	4.54	2.45	0.50	0.36	1.62	3.25	2.57	2.19	1.85	0.43	2.45
Orthoptera																			
Acheta domesticus (adult)	66.6	5.84	4.06	5.58	6.98	3.38	1.56	3.05	6.66	3.57	0.97	0.55	2.11	3.25	3.73	3.31	2.40	0.42	3.47
Acheta domesticus (nymph)	67.2	5.98	4.10	4.76	6.99	3.54	1.48	2.88	6.42	3.62	0.87	0.57	1.88	3.71	3.71	2.79	2.40	0.35	3.32
Sphenar-ium histro (nymphs & adults)	77.0	5.85	5.08	7.16	4.08	4.08	1.46	4.08	6.70	4.39	0.77	1.00	9.01	5.62	5.54	3.93	3.08	0.46	3.93
Isoptera																			
Macrot-ermes bel-licosus (alate)	34.8	3.13	2.42	3.64	3.08	1.37	1.79	1.78	2.72	1.89	0.26	0.65	1.52	1.05		0.41	0.96	0.50	2.55
Macrot-ermes sub-hyalinus (alate)	38.8							1.44	3.09	1.37	0.50	0.35	1.67	1.43			1.62	0.30	1.99
Nasuti-termes corniger (soldier)	62.4	2.39	1.44	2.23	3.21	1.28	0.69	0.77	1.57	1.09	0.14		0.80	1.52	0.69	1.76	1.96		1.22
Hymenoptera																			
Aphis mellifera (larva)	40.5	1.94	1.72	3.28	5.56	1.77	0.95	1.85	2.84	2.50	0.86	0.86	1.42	1.77	2.46	1.42	1.34	0.39	2.11

	Crude protein (%)	Ala (%)	Arg (%)	Asp (%)	Glu (%)	Gly (%)	His (%)	Ile (%)	Leu (%)	Lys (%)	Met (%)	Cys (%)	Phe (%)	Tyr (%)	Pro (%)	Ser (%)	Thr (%)	Trp (%)	Val (%)
Atta mexicana (adult)	46.0	3.04	2.16	4.14	4.78	3.04	1.15	2.44	3.68	2.25	1.56	0.69	4.05	2.16	3.63	2.02	1.98	0.28	2.94
Diptera																			
Copestylum ann & haggi (larva)	37.0	2.37	2.33	3.77	4.77	2.52	1.07	1.48	2.74	2.04	0.70	0.67	2.00	2.44	1.92	1.92	1.81	0.26	2.26
Hermetia illucens (larva)	47.0	2.77	2.07	3.29	4.18	2.40	1.74	2.44	3.48	2.49	0.89		2.44	4.51		1.88	1.83		2.44
Musca autumnalis (pupa)	51.7	2.58	1.30	4.75	5.58	2.25	1.46	1.92	2.94	2.58	1.36		2.19	1.83	1.81	1.84	1.93		2.34
Musca domestica (pupa)	61.4	2.50	3.70	5.30	7.20	2.40	2.00	2.40	3.40	3.80	1.60		3.00	3.80	2.30	1.90	2.10		2.70
Hemiptera																			
Edessa petersii (nymphs & adults)	37.0	3.81	1.67	2.04	3.77	2.85	0.85	1.48	2.63	1.48	1.04	0.33	2.48	4.26	2.55	1.67	1.67	0.19	2.37

Euchistus egglestoni (nymphs & adults)	35.0	3.26	1.51	2.49	3.36	2.10	1.12	1.54	2.45	1.05	0.98	0.35	1.16	1.68	2.35	1.37	1.68	0.21	2.14
Pachilis gigas (nymphs & adults)	64.0	4.93	2.62	4.22	6.59	4.48	1.28	2.69	4.42	2.88	2.30	1.54	9.22	3.71	3.65	2.88	2.30	0.38	3.97
Umbonia reclinata (nymphs & adults)	29.0	2.29	1.33	2.58	5.45	1.39	1.07	1.10	1.97	1.65	0.55	0.41	1.71	1.97	1.57	1.22	1.36	0.17	1.16
Hoplophorion monograma (nymphs & adults)	64.0	4.80	2.88	5.82	7.94	3.84	0.96	2.62	4.93	3.39	1.22	1.34	3.01	5.76	4.29	3.14	2.88	0.64	4.74

Ala – Alanine, Asp – Aspartic acid, Arg – Arginine, Glu – Glutamic acid, Gly – Glycine, His – Histidine, Ile – Isoleucine, Leu – Leucine, Lys – Lysine, Met – Methionine, Cys – Cystine, Phe – Phenylalanine, Tyr – Tyrosine, Pro – Proline, Ser – Serine, Thr – Threonine, Trp – Tryptophan, Val – Valine meals are generally high in unsaturated fatty acids, they are susceptible to oxidation if not treated with an antioxidant during drying and storage. Another possibility is the presence of a compound in the insect meal, which negatively affects palatability. In the wild, many insect species are known to sequester compounds from their foodplants, which cause them to be unpalatable or toxic. A third possibility is the effect of some unknown anti-nutritional factor present in some species of insects. While there is little work in this area, a thiaminase recently has been discovered in both African silkworm pupae (*Anaphe*) and domestic silkworm larvae (*Bombyx mori*).

There is only very limited data available for vitamin analyses of insects. While several species of lepidopteran larvae and the soldiers of one species of termites (*Nasutitermes corniger*) contain significant quantities of preformed vitamin A (retinol), in general, insects do not appear to contain much preformed vitamin A. Insects use a variety of retinoids for vision, which they synthesize from carotenoids in their food. As these retinoids are present only in the insect eye, whole body levels of retinoids are usually very low. There is a single report that honey bee (*Aphis mellifera*) larvae and pupae contain extremely high levels of preformed vitamin A (50,000–154,600 μg retinol/kg dry weight), but the analytical procedure used is not specific for retinol. More recent analysis using high pressure liquid chromatography detected no retinol in honey bee larvae or pupae, and only low levels (850–930 μg retinol/kg) in adult bees (Table 8).

While commercially raised insects appear to contain little or no β-carotene, most wild-caught insects contain a variety of carotenoids (astaxanthin, α-carotene, β-carotene, lutein, lycopene, zeaxanthin, and others), which they accumulate from their food. Most species of vertebrates can convert some of these carotenoids to retinol, so insects containing high levels of carotenoids may be a significant source of vitamin A for insectivorous vertebrates (Table 8).

There is little data on the vitamin E content of insects, but levels are generally low. Wild-caught insects appear to contain more vitamin E than cultured insects, which likely reflects differences in their dietary intake. When mealworms (*Tenebrio molitor* larvae) or house crickets (*Acheta domesticus*) were fed diets high in vitamin E for 7 days, there was only a small increase in the vitamin E content of the crickets and the mealworms. It is not clear whether this reflects vitamin E absorbed by the insect, or is simply a result of the dietary vitamin E retained in the gastrointestinal tract.

B-vitamin analysis of insects is very limited and most of the available data is for thiamin, riboflavin and niacin. All insects tested contained substantial quantities of most of the B-vitamins and choline. It should be noted that several B-vitamins (most notably thiamin and, to a lesser degree, pyridoxine and folic acid) are not heat stable so, processing insects by canning, roasting or boiling is likely to result in a reduction of these vitamins. While insects appear to be a good source of most B-vitamins, a number of insects appear to contain low levels of thiamin. Some of these low levels are likely an effect of heat processing, although the low levels seen for house crickets and superworms (*Zophobas morio* larvae) are for raw, whole insects. Recently, wild African silkworm pupae (*Anaphe*) have been shown to contain high levels of an enzyme which results in the destruction of thiamin (Vitamin B_1). This thiaminase was shown to be relatively heat stable and appears to be responsible for an acute seasonal ataxia reported in humans in Nigeria that was previously linked to *Anaphe* consumption.

There are numerous reports on the fatty acid composition of various insect species, and all of the insects tested contained the essential fatty acid linoleic acid (18:2). There appears to be no consistent pattern in fatty acid profiles across a variety of insect species, although all species contained significant quantities of palmitic, oleic, linoleic and linolenic acid. Some insects have also been shown to contain minor amounts of other fatty acids including lauric acid (12:0), myristoleic acid (14:1), heptadecanoic acid (17:0), heptadecenoic acid (17:1), arachidonic acid (20:4) and benhic acid (22:0) (Table 9).

Nutrient Content of Insects, Table 8 Vitamin content of selected insect species

	Vitamin A (μg retinol/kg)	β-Carotene (μg/kg)	Vitamin E (mg α-tocopherol/kg)	Thiamin (mg/kg)	Riboflavin (mg/kg)	Niacin (mg/kg)	Pantothenate (mg/kg)	Pyridoxine (mg/kg)	Folate (mg/kg)	Biotin (mg/kg)	Vitamin B_{12} (μg/kg)	Choline (mg/kg)
Lepidoptera												
Bombyx mori (larva fed artificial diet)	2,740	ND	34	19.1	54.3	152	125	9.5	4.1	1.4	ND	6,523
Bombyx mori (pupa)						11						
Conimbrasia belina (larva)	60	10		5.8	49.8	119						
Galleria mellonella (larva)	40	ND	21	5.6	17.6	90	49	3.1	1.1	0.7	ND	3,953
Imbrasia epimethea (larva)	470	82		1.8	43.0	118	ND	0.7	0.1	0.3	0.2	
Imbrasia ertli (larva)												
Imbrasia truncata (larva)	330	71		2.9	55.0	118	ND	0.4	0.4	0.5	0.3	
Nudaurelia oyemensis (larva)	320	68		1.6	34.0	101	ND	0.5	0.2	0.3	0.2	
Porthetria dispar (adult with eggs)	100		149									
Usta terpsichore (larva)				40.4	20.9	3						
Coleoptera												
Rhyncophorus ferrugineus (larva)				2.7	14.6	125						
Rhyncophorus palmarum (larva)		18,000	347									

Nutrient Content of Insects, Table 8 Vitamin content of selected insect species (Continued)

	Vitamin A (μg retinol/kg)	β-Carotene (μg/kg)	Vitamin E (mg α-tocopherol/kg)	Thiamin (mg/kg)	Riboflavin (mg/kg)	Niacin (mg/kg)	Pantothenate (mg/kg)	Pyridoxine (mg/kg)	Folate (mg/kg)	Biotin (mg/kg)	Vitamin B_{12} (μg/kg)	Choline (mg/kg)
Rhyncophorus phoenicis (larva)				33.8	25.1	34						
Tenebrio molitor (adult)	ND	ND	ND	2.7	23.4	155	66	22.4	3.8	0.8	15.4	6,671
Tenebrio molitor (larva)	240	ND	20	6.3	21.3	107	69	21.1	4.1	0.8	12.3	4,839
Zophobas morio (larva)	290	ND	21	1.5	17.8	77	46	7.6	1.6	0.8	10.1	4,124
Orthoptera												
Acheta domesticus (adult)	240	ND	43	1.2	110.7	125	75	7.5	4.9	0.6	174.3	4,932
Acheta domesticus (nymph)	140	ND	28	0.8	41.5	143	115	7.6	6.3	0.2	380.8	4,776
Blatella germanica (not specified)	300		179	*Brachytrupes* sp.				9.7	66.7	86		
Crytacanthacris tatarica				8.1	24.5	286						

Gryllotalpa africana				6.9	65.6	167						
Oxya verox				3.4	78.4	100						
Isoptera												
Macrotermes subhyalinus (alate)				1.3	11.5	46						
Nasutitermes corniger (soldier)	20,400		84	*Nasutitermes corniger* (worker)	ND		ND	*Hymenoptera*	*Aphis melifera* (adult female)	850	27	
Aphis mellifera (adult male)	930		10	7,258								
Aphis mellifera (larva)	ND	ND	ND	17.7	39.2	158	51	5.1	ND	1.0	ND	
Oecophylla smaragdina				9.2	33.8	130						
Diptera												
Drosophila melana-gaster (adult)	ND		15									

ND – Not Detected

Nutrient Content of Insects, Table 9 Crude fat content and major fatty acids of selected insect species

	Crude fat (%)	Myristic acid (14:0)	Palmitic acid (16:0)	Palmitoleic acid (16:1)	Stearic acid (18:0)	Oleic acid (18:1)	Linoleic acid (18:2)	Linolenic acid (18:3)	Arachidic acid (20:0)	Other fatty acids[a]
Lepidoptera										
Bombyx mori (larva fed artificial diet)	8.1	ND	0.98	0.03	0.72	1.86	2.05	0.83	0.06	
Bombyx mori (pupa)	37.1		9.72		2.60	13.69	1.56	9.53		
Galleria mellonella (larva)	60.0	0.10	19.18	1.23	0.82	29.88	3.66	0.27	0.07	0.07%–17:1
Heliothis zea (larva fed broad-beans)	18.2	0.10	3.80	0.20	0.40	3.30	1.50	5.50		
Heliothis zea (larva fed artificial diet)	30.2	0.10	7.60	2.90	0.10	12.90	0.70	0.00		
Imbrasia epimethea (larva)	13.3	0.08	3.09	0.08	2.94	1.12	0.93	4.67		
Imbrasia ertli (larva)	12.2	0.12	2.68		0.05	0.24	2.44	1.34	4.63	0.11%–17:0; 0.06%–12:0
Imbrasia truncata (larva)	16.4	0.03	4.03	0.03	3.56	1.21	1.25	6.04		
Nudaurelia oyemensis (larva)	12.2	0.02	2.66	0.07	2.82	0.68	0.70	4.34		
Usta terpsichore (larva)	9.5	0.22	2.60		0.01	0.16	2.58	0.27	0.71	2.82%–17:0
Coleoptera										
Rhyncophorus phoenicis (larva)	46.8	1.17	16.83		0.14	14.03	12.16	0.94	0.28	0.65%–17:0
Tenebrio molitor (adult)	14.9	0.22	2.34	0.17	0.72	4.93	3.77	0.11	0.06	0.06%–17:0; 0.06%–17:1
Tenebrio molitor (larva)	35.0	0.76	6.01	0.92	1.02	14.15	9.13	0.37	0.08	0.08%–17:1

Zophobas morio (larva)	42.0	0.40	12.54	0.17	2.99	15.68	7.81	0.26	0.10	0.17%–17:0; 0.17%–17:1
Orthoptera										
Acheta domesticus (adult)	22.1	0.13	5.06	0.29	1.88	5.00	7.44	0.19	0.13	0.10%–22:0
Acheta domesticus (nymph)	14.4	0.08	2.66	0.14	1.27	2.79	4.80	0.18	0.11	
Isoptera										
Macrotermes bellicosus (alate)	46.1	0.08	21.45	0.96		5.92	15.87	1.77		
Macrotermes subhyalinus (alate)	46.5	0.42	15.35		0.65	4.42	20.04	1.40	0.19	1.21%–17:0; 0.23%–14:1;
Nasutitermes corniger (soldier)	11.2	0.48	0.85	0.11	1.33	3.66	1.24	1.09	0.43	1.03%–20:4; 0.49%–22:0
Nasutitermes corniger (worker)	2.2	0.09	0.21	0.05	0.28	1.08	0.33	ND	0.04	0.04%–12:0; 0.03%–22:0
Hymenoptera										
Aphis mellifera (larva)	20.3	0.52	6.34	0.10	1.83	7.84	0.15	0.16	0.10	0.07%–12:0

ND – Not Detected

[a]Other major fatty acids reported as % followed by fatty acid formula

In a review of insect fatty acid patterns, Thompson reported that several insect orders appeared to have unique fatty acid profiles. These peculiarities included relatively high levels of myristic acid (14:0) in Hemiptera, and palmitoleic acid (16:1) in Diptera. It also appears that linoleic acid (18:2) and linolenic acid (18:3) were virtually absent in Dictyoptera (Mantodea, Blattodea). The data are not shown in the table because crude fat and fatty acid content as a percent of body weight could not be calculated.

In general, it appears that insect fatty acid levels reflect a combination of insect fatty acid synthesis (certain pathways that may be unique for certain species or orders) and the fatty acid composition of the insect's diet. For insects that feed on a single foodplant, the values in the table are probably typical for all members of the species. In contrast, the fatty acid content of generalist feeders like the house cricket, *Acheta domesticus*, is likely to vary widely depending on the diet being fed. In addition, the data for *Rhyncophorus phoenicis* (F.) and *Macrotermes subhyalinus* is for insects that were fried prior to analysis. As such, these analyses reflect both the fat naturally in the insect and that from the cooking oil.

References

Barker D, Fitzpatrick MP, Dierenfeld ES (1998) Nutrient composition of selected whole invertebrates. Zoo Biol 17:123–134

Bukkens SGF (1997) The nutritional value of edible insects. Ecol Food Nutr 36:287–319

DeFoliart GR (1989) The human use of insects as food and as animal feed. Bull Entomol Soc Am 35:22–35

Feltwell J, Rothschild M (1974) Carotenoids in thirty-eight species of Lepidoptera. J Zool 174:441–465

Finke, MD (2002) Complete nutrient composition of commercially raised invertebrates as food for insectivores. Zoo Biol 21:269–285

Finke MD, DeFoliart GR, Benevenga NJ (1987) Use of a four-parameter logistic model to evaluate the protein quality of mixtures of Mormon cricket meal and corn gluten meal in rats. J Nutr 117:1740–1750

Ramos-Elorduy J, Moreno JMP, Prado EE, Perez MA, Otero JL, de Guevara OL (1997) Nutritional value of edible insects from the state of Oaxaca, Mexico. J Food Compost Anal 10:142–157

Thompson SN (1973) A review and comparative characterization of the fatty acid compositions of seven insect orders. Comp Biochem Physiol 45B:467–482

Nutrient Cycling

The transformation of chemical elements from inorganic form in the environment to organic form inorganisms, and then back to inorganic form following decomposition.

Nutritional Castration

Differential feeding of some groups of social insects, with those deprived of much food developing into small, sterile workers.

Nutrition in Insects

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The main reason any animal eats is to acquire the nutrients (including water) that are essential for meeting energetic needs associated with general maintenance and fueling growth and reproduction. In this regard, insects do not differ from other animals. What sets insects apart, however, is that they are able to get their nutrients from a wide range of different food sources that, for various reasons, are unavailable to most other animals. For example, termites and many beetles feed on wood, while cockroaches and crickets feed on dead plant material (detritus). A large number of insects have sucking mouthparts that allow them to feed on plant phloem (e.g., aphids) and plant xylem (e.g., spittlebugs and cicadas), or in the case of the sucking lice and some flies (e.g., mosquitoes) vertebrate blood. Some ants and beetles even get their nutrients from fungus gardens that they themselves actively maintain. From a nutrient standpoint, these foods are all very different from one another, yet, most of the work exploring insect nutrition indicates that nutritional requirements among insects are fairly uniform. This suggests that different insects have evolved specific adaptations that allow them to overcome the nutritional hurdles that prevent other animals from using certain foods as a source of nutrients.

Certain nutrients are considered essential or important for insects, and there are also some interesting nutritional differences that occur between species. Insects also have different ways to solve the problem of balancing nutrient intake in a nutritionally variable world. Examples of the different behavioral and physiological mechanisms employed, and the strategies that have evolved for dealing with nutritionally poor foods and environments are documented.

Qualitative Nutrition

The qualitative nutritional requirements of insects are very similar to other animals as the basic chemical composition of their tissues and their metabolic processes are generally the same. Insects have the ability to biosynthesize some nutrients, but most are obtained from the foods they eat. Those that cannot be biosynthesized are called essential nutrients. Much of what we know about insect nutrition comes from studies using artificial foods, and in general there are three main approaches to understanding insect nutritional requirements. The most common is the deletion method, which measures the effect of eliminating one specific component from a chemically defined artificial diet and then measuring whether the insect can develop on the modified diet under sterile conditions. Once the deletion method identifies which nutrients are essential, the substitution method can be used to test whether analogues of these nutrients also support development. Finally, radiolabeled precursors can be fed to insects to determine which nutrients insects are able to produce endogenously.

Amino Acids and Proteins

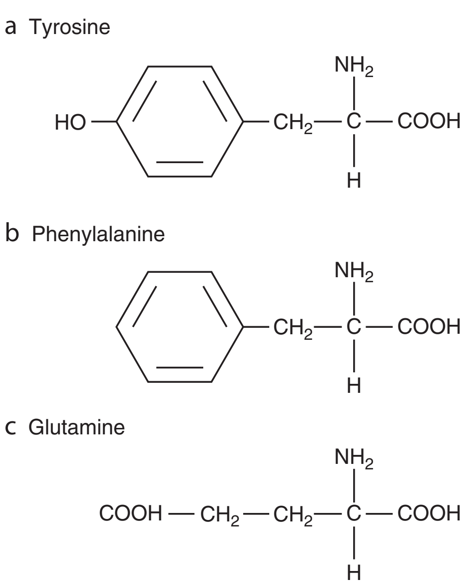
Amino acids are characterized by having a basic nitrogenous group, generally an amino group ($-NH_2$), and an acidic carboxyl group ($-COOH$). They are the building blocks of protein, which are used for structural purposes, as enzymes, for transport and storage, and as receptor molecules. Individual amino acids also serve important physiological functions in insects (e.g., aromatic amino acids such as tyrosine and phenylalanine in morphogenesis, and glutamate as a neurotransmitter). In total, about 200 amino acids have been isolated from biological materials, but only 20 of these are regularly found in proteins. Of these 20 amino acids, usually only ten are considered essential for insects (Table 10). The others, which are considered non-essential, can be synthesized or derived from these ten (Fig. 37).

Dietary proteins are the greatest source of amino acids, although most foods contain at least a small pool of free amino acids. The value of any protein to an insect can vary, however, depending on its digestibility and amino acid content, particularly the number and balance of essential amino acids. This is especially true for plant feeding insects since the amino acid content and balance of foliar proteins can vary significantly from species to species, as well as within a species, due to genetic and environmental variation. Foliar protein profiles can also vary within an individual plant as a result of differences in leaf age (e.g., young leaves tend to be high in protein content while old leaves tend to be protein-poor). In general, the absence of any single essential amino acid from the diet prevents growth, and in some instances, non-essential amino acids (e.g., proline for the silkworm, *Bombyx*) may be required. Even though some amino acids are non-essential, optimal growth usually only occurs when there is a good mixture of non-essential amino acids in the diet. This is because the synthesis of non-essential amino acids and the elimination of remnant compounds following their synthesis can be metabolically expensive. For some insects, the concentration of

Nutrition in Insects, Table 10 **Essential and non-essential amino acids for insects**

Essential	Non-Essential
Arginine	Alanine
Histidine	Asparagine
Isoleusine	Aspartate
Leucine	Cystine
Lysine	Glutamate
Methionine	Glycine
Phenylalanine	Histidine
Threonine	Proline
Tryptophan	Serine
Valine	Tyrosine

Essential amino acids are those that insects cannot synthesize for themselves and must be obtained from the diet or from endosymbionts



Nutrition in Insects, Figure 37 **Examples of important amino acids. Tyrosine and phenylalanine, which are distinguished from other amino acids by their aromatic ring structures, play an integral part in the sclerotization (the hardening of new cuticle following a molt). Among its various roles, glutamate is the principle neurotransmitter at insect nerve/muscle junctions.**

non-essential amino acids needed for optimal growth on an artificial diet may exceed 50% of the total amino acid pool. There are also constraints on which non-essential amino acids can be metabolized. For example, because insects cannot synthesize the aromatic ring in tyrosine, a key amino acid involved in the sclerotization of the cuticle, it can only come from a compound with a similar structure, such as phenylalanine (Table 10).

Carbohydrates

The name carbohydrate is derived from the French hydrate de carbone and, in general, is applied to neutral chemical compounds containing the elements carbon, hydrogen and oxygen, with the last two elements present in the same proportions as in water $(CH_2O)n$. There are exceptions to this rule, though, since some compounds with the general properties of carbohydrates also sometimes contain phosphorous, nitrogen or sulphur. In general, carbohydrates can be split into two main groups: sugars (e.g., glucose, fructose and sucrose) and non-sugars (e.g., starch, dextrin, cellulose). Whether an insect can utilize a particular type of carbohydrate depends upon its digestive capabilities. Most insects can use sugars but, with regard to non-sugars, the situation is much more variable.

Strictly speaking, carbohydrates are not essential nutrients since insects can convert fats and amino acids to carbohydrates (a process called gluconeogenesis). There are, for instance, some insects, such as the screw-worm fly, *Chrysomya*, which normally feeds on live animal tissue, and the wax moth, *Galleria*, that readily grows on artificial diets containing no carbohydrates. For most, however, carbohydrates are considered important because they usually provide the main energy source for metabolic processes and the molecular skeletons for other organic molecules. For example, the desert locust, *Schistocerca*, needs at least 20% of digestible carbohydrates in an artificial diet for good growth. Likewise, the flour beetle, *Tenebrio*, shows optimal growth when it has a diet of 70% carbohydrate, but fails to develop if the concentration drops below 40%.

Lipids

Lipids are a group of substances found in plant and animal tissues, and are insoluble in water but soluble in common organic solvents such as benzene, ether and chloroform. Lipids act as electron carriers, substrate carriers in enzymatic reactions, components of biological membranes and sources and stores of energy. Sterols, fatty acids, carotenoids and fat-soluble vitamins are examples of lipids that are either essential or considered important for insects.

Sterols

Sterols, which serve as structural components in cellular membranes and as precursors for steroid hormones (e.g., molting hormone), are essential nutrients for all insects. This is because insects are unable to biosynthesize the sterol tetracyclic nucleus as is normal for most living organisms (such as vertebrates and plants). For the great majority of animals, including insects, cholesterol is the dominant tissue sterol. This means that predaceous, parasitic and sarcophagous insects always have a ready supply of cholesterol available. In contrast, plants rarely contain cholesterol at appreciable levels so phytophagous insects must either (i) use plant sterols in their existing form, (ii) convert them to cholesterol, or (iii) convert them to some usable form. Hundreds of different sterols have been identified in plants, with sitosterol being the most common (Fig. 39). Sitosterol is differentiated from cholesterol by the presence of an alkyl group on the side-chain (as shown by the arrow in the figures of sterol molecules, and is converted to cholesterol when the alkyl group on the side-chain is removed by the appropriate enzyme. Most plant feeding insects can use sitosterol, but because of metabolic constraints, some plant sterols cannot be converted to cholesterol. Grasshoppers, for example, cannot use phytosterols with double bonds in certain positions. A small group of insects, such as the cactus fly, *Drosophila pachea*, requires very specific phytosterols that are only found in the plants on which they specialize.

Fatty Acids

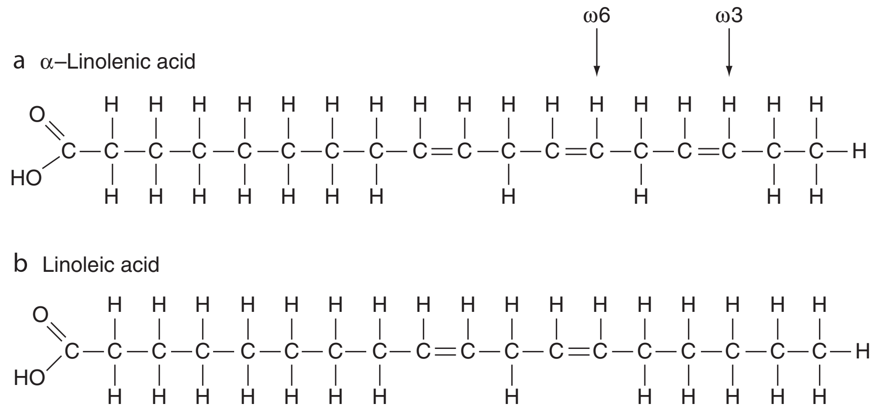
In addition to sterols, most insects have a dietary requirement for polyunsaturated fatty acids. Fatty acids consist of a hydrocarbon chain and have a terminal carboxylic acid group ($-COO^-$). The most common fatty acids in insects have an even number of carbon atoms and chain lengths of 16 or 18 carbon atoms, although chain lengths ranging from 14 to 24 carbon atoms are not uncommon. Unsaturated fatty acids, in contrast to saturated fatty acid, contain a double bond in the hydrocarbon chain; polyunsaturated fatty acids contain two or more double bonds. Many different studies have shown that either linoleic or linolenic acids adequately satisfy this nutritional need. The effect of omitting fatty acids from the diet varies from species to species. For example, in the Lepidoptera and Hymenoptera, adults, but not larva, fail to develop properly if linolenic acid is not in the diet. This suggests it is important in metamorphosis. Linolenic acid also seems to play a role in Both cockroaches and beetles suffer reduced fecundity and produce slow growing nymphs in its absence. With the exception of mosquitoes, it seems Diptera do not require polyunsaturated fatty acids. Larval mosquitoes, however, do require arachidonic acid or related 20- and 22-carbon polyunsaturated fatty acids to survive to adulthood (Fig. 38).

Vitamins

Vitamins are usually defined as organic compounds that are required in small amounts for normal growth and maintenance of life. Insects, as well as most other animals, usually only require them in small quantities. Nonetheless, if a deficiency is incurred, normal metabolic functions may be disrupted and susceptibility to disease may increase. Typically, vitamins are split into two groups based on their solubility in water.

Among the water soluble vitamins are the B vitamins, including thiamine, riboflavin, nicotinic acid, pyridoxine, panthothenic acid, folic acid and biotin, which function as cofactors of the enzymes catalyzing metabolic transformations. Some of these also serve additional roles (e.g., biotin in the enzyme pyruvate carboxylase in honeybees, and folic acid is necessary for nucleic acid biosynthesis). Myo-inositol and choline, which are constituents of some phospholipids, are required in larger amounts than other vitamins. However, because choline can be synthesized from methionine, the quantities needed may be a reflection of the levels of methionine available in the diet. Ascorbic acid, more commonly known as vitamin C, is a dietary requirement for most plant-feeding insects, but not for insects using other types of food.

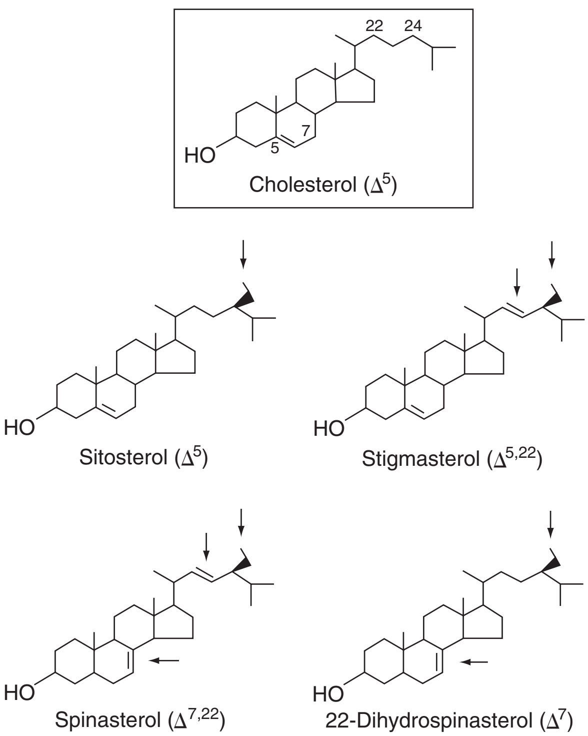
Two fat-soluble vitamins are known to be important for insects. One is β-carotene (provitamin A), which is probably essential as it is the functional component of visual pigments. β-carotene and other carotenoids, which typically have yellow, orange or red colors, are responsible for many of the varied and natural colors for which insects have become well known. Only plants and microorganisms can make carotenoids, so insects, like all animals, must obtain them from their diets. The other lipid-soluble vitamin required by most insects is vitamin E (α-tocopherol). When it is added to diets, some moths and beetles show high fecundity, but a deficiency may negatively affect sperm production, as has been shown in the house cricket.



Nutrition in Insects, Figure 38 **Essential fatty acids. Most insects require a dietary source of polyunsaturated fatty acids with double bonds in the ω 3 and/or ω 6 position.**

Nucleic Acids

Nucleic acids are high molecular weight compounds that store genetic information and provide the blueprint for building proteins. On hydrolysis, nucleic acids yield a mixture of basic nitrogenous compounds (purines and pyrimidines), a pentose (ribose or deoxyribose) and phosphoric acid. Only some of the Diptera, such as the screw-worm (*Cochliomyia*), and *Drosophila* and *Culex* require nucleic acid in the diet, although other Diptera show faster development and less mortality when diets are supplemented with nucleic acids (Fig. 39).



Nutrition in Insects, Figure 39 Sterol structures of interest. Cholesterol, with a double bond at position 5 (Δ 5), is the dominant tissue sterol found in insects. The remaining four sterols are found in plants. The arrows indicate structural differences from cholesterol. Of these four, only sitosterol supports normal growth and development in grasshoppers.

Minerals

Most naturally occurring mineral elements are found in insects because they are constituents of the food insects eat. The term "essential mineral element" is restricted to ones that are known to play a metabolic role in the body. For insects, sodium, potassium, calcium, magnesium, chloride and phosphate are considered essential. However, since most of these elements exist as impurities in any artificial diet, little detailed information exists about the precise amounts insects need.

As in all animals, iron is the central element in cytochromes and a dietary source is required. Zinc and manganese are also essential and play a part in hardening the cuticle of mandibles in insects. Interestingly, some plants hyperaccumulate heavy metals, such as iron, at levels that greatly exceed nutritional requirements. Behavioral studies show that insects given such plants quickly develop learned aversions to them, but that if they are given no alternative, they will eat these plants and suffer reduced growth and high rates of mortality.

Regulation of Nutrient Intake

The nutrient content and profile of foods can be highly variable, particularly for insects that feed on plants or plant parts. Insects have multiple nutritional needs (upwards of 30), but whether insects are able to maximize their fitness is, in part, determined by the extent to which they can regulate the intake of important nutrients. The blend of nutrients an insect requires to meet its structural and energetic needs over a given period is called the "nutrient target." However, because insects cannot absorb or utilize all the nutrients they ingest, they must eat nutrients in amounts that exceed the nutrient target. The mix of nutrients that must be eaten to reach the nutrient target is called the "intake target." Nutrient and intake targets tend to be species-specific and both are known to shift depending on the age, stage of development, reproductive status and physiological state (e.g., bumblebees before and after flight) of the insect.

Recent studies demonstrate that nutrient regulation is a widespread phenomenon in insects. For example, when grasshoppers are given two foods that contain protein and carbohydrates in ratios and amounts that are suboptimal, but which are together complementary (i.e., the intake target lies between the two foods), insects reach their protein–carbohydrate intake target by eating specific proportions and amounts of the two foods. They even reach the protein–carbohydrate intake when these same complementary foods are paired in different ratios (e.g., 3:1, 2:2 or 1:3). Regulatory responses are also shown when grasshoppers are restricted to single foods that have protein–carbohydrate ratios, but not amounts, that are optimal. Regulatory responses under these conditions are called compensatory because total food intake is adjusted. That is, intake is high on foods with low nutrient concentrations, but low on foods with high nutrient concentrations. Mixing between foods to regulate nutrient intake and compensatory feeding responses to different nutrient concentrations have also been regularly demonstrated in caterpillars.

The mechanisms insects use to regulate their nutrient intake have been explored at a number of different levels. Perhaps the most interesting involves a direct feedback involving mouthpart taste-receptors (specifically the maxillary and labial palps) and the blood (also called hemolymph). In grasshoppers, for example, electrophysiological studies have shown that the sensitivity of mouthpart chemoreceptors that respond to amino acids and sugars are inversely proportional to the level of these nutrients in the hemolymph. This means that when amino acid levels in the blood decrease as a result of either not having eaten for a long time or having previously eaten a food with low protein content, the sensitivity of the grasshopper's mouthpart taste receptors to protein-rich foods will increase. As a result, when the grasshopper next encounters a protein-rich food, it will be stimulated to feed. A similar response will occur if blood titres of sugar drop and a carbohydrate rich food is encountered. Interestingly, these responses operate independently of one another. Learning also has been shown to be involved in regulating the intake of both macronutrients (e.g., protein and carbohydrates) and micronutrients (sterols).

Finally, insects are able to employ postingestive regulatory mechanisms to reach their nutrient target. For instance, both grasshoppers and caterpillars are able to differentially utilize excess protein to meet energy requirements when carbohydrates are limiting. In this case, amino acids are deaminated and glucose is generated from the remaining carbon skeleton (i.e., gluconeogenesis). Other noncarbohydrate precursors such as glycerol and fatty acids can also act as a source for the production of glucose. Grasshoppers have also been shown to physically increase their gut size as the nutritional quality of their food decreases. This allows them to ingest greater amounts of food, which increases their ability to process and absorb important nutrients. In cases where nutrients are eaten in excess of requirements, mechanisms also exist to eliminate the surplus. In grasshoppers, for example, excess nitrogen can be converted to uric acid and excreted, but in both grasshoppers and caterpillars, excess carbohydrate can either be respired or converted to lipid and stored.

Nutrient–Allelochemical Interactions

Many foods, particularly plants, contain nonnutritive compounds called allelochemicals, which either deter insect feeding or, when ingested, negatively affect growth and/or reproduction. It is generally believed that these compounds have evolved as a form of defense against herbivores, but recent evidence suggests they may also serve in other capacities (e.g., tannins in fallen oak leaves may aid in the maintenance of soil nutrient levels). Allelochemicals are widespread and in terms of their chemical structures, very diverse. A brief discussion of allelochemicals is warranted as they are known to have a strong impact on insect foraging and nutrient utilization.

When the foods available to an insect vary both in their nutritional and allelochemical composition, foraging decisions probably represent a trade-off between the benefits gained from obtaining an optimal balance of nutrients and the costs of ingesting allelochemicals that may be deleterious. This issue has been explored by presenting locusts with multiple foods that vary in their protein, carbohydrate and tannic acid content. A key point discovered by this research is that the effectiveness of an allelochemical as a defense depends on the nutritional content of the food. For example, when locusts were given a food with an optimal amount and ratio of protein to carbohydrate, they were impervious to the effects of tannic acid even when it was present at concentrations as high as 10%. However, as the protein–carbohydrate ratio and concentrations of the food became increasingly suboptimal, the concentration of tannic acid needed to negatively impact insect performance decreased. Interestingly, the manner in which tannic acid affected the locusts depended on the direction of the protein–carbohydrate imbalance. When tannic acid was in a food with a high carbohydrate/low protein content, it acted as a feeding deterrent. In contrast, when tannic acid was in a high-protein/low-carbohydrate food, it disrupted protein utilization. A choice study showed that the effect of an allelochemical on foraging behavior is, in part, determined by a food's nutrient content. This time, if locusts were given a choice between a high-protein/low-carbohydrate food without tannic acid and a low-protein/high-carbohydrate food with tannic acid, they primarily ate from the former. When the tannic acid was in the high-protein/low-carbohydrate food and absent from the low-protein/high-carbohydrate food, they still slightly preferred the high-protein/low-carbohydrate food even though it contained tannic acid. In both instances, the importance of ingesting protein was cited as the reason for preferring the high protein food. In the first case, excess ingested protein could have been deaminated to make up the carbohydrate deficit, but in the latter case, the benefit gained from eating protein outweighed the costs associated with consuming tannic acid. More recent studies using another allelochemical, gramine, suggest that the manner in which nutrients and allelochemicals interact to affect insect foraging behavior may also be tightly linked to the chemical and structural make-up of the allelochemical, specifically whether it is carbon or nitrogen based.

Extreme Foods

Half of all identified insects species feed on plants, and a significant proportion of these feed on plant material (e.g., wood, phloem, xylem) that is best described as nutritionally inadequate to most species. At least two major adaptations exist that may help to improve this problem. One is the development of symbiotic associations with micro-organisms, the other concerns gut morphology.

Endosymbionts, which appear to be more common than ectosymbionts, can be found in either the alimentary canal, or intracellularly. In most cases, micro-organisms found in the alimentary canal usually come from ingested food and probably contribute very little to the nutrition of the insect. However, detritus-feeders, such as cockroaches and crickets, do contain bacteria in their hindguts that allow them to digest plant polysaccharides such as xylans, pectins and gums, and oligosaccharids, such as raffinose. Some termites also have bacteria in their guts that enable them to fix atmospheric nitrogen, which then can be incorporated into body tissues.

Intracellular micro-organisms are of two types: those found in normal cells, and those with a discrete morphology called mycetocytes. Of these two types, only mycetocytes seem to play a role in the nutrition of insects. They are found in all insect species that feed on vertebrate blood throughout their life and in almost all Hemiptera, except those that feed on tissues other than phloem or xylem. Most wood-feeding beetles and Ischnocera (specialists on feathers and skin debris of birds), plus cockroaches in the family Blattidae and ants in the tribe Camponoti have mycetocyte micro-organisms. Mycetocyte-bound micro-organisms are involved in regulating and maintaining nitrogen levels. In the Blattidae they recycle nitrogen and synthesize a range of essential amino acids, including those containing sulfur. The symbionts of aphids convert non-essential amino acids to essential ones and aphids could not survive without them, because the essential amino acids usually comprise less than 25% of the total amino acid concentration in phloem. Whether endosymbionts provide essential sterols is debatable, but there is some evidence that they may produce some of the B vitamins.

Unique gut morphology may also aid insect nutrition, particularly in phloem and xylem feeders. In some aphids, for example, the presence of a so-called filter chamber(s) in the alimentary canal allows insects to substantially reduce the osmotic concentration of ingested fluid. It is thought that this structural design increases the concentration of important nitrogen containing nutrients in the midgut, which aids the absorption process. In species that do not have a filter chamber, the hind part of the gut lies alongside and is attached closely to one side of the stomach. Alternatively, it has been suggested that the presence of a large stomach in aphids, which feed continuously, is surprising, and that its function may be to dilute, rather than to store incoming food.

Conclusions

As a group, insects are an incredibly diverse and species rich. Estimates for the total number of species currently range from 5 million to 30 million. Certainly some of their unparalleled success is owed to evolved adaptations that allow them to acquire their nutrients from a wide range of different foods. In recent years, our understanding of insect nutrition has been expanding rapidly, in large part because of major technological advances, and some of this information is proving valuable for humans. First, because insect and human physiological processes share much in common, insects make excellent model systems for exploring human health issues related to nutrition. Second, new insights into insect nutrition allow us to develop novel strategies that exploit specific nutritional requirements and constraints, which, in turn, may reduce insect pest populations and the adverse effects associated with insects to our health, crops, homes and buildings.

References

Canavoso LE, Jouni ZE, Karnas KJ, Pennington JE, Wells MA (2001) Fat metabolism in insects. Annu Rev Nutr 21:23–46

Chapman RF (1998) The insects: structure and function, 4th edn. Cambridge University Press, Cambridge, 770 pp

Dadd R (1985) Nutrition: organisms. In: Kerkut GA, Gilbert LI (eds), Comprehensive insect physiology, biochemistry and pharmacology. Pergamon, Oxford, pp 313–390

Simpson SJ, Raubenheimer D (2000) The hungry locust. Adv Study Behav 29:1–44

Nuttalliellidae (Acari)

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The phylogenetic nature of this monotypic family of ticks has been the conjecture of biologists now for three quarters of a century. The single species known is *Nuttalliella namaqua* Bedford, 1931, and is known from only 18 females and three nymphs from the scattered semiarid areas in Namaqualand, North Cape Province of South Africa, Namibia, and from mud nests of swallows in an "arid area" of northwestern Tanzania (112 miles south of Lake Victoria) in East Africa. Single specimens have been taken from skins of a burrowing rodent inhabiting sandy soil, Brant's Karoo rat, *Parotomes brantsii*; a small carnivore, the slender-tailed meerkat, *Suricata hahni*; and from two mud clinging nests of the lesser striped swallow, *Hirundo abyssinica*, from overhanging ledges in a rock kopje or inselberg. Hoogstraal believed that the rock hyrax (*Procavia capensis*) was also a principal host based on Bedford's original description in South Africa who reported that "rock-rabbits" or hyrax were the most common animals on the hill where the tick was originally discovered "under a rock." Bedford, however, suggested that a bird could be a host.

The discovery in Tanzania of *N. namaqua* in the nests of *H. abyssinica* swallows, and the female taken on the ground in 1980 by Dixon (University of Capetown), suggest that birds are at least one of the true hosts. When the mud retort nests decompose or in weathering when abandoned and pieces of mud break off after a period of time, the tick could very well find seclusion under one of the many rocks or boulders on a rocky hill or kopje, or attach itself to a burrowing rodent or a meerkat that plays in the southern African sandy soils. Under overhangs of granitoid boulders in kopjes near Shinyanga of western Tanzania, the author often found other species of Argasid ticks, namely *Argas brumpti*, under rocks, and *Argas africolumbae* (Argasidae) were collected in the same mud nests as the *Nuttalliella*. There is also evidence that birds other than striped swallows can use these nests and be possible hosts. When the spout is broken off the mud nest, the opening is made larger and could accommodate nesting by the cliff chat, *Thamnolaea cinnamomeiventris*, or rock martin, *H. fuligula*. Both of these birds have been reported to use these nests in Tanzania.

Scanning electron microscopy of the external surfaces of *Nuttalliella* reveals an argasid-like tick with certain generalized ixodid-like characters. The female *N. namaqua* spiracle plate reveals a morphology that differs from basic patterns in argasid and ixodid ticks and is unique to the Nuttalliellidae, lacking the pores found in other ticks.

Hoogstraal has proposed that the absence of male specimens suggested that (i) *Nuttalliella* is parthenogenetic, or (ii) males are more secretive and less mobile than females and remain to be discovered, or (iii) the sex ratio is unusually disproportionate.

References

Bedford GAH (1931) *Nuttalliella namaqua*, a new genus and species of tick. Parasitology 23:230–232

El Shoura SM, Hoogstraal H, Roshdy MA (1984) *Nuttalliella namaqua*: female internal morphology. J Parasitol 70:114–20

Hoogstraal H (1985) Argasid and nuttalliellid ticks as parasites and vectors. Adv Parasitol 24:135–238

Keirans JE, Clifford CM, Hoogstraal H, Easton ER (1976) Discovery of *Nuttalliella namaqua* Bedford (Acarina: Ixodoidea: Nuttalliellidae) in Tanzania and redescription of the female based on scanning electron microscopy. Ann Entomol Soc Am 69:926–932

Nycteribiidae

Formerly a family of flies (order Diptera). They (and Streblidae) were commonly are known as bat flies, but are now included in the family Hippoboscidae.

► Flies

Nygma (pl., nygmata)

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Insect wings, due to their complex anatomical structure and long evolutionary history, are organs of significant phylogenetic value. Present on the wings of many insects are nygmata, frequently prominent but enigmatic structures whose presence, anatomy, and function has been discussed for nearly a century. In imaginal wings, nygmata resemble small cuticular "discs" that may occur on the forewing, hindwing, or both. Depending on taxon, they may number from one to several per wing. Although they probably are phylogenetically very old, they are found only in endopterygote insects.

The term “nygma” is a Greek transliteration from the Spanish *punto*, the descriptive term first used in the literature, and which translates into English as “a pricking,” “lesion,” or “puncture.” Alternative terms found in the literature include “corneus points,” “organes facettiques,” “facetic spots,” and “chitenous (sic) dots.” The proliferation of names in the literature indicates partly that it is still not clear whether the structures are homologous in the different groups or, when multiple nygmata occur on a single wing, whether those several nygmata are homologous.

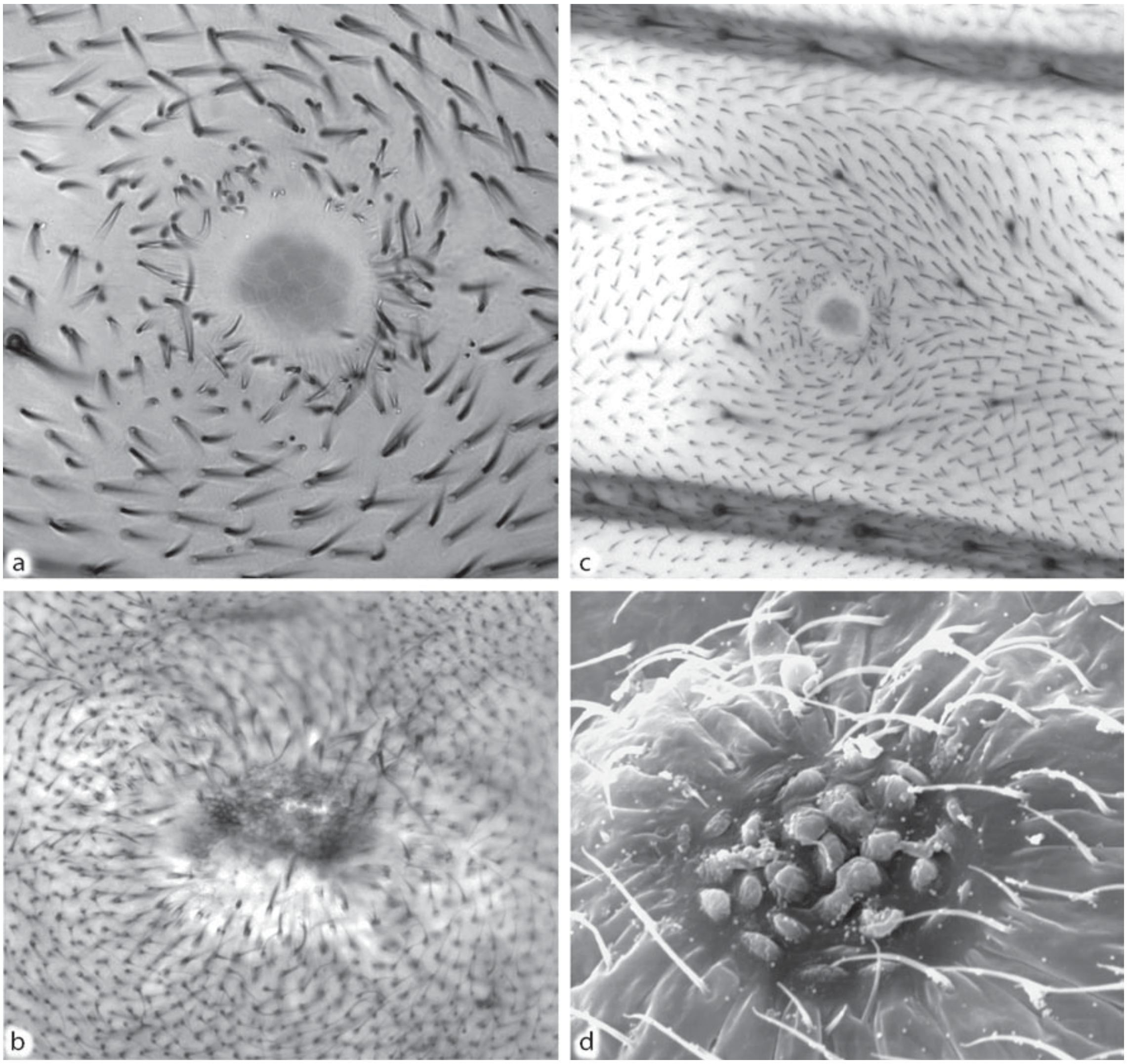
In extant holometabolous insects, nygmata are found in Trichoptera, Mecoptera, Hymenoptera: Symphyta, and some but not all families of “Neuroptera” (Megaloptera, Neuroptera s.s., but not Rhaphidioptera). Notably, nygmata are absent from any known Lepidoptera, some families of Trichoptera, Diptera, and Hymenoptera: Orussoidea and Apocrita. In the groups where they do occur, they have often been used as significant “landmarks” for interpreting venational homology (e.g., Trichoptera). An early report in the literature that a nygma-like structure had been discovered on the wings of *Phymatopterella shannoni* (Brues) (Phoridae) almost certainly refers to a developmentally different structure. Similarly, the raised sclerotized regions found in the “horse-head” cell (1M + 1R1) of some ophionine ichneumonid wasps (e.g., *Enicopsilus* spp.) are substantially different in gross morphology than typical nygmata, and are probably unrelated structures.

Although there is considerable morphological variation in nygmata among taxa in their shape, micro-sculpture, distribution, and constancy of number, it seems reasonable that they are manifestations of the same basic morphological, physiological, or development phenomena. A typical nygma is ~0.1 mm in diameter, circular in outline, bi-convex, and with a surface “blebbed” by the cuticular remnants of epidermal cells. Typically, the wing membrane around the nygma is deformed and acquires pleats directed toward the nygma. Significant deviations occur in several groups, often suggesting a duct-like structure, or assuming a concave aspect with an irregular outline.

All experimental work to date has been descriptive and based entirely on the imaginal structure. Contrary to some earlier reports, imaginal and sub-imaginal nygmata can be seen in some developing pupae (e.g., trichopterans). All discussions in the literature of a functional role for nygmata are speculative; a glandular role has been suggested repeatedly, perhaps serving some function for molting or for storing pheromones. Given that imaginal nygmata are clearly derived from epidermal cells, as indicated by their substructure, and that they occur exclusively in wing membrane, it is unlikely that as imagoes they receive much metabolic support from the hemolymph, whose distribution in the wing is almost completely restricted to the cuticular veins. Perfusion of hemolymph between the upper and lower wing membrane layers may provide some metabolic resources to support active physiological processes in the nygma, but no data are available to support this possibility. Furthermore, there is no evidence that nygmata are innervated by any nerve branches present in the veins.

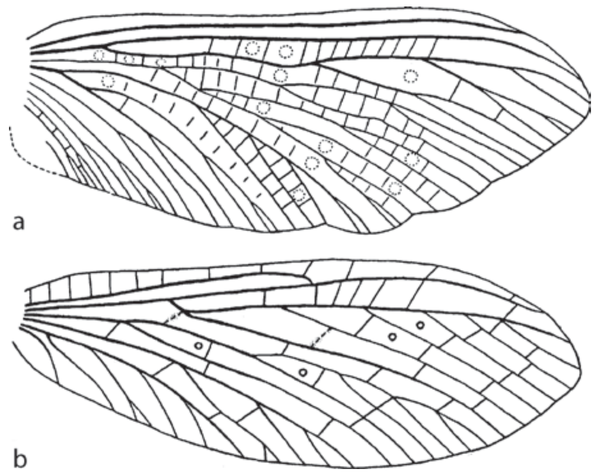
Quite possibly the nygmata have no functional role in fully developed imagoes of extant taxa, but instead are involved with wing development, or apolysis and ecdysis from the pupal cuticle. It is clear that in at least some groups (e.g., Trichoptera) that a nygma can influence the course of a developing vein, such as by causing a vein to bifurcate around a nygma and then anastomose beyond it.

Other than clarifying any functional and developmental roles, the outstanding question is why nygmata are restricted entirely to extant holometabolous groups. Impressions of nygmata can be discerned readily in the fossil wings of extant taxa that still retain them (e.g., Osmylidae remains from China). This suggests the question of whether nygmata are remnants of structures that were found in early pre-endopterygote insects. Illustrated literature of extinct faunas, typically of non-endopterygote groups, suggests



Nygma (pl., nygmata), Figure 40 **Photographs of nygma on wings of extant insects (a) *Panorpa* sp. (Mecoptera: Panorpidae), (b) *Nigronia* sp. (Neuroptera: Corydalidae), (c) *Panorpa* image a, less magnified, (d) *Hydrospyche* sp. (Trichoptera: Hydrospsychidae).**

the possibility that nygmata were present in some of these groups, although the illustrations are insufficient to settle the question. A few examples include the fossil wings of Miscopteridae (Megasecoptera), Cacurgidae (Protorthoptera), and Diaphanopterodea (Paleoptera), which are often illustrated with marks typical of the areas where nygmata occur. Some of these may simply be transferred pigmented areas, but others may represent nygma-like morphological structures. The problem of character interpretation is particularly acute in fossil taxa described as *Diaphanoptera* spp. (Diaphanopteridae), which have been treated as both representative paleopterans and as near-relatives of modern megalopterans. If any *Diaphanoptera* spp. taxa are in fact related to megalopterans, then the wing illustrations could indeed be of nygmata. Other *Diaphanoptera* spp. wings illustrated with "nygmata" that are figured *on* veins are most probably either incorrectly illustrated or simply areas of pigment transfer; no examples are known of nygmata developing in a



Nygma (pl., nygmata), Figure 41 **Drawings of nygma on hind wings of extinct insects (Paleoptera) (a) *Lamproptilia* sp., (b) *Diaphanoptera* sp. (modified from Forbes 1943).**

vein without causing significant deviation to the development of that vein (Figs. 40 and 41).

References

Betten C (1913) An interesting feature in the venation of Helicopsyche, the Molannidae, and the Leptoceridae. Ann Entomol Soc Am 6(1):65–73

Béthoux O, Nel A (2003) Revision of *Diaphanoptera* species and new diagnosis of Diaphanopteridae (Paleoptera: Diaphanopterodea). J Paleontol 77(5):1016–1020

Carpenter FM (1963) Studies on carboniferous insects from Commentry, France: Part V. The genus *Diaphanoptera* and the order Diaphanopterodea. Psyche 70(4):240–256

Forbes WT (1924) The occurrence of nygmata in the wings of Insecta Holometabola. Entomol News 35:230–233

Jolivet P (1955) Recherches sur les organes facettiques des ailles des insectes (1). Bull Inst R Sci Nat Belg 31(7):1–23

Kristensen NP (1989) The New Zealand scorpionfly (*Nannochorista philpotti* comb. n.): wing morphology and its phylogenetic significance. J Zoolog Syst Evol Res 27:106–114

Londt JG (1974) "Corneus spots" in insects. J Entomol Soc S Afr 37(1):5–14

Martynov AV (1925) On the facetic organs on the wings of insects. Trav Soc Nat Leningr 44:1–23

Martynova O (1949) Facetic organs on wings of Mecoptera. Bull Moscow Soc Nat Res, Geol Sect 24:93–95. (Byulleten Moskovskoe Obshchestvo Ispytatelei Prirody Otdel Geologicheskii.)

Navas L (1917) Algunos organos de las alas de los insectos (4a Serie). Asociación Española para el Progresso de los Ciencias, Congreso Sevilla. pp 57–62

Nymph

The immature stage of insects with incomplete metamorphosis (hemimetabolous development). The nymph usually resembles the adult in form except for undeveloped wings. This term also is applied to the second stage of mites.

Nymphalidae

A family of butterflies (order Lepidoptera). They commonly are known as brush-footed butterflies.

► Brush-Footed Butterflies
► Butterflies and Moths

Nymphidae

A family of insects in the order Neuroptera.

► Lacewings, Antlions, and Mantidflies

Nymphomyiid Flies

Members of the family Nymphomyiidae (order Diptera).

► Flies

Nymphomyiidae

A family of flies (order Diptera). They commonly are known as nymphomiid flies.

► Flies

Nyssonidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees, and Sawflies**Nutrient Content of Insects, Table 6 Mineral content of selected insect species (Continued)**

O

Oak Wilt

This fungal disease is an important forest tree pathogen, and is transmitted by nitidulid beetles and others.

► Transmission of Plant Diseases by Insects

Oakworms

Members of the family Dioptidae (order Lepidoptera).

► American False Tiger Moths

► Butterflies and Moths

Obligate Myiasis

Myiasis in which the maggots are obligated to dwell within their animal host.

Obligate Parasitism

Organisms capable of existence only by parasitism.

Obliquebanded Leaf Roller, *Choristoneura rosaceana* (Harris) (Lepidoptera: Tortricidae)

This is an important fruit tree pest in North America.

► Apple Pests and their Management

Obligatory Diapause

A genetically programmed period of diapause (suspended development) that occurs regularly as part of an insect's life cycle. Most insects living in temperate climates have obligatory diapause that allows them to survive winter; this may also occur in climates with a prolonged dry season. The stage of the insect that exhibits diapause may vary among species, but it is consistent within the species. Optional induction of diapause is called facultative diapause.

► Diapause

► Facultative Diapause

Obtect Pupa

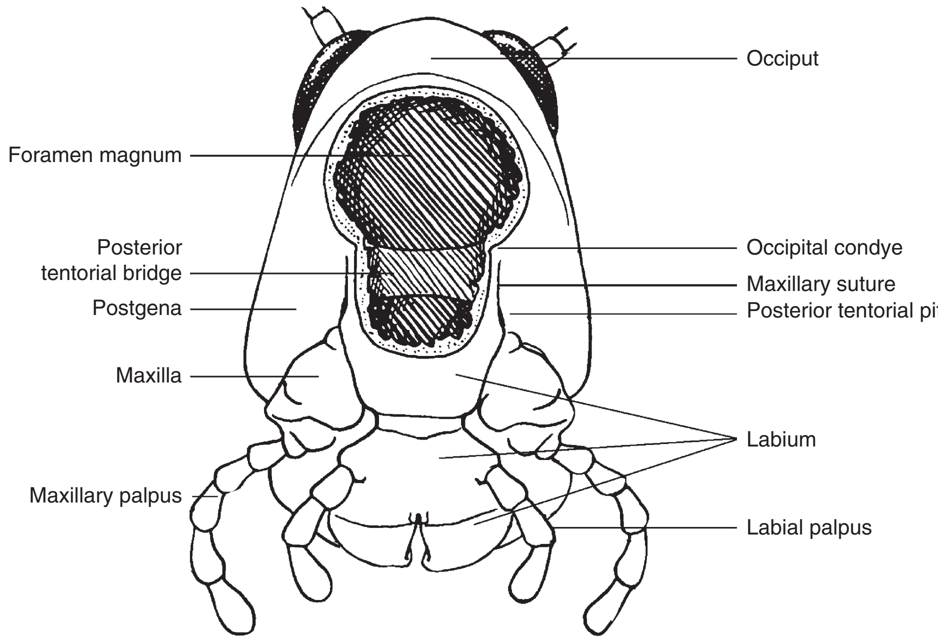
A pupa in which the appendages adhere closely to the body.

Occiput

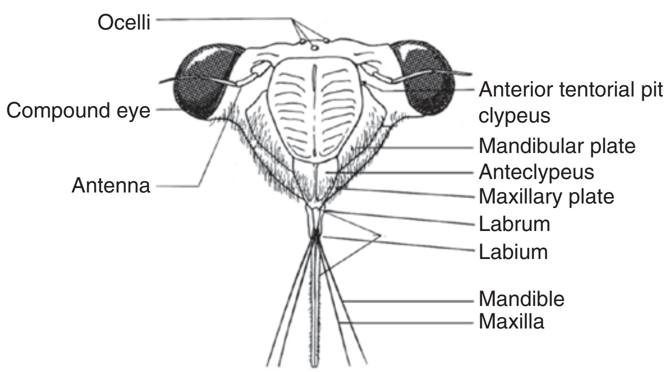
The upper posterior portion of the head capsule (Fig. 1).

Occluded Virus

A virus that produces a dense protein crystal, polyhedral in shape, and containing virions. This virion-containing structure is called a polyhedral inclusion body (PIB). PIBs are large enough to be visible with a light microscope.



Occiput, Figure 1 **The posterior view of the head of a grasshopper (Orthoptera).**



Ocellus (pl. ocelli), Figure 2 **Anterior aspect of the head and mouthparts of a cicada (Hemiptera).**

Occult Virus

A special phase of some viruses, characteristic of latent infections, in which the pathogenic agent is presumed to differ from the infective phase, and in which virions cannot be detected.

Ocellus (pl. ocelli)

The simple eye of an insect, occurring singly or in small clusters, and located dorsally on the head of most adults (Fig. 2) and in the larvae of exopterygote insects. They are similar to the ommatidia of compound eyes in anatomical structure and in function.

► Head of Hexapods

Ochodaeidae

A family of beetles (order Coleoptera). They commonly are known as theochodaeid scarab beetles.

► Beetles

Ochraceous

Yellow tinged with brown. This term is commonly used to describe insect coloration.

Ochsenheimeriidae

A family of moths (order Lepidoptera). They commonly are known as cereal stem moths.

► Cereal Stem Moths
► Butterflies and Moths

Ochteridae

A family of bugs (order Hemiptera) They also are known as velvety shore bugs.

► Bugs

Ockham's Razor

The belief that the simplest explanation of facts is probably the most correct interpretation. Attributed to William Ockham, a fourteenth century philosopher.

Odiniid Flies

Members of the family Odiniidae (order Diptera).

► Flies

Odiniidae

A family of flies (order Diptera). They commonly are known as odiniid flies.

► Flies

Odonata

An order of insects. They commonly are known as dragonflies and damselflies.

► Dragonflies and Damselflies

Odontoceridae

A family of caddisflies (order Trichoptera).

► Caddisflies

Oecophoridae

A family of moths (order Lepidoptera). They commonly are known as concealer moths.

► Concealer Moths
► Butterflies and Moths

Oedemeridae

A family of beetles (order Coleoptera). They commonly are known as false blister beetles.

► Beetles

Oenocytoids

Hemocytes that are important in the melanization process of hemolymph.

► Hemocytes of Insects: Their Morphology and Function

Oestridae

A family of flies (order Diptera). They commonly are known as bot, heel, or warble flies.

► Flies

Oil

Petroleum or plant-derived oil that can be used to control pests on plants; more correctly called horticultural oil.

► Horticultural Oil

Old House Borer, *Hylotrupes bajulus* (Linnaeus) (Coleoptera: Cerambycidae)

This is a species of wood-boring beetle sometimes found infesting structures.

► Wood-Attacking Insects

Old World Butterfly Moths (Lepidoptera: Callidulidae)

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Old World butterfly moths, family Callidulidae, include 102 species, mostly tropical Oriental, in two subfamilies: Griveaudiinae (from Madagascar) and Callidulinae. The family is in the superfamily Calliduloidea, in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults medium size (22–38 mm wingspan), with head scaling average; haustellum naked; labial palpi usually long and porrect; maxillary palpi vestigial. Wings quadratic but with forewing mostly acute or even falcate (rarely rounded) (Fig. 3). Maculation usually colorful, with brown shades plus color patches of red or orange, or more somber (rarely pale). Adults diurnal, flying like some butterflies in quick bursts to alternate leaf perches; resting position with wings held together and upright. Larvae largely unknown, except for two species of Callidulinae which are leafrollers of ferns.

Old World Butterfly Moths (Lepidoptera: Callidulidae), Figure 3 Example of Old World butterfly moths (Callidulidae), *Callidula attenuata* Moore from Taiwan.

References

*Holloway JD (1998) Family Callidulidae In: The moths of Borneo. Kuala Lumpur, Malayan Nature Society (Malayan Nature Journal, 52) 8:7–14, pl. 1, 8

*Kobes LWB (1990) The Callidulidae of Sumatra. In: *Heterocera sumatrana*. Heterocera Sumatrana Society, Göttingen, pp 101–115

*Pagenstecher A (1902) Callidulidae In: Das tierreich. 17:1–25

Seitz A (ed) (1911–1922) Familie: Callidulidae. In: Die grossschmetterlinge der erde. A. Kernan, Stuttgart, 2:207–208, pl. 22, 48 (1911); 10:491–496, pl. 51–57 (1922)

Tschistjakov YA, Belyaev EA (1987) Immature stages of *Pterodecta felderi* (Bremer) and systematic position of the family Callidulidae (Lepidoptera). Tinea suppl. 12:285–289

Old World Harvester Termites

Members of a family of termites (Hodotermitidae).

► Termites

Old World Spiny-Winged Moths (Lepidoptera: Eriocottidae)

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Old World spiny-winged moths, family Eriocottidae, are a small family of 212 known species, mostly African (120 sp.) and Oriental (66 sp.). There are two subfamilies: Eriocottinae and Compsocteninae. The family is part of the superfamily Tineoidea, in the section Tineina, subsection Tineina, of the division Ditrysia. Adults small to medium size (5–50 mm wingspan), with rather elongated wings, often tufted, and with rough head scaling; haustellum naked; maxillary palpi 2 to 3-segmented or 4 to 5-segmented (rarely 1-segmented); labial palpi mostly upcurved, sometimes porrect; antennae filiform, sometimes bipectinate; wings with microtrichia on surfaces. Maculation usually dull gray or brown, but sometimes spotted; rare females are brachypterous (*Deuterotinea*). Adults are mostly diurnally active, or may be crepuscular. Biologies are little known but some larvae reported to tunnel in the soil, possibly feeding on roots or detritus.

References

Dierl W (1970) Compsoctenidae: ein neues. Taxon von familien-status (Lepidoptera). Veröffentlichungen der Zoologische Staatssammlung München, 14:1– 41, pl. 2

Nielsen ES (1978) On the systematic position of the genus *Eriocottis zeller*, 1847, with remarks on the phylogeny of primitive Tineoidea (Lepidoptera). Entomologica Scandinavica 9:279–296

Oleander or Milkweed Aphid, *Aphis nerii* Boyer de Fonscolombe (Hemiptera: Aphididae)

This bright yellow aphid is common is southern climates on several host plants.

► Aphids

Olfactometer

A device for detecting the response of insects to odors. Air is passed over a potential stimulant and insects are induced to move upwind to the source, making a choice or choices along the way to ascertain that the odor, not just air movement or moisture, is providing the stimulus. Traditionally, olfactometers have been Y-tube devices, where walking insects chose between two sources of air flow that blended together. Flight chambers accommodate flying insects in a similar manner, with air flowing over two or more sources of odor, but the insects do not have to traverse tubes.

Oligidic Diet

A diet containing complex organic materials of a poorly defined nature (e.g., pinto beans, dog food, etc.). This is a common method of insect culture. (Contrast with meridic and holidic diets)

Oligoneuriidae

A family of mayflies (order Ephemeroptera).

► Mayflies

Oligophagous

Feeding on a restricted group of organisms; among herbivorous insects, feeding on plants within a single plant family.

Oligotomidae

A family of web-spinners (order Embiidina).

► Web-Spinners

Olive Fruit Curculio, *Rhynchites cribripennis* Desbrochers (Coleoptera: Attelabidae)

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The adult of this curculio is red to reddish brown, except the abdomen and the mandibles which are black. Each elytron has 10 longitudinal grooves, and the base of the elytra is twice as wide as the thorax.

The body length including the rostrum is 5.5–6 mm, and that of the fully grown larva 7 mm. It is distributed over the central and eastern Mediterranean and neighboring regions and as far as Crimea. The olive and the oleaster (wild olive) are reported as the only host plants on which the larvae can grow, but the adults seem to feed also on other Oleaceae.

The olive fruit curculio is semivoltine. The first winter is passed mainly as a fully grown larva in the soil, and the second winter as an adult also in the soil. Overwintered adults come out of the soil from late April to late May and fly to the foliage of olive trees, where they feed for several weeks, first on tender leaves and apical parts of shoots, then on small young fruits. Their feeding holes cause an early drop of fruits, which may be serious in small-fruit cultivars. Economic damage (Fig. 4) is reported only in warm areas with rather dry, non-irrigated soils. From late July to late August the female, after making a hole in the mesocarp with its rostrum to reach the outer part of the endocarp, inserts an egg. The young larva hatches in approximately 10 days, bores through the endocarp which is already lignified, and reaches the seed which it devours completely. Only one larva develops per fruit. Upon completion of its growth, sometime in October or November, the fully grown larva abandons the fruit and overwinters in a cell in the soil. Pupation takes place in the soil at the end of the following summer or early autumn. The adult is formed in winter, and emerges from the soil in spring to feed, mature sexually and reproduce. Thus, the life cycle is completed in two years, and includes a period of larval growth lasting two to three months, followed by a long period of larval dormancy from autumn to the following summer or early autumn, followed by a shorter period of adult dormancy from autumn to spring, followed by a rather long preoviposition period from mid-spring to mid- or late summer.

Olive Fruit Curculio, *Rhynchites cribripennis* Desbrochers (Coleoptera: Attelabidae), Figure 4 Fruit damage caused by adult *Rhynchites cribripennis*, as seen in September.

References

Monaco R (1986) *Rhynchites (Coenorrhinus) cribripennis* Desbr In: Arambourg Y (ed), Traité d2 entomologie oleicole. Conseil Oleicole International, Madrid, Spain, pp 14–19

Silvestri F (1912) Contributo alla conoscenza del rinchite dell' olivo. Bolletino del Laboratorio Zoologia Generale Agraria, Reale Scuola Superiore Agricoltura, Portici 6:151–175

Olive Fruit Fly, *Bactrocera oleae* (Rossi) (=*Dacus oleae*) (Diptera: Tephritidae)

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The olive fruit fly is a major pest of olive in Mediterranean countries. It also occurs in the Canary Islands, East and South Africa, from the Middle East to India, and recently in North America. It was detected California in 1998, probably originating from Mexico, and spread rapidly to all the counties in that state where olive is grown.

Olive fruit fly is oligophagous, infesting in nature only fruits of the genus *Olea*, such as the cultivated olive *O. europaea* ssp. *sativa*, and *O. europaea* ssp. *oleaster* or *sylvestris*. The female introduces an egg into the pulp (mesocarp) of green or ripe olive fruits, after having made with her ovipositor an oviposition slit in the epicarp and a minute chamber underneath in the pulp.

As a rule, it lays one egg per fruit, and under high population densities more. On average, a few hundred eggs per female are laid. Oviposition starts when the fruit has acquired approximately its final size and the epicarp and flesh become soft enough for the ovipositor to penetrate. The larva bores a gallery in the pulp, and when fully grown pupates inside the fruit, as is usually the case in summer when the mesocarp is hard. Or it may drop to the soil where it pupates at a shallow depth, usually in autumn and winter, when the mesocarp is softer and rich in oil. Overwintering takes place as a pupa in the soil, or as an adult in or outside the olive grove. Under favorable conditions, especially of temperature, the life cycle is completed in a little over a month. The adults are long lived and can oviposit for months. Thus, there is overlapping of generations during late summer and autumn, and oviposition by females of the same or different generations continues for weeks or months, until the drop of temperature in late autumn or in winter prevents oviposition. When winter temperatures allow oviposition and larval growth, all preimaginal stages may be found on the trees in winter. For survival and reproduction the adult needs to feed frequently on various organic substances, liquid or solid, such as insect honeydew, flower nectar, other plant exudates, pollen, juices and tissues of damaged or decaying fruit, and, most probably, also microorganisms such as plant surface bacteria.

The adult is 4–5 mm long, and from light to dark brown. It has a whitish to yellowish scutellum (Fig. 5) and the female has a prominent ovipositor. The egg is whitish, 0.7 mm long, and banana-shaped. The larva is whitish to yellowish when growing in green fruits and purplish if in dark-ripe fruits, reaching 7–8 mm. There are three larval instars. The pupa is ellipsoid and light brown.

This fruit fly is multivoltine, completing from 2 to 5 generations per year, depending on the region and local conditions. In northern Italy and southern France, where summer temperatures do not exceed threshold values, three generations are reported at most. In southern Italy, Spain, western Croatia and central Greece, one generation starts in June to July in fruit of the new crop and two more develop in autumn through November or even December, while a fourth one may develop in spring on ripe fruits remaining on the trees. In Jordan, five generations are reported per year. It seems that the continuous development of the fly, which makes finding the number of generations per year uncertain, is interrupted in the north of the Mediterranean principally by winters, at the center by winters as well as summers, and in the south only by hot and dry summers.

Olive Fruit Fly, *Bactrocera oleae* (Rossi) (=*Dacus oleae*) (Diptera: Tephritidae), Figure 5 Male olive fruit fly adult.

There is a period of reproductive immaturity, probably diapause, in late spring and early to mid-summer. During that period of the year the females have undeveloped oocytes and the males do not respond to sex pheromone traps. As the olives become suitable for oviposition, usually in mid-summer, ovarian maturation prevails and oviposition begins. The fly is known to disperse from areas without olive fruit to areas with a new season's crop, and also from olive trees to other trees and vice versa, or from plain to mountain olive groves and vice versa. Long-distance migrations have also been reported. The population increases mostly in autumn, and especially when the autumn weather is humid and relatively warm. The high summer temperatures and low air humidity do not favor this insect.

When the fruit is green, the larva needs the presence of symbiotic bacteria in its digestive tract to use the proteins of the olive mesocarp. These bacteria are housed in a special esophageal diverticulum of the adult female and in the inner surface of her ovipositor. They are smeared over the egg surface during oviposition and enter the young larva's gut at hatching.

The oviposition hole, and the tiny chamber under it, are the usual sites of infection of the fruit by the Dalmatian fungus, *Camarosporium dalmaticum*, also known as *Sphaeropsis* or *Macrophoma dalmatica*. The fungus spreads in the pulp, causing characteristic spots. This lowers the quality of olive oil and makes table olives unsuitable for the market. A midge, *Prolasioptera berlesiana* Paoli, lays an egg in the fruit fly's oviposition chamber next to the fruit fly's egg, and is believed by some scientists to be the vector of the *Camarosporium* fungus. By some authors it is also considered a natural enemy of the fruit fly, because the midge larva often feeds on the fruit fly's egg before feeding on the fungus hyphae. Damage from the olive fruit fly, in conjunction with damage by the fungus that often accompanies it, is serious in many Mediterranean countries, so this fly is considered the most dangerous pest of olive, and control measures are required every year.

The control is usually chemical, consisting of the use of insecticides, usually organophosphorous ones, applied from the ground or the air, depending on the time of year. The insect's population density is assessed by sampling of fruit and adult captures in traps (Fig. 6). In trees of table olive cultivars the "curative" method is generally applied. It aims at killing the larvae already inside the fruits, and consists of cover sprays from the ground, when the percentage of infested fruits reaches the intervention threshold (economic threshold, action threshold). This level in some European countries is set at 2% of fruit infestation, all stages of the life cycle included, but in some other countries at less than 2%. In groves and years favoring the insect, 2–4 such sprays are needed. The sprays should stop well before harvest, to avoid insecticide residues in

Olive Fruit Fly, *Bactrocera oleae* (Rossi) (=*Dacus oleae*) (Diptera: Tephritidae), Figure 6 Glass McPhail fruit fly trap.

the fruit that exceed the official tolerances. This method kills many beneficial entomophagous insects and may result in resurgence of certain scale insects and other enemies of the olive tree. In years of low fruit fly density, the number of cover sprays can be reduced to a minimum, if the sprays are combined with a dense network of traps to mass trap the adult flies.

The "preventive" method is more suitable for olive cultivars destined to oil production. It consists of bait sprays (insecticide plus a food attractant), and aims at killing the adults before they oviposit. The attractant is usually a protein hydrolyzate. If applied from the ground, the bait spray covers only a portion of every tree or every second or even third tree. It is fairly selective, usually does not cause resurgences of other insect or mite pests of the tree, and is less likely to leave undesirable residues in the oil. Bait sprays have also been applied from the air by airplanes or helicopters, but have been prohibited in some countries because of adverse effects on beneficial arthropods and other animals. Yet, because of the relatively low cost and the simultaneous coverage of large areas, some countries continue to use low-volume air spraying. In some countries with extensive olive groves, the application of bait sprays is carried out under the supervision of state agricultural services. The first bait spray, to be effective, should be applied over a wide area. The proper time is determined on the basis of captures of adult flies in McPhail traps baited with a solution of an ammonium salt or of a protein hydrolyzate, on the maturity of the females caught in the traps, and on the hardness of the fruit, making the oviposition possible or not.

In certain groves and years where the fly's population is not dense, mass trapping alone may be effective for oil cultivars. Various traps have been developed. The most effective traps combine a food attractant, a sex pheromone, a proper color, and an insecticide. A trap is hung in every tree. However, when the fly population exceeds a certain density at the start, or later despite the trapping, one or two bait sprays are also necessary.

The sterile insect release method has been tested, in combination with two bait sprays, in northern Greece. The fly density was kept at acceptably low levels, but reasons of technical nature and cost did not favor the application of the method commercially. Biological control has also been tried in certain countries by either introducing the parasitoid *Psyttalia concolor* (Széplegeti) (Hymenoptera: Braconidae) in areas where it did not occur, or by mass rearing and mass releasing it more than once during summer and autumn. The results, although encouraging, were not such as to justify the further application of the method on a wider scale. Mating disruption by distributing in the grove sex pheromone dispensers was also tried, but without success. Other methods, such as attempting to kill the fly's symbiotic bacteria by cover-spraying trees with a bactericide, have not been tested on a widely enough basis to justify use. Integrated pest management strategies for the key insect pests of olive, including the olive fruit fly, for three climatic regions of the Mediterranean Basin are suggested by Katsoyannos (1992).

References

Economopoulos AP, Avtzis N, Zervas G, Tsitsipis J, Haniotakis G, Tsiropoulos G, Manoukas A (1977) Experiments on the control of the olive fly, *Dacus oleae* (Gmelin), by the combined effect of insecticides and releases of gamma-ray sterilized insects. Zeitschrift für angewandte Entomologie 83:201–215

Fletcher BS, Kapatos ET (1983) The influence of temperature, diet and olive fruits on the maturation rates of female olive flies at different times of the year. Entomologia Experimentalis et Applicata 33:244–252

Harpaz I, Gerson U (1966) The "biocomplex" of the olive fruit fly (*Dacus oleae* Gmel.), the olive fruit midge (*Prolasioptera berlesiana* Paoli) and the fungus *Macrophoma dalmatica* Berl. & Vogl. in olive fruits in the Mediterranean basin. Scripta Hierosolymitana 18:81–127

Kapatos ET (1989) Integrated pest management systems of *Dacus oleae* In: Robinson AS, Hooper G (eds), Fruit flies. Their biology, natural enemies and control, vol 3B. Elsevier Science Publishers Amsterdam, The Netherlands, pp 391–398

Katsoyannos P (1992) Olive pests and their control in the near east. FAO Plant Products and Protection Paper 115, FAO Rome, Italy

Neuenschwander P, Michelakis S, Kapatos E (1986) *Dacus oleae* (Gmel.). In: Arambourg Y (ed) Traité d 2 Entomologie Oleicole. Conseil Oleicole International, Madrid, Spain, pp 115–159

Tzanakakis ME, Koveos DS (1986) Inhibition of ovarian maturation in the olive fruit fly *Dacus oleae* (Diptera: Tephritidae), under long photophase and an increase of temperature. Ann Entomol Soc Am 79:15–18

Olive Knot

This bacterial disease of olive can be transmitted by insects, especially files.

► Transmission of Plant Diseases by Insects

Olive Psyllids, *Euphyllura* spp. (Hemiptera: Psyllidae)

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The olive psyllids are small in size, with piercing-sucking mouthparts. Adults and larvae feed on the sap they extract from leaf and flower buds, shoots, flowers, and young fruits. They overwinter as adults, sheltered on the underside of olive twigs and especially at the base of leaves and buds. Oviposition starts usually in early spring. The eggs are inserted with their short pedicel mostly on the inner surface of the young small leaves of apical buds. The larvae produce a white waxy secretion and spherical honeydew droplets covering the infested buds, inflorescences and other tender growth they feed on. The adults need to feed frequently on plant sap, even during the periods of diapause and post-diapause quiescence, for survival.

Three species live on olive in the Mediterranean Basin and the Middle East: *Euphyllura olivina* (Costa), *E. phillyreae* Foerster, and *E. straminea* Loginova. A key distinguishing the three species is given by Lauterer et al. In France and Italy, both *E. olivina* and *E. phillyreae* occur, in the Balkans and Israel both *E. phillyreae* and *E. straminea*, in the Black Sea coast and Caucasus *E. phillyreae*, and in Iraq and Iran both *E. olivina* and *E. straminea*. They infest the cultivated olive, the oleaster (wild olive), species of *Phillyrea*, and one of them also attacks species of *Osmanthus* (all Oleaceae). All three species share the same habits, but differ in voltinism and phenology.

Euphyllura olivina completes from 2 to 4 generations per year, depending on the region and conditions. On an island off the gulf of Naples, Italy, two generations were observed in the first year of observations, with larvae seen from mid-April to late May, and early July to late September, while the second year only one generation was completed, with larvae seen from mid-March to early May. Further north, in Tuscany, in a year of heavy infestation and with olive trees having new tender growth into autumn, three generations were completed, with larvae recorded from early February to mid-April, early April to late July, and early November to mid-February. The third (winter) generation is considered a facultative one. Adults spent the summer in reproductive diapause. In warmer regions such as Tunisia, three generations are completed regularly, and a facultative fourth occurs in some years. The larvae are seen in early March to early June, early May to late June, and late October to early January, and those of the occasional fourth generation in mid-December to early February. In Tunisia, the adults of the first and second generations undergo a summer dormancy, while most of those of the third generation a winter dormancy. In Tunisia, where populations of this insect are often dense, 10 insects per floral raceme in the spring generations are considered as the economic threshold. Above this density, the percentage of drop of inflorescences and reduction of fruit set justify chemical control. A contact insecticide with some vapor action is recommended. Usually, insecticides applied against the olive moth suffice to control this psyllid as well.

Euphyllura phillyreae is univoltine. The single annual generation develops in spring. In northern Greece, the eggs are deposited on olive in April, the larvae develop in April and May, and the adults are formed mostly in the second half of May. The adult females remain in reproductive diapause until mid-December or early January, then in quiescence until February or early March. Reproductive maturation follows when the host tree is at a certain stage of development, so that the larvae can take full advantage of the developing leaf and flower buds and developing inflorescences. In and around Florence, Italy, the adults are formed in June. They undergo a reproductive diapause in summer, followed by a reproductive quiescence from September until January-March. Generally, this species does not cause economic damage.

Euphyllura straminea infests the olive in spring, but little is known about its seasonal development in the rest of the year.

References

Arambourg Y, Chermiti B (1986) Psyllidae. In: Arambourg Y (ed) Traité d' entomologie oleicole. Conseil Oleicole International, Madrid, Spain, pp 163–171

Del Bene G, Gargani E, Landi S (1997) Observations on the life cycle and diapause of *Euphyllura olivina* (Costa) and *Euphyllura phillyreae* Foerster (Homoptera: Aphalaridae). Adv Hortic Sci 11:10–16

Fimiani P (1985) Biological data on *Euphyllura* spp. (Homoptera, Psylloidea) in the Vivara Island (Gulf of Naples). In: Cavalloro R, Crovetti A (eds) Integrated pest control in olive groves. Proceedings CEC/FAO/IOBC International Joint Meeting, Pisa, Italy, 3–6 April 1984 A. A. Balkema, Rotterdam, The Netherlands, pp 266–269

Lauterer P, Prophetou DA, Tzanakakis ME (1986) Occurrence of *Euphyllura phillyreae* Foerster (Homoptera:

Aphalaridae) on olives of the Greek mainland. Ann Entomol Soc Am 79:7–10
Prophetou-Athanasiadou DA (1997) Occurrence of immature stages of olive psyllid *Euphyllura phillyreae* (Hom., Aphalaridae) in *Phillyrea latifolia* and *Olea europaea* in coastal northern Greece. J Appl Entomol 121:383–387
Prophetou-Athanasiadaou DA, Tzanakakis ME (1986) Diapause termination in the olive psyllid *Euphyllura phillyreae*, in the field and in the laboratory Entomologia Experimentalis et Applicata 40:263–272

Omaniidae

A family of bugs (order Hemiptera). They sometimes are called intertidal dwarf bugs.

► Bugs

Omethridae

A family of beetles (order Coleoptera). They commonly are known as false firefly beetles.

► Beetles

Ommatidium (pl. ommatidia)

The individual unit of vision in the compound eye. Often there are large numbers of ommatidia clustered into each compound eye, and each ommatidium is marked externally by a hexagonal facet. The ommatidium structure varies among taxa, but is similar in function. Each contains a rhabdomere as part of a retinular cell, which is the light sensitive area; a lens or cornea that allows light to enter; and a pigment cell surrounding the rhabdomere and shielding the rhabdomere from light that might enter from nearby ommatidia. In some ommatidia the pigment may contract, allowing greater entry of light during low-light conditions.

Omnivorous

Having a broad diet, consisting of both plant and animal material.

Omsk Hemorrhagic Fever

This viral disease is found principally in Siberia, where it is transmitted by ticks.

► Ticks

Onchocerciasis

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Human onchocerciasis, river blindness, is a debilitating disease of the poorest people in Latin America (Brazil, Ecuador, Guatemala, Mexico, Venezuela and Colombia), in Yemen and in countries in East Africa and the West African savanna zone, including Burkina Faso (Upper Volta), Ivory Coast, Ghana, Togo, Benin, Sierra Leone and Guinea. The causative agent, *Onchocerca volvulus*, is a filarial nematode (Order Filariata, Family Onchocercidae) that is transmitted by a black fly or buffalo gnat, *Simulium damnosum* and related species. The disease occurs when embryonic nematodes (microfilariae) migrate to tissues of the eye, causing keratitis and formation of an opacity on the cornea and pupil, causing blindness. This effect on the eye gave rise to a West African term, the "lion's stare". Other terms for the disease include Robles' disease, craw-craw and gale filarienne. Ocular onchocerciasis is the third leading cause of blindness in Africa, affecting over 18 million people; one million have impaired vision and more than 350,000 are blind. This is often evidenced by children leading their blind adults by a stick. Over 80 million Africans are at risk of infection by this parasite.

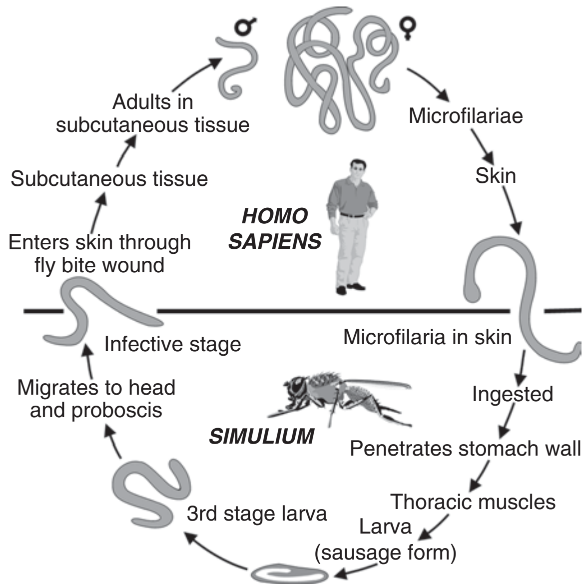
Adults of *O. volvulus* are dioecious, and the male and female worms are usually tightly intertwined in pairs or groups within subcutaneous tissues. The male is 19–42 cm long and 130–210 μm wide, while the female is about 33–50 cm long and 270–400 μm wide. The worms reach maturity within one year, are detectable in subcutaneous tissues, and may live as long as

16 years. They induce the formation of subcutaneous nodules (onchocercomas), particularly above bony prominences such as the elbows, trochanters, iliac crests, knees and the skull. Nodules also form near the waist where the fly bites. The nodules represent the cellular defense response of the host to the presence of the worms. Instead of eggs, *O. volvulus* females deposit millions of embryos (unsheathed microfilariae) that measure 220–360 μm long and 5–9 μm wide with sharply pointed, curved tails.

Persons with severe infections have millions of microfilariae in the skin, the eyes, lymph nodes, and other organs. In addition to severe itching and possibly secondary infection, a victim often experiences severe dermatitis involving hypo- or hyper-pigmentation, and thickening and wrinkling of the skin. The latter symptom often occurs concomitant with scaling or "lizard skin." In some instances, victims exhibit "hanging groin" or adenolymphocele in which the distended groin consists of microfilariae surrounded by lymph nodes and sometimes collagen and smooth muscle fibers. There are reports of onchocerciasis-associated dwarfism in victims infected by *O. volvulus* in Uganda, presumably resulting from microfilarial damage to the pituitary.

The microfilariae occur in the upper dermis where they are ingested when the *Simulium* female inserts her proboscis (Fig. 7). Within the vector's gut, microfilariae migrate through the gut to the thoracic muscles where they undergo successive larval molts to the infective filariform third stage (L_3). The L_3 then migrate to the labrum of the fly and escape into the wound created in the skin of the victim by the fly's piercing-sucking mouthparts.

Larvae of the vector *S. damnosum* (Diptera: Simulidae) develop in fast-running rivers and streams. The eggs are oviposited on vegetation and on moist rocks, to which the resulting larvae and pupae attach. Adult flies live and mate in humid, shaded areas. The female black fly bites people and wildlife to obtain a blood meal for egg development, thus transmitting the infective L_3 stage.



Onchocerciasis, Figure 7 ***Onchocerca volvulus*** **life cycle. (Modified from Wigg, 1993.)**

Prior to 1974, diethylcarbamazine (DEC) was used for desquamation of affected patients. However, it also killed the microfilariae, which induced profound allergic reactions of skin eruptions and anaphylactic shock. Since 1974, the fungicidal antibiotic ivermectin has replaced DEC because it has fewer negative side effects and appears to reduce the microfilarial load, probably by decreasing the reproductive output of adult worms. It also has an apparent prophylactic effect and requires only one oral dose yearly. The use of ivermectin was an integral part of the Onchocerciasis Control Program (OCP), sponsored by the World Health Organization (WHO) in collaboration with several international and intergovernmental agencies along with the local governments of several West African countries. Importantly, Merck & Co., Inc., donated the ivermectin used in the OCP and continues to do so, free of charge, through its Mectizan® Donation Program.

The OCP also employed cocktails of natural and synthetic insecticides as well as educational initiatives to decrease the vector population and to facilitate successful devolution efforts, respectively. The OCP is also recognized as one of the most successful and environmentally conscious control programs that utilized pesticides with the least adverse ecological effects. The program has significantly reduced the incidence of onchocerciasis in West Africa, increased the economic well-being of the people, and realized an estimated economic rate of return of about 18%.

The microfilarial load in the human populations in *Onchocerciasis*-affected areas in both Africa and Latin America is monitored using skin-snip biopsies. Molecular approaches such as the polymerase chain reaction (PCR) are used to monitor *O. volvulus*-infected *Simulium* populations. This technique uses the DNA sequences from *O. volvulus*, to detect infected *S. ochraceum*, a common vector in Guatemala. It has also been used to detect as few as one *S. damnosum* experimentally infected with the parasite, from among 100 uninfected flies. The amplified fragment length polymorphism (AFLP) of the *O. volvulus* DNA is also used to distinguish it from other filarial worms.

References

Aehyung K, Benton B (1995) Cost-benefit analysis of the Onchocerciasis Control Program (OCP). World Bank Tech. Paper # 283. Series on River Blindness Control in West Africa, 18 pp

Anon (1994) OCP:1974–94. World Health Organization, Onchocerciasis Control Programme. WHO/OCP/CTD/94.1, 2nd. 24 pp

Davies JB, Oskam L, Lujan R, Schoone GJ, Kroon CCM, Lopez-Martinez LA, Paniagua-Alvarez AJ (1998) Detection of *Onchocerca volvulus* DNA in pools of wild-caught *Simulium ochraceum* by use of the polymerase chain reaction. Ann Trop Med Parasitol 92:295–304

Duke BO (1971) Onchocerciasis. Br Med Bull 28:66–71

Schmidt GD, Roberts L (1985) Foundations of parasitology, 34th edn. Times Mirror/Mosby College Publishing, St. Louis, Missouri, 775 pp

WHO Information Fact Sheets (2000) Onchocerciasis (river blindness). Fact Sheet No. 95, Accessed 5 March 2008. Available at, http://www.nematodes.org/fgn/news/onchofilfact.html

Wigg D (1993) And then forgot to tell us why. A look at the campaign against river blindness in West Africa. World Band Development Essays. The World Bank, Washington, DC, 44 pp

Onion Maggot, *Delia antiqua* (Meigen) (Diptera: Anthomyiidae)

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Onion maggot (onion fly) is now found throughout the northern hemisphere. It apparently was introduced to North America from Europe soon after European colonists arrived, in the 1600s or 1700s, and was recognized as a serious pest in North America by the early 1800s. It is favored by cool weather, and is a serious pest only in northern areas.

Life History

The number of generations is two or three per year, with a proportion of each generation diapausing as puparia until the next year. At the latitude of Quebec, Canada, adults from overwintering insects appear in May and initiate the first generation, with peak emergence of the first generation occurring in early July. The second generation begins emerging in mid to late August, with peak emergence about the first of September. Third generation insects all enter diapause, forming the overwintering population that emerges the following spring. The proportion of insects entering diapause in the first and second generations is reported to be about 25 and 60%, respectively. During exceptionally warm summers fewer insects enter diapause. Very similar patterns of emergence were observed in the USA.

Oviposition occurs when temperatures attain about 21–26°C. In Pennsylvania, USA, maximum oviposition from the overwintering generation was observed in early June, whereas the first generation adults produced eggs in mid to late July, and the second generation adults produced eggs in early September. The eggs are white and elongate, with one side convex and the other side slightly concave. One end is slightly more pointed than the other end. Eggs measure about 1.2 mm long (range 1.12–1.23 mm) and 0.5 mm wide.

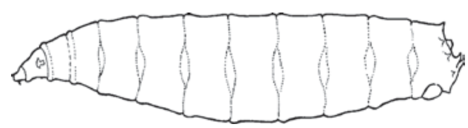
Females tend to deposit clusters of 7–9 eggs daily, and duration of the oviposition period is 30–60 days. In the laboratory, egg production for onion maggot colonies may average 100–250 eggs per female, with individually reared insects producing an average of 500 eggs. Estimates of egg production in the field, however, are considerably less, perhaps 50 per female. The eggs are positioned on or near the host plant, often in soil crevices adjacent to onion plants. If the soil is wet, as occurs immediately following a heavy rain, the adults may deposit their eggs on the foliage. Ovipositing flies are highly attracted to bulbs previously infested with maggots, although low to moderate levels of damage are preferred over high levels of damage. Microbial activity of rotting onion bulbs enhances attractancy of onion volatiles. The soil temperature optimum for oviposition is about 20–22°C. Eggs hatch in about 5.5 days (range 5–7 days) in cool weather, but hatch may be shortened to 2–3 days during the warmth of the summer.

Larvae are whitish, and have three instars. The mouthparts (cephalopharyngeal skeleton) measure 0.38, 0.71, and 0.96 mm in length, respectively, during instars 1–3. When they first hatch, larvae measure only about 1 mm in length, but by the time they have matured, larvae attain a length of about 9–10 mm. Development time is about 3, 4–5, and 9–14 days for instars 1–3, respectively. Total duration of the larval stage is estimated at 15–23 days. The anterior spiracles, which do not become visible until the second instar, bear 12 (range 10–13) finger-like lobes. The number of spiracular lobes is a useful character for differentiating onion maggot larvae from seedcorn maggot, *Delia platura* (Meigen) (Diptera: Anthonyiidae), a species commonly found in association with onions and onion maggots. The spiracles of seedcorn maggot larvae bear only 5–8 lobes.

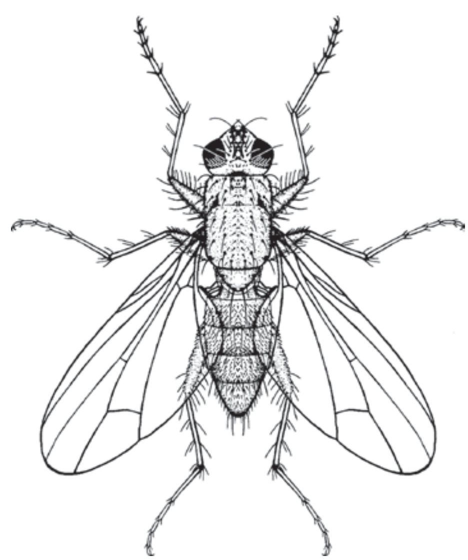
Mature larvae (Fig. 8) form a puparium in the soil. The location of the puparium may be close to the bulb, perhaps among the onion roots, but it sometimes is a considerable distance away, and at a depth of 10–12 cm. Puparium color varies from yellow-brown to dark brown or almost black in color. The puparium measures 4–5 mm in length. Duration of the puparium is from 15–19 days during the spring, 8–14 days during the summer, and 5–6 months during the winter.

The adult is greenish gray in color, and marked with longitudinal dark stripes on the thorax. The legs are black and the wings rather colorless (Fig. 9) with black veins. The adults average about 6 mm in length. Adults usually live 30–50 days if they have adequate food, but may live for 60–70 days. The preoviposition period is often about 10 days, followed by an egg-laying period of about five days.

Onion maggot attacks plants in the family Alliaceae (Amaryllidaceae). Onion is the principal host, but chive, garlic, leek, and shallot are



Onion Maggot, *Delia antiqua* (Meigen) (Diptera: Anthomyiidae), Figure 8 **Mature larva of onion maggot, *Delia antiqua* (Meigen).**



Onion Maggot, *Delia antiqua* (Meigen) (Diptera: Anthomyiidae), Figure 9 **Adult of onion maggot, or onion fly, *Delia antiqua* (Meigen).**

sometimes attacked. Wild onion apparently is not a suitable host. It is possible to rear onion maggot larvae on abnormal hosts such as radish and turnip, but adults normally do not deposit eggs on such plants.

Onion maggot adults are particularly attracted to decaying onions, such as those infected with the soft-rotting bacteria *Erwinia carotovora* or *Fusarium* fungus. Survival may be slightly higher, or development time shorter, for onion maggot larvae feeding on microbe-infected onions. Older onion maggot larvae are usually fully capable of attacking, and developing satisfactorily on, disease-free onions; however, survival of young maggots is poor on mature onions unless they are wounded or infected with disease. Indeed, survival of the third generation of onion maggots is likely dependent on the availability of unhealthy onions.

Numerous insects are known, or suspected, to prey on onion maggots. In North America, parasitoids include *Aleochara bilineata* (Gyllenhal), *A. bipustulata* (Linnaeus), *A. curtula* (Goeze) (all Coleoptera: Staphylinidae), *Aphaereta pallipes* (Say) (Hymenoptera: Braconidae), *Spalangia rugosicollis* Latreille, and *Sphegigaster* sp. (both Hymenoptera: Pteromalidae). Among the common predators are mites (Acari), rove beetles (Coleoptera: Staphylinidae), hister beetles (Coleoptera: Histeridae), sap beetles (Coleoptera: Nitidulidae), ground beetles (Coleoptera: Carabidae), and ants (Hymenoptera: Formicidae). The parasitoids *Aleochara bilineata* and *Aphaereta pallipes* are among the more important mortality agents. Predation is much more difficult to measure, so the relative importance of predators is less certain. However, such predators as *Bembidion quadrimaculatum* L. (Coleoptera: Carabidae) consume 25 onion maggot eggs per day, so predators surely have an important role in onion maggot population biology.

The fungus *Entomophthora muscae* commonly infects onion maggot and many other flies. Dead, spore-covered flies are often found attached to elevated portions of plants following fungus outbreaks. Flies contact fungus, and become infected, both on host plant foliage and in the soil. Death of adults occurs 7–9 days after exposure to conidia. The soil is the principal overwintering reservoir for the fungus. The spring and autumn generations of onion maggot exhibit higher levels of infection.

Damage

Onion maggots can be extremely damaging in northern onion-producing areas. In New York, USA, for example, 40–80% losses are realized regularly if insecticides are not used. Damage to onions often occurs in early to mid summer; damage that occurs earlier in the development of the onion plant is more often due to seedcorn maggot, which may be active as early as April. When onion maggot larvae feed on relatively small onions they may completely hollow out the young bulb, causing rapid death. A single onion maggot larva may kill several seedling onions, whereas as the onions grow larger the larvae are not compelled to disperse to other onions to find food. Later in the season the onions are more tolerant of onion maggot feeding, and there may not be aboveground signs of maggot feeding, but the bulbs can incur additional damage from secondary invaders such as soil-borne fungi and seedcorn maggot. Onions nearing maturity are most susceptible to these secondary organisms. Onions 12 weeks old or older are not very suitable for survival of onion maggots unless they are mechanically damaged or infected with disease. Mechanical damage to bulbs during harvesting can lead to attack by third generation flies on bulbs drying in the field.

There appears to be a close relationship between onion maggot and soft rot of onion caused by *Erwinia carotovora*. The maggot creates wounds where the bacterium can enter the onion. The surface of several stages of the insect may be contaminated with the bacterium, thus aiding dispersal. Also, the bacterium is found in the puparium, which provides protection and may allow survival during inclement periods. The insect also benefits from this relationship, because onion tissue infected with soft rot bacteria are more suitable for development of larvae. The relationship is not entirely specific, however, and several other flies such as seedcorn maggot, and several otitidids (Diptera: Otitidae), are attracted to rotting onions.

Management

Onion maggot flies use both olfactory and visual cues to find their host plant, and this information has been exploited to develop sampling techniques. Flies will orient upwind in response to onion volatiles, and various trap designs employing inverted cones suspended above onion bulbs or baited with the onion chemical n-dipropyl disulfide have been devised to capture adults. Enzymatic yeast hydrolysate is also attractive. Yellow traps are also recommended for capture of onion maggot flies, and sometimes yellow or white sticky traps are baited with onions. Adults prefer to land on horizontal surfaces; therefore, water pan traps may be more appropriate than vertical sticky traps.

Heat unit accumulations have been used to predict developmental rates of onion maggot as an aid to estimating optimal timing of insecticide applications. Careful timing of adult control reduced the number of insecticide treatments from 7–12 annually to only two, with excellent results.

In many areas, insecticides are routinely used to protect against damage by onion maggot. Application of granular or liquid insecticide formulations to the furrow at planting, or over the row after planting, are common. Treatment of seed with insecticides is also beneficial, but some materials are phytotoxic when applied in this manner. Disruption of first generation onion maggot helps protect against damage by later generations even if the insecticide residue has dissipated. However, long-lasting insecticides are more effective, and in the absence of these, adult suppression is practiced to protect against second and third generation onion maggots. Insecticide applications to foliage are common, but in many areas insecticides are also applied to the harvested bulbs drying in windrows. To avoid illegal insecticide residues on onions, it is important to use insecticides that are not very persistent for treatment of dry bulbs. Insecticide resistance is common in many onion-growing areas.

The only significant host of onion maggots is onions, and usually commercially produced onions. Therefore, crop rotation is sometimes suggested as a component of pest management. The potential for onion maggots to cause damage is directly related to the presence of onions previously. However, onion maggots disperse randomly over distances that exceed 2 km, so it is difficult to obtain adequate isolation.

Sanitation is an important component of onion maggot management. Damaged bulbs left in the field are an important food source for overwintering populations, much more so than are cull piles and volunteer onions. Efforts should be made to minimize damage to bulbs when tilling, or at harvest, as these injured bulbs are very suitable for onion maggot larval development.

Soil conditions influence onion maggot, but the relationship of soil to population biology warrants additional research. Egg hatch and larval survival are higher in moist soil. Only if larvae are exposed to saturated soil for protracted periods will high soil moisture levels be a problem. Sites with heavy soil, rich in clay, are less suitable for onion maggot than are sites with organic soil. Onion maggots apparently prefer to oviposit on organic soils.

► Vegetable Pests and their Management

References

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, CA, 729 pp

Finch S (1989) Ecological considerations in the management of *Delia* pest species in vegetable crops. Annu Rev Entomol 34:117–137

Perron JP (1972) Effects of some ecological factors on the onion maggot, *Hylemya antiqua* (Meig.), under field conditions in southwestern. Quebec Ann Entomol Soc Quebec 17:29–45

Oncopoduridae

A family of springtails in the order Collembola.
► Springtails

Onisciform Larva

An oval, flattened larva, resembling some terrestrial isopods.

Oniscigastridae

A family of mayflies (order Ephemeroptera).
► Mayflies

Onychiuridae

A family of springtails in the order Collembola. They commonly are known as blind springtails.
► Springtails

Oocytes

Cells produced by the ovaries that eventually become an ovum (egg cell) after meiosis. They are produced from oogonia and surrounded with follicle cells and sometimes nurse cells.
► Reproduction
► Endocrine Regulation Of Reproduction
► Oogenesis

Oogenesis

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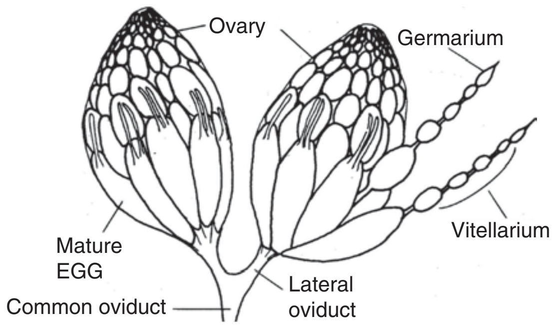
One reason for the evolutionary success of insects is their remarkable capacity to generate large numbers of progeny. Since most insects reproduce sexually, this requires the efficient formation of specialized gametes, a process in females called oogenesis. Females produce eggs that have to accomplish a number of functions. The egg must contain sufficient nutrients to sustain embryonic development, allow gas exchange for respiration, and protect the embryo from a variety of environmental stresses, including large shifts in temperature and water loss by desiccation. This is particularly true for insects that lay their eggs in the external environment (as opposed to ovoviviparous insects that store eggs in the body until hatching). In addition, early stages of insect embryogenesis are very much dependent on regulatory factors stored in the egg during oogenesis, often requiring that these factors be specifically localized. Hence, the relatively simple appearance of the egg masks a surprisingly complex structure that serves a number of different functions all essential for the development of the next generation.

Ovary Structure

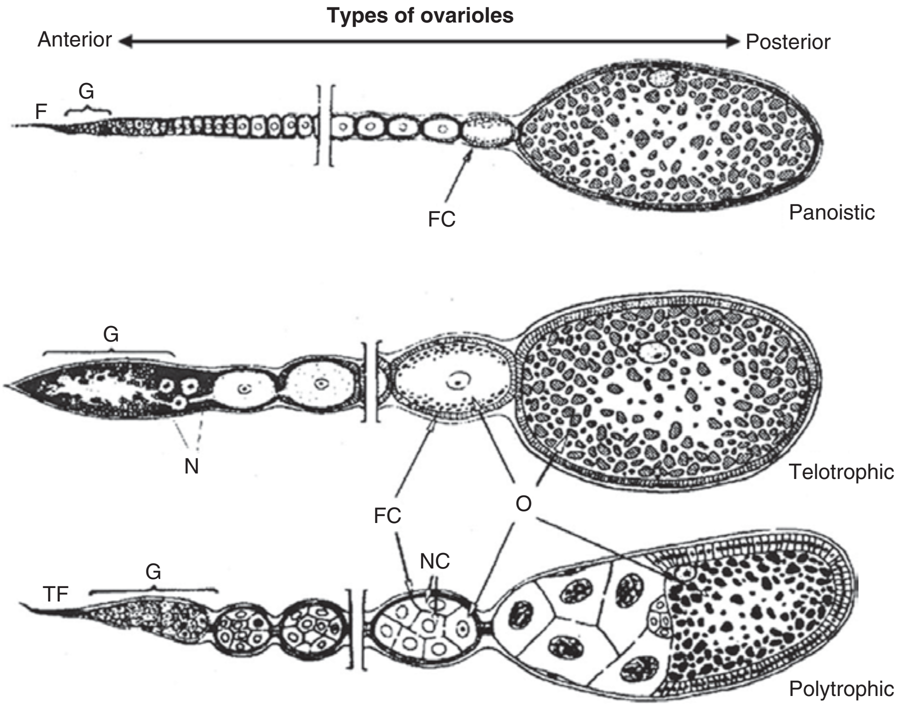
The germline consists of those cells that can directly produce gametes. All other cells are defined as somatic. Oogenesis requires extensive interactions between the soma and germline, with all developmental events taking place in the ovaries. In the adult there are typically two ovaries (Fig. 10), each made up of multiple hollow tubes called ovarioles. At the distal tip of the ovariole is a region called the germarium, which contains undifferentiated germ cells called oogonia. Oogenesis begins when an oogonial cell becomes committed to forming an oocyte and initiates meiosis, which is usually arrested until fertilization. Somatically derived follicle cells then envelop the oocyte to form the egg chamber. Soon the oocyte will begin to take up and store yolk protein, entering the region of the ovariole known as the vitellarium. As new eggs form, older chambers are pushed down the length of the ovariole, differentiating along the way such that the most mature eggs are eventually located at the proximal end next to the oviduct. This developmental sequence results in a linear



Oogenesis, Figure 10 **Structure of the female gonads in *Drosophila*. The ovaries are shown from the dorsal side; two ovarioles are shown on the right. (From Mahowald AP, Kambysellis MP (1980) Oogenesis. In: Ashburner M, Wright TRF (eds) The genetics and biology of *Drosophila*, vol 2c. Academic Press, London, UK, pp 141–224).**

arrangement of sequentially more mature egg chambers, a morphology that is characteristic of insects. As one might expect, there is large species-specific variation in the number of ovarioles per ovary, ranging from a single ovariole in some aphids to over 2,000 in termite queens.

Ovarioles are subdivided into two major types based on the presence and organization of specialized cells that provide trophic support to the oocyte. Panoistic ovarioles are the simplest in morphology (Fig. 11) and represent the most primitive design. In this case, there are no specialized nutritive (trophic) cells to support oocyte development. Instead the oocyte directly absorbs food released by the surrounding follicular epithelium. This means that all germ cells can



Oogenesis, Figure 11 **Variations in the organization of insect ovarioles. A panoistic ovariole contain no specialized nutritive (trophic) cells to support oocyte development. Meroistic ovarioles are of two types. Telotrophic ovarioles contain a cluster of trophic cells (N) located near the germarium. In polytrophic ovarioles, the trophic cells or nurse cells (NC) are grouped near the oocyte to provide necessary macromolecules. FC: follicle cells. G: germarium. N: nutritive cord. NC: nurse cell. O: oocyte. TF: terminal filament. (Modified from Mahowald AP (1972) Oogenesis. In: Counce SJ, Waddington CH (eds) Developmental systems: Insects, vol 1. Academic Press, London, UK, pp 1–47).**

become oocytes. Panoistic ovarioles are found in Apterygota, Ephemerida, Odonata, Orthoptera, and Siphonaptera.

In contrast, most insects have trophic cells whose primary function is to assist in oocyte development. These form meroistic ovaries that can be subdivided into two types. Telotrophic ovarioles (found in Hemiptera and Coleoptera) contain a cluster of trophic cells located near the germarium (in a region sometimes called the tropharium. These are linked by a nutritive cord to oocytes located some distance away in a separate cluster. The cord grows as the oocyte moves proximally, eventually breaking during vitellogenesis.

In polytrophic ovarioles, the trophic cells (also called nurse cells because they "nurse" the oocyte) are grouped near the oocyte to provide necessary macromolecules. They are physically joined to each other and to the oocyte by cytoplasmic bridges. In some cases, the follicle layer surrounds both the nurse cells and the future oocyte, forming a composite egg chamber. The nurse cells eventually degenerate upon maturation of the oocyte. In the other case, the nurse cells form a separate chamber that lies adjacent to the oocyte they are nursing, creating an alternate arrangement of egg chambers and nutritive chambers in the ovariole.

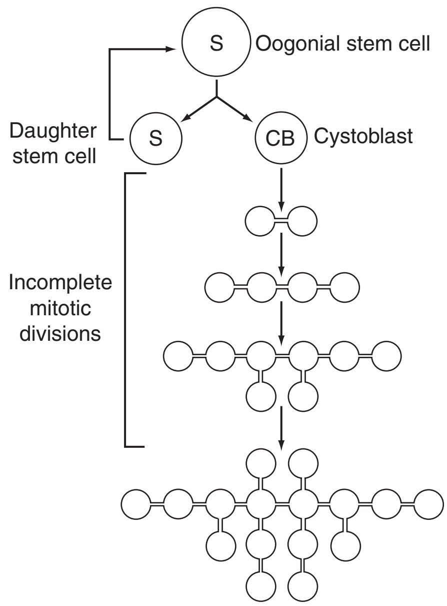
Major Stages of Oogenesis

What follows is a description of the major oogenic events using primarily examples from the fruit fly, *Drosophila melanogaster*. This provides an example of a polytrophic ovary in which the nurse cells are derived from the same germ cell lineage as the oocyte. The first step in oogenesis occurs when an oogonial stem cell undergoes an asymmetric division to produce a daughter stem cell (thereby maintaining the oogonial population) and the precursor to the egg called a cystoblast. In *Drosophila melanogaster*, the cystoblast undergoes a set of four synchronous mitotic divisions to product 16 daughter cells. The divisions are associated with incomplete cytokinesis such that intercellular bridges called ring canals connect the cells. This arrangement allows the rapid exchange of cytoplasmic material, hence the cell cluster can be seen as forming a syncytium or cyst with each interconnected cell called a cystocyte. During these divisions, one cystocyte is committed to become the oocyte and initiates meiosis, which arrests prior to the first meiotic division. The remaining 15 cystocytes differentiate into nurse cells.

The number of cystocyte divisions can vary between species, with as many as 127 nurse cells found in some eggs of *Carabus violaceus*, while the honey bee has 47. In some species, the number of divisions even within the same mother is variable, resulting in eggs with different nurse cell numbers. Variation can also occur in the origin of the nurse cells, as there are examples of some being derived from somatic cells, such as the follicular epithelium.

Once the cystocyte divisions are completed in *Drosophila*, a single layer of approximately 80 somatically derived follicle cells surround the oocyte and nurse cell syncytium to form the egg chamber. Within the next 30 h, the follicle layer will undergo four mitotic divisions (Fig. 12) to give about 1,200 cells. The oocyte positions itself at the posterior end of the egg, while the nurse cells expand in size and undergo endomitosis (DNA replication without cell division). The result is a polyploid nucleus containing about 1,000 times the haploid DNA content. At their largest point the nurse cell nuclei expand to a volume about 2,000 times that of the original cystocyte nucleus. Polyploidy is believed to facilitate the production of the massive amounts of macromolecules the nurse cells must produce to support oocyte development. In contrast, the oocyte nucleus remains arrested in meiosis and is mostly inactive.

Once the egg chamber has formed, it moves into the vitellarium where uptake of yolk proteins begins. Yolk is the principle component of the mature egg, making up about 90% of the total weight. It is a combination of lipids and protein that serves as a nutritive source for the developing embryo. About 60% or more of yolk proteins come from large molecules called vitellogenins made up of a complex of



Oogenesis, Figure 12 Pattern of cell division in the formation of the *Drosophila* egg chamber. Cystocytes are connected by intercellular bridges called ring canals. (From King RC, Cassida JD, Rousset A (1982) The formation of clones of interconnected during gametogenesis in insects. In: King RC, Akai H (eds), Insect ultrastructure. Plenum Press, New York, NY).

glycolipophosphoproteins. Vitellogenins are synthesized primarily by the fat bodies and are secreted into the hemolymph where they are selectively taken up by the oocyte. This process requires vitellogenin-specific receptors and is regulated by insect steroid hormones. Once in the oocyte, the vitellogenins are frequently processed to a more refined structure called vitellin. The absorption and deposition of vitellogenin results in a continuing increase in the size of oocyte. By the end of vitellogenesis, the oocyte will have increased in volume approximately 90,000-fold.

In addition to vitellogenesis, the oocyte receives substantial amounts of macromolecules and organelles from the nurse cells via the ring canals. These include ribosomes, mitochondria, and a large collection of regulatory and structural proteins and RNAs. Much of this movement is probably nonspecific and passive, but there is also evidence for specific transport of macromolecules. This includes a kinesin and microtubule-dependent process that selective moves regulatory RNAs and proteins to the oocyte. Near the end of oogenesis in Drosophila, there is a short period of extremely rapid transport in which the bulk of the nurse cell cytoplasmic contents flows into the oocyte. The oocyte expands from being 50% of egg volume to almost completely filling the available space in less than 30 min. This period of nurse cell "dumping" is associated with nurse cell degeneration and requires the action of actin microfilaments.

Structure of the Mature Egg

The completion of vitellogenesis is associated with the secretion of the vitelline membrane by the follicle cells. The vitelline membrane is a rigid, protein-dense layer that efficiently protects the egg from desiccation and also has a role in embryonic pattern formation. Just above the vitelline membrane is a thin waxy layer followed by the chorion, which makes up the bulk of the eggshell. The chorion is composed of at least 20 proteins, many of which are evolutionarily conserved among insects. They form an intricate cross-linked array providing structural strength and rigidity. Choriogenesis also involves the formation of specialized eggshell structures. The micropyle is the opening through which the sperm enters and is located in the anterior end of the *Drosophila* egg. Near the micropyle are long dorsal filaments that extend outward. These are respiratory structures important for gas exchange. Also in this area is a weakened "collar" called the operculum from which the larva will eventually hatch.

Studies in *Drosophila* and other insects have shown that the internal architecture of the egg is surprisingly complex. The egg displays both anterior-posterior and dorsal-ventral asymmetry with spatially localized collections of regulatory macromolecules. For example, determinants for the specification of germ cells are anchored at the posterior end of the egg while RNAs and proteins required for the patterning of the embryo are distributed in gradients along the anterior-posterior axis. Hence, the spatial polarity of the egg influences the establishment of analogous polarity in the embryo. How this asymmetric distribution of regulatory factors occurs is a complex process involving extensive interactions between the nurse cells, oocyte, and surrounding follicle layer during oogenesis. Additional and more broadly distributed maternally contributed products include those that control early embryonic cell division, gene expression, the cytoskeletal network, and contribute to the determination of embryonic sex. For example, tubulin protein subunits make up about 3% of total egg protein while histone mRNA amounts to 2% of total maternal mRNAs.

Regulation of Oogenesis

The regulation of oogenesis requires a complex interplay of interactions between the soma and germline. Direct contact with the somatic cells at the apical tip of the ovariole (the terminal filament) controls the asymmetric division of the oogonial stem cells in the germarium. Direct physical interactions between the follicle cells and oocyte are necessary to define the shape and polarity of the egg as well as control the differentiation and migration of the follicle cells. Long-range hormonal regulation of oogenesis occurs with juvenile hormone and ecdysteroids, which can alter yolk protein synthesis in the fat bodies and yolk protein uptake in the ovary. Both the maturation and release of eggs are also influenced by environmental factors, such as changes in light cycle, low temperature, and nutrition. These may also involve modulation of steroid hormone levels.

► Hormonal Regulation of Insect Reproduction
► Embryogenesis
► Juveile Hormone
► Ecdysteroids
► Diapause
► Sterile Insect Technique

References

Grünert S, St Johnston D (1996) RNA localization and the development of asymmetry during *Drosophila* oogenesis. Curr Opin Genet Dev 6:395–402

Spradling AC (1993) Developmental genetics of oogenesis. In: Bate M, Martinez Arias A (eds) The development of *Drosophila melanogaster*. Cold Spring Harbor Press, Long Island, NY, pp 1–70

Wilkins AS (1993) Genetic analysis of animal development. Wiley-Liss, Inc., New York, NY

Oogonia

Cells produced by the germarium of ovaries that develop into oocytes and eventually produce eggs.

► Oogenesis

Oötheca

The covering or case of an egg cluster, secreted by accessory glands, and usually used in reference to cockroaches and mantids.

Operating Characteristic

A measure of the accuracy of a classification sample. An operating characteristic curve shows the probability of classifying density below a critical value (e.g., economic threshold) as a function of true mean density. Ideally, probabilities should be near 1 at densities far below the critical value, near 0.5 at densities very near the critical value and near 0 at densities far above the critical value.

► Sampling Arthropods

Operculum (pl. opercula)

A lid or cover.

Opetiidae

A family of flies (order Diptera).

► Flies

Opisthognathous

A condition in which the mouthparts are directed posteriorly.

► Mouthparts of Insects

Opomyzid Flies

Members of the family Opomyzidae (order Diptera).

► Flies

Opomyzidae

A family of flies (order Diptera). They commonly are known as opomyzid flies.

► Flies

Opossum Beetles

Members of the family Monommidae (order Coleoptera).

► Beetles

Opostegidae

A family of moths (order Lepidoptera). They commonly are known as eye-cap moths.

► Eye-Cap Moths

► Butterflies and Moths

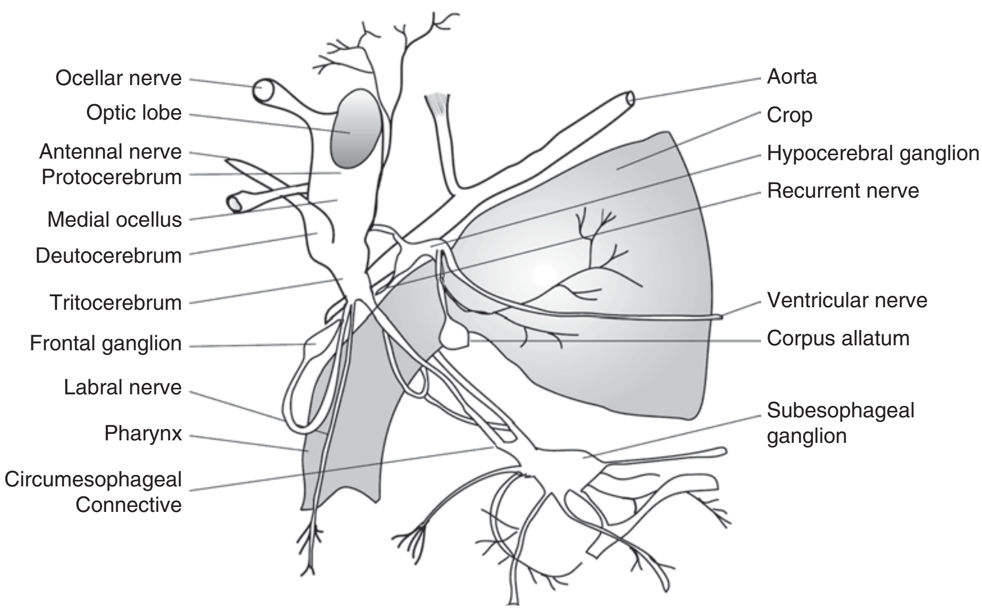
Optic Lobe

Large areas of the brain (protocerebrum) that receive signals from the visual receptors by connecting to the compound eyes (Fig. 13).

► Nervous System

Optimal Foraging

The concept that predators will seek prey that provide the most calories or biomass, as this represents the "optimal" investment of their time for maximizing growth and reproduction. Optimal foraging is also called the profitability concept, or optimal diet model.



Optic Lobe, Figure 13 **Cross section of an insect brain (adapted from Snodgrass, Insect morphology).**

Oral Cavity

The mouth of an insect.

Oral Filter

A filter formed from dense patches of setae on portions of the mouthparts.

Oral Hooks

The mouth hooks of Diptera.

Oral Vibrissae

A pair of stout bristles, larger than adjacent bristles, on the face of a fly (Diptera), between the mystax and the antennae.

Orangedog

This is the name given to the larval stage of the giant swallowtail, *Papilio cresphontes* Cramer (Lepidoptera: Papilionidae).

► Citrus Pests and their Management

Orb

A circle or sphere.

Orbicular

Circular or spherical in outline.

Orbicular Spot

A circular or oval spot found in the discal cell of the front wing of noctuid moths (Lepidoptera: Noctuidae). The shape and color of this spot (which may deviate significantly from circular) has diagnostic value in noctuids.

Orchid Bees (Hymenoptera: Apidae)

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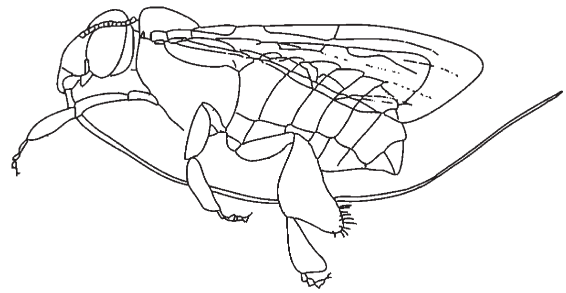
Orchid bees are tropical bees in the tribe Euglossini within the subfamily Bombinae of the family Apidae. They are closely related to the bumblebees and consist of five genera. *Euglossa, Exaerete*, and the monotypic (a genus containing a single species) Aglae possess bright metallic coloring, while *Eulaema* and *Eufriesea* more resemble in size and coloring the typical hairy bumblebee. Most members of the tribe are solitary, while only a few species are parasocial. They are found in neotropical America and prefer species rich virgin forests where their natural habitats range from sea level to nearly 2,000 m. Two peculiarities characterize the euglossine orchid bees and drew the attention of entomologists: (i) both sexes have long tongues, which in some species is longer than the body length, and (ii) males show the unique behavior of collecting fragrances, especially from orchid flowers.

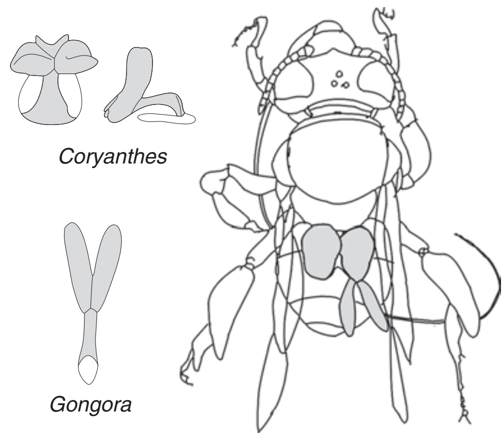
Because of their long tongues, euglossine bees are capable of reaching nectar hidden deep within special floral organs (Fig. 14). Thus, an effective pollination syndrome evolved via the co-adaptation of certain plants and euglossine bees. Changes in floral morphology that excluded short-tongued bees from the nectar source led to specialization by the long-tongued euglossine bees and better floral constancy, as shown by repeated flower visits. Many different plants from different plant families are included in this pollination syndrome (e.g., Bignoniaceae, Apocynaceae, Lecythidaceae, Orchidaceae).

A much more effective pollination syndrome has evolved around the peculiar behavior of male euglossine bees collecting floral fragrances



Orchid Bees (Hymenoptera: Apidae), Figure 14 **Morphological modifications of a male *Euglossa* sp. bee important in its pollination relationship with orchid species. Note the tongue is much longer than the body of the bee and the hind tibia is inflated (drawing by C. Gerlach).**

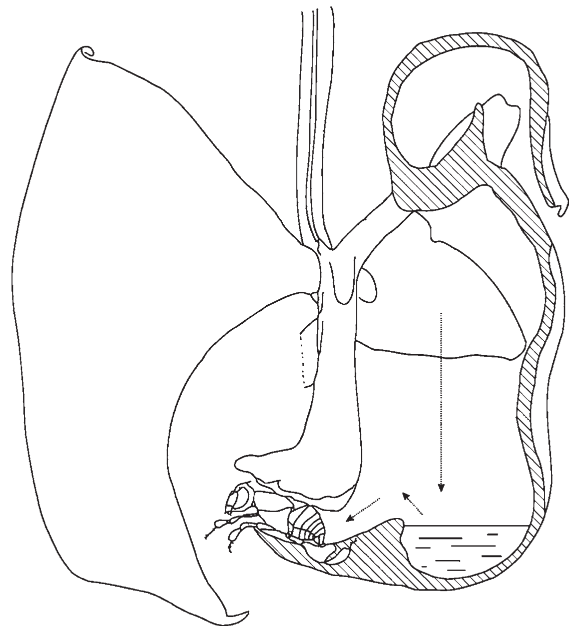
(Figs. 15–17). Males possess special morphological adaptations to help in fragrance collection. Their forelegs bear tarsal brushes with mop-like hairy regions to wipe up the liquid fragrance compounds, the midlegs have velvety patches and special combs to squeeze the fragrance compounds from the soaked mops and the tibiae of the hindlegs are inflated to store the chemicals. These chemicals enter through a slit and are stored in the hairy matrix of the interior. To collect fragrance compounds, the male bee lands on the fragrance source and wipes with his foretarsal brushes, mopping up the liquid fragrance chemicals. When the mops are saturated, the bee takes to the air and, while hovering, transfers the liquid to the slit in the hind tibiae with rapid movements of all the legs. This behavior is normally repeated several times. If the fragrances are present in a crystalline form as solid substances, then the bee first dissolves the fragrance chemicals in secretions from paired cephalic (head) glands, a more effective way to exploit the fragrance source. Then the same process of depositing the resulting liquid in the hind tibiae takes place. It is presumed that the solvent used is selectively absorbed from the hindlegs because the receptacles in the tibiae otherwise would be filled too quickly. The fragrance chemicals stored in the leg do not enter the bee's metabolism. Proof of this comes from the unusual behavior of some male euglossine bees in Brazil that collect great quantities of the insecticide



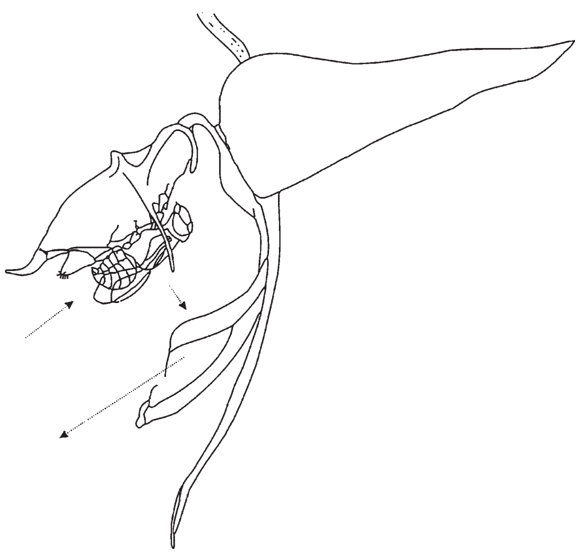
Orchid Bees (Hymenoptera: Apidae), Figure 15 ***Euglossa crassipunctata* with pollinaria of orchids *Gongora* sp. and *Coryanthes mastersiana*. The tip of the *Coryanthes pollinarium* is orientated to the head of the bee, while that of *Gongora* points to the tip of the abdomen. So the bee can enter a *Coryanthes* flower and pollinate it without affecting the *Gongora pollinarium* and vice versa. In the genus *Coryanthes*, the bee enters the flower forward, and leaves it in the same direction while in *Gongora*, the bee enters forward and leaves the flower backward. Note the tongue that is much longer than the bee's body (drawing by C. Gerlach).**

DDT from the walls of treated houses with no negative effects on their health.

The function of the collected fragrance compounds is still unclear. All the hypotheses suggest that they play a role in the reproductive biology of the bees. It was first hypothesized that the males collect the fragrances as precursors of their own pheromones, but bees collecting DDT do not support such a theory. Then it was thought that the males use the fragrances to aggregate and to form "leks," but such a behavior has never been observed in the field. The latest idea is that the males are trying to imitate their nest scent, so the fittest one would be chosen by the female. There are problems in investigating this as the bees are very shy and also are rapid long distance flyers with a need of a large territory. To date, only a few instances of copulate (mating) have been observed and documented.



Orchid Bees (Hymenoptera: Apidae), Figure 16 **Pollination of a *Coryanthes* flower by an *Euglossa* bee. The bee falls into the liquid-filled bucket and escapes via a callus and tunnel formed by the lip and the column. The pollinarium is scraped from the bee's body as it exits the flower. The passage of the bee is marked by arrows. The lip is longitudinally sectioned (drawing by C. Gerlach).**



Orchid Bees (Hymenoptera: Apidae), Figure 17 ***Euglossa* bee pollinates a *Gongora* orchid. Arrows indicate the path of the pollinator (drawing by C. Gerlach).**

The male progenitors of today's euglossine bees likely originally collected their fragrance compounds from decaying wood, for example, or tree wounds. Some plant families took advantage of this behavior and linked themselves to it, evolving flowers with intense fragrance production, sufficient to be collected. Apart from the orchids, Arecaceae (some *Geonoma* spp.), Euphorbiaceae (some *Dalechampia* spp.), Araceae (*Spathiphyllum* and some *Anthurium* spp.) and Solanaceae (some *Solanum* spp., formerly *Cyphomandra*) bear so-called perfume flowers. Within the Orchidaceae, the perfume flower syndrome evolved independently at least five times. More than 800 neotropical orchid species share 180 euglossine bee species as pollinators. Unique in this syndrome is that the floral scent serves as both attractant and reward.

Darwin assumed that the orchid flowers offered food rewards for visiting male euglossine bees. Only in the 1960s was Vogel able to prove that the male bees collected only fragrance compounds at the flowers. After this discovery, the perfume flower syndrome was better investigated and the first floral aromas were identified. Dodson and Dressler used the knowledge of the involved chemical compounds and tested them in the field with revolutionary results. With these chemicals, it was easy to attract male euglossine bees to baits which led to many new bee species being discovered and described. Unfortunately, the newly acquired knowledge was restricted to males. This presents a taxonomic problem as before the perfume flower syndrome was discovered, mainly female bees were collected and named, whereas now mainly males are collected. It is very difficult and sometimes impossible to assign the newly described males to the species already described based on female specimens.

Male euglossine bees are very specific in their choice of fragrances. The floral scent of an orchid normally attracts only one or a few bee species. So optimal conditions for effective pollination evolved. This is a prerequisite for orchid pollination, because the orchid flower gives all the pollen (packaged in a special structure called a pollinarium) to the first visitor of adequate size.

Another important circumstance is that the orchids easily form hybrids which could be avoided here because of the special fragrances. So species which grow sympatrically differ in their fragrances. Hybrids are very seldom seen or are absent because of the unique scent of each species. In orchids, even hybrids between different genera are often produced by man. In nature, these intergeneric crosses are prevented as each orchid genus places its pollinarium onto different parts of the bee's body. Therefore, different orchid genera can use the same bee species (often the same bee individual) as the pollinator, and the respective pollinarium only reaches the correct stigma where it enters like a key in a lock.

The visible pollinarium on the male bee and the easy attraction of males to artificial fragrance baits make euglossine bees a perfect tool for population monitoring of the perfume orchids. The bees fly long distances tending to a trapline of individual orchids and efficiently find all the orchids of interest to them. We can use the bees as scouts to lead us to the hidden flowers in the forest and their pollinarium load tells us which orchid genus was visited (it is known where the different orchid genera deposit their pollinaria on the bee's body). Other ecological information that can be obtained by baiting bees is the knowledge of which bee species pollinate which orchid species. Further, euglossine bees can be used as an indicator of ecosystem health. If the euglossine species have been inventoried in a specific area, one can easily determine if the habitat is still intact based on the numbers of euglossine species attracted to different baits in an area. Richness in euglossine bee species is a direct indicator of richness in the ecosystem.

► Bees
► Wasps, Ants, Bees, and Sawflies

References

Vogel S (1963) Das sexuelle anlockungsprinzip der catasetinen- und stanhopeen-blüten. Osterreichisches Botanische Zeitschrift 110:308–337
Dodson CH, Dressler RL, Hills HG, Adams RM, Williams NH (1969) Biologically active compounds in orchid fragrances. Science 164:1243–1249
Williams NH, Whitten MW (1983) Orchid floral fragrances and male euglossine bees: methods and advances in the last sesquidecade. Biol Bull 164:355–395

Orders

Orders are the major functional divisions of the class Insecta. There are about 30 orders, depending (Table 1) on the system of classification. There is considerable disagreement about whether some groups should be split or grouped, and even if some insect relatives (e.g., the springtails, Collembola) should be considered to be insects.

► Each Individual Order
► Classification
► Phylum

Organic

Chemically, this is a material that contains the elements carbon and hydrogen. Agriculturally, this refers to plants cultured without synthetic fertilizers or pesticides.

Organic Agriculture

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Organic agriculture is a production system that seeks to integrate farming methods and natural ecological processes in a manner that enhances crop yield and quality while improving soils and environmental integrity. Organic farming systems have as their basis the improvement of the agronomic characteristics of soils, stemming from the belief that healthy soils produce healthy crops. Central to this tenet is the establishment and maintenance of appropriate levels of organic

Orders, Table 1 Following is a list of orders, and the number of species known in each group, from several locations

The insect orders, and approximate numbers of described species					
Order Name	**Common Name**	**Number Worldwide**	**Number in the United Kingdom**	**Number in Australia**	**Number in USA & Canada**
The Apterygota (wingless insects with no true metamorphosis)					
Zygentoma (Thysanura)	Silverfish	320	9	23	18
Archaeognatha (Microcoryphia)	Bristletails	250	11	3	20
The Exopterygota (hemimetabolous insects, incomplete metamorphosis)					
Ephemeroptera	Mayflies	2,000	36	124	615
Odonata	Dragonflies and damselflies	5,000	43	248	410
Plecoptera	Stoneflies	1,700	34	84	465
Embiidina	Webspinners	300	0	65	10
Phasmatodea	Stick and leaf insects	3,000	3	132	29
Mantodea	Praying mantids	1,500	0	118	20
Mantophasmato-dea	Gladiators	13	0	0	0
Blattodea	Cockroaches, roaches	4,000	12	439	50
Isoptera	Termites	1,900	0	182	45
Grylloblatodea	Rock crawlers	26	0	0	10
Orthoptera	Grasshoppers, katydids, and crickets	25,000	33	1,513	1,100
Dermaptera	Earwigs	1,200	5	60	20
Zoraptera	Angel insects	30	0	0	2
Psocoptera	Book and bark lice	2,000	68	120	245
Hemiptera	Bugs	100,000	1,410	3,661	9,960
Thysanoptera	Thrips	4,000	180	287	700
Phthiraptera (Mallophaga & Anoplura or Siphunculata)	Chewing and sucking lice	3,500	286	208	975
The Endopterygota (holometabolous insects, complete metamorphosis)					
Megaloptera	Alderflies and dobsonflies	190	2	16	27
Raphidioptera (Raphidiodea)	Snakeflies	188	4	0	18
Neuroptera	Lacewings, ant lions and mantidflies	5,000	54	396	300
Coleoptera	Beetles	370,000	3,700	19,219	24,000

Orders, Table 1 Following is a list of orders, and the number of species known in each group, from several locations (Continued)

The insect orders, and approximate numbers of described species					
Order Name	Common Name	Number Worldwide	Number in the United Kingdom	Number in Australia	Number in USA & Canada
Strepsiptera	Stylopids	600	16	93	110
Mecoptera	Scorpionflies	480	4	20	68
Trichoptera	Caddisflies	7,000	188	260	1,265
Lepidoptera	Butterflies and moths	150,000	2,400	11,221	11,300
Diptera	Flies	100,000	5,700	6,256	17,000
Siphonaptera	Fleas	2,300	53	68	325
Hymenoptera	Wasps, ants, bees, and sawflies.	120,000	6,641	8,834	18,000

Some taxa are poorly known, and there are many areas of the world (especially the tropics) where insect life is poorly documented, so there may be three times as many (or more!) insect species as is shown here

matter and soil micro-organisms involved in nutrient cycling. Soil organic matter and microbial activity are managed by organic farmers through various methods that include crop rotation, green manuring, and the addition of soil amendments such as compost. Organic farming systems also attempt to promote biological diversity on the farm and its surrounding environment. This derives from the assumption that diversity lends balance to a system, and that diverse cropping systems are less likely than simple ones to suffer stresses such as pest outbreaks. However, monoculture is not uncommon in organic farming.

Organic agriculture does not permit the use of synthetically produced fertilizer, pesticides or other artificial compounds. Nitrogen is supplied to crops as composted manure, green manure, and in other naturally occurring forms such as fish-meal, guano, and slaughterhouse by-products. Potassium, phosphorus and micro-nutrients are supplied in mined and other forms such as rock phosphate, limestone, potash and ash.

Organic farmers employ cultural and biological control techniques to manage pests, and may use certain pesticides if both active and inert ingredients conform to regulated standards. Cultural pest management techniques include crop rotation, trap cropping, intercropping, and timing planting to avoid peak pest populations. Biological control in organic systems relies primarily on the conservation of natural enemies. Stable populations of beneficial arthropods are encouraged on organic farms by the presence of diverse crops that offer habitat and alternate food sources such as pollen and nectar. The limited use of pesticides also helps conserve natural enemies. Pesticides that are permitted on organic farms include certain formulations of *Bacillus thuringiensis* and other biological pesticides, botanical pesticides such as pyrethrins and neem (azadirachtins), and horticultural soaps and oils.

Weed management presents a significant challenge for organic farmers, because synthetic herbicides are not permitted. Weeds are controlled mechanically and manually, and with the use of fire and plastic mulches.

Organic farms must undergo a process of certification by an accredited agency in order to sell certified organic produce. Certification assures the consumer that products were grown and processed according to specific standards. Certifying agencies operate on the state level, and some states have several certifying agencies. In 2002, the United States Department of Agriculture established national standards for organic agriculture that regulate the certification of organic farms and the accreditation of certifiers, as well as rules for record keeping and definitions for excluded methods. State certifying agencies may have requirements that are more stringent than the federal standards, but not less stringent. In the United States of America, the Organic Materials Review Institute determines which products can be used on certified organic farms. Protocols have been established for the certified production of organic dairy products, eggs, and livestock as well as vegetables, fruits and grains.

Organic agriculture became the fastest growing agricultural market in the United States in the 1990s, with a twenty percent increase in sales over the decade. Estimated sales of organic vegetables, dairy, and livestock reached $7.8 billion in 2000. Total crop area under organic production in the United States and Canada was estimated at 1.1 million hectares for 2001. There were an estimated 4.4 million hectares devoted to organic agriculture throughout the European Union in 2000, and 7.7 million hectares in Australia and New Zealand. Organic production for domestic and export markets is developing in Latin America, Africa, and Asia, where the land devoted to organic agricultural production in 2000 was estimated at 3.7, 0.06, and 0.09 million hectares respectively.

The fundamental concepts of organic agriculture were derived largely from the principles of biodynamic farming outlined by the Austrian philosopher Rudolf Steiner (1861–1925). Organic agriculture and biodynamic agriculture share an holistic approach to the agroecosystem that emphasizes the alignment of agricultural and natural processes with a view to improving human and environmental health. However, organic agriculture is primarily science-based, while biodynamic agriculture is founded on metaphysical concepts. Organic agriculture is often distinguished from conventional agriculture by the fact that synthetic fertilizers and pesticides are forbidden. The distinguishing characteristic of organic agricultural systems is the commitment to farming in concordance with naturally evolved processes using naturally derived materials. Conventional agricultural systems may employ the tools of organic farming systems. Conventional farmers may also use synthetic compounds and, increasingly, recombinant DNA technology.

References

Green CR (2001) US organic farming emerges in the 1990s: adoption of certified systems. AIB 770. U.S. Department of Agriculture, Economic Research Service Washington, DC

U. S. Department of Agriculture (2002) Agricultural Marketing Service. National Organic Program. Available at, www.ams. usda.gov/nop Accessed 5 March 2008

Willer H, Yussefi M (2002) Organic agriculture worldwide 2001: statistics and future perspectives. Special Report 74. Ecology and Agriculture Foundation, Bad Dürkheim, Germany

Organochlorine

Another term for a chlorinated hydrocarbon insecticide.

► Insecticides

Organophosphate

A class of synthetic insecticides derived from phosphoric acid, and capable of disrupting neurotransmission in insects and vertebrates.

► Insecticides

Oriental Beetle

► Turfgrass Insects and their Management

Oriental Fruit Fly, *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae)

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Oriental fruit fly occurs in tropical regions of Asia, including some Pacific islands and northern Australia, and also in eastern Africa. It became established in Hawaii about 1946. On occasion, Oriental fruit fly has appeared in the USA in California and Florida, but has always been successfully eradicated. It remains a threat to many tropical and subtropical locations.

The taxonomy of this insect is uncertain; there likely are several species within the Oriental fruit fly "complex." Thus, many elements of the life history, including host records, are suspect until confirmed.

Life history

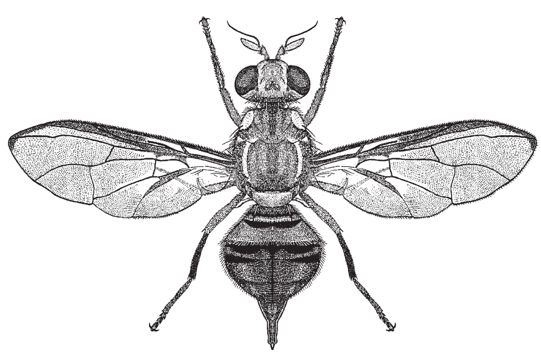
Oriental fruit fly can complete a generation in about 30 days. In tropical climates many overlapping generations per year are reported. Fruit fly abundance typically coincides with availability of ripening fruit, though they tend to be most common in summer and autumn.

Oriental fruit fly eggs average about 1.17 mm in length and 0.21 mm wide. The female may puncture fruit and deposit her eggs, or may take advantage of cracks or other wounds, including the oviposition punctures of other flies. One of the principal reasons that Oriental fruit fly is believed to have successfully displaced Mediterranean fruit fly in Hawaii is that Oriental fruit fly larvae are more competitive when both species of larvae inhabit the same fruit. Eggs may be deposited at a depth of 5–6 mm in soft fruit, whereas they may be very near the surface in hard fruit. The upper and lower developmental thresholds for eggs are estimated at 38 and 12°C, respectively. The average time for egg hatch is 1.6 days, but hatch may be extended to 20 days by cold weather.

Oriental fruit fly larvae are typical in form for tephritid fruit flies: cylindrical and broad posteriorly and tapering to a point at the anterior end. There are three instars; all are whitish in color. First instars range in size from about 1.2 mm to 2.3 mm, whereas second instars range from 2.5–5.7 mm and third instars range from 7.0–11.0 mm. The upper and lower developmental thresholds for larvae are estimated at 34 and 11°C, respectively. Larval development generally requires about 7.8 days, although development time can range from 6–35 days.

Mature larvae leave infested fruit and enter the soil, usually at the base of affected trees, to pupate. The puparia are from 3.8–5.2 mm in length and vary in color from tan to brownish yellow. Pupal development requires about 10.3 days.

The adult fruit fly has a yellow to orange abdomen marked with a black "T." The thorax is predominantly black but bears two yellow stripes laterally. Oriental fruit fly lacks cross bands on its wings. After adults emerge, a period of 6–12 days normally elapses before oviposition can occur. Copulation persists for 2–12 h. Males expel pheromone in a visible form resembling (Fig. 18) smoke. Mating occurs at dusk by flies in aggregations called leks. Mating normally occurs at 4–5 day intervals. Adults continue to produce eggs for about two months. The Oriental fruit fly produces an



Oriental Fruit Fly, *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae), Figure 18 Adult of oriental fruit fly, *Bactrocera dorsalis* (Hendel).

average of over 1,400 eggs per female during a life span of about 80 days. The oviposition rate is reported to be about 130 eggs per day.

Over 120 plants have been reported to serve as hosts of Oriental fruit fly larvae, although many are attacked only during population outbreak conditions. Principal hosts are fruits such as avocado, apple, mango, peach, pear, citrus, coffee, and especially guava. Oriental fruit fly is so highly attracted to guava, and so effective at utilizing this host, that it has displaced Mediterranean fruit fly, *Ceratitis capitata* (Weidemann), as the principal pest of guava and significantly lowered the overall density of Mediterranean fruit fly in Hawaii. Among vegetables, pepper, tomato, and watermelon are reportedly attacked.

Adult flies feed on secretions of extrafloral nectaries, honeydew, rotting fruit, bird dung, and other liquefied items. Adults will survive only three days without water, and six days with water but no sources of carbohydrate. The ability of flies to disperse long distances to obtain food is present in this species.

In the absence of natural enemies, which was the situation in Hawaii immediately after introduction of the fly, very high pest densities are attained. Searches were conducted in many countries for beneficial insects, and a predatory rove beetle (Coleoptera: Staphylinidae) and several hymenopterous parasitoids attacking the egg and larval stages were introduced. Apparently some of the wasps contributed materially to reducing population densities of this damaging fly, because fruit infestation levels declined by 1951. The principal beneficial parasitoid is *Biosteres arisanus* (Sonan), but *Diachasmimorpha longicaudata* (Ashmead) and *Biosteres vandenboschi* (Fullaway) (all Hymenoptera: Braconidae) also are considered important. Over a 7-year period on Oahu, Hawaii, studies found that 68–79% of fly larvae in guava fruit were parasitized. Destruction of eggs by *B. arisanus* was sometimes considerable, up to 80%, probably due to infection of eggs by bacteria and fungi following damage to the chorion by the parasitoid. Overall fruit fly densities are also determined significantly by availability of fruit and warm weather.

Damage

Adult flies sting fruit during the process of oviposition. The presence of larvae is, of course, highly objectionable to consumers. Even if the larva fails to develop, fruit deformities may occur. Also, the oviposition wound is frequently a site for invasion by bacterial and fungal diseases. Other insects such as fruit flies (Hymenoptera: Drosophilidae) and sap beetles (Coleoptera: Nitidulidae) may attack fruit infested by fly larvae. Because many locations lack Oriental fruit fly, quarantine restrictions are frequently imposed that restrict the sale and transport of valuable produce.

Management

Liquid bait traps such as the McPhail trap have long been used in fruit fly detection efforts, but they require considerable maintenance so there is a continuing effort to develop effective but inexpensive trap technology. Methyl eugenol is highly attractive to Oriental fruit fly, but only males are attracted. Yellow and white sticky spheres may be useful for population monitoring. Growers are advised to spray crops when flies become abundant in traps.

Male suppression has been used to eradicate Oriental fruit fly on some islands. Males are lured to a substrate that is impregnated with the attractant methyl eugenol, where flies also come into contact with a lethal dose of insecticide. Bait/insecticide releasers are air-dropped or suspended from trees. Release of sterile male insects also can be used for eradication, alone or in combination with other means of suppression. Insecticides also have been mixed with protein hydrolyzate baits, and sprayed on foliage to affect fly suppression.

Fruit can be protected from flies by being wrapped in netting or bags. Obviously, this approach is limited to small-scale fruit or vegetable production.

► Fruit Flies (Diptera: Tephritidae)
► Tropical Fruit Pests and their Management

References

Vargas RI, Miyashita D, Nishida T (1984) Life history and demographic parameters of three laboratory-reared tephritids (Diptera: Tephritidae). Ann Entomol Soc Am 77:651–656

Vargas RI, Stark JD, Nishida T (1989) Abundance, distribution, and dispersion indices of the Oriental fruit fly and melon fly (Diptera: Tephritidae) on Kauai, Hawaiian Islands. J Econ Entomol 82:1609–1615

Vargas RI, Stark JD, Nishida T (1990) Population dynamics, habitat preference, and seasonal distribution patterns of Oriental fruit fly and melon fly (Diptera: Tephritidae) in an agricultural area. Environ Entomol 19:1820–1828

Vargas RI, Stark JD, Prokopy RJ, Green TA (1991) Response of Oriental fruit fly (Diptera: Tephritidae) and associated parasitoids (Hymenoptera: Braconidae) to different-color spheres. J Econ Entomol 84:1503–1507

Vargas RI, Stark JD, Uchida GK, Purcell M (1993) Opiine parasitoids (Hymenoptera: Braconidae) of Oriental fruit fly (Diptera: Tephritidae) on Kauai Island, Hawaii: islandwide relative abundance and parasitism rates in wild and orchard guava habitats. Environ Entomol 22:246–253

Oriental Parnassian Moths (Lepidoptera: Ratardidae)

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Oriental parnassian moths, family Ratardidae, are butterfly-like moths of the Himalayas and Oriental tropics, with 10 described species, plus a few more still undescribed. The family is in the superfamily Calliduloidea, in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults medium sized (29–87 mm wingspan), but males often much smaller than females; with head rough scaled; haustellum absent; Labial palpi very short; maxillary palpi vestigial; antennae short and mostly bipectinate (reduced in females). Wings broadly rounded (Fig. 19), but males with more acute forewings. Maculation very dimorphic, with females mostly dark browns with pale spots (some with black spots on dark brown), or pale with dark spots (pale females have a vague resemblance to some butterflies of the genus Parnassius), but males with golden markings or more colorful (orange); hindwings dark or similar to forewings. Males in this family were long unknown due to their different maculation from females, and most remain so but for one species where the males had been described in Lymantriidae and another described from Sumatra. Adults are diurnal; females fly slowly like some butterflies (male flight is unknown). Larvae are bark feeders, but biologies and larvae are mostly unknown.

Oriental Parnassian Moths (Lepidoptera: Ratardidae), Figure 19 **Example of Oriental parnassian moths (Ratardidae), *Callosiope bang-haasi* Hering from China.**

References

Heppner JB (1987) A rare moth, *Ratarda tertia* Strand (Lepidoptera: Ratardidae), from Palin, Taiwan. J Taiwan Mus 40:91–94

Hering EM (1925) Die familie der Ratardidae (Lep.). mit Beschreibung 5 neuer Arten. Mitteilungen des Zoologisches Museums Berlin 12:149–158, pl. 1

*Holloway JD (1986) Family Ratardidae. In: The moths of Borneo, Kuala Lumpur, Malayan Nature Society (Malayan Nature Journal, 40) 1:41–42, pl. 68
*Kobes LWR, Ronkay L (1990) The Ratardidae of Sumatra. In: Heterocera sumatrana, Heterocera Sumatrana Society, Göttingen, 6:79–100
Seitz A (ed) (1922) Familie: Ratardidae. Die gross-schmetterlinge der erde, A. Kernen, Stuttgart, 10:389–390, pl. 46, 51

Oriental Realm

The zoogeographic region of India and Southeast Asia south through Indonesia. This region is characterized by having tree shrews, orangutan, and gibbon.

► Zoogeographic Realms

Oriental Swallowtail Moths (Lepidoptera: Epicopeiidae)

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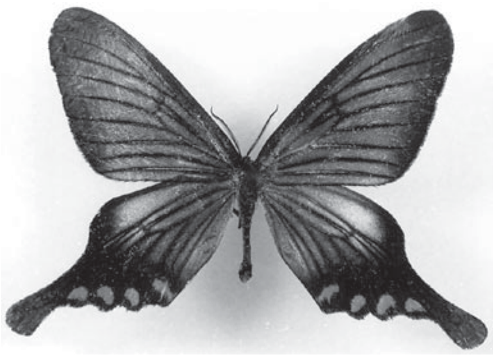
Oriental swallowtail moths, family Epicopeiidae, are a small family with 25 species known; mostly Himalayan and Oriental, but with a few species getting as far north as Japan and Korea. There are two subfamilies: Schistomitrinae and Epicopeiinae. The family is in the superfamily Uranioidea, in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults medium to large (36–126 mm wingspan), with head rough scaled dorsally (frons mostly smooth) and eyes large; haustellum naked; labial palpi small, with second segment long and apical segment reduced; maxillary palpi minute, 1-segmented; antennae filiform to bipectinate and thickened. Wings quadratic, to triangular and somewhat pointed apically; hindwings rounded or tailed (Fig. 20) (rarely longer than forewings; Nossa). Maculation mostly dark brown to black, with few markings or mostly white with dark or colored margins; hindwings similar or tailed and with colored marginal spots. Adults are diurnal; among the larger species seemingly mimicking some tailed Oriental butterflies like in the genera Byasa and Pachliopta (Papilionidae). Resting attitude is with wings outspread. Larvae little known, but leaf feeders with waxy secretions over body. Host plants are in Clethraceae, Cornaceae, Ericaceae, Theaceae, and Ulmaceae.



Oriental Swallowtail Moths (Lepidoptera: Epicopeiidae), Figure 20 **Example of Oriental swallowtail moths. (Epicopeiidae), *Epicopeia hainesii* Holland from Taiwan.**

References

Endo T, Kishida Y (1999) Day-flying moths. Chalcosiinae/Epicopeia. Endless Scientific Information, Tokyo, 119 pp (Endless Collection Series, No. 8) (In Japanese)
*Janet A, Wytsman P (1903) Lepidoptera Heterocera. Family Epicopiidae [sic]. In: Genera insectorum, P Wytsman, Brussels, 16:1–5, 2 pl
Seitz A (ed) (1908–1931) Familie: Epicopeidae [sic]. In: Die gross-schmetterlinge der erde, A Kernen, Stuttgart, 2:35–36, pl. 10 (1909); 2(suppl):51, pl. 10 (1931); 10:57–59, pl. 9–10 (1908)
Sugi S (1972) The distribution, food-plant and early stages of *Schistomitra funeralis* Butler, a diurnal moth (Epiplemidae). Tyô to Ga 23:4–8 (In Japanese)
Yen S-H, Mu J-H, Jean J-L (1995) The life histories and biology of Epicopeiidae of Taiwan. Trans Lepidopterol Soc Jpn 46:175–184

Ormerod, Eleanor Anne

Eleanor Ormerod (Fig. 21) was born May 11, 1828, at Sedbury Park, Gloucestershire, England. Though lacking formal education, she began scientific study in 1852 after finding a rare locust on the grounds of

Ormerod, Eleanor Anne, Figure 21 **Eleanor Ormerod.**

the family estate. In 1868 she responded to a call by the Royal Horticultural Society to make observations on which insects were friends and which were pests, and began to make observations. This activity met with disapproval by her family, however, so entomological work was not conducted in earnest until the death of her father in 1873. She also embraced meteorology, an interest of her brother, and she compiled and analyzed weather data extensively, and published in the Quarterly Journal of the Royal Meteorological Society. She became the first woman fellow of the Meteorological Society, in 1878. Much of her interest in weather was tied to the relationship of weather to insects. She began compiling data on insects and corresponding with others. She eventually produced 24 voluminous annual reports in addition to specialty publications such as "A manual of injurious insects, with methods of prevention and remedy," "Handbook of insects injurious to orchard and bush fruits," "A guide to methods of insect life," and "A textbook of agricultural entomology." Four-page leaflets were prepared for farmers and gratuitously distributed. Thus, she became known as one of the greatest authorities on economic entomology in England and the world. During the conferral of an LL.D. degree to her (the first woman to be so honored) by the University of Edinburgh, she was deemed the "protectress of agriculture and fruits of the earth," a descriptive tribute to her labors to prevent damage by insects. She received many other honors, including an unpaid post as consultant to the Royal Horticulture Society, and the Gold Victoria Medal of the Horticultural Society. She died at St. Albans on July 20, 1901.

References

Anon. (1901) Obituary: Eleanor A. Ormerod, LL.D. Entomologist 34:235–236

Wood M (1999) Meteorologist's profile – Eleanor Anne Ormerod. Weather 54:365–369

Ormyridae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees, and Sawflies

Ornate Pit Scales

Members of the family Cerococcidae, superfamily Coccoidae (order Hemiptera).

► Scales and Mealybugs
► Bugs

Orsodacnid Beetles

Members of the family Orsodacnidae (order Coleoptera).

► Beetles

Orsodacnidae

A family of beetles (order Coleoptera). They commonly are known as orsodacnid beetles.

► Beetles

Ortheziidae

A family of insects in the superfamily Coccoidae (order Hemiptera). They sometimes are called ensign coccids.

► Bugs

Orthoptera

An order of insects. They commonly are known as grasshoppers, katydids, and crickets.

► Grasshoppers, Katydids and Crickets

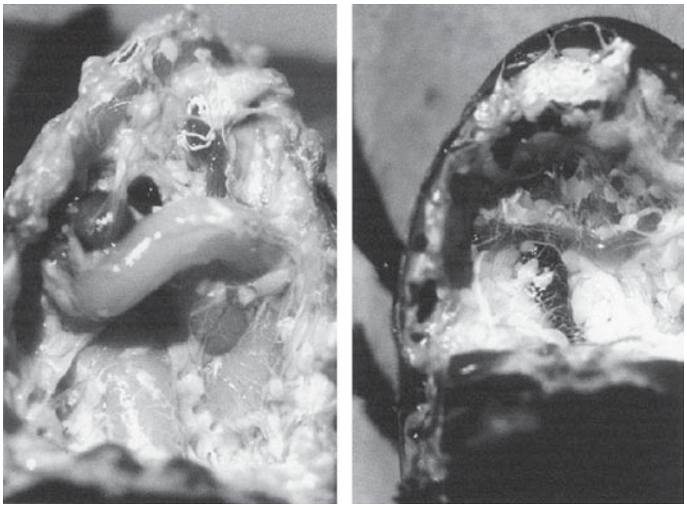
Orussidae

A family of wood wasps (order Hymenoptera, suborder Symphyta). They commonly are known as parasitic wood wasps.

► Wasps, Ants, Bees, and Sawflies

Oryctes Virus and Other Nudiviruses

Various non-occluded, enveloped, rod-shaped viruses, at one time placed in subgroup C of the *Baculoviridae*, have been placed in the pending family Nudiviruses. Members within this family are heterogeneous but do possess the characteristic covalently closed, circular dsDNA genome. The best-studied nudivirus, the *Oryctes* virus, was isolated in the 1960s from the Indian rhinoceros beetle, *Oryctes rhinoceros*. The *Oryctes* virus is one of the few non-occluded insect viruses developed as a microbial control agent. The enveloped, rod-shaped *Oryctes* virus (100 x 200 nm) contains multiple structural peptides (27) of which approximately 14 are associated with the nucleocapsid component. A combination of restriction endonuclease digestions and Southern hybridizations were used to construct a physical map of the 127 kbp *Oryctes* viral genome. DNA hybridization studies revealed little or no homology between the genome of the *Oryctes* virus and the genomes of either GV or NPVs. In nature, the *Oryctes* virus is transmitted when larvae feed on virus-contaminated food. This virus is capable of infecting the larval midgut and fat body tissues. Viral replication results in the production of hypertrophied nuclei. Gross symptoms of the *Oryctes* virus include the disintegration of the fat body, an increase in body turgor pressure, rectal prolapse, and a change in body coloration (Fig. 22). This virus also causes a chronic infection in adult beetles. In this case, viral replication is limited to the midgut region. Dissection of infected adults reveals the presence of a characteristic enlarged white midgut. *Oryctes* virus can replicate in vitro in cells derived from either lepidopteran or dipteran hosts.



Oryctes Virus and Other Nudiviruses, Figure 22 **Dissection of alimentary tract from adult coconut rhinoceros beetle adults. Compare the swollen *Oryctes* virus-infected midgut in panel A to that of the healthy midgut displayed in panel B. (Photograph courtesy of Dr. T. Jackson, Ag Research, New Zealand.)**

Other members within this subfamily include the non-occluded Hz-1 virus, a contaminant of various lepidopteran cell lines, which also has been placed within the nudivirus group. The cytopathic effect caused by Hz-1 virus was observed initially in cell lines established from the bollworm *Helicoverpa zea*. Unlike uninfected lepidopteran cell lines, the Hz-1 infected cell line, when challenged with the *H. zea* NPV, did not produce progeny occlusions but produced a detectable cytopathic effect (CPE). Analysis of the Hz-1 cell line revealed that it was persistently infected with the nonoccluded Hz-1 virus. A third nudivirus has been observed in association with the gonadal tissues (testes, ovary) of *H. zea*. This virus, referred to as gonad-specific virus (GSV), replicates in the various components of both the male and female reproductive tracts. GSV-infected cells contain hypertrophied nuclei that display numerous enveloped, rod-shaped virus particles. The GSV, although highly infectious to the reproductive tissues, does not appear to replicate in other insect tissues. GSV infection results in the atrophy of either ovarian or testicular tissues. The gross symptom of GSV in these colonies was a marked reduction in the production of viable insect eggs due to a nearly 70% incidence of the agonadal condition. The GSV can be both horizontally and vertically transmitted in the *H. zea* colony. This virus, like other baculoviruses, contains a circular dsDNA genome containing 225 kbp. Its relationship to other subgroup C baculoviruses is unknown.

Crickets belonging to the genus *Gryllus* also harbor non-occluded baculovirus-like particles (GrV). Infection by these viruses causes enlargement (bloating) of the abdomen. Handling these infected crickets induces reflex bleeding at both the intersegmental regions and at the termini of abdominal cerci. Hemolymph of infected crickets, characterized as milky and viscous, contains numerous tiny vesicles. Electron microscopy of infected hemolymph samples reveals that these vesicles are membranous sacs filled with enveloped virus particles. These rod-shaped virus particles measure 100 by 154 nm and contain more than 20 structural polypeptides. Histological studies have shown that the fat body is the primary tissue supporting viral replication. Unlike the *Oryctes* virus, the GrV does not replicate in the midgut cells. $CsCl_2$ gradients of nucleic acids extracted from purified virus produced two bands, representing a relaxed and a supercoiled form of dsDNA. Southern blots conducted under low-stringency conditions demonstrated that the GrV did not hybridize to DNA preparations of either the non-occluded *Oryctes* viruses or occluded *Autographa californica* NPV. Attempts to transmit the GrV to healthy crickets by *per os* exposure resulted in low infection levels.

References

Boucias DG, Maruniak JE, Pendland JC (1989) Characterization of a non-occluded baculovirus (subgroup C) from the field cricket, *Gryllus rubens*. Arch Virol 106:93–102

Kelly DC (1976) "Oryctes" virus replication: electron microscopic observations on infected moth and mosquito cells. Virology 69:596–606

Raina AK, Adams JR, Lupiani B, Lynn DE, Kim W, Burand JP, Dougherty EM (2000) Further characterization of the gonad-specific virus of corn earworm, *Helicoverpa zea*. J Invertebr Pathol 76:6–12

Ornate

On the integument of ticks, the presence of an enamel-like color pattern over the base color.

Osborn, Herbert

Herbert Osborn (Fig. 23) was born on March 19, 1856, at Lafayette, Wisconsin, USA. A graduate of Iowa State University (B.S. in 1879, M.S. in 1880), he received an honorary degree of Sc.D. in 1916. He was employed on the faculty at Iowa State and with the United States Department of Agriculture, Division of Entomology, until 1898 when he moved to Ohio State University. At Ohio State he served in several capacities, including director of

Osborn, Herbert, Figure 23 **Herbert Osborn.**

the Ohio Biological Survey. He is remembered, however, as a master teacher of entomology and economic entomology. In the early part of the twentieth century he probably produced more graduate students than any other entomologist. He also was a systematist, with expertise in Cicadellidae and related families, and in Tingidae. Osborn served in many scientific societies, including in the capacity of president of the Entomological Society of America and the American Microscopical Society, and as editor of two journals. His publication list exceeds 300 journal articles and he authored such books as "Insects affecting domestic animals" (1896), "Economic zoology" (1908), "Agricultural entomology" (1916), "Meadow and pasture insects" (1939), and three books on entomological history. He died September 20, 1954.

References

Essig EO (1931) A history of entomology. The Macmillan Company, New York, NY, 1,029 pp

Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Osburn RC (1954) Herbert Osborn. Ann Entomol Soc Am 47:545–547

Osmeterium (pl. osmeteria)

A fleshy, tubular structure that can be everted from a slit in the prothorax of certain caterpillars, producing a pungent odor and used as a defensive display.

Osmoregulation

Regulation of the salt and water concentration in body fluids and cells.

Osmosis

Diffusion of water across a semi-permeable membrane.

Osmylidae

A family of insects in the order Neuroptera.

► Lacewings, Antlions, and Mantidflies

Osten Sacken, C.R.

Karl Robert Romanovitch, Baron von den Osten Sacken, commonly known as C.R. Osten Sacken, was born at St. Petersburg, Russia, on August 21, 1828. Osten Sacken successfully mixed diplomatic service and entomology. Beginning in 1849 he commenced employment with the Imperial Foreign Office in St. Petersburg. At this time in his life he collected broadly, accumulating a collection of most orders but excluding Lepidoptera. In 1856 he became Secretary of the Russian Legation and Consul General of Russia in New York City. He switched his entomological activities at this time, focusing in Diptera, and in 1858 published the "Catalogue of the described Diptera". He resigned his official position in 1871 but remained in the United States (except for visits to Russia) for four years, and collected widely. In 1877 he published the "Catalogue of North American Diptera," and "Catalogue of Western

Diptera." He provided immense collections of Diptera to Loew with the understanding that they were only a loan, as he intended them to form a foundation for North American dipterology. His impact on North American Diptera systematics is best seen in the extent of his North American collection, which is housed at the Museum of Comparative Zoology at Harvard University, and consists of about 3,000 species. Osten Sacken moved to Heidelberg, Germany, in 1877, where he remained until his death on May 20, 1906. Osten Sacken was the outstanding dipterist of his day.

References

Aldrich JM (1906) Baron Osten Sacken. Entomol News 8:269–272
Essig EO (1931) A history of entomology. The Macmillan Company, NY, 1,029 pp
Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp
Papavero N (1971, 1973) Essays on the history of Neotropical Dipterology with special reference to collectors (1750–1905). Museu de Zoologia, Universidade de São Paulo, São Paulo

Ostia

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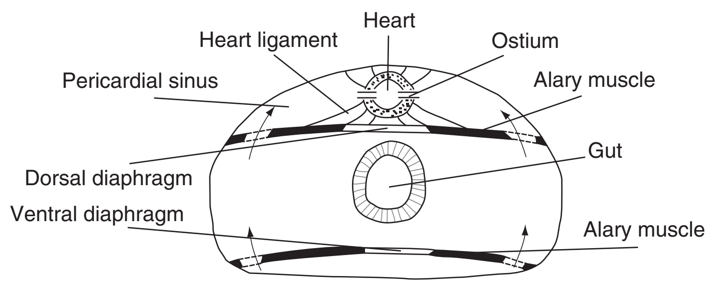
Ostia are small, slit-like, paired openings in the dorsal vessel that allow hemolymph to enter or leave the vessel. Incurrent ostia allow hemolymph to enter during diastole and excurrent ones permit hemolymph to exit. Some Orthoptera have 12 pairs of incurrent ostia, nine in the abdomen and three in the thorax, but most insects have fewer, with 2, 3, or 5 pairs of ostia being common. Ostia more commonly occur in the heart, but may also occur in the aorta. Pairs of ostia are usually located laterally, with one on each side of the heart, but some are ventrally and dorsally located.

Ostial openings tend to occur at the base of shallow pockets or at deeper, funnel-shaped invaginations in the wall of the dorsal vessel (Fig. 24), which often give the heart a chambered appearance. It can be difficult to distinguish incurrent and excurrent ostia. Excurrent ostia more often occur in the thoracic portion of the vessel, but some also occur in the abdomen of some insects. Some ostia do not have well developed valves that control hemolymph flow, and the opening and closing of some may not correlate well with the relaxation-contraction cycle phase. Most incurrent ostia, however, open with the diastole, allowing hemolymph to be sucked in. Some insects have well developed valve flaps in incurrent ostia that open inward; hemolymph is readily aspirated past the valves into the lumen of the heart but during contraction the valve flaps are forced together, thus preventing backflow.

Accessory Pulsatile Hearts

Accessory hearts have several shapes and variable morphology, but all are simple pulsatile, sac-like structures. They occur at a number of places in the



Ostia, Figure 24 **Cross section of an insect abdomen, showing components of the insect circulatory system and direction of hemolymph flow (adapted from Evans, Insect biology).**

body, but most commonly at the base of antennae and wings, and within the leg, usually near the femero-tibial joint, and in the dorsal region of the meso- and metathorax. They assist circulation of hemolymph into and through the appendages. Based upon location, they are usually referred to as leg, antennal, or wing hearts. In most cases, they have no connections to the dorsal vessel. They merely aspirate hemolymph into a sinus cavity through ostial openings and pump it out, or less structured ones consist of little else than a pulsating muscle that aids movement of hemolymph. A mesothoracic accessory heart of *Bombyx mori* aids in pumping hemolymph into the wings. In *B. mori* the metathoracic pulsatile heart is not directly connected to the aorta, although in some other insects it is connected to the aorta. The importance of wing expansion and wing circulation has been mentioned already.

Antennal hearts at the base of the antennae are common, especially in adult Lepidoptera. A complex array of head accessory hearts occurs in *B. mori*, in which the aorta expands into a large sac on the anterior surface of the supraoesophageal ganglion, the "brain." A short transverse tube arises from the sac and terminates in a pair of lateral ampullae, on each side of the head. Each functions as an accessory heart to pump hemolymph into the antenna via an antennal vessel running into the antenna, and to the optic lobe of the brain through a vessel that passes dorsally over the brain to the optic lobe, and ends as an enlarged open sac.

Antennal ampullae in some insects do not have direct connection with the aorta. Generally antennal ampullae have simple attachments by tonofibrillae to the epidermis to keep them in place, and some are attached by tiny muscle strands to the pharynx. Some antennal ampullae have nervous connections, but detailed recordings of nervous control have not been conducted. The structure of the antennal heart in certain earwigs (Dermaptera) may be indicative of the early evolutionary history of accessory antennal hearts. The sac-like ampulla at the base of each antenna in earwigs is connected to an antennal blood vessel that runs to the apex of the antenna. The ampulla is not a muscle itself, and does not have a muscular wall. It is compressed by a small independent muscle running across the ampulla like a strap. A valve-like structure near the origin of the antennal blood vessel prevents hemolymph from flowing back towards the ampulla. When the compression muscle relaxes, the natural elasticity of the ampulla assisted by the pull of elastic fibers attaching the ampulla to the wall of the head promote diastole and filling with hemolymph via a ventral ostium.

Leg hearts are common in some Odonata, Hemiptera, and higher Diptera. There may be a membranous septum between the ventral and dorsal regions of the tibia, and hemolymph is pumped into one channel and returns through the other, aided by muscle contractions in the leg that pump the septum.

Ostiole

A small hole or opening.

► Ostia

Otitidae

Formerly a family of flies (order Diptera). They (and Platystomatidae) were commonly are known as picture-winged flies.

► Flies

Outbreak

In population biology, a marked increase in population density.

Outbreaks of Insects

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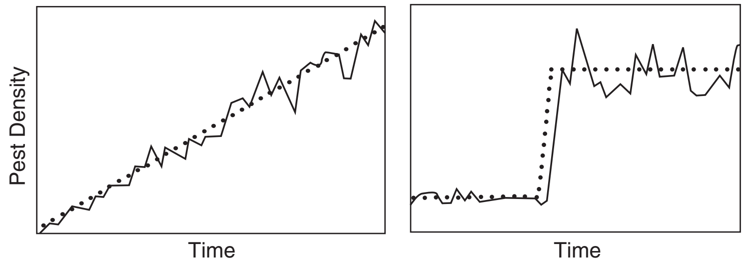
Outbreaks of insect pests have plagued the planet from time immemorial. Naturally, it is important to understand the causes of pest outbreaks, for then it may be possible to control or prevent them from happening by manipulating the causal factors. The general theory of population dynamics recognizes two major kinds of insect outbreaks: "gradient" and "eruptive."

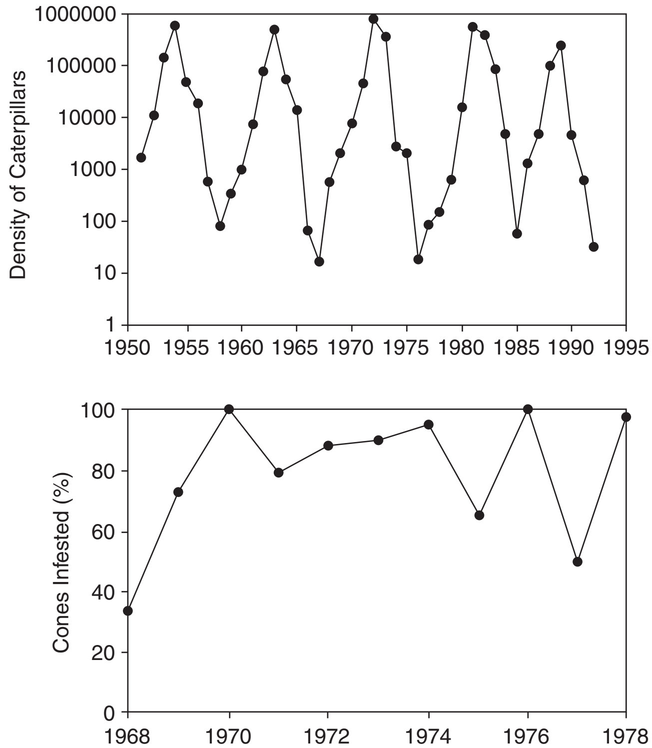
Gradient Outbreaks

The first and most obvious kind of outbreak occurs when the environment changes in some way to favor the pest or disfavor its natural enemies. For example, growing extensive monocultures of a particular plant genotype may provide a huge amount of highly susceptible food for insects that feed on that crop, and/or may create an environment that is less hospitable for some of the natural predators and parasites that attack them. Populations of these pests respond proportionally to certain properties of their external environment so that the average pest density reflects a graded response to these external factors (Fig. 25), hence the name "gradient" outbreak. In technical terms, the equilibrium pest population, estimated by its average density, is a simple direct function of the favorability of the environment, estimated by the abundance of food and/or enemies. Thus, in a changing environment, the pest population will automatically adjust to the equilibrium density as determined by its environment. In agricultural settings, insect environments can change suddenly and dramatically. For example, sowing numerous fields of one crop creates a highly favorable environment, while harvesting all fields simultaneously changes it to a very unfavorable environment. It is not surprising that insect populations rise and fall in response to anthropogenic effects on their environments.

There are two basic types of gradient outbreak (Fig. 26). In the first type, called a "sustained" gradient outbreak, the pest population remains at high densities in certain favorable environments or fluctuates in an irregular manner at the outbreak level. In the second, called a "cyclical" gradient, the pest population oscillates in a regular (cyclic or periodic) manner but the amplitude of oscillation and average density is directly related to the favorability of the environment. Hence, pest outbreaks tend to recur at regular intervals, often every 9 or 10 years, in favorable environments. Cyclical outbreaks are common in forest-dwelling moths, which are often attacked by specialized and effective parasitic wasps and flies. In more general terms, cycles tend to occur whenever populations have a strong negative impact on the favorability of their own environments. In the case of forest moths, large populations provide more food for parasitic insects, which then reproduce more offspring, making the environment less hospitable for future moth populations. Obviously, environments can also be made less favorable when insects



Outbreaks of Insects, Figure 25 **Gradient pest outbreaks: *left*, a gradual improvement in the environment over time results in a proportional increase in the equilibrium density (dashed line) around which the pest population fluctuates (black line); *right*, a sudden increase in the favorability of the environment leads to a sudden change in the equilibrium density (dashed line) around which the pest population fluctuates (black line).**



Outbreaks of Insects, Figure 26 Examples of cyclical and sustained gradient outbreaks: *top*, cyclic outbreaks of the larch budmoth (*Zeiraphera diniana* Guenée) in the Swiss Alps (data from Werner Baltensweiler, ETH Zürich, retired); *bottom*, sustained outbreak of the red pine cone beetle (*Conophthorus resinosae* Hopkins) in a Wisconsin seed production plantation (data from William Mattson, US Forest Service).

destroy or induce changes in the quality of their food plants, so mutual interactions between pest and plant populations can also create the conditions for population cycles.

In contrast, sustained gradients occur when the properties of the environment are not influenced by the size of the population. This is common in agricultural settings because natural enemy populations are often sparse and food supplies are renewed annually by the farmers. However, sustained gradient outbreaks can also occur in more natural forest settings when food supplies or natural enemies do not change in response to the pest population. For example, the reason that cone beetles exhibit sustained gradient outbreaks is that the annual supply of cones is replaced each year and so is more or less independent of previous beetle densities.

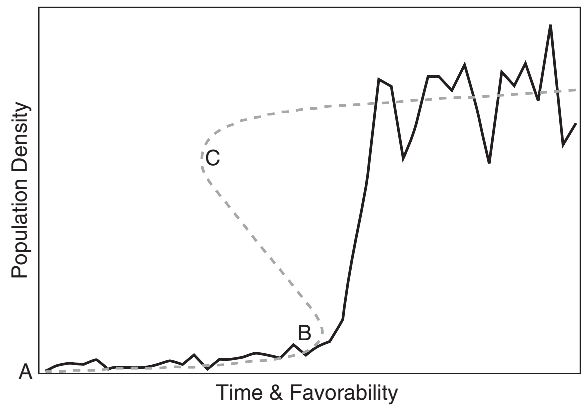
It is also possible to observe a mixture of sustained and cyclical dynamics due to temporary changes in environmental favorability. For example, fir engraver beetle (*Scolytus ventralis* LeConte) populations are normally restricted to a few susceptible fir trees weakened by storms or diseases. In this case, the amount of food available annually is independent of the beetle population size. Occasionally, however, large numbers of firs are weakened by drought or outbreaks of other insects, like the Douglas-fir tussock moth (*Orgia pseudotsugata* McDunnough). Under these conditions, the engraver population increases, kills large numbers of susceptible trees, and then subsides as the food supply is depleted. In this case, an outbreak cycle that is not repeated at regular intervals may be seen. This is called a "pulse" gradient outbreak.

One of the features of gradient outbreaks is that they tend to be restricted to certain locations (e.g., agricultural fields) where the environment is particularly favorable for the pest. The larch budmoth is a good natural example because outbreaks only occur in the high Alps and are never observed in low-elevation larch forests. Gradient outbreaks do not usually spread into adjacent unfavorable habitats because the population automatically adjusts to the less favorable conditions.

Eruptive Outbreaks

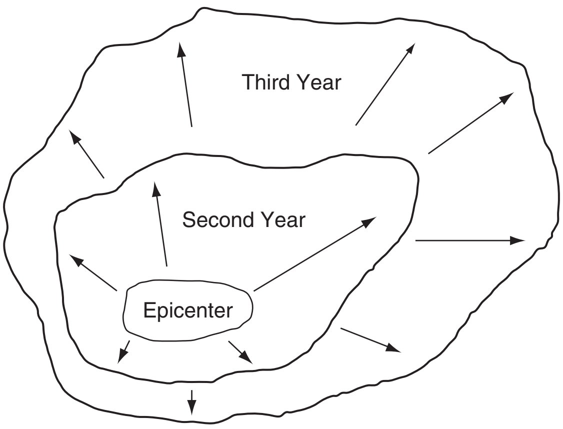
In contrast to gradient outbreaks, eruptive pest populations can spread over vast areas. The reason for this is that eruptive species have a complex equilibrium structure or manifold. Superficially, the eruptive outbreak resembles a gradient outbreak caused by a sudden increase in the favorability of the environment. In the eruptive species, however, the outbreak is not necessarily associated with a major environmental change. In addition, eruptive outbreaks can be triggered by the immigration of pests into a non-outbreak region. Consider, for example, a pest population on the lower arm of the equilibrium manifold close to the point B: If pests move into the area in sufficient numbers to raise the local population above the segment B-C on the manifold, then the population will automatically rise to the upper arm and an outbreak will erupt (Fig. 27). Thus, one of the main characteristics that distinguishes eruptive from gradient outbreaks is that they can spread from local epicenters to cover vast areas. Actually, the segment B-C on the manifold is a repeller, in the sense that the dynamic variables move away from it, while the remainder of the manifold is an attractor, in the sense that trajectories are drawn toward it.

The S-shaped equilibrium structure characteristic of eruptive species is known, technically, as a "fold catastrophe" (notice the fold in the manifold). The term catastrophe is used to describe the sudden and often unexpected jump in the dynamic variable responding to this kind of



Outbreaks of Insects, Figure 27 Eruptive pest outbreak: The environment gradually improves over time but the pest population suddenly and unexpectedly increases to outbreak levels in the absence of any major changes in the environment. The dotted line shows the complex equilibrium manifold and the solid line the pest population fluctuations.

equilibrium structure. The important question, of course, is what causes this fold in the manifold? Without going into details, suffice it to say that fold catastrophes are created by pest species that are able to escape from their predators or overwhelm the resistance of their hosts. For example, generalist predators such as birds are capable of maintaining insect populations at very sparse densities by rapidly moving from one local infestation to another and by switching their attention to the more abundant species. However, this effect becomes inconsequential when the pest population increases above a certain level, called the escape threshold. The mountain pine beetle, *Dendroctonus ponderosae* Hopkins, is an example of the second way in which S-shaped manifolds can be created. This beetle is able to overwhelm resistant trees by rapid mass attack in response to aggregating pheromones (Fig. 28) when populations are large but not when they are small. Finally, it is important to realize that the further the points B and C move to the right, the lower the probability of an outbreak, and that is related to environmental



Outbreaks of Insects, Figure 28 **Spread of an eruptive outbreak from a local epicenter. The theory of outbreaks makes it clear that, in the long run, it is better to manage outbreak species by controlling their environments. Some outbreak management techniques include decreasing the abundance of food or shelter for the pest species, increasing the abundance of natural enemies, or by only growing crops in physical environments unfavorable to the pest. Through activities such as these, the manager may be able to reduce the equilibrium densities of gradient species to tolerable levels or shift the fold of the catastrophe manifold and thereby reduce the likelihood of eruptive outbreaks. A key for identifying pest outbreaks.**

conditions. In the case of the mountain pine beetle, for example, it determined by the average resistance of the trees to beetle attack (i.e., their health and vigor).

As with gradient outbreaks, there are two basic types of eruptions. When the large population does not seriously degrade its environment, the outbreak can persists for several or many years, creating a "sustained" eruption. On the other hand, if the large pest population seriously impacts its environment, as by destroying food plants or attracting natural enemies, then it will automatically return to the lower arm of the manifold and generate an outbreak cycle. If this cycle is repeated at regular intervals it is a "cyclic" eruption, if not, it is a "pulse" eruption.

Management Implications

A key for identifying the type of outbreak is presented in tabular form. The ability to recognize different types of outbreaks is important for pest managers, as different kinds of outbreaks require different management approaches. For example, the use of pesticides to suppress sustained gradient outbreaks is unlikely to be cost-effective because the population will quickly grow back to its original density requiring repeated pesticide applications. On the other hand, eruptive outbreaks can be prevented from spreading by vigorous pest control at the outbreak "epicenter" (the place where the outbreak begins). Here, it may be cost-effective to use pesticides because a single application at the epicenter can, theoretically, prevent the outbreak from spreading. It is imperative that the epicenter be controlled with great vigor and determination, for once an eruptive outbreak has begun to spread it is very difficult to stop.

References

Berryman AA (1999) Principles of population dynamics and their application. Stanley Thornes (Publishers) Ltd., Cheltenham, UK

Barbosa P, Schultz JC (eds) (1987) Insect outbreaks. Academic Press, New York, NY

Berryman AA (1981) Population systems: a general introduction. Plenum Press, New York, NY

Conway GR (ed) (1984) Pest and pathogen control: strategic, tactical, and policy models. John Wiley & Sons, New York, NY

Ovacide

An insecticide that is effective at killing eggs.

Ovariole

One of the egg-producing tubules that collectively form the ovary of female insects.

► Reproduction
► Embryogenesis
► Sterile Insect Technique

Outbreaks of Insects, Table 2 **A key for identifying pest outbreaks**

#	Outbreak characteristics	Outbreak type	Go to #
1a	Spread out from local epicenters to cover large areas. Pests can escape from predators or overwhelm resistant plants.	Eruptive	2
1b	Do not spread far from their point of origin, usually being restricted to specific sites or environmental conditions.	Gradient	4
2a	Go through a single pulse-like cycle at any one location, often being terminated by food depletion and/or the build-up of natural enemy populations.		3
2b	Persist for several or many years at any one location.	Sustained eruption	
3a	Occur at regular intervals, usually 6 to 11 years apart, and never cause severe and widespread mortality to their host.	Cyclical eruption	
3b	Occur at irregular intervals and often cause severe and widespread mortality to their host or are terminated by natural enemy build-up.	Pulse eruption	
4a	Occur at irregular intervals following major environmental disturbances or are permanently associated with a particular site and/or stand conditions.		5
4b	Occur at regular intervals, usually 6 to 11 years apart, rarely cause severe and widespread mortality to their host, and usually terminated by build-up of natural enemies or changes in food quality.	Cyclical gradient	
5a	Occur more-or-less continuously at a particular locality.	Sustained gradient	
5b	Occur at irregular intervals following major environmental disturbances and subside when the environment returns to normal.	Pulse gradient	

Ovary

The assemblage of ovarioles that produce eggs. The ovary terminates into a lateral oviduct, which in turn connects to a common or medial oviduct and allows passage of the eggs to the outside (Fig. 29). The common oviduct usually has associated with it a spermatheca for storage of sperm, and accessory glands for production and storage of secretions that enhance egg deposition or survival.

► Reproduction

Overwintering in Insects

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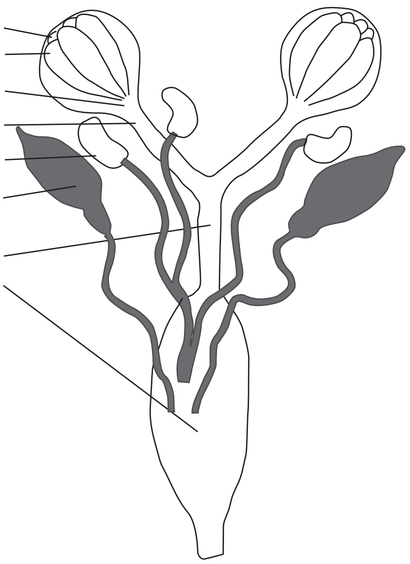
As with animals that inhabit deserts, insects that live in seasonal habitats employ specific strategies and possess special attributes that enable them to survive unfavorable conditions. Winter and its attendant characteristics, low temperatures and inclement weather, occur predictably. It is this predictability that has enabled insects to evolve



Ovary, Figure 29 Diagram of female reproductive system, as found in *Rhagoletis* (Diptera) (adapted from Chapman, The insects: structure and function).

to exploit this inhospitable season efficiently. This article briefly describes how insects get ready to overwinter, which cues inform them to get ready for winter and how they survive the winter once it has begun. Some important terminology used in discussing overwintering follows:

Diapause is the spontaneous state of dormancy occurring in the lives many insects.

Dormancy is a resting or quiescent condition in which metabolism is reduced.

Morph one of the forms present in a polymorphic population.

Phototaxis movement in response to light.

Polymorphism is the existence within a species or population of different forms of individuals.

Thigmotaxis (stereotaxis) the response of an organism to the stimulus of contact with a solid, hence leading to aggregations.

Freeze tolerance is the ability to tolerate the formation of ice crystals in the body tissues or fluids. This occurs extra-cellularly. If it occurs within the cells they would burst.

Freezing intolerant species are those that cannot tolerate freezing.

Freeze avoidance is exhibited by freezing intolerant insects and is facilitated by their ability to supercool.

Supercooling is the ability of a substance to remain unfrozen below their melting point (the melting point is the temperature at which the last ice crystal disappears when a frozen sample is warmed).

The *supercooling point* is the temperature at which spontaneous freezing occurs in a supercooled liquid.

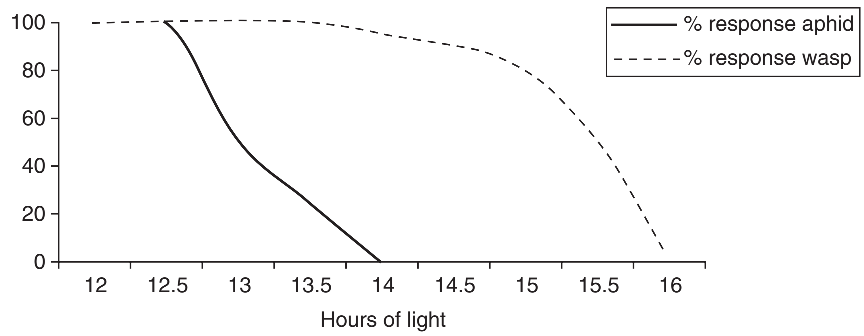
Cold acclimation (cold hardening) is the seasonal increase in cold hardiness that occurs in most species as summer turns to winter and helps prevent death or cryo-injury as temperatures go below those at which normal growth and development occur.

Cues

Insects show a range of responses to the approach of winter, including migration, diapause, polymorphism and dormancy. Whatever response or set of responses they use, it is important that the developmental stage at which they overwinter is reached at the correct time of year. On the other hand, overwintering is expensive in terms of energy and life-history traits and it is thus to the advantage of the insect to delay the onset of the overwintering stage to the last possible moment.

Insects prepare for winter in response to certain cues. These are, as you might expect abiotic, light and temperature being the two primary cues. Usually the insect responds to a combination of the two to ensure that a sudden cold spell in the middle of summer does not send the insect into hibernation prematurely. Winter periods, especially in temperate regions, are characterized by decreasing temperatures and shortening day lengths.

Photoperiod is, of course, the most reliable cue that an insect has to tell it when winter is on the way. Changes in day length follow a regular seasonal pattern, which, especially given the



Overwintering in Insects, Figure 30 **Responses of the aphid *Rhopalosiphum padi* and the wasp *Cotesia rubecula* to day length.**

recent perturbations in weather patterns, is much more reliable than something like temperature or relative humidity. Aphids (Hemiptera: Aphidoidea), for example, respond to a decrease in day length together with a decrease in temperature by producing the morphs known as sexuparae, which in turn produce the sexual stages of their mainly parthenogenetic life cycle, as shown in *Rhopalosiphum padi*, the bird cherry aphid. A response to photoperiod and temperature is also commonly seen in other insect orders (e.g., the braconid wasp *Cotesia rubecula* [Hymenoptera: Braconidae]) (Fig. 30) but in this case the response is for the individuals to go into diapause rather than the production of specialized overwintering morphs, as in the aphid example. Once the insect has ascertained that winter is indeed on the way it has then to ensure that it will survive the winter.

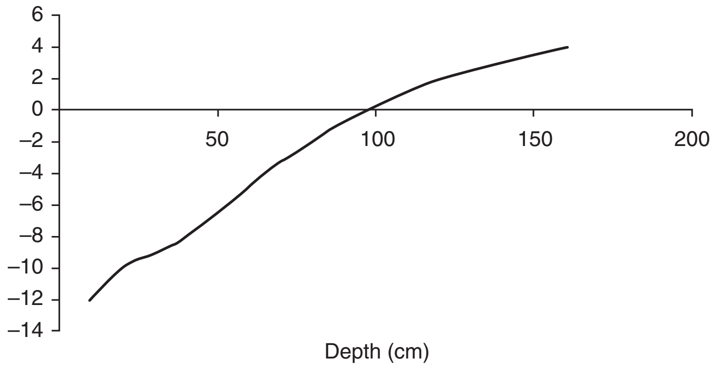
How do insects survive winter? In some parts of the world winter temperatures can reach as low as −40°C and stay there for some considerable time – yet many insect species can survive these temperatures without shelter or fur coats! Although insects may not wear fur coats, they are able to take protective measures against severe weather conditions. There are two basic ways in which insects are able to protect themselves against cold and exposure during winter – behavioral evasive action and/or chemical evasive action. What exactly does this mean? An insect has two basic imperatives that must be met to ensure its overwinter survival. It must find somewhere to pass the winter and at the same time become physiologically ready. Before considering the physiological changes involved, we should first examine the sites where an insect might spend the winter.

Where to Overwinter

A basic requisite is to find somewhere protected from the environment, although sometimes what an insect "sees" as protected is perhaps not the same thing that we think of as a nice cozy site to pass the winter.

Some of the protective factors are not directly under the control of the insect, e.g., snow cover, which acts as a useful buffer against sudden temperature changes and exposure. Insects are, however, able to take advantage of these naturally occurring variables, even if not deliberately. For example, insects that pass the winter just below the soil surface are better protected (both from weather conditions and predation) when the soil is covered by a thick snow layer than when the ground is fully exposed.

The depth at which an insect overwinters can have a marked effect on the temperature experienced by that insect. The deeper one penetrates the soil the greater the differential between air temperature and soil temperature. There is, of course, a cost: the deeper the insect overwinters in the soil, the more energy it expends getting to its



Overwintering in Insects, Figure 31 **Relationship between soil depth and temperature; example is from Russia on a day in January.**

site (Fig. 31). Some insects are better equipped to dig than others. The larvae of Lepidoptera, for example, that are going to spend the winter as a pupa are not as good at digging down as an adult ground beetle (Coleoptera: Carabidae) or mole cricket (Orthoptera: Gryllidae). The other point that must be borne in mind is that if an insect digs down a long way to take advantage of the temperature gradient, it then has a long way to dig back up when spring arrives. For a moth or a butterfly that has just emerged from an underground overwintering pupal case and has soft (albeit unfurled) wings, and then has to dig up through several centimeters of soil, there is a real possibility of wing and body damage. The pine beauty moth, *Panolis flammea* (Lepidoptera: Noctuidae), a common insect of pine forests in northern and western Europe, overwinters as a pupa in the soil. In forests growing on soft peaty or sandy soils they habitually overwinter at depths of from 5–20 cm, depending on the climate. In sites where the soil is very hard and stony, however, they are usually found just beneath the surface to a maximum depth of perhaps 2 cm. Consequently, their overwintering mortality tends to be higher in the latter sites because predators locate them more readily, and they suffer more frost and cold damage due to the reduced buffering effect.

Some insects do not go into full diapause and use a more active strategy to exploit this trade-off. The root borer *Prionus laticollis* (Coleoptera: Cerambycidae) is killed by temperatures below freezing. It overwinters as an apodous (without legs), soft bodied larva, ill-adapted for digging in soil. To compensate for this, the larvae migrate ahead of the lethal temperatures and so only dig when they have to avoid freezing. Another example of non-diapausing active overwintering is shown by the weevil *Strophosomus melanogrammus* (Coleoptera: Curculionidae). This insect overwinters as an adult at the soil surface or above it, remaining mobile and able to feed on the thin bark of trees and shrubs when the temperature is warm enough for it to be active. If temperatures begin to fall below this level it burrows into the soil or into a grass clump. Aphids are also able to successfully overwinter as adults and immature stages by crawling into the middle of grass tussocks where temperature and wind chill effects are buffered. Insects that overwinter beneath the soil surface sometimes are able to move from their normal summer feeding site; for example, the large pine weevil *Hylobius abietis*, a pest of young conifers in restocking sites, moves to mature forests to overwinter in the soil, where the canopy cover gives added protection from frost.

Location of Sites

So how do the insects find their overwintering sites? Many of the sites are located by programmed changes in the behavior of the insects. Seasonal changes in phototaxis, for example, occur in those insects that overwinter in caves or holes. The fly *Pyrellia serena* (Diptera: Muscidae), which overwinters in caves in Europe, becomes negatively phototactic as day lengths shorten and this results in a tendency for the adults to creep into dark enclosed places. Some insects develop a negative phototaxis coupled with a digging reflex. Ladybird beetles, for example, that overwinter in litter layers show this response. Many insects become thigmotactic as winter approaches (i.e., they develop a need to be in contact with each other or to be in confined spaces). The monarch butterfly and many ladybird beetles are notable examples; hence, the spectacular roosting colonies of monarch butterflies, and the large aggregations of ladybird beetles often found in protected sites such as tree stumps or under bark.

Coping with Cold

Even when an insect has found a suitable overwintering site, it is still going to be subjected to low temperature, especially if, for example, it is an immobile overwintering stage such as an aphid egg laid on the buds or bark of a tree. How do insects cope with the extremely low and prolonged temperatures that they are likely to encounter over the winter?

To cope with cold, insects have developed a biochemical response to winter. The concentrations of various compounds within the haemocoel of the insects changes as winter approaches and, in many cases, continues to change as winter progresses. The ability of insects to withstand the low temperatures encountered during the winter is known as cold hardiness.

Cold Hardiness

Insects possess various degrees of cold hardiness and this is achieved by a number of mechanisms. Generally, insects have adopted two main strategies of cold hardiness. They are either freeze tolerant or freeze intolerant. Insects that are freeze tolerant do this by accumulating antifreeze (glycerol is the most abundant substance found in freeze tolerant insects although sorbitol, fructose, sucrose and trehalose are also commonly employed as antifreeze compounds). The amounts of antifreeze vary through the year and are generally in line with requirements (i.e., greatest at the coldest times of the year). In areas such as the Arctic and Antarctic, most species are freeze tolerant.

Freeze intolerant species attempt to avoid freezing by supercooling. Such insects are usually found in cool and cold climates. The majority of cold hardy insects are freezing intolerant and rely on supercooling to avoid lethal freezing. The melting point of water is 0°C, but when a sample is cooled it will not normally freeze at its melting point and will remain unfrozen until cooled to much lower temperatures. Liquids that remain unfrozen at temperatures below their melting point are described as supercooled. It is possible to supercool water to −40°C if it is very pure. Insects can be viewed as liquid containers, and they attempt to keep their water unfrozen. They usually stop feeding in the autumn and clear their digestive systems, because food particles can encourage ice formation. In addition, they increase the amount of antifreeze compounds within their bodies. As with freezing tolerant insects, a seasonal change in antifreeze concentration is seen.

The biochemistry involved in insect overwintering is very complicated, and as molecular techniques improve it is a rapidly developing and important area of research. It is beyond the scope of this article to do more than briefly outline the factors involved. For those wishing a more in-depth treatment, suggestions for further reading can be found at the end of the article.

At the ecological level, it is interesting to note that despite the fact that supercooling points of −20, −30 or even −40°C have been shown in insects, populations of overwintering insects can die out at temperatures much higher than these. For example, populations of the cereal aphids *Sitobion avenae* and *Rhopalosiphum padi* often go locally extinct in southern England despite temperatures being far higher than the reported supercooling points for these aphid species. Eggs of *R. padi*, which are recorded to have a supercooling point of –40°C, also suffer approximately 80% mortality over the winter regardless of the temperatures experienced.

In this context, it important to note that although many experiments on supercooling point determination have shown that insects survive exposure to temperatures close to or at their supercooling points, few experiments retained the insects to check if other factors beside immediate survival had been affected. In many cases, it was later found that cryo-injury had resulted in reduced fecundity and longevity, as well as affecting behavior and motor function.

Overwintering Stages

Insects can pass the winter in a number of different stages, egg, larva, pupa, adult – in fact, every stage of the insect life cycle is used by some insect or other. But why? We have seen that aphid eggs, for example, have supercooling points of –40°C, so why not overwinter as an egg? After all, overwintering as a mobile stage in aphids does not seem very sensible, as we saw in the example above where cereal aphids overwintering as active stages can suffer local extinction. At first sight, it would seem that the obvious answer is to pass the winter as something inconspicuous and/or very protected such as a small extremely cold-hardy egg hidden in the crevices of a tree's bark (as many aphids do) or as a pupa deep under the soil (as many other insects do). Certainly, these two tactics are used widely by insects, but even in Finland where winter temperatures of –30°C are very common, many species of Lepidoptera pass the winter as eggs, larvae, pupae and adults, with some species even using a mixture of life cycle stages. So why do we see this variability in overwintering stage? One suggestion is related to the feeding strategy of the insect. For example, some Lepidoptera such as the gypsy moth (*Lymantria dispar*) or the winter moth (*Operophthera brumata*) which are flush feeders (i.e., they feed on the newly emerging plant tissue in the spring), overwinter in the egg stage and hatch at the same time as the buds on their host plant begin to burst. In fact, this is also the case for many aphid species, particularly those that live on trees or bushes. There are, of course, some insects that confound these rules. The pine beauty moth, for example, is a flush feeder on pine but overwinters as a pupa, emerges as an adult and then lays its eggs. It overcomes the disadvantage of the extra developmental time required by emerging early. The adults emerge from their overwintering pupae before the pines begin to break bud. The eggs are laid in early spring and hatch at the same time as the buds burst so synchrony is still achieved. Some insects have opted for mixed strategies. Some aphids, like the bird cherry aphid, *Rhopalosiphum padi*, are host alternating, and spend part of their life cycle on a woody host and the summer part of its life cycle on grasses and cereals. The standard overwintering strategy is to pass the winter as an egg on bird cherry (*Prunus padus*). It can, however, overwinter as adults and/or nymphs on grasses (anholocyclic overwintering). This has a possible advantage in that if the winter is mild and its active overwintering stages survive they are ready to exploit the grass/cereals much earlier (March/April in southern England) than if they have to hatch from eggs on their primary woody host (March/April in England) and have two generations of multiplication before they make the dangerous migration to grasses and cereals in May/June. On the other hand, if the winter is harsh, then all the active stages will be killed, but because there is an egg population the species is saved. In general, the warmer the climate, the greater the preponderance of anholocyclic overwintering that is found.

Clocks

How do the overwintering insects know when it is time to stop? Not surprisingly, this is done using the same cues as the decision to prepare for overwintering: photoperiod and temperature. It is not entirely as straightforward it sounds. Although winter is, on average, cold in temperate regions, very warm spells in the winter are not uncommon. Thus, it would not be a good idea to emerge and then be covered in snow and ice. The emergence cues are usually a combination of photoperiod and temperature, although some insects have an internal clock that dictates an obligate time in diapause before they start to respond to rises in temperature or lengthening photoperiod. Interestingly enough, some insects require a period of cold before they can break diapause – so for example, face flies, *Musca autumnalis* (Diptera: Muscidae), need a prolonged exposure to low temperatures before they can begin to emerge. The pine beauty moth needs a period of at least eight weeks at sub-developmental temperatures plus a period of 120 days before it will even start to respond to temperature increases. Thus, there is thus a certain degree of variability in the responses seen, although it is not known why such variability exists.

This article has provided a basic overview of the main ecological and physiological strategies involved in insect overwintering. By understanding these strategies and the factors that influence them we are able to make predictions about insect populations and many pests forecasting schemes are now based on the overwintering stages of insects.

► Diapause

References

Danks HV (2006) Insect adaptations to cold and changing environments. Can Entomol 138:1–23

Danks HV (2006) Key themes in the study of seasonal adaptations in insects. II. Life-cycle patterns. Appl Entomol Zool 41:1–13

Hawes TC, Bale JS, Convey P, Worland R (2006) Ecologically realistic modalities in arthropod supercooling point distributions. Eur J Entomol 103:717–723

Leather SR, Bale JS, Walters KFA (1993) The ecology of insect overwintering. Cambridge University Press, Cambridge

Lee RE, Costanzo JP (1998) Biological ice nucleation and ice distribution in cold-hardy ectothermic animals. Annu Rev Physiol 60:55–72

Pfister TD, Storey KB (2006) Insect freeze tolerance: Roles of protein phosphatases and protein kinase A. Insect Biochem Mol Biol 36:18–24

Turnock WJ, Fields PG (2005) Winter climates and coldhardiness in terrestrial insects. Eur J Entomol 102:561–576

Oviduct

One of the tubes that passes eggs from the ovaries to the vagina.

Ovipara

In aphids, a female that produces eggs after mating with a male.

► Aphids

Oviparous

An organism that produces eggs.

Oviposition

The act of depositing eggs.

Ovipositor

The structure, usually in the shape of a tube, that is used to deposit eggs.

► Abdomen Of Hexapods

Ovisac

A waxy secretion produced by females, and enclosing the eggs. In scale insects (Coccoidea), the ovisac often encloses part of the female, or her entire body.

Ovisorption

Resorption of eggs prior to oviposition.

Ovoviviparous

A condition wherein the eggs hatch within the female insect, and the female produces immatures rather than eggs.

Ovum (pl. ova)

A term for the egg.

Owlflies

Members of the family Ascalaphidae (order Neuroptera).

► Lacewings, Antlions, And Mantidflies

Owlet Moths (Lepidoptera: Noctuidae)

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Owlet moths, family Noctuidae (including cutworm moths, dagger moths, forester moths, millers, and underwing moths), are the largest family of Lepidoptera, with about 26,310 described species worldwide; actual fauna likely exceeds 30,000 species. Major regions of biodiversity are in the Neotropics (ca. 8,600 sp.) and the Indo-Australian region (6,500 sp.). The family is in the superfamily Noctuoidea, in the section Cossina, subsection Bombycina, of the division Ditrysia. Numerous subfamilies and tribes have been described and the classification is still in flux, but 26 subfamilies are now recognized segregated into three groups: group Aganainina (including Aganainae; previously in Arctiidae), group Herminiinina (including Herminiinae), and the remaining subfamilies in group Noctuinina (Hypenodinae, Rivulinae, Hypeninae, Catocalinae, Euteliinae, Stictopterinae, Sarrothripinae, Chloephorinae, Nolinae, Plusiinae, Acontiinae, Condicinae, Amphipyrinae, Stiriinae, Psaphidinae, Agaristinae, Cocytiinae, Heliothinae, Acronictinae, Pantheinae, Bryophilinae, Cuculliinae, Hadeninae, and Noctuinae). Some subfamilies, like Aganainae, Herminiinae, Nolinae and Pantheinae, are sometimes considered separate families. Adults (Fig. 32) small to very large (8–305 mm wingspan); a few with clubbed antennae; some with greatly elongated labial palpi (Hypenodinae); abdominal tymbal organs in some groups (e.g., Chloephorinae, Nolinae, and Sarrothripinae). Maculation extremely varied but most species with somber shades of brown or gray, with various markings; some are very colorful. Adults mostly nocturnal but some are crepuscular, and several groups are diurnal (Aganainae, Agaristinae, Cocytiinae, and Heliothinae). Larvae mostly leaf feeders, but many are borers. Host plants include numerous plant families, but the majority of owlet moths are not known biologically. Some agricultural pests are included in the family (e.g., cutworms, armyworms, and others); some *Eublemma* are predaceous on scale insects. The largest adults are females of the Neotropical white witch moth, *Thysania agrippina* (up to 305 mm), while the smallest are among the subfamily Acontiinae.

References

Beck H (1999–2000) Die larven der Europäischen Noctuidae. revision der systematik der Noctuidae (Lepidoptera: Noctuidae). Verlag Eitschberger, Marktleuthen: 4 v. (Herbipoliana, 5)

Chen Y (1999) Lepidoptera Noctuidae. In: Fauna sinica. Insecta. 16. Science Press, Beijing, 1596 pp, pl. 68

Fibiger M (ed) (1990–2001) Noctuidae Europaeae. Entomology Press, Sorø, 7 vol

Lafontaine JD, Poole RW (1987–1998) Noctuoidea. Noctuidae (part). In: Dominick RB et al. (eds) The moths of America

Owlet Moths (Lepidoptera: Noctuidae), Figure 32 **Examples of owlet moths (Noctuidae): *top left*, (subfamily Acontiinae) *Episteme adulatrix* (Kollar) from Nepal; *top right*, (subfamily Catocalinae), *Catocala fraxini* (Linnaeus) from Taiwan; *bottom left*, (subfamily Euteliinae), *Eutelia furcata* (Walker) from Florida, USA; *bottom right*, (subfamily Herminiinae), *Zanclognatha atrilineella* (Grote) from Florida, USA.**

north of Mexico including Greenland. Fasc. 25.1:1–182 (4 pl.) (1991); 26.1:1–249 (5 pl.) (1995); 27.2:1–237 (8 pl.) (1987); 27.3:1–348 (8 pl.) (1998). Wedge Entomological Research Foundation, Washington, 237 pp (8 pl.)
Poole RW (1989) Noctuidae. In: Lepidopterorum catalogus (n.s.). Fasc. 118 [124]. E. J. Brill, Leiden, 3 vol, 1314 pp
Seitz A (ed) (1909–1944) Familie: Noctuidae. In: Die gross-schmetterlinge der erde, A. Kernen, Stuttgart, 3:5–511, pl. 1–75 (1909–1914); 3(suppl.):3, 5–332, pl. 1–26 (1931–1938); 6:3–508, pl. 1–96 (1917–1944); 11:1–496, pl. 1–56 (1912–1938); 15:1–302, pl. 1–41 (1913–1939)
Speidel W, Fänger H, Naumann CM (1996) The phylogeny of the Noctuidae (Lepidoptera). Syst Entomol 21:219–251

Oxaeidae

A family of bees (order Hymenoptera, superfamily Apoidae).

► Bees
► Wasps, Ants, Bees, and Sawflies

Oxycarenidae

A family of bugs (order Hemiptera, suborder Pentamorpha).

► Bugs

Oxychirotidae

A family of moths (order Lepidoptera).

► Butterflies and Moths

Oxytenidae

A family of moths (order Lepidoptera). They also are known as American tropical silkworm moths.

► American Tropical Silkworm Moths
► Butterflies and Moths

P

Pachygronthidae

A family of bugs (order Hemiptera, suborder Pentamorpha).

► Bugs

Pachyneurid Flies

Members of the family Pachyneuridae (order Diptera).

► Flies

Pachyneuridae

A family of flies (order Diptera). They commonly are known as pachyneurid flies.

► Flies

Pachynomidae

A family of bugs (order Hemiptera).

► Bugs

Pachytroctidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice or Psocids

Packard, Alpheus Spring

Alpheus Packard was born on February 19, 1839, at Brunswick, Maine, USA. He graduated from Bowdoin College in 1861, and served from 1864 to 1865 as an assistant surgeon during the American Civil War. After the war he was employed by the Boston Society of Natural History, the Essex Institute, and the Peabody Academy of Science. He was a member of the United States Entomological Commission from 1877 to 1882, and was a professor of zoology and geology at Brown University from 1878 to 1905. Packard (Fig. 1) was a well-rounded naturalist, and wrote on several topics including crustaceans, myriapods, systematic entomology, and economic entomology. He served as chief editor of the journal American Naturalist for 24 years, from 1881 to 1905. He is remembered for his authorship of books including introductory entomology books such as "Guide to the study of insects" (1869), "A text book of entomology" (1898); systematics books such as "Monograph of the geometrid moths or Phalaenidae of the United States" (1876), "Monograph of the bombycine moths of America north of Mexico" in three volumes (1895, 1905, 1914); and economic entomology books such as "Injurious insects, new and little known" (1870), and "Insects injurious to forest and shade trees" (1881). He also authored "Lamarck: the founder of evolution; his life and work, with translations of the writings on organic evolution" in 1901. Packard died at Providence, Rhode Island, on February 14, 1905.

Packard, Alpheus Spring, Figure 1 **Alpheus Packard.**

References

Anon (1905) Alpheus Spring Packard, M.D., Ph.D. Entomol News 16:97–98
Essig EO (1931) A history of entomology. Macmillan, New York, NY, 1,029 pp
Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Paecilomyces

The genus *Paecilomyces* includes a number of plant, nematode, and insect pathogenic species. Of the fifteen entomopathogenic species, *P. farinosus* and *P. fumosoroseus* are used most often in laboratory studies and are therefore the best described. *Paecilomyces* is characterized by having flask-shaped phialides, or phialides with swollen base structures; the phialides taper into a distinct neck and generate conidia that are dry, hyaline, or slightly pigmented. These conidia adhere end-to-end, forming chains as they emerge. Synnematous growth often occurs on insects.

Paecilomyces farinosus has a broad host range, attacking a number of lepidopterans, coleopterans, hymenopterans and hemipterans. Larval stages of these insects are most readily infected, and a recent report on the identification of fungi infecting gypsy moth larvae shows that *P. farinosus* is actually the most prevalent hyphomycete species in these insects. Eggs of some hosts also can be invaded; for example, *P. farinosus* blastospores were observed to adhere to the sticky surface of sawfly eggs, germinate, and penetrate the egg chorion.

Paecilomyces is cultured easily on agar or under submerged conditions. Media such as Sabouraud dextrose or potato dextrose commonly are used. In one study, it was found that *P. farinosus* conidia produced on Sabouraud dextrose medium containing trehalose accumulated this carbohydrate. Trehalose is known to enhance desiccation tolerance so that propagules with a high content of this sugar may be stored longer, and therefore better suited for biocontrol purposes. It is possible that the trehalose in insect hemolymph provides enhanced survival capabilities to *in vivo*-produced conidia. The pathogenicity of *P. farinosus* towards sawfly larvae is improved by *in vivo* passaging and virulence lost during *in vitro* culture (attenuation) can be restored by passage through living hosts. Additionally, it has been suggested that in vivo growth improves infectivity because this process selects for propagules with relatively high levels of cuticle-degrading enzymes.

References

Hajek AE, Elkington JS, Humber, RA (1997) Entomopathogenic Hyphomycetes associated with gypsy moth larvae. Mycologia 89:825–829
Prenerová E, Weyda F (1992) An ultrastructural study of the fungus, *Paecilomyces farinosus* (Deuteromycotina) infecting the eggs of the spruce sawfly *Cephalcia abietis* (Insecta, Hymenoptera). In: Bennettová B, Gelbic I, Soldán T (eds) Advances in regulation of insect reproduction. Czech Academy of Science, Ceske Budejovice, Czech Republic, pp 231–242
Samson RA (1974) *Paecilomyces* and some allied Hyphomycetes. Studies Mycol 6:38–41

Paederina

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A subtribe of the subfamily Paederinae (Coleoptera: Staphylinidae). It now contains 14 genera, of which the most speciose is *Paederus*. The others are *Paederidus*, *Parameropaederus*, *Lobopaederus*, *Megalopaederus*, *Eupaederus*, *Diplopaederus*, *Oncopaederus*, *Allopaederus*, *Madecapaederus*, *Oreopaederus*, *Pachypaederus*, and *Uncopaederus*. Cladistic methods have not yet been used to study the phylogeny of this subtribe which contains 623 + described species, so the assignment of species to genera is subject to change.

► Dermatitis Linearis
► *Paederus*
► Pederin
► Rove Beetles (Coleoptera: Staphylinidae)

Reference

Frank JH (1988) *Paederus,* sensu lato (Coleoptera: Staphylinidae): an index and review of the taxa. Insecta Mundi 2:97–159

Paederus Fabricius (Coleoptera: Staphylinidae: Paederinae)

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One of the 14 genera of the subtribe Paederina of the subfamily Paederinae of the beetle family Staphylinidae. Hundreds of species of the genus *Paederus* have been described, from all continents except Antarctica and from many islands, especially in the tropics. Nevertheless, they form a very small proportion of the total number of known species of the huge family Staphylinidae (rove beetles).

Adults of most *Paederus* species are unusual among Paederinae in that they are active in broad daylight and climb on vegetation, especially in moist habitats (adults of most other Paederinae, indeed of most Staphylinidae, conceal themselves during daylight hours). Adults of some *Paederus* species are winged and can fly, whereas others are brachypterous or apterous, and flightless. Flight of winged adults has been recorded at night, when they are attracted to incandescent and fluorescent light. Adults of many species are known only from a few specimens, and seem to be rare. Adults of a few are at times very abundant, especially in tropical countries, and some of these serve as useful predators of agricultural pest insects, for example, on rice, maize, and sweetpotato in eastern and southern Asia, South America, and Africa.

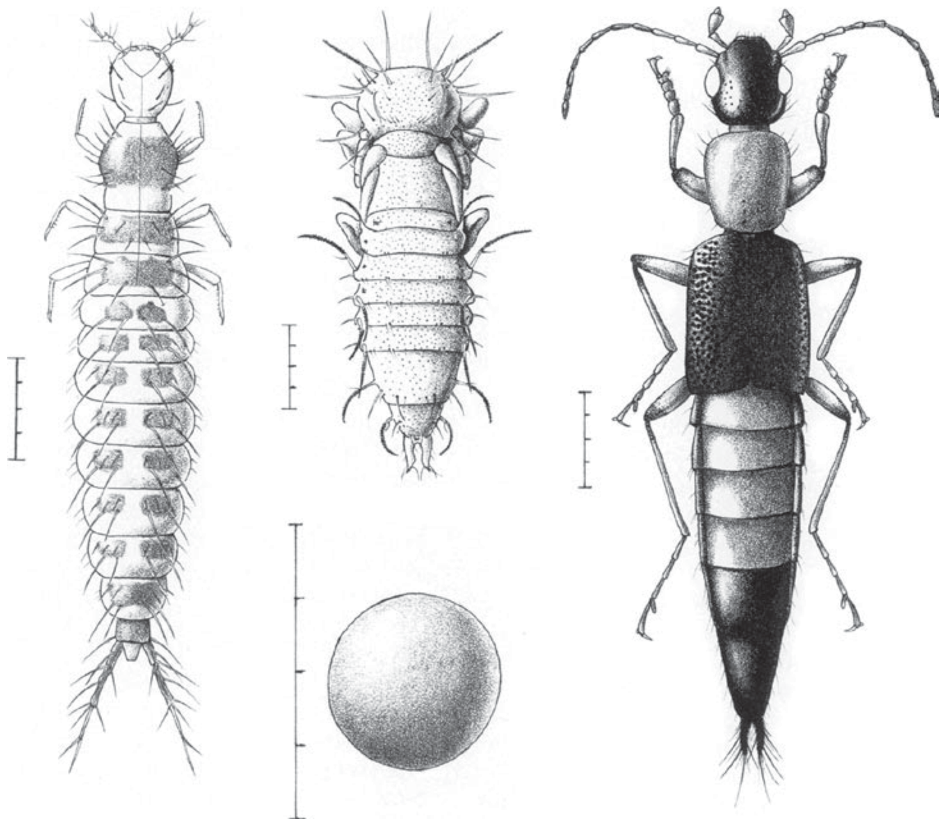
Paederus species (Table 1) have life cycles similar to those of other Staphylinidae, with egg, larval, and pupal stages (Fig. 2). The adult shown has the typical color pattern of black head, orange prothorax, and orange abdomen with black apex, and blue elytra. Like other members of the subfamily Paederinae, the larvae have only two developmental stages (instars); in contrast, most other Staphylinidae have three In temperate regions there may be only one generation per year, but in tropical regions there may be several. Timing and number of generations depends upon climate, in that annual variation (colder temperatures and drier conditions) limit what could become continuous generations under totally favorable conditions. Larvae prey on smaller invertebrates.

That adults of one or more species of *Paederus* produce a chemical toxin was known in Chinese medicine as early as 739 A.D., and the toxin was used medicinally. That adults of some *Paederus* species release toxins when crushed, and these toxins produce dermatitis on human skin was gradually made known to western medicine, beginning in 1901. This gave flying adults of some *Paederus* species pest status in some places and some times of year. The reason is that flying adults are attracted to incandescent and fluorescent light, thus come into contact with humans near such light, may accidentally be crushed by hands or other bodily parts on human skin, and are thus caused to release toxin. The beetles do not attack people! The toxins circulate in the hemolymph of adults, eggs, larvae, and pupae. Those that have caused dermatitis or have experimentally released toxins are listed in the following table.

***Paederus* Fabricius (Coleoptera: Staphylinidae: Paederinae), Table 1 Species causing dermatitis (D) or shown experimentally (E) to produce toxins, with current generic assignment**

Species	Location	D or E
Megalopaederus poweri (Sharp)	Japan	E
Paederidus albipilis (Solsky)	Tadzhikistan	E
Paederidus rubrothoracicus (Goeze)	France, Romania	E
Paederidus ruficollis (F.)	Georgia	E
Paederus alternans Walker	India, Vietnam	D
Paederus amazonicus Sharp	Brazil	D
Paederus brasiliensis Erichson	Argentina, Brazil	D
Paederus brevipennis Lacordaire	Italy	E
Paederus columbinus Laporte	Brazil, Venezuela	D
Paederus cruenticollis Germar	Australia	D
Paederus eximius Reiche = *crebre-punctatus* Eppelsheim	Kenya	D
Paederus ferus Erichson	Argentina	D
Paederus fuscipes Curtis	China, India, Indonesia, Iran, Italy, Japan, Russia, Taiwan, Thailand, Turkey	D
Paederus iliensis Coiffait	Iran	D
Paederus ilsae Bernhauer	Israel, Iran	D
Paederus laetus Erichson	Guatemala	D
Paederus limnophilus Heer	Romania	E
Paederus littoralis Gravenhorst	France, Italy	E
Paederus melampus Erichson	India	D
Paederus melanurus Aragona	Italy	E
Paederus ornaticornis Sharp = *irritans* Chapin	Ecuador	D
Paederus parallelus Weise	Japan	E
Paederus riparius (L.)	Russia	D
Paederus rufocyaneus Bernhauer	Malawi	D
Paederus rutilicornis Erichson	Brazil	E
Paederus sabaeus Erichson	Cameroon, Congo-Brazzaville, Congo-Kinshasa, Namibia, Nigeria, Sierra Leone, Tanzania, Uganda	D
Paederus signaticornis Sharp	Guatemala, Panama	D
Paederus tamulus Erichson	China	D

After Frank and Kanamitsu (1987) with slight update. The 28 species here listed are only a few of the 623 + species of the subtribe, and their generic assignment may change after future taxonomic revisions. Note that one of them is now assigned to genus *Megalopaederus*, and three to genus *Paederidus*. Species causing dermatitis in Malaysia, Papua New Guinea, and Sri Lanka have not been specifically identified.



Paederus Fabricius (Coleoptera: Staphylinidae: Paederinae), Figure 2 ***Paederus* egg, larva, and pupa, with *P. fuscipes* adult. From Frank JH, Kanamitsu K (1987) *Paederus* sensu lato (Coleoptera: Staphylinidae): natural history and medical importance. J Med Entomol 24:155–191, reproduced by permission of the Entomological Society of America.**

Various early assumptions about the chemical nature, site of production, and purpose of the toxins were later shown to be unfounded. The toxins have not been shown to be present in any group of beetles other than the subtribe Paederina, so are unique among beetles to this subtribe. Further, the toxins have been demonstrated to be present in very few of the species in the subtribe, most of which belong to the genus *Paederus*, whereas their presence could not be demonstrated in some species of the subtribe that have been tested. For the present, we must conclude that the toxins are absent from some, perhaps most, species of the subtribe. The toxins are described under Pederin.

► Dermatitis Linearis
► Paederina
► Pederin
► Rove Beetles (Coleoptera: Staphylinidae)

References

Frank JH (1988) *Paederus*, sensu lato (Coleoptera: Staphylinidae): an index and review of the taxa. Insecta Mundi 2:97–159

Frank JH, Kanamitsu K (1987) *Paederus* sensu lato (Coleoptera: Staphylinidae): natural history and medical importance. J Med Entomol 24:155–191

Kellner RL (2002) Molecular identification of an endosymbiotic bacterium associated with protein biosynthesis in *Paederus sabaeus* (Coleoptera: Staphylinidae). Insect Biochem Mol Biol 32:389–395

Kellner RLL, Dettner K (1996) Differential efficacy of toxin pederin in deterring potential arthropod predators of *Paederus* (Coleoptera: Staphylinidae) offspring. Oecologia 107:293–300

Paedogenesis

An unusual form of reproduction in which reproduction commences in the immature stage, usually by activation of the ovaries of immature parthenogenetic females.

Paedomorphosis

The retention of juvenile characters of the ancestral form by the later developmental forms or adult of the modern, descendent form.

Paenibacillus

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Although there are several species of endospore-forming bacteria in the genus *Paenibacillus*, only a few are the causative agents of disease in insects. These are not as well known or studied as the important insecticidal species, *Bacillus thuringiensis*, but they affect economically important insects and therefore have drawn some attention. These bacteria are *Paenibacillus larvae* subsp. *larvae*, *P. larvae* subsp. *pulvifaciens*, *P. popilliae* and *P. lentimorbus*.

Paenibacillus larvae subsp. *larvae* and *P. larvae* subsp. *pulvifaciens* are closely related, having about 90% DNA similarity. However, they are distinguishable at the subspecies level by SDS-PAGE of whole cell proteins, by DNA fingerprinting (AFLP analysis), by a few biochemical tests and by the pathology of the disease produced. *P. larvae* subsp. *larvae* causes American foulbrood and *P. larvae* subsp. *pulvifaciens* causes powdery scale disease in larval honeybees. The bacteria are gram positive, catalase negative and have fastidious nutrition. Larvae are infected by ingesting bacterial spores contaminating their food. Spores germinate in the larval midgut, penetrate the midgut epithelium by phagocytosis and produce a systemic bacteremia resulting in larval death. Vegetative cells sporulate in the dying larvae and provide a source of spores for further infections. Spores can survive for years in larval food, in soil, or in larval cadavers. Adult bees can carry bacterial spores in their digestive tract but are immune to the disease. The bacteria are susceptible to a variety of antibiotics, and oxytetracycline has been used prophylactically or to treat diseased colonies to suppress symptoms. There are reports of the development of bacterial resistance to this antibiotic, and its use is not allowed in some countries.

Paenibacillus popilliae and *P. lentimorbus* are the causative agents of milky disease in various larvae of the family Scarabaeidae. These two species are distinguishable by DNA similarity studies but are quite similar in the usual bacteriological tests. They are facultative, nutritionally fastidious, spore-forming, and present a gram positive cell wall profile although the Gram stain is reported to be negative during vegetative growth. It has been suggested that there should be a single species (*P. popilliae*) and that *P. lentimorbus* should be a subspecies within that species, a situation similar to that of *P. larvae*. The species were originally separated by the production of a parasporal inclusion by *P. popilliae* and the absence of this body in *P. lentimorbus*. However, the DNA similarity study demonstrated that most isolates (although not the type strain) of *P. lentimorbus* also produce paraspores. *P. popilliae*, the subject of most physiological studies, appears to lack a complete tricarboxylic acid cycle and is catalase negative. Although *P. popilliae* grows better in air than without air, growth is better in 10% oxygen than in the 21% oxygen present in air. It is possible that the enzyme deficiencies may be related to the inability of these bacteria to sporulate *in vitro*.

There is no direct evidence that the protein composing the parasporal body plays any role in the course of the disease process. The gene encoding the parasporal protein has been cloned and sequenced, and was shown to have significant similarity to genes encoding the parasporal proteins of *Bacillus thuringiensis*.

The course of infection in scarab larvae is initiated following ingestion of spores. Over the period of 2–4 weeks, spores germinate in the larval gut, vegetative cells penetrate the epithelium, proliferate in the hemolymph, and finally sporulate in the hemolymph. The dead larva displays a turbid or milky hemolymph giving the name "milky disease." As the larval cadaver disintegrates, spores are released into the soil and may be consumed by larvae feeding on plant roots. Insecticides containing *P. popilliae* spores have been produced by collecting larvae in the field, infecting them in the laboratory, blending the spores (and larval debris) with inert carrier, and dispersing the product into soil. Although the bacteria can be grown in bacteriological media, they sporulate poorly outside larvae, and this has frustrated attempts to produce large volumes of spores by fermentation techniques.

The inability of all these insect pathogenic paenibacilli to produce large quantities of spores outside larvae has been the subject of much research. A variety of empirical methods to achieve *in vitro* sporulation have been attempted without success. Until the underlying relationships between sporulation and the peculiarities of the metabolism of these bacteria are better understood, *in vitro* sporulation is likely to remain elusive.

References

Davidson EW (1973) Ultrastructure of American foulbrood disease pathogenesis in larvae of the worker honeybee, *Apis mellifera*. J Invertebr Pathol 21:53–61

Hanseh H, Brodsgaard CJ (1999) American foulbrood: a review of its biology, diagnosis and control. Bee World 80:5–23

Stahly DP, Andrews RE, Yousten AA (1991) The genus *Bacillus*: insect pathogens. In: Balows A, Truper H, Dworkin M, Harder W, Schleifer K (eds) The Procaryotes, a handbook on the biology of bacteria, 2nd edn. Springer-Verlag, New York, NY, pp 1697–1745

Paenibacillus larvae = (Bacillus larvae) Bacteria

The bacterium responsible for causing American foulbrood in honey bees.

► American Foulbrood

► *Paenibacillus*

Painter, Reginald Henry

Reginald Painter was born on September 12, 1901, at Brownswood, Texas, USA. He received a B.A. (1922) and M.A. (1924) from the University of Texas, and a Ph.D. from Ohio State University (1926). He immediately joined the faculty at Kansas State University, where he remained for his entire career except for brief periods in Honduras and Guatemala. Painter became widely recognized as the leading authority of plant resistance to insects. He worked cooperatively with plant breeders in the production of sorghum, wheat, and alfalfa varieties resistant to insect pests. He also documented the existence of insect biotypes that could overcome host plant resistance. He is remembered for his authorship of "Insect resistance in crop plants," which was the major synthesis and leading work on the subject for decades. Painter also had a strong interest in Bombyliidae, and he and his wife described several new genera and numerous new species from North and Central America, and redescribed many European species. Painter was a fellow of the Entomological Society of America and the American Association for the Advancement of Science, and was awarded the Gamma Sigma Delta International Award for Distinguished Service to Agriculture. He died on December 23, 1968, in Mexico City.

Reference

Anon (1969) Reginald Henry Painter 1901–1969. J Econ Entomol 62:759

Palaeosetidae

A family of moths (order Lepidoptera). They also are known as minature ghost moths.

► Miniature Ghost Moths

► Butterflies and Moths

Palaeosetode

A family of moths (order Lepidoptera). They also are known as minature ghost moths.

► Minature Ghost Moths

► Butterflies and Moths

Palaephatidae

A family of moths (order Lepidoptera). They also are known as Gondwanaland moths.

► Gondwanaland Moths

► Butterflies and Moths

Palearctic Realm

The Palearctic realm is a zoogeographic region encompassing Europe and Asia except for Southeast Asia. The fauna consists of such animals as vireos, wood warblers, deer, bison and wolves, and is quite similar to the fauna of the Nearctic realm (North America). Thus, the Palearctic and Nearctic realms often are combined into a larger region called the Holarctic realm.

► Zoogeographic Realms

Paleoentomology

The study of fossil and extinct insects.

Pale Lice

Members of the family Linognathidae (order Phthiraptera).

► Chewing and Sucking Lice

Paleopterous

Lacking the ability to fold the wings backward over the abdomen.

Pale Western Cutworm, *Agrotis orthogonia* (Morrison) (Lepidoptera: Noctuidae)

The larvae of this moth attack wheat in the Great Plains region of USA.

► Wheat Pests and Their Management

Palidium

A portion of the raster in scarab larvae.

Palindrome

A DNA sequence in two strands that reads the same in both directions.

Pallopteridae

A family of flies (order Diptera). They commonly are known as flutter flies.

► Flies

Palm Beetles

Members of the family Mycteridae (order Coleoptera).

► Beetles

Palmetto Beetles

Members of the family Smicripidae (order Coleoptera).

► Beetles

Palm Insects

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The Palmae are one of the largest plant families, with about 2,600 species. The family is concentrated in the humid lowland tropics, extending to extra-tropical warm regions of the world, including deserts and regions with a Mediterranean climate. A few cold-hardy species can be grown outdoors as far north as Britain. Members of the palm family are easily recognized by their large leaves, or fronds, which occur in two general forms, pinnate and palmate. Palms range in size from less than a meter tall at maturity to arborescent forms such as *Ceroxylon* spp., which may reach a trunk height of more than 65 m and are among the tallest plants in the plant kingdom. Different species have solitary or multiple stems, and stem diameters range from less than a centimeter (e.g., *Chamaedorea* spp.) to 1.8 m in *Jubaea chilensis* (Molina) Baillon.

Palms are important components of the plant communities of warm regions. Their broad fronds and deep leaf axils provide shelter for birds, reptiles, mammals and other animals. The fruits of many species of palms are a prime food source for vertebrate animals. The fronds, leaf axils and stems support a diversity of epiphytes.

Many of the species are sources of economic products, including fruits, beverages, and fiber products. Some species have been cultivated since prehistoric times, notably the coconut palm, *Cocos nucifera* L., the African oil palm, *Elaeis guineensis* Jacquin, the date palm, *Phoenix dactylifera* L., and the peach-palm, *Bactris gasipaes* Kunth. Commercial palm cultivation has expanded along with a general expansion in agriculture beginning in the nineteenth century, and the use of palms as landscape and interior plants has increased dramatically in recent decades. Increasing interest in the culture of palms, along with recognition of the importance of tropical life in the world ecosystem, has stimulated a need for knowledge of the insects associated with these plants.

Palms as Hosts of Insects

The foliage, stems, roots, flowers, and fruits of palms provide food for insects that are undoubtedly important components of their respective ecosystems. Palms constitute a highly stable resource for insects that are adapted to them. They produce foliage periodically throughout the year, so that not only is green tissue continually available to leaf-feeders, but also is present both as fresh foliage and in subsequent stages of maturity. Thus, palms may be food sources for both insects that feed on young foliage and those adapted to feed on mature foliage. The broad fronds are relatively easy targets for insects searching for food sources. Other matters being equal, insects can more readily colonize a large palm leaf than the multitude of small leaves of dicotyledons. The stiff foliage of palms provides superior protection from heavy rain and sunlight. On the other hand, the rigidity of palm foliage is largely due to its high fiber content, which poses a challenge to phytophagous insects.

The stems of palms are highly fibrous, and in some species are extremely hard, especially in the peripheral zone ("rind"). As in monocotyledons in general, the stems, once formed, do not undergo radial growth. There is no cambium or bark, thus no habitat for bark beetles. Some important insect pests of palms are species that bore in the fleshy tissue of buds or rachises. Some insects that bore in the petiole or bud may enter the stem tissue. Few insect species bore directly into palm stems.

The roots of palms are poor nutritionally except at the root tips, and few insects are associated with them.

Palm flowers are generally entomophilous. The inflorescences typically support massive numbers of small, shallow flowers of pale color, often with a strong fragrance. Flowers are produced at different intervals in different species, e.g., monthly in coconut, yearly in date palm, and at the end of the life of the plant in *Corypha* spp.

Although many palm fruits serve as important food resources for vertebrate animals, they are probably less important as food sources for insects.

Severe damage by insects to palms in the wild has been reported, but this is probably rare. As in other crops, palms seem to be most susceptible to destruction by insects when grown in dense monocultures.

The Insect Fauna of Palms

There are striking similarities in the insect fauna associated with palms in different regions. Most of the significant palmivorous insect species are in one of six orders: Orthoptera, Phasmatodea, Hemiptera, Thysanoptera, Coleoptera, and Lepidoptera. Within each of these orders, palmivorous insects are concentrated in particular families, most of which are represented by different species in disparate regions.

Insects that are restricted to palms usually attack a range of several different species of this family, although some insects are restricted to a single genus or species e.g., *Xylastodoris luteolus* Barber (Hemiptera: Thamastocoridae), which is known only on Cuban royal palms, *Roystonea regia* [Kunth] O. F. Cook. Probably no species of insect is adapted to feed on all species of palms. Some palmivorous species also feed on bananas, pandans, or other large monocotyledons, but not on dicotyledons. Many of the pests of palms in cultivation are highly polyphagous species that also attack dicotyledons, such as citrus, coffee, cacao, etc.

The diversity of palmivorous insects in different regions tends to reflect the respective diversity of palms: greater numbers of palmivorous species are known in regions rich in palms, including Southeast Asia and South America, and fewer in regions poor in palm diversity such as tropical Africa.

Defoliators

Caterpillars (Lepidoptera) that feed on palm foliage are found in virtually all palm-growing regions except desert regions, such as in North Africa and the Middle East. Psychidae, Gelechioidea, Zygaenidae, Limacodidae, Hesperiidae, and Nymphalidae are represented by species on palms in most regions.

Important species of bagworms (Psychidae) on palms include *Oiketicus kirbyi* Guilding in tropical America, and *Metissa plana* Walker, *Cremastopsyche pendula* Joanna, and *Mahasena corbetti* Tams (the coconut case caterpillar), in Southeast Asia.

Species of Gelechioidea include the coconut blackheaded caterpillar, *Opisina arenosella* Walker (Oecophoridae), of southern Asia, the coconut flat moth, *Agonoxena argaula* Meyrick (Agonoxenidae) of Oceania, and the palm leaf skeletonizer, *Homaledra sabalella* (Chambers)(Coleophoridae) of the southeastern U.S. and western Caribbean.

The coconut leaf moth, *Artona catoxantha* Hampson, of Southeast Asia, and *Homophylotis catori* Jordan, a pest of coconut palms in West Africa, are two of several important species of palmivorous Zygaenidae. The levuana moth, *Levuana iridescens* Bethune-Baker, decimated coconut plantations in Fiji in the early part of the twentieth century, but became nearly (or possibly completely) extinct as a result of a famous biological control campaign in which *Bessa remota* Aldrich (Diptera: Tachinidae), a natural enemy of *A. catoxantha* in the Malay Peninsula, was imported and established in Fiji.

Species of the zygaenoid family Limacodidae occur on palms in probably all humid tropical regions, and are richest in Southeast Asia, where more than 60 species have been reported on palms. Certain species of Limacodidae are among the most damaging of palm defoliators.

Larvae of many species of skippers (Hesperiidae) feed on monocotyledons, and species of this family are defoliators on palms in most humid tropical regions.

The brushfooted butterflies (Nymphalidae) are represented on palms in the eastern hemisphere by species of Amathusiinae, and in the western hemisphere by Brassolinae and Satyrinae. The adults are large, showy butterflies, much sought after by collectors, and their large, gregarious larvae are highly destructive to foliage.

Worldwide, beetles (Coleoptera) are second in importance to Lepidoptera as palm defoliators, but in certain localities they may equal or surpass Lepidoptera in this respect. Most are in the subfamily Hispinae of the leaf beetle family Chrysomelidae. Most are leaf miners, but a few are superficial leaf feeders.

Several species each of walking-sticks (Phasmatodea) and longhorned grasshoppers (Orthoptera: Tettigoniidae) are important pests of coconut palms in some islands of Oceania. They are polyphagous, their status as pests of coconut palms reflecting the overwhelming importance of these palms on some Pacific islands.

Sap-Feeders

Relatively few true bugs (Hemiptera: Heteroptera) feed on palm foliage, but several species are important pests. *Stephanitis typica* Distant (Tingidae) is widely distributed on coconut palms, bananas, and probably other arborescent monocotyledons in Asia. It is sometimes considered a pest in coconut palm nurseries, and has been shown to be a vector of Kerala coconut decline, also known as coconut root (wilt) disease, of mature coconut palm in southern Asia.

Thaumastocoridae are a small family closely related to Tingidae with 17 known species, six of which are found in the western hemisphere, specifically on palms in tropical America. The 11 eastern hemisphere species are associated with various dicotyledons.

There are only two species of Miridae, the largest family of Heteroptera, of significance on palms: *Carvalhoia arecae* Miller and China, a pest of betel-nut palm, *Areca catechu* L., in India, and *Parasthenaridea arecae* Miller, which has a similar biology in the Malay Peninsula.

Several species of *Lincus* (Pentatomidae) are considered vectors of protozoans that cause marchitez sorpresiva (sudden wilt) of African oil palm, and heartrot of coconut palms, respectively, in northern South America.

The Auchenorrhyncha on palm foliage are much more diverse than the Heteroptera. As in other major taxa, palmivorous species are concentrated in certain families, notably the superfamily Fulgoroidea (planthoppers). The fulgoroid family Derbidae has the highest diversity and widest distribution of Auchenorrhyncha on palms. Only the adults visit palms, typically in sparse numbers. Their nymphs are believed to feed on fungi, and the numbers on palms of one species, *Cedusa inflata* (Ball), were shown to be related to the proximity of decaying plant debris.

Although Cixiidae are less diverse on palms than Derbidae, a few palm-associated species of this family are widely distributed. Attention has been drawn to this family because two species are considered vectors of palm diseases. *Myndus crudus* Van Duzee is a vector of lethal yellowing (LY), which affects almost 40 species of palms in Florida and parts of the Caribbean Region. This insect passes its immature stages on grasses and the adults move to palms. Thus, ground cover management in plantations has been investigated as a method of reducing LY vector populations. *Myndus taffini* Bonfils is a vector of foliar decay of coconut palm in Vanuatu.

Although Cicadellidae are the largest family of Auchenorrhyncha, leafhoppers are not well represented on palm foliage.

The Sternorrhyncha are the best represented suborder on palms, Coccoidea accounting for most of this diversity. Of the few aphid species (Aphididae) reported on palms, two very similar species of *Cerataphis* of an unusual aphid subfamily, Hormaphidinae, have been spread to many tropical countries where they are known only on palms and considered occasional pests. Often their presence is signaled by a thick crust of sootymold over the palm foliage, along with multitudes of honeydew-seeking ants. In their native Southeast Asia, they alternate between palms and certain dicotyledonous trees.

Whiteflies (Aleyrodidae) are more diverse in the tropics than the Aphididae, and nearly 50 species have been reported on palms. Whiteflies probably can be found on palms in most tropical localities, but are not known on date palms in arid regions. Their populations are typically sparse, except in a few recorded cases in which whiteflies recently introduced into new areas have achieved dense enough populations to be considered pests.

Ten of the 20 families of the superfamily Coccoidea have species reported on palms, and it is the superfamily of insects represented on palms by the most species. Palms appear to be particularly favorable hosts for these insects. Coccoidea invade new host plants primarily via the wingless crawler stage (first instar), thus the large fronds of palms and their "evergreen" quality (i.e., continual availability) facilitate the establishment of these passively dispersed insects, and their fibrous tissues provide firm surfaces upon which Coccoidea fabricate their scales. The larger coccoid families, viz., mealybugs (Pseudococcidae), soft scale insects (Coccidae), and armored scale insects (Diaspididae), each contain numerous species that infest palms, and species of each group are known only on palms. As discussed below, several taxa of Coccoidea have special relationships with palms.

The armored scale insects comprise the largest family of Coccoidea. Of the more than 100 species of this family reported from palms, about 15 are recognized as important pests of these plants. Most of the latter are widely distributed, polyphagous insects that are pests of various crop trees and ornamental plants in addition to palms. Among the most notorious of these is the coconut scale, *Aspidiotus destructor* (Signoret), which originated in the tropics of the eastern hemisphere and is now pantropical. Classical biological control of this insect has been successful in many countries but not in others.

The white date scale, *Parlatoria blanchardi* (Targioni-Tozzetti), is an example of an armored scale insect reported exclusively on palms. It is especially frequent on palms of the date palm genus, *Phoenix*. Native to North Africa and the Middle East, where it is sometimes a serious pest, it was introduced accidentally into the date-growing region of the southwestern U.S. during the late 1800s, but was eradicated after a long campaign.

Several families of Coccoidea have special relationships with palms and are thus of exceptional interest to coccidologists. The pit-scale family, Asterolecaniidae, has about 400 species, 29 of which are reported only from palms. Many species of this family induce pit-like galls on their hosts, a characteristic not shared with the palm-infesting species. Phoenicococcidae and Halimococcidae are restricted to palms and related monocotyledons, as is *Comstockiella*, which is a genus of uncertain familial status. Beesoniidae are a family of nine species, four of which are found on palms in tropical America. Curiously, the five species native to the tropics of the eastern hemisphere are gall-makers on dicotyledonous trees.

Thysanoptera are usually not particularly common on palms, but certain species, including the greenhouse thrips, *Heliothrips haemorrhoidalis* (Bouché), a ubiquitous and highly polyphagous pest, sometimes causes superficial damage to palm foliage.

Pests of Flowers and Fruits

The inflorescences of palms may be attacked by various insects, whose feeding causes immature dropping of flowers and fruits. Examples include caterpillars of *Tirathaba* spp. (Galleriidae) and *Batachedra* spp. (Coleophoridae), and a stink bug, *Axiagastus cambelli* Distant (Hemiptera: Pentatomidae). Some species of weevils consume floral parts of palms, in the process serving as pollinators.

Fruits of palms are more important food sources for birds and mammals than for insects. Certain true bugs (Hemiptera: Heteroptera) including *Amblypelta cocophaga* China in the Solomon Islands and *Pseudotheraptus wayi* Brown (Coreidae) in Africa, attack fruits of various plants including young coconut fruits, causing premature fruit-drop. Scale insects that infest palm fruits are generally eurymerous species that also infest leaves, stems, etc.

Nitidulid beetles such as *Carpophilus hemipterus* (L.), *C. dimidiatus* (F.), *C. humeralis* (F.), and *Haptoncus luteolus* (Erichson), are economically important pests of ripening and curing dates in the Coachella Valley of California. Certain varieties of dates are very susceptible to the date stone beetle, *Coccotrypes dactyliperda* (F.) (Scolytinae). Females of this beetle oviposit in unripened fruit and the larvae penetrate the seed and develop inside, while subsequent generations may develop in fruit tissue.

Fruit flies (Diptera: Tephritidae), a major fruit infesting family, do not normally infest palm fruits.

Bud, Petiole, Stem and Root Borers

Several species of scarab beetles (Scarabaeidae) in the subfamily Dynastinae are pests of palms, the most notorious of which is the coconut rhinoceros beetle, *Oryctes rhinoceros* L., a pest of coconut palm in Oceania. The adults bore into the bud, so that when the leaves unfold, large portions have been consumed. The grubs live in decaying vegetation. Several additional species of *Oryctes* are pests of palms in Asia and Africa. In tropical America, several species of *Strategus* are known to bore in the stem bases, or in roots of seedling palms.

Jebusea hammerschmidti Reich (Coleoptera: Cerambycidae) is an important pest of date palms. The adult longhorned beetle females oviposit on palm foliage, and larvae bore into petioles and eventually may enter the trunk.

Dinapate wrightii Horn (Coleoptera: Bostrichidae) bores into the crown and then down into trunk of mature palms, including *Washingtonia* spp. and *Phoenix* spp. Known until recently only in southern California, this species has extended its range in the southwestern U.S. This largest bostrichid in the world (30–50 mm long) makes extensive galleries that weaken the trunk so that it may break in high winds. *Dinapate hughleechi* Cooper is a similar species on palms in Mexico.

The grubs of several species of *Rhynchophorus* (Coleoptera: Curculionidae) bore in the meristem (bud) and sometimes from there into the stems of palms. These weevils include *R. palmarum* (L.) in the American tropics, *R. cruentatus* (F.) in the southeastern U.S., *R. phoenicis* (F.) in Africa, and *R. ferrigeneus* Olivier, the latter which is currently the most widely distributed, having been spread from Asia and Oceania to Africa, the Middle East, and more recently to Southern Europe. *Rhynchophorus palmarum* is a significant pest by itself but it can also vector the red ring nematode, *Bursaphelenchus cocophilus* (Cobb), which causes red ring, a lethal disease of coconut and African oil palms in the American tropics, and little leaf, a chronic disease of these palms.

A second group of weevils important on palms is the tribe Sphenophorini, the New and Old World billbugs. *Metamasius* has 15 species that are reported on palms in tropical America. *Metamasius hemipterus* (L.), considered probably the most damaging, bores into petiole bases, often causing enough damage that they break off. Sometimes they penetrate far enough into the stem to cause superficial damage. *Rhabdoscelus obscurus* (Boisduval) causes similar damage to palms in Queensland, Australia.

Ambrosia beetles (Curculionidae: Scolytinae and Platypodinae) are among the few beetles that bore directly into palm stems (not via the bud or petioles). Extremely small insects, they make narrow galleries in which they culture specific fungi on which they feed. They do not feed on the tissue of palms themselves. They usually attack only stressed palms.

Castnia daedalus Cramer (Lepidoptera: Castniidae) is a large moth whose caterpillars bore between petiole bases and the trunk of palms, causing the fronds to buckle and sometimes damaging the stem surface. It is widely distributed in South America.

Opogona sacchari (Bojer)(Lepidoptera: Tineidae) is a small moth whose larvae bore in stems of various monocotyledons, including some palms, mostly under nursery conditions. The larvae are apt to begin the attack by feeding on damaged stem tissue, and then may continue feeding and making a gallery in healthy stem tissue, at times penetrating into the roots.

The larvae of *Sagalassa valida* Walker (Lepidoptera: Glyphipterigidae) bore in roots of African oil palm in Colombia. Females oviposit near the base of the stems, from which the larvae penetrate the roots, hollowing them out and sometimes causing extensive death of primary roots.

Pollinators

Although in date palms and other species, pollen transfer is partially or exclusively anemophilous, i.e., by air currents, the vast majority of palm species have entomophilous flowers, i.e., that are pollinated by insects. Thus, palm flowers are often scenes of intense insect life. Coleoptera, Hymenoptera, and Diptera are the best-represented orders. Weevils (Coleoptera: Curculionidae) and stingless bees (Hymenoptera: Apidae: Meliponinae) are particularly important. Lepidoptera are of far less importance in palm pollination. Other insects, e.g., Thysanoptera, may be significant in pollinating some species in some localities. Some pollinators, e.g., certain weevils, also consume somatic floral tissue, the damage of which may be vastly offset by their benefits as pollinators. *Elaeidobius kamerunicus* (Faust) (Curculionidae), the major pollinator of African oil palm in West Africa, has been introduced into other tropical countries to increase fruit production in this palm.

References

Broschat TK, Meerow AW (2000) Ornamental palm horticulture. University Press of Florida, Tallahassee, FL, 255 pp

Carpenter JB, Elmer HS (1978) Pests and diseases of the date palm. Agriculture Handbook No. 527, U.S. Department of Agriculture, Washington, DC, 42 pp

Cock MJW Godfray HCJ, Holloway JD (eds) (1987) Slug and nettle caterpillars. The biology, taxonomy and control of the Limacodidae of economic importance on palms in south-east Asia. CABI Publications, Wallingford, UK, 270 pp

Corner EJH (1966) The natural history of palms. Weidenfeld and Nicholson, London, UK, 393 pp

Howard FW, Moore D, Giblin-Davis RM, Abad RG (2001) Insects on palms. CABI Publications, Wallingford, UK, 400 pp

Jones DL (1995) Palms throughout the world. Smithsonian Institution Press, Washington, DC, 410 pp

Lepesme P (1947) Les insectes des palmiers. Paul Lechavalier, Paris, France, 903 pp

Tothill JD, Taylor THC, Paine RW (1930) The coconut moth in Fiji. Imperial Bureau of Entomology, London, UK

Palm Moths (Lepidoptera: Agonoxenidae)

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Palm moths, family Agonoxenidae, are a small family of 68 known species, in all faunal regions for subfamily Blastodacninae but only South Pacific for four of the species of subfamily Agonoxeninae (plus one from Argentina). The family is part of the superfamily Gelechioidea in the section Tineina, subsection Tineina, of the division Ditrysia. Adults small (6–15 mm wingspan), with head smooth-scaled; haustellum scaled; labial palpi recurved; maxillary palpi small, 1-segmented. Wings elongated, usually with very narrow hindwings with long fringes. Maculation varied, often yellow or brown shades with some markings, but a few are colorful and with iridescent markings. Adults are diurnal. Larvae are leaf skeletonizers, or borers in leaves, stems, and fruits; rarely gall-makers. Host plants mostly in Rosaceae for Blastodacninae and Palmae for Agonoxeninae. A few are economic.

References

Bradley JD (1965) A comparative study of the coconut flat moth (*Agonoxena argaula* Meyr.) and its allies, including a new species (Lepidoptera, Agonoxenidae). Bull Entomol Res 56:453–472

Diakonoff AN (1939) Notes on Microlepidoptera. II. Remarks on some species of the genus *Blastodacna* Wocke (Fam. Cosmopterygidae). Tijdschrift voor Entomol 82:64–77

Hodges RW (1997) A new agonoxenine moth damaging *Araucaria araucana* needles in western Argentina and notes on the Neotropical agonoxenine fauna (Lepidoptera: Gelechioidea: Elachistidae). Proc Entomol Soc Washington 99:267–278

Karsholt O (1997) The genus *Chrysoclista* Stainton, 1854 in Europe (Lepidoptera, Agonoxenidae). Entomol Meddelelser 65:29–33

Lucchese E (1942) Contributi alla conoscenza dei lepidotteri del melo 5. Blastodacna putripennella Zell. Bolletino Rurale del Laboratorio di Entomologia Agraria Portici 5:175–195

Palm Scales

Members of the families Phoenicococcidae and Halimococcidae, superfamily Coccoidea (order Hemiptera).

► Scale Insects and Mealybugs

► Bugs

Palm, Thure

Thure Palm was born near Ystad in southern Sweden on January 30, 1894. He became interested in insects as a child, and in 1918 became a forestry officer. About 1926 he began to study beetles of importance to forestry and in 1951 published a book on insects of importance to wood and bark in northern Sweden, and in 1959 another for middle and southern Sweden. He also published over 200 papers on systematics, ecology, and faunistics, and was one of the most recognized Swedish coleopterists of modern time. He received an honorary doctoral degree from the University of Lund in 1953. He died at Malmö, Sweden, on May 2, 1987.

Reference

Herman LH (2001) Palm, Thure. Bull Am Mus Nat Hist 265:121–122

Palp (pl., palps)

Small, paired, segmented sensory appendages attached to the maxilla or labium; more correctly called palpus (Figs. 3 and 4).

► Palpus

► Mouthparts of Hexapods

Palpifer

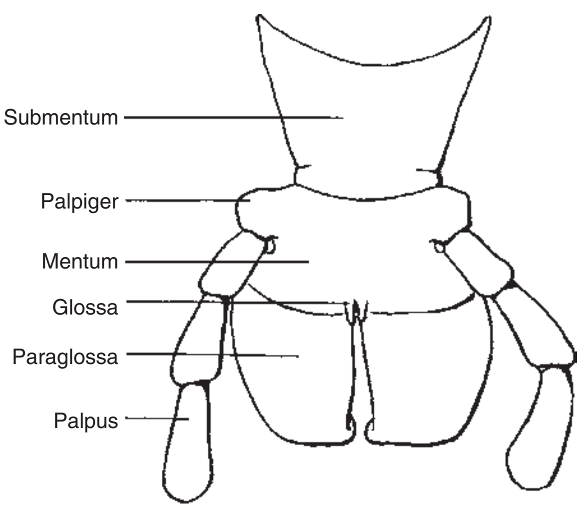
A small sclerite that bears the maxillary palpus, and is connected to the stipes.

► Mouthparts of Hexapods

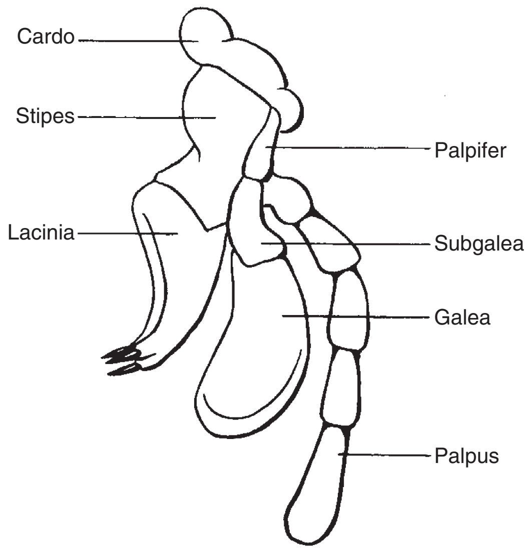
Palpiger

A small sclerite that bears the labial palpus, and is connected to the mentum (Fig. 4).

► Mouthparts of Hexapods



Palp (pl., palps), Figure 3 **External aspect of the labium in an adult grasshopper, showing some major elements.**



Palpiger, Figure 4 **External lateral aspect of the left maxilla in an adult grasshopper, showing some major elements.**

Palpus (pl., palpi)

Small, paired, segmented sensory appendages attached to the maxilla or labium; also called palp (Figs. 3 and 4).
► Mouthparts of Hexapods

Pamphilidae

A family of sawflies (order Hymenoptera, Suborder Symphyta). They commonly are known as web-spinning or leaf-rolling sawflies.
► Wasps, Ants, Bees and Sawflies

Pamphiliidae

A family of sawflies (order Hymenoptera, suborder Symphyta). They commonly are known as web-spinning or leaf-rolling sawflies.
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Panoistic Ovaries

Ovaries in which the oocytes lack nurse cells (contrast with meroistic ovaries).

Panorpidae

A family of scorpionflies (order Mecoptera). They are known as common scorpionflies.
► Scorpionflies

Panorpodidae

A family of scorpionflies (order Mecoptera). They commonly are known as short-faced scorpionflies.
► Scorpionflies

Panthophthalmidae

A family of flies (order Diptera).
► Flies

Panzootic

A condition wherein a disease affects all, or a large proportion of the animals of a region; extensively epizootic.

Paper Wasps

Members of the family Vespidae (order Hymenoptera).
► Wasps, Ants, Bees and Sawflies

Papilionidae

A family of butterflies (order Lepidoptera). They commonly are known as swallowtails.
► Swallowtails
► Butterflies and Moths

Papilla (pl., papillae)

A small nipple-like elevation.

Parabiosis

Use of the same nest and sometimes the same odor trails by colonies of different species, which nevertheless maintain separate broods.

Paradichlorobenzene

This solid, white, aromatic product is also known as 1,4 dichlorobenzene. It is most commonly used as a deodorizer in urinals, but also as an insect repellent and insecticide to protect wool products from clothes moths and dermestid beetles. It is sold as "moth flakes" and "para crystals," among others, and competes with naphthalene for this market. It sublimates are room temperatures, forming a vapor, and has proven useful to entomologists to protect insect collections from dermestids. Its toxicity should be considered, however, if prolonged exposure is anticipated. Outdoor uses include application around the bases of fruit trees to deter oviposition and survival of wood boring insects such as peach tree borer, *Synanthedon exitiosa* (Lepidoptera: Sesiidae), though this is not a legal use in all areas.

Paraglossa

A paired labial structure, often jointed, found at each side of the ligula.
► Mouthparts of Hexapods

Parajapygidae

A family of diplurans (order Diplura).
► Diplurans

Parallel Evolution

The evolution along similar lines by taxa that were separated geographically at an earlier stage in history.

Parameres

Structures in the male genitalia of insects; lobes at the base of the aedeagus.
► Abdomen of Hexapods

Paraphrynoveliidae

A family of bugs (order Hemiptera).
► Bugs

Paraphyletic

A taxonomic group that does not include all the descendents of an ancestral form.
► Phylogenetics

Paraphyletic Group

Taxa that do not contain all the recent descendents of a single past species. Insect orders are now not clearly polyphyletic, though some artificial classifications in the past or present are polyphyletic (e.g., grouping all wingless insects into a single taxon) (contrast with polyphyletic and monophyletic groups).

Parapodium

Primitive or false legs or feet. Segmented abdominal processes of symphylans.

Paraproct

One of the two lobes bordering the anus and formed from the ventrolateral parts of the epiproct.
► Abdomen of Hexapods

Parasite

An organism that obtains its food by feeding on the body of another organism, its host, without killing the host.

Parasitic Castration

Any process that interferes with or inhibits the production of mature ova or spermatozoa in the gonads of an organism.

Parasitic Flat Bark Beetles

Members of the family Passandridae (order Coleoptera).

► Beetles

Parasitic Hymenoptera (Parasitica)

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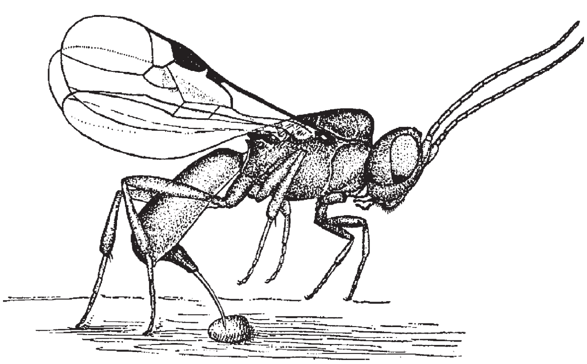
The order Hymenoptera has traditionally been separated into three groups: the suborder Symphyta (sawflies), and the suborder Apocrita, which is subdivided into the Aculeata (bees, wasps and ants) and Parasitica (= Terebrantia). Whereas the Symphyta are monophyletic and the Aculeata holophyletic, the Parasitica are a paraphyletic assemblage of taxa that does not have a formal taxonomic status. But the families comprising the Parasitica share a similarity in basal biology and fill important ecological niches that are of great economic importance, which makes the group a useful one to distinguish. When discussing this group, most modern workers use the term "parasitoid" to denote insects whose larvae feed on and usually kill an arthropod host, to distinguish them from true parasites, which generally do not kill their hosts. The higher classification is still unsettled, but one current scheme recognizes 11 superfamilies and 48 families. Other hymenopteran parasitoids are found in both the Symphyta (family Orussidae) and Aculeata (superfamily Chysidoidea and families Scoliidae, Tiphiidae, Mutillidae, Sapygidae, Pompilidae, Rhopalosomatidae and Bradynobaenidae) (Fig. 5).

Adult Morphology

Given their paraphyletic status, the Parasitica have no unique morphological character, though they are usually smaller and have reduced wing venation compared to the symphyta and Aculeata. Additionally, the Symphyta have no constriction between their first (propodeum) and second (petiole) abdominal segment (although in some very small Parasitica the petiole is reduced in size, and the constriction is not easily evident), while the ovipositor in the Aculeata has been modified to form a sting and no longer acts as an egg-placing device. Adult Parasitica range in body length (excluding antennae and ovipositors) from 0.2 mm to 6 cm, but the vast majority are 5 mm or less. The reduction or absence of wings is found in many families.



Parasitic Hymenoptera (Parasitica), Figure 5 Adult of *Chelonous shoshoneanorum* Viereck (Hymenoptera: Braconidae) ovipositing within egg of moth (from U.S. Department of Agriculture).

Parasitic Hymenoptera (Parasitica), Table 2 **Families of the parasitica, their mode of parasitism, and hosts**

				Mode		Host	
Superfamily	Family	1°	2°	Hemi	Holo	Arach	Phyto
Ichneumonoidea	Braconidae	++	+	++	++		+
	Ichneumonidae	++	++	++	++	++	
Evanioidea	Evaniidae	++		++			
	Gasteruptiidae	++			++		
	Aulacidae	++			++		
Stephanoidea	Stephanidae	++			++		
Megalyroidea	Megalyridae	++			++		
Trigonalyoidea	Trigonalyidae	++	++		++		
Cynipoidea	Ibaliidae	++			++		
	Liopteridae	++			++		
	Figitidae	++	++		++		
	Cynipidae	N/A	N/A			++	
Proctotrupoidea	Vanhorniidae	++			++		
	Pelecinidae	++			++		
	Austroniidae						
	Maamingidae						
	Monomachidae	++			++		
	Peradeniidae						
	Renyxidae						
	Roproniidae				?		
	Heloridae	++			++		
	Diapriidae	++	+		++		
	Proctotrupidae	++			++		
Platygastroidea	Scelionidae	++	+	++	++	++	
Platygastridae		++		++	++		++
Ceraphronoidea	Ceraphronidae	++	++	++	++		
	Megaspilidae	++	++	++	++		
Mymaromma-toidea	Mymarommatidae						

Parasitic Hymenoptera (Parasitica), Table 2 Families of the parasitica, their mode of parasitism, and hosts (Continued)

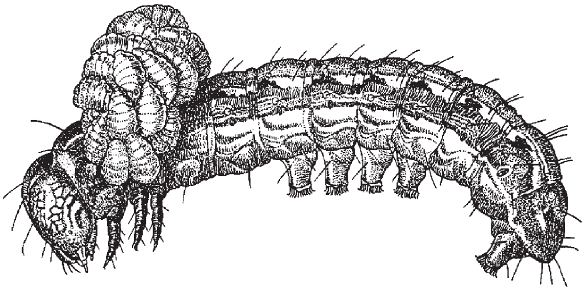
				Mode		Host	
Superfamily	Family	1°	2°	Hemi	Holo	Arach	Phyto
Chalcidoidea	Mymaridae	++		++	++		
	Chalcididae	++	++		++		
	Leucospidae	++			++		
	Eurytomidae	++	+	++	++	+	++
	Pteromalidae	++	++	++	++	+	+
	Agaonidae	N/A	N/A			++	
	Torymidae	++	+	++	++		+
	Ormyridae	++	+?		++		
	Perilampidae	++	++	++	++		
	Eucharitidae	++			++		
	Eupelmidae	++	++	++	++	++	
	Tanaostigmatidae	++			++		++
	Encyrtidae	++	++	++	++	++	
	Aphelinidae	++	++	++	++		
	Signiphoridae	++	++	++	++		
	Tetracampidae	++			++		
	Rotoitidae						
	Eulophidae	++	++	++	++	++	+
	Elasmidae	++	++		++		
	Trichogrammatidae	++	+	++	++		

Sexual dimorphism occurs in several groups as well, but is usually limited to differences in antennae, abdominal morphology and color patterns; the most extreme cases are found in the Agaonidae, which have been highly modified as pollinators of figs.

Immature Stages

There are several morphological egg types. The hymenopteriform is several times longer than wide with rounded poles, and is the most common. The acuminate egg is typically long and narrow, and is adapted for extrusion from longer ovipositors. The stalked egg is elongate with a constricted stalk-like projection from one or both poles. The pedicellate egg is a modification of the stalked egg, in which one end is anchored to the host. The encyrtidiform egg resembles a double-bodied dumbbell while in the ovary, but after oviposition one end collapses and it then resembles a stalked egg. Eggs also can be (Fig. 6) classified as lecithal (which are relatively larger and more yolky), or alecithal (which are smaller and physiologically less expensive to produce).

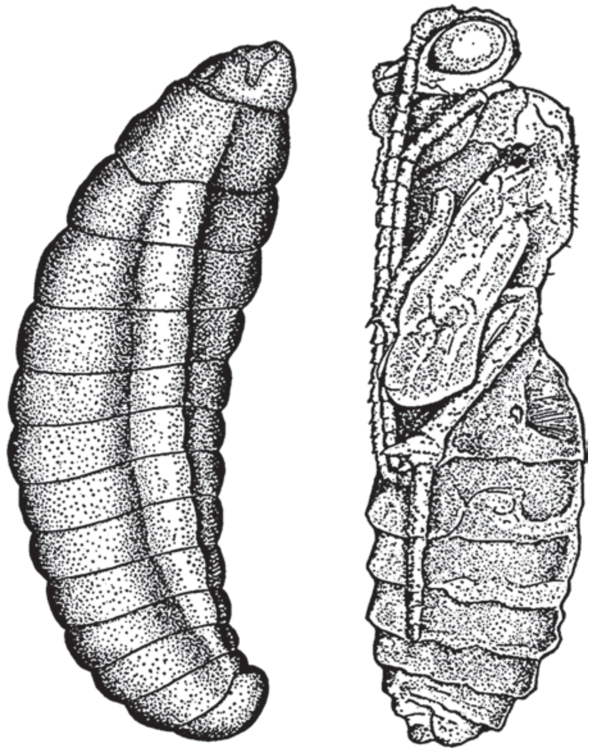
There are one to five larval instars. The greatest variation in morphology occurs in the first instar, where up to 14 types have been distinguished. The most common is hymenopteriform, which is spindle-shaped and maggotlike, and is generally smooth without any conspicuous structures. Subsequent



Parasitic Hymenoptera (Parasitica), Figure 6 **Larvae of an ectoparasitic wasp, *Euplectrus* sp. (Hymenoptera: Eulophidae) feeding externally on a caterpillar (from USDA).**

instars of almost all families take this form as well, and their identification can be very difficult, though families may be distinguished by their scleriterized head structures. Another larval form is the planidium of Eucharitidae and Perilampidae, which is a free-living stage that actively seeks out its host, and has heavier body scleritization. Adult solitary parasitoids optimally deposit only one egg per host. Under some conditions, when more than one egg is deposited, superparasitism may occur, leading to competition between the hatching larvae. Some larvae have well-developed mandibles which can destroy competitors physically, while physiological suppression, selective starvation and suffocation may suppress the supernumerary larvae, although the exact mechanisms are not yet fully understood. In some polyembryonic broods, a precocious "guard" morph is produced that defends its siblings from other larvae, but fails to mature itself. Larvae have a closed midgut, so they cannot expel waste which may foul their environment. Upon completion of feeding, the larvae enter a prepupal stage, when the midgut opens, and the stored wastes are finally expelled and bundled with the last larval skin as a meconial pellet (Fig. 7).

The larvae of many species pupate within the host remains, and do not spin cocoons. Upon death, some hosts become mummified, which effectively provides the same protection to the parasitoid pupa as a cocoon does, but without the physiological expenditure of producing silk. However, most of the Ichneumonidea and a few



Parasitic Hymenoptera (Parasitica), Figure 7 **The larval (*left*) and pupal (*right*) stages of an endoparasitic wasp, *Agathis gibbosas* (Say) (Hymenoptera: Braconidae) (from USDA).**

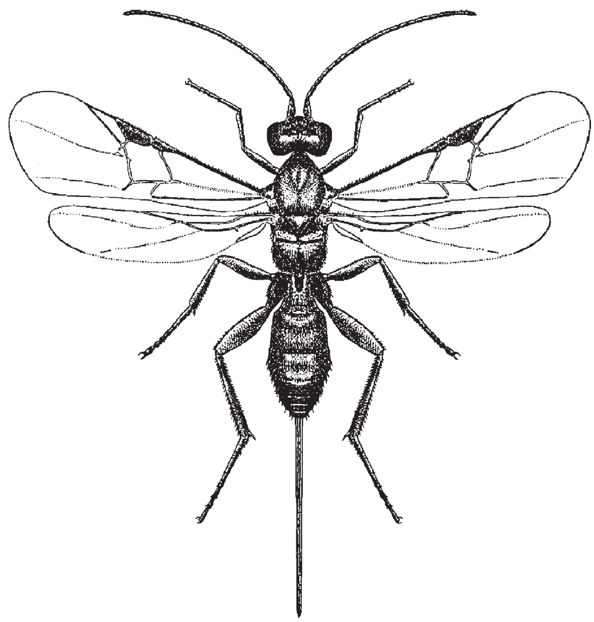
Chalcidoidea do produce silk cocoons, some of the most notable being gregarious microgastrine braconids, which feed internally in their Lepidoptera hosts, but emerge to pupate on the outside of their host by the dozens.

Biology

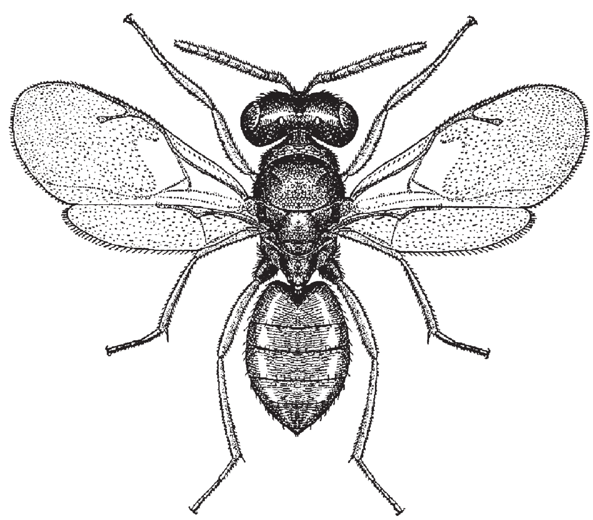
Like other Hymenoptera, most of the Parasitica have a haplo-diploid reproductive strategy, where a fertilized (diploid) egg produces a female, and an unfertilized (haploid) egg produces a male (arrhenotokous parthenogenesis). Thus, by controlling fertilization, ovipositing females can choose what sex egg to allocate after inspecting the prospective host. In some groups, thelytokous parthenogenesis occurs, where males are unknown and unfertilized females produce only females. In several groups of Chalcidoidea, thelytoky can be induced through infection by *Wolbachia* bacteria. Finally, deuterotokous parthenogenesis occurs in a few species, where unfertilized eggs can produce both males and females; in this case, males appear to be sexually non-functional. Two strategies of egg-production have been characterized in the Parasitica: synovigenesis, where females successively develop a number of eggs (generally lecithal), throughout her lifetime, and proovigenesis, where ovigenesis is completed soon after females emerge from the pupa, and thus have only a fixed number of eggs (generally alecithal) to lay (Fig. 8).

In some groups, adult morphology varies based on environmental factors, typically depending upon the size or choice of host. The most dramatic changes occur in the gall-inducing Cynipidae, which undergo an alternation of generations (heterogony) – a sexual generation of females and males, and a non-sexual (agamic) generation of females. Often the adult morphology and the gall structure and site differs considerably between the two generations.

Parasitoids can be classified in several ways. (i) Endoparasitoids develop internally in the host, and ectoparasitoids develop externally (though a few species may begin their development internally and finish externally). (ii) They also can be separated based on the variety of hosts they may attack, ranging from monophagy (specialists attacking only one species or a few closely related species) through oligophagy to polyphagy (generalists attacking hosts in a wide variety of taxa). This range of hosts is a continuum with few well-defined parameters (Fig. 9), and very few species are properly placed at either extreme. Nevertheless, the concept of a generalist versus a specialist plays an important role in biological control applications. (iii) Most parasitoids develop as a single individual per host; they are called solitary parasitoids. When two or more larvae can successfully develop in a single host, they are called gregarious parasitoids. The most extreme example of gregarious parasitism involves polyembryony, the production of several larvae from a single egg. Polyembryony is found in a few species of Platygastridae and Braconidae, and virtually the entire tribe of Copidosomatini (Encyrtidae), where one egg may produce up to 3,000 larvae.



Parasitic Hymenoptera (Parasitica), Figure 8 Adult of *Agathis gibbosas* (Say) (Hymenoptera: Braconidae) (from USDA).



Parasitic Hymenoptera (Parasitica), Figure 9 Adult of *Pteromalus eurymi* Gahan (Hymenoptera: Pteromalidae) (from USDA).

(iv) Parasitoids also can be classified by the stage of host attacked and the span of host stages during parasitoid development, e.g., egg, egg-larval, egg-pupal, larval, larval-pupal, etc. (v) When a host is killed without undergoing further development, the parasitoid is classified as an idiobiont. Conversely, koinobiont parasitoids allow their hosts to continue developing after the initial parasitism, thus ultimately providing a larger food source for their larvae. (vi) Parasitoids which do not attack other parasitoids are primary parasitoids; those which develop at the expense of other parasitoids (exclusive of those which may kill competing parasitoids but do not rely upon them for development) are hyperparasitoids. Hyperparasitism can be obligate or facultative. Most hyperparasitoids attack primary parasitoids and are called secondary parasitoids, but tertiary and even quaternary parasitoids can occur facultatively. Hyperparasitoids which attack their definitive host after it has killed its own host may be referred to as pseudohyperparasitoids. Finally, an unusual form, heteronomous hyperparasitism, occurs in a few Aphelinidae; in these species the females always develop as primary endoparasitoids of scales or whiteflies, but the conspecific males can develop in several different ways: as diphagous parasitoids (primary ectoparasitoids of the same host), as heteronomous hyperparasitoids (obligate or facultative hyperparasitoids on their own [= autoparasitism] on other species), or remarkably, as heterotrophic parasitoids (primary parasitoids of Lepidoptera eggs).

Hosts have evolved several lines of defense against parasitism, using morphological, behavioral and physiological adaptations. Chief among the latter is the encapsulation of foreign objects mediated by haemocytes. Endoparasitoids in return have developed several strategies to ensure their success, including: (i) avoidance by oviposition into specific sites of the host not accessible to its hemocytes; (ii) attack though the injection of viruses, teratocytes (=giant cells, trophic cells or trophoserosa cells), or venom along with the egg; and (iii) passive defense through morphological adapations of the egg which inhibit encapsulation.

The primary source of nutrition for parasitoids is the host of the larva. However, many species also feed as adults to maximize their reproductive capacity and life-span, typically feeding on honeydew, nectar and other plant secretions. Additionally, the females of many species will feed on the hosts as well (host-feeding), in some cases leading to the death of the host.

Although most of the Parasitica are true parasitoids, in some groups a single larva will feed on a number of prey found in an enclosed area (typically an egg mass or several small larvae in a gall or cell), and thus are actually predators. In a few groups (Agaonidae, Eurytomidae, Pteromalidae, Torymidae, Tanaostigmidae, Eulophidae, Braconidae, Cynipidae, and Platygastridae) there have been revisions to phytophagy, in many cases marked by gall formation.

Adults have developed some remarkable abilities to parasitize otherwise protected hosts. Two species (a mymarid and a trichogrammatid) are fully aquatic, using their wings and legs as oars, while an ichneumonid species can stay underwater for 30 min searching for prey. The deliberate use of another species for transport is termed phoresy, and several Parasitica species practice it. Scelionid and trichogrammatid females will ride on the female adult of their hosts, so that they may immediately parasitize newly laid eggs. Phoresy has also been recorded in the Torymidae and Pteromalidae.

Biological Control

In biological control programs, it is essential to use agents which do not attack non-target organisms, and parasitoids of insect pests in general tend to be more host-specific than predators. Thus the parasitic Hymenoptera, which comprise more parasitoid species than any other group, provide the greatest pool of potential agents against insect pests. In classical biological control programs, the majority of successes have been through importations of agents from three parasitic families:

Aphelinidae, Encyrtidae and Braconidae. In mass-culturing and release programs, the Trichogrammatidae, Braconidae and Pteromalidae have been heavily relied on. The most important families (and some of the principal taxa of pests they are used against) are as follows:

Chalicidoidea

- Aphelinidae (Aphoidea, Diaspidae, Aleyrodidae and Lepidoptera)
- Encyrtidae (Pseudococcidae and Coccidae)
- Trichogramatidae (Lepidoptera)
- Eulophidae (Chrysomelidae and Lepidoptera)
- Mymaridae (Cicadellidae)
- Pteromalidae (Muscidae)

Ichneumonoidea

- Braconidae (Aphoidea, Lepidoptera and Tephritidae)
- Ichneumonidae (Lepidoptera and Curculionidae)

Platygastroidea

- Scelionidae (Pentatomidae and Noctuidae)
- Platygastridae (Aleyrodidae)

Fossil Parasitica

The parasitica appear to have arisen in the Jurassic Period, based on the fossil remains from that time of 13 extinct families reputably assignable to the group. By the Cretaceous period, several modern families had appeared, while almost every extant family is known from the oligocene period. Parasitic Hymenoptera fossils are known from both amber and sedimentary deposits, and from Australia, Asia, Europe and North and South America.

► Wasps, Ants Bees and Sawflies

References

Gauld I, Bolton B (1988) The Hymenoptera. Oxford University Press and British Museum (Natural History), Oxford, UK, 332 pp

Godfray HCJ (1994) Parasitoids. Behavioral and evolutionary ecology. Princeton University Press, Princeton, NJ, 473 pp

Goulet H, Huber JT (eds) (1993) Hymenoptera of the world: an identification guide to families. Agriculture Canada Publications, Ottawa, Canada, 668 pp

Gupta VK (ed) (1988) Advances in parasitic Hymenoptera research: Proceedings of the second Conference on the taxonomy and biology of parasitic Hymenoptera held at the University of Florida, Gainesville, FL, 19–21 November 1987, EJ Brill, Leiden, The Netherlands, 546 pp

Hanson PE, Gauld ID (1995) The Hymenoptera of Costa Rica. Oxford University Press and British Museum (Natural History), Oxford, UK, 893 pp

Waage J, Greathead D (eds) (1986) Insect parasitoids. Academic Press, London, UK, 389 pp

Parasitic Wood Wasps

Members of the family Orussidae (order Hymenoptera: suborder Symphyta).

► Wasps, Ants, Bees and Sawflies

Parasitism

Living on or in another organism, and using that host to obtain food. The parasitic relationship is usually debilitating for the host, and sometimes fatal, though fatal conditions are perhaps more correctly termed parasitoidism.

Parasitism of Lepidoptera Defoliators in Sunflower and Legume Crops, and Adjacent Vegetation in the Pampas of Argentina

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Pampean grasslands were dramatically modified after the introduction of exotic plant species for livestock industry and agriculture during the last century. A succession of wheat, maize, linseed, green pastures (mainly alfalfa and clover), sunflower, grain sorghum, and lastly soybean crops have changed the original grassland community structure and function. To date, the landscape in the Pampas comprises an assortment of secondary natural grasslands, and farming and crop fields with differential degrees of disturbance (i.e., use of agrochemical, planting techniques, etc.). Soybean and wheat are the major summer and winter crops, respectively. Extensive cropping and grazing are dominant practices, but allocation of land for each fluctuates according to changes in market demand and technology. Relicts of native plus introduced flora and fauna can be found in small areas of abandoned land, and in corridors alongside roads and railways. Together they cover a significant proportion of the pampean landscape.

Most regions of the world suffer the effects of invasions by introduced crops. In the case of insect communities, crops are colonized by herbivorous species; the recruitment is influenced by the natural reservoir of fauna associated with native (wild) plants chemotaxonomically related to that exotic crop, as well as by the deficiency of a broad spectrum of defensive allomones that make plants vulnerable.

Predators, parasitoids and pathogens attack herbivorous insects. Parasitoid insects are defined as entomophagous insects. Parasitoid larval stages feed internally (endoparasitoid) or externally (ectoparasitoid) upon arthropods, usually other insects, killing their hosts. One or more individuals can be obtained from a single host (solitary, gregarious or embryonic parasitoids). Parasitoids can attack a taxonomically broad range of insect orders and all developmental stages, and they themselves often are subject to attack by parasitoids; thus, they can be distinguished as primary, secondary or hyperparasitoids. Given their importance and ubiquity (probably over 1 million species), and because they can play a critical role in limiting the abundance of their hosts, parasitoids are considered to be very reliable candidates for biological control of pests.

Unfortunately, changes in natural insect communities during the agricultural expansion in the Pampas are poorly documented. However, it is interesting to investigate current insect complexes in a landscape scale, and to examine both historical and ecological processes. Insect community structure, life cycles, and interactions allow reconstruction of part of the past native communities and enable us to understand contemporary dispersion and refuges of insects in the region. It also indicates the potential use of natural enemies in the context of the biological control of pests through conservation tactics.

Larval stage of Lepidoptera naturally supports a large number of parasitoids, and non-crop habitats associated with agricultural fields provide these and other beneficial arthropods with alternate hosts or prey, food and water resources, shelter, favorable microclimates, overwintering sites, mates and refuges from pesticides.

In crops such as soybean, sunflower, alfalfa and mixed clover-grass pastures, and in monospecific patches of *Melilotus alba* L. and *Galega officinalis* L., two naturally occurring legumes alongside roads and railroads, and in crop borders in the northwest of Buenos Aires province (34°4' S, 58–60°00' W), a total of 28 Lepidoptera defoliator species can be found. These species are polyphagous and multivoltine, some are migratory and some may hibernate or overwinter. They belong to the following families: Noctuidae (21 species), Pyralidae and Geometridae (2 species each), and Tortricidae, Pieridae and Arctiidae (1 species each). Soybean supports 10 species, pastures 9, legume patches 8, and sunflower crop only 2.

Rachiplusia nu Guenée (Noctuidae) is the dominant species, being recovered from all six habitats; *Paracles vulpina* (Hübner) (Noctuidae) is found in four (both pastures and non-crops); and *Colias lesbia* Fabricius (Pieridae), *Pseudoleucania minna* (Butler), Faronta albina (Hübner) (Noctuidae) and *Spilosoma virginica* (Fabricius) (Arctiidae) in three (soybean, and both pastures; alfalfa, clover and *G. officinalis*; and soybean, sunflower and *G. officinalis*, respectively). But in general, most species are observed in one or two out of six plant habitats.

Numerous parasitoid species attack the larval stage of defoliators of soybean. Nine out of ten host species are attacked at least by one primary endoparasitoid species; all categorized as koinobionts (parasitoids associated with exposed hosts and which permit them to continue to move, feed and defend themselves). Hyperparasitoids are not found. The parasitoid assemblage comprises 30 species; they belong to Hymenoptera (4 families, 17 species) and Diptera (1 family, 13 species). *Campoletis grioti*, *Copidosoma floridanum*, *Cotesia marginiventris*, *Rogas nigriceps*, *Voria ruralis*, *Cotesia* spp., *Microgaster* spp., and *Chetogena* spp. are the most common species. Most species are solitary, some gregarious, and one polyembrionic. The number of parasitoid species attacking each host is different, highest for *R. nu* (11) and lower for *Eulia loxonepes* and *Elasmopalpus lignosellus* (1). Likewise, differences are found in parasitoid abundance (number of individuals) when comparing host species; in particular for *R. nu*, the high number of parasitoid species and number of individuals reveal the importance of parasitoids as mortality agents and point out for their preservation in protected areas. When parasitoid guild analysis is used to explore the determinants of species richness and structure of parasitoid complexes, it can be observed that the number of parasitoid guilds differs among hosts: four parasitoid guilds were recorded for *R. nu*: egg-prepupal, early larval, late larval, and larval-pupal; two for *S. virginica*: late larval, and larval-pupal, and *C. lesbia*: early larval and larval-pupal; and one for *A. gemmatalis* and *L. biffidalis*: early larval. *Elasmopalpus lignosellus* and *E. loxonepes* are parasitized by one species each (*C. marginiventris* and *Apanteles* or *Cotesia* sp., respectively).

Parasitoid assemblages from each host differ in species composition, levels of parasitism and number of guilds. Besides historical processes, some of these differences could be associated to ecological factors, such as host

Parasitism of Lepidoptera Defoliators in Sunflower and Legume Crops, and Adjacent Vegetation in the Pampas of Argentina, Table 3 Lepidoptera species inhabiting crops and corridor vegetation in northwest Buenos Aires Province, Pampean region, Argentina

Habitat plants	Lepidoptera species
Soybean	*Anticarsia gemmatalis* (Hübner), *Heliothis* spp. complex, and *Spodoptera frugiperda* (J.E. Smith), *Rachiplusia* nu (Guenée), and *S. ornithogalli* (Guenée) (Noctuidae), *Elasmopalpus lignosellus* Zeller *and Loxostege biffidalis* (Fabricius) (Pyralidae), *Colias lesbia* (Fabricius) (Pieridae), *Eulia loxonepes* Meyrick (Tortricidae), *Spilosoma virginica* (Fabricius) (Arctiidae)
Sunflower	*R. nu, S. virginica*
Alfalfa	*Paracles vulpina* (Hübner), *Leucania jaliscana* Schaus, and *Pseudoleucania minna* (Butler) (Noctuidae), *R. nu, C. lesbia*, 1 unidentified species (Geometridae), 3 unidentified species (Noctuidae)
Mixed – Clover	*Faronta albilinea* (Hübner), and *Mocis phasianioides* (Guenée) (Noctuidae), *P. minna, R. nu, C. lesbia, P. vulpina*, 3 unidentified species (Noctuidae)
M. alba	*R. nu, P. vulpina, F. albilinea, S. virginica,* 3 unidentified species (Noctuidae), 1 unidentified species (Geometridae)
G. officinalis	*Elaphia repanda* (Schaus), and *Helicoverpa gelotopoeon* (Dyar) (Noctuidae), *P. minna, M. phasianoides, S. virginica, F. albilinea, R. nu, P. vulpine*

Parasitism of Lepidoptera Defoliators in Sunflower and Legume Crops, and Adjacent Vegetation in the Pampas of Argentina, Table 4 The parasitoid complex of defoliator Lepidoptera species on soybean crops in northwest Buenos Aires Province, Pampean region, Argentina

Hosts					
Parasitoid complex	*R. nu*	*A. gemmatalis*	*S. virginica*	*C. lesbia*	*L. biffidalis*
Egg prepupal endoparasitoids					
Encyrtidae					
Copidosoma floridanum	x				
Early larval endoparasitoids					
Braconidae					
Apanteles lesbiae				x	
Apanteles or Cotesia sp.					
Cotesia marginiventris	x				
Cotesia a					
Cotesia b			x		
Meteorus rubens		x			x
Microgaster a	x				
Microgaster b					
Rogas nigriceps	x				
Ichneumonidae					
Campoletis grioti	x				
Campoletis a	x				
Campoletis b					
Campoletis c					
Hymenoptera					
Unidentified sp. 1					
Unidentified sp. 2					x
Late larval endoparasitoids					
Tachinidae					
Voria ruralis complex	x				
Chetogena a and *Lespezia aletie*			x		
Patelloa similis and *Lespezia* sp.			x		
Sturmia sp.			x		
Unidentified sp. 3	x				

Parasitism of Lepidoptera Defoliators in Sunflower and Legume Crops, and Adjacent Vegetation in the Pampas of Argentina, Table 4 The parasitoid complex of defoliator Lepidoptera species on soybean crops in Northwest Buenos Aires Province, Pampean region, Argentina (Continued)

Hosts					
Parasitoid complex	*R. nu*	*A. gemmatalis*	*S. virginica*	*C. lesbia*	*L. biffidalis*
Unidentified sp. 4	x				
Unidentified sp. 5			x		
Chetogena c				x	
Larval-pupal endoparasitoids					
Tachinidae					
Winthemia sp.	x				
Chetogena b			x		

abundance patterns, including constancy and predictability in time and space.

Rachiplusia nu has the most complex parasitoid assemblage, and this could be explained by its higher abundance and constancy than the other host species, and the development of two generations within the crop cycle. We might expect to find more similarity in parasitoid assemblages between *R. nu* and *A. gemmatalis*, considering they belong to the same family. However, *A. gemmatalis*, a tropical species, is possibly in the limit of its geographical distribution, having one generation a year at the end of the crop cycle and sporadic occurrence in the study area. Its lower predictability, compared to *R. nu*, could account, at least to some extent, for the observed differences. The fact that *S. virginica* does not support parasitoid guilds composed of hymenopteran species could be attributed to the long setae in the host body that, in general, would prevent the attack of wasps lacking a long ovipositor, but not for tachinids, since they can lay eggs in foliage or attach eggs on the host integument. The simplicity of the parasitoid guild structure associated with *C. lesbia* and *L. biffidalis* could be related to their low abundance.

From a regional perspective, *R. nu* population abundance is higher in summer crops, followed by multi annual crops and lower in non-crop habitats, though some low densities are registered for alfalfa and mixed clover-grass pastures. *Rachiplusia nu* larvae support 18 primary endoparasitoid species in plant habitats other than soybean, including two hyperparasitoids species registered in sunflower crops. Comparatively, the number of parasitoid species and the number of parasitized hosts is greater in crop than in non-crop habitats, ranging from 11 in sunflower (as in soybean) to four in *G. officinalis* and *M. albus*. Some species are coincidental with those registered for the soybean crop. *Copidosoma floridanum*, *R. nigriceps*, and *V. ruralis* again are the species consistently reared in five plant habitats, whereas *Casinaria* sp. is found for the first time for *R. nu* and in the five sites. The most frequently abundant parasitoid species in crop habitats is *C. floridanum*; the remaining species have lower incidence on *R. nu*. The parasitism in non-cultivated habitats is very low.

Parasitoid guild analysis yields differences for *R. nu* parasitoid assemblages among plant habitats: four parasitoid guilds are found in sunflower and in soybean (egg-prepupal, early larval, late larval and larval pupal); three in mixed clover-grass, alfalfa and *M. albus* (egg-prepupal, early larval, and late larval), and two in *G. officinalis* (early larval and late larval) (Fig. 10).

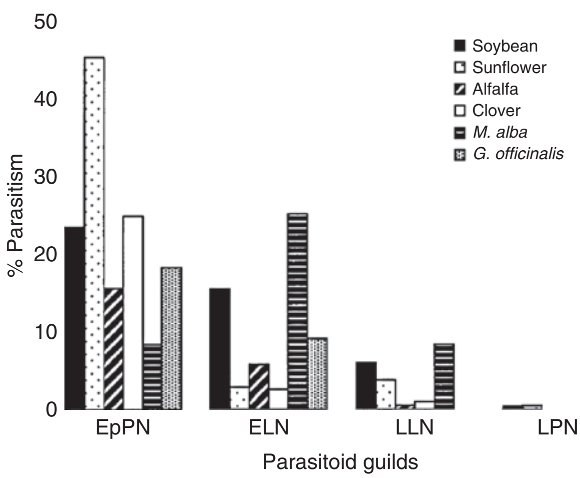
Parasitism of Lepidoptera Defoliators in Sunflower and Legume Crops, and Adjacent Vegetation in the Pampas of Argentina, Table 5 **The parasitoid complex of *R. nu* larvae on crops and corridor vegetation in northwest Buenos Aires Province, Pampean region, Argentina**

Plant habitats					
Parasitoid complex	Sunflower	Alfalfa	Clover	*M. alba*	*G. officinalis*
Egg prepupal endoparasitoids					
Encyrtidae					
Copidosoma floridanum	x	x	x	x	x
Early larval endoparasitoids					
Braconidae					
Cotesia marginiventris		x			
Microgaster sp.	x	x	x		x
Rogas nigriceps	x	x	x		x
Rogas sp.		x			
Ichneumonidae					
Campoletis grioti	x	x			
Campoletis d	x				
Campoletis e			x		x
Casinaria sp.	x	x	x	x	x
Hymenoptera					
Unidentified sp. 6[a]	x				
Unidentified sp. 7[a]	x				
Unidentified sp. 8				x	
Unidentified sp. 9[b]					x
Late larval endoparasitoids					
Tachinidae					
Voria ruralis complex	x		x		x
Unidentified sp. 10[a]	x				
Unidentified sp. 11[a]		x			
Unidentified sp. 12[b]				x	
Larval-pupal endoparasitoids					
Tachinidae					
Winthemia sp.	x				
Hyperparasitoids					
Chalcididae					
Unidentified sp. 13	x				

Parasitism of Lepidoptera Defoliators in Sunflower and Legume Crops, and Adjacent Vegetation in the Pampas of Argentina, Table 5 The parasitoid complex of *R. nu* larvae on crops and corridor vegetation in northwest Buenos Aires Province, Pampean region, Argentina (Continued)

Plant habitats					
Parasitoid complex	Sunflower	Alfalfa	Clover	*M. alba*	*G. officinalis*
from *Casinaria* sp.)					
Unidentified sp. 14	x				
(from Tachinidae)					

[a]only the pupa was obtained
[b]only larvae were obtained



Parasitism of Lepidoptera Defoliators in Sunflower and Legume Crops, and Adjacent Vegetation in the Pampas of Argentina, Figure 10 A comparison of levels of parasitism for the four larval parasitoid guilds associated with *Rachiplusia nu* (Guenée) (Lepidoptera: Noctuidae) in six Pampean plant habitats (Argentina).

In this region, only four out of seven potential parasitoid guilds defined for Lepidoptera are recorded, suggesting that potential host niches are not totally utilized. Parasitoid species belonging to guilds that attack earlier host stages are responsible for higher levels of parasitism than those attacking later developmental stages. At present, Lepidoptera defoliators occur infrequently at damaging levels and only in limited areas. The action of parasitoids seems to be, in part, responsible for maintaining defoliator populations in crops at low levels.

References

Hall AJ, Rebella, CM, Ghersa, CM, Culot, JP (1992) Field-crop systems of the Pampas. In: Pearson CJ (ed) Ecosystems of the world, vol 1: Field crop ecosystems. Elsevier Science Publishers, Amsterdam, The Netherlands, pp 413–450

Hawkins BA, Sheehan W (1994) Parasitoid community ecology. Oxford University Press, Oxford, UK, 516 pp

Luna MG, Sánchez NE (1999a) Specific composition and abundance of the soybean defoliator Lepidoptera community in northwest Buenos Aires province, Argentina. Rev Soc Entomol Argent 58:67–75

Luna MG, Sánchez NE (1999b) Parasitoid assemblages of soybean defoliator Lepidoptera in north-western Buenos Aires province, Argentina. Agric For Entomol 1:255–260

Mills NJ (1994) Parasitoid guilds: defining the structure of the parasitoid communities of endopterygote insect hosts. Environ Entomol 23:1066–1083

Quicke DLJ (1997) Parasitic wasps. Chapman and Hall, New York, NY, 485 pp

Parasitization

Parasitism. This is not a widely accepted term.

Parasitoid

A parasite that kills its host at about the time the parasite completes it development.

Parasitoidism

Parasitism resulting in death of the host. This is not a widely accepted term.

Parasocial Behavior

A level of social behavior less developed than eusocial behavior. This type of sociality includes cooperative behaviors within the same generation of insects, namely communal, quasisocial, and semisocial behavior.

- ► Solitary
- ► Subsocial
- ► Communal
- ► Quasisocial
- ► Semisocial
- ► Eusocial Behavior
- ► Sociality in Insects

Parasporal Body

A particle which lies alongside the spore or is included in the sporangium along with the spore, formed during sporulation of a number of *Bacillus* and *Paenibacillus* species. If the inclusion is a crystalloid, the species is called crystalliferous. It is usually diamond-shaped (bipyramidal). When digested it releases an endotoxin.

Paratype

Any specimen in the series from which the species description was completed, other than the holotype specimen.

Parental Care In Heteroptera (Hemiptera: Prosorhynche)

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The term "parental care" refers to the set of activities that parents carry out to provide protection to their offspring. In the Heteroptera it was first described in the acanthosomatid *Elasmucha grisea* by Adolph Modeer in 1764. It is known to occur in four infraorders and 14 families, and possibly it is an ancestral character that appeared early by convergence, later to be replaced by less costly behaviors. Species providing parental care are called "social" species, and those that do not called "asocial." Generally with social insects, brood caring is exerted by the mother because she is the sex that invests the most in her descendants and because she is certain of her maternity. Under these conditions, the investment she makes in brood caring is compensated for by her increased reproductive fitness. As it will be explained later, however, Heteroptera do not conform to this hypothesis. Also, the male usually does not cooperate in brood caring, although there are remarkable exceptions. The male bases his reproductive fitness on promiscuity. Parental care in Heteroptera poses some evolutionary dilemmas, because investment by parents in brood care reduces the fecundity of parents, and does not always enhance survival of offspring. Thus, this is not widespread in Hemiptera.

Models of Parental Care in the Heteroptera

The simplest expression of parental care is to take care of the clutch, laying it in protected places, and laying it in an environment that is favorable for the hatching young. This protection can be accompanied by aggressive behavior with respect to the predators or parasitoids that want to attack the offspring. Some morphologies favor the mechanical protection of the clutch. For example, a shield bug female can protect with her own body the clutch she lays on the ground. When moving to vegetables, the shield shape was maintained as it provides a good protection to the eggs. Later on, other means of clutch protection were developed, and the shield shape remained like a relict, although it no longer was essential for protection of the clutch. It is difficult to establish the limits of the most elaborate expression of parental care, but is usually interpreted to occur when one or both parents remain associated with their offspring, nourish them, and protect them during one or more stages of development. It can constitute the basis of incipient sociality.

Origin of Parental Care in Heteroptera

The first hemipteroid lineages appeared 260 million years ago, likely derived from scavengers that lived, fed and copulated on the ground. They moved to roots, later became predators, and finally changed to a phytophagous regime. The threat of drought and depredation in terrestrial habitats favored egg-laying in damp places on the ground, and stimulated their guarding behavior with respect to edaphic predators (as in cydnids of the subfamily Sehirinae do nowadays). When moving to aerial habitats (plants), laying clusters of eggs was retained, but the clutch was exposed to drying. The female protects her clutch to guarantee its persistence until the following generation. In order to balance the costs of this maternal protecting activity, clutches become larger-sized, but at the same time larger size made them more vulnerable to predators and parasitoids, and a positive feedback leading to establishment of parental behavior began. Only a major change in reproductive strategies allows them to escape that feedback. The clutch-protection behaviors are derived from defensive behavior (e.g., wing movement/flight behavior) and of feeding behavior that already existed in the asocial species. The aquatic habitat of Gerromorpha and the Nepomorpha reduces the dangers of desiccation and predation for these groups, and the appearance of parental behavior may be due to other factors.

Costs of Parental Care Behavior

Accomplishing the tasks of brood caring involves costs for the parent who makes them. On the one hand, the caring individual is more exposed to the attack of antagonists (e.g., the probabilities of mortality of social females of the tingid *Gargaphia* are three times higher than the mortality of asocial females). In addition, if the caring parent is female, her fecundity is reduced because, while taking care of brood, she does not lay eggs, which favors semelparity (a single act of oviposition). The total lifetime fecundity of the asocial species is significantly greater than that of the social species. For example, in *Gargaphia* the female spends more than half of her life in the care of brood, a time during which she does not proceed with another egg-laying episode. Semelparity also leads to a situation where the first, and perhaps only, clutch is much larger than that of corresponding non-nursing species. The vulnerability of the female nursemaid to predation is increased, though increase in clutch size also occurs to balance the cost of the caring behavior. In many cases brood caring is incompatible with the feeding of the parent, especially in predator species. This is of great relevance if the mother is the caring sex, as then she cannot accumulate reserves for the following clutch, thus compromising her future fecundity. Interestingly, only 10% of the Hemiptera with maternal care are predators.

Benefits of Parental Care Behavior

The benefit of parental care might be expected to result in greater survival of the offspring of the social species (Table 6). In Heteroptera, when comparing the success that parental care offers in respect to other strategies of protection, such as insertion of eggs into the vegetation or dissemination, it is not evident that caring behavior is more effective. For example, the mortality of the aggregated clutches of *Gargaphia* not being nursed is 56%, whereas in *Corytucha*, with scattered, unattended clutches the mortality is 29%. In addition, if parental care was

Parental Care In Heteroptera (Hemiptera: Prosorhynche), Table 6 Relative protective value of hemipteran oviposition behavior

	Protection index
Clutch size	
Eggs laid singly	5
Eggs in small groups	3
Eggs in large groups	1
Oviposition site	
On terrestrial substrate	1
On aquatic substrate	2
Elevated on stalks	3
Hidden in natural crevices	4
Glued to conspecific	5
Glued to spider web	5
Given to male for care	5
Eggs retained until hatching	5
Inserted into plant tissue	6
Protective secretion	
Eggs covered with protection secretion	2

especially beneficial and adaptive, it might appear more often in the derived species. In turn, adaptative radiation should lead to the appearance of new morphological or ethological traits (apomorphies). It might also be expected that social species are able to colonize more hostile habitats, or are more protected against attack by parasitoids or predators than those that do not take care of their offspring. However, there is no evidence to support those expectations. The groups with parental care are not the most evolved within each taxon (infraorder, family, genus), and do not differ either morphologically or ethologically from the asocial species. They do not occupy especially hostile niches either. Overall, it may be concluded that maternal care is a plesiomorphic (ancestral) character that does not require the appearance of special morphological and ethological traits. The trade-off between costs and benefits shows that it does not imply improvements for offspring fitness. Paternal care is a by-product of females abandoning brood caring, and it is only supported because males benefit reproductively from this caring behavior. Therefore, the difficulty is not to implement maternal care as a vital strategy, but rather to get rid of this expensive behavior that does not bring along with it reproductive benefits.

Replacement of Parental Care by Other Protective Strategies

The substitution of brood guarding by other means of protection has several aspects. In the first place, because it is the mother that usually performs brood caring, and is the parent that pays the greatest cost for this action, changes in her behavior tend to reduce the cost of her actions.

One strategy consists of defending the clutch only when it is in danger, making clutch defense compatible with periods of feeding by the mother. In certain species, the female protects the brood only when she is old, and chances of producing a new clutch are very low; in other words, when it turns out more beneficial to protect her (probably) last clutch rather than to abandon it to try to make another (improbable) clutch.

Another strategy is egg dumping, wherein the (dumping) female lays the eggs within or next to the clutch of another (resident or host) female, who eventually broods her own clutch and the dumped clutches simultaneously. Egg dumping has been described in the tingids *Gargaphia* sp. and *Leptobyrsa decora*, and may also occur in the coreid *Physomerus grossipes*, in the aradids *Neurocterus hochstetteri* and maybe *N. pseudonymus*, and in the reduviids *Rhynocoris carmelita* and *Pisilinus tipuliformis*. For egg dumping to arise, some prerequisites are required. First of all, maternal care is needed. Also, opportunity for iteroparity (repeated reproduction) to benefit from avoiding maternal care must exist. Good synchrony in reproduction within the species is also required in order for the dumping female to have a clutch of eggs to contribute to a receptive resident female, and also to assure that the eggs and young develop at about the same rates so the resident female will not give up protective behavior too early. Egg dumping is also facilitated if breeding individuals are aggregated, making it easier to find a host female.

The (dumper) females that transfer the care of their eggs to a (guarding) female produce a new clutch immediately, while oogenesis is suspended in guarding females. In light of the trade-off between care and future reproduction, two powerful forms of selection compete. On one hand, selection acts for protection of young; on the other, it acts against maternal behavior. The receiving female cannot easily escape her guarding role and transform into an egg layer. Immediately after egg-laying, decrease in juvenile hormone titer promotes guarding behavior, a condition that does not revert even if opportunities arise to do so. On the contrary, high juvenile hormone titer promotes oogenesis and laying, thus egg dumping. The resident female benefits from the lessened impact of parasitoids and predators on her own descendants. Resident eggs are placed in the middle of the clutch, where mortality is about 23%, whereas dumped eggs are placed peripherally (60% of perimeter eggs are dumped), where mortality is about 37%. Thus, dumped eggs provide a buffer zone of protection. Resident nymphs benefit from dilution among nymphs produced by dumper females, dilution making them perhaps less vulnerable to predators and parasitoids. A greater percentage of host offspring survives as brood size increases. Egg dumping can be said to be mutualistic between conspecific females. In fact, in the case of *G. solani*, only 10% of the females try to prevent egg dumping, and apparent attempts to attract egg dumpers have been reported. Perhaps volatiles deposited on the clutch by the host mother may be cues for dumping females. Dumper females are high-quality females, who may increase their reproductive fitness by avoiding the costs of maternal care. In *G. solani*, an increase of 20% fitness has been reported, perhaps due to higher survival rates of dumper females. To achieve benefits, a female must dump once or twice in her life. Dumping twice results in tripling of lifetime reproduction.

Forces that may have enhanced egg dumping are simple natural selection (resulting in direct benefits to fitness) and/or kin selection (indirect benefits to fitness). No mechanism of mutual recognition between relatives has been reported, but aggregation of reproductive conspecifics may increase the chances of dumping in kin clutches.

Finally, the mother can detach herself from brood caring and transfer it to the father. Since the costs of maternal care are higher in predatory species (maternal care and patrolling to hunt prey are incompatible activities), it is no wonder that the paternal care has been developed in belostomatids and reduviids, both families of predatory insects.

Other strategies have allowed some Heteroptera to avoid brood caring. A first opportunity had to be to avoid large-sized clutches, scattering them in time and space. This change was beneficial, as observed by the mortality by depredation of the clutches of *Gargaphia* (56%; large-sized clutches) and those of *Corytucha* (29%; scattered, smaller clutches). Scattered clutches are preferred, as the Piesmatidae and the Berytidae do, laying 1–3 eggs every day. Triatominae drop the eggs as they walk. In the case of massive clutches, they may be hidden, as lygeids, dipsocorids and thaumastocorids do. Protection is increased if the clutch is covered with extra secretions, as occurs in urostylids and reduviids of the subfamily Holptilinae. Oothecas can even be produced (with a shellac-like covering), as occurs in the plataspids and many reduviids of the subfamily Harpactorinae. When moving to plants, eggs may be laid on the leave or stem surface (epiphytic oviposition), and must be more resistant to desiccation by means of a thicker chorion. Those eggs may be larger and produce larger hatchlings. However, they are very attractive to the antagonists, unless they are protected. A better option is to insert eggs in plant tissues (endophytic oviposition), resulting in lower risk of mortality due to desiccation. The cost of this endophytic oviposition strategy was the reduction of egg size, which implies smaller hatchlings, but a beneficial side-effect is better protection from antagonists. An intermediate option between maternal care and asocial behavior are ovoviviparous (as is the case in some Microphysidae) or viviparous (as in some Anthocoridsae and Aradidae) strategies, which are compatible with food searching, although not with a new reproductive episode. Therefore, by means of changing the location or size of the clutch, most Heteroptera (95% of the species) have left the parental option in favor of other alternatives that protect the clutch without invoking reduced survival or fecundity.

Persistence of Maternal Care

Clearly there are alternatives to maternal care behavior. If, in spite of its disadvantages or lack of advantages, maternal behavior persists in some groups of Heteroptera, it is likely due to lack of alternatives. Maternal behavior therefore remains as a relict trait. An example of why maternal care might persist might include withering of the host plant before embryonic development has been completed, or insertion of eggs into the withered plant would not afford protection. Or, as happens in *Parastrachia japonensis*, food (fruits of *Schoepfia jasminodora*) is available only seasonally, and this factor leads inevitably to the semelparity, even if maternal care did not exist. In other words, the care of offspring does not represent any cost with respect to the future fecundity. Maternal care usually appears or is maintained with semelparity, that in turn is conditioned by diverse ecological exigencies, e.g., climate, food, mates. In these cases, reproduction happens only a few times, and it is associated with very large-sized clutches, taking advantage of the abundance of the limiting resource.

Groups That Display Maternal Care in Heteroptera

Nepomorpha: Gelastocoridae (*Nethra martini*), Gerridae (*Halobates*)

Leptopodomorpha: Saldidae (*Aepophilus*)

Cimicomorpha: Reduviidae Harpactocorinae (*Pisilus*, *Endochus*, *Rhinocoris*) and Emesinae (*Ghinallelia*); Tingidae (*Gargaphia*, *Leptobyrsa*, *Phyllomorpha*)

Pentatomorpha: Aradidae (*Mezira, Neuroctenus, Ctenoneurus, Brachyrhynchus)*; Coreidae *(Physomerus)*; Cydnidae *(Sehirus, Adomerus, Canthophorus, Tritomegas, Brachypelta, Legnotus, Parastrachia)*; Acanthosomatidae *(Anaxandra, Elasmucha, Sastragala)*; Scutelleridae *(Cantao, Augocoris, Pachycoris, Tectocoris)*; Phloeidae *(Phloea, Phloeophana)*; Dinidoridae *(Cyclopelta)*; Tessaratomidae *(Pygoplatys, Erga)*

Examples of Maternal Care

Tingidae

All the species of the genus *Gargaphia* (more than 60) perform maternal care and live on Solanaceae. The mother watches the egg clutches. The nymphs seek an unopened leaf, where they take refuge. When predators (e.g., nabids) approach, the mother faces them, extending and raising the wings. The mother may even perish in this defensive act. *Gargaphia solani*, after copulation, performs egg-laying over a period of about a day and a half on the lower surface of the foliage. Altogether she lays more than 100 eggs. The female protects her offspring until they reach maturity, and she accompanies them when they move to look for new food and refuge. The mother prevents the fragmentation of the group by directing all brood into a compact group. This behavior allows 30% of the descendants to reach the adult stage, as opposed to 3% of other genera of the same family which do not take care of brood. Genus *Leptobyrsa* performs a very similar maternal care.

The case of *Phyllomorpha laciniata* (golden egg bug) is somewhat controversial. Adults carry eggs on their backs. Males, in fact, carry double the number of eggs that are carried by a female.

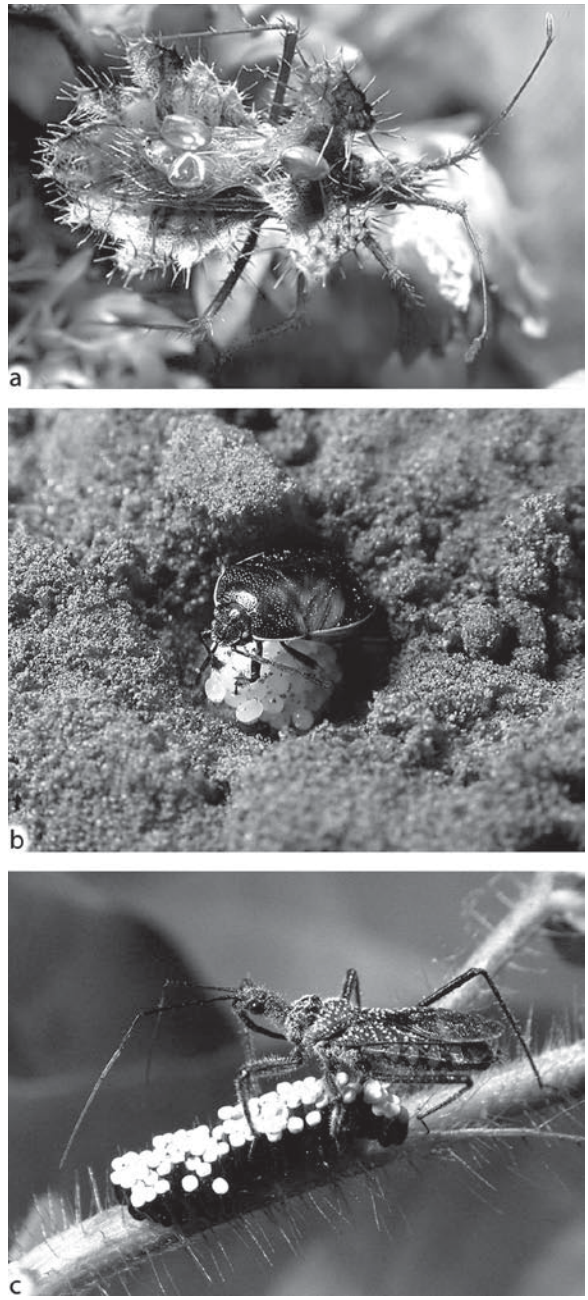
Phyllomorpha laciniata populations have a sex-ratio that is male-biased. Copulation is quite arduous (20 h under laboratory conditions), and afterwards the male stays with the female to prevent her from future copulations. During that entire period of time, males cannot avoid the gravid females that desire to lay their eggs on his back. Also females may have to tolerate gravid females gluing eggs on their backs. As the egg-carrying male does not modify his behavior, some authors do not consider the case of *P. laciniata* an example of paternal care. Rather it would be a maternal strategy, because her clutch obtains additional care when affixed to the back of conspecifics, either males or females. The ovipositing female benefits, of course, by being freed of brood caring. In this case, it may be that the males are victims of social parasitism inflicted on them by egg-laying females, and back-brooding is the price he must pay to keep a mate. This would be the case also of the gerrid *Halobates* and the reduviid *Stenolemus arachniphagus*, as they also display male back-brooding.

Coreidae

The female of *Physomerus grossipes* keeps large-sized clutches stuck to vegetation. She gives the offspring predigested food, and also the symbiotic microorganisms they will need in the future.

Cydnidae

The simplest form of protection is that the female places the clutch in cracks in the soil and watches them (Fig. 11). However, in some cases, the behavior is more complex. *Parastrachia japonica* lives in laurisilva (laurel) forests, and congregates in short trees of different genera, forming groups of up to 4,000 individuals. The fertilized females usually move away from the group (moving up to 2 km) before locating a small depression in the litter (she also may excavate this depression) which may



Parental Care In Heteroptera (Hemiptera: Prosorhynche), Figure 11 **Parental behavior in Heteroptera: (a) Golden egg bug, *Phyllomorpha laciniata* (Hemiptera: Coreidae) with eggs carried on its back (photo courtesy of Arja Kaitala); (b) egg guarding by *Sehirus cinctus* (Cydnidae); (c) egg guarding by *Rhinocoris tristis* (Reduviidae) (photos b and c courtesy of Doug Tallamy, University of Delaware).**

serve as an oviposition site. The eggs of the clutch are glued together, and in case of danger they may be transported by the mother with the aid of the tip of the rostrum ("rostripulation") beneath her body. If the danger increases, the female will try to drive away the predator. The mother protects the offspring until they reach the third instar. In addition, the female actively provides food to her brood. With the tip of rostrum, she gathers the falling fruits (drupes) of *Schoepfia jasminodora*, which are inaccessible to the nymphs. She moves the drupes to the developing nymphs, who congregate in numbers from 2 to 10 per drupe. It appears that collective enzyme injection by the nymphs is the only way to soften the interior of the drupes and allow ingestion. The females of *Legnotus limbatus*, *Sehirus bicolor* and *Sehirus nievimarginatus* also rostripulate the clutch, and they protect the young until the second instar.

Acanthosomatidae

Usually, maternal care consists of protecting large-sized clutches stuck to the leaves (Fig. 12). The female of *Elasmucha grisea* (parent bug) locates herself on the clutch (40–50 eggs) and protects it with her own body, without abandoning it even to feed herself. The care can be prolonged until the third instar, but by this time the mother remains beside the offspring, because they are too big to be shielded. The nymphs tend to aggregate, which facilitates maternal care. *Elasmucha grisea* can be considered a subsocial species, because the females often nurse their young collectively. This shared guarding behavior induces greater clutch size. In addition, the survival of the offspring is increased two-fold. The negative aspect of the shared guarding behavior is that the group becomes more tempting to insectivorous birds. This may explain why this behavior is observed, at most, in 30% of the females. *Elasmucha fieberi* behaves very similar to the previous species, but less is known. The female of *Elasmothetus interstinctus* protects her brood with her own body, before and after hatching, orienting herself toward the source of danger. The mother follows the movements of the brood, protecting them like an umbrella. The protection lasts only during the first instar. After the first molt, the nymphs preserve a certain gregarious instinct, but finally separate.

Phloeidae

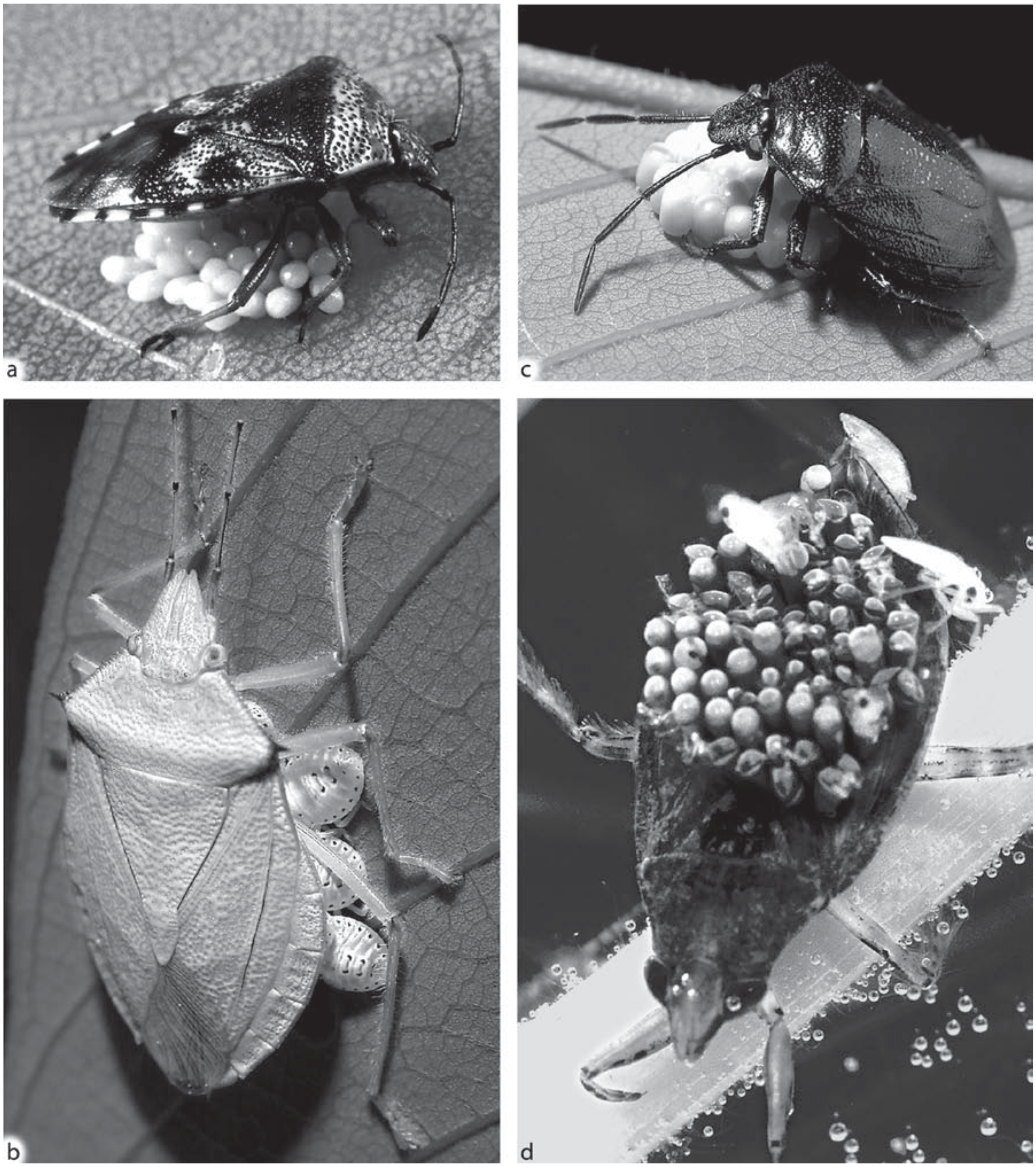
The female lays eggs in crevices of the host tree, and soon she covers the crevices with her body. The newly hatched nymphs seem to feed themselves on the mother, since their mouthparts are still too short to pierce the hard bark of the tree. In this case, the reason for maternal care is feeding, more than the protection from antagonists.

Tessaratomidae

Pygoplatys sp. and *Erga* sp. glue clutches of eggs to plants, and look after them. The female of *Pygoplatys acutus* protects, under her body, a mass of more than 30 nymphs. These attach firmly to their mother and she may even walk or fly without losing any nymphs. The mother is able to nourish herself on several plants, but not the nymphs.

Paternal Care

The concept of paternal care includes only those cases in which the father, alone or together with the female, is involved in the direct brood care, either of eggs or nymphs. It does not include cases where the father provides nuptial gifts (including spermatophores) to the future mate as prezygotic investment in the offspring. Although there have been attempts to relate paternal care to the type of fertilization, there are examples of paternal care both in species with external fertilization (when the male has greater certainty as far as his paternity) and in species with internal fertilization (as is the case in Heteroptera).



Parental Care In Heteroptera (Hemiptera: Prosorhynche), Figure 12 **More parental behavior in Heteroptera: (a) acanthosomatid guarding eggs; (b) Colombian pentatomid guarding nymphs; (c) *Antiteuchus tripterus* (Pentatomidae) guarding eggs; (d) Male *Belostoma* water bug with eggs and hatching nymphs on his back (photos courtesy of Doug Tallamy, University of Delaware).**

The transference of brood care to the male benefits the female. On the one hand, it releases her from limitations on her future fecundity, by allowing her greater freedom to feed and ability to escape predation (according to the enhanced fecundity hypothesis). On the other hand, it allows her to identify the males with better genes (handicap principle). In this second hypothesis, a male that successfully takes care of the offspring displays good genes, because the attention to brood care exposes him to greater risks than when he is not nursing the brood, just as happens in the case of maternal care. Paternal care is then a sexually selected character. The benefits of transferring brood-caring to the male are more evident in the predatory groups, where it is not possible to predate and nurse at the same time, so the female decidedly compromises her future fecundity.

Exclusive paternal care often occurs when the populations are in restricted spaces. This favors the promiscuity of the brooding male, which is constrained to a discrete space. Also, male caring behavior is frequently associated with populations in which the sex ratio is 1:1 or female-biased. If there were not selection in effect with regard to paternal behavior, it might be advantageous for the male to increase his fitness by promiscuity via scramble competition, leaving the brood unattended. On the other hand, if the density of females was very low the attachment of the male to the brood, which restricts his movement, might result in too few mating opportunities for him.

In Reduviidae it has been observed that the males are much more numerous on their host plants than the females. The time that the male remains with the offspring is directly related to the number of matings that he obtains in that place.

Often the female will choose a male that already has a clutch in his care, and the male will welcome an additional clutch and even will take care of clutches that are not his because this makes him attractive. Desire to become attractive even leads to the males robbing eggs that are being nursed by other males. An exception to this norm are Belostomatidae, in which bouts of oviposition and copulation alternate. In other words, in Belostomatidae the male makes sure that the clutch is his (natural selection). Male Belostomatinae, which are back-brooders, allow eggs that are not his, but prefer to assure their paternity. In this case the limiting factor could be the surface of the male's back. However, a Lethocerinae male, emergent-brooder (lays the clutch in the vegetation of the surroundings, a much less restricted space), willingly accepts clutches from several females, even if they haven't mated with him, because in doing so he becomes more attractive. The most difficult period for the female to choose a mate is at the beginning of the egg-laying period, when no male is protecting a clutch. The female must take considerable risk, and in case of failure (i.e., the male does not care for the offspring correctly), it may be assumed that this first clutch is only one fraction of her total fecundity. A possible signal of future good parental behavior would be the interest the male shows in receiving a clutch. Perhaps in these cases of uncertainty the first clutch is less numerous than the rest, but this has not been assessed. In the Heteroptera, the absence of activities that show the responsibility of the future father make the selection by the female more difficult.

In summary, paternal care is developed if it is compatible with male promiscuity at the same level as if the father did not take care of the offspring. This assumes that the father is associated to his offspring when they are hatched, and that paternal care is related to guaranteed paternity (both achieved as the female immediately lays eggs after mating). Paternal care is too risky not to be balanced by improved mating success associated with such behavior. Normally the caring male courts his mates where oviposition occurs, or he rides inseminated females until egg-laying occurs. Promiscuity is more common in the species with exclusive paternal care, the sex ratio is 1:1, or the population is highly female-biased. In such cases, the male becomes the limiting sex, and is sought after by the female (reversal of the typical sexual role). In addition, the females are iteroparous, and the opportunities for male promiscuity are numerous.

Groups That Display Paternal Care

Belostomatidae

In this family, exclusive paternal care is obligated, which means that in 99% of the cases, care is performed by the male. This was first observed in Belostomatinae at the beginning of twentieth century by Torre Bueno. In the fossil record, *Mesobelostomum*, a Lethocerinae from Solnhofen limestone (southern Germany), most probably brooded. Males require less food than females, predation efficiency is reduced by brooding, and females with a richer nutrition increase clutch size, so that Belostomatidae are a good example of paternal care selected by the enhanced fecundity hypothesis. Typically, bouts of copulation (up to 30) and oviposition alternate.

In *Lethocerus* (subfamily Lethocerinae), paternal care was first described in the late 1970s, and is called emergent-brooding. Sexes meet through the ripple signals performed by the male. Males that signal longer obtain more copulations than males that signal more briefly. In some species, males may also signal acoustically. Low frequency ripples may also be an attractive signal for predatory water spiders. Males may mate sequentially with several females, and their eggs will form a large egg clutch that will be attended by the polygynous father. In *Lethorecus americanus*, a male can take care of eight clutches simultaneously. The female glues the clutch in a plant stem or another emergent substrate along the pond margin. The adhesive is a hydrophilic mucopolysaccharide, which may contribute to moisture retention. It has been reported that *L. maximum* in Trinidad selects the oviposition height above water level depending on the season, higher in the rainy season. After each copulation bout, the female climbs out and lays 1–3 eggs, embedding them in a foamy substance produced by annex glands in her reproductive system. The eggs are then laid in a bubble net. When she completes her final oviposition, she abandons the clutch and never returns to it. Most probably, females never brood, because when left with no male after copulation she stops egg-laying and soon deserts her eggs, leaving the incomplete batch unattended. Laying eggs outside the water is complicated by the challenge of drought. In this case, paternal care will involve shading the clutch and periodically sprinkling it with the water that drains off his body. In very dry conditions, where water would evaporate prior to the male reaching the clutch, he imbibes water and regurgitates it onto the eggs. In *L. medius*, eggs were wetted every 30 min. Moreover, the father displays aggressively if threatened, especially against birds or any threat coming from above. Locating the clutch in the emergent substrate seems to be mediated by a scent delivered by the metathoracic scent gland system (MSGS). As the female has to track the clutch for a shorter time than males, the metathoracic scent gland system in females is much smaller than in males.

Males of Lethocerinae are not an active part of the population while nursing, and although sex ratio is nearly 1:1, the operational sex ratio is female-biased and females compete for the opposite sex. However, the wave motion the male produces to sprinkle the clutch is very similar to that produced when searching for mates. So females track this sign as to a possible mate, and as a result, brooding males do not lose chances for promiscuity, which is also reinforced by their caring behavior. If no other available mate is found, the female may attack the nursing male with the front legs and the rostrum and destroy the clutch, which stimulates a new mating. The male keeps an ambivalent attitude, because he tries to defend the old clutch and copulate with the attacking female at the same time. Only in about 30% of the cases are the caring males able to fend off the attacks by the females. Females may also drive the male away from the clutch he is caring for, copulate with him, and force him to brood the new clutch. The older nymphs of other clutches also may cannibalize eggs about to hatch. The older the clutch, the greater the amount of time the male spends next to it, seeking to avoid an encounter with a reproductive female that could spoil his investment in the brood.

Belostomatinae perform back-brooding. Courtship begins with "push-ups." Only after one or more couplings does the male allow the female to glue the eggs on his back. As in Lethocerinae, copulations and egg-laying alternate. One to four eggs are laid per oviposition effort. Males do not copulate while an egg pad is fixed to their back, and this is a very important restriction since mating season lasts 60–90 days. Periodically, the male cleans, aerates and wets the eggs with his hind legs. In Belostomatinae, the risk is drowning, as the oxygen and carbon dioxide diffusion rates in water are not sufficient to assure survival of the clutch. To enhance gas exchange, the male floats at the surface of the water, which is a very risky behavior because while doing so he is exposed to predators. Females and unencumbered males never behave in such a way. While underwater, the male aerates the clutch through brood pumping, a behavior that increases the flow of water over the surface of eggs. Brood pumping may be a plesiomorphic (ancestral) trait, modified from display-pumping. Lastly, the male may move its hind legs to brush and circulate water over the egg clutch (brood-stroking). In this way he also keeps informed about eggs still attached to his back. It has been experimentally verified that the eggs nursed in such ways have the highest percentage of hatching, as opposed to those which remain submerged in water, above the water surface, or pass from aerial habitat to the aquatic one but without receiving greater attention. Back oviposition sites are the limiting vital resource in the belostomatine giant waterbugs. Occasionally, eggs may also be laid on the female's back.

Under stressed conditions, the male may kick off an egg clutch, leading to egg abortion. Probabilities on kicking off an egg clutch depends on clutch size and age (i.e., on the male's invested effort). Also, the egg clutch is kicked off when all eggs have hatched, which occurs about 14 days after egg-laying. Death of the clutch may also occur when the male does not emerge from the water due to threats of predation; the developing embryos drown. Oophagy arises when the probabilities of eggs hatching are very low, and with ingestion of eggs the male partly recovers the energy invested in their care. As there is no need for clutch tracking in Belostomatidae, they lack the metathoracic scent gland system.

Brood caring means an elevated cost to the male, including a greater risk of predation, a smaller probability of successful hunting or of dispersing (the eggs glued on the back immobilize the wings), and perhaps also a smaller probability of fertilizing eggs. However, the male assumes these costs because he has certainty of paternity. Indeed, he accepts the clutch laid by the female with which he has just mated, because in these species sperm precedence is the rule (last in, first out).

The enormous size of the Belostomatidae (somewhat over 110 mm) seems to be related to paternal care, a trait following ancillary selection (selected by a primary trait, which is large size). Larger size opens new opportunities for preying on vertebrates. Great size is achievable due to prolonged life cycles and additional instars. However, this is a risky option, as nymphs are unable to fly and they may need to escape from temporary ponds. Such ephemeral habitats would be more suitable for insects with rapid development. On the other hand, a life cycle with five (rarely four) molts is fixed in Heteroptera. As a consequence, the only way to reach this great size is being born of very large eggs, which carries with it the constraint of higher metabolic demand, often exceeding the gas diffusion rate in water and threatening the survival of the embryos. If egg-laying on shore is adopted, which benefits from higher gas diffusion rates, the risk of desiccation arises. Adaptation to a water habitat relaxes the need for chorion protection against drought as compared with terrestrial bugs. Belostomatid egg yolk is richer in proteins than in lipids, and more water is needed to metabolize proteins. Paternal care in Belostomatidae not only counteracts the challenges of drowning (Belostomatinae) or desiccation (Lethocerinae), which are necessary to assure embryo survival, but frees the female from those tasks and leaves her ready again for reproduction (iteroparity). Perhaps some ancestral characters produced an adaptation to emergent-brooding. This could result from alternating oviposition and copulation, with the father remaining in the vicinity of hatching eggs (initially as a postinsemination association, to prevent further couplings of the female). This could include fighting against potential predators and inhibiting cannibalism on the part of the male. Also, the eggs benefit from being removed from the water as this inhibits growth of algae and fungi, but need to be moistened periodically to avoid desiccation. The result might be the evolution of emergent-brooding from a non-brooding ancestor. Back-brooding could have been produced by accident due to absence of emergent substrates, but the adaptiveness of breathing behavior is a consideration.

Reduviidae

In *R. tristis*, the male remains on the female's back and copulates with her until egg-laying. The female glues the clutch to a leaf of a plant. As egg-laying is completed, the male begins to nurse the offspring. For a short period of time, the female will come back to copulate again with the guarding male, laying additional egg batches. Other females will approach the guarding male and will mate with him, adding more eggs to the initial clutch. Also, females who didn't mate with him are allowed to contribute to the egg mass. In *R. tristis*, it has been shown that a male may protect up to ten clutches of five different females. As long as the father is caring, he will chase off parasitic wasps and other threats, although he is not always successful. During this period he does not feed, as this would mean abandonment of the egg mass to look for prey. Several males may congregate on the same plant, but this does not harm their chances of promiscuity. On the contrary, this situation benefits both sexes. Each male can fertilize several females, and each female can successively mate and lay eggs fertilized by several males, resulting in a greater genetic variability for their offspring. It has been recently reported that if the male abandons the clutch, a contributing female (a female whose eggs are part of the defended clutch) may replace him in guarding the offspring. In *Zelus* sp., *R. albopilosus* and *R. albopunctatus*, the father also takes care of clutches from several females, with which he may or may not have mated. Males fight to control an oviposition place, waiting for the females to arrive. In *Rhinocoris*, parental care ends as soon as eggs hatch, but in *Zelus* the male remains with the young until they disperse.

Coreidae

In the males of *Plunetis yurupucu* and *P. porosus*, the clutch is glued to the ventral abdominal sclerites of the male. This location suggests something more than simple passive cooperation on the part of the male. In a single population of *Scoloposcerus uhleri* it has been observed that the males carry the clutch stuck to the back, although this is not the case with the females.

Aradidae

In the genus *Neuroctenus*, it is not certain that the female which abandons the offspring is replaced by a male. In any case, she is replaced by another adult who guards the clutch until it hatches. It could be another female, because Aradidae typically make communal clutches.

► Bugs (Hemiptera)
► Sociality of Insects
► Gregarious Behavior in Insects

References

Gogala M, Yong H-S, Brühl C (1998) Maternal care in *Pygoplatys* bugs (Heteroptera, Tessaratomidae). Eur J Entomol 95:311–315

Smith RL (1997) Evolution of paternal care in the giant water bugs (Heteroptera: Belostomatidae). In: Choe JC, Crespi BJ (eds) The evolution of social behavior in insects and arachnids. Cambridge University Press, NY, pp 116–149

Tachikawa S, Schaefer C (1985) Biology of *Parastrachia japonensis* (Hemiptera: Pentatomoidea: Cydnidae). Ann Entomol Soc Am 78:387–397

Tallamy DW (2000) Maternal lace bugs: to care or not to care? Wings 23:3–7
Tallamy DW (2001) Evolution of exclusive paternal care in arthropods. Ann Rev Entomol 46:139–65
Tallamy DW, Schaefer C (1997) Maternal care in the Hemiptera: ancestry, alternatives, and current adaptative values. In: Choe JC, Crespi BJ (eds) The evolution of social behavior in insects and arachnids. Cambridge University Press, NY, pp 94–115

Parental Investment

Behaviors displayed by the parent insects to increase the probability that their offspring will survive and reproduce, at the expense of the parent's ability to produce more offspring. Females are considered to invest more in offspring than males. Social behavior is considered to be a high degree of parental investment because parents invest in brood care.

Parietals

The lateral areas of the insect head between the frontal and occipital areas. Each parietal consists of the antenna, compound eye, and lateral ocelli.

Parnassian Moths (Lepidoptera: Pterothysanidae)

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Parnassian moths, family Pterothysanidae, include 19 species from southern Africa (seven sp.) and Southeast Asia (12 sp.). There are two subfamilies: Pterothysaninae and Hibrildinae (the latter subfamily also considered in Eupterotidae in some classifications). The family is in the superfamily Calliduloidea, in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults medium size (55–75 mm wingspan), with head scaling average; haustellum naked; labial palpi porrect; maxillary palpi vestigial; antennae filiform or bipectinate. Wings rounded (Fig. 13) Maculation pale and spotted, sometimes translucent (Hibrildinae); some with long hair-like setae from hindwing margin (Pterothysaninae). Adults diurnal; possibly also crepuscular. Biologies and larvae remain unknown.

Parnassian Moths (Lepidoptera: Pterothysanidae), Figure 13 Example of parnassian moths (Pterothysanidae), *Hibrildes ansorgei* Kirby from Mozambique.

References

Hampson GF (1892) Family Pterothysanidae. In: Blanford WT (ed) Fauna of British India, including Ceylon and Burma. moths, vol 1. Taylor & Francis, London, pp 430–432
Hering EM (1926) Familie: Pterothysanidae. In: Seitz A (ed) Die Gross-Schmetterlinge der Erde. 10. Die afrikanischen Spinner und Schwärmer. A. Kernen, Stuttgart, pp 123–125, pl 19
Minet J (1987) Description d' une chrysalide de Pterothysaninae (Lep Callidulidae). Nouvelle Revue d' Entomologique (n.s.) 4:312
Seitz A (ed) (1926) Gattung: *Pterothysanus*. In: Die Gross-Schmetterlinge der Erde, vol 10. A. Kernen, Stuttgart, 277 pp, pl 26, 30

Paronellidae

A family of springtails in the order Collembola.
► Springtails

Parsimony

Events that are the result of the fewest intervening steps or processes. In systematics, evolution is assumed to proceed along the course with the fewest number of steps.

Pars Intercerebralis

The pars intercerebralis is the dorsomedial portion of the protocerebrum. The insect brain consists of the protocerebrum (the forebrain), mesocerebrum (middle brain), and tritocerebrum (hind brain). The protocerebrum innervates the eyes and ocelli.

► Nervous System

Parthenogenesis

Development from an egg that has not been fertilized. Reproduction without fertilization.

Parthenogenetic Reproduction

Asexual reproduction. (contrast with sexual reproduction).

► Parthenogenesis

Parvovirus

Parvoviruses, the smallest DNA viruses, are contained within the genera *Parvovirus*, *Erythrovirus*, *Dependovirus*, *Iteravirus*, *Contravirus*, and *Densovirus*. Members of the *Parvovirus*, *Erythrovirus*, and *Dependovirus* infect vertebrates, whereas the host range of genera *Contravirus*, *Iteravirus*, and *Densovirus* is restricted to arthropods. The dependoviruses require a helper virus for replication; the vertebrate parvoviruses and the Densovirinae are autonomous viruses. Autonomous parvoviruses replicate through a variety of double-stranded linear DNA intermediates in mitotically active host cells.The canine and human B-19 parvoviruses are simple icosahedral viruses that are constructed from 60 protein subunits or protomers that contain three structural proteins. The insect parvoviruses produce a small, non-enveloped icosahedron (20–24 nm diameter) composed of four structural polypeptides (VP1-VP4). These viruses, like other parvoviruses, possess a relatively high DNA/protein ratio (about 37%), which confers a characteristic heavy buoyant density (about 1.40 g/cm^3) in $CsCl_2$ gradients. These viruses are very stable and are resistant to exposure to pH 3–9, solvents ($CHCl_3$), and temperature (58°C, 1 h). Insect parvoviruses, like their vertebrate counterparts, replicate only in actively multiplying insect cells. The parvovirus replication takes place in the cell nucleus and is closely affiliated to cellular DNA replication events. Parvoviruses are not capable of stimulating DNA replication in resting cells; replication of these viruses requires host cells to go through the S phase. The insect parvoviruses undergo a non-lytic cycle in cell culture.

The subfamily Densovirinae (DNVs) contains members that have been isolated mainly from dipteran and lepidopteran hosts. The DNVs in the genus *Densovirus* contain a 6 kb genome which codes for structural and non-structural proteins on separate strands. Many of these viruses are polytropic and replicate in the nuclei of all insect tissues except the midgut. The *Bombyx mori* densovirus, the sole member of the genus Iteravirus, contains a smaller genome (about 5.0 kb) that codes for all proteins on one strand and is able to replicate only in midgut cells. Members of the third genus, the *Contravirus*, have been reported to cause persistent, non-lytic infections in mosquito cell lines and have been shown to be vertically transmitted in *Aedes*. These viruses possess a 4.0 kb genome and have open-reading frames (ORFs) on the plus strand and/or negative strands. The mosquito DNVs have been examined for potential vectors for the delivery and expression of foreign genes in mosquito cells. These polytropic DNVs share characteristics of both the *Densovirus* and *Iteravirus* groups. However, unlike the lepidopteran DNVs that encapsidate plus and negative strands at equal frequency, the *Aedes* DNVs encapsidate only 15% of the plus polarity strand.

The best-studied insect parvoviruses include the *Bombyx* DNVs, the causal agents of densonucleosis in the silkworm *Bombyx mori*. Two forms, DNV-1 and DNV-2, have been detected in silkworm populations. Both DNV-1 and DNV-2 replicate in the nuclei of midgut columnar cells. The DNV-1 (*Ina* isolate) induces infected midgut cells to be discharged into the gut lumen. DNV-2 infected cells are not as readily discharged as those infected with DNV-1. In nature, both DNV-1 and DNV-2 are able to cause chronic infections in larvae of the mulberry pyralid, *Glyphodes pyloalis*. More than 50% of field-collected *G. pyloalis* larvae screened with anti-DNV rabbit antisera were infected with DNV and/or the infectious flacherie virus. It is believed that this DNV overwinters in diapausing *G. pyloalis* and is transmitted to silkworms via contamination of mulberry foliage by prior generations of DNV-infected *G. pyloalis* larvae.

References

Bando H, Hayakawa T, Asano S, Sahara K, Nakagaki M, Iizuka T (1995) Analysis of the genetic information of a DNA segment of a new virus from silkworm. Arch Virol 140:1147–1155

Berns K (1990) *Parvovirus* replication. Microbiol Rev 54:316–329

O'Neill SL, Kittayapong P, Braid HR, Andreadis TG, Gonzalez JP, Tesh RB (1995) Insect denosoviruses may be widespread in mosquito cell lines. J Gen Virol 76:2067–2074

Pass, Bobby Clifton

Bobby Pass was born in Blount County, Alabama, in 1931. He received his B.S. and M.S. degrees from Auburn University, and a Ph.D. from Clemson University, the latter in 1962. He immediately joined the faculty of the University of Kentucky, where he served his entire professional career. He became department chairman after only 6 years of service, and served in that capacity for 33 years. He also served as the State Entomologist of Kentucky, a regulatory position. Known for his administrative prowess, Bobby Pass had a pioneering role in the promotion of IPM. He also played a major role in Kentucky's teaching programs, and did much to enhance the University of Kentucky's reputation in entomology. He served as president of the Entomological Society of America, and was active in the regional and national society. He died on December 12, 2001, 15 years after receiving a heart transplant, making him, at that time, one of the longest-living recipients of this operation.

Reference

Yeargan KV, Knapp FW (2002) Dr. Bobby Clifton Pass. Am Entomol 48:123–124

Passalidae

A family of beetles (order Coleoptera). They commonly are known as bess beetles.

► Beetles

Passandridae

A family of beetles (order Coleoptera). They commonly are known as parasitic flat bark beetles.

► Beetles

Passive Dispersal

The redistribution of animals caused by external agents such as wind or movement of seeds. The small size of insects allows passive dispersal frequently (contrast with active dispersal).

Passive Flight

One form of flight, found particularly in heavy bodied species, lacks wingbeat and fails to create thrust. This is basically a gliding or parachuting form of flight. The other basic form of flight is flapping flight.

Patagium (pl., patagia)

A small flap or lobe at the anterior edge of the forewing of some insects. It is also known as the tegula.

► Wings of Insects

Patch Dynamics

The concept that communities are not homogeneous, rather consisting of a mosaic of patches, with differing rates of biotic and abiotic interactions and disturbances.

Patch, Edith Marion

Edith Patch was born at Worcester, Massachusetts, USA, on July 27, 1876. Her family moved to Minnesota in 1884, where she had ample opportunity to live with, and observe nature. She was particularly fascinated with the monarch butterfly and at an early age came to love entomology. She entered the University of Minnesota in 1897 and received her B.S. in 1901. It was here that she was introduced to aphids, a subject that came to dominate her life. Unable to gain employment because entomology was not yet regarded an appropriate field for women, she taught high school for 2 years. However, in 1903 she was invited to organize a Department of Entomology at the University of Maine. During leaves of absence from Maine she studied at Cornell University, and was granted a Ph.D. in 1911. She served as head of the entomology department at the University of Maine until her retirement in 1937. Edith Patch wrote about 80 technical publications on insects, mostly concerning aphids, but also including many of Maine's important pests. She was interested both in taxonomy and economic entomology. Among her important works were "Aphididae of Connecticut" (1923) and "Food-plant catalogue of the aphids of the world" (1938). She was especially supportive of other students and scholars, and a significant amount of her time was devoted to assisting others to learn aphidology or in identifying aphids for others. Patch also wrote about 40 popular articles on scientific topics, about 100 nature stories for children, and 17 books on natural history for children. She was elected the first woman president of the Entomological Society of America and received many other honors and recognitions associated with her expertise in aphids. She died at Orono, Maine, on September 27, 1954.

References

Adams JB, Simpson GW (1955) Edith Marion Patch 1876–1954. Ann Entomol Soc Am 48:313–314

Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Stoetzel MB (1990) Edith Marion Patch: her life as an entomologist and as a writer of children's books. Am Entomol 36:114–118

Patchy Environment

A habitat within which occurs significant variability in suitability for an organism of interest.

Patella

In arachnids, a leg segment between the femur and the tibia.

Pathogen

A virus, bacterium, parasitic protozoan or other microorganism that causes disease by invading the body of a host; infection is not always disease because infection does not always lead to injury of the host.

Pathogenesis

The ill health or death of an organism caused by a pathogenic microorganism.

Pathogenicity

The ability of a pathogen to cause disease.

Pathogen Transmission by Arthropods

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Vector arthropods are those on, or in, which pathogenic organisms can survive and be transferred. Parasites transmitted by arthropods range widely from eukaryotes, including helminths, to prokaryotes and viruses. Some of them, for example, the sporogenic *Anthrax* bacterium (a prokaryote) and myxoplasmosis (a virus that affects rabbits) survive long enough on the mouthparts of bloodsucking insects such as horseflies and fleas that they are capable of contaminating vertebrate hosts. Regurgitation or the feces of their arthropod host disperse other pathogens that survive in the gut of non-bloodsucking insects such as cockroaches and domestic flies. Representatives of these groups are called contaminators. The efficiency of contamination depends upon the ability of the pathogenic agents to survive in, or on, the body of their temporary vector. The food of man or of animals can also be infected by pathogens transferred by these arthropods. In most cases, this type of transmission is occasional. However, for example, diarrhea agents can be transmitted in poorly managed hospitals where flies or cockroaches are abundant. There are some examples of persistent transmission. For example, the myxomatosis virus, which is capable of surviving for a long time on the mouthparts of *Spilopsyllus cuniculi* fleas, is transmitted from rabbit to rabbit by this vector only. In this case, the flea is an obligate, specific vector. However, this is an exception to the rule.

The term specific vector is mainly used to define the large group of vectors, mostly bloodsuckers, whose body provides not only a pathogen's survival, but also its propagation to the level of an invasive stage capable of infecting a vertebrate host.

Specificity of bloodsucking vectors is defined by the following criteria:

Any pathogen that consumes the energy sources accumulated by its bloodsucking host. The parasite propagates to enhance its chances of transmission.

A specific stage in the pathogen's life cycle is developed inside the arthropod host. This developmental stage can be distinguished morphologically (helminths, Protozoa, agent of plague) or antigenically (bacteria, viruses) or genetically using PCR for DNA/RNA identification (all pathogens).

Highly efficient mechanisms of transmission through injection or other specific contamination are characteristic.

The pathogen transmitted is relatively harmless to the vector either at the individual or at the population level.

It possesses both a) an adequate level of pathogen for the vector to be infected on a vertebrate host, and b) the ability for vector infection on an aviremic host. (An aviremic host is one that is tolerant to infection or it develops the infection much later than bloodsuckers are able to exchange the pathogen between infected and naive specimens).

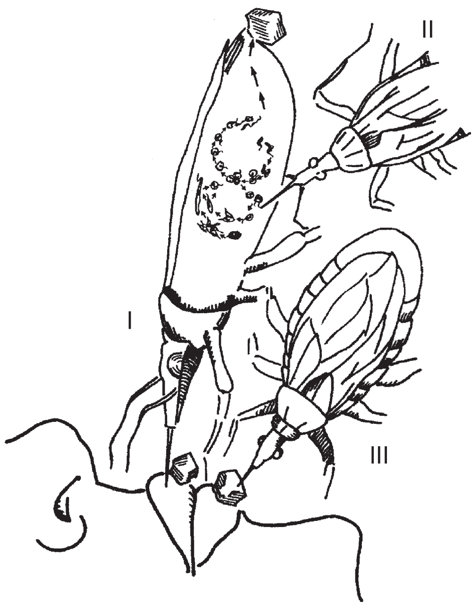
The malaria agent *Plasmodium* is the best example of items 1 and 2. Only sexual forms that are not very abundant in the host blood can develop in the mosquito host. In the sporocysts of *Plasmodium*, the numbers increase a thousand-fold. Individual sporozoites flooding out with mosquito saliva can infect a vertebrate host.

There are many mechanisms of parasite transmission. The most widespread mechanism is pathogen transmission through the bite of a bloodsucker (Fig. 14). Pathogens are transmitted in the ectoparasite's saliva. All mites and ticks, mosquitoes, gnats, sand flies and tsetse flies demonstrate this mechanism of transmission. Helminthes infest the host during the bite of a fly, but not with saliva. Using their "knife and scissors" mouthpart they are able to perforate the bloodsucker's soft labium that remains in tight contact with the wound they make in the host. Passive specific contamination is typical of triatomid bugs, also called "kissing bugs" because they often sting a sleeping person's mouth where the skin is thin. Their feces infected by the Chagas disease agent are dropped over a small wound made by the bug's "dagger-like" mouthparts. Lice-borne pathogens contaminate scratches in human skin either with infected feces or with crushed louse bodies whose guts are full of *Rickettsia* (red typhus) agents. Louse saliva is a highly itchy substance and stimulates both the scratching and the subsequent lice crushing. Bugs and lice are, therefore, not only specific hosts, but specific contaminators also.

The mouthparts of ectoparasitic mites, ticks and insects are highly varied in construction, but invariably well adapted to blood sucking. The stiff "daggers and scissors" of a horse-flea's mouthparts enable rapid blood-sucking in spite of the rough skin of its host. The fine, delicate vein-opening apparatus of sand flies account for their Latin name, Phlebotominae, "phlebo-tomeo" meaning "vein dissection." The long, sword-like, flexible, often serrate mouthparts of mosquitoes and fleas enable them not only to pierce the host's skin, but also to penetrate the blood vessels. The rough, scissors-like tick chelicerae provide a relatively large hole in the host skin, inside which the hooked hypostome is inserted to ensure tick attachment. Very often, a special kind of saliva, which hardens in contact with air and is thus termed cement, anchors the tick mouthparts in the skin. This is necessary to fix a hard tick whose feeding takes several days. Saliva of bloodsucking arthropods is rightly called a pharmacological laboratory, as it either serves to irritate the host skin (lice) or to anesthetize the place of the bite (triatomid bugs, ticks and mites), or to dilate host's blood vessels and suppress blood clotting. Tick saliva is perhaps the most multifunctional in suppressing not only blood clotting, but also host immune reactions. The more detailed the study of bloodsuckers' saliva, the more diverse are the features disclosed. The presence of specific insect- or tick-borne pathogens not only alters arthropod host behavior (e.g., tick-borne encephalitis virus enhances the vector's locomotor activity) but also its saliva. For example, the malaria agent appears to disable the production of the enzyme apyrase by the mosquito salivary glands. As a result, the duration of bloodsucking is extended, and a considerable increase in sporozoite transmission to the vertebrate host is observed.

Blood consumption from vertebrate hosts is an absolute prerequisite to survival of bloodsucking arthropods. Yet, blood is the main, but not the only, pathway of pathogen transmission. Devouring the gut content of older individuals is relatively common among bloodsuckers. For example, the larvae and nymphs of triatomid bugs very often behave as cannibals, piercing the body of adults and sucking their blood content, which might be infected by *Trypanosoma cruzi*. Sucking the adult feces is also typical of these contaminators. Four pathways of pathogen transmission can be seen in this picture: two types of contamination (both from and to, the insect) and two routes of pathogen acquisition (with blood of a vertebrate or an invertebrate host) (Fig. 14).

Often enough, subadults of soft ticks suck the gut content of older individuals which have fed, thus engulfing relapsing tick fever pathogens (e.g., *Borrelia duttoni*). Likewise, there are several modes of transmission and circulation of the plague agent *Yersenia pestis* (Fig. 15) which is usually transmitted through a flea bite (donor rodent - to flea - to recipient rodent). However, it can also be acquired by the direct contact of a healthy person with an ill one in cases of the pulmonary form of the disease, or, carried from a bloodfed, infected, soft tick to a hungry flea. At present, a telluric way of plague agent maintenance is in debate. *Yersenia pestis* pathogens can be preserved and are capable of re-entering the animal/flea circle at a later time. *Anthrax* bacilli in the spore form can remain preserved in the soil for decades and then infect wild animals or livestock.



Pathogen Transmission by Arthropods, Figure 14 Specific contamination and cannibalistic routes of Chagas disease agent. I – specific contamination: infected feces contaminate the wound made by the bug; II – cannibalistic route: hungry nymph consumes trypanosomes from the fed adult's gut; III – contamination route: hungry nymph consumes agent from the drop of fresh feces with trypanosomes.

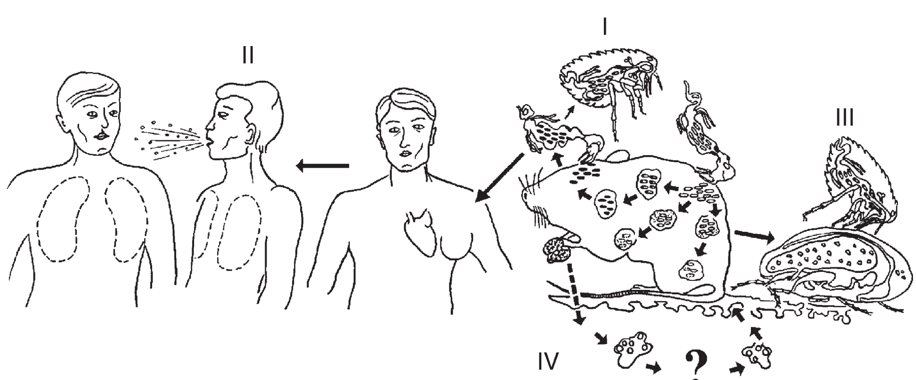
Anthrax kills the vertebrate host while horse flies feeding on the dying or freshly dead animals may disseminate this agent as contaminators. Horse flies carry the spores on their mouthparts. Even a typical vector-borne pathogen such as the malaria agent can circulate by transmission from an infected mother to a child or from an infected person to a healthy one by blood transfusion. In these cases, asexual forms of the parasite are transmitted.

The pathways of tick-borne pathogen transmission seem the most complex. The most studied examples concern the tick-borne encephalitis virus, an agent that is the most dangerous to man.

The first, "classical" pathway demonstrates infected blood consumption by an adult female tick feeding on a vertebrate showing viremia (high concentrations of the virus in host blood). For a long time, this pathway was believed to be the main one. It includes:

Transovarial transmission, implying infected blood consumption and pathogen transmission to the egg (beginning of the F1 progeny). Transovarial virus transmission has also been proven for Diptera: mosquitoes as vectors of yellow and dengue fevers, and sand flies as vectors of phleboviruses (for example, papattasi fever).

Transphasic transmission must include at least one of the following steps: transmission of a pathogen from fed and infected larvae to nymphs; survival



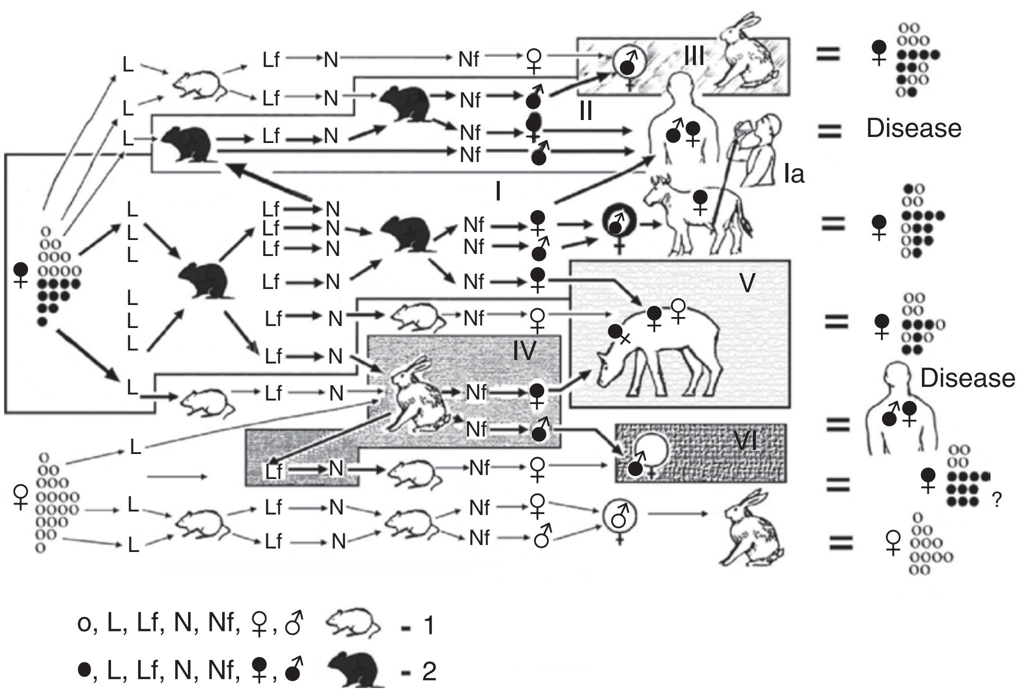
Pathogen Transmission by Arthropods, Figure 15 Plague agent routes of transmission and circulation. I – system: flea, *Yersenia pestis* and susceptible rodent; II – generalized and aerial forms of plague; III – *Ornithodoros* as a "living can" of *Y. pestis* for fleas; IV – possible phytophase of the *Y. pestis* cycle (telluric hypothesis).

of the pathogen in hungry and fed nymphs and its transmission to adults following the nymph's molt. Adults can transmit the virus to humans and animals. Transphasic transmission is also typical of *Borrelia*, the relapsing tick fever agent transmitted by soft ticks, and of the Lyme disease agent transmitted by hard ticks of the genus *Ixodes*.

The sexual transmission of tick-borne encephalitis (TBE) virus and Lyme disease agents from males to females has been proved as well.

A cannibalistic type of pathogen exchange cannot be excluded as, for example, *Ixodes* tick males sometimes feed not only on fed females but also on hungry specimens.

At present, the classical pathway of pathogen transmission is no longer considered to be the main one. Pathogen exchanges between co-feeding vector specimens belonging to various age groups, for example, nymphs and larvae of ticks, or different generations, is now theoretically the most efficient way of spreading the viruses and other pathogens from infected individuals to uninfected ones. Ticks issuing saliva near each other may transfer regurgitated pathogens while feeding in the same site of inflammation in the host skin. This type of transmission is called transsalival and may occur both on viremic and aviremic vertebrate hosts (Fig. 16).



Pathogen Transmission by Arthropods, Figure 16 Tick-borne encephalitis virus routes of transmission. I – "classical" (transmissive) route from egg to egg by feeding on the susceptible vertebrate animals with threshold quantity of virus in the blood; Ia – human infection by virus contained in goat or cow milk; II – transphasic transmission: naïve larva gets virus on infected susceptible vertebrate animal; III – sexual transmission: infected male transmits virus to naïve female during copulation; IV – virus exchange between infected nymphs and naïve larvae co-feeding not near each other on the vertebrate animal without viremia (distant transmission); V – virus exchange between specimens co-feeding near each other on aviremic (not susceptible to the virus) animal (transsalival transmission); VI cannibalistic route of transmission: infected male consumes hemolymph from naïve female and injects virus-infected saliva into her body; 1 – naïve tick and vertebrate animal: o – ova, L – larva, Lf – fed larva, N – nymph, Nf – fed nymph.

Similar exchanges of pathogens, not only of viruses but of borreliae as well, occur when ticks feed separately on infected and aviremic animals. This type of transmission is termed infection on an aviremic host, or distant infection. The mechanism by which this exchange occurs is enabled by the host immune cells, which transfer absorbed pathogens from one area of inflammation to another.

The many forms of pathogen transmission ensure the effective transmission of infection by bloodsucking insects, mites and ticks.

References

Alekseev AN (1993) Tick-tick-borne pathogen system and its emergent qualities. Zoological Institute RAS, St. Petersburg, Russia, 204 pp

Alekseev AN, Chunikhin SP (1991) Virus exchange in ticks feeding on vertebrate host in the absence of viremia (distant transmission). Med. Parazitologiya i parazitamye bolezni (Moscow) 2:50–54

Alekseev AN, Kondrshova ZN (1985) Organism of arthropods as environment for pathogens. Academy of Science of the USSR Urals Branch, Sverdlovsk, USSR, 181 pp

Jones LD, Davies CR, Steele GM, Nuttall PA (1987) A novel mode of arbovirus transmission involving a nonviremic host. Science 237:775–777

Kennedy CR (1975) Ecological animal parasitology. Blackwell, Oxford, UK, 163 pp

Ribeiro JMC (1995) Blood-feeding arthropods: live syringes or invertebrate pharmacologists? Infect Agents Dis 4:143–152

Pathogens of Whiteflies (Hemiptera: Aleyrodidae)

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Whiteflies are tropical and subtropical in origin, and can be serious pests in greenhouses and on house plants. In the United States, whiteflies were considered secondary pests in agricultural field crops until outbreaks of the silverleaf whitefly (*Bemisia argentifolii*) began to occur in the late 1980s. Before the development of the silverleaf whitefly problems in the U.S., whiteflies were mainly greenhouse pests, and occasionally pests on certain other subtropical crops, such as citrus. The silverleaf whitefly has a wide host range, including cotton, melon, soybean, and a variety of vegetable crops.

Whiteflies are very small insects, and like other Hemiptera, they have sucking mouthparts. Insect pathogens (also known as entomopathogens) in the groups bacteria, viruses, rickettsia, and protozoans nearly always infect hosts through the alimentary tract, and so the host must ingest the pathogen to become infected. Because whiteflies suck the phloem from plants, the only means by which they might ingest these pathogen groups is if they occur in the plant phloem. Entomopathogens have been known to occur and even grow within plants, but it is not very common, and for that reason, these pathogens are rare in whiteflies. This situation should not be confused with its reverse, that is, where the insect acts as a vector for plant pathogens, a much more common phenomenon. Whiteflies do act as vectors for plant pathogenic viruses, particularly the Gemini viruses.

Nearly all known whitefly pathogens are fungi, which can infect their hosts directly through the exoskeleton. Fungi in the phylum Deuteromycotina are the asexual fungi, and most all pathogens of whiteflies belong to this group. Conidia, asexually produced spores, are the infective units. These spores attach to the outside of the host, where they germinate, producing a germ tube. The germ tube will grow along the cuticle of the host until it finds a suitable site to penetrate and cause infection. The invasion process varies somewhat between species, but a good general description can be found by Hajak and St. Leger (1994).

Aschersonia spp. are fungal pathogens commonly found in whiteflies in the genus *Trialeuroides*. These fungi belong to the class Coelomycetes and are specific to whiteflies and coccids. Twenty-five species have been isolated from whiteflies. They produce conidia in structures called pycnidia. Different species of *Aschersonia* can be distinguished by the color of the conidia – usually reddish, orange, or yellow. *Aschersonia conidia* are coated in a hydrophilic mucus layer. This mucus is somewhat sticky and prevents them from readily being dispersed by wind, so *Aschersonia conidia* are usually dispersed by rainfall. Young whitefly nymphs are the most susceptible life stage, with the older nymphal stages being progressively less susceptible, and the adults resistant, to infection.

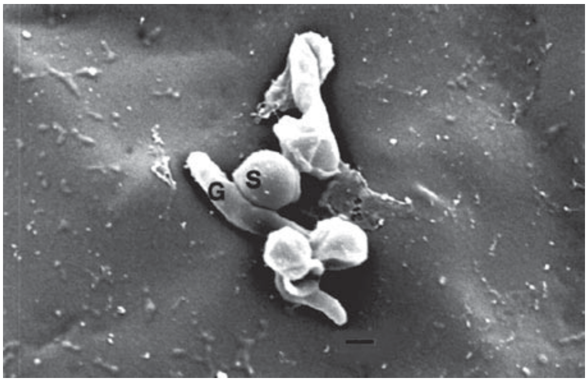
Other fungi that have been found in populations of *Trialeuroides* whitefly nymphs include *Verticillium lecanii*, *Paecilomyces fumosoroseus*, *Aphanocladium album*, and *Beauveria bassiana*. All these belong to the class Hyphomycetes. The nymphs are most commonly infected, but adults have been found infected with *Paecilomyces farinosis*, *Paecilomyces fumosoroseus*, *Verticillium fusisporum*, and *Erynia radicans*. Unlike the other fungi mentioned so far, *Paecilomyces* spp. and *Beauveria bassiana* produce dry conidia without a mucous coating. These may be dispersed by either rain or wind, but the spores are dried and shriveled and require high levels of moisture for germination. This moisture may come from rain, dew, or high levels of relative humidity that sometimes occur at the plant surface.

Aschersonia has rarely been isolated from *Bemisia* whitefly species. Pathogens in the genera *Verticillium* and *Paecilomyces* are much more common. *Beauveria bassiana* has been shown to infect nymphs of *Bemisia* whiteflies if they are sprayed with conidial suspensions, but no epizootics in untreated whitefly populations have been reported.

Pathogens of whiteflies have been used as biological control agents to control pest outbreaks. Using pathogens as biological control agents is also called microbial control, and is done two different ways: by natural epizootics and augmentative use. When whitefly populations reach outbreak levels and climatic conditions are right (usually during times of high rainfall), then fungal pathogens can cause epizootics. Epizootics of fungal pathogens in whiteflies can be quite striking and lead to a rapid decline in host populations. The limitation of natural epizootics as a pest control strategy is that growers have little control over their occurrence, and they often do not occur until host populations are high, which means that crop damage is likely to have already occurred. However, natural occurrences of fungal pathogens may control whitefly populations more often than is recognized.

Augmentative control is when a natural enemy is mass cultured and then released for biological control. The control agent may or may not be expected to establish in the region. It is the mass release that leads to control. This approach is common for microbial control agents; *Aschersonia*, *Verticillium lecanii*, *Paecilomyces fumosoroseus*, and *Beauveria bassiana* (Fig. 17) have all been produced for commercial sale as myco-pesticides against whiteflies. Most myco-pesticides used for whiteflies contain fungal spores, either conidia or blastospores, as the active ingredient. Conidia have a longer shelf- and field-life, but can only be produced on a solid substrate. Blastospores are produced during liquid fermentation. Liquid fermentation tends to be faster and less labor intensive than fermentation on a solid substrate.

These myco-pesticides have tended to work better in greenhouses than in field crops. The



Pathogens of Whiteflies (Hemiptera: Aleyrodidae), Figure 17 Four conidia of the fungus *Beauveria bassiana* germinating on the cuticle of a nymph of the silverleaf whitefly. S = conidial spore, G = germ tube, Bar = 1 µm.

reasons for this are surely many-fold, but the fact that greenhouses tend to be more controlled environments is probably a major factor. Temperature and relative humidity can have a dramatic impact on infection levels, and these factors are more controlled in greenhouses. The high levels of humidity in greenhouses are conducive to infection. Conidia and blastospores also are very sensitive to ultraviolet radiation, which is generally lower in a greenhouse than the field, just by the nature of a greenhouse (greenhouse materials such as glass, plastic, shade cloths, etc., block some light from entering). Lower ultraviolet light levels extend the life of the spores and their activity. In the field, mass immigration of new adult whiteflies into a treated field can lead to whitefly population increases if conditions are not conducive to disease transmission of the fungus from treated insects to new, uninfected hosts.

References

Fransen J (1990) Natural enemies of whiteflies: fungi. In: Gerling D Whiteflies: their bionomics, pest status and management. Intercept, Ltd., Andover, UK, pp 211–225

Gindin G, Geschtovt NU, Raccah B, Barash I (2000) Pathogenicity of *Verticillium lecanii* to different developmental stages of the silverleaf whitefly, *Bemisia argentifolii*. Phytoparasitica 28:229–239

Hajek AE, St Leger RJ (1994) Interactions between fungal pathogens and insect hosts. Ann Rev Entomol 39:293–322

Lacey LA, Fransen JJ, Carruthers R (1996) Global distribution of naturally occurring fungi of *Bemisia*, their biologies and use as biological control agents. in Gerling D (ed) *Bemisia* 1995: taxonomy, biology, damage control and management. Intercept, Ltd., Andover, UK, pp 401–433

Wraight SP, Carruthers RI, Jaronski ST, Bradley CA, Garza CJ, Galaini-Wraight S (2000) Evaluation of the entomopathogenic fungi *Beauveria bassiana* and *Paecilomyces fumosoroseus* for microbial control of the silverleaf whitefly, *Bemisia argentifolii*. Biol Control 17:203–217

Pathology

The science that deals with all aspects of disease.

Pathotype

An intraspecific variant of a pathogen, distinguished by variation in pathogenicity on a specific host relative to other pathogens of the same type.

Pathway

From a regulatory perspective, any means that allows the entry or spread of a pest into a new area.

Patrolling

In honey bees, the act of investigating the interior of the nest by workers. Such behavior allows the nest to detect and respond to problems quickly.

Patronym

In nomenclature, a scientific name of a taxon based upon the name of a person. When such a name is dedicated to a living person, it is said to be named for that person. When it is dedicated to a deceased person, it is said to be named after that person.

Paurometabolous Development

This is a type of incomplete metamorphosis (hemimetabolous development) found in some aquatic insects (Odonata, Ephemeroptera, Plecoptera). Unlike terrestrial insects displaying the typical form of incomplete metamorphosis, in which the immature and adult stages are substantially the same in body form (differing principally in the presence of fully formed wings among the adults), immature and adult stages of these aquatic insects differ slightly to significantly in appearance as compared to their adults. However, they lack a pupal stage, which is characteristic of insects with complete metamorphosis (holometabolous development). Because these insects depart from the typical pattern of hemimetabolous development, they sometimes are said to have paurometabolous development or gradual metamorphosis. Consistent with this differentiation, the immature are sometimes called naiads rather than nymphs. (contrast with hemimetabolous development, holometabolous development).

► Metamorphosis

Paykull, Gustaf

Gustaf Paykull was born at Stockholm, Sweden, on August 21, 1757. Educated initially by tutors, Paykull was likely influenced by Linnaeus, and developed interest in natural history, literature, and poetry. His literary successes were limited at the University of Uppsala, and he began to concentrate more on natural history. Beginning in 1779 he worked in government administration, though he found pleasure in collecting, and he also learned that this activity earned him respect from colleagues. He went on to build an extensive private collection of natural objects. He produced monographic treatments on several groups of beetles in the late 1700s, culminating in his "Insecta Svecica" (1798–1800). Paykull traveled widely, and collected birds, mammals, and fish in addition to insects. His eagerness to amass a large collection earned him the ire of some colleagues, however, as some borrowed specimens apparently were not returned. He was honored by election to the Swedish Academy of Sciences in 1791. Paykull died at Stockholm on January 28, 1826.

Reference

Herman LH (2001) Paykull, Gustaf. Bull Am Mus Nat Hist 265:122–123

Pban

A neuropeptide that controls synthesis of pheromone in glands of some female moths.

► Reproduction

PCR

See polymerase chain reaction.

PCR-RFLP

A technique that combines the PCR and RFLP analyses. Genomic DNA is amplified by traditional PCR. Once the DNA is amplified, it is cut with restriction enzymes, electrophoresed, and visualized by ethidium bromide staining. Because the DNA was amplified by the PCR, the DNA fragments can be visualized without having to blot and probe the labeled probe, making PCR-RFLP more efficient and inexpensive than traditional RFLP analysis.

Pea Aphid, *Acyrthosiphon pisum* (Harris) (Hemiptera: Aphididae)

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The origin of pea aphid is likely Europe or Asia, although it is now found throughout the world in regions with temperate climates. In recent years, a closely related species with similar biology, *Acyrthosiphon kondoi* Shinji, has also spread nearly worldwide and attacks some of the same crops.

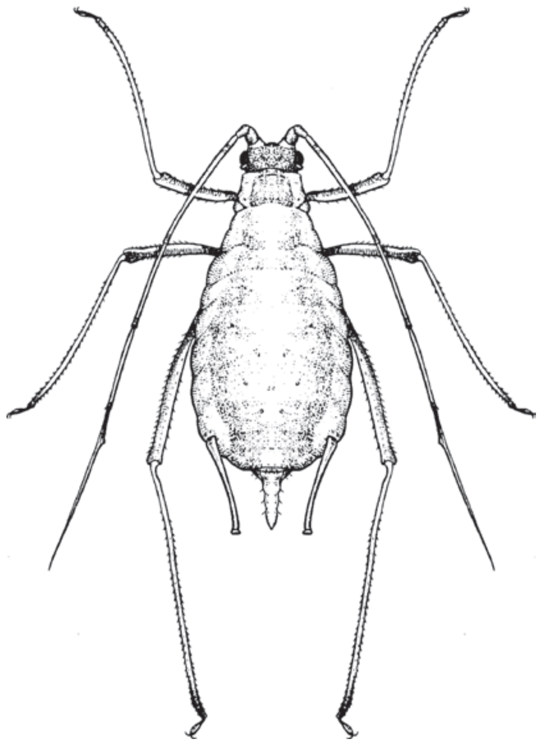
Life History

Pea aphids complete their life cycle quickly. These aphids can reach maturity and begin reproduction 10–12 days after birth. The number of generations completed annually by pea aphid is estimated at about 13 in cooler climates and over 20 in warmer climates. The overwintering stage of pea aphid varies with climate; in cold regions the eggs overwinter, in warm areas females persist, and in temperate climates both eggs and females can be found during winter months. Unlike many species of aphids, these species do not migrate to a woody host for overwintering. However, they do commonly disperse from annual legumes in the summer to perennial legumes such as alfalfa and clover in the autumn, so the difference in behavior is not great.

The egg is elliptical in shape, measuring about 0.75–0.80 mm long and 0.35–0.40 mm wide. Initially pale to bluish green in color, the eggs soon turn shiny black. Eggs commonly hatch in early spring. After developing on alfalfa or clover for several generations, overwintered populations produce winged females which disperse to uninfested plants. New hosts include both peas and forage legumes.

Pea aphid has four instars. Instar duration is about 2.7, 2.6, 2.7, and 3.6 days, respectively, at 15°C. Optimal temperatures are about 10–15°C for survival and fecundity, but 20–25°C for rapid development. Throughout development the nymphs are pale green in color. The body length increases from about 0.9, to 1.2, 1.7, and 2.0 mm in instars 1–4, respectively. The tip of the cornicles, distal portion of the tibia, and the tarsi are blackish throughout development. The instars are best separated by cornicle length, with lengths of <0.21, 0.21–0.36, 0.37–0.58, and >0.58 mm in instars 1–4, respectively.

Through most of the year, pea aphid reproduces parthenogenetically (viviparously), females giving birth without mating. Reproduction commences about 2.4 days after attainment of the adult stage. Reproducing females may be either winged (alate) or wingless (apterous) (Fig. 18). These are relatively large aphids, the apterae measuring about 2.3–2.7 mm and the alatae about 3.0–3.5 mm in length. Both winged and wingless forms are pale green with black at the tips of the rather long cornicles (Fig. 18), although in the alate form the head and thorax tend toward yellow-brown. Both forms also have long legs, principally green but with the tips of the tibia, and the entire tarsi, blackish in color. The wings of the alatae are colorless. Pea aphid sometimes exhibits red body color rather than green. The basis for the color forms is genetic, and in crosses the red form is dominant. Red color



Pea Aphid, *Acyrthosiphon pisum* (Harris) (Hemiptera: Aphididae), Figure 18 Wingless adult female of pea aphid, *Acyrthosiphon pisum* (Harris).

forms rarely are found on pea, but are sometimes found on red clover and alfalfa. Females typically begin production of offspring 10–12 days after birth. Mean number of nymphs produced per female is estimated at about 70–100, although some individuals produce up to 150 offspring. The rate of reproduction is highest early in life, with as many as 14 nymphs being produced per day by each female. Near the end of her life (mean of 40 days), an aphid may be producing less than one nymph per day. The average rate of reproduction is estimated at 7 per day, but apterous females produce 8.5 per day whereas alatae produce only 3.8 per day. The aphids seem to form only small colonies on pea, with frequent dispersal of alatae as densities increase. Maturation of pea plants also results in development of alatae, and their dispersal.

Sexual forms are produced by pea aphid in the autumn in response to shorter day lengths and cooler temperatures, and males and females may be alate or apterous. The females greatly resemble the apterous viviparous females, differing principally in size. Oviparous females measure only about 2.0–2.2 mm long. The greenish males also bear brown coloration on the thorax, and usually brown or yellowish brown on the head and abdomen. The males measure less than 2.0 mm long. Production of sexual forms is less predictable than in many other species of aphids. For example, oviparous females may be produced by either alate or apterous females, and the same female may produce both viviparous and oviparous forms alternately. Fecundity of oviparous forms seems to be unknown, but based on examination of ovaries, at least 25 eggs are produced by each female.

The aphids produce and respond to alarm pheromone. Pheromone production normally results when aphids are disturbed, and the standard response by aphids is to walk away from the source of the pheromone or to drop from the plant. Responsiveness to pheromone is increased when the substrate is vibrated. Young instars are less responsive.

Pea aphids are known principally as pests of Leguminosae. Because they are efficient vectors of plant viruses, however, they also cause loss in crops on which they normally do not feed, such as cucurbits.

Pea aphid is prone to develop races or subspecies with slightly different host ranges, so populations may differ somewhat in their damage potential to specific legumes. Pea is the most suitable vegetable host for this species, and faba bean and lentil are sometimes damaged. Other hosts that are important in pea aphid biology are alfalfa, sweet pea, vetch, and such clovers as alsike clover, red clover, white clover, and sweet clover.

A large number of natural enemies of pea aphid have been documented. Flower fly (Diptera: Syrphidae) and ladybird larvae (Coleoptera: Coccinellidae) species are most numerous among the natural enemies, and sometimes quite important in regulating aphid population densities. However, fungi and wasps (Hymenoptera: principally Braconidae) also are very important, with introduced species of *Aphidius* normally dominant. The braconid *Aphidius ervi* Haliday is often reported to be the most important parasitoid, and was observed in North America soon after the introduction of pea aphid, probably being introduced simultaneously. Initially it did not provide effective suppression, and other introductions of beneficial species were made, apparently including additional subspecies or races of *A. ervi*. Among the other species introduced were *A. smithi* Sharma & Subba Rao; *A. eadyi* Stary, Gonzalez, & Hall; *A. urticae* Haliday; and *A. staryi* Chen, Gonzalez, & Luhman. Apparently there has been displacement among species and strains of parasitoids, with the native *A. pisivorus* Smith displaced by imported *A. smithi*, and then the latter species displaced by *A. ervi*.

A rather predictable cycle of events is observed in many pea aphid populations. After building to high densities on either forage legumes or peas in the spring months, predators, parasites, and fungi take a toll. Both the natural enemy densities and weather are unfavorable at mid-summer, and aphid populations decline. Warm, humid weather, in particular, favors development of fungal epizootics among pea aphids. With the subsequent collapse of natural enemy populations and the return of cooler, more favorable weather for aphids in the autumn, pea aphid populations typically increase again. In Canada and other northern latitudes the aphid populations may not attain high densities until late summer, so there is only one population peak.

In addition to the effect of weather on disease incidence, there also can be direct effects of weather on pea aphids. In cold climates, which are normally characterized by abundant snowfall, egg survival rates are high and overwintering success is not highly variable. In mild-winter areas, overwintering success is more variable. Mild winters favor the survival of overwintering females and eggs. During cold winters, however, when temperatures fall below freezing, neither adults nor eggs survive well. In addition to the cold temperatures, the lack of snow cover is thought to reduce the overwintering success rate. Also, aphids are especially susceptible to destruction by such adverse weather as heavy rainfall in the early part of the season, soon after egg hatch. The lower developmental threshold for pea aphid is about 5.5°C, whereas that of its principal parasitoids is 6–7°C. The higher developmental threshold of the parasitoids allows the aphid populations to increase to higher densities during cool spring weather.

Damage

Pea aphids cause direct injury by removal of plant sap from leaves, stems, blossoms, and pods. Aphids feeding on foliage disrupt the flow of plant photosynthates to the plant roots. Nitrogen fixing bacteria inhabiting the nodules on roots of legumes are affected by availability of phytosynthates. Thus, aphid feeding decreases nitrogen fixation and plant growth. Both young and mature plants are affected. Damage may not be apparent if aphid populations are low, but at high densities foliage may turn brown, pods are only partially filled, or fewer pods are produced. Under extreme conditions young plants are killed.

Pea plants may support aphids throughout the growing season, but not all stages of plant growth are equally susceptible to damage. The flowering and pod-filling stages were most susceptible to injury. Plants infested prior to the reproductive stage recover from damage if the aphids are removed, resulting in no reduction in yield. The treatment threshold was estimated to be about 2–3 aphids per stem tip, or 9–12 aphids per sweep.

Acyrthosiphon species commonly vector plant viruses. Over 30 viruses are known to be transmitted by pea aphid. Because pea aphid develop large populations on many legume hosts, particularly extensively planted forages such as alfalfa, they provide numerous potential vectors to cropping areas. In some instances they are important vectors in crops on which they do not normally feed. For example, watermelon mosaic virus and zucchini yellow mosaic virus are transmitted to cucurbits by both pea aphid and blue alfalfa aphid. They are very important in vectoring legume viruses also, including pea enation mosaic, one of the most prevalent virus diseases of peas.

Management

Aphids may be sampled by various methods, including direct visual examination of plants, sweeping, vacuum sampling, and trapping. Sweep net sampling is usually recommended.

Both soil-applied and foliar insecticides are commonly used to protect plants from injury by pea aphid. Systemic and nonsystemic products are used. The susceptibility of aphids to foliar insecticide is increased slightly when alarm pheromone is released near aphid-infested plants, presumably because the elevated activity level associated with pheromone release increases contact with insecticide.

Crop management is a key factor in preventing damage by pea aphid. Because alfalfa and clover are the common overwintering sites, they serve as the source of inoculum for surrounding areas. Such crops can be sprayed with insecticide or harvested before aphid populations produce alate forms, resulting in the destruction of most potential dispersants. Destruction of crop residue by burning also disrupts aphid populations by destroying overwintering aphids.

Forage legumes may serve as sources of plant viruses for both legume and nonlegume vegetable crops, and pea aphid serves as an effective vector. For example, the incidence of bean yellow mosaic virus in bean is related to the proximity of clover. Also, emigration of aphids from alfalfa to other crops increases following cutting.

Pea leaf roll, pea enation mosaic, and some other *Acyrthosiphon*-transmitted viruses are circulative viruses, persisting for the duration of the vector's life. Such viruses usually require extensive feeding for successful transmission; thus, insecticides can be helpful in protecting against disease. Research has shown that incidence of pea leaf roll virus can be decreased by application of systemic insecticides. Insecticides are less useful for stylet-borne viruses, which are transmitted quickly. Interestingly, stylet-borne virus transmission is often reduced by application of oils to plants, but oil does not greatly reduce transmission of circulative viruses such as pea enation virus. The differential effectiveness of oil is likely due to the tendency of oil to inhibit probing by transient alatae, but not feeding by colonizing aphids.

Peas differ in their susceptibility to pea aphid. Resistance is reflected in differences in aphid weight, longevity, time to maturity, and progeny and honeydew production on many plant cultivars, and in plant tolerance to aphids in a few varieties. Although aphid performance differs among pea cultivars, none are immune to attack. Faba bean cultivars, although differing with respect to aphid performance, similarly display little practical resistance to pea aphid. Pea plant morphology affects aphid success indirectly by influencing searching effectiveness of aphid predators, but this form of resistance has not been exploited by pea breeders.

► Aphids

References

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, CA, 729 pp

Cook WC (1963) Ecology of the pea aphid in the Blue Mountain area of eastern Washington and Oregon. USDA Technical Bulletin 1287, 48 pp

Hutchison WD, Hogg DB (1984) Demographic statistics for the pea aphid (Homoptera: Aphididae) in Wisconsin and a comparison with other populations. Environ Entomol 13:1173–1181

Peach Silver Mite, *Aculus cornutus* Banks (Acarina: Eriophyidae)

This mite damages peach tree foliage throughout the world.

► Four-Legged Mites

Peairs, Leonard Marion

Leonard Peairs was born at Leonard, Kansas, USA, on June 5, 1886. He obtained his B.S. and M.S. degrees from Kansas State University in 1905 and 1907, respectively. For several years he worked at the University of Illinois, University of Maryland, and Kansas State, but in 1912 he accepted employment at West Virginia University where he remained until retirement in 1952. In 1925 he received a doctorate from the University of Chicago. Peairs is best known as a co-author of the text "Insect pests of farm, garden, and orchard" (with E.D. Sanderson, 1921 and subsequent editions). He served as editor of the "Journal of Economic Entomology" from 1940 to 1953. Peairs died on January 29, 1956.

Reference

Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Pea Leafminer, *Liriomyza huidobrensis* (Blanchard) (Diptera: Agromyzidae)

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What is known today as the pea leafminer was originally described as five different fly species: *Agromyza huidobrensis* Blanchard (1926, Brazil), *Liriomyza huidobrensis* Blanchard (1938, Argentina), *L. cucumifoliae* Blanchard (1938, Argentina), *L. langei* Frick (1951, California), and *L. dianthi* Frick (1958, California). In 1973, Spencer synonymized the California and South American species under the name *Liriomyza huidobrensis*. Recent genetic evidence (in addition to observations of behavioral differences) strongly suggests that the species occurring in California and Hawaii is different from the South American species and that the name *L. langei* should be resurrected.

The pea leafminer is a small fly, less than 2.5 mm long, with a generally black body, and yellow face, frons and scutellum. Salient characteristics that distinguish *L. huidobrensis* from other members of the genus are as follows: the vertical bristles on the head are on a dark background contiguous with the black hind margin of the eye; the antennal segments are yellowish-brown and the distal third of the third segment is sometimes darkened; and the hind-corners of the mesonotum adjoining the scutellum are black. The posterior spiracles of the puparia have 6–9 pores.

Liriomyza huidobrensis was not considered a pest prior to the 1970s, when in South America, large amounts of insecticides were applied against the gelechid potato moth, *Scrobipalpula absoluta* (Meyrick). The leafminer became resistant to these insecticides and emerged as a secondary pest. In the late 1980s it spread from South America to Europe on cut flowers, quickly spread throughout Europe, and arrived in Israel in the early 1990s. The South American species also has spread to Kenya, South Africa and Indonesia.

The pea leafminer is truly polyphagous, feeding on a large number of flowers, vegetables and weeds. Some of the more important economic plants are Cucurbitaceae (gherkin, cucumber, melon), Leguminosae (numerous bean species), Solanaceae (pepper, tomato, potato, eggplant), Caryophyllaceae (*Dianthus* spp., *Gypsophilla* spp.), Chenopodiaceae (spinach, beet), Compositae (thistle, endive, aster, *Chrysanthemum* spp., *Gerbera* spp., lettuce), Cruciferae (Chinese cabbage, radish), Umbelliferae (carrot, celery, parsley), and Violaceae (*Viola* spp.).

Damage to plants occurs in two forms: aesthetic damage from feeding punctures and tunnels, and reduction of photosynthesis. Adult females puncture top and bottom surfaces of leaves with their ovipositor and feed on the plant juices. Adult males also feed at these same holes. The amount of stippling varies with plant species, varying from about 50 to 300 per day. Additionally, females lay eggs on the underside of leaves; larvae hatch and mine the leaves. Larval mines are typically along the midrib and lateral veins, although not exclusively so. Even in leaves with one larval mine, photosynthetic rates are significantly reduced because larval tunnels are in the spongy mesophyll where chloroplasts are located. The feeding punctures also significantly reduce photosynthetic rates and stomatal and mesophyll conductance.

Female flies live less than three weeks and males about a week. During her lifetime, a female lays an average of 8–14 eggs per day after a 1–2 day pre-ovipositional period. The egg stage lasts about 2–3 days depending on temperature and host plant. There are three instars in the leaf, and the mines become progressively larger with each molt. The duration of the larval stage depends on temperature and host plant, but averages about one week. The third instar chews a hole in the leaf surface and emerges completely from the leaf to pupate. There is a prepupal stage of 4–5 h duration between formation of the puparium and actual pupation. Pupae vary in color from a light brown to almost black, and live about one week.

Control measures for greenhouse and open field crops include biological, cultural/mechanical, chemical, and use of resistant plants. Biological control measures in greenhouses with releases of *Dacnusa sibirica* Telenga, *Opius pallipes* Wesmael and *Diglyphus isaea* Walker wasp parasitoids have been very successful on various crops. While natural parasitism in the field sometimes may be quite high, it is insufficient to control the leafminer. Release trials have shown that it is economically unfeasible to release sufficient parasitoids to achieve control in open field situations in celery. Some success has been achieved in applying entomopathogenic nematodes (*Steinernema feltiae* (Filipjev)) for control of the leafminer.

Cultural/mechanical control measures are relatively few in number. It is always important to maintain good agricultural practices – removing harvested plants from fields, maintaining control over weeds, etc. – to prevent the buildup of populations in these reservoirs. However, to date, trials with traps plants have been unsuccessful. Attempts have been made at mass trapping flies by circumscribing greenhouses with yellow sticky sheets or by dragging sheets of oil coated yellow plastic just above crops in open fields; these methods have reduced the numbers flies but have not significantly controlled the situation. Similarly, vacuum removal of flies has had limited success because they quickly reinvade the field. In South America, trials have been proceeding on developing cultivars of potatoes that are resistant to the leafminer by developing plants with a high density of glandular trichomes that interfere with feeding and oviposition.

Chemical control measures have had mixed results. The leafminer was discovered in Israel when conventional insecticides failed to control what were thought to be adult *L. trifolii*. Growers in Indonesia spray 2–3 times a week with a variety of 35 conventional insecticides in attempts to control the fly, with unsatisfactory results. On the other hand, efforts to control the larvae with translaminar insecticides (neem, cyromazine, abamectin, and spinosad) have been successful. Timing of insecticide application with these translaminar insecticides is critical and requires educating growers to treat the (unseen) larval population and not wait until large numbers of adults are observed, when insecticides essentially are useless.

References

Parrella MP, Jones VP, Youngman RR, Lebeck LM (1985) Effect of leaf mining and leaf stippling of *Liriomyza* spp. on photosynthetic rates of chrysanthemum. Ann Entomol Soc Am 78:90–93

Rauf A, Shepard BM, Johnson MW (2000) Leafminers in vegetables, ornamental plants and weeds in Indonesia: surveys of host crops, species composition and parasitoids. Int J Pest Manag 45:257–266

Scheffer SJ (2000) Molecular evidence of cryptic species within the ea leafminer *Liriomyza huidobrensis* (Diptera: Agromyzidae). J Econ Entomol 93:1146–1151

Spencer KA (1973) Agromyzidae (Diptera) of economic importance. Ser Entomol (The Hague) 9:1–444

Weintraub PG, Horowitz AR (1995) The newest leafminer pest in Israel, *Liriomyza huidobrensis*. Phytoparasitica 23:177–184

Pear Decline

This is a widespread disease of pear trees that is transmitted by pear psylla.

► Transmission of Plant Diseases by Insects
► Pear Psylla

Pear Psylla, *Cacopsylla pyricola* (Foerster) (Hemiptera: Psyllidae)

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At least seven species of pear-feeding psyllids in the genus *Cacopsylla* are recognized from Europe and North America, with unknown numbers of additional species occurring in Asia. Several of these species are pests of commercial pear (*Pyrus*), most notably *Cacopsylla pyricola* (Foerster) in North America and Europe, and *C. pyri* (L.) in Europe. The North American psyllid, *C. pyricola*, is not native to North America, but was introduced into the eastern United States in the early 1800s on infested pear seedlings imported from Europe. The pest rapidly dispersed from the eastern U.S., ultimately reaching the pear-growing regions of western North America in the early 1900s. The species apparently now occurs in all pear-growing regions of North America. With codling moth, *Cydia pomonella* (L.), pear psylla is the major insect pest attacking commercial pears in North America. It is estimated that 50–80% of the costs associated with controlling arthropod pests in pear orchards are directed at pear psylla and a few other soft-bodied arthropods.

The adult pear psylla (Fig. 19) is 2–2.5 mm in length, and in appearance resembles a miniature cicada. The insect is greenish to dark brown in color, depending upon time of year, as discussed below. Wings are held roof-like over the abdomen. Eggs are yellow and elongate, having a curled filament extending from one end. The eggs are inserted partially into the host plant, anchored by a small pedicel that appears to function at least partially in uptake of water from the host plant. Nymphs are yellow at hatch, becoming darker with successive molts. Late instar nymphs are flat and oval in shape, having large obvious wing pads. Nymphs of all ages have a pair of conspicuous red eyes at the front of the head (Fig. 19).

Pear Psylla, *Cacopsylla pyricola* (Foerster) (Hemiptera: Psyllidae), Figure 19 Adult pear psylla.

Pear psylla has a somewhat unusual life cycle. The species is seasonally dimorphic, producing a large, dark overwintering adult, or winterform, that is quite distinct from the smaller and light-colored summerform adult. The dimorphism is controlled by photoperiod; nymphs experiencing short-day condition develop into winterform adults, whereas those experiencing long-day conditions develop into summerform adults. The dimorphism is striking enough that the two morphotypes were once considered to be separate species. Pear psylla overwinters both in the pear orchard and outside of the orchard, often on other tree fruit species. Dispersal from the pear orchard in autumn by Pacific Northwest populations of psylla occurs in October and November, coinciding with leaf fall in pear. Reentry into the pear orchard by post-diapause winterforms begins in February. Pear psylla reallocates among orchards between fall and spring associated with this dispersal behavior.

Winterform adults overwinter in reproductive diapause, characterized by immature ovaries and a lack of mating. Diapause ends in mid-winter; in the Pacific Northwest, cold temperatures keep the insect quiescent until late winter. Egg-laying by post-diapause winterforms begins in late February or early March in Oregon and Washington growing regions. The first eggs are deposited directly in wood at the base of fruit and leaf buds. Oviposition then shifts to newly emerging foliage as it becomes available. Fecundity of the overwintered female is quite high, exceeding 1,000 eggs per female. There are five nymphal instars, requiring 3–4 weeks to complete development at moderate (20–25°C) temperatures. Offspring of the overwintered adults eventually eclose as summerform adults, in Washington growing regions first appearing in early May. Pear psylla has 2–4 summerform generations per year depending upon latitude. Fecundity of the summerform adult is lower than that of the winterform adult.

Pear psylla causes several types of damage in pear orchards: fruit russet, psylla shock, and pear decline. Of these, russet is of most concern to growers, and management protocols are generally aimed at preventing this injury. Fruit russet is caused by the feeding activities of nymphs. Immature pear psylla ingest large quantities of plant juices that are eliminated as honeydew during the digestive process. Nymph-produced honeydew is in the form of a syrupy liquid, and if the product is in contact with fruit for extended periods of time it causes dark blotches or streaks on the fruit surface. If the marking is highly noticeable, the fruit may be downgraded at harvest. The damage is exacerbated by a sooty mold fungus that colonizes honeydew.

Psylla shock is also caused by nymphs. At high densities, pear psylla causes tree stunting, premature leaf drop, reduced fruit size, and premature fruit drop, symptoms collectively termed psylla shock. Substantial losses in yield may accompany this damage, and the effects may actually carryover from one year to the next, even in the absence of high psylla densities the second year.

Lastly, adult pear psylla vector a mycoplasma-like organism that is responsible for pear decline disease. The pathogen causes sieve-tube necrosis at the graft union, preventing tree-synthesized nutrients from reaching the roots. Symptoms of the disease include a slow to rapid decline in tree vigor, accompanied by reduced yield and often eventual death of the tree. Resistant rootstock has largely eliminated this problem from North American pear production.

Control recommendations for pear psylla generally emphasize destruction of the overwintered generation and offspring of the overwintered generation, as it is very difficult to control the summer generations. Successful control in early spring is necessary to prevent unmanageable problems during the growing season. Also, it is necessary to manage the spring generation because contamination of fruit by honeydew early in the growing season almost ensures that the fruit will be damaged by russet. A typical program for overwintered adults is characterized by the use of horticultural mineral oil, sulfur, and insecticide, the latter generally being a synthetic pyrethroid or chlorinated hydrocarbon. The initial applications occur in late winter when pear is still dormant, with additional applications repeated as necessary as the tree breaks dormancy. The initial spray should be delayed until re-entry by psylla into the orchard is mostly complete, but before significant levels of egg-laying has occurred. The oil applications cause delays in egg-laying by the returning winterform adults, resulting in increased synchronization of egg hatch in early spring. This increased synchrony simplifies subsequent pesticide-based control efforts. Summer control of pear psylla has become increasingly difficult because of resistance to insecticides. Currently, summer chemicals used include Mitac (amitraz), Agri-Mek (avermectin), and a neonicotinyl, Provado. Other products found to be useful against pear psylla include insect growth regulators, applied in spring, and kaolin particle film, used from late-winter through bloom. Kaolin is a wettable powder that dries to a white film on the tree and is an extremely effective feeding and oviposition deterrent to pear psylla. In some pear production areas of Washington State, the kaolin product Surround has substantially replaced the more traditional spring chemical controls.

Growers have certain horticultural practices that they use to simplify management. These practices include primarily strategies that make the tree less suitable or less attractive to psylla. For example, it is recommended that growers use only enough nitrogen fertilizer to produce good fruit set and fruit size, as excessive nitrogen leads to outbreaks of pear psylla. Similarly, pear trees should not be over-pruned, as this may prompt extensive growth of new foliage which is highly attractive to adults. Suckers and water sprouts should be removed from limbs, as these are a source of highly nutritious foliage.

The primary means of monitoring pear psylla for management decisions are by use of a beat tray (for sampling adults) and by taking leaf samples (for immature stages). The beat tray method involves holding a white, cloth-covered tray (generally $45 \times 45\ cm^2$ in size) beneath a horizontal limb, and sharply jarring the limb with a piece of stiff rubber hose. Psylla that are dislodged onto the tray are then counted. Recommended sample sizes are 25 trays (trees) per 10–20 acre (about 4–8 ha) pear block. Samples should be taken at random locations throughout the block. For the immature stages, samples taken during the first generation should consist of fruit spurs, examined either with a hand lens or beneath a dissecting microscope. Recommended sample sizes are at least 10 spurs per block. Additional samples taken just after bloom may also be necessary. For these samples, one fully expanded leaf should be taken from each sampled spur, with 2 spurs taken per tree and 20 trees sampled per 20 acre pear block. Mid-season leaf samples for psylla eggs and nymphs should be taken from actively growing shoots, near the top of the tree if possible. Extension personnel recommend taking 50 leaves per block, comprising a mix of young and old leaves.

Treatment thresholds tend to be fairly inexact and assume that the type of damage to be prevented is fruit russet (having a lower threshold than that for psylla shock, the latter requiring high densities of nymphs). Thresholds for adult psylla are one or two per ten trays during late winter before the dormant spray, and one or two per tray during the spring and summer growing seasons. For the immature stages, treatment thresholds are 1–2 eggs or nymphs per fruit cluster in spring, and 0.25–0.5 nymphs per leaf during the summer sampling periods. It should be noted that susceptibility of fruit to russet damage depends upon a number of factors, including pear variety (naturally russetted varieties such as "Bosc" are less susceptible than clear-skinned varieties such as "Anjou"), fruit destination (russet is of little importance in fruit destined to be canned), and age of the fruit when marked. Thus, threshold decisions for psylla control depend upon factors other than just psylla density.

Lastly, natural enemies have the potential to play a large role in controlling pear psylla. Many scientists consider pear psylla to be an induced pest, in that insecticide use destroys natural enemies that would otherwise keep psylla in check. Pear psylla is attacked by a variety of specialist and generalist natural enemies. One of its most important enemies is a specialist parasitoid, *Trechnites insidiosus* (Crawford) (Hymenoptera: Encyrtidae), that may cause very high levels of parasitism in reduced-insecticide orchards. Predatory true bugs, including species of Anthocoridae (*Anthocoris* spp.) and Miridae (*Deraeocoris brevis* (Uhler), *Campylomma verbasci* (Meyer)) are very efficient predators of pear psylla and other soft-bodied pests in pear orchards. Ladybug beetles (Coleoptera: Coccinellidae), lacewing larvae (Neuroptera), and European earwig (*Forficula auricularia* L.) also prey on eggs and nymphs of pear psylla. The relative importance of the various taxa in controlling pear psylla remains unexplored, and merits study.

References

Beers EH, Brunner JF, Willet MJ, Warner GM (1993) Orchard pest management: a resource book for the Pacific Northwest. Good Fruit Grower, Yakima, WA, USA

Horton DR (1999) Monitoring of pear psylla for pest management decisions and research. Integr Pest Manage Rev 4:1–20

Unruh TR, Westigard PH, Hagen KS (1994) Pear psylla *Cacopsylla pyricola* (Forster) Homoptera: Psyllidae. In: Andres L, Goeden RD, Jackson G, Beardsley J (eds) Biological control in the western region. DANR Publications, University of California, Berkeley, CA, pp 95–100

VanBuskirk PD, Hilton RJ, Simone N, Alway T (1999) Orchard pest monitoring guide for pears: a resource book for the Pacific Northwest. Good Fruit Grower, Yakima, Washington

Westigard PH, Zwick, RW (1972) The pear psylla in Oregon. Oregon State University, Agricultural Experiment Station Technical Bulletin 122, Corvallis, Oregon

Pebrine

A disease of the silkworm caused by the microsporidian *Nosema bombycis*.

Pecaroecidae

A family of sucking lice (order Phthiraptera). They sometimes are called peccary lice.

► Chewing and Sucking Lice

Peccary Lice

Members of the family Pecaroecidae (order Phthiraptera).

► Chewing and Sucking Lice

Peck, William Dandridge

William Peck was born at Boston, Massachusetts, USA, on May 8, 1763. He is sometimes known as America's first native entomologist, as those preceding him were immigrants from Europe. Peck graduated from Harvard University in 1782 and though he aspired to be a physician, he entered business, an occupation he found to be unsatisfactory. He and his father (a naval architect who also was discontented) moved to a small farm at Kittery, Maine, were he spent the next 20 years isolated but studying nature. He became an authority on plants, birds, fishes, and insects. In 1794 he published the first American paper on systematics, a description of four fishes. He began writing on insects in 1795 and won a prize from the Massachusetts Society for Promoting Agriculture for his publication on cankerworm in 1796. In 1805 he became a professor of Natural History

Peck, William Dandridge, Figure 20 **William Peck.**

at Harvard University and he went to Europe to study botanic gardens in preparation for establishment of a botanic garden at Harvard. There he became acquainted with important European naturalists including Linnaeus. He described a few species of insects, but unlike most naturalists and entomologists of the period, was more interested in the economic aspects of entomology. Peck (Fig. 20) taught a course on entomology while at Harvard, undoubtedly the first course of its kind in the United States. He published such articles as "The description and history of the cankerworm" (1795), "Natural history of the slugworm" (1799), and "Some notice of the insect which destroys the locust tree" (1819). He died at Cambridge, Massachusetts, on October 8, 1822.

References

Essig EO (1931) A history of entomology. Macmillan, New York, NY, 1,029 pp

Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Pecten

Any series of bristles arranged like a comb. This term (or pecten teeth) is sometimes applied to rows of spines on the legs of pollen-gathering bees.

Pectinate

Having a series of slender projections from a slender shaft. Comb-like.

► Antennae of Hexapods

Pederin

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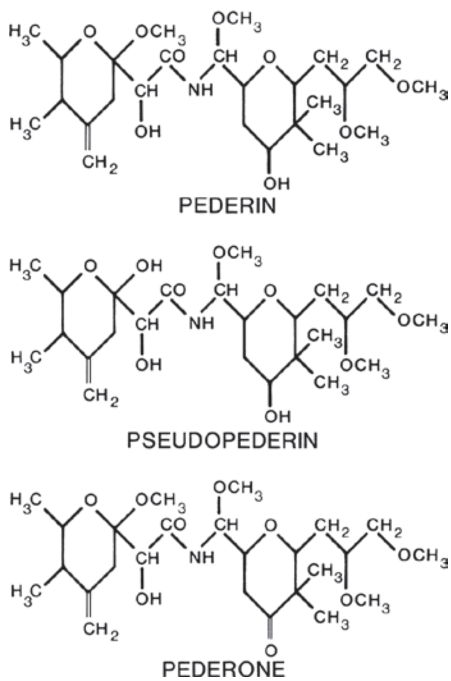
One of three toxins produced within some adult females of some species of *Paederus* and allied genera within the subtribe Paederina (Coleoptera: Staphylinidae: Paederinae). It is an amide with two tetrahydropyran rings, pederamide and pedaldehyde. The other two toxins are pseudopederin and pederone (Fig. 21).

Pederin is the most complex non-proteinaceous insect secretion known. It is among the most potent animal products known, more so than *Latrodectus* venom, which is 15 times more potent than cobra venom. It is a DNA-inhibitor and acts at the cellular level by blocking mitosis.

Pederin is produced within some females (those that contain certain endosymbiotic bacteria [+ females] and not within other females of the same species lacking endosymbiotic bacteria [-females, also called aposymbiotic females]) of some species of the staphylinid subtribe Paederina. It circulates in the hemolymph. It is accumulated in the eggs and thus is transferred to later stages (larvae, pupae, and resultant adults, male and female). Adult males and females are able to acquire pederin by cannibalism on their own immature stages. Those females in which bacteria



Pederin, Figure 21 The structure of pederin, pseudopederin, and pederone. From Frank JH, Kanamitsu K (1987) *Paederus* sensu lato (Coleoptera: Staphylinidae): natural history and medical importance. J Med Entomol 24:155–191, reproduced by permission of the Entomological Society of America.

produce the toxin [+ females] typically contain much higher levels of it than do males (or females that do not produce it [- females]). The ability to produce it seems to be a matrilineal trait, because production does not seem heritable from males. The ability to produce it can be destroyed by use of certain antibiotics. Related toxins are produced in certain marine sponges.

Pederin is expressed from adult beetles when they are crushed. This occurs when adult beetles of some species fly to light (incandescent and fluorescent), inadvertently land on humans adjacent to the light, and are crushed (by human body parts) against the skin. The beetles do not attack people – instead, the harm is self-inflicted by humans. Typically, a hand is used to crush a beetle, and smears the exudate (pederin) in a line across the skin. Within 24-h a linear red mark of dermatitis is seen on the skin, thus the name "dermatitis linearis," or an injured eye swells and closes, causing temporary blindness.

It has been synthesized and, in pure form, it is a crystalline amide soluble in alcohol and water. It is more toxic externally and internally to rabbits, rats, mice, and guinea pigs than to hedgehogs, chickens, frogs, and toads. That suggests its purpose is not as a defensive secretion against vertebrate predators. It is not known to be toxic to insects, is not attractive to insects, and has little effect against bacteria. However, it has a demonstrated function in defense of the beetles against spiders, to which it is toxic. Other possible natural functions await exploration.

Experimentally, it has suppressed cancerous tumors in mice, rats, and plants, stimulated regeneration of damaged tissues, healed chronic necrotic lesions in geriatric patients, and induced cell fusion in human skin fibroblasts.

► *Paederus*
► Paederina
► Dermatitis Linearis
► Rove Beetles (Coleoptera: Staphylinidae)

References

Cardani C, Ghiringhelli D, Quilico A, Selva A (1967) The structure of pederone, a novel substance from *Paederus* (Coleoptera: Staphylinidae). Tetrahedron Lett 41: 4023–4025

Frank JH, Kanamitsu K (1987) *Paederus* sensu lato (Coleoptera: Staphylinidae): natural history and medical importance. J Med Entomol 24:155–191

Kellner RL (2002) Molecular identification of an endosymbiotic bacterium associated with protein biosynthesis in *Paederus sabaeus* (Coleoptera: Staphylinidae). Insect Biochem Mol Biol 32:389–395

Kellner RLL, Dettner K (1996) Differential efficacy of toxin pederin in deterring potential arthropod predators of *Paederus* (Coleoptera: Staphylinidae) offspring. Oecologia 107:293–300

Pavan M (1982) Summary of the present data on pederin. Pubblicazioni dell'Istituto di Entomologia dell'Università di Pavia 1982 (23), 61 pp

Pavan M, Bo G (1952) Ricerche sulla differenziabilità, natura e attività del principio tossico di *Paederus fuscipes* Curt. Memorie della Società Entomologica Italiana 31:67–82

Quilico A, Cardani C, Ghiringhelli D, Pavan M (1961) Pederina e pseudopederina. La Chimica e l'Industria 43:1434–1436

Pedicel

The constricted region of the abdomen in Hymenoptera. In ants the pedicel bears one or more upright lobes; the first segment is the petiole, the second the post-petiole. This term also is applied to the second segment of the antenna (Fig. 22).

► Antennae of Hexapods

Pedicinidae

A family of sucking lice (order Phthiraptera).

► Chewing and Sucking Lice

Pediculosis

The presence of lice on the body (= phthiriasis).

► Chewing and Sucking Lice (Phthiraptera)

► Human Lice

Pediculidae

A family of sucking lice (order Phthiraptera). They sometimes are called body lice.

► Chewing and Sucking Lice

► Human Lice

Pedipalps

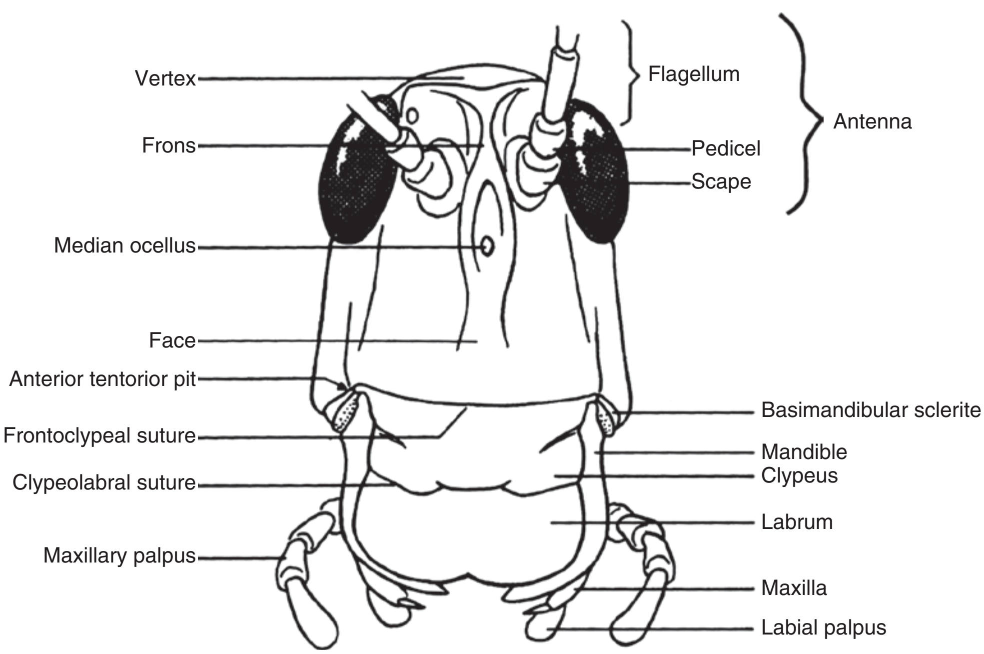
The second pair of appendages of an arachnid.

Pelagic Community

A group of organisms inhabiting the open sea, as opposed to the edge, or inlet of the sea or juncture of a river and an ocean (called estuarine).

Pedunculate

A structure positioned on a narrow stalk or stem-like structure (= petiolate).



Pedicel, Figure 22 Front view of the head of an adult grasshopper, showing some major elements.

Pelecinidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Pelecinid Wasps (Hymenoptera: Pelecinidae)

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Pelecinidae is a family of parasitic wasps with extant species found only in the New World. The family is contained within the superfamily Proctotrupoidea. This superfamily includes roughly 10–12 families, depending on the classification used, with the Diapriidae and Proctotrupidae containing the largest numbers of species. The others are considered to be relict families and contain few species. The Proctotrupoidea is probably paraphyletic. Most proctotrupoid families contain primarily small to minute wasps only a few millimeters in length, but the Pelecinidae is a notable exception, as described below.

Only one extant genus and three species of pelecinids are recognized: *Pelecinus thoracicus* Klug, *Pelecinus dichrous* Perty, and *Pelecinus polyturator* (Drury). *Pelecinus thoracicus* is found in western Mexico, and *P. dichrous* ranges across northern Argentina, Uruguay, Paraguay, and southeastern Brazil. *Pelecinus polyturator* has by far the largest latitudinal range, extending from southeastern Canada through the eastern and central United States and Mexico south to northern Argentina. Female *Pelecinus* are large (up to 7 cm in length), slender insects characterized by a very long, flexible metasoma (abdominal region), and swollen hind tibiae. Males are roughly half the length of females, with the posterior region of the metasoma swollen, giving the metasoma a club-shaped appearance. Both sexes have shortened basal tarsomeres of the hind legs. Body coloration of Nearctic specimens is almost always uniformly shiny black, with a white ring on each antenna. Specimens from tropical regions can be more variable, with red or reddish brown body coloration present. *Pelecinus* hold the wings elevated over the thorax at rest, rather than folding them flat over the back as most wasps do. The forewings are dark along the front edge, and this darkening may sometimes extend to some or even the entire wing. Wing venation is reduced in *Pelecinus*, which is an unusual feature for such large wasps. Reduced venation among wasps is generally confined to very small species.

Fossil Pelecinids

The fossil record has yielded several species of extinct pelecinids in the genera *Protopelecinus* and *Pelecinopteron*. Most of these have been found in Russia, Siberia, Mongolia, and the Baltic region. There is some disagreement regarding the status of several other controversial genera and species of fossil wasps uncovered primarily in China. These include members of the genera *Iscopinus*, *Sinopelecinus*, *Eopelecinus*, *Scorpiopelecinus*, and *Allopelecinus*, collectively referred to as "sinopelecines." Some consider these fossil wasps to be stem-group members of the Pelecinidae, and place them in the subfamily Iscopininae within the Pelecinidae. However, the prevailing view currently favors separation of these latter genera into their own family, the Iscopinidae, closely related to the Pelecinidae. Paleoentomological research on the pelecinids is very active, and hopefully future discoveries will clarify the evolutionary relationships among these groups. All of these fossil pelecinids and sinopelecines are small in body size (a centimeter or less in body length), in contrast to the much larger extant *Pelecinus*. Furthermore, a new fossil pelecinid species, representing a new genus, has recently been discovered in Cretaceous amber from New Jersey, USA. This "pygmy pelecinid," *Helopelecinus pygmaeus*, measures only about 6.5 mm in length, and represents the first pelecinid recorded in Cretaceous amber. All of the fossil pelecinids and sinopelecines have reduced wing venation, as is common among small parasitic wasps. This may explain why extant *Pelecinus* have reduced wing venation, even though they are quite large wasps. This condition may be an evolutionary holdover from smaller pelecinid ancestors. Effects of this evolutionarily constrained wing vein reduction on flight biomechanics of modern pelecinids is a potentially exciting area of research.

Ecology and Natural History

Despite their large size and striking appearance, relatively little is known of modern pelecinid ecology and natural history. Most published work has been on *P. polyturator* (Fig. 23). The vast majority of *P. polyturator* found in North America are females, as discussed below. Female *P. polyturator* are fairly common in the lower strata of hardwood forests, and are generally easily captured because of their slow flight. Once captured, the wasp may attempt to defend herself by stabbing with the metasoma, but has difficulty penetrating the skin. The relatively rare (at least in the northern part of their range) males are reportedly faster and more wary. *Pelecinus polyturator* are solitary endoparasitoids that primarily parasitize June beetle grubs of several species in the genus *Phyllophaga*, although *Podischnus agenor* has also been recorded as a host. Parasitism rates are reportedly very low, 1–3%, which suggests that *P. polyturator* is probably not an important factor in regulating host populations. *Pelecinus polyturator* host location behavior has been studied in a single hand-collected female kept in a terrarium with 6 cm of potting soil and 24 third-instar *Phyllophaga* grubs. The *P. polyturator* inserted her metasoma below the soil surface, probing both vertically and horizontally in the soil. She was able to reach grubs up to 5 cm below the soil surface. Several discrete insertions were observed, lasting from about one to almost seven minutes. Studies of larval *P. polyturator* dissected from *Phyllophaga* hosts have recorded lengths of 3.3–5.3 mm for first instars. The larvae were extracted from the posterior two-thirds of the host abdomen. They were dissected from hosts in the spring, which suggests that *P. polyturator* overwinter as late first instars within the host larva. The substantial size variation in adult *P. polyturator* may be associated with size variation in larvae of different host species.

Pelecinid Wasps (Hymenoptera: Pelecinidae), Figure 23 ***Pelecinus polyturator*** **(Drury) (Hymenoptera: Pelecinidae) is found throughout the Americas. (Photo by Lyle Buss.)**

Geographic Patterns

Pelecinus polyturator exhibits an interesting geographical pattern that was noted as early as 1928. In the southern, tropical part of its range, *P. polyturator* populations are bisexual and males are quite common. However, in the northern, temperate part of the range *P. polyturator* populations consist almost exclusively of females, which reproduce via parthenogenesis, development of an unfertilized egg into an adult. Males are very rare at northern latitudes, comprising at most 4% of the total population in Canada and the USA. This geographical pattern is known in a variety of animal groups, including some other insects, and has been given the name "geographic parthenogenesis." It has been suggested that this pattern occurs because parthenogenetic reproduction is evolutionarily favored over sexual reproduction in more marginal habitats (higher latitudes and altitudes, xeric vs. mesic habitats, disturbed vs. undisturbed habitats). These marginal habitats generally have lower populations, lower biodiversity, and fewer biotic interactions such as predation, parasitism, and competition. Thus, parthenogenetic populations should be more adaptive in these types of habitats because (i) finding a mate is unnecessary, which is advantageous at low population densities when finding a mate would be difficult, and (ii) fewer biotic interactions mean less selective pressure for the increased genetic diversity associated with sexual reproduction. It has been suggested that parthenogenetic populations of *P. polyturator* in Wisconsin may be associated with Pleistocene events, with all-female populations colonizing the recently unglaciated areas. It has also been suggested that the presence of *P. polyturator* males in a relatively small area in southeastern Wisconsin may represent the beginnings of displacement of a parthenogenetic population by a sexually reproducing population. Perhaps current climate change patterns could also have an impact on *Pelecinus* life history strategies.

The Pelecinidae represents a fascinating group of wasps and a rewarding subject of study. Continued research will undoubtedly provide further glimpses into the evolution, ecology, and biogeography of this enigmatic group.

References

Bennett AMR (2003) Host location behavior in *Pelecinus polyturator* (Hymenoptera: Pelecinidae). J Entomol Soc Ontario 134:131–134

Brues CT (1928) A note on the genus *Pelecinus*. Psyche 35:205–209

Engel MS, Grimaldi DA (2006) A diminutive pelecinid wasp in Cretaceous amber from New Jersey (Hymenoptera: Pelecinidae). Northeast Nat 13:291–297

Haichun Z, Rasnitsyn, AP, Junfeng Z (2002) Pelecinid wasps (Insecta: Hymenoptera: Proctotrupoidea) from the Yixian Formation of western Liaoning, China. Cretaceous Res 23:87–98

Johnson NF (1998) The fossil pelecinids *Pelecinopteron* Brues and *Iscopinus* Kozlov (Hymenoptera: Proctotrupoidea: Pelecinidae). Proc Entomol Soc Washington 100:1–6

Johnson NF, Musetti L (1999) Revision of the proctotrupoid genus *Pelecinus* Latreille (Hymenoptera: Pelecinidae). J Nat Hist 33:1513–1543

Johnson NF, Musetti L. The *Pelecinus* Project. Available at http://hymfiles.biosci.ohio-state.edu/projects/tpp/. Accessed 27 March 2008

Johnson NF, Musetti L, Johnson JB, Katovich K (1999) The larva of *Pelecinus polyturator* (Drury) (Hymenoptera: Pelecinidae). Proc Entomol Soc Washington 101:64–68

Junfeng Z, Rasnitsyn AP (2006) New extinct taxa of Pelecinidae sensu lato (Hymenoptera: Proctotrupoidea) in the Laiyang Formation, Shandong, China. Cretaceous Res 27:684–688

Young DK (1990) Distribution of *Pelecinus polyturator* in Wisconsin (Hymenoptera: Pelecinidae), with speculations regarding geographical parthenogenesis. Great Lakes Entomol 23:1–4

Pelecorhynchid Flies

Members of the family Pelecorhynchidae (order Diptera).

► Flies

Pelecorhynchidae

A family of flies (order Diptera). They commonly are known as pelecorhynchid flies.

► Flies

Peloridiidae

A family of bugs (order Hemiptera, suborder Coleorrhyncha). They also are known as moss bugs.

► Bugs

Peltoperlidae

A family of stoneflies (order Plecoptera). They sometimes are called roach stoneflies.

► Stoneflies

Pemphredonidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Penis (pl., penes)

The male intromittent organ. The aedeagus.

► Abdomen of Hexapods

Pentatomidae

A family of bugs (order Hemiptera). They sometimes are called stink bugs or shield bugs.

► Bugs

Penultimate

The next to the last. For example, the penultimate instar for a lepidopteran with six larval instars is the fifth instar.

Pepper Weevil, *Anthonomus eugenii* Cano (Coleoptera: Curculionidae)

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The pepper weevil, *Anthonomus eugenii* Cano (Coleoptera: Curculionidae), is a serious pest of peppers, *Capsicum* spp., causing millions of dollars damage annually in the southern U.S.A., Mexico, Central America, Hawaii and several Caribbean islands. Pepper weevil damages the pepper crop by directly feeding and ovipositing in the fruit, causing premature abscision of all stages of peppers from flower buds to maturing pods. This insect is generally more prevalent in warm climates and, based on the earliest records of this insect and the corresponding first records of a principal host plant group, the domesticated *Capsicum* spp. around 7000 B.C. in Mexico, it is probably native to Mexico or surrounding regions. The reason pepper weevil is such an important pest relates to the difficulty of controlling this insect once it has become established in the field. Larvae feed within pepper pods, and are protected from insecticide sprays. Also, since the level of weevils required to cause economic loss is so low, detection of this pest when it reaches an action threshold is time consuming and relatively difficult. The economic impact of pepper weevil as a pest of peppers in the U.S.A. is conservatively estimated at $5–$20 million annually and the impact of pepper weevil on Mexican pepper production is probably much greater. Current factors that keep potential losses due to pepper weevil from reaching 50–100% in more areas in the U.S. are the availability of effective insecticides and local eradications from harsh winters or the absence of host plants causing local extinctions.

The introduction of pepper weevil from Mexico into Texas is thought to have occurred through fresh market transport. In the USA, it occurs in Hawaii, California, Arizona, Texas, Louisiana, Florida, Georgia, North Carolina, and New Jersey. Outside the U.S. it occurs in Mexico, Guatemala, and El Salvador. Additional areas infested include Honduras, Puerto Rico, and Costa Rica. There is a report of pepper weevils in greenhouse production of pepper in Canada, apparently introduced on pepper transplants from southern California. This illustrates that pepper weevil can be introduced into any area that will sustain host plants for the pepper weevil and that re-infestations can even occur in areas where pepper weevil is periodically eradicated or does not normally exist because of climatic conditions.

The pepper weevil shares the same biological characteristics of many of the other 330 species of the genus *Anthonomus*. Adults are oligophagous, and females lay eggs in flower buds or fruit. Larvae complete development within immature buds or fruit, causing premature bud and fruit abscision (fruit drop). The pepper weevil has three larval instars and multiple generations per year. Reported generation times for the pepper weevil varies widely among different investigators from 10 to 40 days, with perhaps the largest differences occurring between summer and fall observations. Generation time, the number of generations per year (5–8), and longevity of adults (79–316 days) are determined primarily by host availability and temperature. The oviposition period ranges from 16 to 129 days and averages 30 days. Feeding and development of pepper weevil is limited to two host plant genera, *Capsicum* and *Solanum*, and limited in its northern distribution by temperature with the exception of introduction of infested plant material into northern greenhouses. The development time in pepper can be as short as 12 days, and in nightshade as short as 11 days.

Temperature data associated with development time were reported by several investigators. Emergence on artificial diet was observed in 17–18 days at 25.7–27.7°C and 70% relative humidity (RH). An average generation time of 17.5 days at 23.9–26.7°C and 60–85% RH. A mean generation time on bell pepper of 14.2 days at 25.7–27.7°C and 40–100% RH. Pepper weevil development has been related to growth stage and temperature by a regression of 1/days development (Y) to °C (X) for the period of adults to new emergence as

$$Y = -1.075 + 0.059X, R\hat{}^2 = 0.95$$

This data has been used to develop predictive models for pepper weevil population development in the field.

Several efforts have been made to define the relationship of crop damage to weevil infestation level. A pepper weevil population density exceeding 1 pepper weevil/100 terminal pepper buds can be economically damaging. Infestation levels of 5% damaged terminals, 1 pepper weevil/10 whole pepper plants, and 1 pepper weevil/400 terminal buds also were shown to result in significant economic loss in high-yielding bell peppers. The frequency of pepper weevil oviposition per fruit is a factor of time, pepper weevil population density, pepper fruit size and the plant variety. Varietal differences in peppers may affect host preference and these effects are thought to be negligible under heavy feeding and oviposition pressure. However, studies indicate that plant structure, number of fruiting buds per plant, etc., may affect the plant's ability to maintain greater numbers of unaffected mature pods.

Early attempts at scouting pepper weevil populations were simply presence determinations and, in many cases, the presence of fallen fruit was the first indication of a pepper weevil infestation. Examination of fallen buds for presence of pepper weevil immatures early in the season is a means of determining the presence of pepper weevil in the field. Counting fallen fruit or using a beat cloth are unacceptable sampling methods for timing pepper weevil control. However, inspecting terminal buds or bud clusters for pepper weevil adults was effective in predicting subsequent infestations. Yellow sticky trap captures correlate well with direct adult pepper weevil counts, using whole plant inspections, and the use of traps is an alternative to the more intensive and costly direct count method. It is also possible to monitor feeding or ovipositional damage to terminal bud clusters as a method for determining the presence of pepper weevil in commercial pepper fields.

The dispersion of pepper weevil has been investigated in several locations. The dispersion index developed for pepper weevil adults in Puerto Rico indicated that adult populations exhibited a moderately clumped dispersion in the field with a negative binomial k = 2.5. In Florida, weevils concentrate along field margins. Clumping patterns of pepper weevil have been confirmed in non-bell peppers. Early in the season, pepper weevil distribution is moderately to highly clumped and that there is generally a concentration of weevils along pepper field margins.

The majority of research literature on pepper weevil control is associated with chemical control. Natural enemies of the pepper weevil include various predators (e.g., *Solenopsis geminata*, *Strunella magna*, *Tetramorium guineese*) and parasites (e.g., *Pyometes venticosis*, *Catolaccus incertus*, *Pediculoides* *ventricosus*, *Bracon mellitor*, *Habrocytus piercei* and *Zatropis incertus*, *Catolaccus hunterii* and a new species of Braconidae, *Triaspis eugenii*). Classical biological control for pepper weevil was attempted with *Eupelmus cushmani* (Crawford) and *Catolaccus hunterii* Crawford in Hawaii, and with *Bracon vestiticida* (Vierick) in southern California with some establishment, but no documented success.

Movement to and from secondary host material and cull sites has been implicated as one of the primary causes for periodic re-infestation in commercial pepper fields. Also, because pepper weevil has been reported to reproduce on nightshade, *Solanum* spp., movement from nightshade to pepper is an important management consideration. Crop residue destruction, transplant sanitation, and nightshade management have been recommended as effective cultural controls of pepper weevil. Even so, caution should be taken with the timing of destruction of host material since the lack of oviposition sites may trigger the migration of weevils, as has been suggested with the boll weevil.

Considerable research needs to be conducted on pepper weevil. Pepper weevil pheromonal sex attraction and the use of yellow sticky traps are important in pepper weevil sampling and management. The males produce an airborne chemical that is attractant to the female, and males are not as attracted. More definitive information is needed on alternative management tactics, such as biological control, mating disruption with pheromones, natural mortality factors, and general ecology of pepper weevil, which ultimately will prove critical for managing this pest.

References

Burke HR, Woodruff RE (1980) The pepper weevil *Anthonomus eugenii* Cano (Coleoptera: Curculionidae) in Florida. Florida Department of Agriculture and Consumer Services, Division of Plant Industry, Circular 219, Gainesville, FL, 4 pp

Riley DG, King E (1994) Biology and management of the pepper weevil: a review. Trends Agric Sci 2:109–121

Riley DG (1992) The pepper weevil and its management. Texas A&M Agricultural Extension Leaflet-5069, 6 pp

Wilson RJ (1986) Observations on the behavior and host relations of the pepper weevil *Anthonomus eugenii* Cano (Coleoptera: Curculionidae) in Florida. M.S. Thesis, University of Florida, Gainesville, FL, 94 pp

Peradeniidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Perennial

A plant that lives at least 3 years and reproduces at least twice.

Pergidae

A family of sawflies (order Hymenoptera, suborder Symphyta).

► Wasps, Ants, Bees and Sawflies

Pericardial Cells

Loose clusters of cells that are found on or near the external surface of the heart. They are believed to have a phagocytic function, removing particulate matter from the hemolymph.

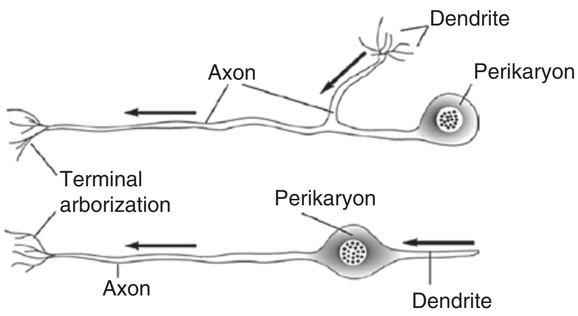
Pericardial Sinus

A space around the heart, bordered below by the dorsal diaphragm.

Perikaryon (pl., perikarya)

The cell body in a nerve cell. Also known as the soma (Fig. 24).

► Nervous System



Perikaryon (pl., perikarya), Figure 24 **Diagrams of insect nerve cells showing direction of nervous impulse (adapted from Chapman, The insects: structure and function)**

Perilampidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Perilestidae

A family of damselflies (order Odonata).

► Dragonflies and Damselflies

Periodical Cicadas, *Magicicada* spp. (Hemiptera: Cicadidae)

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Periodical cicadas (genus *Magicicada* Davis) are named for their extraordinarily regular adult appearances, caused by near-perfect synchronous development of the underground nymphs. Long life cycles of 13 or 17 years and large adult populations (up to about 3.75 million/ha, or 1.5 million/acre) make their periodicity events (Fig. 25) especially remarkable. Their importance has been long-standing, as can be seen in the following quote:

Periodical Cicadas, *Magicicada* Spp. (Hemiptera: Cicadidae), Figure 25 **Periodical cicadas emerge synchronously.**

“And the spring before, especially all the month of May, there was such a quantity of a great sort of flies like for bigness to wasps or bumblebees, which came out of holes in the ground and replenished all the woods, and ate the green things, and made such a constant yelling noise as made all the woods ring of them, and ready to deaf the hearers. They have not by the English been heard or seen before, or since.” – William Bradford, second governor of Plymouth Colony, 1633

Up to four reproductively isolated *Magicicada* species commonly emerge together, apparently due to a dependence on predator satiation. *Magicicada* inhabit deciduous forests of the United States east of the Great Plains. Although locally synchronized, periodical cicadas in different regions mature and emerge in different years.

Although cicadas in other parts of the world sometimes damage crops such as asparagus and sugarcane, the periodical cicadas are not significant agricultural pests. Also, they are not harmful to humans or other animals.

The common name "periodical cicada" formally applies to *Magicicada septendecim* alone, but the plural form is widely applied to all members of the genus. No other strictly periodical cicada species are known. In the United States, the term "locust" is often incorrectly applied to cicadas (e.g., "17-year locust").

Morphology and Classification

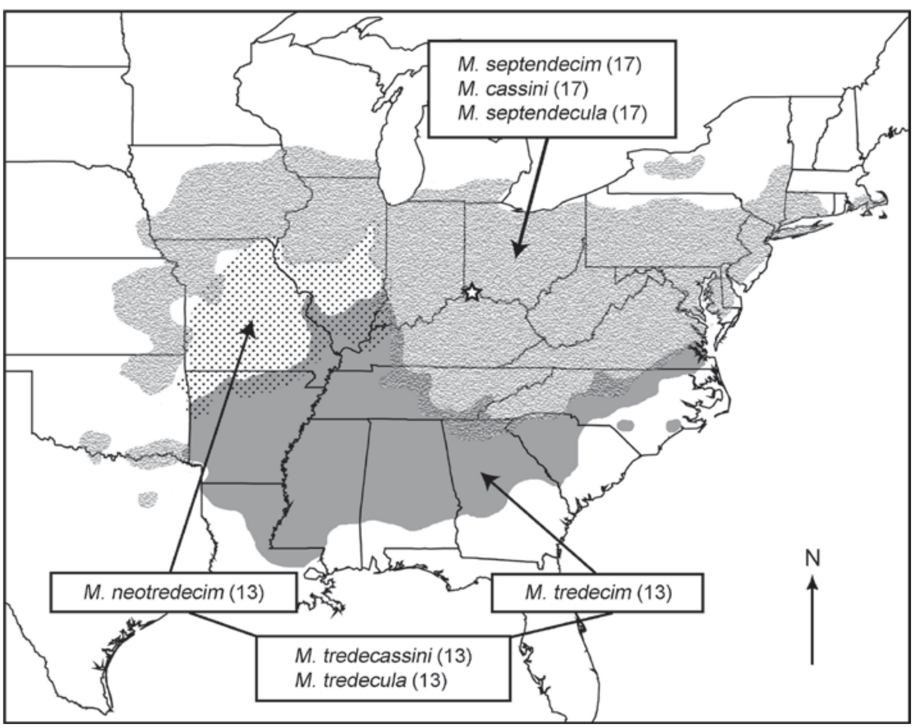
Periodical cicadas are medium-sized, about 2.5–4 cm from head to closed wingtip, with black-and-orange body coloration, striking red eyes, and orange-veined wings with distal infuscations. The seven *Magicicada* species (Fig. 26) are distinguishable by color pattern, song characters, and life cycle length. Three species groups are evident, the decim, cassini, and decula groups, and in each group one pair of species is distinguishable only by life cycle.

The relatives of *Magicicada* within the Cicadidae remain unknown. Morphological and genetic evidence supports their placement in the tribe Taphurini, subtribe Tryellina, but this largely Old World subtribe is represented in the Americas only by *Magicicada* and by a poorly known species recorded from Guatemala (*Chrysolasia guatemalena* (Distant, 1883)). Periodical cicadas are not related to the so-called "annual" cicadas of the genera *Okanagana* (which they resemble in appearance), *Tibicen*, and *Diceroprocta* that emerge throughout North America every summer.

Distribution

Species

The 17-year species are generally northern and range from Massachusetts to Iowa to Texas and



Periodical Cicadas, *Magicicada* Spp. (Hemiptera: Cicadidae), Figure 26 Distributions of the seven *Magicicada* species. The star marks a newly reported, disjunct 13-year population.

Periodical Cicadas, *Magicicada* Spp. (Hemiptera: Cicadidae), Table 7 Distinguishing characters of Magicicada species. Body length is the approximate distance from the tip of the head to the tip of the abdomen (holotype male, allotype female). Pronotal extension is the pronotal margin between the eye and wing articulation. Sternite color states are as follows: A, orange with dark centers; B, mostly orange; C, black, or with narrow orange bands less than one third of the sternite width; D, always with orange bands about one half of the sternite width. Phrase length is the duration of one song phrase. Song types are as follows: (i) pure tone, musical buzz ending in a drop in pitch (usually 2–3 song phrases between flights); (ii) rapid tick series then broad-spectrum buzz that rises and falls in pitch (usually 1–2 phrases between flights); (iii) repeated broad-spectrum chip-buzz phrases followed by chips without buzzes (usually one phrase between flights)

Species	Author (Year)	Life cycle	Body length (mm)	Pronotal extension color	Sternite color (each)	Dominant song pitch (kHz)	Phrase length (sec)	Song type
M. septendecim	Linnaeus (1758)	17	28,29	orange	A	1.25–1.5	1.5–4	1
M. neotredecim	Marshall and Cooley (2000)	13	28,29	orange	A	1.25–1.9	1.5–4	1
M. tredecim	Walsh and Riley (1868)	13	29,33	orange	B	1–1.25	1.5–4	1
M. cassini	Fisher (1851)	17	24,27	black	C	>3	2–4	2
M. tredecassini	Alexander and Moore (1962)	13	25,26	black	C	>3	2–4	2
M. septendecula	Alexander and Moore (1962)	17	24,26	black	D	>3	7–14	3
M. tredecula	Alexander and Moore (1962)	13	24,27	black	D	>3	7–14	3

northern Georgia (Fig. 26). All three are broadly sympatric (co-occurring) and synchronic (emerging together) (Fig. 27). The 13-year species, also synchronic, have more complex spatial relationships. *Magicicada tredecassini* and *M. tredecula* are sympatric from Maryland to Louisiana and north into Missouri and Illinois. The 13-year -decim species each inhabit part of the *M. tredecassini* + *M. tredecula* range and overlap one another along a zone extending from Arkansas to Indiana; in this zone, all four 13-year species emerge together. The northernmost *Magicicada* populations contain only *M. septendecim*, the most southwestern populations contain only *M. cassini*, and the -cassini species are locally rare or absent in the southeast. Periodical cicadas have been recorded from Ontario, Canada, but may now be extinct there.

Recent information suggests that an isolated 13-year population exists near Cincinnati, Ohio, surrounded by 17-year populations that have obscured its appearances historically. The next opportunity to confirm this population will arrive in 2014.

Broods

Same-cycle *Magicicada* populations in different regions have become temporally isolated by large-scale life cycle errors. The term *brood* is used for a set of such populations that emerge in the same year. There are twelve 17-year cicada broods and three

13-year broods (Table 8), most containing geographically contiguous populations. The broods have been named with Roman numerals reflecting their order of appearance, I-XVII for the 17 year broods and XVIII-XXX for the 13-year broods. Many brood numbers refer to years in the cycle for which no corresponding population is known. Some "empty" broods were recorded historically but have gone extinct, such as Brood XI in New England and Brood XXI in the Apalachicola River valley in Florida.

Most woods contain only one *Magicicada* brood, probably because resource levels are inadequate to support two populations large enough to satiate predators (see Predator satiation, below). As a result, the broods are mostly parapatric, meaning that their ranges overlap only along their edges. Some maps show extensive overlap between the 17-year broods XIV, X, VI, and II in the eastern states, and between the 13-year broods XIX and XXIII in the south. This may indicate that broods separated by four years or more experience reduced competition. However, some apparent overlap is explained by mistaken identification of straggling cicadas (see Life cycle plasticity, below) and imprecise county-level distribution records. Where two broods of different life cycles meet or overlap, local co-emergences occur every 13 × 17 or 221 years.

Predator Satiation

Many predators eat periodical cicadas when they emerge as adults, but the long periods between emergences prevent the predator populations from building up in response. Escape from ecological control by predators allows periodical cicada populations to reach extraordinary adult densities ranging from 8,000/ha–3.5 million/ha. Many cicadas and few predators means that the risk of being eaten is low for an individual cicada as long as it appears in synchrony with the brood. Furthermore, periodical cicadas have evolved in low-risk aggregations for so long that subsequent adaptations (e.g., precise but slow flight, low wariness, conspicuous mating behavior and bright coloration) have made them easy to catch and therefore dependent on large populations. Reproductive success increases with *Magicicada* population density, while adult mortality decreases. When periodical cicadas emerge in comparatively low numbers (roughly <5,000/ha), local predators easily drive the population extinct.

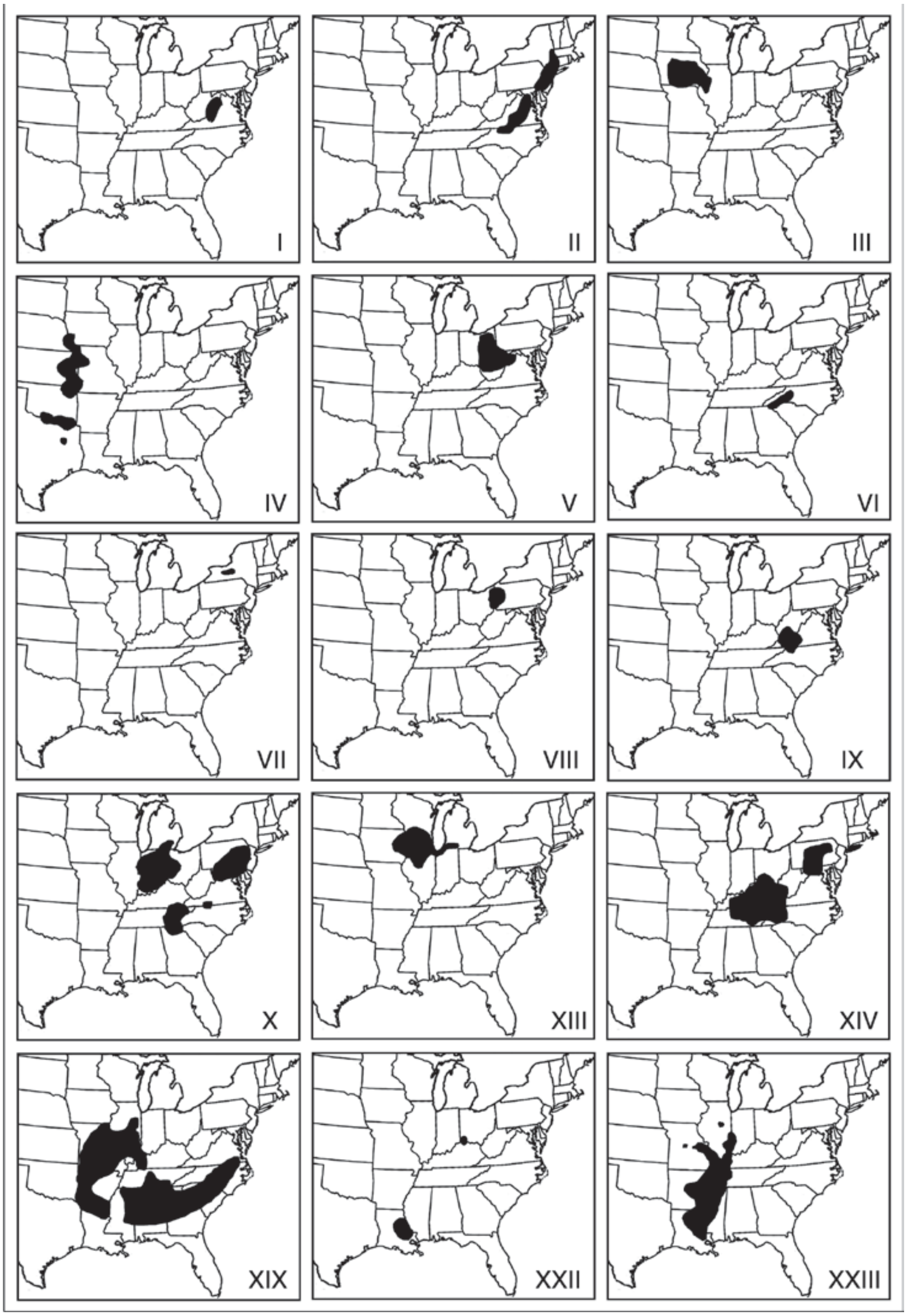
Juvenile Life History

Nymphal Development

Periodical cicadas begin life as eggs laid in pencil-sized twigs of trees or other woody vegetation. The eggs hatch six to ten weeks later, in midsummer, and the first-instar nymphs drop to the ground and seek feeding sites on small roots. Mortality approaches 98% during the first 2 years. All species pass through five instars and gradually move to larger roots. The durations of the first through fifth instars of 17-year cicadas have been estimated at 1, 2–3, 3, 5, and 5–6 years, respectively, with considerable variation across populations. Growth rates of 13-year nymphs differ from those of 17-year nymphs mainly in the first two instars. Nymphal growth rates also vary within populations; up to three instars can be observed at once although all eventually emerge together. Periodical cicadas, like all cicadas, suck fluids from plant xylem tissue, which is low in nutrients. Variation in growth rates within populations, together with considerable size variation among adults, suggest that competition for limited nutritive resources is important in dense *Magicicada* populations.

Life Cycle Timing

The mechanisms by which periodical cicadas "count" 13 or 17 years are unknown, but environmental cues are likely involved, such as temperature



Periodical Cicadas, *Magicicada* Spp. (Hemiptera: Cicadidae), Figure 27 Distributions of the fifteen extant periodical cicada broods.

or other cues detected via their host plants. In one study, 15-year-old nymphs transferred to roots of greenhouse trees emerged in the 17th "greenhouse season," rather than their 17th year, when the seasonal cycle of the trees was artificially accelerated. Observations of off-schedule emergences also implicate external cues in developmental timing (see Life cycle plasticity, below).

Periodical Cicadas, *Magicicada* Spp. (Hemiptera: Cicadidae), Table 8 Recent and predicted emergences of the fifteen extant periodical cicada broods

Year	17	13	Year	17	13	Year	17	13
1961	I		1984	VII		2007	XIII	
1962	II	XXII	1985	VIII	XIX	2008	XIV	
1963	III	XXIII	1986	IX		2009		
1964	IV		1987	X		2010		
1965	V		1988		XXII	2011		XIX
1966	VI		1989		XXIII	2012	I	
1967	VII		1990	XIII		2013	II	
1968	VIII		1991	XIV		2014	III	XXII
1969	IX		1992			2015	IV	XXIII
1970	X		1993			2016	V	
1971			1994			2017	VI	
1972		XIX	1995	I		2018	VII	
1973	XIII		1996	II		2019	VIII	
1974	XIV		1997	III		2020	IX	
1975		XXII	1998	IV	XIX	2021	X	
1976		XXIII	1999	V		2022		
1977			2000	VI		2023		
1978	I		2001	VII	XXII	2024	XIII	XIX
1979	II		2002	VIII	XXIII	2025	XIV	
1980	III		2003	IX		2026		
1981	IV		2004	X		2027		XXII
1982	V		2005			2028		XXIII
1983	VI		2006			2029	I	

Emergence and Teneral Period

In the spring, a few weeks prior to emergence, *Magicicada* nymphs construct emergence tunnels which they sometimes cap with mud "turrets" of unknown function. The nymphs wait below until the soil temperature reaches approximately 18°C at 20 cm depth. This threshold is reached in late April or early May in southern populations, and late May or early June in northern ones. Although temperature variation spreads the emergence over one to two weeks, a large fraction of the population may emerge on a single night, creating an extraordinary spectacle as thousands of ghostly-white teneral cicadas dangle from cast exoskeletons. The adult sex ratio is close to 50:50, but males emerge a few days earlier on average, a phenomenon called protandry. Emergence occurs after sunset, and ecdysis requires approximately one hour. Lack of perching space in dense emergences can cause a high rate of failed ecdysis.

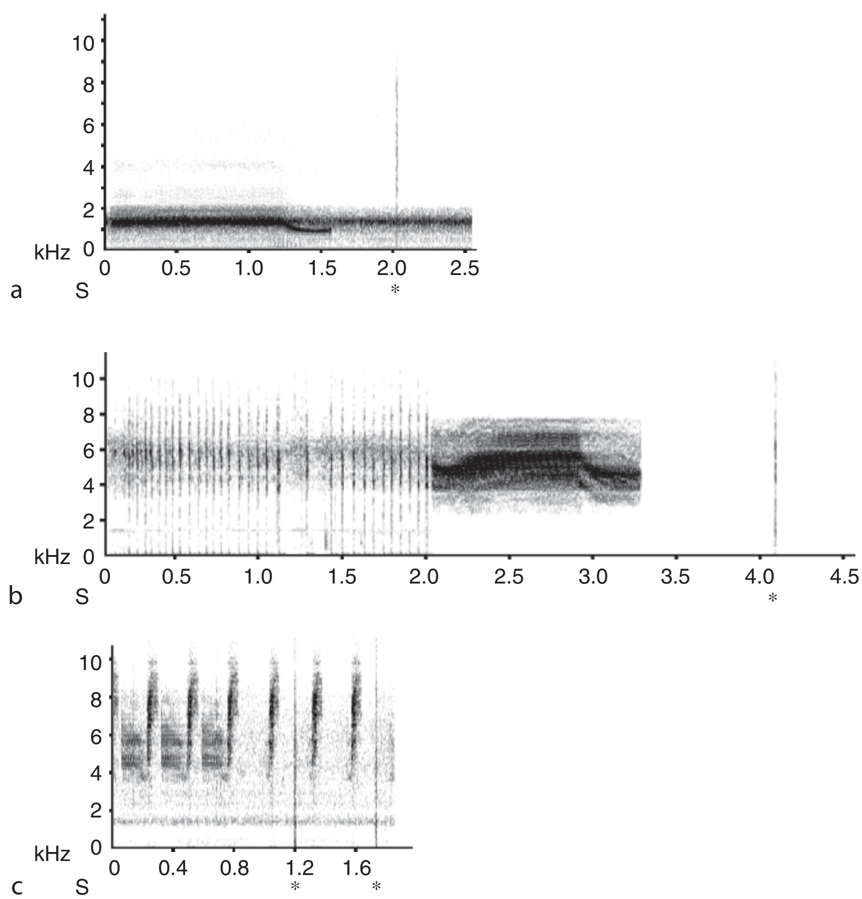
Complete hardening of the exoskeleton requires 5 days or more, depending on temperature, which explains the puzzling silence that immediately follows a large emergence. Once fully mature, males begin chorusing and females become sexually receptive. Individual adult cicadas survive approximately 2–4 weeks after emergence.

Adult Life History and Behavior

Chorusing and Mating

Males of all species fly to sunlit vegetation and alternate singing bouts of 1–3 song phrases with short flights. Both sexes are attracted to conspecific song, and periodical cicadas aggregate in chorusing centers that gradually move as the emergence progresses. These mating aggregations are viewed as non-resource-based leks, reflecting the absence of resources offered by males and the opportunity for female choice. Leks of different species frequently overlap, but the species are reproductively isolated by distinctive male songs and female phonoresponses (Fig. 28). Chorusing by the -decim species is most intense in the morning, -cassini activity peaks in the afternoon, and -decula peak at midday.

When ready to mate, females reply to conspecific males with wing-flicks after the male song phrase (in -decim and -cassini species) or after each of several cueing notes within the male song (-decula species). Males hearing or seeing wing-flick responses move toward the female and, in -decim and -cassini, switch to a courtship song of linked song phrases without gaps. Receptive females signal their continued willingness to mate



Periodical Cicadas, *Magicicada* Spp. (Hemiptera: Cicadidae), Figure 28 **Sonogram of one song phrase from the (A) -decim, (B) -cassini, and (C) -decula species group, including female wing-flick reply sound (marked with an asterisk) after species-specific delay. Only a central fragment of the long (7–12 sec) -decula phrase is shown. Note that the timescales are not equivalent, and that the -decim song phrase includes a strong acoustic background from other males.**

by remaining still. Before copulation, the male switches to a second courtship song of staccato buzzes and makes initial contact with a vibrating foreleg. Acoustic courtship ends when copulation begins (Fig. 29). Mating lasts several hours and results in the deposition of a hardened copulatory plug in the female's genital tract. Most females mate once, although disruption of copulation can induce remating. Males can mate many times.

The synchronized emergence and the rarity of female remating lead to intense male competition for mates. Males listen and watch for female replies to the songs of competitor males as well as their own. While courting a female, a -decim or -cassini male will obscure the downslurs of nearby conspecifics with "interference buzzes" that prevent the female from hearing (and responding to) the potential competitors. High density and protandry of *Magicicada* choruses encourages lengthy courtships between mature males and still partially teneral, marginally receptive females. This, in turn, leads males to attempt mistaken courtships of conspecific males, other *Magicicada* individuals, and even inanimate objects.

Periodical Cicadas, *Magicicada* Spp. (Hemiptera: Cicadidae), Figure 29 **Mating pair of *Magicicada septendecim*.**

Under optimal conditions of light, warmth, and cicada density, males of the -cassini siblings exhibit synchronized chorusing behavior. In this "giant game of musical chairs," thousands of males together alternate synchronous song phrases with short flights, creating dramatic waves of song across the forest.

Oviposition

Mated females deposit eggs into twigs in forked rows using a sharp ovipositor, about twenty eggs per 1.5 cm egg clutch or "eggnest," and about 400–600 eggs per female. Eggnests from the three -decim species are wider and V-shaped, with ragged wood fibers. Those of the -cassini species are smaller and less ragged, and -decula eggnests have a braided appearance. Eggnest scars can be located and sometimes identified to species for many years. When oviposition space is scarce, damage from ovipositing females can cause breakage, or "flagging," of peripheral twigs. Perhaps because of the risk of flagging, female *Magicicada* avoid overlapping eggnests, even while demonstrating aggregative behavior at a larger spatial scale.

Ecology

The 17-year species have overlapping but distinguishable habitat preferences that are sometimes obscured in man-made environments. *Magicicada cassini* prefers deciduous lowland and floodplain woods, while *M. septendecim* and *M. septendecula* prefer deciduous upland woods, especially forest-prairie ecotones in the case of *M. septendecula*. Adult host plant affinities reflect these habitat preferences (e.g., *M. cassini* on elm and ash, and *M. septendecula* on hickory), although all species can use a variety of woody tree, shrub, and vine species. Host plant affinities of the 13- and 17-year siblings are indistinguishable. Adult periodical cicadas do not use soft plants such as grasses or forbs except as perches during ecdysis.

All *Magicicada* species avoid ovipositing in resinous conifers because sap seals the eggnests before hatching. Nymphs survive on roots of a wide variety of plants, including deciduous and coniferous trees.

Control Measures

Periodical cicadas require deciduous woods and do not affect most crops. They are not toxic or otherwise harmful to humans or other animals. Orchards, nurseries and gardens are sometimes affected when oviposition damages young trees and shrubs, and feeding by nymphs can reduce fruit yields. Adult xylem feeding does not cause noticeable damage. Some soil pesticides can kill cicada nymphs, but adult cicada populations are generally too large to be controlled by pesticides. Brood emergence schedules can be used to optimize the planting of young trees, and mesh covering (<1/2 cm gap) tied at the trunk protects saplings from females seeking oviposition sites.

Fungal Infection by *Massospora*

Periodical cicadas are tracked by one synchronized parasitoid, the entomopathogenic fungus *Massospora cicadina* Peck. The *Massospora* life cycle involves two stages that infect different cicadas in the same population. The first stage begins when nymphs are infected by diploid resting spores from the soil before emergence. During the first week after emergence, the fungus converts the contents of the abdomen into haploid conidiospores that will infect more cicadas from the same emergence. As the abdomen swells, the abdominal sclerites fall off and expose the chalky mass of spores. The fungus leaves the head and thorax intact and the cicada remains active, but both males and females infected with this stage become unnaturally sexually receptive. Infected males even wing-flick to other males, causing frequent male-male copulatory attempts. Infected females cannot complete normal mating and wing-flick to males until they die. Sexual contact may be important for conidiospore transfer.

Cicadas infected by conidiospores develop the second phase of the *Massospora* life cycle, a similar syndrome that eventually exposes a brown, fluffy mass of resting spores. These spores are dispersed over the soil by cicada movements, ready to infect the next generation of nymphs. No increased sexual receptivity is caused by the second *Massospora* stage, which does not gain from spreading spores to adult cicadas.

Life Cycle Plasticity and Speciation

Because each *Magicicada* species is most closely related to one with the alternative life cycle, periodical cicada speciation likely involves permanent life cycle shifts. Clues to the mechanism of speciation can be observed in the pattern of straggling, or off-schedule emergences of cicadas. Both premature and delayed straggling events have been recorded, with 1- and 4-year premature emergences especially common. Not surprisingly, geographically adjacent broods are often separated by 1 or 4 years. In addition, broods separated by 1 year are usually oriented north-south, with the earlier emerging brood found to the north. Brood formation occurs, then, when a rare environmental stimulus (e.g., climate shock) causes sufficient numbers of cicadas to emerge off-schedule and satiate predators.

For life cycle shifts to cause speciation, a permanent life cycle change must evolve, which implies an environmental cue that is maintained for generations. Such an evolutionary event has been proposed for *Magicicada neotredecim*. This 13-year species evolved recently from its 17-year relative *M. septendecim*, perhaps when sudden and extended mid-Holocene warming triggered a widespread four-year acceleration in development. Subsequent overlap and interaction between *M. neotredecim* and its 13-year relative, *M. tredecim*, led to reproductive character displacement in male song pitch and female song preferences.

Interspecific hybridization between the -decim, -cassini, and -decula groups can be encouraged in cages and leads to reproductively viable first-instar offspring, although adult hybrids have not been observed. Thirteen- and 17-year siblings apparently interbreed during their temporally and spatially limited co-emergences, although the genetic consequences of this for population divergence remain unknown.

Evolution of Periodicity

Many theories exist to explain the origin of life cycles that are extraordinarily long, developmentally synchronized, and prime-numbered. A popular "arms race" theory proposes that the *Magicicada* ancestor evolved a long life cycle to escape exploitation by a synchronized predator or parasite species, eventually settling on a prime-numbered solution that the parasitoid could not overlap with a shorter, common-factor cycle. This theory does not explain why just seven cicada species are periodical out of thousands worldwide.

Mathematical theories have shown that long, periodical cycles can arise from an interaction between demand for predator satiation and within-species competition for resources. But reliance on predator satiation is difficult to explain without pre-existing long, periodical life cycles. This illustrates the "chicken-and-egg" challenge presented by *Magicicada*.

More recent scenarios have focused on the climates that faced the *Magicicada* ancestor in eastern North America during the Pleistocene Epoch, when repeated glaciations spread cold, unstable conditions southward. Life cycles may have lengthened initially as a developmental side-effect of cold temperatures on nymphal metabolic rates. Alternatively, initial cycle lengthening may have occurred by natural selection because cicadas with longer cycles were less likely to emerge during unpredictable sets of cold years, when temperatures were too low for adult reproduction. Longer juvenile periods would increase cumulative juvenile mortality, creating selection for developmental synchrony (periodicity). Selection for developmental synchrony may have lengthened life cycles further if nutrient limitation prevents nymphs from emerging earlier. Finally, selection against hybridization between ancestral periodical populations with different life cycles (which would impede periodicity) might have favored those with rarely interacting prime-numbered lengths.

References

Alexander RD, Moore TE (1962) The evolutionary relationships of 17-year and 13-year cicadas, and three new species (Homoptera, Cicadidae, *Magicicada*). Univ Michigan Mus Zool Misc Publ 121:1–59

Dybas HS, Lloyd M (1974) The habitats of 17-year periodical cicadas (Homoptera: Cicadidae: *Magicicada* spp.). Ecol Monograph 44:279–324

Karban R (1986) Prolonged development in cicadas. In: Taylor F, Karban R (eds) Evolution of insect life cycles. Springer-Verlag, NY, pp 222–235

Kritsky G (2004) Periodical cicadas: the plague and the puzzle. Indiana Academy of Science, Indianapolis, Indiana

Lloyd M, Dybas HS (1966) The periodical cicada problem. II. Evolution. Evolution 20:466–505

Marshall DC, Cooley JR (2000) Reproductive character displacement and speciation in periodical cicadas, with description of a new species, 13-year *Magicicada neotredecim*. Evolution 54:1313–1325

Marlatt CL (1907) The periodical cicada. USDA Bureau of Entomology Bulletin 71:1–181

White J, Lloyd M (1975) Growth rates of 17- and 13-year periodical cicadas. Am Midland Nat 94:127–143

Williams KS, Simon C (1995) The ecology, behavior, and evolution of periodical cicadas. Ann Rev Entomol 40:269–295

Peripsocidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice or Psocids

Periscelidid Flies

Members of the family Periscelididae (order Diptera).
► Flies

Periscelididae

A family of flies (order Diptera). They commonly are known as periscelidid flies.
► Flies

Perissommatidae

A family of flies (order Diptera).
► Flies

Peristome

In Diptera, the membranous area surrounding the base of the mouth.

Peritreme

Any sclerite bearing a body opening, particularly a spiracle. A sclerotic ring around a spiracle.

Peritrophic Membrane

A porous sheath lining the midgut and protecting the midgut cells from abrasion by the food, penetration by microbial pathogens, and the degradatory properties of digestive enzymes. It is secreted continuously along the length of the midgut (type I peritrophic membrane) or from the anterior portion of the midgut only (type II peritrophic membrane).
► Alimentary Canal and Digestion

Perlidae

A family of stoneflies (order Plecoptera). They sometimes are called common stoneflies.
► Stoneflies

Perlodidae

A family of stoneflies (order Plecoptera).
► Stoneflies

Peroral

By way of or through the mouth; *per os*.

per os

By way of the mouth; peroral.

Persistent Virus

A virus that passes through the body of the vector, and that usually persists for the remainder of the vector's life.

Pest Free Area

From a regulatory perspective, this is an area in which a pest does not occur, as demonstrated by scientific evidence, and in which this condition is being officially maintained.
► Pest Risk Analysis (Assessment)

Pesticide

A material that kills pests. This term is often used to describe insecticides, which are pesticides that kill insects.

Pesticide Hormoligosis

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Hormoligosis (from the Greek: *hormo* = excite and *oligo* = small quantities) is a term applied to the phenomenon in which sublethal quantities of stress agents such as chemicals, antibiotics, hormones, temperature, radiation, and minor wounds are stimulatory to an organism by providing increased efficiency to develop new or better systems to cope in a suboptimum environment.

The occurrence of pesticide hormoligosis in agriculture is well documented and may be a common phenomenon, but it is rarely monitored so we are uncertain of its importance in fostering outbreaks of certain pests or in accounting for failures in pest control programs. The purpose of this section is, therefore, to review the state-of-the-art of pesticide hormoligosis and to discuss controversial hypotheses on the reasons for the resurgence of certain arthropod pests and the drastic increase in their populations. Medical studies show that (i) stimulation of tissue repair after a sublethal dose of CCl_4 (i.e., chemically induced hepatotoxicity) appears to be the central mechanism in protection against death from a subsequent large dose; (ii) sublethal environmental stresses by exposure to ethanol (5%, v/v), acid (HCl, pH 4.5–5.0), H_2O_2 (500 ppm) or NaCl (7%, w/v), protects *Listeria monocytogenes* against lethal preservation factors by increasing its resistance to lethal doses of the corresponding factors; and (iii) pre-exposure of *Vibrio cholerae* cells to sublethal dose of 1.7 Gy X-rays makes these cells 3–38-fold more resistant to the subsequent challenge by X-rays.

In spite of a good initial kill at the time of treatment, different pesticides and even carrier materials and diluents used on orchard or field crops are reported to cause a tremendous increase of the pest against which they have been applied. Furthermore, spray applications are sometimes followed by serious outbreaks, not of the pest against which they were applied, but of other phytophagous insects and mites which, prior to the treatment, were in very small numbers too low to be of economic importance. Both types of increases, usually called pest resurgence, have been recorded in different climatic conditions (namely, temperate, subtropical and tropical regions) and for many species of the following families of mites or insects: Tetranychidae, Eriophyidae, Tarsonemidae, Coccidae, Aphidae, Aleyrodidae, Cicadellidae, Noctuidae, Tortricidae (=Olethreutidae), Yponomeutidae, Trypetidae, Agromyzidae, and the order Collembola. Spread of this phenomenon over a number of very different groups of phytophagous arthropods, and its occurrence after application of pesticides using different modes of action and under different climatic conditions, indicates that chemical control in these cases upsets the population dynamics of the pests in question.

For an explanation of this phenomenon, three hypotheses usually are suggested: (i) The reduction of natural enemies by the pesticides; (ii) pesticide-induced reproductive stimulation of phytophagous arthropods; and (iii) the removal of competitive species. Two additional factors also have been proposed: (i) altered host plant quality caused by agrochemicals, and (ii) the pesticide-induced irritation causing pest dispersal. Although sporadic literature confirms the validity of the second hypothesis (i.e., pesticide-induced reproductive stimulation of phytophagous arthropods), and its importance in pest resurgences, most information on the subject refers chiefly to the destructive effects of pesticides on the natural enemies of the phytophagous species and, to a lesser extent, to the removal of competitive fauna. Critical information needed to substantiate the importance of natural enemies in regulating pest populations includes: (a) a negative correlation between the number of natural enemies and pests, (b) proof that the natural enemies were the limiting factor to the density of the population, and (c) an exclusion of stimulating influences of the pesticide on the pest directly or via the plant. The less well-known phenomenon, pesticide-induced reproductive stimulation of phytophagous arthropods, comprises the backbone of pesticide hormoligosis and is the focus here.

There is considerable evidence of a favorable effect of some pesticides on the biotic potential of arthropods. For example, a drastic increase in the population of the fruit tree red spider mite, *Metatetranychus ulmi* (Koch) [*Panonychus ulmi* Koch], following the application of DDT has been demonstrated in The Netherlands since the late 1940s. Studies on the sublethal effect of DDT on oviposition of this mite revealed stimulation of egg production at a DDT concentration much lower than the recommended rates (Table 9).

In California, the results of a 3-year field and greenhouse study with DDT on natural populations and fecundity tests in small cages on the European red mite, *Paratetranychus pilosus* C. & F., failed to support the theory of destruction of the natural enemies as the primary cause of the mite outbreaks. Some of the results were, however, consistent with the idea of a physiological stimulus to reproduction under DDT influence.

Pesticide Hormoligosis, Table 9 Oviposition of *Panonychus ulmi* Koch on leaf discs treated with different concentrations of DDT dust during a 8–10-day observation

Treatment	Total eggs produced by ten females[a]	Egg production (index)
Control	37	100.0
1/8	78	210.8
1/4	24	64.9
1/2	31	83.8
1	23	62.2

[a]Average of five replicates(1 = field application rate amounting to 2.5 g/m^2 of dust containing 5% DDT; See Hueck DJ, Huenen DJ, Den Boer PJ, Jaeger-Draafsel E (1950) The increase of egg production of the fruit tree red spider mite (*Metatetranychus ulmi* Koch) under influence DDT. Physiol comp oecol 2:371–375, for more details)

Although some scientists at first thought that the mite resurgence was solely attributable to an elimination of the natural enemies of the mites, others posed the question of the possible involvement of a change in the physiology of the mites, or in their host, or both. It was found that DDT treatments produced an increase of mite populations above that occurring on check trees which was not explainable by a reduction of the natural enemies.

In order to find the reason for the mite's resurgence, apple trees with a moderate infestation of red spider mites were sprayed with parathion which killed all mites that were not in the egg stage, and all predators. Following the application of parathion, a number of trees were sprayed with DDT. Afterward, the numbers of all stages of red spider mites were counted every second day. An examination of the resulting data showed that egg production had been substantially higher on DDT-sprayed trees than on the check trees. Laboratory experiments also showed that the egg production of the mites feeding on leaf discs dusted with 5% DDT was significantly greater than those feeding on untreated discs. Both experiments, however, were not designed to explore whether the stimulating factor was caused by a direct influence of the pesticide, or via the plant. Coding moth adults, exposed to various sublethal doses of several insecticides, demonstrated stimulation of oviposition at concentrations where the females are under stress. Wherever the stress factors are not remarkable, oviposition is not stimulated.

More recent studies on population changes of spider mites (Acari: Tetranychidae) following insecticide applications in corn have shown that the exposure of twospotted spider mite (*Tetranychus urticae* Koch) to sublethal doses of permethrin leads to an increase in dispersal behavior (under laboratory conditions) and to an increase in population densities (under field conditions).

Stimulation of some vegetable plants by DDT with an action resembling that of some plant hormones suggests direct or indirect effect of sublethal doses of pesticides on phytophagous pests, but no field experiments or laboratory/greenhouse tests have been conducted either on intact or on excised plants (i.e., leaf discs). Nevertheless, numerous scientists have suggested the host-plant physiology hypothesis for the observed data on the reproductive stimulation of mites/insects whenever the hypothesis on the reduction in natural enemies is refuted. This hypothesis warrants additional research.

References

Abivardi C, Weber DC, Dorn S (1998) Effect of azinphos-methyl and pyrifenox on reproductive performance of *Cydia pomonella* L. (Lepidoptera: Tortricidae) at recommended rates and lower concentrations. Ann Appl Biol 132:19–33

Abivardi C, Weber DC, Dorn S (1999) Effects of carbaryl and cyhexatin on survival and reproductive behaviour of *Cydia pomonella* (Lepidoptera: Tortricidae). Ann Appl Biol 134:143–151

Chapman RK, Allen TC (1948) Stimulation and suppression of some vegetable plants by DDT. J Econ Entomol 41:616–623

Hueck DJ, Huenen DJ, Den Boer PJ, Jaeger-Draafsel E (1950) The increase of egg production of the fruit tree red spider mite (*Metatetranychus ulmi* Koch) under influence DDT. Physiol comp oecol 2:371–375

Luckey TJ (1968) Insecticide hormoligosis. J Econ Entomol 61:7–12

Pesticide Resistance Management

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"Integrated Pest Management" (IPM) and "Management of Pesticide Resistance in pest arthropods" (MPR) are usually perceived to be distinct topics, but have equivalent goals and methods. Effective management of resistance to pesticides and effective IPM programs require that we employ a holistic and multitactic management strategy. A key component of a holistic and multitactic strategy will include enhancing the compatibility of pesticides and biological control agents.

Resistance to pesticides is an extremely important problem. At least 440 arthropod species have become resistant to insecticides and acaricides, with many species having become resistant to all the major classes of such products. Resistance to pesticides in weeds, plant pathogens, and nematodes also is increasing, although somewhat more slowly.

Developing and registering new pesticides is an elaborate, and increasingly expensive, business in most parts of the world. Thus, pesticide producers should be increasingly interested in extending the economic life of their products in order to maximize a return on their investment. Likewise, pest management specialists want to preserve registered pesticides. This is especially true for products that are effective against arthropod pests in minor crops such as vegetables, which may be ignored by pesticide companies because they are a relatively small market compared to field crops. Registration of new pesticides is likely to be more difficult and expensive in the future, which could leave some pest management specialists with extremely limited options for managing certain recalcitrant pests.

A few environmentalists have argued that we do not need pesticides, that they will soon be outlawed, or that they will become unimportant because transgenic crops resistant to pests and diseases will dominate the market, and that pesticide resistance will no longer be an important issue. However, it is unrealistic to eliminate all pesticides from agriculture; there are significant arthropod pests for which we have no other effective control tactic. Pesticides are effective tools for fighting outbreaks and emergency pest problems. Pesticides are often required to control plant pathogens, weeds, or nematodes because they cannot be controlled by alternative methods at this time.

Research on Resistance in Arthropods

Scientists have approached the problem of pesticide resistance in a variety of ways. Fundamental research over the past 40 years has produced insights into resistance mechanisms and the mode of inheritance of resistance in arthropods. Simulation models have been developed to evaluate different options for managing resistance, but these models may not be applicable to a specific situation.

The debate over whether to recommend alternation of different pesticides or to recommend mixtures of different pesticides as appropriate methods for slowing the development of resistance remains controversial. Each management approach is dependent upon specific genetic and operational assumptions associated with the resistance mechanisms and mode of inheritance of the resistance in the specific pest population, as well as application methods and timing, and details of the biology of the pest. If one or more of these assumptions are not valid, then the management recommendations may not result in the intended preservation of the pesticide. Furthermore, few field data are available to support adopting either alternation or mixtures, or other resistance management concepts.

The hypothesis that reduced fitness, which is often associated with pesticide resistance alleles, could be used in resistance management programs continues to be controversial. The concept of reduced fitness may have limited application because not all resistance alleles confer lowered fitness and selection for modifying genes that restore fitness to individuals carrying resistance alleles can occur in the field.

Various monitoring techniques have been developed to identify resistant insects or mites and detect their establishment and spread. These monitoring methods are particularly useful for documenting that resistance has developed, but monitoring methods that would allow us to detect rare resistant individuals in populations in sufficient time that operational pest management programs could be altered remains difficult and expensive to execute.

Resistance management research programs and IPM research programs have had fairly distinct identities to date. The current scenario usually goes something like this: Once a pesticide has been registered and used, and resistant individuals have been detected in populations, people begin to discuss developing and implementing a resistance management program. This approach is short sighted because an effective program is exceedingly difficult to execute in sufficient time to have the desired results.

Developing a resistance management program may take several years; studies typically are conducted to develop an appropriate monitoring method, estimate the frequency of resistant individuals in populations, detect cross resistances, and evaluate mode of inheritance and stability of the resistance. Meanwhile, unless pesticide applications are discontinued, selection for resistance continues. Because the initial detection of resistance usually requires that resistant individuals comprise 5% of the population, by the time resistant individuals are detected additional pesticide applications are likely to increase significantly their frequency in the population. This scenario is particularly familiar with pests such as aphids, spider mites, whiteflies, and leafminers with a high reproductive rate and multiple generations a year.

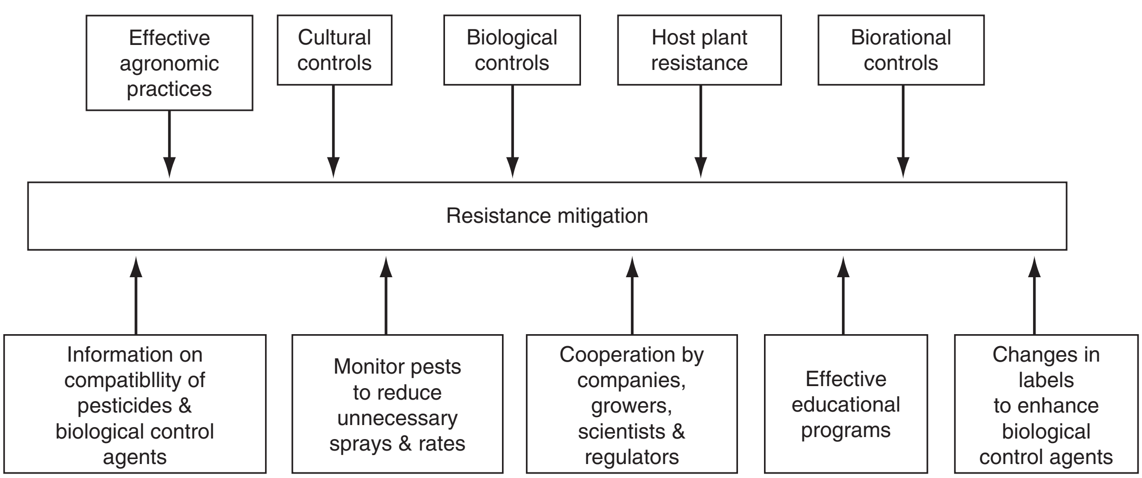
The experiences of scientists studying pesticide resistance in ubiquitous pests in other geographic regions can alert pest managers to a potential problem, but this seems to be an inefficient method for managing resistance in arthropods and it is possible for two different populations of the same species to respond to selection for resistance in different ways because different resistance alleles may be present in the different populations. Mechanisms may vary, the mode of inheritance may vary, and the degree of reduction in fitness associated with the resistance may vary because resistance alleles at each site are different. Because it is difficult to sample rare individuals in natural populations, monitoring programs, if employed other than as a method to document a problem once it has developed, may not be cost effective. Waiting until the pest becomes resistant before instituting a resistance management program is ineffective.

Resistance Management and IPM

A better paradigm for managing resistance in arthropods involves altering pesticide use patterns. Nearly everyone will agree that reducing pesticide use is an effective resistance management tactic. What is more controversial is whether resistance management programs should include altering the way pesticides are developed and registered. Also, many pest managers have been slow to recognize that resistance management must be a broad-based, multitactic endeavor (Fig. 30).

It seems reasonable to assume that nearly all major insect and mite pests will develop resistances to all classes of pesticides given sufficient selection pressure over sufficient time. There may be some exceptions, but this generalization appears reasonable given the documented record of resistance development in arthropod pests during the past 40 years. Resistance to stress is a fundamental and natural response by living organisms. On an evolutionary time scale we should expect insects to have developed multiple and diverse mechanisms to survive extreme temperatures, allelochemicals, and other environmental stresses. We should expect most insects and mites to develop resistance to most pesticides if subjected to appropriate and sustained selection. While new pesticide classes have been proclaimed to be a potential "silver bullet" and not amenable to resistance development, these hopes have been misplaced repeatedly. It seems appropriate to assume that the development of resistance is nearly inevitable and the issue is not whether resistance will develop, but when. With this assumption, resistance management programs have the goal of delaying, rather than preventing, resistance.

Growers and pest management experts cannot afford to rely on pesticides as their primary management tool. There are increasing social, economic, and ecological pressures to reduce pesticide use and to increase the use of nonchemical control tactics such as host plant resistance, cultural controls, biological controls and biorational control methods such as mass trapping, sterile insect release programs and mating disruption. There is an increasing emphasis to use pesticides that are nontoxic to biological control agents, and that have minimal impacts on the environment and on human health. The compatibility of pesticides with natural enemies and other nonchemical management tactics is critical for improving pest management programs and environmental quality,



Pesticide Resistance Management, Figure 30 Effective resistance management programs incorporate multiple tactics as part of a fully integrated pest management program. Pesticides should be used only when needed, at the lowest rates possible, and in a manner that reduces negative effects on arthropod natural enemies. Ideally, pesticide labels would include information about their effects on natural enemies.

as well as for managing resistance to pesticides in pest arthropods. Enhancing the compatibility of pesticides and biological control agents is complex and sometimes difficult, but can play handsome dividends in improved pest control and pesticide resistance management.

Changing the way pesticides are registered could become part of an effective resistance management strategy and would have the benefit of achieving improved integrated pest management. For example, some pesticides are relatively nontoxic to important natural enemies in cropping systems when applied at low rates, but the recommended application rates are too high. Use at the high rates thus disrupts effective natural enemies, leading to additional pesticide applications, which exert unnecessary selection for resistance in the pest. Under these circumstances, it may be appropriate for the label to contain two different directions for use; one rate could be recommended for the strategy of relying on pesticides to provide control. A lower rate could be recommended for use in an IPM program when it is known that effective natural enemies are present but need help to suppress the pest population(s). This approach to labeling could reduce the number of pesticide applications and reduce rates, which would reduce selection for resistance in both target and nontarget pests in the cropping system.

Another innovation in pesticide registration would require that the toxicity of the pesticide to a selected list of biological control agents be determined for each cropping system. This information should be provided, either on the label or in readily available computerized data bases, perhaps via the internet. Without such information, pesticides may be used that disrupt effective natural enemies. This often results in unnecessary use of pesticides, leading to more rapid evolution of pesticide resistance in pests. Enhancing biological control not only can lead to improved pest management, but is an essential tool in managing pesticide resistance.

How could information about the toxicity of pesticides to biological control agents best be made available to the end user? How should bioassays be conducted to evaluate pesticide selectivity? There are no simple answers. Data on pesticide toxicity to natural enemies often is buried in publications or reports that pest managers and farmers cannot find easily. Unfortunately, even if the data can be found, it is not easy to interpret bioassay data obtained by different scientists using different methods. Different bioassay methods can produce different conclusions about the toxicity of pesticides to natural enemies, and it is often difficult to predict the effects of pesticides under field conditions based on laboratory assays. Thus, the recommendation that labels or data bases be developed with information on the impact of pesticides on natural enemies requires considerable discussion and additional research. Should pesticide companies conduct the research using standard bioassay methods? Should a consortium of pest management scientists conduct the assays? Who should pay for the research? What species of natural enemies should be tested? This concept is not new; in Europe standardized bioassays already are conducted on selected natural enemy species by a scientific working group concerned about managing pests in glasshouses. Whether this model can be used elsewhere should be explored. Increased international consultation and cooperation between scientists, regulatory agencies, and pesticide companies could resolve many of the questions raised above.

Evolution of pesticide resistance in pests has been shown by computer simulations of predator and prey interactions to be slowed by reduced pesticide use. There is general agreement that reduced pesticide use is one of the essential elements of any resistance management program. Thus, the compatibility of pesticides and biological control agents is a crucial issue in pesticide resistance management.

Attempts to manage pesticide resistance (Table 10) in pest arthropods generally has involved making relatively minor tactical shifts in use patterns. A major shift in how we think about pesticide development and use could provide more effective resistance management tactics. The

Pesticide Resistance Management, Table 10 Important assumptions of resistance management models; violation of the assumptions could make management decisions based on these models ineffective (modified from Hoy 1998)

Model type	Assumptions
Mixtures	Resistance to each product is monogenic
	No cross resistance occurs between products in the mixture
	Resistant individuals are rare in the population
	Products have equal persistence
	Some of the population remain untreated (refuge)
	Resistance is functionally recessive (only homozygotes survive exposure)
Mosaics	Susceptible individuals are maintained and able to move into surrounding patches
	Negative cross resistance or fitness costs associated with the resistance may be required
Rotations	The frequency of individuals resistant to one product will decline during application of the alternative product, which is true if there is negative cross resistance (rare), a substantial fitness cost associated with resistance, or immigration of susceptible individuals occurs
High-dose strategy	Assumes complete coverage, effective kill of all individuals, ignores negative effects on secondary pests and their natural enemies or the environment

strategy should be to manage use of the pesticide, even before it is fully developed and registered. If this strategy is adopted, decisions on application rates and the numbers of applications per growing season would be made with the understanding that they affect the speed with which resistance will develop. In some cases, new products may not be registered for specific crops because they are toxic to biological control agents in that crop and thus could disrupt effective IPM programs in place.

Pesticide-Resistant Natural Enemies

Pesticide-resistant natural enemies are a special category of pesticide selectivity. Relatively few natural enemies have developed resistance to pesticides through natural selection, but several have been important in effective IPM programs. Artificial selection of phytoseiid predators for pesticide resistance can be a practical and cost effective tactic for the biological control of spider mites. Field tests have been conducted with several laboratory-selected phytoseiid species and some are being used in IPM programs.

Selection of pesticide-resistant strains of parasitoids and predatory insects have been conducted and some strains have been evaluated for incorporation into IPM programs. The use of mutagenesis and recombinant DNA techniques could improve the efficiency of such genetic improvement projects. However, development of pesticide-resistant natural enemies is time consuming and expensive and should not be considered before exploring other, less expensive, options for IPM and pesticide resistance management.

Pesticides are powerful and effective pest management tools. Some can be highly selective, rapid in their impact, adaptable to many situations, and relatively economical. Thus, preserving pesticides is essential. Effective paradigms for resistance management are not yet deployed because resistance management and IPM have been considered separate issues. Effective programs will acknowledge the role of biological control, host plant resistance, cultural controls, and biorational controls such as mating disruption, insect growth regulators, and mass trapping. A key issue should always be whether pesticides can be used in a precise and selective manner without disrupting natural enemies.

References

Croft BA (1990) Arthropod biological control agents and pesticides. Wiley-Interscience Publishers, New York, NY

Georghiou GP, Saito T (eds) (1983) Pest resistance to pesticides. Plenum Press, New York, NY

Hoy MA (1998) Myths, models and mitigation of resistance to pesticides. Philosophical Trans R Soc Lond B 252:1787–1795

Hull LA, Beers EH (1985) Ecological selectivity: modifying chemical control practices to preserve natural enemies. In: Hoy MA, Herzog DC (eds) Biological control in agricultural IPM systems. Academic Publishers, Orlando, FL, pp 103–122

National Academy of Sciences (1986) Pesticide resistance: strategies and tactics for management. National Academy Press, Washington, DC

Roush RT, Tabashnik BE (eds) (1990) Pesticide resistance in arthropods. Chapman and Hall, New York, NY

Tabashnik BE, Croft BA (1985) Evolution of pesticide resistance in apple pests and their natural enemies. Entomophaga 30:37–49

Pest Resurgence

Increase in abundance of pests, rapidly and sometimes to higher than previous levels, following actions made to suppress them.

Pest Risk Analysis (Assessment)

The process of evaluating biological or other scientific or economic evidence to determine whether a pest should be regulated, and the strength of any regulatory measures to be directed against it.

Biological pollution, the inadvertent introduction or invasion of nonindigenous species, is one of the most serious ecological problems facing contemporary societies. The greatly expanded "free trade" policies of the modern world have greatly exacerbated the problems with alien invasive organisms. Environmental autonomy, or the ability of a nation to protect its own flora and fauna, has usually been relegated to secondary importance; economic benefits seem to be more important than ecological benefits in most areas of the world. There are ample legal grounds for countries to act to protect human, animal or plant life or health, provided that "protective" acts are not economic acts disguised as environmental actions. Thus, there must be ample scientific justification for such protective acts. Pest risk analysis is a means of obtaining objective assessment of the hazards associated with pest introduction.

Pest risk analysis should identify hazards, quantify risks, and identify management options and strategies. The assessment should provide a reasonable estimation of overall risk. The ability of an introduced organism to become established involves a mixture of inherent (biological) and environmental characteristics. There is a great deal of uncertainty associated with such estimates.

Biosecurity hazards can be classified into three groups: vectors, pathways, and species. Vectors are the means of introduction (e.g., fruit or flower contamination). Pathways are the specific routes of introduction; shipping (air or sea transport) usually is implicated. The species of concern may be easily identified in some cases, but often multiple threats exist. For biosecurity hazards to be adequately assessed, the entire suite of vector, pathway, and species issues must be known.

Most hazard identification is calculated deductively. Deductive techniques rely on examination of what has occurred in the past. Though valuable, past experience is not entirely inclusive, and new hazards may exist. Alternatively, inductive techniques are sometimes employed, including logic tree analysis, hazard and operability analysis, and failure modes and effects analysis. These latter techniques help identify possible, though not necessarily probable, events that can be overlooked during deductive assessment because they may have not occurred previously.

Quantifying risks determines the likelihood and consequences of biological pollution. Few quantitative data are available to assist in this process, so it tends to be more qualitative than quantitative. However, quantitative assessments are subject to scientific scrutiny, and so may be "testable," and amenable to revision and improvement. A typical risk assessment model consists of a calculation of the probability of establishment [P] – the product of association with a pathway [Xa], entry potential [Xe], colonization potential [Xc], and spread potential [Xs]): P = [Xa] [Xe] [Xc] [Xs]. The consequences of establishment [C] are calculated by summation of the economic impact potential [X], environmental impact potential [Y], and "perceived impact" (social and political influences) [Z]: C = X + Y + Z.

Ultimately, the goal of pest risk assessment is to manage or eliminate introductions or reduce the rates of invasion. Thus, risk analysis seeks to identify weak links in the invasion sequence, identify where additional information is needed, identify the optimal management processes, and determine the probability and costs of failure.

► Invasive Species

References

Andow DA (2003) Pathways-based risk assessment of exotic species invasions. In: Ruiz G.M, Carlton JT (eds) Invasive species. Vectors and management strategies. Island Press, Washington, DC, pp 439–455

Hayes KR (2003) Biosecurity and the role of risk assessment. In: Ruiz GM, Carlton JT (eds) Invasive species. Vectors and management strategies. Island Press, Washington, DC, pp 382–414

National Research Council. (2002) Predicting invasions of nonindigenous plants and plant pests. National Academy Press, Washington, DC, 194 pp

Orr R (2003) Generic nonindigenous aquatic organisms risk analysis review process. In Ruiz GM, Carlton JT (eds) Invasive species. Vectors and management strategies. Island Press, Washington, DC, pp 415–438

Ruiz GM, Carlton JT (2003) Invasion vectors: a conceptual framework for management. In: Ruiz GM, Carlton JT (eds.) Invasive species. Vectors and management strategies. Island Press, Washington, DC, pp 459–504

Pests and their Natural Enemies (Parasitoids and/or Predators) in the Middle East

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The Middle East is a geographic region comprising a territory in which Asia, Africa, and Europe converge and which includes the Mediterranean Sea, the Red Sea, and the Persian Gulf. To the south, the Sahara Desert divides it from Tropical Africa; to the north, its outer limits lie in the latitude of the Black and Caspian Seas. On the east it extends as far as the Indian subcontinent, while its western limits lie at about the longitude of the Aegean Sea.

Agriculture is the most important activity in the Middle East in terms of the number of people it employs; in some countries it provides a substantial part of the gross domestic economy. Rainfed farming is possible only in these limited areas that receive more than 8 inches (800 mm) of rain annually, and then only for winter crops, because the summer is dry everywhere. A perennial supply of irrigation water is available from the Middle East's two great river systems, the Nile in Egypt and the Tigris-Euphrates system in Iraq and Syria. The agriculture these rivers support is highly productive. Irrigation water is also obtainable from underground water resources. These include renewable ground water resources, continually resupplied from precipitation and subterranean flow, and nonrenewable resources such as the fossil water deposits of the Sahara and Arabian peninsula. Another important agricultural resource of the Middle East is the region's grazing lands.

The largest vegetable production area in the world is in Asia, with 61% of total production and an annual growth rate of 5.1% per year. Over 100 types of vegetable crops are grown and consumed. Developing countries account for 61% of world vegetable production. China has the highest proportion of vegetable production, with South Asia is second with 19.4% of developing countries' vegetable production, followed by the Near East (8.5%) and East and South East Asia (9.1%). In terms of income generation, vegetable production has an important economic significance in developing countries. In many developing countries, the return per hectare for vegetable crops is twice the return for rice crops. Small-holder producers with limited mechanization carry out most production. This also increases the opportunities for on-farm employment. In 1996, developing countries accounted for 72% of world fresh fruit production.

According to FAO (1998), citrus is the most important fruit crop with world production at 87 million tons and increasing at an annual rate of 3.4% per year. Bananas are the second most important fruit commodity with 82 million tons and an annual growth increase of 2.7%. Most of the world banana production occurs in the developing countries of Latin America, Asia and Africa. Tomatoes are the third most important crop with 80 million tons of annual production and an annual production increase of 2.9% per year. Grapes are the fourth most important fruit crop with 55 million tons of annual production. Apples are the fifth most important fruit crop with 49 million tons of annual production.

Following is a list of key pests, sorted by crop known to be important in the Middle East. Indented beneath each pest is a list of natural enemies of each pest found in this region, and where they are known to occur.

Key insect and mite pests and their determined natural enemies in the Middle East (natural enemies are indented under their hosts)

a. Information for each crop is arranged as follows: name of the crop; scientific name of pest(s); scientific name of natural enemy(ies) (parasitoid or predator), if available; country where species were encountered and studied.
b. Reference in Arab Journal of Plant Protection.
c. Seventh Arab Congress of Plant Protection. 22–26 October 2000. Amman, Jordan. Abstract Book.
d. Gerling, D. 1990. Whiteflies: their Bionomics, Pest Status and Management.

Alliaceae

Garlic

Thrips tabaci Lindeman (Thysanoptera: Thripidae); Egypt[c], Lebanon

Onion

Thrips tabaci Lindeman (Thysanoptera: Thripidae); Jordan[c], Saudi Arabia

Anacardiaceae

Pistachio Tree

Agonoscena targionii (Licht.) (Hemiptera: Psyllidae)
- *Adonia variegata* Goetze (Coleoptera: Coccinellidae); Lebanon, Syria
- *Anthocorus minki* Dohrm (Hemiptera: Anthocoridae); Syria
- *Camphylomma* sp. (Hemiptera: Miridae); Syria
- *Chilocorus bipustulatus* (L.) (Coleoptera: Coccinellidae); Jordan, Lebanon, Syria
- *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae); Jordan, Syria
- *Coccinella novemnotata* Herbst (Coleoptera: Coccinellidae); Syria
- *Coccinella septempunctata* (L.) (Coleoptera: Coccinellidae); Iraq, Lebanon, Syria
- *Coccinella tredecimpunctata* (L.) (Coleoptera: Coccinellidae); Syria
- *Coccinella undecimpunctata* (L.) (Coleoptera: Coccinellidae); Iraq, Lebanon, Syria
- *Geocoris* sp. (Hemiptera: Lygaeidae); Syria
- *Hyperaspis quadrimaculatus* Redt. (Coleoptera: Coccinellidae); Syria, Turkey
- *Nabis ferrus* L. (Hemiptera: Nabidae); Syria

Orius horvathi (Reuter) (Hemiptera: Anthocoridae); Syria
Psyllaephagus pistaciae (Hymenoptera: Encyrtidae); Syria
Rhizophagus sp. (Coleoptera: Rizophagidae); Syria
Scymnus sp. (Coleoptera: Coccinellidae); Syria
Stethorus sp. (Coleoptera: Coccinellidae); Syria
Syrphus sp. (Diptera: Syrphidae); Lebanon, Syria
Capnodis cariosa Pall. (Coleoptera: Buprestidae); Lebanon, Syria
Hylesinus vestitus M. & R. (Coleoptera: Curculionidae: Scolytinae); Syria[c]
Cheiropachus quadrum F. (Hymenoptera: Pteromalidae); Syria
Clerus mutillarius Fisch. (Coleoptera: Cleridae); Syria
Dendrosoter protuberans (Nees) (Hymenoptera: Braconidae); Syria
Denops albofasciata K. (Coleoptera: Cleridae); Syria
Iponemus sp. (Acari: Tarsonemidae); Syria, Lebanon, Turkey
Tarsonemus sp. (Acari: Tarsonemidae); Syria
Thanasimus formicarius (L.) (Coleoptera:Cleridae); Syria
Thaumetopoea solitaria (Fr.) (Lepidoptera: Thaumetopoeidae); Iraq, Iran, Lebanon, Syria, Turkey

Arecaceae/Palmae

Palm

Apate monachus F. (Coleoptera: Bostrychidae); Algeria[c]
Arenipses sabella Hampson (Lepidoptera: Pyralidae); Algeria, Iran, Iraq, Libya, Saudi Arabia
Batrachedra amydraula Meyrick (Lepidoptera: Cosmopterygidae); Egypt, Iraq, Libya, Saudi Arabia
Ecotomyelois ceratoniae (carob moth)
Habrobracon hebetor Say (Hymenoptera: Braconidae); Tunisia[c]
Ephestia cautella (Walker) (Lepidoptera:Pyralididae); Iraq and Libya[c]
Bracon hebetor Say. (Hymenoptera: Braconidae); Iraq[c]
Icerya purchasi Mask. (Hemiptera: Margarodidae); Libya
Jebusea hammerschmidti Reiche (Coleoptera: Cerambycidae); Iraq, Saudi Arabia
Ommatissus binotatus Berg. (Hemiptera: Tropiduchidae); Algeria, Egypt, Libya
Chilocorus bipustulatus (L.) (Coleoptera: Coccinellidae); Iraq
Chrysopa carnea Steph. (Neuroptera: Chrysopidae); Iraq
Coccinella septempunctata L. (Coleoptera: Coccinellidae); Iraq
Coccinella undecimpunctata L. (Coleoptera: Coccinellidae); Iraq
Oryctes elegans Prell (Coleoptera: Scarabaeidae); Iraq[c] & Qatar[c], Saudi Arabia
Paratetranychus afrasiaticus (McG.) (Acari: Tetranychidae); Saudi Arabia
Parlatoria blanchardi Targioni-Tozzetti (Hemiptera: Diaspididae); Egypt, Iran, Iraq[b], Jordan, Libya, Palestine, Saudi Arabia
Phoenococcus marlatti Cock (Hemiptera: Phoenicococcidae); Libya
Phonapate frontalis Farhr. (Coleoptera:Bostrychidae); Iraq, Libya, Saudi Arabia
Planococcus citri (Risso) (Hemiptera: Pseudococcidae); Libya
Pseudophilus testaceus Gahan (Coleoptera: Curculionidae); Iraq & Qatar[c]
Rhynchophorus ferrugineus Fabricius (Coleoptera: Curculionidae); Egypt[c], Qatar[c], & Saudi Arabia
Schistocerca gregaria Forsk. (Orthoptera: Acrididae); Iraq, Jordan, Lebanon, Libya, Palestine, Saudi Arabia, Syria, Turkey

Brassicaceae (Cruciferae)

Cabbage

Aporia crataegi (L.) (Lepidoptera: Pieridae)
Apanteles (*Cotesia*) *glomeratus* L. (Hymenoptera: Braconidae); Lebanon, Syria
Bemisia tabaci Genn. (Hemiptera/Hemiptera: Aleyrodidae)
Clitostethus arcuatus Rossi (Coleoptera: Coccinellidae); Syria[c]

Brevicoryne brassicae L. (Hemiptera: Aphididae)
Aphidius brassicae March. (Hymenoptera: Braconidae); Lebanon
Diaeretiella rapae Mc' Intosh (Hymenoptera: Braconidae); Jordan, Lebanon, Syria
Pieris brassicae L. (Lepidoptera: Pieridae)
Cotesia glomeratus L. (Hymenoptera: Braconidae); Lebanon, Syria
Brachymeria intermedia Nees (Hymenoptera: Chalcididae); Lebanon
Compsilura sp. (Diptera: Tachinidae); Syria
Hyposoter sp. (Hymenoptera: Ichneumonidae); Syria
Spodoptera littoralis (Boisd.) (Lepidoptera: Noctuidae); Egypt, Lebanon, Iraq[b]

Cauliflower

Bemisia tabaci Genn. (Hemiptera: Aleyrodidae)
Clitostethus arcuatus Rossi (Coleoptera: Coccinellidae); Syria[b]
Spodoptera littoralis Boisduval (Lepidoptera: Noctuidae); Iraq[b]

Kohlrabi (*Brassica oleraceae* var. *caularapa*)

Atherigona orientalis (Schinner) (Diptera: Muscidae); Iraq[b]
Baris opiparis Jacquilin DuVal (Coleoptera: Curculionidae); Iraq[b]
Hellula undalis (Fabricius) (Lepidoptera: Pyralidae); Iraq[b]

Chenopodiaceae

Sugarbeet

Agrotis segetum (Schiff) (Lepidoptera: Noctuidae); Lebanon, Syria
Spodoptera exigua (Hübner) (Lepidoptera: Noctuidae); Lebanon, Iraq, Syria

Cucurbitaceae

Cucumber

Aphis gossypii Glover (Hemiptera: Aphididae)
Aphidius colemani Vierck (Hymenoptera: Aphidiidae); Algeria[c], Egypt[c], Lebanon, Saudi Arabia, Syria
Bemisia tabaci Genn. (Hemiptera: Aleyrodidae); Egypt[c], Lebanon, Syria[b]
Empoasca decipiens Paoli (Hemiptera: Cicadellidae); Egypt[c], Jordan, Lebanon, Syria
Henosepilachna elaterii Rossi (Coleoptera: Coccinellidae); Sudan[b]
Liriomyza cicerina Rond. (Diptera: Agromyzidae)
Diglyphus isaea (Walker) (Hymenoptera: Eulophidae); Syria
Liriomyza huidobrensis (Blanchard) (Diptera: Agromyzidae)
Diglyphus isaea (Walker) (Hymenoptera: Eulophidae); Syria
Hemiptarsenus sp. (Hymenoptera: Eulophidae); Syria
Neochrysocharis formosa (Westwood) (Hymenoptera: Eulophidae); Jordan, Lebanon, Syria
Halticoptera sp. (Hymenoptera: Pteromalidae); Syria
Liriomyza trifolii (Burgess) (Diptera: Agromyzidae)
Diglyphus isaea (Walker) (Hymenoptera: Eulophidae); Syria
Tetranychus urticae Koch (Acari: Tetranychidae)
Phytoseiulus persimilis (Acarina: Phytoseiidae); Lebanon & Syria[b]
Thrips tabaci Lindeman (Thysanoptera: Thripidae); Egypt[c], Syria[b]
Trialeurodes vaporariorum Westwood (Hemiptera: Aleyrodidae); Syria[b]

Melon

Acytopeus (Baris) curvirostris (Tourn.) (Coleoptera: Curculionidae)
Sarcophaga sp. (Diptera: Sarcophagidae); Saudi Arabia
Aphis gossypii Glover (Hemiptera: Aphididae)
Aphelinus gossypii (Timberlake) (Hymenoptera: Aphelinidae); Jordan[c], Lebanon, Syria

Dacus ciliatus Lw. (Diptera: Tephritidae); Egypt Lebanon, Saudi Arabia, Syria, Sudan

Eudioptes (Margaronia) indica Sn. (Lepidoptera: Pyralidae); Saudi Arabia, Syria

Myopardalis pardalina Bigot (Diptera: Tephritidae); Lebanon, Syria

Squash

Aphis gossypii Glover (Hemiptera: Aphididae); Egypt[c], Lebanon, Syria

Bemisia tabaci Genn. Genn. (Hemiptera: Aleyrodidae); Egypt[c], Lebanon, Syria

Empoasca decipiens Paoli (Hemiptera: Cicadellidae); Egypt[c], Lebanon, Syria

Watermelon

Acytopeus (Baris) curvirostris (Tourn.) (Coleoptera: Curculionidae)

- *Sarcophaga* sp. (Diptera: Sarcophagidae); Saudi Arabia

Aphis gossypii Glover (Hemiptera: Aphididae)

- *Aphelinus gossypii* (Timberlake) (Hymenoptera: Aphelinidae); Jordan[c], Lebanon, Syria

Trichoplusia ni (Hübner) (Lepidoptera: Noctuidae); Lebanon

Fagaceae

Cork oak

Cerambyx cerdo L. (Coleoptera: Cerambycidae); Algeria[c]

Platypus cylindrus F. (Coleoptera: Platypodidae); Algeria[c]

Oak

Malacosoma neustria L. (Lepidoptera: Lasiocampidae); Libya[c]

Gramineae/Poaceae

Barley

Cephus pygmaeus L. (Hymenoptera: Cephidae)

- *Collyria coxator* Villers (Hymenoptera: Ichneumonidae); Syria[b]
- *Collyria orientator* Aubert (Hymenoptera: Ichneumonidae); Syria[b]
- *Bracon terebrella* Wesmael (Hymenoptera: Braconidae); Syria[b]

Cnephasia pumicana Zeller (Lepidoptera: Tortricidae); Syria[c]

Diuraphis noxia Kurdjumov (Hemiptera: Aphididae)

- *Syrphus* sp. (Diptera: Syrphidae); Syria[b]
- *Leucopis* sp. (Diptera: Chamaemyiidae); Syria[b]
- *Coccinella septempunctata* L. (Coleoptera: Coccinellidae); Syria[b]
- *Diaretiella rapae* (Hymenoptera: Aphidiidae); Syria[b]
- *Praon* sp. (Hymenoptera: Aphidiidae); Syria[b]
- *Aphidius colemani* (Hymenoptera: Aphidiidae); Syria[b]

Eurygaster integriceps Puton (Hemiptera: Scutelleridae); Iran[b], Iraq, Syria[c], Turkey

- *Asolcus* sp. (Hymenoptera, Scelionidae); Iran, Syria
- *Microphanurus vasilievi* (Mayr) (Hymenoptera); Iran, Syria

Haplothrips tritici Kurd (Thysanoptera: Phlaeothripidae); Syria[c]

Oria musculosa Hübner (Lepidoptera: Noctuidae); Syria[c]

Porphyrophora tritici Bodenheimer (Hemiptera: Margarodidae); Syria[b]

Rhopalosiphum maidis Fitch (Hemiptera:Aphididae); Iraq, Lebanon, Syria[c]

Rhopalosiphum padi L. (Hemiptera: Aphididae); Iraq[b]

Schizaphis graminum (Rondani) (Hemiptera: Aphididae); Iraq

Sitotroga cerealella (Olivier) (Lepidoptera: Gelechiidae); Iraq

Tracheus judaicus Konow (Hymenoptera: Cephidae)

- *Collyria coxator* Villers (Hymenoptera: Ichneumonidae); Syria[b]
- *C. orientator* Aubert (Hymenoptera: Ichneumonidae); Syria[b]

Bracon terebrella Wesmael (Hymenoptera: Braconidae); Syria[b]

Trachelus libanensis Andre (Hymenoptera:Cephidae)

Collyria coxator Villers (Hymenoptera: Ichneumonidae); Syria[b]

C. orientator Aubert (Hymenoptera: Ichneumonidae); Syria[b]

Bracon terebrella Wesmael (Hymenoptera: Braconidae); Syria[b]

Corn

Cicadulina chinai Ghauri (Hemiptera: Cicadellidae); Egypt[c]

Cicadulina bipuncellazea China (Hemiptera: Cicadellidae); Egypt[c]

Empoasca descipiens Paoli (Hemiptera: Cicadellidae); Egypt[c], Jordan, Lebanon, Syria

Empoasca decedens Paoli (Hemiptera: Cicadellidae); Egypt[c]

Ostrinia (Pyrausta) *nubilalis* (Hübner) (Lepidoptera: Pyrlidae); Lebanon

Sogatella vibix (Haupt) (Hemiptera: Delphacidae); Egypt[c]

Sogatella furicifera Horv (Hemiptera: Delphacidae); Egypt[c]

Rhopalosiphum maidis Fitch (Hemiptera: Aphididae)

Coccinella septempuncata L. (Coleoptera: Coccinellidae); Iraq, Lebanon, Saudi Arabia, Syria

Sesamia cretica Led. (Lepidoptera: Agrotidae); Jordan, Saudi Arabia

Bracon spp. (Hymenoptera: Braconidae); Iraq, Syria

Coccinella septempuncata L. (Coleoptera: Coccinellidae); Iraq, Lebanon, Syria

Coccinella undecimpuncata L. (Coleoptera: Coccinellidae); Iraq, Lebanon, Syria

Orius albidepennis (Reut.) (Hemiptera: Anthocoridae); Iraq

Platytelenomus hylas Nixon (Hymenoptera: Scelionidae); Egypt[c]

Telenomus sp. (Hymenoptera: Scelionidae); Iraq

Tribolium castaneum (Herbst) (Coleoptera: Tenebrionidae)

Platytelenomus hylas Nixon (Hymenoptera: Scelionidae); Iraq[b]

Rice

Sitophilus oryzae L. (Coleoptera: Curculionidae); Iraq[b]

Trogoderma granarium Everts (Coleoptera: Dermestidae); Iraq[b]

Sorghum

Atherigona yorki Deeming (Diptera: Muscidae); Yemen[b]

Chilo partellus Swinhoe (Lepidoptera: Pyralidae); Yemen[b]

Sesamia cretica Lederer (Lepidoptera: Noctuidae); Yemen[b]

Sugarcane

Chilo agamemnon Bleszynski (Lepidoptera: Pyralidae)

Trichogramma evanescens West. (Hymenoptera: Tricogrammatidae); Egypt[b]

Wheat

Cephus pygmaeus L. (Hymenoptera: Cephidae)

Collyria coxator Villers (Hymenoptera: Ichneumonidae); Syria[b]

Collyria orientator Aubert (Hymenoptera: Ichneumonidae); Syria[b]

Bracon terebrella Wesmael (Hymenoptera: Braconidae); Syria[b]

Diuraphis noxia (Mordvilko) (Hemiptera: Aphididae)

Coccinella septempuncata L. (Coleoptera: Coccinellidae); Lebanon and Syria[b]

Leucopis sp. (Chamaemiiydae: Diptera); Lebanon, Syria

Syrphus sp. (Diptera: Syrphidae); Lebanon, Syria

Aphidius colemani Viereck (Hymenoptera: Braconidae); Lebanon, Syria

Diaeretiella rapae Mc' Intosh (Hymenoptera: Braconidae); Jordan, Lebanon, Syria

Praon sp. (Hymenoptera: Braconidae); Lebanon, Syria

Eurygaster integriceps Puton (Hemiptera: Scutelleridae); Iraq, Lebanon, Turkey

Asolcus sp. (Hymenoptera: Scelionidae); Iran, Syria
Microphanurus vasilievi (Mayr) (Hymenoptera); Iran, Syria
Trissolcus sp. (Hymenoptera: Scelionidae); Syria[c]
Exaeretopus tritici Williams (Hemiptera: Coccidae); Iraq[b]
Lytta vesicatoria (L.) (Coleoptera: Meloidae); Algeria[c]
Mayetiola destructor (Say) (Diptera: Cecidomyiidae); Morocco, Tunisia[c]
Metopolophium dirhodum (Walker) (Hemiptera: Aphididae)
Coccinella septempuncata L. (Coleoptera: Coccienllidae); Lebanon, Syria
Oria musculosa Hübner (Lepidoptera: Noctuidae); Syria
Oulema melanopus (L.) (Coleoptera: Chrysomelidae); Syria[b]
Rhopalosiphum padi (L.) (Hemiptera: Aphididae)
Coccinella septempuctata L. (Coleoptera: Coccinellidae); Syria[c]
Harmonia axyridis Pallas (Coleoptera: Coccinellidae); Syria[c]
Sitobion avenae (Fabricius) (Hemiptera: Aphididae)
Coccinella septempuncata L. (Coleoptera: Coccinellidae); Lebanon, Syria
Trachelus judaicus Konow (Hymenoptera: Cephidae)
Collyria coxator Villers (Hymenoptera: Ichneumonidae); Syria[b]
Collyria orientator Aubert (Hymenoptera: Ichneumonidae); Syria[b]
Bracon terebrella Wesmael (Hymenoptera: Braconidae); Syria[b]
Trachelus libanensis Andre (Hymenoptera: Cephidae)
Collyria coxator Villers (Hymenoptera: Ichneumonidae); Syria[b]
Collyria orientator Aubert (Hymenoptera: Ichneumonidae); Syria[b]
Bracon terebrella Wesmael (Hymenoptera: Braconidae); Syria[b]

Leguminoseae

Alfalfa

Sitona discoideus Gyllenhal (Coleoptera: Curculionidae)
Anaphes diana (Girault) (Hymenoptera: Mymaridae); Syria
Sitona lineatus (L.) (Coleoptera: Curculionidae); Lebanon, Syria
Spodoptera exigua (Hübner) (Lepidoptera: Noctuidae)
Chrysopa vulgaris L. (Hymenoptera: Chrysopidae); Libya[b]
Coccinella novemnotata Herbst (Coleoptera: Coccinellidae); Libya[b]
Coccinella septumpunctata L. (Coleoptera: Coccinellidae); Libya[b]
Coccinella undecimpunctata L. (Coleoptera: Coccinellidae); Libya[b]
Hippodamia tredecimpunctata tibialis (Say) (Coleoptera: Coccinellidae); Libya[b]
Nabis ferrus L. (Hemiptera: Nabidae); Libya[b]
Syrphus corollae Fabricius (Diptera: Syrphidae); Libya[b]
Tripolitanus sp. (Diptera: Asilidae); Libya[b]
Spodoptera littoralis (Boisd.) (Lepidoptera: Noctuidae); Egypt, Iraq, Lebanon, Saudi Arabia, Syria
Therioaphis maculata (Buckton) (Hemiptera: Aphididae)
Chrysopa vulgaris L. (Hymenoptera: Chrysopidae); Libya[b]
Coccinella novemnotata Herbst (Coleoptera: Coccinellidae); Libya[b]
Coccinella septumpunctata L. (Coleoptera: Coccinellidae); Libya[b]
Hippodamia tredecimpunctata (L.) (Coleoptera: Coccinellidae); Libya[b]
Coccinella undecimpunctata L. (Coleoptera: Coccinellidae); Libya[b]
Nabis ferrus L. (Hemiptera: Nabidae); Libya[b]
Syrphus corollae Fabricius (Diptera: Syrphidae); Libya[b]
Tripolitanus sp. (Diptera: Asilidae); Libya[b]
Therioaphis trifolii Monell (Hemiptera: Aphididae)
Aphelinus asychis Walker (Hymenoptera: Aphelinidae); Syria
Aphelinus semiflavus Howard (Hymenoptera: Aphelinidae); Syria
Coccinella septumpunctata L. (Coleoptera: Coccinellidae); Iraq, Lebanon, Syria
Malacocoris sp. (Hemiptera: Miridae); Syria
Praon exoletum (Needs) (Hymenoptera: Aphidiidae); Lebanon, Syria

Praon palitans Muesebeck (Hymenoptera: Aphidiidae); Lebanon, Palestine, Saudi Arabia

Trioxys complanatus Quilis Pérez (Hymenoptera: Aphidiidae); Lebanon

Trioxys utilis Muesebeck (Hymenoptera: Aphidiidae); Lebanon, Palestine, Syria

Beans

Aphis craccivora Koch (Hemiptera: Aphididae); Egypt[b]

Aphis fabae Scopoli (Hemiptera: Aphididae)

Coccinella septempunctata L. (Coleoptera: Coccinellidae); Syria[c]

Harmonia axyridis Pallas (Coleoptera: Coccinellidae); Syria[c]

Chrysoperla carnea (Stephens) (Neuroptera: Chrysopidae); Jordan, Syria

Didea sp. (Diptera: Syrphidae); Syria

Epistrophella sp. (Diptera: Syrphidae); Syria

Episyrphus balteatus De Geer (Diptera: Syrphidae); Lebanon, Syria

Eristalis sp.; Syria

Lysiphlebus confusus Tremblay & Eady (Hymenoptera: Aphidiidae); Lebanon

Melanostoma sp. (Diptera: Syrphidae); Syria

Scaeva sp. (Diptera: Syrphidae); Syria

Scymnus apetzi Mulsant (Coleoptera: Coccinellidae); Jordan, Lebanon, Syria

Trioxys angelicae (Haliday) (Hymenoptera: Aphidiidae); Lebanon

Bemisia tabaci (Gennadius) (Hemiptera: Aleyrodidae); Iraq, Jordan, Lebanon

Clitostethus arcuatus Rossi (Coleoptera: Coccinellidae); Syria[c]

Liriomyza cicerina Rondani (Diptera: Agromyzidae)

Diglyphus isaea (Walker) (Hymenoptera: Eulophidae); Syria

Liriomyza huidobrensis (Blanchard) (Diptera: Agromyzidae)

Chrysocharis orbicularis (Nees) (Hymenoptera: Eulophidae); Lebanon

Crossopalpus sp. (Diptera: Empididae); Syria

Diglyphus isaea (Walker) (Hymenoptera: Eulophidae); Syria

Halticoptera sp. (Hymenoptera: Pteromalidae); Syria

Hemiptarsenus sp. (Hymenoptera: Eulophidae); Syria

Neochrysocharis formosa (Westwood) (Hymenoptera: Eulophidae); Jordan, Lebanon, Syria

Nordlanderia sp. (Hymenoptera: Eucoilidae); Lebanon

Opius sp. (Hymenoptera: Braconidae); Syria

Pediobius acantha (Walker) (Hymenoptera: Eulophidae); Syria

Platypalpus sp. (Diptera: Empididae); Syria

Liriomyza trifolii (Burgess) (Diptera: Agromyzidae)

Diglyphus isaea (Walker) (Hymenoptera: Eulophidae); Syria

Lixus algirus L. (Coleoptera: Curculionidae); Syria[b]

Melanagromyza (*Agromyza*) *phaseoli* Coq. (Diptera: Agromyzidae); Lebanon

Rhopalosiphum padi L. (Hemiptera: Aphididae)

Coccinella septempuctata L. (Coleoptera: Coccinellidae); Syria[c]

Harmonia axyridis Pallas (Coleoptera: Coccinellidae); Syria[c]

Sitona crinitus H. (Coleoptera: Curculionidae); Syria[c]

Tetranychus urticae Koch (Acari: Tetranychidae)

Phytoseiulus persimilis (Acarina: Phytoseiidae); Lebanon & Syria[b]

Trialeurodes ricini Misra (Hemiptera: Aleyrodidae)

Clitostethus arcuatus Rossi (Coleoptera: Coccinellidae); Jordan[c]

Chickpeas

Heliocoverpa (*Heliothis*) *armigera* Hb. (Lepidoptera: Noctuidae); Jordan, Lebanon

Cynopterus sp. (Hymenoptera: Braconidae); Syria

Bracon hebetor (Say.) (Hymenoptera: Braconidae); Iraq, Syria

Campoletis sp. (Hymenoptera: Ichneumonidae); Syria

Liriomyza cicerina Rondani (Diptera: Agromyzidae)

Opius sp. (Hymenoptera: Braconidae); Syria

Dygliphus isaea (Walker) (Hymenoptera: Eulophidae); Syria

Lixus algirus L. (Coleoptera: Curculionidae); Syria[b]

Sitona lineatus (L.) (Coleoptera: Curculionidae); Lebanon, Syria[b]

Lentils

Heliothis spp. (Lepidoptera: Noctuidae); Syria[b]
Liriomyza cicerina Rondani (Diptera: Agromyzidae); Syria[b]
Lixus algirus L. (Coleoptera: Curculionidae); Syria[b]
Sitona lineatus (L.) (Coleoptera: Curculionidae); Lebanon, Syria[b]
Smynthurodes betae Westwood (Hemiptera: Aphididae)
Chrysotoxum intermedium Meigen (Diptera: Syrphidae); Syria, Turkey
Hyperaspis quadrimaculatus Redt. (Coleoptera: Coccinellidae); Syria, Turkey

Soybeans

Aphis gossypii (Glover) (Hemiptera: Aphididae); Egypt[b]
Bemisia tabaci Gennadius (Hemiptera: Aleyrodidae); Egypt[b]
Earias insulana Boisduval (Lepidoptera: Noctuidae); Egypt[b]
Empoasca lybica De Bergevin (Hemiptera: Cicadellidae); Egypt[b]
Platyedra (*Pectinophora*) *gossypiella* (Saunders) (Lepidoptera: Gelechiidae); Egypt[b]
Spodoptera littoralis Boisduval (Lepidoptera: Noctuidae); Egypt[b]
Tetranychus cinnabarinus (Boisduval) (Acari: Tetranychidae); Egypt[b]

Lythracaea

Pomegranate

Aphis punicae Passerini (Hemiptera: Aphididae)
Aphidius sp. (Hemiptera: Aphidiidae); Libya[c]
Coccinella novemnotata Herbst (Coleoptera: Coccinellidae); Libya[c]
Scymnus nubilus Mulsant (Coleoptera: Coccinellidae); Libya[c]
Scymnus syriacus Mars. (Coleoptera: Coccinellidae); Libya[c]
Syrphus corollae Fab. (Diptera: Syrphidae); Libya[c]
Ectomyelois ceratoniae Zeller (Lepidoptera: Pyralidae)
Apanteles angaleti Muesebeck (Hymenoptera: Braconidae); Iraq[c]
Siphoninus phillyreae (Haliday) (Hemiptera: Aleyrodidae)
Eretmocerus sp. (Hymenoptera: Aphelinidae); Jordan, Syria
Encarsia formosa Gahan (Hymenoptera: Aphelinidae); Jordan, Syria
Tenuipalpus punicae P. & B. (Acari: Tenuipalpidae); Iraq[b]
Virachola (Deudorix) livia Klug (Lepidoptera: Lycaenidae)
Brachymeria sp. (Hymenoptera: Chalcididae); Jordan

Malvaceae

Cotton

Aphis gossypii Glov. (Hemiptera: Aphididae)
Aphelinus gossypii (Temberlack) (Hymenoptera: Aphelinidae); Jordan
Geocoris megacephalus (Rossi) (Hemiptera: Lygaeidae); Syria
Hyperaspis variegata Goeze (Coleoptera: Coccinellidae); Lebanon
Orius laevigatus (Fieber) (Hemiptera: Anthocoridae); Syria
Scymnus levaillanti Mulsant (Coleoptera: Coccinellidae); Jordan, Syria
Scymnus quadriguttatus Capra (Coleoptera: Coccinellidae); Syria
Scymnus subvillosus (Goeze) (Coleoptera: Coccinellidae); Jordan, Lebanon, Syria
Trioxys angelicae (Haliday) (Hymenoptera: Aphidiidae); Lebanon
Bemisia tabaci Gennadius; Egypt[c]
Campylomma diversicornis Reuter (Hemiptera: Miridae); Syria
Deraeocoris punctulatus (Fallen) (Hemiptera: Miridae); Syria
Encarsia lutea (Masi) (Hymenoptera: Aphelinidae); Jordan, Syria
Eretmocerus mundus Mercet (Hymenoptera: Aphelinidae); Jordan, Syria
Macrolophus sp. (Hemiptera: Miridae); Syria

Earias insulana Boisduval (Lepidoptera: Noctuidae); Egypt[b], Iraq, Iran, Turkey

Trichogramma brassicae Bezdenko (Hymenoptera: Trichogrammatidae); Syria

Helicoverpa armigera Hübner (Lepidoptera: Noctuidae)

Bracon (*Haprobracon*) *brevicornis* Wesmael (Hymenoptera: Braconidae); Syria

Haprobracon hebetor Say (Hymenoptera: Braconidae); Syria

Trichogramma brassicae Bezdenko (Hymenoptera: Trichogrammatidae); Syria

Trichogramma chilonis Ishii (Hymenoptera: Trichogrammatidae); Syria

Trichogramma principium Sugonyaev-Sorokina (Hymenoptera: Trichogrammatidae); Syria

Platyedra (*Pectinophora*) *gossypiella* (Saunders) (Lepidoptera: Gelechiidae); Egypt[b], Sudan, Syria

Spodoptera litoralis Boisduval (Lepidoptera: Noctuidae); Eygpt[b]

Tetranychus cinnabarinus (Boisduval) (Acari: Tetranychidae)

Chrysoperla carnea (Stephens) (Neuroptera: Chrysopidae); Syria

Exochomus pubscens Kuster (Coleoptera: Coccinellidae); Jordan

Okra

Bemisia tabaci Gennadius. (Hemiptera: Aleyrodidae)

Clitostethus arcuatus Rossi (Coleoptera: Coccinellidae); Syria[c]

Earias insulana Boisduval (Lepidoptera: Noctuidae); Lebanon, Saudi Arabia

Oleaceae

Olives

Acaudaleyrodes olivinus Silvestri (Hemiptera: Aleyrodidae)

Encarsia spp.; Jordan

Bactrocera (*Dacus*) *oleae* Gmelin (Diptera: Tephritidae); Libya[c]

Carpophilus mutilatus Er. (Coleoptera: Nitidulidae); Lebanon

Cyrtoptyx dacicida Masi (Hymenoptera: Pteromalidae); Lebanon

Cyrtoptyx latipes (Rondani) (Hymenoptera: Pteromalidae); Egypt[c]

Eupelmus sp. (Hymenoptera: Eupelmidae); Egypt[c]

Eupelmus urozonus Dal. (Hymenoptera: Eupelmidae); Lebanon

Eurytoma rosae Nees (Hymenoptera: Eurytomidae); Lebanon

Eurytoma martelli M. (Hymenoptera: Eurytomidae); Egypt[c], Syria

Macroneura sp. (Hymenoptera: Eupelmidae); Egypt[c]

Opius concolor Szépligeti (Hymenoptera: Braconidae); Egypt[c],Lebanon, Palestine, Syria

Platygaster sp. (Hymenoptera: Scelionidae); Lebanon

Pnigalio agraules W. (Hymenoptera: Eulophidae); Egypt[c]

Pnigalio mediterraneus Ferriere & Delucchi (Hymenoptera: Eulophidae); Lebanon, Syria

Prolasioptera berlesiana Paoli (Diptera: Cecidomyidae); Lebanon

Synopeas sp. (Hymenoptera: Scelionidae); Lebanon

Clinodiplosis oleisuga Targ. (Diptera: Cecidomyiidae)

Inostema sp. (Hymenoptera: Platygasteridae); Syria, Jordan, Lebanon

Leptacis sp. (Hymenoptera: Platygasteridae); Syria

Dasyneura (*Perrisia*) *oleae* (Loew) (Diptera: Cecidomyiidae)

Aprostocetus sp. (Hymenoptera: Eulophidae); Jordan, Lebanon

Platygaster apicalis Thomas; Syria

Platygaster oleae Szeleny; Jordan, Syria

Euphyllura straminea Loginova (Hemiptera: Psyllidae)

Anthocoris nemoralis (Fabricius) (Hemiptera: Anthocoridae); Syria

Anthocoris nomorum L. (Hemiptera: Anthocoridae); Lebanon, Syria

Crysoperla carnea (Stephens) (Neuroptera: Chrysopidae); Jordan, Lebanon, Syria

Euphyllura olivina Costa (Hemiptera: Psyllidae)

Anthocoris nemoralis (Fabricius) (Hemiptera: Anthocoridae); Syria

Anthocoris nomorum L. (Hemiptera: Anthocoridae); Lebanon, Syria

Parlatoria oleae (Clovée) (Hemiptera: Diaspididae)

Chilocorus bipustulatus (L.) (Coleoptera: Coccinellidae; Jordan, Lebanon, Syria

Phloeotribus scarabeoides (Bern.) (Coleoptera: Curculionidae: Scolytinae); Lebanon, Morocco[c], Syria

Prays oleellus F. (Lepidoptera: Hyponomeutidae)

Ageniaspis fuscicollis (Dalman) (Hymenoptera: Encyrtidae); Lebanon

Apanteles dilectus Haliday (Hymenoptera: Braconidae); Lebanon

Chelonus elaeaphilus Silv. (Hymenoptera: Braconidae); Lebanon

Chrysocharis sp. (Hymenoptera: Eulophidae); Lebanon

Cirrospilus elongatus Boucek (Hymenoptera: Eulophidae); Lebanon

Elasmus flabellatus Fonscolombe (Hymenoptera: Elasmidae); Lebanon

Himertosoma sp. Schmiedeknecht (Hymenoptera: Ichneumonidae); Syria

Phytomyptera sp. Rond. (Diptera: Tachinidae); Lebanon

Trichogramma oleae Voegelé-Pointel (Hymenoptera: Trichogrammatidae); Syria

Saissetia oleae (Bern.) (Hemiptera: Coccidae)

Chilocorus bipustulatus (L.) (Coleoptera: Coccinellidae); Jordan, Lebanon, Syria

Scutellista cyanea Motschulsky (Hymenoptera: Ormyridae); Lebanon, Syria

Pedaliaceae

Sesame

Asphondylia sesami Felt (Diptera: Cecidomyiidae); Yemen[b]

Antigastra catalaunalis Duponchel (Lepidoptera: Pyralidae); Yemen[b]

Pinaceae

Cedars

Cephalcia tannourinensis Chevin (Hymenoptera: Pamphiliidae); Lebanon

Dasineura cedri Coutin (Diptera: Cecidomyiidae); Lebanon

Thaumetopoea pityocampa Schiff. (Lepidoptera: Thaumetopoeidae)

Anastatus bifasciatus Fonsc. (Hymenoptera: Eupelmidae); Lebanon, Morocco[b]

Baryscapus (*Tetrastichus*) *servadeii* (Dom.) (Hymenoptera: Eulophidae); Lebanon, Morocco[b]

Ooencyrtus pityocampae Mercet (Hymenoptera: Encyrtidae); Lebanon, Morocco[b]

Trichogramma embryophagum Hartig (Hymenoptera: Trichogrammatidae); Morocco[b]

Pine

Aspidiotes hederae (Vallot) (Hemiptera: Diaspididae)

Chilocorus bipustulatus (L.) (Coleoptera: Coccinellidae); Jordan, Lebanon, Syria

Eulachnus rileyi (Williams) (Hemiptera: Lachnidae); Iraq[b]

Thaumetopoea pityocampa (Den. and Schiff.) (Lepidoptera: Thaumetopoeidae)

Anastatus bifasciatus Fonsc. (Hymenoptera: Eupelmidae); Morocco[b]

Baryscapus (*Tetrastichus*) *servadeii* (Domenichini) (Hymenoptera: Eulophidae); Syria[c]

Calosoma sycophanta L. (Coleoptera: Carabidae); Lebanon, Syria

Ooencyrtus pityocampae (Mercet) (Hymenoptera: Encyrtidae); Morocco[b], Syria[c]

Phryxe caudata (Rondani) (Diptera: Tachinidae); Syria

Trichogramma embryophagum Hartig. (Hymenoptera: Trichogrammatidae); Morocco[b], Syria[c]

Thaumetopoea wilkinsoni Tams. (Lepidoptera: Thaumetopoeidae)

Anastatus bifasciatus Fonsc. (Hymenoptera: Eupelmidae); Lebanon[c]

Baryscapus (*Tetrastichus*) *servadeii* (Domenichini) (Hymenoptera: Eulophidae); Lebanon

Compsilura concinnata (Meigen) (Diptera: Tachinidae); Lebanon

Ooencyrtus pityocampae (Mercet) (Hymenoptera: Encyrtidae); Lebanon

Phryxe caudata (Rondani) (Diptera: Tachinidae); Lebanon

Rosaceae

Almond

Aporia crataegi L. (Lepidoptera: Pieridae)
Apanteles glomeratus (L.) (Hymenoptera: Braconidae); Lebanon, Syria
Microbracon kikpatricki Wilk. (Hymenoptera: Braconidae); Syria
Trichogramma semblidus (Aurivilius) (Hymenoptera: Trichogrammatidae); Syria
Brachycaudus amygdalinus (Schout.) (Hemiptera: Aphididae)
Aphidius matricariae Hal. (Hymenoptera: Aphidiidae); Lebanon, Syria
Aphidoletes aphidimyza (Rondani) (Diptera: Cecidomyiidae); Lebanon, Syria
Deraeocoris pallens (Reuter) (Hemiptera: Miridae); Lebanon
Exochomus quadripustulatus (L.) (Coleoptera: Coccinellidae); Lebanon, Syria
Leucopis sp. (Diptera: Chamaemyiidae); Lebanon, Syria
Scymnus subvillosus (Goeze) (Coleoptera: Coccinellidae); Jordan, Lebanon, Syria
Synharmonia conglobata (L.) (Coleoptera: Coccinellidae); Lebanon, Syria
Cimbex quadrimaculatus Muell. (Hymenoptera: Tenthredinidae); Cyprus, Lebanon, Syria, Turkey
Spilocryptis cimbicis Tschek. (Hymenoptera: Ichneumonidae); Palestine
Eriogaster amygdali talhouki Wilts. (Lepidoptera: Lasiocampidae); Lebanon
Eurytoma amygdali End. (Hymenoptera: Eurytomidae); Palestine
Ascogaster sp. (Hymenoptera: Braconidae); Syria
Mesochorus nigripes Ratz. (Hymenoptera: Ichneumonidae); Syria
Plastotorymus amygdali n.sp. (Hymenoptera: Torymidae); Jordan, Syria
Saltis sp. (Araneae); Lebanon
Syntomaspis sp. (Hymenoptera: Torymidae); Syria
Neurotoma nemoralis L. (Hymenoptera: Pamphiliidae)
Sinophorus (*Limnerium*) *crassifemur* (Thomson) (Hymenoptera: Ichneumonidae); Syria
Pterochloroides persicae (Cholod) (Hemiptera: Lachnidae); Lebanon, Syria
Pauesia sp. (Hymenoptera: Braconidae); Yemen[b]

Apple

Aphis pomi DeGeer (Hemiptera: Aphididae)
Adalia bipunctata (L.) (Coleoptera: Coccinellidae); Lebanon, Jordan, Syria
Adalia decempunctata (L.) (Coleoptera: Coccinellidae); Lebanon, Syria
Harmonia quadripunctata (Melsheimer) (Coleoptera: Coccinellidae); Jordan
Bryobia sp. (Acari: Tetranychidae)
Typhlodromus kettanehi Dosse (Acari: Phytoseiidae); Lebanon
Capnodis tenebrionis L. (Coleoptera: Buprestidae); Lebanon
Cenopalpus pulcher (Canestrini and Fanzago) (Acari: Tenuipalpidae)
Amblyseius finlandicus Ondemans (Acari: Phytoseiidae); Lebanon[b]
Phytoseius ocellatus Bayan (Acari: Phytoseiidae); Lebanon[b]
Typhlodromus invectus Chant (Acari:Phytoseiidae); Lebanon[b]
Typhlodromus kettanehi Dosse (Acari:Phytoseiidae); Lebanon[b]
Typhlodromus pyri Scheuten (Acari:Phytoseiidae); Lebanon[b]
Ceratitis capitata Weid. (Diptera: Tephritidae); Jordan, Lebanon, Syria[c]
Cydia pomonella L. (Lepidoptera: Olethreutidae)
Ascogaster quadridentata Wesml. (Hymenoptera: Braconidae); Syria[c]
Dibrachys cavus (Walker) (Hymenoptera: Pteromalidae); Lebanon
Itoplectis maculator F. (Hymenoptera: Ichneumonidae); Syria[c]
Liotryphon caudatus Ratz. (Hymenoptera: Ichneumonidae); Syria[c]
Microdus rufipes Nees (Hymenoptera:Braconidae); Syria[c]
Perilampus sp. (Hymenoptera: Perilampidae); Lebanon

Perilampus tritis Mayr (Hymenoptera: Perilampidae); Syria[c]
Pristomerus vulnerator Gravenhorst (Hymenoptera: Ichneumonidae); Syria[c]
Trichogramma sp. (Hymenoptera: Trichogrammatidae); Syria[c]
Trichomma enecator Rossi (Hymenoptera: Ichneumonidae); Syria[c]
Dysaphis plantaginea (Passerini) (Hemiptera: Aphididae); Lebanon
Dysaphis pyri Boy. (Hemiptera: Aphididae); Iraq[b]
Eriosoma lanigerum Hausm (Hemiptera:Aphididae)
Adalia bipunctata L. (Coleoptera: Coccinellidae); Jordan, Lebanon, Syria
Aphelinus mali (Haldeman) (Hymenoptera: Aphelinidae); Lebanon
Coccinella septempunctata L. (Coleoptera: Coccinellidae); Lebanon, Jordan, Syria
Oenopia conglobata (L.) (Coleoptera:Coccinellidae); Syria, Jordan
Leucoptera scitella Costa (Lepidoptera: Lyonetidae); Algeria[c]
Malacosoma neustria (L.) (Lepidoptera: Lasiocampidae); Libya[c]
Panonychus ulmi (Koch) (Acari: Tetranychidae)
Amblyseius andersoni Chant (Acari: Phytoseiidae); Algeria[c]
Phytoseiulus persimilis Athias-Henriot (Acari: Phytoseiidae); Algeria[c]
Phytoseius plumifer (C. & F.) (Acari: Phytoseiidae); Lebanon
Stethorus gilvifrons (Muslant) (Coleoptera: Coccinellidae); Iraq, Jordan, Lebanon, Syria
Zetzellia mali Oud. (Acari: Stigmaeidae); Lebanon, Syria
Zetzellia talhouki Dosse (Acari: Stigmaiedae); Lebanon
Pterochloroides persicae (Cholod) (Hemiptera: Lachnidae); Lebanon, Syria
Pauesia sp. (Hymenoptera: Aphidiidae); Yemen[c]
Tetranychus urticae Koch (Acari: Tetranychidae)
Amblyseius andersoni (Acari: Phytoseiidae); Algeria[c]
Phytoseiilus persimilis Athias-Henriot (Acari: Phytoseiidae); Algeria[c]
Stethorus gilvifrons (Muslant) (Coccinellidae); Iraq, Jordan, Lebanon, Syria
Zetzellia spp. (Acari: Stigmaeidae); Lebanon, Syria
Tetranychus turkestani Ugarov & Nikolski (Acari: Tetranychidae)
Stethorus gilvifrons (Muslant) (Coccinellidae); Iraq, Jordan, Lebanon, Syria
Tydeus californicus Banks (Acari: Tydeidae); Lebanon[b]
Zeuzera pyrina (L.) (Lepidoptera: Cossidae) Algeria[c], Lebanon, Libya[c], Syria

Peach

Anarsia lineatella Zell. (Lepidoptera: Gelechidae); Palestine, Syria
Aetecerus discolor Wesm. (Hymenoptera: Ichneumonidae); Lebanon
Aulacorthum solani (Kaltenbach) (Hemiptera: Aphididae)
Aphidius matricariae Hal. (Hymenoptera: Aphidiidae); Lebanon, Syria
Bactrocera zonata (Saunders) (Diptera: Tephritidae); Egypt, Middle East[c]
Brachycaudus amygdalinus (Schout.) (Hemiptera: Aphididae)
Episyrphus balteatus (De Geer) (Diptera: Syrphidae); Lebanon, Syria
Brachycaudus helichrysi (Kalt.) (Hemiptera: Aphididae); Iraq, Jordan, Saudi Arabia
Episyrphus balteatus (De Geer) (Diptera: Syrphidae); Lebanon, Syria
Ceratitis capitata Weid. (Diptera: Tephritidae); Egypt, Jordan, Lebanon, Syria[c]
Myzus persicae (Hemiptera: Aphididae)
Praon sp. (Hymenoptera: Aphidiidae); Syria
Syrphus ribessii (L.) (Diptera: Syrphidae); Lebanon, Syria
Trioxys angelicae (Haliday) (Hymenoptera: Aphidiidae); Lebanon, Tunisia[c]
Neurotoma nemoralis L. (Hymenoptera: Pamphiliidae)
Sinophorus (*Limnerium*) *crassifemur* (Thomson) (Hymenoptera: Ichneumonidae); Syria

Pterochloroides persicae (Cholod) (Hemiptera: Lachnidae)
Syrphus sp. (Diptera: Syrphidae); Lebanon, Syria
Pauesia antennata (Mukerji) (Hymenoptera: Braconidae); Yemen

Pear

Apiomyia bergenstammi (Wachtl.) (Diptera: Cecidomyiidae)
Oxyglypta rugosa Rushka (Chalcididae); Lebanon, Syria
Cacopsylla bidens (Sulc.) (Hemiptera: Psyllidae); Lebanon, Syria
Capnodis tenebrionis L. (Coleoptera: Buprestidae); Lebanon
Ceratitis capitata Weid. (Diptera: Tephritidae); Egypt, Jordan[b], Lebanon, Syria[c]
Dysaphis pyri Boy. (Hemiptera: Aphididae); Iraq[b]
Zeuzera pyrina (L.) (Lepidoptera: Cossidae); Algeria[c], Lebanon, Libya[c], Syria

Plum

Acalitus phloeocoptes Nal. (Acari: Eriophyidae)
Typhlodromous invectus Chant (Acari: Phytoseiidae); Lebanon[b]
Zetzellia talhouki Dosse (Acari: Stigmaeidae); Lebanon[b]
Aculus fockeui (Nalepa and Trouessart) (Acari: Eriophyidae)
Zetzellia talhouki Dosse (Acari: Stigmaeidae); Lebanon[b]
Typhlodromous invectus Chant (Acari: Phytoseiidae); Lebanon[b]
Bryobia rubrioculus (Scheuten) (Acari: Tetranychidae)
Typhlodromous invectus Chant (Acari: Phytoseiidae); Lebanon[b]
Zetzellia talhouki Dosse (Acari: Stigmaeidae); Lebanon[b]
Cenopalpus lanceolatisetae Attiah (Acari: Tenuipalpidae)
Typhlodromous invectus Chant (Acari: Phytoseiidae); Lebanon[b]
Zetzellia talhouki Dosse (Acari: Stigmaeidae); Lebanon[b]
Diptacus gigantorhynchus (Nalepa) (Acari: Diptilomiopidae)
Typhlodromous invectus Chant (Acari: Phytoseiidae); Lebanon[b]
Zetzellia talhouki Dosse (Acari: Stigmaeidae); Lebanon[b]
Eotetranychus carpini (Oudemams) (Acari: Tetranychidae)
Typhlodromous invectus Chant (Acari: Phytoseiidae); Lebanon[b]
Zetzellia talhouki Dosse (Acari: Stigmaeidae); Lebanon[b]
Hyalopterus pruni (Geoffroy) (Hemiptera: Aphididae)
Adonia variegata (Goeze) (Coleoptera: Coccinellidae); Lebanon, Syria
Ephedrus plagiator (Nees) (Hymenoptera: Braconidae); Lebanon, Iraq[b]
Syrphus ribesii L. (Diptera: Syrphidae); Lebanon, Syria
Phyllocoptes abaenus Keifer (Acari: Eriophyidae)
Typhlodromous invectus Chant (Acari: Phytoseiidae); Lebanon[b]
Zetzellia talhouki Dosse (Acari: Stigmaeidae); Lebanon[b]
Tetranychus cinnabarinus Boisd. (Acari: Tetranychidae); Saudi Arabia, Syria
Typhlodromous invectus Chant (Acari: Phytoseiidae); Lebanon[b]
Zetzellia talhouki Dosse (Acari: Stigmaeidae); Lebanon[b]
Tetranychus urticae Koch (Acari: Tetranychidae); Saudi Arabia, Syria
Typhlodromous invectus Chant (Acari: Phytoseiidae); Lebanon[b]
Zetzellia talhouki Dosse (Acari: Stigmaeidae); Lebanon[b]

Quince

Capnodis tenebrionis L. (Coleoptera: Buprestidae); Algeria
Ceratitis capitata Weid. (Diptera: Tephritidae); Jordan[b]
Recurvaria nanella Hb. (Lepidoptera: Gelechidae); Lebanon
Macrocentrus abdominalis F. (Hymenoptera: Braconidae); Syria
Orgilus obscurator Nees (Hymenoptera: Braconidae); Syria

Strawberry

Phytonemus (*Steneotarsonemus*) *pallidus* (Banks) (Acarina: Tarsonemidae); Lebanon
Tetranychus cinnabarinus (Boisduval) (Acari: Tetranychidae); Lebanon

Tetranychus urticae Koch
Phytoseiulus persimilis Athias-Henriot (Acari: Phytoseiidae); Egypt[c], Lebanon

Rutaceae

Citrus

Acaudaleyrodes citri (Priesner & Hosni) (Hemiptera: Aleyrodidae)
Cales noaki Howard (Hymenoptera: Aphelinidae); Syria[c]
Encarsia lahorensis (Howard) (Hymenoptera: Aphelinidae); Syria[c]
Encarsia lutea (Masi) (Hymenoptera: Aphelinidae); Middle East[d]
Acrythosiphon lactucae (Tlja.) (Hemiptera: Aphididae)
Scymnus apetzi Mulsant (Coleoptera: Coccinellidae); Jordan, Lebanon, Syria
Aleurothrixus floccosus (Maskell) (Hemiptera: Aleyrodidae)-Syria[c]
Encarsia lahorensis (Howard) (Hymenoptera: Aphelinidae); Syria[c]
Aonidiella aurantii (Maskell) (Hemiptera: Diaspididae)
Aphytis chrysomphali (Mercet) (Hymenoptera: Aphelinidae); Lebanon, Syria
Aphis citricola (Van der Goot) (Hemiptera: Aphididae); Syria[c]
Aphis gossypii (Glover) (Hemiptera: Aphididae); Iraq, Jordan, Lebanon, Saudi Arabia, Syria[c]
Aspidiotus hederae Vallot (Hemiptera: Diaspididae)
Rhizobius lophanthae (Blaisdell) (Coleoptera: Coccinellidae); Jordan, Syria
Bemisia tabaci Genn. (Hemiptera: Aleyrodidae)
Encarsia lutea (Masi) (Hymenoptera: Aphelinidae); Middle East[d]
Euseius scutalis (Athias-Henriot) (Acari: Phytoseiidae); Jordan[b]
Brevipalpus lewisi McGregor (Acari: Tetranychidae)
Euseius scutalis (Athias-Henriot) (Acari: Phytoseiidae); Jordan[b]
Ceratitis capitata Wied. (Diptera: Tephritidae); Jordan, Lebanon, Syria[c]
Ceroplastes floridensis Comostock (Hemiptera: Coccidae)
Scutellista cyanea Motsch (Hymenoptera: Pteromalidae); Lebanon, Syria[c]
Chrysomphalus ficus Ashm (Hemiptera: Coccidae)
Aphytis chrysomphali (Mercer) (Hymenoptera: Aphelinidae); Lebanon, Syria
Dialeurodes citri Ashmead (Hemiptera: Aleyrodidae)
Cales noaki Howard (Hymenoptera: Aphelinidae); Syria[c]
Encarsia lahorensis (Howard) (Hymenoptera: Aphelinidae); Syria[c]
Encarsia sp. (Hymenoptera: Aphelinidae); Syria
Diaphorina citri Kuw. (Hemiptera: Psyllidae)
Chilomenes vicina (Muls.) (Coleoptera: Coccinellidae); Saudi Arabia
Diaphorencyrtus aligarhensis (Shafee, Alam & Agaral) (Hymenoptera: Encyrtidae); Saudi Arabia
Duraphis noxia (Kurdjumov) (Hemiptera: Aphididae)
Aphidius colemani Viereck (Hymenoptera: Braconidae); Lebanon, Syria
Aphidius matricariae (Hymenoptera: Braconidae); Lebanon, Syria
Ephedrus persicae Frogatt (Hymenoptera: Braconidae); Lebanon
Lysiphlebus fabarum Marshal (Hymenoptera: Braconidae); Lebanon[b]
Praon volucre (Hymenoptera: Braconidae); Lebanon[b]
Trioxys angelicae Haliday (Hymenoptera: Braconidae); Lebanon[b]
Eriophyes (*Aceria*) *sheldoni* (Ewing) (Acari: Eriophyidae)
Phytoseiulus (*Phytoseides*) sp. (Acari: Phytoseiidae); Lebanon, Syria
Eutetranychus orientalis (Klein) (Acari: Tetranychidae)
Euseius scutalis (Athias-Henriot) (Acari: Phytoseiidae); Jordan[b]
Exochomus nigromaculatus (Goeze.) (Coleoptera: Coccinellidae); Jordan, Lebanon, Syria
Heliothrips haemorrhoidalis Bouche (Thysanoptera: Thripidae)
Franklinothrips megalops (*myrmecaeformis*) (Thysanoptera: Aeolothripidae); Lebanon, Palestine
Icerya purchasi Mask. (Hemiptera: Margarodidae)
Rodalia cardinalis (Mulsant) (Coleoptera: Coccinellidae)
Macrosiphum euphorbiae (Thomas) (Hemiptera: Aphididae); Syria[c]
Microtermes najdensis Harris (Isoptera: Termitidae); Saudi Arabia

Nipaecoccus viridis (Newstead) (Hemiptera: Pseudococcidae); Iraq, Jordan, Lebanon, Saudi Arabia

Anagyrus (*Agraensis*) *indicus* Shafee, Alam, & Agarwal (Hymenoptera: Encyrtidae); Jordan, Syria

Anagyrus kamali Moursi (Hymenoptera: Encyrtidae); Jordan

Anagyrus pseudococci Girault (Hymenoptera: Encyrtidae); Saudi Arabia

Chrysopa nr. *gobiensis* (Tjeder) (Neuroptera: Chrysopidae); Saudi Arabia

Exochomus marginipennis Leconte (Coleoptera: Coccinellidae); Saudi Arabia

Hyperaspis sp. (Coleoptera: Coccinellidae); Saudi Arabia

Nephus bipunctatus (includens) Kirsch (Coleoptera: Coccinellidae); Jordan, Syria

Scymnus sp. (Coleoptera: Coccinellidae); Saudi Arabia

Panonychus citri (McGregor) (Acari: Tetranychidae)

Amblyseius (*Iphiseius*) *degenrans* Berlese (Acari: Phytoseiidae); Syria; Lebanon, Saudi Arabia

Neoceiulus (*Amblyseius*) *californicus* McGregor (Acari: Phytoseiidae); Syria

Phytoseiulus (*Phytoseides*) sp. (Acari: Phytoseiidae); Syria

Papilio demodocus (Esper) (Lepidoptera: Papillionidae); Saudi Arabia

Papilio demolus L. (Lepidoptera: Papillionidae); Saudi Arabia

Parabemisia myricae Kowana (Hemiptera: Aleyrodidae)

Cales noaki Howard (Hymenoptera: Aphelinidae); Syria[c]

Encarsia lahorensis (Hymenoptera: Aphelinidae); Syria[c]

Eretmocerus sp. (Hymenoptera: Aphelinidae): Israel[d]

Paraleyrodes minei Iaccarino (Hemiptera: Aleyrodidae)

Cales noaki Howard (Hymenoptera: Aphelinidae); Syria[c]

Encarsia lahorensis (Hymenoptera: Aphelinidae); Syria[c]

Phyllocnistis citrella (Stainton) (Lepidoptera: Gracillariidae); Saudi Arabia

Ageniaspis citricola Logvinovskaya (Hymenoptera: Encyrtidae); Syria

Chrysoperla carnea (Stephens) (Neuroptera: Chrysopidae); Jordan, Syria

Cirrospilus ingenus (Gahan) (Hymenoptera: Eulophidae); Syria

Cirrospilus luteus (Hymenoptera: Eulophidae); Lebanon

Cirrospilus lyncus (Walker) (Hymenoptera: Eulophidae); Lebanon

Cirrospilus nr. *lyncus* (Walker) (Hymenoptera: Eulophidae); Syria

Cirrospilus pictus (Nees) (Hymenoptera: Eulophidae); Jordan

Cirrospilus quadristriatus (Subba Rao & Ramamani) (Hymenoptera: Eulophidae); Jordan, Syria

Cirrospilus sp. (Hymenoptera: Eulophidae); Algeria[c]

Citrostichus phyllocnistoides (Hymenoptera: Eulophidae); Syria

Neochrysocharis formosa (Westwood) (Hymenoptera: Eulophidae); Jordan, Syria

Pnigalio spp. (Boucek) (Hymenoptera: Eulophidae); Algeria[c], Jordan, Lebanon, Syria

Ratzeburgiola incompleta (Boucek) (Hymenoptera: Eulophidae); Jordan, Syria, Saudi Arabia

Semielacher petiolatus (Girault) (Hymenoptera: Eulophidae); Algeria[c], Syria

Stenomesius japonicus (Ashmead) (Hymenoptera: Eulophidae); Syria

Sympiesis spp. (Hymenoptera: Eulophidae); Syria

Phyllocoptruta oleivora (Ashmead) (Acarina: Eriophyidae); Saudi Arabia

Phytoseiulus (*Phytoseides*) sp. (Acari: Phytoseiidae); Lebanon, Syria

Planococcus (*Psuedococcus*) *citri* (Risso) (Hemiptera: Pseudococcidae)

Cryptolaemus montruzieri (Mulsant) (Coleoptera: Coccinellidae), Syria[c]

Planococcus spp. (Hemiptera: Pseudococcidae); Saudi Arabia

Anagyrus (*agraensis*) *indicus* Shafee, Alam, & Agarwal (Hymenoptera: Encyrtidae); Jordan, Syria

Pseudococcus adonidum (L.) (Hemiptera: Pseudococcidae)

Cryptolaemus montruzieri (Mulsant) (Coleoptera: Coccinellidae), Syria[c]

Leptomastix dactylopii Howard (Hymenoptera: Encyrtidae); Syria

Nephus bipunctatus (*includens*) Kirsch (Coleoptera: Coccinellidae); Jordan, Syria

Prays citri Miller (Lepidoptera, Hyponomentidae); Egypt[b]

Bracon hebetor Say. (Hymenoptera: Braconidae); Iraq, Syria

Elasmus steffani (Hymenoptera: Elasmidae); Syria

Scirtothrips citri (Moulton) (Thysanoptera: Thripidae)
Euseius scutalis (Athias-Henriot) (Acari: Phytoseiidae); Jordan[b]
Tetranychus cinnabarinus (Boisd.) (Acari: Tetranychidae)
Exochomus nigromaculatus (Goeze.) (Coleoptera: Coccinellidae); Jordan, Lebanon, Syria
Stethorus gilvifrons Muls. (Coleoptera: Coccinellidae); Lebanon
Tetranychus turkestani Ugarov & Nikolski (Acari: Tetranychidae)
Stethorus gilvifrons (Muslant) (Coleoptera: Coccinellidae); Iraq, Jordan, Lebanon, Syria
Chrysoperla carnea Steph. (Neuroptera: Chrysopidae); Iraq
Toxoptera aurantii (Boyer de Fonscolombe) (Hemiptera: Aphididae)
Aphidius colemani Viereck (Hymenoptera: Braconidae); Lebanon, Syria
Aphidius matricariae (Hymenoptera: Braconidae); Lebanon, Syria
Ephedrus persicae Frogatt (Hymenoptera: Braconidae); Lebanon
Lysiphlebus fabarum Marshal (Hymenoptera: Braconidae); Lebanon[b]
Praon volucre; Lebanon[b]
Trioxys angelicae Haliday (Hymenoptera: Braconidae); Lebanon[b]

Solanaceae

Eggplant

Aphis gossypii (Glover) (Hemiptera: Aphididae); Iraq, Jordan, Lebanon, Saudi Arabia
Bemisia tabaci Gen. (Hemiptera: Aleyrodidae); Algeria[c]
Clitostethus arcuatus Rossi (Coleoptera: Coccinellidae); Iraq, Syria[c]
Orius albidipennis Reut. (Hemiptera: Anthocoridae); Iraq[b]
Leucinodes orbonalis Guen. (Lepidoptera: Pyralidae); Egypt, Lebanon, Saudi Arabia
Tetranychus urticae Koch (Acari: Tetranychidae)
Phytoseiulus persimilis (Acari: Phytoseiidae); Lebanon & Syria[b]

Potato

Gnorimoschema (*Phthorimaea*) *operculella* Zeller (Lepidoptera: Gelechiidae); Cyprus, Egypt, Iraq[b] & Jordan, Lebanon, Saudi Arabia, Syria
Chelonus phthoremiaeae Gahan (Hymenoptera: Braconidae); Tunisia
Macrosiphum euphorbiae (Thomas) (Hemiptera: Aphididae); Algeria[c]
Myzus persicae (Sulzer) (Hemiptera: Aphididae); Algeria[c], Lebanon, Saudi Arabia, Syria

Tomato

Aculops (= *Vasates*) *lycopersici* (Massee) (Acari: Eriophyidae); Lebanon, Saudi Arabia
Bemisia tabaci Gennadius (Hemiptera: Aleyrodidae); Egypt[c], Lebanon, Saudi Arabia, Syria, Yemen
Encarsia spp. (Hymenoptera: Aphelinidae); Jordan
Helicoverpa (*Heliothes*) *armigera* Hb. (Lepidoptera: Noctuidae); Egypt, Lebanon, Saudi Arabia, Syria, Yemen[b]
Liriomyza bryoniae Kalt. (Diptera: Agromyzidae); Iraq[c]

Urticaceae

Figs

Ceratitis capitata Weid. (Diptera: Tephritidae); Jordan, Syria[c]
Ceroplastes rusci L. (Hemiptera: Coccidae)
Ancytus sp.; Syria; Libya[c]
Coccidophaga scitula Ramb. (Lepidoptera); Lebanon
Scutellista cyanea (Motschulsky) (Hymenoptera: Pteromalidae); Jordan, Lebanon, Syria
Tetrastichus sp. (Hymenoptera: Eulophidae); Jordan, Lebanon, Syria
Ephestia cautella (Walker) (Lepidoptera: Pyralididae)
Bracon hebetor Say. (Hymenoptera: Braconidae); Iraq, Syria
Hypoborus ficus Er. (Coleoptera: Scolytidae)
Sycoster lavagnei (Hymenoptera: Braconidae); Lebanon
Rhycaphytoptus ficifoliae K. (Acari: Rhyncaphytoptidae); Iraq[b]

Silba adipata McAlpine (Diptera: Lonchaeidae); Iraq, Lebanon, Turkey

Mulberry

Icerya aegyptiaca Douglas (Hemiptera: Margarodidae)
Amblyseius swirskii Athias-Henriot (Acari: Phytoseiidae); Egypt[c]
Euseius scutalis (Acari: Phytoseiidae) (Athias-Henriot); Egypt[c]
Pseudococcus citri Risso (Hemiptera: Pseudococcidae)
Amblyseius swirskii Athias-Henriot (Acari: Phytoseiidae); Egypt[c]
Euseius scutalis (Acari: Phytoseiidae) (Athias-Henriot); Egypt[c]
Tetranychus urticae Kock. (Acari: Tetranychidae)
Amblyseius swirskii Athias-Henriot (Acari: Phytoseiidae); Egypt[c]
Euseius scutalis (Acari: Phytoseiidae) (Athias-Henriot); Egypt[c]

Vitaceae

Grapes

Colomerus (*Eriophyes*) *vitis* (Pangest) (Acari: Eriophyiidae); Lebanon
Euseius scutalis Athias-Henriot (Acari: Phytoseiidae); Jordan
Lobesia botrana Denis & Schiffermüller (Lepidoptera: Tortricidae); Iran[c], Jordan[c]
Ascogaster quadridentata (Wesmael) (Hymenoptera: Braconidae); Jordan, Syria
Bassus (*Microdus*) *dimidiator* (Nees) (Hymenoptera: Braconidae); Syria
Bracon brevicornis (Wesmael) (Hymenoptera: Braconidae); Syria
Coccinella septempunctata L. (Coleoptera: Coccinellidae); Iraq, Lebanon, Syria
Dibrachys boarmiae (Walker) (Hymenoptera: Pteromalidae); Syria
Pristomerus sp. (Hymenoptera: Ichneumonidae); Syria
Planococcus (*Pseudococcus*) *citri* (Risso) (Hemiptera: Psuedococcidae); Lebanon[b], Syria
Theresimima (*Procris*) *ampelophaga* B.-B. (Lepidoptera: Zygaenidae); Jordan, Lebanon, Syria
Viteus vitifolii (Fitch.) (Hemiptera: Phylloxeridae); Jordan, Lebanon, Syria

Miscellaneous

Stone fruit trees

Capnodis tenebrionis L. (Coleoptera: Buprestidae); Jordan[c], Lebanon, Syria
Capnodis carbonaria Klug. (Coleoptera: Buprestidae); Jordan[c], Lebanon, Syria

Storage pests

Beans (Leguminosaea)

Bruchus dentipes Baudi (Coleoptera: Bruchidae)
Triaspis thoracicus (Curtis) (Hymenoptera: Braconidae); Syria
Callosobruchus chinensis L. (Coleoptera: Bruchidae); Syria[b]

Chickpeas (Leguminosaea)

Bruchus dentipes Baudi (Coloeptera: Bruchidae); Syria[b]
Callosobruchus chinensis L. (Coloeptera: Bruchidae); Syria[b]
Trogoderma granarium Everts (Coleoptera: Dermestidae); Iraq[b]

Cotton (Malvaceae)

Tribolium castaneum (Herbst) (Coleoptera: Tenebrionidae)
Trichogramma principium (Hymenoptera: Trichogrammatidae); Iraq[b]

Cowpeas (Leguminosaea)

Collosobruchus maculatus F. (Coleoptera: Bruchidae); Iraq[b], Syria

Lentils (Leguminosaea)

Bruchus dentipes Baudi (Coleoptera: Bruchidae); Syria[b]

Callosobruchus chinensis L. (Coleoptera: Bruchidae); Syria[b]

Sesame (Pedaliaceae)

*Trog*oderma granarium Everts (Coleoptera: Dermestidae); Iraq[b]

Sunflower (Asteraceae/Compositae)

Trogoderma granarium Everts (Coleoptera: Dermestidae); Iraq[b]

Wheat (Gramineae/Poaceae)

Sitotroga cereallella (Olivier) (Lepidoptera: Gelechiidae); Iraq

Trogoderma granarium Everts (Coleoptera: Dermestidae); Iraq[b]

Vegetables

*Agrotis ipsilo*n (Rottemburg) (Lepidoptera: Noctuidae); Lebanon, Saudi Arabia, Syria

Apanteles ruficrus Hal. (Hymenoptera: Braconidae); Egypt

Earias biplaga Walker (Lepidoptera: Noctuidae); Egypt, Lebanon, Saudi Arabia, Syria

Empoasca lybica De Bergevin (Hemiptera: Cicadellidae); Egyptb, Lebanon, Saudi Arabia, Sudan, Syria

Tetranychus cinnabarinus (Boisduval) (Acari: Tetranychidae); Egypt[b]

Spodoptera exigua (Hb.) (Lepidoptera: Noctuidae); Egypt, Lebanon, Saudi Arabia, Syria

Trichoplusiani (Hübner) (Lepidoptera: Noctuidae); Egypt, Lebanon, Saudi Arabia

References

Al-Matni W, Samara H (2001) Natural enemies of insects recorded in Syria and neighboring countries. Version 2. Dar An-Nokhba, Damascus, Syria

Arab Journal of Plant Protection. A scientific journal published by the Arab Society for Plant Protection, Volumes 1 (1983)-14 (1996), 19 (2001). Beirut, Lebanon

Gerling D (1990) Whiteflies: their bionomics, pest status and management. Intercept Ltd., Andover, UK

Kawar NS, Al-Ajlan AM, Yassin M (1995) The most important insect and mite pests on major crops in the west region of Saudi Arabia. Ministry of Agriculture and Water Resources, Agricultural Research Center in Makka Al-Mukarrama and Jaddah, Saudi Arabia, and Food and Agriculture Organization (FAO)

Talhouk AS (2002) Insects and mites injurious to crops in middle eastern countries, 2nd edn. American University of Beirut Press. Beirut, Lebanon

Pest Species

Any species that humans consider to be undesirable. More often, a pest is considered to be a species that competes with humans for food, fiber, or shelter, or transmits diseases to humans or livestock, or affects the comfort of humans.

Petaluridae

A family of dragonflies (order Odonata). They commonly are known as graybacks.

► Dragonflies and Damselflies

Petiolate

Attached by a narrow stem or stalk (a petiole).

Petiole

Stalk that connects the leaf to a stem. In Hymenoptera, it is sometimes used to describe the first section of the narrow stalk-like abdominal segment, or "waist."

► Abdomen of Hexapods

Petrunkevitch, Alexander

Alexander Petrunkevitch was born at Pliski, Russia, in December 1875. He was born into a noble family, and at an early age displayed interest in both zoology and the literary arts. His liberal politics forced him to leave Russia, and he moved to Germany, where he came under the influence of August Weismann. He completed a Ph.D. dissertation in 1900 on the cytology and embryonic development of the honey bee, and married an American. They moved to the United States in 1903, and he became a lecturer at Harvard University in Boston, and then acting professor of Zoology at Indiana University, though he commuted regularly to Massachusetts to be with his wife, who had become ill. He moved to Yale University when his wife contracted tuberculosis, becoming an assistant professor in 1911 and a full professor in 1917. Petrunkevitch made important contributions to the study of arachnids. Among his important publications were "A synomic index-catalogue of spiders of North, Central and South America" (1911)," "On families of spiders" (1923), "Catalog of American spiders-part I" (1939), and "An inquiry into the natural classification of spiders, based on a study of their internal anatomy" (1933). He died in New Haven, Connecticut, on March 9, 1964.

Reference

Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Phacopteronidae

A family of bugs (order Hemiptera, superfamily Psylloidea).

► Bugs

Phage (Bacteriophage)

A virus that attacks bacteria. Frequently used as vectors for carrying foreign DNA into cells by genetic engineers.

Phalacridae

A family of beetles (order Coleoptera). They commonly are known as shining flower beetles.

► Beetles

Phagocytes

Cells that are capable of moving in the insect body and engulfing or destroying small foreign bodies such as microorganisms.

Phagostimulant

A substance that induces feeding.

Phagocytosis

The process of ingestion and digestion by cells, especially the ingestion or engulfing of microorganisms and other small particles by blood cells.

Phallus

The intromittent (copulatory) organ of insects; the aedeagus and any processes found at its base.

Phantom Crane Flies

Members of the family Ptychopteridae (order Diptera).

► Flies

Phantom Midges

Members of the family Chaoboridae (order Diptera).

► Flies

Pharate

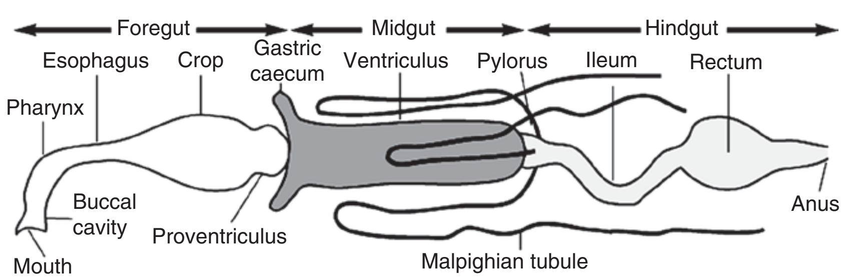
The stage at which molting has started but the insect has not yet cast off the old cuticle.

Pharynx

The anterior portion of the foregut immediately behind the buccal cavity (Fig. 31).

► Alimentary System

► Alimentary Canal and Digestion



Pharynx, Figure 31 Generalized insect alimentary system (adapted from Chapman, The insects: structure and function).

Phase Polymorphism in Locusts

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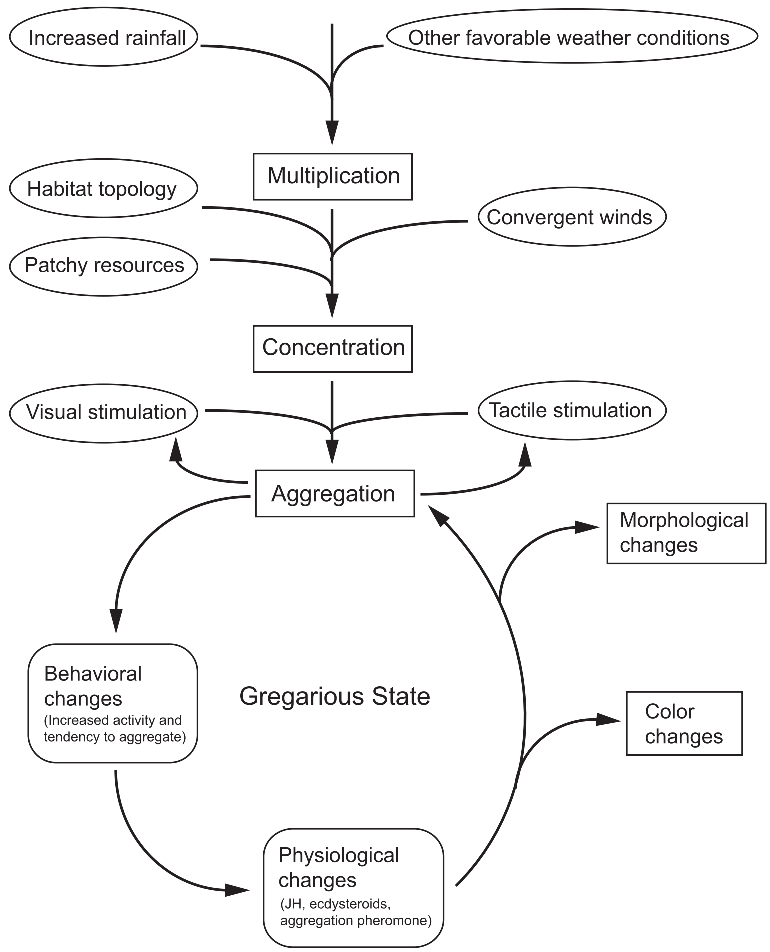
Insects regularly encounter large fluctuations in environmental conditions to which they must adapt in order to survive. Some of these conditions include temperature change, photoperiod, host plant quality and availability, and conspecific and heterospecific species density. These conditions can change rapidly and, in order to survive, insects must adapt to them within a single or only a few generations. One way insects can accomplish this is through a physiological change such as polymorphism. Polymorphism is the presence of multiple phenotypes of organisms in the same species, accomplished through differential gene expression. Polymorphism can affect several aspects of an insect's biology such as behavior, appearance, reproductive capability, or dispersal ability. This is often accomplished through a complex series of events, which at the most basic level involves differences in gene transcription and translation. Polymorphisms occur across the animal kingdom and, of course, in Insecta. Polymorphism affecting dispersal capability, often called dispersal phase polymorphism, occurs in Psocoptera, Thysanoptera, Hemiptera, Coleoptera, Diptera, Lepidoptera, and Hymenoptera. The variety of polymorphisms, and the broad range of taxa in which polymorphisms occur, implies that there must be some benefit in possessing the ability to change in response to environmental conditions.

Dispersal Polymorphism

Dispersal polymorphisms have been widely studied, and the knowledge gained has led to some insights into why a mechanism like polymorphism would evolve. A change such as an insect's ability to disperse should be related to large-scale changes in the environment that would necessitate dispersal to a new one. Therefore, dispersal should be essential in temporary habitats, but minimized in persistent habitats. However, this does not always hold true. Other factors such as crowding, host plant condition, temperature, and photoperiod have been shown to influence dispersal capability. These factors may either initiate or intensify the process.

Dispersal polymorphism is most easily recognized in insects as differences in wing size, but can also be expressed as differences in flight muscle mass, behavior, and storage and metabolism of energy reserves. Migration from an unsuitable habitat to a more suitable one requires relatively greater energy reserves. Many species exhibiting wing polymorphism have their flight capability negatively correlated with age at first reproduction and fecundity. Insects that show this negative correlation in having their macropterous forms less fecund than their brachypterous forms include grasshoppers, crickets (both Orthoptera), planthoppers, aphids, waterstriders, veliids, water boatmen, seed bugs (all Hemiptera), and pea weevils (Coleoptera). Other costs of being macropterous include decreased longevity, and reduced egg or offspring size. Negative correlations between dispersal ability and reproduction have led to the notion that there is a trade-off between flight capability and reproduction, two very energetically expensive processes. General maintenance costs in herbivorous insects can comprise up to thirty percent of their total energy budget. With such a large amount of resources being dedicated to maintenance, reducing the amount of tissue having to be maintained would be an easy way to save resources. In brachypterous forms, this is exactly what happens. Reduction of wing size and flight muscle mass saves energy in the production of these tissues and reduces the overall costs of maintenance in the insect. Reduction of tissues can occur during development or after development, by breaking down already-present tissues. Histolysis of flight muscle in the Colorado potato beetle, *Leptinotarsa decemlineata*, before it overwinters is thought to conserve energy. Flight muscle proteins are adsorbed by growing oocytes in *Dysdercus cingulatus* bugs. This example provides evidence that energy saved from reducing flight muscle mass can be used directly in the production of oocytes, and that a trade-off between dispersal ability and reproduction is possible. In terms of evolution, it would make sense that those insects not needing to disperse or migrate should not waste energy on producing and maintaining expensive flight muscles. However, there is another aspect that must be considered, and that is the timing of phase determination, or the time an individual becomes committed to a particular phase. In general, there are two modes of phase determination timing, early and late. Each of these modes has particular evolutionary advantages and disadvantages. Early-stage determination allows maximum commitment of resources and more efficient morphs. This can be beneficial in environments that change slowly over time, but when environmental changes occur rapidly it would be more advantageous to be able to adapt quickly. Late-stage development allows this adaptation to sudden changes in conditions.

There are many reasons why it might have been advantageous for polymorphism to have evolved. In fact, the diversity of taxa possessing polymorphism, and variety of mechanisms and stimuli involved, suggest it has evolved independently many times throughout Insecta. One group of insects in which development of polymorphism has been advantageous for is the orthopteran family Acrididae, particularly the locusts. Locust phases exhibit marked differences in behavior, physiology, biochemistry, morphology, and pigmentation. These differences were so dissimilar that locusts exhibiting them were thought to be different species. Boris A. Uvarov realized that the different phases were actually the same species and coined the term phase polymorphism for referring to the shifts in phase occurring in locusts (Fig. 32).



Phase Polymorphism in Locusts, Figure 32 **Major component processes of phase transformation in locusts.**

Environmental Factors Inducing Phase Differentiation in Locusts

Phase determination in locusts is largely based on the degree of crowding or density of the locusts, and the length of time to which they are exposed to this density. Increases in favorable weather conditions such as rainfall and food quality can cause a general increase in abundance of individuals. With increased population numbers, crowding of individuals is more likely, and can be promoted by such things as convergent winds, habitat topologies, and patchy distributions in harborages, food distribution, and oviposition sites. As crowding occurs due to these factors, behavior is altered to promote further crowding. This causes a positive feedback loop that, in combination with continued favorable environmental conditions, pushes the population further towards the gregarious phase.

Differences Between Phase States: Solitarious Versus Gregarious

Phase polymorphisms often exhibit a continuum of states with two extremes, one being the solitarious state and the other the gregarious state (Table 11). The intermediate state is sometimes called "transiens." In populations with low densities, individuals are in the solitarious state and are relatively inactive, exhibit cryptic coloration, and are widely dispersed, avoiding one

Phase Polymorphism in Locusts, Table 11 Some differences between locust phases

	Solitarious	Gregarious
Behavior		
Tendency to aggregation	Absent	Present
Aggressive toward conspecifics	Yes	No
Activity level	Lower	Higher
Activity rhythm	Not synchronized	Synchronized
Adult flight	Nocturnal	Diurnal
Physiology		
Hemolymph polypeptides	3 specific	17 specific
Juvenile hormone levels	Higher	Lower
Nymphal ecdysteroid levels	Lower	Higher
Adult ecdysteroid levels	Higher	Lower
Lipid reserves	Lower	Higher
Carbohydrate level	Lower	Higher
Respiratory rate	Slower	Faster
Adipokenetic reaction	Lower	Higher
Glycolytic enzyme levels	Lower	Higher
Early mortality of young	Higher	Lower
Extra larval molt	Yes	No
Nymphal development rate	Slower	Faster
Adult sexual maturation rate	Faster	Slower
Fecundity	More, smaller eggs	Fewer, larger eggs
Life span	Longer	Shorter
Nymphal coloration	Cryptic/Uniform	Dark patterns on light background
Adult coloration	No change	Changes with sexual maturation
Morphology		
Overall size	Larger	Smaller
Head	Smaller	Larger
Tegmen	Shorter	Longer
Hind femur	Longer	Shorter
Sexual-size dimorphism	Pronounced	Slight

another. In populations with high densities, individuals are in the gregarious state and are relatively active, exhibit dark coloration and markings (depending on the species), and are crowded on patchy resources where they tend to aggregate.

Developmental and Reproductive Differences

Solitarious and gregarious locusts exhibit differences in several characters, two of these being developmental rate and fecundity. For example, *Schistocerca* *gregaria* (Orthoptera: Acrididae), when reared under isolated conditions, undergoes an extra larval molt. The incidence of the extra larval molt increases with the duration of isolated development. In the grasshopper *Humbe tenuicornis* (Orthoptera: Acrididae), laboratory reared, adult isolated females are significantly larger and live longer. In general, adult solitarious females of grasshoppers and locusts mature more rapidly and deposit more eggs than do adults from crowded culture. The onset of egg production begins 5 days earlier in solitarious *S. gregaria* than in gregarious forms. Solitarious females of *S. gregaria* produce a greater number of eggs per pod than gregarious females, and have an increased number of ovarioles and a decrease in the number of nonfunctional oocytes.

Metabolic Differences

Another way in which the phase states of locusts differ is in the amount of metabolically derived storage compounds present, and the ability to convert these compounds to energy. Nymphs of solitarious *S. gregaria*, when compared to gregarious individuals, show low carbohydrate levels in the hemolymph and a reduced respiratory rate as evidence of a reduced metabolism. In nymphs of *Locusta migratoria* (Orthoptera: Acrididae) and *Aiolopus thalassinus* (Orthoptera: Acrididae) reared at high population density, CO_2 release is significantly higher than those reared in solitude. Gregarious nymphs and adults of *L. migratoria* show increased lipid levels in their hemolymph when compared to solitarious individuals. In *S. gregaria*, newly emerged solitarious females have relatively smaller fat bodies and less absolute triacylglycerol reserves. Lipid storage is an important factor in an insect's ability to migrate long distances, and phase specific differences in lipid content of the hemolymph may be partly responsible for differences in dispersal ability of the phases. Locusts can also differ in their ability to utilize ingested and stored nutrients, which could also affect dispersal ability. The adipokenetic reaction, which is responsible for the mobilization of lipids, can be induced by a 60 min flight in the laboratory. The reaction is distinctly higher in gregarious females than in solitarious females of *S. gregaria*. In *L. migratoria*, glycolytic enzymes are expressed at different levels in solitarious and gregarious forms. Different isoenzymes of aldose appear at high and low densities, and 2-glycerol-3-phosphate dehydrogenase isoenzymes (enzymes that break down compounds important in lipid metabolism) are higher in low-density larvae. Physiological changes such as these tend to change rapidly in response to changes in density. Such evidence provides more support for the idea that gregarious locusts are better equipped for migratory flights. Paired with the fact that fecundity is reduced, it provides additional evidence for a trade-off between flight capability and reproduction.

Morphological Differences

Phase differences in physical characteristics such as tegmen and femur length are very common in locusts, and are often used in studies to define the phase state of an individual. However, morphometrics should not be used in studies where immediate changes must be recorded, for it may take several generations to see the full effect of treatment on morphometric measurements. For example, in a recent study, two natural subpopulations were brought into laboratory, reared, and phase state determined. The gregarious subpopulation was reared under crowded conditions, while the solitarious subpopulation was reared in isolation. The F/C (femur/width of head between the eyes) ratios of both the original populations were within the solitarious range. But, after two laboratory generations, the F/C ratios of gregarious females had more gregarious F/C ratios than when compared to their parents, or to the solitarious population. What advantages such changes might provide are uncertain, but in locusts it seems to enhance dispersal ability. Locust phases have also been shown to differ in the selectivity and abundance of antennal sensilla. It is thought that such differences might influence density dependent responses by changing the way an individual perceives certain stimuli.

Chromatic Differences

Some of the most obvious characters by which gregarious and solitarious individuals differ are differences in background color, and presence and intensity of dark markings on the body. In locusts, cryptic coloration is generally found in low density populations. Solitarious nymphs of *L. migratoria* show various body colors, depending on habitat, some of these include green, brown, red, and black. In *S. gregaria*, solitarious nymphs are green for the most part, while gregarious nymphs are noticeably melanized. In both of the aforementioned species, gregarious nymphs become more similar to each other in coloration, with distinct black patterns on an orange background. For locusts which tend to bask, darkened cuticle could improve absorption of solar radiation adsorption and cause an increase in nymphal development rate. Such darkening of the cuticle could have been a mechanism evolved to offset the reduced development rates and reproduction exhibited by many gregarious locusts. Research up to this point has shown there to be several compounds responsible for controlling the pigmentation between different phases in locusts. Some of these include juvenile hormone and [His7]-corazonin.

Behavioral Differences

While the changes in color and morphology are easily quantified and evaluated, they may take several generations to manifest themselves. Moreover, they do not necessarily occur in all locusts. A variant population of *L. migratoria* in Israel shows no morphometric or chromatic responses to density. It does, however, show a behavioral response. Behavioral changes are imposed rapidly and are one of first characters to vary in response to density changes. This makes behavioral differences relatively useful in studies, where they can help separate gregarious from solitarious states. The disadvantage of using behavioral differences to determine phase state is that they are hard to quantify and measure accurately, and the measurements taken can be subjective. Another factor that may hinder quantifying behavior is that relative intensity of behavioral responses depends on the degree and duration of crowding experienced by the insect, and by previous generations, and that behavior tends to be the most labile component in phase transition.

Many different aspects of behavior vary between gregarious and solitarious individuals, such as aggregation, general activity level, mating, and oviposition, with aggregation being the most prominent and well studied. Locusts in the gregarious phase show a propensity to aggregate and form bands or swarms. Crowded insects are generally more active and orient towards other individuals, which may lead to behaviors associated with aggregation, such as marching and swarming. The exact opposite occurs in solitarious locusts, which tend to avoid one another and even show aggressive behavior toward each other. Reproductive behaviors such as mating and oviposition are also phase dependent. For male locusts under crowded conditions, mate-finding is not an issue, and sperm competition becomes their main dilemma, which increases mate guarding behavior. Female *S. gregaria* locusts under crowded conditions deposit eggs at common sites, and this aggregated oviposition may be pheromone mediated.

Stimuli Inducing or Enhancing Phase State

The induction of a phase state involves a series of steps. The first is stimuli that induce the phase change. The second is the physiological processes that are initiated by these stimuli. The third is the visible change or difference that occurs between phases. Following are four types of stimuli that occur in a group of locusts that induce or enhance phase state in locusts: visual, auditory, chemical, and tactile.

Tactile Stimuli

Tactile stimulation seems to be the most potent stimulus inducing the gregarious state, with all other stimuli further enhancing its effect. Even tactile stimulation with paper maché balls or millet seeds can induce a phase change. This is not to say that only tactile stimulation induces the gregarious phase. Many stimuli can initiate a phase change when in combination with each other, while a few can initiate a weak response. Nymphs of *S. gregaria*, when reared in contact with other locusts (either conspecific or heterospecific), develop black markings. However, full development of the yellow background color in final instar nymphs only occurs when nymphs are reared with conspecifics. Visual and chemical stimuli can cause black coloration, but black coloration is not enhanced by the addition of tactile stimulation. Tactile stimulation inducing gregarious characteristics is particularly effective on the hind femora in *S. gregaria*, where both exteroceptive and proprioceptive mechanosensory components were found to be involved, traveling through leg nerves. Tactile stimulation is a key component in the positive feed-back loop that drives a population towards being more gregarious. As locusts get closer, physical contact induces a behavioral change which brings them even closer together increasing the stimulus which further alters their behavior to the gregarious state.

Visual Stimuli

Visual stimuli play an important role in attraction in gregarious locusts and repulsion in solitary locusts over short distances. By influencing the density of locusts, by either attraction or repulsion, visual stimuli can indirectly affect phase state. However, there is some evidence that visual stimuli are important in determination of phase state. In *S. gregaria*, visual and olfactory stimuli are weakly stimulating when presented alone, unless the period of exposure is greater than 24 h, in which case visual stimuli are moderately stimulating. But, when presented together, they have marked effects on behavior, causing individuals to become more gregarious. In nymphs of *S. gregaria*, olfactory contact with gregarious conspecific or heterospecific locusts fails to induce a behavioral change, but, when presented with visual and olfactory stimuli, behavioral gregarization occurs. This clearly shows that visual and olfactory stimuli are necessary for shifting phase states in the absence of tactile stimuli.

Chemical Stimuli: Olfactory and Contact Chemicals

In general, there are two types of chemical signals an insect can perceive, those produced by volatile chemicals and those produced by contact chemicals. The roles that chemical signals play in phase determination in locusts have been strongly debated, and the debate has been fueled by conflicting evidence from different studies.

One chemical that is currently under debate is phenylacetonitrile. Gregarious males of *S. gregaria*, when becoming sexually mature, release large amounts of a blend of chemicals thought to be active as an aggregation pheromone. Phenylacetonitrile was originally described as the main component of this aggregation pheromone blend, which also contains low amounts of phenol, guaiacol, and benzaldehyde. This aggregation pheromone supposedly can cause locusts to aggregate and perhaps play an important role in arrestment and recruitment of solitary individuals into gregarious groups.

However, in some studies phenylacetonitrile has no attractiveness to fifth instars, or young or mature adults of either sex, suggesting that phenylacetonitrile is not involved in aggregation. An alternative hypothesis as to the function of phenylacetonitrile is that it may function in reproductive behavior under crowded conditions, because of its association with male maturation and increased competition. It has been reported that phenylacetonitrile is released only if other mature males are present, and the amount released depends on the number of males present. Phenylacetonitrile may also act as an antiaphrodisiac by "hiding" the female and preventing other males from attempting to mount the guarded female, enhancing their mate guarding ability. It also prevents homosexual encounters, which could occur often under crowded conditions. However, it is possible that phenylacetonitrile can affect both aggregation and reproductive behavior, and that the response is somehow dependent on age and level of juvenile hormone. Regardless of its function, changes in emission of aggregation pheromone by adult desert locusts occur rapidly in response to shifts from crowded to solitary rearing conditions, and vice versa. Aggregation pheromone production is so sensitive to density change that there is greater production at a density of four than at two, and it is because of this sensitivity that some have suggested pheromone production be used as a way to measure phase change.

Non-volatile contact chemicals may also play a role in phase determination. Cuticular hydrocarbons have a gregarizing effect on behavior in adult *S. gregaria*, though exposure to cuticular hydrocarbons, either as a single treatment or in combination with mechanical or visual treatments, does not elicit any measurable behavioral gregarization in fifth instars of *S. gregaria*. In another study, locust odor caused an attraction to stimulus source but did not have a gregarizing effect, while chemotactile stimuli had a gregarizing effect but was not attractive to locusts. While the action of cuticular hydrocarbons is debatable, one thing is for sure, and that is cuticular hydrocarbons of gregarious *L. migratoria* and S. *gregaria* differ considerably, as full development of the yellow background color in the last instar of *S. gregaria* nymphs only develops when they are in contact with conspecifics. This implies the presence of species-specific chemical cues or contact pheromones.

Some Physiological Mechanisms Behind Phase Polymorphism

At the core of all the different characteristics that separate gregarious and solitarious locust, and the stimuli which induce these differences, are the physiological and biochemical reactions that occur within the organism. In *S. gregaria*, 17 polypeptides are specific to the gregarious phase and three are specific to the solitarious phase. The presence and quantity of these polypeptides are affected by rearing density and juvenile hormone. This is clear evidence that the different phases of locusts exhibit differences in gene transcription and/or translation. Differences in physiology between gregarious and solitarious phases include hemolymph polypeptides, the density dependent yellow protein, neurotransmitters, juvenile hormone, ecdysteroids, neuropeptides such as corazonin, neuroparsins, and insulin, pheromones such as phenylacetonitrile, and protease inhibitors. Hormones have been especially well investigated.

Juvenile Hormone (JH) and its Analogues

The function of JH has been researched extensively in insects, and its function in phase polymorphism is no exception. JH has been shown to affect several aspects of the differences between phase states. When gregarious male locusts are treated with JH, nine of the 17 gregarious-specific polypeptides are no longer expressed, and two of the three solitarious-specific polypeptides are newly expressed. Thus, JH appears to have a solitarizing effect. Cryptic coloration that is associated with the solitary phase, such as green, is induced by the application of JH in *L. migratoria*, *S. gregaria*, and *S. americana*. JH and its analogues have been shown to have a solitarizing effect on the maximum weight and weight gain in *S. gregaria*. Application of JHIII to gregarious females increases weight gain to maximum weight by 4 days. BASF 228743 (a JH analogue) shows a stronger effect than JHIII, and allows gregarious females to attain a higher maximum weight than solitarious females. JH analogues, and not so much JHIII, reduce aggregation in *S. gregaria* and *L. migratoria* larvae, again a solitarizing effect.

JH and JH analogues have also been shown to take part in the energetic trade-off between flight capability and reproduction. Most of the evidence for this has come from studies on *S. gregaria*. Treatment of gregarious females with JH or JH analogous reduces fat body content levels to levels characteristic of solitarious females. The application of JH also suppresses the adipokenetic reaction in gregarious females as compared to gregarious control females. The appearance of vitellogenin in hemolymph occurs at 7 days for solitarious females, and at 12 days for gregarious females. Application of JH or JH analogous causes gregarious time periods to be more like solitarious ones. Treatment with JH or JH analogous causes an early onset of oocyte development in gregarious females as compared to untreated gregarious females. JH seems to be in control of two very important mechanisms that regulate a trade-off between energy storage for flight, and energy utilization for reproduction. The effects of JH on these processes also seem to be solitarizing, and it may be safe to say that, in general, JH is responsible for several characteristics exhibited by the solitarious phase.

Ecdysteroids

Originally, ecdysone was identified as an insect molting hormone, but ecdysone also occurs in adults in which no molting occurs. Therefore, there must be some other purpose for ecdysone to be present. It is known that prothoracic glands in locusts persist into adult at least until sexual maturation occurs. However, they do not release any significant amount of ecdysteroids in male or female, solitarious or gregarious adult *S. gregaria*. The removal of prothoracic glands from adult *L. migratoria* does not affect the titre of ecdysteroids in the hemolymph. Therefore, ecdysteroids must be originating from some other tissue. Indeed, ecdysteroids are found to be present in eggs and the ecdysteroids originate from the ovaries, which can release the chemical into the hemolymph in some species.

One important function of ecdysteroids could be the control of vitellogenin production, which was documented in *L. migratoria*. The same may be true for *S. gregaria*. Ecdysteroid titres of adult solitarious *S. gregaria* are much higher than in gregarious adults. Maximum levels of hemolymph ecdysteroids in gregarious females are about 150 ng of 20-hydroxyecdysone/ml, as compared to 400 ng of 20-hydroxyecdysone/ml found in solitarious females. There are two peaks in the ecdysteroid titre in *S. gregaria* males and females. In females, the first peak occurs with the first release of vitellogenin synthesis, while the second is timed with egg chorionation. In males, the first peak may control spermatogenesis and accessory gland function, while the second peak coincides with production of pheromones involved in aggregation and maturation. Thus, ecdysteroids are intimately involved in sexual maturation and perhaps interact with JH.

Corazonin

Corazonin is a neurohormone often associated with the corpus cardiacum, and it and similar compounds occur in many arthropods including crustaceans. In insects, it most commonly occurs as one of two forms, [His7]-corazonin or [Arg7]-corazonin. [His7]-corazonin was first discovered in *S. americana*. At the time of discovery, however, its function was unknown. [Arg7]-corazonin, a variant of corazonin that differs by a single amino acid (arginine instead of histine) was first isolated from the corpus cardiacum of the American cockroach, *Periplaneta americana*, as a potent cardiostimulatory peptide. Later studies showed that neither form of corazonin had cariostimulatory effects on *S. americana*, leaving its function in locusts unknown. Subsequent studies have shown that corazonin affects dark pigmentation in locusts. The albinism in the well known Okinawa strain of

L. migratoria is caused by a deficiency of peptides present in the central nervous system, one of these being corazonin. Implantation of a brain or corpus cardiacum taken from normal individuals, *S. gregaria*, other acridids, cockroaches, katydids, crickets, and moths, or injection of methanolic extract, induces dark color in albinos. Injection of [His7]-corazonin, at doses as low as 10 fmol (femtomole, 10^{-15}), induces dark coloration in nymphs of both *L. migratoria* and *S. gregaria*. The response to corazonin is dose dependent, and the higher the dose the darker the color, with very high doses turning most species completely black. Timing of injection is also important. As time of injection is delayed individuals become less black and develop lighter color backgrounds with dark markings. Therefore, both the amount and timing of corazonin present are important in causing the dark coloration exhibited by many gregarious locusts. Corazonin may also have gregarizing effects on behavior and morphological characters such as the number of antennal sensilla.

Proliferation of the Gregarious State

Changes in a locust's phase are not only influenced by the individual's crowding experience, but also by its parents' exposure. This may help explain why locust plagues can persist for several years. Boris A. Uvarov was one of the first scientists to mention that the parental experience of crowding may be transmitted to the next generation of locusts. Some of the first evidence for this was the discovery of behaviorally active compounds that elicit aggregated oviposition are found in the froth of egg pods and include acetophenone and veratrole. Additionally, straight chain unsaturated ketones occur in the sand around oviposition sites and may increase the aggregation response. However, the color and gregarious state of hatchlings is not directly related to the density of egg pods in the area, but is more heavily influenced by the crowding experienced by the adult females. Perhaps the crowding of egg pods is a way of promoting gregarization after hatch by increasing the density of hatchlings in a particular area. It may be possible that these compounds have multiple functions, acting as an attractant for oviposition and as a gregarizing factor for newly hatched nymphs. In response to crowding, accessory glands produce water soluble compounds that can be found in the egg foam that result in the gregarization of developing hatchlings. These compounds were shown to be effective only if present in the first few hours after oviposition. It is unclear if the aforementioned compounds are identical to the oviposition aggregation compounds mentioned earlier.

Compounds found in the egg foam are not the only chemicals responsible for the gregarization of newly hatched nymphs. The hatchlings of gregarious females contain five times more ecdysteroids than those of solitarious females. Eggs of gregarious and solitarious females contain similar ratios of ecdysteroids, but occur at significantly higher levels in the eggs of gregarious females. Eggs from solitary females that experience crowding soon before oviposition show no increase in the amount of ecdysteroid present, suggesting the necessity for a prolonged exposure to crowding. Over incubation time, the change in levels of ecdysteroid content of eggs from gregarious females does not follow the same pattern as levels in eggs from solitarious females. Solitary eggs show a continuous increase in the levels of ecdysteroids, while gregarious eggs show two peaks followed by a decline in ecdysteroid content. This may help explain why adult solitarious locusts have high levels of ecdysteroids while gregarious locusts have low levels. The role of ecdysteroids in the proliferation of the gregarious state is not yet completely understood and it is unclear why ecdysteroid level would differ from egg and nymphal stage to adulthood. What is certain is that the transition to and subsequent retention and proliferation of the gregarious state contains a multitude of interactions that should be further studied.

► Polyphenism in Insects and Juvenile Hormone (JH)
► Corazonin

References

Applebaum SW, Heifetz Y (1999) Density-dependent physiological phase in insects. Ann Rev Entomol 44:317–341

Breuer M, Hoste B, De Loof A (2003) The endocrine control of phase transition: some new aspects. Physiol Entomol 28:3–10

Hassanali A, Njagi PGN, Bashir MO (2005) Chemical ecology of locusts and related acridids. Ann Rev Entomol 50:223–245

Simpson SJ, Sword GA, De Loof A (2005) Advances, controversies and consensus in locust phase polymorphism research. J Orthoptera Res 14:213–222

Zera AJ, Denno RF (1997) Physiology and ecology of dispersal polymorphism in insects. Ann Rev Entomol 42:207–230

Phasic Receptors

Sensory neurons that adapt rapidly to continuing steady stimuli, with the receptor potential falling, and the neuron becoming relatively insensitive. (contrast with tonic receptors).

Phasmatidae

A family of walkingsticks (order Phasmatodea). They commonly are known as winged walkingsticks.

► Walkingsticks and Leaf Insects

Phasmatodea

An order of insects. They commonly are known as walkingsticks and leaf insects.

► Walkingsticks and Leaf Insects

Phenacoleachiidae

A family of insects in the superfamily Coccoidae (order Hemiptera).

► Bugs

Phengodidae

A family of beetles (order Coleoptera). They commonly are known as glowworms.

► Beetles

Phenogram

A branching diagram that links different taxa by estimating overall similarity based on data from characters. Characters are not evaluated as to whether they are primitive or derived.

Phenological Asynchrony

Lack of simultaneous occurrence between an insect and its host, or lack of correspondence between traits of organisms (contrast with phenological synchrony).

Phenological Synchrony

Seasonal correspondence between an insect and its host, or seasonal correspondence between traits of organisms (contrast with phenological asynchrony).

Phenology

The seasonal life history of a plant or animal, especially in relation to weather and climate.

Phenology Models for Pest Management

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All living organisms use various "substances" for their energy, body growth, and tissue maintenance.

Enzymes control the use of those substances. Enzymes are very large, complex protein molecules that are formed within cells.

Enzymes have very important roles to play within the life of an organism. In the most general terms, they function to increase the rate of various chemical reactions (catalysts). In more specific terms, they are involved in the removal of electrons from some chemical compounds, the transfer of chemical groups from some compounds to others, the "breaking apart" of larger molecules (digestion), and the linking together of some molecules. Their function within an organism is affected by several factors, one of which is temperature.

For those reactions in which enzymes are involved, there is a range of temperatures within which they will take place. For temperatures that are less than the least value in that range, no reactions will occur. For temperatures that are greater than the greatest value in that range, the enzyme is denatured and coagulates, so no reactions will occur. For temperatures within that range, the rate of reactions increases with increasing temperatures.

The most general measure of enzymatic activity within an organism is, of course, "growth." Growth can be measured in many ways, two of which are the length or height of an organism, and its weight. The growth of an insect to certain discrete stages, such as the larval, pupal, or adult stages, is often referred to as "development." When development is linked with temperature, it is referred to as "phenology."

Growth and development of some organisms, such as humans, may be independent of the temperature that is outside their bodies because their body temperature is fairly constant and always warm. Such organisms are called "homoiotherms." Due to their relatively constant cellular temperatures, the growth of homoiotherms proceeds at a constant rate which can be predicted by "calendar time" (i.e., days, weeks, months, years).

In contrast, development of some other organisms, such as insects, cannot be predicted using calendar time because their body temperature is not maintained at a constant, warm level. Rather, their body temperature largely fluctuates with environmental temperatures. Such organisms are called "poikilotherms." As the cellular temperatures of poikilotherms are not constant, and the level of enzymatic activity is linked with environmental temperatures, their growth and development can usually be predicted through "thermal time."

Thermal time is calculated by first determining the amount of heat that is experienced during a 24 h period. That heat can be expressed as units of heat, or "heat units," also known as degree-days, day-degrees, and thermal units (more on that later). Thermal units are daily amounts of the total heat needed for a poikilotherm to develop to a given growth stage. The total heat needed before a poikilotherm will grow to that stage is sometimes called the effective cumulative temperature, required degree-days, or required thermal summation.

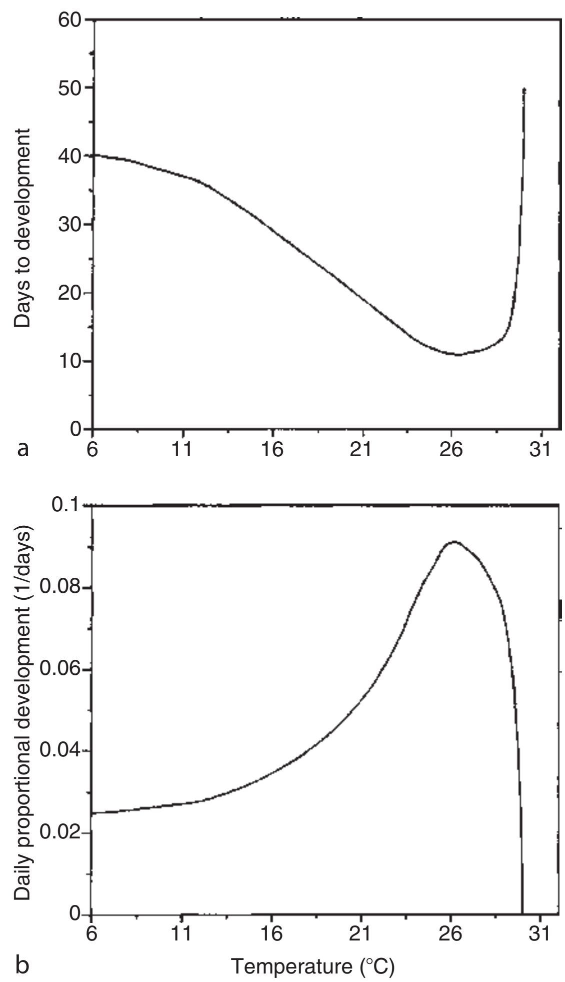
Thermal time can be used to predict the growth of an individual insect by having pest managers calculate and sum thermal units, from one 24-h period to another, until that sum equals the required thermal summation; the date on which that occurs is, theoretically, the date on which the growth of that insect has reached a specific stage. Pest managers often wish to predict insect developmental events, such as egg hatch, which can signal the onset of crop damage.

Growth and Development of Populations

Knowledge of how temperatures influence the growth and development of just one insect can also be used to predict the growth and development of many insects of the same species (population). Measures used to predict the development of populations, however, necessarily differ from those that are used to predict the development of individuals. This is so because pest managers who want to predict the date on which just one larva will develop to, for example, its third instar would calculate and sum thermal units, beginning at oviposition, and declare that individual as being in the third instar on the date that summed thermal units equals the required thermal summation. For a population, however, numerous eggs will be laid over several days or weeks. Consequently, individuals that hatch from the first eggs laid will develop to the third instar sooner than will individuals that hatch from the last eggs laid. Thus, when predicting developmental events for populations, pest managers may want to determine, in the context of this example, the date on which those first larvae develop to the third instar. Other population events, such as the peak occurrence of third instar larvae, may also be predicted. This process of calculating and summing thermal units, until they reach the required thermal summation, for the purpose of predicting a population event, is called phenological modeling, and the models used for making such predictions are called phenology models. Phenology models can be constructed through the conduct of laboratory experiments or field studies.

Constructing Phenology Models Through the Conduct of Laboratory Experiments

When constructing phenology models through the conduct of laboratory experiments, several environmental chambers are used at the same time, with each being set at a different temperature. Temperatures should vary widely so as to encompass the extremes within which enzymatic activity occurs. Next, a laboratory colony of the insect is accessed, with many individuals being used in the study (experimental subjects). Then, experimental subjects are divided into as many groups as there are chambers, with each group being placed into its respective chamber. Next, all individuals are provided with sustenance (either artificial diet or a host), and monitored daily. The number of days required for each individual to grow to a given stage is then recorded. If the average or median of those days is calculated and graphed on temperatures, the resulting chart should look like that shown in the following figure (responses of experimental subjects that did not develop to the desired growth stage, at the coldest and warmest temperatures, were excluded from this graph). The upper portion of the figure (Fig. 33) shows that the number of days needed for insect growth to a given stage decreased with increasing temperatures, up to a point, after which the number of days increased; that increase was caused by temperatures being so warm that basic physiological processes were disrupted, causing retarded growth and death.

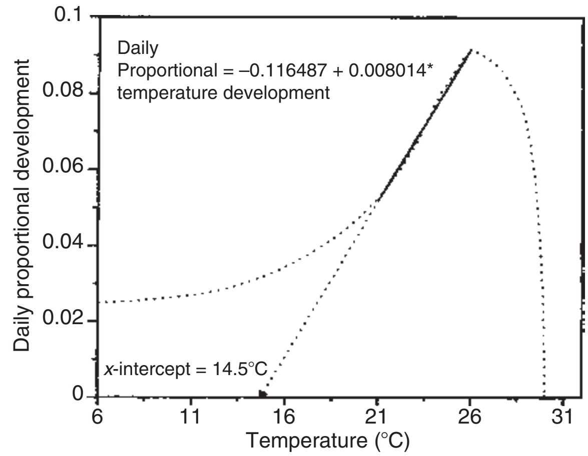


Phenology Models for Pest Management, Figure 33 Average days needed before a hypothetical insect will to develop to a certain growth stage, at various temperatures (A), and the inverse of those days (B), which expresses development on a daily basis.

Such information is not directly used to predict insect development. However, the information can be used to predict insect development if pest managers invert those values to express growth on a daily basis (the lower portion of the figure). Then, either a linear thermal unit function or a nonlinear developmental function is fitted to part or all of the data; that function is then used to predict insect phenological development.

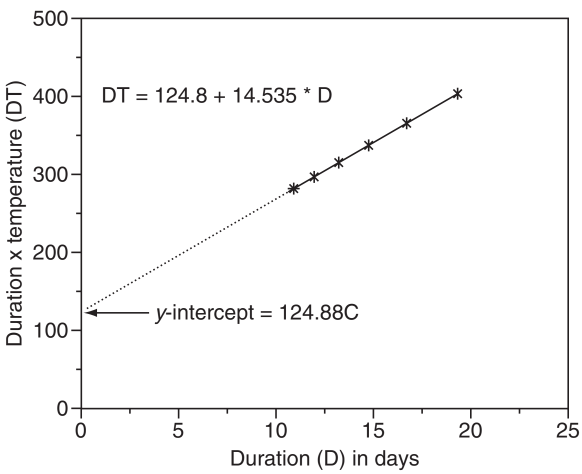
Predicting Insect Development with a Linear Thermal Unit Function

A linear thermal unit function is calculated by trimming the nonlinear portion from the relationship, and mathematically fitting a straight line to what is left. The resulting "straight line" is then extrapolated to where it crosses the x-axis (x-intercept); the temperature corresponding with that point is the developmental zero temperature or lower developmental threshold (Fig. 34). Hypothetically, that value is the lowest temperature at which insect growth will occur. Next, the required thermal summation is calculated. One way to do that is to invert the value of the slope from the straight line (i.e., 1/0.008014 = 124.8°C). Another way to do that is to multiply the effective temperature of each growth chamber (effective temperature = temperature of growth chamber–lower developmental threshold) by the average or median number of days that were required for development (Fig. 35). A third way to do that is to multiply each average or median number of days that were required for development by their respective temperature, then calculate a straight line between that product and the average or median number of days that were required for development. When that is done, the point where that line crosses the y-axis (y-intercept) (124.8°C) is the required thermal summation and the slope of that line (14.5°C) is the lower developmental threshold. Regardless of how the required thermal summation and lower developmental threshold are calculated, those values are then used to predict phenological events in the field.



Phenology Models for Pest Management, Figure 34
One way the lowest temperature at which insect development will first occur (lower developmental threshold) can be estimated is to trim the nonlinear portions from the daily developmental curve, then mathematically fit a straight line to the rest; the lower developmental threshold is the temperature where the straight line crosses the x-axis (14.5°C), and the total amount of heat needed for the insect to develop is the inverse of the slope (i.e., 1/0.008014 = 124.8°C).

That is done by first obtaining average daily temperatures from locations where the predictions are to be made. One way to do that is to add the daily maximum and minimum temperatures together, then divide that sum by two ("rectangle" method). There are other ways that can be done, one of which is to use a "sine-wave" method. Next, daily thermal units are calculated by subtracting the lower developmental threshold from the average daily temperature; if that difference is less than zero, daily thermal units are set equal to zero. Thermal units are calculated for each 24-h period and summed until they equal the required thermal summation. Theoretically, the date on which that happens is the date on which the developmental event occurs.



Phenology Models for Pest Management, Figure 35
Another way the lowest temperature at which insect development will first occur (lower developmental threshold) can be estimated is to trim the nonlinear portions from the relationship, multiply the average (or median) days to development (D) by their respective temperatures (T), and mathematically draw a straight line between that product and D; the lower developmental threshold is the slope of that straight line (14.535°C), and the total amount of heat needed for the insect to develop is the value for DT where the straight line crosses the y-axis (124.8°C).

Predicting Insect Development with a Nonlinear Developmental Function

Nonlinear developmental functions can be constructed by fitting a mathematical equation to both the linear and nonlinear portions of the relationship curve. Several such equations could be used to do this, some of which are based on theory (theoretical equations), and others are based on fitting techniques (empirical equations). In addition, some of these equations will provide estimates of the lower developmental threshold. Whichever type of equation is chosen, it is then used to calculate proportional insect development, given some measure of daily heat. Such calculations are made for each 24 h period, with those proportions being added, from 1 day to the next, until that sum equals 1.0. Theoretically, the date on which that sum equals 1.0 is the date on which the phenological event occurs.

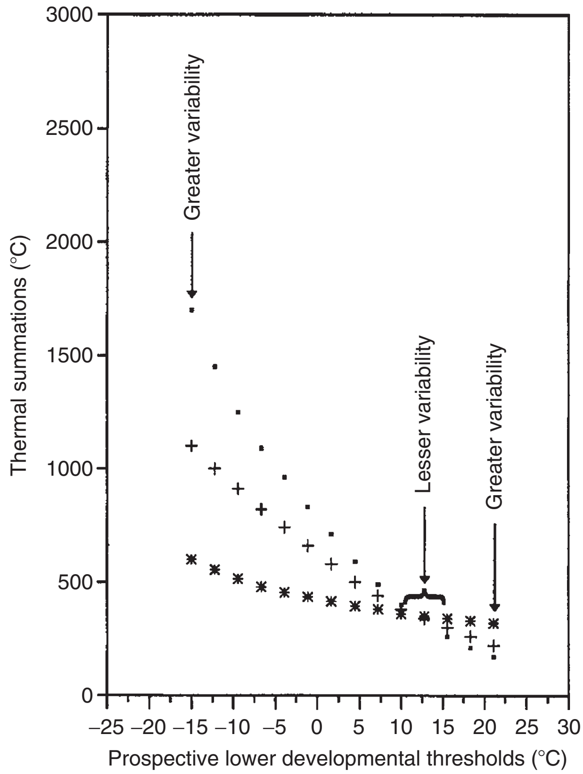
Constructing Phenology Models Through the Use of Field Studies

If the insect cannot be reared on artificial diet, or if its host cannot be grown in the greenhouse and placed in environmental chambers, then phenology models must be constructed through the use of field studies. This can be done in several ways, one of which is to find a location at which the insect is known to habit, and visit that location every day until the phenological event occurs; that date is then recorded. This process is repeated for many years. Next, daily maximum and minimum temperatures are procured from the nearest weather station, for each year the observations were made, beginning on a selected starting date and ending on the dates the phenological event occurred. These temperatures are saved in separate computer files, with each year of temperatures comprising a single file (temperature data sets).

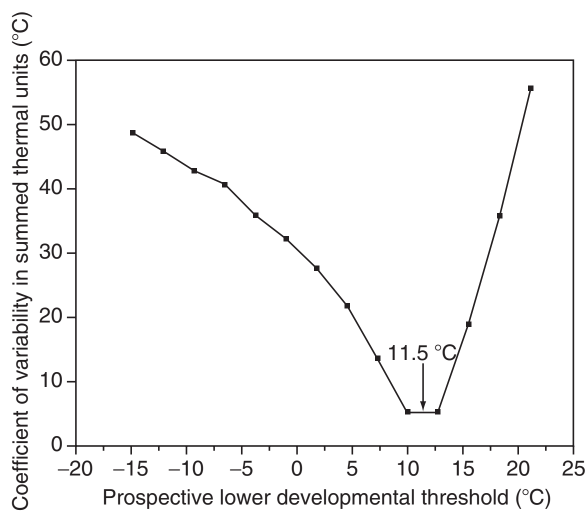
Initially, as pest managers do not know what value to use for the lower developmental threshold, several prospective values (prospective lower developmental thresholds) are chosen to calculate and sum prospective thermal units (prospective thermal summations). This is done with each temperature data set. For example, if there were just 3 years of field observations, and their corresponding temperature data sets were used to calculate prospective thermal summations with each of fourteen prospective lower developmental thresholds, a plot of prospective thermal summations on prospective lower developmental thresholds may look like that shown in Figure 36. Note that the spread between prospective thermal summations is greater at both ends of the plot.

Using this data, there are several methods by which a pest manager can actually calculate the lower developmental threshold. Two methods discussed here are the least variability and the modified regression methods. The least variability method involves calculating a simple measure of variability, or spread, in the required thermal summations, then determines the prospective lower developmental threshold(s) for which that variability is least. This approach clearly shows that prospective lower developmental thresholds which ranged from 10 to 13°C provided the least variability in the required thermal summation and, therefore, would work equally well as the lower developmental threshold. When all temperatures within a range are equally acceptable, their mid-point value is calculated (11.5°C) and used as the lower developmental threshold. Next, the chosen lower developmental threshold is used to calculate and sum thermal units, separately for each temperature data set. An average or median of those values is then calculated and used as the required thermal summation in the phenology model.

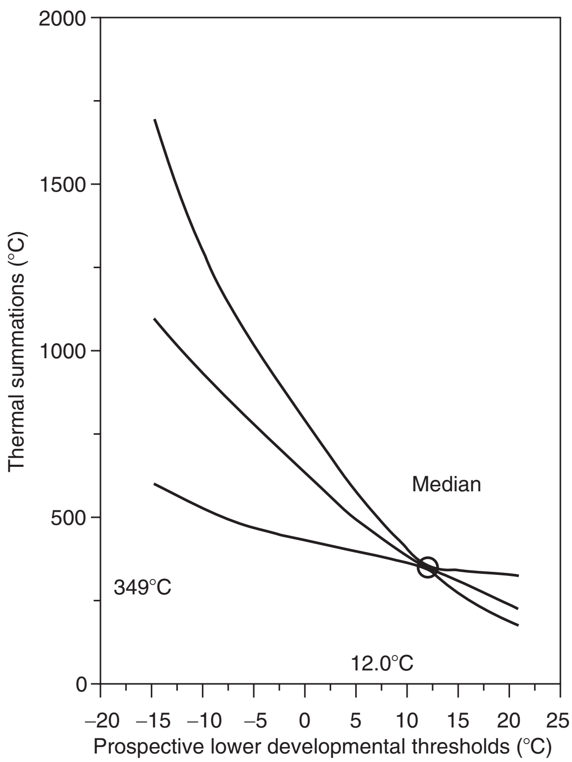
The modified regression method is used by first calculating mathematical equations that realistically express the curve-type relations; the use of such equations produces a set of curves. These equations are then used to determine mathematically where those curves cross, or have a point of closest convergence. Each such crossing point, or point of closest convergence (Fig. 38), corresponds with an individual estimate of a required thermal summation (y-axis) and lower developmental threshold (x-axis). Then, the average or median of those estimates is calculated and used in the phenology model as the required thermal summation and lower developmental threshold. The modified regression method is extremely difficult to use without the aid of a computer. Fortunately, a computer program (CALFUN) is available and can be used



Phenology Models for Pest Management, Figure 36 **Typical curve-like relations between prospective thermal summations and prospective lower developmental thresholds that are seen in the temperate climes; the area of lesser variability corresponds with estimates of values for the required thermal summation (y-axis).**



Phenology Models for Pest Management, Figure 37 **A typical plot of the variability in the data, on values for prospective lower developmental threshold (x-axis); values for prospective lower developmental threshold at which the variability was least are used as estimates of lower developmental threshold (in this case, their mid-point value, 11.5°C, was selected).**



Phenology Models for Pest Management, Figure 38 Results from developing mathematical equations (curves) showing their generalized area of convergence (encircled area); corresponding values for prospective required thermal summation (y-axis) (349°C) and prospective lower developmental threshold (x-axis) (12.0°C) are estimates of the required thermal summation and the lower developmental threshold, respectively.

to quickly and easily perform these calculations. CALFUN can be obtained from the World Wide Web at the following URL: http://w3.uwyo.edu/~dlegg/calfun.html.

Once values for the lower developmental threshold and required thermal summation are calculated, the value for the threshold is used to calculate daily thermal units, which are summed until the date on which that sum equals the required thermal summation. Theoretically, that is the date on which the phenological event occurs.

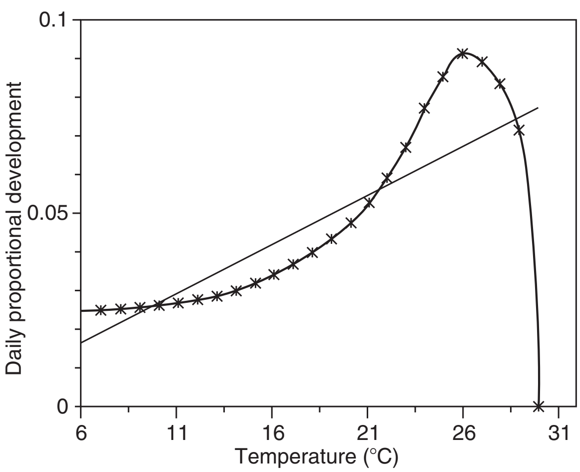
Concluding Remarks

There are advantages and disadvantages to developing phenology models in the laboratory and in the field. One advantage to developing phenology models in the laboratory is that values for the lower developmental threshold are biologically meaningful. That is, they represent temperatures at which growth and development will first occur. One potential disadvantage to developing phenology models in the laboratory, however, is that they must make use of temperatures that actually occur where the insect is found. Those places include soil, dung, fruit, and plant tissues (substrate). As phenology models often make use of air temperatures to calculate either daily thermal units or proportional daily development, it may be necessary to convert those temperatures into substrate temperatures before laboratory-based phenology models will be effective.

One advantage to developing phenology models from field studies may be that converting air temperatures into substrate temperatures will not be necessary. This is so because field-developed phenology models appear to have the air temperature-substrate temperature relationship already factored into the values that are calculated for required thermal summation and lower developmental threshold. This, however, suggests one disadvantage to calculating lower developmental thresholds and required thermal summations from field studies; their values may not be biologically meaningful.

Phenology models that are based on nonlinear thermal unit functions are sometimes thought of as being superior to those that are based on linear thermal unit functions. This is so because nonlinear thermal unit functions best describe the relation between insect growth and a wide range of temperatures. However, many insects have behaviors that, when exhibited, help regulate their body temperatures to some extent (thermal regulation). For example, many grasshoppers will climb plants to escape uncomfortably warm temperatures near the ground, or will climb plants to better impact sunshine, on cool mornings, so they will warm rapidly. Also, many grasshopper species will turn their bodies in such a way as to "bask" in sunshine, thereby keeping their cellular temperatures warmer, for longer periods of time, throughout a chilly day. Such behaviors may largely serve to keep insect growth within the linear portion of their developmental curves. If that is true, then phenology models that are based on linear thermal unit functions will be superior to those that are based on nonlinear developmental functions when predicting phenological events in the field. However, if such behaviors do not keep insect development within the linear portion of their developmental curves, then phenology models that are based on nonlinear developmental functions will be superior to those that are based on linear developmental functions when predicting phenological events in the field (Fig. 39).

Finally, the performance of many phenology models may be acceptable when they are used to predict insect phenological development in most fields, orchards, or pastures (target populations), but unacceptable in some others. Unacceptable performances may occur when the temperatures recorded at the location of a weather station do not reflect the temperatures that occur at some target populations. Such discrepancies can occur for several reasons, but most involve localized site-specific features such as soil types, plant litter, or slope of terrain relative to the angle of the sun. For some combinations of these features, the area of the target population may be warmed much more than the area of the weather station, resulting in accelerated insect development relative to the output of a phenology model that is using temperatures recorded at the weather station. For other combinations, however, the area of the target population may be much cooler than the area where the weather station is located, thus resulting in retarded insect development relative to the output of a phenology model that is using temperatures recorded at the weather station. For those target populations where such site-specific features can cause phenology models to perform poorly, it may be necessary to make use of on-site temperature recorders. The use of temperatures from these recorders should result in acceptable predictions of insect phenological events.



Phenology Models for Pest Management, Figure 39 **Results from using a linear model (straight line) and nonlinear model (curve) to describe the observed proportions of daily development (asterisks); note that the nonlinear model best describes observed daily proportional development over a wide range of temperatures.**

References

Higley LG, Pedigo LP, Ostlie KR (1986) DEGDAY: a program for calculating degree-days, and assumptions behind the degree-day approach. Environ Entomol 15:999–1005

Ikemoto T, Takai K (2000) A new linearized formula for the law of total effective temperature and the evaluation of line-fitting methods with both variables subject to error. Environ Entomol 29:671–682

Legg DE, Van Vleet SM, Lloyd JE, Zimmerman KM (1998) Calculating lower developmental thresholds of insects from field studies. In: Pandalai SG (ed) Recent research developments in entomology, vol 2. Research Signpost Press, Trivandrum, India, pp 163–172

Pruess KP (1983) Day-degree methods for pest management. Environ Entomol 12:613–619

Wagner TL, Olson RL, Willers JL (1991) Modeling arthropod development time. J Agric Entomol 8:251–270

Phenotype

The physical appearance of an individual that are determined by both genotype and environment (contrast with genotype).

Phenotypic Plasticity

This is the property of a genotype being able to produce different phenotypes in response to different environmental conditions. Evolution can channel organisms into a stabilized phenotype, with little plasticity, that is well developed for a certain function or environment. Alternatively, it can lead to a more flexible phenotype, producing a robust organism that varies according to environmental stimuli. This latter condition is more common than generally acknowledged. Some of these flexible or "plastic" phenotypes show gradual change in response to environmental variation, without producing discretely different subsets, and are called "reaction norms." Some phenotypes produce discretely different (lacking intermediate forms) intraspecific variation, and this is called "polyphenism." Polyphenisms (= polymorphisms) are adaptations to reliable and predictable variations in the environment.

In most cases, a genotype gives rise not to a single phenotype, but a range of phenotypes. Thus, phenotypes are a product of the genotype and the environment, and results in the expression of alternative morphology, behavior, and performance. The resulting plasticity is important in ecological and evolutionary success of the organism. Phenotypic plasticity can act as a buffering agent against environmental variation. We might expect, then, to find phenotypic plasticity most pronounced in organisms inhabiting heterogeneous environments. Phenotypic plasticity favors host race formation in insects, and sympatric speciation.

► Polyphenism
► Polymorphism in Locusts
► Polyphenism and Juvenile Hormone (JH)
► Castes

References

Ananthakrishnan TN, Whitman D (eds) (2005) Insect phenotypic plasticity. Diversity of responses. Science Publishers, Enfield, New Hampshire, 213 pp

De Jong G (1995) Phenotypic plasticity as a product of selection in a variable environment. Am Nat 145:493–512

Evans JD, Wheeler DE (2001) Gene expression and the evolution of insect polyphenisms. Bioessays 23:62–68

Nijout HF (2003) Development and evolution of adaptive polyphenisms. Evol Dev 5:9–18

Pigliucci M (2001) Phenotypic plasticity. Beyond nature and nurture. The Johns Hopkins University Press, Baltimore, MD, 328 pp

Scheiner SM (1993) Genetics and evolution of phenotypic plasticity. Ann Rev Ecol Syst 24:35–68

Pheromone

Chemical substance secreted externally into the environment that affects the behavior or physiology of other members of the same species. Pheromones are a type of semiochemical.

► Chemical Ecology
► Alarm Pheromones
► Sex Pheromones

Pheromones

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When we hear the term "pheromone," our thoughts automatically turn to love! Pheromones certainly are involved in getting the sexes together (not only insects, but most animals, and possibly even humans, use sex pheromones to facilitate reproduction) but they have myriad other functions in the lives of insects as well. Males and females, sometimes both sexes, within a species may produce pheromones to coordinate their life histories. Simply defined, pheromones are one type of semiochemical (chemical compound that mediates interactions between organisms) that carry information between organisms of the same species. The term is derived from the Greek verbs "pherein" (to carry) and "horman" (to excite or to stimulate). Thus, pheromones are chemical substances that, when secreted to the outside of an organism, cause a specific reaction in a receiving organism of the same species.

Types of Pheromones

Pheromones can be classified by the effect that they have on the receiving organism. They may be "releaser" pheromones, where the receiving organism immediately performs a stereotypical behavior or sequence of behaviors upon perceiving the pheromone. For example, when flying male moths perceive the volatile, sex attractant pheromone of a female moth, they immediately turn upwind, and begin casting, a flight behavior characterized by large-amplitude horizontal excursions with no forward movement. This behavior, and the subsequent upwind flight, help them locate the source of the odor, which is the virgin female. The second type of pheromone is a "primer" pheromone. These pheromones set in motion complex physiological changes, such as development or sexual maturation, in the receiving organism. For example, mandibular gland pheromone produced by queen honeybees inhibits initiation of queen rearing and regulates division of labor in the worker caste through effects on the worker bees' juvenile hormone levels.

Pheromones may be categorized based on the function they appear to have in the insect. For example, chemicals released by an insect under attack by a predator may be termed an alarm pheromone if other individuals of the same species react to it by dispersing, running around frantically, jumping off the plant, or displaying some other type of alarmed behavior. Many types of pheromones have been described based on their supposed function in a species: sex attractant pheromone, courtship pheromone, marking pheromone, oviposition deterrent pheromone, aggregation pheromone, and the many pheromones used in the lives of social insects for the purposes of recruitment, nest-mate recognition, and trail laying.

The Early Days of Pheromone Research

The history of pheromone research is relatively recent. It has been observed since the 1700s that male moths are attracted to female moths of the same species. Jean-Henri Fabre, a French naturalist active in the late 1800s, was the first to perform experiments to test the attraction of male moths to females and to suggest a mechanism to explain his observations. His experiments began after a chance observation, as great scientific discoveries often do. He was keeping a pupa of the Great Peacock moth, *Saturnia pyri*, in his office. One day the moth enclosed and it happened to be female. That night he and his young son went into his office and, because the window had been left open, found twenty male *S. pyri* moths fluttering about the room. He originally thought that the virgin female moth was producing some sort of X-rays or some form of "etheric" waves to signal males. However, after several years of experiments with this species, and several others, he concluded, as astounding as it seemed to him, that female moths were producing an odor that was attractive to males from a great distance.

It was not until the epic research of German chemists, Adolf Butenandt and his colleagues, that the first pheromone was identified. This group was interested in the potential use of insect sex pheromones in management of agricultural pests. They began isolating the sex attractant pheromone of the silkworm moth, *Bombyx mori*, in 1939, choosing this beneficial lepidopteran as a model because of the ease of obtaining large numbers of insects for chemical isolation. Twenty years, and 500,000 female moths later, they had succeeded in isolating and identifying one component of the silkworm's female-produced sex attractant pheromone, which they termed "bombykol." Their success was remarkable because of the meager tools that these analytical chemists had at their disposal. They were dealing with much smaller amounts of chemicals than were analyzed routinely at the time. Today, insect pheromones often can be isolated, identified and synthesized within 6 months, depending on their complexity. Amazingly, with today's analytical instrumentation (gas chromatographs and mass spectrometers), we can measure easily the amount of pheromone a single female insect releases over only an hour's period of time.

Pheromone Biosynthesis

Many insects biosynthesize their pheromones de novo, meaning that they break down their food into small molecules which they then use as the building blocks for their pheromones. For example, the female-produced sex attractant pheromones of most moth species analyzed so far are straight-chain hydrocarbon molecules with oxygen-containing functional groups (alcohols, aldehydes and acetates), varying in length from 8 to 18 carbon atoms. The molecules usually are made by the end-to-end addition of acetate molecules, two-carbon-atom building blocks which are end-products of fatty acid metabolism.

Other insects however, biosynthesize their pheromones from specific plant-derived molecules, processing them only minimally before use as a pheromone. This occurs commonly in several species of ithomiine and danaiid butterflies (like the monarch butterfly) and tiger moths (family Arctiidae). In these species, the male butterfly sequesters plant compounds, either from its larval food or, as an adult, from plant species that are visited solely for the purpose of collecting these molecules, and modifies them slightly for use as an aphrodisiac or courtship pheromone. These pheromones are produced in specialized glands at the tip of the male's abdomen and are either sprinkled on the female or wafted in front of her from modified scales called hair pencils or inflatable, eversible sacs called coremata. Perception of the courtship pheromone may allow the female to judge the fitness of the courting male and will result in mating if she deems him "fit."

Pheromone components may be made, not by the insect itself, but by symbiotic microorganisms that live within the insect's body. For example, the spruce bark beetle, *Ips typographus* (family Scolytidae), a devastating pest of forest trees in Europe, has a symbiotic relationship with yeast fungi. When pioneer beetles first attack healthy trees, they release a multi-component aggregation pheromone that attracts more beetles to help overwhelm the tree's sticky and toxic resin defense. One of the components of this aggregation pheromone (cis-verbenol) is produced as a detoxification product of a terpene defensive compound in the tree (α-pinene) by yeast found in the hindgut of the colonizing beetles. After there is adequate colonization of the tree and its defense has been breached, the yeast transforms cis-verbenol to verbenone, which acts as an anti-aggregation pheromone stopping further colonization and reducing the negative effects of beetle overcrowding and competition.

Finally, some insects may use plant compounds directly as pheromones without further modification. The euglossine orchid bees (family Apidae) are pollinators of orchids in the New World tropics, with each species of bee usually visiting and pollinating only one species of orchid. In this group of bees, the males, never the females, pollinate the orchids. The bees gain no nectar or pollen reward but instead collect large quantities of fragrances that the orchids produce. These fragrances are stored in specialized organs in the hind femora of the bees and are hypothesized to be used to facilitate mating. The stored orchid volatiles attract other male bees to a mating display, or a lek, to which female bees are subsequently attracted. Females at these leks can possibly choose specific males to mate with based on the quality or quantity of the orchid fragrance they have collected.

Pheromones are made in exocrine glands, specialized glands that are found on various portions of the body, usually in the epidermis. The glandular secretions are released to the outside of the body. Pheromones usually are released only at certain times of the day or night based on an internal biological rhythm. Most pheromones are volatile, small molecules borne in the air and are perceived by olfactory chemoreceptors on the antennae. Some pheromones are larger, less volatile, or even nonvolatile, molecules that are perceived by contact chemoreceptors found on the ovipositor, antennae, and elsewhere.

Use of Pheromones by Insects and Humans

Chemical communication via pheromones has tremendous benefit to insect species that may not have extensive adaptations for visual or acoustic communication. Thus, pheromone production is extremely common and widespread among the class Insecta. However, there are costs associated with the production of pheromones. One of the major costs is the fact that many predatory and parasitic insects have evolved the ability to perceive these pheromones and can eavesdrop on the communication going on between members of their prey species. For example, several species of predaceous clerid beetles are attracted to the aggregation pheromone of bark beetles. Species of *Trichogramma*, minute hymenopterans that often parasitize the eggs of Lepidoptera, are attracted to the sex attractant pheromone of female moths. Female parasitoids of several species of tephritid fruit flies are stimulated to search a fruit for hidden host larvae when they perceive the nonvolatile host-marking pheromone laid down on the fruit by the ovipositing female fruit fly. Some species of predator have even evolved the ability to produce the pheromone of their prey and thus lure their prey to them. For example, the females of several species of bolas spiders, *Mastophora* spp., produce the sex attractant pheromone of the females of the moth species on which they prey. When the male moth approaches the bolas spider, expecting to find a virgin female moth, he is captured by a sticky bolas that the spider launches at him.

The list of such examples of illicit communication is endless and illustrates the fascinating odorous world in which insects live, and of which we humans largely are unaware due to our poor sense of smell. Despite being unable to directly experience this hubbub of chemical communication, we have taken advantage of it to help control pestiferous insects that harm our food supply. We have used insect pheromones to detect the presence of pest insects as an early warning of their immigration into an area, to time insecticide applications or other control measures, and to document arrival of quarantine pests in pest-free areas. Pheromone monitoring also can be used to quantify insect populations or, at least, to indicate whether populations are declining or increasing. We have used pheromones to disrupt insect's mating behavior. For example, the pink bollworm, *Pectinophora gossypiella*, an economically important pyralid moth pest of cotton in both the Old and New World, is managed almost exclusively now by the area-wide application of Gossyplure, a synthetic version of the female's sex attractant pheromone. The pheromone is formulated for slow release and is dispersed over large acreages of cotton. The multiple point sources of pheromone in the field make it very difficult for the male bollworm moth to find virgin females and mate with them, thus slowing population increase and the associated yield loss.

Pheromones also are used in mass trapping and attract and kill strategies. In mass trapping of bark beetles for example, large vertical funnel traps are baited with aggregation pheromones. Bark beetles are attracted to the tall, cylindrical funnel traps (which visually mimic trees) and are trapped in the funnels, thus taking them out of the population. In the attract and kill strategy, insects are attracted to a pheromone-impregnated substrate that also has been treated with an insecticide or sterilant so that the insects are excluded from the breeding population. The addition of the house fly sex pheromone, (Z)-9-tricosene, to granular food baits impregnated with an insecticide greatly improved control of house flies in commercial animal production facilities over use of an insecticide-treated food bait alone.

To date, the majority of pheromones that have been used in pest management are female-produced sex attractant pheromones and bark beetle aggregation pheromones. Other pheromones that have potential are the anti-aggregation pheromones of bark beetles that may have potential to prevent infestation of trees, oviposition-deterring pheromones of fruit flies and other insects to prevent oviposition in crops, and alarm pheromones of aphids that increase aphid movement in the area of the alarm pheromone, thus making the aphids more likely to contact a lethal dose of insecticide or to be noticed by visually orienting predators or parasitoids.

► Social Insect Pheromones
► Alarm Pheromones
► Sex Attractant Pheromones
► Marking Pheromones

References

Cardé RT, Minks AK (1995) Control of moth pests by mating disruption: successes and constraints. Annu Rev Entomol 40:559–585

Hardie J, Minks AK (eds) (1999) Pheromones of non-lepidopteran insects associated with agricultural plants. CABI Publishing, New York, NY, 466 pp

Haynes KF, Yeargan KV (1999) Exploitation of intraspecific communication systems: illicit signalers and receiver. Ann Entomol Soc Am 92:960–970

Howse P, Stevens I, Jones O (1998) Insect pheromones and their use in pest management. Chapman & Hall, London, UK, 369 pp

Wyatt TD (2002) Pheromones and animal behaviour: communication by smell and taste. Cambridge University Press, Cambridge, UK

Pheromone Parsimony

A phenomenon wherein the same pheromone can serve multiple functions. For example, a marking pheromone may also function as an aggregation pheromone, an antimicrobial agent, and a kairomone.

Phialides

Specialized cells with one or more open ends from which conidia are produced in basipetal succession. Thus, the apical conidia are the oldest.

Philanthidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Philopotamidae

A family of caddisflies (order Trichoptera). They commonly are known as finger-net caddisflies or silken-tube spinners.

► Caddisflies

Philopteridae

A family of chewing lice (order Phthiraptera). They sometimes are called bird lice.

► Chewing and Sucking Lice

Philotarsidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice and Psocids

Phlaeothripidae

A family of thrips (order Thysanoptera).

► Thrips

Phloeidae

A family of bugs (order Hemiptera, suborder Pentamorpha).

► Bugs

Phoenician Billbug, *Sphenophorus phoeniciensis* Chittenden (Coleoptera: Curculionidae)

This turfgrass pest affects grass in the southwestern USA.

► Turfgrass Insects and Their Management

Phoenicococcidae

A family of insects in the superfamily Coccoidae (order Hemiptera). They sometimes are called palm scales.

► Scale Insects, Mealybugs
► Bugs

Phonotaxis

Taxis response with respect to sound.

Phoracantha longicorn Beetles (Coleoptera: Cerambycidae)

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The genus *Phoracantha* Newman belongs to the family Cerambycidae of the order Coleoptera.

Order: Coleoptera
Family: Cerambycidae
Subfamily: Cerambycinae
Tribe: Phoracanthini
Genus: *Phoracantha*

External Morphology

Phoracantha adults range from 14 to 48 mm in length. Body is pale, yellowish, reddish to blackish brown with elytra having colored fasciae in most species, usually zigzag, arranged transversely. At least antennal segments 3–6 are unispined or bispined at apex. The prothorax is wider than long, with depressed hairs, and the pronotum has a spine or strong prominent conical process at each side. The elytral apex is usually bispined, at least spined at marginal angle. The femora are lineate or gradually thickened. Larvae have an elongate, cylindrical body shape.

Biodiversity and Distribution

Phoracantha has 40 known species and is the most speciose genus of the tribe Phoracanthini. This genus is mainly distributed in southern Australia, and some species occur in northern Australia and New Guinea. Only two species are endemic to Papua New Guinea. In Australia, these beetles are predominantly along the coast, with only one species, *P. tuberalis*, restricted to the center of the Australian continent. About eight widely distributed species occur in both coastal and central areas. Several species are known to be introduced to other parts of the world, for example, *P. semipunctata* and *P. recurva* now occur in all zoogeographic regions except the Oriental Region.

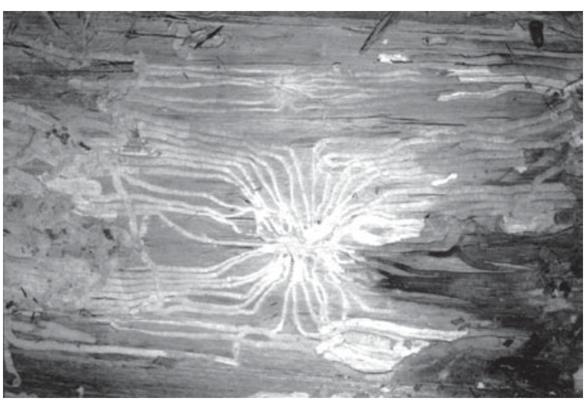
Habitat, Host and Life Cycle

Many *Phoracantha* species are associated with the tree genus *Eucalyptus* and a few with *Acacia*. Adults are active during the night, hiding in daytime under loose bark or in crevices, and can be attracted by light. Larvae bore into trunks or branches of trees. Biologically, the borers can be divided into two groups: (i) dead/dying tree consumers, including *P. semipunctata*, *P. recurva*, *P. tricuspis* and *P. punctata*, and (ii) living tree consumers, including *P. mastersi*, *P. acanthocera*, *P. frenchi*, *P. impavida*, *P. synonyma*, *P. solida* and *P. odewahni*. These are clearly defined functional groups, and the species can be allocated clearly to one or other of these (Figs. 40–42).

The members of the dead/dying tree consumers have 1–2 generations a year, attacking newly felled and dying trees, of all ages, of *Eucalyptus* species. More than 50 eucalypt species are host plants of this group. The group is distributed in both northern and southern parts of Australia. Adults lay eggs in large batches under loose bark, or in crevices, with each egg mass consisting of 23–340 eggs. The larvae feed in and under the bark for 2–6 months, making regular tunnels up to 1.5 m long, either in a straight line or twisted, radiating from the egg mass in all directions. When mature, the larvae bore into hardwood to pupate at a depth of up to 20 cm from surface. In general, this group of consumers damages trees because of the large number of larvae produced.

The living tree consumers need from 2 to 3 years to complete their life cycle. They attack living trees of all ages, but particularly young trees aged from 6 to 20 years. They have a much narrower

Phoracantha longicorn Beetles (Coleoptera: Cerambycidae), Figure 40 ***P. recurva*** **adult.**



Phoracantha longicorn Beetles (Coleoptera: Cerambycidae), Figure 41 **Tunnels in a eucalyptus tree made by** ***P. semipunctata*****.**

Phoracantha longicorn Beetles (Coleoptera: Cerambycidae), Figure 42 **Tunnel in a eucalyptus tree made by** ***P. acanthocera*****.**

range of host plants than the dead/dying tree consumers, only about 20 eucalypt species have been recorded as their hosts, with each longicorn species having its own eucalypt hosts. In addition, they are distributed in either southern or northern parts of Australia. Eggs are laid singly or in only small batches, in bark cracks or the sites of injuries, with each egg mass consisting of 1–18 eggs. The larvae do not make the radial or parallel tunnels as dead/dying consumers do, but their activities make 1–6 large damaged areas under the bark and they may bore into the hardwood several times before pupating there. In general, one tree supports only one species of living tree consumers, and one or a few larvae. In many cases, even a couple of larvae can kill a tree.

Insect Natural Enemies

Insect natural enemies cause substantial mortality of *Phoracantha*. Parasitoids are mainly recorded from Hymenoptera, including three families and

13 species. The genera *Callibracon*, *Syngaster* and *Jarra* of Braconidae are major larval parasitoids and *Avetianella* from Encyrtidae is the only known egg parasitoid of *Phoracantha*. Some of these parasites have been introduced to North America and South Africa for biological control of *P. semipunctata* and *P. recurva*. Known predators are mainly from coleopteran families Cleridae and Colydiidae. The clerid genera *Stigmatium*, *Trogodendron* and *Tenerus* attack *Phoracantha* larvae, and the colydiid genera *Bothrideres*, *Deretaphrus*, *Phormesa* and *Teredalaemus* prey on either adults or larvae. *Stigmatium gilberti* was observed to feed on *Phoracantha* eggs as well.

Economic and Ecological Importance

Most phoracanthine species of economic importance are placed in this genus and some species are serious pests of eucalypt forests in various states of Australia and many countries around the world. The widely distributed species are more likely to become pests in Australia and elsewhere. For example, *P. semipunctata* and *P. recurva* have now been established in many countries in Africa, South and North America, and the Mediterranean region, and have become serious pests of *Eucalyptus* plantations in these regions. They feed mainly on dead or stressed trees, and can survive lengthy shipment in logs between continents. Other species such as *P. obscura*, *P. punctata* and *P. tricupis*, have similar necessities and life cycles and can cause serious damage to *Eucalyptus* outside Australia if introduced. The dead/dying tree consumers are important in recycling dead and sickly trees in nature and promoting re-growth of forest.

The species *P. solida*, *P. synonyma*, and *P. acanthocera* have wider geographic adaptation than most other *Phoracantha* species, and have become pests of Australian *Eucalyptus* forests. Of these species, *P. acanthocera* has become a serious pest in all southern states of Australia. Because these species mainly live on healthy trees, they may not be able to survive lengthy shipment in logs. So far, none of them has been reported to have established outside Australia. However, if these species are accidentally introduced into other regions, they may be more harmful than dead/dying tree consumers to *Eucalyptus* plantations. Species other than those mentioned above appear not to be able to adapt to a wide range of environments and are less likely to become important pests in Australia or other countries, except one species, *P. mastersi*, which is a fairly serious pest in southeastern Australia, particularly in Tasmania.

References

Austin AD, Quicke DLJ, Marsh PM (1994) The hymenopterous parasitoids of eucalypt longicorn beetles, *Phoracantha* spp. (Coleoptera: Cerambycidae) in Australia. Bull Entomol Res 84:145–174

Moore KM (1963) Observations on some Australian forest insects, 15. Some mortality factors of *Phoracantha semipunctata* (F.) (Coleoptera: Cerambycidae), vol 88. Proceedings of the Linnean Society of New South Wales, pp 221–229

Wang Q (1995) A taxonomic revision of the Australian genus *Phoracantha* (Coleoptera: Cerambycidae). Invert Taxonomy 9:865–958

Wang Q, Thornton IWB, New TR (1999) A cladistic analysis of the phoracanthine genus *Phoracantha* Newman (Coleoptera: Cerambycidae: Cerambycinae), with discussion of biogeographic distribution and pest status. Ann Entomol Soc Am 92:631–638

Phoresy

A symbiotic relationship with transport of one organism by another. Phoretic relationships display little or no pathology to the host. Many insects, nematodes, and microbial organisms have phoretic associations with insects.

Phoridae

A family of flies (order Diptera). They commonly are known humpbacked flies.

► Flies (Diptera)
► Myiasis

Phryganeidae

A family of caddisflies (order Trichoptera). They commonly are known as large caddisflies.

► Caddisflies

Phosphorylation

The combination of phosphoric acid with a compound. Many proteins in eukaryotes are phosphorylated.

Photodynamic Action in Pest Control and Medicine

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In most cases, life depends on light. For instance, photosynthesis (the process by which plants derive the energy needed for growth) provides almost all food for both humans and animals. Light has profound implications for the field of medicine. While it works as a cause of disease (e.g., UV damage of DNA) it also may be applied as a therapeutic agent (cf. photodynamic therapy). Additionally, light also acts as a means for plant defense against herbivorous animals including insects.

In contrast to the normal photobiological processes that are essential to the physiology of living organisms such as photosynthesis in green plants, biological systems also can be damaged and destroyed by non-physiological photochemical reactions after light absorption. These reactions are the result of the interference of certain dyes and many secondary plant products known as photosensitizers that are carried out either in the presence or the absence of oxygen. The latter category, which is realized under anaerobic conditions, is much less common.

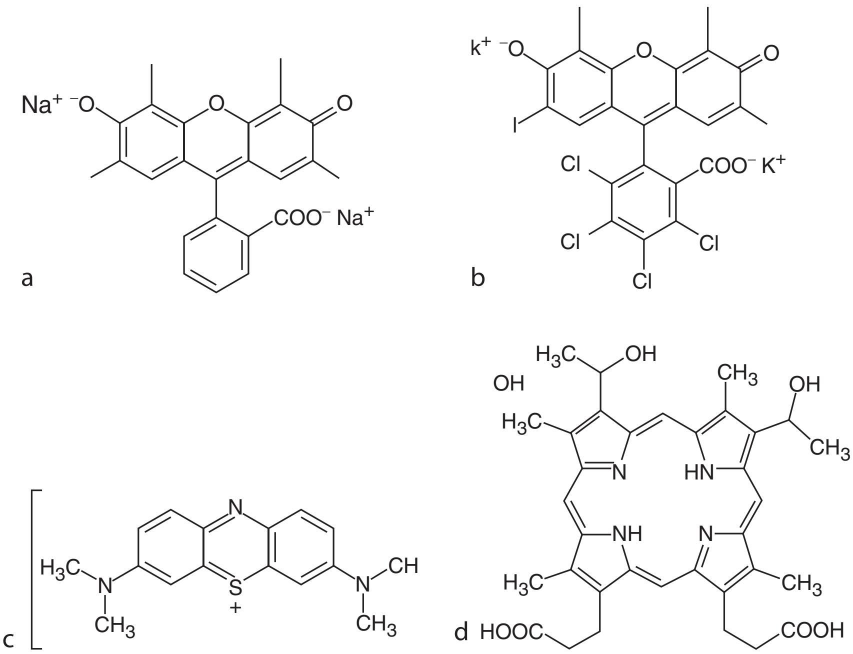
The question of potential hazards to humans arises with the wide use of photodynamic sensitizers in foods, drugs and cosmetics. In addition, there is considerable experimental evidence on the photodynamic effects of several popular dyes as highly active insecticides, and some clear evidence for photocarcinogenicity of certain phototoxic agents (Fig. 43).

The term photodynamic action or "photodynamische Erscheinung" was suggested in 1904 by Tappeiner and Jodlbauer to differentiate this activity from the photosensitization of photographic plates by dyes. Much later, Spikes and Glad defined photodynamic action as the killing or damaging of an organism, cell, or virus, or the chemical modification of a (bio-) molecule in the presence of a sensitizing dye and molecular oxygen. However, considering recent discovery of the photodynamic action in some important groups of phytochemicals, such as furanocoumarins, polyacetylenes and their thiophene derivatives, cercosporin, hypericin, and numerous photosensitizing drugs, which exclusively work at the near UV range (300–400 nm), it is apparent that photodynamic action is not limited to dyes, but includes many biomolecules (Fig. 44).

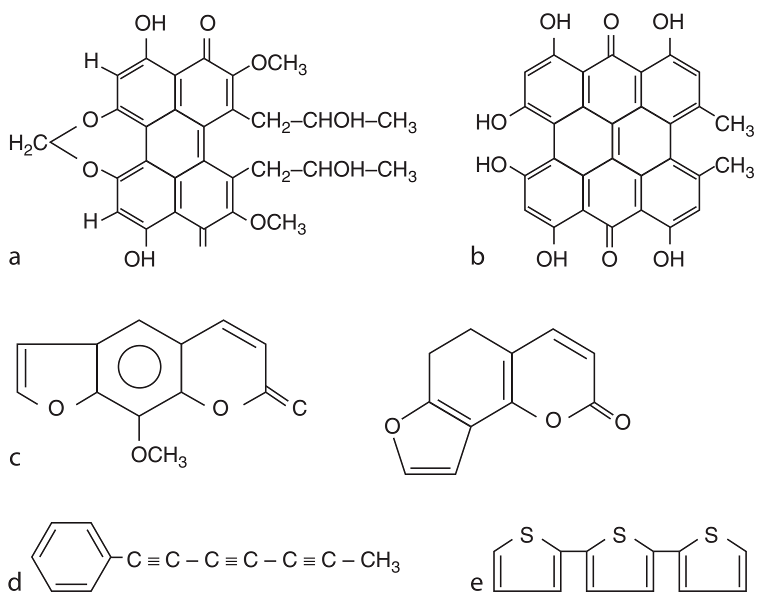
O_2 Metabolism

The oxidative processes that are fundamental to photodynamic action differ greatly from normal cellular metabolism. Differences include:

1. While the respiratory quotient, i.e., the ratio between CO_2 production and O_2, is near unity for normal aerobic metabolism, the ratio during photodynamic action is up to 20-fold lower than the former (e.g., 0.048 vs 1.00).
2. Normal O_2 metabolism is virtually abolished if the structure of the cell is destroyed. Whereas, the O_2 uptake during photodynamic action has been found to remain the same for both intact or hemolyzed red blood cells.
3. While cyanide inhibits normal O_2 metabolism, it increases the uptake of O_2 in photodynamic action.
4. Normal O_2 metabolism is destroyed by heat, whereas boiling does not abolish the photosensitized uptake of O_2.



Photodynamic Action in Pest Control and Medicine, Figure 43 **Some examples of several dyes with photodynamic action: i.e., halogenated dyes – e.g., (a) Erythrosin ($C_{20}H_6I_4Na_2O_5$), (b) Rose Bengal ($C_{20}H_2Cl_4I_4K_2O_5$) and (c) Methylene Blue ($C_{16}H_{18}Cl\text{-}N_3S$); and non-halogenated dyes – e.g., (d) Hematoporphyrin ($C_{34}H_{38}N_4O_6$).**



Photodynamic Action in Pest Control and Medicine, Figure 44 **Chemical structures of several secondary plant products with photodynamic action: (a) cercosporin; (b) hypericin; (c) furanocoumarins (left, linear: e.g., 8-methoxypsoralen, i.e., 8-MOP or xanthotoxin; and right, angular: e.g., angelicin); and finally polyacetylenes (e.g., phyenylheptatriyne) and their thiophenes – e.g., α-terthienyl (d and e, respectively).**

Light Absorption

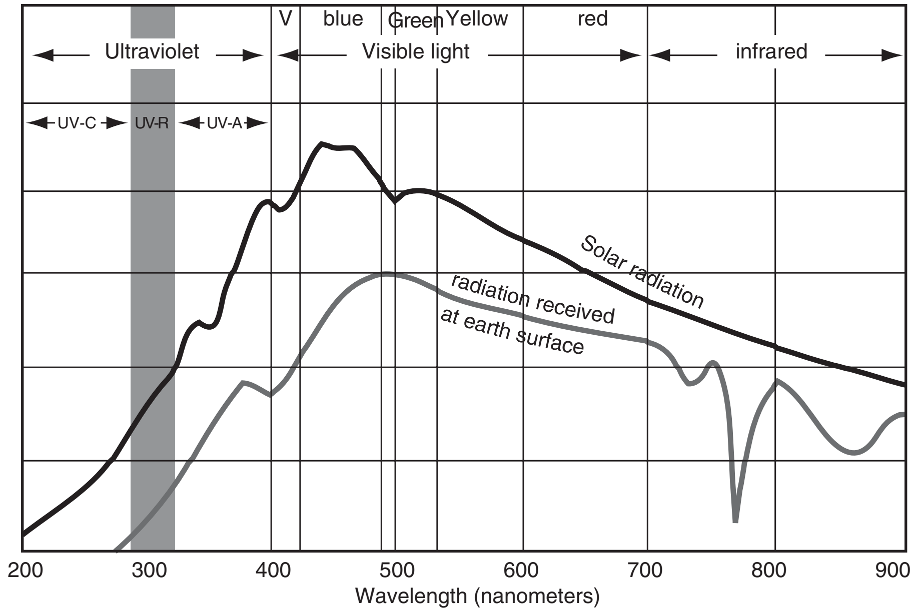
The first step of photodynamic action is absorption of light by a sensitizer (Fig. 45).

An important aspect of the photodynamic effect is that the active wavelengths are longer than 300 nm. Therefore, it is restricted to the regions of the electromagnetic spectrum that penetrates the Earth's atmosphere: i.e., some parts of the UV (300–400 nm), and entire spectrum of the visible light (400–700 nm). The destructive effect of the short-wave lengths (less than 300 or 330 nm) are well documented. However because the ozone layer absorbs almost all energy below 280–290 nm, the destructive region of solar light is confined to a narrow range (i.e., 280–330 nm).

The extent of penetration of ultraviolet (UV) and visible radiation into skin varies considerably. While UV-C (200–280 nm) does not penetrate beyond the epidermis, UV-B (280–320 nm) and UV-A (320–400 nm) enter the dermis; and visible light penetrates further into the subcutaneous tissue. UV penetration into tissue is estimated at less than 0.1 mm, whereas the typical penetration depth in living tissue of the red light used for photodynamic therapy ranges between 1 and 3 mm.

Mechanisms

When the absorption of a quantum of radiation excites a sensitizer, the energy imparted by this excitation is related to wavelength by the following equation: $E = hv$, where E is the energy of radiation, h is Planck's constant (i.e., 2.8591), and v is the frequency of the radiation. On the other hand, as $v = c/\Lambda$, where c is the velocity of light and Λ the wavelength, one can substitute to obtain $E = hc/\Lambda$ (i.e., $2.8591 \times 10^5/\Lambda$). From this relationship, the energy imparted at a given wavelength can be determined. Basically, the shorter the wavelength, the higher the energy. At 300 nm, for example, 95.3 kcal/mole would be imparted to the molecule, which is sufficient to disrupt most covalent



Photodynamic Action in Pest Control and Medicine, Figure 45 **Solar radiation and its participating spectra received at the Earth's surface: i.e., (1) ultraviolet (≤400 nm), (2) visible light including violet (abbreviated by V; ca. 400–420 nm), green (420–490 nm), yellow (490-ca 600 nm) and red (600–700 nm), and finally (3) infrared (700–900 nm). Adapted from The Ozone Layer (UNEP, Nairobi, 1987).**

bonds. Basic to any energy transfer is that the molecule in question must exhibit an absorption spectrum at the wavelengths of excitation, and this absorption generally follows Beers law ($I = I_0 10^{-Ebc}$).

Phytodynamic action begins when a sensitizer (Sens) absorbs light, giving an excited state (Sens*), often (but not always), the triplet. Sens* can either react directly with the substrate (Type I reaction; less common) or with oxygen (Type II reaction). Therefore, high substrate concentrations (as well as electron-rich or hydrogen-atom-donating substrates) promote Type I reactions and high oxygen concentrations favor Type II reactions. Furthermore, in biological systems, where binding of sensitizer to substrate is common, Type I reactions are particularly favorable. While a type I reaction results in hydrogen atom or electron transfer, yielding radicals or radical ions, a type II reaction leads mainly to singlet molecular oxygen by energy transfer.

Singlet oxygen can be produced in high yield in the Type II reaction by energy transfer from Sens*. It is an electronically excited state of oxygen, with a lifetime that varies about 3–4 µs in water and as long as 0.1 s in solvents with no hydrogen atoms. In biological lipids and membranes, it probably has a lifetime considerably shorter than that in most organic solvents because of quenching by proteins and escape from the membrane into cytosol. The mechanism of action of the halogenated xanthene dyes such as rose bengal and erythrosin is considered to occur by a Type II mechanism.

The dye photosensitizer does not enter into the toxic reaction. The photosensitizer is a catalyst, not a participant. A single dye molecule is able to cycle through light absorbance, movement to the excited singlet state, transfer to the excited triplet state, sensitization of the ground state oxygen to the excited singlet state, and eventual return to the ground singlet state of the dye in approximately 10 ms, or less. It is then possible that a single dye molecule could be responsible for the generation of thousands of molecules of singlet oxygen per minute. A single dye molecule is then capable of initiating oxidation reactions which can destroy thousands of different target molecules rather than the single target molecule destroyed by a single organophosphate molecule, for instance.

Photodynamic action (photochemical damage by oxygen) is caused by oxidation of biological target molecules, and can lead to (i) membrane lysis by oxidation of unsaturated fatty acids and cholesterol, (ii) enzyme deactivation by oxidation of amino acids (methionine, histidine, tryptophan, tyrosine and cysteine), and (iii) oxidative destruction of nucleic acid bases (primarily guanine).

The responses of living organisms to photosensitized modification are varied, ranging from mild irritation to death. The precise nature of the response depends on many factors, but the majority of cases can be explained based on the changes produced in individual cells. Cellular photomodification is in fact a multi-step process which is carried out in six steps.

Step 1: The photosensitizer must get to the target cell. This involves introduction into the organism during feeding, via injection or diffusion. Once in the organism, the photosensitizer may be carried in combination with proteins, lipoproteins, or other molecules. At the target cell, the photosensitizer may need to diffuse through a vascular wall, a cell wall and/or a cell membrane. Ultimately, it must localize at or near the site of photomodification. Variations in any of these processes can significantly alter the final effect.

Step 2: Once the sensitizer has reached its site of action, it may remain free or may be bound to various biomolecules. It can also be metabolized to a form that may be more effective or less effective as a photosensitizer. The use of precursors, such as δ-aminolevulinic acid which is metabolized by the organism to a photosensitizing porphyrin, is an example of this possibility.

Step 3: At the site of action the sensitizer must be able to absorb light. This ability can be altered by the environment and physical state of the sensitizer in the organism. Binding, aggregation, metabolism and altered dielectric constant (as in a lipid membrane) are all variables that may significantly alter the absorption spectrum of the sensitizer.

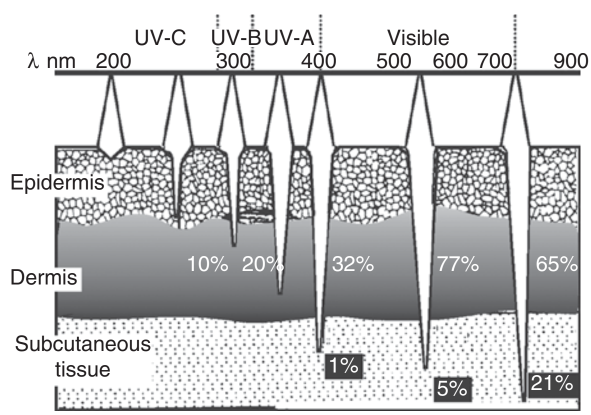
Step 4: After absorbing light, the sensitizer must make use of the energy in a way that effects a change in the cell. It may transfer energy to oxygen creating an electronically excited state such as singlet oxygen, which can then react with a cellular structure nearby. Alternatively, it can react directly with cellular biomolecules. But, in the cellular environment, it may also be quenched by the impressive array of antioxidants available in cells. Therefore, the excited state properties and reactivities of photosensitizers in vivo will not always be the same as they are in simple solution.

Step 5: The next step is the reaction of either the excited state sensitizer or a reactive intermediate, such as singlet oxygen, with cellular biomolecules which critically impair cell function and/or survival. Many biomolecules and cellular structures are photomodifiable, but not all of these affect cells in ways that result in cell death or irreparable damage. For example, it has been known for many years that cell lipids are peroxidized by photosensitized modification, but a definitive link between that peroxidation and cell killing has remained elusive.

Step 6: Finally, if enough critical cells in an organism are affected, then the foregoing steps will result in death or impairment of function. While each of these steps is critical and can significantly affect the degree of cellular modification, an in-depth analysis of Step 5 follows, namely the reactions of photosensitizer and light which lead to the critical impairment of cell function.

Effects of Photosensitizers and Light on Cells

Photosensitizers and light can affect a variety of biomolecules and cellular structures. Proteins, lipids and nucleic acids are all susceptible to photomodification. Carbohydrates are much less sensitive. This means that direct effects on cellular energy stores in the form of glucose or glycogen are unlikely to be significant. Conversely, effects on enzymes, nuclear DNA and lipid membranes may be important. Several sensitizers are accumulated in lysosomes where they may sensitize swelling and increase permeability of the lysosomal membrane allowing enzymes to be released from the lysosome. Other sensitizers seem to localize in mitochondria where they cause swelling and can affect the function of membrane-bound enzymes involved in energy production for the cell. Finally, a large variety of sensitizers, including many of the porphyrins and xanthene dyes, localize in the plasma membrane (and perhaps other membranes) altering the permeability properties of the surface membrane of the cell when illuminated, either by affecting membrane proteins or lipids. To summarize, photodynamic action involves photooxidation of various substrates which results in inactivation of biological systems, distortion of membranes, inactivation of enzymes, photocarcinogenesis, cell death and losses in other functions (Fig. 46).



Photodynamic Action in Pest Control and Medicine, Figure 46 **Extent of penetration of ultraviolet (UV) and visible light into human skin. The drawing is from the late BE Johnson, Department of Dermatology, University of Dundee (Scotland, UK). Courtesy of Springer Verlag and the editors of Photosensitization: Molecular, Cellular and Medical Aspects (G Moreno, RH Pottier, TG Truscott: 1988).**

How Do Photosensitizers and Light Kill Cells?

The above-mentioned effects of photosensitizers and light on cells offer many possible means by which a cell may be killed. Lysosomes may release degradative enzymes into the cytoplasm, mitochondrial production of ATP may be inhibited, plasma membrane barrier function may be compromised, and DNA damage may prevent cell replication and/or impair transcription required for protein synthesis and normal cell function. But some of these effects are critically related to cell death and others are merely consequences of the process of cell death.

Presently two major forms of cell death are recognized. One form, known as necrotic death or necrosis, is a degenerative cell death resulting from severe cell injury. The second form, known as apoptotic death or apoptosis, is a programmed cell death which is a cellularly controlled process. The death can occur under pathological conditions, such as cell injury, but also appears to be the mechanism by which organisms delete certain cell populations when they are no longer needed in the developmental process. While a hallmark of apoptosis is a selective cleavage of DNA, necrosis produces a random degradation of DNA.

An increase in intracellular calcium concentration has been suggested as the trigger of both forms of cell death (i.e., apoptotic and necrotic). Even cells which tolerate transient elevation of intracellular calcium concentration as part of their normal function, e.g., contracting cardiac cells where such elevation of calcium serves as the trigger for contraction, cannot tolerate this increased concentration continuously. It is well known that cardiac cells are susceptible to destruction by calcium overload. It has been documented that cellular photosensitization produces cell death by an apoptotic mechanism. Although apoptosis is a carefully orchestrated series of reactions within the cell leading ultimately to death, calcium is the trigger for this process. Thus, one should look for the mechanism that can increase intracellular calcium concentration as the seminal effect of photosensitization. As it is known that cell membranes are responsible for maintaining the very low calcium concentrations inside normal cells, i.e., 10^{-7} M, an obvious way for such increase is by a change in membrane permeability to calcium.

Multiple Mechanisms of Xanthene Dyes in Insects

Based on the foregoing studies on the toxicity of several xanthene dyes on insects, multiple mechanisms should be considered: e.g., light dependent mechanism, light independent mechanism and developmental toxicity mechanism.

Light dependent mechanism (or photodynamic action) in insects involves the ingestion of the dye by the insect, followed by exposure to a visible light source which results in the death of an insect. It is quite fast and needs comparatively lower concentrations of the photosensitizer and a source of light. In contrast, the light independent mechanism is slow, needs a higher concentration of sensitizer and operates in the absence of light.

In the developmental toxicity mechanism, the insect is exposed to a sublethal dose of the compound in the earlier stages of development. This results in mortality or some adverse morphological abnormalities during development, such as delayed development, growth retardation, and changes in fecunditiy and fertility.

Photodynamic Dyes

With the exception of hematoporphyrin, a substance known to be derivable from hemoglobin or hemin, other dyes studied for their photodynamic action are mainly confined to the synthetic dye molecules with halogenated structures.

The first documented (although qualitative) study in which light was understood to cause an enhancement of a chemically induced toxic effect was that of A. Marcacci in 1888. He reported that alkaloids were more effective against seeds, plants, fermentations, and amphibian eggs in sunlight than in the dark. This appears to be the first formal report that some materials have a light-enhanced toxic effect, even though a few dyes were already used for their anti-bacterial properties without recognition of the involvement of light action.

In 1900, a study on the toxicity of a dye (acridine) toward paramecia reported the results of the first quantitative studies on photodynamic action. Low concentrations of acridine and other dyes (at 50 ppm), which had no effect on microorganisms such as paramecium in the dark, were found to lead to a rapid death on illumination in the presence of oxygen. An increase of 2–3 orders of magnitude in the acridine sensitized mortality of paramecia was recorded. Also, those light rays which generated the greatest fluorescence in the dyes induced the largest biological reaction.

Following this discovery, it was soon established that many dyes and pigments could sensitize almost any type of biological system (plants, animals, cells, viruses, biologically important molecules) and result in cell damage, induction of mutations or cancer, and death.

Photodynamic Effect of Rose Bengal and Erythrosin Against Insects

The first reported use of photodynamic action against an insect target was a study of *Anopheles* and *Culex* mosquito larvae, which were shown to be susceptible to solutions of several classes of dyes in direct sunlight. The most active dyes were the halogenated fluorescein derivatives, erythrosin and rose bengal, alone and in mixture. There were no deaths reported from populations used as control for the effect of dye or light alone. A mixture of rose bengal and erythrosin was found to be the most effective, showing high larvicidal activity at a dilution of one part of dye-mixture in 1.5 million parts of water in direct sunlight. Damage to larval alimentary tract was noted.

Another study found that *Anopheles maculipennis* larvae with a series of dye solutions (10 ppm (W/V)) and exposed to sunlight were sensitive to dyes. Field tests in small ponds demonstrated that rose bengal or acridine red caused 100% mortality, and erythrosin in about 90% mortality. However, eosin and fluorescein were ineffective. The larvae of another species of *Anopheles* (*A. superpictus*) and those of *Aedes aegypti* were also similarly sensitive, whereas there was no effect on the mosquito fish (*Gambusia* sp.) that were present.

The modern era of photodynamic insecticide studies began with the report of T.P. Yoho and associates in 1971. The paucity of literature on the effects of phototoxic agents on insects, until this period, is not surprising. Light often has been a forgotten or underestimated factor in the study of insects. Even until recently little attention has been paid to its role as a parameter in the mortality of insects.

Yoho's group at West Virginia University published several investigations on the efficacy of photodynamic action against the adult house fly using primarily the halogenated series of dyes. These papers compared toxicological data with the parameters of light source and intensity, dye structure and concentration in the diet, source of light, and length of light exposure. It was observed that all house flies fed on diets containing either rhodamine (625 ppm) or erythrosin B (1,250 ppm) were killed after a 3-h exposure to light, whereas, when the dye-fed house flies were kept in the dark, no adverse effect was observed. It was also reported that the midgut epithelial cells appeared to be damaged and that the external symptoms associated with toxicity suggested an involvement with the nervous system.

Yoho and associates also studied a series of 14 food, drug and cosmetic dyes for efficacy in photodynamic toxicity to house fly adults. Nine of the 14 dyes tested produced up to 100% mortality in illuminated flies, particularly in those receiving liquid diets with a concentration as low as 0.25% dye (2,500 ppm). Lower concentrations were not tested.

The results of these investigations motivated other scientists to work on insecticidal properties of a series of common dyes. It also led to the registration of a formulation of erythrosin B under the name of "Synerid."

Practical Aspects of Erythrosin B in Insect Control

In 1980, G. D. Pimprikar and associates reported on their attempts to control house flies in a commercial caged layer house, under minimal light, using weekly applications of aqueous solutions of erythrosin B directly on the manure (about 650 mg a.i./m^2). They reported decreases of adults and larval house flies up to 90% with respect to pretreatment levels with no change in the beneficial soldier fly larval population. Their additional studies on the effects of several fluorescein derivatives in the diet on each developmental stage of the housefly revealed that the treated adults exhibited lowered fecundity, the eggs had a reduced viability, and mortality was observed in each life stage of the house fly. This experiment which was also conducted under minimal light, required a relatively large amount of dyes for 100% mortality: e.g., 0.5 g a.i./kg diet for rose bengal and 2 g a.i./kg for erythrosin B.

In 1981, T. L. Carpenter and associates reported on the role of fluorescein on enhancement of the phototoxicity of rose bengal, and some other xanthene dyes, towards *Aedes* larvae. Subsequently, a United States patent was issued covering the synergism of a nontoxic dye with a demonstrated toxic dye in both house fly and mosquito systems. Further studies resulted in an over twofold increase in the toxicity of erythrosin B against house flies.

In 1983, N. C. Respicio and J. R. Heitz reported development of resistance to erythrosin B in the house fly. While a laboratory strain developed only sixfold resistance after 40 generations, a wild strain experienced a 48-fold resistance after 32 generations of exposure to increasing levels of erythrosin B in the diet. Upon removal of the selection pressure for 20 generations, the resistance remained constant. Furthermore, the erythrosin B-resistant strain was cross-resistant to phloxin B and rose bengal, as it is to be expected since they function by same mechanism. Whereas, no cross-resistance of the resistant strain to conventional insecticides was observed.

In 1984, Primprikar and Heitz observed an unusually high insecticidal activity in *Aedes* mosquito larvae which had been illuminated after exposure to the insoluble free acid forms of the xanthene dyes. In all previous studies, the larvae had been treated with the water soluble salt forms of the dyes and the larvae consumed the dye as they ingested in the water. With the insoluble dyes they were able to filter feed on dye particles and thereby receive higher levels of these chemicals. Toxicity ratios ranged up to 2 orders of magnitude between the soluble and insoluble forms of the same compound.

A simultaneous report of Carpenter and associates showed that insoluble forms of the xanthene dyes were tenfold more effective against *Culex* mosquito larvae than the soluble forms, when used at the same dosage. They also reported that when the insoluble forms of the dyes were dispersed with a surfactant, such as sodium lauryl sulfate, the dyes were 50- to 60-fold more effective than the soluble forms. Depending on the concentrations under consideration, the increase in toxicity ranged from 26- to 229-fold for erythrosin B and 13- to 206-fold for rose bengal. Therefore, doses of free acid, dispersed formulations were in the lower ppm to upper ppb range for up to 24 h of light exposure.

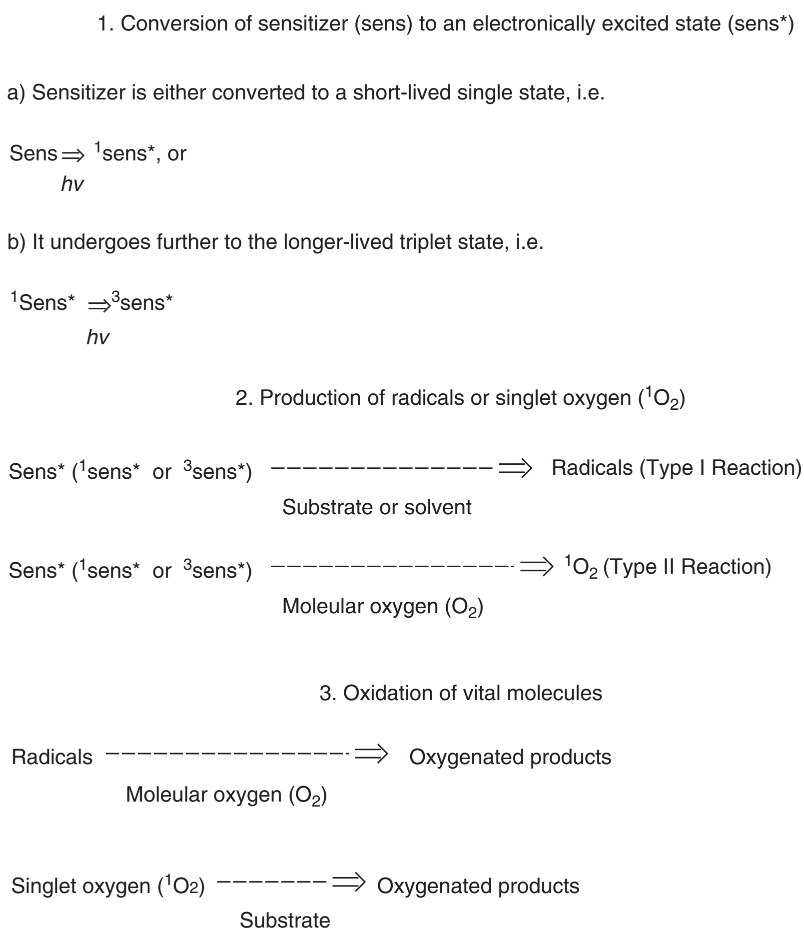
In 1985, Carpenter and associates reported that a series of eight dispersants for use with the insoluble forms of the dyes were evaluated and none were toxic alone. Erythrosyin B, dispersed with sodium dodecyl sulfate, was the most toxic against *Culex* mosquito larvae. In small-scale field tests, this formulation caused significant reductions in larval and emergent adult populations of *Culex* mosquitoes at concentrations ranging from 0.25 to 8.0 ppm. Nevertheless, possible limitation of the activity in "naturally basic waters," as a result of conversion of Erythrosin B to the soluble ionized form, was suggested.

Following the studies on phototoxic activity of erythrosin B against insects, a formulation of this dye has been registered under the name of "Synerid Fly Control B." Presently, this is the only dye commercially available for insect control.

Mode of Action of Photosensitizing Dyes in Insects

Photoactive dyes were found to have numerous effects on insects (Fig. 47). Acetylcholinesterase from the black imported ant and the boll weevil was susceptible to dye-sensitized photooxidation in vitro, but levels were not depressed in insects killed by photodynamic action. It was also reported that in the American or Oriental cockroach, photodynamic action induced by rose bengal or erythrosin B caused a significant decrease in hemolymph (over 90% reduction by erythrosin B) and a large increase in the crop volume (over threefold increase in erythosin B treatment). Furthermore, photodynamic action induced by erythrosin B resulted in up to 40% reduction of hemocytes relative to controls.

Under fluoroscent light and at rose bengal treatment levels of 1–20 ppm, *Culex* larvae were



Photodynamic Action in Pest Control and Medicine, Figure 47 **A schematized version of reactions involved in the process of photodynamic action. These include (1) conversion of sensitizer to an electronically excited state, (2) production of radicals or singlet oxygen, and (3) oxidation of vital molecules. Energy (E) imparted by this excitation is related to Planck's constant (h) and the frequency of radiation (v) (see the text).**

more susceptible than *Aedes* larvae, and early instars were more susceptible than later instars. Physiological and morphological abnormalities were observed in the pupal and adult stages when the mosquito was treated during the larval period, suggesting improper chitin formation in the insect. This sometimes resulted in incomplete release of the pupal stage from the larval cuticle and of the adult stage from the pupal cuticle. Where this was observed, mortality resulted. They also observed larval-pupal intermediates similar to those found after treatment with insect growth regulators.

The abnormalities observed in insects have led to the hypothesis that these photosensitizers may have an effect on the molting hormones. There is experimental evidence that the titers of the two most prominent molting hormones in insects (e.g., α-ecdysone and β-ecdysone) are distinctly different in the erythrosin B-treated insects as compared to the control insects. According to these studies the imbalance of the molting hormone titers during the critical stages of development may contribute to the abortive molting or to the development of morphologically abnormal individuals.

Persistence of Erythrosin in Biological System

In 1981, T.E. Fairbrother and associates made a comprehensive study of the toxicological effects of erythrosin B and rose bengal on the face fly. These dyes were incorporated with manure, either by hand or by passage of the dye through cattle. When larvae developed on the manure containing either erythrosin B or rose bengal, mortality was observed at each life stage. Wing deformation in some emerging adults and incomplete removal from the puparium were also recorded.

Adults, held from emergence and illuminated with visible light, were observed to have a much higher mortality than controls, thus suggesting that dye sequestered in the insect body during development from larvae to adult was responsible for the toxicity. This is the first report of photodynamic action occurring in a life stage different from the life stage in which the dye was ingested. This was confirmed in 1982 by studies of the inhibition of growth and the photodynamic action caused by rose bengal and erythrosin B in the housefly. House flies which had consumed a nonlethal amount of dye in the larval period exhibited a considerable light-dependent toxicity in the adult stage.

Effect of Photosensitizing Dyes on Other Organisms

Although most of the photodynamic studies with the fluoroscein dyes concerned insects, and to some extent other animals, phototoxicity of eosin to chloroplasts and that of erythrosin B to the infectious third stage larvae of gastrointestinal nematodes have been recorded. Furthermore, the effect of photodynamic action on the eggs of sea urchins also has been reported. Simultaneous irradiation of eggs of sea urchins (*Paracentrotus lividus*), incubated in 0.1 mmol/l solutions of two singlet oxygen sensitizers (i.e hematoporphyrin derivative- Hpd- at 60 ppm or rose bengal- RB- at 102 ppm solutions), led to different phototoxic reactions. For example, inhibition in formation of fertilization membrane (which is required to inhibit polyspermy), shrinkage of the egg surface, appearance of many small holes in the eggs, formation of larger holes, breakage of the eggs, and finally leakage of cytoplasm.

For additional information on properties of photosensitizing dyes refer to the following section.

Photodynamic Therapy

The use of photoactive dyes as therapeutic agents (i.e., photodynamic therapy) only began in the 1960s. In 1966, Lipson reported on the practical treatment of a patient with metastatic chest wall breast cancer by a hematoporphyrin derivative. Photosensitizing dyes are currently being investigated as potential agents in the photochemotherapeutic treatment of tumors and for other medical applications. In Canada, the use of hematoporphyrin derivatives in tumor phototherapy has recently received approval for clinical use. Furthermore, second-generation photosensitizers such as phthalocyanines or benzoporphyrins that absorb in the far-red or near-infrared region are receiving increasing attention because of the ability of light of these wavelengths to penetrate tissue. Such absorption properties would permit deeper penetration of exciting light into the skin and lower doses of photosensitizer.

The laser beam (632 nm) has also been successfully used for endoscopic photodynamic therapy of gastrointenstinal neoplasms, following a 60 min infusion of the patient with hematoporphyrin (2.5–5.0 mg/kg of body weight). Furthermore, the controlled application of photosensitization has been exploited for the relief of the symptoms of some skin diseases, and therapy of different types of malignant tumors.

Viral components, including nucleic acids and lipid-rich envelopes, are potential targets for photochemical attack. Indeed, a number of photosensitizers have been able to inactivate viruses at both the DNA and the envelope levels. Nevertheless, it has been shown that enveloped viruses are significantly more sensitive (by several orders of magnitude) to photodynamic destruction than are non-enveloped viruses.

Hematoporphyrin, also known as photofrin or porphyrin, is the only photosensitizer to date to have been used extensively in the clinical treatment of a variety of malignancies. Since it is activated at a wavelength of 630–635 nm, a wavelength that is seriously decreased by hemoglobin, its antiviral activity in blood (in vivo) is expected to be reduced. Notwithstanding this fact, it has been found to inactivate a number of human viruses in tissue culture or blood: i.e., HSV (type 1 and type 2), VSV, CMV, measles, SIV, and HIV (all of which are enveloped viruses). In contrast, non-enveloped viruses have been shown to be unaffected: e.g., ECHO 21, poliovirus (P1) and adenovirus (AD12).

Because there is differential photodynamic activity of hematoporphyrin on enveloped and non-enveloped viruses, inactivation of the virus envelope is suggested. Photoactivation occurs primarily as a result of the oxidative modification of the lipid and protein components of the viral envelope. The inactivated virus is then unable to adsorb to or to penetrate into host cells, hence it cannot initiate an infection or induce the formation of viral antigens. Two other groups of photosensitizers, psoralens and hypericin, also have been found to be virucidal agents.

Extent of Penetration

Although UV, visible, or near infrared radiation could be possible energy sources for photodynamic therapy of patients, UV radiation is considered disadvantageous because of low penetration. In the course of studies on photodynamic therapy of tumors in humans, it was soon recognized that by using hematoporphyrin derivative and long wavelength light (e.g., red: above 600 nm), both greater activity and deeper tissue penetration could be achieved. While UV penetration into tissue is estimated at less than 0.1 mm, the typical penetration depth in living tissue of the red light used for photodynamic therapy ranges between 1 and 3 mm.

Mode of Action in Photodynamic Therapy

Singlet oxygen is the basis for photodynamic killing of cells for several classes of sensitizers, including xanthene dyes such as rose bengal. Although both proteins and lipids are photooxidized, proteins are generally believed to be a critical target leading to the disruption of function in cell membranes. Singlet oxygen is a genotoxic substance which can be produced in vivo, inside or outside cells causing severe damage to various biological macromolecules, even to those deeply embedded inside the cells such as DNA.

Aerobic organisms have evolved antioxidant defenses against most reactive oxygen species (e.g., superoxide dismutase, catalase, glutathione peroxidase and DNA repair enzymes, and low molecular weight agents such as α-tocopherol, β-carotene and ascorbic acid), but the antioxidation mechanism does not appear to be always effective. In this case, when active oxygen species are not adequately removed, an oxidative stress situation appears in the cell resulting in major metabolic dysfunctions. These include membrane peroxidation, rise in intracellular free calcium ions, cytoskeletal disruption and DNA damage. Singlet oxygen can mediate the oxidation of major cellular molecules. DNA, proteins and lipids are all at risk. When singlet oxygen is generated inside cells, it is very genotoxic leading to an important mutagenic effect. When singlet oxygen is produced extracellularly, it reacts with the lipids of the cellular membrane as the major target. In addition, DNA also can be attacked. Reactions leading to peroxidation of the membrane and DNA are discussed by Legrand-Poels et al. (1993).

Effect on Tumor and Non-target Tissues

Tumor destruction in photodynamic therapy is the result of the combination of direct cellular toxicity and damage to tumor microvasculature. It has long been realized that a significant proportion of photodynamic tissue destruction involves the vasculature. These phenomena appear to be caused by tissue interactions with toxic oxygen compounds which are formed when light interacts with photosensitizing agents.

The targets of photodynamic sensitizers such as hematoporphyrin are predominately the plasma membrane, mitochondria and lysosomes and, to a lesser extent, nuclear sites. Photodynamic treatment has been reported to affect transmembrane transport systems in fibroblasts, to influence lipid bilayer membranes, and to alter membrane potential in renal cells. Although nuclear aberrations, mutagenicity, micronuclei and strand breakage occur in photodynamically treated patients, the induced abnormalities may not be severe enough to cause side effects in these patients. However, there is no question that major changes occur to both tumor and surrounding normal microvasculature during and following photodynamic therapy. Changes in the endothelium, smooth muscle contraction, and increased capillary permeability have also been observed during therapy.

In addition, the oxidative stress which is mediated by intracellular generation of singlet oxygen by rose bengal photosensitization in cell culture, has been found to reactivate HIV-1 from latently infected lymphocytes and monocytes. It is a possibility that HIV-1 reactivation caused by rose bengal leads to AIDS progression by impairing the antigen presentation function or increasing infection of the adjacent T cell population of the skin, in vivo.

Cellular porphyrin distribution by fluorescence microscopy shows staining of the nuclear membrane without induction of damage. Recent experiments revealed an initial fast (within minutes) and uniform penetration of the dyes into the nuclear envelope and chromocenters. This may indicate that the matrix between the nuclear membranes is a primary target for the dyes.

Risks and Benefits

Analysis of the risks and benefits of photodynamic action is very complex, especially when the photodynamic therapy of patients suffering from malignancies, AIDS or other disorders is taken into consideration and photodynamic effects in humans such as photosensitive porphyrias (i.e., porphyrin metabolism disorders), drug photosensitivity, and photoallergies are included.

With the application of laser beam technology in endoscopic photodynamic therapy, successful treatment of certain internal cancers has been achieved (e.g., gastrointenstinal neoplasms), and experimental results from photoinactivation of viruses by hematoporphorin derivatives in cell-containing blood products also are promising. In fact, with the impressive light-mediated activity of hematoporphyrin, a new chapter in clinical trials for the treatment of HIV-infection and AIDS has been opened. Furthermore, the discovery of the second-generation photosensitizers that absorb in the far-red or near infrared region (e.g., phthalocyanines or benzoporphyrins) is promising because of the ability of these light wavelengths to penetrate tissue. Such absorption properties would permit deeper penetration of exciting light into the skin and lower doses of photosensitizer.

The simultaneous appearance of numerous reports on the success of phototoxins as insecticides also has played a great role in a growing optimism concerning the future of photodynamic agents in agriculture. This is manifested by the recent registration of erythrosin B in the U.S.A. for insect control.

Both the economic and the environmental aspects of using photodynamic pesticides, with special reference to dyes, have been studied. While some literature lists the prospects of using photodynamic dyes, others suggest the potential dangers of food, drug, and cosmetic dyes. Often they are considered to be extremely safe and pose no threat to the health or welfare of the applicator or environment in field usage, with many of them being registered as food additives. Arguments have been presented for speedy registration, requiring few label restrictions, and limited toxicological testing of the photoactive dyes.

An important reason for serious concern about the environmental threat of the photodynamic agents is the method by which their toxicity is evaluated. Since light has not been considered as a parameter, in many toxicological data which are usually presented by LD_{50} for rats or mice, the validity of such data needs to be reexamined before making a general conclusion on safety.

Because the time required for initiation of phototoxicity is very low, detoxification does not appear to prevent sublethal toxicity. Therefore, development of new strategies in the marketing of foods, drugs and cosmetics and new techniques in toxicological studies of these compounds (using light as a parameter) is indispensable. More needs to be known about the long-term effects of these materials and their terminal residues, including their use as insecticides.

References

Blum HF (1964) Photodynamic action and diseases caused by light. Hafner Publishing, New York, NY, 309 pp

Fondu M, van Gindertael-Zegers H, Bronkers G, Stein H, Carton P (eds) (1988) Food additives tables, updated edition. Compiled by Food Law Research Centre, University of Brussels. Elsevier, Amsterdam, The Netherlands (unpaginated)

Heitz JR, Downum KR (eds) (1987) Light-activated pesticides. ACS Symposium Series 339, Washington, DC, 339 pp

Heitz JR, Downum KR (eds) (1995) Light-activated pest control. ACS Symposium Series 616, Washington, DC, 279 pp

Legrand-Poels S, Hoebeke M, Vaira D, Rentier B, Piette J (1993) HIV-1 promoter activation following an oxidative stress mediated by singlet oxygen. J Photochem Photobiol B 17:229–237

North J, Neyndorff J, Levy JG (1993) Photosensitizers as virucidal agents. J Photochem Photobiol B 17:99–108

Photokinesis

Kinesis response with respect to a gradient of light.

Photoperiod

Daylength. Length of daylight during a 24-h day-night cycle.

► Diapause

Photoperiodism

Response of an organism to periodic changes in day length.

Photosynthesis

The utilization by plants of the energy provided by sunlight to split water and fix (synthesize) carbon dioxide into sugars.

Phototaxis

The taxis response of a cell or organisms toward or away from light.

Phragma (pl., phragmata)

An internally projecting structure or internal ridge in the insect body, usually an extension of the endoskeleton, but also a membrane that partitions the body.

Phragmosis

A condition in which the head or tip of the abdomen is used as a plug for the nest entrance. This behavior occurs in ants and termites, usually performed by the soldiers.

Phthiriasis

A disease of the skin resulting from an infestation of sucking lice (pediculosis).

► Human Lice

Phthiraptera

An order of ectoparasitic insects affecting mammals and birds. Considered by some to be divided into two orders, Mallophaga (chewing lice) and Siphunculata or Anoplura (sucking lice).

► Chewing and Sucking Lice

Phyletic Lines

Links drawn between present and past taxa that imply their evolutionary relationships.

Phyletic Speciation

The gradual transformation of one species into another without an increase in species number at any time within the lineage. Also called vertical evolution or speciation.

Phylogenetic Tree

A graphic representation of the evolutionary history of a group of taxa or genes.

Phylogenetics

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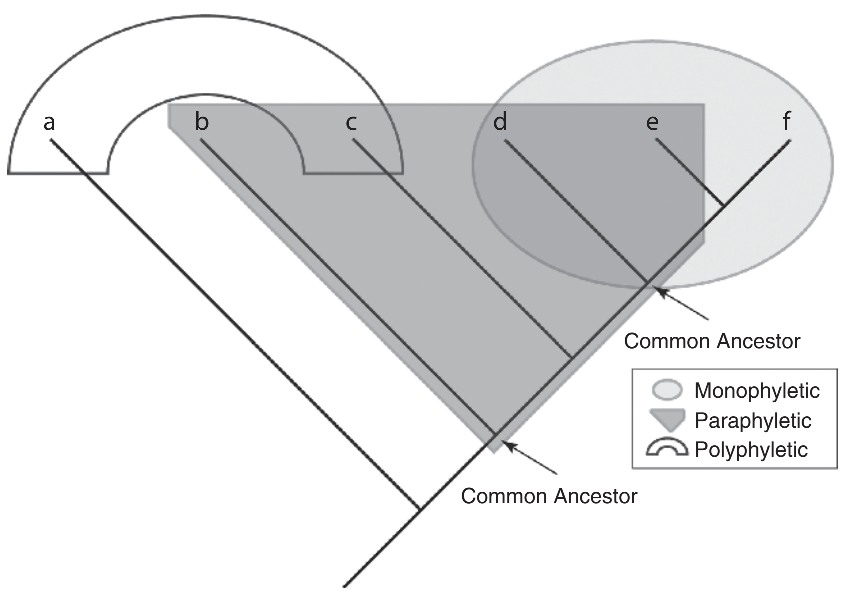
Phylogenetics is a relatively young and rapidly growing subdiscipline of the much older and larger discipline known as systematics. There are three complementary subdisciplines within systematics: taxonomy, classification, and phylogenetics. While taxonomy is used to describe the Earth's biodiversity through identifying "kinds" and placing like kinds into definable groups, based on variation (usually termed species), and classification is used to arrange these species into a hierarchical scheme of relationships (class, order, family, etc.), phylogenetics is often used to unite both taxonomy and classification by organizing the accumulated data from each species into groups representing a broader biological context. This context is usually one of evolutionary significance. One of the main purposes of phylogenetics is to unite related organisms into a natural or monophyletic group. A monophyletic group is an assemblage of organisms that includes a common ancestor and all of its descendants. Occasionally, taxa are assembled into groups that represent artificial groupings of organisms, i.e., those which are not natural. These groupings, which are called para- or polyphyletic, have fallen into disfavor as they exclude closely related taxa. A paraphyletic group contains a common ancestor but does not include all the descendants of that ancestor. A polyphyletic group does not contain the common ancestor nor all close relatives of a group of taxa. Determining whether a group is mono-, para-, or polyphyletic is done by including species of a hypothesized group in a phylogenetic analysis, which groups species based on inferences of their shared ancestry (Fig. 48). Homology is the similarity of biological structures due to shared ancestry; thus statements of homology are hypotheses about the origin and similarity of biological features among organisms. There are many forms of biological data upon which homology statements can be based, such as DNA, morphological, or behavioral data. Phylogenetics offers a rigorous framework by which multiple homology statements can be tested simultaneously, resulting in phylogenetic trees that represent patterns of relatedness, like a very large "family tree." Phylogenetics is the process by which hypotheses of evolutionary relationship (phylogeny) can be formulated and tested. A revised classification is a desired outcome of phylogenetics.

Since phylogenetics is dependant on our ability to make homology statements based on data gathered from both extant and extinct organisms, a knowledge of Earth's biodiversity is essential. Building phylogenetic trees that reflect monophyletic groups is essential to scientists researching the processes of evolution. Many insects have interesting behaviors such as flight, communication and sociality, to name only a few, that are central to understanding many of the biological processes observed among insects and that have served to shape their evolutionary history for millions of years. The phylogenetics of insects is made more interesting given that insects are the most diverse group of organisms on the planet, and as such, they have the most diverse range of morphologies, behaviors, ecological adaptations and natural histories. Organizing the diversity of



Phylogenetics, Figure 48 **An illustration of the three types of groupings: monophyletic, paraphyletic and polyphyletic. Phylogenetics seeks to identify, categorize and name only monophyletic groups. Note that there is no common ancestor for a group that is polyphyletic.**

insects into monophyletic groups within a phylogenetic framework is a major task and will be the chief focus for the field of phylogenetics for many years to come.

What Types of Data Are Used in Insect Phylogenetics?

Phylogenetics is dependent on data gathered from heritable variation that can be directly compared via homology statements. Scientists have to be sure that each character within the data set being compared is homologous across all species or kinds in the data set. For example, it would not do to compare the elytra of a beetle with the wings of a bird because beetle elytra and bird wings do not share a common origin, have special similarity or share similarity in their position, even though they are both part of the flight mechanisms for their respective organisms. Structures such as bird wings and beetle elytra share no evolutionary or developmental past and are called analogous characters. Only homologous characters should be used within a phylogenetic analysis. Traditionally, the most common type of data used within insect phylogenetic analyses is morphological data, although molecular data is fast becoming the norm among most of today's phylogenetic research. Other types of information such as behavior, ecology, physiology and developmental characters can also be used to reconstruct phylogenetic relationships.

Morphological Data

Insects have a great deal of morphological variation due to the number of ecological niches they inhabit and their diversity. Insects make use of most of the organic materials on Earth, from dung to flesh, from fungi to trees, and from mud to silk. Insects eat, produce, construct, and even culture these materials. The morphological diversity and innovation found among insects is unmatched by any other group of organisms. This astounding morphological variation is made even more impressive by the insect's ability to metamorphose. While many insects, such as grasshoppers, feed on the same diet and inhabit a similar ecological niche their whole lives, most holometabolous insects exhibit morphological changes reflective of a shift in ecological niche during the immature and adult life stages. For example, female mosquito larvae have opposed mandibles and feed mostly on detritus or micro-organisms. However, as adults their mouthparts have become modified into a serrated syringe-like structure suitable for piercing skin and extracting blood. There are also extreme shifts in the morphology of some hemimetabolous insects due to changes in ecological niches during the immature and adult life stages. For example, mayflies, dragonflies and stoneflies are aquatic during their immature stages and undergo large morphological changes in gill, eye, and skeletal morphology to become successful terrestrial adults. Many insects undergo lesser modifications of their morphology between instars (each developmental stage between moults (ecdysis) until the adult stage is reached) such as praying-mantids, true bugs, thrips, and strepsipterans. These shifts in morphology have evolved in response to factors such as food shortages, the need for protection, or life stage requirements.

Morphological data is also crucial to phylogenetic studies that seek to include insects from the fossil record since fossils (with the rare exception of some encased in amber) by definition lack DNA. Fossils also play a major role in allowing scientists to better understand the current morphological adaptations we see among related present-day taxa because they often exhibit the more primitive forms of morphological features.

Molecular Data

Today phylogenetic analyses are increasingly including molecular data for several reasons. Over the past decade, the amplification, comparison and analysis of DNA sequence data have become more straightforward, reliable, faster, cheaper, and more routine than ever. This trend will likely continue. Further, both mitochondrial and nuclear genomes are being isolated from insects to form phylogenetic hypotheses. There are, however, still challenges to using molecular data within a phylogenetic context. The software used to align sequence data (i.e., provide homology statements between nucleotides of a DNA sequence) and perform phylogenetic analyses is still inadequate for large data sets consisting of more than ~600 specimens for only a few genes. Nonetheless, molecular methods have proven to be very powerful and insightful for resolving many questions concerning insect phylogenetics.

Molecular data has also proven to be helpful when resolving relationships among species or groups of insects that have evolved unique morphological or behavioral adaptations that are difficult to homologize with existing data (see below, What is going on in insect phylogenetic studies?).

Combined Analysis or Total Evidence

It is widely accepted that a powerful approach for generating phylogenetic hypotheses is to combine large amounts of morphological and molecular data within a single analyses. This is referred to as a combined or total evidence analysis. This approach is generally preferred because it allows molecular, morphological, and any other type of data, to influence the resulting phylogenetic hypothesis in the same analysis simultaneously. This technique often produces more robust estimates of phylogenetic relationships and evolutionary hypotheses than when using only one type of data. Simply put, a total evidence analysis produces a phylogenetic hypothesis generated from the largest amount of data at hand and in which all the data contributes to the construction of the hypothesis.

What Are the Major Modern Methodologies Used in Phylogenetics?

Phylogenetic analyses result in tree diagrams called phylogenies, or simply, trees. Tree reconstruction within phylogenetics is no simple task. The number of possible trees increases dramatically as the number of taxa (individual specimens or gene sequences) included in the analysis increases (Fig. 49). The total number of possible trees for a given number of taxa (n) can be determined with the following formula:

$$\frac{(2n-3!)}{2^{n-r}(n-2)}$$

As there are so many potential trees when even a small number of taxa are included within a phylogenetic analysis (e.g., ~14 million potential trees for 12 taxa), there are multiple methods for tree reconstruction currently employed today. Modern analyses are performed almost exclusively using three major methods: Maximum Parsimony (called simply MP or parsimony) and two model based statistical approaches: Maximum Likelihood (ML) and Bayesian.

Maximum Parsimony

Maximum Parsimony (MP) is simplistic in its approach to phylogenetic analysis. MP finds its origins in "Occam's Razor," *lex parsimoniae*, which states that the explanation of a phenomenon that makes the fewest assumptions is the preferred explanation. Trees are scored such that the most parsimonious, or simplest, explanation for relationships among the taxa included in the analysis given the data is most defensible. Thus, the tree that is most parsimonious has the fewest evolutionary steps and is the favored hypothesis. This approach does not mandate that evolution always occurs in a parsimonious fashion, but rather uses the principle of parsimony to choose among competing phylogenetic hypotheses (i.e., phylogenetic trees).

MP is commonly used among entomologists, especially those using morphological data. It is also useful for molecular sequence data and generally gives very similar results to those generated by both maximum likelihood and Bayesian approaches. The most often cited weakness of MP is that of "long branch attraction" when using molecular data. Because there are only four possible nucleotides at any given site along a DNA sequence, the result is an increased probability of two or more taxa with rapidly evolving DNA (i.e., high substitution rates) to evolve the same nucleotide at the same position. Long branch attraction takes place when at least two taxa representing rapidly evolving lineages are inferred to be closely related, due to similarities along their rapidly evolving DNA, when in fact they are not. This problem is often overcome in MP analyses by including a broader range of taxa and thus more diversity in molecular sequence data that serves to break up phylogenetic relationships that could be potentially recovered as a result of long branch attraction.

Statistical Approaches

Maximum Likelihood (ML). ML is used with molecular sequence data and is a more complex approach to tree reconstruction than MP. ML differs from MP in that an explicit model of sequence evolution is used to provide an approximation of the data's origin. In addition, because this approach is model-based, it is viewed as a parametric approach to estimating phylogenetic hypotheses. ML is seen by many systematists as a more attractive method because of its statistical foundation.

Although becoming more rapid, ML is still a slow process for large data sets. Until computer computational power catches up with the demands of imposing a complex model over large molecular data sets, MP will continue to be used. However, ML is probably used more often than parsimony for moderately sized data sets. In general, both ML and MP usually converge on the same phylogenetic relationships. Although ML outperforms MP in some respects (e.g., it is less susceptible to long branch attraction), its utility is directly linked to the ability of the model used during tree reconstruction to represent the data accurately. A model that does not accurately represent the data will bias the resulting tree.

# of taxa	Resulting # of possible trees
3	3
4	15
5	105
6	945
7	10,395
8	135,135
9	2,027,025
10	34,459,425
11	654,729,075
12	13,749,310,575
13	316,234,143,225
14	7,905,853,580,625
15	213,458,046,676,875
16	6,190,283,353,629,370
17	191,898,783,962,510,000
18	6,332,659,870,762,850,000
19	221,643,095,476,699,000,000
20	8,200,794,532,637,890,000,000

Phylogenetics, Figure 49 The approximated number of possible phylogenetic trees for 3–20 taxa (after Schuh (2000)).

Bayesian

This approach to tree reconstruction is a recent development but is becoming more and more prevalent. Bayesian phylogenetics finds its origins in Bayesian statistics, and uses *a priori* evidence (prior probabilities, although rarely used in phylogenetics) to infer a revised probability (posterior probabilities) that a phylogenetic hypothesis may be true. Bayesian analyses use the likelihood function and the same evolutionary models for DNA sequence data as ML. Just as with ML, an estimate of Bayesian phylogenetic relationships is only as good as the model used to estimate them.

Morphological models, that use the likelihood function generated from the data, can be employed in a Bayesian framework. These models have been shown to perform well with morphological data, demonstrating that simultaneous analyses of both morphological and molecular data can be performed using Bayesian as well as MP methods.

Bayesian analyses employ a Markov chain Monte Carlo process to provide a sample of trees based on their likelihood and thus can produce a credible sample of trees from which a probability of relationship among groups and taxa can be directly estimated. Many phylogeneticists view this ability, coupled with the speed of Bayesian analyses (which is generally much quicker than ML), as a great benefit.

What Is Going on in Insect Phylogenetic Studies?

Over the last decade there has been an influx of large scale phylogenetic studies undertaken by the entomological community. These efforts are producing significant phylogenetic estimates of relationship between the orders of insects and within some of the largest orders of insects (e.g., Hymenoptera, Lepidoptera, Diptera and Coleoptera). From these phylogenetic reconstructions, entomologists can directly test hypotheses of evolution and diversification across higher taxa.

Current research has led to the resolution of novel hypotheses concerning some of the more problematic relationships among the orders of Insecta. For example, (i) the relationship among the lineages of the group Dictyoptera (orders Mantodea, Isoptera and Blattodea) has long been in question and there is now an increasing amount of data that supports Isoptera as a derived group within Blattodea. Placing Isoptera within the Blattodea allows scientists to examine and answer questions concerning the evolution of gut endosymbionts that allow for the digestion of cellulose for both termites and some cockroaches. (ii) Strepsiptera has also been a problematic order as many systematists have long thought it was most closely related to Coleoptera. Currently, molecular data combined with morphological data support Strepsiptera as being most closely related to Diptera, forming the group Halteria, in reference to the halteres that both groups possess in place of well developed wings. This research has lead to the discovery that by manipulating only one gene, halteres can occur on either the meso- or metathorax. (iii) Another major dilemma within the classification of Insecta is the "Paleoptera problem." Paleoptera is composed of Ephemeroptera (mayflies) and Odonata (dragonflies and damselflies) and both are hypothesized to represent the most primitive forms of extant winged insects. The relationship between these two primitive groups of living insects as well as to the other insect orders has long been debated as these relationships appear directly linked to the origin and evolution of insect flight. The most convincing evidence to date is based on both morphological and molecular data which indicate the Ephemeroptera as the most primitive form of extant winged insects.

References

Grimaldi D, Engel MS (2005) Evolution of the insects. Cambridge University Press, New York, NY, 772 pp

Huelsenbeck JP, Crandall KA (1997) Phylogeny estimation and hypothesis testing using maximum likelihood. Annu Rev Ecol Syst 28:437–466

Huelsenbeck JP, Ronquist F, Nielsen R, Bollback JP (2001) Bayesian inference of phylogeny and its impact on evolutionary biology. Science 294(5550):2310–2314

Schuh RT (2000) Biological systematics: principles and applications. Cornell University Press, Ithaca, NY, 256 pp

Wheeler WC, Whiting MF, Carpenter JC, Wheeler QD (2001) The phylogeny of the insect orders. Cladistics 12:1–57

Phylogeny

The history of evolution of a group of taxa or their genes. The ordering of species and their ancestors into higher taxa based on evolutionary relationships.

► Classification
► Phyogenetics

Phylosphere

The microenvironment associated with an individual plant leaf.

Phylloxerans

Members of the family Phylloxeridae (order Hemiptera).
► Bugs

Phylloxeridae

A family of insects in the order Hemiptera. They sometimes are called phylloxerans.
► Bugs

Phylum (pl., phyla)

A unit of classification, one of the major divisions of the kingdom and containing several classes. Class Insecta generally is placed in the Phylum Arthropoda of the Kingdom Animalia, as follows:

Phylum: Arthropoda
- Subphylum Trilobita – Trilobites (these are extinct)
- Subphylum – Chelicerata
  - Class Merostomata – Horseshoe crabs
  - Class Arachnida – Arachnids (scorpions, spiders, ticks, mites, etc.)
  - Class Pycnogonida – Sea spiders
  - Subphylum Crustacea – Crustaceans (amphipods, isopods, shrimp, etc.)
- Subphylum Atelocerata
  - Class Diplopoda – Millipedes
  - Class Chilopoda – Centipedes
  - Class Pauropoda – Pauropods
  - Class Symphyla – Symphylans
  - Class Entognatha – Collembolans, proturans, diplurans
  - Class Insecta – Insects

In this classification system, the class Entognatha and the class Insecta are separate, though they can be placed together into the superclass Hexapoda. Formerly, however, Entognaths were commonly considered to be in Insecta. other variations also exist.
► Classification
► Orders

Physical Control

Control techniques that are based on physical properties of the environment to kill insects. examples of physical control include cold storage, heating, burning, and modification of the gaseous atmosphere in storage.
► Physical Management of Insect Pests

Physical Gill

A bubble of air that adheres to the body of aquatic insects, providing a reservoir of air or plastron.
► Tracheal System and Respiratory Gas Exchange

Physical Management of Insect Pests

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Physical control methods aim to prevent or reduce pest invasion into a crop. Various physical means function either mechanically or by affecting insects' viability or behavior. For example, insect suction devices, insect glue, and electromagnetic energy suppress insect populations. Insect exclusion screens also reduce insect density, though not through mortality. Also, color and chemicals are used to change insect behavior. Physical control methods may have some shortcomings, which must be weighed against their advantages. Physical control methods generally do not interfere with other control methods. Screens are often crucial for the implementation of Integrated Pest Management (IPM) programs. They enable the use of biological control agents as well as the use of insect pollinators. Generally, most physical control methods are environmentally safe, fit well into IPM strategies, and greatly reduce the use of chemical control.

Insect-Proof Screens and Covers

The physical exclusion of insects from a greenhouse or open field is aimed at preventing direct crop damage by insects in general, and the incidence of insect borne virus diseases in particular. Additional outcomes of the reduction of pest damage are a marked reduction in the use of pesticides, the ability to use biocontrol agents as a complementary control measure, and more effective use of insect pollinators. Pest exclusion can be obtained by applying appropriate fabrics, of mesh aperture smaller than the insects' body width, or by fitting insect repellent fabrics. These fabrics are positioned over the plants in open fields, or attached to ventilators and doorways of greenhouses. Due to the exclusion feature of the technique, the fabrics must be applied before the crop is sown or planted because they do not suppress insect populations. Screens impede ventilation and sunlight; thus, to avoid adverse effects on crops and their susceptibility to diseases, compromises are necessary in the management of air flow, light, temperature and humidity. Various types of screens and plastic covers are known to exclude insects, and the challenge for the grower is to select the type of screening best suited to solve his specific problems. Although screening is a very efficient way to prevent primary pest penetration, some pest individuals manage to enter the greenhouses, despite all efforts. These insects may build up an indoor population and cause damage. When they exceed the economic threshold level it is necessary to apply complementary control measures, such as biocontrol or environmentally safe insecticides, which would be useless without the netting. The success of pest exclusion, especially its success in preventing insect-borne viruses, has led recently to a rapid increase in the area of screened greenhouse, primarily in subtropical climate regions.

Specifications of Insect Exclusion Covers

Insect-proof covers are a general name for many types of plastic sheets and screens that prevent insects from reaching the crop. There are today several companies manufacturing or supplying screens differing from each other in aspects of mesh density and thread gauge. These variations provide differing rates of ventilation but also different rates of insect penetration. The optimal screen will be the one that maintains the indoor population density independent from the outdoor population density, but still allow ventilation. For example, if the accepted economic threshold level for tomato yellow leaf curl virus infection is 10% of virus-infected plants at the end of the season, the threshold for the whitefly population density in the greenhouse will be 1.4 whitefly/trap/day or 10 whiteflies/trap/week. As long as whitefly catches are below this threshold, growers do not need to apply complementary control means. Screens can solve the problem economically and almost by themselves. To be effective, screens must be installed prior to the pests' appearance; and all openings must be totally covered by screens, including the entrance, which needs to employ air locks. Screen maintenance (repairing rips) is of paramount importance. Furthermore, plants must be quarantined before they go into production areas, to ensure they are pest free before planting. Even with these precautions, which are not without cost, some penetration by pests may occur and require complementary pest control measures.

Microperforated and Unwoven Sheets

Agronet® and FastStart® are clear, microperforated polyethylene fabrics. Reemay® and Agryl are unwoven, polyester and polypropylene porous sheets. All are light materials (17 g/m^2) that can be applied loosely, directly over transplants or seeded soil, without the need for mechanical support. Plants easily support these materials. They are used in the open field, in early spring, as spun-bonded row covers, to enhance plant growth and to increase yield. At the same time, they also proved to protect plants from insects. Reemay® is known to efficiently protect squash from *Bemisia*-borne viruses (in California), and pepper from aphid borne viruses (in Spain). FastStart® protects plants from flea beetles, root flies, moths and insect transmitted diseases (in the U.S.). Indoors, Agryl® is used to protect organically grown tomatoes from virus transmission by *Bemisia* (in Israel). High environmental temperatures may damage plant parts that are in contact with the fabrics.

Woven Screens (Whitefly Exclusion Screens)

The conventionally woven "Whitefly Exclusion Screens" – generally known as 50-Mesh®, Anti Whitefly®, or AntiVirus®, and by many other commercial names – are produced from plain, woven, white plastic yarns. These screens are made of yarns 210–230 μm thick; 24–28 yarns/in. in warp (about 10/cm), and 54–56 yarns/in. (about 20/cm) in weft, resulting in slots of rectangular shape. The limiting factor for blocking the whiteflies is the smaller width of the slot, approximately 240 μm. Insects' ability to pass through a barrier cannot be predicted solely from thoracic width and hole size. Screens are three-dimensional fabrics with a specific hole geometry, which is an important element in insect exclusion. The blocking efficacy of any screen must be tested in laboratory and/or field trials. The elongated shape of the slot improves air and light passage. However, elongating the slot more will enable the threads to slide, and whiteflies to penetrate. These screens, though developed primarily to block penetration by *Bemisia* whitefly, also exclude all insects larger than *Bemisia*, e.g., moths, beetles, leafminers, aphids, plant hoppers, and psyllids; thus they also prevent epidemics of aphid-borne viruses.

Knitted Shade Screens

The mesh of knitted screens is defined by the percentage of shade (e.g., 30, 40 and 50%) that they produce. Because of irregularity in the shape of the holes, whiteflies are not excluded. Reducing the size of the screen holes until they are capable of blocking whiteflies reduces ventilation to an impractical level. However, insects bigger than whiteflies, and birds, might well be excluded.

Knitted-Woven Screen

A new type of plastic screen (SuperNet®) is under development. It is produced by a combination of knitting and weaving. This technique produces a screening with slots almost three times longer than those of the commercial woven screen, while keeping the width of the slot smaller than whitefly body size. This screen possesses high blockage capacity for whiteflies, similar to that of conventional woven screens, but with improved ventilation.

Thrips Exclusion

Thrips are the smallest of common insect pests, with a body width of only 245 μm. They move freely through whitefly-proof woven screens. However, thrips are strongly affected by color. As a result, a high proportion of the thrips population (50%) is excluded in the field, due to the optical features of the screen's material. To improve this still-insufficient rate of exclusion, a very fine mesh screen is needed (Bugbed-12®, NoThrips®), but this hampers ventilation too much. Nevertheless, a loose shading screen of aluminum color, through which even whiteflies penetrate freely, reduces thrips penetration by 55%, contrary to a screen, similar in structure but white in color, which attracts many thrips (similarly to a white mulch).

Greenhouse Ventilation, Insect Invasion and Screens

The use of insect-proof screens reduces natural ventilation, which may in turn increase temperature and air humidity to harmful levels. This is even more likely if the greenhouse area exceeds about 1,000 m^2. In this case, natural ventilation may become insufficient, because the area of the side-openings becomes proportionately too small for the greenhouse area. Consequently, natural ventilation becomes ineffective. Forced ventilation may minimize these harmful effects, but the type of ventilation system strongly affects the influx of insects into the greenhouse. The use of vents that exhaust air from the greenhouse causes underpressure, and many insects are sucked into the structure. Alternatively, overpressure, induced by actively pushing air into the greenhouse through an insect-proof filter, reduces the influx of insect pests significantly even in unscreened greenhouses. In large greenhouses (greater than 1,000 m^2) natural roof ventilation is crucial. Obviously, the roof openings must also be protected by an appropriate insect exclusion screen.

Insect Suction Devices

Efficient removal of certain flying and non-flying insects (e.g., aphids, Colorado potato beetles, leafminers, and whiteflies) is possible with modern vacuuming machinery. Vacuum treatments, applied either prophylactically or whenever the insect population exceeds a certain threshold level, reduce populations markedly. One of many examples is the Biovac, a tractor-propelled vacuum device that can be used to control tarnished plant bug populations in strawberry crops. Field trials have demonstrated the additional benefits of enhanced pollen dispersal in strawberries coupled with no reduction in beneficial honey bee pollinators (which are able to fly out of the path of the vacuum machine). Greenhouses present unique problems due to their physical structure, but special equipment could be developed, with vacuum machines running automatically on overhead tracks. Vacuum devices are completely compatible with all forms of pest control, and can even be used in biological control by reducing pest levels before releases of natural enemies.

Insect Glue (Polybutene)

"Insect glues," e.g., polybutenes, are synthetic hydrocarbon polymers. Glue viscosity is proportional to chain length; the longer the chain, the higher the viscosity. Viscosity ranges from 0.3, a liquid with little tackiness, to 600, a very viscous grease-like material with a high degree of tackiness. "Thripstick" is a commercial mixture consisting of polybutene, an emulsifying agent, an insecticide, and water. It is sprayed under greenhouse crops, either on the floor covering or the soil. It does not affect natural enemies. It has been used successfully to control two typical soil-pupating insects: thrips and leafminer flies.

Electromagnetic Energy

The effect of electromagnetic energy on organisms is incompletely understood, although in general, longer wavelengths produce heating effects and shorter wavelength radiation produces chemical effects, including ionization of the absorbing media.

Longwaves: Radio Frequencies (RF) and Infrared (IR)

The use of RF for pest control has been frequently considered, mainly in grains, foodstuffs, and wood.

RF energy was found to be effective against some moth larvae, e.g., the pink bollworm in cotton seeds. Still, no practical large-scale applications have been yet developed. It appears that major improvements in efficiency of RF treatments are necessary for the method to become practical. Potential uses of IR for insect control involve two generally different concepts. One concept is the use of radiation directly applied to the insects or to the infested material. The other concept is based on the insect's suspected ability to sense infrared radiation and man's ingenuity in employing this knowledge in some way to achieve control, e.g., by attracting specific insects to IR lured traps for monitoring and control purposes.

Ultraviolet (UV) Radiation

Insects (e.g., aphids, whiteflies and honey bees) are sensitive to much shorter wavelengths of light than man, and may visualize the part reaching into the UV portion of the spectrum. The responsive region for insects lies, generally, between 700 nm and about 253 nm. Insects respond to visible and UV radiation in many ways, physiologically and behaviorally. The insects may be affected by the quality, intensity, and duration of light, either directly or indirectly through the host-plant. One aspect of major interest for control is that of phototaxis, movement toward or away from light. The effect of UV radiation on insects' photoperiod, diapause, and sterilization are also of interest. Investigations on insect control with UV radiation have taken two approaches: (i) the use of low-level illumination to manipulate attractive or behavioral responses, and (ii) the use of high intensity irradiation that produces adverse physiological responses. UV (black light) lured traps are used to monitor noctuid insects. UV-absorbing plastic sheets, used as a greenhouse roof cover, reduce to some extent the immigration of whiteflies, probably due to a retarding effect of their UV reflection features. Exposure of newly emerged virgin adults of *Bemisia* for 15 min to the radiation of a "Hanovia model II" ultraviolet lamp, causes complete sterilization of the males and partial sterilization of the females. Sterilization of both male and female adults can also be induced by irradiation of pupae during the last day before emergence, whereas fecundity of females is not significantly affected.

Gamma Irradiation: A Postharvest Treatment

Whiteflies, leafminer flies, and thrips are considered "quarantine pests," even at numbers far below the conventional economic threshold. Gamma irradiation, originating from 60Co, is used with doses of 2.5–200 krad/h (25–2,000 GY/h). For example, 200 krad are lethal to eggs and all immature stages of the leafminer *Liriomyza trifolii* on bean seedlings. At doses of 75 krad or less larvae survive to pupate, but do not give rise to adults. Larval and pupal radiosensitivity decrease with increasing age. Eggs and prepupae are more susceptible to radiation than other stages. Very few flies emerge from eggs or first instar larvae irradiated by 4–5 krad, and those that do are all impaired and die within 24 h. Doses of 20 krad kill eggs and all larval stages of *Bemisia* on cotton seedlings. *Spodoptera littoralis* eggs in chrysanthemum flowers are killed by a dose of 50 krad, and neonate larvae by 125 krad. Consequently, the higher dose is suitable to eliminate the pest in flowers for export.

Air Ion Stimulation

In one study, an air ion generator-emitter complex, installed above tomato plants grown in a commercial soilless culture, caused a marked decrease in greenhouse whitefly infestation and no chemical treatment was needed. When the air ion treatment was halted for 10 days whiteflies appeared. When the air ion generator was reactivated, there was a prompt reduction in whitefly activity. It appears that negative air ions diminish whitefly activity and prevent their population growth.

Visible Light

Attractive Colors

Color lured traps are an efficient monitoring device. Yellow sticky traps are used for monitoring a insects such as whiteflies, aphids, thrips, and various flies (e.g., leafminer flies, fungus flies, etc.). Blue sticky traps are more specific, attracting mainly flower-infesting insects such as thrips and the flower chafer, *Epicometis squalida*. The highly significant correlation between the number of trapped whiteflies and the number of tomato yellow leaf curl virus infected plants turns the traps into a very helpful monitoring device for control decision making.

Ground Colors and Whitefly Trapping

Ground colors affect the number of whiteflies trapped by yellow sticky traps. The highest numbers are attracted to traps placed on bare soil (100%). Black, white, and glittering transparent plastic mulches, white and aluminum colored insect screens, kaolin sprayed whitened soil, all reduce the insect catches. In the following decreasing order from black to the various white and aluminum colored backgrounds. Glittering transparent plastic and Kaolin sprayed soil are the most repellent backgrounds. This indicates the importance of reflective light when mulching is selected as a mean of control, or when traps are exposed for monitoring purpose.

The number of trapped thrips is also strongly affected by background colors. Aluminum colored backgrounds, commercial white-appearing whitefly exclusion screens, or transparent plastic sheets, significantly reduce the numbers of alighting thrips. This may explain the relatively scarce appearance of thrips in structures covered by the commercially used whitefly exclusion screens. Conclusively, thrips are affected not only by the screen mesh but also by its color. Thus, the population can be reduced drastically by using a proper combination of mesh and color screen.

Mass Trapping

Attempts to control greenhouse whitefly populations through mass trappings in greenhouses give controversial results. Some claim success while others do not, since many whiteflies are found on the plants despite the fact that many are caught on yellow sticky strips.

Colored Screens

The incidence of aphid-borne virus infection in paprika is reduced significantly by using a white screen, even when the holes were larger than aphids and the screens are not a mechanical barrier. Attempts to increase screen holes, by combining the mechanical effect of the screen with a behavioral effect of colors to exclude *Bemisia tabaci*, turn out to be insufficient. Although whiteflies react to colors, it seems that the crucial restricting mechanism of screens is mechanical rather than behavioral. The behavior of the western flower thrips is more affected by colors.

Mulches

The mode of action of mulches is not fully understood. White mulch attracts thrips to the crop, aluminum colored mulch repels them, and yellow mulch delays tomato infection by tomato yellow leaf curl virus vectored by *Bemisia tabaci*. Before using mulches their effects must be carefully investigated for each circumstance.

Whitewashes

Whitewashes are white suspensions which contain 2.5–6% Zn. They are used as repellents inert reflective materials like Ca, and various adjuvant like stickers and spreaders. They are sprayed directly onto the crop's leaves to make them white. Whitewash increases potato leaf reflectivity in the visible spectrum by 130–250%, and markedly reduces the overall number of aphids landing in whitewash-treated plots. However, different aphid species respond differently; *Myzus persicae* (Sulzer) and *Aphis fabae* Scopoli are repelled, whereas *A. gossypii* Glover is attracted to whitewash-treated pots. A water solution of Kaolin reduces remarkably both the alighting and the development of *Bemisia*, on melons and zucchini plants.

Photoperiod

Many physiological processes depend on the length of the light period. Under long day conditions, whitefly development is quicker, the progenies' body size is larger and the females lay more eggs. Sex ratio is not affected by the length of the day. Finally, the population growth rate is enhanced under long day conditions. Adult emergence time is often synchronized by the diurnal rhythm under which the immature stages had developed. Many insects survive hard living conditions by diapausing (during wintering) or aestivating during summer. In most insects, the length of the day regulates the initiation of diapause or aestivation, and its end. By artificially changing the photoperiod, the process can be disrupted and the insects die in the course of the season.

Chemically Induced Behavior Modifiers

Chemically induced behavior modifications are a well-known phenomenon in nature in general, and in insects in particular. Formulations based on safe active ingredients can act both as repellents and as physical poisons. Nontoxic, or safe active ingredients, such as behavior modifiers, repellents, knockdown agents, and physical poisons, are used to protect people and their animals, and can be used to protect crop plants. However, many of those compounds cannot yet be applied to foliage due to the phytotoxicity of their chemicals, emulsifiers, or other necessary additives. Some soaps and vegetable oils (e.g., sunflower, soybean, pea nuts, and ricinusoil) and many more chemicals are included in this group of insect behavior modifiers.

References

Berlinger MJ, Lebiush-Mordechi S (1996) Physical methods for the control of *Bemisia*. pp 617–634. In: Gerling D, Mayer RT (eds) (1995) *Bemisia*: Taxonomy, biology, damage, control and management. Intercept Ltd., Andover, Hants, UK, 702 pp

Berlinger MJ, Jarvis WR, Jewett TJ, Lebiush-Mordechi S (1999) Managing the greenhouse, crop and crop environment. pp 97–123. In: Albajes R, Gullino ML, Lenteren JC, van Elad Y (eds) Integrated pest and disease management in greenhouse crops. Kluwer Academic Publishers, Dordrecht, The Netherlands. 545 pp

Cohen S, Berlinger MJ (1986) Transmission and cultural control of whitefly-borne viruses. Agriculture, Ecosystems and Environment 17:89–97

Kilgore WW, Doutt RL (eds) (1967) Pest control: biological, physical, and selected chemical methods. Academic Press, New York, NY, 477 pp

Taylor RAJ, Shalhevet S, Spharim I, Berlinger MJ, Lebiush-Mordechi S (2001) Economic evaluation of insect-proof screens for preventing tomato yellow leaf curl virus of tomatoes in Israel. Crop Protection 20:561–569

Vincent C, Panneton B, Fleurat-Lessard F (Coord.) (2000) La Lutte Physique en Phytoprotection. INRA – Institut National de la Recherche Agronomique, Paris, France, 347 pp

Phytoecdysones

Ecdysone-like chemicals found in plants that affect the growth and development of insects, providing a basis for resistance of the plants to insect herbivory.

Phytophage

An organism that feeds on plant tissue (= herbivore).

Phytophagous

Feeding on plants or plant products.

Phytophagy

Feeding on plants (= herbivory). Arthropods feeding on plants are said to be phytophagous (phytophages) or herbivorous, though herbivory can be more narrowly defined as feeding on herbage, which consists of grass and other low-growing plants, not trees.

Phytophagy is one of the most common ways of living displayed by insects. Just under half of all insect species feed on plants, with the balance being either predatory or parasitic (feeding on other insects), or saprophagous (feeding on decaying material). The taxa feeding on plants tend to be among the more modern orders and contain the most species. Most evolved in response to the increased availability of modern plants (Spermatophyta), and include the orders Hemiptera, Thysanoptera, Lepidoptera, Coleoptera, Hymenoptera, and Diptera.

► Food Habits of Insects
► Allelochemicals
► Plant Secondary Compounds and Phytophagous Insects
► Graminivory
► Granivory
► Folivory
► Herbivory

References

Southwood TRE (1972) The insect/plant relationship – an evolutionary perspective. In: van Emden HF (ed) Insect/plant relationships. Blackwell Scientific, Oxford, UK, pp 3–30

Strong DR, Lawton JH, Southwood TRE (1984). Insects on plants. Community patterns and mechanisms. Harvard University Press, Cambridge, MA, 313 pp

Phytosanitary Procedure

Officially prescribed methods for performing inspections, surveys, tests, or treatments in connection with regulated pests.

► Regulatory Entomology
► Sampling Arthropods

Phytosanitary Regulation

Official rules to prevent the introduction and spread of pests by regulating production, movement, or presence of commodities or other articles or personnel. This is normally enforced by establishment of phytosanitary procedures, and certification procedures.

► Regulatory Entomology

Phytoseiid Mites (Acari: Phytoseiidae)

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The family Phytoseiidae consists of approximately 1,700 species of small mites (200–500 μ) mostly predatory, free-living, terrestrial, and known throughout the world, except the Antarctica. They belong to the order Acari, suborder Mesostigmata, Family Phytoseiidae, subfamilies Amblyseiinae, Phytoseiinae, and Typhlodrominae (Fig. 50). The life cycle consists of the egg, larva, protonymph, deutonymph and adult. They are found on many plant species, soil, and debris. Published accounts of food sources include pollen, fungi, nematodes, mites, scale insects, whiteflies, and other small arthropods.

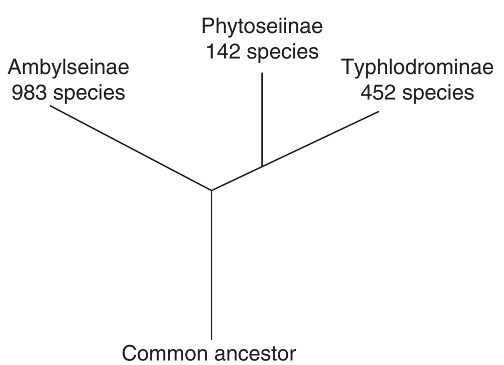
They have attracted attention due to their role in the biological control of small arthropods and are included in some integrated pest management programs to reduce the need of pesticides. Some of the species that are mass-reared and sold for use in biological control programs are: *Phytoseiulus persimilis* Athias-Henriot is predaceous on spider mites world wide; *Metaseilus occidentalis* (Nesbitt) is predatory on spider mites on apples, grapes, peaches and almonds in California, but is less effective on the genera *Panonychus*, *Bryobia*, and *Eotetranychus*; *Typhlodromus pyri* Scheuten is predatory on the twospotted spider mite, *Tetranychus urticae* (Koch) world wide and the European red mite, *Panonychus ulmi* (Koch) in Europe and apples in New Zealand; *Neoseiulus alpinus* (Schweizer) is an effective predator of the cyclamen mite on strawberries in Florida; *Euseius hibisci* (Chant) is considered to be an effective predator of the sixspotted mite, *Eotetranychus sexmaculatus* (Riley) in California.

Classification

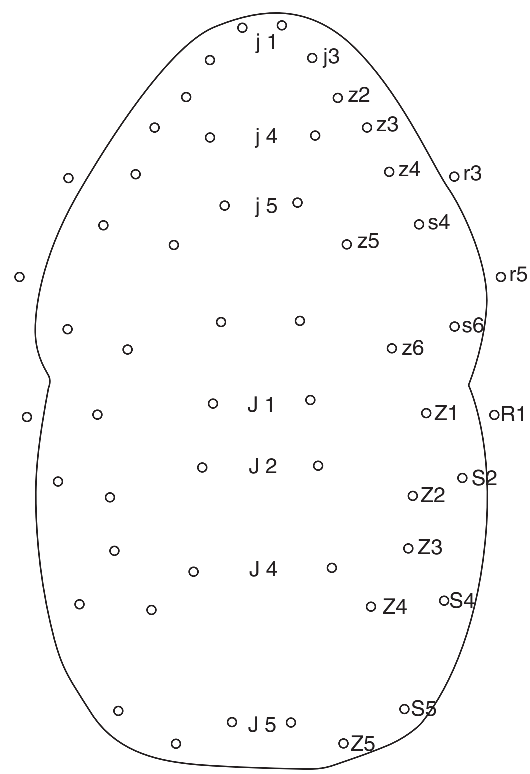
The evolution in the Phytoseiidae has been marked by the loss of many of the idiosomal setae as shown in the schematic view of a phytoseiid mite (Fig. 51). Three subfamilies are recognized by the absence of z3 and s6 in the Amblyseiinae Muma as shown in *Amblyseius mazatlanus* Denmark and Muma (Fig. 52), either or both setae z3 and s6 present and setae Z1, S2, S4, and S5 absent in the Phytoseiinae Berlese as shown in *Phytoseius chanti* Denmark (Fig. 53), and one of the setae Z1, S2, S4, and S5 present in Typhlodrominae Chant and McMurtry as shown in *Typhlodromus swirskii* Denmark (Fig. 54). There have been many attempts to classify the phytoseiids as shown in the suprageneric classification of the Phytoseiidae by various taxonomists (see Table 12).

Ecology

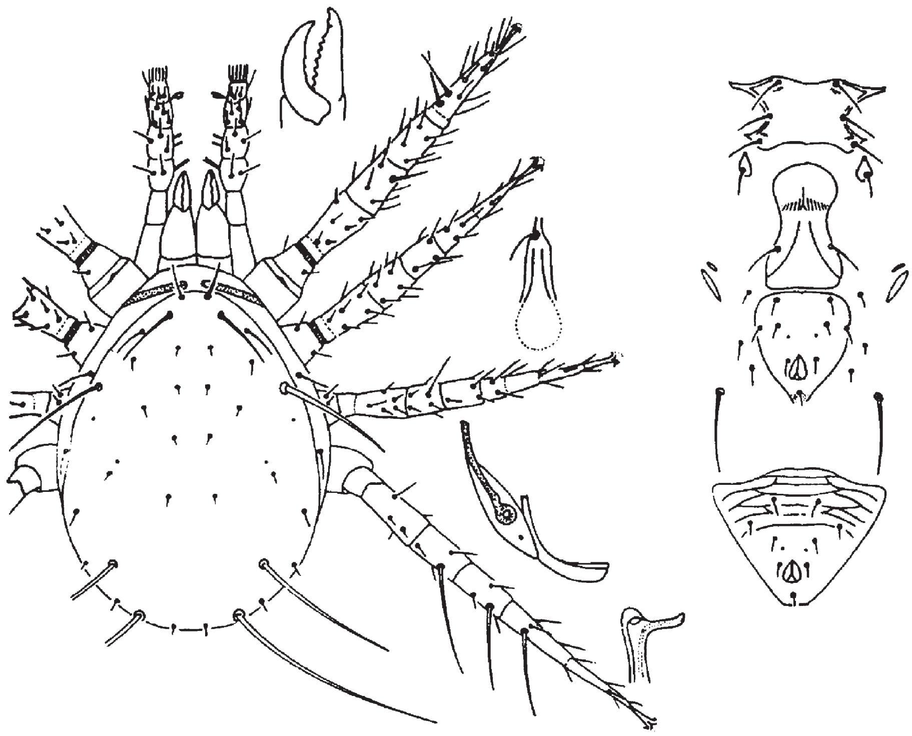
The important role that the phytoseiids play in the ecology of agriculture crops and ornamental



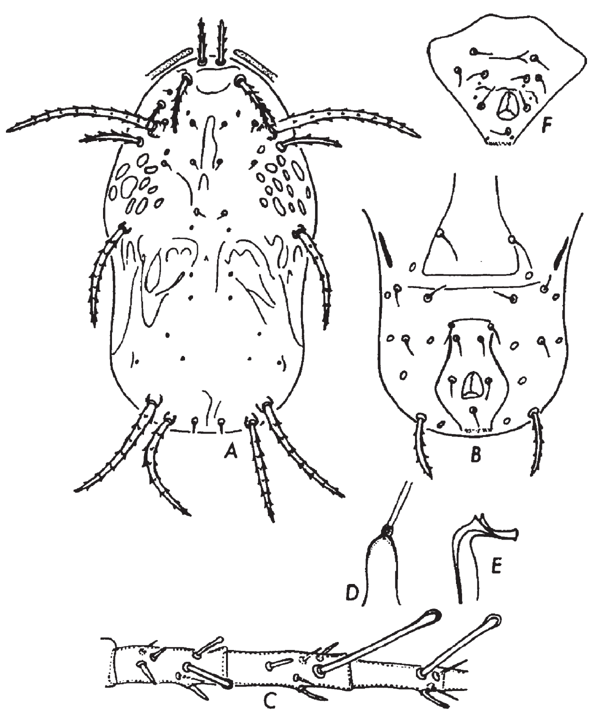
Phytoseiid Mites (Acari: Phytoseiidae), Figure 50 Probably phylogenetic relationships of the Amblyseiinae, Phytoseiinae, and Typhlodrominae (after Chant and McMurtry).



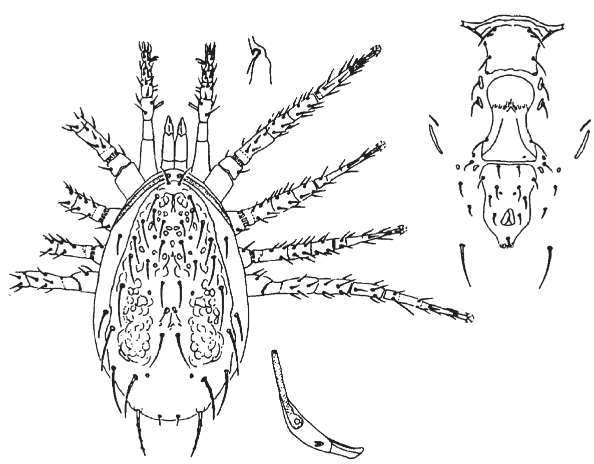
Phytoseiid Mites (Acari: Phytoseiidae), Figure 51 Schematic view of a hypothetical adult phytoseiid mite showing the 27 pairs of dorsal setae known to occur in the family (after Chant and Yoshida-Shaul).



Phytoseiid Mites (Acari: Phytoseiidae), Figure 52 **Diagram of *Amblyseius mazatlanus* Denmark and Muma, an example of the subfamily Amblyseiinae.**



Phytoseiid Mites (Acari: Phytoseiidae), Figure 53 **Diagram of *Phytoseius chanti* Denmark, an example of the subfamily Phytoseiinae.**



Phytoseiid Mites (Acari: Phytoseiidae), Figure 54 **Diagram of *Typhlodromus swirskii* Denmark, and example of subfamily Typhlodrominae (Cydnodromellinae).**

plants is poorly understood because the biology is known only for a few species. Phytophagous mites are involved in losses to agricultural, medicinal, forestry textile, fruit, ornamental and forage crops. While the availability and use of pesticides in

Phytoseiid Mites (Acari: Phytoseiidae), Table 12 Various approaches to suprageneric classification of the Phytoseiidae

Berlese[a]	Vitzhum[b]	Baker and Wharton[c]	Karg[d]
Family Laelapidae	Family Laelapidae	Family Phytoseiideae	Family Typhlodromidae
Tribe *Phytoseiini*	Subfamily Phytoseiinae	Subfamily Phytoseiinae	
		Subfamily Podocinae[e]	
Muma[f]	Hirschman[g]	Chant[h]	Karg[i]
Family Phytoseiidae	Family Gamasidae	Family Phytoseiidae	Family Typhlodromidae
Subfamily Phytoseiinae		Subfamily Phytoseiinae	Subfamily Phytoseiinae
Subfamily Macroseiinae		Subfamily Otopheidomeninae[e]	Subfamily Otopheidomeninae[e]
Subfamily Amblyseiinae			Subfamily Blattisociinae[e]
Subfamily Aceodrominae[e]			
Muma[j]	Wainstein[k]	Chaudhri[1]	Aruntunjan[m]
Family Phytoseiidae	Family Phytoseiidae	Family Phytoseiidae	Family Phytoseiidae
		Subfamily Gnoriminae	Tribe Amblyseiini
Subfamily Macroseiinae	Subfamily Phytoseiinae		Tribe Phytoseiini
Subfamily Amblyseiinae	Subfamily Macroseiinae		Tribe Typhlodromini
Subfamily Phytoseiinae	Subfamily Treatiinae[e]		Tribe Macroseiini
	Subfamily Evansoseiinae		Tribe Iphiseiini
	Subfamily Gigagnathinae		
Krantz[n]	Karg[o]	Chant & McMurtry[p]	Kolodochka[q]
Superfamily Phytoseioidea	Family Phytoseiidae	Family Phytoseiidae	Family Phytoseiidae
Family Phytoseiidae	Subfamily Phytoseiinae	Subfamily Amblyseiinae	Subfamily Phytoseiinae
Family Otopheidomenidae[e]	Subfamily Blattisociinae[e]	Subfamily Phytoseiinae	Subfamily Cydnodromellinae
Family Ameroseiidae[e]	Subfamily Macroseiinae	Subfamily Typhlodrominae	Tribe Amblyseiini

Phytoseiid Mites (Acari: Phytoseiidae), Table 12 Various approaches to suprageneric classification of the Phytoseiidae (Continued)

Berlese[a]	Vitzhum[b]	Baker and Wharton[c]	Karg[d]
Family Podocinidae[e]	Subfamily Treatiinae[e]		Tribe Kampimodromini
Family Epicriidae[e]			Tribe Phytoseiini
			Tribe Typhlodromini
			Tribe Seiulini
			Tribe Paraseiulini
			Tribe Anthoseiini

[a]Berlese A (1913) Systema Acarorum genera in familiis suis disposita. Acar. Italica 1–2:3–19
[b]von Vitzhum H (1941) Acarina. In: Brons H (ed) Klassen und Ordnungen des Tierreichs 5, Akad. Verlag. M. B. H. Leipzig, pp 764–767
[c]Baker EW, Wharton GW (1952) An introduction to acarology. The Macmillan Company, New York, NY, 465 pp
[d]Karg W (1960) Zur Kenntnis der Typhlodromiden (Acarina: Parasitiformes) aus Acker und Grunlandboden. Z Ang Entomol 47:440–452
[e]Species in this group are not currently placed in the Phytoseiidae
[f]Muma MH (1961) Subfamilies, genera, and species of Phytoseiidae (Acarina: Mesostigmata). Fla State Mus Biol Sci 5:267–302
[g]Hirschmann W (1962) Gangsystematik der Parasitiformes. Acarologia Schrift. Vergleichende Milbenkunde, Hirschmann-Verlag, Furth/Bay, 5(5–6):80 pp
[h]Chant DA (1965) Generic concepts in the family Phytoseiidae (Acarina: Mesostigmata). Can Entomol 97:351–374
[i]Karg W (1976) To the knowledge of the Superfamily Phytoseiodea Karg, 1965. Zool Jb Syst 103 [In German]
[j]Muma MH, Denmark HA, De Leon D (1970) Phytoseiidae of Florida. Arthropods of Florida and neighboring land areas, 6. Florida Department of Agriculture and Consumer Services, Division of Plant Industry, Gainesville, FL, 150 pp
[k]Wainstein BA (1962) Revision du genre *Typhlodromus* Scheuten, 1857. Et systematique de la famille des Phytoseiidae (Berlese, 1916) (Acarina: Parasitiformes). Acarologia 4:5–30
[l]Chaudhri WM (1975) New subfamily Gnoriminae (Acarina: Phytoseiidae) with the new genus *Gnorimus* and description of new species *Gnorimus tabella* from Pakistan. Pak J Agric Sci 12:99–102
[m]Aruntunjan ES (1977) Identification manual of phytoseiid mites of agriculture crops of Armenian S.S.R. An. Armenian SSR Erevan. 177 pp. [In Russian]
[n]Krantz GW (1978) A manual of Acarology, 2nd edn. Oregon State University Book Store, Corvallis, OR, 50 pp
[o]Karg W (1983) Systematische Untersuchung der Gattungen und mit der Beschreibung van 8 neuen Arten. Mitt Zool Mus Berlin 59:293–328
[p]Chant DA, McMurtry JA (1994) A review of the subfamilies Phytoseiinae and Typhlodrominae (Acari: Phytoseiidae). Int J Acarol 20:223–310
[q]Kolodochka LA (1998) Two new tribes and the main results of a revision of Palearctic phytoseiid mites (Parasitiformes, Phytoseiidae) with the family system concept. 32(1–2):51–63

agriculture now is essential, alternative control strategies of mites must be developed. The cost of pesticides, the development of pesticide resistance and sustaining competitive food exports to foreign markets dictate the need for new tactics of control. Students with an interest in Phytoseiidae could make a meaningful contribution by researching the biology of some of the species that are routinely collected on fruit and/or vegetable crops. IPM programs can always use additional predators to help reduce pest problems.

References

Baker EW, Wharton GW (1952) An introduction to acarology. The Macmillan Company, New York, NY, 465 pp
Chant DA, McMurtry JA (1994) A review of the subfamilies Phytoseiinae and Trophlodrominae (Acari: Phytoseiidae). Int J Acarol 20:223–310
Kranz GW (1978) A manual of acarology, 2nd edn. Oregon State University Book Stores, Corvallis, OR, 509 pp
Muma MH (1961) Subfamilies, genera, and species of Phytoseiidae (Acarina: Megostigmata). Fla State Mus Bull Biol Sci 5:267–302
Muma MH, Denmark HA, DeLeon D (1970) Phytoseiidae of Florida. Arthropods of Florida and neighboring land areas, 6. Florida Department of Agriculture and Consumer Services, Division of Plant Industry, Gainesville, FL, 150 pp

Phytotelmata

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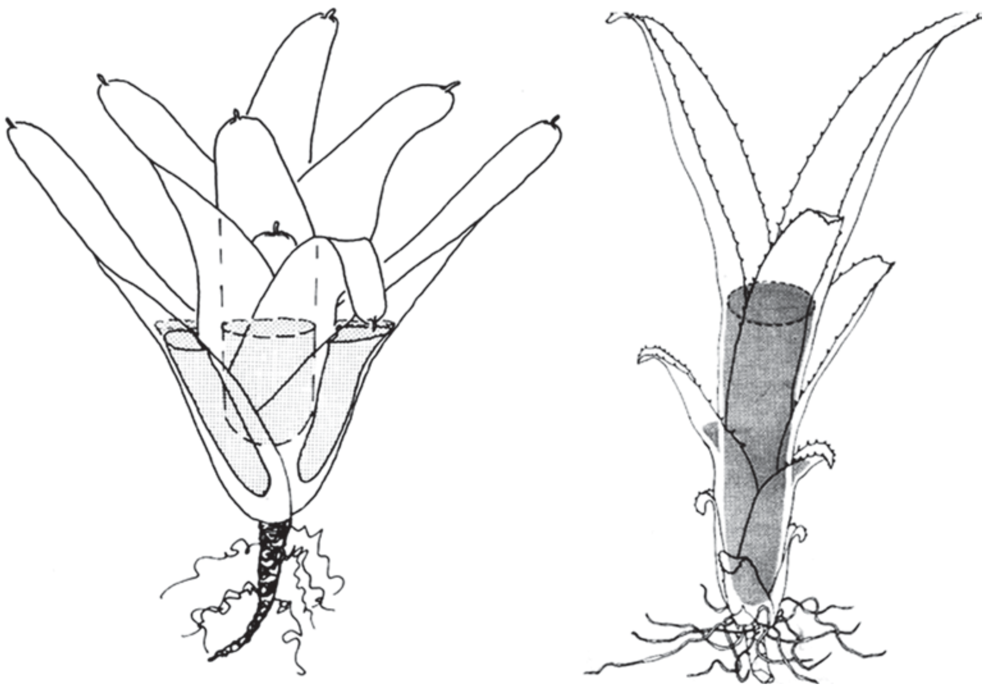
Phytotelmata are pools of water impounded by terrestrial plants. The structures that impound them are modified leaves, leaf axils, flowers, perforated internodes of plants that have internodes (such as bamboos), rot-holes in tree trunks or branches (henceforth called treeholes), open fruits, and fallen leaves. This expression, derived from the Greek words for plant and pool, was coined by Varga (1928) who wrote in German, with a companion paper in Hungarian. Maguire (1971) popularized its acceptance into English. The plural is phytotelmata (correctly pronounced phyto.TELM. ata, where the capital letters indicate location of the stressed syllable), in keeping with other plural words ending in -ata in Greek such as stemmata and stomata. The singular is phytotelma (compare with soma, stemma and stoma). The singular has been further Anglicized to phytotelm, which serves as a noun and as an adjective.

Phytotelmata formed by leaves, flowers and internodes of living plants are found in members of at least 29 plant families, mostly monocotyledons. They are Agavaceae, Amaryllidaceae, Araceae, Bromeliaceae, Campanulaceae, Cannaceae, Cephalotaceae, Commelinaceae, Compositae, Cyperaceae, Dipsacaceae, Eriocaulaceae, Euphorbiaceae, Gesneriaceae, Gramineae, Heliconiaceae, Hanguaceae, Liliaceae, Marantaceae, Musaceae, Nepenthaceae, Palmae, Pandanaceae, Rafflesiaceae, Sarraceniaceae, Strelitziaceae, Typhaceae, Umbelliferae, and Zingiberaceae. A list of plant families providing fruits or fallen leaves that form phytotelmata has not been compiled, but would be long. Treeholes are formed in just about any plant family containing hardwood trees.

Some of the plants that form phytotelmata are carnivorous. The pitcher plant families (Cephalotaceae, Nepenthaceae, and Sarraceniaceae) are not closely related to one another. Pitcher plants have modified leaves that trap and digest terrestrial arthropods as a source of nutrients for the plant. Despite the digestive fluids produced, specialist aquatic arthropods (mites and insect larvae) dwell in the pitchers of some species of *Sarracenia* (North America) and *Nepenthes* (southeast Asia and Madagascar). Carnivory is also displayed by some members of two genera of bromeliads, *Catopsis* and *Brocchinia*, although because there is no evidence of plant-produced digestive fluids, these plants have been dubbed "proto-carnivorous" by purists. In them, prey organisms are broken down by autolysis and then the products became available for uptake by the plant. Specialist aquatic insect larvae dwell in the water-impounding leaf axils of these bromeliads (Fig. 55).



Phytodelmata, Figure 55 **Figures show how the architecture of two bromeliads affects distribution of phytotelmata: left, *Billbergia pyramidalis*, right, *Aechmea nudicaulis*.**

Bromeliads are a family (Bromeliaceae) of monocotyledons with about 2,500 described species. Almost all of them are native to the neotropics. They include many species whose growth form impounds water and many that do not. Phytotelmata held by water-impounding species range from small bodies of water in several to many leaf axils (typified by some plants of the genera *Tillandsia* and *Guzmania*), or the formation of a large central tank formed by a few leaves (typified by some plants of the genera *Aechmea* and *Neoregelia*). Very many bromeliad species are epiphytic whereas others grow on the ground. None of the epiphytic species is believed to be parasitic on trees. Instead, the roots serve only as holdfasts, and water and nutrients are absorbed through pores on the leaves from the impounded water. Wet neotropical forests may support dense populations of such epiphytic bromeliads which have been likened to "aquaria in the treetops." Some bromeliads that grow on the ground dwell on rock surfaces, some in rather arid habitats and others in swamps, and in these the roots may absorb nutrients. Some of the ground-dwelling bromeliads provide phytotelmata. One species of one ground-dwelling genus (*Ananas comosus*) is an important crop plant (pineapple). Many genera, species, and hybrids are grown as ornamental plants; although many of these are epiphytic in nature, horticulturists have learned how by use of well-drained media, most may be grown in pots. The food-chains in bromeliad phytotelmata are of two basic kinds. In the phytotelmata provided by epiphytic bromeliads, rainwater falling through tree canopies is there enriched by leachates (to form throughfall), and is impounded by the plants together with debris (leaves, twigs, and seeds) of the trees. The plant obtains its nutrients from the impounded water. Various organisms inhabit the impounded water. In the phytotelmata provided by ground-dwelling bromeliads, debris trapped tends to be sparser (for lack of a tree canopy overhead), algae tend to grow in the water, and these algae form the basis of a food chain. A third kind of food chain is formed in those few bromeliads that grow in sun-exposed bromeliads and have developed carnivorous habits.

Heliconia is a genus of some 200 + species distributed in the neotropics and in some Pacific islands. It is now placed in the family Heliconiaceae, although in the past it has been variously assigned to Musaceae and Strelitziaceae. Floral spikes are pendent in some species, upright in others. Flower bracts in upright flowers may hold from a few drops to about 90 ml of water, depending upon species. Flowers emerge through this water and perhaps are thus protected to some extend from herbivory by it. At all events, the presence of water seems important to some species because they do not rely totally upon rainfall to replenish the water, but are able to pump water into the bracts. After flower fertilization, which is believed to be performed by hummingbirds or bats, the flower petals decompose in this water. The flowers are the basis of a food chain that nourishes various invertebrate animals. The first invertebrates to invade are specialist aquatic insect larvae. As the contents of each bract age, and as bract walls are damaged by vertebrate animals, the water level in the bract declines, and the bract risks invasion by semi-aquatic or even non-aquatic insects. However, the seed walls are extremely hard and thus very resistant to attack by insects. Each seed is enclosed within a fleshy, typically blue, pericarp, which doubtless makes it attractive to vertebrate animals and serves to disperse the seeds. During the flowering season, each floral spike at any time typically presents a succession, from youngest, unopened bracts at the apex, to older bracts with formed seeds.

It is not clear that other plants that impound water in leaf axils or floral parts use the water in any way. Most of these plants are monocotyledons. Fallen leaves may provide ephemeral, nutrient-poor phytotelmata during rainy seasons. Fruit husks may provide nutrient-richer phytotelmata. One example of the latter is the husks of cacao, which are usually left in piles in cacao plantations after harvest.

Treeholes provide phytotelmata in all but one continent. Those in an appropriate position in a tree trunk or large branch may be filled by stemflow. Part of the rainfall striking a tree canopy falls through it (after enrichment) as throughfall. Another part runs down branches and trunks, picking up leached materials and debris, as stemflow. Dead leaves and other debris from the canopy above may be blown into well-placed treeholes. All these materials decomposing inside treeholes provide a nutrient soup, which typically is not wasted by invertebrate animals. Some trees whose stem gives rise aboveground to roots, form bark-lined basal treeholes, which may likewise impound water. Not all treeholes impound water, not just because they are not in an appropriate position to collect stemflow, but because they have more than one opening, and leak. Some treeholes rarely receive stemflow and may be dry or almost so for months of each year. Rainfall fluxes are as important to the inhabitants of treehole phytotelmata as they are to the inhabitants of bromeliad phytotelmata.

Bamboos provide phytotelmata by one of two methods. If the stem is snapped or cut, the standing part, whose lower limit is marked by a node, can accumulate rainwater and debris. In some tropical countries, however, Coleoptera may make a small lateral hole into an internode, and this may accumulate water by stemflow. This small hole may limit access by flying insects, but some insects have adapted to injecting their eggs, giving rise to aquatic larvae, through it. The inner lining of the internode provides some nutrients.

The phytotelmata provide habitats for various aquatic invertebrates, including insects; these aquatic organisms and their habitat are of main concern in this article as "phytotelmatous." However, the plant structures around the phytotelmata provide habitat for some non-aquatic invertebrates that interact as predators with the aquatic fauna, much as do banks of ponds and streams. Other invertebrates (including insects) that dwell around the edges of phytotelmata, but that do not interact with the aquatic organisms, are numerous, but cannot be construed as part of the phytotelm fauna. Thus, lepidopterous larvae that feed on decomposing materials in non-water-holding outer leaf axils of bromeliads are not "phytotelmatous," nor are cockroaches nor ants. A few vertebrate animals, mainly frogs, have evolved to become specialist inhabitants of bromeliad phytotelmata or treeholes, laying their eggs nowhere else. But almost all phytotelm specialists are invertebrates.

Specialist inhabitants of phytotelmata typically do not harm the plant hosts. Some appear to be mutualists. In bromeliads, invertebrates (and bacteria and fungi) break down debris and may make it more easily taken up as nutrients by the leaves. Algae growing in sun-exposed bromeliad phytotelmata may perhaps compete with the plant host for nutrients, but the action of chironomid larvae is to feed on the algae, thus benefiting the host in two ways. In Heliconia bracts, it does not matter that decomposing petals are eaten by syrphid larvae after fertilization of the flowers has occurred. It does not matter that inner walls of bracts are scraped by hispine chrysomelid larvae once the seeds have formed.

Regulation of populations of invertebrates in phytotelmata takes several forms. Rainfall fluxes are, of course, of paramount importance in almost all, for the phytotelmata would not exist without rainfall. Rainfall, in the form of throughfall and stemflow, is also important for the provision of many nutrients in many phytotelmata. With water and nutrients and detritus that form the basis of the food chains, the next level of most food webs consists of saprovores (that feed on detritus) or, in phytotelmata that support algal growth, of herbivores (that feed on algae). Then, if the web is complex enough, come one or two levels of predators. Population regulation of the saprovores is brought about either by competition for resources, or by predation. It is of course the organisms that are lower in the food web (chain, pyramid) that are the most abundant.

Invertebrate animals that occupy at least some phytotelmata include rotifers, aquatic oligochaete worms, crustaceans (ostracods, copepods, and decapods), aquatic mites, and representatives of some orders of insects. Aquatic insect larvae are best represented in diversity and numbers of individuals by Diptera. For example, over 200 species of Culicidae are known from bromeliad phytotelmata alone. Culicidae are reported from all the other groups of phytotelmata, from pitcher plants through bamboo internodes to Heliconia floral bracts and fruit husks and fallen leaves. But Ceratopogonidae, Chironomidae, Psychodidae, Richardiidae, Stratiomyidae, and Syrphidae may be heavily represented in numbers of individuals, and the list of dipterous families does not end there. The abundance of individuals of numerous species of Diptera is because they are low in the food web. Those dipterous larvae that feed as predators are much less abundant. Adults and larvae of aquatic Coleoptera (Hydrophilidae, Dytiscidae, Scirtidae) are known from some bromeliad phytotelmata, as are adults and nymphs of Veliidae (Hemiptera). Fewer aquatic coleopterous families and far fewer species are reported from treeholes and Heliconia bracts. Nymphs of Trichoptera are recorded from bromeliad phytotelmata, and nymphs of Odonata from bromeliads and treeholes.

Phytotelmata inhabitants exhibit a full range of specialization. Some species inhabit many kinds of water bodies, whereas others inhabit only small bodies of water. Among the latter, some inhabit various kinds of phytotelmata, whereas the ultimate specialists inhabit only one kind (for example, only bracts of one or more species of Heliconia). The means by which most specialist insects select the places in which to oviposit is unknown. However, perception of volatile chemicals plays a role in some, and vision, including color vision, in some. Flightless invertebrate animals may have little control in the matter of dispersing from one phytotelm to another, beyond hitching a ride (phoresy) on some larger, more mobile organism that just may be about to disperse to another phytotelm.

References

Frank JH (1996) Bromeliad phytotelmata. Available at http://bromeliadbiota.ifas.ufl.edu

Frank JH, Lounibos LP (eds) (1983) Phytotelmata:terrestrial plants as hosts for aquatic insect communities. Plexus, Medford, NJ, 293 pp
Kitching RL (2000) Food webs and container habitats: the natural history and ecology of phytotelmata. Cambridge University Press, Cambridge, England, 431 pp
Kitching RL (2001) Food webs in phytotelmata: "bottom-up" and "top-down" explanations for community structure. Annu Rev Entomol 46:729–760
Maguire B (1971) Phytotelmata: biota and community structure determination in plant-held waters. Annu Rev Ecol Syst 2:439–464
Varga L (1928) Ein interessanter Biotop der Biocönose von Wasserorganismen. Biologisches Zentralblatt 48:143–162

Phytotoxemia

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Symptoms of plant disease that are induced from the effects of insect/mite feeding and introduced salivary compounds (phytotoxins) are called phytotoxemias or plant toxemias. Categories of phytotoxemias include: (i) local lesions at the feeding point; (ii) local lesions with development of secondary symptoms; (iii) tissue malformations; and (iv) translocated phytotoxins. An arthropod that is capable of producing a phytotoxemia is sometimes described as being "toxiniferous."

Phytotoxemias are almost entirely produced by arthropods that suck plant fluids, and primarily involve Hemiptera. Some Hemiptera, gall making insects found within other orders, and some mites (Tetranychidae and Eriophyiidae) are also considered capable of producing certain phytotoxemias.

The nature of the toxins involved in a phytotoxemia is little understood, but apparently often includes enzymes adapted to the insect diet that have adverse effects on the host. Various pectinases, proteases, amylases, saccarhases, lipases and pheonolases are among the compounds identified that produce phytotoxemias. The effects of such phytotoxic compounds may vary depending on the response of the host plant. For example, the potato/tomato psyllid, *Paratrioza cockerelli*, is a species that produces serious systemic injuries to potatoes and tomatoes, but has little effect when feeding on eggplant and pepper.

Induction of a phtytoxemia is usually related directly to the presence of the insect responsible, and once the insect is removed no further damage occurs. However, if the damage is severe the plant may not recover. To prevent a phytotoxemia, usually the insect must be prevented from feeding, or killed soon after it begins feeding. In some cases, plant varieties are known that are resistant to injury.

Phytotoxicity

Damage to a plant due to contact with a chemical toxin.

Piceous

Very dark, black.

Pickett, Allison Deforest

A.D. Pickett was a pioneer in the field of insect pest management, but his important contributions to minimizing pesticidal inputs into crop production have often been overlooked. Pickett was born in Lower Kars, New Brunswick, Canada, in 1900. He attended Nova Scotia Agricultural College, Ontario Agricultural College, Macdonald College, and was granted a B.Sc. from McGill University in 1929. He worked at the Dominion Entomological Laboratory and was appointed the first Provincial Agricultural Representative for Kings County, Nova Scotia. He served as the Provincial Entomologist for Nova Scotia from 1929 to 1939, and developed into an outstanding teacher of zoology and genetics at the Nova Scotia Agricultural College. During this period he also served as extension entomologist. From 1933 to 1937 he served as Head of the Horticulture and Biology section and conducted graduate research on apple maggot strains, for which he was awarded a M.Sc. degree from McGill University in 1936.

Pickett was appointed Officer-In-Charge of the Dominion Entomological laboratory in 1939 and then Head in 1950. During this period he led a very productive research team at Kentville focusing on integration of biological and chemical control of fruit pests. For this innovative research in an era when chemical insecticides were highly regarded, Pickett was awarded an honorary D.Sc. degree from McGill University in 1959. The program that became known as "Pickett's modified spray program" earned him international recognition.

Pickett was honored by the naming of the A.D. Pickett Entomological Museum and Research Laboratory at Nova Scotia Agricultural College in 1984. He reciprocated by endowing the W.H. Brittain Memorial Fund at Macdonald College in recognition of the support and inspiration from Professor W.H. Brittain of Macdonald. Lastly, Dalhousie University of Halifax, Nova Scotia, awarded him an honorary L.L.D. degree in 1989. He died on September 18, 1991.

Reference

LeBlanc J-PR (1991) Allison Deforest Pickett (1900–1991). Bull Entomol Soc Can 23:198–199

Pickleworm, *Diaphania nitidalis* (Stoll) (Lepidoptera: Pyralidae)

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Pickleworm is a tropical insect which occurs widely in Central and South America and the Caribbean. It can survive in subtropical climates, such as the southernmost USA, but regularly survives the winter in the USA only in southern Florida and perhaps south Texas. Pickleworm is highly dispersive, and invades much of the southeastern USA each summer. Although it regularly takes 1 or 2 months for the dispersing pickleworms to move north from Florida to the Carolinas, in some years they reach locations as far north as Michigan and Connecticut. Presumably they are assisted in their northward dispersal by favorable wind patterns. In Canada, pickleworm has occasionally been found in southern Ontario. In Puerto Rico, it is more common in the mountains than at low elevations, and is not found at all in dry areas of the island.

Life History

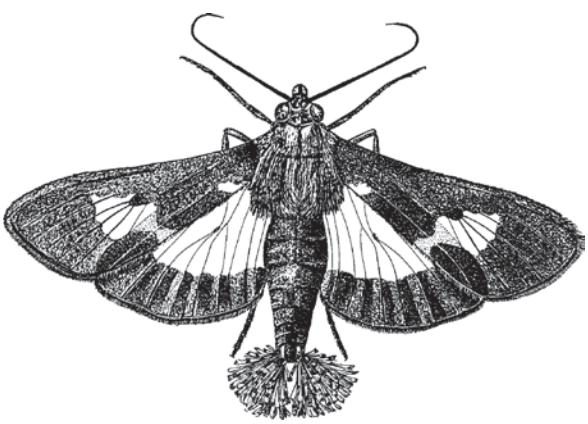
The pickleworm can complete its life cycle in about 30 days. Over much of its range, multiple and overlapping generations may occur annually, but as few as one generation occurs at the limits of its range.

The eggs are minute, measuring only about 0.4–0.6 mm wide and 0.8 mm long. The shape varies from spherical to flattened. Their color is white initially, but changes to yellow after about 24 h. The eggs are distributed in small clusters, usually 2–7 per cluster. They are deposited principally on the buds, flowers, and other actively growing portions of the plant. Hatching occurs in about 4 days. Egg production is 300–400 eggs per female.

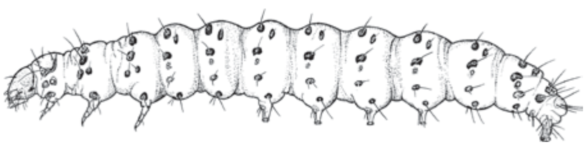
There are five instars. Total larval development time averages 14 days. Mean duration (range) of each instar is about 2.5 (2–3), 2 (1–3), 2 (1–3), 2.5 (2–3), and 5 (4–7) days, respectively. Head capsule widths for the five instars are about 0.25, 0.42, 0.75, 1.12, and 1.65 mm, respectively. Body lengths average 1.6, 2.5, 4.0, 10, and 15 mm during instars 1–5, respectively. Young larvae are nearly white in color with numerous dark gray or black spots (Fig. 56). The dark spots are lost at the molt to the fifth instar. Larval color during the last instar is somewhat variable, depending largely on the insect's food source. For example, they tend to be orange when feeding on blossoms, green when feeding on stem tissue, and white when feeding on fruit. Prior to pupation, larvae tend to turn a dark copper color. When mature, larvae often attain a length of 2.5 cm.

Pupation usually occurs in a leaf fold; often dead, dry material is used. There is only weak evidence of a cocoon, usually just a few strands of silk. The pupa is elongate, measuring about 13 mm in length and 4 mm in width. It is light brown to dark brown in color, and tapers to a point at both ends. Pupation usually lasts about 8–9 days.

Emerging moths fly during much of the evening hours, but most flight occurs 3–5 h after sundown, with peak flight at approximately midnight. The female moth produces a pheromone that attracts males, with peak production occurring at 5–7 h after sunset. Moths are fairly distinctive in appearance. The central portion of both the front and hind wings is a semi-transparent yellow color, with an iridescent purplish reflection. The wings are bordered in dark brown (Fig. 57). The wing expanse is about 3 cm. Both sexes often display brushy hairpencils at the tip of the abdomen. Moths are not found in the field during the daylight hours, and probably disperse to adjacent wooded or weedy areas during the heat of the day. Moths do not produce eggs until they are several days old.



Pickleworm, *Diaphania nitidalis* (Stoll) (Lepidoptera: Pyralidae), Figure 56 **Adult pickleworm, *Diaphania nitidalis* (Stoll).**



Pickleworm, *Diaphania nitidalis* (Stoll) (Lepidoptera: Pyralidae), Figure 57 **Young larva of pickleworm, *Diaphania nitidalis* (Stoll).**

Pickleworm feeds only on cucurbits, but both wild and cultivated species are suitable hosts. Creeping cucumber, *Melothria pendula*, is considered to be an important wild host. Summer squash and the winter squash species are good hosts. Pumpkin is of variable quality as a host, probably because pumpkins have been bred from several *Cucurbita* species. The *Cucumis* species, cucumber, gherkin, and cantaloupe, are attacked but not preferred. Among all cucurbits, summer squash is most preferred, and most heavily damaged. Cultivars vary widely in susceptibility to attack, but truly resistant cultivars are unknown. Cucurbits are intolerant of cold weather. Although diapause is unknown in pickleworm, it is the lack of host plants during the winter months that functionally limits the distribution of pickleworm.

Pickleworm has several natural enemies, but none reliably suppress damage. Generalist predators such as *Calosoma* spp. and *Harpalus* (both Coleoptera: Carabidae), the soldier beetle *Chauliognathus pennsylvanicus* DeGeer (Coleoptera: Cantharidae), and the red imported fire ant *Solanopsis invicta* Buren (Hymenoptera: Formicidae) have been reported to be important mortality factors. Also, several parasitoids are known, including *Apanteles* sp., *Hypomicrogaster diaphaniae* (Muesebeck), *Pristomerus spinator* (Fabricius) (all Hymenoptera: Braconidae), *Casinaria infesta* (Cresson), *Temelucha* sp. (both Ichneumonidae), and undetermined trichogrammatids. The braconid *Cardiochiles diaphaniae* Marsh (Hymenoptera: Braconidae) has been imported from Colombia and released into Florida and Puerto Rico in an attempt to obtain higher levels of parasitism.

Damage

Pickleworm may damage summer and winter squash, cucumber, cantaloupe, and pumpkin.

Watermelon is an unusual host. The blossom is a favored feeding site, especially for young larvae. In plants with large blossoms, such as summer squash, larvae may complete their development without entering fruit. They may also move from blossom to blossom, feeding and destroying the plant's capacity to produce fruit. Very often, however, the larva burrows into the fruit. The larva's entrance is marked by a small hole, through which frass is extruded. The presence of the insect makes fruit unmarketable, and fungal or bacterial diseases often develop once entry has occurred. If larvae burrow into fruit just before harvest, their presence is difficult to detect, yet a considerable amount of larval growth and feeding damage may occur. When all blossoms and fruit have been destroyed, larvae will attack the vines, especially the apical meristem. Cantaloupe is not a preferred host, and larvae often seem reluctant to burrow into the fruit. Rather, they feed on the surface or "rind," causing scars. Thus, pickleworm is sometimes referred to as "rindworm."

Management

It is very difficult to scout for this insect and predict its appearance. Moths are not attracted to light traps, and pheromone traps have had limited success. Pheromone lures are not currently available commercially. The small eggs, night-flying behavior, and inability to trap the insect reliably lead most growers to depend on preventative applications of insecticides.

Cucurbit producers in areas where pickleworm damage is likely to occur usually apply chemical insecticides from the onset of fruiting through harvest. The internal feeding behavior of larvae, which is so difficult to detect at harvest, causes particular emphasis on prevention of damage. In areas that are on the fringe of the normal range there are many seasons when damage will not occur, but producers apply insecticides as a preventative measure because prediction of occurrence is so difficult.

Pollinators, particularly honeybees, are very important in cucurbit production, and insecticide application can interfere with pollination by killing honeybees. If insecticides are to be applied when blossoms are present, it is advisable to use insecticides with little residual activity, and to apply insecticides late in the day, when honeybee activity is minimal.

The entomopathogenic nematode *Steinernema carpocapsae* has been shown to effectively suppress pickleworm injury in squash. Nematode survival is quite good in large-blossomed squash, where the nematodes can kill the young pickleworm before it burrows into the fruit. This approach is probably ineffective for species with small, open blossoms such as cucumber, however, because the nematodes die quickly when exposed to sunlight. *Bacillus thuringiensis* will kill pickleworm, but is usually not recommended because the internal feeding behavior puts the feeding larvae beyond the reach of a stomach-active toxin.

It is possible to cover plants with screen or row covers to prevent moths from depositing eggs on the foliage. However, because the plants must be pollinated, usually by honey bees, some allowance must be made to leave the plants uncovered. Given the night-flying behavior of the moths and the daytime activities of honeybees, this is not a difficult task on a small planting but is prohibitive on large acreage.

Some growers are able to prevent plant injury through careful timing of their cropping cycle. By planting early, it is often possible to harvest part of the crop before pickleworms appear. Usually the crop is eventually infested, so some yield is lost. Plowing under of the crop residue is recommended to destroy pupae in the leaf debris.

Squash can be used as a trap crop to keep pickleworm from attacking cantaloupe, a less preferred host. Destruction of squash blossoms, or even the entire plant, should be done periodically to keep pickleworms from exhausting the food supply and then moving onto adjacent cantaloupes.

References

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, CA, 729 pp
Dupree M, Bissell TL, Beckham CM (1955) The pickleworm and its control. Georgia Agric Exp Station Bull 5:1–34
Elsey KD, Klun JA, Schwarz M (1991) Forecasting pickleworm (Lepidoptera: Pyralidae) larval infestations using sex pheromone traps. J Econ Entomol 84:1837–1841
Elsey KD, McFadden TL, Cuthbert RB (1984) Improved rearing system for pickleworm and melonworm (Lepidoptera: Pyralidae). J Econ Entomol 77:1070–1072
Valles SM, Capinera JL, Teal PEA (1991) Evaluation of pheromone trap design, height, and efficiency for capture of male *Diaphania nitidalis* (Lepidoptera: Pyralidae) in a field cage. Environ Entomol 20:1274–1278
Valles SM, Heath RR, Capinera JL (1992) Production and release of sex pheromone by *Diaphania nitidalis* (Lepidoptera: Pyralidae): periodicity, age, and density effects. Ann Entomol Soc Am 85:731–735

Picture-Winged Flies

Members of the family Ulidiidae and Platystomatidae (order Diptera).

► Flies

Picture-Winged Leaf Moths (Lepidoptera: Thyrididae)

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Picture-winged leaf moths, family Thyrididae, total 794 species worldwide, nearly all tropical, with nearly half the species Indo-Australian (only a few species are in the Nearctic and Palearctic regions); actual fauna likely exceeds 1,200 species. There are six subfamilies: Simaethistinae, Whalleyaninae, Argyrotypinae, Thyridinae, Siculodinae, and Striglininae. The first three subfamilies are sometimes treated as separate families. The family is in the superfamily Pyraloidea in the section Tineina, subsection Tineina, of the division Ditrysia (sometimes placed in its own superfamily, Thyridoidea). Adults small to large (9–90 mm wingspan), with head scaling average; haustellum naked; labial palpi upcurved or slightly porrect; maxillary palpi 1- to 2-segmented. Maculation varied, often dark with light spots, or shades of brown to mimic dead leaves, or very colorful; many with wing margins irregular in shape, or leaf-like. Adults are diurnal or crepuscular. Larvae are leafrollers (one Australian species is gregarious), or borers in stems and flower racemes; a few are gall makers. A number of host plants are used. Only a few species are economic. The subfamily Whalleyaninae and its nominate genus *Whalleyana* are named after the British lepidopterist Paul E. S. Whalley.

References

de Freina JJ, Witt TJ (1990) Familie Thyridae Herrich-Schäffer 1846. Fensterschwärmer (= Thyrididae Hampson 1897). In Die Bombyces und Sphinges der Westpalaearktis, 2:69–71, pl. 10. Forschung & Wissenschaft Verlag, Munich
Thiele JHR (1994) Thyrididae. In: Ebert G (ed) Die Schmetterlinge Baden-Württembergs. Bd. 3. Nachfalter, 505–514. Verlag Eugen Ulmer, Stuttgart
Whalley PES (1964) Catalogue of the world genera of the Thyrididae (Lepidoptera) with type selection and synonymy. Ann Magazine Nat Hist (13) 7:115–127
Whalley PES (1971) The Thyrididae (Lepidoptera) of Africa and its islands. A taxonomic and zoogeographic study. Bull Br Mus (Nat Hist) Entomol Suppl 17:1–198, 68 pl
Whalley PES (1976) Tropical leaf moths: a monograph of the subfamily Striglininae (Thyrididae). British Museum (Natural History), London, 194 pp, 68 pl

Pierce's Disease Of Grape

This bacteria disease of grapes is transmitted by certain leafhoppers.

► Transmission of Plant Diseases by Insects

Pieridae

A family of butterflies (order Lepidoptera). They commonly are known as yellows-white butterflies, yellows, whites, and sulfurs.

► Yellow-White Butterflies
► Butterflies and Moths
► Transmission of *Xylella fastidiosa* Bacteria by Xylem-feeding Insects

Piesmatidae

A family of bugs (order Hemiptera). They sometimes are called ash-gray leaf bugs.

► Bugs

Pile

Having a covering of thick, erect setae that give the appearance of fur (= setose or pilose).

Pileiform

Having the form of an umbrella-shaped cap (pileus) (= agariciform).

Pilifer

A small projection, resembling a small mandible, at each side of the clypeus in Lepidoptera.

Pill Beetles

Members of the family Byrrhidae (order Coleoptera).

► Beetles

Pillbugs and Sowbugs, or Woodlice (Isopoda)

The terrestrial isopods known as pillbugs and sowbugs in North America are collectively known as "woodlice" in Europe. The term "woodlice" conveniently depicts their relatedness and preferred habitat, and deserves wider recognition and use in North America. Consistent with this is the fact that many of the pillbugs and sowbugs now found in North America seem to be immigrants from Europe. Indeed, several species have become almost cosmopolitan.

Classification

Woodlice are arthropods in the subphylum Crustacea, whereas insects are in the subphylum Atelocerata. Like many other terrestrial arthropods, they are commonly confused with insects. However, they are more closely related to shrimp and crabs than to insects, as shown below:

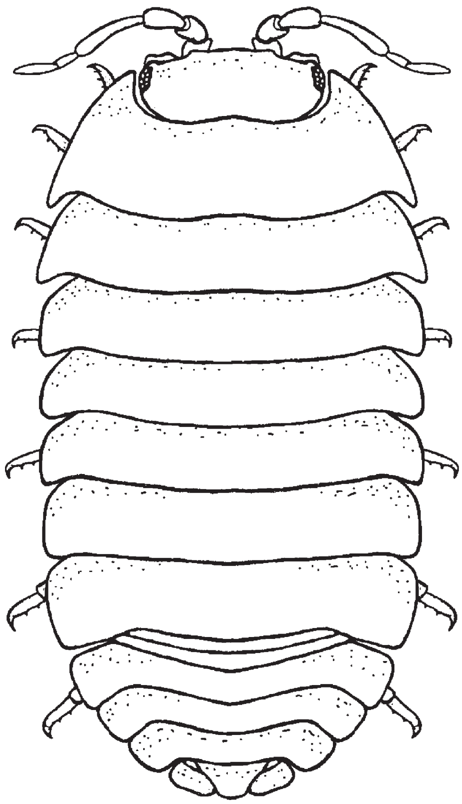
Phylum: Arthropoda
- Subphylum: Trilobita – Trilobites (these are extinct)
- Subphylum: Chelicerata
  - Class: Merostomata – Horseshoe crabs
  - Class: Arachnida – Arachnids (scorpions, spiders, ticks, mites, etc.)
  - Class: Pycnogonida – Sea spiders
- Subphylum: Atelocerata
  - Class: Diplopoda – Millipedes
  - Class: Chilopoda – Centipedes
  - Class: Pauropoda – Pauropods
  - Class: Symphyla – Symphylans
  - Class: Entognatha – Collembolans, proturans, diplurans
  - Class: Insecta – Insects
- Subphylum: Crustacea – Crustaceans (isopods, shrimp, crabs, etc.)
  - Class: Malacostraca
    - Superorder: Peracarida – Amphipods, isopods, etc.
      - Order: Isopoda

Class Malacostraca contains about two thirds of all crustacean species, including all of the larger forms. The three principal orders of malacostracans are the Isopoda, Amphipoda, and the Decapoda. The latter is best known to most people, as it contains the crayfish, lobsters, crabs and shrip. The woodlice are found in several families of Isopoda within the suborder Oniscidea. Many Isopods are marine, and a few live in freshwater habitats, but the member of the suborder Oniscidea are terrestrial. The members of the suborder Oniscidea are the most successful (diverse) of the land-dwelling Crustacea. The herbivorous and detritivores of the suborder Oniscidea are considered to be relatively primitive; the more advanced groups of Isopoda are carnivores, predators and parasites.

Life Cycle and Description

Though superficially similar to insects because they have a rigid exoskeleton and jointed appendages, there are some important differences. As in insects, the body of woodlice is divided into three major regions: the head, which bears the antennae and mouthparts; the thorax or pereion which bears the legs but never wings; and the abdomen or pleon. The head bears two pairs of antennae instead of the one pair found in insects, but one pair of the antennae in woodlice is greatly reduced in size and therefore not often observed. The pereion (thorax) consists of seven segments instead of the three found in insects, with each segment bearing a pair of legs ventrally. The pleon (abdomen) consists of six segments, but invariably is much smaller than the pereion. The ventral surface of the pleon bears plate-like structures, and is an important site for gas exchange. A terminal pair of tail-like appendages, called uropods, may be located at the tip of the pleon. Uropods are present in sowbugs but absent in pillbugs (Figs. 58 and 59). Sowbugs cannot completely roll into a ball, though pillbugs are capable of this behavior. Because they can roll into a ball, pillbugs are sometimes called roly-polys.

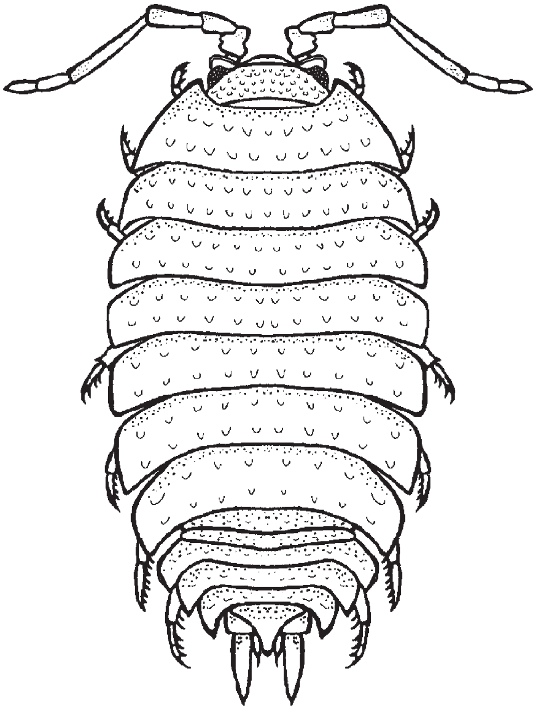
The female woodlouse carries her eggs and young about with her in a special compartment, called the marsupium, on the underside of her body. Fertilized eggs are inserted into the marsupium where the embryos (and later the young) obtain water, oxygen and nutrients from a nutritive fluid called, appropriately, marsupial fluid. The eggs may be up to 0.7 mm in diameter, and in some species over 100 eggs may be produced. The eggs persist for 3–4 weeks, then hatch, but the young remain in the marsupium for another 1–2 weeks before crawling out. They are only two mm in length at this stage of development. Woodlice commonly produce offspring 1–3 times/year, with spring and autumn broods most common. Woodlice often survive for longer than a year, with longevity of 2–5 years not uncommon.



Pillbugs and Sowbugs, or Woodlice (Isopoda), Figure 58 An adult pillbug, *Armadillidium vulgare*.

Woodlice often produce 20–40 young, and 1–3 broods per season. Brood size was positively correlated with female size. The young are highly gregarious, and sometimes cannibalistic. Once they have left the female they molt, usually within 24 h, acquiring a seventh pereion segment. After an additional 14 days a second molt occurs, and a seventh pair of legs is produced. Thereafter they do not change in morphology, other than to increase in size. The interval between molts is 1–2 weeks until the age of about 20 weeks, and molting continues irregularly for the remainder of their life, including adulthood. Molting occurs in two stages, with the posterior portion of the body shedding its old skin first, followed about three days later by the anterior portion.

Woodlice often attain a length of 8.5–18.0 mm as they reach adulthood. The width of the body is about half of its length. Woodlice are somewhat flattened and elongate oval in shape, seven pairs of



Pillbugs and Sowbugs, or Woodlice (Isopoda), Figure 59 **Adult of dooryard sowbug, *Porcellio scaber*.**

legs and 13 body segments are apparent, and they have long, jointed antennae. Eyes are evident on the side of the head. They are brownish or grayish in general body color, though often marked with areas of black, red, orange or yellow.

Ecology

Woodlice generally feed on dead plant material, though they also accept dead animal remains and dung, and occasionally ingest bacteria, fungi, and living plants. They are best viewed as decomposers, similar to earthworms, breaking down plant material and mixing it with mineral particles to produce soil. However, they are not the first organisms to attack leaf litter, waiting until microorganisms have begun the degradation process. Also, they sometimes have the unfortunate habit of grazing on plants, particularly seedlings. Woodlice occasionally attack seedlings above-ground, feeding especially on stems and young leaves, and below-ground, feeding on roots. Woodlice are most common in soils with neutral or alkaline pH, good crumb structure, high organic matter content, and where soil bacteria and other macro-decomposers such as earthworms and millipedes flourish. They tend to be absent from acid and waterlogged soil. Due either to the disturbance or lack of shelter, woodlice are virtually absent from thoroughly tilled land. On the other hand, straw or other coarse mulch provides good habitat for woodlice and can lead to crop damage. They have adapted well to humans and human habitations, and are often considered to be anthropophilic, but they also survive well in forests and grasslands, particularly if they can find shelter beneath logs and rocks. They are nocturanal.

Woodlice are parasitized by species of tachinids (Diptera: Tachinidae), with most displaying a fairly specific host range. Predation and cannibalism are known to occur, but it is uncertain whether these are important mortality factors in nature. Lizards, salamanders, shrews, spiders, centipedes, and ground beetles (Coleoptera: Carabidae) will eat woodlice. An iridovirus has been found to occur in woodlice populations in California. In addition to causing a slight blue to purple discoloration in infected woodlice, the longevity of infected hosts is greatly reduced when woodlice are infected with iridovirus. Fungus, nematode, and protozoan parasites seem to be of little importance.

References

Paris OH (1963) The ecology of *Armadillidium vulgare* (Isopoda: Oniscoidea) in California grassland: food, enemies, and weather. Ecol Monogr 33:1–22

Sutton S (1972) Woodlice. Pergamon Press, Oxford, UK

Warburg MR (1993) Evolutionary biology of land isopods. Springer, Berlin

Pilose

Covered with soft hair.

Pine and Spruce Aphids

Members of the family Adelgidae (order Hemiptera).

► Aphids
► Bugs

Pine Tip Moths, *Rhyacionia* spp. (Lepidoptera: Tortricidae)

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There are approximately 35 known species of pine tip moths distributed throughout the palearctic and nearctic regions of the world. However, the greatest diversity of species within the genus *Rhyacionia* is found in the western United States. As their name implies, pine tip moths feed exclusively on pine trees. A few species are economically important, particularly in the southeastern and western United States.

Tip moth larvae feed within the buds and shoots of their host. Damage caused by tip moths is usually visible by the appearance of small accumulations of pine resin which collect around the entrance wound. The terminal portion of the infested shoot eventually turns brown as it is hollowed out by the burrowing larvae. The tree is normally not killed by this pest unless repeated, severe infestations occur. However, significant losses in growth and wood quality are common. Tip moths are primarily a problem in intensively managed pine plantations where slow growth and poorer wood quality can result in economic losses.

The biologies of tip moths within the genus *Rhyacionia* are similar. Adults normally emerge in spring from infested shoots, duff, or soil. The majority of species studied are univoltine, however, some have multiple generations per year. Adults are often inactive during much of the day, with mating generally occurring at dusk or later during the night. Females release a sex pheromone to attract males for mating. Oviposition occurs on the needles, buds, or shoots of the host tree. Eggs may be deposited singly or in clusters. First instar larvae generally mine the needles while later instars enter the shoot, feeding on pith and cambium tissue. Pupation occurs within the shoot, on or in the ground below the host tree, or in cocoons just below the soil, often attached to the root collar. Univoltine species generally overwinter as pupae on the ground. An important exception is the European pine shoot moth, *Rhyacionia buoliana*, which overwinters as a larvae in the buds, completing feeding the following spring. Multivoltine species usually spend the winter as pupae within the shoots.

The greatest diversity of species occurs in the southern Rocky Mountains in Colorado, New Mexico, and Arizona, most of which are associated with Ponderosa pine. However, the most economically significant tip moth species, the Nantucket pine tip moth, *Rhyacionia frustrana*, occurs in the eastern United States. This species attacks a number of pine species, but is primarily a problem on the vast acreage of intensively managed loblolly pine (*Pinus taeda*) plantations throughout the Southeast. For this reason, an extensive amount of research has been done on this pest compared to most other species of *Rhyacionia*, for which even the most basic information is lacking. Another significant pest is the European pine shoot moth, *Rhyacionia buoliana*, which was accidentally introduced into North America in the early 1900s. It is a sporadic pest of pine plantations in the Northeast, the Lake States, and the Pacific Northwest.

In most cases, prevention of pine tip moth infestations involves planting pines on suitable sites within their native range and avoiding intensive management practices (herbicides, pesticides, fertilizers, etc.). Chemical control is a viable option for preventing damage but has seldom been used historically due to a lack of perceived threat from these non-lethal forest pests. Recent research on Nantucket pine tip moth, however, has demonstrated that substantial growth losses can occur in pine plantations that receive repeated damage, even at seemingly low levels. These pests are likely to become more important in the future as forest management becomes increasingly intensive in order to meet the wood and paper demands of a rapidly growing population.

References

Asaro C, Fettig CJ, McCravy KW, Nowak JT, Berisford CW (2003) The Nantucket pine tip moth (Lepidoptera: Tortricidae): a literature review with management implications. J Entomol Sci 38:1–40
Berisford CW (1988) The Nantucket pine tip moth. In Berryman AA (ed) Dynamics of forest insect populations: patterns, causes, implications. Plenum Publishing Corp., New York, NY
Miller WE (1967) The European pine shoot moth: ecology and control in the lake states. For Sci Monogr 14:1–72
Powell JA, Miller WE (1978) Nearctic pine tip moths of the genus *Rhyacionia*: biosystematic review (Lepidoptera: Tortricidae, Olethreutidae). USDA Agricultural Handbook No. 514

Pine Weevil, *Hylobius abietis* Linnaeus (Coleoptera: Curculionidae)

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Hylobius abietis (Fig. 60) L. feed on the stem bark of conifer seedlings. In the absence of appropriate control measures, the damage may reach a level that rules out planting as a means of conifer regeneration. It is distributed throughout the coniferous forests of northern Eurasia, including the British Isles and Japan. Other *Hylobius* species cause damage of a similar type, both within this area, and in North America. Soon after the introduction of clear felling systems in Central Europe, damage by *H. abietis* became wide-spread.

Pine weevil adults are blackish brown, robust-looking insects with a body length between 9 and 14 mm. Their antennae are located near the tip of the snout. Small tufts of yellow hair form characteristic patterns on the thorax and the abdomen, but are often worn off in older individuals that have spent a long time burrowing in the soil. The yellowish-white larvae are footless, curved and wrinkled, with a brown head capsule. Fully grown, fifth instar larvae attain a body length of about 15 mm.

Pine Weevil, *Hylobius abietis* Linnaeus (Coleoptera: Curculionidae), Figure 60 ***Hylobius abietis*.**

Migration

Upon logging of coniferous trees, volatile substances such as terpenes emanate from stumps and logging debris, particularly in clear-cuts when temperatures rise at the onset of summer. These volatiles attract weevils that have emerged from their hibernation sites in the forest floor. A main migration flight, usually lasting for a week or two, starts when maximum temperatures approach 25°C. The weevils take off into the wind to drift along. They have been observed flying above the forest canopy and are likely to land when sensing the strong bouquet of conifer volatiles. Migrants may end up in the wrong place, such as lumberyards and newly built wooden houses, and at sawmills, they can be found in great abundance on heaps of fresh sawdust. However, a large part of the migrants reach areas with fresh conifer stumps, where a new generation of weevils can reproduce in the roots. After the spring migration the weevils rarely fly for the rest of the season.

Oviposition

As both sexes are attracted by volatiles from fresh stumps, they will meet in the immigration areas. It is doubtful that sex pheromones play a role, other than maybe at close range. Upon mating, an extensive period of oviposition starts using roots with a diameter of at least 1 cm. Clear-cut areas offer an abundance of suitable breeding substrate. During the growth season, a female may lay several dozen eggs, which are laid singly, either in small cavities that she gnaws in the root phloem, or simply in the soil. When the soil is dry, the latter option seems to be avoided. Egg larvae hatching in the soil apparently use chemical clues to find suitable roots and may cover considerable distances during their underground migration. Throughout the egg-laying period, the weevils feed on local vegetation, including conifer seedlings. In cool areas, the oviposition may come to a halt by the onset of winter, to be resumed the next spring in stumps that remain fresh enough. The adults may survive for two, or even three seasons.

Development

Inside the subterranean stump roots, the offspring is protected against extreme weather and some of their natural enemies. The weevil larvae go through five stages during which they dig long, winding galleries in the phloem and outer xylem of the roots. Ambient temperature determines the developmental speed: at a stable 23°C, they are full-grown 40 days after the egg is laid, while at 12°C, the development takes more than 100 days. In their last instar, which in warmer areas may be reached the first autumn, the larvae construct an oblong pupal chamber. In thick-barked roots, this is dug out at the interface between phloem and xylem; where root bark is thin, the chamber is excavated in the wood and the entrance is closed from the inside with a plug of frass. If temperatures stay below about 21°C during their fifth instar, the larvae enter a diapause, which is broken after hibernation. Thus, a diapause is a regular feature of the weevil life cycle in cold boreal forest soils. After pupation, the adults remain in the pupal chamber while their exoskeleton hardens. They may then make their way to the surface, but if hatching occurs late in the season, they over-winter in the pupal chamber. Pine weevils hibernate at various larval stages or as adults, but not as eggs or pupae. Before migrating to other areas with fresh breeding material, the young adults go through an intensive period of feeding to develop their energy reserves and sexual organs.

The prolonged period of oviposition, the temperature-dependant development, and the facultative diapause lead to a highly variable generation time. In southern Scandinavia and Finland, a 2-year life cycle dominates; in the north, generation time stretches to 4 years or more. A mountainous landscape adds to the variability because the microclimate of steep, sunny and shady slopes are quite different. The survival of the immature stages is related to the generation time; a prolonged development means a higher risk of parasitation and predation, as well as increased competition from root-inhabiting fungi and other insects. A prolonged presence of the parental generation and a highly variable development of their offspring mean that the population remains high for several years. This is reflected in the period of damage.

Damage to the Conifer Seedlings

The adult pine weevil damages seedlings by eating the phloem of the above-ground stem. Moderate stem feeding often results in small, irregular "pockmarks" in the bark. A healthy plant may survive this damage and callus tissue soon covers the wounds. Severe attacks can girdle the stem, thereby interrupting photosynthate translocation and impairing water flow in the seedlings. The weevils prefer larger seedlings over smaller, but the former generally survive better. The damage occurs in natural regeneration as well as on planted seedlings, but in the former case, it often goes unnoticed because of an abundance of seedlings. Attack on planted seedlings is more likely to be noticed and generally has more serious consequences because the plants are distributed at an economically set distance. Both endemic and introduced coniferous species are attacked, as well as a number of other trees and weeds. Popular names in Europe often refer to the conifer that is most commonly attacked. As opposed to the stem feeding, larval tunneling in the roots can be considered useful because it accelerates stump decomposition and nutrient recycling.

If planted seedlings are not given appropriate protection, the mortality rate may be unacceptably high (for example, in southern Scandinavia, the mortality frequently exceeds 50%). The damage is often patchy, resulting in gaps in the future forest stand. The severity of damage is influenced by a variety of factors: the local environment and silvicultural practices both play a role. Regionally speaking, the damage is more severe in the southern parts of the pine weevil's range, probably due to more favorable conditions for the immature stages. Ground vegetation may be important, since the weevils can feed on a variety of plants. Upon clear cutting on lush sites, when thick vegetation is cut back, the ground vegetation will often succumb to sun-exposure, leaving new-planted seedlings as an extra welcome food for the weevils. Burned areas are particularly prone to damage. The common practice of extending felling coups from year to year facilitates migration to nearby breeding sites and in such cases, the population may build up to very high levels. Damage may become so severe that planting must be postponed for years. This practice, known in German as "Schlagruhe," may imply serious weed problems on sites with thick vegetation.

Control

Before World War II, a wide variety of control methods were used, including removing stumps, digging trap pits from which the weevils could not escape, using fresh stem sections and bark pieces to lure the insects, and a wide variety of stem treatments, including mechanical as well as chemical. After World War II, stem application of DDT was thought to solve the pine weevil problem for the future. DDT was thought to be both efficient and harmless. At least in more northern regions, the protective effect of DDT lasted for 2 years, protecting the seedlings during the most critical periods. Lindane (γ-BHC) was added to the compounds to accelerate the killing. When these chlorinated hydrocarbons were banned for environmental reasons in the 1970s, pyrethroids such as permethrin became the preferred chemicals. Although pyrethroids do not accumulate in food webs like the chlorinated hydrocarbons, environmental groups oppose their use, even when they are applied in nurseries. The European Commission may not allow the use of permethrin for forest seedling protection in the future.

Currently, the alternatives to insecticides are a mixed bag of silvicultural and technical methods. Substitution of clear felling and planting with natural regeneration methods would reduce the problem. However, this is often difficult in spruce forests because the shallow-rooted seed trees that are left are prone to wind felling. More deep-rooted species, e.g., Scots pine, are indeed often naturally regenerated. Here, a moderately dense shelterwood stand may significantly reduce seedling damage. This is partly due to the weevils' feeding on twig bark in the canopy and on superficial tree roots. Soil scarification also reduces feeding, particularly where seedlings are planted in exposed mineral soil. This effect diminishes gradually as the scarified patches fill up with vegetation and litter. Planting on small mounds of mineral soil is an improvement of the scarification method, though expensive. A variety of stem protecting devices exist, including coats of wax or latex, and various objects made from plastic, paper, etc., that are fitted around the seedling. At present, none of these devices seem to be reliable for a prolonged period of time; some are efficient for one season, but fail the next. Some of the designs may cause damage to the plant roots.

The pine weevil has a variety of natural enemies, such as parasitoids, and invertebrate and vertebrate predators. However, these organisms rarely seem to make significant inroads on the populations. In some cases, this may be because the immature stages are relatively inaccessible in their subterranean hiding places. Fungi and nematodes kill weevils, and nematodes may possibly become an active means to destroy the soil-dwelling stages, provided strains can be found that are active in cool soils. The artificial application of fungi to occupy the phloem of stumps could render this substrate less useful for the larvae, but success depends on how fast the hyphae are able to permeate the substrate. Considerable efforts are allocated to the search for chemicals with repellant and antifeedant properties, potentially to include them in stem protectants. Recently, a repellent substance has been patented, which occurs in excrements that the egg-laying females deposit next to their eggs, probably as a warning to other pine weevils. It seems unlikely that the pine weevil will easily adapt to this natural signal.

A panacea to the pine weevil problem does not seem likely. In areas where clear cutting remains a dominant way of regenerating conifers, the pine weevil is likely to retain its unique position as a headache for foresters and an expensive enemy of commercial forestry.

References

Bejer-Petersen B, Juutinen P, Kangas E, Bakke A, Butovitsch V, Eidmann H, Heqvist KJ, Lekander B (1962) Studies on *Hylobius abietis* L. I. Development and life cycle in the Nordic countries. Acta Entomol Fenn 17:1–106

Leather SR, Day KR, Salisbury AN (1999) The biology and ecology of the large pine weevil, *Hylobius abiestis* (Coleoptera: Curculionidae): a problem of dispersal? Bull Entomol Res 89:3–16

Nordlander G, Nordenhem H, Bylund H (1997) Oviposition patterns of the pine weevil *Hylobius abietis*. Entomol Exp Appl 85:1–9

Ratzeburg JT (1839) Die Forst-Insekten, Berlin, Germany

Örlander G, Nordlander G, Wallerts K, Nordenhem H (2000) Feeding in the crowns of Scots pine trees by the pine weevil *Hylobius abietis*. Scand J For Res 15:194–201

Pine Wilt

This is an insect-transmitted disease of pine trees caused by nematodes.

► Transmission of Plant Diseases by Insects

Pine-Flower Snout Beetles

Members of the family Nemonychidae (order Coleoptera).

► Beetles

Pin-Hole Borers

Some members of the subfamily Platypodinae (order Coleoptera, family Curculionidae).

► Beetles

Pink Hibiscus Mealybug, *Maconellicoccus hirsutus* Green (Hemiptera: Pseudococcidae)

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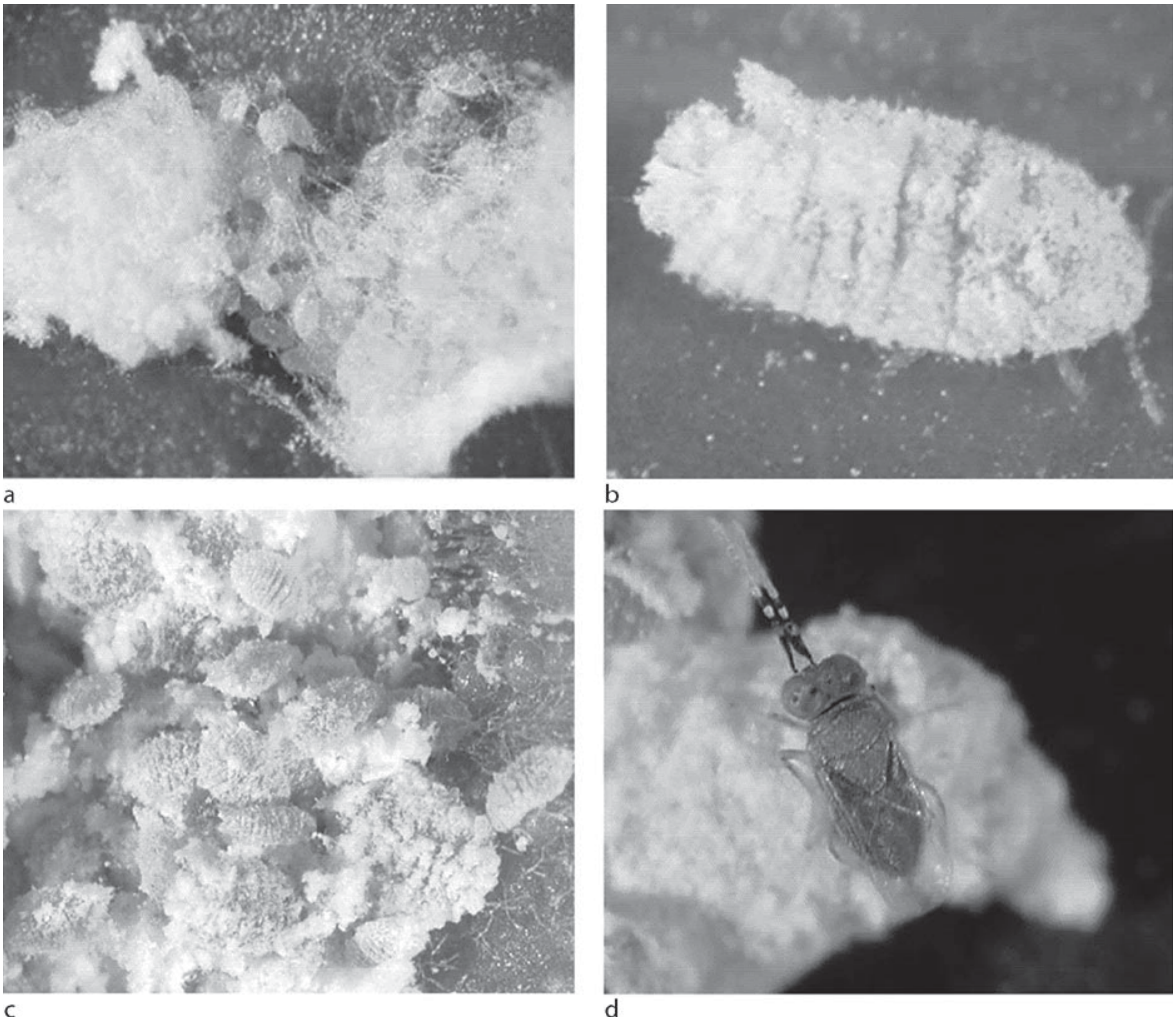
The pink hibiscus mealybug, *Maconellicoccus hirsutus* (Green), is native within the area encompassing Southeast Asia and nearby Australia. Its host range is very large, exceeding over 200 perennial and annual plant species, many of which are important in agriculture and as ornamentals. During the early part of the twentieth century, its range extended into Central Asia and Egypt. Within Egypt, it was a very significant pest of several common plant species, including cotton. Initially, a predatory beetle species (*Cryptolaemus montrouzieri*) was reared and introduced in large numbers. This provided some short-term relief; however, it was not until several parasite species were introduced that high levels of control were sustained. The pink hibiscus mealybug appeared first in the Western Hemisphere in Hawaii in 1984 and in the Caribbean island of Grenada and neighboring islands in 1994. In subsequent years, it spread to over 27 island countries in the Caribbean and in 1999, it was found in southern California, USA, the adjoining border region of northern Mexico, and the Central American country of Belize. By 2000, it was discovered in the Bahamas and northern South America (i.e., Venezuela/Guyana region), and attained Florida, USA, in 2002.

Female pink hibiscus mealybugs pass through three immature nymphal stages prior to developing into wingless adults. Most commonly, egg masses (i.e., ovisacs) (Fig. 61) containing several hundred eggs are laid at nearly the same location on a plant where the female developed. They lay one ovisac during their life. Total egg production ranges widely and is dependent on the host plant. Several hundred eggs are produced by females that have developed on potato sprouts, whereas 600 or more eggs often are laid by females that have developed on pumpkin fruit. At temperatures ranging from 26 to 33°C, the total development time from egg to gravid female takes 4–5 weeks. This includes approximately 5 days for egg hatch, 7 days for first and second instar female nymphs, 8 days for third instars and approximately another week for adult females to fully mature and begin laying eggs. As adults, females undergo a considerable increase in size (approximately 2- to 3-fold) prior to laying eggs. In contrast, although male pink hibiscus mealybugs look essentially identical to female mealybugs as first instars and most of the second life stage, male nymphs take on a considerably different appearance as late second instar nymphs. They become elongate and begin to sport small wing buds that become accentuated in third and fourth instars. As late second instars to the time males emerge as winged adults, they live clustered together as small groups within flocculent mounds of waxy material. During these late stages of development, the males are developing within a cocoon-like structure. Females also produce an abundant white, waxy substance that covers their bodies. Male pink hibiscus mealybugs have four immature nymphal stages. There is a third instar life stage of very short duration (lasting for little more than a day) and a fourth nymphal life stage lasting for 5–6 days prior to emerging as a winged adult.

First instar nymphs are referred to as crawlers because they are very actively moving at this stage. The crawlers and all other immature stages range in color from orange to medium pink. Adult females have a very dark pink coloration. Wax is present on all stages; however, it is especially abundant on third instar and adults. Although many mealybug species are field identified by specific patterns of wax filaments extending from the perimeter of the body or very long filaments extending from the posterior, the pink hibiscus mealybug produces no distinct pattern of filaments. As a result of the delicate nature of wax filaments, field identification of mealybug species typically requires viewing the characteristics of numerous individuals in a group as opposed to one isolated mealybug. The life stage of preserved pink hibiscus mealybug specimens can be accurately identified by the number of antennal segments. First and second instar nymphs have six segments, third instar females have seven segments, whereas adult females have nine-segmented antennae.

The pink hibiscus mealybug undergoes numerous generations each year. Population increase is dependent on temperature and



Pink Hibiscus Mealybug, *Maconellicoccus hirsutus* Green (Hemiptera: Pseudococcidae), Figure 61 Pink hibiscus mealybug (*upper left*) ovisac, (*upper right*) young adult female, (*lower left*) cluster of nymphs and adult females, (*lower right*) parasitoid *Anagyrus kamali* female.

suitability of host plants, which is often linked to moisture availability. The pink hibiscus mealybug performs well at moderate to high temperatures (exceeding 38°C). In the tropical and subtropical regions, this mealybug species reproduces continuously throughout the year, having abundant host plant material and temperatures ranging from 22°C and above. In the more temperate areas of its distribution in the northern hemisphere, the pink hibiscus mealybug population is difficult to find from winter to late spring. From June to September, population densities may increase dramatically in the absence of effective natural enemies. From November onward, the population declines as certain host species (especially mulberry) drop their leaves, causing the mealybugs to move from the growing regions of the tree (i.e., branch terminals) to larger branches that often contain crevices in rough bark, well suited for providing protection. Essentially all life stages are present during the winter period, although later instars and adult female mealybugs are more common.

As previously stated, *Cryptolaemus montrouzieri* is cited as an important biological control agent within its presumed native range. It has also been used with some success within new regions where the pink hibiscus mealybug has become established. Parasites also play a very important role in population regulation. *Anagyrus kamali* (family Encyrtidae) is among several agents that have had a long-term impact on the pink hibiscus mealybug in Egypt and has been the most important natural enemy introduced to date to control the pink hibiscus mealybug in the Western Hemisphere. This parasitoid has reduced mealybug population densities by 90% or more in St. Kitts, West Indies; St. Thomas and St. Croix in the U.S. Virgin Islands, Puerto Rico, Belize, Bahamas and California, USA, resulting in a highly successful biological control program.

References

Ghose SK (1972) Biology of the mealybug *Maconellicoccus hirsutus* Green (Pseudococcidae: Hemiptera). Indian Agric 16:323–332

Hall WJ (1926) The hibiscus mealybug (*Phenacoccus hirsutus*, Green) in Egypt in 1925 with notes on the introduction of *Cryptolaemus montrouzieri*, Muls. Ministry of Agriculture, Cairo, Egypt. Technical and Scientific Service Bulletin No. 70, 19 pp

Kairo MTK, Pollard GV, Peterkin DD, Lopez VF (2000) Biological control of the hibiscus mealybug, *Maconellicoccus hirsutus* Green (Hemiptera: Pseudococcidae) in the Caribbean. Integr Pest Manage Rev 5:241–254

Mani M (1989) A review of the pink mealybug – *Maconellicoccus hirsutus* (Green). Insect Sci Appl 10:157–167

Persad A, Khan A (2002) Comparison of life table parameters for *Maconellicoccus hirsutus*, *Anagyrus kamali*, *Cryptolaemus montrouzieri* and *Scymnus coccivora*. Biocontrol 47:137–149

Sagarra LA, Vincent C, Stewart RK (2001) Body size as an indicator of parasitoid quality in male and female *Anagyrus kamali* (Hymenoptera: Encyrtidae). Bull Entomol Res 91:363–367

Piophilidae

A family of flies (order Diptera). They commonly are known as skipper flies.

► Flies

Pipunculidae

A family of flies (order Diptera). They commonly are known as big-headed flies.

► Flies

Piroplasmosis: *Babesia* and *Theileria*

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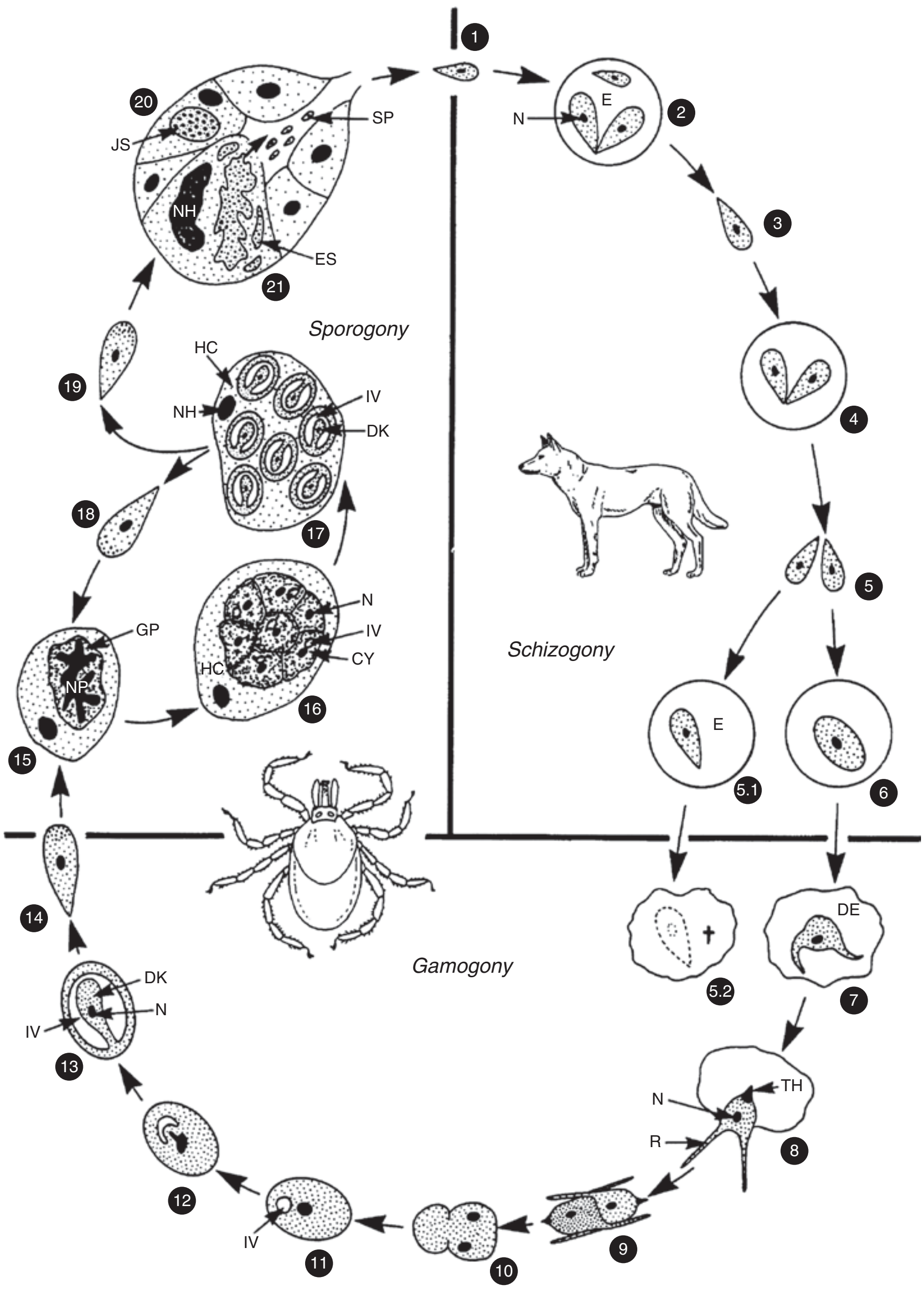
The Piroplasmea, a class of protozoa, are transmitted to vertebrates by ticks. Piroplasms infect erythrocytes (RBCs), and some also attack leukocytes. Species from two genera, *Babesia* and *Theileria*, cause serious diseases in dogs, cattle, sheep, and goats.

Babesia

Some 99 species of *Babesia* are parasites of nine orders of mammals. We shall consider only those species that cause babesiosis in dogs, ruminants and humans.

Canine babesiosis, also known as canine piroplasmosis or malignant jaundice, is caused by *Babesia canis* and *B. gibsoni*. The former is cosmopolitan, especially in warm climates, while the latter is found in Asia and North America. Both are pathogenic in dogs. *B. canis* is transmitted by the brown dog tick *Rhipicephalus sanguineus*. The extent of pathology in the dog is dependent on the virulence of the strain of *B. canis*.

The life cycle of *Babesia canis* is typical of other species of *Babesia*. The sporozoite is introduced into the vertebrate host via the saliva of *R. sanguineus*. Sporozoites invade the host's RBCs where they develop via binary fission into merozoites. Eventually these RBCs rupture, releasing the parasites to invade other RBCs. Merozoites develop into gamonts in some RBCs. Gamonts infect ticks when a bloodmeal is taken. The



Piroplasmosis: *Babesia and Theileria*, Figure 62 **Diagram of the life cycle of Babesia canis. An infectious tick introduces sporozoites (1) into the blood of its host and the sporozoites; they undergo binary fission in the red blood cells (RBCs) (2–4); the merozoites differentiate into gamonts also within RBCs (5, 6). When infectious blood is ingested by a tick, gamogony and fertilization occur in the gut of the tick (7–13), and then the kinete (14) enters cells of the salivary gland where sporogony takes place (15–20). Abbreviations: CY, cytomere; DE, digested RBC; DK, developing kinete; E, RBC; ES, enlarged sporont forming sporozoites; GP, growing parasite or polymorphic stage; HC, host cell; IV, inner vacuole; N, nucleus; NH, nucleus of host cell; R, raylike protrusion; SP, sporozoite; Th, thornlike apical structure; YS, young meront. (From Marquardt et al. (2000), used with permission of Harcourt Academic Press.)**

development of sporozoites into gamonts is an asexual form of reproduction known as schizogony. It allows the rapid build-up of the parasite in the host. Within the tick's midgut, sexual reproduction occurs in a process known as gamogony. The fertilized kinete then enters cells of the salivary gland where sporogony takes place. This is a process of asexual reproduction that results in the production of large numbers of sporozoites. The kinete can also infect the ovaries which allows transovarial transmission to new larvae and produces a new generation of infected ticks. Babesia canis are also transmitted from one life stage to another in a process named transstadial transmission.

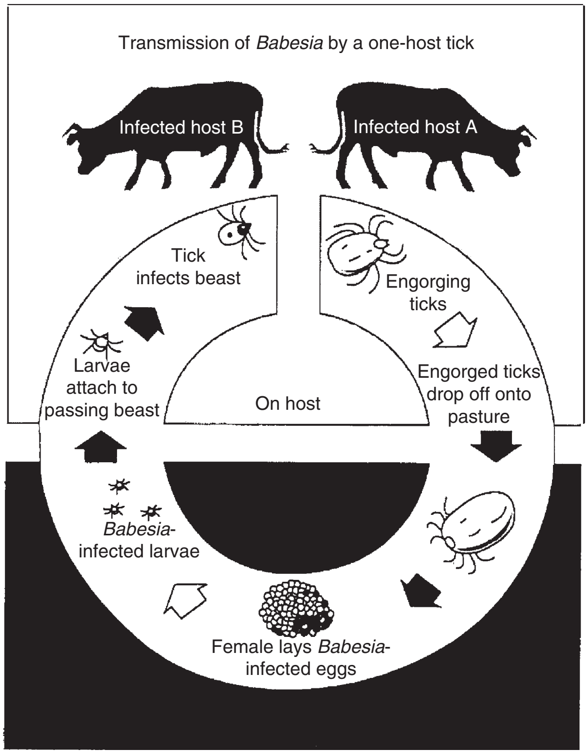
Most of the symptoms of the different babesioses including canine babesioses, can be traced to the breakdown of infected RBCs and the release of toxic products. This can result in anemia, enlarged spleen, kidney damage and sometimes impaired circulation of blood. Dogs that recover from canine babesiosis are immune to future infections. As with other babesiosis, diagnosis is made by identifying the parasite within RBCs. Several drugs are effective against canine babesiosis.

Two species of *Babesia* are parasites of sheep: *Babesia motasi* and *Babesia ovis*. Some strains of *B. motasi* will infect goats as well as sheep. *Babesia motasi* produces a severe disease but is even more pathogenic when it is accompanied by infections of *Theileria* and or *Ehrlichia*. *Babesia ovis* is found in equatorial Africa north to the Sahara, in the Mediterranean area throughout Europe, and portions of the former USSR. It is believed to be transmitted by *Rhipicephalus bursa* and *R. evertsi* outside of Asia, and *R. bursa* in the former USSR. The latter tick can transmit *B. ovis* transovarially through at least 44 generations. *Babesia motasi* occurs in equatorial Africa north to the Sahara, the Mediterranean area and Europe. It is believed to be transmitted by species of *Haemaphysalis* in Europe. Sheep infected with *Babesia* can act as carriers for up to 2 years.

Horses and other equids are infected by *Babesia caballi* which causes equine piroplasmosis worldwide. Mortality in domestic horses is less than 50%, but strains with differing virulence exist. Over ten species of ticks can vector *B. caballi*. *Dermacentor nitens* transmits the parasite in the United States, Central and South America.

Bovine babesioses is caused by seven species of *Babesia* and is transmitted by several species of ticks. Domestic cattle are at high risk from babesiosis worldwide. Two of the seven species that cause bovine babesiosis, *Babesia bovis* and *Babesia bigemina*, are widely distributed in Africa, Asia, Europe, Australia and Central and South America. *Babesia bovis* is transmitted by species of *Boophilus*, especially *B. microplus* and *B. decoloratus* in tropical and subtropical areas, and by *Rhipicephalus bursa* in southern Europe. Transmission by a one-host tick such as *B. microplus* and other species of *Boophilus* is described in the accompanying figure. The female tick becomes infected during feeding and transmits the pathogen transovarially to larvae that infect cattle as they feed. Many factors are related to the success of this transmission cycle (Fig. 63).

Babesia bigemina causes Texas cattle fever, also known as Red water fever or splenetic fever. Feeding ticks transmit the parasite. The African strain of *B. bigemina* is the most pathogenic, the Australian strain less so. The tick vector in the USA is *Boophilus annulatus*. Texas cattle fever is important historically because it is the first disease caused by a protozoan parasite that was shown to be transmitted by a blood feeding arthropod. The disease was first noticed during the cattle drives in the mid 1800s, and was officially described in 1888 as Texas cattle fever. Efforts to eradicate Texas cattle fever started at the turn of the century with the goal of eliminating the disease in the southeast part of the country, especially Texas and Florida. The ability to control cattle movement into Florida resulted in success in eliminating Texas cattle fever in that state by the 1930s. Because of its long border with Mexico, control of cattle movement into Texas was more difficult. Even so, the disease has largely been eliminated as a problem though there is still a sub-symptomatic level of infection in some Texas herds.



Piroplasmosis: *Babesia* and *Theileria*, Figure 63 **Diagrammatic representation of the transmission of a *Babesia* species by a one-host tick. The upper half shows the ticks attaching, feeding, and dropping from the host, while the lower half shows the events that occur in the pasture. Factors affecting the success of the transmission cycle include: (1) the concentration of infected erythrocytes; (2) number of infected, replete females dropping from the diseased host; (3) proportion of engorged females that lay eggs; (4) proportion of eggs that hatch; (5) the proportion of the larval population that is infected with the pathogen; (6) the number of infected larvae attaching to susceptible bovine hosts each day; (7) host immunity (natural and acquired) to infection; and (8) host resistance to tick parasitism. (From Sonenshine (1993), used with permission of Oxford University Press.)**

Five other species of *Babesia* are not distributed as widely as *B. bovis* and *B. bigemina*. *Babesia* major occurs in Europe and the Middle East where it causes a disease in cattle with limited mortality. *Haemaphysalis punctata* vectors *B. major* which is transmitted transovarially in the tick. *Babesia jakimovi* occurs in Siberia where it causes a disease in cattle that has high mortality. It is transmitted by species of *Ixodes*. The pathogen is transmitted transovarially in its vectors. Adults of the next generation of ticks are the infective stage. *Babesia divergens* occurs in Europe and causes a disease that can produce a parasitemia in cattle with as high as 24% of RBCs infected. The pathogen is transmitted by *Ixodes ricinus*. The adult tick picks up the pathogen during feeding and transmits it transovarially. All feeding stages of the next generation can transmit the pathogen to cattle. *Babesia ocultans* occurs in South Africa, and *Babesia ovata* in Japan.

Clinical symptoms of babesiosis are seen 8–16 days following infection. Most of the symptoms result from infected RBCs which eventually break down releasing hemoglobin and metabolic byproducts of the parasite. This results in a fever that can rise to over 40°C and anemia. Hemoglobin creates the characteristic red tinge of the urine. *Babesia bovis* infections can produce a hypertensive shock syndrome where sick animals quit feeding and become listless. Often dry bloodstained feces occur. Parasitized animals may develop sunken eyes and muscle tremors. Symptoms can be severe especially in older animals. Newborn calves are protected by maternal antibodies.

Cattle are able to develop immunity to infection with *Babesia* species. Persistent subclinical infections causes acquired immunity. Calves also get immunity from their mothers that can last several months, and if infected, calves develop an even stronger immunity that can last for up to 4 years. Some breeds of cattle are naturally more resistant to the disease, so they are preferred in areas where there is a high level of infected ticks. Currently the best control of the disease is by dipping and spraying the animals to control tick infestations. A vaccine used in Australia has had some success.

Four species of *Babesia* have been found in humans: *B. bovis* and *B. divergens* whose normal host are oxen, *B. equi* whose normal host are horses, and *B. microti* whose normal host are rodents. Piroplasmosis in humans is rare and those without a spleen are the most susceptible. *Babesia microti* can infect individuals with a normal spleen. *Babesia microti* is transmitted by *Ixodes ricinus* and *I. trianguliceps* in Europe, and *I. scapularis* in the USA. Symptoms of human babesiosis are similar to those of malaria, but the disease lacks the periodicity found in malaria.

Theileria

Theileria spp. are parasites of domestic and wild ruminants, and domestic and wild felines. Six species infect cattle: *Theileria parva*, *Theileria annulata*, *Theileria orientalis*, *Theileria mutans*, *Theileria taurotragi* and *Theileria velifera*. The most serious diseases are caused by *T. parva* and *T. annulata*. These two pathogens are considered later. *Theileria orientalis* occurs worldwide and is transmitted by several ixodids. In western Eurasia, through the northwest of Africa, it is transmitted by *Haemaphsalis punctata*, but in the eastern Asia and Australia it is transmitted by *H. longicornis*. Usually *T. orientalis* causes a mild disease, but in susceptible breeds of cattle it can produce a severe anemia. *Theileria orientalis* may be a synonym of *T. buffeli* and *T. sergenti*. *Theileria mutans* occurs throughout tropical Africa. Its principle vector is *Amblyomma variegatum*. *Theileria mutans* is usually not very pathogenic, although a pathogenic strain of the parasite exists in East Africa that can produce severe anemia with up to 45% of the host's RBCs infected. *Theileria taurotragi* infects cattle in eastern, central and southern Africa, and can also infect sheep and goats. The pathogen is transmitted by *Rhipicephalus appendiculatus*, *R. zambeziensis* and *R. pulchellus*. *Theileria taurotragi* produces a mild or subclinical disease in cattle but can produce a fatal disease in eland. *Theileria velifera* is found throughout Africa south of the Sahara. It is transmitted by *Amblyomma variegatum*, *A. hebraeum* and *A. lepidum*. The parasite causes a disease of low pathogenicity. *Theileria cervi* is a parasite of cervids in Europe and the United States. In the USA the pathogen is transmitted by *Amblyomma americanum*. The pathogen is common in white-tailed deer (*Odocoileus virginianus*) in the south and southeastern states. No clinical manifestations of these infections occur.

Theileria parva causes East Coast Fever, the most serious of the diseases caused by *Theileria* in cattle. It is transmitted by *Rhipicephalus appendiculatus*. East Coast Fever was first described in east Africa at the start of the seventeenth century. By 1901–1902 it had spread to southern Africa. The incubation period for East Coast Fever is 10–25 days. Symptoms include fever, swollen lymph nodes and emaciation. Most of the damage is to the lymphatic system, especially the lymph nodes and spleen, but other organs including the kidney, lungs and liver may also be affected. Older animals are more susceptible to East Coast Fever than younger animals. The most common control of East Coast Fever is to kill the vector ticks. Antigenic diversity exists in *T. parva*, and this can complicate the outcome of the disease. In addition, strains of *T. parva* exist that have different virulence. Virulence is also tied to the tick vector, and some ticks only transmit a 100% fatal form of the parasite. The disease is believed to have originated in African buffalo *Syrlcerus caffer* which acts as a reservoir. East Coast Fever is a benign disease in the buffalo.

An important concept in understanding East Coast Fever is endemic stability, which is defined as the condition in a given cattle herd (or population) where a large majority of individuals become infected and immune by 6 months of age, with little or no clinical symptoms. Endemic stability occurs when the cattle have a low innate susceptibility to the pathology of East Coast Fever; when *R. appendiculatus* infestation occurs throughout the year; and when most of young calves are exposed to a low *T. parva* challenge. Eradication of the tick vectors in endemic areas can result in the loss of endemic stability. Subsequent relaxation of control measures in these areas has often resulted in a rapid increase in the tick population with the return of severe epidemics of East Coast Fever.

The life cycle of *Theileria parva* is similar to that of *Babesia canis*, but differs in that lymphocytes are invaded as well as RBCs. The infectious stage of the parasite is the sporozoite. These first invade lymphocytes in the lymph nodes, unlike *Babesia canis* sporozoites. In lymphocytes, the sporozoites undergo schizogony and multiply, then invade RBCs. Erythrocytic schizogony is rare or absent. Infected RBCs are transmitted to the tick where they undergo gamogony and fertilization in the midgut, then invade salivary gland cells. Here sporogony occurs, resulting in sporozoites that are transmitted to the vertebrate host with the tick's saliva. In the tick vector, transstadial transmission occurs but not transovarial transmission.

Theileria annulata causes Mediterranean or tropical theileriosis in cattle. The pathogen is found throughout northern Africa, into the Middle East including Saudi Arabia, Turkey, southern Europe through the Caucasian area into India and China. It is transmitted by species of *Hyalomma*. Common vectors include *H. anatolicum anatolicum*, *H. detritum* and *H. asiaticum*. Tropical theileriosis is a milder disease than ECF and has a much lower mortality in cattle. However, it is an economically important impediment to livestock improvement. In enzootic areas, *Bos taurus* cattle can have a mortality of 40–80%, and *Bos indicus* cattle, which are more resistant to *T. annulata*, can have as much as 20% mortality, mostly in calves. Symptoms include fever, swollen lymph glands, weight loss, anorexia, and apathy. A generalized leucocytosis occurs with great reduction in RBCs, resulting in hemolytic anemia. Organs that are damaged are mostly similar to those damaged in East Coast Fever. Erythrocytic schizogony is common in the life cycle of *T. annulata*. Cattle that survive the disease develop a persistent immunity.

Several species of *Theileria* infect small ruminants. *Theileria hirci* occurs in eastern and southern Europe, the Near and Middle East and in northern Africa. It is transmitted by *Hyalomma anatolicum*. It produces a disease that is highly pathogenic in sheep and goats. *Theileria separata*, a non pathogenic parasite of sheep, is found in Tanzania and is transmitted by *Ripicephalus evertsi*. *Theileria ovis* is worldwide in distribution and is transmitted by many different ticks, including species of *Ornithodorus*, *Hyalomma*, *Haemaphysalis*, *Dermacentor* and *Rhipicephalus*. It produces a disease with little or no pathogenicity in sheep and goats.

Wild and domestic cats are infected by *Theileria felis*, which causes feline cytauxzoonosis in the United States. It is transmitted by *Dermacentor variabilis*. The disease can be fatal unless treated. Cougars and bobcats are carriers of the disease, but show no symptoms.

► Ticks

References

Kettle DS (1995) Medical and veterinary entomology, 2nd edn. CAB International, Wallingford, UK, 725 pp

Kocan AA, Kocan KM (1991). Tick-transmitted protozoan diseases of wildlife in North America. Bull Soc Vector Ecol 16:94–108

Norval RAI, Perry BD, Young AS (1992) The epidemiology of Theileriosis in Africa. Academic Press, San Diego, CA, 481 pp

Sonenshine DE (1993) Biology of ticks, vol. 2. Oxford University Press, New York, NY, 465 pp

Sonenshine DE, Mather TN (eds) (1994) Ecological dynamics of tick-borne zoonoses. Oxford University Press, New York, NY, 447 pp

Pistachio Seed Wasps

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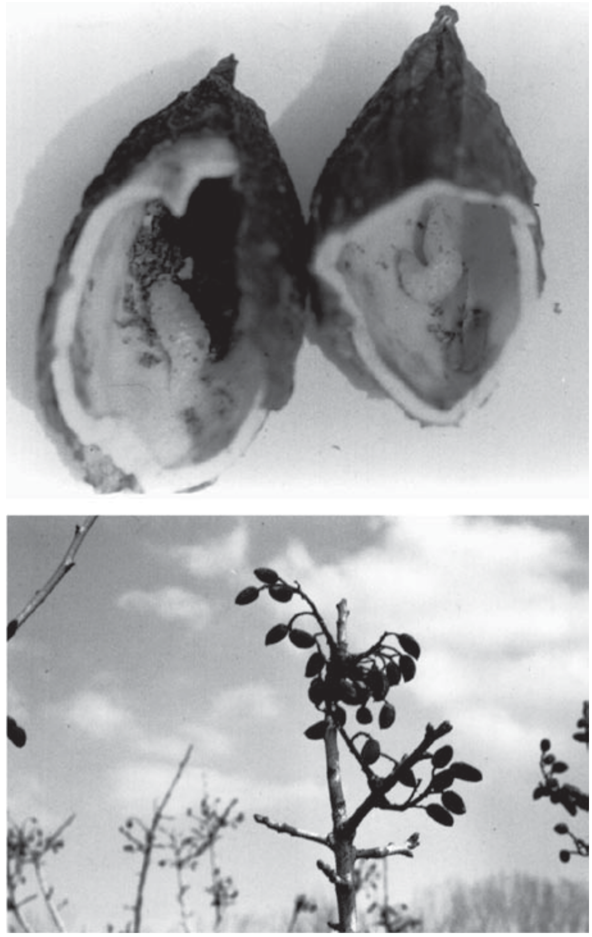
Two species of such wasps are known pests of pistachio because they destroy the fruit. They belong to different families of the Hymenoptera, and their population densities vary with the region and with time. In some orchards the two species co-exist, but one of them usually outnumbers the other. In addition to fruits of the cultivated pistachio, *Pistacia vera*, both these wasps infest also fruits of *P. terebinthus*.

Eurytoma plotnikovi Nikol' Skaya (Eurytomidae)

The adult female is 4–5 mm long and has a reddish brown head and thorax, yellowish red abdomen and red eyes. The legs and the two basal antennal articles may have a lighter color, but this varies with the region. The antennae have ten segments, with the basal one, the scape, being three times as long as the next one. The male is usually black and a little shorter than the female. The larva is whitish, tapering in both ends, apodous, curved, and is 6 mm in length when fully grown. It occurs from the Mediterranean region east to central Asia.

This wasp is univoltine. However, some individuals may complete their life cycle in 2 years because of prolonged diapause. It overwinters as a fully-grown larva inside the fruit, whether the infested fruit remains on the tree throughout winter or has fallen to the ground. Pupation occurs also inside the fruit, sometime in May, and the adult emerges in late May to late June, after boring an exit hole in the fruit with its mandibles. Oviposition occurs in June. Using her ovipositor, the female inserts her egg near the tip of the fruit. The stalked egg is usually placed on the inner wall of the endocarp. The oviposition hole darkens, is easily seen, and may offer entry to plant pathogenic fungi. The larva (Fig. 64) first feeds on the still tender inner layers of the endocarp, and later, in July to August, on the seed, which it consumes completely or almost so. There it remains in diapause until the following spring. In coastal northern Greece, diapause is terminated between early April and early May, with high temperatures and long days leading to diapause termination. The infested fruits become mummified, and as a rule remain on the tree after the leaves have fallen in autumn. Yet, if the fruits are also infected by a fungus, they mostly drop to the ground, usually in autumn.



Pistachio Seed Wasps, Figure 64 **Fully-grown larvae of *E. plotnikovi* within infested mummified pistachios (*above*), and infested mummified fruits remaining on the tree after harvest (*below*).**

This seed wasp is among the most destructive pests of pistachio in many countries. Thus, control measures are generally needed. One such measure is the collection and destruction of all mummified fruits, whether they are on the tree or the ground. This measure to be effective should be applied by all neighboring growers. If fruit collection in a given area cannot be practiced, one or two insecticidal sprays are needed. The insecticide should preferably be systemic, but contact ones of long residual action also proved effective. The proper time is determined by following the exit of adult wasps from infested fruits kept in cages in the orchard. In Cyprus, a spray applied 3 days after the exit of the first wasps from caged fruits, gave satisfactory protection of the crop.

Megastigmus pistaciae Walker (Torymidae)

The adult female has a golden yellow body, with grey-yellow head, red eyes and reddish reflections on the abdomen. Its length is variable, from 3 to 5.5 or even 6 mm. The front wings have a dark oval spot near the costa. The male is reddish yellow. Males are rare. The larva is grayish white, apodous, curved, narrower in both ends and 6 mm long when fully grown. It occurs in southern Europe, northern Africa, the Black Sea coast, the Middle East, Iran, Central Asia, and the United States.

Oviposition takes place in the fruit and the larva consumes the seed, much like *Eurytoma plotnikovi*, above. In Iran and Tunisia it is reported to be bivoltine. It overwinters as a larva inside the pistachio seeds, pupates in spring, and emerges as an adult in spring or early summer. In Tunisia, the adults of the second generation are seen in April-June, and those of the first in July to August. Overwintering larvae are produced from eggs of both generations. In Iran, adults emerge in mid-April to late May and in mid-June and oviposit shortly before the endocarp is completely hardened.

In California, in addition to pistachios, this wasp often infests the seeds of *Pistacia chinensis*, a common ornamental, as well as fruits of other plants of the same genus. Adult trapping and emergence records indicate two generations per year, with adults being active in June and August to September. Yet, adults emerging during the second period are evidently unable to oviposit through the endocarp which is already hard. Therefore, it is possible that only one generation develops in pistachios in California. This is supported by the fact that a high percentage of larvae of the first generation enter diapause, to give adults in the following spring. A possible second generation may develop in fruits of other species of *Pistacia* having an endocarp that hardens later than that of pistachio.

Damage is similar to that by *E. plotnikovi* and, when it reaches economic levels, control should be applied in spring against the adults. Careful collection and destruction of the fruits housing the diapausing larvae are also effective, if applied by all the growers of a given area, and provided that no other species of host trees are in the vicinity.

References

Davatchi A (1956) Sur quelques insectes nuisibles au pistachier en Iran. Revue de Pathologie Végétale et Entomologie Agricole de France 35:17–26

Haralambidis CG, Tzanakakis ME (2000) Time of diapause termination in the pistachio seed wasp *Eurytoma plotnikovi* (Hymenoptera: Eurytomidae) in northern Greece and under certain photoperiods and temperatures. Entomol Hellenica 13:43–50

Jarraya A, Bernard J (1971) Premières observations bioécologiques sur *Megastigmus pistaciae* en Tunisie. Annales Institut National de la Recherche Agronomique de Tunisie 44:1–28

Rice RE, Michailides TJ (1988) Pistachio seed chalcid, *Megastigmus pistaciae* Walker (Hymenoptera: Torymidae), in California. J Econ Entomol 81:1446–1449

Pit Scales

Members of the family Asterolecaniidae, superfamily Coccoidae (order Hemiptera).

► Bugs

Plague: Biology and Epidemiology

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Plague, also called the black death, is an infectious bacterial disease of humans caused by *Yersinia* (*Pasteurella*) *pestis*. The bacterium is a non-motile, gram negative, plump coccobacillus that is transmitted through the bite of the rat flea, *Xenopsylla cheopis,* from susceptible rat hosts, primarily the domestic rat, *Rattus rattus*. People may sometimes become infected by handling other rodents such as prairie dogs that have sylvatic plague and harbor the infected fleas. The infected rodent populations are often decimated by the disease and the hungry fleas abandon the host carcasses in search of new hosts, often domestic rats, cats or even humans. Direct bacterial infection can occur in humans who handle dead rodents or who care for infected domestic cats. In such cases, the bacterium may enter an open wound. Airborne bacterium in the cough of an infected cat or human can also be the source of infection (pneumonic plague).

In the Middle Ages, plague killed millions of people in Europe and, from 1924 to 1925, there was an urban plague epidemic in Los Angeles. Since 1974, small scattered foci of the plague were identified in northern regions of China and other Asian countries, Southern Africa and Madagascar, and in Brazil. In the United States, between 1970 and 1998, small foci have been confined to rural areas of Arizona, California, Colorado, and New Mexico with 36 or as many as 191 cases reported from each of these regions.

Plague induces three types of clinical pathologies in human hosts: the bubonic, primary pneumonic, and primary septicemic plague. Of these, the bubonic plague is the most common and is caused by the bite of an infected flea. Within 2–4 days of infection the person experiences chills, high fever, headache, nausea, and vomiting. There is also evidence of rapid pulse and rapid breathing accompanied by anxiety. Physiologically, the neutrophile leukocyte counts are rapidly elevated. Concomitant with these symptoms, single or multiple enlarged hemorrhagic lymph nodes, the "bubo" (hence the name bubonic plague), appear and are painful and tender. If treated early with antibiotics such as streptomycin, gentamicin, tetracycline, or chloramphenicol, the infection is often eliminated. However, if treatment is delayed, death ensues within 24 h as a result of toxemia even though the bacteria are killed by the antibiotic. About one in seven patients in the United States dies from the disease. Mild variations of the disease (plague minor) may occur and involve minimal toxemia with small "buboes" which contain evidence of the bacterium (thus resulting in the diagnosis). However, these patients frequently survive. Other patients may serve as "carriers" with temporary bacterial infection in the throat (transient pharyngeal carrier) but who may have no manifestations of the disease.

Patients with primary septicemic plague may occur in about 1% of cases. The disease pathogenesis is not as clear-cut as in bubonic plague infections. Sudden fever, meningitis, hemorrhage and pneumonia are common. Presumably, the infection is induced by direct introduction of the bacillin into a blood vessel.

Primary pneumonic plague is contracted by inhalation of the bacterium in aerosol form from coughing patients, and from airborne bacilli released from the remains of infected people or animal carcasses. There is a 48–60 h incubation period, followed by sudden chills and fever. The sputum and other body exhudates of persons with primary pneumonic plague are replete with *Y. pestis* bacilli but the individual exhibits no symptoms of pneumonia. Death occurs within one or two days after infection, as a result of respiratory distress and toxic shock.

The vector of the bacterium, the (Oriental) rat flea, *Xenopsylla cheopis*, like other fleas, belongs to the insect Order Siphonaptera. Unlike most other insects, fleas have a bilaterally flattened body and possess jumping legs than enable them to jump more than 100 times their body length, and even to heights of more than 30 cm. They have piercing-sucking mouthparts that enable them to pierce the skin of their rodent or human host and siphon the blood. The proteins in the blood are important for flea egg development. Fleas have a holometabolous form of development involving an egg, larval and pupal stages, and the adult male and female.

The eggs (about 0.5 mm long) do not adhere to the rat's body but usually fall off into the nest. After 2–21 days, depending on temperature, one larva hatches/egg and feeds upon the detritus and flea feces. There are three larval instars that require 9–15 days to reach the pupal stage. Larvae have a somewhat cylindrical body, have no legs or other appendages, and are covered with long setae. They have chewing mouthparts. A mature larva may measure up to 4 mm long. The pupal stage lasts 5–7 days but can be prolonged if temperatures are low. The pupa may spin a silken cocoon around itself. Adults may live for 38–100 days, depending on the humidity. Such longevity has epidemiological implications, particularly in relation to plague as they may allow the pathogen to survive long after an outbreak has been though to be eliminated.

Several public health and environmental management strategies have been established in the United States to prevent plague infections. These involve sanitation measures to reduce rodent infestations where people work, securing grain and other food storage areas from rodent entry, use of rodenticides in areas (e.g., ships and docks) where rodents may breed, and applying insecticides to kill fleas, particularly in rodent nests where flea eggs, larvae, or pupae may be sequestered.

► Fleas
► History and Insects

References

Binford CH, Connor DH (1976) Pathology of tropical and extraordinary diseases, an atlas, vol 1. Armed Forces Institute of Pathology, Washington, DC, 339 pp

Centers for Disease Control (2002) A quick guide to plague. Available at http://www.cdc.gov/ncidod/dvbid/dvbid.htm. Department of Health and Human Services

Schmidt GD, Roberts LS (1989) Foundations of parasitology, 4th edn. Times Mirror/Mosby College Publishing, St. Louis, MO, 750 pp

Youmans GP, Paterson PY, Sommers HM (1980) The biologic and clinical basis of infectious diseases. W.B. Saunders, London, UK, 849 pp

Planidiiform Larva

A flattened body form found in the active first instar of certain parasitoids in the orders Diptera and Hymenoptera. This mobile stage, occurring before the insect penetrates the host, is called a planidium (pl., planidia).

Planidium

In certain insects that undergo hypermetamorphosis, the first instar larva, which is legless and somewhat flattened. This is found in certain Diptera and Hymenoptera (contrast with triungulin).

Planta (pl., plantae)

The basal joint of the posterior tarsus in pollen-gathering Hymenoptera.

Plant Bugs (Hemiptera: Miridae)

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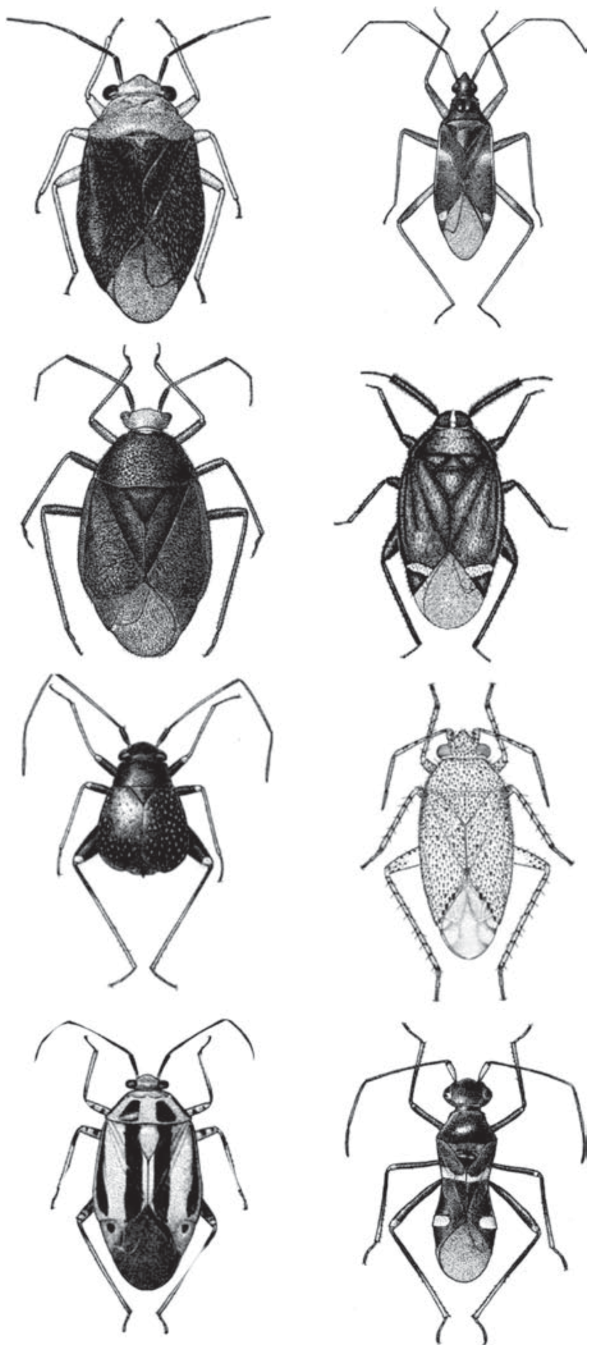
The family Miridae, often referred to as plant bugs, is the largest true bug family. Worldwide, more than 10,000 species of Miridae are known, but this number is expected to more than double once the tropical faunas are more thoroughly studied. Plant bugs belong to the superfamily Miroidea, infraorder Cimicomorpha, and suborder Heteroptera, within the order Hemiptera. Also included in Miroidea are the families Joppeicidae, Microphysidae, Thaumastocoridae, and Tingidae.

Eight mirid subfamilies are currently recognized (Fig. 65), primarily on the basis of pretarsal structures and male genitalia. Mirinae is by far the largest subfamily, followed in size by Phylinae, Orthotylinae, Bryocorinae, Deraeocorinae, Cylapinae, Isometopinae, and Psallopinae. Mirinae are characterized largely by the apically divergent parempodia on the claws and male genitalia with an inflatable aedeagal membrane; Phylinae, by hairlike or setiform parempodia and straplike male genitalia; Orthotylinae, by apically convergent parempodia, unique secondary gonopore, and frequently complex vesica and parameres; Bryocorinae, by the often stout mouthparts and tarsi, frequently single-celled hemelytral membrane, and fleshy pseudopulvilli on the claws; Deraeocorinae, by the basally toothed claws and generally punctate pronotum and hemelytra; Cylapinae, by the apically notched claws, setiform parempodia, long slender antennae and legs, and often stylate eyes; Isometopinae, by the setiform parempodia, often apically toothed claws, two-segmented tarsi, plesiomorphic ocelli, strongly modified head, and single-celled hemelytral membrane; and Psallopinae, by setiform parempodia, apically toothed claws, two-segmented tarsi, head structure, and single-celled hemelytral membrane.

Morphology

Adults range in size from 1.5 mm or less in some bryocorines, orthotylines, and phylines to more than 15 mm in certain restheniine Mirinae. Plant



Plant Bugs (Hemiptera: Miridae), Figure 65 **Some plant bugs: (*top row left*) the yucca plant bug, *Halticotoma valida* (Bryocorinae): 3.0–3.5 mm long. North America (by Elsie Herbold Froeschner, courtesy of the Smithsonian Institution); (*top row right*) *Fulvius imbecilis* (Cylapinae): 4.00 mm long. North America (by Elsie Herbold Froeschner, courtesy of the Smithsonian Institution); (*second row left*) *Bothynotus modestus* (Deraeocorinae): 5.0 mm long. North America (by Elsie Herbold Froeschner, courtesy of the Smithsonian Institution); (*second row right*) *Myiomma cixiiforme* (Isometopinae): 3.00 mm long. North America (by Thomas J. Henry, courtesy of the U.S. Department of Agriculture); (*third row left*) the garden fleahopper, *Halticus bractatus* (Orthotylinae): 1.5–2.0 mm long. North, Central, and South America (by Elsie Herbold Froeschner, courtesy of the Smithsonian Institution); (*third row right*) the cotton fleahopper, *Pseudatomoscelis seriata* (Phylinae): 3.0–3.5 mm long. North and Central America, West Indies (by Linda H. Lawrence, courtesy of the U.S. Department of Agriculture); (*bottom row left*) the fourlined plant bug, *Poecilocapsus lineatus* (Mirinae): 7.0–7.5 mm long. North America (by Elsie Herbold Froeschner, courtesy of the Smithsonian Institution); (*bottom row right*) *Sericophanes heidemanni* (Orthotylinae): 3.0–3.5 mm long. North America (by Elsie Herbold Froeschner, courtesy of the Smithsonian Institution).**

bugs can be described as delicate and are well known for their tendency to lose appendages when preserved in alcohol. Many Miridae often are brightly colored, ranging from bright, shiny yellow to vivid orange or red and black. Others are more cryptically colored green, gray, brown, or black, closely resembling leaves, stems, flowers, and bark of their hosts. Mirids may be nearly glabrous or may possess diverse kinds of setae, ranging from simple and hairlike to thick and woolly, silky, or even flattened and scalelike.

The family is characterized by a four-segmented antenna, four-segmented labium, primarily three-segmented tarsi (only two segments in Isometopinae, Psallopinae, and some Bryocorinae and Cylapinae); declivent to porrect head, lacking ocelli (except in Isometopinae); trapeziform pronotum, often bearing paired callosities or swellings on the anterior half; paired lateroventral scent glands on the metathorax; and asymmetrical male parameres or clasping structures. Miridae have two pairs of wings, the characteristic hemelytra or forewings, and shorter, membranous hind wings. The hemelytron of fully winged or macropterous Miridae possesses a triangular-shaped cuneus, one or two closed cells on the apical membrane, and a widened costal area frequently referred as the embolium. Miridae can also have varying degrees of hemelytral short wingedness or brachyptery, ranging from only a reduced apical membrane to the absence of even wing stubs. Some taxa exhibit beetlelike (coleopteroid) hemelytral modifications. While brachyptery can be exhibited by either sex, it occurs most often in females. Myrmecomorphy, or a resemblance to ants, is a common adaptation in many groups, generally characterized by a rounded head well separated from a sometimes anteriorly narrowed pronotum, and constricted hemelytra (or a basally constricted abdomen in brachypterous forms) to give the image of three antlike body sections.

Mirid eggs, sometimes described as banana- or cigar-shaped, are elongate and slender, straight to weakly curved, and generally 0.6–2.5 mm long. They are typically creamy or white. The egg shell or chorion usually is smooth but may bear faint hexagonal sculpturing. A characteristic operculum or egg cap, bearing two micropyles, is always present. Eggs frequently are inserted singly but can be laid in groups of 2 or 3 to 20 or more on their host and usually are deposited deep within leaf or stem tissue, within structures such as lenticels, or tucked tightly within leaf bundles or sheaths of grasses and other plants. The operculum usually remains visible and flush with the surrounding tissue until eclosion.

Nymphs or larvae (as they often are called outside the U.S.) undergo gradual or paurometabolous metamorphosis. Nymphs resemble adults in general appearance, differing primarily in body proportions (particularly the head, thorax, and appendages), pigmentation, two-segmented tarsi, and the lack of wings and reproductive structures. Each instar possesses a characteristic dorsal abdominal scent gland, the opening of which is visible between abdominal terga III and IV. All but a few species undergo five stages. Instars I and II lack wing pads and the meso- and metanotal segments are of nearly equal length; traces of wing pads appear in instar III, with the metanotum becoming wider than the mesonotum; larger wing pads extending onto the abdomen develop on the metanotum in instar IV; and fully developed pads extending well onto the abdomen are present in instar V. The ovipositor in females or the genital capsule of males sometimes are visible through the cuticle in fifth instars, but are not functional until the adult stage.

Habitats and Host Plants

As the common name "plant bugs" suggests, mirids are mainly plant inhabitants. Though often underappreciated for their species richness, they are among the most common insects found on herbs, shrubs, and trees. Plant bugs are common not only in managed systems and ruderal sites such as vacant lots but also in specialized communities such as granite outcrops, pine barrens, serpentine barrens, and shale barrens. They can be found from below sea level to an altitude of nearly 5,400 m.

Mirids develop principally on coniferous gymnosperms and dicotyledonous and monocotyledonous angiosperms. Twenty or more mirid species can be found on a single species of oak or pine. In arid regions of the southwestern United States and Mexico, shrubs such as ephedra (*Ephedra*), mesquite (*Prosopis*), rabbit-brush (*Chrysothamnus*), sagebrush (*Artemisia*), and saltbush (*Atriplex*) also are characterized by a diverse plant bug fauna. Some shrub- and tree-inhabiting Miridae are most numerous on isolated plants, in hedgerows, or along forest edges. Other species prefer shaded habitats or are shade tolerant. A few species are associated with fungi, especially those that grow on logs and tree trunks. The first moss-feeding plant bug was recently described from Japan. While no mirids are truly aquatic, those species that live on plants in or on the edge of water, such as water-hyacinth, might be considered semiaquatic. The Miridae also include species that are found in the litter layer, in ant nests, and in webs of subsocial spiders.

The Miridae are mostly a host-restricted group. Diet breadth ranges from strict monophagy, feeding only on one plant species, to polyphagy. Among well-known generalists are the European tarnished plant bug (*Lygus rugulipennis*) in Eurasia and the tarnished plant bug (*L. lineolaris*) in North America. Even large, agriculturally important genera such as *Lygus*, which tend to be dominated by broadly polyphagous species, usually contain specialists of narrow host range. Although predatory mirids typically show broader host associations than do plant feeders, species of mainly predacious genera, such as *Deraeocoris* and *Phytocoris*, often develop only on one plant genus (e.g., pine or oak).

Life History and Habits

In temperate regions, most mirids that feed on woody plants overwinter as eggs inserted into various plant parts or in crevices on the host. In spring, the hatching of diapausing eggs often is synchronized with budbreak of host plants and is triggered by water uptake of the host. Plant bugs that feed on trees and shrubs tend to produce only one annual generation – that is, populations are univoltine. Overwintering in the adult stage is typical of multivoltine species found on herbaceous weeds, including grasses, and field crops. Among other plant bugs overwintering as adults are some species of the predacious genus *Deraeocoris*.

Nymphal development, which generally is inversely proportional to temperature, can be completed in 12–35 days, depending on the species, temperature, and diet. Males of many species emerge slightly earlier than females (i.e., exhibit protandry). A sex pheromone released by the female attracts the male in certain species of the subfamilies Bryocorinae, Mirinae, and Phylinae. Olfactory receptors on the antennae allow males to detect the female pheromones. After a short premating period (usually only several days), mating takes place on the host plant. Elaborate courtship behavior may or may not be involved, depending on the species. Multiple matings apparently are common. In many species, mated females deposit about 30–100 eggs, but fecundity can be lower or as high as several hundred eggs. The insertion of eggs into host tissue, referred to as endophytic, reduces water loss, minimizes winter mortality, and provides some protection from natural enemies. As noted above, endophytic oviposition also is important in establishing contact with the host's vascular system so that egg hatch of plant-feeding species can be synchronized with host phenology.

Eggs of plant bugs are moved readily in shipments of nursery stock; the usually inconspicuous eggs are unlikely to be detected by plant-regulatory inspectors. Consequently, numerous Old World mirids have been accidentally introduced into North America and have become established in the Nearctic fauna.

Plant-feeding mirids generally use high-nitrogen resources, including buds, meristems, young leaves, pollen, and ovules. Most plant bugs are mesophyll rather than vascular-tissue feeders. Phytophagous members of the family, as feeders on liquefied solids, should not be considered sap feeders. Predatory mirids also suck up liquefied solids. Mirids have been described as lacerate (or macerate) and flush feeders. Their flexible stylets (paired maxillae and mandibles) macerate mesophyll cells, or prey tissues in the case of predators, and digestive enzymes from their saliva liquefy plant or animal material so that it can be imbibed through the narrow food canal. Although mirids do not tap into sieve tubes as aphids and certain other phloem-feeding hemipterans do, some species do feed from vascular tissues of their host plants. Adults of both leaf- and flower-feeding species sometimes disperse to other plant species to feed on nectar and pollen.

Mirids probably exhibit greater trophic plasticity than bugs of any other hemipteran family. Even important plant pests such as lygus bugs can be scavengers and facultative predators. Other plant bugs are mostly or entirely predacious. Predatory species range from multivoltine generalists that during the season track various prey over a wide range of host plants to univoltine specialists that feed only on a certain type of prey on a particular plant genus. Thus, some mirids prey only on oak-infesting scale insects, whereas others specialize on thrips or lace bugs.

Economic Importance

The Miridae sometimes are stated to be important vectors of plant pathogens. Although some species help disseminate fungal and bacterial pathogens, plant bugs are not among the principal vectors of plant viruses. The bugs' destruction of plant cells presumably makes it difficult for obligate parasites to infect the host plant, and their salivary secretions might inactivate plant viruses. Moreover, as mesophyll feeders, mirids would not be expected to vector phloem-limited viruses.

Mirids, however, are significant pests of numerous crops, including alfalfa, apple, cocoa, coffee, cotton, guava, peach, sorghum, strawberry, sugar beet, and tea. Symptoms of plant bug injury range from foliar chlorosis, crinkling, and shot holing to lesions, cankers, and abnormal growth patterns such as stunting, bushiness, multiple leadering, and witches'-brooming. Because symptoms of mirid feeding can be so similar to those caused by abiotic factors, as well as by other insects and plant pathogens such as fungi, bacteria, and viruses, their injury often is misdiagnosed.

Millions of dollars are spent each year in attempts to control lygus bugs and other mirids that affect cotton production in the United States. An intensive, and sometimes excessive, use of insecticides against cotton-infesting plant bugs has led not only to outbreaks of secondary pest species but also the development of insecticide tolerance or resistance among mirid populations. Certain species of the subfamily Bryocorinae, which are key pests that limit the production of cocoa in West Africa, also have developed resistance to chlorinated hydrocarbon insecticides.

The agricultural importance of plant bugs also extends to predacious species. Some of the most successful examples of long-term biological control involve the use of Miridae that feed on eggs of delphacid planthoppers. For example, the introduction into Hawaii of a mirid (*Tytthus mundulus*) from Australia has been credited with saving the Hawaiian sugar cane industry from an exotic pest, the sugarcane delphacid. Another case of successful classical biological control involves a non-native predatory plant bug that preys on an introduced planthopper that attacks taro in Hawaii. Other predacious mirids help suppress populations of rice-infesting planthoppers. Numerous crops benefit from native species of Miridae that prey on mites, thrips, leafhoppers, psyllids, whiteflies, scale insects, aphids, lace bugs, and the eggs, larvae, and pupae of various beetles, flies, and moths. These naturally occurring predators should be conserved in pest management programs. Since the 1980s, dicyphine Bryocorinae have been studied and used successfully against thrips, whiteflies, and aphids that are pests of greenhouse crops.

In addition, some mirids penetrate mummified aphids, killing the larvae, prepupae, or pupae of the parasitic wasp within the mummies. Plant bugs sometimes also prey on various life stages of insects intentionally released as biological control agents of weeds. Mirids might impair the effectiveness of parasitic wasps that are enemies of crop-infesting aphids and herbivores released for the biological control of weeds, but the potential detrimental effect of such predation on population dynamics of the prey species is unknown.

Natural Enemies

In all their life stages, mirids are subject to attack by a diversity of predators, parasitoids, and microbial pathogens. Among vertebrate enemies are lizards, frogs, toads, and birds. An even more diverse group of invertebrate predators helps suppress plant bug numbers. Generalist predators include spiders, big-eyed bugs (geocorids), damsel bugs (nabids), minute pirate or flower bugs (anthocorids), assassin bugs (reduviids), mantids, and ants. Well-known families such as lady beetles (coccinellids) and flower flies (syrphids) include predators of mirids, but members of these groups are unimportant natural enemies of plant bugs. Despite being partially or completely concealed in crevices or plant tissues, the eggs of mirids are killed by parasitic wasps. The most important egg parasitoids belong to the family Mymaridae. Mirid nymphs are killed by wasps of the family Braconidae, specifically certain specialized parasitoids of the subfamily Euphorinae. At times, euphorine braconids cause population crashes of injurious mirids.

Other biotic agents that can limit plant bug populations are parasitic nematodes (mermithids) and various microbial pathogens. Fungi are more important natural enemies of mirids than are bacteria or protozoa. Laboratory cultures, however, can be decimated by bacteria and microsporidian protozoa. No virus diseases of mirids are known.

► Bugs (Hemiptera)

References

Henry TJ, Wheeler AG Jr (1988) Family Miridae Hahn, 1833 (Capsidae Burmeister, 1835). The plant bugs. In: Henry TJ, Froeschner RC (eds) Catalog of the Heteroptera, or true bugs, of Canada and continental United States. E. J. Brill, Leiden, The Netherlands, pp 251–507

Schuh RT (1995) Plant bugs of the world (Insecta: Heteroptera: Miridae): systematic catalog, distributions, host list, and bibliography. New York Entomological Society, New York, NY, 1329 pp

Schuh RT, Slater JA (1995) True bugs of the world (Hemiptera: Heteroptera): classification and natural history. Cornell University Press, Ithaca, NY, 336 pp

Wheeler AG Jr (2001) Biology of the plant bugs (Hemiptera: Miridae): pests, predators, opportunists. Cornell University Press, Ithaca, NY, 507 pp

Wheeler AG Jr, Henry TJ (1992) A synthesis of the holarctic Miridae (Heteroptera): distribution, biology, and origin, with emphasis on North America. Thomas Say Foundation Monograph, vol 15. Entomological Society of America, Lanham, MD, 282 pp

Plant Compensation

Feeding by insects does not always result in less productivity of plants, due to compensatory physiological processes in the injured plant. Insect feeding can actually stimulate a plant to grow more than an uninjured plant, but more often results in partial compensation for the removed plant tissue, resulting in less damage than expected. Compensatory processes function best at low levels of damage, and are due to such factors as removal of apical dominance, removal of less productive tissue, increased penetration by light, and reduction in carbohydrate-induced inhibition of photosynthesis.

Plant Extrafloral Nectaries

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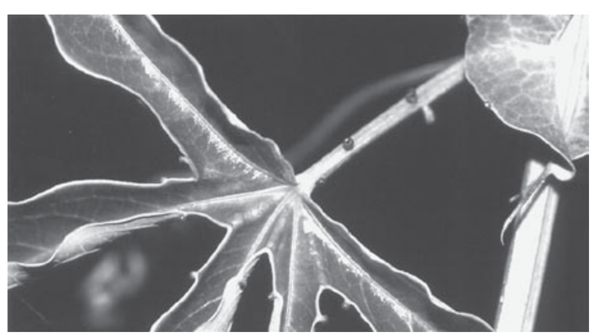
It is well known that plant flowers produce nectar that is important in encouraging pollination, as well as providing food for bats, birds and insects (Fig. 66). However, few people are aware of plant extrafloral nectaries that are nectar-producing glands physically apart from the flower. Extrafloral nectaries have been identified in more than 2,000 plant species in more than 64 families. For example, in nine cerrado areas of Brazil's São Paulo and Mato Grosso states, the plant families Mimosaceae, Bignoniaceae and Vochysiaceae contained the highest frequency of extrafloral nectaries.

Several review articles dealing with extrafloral nectaries or related ecological relationships and at least one book is available. In this article we briefly summarize some aspects of current knowledge about plant extrafloral nectaries and discuss their role and significance to parasitic and predatory arthropods that are important biological control agents.

Extrafloral nectaries were distinguished from floral nectaries in 1762. In 1874 Delpino described extra-nuptial nectary glands. Studies of extrafloral nectaries on plants from various families and habitats provide data on the location, morphology, and abundance of extrafloral nectaries. Approximately 93 angiosperm families with 2,000 species have extrafloral nectaries, but monocotyledons have few taxa with extrafloral nectaries. Plants with extrafloral nectaries tend to be woody and perennial. Extrafloral nectaries are often found on plant species that grow as vines (Fig. 67). Aquatic plants appear to be entirely devoid of extrafloral nectaries. The presence or absence of extrafloral nectaries may vary even among closely related species or cultivars. Whereas up to 80% of plants in tropical habitats have extrafloral nectaries, the proportion of plants in temperate climates varies widely. Only 14% of plants sampled in Nebraska had extrafloral nectaries. In plant communities similar to those of Nebraska, no plants in northern California were found to have extrafloral nectaries. The percent of plant cover with extrafloral nectaries in a myriad of habitats varies from 0 to 80%. Plants with extrafloral nectaries are few in number in areas that do not have ants. For example, at higher elevations in Jamaica in comparison to sea level habitats, ants and plants with extrafloral nectaries were significantly lower. Hawaii is an excellent example with few species of native plants with extrafloral nectaries. Extrafloral nectaries often occur on plants noted for toxicity, thorns, or coriaceous leaves. An interesting model predicting the probability of development of mutualistic associations among plants and ants indicates a probability of 1.0 when ants are "omnipresent" and predicts only low probability when ants are few, and then only under very narrow conditions.

Plant Extrafloral Nectaries, Figure 66 Ants frequently visit the nectaries of the vine *Smilax* sp.



Plant Extrafloral Nectaries, Figure 67 The knob-shaped extrafloral nectaries of the passion vine, *Passiflora* sp.

Some Plant Families with Extrafloral Nectaries

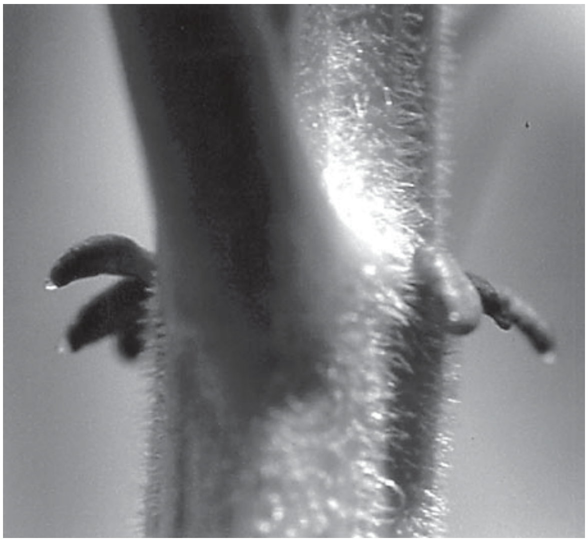
- Asclepiadaceae
- Bignoniaceae
- Caesalpiniaceae
- Caprifoliaceae
- Compositae
- Convolvulaceae
- Curbubitaceae
- Euphorbiaceae
- Fabaceae
- Leguminaceae
- Liliaceae
- Malvaceae
- Mimosaceae
- Papilionaceae
- Rosaceae
- Salicaceae

Plant Extrafloral Nectaries, Figure 68 **Ants frequently visit the large extrafloral nectaries of the elderberry, *Sambucus* sp.**

Location and Morphology

Extrafloral nectary glands may be located on leaf laminae, petioles, rachids, bracts, stipules, pedicels, fruit, and most any above ground plant parts. Their size, shape and secretions vary with plant taxa. Extrafloral nectaries on Nebraska plants are most common (73%) on the foliage. Elderberry, *Sambucus nigra*, extrafloral nectaries (Figs. 68 and 69) are stalk-like on the base of leaves with nectar-producing tissue on top with a single central vascular bundle of dense cytoplasm with a well-developed endoplasmic reticulum. Light microscopy shows that very young nonsecreting nectaries are less than 2 mm, still-growing nectaries with nectar droplets are 2–4 mm and full-grown nectaries are 5–6 mm with small vacuoles fused to large vacuoles.

Apocynaceae, for example *Nerium odorum* L., have extrafloral nectaries on the adaxial surface at the junction of petiole and lamina with short apices, one or two to six to seven



Plant Extrafloral Nectaries, Figure 69 **The large extrafloral nectaries of the elderberry, *Sambucus* sp., produce large droplets of nectar.**

nonvascular nectaries develop on each leaf axial. These nectaries are active on young leaves and dry on mature leaves. *Ipomoea carnea* has two types of extrafloral nectaries with one set of two located on the distal end of the petiole. These mature before the lumina. The other set of five in a ring is on the pedicel which develop with flower buds. Nectar is produced continuously with no change in rate. *Rincinus communis* has extrafloral nectaries found on the lower side of petioles and at the base of leaves with normally three to seven per leaf. Nearly all *Prunus* spp. have extrafloral nectaries, notable exceptions include the low-chill peach, *P. persica*, cultivars "JunePrince" and "GoldPrince" developed by commercial breeding programs. Peach nectaries are globose or reniform and located on the leaf petioles. Cherry laurel, *P. laurocerasus* L., has histoid extrafloral nectaries on the lower leaf surfaces. *Calotropis gigantea* and *Wattakaka volubilis* (Asclepiadaceae) have multiple nectaries at the junction of the petiole and lamina. *Cipadessa baccifera* (Roth.) (Meliaceae) have 25–35 extrafloral nectaries per leaf. The nectaries occur mostly on the abaxial surface of the rachis. Magnified, the extrafloral nectaries appear as ridges and are green on immature leaves and reddish brown on mature leaves. The nectaries of the angiosperm, *Pteraduim aqualinum*, are smooth protrusions located on the stipe and frond and consist of vascular tissue with abundant mitochondria with well-developed vacuoles, a large number of plasmodesmita and less dense cytoplasm. Extrafloral nectaries of cotton, *Gossypium hirsutum*, are closely packed papillae in a pyriform depression on the lower midvein of the leaves. Peak secretion of cotton extrafloral nectaries occurs in July. *Passiflora incarnata* has two sets of extrafloral nectaries, one set is located on the glands of the petiole at the base of each leaf and the other set consists of pairs of glandular bodies on each of three bracts directly underneath the flower or bud. *Dioscorea rotundata* has extrafloral nectaries embedded in the leaf lamina with the pore opening on the lower leaf surface. Each gland is closely associated with leaf veins. Vetches have stipular nectaries present on young plants.

Some Species with Extrafloral Nectaries

- *Abutilon* (Indian mallow)
- *Ailanthus altissima* (silk tree)
- *Allamanda nerifolia*
- *Aphelandra* (tropical herb or shrub)
- *Callecarpa* (beauty berry)
- *Campsis radicans* (trumpet creeper)
- *Cassia fasciculatus* (partridge pea)
- *Catalpa speciosa* (Indian bean)
- *Cattleya* (orchids)
- *Cissus rhombifolia* (ivy)
- *Clerodendron* (tube flower)
- *Costus* (spiral ginger)
- *Crotolaria striata*
- Croton
- Curcurbits
- *Dioscorea* sp. (air potato)
- *Fraxinus* sp. (ash)
- *Fritillaria* sp. (N. Am. lily)
- *Gossypium hirsutum* (cotton)
- *Helianthus* sp. (sunflower)
- *Helionthella quinquenervis* (W. N. Am. herb)
- *Hibiscus* sp.
- *Hoya* sp.
- *Impatiens balsamina*
- *Ipomoea pandurata* (morning glory)
- *Osmanthus* sp. (devil weed)
- *Oxypetalum* sp. (S. Am. shrub)
- *Paeonia* sp. (peony)
- *Passiflora incarnata* (passion flower)
- *Pennisetum* sp. (tropical grass)
- *Phaseolus* sp. (beans)
- *Polygonium* sp. (knot, smartweed)
- *Prunus* spp. (peach) most of 431 species have
- *Pteridium aquilinum* (bracken)
- *Ricinus communis* (castor bean)
- *Robinia pseudoacacia* (black locust)
- *Salix* sp. (willow)
- *Sambucus nigra* (elderberry)
- *Smilax macrophylla* (green briar)
- *Thunbergia grandifloria* (blue trumpet vine)
- *Viburnum opalus*, *V. americanum*

- *Vicia sativa* (vetch)
- *Vigna unguiculata* (cowpeas)

The Location of Some Extrafloral Nectaries on the Plant

- *Ailanthus*: leaf margins
- *Allamanda*: leaf axils
- *Callecarpa*: adaxial surface near veins at leaf base
- *Cassia*: petiole
- *Cissus*: stipule
- *Costus*: outer surface of floral bracts
- *Crotalaria*: flower stalk
- Croton: petiole
- Curcurbits: lamina, pendunular bracts, abaxial surface of calyx
- *Fraxinus*: glandular trichomes on lower leaf surface
- *Gossypium*: leaf or flower bracts
- *Helianthus*: flower bracts and phyllaries
- *Hibiscus*: sunken, elongate cavity part of midvein adaxial surface
- *Hoya*: upper leaf surface
- *Impatiens*: petiole and leaves
- *Ipomoea*: lower leaf surface, petiole, pedicel just below junction with sepals
- *Osmanthus*: glandular trichomes on lower leaf surface
- *Passiflora*: petiole, bud and flower bracts
- *Phaseolus*: on the cushion-like compressed lateral branches on the inflorescence axis
- *Prunus*: distal part of leaf petiole/leaf blade, adaxial leaf
- *Pteridium*: stipe and fronds
- *Ricinus*: leaf and inflorescence
- *Robinia*: stipules
- *Salix*: leaves
- *Sambucus*: stipules
- *Smilax*: tiny, flattened on lower leaf surface
- *Thunbergia*: sepals
- *Viburnum*: lower leaf surface near petiole
- *Vicia*: stipules
- *Vigna*: stipules and inflorescence stalk

Composition and Periodicity

The most prevalent components of floral nectar are a combination of fructose, glucose, and sucrose in various proportions with other sugars such as maltose, trehalose, metazelose, methyl-glucose. The content of extrafloral nectaries differs from floral nectar even on the same plant, varies by taxa, and may or may not flow in a daily pattern. The composition of extrafloral nectaries secretion is about 95% sugar – predominantly sucrose, glucose and fructose – with the other 5% consisting of a wide array of amino acids, proteins and other important nutrients. Extrafloral nectar contains significantly higher numbers of amino acids and non-protein amino acids than does floral nectar. All of the common amino acids in floral nectaries are also equally common in extrafloral nectaries. Other components of extrafloral nectaries may include acids, proteins, lipids, and other organic compounds.

Factors which determine the concentration of the nectar solution include proximity of the phloem vessels, proportion of xylem in the vascular trace, photosynthetic rates of associated organs and local climatic conditions. The volume of extrafloral nectar is strongly affected by evaporation. *Ricinus communis*, castor bean, extrafloral nectar is mostly sugars supplied by the phloem, with the xylem supplying some water. The nectar has lower levels of amino acids than the phloem. Cherry laurel has extrafloral nectaries that produce fructose, glucose, saccharose, and 38% dry substances.

Extrafloral nectaries have a longer secretion period than floral nectaries but often do not have a concise diurnal secretion pattern. Studies have shown that the peak secretion of extrafloral nectaries can occur in the morning and the evening or can be relatively constant day and night. Extrafloral nectaries secretion often begins several weeks prior to flowering and may last through the flowering period. The most active extrafloral nectaries usually occur at the same time with and are associated with plant reproductive organs. In temperate zones peak extrafloral nectaries activity occurs during the middle of the growing season, whereas in tropical habitats secretion may occur continuously during the year. Artificial leaf damage to *Macaranga tanarius* L. induced greater flow from extrafloral nectaries for the next 3 days. Jasmonic acid was found to be the induced chemical responsible for the increase in nectar production rate.

Function and Ecological Interactions

Two hypotheses have been presented to explain the function of extrafloral nectaries. One theory holds the function of extrafloral nectaries as one of a purely physiological function enabling plant waste elimination from metabolism. This hypothesis suggests that extrafloral nectaries may serve as "sap valves" to release extra sugars (Fig. 69). The other theory suggests that the function of extrafloral nectaries is one of plant defense. Extrafloral nectaries may attract ants to protect plants against herbivores, may attract pollinators, as defense against ant-hemipteran mutualisms or may attract ants away from florets to protect from nectar thieving and interference with pollination. Of the plant species with extrafloral nectaries that have been studied, most of the results, although not all, have supported the plant defense hypothesis. It is well documented that many insects use extrafloral nectaries and it is easy to observe beneficial insects such as parasitic Hymenoptera and ladybird beetles feeding on extrafloral nectaries. Many species of ants are found in association with plants having extrafloral nectaries and are thought to be manipulated by the plant using its extrafloral nectaries. Removal of extrafloral nectaries from cotton decreased field populations of both phytophagous (60% reduction) and predacious insects (17–35% reduction). Interestingly, a great many species of vines have extrafloral nectaries and the evolution and selection for extrafloral nectaries is hypothesized to occur as a direct result of the ants using the vines as natural pathways into the forest canopy. Sparsity of extrafloral nectaries in Hawaii seems consistent with a plant antiherbivore defense system that does not function in the absence of ants.

There are five ways in which plants may benefit from interactions with ants: (i) ants protect plants against herbivores, (ii) ants prune neighboring plants which promotes growth and survival of host plants, (iii) ants feed plants with essential nutrients, (iv) ants disperse seeds and fruit, and (v) ants pollinate plants. Studies of the mutualism between plants and ants show that mutualistic association may vary with time, habitat, aggressiveness of ants, and the ability of herbivores to overcome ant predation. Mutualism is favored when the investment in nectar and nectaries is low with high herbivore damage, effective alternative defenses are not

Plant Extrafloral Nectaries, Figure 70 **The introduced ladybird, *Harmonia axyridis*, feeds from the extrafloral nectaries of the elderberry, *Sambucus* sp.**

available, and effective defenses are provided by ants. For mutualism using extrafloral nectaries to be favored, ants must be omnipresent. However, direct predation by ants may be unnecessary; the mere presence of the ants may be enough. In order for ants to truly be considered as "protectors" of plants they must have the characteristics of aggressive behavior against feeding herbivores, daily activity patterns to provide 24-h protection, actively forage for a plants herbivores, actively forage in large numbers, have nest locations in close proximity to the extrafloral nectaries plant and be able to move (nest mobility) the nest close to extrafloral nectaries plants.

Passiflora incarnata has two sets of extrafloral nectaries. These extrafloral nectaries are visited by five species of ants and the number of ants was correlated positively with the number of extrafloral nectaries and negatively with herbivores. The number of fruit produced was greater on plants with extrafloral nectaries than without. Studies on *Cassia* sp. showed that ant visitation resulted in decreased herbivore numbers and leaf loss with increased growth but did not result in seed set differences. Continuous production of nectar is necessary to attract ants and ant activity follows the secretion patterns of extrafloral nectaries. This continuous production is evident in extrafloral nectaries, but not floral nectaries.

While ant visitation does not affect the reproductive output of plants, it is advantageous if ants protect plants during growth because pollinators are increased by large floral display, and a surplus of initial fruit and seeds may allow a plant to selectively abort genetically inferior progeny. Another way extrafloral nectaries may function is to protect plants against ant-hemipteran mutualism. By supplying nectar to ants, extrafloral nectaries distract the ants from the honeydew produced by the Hemiptera, and the plant incurs less hemipteran damage. Plant antiherbivore mechanisms are often reduced in commercial crops.

The evolution of nectar rewards may illustrate a correlation between plants and ants that provides a consistent plant defense system. The plant may select for biological control by ant protection which probably reduces the potential of damage by herbivores resistant to chemical or structural barriers provided by the plant. Natural selection may operate to optimize the production of nectar from extrafloral nectaries, balancing the cost for production with benefit in leaf and fruit production. A model for facultative mutualism predicts a positive correlation between extrafloral nectaries and ant abundance. Extrafloral nectaries selection is stronger for species that encounter ants frequently. Extrafloral nectaries are expected to be more abundant in vines and may be favored in seasonal environments. Extrafloral nectaries may result in ant symbiosis, not cause it. In Nebraska the occurrence of ants was not related to the distribution of plants with extrafloral nectaries.

Extrafloral nectaries may also function to attract ants to plants which use the ants to disperse seeds. Plants with ants have significantly fewer predators because ants may interfere with predator oviposition. Major herbivorous insects are more likely to be parasitized on plants with high quality nectar that attract parasites. Ants decrease the amount of time *Eurybia* larvae are on inflorescences. Diptera seem more prevalent on *Aerobe* sp.-infested plants.

Ant exclusion studies have shown that removing ants from plants did not lessen the number of ants visiting extrafloral nectaries; however, sugar would not attract ants to plants. Exclusion of ants increased the number of insects on developing capitula but did not affect pollination. *Mentzelia nuda* (Loasaceae), a short wild perennial, has extrafloral nectaries which secrete after flowering, and attract ants, which significantly enhances seed set. The number of ants increases sharply when extrafloral nectar is available, which indicates that ant foragers can respond to a new food source. On black cherry, extrafloral nectaries are most active when ants are most able to prey on herbivores.

Ants visiting extrafloral nectaries may add to an increase in plant fitness by deterring leaf, seed, and flower herbivores and this in turn may increase the number of seeds produced. The defense of plant parts by ants appears to be a flexible interaction using diverse ant species and repelling various types of herbivores. Extrafloral nectaries on flowers may increase parasitoid survivorship, fecundity, retention and pest suppression. In Costa Rica, studies have shown more buds mature to ripe fruit on plants with extrafloral nectaries and a higher ant visitation rate. Ant activity followed the secretion pattern of extrafloral nectaries. Total number of seeds per cyme was significantly higher on plants with ants.

While ants are the most common visitors to extrafloral nectaries, and 30 species of ants have been observed visiting *Passiflora*, extrafloral nectaries are attractive to many families of arthropods. Over an 8-day period, 3,941 insects, including 40 families, 77 genera, and 100 species were observed visiting extrafloral nectaries of *I. carnea* in Costa Rica. The insects included Coleoptera (Fig. 70), Hemiptera, Lepidoptera, Neuroptera, Diptera, and Hymenoptera. Extrafloral nectaries on cotton attract parasitoids and increase the retention time and rate of parasitism. Extrafloral nectaries serve as an important supplementary food source of many insects, including predatory mites on cotton during times of stress when usual food sources are scarce, and are an important nutritional source for parasitic Hymenoptera. Even spiders may respond to the presence of extrafloral nectaries as the presence of salticids are known to enhance seed production of *Chamaecrista nictitans* (Caesalpiniaceae). Nineteen genera and 41 species of ladybird beetles, Coccinellidae, have been observed feeding on extrafloral nectaries.

Extrafloral nectaries offer an important supplemental food source for many beneficial insects (and too, to phytophagous insects including some pest species), particularly during extreme weather conditions such as drought and other times of the year when prey are scarce. Extrafloral nectaries may be valuable if not critical components in the ecology of landscapes. Passion flower, *Passiflora* spp., partridge pea, *Cassia* spp., hairy vetch, *Vicia* sp. and elderberry, *Sambucus* spp., are common examples of plants with large extrafloral nectaries on the leaves and/or stems. A great many opportunities exist to further our understanding of extrafloral nectaries as much remains unknown about the important ecological roles extrafloral nectaries may play. Exploiting extrafloral nectaries and other natural ecosystem functions that increase the presence and effect of natural enemies of pests have great potential to help reduce further the need for conventional pest controls in commercial agriculture and urban landscapes.

► Ant-plant Interactions
► Conservation Biological Control

References

Beatie AJ (1985) The evolutionary ecological ant-plant mutualism. Cambridge University Press, Cambridge, 182 pp

Elias TS, Bently B (eds) (1979) The biology of nectaries. Columbia University Press, New York, NY

Galetto L, Bernardello L (1992) Extrafloral nectaries that attract ants in Bromeliacea: structure and nectar composition. Can J Bot 70:1101–1106

Grout BW, Williams A (1980) Extrafloral nectaries of *Dioscorea rotnndata* Poir.: their structure and secretions. Ann Bot 46:255–258

Keeler KH (1977) The extrafloral nectaries of *Ipomoea carnea* (Convolvulaceae). Am J Bot 64:1182–1188

Oliveira PS, Oliveira-filho A (1991) Distribution of extrafloral nectaries in the woody flora of tropical communities in western Brazil. In: Price P, Lewisohn T, Fernandes G, Benson W (eds) Plant-animal interactions; evolutionary ecology in tropical and temperate regions. Wiley, New York, NY, pp 163–175

Planthopper Parasite Moths (Lepidoptera: Epipyropidae)

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Planthopper parasite moths, family Epipyropidae, total 40 described species, with at least another 30 known species awaiting naming. Species are known from all faunal regions, but are most diverse in Australia. Two subfamilies are known: Epipyropinae and Heteropsychinae. The family is in the superfamily Cossoidea (series Limacodiformes)

Planthopper Parasite Moths (Lepidoptera: Epipyropidae), Figure 71 **Example of planthopper parasite moths (Epipyropidae), *Fulgoraecia exigua* (H. Edwards) from Florida, USA.**

in the section Cossina, subsection Cossina, of the division Ditrysia. Adults are minute to small (4–35 mm wingspan), with head scaling mostly roughened; haustellum absent; labial palpi minute; maxillary palpi absent; antennae bipectinate in males and rather conspicuous. Body robust. Wings quadratic and broadly rounded (Fig. 71). Maculation mostly black or dark brown; sometimes with some spots and iridescence. Adults are crepuscular and nocturnal; females are sedentary. Larvae slug-like with rounded dorsum; parasitic on fulgorids and planthoppers (Hemiptera). Eggs are laid on various plants and upon hatching, larvae search for suitable hemipteran hosts to parasitize.

References

Davis DR (2004) The ectoparasitic moths of the family Epipyropidae of the world (Lepidoptera: Zygaenoidea). Smithson Contrib Zool (in press)

de Freina JJ, Witt TJ (1990) Familie Epipyropidae Dyar [1903] 1902. In Die Bombyces und Sphinges der Westpalaearktis, 2:72–73, pl. 10. Forschung & Wissenschaft Verlag, Munich

Kato M (1940) A monograph of Epipyropidae (Lepidoptera). Entomol World 8(72):67–94, 4 pl

Sick H (1939) Familie: Epipyropidae. In: Seitz A (ed) Die Gross-Schmetterlinge der Erde. Teil 6. Die amerikanischen Spinner und Schwärmer, pl. 168. A. Kernen, Stuttgart, pp 1313–1315

Viette PEL (1960) Les epipyropides de Madagascar (Lépidoptères parasites). Lambillionea 60:41–46

Planthoppers (Hemiptera: Fulgoroidea)

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Current cladistic and molecular studies are resolving their placement in the Hemiptera and the placement of odd genera and tribes within families. Perhaps only 20% of the species of the superfamily are described.

Order: Hemiptera
Suborder: Fulgoromorpha
Superfamily: Fulgoroidea
Families: 16–21, consensus not yet reached

Morphology

The superfamily is usually identified by the placement of the eyes, antennae, and lateral ocelli on the genae, which are separated from the front of the head by lateral carinae; by the tegula, a small plate covering the base of the wing; a y-shaped claval vein in the forewing; and rows of spines at the apex of the hind tibia and first tarsomere. Specimens measure from 2 mm to 10 cm (4 in.).

Phylogeny

At the moment, but still subject to change, we believe the Sternorrhyncha are the sister group of the rest of the Hemiptera. Next, the Fulgoromorpha (the suborder, which is equal to the superfamily Fulgoroidea) are separated as the sister group of the Heteroptera + Coleorrhyncha + Cicadomorpha (Cicadoidea, Cercopoidea, and Cicadelloidea).

Within the Fulgoroidea there are from 16 to 21 families, three with only one or two genera. Each family will be listed and discussed after some general characters are mentioned. These families are divided into two or three clades, depending upon the author. The Delphacidae and Cixiidae both have a sword-shaped ovipositor. The rest do not. They are divided by the number of spines on the second hind tarsomere into two groups. One has a row of spines and includes the Meenoplidae and its sister group Kinnaridae, Derbidae, Achilidae, Achilixiidae, Dictyopharidae and its sister group Fulgoridae, and also the Cixiidae and Delphacidae. The nymphs of the first five families of this group and of the Cixiidae are thought to live underground or in association with the ground. The last group includes the Acanaloniidae, Caliscelidae, Issidae, Nogodinidae, Ricaniidae, Flatidae, Tropiduchidae, Tettigometridae, Lophopidae, Eurybrachidae, and the two small families Hypochthonellidae and Gengidae.

Habitats

Eight of the families are found on all the continents but Antarctica, and some are found in each major biome, including forests, grasslands, deserts, tropical rainforests, and arctic tundra. Three families are worldwide except for the Palearctic (fulgorids, nogodinids, acanaloniids), one except for the Nearctic (ricaniids), one except for the Holarctic (lophopids). The tettigometrids are not found in the New World or Australia. The Nearctic and Palearctic have 12 families each, Australia 15, the Neotropics 16 or 17, and Africa (lacking kinnarids and achilixiids) and the Orient (lacking gengids and hypochthonellids) each 19.

Most adults feed on plant parts above ground. Nymphs of cixiids are found in cavities underground, feeding on plant roots, often grasses. Nymphs of achilids and derbids have been found in cavities in rotten wood or under bark, where they are thought to feed on fungi. Kinnarid and meenoplid nymphs are supposed to be associated with soil, as are the three smallest families, achilixiids, gengids, and hypochthonellids. The other families, as far as reported, have the nymphs on the leaves and trunks of the same hosts as the adults.

Eggs are placed in several substrates. In delphacids and cixiids, they are inserted into the soil or plant tissue with a sword-shaped ovipositor. Derbids, achilids, kinnarids and meenoplids are thought to have a raking-sweeping type of oviposition, where the substrate is moved and the eggs are attached to small particles such as bark. Fulgoroids, dictyopharids, and eurybrachids are thought to glue eggs to plant surfaces, and the rest have a secondarily derived piercing excavating ovipositor. Most cover their eggs with wax. Two genera of issids (two in Europe, and one in California) carry dry soil in an internal sac and mix it with body fluids to form mud egg cases.

Adults of four families, cixiids, meenoplids, kinnarids, and delphacids, have been found adapted to caves, with eyes reduced or absent, wings often reduced, and loss of pigment, and adults of hypochthonellids burrow through the soil. Cavernicolous species have been found in caves or lava tubes chiefly in Australia and Hawaii, but also in Thailand, Mexico, New Caledonia, the Canary Islands, Galapagos Islands, and Western Samoa.

Fulgoroidea are one of the groups that have been successful reaching and establishing themselves on islands. Delphacids are the most successful and widespread, and obviously traveled as aerial flotsam, as they have been found in samples taken in nets on the prows of ships in the Pacific. Often they have maintained their specific identity, which may indicate repeated gene flow to the islands. In other cases, such as Hawaii, they have speciated successfully. Actually, 13 families have reached oceanic islands, including all of the families with nymphs associated with the soil (except hypochthonellids and gengids with their three species total), suggesting that rafting may be involved in some cases.

Hosts

Fulgoroidea, as far as is known, feed on phloem of plants, through roots, trunks or leaves, except for the Achilidae and Derbidae, which are thought to feed on fungus, at least as nymphs. In a few cases this has been demonstrated in various families of the order through histological studies of plant parts, tracing the stylet sheath secreted by the insect through or between the cells to a cell or to the phloem or xylem tubes. In others it is accepted because of the production of honeydew. Some species are known to be monophagous, but a flatid, *Metcalfa pruinosa* (Say), has been reported from 100 plants in the United States, and now has been accidentally introduced into Italy, where it has been found to be a pest of grapes especially, either the wax from the insect or sooty mold from the honey dew detracting from the appearance of the fruit. Monocots are popular hosts, especially rice, sugarcane, corn, and palms. Wilson et al. (1994) list the hosts for as many species as they could find references, finding ten families feeding on Pteridophyta, sevenon Gymnospermae, all but two of the 16 common families (Eurybrachidae and Nogodinidae) on Monocotyledoneae, and all on Dicotyledoneae. They also give fossil history and differing phylogenies of the group to consider the evolution of host plant use.

Pest Species

Fulgoroidea are implicated in rice diseases in the orient, lethal yellowing of palms in the Caribbean and Florida, and Dubas-bug-caused death of date palms in the middle east. An unusual pest is the ricaniid *Scolypopa australis* Walker from Australia, which, although it has many hosts, sometimes feeds on a poisonous plant tutu, *Coriaria arborea* Lindsay, producing a poisonous honeydew. In times of poor nectar supply, honey bees feed on the honeydew and produce a honey poisonous to man. A list of species reported as pests of crops is reported in Wilson and O' Brien (1987).

Communication

Although the cicadas communicate by airborne sounds, the Fulgoromorpha and the rest of the Cicadomorpha communicate by substrate-transmitted sounds scarcely or not audible to the human ear. Males and females in the families studied (cixiids, delphacids, dictyopharids) each have species specific mating sounds, with the males usually initiating the sounds and the females responding. Although the male genitalia are very complex and almost always species specific, the calls are considered significant in mating isolation as well as mate finding. Fulgoroids are not thought to produce pheromones.

Wax Production

Wax (actually a 60–80 carbon atom ester of 30–40 carbon acids and alcohols) is produced in most nymphs and females and some males in most members of the superfamily (rare in delphacids, only the vision of *Saccharosydne sacchivora* (Westwood) with waxy tufts comes to mind). Chemically it shares compounds found in the wooly alder aphid and the cochineal scale. Most of the wax is produced through hundreds of flower-shaped glands in wax plates on the sixth, seventh, and eighth abdominal tergites. Hollow strands are produced which touch each other to form another hollow tube. Small clumps of gland cells are usually found around the spiracles also. Wax particles as opposed to strands may also simply be excreted through the integument almost anywhere on the body, including the wings in some species, without an external gland visible by means of scanning electron microscopy.

What is the function of wax? Females cover the eggs with it and reports show the wax hides the eggs, repels water running over eggs, and may protect the eggs and nymphs from parasites. It is also thought to keep the nymphs in enclosed places from becoming sticky with their own honeydew, to aid escape from spider webs, to reflect ultraviolet light to aid species recognition (insects see in the ultraviolet), etc. Fulgoroidea feed on sugary phloem which they need to ingest in excess to get N for growth, and they need to get rid of sugars because of their osmotic effect on the hemolymph, but they don't have filter chambers. Might they simply have produced more of these high molecular weight compounds, some of which are similar in wax and in cuticular wax, to get rid of the excess sugar, and retained them for both physical and physiological benefits?

Other Behavior

The genera *Megamelus* (Delphacidae) and *Taosa* (Dictyopharidae) are able to live on emergent aquatic plants without all of the jumping nymphs drowning. Some of the fulgorids have favorite trees in the jungle and may be found on them for weeks at a time and year after year. A tribe of derbids can roll its wings longitudinally, presumably for protection from tropical rain drops. Tettigometrids, in a commensal arrangement with ants, can increase the production of figs. Poison honeydew from a ricaniid can be incorporated into honey, making it poisonous to humans.

Predators and Parasites

Four families of insects are parasitoids of planthoppers and leafhoppers, the Pipunculidae (Diptera), Dryinidae (Hymenoptera), Halictophagidae (Strepsiptera), and Epipyropidae (Lepidoptera), the latter inserting their mandibles through the intersegmental membranes and feeding on the hemolymph of several families of Fulgoroidea in the Nearctic, Neotropics, and Asia. Egg parasites include the Hymenoptera Mymaridae, Trichogrammatidae, Eulophidae, and Aphelinidae. Nematodes may also be parasitoids of nymphs and adults.

Birds are important predators. Up to 71% of the insects in stomachs of flycatchers have been found to be fulgoroids. It is assumed that other insectivores also eat them, although perhaps not preferentially. Man, from fear, is a killer of one genus in Brazil (see Fulgoridae, below).

Family Synopsis

Each family will be discussed alphabetically (refer to the listing above for phylogenetic sequence). If there is a single character that can separate that family from other Fulgoroidea, it will be mentioned. Otherwise, consult O' Brien and Wilson (1985) for a key, illustrations of morphology, and a general introduction to the superfamily.

Acanaloniidae

This mostly New World family can usually be recognized by the lateral flattening, reticulate venation, and green color in specimens of small to medium size, 4–12 mm. long. It was placed in the issids by Fennah (1954) but resurrected by Emelyanov (1999).

Achilidae

This worldwide family can be identified by the tips of the forewings overlapping at rest except in a few genera. A key to genera of the world is provided by Fennah in 1950. One species in Australia is found in termite nests. At present there is a disproportionate number of genera with few species in them in this family.

Achilixiidae

This small family of two genera and 24 species is found in the Neotropics and the Philippines and Borneo. They may be identified by a lateral projection of the abdomen topped by cup-like depressions. They are from 4 to 8 mm long. Bennini in the Cixiidae have a similar projection, but the top surface varies, and the cixiids have a branched spine in each depression. Achilixiids have been placed in the achilids, derbids, cixiids, and kinnarids. The function of the projection is unknown.

Caliscelidae

This worldwide group is found on bunch grasses in South America, grasses and sedges in the U.S., and also palms and bamboo elsewhere. It was only recently raised to family level (removed from the Issidae). They are small (3–6 mm long) and brachypterous, and are often taken for weevils or Heteroptera nymphs. Some are associated with ants.

Cixiidae

Female cixiids can be identified by a sword-shaped ovipositor and no moveable tarsal spur (delphacids also have the sword-shaped ovipositor). Males need a composite of characters. They are small or medium sized, from 3 to 13 mm long. Of worldwide distribution, they are probably the second most economically important group of Fulgoroidea because they transmit lethal yellowing of palms and other phytoplasmas.

Some have become of interest recently because they have adapted from epigean adults with nymphs feeding on roots underground to fully cave adapted species, with loss of eyes and pigment. This is particularly interesting in Hawaii, where some Oliarus have invaded lava tubes, which we have begun to date. Evidence from their recorded mating calls shows that cave species on Mauna Loa and Mauna Kea are more closely related to the epigean species above ground above them than the troglobitic (cavernicolous) species of the other mountain, even though there are fissures in the lava which would allow them to travel great distances underground.

Delphacidae

The delphacids can be recognized by the movable spur on the hind tibia. When sorting collections by eye, these specimens, 1–6 mm long, may usually be picked out of Auchenorrhyncha by their antennae sticking out from the side of their head, more visibly than other families. Economically, they are the most important of the Fulgoroidea. The Delphacidae include at least 55 species that feed on economic plants, including some major pests of agricultural crops, such as rice, sugarcane, maize, taro, and cereals. Plant damage results both from direct feeding, and the transmission of plant diseases, particularly viral diseases (e.g., Fiji disease of sugarcane by *Perkinsiella saccharicida*, rice grassy stunt and rice ragged stunt by *Nilaparvata* spp. (*Nilaparvata lugens*, a rice pest, cost China an estimated US $400 million loss in 1990), rice hoja blanca by *Tagosodes* spp., rice yellows by *Sogatella furcifera*, cereal mosaic and oat rosette virus by *Laodelpax striatella*, maize mosaic and maize stripe viruses by *Peregrinus maidus*). Note that the above list of delphacid-vectored plant diseases includes five of the top ten major world food crops (wheat, rice, corn, barley, and sugarcane), plus, at least three delphacid species are known to feed on sorghum.

Delphacids are carried easily by air currents. Rice pests reinvade Japan each year from China, and delphacids have probably reached every island in the world, but sometimes do not form new species on islands, presumably because other introductions of the same species do not allow reproductive isolation. They, and cixiids, seem most tolerant of cold habitats.

Derbidae

The derbids have a number of characteristic shapes, varying in size from 4 to 16 mm. It may be the possibility of tropical raindrops plastering their wings to a substrate with subsequent death that has favored the selection of multiple resting positions. Many have roof-like wings and sit head-up on plants, often grasses. Others, Mysidiini, are moth-like and hold their wings flat against the underside of broad leaves. Specimens of Zoraidini hang upside down, frequently on palm leaves, with the wings held together under the back, forming a T-shape with the body in lateral view. Specimens of Dawnarioidini have the ability to roll each pair of wings into a longitudinal tube, which is held above the body and to the side, forming a V shape in caudal view. Specimens tend to congregate on the same leaf or on the same plant.

Dictyopharidae

The dictyopharids, sister group of the fulgorids, are often green and with a head projection, but do need to be keyed to family. They vary in length from 3 to 33 mm. One genus, *Taosa*, lives on aquatic plants and a species is being tested to see whether it is host specific and may be used for biological control of water hyacinth. The nymphs seem to be able to fall onto the water and get out again, perhaps because of broad spines on the hind tibiae and tarsi. A desert loving subfamily, Orgerinae, is small and brachypterous and lacks the tegulae found in the rest of the Fulgoroidea.

Eurybrachidae

Found in Africa, the Orient, and Australia, these insects usually can be identified by the rectangularly (not triangularly) shaped wings, the frons being 3× as broad as long, and the second hind tarsomere lacking spines. Usually the forewings are opaque and colored. They measure 8–28 mm in length. In Australia they are associated with *Eucalyptus* and *Acacia*. In both an Asian and African genus, the forewings are modified with a projection that looks like an antenna, and the hind wings with one that bends downward like a snout, so the insect appears to have two heads, but the false one is the more obvious.

Flatidae

This family has the second most colorful and second largest specimens (4.5–32 mm) of the superfamily after Fulgoridae. They can be identified by having pustules in the basal half of the clavus plus the costal area transversed by many parallel veinlets. Many species (46%) are polyphagous, so introduced species may become pests, as *Metcalfa pruinosa* (Say) has in Italy and Southern Europe, introduced from the U.S.; *Siphanta acuta* (Walker) may become a pest in Hawaii and California, introduced from Australia or New Zealand; and *Melormenis basalis* (Walker) may in Florida, introduced from the West Indies.

Fulgoridae

This family, known for large (up to 10 cm) and colorful specimens, is also known for large and colorful legends. It can be identified by cross veins in the hind wings. The largest number of genera and greatest variation in the head shape are in the Neotropics, but the greatest variation in color occurs in Asia. This family does not reach the Palearctic. The nominate genus, *Fulgora*, was called a lantern fly because of its large peanut shaped head that suggested a lantern and was reported to produce light, with the last report in 1951. Now it is accepted that it does not bioluminesce, but the natives in the South American jungle still fear it, saying it kills anything it touches, perhaps because the head looks like an alligator in lateral view, with a false eye spot, a false nostril on the top of its head and a row of false teeth. Presumably this mimicry works on birds and perhaps monkeys, and perhaps man in the past, when the medicine man carried a dead Fulgora in his amulet bag. But a Brazilian ethnoentomologist, Eraldo Medeiros Costa Neto, says now people get a big stick and try to kill the insects. Male college students, on the other hand, from Mexico to Argentina, have asked if they will die if bitten by a Fulgora if not saved by having sex within 24 h.

Gengidae

This family of two genera and two species is found in the Union of South Africa. Their nearest relative is thought to be Eurybrachidae.

Hypochthonellidae

This family is known from adults and nymphs of one species taken underground on the roots of corn, tobacco, and peanuts in Southern Zimbabwe. The compound eyes are obsolescent, the ocelli absent. The wings are brachypterous and the adult described as maggot-like. It most seems to resemble Flatidae.

Issidae

This large family of small to medium insects, 2–19 mm long, are often brown and a rounded diamond shape from above. There is still a question whether the family is monophyletic. Females of one genus, *Hysteropterum*, which occurs in Europe and the U.S. (and a second genus in Europe), scratch up dirt and store it in a sac near the ovipositor and use it with bodily secretions to make a mud case for the eggs.

Kinnaridae

Kinnaridae and Meenoplidae are sister groups, identified by wax on the females on their chevron-shaped sixth to eighth tergites, or the wax plates, if the wax is lacking. Both are thought to have nymphs that live underground or near the ground. Kinnarids are found primarily in the New World, and are especially common in the West Indies. They are from 2 to 8 mm in length.

Lophopidae

The Lophopidae, found everywhere but in North America and Europe, with one genus (*Carrionia*) in South America, are the first family to have a complete modern cladistic treatment at the generic level. *Pyrilla perpusilla* (Walker) can be a pest of sugarcane, rice, and corn in India. Lophopids vary in shape and color and in length from 6 to 15 mm. A fossil has been found in North America, although no species are present there now.

Meenoplidae

The meenoplids, a small family of small insects, 3–7 mm, can be recognized by the combination of chevron shaped wax-bearing 6–8 tergites in the females and pustules on one or both claval veins. Kinnarids, their sister group, have the same shape of the wax glands, but lack the pustules on the forewing. Meenoplids are not found in the New World and are associated with the soil in the literature. Cave dwelling species are found in Australia, New Caledonia, the Canary Islands and Western Samoa.

Nogodinidae

Tribes in the nogodinids, lacking in the Palearctic, are still being moved from family to family in the hope of delineating a monophyletic group. Wings are usually broadly oval, usually membranous or with a membranous cell. They vary in size from 4 to 17 mm. Fennah moved some of the issids in California to nogodinids and acanaloniids to issids; Emelyanov (1999) moved both Caliscelinae and Acanaloninae back to families, and moved Bladininae to Issidae, based primarily on the structure of the ovipositor.

Ricaniidae

Sub-triangular fore wings separate most species of this family from the rest of the Fulgoroidea. They are found everywhere but in the Nearctic, range from 6 to 20 mm, and are usually membranous with dark patterns or dark with membranous areas. *Scolypopa australis* can cause honey poisoning.

Tettigometridae

Tettigometrids lack some of the characters usually found in Fulgoroidea. They have been considered the most primitive, but now are considered among the more recent families. They are not found in the New World or Australia, are 3–7 mm long, with the wings shaped to the body, and lack a jumping apparatus. They are often associated with ants which remove their honeydew and protect them in return. In tropical Africa Camponotus ants which feed on the honeydew of *Hilda undata* (Walker) can reduce the predation on pollinators and figs by other species of ants.

Tropiduchidae

Tropiduchids are found worldwide and can be identified in most species by a transverse groove between the apex and disk of the mesonotum. They are usually green, depressed, and similar to dictyopharids but have only one pair of spines on the hind tarsomere and the venation is different with fewer apical cells. Sizes range from 5 to 13 mm. *Ommatissus lybicus*, the Dubas bug, can kill date trees in the Middle East.

Current Status

In no country of the world can one identify all of the species of one family of Fulgoromorpha with a single reference except England, Scandinavia, New Zealand, and perhaps Taiwan. But new species are still being discovered in Taiwan. Europeans say they can identify the species of Middle Europe, but Spain and Portugal, southern Italy, and Greece and Turkey are poorly known. Also, the U.S. and Canadian faunas are known and most species can be identified, with the western flatids and delphacids being the most troublesome. There are many papers on the fauna of national parks in Africa, but nothing I know of that relates the Entomofaunal regions to these papers. European museums have many species from the Orient, so perhaps some sort of monograph might be done, but surely many species have not been discovered. Australia has many species to be described. South America is virtually unknown. Judging from 852 described species in the U.S. and Canada and 750 in Taiwan, their museums are obviously incomplete.

Further Information

The Metcalf catalog is superb, with notes on whether each paper cited contains information on keys, description, illustrations, biology, host, etc. Unfortunately, it is out of date, as is the bibliography that accompanies it.

Review papers which provide an introduction to the superfamily (O' Brien and Wilson 1985), to pest species (Wilson and O' Brien), to behavior (O' Brien 2002), to host preferences (Wilson et al.) are listed below. The book "The Planthoppers and Leafhoppers" (Nault and Rodriguez, eds 1985) and a volume of Denisia (2002) provide a series of papers of related review articles.

Fennah (1950) keyed the achilid genera of the world. Fennah also has provided keys to Neotropical genera in derbids, dictyopharids, kinnarids, and tropiduchids, and in the "Fulgoroidea of Fiji" a key to Australasian cixiids, delphacids, derbids, and Pacific issids, tropiduchids and ricaniids. Earlier treatments of the world fauna, or a large part, such as Melichar's (1898–1915) can be located in Metcalf's catalogue. A recent paper (1998) keyed the genera of Lophopidae, and subsequent ones, also by Soulier-Perkins (2000, 2001), describe their phylogeny and biogeography. Denno and his students have done many ecological studies to provide a theoretical background for pest management practices, emphasizing studies on the effect of brachyptery in a dimorphic species.

Bourgoin, Campbell, Asche, and Emelyanov are doing phylogenetic studies between and within families. Porion (1994) and Nagai and Porion (1996) have provided photographic atlases and checklists of the Fulgoridae of America, and of Asia and Australia, with many colored plates.

► Bugs (Hemiptera)

References

Holzinger WE (ed) (2002) Zikaden – leafhoppers, planthoppers and cicadas (Insecta: Hemiptera: Auchenorrhyncha). Denisia 4, Verlag Biologiezentrum, Linz, Austria, 556 pp

Mason RT, Fales HM, Jones TH, O'Brien LB, Taylor TW, Hogue CL, Blum MS (1989) Characterization of fulgorid waxes (Homoptera: Fulgoridae: Insecta). Insect Biochem 19:737–740

Metcalf ZP (1942) A bibliography of the Homoptera (Auchenorrhyncha), vols 1 and 2. North Carolina State College, Raleigh, NC

Metcalf ZP (1932–1946) General catalogue of the Hemiptera. Fasc. IV. Fulgoroidea. Parts 1–10. Smith College, Northampton, MA

Metcalf ZP (1954–1958) General catalogue of the Hemiptera. Fasc. IV. Fulgoroidea. Parts 11–18. North Carolina State University, Raleigh, NC

Nault LR, Rodriquez JG (eds) (1985) The leafhoppers and planthoppers. Wiley, New York, NY

O' Brien LB, Wilson SW (1985) Planthopper systematics and external morphology. In: Nault LR, Rodriquez JG (eds) The leafhoppers and planthoppers. Wiley, New York, NY, pp 61–102

Wilson MR (1988) Ronald G Fennah, 1910–1987. Obituary and list of publications. Entomologist's Monthly Magazine 124:167–176

Wilson SW, O' Brien LB (1987) A survey of planthopper pests of economically important plants (Homoptera: Fulgoroidea). In: Wilson MR, Nault LR (eds) Proceedings of the Second International Workshop on Leafhoppers and Planthoppers of Economic Importance, held in Provo, Utah, USA, 28th July – 1st August 1986. CIE, London, UK, pp 343–360

Wilson SW, Denno RF, Mitter C, Wilson MR (1994) Evolutionary patterns of host plant use by delphacid planthoppers and their relatives. In: Denno RF, Perfect TJ (eds) Planthoppers: their ecology and management. Chapman and Hall, New York, NY, pp 7–113

Plant Lice

Members of the family Aphididae (order Hemiptera).

► Bugs
► Aphids

Plant Resistance to Insects

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Plant resistance to insects is a natural phenomenon based on plant self-defense mechanisms. It results from insect-plant co-evolution and is crucial for their co-existence. During plant domestication, some important features of plant resistance may be inadvertantly removed by the breeders, increasing their susceptibility. This necessitates additional selection for resistance factors.

When plant breeding was still performed under field conditions, the most susceptible plants were so badly damaged by insects that they were lost from the breeding pool before they produced seeds. Thus, the plant population retained a natural resistance to insects. After World War II, however, massive use of insecticides by plant breeders accelerated the loss of natural resistance in crop plants, because it allowed the conservation of plants that were high yielding but, on the other hand, very sensitive to insects. As a result, these modern, high valuable cultivars must be continuously protected against pests. The solution to this problem lies in an attempt to reincorporate resistance into the modern crop varieties. This task requires a clear definition of the breeding target(s), adequate source(s) of resistance, and development of methods to evaluate resistance that are reliable, inexpensive and rapid. Plants and insects are very dynamic, and highly developed organisms with a good capacity for adaptation to ever-changing environments. Because insects are capable of evolving, and overcoming plant resistance, a suggested strategy is to implement an Integrated Pest Management (IPM) program that combines partial plant resistance with nontoxic (e.g., biological, physical, biorational) control measures.

The Nature of Insect Damage to Plants: Direct Versus Indirect Damage

There are two main types of insect damage to plants: (i) Direct damage is caused by insect feeding on the plant resources. This may be accompanied by insect excretion of honeydew, on which a black sooty mold develops. The damage is correlated with pest population size. (ii) Indirect damage is caused by the insect transmission of plant diseases (viruses, mycoplasma, etc.), and can be caused by a rather low vector population. Accordingly, the crop resistance breeding program should include two different breeding concepts: (i) Prevention of direct (quantitative) damage will be achieved by suppressing pest population buildup, to keep it below the "Economic Injury Level" (EIL). (ii) Indirect damage can be prevented by breeding for "vector resistance," minimizing virus transmission by insect vectors.

Definitions of Plant Resistance to Pests

Plant resistance is defined as any reduction in plant acceptance, in pest population growth rate, or in the damage cause by pests, that is due to inherited self-defense mechanisms in the plant. If the EIL is not reached until the end of the crop production season, the plants are considered resistant (R) to that specific pest. If the EIL is exceeded during the crop production season, the plants are considered partially resistant (PR). If the EIL is reached even before the crop production has started, the plants are designated as susceptible (S). Immune plants are plants which are not attacked at all, whereas tolerant plants are plants which possess a high EIL.

Mechanisms of Resistance

The mechanisms of resistance can be divided into two major categories: antixenosis and antibiosis, which often occur together. Antixenosis is related to arthropod behavior that leads away from plant damage, whereas antibiosis is related to poor performance or lethal effects on different stages of the target insect. Although complete resistance to insects has been found and used, it is rather exceptional. On the other hand, the more frequently occurring partial resistance tends to be more durable, which is an important advantage for the development of stable agro-ecosystems. Introducing partial resistance requires more sophisticated testing methods.

Plant resistance to insect pests based on recombinant proteinase inhibitors (PIs) could interfere with natural enemies of target pests, as their own proteolytic systems may also be sensitive to broad-spectrum proteinase inhibitors.

Vector Resistance

Resistance to vectors is a special case of plant resistance to pests. Vector resistance is the tendency of plants, which are by themselves virus-susceptible, to escape infection by preventing the vector from transmitting the virus. Hypothetically, two mechanisms of plant resistance are recognized: resistance or tolerance to the virus itself, and resistance to the vector which transmits the virus.

Various insects transmit virus diseases to plants. Most insect vectors belong to the Hemiptera (e.g., aphids, whiteflies, mealybugs, psyllids). All are phytophagous, piercing the plant with their mouthparts (stylets) to suck sap from the plant tissues. Viruses are transmitted in a rather short time of inoculation-feeding, usually within minutes when they are "stylet-borne" (non-persistent) viruses, or within few hours if they are "circulative" (semi-persistent or persistent) viruses. Stylet-born viruses are "mechanically transmitted" when the insect probes the plant, whereas circulative virus transmission requires vector feeding upon the plant.

The advantage of breeding resistance to the insect vector is twofold: it can be integrated with plant resistance, or tolerance, to the virus itself, and plant resistance to insects is expected to be of greater durability than plant resistance to viruses. Several plant features can be responsible for this kind of resistance: hairy leaves, sticky and poisonous secretions, and intrinsic factors in plants which influence the settling, acceptance, and feeding behavior of the insect vector (such as the secretion of an aphid alarm pheromone mimic by the plant).

Some projects have been based on the advantage of breeding vector resistance. A significant reduction of Tungro virus was achieved in rice by the use of cultivars resistant to the leafhopper vector, *Nephotetix impicticeps*. A similar result was obtained by using cultivars resistant to *Nilaoarvata lugens*, the vector of the grassy stunt virus in rice. Resistance to *Aphis gossypii* of *Cucumis melo* prevented the transmission of cucumber mosaic virus (CMV). *Solanum polyadenium*, *S. berthaultii* and *S. tarijense* reduced attacks by aphids, and thereby reduced the viruses they transmit to potatoes. Cassava cultivars, which are partially resistant to *B. tabaci*, significantly reduce the incidence of African cassava virus.

This type of resistance may have also some drawbacks because it is vector specific, but not virus specific. The resistance to CMV transmission in muskmelon, for example, appears to be associated with nonpreference for *Aphis gossypii*. Though this plant was completely resistant to the transmission of several strains of cucumber mosaic virus (CMV) by *A. gossypii*, it was susceptible to inoculation by *Myzus persicae*. Furthermore, once this cultivar became infected, it was a source of CMV for both *A. gossypii*, and *M. persicae*. This cultivar is also resistant to CMV transmission by several clones of *A. gossypii*, and to the transmission of some other viruses as watermelon virus 1 (WMV_1), WMV_2, and muskmelon yellow stunt virus (MYSV) by this vector. However, it was susceptible to the transmission of these viruses by several other aphid species. Conclusively, this type of resistance to transmission is vector specific, but not virus specific.

Methodology: Evaluating Plant-Resistance to Insects

Methods to evaluate levels of plant resistance to both the direct or and indirect types of damage are crucial for any breeding program of plant resistance. The method should be quick, cheap, and reliable.

One of the first steps to a deliberate exploitation of genetic variation in host-plant resistance would be large-scale screening of a wide collection of varieties, breeding materials, or related wild species. The search for resistance should not be limited to free-choice experiments since the differences found are obscured when varieties are grown in monoculture. Thus, at least the most promising materials should be tested by non-choice experiments as well, to make sure that the differences found are based on true resistance and not merely on preference (antixenosis). Results should be carefully interpreted and conclusions limited to the varieties used in the experiments. Laboratory studies must, likewise, be cautiously viewed because laboratory cultures of insects suffer greatly reduced genetic variability. The strain and origin of the insects used should also be specified.

Plant Resistance to Pests Causing Direct Damage

Direct damage is usually correlated with pest population densities. Hence, host preference, rates of feeding, and rates of the pest population built-up, like the "innate capacity of population increase" (r_m), provide powerful tools for choosing a suitable source of resistance and for determining the level of resistance among the progenies. A quick and reliable test of resistance, in plants in which a sticky exudate is the mechanism of resistance, is the "sugar-test." Fine-ground crystallized "tea" sugar is spread on the tested leaf, the excess of sugar is shaken off, and a leaf diskette of a determined area is punched out from the treated leaf. The sugar is washed off from the leaf diskette, and the amount of sugar in the aqueous solution is determined with a refractometer by means of a pre-prepared correlation graph.

An additional method to evaluate plant resistance is based on the expression of resistance in in-vitro derived callus tissue rather than in seedlings or complete plants.

Evaluation of Vector Resistance

Plant resistance to stylet-born viruses may be evaluated by confining viruliferous insects (insects contaminated with plant virus) onto test-plant seedlings. After the virus incubation time has passed, the percentage of plants showing virus symptoms is determined.

A much quicker technique is, once a correlation graph has been produced, to relate virus incidence to the amount of feeding or to the excretion rates. For example, the amount of excreted honeydew often directly reflects the probability of TYLCV transmission by *B. tabaci*. The rate of honeydew excretion can be quantified by counting the number of droplets, or by determining the amount of sugar in the excreted honeydew. The honeydew can be collected by confining the whitefly adults onto the underside of a healthy tomato leaflet by means of a clip-on-cage, or by a modified "Munger-cell." If a detached leaf is used, its petiole must be kept moistened to avoid leaf desiccation during the test. The honeydew can then be collected on a piece of filter-paper, and treated with a reagent (Ninhydrin 0.2%) that stains the amino acids of the honeydew blue. The droplets can then be easily counted. To determine the total sugars, the honeydew is collected on a microscope glass cover slide and washed off with 1 ml of distilled water, to which 2 ml of a 0.2% Anthrone solution had been added. The optical density of this solution is then recorded by a spectrophotometer at 620 nm. The absolute amount of sugars in the honeydew is then derived from a pre-prepared calibration curve. Such tests are performed within 4 or 24 h.

Sources of Resistance

Genetic sources of resistance to insects can be introgressed into modern crop cultivars. Many "old" or "primitive" varieties of crops that have been under cultivation for a long time, such as rice, eggplants, cucumbers, etc., can be investigated as sources for resistance. However, such "new world" crops as tomato, potato, pepper or corn, which have been under cultivation for a relatively short period of time, often lack known resistant cultivars, so resistance must be searched for and acquired from wild plants that can be interbred with these crops. Some examples are given below.

Soybeans

Leaf pubescence influences oviposition of *Bemisia* on soybean, *Glycine max*. More eggs are laid on hirsute and pubescent than on glabrous isoline. The within-plant distribution of eggs is related to trichome density.

Cotton

Glabrous cotton confers resistance to the *Heliothis* spp., but numbers of tarnished plant bugs and cotton flea-hoppers are greater on pilose lines; damage is reduced depending on the degree of pilosity. *High gossypol*, due to genetic increase of gossypol naturally occurring in cotton, causes the death of larvae through antibiosis and phagodeterrence. It was found to inhibit protease and amylase activity in *Spodoptera littoralis* larvae. High tannin causes antibiosis and feeding deterrence to *Heliothis* spp. *Nectariless* has been shown to be a resistance character for pink bollworm based on antibosis. (Transgenic cotton, to which the gene responsible to the development of the toxin of *Bacillus thuringiensis* has been transferred by genetic engineering manipulations).

Engineered Resistance

There is interest in more rapidly creating plant resistance to insects. An induced method for obtaining resistant mutants might be achieved by irradiation or by transgenic manipulations. Plant genetic engineering offers opportunities for the creation of insect-resistant plants by insertion and expression of entomopathogenic proteins.

Techniques for gene transfer have been developed for most crop plants, but current prospects for engineering resistance to insects are limited by our lack of identified candidate genes to transfer, our elementary stage of understanding of gene regulation in plants, and uncertainty about the acceptance of engineered organisms by society. Most plants genetically engineered for resistance to insects and currently being tested in the field derive their resistance from a protein endotoxin from one of the many strains of *Bt* (*Bacillus thuringiensis*), a bacterium long used as a microbial insecticide. Examples of this are transgenic cotton or potato plants to which the *Bt* toxin gene had been transferred, or transgenic clones of *Bt*-1 that impose resistance to the potato tuber moth. Some tomato varieties, bearing the Mi-1.2 gene, which provides resistance to nematodes (*Meloidogyne* spp.) and to the potato aphid (*Macrosiphum euphorbiae*), are also less preferred by *Bemisia tabaci* than varieties that do not bear this gene.

The potato proteinase inhibitor gene, pin2, was introduced into several rice varieties and inherited. Bioassay for insect resistance with the fifth-generation transgenic rice plants showed that transgenic rice plants had increased resistance to a major rice insect pest, pink stem borer (*Sesamia inferens*).

Environmental Factors Affecting Resistance

Environmental factors such as day-length, light intensity and plant nutrition, affect not only the development and behavior of the insects but also the morphology and physiology of the plant. Temperatures, drought, plant nutrition, plant age and previous virus-infection may also affect the hostplant preference of the insect, which is then expressed as variations in plant resistance by making a susceptible plant to appear "resistant." Furthermore, the conditions under which the resistance-test are performed must also be optimized, standardized and noted.

The Effect of Light Intensity and Photoperiod

Some *Lycopersicon pennellii* and *L. hirsutum* f. *glabratum* accessions are always resistant to *B. tabaci*, some are always susceptible, but in some accessions the resistance varies according growth conditions, summer or winter. Both light intensity and day-length (photoperiod) affect their resistance to *B. tabaci*, *Manduca sexta*, and to *Leptinotarsa decemlineata*. Furthermore, 2-tridecanone, a toxin important in the resistance of *L. hirsutum* f. *glabratum* accessions, is significantly more abundant in plants grown under long day than under short-day regime. Accessions of *L. hirsutum* f. *glabratum* varied in their resistance to *B. tabaci* when grown under low light intensity, independent of day-length. In the case of *L. pennellii* accessions, only plants grown under low light intensity and a short-day regime are susceptible. The density of glandular trichomes, which secrete 2-tridecanone, is influenced by an interaction between day length and light intensity. Hence, the transition from resistance to susceptibility and vice versa took about 3–4 weeks and found its expression in the leaves, which had grown under the new conditions. The resistance can be noted clearly by the stickiness of the leaves, as quantified by the "sugar test." Day length also has significant effects on the expression of resistance in *L. hirsutum* leaves to *L. decemlineata*, through the tomatine content of the leaves which affects the rate of feeding.

The Effect of Plant Nutrition

Concerning their effects on insects, plant biochemicals may be divided into nutrients and non-nutrients. The effect of nutrients on hostplant specificity is small. Variations in nutrient value of plants are usually not significant. Furthermore, most species of insects do not differ greatly in their qualitative requirements for nutrients. Thus, although the host plant obviously has to satisfy the nutritional requirements of the insect, it does not seem likely that the insects' nutritional requirements play more than a minor role in host plant specificity. Allelochemics (non-nutritional chemicals produced by an organism) which affect the growth, health, behavior, or population biology of insects, can be extremely important factors in host plant resistance. They may also interact with the nutrients.

In cultivated crops, artificial fertilization may have an important impact on insect-host-plant relations. In many crops, nitrogen fertilizer increases the number of pests because they affect the suitability of the plant. But in some pest-crop systems, the same nitrogen levels may have a negative impact on plant resistance; this can occur in forests and, less often, in grass, where nitrogen decreases pest numbers for reasons which are unclear. Generally, pest populations increase when the host plants are over-fertilized, especially when nitrogen is in excess. High N-levels in the hostplant cause an increase in aphid populations. In whitefly, increasing N-levels in the plant nutrition causes an increase in the intrinsic rate of natural population growth (r_m) due to an increase in survival, fecundity, respiration rate, net reproductive rate (R_0), followed be an decrease of generation time and in the doubling time of the populations.

Increasing population growth enhances not only direct damage but also the development of resistance to pesticides, which will undoubtedly result in positive feedback by a significant, and completely unwanted, increase in pesticide application.

The effects of P and K, as well as minor and trace elements, are less clear. The idea that K is outstandingly important in conferring "resistance" to pest attack has found little support. Undoubtedly, the composition of cell sap is affected by the nutrients applied to soil as N, P and K, and may sometimes enhance or reduce the real resistance of the crop to particular pests by modifying non-preference or antibiosis. The effects might well operate in different directions for a variety of pests attacking the same crop.

Glucosinolates and the availability of free amino acids in the phloem affects the feeding behavior and development of the specialist cabbage aphid, *Brevicoryne brassicae*, and of the generalist peach potato aphid, *Myzus persicae*, on *Brassica* species and cultivated cabbage.

► Allellochemicals
► Plant Secondary Compounds
► Trichomes and Insects

References

Berlinger MJ, Tamim M, Tal M, Miller AR (1997) Resistance mechanisms of *Lycopersicon pennellii* (Corr.) D' Arcy accessions to *Spodoptera littoralis* (Boisduval) (Lepidoptera: Noctuidae). J Econ Entomol 90:1690–1696

Frutos R, Rang C, Royer F (1999) Managing insect resistance to plants producing *Bacillus thuringiensis* toxins [Review]. Crit Rev Biotechnol 19:227–276

Heinrichs EA (ed) (1988) Plant stress-insect interaction. Wiley, New York, NY, 492 pp

Jouanin L, Bonade-Bottino M, Girard C, Morrot G, Giband M (1998) Transgenic plants for insect resistance [Review]. Plant Sci 131:1–11

Maxwell FG, Jennings PR (eds) (1980) Breeding plants resistant to insects. Wiley, New York, NY, 683 pp

de Ponti OMB, Romanov LR, Berlinger MJ (1990) Whitefly-plant relationships. In: Gerling D (ed) Whiteflies: their bionomics, pest status and management. Intercept, Andover, Hants, UK, pp 91–106

Smith CM (1989) Plant resistance to insects: a fundamental approach. Wiley, New York, NY, 286 pp

Plant Secondary Compounds and Phytophagous Insects

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Although phytophagy is limited to eight (Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Orthoptera, Phasmatodea and Thysanoptera) of the approximately thirty orders of insects, the diversity of herbivorous insect species is extensive. While the total number of phytophagous insect species is difficult to assess because of the overwhelming diversity of insects as a group and the large number of non-described species, it has been estimated that approximately 46% (or 361,000) of the almost 800,000 species of insects are herbivorous. Because plants and animals differ substantially in their chemical makeup (plants are composed primarily of C-based carbohydrates, while the primary biological macromolecules of animals are N-based proteins), strictly phytophagous animals face two major hurdles during feeding. First, nitrogen accounts for approximately 7–14% of the dry mass of animal cells, while plants rarely exceed 7% and are typically much lower. As a result, plants are nutritionally sub-optimal and N often is limiting for herbivores. Numerous studies have documented the direct positive relationship between N fertilization of host plants and increased size, fecundity and population density of plant-feeding insects.

Second, plants may employ either physical defenses such as thorns or trichomes, chemical defenses, or both for protection from attack by phytophages. Secondary compounds are substances that have no known metabolic function (i.e., they are not constituents of any known primary metabolic pathway). Moreover, secondary compounds are often energetically expensive to produce and, although a defensive role of plant chemicals was proposed more than 100 years ago, it wasn't until Fraenkel in the 1950–1960s specifically noted that host-location and feeding behavior of herbivores is regulated by plant secondary compounds. Secondary metabolites can be classified according to their concentration within plant tissues. Generally, plants or plant parts that are low in abundance (i.e., non-apparent to herbivores) produce qualitative defensive compounds that interfere with metabolic pathways of herbivores; whereas, common (i.e., apparent) plants or plant parts are more likely to be defended by quantitative compounds, which are produced in much higher concentrations and reduce the digestibility of the plant material. The concept of strategic chemical defense of plants, based on the visibility of the plant to searching herbivores, is referred to as the "plant apparency hypothesis" of chemical defense.

Secondary compounds can be broadly classified into two groups: N-containing and non-N-containing (Table 13). Among the N-containing compounds, non-protein amino acids, which are commonly found in the seeds of legumes, act as anti-metabolites because they are structurally similar to one of the twenty amino acids required for normal protein synthesis. For example, azetidine 2-carboxylic acid is structurally very similar to the protein amino acid proline and, as a result, it is mistakenly incorporated into the structural and enzymatic proteins of herbivores that consume the seeds. Incorporation of these toxic non-protein amino acids by non-adapted herbivores is likely to be fatal. However, some specialist seed-eating bruchid beetles have evolved the ability to overcome these toxic amino acids. For instance, larvae of *Caryedes brasiliensis* feed exclusively on seeds of the tropical legume *Dioclea megacarpa*, which contains high levels of the non-protein amino acid canavanine. Canavanine is similar structurally to the protein amino acid arginine. However, this bruchid beetle has very specific arginyl t-RNA synthetase, which discriminates between arginine and canavanine so that the latter is not incorporated into the insect's proteins. Glucosinolates, characteristic of the mustard family (Brassicaceae), are another important group of N-containing secondary compounds that also possess sulfur. While the glucosinolates vary in their side chains, they all contain thioglucose and sulfate moieties. Plants such as mustard and horseradish that synthesize glucosinolates also produce thioglucosidase, which enzymatically hydrolyzes glucosinolates by cleaving glucose and HSO_4^- from the parent molecule to produce isothiocyanate, thiocyanate or nitrile. Although glucosinolates are isolated from the thioglucosidase within the intact plant tissues, disruption of the plant structure by chewing or grinding action will cause glucosinolates to mix with the thioglucosidases resulting in hydrolysis and release of mustard oils. These pungent compounds (mustard oils) can cause blistering, irritation of mucous membranes including the alimentary canal, and they result in rejection of plant tissue containing them by non-adapted insects. For

Plant Secondary Compounds and Phytophagous Insects, Table 13 Select classes of secondary compounds produced by plants and their major effects on non-adapted insect herbivores (see text for details)

Classification	Class	Example	Common source	Effects on non-adapted insects
N-containing				
	Non-protein amino acids	Canavanine	Legume seeds	Antimetabolite, malfunctioning proteins
	Glucosinolates	Sinigrin	Mustard family	Anti-feedant, blistering, irritation of mucus membranes
Non-N-containing				
	Rotenoids	Rotenone	Legume	Inhibition of cellular respiration
			Roots	
	Pyrethrins	Pyrethrin I	Flower heads of *Chrysanthemum cinearifolium*	Paralysis
	Proanthocyanidins	Procyanidin	Most classes of woody plants, such as oaks	Precipitation of plant and insect proteins, reduction in insect size, performance and fecundity

instance, a concentration of ≥0.1% sinigrin (a glucosinolate) infiltrated into celery leaves was fatal to the non-adapted black swallowtail (*Papilio polyxenes*). Moreover, plant concentrations of as little as 0.01% sinigrin increased the development time of larva to pupa by 21%, reduced pupal mass by approximately 28%, and adult females laid 31% fewer eggs compared to insects reared on control plants containing no sinigrin. In addition, females, which had been reared as larvae on 0.01% sinigrin, only produced half as many viable eggs as females that had been cultured on plants containing no sinigrin. However, specialist herbivores such as the cabbage butterfly (*Pieris brassicae*), which feed exclusively on mustards, may utilize the pungent glucosinolates or their hydrolytic products for host location and to stimulate gustation. The cabbage butterfly may even reject artificial diet unless it contains glucosinolates or mustard oils.

The non-N-containing secondary compounds include some economically important substances such as the rotenoids and pyrethrins, which are used commercially to control insect pests of crops and turf grasses. The rotenoids (such as rotenone), primarily isolated from the roots of tropical legumes, prevent cellular oxygen uptake in insects by inhibiting NADH-dependent dehydrogenase activity associated with the electron transport system of mitochondria. Rotenoids are highly toxic to insects and as little as 0.003 g/g body mass was lethal to the silkworm (*Bombyx mori*). Pyrethrins, which may disrupt the permeability of nerve cell membranes to sodium ions, causes paralysis and death of insects.

Among the most widespread of the quantitative defensive compounds are the non-N-containing tannins. These C-based defensive compounds can be divided into two categories: hydrolyzable, which are derivatives of phenolic acids and condensed (proanthocyanidins), which are often of higher molecular mass. The name "tannin" refers to the ability of these substances to render animal hides into leather, which are much more resistant to water infiltration. Their ability to "tan" leather is based on the formation of hydrogen bond cross-links between tannin and protein molecules. The protein binding ability of tannins also provides protection to the plant from herbivores. Defensive tannins typically are stored in vacuoles, which prevents them from interacting with the plant's proteins. Upon disruption of the vacuoles, which occurs during herbivore feeding activities, tannins are released from the ruptured vacuoles and they quickly combine with available proteins. As a result, tannins greatly decrease the quality of the plant tissue by combining with two important groups of proteins. First, they combine with plant protein, which reduces the ability of proteases such as trypsin to digest them into simpler polypeptides for N metabolism in the herbivore. Second, they bind to the digestive enzymes of the phytophage, thereby reducing their ability to breakdown plant proteins (and other enzymatically digested compounds). This non-selective cross-linkage of proteins (both host's and herbivore's) can reduce the N availability (and hence quality) of the plant. The negative relationship between tannin levels and insect herbivore abundance was most clearly demonstrated by Feeny (1970) for the winter moth, *Operophtera brumata*, which feeds on leaves of the oak *Quercus robur*. Larvae of the winter moth feed on oak leaves during the spring, but quickly cease feeding on the oaks by mid-June when they search for alternative hosts. This sudden decrease in feeding activity is inversely correlated with levels of leaf tannin, which are low during the spring and rapidly increase during the summer. In laboratory studies, larvae of the winter moth reared on oak leaves collected on May 16 (prior to tannin buildup) were approximately 2.5 times heavier (peak mass) than larvae reared on leaves collected on May 29 (when tannin accumulation had reached approximately 1% of the dry leaf mass). The decrease in larval mass is important biologically because numerous studies have documented the correlation between larval or pupal mass and insect fecundity.

In summary, most vascular plants probably contain one or more secondary compounds. Although a defensive role has been hypothesized for secondary compounds, it is unclear whether this description is suitable in all cases. For instance, tannins (along with lignins) also help strengthen plant structures and prevent invasion by pathogens, in addition to their anti-herbivore role. Moreover, secondary compounds, while protecting the plant from attack by non-adapted herbivores, may actually serve as host selection cues and feeding stimulants for adapted insects. Although many of these substances such as tannins have general anti-herbivore properties and offer the plant protection from most herbivores, others such as such as pyrethrins offer protection from insect phytophages in particular.

► Allellochemicals

References

Bernays EA, Chapman RF (1994) Host-plant selection by phytophagous insects. Chapman and Hall, New York, NY, 312 pp

Erickson JM, Feeny P (1974) Sinigrin: a chemical barrier to the black swallowtail butterfly, *Papilio polyxenes*. Ecology 55:103–111

Feeny P (1970) Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology 51:565–581

Harbourne JB (1994) Introduction to ecological biochemistry, 4th edn. Academic Press, London, UK, 356 pp

Slansky F Jr, Rodriquez JG (eds) (1987) Nutritional ecology of insects, mites, spiders and related invertebrates. Wiley Interscience, New York, NY, 1016 pp

Spencer KC (1988) Chemical mediation of coevolution. Academic Press, San Diego, CA, 609 pp

Strong DR, Lawton JH, Southwood R (1984) Insects on plants: community patterns and mechanisms. Harvard University Press, Cambridge, MA, 313 pp

Rosenthal GA, Janzen DH (eds) (1979) Herbivores: their interaction with secondary plant metabolites. Academic Press, Orlando, FL, 718 pp

Plant Viruses and Insects

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The principal families of insect vectors which cause the most damage to agricultural crops through the spread of plant diseases are in the order Hemiptera, and include the aphids, leafhoppers, delphacid planthoppers and whiteflies. Another important group of insect vectors found worldwide is the order Thysanoptera, the thrips. Other insects also spread plant diseases; however, aphids alone are responsible for spreading the majority of known plant viral diseases, followed closely by the leafhoppers, whiteflies, and thrips. The known number of plant disease vectors within these taxa is large, including Cicadellidae (leafhoppers, containing 49 known vector species), Aphididae (aphids, with the majority of 192 vector species), Aleyrodidae (whiteflies, with three vector species) and Thripidae (thrips, with eight known vector species). Of course, these numbers change every year with the description and discovery of new viral diseases and new insect vectors. Furthermore, a group with only a few insect vectors still may be able to carry and spread a huge number of viral diseases to many different host plants, as occurs in the whiteflies and thrips.

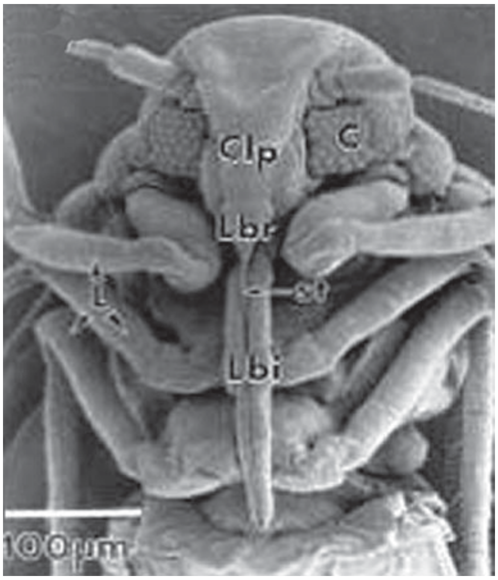
In 1997, more than 380 viruses were known to be transmitted by these insect vectors; however, in the last 5 years the number has increased greatly (about 600 in 2001) and is increasing every year. This dramatic increase has been due in part to our ability to detect and characterize viral diseases more accurately, and also due to increased travel and trade between countries, which often result in the accidental introduction of either diseases or insects from one country into another.

Components Involved in Disease Epidemiology

The epidemiology of plant diseases caused by insect-carried plant pathogens involves four main components: the pathogen, the insects, the plant and the environment. Thus, the transmission of a plant pathogen by an insect to a plant appears relatively simple. However, this situation is highly complex when one examines all the possible elements that can influence these interactions. The availability of the pathogen is affected by its quantity, location, and the strain within the plant. The insect's biology is influenced by population size, number of generations, longevity, dispersal patterns, feeding behavior and interactions with the pathogen. The plant's performance can be influenced by its level of susceptibility to the pathogen, multiple infections of different strains, and/or different pathogens, susceptibility to the insect, the location and stage of growth when exposed to the pathogen and insect. Environmental factors add another level of complexity as temperature, moisture, air currents, and cultural practices come into play. The discovery of a new plant pathogen that is carried and spread by an insect is usually the beginning of a long and difficult task toward understanding its epidemiology (all the elements that influence the development and spread of a plant disease).

Insect Feeding Mechanisms

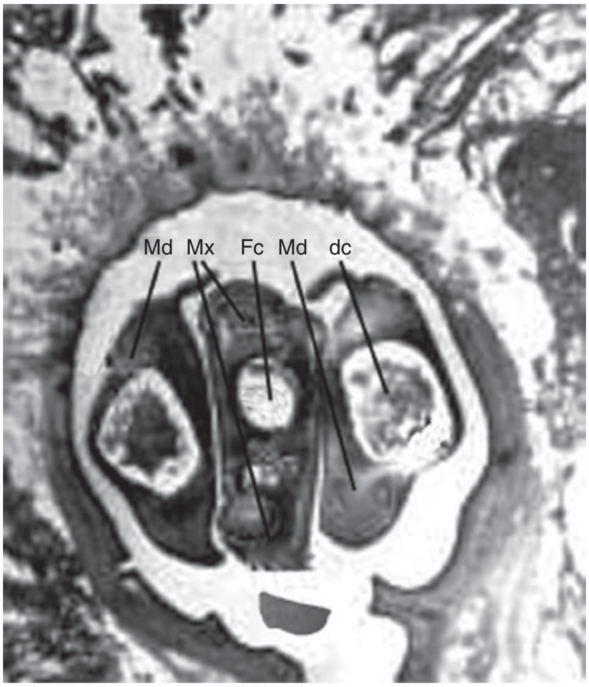
The traits of morphology that contributes to the ability of these insects to transmit plant diseases so efficiently is their piercing-sucking feeding style. Insects in the order Hemiptera (aphids, leafhoppers, whiteflies), and Thysanoptera (thrips) have similar basic morphologies of the head and body (Fig. 72–74). In the accompanying scanning electron micrograph you can see the compound eyes, and the proboscis of the insect. In Thrips this proboscis is referred to as a mouthcone due to the thick, short nature of the structure. The proboscis helps support the stylets as the insect works its stylets into the plant cells. The stylets are under muscular control so that they can be extended into the plant tissues. The stylets are each curved and are held against each other so that they go straight, one pushing and sliding against the other. However, when one stylet moves in front of the other the curve pushes the stylet in a lateral, sideways direction. Thus, the insect controls the direction in which it moves the stylets.



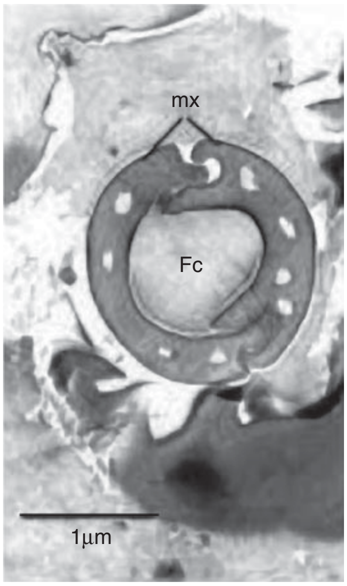
Plant Viruses and Insects, Figure 72 **Scanning electron micrograph (SEM) of the whitefly *Bemisia tabaci* showing the ventral surface. Body parts are as follows: C, compound eye; Clp, clypeus; Lbi, labium; Lbr, labrum; L, legs; St, stylet bundle.**

Some leafhoppers feed in a manner whereby they will pierce into the plant tissues and then proceed to feed in a clockwise or counter-clockwise procession, emptying cells as they go, thus creating an emptied out "spot" in the plant leaf, called a stiple. Others feed directly from the vascular tissues of plants, the phloem or xylem.

All these insects have piercing-sucking mouthparts that allow them to feed on plants while causing minimal damage. This is important for virus transmission, as viruses require a living cell to reproduce. The insects use paired maxillary stylets to form a suction tube that is inserted into plant cells, similar to a flexible syringe needle. In the Hemiptera, these stylets form two canals, the food canal, and a smaller salivary canal where the saliva of the insect comes out during feeding. The Thysanoptera are unique in that thrips stylets form a single canal used for both sucking up plant fluids and to secrete saliva. The insect salivary secretions have several functions. There are at least two types of saliva, one is liquid and aids in the digestion of plant cells and cell debris so that they



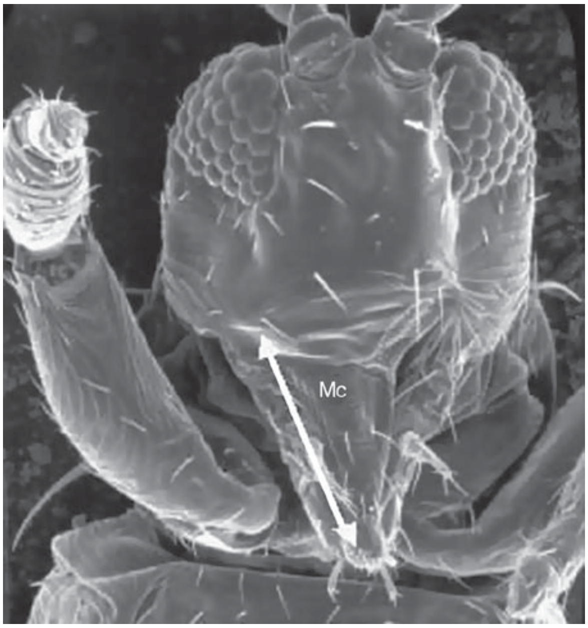
Plant Viruses and Insects, Figure 73 **Cross section showing stylets of a whitefly, with separate food and salivary canals: *Dc*, dendritic canal; *Fc*, food canal; *Md*, mandibular stylet; *Mx*, maxillary stylet; *Sc*, salivary canal.**



Plant Viruses and Insects, Figure 74 **Cross section showing stylets of a thrips, with single canal used for salivation and food intake: *Fc*, food canal; *Mx*, maxillary stylet.**

can be ingested, sucked up through the food canal. Another solidifies or hardens during feeding which functions to form a salivary sheath to help prevent leakage around the inserted stylets, and to hold the stylets firmly in place during feeding. The saliva also is thought to prevent or hinder the plant's response to repair its damaged cells so the insect can continue feeding once it finds the desired location inside the plant (i.e., the phloem or xylem).

There are also mandibular stylets. These are paired, thicker stylets on the outside of the maxillary stylets. The aphids, leafhoppers and whiteflies all have symmetrical, paired, matching mandibular stylets which function to pierce the hard epidermis of plants and to assist attaching the insect firmly to the plant surface. Only the thrips have an asymmetrical morphology with one of the mandibular stylets being reduced or absent, and the remaining stylet being closed at the end, forming a needle-like structure, closed at the end (Fig. 75). The thrips use the single, mandibular stylet to pierce a hole into the epidermis of the plant surface so that the slender, paired maxillary stylets can be inserted to feed in a piercing-sucking manner from plant cells that are deeper.



Plant Viruses and Insects, Figure 75 Scanning electron micrograph of a thrips showing the face and mouthparts: *Mc*, mouthcone.

By being able to feed in such a precise and direct manner, insects that feed in a piercing-sucking manner can avoid many of the plant's natural defenses. These insects also can deposit viruses directly into specific tissues from which they feed, such as into the vascular tissues of a plant. Once a virus has been introduced into the vascular tissues, it can spread rapidly throughout the plant to cause disease. Furthermore, piercing-sucking feeders cause less damage to the plant than a chewing insect, so plant cells that are infected with a virus often survive the feeding and support virus survival within the plant.

Inside the head there are several valves whereby the insects can stop the procession of food into their midgut. The plant sap is drawn up the food canal of the maxillary stylets. The food is then held in place by the precibarial valve where it is tasted by gustatory sensilla. The food is then drawn into the cibarium, the pumping chamber of the mouth. The cibarium also has gustatory sensilla for tasting and evaluating the quality of the food as the insect sucks up the plant sap. The food then passes the esophageal valve and enters the esophagus and passes through to the midgut which is the area of the alimentary tract where most nutrients are absorbed. In most plant sap-feeding insects, there is a region of the midgut where the hindgut coils around and is attached to it. This is the filter-chamber region of the insect's alimentary canal. Plant phloem and xylem, the liquids within plants' vascular tissues, are full of water; insects which feed on these as a primary food source have adapted over time the ability to shunt or direct excess water directly into the hindgut. This allows the insect to concentrate food and nutrients in the midgut for maximum absorption and to release excess water without having to process it through the midgut.

Tools to Understand Feeding (Electronic Monitoring of Insect Feeding)

Scientist have many methods to study insect/virus interactions. One such method is the invention of an electronic feeding monitor system, EMS, that allows someone to measure aspects of feeding as they occur. This is very important in studies where the amount of time an insect spends feeding needs to be measured. The EMS allows the scientist to know how many times an insect inserts its stylets into a plant, how long the insect fed, and if the insect was feeding from the phloem or xylem tissues within the plant. Being able to examine insect feeding so closely enables the early selection of crop varieties that may have resistance to insect feeding before they are planted in the field. Plant varieties which can disrupt insect feeding may be useful to prevent the transmission of some virus diseases. The EMS works by running a low voltage of electricity through a plant, usually by placing a copper electrode into the moist soil of a potted plant. The insect then has a fine gold wire glued onto its back, using electrical-conductive paint, so that the electricity will pass up through the plant, and then through the insect when it inserts its stylets into the plant. When the insect either salivates out, or ingests plant fluids up the food canal, the electricity passes through the insect, which acts as a variable resistor, and goes back into the EMS, which then amplifies the signal so that it can be recorded.

Insect Vector–Plant Pathogen Interactions

There have been two systems of terminology established to describe the association and transmission of plant diseases by insect vectors which feed in a piercing-sucking manner. One is based on how long the virus persists in the insect vector, and the second is based on the route of virus movement through the insect vector. They can be combined as follows: (i) the non-persistently transmitted, stylet-borne viruses; (ii) the semi-persistently transmitted, foregut-borne viruses; (iii) the persistently transmitted, circulative viruses; and (iv) the persistently transmitted, propagative viruses. Using this terminology, virus "transmission" is referred to as "non-persistent," "semi-persistent," or "persistent".

The way a virus moves through the insect vector then is described by the terms: "circulative" or "propagative." Circulative viruses pass into the insect hemolymph and circulate through the insects before being salivated back out during feeding. This involves the ability of the virus to pass several barriers within the insect, passing through the midgut membranes, and then the salivary gland membranes, to be able to be released back out with the saliva. These types of viruses do not replicate inside their insect vectors but merely pass through the insect. Viruses that reproduce inside the insect are considered propagative. Propagative viruses are able to enter the insect hemolymph but they also replicate once they infect an insect. As one would expect, a virus that is circulative is retained in the insect for a longer period of time than a virus that is non-circulative and merely stuck to the insects' stylets (stylet-borne) or foregut (foregut-borne virus). Viruses that are propagative (replicating in the insect) are retained for the life of the insect.

Non-persistently transmitted, stylet-borne viruses are transmitted into the plant during short durations of feeding. Virus acquisition (the ingestion of a virus that results in the insect's ability to transmit the virus to a plant), is brief, often just a few seconds of feeding. There is no latent period (the time that passes between when the virus is acquired and when it can be transmitted to a plant). Since these types of viruses usually are binding to the insect's stylets for only a brief period of time, the insect does not retain the ability to transmit the virus for long periods. Usually, virus transmissibility is lost after a few minutes of feeding on a non-infected plant. Aphids transmit the majority of non-persistently transmitted viruses. The ability of viruses to bind to the insect's stylets is aided by a helper component (a virus encoded, non-structural protein produced only in infected plants). During subsequent periods of feeding the virus is released, or washed from the stylets, thus depositing virus into the plant tissues.

Semi-persistently transmitted, foregut-born viruses are transmitted into the plant during longer durations of feeding (minutes). Virus acquisition increases with increased time spent feeding (minutes to hours), and the virus stays in association with the insect for several hours, being able to be transmitted into other plants. The virus is thought to be binding in the anterior areas of the alimentary tract, along the stylets to the foregut, and a few virus particles are released during each act of feeding. There is no latent period, the virus does not replicate, and the insect will lose the ability to transmit the virus during its life.

Persistently transmitted, circulative viruses do not replicate in the insect vector. These types of viruses are acquired and transmitted during long periods of feeding (minutes to hours), and there is a latent period of hours to days before the virus can be transmitted to another plant. This makes sense as the virus must move through the insect body and get into the salivary glands to be salivated back out before transmission can occur. Virus retention is long, but is dependent upon the amount of virus acquired into the insect body, and may last for the life of the insect, usually around 30 days.

Persistently transmitted, propagative viruses do replicate inside the insect. Virus acquisition time takes hours to days of feeding. The latent period can take weeks before an insect can transmit virus. The virus is retained for the life of the insect and often the virus is passed to the eggs (transovarial transmission).

Some Insect-Transmitted Viral Plant Diseases

Aphids

Of all known aphids, about 250 are considered serious pests. They are pests because of their feeding, which reduces the vitality of the crops they feed on, but primarily due to the transmission of viral plant diseases. Perhaps the most important aphid pest is *Myzus persicae*, often referred to as the green peach aphid. *M. persicae* is a green or slightly reddish aphid which has peach as its primary host and a wide range of secondary hosts, including many brassicas. *M. persicae* is cosmopolitan in temperate climates occurring in the U.S.A., and a fair portion of Europe including the United Kingdom. Though it seldom occurs in numbers large enough to cause direct damage from feeding pressure, it is capable of transmitting and spreading over 100 viruses including the potato leaf roll, potato virus Y, yellow net and yellows viruses of sugar beet, cauliflower mosaic, plum pox, cucumber mosaic, lettuce mosaic, and turnip mosaic virus.

The pea aphid, *Acyrthosiphum pisum*, is a large green aphid with long antennae and legs. The pea aphid is found on many leguminous plants and transmits Lucerne mosaic virus, pea leaf-roll virus, pea enation mosaic virus and pea mosaic virus in the United Kingdom, and pea enation mosaic virus in the U.S.A. The cabbage aphid, *Brevicoryne brassicae*, is a serious pest of the major cabbage crops, cabbages, cauliflowers and Brussels sprouts. The main cause of its pest status is the transmission of cauliflower mosaic and turnip mosaic virus. The brown citrus aphid, *Toxoptera citricida*, is a dark, black, aphid that is the main vector of citrus tristeza virus in the subtropics and tropics. The melon aphid or cotton aphid, *Aphis gossypii*, also is an important aphid vector of viral diseases in citrus and on many other agricultural crops.

The control of aphid pests currently still involves large amounts of pesticides in most countries, but other more ecologically friendly methods have been used in other places for some time. These generally involve biological control, mostly the use of *Hymenopteran parasitoids*. These are small wasps that lay their eggs inside the aphids. Other methods include plant improvement, and monitoring aphid dispersal to predict when a pre-emptive spraying in smaller amounts might be effective. The most important element of insect pest control for all of us is education. Farmers as well as the general public need to become better informed as to the alternatives to, and proper uses of, insecticides.

Leafhoppers

A large group of plant viruses, the plant rhabdovirus group, consists of more than 70 members. They are transmitted by aphids, leafhoppers, planthoppers, lacebugs, and mites. These viruses infect and replicate in the insect cells, but each virus is specific to its insect vector. Some of them also can be transmitted mechanically, through artificial means using plant sap from infected plants. Another important leafhopper-transmitted virus is maize chlorotic dwarf virus (MCDV). This virus is a semi-persistently transmitted, foregut-borne virus, and is restricted to the phloem of maize. Transmission of this virus requires a protein that is produced by virus-infected plants. This protein, called the helper component (HC), is suspected to bind to receptor-like structures in the food canal of leafhoppers, thereby forming a matrix to which virus particles attach. Viruses are then slowly released from this matrix during feeding and, consequently, are transmitted to other plants when leafhoppers fly to neighboring plants and then feed. The insect vector of maize chlorotic dwarf virus is the leafhopper, *Graminella nigrifons*.

The beet leafhopper (*Circulifer tenellus*) is one of the most important insect pests of sugarbeets in the western United States because it is the vector of beet curly top virus, BCTV. Curly top virus is a severely devastating plant virus that affects more than 300 broad-leaved plants. Tomato, bean, squash, cucumber, melon, spinach, table beet, pepper, and some flowering plants are the most common cultivated plants affected in the western United States. Leafhopper populations survive on weeds and cultivated plants infected with curly top virus which serve as reservoirs for both the insect and virus. Leafhoppers are able to acquire the virus during very short feeding times. The leafhopper retains the ability to transmit BCTV for a month or more after acquisition.

Whiteflies

In the past decade, whiteflies as pests and vectors of plant viruses have become one of the most serious crop protection problems in the tropics and subtropics. Yearly losses are estimated in the hundreds of millions of dollars. Several species of whitefly cause crop losses through direct feeding, while others are important in virus transmission. *Bemisia tabaci*, for example, is the vector of African cassava mosaic, bean golden mosaic, bean dwarf mosaic, bean calico mosaic, tomato yellow leaf-curl, tomato mottle, and other *Begomoviruses* in the family Geminiviridae, affecting crops worldwide.

With the spread of an especially aggressive biotype of *B. tabaci* into the New World tropics (*B. argentifolii*), crop losses likely will continue to increase, resulting in higher pesticide use on tomatoes, beans, cassava, cotton, cucurbits, potatoes, sweet potatoes and other crops. There is an urgent need to develop integrated pest management systems aimed at reducing insecticide use and which will help re-establish the ecological equilibrium of predators, parasitoids, and microbial controls. Needed are crop varieties with resistance to the whiteflies, and/or to the whitefly-transmitted viral diseases.

This problem is manifested in the fact that whiteflies and the viruses they carry can potentially infect many different host plants, including agricultural crops and weeds. A pest problem on one crop, such as beans, cannot be tackled as a single problem, as neighboring crops or weeds also may be affecting the disease spread. The different viruses and forms of the whitefly also are difficult to identify, and/or separate on the basis of symptoms or morphology. Determining where the problems in food crops are coming from becomes almost impossible. Proper diagnosis of the problem depends on using sophisticated molecular techniques to characterize the viruses and whitefly vectors, followed by epidemiological work, usually based on dynamic modeling, to understand the incidence of disease spread.

Thrips

Thrips species in the genus *Frankliniella* are commonly referred to as flower thrips. The western flower thrips, *F. occidentalis*, has a worldwide distribution and is considered the primary vector of tospoviruses. Thrips feed on over 600 different plants and crops, especially on flowering plants where they also feed on pollen. Many thrips are pests of commercial crops due to their damage to flowers. Also, their feeding causes stunting, deformed and unmarketable fruits and vegetables.

Thrips in the genera *Frankliniella* sp. and *Thrips* sp. also spread plant diseases through the transmission of viruses such as tospoviruses. Tomato spotted wilt virus is the type member of the genus *Tospovirus* in the family Bunyaviridae. These enveloped viruses are considered among the most damaging of emerging plant pathogens around the world. Virus members also include the impatiens necrotic spot viruses, which infect many ornamental plants. Tospoviruses can kill plants or reduce yields of marketable fruits and vegetables (i.e., lettuce, tomato, peanut, watermelon and ornamental crops). To transmit tospoviruses, thrips must acquire the virus during the larval stage. Most thrips species overwinter as either adults or as pupae. A typical flower thrips generation time varies from between 7 and 22 days depending on the temperature. The eggs are about 0.2 mm long and reniform (kidney shaped); they take on average 3 days to hatch. Thrips have two larval stages, then go through a prepupal and a pupal stage. Adults take between 1 and 4 days to reach sexual maturity. The females of the suborder Terebrantia are equipped with an ovipositor which they use to cut slits into plant tissue into which they insert their eggs one per slit, while females of the suborder Tubulifera, which lack an ovipositor, lay their eggs on the outside surface of plants, either singly or in small groups.

References

Hunter WB, Backus EA (1989) Comparison of feeding behavior of the potato leafhopper *Empoasca fabae* (Homoptera: Cicadellidae) on alfalfa and broad bean leaves. Environ Entomol 18:473–480

Hunter WB, Ullman DE (1992) Anatomy and ultrastructure of the piercing-sucking mouthparts and paraglossal sensilla of *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae). Int J Insect Morphol Embryol 21:17–35

Hunter WB, Ullman DE, Moore A (1994) Electronic monitoring: characterizing the feeding behavior of western flower thrips (Thysanoptera: Thripidae). In: Ellsbury MM, Backus EA, Ullman DL (eds) History, development, and application of AC electronic insect feeding monitors. Thomas Say Publications in Entomology, Entomological Society of America, Lanham, MD, pp 73–85

Hunter WB, Hiebert E, Webb SE, Polston JE (1996) Precibarial and cibarial chemosensilla in the whitefly, *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae). Int J Insect Morphol Embryol 25:295–304

Nault LR (1997) Arthropod transmission of plant viruses: a new synthesis. Ann Entomol Soc Am 90:521–541

Plasmatocyte

A common type of hemocyte capable of phagocytic, encapsulation and secretory functions.

► Hemocytes of Insects: Their Morphology and Function

Plasmid

Circular, dsDNA molecules found in bacteria that are often used in cloning. Plasmids are independent, stable, self-replicating, and often confer resistance to antibiotics. Often used in recombinant DNA work as vectors of foreign DNA.

Plasterer Bees

Members of the family Colletidae (order Hymenoptera, superfamily Apoidae).

► Bees
► Wasps, Ants, Bees and Sawflies

Plastron

Hairs or a tube-like process in which the cuticle of an insect or egg chorion holds a bubble of air through which gas exchange can occur while the insect is submerged in water. A physical gill.

► Eggs of Insects

Plataspidae

A family of bugs (order Hemiptera, suborder Pentamorpha).

► Bugs

Plate-Thigh Beetles

Members of the family Eucinetidae (order Coleoptera).

► Beetles

Platygastridae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Platypezidae

A family of flies (order Diptera). They commonly are known as flat-footed flies.

► Flies

Platypodidae

Considered by some to be a family of beetles (order Coleoptera). They commonly are known as pin-hole borers. Here they are treated as a subfamily (Platypodinae) of Curculionidae.

► Beetles

Platystictidae

A family of damselflies (order Odonata).

► Dragonflies and Damselflies

Platystomatidae

A family of flies (order Diptera). They (and Otitidae) commonly are known as picture-winged flies, but Otitidae is now considered to be part of Ulidiidae.

► Flies

Pleasing Fungus Beetles

Members of the family Erotylidae (order Coleoptera).

► Beetles

Pleasing Lacewings

Members of the family Dilaridae (order Neuroptera).

► Lacewings, Antlions and Mantidflies

Plecomidae

A family of beetles (order Coleoptera). They commonly are known as rain beetles.

► Beetles

Plecomidae

A family of beetles (order Coleoptera). They commonly are known as rain beetles.

► Beetles

Plecoptera

An order of insects. They commonly are known as stoneflies.

► Stoneflies

Pleidae

A family of bugs (order Hemiptera). They sometimes are called pygmy backswimmers.

► Bugs

Pleiotropic

Term used to describe a gene that affects more than one, apparently unrelated, trait.

Pleural

An adjective describing the lateral region of an insect, or features found laterally.

Plesiomorphy

When considering classification and phylogeny, an ancestral or primitive character state.

Pleuron (pl., pleura)

The lateral plates of the insect body segments, especially the thoracic segments.

► Thorax of Hexapods

Plica

A longitudinal fold or wrinkle in the wing of an insect.

Plokiophilidae

A family of bugs (order Hemiptera). They sometimes are called web-lovers.

► Bugs

Plumaridae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Plum Curculio, *Conotrachelus nenuphar* Herbst (Coleoptera: Curculionidae)

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The plum curculio, *Conotrachelus nenuphar* Herbst (Coleoptera: Curculionidae), is an important pest of pome and stone fruit orchards in North America. The insect is distributed from Quebec to Florida, east of the Rocky Mountains and in Utah. Two strains are found: a northern and a southern strain, which have, respectively, one and two generations per year.

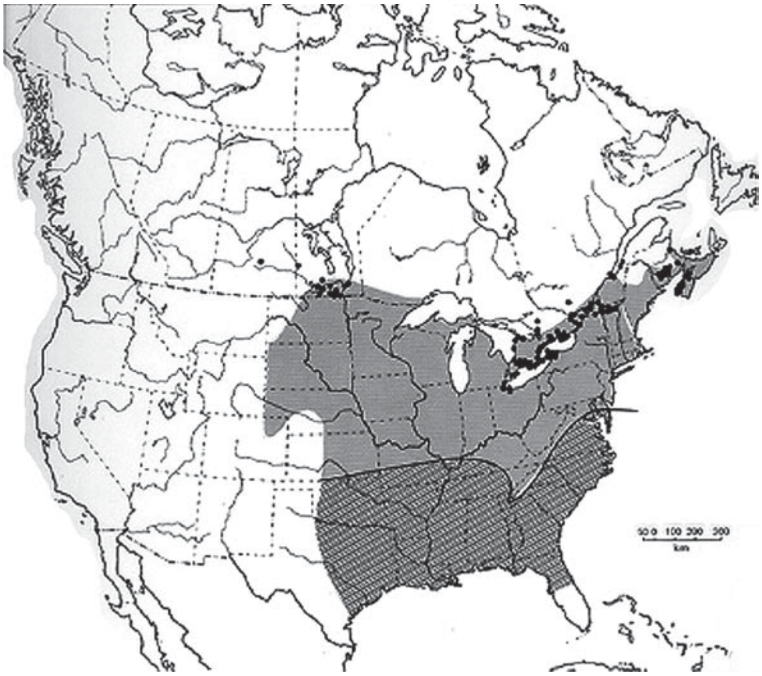
Life Cycle

C. nenuphar overwinters as adults in plant debris, preferably under maple leaves. The pest is univoltine in the northern part of its range (north of Virginia, USA) and at least partially multivoltine in southern areas including populations present in mid-Atlantic regions of West Virginia and New Jersey (Fig. 76). Spring emergence times vary with geographical location. In Quebec (Canada), overwintered adults emerge in late April when apple trees of cv. McIntosh reach the "green tip stage." Emergence reaches a peak from 6 days before full bloom to 10 days after petal fall. In southwestern Quebec emergence may take 3–4 weeks to complete. In Ontario (Canada), emergence begins at end of April and is nearly complete by early June, but continues until late June or early July. In Texas, emergence occurs from late March to early May. Adults begin to emerge and become active when mean daily temperatures reach approximately 13–15°C.

After emergence, adults remain on the surface of the soil for some time before appearing on the trees, where they feed on the new shoots and blossoms until fruit becomes available. In spring, adults invade orchards mainly from the surrounding woodland. In Quebec, the adult population peaks somewhere between the tight cluster stage and 10 days after petal fall on apple. The highest distance covered by the adults, mainly by walking, was recorded from the tight cluster stage until physiological fruit drop in late June. In southern regions in the United States, adult populations on peach and plum peak at least 1 month earlier.

In Ontario, oviposition begins in late May and continues until early August. The timing of oviposition varies with climate. In New York State, it was estimated that 60% of total fruit damage by oviposition is accomplished when 230 day-degrees (above 10°C) had accumulated after petal fall in apple (mid-June on average in that region).

Eggs are laid in an epidermal cavity in the fruit that the female excavates. The skin is cut into a distinctive crescent-shaped slit, which partially surrounds the egg. The eggs and young



Plum Curculio, *Conotrachelus nenuphar* Herbst (Coleoptera: Curculionidae), Figure 76 **Distribution of plum curculio in North America. The map shows the area inhabited by both the northern (single generation per year) and southern (more than one per year) strains.**

larvae are sensitive to internal pressure and other unfavorable effects of fruit growth. Eggs crushed by rapidly growing apple fruit may account for varietal differences in the susceptibility to attack by *C. nenuphar*. The gum exudate from egg-laying scars on half-grown plums can kill the larvae. More than one larva can develop in a single fruit. The abundance of fruit has a significant influence on *C. nenuphar* population dynamics and a poor crop may lead to a marked decrease in population size. The larvae feed in the fruit, which usually drops prematurely unless egg or larval development is interrupted in its early stages. The time spent in the fruit varies from 15 to 18 days. When fully fed, the larvae leave the fruit and pupate in cells in the soil. The time spent in the soil depends on temperature and humidity but varies from 3 weeks to more than 5 weeks, the longer periods generally occurring in the northernmost part of its range.

The summer generation of adults emerges over a long period from July to October in Ontario, and Maine, with a peak of emergence in September. In Georgia, approximately 50–75% of females lay eggs in the same year, giving a partial second generation. The adults leave the trees and search for overwintering sites in September and October. In caged experiments in Quebec, 93% of adults overwintered at the soil surface under leaves and other debris, 4% were found in the top inch of the soil and the remainder overwintered deeper in the soil. In Virginia, weevils were found hibernating up to 15 cm deep in loose soil and in clay, at an average depth of 6 cm.

Host Plants

Plums, peaches, apricots and nectarines are the preferred hosts of *C. nenuphar*, but apples are also widely affected. Other economically important hosts include sweet cherry, sour cherry and blueberry. Apples are less damaged in areas adjacent to peach orchards than in areas where peaches are not grown. Peaches are often scarred and deformed by the feeding and egg punctures of *C. nenuphar*, with larvae developing successfully and leaving the fruit to pupate. There are varietal differences in the susceptibility of apples, with eggs being destroyed and larval establishment being prevented by fruit growth in some cultivars.

Damage and Economic Impact

Second only to the codling moth (*Cydia pomonella*), *C. nenuphar* is regarded as the most serious pest of pome and stone fruit in eastern North America. For example, in Quebec up to 85% of harvested apples may be damaged by *C. nenuphar* in unsprayed orchards. Plum curculio damage returns to levels of economic importance 1–3 years after cessation of pesticide spraying.

On apple, *C. nenuphar* can cause three types of external damage. In spring, males and females feed on, and females oviposit in, young fruit, leaving behind small round feeding punctures and marking them with characteristic half-moon shaped scars (Fig. 77), respectively; and in spring and summer, the adults puncture the fruit causing round (2–3 mm diameter), feeding scars (Fig. 78).

Plum Curculio, *Conotrachelus nenuphar* Herbst (Coleoptera: Curculionidae), Figure 77 Oviposition scar on the surface of an apple.

Plum Curculio, *Conotrachelus nenuphar* Herbst (Coleoptera: Curculionidae), Figure 78 Adults and feeding punctures on young fruit.

The appearance of plum curculio damage is highly variable and, of all fruit damage rated by IPM specialists, damage caused by plum curculio had the lowest agreement level, i.e., 71.8%. Internal damage to the fruit is caused by larval feeding and exit holes. Most infested fruits drop prematurely in June, though cherries rot on the trees. Larvae release pectic enzymes and cellulase while they feed internally aiding in fruit abscission. Adult feeding may also cause marginal damage to leaves and blossoms.

Management of the Plum Curculio

Insecticide treatments are usually recommended against the adults at petal fall and once or twice thereafter at 10- to 14-day intervals. No resistance to synthetic insecticides has yet been reported for this pest. Alternatives to insecticides are discussed hereafter.

Behavioral Studies

Observations on the behavior of adults, both in the field and in cages, Using Zn^{65} as a marker to track adults has led to the design of better IPM programs for plum curculio. In autumn, most adults labeled with Zn^{65} moved from orchards to surrounding woodlots. After overwintering, the returning plum curculios gradually invade adjacent apple orchards between pink and petal fall, after spending several days on the ground under the perimeter rows of trees, which most of them then climb. From full bloom to 9 days after fruit set, plum curculio adults were found to be active mainly during the night. In field cages, adults labeled with Zn^{65} also showed a similar diel periodicity while foraging on dwarf apple trees. Because adults are most active in the trees at night, it is recommended that insecticide treatments are likely to be most effective if applied during the first hours of darkness.

There have been several attempts to relate adult activity to ambient temperature in order to optimize the timing of insecticide treatments. Two approaches have been investigated: the development of a trap to evaluate adult populations and establish a relationship between population levels to risks and the development of day-degree models to predict the appearance of damage in orchards. Neither of these methods has been used in isolation to manage populations of *C. nenuphar*. A model predicting the nocturnal activity of *C. nenuphar* hourly has recently been developed and is currently under validation.

Treatment of Peripheral Zones of Apple Orchards

The strategy to treat 20 m-wide peripheral zones of apple orchards (when needed) in spring is based on the fact that plum curculio damage is frequently more abundant at this time in peripheral zones, and that during the tight cluster stage most plum curculio adults move only 1–4 m/day when returning to the orchards from their overwintering sites in adjacent woodlots. During this 5–20 day reinvasion period in southern Quebec, petal fall appears as the most appropriate time for a peripheral zone treatment.

Using this approach in a 1.7 ha experimental orchard (with standard-size trees) in Quebec, fruit damage at harvest was reduced from 57 to 2.4%, while reducing the amount of insecticide used by 70%, and the plum curculio adult population by 83%. These results were consistent over a 2-year period in one locality, under high population pressure. The mortality data were based on recaptures of plum curculio adults, radio-labeled with Zn^{65}, that had been released in a woodlot adjacent to an orchard in which the peripheral zones had been treated with insecticides.

Peripheral-zone spraying has been validated in commercial orchards and compared for effectiveness with full-block spraying in four commercial apple orchards in southern Quebec. Plum curculio damage at harvest was less than 0.7 and 0.8% fruit in plots receiving peripheral and full-plot sprays, respectively; and most damaged apples (95%) were found in peripheral zones.

Trapping Methods

The best (although tedious) monitoring method available for plum curculio in commercial orchards still remains careful examination of thousands of small fruit to detect fresh egg-laying scars. In Quebec a threshold of 1% damaged fruit, based on careful monitoring of fruit three times a week, was successfully used for managing localized peripheral zone treatments following full-block treatment at petal fall. A lower threshold and daily monitoring would be required, however, in areas where the pest pressure is very high. Limb tapping as a monitoring technique is not popular with growers because beating sticks damage the trees, and accuracy varies with cultivar, tree shape, time of day and scout experience.

There have been several studies aimed at improving the timing of insecticide treatments by monitoring adult plum curculios with traps designed for other curculionids or with novel trapping methods. Inverted polyethylene funnels have been evaluated by hanging them beneath tree trunks to capture falling adults. Unbaited sticky-coated green plastic spheres (3 and 8 cm diameter) and sticky-coated green thinning apples (3 cm diameter) hung in host trees, PVC pitfall traps placed beneath host trees, 5 cm bands coated with a sticky substance encircling tree trunks, and unbaited and baited (baited with boll weevil pheromone, grandlure) boll weevil traps placed on vertical stakes between woods and commercial orchards have also been tested. However, no plum curculios were captured on sticky bands and very few were captured in pitfall and boll weevil traps. Black pyramid traps placed next to apple tree trunks, originally designed to mimic the visual silhouette of the trunk of a pecan tree and used to monitor pecan weevil, *Curculio caryae*, captured significantly more plum curculios than those traps placed between apple trees, between apple trees and an adjacent wood lot, and between apple trees and an adjacent field.

However, occurrence of plum curculios in these pyramid traps did not coincide with temporal occurrence of ovipositional injury nor did number of adults captured coincide with levels of ovipositional injury, possibly because of abiotic factors. In experiments designed to learn how plum curculios move into host fruit trees, adults dislodged from apple trees tended to walk off a small collecting frame when ambient temperatures were below 20°C, but fly to a host tree canopy or inter-tree space when temperatures were 20°C or above. This indicates that plum curculios are likely to bypass any sort of trap designed to intercept crawling individuals such as black pyramid traps placed next to tree trunks when temperatures are above 20°C. Therefore, traps that capture flying plum curculio adults as they enter the orchard or after arrival in the host tree canopy also have been evaluated. Clear Plexiglas panels have been evaluated for their ability to intercept flying adults. The circle trap consists of a wire screen cage capped with an inverted screen funnel and attached to a limb; it is designed to intercept foraging adults walking on tree limbs or on the tree trunk, and not to attract adults based on stimulating visual cues. A third trap type that has been evaluated in host tree canopies is the branch-mimicking cylinder trap, designed to exploit visual cues provided by an upright twig. So far, none of these unbaited trap types have shown sufficient attractiveness or reliability to replace the visual examination of fruitlets as the recommended monitoring technique. However, addition of attractants to trap types is considered to be the next logical step for their improvement.

Attractants

Numerous species of weevils are attracted to host plant volatiles or specific compounds present in host plant volatiles, including the banana weevil, *Cosmopolites sordidus* (Germar), the cabbage seed weevil, *Ceutorhynchus assimilis* (Paykull), the pea weevil, *Sitona lineatus* (L.), and the red weevil, *Rhynchophorus ferrugineus* F.

Attempts to identify potential attractants for adult plum curculios were first published in the 1920s. It was reported that adult plum curculios are attracted to salicyl-aldehyde early in the season and gallic acid later in the season. More recently, much effort has focused on identification of potential attractants. In the 1980s, fresh apple juice and synthetic apple blossom fragrance were evaluated, and in the 1990s stored apples, fresh apple branchlets, and ammonium carbonate as potential attractants were also evaluated: all proved unsuccessful. Chemically uncharacterized host apple odor from water- and hexane-based extracts was most attractive between bloom and 2 weeks after bloom. Furthermore, volatiles released from punctured plums were very attractive to plum curculios in laboratory bioassays. Specific compounds identified from plum and/or apple volatiles and found to be attractive to plum curculio as evidenced by laboratory and/or field bioassays include ethyl isovalerate, limonene, benzaldehyde, benzyl alcohol, decanal, E-2-hexenal, geranyl proprionate, and hexyl acetate. Because odors of host fruit were significantly less attractive at 4 and 8 cm than at 2 cm from plum curculios, fruit odor-based traps may not be useful in commercial orchards. However, host plant volatiles often synergize or enhance insect responses to sex and/or aggregation pheromones. In the family Curculionidae, male-produced pheromones have been documented in at least 21 species and enhancement of attraction to them by the presence of host plant volatiles have been documented in at least 18 species.

Some antennal sensory structures on plum curculio are similar to pheromone receptors found on related curculionids. Researchers recently isolated and subsequently synthesized an aggregation pheromone from male plum curculios: (+)-(1R,2S)-Methyl-2-(1-methylethenyl) cyclobutaneacetic acid. This pheromone, which they named grandisoic acid, is attractive to both sexes. Attempts to use live adults in pyramid traps were unsuccessful, baited traps being no more attractive than unbaited traps, possibly because of repulsive distress signals emitted by the curculios. However, lures impregnated with a racemic mixture of grandisoic acid have been reported to significantly increase the number of plum curculios trapped in pyramid traps. A two-fold increase in attractiveness when the lure was used in conjunction with small amounts of green leaf volatiles; high amounts showed a repulsive effect. More recently, it has been demonstrated that pyramid and sticky Plexiglas panel traps baited with a combination of grandisoic acid and benzaldehyde and placed close to woods and adjacent to orchards, captured more immigrating plum curculios than grandisoic acid alone or unbaited traps. This combination of attractants has been deployed within apple tree canopies to aggregate plum curculios and to monitor seasonal activity. This monitoring technique is termed a “trap free” approach.

Biological Control

Several natural enemies have been recovered from *C. nenuphar* but none are able to provide an effective alternative to chemical insecticides in commercial orchards. Several nematode species have been tested and found to be effective as larvicides against *C. nenuphar*. In the laboratory, 95% larval mortality was reported at 400 *Steinernema carpocapsae*/larva. At 200–400 nematodes/larva, 73.4% larval mortality was achieved in natural sods. Nematode treatments would also affect other pests, such as the larvae of *Hoplocampa testudinea* (apple sawfly). The application of nematode treatments to the soil would not prevent damage to apples, but would lower *C. nenuphar* and *H. testudinea* populations for the subsequent growing season.

Repeated applications of *S. carpocapsae* to the foliage or aerial parts of apple trees were tested to prevent damage to the fruit. In caged environments, localized application of nematodes at the base of tree trunks significantly reduced adult populations (82–100% mortality).

► Apple Pests and Their Management

References

Chouinard G, Hill SB, Vincent C (1993) Spring behavior of the plum curculio (Coleoptera: Curculionidae) within caged dwarf apple trees. Ann Entomol Soc Am 86:333–340

Lafleur G, Hill SB, Vincent C (1987) Fall migration, hibernation site selection and associated winter mortality of plum curculio (Coleoptera: Curculionidae) in a Quebec apple orchard. J Econ Entomol 80:1152–1172

Racette G, Chouinard G, Vincent C, Hill SB (1992) Ecology and management of plum curculio, *Conotrachelus nenuphar* (Coleoptera: Curculionidae), in apple orchards. Phytoprotection 73:85–100

Vincent C, Chouinard G, Hill SB (1999) Progress in plum curculio management: a review. Agric Ecosyst Environ 73:167–175

Vincent C, Chouinard G, Bostanian NJ, Morin Y (1997) Peripheral zone treatments for plum curculio management: validation in commercial apple orchards. Entomol Exp Appl 84:1–8

Plume Moths (Lepidoptera: Pterophoridae)

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Adult plume moths are generally small, with wingspans of about 2 cm, but range from 6 to 40 mm. They are easily recognized by their characteristic T-shaped resting posture with the narrow forewings held perpendicular to the body and the hindwings tucked under or folded within the forewings. The wings are often divided into lobes, or plumes, with long fringe scales accentuating the feather-like appearance (Figs. 79–81). The fore- and hindwing are typically divided into two and three lobes, respectively, but one subfamily, Deuterocopinae, has one or two additional clefts in the forewing, and the subfamilies Agdistinae and Ochyroticinae have both wings entire. Many species are plain white or mottled gray or brown. Others are more striking, with banded legs, scale tufts at the tibial spurs, and wing maculation that includes clusters of spatulate scales mixed within the linear fringe scales. Worldwide, 1,139 species and 92 genera are reported in the most recent world catalogue, with at least another 300 new species anticipated, especially from tropical regions. The group has been divided into four or five subfamilies by different authors. Genera of the subfamily Platyptiliinae have been recently included within the Pterophorinae.

Morphology and Family Characters

Adults

Aside from cleft wings, the primary defining character for the family, present in all genera and species, is rows of stout sclerotized scales arising from the underside of the hindwing median and cubital veins. These scales were once referred to as androconial scales, but occur in both males and females, and have since been termed venous scales. There are no apparent openings in these scales and their functional significance, if any, is still unknown. The Macropiratidae, generally accepted as the sister taxon to the pterophorids and treated as a subfamily of Pterophoridae by some authors, do not have venous scales. Pterophorid hind legs are proportionally long, most with two pairs of enlarged tibial spurs. The hind legs are not used for grasping but are held against the abdomen or away from the body at an angle similar to most Heliodinidae, Schreckensteiniidae, and stathmopodine Oecophoridae. The abdomen is long and narrow, with scale tufts often associated with the genitalia. Females have an eversible bilobed pheromone gland just above the ovipositor. Many species require dissection and preparation of genitalia slides for determination.

Immature Stages

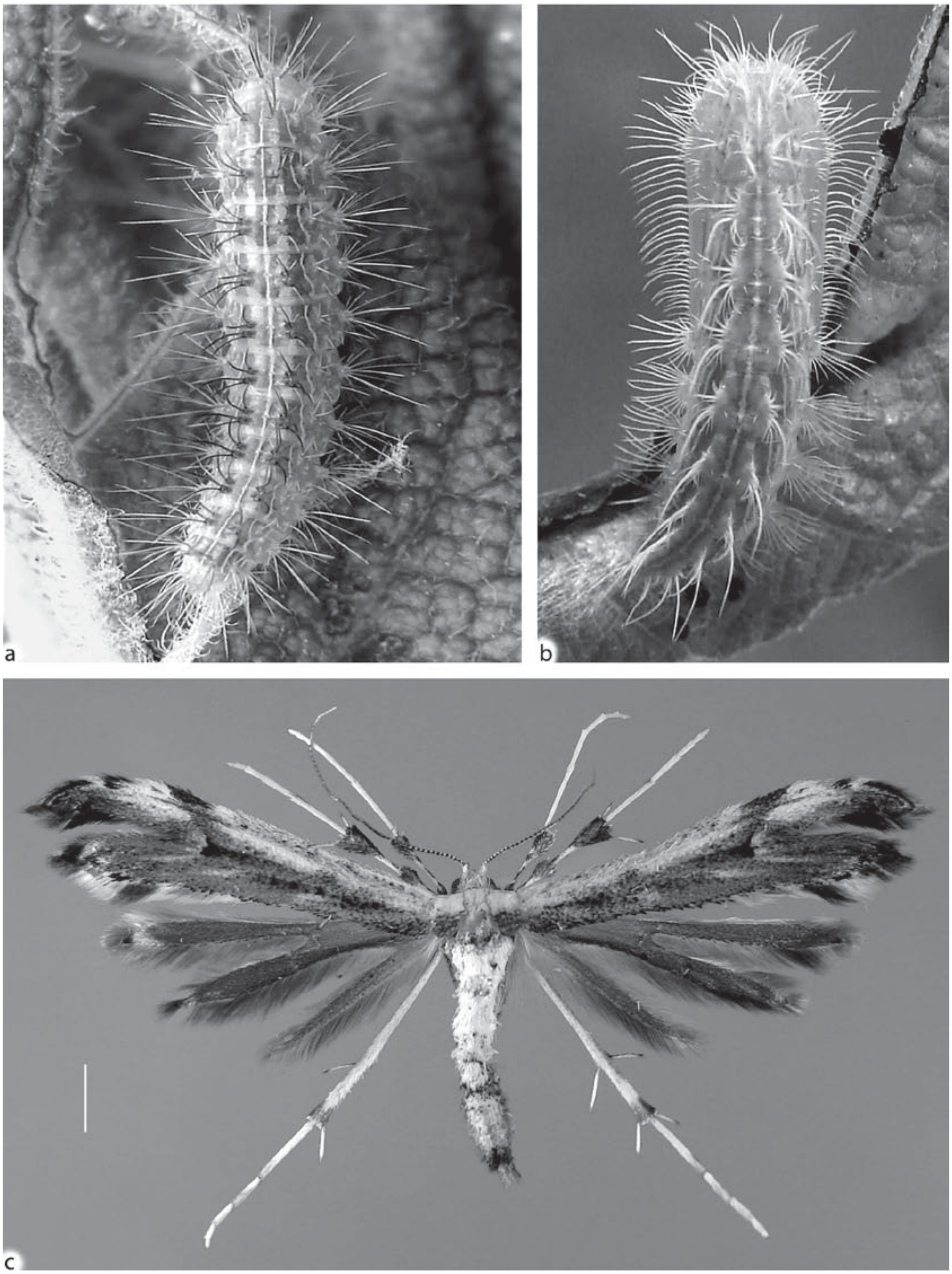
Eggs are oval to oblong, generally under 1 mm in length. The color varies by age and species but is usually white to yellowish or light green and they often appear glossy. The chorion surface is smooth, pitted, or finely reticulated.

Larvae of most species have secondary setae or spinules, subprimary seta L3 present on the prothorax, 2 SV setae present on all three thoracic segments, and crochets on the prolegs arranged in a uniordinal mesopenellipse. The prolegs are usually slender and peg-like, except in some of the borers. Larvae of external feeders are sometimes cryptic, with ingested plant material showing through the cuticle, or fairly easy to spot with contrasting longitudinal bands. The setae tend to be long, both primary and abundant secondary setae often blending in with the host-plant trichomes. Internal feeders are less colorful, either plain or cream-colored or with pink to red markings, with shorter and fewer secondary setae and shorter or reduced prolegs. Some internal feeders have sclerotized anal plates with thorn-like terminal structures. Secondary setae are localized, scattered, or radiate from verrucae or verruca-like tubercles, often with a distinct central primary seta. Setal morphology is diverse and quite remarkable, ranging from simple setae with pointed tips, to modified setae with spiculate or barbed margins, flattened scale-like setae, and apically modified setae with blunt, inflated, capitate, spatulate, tined, or conspicuously forked tips. In some genera including *Buckleria*, *Dejongia*, *Megalorhipida*, and *Trichoptilus*, inflated, or hollow, open-tipped glandular setae exude a viscous, sticky fluid, which accumulates in a droplet at the end of the seta.

Pupae exhibit a variety of shapes and some are fairly colorful. Many appear quite spiny, with secondary setae and tubercles carried over from the larval stage, including lateral verrucae (Fig. 79). In addition, fringes of secondary setae are frequently present along the lateral margin of the forewing and antenna. In several genera, dorsal abdominal tubercles are noticeably enlarged on the third abdominal segment. All pterophorid pupae have the first three abdominal segments fused, making movement only possible below the third segment. Related families, such as Macropiratidae, have the first four segments fused. Most species have two distinct patches of hooked setae or hamuli on the ventral surface of the tenth abdominal segment for anchoring to a silk pad spun by the larva.

Host Plant Associations

Pterophorid larvae feed on various plants representing about 70 different families. They are predominantly associated with the family Asteraceae (Compositae) with more than a third of the recorded hosts belonging to this family. Next to the composites, Lamiaceae are the second most common host family, with the whole order Lamiales including about 23% of the recorded hosts. The family Fabaceae or legumes also includes many hosts, especially in the tropics and subtropics. Other families with several hosts include Plantaginaceae, Convolvulaceae, Vitaceae, Rosaceae, Orobanchaceae,



Plume Moths (Lepidoptera: Pterophoridae), Figure 79 ***Oidaematophorus eupatorii*: (a) larva, (b) pupa, and (c) adult. Line = 2 mm.**

Gentianaceae, Amaranthaceae, Dipsacaceae, and Plumbaginaceae. Certain pterophorid genera are strongly associated with specific host families or genera, while a few, such as the pantropical species *Sphenarches anisodactylus* (Walker), are polyphagous.

Distribution

Plume moths are found in all faunal regions and a range of different habitats extending to arctic and sub arctic zones of Greenland and Iceland, high elevations in the Alps where the genus *Stenoptilia* is diverse, and arid or saline areas where the genus *Agdistis* is well represented. While many species are restricted to certain regions or habitats, others such as the morning glory plume moth, *Emmelina monodactyla* (Linnaeus), are widespread and occur in several faunal regions. Species occurring in tropical and subtropical areas tend to have multiple or continuous broods.

Life Histories, Habits and Behavior

Adults

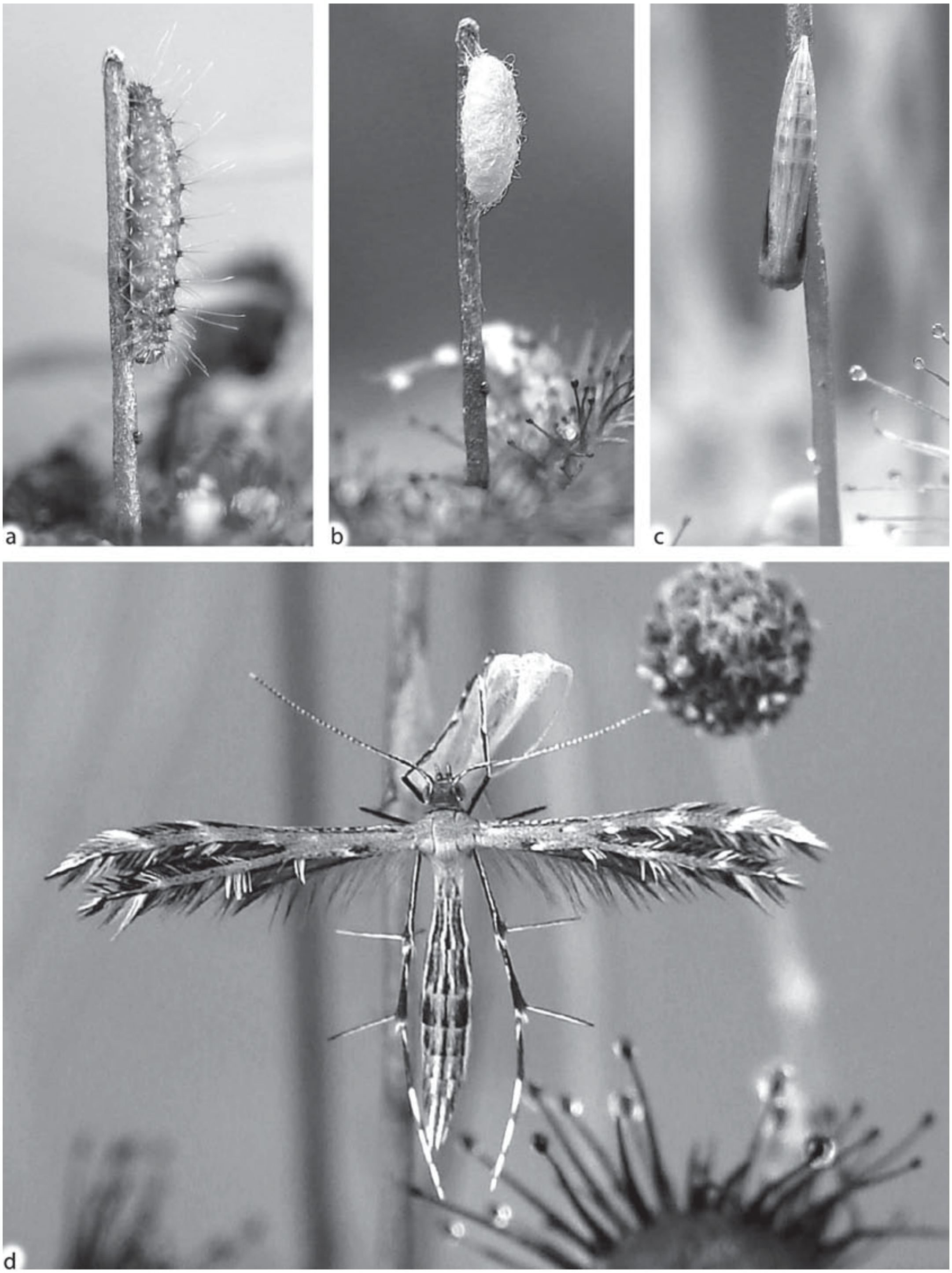
Plume moths typically fly for short distances before alighting and are easily tracked by day or followed with a headlamp at night. Adults are active early in the evening, at night, and may also be collected by sweeping or beating vegetation in shady areas during the day, or collected in the vicinity of larval hostplants. A few species actively seek nectar by day, even in sunlit areas. Both males and females are attracted to lights at night. Eggs are deposited singly or close together in loose groups, usually directly on the hostplant and in specific locations such as tender leaves, flower buds, or shoots where the first instar larvae will feed. In species where first instar larvae overwinter or diapause within the egg chorion, eggs may be placed on persisting structures such as at branch axils of woody stems.

Larvae

Pterophorid larvae exhibit a wide range of feeding habits which vary with hostplant species, growth stage, season, and availability of preferred plant parts. Certain species feed on whatever part of the host is available, while others are specialists, seeking out specific structures such as developing seeds or immature anthers within flower buds. Early instar larvae tend to feed on softer tissues, foliage feeders starting out on terminal shoots before consuming mature leaves. Stem borers such as the golden-rod borer, *Hellinsia kellicottii* (Fish) and the *Baccharis* borer *H. balanotes* (Meyrick) typically feed in shoots or flowers before re-entering the stem or branch lower to the ground, some feeding and hibernating in the lower stem and roots. Two species of *Adaina* are known to produce stem galls. Externally feeding larvae tend to initially resist movement when disturbed while internally feeding species, such as flower and stem borers react more readily when agitated, the stem borers quickly retreating to the lower extent of their burrows. Most are solitary feeders, with only one larva found per shoot, but a few, such as the common nearctic species, *Oidaematophorus eupatorii* (Fernald), are gregarious, with several young larvae webbing together the upper shoot and young leaves of species of *Eupatorium* (Joe-Pye Weed) (Fig. 79).

Sundew Plume Moths

The sundew plume moth (Fig. 80), *Buckleria parvula* (Barnes and Lindsey) (formerly *Trichoptilus parvulus* Barnes and Lindsey, 1921), is one of the most fascinating species because the larvae feed on the carnivorous plant genus *Drosera*. These plants have glandular trichomes that ordinarily trap small insects. Reaching only 8 mm in length, these tiny plume moth larvae ingest the sticky fluid at the trichome tips and will mow down a whole patch of these hairs before feeding on the rest of a leaf. Feeding mostly at night, in addition to leaves, larvae will also eat dead insects trapped by the leaves and crawl up the inflorescence stalks to feed on the flower buds. Larvae may be found resting on the undersurface of the leaves or on the inflorescence stalks during the day but are usually difficult to spot because their reddish color, especially in younger larvae, blends in with the plants (Fig. 80).



Plume Moths (Lepidoptera: Pterophoridae), Figure 80 **Plume moths (Lepidoptera: Pterophoridae): (a) parasitized larva of the sundew plume moth, *Buckleria parvula*; (b) cocoon of *Cotesia* wasp spun by parasitoid larva emerging from the same moth larva; (c) pupa of sundew plume moth 12 h before emergence; (d) newly emerged sundew plume moth adult perching on pupal skin.**

Plume Moths (Lepidoptera: Pterophoridae), Figure 81 Examples of economically important plume moths: rose plume moth, *Cnaemidophorus rhododactyla* (above); artichoke plume moth, *Platyptilia carduidactyla* (below). Line = 2 mm.

While successfully avoiding the peril of the sundew's sticky traps, larvae frequently fall prey to a species of *Cotesia* wasp (Braconidae). A single wasp larva emerges from the final instar pterophorid larva and immediately spins its cocoon, leaving the pterophorid crawling around for hours before it finally expires. In contrast to the moth larvae, the white cocoons of the parasitoid larvae are easily spotted on the *Drosera* leaves or inflorescences, and persist long after the wasp emerges after a pupal stage of about 6 days. Several spent cocoons may be found on a single plant. In some populations more than half the pterophorid larvae are parasitized.

The plume moth larvae that manage to avoid the wasps pupate on the inflorescence stalks or on nearby blades of grass and in this particular genus, are always positioned with the head facing down. The pupa is light green, changing to yellowish-tan and brown before emerging after up to 11 days. The newly emerged moth clings to the pupal skin while the wings, at first drooping at an angle, expand and are held fully erect, perpendicular to the body.

Buckleria parvula is found in the southeastern United States, with larvae collected from May to October on several different species of sundews. These plants grow in damp areas of pine flatwoods, bogs, lake shores, seasonal ponds, and drainage ditches with nutrient poor soil. Four other species of sundew moths are known, *B. paludum* (Zeller) from the Palearctic and Oriental Regions, *B. girardi* Gibeaux and *B. madecassea* Gibeaux from the Ethiopian Region, and *B. brasilia* Gielis from the Neotropical Region.

Economic Species

Most plume moths infest plants of little economic or cultural significance but a few are pests of crops, ornamentals, or are of value for the biological control of nuisance weeds. The artichoke plume moth, *Platyptilia carduidactyla* (Riley) is a well known pest of the globe artichoke, *Cynara scolymus* (L.) (Fig. 81). Larvae feed in the stems, shoots, and developing flower heads of artichoke in California, as well as native thistles throughout much of the Nearctic Region. Studies of the male calling pheromone produced by adult females have been an important component in control applications including traps for monitoring populations, mating disruption, and mass trapping. Also in the Nearctic Region, the grape plume moth, *Geina periscelidactyla* (Fitch), is a minor pest of cultivated grape, feeding and webbing together young leaves and shoots. This species is more commonly found on wild than cultivated grape species. *Geina sheppardi* Landry and *Sphenarches ontario* (McDunnough) also feed on certain species of wild grape, the larvae of both feeding on the inflorescences.

Some ornamental plant pests include the snapdragon plume moth, *Stenoptilodes antirrhina* (Lange) on *Antirrhinum*, the geranium plume moth, *Amblyptilia pica* (Walsingham) on *Pelargonium*, and the calendula plume moth, *Platyptilia williamsii* Grinnell on marigolds (*Calendula* spp.). Larvae of the rose plume moth (Fig. 81), *Cnaemidophorus rhododactylus* (Denis & Schiffermüller) feed on leaf shoots and flower buds of cultivated roses in temperate areas of the Palearctic and Oriental Regions. It was introduced from Europe to the northeastern United States sometime in the early 1800s. The wing maculation and banded legs of the adults make this one of the most attractive species, despite its minor pest status. The first instar larvae have the interesting habit of not feeding upon hatching but spinning tiny spherical silk hibernacula in which they overwinter.

Several pterophorids have been investigated as potential biological control agents of various weeds. Two European species have been introduced to Australia, *Wheeleria spilodactyla* (Curtis) to control horehound, *Marrubium vulgare* L., and *Platyptilia isodactyla* (Zeller) to control tansy ragwort, *Senecio jacobaea* L. *Hellinsia balanotes* has also been introduced to Australia from the United States for control of *Baccharis halimifolia* L. In Hawaii, *Hellinsia beneficus* (Yano & Heppner) was introduced from Mexico to control *Ageratina riparia* (Regel) R.M. King & H.Rob. The lantana plume moth *Lantanophaga pusillidactyla* (Walker) was likewise introduced from Mexico to control *Lantana camara* L. in Hawaii as early as 1902. A European species, *Agdistis tamaricis* (Zeller) is under consideration as a potential control agent of saltcedar, *Tamarix ramosissima* Ledeb. in the southwestern United States.

► Butterflies and Moths
► Insectivorous Plants

References

Arenberger E (1995) Pterophoridae. In: Amsel HG, Gaedike R (eds) Microlepidoptera Palaearctica 9. Goecke & Evers, Keltern-Weiler, Germany, 411 pp

Arenberger E (2002) Pterophoridae, 2. Teilband. In: Amsel HG, Gregor FG, Reisser H (eds) Microlepidoptera Palaearctica 11. Goecke & Evers, Keltern-Weiler, Germany, 287 pp

Gielis C (1993) Generic revision of the superfamily Pterophoroidea (Lepidoptera). Zoologische Verhandelingen Leiden 290:1–139

Gielis C (2003) Pterophoridae & Alucitoidea. World Catalogue of Insects 4: 1–198

Gielis C (2006) Review of the Neotropical species of the Family Pterophoridae, part I: Ochyroticinae, Deuterocopinae, Pterophorinae (Platyptiliini, Exelastini, Oxyptilini) (Lepidoptera). Zoologische Mededelingen Leiden 80:1–290

Matthews DL (2006) Larvae and pupae of Nearctic Pterophoridae: a synopsis of life histories, morphology, and taxonomy (Lepidoptera: Pterophoroidea). Unpublished Ph.D. Dissertation, University of Florida, Gainesville, FL, 959 pp

Matthews DL, Lott TA (2005) Larval hostplants of the Pterophoridae (Lepidoptera: Pterophoroidea). Mem Am Entomol Inst 76:1–324

Plumose

Feather-like structure with a single thick stem and numerous parallel branches. This term usually is used to describe the antennae of Lepidoptera.

► Antennae of Hexapods

Plutellidae

A family of moths (order Lepidoptera). They commonly are known as diamondback moths.

► Diamondback Moths
► Butterflies and Moths

Poduridae

A family of springtails (order Collembala). They commonly are known as water springtails.

► Springtails

Poikilothermic

Cold-blooded animals; animals (including insects) that lack an internal temperature regulation system, and so tend to have body temperatures that mirror the temperature of their environment. Poikilothermic animals actually use behavior and heat generated by muscles to adjust their temperature to some degree (contrast with homeothermic).

Polar Filament

A hollow, thread-like organelle associated with a microsporidian spore that extrudes, and allows the sporoplasm to pass to the exterior and to inoculate a cell.

Pollen Basket

A specialized scopa, or pollen holding apparatus, found in bumble bees and honey bees. The pollen basket consists of the broad, concave hind tibia surrounded by a fringe of long hairs. *A. corbicula*.

Pollenose

Covered with a loose, dusty yellow material resembling pollen, and which can be rubbed off the surface of an insect.

Pollen Pot

A container made from soft cerumen by stingless bees, and used to store pollen.

Pollen Rake

A comb-like row of bristles at the tip of the hind tibia of bees.

Pollination and Flower Visitation

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Insects are the most common and abundant pollinators of flowering plants, far surpassing the other winged pollinators, the birds and bats. Other insects (anthophiles) visit flowers but do not necessarily pollinate them. The history of the relationships between insects (both pollinators and anthophiles) and flowers is long and varied. Their modern-day importance in ecosystem functioning and agricultural production has made them the subject of numerous scientific studies.

Evolutionary Overview

The relationships of insects and the sexual reproductive organs of plants may be as ancient as the insects and terrestrial plants themselves. Such relationships probably preceded pollination to a time before pollen existed. The first terrestrial plants produced unicellular spores that may have been food for the first terrestrial insects, probably Collembola. Thus, some 400 million years ago in Devonian time, *Rhyniella* (Collembola) and its relatives may have consumed the spores of *Rhynia* and its relatives (primitive vascular plants known only from fossils). Other arthropods have been found in association with the sporangia of plants of that time also. By the time the Carboniferous forests dominated major parts of the globe, insects were well represented in the fauna. Several extinct orders are known to have had elongated mouthparts, reminiscent of those associated today with insects that suck liquids from tubular structures, such as flowers. Moreover, spores (microspores) have been found associated with those insects, particularly on their mouthparts and their wing bases. Reproductive organs of the plants of the Carboniferous, and earlier, had structures (bracts) that formed tubes leading to the micropylar droplet (the germination medium for the microspores) above the megaspore retained on the parent plant. By mid-Mesozoic, some cycadoid gymnosperms appear to have had apparently showy structures embracing the sexual sporangia. Thus, a firm trend towards the insect-plant mutualism of pollination seems to have roots extending into the past well before the advent of the Angiospermae (the flowering plants), a Cretaceous phenomenon of some 160 million years ago.

Insect pollination is generally thought of as being associated with flowering plants, Angiospermae, but it is now realized that most extant Cycadaceae (one family of the non-flowering Gymnospermae) seem to be pollinated by insects also. Both groups of plants produce pollen (i.e., microgametophytes of two or three cells) that must move from the microsporangia to the megasporangia, in which fertilization of ovules takes place, followed by embryogenesis, seed development, and fructification. Which insects were the first pollen vectors (i.e., pollinators) is a matter of debate. Both Diptera and Coleoptera have been suggested (reviewed by Labandiera and Bernhardt, respectively). Perhaps there is no reason to assume that the two suggestions are mutually exclusive.

Within Diptera, short-horned flies are noted having tubular mouthparts that fit with feeding at flowers. Coleoptera as early pollinators are thought to have been associated with heavily constructed flowers (such as those of Magnoliaceae, the magnolias) in which they fed on floral tissues (tepals and ovaries) and pollen, spreading pollen between flowers by "mess and soil." Nowadays, Diptera, Coleoptera, Hymenoptera, and Lepidoptera are the most conspicuous and well-known of pollinators and anthophiles (flower visitors that are not necessarily pollinators). These orders and several minor orders associated with anthophily and pollination are discussed below (Taxonomic diversity).

The details of how flowers attract insects are discussed under "Floral advertising." The benefits that anthophiles reap from flowers (pollen, nectar, and other foods, oviposition sites, mates, and comfort) are discussed under "Floral rewards." Flowers and their symbiont insects comprise evolving and functional ecosystems in a complex interplay of mutualisms and competition (community and co-evolutionary ecology) that are becoming recognized, along with biological diversity, as being crucial to conservation.

Taxonomic Diversity

The Hymenoptera are well known as flower visitors and pollinators, primarily because of the bees (Apoidea) (Fig. 82), which are thought to have co-evolved with reproductive structures of plants, especially flowers. They are adept at handling flowers, gathering pollen (mostly as provisions for their brood) and imbibing nectar. Their specialized, plumose body hairs entrap pollen as they move from flower to flower so that they are effective pollen vectors and pollinators. Honeybees and bumblebees are quick students of floral colors, shapes, and complexity and are efficient foragers. Some bees have special relationships with oil-providing, and gum-providing flowers. The closely related Sphecidae are mostly predatory, but like other families of wasps (Pompilidae and Vespidae), often are seen at flowers feeding mostly on floral or extrafloral nectar. The Masaridae (Vespoidea) are almost all vegetarian and are especially associated with anthophily. The ants (Formicidae) also may frequent flowers. There are only a few examples of ant pollination, but their association with flowers and

Pollination and Flower Visitation, Figure 82 **Honeybee, *Apis mellifera*, a common daytime visitor of flowers (photo Andrei Sourakov).**

extra-floral nectaries often protects the flowers and seeds from predation. Most other families in the suborder Apocrita are parasitoids. There are many examples of these kinds of wasps feeding from nectar at flowers. Because they mostly have unspecialized and short mouthparts, they are found mainly on open-bowl shaped flowers with exposed nectar. Indeed, floral nectar may be a crucial resource to fuel their activities, especially as young adults that have not yet found hosts or mates. Among the herbivorous families of Apocrita are the Cynipidae (the gall wasps) and several species of seed-eating and gall-forming Chalcidoidea. Notorious among the chalcidoids are the Agaonidae, the fig wasps, which have tightly co-evolved relationships with *Ficus* species (figs). The wasps oviposit in the enclosed inflorescence (flower). The larvae then mature as the fig inflorescence ripens into a complex infructescence. The newly emerged adult female wasps collect pollen in specialized pouches and seek out new inflorescences in which to lay their eggs. Pollination of the fig inflorescences occurs as a byproduct of the reproductive behavior of the wasp species.

Among the Symphyta (the other suborder of the Hymenoptera which includes the sawflies), anthophily is less well studied. They sometimes are found on flowers, often well dusted with pollen, and feed on nectar. Some species seem to be associated with pollination, especially of orchids in Australia.

The Diptera are highly diverse as flower visitors. Many families of long-horned flies (Nematocera) derive their carbohydrate nutrition from feeding at flowers. This habit is especially well studied in mosquitoes (Culicidae). Males feed on floral nectar for fuel in swarming flight, and females may feed on nectar prior to searching for mates and blood. Some orchids are pollinated by mosquitoes. The idea that blackflies (Simuliidae) are pollinators of blueberries (*Vaccinium* spp.) is not correct, but nectar feeding is known in this group. Nectar feeding and pollination is attributed to most nematocerous families, especially in relation to floral mimicry. Some plant groups, notably Araceae and Aristolochiaceae, attract flies by scents and colors that mimic such fly-attracting substrates as dung, carrion, musk, and fungi. Among the midges (Ceratopoginidae) are a few specialized species that bite open pollen grains to feed. Cacao is pollinated by midges. Among short-horned flies (Brachycera) there are also many flower visiting species. Particularly interesting are the long-tongued Tabanidae (horse flies) and Nemestrinidae (tangle-veined flies) of southern Africa. Some species have highly specialized pollinating relationships with plants in the iris family (Iridaceae). The flower flies, or hover flies (Syrphidae), are probably the best known of the Brachycera for their close associations and pollinating activities with a wide variety of plants. Among the Diptera, the 50 families of acalypterate muscoids are poorly represented as flower visitors, with records associated with only the pomace flies (Drosophilidae) for which yeasts and floral nectars are parts of the symbioses. The calypterate muscoids generally are well known as flower visitors. Their roles as pollinators have been explored in various plants, including the umbels (Apiaceae), and especially the mimetic Araceae, Aristolochiaceae, and Rafflesiaceae.

Almost all Lepidoptera visit flowers and imbibe nectar. The exceptions are those that do not feed as adults (some microlepidoptera) and perhaps some of the specialized moths that feed on animal secretions, and even blood. Some Micropterigidae feed directly on pollen. Also, a few butterflies (for example, *Heliconius*, *Parides*, *Battus*) use pollen as food. They place pollen into floral nectar and make a "pollen soup." They then imbibe the nectar enriched with the eluents of the pollen. Most butterflies and moths have elongated, tubular mouthparts and imbibe nectar that is dilute (less than 45% sugars). One of the longest proboscides is that of *Xanthopan morgani* f. *praedicta* (Sphingidae), the existence of which was predicted on the basis of an orchid from Madagascar, *Angraecum sesquipedale*, with its 25–30 cm nectariferous spur. Some moths (for example, *Plusia gamma*) secrete saliva and dilute heavy nectar at open-bowl shaped flowers.

Moths, particular Sphingidae, hover while feeding at flowers and have high energy demands. The flowers they visit and pollinate tend to be presented with outward facing tubes (like trumpets) and secrete copious nectar. They are also often heavily scented. The nectar of flowers visited by hawkmoths are weak in amino acids. It has been suggested that too much amino acids ingested with large amounts of nectar could be toxic. Many pestiferous moths feed extensively at flowers, but their activities, being nocturnal, are not well understood. The army cutworm moth (*Euxoa auxilliaris*) is migratory from the U.S. plains to the Rocky Mountain alpine ecosystem. In the summer, the moth does not aestivate (become quiescent), but feeds extensively on floral nectar, converting the sugars to fat before return migration and sexual maturation. The resident moths of the same family (Noctuidae) do not show that pattern of activity and reproductive diapause.

Some special relationships have co-evolved between Lepidoptera and flowering plants. One of the best studied is that between *Yucca* spp. (Liliaceae) and its pollinating moths (*Tegeticula*). These moths gather pollen in their mouthparts and carry it between flowers of different plants, stuff the pollen mass into the stigma of the flower, and then lay their eggs in the floral ovary. As the ovary matures, the larvae eat some of the developing seeds. There are other similar, but less well appreciated examples (for example, *Hadena bicruris* and its oviposition behavior on *Silene alba*).

Butterflies are diurnal and less energy demanding than moths in their flower visiting. Many of the flowers with which they are associated have tubular corollas that flare and provide landing platforms for the settling butterflies. The flowers are often brightly colored, sometimes distinctly reddish, and mostly not strongly scented. Butterflies often forage sporadically, visiting flowers that may be widely spaced and not visiting those along the way. Pollination by butterflies has been rarely proven to be important, mostly because specific studies have not been made. For migratory butterflies, especially the monarch (*Danaus plexippus*), considering the importance of nectar corridors is part of conservation efforts.

The Coleoptera is a hugely diverse order and members of about 30 families have been recorded from flowers. Members of the suborder Adephaga (i.e., Caraboidea) are not flower visitors, although a few records have been made. Among the suborder Polyphaga, flower visiting is widespread among the families, but not in any apparently systematic way. Among the Hydrophiloidea and Staphylinoidea, anthophily is recorded only for a few Hydrophilidae (or Hydraenidae) and Staphylinidae and Ptiliidae, respectively. The Scarabaeoidea has anthophiles in the Scarabaeidae, with pollination relationships ascribed to a few species. There are a few records of anthophiles in the Elateroidea (Elateridae), the Buprestoidea (Buprestidae), the Cantharoidea (especially in the Cantharidae, and a few in the Lycidae) and in Dermestoidea (Dermestidae). In the Cleroidea, flower visiting is well represented in the most diverse families (Cleridae, Melyridae). Among the wide array of families in the Cucujoidea is a smattering of anthophilous families (Nitidulidae, Rhizophagidae, Coccinellidae, Lagriidae especially some Scraptiidae, Mordellidae, Oedemeridae, and few Anthicidae). The Chrysomeloidea has anthophily recorded from a few Cerambycidae, Bruchidae, more Chrysomelidae, and many Curculionidae. Only the Melyridae, Mordellidae, and Oedomeridae seem to be exclusively anthophilous, however, the nature of the relationships of those beetles with flowers is mostly unknown.

A wide variety of other taxa use flowers in various ways. Collembola have been recorded from flowers from all over the world. They seem to be mostly pollenophagous, but some feed on nectar. There are a few records of Plecoptera (stoneflies) on flowers. Among the Orthopteroid orders, flower visiting is known, but rarely studied. Some Dictyoptera visit flowers. For example, cockroaches may be found in the inflorescences of palms and may be involved in some pollination in the canopy of tropical forests. Some mantids use flowers as sites from which to ambush prey and some have floral-mimicking coloration. Dermaptera (earwigs) often are found in flowers, but seem to be mostly destructive, feeding on the stamens and pistils. Among the Grylloptera, some long-horn grasshoppers (Tettigoniidae, especially *Conocephalus*) also feed destructively on flowers. The Australian Zaprochilidae have elongated heads and prognathous mouthparts that suggest floral feeding. The Orthoptera proper (short-horned grasshoppers) are not often found in flowers, but some, as nymphs, may feed destructively there.

Various Hemiptera sometimes are encountered feeding in flowers, notably Nabidae, Miridae, Lygaeidae, Coreidae, Pentatomidae, and Phymatidae. Among the phymatids, both nymphal and adult ambush bugs are well known to take prey at flowers. The way they choose which flowers to use seems to reflect ease of movement, alate adults being less choosy than strictly ambulatory nymphs. The importance of various predatory Hemiptera in biocontrol suggests that much more needs to be known about their nutritional needs outside their prey. Among the hemipterans, flower visiting is not well known, but some mimic flowers or inflorescences in group activity (for example, Flattidae).

The thrips (Thysanoptera) often are found in flowers. Some have specialized asymmetrical pairs of mandibles that allow them to crush pollen grains. Thrips can build up huge populations in flowers, and may be pestiferous in the horticultural trade. They are invoked as pollinators in some special situations. In the Malaysian forest trees (Dipterocarpaceae), the development of thrips populations has been associated with multi-specific plant flowering phenology, sexual reproductive strategies (breeding systems), and pollination.

The potential for lacewings (Neuroptera) for biocontrol of pest insects has stimulated research into their flower visiting activities and nutritional needs. It seems that nectar or pollen feeding, or both, is important for their longevity and persistence.

Floral Advertising

Flowers can be considered as advertisements for plant sex. Primarily, they exploit the senses of vision and smell, but at close range and on flowers, taste and touch come into play. Color vision is general in insects. It is like color vision in human beings because, in most species studied, three primary colors are involved (trichromacy) but, unlike in human beings, the primary colors are ultraviolet (UV), blue (B), and green (G) rather than B, G, and red (R). Some insects seem to have tetrachromatic (UV, B, G, R) color vision, while others are deuteranopes (UV, B+G) Most of our understanding of color vision in insects comes from the western honeybee (*Apis mellifera*). The neural coding is also different from our own, so that brightness is not important and the green receptor is involved in other visual tasks as well as resolving colors. Thus, in studies of colors of objects of interest to insects, the whole insect visual spectrum must be considered, not just UV and not just the B and G parts of the spectrum. Many flowers show UV patterns that are invisible to people. In general, more architecturally complex flowers with hidden rewards and sexual organs tend to have color pattern guides (UV or not) more often than simpler, open flowers.

It has been assumed that floral color and size act as long-distance attraction for floral visitors. However, recent research has shown that discs of about 8 cm diameter become visible to honeybees only at a range of less than a meter. Moreover, the colored discs must have color and green contrast with the background to be even that visible. Without green contrast, the distance for detection declines to a few centimeters. The green receptor is involved in the detection of the edges of shapes, movement of objects, shape recognition, and such tasks as landing after flight. Another component of flower form that has been investigated recently is the importance of the dissectedness of the outline. It was assumed that dissectedness of the outline added attractiveness to flowers, but circular targets are detected over longer distances than those of the same diameter with variously dissected outlines.

Flowers produce a wide variety of scents. Some are mimetic, as noted above under Diptera and Coleoptera as flower visitors and pollinators. "Heavy" floral scents are associated with flowers that bloom and are pollinated at night, mostly by moths. Those scents are assumed to attract pollinators over long distances, and the highly developed olfactory sense of the moths is well known. Diurnally blooming flowers tend to have more delicate "floral" scents. These seem to be used by floral visitors at close range. Different parts of flowers emit different smells that are used in orientation. Once the visitor has landed, the definition of scent and taste becomes blurred, as antennation allows the visitors to follow odor/taste guides on the surface of the floral parts.

Coupled to the subtleties of floral size, shape, color, color patterns, scent, and odor/taste guides may be the role of micro-textural features of the floral epidermis. Insects, at least bees, have been shown to use and to learn "micro-Braille" while foraging. The features on the floral surface match the scale of antennal sensilla in size and spacing.

Floral Rewards

Pollen is probably the most important of floral food rewards for anthophiles, but may have been coupled with sugary drinks (nectar) since the association of spores and micropylar droplets in the Carboniferous. Pollen of entomophilous (insect-pollinated) plants is generally highly nutritious. Depending on the plant species of origin, it contains variable amounts of protein (even up to about 60%), many amino acids (including those essential for animal nutrition), lipids (up to about 20%), starch (up to 22%) and most minor, but important, nutrients such as vitamins, sterols, and minerals. Entomophilous pollen is also characterized often by external ornamentation (spines in Asteraceae, Cucurbitaceae, Malvaceae, Cactaceae; tubercules and ridges) and by having an external, oily pollenkitt. Both features enhance adherence to the bodies of pollinating insects for dispersal. Pollen is ingested whole by most insects, and the nutritive protoplast is digested by enzymes that diffuse in so the nutrients diffuse out into the gut lumen. There are some insects that chew or bite pollen grains to extract the nutrition, among them *Atrichopogon* (Diptera: Ceratopogonidae), various thrips (Thysanoptera), some beetles, and Collembola. Pollen ingestion by some Diptera and Coleoptera is associated with maturation of their sexual organs, especially of the ovaries and ova in females. During nesting by bees, pollen is gathered by females and stored as "bee bread" or larval food. The females in most families have specialized pollen collecting (parts of the legs) and carrying organs (scopae, corbiculae). Most female solitary bees lay their eggs on a loaf of bee bread within the cells of the nests.

Nectar is a sugary liquid secreted by various parts of plants, including flowers. Floral nectar is comparatively well studied and is the primary fuel for flight in many insects. The energy content (5 cal/mg of sugar) of nectar depends on the volume produced and its sugar concentration. The concentration of sugars reflects the capacities of various insects to imbibe liquids of different viscosities. The nectar imbibed by long-tongued insects such as Lepidoptera, some Diptera (e.g., Nemestrinidae, some Tabanidae, Bombyliidae), and some Apoidea (Bombinae, Euglossinae) is usually watery (around 30% sugars), whereas that taken by short-tongued and lapping insects (e.g., Muscidae) may even be crystalline. The main sugars (sucrose (a disaccharide), glucose, and fructose (monosaccharides)) vary with plant family and type of pollinator. Some generalizations can be made about pollinator type and the ratio of sucrose to fructose and glucose in nectar. If this ratio is high, pollination by insects with short proboscides (Diptera, short-tongued bees) is expected; if it is low, pollination by insects with long proboscides (Lepidoptera, long-tongued bees) is expected. Floral nectar contains minor constituents, among which amino acids are the best understood. Floral nectars consumed by insects (e.g., many Diptera, bees) with nitrogen-rich diets tend to have lower titers of amino acids than do those consumed by insects that do not feed on nitrogen-rich diets (e.g., most Lepidoptera, long-tongued Diptera). The role of amino acids in nectar in the nutrition of anthophiles has been investigated rarely, but it is known that some insects have greater longevity when allowed to feed on nectar rather than on syrup of the same sugar concentration. Little is known of the other minor constituents, save their presence. Lipids often are accompanied by antioxidants (for example, ascorbic acid) and may be involved in reducing evaporation rates of water from exposed nectars.

Among the Apoidea (especially *Centris* species in the subfamily Anthophorinae) are specialists that collect floral oils from the flowers of certain families of plants, such as Malpighiaceae and Krameriaceae. These bees use the oils for provisioning their nests and collect it on specialized tarsal brushes. Many bees collect resins and gums, but some flowers provide it as a reward for their pollinators. *Dalechampia* species and *Clusia* species are well-known provenders of gums that the bees use in nest construction. Among the Euglossinae (Apidae) are species in which male bees collect floral scents, especially of orchids, that they use as olfactory attractants for mates in lekking behavior.

Other Floral Rewards: Heat, Floral Tissue, Sex

Some blossoms become heated. Among the mimetic Araceae, such as jack-in-the-pulpit and skunk cabbage, endogenous heat production is well known. The pollinators of these plants are various flies and beetles that become temporarily trapped in female phase blossoms that become male as the stigmas senesce and anthers shed pollen, which is when the pollinators are liberated. The heat helps drive off the mimetic scents (dung, carrion, musk), speed floral and insect development, and bring the pollinator sexes together for mating. Other flowers trap the heat of the sun by various means. Parabolic diaheliotropic (sun-following) flowers may warm their insect visitors by six or more degrees Celsius. Such heating improves speed of mobility, and, it seems, optical and other neural processing. Catkins of willows (*Salix* spp.) act as hairy heat traps and offer shelter and warmth to small insects, such as non-biting midges (Chironomidae) in the Arctic. Some insects, especially male bees, sleep in flowers. The males of the hoary squash bee (*Peponapis pruinosa*: Anthophorinae) sleep, often in small bachelor parties, in the spent flowers of squash and pumpkin (*Cucurbita* spp.) that open and close in a single day.

A wide variety of insects feed on floral tissues, apart from pollen. Many, for example, caterpillars, maggots, earwigs, thrips, and some beetles, probably are not pollinators, but some are. Notorious are the highly mutualistic interactions between figs and fig-wasps, yucca and yucca-moths, globeflowers and the anthomyiid flies, oil palms and its pollinating weevils, and some special fly-pollinated flowers (for example, *Siparuna* species (Monimiaceae)). The flowers, mostly the female parts and resulting fruit (except in oil palm and *Siparuna*), serve as oviposition sites and for brood food. The adult insects are the pollinators. Some thrips breed in flowers, becoming serious horticultural pests in some situations. Other sorts of floral tissues seem to be fed on by some anthophiles and pollinators. Special structures, food bodies and staminodes with pollen substitute (for example, in Melastomataceae) are eaten or collected by various insects, including bees.

There are a few flower visiting arthropods that use flowers as sites for prey capture. Well known are some species of crab spider (for example, *Misumena* species (Thomisidae)) and ambush bugs (*Phymata* species (Reduviidae)). These predators choose their ambush sites according to energetic constraints of changing site. For example, adult female crab spiders that walk slowly from place to place are most careful in choice, immature and apterous bugs are also fastidious, but adult alate ambush bugs choose quickly and switch sites readily. Some tropical mantids are cryptically colored to match the flowers they use. Some crab spiders may be able to change color to match their floral host.

Flowers may be mating sites for some insects, as recorded for a few species of bees. Some insects, such as the males of some orchid bees (*Euglossa* spp. (Euglossini)) and some flies collect floral scents that become attractive to mates.

Energetics: Time and Motion

A great deal has been learned about optimal foraging from insect and flower relations. Bees, especially bumblebees (*Bombus* spp.), are central place foragers (i.e., they forage from a home, the nest), are conspicuous and quite easily followed. Their foraging illustrates the range of behaviors that exemplify maximizing energy gathering while minimizing energy expenditure. Foraging bumblebees tend to follow the same general path from one trip to the next. Thus, they are familiar with their area. They also tend to visit the same patches of flowers on sequential trips, a behavior sometimes called "trap-lining." Within a patch, bumblebees usually show a "forwarding" path, but this may involve sharp turns to left or right and visiting mostly "next-closest" blooms if resources present are relatively abundant and rich. If resources are sparse, the bees tend to veer back and forth much less between sequentially visited blooms, and often overfly the "next closest." Thus, in a rich patch they visit more and stay longer, but in a poor patch, they sample and depart quickly. On the blooming plants, the bees tend to act systematically. For example, on tall inflorescences, they start at the lowermost open flowers and work upwards. The energetic implications are for efficiency, crawling vertically instead of flying, and flying down between adjacent inflorescences. Mostly, such inflorescences have female-phase older flowers and male-phase younger flowers (protandrous flowers), with more dilute nectar below and less, but sweeter, above. Most of the studies that exemplify those movement patterns have been made in meadow-like situations. On trees, with vertically arranged arrays of blooms, the same within-patch pattern has been noted. However bees treat inflorescences close to each other as a unit and continue upward but they treat separated (more than 10 cm apart) inflorescences as individuals and so show a generally descending overall direction. The implications for pollination of trees remains to be explored.

Flowers are variable in their anatomical complexity. Thus, simple, open-bowl-shaped flowers are easily exploited, but complex flowers with intricate mechanisms and hidden rewards require skill on the part of the pollinators to use. Experiments with bumblebees have shown that learning to manipulate complex flowers with skill, accuracy, and speed requires learning and an investment of time. That investment can pay off through the much greater amounts of reward in complex flowers versus simple ones. Of course, if too many bees invest in the learning when there are few flowers, loss in profitability from investing in learning may result.

The models of optimal foraging by bumblebees can be extrapolated to predator and prey interactions, but blossoms do not try to escape (quite the contrary, they advertise their presence), worker bees forage for the colony rather than for themselves, and their demise as individuals is not as drastic a loss for the next generation as in non-eusocial animals. Nevertheless, in such flower-visiting animals as sphinx moths and hummingbirds, the similarities in foraging patterns are remarkable. Butterflies tend to forage in a much more haphazard fashion, sipping nectar at flowers as they need energy (Fig. 83).

Floral specialization and constancy in the broad sense include the tight interspecific interactions between specialized pollinators and their partner flowering plants (for example, *Yucca* and *Tegeticula* (Lepidoptera), *Ficus* and *Agaonidae* (Hymenoptera), oil palm and *Elaeidobius* spp. (Coleoptera), *Siparuna* and Mycetophilidae (Diptera), and the myriad bees and flower specializations. The terms mono-, oligo-, and polylectic (or -tropic) refer to anthophiles that use one, a few, and many

Pollination and Flower Visitation, Figure 83 Moths such as this sphinx moth visit flowers at dusk or during the evening (photo R. J. Barnas).

floral resources. The equivalent botanical terms for flowers are mono-, oligo-, and polyphilic. Entomologists and naturalists have made observations of apparent, but unexplained, floral specializations in other groups of insects in which generalist anthophily might be otherwise expected (e.g., in Syrphidae (Diptera), other Diptera, and some Coleoptera). Apparent floral "specialization" (mono- or oligolecty) may be thrust upon anthophiles by lack of a diversity of flowers upon which to forage. Presented with more kinds of flowers, such anthophiles would presumably expand their foraging base. Constancy is a term best reserved for oligo- or polyleges that restrict their visits to the flowers of one species of plant, even when others are in bloom. Such constancy is well explored by studies of social bees (Apidae) in which individuals from a single colony may be constant to the flowers of a particular plant for a short period before switching to another, while other individuals from the same colony may be constant to yet a different species, and so on. The benefits of constancy are clear from the viewpoint of intraspecific pollination, and from the anthophile's viewpoint, in efficiency of learning to forage quickly and accurately. Such foragers, either as colonies as in honeybees, or as individuals, have species of plants that can be called "majors" and "minors" so that they sample the floral resources in their areas and can switch as resource availability, type or quality change in the habitat or according to the colonies' needs (Fig. 84).

Pollination and Flower Visitation, Figure 84 Scanning electron micrograph of pollen of the oil palm (*Elaeis guineesis*) on the snout and compound eye of a weevil, *Elaeidobius kamerunicus*, the major pollinator of oil palm.

Ecosystems, Community and Co- Evolutionary Ecology

Various ecosystems and communities have particular assemblages of plants and pollinators, for example, the Arctic, New Zealand, and alpine communities with pollination predominantly by flies. In general, there appears to be a positive relation between phytosociological progression (by succession, habitat, or geographic area, or combinations thereof) and specialization and diversity in pollination mechanisms. How those various diversities of pollination partnerships came about evolutionarily may be outlined as follows. Starting with the idea that flowers may sometimes compete for pollinator services and sometimes pollinators may compete for floral resources, it can be invoked that some individuals and some species fare better than others. If the direction of competition remains the same over a period of time, one would expect some evolutionary changes to take place in some of the partners. These changes would involve directional selection and character displacement to result in better adaptedness in species of any group, or of groups of species comprising the partnerships. Thus, the assemblage of flowers and pollinators might change in species abundances and diversities as generalists become more specialized through pressures of resource partitioning (increased reliability of pollination for the plants by specialist pollinators, and lesser interspecific competition for floral resources for the pollinators). The direction of competition probably naturally fluctuates over the short term (years to centuries), but with long-term (thousands to millions of years) trends. It is presumably through those processes, and their reversals, that the complexity of pollination, and other ecosystem functions, has arisen. The extreme situation of the evolution of eusocial pollinators (which are found everywhere from tropical forests to high arctic tundra and exhibit constancy and specialization) has depended on a flora of plants with short-lived flowers (from open-bowl shaped ones visited by a wide diversity of pollinators to specialized ones that only the eusocial pollinators can service) blooming in sequence throughout the long life-span of the insect colony. Co-evolution in pollination is a complex process.

Pollination for Food and Fiber Production

Although many agricultural crops are independent of insects for pollination (wind pollination in grains, self-pollination in some seed crops and vegetables), others require insect pollination. Honeybees (*Apis mellifera* and *A. cerana*) are especially important, and stingless bees (Meliponini) are gaining recognition also. The importance of leafcutting bees (especially *Megachile rotundata*) in agriculture came to prominence for production of alfalfa seed and the culture of these bees is now a multi-million dollar industry. In Japan especially, but also in other places, mason or orchard bees (*Osmia* spp. (Megachilidae)) are managed as pollinators for use in fruit production. Bumblebees (*Bombus* spp. (Apidae)) are now firmly entrenched as part of technology for greenhouse production, especially of tomatoes, around the world. Flies (especially Calliphoridae) are used in pollination of some crops (for example, seed production for onions, carrots, parsnips), and are probably the principal pollinators of mango. Midges (Ceratopogonidae) are the principal pollinators of cacao. Rotting vegetation is used in plantations to provide oviposition sites and food for the maggots to assure adequate pollinator forces for the crop. Some beetles (Nitidulidae) are the principal pollinators of Annonaceae. In these, and other crops for which even less is known, much research is needed to determine how to provide the pollination forces needed from crop production.

The importance of pollinators to forest sustainability has been hardly investigated, but it seems reasonable to suggest, from evidence in Costa Rica, Thailand, and Canada (Ontario, Quebec, New Brunswick) that pollination has been adversely affected by human activities (logging, pesticide applications, fragmentation). Grasslands in South Africa and Canada also seem to be suffering declines in pollinators and pollination through overgrazing.

As mentioned, honeybees (*Apis* spp.) are especially important pollinators in agriculture throughout the world, and where they are native, are part of the natural ecosystem. Beekeeping has come to grips with the issues of pesticide kills, but recently in Europe and North America, has suffered major setbacks with the spread of exotic diseases. Varroa mites transmitted from the natural host, the Asiatic hive bee *Apis cerana*, onto the western honeybee, *A. mellifera*, continue to adversely impact natural, feral, and managed colonies. Conversely, diseases of the western honeybee have been transmitted to Asiatic species. In some places now, honeybees are in too short supply to service growers' needs. Moreover, as beekeeping has come to require more intensive management to maintain healthy, strong colonies, the costs of pollination services have risen. In some places, notably in China and parts of Nepal, bees are so scarce that apple pollination is now done by hand.

The economic impact of pollinator shortages are crops failing to reach potential yield levels locally, regionally, nationally, or globally. The effects, depending on scale, may be rising prices or farmers being unable to produce with profit. Whatever the effect, prices to consumers rise. The needs for pollinator conservation are clear.

Insect Conservation

There are relatively few insects on lists of rare and endangered life forms by comparison with birds, mammals, and plants. Most insects on such lists are butterflies. Flower relations and pollination are central to conservation because rare and endangered flowering plants must have their mutualists with them in their habitats if the populations are to persist. Thus, pollinators and seed dispersers must be included in conservation and restoration planning. That approach is being embraced in Hawaii for plant conservation, especially for endangered bird-pollinated plants. Also in the Carolinian forest fragments of southern Ontario, sensitivity to the need for pollinators in rare plant conservation is recognized. Several magnificent trees, for example, cucumber magnolia, Kentucky coffee tree, and the native paw, fail to set fruit for various reasons such as pollinator limitation and wide spacing of trees.

The vicious cycle involving the demise of pollination mutualisms and the partners of those mutualisms proceeds as follows. The general habitat is stressed (by fragmentation, pollution, etc.) so that one or more components become scarce. If one of the dwindling components is part of a crucial mutualism, such as pollination or seed dispersal, then the partner not directly affected by the stress becomes indirectly affected and dwindles too. As the community become simplified by erosion of diversity and abundance, other components become adversely affected. So the system, as a whole, can be seen to become less and less diverse in terms of species present and the interactions that make for a functioning ecosystem. The complex is simplified, and a different ecosystem becomes established.

There is now global concern for the demise of pollination in agricultural and forest ecosystems. In agriculture, pollination services are variously threatened by adversity, disease, and pests in beekeeping (for example, fluctuating honey prices, mite and other diseases, small hive beetle); pesticide poisonings of pollinators; expansive cultural practices that remove pollinator habitat from proximity to crops (for example, as happened by expanded alfalfa seed production fields in the Canadian prairies in the 1940s and 1950s); and reduction in the amount of natural or semi-natural areas in agricultural regions. In forestry, large scale clear-cutting, especially now in the tropics (the effects in much of the temperate world are now largely unrecorded history), seems to be adversely affecting populations of various flower visiting insects. Some insects, notably generalist bees, seem to have a remarkable propensity for persistence, but many specialists do not have that capacity.

Pollination deficits in agriculture are documented in various parts of the world and have become common enough to prompt major international concern, especially for sustainable food and fiber production for human life. The International Convention on Biological Diversity acted over 1998–2002 through the International Pollinators Initiative of the Food and Agriculture Organization of the United Nations. Various other national and continental programs also have started (for example, the World Conservation Union, and various regional initiatives such as the North American Pollination Protection Campaign and the African Pollinators Initiative).

► Pollination by Yucca Moths
► Night Blooming Plants and Their Insect Pollinators
► Bees
► Honey Bee
► Alfalfa Leafcutting Bee
► Apiculture
► Plant Extrafloral Nectaries

References

Bernhardt P (2000) Convergent evolution and adaptive radiation of beetle-pollinated angiosperms. Plant Syst Evol 222:293–320

Dobson HEM, Bergström G (2000) The ecology and evolution of pollen odors. Plant Syst Evol 222:63–87

Free JB (1993) Insect pollination of crops, 2nd edn. Academic Press, London, UK

Heinrich B (1979) Bumblebee economics. Harvard University Press, Cambridge, MA

Kevan PG, Baker HG (1983) Insects as flower visitors and pollinators. Annu Rev Entomol 28:407–453

Kevan PG, Baker HG (1999) Insects on flowers. In: Huffaker CB, Gutierrez AP (eds) Ecological entomology, 2nd edn. Wiley, New York, NY, pp 553–584

Labandeira C (1998) How old is the flower and the fly? Science 280:57–59

Lloyd DG, Barrett SCH (eds) (1996) Floral biology: studies on floral evolution in animal-pollinated plants. Chapman and Hall, New York, NY

Proctor M, Yeo P, Lack AJ (1996) The natural history of pollination. Timber Press, Portland, OR

Roulston TH, Cane JH (2000) Pollen nutritional content and digestibility for animals. Plant Syst Evol 222:187–209

Pollination by *Osmia* Bees (Hymenoptera: Megachilidae)

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Most of the plants of agricultural value are angiosperms, plants characterized by the presence of flowers with ovaries formed by one or more carpels. The flowers are normally hermaphroditic, having both male and female reproductive organs, but there are also plants with unisexual flowers. The reproductive organs of insect-pollinated plants correspond to the morphological and behavioral characteristics of the pollinators, and result from the co-evolution of the plant and pollinator.

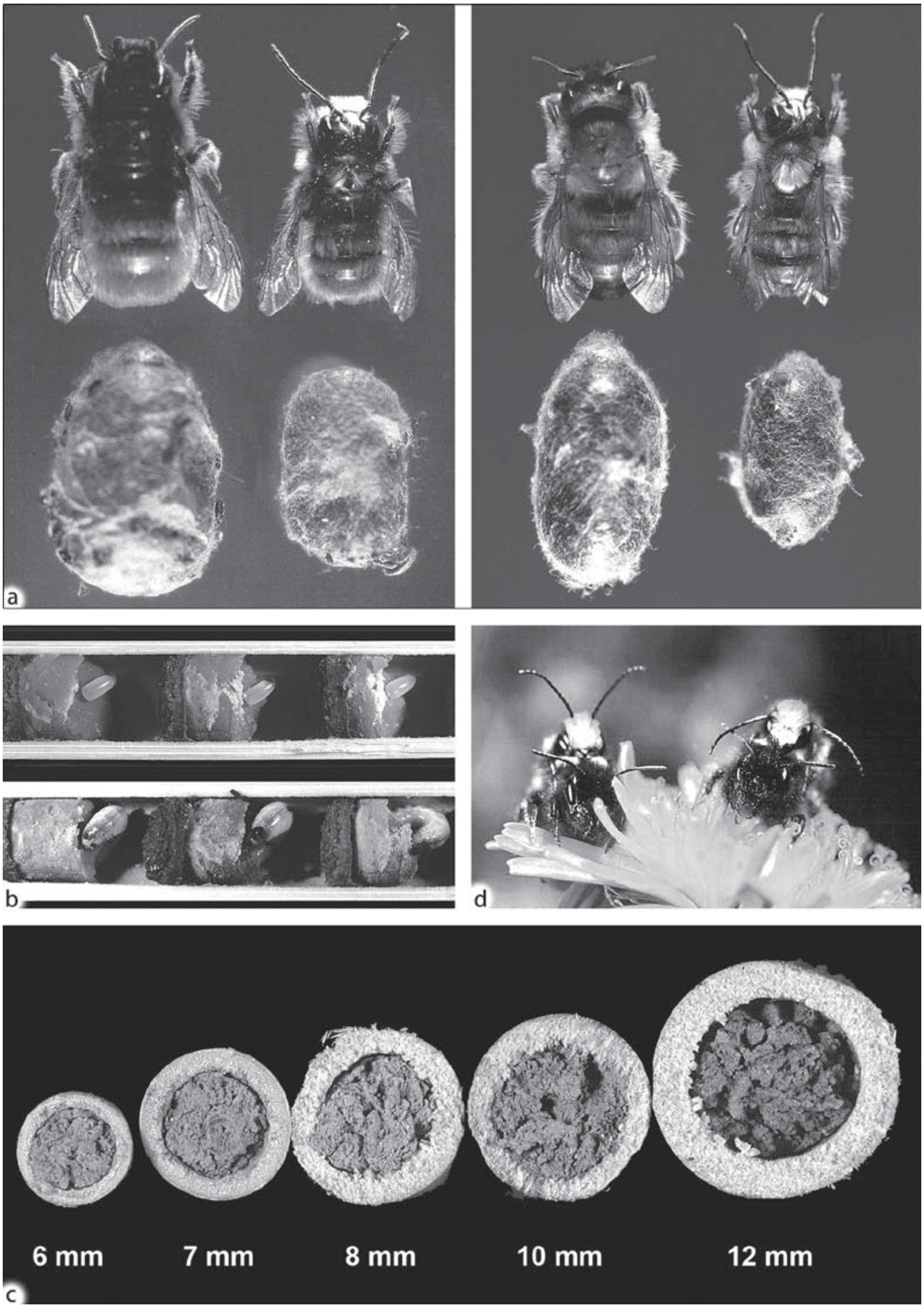
In an hermaphroditic flower, the male organ is represented by one or more stamens, each formed by a filament terminating in an anther in which pollen grains are formed. The female apparatus is formed by one or more carpels joined together in various ways to form the ovary containing immature seeds, and from which a slender column, or style, arises and culminates in an expanded tip or stigma.

There are two phases in the reproductive process, pollination and fertilization. Pollination is the transport of pollen from the stamen (anther) to the stigma; fertilization is the fusion of the two germinal cells and all the biochemical exchanges that follow. Once on the stigma, the pollen granule is held by the papillae, which cover the surface, and possibly by exudates. When the pollen granule comes in contact with the stigma it germinates; it then develops and forms the pollen tube, which grows through the style, reaching and fertilizing the ovule. There are numerous agents responsible for pollination: wind, water, insects and some vertebrates.

Many crops of agricultural interest are mainly insect-pollinated, so the work of pollinating insects is often necessary or at least useful for a bountiful harvest. Among the pollinating insects, bees are most widely employed to obtain pollination service. The transport of pollen from flower to flower occurs during a short period of blossoming, so it is imperative that these pollinators be active at the correct time.

Many wild bees are favored by warm weather, even though different species vary in their temperature optima. *Osmia* species (Fig. 85), depending on the species, are active from February (*Osmia cornuta*) to September (*Osmia caerulescen*) and they can forage under cool and cloudy weather. They are found in all kinds of environments, though they prefer open, sunny habitats and a variety of flora. Almost all *Osmia* species are gentle, not aggressive, and have a brief nesting period. These characteristics are associated with the ease at which *Osmia* can be induced to nest in artificial nests. This, and their strong gregarious nesting tendencies, are the base for the management and multiplication of these insects for crop pollination.

The use of *Osmia* for pollination of orchards was first attempted during the second half of the last century in Japan with the species *Osmia cornifrons*. From the very beginning, satisfactory results were obtained in using these species as orchard pollinators, and the practice has been continued and advanced to the present day. Today



Pollination by *Osmia* Bees (Hymenoptera: Megachilidae), Figure 85 ***Osmia* bees: (a) *Osmia cornuta* Latr., female and male with cocoons (left) and *Osmia rufa* L. female and male with cocoons (right). (b) *Osmia cornuta* Latr. newly laid eggs (above) and larvae (below). (c) Cane (*Arundo donax* L.) segments of suitable diameter for the nesting of *Osmia rufa* (6–8 mm) and *Osmia cornuta* (8–12 mm). Mud seals are visible. (d) *Osmia cornuta* Latr. mating on a *Taraxacum officinalis* flower.**

the majority of apple orchards in Japan are pollinated with the aid of *Osmia*.

During the 1970s and 1980s, investigators in the USA started investigating the native American species *Osmia lignaria* as a pollinator of orchards, then somewhat later began examining the possibility of using a species introduced from Japan (*O. cornifrons*) for this purpose. At the same time, investigations were initiated on the possibility of using *Osmia rufa* as pollinators in Denmark and England, and *Osmia cornuta* in Spain, Serbia, and Italy. The technology of raising *O. cornuta* is well known, and this bee can be reared in the desired numbers.

The use of these bees for field pollination cultivations has been very successful, especially for early-flowering fruit trees. Good results have also been obtained recently for pollination of crops grown in confined environments.

Osmia Biology

Osmia bees are found in the order Hymenoptera, suborder Apocrita, superfamily Apoidea, and family Megachilidae. The genus *Osmia* Panzer consists of 213 species. They are spread over the old and new world in the Palearctic, Nearctic and Ethiopian regions, but are not found in the Indo-Australian and Neotropical regions. In most cases, *Osmia* spp. show a well-defined sexual dimorphism and an obligatory univoltine type of life cycle. They spend the winter in their cocoons as diapausing, fully-formed adults. Each cocoon is found inside a pedotrophic cell (each cell contains an egg and stored food in a suitable amount for the newly hatched larva). Often the cells are placed in a series of rows inside the nests. The latter are sometimes made in wall cavities, old snail shells, old nests of other insects, hollow canes or stems of plants (Fig. 85). *Osmia* nests have also been found in electric outlet holes and in other kinds of cavities. However, nesting always occurs in pre-existing cavities and usually with well-ordered rows of cells. Nesting females use cavities without contributing to building them. In some cases, as for example with *Osmia coerulescens*, nesting does not consist of ordered rows of cells.

In spring, generally between February and July, according to the species, adults emerge from the cocoon. The emergence of the adults is protandrous; males tend to emerge about a week earlier than the females. When females emerge, mating occurs. Mating can occur on a flower, on the ground, or close to the nest, but never in flight.

Field Pollination

Because the bees collect pollen and nectar from flowers that are near their nests, and they generally will not fly more than 100 m away from the nest, good pollination is achieved by placing nests and cocoons in the orchard with spacing of about 20–50 m. A good rule for open field pollination is to build a shelter in the middle of the field and place a large number of artificial nests inside, together with aerated dark boxes containing cocoons with insects ready to emerge. These containers must be kept away from direct sunlight or the insect-containing cocoons will generate high concentrations of CO_2, which quickly causes high mortality. Furthermore, in order to avoid the dispersal of females that are seeking nesting locations, it is desirable to put artificial nests in the field, thereby retaining the females. Good results have been obtained by distributing ten artificial nests, each containing a hundred tunnels, per hectare.

As a general rule, two to five females per fruit tree in blossom is sufficient to achieve 50–90% of pollination, depending on the orchard. A single hectare of apple or pear trees requires 350–500 nesting females of *O. cornuta*, 500–600 *O. cornifrons*, and 600–1,800 *O. lignaria*, and 1,000 *O. rufa*.

Pear

Most varieties of cultivated pear are self-incompatible, and although self-pollination occurs in some cultivars, fruit-set generally benefits from cross-pollination. Pear flowers usually produce small amounts of nectar with low sugar concentration, so they are not very attractive to honey bees. Honey bees visiting pear blossoms often switch to other, more rewarding plants, resulting in insufficient pollination and poor yields. Moreover, seed-set is important in commercial pear production, and seed number increases with insect pollination. Pears with large numbers of seed are larger and have better shape and flavor than those with small numbers of seeds. Unlike the case with honey bees, *O. cornuta* readily visit pear flowers to collect pollen, despite the low nectar content and quality. Most of the pollen provisions in their cells contain 100% pear pollen, and pollination effectiveness of *O. cornuta* on pear is very high. Thus, *O. cornuta* is a suitable pollinator for pear flowers. *Osmia cornuta* stocking rates for adequate pear pollination have been estimated to be very similar to those estimated for apple (500 nesting females per hectare).

Apricot

This tree blossoms when there are still great differences in temperature, and with frequent frost at night. Many varieties of this plant are self-pollinating, but cross-pollination also occurs. The use of *Osmia* bees on apricot trees can be extremely profitable for the following reasons: *Osmia* bees fly at 10–13°C and tolerate night temperatures below zero; and during this period there are very few competing flowers. The activity of a hundred females per hectare is sufficient to increase fruit set by 30–50%. The same results occur with respect to almond, pear and apple trees.

Chinese-Japanese Plum Cv "Angeleno"

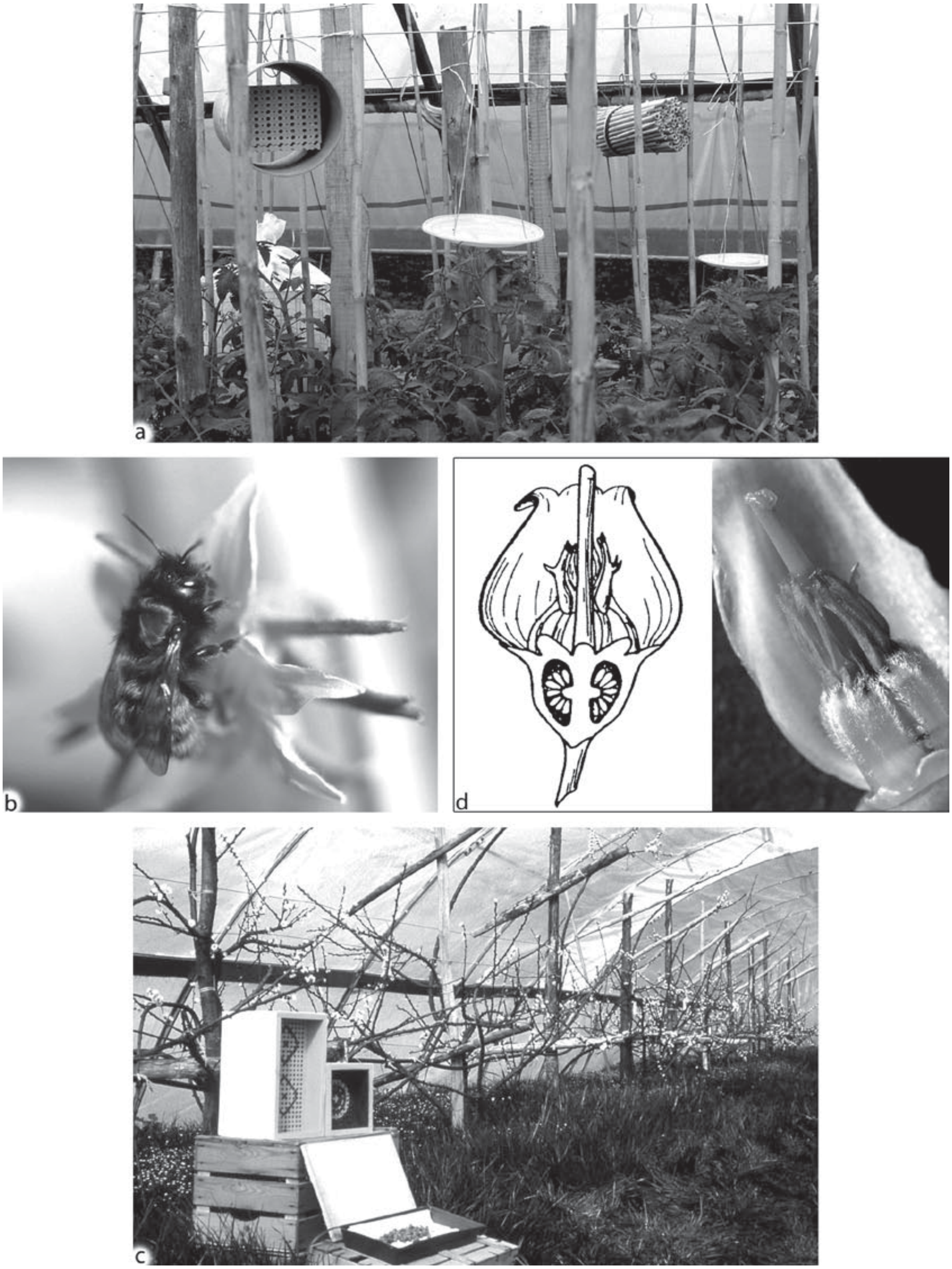
Depending on latitude, the cultivation of this plant has two major difficulties due to limited self-pollination and low nectar production, causing these plants to be unattractive to most pollinating insects. However, *O. cornuta* and *O. rufa* are good pollinators for these plants because they are more attracted by pollen than by nectar, like honey bees and bumble bees. They gather great quantities of pollen as a food reserve for the nest, and gain enough nectar to produce the metabolic energy for flight. For flight they need relatively little sugar, though the presence of flowers is very useful. The reward for the pollination service is therefore mostly pollen, which the *Osmia* gather up in great quantities with the hairs of the ventral part of their abdomen and carry back to their nest. A hundred or so females per hectare are sufficient to obtain an optimal percentage of fruit setting.

Oil-Rape

This crop is very attractive to bees due to the large amount of nectar and pollen. Megachilid bees pollinate this plant with an efficiency comparable to that of honey bees. This crop is a good food source because a large amount of pollen is associated with extensive blossom production, so that the flying and nesting activities can persist for at least one month. With this crop, *Osmia* population densities can increase five-fold.

Cultivation in Greenhouses

Recently it has been shown that *Osmia* are well adapted for pollination in greenhouses, though they do not reproduce well in these structures. Structures containing *Osmia* as pollinators must have side netting or other mechanisms to prevent the bees from escaping. Furthermore, it is very important that structural poles have no holes opening into the greenhouse as these bees are attracted to such openings and tend to get caught and perish inside. *Osmia* are good pollinators for horticultural crops, and extremely positive results have been obtained in the cultivation of tomato (Fig. 86) , pepper and of small fruits such as strawberry, blackberry and raspberry.



Pollination by *Osmia* Bees (Hymenoptera: Megachilidae), Figure 86 **More pollination: (a) Cultivation of tomato in a greenhouse; two types of artificial nest traps and an artificial nectar flower are visible. (b) *Osmia cornuta* female on a tomato flower. (c) A shelter with artificial nests near a planting of apricot trees. (d) Flowers of the genus *Vaccinium*: drawing of a *Vaccinium ashei* flower – the stigma edge is over the corolla (left); *Vaccinium corymbosum* flower – the stigma edge is inside the corolla (right)**

As in the use of these bees in the open field, in the greenhouse the cocoons must be placed in aerated containers away from direct sunlight. In the case of tomato pollination, because the tomato flower has no nectar for food, it is necessary to place "artificial flowers" inside the greenhouse. These can be made with yellow plastic picnic plates containing sugar-water solution, and they may be hung from the ceiling of the greenhouse. *Osmia* learn easily and quickly include the artificial flowers in their foraging flights to obtain glucose for their own metabolic needs.

Five artificial nests each containing about 50 tunnels and 300 females are necessary for a surface of about 1,500 m^2. To accommodate variation in flowering of tomato plants, it is useful to plan the release of *Osmia* in groups of 30–40 females at a time, in successive intervals of at least 5 days, to be sure of continuing flower pollination. Alternatively, it can be helpful to cultivate tomato plants in conjunction with other nectar-producing horticultural plants such as zucchini, melon, pepper or with *Facelia* sp. flowers.

Considerable financial economy is obtained using bees for pollination. This results from lower manpower costs, and the lack of need for wind generators and mechanical vibrators to facilitate pollination. Also, bees provide better fruit and berry set, and in the case of tomato, they avoid problems with parthenocarpic fruit obtained with phytoregulators. Pollination is especially useful for small fruit production because the flowers have abundant nectar and are generally very attractive to bees.

Blackberry, Strawberry and Raspberry

The flowers of these plants have abundant nectar and are generally very attractive to bees. *Osmia* pollination (Fig. 87) benefits these crops in three principal ways. The first is the increase in fruit size due to better pollination. The second is more uniform fruit due to more uniform fertilization of the drupes (or in the case of the strawberry, achenes). The third important benefit is the reduction of the number of treatments against *Botrytis cinerea*. For example, in the case of raspberry cultivation the treatments are reduced from six to one. The explanation of this phenomenon is the decrease of the nectar volume due to the foraging activity of the bees. In the greenhouse environment, excess nectar stagnates and becomes sticky, thus often causing the sticking together of the sepals and the small drupes and creating a suitable substrate for *Botrytis cinerea*.

Blueberry

Research on pollination of the American giant blueberry (*Vaccinium corymbosum*) by *O. cornuta* in confined environments showed that this bee did not have the pollination efficiency of honeybees and bumblebees. This result is in contrast with the pollination of the blueberry *Vaccinium ashei* using *Osmia ribifloris* in open field conditions. This bee showed a higher efficiency in pollinating blueberry flowers than did the honeybee. It is quite interesting that the morphology of the flower is different in the two species. The *V. ashei* shows the stigma coming out from the corolla while the *V. corymbosum* has the stigma inside the corolla. The *Osmia* bees gather pollen directly with the ventral brush so it is quite difficult for them to collect pollen from the *Vaccinium* sp. that have a very small and deep corolla. So pollination occurs only during nectar sucking visits, and flowers with exposed stigma gain more from *Osmia* visits than those with internal stigma.

Seed and Red Cabbage

Research with *O. cornuta* demonstrated that both these plants are effectively pollinated by the bee in a confined environment. Also, seed yield was double of that obtained with honeybees. These plants are also good candidates for *Osmia* rearing because the population increases

Pollination by *Osmia* Bees (Hymenoptera: Megachilidae), Figure 87 ***Osmia* pollination: (a) *Osmia cornuta* Latr. female collecting nectar from a flower (left); an *Osmia* female on its back showing the collected pollen (right). (b) Nesting shelter in a plum orchard (left); assembled artificial nest trap in a field of Chinese-Japanese plum, variety Angeleno (right).**

three to five times in confined environments with these plants.

Lucerne and White Clover

O. cornuta and *O. rufa* in a density of 0.50 females/m^2 have been used for pollination of both lucerne and white clover breeding material grown in mesh cages (10 m^2) in summer. For lucerne pollination, *O. cornuta* produce a yield of 8.1 kg/ha while *O. rufa* give a yield of 5.3 kg/ha. Similar results have been obtained for white clover. Both species did not reach the efficiency of *Megachile rotundata* (250 kg/ha), probably due to the high summer temperatures. However, *O. cornuta* show a great efficiency (175 kg/ha) in pollinating off-season in white clover grown in a growth cabinet during winter (24°C/18°C day/night and 16 h photoperiod) if used in a density of 5 females/m^2.

Inhibition of Pollen Germination

For several reasons, bees differ in their pollination capability. One important factor favoring *Osmia* bees relates to inhibition of pollen germination by the bees. *Osmia* gather pollen from the flower anthers without manipulating them. After visiting several flowers, the female bee returns to her nest to discharge the pollen. Pollen gathered by these bees remains viable until the bee discharges it into her nest. In contrast, honeybees and bumblebees quickly inhibit the germination of the gathered pollen. They immediately store the collected pollen in structures called curbicula as they gather it, and this process inhibits germination of pollen. For example, when pollen is compared from anthers and from curbicula, germination rates are reduced 50% in the latter case. Thus, *Osmia* bees are quite effective pollinators.

This is not to say that *Osmia* do not affect pollen. When depositing the pollen in her nest, the *Osmia* female presses the newly gathered pollen on the pollen provision with her clypeus. Extracts of the heads, possibly secretions of the mandibular glands, have been shown to inhibit pollen germination by 75%. The nature of the inhibitor is not known.

► Bees
► Honey Bee
► Pollination and Flower Visitation

References

Bosch J, Kemp W (2001) How to manage the blue orchard bee as an orchard pollinator. SARE, Sustainable Agriculture Network, Handbook series book 5. Beltsville, MD, USA, 87 pp

Felicioli A (2000) Le osmie. In: Pinzauti M (ed) Api e impollinazione. Giunta Regionale Toscana, Firenze, Italy, pp 159–188

Krunić MD, Stanisavljević LZ (2006) In: Stankovic L (ed) The Biology of European orchard bee *Osmia cornuta*. Faculty of Biology, University of Belgrade, Belgrade, Serbia, 137 pp

Pollination by Yucca Moths

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Yucca moths provide one of the best understood examples of obligate pollination mutualism, in which the female adult pollinates the flowers of her host plant and her larval progeny consume some of the developing seeds. The yucca moth and its relationship with the yuccas was first described from Missouri in 1872 by Charles V. Riley. At least 25 species of *Tegeticula* and *Parategeticula* (Lepidoptera: Prodoxidae) serve as the exclusive pollinators of an estimated 30–40 species of yucca (*Yucca* and *Hesperoyucca*, Agavaceae). Yuccas have white, usually fragrant flowers in a large panicle, but have effectively lost nectar production and produce very little pollen, thus, they only attract a limited range of floral visitors. A modified urn-shaped stigma of the floral ovary makes pollination unlikely by casual brushing, and only the moths have been documented to be pollinators. The plants can reproduce vegetatively, but the moths appear to be critical for sexual propagation. Geographically limited to the Americas, the moths and yuccas are distributed from southwestern Canada southward at least to northern Belize, with the highest species diversity in arid and semiarid portions of western North America. Over the past two centuries, contiguous yucca range expansion through horticulture in the interior of eastern North America led to rapid colonization by the moths. Within decades, they spread northward to southeastern Canada and westward to the edge of the Great Plains (Fig. 88).

Early studies held that four yucca moth species, including one thought to feed on all but two

Pollination by Yucca Moths, Figure 88 **Yucca moth pollinating a yucca flower.**

yuccas, served as pollinators of all yuccas. Recent studies based on behavioral, morphological, and DNA sequence data have shown that the polyphagous species, *T. yuccasella*, in fact is a large species complex with species ranging in diet breadth from monophagy to feeding on as many as seven host species. Adult moths have a wingspan of 15–35 mm, and range in color from solid white to black, a mix of white and black, or sand-colored. The female has unique tentacular mouthparts at the tip of the first segment of the maxillary palp. With a single exception, all species are nocturnal. Adults, which are estimated to live 2–4 days, emerge during the flowering period of their host, and mate during their first night. Flowering host plants are likely found through a combination of visual cues and prominent floral scent cues. The female then visits yucca flowers to gather pollen by dragging her tentacles across the anthers. The highly sticky pollen is compacted and then held under the head. The female next seeks out flowers where she can oviposit. *Tegeticula* species use a cutting ovipositor to insert eggs one at a time at different positions in the pistil, whereas *Parategeticula* females create grooves in petals or pedicels where eggs are laid. After oviposition, the female removes a pollen batch from her load with her tentacles, walks to the stigma, and pollinates the flower by probing 10–20 times into the stigmatic cavity. In so doing, she assures that lack of pollination will not prevent fruit formation, which is critical because seeds, or modified seed tissue, is the sole food item of yucca moth larvae. Overexploitation by the moths is prevented by selective abscission of flowers that have received many eggs, and possibly by other mechanisms as well. Depending on the species, females may lay one or many eggs per flower, but typically only a handful of larvae from any one female will exist in a fruit, in part because of egg mortality. The larva hatches from the egg within a week in most species, and feeds on developing yucca seeds during fruit maturation. The fully fed larva exits the fruit, and diapauses inside a dense cocoon in the soil for one or more years. Pupation generally takes place a few weeks before adult emergence. In one tropical species, there may be no diapause.

DNA-based phylogenetic analyses of the moths suggest an estimated minimum age of 40 million years of the obligate moth-plant mutualism, and also reveal that the pollination behavior arose shortly after the moth lineage had colonized the yuccas from the Nolinaceae, a coexisting family of woody monocots in arid regions. A rapid diversification over the past five million years in the northern part of the range gave rise to about half of the extant species, including two species that have reverted to antagonism by having lost functional tentacles and pollination behavior. Instead, they oviposit directly into yucca fruits, and rely on coexisting pollinator species for the creation of yucca seeds.

References

Riley CV (1892) The yucca moths and yucca pollination. Annu Rep Mo Bot Gard 3:99–158

Pellmyr O (1999) A systematic revision of the yucca moths in the *Tegeticula yuccasella* complex north of Mexico. Syst Entomol 24:243–271

Pellmyr O, Leebens-Mack J (2000) Reversal of mutualism as a mechanism for adaptive radiation in yucca moths. Am Nat 156:S62–S76

Pellmyr O (2002) Yuccas, yucca moths and coevolution: a review. Ann Mo Bot Gard 90:35–55

Pollinator

The agent of pollen transfer in plants, often bees.

► Pollination and Flower Visitation

Pollution and Terrestrial Arthropods

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Pollution, the unwanted and undesirable presence of a chemical or compound, is unfortunately common. The problem is global, affecting all continents and nations, and frequently crossing natural and political boundaries. Specific occurrences may be quite localized (such as waste-water runoff from mining operations) or cover exceptionally broad geographic areas (like acidic precipitation in northern Europe or the entire northeastern USA plus adjacent regions of Canada).

Problems with pollution are not new; air and soil contamination have been reported for thousands of years. Over 2,000 years ago, the Roman poet, Horace, complained about soot damaging the walls of temples. However, the problem has become substantially worse since the Industrial Revolution, with the large scale production and transport of many toxic materials. Most countries evolve through a period of intense industrialization, where the primary goal is to raise the standard of living for the population. During this period the environmental effects of pollutants are not considered a primary concern. As countries become more affluent, the desire for improving environmental quality increases, but nationalistic concerns, economic costs of less polluting technologies, and long standing patterns of industrial production work to impede changes that can reduce contaminants. Even in situations where pollution has been largely eliminated, a "legacy" of contamination may still exist. Thus, the problem of pollution is likely to continue for the foreseeable future.

Solving our existing problems of environmental contamination and mitigating the effects of contaminants on living organisms are difficult because of the incredible variety of sources and forms of pollution. Even an abbreviated list of pollutants would include thousands of industrial by-products, pesticide residues from chemicals that have been banned from use, a variety of toxic metals and chemicals in mining waste, many compounds produced by burning fossil fuels, the by-products of warfare, chemicals used in electrical generation/transport machinery, fuel additives, as well as a host of other materials. Each pollutant has the potential to disrupt ecosystems. Some have minimal effects, others have contaminated soils so that plants or animals from these areas cannot be eaten. A few have created wastelands, where the ground has become too toxic to support even the most basic organisms in an ecosystem.

Terrestrial arthropods are critical to the functioning of ecosystems. Because they are at the base of the food web, changes in population densities of arthropods can have profound effects on higher level organisms that depend on them. Insects and their relatives are used as food by many birds and mammals. Many arthropods are beneficial, serving to keep pest populations under control, thereby preventing damaging outbreaks. Others pollinate plants, disseminate seeds, and produce structures used by countless other organisms. Disruption of any of these activities can have disastrous effects on an ecosystem. Thus, arthropods are often the first animals examined when ecosystems become polluted.

Interestingly, direct contact with most pollutants generally does not harm terrestrial arthropods. Populations of arthropods are more commonly affected when pollutants are ingested, or if the pollutants change the quality or quantity of their food. These effects can be either positive or negative. The following sections summarize the major types of pollutants and their effects on arthropods.

Air Pollutants

Air pollution takes many forms. Some of the more common pollutants contain products resulting from fossil fuel combustion include ozone, carbon dioxide (CO_2) and carbon monoxide (CO), acidic precipitation (acidic fogs and acid rain), and many related compounds. In nearly all scientific studies, direct exposure to high concentrations of these contaminants does not physically harm arthropods. However, air pollution can alter plant chemistry, and thereby change the nutritional value of plants or their chemical defenses against arthropods. Examples are provided for ozone, acid fog, and CO_2.

Ozone is a remarkably active compound generated when combustion products from fuel are exposed to sunlight. Even moderate levels of ozone can damage plants and cause modifications in the form and content of plant nutrients. Exposure to ozone often increases availability of a key nutrient, nitrogen, which is critical for arthropod growth. This nutrient is very important, and frequently determines how fast an arthropod can grow, and if it will survive. Thus, insects such as the tomato pinworm, a key agricultural pest throughout the southern United States and Mexico, grow about 10% faster and survive at twice the rate if feeding on plants exposed to ozone. If ozone exposure is very high, then plants can become so damaged that arthropod populations can no longer survive. Like many toxic substances, the concentration of the contaminant, and the duration of exposure will determine if the pollutant is a benefit or detriment to arthropods.

The levels of CO_2 in the earth's atmosphere have been increasing dramatically since the industrial revolution. CO_2 concentration in the atmosphere has increased from 270 to 280 ppm to the current level of 355–360 ppm. This represents an increase of ~27% in a relatively short period of time. Scientists already have shown that increasing levels of atmospheric CO_2 can have substantial effects on plant suitability for arthropods. Because arthropods (like all animals) are mostly made of nitrogen, those feeding on plants have to separate the relatively small amounts of nitrogen from plant material consisting mostly of carbon. Plants grown in elevated concentrations of CO_2 have increased levels of carbon (from the carbon availability in the CO_2), and substantially reduced amounts of nitrogen. Most arthropods respond to this problem by simply eating more plant material. Some eat twice as much. Others cannot cope with the relative lack of nitrogen, and develop more slowly or even die. Changing CO_2 levels will therefore have significant effects on the plants that arthropods can eat, and how much damage is caused by their feeding.

Acid deposition in the form of "acid rain" or acidic fogs is common in North America. Although terrestrial arthropods are not typically affected by direct exposure, their food plants are often damaged. Typical damage symptoms include lesion development, weathering of leaf surface waxes, foliar leaching, premature leaf fall, changes in plant nitrogen form and content, or even plant death. All of these can impact arthropod populations. Encounters with lesions can change arthropod feeding patterns. Leaf waxes are important cues used by some arthropods to identify a particular plant as a food source, and changes in waxes can make normally acceptable plants unrecognizable. Early leaf loss shortens the time available for leaf-feeding arthropods to develop. Changes in plant nitrogen form and content and plant defensive chemistry generally have profound impacts on arthropods. Some acidic fogs contain high levels of nitrogen, and may act as a fertilizer. In some instances this provides the arthropod with a more nutritious food source, allowing populations to increase. In other cases, the plants use the additional nitrogen to produce defensive chemicals that can suppress insect populations. The death of large areas of trees caused by acid rain and acidic fogs in eastern North America and some parts of Europe have dramatic effects on abundance of many arthropod species that survive on the affected tree species.

Pollutants that Transfer from Water to Soil

Many common water pollutants are readily transferred from water to soil or directly from water to plants. Terrestrial arthropods are then exposed to these materials. Some of the more common waterborne pollutants include hexavalent chromium, MTBE (methyl tertiary butyl ether), and selenium. Each of these widespread contaminants has different effects on insects.

Hexavalent chromium is one of the most common contact sensitizers in industrialized countries and is associated with numerous materials and processes, including chrome plating baths, chrome colors and dyes, cement, tanning agents, wood preservatives, anticorrosive agents, welding fumes, lubricating oils and greases, cleaning materials, and textile production. Due to the past and present use of chromium in so many industries, it is a widespread pollutant. When ingested, this material has been shown to cause a decrease in growth and fecundity in arthropods.

MTBE is a gasoline additive used to elevate the oxygenate level in gasoline. This helps the gasoline burn more completely, reducing the production of some contaminants associated with automobile exhaust. Unfortunately, this chemical has leaked into the groundwater at over 385,000 sites nationwide due to poorly sealed underground fuel storage tanks. MTBE has now been detected in 21% of 480 wells in regions using MTBE as a gasoline additive. In addition, findings from the National Water Quality Assessment Program indicate that MTBE is the second most frequently detected volatile organic compound in ground water and urban streams. Preliminary data suggest that this material can slow development of some arthropod species.

Selenium is found in contaminated soils throughout western North America. Soil accumulation is associated with agricultural irrigation, geochemical processes, mining, and a variety of other industrial sources and frequently results in significant effects on animal and human health. Although selenium is an essential trace nutrient important to humans and most other animals, toxicity occurs at high concentrations due to replacement of sulfur with Se in amino acids resulting in incorrect folding of the protein and consequently malformed, nonfunctional proteins and enzymes. Remediation strategies include removal of soil selenium by plant accumulation, harvest, and removal. Use of plants in soil remediation programs results in the availability of selenium to plant eating arthropods. Ingestion of selenium in plants by arthropods generally results in slowed growth, reduced egg production, and higher mortality.

Pollutants that transfer from water to the soil are likely to be long term problems for arthropods. Contaminated aquifers will be used for irrigation, and plant feeding organisms will be exposed to these pollutants throughout their lives. The long term effects of such exposures, and the possible interactions between the various water-borne contaminants, is not yet known.

The Special Case of Metals

Eighty-seven of the elements on the periodic table are considered metals or metalloids (elements which act like metals). These metals are toxic at relatively low levels to terrestrial arthropods and many other organisms. Although natural mineral deposits containing metals occur around the world, and the erosion of rocks and volcanoes release metals into the atmosphere, contamination of soils by metals is most often associated with human activity. In our industrial society, metals are one of the most commonly used raw materials. Consequently, waste-water runoff from mining, metal refining, sewage sludge, and other anthropogenic sources contain high levels of metals that pollute water and soil. Additionally, gas exhaust, energy and fuel production, smelters, and foundries emit metals as airborne particulates. Sources of contamination often contain mixtures of several metals or metalloids making analysis of the effects of any one element difficult to determine in a field setting.

Airborne particulates containing metals may land on the surface of food plants of arthropods, damaging plant photosynthetic systems and resulting in altered plant chemistry and nutrition for herbivores. Contamination of soils also allows for plant uptake of many metals making these metals available to herbivores. Additionally, decaying plant materials containing metals are consumed by soil and leaf litter dwelling arthropods. Metals have been shown to accumulate in the tissues of some arthropods making them more available to predatory and parasitic arthropods, as well as higher animals that eat arthropods. This can lead to biomagnification, where pollutants accumulate in the tissues of animals as they consume the contaminated arthropods.

Toxicity of metals to terrestrial arthropods has been demonstrated in the field as well as in the laboratory. Because metals are such a large and diverse group of elements it is not surprising that the mode of action and concentrations resulting in toxicity to terrestrial arthropods are variable. Additionally, arthropods themselves differ in their ability to tolerate environments containing metals. Some arthropods are able to excrete small amounts of metals and thereby avoid toxic effects at low levels of pollution. However, at slightly higher concentrations the presence of metals may result in their incorporation into proteins and enzymes, altering their ability to function properly in the arthropod system. Some metals interfere with metabolic pathways in arthropods resulting in reduced total body protein. Additionally, metals can affect the energy source of insects, the fat body. Collectively, these effects often result in impaired growth and development and the disruption of reproduction. Therefore, not surprisingly, arthropod abundance and species diversity are usually diminished in areas where metal pollution is present.

Conclusion

All of these pollutants, whether airborne, carried by water, or present in contaminated soil, can affect population development and survival of terrestrial arthropods. Because of this, all of these contaminants can influence how communities of arthropods, and the higher animals that feed on them, will function within ecosystems. Scientists are just beginning to understand the long term effects of these pollutants on terrestrial organisms.

References

Agrawal SB, Agrawal M (2000) Environmental pollution and plant responses. Lewis, Boca Raton, FL

Coviella C, Trumble JT (1999) Elevated atmospheric CO_2. and insect-plant interactions: implications for insect conservation. Conserv Biol 13:700–712

Frankenberger WT, Engberg RA (eds) (1998) Environmental chemistry of selenium. Marcel Dekker, New York, NY

Heliövaara K, Väisänen R (1993) Insects and pollution. CRC, Boca Raton, FL

Legge AH, Krupa SV (1986) Air pollutants and their effects on the terrestrial ecosystem. Wiley, New York, NY

Polyacetylenes (and Their Thiophene Derivatives)

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Investigations carried out in the second half of the last century have suggested that certain secondary metabolites from plants, including polyacetylenes and their thiophene derivatives, exert photodynamic action. As discoveries are made, the number of natural photodynamic sensitizers of this group is increasing.

Structure

Polyacetylenes have a conjugated double and triple bond system, or may be biosynthetically cyclized into thiophene compounds such as α-terthienyl. The chemistry and the natural distribution of polyacetylenic compounds have been comprehensively described elsewhere (see "Naturally occurring acetylenes" by Bohlmann et al., 1973).

During studies on the structure activity relationship in these compounds, more than two dozen polyacetylenes and thiophene derivatives, originating from the plant family Asteraceae, have been extensively tested against various biological systems. In general, aliphatic compounds containing fewer than three conjugated acetylenic bonds do not exhibit phototoxic effects. Furthermore, in a study using the microorganisms *Escherichia coli* and *Saccharomyces cerevisiae*, it was found that thiophene derivatives generally were more phototoxic than polyacetylenes.

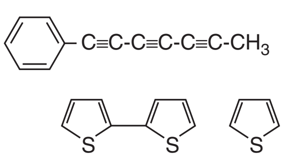
Occurrence in Plants

Polyacetylenes and thiophene derivatives are a very large group of secondary compounds whose photosensitizing properties in insects were first reported in 1975 by Arnason's team at the University of British Columbia in Canada. These compounds have been considered characteristic of taxonomically advanced plant families such as Asteraceae, Apiaceae, Araliaceae and Campanulaceae, as well as certain groups of Basidomycete fungi (Fig. 89). The greatest diversity is found in the Asteraceae where many polyacetylenes occur in roots, and some in the aerial parts of the members of this family.

Activity

Although the first report on the biological activity of α-terthienyl, a thiophene, as a nematocide goes back to 1958, its photoactive properties were not noticed until 1972 when the treated nematodes were exposed to near UV-A light. This was the beginning of a series of studies on the photosensitization of polyacetylenes and thiophene derivatives mediated by UV-A. Since then, numerous articles on different aspects of their activity have been published. With few exceptions, most of the studies concern insects.

$CH_3\text{-}CH{=}CH\text{-}(C{=}C)_2\text{-}(CH{=}CH)_2(CH_2)_4CH{=}CH_2$



Polyacetylenes (and Their Thiophene Derivatives), Figure 89 Chemical structure of polyacetylenes and their thiophenes: above, straight-chain aliphatic acetylenes (e.g., heptadeca tetraene diyne); middle, partly cyclized (e.g., PHT: phenylheptatriyne); and, below, their thiophene derivatives (e.g., α-terthienyl).

Although the photosensitizing properties of polyacetylenes on insects was reported in 1975, the presence of a polyacetylene, 8-cis-decene-4,6-diyonic acid, in insects had been recorded earlier (1968). This compound was isolated from the thoracic and abdominal glands of the cantharid beetle, *Chauliognathus lecontei*.

Twenty-four polyacetylenes (and thiophene derivatives) isolated from species in the Asteraceae were screened by Arnason and associates for their near-UV mediated larvicidal properties to *Aedes aegypti* mosquitoes. One of these, α-terthienyl that was extracted from *Tagetes,* was found to be more toxic than DDT in the presence of UV-A. Since this discovery, studies on the photodynamic action of α-terthienyl have attracted more interest.

Further studies revealed that both phenylheptatriyne (PHT) and α-terthienyl exhibited ovicidal activity against the eggs of the fruit fly, *Drosophila melanogaster*, in the dark. It was reported, however, that irradiation by UV-A respectively enhanced the toxicity by 37- and 4,333-fold.

In 1984, additional investigations on the UV-mediated activity of α-terthienyl against the tobacco hornworm, exhibited delayed and abnormal pupal formation with no subsequent adult emergence. During the same year, the first example of the inactivation of acetylcholinesterase *in vivo* by a photoactive pesticide, α-terthienyl and its two isomers, was documented by Kagan and associates. A high rate of inactivation (ca. 65–90%) occurred within a few minutes when fourth instar larvae of *Aedes aegypti* mosquitoes were treated with this phototoxin or either of its two isomers in the presence of UV-A.

In 1985, a Canadian patent was awarded covering the control of pests (algae, fungi, nematodes, or herbivorous invertebrates) by polyacetylenes. During the same year, the successful synthesis of α-terthienyl was reported. In field trials, effective control of third- and fourth-instar larvae of *Aedes* *intrudens* mosquitoes was achieved with the application of 0.1 kg/ha to natural breeding pools. This compound (α-terthienyl) was found to have a half-life of about 4 h in sunlight.

Studies on the photobiological activity of polyacetylenes and thiophene derivatives are relatively new, therefore few reports are available on their phototoxicity to organisms other than insects. Nevertheless, the broad spectrum of activity in different photoactive molecules, including dyes and furanocoumarins, is well documented. Based on a wide range of biological activity reported from several non-phototoxic studies on polyacetylenes, neither photoactive polyacetylenes nor thiophene derivatives are believed to be the exceptions. For instance, α-terthienyl (a thiophene) that has been patented for use against algae, fungi, weeds, nematodes, insects and other herbivorous invertebrates, also has been found as a potent fish poison. It also results in damage to red blood cells and human skin in the presence of UV-A. Furthermore, phenylheptatriyne (PHT), identified as the major polyacetylenic constituent of the leaves and stems of *Bidens pilosa*, is phototoxic to yeasts and bacteria when mediated by the near UV. PHT, which is present in the cuticle of *Bidens pilosa* (up to 600 ppm), strongly inhibits the germination and growth of *Fusarium culmorum* in the presence of UV, but not in the dark.

Mode of Action of Polyacetylenes and Thiophene Derivatives

In spite of over a century of research on photodynamic action, little is known about the selectivity of phototoxins. In contrast, most photoactive agents including polyacetylenes and their thiophene derivatives have shown a wide spectrum of activity. For example, many polyacetylenes and thiophene derivatives are reported to be toxic to a wide range of microorganisms and to human skin fibroblasts in the presence of UV-A. A thiophene (α-terthienyl) causes photodermatitis in human skin characterized by immediate severe erythema on exposure to sunlight and long lasting hyperpigmentation. There is evidence that this compound, in the presence of UV-A, damages DNA since it induces unscheduled DNA synthesis.

Unlike the linear furanocoumarins, e.g., 8-MOP, that kill cells by a photoinduced modification of DNA, photoactive polyacetylenes and their thiophenes attack the cell membrane by photodynamic as well as by oxygen-independent mechanisms. However, as in the case of furanocoumarins, photosensitization is mediated by the near-UV region (UV-A: 320–400 nm).

In general, straight chain aliphatic acetylenes, which are well known for their instability in vitro, have a non-oxidative mode of action that probably involves the formation of free radicals upon photoexcitation (i.e., Type I Reaction). Thiophenes, however, are Type II photodynamic photosensitizers that damage membranes via catalytic generation of singlet oxygen.

Generation of superoxide anion radicals by α-terthienyl in the anal gills of *Aedes aegypti* mosquito larvae recently has been observed. On the basis of this observation, the phototoxic action of α-terthienyl is suggested. Other investigators who have examined the metabolism of α-terthienyl in the mosquito *Culex tarsalis* found that pretreatment of the larvae with piperonyl butoxide increased larval susceptibility to α-terthienyl and reduced the rate of elimination of this substance.

Partly cyclized aromatic acetylenes such as phenylheptatriyne, which are intermediate in structure between the aliphatic compounds and the thiophenes, apparently exhibit both photodynamic and non-photodynamic processes. It was subsequently found that phenylheptatriyne and other polyacetylenes are photodynamic toward some organisms, including *E. coli*, but are partially non-photodynamic in other systems, including the microorganism *Saccharomyces*.

Most acetylenes are able to produce singlet oxygen in vitro at levels that do not fully account for their phototoxic effects. For example, after removal of oxygen, phenylheptatriyne showed only partial or no decrease in phototoxicity to microorganisms or photohemolysis of erythrocytes.

It should be mentioned that many biologically active acetylenes, such as falcarinone, falcarindiol, oenanthotoxin, capillin, *Matricaria* ester and its derivatives, and cicutotoxin, are not light-activated. Interestingly, falcarindiol, recently identified as a potent phytoalexin in fungal infections, was found to stimulate oviposition by the carrot fly, *Daucus carota*.

All photoactive representatives of dyes, furanocoumarins, polyacetylenes and their thiophene derivatives, including cercosporin and hypericin, have shown a wide spectrum of activity. For example, it has been demonstrated that furanocoumarins, upon activation by light, are powerful antimicrobial agents, nematocides, molluscicides, piscicides and powerful skin photosensitizers against man and animals.

Many polyacetylenes and thiophene derivatives recently have been shown to be toxic to a wide range of microorganisms and to human skin fibroblasts, in the presence of UV-A. A thiophene (α-terthienyl) causes serious photodermatitis in human skin, characterized by immediate severe erythema on exposure to sunlight and long lasting hyperpigmentation. There is evidence that this compound, in the presence of UV-A, damages DNA since it induces unscheduled DNA synthesis. For these reasons, there may be genetic risk associated with polyacetylenes and thiophene derivatives.

References

Arnason T, Swain T, Wat C-K, Graham EA, Partington S, Towers GHN, Lam J (1981) Mosquito larvicidal activity of polyacetylenes from species in the Asteraceae. Biochem Syst Ecol 9:63–68

Arnason T, Towers GHN, Philogène BJR, Lambert JDH (1983) The role of natural photosensitizers in plant resistance to insects. In: Hedin PA (ed) Plant resistance to insects. ACS Symposium Series 208. Washington, DC, pp 139–151

Bohlmann F, Burkhardt T, Zdero C (1973) Naturally occurring acetylenes. Academic Press, London, UK, 547 pp

Champagne DE, Arnason JT, Philogène BJR, Morand P, Lam J (1986) Light-mediated allelochemical effects of naturally occurring polyacetylenes and thiophenes from Asteraceae on herbivorous insects. J Chem Ecol 12:835–858

Christensen LP (1998) Biological activities of naturally occurring acetylenes and related compounds from higher plants. Recent Res Dev Phytochem 2:227–257

Heitz JR, Downum KR (eds) (1987) Light-activated pesticides. ACS Symposium Series 339. Washington, DC, 339 pp

Polyacridamide Gel Electrophoresis

A process by which molecules are separated based on their size and charge, using a polyacridamide gel and electrical current.

Polyandry

Mating of a female with several males.

Polycentropodidae

A family of caddisflies (order Trichoptera). They (as well as Psychomyiidae) commonly are known as trumpet-net and tube-making caddisflies.

► Caddisflies

Polyctenidae

A family of bugs (order Hemiptera). They sometimes are called bat bugs.

► Bugs

Polyculture

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Polyculture is the planting of two or more crops in the same field at the same time. Often the terms *polyculture* and *intercropping* are used interchangeably. However, polyculture is a broader term since it can include not only crop plants but even weeds, nursery and insectary plants, windbreaks, or hedgerows that may be intentionally included in the farming system. *Multiple cropping* is an even more inclusive term that includes both polyculture or intercropping (multiple crops grown at the same time) and crop rotation or sequential cropping (crops grown at different times). In contrast to polyculture, *monoculture* refers to a system in which only one crop is grown.

Types of Polyculture Systems

A variety of different types of intercropping systems and their combinations are possible (Fig. 90). In mixed intercropping, crops are planted without any arrangement in rows. In *row intercropping* or *strip cropping*, crops are planted in alternating rows or strips, for easier mechanization than in mixed intercropping. In *relay cropping*, one intercropped species is planted during the life cycle of another crop plant. Vining crops such as beans or cucurbits planted into an existing corn crop is a common relay crop system, since the growing vines can use the mature or dead corn stalks for support. *Agroforestry* is a type of intercropping system (either mixed or in rows) in which trees are included along with other crops. Use of hedgerows, buffer strips, and windbreaks may not be considered intercropping because they do not involve traditional crops, but they are important elements of polyculture that provide increased plant diversity in the agroecosystem.

Polyculture, Figure 90 Examples of intercropping: intercropped strips of cassava and beans next to a row of sugarcane (above); windbreaks in this eggplant field provide increased border area and inject plant diversity into the system (below).

Advantages and Disadvantages of Polyculture

Polyculture offers a number of advantages over monoculture. A crucial element for small farmers and subsistence farmers is diversification, spreading any risk of crop failure or serious damage over a number of different crops. With monoculture, the entire farm may be at risk if a serious problem affects the key crop. Intercropping systems may offer increased yield per unit of land for several reasons. Plant species with different rooting depths, light requirements, and nutrient requirements may partition and share resources more efficiently than plants of the same species. Open areas and spaces between rows are utilized more efficiently for additional crop production, which also aids in weed management. Increased plant diversity can be beneficial in managing pests, particularly herbivorous insects. On the other hand, a grower of a large monoculture has specialized in the production of one crop, and may have invested heavily in equipment and infrastructure specific to that crop. Mechanization is a particular difficulty with polyculture systems, particularly mixed intercropping, which can involve substantial labor input.

Polyculture and Insect Pest Management Theory

Several hypotheses have been proposed to explain the reduction of insect pests in polyculture relative to monoculture: the disruptive-crop hypothesis, the natural enemies hypothesis, and the trap crop hypothesis. Of these, the first two appear to be more important in practice, but results vary with the specific insects and crops involved. In some systems, no advantage may be obtained by intercropping.

The *disruptive-crop hypothesis* (sometimes called the resource concentration hypothesis) states that insect herbivores are more likely to locate and remain in a concentrated patch of the host plant. Insects relying on olfactory cues from a host plant may be disrupted by strong volatiles from other plant species. Insects relying on visual cues may have difficulty in recognizing concentrations of host plants, specific vegetation colors, or backgrounds when these are disrupted by intercropped species. Once inside a patch of mixed plant species, weak fliers such as whiteflies or aphids may waste time and energy landing on or probing plants that are not optimal hosts. Highly mobile insects like some chrysomelid beetles may emigrate more quickly if preferred food plants are not easily located.

The *natural enemies hypothesis* states that potential enemies of pest insects are more abundant in mixed systems than in monoculture. This appears to be particularly true for generalist predators and parasitoids, but less so for highly specialized parasitoids that are strongly dependent on their hosts. In general, a mixed cropping system offers more sources of pollen and nectar, alternative prey, and more varied microhabitats and plant architecture to potential predators and parasitoids.

Trap cropping involves attracting a pest species away from a valuable cash crop. A classic example is the use of strips of alfalfa to attract damaging *Lygus* bugs away from cotton. More common is the use of early planting or an early maturing variety of the crop plant to attract pests, and then destroying pests and early plants before the main crop is planted. This method can preemptively remove pests and reduce insecticide costs by treating a small trap crop rather than a large field. However, use of trap crops can be risky, since improper timing or management of the trap crop can lure more pests into the area or provide a host on which pests can build up.

Polyculture for Insect Management in Practice

Farm sites can be diversified to maximize the benefits of polyculture for managing insect pests and encouraging their natural enemies. A key step is the maintenance of areas adjacent to fields as sources and refuges for beneficial insects. Natural or semi-natural areas are particularly useful for this purpose, but orchards or other perennial crops also provide permanent and stable habitat. Reduced mowing of perennial legumes and meadows can maintain important sources of pollen for hymenopterous parasitoids, and for Diptera and other predators. *Farmscaping* is a term used to describe the incorporation of hedgerows, insectary plants, cover crops, and other elements of polyculture into the overall farm design.

Edge effects from adjacent landscape are strongest at field margins. Opportunities exist to increase edge effects by subdividing large fields into smaller units, utilizing long fields or strips for crop plantings, subdividing fields with windbreaks, including strips of cover crops or insectary plants within the field, and intercropping with diverse crop species.

Many plants in the carrot (Umbelliferae), composite (Compositae), and mint (Lamiaceae) families are useful insectary plants, including important crop plants as well as many wildflowers and native plants more suitable for border or hedgerow areas. Cover crops such as buckwheat, vetch, cowpea, and various clovers are useful insectary plants as well. Aromatic herbs as intercrops may be disruptive to specialist herbivores. Plant choices for polyculture vary widely with local conditions and cropping systems, so it is necessary for growers to test and experiment locally to develop the combinations most suitable for their ecosystems.

► Flower Strips as Conservation Areas for Pest Management
► Organic Agriculture
► Conservation Biological Control
► Host Plant Selection By Insects
► Plant Extrafloral Nectaries

References

Altieri MA (1994) Biodiversity and pest management in agroecosystems. Food Products Press, New York

Powers LE, McSorley R (2000) Ecological principles of agriculture. Delmar Thomson Learning, Albany, NY

Smith HA, McSorley R (2000) Intercropping and pest management: a review of major concepts. Am Entomol 46:154–161

Stary P, Pike KS (1999) Uses of beneficial insect diversity in agroecosystem management. In: Collins WW, Qualset CO (eds) Biodiversity in agroecosystems. CRC, Boca Raton, FL, pp 49–67

Vandermeer JH (1992) The ecology of intercropping. Cambridge University Press, Cambridge, UK

Polydnaviruses (Parasitoid Related Viruses)

Members of the family Polydnaviridae are unique to insects and possess enveloped, quasicylindrical (helical symmetry) nucleocapsids which encapsidate multiple (20–30) dsDNA molecules having a composite size of 200–280 kbp. Historically, these viruses were originally placed in subgroup D of the family Baculoviridae. Polydnaviruses replicate exclusively in the nuclei of the calyx cells located in the female reproductive tract of adult hymenopterans. Two genera of polydnaviruses are recognized: the *Bracovirus and Ichnovirus* detected in braconids and ichneumonids, respectively. Bracoviruses are rod-shaped, have a width of 35–40 nm, and can vary in length from 30 to 200 nm. The nucleocapsids are enveloped by a single unit membrane (one or more nucleocapsids/membrane) that is formed de novo in the nuclei of calyx cell. Progeny bracoviruses are released through cytolysis of calyx cells. Ichnoviruses have a fusiform morphology (about 100–350 nm), possess a lenticular nucleocapsid, and contain a two-unit membrane, the first formed in the nucleus and the second acquired via budding through the cell membrane of infected calyx cells. Both the bracoviruses and ichnoviruses are complex particles and contain 20 to more than 30 structural proteins ranging from 10 to 100 kDa.

The key characteristic of the polydnaviruses is the heterodispersed double-stranded circular DNA genome. In the mid-1970s, numerous enveloped virus particles were detected in the calyx epithelial cells of the accessory glands of female parasitoids. Polydnaviruses can be purified easily from dissected calyx tissue using density gradient centrifugation methods. Polydnavirus DNA preparations applied to $CsCl_2$ gradients containing ethidium bromide produce two bands, representing the relaxed circular and superhelical DNA molecules. Kleinschmidt spreads of these preparations revealed a complex of circular DNA molecules ranging from 1.5 to 8.0 × 10^6 Da. Agarose gel electrophoresis of polydnavirus DNA preparations produced more than twenty bands ranging from 2 to more than 28 kbp. The bands detected in these gels were present in nonequimolar ratios. Hybridization studies, utilizing DNA extracted from agarose gels and labeled in vitro with ^{32}P as probes for Southerns, demonstrated that more than 80% of the electrophoretically separated bands were unique DNA molecules. The relative number of DNA molecules packaged within the polydnavirus nucleocapsid differs between the *Ichnovirus* and *Bracovirus*. It has been proposed that the different *Ichnovirus* DNA molecules are encapsidated together within a single particle. However, certain bracoviruses, characterized by possessing nucleocapsids of variable length, are believed to encapsidate a single DNA molecule. Kleinschmidt spreads of DNA released from osmotically shocked preparations of the bracovirus of *Chelonus inavitus* revealed that each nucleocapsid released a single DNA molecule, suggesting the presence of a population of virions. The helical symmetry of these viruses allows for differential packaging of DNA; the longer the helix, the larger the encapsidated dsDNA fragments.

In most cases, polydnaviruses replicate in the calyx cells of female wasps and release progeny virus particles into the calyx lumen. In the calyx cells, polydnavirus morphogenesis is observed at the pupal-adult stage of wasp development and is regulated in part by 20-hydroxyecdysone. Within a specific parasitoid population, these vertically transmitted viruses are found in 100% of egg and sperm cells, suggesting a Mendalian transmission mode. In certain ichnoviruses, including the *Campoletis sonorensis* viruses (CsV) and *Hyposoter fugitivus* (HfPV), the polydnavirus DNA is integrated into the chromosomal DNA of both the parasitoid and in selected lepidopteran cell lines. Cloned polydnavirus DNA hybridized to Southern blots detected off-size fragments in REN digests of chromosomal preparations of both parasitoid and selected insect cell lines. The stable integration of complete, unarranged polydnavirus DNA into wasp chromosomes suggests that these viruses may be transmitted as proviruses. Therefore, it has been proposed that the polydnavirus has two replicative pathways. First, it exists as a linear chromosomal provirus responsible for transmission in the wasp and, secondly, as an encapsidated circular DNA produced within the calyx cells during the pupal-adult stages. The circular DNAs, packaged into virus particles, are released during oviposition into the parasitoid's host.

Deposition of polydnaviruses during oviposition into the host plays an important role in the survival and development of the parasitoid egg. Parasitoid eggs explanted from the wasp ovary and implanted into host larvae are readily recognized as non-self, encapsulated by circulating hemocytes, and killed. However, the combination of viable polydnavirus and the egg implants results in the survival and development of the parasitoid. The observed obligatory mutualism observed between polydnaviruses and their respective wasp species is unique. The polydnaviruses delivered with the parasitoid egg during oviposition do not replicate in host lepidopteran cells; nevertheless, polydnaviruses mediate dramatic changes in host physiology. In addition to the polydnavirus, wasps deliver host-modulating substances, including venom, ovarian-secreted proteins, and/or specialized teratocyte cells that may complement the activity of polydnaviruses. The polydnaviruses delivered into the lepidopteran host are able to penetrate various cell types, undergo partial transcription, and produce m-RNA and selected viral proteins within several hours of oviposition. Host granulocytes and plasmatocytes, as well as the hemopoietic tissues (hemocyte stem cells) and prohemocytes, are the primary targets of the polydnaviruses. The presence of polydnavirus causes a marked depletion of immunoresponsive cells, disrupts the actin cytoskeleton of plasmatocytes and granulocytes, and may induce apoptosis (programmed cell death) of targeted hemocytes. The disruption of cellular actin inhibits the ability of these cells to adhere to and spread over non-self, resulting in the inhibition of the encapsulation response. The polydnavirus-mediated inhibition of the host cellular defense has been shown recently to increase the susceptibility of host larvae to other disease agents such as baculoviruses. Apoptosis of the granulocytes, characterized by cellular blebbing and fragmentation of chromosomal DNA, seen as a ladder of DNA molecules on agarose gels, results in depletion of functional granulocytes. Although the polydnaviruses are able to suppress the host cellular defense, the humoral response which involves the induction and synthesis of the anti-microbial cationic proteins remains functional in the parasitized hosts.

References

Beckage N (1998) Modulation of immune responses to parasitoids by polydnaviruses. Parasitology 116 (Suppl): S57–S64

Edson K, Vinson SB, Stoltz D, Summers M (1981) Virus in a parasitoid wasp: suppression of the cellular immune response in the parasitoid's host. Science 211:582–583

Fleming J, Summers M (1991) Polydnavirus DNA is integrated in the DNA of its parasitoid wasp host. Proc Natl Acad Sci USA 88:9770–9774

Lavine M, Beckage N (1995) Polydnaviruses: potent mediators of host insect immune dysfunction. Parasitol Today 111:368–377

Whitfield JB (2002) Estimating the age of the polydnavirus/braconid wasp symbiosis. Proc Natl Acad Sci USA 99:7508–7513

Polydomous

Social insects in which single colonies occupy more than one nest.

Polyembryony

Production of more than one embryo from a single egg, a condition found in some Hymenoptera in the families Braconidae, Dryinidae, Encyrtidae, and Platygasteridae.

Polyethism

Division of labor among members of a colony of social insects. This includes caste-based polyethism, wherein different forms perform different functions, and age-based polyethism, wherein individuals perform different functions as they age.

Polygenic Resistance

Resistance of a host to a "parasite" based on many genes.

Polyhedron (pl., polyhedra)

Crystal-like inclusion bodies produced in the cells of tissues affected by certain insect viruses; ordinarily the polyhedrosis-virus particles formed in the nuclei of the host cells are rod-shaped, while those formed in the cytoplasm are polyhedral or approximately spherical.

Polyhedrosis (pl., polyhedroses)

A virus disease of certain insects characterized by the formation of polyhedral inclusions in the tissues of the infected insect; if the inclusion bodies (polyhedra) are formed in the nuclei of the infected cells, the disease is known as a "nuclear polyhedrosis." If the inclusions are formed in the cytoplasm, the disease is known as a "cytoplasmic polyhedrosis."

► Baculoviruses

Polygyny

The existence of more than one egg-producing queen in a single colony. Primary polygyny is a condition wherein the queens form a colony simultaneously; secondary polygyny occurs when supplementary queens are added after the colony is founded.

► Sociality of Insects

Polymer

A chemical compound consisting of a long chain of identical or similar units.

Polymerase Chain Reaction (PCR)

A method for amplifying DNA by means of DNA polymerases such as *Taq* DNA polymerase. PCR fundamentally involves denaturing double-stranded DNA, adding dNTPs, DNA polymerase, and primers. DNA synthesis occurs, resulting in a doubling of the number of DNA molecules defined by the primers. Additional rounds of denaturation and synthesis occur, resulting in a geometric increase in DNA molecules because each newly synthesized molecule can serve as the template for subsequent DNA amplification. Modifications of the PCR reaction have been developed for special purposes. PCR is used to clone genes, produce probes, produce ssDNA for sequencing, and carry out site-directed mutagenesis. DNA sequence differences are used to identify individuals, populations, and species.

Polymitarcyidae

A family of mayflies (order Ephemeroptera).

► Mayflies

Polymorphism

More than distinct one body form (phenotype) within the same stage of a species. Two or more genetically different classes in the same interbreeding population. (contrast with polyphenism).

Polyphaga

One of four suborders of beetles (Coleoptera), and one of two suborders that contain numerous and important beetles (the other is suborder Adephaga). It is comprised of numerous important families, including Scarabaeidae, Elateridae, Lampyridae, Cantharidae, Dermestidae, Cleridae, Coccinellidae, Tenebrionidae, Cerambycidae, and Curculionidae.

► Beetles (Coleoptera)

Polyphagidae

A family of cockroaches (order Blattodea).

► Cockroaches

Polyphagous

Feeding broadly. In herbivores, feeding on more than one family of plants.

Polyphenism in Insects and Juvenile Hormone (JH)

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Borsi, Durg, India

Polyphenisms are adaptations of a genotype to produce different phenotypes under different environmental conditions. Polyphenisms may be considered to be a form of polymorphism. Presumably the different phenotypes favor survival in these different environments. During the past several decades there has been a growing realization that JH is widely involved in development of polyphenism in insects.

A good model for examining the importance of JH in polyphenism is tobacco hornworm, *Manduca sexta*. A black mutant race of *M. sexta* produces larvae that are black in color at temperatures between 20 and 28°C. If the larvae of this race are heat shocked (by exposure for 6 h before apolysis, the first step in molting) at the molt between the fourth and fifth instar, a range of color variants is produced, ranging from the original black to nearly normal green. Among the larvae obtained this way, a monophenic line can be obtained by selecting black larvae in each generation. Also, a polyphenic line can be obtained by selection of normal green larvae. In each generation, larvae are subjected to heat shock and segregated by color. A control line is also maintained, given heat shock in each generation, but no color segregation is practiced. The monophenic line loses response to heat treatment after about the seventh generation, i.e., the heat treatment now produces only black larvae. In the polyphenic line, the body color remains green even at 28°C. In the control line, the body color shows continuous variation between the black color of the mutant race, and nearly fully green color, indicating polygenic control of body color. When the neck and the base of the abdomen of larvae are ligated in both the monophenic line and the polyphenic line, we infer that secretions from the head are needed for melanizing the body color. JH titers in the larvae of the two selection lines are different during the sensitive period, i.e., the time for heat shock. The titer of JH in the polyphenic line after heat shock is much higher than in the monophenic line. Obviously it is the JH titer that determines the extent of melanization. Selections in the two lines clearly indicate that genes control the extent of formation and deposition of melanin in the epidermis. Observations in the control line suggest polygenic control. From this study it may be further inferred that JH acts as a "middle man" between the genome on one hand and melanin synthesis and deposition on the other.

The hornworm manipulations demonstrate that a part of genetic variability may remain masked and unexpressed in the phenotype, but an environmental change may trigger expression of this part of the genome, and consequent polyphenism. The phenomenon may help survival under changed environmental conditions and, therefore, has been referred to as "genetic accommodation." As suggested above, JH plays the role of a mediator in development of melanization.

Polyphenism is also well studied in bruchids (Coleoptera: Bruchidae). In *Callosobruchus analis* and *C. maculatus* there is a "flightless" form (referred to as "A" phase) and "flight" form (called the "B" phase). The "flight" individuals are highly melanic in body color, and those in the "flightless" phase are much less so. In both bruchid species there are also intermediate forms with intermediate states of melanization. Crowding, high temperatures, and high humidity increase the proportion of melanic forms. Under natural conditions, larval crowding in a legume store brings about significant elevation of both temperature and humidity. Selection for 10 generations in high density cultures to favor the "B" or highly melanic phase, or to favor the "A" or lightly colored phase, results in markedly different phenotypes. When selection is then relaxed, the second post-selection generation of bruchids are all "B" in "B" favored cultures, and in the "A" cultures nearly all are "A." Hence, as in the case of *Manduca sexta*, genetic control of melanization may be inferred. Occurrence of intermediate forms between "A" and "B" phases in a continuous series in an ordinary culture in either of the two bruchid species, mentioned above, suggests polygenic control of phase determination in them.

When adults of *C. analis* that have recently eclosed are treated with an extract of cockroach corpora allata, a JH analogue, or the bruchid's own JH by implantation in the abdomen with the severed heads from well-sclerotized conspecifics, the effects of JH are evident. In all these experiments, there is a significant increase in the proportion of "A" individuals, as compared to controls (which have received either application of solvents without JH or implants of coxae of legs in place of heads). That in any of these experiments 100% of the individuals do not become "A" points to polygenic control of phase determination, and shows that some individuals do not have genetic proclivity to respond to increased titer of JH.

Bruchids and other phytophagous beetles show polyphenism elsewhere in their organization. In the phase "B" males of *Callosobruchus analis* and *C. maculates*, retournement of the aedeagus is anticlockwise, while in "A" males it is clockwise. (Retournement is rotation of the male aedeagus during development about its longitudinal axis). In Phytophaga (Phytophaga = Chrysomelidae + Bruchidae + Cerambycidae), the rotation is through 180°, so that the ventral surface of the organ becomes dorsal and vice versa ("clockwise" and "anticlockwise" refer to the direction of the rotation, as seen from the caudal end). Deficiency of JH promotes appearance of the "B" phase, which is characterized both by a high degree of melanization as well as anticlockwise retournement.

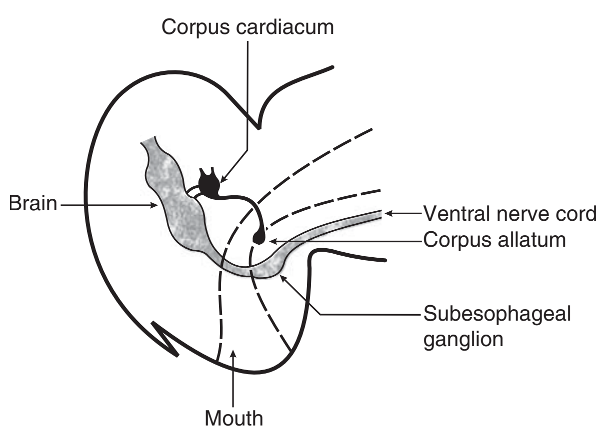
Among other insects, there are instances of polyphenism similar to what is documented in bruchids. *Zygogramma suturalis*, a chrysomelid that was introduced in northern Caucasus from North America for biological control of the ragweed *Ambrosia artemisiifolia* displays some elements of polyphenism. The introduced beetle forms a "solitary population wave" (SPW), moving ahead and effectively destroying the weed. As the SPW advances, two remarkable changes take place in the beetles: increasing melanization of the body color, and appearance of flight capacity, even though in the home country the beetle is a non-flying species. The formation of "flyers" takes place under high population density conditions within the SPW. As noted above, high population density in a bruchid culture induces appearance of "flight" and melanized individuals. If JH levels were determined in the SPW, it is likely that further resemblance with polyphenism in bruchids may be demonstrated.

JH titer is regulated by a balance between synthesis and degradation, and the degradation is brought about by the enzyme JHE (JH esterase). Higher JHE titer suppresses reproduction in the migratory phase of butterflies. The migratory phase is correlated with lowering of JH titer in several insects, including the beetles *Melolontha melolontha* and *Leptinotarsa decemlineata*. *Chrysolina aurichalcea* is a leaf beetle that normally is brachypterous and flightless. However, there are populations of this species in which some individuals fly. The flying individuals are all females with underdeveloped ovaries. Flying individuals have longer and thicker wings, and are pigmented deep red basally.

Locusts also show polyphenism similar to that of bruchids. Locusts are grasshoppers, which, under certain environmental conditions produce a swarming or migratory phase. Their swarms are formed in limited areas with vegetation, and surrounded by long stretches of arid land. When locust species multiply in such a breeding area for some time and their population density increases, darkly pigmented and more active hoppers begin to appear, replacing the green forms that predominated previously. If population densities remain high they leave the breeding area as a swarm. The involvement of corpora allata (CA), the gland that produces JH in phase determination in the locust *Locusta* (Fig. 91) , has long been known. Implantation of CA from another hopper in the body of a hopper in a crowded culture results in changes in the implant-receiving hopper, so that the adult developing from it shows characteristics of the non-swarming phase. In addition, if CA are removed in the fourth instar of *Locusta*, the dark pigmentation characteristic of the swarming phase appears in the fifth instar. Thus, in this case too, JH is involved in production of polyphenism.

The role of JH in locust phase production is limited. Juvenile hormone modulates cuticular melanization and the rate of reproductive maturation, regulating vitellogenesis at the transcriptional level and nonspecifically stimulating the translational capacity of the locust fat body. However, JH does not appear to be involved in behavioral phase transition of locusts. Long-term treatment of crowded nymphs with the JH analog methoprene does not reduce development of their gregarious behavior. So although JH induces certain solitarious characteristics such as green coloration, it is not the primary cause of phase transition.

JH influences caste differentiation in the bees. Topical application of JH on three-day-old



Polyphenism in Insects and Juvenile Hormone (JH), Figure 91 A vertical longitudinal cut through the head of *Locusta* to show location of the corpora allata.

worker honey bee larvae results in development of queen-like features. Polyploidization of CA cells through endomitosis is complete at the beginning of the fifth instar in a queen larva, and at the end of the fifth instar in a worker larva. At the end of the larval development, the CA volume in a queen larva is twice that in a worker larva. This is indicative of higher JH activity during queen bee differentiation.

Similarly, a single application of JH to the first or the second instar larva of the bumblebee, *Bombus terrestris*, in a young colony that has just been started by the queen, and in which all larvae are destined to be workers, leads to the treated larva developing into a queen. However, this treatment to older colonies does not produce a clear-cut result, as in such colonies some larvae, without any treatment, develop into queens.

The role of JH in insect polyphenism is becoming clearer. JH is involved in the control of gene switching and it exerts this control only during certain critical periods. Thus, the presence or level of JH during a critical period results in expression of alternative developmental pathways. There are relatively brief critical periods of hormone sensitivity during which the development switch occurs, although the hormone sensitive periods of different tissues occur at different times during development. It is important to note that change of environs, often with change of habitat, may alter JH concentration in the hormone sensitive period, and thus alter developmental path. Thus, it may be concluded that involvement of JH in development of polyphenism is widely found among insects. Whether it is universal among insects cannot be inferred at this stage. JH is known to be a hormone with multiple effects in the postembryonic development of insects. It seems that initiation of some programmed changes in insect's postembryonic life has become tied to certain JH concentrations, which may be regulated by sensory perception of certain environmental changes acting through the neuroendocrine integration in the region of corpora cardiaca; hence, polyphenism.

► Phase Polymorphism in Locusts
► Corazonin
► Grasshoppers and Locusts

References

Bartolotti L, Duchateau MJ, Sbrenna G (2001) Effect of juvenile hormone on caste determination and colony processes in the bumblebee *Bombus terrestris*. Entomol Exp Appl 101:143–158

Breuer M, Hoste B, De Loof A (2003) The endocrine control of phase transition: some new aspects. Physiol Entomol 28:3–10

George J, Verma KK (1997) Variability in *Callosobruchus chinensis* L. and evolution of polymorphism in *Callosobruchus* (Coleoptera, Bruchidae). Russ Entomol J 6:41–48

George J, Verma KK (1999) Laboratory rearing of the "active" phase of *Callosobruchus maculatus* F. (Coleoptera, Bruchidae). Indian J Exp Biol 37:584–588

Kovalev OV (2004) The solitary population wave, a physical phenomenon accompanying the introduction of a chrysomelid. In: Jolivet P, Santiago-Blay JA, Schmitt M (eds) New developments in the biology of chrysomelidae. S.P.B. Academic Publishing bv, The Hague, The Netherlands, pp 591–601

Suzuki Y, Nijhout F (2006) Evolution of polyphenism by genetic accommodation. Science 311:650–652

Tiwary PN, Verma KK (1989a) Studies on polymorphism in *Callosobruchus analis* (Coleoptera, Bruchidae). I. Characteristics of phases. Entomography 6:269–290

Tiwary PN, Verma KK (1989b) Studies on polymorphism in *Callosobruchus analis* (Coleoptera, Bruchidae). II. Endocrine control of polymorphism. Entomography 6:291–300

Tiwary PN, Verma KK (1989c) Studies on polymorphism in *Callosobruchus analis* (Coleoptera, Bruchidae). III. Mechanism of phase determination. Entomography 6:301–316

Tiwary PN, Verma KK (1989d) Studies on polymorphism in *Callosobruchus analis* (Coleoptera, Bruchidae). IV. Significance of polymorphism. Entomography 6:317–325

Polyphenism

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The condition of having two or more discrete phenotypes, without intermediates, resulting from

Polyphenism, Table 14 Some examples of polyphenisms, the agent invoking the polyphenism, and the inductive environment that triggers the polyphenic developmental switch

Polyphenism	Selective agent (to which the polyphenism is an adaptation)	Inducing stimulus
Seasonal	Lethal temperature, food scarcity	Photoperiod, nonlethal temperature
Phase in aphids	Food quantity or quality	Crowding, temperature, photoperiod
Phase in locusts	Food quantity or quality	Crowding, food quality
Phase in caterpillars	Predation	Food quality
Horn length	Mating success	Food quantity or quality
Wing length	Food quantity or quality	Crowding, photoperiod
Caste in ants (soldiers)	Food quantity or quality	Food quality, pheromones
Caste in ants (reproductives)	Reproduction	Pheromones, overwintering
Caste in bees	Reproduction	Nutrition, pheromones
Diapause	Lethal temperature	Photoperiod, nonlethal temperature

Adapted from Nijout, 2003

discrete phenotypic plasticity. Evolution can channel organisms into a stabilized phenotype, with little plasticity, that is well developed for a certain function or environment. Alternatively, it can lead to a more flexible phenotype, producing a robust organism. Some phenotypes show gradual change in response to environmental variation, without producing discretely different subsets, and are called "reaction norms." Some phenotypes produce discretely different (lacking intermediate forms) intraspecific variation, and this is called "polyphenism." Polyphenisms are adaptations to reliable and somewhat predictable variations in the environment. This is also known as polymorphism, especially in the older literature. Some examples are given in Table 14. Note that the inducing environment is not the same as the selective environment.

Many insects have evolved a critical period in development when they are sensitive to inducing stimuli, and this critical period occurs well in advance of the occurrence of the alternative phenotype. Thus, token stimuli such as day length signal the onset of lethal temperatures, the selective agent.

The developmental switch that leads to alternative phenotypes is regulated by hormones. Insects express both larval and adult polyphenisms. The stimulus for adult polyphenism occurs in the larval stage, and at a hormone-sensitive period an alternative development pathway is initiated. The hormones controlling polyphenic development generally are the same as those controlling molting and metamorphosis: ecdysone and juvenile hormone. The hormones trigger different patterns of gene expression, leading to alternative phenotypes.

► Castes
► Polymorphism in Locusts
► Polyphenism and Juvenile Hormone (JH)
► Phenotypic Plasticity

References

Ananthakrishnan TN, Whitman D (eds) (2005) Insect phenotypic plasticity. Diversity of responses. Science, Enfield, New Hampshire, 213 pp

Evans JD, Wheeler DE (2001) Gene expression and the evolution of insect polyphenisms. Bioessays 23:62–68

Miura T (2005) Developmental regulation of caste-specific characters in social-insect polyphenism. Evol Dev 7:122–129

Nijout HF (1999) Control mechanisms of polyphenic development in insects. Bioscience 49:181–192

Nijout HF (2003) Development and evolution of adaptive polyphenisms. Evol Dev 5:9–18

Polyphyletic Group

Taxa that do not contain all the recent descendents of a single past species, but those excluded from the group are descended from a species of the group that is younger than the stem-species. Often it is difficult to distinguish paraphyletic from polyphyletic taxa.

► Phylogenetics

Polyplacidae

A family of sucking lice (order Phthiraptera). They sometimes are called spiny rat lice.

► Chewing and Sucking Lice

Polyploidy

An increase in the number of copies of the haploid genome. Most individuals are 2n, but species are known that are polyploid (3n, 4n, 5n, 6n), and such species are parthenogenetic because of the difficulty of maintaining normal meiosis. Many insect species have tissues that are polyploid, such as the salivary glands, nurse cells of the ovary, and germ line tissues.

Polypodous

Used to describe an organism with many legs. Including prolegs, caterpillar (Lepidoptera) and sawfly (Hymenoptera) larvae are polypodous. Most insects have hexapodous (six legs) larvae and a few have apodous (no legs) larvae.

Polypore Fungus Beetles

Members of the family Tetratomidae (order Coleoptera).

► Beetles

Polystoechotidae

A family of insects in the order Neuroptera. They commonly are known as giant lacewings.

► Lacewings, Antlions, and Mantidflies

Polytene Chromosomes

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Polytene chromosomes, also referred to as giant chromosomes, are huge, transversely banded ribbons of DNA. Compared with typical interphase chromosomes, they are longer by one hundred times or more and have diameters thousands of times greater. Only Collembola and Diptera among the hexapods have polytene chromosomes, which were first described in larval midges in 1881, and in Collembola in 1961. These giant chromosomes are formed in tissues that grow by cellular enlargement rather than by an increase in cell number. In contrast to a typical mitotic cycle, the homologues of polytene chromosomes typically remain paired and do not participate in the mitotic cycle of coiling and uncoiling. The sister chromatids remain paired at the end of each replication cycle, and the nuclear membrane and nucleoli remain intact throughout replication. The end product of the replication cycles is a nucleus with a haploid number of chromosomes, each containing up to 2,000 or more parallel strands. In the Collembola, however, the polytene chromosomes typically remain unpaired and the nuclei contain the diploid number (Fig. 92).

Polytene chromosomes of Diptera are found in a wide variety of larval, pupal and adult tissues, but they are best developed in tissues with a high level of secretory activity, such as the salivary glands, midgut, fat body, and Malpighian tubules. Larval salivary glands typically yield the finest preparations, as represented by the photographs of the genus *Drosophila*, which often are featured

Polytene Chromosomes, Figure 92 **Section of giant, polytene chromosome from salivary gland of larval black fly.**

in textbooks. Polytene chromosomes are also present to varying degrees in ovarian nurse cells and trichogen cells. In the Collembola, polytene chromosomes are well developed in the salivary gland cells.

The enormous size of the polytene chromosomes and the constancy of the series of light and dark bands, seen most easily in stained preparations, provide a wealth of taxonomic, phylogenetic, and genetic information. The banding patterns of the chromosomes can be photographed or drawn and then mapped by assigning sectional numbers and letters so that every band or puff can be referenced. The banding sequences tend to be species specific, with at least a segment of the total polytene complement of each species having a unique sequence of bands. These unique segments are created by one or more rearrangements, typically inversions, which reorient the sequence of bands. Nonetheless, examples of homosequential species (i.e., species with identical banding sequences) are known among taxa such as drosophilids and black flies. Inverted sequences often appear in the heterozygous condition, forming knots or loops in the chromosomes, as the sequences of each chromosomal homologue attempt to pair. An absence of heterozygous inversions in the presence of two opposite banding sequences indicates a lack of hybridization, providing evidence of reproductive isolation. Polytene chromosomes, consequently, have been used to reveal morphologically similar species (i.e., sibling species) through the absence of hybrids. The evolutionary relationships of insects also can be reconstructed on the basis of uniquely shared banding sequences. Not all Diptera have polytene chromosomes amenable to band-by-band analysis. In many taxa, the polytene chromosomes are under replicated or sticky and fragmented, making analysis of banding patterns difficult.

References

Ashburner M (1970) Function and structure of polytene chromosomes during insect development. Adv Insect Physiol 7:1–95

Beermann W (ed) (1972) Developmental studies on giant chromosomes. Results and problems in cell differentiation, vol 4. Springer-Verlag, New York, NY, 227 pp

Polythoridae

A family of damselflies (order Odonata).

► Dragonflies and Damselflies

Polyunsaturated Fatty Acids

A dietary source of polyunsaturated fatty acids is required by many insects. Linoleic acid and linolenic acid satisfy their need. Lack of these dietary components often results in slow growth and deformed wings in the adult stage.

Pomace Flies

Members of the family Drosophilidae (order Diptera).

► Flies

Pomerantsev, Boris Ivanovich

IGOR USPENSKY

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B.I. Pomerantsev was born in St. Petersburg on March 3, 1903. Later the family moved to Saratov where he studied in a local high school. After his father died in 1917, he had to work and tried his hand at many jobs: agricultural worker, docker and sailor on the Volga River, and even a musician in a military orchestra. He left school in 1920 and entered the hydrotechnical faculty of the State University of Saratov. However, the faculty was soon closed and only in 1924 could he continue his education in the Institute of Applied Zoology and Phytopathology in Leningrad. There he began work on pyroplasmosis of cattle and ixodid ticks as vectors of the disease in Novgorod Region. He graduated from the Institute in 1929 as an entomologist specializing in ticks. From 1930 through 1933 he worked in the All-Union Institute of Plant Protection in the Department of Stock-Raising Pests, and in 1934 he was invited to the Department of Parasitology of the Zoological Institute of the USSR Academy of Sciences. Since he already had good experience in ecological studies of ticks, he concentrated his research on tick morphology and taxonomy. He collected unique material from various regions of Russia and described eight new species of ticks that remain valid today. While preparing the monograph on ixodid ticks of the USSR, he presented important arguments for his classification of ticks and considered the directions of tick evolution. He was excellent in drawing and illustrated all his scientific works. In 1939 he worked in the Far East of the USSR studying tick-borne encephalitis, a severe viral infection which emerged at that time. While making a survey over the taiga forest, he was bitten by many *Ixodes persulcatus* ticks, the main vectors of the virus, and despite immediate vaccination, the disease developed and he passed away on June 22, 1939. He had no time to complete his Ph.D. thesis. All his main works were published after his tragic death. Two of his basic papers and his monograph, the first of its kind in the world, were translated into English: "Basic directions of evolution of the Ixodoidea" (NAMRU3–13); "On the structure and organization of the Ixodoidea (Acarina, Parasitiformes)" (NAMRU3–55); and "Ixodid Ticks (Ixodidae)" (G. Anastos [Ed.],The American Institute of Biological Sciences, Washington, DC). Even now, these works are cited in publications concerning tick taxonomy and evolution. Two species of ticks were named after him: *Ixodes pomeranzevi* and *Dermacentor pomerantzevi*.

Reference

Pavlovsky EN (1947) B.I. Pomerantsev (1903–1939). Parazitologichesky Sbornik 9:5–12 (in Russian)

Pompilidae

A family of wasps (order Hymenoptera). They commonly are known as spider wasps.

► Wasps, Ants, Bees and Sawflies

Popularity of Insects

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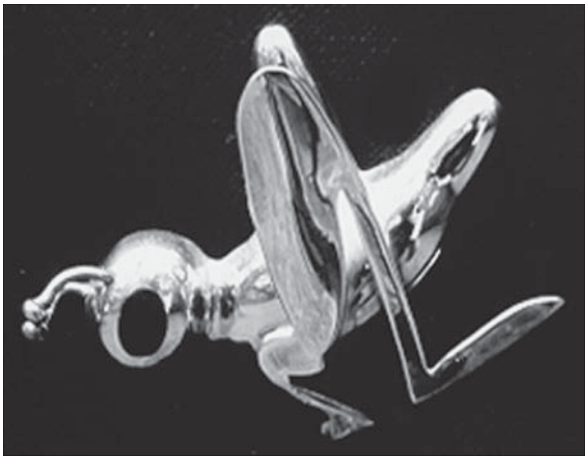
In terms of numbers of species, insects are the largest group of animals by far. There are approximately one million named species of insects, and most recent estimates suggest there are three to four million more in the world yet to be discovered. Insects also are among the most abundant in terms of sheer numbers. Dr. E.O. Wilson has estimated that there may be as many as 10,000,000,000,000,000,000 (10 quintillion) individual insects in the world.

Because of the great numbers and spectacular appearance of insects, everyone has some familiarity with them. Throughout history, insects have permeated almost every area of human society – a fact that is well documented on the web site, *Cultural Entomology Online*. Most people have some opinion, either positive or negative, about insects. Currently, insects and other arthropods are enormously popular. Everywhere one looks there is evidence of this popularity. It is virtually impossible to visit the jewelry departments of large department stores without seeing insect necklaces, pins, and earrings (Fig. 93). Also, insects are commonly featured as prints for fabrics used in women's clothes (Fig. 94). Butterflies were proclaimed to be a "fashion statement" in a recent (June 14, 2002) article in the *Life* section of *USA Today*. The article stated, "This season, butterflies are fluttering across ankle straps and purses, up-dos, and jean pockets." While butterflies are certainly the most popular insects featured in fashion, dragonflies, damselflies, bees, and ladybugs are also extremely popular.

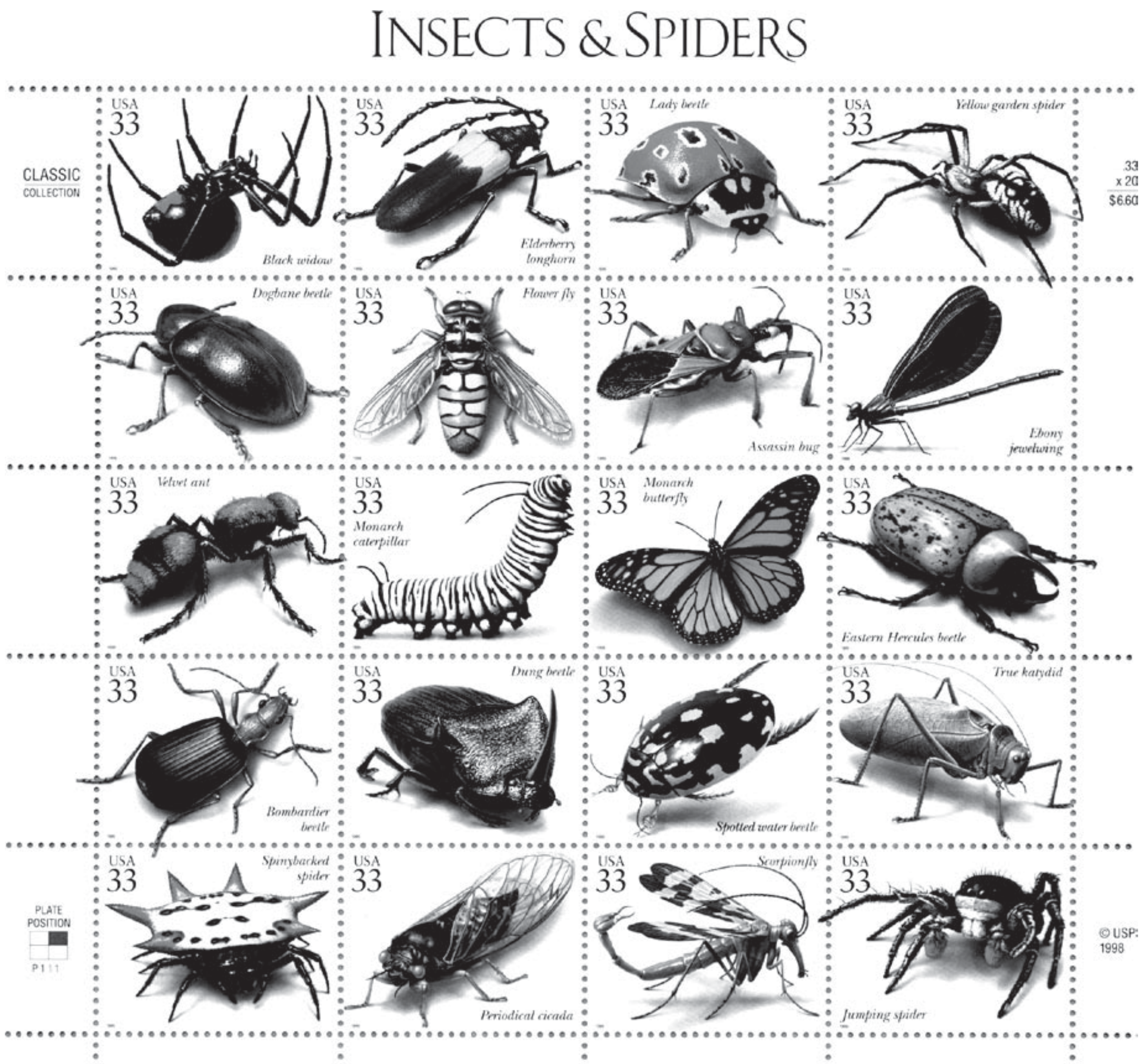


Popularity of Insects, Figure 93 **Grasshopper jewelry pin.**

Insects also are prevalent in photography and art. Kjell B. Sandved spent 24 years photographing all the letters of the alphabet and the numerals from one to nine and zero from the wings of butterflies. Many of these photographs are now featured in three magnificent posters and a book available at his butterfly alphabet web site. Even the United States Postal Service has recognized the popularity of insects. In October of 1999, the Postal Service issued a sheet of magnificent 33¢ postage stamps that featured an outstanding selection of sixteen species of insects and four species of spiders (Fig. 95). The insects and spiders sheet of stamps was ranked fourth on the Postal Service's list of the "Top 20 Commemorative Stamps of All Time."

An area of growing interest is the use of insects as human food. There are several web sites that have links to insect recipes, nutrition facts and food insect festivals. Also, there are a number of

Popularity of Insects, Figure 94 **Fabrics with butterfly and dragonfly designs.**

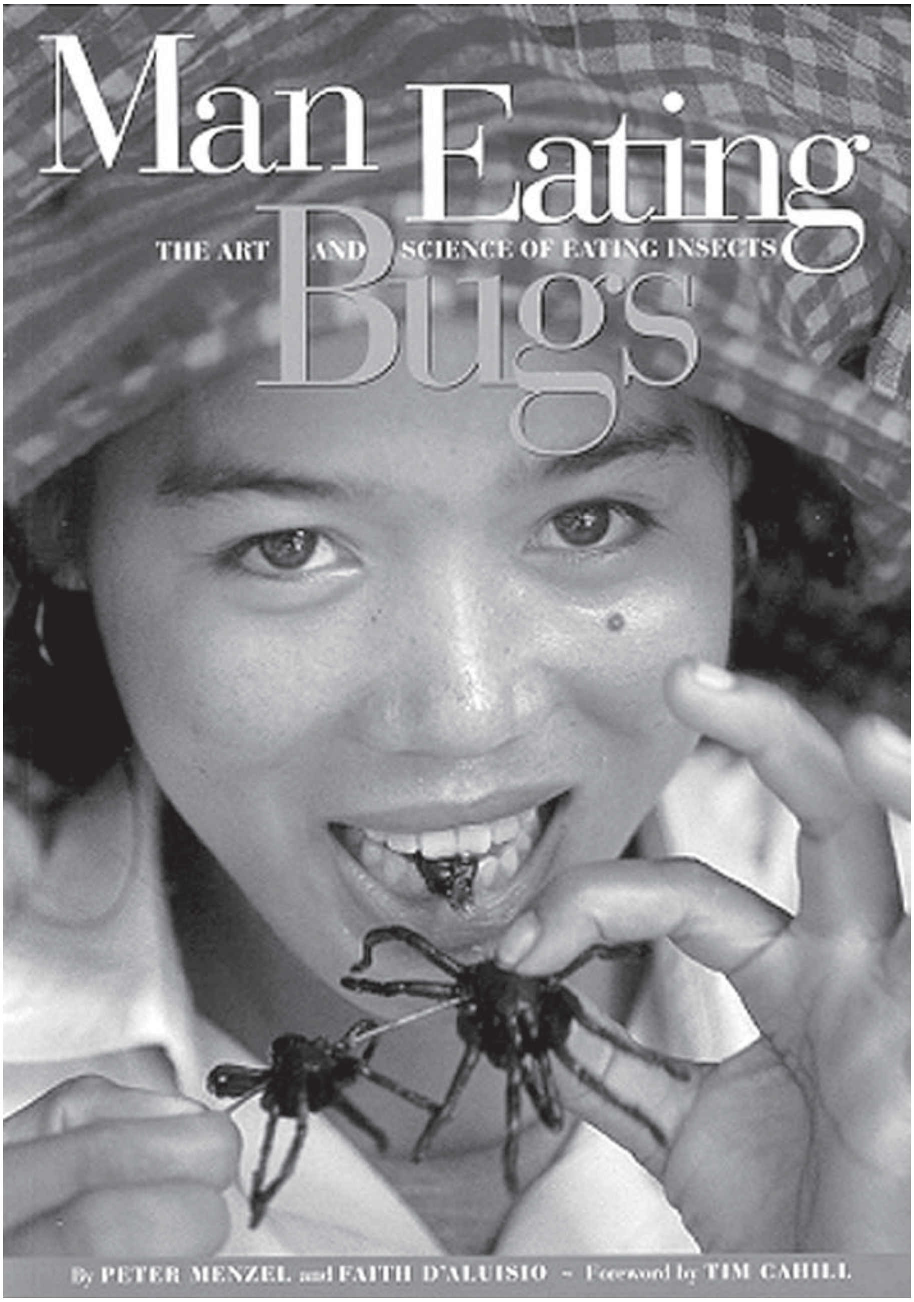


Popularity of Insects, Figure 95 **Insect and spider stamps. Stamp Design © 1999. U.S. Postal Service. Reproduced with permission. All rights reserved.**

excellent books devoted to the subject. One, *Man Eating Bugs* (Fig. 96) by Peter Menzel and Faith D'Aluisio, is a fascinating account (with numerous color pictures) of the use of insects as human food around the world.

Numerous television and magazine commercials and movies have used insects as actors. Recent popular animated movies featuring insects include PDI/Dreamworks' *ANTZ* and Pixar/Disney's *A Bug's Life*. Films with outstanding video of living insects include Galatee Films' *Microcosmos* and the BBC's outstanding three part educational video series for television, *Alien Empire*. All of these videos are currently available for purchase from online sources. Also, forensic entomology (use of insects as evidence by law enforcement agencies) has become popularized on the *Crime Scene Investigations* television series.

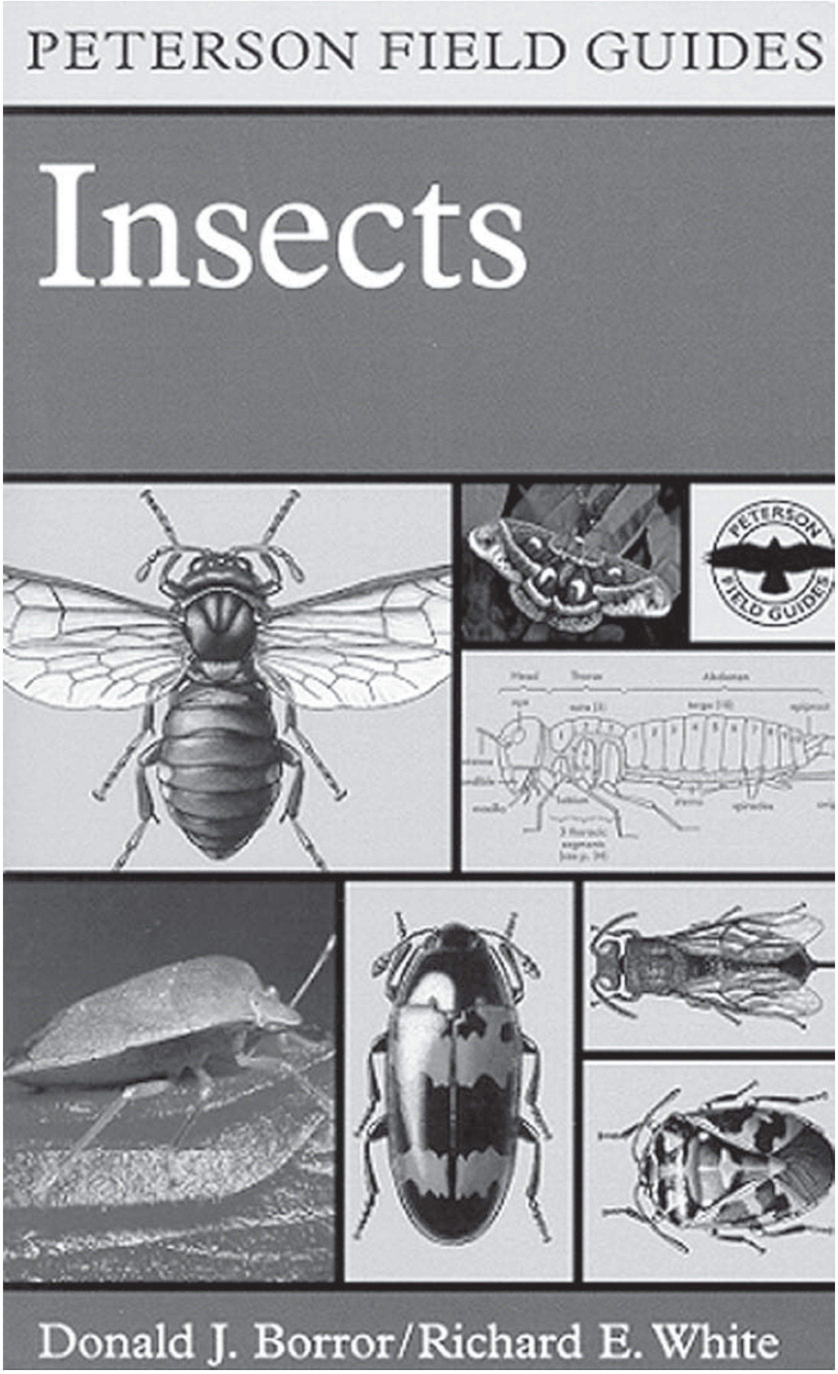
Adding to the popularity of insects is the abundance of excellent insect books for all age groups from young children to adults. For young children there are books that use insects to teach moral values and desired behaviors in addition to those that feature insect identification and behavior. For older



Popularity of Insects, Figure 96 Front cover of *Man Eating Bugs*. Used with permission of Ten Speed Press.

children and adults, there are a variety of outstanding field guides to the insects and specialized books that address a wide variety of specialized topics related to insects. Representative selections of insect books (Fig. 97) are found in the natural history sections of all of the major bookstores, or more complete lists may be found by using the search engines of online booksellers. Also, books as well as many other items (insect videos, posters, t-shirts, puppets, collecting supplies, etc.) of entomological interest are available from entomological supply catalogs – some of which are available online.

Many societies and organizations have contributed to the popularization of entomology. For children, most state 4-H programs have entomology projects, and the Boy Scouts of America has



Popularity of Insects, Figure 97 **Front cover of Insects (Peterson Field Guide Series). Used with permission of Houghton Mifflin Company.**

an "Insect Study" merit badge. The Young Entomologists' Society is another excellent choice for children. National and state professional entomological societies have annual meetings – often with special outreach programs to schoolchildren in the localities where meetings are held. Many countries throughout the world have their own entomological societies. In the United States, the Entomological Society of America (ESA) is the leading entomological society. It has a wealth of educational material on its web site and sponsors educational programs for children and teachers at each of its annual meetings. Of special interest is the ESA's web page on frequently asked questions on entomology. The web addresses for ESA, other entomological societies in the United States, and those throughout the world are found in the accompanying Table 15 of web addresses.

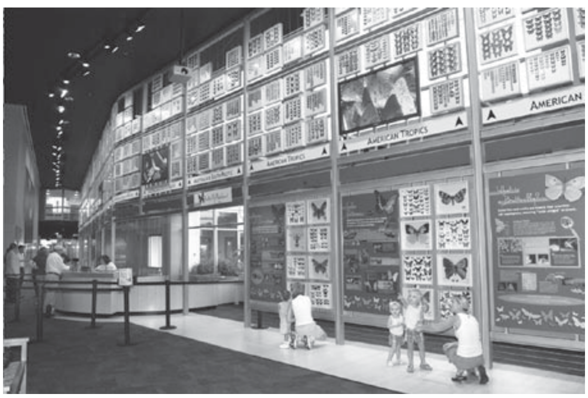
The success of insect zoos and butterfly pavilions are testimonials to the current popularity of insects. In contrast to most museums that may house millions of dead insects, the zoos and butterfly pavilions display live insects. In the case of the butterfly pavilions, the butterflies are free-flying and often land on the human visitors. Many large cities either have insect zoos or are in the process of building them. The Audubon Insectarium in New Orleans bills itself as the largest freestanding museum in the United States devoted to insects, and projects an estimated annual visitation of 400,000 and an estimated economic impact for the city of $87,000,000.

The University of Florida's McGuire Center for Lepidoptera and Biodiversity in Gainesville has a screened butterfly vivarium, "The Butterfly Rainforest" (Fig. 98), with hundreds of free-flying butterflies from around the world allowing visitors to get up-close with the butterflies. There is also a

Popularity of Insects, Table 15 Selected entomological web sites

The Entomology Index of Internet Resources	http://www.ent.iastate.edu/list/
Entomological Society of America	www.entsoc.org
Entomological Societies	www.amnh.org/learn/biodiversity_counts/know_more/w_entomsoc.htm
World's Entomological Societies	www.sciref.org/links/EntSoc/eslists.htm (case sensitive)
Young Entomologists' Society	members.aol.com/yesbugs/bugclub.html
National 4-H headquarters	http://www.national4-hheadquarters.gov/
Boy Scouts of America Insect Study Merit Badge	www.usscouts.org/usscouts/mb/mb065.html
Links to University Entomology Departments	www.entsoc.org/resources/education/colleges.htm
Frequently Asked Questions on Entomology	www.entsoc.org/resources/faq.htm
Featured Creatures	creatures.ifas.ufl.edu
Best of the Bugs website	pests.ifas.ufl.edu/bestbugs
Insect Zoos, Museums, and Butterfly Gardens in North America	http://www.entsoc.org/resources/links/zoos.htm
Public Butterfly Gardens & Zoos	Butterflywebsite.com/gardens/index.cfm
NABA Butterfly Gardening Guides	www.naba.org/pubs/bgh.html
North American Butterfly Association (NABA)	www.naba.org
Butterflies and Moths of North America	www.butterfliesandmoths.org/
Y.E.S. Minibeast Merchandise Mall	members.aol.com/YESsales/mainmenu.html
Bioquip Products	www.bioquip.com
Carolina Biological Supply Company	www.carolina.com
Butterfly Alphabet Posters & Book	www.butterflyalphabet.com
The Cultural Entomology Digest OnLine	www.insects.org/ced/index.html
The Food Insects Newsletter, Inc.	www.hollowtop.com/finl_html/finl.html
The Bay Area Bug Eating Society	www.planetscott.com/babes/

Popularity of Insects, Figure 98 **University of Florida Butterfly Rainforest.**



Popularity of Insects, Figure 99 **University of Florida Wall of Wings.**

"Wall of Wings" (Fig. 99) educational exhibit that features thousands of specimens, photographs, and videos of moths and butterflies. The McGuire Center also houses the world's second largest Lepidoptera research collection.

The popularity of butterflies has spawned a lot of interest in creating butterfly gardens in city parks, K-12 schools, and home lawns. Because different butterfly species prefer different species of flowering plants as nectar sources for the adults and host plants for the caterpillars, creating a butterfly garden requires knowledge of the appropriate plants for each geographic area. To meet this need, there are many excellent regional butterfly gardening books. One may find books specific to a region at local bookstores or by searching the web sites of online booksellers. Also, there is a wealth of information on the web including a good selection of free downloadable regional butterfly gardening guides on the web site of the North American Butterfly Association (NABA). NABA also sponsors a large number of butterfly counts throughout North America. Dates and localities for the butterfly counts are found on the NABA web site. These butterfly counts are an excellent opportunity to learn the local butterflies. A number of excellent national, regional and state butterfly books with color photographs are available to assist with identification of butterflies. On the "Butterflies of North America" web site, one may select a state and see a list of links to color photographs and biological accounts of butterflies for that state.

Releasing butterflies at weddings has become a very popular but somewhat controversial practice. According to the International Butterfly Breeders Association, there are hundreds of commercial butterfly farms in the United States that raise butterflies for schools and for release at special events. Some scientists do not approve of the releases because of the potential harmful effects of the released butterflies (that may not originate from the same area in which they are to be released) mating with local butterflies. There is concern that the progeny resulting from these matings may not be as well adapted to survive. Also, the United States Department of Agriculture is concerned that some of the butterflies may pose a threat as plant pests and has proposed regulations to restrict releases of all but a few species.

Schools and universities have played a major role in educating the public about insects. Elementary school teachers frequently utilize insects in their teaching. A number of major university entomology departments offer entomology courses designed for education majors. Also entomology courses are offered at many universities as electives or to meet general education biology requirements for non-science majors. Some of these courses have enrollments of greater than 500 students per semester.

A few university entomology departments conduct insect fairs for the general public. The best

Popularity of Insects, Figure 100 **Roachhill Downs at Purdue University's Bug Bowl.**

Popularity of Insects, Figure 101 **Cricket-spitting at Purdue University's Bug Bowl.**

of these is Purdue University's "Bug Bowl" (Fig. 100) organized by Professor Tom Turpin. Over 12,000 people attend Bug Bowl each year. These fairs offer a combination of hands-on educational experiences and entertainment. Two of the most popular events at Bug Bowl are "Roachhill Downs," a miniature race track with preserved cockroaches sitting in the stands, where live cockroaches race and an event that is now sweeping the nation, "cricket-spitting" (Fig. 101). The current world record for cricket spitting is 30 feet, 1 and ¼ in.

The popularity of insects is certain to continue to grow in the future. As with many other subjects, the world wide web will play a major role. There is already a wealth of information about this fascinating group of animals available online – just a few "clicks" away.

References

Arnett RH, Jaques RL Jr (1981) Simon & Schuster's guide to insects. Simon and Schuster, New York, NY
Borror DJ, White RE (1970) Insects (Peterson Field Guides). Houghton Mifflin, Boston, MA
McGavin GC (2000) Insects spiders and other terrestrial arthropods. Dorling Kindersley, New York, NY
Milne L, Milne M (1980) The Audubon Society field guide to North American insects and spiders. Alfred A. Knopf, New York, NY
Berenbaum MR (1989) Ninety-nine gnats, nits, and nibblers. University of Illinois Press, Urbana, IL
Glassberg J (1999) Butterflies through binoculars: the East. Oxford University Press, New York, NY
Glassberg J (2001) Butterflies through binoculars: the West. Oxford University Press, New York, NY
Akre RD, Paulson GS, Catts EP (1992) Insects did it 1st. Ye Galleon Press, Fairfield, WA
Wangberg JK (2001) Six-legged sex – the erotic sex lives of bugs. Fulcrum, Golden, CO
Menzel P, D'Aluisio F (1998) Man eating bugs – the art and science of eating insects. Ten Speed Press, Berkeley, CA

Population

A group of individuals of one species that occupy the same area at the same time and generally interbreed.

Population Density

The number of organisms expressed as a unit of space (e.g., insects per plant, per square meter, or per cubic centimeter).

Population Dynamics

The changes in population sizes over time, and the factors responsible for these changes.

Population Ecology

The study in time and space of populations, their density and distribution, relative to factors causing changes in the populations.

Population Index

A sampling method that attempts to provide an indirect estimate of population density based on an associated product (e.g., frass) or effect (e.g., defoliation).

► Sampling Arthropods

Population Pyramid

A method of illustrating the age structure of a population diagrammatically by placing the youngest members of the population at the base and by stacking successive age classes above it.

Population Regulation

Maintenance of a relatively consistent population size and density. Some factor causes population density to increase when it is low, and to decrease when it is high.

Population Resilience

The ability of a population to adapt to change in its density or environment.

Pore Canal

Canals running from the epidermis through the procuticle, and used for transport of waxes, cement, and sometimes other substances to the surface (epicuticle) of the insect. The pore canals do not penetrate the epicuticle, though smaller canals called wax channels do penetrate the epicuticle.

► Cuticle

Porrect

Labial palps that protrude straight forward (not curved upward) in a pronounced manner, such as is found in Pyralidae.

Post-Emergence Treatment

Treatment of a plant, usually with a pesticide, after the plant has emerged from the soil.

Posterior

The hind region of the body, or referring to the end containing the anus.

Postoccipital Suture

A suture that marks the presence of an internal ridge, the postoccipital ridge, to which dorsal prothoracic muscles and head muscles are attached.

► Head of Hexapods

Postocular Area

An area of the head behind the eyes.

► Head of Hexapods

Postpetiole

The second segment of the “waist” (petiole) of an ant.

Post-Plant

Reference to treatments applied to a crop after planting.

Postscutellum

A small portion of the thoracic notum immediately behind the scutellum.

► Thorax of Hexapods

Potamanthidae

A family of mayflies (order Ephemeroptera).

► Mayflies

Potamocoridae

A family of bugs (order Hemiptera).

► Bugs

Potato Aphid, *Macrosiphum euphorbiae* (Thomas) (Hemiptera: Aphididae)

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Potato aphid is a highly variable species, and may eventually be shown to be a species complex. The origin of potato aphid is thought to be North America, though it is now found widely around the world.

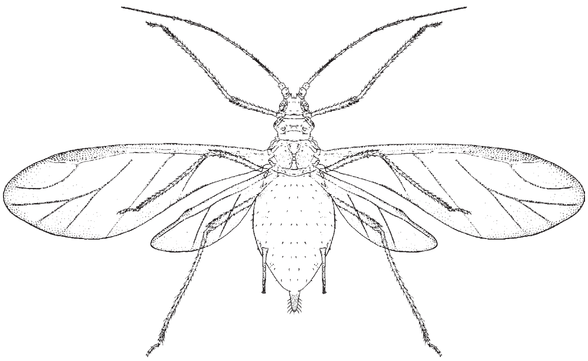
Life History

In northern areas this aphid has a sexual component to its life cycle and overwinters in the egg stage. In the spring this aphid feeds on rose, where 2–6 generations are completed. The aphids abandon the rose in the summer months and fly or walk to other suitable hosts, where several additional generations occur and high densities are attained. In the autumn, the winged forms disperse, usually back to rose. On rose, autumn migrant females, oviparous (egg-laying) females and males are found, mating occurs, and overwintering eggs are produced by oviparous females. In mild-winter regions, the sexual form is not produced or is not the only stage overwintering, as the aphid reproduces parthenogenetically (viviparously) throughout the year.

Apparently there are five nymphal instars, the mean durations of which are1.7, 1.9, 2.1, 2.4, and 1.5 days, respectively, for apterous forms. However, four instars have also been reported.

These aphids differ considerably in appearance, not only because of the different sexual forms but because they typically produce two discrete color forms, one green and the other pink. It is not surprising, therefore, that one of the common names sometimes applied to this species is the "pink and green aphid." The most common form is the adult wingless (apterous) parthenogenetic form, which predominates during the summer months. The body is green or pink in color, and free of dark markings. The cornicles are quite long, and dark at the tips. The tubercles at the base of the antennae diverge or point outward, unlike the other common potato-infesting aphids. This aphid, in its apterous form, measures about 3.0–4.0 mm long, making this the largest of the common potato-infesting aphid species. The adult winged (alate) parthenogenetic form also is abundant in the summer, especially when aphid densities are high or the nutritional quality of the host plant dissipates. This form has the same pink or green body color with cornicles that are darker distally, but bears transparent wings with dusky veins and is slightly smaller in size, about 2.1–3.4 mm long.

In the spring in warm weather areas, winged viviparous females (Fig. 102) disperse from the winter hosts in early spring to young warm-season plants such as weeds and potato. They often remain on these hosts until the plants deteriorate, often



Potato Aphid, *Macrosiphum Euphorbiae* (Thomas) (Hemiptera: Aphididae), Figure 102 Winged adult female of potato aphid, *Macrosiphum euphorbiae* (Thomas).

from overcrowding by aphids. The hot weather of summer does not favor the aphids, and their numbers greatly diminish, but begin to increase again in the autumn. They are abundant in the winter on cool-season plants such as spinach, cole crops, and weeds. Viviparous females live for about 30 days, with 10 days in the nymphal stage and the remainder as adults. Occasionally they will survive up to 50 days. They produce, on average, about 50 young aphids, but sometimes up to 80 offspring, at a rate of about 2.5 per day.

The sexual forms also differ in appearance, both due to sexual differences and in comparison with the parthenogenetic forms. In the oviparous female, wings are absent. The head and thorax are whitish, the abdomen pinkish or greenish, and the tibiae are dark. This form measures only about 2.15 mm long. The male has wings. The male also has a dark head and thorax, with a brownish green abdomen and dark appendages. The male measures less than 1.6 mm long.

Potato aphid is polyphagous, though its predominant hosts are potato, tomato, and sometimes corn in the summer, and wild or cultivated rose in the winter and spring. Sometimes spinach and lettuce are heavily infested during the autumn months. Potato aphid may be found in association with other crops such as clover, field corn, hops, peach, pawpaw, soybean, strawberry, sugarbeet, sunflower, and tobacco. It also infests such flowers as canna, geranium, gladiolus, hollyhock, iris, lily, poppy, rose, rudbeckia, and tulip. Among the weed hosts are groundcherry, *Physalis* spp.; hoary cress, *Lepidium draba*; jimsonweed, *Datura stramonium*; lambsquarters, *Chenopodium album*; matrimony vine, *Lycium* sp.; morning glory, *Ipomoea purpurea*; pepper vine, *Solanum jasminoides*; pigweed, *Amaranthus* spp.; pepperweed, *Lepidium* spp.; plantain, *Plantago* spp.; ragweed, *Ambrosia* spp.; roundleaved mallow, *Malva rotundifolia*; shepherdspurse, *Capsella bursa-pastoris*; sow thistle, *Sonchus oleraceus*; smartweed, *Polygonum* spp.; wild lettuce, *Lactuca* sp.; and winter cress, *Barbarea vulgaris*. These aphids commonly move from host to host as the quality of the plants deteriorates due to seasonal changes. They are capable, however, of feeding indefinitely on the same hosts if the plants remain nutritionally suitable. Although rose is normally reported to be the overwintering host in cold climates, there are occasional reports that either apterae (wingless forms) or eggs are found during the winter months in cold climates on such diverse plants as asparagus, raspberry, and various weeds.

Potato aphid has many natural enemies, as is commonly the case with aphids. Most of the common ladybirds (Coleoptera: Coccinellidae), some lacewings (Neuroptera: Chrysopidae), flower flies (Diptera: Syrphidae), and the predatory midge *Aphidoletes aphidomyza* (Rondani) are reported to prey on potato aphid. Ground beetles (Coleoptera: Carabidae) affect aphid populations, but not as greatly as canopy-level predators.

Among the parasitoids of potato aphid are *Aphidius*, *Diaeretiella*, *Ephedrus*, and *Praon* spp. (all Hymenoptera: Aphidiidae) and *Aphelinus* and *Dahlbominus* spp. (both Hymenoptera: Eulophidae). Only *Aphidius nigripes* Ashmead is regularly abundant.

Several closely related species of fungi affect potato aphid, and are thought to be suppressive. Frequency of fungal epizootics is positively correlated with aphid density. High levels of rainfall, though perhaps aiding in development of epizootics, are not a necessary prerequisite.

Damage

Young tissue, usually the growing tip of the plant, is first attacked by potato aphids. As the aphids multiply they spread over the entire plant, removing plant sap throughout. The leaves take on a distorted appearance, with the leaf edges turned downward. This form of injury is typical of many aphids, on a variety of plants, but is especially evident on potato infested with potato aphid. Potato plants may die back from the tip downward, and heavy infestation can kill potato plants. Leaves may be covered with honeydew and sooty mold. At times, potato aphid can be the most important pest of potato.

On tomato, pepper, and eggplant the leaf deformities are less apparent though stunting of the growing tips is evident. The blossoms are especially preferred in the latter hosts, and blossom drop or fruit deformities may occur. Potato aphid infestation resulted in higher sunscald damage to tomato fruit, presumably due to reduced shading by foliage.

In the northwestern United States, potato aphid is very abundant on corn, often covering the lower surface of leaves. Despite its great abundance, it does not cause plant deformities and is not considered to be a serious pest on this crop. In lettuce, potato aphid may be a contaminant that reduces marketability, particularly the ability to ship the crop to other nations.

Potato aphid can transmit a large number of plant viruses, though it is not considered to be an especially effective vector. Among the viruses transmitted to potato and tomato are cucumber mosaic virus and potato virus Y.

Management

Suction traps have been used to capture winged forms of potato aphid, and although useful for determining presence of the aphids they are not very predictive of crop infestation levels. Periodic placement of plants in pots in fields, or "plant traps" has also been used in monitoring, and data obtained from plant traps correlates with suction trap estimates. Population estimates are usually attained by visual examination, although yellow water pan traps are useful for estimating invasion by alate aphids.

Foliar insecticides are applied for aphid suppression. Broad-spectrum insecticides are usually used because of the other, often more serious, pests associated with solanaceous crops. Because they are not important virus vectors, however, high numbers of aphids can be tolerated. Chemical suppression is not usually recommended unless half of the leaves are infested. Soaps, detergents, and oils can be used against aphids, but care should be taken not to burn the plants.

Studies conducted in Maine, USA, demonstrated that planting practices could influence damage to potato. Delay of planting from early May, to late May or early June, resulted in up to 90% reduction in aphid infestation. Early hilling operations, wherein row ridges are heightened with soil from the row middles, similarly deprived dispersing aphids of young plant tissue, resulting in lower aphid densities.

Cultural practices can also interfere with aphid host selection behavior. Reflective mulches, particularly aluminum mulch, are sometimes recommended for disruption of aphid invasion of crops. Evaluation of aluminum mulch in potato, however, showed that the beneficial effect of the reflective mulch was slight or of short duration, and therefore impractical. The undersowing of potato with rye grass also affects aphids, resulting in reduced aphid densities in fields with grass, and no loss in crop yield.

In northern climates, aphids deposit overwintering eggs upon wild and cultivated rose, and develop on these plants in the spring. Therefore, it is desirable to destroy, or treat with an insecticide, such overwintering sites before the aphids disperse to crops. Increasingly, aphids are shipped northward from southern climates on young plants, or overwinter in northern areas in greenhouses. Care should be taken to keep from introducing aphids into fields on transplants.

There are significant differences in susceptibility to aphid infestation among tomato, lettuce, and to a lesser degree potato, varieties. The basis for resistance in lettuce is uncertain, but butterhead varieties are less susceptible to infestation.

References

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, 729 pp

Smith LB (1919) The life history and biology of the pink and green aphid (*Macrosiphum solanifolii* Ashmead). Va Truck Exp Stn Bull 27:27–79

Potato Flea Beetle, *Epitrix cucumeris* (Harris) (Coleoptera: Chrysomelidae)

Both adults and larvae of this small insect may damage potatoes.

► Potato Pests and Their Management

Potato Leafhopper, *Empoasca fabae* (Harris) (Hemiptera: Cicadellidae

This insect is known for its ability to inflict "hopper burn" on plants.

► Potato Pests and Their Management
► Alfalfa (Lucerne) Pests and Their Management

Potato Pests and Their Management

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Potato is one of the crops that receives the heaviest use of pesticides in the world. This over reliance on insecticides has resulted in the development of pest resistance and the emergence of pests that were previously considered to be of minor economic importance.

Potato pest integrated pest management (IPM) programs should incorporate alternatives to chemical control. Pest control decisions using an IPM approach will help to reduce production costs by decreasing pesticide use. The final result of reduced pest control costs will be higher income for growers and reduced health risks for all people involved in crop management.

Managing pests successfully, using any method, depends on being able to reliably identify and monitor pest populations at each life stage. In North America, this means principally the Colorado potato beetle, the green peach aphid, and wireworms, which are considered major potato pests in most potato growing areas.

Colorado Potato Beetle

The Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae), is probably the most important pest in all potato-growing areas in the United States and has spread to the rest of the continent, Europe and Asia. Potato yields are reduced and plants sometimes killed by the adult and larval leaf feeding. Larvae cause most of the defoliation, consuming about four times more than the adults. Leaf feeding has the highest effect on yields when it occurs within two weeks of flowering. The few tubers produced by damaged plants are stunted and possibly unmarketable. Potato plants still can tolerate some defoliation without a yield reduction: up to 25% prior to flowering, between 10 and 15% when tubers are beginning to bulk, and up to 20% for the last 3 weeks of the growing season.

This beetle was first recognized as a potato pest in 1859. The high reproductive potential and the fact that this pest has become resistant to almost all the insecticides that have been used against it, make the Colorado potato beetle such an important pest. One possible explanation for the ability to develop resistant to many insecticides is that this beetle evolved on a family of plants (Solanaceae) that contains high concentrations of toxins, and during the evolution process the beetle developed the ability to detoxify ingested toxins.

The adult is about 10 mm long, with yellow rounded and convex wing covers (elytra) marked with 10 black stripes. The eggs are orange-yellow, and found in clusters of about 30 on the underside of leaves. The larvae are 3–12.5 mm long and have slug-like, soft-skinned, brick red to orange, humped bodies with two rows of black spots on each side, six legs and a black head.

Biology

In temperate regions, adults spend the winter buried 10–25 cm deep in the soil. Adults emerge in the spring just as the first volunteer potatoes appear. Potato fields are usually rotated; therefore, beetles emerge and feed in the same field on volunteer potatoes or weed hosts and then fly to find a new host field. Recently emerged beetles either mate close to the overwintering sites or fly to new potato fields. Females are able to retain sperm from the last season's mating, and to produce viable eggs without new copulation in the spring. Beetles are able to fly several kilometers. Colonizing beetles first feed and then oviposit within a week, depending on temperature. Females lay up to 800 eggs over a 4- to 5-week period. The extended egg laying period means that larvae may be present in the field for four to five weeks. In Idaho and the northeastern states, the eggs begin to hatch at the end of May or first week of June and hatch in 4–9 days depending upon temperatures. Young larvae remain close to the egg mass but begin to move throughout the plant as that leaf is consumed. The larvae pass through four growth stages in as little as 8–10 days with average temperatures of about 30°C, while it will take longer with lower temperatures. The fourth and final growth stage consumes three times as much as the other three stages together.

The mature larvae drop from the plant and build cells in the soil where they pupate and transform into adults in 1–2 weeks. The new summer generation of adults emerges and lays eggs in that field or an adjacent field, and then migrates to overwinter. At higher elevations, the beetle may have only a single generation or a partial second generation, which feeds only briefly and then migrates to the overwintering sites without reproduction.

Management

There are several effective ways of dealing with this pest, including cultural, biological, physical and chemical practices, several of which work best in combination. Keep in mind that potato beetle control practices in one field may affect nearby fields.

Crop Rotations

Crop rotations help in delaying or reducing beetle pressure. Planting cereal grains after potatoes aids in reducing migrations because cereals are poor launch sites for the beetles. Planting new potato fields as far from last year's fields as possible (at least 400 m) will reduce the number of immigrant overwintering beetles in the new field.

Control of Volunteers and Weeds

Because overwintering adults will need to feed before walking or flying into new fields, controlling volunteer potatoes, and weeds such as nightshades, is important, as they are a preferred and early food source for these emerging adults. This tactic does not provide complete control. Therefore, it is important to scout fields to see whether additional control methods are needed.

Other methods that have proven fairly effective are the use of plastic-lined trenches, propane flamers, and vacuums. Plastic-lined trenches are arranged on the edge of a field and beetles are trapped early in the season when they walk towards the crop and at the end of the season when they move out of the field to overwintering sites.

Chemical Control and Management of Insecticide Resistance

We currently have several insecticides that are very effective. However, as mentioned before, this pest has a great ability to develop resistance to almost all different classes of insecticides. In most cases, the choice of an insecticide is based on price, effectiveness, and ease of application. It is well known that the repeated use of the same insecticide or other insecticides from the same chemical class in the same year or in successive years will accelerate the development of resistance. With a little planning and forethought insecticide programs can be developed that will allow usage of older and newly developed insecticides for a prolonged period of time.

Mixtures of insecticides are not generally recommended. Potato beetles can develop tolerance to components of the insecticide mixture and the resultant resistance may be more permanent and more difficult to manage than one developed separately to each of the active ingredients present in the mixture.

Insecticides that are not harmful to beneficial organisms should be used because natural enemies play a major role in the management of resistance. They reduce potato beetle populations regardless of the pest's resistance and act against the selection of resistant populations.

Insecticides should only be used when needed. As mentioned before, potato plants can tolerate some defoliation without a yield reduction. Once populations become damaging, insecticides can be applied either at planting or to the foliage after emergence of the plants. Systemic insecticides applied at planting are effective not only against the beetles, but also in controlling aphids. If the systemic insecticide is no longer protecting the crop when tubers are beginning to bulk (within two weeks of flowering) a foliar insecticide application may be necessary.

It is not always necessary to spray foliar insecticides over the whole field. When crops are rotated, the arriving beetles will concentrates at the edge of the new fields and defoliated plants will be restricted to field edges. Thus, treating only this area may be adequate.

Young larvae are most susceptible to insecticides. Since the older larvae are responsible for 75% of the feeding damage, early treatment will also prevent economic damage. The foliar application will be more effective when 15–30% of the beetle eggs have hatched, and will be justified with defoliation from larvae above 10–15%.

Biological Control

Not all the Colorado potato beetle eggs deposited early in the spring will become adults. Several beneficial insects that feed on eggs and young larvae will reduce the number of adults in the first spring generation. Ground beetles, predatory stinkbugs, ladybird beetles, and collops beetles are some of the predators that may reduce potato beetle populations. There also are pathogenic fungi such as *Beauveria bassiana* and *Paecilomyces farinosus* that infect and reduce potato beetle populations. However, the limited knowledge about natural enemies and the reliance on insecticides have limited their usefulness. Natural enemies can be protected by using "biorational" approaches such as microbial insecticides, mineral and vegetable oils, neem, and fermentation-based products that are toxic only to the Colorado potato beetle. Toxins from strains of the naturally occurring bacterium *Bacillus thuringiensis* (*B.t.*) are commercially available and have good potential for use in combination with natural enemies because of their specificity to potato beetle.

Green Peach Aphid

The green peach aphid, *Myzus persicae* (Salzer) (Hemiptera: Aphididae), is a European native that occurs throughout the world on a diverse host range of over 875 species of plants. It is the most common and abundant aphids in North America. It is considered one of the most difficult insect species to control due to its high reproductive potential and diverse host range. It seriously damages many crop plants directly by feeding, and also transmits more than 100 viruses to cultivated crops. Aphid numbers may occasionally be high enough to cause damage to potato crops by excessive removal of sap, but main losses occur when it transmits potato leafroll virus (PLRV). The virus causes yield reduction and reduced quality. Green peach aphid is by far the most efficient PLRV vector.

Green peach aphid may be winged or wingless. Wingless forms are yellow-green to pinkish. Winged green peach aphids are pale or bright green with a dark head and thorax. The irregular dark patches on the abdomen are characteristic but not unique. Not all winged aphids in potato fields are green peach aphids. Many species of winged aphids that have developed on other crops or weeds may be present.

Biology

The life cycle of aphids in general is very unusual and complicated. It includes several body forms, and a sexual and an asexual mode of reproduction. Asexual reproduction occurs during the growing season when females give birth to live females (they do not lay eggs, as it is usually the case with insects) for 10–25 generations. Sexual females produce eggs in the fall.

In the north, green peach aphid overwinters as eggs on the primary host, the peach tree. However, in southern regions and during mild winters aphids can also overwinter on several weeds, such as mustards, nightshade and ground cherries.

When green peach aphid overwinters on peach and nectarine trees, wingless females known as "the stem mothers" hatch from eggs that were laid near the buds in the previous fall, and produce live nymphs without mating. Eggs may hatch in response to warm periods as early as late January or early February. At high elevations egg hatching may not occur until April. The green peach aphid remains on the host tree in the spring until leaves are fully expanded. Then, winged aphids, known as "spring migrants," are produced. These spring migrants fly to secondary hosts, which may be weeds, crop plants or ornamentals. Up to 40,000 spring migrants may be produced on one tree.

Although long-distance, wind-aided flights are possible, most winged migrants establish colonies near the winter host if summer host plants are present. They search for suitable hosts by making a series of short random flights. When an acceptable host is located the aphid feeds and deposits as many as 20 nymphs. Then the aphid takes flight and the process is repeated.

Once hosts mature, another winged form is produced, the "summer migrant." Summer migrants usually land in greatest numbers on the edges of potato fields. Summer development of populations is strongly influenced by weather. Sudden hot or cold periods, high winds and hard rains or hail can significantly reduce populations. Summer migrants produce nymphs that can complete development in as short as 6 days and they in turn begin producing young 2 or 3 days later. Maximum reproduction occurs at temperatures between 24 and 30°C. Reproduction is sharply reduced at temperatures above 35°C and reproduction slows as temperatures are lowered from the optimum range. Temperatures under the vine canopy, where the aphids are reproducing, are less extreme than in the open. In general, weather conditions that favor high tuber yields also favor aphid reproduction. Each aphid is capable of producing 30–80 nymphs over a period of 10–20 days. They tend to deposit nymphs on a series of plants instead of putting them all on one plant. Where population peaks result in extreme crowding, winged aphids develop and move out of the field, thereby greatly reducing numbers. Declines in populations also may be associated with periods of extremely high temperatures and with a decline in potato vine condition.

The cold weather in the fall and/or the lack of suitable hosts triggers the production of winged aphids, which will be the ones returning to the primary host. These are the "fall migrants." One type of winged migrant aphid deposits nymphs on leaves of peach trees. These nymphs develop into wingless sexual females. The other type of winged migrant is the sexual male, which mates with the wingless female. Each female then deposits 5–15 eggs on or near the axillary buds. Total number of eggs per tree is extremely variable but may exceed 10,000 in mild falls when aphid activity continues into late November.

Management

A successful integrated pest management program should include methods aimed to breaking the life cycle of this aphid, such as applying insecticides to control the aphid, and eliminating or treating overwintering and secondary hosts.

Cultural Control

The number of green peach aphids present in the spring to infest crops depends upon winter survival. The common means of overwintering is on the winter host in the egg stage. Peach trees are the most common winter hosts, although apricots and other species of *Prunus* are infested on rare occasions. Fields near commercial peach orchards, or urban areas with backyard and abandoned peach trees, usually have higher populations than those in isolated areas. If spring and summer weather are favorable for aphid development a single peach tree can potentially produce enough winged aphids to initiate economic infestations on at least 500 acres of potatoes. Removing and replacing peach and apricot trees and spraying insecticides on commercial peach orchards are valid attempts to prevent aphid buildup.

Seed production areas at high elevations and commercial production areas with severe winters are usually too cold for survival of primary host plants. However, it is not unusual to observe potato fields in these areas close to towns with high aphid populations and high PLRV incidence. This is because many of the bedding plants that homeowners buy in local greenhouses are infested with green peach aphids. In Idaho for example, a 1990 survey of bedding plants that were introduced from surrounding states and were commercially available in all seed production areas of eastern Idaho, revealed that 37% of these plants were infested with green peach aphids and, therefore, home gardens represented a major source of aphid infestations in seed production areas in that state. Aphids moving directly from home gardens to potato plantings often transport viruses because home garden potato plants often have a high rate of disease infection.

Elimination of aphids on bedding plants is a very important part in the success of any integrated pest management program of green peach aphid and PLRV. Campaigns oriented to educate home gardeners about the importance of buying and planting bedding plants with no aphids are needed.

Many winged aphids from peach trees and other sources appear before crops are available for colonization. The ground cover of overwintering orchards usually includes suitable hosts that may become heavily infested. Early infestations commonly occur on a number of weeds including species of mustards, nightshade and ground cherries. Winged forms produced on these weeds later infest crop plants, including potatoes, and high numbers may appear during a short period when one or more species of weeds dry up or mature.

Where the winters are mild, aphid colonies can survive the winter outside on plants that maintain green growth. In areas where minimum temperatures are too severe for plant growth, plants near canals, springs, or adjacent to heated buildings may be infested because of the higher minimum temperatures at these locations. This kind of overwintering occurs primarily in low elevation potato-growing areas or protected places, and except in unusually mild winters or local situations, is less important than the other two aphid sources discussed.

General insecticide application guidelines based upon aphid numbers are used in some areas. When making counts, sample several areas of a field because aphid numbers are usually highest on field margins, including weeds. Nightshades are one of the preferred weeds.

When scouting, it is important to keep in mind that green peach aphid prefers to infest lower portions of potato plants. After periods of cool cloudy weather tops of plants may be infested. Colonies will also develop on upper portions of plants where crowding occurs. Aphid reproduction is favored by dense vigorous vine growth.

Early aphid migrants not controlled on time will form colonies. Therefore, detection of few aphids and application of insecticides on time will prevent the formation of these colonies. It is important to inspect the fields every 3–4 days and watch for the presence of surviving, wingless aphids.

Biological Control

Predators, parasitoids and pathogens affect aphid populations and may keep aphids below economic levels in particular situations. The sudden decline of aphid population late in the season may be associated with several factors of which the action of predators is often dominant. However, applications of insecticides and fungicides against other potato pests reduce or even eliminate populations of natural enemies, allowing aphid populations to increase rapidly. For this reason, high populations of aphids can sometime be observed after the application of an insecticide against Colorado potato beetle and potato leafhopper.

Chemical Control and Management of Insecticide Resistance

The green peach aphid is difficult to control because of the high reproduction capacity, and because it has developed resistance to at least 69 insecticides representing all major classes. However, it is critical to control aphid in production areas with PLRV susceptible cultivars such as Russet Burbank. Most of the principles of chemical control of Colorado potato beetle explained above apply also to green peach aphid.

Alternating insecticide use among the major insecticide groups reduces the development of resistance. Some systemics can give adequate aphid control and also reduce Colorado potato beetle, wireworm, or nematode numbers. Cost of the insecticide may be an important consideration.

The effectiveness of any insecticide used intensely in an area will be reduced significantly after a few years. Preventing or reducing speed with which resistance develops depends mainly on reducing insecticide use to the bare minimum necessary for economic crop production. It is important to note that not all insecticides that kill aphids prevent virus transmission.

Timing the application of an insecticide is as critical as selecting it. Applying systemic insecticides to the soil at the time of planting effectively controls aphids. At high elevations where mid- to late-season pressure from winged aphids is light, these applications may provide season-long protection. At lower elevations, one or more foliar applications of insecticide may be necessary after about midseason. Application of foliar insecticides should begin when one to three wingless aphids per 100 leaves are detected. This is a very low threshold for most scouting programs to detect with confidence.

Wireworms

Wireworms are becoming increasingly important in several potato-growing areas in North America.

Two of the possible reasons for this are the increased rotation with grasses for the cattle industry, and the removal of insecticides with long residual activity in the soil. The adults, known as click beetles, produce little or no damage and the larval stage causes the damage to seedlings and underground parts of annual crops by feeding on seeds and tunneling potato seeds and tubers. There are 885 species of wireworms (family Elateridae) in the United States. Three species of wireworms commonly damage potatoes in western North America. The sugarbeet wireworm, *Limonius californicus* (Mannerheim), and the Pacific Coast wireworm, *L. canus* LeConte, are found in soils that have been under irrigation for three or more years. The Great Basin wireworm, *Ctenicera pruinina* (Horn), infests soils previously farmed without irrigation, in pasture, or soils recently brought under cultivation. Although crop losses from wireworms are only sporadic, these are substantial (5–25%) in some places.

Wireworm larvae are about 2.5 cm long when fully mature, hard-bodied, slender, cylindrical, glossy, small-legged, and yellow-to-light brown. They feed on potato seed pieces and underground stems during the spring. This early feeding opens the seed pieces and stems to rotting organisms, which can result in poor or weak stands of potatoes. Wireworms also burrow into developing tubers. The holes look as if they were made by stabbing the tuber with a nail and usually are lined with potato skin.

Biology

The life cycle of our most common wireworms requires 3–4 years under favorable conditions. Wireworms spend the winter in the soil either as partially grown larvae or as new adults in overwintering cells. Adults work their way to the soil surface in the spring when soil temperatures reach 13°C or above. These adults require little or no food and cause no economic damage. The female mates soon after emerging from the soil, then burrows back into the soil and lays eggs at depths of 2–20 cm in several locations. The sugarbeet wireworm prefers vegetated areas for oviposition. Infestations are often spotty because oviposition is not uniform and some localities are more favorable for larval development than others.

Wireworm larvae cause the most severe feeding damage during their second and third years. In the spring, when soil temperatures reach 13°C or above, the larvae move toward the soil surface from depths of 6–24 in. where they have spent the winter. When soil surface temperatures reach 27°C or higher, they move downward again. In irrigated fields with complete foliage cover, this higher temperature level may not be reached. During the third or fourth season, mature larvae transform to fragile pupae in earthen cells. In 3–4 weeks the pupae change to adults, which remain in the earthen cells until the following spring. Wireworms in all stages may be present in the soil during any growing season.

Management

Because of the similarities in the biology of wireworms, the same management approaches apply to all the species. USDA standards for U.S. No. 1, U.S. Commercial, and U.S. No. 2 potatoes allow only 6% external defects. These includes soil or other foreign matter, sunburn, greening, growth cracks, air cracks, scab, rhizoctonia and mechanical damage, as well as insect damage. If allowance is made for defects other than wireworm damage, only to a small percentage of wireworm injury is allowable.

Detecting wireworm infestations and determining size of wireworm populations is not easy. Baiting gives a very poor estimate of population size but is a quick way to determine whether wireworms are present. Baits have to be buried in the ground one month before planting to determine the need for insecticide treatment. If wireworms are found in baits, soil sampling can be used to estimate the population density. An understanding of wireworm larval movement in soil is needed to design an effective sampling method. There are no reliable economic thresholds for wireworms.

Carrots, corn, wheat, and coarse-ground whole-wheat flour buried about 7 cm in the soil are good baits. Wrap a few grams of flour in a scrap of nylon mesh with the tail end of the mesh protruding from the soil. Randomly place these baits or carrots in a field. Mark the bait locations clearly. The more bait locations used, the greater the chance of discovering an infestation. After 2–3 days, dig up the bait and check for wireworms. Baits are not effective in soils that are very dry, wet, or cold, or if excessive organic residue is present. Covering bait stations with dark plastic will allow sampling earlier in the season when soil temperatures are cooler.

Most of the insecticides used to control wireworms are relatively old. Wireworms can be suppressed by broadcast or band treatments, by fumigation, or with seed treatments. Usually, controlling wireworms in one crop of a 2–4 year rotation will reduce wireworm damage in the other crops. For broadcast treatments, apply granules or emulsifiable concentrates evenly over the soil and incorporate immediately. Depth of incorporation varies depending upon the insecticide selected. Granular insecticides may be used as band treatments at planting time. These should be applied in narrow bands 7–10 cm below the seed piece in the seed piece furrow at planting time. Fumigants may be used to control high wireworm populations but a combination of broadcast and band treatments may be more economical to use, depending on the pest complex. Seed treatment insecticides used to control Colorado potato beetle and green peach aphid have also proven effective at reducing wireworm damage. Keep in mind that even the best insecticides will not kill all the wireworms and a small percent of a large population could still cause economic damage.

Certain cultural control practices can also be effective. One practice is to avoid rotations that include clovers and grasses. Because soil dryness can kill many wireworms in an infested field, fallowing a field will reduce wireworm numbers, but the control achieved must be weighed against the income lost from missing a crop year. It is important to keep in mind that when soils dry out in potato fields, wireworms may seek moisture from tubers, therefore increasing the wireworm damage. Plowing a dry field during the first 10 days of August can break up the pupal cases. In fields where populations have been reduced, potatoes, a susceptible crop, should be planted the first year in rotation followed by less susceptible crops such as sugarbeets, beans or corn in the ensuing years. If wireworm populations are very high in a certain field, perhaps potatoes should not be planted in that field. Avoid planting potatoes in fields that have had several successive years of cereal grains and/or corn.

Known natural enemies of wireworms include birds, carabid and staphylinid beetles, entomopathogenic nematodes, and pathogenic fungi such as *Beauveria* sp. and *Metarhizium* sp. However, there is not much information on the real effect of these natural enemies.

Secondary Pests in Alphabetical Order

Blister Beetles

Four species of blister beetles commonly damage potato: the spotted blister beetle, *Epicauta maculata* (Say), the ash-gray blister beetle, *Epicauta fabricii* (LeConte), the Nuttall blister beetle, *Lytta nutalli* Say, and the punctured blister beetle, *Epicauta puncticollis* Mannerheim. They are elongate (1.5–3 cm) with conspicuous heads and necks. The wing covers are soft and do not completely cover the tip of the abdomen. The beetles cluster on the tips of the plants causing leaf ragging and stunted plants. Severe damage, however, is not common. The adults first appear in the summer and live about 45 days. They are usually abundant only in areas adjacent to rangeland where the larval stages are predatory on grasshopper eggs.

Check field edges in years of heavy grasshopper infestations. The beetles are strong flyers and often fly from an area before damage is detected and controls can be applied. If beetles remain in the field and continue to defoliate field edges, border sprays will eventually alleviate the problem. If defoliation remains below 10–15%, controls are probably not needed.

Cutworms and Armyworms

Cutworms are soil dwelling caterpillars having a smooth appearance, three pairs of legs and five pairs of prolegs. Some species may be up to 5 cm long when mature. The black cutworm, *Agrotis ipsilon* (Hufnagel) (gray to black upper half and distinct greasy appearance), variegated cutworm, *Peridroma saucia* (Hübner) (top line of small, pale spots more distinct on front portion), spotted cutworm, *Xestia* spp. (pairs of black oblique marks on top of last four segments) army cutworm, *Euxoa auxiliaris* (Grote) (body gray with darker top-lateral and spiracle stripes), and the red-backed cutworm, *Euxoa ochrogaster* (Guenée) (top often distinctly reddish bordered with dark bands), feed at night. During the day they can be found under clods of soil or in cracks in the ground near injured plants. The western yellowstriped armyworm, *Spodoptera praefica* (Grote), feeds during the day and like the army cutworm may migrate in mass into potato fields from adjacent crops. Cutworms either cut off stems at or below ground level or strip the foliage during the growing season. They also feed on tubers that are exposed on the surface or accessible through cracks in the soil.

Cutworms spend the winter as partly grown larvae or pupae in the soil. One to several generations occur per season depending upon which cutworm is involved. The adults are dusky-brown to gray miller moths and are commonly observed flying around lights during the warmer seasons.

Control programs are aimed only at seriously damaging infestations because natural enemies generally hold the populations in check. Some defoliation from cutworms can be tolerated. Keeping defoliation between 10 and 15% will generally prevent yield loss. Weed control in previous crops and along field edges also aids in reducing cutworm damage.

Flea Beetles

Adult western potato flea beetles, *Epitrix subcrinita* LeConte, and potato flea beetle, *Epitrix cucumeris* (Harris), seldom cause damage severe enough to warrant control but extensive leaf feeding by adults may be an indication of later tuber infestation by larvae. Injury on the surface of the potato tuber consists of rough, winding trails up to 2 mm wide and of varying length. Internal tuber injury consists of shallow, narrow brown subsurface feeding tunnels. These tunnels occur singly or in groups, and are about 1 mm in diameter and up to 6 mm deep. Fungi often fill the tunnels. When potatoes are processed, these injuries must be removed by deep peeling to prevent discolored products.

The adults are about 2 mm in length and metallic greenish-black in color. Adults are active in the spring and feed in weeds until the potato plants emerge. Small, round holes in potato leaves are indicative of adult feeding. Females scatter their eggs in the soil at the base of the potato plants. The eggs hatch in 10 days and the tiny whitish larvae feed on underground stems, roots and tubers for 3–4 weeks. There are 1 or 2 generations a year depending on location. Adult western potato flea beetles hibernate under leaves, grass or trash, on margins of fields, along ditch banks and other protected places.

The tuber flea beetle, *Epitrix tuberis* Gentner, occurs in the major potato growing areas of the Northwest except southern Idaho and eastern Oregon. Extensive leaf feeding by adults will cause defoliation of the plants and reduce tuber growth.

Adults chew small holes in leaves, and extensive feeding causes a sieve-like appearance. Severely damaged leaves turn brown and die. Flea beetles can transmit potato diseases, such as spindle tuber and brown rot, and the leaf wounds may allow entry of air or waterborne disease organisms. The appearance and life cycle of the tuber flea beetle are very similar to those of the western potato flea beetle.

Larval damage is much more severe because the larval tunnel goes up to 12 mm directly into the tuber whereas the western potato flea beetle burrows under the peel and seldom penetrates over 6 mm. Some lots of potatoes may be unsuitable for processing when damage by the tuber flea beetle is extensive.

Management

Soil applications of systemic insecticides and foliar applications of insecticides for Colorado potato beetle and green peach aphid control hold flea beetle populations to sub-economic levels.

Garden Symphylan

The garden symphylan, *Scutigerella immaculata* (Newport), is not a widespread pest, but it can limit potato production in some localities. Symphylan feeding on the root hairs and rootlets may stunt plant growth before tuber formation. Damage to developing tubers consists of tiny holes in the skin with an undercut cavity lined with hard, dark, corky tissue around each point of injury. Damaged tubers are unmarketable.

Garden symphylans are not insects but are a more primitive centipede-like animal. The adults are white and live below the surface in loose soil where they appear to constantly run in and out among the particles. Symphylans move rapidly away from light, so you must look quickly after exposing the tubers or soil to see them.

Symphylans lay their eggs in the spring or early summer in cavities in the soil. The eggs hatch in 1–3 weeks. Under favorable conditions, a new brood develops in 60 days and the adults may live for several years. Optimum temperatures for activity of symphylans are from 10 to 21°C. They readily move up and down in the soil to stay within this range.

Management

Control measures must be very thorough if root crops are to be grown in symphylan- infested soils. Fall fumigation of infested areas can be effective. Insecticides should be broadcast in the spring as close to planting as possible and thorough coverage is essential. Carefully watch the field history for symphylan damage. If damage has not occurred in other crops, damage should be minimal to potatoes.

Grasshoppers

Grasshoppers are pests of potatoes only during years when they migrate out of uncultivated areas. Usually their populations are small and their damage is inconsequential. During outbreak years they can defoliate potatoes and transmit viruses, causing spindle tuber and unmottled curly dwarf.

The several species of grasshoppers that cause the most damage to potatoes are the migratory grasshopper, *Melanoplus sanguinipes* (Fabricius), clearwinged grasshopper, *Camnula pellucida* (Scudder), and the redlegged grasshopper, *Melanoplus femurrubrum* (DeGeer).

Other species may cause local, periodic problems. Grasshoppers lay their eggs in inch-long pods, each containing 10–75 eggs, deposited slightly below the surface of the soil in late summer or fall. Each female may lay from 8 to 20 pods.

Hard uncultivated ground is preferred for ovipositing although eggs are sometimes found on the edges of cultivated fields, along ditch banks, in pastures and hay fields. The eggs hatch in the spring depending upon the weather conditions and grasshopper species. The nymphs resemble the adults, but are smaller and without wings. There is one generation per year and the nymphs become mature in summer or early fall.

Management

Control programs need to be initiated only when problems develop. In outbreak years, area-wide programs are more effective than field-by-field treatment for grasshoppers. Also, in outbreak years, watch for blister beetles that may move into the field edge and cause local defoliation.

Leafhoppers

The potato leafhopper, *Empoasca fabae* (Harris), is a North American species considered to be one of the most destructive potato pests in northeastern and midwestern United States. In the West, however, the intermountain potato leafhopper, *Empoasca filamenta* Delong, is important. Nymphs and adults of leafhoppers feed on the undersurface of potato leaves and cause a speckled or white stippled appearance on the lower leaves. Adults are wedge-shaped, green insects with white markings and are about 4 mm long. Nymphs are similar in color but are smaller and lack wings. The intermountain leafhopper does not cause "hopper burn" or leaf scorching to potatoes like the eastern potato leafhopper. The adults pass the winter in grass and weeds along the field margins and in other areas where they have at least one generation before they move to potato fields.

Management

Control measures specifically for the leafhopper in the West are rarely warranted. Soil applications of systemic insecticides for other pests effectively control the intermountain potato leafhopper. In the East, foliar applications of insecticides are warranted when potato leafhopper is abundant.

Witches' Broom and Leafhoppers

There are several diseases produced by phytoplasmas in potato. Leafhopper species in the family Cicadellidae have been implied in the transmission of phytoplasmas. Phytoplasmas are pathogens transmitted in persistent form; therefore require long periods of acquisition and an incubation period.

One of these diseases, the disease known as witches' broom, has been reported occurring sporadically in some seed production areas. This disease produces a severe halting of plant growth due to the shortening of stems, and also induces marginal chlorosis of the leaves. The plants do not produce tubers, or only some small ones with enlarged buds.

The control of the diseases caused by phytoplasmas depends exclusively on the use of seed free of these diseases. For this reason, seed must be produced in areas that are known to be free of the vector, and all plants showing some of the described symptoms must be eliminated. Tubers showing proliferation of buds must be eliminated. The control of vectors is not a practical measure and perhaps it only can be used in conditions where the vector remains in the field or forms colonies on the crop.

Leather Jackets

Severe damage by the leather jacket, *Tipula dorsimacula* (Walker), may occur in fields planted with potatoes following spring plowing of alfalfa or in low, moist, weedy areas in the field. Larvae feed on tubers, causing round punctures varying from shallow depressions to inch-deep holes.

Leather jackets overwinter in the soil as mature or nearly mature larvae. Adults emerge in the spring and deposit eggs in the vicinity of plant refuse. The larvae initially feed on the decomposing plant tissue in the soil but later transfer to developing tubers.

Mature larvae are about 3–4 cm long, gray to gray-brown, and have characteristic fleshy anal projections. Their skin resembles leather, giving rise to the common name leather jacket. The adult fly is about 2.5 cm long with long, fragile legs that may drop off when the insect is handled. Adults look like giant mosquitoes.

Management

Control consists of avoiding spring incorporation of alfalfa green manure, weed control, and water management to prevent water-soaked areas.

Loopers

The most common loopers found in potato fields are the cabbage looper, *Trichoplusia ni* (Hübner) and the alfalfa looper, *Autographa californica* (Speyer).

Damage is caused by the greenish, white-striped larvae which may be 3 cm long when mature. They differ from cutworms in that they only have three pairs of prolegs. The middle of the larva is characteristically humped up when the insect rests or moves and for this reason they are often called measuring worms. Defoliation usually starts in the middle of the plant. The adult is a gray-brown miller moth that looks like a cutworm adult. There are 2–3 generations per year.

Management

Loopers seldom become a serious pest of potatoes even though they may build up high numbers. Damage usually occurs just after the vines have gone into senescence. Loopers often are found with cutworms and are blamed for the cutworm damage because the cutworms are hidden during the day. As long as defoliation remains below 10–15%, control measures are seldom warranted. Foliar sprays applied for Colorado potato beetle will usually control loopers as well.

Lygus Bugs

Lygus bugs, *Lygus elisus* Van Duzee and *Lygus hesperus* Knight, are general feeders found on most plants and trees. Damage by lygus is the result of their sucking sap from buds and leaves. Lygus bugs inject a toxin during feeding which kills the area fed upon or causes distorted growth.

Immature lygus bugs (nymphs) are smooth glossy green insects that are similar in size to aphids, but move rapidly when disturbed. Several overlapping generations occur each year that require about 6 weeks each.

Adult lygus are 6–7 mm long, green to brown bugs with a yellow triangle on the back. They hibernate in debris in fields or field margins. The insects are strong flyers and move from field to field. They usually move into a potato field just after an adjoining field is harvested or has matured. Damage is most severe on field margins.

Management

Control is seldom necessary because lygus bugs are a sporadic pest. Damage is not often noticed until the lygus bugs have left the field.

Potato Aphid

The potato aphid, *Macrosiphum euphorbiae* (Thomas), occurs in most potato growing areas, but infestations are usually not economically important for crops grown for table stock. The aphid is an efficient vector of potato virus Y and PLRV and is therefore important to seed potato production.

The aphid overwinters in the egg stage on rose bushes. Infestations develop on this host in the spring and winged forms are produced after several generations. These fly to various summer hosts that include tomatoes, ground cherry and nightshade in addition to potatoes. Nightshade weeds are apparently the preferred host.

Infestations of potato aphids usually develop on the upper parts of potato plants. This is in contrast to the green peach aphid, which usually occurs on the lower leaves. The potato aphid is green and more elongate and larger (3–4 mm) than the green peach aphid. The cauda (tip of the abdomen) is long, extending beyond the tips of the cornicles. The cauda of the green peach aphid is less conspicuous and extends about to the tips of the cornicles. The frontal tubercles of both species are prominent but they are rounded in the potato aphid and angular, appearing boxlike, in the green peach aphid. When exposed to sunlight, potato aphids rapidly move to the opposite side of the leaf while green peach aphid will not move.

Management

Plant certified seed to avoid transmission of Potato Virus Y or plant a variety not susceptible to PVY. Other control measures are seldom warranted. The same management recommendation to reduce virus spread by green peach aphid apply also to this aphid.

Thrips

Two species of thrips are associated with foliar damage to potatoes. These species are the onion thrips, *Thrips tabaci* Lindeman, and the western flower thrips, *Frankliniella occidentalis* (Pergande). Thrips cause damage by severely scarring the undersides of leaves and "silvering" the tops of leaves. Extensive damage causes the leaves to become dry and drop. Defoliated plants never recover.

Damage by thrips is usually restricted to the outside 3–5 rows adjoining wasteland, grain or dry pastures. Occasionally small fields are totally infested. Thrips move into potato fields when alfalfa is harvested or as grass or grain hosts dry during June or July. Similar damage can be caused by windburn, blown sand or by leaves being hit directly by water from sprinklers.

Thrips are tiny, yellow, brown, or white (nymphs) insects that feed at night or on cloudy days. They rasp and puncture the leaf tissue with their saber-like mouthparts and swallow the sap together with bits of leaf tissue. During the day they are found in cracks in the soil or along leaf veins on the plants.

Management

Thrips are generally kept in check by predators and seldom become a problem. When damage occurs, the thrips population has usually declined before the cause is discovered. If thrips remain in potatoes and halt growth, control measures are warranted.

Twospotted Spider Mite

Twospotted spider mites, *Tetranychus urticae* Koch, develop some years in potato fields. Problems usually occur downwind from infested bean, corn, alfalfa or clover seed fields or along dusty roads. Spider mites damage plants by puncturing the leaf tissue with their mouthparts to extract the plant juices. Injured cells and those surrounding the injury die, causing loss of chlorophyll. The injury first looks like stippling or small blotching, turning yellowish, then brown. These injury blotches come together causing the leaf to be brittle and brown. In severe infestations brown areas can progress rapidly across the field.

Adult mites are one mm long, yellow, with a dark spot on either side of the body. Nymphs are similar but smaller. Eggs are clear, round spheres found in the feeding areas.

Spider mites overwinter as adults in the soil or in debris in fields, fencerows or field margins. The adult female emerges and lays eggs on the undersides of plant foliage in late spring. A female can lay 20 eggs a day with a total of 300 eggs during her lifetime. The eggs hatch in 3–5 days. During hot weather the young develop to adults in 7–9 days. The female spins a fine web over the leaf, which apparently protects the eggs and mites from rain and predators. In severe infestations the leaves are tied together with dirty webbing. When populations become severely crowded, mites climb to the top of a plant or post and secrete a web strand. Some mites are then carried by the wind. This is why sudden infestations commonly develop downwind from previously infested fields.

Management

Sprinkler irrigation washes the foliage, breaking webs and dislodging the mites, thereby reducing

Potato Pests and Their Management, Table 16 Insecticides available for use against potato pests

Class	Commercial name	Common name	Site/mode of action	Application method	Pest controlled
Biological	Raven	*Bacillus thuringiensis* var. *kurstaki*	Stomach poison	Foliar	CPB
	Novador, M-Track	*Bacillus thuringiensis* var. *tenebrionis*	Stomach poison	Foliar	CPB
	Colorado Potato Beetle Beater (Bonide)	*Bacillus thuringiensis* var. *san diego*	Stomach poison	Foliar	CPB
	Agri-Mek, Avid	Abamectin	Neurotoxin, GABA inhibitor	Foliar	CPB
	Success	Spinosad	Gamma receptor (neurotoxin)	Foliar	CPB
Botanical	Azatin XL Plus BioNeem Margosan-O Neemix	Azadirachtin	Interference with molting, repellent	Foliar	CPB
	Rotenone/Pyrethrin Spray (Bonide)	Rotenone	Respiratory enzyme inhibitors of fish and insects, not mammals	Foliar	CPB
Carbamate	Temik 15G	Aldicarb	Central nervous system/acetyl-cholinesterase inhibitor	At planting	Aphids, CPB
	Furadan 4F	Carbofuran	Central nervous system/acetyl-cholinesterase inhibitor	Foliar and at planting	Aphids, CPB, wire-worms, fleabeetles
	Sevin	Carbaryl	Central nervous system/acetyl-cholinesterase inhibitor	Foliar	CPB, leafhoppers, fleabeetles, cut-worms, armyworms
	Vydate	Oxamyl	Central nervous system/acetyl-cholinesterase inhibitor	In-furrow at planting or foliar	Aphids, CPB, fleabeetles
Chloronicotinyl	Admire 2F	Imidacloprid	Central nervous system/ neurotoxin	In-furrow at planting or seed treatment	Aphids, CPB, leafhop-pers, fleabeetles
	Genesis	Imidacloprid	Central nervous system/ neurotoxin	Seed treatment	CPB
	Gaucho-MZ	Imidacloprid	Central nervous system/ neurotoxin	Seed treatment	Aphids, CPB

Potato Pests and Their Management, Table 16 **Insecticides available for use against potato pests**

Class	Commercial name	Common name	Site/mode of action	Application method	Pest controlled
	Provado	Imidacloprid	Central Nervous System/ neurotoxin	Foliar	Aphids, CPB
Chloronicotinyl; pyrethroid	Leverage	Imidacloprid; cyfluthrin	Central nervous system/interferes with the nicotine type acetylcholine receptor; sodium channel	Foliar	Aphids, CPB, plant bugs, flea beetles, cutworms, loopers, leafhoppers,
Cyclodiene	Thiodan 3EC, and 50WP, Phaser 3EC and 50WSB, Endosulfan 3EC and 50WSB	Endosulfan	Central nervous system/sodium and potassium balance in neurons	Foliar and chemigation	Aphids, CPB, fleabeetles
Inorganic	Kryocide, Cryolite	Sodium aluminofluoride	Inhibits enzymes with iron, calcium or magnesium centers	Foliar	CPB
Organochlorine	Methoxychlor	Methoxychlor	Central nervous system depression	Foliar	CPB
Organophosphate	Guthion	Azinphos-methyl	Central nervous system/acetylcholinesterase inhibitor	Foliar	CPB, Leafhoppers, fleabeetles
	Diazinon	Diazinon	Central nervous system/acetylcholinesterase inhibitor	Broadcast preplant	Wireworms, fleabeetles
	Di-Syston 15%G	Disulfoton	Central nervous system/acetylcholinesterase inhibitor	In-furrow at planting	Aphids, CPB
	Di-Syston 8EC	Disulfoton	Central nervous system/acetylcholinesterase inhibitor	Foliar, may be applied by chemigation	Aphids, CPB
	Lorsban	Chlorpyrifos	Central Nervous System/cholinesterase inhibitor	At planting to postemergence	wireworms
	Monitor	Methamidophos	Central nervous system/acetylcholinesterase inhibitor	Foliar	Aphids, CPB, Fleabeetles, cutworms, armyworms
	Penncap-M	Methyl parathion	Central nervous system/acetylcholinesterase inhibitor	Foliar	CPB

Potato Pests and Their Management, Table 16 Insecticides available for use against potato pests (Continued)

Class	Commercial name	Common name	Site/mode of action	Application method	Pest controlled
	Thimet 15G and 20G, Phorate 20G	Phorate	Central nervous system/acetylcholinesterase inhibitor	In-furrow at planting or side dress at hilling	Aphids, CPB, wireworms, fleabeetles
	Imidan 70-WSB	Phosmet	Central nervous system/acetylcholinesterase inhibitor	Foliar	CPB, fleabeetles
Pyridine Azomethine	Fulfill	Pymetrozine	Central nervous system/interferes with the nicotinic acetylcholine receptor Anti-feeding	Foliar	Aphids
Pyrethroid	Baythroid 2	Cyfluthrin	Central nervous system/axonic poison, sodium channel disrupter	Foliar	CPB
	Ambush, Pounce	Permethrin	Central nervous system/axonic poison, sodium channel disrupter	Foliar	Aphids, CPB, leafhoppers, cutworms, armyworms
	Asana XL	Esfenvalerate	Central nervous system/axonic poison, sodium channel disrupter	Foliar	Aphids, CPB, fleabeetles, cutworms, armyworms
Second-generation neonicotinoids	Actara	Thiamethoxam	Central nervous system/interferes with the nicotinic acetylcholine receptor Anti-feeding	Foliar	Aphids, CPB, leafhoppers, wireworms
	Platinum	Thiamethoxam	Central Nervous System/interferes with the nicotinic acetylcholine receptor Anti-feeding	Soil applied	Aphids, CPB, leafhoppers, wireworms

Note: For specific rates and time of application for a given product refer to manufacturer recommendations.

populations. There are many predators that attack spider mites, but because insecticides kill many of these, mite outbreaks often follow treatments for aphids or other foliar pests. Since potatoes are usually grown under optimum conditions and spider mites prefer stressed plants, serious problems are not common.

White Grubs

The two species of white grubs that frequently damage potatoes are the carrot beetle, *Bothynus gibbosus* (DeGeer), and the ten-lined June beetle, *Polyphylla decemlineata* (Say). Both species are more abundant in sandy soils where grass sod or large quantities of organic matter, such as manure, have been plowed into the soil before potatoes are planted.

The larvae are 2.5–3 cm long, C-shaped, dirty white in color with a glossy smooth skin, brown head and six prominent legs. Their large abdomen is transparent, allowing the body contents to be seen through the skin. This stage attacks the tubers, causing feeding cavities in the potato which are from 8 to 12 mm in diameter, rough, irregularly shaped and wider than deep. In severe infestations more than half of the tuber may be consumed.

The carrot beetle has an annual life cycle while the ten-lined June beetle spends 2–3 years as a grub. Adults of both beetles are awkward flyers. During May and June they feed on leaves of trees at night, and are attracted to lights, thus the name June beetles.

Management

Control of white grubs is difficult because they are found in soils with high organic content, which tend to inactivate insecticides. Currently no insecticides are registered on potatoes for white grubs. But, wireworm materials have been somewhat effective in controlling white grubs. Good weed control may also help reduce grub damage.

References

Casagrande RA (1987) The Colorado potato beetle: 125 years of mismanagement. Bull Entomol Soc Am 18:142–150

Rowe RC (ed) (1993) Potato health management. APS, St. Paul, MN, pp 103–115

Harcourt DG (1971) Population dynamics of *Leptinotarsa decemlineata* (Say) in eastern Ontario. III. Major population processes. Can Entomol 103:1049–1061

MacGillivray ME (1979) Aphids infesting potatoes in Canada: a field guide. Minister of Supply and Services, Canada, 23 pp

Zehnder GW, Powelson ML, Jansson RK, Raman KV (eds) (1997) Advances in potato pest biology and management. APS, St. Paul, MN, 655 pp

Potato Tuberworm, *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae)

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Potato tuberworm apparently is native to southern North America, but is now spread throughout the world in areas with warm, dry climates such as southern Europe, northern and southern Africa, India, Australia, and Central and South America. The transport of tubers infested with insects causes extensive dissemination of this pest, and also results in occurrence records where this insect does not exist permanently.

Life History

A life cycle may be completed in 15–90 days, so depending on weather the number of generations is reported to range from 2 to 13 annually. In warm climates, the generations overlap and cannot be distinguished easily. Potato tuberworm normally cannot withstand freezing, so in cold climates overwintering survival by larvae is poor except within potatoes in storage or in cull piles.

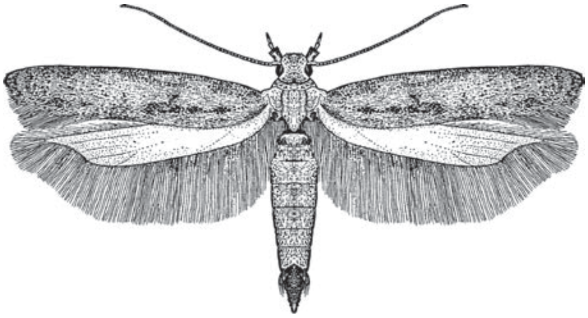
Eggs are deposited singly or in poorly defined clusters of a few eggs, usually on the underside of leaves. If deposited on potatoes in storage, however, the egg clusters tend to be larger, up to 30 eggs. Tubers tend to be heavily infested if they are exposed, i.e., not covered with soil. There also are reports of oviposition on soil adjacent to plants. The egg is elliptical in shape, and measures about 0.48 mm long and 0.36 mm wide. Initially white in color, eggs turn yellow and acquire a distinct iridescence with age. Duration of the egg stage is only about five days during the summer but may reach 30 days during cool weather.

At hatching, larvae normally begin to burrow almost immediately. Larvae normally mine the leaves, but occasionally the petioles and stems, and sometimes burrow into tubers. The older or lower leaves are preferred. Larvae often plug the entrance to their burrow with excrement, but extrude the cast skins and head capsules. Sometimes considerable amounts of silk are produced by larvae, usually when they are forced to traverse the leaf surface, but also to plug larval burrows and to web together leaves. There are four larval instars. Mean head capsule widths are about 0.20, 0.36, 0.60, and 1.13 mm for instars 1–4, respectively. Body lengths are about 1.1, 2.0, 4.5, and 7.0 mm, respectively. Mean duration (range) of the instars is about 3.5 (2–6), 2.5 (2–3), 3.1 (2–4), and 7.3 (5–12) days, respectively. Initially white in color with a black head and thoracic plate, the larva acquires additional color as it grows. In the mature larva, the head, thoracic plate and thoracic legs are black in color. The body is principally white, with pink or greenish-pink dorsally. There are five pairs of prolegs. The anal plate is yellow. Duration of the larval period may require only 14 days during the summer, but up to 70 days during the winter months.

Pupation occurs in the soil, or just beneath the epidermis of the leaf or tuber. Prior to pupation, the larva spins a silk cocoon that is usually covered with leaf trash, fecal material, soil particles, and other debris. Initially white or yellow, the pupa eventually becomes dark mahogany in color. The form of the pupa is typical of Lepidoptera, wider at the anterior end, tapering to a point at the posterior end, and with the partially developed wings twisted ventrally. The tip of the abdomen bears a hook and a circle of spines. It measures about 6 mm in length. Mean duration (range) of the pupal period is 11.6 (8–14) days.

The adult stage (Fig. 103) is a small grayish-brown moth with a wing span of 12–16 mm. The wings, especially the hind wings, are fringed. The forewings are marked with dark spots, the spots usually coalescing to form a dark longitudinal streak or a row of dark spots. The wings, abdomen, and legs also are tinged with yellow scales. The moths are nocturnal, hiding during the day beneath debris and clods of soil. Mating occurs within two days of moth emergence. Oviposition is usually completed in 6–17 days, with females each producing 150–250 eggs. Longevity rarely extends beyond 21 days. A sex pheromone has been identified and can be used for trapping under field conditions.

This insect feeds almost entirely on members of the plant family Solanaceae. Vegetable crops supporting potato tuberworm include eggplant, pepper, potato, and tomato, though potato is the only frequent host. Tobacco is sometimes affected, and potato tuberworm is sometimes called "tobacco splitworm" when it is associated with this host. Solanaceous weeds such as bittersweet, *Solanum dulcamara*; black nightshade, *S. nigrum*; groundcherry, *Physalis* spp.; henbane, *Hyoscyamus* sp.; horsenettle, *S. carolinense*; jimson weed, *Datura stramonium*; and matrimony vine, *Lycium europaeum*; also serve as hosts.

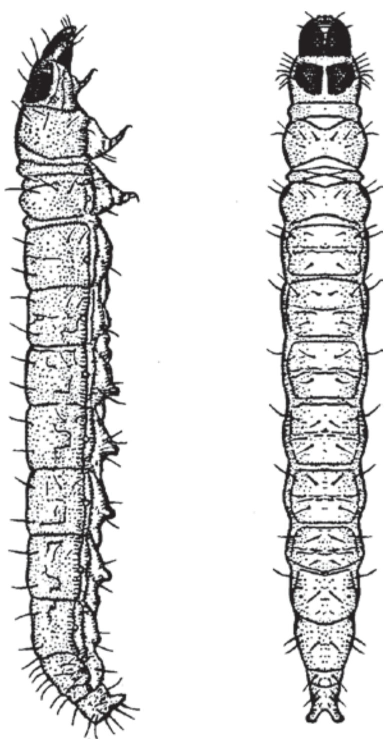


Potato Tuberworm, *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae), Figure 103 Adult of potato tuberworm, *Phthorimaea operculella* (Zeller).

Natural enemies affect the egg, larval (Fig. 104), and pupal stages of potato tuberworm, though they are much more effective when the tuberworms are feeding on the aerial portions of the plant rather than within tubers. Among the parasitoids known to affect potato tuberworm are numerous species of Braconidae, Encyrtidae, Eulophidae, Ichneumonidae, Mymaridae, Pteromalidae, Scelionidae, and Trichogrammatidae (all Hymenoptera).

Other natural enemies are less important. Several general predators have been noted to feed on tuberworm, including the ants *Pheidole* and *Lasius* spp. (Hymenoptera: Formicidae), pirate bugs (Hemiptera: Anthocoridae), shield bugs (Hemiptera: Pentatomidae), and rove beetles (Coleoptera: Staphylinidae). Diseases have been noted, but seem to be of little natural significance.

Weather is thought to affect the abundance of potato tuberworm. Summers that are unusually warm and dry favor increase in tuberworm populations.



Potato Tuberworm, *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae), Figure 104 **Larva of potato tuberworm, *Phthorimaea operculella* (Zeller), dorsal and lateral views.**

Damage

Leaf mining is the most common habit of potato tuberworm, but mining of the tuber or fruit is the most damaging. Mining normally is restricted to the foliage as long as it is green and succulent. Larvae may also mine the stems, usually working downward. If the tuber or fruit is attacked, the mining may occur near the epidermis, or larvae may burrow deeply. The tunnels in potato tubers normally fill with fungus. Tunneling not only destroys the food quality of the tubers, but also the sprouting potential of tubers that are to be used for propagation.

Management

Pheromone traps are effective for monitoring potato tuberworm populations, and usually there is a good correlation between trap catches and damage levels. Various types of traps can be used effectively with pheromone lures.

Tuberworm often is controlled by application of insecticide to foliage, though in some parts of the world resistance to insecticides is a problem. Also, insecticides interfere with predators and parasitoids of tuberworm, which can be quite effective, so it is prudent to determine that tuberworm is present in potentially damaging numbers before implementing an insecticide-based management effort. Biological insecticides, particularly the bacterium *Bacillus thuringiensis*, are recommended for protection of potato tubers in storage, but not usually in the field. Suppression in the field is possible with *B. thuringiensis*, but several applications may be required.

Cultural practices can greatly affect susceptibility of potato to potato tuberworm. Overwintering populations tend to be low, with tuberworm populations increasing through the year. Thus, areas where more than one potato crop are cultivated tend to experience greater loss by tuberworm, and greatest damage occurs late in the season. In some regions, potato production has been limited to the spring months to eliminate the nearly year-long availability of potatoes for tuberworm breeding.

Sanitation is extremely important in potato tuberworm management. Potatoes held in storage or in cull piles are potential sources of infestation. Similarly, potatoes left in the field, volunteer plants, and solanaceous weeds can support tuberworms. Harvested potatoes should not be left in the field overnight as this is when oviposition occurs.

If vines are killed before senescence and tubers harvested soon thereafter, the level of tuber infestation is low. Delayed harvest increases the exposure of tubers to ovipositing moths. Infestation of tubers is especially likely if there are cracks in the soil, allowing access by tuberworm. Soil depths of 5 cm or more protect tubers from infestation. Sandy soil can also be a problem if rainfall washes away soil, exposing tubers. Irrigation practices greatly affect soil condition, with furrow irrigation producing more cracks than overhead irrigation. Frequent irrigation helps to prevent soil cracking. Hilling of the soil, wherein soil is scraped from between the rows and deposited at the base of the plants, helps to deny access by tuberworm to tubers. Deep planting of potato seed, and culture of varieties that do not produce shallow tubers, also reduce incidence of tuberworm damage.

The sex pheromone can be used to manipulate populations. Mass trapping can be used to reduce damage in the field. Trapping, and disruption of mating by saturation of the atmosphere and confusion of the moths, works best for potatoes in storage.

References

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, 729 pp

Das GP, Raman KV (1994) Alternate hosts of the potato tuber moth, *Phthorimaea operculella* (Zeller). Crop Prot 13:83–86

Poos FW, Peters HS (1927) The potato tuber worm. Va Truck Exp Stn Bull 61:597–630

Trivedi TP, Rajagopal D (1992) Distribution, biology, ecology and management of potato tuber moth, *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae): a review. Trop Pest Manag 38:279–285

Potter, Charles

Charles Potter was born in England on January 3, 1907, and rose to become one of the most important workers in chemical insecticides. Beginning in the 1930s with his work on stored product pests at Imperial College, London, Potter made critical observations showing that pyrethrum formulations could be residual under the conditions of a darkened warehouse. To make proper studies of toxicity, laboratory bioassay techniques including precision spray applicators had to be developed. At the Rothamsted Experimental Station, Potter worked vigorously at developing improved techniques to assess potency of pest control materials, resulting in development of an apparatus to become known as the "Potter spraying tower." He served as head of the Insecticides and Fungicides Department, a group that grew and prospered under his direction. Potter's group was active in the introduction of organochlorine and organophosphate insecticides into commercial agriculture, and also was active in solving some of the resulting problems. They greatly improved our knowledge of structure-activity relationships, mode of action, the activities of systemic chemicals, biological and operational properties that affected efficacy, and insecticide resistance. Importantly, he remained convinced, and committed to, the notion that a synthetic material could be developed that had the beneficial attributes of natural pyrethrins. This led to development and introduction of pyrethroid insecticides, a revolutionary class of pest control materials. For his contributions to pesticide research, Potter received numerous awards and honors, including a Congressional Medal from the Third International Congress of Crop Protection, and a team award from UNESCO for development of more photostable pyrethroids. He also served as vice president of the Royal Entomological Society and president of the Association of Applied Biologists. He died on December 10, 1989.

Reference

Needham PH (1990) Charles Potter DSc, DIC, FIBiol, FRES. Antenna 14:57–60

Potter Wasps

Members of the family Vespidae (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Poultry Lice

Members of the family Menoponidae (order Phthiraptera).

► Chewing and Sucking Lice

Pour-On

A type of pesticide treatment of animals wherein the liquid pesticide formulation is poured on the animal, usually in high volume.

Powassan Encephalitis

This tick-borne disease affects several species of animals.

► Ticks

Powderpost Beetles (Coleoptera: Bostrichidae: Lyctinae)

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The Lyctinae are commonly known as powderpost beetles because of the propensity of the larvae to reduce sapwood, particularly of hardwoods, into a powdery frass. The Lyctinae are worldwide in distribution, each region having an indigenous fauna plus established introduced species. They predominantly are tropical and temperate in distribution. The classification of powderpost beetles is as follows:

Order: Coleoptera
Suborder: Polyphaga
Superfamily: Bostrychoidea
Family: Bostrichidae
Subfamily: Lyctinae

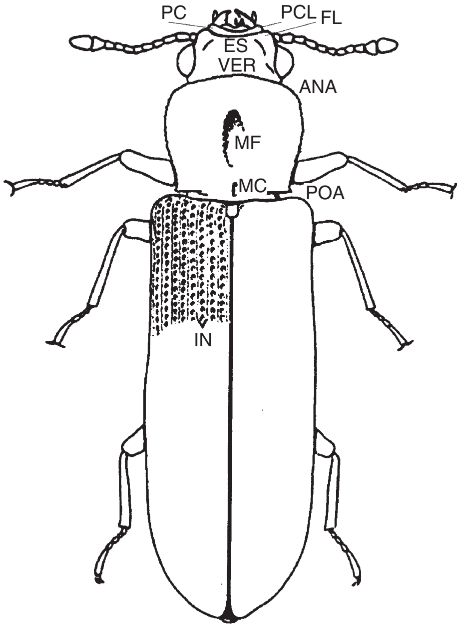
The two tribes of the Lyctinae are the lyctini and trogoxylini. the major genera of lyctini are *Lyctus, Acantholyctus*, *Lyctodon*, *Lycthoplites*, *Minthea*, *Lyctoxylon*. The major genera of trogoxylini are *Trogoxylon*, *Tristaria*, *Lyctopsis*, *Lyctoderma*, *Cephalotoma*, *Phyllyctus*. There are ~70 species of powderpost beetles, of which 11 species occur or have become established in the united states. *Lyctus planicollis* LeC., *Lyctus linearis* (Goeze), and *Trogoxylon parallelopipedum* (Melsh.) are the most common in the United States.

External Morphology

Powderpost beetles are small, 2–7.5 mm in length, reddish-brown to black beetles without distinctive spots or markings. They are elongate, body flattened dorso-ventrally, with a prominent, slightly deflexed head constricted behind the eyes. The antennae are 11-segmented, with a two-segmented terminal club, inserted immediately anterior of the eyes. The prothorax is somewhat flattened, and does not form a hood over the head (Fig. 105). The tarsi are all five-segmented, with the first segment very small and the fifth segment almost as long as all the preceding segments combined. The tarsal claws are simple.

Life History and Habits

Adult powderpost beetles are sexually mature upon emergence. Copulation occurs soon afterward. Oviposition takes place 2–3 days after mating. The female may feed on the surface of the wood by



Powderpost Beetles (Coleoptera: Bostrichidae: Lyctinae), Figure 105 External morphology of a generalized adult powderpost beetle, dorsal aspect. ANA, anterior angle of pronotum; ES, epicranial suture; FL, frontal lobe; IN, interspace; MC, median canaliculation; MF, median fovea; PC, postclypeus; PCL, postclypeal lobe; POA, posterior angle of pronotum; VER, vertex.

gnawing the torn fibers, possibly to detect the suitability of the timber for oviposition in relation to food value for the larvae. The female extends the long, flexible ovipositor directly into the lumen of the vessel, tracheae, or pores of the wood. The translucent white cylindrical eggs are laid in depths of from 0.5 to 1 mm. Those woods in which the vessels are most numerous are more liable to heavy attack. The diameter of the vessels in which oviposition occurs is a great importance, as it must be large enough for insertion of the ovipositor. Depending upon temperature, the incubation period may vary from 6 to 20 days. The larva, on hatching, is white and straight bodied, armed at the rear end, and with a pair of small spines. After the first molt, the larva assumes a curved form. The young larva usually tunnels with the grain of the wood. In the later stages, the larval tunnel takes an irregular course. Tunnels approaching the surface of infested wood do not penetrate it but leave a thin, unbroken layer. The larva may remain in the wood for about 10 months, the length of time varying with the temperature, moisture, and condition of the wood. The larva possesses large spiracles on the eighth abdominal segment. When fully matured, it bores its way near the surface of the wood and builds a pupal chamber. The pupal period lasts 12–30 days, though this again is variable. When transformation from pupa to adult occurs, the beetle cuts its way to the surface. When emerging, it generally pushes some of the fine dust in front of it, and as a result, small piles of dust often can be seen near new holes. These emergence or flight holes are about 2 or 3 mm in diameter.

The larva feeds mainly on the sapwood of hardwoods, such as oak, ash, hickory, mahogany and bamboo. The chief source of food of the larva is the starch in the cell content of the wood. The cell wall is not digested. Besides starch, certain sugars, disaccharides and a polysaccharide, as well as protein, are necessary constituents of the larval food. As the presence of starch in sapwood is essential for infestation to occur, the greater the starch content, the greater the possible extent of damage. Below a minimum concentration of starch, no attack occurs. Moisture also is essential for the normal development of the larva. It will thrive in wood with a moisture content of between 8 and 30%.

Predators and Parasites

Predators and parasites are not a factor in the artificial control of the powderpost beetles. Various Hymenoptera have been found to parasitize these beetles. Clerid beetles (Coleoptera) have been reported as predators.

Economic Importance

The destructiveness of powderpost beetles to wood and wood products is second only to that of termites. The annual loss of lumber and wood products runs into millions of dollars. As noted previously, powderpost larvae primarily attach to the sapwood of hardwoods. They are more often found in recently dried wood than in old wood. They attack lumber that is used for hardwood floors, crating, furniture, plywood, implement handles, and gun stocks. The damage consists of the destruction of the wood, resulting in a powdery frass as the larvae tunnel their way through the sapwood. When the adult beetles emerge, they further damage the wood by producing exit or flight holes.

Control Measures

The control of powderpost beetles in wood may be accomplished by heat treatment, fumigation, chemical treatment, and good lumber yard and saw mill sanitation.

► Wood-Attacking Insects

References

Gerberg EJ (1957) A revision of the New World species of powder-post beetles belonging to the family Lyctidae. U.S. Department of Agriculture Technical Bulletin No. 1157. 55 pp, 14 pls

Hickin NE (1963) The insect factor in wood decay. Hutchinson, London, UK, 336 pp

Ivie MA (2002) Bostrichidae. In: Arnett RH, Thomas MC, Skelley PE, Frank JH (eds) American beetles, vol 2. Boca Raton, FL, CRC, pp 233–244

Powderpost Termites

A group of termites in the family Kalotermitidae known to attack dry wood not in contact with soil, and reduce it to powder.

► Termites

Powdery Mildew

Though also wind-transmitted, these fungi also are transmitted by insects.

► Transmission of Plant Diseases by Insects

Praying Mantids (Mantodea)

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There is some debate about the most appropriate taxonomic position of praying mantids (or mantises). They are considered orthopteroid insects because they appear to have much in common with cockroaches, grasshoppers, crickets, and stick insects, all of which used to be lumped together with mantids within the order Orthoptera. Morphological and molecular evidence suggests that mantids are, in fact, most closely related to Blattodea (cockroaches) and Isoptera (termites), but most authors feel that the 1,900 or so species of mantids are sufficiently different from these groups to be classified separately: Order Dictyoptera, Suborder Mantodea. There are eight families and 28 subfamilies in this suborder:

Amorphoscelididae, containing two subfamilies from Africa and Australia

Chaeteessidae, with only one Neotropical genus, *Chaeteessa*

Empusidae, consisting of eight genera in Africa and Asia

Eremiaphilidae, ground-dwelling mantids of Africa and Asia

Hymenopodidae, with three subfamilies, including tropical flower mimics

Mantidae, the most important family with 21 subfamilies and 263 genera

Mantoididae, with a single Neotropical genus, *Mantoida*

Metallyticidae, with a single Malaysian genus, *Metallyticus*

Distinguishing Characteristics

The praying mantis (from the Greek for "prophet") derives both its name and its livelihood from the contradictory morphology and function of the prothoracic legs. When folded against the body, these appendages give the insect the appearance of prayer. However, when an unwary wasp or cricket happens by, the legs unfold at great speed, trapping the prey item in a nearly unbreakable grip between the scimitar-like apical claw of the tibia and the discoidal spines lining the anterior surface of the femur. In addition to the raptorial front legs, the most obvious physical features of mantids are an elongated prothorax and a highly mobile head with which the insect can actually look over its shoulder. Mantids employ accurate binocular vision to assess prey (or enemy) size and distance, and at least some species have an ear that can detect the ultrasound emitted by insectivorous bats hunting the night sky for prey.

Most orthopteroid insects are either herbivores or omnivores, but all mantids are carnivores. Aside from this commonality, mantids are otherwise quite diverse in form and function. There are, for instance, two distinct modes of predation. Most species are sit-and-wait ambush predators such as the leaf mimic, *Phyllocrania illudens,* from Madagascar, the spectacular Malaysian flower mimic, *Hymenopus coronatus*, and the simply cryptic European mantis, *Mantis religiosa*. However, some species are active hunters that run down their prey, such as the North American species, *Yersiniops sophronicum.* Most mantids are winged and sexually dimorphic, but *Brunneria borealis* from the southern U.S.A. is a wingless, completely parthenogenetic female species. In many winged species, only the male has appreciable flight capability; the wings of females often are too small for flight, but can be used in defense (deimatic displays) or to help disperse sex pheromones. Since males cannot by themselves colonize new habitats, the dispersal of mantid populations within a region is generally slow.

Adult body size varies greatly among species; the smallest known species being *Mantoida tenuis* (1 cm) and the largest is *Ischnomantis gigantas* (17 cm). The genetics of sex determination also differs among mantids: males of some species are XO, while many others are XXY.

Life History

Most species of mantids are relatively rare and narrowly distributed in the tropics, an extreme example of which is *Galapagos solitaria*, which is only found on three of the Galapagos Islands. However, some temperate zone species are both abundant and widely distributed. Thus, in spite of the vastly greater diversity of tropical mantids, we know much more about the biology of a few temperate zone species. The best known, most ubiquitous species undoubtedly is the Chinese mantis, *Tenodera aridifolia sinensis*, which occurs throughout much of Eurasia and (through introduction) eastern North America. The life cycle of this species is closely governed by seasonality, typical of many large-bodied, semelparous insects in temperate regions. Egg hatch for the Chinese mantis occurs in the spring, followed by a long maturation period during the summer and sexual maturity early in the fall. Nymphs develop through six or seven instars, during which they may increase from 10 mm to 10 cm in body length. By the time they are adults, males outnumber females by as much as 2:1 (Fig. 106). In the fall, adult females emit pheromones to attract males, and perhaps other females as well. The adaptive utility of the first function is obvious; the latter may be explained as a mechanism to increase the total pheromone concentration in the area of grouped females, resulting in a higher probability that males will be attracted.

After mating, a female deposits one or (infrequently) more oothecae on a stalk of vegetation, each ootheca containing from 60 to 300 eggs, and constituting as much as 50% of the female's pre-oviposition weight, a considerable parental investment at a time when prey are becoming scarce (Fig. 107). The eggs of this and many other species are subject to mortality from parasitoid wasps and, if deposited far enough above the ground, foraging birds.

Praying Mantids (Mantodea), Figure 106 **Three male *Tenodera sinensis* competing to mate with the same female. Males typically outnumber females at the beginning of the adult portion of the life cycle, but sexual cannibalism may reduce the discrepancy by the end of the season.**

Praying Mantids (Mantodea), Figure 107 **Female *Tenodera sinensis* with her ootheca. The egg mass weighs about as much as she does after oviposition.**

Adults die with the onset of cold weather, and eggs over-winter. Unlike the European mantis, *Mantis religiosa,* the eggs of which have an obligatory cold diapause, the eggs of the Chinese mantis begin to develop as soon as they are laid, so an extended fall can be lethal if egg hatch occurs before onset of winter. This limits the southern distribution of this species, and extreme cold limits the northern range by desiccating the eggs during winter. Although successive generations of temperate zone species do not overlap, adult females of some tropical species, such as *Cardioptera brachyptera*, live long enough to exhibit parental care by guarding their oothecae and hatchlings against predators.

Mantids in general, and females in particular, are famous cannibals. This trait has led some authors to speculate that a male commits "adaptive suicide" by allowing his mate to consume him, thus contributing to the fitness of his offspring by providing nourishment for egg production. This popular notion is unlikely to be true because females begin to produce their first clutch of eggs before they mate, and the male victim has no assurance of paternity because females may attract and copulate with many males. Furthermore, although sexual cannibalism is frequently observed in the laboratory, under natural conditions males usually escape their first sexual encounter to mate with other females (however, the more mating attempts the greater the probability of being eaten). The simplest explanation for sexual cannibalism is that a very hungry female will eat her suitor before copulation can begin, a mildly hungry female will eat him during or shortly following copulation (if she can catch him), and a female that is less hungry than amorous will let him go. In the first two instances the male does indeed contribute to his mate's nutrition, and therefore to her fitness, but not necessarily to his own because she actually may have been inseminated by a previous male. Considering that females often are food limited at the end of the season and that there are fewer of them than of males, cannibalism of male mantids may be a female's best strategy for producing a healthy ootheca in many instances.

Ecology and Economic Importance

Praying mantids have a tritrophic niche, i.e., they simultaneously occupy two consumer trophic levels in natural ecosystems by virtue of feeding on herbivores, other carnivores and pollen. Mantids, therefore, can compete with other predator species (e.g., spiders) for food, eat other predators, compete with each other, or cannibalize each other. The fact that all of these processes may be occurring at the same time in the same ecosystem can complicate prediction of the impact of these predators on ecosystem structure and dynamics. Predators of mantids include larger spiders and vertebrates such as birds, lizards, and snakes. Other enemies include chalcoid wasps that are parasitic on eggs, and tachinid flies that parasitize nymphs.

Field experiments have shown that mantids exert both direct (prey reduction) and indirect (prey enhancement) effects on arthropod assemblages. Indirect effects occur because competition with, or predation on, other predators may reduce predation on some herbivorous arthropods. An experiment in a complex old-field ecosystem revealed that mantids had a positive effect on plant productivity by reducing herbivorous insects, a direct effect known as a trophic cascade because it ramified two trophic levels down from the predators. However, in another study, mantid nymphs indirectly enhanced aphid densities by reducing spider populations. This kind of unpredictability has important implications for one of the most persistent ideas about mantids, that they are good biological control agents. To that dubious end, oothecae of *Tenodera aridifolia sinensis* are sold and distributed through the mail by organic gardening suppliers. Although this has resulted in much of the broad regional distribution of this species in the U.S., the value of these animals to pest control is dubious at best. Because they are generalists, they eat anything that moves within a suitable size range, and this includes spiders, wasps, bees, butterflies, and other desirable species as well as deleterious herbivores (Fig. 108). In fact, flower-foraging insects such as bees may constitute a significant portion of their diet at the end of the season when grasshoppers and other herbivorous prey are becoming scarce. Thus, planting mantids in one's garden is not necessarily an efficacious way to control pests. There is also a chance that by spreading this exotic species around the country we may be affecting native arthropod assemblages, including native mantid species such as *Stagmomantis carolina*, which often is eaten by the larger Chinese mantid.

Praying Mantids (Mantodea), Figure 108 Adult female *Tenodera sinensis* feeding on a bee. Pollinators such as bees, wasps, and butterflies are frequent prey, especially for adult mantids.

References

Fagan WF, Moran MD, Rango JJ, Hurd LE (2002) Community effects of praying mantids: a meta-analysis of the influences of species identity and experimental design. Ecol Entomol 27:1–11

Helfer JR (1963) How to know the grasshoppers, cockroaches and their allies. W. C. Brown, Dubuque, Iowa, 353 pp

Hurd LE, Eisenberg RM (1990) Arthropod community responses to manipulation of a bitrophic predator guild. Ecology 76:2107–2114

Preston-Mafham K (1990) Grasshoppers and mantids of the world. Facts on file. New York, NY, 192 pp

Prete FR, Wells H, Wells PH, Hurd LE (eds) (1999) The praying mantids. Johns Hopkins University Press, Baltimore, MD, 362 pp

Precinction

The occurrence of taxonomic groups restricted to, and having originated in, a given geographical region. Most writers use the word endemism to label this condition, but the word endemism is based on the word endemic. The word endemic was first used in ecology in the early 17th century, and has consistently been used in that sense. More than 250 years later, it was misappropriated and used in another sense in biogeography.

► Endemic
► Endemism
► Precinctive

Precinctive

Native to a specified area, and not occurring elsewhere.

► Invasive Pests

Precision

A statistical measure of the repeatability of an estimate relative to a group of estimates from the same population at the same time. Typically measured as the quotient of the standard error of the mean over the mean. Low numerical values indicate high precision, high numerical values indicate low precision. Precision is a key element in developing and evaluating the performance of sampling plans.

► Sampling Arthropods

Preclearance

From a regulatory perspective, this is the certification that in the country of origin, an imported commodity was free of infestation, or produced in a manner that would eliminate risk of infestation. Such commodities are inspected under the supervision of the national plant/animal protection organization of the country of destination.

► Invasive Species
► Regulatory Entomology

Precocenes

Chemical substances from the common bedding plant *Ageratum houstonianum* that affect the development of some insects by causing atrophy of the corpora allata and causing precocious maturity and production of sterile adults.

Predaceous (Predacious)

Animals that attack and feed upon (prey upon) other animals. Ecologists sometimes consider consumption of plants by animals to be predation, but entomologists call such animals herbivores and this process herbivory.

Predaceous Diving Beetles

Members of the family Dytiscidae (order Coleoptera).

► Beetles

Predation: The Role of Generalist Predators in Biodiversity and Biological Control

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The term "generalist predator" is nearly redundant. The diets of the vast majority of predators are far less specialized than many herbivore-plant associations in which, for example, the life cycle of a phloem-feeding treehopper (Hemiptera: Membracidae) in the temperate zone may be completely dependent on the seasonal phenology of a single species of tree. Although some groups such as ladybird beetles (Coleoptera: Coccinellidae) are relatively specialized on a few related prey species (in this case, mainly aphids or scale insects), the vast majority of predators feed on varied prey. A far more typical group of coleopteran predators, beetles in the family Carabidae, will take nearly anything that moves within a size range they can physically handle, regardless of taxonomic position. Thus, the most important factor determining the niche (ecological role) of insect predators undoubtedly is breadth of diet.

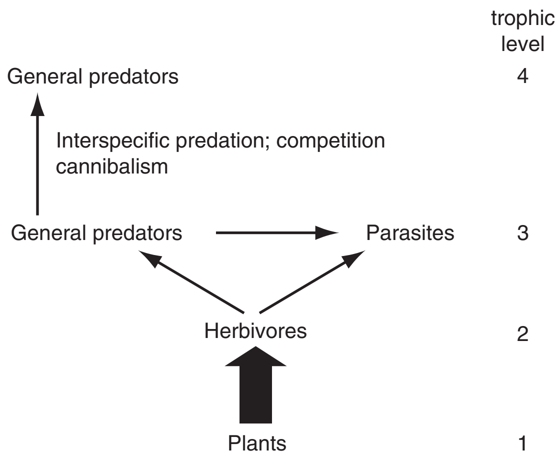
The Niche of Generalist Predators

Predatory insects are fewer in number than herbivores owing to the constraints of the second law of thermodynamics, which dictates that the energy available to higher trophic levels in a food chain diminishes with each transfer. This is why food chains often are represented as pyramids, getting smaller from the ground floor (plants), through the consumer levels, with top carnivores occupying the narrow tip. Most predators are probably generalists because carnivores that feed broadly can sustain larger populations than those specializing on one or a few prey species. A specialist will starve if its prey population gets too low, but a generalist can sustain its population size on alternate prey even if preferred prey species become scarce (see functional response, below). This is a key tenet of niche theory: resource generalists are more buffered against fluctuation in those resources than are specialists.

A voluminous literature suggests that phytophagous insects do not often compete, i.e., are not routinely food limited, whereas most studies that have addressed the question have found that predators usually are limited by their prey. In spite of this apparent thermodynamic disadvantage of the predatory lifestyle, feeding on animal prey does provide one potential advantage over vegetarian fare: higher quality protein. There are even many examples in the animal kingdom of predominately herbivorous animals that are carnivorous as juveniles (when growth is important) or as adults during reproduction (for egg production). After all, adult female mosquitoes (Diptera: Culicidae) feed on blood to make eggs.

Most major insect orders have predaceous members. These may be dedicated carnivores such as dragonflies and damselflies (Odonata), mantids (Dictyoptera), ambush bugs (Hemiptera), and lacewings (Neuroptera), or they may be omnivores such as ants (Hymenoptera), earwigs (Dermaptera), and crickets (Orthoptera). The manner of predation also varies widely: carabid beetles (Coleoptera) chew their victims, while reduviid bugs (Hemiptera) suck them dry as do spiders; water scorpions (Hemiptera) and some mantids, like orb weaving spiders, are sit-and-wait ambush predators, while wasps (Hymenoptera) tend to be active hunters. Some, such as the aquatic naiads of Odonata, will even include vertebrates in their diets. These predators, and others such as diving beetles (family Dytiscidae) and giant water bugs (family Belostomatidae) are particularly adept at capturing small fish and tadpoles.

The amount of research on predatory insects is far exceeded by work on herbivores, for the obvious reason that most insect pests are herbivorous. For that reason, we know much more about plant feeders than about the insects that eat them. Our growing awareness of the environmental hazards of biocide use has contributed to research on some



Predation: The Role of Generalist Predators in Biodiversity and Biological Control, Figure 109 The trophic position of generalist predators is complicated by the varied interactions that can take place among them, as well as by their relationship with the rest of the community. Arrows represent direction and relative amount (line thickness) of energy flow in food webs topped by general arthropod predators, illustrating their bitrophic position as members of both the third and fourth trophic levels.

predatory species to investigate their potential for biological pest control. However, we still have much to learn about how predators fit into complex natural communities.

The Predator Guild and Community Interactions

A guild is a group of species that use a common resource base. A community of organisms within a habitat generally comprises many guilds using many different, sometimes overlapping, resources. Guilds often consist of species that are not particularly closely related, but that have overlapping resource requirements. Thus, a guild of predatory animals that feed on ground-dwelling arthropods may consist of such invertebrates as wolf spiders, scorpions and tiger beetles, along with vertebrates such as lizards and shrews (Fig. 109).

Generalist arthropod predators typically are bitrophic: they simultaneously occupy the third and fourth trophic levels by virtue of feeding both on herbivores and on each other. As a consequence, species within generalist predator guilds may compete with each other for common prey resources, or they may eat each other. Predation can be either between species or among individuals within the same species, because most generalist predators are cannibals. In fact, cannibalism often has been proposed as a mechanism of population regulation in such predators because the frequency of cannibalism is expected to increase as population density increases, resulting in negative feedback between population size and cannibalism. The selective advantage of cannibalism is simply that a cannibalistic individual can increase its Darwinian fitness by eating members of its own cohort when alternate prey are scarce. The combination of cannibalism and interspecific predation within predator guilds has become known as intraguild predation.

The combination of competition, interspecific predation, and cannibalism not only influences coexistence within this guild, it also complicates the impact of these predators on the rest of the community. Both competition for scarce prey and intraguild predation can occur even among predators of different phyla (e.g., between amphibian larvae and aquatic insects). There is yet another wrinkle in the food web. It has been suggested that predators be thought of as mutualists of plants, because plants supply them herbivore prey and they in turn reduce damage from herbivory. However, predators such as ambush bugs and crab spiders can be viewed as competitors with plants for a common resource: pollinating insects such as bees and butterflies.

In view of the complex relationship of generalist predators to each other and to the rest of the community, it is not surprising that we do not yet have good predictive models of their impact on diverse insect assemblages. Finding out how generalist predators affect highly diverse natural communities requires careful experimentation in the field, in which predators are either eliminated or their densities augmented in replicated plots, and the results are compared with control plots with normal predator levels. These experiments usually are difficult to perform, and the resultant data (usually in the form of changes in numbers of individuals or biomass among resident species) are nearly always highly variable, necessitating relatively complex statistical analysis. For these reasons, such experiments are not as common in the literature as are laboratory tests of predator feeding, or experiments using low diversity agricultural plots.

Interpretation of the results of experimental predator manipulations on a target community often can be difficult. When a target (prey) population declines, the cause is usually a direct effect of predation. However, frequently predators actually increase populations of prey species, an indirect effect of their feeding on competitors or on other predators of these prey. In a diverse species assemblage, both kinds of results often occur in the same experiment. The potential combinations of positive and negative effects on prey may even serve to cancel out the overall impact of predators on prey assemblages. Our current understanding of these interactions is still too limited to make reliable predictions of which of these effects will be important prior to adding predators to arthropod assemblages. Clearly, more research is needed.

If predators affect herbivore populations, they may as a result affect the plants on which these herbivores feed. This kind of "top down" effect of predators on successively lower trophic levels is one kind of what is known as a trophic cascade. The other kind, "bottom up," is when plants are demonstrated to control herbivores (rather than the reverse), and herbivores in turn control predators. Trophic cascades are the subject of a growing literature among theoreticians and experimentalists in ecology, and people involved in biological control are obviously interested in the potential for predators to exert top down control. Unfortunately, there are as yet few experiments in the field demonstrating that arthropod predators can exert top down control. One experiment in a simplified agricultural system showed that spiders could boost plant productivity by reducing herbivores; another experiment demonstrated the same sort of effect for praying mantids in a complex natural community. This may seem promising, but before we can make any kind of general prediction, we need many more studies under various conditions.

Generalist Predators and Biological Control

There are some good examples of biological control of pest species using specialized predators, e.g., the control of scale insects on California citrus by the introduction of the Australian ladybird beetle, *Rodolia cardinalis*. Some evidence suggests that at least some arthropod generalists, such as mites and spiders, can significantly reduce herbivore populations in simplified experimental agricultural system, but very few data have been generated as to the effects of this predation on plants. It is therefore reasonable to ask whether generalist insect predators may be useful in the control of those herbivorous and parasitic species that have exceeded the human economic and nuisance threshold: pests.

Pest species are virtually defined as populations that are out of control, and in order to control a pest population, a predator must track its prey closely. This generally requires two kinds of reactions to changes in the size of a prey population by a predator: numerical and functional responses. Numerical response simply means that a predator can adjust its population size to exploit changes in the prey population. The two ways to do this are through increased reproductive output, and high rates of dispersal into areas of high prey density (and, conversely, reduced reproduction and emigration when prey become scarce, to avoid complete starvation). Both of these mechanisms would entail a time lag in predator response, even if the predator were a specialist; this time lag would likely be much longer for a generalized predator.

Functional response is an increase in per capita feeding rate as prey become more abundant. Ideally, a predator should "switch" from generalized feeding on many prey species to focus on the rapidly increasing pest population in a frequency-dependent manner. This entails recognition of specific chemical, tactile, or visual cues provided by the pest species from among all the other prey signals in the environment at the time. This would seem unlikely for a generalist predator, an animal adapted to hunting or ambushing a variety of prey species in a food-limited environment, but even an omnivore may have preference for a specific item from among its dietary choices. The criteria for prey preference in predators vary, but include such factors as ease of capture and nutritional value. The net gain to the predator for an item of prey, when costs of finding and capturing prey are balanced against nutritive gain, are included in the theoretical construct known as optimal foraging theory. This theory predicts that selection will favor those (optimal) behaviors that maximize net return on an animal's foraging expenditure. However, even if a predator did switch to increase its feeding rate on a specific pest, it would reach a satiation level past which further increases in prey density could elicit no faster capture rate per individual predator. Unless this functional response were accompanied by a good numerical response, it would be unlikely to work.

The general unpredictability of community-wide effects of adding predators to experimental systems discussed in the previous section argues against their use in the absence of careful prior study. A predator may feed broadly enough that its diet encompasses a pest species, but once introduced it may exhibit preference for other prey, either benign or beneficial. The fact is that generalist predators may eat as many or more beneficial species as they do pests, and the tradeoff between positive and negative effects of these predators in our gardens can make them unreliable biocontrol agents.

Value of Predators to Biodiversity

It is becoming increasingly obvious that predators of all kinds play a critical role in the maintenance of biodiversity. So, to the extent that humans are concerned with the variety of life forms in nature, we should pay attention to the carnivores. Human history is rife with examples of human extirpation of vertebrate carnivores, as we have spread ourselves across the habitable world. This has happened largely because tigers, wolves, rattlesnakes, and hawks have been perceived to compete with us for what we eat (including domesticated animals), or are feared because they can harm us. As a result, we have a superabundance of animals like deer, rabbits, rats, and groundhogs, but a general decline in biological diversity in proximity to human settlements.

Among arthropods, predators have been implicated as important selective agents in the evolution of herbivore-plant systems. Evidence of strong natural selection exerted by predators includes the numerous examples of adaptations among herbivorous insects to detect and avoid them. This includes remote sensing to chemically identify the whereabouts of an enemy, clearly a case for considerable evolutionary fine-tuning of a prey to its predator. It seems quite likely that predators play an important role in controlling the diversity of the arthropod portion of the biosphere. This is a large slice of life indeed, considering that about 64% of all species identified so far are insects, so it would not be surprising if much of the rest of global biodiversity depended on them as well.

Adding exotic predators to control pest species may have the undesirable effect of decreasing native insect diversity. Some studies have suggested that introduced predators can interfere with native species, resulting in loss of control over prey populations through release from predation, i.e., making a bad situation worse in terms of levels of pest populations. Or, an introduced predator may simply displace, through competition or intraguild predation, a native predator. An example of this is the Chinese praying mantis, *Tenodera sinensis*, introduced into the United States a little more than 100 years ago. This species has not only become the most abundant and widespread mantid in this country (mainly by human transport of egg cases), it has displaced one of our native species, the Carolina mantid, *Stagmomantis carolina*, from some habitats in North Carolina. In this case, the mechanism is predation: both species lay their eggs on loblolly pines, but the Chinese mantid is larger and finds the Carolina mantid easy prey. It is therefore uncommon to find both species persisting in the same habitat for very long.

Whatever their effects, once introduced insects can be very hard to remove from their adopted home. In archipelagos such as Hawaii and the Galápagos, where entomologists have been keeping score, the proportion of exotic insects making up the species list has been growing at an alarming rate ever since these islands were colonized. Most biologists recognize diet breadth as one indication of how likely an animal is to be invasive. The very fact of their broad diet can make generalist predators ideal invasive species, preadapted for survival in novel habitats with a naive (unadapted) prey assemblage. Given that species invasions are second only to habitat loss as a threat to global biological diversity, and that uncountable introductions have been made inadvertently through global human travel and commerce, we certainly must be especially careful about introducing insects intentionally.

References

Bernays E, Graham M (1988) On the evolution of host specificity in phytophagous arthropods. Ecology 69:886–892

Hassell MP (1978) Arthropod predator-prey systems. Princeton University Press, Princeton, NJ

Hurd LE (1999) Ecology of praying mantids. In: Prete FR, Wells H, Wells P, Hurd LE (eds) The praying mantids. Johns Hopkins University Press, Baltimore, MD, pp 43–60

Polis GA, Myers CA, Holt RD (1989) The ecology and evolution of intraguild predation: potential competitors that eat each other. Annu Rev Ecol Syst 20:297–330

Sih A, Crowley P, McPeek M, Petranka J, Strohmeier K (1985) Predation, competition and prey communities: a review of field experiments. Annu Rev Ecol Syst 16:269–311

Predator

In entomology, animals that feed on insects, and must eat several or many insects in order to complete their life cycle.

Predatory Guild

A group of different types of organisms that feed on the same resource, such as a developmental stage of an insect.

Predatory Stink Bugs (Hemiptera: Pentatomidae, Asopinae)

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The subfamily Asopinae belongs to the family Pentatomidae of the suborder Heteroptera (true bugs). About 300 species in 69 genera have been described worldwide.

Order: Hemiptera
Suborder: Heteroptera
Infraorder: Pentatomomorpha
Superfamily: Pentatomoidea
Family: Pentatomidae
Subfamily: Asopinae

External Morphology

Like other Pentatomidae, predatory stink bugs or soldier bugs are of moderate to large size, ranging in length from 7 to 25 mm, and are broadly elliptical in shape. The piercing-sucking mouthparts of predatory stink bugs consist of a four-segmented rostrum or beak (labium) forming a sheath that encloses two mandibular and two maxillary stylets. Whereas the rostrum of phytophagous pentatomids is slender, asopines are characterized by having a thickened rostrum.

In asopines, the first segment of the rostrum is markedly thickened and free, which enables the rostrum to swing forward fully, making it easier for the predator to feed on active prey. The appearance of the rostrum can be a useful diagnostic character for distinguishing the beneficial predatory pentatomids from potentially harmful phytophagous pentatomids in the field. The triangular mesothoracic shield, called the scutellum, is usually much shorter than the abdomen, but in some genera it is enlarged, covering most of the abdominal dorsum. The males of Asopinae are unique in combining the presence of genital plates with a thecal shield. The shape of the male claspers or parameres is the most reliable diagnostic characteristic for the identification of species.

Habitat and Food

Predatory stink bugs are found in a wide range of natural and agricultural habitats, but many species appear to prefer shrubland and woods. The Asopinae are set apart from the other pentatomid subfamilies by their essentially predaceous feeding habits. It is believed that the Pentatomomorpha have arisen as plant feeders and that only the subfamily Asopinae has secondarily become predaceous. First instars do not attack prey and only need moisture, mainly in the form of plant juices, to develop. Although, for some species, partial development on certain plant-based diets has been reported, nymphs from the second instar on require animal-based diets to complete development. Nymphs and adults, however, are often observed to take up plant juices or free water in addition to feeding on animal prey. Plant feeding primarily provides moisture, but it may also furnish certain nutrients to the bugs. This habit may help predatory stink bugs to sustain their populations in times of prey scarcity. In contrast to some other zoophytophagous heteropterans, plant-feeding asopines have not been reported to injure plants.

Predatory stink bugs attack mainly slow-moving, soft-bodied insects, primarily larval forms of the Lepidoptera, Coleoptera and Hymenoptera. Very few, if any, Asopinae are truly host-specific. Nevertheless, whereas some asopine bugs are generalist predators, attacking a wide array of prey in a diversity of habitats, others appear to be more closely associated with a limited number of insect species and occur in only a few habitats. It has been hypothesized that there may be an evolutionary progression from the drab asopines, which feed rather generally, to the brightly colored asopines, which prefer larvae of Chrysomelidae and, to a lesser extent, Coccinellidae.

Life History

The eggs are usually laid in masses. In some species (e.g., *Podisus*), the eggs bear prominent micropylar processes. There are five nymphal instars. The nymphs take a few weeks to develop, depending on temperature and food. Newly emerged nymphs are highly gregarious, whereas later instars become progressively more solitary with each molt. First instars are not predaceous and take up only water or plant juices; occasionally, they also feed on unhatched eggs. From the second instar on, nymphs begin searching for prey shortly after molting. The nymphs will feed up to 1–2 days before the next molt; at that time, their activity drops and the nymphs will remain resting in a concealed place in preparation for the oncoming molt. Small nymphs tend to attack prey and feed collectively, particularly when the prey is large. Larger nymphs and adults prefer to attack prey individually. Under conditions of food shortage, the nymphs and the adults are highly cannibalistic. The adults are long-lived, with reported longevities of 15 days to more than 3 months, and they lay eggs throughout their entire lifetime. The adults usually move by crawling, but some species (including *Podisus maculiventris*) are also noted to be good flyers. Field surveys suggest that scelionid egg parasitoids, such as *Trissolcus* and *Telenomus* spp., are the most important natural enemies of predatory stink bugs.

Prey Location and Capture

Predatory stink bugs use visual, chemical and tactile cues to locate and recognize their prey. Vision appears to be the most important sense used by the bugs to locate prey. *Podisus maculiventris* and other asopine bugs react to moving prey at distances up to 10 cm, but their reactive distance to immobile prey is considerably less and detection often seems to occur at antennal or rostral contact. Evidence is accumulating that several asopines can also use airborne chemical cues for prey detection. Both *Podisus maculiventris* and *Perillus bioculatus* are sensitive to systemic volatiles produced by plants in response to prey feeding. *Eocanthecona furcellata* is attracted to its lepidopterous prey based, in part, on a volatile component derived from the chlorophyll ingested by the prey. Further, it has been demonstrated that *Podisus maculiventris* can use vibrations of the substrate as cues for prey location. Prey recognition is based primarily on antennal and rostral contact. Asopines are rather timid predators. After finding the prey and orienting to it, the bugs may spend from several minutes up to an hour stealthily approaching it, often keeping their beak extended forward. The stylets are usually inserted at soft areas of the prey body. During attacking and feeding, the only contact between predator and prey is by the rostrum and stylets. When stylet penetration is perceived by the prey, many prey species will try to escape by vigorous body movements. The harpoonlike structure of the mandibular stylets enables a tenacious hold on the prey during this struggle. Further, predatory pentatomids are presumed to inject a salivary toxin into the prey body that quickly immobilizes it. During feeding, body tissues of the prey are liquefied by the injection of digestive enzymes and by the lacerating action of the stylets. The liquid and partly digested food can then be sucked up through the rostrum. This "solid-to-liquid" feeding process enables the predator to use most of the body tissues of the prey.

Pheromones

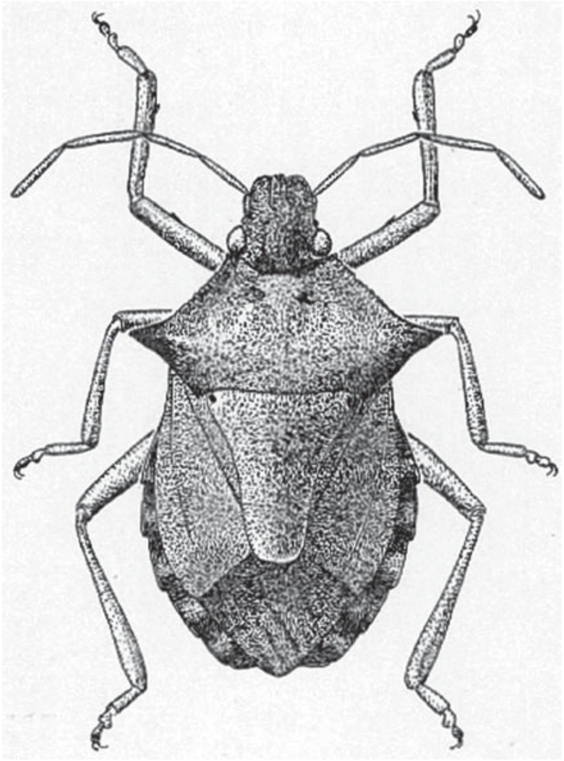
Both male and female asopines possess a metathoracic scent gland from which they discharge a disagreeable odor when disturbed, hence the name "stink bugs." In addition, many species of predatory stink bugs have discrete pheromone glands, which belong to one of two types: dorsal abdominal glands (in both sexes) or sternal glands (in males only). Species with dorsal abdominal glands are mostly polyphagous predators (e.g., *Podisus*, *Zicrona*), whereas those with sternal glands often appear to be more specialized predators (e.g., *Perillus*, *Stiretrus*).

The best known pheromone system is that of the spined soldier bug, *Podisus maculiventris*. Adult males of this species possess hypertrophied dorsal abdominal glands that produce secretions that function as long-range attractants for adults and immatures of both sexes. Immature predators are thought to use the male pheromone as a cue indicating the presence of prey. In the United States, attractors with a synthetic pheromone are commercially available to lure spined soldier bugs to target areas in early spring when the adults emerge from overwintering. Pheromone-baited traps can also be employed to capture large numbers of predators that can be used to establish mass cultures.

Economic Importance

Several predatory pentatomids are believed to have a future for the biological control of various economically important crop pests in different parts of the world. To date, however, the only asopine that has been commercially available for augmentative biological control in North America and Europe is the spined soldier bug, *Podisus* *maculiventris*. This species is native to North America and has shown good capacity to control a variety of insect pests in field and greenhouse crops, orchards and forests, including the Colorado potato beetle, *Leptinotarsa decemlineata*, and several leaf-feeding caterpillars. The two-spotted stink bug, *Perillus bioculatus*, is another important natural enemy of the Colorado potato beetle in North America. *Podisus nigrispinus* is the most common predatory stink bug in South America. The insect has been the subject of conservation and augmentation biological control programs against leaf-feeding caterpillars in forests, including Eucalyptus stands in Brazil. In Southeast Asia and India, *Eocanthecona furcellata* has received increasing attention for its potential to control outbreaks of lepidopterous and coleopterous defoliators. *Picromerus bidens* (Fig. 110) was originally a widely distributed Palearctic species, but it has been found in the northeastern United States and eastern Canada since its (accidental) introduction sometime before 1932. Although its biology has been studied to some extent, few studies have attempted to quantify its predatory effectiveness. Given that only 10% of the nearly 300 known species of Asopinae has been studied in more or less detail, obviously an enormous biocontrol potential remains to be investigated.

► Stink Bugs (Hemiptera: Pentatomidae) Emphasizing Economic Importance
► Bugs (Hemiptera)



Predatory Stink Bugs (Hemiptera: Pentatomidae, Asopinae), Figure 110 **Line drawing: *Picromerus bidens* (taken from T.J. Henry and R.C. Froeschner, 1988. Catalog of the Heteroptera, or True Bugs of Canada and the Continental United States. E.J. Brill).**

References

Aldrich JR (1999) Predators. In: Hardie J, Minks AK (eds) Pheromones of non-lepidopteran insects associated with agricultural plants. CAB International, Wallingford, UK, pp 357–381

De Clercq P (2005) *Podisus* online. Available at http://users.ugent.be/~padclerc/

De Clercq, P (2000) Predaceous stinkbugs (Pentatomidae: Asopinae). In: Schaefer CW, Panizzi AR (eds) Heteroptera of economic importance. CRC, Boca Raton, FL

Thomas DB (1992) Taxonomic synopsis of the asopine Pentatomidae (Heteroptera) of the Western Hemisphere. The Thomas Say Foundation monographs, vol 15. Entomological Society of America, Lanham, MD

Thomas DB (1994) Taxonomic synopsis of the Old World asopine genera (Heteroptera: Pentatomidae). Insecta Mundi 8:145–212

Predisposing Factors

Factors which, by their actions, render an organism susceptible to a certain disease; conferring a tendency to disease.

Pre-Emergence Treatment

Treatment of a plant, usually with a pesticide, before the plant has emerged from the soil.

Pre-Planting Treatment

Reference to a treatment applied to a crop before planting.

Prepupa

A generally quiescent, occasionally active but non-feeding, stage of insects at the end of the immature development period. The period immediately preceding the molt to the adult stage. In thrips, it is the third instar.

Prescutum

The anterior portion of the meso- and metanotum.

► Thorax of Hexapods

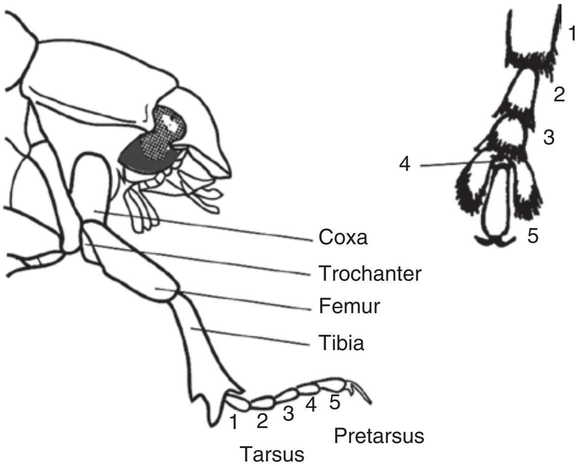
Presocial Behavior

Expression of one or two (but not all three) of the following traits of sociality: individuals of the same species cooperate in caring for the young; there is division of reproductive behavior, with more or less sterile individuals working on behalf of the fecund individuals; overlap of at least two generations in life stages contributing to colony labor, so that offspring can assist parents during some period of their life. Thus, presocial behavior is considered to include all the stages intermediate between solitary and eusocial behavior.

► Subsocial
► Communal
► Quasisocial
► Semisocial
► Eusocial Behavior

Prevalence

The frequency of occurrence. In ecology, the proportion of inhabitable sites or areas inhabited by



Pretarsus, Figure 111 Leg of a beetle (Coleoptera: Scarabaeidae) leg showing its component parts, and a close-up of one type of beetle tarsus (foot).

an organism. With respect to epizootiology, the total number of cases of a particular disease at a given moment of time, in a given population.

Pretarsus

The terminal portion of the leg. The tarsal claws and associated structures (Fig. 111).

► Legs of Hexapods

Prey

In entomology, insects that are eaten by predatory animals (including other insects). If the insect is killed by a parasitoid or pathogen, the insect is called a host, not the prey.

Primary Parasitoid

A parasitoid of a host, not of another parasitoid.

Primary Production

Production by green plants (contrast with secondary production).

Primary Productivity

The rate at which biomass is produced by plants, expressed on a per unit area basis.

Primary Reproductives

In social insects, the pair of insects that founds the colony.

Primer

In molecular biology, a short oligonucleotide that is attached to a ssDNA molecule in order to provide a site at which DNA replication can begin.

Primer Pheromone

A pheromone that acts to modify the physiological condition of an animal (contrast with releaser pheromone).

Primitive Caddisflies

Members of the family Rhyacophilidae (order Trichoptera).
► Caddisflies

Primitive Carrion Beetles

Members of the family Agyrtidae (order Coleoptera).
► Beetles

Primitive Crane Flies

Members of the family Tanyderidae (order Diptera).
► Flies

Primitive Dampwood Termites

Members of the termite family Termopsidae.
► Termites

Primitive Weevils

Members of the family Belidae (order Coleoptera).
► Beetles

Prionoglaridae

A family of psocids (order Psocoptera).
► Bark-Lice, Book-Lice or Psocids

Probability Model

In sampling, a mathematical description of the dispersion or distribution of individuals in a population based on numbers per sample unit. Common models include Poisson, Negative-binomial, Binomial, Normal, and Neyman Type A. Such models can form the foundation of a sampling plan.
► Sampling Arthropods

Probe

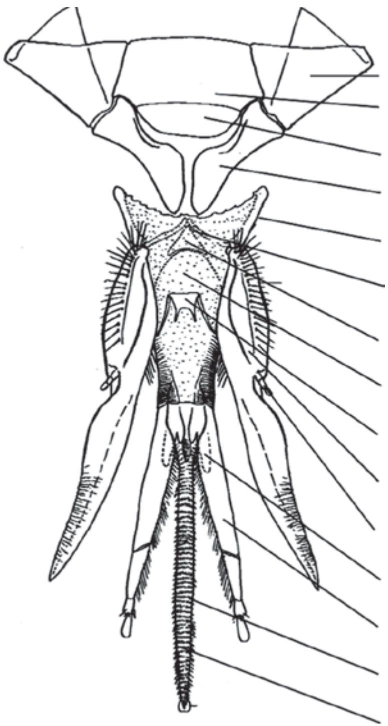
A probe is a molecule labeled with radioactive isotopes or another tag that is used to identify or isolate a gene, gene product, or protein.

Proboscis

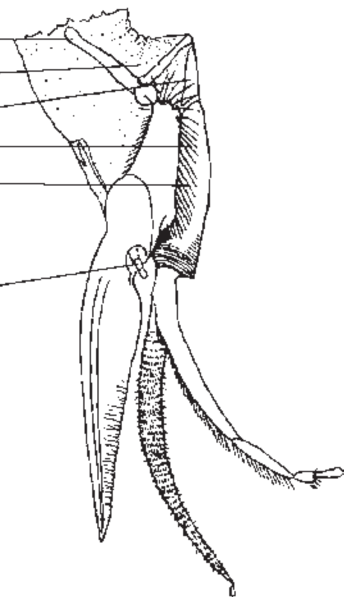
The tube-like or beak-like mouthparts or sucking apparatus of insects that are modified to feed on liquid food (Figs. 112–114).

Process

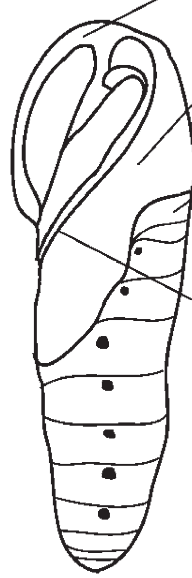
Any projection or prominent part of the body that projects from the surface, but that does not warrant a specific name; examples include bumps, warts, and tubercles.



Proboscis, Figure 112 Anterior aspect of a proboscis (Diptera).



Proboscis, Figure 113 Left lateral aspect of a proboscis (Diptera).



Proboscis, Figure 114 Side view of a moth pupa (Lepidoptera: Sphingidae) showing the proboscis.

Proctodeum

The hindgut of insects.

► Alimentary Canal and Digestion

Proctotrupidae

A family of wasps (order Hymenoptera).

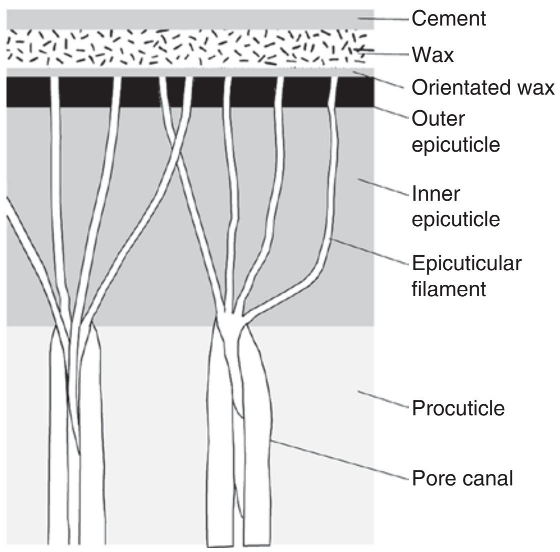
► Wasps, Ants, Bees and Sawflies

Procuticle

The inner zone of the cuticle, divisible into the hard, outer, dark exocuticle and the soft, inner, light endocuticle, and containing primarily chitin and protein. The procuticle exists during molting, before the inner layers of the cuticle (exocuticle and endocuticle) are sclerotized into distinct layers, but this is a temporary condition (Fig. 115).

► Cuticle

► Epicuticle



Procuticle, Figure 115 **Cross section of the insect epicuticle (adapted from Chapman, The insects: structure and function).**

Prodoxidae

A family of moths (order Lepidoptera). They commonly are known as yucca moths.

► Yucca Moths

► Butterflies and Moths

Profitability Concept

The concept that predators will seek prey that provide the most calories or biomass, as this represent the "most profitable" investment of their time by maximizing growth and reproduction. This can also be called optimal foraging.

Prognathous

A condition in which the head is horizontal and the mouthparts are directed forward. This is particularly common in burrowing and predatory species.

► Mouthparts of Insects

Progressive Provisioning

Among social insects, the act of provisioning the larva at intervals during its development, as opposed to mass provisioning.

Prohemocyte

Very small hemocytes, possibly giving rise to other types of hemocytes.

► Hemocytes of Insects: Their Morphology and Function

Projapygidae

A family of diplurans (order Diplura).

► Diplurans

Prokaryote

An organism whose cells lack a distinct nucleus.

Prokopy, Ronald J

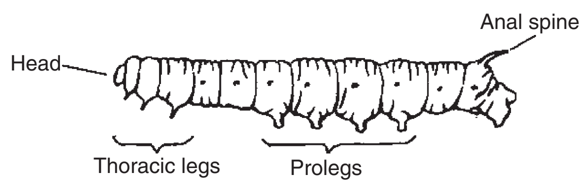
Ron Prokopy was known for innovative and insightful research on insect behavior that led to new approaches to effective pest management. He was born September 28, 1935 in Danbury, Connecticut, USA. He was raised on the family apple farm, an experience that likely explains his life-long fascination with apple pest management in general, and apple maggot in particular. After earning a B.S. and Ph.D. degree from Cornell University in 1964, Prokopy joined the Connecticut Agricultural Experiment Station, working on apple pests. There he was influenced by Jim Kring, who was studying host location by flying aphids. Prokopy initiated study of the visual orientation of apple maggot flies, examining how shape, color, and size of fruit and foliage influence fly behavior. A trademark of Prokopy's work then, and throughout his career, was the direct observation of these day-active insects. He manipulated the insects or their environment, either in cages or in the field, then watched and recorded their unusual and unanticipated actions for hours.

Prokopy traveled to Europe beginning in 1968, working in Poland, Switzerland, and Greece, but also worked with Guy Bush in Texas before settling into the "Prokopy Bio-Experimental Farm in Wisconsin." In 1975, he joined the University of Massachusetts, where he conducted research and educational programs for apple growers, and taught a course in insect pest management. His mission while in Massachusetts was to reduce or eliminate insecticides, a tall order for an industry grown accustomed to blemish-free fruit. Unlike most extensionists, Prokopy eschewed presentations about new and more effective insecticides, focusing on insect behavior. Perhaps because he had his own commercial orchard, growers listened to his advice, and gradually insecticide use was reduced. But Prokopy's personal intensity, knowledge, and integrity also contributed to his success in changing the attitudes and actions of growers, and they were soon great supporters of his philosophy. This high level of commitment, and a seemingly unending supply of energy, made him a popular mentor and collaborator.

Prokopy was a popular speaker and a prolific author. He published about 275 journal articles during his career, and over 400 scientific publications in total. He pioneered research on apple maggot fruit marking pheromone, and on using red, spherical sticky traps for population monitoring and removal trapping. Prokopy received many honors and awards. From the Entomological Society of America he received the Distinguished Service Award in Extension, founder's Memorial Award, Buzzard Award, and was named a Fellow of the Society. He also received a Guggenheim Fellowship, and a Fulbright Fellowship, and received both research and extension awards from the University of Massachusetts. Ron Prokopy died on May 14, 2004 in Greenfield, Massachusetts.

Reference

Cardé RT, Stoffolano JG Jr (2004) Ron Prokopy 1935–2004. Physiol Entomol 29:489–490



Proleg, Figure 116 **Lateral view of a "hornworm" caterpillar (Lepidoptera: Sphingidae).**

Prolarvae

Newly hatched larvae without completely functional legs, and incompletely sclerotized integument. Such larvae often remain aggregated.

Proleg

A fleshy, unsegmented appendage serving as a leg and found on the abdomen of some holometabolous insects, particularly caterpillars and sawflies (Fig. 116).

Prominence

A section of the body that is raised, elevated, or projecting.

Prominent Moths (Lepidoptera: Notodontidae)

JOHN B. HEPPNER
Florida State Collection of Arthropods, Gainesville, FL, USA

Prominent moths, family Notodontidae (including processionary moths), total 3,562 species from all faunal regions, most from the Neotropics (1,766 sp.); actual world fauna likely exceeds 4,000 species. The family is in the superfamily Noctuoidea, in the section Cossina, subsection Bombycina, of the division Ditrysia. The subfamily classification varies, but currently involves eight subfamilies, with segregation into three groups: Oenosandrinina (for Oenosandrinae, with three species in Australia), Thaumetopoeinina (for Thaumetopoeinae, and Notodontinina (for the remaining six subfamilies). Dioptidae (including Doinae) are sometimes included in Notodontidae. Adults small to very large (20–124 mm wingspan); some with massive bodies. Maculation varied, but many with subdued browns and grays; some white and a few more colorful or with iridescent markings. Adults mostly nocturnal. Larvae are leaf feeders, sometimes gregarious (especially among Thaumetopoeinae) and feeding nocturnally. Host plants include a large variety of plant families, especially for broadleaf forest trees. A number of economic species are known, especially among the processionary caterpillars (subfamily Thaumetopoeoinae) (Fig. 117).

References

Bender R (1985) Notodontidae von Sumatra. In: Heterocera Sumatrana, vol 5. Heterocera Sumatrana Society, Keltern, pp 1–101, 14 pl

Bryner R (2000) Notodontidae – Zahnspinner. In: Schmetterlinge und ihre Lebensräume: Arten-Gefährdung-Schutz. Schweiz und angrenzenden Gebiete, 3:403–524, pl 20–23, 25. Pro Natura-Schweizerische Bund fuer Naturschutz, Basel

Kiriakoff SG (1964–1970) Lepidoptera. Familia Notodontidae. In: Genera Insectorum, 217(A):1–213, 11 pl (1964); 217(B): 1–238, 8 pl (1967); 217(C): 1–269, 11 pl (1968); 217(A) (Suppl): 1–74 (1970); 219: 1–54, 3 pl (1970). Brussels

Prominent Moths (Lepidoptera: Notodontidae), Figure 117 Example of prominent moths (Notodontidae), *Epicoma melanosticta* Donovan from Australia.

Miller JS (1991) Cladistics and classification of the Notodontidae (Lepidioptera: Noctuoidea) based on larval and adult morphology. Bull Am Mus Nat Hist 204:1–230

Schintlmeister A (1992) Die Zahnspinner Chinas (Lepidoptera, Notodontidae). Nachrichten des Entomologischen Verein Apollo Supplement 11:1–343

Seitz A (ed) (1912–1934) Familie: Notodontidae. In: Die Gross-Schmetterlinge der Erde, 2:281–319, pl 44–49, 56 (1912); 2 (Suppl):172–186, 286, pl 14–15 (1933–34); 6:901–1070, pl 143–159 (1931–34); 10:605–655, pl 79–84 (1930); 14:401–444, pl 68–72 (1928). A. Kernen, Stuttgart

Promoter

A region of DNA crucial to the accuracy and rate of transcription initiation. Usually immediately upstream of the gene itself.

Pronotal Comb

In fleas, a row of strong spines on the posterior margin of the pronotum.

Pronotum

The upper or dorsal surface of the prothorax, often shield-like in form.

► Thorax of Hexapods

Pronunciation of Scientific Names and Terms

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Many words of Greek and Latin origin are used in entomology and are of two kinds. The first kind is words that have been adopted into English and other modern languages to describe forms, structures and processes. The second kind is the Latin (scientific) names of taxa at all classificatory levels. Their pronunciation has caused confusion.

Once, Latin was a living language. For many hundreds of years after the fall of Rome, Latin was the common language in western Europe, a means by which educated people in various countries communicated. That is why Linnaeus in the eighteenth century wrote his Systema Naturae in Latin rather than in his native Swedish. It is why Latin was used for binominal nomenclature. Later, French and then English became widely used, and the editions of the International Code of Zoological Nomenclature are written in those two languages although the names of taxa are still nominally Latin and follow the rules of Latin grammar.

Even by the time of Linnaeus, Latin pronunciation had diverged from country to country in western Europe to acquire the characteristics of each native language. By the late nineteenth century, Latin as pronounced in England (and, by extension, also in the USA, Australia, Canada, and New Zealand) had acquired the vowel and diphthong sounds of English, whereas Latin as pronounced in France had acquired some peculiarities of French. Likewise in Germany and Italy. Although Latin was written identically in countries of western Europe, it no longer was pronounced the same. In recognition of this problem, Latin scholars met to reconstruct pronunciation of Roman Latin, and then to begin its teaching in the early decades of the twentieth century. By the mid twentieth century, Latin pronunciation as taught in Latin classes in England, the USA, other English-speaking countries, and countries of continental Europe was once again (more or less) uniform. So we may talk about two systems of Latin pronunciation: corrupted Latin as used in the nineteenth century in English (and differently in other modern languages), and restored Latin as now taught in Latin classes.

But, damage of two forms already had been done. First, many Latin words had been adopted into English and the corrupted form had become the norm in English, as shown for a few words below (Table 17).

Pronunciation of Scientific Names and Terms, Table 17 **Examples of correct (restored) and corrupted English pronunciation of Latin**

Latin word	Restored Latin pronunciation	Corrupted English pronunciation
Alumnae	alumn.eye	alumn.ee
Alumni	alumn.ee	alumn.eye
Larvae	lar.why	lar.vee
Pupae	poop.eye	pyoo.pee

This corrupted English pronunciation is broadly used in biology, medicine and law, and is now engrained in English. We have to accept that such words are English, adopted from Latin, spelled as in Latin, but not pronounced as Latin is now taught. After all, English has adopted and mispronounced many words from other foreign languages. The words beau, bouquet, boutique, lieutenant and lingerie have been adopted from French. They are now used in France, are not relics of a long-defunct language, but yet are commonly mispronounced by English-speakers. The same kinds of changes have befallen other modern languages. French and Spanish too, despite regulation by academies designed to preserve their purity, have adopted, corrupted and mispronounced words from other languages, including English. They have likewise adopted words from Latin, and changed not only their pronunciation but also their spelling.

The International Code of Zoological Nomenclature specifies how scientific names of animals are to be formed. But it does not specify how they should be pronounced.

The most widely used basic entomology textbook in the USA (Borror et al., 1989) provides a few pages about construction of names of scientific names of insects. This explanation for the most part is good and useful. However, as to sounds of vowels, consonants, and diphthongs, it explains only the corrupted English pronunciation as taught in Latin classes in the USA in the nineteenth century. Its instructions are thus out of line with the way that Latin has been taught for the last 50 years. It promotes an outdated system that makes the pronunciation very hard to understand by anyone who learned Latin and/or pronunciation of scientific names in non-English-speaking countries. Generations of entomologists have relied upon this textbook to explain the latest classification of insects,

Pronunciation of Scientific Names and Terms, Table 18 **Pronunciation of Latin vowels, consonants, and diphthongs as now taught in Latin classes**

Vowels	Consonants
a (short) as in apple	b (as in English)
a (long) as in father	c as in cat
e (short) as in get	ch as English k (or k-h)
e (long) as in they	d (as in English)
i (short) as in pit	f (as in English)
i (long) as in machine	g as in go
o (short) as in not	h as in hence
o (long) as in note	i (consonant i [= j]) as y in yes
u (short) as in full	k (as in English)
u (long) as in brute	l (as in English)
y as "ew" but without any trace of y sound	m as in man n (as in English)
	ph as English p (or p-h)
Diphthongs	q as in quite
ae as y in English try	r always rolled
au as ou in English house	s as in sister
ei as in English rein	t as in tanned
eu as "ay-oo" (stress the "ay")	th as English t
oe as oi in English foil	v as English w
ui as in English we	x as in six
	z as in zero

most without realizing they were being subjected to an outdated concept of Latin pronunciation.

English-speaking botanists have been faced with the same dilemma. However, Stearn (1983) explains the restored Latin pronunciation together with the corrupted English pronunciation.

Restored Latin is the best hope of English-speaking entomologists to be able to communicate names of taxa to entomologists whose native language is something other than English, and to convert international congresses of entomology from something other than towers of Babel. Our objective should be to promote international communication by having a standard system for pronouncing scientific names. It should not be to perpetuate a corrupted, outdated, English mispronunciation of Latin, and even less to foist this on foreigners as being "Latin." Pronunciation of Latin vowels, consonants and diphthongs according to the restored system is explained in Table 18. It should not be difficult to learn, especially by anyone who has studied Italian or Spanish. It is further explained in modern textbooks on Latin grammar and in modern Latin dictionaries.

References

Borror DJ, Triplehorn CA, Johnson NF (1989) An introduction to the study of insects, 6th edn. Saunders College Publishers, Philadelphia, PA, xiv + 875 pp

International Commission for Zoological Nomenclature (1999) International code of zoological nomenclature, 4th edn. International Trust for Zoological Nomenclature, London, England, xxix + 306 pp

Stearn WT (1983) Botanical Latin: history, grammar, syntax, terminology, and vocabulary, 3rd edn. David and Charles, Devon, UK, xiv + 566 pp

Propagative Transmission

Transmission of an arthropod transmitted disease wherein the causal organism does not undergo cyclical changes, but multiplies in the body of the arthropod vector.

► Mechanical Transmission
► Cyclo-Developmental Transmission
► Cyclo-Propagative Transmission

Propagule

A general term used to describe a reproductive (propagative) stage that will give rise to a new organism, usually in plants (seeds, corms, bulbs) but also in invertebrates (eggs, cysts).

Prophylactic Control

Preventative control. Control procedures implemented in a pre-emptive manner to avoid the possibility of damage.

Propleuron

A lateral portion of the prothorax.

► Thorax of Hexapods

Propolis

The resins and waxes collected by bees and used in construction of nests, and in sealing cracks in the nest wall.

Proprioreceptor

An internal sensory receptor that senses the internal body condition including relative position of a body's components.

Propupa

The first of the quiescent instars in Thysanoptera; this stage lacks functional mouthparts.

Prosopistomatidae

A family of mayflies (order Ephemeroptera).

► Mayflies

Prosternum

The sclerite between the front legs.

► Thorax of Hexapods

Prostomidae

A family of beetles (order Coleoptera). They commonly are known as juglar-horned beetles.

► Beetles

Prostomium

A preoral, unsegmented portion of the body, anterior to the first true body segment. This is also known as the acron.

Protease

An enzyme that degrades proteins.

Protein

The polymeric compounds made up of amino acids.

Protelean Parasite

A insect that develops parasitically during the larval stage, and kills the host. The larva kills but a single host, and the adult stage is free living. A more popular term for this is "parasitoid."

Proteneuridae

A family of damselflies (order Odonata).

► Dragonflies and Damselflies

Protentomidae

A family of proturans (order Protura).

► Proturans

Proteomics

The science and process of analyzing and cataloging all the proteins encoded by a genome (a proteome). Currently the majority of all known and predicted proteins have no known cellular function. Determining protein function on a genomewide scale can provide critical clues to the metabolism of cells and organisms. Proteomics involves understanding the biochemistry of proteins, processes and pathways. Two-dimensional gel analyses were used in the late 1970s to identify proteins active (expressed) in different tissues at different times. Now, biological mass spectrometry is a powerful method for protein analysis, involving identification or localization of proteins and interactions of proteins.

Prothoracic Glands

Endocrine glands found in the thorax and secreting molting hormone (ecdysone) or a closely related ecdysteroid. They are activated by PTTH during the immature stage, and degenerate during or soon after metamorphosis.

► Ecdysone Agonists
► Ecdysteroids
► Endocrine Regulation of Insect Reproduction
► Metamorphosis
► Prothoracicotropic Hormone

Prothoracicotropic Hormone

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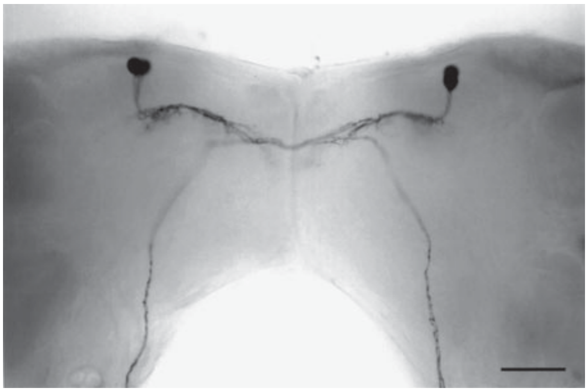
The growth and molting of insects are cyclical phenomena and are brought about predominantly by two hormones, one produced by neurosecretory cells in the insect's brain, and the other by glands in the prothorax, the prothoracic glands. Periodically, specific neurosecretory cells of the brain synthesize a hormone, the prothoracicotropic hormone (PTTH), that acts on the prothoracic glands, which, in turn, respond to this stimulus by synthesizing and releasing a steroid hormone [ecdysone (E), or 3-dehydroecdysone (3-dE), depending upon the species)] that is ultimately converted at target tissues to 20-hydroxyecdysone (20E), the principle molting hormone of insects. 20E then interacts with various target cells via binding to a high affinity nuclear receptor, which then modulates the expression of specific genes and ultimately, regulates cell growth and differentiation. In the case of the epidermal cells, 20E causes them to deposit a new cuticle and, thus, initiates the molting process. The cyclical synthesis and release of PTTH by the neurosecretory cells of the brain is elicited by environmental factors such as photoperiod, temperature, nutritional state, etc. In the case of moths and butterflies, such as the tobacco hornworm *Manduca sexta*, photoperiod and temperature are important and, indeed, the brain appears to possess an extraretinal photoreceptor, i.e., these PTTH-producing neurosecretory cells may be a self-contained unit directly perceiving the light signal, or perhaps the light signal is transduced elsewhere and the information transferred to these neurosecretory cells.

More than eight decades ago, the Polish biologist Stefan Kopeć first suggested that the control of insect molting was mediated by neurohormones. Using larvae of the gypsy moth, he extirpated the brains of these insects and showed that these "de-brained" insects lived for several weeks. If the brains were removed ten days or more after the final larval molt, pupation occurred and brainless, but otherwise normal, moths emerged. However, if the brain was removed prior to the tenth day, the caterpillars failed to pupate (i.e., undergo a metamorphic molt) although they survived for a long time. He also showed that if the larvae were divided into two hemolymph-tight compartments by a ligature posterior to the thorax, both the anterior and the posterior portions pupated simultaneously if tied off after the tenth day, but only the anterior portion pupated if ligation occurred prior to this critical period. Kopeć concluded from these studies that the brain liberates a substance into the hemolymph that is essential for pupation, and that it is released on or about the tenth day after the final larval molt. Indeed, not only was this the beginning of the field of insect neuroendocrinology, but it was also the beginning of the science of neuroendocrinology in general, and led to the now accepted dogma that the nervous system of almost all animals functions as an endocrine gland.

About fifteen years after the work of Kopeć, the great British biologist, Vincent Wigglesworth, showed that decapitation of the blood-sucking hemipteran (bug) nymph *Rhodnius prolixus*, within three or four days after feeding, prevented molting, but that decapitation after this period did not. He concluded that there is a factor within the head (i.e., a portion of the brain) that initiates the molting process. These sorts of experiments have been verified consistently in literally hundreds of species over the past seventy years. Further studies in the 1940s showed that regions of the brain containing large neurosecretory cells were the active portions of this neuroendocrine organ. The classic studies of Piepho (Germany), Fukuda (Japan) and Williams (USA) in the 1940s showed dramatically, again via surgical manipulations, that the brain hormone (PTTH) exerted its effect humorally on the prothoracic glands. When the product of the prothoracic glands was identified as ecdysone in the 1950s, it was hypothesized that PTTH elicited, or enhanced, the synthesis and secretion of ecdysone from the prothoracic glands. This finding of a brain-prothoracic gland (neuropeptide-steroidogenesis) axis was of real interest both to insect physiologists examining the control of insect molting and to those interested in evolution, because this system is quite analogous to the mammalian ACTH-adrenal cortex axis in both a general way, and subsequently, in many details of its transductory biochemistry.

The presence of neurosecretory cells in the nervous system is a very early event in the evolution of animals with data indicating their existence in organisms as primitive as coelenterates (*Hydra*). It should be noted that there are reports that prothoracic glands can also be controlled neurologically by neurons from the brain in some insects, and it has even been suggested that there is direct transport of neurosecretory products by way of channels in the basal lamina, an extracellular matrix that covers all insect tissues. For the most part, however, there is a consensus that PTTH leaves the brain, is stored in a neurohemal organ attached to the brain (the corpus allatum), is released into the hemolymph at specific times and activates the prothoracic gland (Fig. 118).



Prothoracicotropic Hormone, Figure 118 Immunochemical detection of PTTH in the brain of a day-0 *Manduca sexta* pupa. Note staining in two cell bodies (prothoracicotropes) in each hemisphere of the brain and the crossing of the axon tracts as they move posteriorly to ultimately end in the corpus allatum (not shown) (from Gilbert et al., 2000).

By the 1970s, investigators began to examine the mechanisms by which PTTH might activate the prothoracic glands to synthesize ecdysone. It was believed by some that in order to study the complex transductory mechanisms involved in ecdysone biosynthesis, it would be much too difficult to work with the whole insect. They therefore attempted, and achieved, a model in which the prothoracic glands of M. *sexta* were placed in a culture medium (in vitro) in which they can live and function in an almost normal way for several weeks. Such glands were shown to synthesize and release 3-dE which was subsequently converted to E and then 20E. It was demonstrated that extracts of the brain of the tobacco hornworm could stimulate the synthesis of 3dE in a consistent and predictable way. Of great importance was the observation that the right and left prothoracic glands of this insect secreted the same quantity of 3dE in vitro so that one gland of a single insect could be experimentally manipulated, with the other serving as the control. With this in vitro assay, a great deal has been learned about how the PTTH signal is transduced into enhanced ecdysteroid synthesis in the prothoracic gland.

The first indication that a mammalian-like signaling mechanism was utilized was the finding that brain extract stimulated the rapid synthesis of cyclic AMP (cAMP) in the prothoracic glands, and that this was followed by 3dE biosynthesis. (In reality, it is the mammal that used an insect-like signaling mechanism because insects evolved several hundred million years before mammals.) With this in vitro bioassay, it was also possible to assay particular parts of the *Manduca* brain as noted previously, and by dissecting out specific neurosecretory cells with an eyebrow hair, it was shown that there were two neurosecretory cells in each side of the brain of the insect that contained PTTH. These so-called prothoracicotropes contained varying amounts of PTTH activity during development. It was shown by immunocytochemical means that axons from these neurosecretory cells extend posteriorly and laterally such that they cross and terminate in the neurohemal organs (corpora allata) where PTTH is stored. Thus, the so-called critical period shown by Kopeć, Wigglesworth and many others is actually the time when PTTH is released from these neurohemal organs into the hemolymph due to one of a variety of environmental and physiological signals. It is of interest that cAMP is also a principal component of the signal transductory cascade in the mammalian ACTH (from the pituitary gland)- adrenal cortex axis.

Most of the data discussed here were generated using PTTH-containing brain extracts to study how PTTH activates ecdysteroid synthesis in the prothoracic glands. Consequently, there have been frequent questions as to whether all the changes in prothoracic gland biochemistry that are elicited by brain extracts are due solely to the effect of PTTH. However, very recently, the *Manduca* PTTH has been cloned, the nucleotide sequence determined and purified, recombinant PTTH produced by transformed cells. The use of this pure, recombinant PTTH in the in vitro system has confirmed all observations on the prothoracic gland that were made using the brain extract.

PTTH-Prothoracic Gland Interactions

PTTH has now been purified and cloned, first from the domestic silkmoth *Bombyx mori*, and subsequently from several other moths (Lepidoptera). The analysis of the PTTH protein and gene sequences indicates that this hormone is synthesized as a prohormone that is processed into a shorter homodimeric molecule (25–30 kDa) as it is transported down the axons of the prothoracicotropes to their termini in the corpus allatum. The structure specified by intra-monomeric, cystine-cystine bonds is essential for the bioactivity of the hormone. Lepidopteran PTTHs clearly comprise a family of proteins, based on the distribution of cystine-cystine bonds, charged amino acids and hydrophilic regions, but these PTTHs are essentially species-specific in action, indicating that the amino acid sequence (primary structure) is likely important for bioactivity. Outside of the Lepidoptera, the structure of PTTH remains conjectural although the PTTH of the fruit fly *Drosophila melanogaster*, appears to be highly glycosylated and considerably larger than those of the moths. These results suggest two possibilities. First, PTTHs have diverged from an ancestral molecule to such a degree that PTTHs from different taxa have only limited structural similarity with minimal amino acid conservation. Second, PTTHs from different taxa (e.g., flies vs. moths) have evolved from different ancestral proteins, and their only similarity is their ability to elicit ecdysteroid synthesis by the prothoracic gland. Current data cannot resolve this issue.

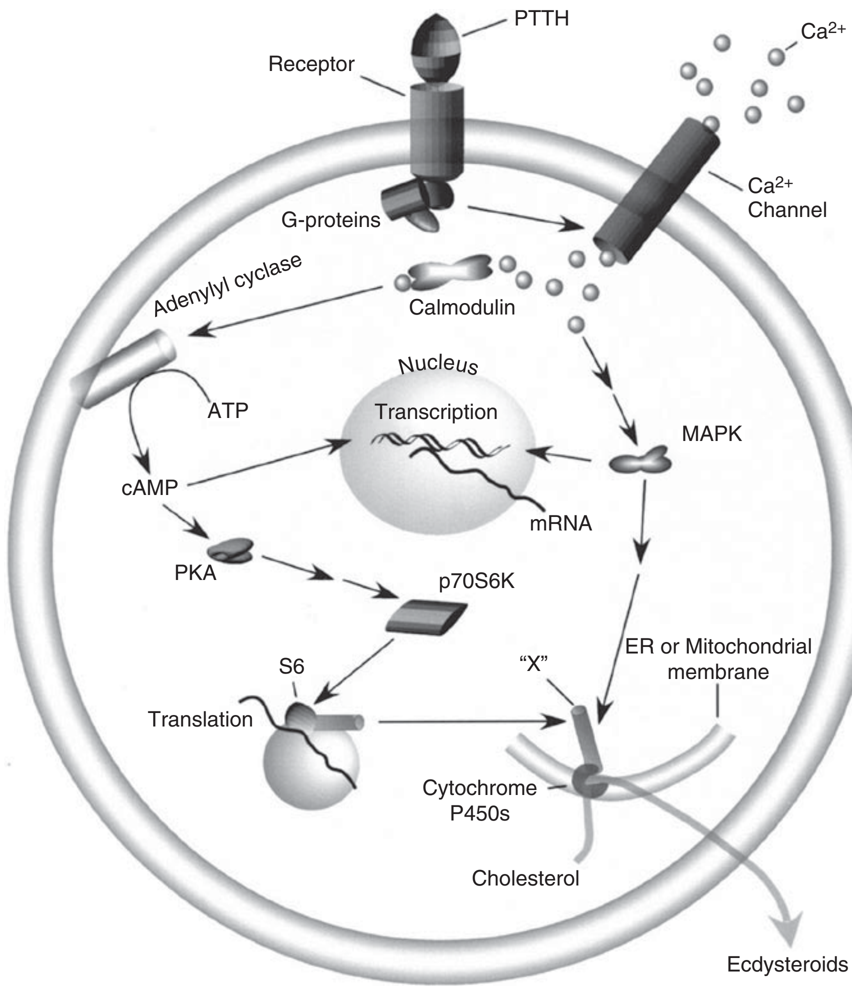
Periodic increases in ecdysteroid titer are critical to pre-adult insect development, as discussed above, and reflect activation of the prothoracic gland by PTTH. PTTH release occurs in particular daily time "windows," following the integration of a variety of factors, such as time since last molt, nutritional status and physical size. How and where such factors are sensed is unknown, but studies do indicate that PTTH release is acutely controlled by the muscarinic class of acetylcholine-releasing neurons. A neuroendocrine modulation of PTTH release has recently been demonstrated in the cockroach *Periplaneta americana*, involving the neurohormone melatonin, which mediates day-night physiological differences in many organisms. While daily cycles of melatonin and PTTH levels are not seen in *Periplaneta*, melatonin could be involved in controlling a daily cycle of PTTH release described in *Rhodnius*.

Changes in PTTH release during *Bombyx* development have been investigated using prothoracic glands in vitro as well as antibodies against PTTH. Although these two approaches were not in complete agreement, both indicate that major peaks of ecdysteroid secretion by the prothoracic gland are preceded by, and partly overlap with, high PTTH titers, and that some episodes of increased PTTH titer are not associated with obvious ecdysteroid production. This latter observation supports the hypothesis that PTTH may have functions in addition to the regulation of prothoracic gland ecdysteroidogenesis.

PTTH may not be the only molecule that stimulates ecdysteroidogenesis by the prothoracic gland, but our knowledge of the nature of other molecules, their biological significance and their modes of action, is rudimentary and preliminary. A brain-derived "small PTTH" (MW < 10,000) of *Manduca* is the best characterized of three candidate factors. Small PTTH stimulates ecdysteroid synthesis in larval glands in vitro, but is only weakly active when applied to pupal glands. Small PTTH appears to stimulate the same second messenger cascades as big PTTH (Ca^{2+} and cAMP: see below), suggesting that it might be an active proteolytic fragment of PTTH, generated during PTTH purification. Conclusive evidence that small PTTH is released into the circulation is lacking. Other candidate ecdysteroidogenic factors that can act upon the prothoracic gland in vitro have been partially purified from lepidopteran proctodaea (*Manduca sexta*, *Lymantria dispar* and *Ostrinia nubilalis*). Given the precedent of the vertebrate gut as an endocrine organ, such findings may not be surprising, but definite roles have yet to be demonstrated in vivo for these incompletely characterized insect molecules. It also would not be surprising if there were negative regulators (inhibitors) of prothoracic gland ecdysteroid synthesis and, indeed, at least two candidate molecules have been isolated, one from fly ovaries and a second from a moth brain, but the in vivo significance of these data remains conjectural (Fig. 119).

The PTTH Transductory Cascade

In the 1970s, studies of the *Manduca* prothoracic gland showed that levels of cAMP, an important intracellular second messenger, were elevated during periods of increased ecdysteroid synthesis (Fig. 119). Further research demonstrated that PTTH stimulated a rapid increase in gland cAMP



Prothoracicotropic Hormone, Figure 119 **A model for the major PTTH-stimulated biochemical events that occur in prothoracic gland cells. Proteins and processes connected by single arrows are likely to be directly interacting, while two arrows indicate the probable interposition of one or more additional proteins or events. PTTH, Prothoracicotropic hormone; cAMP, cyclic adenosine monophosphate; p70S6K, 70 kDa molecular weight S6 kinase; S6, ribosomal protein S6; MAPK, mitogen-associated protein kinase; ER, endoplasmic reticulum; "x," hypothesized, newly synthesized protein that regulates the rate of ecdysteroid synthesis in prothoracic glands stimulated by PTTH.**

content in vitro, detectable within minutes. However, cAMP generation is not the first intracellular change triggered by PTTH. Experiments revealed that cAMP generation was dependent on the influx of extracellular Ca^{2+}, suggesting that cAMP synthesis required Ca^{2+}-calmodulin dependent adenylyl cyclase activity, which is indeed present in prothoracic glands. A variety of Ca^{2+} channels exist in many cell types and it is not clear which type opens in response to PTTH, let alone the mechanism by which PTTH accomplishes this action. G-proteins, small proteins often associated with peptide hormone receptors, may be involved directly in Ca^{2+} channel opening, but other data indicate that cAMP could be involved in such channel regulation. The observation that PTTH stimulates rapid synthesis of cAMP indicates, based on our knowledge of analogous systems in vertebrates, that the PTTH receptor is likely to be situated in the cell membrane, and that binding of PTTH to the receptor is the first step in PTTH signal transduction. Furthermore, the PTTH receptor is predicted to belong to the family of proteins known as G-protein coupled receptors, and to possess an extracellular region that binds PTTH. Nevertheless, knowledge of the earliest events stimulated by PTTH in prothoracic glands is incomplete.

As intracellular levels of cAMP rise, the important cAMP-dependent kinase, protein kinase A (PKA), is rapidly activated in the prothoracic glands. (Kinases regulate the function of other proteins via the addition of phosphate groups.) However, the natural substrates of PTTH-stimulated PKA activity are not known, and a requirement for PKA activity in PTTH-stimulated ecdysteroidogenesis has not been proven unequivocally. It is clear that analogs of cAMP that enter the prothoracic gland stimulate ecdysteroidogenesis and that an inhibitory, stereoisomeric analog of cAMP blocks PTTH-stimulated ecdysteroidogenesis. However, PKA is not the only protein dependent on cAMP for activity, and, therefore, the possibility remains that proteins other than PKA transduce the PTTH signal into eventual ecdysteroid synthesis. For example, a mammalian cAMP-dependent guanine nucleotide exchange factor has been discovered that activates small G-proteins, leading to phosphorylation-dependent events, including the activation of the 70 kDa S6 kinase, a known target in PTTH action.

PTTH stimulates a number of protein phosphorylations in the prothoracic gland via PKA, mitogen-activated protein kinases (MAPKs) and perhaps other kinases. The most prominent and consistent phosphorylated protein is the ribosomal protein S6. The importance of S6 phosphorylation in PTTH-stimulated ecdysteroid synthesis was demonstrated in studies using the drug rapamycin, which blocks S6 phosphorylation by inhibiting the activation of the 70 kDa S6 kinase. In the prothoracic gland, rapamycin inhibits not only S6 phosphorylation, but also PTTH-dependent ecdysteroid and protein synthesis. In vertebrate cells, S6 phosphorylation increases the rate of protein synthesis, especially of mRNAs possessing a polypyrimidine tract at their 5′ transcriptional end, and it is likely that it acts similarly in insect cells. The activation of MAPKs in PTTH-dependent signal transduction has only recently been demonstrated, along with the ability of MAPK inhibitors to inhibit ecdysteroid synthesis. Like the ribosomal protein S6, MAPKs can regulate translation, although by another route, but whether this regulation occurs in the prothoracic glands is currently unknown.

Vertebrate and insect steroidogenic cells share many intracellular mechanisms that function in the regulation of steroid hormone synthesis, as noted previously. In both groups, peptide hormones produced by neurons or brain-associated cells bind to cell membrane receptors associated with G-proteins, with a subsequent generation of cAMP. Increases in intracellular Ca^{2+} occur, as do multiple protein phosphorylations, including that of the ribosomal protein S6. In both taxa, the final transductory step in acutely up-regulating steroid hormone production appears to be the synthesis of one or more short-lived proteins that abolish a rate-limiting bottleneck in the steroid synthesis pathway. In vertebrates, two such proteins are believed to facilitate the movement of cholesterol across the mitochondrial membrane, which is the rate-limiting step in vertebrate steroid hormone production. In insects, the rate-limiting step in ecdysteroid synthesis has not yet been characterized, but recent data from *Drosophila* suggest it may well involve movement of ecdysteroid precursors between intracellular compartments, like the endoplasmic reticulum and the mitochondrion, and that a carrier protein may be involved. Furthermore, it is known that PTTH-stimulated ecdysteroid synthesis in *Manduca* requires protein synthesis, as demonstrated by the ability of translation inhibitors to block PTTH-stimulated ecdysteroid synthesis, and that PTTH stimulates the synthesis of about ten specific proteins.

PTTH might also regulate other cell types besides those of the prothoracic gland. A thorough discussion of this topic is not within the scope of this review, but it is noteworthy that significant levels of PTTH are present in adult brains, by which time the prothoracic glands have disappeared due to programmed cell death. This observation suggests that PTTH likely regulates cellular processes other than prothoracic gland ecdysteroid synthesis.

A number of the important PTTH-related events in the prothoracic gland is now known. However, knowledge about the events that occur in prothoracic gland cells after PTTH stimulation is still fairly incomplete. For instance, nothing is known about possible PTTH-elicited long term changes in the levels of ecdysteroid-synthesizing enzymes (cytochrome P450s) via either translation or transcription, an effect that might be expected based on vertebrate studies. The PTTH-stimulated activation of a mitogen-activated protein kinase is suggestive in this context, as this family of kinases can migrate into the nucleus to regulate transcription. Furthermore, there are enormous gaps in our knowledge of the events that occur between PTTH contacting a prothoracic gland cell and S6 phosphorylation, and between this phosphorylation and the first steps in the conversion of cholesterol to ecdysteroid. It is likely that continued, integrated molecular and biochemical studies of the PTTH control of ecdysteroid synthesis will fill many of these gaps in our knowledge and that major revisions in our current understanding will surely be necessary in the future.

► Ecdysteroids
► Ecdysone Agonists
► Diapause

References

Gilbert LI, Combest W, Smith W, Meller V, Rountree D (1988) Neuropeptides, second messengers and insect molting. Bioessays 8:153–157

Gilbert LI, Rybczynski R, Warren JT (2002) Control and biochemical nature of the ecdysteroidogenic pathway. Annu Rev Entomol 47:883–916

Gilbert LI, Rybczynski R, Song Q, Mizoguchi A, Morreale R, Smith WA, Matubayashi H, Shionoya M, Nagata S, Kataoka H (2000) Dynamic regulation of prothoracic gland ecdysteroidogenesis: *Manduca sexta* recombinant prothoracicotropic hormone and brain extracts have identical effects. Insect Biochem Mol Biol 30:1079–1089

Henrich V, Rybczynski R, Gilbert LI (1999) Peptide hormones, steroid hormones and puffs: mechanisms and models in insect development. In: Litwack G (ed) Vitamins and hormones. San Diego, CA, Academic Press, pp 73–125

Rybczynski R, Bell S, Gilbert LI (2001) Activation of an extracellular signal-related kinase (ERK) by the insect prothoracicotropic hormone. Mol Cell Endocrinol 184:1–11

Song Q, Gilbert LI (1997) Molecular cloning, developmental expression, and phosphorylation of ribosomal protein S6 in the endocrine gland responsible for insect molting. J Biol Chem 272:4429–4435

Prothoracic Plate

Equivalent to thoracic plate.

Prothorax

The most anterior of the three thoracic segments, bearing the first pair of legs.

► Thorax of Hexapods

Protocerebrum

The largest and most anterior segment of the insect brain, that innervates the compound eyes and ocelli (Fig. 120).

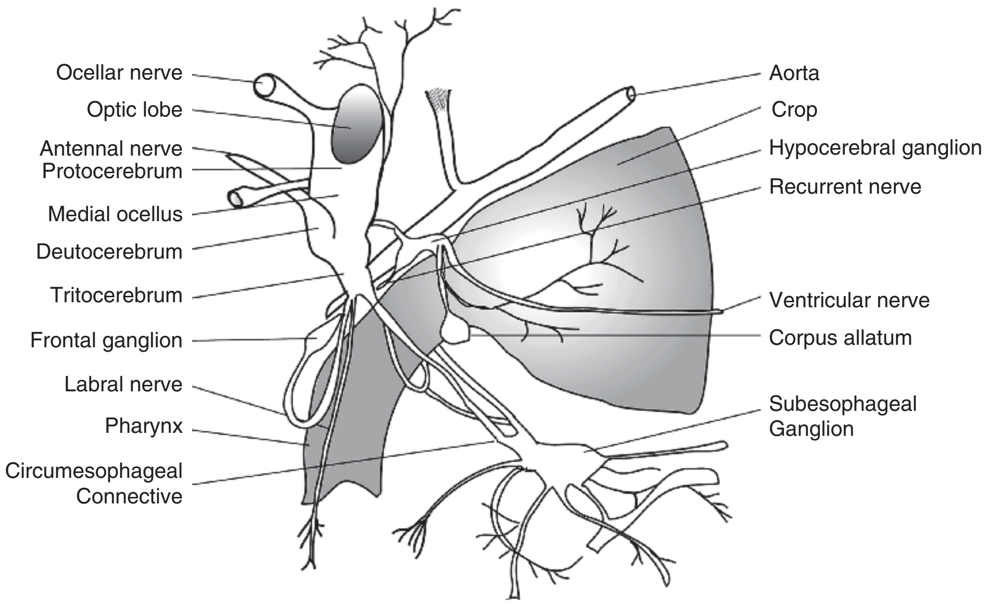
► Nervous System

Protonymph

In mites (Acari), the second instar.

Protopodite

The basal portion of a segmented appendage.



Protocerebrum, Figure 120 Diagram of the insect brain, lateral view (adapted from Snodgrass, Insect morphology).

Prototheoridae

A family of moths (order Lepidoptera). They also are known as African primitive ghost moths.

► African Primitive Ghost Moths
► Butterflies and Moths

Protuberance

A projection.

Proturans (Protura)

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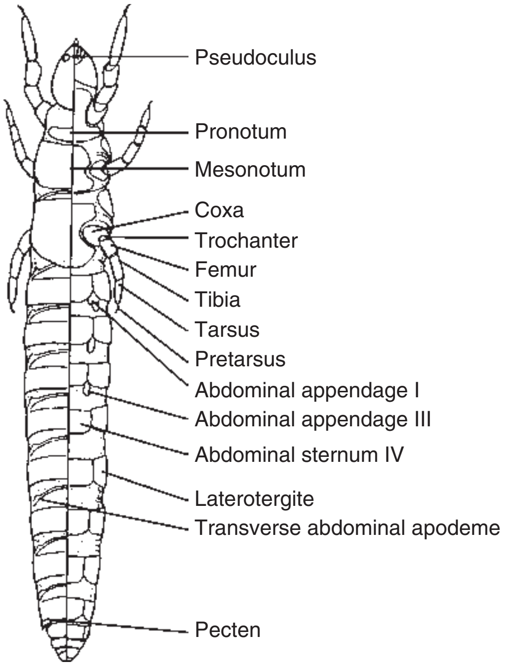
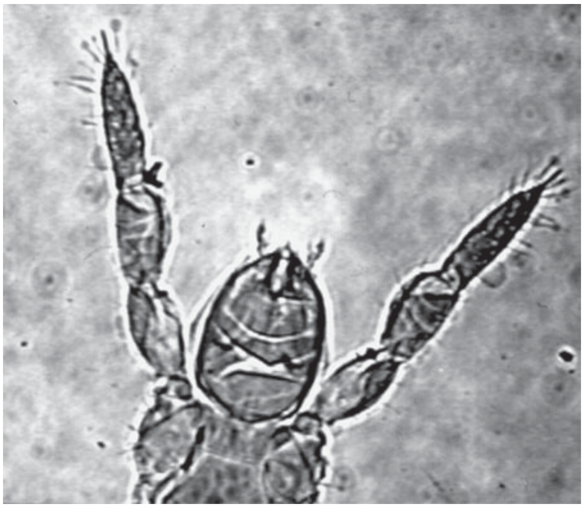
The order Protura consists of minute soil-inhabiting hexapods characterized by the lack of eyes and antenna, a 12 segmented abdomen and development by anamorphosis. The first three abdominal segments have small leg-like appendages that are capable of movement (Fig. 121). The first pair of legs have enlarged foretarsi that are covered with many types of setae and sensilla and function as antenna (Figs. 122 and 123). The first Proturan species discovered, *Acerentomon doderoi*, was described in 1907 by Silvestri. Some researchers believe that Protura is a sister group to the Collembola, though Protura may be a separate class. Here, it is included in the class Entognatha. Protura have a worldwide distribution with over 500 described species divided into two distinct suborders: Eosentomoidea and Acerentomoidea with nine families:

Class: Entognatha
Order: Protura
Suborder: Eosentomoidea
Family: Eosentomidae
Family: Sinentomidae
Suborder: Acerentomoidea
Family: Acerentomidae
Family: Protentomidae
Family: Hesperentomidae
Family: Berberentomidae
Family: Nipponentomidae
Family: Acerellida
Family: Antelientomidae

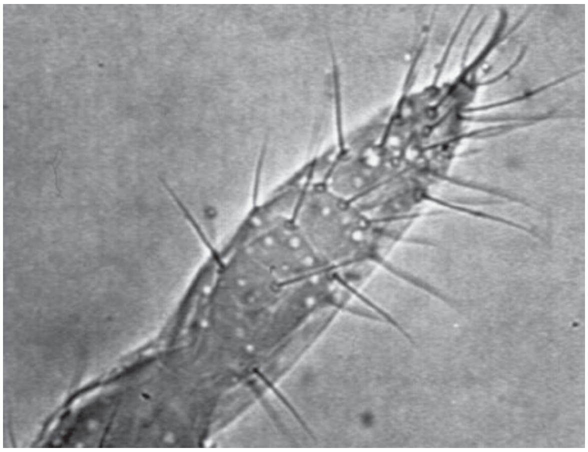
Proturans in the Eosentomoidea possess spiracular openings on the meso- and metathorax



Proturans (Protura), Figure 121 **Diagram of a proturan: left, dorsal view; right, ventral view.**



Proturans (Protura), Figure 122 **Foretarsi of *Eosentomon maryae* Tipping.**



Proturans (Protura), Figure 123 **Close-up of foretarsi showing setae and sensilla.**

connected to a primitive tracheal system. Proturans in the Acerentomoidea are without specialized respiratory structures and respire directly through the cuticle.

Proturans exhibit anamorphosis, a type of development that adds a body segment after a molt. The first stage, or prelarva, is hatched from the egg with nine abdominal segments and weakly developed mouthparts. The second stage or Larva I also has nine abdominal segments but with fully developed mouthparts. Larva II has an additional abdominal segment added between the eighth segment and the telson, or last abdominal segment. The next stage is the maturus junior which has eleven abdominal segments. The maturus junior molts to the adult stage except for males in the family Acerentomidae, which have an additional stage known as the pre-imago. The pre-imago has partially developed internal genitalia. It is not known if the adult stage continues to molt throughout the remainder of its life.

The life-history of Protura is poorly understood. Many species can be found in leaf litter, soil that is rich in organic matter, and dead wood. Similarly, the diet of protura is not well known. Their mouthparts are entognathous and most species appear to have modifications for feeding on fungi; however, some species have styletiform or grinding structures. Like most soil arthropods, proturans most likely feed on a variety materials including plants and fungi as well as scavenging on dead arthropods. In culture, Proturans have been observing feeding on mushroom powder, dead mites, and mycorrhizal fungi.

Protura can be collected from soil and leaf litter with Berlese funnels or by the centrifugation sugar flotation technique. They can be stored in 70% ethanol until mounted on permanent microscope slides with Hoyer's or other clearing medium.

Like many other soil arthropod groups, relatively few proturans have been described by taxonomists. Not surprisingly, distribution records for this group are far from adequate to attempt to understand their biogeography. Undoubtedly, there are many hundreds of species yet to be found from the tropics as well as temperate climate areas.

References

Imadaté G (1974) Fauna Japonica Protura (Insecta). Keigaku, Tokyo, Japan, 351 pp

Nosek J (1973) The European Protura: their taxonomy, ecology and distribution with keys for determination. Museum d' Histoire Naturelle, Geneva, Switzerland, 345 pp

Tuxen SL (1964) The Protura. A revision of the species of the world with keys for determination. Hermann, Paris, France, 360 pp

Provancher, (L' abbé) Léon

Léon Provancher was born at Bécancour, Quebec, Canada, on March 10, 1820. Educated for the Catholic priesthood and later designated Abbot, he eventually gave up this work due to poor health and moved to Cap Rouge, Quebec. There he devoted his time to the natural sciences, including botany, birds, molluscs, worms, and entomology. In 1869 he began publication of the journal "Le Naturaliste Canadien," which was nearly 8,000 pages long before being terminated for lack of support. Also, he commenced publication of the "Petite Faune Entomologique du Canada," which began with a volume on Coleoptera, published in 1877, and eventually included treatises on Orthoptera, Neuroptera, Hymenoptera, and Hemiptera. He labored on this project until 1890, and his most important contributions are on Hymenoptera and Hemiptera. He described hundreds of insects, including 923 species of Hymenoptera alone. This is a particularly remarkable achievement because he was isolated from libraries and collections. He died at Cap Rouge, Canada, on March 23, 1892.

References

Anon (1895) L' Abbe Provancher. Entomol News 6:7

Essig EO (1931) A history of entomology. Macmillan, New York, 1029 pp

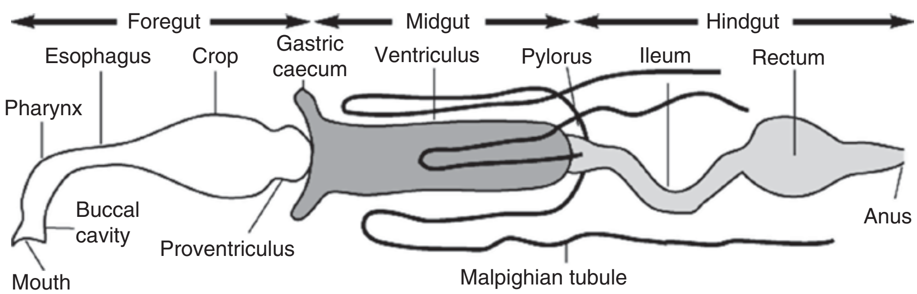
Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Proventriculus

A valve that controls entry of food into the midgut, and located at the terminus of the foregut (Fig. 124). It is a muscular organ and capable of some grinding action.

► Alimentary System

► Alimentary Canal and Digestion



Proventriculus, Figure 124 **Generalized insect alimentary system (adapted from Chapman, The insects: structure and function).**

Proximal

Pertaining to the part of an appendage closer to the body.

Pruinose

Covered with whitish waxy powder. This condition is common in aphids and scales.

Psephenidae

A family of beetles (order Coleoptera). They commonly are known as water-penny beetles.

► Beetles

Pseudergate

In lower termites, a caste from individuals regressing from nymphs, or derived from larvae. In either case, they comprise the worker caste, but can develop into other castes following additional molts.

Pseudironidae

A family of mayflies (order Ephemeroptera).

► Mayflies

Pseudoantagonism

An aggressive response by pollinators to orchids that appear to be invaders of the pollinator's territory. The pollinator's response can result in pollination of the orchids.

Pseudocaeciliidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice, or Psocids

Pseudococcidae

A family of insects in the superfamily Coccoidae (order Hemiptera). They sometimes are called mealybugs.

► Scale Insects and Mealybugs
► Bugs

Pseudocopulation

A copulatory response by male pollinators to orchids that mimic females of the pollinator species. The pollinator's response can result in pollination of the orchids.

Pseudo-Curly Top Treehopper, *Micrutalis malleifera* (Fowler) (Hemiptera: Membracidae)

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The pseudo-curly top treehopper or nightshade treehopper, *Micruotalis malleifera* (Fowler), is the only known member of Membracidae to transmit any plant disease agent. This insect was first reported to transmit tomato pseudo-curly top virus (PCTV) in south Florida in 1957. PCTV is now recognized as a member of Geminiviridae based on the inclusion body in the infected cell, serological tests, and sequence evidence. PCTV is transmitted by *M. malleifera* in a semipersistent-circulative manner. Transmission can also be achieved by injecting the treehopper vector with either crude sap or partially purified virus preparation. The transmission efficiency by sap injection is estimated at 30%. Both adults and nymphs are efficient vectors of PCTV. Nymphs retain the virus transmissibility after molting. The transmission efficiency reaches 60% after a 6-h acquisition access period (AAP). The median incubation period of PCTV in *M. malleifera* is estimated at 15 h after a 6-h AAP. The average retention period in the vector is 12 days. Pseudo-curly top disease has been a chronic problem in tomato production in south Florida since the 1940s. The incidence of pseudo-curly top on tomato reaches as high as 50% in some years. PCTV host plants include tomato (*Lycopersicon esculentum* Mill.), eggplant (*Solanum melongena* L.), night shade (*S. nigrum* L.), lettuce (*Lettuca sativa* L.), ragweed (*Ambrosia* sp.), tobacco (*Nicotiana glutinosa* L.), chickweed (*Stallaria medea* L.) and jimson weed (*Datura stramonium* L.).

At 25 ± 1°C using eggplant, nighshade, and ground cherry (*Physalis floridana* Rydb.) as rearing hosts, all *M. malleifera* nymphs display five instars. The average developmental times for instars 1–5 are 4.6, 4.3, 4.4, 5.4 and 7.8 days, respectively, on eggplant; 4.8, 4.5, 4.6, 5.2, 7.6 days, respectively, on nightshade; and 4.6, 4.3, 4.4, 5.4 and 7.8 days, respectively, on ground cherry. The size of instars 1–5 averages as follows: 1.3 mm long and 0.4 mm wide for the first instar, 1.7 mm long and 0.6 mm wide for the second instar, 2.3 mm long and 0.8 mm wide for the third instar, 3.1 mm long and 1.2 mm wide for the fourth instar, and 4.2 mm long and 1.8 mm wide for the fifth instar.

The average adult longevities for females and males are 56.1 and 37.2 days on eggplant, 33.7 and 30.6 days on nightshade and 12.0 and 10.6 days ground cherry, respectively. The adult female is 4.6 mm in length and 2.5 in width. The male is 4.2 mm long and 2.2 mm wide. The eggs are deposited mainly on terminal stems and petioles, but often eggs are found on eggplant leaves. The eggs are imbedded under the epidermal layer with a portion of the egg exposed. The egg is translucent, with one blunt end, and averages 0.9 mm long, 0.3 mm wide. At 25 ± 1°C, the average egg incubation period is 13.6 days (range: 12–16 days). The mean preoviposition period is 3.6 days. The oviposition period is 51.3 days on eggplant. The average number of eggs per day per female is 2.04. The average number eggs laid per female is 55. Both nymphs and adults are very placid and docile.

Tomato pseudo-curly top is not an economically important problem in tomato production areas. Nightshade plant is the main host for both PCTV and *M. malleifera*, which can be effectively controlled in the field and the adjacent areas.

References

Briddon RB, Bedford ID, Tsai JH, Markham PG (1996) Analysis of the necleotide sequence of the treehopper-transmitted geminivirus, tomato pseudo-curly top virus, suggests a recombinant origin. Virology 219:387–394

McDaniel LL, Tsai JH (1990) Partial characterization and serological analysis of pseudo-curly top virus. Plant Dis 74:17–21

Simons JN (1962a) The pseudo-curly top disease in south Florida. J Econ Entomol 55:358–363

Simons JN (1962b) Life-history and behavioral studies on *Micrutalis malleifera*, a vector of pseudo-curly top virus. J Econ Entomol 55:363–365

Simons JN, Coe DM (1958) Transmission of pseudo-curly top virus in Florida by a treehopper. Virology 6:43–48

Tsai JH (1989) Biology and ecology of treehopper transmission of a geminivirus. In: Proceedings of 6th International conference on comparative and applied virology, Banff, Alberta, Canada, 15–21 October. Symposium Abstract W7–3

Tsai JH, Brown LG (1991) Pseudo-curly top of tomato. Plant Pathology Circular No. 344. Florida Department of Agriculture and Consumer Services, Gainesville, FL

Tsai JH (2002) Bionomics of *Micrutalis malleifera* Fowler and its transmission of pseudo-curly top virus. In: Harris KF, Smith OP, Duffus JE (eds) Virus-insect-plant interactions. New York, NY, Academic Press, pp 351–361

Pseudomyiasis

Myiasis of the intestinal tract (=enteric myiasis) resulting from accidental ingestion of eggs or larvae of flies. The flies involved usually are members of the families Muscidae and Sarcophagidae, and the myiasis is only temporary.

► Myiasis

Pseudophasmatidae

A family of walkingsticks (order Phasmatodea). They commonly are known as striped walkingsticks.

► Walkingsticks and Leaf Insects

Pseudopod

A soft, foot-like appendage, especially on larvae of Diptera.

Pseudopositor

A tube-like modification of the tip of the abdomen in certain female insects.

► Abdomen of Hexapods

Pseudoparasitism

A response by parasitoids to orchids that are apparent potential hosts. The parasitoid's response results in increased pollination of the orchids.

Pseudostigmatidae

A family of damselflies (order Odonata).

► Dragonflies and Damselflies

Psilidae

A family of flies (order Diptera). They commonly are known as rustflies.

► Flies

Psilopsocidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice or Psocids

Psocidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice, or Psocids

Psocids

Members of the insect order Psocoptera.

► Bark-Lice, Book-Lice or Psocids

Psocoptera

An order of insects, formerly known as Corrodentia. They commonly are known as bark-lice, book-lice, or psocids.

► Bark-Lice, Book-Lice or Psocids

Psoquillidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice, or Psocids

Psychiatry and Insects: Phobias and Delusions of Insect Infestations in Humans

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Insects are an integral and influential part of our culture, as illustrated by their infiltration of our language, arts, history, philosophy, and religion. However, as human society has become progressively more urbanized, insects have become progressively more estranged. As significant but increasingly intangible elements of our culture, insects now feature prominently in certain psychiatric disorders, much as do religious and extraterrestrial elements. Our perception of insects can range from appropriate apprehension when faced with the possibility of a bee sting, through subclinical and clinical insects phobias, to full blown psychotic delusions of insect attacks and infestations. Here we examine firstly phobias about insects, or entomophobia, which includes acarophobia (scabies) and arachnophobia (spiders). Secondly, we deal with the rarer and more serious delusions about insects which are experienced in some psychiatric disorders.

Most people are at least wary, if not fearful, of certain insects (more correctly arthropods). This may be a reasonable fear based on knowledge or experience (bees, wasps, spiders, mosquitoes), an unreasonable but culturally understandable repulsion (cockroaches or flies), or a misplaced fear resulting from inadequate information (dragonflies, moths, crickets). A true insect phobia, on the other hand, is defined as a "persistent irrational fear of and compelling desire to avoid insects," which results in significant distress in the sufferer despite recognition that the fear is excessive or unreasonable. The syndrome represents only the tip on an iceberg, with much unnecessary avoidance behavior never reaching a level where medical attention is sought or necessary.

Although insect phobias probably occurred before recorded history, insects are less likely to have been phobic objects in the past. In hygienically urbanized western societies, many people have little first hand experience of insects other than common flies, mosquitoes, cockroaches and ants. Such urban societies are not as mentally or physically prepared for arthropod encounters as are rural communities.

It is not unreasonable to assume that the danger and annoyance insects have caused to man over the millennia has resulted in an ingrained fear of insects in most societies. Bites and stings to humans and domestic animals act not only as stimulators of toxic and allergic reactions, but insects have been the vectors of potentially fatal diseases since prehistoric times (e.g., dengue or malaria). This explanation, however, is likely to account only for some cases at the non-clinical end of the phobic spectrum, not the genuine phobias which satisfy the definition given above. In the latter clinical cases, as in other phobias, the more likely cause is a displacement of diffuse anxiety to an external focus which can be avoided. The choice of insects as the phobic object may be random, symbolic, or perfectly logical. When symbolic the insects often represent filth and soiling. An example of a "logical" choice of insects as phobic objects is illustrated by the example of a 3-year old girl with an insect phobia, whose symptoms resulted from her being told that her sister with pneumonia had died from a "bug"!

Treatment for entomophobia (and other phobic disorders) is highly specialized, and is largely determined by the therapist's individual preferences. Methods which have been applied in the past include supportive psychotherapy, desensitization, insight psychotherapy, drug therapy (anxiolytics), modeling, hypnotic regression and reframing, implosive therapy, and combinations of these therapies.

Some detailed information about which insects are dangerous and which are not is probably one of the most useful things that an entomologist can contribute to people unfortunate enough to suffer from this disorder. For example, as most entomologists will know, dragonflies are quite harmless, despite their fearsome name and the fact that they feature as phobic objects in many a person's entomophobia. It is useful to remember that only blood feeders (mosquitoes, fleas, ticks, bedbugs) actively pursue humans. The more common phobic objects (spiders, bees) never bite or sting unless trapped or seriously threatened. The former category comprises insects which are associated with poverty or poor sanitation, but perhaps surprisingly, insects in the latter category are feared the most despite being beneficial to man.

"Delusions of parasitosis" can be defined as an unshakeable false belief that live organisms are present in the skin. The disorder was first described in 1894 by Thibierge, who named it acarophobia. Confusingly the syndrome has also been referred to as dermatophobia, parasitophobia, and entomophobia. In 1946 Wilson and Miller more correctly referred to the disorder as delusions of parasitosis. The "offending" organisms range from insects to worms and bacteria, the type often depending upon the parasitological knowledge of the patient. Delusions of parasitosis constitute a symptom complex rather than a disease entity, and are found in a variety of physical and mental diseases. The condition can be difficult to differentiate from entomophobia, particularly when there is a phobia of infestation. Patients with delusions of parasitosis actually experience the state of being infested. This is fundamentally different from having a fear of becoming infested, which falls into the category of entomophobia. Even though the syndrome is a psychiatric disorder, patients usually visit a dermatologist rather than a psychiatrist, since they are convinced they have a dermatological problem. Referral to a psychiatrist is nearly always rejected, and the dermatologist has the difficult task of treating these patients.

The syndrome may be preceded by an original and very real arthropod infestation acting as a "trigger." Other possible triggers include the itch resulting from systemic disease (diabetes, TB, syphilis) or from alcohol withdrawal ("the DT's" – delirium tremens). The sufferer usually complains about itching, biting, stinging, burning and crawling sensations. Insects are often described as black or white, jumping, and sometimes emerging from cosmetics or toothpaste. The "matchbox" sign is ominous, where the patient brings unidentifiable specimens to the doctor or pest controller at the first visit. Microscopic examination of the contents usually reveals only lint, scabs, or other household dust. Such negative findings invariably lead to more intense collection and presentation of specimens by the sufferer. One can often elicit a list of attempted treatments including all imaginable varieties of detergents, balms and poisons. Thus there may be excoriations produced by the fingernails on the skin as well as signs of chemical burns as a result of attempts to kill the parasites. The patient is compelled to dig the parasites out, especially before going to bed, and often resorts to the use of a knife, tweezer or other sharp implement, leaving skin lesions consistent therewith.

Because of the variety of diseases in which delusions of parasitosis occur, there is no generally accepted approach to treatment. Psychotherapy and psychoanalysis have been successful in treating delusions of parasitosis associated with repressed conflicts over sexuality and aggression, and drug treatment can provide significant relief of both itch and delusions. A number of other treatments are used less frequently or have fallen out of favor (including ECT – electroconvulsive therapy).

The prognosis is quite variable, and often dependent on those other diagnosed or undiagnosed diseases which contribute to the symptomatology. The itch (formication) of delirium tremens, for example, has an excellent prognosis, but the prognosis is worse in schizophrenia. The prognosis in patients suffering from paranoid conditions is very poor, because these cases are usually not very subjectable to effective treatment. One author describes paranoiacs who would dig into their skins "up to the time of involuntary parting, and who probably still dig, under somebody else's auspices"!

The details of natural history of the infesting organisms related by patients are often quite complex, and depend upon the patients' previous entomological knowledge. Imagined animals range from fleas, lice and scabies through itchmites, bedbugs and worms, to nondescript "black things" and insects new to science. The therapist must assess the feasibility of these details by consulting medical entomology texts or local entomologists. It is important to remember that psychiatric patients can be the unwilling hosts of real lice, mites, and bedbugs as easily as can anyone else.

References

Bourgeois M, Amestov JM, Durand J (1981) Délires d' infestation, dermatozooes et ectoparasitoses délirantes, syndrome d' Ekbom. Ann Med Psychol 139:819–828

Ekbom KA (1938) Der praesenile Dermatozoenwahn. Acta Psychiatr Neurol Scand 13:227–259

Olkowski H, Olkowski W (1976) Entomophobia in the urban ecosystem, some observations and suggestions. Bull Entomol Soc Am 22:313–317

Trabert W (1995) 100 years of delusional parasitosis; meta-analysis of 1,223 case reports. Psychopathology 28:238–246

Thibierge G (1894) Les acarophobes. Rev Gen Clin Ther 8:373–376

Waldron WG (1962) The role of the entomologist in delusory parasitosis (entomophobia). Bull Entomol Soc Am 82:81–83

Weinstein P (1994) Insects in psychiatry. Cult Entomol 1:10–15

Wilson JW, Miller HE (1946) Delusion of parasitosis (acarophobia). Arch Dermatol Syphilol 54:39–56

Psychidae

A family of moths (order Lepidoptera). They commonly are known as bagworm moths.

► Bagworm Moths
► Butterflies and Moths

Psychodidae

A family of flies (order Diptera). They commonly are known as moth flies and sand flies.

► Flies

Psychomyiidae

A family of caddisflies (order Trichoptera). They (as well as Polycentropodidae) commonly are known as trumpet-net and tube-making caddisflies.

► Caddisflies

Psychopsidae

A family of insects in the order Neuroptera.

► Lacewings, Antlions and Mantidflies

Psyllidae

A family of insects in the order Hemiptera. They sometimes are called psyllids or lerp insects.

► Bugs

Psyllids

Members of the family Psyllidae (order Hemiptera).

► Bugs

Psyllipsocidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice or Psocids

Pteridophagy

Fern feeding. Arthropods that feed on ferns are said to be pteridophagous or pteridophages. Surprisingly few insects feed on ferns; most are associated with the more modern angiosperms. The relative lack of insect feeding on ferns is attributed to both chemical and morphological attributes of ferns, though several groups of insects have adapted to use ferns as a food substrate. Most pteridophagous insects are moths (Lepidoptera), and include members of the families Tineidae, Oecophoridae, Pyralidae, Callidulidae, Geometridae, and Noctuidae, though fern feeding is not limited to moths.

► Food Habits of Insects

Pterolonchidae

A family of moths (order Lepidoptera). They are commonly called lance-wing moths.

► Lance-Wing Moths
► Butterflies and Moths

Pteromalidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Pteronarcidae

A family of stoneflies (order Plecoptera). They sometimes are called giant stoneflies.

► Stoneflies

Pterophoridae

A family of moths (order Lepidoptera). They commonly are known as plume moths.

► Plume Moths
► Butterflies and Moths

Pterostigma

The dense, often discolored portion of the costal margin of a wing, usually at the end of the radius. This is also known as the stigma.

► Wings of Insects

Pterothorax

The fused meso- and meta-thorax found in certain winged insects.

► Thorax of Hexapods

Pterothysanidae

A family of moths (order Lepidoptera) also known as Parnassian moths.

► Parnassian Moths
► Butterflies and Moths

Pterygote

An insect bearing wings, or derived from winged ancestors. A member of the Class Insecta, subclass Pterygota.

Pthiraptera

An order name in some classification systems, and comprised of Mallophaga (chewing lice) and Siphunculata (sucking lice).

► Chewing and Sucking Lice

Pthiridae

A family of sucking lice (order Phthiraptera). They sometimes are called pubic lice.

► Chewing and Sucking Lice
► Human Lice

Ptiliidae

A family of beetles (order Coleoptera). They commonly are known as feather-winged beetles.

► Beetles

Ptilinum

An inflatable organ on the front of the head, thrust out from a suture just above the base of the antennae, in higher flies. It is expanded when the adult insect is escaping from the puparium.

Ptilodactylid Beetles

Members of the family Ptilodactylidae (order Coleoptera).

► Beetles

Ptilodactylidae

A family of beetles (order Coleoptera). They commonly are known as ptilodactylid beetles.

► Beetles

Ptiloneuridae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice or Psocids

Ptinidae

A family of beetles (order Coleoptera). They commonly are known as spider beetles.

► Beetles

PTTH

Abbreviation for prothoracicotropic hormone.

Ptychopteridae

A family of flies (order Diptera). They commonly are known as phantom crane flies.

► Flies

Pubescence

A covering of setae (hairs).

Pubescent

Covered with hair-like structures (setae in insects, trichomes in plants).

Pubic Lice

Members of the family Pthiridae (order Phthiraptera).

► Chewing and Sucking Lice

►Human Lice

Puddling Behavior by Lepidoptera

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Visitation of mud puddles and patches of moist soil – puddling – is common among many Lepidoptera, as well as other insects such as leafhoppers (Cicadellidae). The phenomenon is most conspicuous among brightly colored butterflies that often form large aggregations at roadside puddles, along streams, or beside pastureland ponds. Among butterflies such as pierids and swallowtails, the presence of one individual often serves as a catalyst for the formation of these aggregations. Puddling is also common among many species of moths and leafhoppers, which are more scattered on the soil at night and do not form the spectacular mud-puddle clubs often seen in diurnal Lepidoptera (Fig. 125).

Puddling Behavior by Lepidoptera, Figure 125 **Streamside aggregation of puddling pierid butterflies.**

Some puddling species of Lepidoptera pump water through their guts, exuding droplets of water from the tip of the abdomen. Certain species of notodontid moths sit on a film of water and pump large quantities of fluid through their guts, discharging up to 8.5 ml/h in rhythmic jets up to 30 cm. Even dry patches of soil are visited by some species of butterflies and moths that can moisten the substrate with a bead of saliva passed down the proboscis. Some skippers moisten the substrate by flexing the tip of the abdomen beneath the body and exuding a drop of fluid that they reimbibe.

Although puddling behavior can have different functions such as acquisition of water and thermoregulation, it is believed to play an important role in the procurement of salts, particularly sodium, which is in short supply for many herbivorous insects. Sodium can increase reproductive success significantly for both males and females. Whether the insects are butterflies, moths, or leafhoppers, the sex ratio typically is exclusively or predominantly in favor of males. The few females that visit soil are usually old and worn. The explanation for the biased sex ratio lies in the need to acquire salts for mating. When males pass a spermatophore (packet of sperm) to females, they lose a significant amount of salts that can be reacquired most readily from salt-rich sources, particularly soil and animal products such as dung, sweat, urine, and the exudates of carcasses. The dung of carnivores has a greater attraction than that of herbivorous mammals, presumably because of the richer supply of sodium. Females, although they lose a significant amount of sodium when they lay their eggs, are able to replenish their supplies, in part, from sodium in the male's spermatophore, which is passed to the female during mating. In their first mating, males may transfer a third of their abdominal sodium to a female.

References

Adler PH (1982) Nocturnal occurrences of leafhoppers (Homoptera: Cicadellidae) at soil. J Kansas Entomol Soc 55:73–74

Adler PH, Pearson DL (1982) Why do male butterflies visit mud puddles? Can J Zool 60:322–325

Adler PH (1982) Soil-and puddle-visiting habits of moths. J Lepidopterists Soc 36:161–173

Arms K, Feeny P, Lederhouse RC (1974) Sodium: stimulus for puddling behavior by tiger swallowtail butterflies, *Papilio glaucus*. *Science* 185:372–374

Pivnick KA, McNeil JN (1987) Puddling in butterflies: sodium affects reproductive success in *Thymelicus lineola*. Physiol Entomol 12:461–472

Smedley SR, Eisner T (1996) Sodium: a male moth's gift to its offspring. Proc Natl Acad Sci USA 93:809–813

Puffing

A swelling in the giant polytene chromosomes of salivary glands of many dipterans.

Pulicidae

A family of fleas (order Siphonaptera). They sometimes are known as common fleas.

► Fleas

Pulsatile Organ

This is a pulsating heart-like organ. The function is to maintain circulation through the appendages, including the wings.

Pulvillus (pl., pulvilli)

Soft pad-like structures found between the tarsal claws, and the short, stiff hairs on the underside of the tarsal joints.

Punctate

Containing impressed points, punctures, or dimples.

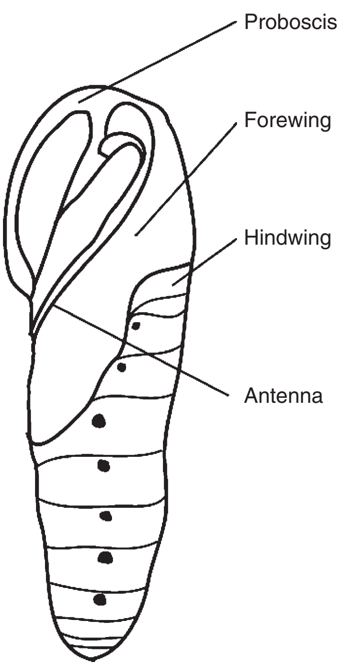
Punkies

Members of the family Ceratopogonidae (order Diptera).

► Flies

Pupa

The nonfeeding, immobile stage between the larval and adult stages in insects with complete metamorphosis. A stage where major reorganization of the body take place (Fig. 126).



Pupa, Figure 126 **Side view of a moth pupa (Lepidoptera: Sphingidae).**

Pupariation

Formation of the puparium by larval Diptera.

Puparium (pl., puparia)

The hardened, thickened integument of the last instar larva of Diptera, in which the pupa is formed.

Pupation

Formation of the pupal stage in holometabolous insects.

Pupiparous

Giving birth to fully developed larvae that are ready to pupate.

Purple Scale, *Cornuaspis beckii* (Newman) (Hemiptera: Diaspididae)

This can be an important citrus pest, but it is susceptible to parasitism.

► Citrus Pests and Their Management

Push-Pull Strategy for Insect Pest Management

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The "push-pull" strategy, a novel tool for integrated pest management programs, uses a combination of behavior-modifying stimuli to manipulate the distribution and abundance of insect pests and/or natural enemies. In this strategy, the pests are repelled or deterred away from the main crop (push) by using stimuli that mask host apparency or are repellent or deterrent. The pests are simultaneously attracted (pull), using highly apparent and attractive stimuli, to other areas such as traps or trap crops where they are concentrated, facilitating their control.

The term "push-pull" was first conceived as a strategy for insect pest management by Pyke, Rice, Sabine and Zaluki in Australia in 1987. They investigated the use of repellent and attractive stimuli, deployed in tandem, to manipulate the distribution of *Heliocoverpa* spp. in cotton to reduce reliance on insecticides, to which the moths were becoming resistant. The concept was later formalized and refined by Miller and Cowles in the US in 1990, who termed the strategy "stimulo-deterrent diversion" while developing alternatives to insecticides for control of the onion fly, *Delia antiqua*.

The development of a reliable, robust, and sustainable push-pull strategy requires a clear scientific understanding of the pest's biology and the behavioral/chemical ecology of the interactions with its hosts, conspecifics, and natural enemies. The specific combination of components differs in each strategy according to the pest to be controlled (its specificity, sensory abilities, and mobility) and the resource targeted for protection.

Among several push-pull strategies under development or used in practice for insect pest control, the most successful example of the push-pull strategy currently being used by farmers was developed in Africa for controlling stemborers on cereal crops. This strategy was developed using technologies appropriate to resource poor farmers and has shown a high adoption rate and spontaneous technology transfer by farmers, resulting in significant impact on food security by increased farm production in the region.

Management of Cereal Stemborers in Africa Through Push-Pull Strategy

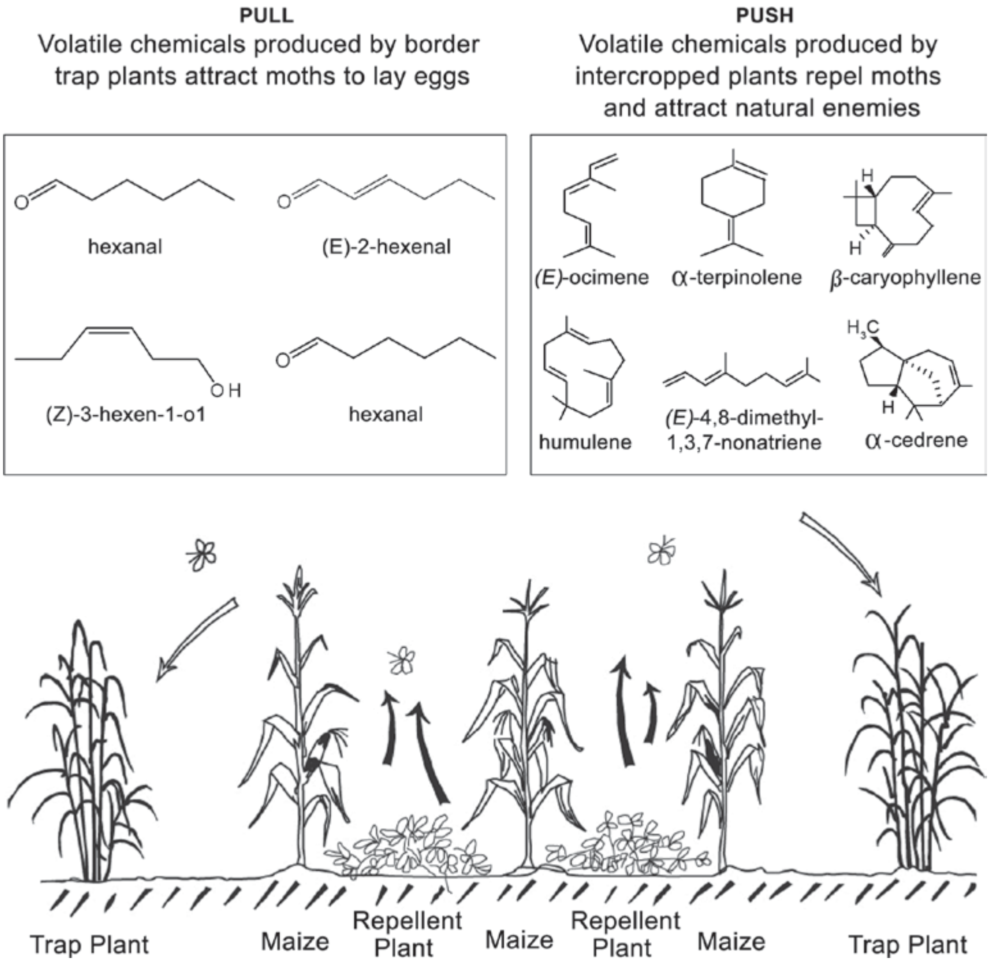
Maize and sorghum are the principal food and cash crops for millions of the poorest people in the predominantly mixed crop-livestock farming systems of eastern Africa. Stemborers are one of the major constraints to increased maize production. At least four species of stem borers (*Chilo partellus*, *Eldana saccharina*, *Busseola fusca* and *Sesamia calamistis*) infest maize and sorghum crops in the region, causing reported yield losses of 30–40% of potential output. Stemborers are difficult to control, largely because of the cryptic and nocturnal habits of the adult moths and the protection provided by the stem of the host crop for immature stages. The main method of stemborer control, which is recommended to farmers by the Ministry of Agriculture in these countries, is use of chemical pesticides. However, chemical control of stemborers is uneconomical and impractical to many resource-poor, small-scale farmers. Therefore, reducing the losses caused by stemborers through improved management strategies is urgently needed which could significantly increase cereal production, and result in better nutrition and purchasing power for many maize and sorghum producers. To put stemborer control within the reach of African farmers, simple and relatively inexpensive measures need to be developed and tailored to the diversity of African farming systems. Several national and international agricultural research centers continue to devote increasingly scarce resources towards the development of technologies intended to increase farm production through stemborer management but with little impact.

A push-pull strategy for managing cereal stemborers in Africa was developed by scientists of the International Centre of Insect Physiology and Ecology (ICIPE) in Kenya and Rothamsted Research in the United Kingdom, in collaboration with other research organizations in eastern Africa. The strategy involves combined use of intercrops and trap crops, using plants that are appropriate to the farmers. This push-pull strategy does not use any chemical deterrents or toxins, but uses repellent plants to deter the pest from the main crop. The trap plants used in this push-pull strategy have the inherent ability of not allowing development of trapped stemborers, thus reducing the number of trapped insects. The strategy also attempts to fully exploit the natural enemies in the cereal farming system.

The push-pull strategy for cereal stemborers involves trapping stemborers on highly attractant trap plants (pull) while driving them away from the main crop using repellent intercrops (push). Plants that have been identified as effective in the push-pull tactics include Napier grass (*Pennisetum purpureum*), Sudan grass (*Sorghum vulgare sudanense*), molasses grass (*Melinis minutiflora*), and desmodium (*Desmodium uncinatum* and *Desmodium intortum*). Napier grass and Sudan grass are used as trap plants, whereas molasses grass and desmodium repel ovipositing stemborers. Molasses grass, when intercropped with maize, not only reduced infestation of the maize by stemborers, but also increased stemborer parasitism by a natural enemy, *Cotesia sesamiae* (Fig. 127). All four plants are of economic importance to farmers in eastern Africa as livestock fodder and have shown great potential in stemborer and striga management in farmer participatory on-farm trials. These innovations have found ready acceptance among the resource-poor farmers in Africa. Although directed at resource-poor farmers, lessons can be learned and applied to organic or low-input agricultural systems. More than ten thousand farmers in eastern Africa are now using push-pull strategies to protect their maize and sorghum from cereal stemborers.

How Push-Pull Strategy Works

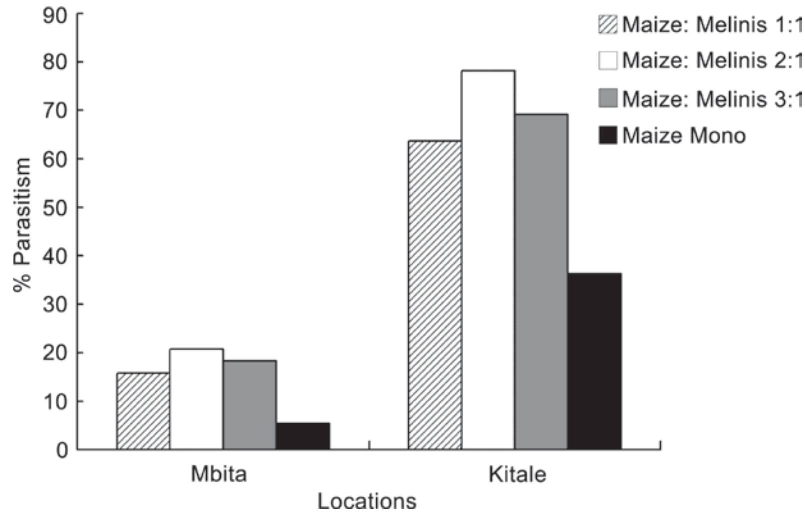
The push-pull strategy undertakes a holistic approach in exploiting chemical ecology and agrobiodiversity. The plant chemistry responsible for stemborer control involves release of attractive volatiles from the trap plants and repellent volatiles from the intercrops. To understand the



Push-Pull Strategy for Insect Pest Management, Figure 127 A diagrammatic presentation on how push-pull strategy works for cereal stemborers.

chemical ecology of the push-pull system, volatile chemicals from trap and repellent plants have been investigated using gas chromatography (GC) coupled-electroantennography on the antennae of stemborers and their natural enemies. GC peaks consistently associated with EAG activity were tentatively identified by GC coupled-mass spectrometry (GC-MS), and identity was confirmed using authentic samples.

A general hypothesis developed during this work on insect pests is that non-host plants are recognized by colonizing insects through the release of repellent or masking semiochemicals, although it is almost inevitable that compounds also produced by hosts will be present (Fig. 126). In this case, the host cereal plants and the non-host *M. minutiflora* would be expected to have a number of volatiles in common as they are both members of the Poaceae family. For *M. minutiflora*, five new peaks with EAG activity were identified, in addition to the attractant compounds and others normally produced by members of the Poaceae. These are: (*E*)-β-ocimene, a-terpinolene, β-caryophyllene, humulene, and (*E*)-4,8-dimethyl-1,3,7-nonatriene. Ocimene and nonatriene had already been encountered as semiochemicals produced during damage to plants by herbivorous insects. It is likely that these compounds, being associated with a high level of stemborer colonization and, in some circumstances, acting as foraging



Push-Pull Strategy for Insect Pest Management, Figure 128 **Parasitism of stemborer larvae by *Cotesia sesameae* in maize-*M. minutiflora* intercrops planted in various ratios.**

cues for parasitoids, would be repellent to ovipositing stemborers. This was subsequently demonstrated in behavioral tests. Investigating the legume volatiles, it was shown that *D. uncinatum* also produced the ocimene and nonatriene, together with large amounts of other sesquiterpenes, including α-cedrene.

Six host volatiles were found to be attractive to gravid stemborers: nonanal, napthalene, 4-allylanisole, eugenol and linalool. Recent studies have indicated that the differential preference of moths between maize and sorghum and Napier grass trap crops is related to a large burst of four electrophysiologically active green leaf volatiles released from the trap crop plants within the two hours of the scotophase, the time at which stemborers fly and most oviposition occurs. Although stemborers oviposit heavily on Napier grass, it produces a gummy substance which restricts larval development and only few survive to adulthood.

A trap crop of Sudan grass also increased efficiency of stemborer natural enemies. In a maize field surrounded by a border of Sudan grass, the parasitization of stemborers increased significantly relative to fields without grass borders.

Benefits of Push-Pull Strategy

The principles of the push-pull strategy are to maximize control efficacy, efficiency, sustainability, and outputs, while minimizing negative environmental effects. Although each individual component of the strategy may not be as effective as a broad-spectrum insecticide at reducing pest numbers, the efficacy is increased through tandem deployment of push and pull components. The push and pull components are generally nontoxic and, therefore, the strategies are usually integrated with biological control.

The push-pull strategy developed for stemborers is a good example how basic research can be linked with technology transfer, with farmer participation leading to spontaneous technology transfer between farmers. The push-pull technology has the potential to improve the livelihoods of small-holder farmers and rural families, increase agricultural productivity and improve environmental sustainability. The push-pull strategy, now adopted by more than 10,000 households in 19 districts in Kenya, five districts in Uganda, and two districts in Tanzania has helped participating farmers to increase their maize yields by an average of 20% in areas where only stemborers are present and by more than 50% in areas where both stemborers and striga weed are problems. It constitutes an integrated system that addresses concurrently problems of stemborers, striga weed, soil fertility and soil moisture retention. It opens up significant opportunities for income generation by small-holder farmers and, represents a platform technology around which new income generation and human nutritional components, such as livestock keeping, can be added.

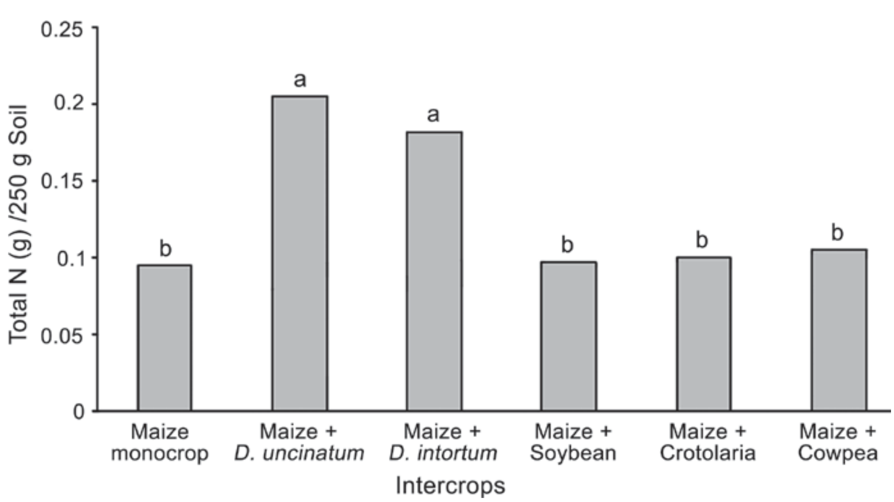
Increased maize yields accompanied by the following additional features of the technology have contributed to the high farmer adoption rates of push-pull technology in eastern Africa:

Reduced Soil Erosion and Increased Soil Fertility

Soil erosion and low fertility are very common problems in eastern Africa. The push-pull strategy has exploited some of the existing practices to address these problems in a multi-functional context. For example, the cultivation of Napier grass for livestock fodder and soil conservation now assumes an additional rationale as a trap plant for stemborer management. Similarly, desmodium, a nitrogen-fixing legume, already grown for improving soil fertility and for quality fodder, is also an effective stemborer repellent and striga weed suppressant. Intercropping desmodium with maize reduces the need for external mineral nitrogen inputs, which are costly and unaffordable by most small-holder rural people, and improves the use efficiency of other inputs. A long-term study in Kenya demonstrated a significant increase in total nitrogen (Fig. 129) on field plots under maize-desmodium intercropping for 3 years than those maize fields intercropped with other legumes.

Striga Weed Control

Witchweed or *Striga* (Scrophulariaceae) are obligate root parasites of cereal crops that inhibit host growth via two processes, competition for nutrients and impairment of photosynthesis. *Striga* infests 40% of Africa's arable land and causes a loss of $7–11 billion to agricultural economy. Among the 23 species of striga prevalent in Africa, *Striga hermonthica* is the most socio-economically important. In western Kenya, it is estimated that 76% of land planted to maize and sorghum, *Sorghum bicolor* (L.) Moench, is infested with *S. hermonthica*, causing up to 100% yield losses equivalent to annual losses estimated at $40.8 million. *Striga hermonthica* infestation continues to extend to new areas in the region as farmers



Push-Pull Strategy for Insect Pest Management, Figure 129 **Total nitrogen (N) levels in the soil under different intercrops in western Kenya (after Khan et al., 2006).**

abandon heavily infested fields for new ones. The push-pull strategy provides significant suppression of striga through intercropping maize or sorghum with desmodium, a repellent plant for stemborers. The protection employed by desmodium in striga suppression has been established to involve a combination of mechanisms ranging from increased availability of nitrogen, soil shading, and an allelopathic root exudation. Exudates from desmodium roots possess striga seed germination stimulation and radical growth inhibition properties which diminish striga seeds through suicidal germination and a continual reduction of the soil seed bank. This combination provides a novel means of *in situ* reduction of striga seed bank in the soil. Additionally, because desmodium is a perennial crop, it is able to exert its striga control effect even when the host crop is out of season, an attribute that makes it a more superior trap crop than most of the other legumes that have been reported to give some limited level of striga control.

Enhanced Biodiversity

Biodiversity in agroecosystems has been reduced greatly in the last decades as a result of intensification of cereal agricultural systems, while empirical data show that agroecosystems with an enhanced overall biodiversity have relatively fewer pest problems. As a result of this observation it has often been stated that enhancement of biodiversity within agroecosystems can greatly contribute to the development of sustainable crop protection systems with a reduced reliance on pesticides. Biodiversity has an intricate role in the functioning of natural and agricultural ecosystems since it performs a variety of ecological services, mediating processes such as genetic introgession, natural control, nutrient cycling and decomposition. Farming practices that conserve such biodiversity as ground fauna and pests' natural enemies may be a practical alternative to manage pests in agricultural systems. Results from Kenya indicate that the push-pull strategy is associated with an overall enhancement of beneficial predator abundance (Fig. 130).

Livestock Production and Human Health

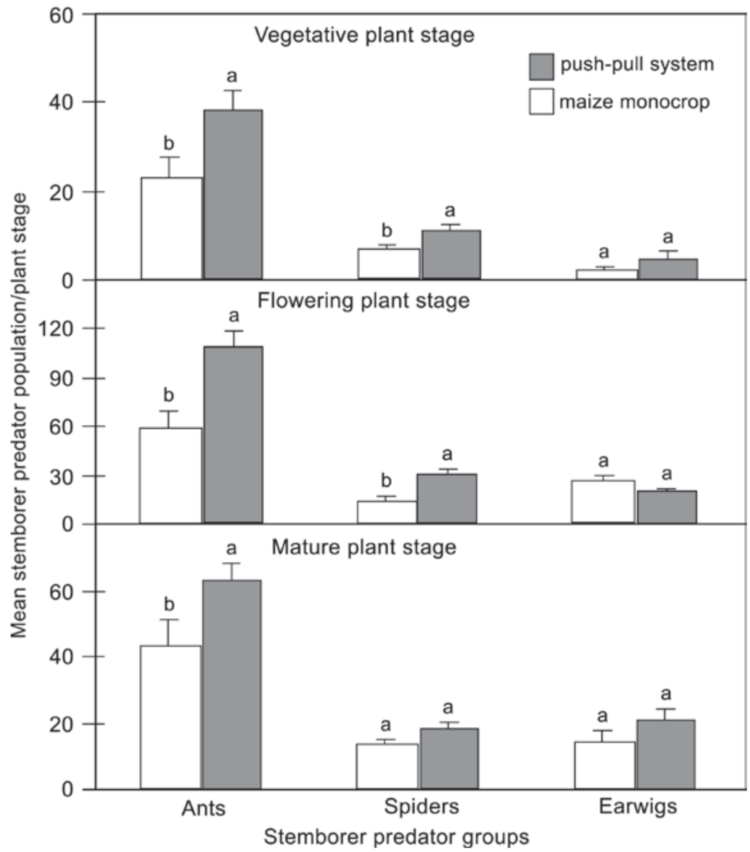
Enhancing the production of fodder plants in local communities demonstrates clear beneficial impacts on health indices, especially for children. By promoting dairy cattle, human health is likely to improve because of high quality milk.

The research outputs have potential to contribute significantly to increased livestock production by providing quality fodder, especially on small farms where pressure for land is high. Dairy cows and dairy goats are emerging as important income alternatives in such situations. With the participation of such partners as Heifer International, more resource-constrained farmers are likely to benefit from dairy animals.

The Suba district of Kenya, a milk-deficit region on the shores of Lake Victoria which has mostly indigenous (zebu) livestock, produced only 7 million liters of milk, far short of the estimated annual demand of 13 million liters. A major constraint to keeping improved dairy cattle for milk production has been the unstable availability and seasonality of feed, which often is low quality. The push-pull strategy, which integrates crop and fodder production, has been adopted by more than 700 farmers in this district. This has resulted in enhanced livestock production and improved milk supply because there now is more and higher-quality feed available for cattle. The number of improved dairy cattle in the district has increased by 500, contributing to a 1 million liter increase in milk production.

Economics of Push-Pull

The contribution of the push-pull strategies to food security cannot be over-emphasized. Intercropping or mixed cropping of maize, grasses and fodder legumes has enabled farmers in Kenya to



Push-Pull Strategy for Insect Pest Management, Figure 130 Stemborer predator populations at the vegetative, flowering and mature stages of maize plants in Lambwe, Kenya (after Midega and Khan, 2003. Insect Science and its Application 23:301–308).

increase crop yields, and thus improve their food security and gross benefits. This feature of the technology is suitable for mixed farming conditions, which are prevalent in eastern Africa. Using a semi-structured questionnaire, data were collected on crop performance, stemborer infestation, *Striga* infestation and yield of the different crops. Economic data on input and output amounts, and labor were collected. All crop management decisions were made by the farmers themselves, with technical backstopping from extension staff on management of the desmodium and Napier grass. In addition, baseline information was collected on the households detailing the household sizes and composition, off-farm activities, the farm sizes, the number of cattle, education level of different members of the households and labor availability. An analysis of expenses incurred and revenues accrued in a season was carried out on the push-pull technology and farmers' own practice. The yield of maize from the push-pull technology and the farmers' practice, the revenues generated from all the farm outputs in a season, the expenses incurred to generate that revenue and the gross benefits accruing to the farmers were investigated in the different districts in Kenya. The results showed that although total labor cost and total variable cost were lower in farmers' practice as compared to push-pull fields, total gross revenue and gross benefit of push-pull were significantly higher (Table 19). As important, though less quantifiable, is the reduction in risk that push-pull strategy provides as the build-up of more fertile, water-retaining soil systems give added protection to crops in periods of water shortage and stress.

Future Directions

The push-pull technology for stemborer control is expanding in eastern Africa via small-holder farmers and has significant impacts on food security and income generation for resource-poor maize farmers. On-station and on-farm trials have also demonstrated that push-pull strategies could also be used for control of stemborers in sorghum and millet, and further on-farm research and development is needed to understand the full potential of this strategy for sorghum and millet farmers in arid and semiarid parts of Africa. Pest management options in these regions are affected by low rainfall, the extent to which cattle are kept, and the fact that the cattle are largely free-grazing. However, wherever these approaches are adapted to the specific needs of local farming practices and communities, it is essential that the scientific basis for the modified systems should be clarified and explained by appropriate research.

The major constraint to widespread technology transfer of push-pull has been availability of desmodium seed. Several pathways have emerged, including involvement of a private seed company, community-based seed production, and vegetative propagation among farmers adopting push-pull technologies. The relative merits of these pathways in stimulating autonomous diffusion of the technologies are being analyzed and compared. In addition, the role of different reinforcing interventions such as mass media, information bulletins, field days, farmer teachers, farmer field schools, etc., are being evaluated and the most cost-effective ones will be identified. The relationship between household socio-economic status and land labor ratio in different areas, and the performance of different diffusion mechanisms are also being clarified.

For long-term sustainability of the push-pull system and its placement on a strong scientific foundation, there is also ongoing work on developing tools for quality control of the performance of new push and pull components, to enhance understanding of soil nutrient dynamics in long term push-pull fields, and to study and solve emerging problems of a previously unrecognized pest (a pollen beetle attacking desmodium), and a disease of the companion crops (phytoplasma disease of Napier grass).

Push-Pull Strategy for Insect Pest Management, Table 19 Economics of push-pull strategy as compared to farmer's practice in six districts in Kenya

Districts	Total Labor Cost ($)/ha		Total Variable Cost ($)/ha		Total Gross Revenue ($)/ha		Gross Benefit ($)/ ha	
	Push-pull	Farmers' Practice	Push-pull	Farmers' Practice	Push-pull	Farmers' Practice	Push-pull	Farmers' Practice
Trans/ Nzoia[a]	223 ± 1.2	128 ± 1.5	493 ± 1.6	374 ± 2.0	1290 ± 27.7	628 ± 32.4	797 ± 28.0	254 ± 31.0
Suba[a]	167 ± 1.6	134 ± 0.4	278 ± 1.1	250 ± 0.7	679 ± 10.2	329 ± 5.9	401 ± 9.9	79 ± 5.7
Bungoma[b]	247 ± 3.8	222 ± 2.3	331 ± 3.9	300 ± 2.8	867 ± 22.6	415 ± 8.6	536 ± 21.3	115 ± 9.9
Busia[b]	222 ± 1.7	118 ± 0.3	321 ± 1.9	243 ± 0.6	862 ± 11.9	418 ± 2.9	541 ± 12.7	175 ± 2.9
Kisii[b]	184 ± 1.8	140 ± 1.1	246 ± 2.1	210 ± 1.0	733 ± 6.4	334 ± 15.7	487 ± 5.3	134 ± 15.9
Vihiga[c]	227 ± 1.9	128 ± 1.0	359 ± 2.3	331 ± 1.5	785 ± 12	423.1 ± 7.1	426 ± 13.4	92 ± 7.0

Khan et al., unpublished

[a–c]Represent data averages for 7 years, 4 years and 3 years respectively. All the parameters studied were significantly lower in the farmers' practice than in the "push-pull" technology in all the districts ($p < 0.05$)

Current studies in these areas will be continued and tools that emerge will be optimized and incorporated into the push-pull dissemination activities. In addition, several new science-led maize production and protection technologies (such as Bt maize) have been developed by other research institutes, the effectiveness and sustainability of which need to be compared with push-pull strategies over a longer time scale. Questions relating to potential integration of these technologies or their complementarities have been raised and need to be evaluated in continued collaboration with other centers. Demonstration of the relative productivity of integrated approaches and their socio-economics, including the possibility of forward linkages, as well as collaborative undertakings with other institutions, will be important.

From the present example of the push-pull strategy it can be seen that understanding the interactions of plants with insects can yield new ways of exploiting plant defense. Basic science, and particularly understanding the chemical ecology of plant-insect interactions by combined analytical-chemical, neurophysiological and behavioral studies, can lead to practical developments to help resource-poor farmers.

Although the experience to date has been restricted to cereal-based farming systems, we believe that the general approach is applicable to a much wider range of pest problems in a variety of crops, and thus can serve as a model for other researchers in their efforts to minimize pest-induced yield losses in an economically and environmentally sustainable manner. This push-pull strategy for cereal stemborers lays the foundation for still wider application of these principles and serves as a model for the management of other pests in Africa and beyond.

References

Chamberlain K, Khan ZR, Pickett JA, Toshova T, Wadhams LJ (2006) Diel periodicity in the production of green leaf volatiles by wild and cultivated host plants of stemborer moths, *Chilo partellus* and *Busseola fusca*. J Chem Ecol 32:565–577

Cook SM, Khan ZR, Pickett JA (2007) The use of "push-pull" strategies in integrated pest management. Annu Rev Entomol 52:375–400

Kfir R, Overholt WA, Khan ZR, Polaszek A (2002) Biology and management of economically important cereal stem borers in Africa. Annu Rev Entomol 47:701–731

Khan ZR, Ampong-Nyarko K, Chiliswa P, Hassanali A, Kimani S, Lwande W, Overholt WA, Pickett JA, Smart LE, Wadhams LJ, Woodcock CM (1997) Intercropping increases parasitism of pests. Nature (London) 388:631–632

Khan ZR, Chiliswa P, Ampong-Nyarko K, Smart LE, Polaszek A, Wandera J, Mulaa MA (1997) Utilisation of wild gramineous plants for management of cereal stemborers in Africa. Insect Sci Appl 17:143–150

Khan ZR, Pickett JA, Berg J, van den Wadhams LJ, Woodcock CM (2000) Exploiting chemical ecology and species diversity: stemborer and striga control for maize and sorghum in Africa. Pest Manag Sci 56:957–962

Khan ZR, Pickett JA, Wadhams L, Muyekho F (2001) Habitat management for the control of cereal stem borers in maize in Kenya. Insect Sci Appl 21:375–380

Khan ZR, Pickett JA (2004) The "push-pull" strategy for stemborer management: a case study in exploiting biodiversity and chemical ecology. In: Gurr G, Waratten SD, Altieri MA (eds) Ecological engineering for pest management: advances in habitat manipulations for arthropods. CSIRO/CABI, pp 155–164

Khan ZR, Hassanali A, Pickett, JA (2006) Managing polycropping to enhance soil system productivity: a case study from Africa. In: Uphoff N (ed) Biological approaches to sustainable soil systems. CRC, New York, pp 575–586

Miller JR, Cowles RS (1990) Stimulo-deterrent diversion: a concept and its possible application to onion maggot control. J Chem Ecol 16:3197–3212

Pickett JA, Bruce TJA, Chamberlain K, Hassanali A, Khan ZR, Matthes MC, Napier JA, Smart LE, Wadhams LJ, Woodcock CM (2006) Plant volatiles yielding new ways to exploit plant defense. In: Dicke M, Takken W (eds) Chemical ecology: from gene to ecosystem. The Netherlands, Springer, pp 161–173

Pyke B, Rice M, Sabine B, Zalucki MP (1987) The push-pull strategy – behavioural control of *Heliothis*. Aust Cotton Grower May–July:7–9

Putoidae

A family of insects in the superfamily Coccoidae (order Hemiptera). They are sometimes called giant mealybugs.

► Scale Insects and Mealybugs, Bugs

Putzeys, Jules Antoine Adolphe Henri

Jules Putzeys, an early Belgian entomologist, was born at Liège, Belgium, on May 1, 1809. He received a doctoral degree from the University of Liège in 1929, and assumed a successful administrative and judicial career. However, he was fascinated by insects, and studied Lepidoptera, Odonata, and especially Coleoptera. In the case of the latter group, he specialized in Cicindelidae, Carabidae, and Pselaphidae. He served as president of the Entomological Society of Belgium from 1874 to 1876, and remained active in the society afterwards. His most important publications were "Prémices entomolgiques" and "Monographie de *Clivina* et des genres voisins." He died on January 2, 1882.

Reference

De Borre AP (1882) Notice nécrologique sur Jules Putzeys. Ann Soc Entomol Belg 26:iiii–vii

Pygidicranidae

A family of earwigs (order Dermaptera).
► Earwigs

Pygidium

The tergum of the last abdominal segment. The supraanal plate. This is the segment often left uncovered by the elytra of beetles.

Pygiopsyllidae

A family of fleas (order Siphonaptera).
► Fleas

Pygmy Backswimmers

Members of the family Pleidae (order Hemiptera).
► Bugs

Pygmy Grasshoppers

A family of grasshoppers (Tetrigidae) in the order Orthoptera.
► Grasshoppers, Katydids and Crickets

Pygmy Mole Crickets

A family of grasshoppers (Tridatylidae) in the order Orthoptera.
► Grasshoppers, Katydids and Crickets

Pygmy Moths (Lepidoptera: Nepticulidae)

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Gainesville, FL, USA

Pygmy moths, family Nepticulidae, comprise the most minute moths known, with 868 species described in the world from all faunal regions, although most (over 510 sp.) are from the Palearctic region. The total fauna likely exceeds 1,200 species worldwide. The family, together with Opostegidae, forms the superfamily Nepticuloidea, in the section Nepticulina of division Monotrysia, in the infraorder Heteroneura. There are two subfamilies: Pectinivalvinae and Nepticulinae. Adults minute to small (2.5–8 mm wingspan), with head rough-scaled and with a large head tuft of scales, often distinctly colored; haustellum is short and naked (unscaled); labial palpi short, dropping and 3-segmented; maxillary palpi 5-segmented and folded; antennae have an eye-cap developed on the basal segment. Wing maculation is gray or brown, or more brightly colored, sometimes with metallic iridecense. Wing venation is heteroneurous but greatly reduced, with large fringes of hair-like scales on the wing margins and frenular bristles for wing coupling. Adults are diurnally active. Larvae are leafminers, usually blotch mines, although some also mine other plant parts; a variety of host plants are used.

References

Johansson R, Nielsen ES, Nieukerken EJ, van Gustafson B (1990) The Nepticulidae and Opostegidae (Lepidoptera) of North West Europe. In: Brill EJ (ed) Fauna Entomologica Scandinavica (2 parts). Leiden, E.J. Brill, pp 231–739

Newton PJ, Wilkinson C (1982) A taxonomic revision of the North American species of *Stigmella* (Lepidoptera: Nepticulidae). Syst Entomol 7:367–463

Puplesis RK (1994) The Nepticulidae of Eastern Europe and Asia: Western, central and eastern parts. Backhuys, Leiden, 291 pp

Puplesis R, Robinson GS (2000) A review of the Central and South American Nepticulidae (Lepidoptera) with special reference to Belize. Bull Nat Hist Mus Entomol 69:(1)3–114

Scoble MJ (1978) Nepticulidae of southern Africa: a taxonomic revision of the genus *Stigmella* Schrank (Lepidoptera: Monotrysia). Ann Transvaal Mus 31:1–129

Pyloric Valve

The valve between the midgut and the hindgut.

Pyralidae

A family of moths (order Lepidoptera). They commonly are known as snout and grass moths.

► Snout Moths
► Butterflies and Moths

Pyrethroids

Synthetic insecticides that are structurally similar to the toxic components of pyrethrum.

► Insecticides

Pyrethrum

Natural insecticide derived from certain plants in the genus *Chrysanthemum*. Pyrethrum is highly valued for its rapid effects on insects and low toxicity to mammals.

► Botanical Insecticides
► Pyrethrum and Persian Insect Powder

Pyrethrum and Persian Insect Powder

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There are numerous examples of plant natural products with interesting agrochemical properties; however, few plant products have had a major role in the development of commercial insecticides. The most important and significant actual application of a plant natural product is pyrethrum or Persian Insect Powder. This powder also has been known as Dalmatian and Japanese powders, or Buhach. The latter powder was produced by the Buhach Producing and Manufacturing Company in California, USA, starting in 1876 from the seeds of Dalmatian pyrethrum.

Pyrethrum powders are made from the dried flowers of several *Chrysanthemum* of the family Compositae. The Persian Insect Powder, obtained from the dried flowers of Persian pyrethrum (*Chrysanthemum coccineum* Willd.), is easily distinguished from those of the Dalmatian pyrethrum (*C. cinerariaefolium* Vis.) by the purple color of the ray florets. As a result, the Persian Insect Powder is darker in color than the Dalmatian Powder. The plants yielding pyrethrum are also known as pyrethrum. Several other species of *Chrysanthemum* such as *C. achilleae* L., *C. myconis* L., *C. parthenium* Bernh., *C. segetum* L., also are recorded to have toxic properties against insects, but *C. coronarium* L., *C. indicum* L., *C. leucanthemum* L. and *C. frutescens.* L. have only negligible toxicity (Fig. 131).

Pyrethrum and Persian Insect Powder, Figure 131 **Pyrethrum powders are made from the dried flowers of several *Chrysanthemum* species, including the Persian pyrethrum (*Chrysanthemum coccineum* Willd.), which belong to the family Compositae. Persian pyrethrum is now principally grown for ornamental purposes and exists in many different horticultural forms and colors.**

History

The use of powdered dry flower of pyrethrum as an insecticide was a long-established folk practice in the Caucasus region and northwest Iran. This powder, known as "Persian Insect Powder" or "Persian Dust," became an article of trade during the eighteenth century and was exported by caravan from Persia, which is now called Iran. It was introduced into Europe in the 1820s, where it was processed and commercialized. The insecticide's efficacy soon became so apparent that the supply reaching Europe was insufficient to meet the demand. The situation changed, however, when an Armenian merchant discovered the secret of its preparation while traveling in the Caucasus and his son started manufacturing the powder on a large scale in 1828. In spite of this, there were still constraints on the supply. Hand collection of the flowers has always demanded low labor costs and, as a result, has limited its major growing regions to developing countries.

The Persian Insect Powder is reported to have been a mixture of the ground flowers of *C. roseum* Adams and *C. carneum* Bieb. Nevertheless, only the former species is distributed in highlands (up to 2,000 m above the sea level) of Armenia, Caucasus and northern Iran and both species may be synonyms for *C. coccineum* Willd. Commercial cultivation of this species started in Armenia in 1828, and continued until 1840, when the greater insecticidal activity of *C. cinerariaefolium* (known as "Dalmatian Pyrethrum" or "Dalmatian Powder") became known.

The Persian Insect Powder was introduced into Europe in 1828 and into the United States in 1876, and then into Japan, Africa, and South America. Parallel to this development, the "Dalmatian Pyrethrum," which exists naturally along the east coast of the Adriatic Sea extending from Italy to northern Albania and up into the mountainous regions of Croatia, Bosnia and Herzegovina, and Montenegro, was cultivated in 1840 in Dalmatia (a historic region along the Adriatic coasts of Yugoslavia, now part of Croatia). The crop was later introduced into many parts of the world. An interesting story traces the discovery of the effect of the Dalmatian pyrethrum to a German woman of Dubrovnik, Dalmatia, who picked a bunch of flowers for their beauty. When they withered she threw them into a corner where, several weeks later, they were found surrounded by dead insects. She associated the death of the insects with insecticidal property of the flowers and embarked in the business of manufacturing pyrethrum powder.

Use and Formulations

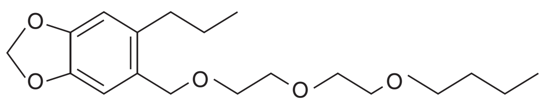
The use of pyrethrum spread rapidly because, in the doses necessary to kill household insects, it is nontoxic to humans and domestic animals. The initial uses of pyrethrum was mainly against insects of public health importance. About 1916, kerosene extracts of pyrethrum flowers appeared on the market and were used widely as sprays against flies and mosquitoes. Until the outbreak of World War II, its principal application was as a dust for household use against bed-bugs, fleas, cockroaches and similar pests. It was not until 1918 that pyrethrum sprays were offered on the market for household use. One of the main uses of pyrethrum today is in the preparation of such sprays. Fly sprays for the protection of cattle were also developed. The main supply now is in the form of extracts in hydrocarbon solvents, concentrated to 25%. Furthermore, mosquito coils made from 1.3% pyrethrum powder are widely used in tropical areas. The slow-burning coils are ignited and the smoke acts both as a killing agent and as a repellent. These coils initially irritate the mosquitoes and then motivate them to fly from the source of the stimuli.

Pyrethrum also is one of the most widely used insecticides for controlling insects in stored products because of its low mammalian toxicity, broad spectrum of activity and short residual life. There are many pyrethrum products formulated for stored products insect control. These range from consumer liquid and aerosol products for control of the insects in private homes, to a wide variety of professional products for use by commercial pesticide applicators. In the latter category, the formulations are either used to protect commodities through direct application to grain (including repellent treatments to packaging material), or for space, contact, and spot treatments within food handling establishments. They include, but are not limited to, bakeries, cafeterias, canneries, commercial airplanes, hospitals, mobile caterers, restaurants, schools and supermarkets.

In agriculture, pyrethrum is unique in being exempt from the establishment of tolerances when applied to growing crops. As a result of having a zero-day preharvest interval, it can be used even on the day of harvest. Furthermore, its broad spectrum of activity as well as its renowned capacity for rapid knock-down allows it to be used against a wide range of agricultural insects. However, because of its very low stability, it is not cost-effective on major crops with large acreages where other insecticides, especially photostable pyrethroids, may be used. Nevertheless, the characteristics listed above make it an ideal insecticide for small fields. In addition, one of the traditional agricultural uses of pyrethrum is a tank-mixture at low application rates (about 10–20 g pyrethrum per ha) with conventional insecticides. This type of mixture exploits the rapid action of pyrethrum on the insect nervous system because insects which are agitated by the action of pyrethrum are exposed to greater quantities of both pyrethrum and the insecticide in the mixture.

Synergists

It has been known since the 1930s that both the knock-down and the killing effects of pyrethrum and some pyrethroids can be greatly optimized by adding synergists that have little or no toxicity alone. During this period, a number of synergists such as sesamin were discovered. Piperonyl butoxide, the most widely used synergist, was the first highly effective synergist found to potentiate the pyrethrum by 5- to 20-fold. Although the mode of action of synergists is not completely understood, one of their activities is believed to inhibit the oxidative and/or hydrolytic metabolism of the insecticide within the insect (Fig. 132).



Piperonyl butoxide

Pyrethrum and Persian Insect Powder, Figure 132 Piperonyl butoxide, the most widely used synergist, is the first highly effective synergist found to potentiate pyrethrum at the range of 5- to 20-fold.

The Pyrethrum Plant

There is considerable confusion in the literature about the taxonomy of pyrethrum (i.e., the plant species from which pyrethrum has been obtained). Recent revisions have even changed the genus *Chrysanthemum* to *Tanacetum*. As a result, the two species of plants with historical and commercial importance, namely the Persian Insect Flower (painted daisy, having red flowers) and the Dalmatian Insect Flower (having white flowers) are respectively considered *Tanacetum coccineum* (Willd.) Grierson and *Tanacetum cinerariifolium* (Trevir) Schultz-Bip, though entomologists continue to refer to these plants as *Chrysanthemum* spp. Both are daisy-like herbaceous perennials belonging to the sunflower family (Compositae).

Pyrethrum is a perennial herbaceous plant which, to the casual observer, resembles the ordinary field daisy. When the plant flowers, many shoots originate from the crown and grow on average to 75 cm. The leaves are petioled and finely cut. The shoots branch a few times before terminating into a white (or red, according to the species), daisy-like flower that consists of a few to several hundred flowers per plant. The flower head of pyrethrum, like any other species belonging to the family Compositae, is a compound inflorescence with small flowers, the florets, aggregated together on a convex receptacle (known as the capitulum). The florets are of two kinds: the disc florets and the ray florets. While disc florets with yellow corollas occupy the center of the receptacle, the ray florets with white corollas form the outer rim of the flower head. The disc florets possess both male and female organs, but the ray florets are unisexual (female alone). In contrast to *C. cinerariaefolium* which possesses white ray florets, the ray florets of *C. coccineum* maybe pink, rose, carmine, crimson or, rarely, white. Moreover, the dried flowers of the latter species is easily distinguished from the former by the purple color of the ray florets and the ten-ribbed achenes (instead of five ribs in *C. cinerariaefolium*). *C. coccineum* produces fewer flowering shoots than *C. cinerariaefolium* and is said to be somewhat more resistant to disease and injury. Commercial flowers vary from 6 to 24 mm in width and from 70 to 300 mg in weight.

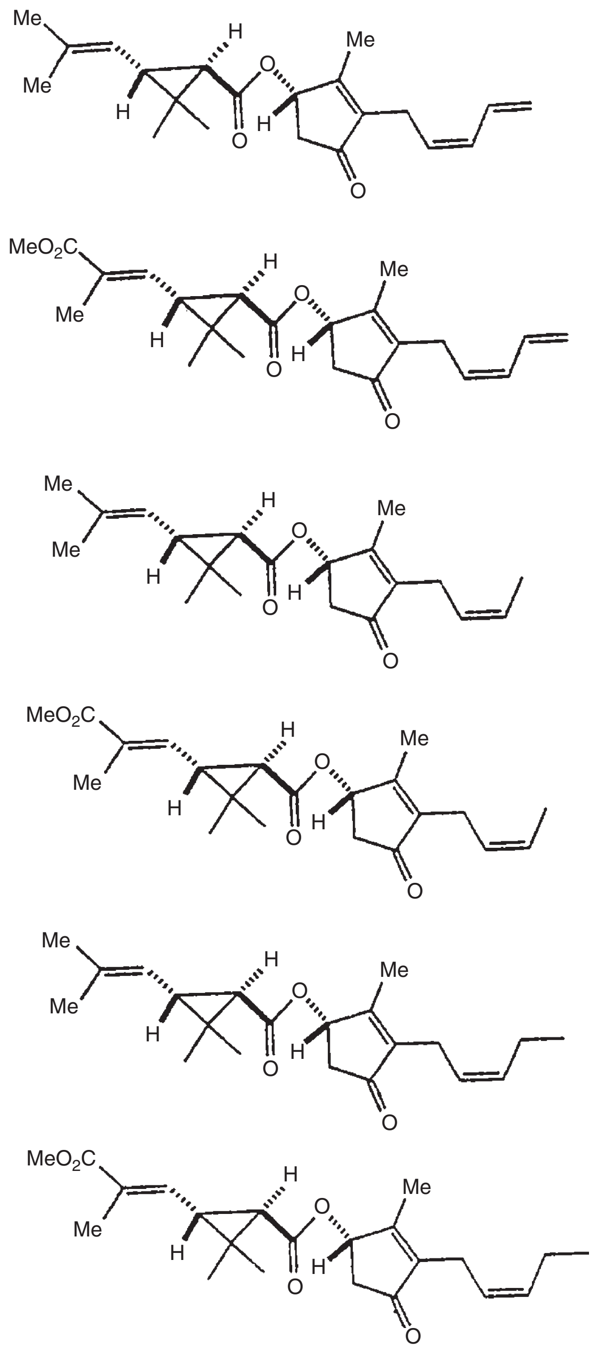
Pyrethrum Production

Pyrethrum propagates easily through different methods including seeds, vegetative splits, stem cuttings rooted under mist and tissue culture. World production of pyrethrum is about 20,000 tons/year. Although the original homes of the commercial flowers of pyrethrum have been Iran, Armenia and Caucasus, a closely related species is now grown in the highlands of East Africa (in particular Kenya, Tanzania, Rwanda and Zaire), Australia (mainly Tasmania), and Papua New Guinea. Eastern Africa, however, remains the main source of supply. For example, from a worldwide production of about 18,000 metric tons in 1992, Kenya alone contributed about 70%. Historically, the major pyrethrum producing countries have been Yugoslavia (until World War I) and Japan (until World War II). By 1941, however, Kenya overtook Japan as the main world producer and Japan ceased to be a significant pyrethrum producer.

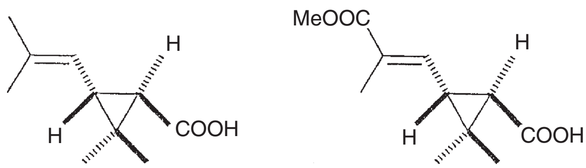
Today, the main commercial source of pyrethrum is the mature flower of *Chrysanthemum* (*Tanacetum*) *cinerariaefolium* Vis., cultivated principally in Kenya and Tanzania at elevations over 1,500 m above sea level. In Kenya, pyrethrum is cultivated almost entirely by about 60,000 small-scale farmers. The crop is not only the main source of cash income for these farmers, but it also provides a major source of export revenue for the country. Pyrethrum cultivation is optimal in the temperatures that occur in the highlands of Kenya (1,800–2,900 m above sea level). Well-drained soils with moderate organic matter are ideal for crop production. New stands in Kenya are established either from seed or from clonal propagation. In commercial plantations of pyrethrum in Kenya, the first picking of mature flowers occurs shortly after flowering and within 3–4 months after transplanting. It is carried out at intervals of 10–14 days and continues for ten consecutive months. At the end of this period, the stand is cut back to remove the dead and unproductive plant material. This practice allows the plant to rest and to get ready for growth in the next season. Flower picking is done by hand, then the flowers are dried and delivered to the factory where crude (oleoresin) as well as high-quality refined extract concentrates are produced. About fifteen parts of pyrethrum flowers are required to produce one part of oleoresin, and up to fourteen parts of oleoresin are required to obtain one part of toxic principle of pyrethrum. A small quantity of fine pyrethrum powder is also prepared for sale to manufacturers of insecticide dusts and mosquito coils. It is interesting to note that *C. coccineum* (the origin of Persian Insect Powder) is now principally grown for ornamental purposes and exists in many different horticultural forms.

Active Ingredients

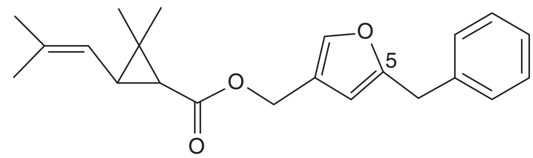
The actual investigation on the active components of pyrethrum was carried out by two Swiss chemists (H. Staudinger and L. Ruzicka) at Zurich from 1910 to 1916, but their results were not published until 1924. They discovered that the chief insecticidal components of natural pyrethrum consist of six closely related esters (namely, pyrethrin I, pyrethrin II, cinerin I, cinerin II, jasmolin I, and jasmolin II) (Fig. 133). While esters of series I are derivatives of chrysanthemic acid and have excellent insect killing activity, esters of series II which are derived from pyrethric acid have high knock-down



Pyrethrum and Persian Insect Powder, Figure 133 Structures of chief insecticidal components of natural pyrethrum discovered by Swiss chemists at Zurich (H. Staudinger and L. Ruzicka) during the years 1910–1916: From top to bottom: Pyrethrin I, Pyrethrin II, Cinerin I, Cinerin II, Jasmolin I and Jasmolin II.



Pyrethrum and Persian Insect Powder, Figure 134 Structures of chrysanthemic acid (left) and pyrethric acid (right).



Pyrethroids, Figure 135 *Resmethrin*: The first commercially competitive pyrethrin analog developed by the Rothamsted group.

properties. In commerce, flower heads containing at least 0.7% active constituents are extracted by solvents. The extract is then further processed to get a standard 25% concentrate which consists of about 10% pyrethrin I, 9% pyrethrin II, 2% cinerin I, 3% cinerin II, 1% jasmolin I and 1.1% jasmolin II. The amount of insecticidal constituents of pyrethrum varies, depending on the source. While Kenya flowers are the richest, containing about 1.3% active compounds, some strains developed recently may yield over 2% active compounds. It is interesting to note that pyrethrum continues to compete with synthetic insecticides in the specialized areas where selectivity and low environmental hazard are most important. Furthermore, because of the selective and relatively small-scale uses of pyrethrum during the past centuries, there has been relatively little development of insect resistance. In spite of this, the synthetic pyrethroids may threaten the commercial use of pyrethrum in the future because over-application may lead to a proliferation of pyrethroid-pyrethrum cross-resistant insects.

Pyrethroids

Among the classes of insecticides, the aforementioned six molecules (described under active ingredients) are unique for the intensity of their very rapid action against many species of insects and for their minimal hazard to mammals under normal conditions. Nevertheless, all six esters decompose rapidly and lose their insecticidal activity on exposure to air and light. Therefore, the natural compounds and earlier synthetic analogs are generally suitable only for indoor or protected applications.

In fact, the development of the first commercially competitive pyrethrin analog (resmethrin) by the Rothamsted group, led by Michael Elliott, represents an important milestone in agrochemical research (Fig. 135). This discovery subsequently inspired chemical companies to develop a wide spectrum of new synthetic pyrethroids. The discovery of related synthetic pyrethroids stable enough for agricultural applications beginning in the 1970s, has been a revolutionary step toward the production of numerous potent and stable analogs with very low mammalian toxicity. While some pyrethroids are applied with a field rate as low as 2.5 g ha^{-1} (e.g., Deltamethrin), the LD_{50} (acute oral toxicity to rats) of some of them may amount to over 4,200 mg kg^{-1} (e.g., Etofenprox). These analogs, which possess favorable properties like those of the natural compounds and at the same time have much greater potency and stability, now constitute about one-quarter of all the insecticides used worldwide. Surprisingly, the small change in structure between the natural and synthetic products has led to a 34-fold increase in its toxicity to houseflies. The addition of synergists in formulations may still lead to much higher activity.

References

Benner JP (1994) Pesticides from nature. I. Crop protection agents from higher plants – an overview. In: Copping LG (ed) Crop protection agents from nature: natural products and analogues. Cambridge, UK, The Royal Society of Chemistry, pp 217–229

Casida JE (ed) (1973) Pyrethrum – the natural insecticides. Academic Press, New York, NY, 329 pp
Casida JE, Quistad GB (eds) (1995) Pyrethrum flowers: production, chemistry, toxicology, and uses. Oxford University Press, Oxford, UK, 356 pp
Elliott M (1994) Synthetic insecticides related to the natural pyrethrins. In: Copping LG (ed) Crop protection agents from nature: natural products and analogues. Cambridge, UK, The Royal Society of Chemistry, pp 254–300
Holman HJ (1940) A survey of insecticide materials of vegetable origin. The Imperial Institute, London, UK, 155 pp
Zargari A (1992) Medicinal plants, 5th edn. vol 3, Tehran University Publications, Tehran, Iran, 889 pp (in Persian)

Pyrgotid Flies

Members of the family Pyrgotidae (order Diptera).

► Flies

Pyrgotidae

A family of flies (order Diptera). They commonly are known as pyrgotid flies.

► Flies

Pyrochroidae

A family of beetles (order Coleoptera). They commonly are known as fire-colored beetles.

► Beetles

Pyrophilous Insects

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Pyrophilous ("fire-loving") organisms are those that are substantially favored by fire. Pyrophilous species are known among plants, fungi, and animals, including numerous pyrophilous insects. Pyrophilous insects are known from at least 25 families in the orders Hemiptera, Lepidoptera, Diptera, and Coleoptera. As concern about the preservation of biodiversity grows, there is an increasing interest in the effects, positive or negative, of ecological disturbances such as fire on biodiversity. This interest has been reflected by increasing research on the behavior of pyrophilous insects, and on the effects of fire on insect diversity in general.

Sensory Receptors and Behavior

Many species of insects gravitate to newly burned forests because they can use the resources that are available in the recently killed or weakened trees. Some of these insects can evidently detect burned habitats over long distances. Three species, all beetles, have been found that have evolved impressive sensory organs that allow them to locate burned habitats, and also probably help them avoid being burned. Two of these, *Melanophila acuminata* and *Merimna atrata*, are in the jewel beetle family, Buprestidae. The third is an acanthocnemid, *Acanthocnemus nigricans*. The most well-known of these species is *M. acuminata*, which, like most buprestids, is a wood boring beetle in the larval stages. The behavior and physiological adaptations that this beetle displays suggests that it is, to a great extent, dependent on fire for persistence. *Melanophila acuminata* is found throughout the holarctic region and also in parts of the nearctic region. *Merimna atrata* and *A. nigricans* are both found in Australia. The former species is endemic, whereas the latter species has been introduced into parts of Europe, Asia, and Africa.

Melanophila acuminata, *M. atrata*, and *A. nigricans* all contain specialized sensilla that are capable of detecting infrared radiation (IR); however, the morphology and physiology of the IR organs from the three species are very distinct. The IR receptors of *M. atrata* and *A. nigricans* function as very sensitive thermoreceptors that can detect low-level thermal radiation, particularly in the IR range. *Merimna atrata* has four IR receptors, two each on the second and third abdominal sternites. Each is innervated by one multipolar neuron which has a highly branched terminal dendritic mass with a large number of mitochondria. These receptors are similar in structure to the heat-sensitive labial pits found on the lips of boas and pythons. *Acanthocnemus nigricans* has a pair of IR receptors on the prothorax, but these are more complex than those of *M. atrata*. Each receptor is well-supplied with mitochondria, as in *M. atrata*. However, in *A. nigricans*, each receptor has about 30 multipolar neurons. The number and arrangement of the neurons in *A. nigricans* suggest that a mosaic of different temperatures can be detected across the receptor, such as would occur when the beetle is moving laterally or vertically in relation to the IR source. Also, unlike the IR organs of *M. atrata*, those of *A. nigricans* have an air-filled chamber under the cuticle. It has been suggested that this chamber increases the sensitivity of the IR receptors of *A. nigricans*. The IR receptors of *A. nigricans* share striking similarities with those of the pit vipers, a case of convergent evolution in two widely separate taxonomic groups.

Most of the research on IR sensilla has focused on *M. acuminata*. This species usually breeds in dead or dying coniferous trees. These beetles help begin the post-fire decomposition process by ovipositing in newly killed trees. Often this process begins even while the forest is still burning. *Melanophila acuminata* has two metathoracic pit organs. The pit organs are located adjacent to the mesothoracic coxae beneath the legs on each side of the thorax. These pit organs are exposed during flight, but concealed by the legs when not in flight. The pit organs contain 50–100 sensilla. Each sensillum consists of a spherule which lacks an exocuticle but contains a single dendrite. The spherule of each sensillum contains three regions: (i) an amorphous core, (ii) a region of unstructured cuticle with irregular lacunae, and (iii) an outer mantle of helical arranged cuticle. Each spherule is innervated by a single, bipolar neuron which consists of a 25–35 nm ciliary dendrite. The spherule transduces IR radiation into a micromechanical stimulus, which is measured by a mechanoreceptor. Thus, unlike the IR sensilla of *M. atrata* and *A. nigricans*, those of *M. acuminata* act as mechanoreceptors rather than thermoreceptors. Each sensillum in *M. acuminata* is also associated with a wax gland. The wax gland protects the sensillum from dirt, smoke, and desiccation.

Due to the discovery of the metathoracic pit organs in some, but not all, *Melanophila* species, the genus *Melanophila* was reclassified in 1937 and a subgenus *Melanophila* was created to include only the species that have the thoracic pit organs. Two other subgenera (*Phaenops* and *Xenomelanophila*) were created which contained the species that did not have the thoracic pit organs. Seven out of fifteen species in the genus are contained in the subgenus *Melanophila*. All seven of these species possess the thoracic pit organs which function in IR detection. Species that lack the thoracic pit organs do not tend to fly to forest fires. This suggests that the thoracic pit organs are associated with pyrophilous behavior. There are numerous reports of *Melanophila* congregating at fire sources. According to Canadian entomologist William G. Evans, "it is a common observation that species of *Melanophila* often inhabit a dead tree to the exclusion of other borers of freshly killed wood, indicating that they had completely occupied the tree before the other forms arrived."

Evans performed a variety of experiments on *M. acuminata*. He discovered that the pit organs were capable of detecting infrared radiation, which was the first description of an IR-detecting organ in an insect. He found that the beetles responded to infrared radiation by twitching their antennae on the stimulated side. Evans suggested that the IR organs would function tropotactically for long-range orientation, and that thermoreceptors in the antennae would function for short-range orientation.

However, physiological studies contradicted Evans' hypothesis. These studies showed that the antennae of *M. acuminata* reacted to volatiles generated by smoldering wood. They also showed that the beetles are attracted to the forest fires by a combination of olfactory cues and IR radiation. These studies also provided clues on the antennae of female *M. acuminata*. The female's antennae possess 20–30 companiform-like organs, but the function is still unclear. The males' antennae lack these 20–30 companiform-like organs. It was suggested that the organs may assist females in the identification of the optimal or threshold temperatures within the bark for ovipositing of eggs.

There are three factors involved in the ability of *M. acuminata* to detect forest fires using IR receptors: (i) the IR receptors respond to wavelengths between 2.4 and 4.0 nm, with a maximum sensitivity at 3.0 nm, (ii) forest fires burn at temperatures between 435 and 1150°C, which corresponds to the IR wavelengths that *M. acuminata* receptors respond to, and (iii) the atmosphere does not absorb infrared radiation evenly, with very little absorption between 3 and 5 nm. Because these three factors are maximized around 3 nm, IR provides an ideal means for the detection of forest fires.

There is anecdotal evidence that *Melanophila* can detect fires from great distances. A large swarm of *Melanophila* was observed at an oil fire in Coalinga, California. The oil fire reportedly was over 50 miles away from the nearest coniferous forest which would have provided a source of the beetles. The distance that *Melanophila* can detect infrared radiation is estimated to be around 1 km on flat terrain and 5 km for mountainous terrain. The mechanism by which *Melanophila* can detect forest fires from greater distances is unknown, but reports suggest that *Melanophila* beetles are attracted over long distances by smoke from a variety of burning materials including wood, oil, mill refuse, smelter products, and possibly tobacco. Over shorter distances, the beetles are aroused by heat. When a beetle is in the vicinity of the heated source, it will fly quickly and run about over hot surfaces. Reports also suggest that light plays a role in the beetle's attraction to forest fires.

Despite the evidence linking pyrophilous insects with fires, there is still some question regarding the extent to which pyrophilous insects depend on forest fires *per se*. Some have suggested that healthy trees are resistant to attack by *Melanophila*, and that these beetles depend on dying trees for the larvae to develop to maturity. Since fire is not the only mechanism that injures trees to the point of death, it may be that other tree stressors could provide suitable habitat for *Melanophila*. Perhaps fire just provides a convenient means of locating stressed trees.

In addition to specialized sensory organs, some pyrophilous insects have other traits that would seem to be adaptive for an organism that must locate fires over long distances. *Melanophila acuminata* has been found to have lower wing load and greater flight-muscle mass than do closely related non-pyrophilous species, which would seem to be advantageous to an insect that must colonize patchy and unpredictable habitats quickly. These adaptive advantages are underscored by studies showing that *M. acuminata* has lower fecundity than closely related non-pyrophilous species, probably due to the greater size of the pterothorax, which extends deeper into the abdomen in *M. acuminata*, reducing the amount of space for the gonads. *Melanophila acuminata* also have less synchronized development, and emerge over a greater time span, than do closely related non-pyrophilous species. It has been suggested that this is an evolutionary "bet-hedging" strategy to optimize the chances of finding fires that are temporally unpredictable.

Ecology and Natural History

The pyrophilous biota of regions with frequent fires (South Africa, Australia, Mediterranean Europe, and the southern USA) is dominated by vascular plants. In boreal forests, on the other hand, pyrophilous fungi and insects are more common. A possible ecological explanation for this pattern may lie in the greater amount of nutrients in the humus layer of boreal forests. Fire helps to release these nutrients. Since most pyrophilous fungi and insects are decomposers, they may benefit from the increased availability of nutrients after a fire. Many pyrophilous insects also feed on the wood-living ascomycetes associated with recently burned forests. Pyrophilous insects seem to develop in burned forests within 1–5 years after a fire. Some, such as *M. acuminata*, can arrive in swarms at the site of a forest fire within 24 h. Many of these insects are specialists on dead and dying wood, taking advantage of the resources available and the reduced defensive capabilities of the weakened trees. These insects can be crucial to the breakdown of coarse woody debris and post-disturbance nutrient cycling. The reduced competition and warmer microclimate, particularly in boreal forests, may also provide selective pressures for pyrophilous behavior. These insects can develop a specialist community, which contains a range of ecological groups. Because pyrophilous insects can create new communities that include a wide variety of ecological groups, they can provide interesting information about prehistoric fires. For example, the presence of pyrophilous insects in prehistoric forests likely indicates burning of exposed wood rather than burned buried wood within a peat body.

Fire, or fire-suppression, can have effects on the diversity of non-pyrophilous as well as pyrophilous insect species. Fire-induced mortality of ground- and wood-living insects can be substantial, depending on the severity of the fire. However, disturbed forests often show an increase in insect diversity over undisturbed forests. The use of prescribed fire in Finnish boreal forests has been shown to be beneficial for many beetle species, including some threatened ground beetle species. Many insects that are not strictly pyrophilous still depend on the dead trees and decaying wood that result from forest fires. This seems to be particularly true in boreal forests, where fire is one of the most important factors influencing the structural and biological diversity of the forest. As forest management becomes more biodiversity-oriented, management approaches such as green-tree retention (retention of live trees after harvest) and prescribed burning will probably increase in importance. These practices make it possible to imitate the effects of wildfires, creating resources for species that require dead or dying wood, while maintaining some of the structural diversity that is lacking after traditional clear-cutting.

Fire is one of the most important causes of disturbance in forest ecosystems. Pyrophilous insects have evolved complex means of locating recently burned forests, taking advantage of the habitats and resources provided by fire. In addition, many non-pyrophilous insect species benefit from the diverse habitats created by fire. Research on the relationships between fire and insects will remain an exciting area of inquiry for the foreseeable future.

References

Evans WG (1964) Infrared receptors in *Melanophila acuminata* Degeer. Nature 202:211

Hyvärinen E, Kouki J, Martikainen P, Lappalainen H (2005) Short-term effects of controlled burning and green-tree retention on beetle (Coleoptera) assemblages in managed boreal forests. Forest Ecol Manag 212:315–332

Martikainen P, Kouki J, Heikkala O (2006) The effects of green tree retention and subsequent prescribed burning on ground beetles (Coleoptera: Carabidae) in boreal pine-dominated forests. Ecography 29:659–670

McCullough DG, Werner RA, Neumann D (1998) Fire and insects in northern and boreal forest ecosystems of North America. Ann Rev Entomol 43:107–127

Schmitz H, Bleckmann H, Murtz M (1997) Infrared detection in a beetle. Nature 386:773–774

Schmitz H, Trenner S (2003) Electrophysiological characterization of the multipolar thermoreceptors in the "fire-beetle" *Merimna atrata* and comparison with the infrared sensilla of *Melanophila acuminata* (both Coleoptera, Buprestidae). J Comp Physiol A 189:715–722

Whitehouse NJ (2000) Forest fires and insects: palaeoentomological research from a subfossil burnt forest. Palaeogeogr Palaeoclimatol Palaeoecol 164:231–246

Wikars L-O (1997) Effects of forest fire and the ecology of fire-adapted insects. Comprehensive summaries of Uppsala dissertations from the faculty of science and technology 272. Acta Universitatis Upsaliensis, Upsala, Sweden, 35 pp

Wikars L-O (2002) Dependence on fire in wood-living insects: An experiment with burned and unburned spruce and birch logs. J Insect Conserv 6:1–12

Pyrrhocoridae

A family of bugs (order Hemiptera). They sometimes are called red bugs or cotton stainers.

► Bugs

Pythidae

A family of beetles (order Coleoptera). They commonly are known as dead log bark beetles.

► Beetles

Pyrrolizidine Alkaloids and Tiger Moths (Lepidoptera: Arctiidae)

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Tiger moths (Arctiidae) are known for their bright aposematic coloration meant to repel predators. Their caterpillars often feed on alkaloid-rich host plants, and it is thought that the noxious substances ingested with the leaves determine the toxicity of both larvae and adults. Laboratory rats die when injected with a dose of arctic alkaloid, and we can safely assume that a natural predator will at least get sick after tasting these brightly colored (and thus memorable) insects, and will avoid eating them in the future. Probably due to these substances, many species of tiger moths were able to become diurnal (daytime) fliers, and many other moths, butterflies, and even beetles form Müllerian mimicry complexes: they all resemble alkaloid-containing arctiid species, so predators should view them all as distasteful.

It has been also suggested that the toxic substances might be synthesized anew by arctiids. In fact, it is the ability of caterpillars to tolerate the noxious compounds secreted for defense against predators that allows them to feed on the toxic plant species (Fig. 136). Indeed, the role of pyrrolizidine alkaloids in the biology of arctiid moths is complex.

The significance of pyrrolizidine alkaloids ingested by the larvae in the reproductive biology of arctiids has been studied extensively. It was shown that alkaloids of the arctiid *Creatonotus gangis* L. influence the morphology and chemistry of coremata (large abdominal hair-covered tubes, which are expanded by a male during the courtship, emitting pheromones). The main compound responsible for the scent can be secreted only when

Pyrrolizidine Alkaloids and Tiger Moths (Lepidoptera: Arctiidae), Figure 136 **Arctiid, *Euchromia collaris*, and noctuid, *Asota* sp., feeding on alkaloid-rich tissues of a Tree Heliotrope, *Tournefortia argentata*. Solomon Islands.**

pyrrolizidine alkaloids are present in the larval diet. The size and weight of coremata is also proportional to the amount of alkaloids ingested by the larva.

Numerous brightly colored arctiid moths are attracted to the damaged and wilting tissues of Tree Heliotrope (*Tournefortia argentata*, Boraginaceae), feeding on sap exuded from leaves and branches. Pyrrolizidine alkaloids that are obtained through feeding on the decomposing plant matter by adult butterflies are used to synthesize danaidone, a compound found in the pheromone secretion of the hair-pencil organ in males that serves as a sexual attractant. Hence, one might assume that alkaloids ingested by the adult tiger moths also are used for pheromone production, or at least for boosting their chemical defense against predators. However, research on several tiger moth species in Florida found that moths instead are seeking pyrrolizidine alkaloids as nitrogen-rich nutrients, which they utilize differently depending on their sex. Egg productivity by females who were mated to alkaloid-deprived males was significantly lower than those of females whose mates had a chance to feed on alkaloid-containing plants. Only young males usually feed on pyrrolizidine alkaloids, subsequently passing nutrients with the spermatophore to a female during the copulation. The spermatophore is then stored in the female's bursa copulatrix and is used up gradually. Unlike males, females seek pyrrolizidine alkaloids after they spend several days on the wing. Alkaloids apparently are metabolized by females, enhancing egg production in their nutrient-depleted abdomens. For an unknown reason, only males or only females of each species in Florida feed on the alkaloids, but on the Solomon Islands, either sex of arctiids feed, with mating also occurring at the congregation sites.

The exact reasons for the phenomenon described above is yet to be understood, but it is clear that multiple biochemical mechanisms underlie the attraction of arctiid moths to various alkaloid-containing plants.

References

Boppré M, Schneider D (1989) The biology of *Creatonotos* (Lepidoptera: Arctiidae) with special reference to the androconial system. Zool J Linn Soc 96:339–356

Goss GJ (1979) The interaction between moths and plants containing pyrrolizidine alkaloids. Environ Entomol 8:487–493

Hartmann T, Biller A, Witte L, Ernst L, Boppré M (1990) Transformation of plant pyrrolizidine alkaloids into novel insect alkaloids by arctiid moths (Lepidoptera). Biochem Syst Ecol 18:549–554

Rotshild M, Alpin RT, Cockrum PA, Edgar JA, Fairweather P, Lees R (1979) Pyrrolizidine alkaloids in arctiid moths (Lep.) with a discussion on host plant relationships and the role of these secondary plant substances in the Arctiidae. Biol J Linn Soc 12:305–326

Q

Q-Fever

A rickettsial disease originally of marsupials in Australia, but now affecting animals worldwide. The agent is *Coxiella burnetii*. It is transmitted by several ticks, and also affects livestock (cattle, sheep, goats) and other animals. It is excreted in urine, feces, and amniotic fluid. It can also affect humans, though transmission normally is by inhalation, so it occurs principally among ranch and slaughterhouse workers. Occasionally milk may be contaminated. Q-fever is easily contracted because only a few bacteria are needed to initiate infection. In most cases, Q-fever causes only mild discomfort and goes undiagnosed. Symptoms include fever, headache, and pneumonia, and sometimes hepatitis. Acute Q-fever kills few people, and humans generally recover within a few months without treatment. Chronic Q-fever may develop months or years after exposure to the acute form. This is a more serious problem, often affecting the heart, and resulting in up to 65% mortality.

► Ticks

Quadrat

A sampling unit used to assess population density.

Qualitative Defenses (of Plants)

These are chemical defenses that are toxic, including alkaloids, cardiac glycosides, mustard oils and phytoecdysones, and which are produced by plants to deter herbivory by insects. Qualitative defenses tend to be low molecular weight chemicals that are active at low concentrations, and often are found in unpredictable (short-lived) plant tissues (contrast with quantitative defenses).

Quantitative Defenses (of Plants)

These are chemical defenses that possess protein-complexing and digestibility reducing abilities such as tannins, resins and enzyme inhibitors, and which are produced by plants to deter herbivory by insects. Quantitative defenses are produced in high concentrations in plant tissue, especially in predictable (long-lasting) plant tissues where they are compartmentalized to protect against autotoxicity problems (contrast with qualitative defenses).

Quarantine

Protocols established to prevent entry of an unwanted organism into an area, or out of an area. Also a building constructed to contain organisms, usually for research or breeding.

Quarantine Facility

A specially designed building or containment facility that is designed to keep organisms isolated.

In entomology, quarantine facilities are sometimes used when working with insect-transmitted diseases, thereby assuring that only trained and properly protected personnel are exposed, and reducing the risk that infected arthropods will transmit the disease. More commonly, however, quarantines are used to contain biological control agents until their identity can be verified, they can be certified to be free of unwanted contamination (parasitoids, disease), and that they are safe to release (will affect only the target insect or weed). Key elements of quarantines are secure construction (cracks, seams and crevices are filled, including voids in walls and spaces around electrical outlets), solid rather than suspended ceiling, filtering of air with hepa-filters, heat or chemical treatment of liquid and solid waste, negative air pressure within the quarantine, interlocked triple door systems to reduce likelihood of escape, light traps or electrocuting light traps to capture flying insects, availability of garments to be worn in quarantine but not removed, and access limited only to trained personnel.

Quarantine Pest

A pest of potential economic importance to an area and not yet present in that area, or being of limited distribution and being officially controlled in that area. In the latter case, the area within which a quarantine pest is present and being controlled, is called a "quarantine area."

► Invasive Species
► Regulatory Entomology

Quasisocial Behavior

A level of sociality less than eusocial behavior. A type of presocial behavior. It involves individuals of the same generation sharing a nest and cooperating in brood care.

► Presocial
► Solitary
► Communal
► Subsocial
► Semisocial
► Eusocial Behavior

Quaternary Period

A geological period of the Cenozoic era, extending from about 2 million years ago to the present.

Queen

The primary reproductive in semisocial or eusocial insects.

Queensland Tick Typhus

This is a tick-borne disease found in Australia.

► Ticks

Queen Substance

A pheromone component produced by honey bee queens that regulates several aspects of hive function and mating.

Quiescence

A reversible state of inactivity initiated by adverse environmental conditions. Quiescence is also sometimes known as torpor.

► Diapause

Quiet-Calling Katydids

A subfamily of katydids (Meconematinae) in the order Orthoptera: Tettigoniidae.

► Grasshoppers
► Katydids and Crickets

R

Rabb, Robert Lamar

Bob Rabb is remembered as a pioneer in the field of Integrated Pest Management (IPM). He co-hosted perhaps the first international conference on IPM, in 1970. The proceedings of the conference were published as "Concepts in Pest Management" and this treatise remains as relevant today as it was at the time of publication. His interests in implementation of IPM and in applied ecology also resulted in publication (in 1979) of a book "Movement of highly mobile insects: concepts and methodology in research." Naturally, anyone interested in movement realizes that insects exist in places other than crop fields, so he conducted research on how the entire landscape influences pest abundance.

Bob Rabb was born August 6, 1919, in Lenoir, North Carolina, USA, and grew up in rural North Carolina where he learned to appreciate nature. He enrolled at North Carolina State University, with his formal education culminating in receipt of a Ph.D. from North Carolina State in 1953. Rabb also spent most of his career as a faculty member there, and was named W.N. Reynolds Professor of Entomology in 1981. He was also recognized by the Entomological Society of America, receiving the Geigy Award and the Founders' Memorial Award. He died on July 31, 2006.

Reference

Gould F, McNeil J (2007) Robert Lamar Rabb. Am Entomol 53:125–126

Rabbit Fever

Also known as Tularemia, this is a serious infectious disease caused by the bacterium *Francisella tularensis*. The disease is endemic in North America, and parts of Europe and Asia. The primary vectors are ticks and deer flies, but occasionally the disease can also be spread through other arthropods. Animals such as rabbits and muskrats serve as reservoir hosts. The disease is named after Tulare County, California, where in 1911 the disease was studied in squirrel and human populations.

► Ticks

Race

A geographically or genetically distinct subgroup of a species.

Radiolabeling

The attachment of a radioactive atom to a molecule, incorporation of ^{32}P-dNTPs into DNA.

Radial Cell

A cell of the wing bordered anteriorly by a branch of the radius.

► Wings of Insects

Radial Sector

The lower of the two branches of the radius.

Radius

The third of the longitudinal wing veins, between the subcosta and the media. It is subdivided into up to five branches.

► Wings of Insects

Radoshkowsky, Octavius John

Octavius Radoshkowsky (Radochkoowsky, Radochkoffsky, Radoszkowskii, etc.) was born in Lomza, Poland on August 7, 1820. He was born into the Polish nobility and educated in Poland. His training also included the military, and he served in the Polish artillery, retiring as Lieutenant-General in 1879. Radoshkowsky had a general interest in entomology, and is considered a systematist and faunist. However, he favored the Hymenoptera, and is best known for his contributions to the Hymenoptera of the Russian Empire. Perhaps his most important contribution, however, is his role in founding and supporting the Russian Entomological Society. He was a founding member, and in his capacity of President he did much to ensure the stability of the Society by acquiring a residence and annual subsidy. He served as president from 1867 to 1880. Due to serious illness and family circumstances Radoshkowsky relocated from Russia to Poland. He died in Warsaw, Poland, on May 1, 1895.

Reference

Essig EO (1931) A history of entomology. Macmillan, New York, 1029 pp

Rain Beetles

Members of the family Pleocomidae (order Coleoptera).

► Beetles

Rallidentidae

A family of mayflies (order Ephemeroptera).

► Mayflies

Random Distribution

A distribution of organisms that lack pattern or order. The distribution is indistinguishable from a pattern based on chance.

Random Sampling

A method of allocating sampling units within a sampling universe in which each sample unit has an equal chance of being selected. Random sampling ensures an unbiased estimate, but is rarely used in the practice of arthropod sampling due to time and cost constraints.

► Sampling Arthropods

RAPD-PCR

RAPD is derived from the term "Random Amplified Polymorphic DNA." It is a type of PCR using single primers of arbitrary nucleotide sequence consisting of nine or ten nucleotides with a 50–80% G + C content, and no palindromic sequences. These 10mers can act as a primer for PCR and yield reproducible polymorphisms from random segments of genomic DNA.

Raphidiid Snakeflies

Some members of the family Raphidiidae (order Raphidioptera).

► Snakeflies

Raphidiidae

A family of insects in the order Raphidioptera. They commonly are known as raphidiid snakeflies.
► Snakeflies

Raphidioptera

An order of insects. They commonly are known as snakeflies.
► Snakeflies

Rapsmatidae

A family of insects in the order Neuroptera.
►Lacewings, Antlions, and Mantidflies

Raptorial

Suitable for grasping prey. This term usually is used to describe legs.

Rasorial

This describes appendages or structures adapted for, or used for, scratching. In insects, these are normally leg structures.

Raspberry Cane Borer, *Oberea bimaculara* (Olivier) (Coleoptera: Cerambycidea)

As the name suggests, this species of beetle damages the canes (stems) of raspberry.
► Small Fruit Pests and their Management

Raspberry Fruit Worm, *Byturus unicolor* (Say) (Coleoptera: Byturidae)

This fruit-feeding beetle is found in eastern North America.
► Small Fruit Pests and their Management

Raster

A complex of hairs, spines and bare areas on the ventral surface of the last abdominal segment of scarab beetle larvae.

Ratardidae

A family of moths (order Lepidoptera) also known as Oriental Parnassian moths.
► Oriental Parnassian Moths
► Butterflies and Moths

Ratemiidae

A family of sucking lice (order Phthiraptera).
► Chewing and Sucking Lice

Rearing of Insects

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Insect rearing is not much different from other forms of animal husbandry and it has similar rewards for a person who is patient, persistent, observant, and reasonably well organized. It is generally safe for humans unless they are hypersensitive to insect proteins, react to the physical irritation of insects or their body parts, work with insects that sting or bite, or expose themselves to toxic substances used in the rearing procedures. Rearing methods can be a simple duplication of nature, such as holding insects and their food plants or animals in cages. In other cases, it can take years to develop a method to successfully rear a very specialized insect, often with breakthroughs based on discovering details about its life history. Methods can also be derived empirically by experimenting with a variety of materials and procedures, until success is achieved. Regardless, the satisfaction in rearing at least the immature stages of insects can be an exciting and fulfilling hobby or vocation.

Once insects have been held to the adult stage, having undergone incomplete (nymphs) or complete (larvae) metamorphosis, the challenge is to induce mating and oviposition of viable eggs. An insect species will mate only in an environment that has the necessary conditions, such as courtship cues, adequate temperature and humidity, appropriate light levels, and often food. Oviposition usually requires a specialized substrate that duplicates or mimics the insect's natural situation. Substrates typically protect the eggs from predators and parasites, and locate them in proximity to larval food. However, given no choice in captivity, some insects will mate and the females will scatter their eggs under completely artificial conditions. First instar larvae of these species travel considerable distances in search of suitable habitats and food.

Taking into consideration the wide range of life histories (e.g., terrestrial, aquatic, subterranean, plant or animal feeding, parasitic, predatory), insect rearing can be approached much the same as raising chickens, rodents or fish. Suitable founders must be collected or purchased, specialized facilities designed and constructed, equipment obtained and in most cases modified, materials and supplies tested, and site-specific rearing procedures established. Both immature and adult insects normally need food, usually with specific nutritional and physical characteristics, presented in certain kinds of containers. Once obtained, fertile eggs may require surface sterilization and incubation in carefully controlled environments. Colonies also must be protected from pathogens and predators, as well as environmental and procedural failures. The rearing processes and insect life history characteristics are checked every generation, e.g., rate of development, pupal weight or adult size, percent emergence and mating, and the number of viable eggs.

Selecting an Insect to Rear

Virtually any insect can be collected as an egg, larva or nymph and maintained through stages in metamorphoses until it becomes an adult. However, it is considerably more difficult to establish a colony that produces continuous generations. Knowledge is required about the species' habitat, natural food and behavior. Re-creation of soil and aquatic environments, symbiotic relationships, and specialized foods can make rearing difficult. Some insects undergo temperature- and photoperiod-dependent diapause or require host plant cues to terminate multi-year cycles. Feeding by trophallaxis may necessitate maintenance of an entire colony, as in termites, ants and other social insects. Because of these and other peculiar life history characteristics, the easiest insects to rear are relatively small, multivoltine (more than one generation per year), plant-feeding, terrestrial species with wide host ranges and few unusual environmental requirements. Commonly cultured insects include pests of common crops, stored products or landscape plants, as well as abundant species that are not pests. Examples include armyworms, loopers, hornworms, mealworms, weevils, mealybugs, aphids, ants, grasshoppers, and lady beetles.

There are published lists and specialized directories of arthropod cultures, e.g., Drosophila spp. strains. "Arthropod Species in Culture" listed colonies of the following taxonomic orders (species, colonies): Acari (41, 77), Anoplura (1, 1), Coleoptera (78, 266), Diptera (168, 301), Hemiptera (90, 206), Hymenoptera (119, 169), Lepidoptera (101, 308), Mallophaga (3, 3), Neuroptera (2, 2), Orthoptera (64, 203), Siphonaptera (2, 7), and Thysanura (4, 11). The most numerous colonies were the twospotted spider mite, *Tetranychus urticae* (24), confused flower beetle, *Tribolium confusum* (21), yellow fever mosquito, *Aedes aegypti* (21), housefly, *Musca domestica* (28), tobacco budworm, *Heliothis virescens* (25), and American cockroach, *Periplaneta americana* (26). "Suppliers of Beneficial Organisms in North America" is maintained by the California

Environmental Protection Agency (http://www.cdpr.ca.gov). This publication lists more than 130 species of beneficial organisms available from 142 suppliers. The species are classified as predatory mites (17 species, 325 suppliers), parasitic nematodes (6, 111), stored product pest parasites and predators (4, 13), aphid parasites and predators (17, 361), whitefly parasites and predators (9, 268), parasites and predators for greenhouse pests (23, 504), scale and mealybug parasites and predators (7, 149), insect egg parasites (12, 238), moth and butterfly larval parasites (6, 30), filth fly parasites (8, 143), other insect parasites (4, 9), general predators (21, 410) and weed controls (36, 50). The most popular species were the lacewings *Chrysoperla carnea* (65 suppliers) and *C. rufilabris* (54), mealybug destroyer, *Cryptolaemus montrouzieri* (52), whitefly parasite, *Encarsia formosa* (54), convergent lady beetle, *Hippodamia convergens* (56), predatory mite, *Phytoseiulus persimilis* (54), and a parasitoid of moth eggs, *Trichogramma pretiosum* (77). Many more species could be reared using the techniques developed for their close relatives.

Founding a Colony

Insect colonies are initiated from field-collected specimens or previously established colonies. Any developmental stage can be used, but surface-sterilized eggs are less likely to introduce a pathogen. Eggs are generally used to initiate a colony from another colony because they are durable and easy to ship. However, eggs may be difficult to find in nature, and subsequent larvae or nymphs often suffer high levels of mortality because they are parasitized or, if viable, are not yet laboratory adapted. Thus, it is generally advisable to collect pupae or large nymphs, hold them in individual containers for parasite and pathogen screening, combine the adults in mating cages with food and a suitable oviposition substrate, and collect and treat the eggs for use in establishing a colony. From either source, field or insectary, the degree of success achieved will depend on the quality of colonized insects and skill with which they are reared. Many species that can be colonized and reared for multiple generations are on average much larger, healthier (free of malnutrition, pathogens, parasites and predators), uniform in growth, and more active and fertile than those in nature.

Facilities and Equipment

Insect rearing facilities have evolved from so-called "insectary" buildings with ambient temperature and humidity, to highly controlled facilities that contain insects under high security. Insectaries provide adequate environments for rearing insects in semi-natural conditions on host plants or animals. However, pathogens, parasitoids and predators are not controlled and workers are exposed to potentially dangerous pathogens and allergens. Conversely, temperature, humidity, air quality and quantity, light quality and photoperiod, sanitation, and security are closely maintained in rearing facilities. Insects and supplies are carefully screened for contaminants before they are admitted, and human access and exposure are limited. All openings to a rearing facility are sealed or filtered to prevent insects from entering or leaving, particularly in quarantine facilities. These rearing facilities range from small rooms with single occupants to massive factories with hundreds of workers. Regardless, they must be well insulated and have highly filtered, re-circulated air to be cost efficient. A garage or out-building can easily be modified to serve as an insect rearing facility.

Equipment is required to provide suitable environments, handle the insects, move and store materials and supplies, observe specimens, assure sanitation, and prepare diets. The environment is maintained by air conditioners, fans, humidifiers and de-humidifiers, mechanical or electrostatic air filters, and incandescent and fluorescent lighting. Tables, chairs, a deep sink, and perhaps a dishwasher are also needed. A dedicated refrigerator is required for storing diet ingredients and a freezer can be used to chill insects for handling. A binocular microscope may be needed to determine sex, screen for parasites and predators, or determine species. Specialized techniques and a high-powered microscope would be required to identify insect pathogens. Laboratory carts with wheels can be very useful for moving insects, materials and supplies. A cooker and blender must be provided to work with gelled diets.

Materials and Supplies

Typical insect rearing materials include hardware cloth, screen, or Plexiglas® for making cages; wood or metal framing; shelves and supports, and oviposition substrates. Materials may also be needed to modify rearing containers, support diets, and build small devices for handling insects. Supplies for insect rearing are similar to those found in a family kitchen, including products for preparing and serving diets, protecting tables, and cleaning and sanitizing surfaces. Egg treatment is not much different than cleaning fresh vegetables with a mild bleach solution. Cotton and sponges are used to hold liquids and prevent feeding insects from drowning. All kinds of paper and plastic containers are used as purchased or modified for insect rearing (Fig. 1). The most specialized supplies are often dietary ingredients for larvae or nymphs. Diets may be natural, such as certain fruits and vegetables, or formulated from specific nutrients. Medical and veterinary pests are usually maintained on living hosts, although mosquitoes can be reared in trays containing water and food. Most materials and supplies for rearing insects are reasonably inexpensive and specialized diets can be purchased to avoid their preparation (Table 1 and 2).

Insect Rearing Procedures

Insect eggs are resilient and generally do not require special care unless handled. Newly emerged larvae or nymphs can remain on the plant or animal host until it is no longer suitable for their development. They can then be transferred to new hosts or simply held for pupation, or additional molts if they have incomplete metamorphosis. Eggs are often surface sterilized with 10% bleach solution or another germicidal chemical to eliminate microorganisms, particularly if they are field collected. This procedure requires individual eggs to be removed from bundles and substrates. The bleach solution dissolves the cement and outer layer of the chorion, thus freeing the eggs. However, this treatment renders them susceptible to desiccation or drowning, so they must be handled carefully. Surface sterilization is recommended if eggs are to be placed in containers of artificial diet (Fig. 2).

Larvae and nymphs are maintained in containers or cages that provide diet, surface area, appropriate environments, and protection from contamination. The diet must induce feeding, provide adequate nutrition and not deteriorate during the insect's development. As the insects grow, they require more food, space and separation from considerable amounts of frass (feces). Overcrowded larvae often become cannibalistic. The containers and cages buffer the developing insects from extremes in temperature and relative humidity, as does the rearing facility and holding room. Air circulation is important to balance moisture and minimize vertical stratification in holding areas.

Adult colonies are derived from pupae or nymphs that have been sexed, selected for desired characteristics, and screened for parasites, pathogens, and other contaminants. If closely related insects are being reared, a contaminant can be the wrong species. Food, water and a suitable oviposition substrate are usually provided in a container or cage and, as with the immatures, it is essential to control the environment. A considerable amount of testing may be required to provide the necessary conditions for mating and oviposition. Depending on the kind of insect, these conditions can involve space, lighting, attractants, sex ratios, airflow, host

Rearing of Insects, Figure 1 **Rearing a small colony of blister beetles: upper left, adults on desert sunflower; upper right, eggs under a flower; lower left, artificial diet and glass bee cells; and lower right, artificial flower with reared pupae and adults.**

cues, complex courtship behavior, and so forth. Production of viable eggs is usually the greatest problem to overcome in establishing a continuous colony of insects.

Food for Immature and Adult Insects

Insects that feed on plants and animals are often maintained on their natural hosts or associated tissues, such as leaves, fruit, meat or blood (Table 3). This requires that the hosts be reared continuously or tissues be collected and kept fresh. With insect life cycles extending from a few days to several years, providing host material can be the most time consuming effort in insect rearing. This is particularly true for predatory and parasitic insects because three trophic levels must be synchronized: the initial plant or animal, second level host and beneficial insect. Consequently, insects are often selected for rearing that feed on human and animal food as immatures and adults, or require only sugar water or nothing as adults. These include crickets, wax moths, cockroaches, stored product pests, certain beetles and grasshoppers, and a wide variety of flies. So, some cockroaches eat dry dog food, grasshoppers eat lettuce, plant bugs eat green beans, flies eat fruit, and so forth. Gelled (often agar-based) diets have been developed to provide water with the food and incorporate preservatives. These kinds of diets can be prepared using published formulas or purchased along with the insects from specialized companies. Diets must be fresh because the ingredients can deteriorate during prolonged storage.

Isolation and Sanitation

Insects and their diets attract a host of competitors, predators, parasites and pathogens. Even a very small colony can easily become infested with scavenger or predatory mites, ants, cockroaches,

Rearing of Insects, Table 1 Partial list of sources for insects, rearing supplies and associated information

Company/institution	Web site addresses (http://)
Assn. of Natural Bio-control Producers	www.anbp.org
Bio Quip Products, Inc.	www.bioquip.com
BioServe	www.bio-serv.com/insect/home.html
Carolina Biological Supply	www.carolina.com
Combined Scientific Supplies	www.overland.net/~insects/
Educational Science	educationalscience.com/breedingsupplies.htm
Entomos	www.entomos.com/
Princ. and Proc. for Rearing Qual. Insects	www.msstate.edu/Entomology/Rearingwksp.html
Southland Products	www.tecinfo.net/~southland/
Suppliers of Beneficial Organisms in N.A.	www.cdpr.ca.gov
Ward's Natural Science Establishment, Inc	www.wardsci.com/
Young Entomologists' Society	members.aol.com/yesbugs/bugclub.html

Rearing of Insects, Table 2 Examples of simple diets for rearing insects, in this case bollworms (moths)

Vanderzant and Richardson (1962)	Shorey and Hale (1965)	King and Hartley (1985)
Wheat germ	Pinto beans	Wheat germ
Casein	Brewers' yeast	Soybean flour
Agar	Agar	Agar
Sugar	–	Sugar
–	Methyl *p*-hydroxybenzoate	Methyl paraben
–	Sorbic acid	Sorbic acid
–	Formaldehyde	Aureomycin®
Ascorbic acid	Ascorbic acid	Vitamin mix
Choline chloride	–	–
B vitamins	–	–
Inositol	–	–
–	–	Wesson salt
Water	Water	Water

Note that many of the components are diet preservatives, not nutrients.

flies and gnats. Most of these kinds of problems can be solved with cleanliness and barriers. Germicidal soaps and a 5% solution of commercial bleach will provide surface sterilization with minimal corrosion. Barriers include sealed walls, electrical outlets and plumbing, reach-in boxes, screened or solid cages, paper and plastic containers, and plastic bags. Food should be stored in a refrigerator or freezer. Rough surfaces, drop ceilings, porous materials and cracks are difficult to sanitize. Positive air pressure helps to keep contaminants from entering and rearing procedures should be accomplished from clean to dirty, with no backtracking. Normally, parasites that penetrate

Rearing of Insects, Figure 2 **Industrial rearing of the Mediterranean fruit fly: upper left, adult fruit fly; upper right, papaya infested with larvae; lower left, trays of larvae on artificial diet; and lower right, rearing facility at Metapa, Mexico.**

Rearing of Insects, Table 3 **Typical purposes for rearing insects and primary requirements for their production and quality**

Purpose for insects	Primary requirements
Enjoyment	Appearance, behavior, longevity
Research	Uniformity, reliability
Pest management	Behavior, reliability, cost
Display	Appearance, behavior, longevity
Education	Appearance, behavior, cost
Human food	Size, taste, cost
Animal food	Size, behavior, taste, cost
Natural products	Size, yield, cost
Fish bait	Appearance, behavior, cost
Biodiversity	Heterogeneity, behavior

barriers can be eliminated by breaking their life cycles, possible because they develop more rapidly than their hosts. Potentially parasitized insects are isolated from the colony until they are determined to be clean. Pathogens can be more problematic because they are difficult to detect and identify. In practice, diseased insects are carefully discarded and the colony is screened until symptoms cease, often without determining the exact cause. Sanitation and surveillance are increased concomitantly. As in kitchens, some of the bacteria that contaminate insect diets are human pathogens.

Quality of Reared Insects

Care must be taken to assure the quality of artificially reared insects relative to their intended purpose. Yield, size, sex ratio, rate of development, egg production and mobility are typically monitored depending on the situation. It is also important to keep track of environmental conditions, e.g., temperature, relative humidity, light quality and photoperiod, sanitation, materials and supplies, and work performed. Often check sheets are used for monitoring insect production and quality control charts with averages and ranges suffice for life history and behavioral measurements. This kind of information is required to "troubleshoot" the rearing process and determine causes of failures to produce acceptable insects. Virtually all severe insect rearing problems result from failure to perform standard operating procedures or defective environmental controls. Once established, rearing operations become routine and individual procedures easy to forget.

As in animal husbandry, insect rearing expertise develops with experience and knowledge gained by trial and error, and by studying information developed by others. It is considered both an art and science, requiring a "brown thumb" analogous with the green thumb of the gardener. The fastest way to learn new techniques is to visit established insect rearing facilities, talk with colleagues individually and at conferences, participate in an organized course, and read technical publications. Facilities and contacts can be located by Land Grant University faculty members, perhaps at extension and research centers, and state department of agriculture and U.S. Department of Agriculture scientists. Currently, the only comprehensive insect rearing course in the United States is a weeklong, intensive workshop taught twice each year at Mississippi State University. Written information on insect rearing techniques is scattered mostly in the methods sections of scientific papers or accumulated in difficult to locate, out-of-print books. Although there are many others, the following journals have tended to publish papers on insect rearing: Annals of the Entomological Society of America, Entomologia Experimentalis et Applicata, Florida Entomologist, Journal of Insect Science, BioControl (formerly Entomophaga), and specialized publications, such as the Journal of the Lepidopterists' Society and Journal of Apicultural Research. Commercial suppliers of insects, diets and educational materials are an excellent source of information on rearing (see Table 2). It can also be advantageous to adapt methods from books on rearing agricultural pests, such as the boll weevil (Curculionidae), screwworm (Calliphoridae), corn earworm (Noctuidae), or tobacco hornworm (Sphingidae). It will require some searching but there is a considerable amount of invaluable information on insect rearing.

► Nutrition in Insects

References

Anderson TE, Leppla NC (1992) Advances in insect rearing for research and pest management. Westview Press, Boulder, CO, 519 pp

Leppla NC, Ashley TR (1978) Facilities for insect research and production. U.S. Department of Agriculture Technical Bulletin No. 1576, 86 pp

Needham JG, Galtsoff PS, Lutz FE, Welch PS (1937) Culture methods for invertebrate animals. Comstock, Ithaca, NY, 590 pp

Peterson A (1964) Entomological techniques, how to work with insects. Entomological Reprint Specialists, Los Angeles, CA, 435 pp

Singh P (1977) Artificial diets for insects, mites, and spiders. Plenum, New York, NY, 594 pp

Singh P, Moore RF (1985) Handbook of insect rearing, vols 1 and 2. Elsevier, Amsterdam, The Netherlands, 488 and 514 pp

Smith CN (1966) Insect colonization and mass production. Academic Press, New York, NY, 618 pp

Villiard P (1969) Moths and how to rear them. Funk and Wagnalls, New York, NY, 242 pp

De Re' Aumur, René Antoine Ferchault

René Antoine Ferchault de Réaumur was born in 1683 at La Rochelle, France. He achieved success early in life, being elected to the Academy of Sciences at the age of 24, after publication of some important work on geometry. He worked principally as a naturalist, publishing articles on regeneration of lost appendages by crustaceans, fossils, luminescence by molluscs, the digestive systems in birds, and other topics. Not until 1734 did he begin publishing on insects, but by 1742 he had authored his "Memoires pour servir à l' histoire des insectes" in six volumes, and had begun a seventh volume, on beetles. In this treatise he gave a clear picture of insects and insect habits, and their relationship with nature. In addition to the natural history of insects, he attempted to develop a classification system based on behavior. Thus, he grouped insects, worms, molluscs, and reptiles together. Though this seems strange now, as we are conditioned to classification systems based on structure, classification was still in its formative stages and much more unusual systems had been proposed. This publication gave him prominence among naturalists, and his work remains a classic example of careful observation. However, Réaumur contributed to science and technology in many ways, including invention of a thermometer, the use of porcelain for thermometers, improved steel production and enhanced the economy of tin plate production.

Reference

Pellett KL (1929) Lives of famous beekeepers, René Antoine Ferchault de Réaumur. Am Bee J 69:193–201

Recapture Technique of Sampling

An absolute method of sampling that involves capture of insects, marking of captured insects, release of the marked insects, and then recapture of marked and unmarked insects from the natural population. After the recapture effort, the proportion of marked insects is used to estimate the initial population size.

► Sampling of Arthropods

Recombinant DNA Technology

All the techniques involved in the construction, study and use of recombinant DNA molecules. Often abbreviated rDNA, which can be confused with ribosomal DNA.

Recombination

A physical process that can lead to the exchange of segments of two DNA molecules and which can result in progeny from a cross between two different parents with combinations of alleles not displayed by either parent.

Recruitment Trail

An odor trail produced by an individual worker that is used to recruit nestmates to a location where other workers are needed: a food source, nest site, a breach in the nest wall, etc.

► Pheromones

Rectal Gill

A tracheal gill occurring in the anterior region of the rectum in naiads of Anisoptera (Odonata).

Rectal Myiasis

A form of myiasis that occurs in the intestine or anus. Fly larvae invade these areas and complete their development internally, in the rectum of the host. Among flies associated with this are rat-tailed maggot, *Eristalis tenax* (L.) (Syrphidae); latrine fly, *Fannia scalaris* (Fabricius) (Fanniidae); false stable fly, *Muscinia stabulans* (Fallen) (Muscidae); and lesser house fly, *Fannia canicularis* (L.) (Fanniidae).

► Myiasis

Rectal Pad

A section of the rectum containing enlarged cells that take up water and ions from the rectum.

Rectum

The posterior region of the hindgut leading to the anus (Fig. 3).

► Alimentary System

► Alimentary Canal and Digestion

Recurrent Vein

A crossvein, often extending obliquely, and usually associated with the costa and subcosta, though this varies among taxa.

► Wings of Insects

Red Bugs

Members of the family Pyrrhocoridae (order Hemiptera).

► Bugs

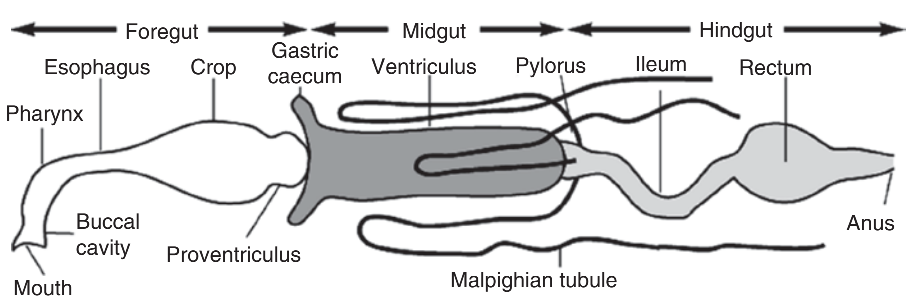
Red Flour Beetle, *Tribolium confusum* Jacquilin du Val (Coleoptera: Tenebrionidae)

This is a common flour pest, and is difficult to control.

► Stored Grain and Flour Insects

Redi, Francesco

Francesco Redi (Fig. 4) was born at Arezzo, Italy, on February 18, 1626. After earning a degree in medicine, he became a tutor for five years, but then moved to Florence where he became physician to the Grand Dukes Ferdinand II and Cosimo III. He conducted much experimentation aimed at improving medicine, but also was proficient at poetry and music. Among his scientific publications are "Observations on vipers," "Experiments on the generation of insects," and "Medical consulting." Among his literary contributions are the "Bacco in Toscana," and "Arianna inferma." He is best remembered for his work establishing that insects are not produced by spontaneous generation, but rather are derived from other insects. Perhaps more importantly, by working with the development of fly larvae on meat he demonstrated the value of experimentation, and the value of changing one variable at a time in elucidating biology. He died at Pisa, Italy, on March 1, 1698.



Rectum, Figure 3 Generalized insect alimentary system (adapted from Chapman, The insects: structure and function).

Redi, Francesco, Figure 4 Francesco Redi.

Reference

Anonymous (2002) Franceso Redi – scientific works. Available at http://galileo.imss.firenze.it/mutli/redi/eopere.html. Accessed August 2002

Red Imported Fire Ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae)

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The red imported fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae), is a social insect that produces hills or mounds in open areas where the colonies reside, although colonies occasionally occur indoors, near and within structures, such as utility housings or tree trunks. Fire ant mounds may reach 30–40 cm high and 30–50 cm in diameter with no holes or central entrance hole on the mound's surface. Inside, mounds have interconnecting galleries that may extend 30–40 cm deep, although some tunnels can penetrate to the water table. In response to solar radiation and ambient conditions, fire ants move within the mound seeking optimum temperature for the development of brood (eggs, larvae and pupae), a process called thermoregulation. Foraging worker ants enter and exit through tunnels radiating up to 5–10 m away from the mound. The disturbance of mounds results in a rapid defensive response by worker ants, which quickly run up vertical surfaces to bite and sting any objects encountered.

Two forms of imported fire ant colonies occur: the single queen (monogyne) and the multiple queen (polygyne) forms, the latter containing two or more inseminated, reproductively active queen ants. Worker ants in single queen colonies eliminate additional queens and respond defensively to neighboring colonies to maintain territories. Multiple queen colony worker ants do not display territorial behavior and, consequently, they can produce 3–10 times as many ant mounds in a given area of land and result in 500 mounds and 50 million ants per ha. Areas infested with the single queen form normally have 50–75 mounds per ha.

Description

A mature colony can contain over 200,000–400,000 sterile, female worker ants. These ants range in length from 1.5 to 5 mm and are dark reddish brown with black abdomens. Worker ants build up the colony, care for the queen and brood, defend the colony and forage for food. Their functions within the colony are determined by the size and needs of the colony, and by the age of the worker ant. The younger workers serve as nurse ants, which tend and move the queen and brood. Older workers serve as reserves to defend the colony and to construct and maintain the mound. The oldest worker ants become foragers.

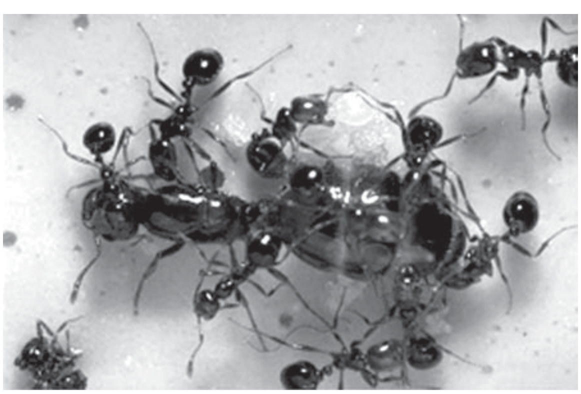
Developmental stages include eggs, larvae and pupae, referred to as brood. The eggs are spherical and creamy white. The larvae are legless, cream-colored and grub-like with distinct head capsules. Pupae resemble worker ants and are initially creamy white turning darker before the adult ants emerge (eclose).

Winged, reproductive, male ants develop from eggs that are not fertilized. Fertilized eggs can develop into either sterile, female worker ants, or winged, reproductive females depending upon the nutrition provided to the larval stages and the chemical signals (juvenile hormone level and pheromones) within the colony. Winged, female reproductives are reddish-brown, while males are shiny black with smaller heads. These ants stay in the colony until conditions exist for their nuptial flight. Queen ants (mated, female reproductives) are larger (9 mm) and have no wings (Fig. 5).

Spread

Spread occurs naturally (through mating flights, ground migration and floating colonies on water during floods) and artificially (by humans through shipment of infested articles like nursery potting media, sod, bales of hay, or soil). It is limited primarily by the availability of soil moisture and cold temperatures. Predictions suggest the ant is unable to survive where the minimum yearly temperatures are less than −12.3 to −17.8°C.

Mating flights occur mid-day (10:00 a.m. to 2:00 p.m.) during the first sunny days after a period of rainy weather when temperature are suitable (24°C) at any time of the year, but mainly in the spring and the fall. Winged male and female reproductives (also called sexuals or alates) couple in the air (90–300 m high). The males die after mating, but the females seeking a nesting site are attracted to shiny surfaces (e.g., water surfaces, shiny truck beds) and land within a mile (1.6 km) or two unless carried farther by the wind.



Red Imported Fire Ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae), Figure 5 Fire ant queen and workers.

Colony Formation

Newly mated females that survive the nuptial flight and that reach suitable nesting habitats (estimated to be about 1% due to predation and other mortality factors), remove their wings and burrow into the ground (Fig. 6). Sealed in a chamber that they dig, these females begin to lay eggs (10–20 per day) that

Red Imported Fire Ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae), Figure 6 Fire ant mound at base of tree.

hatch into larvae in 6–10 days, which are fed from energy produced from the breakdown of flight muscles, infertile (trophic) eggs, young larvae and oil reserves. The first worker ants emerging are uniformly small and are called minums or nanitics.

Life Cycle

Each queen ant can produce about 800 eggs per day. The eggs hatch in 8–10 days and the larvae develop through four stages (instars) over 12–15 days before pupating for a period of 9–16 days. Development requires 22–37 days, depending on the temperature. Most worker ants live 60–150 days with larger ants living longer, but during cooler weather, workers can survive for 8 months or more. Newly established colonies develop winged, reproductive ants after about 6–8 months and can produce 4,000–6,000 alates per year. Queen ants can live for more than 7 years.

Habitat and Food Source(s)

Ants communicate through vision (sight), vibration (sound), touch and chemicals (pheromones, including a queen pheromone that attract workers and may suppress dealation and reproduction, and a trail pheromone produced by Dufour's gland associated with the worker ant stinger). They forage when temperatures range from 22 to 36°C. Upon locating food resources, they develop a trail using a pheromone that directs other worker ants to the site. Fire ants are omnivores, consuming sugars (carbohydrates), certain amino acids, ions in solution and some oils containing polyunsaturated fatty acids. Although they primarily consume other arthropods and the honeydew produced by some types of sucking insects (Hemiptera), they will also consume seeds and other plant parts like developing or ripening fruit, and dead plant and animal tissues.

Worker ant mouthparts are for biting and sipping liquids. Worker ants consume only liquids and particles <0.9 μm, storing food in their crops and their postpharyngeal gland (oils only) until feeding it to other worker ants and ultimately, to larvae and queen(s) – a process called trophalaxis. Young larval stages (instars) are fed regurgitated liquid food only. However, the last (fourth) larval stage can ingest solid food particles. Worker ants place bits of solid food in a small depression (called a food basket or praesaepium) just in front of and beneath the larva's mouth (an area called the presternum). They digest the proteins externally (extraorally) by secreting enzymes and by chewing and swallowing smaller particles.

Pest Status

Like a weed species, the aggressive and abundant imported fire ant reduces biodiversity, particularly other ant species, in newly infested areas. These soil-dwelling ant colonies are most commonly found in urban, agricultural and non-agricultural areas and affect people, livestock, wildlife and the flora and fauna of infested lands. Although the exact economic costs of fire ant damage and control are unknown, estimates for the southeastern United States have been more than a half billion to several billion dollars per year. The cost of producing agricultural commodities, such as nursery and sod production, has increased in infested areas. There, quarantine regulations mandate treatment of materials to be shipped to non-infested areas.

Medical Importance

For most people, contact with the ants is merely an irritation and a nuisance, but for some people (particularly very young, old or indigent people), the ant's sting can result in medically serious problems or even (rarely) death. Imported fire ant workers are highly defensive and aggressive. When disturbed, they run up vertical objects quickly (8 cm/5 s) en masse (tens to hundreds) and seem to bite (with their mandibles) and sting (with their modified ovipositor) all at once. The venom injected produces a burning, fire-like sensation for which the ant gets its common name: fire ant. Each worker ant can sting repeatedly. Queen ants do not sting, but they do contain venom. Surveys have documented that more than 50% of the people living in infested areas are stung by the ant annually. Most people can tolerate multiple stings, but may have problems with secondary infections at the sites of the stings. However, about 0.6–6.0% of people stung are sensitive to the venom and can experience serious medical problems from even one sting.

The venom produces a fluid-filled pustule within a day or so (10–12 h) of being stung (Fig. 7). The venom consists of aliphatic substituted alkaloids that are cytotoxic (cell-killing), and a small amount of protein, which is responsible for allergic responses (swelling or edema, and anaphylactic shock characterized by swelling, sweating and shortness of breath that can lead to respiratory arrest and heart failure). The pustules persist for several weeks and may leave scars. Ruptured pustules can become infected.

The ants also affect people indirectly by modifying their behavior to avoid contact with the ant. There are also increased health and environmental risks associated with insecticide application or other attempts to control this pest.

Red Imported Fire Ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae), Figure 7 Pustules on hand resulting from fire ant stings.

Equipment Damage

The ants or entire colonies move into buildings or vehicles seeking favorable nesting sites, particularly during flooding and very hot, dry conditions. Fire ant foraging and nesting activities can result in failure of many types mechanical (e.g., hay harvesting machinery, sprinkler systems) and electrical equipment (e.g., air conditioner units, traffic box switching mechanisms).

Agricultural and Ecological Impact

In addition to being considered medically important pests of people, pets, livestock and wildlife, imported fire ants can also damage crops such as corn, sorghum, okra, potatoes, sunflowers and others by feeding on the seeds, seedlings and developing fruit. Predatory activities of fire ants suppress populations of ticks, chiggers, caterpillars and other insects. Predatory activity attributes to wildlife reductions in some areas. Many animals are also affected by these stinging ants, particularly those that cannot quickly move away from the threat (e.g., very young, old, or confined animals). Ants recruit to moist areas of the body (eyes, genitals), yolk of hatching birds and wounds, and begin stinging when disturbed. Stings result in injury such as blindness, swelling or death. Indirectly, animals avoid infested food, water and nesting areas. The ants can reduce food sources for some insect-eating (insectivorous) animals, such as some birds and lizards, and they may compete with seed-feeding (gramnivorous) animals for food, or by altering the distribution and composition of plant communities.

In addition to direct damage to plants, they also aggravate populations of other insect plant pests like some Hemiptera (aphids, scale insects, mealybugs) by protecting them from natural enemies as the ants consume the sugary honeydew produced by these pests. However, the ants primarily prey on arthropods, such as some species of ticks, many caterpillars and other insects often considered pests.

This behavior can provide benefits to producers of cotton, sugarcane and other commodities.

History of Spread

The fire ants comprise a group of 18–20 insects species native to the New World within the genus, *Solenopsis*, which contains about 200 species including "thief ants" (an ant species, most of which are incapable of stinging humans, nesting close to other ant nests and robbing them of stored food and brood). The black imported fire ant, *S. richteri* Forel, was accidentally introduced from the Paraguay River drainage area of South America to the U.S. port of Mobile, Alabama in 1918. The red imported fire ant, *S. invicta*, is believed to have been introduced from northern Argentina or southern Brazil to the same U.S. port around the early 1930s. *S. invicta* spread westward at about 198 km per year.

Several native fire ant species occurred in the U.S. before *S. invicta* and *S. richteri* Forel arrived: *S. xyloni* McCook, the southern fire ant; *S. geminata* (Fab.), the tropical fire ant; and, two desert-adapted species, *S. aurea* Wheeler and *S. amblychila* Wheeler. While *S. xyloni* and *S. geminata* have also been considered to be pest ants, they have been largely displaced in the southeastern U.S. by the red and black imported fire ants. Imported fire ants occur at higher densities than native fire ant species, leading to increased human contact and problems. In the U.S., *S. richeteri* occurs in northern areas of Alabama, Mississippi, Georgia and southern Tennessee, with a sexually reproductive hybrid population of *S. invicta* and *S. richteri* throughout the remainder of these states and part of Georgia.

Solenopsis invicta now occupies 128 million ha (316 million acres) in nine southeastern states (Alabama, Arkansas, Florida, Georgia, Louisiana, Mississippi, North Carolina, South Carolina, Texas) in the U.S. with limited infestations in Arizona, Oklahoma, Tennessee, New Mexico and California. Infestations also occur in a number of island countries in the Carribean including Puerto Rico, the Bahamas, the British and U.S. Virgin Islands, Antigua and Trinidad. The species has recently been detected in New Zealand and Australia (Brisbane).

History of Control Efforts in the U.S

- 1929 – Imported fire ant first detected in the northern Mobile area and Spring Hill, Alabama
- February 1937 – First organized control program in Baldwin County, Alabama (1–3 ounces 48% calcium cyanide dust per mound); 2,000 acres or 800 ha treated
- 1948 – Mississippi spends $15,000 to treat ant mounds with chlordane dust; Alabama and Louisiana provide chlordane to farmers free or at cost
- 1957 – Arkansas conducts 12,000 acre eradication project in Union County, and the city of El Dorado applied heptachlor (2 lb/acre) by air; congress appropriates $2.4 million for USDA to begin a federal-state cooperative control and eradication program dedicated to the use of aerial and granular applications of heptachlor and dieldrin (2 lb a.i./acre)
- 1958 – Mandated treatments of regulated items initiated to comply with USDA imported fire ant quarantine regulations
- 1960 – Heptachlor rate lowered to 0.25 lb a.i./acre with two applications, 3 and 6 months apart
- Early 1960s – Growing concerns about the detrimental effects of treatments to wildlife, contamination of food and crops ended the program
- 1962 – Lofgren develops conventional bait formulation; mirex developed as an active ingredient: mirex (0.3%) dissolved in soybean oil (14.7%) on impregnated corn grits (85%)
- 1962–1978 – 140 Million acres treated with mirex bait by ground and aerial equipment, although many treatments consisted of three applications to the same area; thus, ~46.6 million acres were actually treated
- 1967 – Feasibility studies were initiated by USDA-ARS in Gainesville, Florida, to use mirex to eradicate imported fire ants

- Late-1960s to early 1970s – mirex residues found in environment, non-target organisms and to be toxic to estuarine organisms
- 1970–1971 – U.S. Department of Interior bans all mirex uses; EPA issues notice of cancellation of mirex
- 1977 – Mirex reported to be a potential carcinogen; EPA cancelled registrations December 31
- 1978 – Amdro® (hydamethylnon with oleic or linoleic acid added to increase oil solubility formulated in soybean oil (20%) on a pregelled defatted corn grit carrier) tested
- 1980 – Amdro registered by EPA for use on pastures, range grasses, lawns, turf and nonagricultural lands
- 1983 – Prodrone, the first insect growth regulator (IGR) is registered by the EPA
- 1985 – Logic® (fenoxycarb), another IGR, registered by the EPA
- 1986 – Ascend®/Affirm® (abamectin) registered by the EPA
- 1995–2000 – Biological control efforts initiated using importation and release of phorid flies (*Pseudacteon tricuspis* and others) and manipulation of a disease, *Thelohania solenopsae*
- 1998 – Distance®/Spectractide® Fire Ant Bait (pyriproxifen), another IGR, registered by the EPA
- 1998 – Extinguish™ (methoprene), another IGR, registered by the EPA for use in croplands in which other baits can not be applied
- 2000 – Justice®, Eliminator®, Strike® Fire Ant Baits and others containing spinosad (spinosyns A and B combined), a new insecticide class (spinosyn derived from bacterium, *Saccharopolyspora spinosa Mertz* and Yao) registered by EPA
- 2000 – Chipco® FireStar® and TopChoice® (fipronil bait and granular products, a phenyl pyrazole insecticide), approved by EPA

References

Drees BM, Barr CL, Vinson SB, Gold RE, Merchant ME, Riggs N, Lennon L, Russell S, Nester P, Kostroun D, Sparks B, Pollet D, Shanklin D, Vail K, Flanders K, Horton PM, Oi D, Koehler PG, Vogt JT (2000) Managing imported fire ants in urban areas. B-6043. Texas A&M University, College Station, TX, USA, 20 pp

Drees BM, Barr CL, Shanklin DR, Pollet DK, Flanders K, Sparks B, Vail K (1999) Managing red imported fire ants in agriculture. B-6076. Texas Imported Fire Ant Research and Management Plan. Texas A&M University, College Station, TX, USA, 20 pp

Taber SW (2000) Fire ants. Texas A&M University Press, College Station, TX, USA, 308 pp

Vinson SB (1997) Invasion of the red imported fire ant (Hymenoptera: Formicidae) – spread, biology, and impact. Am Entomol 43:23–39

Williams DF, Collins HL, Oi DH (2001) The red imported fire ant (Hymenoptera: Formicidae): an historical perspective of treatment programs and the development of chemical baits for control. Am Entomol 47:146–159

Red Imported Fire Ant Territorial Behavior

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The imported fire ant, Solenopsis invicta Buren, is a stinging social insect indigenous to parts of Brazil, Paraguay, and Argentina, and it was accidentally introduced to the United States in Alabama in 1929. The fire ant has since spread across the southern United States and Puerto Rico, and because of its venomous sting, it is widely viewed as being an exotic pest. Queens start colonies after nuptial flights that occur year round, but peak flight activity occurs between May and August. Colonies can produce 3,000–5,000 queens each year, and fire ant reproduction in a colony can be accomplished by a single queen or by multiple queens in polygynous colonies. Queens are morphologically distinct from other individuals in the colony, but workers range in length from 2 to 6 mm and definite subcastes among workers have not been identified.

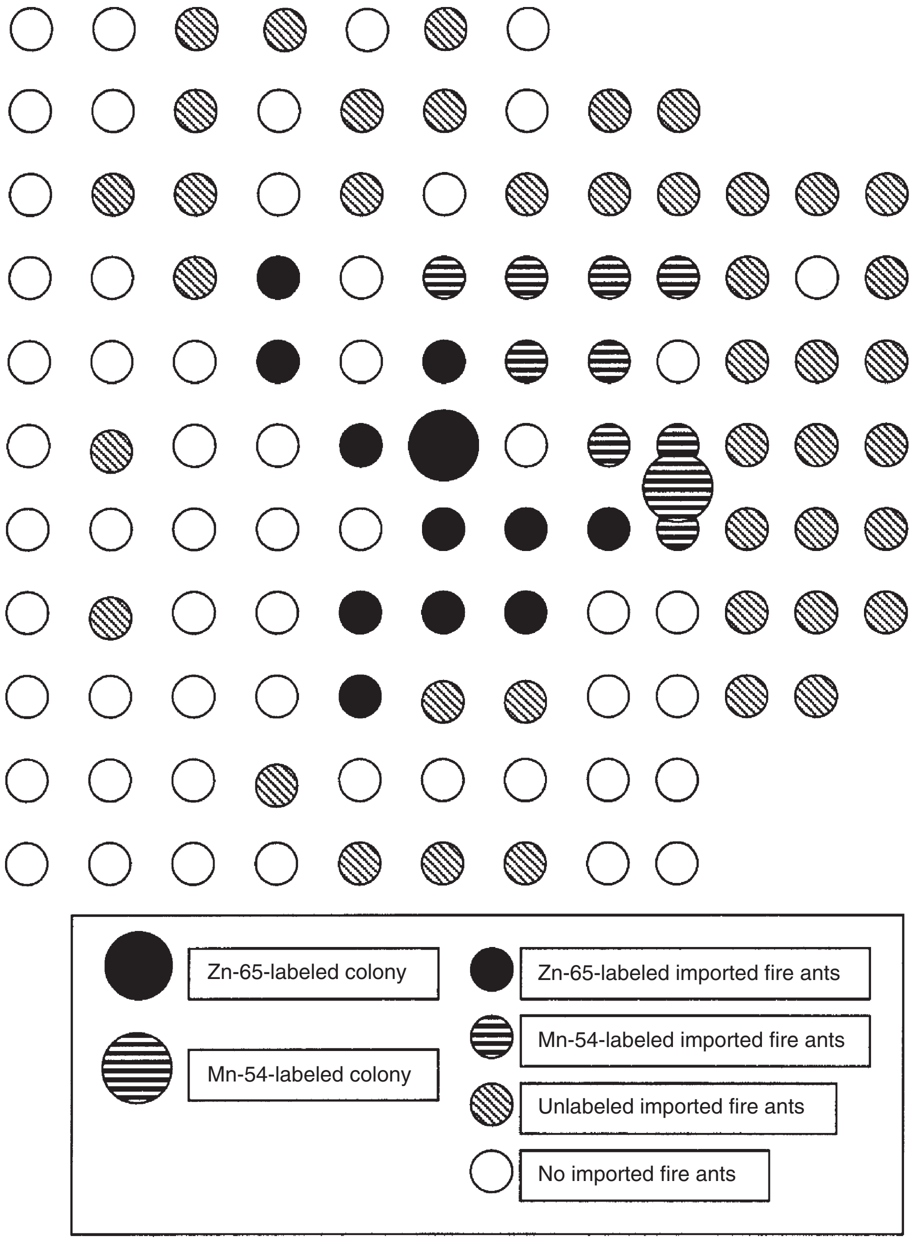
Fire ants establish colony mounds with subterranean galleries that can support populations of 50,000–230,000 workers. Mound densities of up to 2,500/ha, but usually <250 mounds/ha have been reported in pastures, cultivated areas, unattended woodlands, and disturbed habitats. Tunnels radiate 2–12 mm below ground level from each colony mound. One colony's tunnel system was exhumed and its tunnels were found to collectively extend 84 m. Tunnel exits occur intermittently and they facilitate access to foraging areas. Fire ants are omnivorous and they feed on a wide diversity of arthropods, molluscs, plant material, honeydew produced by hemipteran insects, and nectar. Mass foraging at specific sites is initiated by a trail pheromone secreted by a gland and extruded through the stinger of scout workers inside tunnel systems.

Dyes ingested by fire ants helped to show that, between two different fire ant colonies, fire ants from the two colonies did not forage at the same places, and it was suggested that the fire ants exhibited intraspecific territorial behavior. Another study labeled one fire ant colony with radioactive Zn-65 ingested with molasses and spread throughout the colony by trophallaxis, and a nearby colony was similarly radiolabeled with Mn-54. The territories of both fire ant colonies were shown to be discrete and dynamic over 20 consecutive days (Fig. 8). Fire ant colonies in weedy and weed-free sugarcane habitats were labeled with the nonradioactive, stable-activable tracer element samarium. Instrumental neutron activation analyses of the samarium marker revealed that the tagged ants foraged at significantly more sampling stations in weed-free sugarcane habitats than in weedy sugarcane habitats. The smaller territorial size in weedy areas was a result of more dense prey populations, which permitted greater numbers of fire ant colonies per unit area than weed-free sugarcane habitats. It was suggested that a heavily infested area could be completely occupied by a contiguous patchwork of fire ant territories defended by different colonies.

There are nine traits that have contributed to the fire ant's rapid adaptation to the southeastern United States, including a large colony population size, a general omnivorous diet, mass foraging recruitment, massive aerial dissemination of reproductive females, the stinging mechanism. Three traits are related to territoriality: (i) tunneling behavior offers protection from trail disruption, (ii) utilizing foraging areas in water-saturated soil permits access to established territories in areas subject to flooding, and (iii) defending temporally dynamic territory boundaries that permit efficient use of foraging areas when specific sites have been depleted.

The fire ant's adaptability and competitiveness have enabled it to become widely established in the southeastern United States despite the presence of other, indigenous ant species. Transect studies have shown that 92–100% of baited sampling sites can be monopolized by fire ants. Since its introduction to the southeastern United States, the fire ant has been a significant competitive force upon the distribution of other formicid species, and species that had previously predominated were frequently displaced. The fire ant has become the dominant formicid species in the southeastern United States. Generally, fire ants can overpower indigenous ant species in combat. Even the Floridian poneroid ant, *Lasius neoniger* Emery, which uses mandibular and chemical defenses to eliminate 2.4 fire ants for every *L. neoniger* killed, eventually succumbs to attrition because of the sheer magnitude of fire ant colony populations. All attempts to control fire ants with mirex applications resulted in the suppression of other ant species, including the tropical fire ant, *Solenopsis geminata* (F.), and *S. xyloni* McCook. Some researchers have suggested that the use of toxins for fire ant eradication has instead contributed to its proliferation in the United States because of fire ant resurgences at the expense of other ant species.

After dominating its niche, the fire ant appears to reach an equilibrium with native ant species. Cohabitation of an area with the competitive fire ant is a result of (i) strategies by other species that exploit other resources in habitat-diverse environments, (ii) chemical repellency by some ant species (e.g., *Monomorium minimum* (Buckley)), (iii) high mobility (e.g., *Aphaenogaster rudis* Emery can



Red Imported Fire Ant Territorial Behavior, Figure 8 **Day 12 of 20 consecutive days of collecting imported fire ants on a 3 m × 3 m grid in a grassy field in southern Louisiana. Each point on the grid was a 35-ml plastic cup buried to the lip and baited at 1,000 h with raw animal fat for 1.5 h. Imported fire ants labeled with Zn-65 and Mn-45 were detected using an autogramma solid scintillation detector with a multichannel analyzer.**

move faster than the fire ant), or (iv) proximity to resources. The latter two strategies each contribute to the reduction of recruitment time to essential resources so that opportunities for foraging can be capitalized upon with greater success even within fire ant territories. One study demonstrated that three formicid species sympatric with the fire ant had similarly rapid recruitment times.

The territorial behavior of the fire ant, in combination with the other characteristics that enhance its competitiveness, has permitted this exotic ant to become widely established in the United States. In areas that can support high numbers of fire ants, territories abut each other, and they continuously shift over time to compensate for changes in prey availability (some of which might be caused by predation by the fire ant). The fire ant's offensive, defensive, and foraging capabilities in such conditions have displaced native ant species, but, on the other hand, the fire ant, because of the same characteristics, has emerged as the key predator of some economically important pests, including the boll weevil, *Anthonomus grandis grandis* Boheman, in parts of Texas, and the sugarcane borer, *Diatraea saccharalis* (F.), in Louisiana.

References

Levings SC, Traniello FA (1981) Territoriality, nest dispersion, and community structure in ants. Psyche 88:265–319

Markin GP, Neal JO, Dillier J (1975) Foraging tunnels of the red imported fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae). J Kans Entomol Soc 48:83–89

Showler AT, Reagan TE (1987) Ecological interactions of the red imported fire ant in the southeastern United States. J Entomol Sci Suppl 1:52–64

Showler AT, Knaus RM, Reagan TE (1989) Foraging territoriality of the imported fire ant, *Solenpsis invicta* Buren, in sugarcane as determined by neutron activation analysis. Insectes Soc 36:235–239

Showler AT, Knaus RM, Reagan TE (1990) Studies of the territorial dynamics of the red imported fire ant (*Solenopsis invicta* Buren Hymenoptera: Formicidae). Agric Ecosyst Environ 30:97–105

Wilson NL, Dillier JH, Markin GP (1971) Foraging territories of imported fire ants. Ann Entomol Soc Am 64:660–665

Redlegged Grasshopper, *Melanoplus femurrubrum* (Degeer) (Orthoptera: Acrididae)

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The redlegged grasshopper is known from nearly all of the United States and southern Canada, and its distribution also extends south through most of Mexico. In portions of the southeastern USA, on the coastal plain from eastern North Carolina to southern Mississippi and Louisiana, and including all of Florida, it is replaced by a very similar form, *M. propinquus* Scudder, which appears to be a separate species. These are native insects.

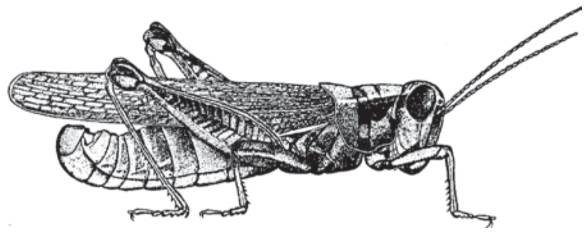
Life History

There is one generation per year throughout the range of these species, with the egg stage overwintering. Eggs hatch in late spring and adults are present from July until they are killed by heavy frost. The following information is derived from studies of *M. femurrubrum*, but likely applies equally well to *M. propinquus*.

The eggs are elongate-cylindrical in shape, and widest at the middle. They measure 4.1–4.6 mm in length and 0.9–1.5 mm in diameter. Their color is yellowish brown or creamy white. The eggs are deposited in structures called pods, which consist of two columns of eggs arranged in parallel rows. The pod, which is secreted by the female during oviposition, consists of frothy material secreted between, and covering, the eggs. The pod is a curved cylinder in form, and measures about 20–25 mm in length and 3–5 mm in diameter. It is buried in the soil, and normally contains 20–26 eggs per pod. The upper portion of the pod consists solely of froth, and the young grasshoppers chew their way through this material to escape from the soil. Eggs are often deposited among the roots of grasses and weeds, particularly along the edges of crop fields. The female can produce 300 eggs during its lifetime. These are not early-season grasshoppers. Hatching occurs about 3 weeks after hatching of twostriped grasshopper, *Melanoplus bivittatus* (Say), 2 weeks after migratory grasshopper, *Melanoplus sanguinipes* (Fabricius), and about the same time as differential grasshopper, *Melanoplus differentialis* (Thomas), with which redlegged grasshopper may co-occur. The period of hatching is extended, however, so nymphs can be found during most of the summer.

Development of the nymphal stage normally requires about 40 days, during which there usually are five to six instars. Throughout their development they are yellowish in color, but marked with a broad black stripe that extends across the face, eyes and prothorax, and onto the abdomen. They also bear a second, less discrete black stripe that is below, but parallel to, the aforementioned stripe, and that arches across the lateral lobe of the prothorax. The outer face of the femora are marked with a broad black stripe. The underside is yellowish. The hind tibiae are yellow or gray, and bear black spines. The overall body length of nymphs is 4–5.6, 6.2–7.2, 7.4–9.7, 10–15.5, and 16.5–22.5 mm for instars 1–5, respectively. Antennal segment numbers increase from 12–14 to 15–16, 17–19, 22–24, and 24–26 in the corresponding instars. In Virginia, total nymphal development times for grasshoppers displaying a total of six instars averaged 67, 42, 31, and 29 days when cultured at 26.5, 30, 35, and 38°C, respectively. Nymphs developing through seven instars required 5–10 additional days, depending on the rearing temperature. Mean instar development time was reported to be 3.6, 4.1, 4.7, 5.0, 5.8, and 7.9 days for instars 1–6 when cultured at 35°C, an optimal temperature. Nymphs change their behavior in response to temperature, with feeding commencing at 20–24°C, and nymphs moving to elevated perches to escape the heat when the air temperature or soil temperature gets high. Like most grasshoppers, they tend to remain inactive, even at high temperatures, in the absence of sunlight.

The adults are medium-sized grasshoppers, the males measuring 17–23 mm in length, and the females 18–27 mm (Fig. 9). They are reddish brown or grayish brown dorsally and yellow or yellowish green ventrally. The forewings lack distinct markings; the hind wings are colorless. The lateral lobe of the pronotum is usually marked with a distinct black area. The outer face of the hind femora is yellowish but bears an indistinct dark stripe. The hind tibiae are almost always



Redlegged Grasshopper, *Melanoplus femurrubrum* (Degeer) (Orthoptera: Acrididae), Figure 9 Adult male of redlegged grasshopper, *Melanoplus femurrubrum* (DeGeer).

deep red with black spines, and are the basis for the common name of these grasshoppers. In the male, the tip of the abdomen is rather bulbous, with the subgenital plate bearing a broad U-shaped depression apically. The cerci narrow rapidly from the base, with the distal third narrow and the tip either angled (*M. femurrubrum*) or rounded (*M. propinquus*).

The males, but not the females, of these two species are easily separated by the genitalia. In *M. femurrubrum*, the cerci are flattened at the tip, forming an acute angle dorsally. The cerci at the midpoint are relatively broad, about one-half the maximum width at the base. The furcula in this species diverge from the base and then converge distally, the space between the arms of the furcula forming a "U." In contrast, in *M. propinquus* the tips of the cerci are rounded, and the cerci are relatively narrow at the midpoint, about one-third the maximum width at the base. The furcula diverge more strongly, the space between the arms forming a "V."

Adults normally roost at night on the tops of tall grasses and weeds. Early in the morning they crawl down the plant and resume feeding when the air temperature warms, often moving along the soil in search of food. As is the case with nymphs, the adults ascend vegetation to escape high temperatures. In the evening they perch again on elevated roosts where they remain until they are warmed by sunlight in the morning. Females have a preoviposition period of 9–15 days before they commence egg laying. Redlegged grasshopper is a fairly strong flier and can fly 10 m if disturbed.

These species are polyphagous, feeding on a broad range of plants and apparently preferring a dietary mixture over a single food plant, and broadleaf plants over grasses. The preferred habitat is tall vegetation in pastures, fence rows, along irrigation ditches and roadways, and in fallow agricultural fields which have become weedy. The redlegged grasshoppers are known throughout North America for damage to crops, attacking alfalfa, barley, birdsfoot trefoil, clover, corn, lespedeza, oat, orchardgrass, soybean, timothy, tobacco, and vetch in addition to vegetables. Among the uncultivated plants eaten are aster, *Aster* spp.; Kentucky bluegrass, *Poa pratensis*; brown knapweed, *Centaurea jacea*; cinquefoil, *Potentilla argentea*; dandelion, *Taraxacum officinale*; fleabane, *Erigeron divergens*; goldenrod, *Solidago canadensis*; kochia, *Kochia scoparia*; Russian thistle, *Salsola kali*; smooth brome, *Bromus inermis*; sweet clover, *Melilotus officinalis*; wavyleaf thistle, *Cirsium undulatum*; western ragweed, *Ambrosia psilostachya*; and likely many others. The weeds fed upon most frequently in North Dakota alfalfa fields were reported to be kochia, *Kochia scoparia*; field bindweed, *Convolvulus arvensis*; awnless bromegrass, *Bromis inermis*; and foxtail, *Setaria* spp. On prairie, redlegged grasshopper ate primarily Kentucky bluegrass, *Poa pratensis*; western ragweed, *Ambrosia psilostachya*; golden aster, *Chrysopsis villosa*; tansy mustard, *Descurainia sophia*; and leadplant, *Amorpha canescens*.

Like most grasshoppers, redlegged grasshopper is favored by hot weather. Long-term periods of drought and hot weather favor population increase, especially in northern areas that normally are cooler. A certain amount of precipitation is necessary to provide adequate food for the grasshoppers, of course, but prolonged cool, wet weather, especially during the period of egg hatch, is detrimental for grasshopper survival. The late onset of winter can favor grasshopper population increase because it allows adults additional time to produce eggs.

Damage

Redlegged grasshopper is a defoliator, often removing all leaf tissue and leaving only plant stems. Lower densities leave plants ragged or tattered. Redlegged grasshopper is a common component of the grasshopper complex that affects plants growing along the margins of fields, though only causing extensive damage during periods of very high density. Redlegged grasshopper is capable of developing high densities and migratory tendencies during periods of drought, and may be found mixed into swarms of migratory grasshopper, *Melanoplus sanguinipes* (Fabricius).

Management

Liquid formulations of insecticides are commonly applied to foliage to protect against damage. Because grasshoppers rarely develop in crops, but instead invade from weedy areas, it is often the edges of crop fields that are most injured. Therefore, application of insecticide to the borders of crop fields is often adequate to protect an entire field. It is even better to apply insecticides to the developing grasshopper populations in weedy areas before they move to crops. This not only minimizes damage to crop plants, but often results in younger grasshoppers being targeted for elimination. Younger grasshoppers are more susceptible to insecticides, with large nymphs and adults sometimes difficult to kill.

Application of insecticide-treated bait is an effective alternative to foliar treatments for *Melanoplus* spp. because these grasshoppers spend considerable time on the soil where they come into contact with baits. Bait formulations are bulky and more difficult to apply than liquid products, so they are less often used, but have the advantage of limiting exposure of crops to insecticide residue and of minimizing mortality of beneficial insects such as predators and parasitoids due to insecticide exposure. Also, the total amount of insecticide active ingredient necessary to obtain control is usually considerably less when applied by bait because the grasshoppers actively seek out and ingest the toxin. Finally, for relatively expensive products that must be ingested to be effective, such as microbial insecticides, baits are the most effective delivery system.

The attractant used most commonly for grasshopper bait is flaky wheat bran, though other products such as rolled oats are sometimes suggested. No additives, other than insecticide (usually 5% active ingredient), are necessary because the wheat bran alone is quite attractive to *Melanoplus* grasshoppers. Other additives such as sawdust, water, vegetable or mineral oil, molasses, amyl acetate, salt, or sugar have been suggested, but provide little or no additional benefit over dry bran. The bait should be broadcast widely to maximize the likelihood of grasshopper contact, and should be applied while grasshoppers are in the late instars because adults ingest less bait.

Elimination of weeds within, and adjacent to, crops is the most important cultural practice, and can have material benefit in preventing damage to crop borders. However, during periods of weather when grasshoppers become numerous they may move long distances and invade crops.

Tillage is an effective practice for destruction of eggs. Deep tillage and burial are required, shallow tillage having little effect. All the crop-feeding *Melanoplus* species deposit some eggs in crop fields, especially during periods of abundance, but it is fence row, irrigation ditch, field edge, and roadside areas that tend to be the favorite oviposition sites, so tillage is not entirely satisfactory unless other steps are taken to eliminate grasshopper egg pods from these areas that cannot be tilled. Though providing suppressive effects, deep tillage is not consistent with the soil and water management practices in many areas, so may not be a good option.

Row covers, netting, and similar physical barriers can provide protection against grasshoppers. This approach obviously is limited to small plantings, and can interfere with pollination. Also, grasshoppers are capable of chewing through all except metal screening, so this approach does not guarantee complete protection.

The opportunities for biological control are limited. The microsporidian pathogen *Nosema locustae* is well studied as a microbial control agent of *Melanoplus* spp. and is available commercially. It is fairly stable, and easily disseminated to grasshoppers on bait. However, its usefulness is severely limited by the long period of time that is required to induce mortality and reduction in feeding and fecundity. Also, the level of mortality induced by consumption of *Nosema* is quite low, often imperceptible. It is best used over very large areas, not just on individual farms, and should be applied at least one year in advance of the development of potentially damaging populations.

Fungi have also been investigated for grasshopper suppression. A grasshopper strain of *Beauveria bassiana* has been effective in some trials, and *Metarhizium anisopliae* var. *acridum* has worked well for grasshopper and locust suppression in Africa and Australia, so it may prove useful for *Melanoplus* spp. Behavioral thermoregulation by grasshoppers, wherein they bask in the sun and raise their body temperatures, is potentially a limiting factor for use of fungi. Basking grasshoppers easily attain temperatures in excess of 35°C; such high temperatures decrease or even prevent disease development in infected grasshoppers. Inconsistent quality control in production of fungi also limits use of these organisms for grasshopper control.

► Grasshopper Pests in North America
► Grasshoppers and Locusts as Agricultural Pests
► Grasshoppers, Katydids and Crickets

References

Bellinger RG, Pienkowski RL (1989) Polymorphic development in relation to the life history of *Melanoplus femurrubrum* (Orthoptera: Acrididae). Ann Entomol Soc Am 82:166–171

Capinera JL, Scott RD, Walker TJ (2004) Field guide to the grasshoppers, katydids, and crickets of the United States. Cornell University Press, Ithaca, NY, 249 pp

Parker JR (1939) Grasshoppers and their control. USDA Farmers' Bulletin 1828, 37 pp
Pfadt RE (2002) Field guide to common western grasshoppers. Wyoming Agricultural Experiment Station Bulletin 912, 288 pp
Shotwell RL (1941) Life histories and habits of some grasshoppers of economic importance on the Great Plains. USDA Technical Bulletin 774, 48 pp

Red Muscardine

This term has been used to denote various mycoses of insects, caused by species of hyphomycetous fungi and characterized by the appearance of pink to brick-red colors on the body of the dying or dead hosts; certain strains of *Beauveria bassiana* are responsible for a red muscardine of silkworm larvae; *Sorosporella uvella* causes a red muscardine of cutworm larvae (Noctuidae) as well as other insects.

► Muscardine
► *Beauveria*

Red Palm Mite, *Raoiella indica* Hirst (Acari: Prostigmata: Tenuipalpidae)

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The red palm mite, *Raoiella indica* is a serious pest of coconuts, date palms and other palm species, as well as a pest of bananas, in different parts of the world (Table 4). It is also known as the coconut mite, coconut red mite, red date palm mite, leaflet false spider mite, frond crimson mite, or scarlet mite. It has long been known from southern Asia and portions of the Middle East, including India, Philippines, Mauritius, Reunion, Malaysia, Israel and Egypt. Recently it became established in the Western Hemisphere in the Leeward Islands of the Caribbean and in Florida, where it is infesting palms, banana, ginger, bird of paradise and other plants within the Musaceae. Palms are the principal host. It has now moved to South America and likely will be widespread in most of the Neotropics before long.

Description of Stages

Adult female red palm mites are red, typically with dark patches on the body dorsolaterally, and about 0.32 mm long. Males are smaller than females and taper to a point posteriorly, giving them a triangular shape. Females are more oval. Dorsal setae are present on both sexes. The body of the red palm mite does not have a striae. The first pair of dorsocentral hysterosomal setae is longer than the others; the fourth pair of dorsosublateral setae is shorter than the first pair. All dorsal body setae are slightly clublike and serrate. The larvae are reddish and sluggish. The minute eggs (0.09 mm × 0.12 mm) are oblong smooth and red in patches of 100–300, and attached to the abaxial (lower) leaf surface by a slender stalk.

Life Cycle

Under laboratory conditions, at temperatures between 24 and 26°C and 60% RH, females completed their development in 24.5 days and males in 20.6 days; adult longevity was 50.9 days for females and 21.6 days for males. Fertilized females produced an average of 22 eggs and virgin females 18.4 eggs. In Mauritius, the preoviposition period is 3 days in summer and 7 days during the winter. Females lay an average of 2 eggs per day over an average oviposition period of 27 days for a total of about 50 eggs per female. The time for development of each life stage is: egg, 6.1–6.5 days; larva, 5.7–9.5 days; protonymph, 5.4–6.5 days; and deutonymph, 4.1–10.5 days. The time required to complete the life cycle is 21–33 days. Developmental ranges are influenced by temperature, RH and host plant.

Red Palm Mite, *Raoiella indica* Hirst (Acari: Prostigmata: Tenuipalpidae), Table 4 **Host plant species of *Raoiella indica***

Plant species	Family	Distribution
Aiphanes sp.	Arecaceae	St. Lucia
Areca catechu L.	Arecaceae	Asia
Areca sp.	Arecaceae	Asia
Cocos nucifera L.	Arecaceae	Asia, Mauritius, St. Lucia, Martinique, Dominica, Trinidad, Guadeloupe, St. Martin
Dictyosperma album (Borg.)	Arecaceae	Asia
Dypsis lutescens (H. Wendl.)	Arecaceae	Asia
Phoenix dactilifera	Arecaceae	Asia, Mauritius, Israel, Egypt
Syagrus ramanzoffianum Glassman	Arecaceae	St. Lucia
Veitchia merrillii (Becc.)	Arecaceae	St. Lucia, Martinique
Licuala grandis H. Wendl.	Arecaceae	Guadeloupe
Caryota mitis Lour.	Arecaceae	Guadeloupe
Pricthardia pacifica B. C. Seem	Arecaceae	Guadeloupe
Washingtonia robusta H. E. Moore	Arecaceae	Guadeloupe
Musa spp.	Musaceae	Trinidad
Musa acuminata Colla	Musaceae	St. Lucia, Dominica
M. balbisiana Colla	Musaceae	St. Lucia, Dominica
Musa uranoscopus Lour.	Musaceae	St. Lucia
Musa x paradisiacal L.	Musaceae	St. Lucia, Dominica
Ocimum basilicum L.	Lamiaceae	Asia
Undetermined ginger	Zingiberaceae	St. Lucia
Undetermined heliconia	Heliconaceae	Trinidad
Heliconia rostrata R	Heliconaceae	Guadeloupe
Strelitzia reginae Banks	Stretlitziaceae	Guadeloupe
Alpinia purpurata Vieill. ex. Schum.	Zingiberaceae	Guadeloupe
Etlingera elatior (Jack.) R. M. Smith	Zingiberaceae	Guadeloupe

Seasonality

These mites are generally abundant in Mauritius on coconut from September to March, except when heavy rains occur during November and January. Starting in April, there is normally a decline in populations, which continues through August. In the summer, the plants appear sickly and yellowish, a condition that may be the combined result of mite feeding and dry season conditions. Population increase is positively correlated with leaf moisture, crude protein and nitrogen levels in leaves in different coconut varieties.

Dispersal

Raoiella indica disperses by wind currents and transport of infested plants or leaves. One of the most common ways of dispersal is through human activity in tourist areas where persons will come in contact with ornamental palms.

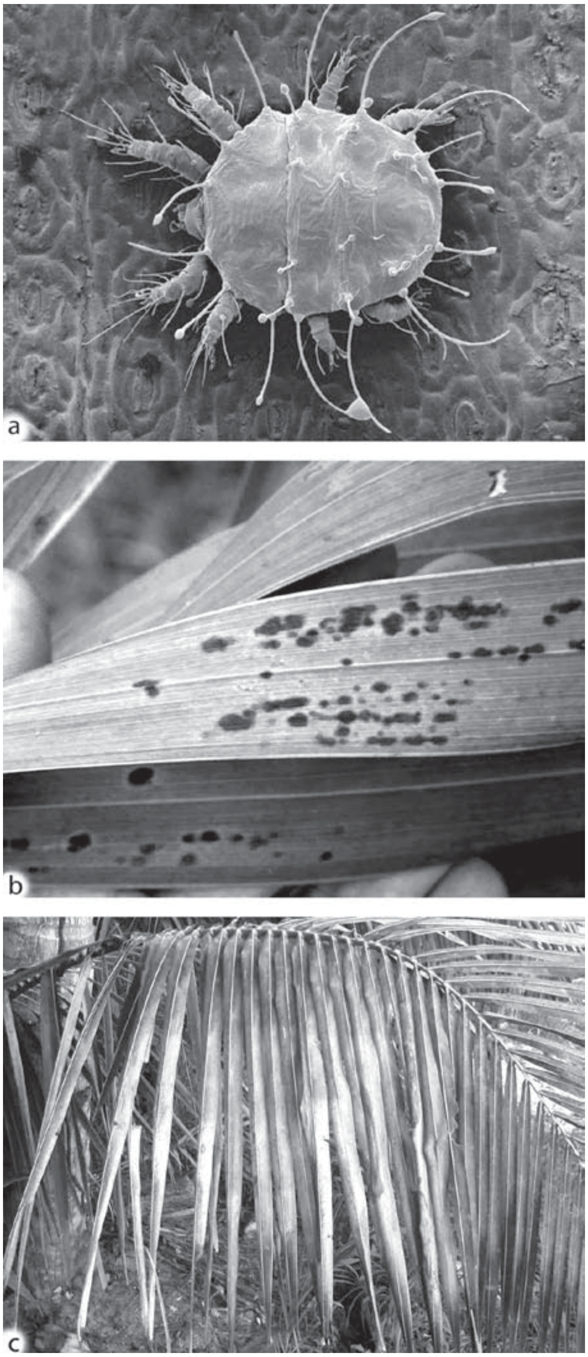
Damage

Raoiella indica lives on abaxial surfaces of coconut leaves. A higher number of mites tend to occur on the lower leaves. Mites are located in groups ranging in number from 20 to 300 individuals (eggs, larvae, protonymphs and deutonymphs). There is no data regarding within-plant distribution in other host plants. Young coconut palms are most severely injured, but mature plants also are damaged.

Extensive yellowing of lower leaves may be symptomatic of either red palm mite feeding, or any of several pests or diseases of palms and other arborescent monocots. For example, red palm mite damage has sometimes been misdiagnosed in the field as lethal yellowing, a highly prevalent disease of palms in southern Florida and various countries of the Caribbean Basin. Like the effects of red palm mite feeding, lethal yellowing infection results in extensive chlorosis of the lower leaves. However, in a very early stage of lethal yellowing disease, the emerging inflorescences become distorted and the male flowers, normally of an ivory, yellow, or orange color depending on variety, turn brown, and the coconuts of all stages of development drop from the tree. Of course, a key symptom that distinguishes red palm mite damage (Fig. 10) from lethal yellowing is the presence of dense populations of a red mite visible with the naked eye on the abaxial surfaces of older foliage. The exuviae (cuticle tissue discarded at molting) of red palm mites may be present as scaly patches on the leaf surface.

Chemical Control

Current knowledge of the effectiveness of chemical control of the red palm mite is based mostly on research in India and the Middle East. In the Middle East, insecticide applications are used in



Red Palm Mite, *Raoiella indica* Hirst (Acari: Prostigmata: Tenuipalpidae), Figure 10 **Red palm mite and damage: (a) Scanning electron microscope photograph of red palm mite (photo by Eric Erbe and Chris Pooley, USDA-ARS); (b) Spotting of coconut foliage caused by red palm mite (photo by J. E. Peña); (c) Bronzing of coconut foliage caused by red palm mite (photo by J. E. Peña).**

cases of high density of the mite when it is affecting date palm. In India, the application of neem oil sprays mixed with sulfur after a thorough cleaning of the coconut crown showed good results. The extract is sprayed from above, 5–6 times per year, and is possible with a sprayer-head attached to a long pole. The application of neem resulted in a yield increase of 25%. Parathion causes a decrease in mite density 14 days after application, followed by an increase of the mite population. Several systemic insecticides exhibited toxicity to the larvae, nymphs and adults. Phosphamidon was considered slightly superior to monocrotophos, dimethoate, formothion and demeton-methyl. However, these products are not registered to be used in coconuts or bananas everywhere.

Chemical control of other Tenuipalpidae in crops such as citrus have shown that in combination with petroleum oil, insecticides such as pyridaben, fenbutatin-oxide, dicofol or high rates of sulfur provided at least 35 days of control. Abamectin and emamectin can be used to control larvae, nymphs and adults of *Brevipalpus phoenicis*. However, abamectin was found to be slightly and moderately noxious to predacious mites, while emamectin was shown to be innocuous and slightly noxious to phytoseiids.

Natural Enemies

In India, during a survey for the indigenous predators, several predators were discovered preying on *R. indica*. The phytoseiid mite, *Amblyseius channabasavanni* and lady beetle, *Stethorus keralicus* Kapur (Coleoptera: Coccinellidae) were considered to be the most important predatory species. *S. kerlaicus* was observed feeding throughout the year on *R. indica* infesting coconut and areca palms in India. In the United Arab Emirates, there is natural control for the scarlet mite, but the natural enemies responsible for this control apparently are unknown. *A. channabasavanni* females effectively consume eggs and females of *R. indica*. Alternate food sources in the field include *Tetranychus fijiensis*, eggs and crawlers of scale insects and mealybugs that infest arecanut leaves. The field population of the predator is highest during May through June when *R. indica* populations are at their peak.

In Mauritius, the principal predator of *R. indica* in coconut plantations was *Typhlodromus caudatus* Chant (*Amblyseius caudatus* Berlese). The life cycle of this mite within a range of temperatures from 18 to 24.3°C required 15 to 6 days, respectively. Nymphs and adults of this phytoseiid can consume an average of 10.6 eggs per day and a total of 493 eggs during their active life cycle. In India, *Amblyseius longispinus* (=*Neoseiulus longispinus* Evans 1952) (Acari: Phytoseiidae) and *Stethorus parcempunctatus* and *Jauravia* sp. (Coleoptera: Coccinellidae) are important natural enemies in the area of Karnanka, while in the area of Kerala the prevalent predators are *A. channabasavannai* and *Stethorus tetranychi* Kapur. In India, *Amblyseius raoiellis* also is known to prey on *R. indica*. Nothing is known about the biology of this species. A related mite, *Amblyseius near raoiellis* has been collected in lime and mango in southern Florida fruits infested with *Brevipalpus phoenicis*. The predaceous mite *Neoseiulus longispinosus* (Evans), an old world species, was observed preying on *R. indica* in Saint Lucia. Other natural enemies reported preying on *R. indica* in the Caribbean are *Amblyseius largoensis* (Phytoseiidae), *Armascirus taurus* (Kraemer) (Cunaxidae) and *Telsimia ephippiger* Chapin (Coccinellidae: Coleoptera).

A small portion of *R. indica* mites have been observed to be infected by a fungus, possibly, *Hirsutella* spp. The tenuipalpid *Brevipalpus phoenicis* can be infected by some isolates of *Hirsutella thompsoni*.

References

Etienne J, Fletchmann CHW (2006) First record of *Raoiella indica* (Hirst, 1924) (Acari: Tenuipalpidae) in Guadeloupe and Saint Martin, West Indies. Int J Acarol 32:331–332

Gerson U, Venezian A, Blumberg D (1983) Phytophagous mites on date palms in Israel. Fruits 38:133–135

Howard FW, Moore D, Giblin-Davis RM, Abad RG (2001) Insects on palms. CABI, Wallingford, UK, 400 pp

Jepson LR, Keifer H, Baker EW (1975) Mites injurious to economic plants. University of California Press, Berkeley, CA, 614 pp

Jayaraj J, Natarajan K, Ramasubramanian G (1991) Control of *Raoiella indica* Hirst (Tenuipalpidae: Acari) on coconut with pesticides. Indian Coconut J 22:7–9

Red Palm Weevil, *Rhynchophorus ferrugineus* (Olivier) (Coleoptera: Curculionidae)

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Date palm, *Phoenix dactylifera* L. (Palmales: Palmae), is one of the oldest fruit trees in the world and is mentioned in the Qur'an and the Bible. There are approximately 100 million date palms worldwide, of which 62 million can be found in the Arab region. The origin of the date palm is uncertain. Some claim that the date palm first originated in Babel, Iraq, while others believe that it originated in Dareen or Hofuf, Saudi Arabia, or Harqan, an island on the Arabian Gulf in Bahrain.

The date palm is a perennial and can live about 150 years. The female date palm normally begins to bear dates within an average of five years from the time of planting of the offshoot. The Middle East and North Africa are the major date palm producing areas of the world.

The red palm weevil, *Rhynchophorus ferrugineus* (Olivier) (Coleoptera: Curculionidae), is the most dangerous and deadly pest of the date palm, as well as coconut, palm oil, sago and 13 other palm species.

Information on red palm weevil was first published in 1891 in India. This pest was first described as a serious pest of the coconut palm in 1906, while in 1917 it was described as a serious pest of the date palm in the Punjab, India. In 1918, red palm weevil caused serious damage to the date palm in Mesopotamia (Iraq), but no insect specimens were collected to confirm it. Red palm weevil entered and was discovered during the mid-1980s in the Arabian Gulf countries. However, it has become a most destructive pest of date palms in the Middle East.

Distribution of Red Palm Weevil

The red palm weevil occurs in the following countries: Bahrain, Bangladesh, Burma, Cambodia, China, Cyprus, Egypt, France, Greece, India, Indonesia, Iran, Iraq, Israel, Italy and Sicily, Japan, Jordan, Kuwait, Laos, Myanmar, Oman, Pakistan, Palestine, Philippines, Qatar, Saudi Arabia, Singapore, Spain, Sri Lanka, Syria, Taiwan, Thailand, Turkey, United Arab Emirates, Vietnam, and in Oceania: Papua New Guinea, Solomon Islands, Western Samoa.

Life Cycle

All stages (egg, larva, pupa and adult) are spent inside the palm itself and the life cycle cannot be completed elsewhere. The female deposits about 300 eggs in separate holes or injuries on the palm. Eggs hatch in 2–5 days into legless grubs, which bore into the interior of the palm, moving by peristaltic muscular contractions of the body and feeding on the soft succulent tissues, discarding all fibrous material. The larval period varies from 1 to 3 months. The grubs pupate in elongate oval, cylindrical cocoons made out of fibrous strands. At the end of the 14–21-day pupation period, the adult weevils emerge. Thus, the life cycle is about 4 months.

All kinds of palms are probably suitable for the development of the red palm weevil, which has been found on the following palms: coconut palm, date palm, nigbong palm, ornamental palm, palm oil, palmyra palm, royal palm, sago palm, sedang palm, sugar palm, talipot palm, and the wild date (toddy) palm.

Eggs

The eggs are creamy white in color, long and oval in shape. The average size of an egg is 2.6 mm long and 1.1 mm wide.

Larva (grub)

The full-grown larva is conical in shape and is a legless fleshy grub. It appears yellowish brown, while the newly hatched larva is yellowish white in color, with a brown head. The length of the full-grown larva is 50 mm and the width is 20 mm. The head is brown in color and bent downwards. Mouthparts are well developed and strongly chitinized, which enables the grub to burrow into the trunk. However, the grub requires a moist environment.

Cocoon

When about to pupate, the larva constructs a cocoon of fibers from the palm. The cocoon is oval in shape, with an average length of 60 mm and a width of 30 mm.

Pupa

The pupa is at first cream colored but later turns brown. The head is bent ventrally, the rostrum reaching the tibiae of the first pair of legs. The antennae and eyes are quite prominent. The elytra and wings are brought down ventrally, passing underneath the femora and tibiae of the second pair of legs, overlapping the third pair of legs and meeting in the middle of the abdomen. The average length of the pupa is 35 mm and the width is 15 mm.

Adult

The adult weevil is a reddish brown cylinder with a long prominent curved snout. It varies considerably in size and is about 35 mm in length and 12 mm in width. The head and rostrum comprise about one third of the total length (Fig. 11).

The mouthparts are elongated in the form of a slender snout or rostrum, which bears a small pair of biting jaws at the end and a pair of antennae near the base. The rostrum is reddish brown dorsally, and ventrally it is dark brown. In the male, the dorsal apical half of the snout is covered with a pad of short brownish hairs; the snout of the female is bare, more slender, curved and a little longer. The antennae consist of the scape and funicle. The eyes are black and separated on both sides of the base of the rostrum.

The pronotum is reddish brown in color and has a few black spots. These black spots are variable in shape, size and number. The elytra are dark red, strongly ribbed longitudinally, and do not cover the abdomen completely. The wings are brown in color and the weevils are capable of strong flight.

The male weevil has a tuft of soft reddish brown hairs along the dorsal aspect of the snout; this tuft is absent in the female. Also, the male produces an aggregation pheromone "ferrugineol" and/or "ferrolure" (4-methyl-5-nonanol), which is a synthetic lure used in the pheromone bucket traps.

Red Palm Weevil, *Rhynchophorus ferrugineus* (Olivier) (Coleoptera: Curculionidae), Figure 11 **Red palm weevil, *Rhynchophorus ferrugineus*, life cycle: larvae, cocoon, pupa, adult.**

Economic Importance and Damage

Normally, the red palm weevil infests palms below the age of 20 years, where the stem of the young palm is soft, juicy and easily penetrated. The weevils are destructive pests to palms.

The larvae are responsible for damaging the palm, and once they have gained access, the death of the palm generally ensues. The larvae normally never come to the surface, since they begin life inside the palm. Therefore, neither the damage nor the larvae can be seen. However, the trunk of the palm can be infested in any part, including the crown.

The damage caused by only a few larvae is astonishing. Even one larva may cause considerable damage for a young palm (offshoot). It is difficult to assess the actual loss caused by this pest, but undoubtedly it affects the production of date palms.

Methods of Control

Integrated Pest Management (IPM)

Because the red palm weevil is difficult to control with just one method, several combinations of control methods should be applied as follows:

Plant Quarantine

The transport of offshoots as planting material from infested areas can contribute to the spread of the pest. Strict quarantine at international and national levels should be applied.

Cultural Control

Field sanitation and cultural practices are some of the important components to prevent weevil infestation.

- Clean the crowns of the palms periodically to prevent decaying of organic debris in leaf axils
- Avoid cuts and injuries
- When green leaves are cut, cut them at 120 cm away from the base
- Cutting of steps in palms for easy climbing is to be avoided, as this provides sites for egg laying by weevils
- As palms affected by leaf rot and bud rot diseases are more prone to weevil infestation, they are to be treated with suitable fungicides; after that, application of an insecticide to prevent egg laying by weevils is essential
- Destroy all dead palms harboring the pest by cutting and burning

Mechanical Control

Dead palms or palms beyond recovery should be split open to expose the different stages of the pest present inside. The debris, including the outer logs and the crowns, should be burned.

Trapping Weevils

Trapping and destroying the weevils is another method to control the pest population. Trapping also is used to detect the presence of the pest in the field and also to assess the population.

The aggregation pheromone lure of red palm weevil is used to attract the weevils to the bucket traps which contain pieces of palm stem as food and a solution of insecticide.

Biological Control

No effective biological agent has been found that can be employed for the biological control of the pest.

Chemical Control

The wounds produced on palms due to cultural practices as well as anther wounds are favorite sites of oviposition by the female weevils. Treatment of such wounds by soaking them with insecticides can be an effective way to prevent red palm weevil entry into palms.

Once infestation is detected in a palm, curative control must be applied. If the infestation is in the crown, remove the affected and damaged portions and apply insecticide suspension. In case of infestation in the trunk, the infested part should be cleaned and plugged with a mixture of mud and insecticide.

Several insecticides under laboratory and field conditions are tested in order to evaluate the best insecticide that will affect the different stages of the weevil.

Training and Education

The cooperation of the farmer is essential in order to successfully implement weevil management. For any large-scale pest management program to succeed, it is imperative that farmers cooperate and become involved at the operational level. This can be achieved by making farmers aware of the seriousness of the problem and training them in various IPM skills.

References

Ajlan AM, Abdulsalam KS (2000) Efficiency of some pheromone traps for controlling red palm weevil, *Rhynchophorus ferrugineus* (Olivier) (Coleoptera: Curculionidae), under Saudi Arabia conditions. Bull Ent Soc Egypt Econ Ser 27:109–120

Ajlan AM, Shawir MS, Abo-El-Saad M, Rezk MA, Abdulsalam KS (2000) Laboratory evaluation of certain organophosphorus insecticides against the red palm weevil, *Rhynchophorus ferrugineus* (Olivier). Sci J King Faisal Univ (Basic Appl Sci) 1:15–26

Faleiro JR (2006) A review of the issues and management of the red palm weevil *Rhynchophorus ferrugineus* (Coleoptera: Rhynchophoridae) in coconut and date palm during the last one hundred years. Int J Trop Insect Sci 26:135–154

Hallett RH, Gries G, Borden JH, Czyzewska E, Oehlschlager AC, Pierce HD Jr, Angerilli NPD, Rauf A (1993) Aggregation pheromones of two Asian palm weevils, *Rhynchophorus ferrugineus* and *R. vulneratus*. Naturwissenschafen 80:328–331

Murphy ST, Briscoe BR (1999) The red palm weevil as an alien invasive: biology and the prospects for biological control as a component of IPM. Biocontrol News Inf 20:35N–46N

Nirula KK (1956) Investigations on the pests of coconut palm. IV. *Rhynchophorus ferrugineus* F. Indian Coconut J 9:229–247

Red Ring of Coconut Palms

This insect-transmitted disease of palm trees is caused by nematodes.

► Transmission of Plant Diseases by Insects

Redtenbacher, Ludwig

Ludwig Redtenbacher was a noted Austrian entomologist, and a noted coleopterist. His most important contribution was the Coleoptera treatise of "Fauna Austriaca." He also served as director of the Royal Vienna Zoological Museum. He died in 1876 at the age of 63.

Reference

Anonymous (1876) Dr. Ludwig Redtenbacher. Entomologist's Mon Mag 12:238

Reduviidae

A family of bugs (order Hemiptera). They sometimes are called assassin bugs, ambush bugs, or kissing bugs.

► Bugs
► Assassin Bugs, Kissing Bugs, and Others

Red Water Fever

This tick-transmitted disease is also known as Texas cattle fever and splenetic fever.

► Piroplasmosis

Reed, Walter

Reed was born on September 13, 1851, in Belroi, Virginia, USA. Initially, he studied classics at the University of Virginia, but soon became interested in medicine and graduated as a doctor of medicine in 1869 at the age of 18. He then obtained a second degree at Bellevue Medical College in New York and held several hospital posts as a physician. By 1875, however, he elected to join the military and was commissioned a first lieutenant in the Army Medical Corps.

Reed married in 1876 and transferred to Fort Lowell in Arizona. For 18 years he moved from station to station on the western frontier, but in 1889 he was appointed attending surgeon and examiner of recruits at Baltimore, Maryland. Here he gained access to Johns Hopkins Hospital, and was able to enroll in courses in pathology and bacteriology. In 1893, he was appointed a major in the Medical Corps. In 1898, he was appointed chairman of a committee to investigate the spread of typhoid fever in military camps, which he found to be caused by contact and by flies, and this success led to his interest in the problem of yellow fever.

Yellow fever, which likely was introduced along with slaves from Africa, plagued the port cities of the western hemisphere in the nineteenth century. It was called "yellow jack" and was the most dreaded and deadly disease of the time. The epidemiology of this disease was unknown, but generally it was thought that the disease was spread on articles of bedding and clothing. However, in 1881 the Cuban physician Carlos Juan Finlay began to promote the idea that the disease was spread by mosquitoes. The role of mosquitoes remained unproven, even though the Italian bacteriologist Guiseppe Sanarelli claimed in 1896 that he had identified the causative organism, which he called *Bacillus icteroides*.

With the commencement of the Spanish-American War, there was concern about the health of American troops during the summer months when yellow fever was prevalent in Cuba. In 1900, Reed was deployed to Cuba, where he worked with Finlay and others to identify the cause of yellow fever. They quickly discarded the idea that it was caused by bacteria, and it would not be shown for another 20 years that a virus was involved. Finlay persisted in his belief that the mosquito *Aedes aegypti* was the vector, but there was no direct proof of its involvement. The research team agonized over using human subjects to assess the role of mosquitoes in yellow fever transmission because it was so deadly, so they decided to test their theories on themselves before subjecting others to exposure. After allowing for an incubation period for the virus (mosquitoes had to ingest the virus within three days of the patient becoming inoculated, and then required another 12 days before they could transmit the disease), they were able to accomplish transmission by mosquitoes. Unfortunately, some of the research team became ill and died, as did subsequent volunteers. They also demonstrated that dirty bedding and foul air were not implicated in spread of the disease.

It fell to others, particularly William Gorgas, to implement sanitation practices that eliminated mosquitoes and alleviated the threat of yellow fever transmission, but history awards Reed most of the credit for identifying the importance of mosquitoes. In truth, the idea that mosquitoes were involved was not a novel idea and did not originate with Reed. However, it was the team led by Reed that eventually established the relationship of mosquitoes to yellow fever, and stimulated the sanitation practices that would eventually largely eliminate the threat of yellow fever. For example, in 1901 only 18 people in Havana succumbed to yellow fever, whereas thousands had died in earlier years.

Major Reed returned to the USA and to great acclaim. He was awarded honorary degrees from Harvard University and the University of Michigan. Perhaps most significantly, the medical facility now known as the Walter Reed Army Medical Center was named in his honor. Walter Reed died on November 23, 1902, at Washington, DC, only two years after his stunning discoveries in Cuba.

► History and Insects
► Yellow Fever
► Gorgas
► William Crawford

References

Pierce JR, Writer JV (2005) Yellow jack – how yellow fever ravaged America and Walter Reed discovered its deadly secrets. Wiley, Hoboken, NJ, 278 pp

Writer JV (1997) Did the mosquito do it? Am Hist 31:44–52

Reflex Bleeding (Autohemorrhage)

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Insects are organic chemists without equal among the terrestrial metazoa. Chemicals used by insects may be acquired by *de novo* synthesis (autogenously), or exogenously by dietary sequestration of secondary compounds from plants, insect prey, or parental transfer; they may even be appropriated from endosymbionts. Not surprisingly, insect defensive chemical ecology is a field of both great breadth and depth, and its study incorporates anatomy, ethology, physiology, development, phylogeny, and predator-prey and plant-insect ecology, and has been the focus of several extensive review articles. The biosynthetic pathways by which many insects come to possess their vast chemical inventory are increasingly well known, and many powerful experimental tools and techniques are available for analyzing compounds and their synthesis, such as gas chromatography, HPLC, NMR, mass spectroscopy, PCR, and radioisotope label tracking.

The manner in which insects present their defensive compounds is also diverse. For a chemical defense to function well, the insect needs to present to a potential attacker either a toxic chemical or some evidence that they contain a toxin of some kind. Ideally, this will happen before the prey insect is wounded or killed. Frequently, chemical defenses co-occur with aposematic coloration, and insects so protected often make no attempt at being inconspicuous while feeding or mating. Insects that defend themselves by actively presenting the toxic compound either by a device or behavior are known as "phanerotoxic." Reflex bleeding, or autohemorrhage, combines both elements into one physiological and behavioral phenomenon. The insect presents hemolymph, through integumental ruptures or specialized cuticular structures, compounds that are either chemically or mechanically repellent to the attacker.

A wide diversity of defense mechanisms has fallen, perhaps overly loosely, under the term reflex bleeding. Charles Hollande, in the early 1900s, was one of the first to bring order to the accumulating evidence of secretion-based defenses in insects. Even though his work was thorough and well illustrated, a number of phenomena that didn't strictly involve hemolymph were treated as reflex bleeding. While Cuenot (1894) was the first to use the term "reflex bleeding/blood" (saignée [saignement] réflexe), Hollande was the first to apply the term "autohemorrhage" (Autohémorrhée). Part of the terminological problem is due simply to the vast diversity of behaviors and physiologies possessed by insects; a single term is not likely to capture the defense response of both a stonefly and a meloid beetle. In some cases, such as in some sawflies and chrysomelids, the basic phenomenon will involve only glanduliferous products, regions where glandular products may mix with hemolymph upon release, or a genuine release of hemolymph through a deliberately made tear in the cuticle.

Thus far, only four, or possibly five (a questionable example from Lepidoptera), orders of insects contain taxa known to engage in reflex bleeding as a defense mechanism. Why the phenomenon has not evolved more often is a puzzle in its own right, but may be due partly to the fact that a series of anatomical, behavioral, and physiological processes are involved, and "coordinating" them into one phenomenon may not have happened often. Also, using hemolymph as a defense mechanism is metabolically expensive, and it is possible that hemolymph-mediated chemical defense represents an "evolutionary stage." In many groups where reflex bleeding is known, related lineages rely entirely upon glanduliferous secretions, perhaps reflecting evolution away from a defense method that includes the extravagance of hemolymph. Overall, the phenomenon might be more widespread but unrecognized, as indicated by the recent observation of bleeding in Cercropidae: Homoptera by Peck, discussed below.

Reflex Bleeding in Plecoptera

Experimental work on adults of the stonefly species *Pteronarcys proteus* Newman (Pteronarcidae) and *Peltoperla maria* Needham and Smith (Peltoperlidae) revealed that these species bleed from the intersegmental membrane of the coxo-trochanteral and tibio-femoral joints when disturbed. The liberated fluid is yellow-orange, contains hemocytes, spreads quickly, and coagulates quickly after contact with an attacker. Cursory chemical assays performed on the hemolymph for known defensive volatile compounds failed to identify any, and the hemolymph was not found to be distasteful to either ants or the investigator. When harassed by ants in experimental conditions, the stoneflies exuded hemolymph from the nearest affected leg. Hemolymph contact with ant mouthparts and antennae elicited a "head-plowing" behavior, presumably in an attempt to rid the body of hemolymph, wherein the ants plowed their heads into the substrate. This behavior actually enhanced coagulation rate and increased the spread of hemolymph over the body.

Defense is apparently achieved by the mechanical properties of coagulating blood, and perhaps also by the mode of delivery. In *Pteronarcys*, the hemolymph can be expelled so forcibly that it makes an audible popping sound, spraying fluid up to twenty-five centimeters. Even though the fluid was not repellent to mice, they were noticeably "startled" by the popping sound. The anatomical or physiological basis for autohemorrhage was not clarified, but is presumed to be increased hemolymph pressure that causes the intersegmental membrane to rupture.

Reflex Bleeding in Homoptera: Cercopidae

Reflex bleeding was recently reported from forty-two species of neotropical froghoppers in the tribes Tomaspidini and Ischnorhinini, adults of which were able to exude hemolymph from their pretarsal pads. The species examined had identifiable lines of weakness in the membrane of the pretarsal pad, and rupture along the lines of weakness was apparently caused by increased hemolymph pressure generated by contraction of the abdomen. No hemolymph was sprayed from the wound, which instead formed a globule maintained by surface tension. Staged encounters with predatory taxa such as ants (*Solenopsis* sp.), beetles (*Paederus* sp.), spiders (Agelenidae sp.), and anole lizards (*Anolis* sp.) failed to demonstrate any chemical or mechanical benefit to the cercopid from the reflex blood, and in almost all cases the froghoppers were acceptable prey. Autohemorrhage in this instance might serve as a startle mechanism that is functionally linked to the cercopid's tremendous jumping ability.

Reflex Bleeding in Lepidoptera

A baculovirus-induced pathology in *Heliconius himera* (Nymphalidae) was recently described as "reflex bleeding." Typical baculovirus-mediated pathology causes the caterpillar to liquefy. Viral genes encoding chitinases and proteases that are transcribed by the host cause the integument ruptures, which releases infective occlusion bodies (OB's) into the environment and makes them available for consumption by another host. In this case, the virus caused a slow release of OB's from hemolymph, delivered through cuticular spines after slight mechanical disruption, and was thus considered a type of reflex bleeding. Whether this phenomenon shares any of the main properties of reflex bleeding is open for debate, because rupture in this case is defensively moot, with the moribund insect apparently receiving nothing of defensive value from rupture.

Reflex Bleeding in Hymenoptera: Symphyta

Sawfly larvae are often protected by chemicals sequestered from their food, such as the terpenoids that diprionids and pergids regurgitate when harassed. This alone is an effective defense when multiplied by the dozens of nest-mates that may be feeding in an aggregation. However, only larvae from the tenthredinid subfamilies Allantinae, Blennocampinae, and Selandriinae are known to bleed reflexively when disturbed. *Athalia rosae* (L.) (turnip sawfly; Allantinae) is a well-studied model for the chemical, ecological, and anatomical attributes of reflex bleeding. Turnip sawflies and many other specialists sequester glucosinolates (e.g., sinalbin, siningrin, and glucobarbarin) from the cruciferous (Brassicaceae) plants on which they feed, and increase the concentration of these chemicals in their hemolymph well above that found in the leaves. The glucosinolates may be transferred unmodified through the pupal and into the imaginal stage. Experiments with *Myrmica rubra* worker ants and foraging yellowjacket *Vespula vulgaris* (L.) demonstrated that the reflex fluid significantly deterred predator foraging activity.

Experiments with species in the blennocampine tribe Phymatocerini led to the "easy bleeding-harmful hemolymph" hypotheses, which link the degree to which the integument is prone to rupture with the degree of hemolymph repellency, and remarkably good correlation was found between these variables. Scanning electron and light microscopy analysis showed that there was also a correlation between the density and distribution of "spider-like" microstructures and the propensity of the integument to rupture easily.

Reflex Bleeding in Coleoptera

Lampyridae

Lampyrids exude a sticky milky fluid from their elytra and pronotum when disturbed. There is clearly a mechanical-defensive role for the exudate, and staining and amino-acid analysis demonstrated that the fluid was identical in composition to the hemolymph. Lampyrids experimentally challenged by the ants *Pogonomyrmex badius* (Latreille) and *Crematogaster atkinsoni* (Wheeler) were able to reflex bleed repeatedly from regions proximate to the attacked area. The basis for the effectiveness appeared to be the coagulation mechanism, which developed quickly as the blood was smeared between the ants' mouthparts, legs, and antennae; affected ants immediately stopped their attack and engaged frantically in cleaning activities.

Light and electron microscopic examination of areas prone to bleeding, the elytral and pronotal margins and region around the antennal sockets, revealed that the bleeding sites are located in small, scattered, shallow depressions where the cuticle is very thin, and hydrostatic pressure seems to be responsible for forcing blood to rupture the integument. *Photinus pyralis* seems capable under experimental conditions of bleeding itself to death when repeatedly provoked. Further protection is provided by chemical constituents that impart a strong smell and repellent taste sufficient to deter many vertebrate predators. However, deterrence is not absolute and many invertebrate and some vertebrate predators will accept lampyrids as prey.

In a study of *Photinus* blood, steroid derivatives were found to be the major chemical repellent. These compounds, called lucibufagins, were shown by NMR and mass spectroscopic analysis to be similar to bufadienolides, previously known only from bufonid toads and some plants. Experimental manipulations with thrushes demonstrated that both whole *Photinus* specimens and extracts of lucibufagin applied to otherwise palatable *Tenebrio* larvae were rendered unacceptable. It is unlikely that *Photinus* synthesize lucibufagins *de novo*, because insects in general are unable to synthesize sterol rings, but instead modify existing cholesterol derivatives through additions to the backbone. *Photuris* sp. females are infamous "femmes fatales" that engage in aggressive mimicry with *Photinus* sp. males, which are able to synthesize lucibufagins. Male *Photinus* sp. respond to the flash signal of female *Photuris* sp., whereupon they are killed and eaten by the female. Females gain not only nutrients for egg provisioning, but also lucibufagins that enhance their defenses.

Lycidae

Lycids are related to lampyrids but do not appear to have the same mechanisms as lampyrids, even though they synthesize or sequester several toxic compounds. Many, such as *Metriorrhynchus rhipidius*, are aposematically colored species that feed openly in large aggregations on early summer flowers. Experiments suggest that lycids participate in an extensive Müllerian mimicry group, involving other families of beetles (e.g., Cerambycidae, Buprestidae, and Meloidae) and other insects (certain flies and moths). The basis for the mimicry is believed to revolve around offensive odorant and taste chemicals, such as substituted quinolines, dihydromatricariate, and 3-phenylpropanamide. The claim that lycids engage in reflex bleeding as part of the defense strategy is less clear than in other beetle families, because the liberated fluid was not unequivocally demonstrated to be hemolymph. The polyyne dihydromatricaria acid, a principal component of the fluid, is also produced by *Chauliognathus lecontei* Champion (Cantharidae), in which species it is released from dedicated defense glands and contains no hemolymph. Given that Cantharidae and Lycidae are thought to be closely related, it is open for debate whether the co-occurrence of dihydromatricaria is due to a genuine, and interesting, difference in delivery mechanism, or the result of a glandular secretion inadvertently contaminated during experimental analysis with hemolymph.

Chrysomelidae

Many of the chrysomelids examined to date contain a variety of compounds that are either toxic or repellent. Larval chrysomelids, which often feed in exposed locations, are particularly vulnerable to predators. Their defensive repertoire involves the sequestration and modification of cardiac glycosides (*Chrysolina*), steroid-derived cucurbitacins (Galerucinae), triterpene saponins (*Doryphorina*), and salicylaldehydes (larval *Chrysomelina*). They also autogenously synthesize pyrrolizidine alkaloid *N*-oxides (*Oreina* sp., *Platyphora* sp.), methylcyclopentanonid monoterpenes ("iridoids," *Chrysomelina*), and modified amino acid moieties of glucosides (adult *Chrysomelina*).

Defensive reflex bleeding by *Diabrotica undecimpunctata* Jac. (spotted cucumber beetle) larvae effectively deterred foraging *Solenopsis* sp. ants. Exudate, containing cucurbitacins, is produced from ruptures in the cervical and intersegmental membranes between the last two abdominal segments. The basis for defense, however, seems to be essentially mechanical. Attacking ants could become so entangled by the coagulating hemolymph that they perished, and experiments with mice demonstrated that they were non-toxic.

Larvae of the chrysomelid *Agelastica alni* (L.) (Galerucinae, Sermylini) reflexively bleeds a mixture of both hemolymph and exocrine glandular secretion. When molested, *Agelastica* larvae evert a cuticular sac-like structure that normally resides inside dorsolaterally located tubercles on abdominal segments 1–8. Examination of the exudate demonstrated that hemocytes were present. Examination of the structures at the blood release site showed that muscles and a glandular cell are associated with the cuticular sac.

The majority of chrysomelid species do not reflexively bleed but still sequester toxic or deterrent compounds in their hemolymph for permanent storage or as an intermediate step before delivery to specialized glands. Indeed, the line between hemolymph fluids that are reflexively bled or released under slight trauma can be thin, as illustrated previously by the "easy bleeding" Symphyta larvae. The phenomenon almost certainly is more widespread than currently recognized.

In chrysomelids, in particular, the distinction between purely glanduliferous secretions, reflex blood compounds, and other delivery modalities becomes complicated. Variation within the single subfamily Chrysomelinae is extensive, with reflex bleeding also known from buccal sites (e.g., *Timarcha* sp., in this species the fluid contains anthraquinones). Bleeding in this case appears to be partly contingent on the age of the adult insect and degree of membrane sclerotization.

Meloidae and Oedemeridae

Meloid beetles synthesize the primary defensive compound cantharidin (from Kantharos (Gr.) = beetle), and a tremendous amount of information on the biosynthetic and ecological aspects of cantharidin is available. Meloids share affinity with oedemerids and stenotrachelids, but oedemerids seem to be the only group other than meloids to synthesize cantharidin.

Use of "blister beetles" in folk medicine is ancient, and work with Meloidae began relatively early in the history of entomology. As early as 1810, pure cantharidin could be extracted from *Lytta vesicatoria* L. It was much later (1896) that reflex bleeding was first proposed as a putatively defensive phenomenon in *Meloe proscarabeus* L., which exudes an oily fluid from tibio-tarsal joints when disturbed.

Biosynthetic and ecological studies demonstrate that cantharidin synthesis forms a key component in an extensive ecological web of predator-prey interactions and courtship behavior. Cantharidin and cantharidin derivatives are synthesized endogenously by the condensation of three isoprenoid units to form the C_{15} sesquiterpene farnesol, followed by extensive degradation to yield the monoterpene anhydride. Cantharamides can also be extracted from meloids, wherein the anhydride oxygen is replaced by a basic amino-acid moiety. Palasonin, a cantharidin-like molecule, has also been isolated from meloids, clerids, and staphylinids, but previously had been known only from *Butea frondosa* Roxb. (Fabaceae). Palasonin is structurally similar to cantharidin, but experiments revealed that palasonin was not sequestered from the plant. The occurrence of cantharidin and palasonin in clerid and staphylinid beetles is believed to be due to the canthariphilous habits of many species in those families.

The bionomics of cantharidin synthesis of *Epicauta funebris* Horn (ebony blister beetle) from egg hatch through adulthood has been traced, and reveals that cantharidin has an important and complicated role in *E. funebris* biology. Triungulid larvae, which hatch from the egg with low cantharidin levels, gradually increase cantharidin concentrations 10^{-2} to 10 μg per individual over five instars. Cantharidin synthesis resumes only in imaginal males, wherein a so-called "cantharidin kidney" sequesters cantharidin in high quantities. Females, which quickly lose their endogenous supply of cantharidin, are "rearmed" during copulation as part of the males' spermatophore. Males replenish their supply after several days, and the females, depending on the species, may or may not pass significant amounts to the eggs.

Both larvae and adults are protected by cantharidin. Larvae store the chemical in the alimentary canal and regurgitate cantharidin in a milky, white fluid when disturbed. Adult males can store large quantities of cantharidin and synthesize several hundred milligrams per day. After 60–90 days they may possess >15 mg of cantharidin, or >20% of their dry body mass.

Reflexively bled cantharidin is broadly effective at deterring predators from an attack. *Pogonomyrmex occidentalis* (Cresson) ants quickly abandon an attack and the ants remove the beetle from the colony area while it is in a catalepsis. Ants and the predatory beetle *Calosoma prominens* (LeConte) engaged in cleansing behaviors in an attempt to remove the oil from their antennae and mandibles. Experiments with cantharidin extract revealed that cantharidin is a feeding deterrent at extremely low concentrations, making sugar water unpalatable to *Formica exsectoides* (Forel) ants at a concentration of 0.77×10^{-5} M.

Many species of insects actively seek cantharidin and incorporate it into one or more of their life-history traits, and some seem to use it as a proxy aggregation pheromone. However, most canthariphilous insects use cantharidin for their own protection or during and after courtship. Male *Schizotus pectinicornis* (L.) (Pyrochroidae) acquire dietary cantharidin in an unknown manner and transfer it to females during copulation. Females then transfer small amounts to the eggshells. *Neopyrochroa flabellata* (Fabricius) uses cantharidin during courtship, with males acquiring dietary cantharidin and advertising this fact to females during courtship displays. A frontal interocular cleft is used for cantharidin display, which, via secretion from a cephalic gland, is laced with previously ingested cantharidin. Females are able to gauge male quality by sampling from this cleft, and if they deem the male suitable, the female receives a large supply of cantharidin as part of his spermatophore. If they accept the mate, they distribute the cantharidin to their eggs, which become significantly protected from attack.

Coccinellidae

Coccinellid reflex bleeding, the ecological role that this behavior plays, and the pharmacological properties of the chemicals within the blood, are now well understood. The presence of hemocyte cells in reflex fluid has been documented in seven-spotted lady beetle, *Coccinella septempunctata* L., and the Mexican bean beetle, *Epilachna varivestis* Mulsant, and is presumably widespread in the family. Reflex bleeding in adults is restricted to the tibio-femoral joints (typically to the leg nearest the provocation) but continued attack will elicit autohemorrhage from other joints and prompt thanatosis. Many larvae possess extensively branched spines along their dorsum and can discharge blood from the tips of the spines when touched. For both larvae and adults, hemolymph functions as both a mechanical and chemical deterrent, and causes ants to frantically clean coagulating blood from their mouthparts, legs, and antennae. Larvae and adults were able to withstand a significant but undetermined amount of fluid loss and recover fully.

Epilachna varivestis hemolymph contains euphococcinine ($C_9H_{15}NO$), a homotropane alkaloid, which provides varying degrees of protection from attacking ants and spiders. Feeding tests with *Monomorium pharaonis* (L.) ants demonstrated that euphococcinine renders sugar solutions unpalatable at a concentration at 10^{-2} M, which is roughly equivalent to the concentration in reflex blood (−1.5 μg/mg body weight). *Hyperaspis trifurcata* Schaeffer larvae sequester unmodified carminic acid, which is produced by their prey, *Dactylopius* spp. (cochineal bugs) (Homoptera: Coccidae).

Coccinellids are also excellent alkaloid synthesizers, with an ever increasing list of alkaloid derivatives appearing in the literature. A curious example of chemical convergence between coccinellids and cantharids is that the coccinellid alkaloids precoccinelline (*C. septempunctata*) and hippodaminae (*Hippodamia convergens* Guérin-Méneville, convergent lady beetle) are also synthesized by *Chauliognathus pulchellus* (Macleay). The piperidine derivative 3-hydroxypiperidin-2-one appears to be an extremely potent component of *Harmonia axyridis* (multicolored Asian lady beetle) hemolymph, and is chemically similar to the venom of *Solenopsis invicta* (red imported fire ant).

A major group of defensive compounds are the lactone-derived class of "macrocyclic polyamines," a group so diverse within even one insect (*E. varivestis*) that it has been described as a type of "combinatorial chemistry." NMR experiments on pupal *E. varivestis* hemolymph revealed an entire class of previously unknown compounds that is based on cyclic oligomerization of five, six, or seven units of 10-(2-hydroxyethylamino) undecanoic acid. Synthesis of these molecules, named polyazamacrolides (PAML's), starts with L-alanine. The macrocyclic polyamines can reach massive ring sizes consisting of more than 98 members of the 5-, 6-, or

7-(2-hydroxyethylanino) alkanoic acids, each of which is incorporated randomly into the ring.

Evolution of Reflex Bleeding

Several considerations of evolutionary significance are raised by the phenomenon of reflex bleeding, whether the hemolymph released is laced with toxic compounds or not. As noted above, there may be an evolutionary "thin line" between integument that is disrupted easily by a probing predator and one that is predisposed to rupture by minimal force, perhaps provided by increased hemolymph pressure. An obviously maladaptive situation arises if the integument is so prone to rupture that any environmental insult results in a tear. Physical properties of the integument underlie the tendency to tear, but a hormonal or nervous interaction might allow the insect to limit rupture only to those circumstances where it would be beneficial.

Convergence seems to underlie the phenomenon of reflex bleeding from the leg. With the exception of the cercopids that bleed from the pretarsal pad membrane, the locus of rupture is the tibio-femoral joint (coccinellids, meloids, *Pteronarcys proteus*, *Peltoperla maria*). At least for coccinellids and meloids, reflex bleeding is linked with thanatosis, or feigning death. This behavior, with the legs pulled tightly in to the body, might have preceded integument rupture, in this case as one component in an exaptational suite of characters. A common thread in the published reports is the *expectation* that increased hemolymph pressure is responsible for tearing the leg intersegmental membrane, but such a mechanism is largely unverified. In the cases where morphological features suggestive of hemolymph-pressure mediated rupture do occur (e.g., Cercopidae), no other anatomical structures (such as accessory pulsatile organ or muscle) responsible for causing the increased pressure has been identified.

A second component, one nearly an *a priori* condition for reflex bleeding to be adaptive, is an efficient coagulation mechanism that reduces blood loss. Rapid coagulation is always associated with generalized reflex bleeding and is a non-trivial defense even in the absence of toxic compounds. Hemolymph-coagulating mechanisms in insects, coupled with integument repair (and wound repair in general) also may be involved in the exaptational puzzle that engendered the apparent repeated evolution of the phenomenon. The prophenol oxidase cascade is apparently a key physiological process. Another convergent phenomenon of an insect under attack is the ability to localize the hemorrhage to the region of insult, generalizing to more appendages or greater integument rupture only under relentless provocation. Because hemolymph is a metabolically expensive product and insects rely largely on hydrostatic integrity, minimizing fluid loss would be adaptive. At least in the case of the sawfly *Athalia rosae*, the larva can "suck" back the hemolymph that has bled.

An outstanding puzzle that also has received little attention in the literature is the mechanism employed by insects sequestering toxic chemicals to avoid autointoxication, especially those that circulate toxins in the hemolymph. For instance, cantharidin is a potent toxin that binds to protein phosphatase 2A, a metabolic constituent of all eukaryote cells. Presumably a mechanism prevents cantharidin from disrupting this system. A corollary to this question is similarly unanswered: what underlies the ability of a predator, or exploiter of the toxin as a resource, to avoid intoxication?

Perhaps most interesting is the evolution of an entire ecology involving the acquisition of the active compounds. Lampyrids, coccinellids, and especially meloids, participate in an extensive ecological economy where defensive compounds are the currency in demand. Insects with canthariphilous habits are known from four orders and six families, especially the beetle families Anthicidae and Pyrochroidae, and mirids in the genus *Hadronema* predominating. In many cases, cantharidin may serve as an aggregation pheromone, but why so many species would convergently use an obscure chemical with a restricted distribution in insects and no known plant origin is puzzling in its own right. Bryocorinae mirids are known to be "parasitic" on meloids, several species of which pierce the beetle's membranes and suck cantharidin-containing hemolymph. Other insects that are either predatory or parasitic on cantharidin-laden meloids are *Atrichopogon* midges (Ceratopogonidae) and *Pedilus* beetles (Pyrochroidae: Pedilinae).

References

Benfield EF (1974) Autohemorrhage in two stoneflies (Plecoptera) and its effectiveness as a defense mechanism. Ann Entomol Soc Am 67:739–742.

Boevé J-L, Ducarne V, Mertens T, Bouillard P, Angeli S (2004) Surface structure, model and mechanism of an insect integument adapted to be damaged easily. J Nanobiotechnol 2:10–21

Bünnige M, Hilker M (1999) Larval exocrine glands in the galerucine *Agelastica alni* L. (Coleoptera: Chrysolmelidae): their morphology and possible functions. Chemoecology 9:55–62

Carrel JE, McCairel MH, Slagle AJ, Doom DP, Brill J, McCormick JP (1993) Cantharidin production in a blister beetle. Experientia 49:171–174

Eisner T, Goetz MA, Hill DE, Smedley SR, Meinwald J (1997) Firefly "femmes fatales" acquire defensive steroids (lucibufagins) from their firefly prey. Proc Natl Acad Sci 94:9723–9728

Glisan-King A, Meinwald J (1996) Review of the defensive chemistry of coccinellids. Chem Rev 96:1105–1122

Hay-Roe MM, Boucias DG, Shapiro AM, Becnel JJ (2003) A newly discovered baculovirus induces reflex bleeding in the butterfly *Heliconius himera* (Nymphalidae: Heliconinae). J Invertebr Pathol 84:59–62

Laurent P, Braekman J-C, Daloze D (2005) Insect chemical defenses. Top Curr Chem 240:167–229

Peck DC (2000) Reflex bleeding in froghopppers (Homoptera: Cercopidae): variation in behavior and taxonomic distribution. Ann Entomol Soc Am 93:1186–1194

Young DK (1984) Field records and observations of insects associated with cantharidin. Great Lakes Entomol 17:194–199

Refuge (pl., refugia)

An area, usually untreated with insecticides, where insects can be preserved. This term usually is used in the context of preserving beneficial insects or pesticide susceptible insects.

Regeneration

Regrowth of a portion of the body (usually legs in arthropods) that has been lost through injury or autotomy (deliberate shedding of the body part).

Regenerative Cells

Cells found in the midgut that gradually grow and replace midgut cells that have been lost through age, wear, or other damage.

Regulated Area

An area into which, within which, and/or from which plants or animals, plant or animal products, or other regulated articles are subjected to regulatory measures in order to prevent introduction and/or spread of regulated pests.

► Regulatory Entomology

Regulation of Sex Pheromone Production in Moths

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Pheromones are chemicals secreted to the outside of the body to influence the behavior of other individuals, generally within the same species. Sex, aggregation and alarm are some of the common pheromones in insects. Sex pheromones are produced by individuals of one sex, to attract from a distance, members of the opposite sex for mating. On the other hand, contact sex pheromones present in some insects do not elucidate long range attraction, but help in keeping the pairs together thereby facilitating mating. Most species of moths are nocturnal in habit with all the essential activities confined to the dark period of the day. Communication between sexes is almost exclusively mediated through sex pheromones, usually released by the female.

It appears that attraction between sexes in moths had been observed as early as 1690. However, the first insect sex pheromone to be chemically identified was that of the female silkworm, *Bombyx mori*, in 1959. It took 20 years and 500,000 female abdomens to identify this pheromone. With introduction of analytical methods such as high pressure liquid chromatography, gas chromatography and combined gas chromatography and mass spectrometry, it is now possible to identify a pheromone from as few as 1–10 moths. Most moth pheromones consist of olefinic aldehydes, alcohols, or acetates with 10–20 carbon atoms and one or more sites of unsaturation. The pheromones may consist of a single compound, a specific blend of geometric isomers or a mixture of several components, produced in very small (nanogram) quantities in specialized glands or cells generally located on the telescoping ovipositor of the female. The act of releasing pheromones is commonly referred to as "calling."

Most lepidopteran sex pheromones are synthesized de novo from fatty acids corresponding in chain length, double bond position, and stereo chemistry to the type of pheromone produced. Biosynthesis of these acids takes place specifically in the pheromone gland rather than elsewhere in the insect. Typically, the starting material is an acetate that is converted to palmitic acid through fatty acid synthetase; however, preformed acids, such as oleic, linoleic, or linolenic acid, as well as amino acids, may be directly utilized by several species. Subsequent steps are controlled by two key enzyme systems: the microsomal β-oxidation, which results in limited chain shortening by two carbons, and a Δ 11 desaturase, which yields acids with unsaturation at the 11 to 12 position. In the corn earworm, *Helicoverpa zea*, Z-11-hexadecenal the major pheromone component (more than 90%), is produced by oxidation of the corresponding alcohol.

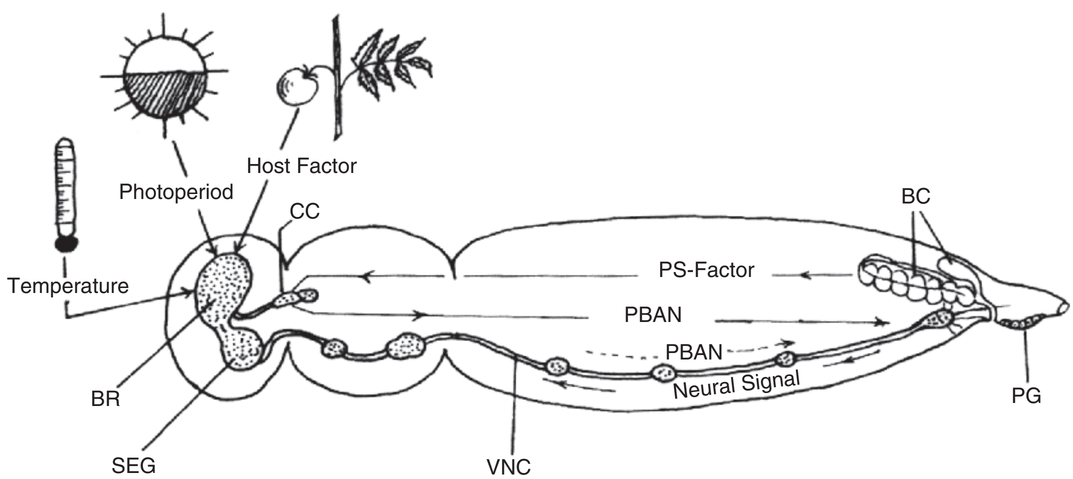
With sexual activity confined to a certain period of the 24-h day, there is no point in producing a pheromone when it is not needed. Therefore, photoperiod appears to be the major external factor regulating pheromone production in moths. This is particularly true of nocturnal species. However, as we will see later, there are other factors that can impact the regulation of pheromone production. We will use the corn earworm as a model to illustrate the intricacies of pheromone production. Corn earworm, like many moths is a nocturnal species. Sex pheromone is produced only during the night (average amount during peak production is ~100 ng), and females have negligible amounts of pheromone in their glands during the day. This diurnal periodicity of pheromone production is controlled by a peptide neurohormone. The hormone is produced in three groups of neurosecretory cells in the subesophageal ganglion and has been named the pheromone biosynthesis activating neuropeptide (PBAN). In the corn earworm and several other species of moths, PBAN is a 33 amino acid residue peptide. It is released into the hemolymph and activates pheromone production at the onset of scotophase. This was demonstrated by a simple bioassay which involved neck-ligating a female to stop pheromone production, followed by injection of either a homogenate of the brain-subesophageal ganglion, or synthetic PBAN into the abdomen of the ligated female. Pheromone titers were then determined by gas chromatography of the pheromone gland extract. One could also conduct the bioassay on a photophase female, without having to ligate it. However, in the gypsy moth the pheromonotropic signal is carried via the ventral nerve cord to the pheromone gland area to activate pheromone production.

The scenario presented for the corn earworm is not universal among moths. For example, species such as the black cutworm and oriental armyworm, which undertake seasonal migration, show delayed sexual maturation as well as delay in initiation of calling. It has been shown that juvenile hormone and PBAN are both involved in regulating pheromone production in these insects. The redbanded leafroller presents a rare case in which it is suggested that PBAN causes the release of a second factor from bursa copulatrix that stimulates pheromone production. In the cabbage looper, females maintain a high titer of pheromone during both day and night. The pheromone glands become competent to produce pheromone prior to adult eclosion and in response to reduction in ecdysone level. The subesophageal ganglion in this species contains PBAN-like pheromonotropic activity, but its exact role is not clear (Fig. 12).

Most neuropeptide hormones interact with surface receptors to activate second messengers which amplify the initial peptide-receptor signal. The second messengers may be small organic molecules such as cAMP, cGMP, ions such as calcium and hydrogen, or inositol phosphate. PBAN has been shown to increase intracellular cAMP levels, and calcium has been reported to be essential for mediating the pheromonotropic response. A G protein-coupled receptor from pheromone glands of *H. zea* was recently cloned. Genes encoding PBAN have been cloned from several insects. Besides PBAN, these genes carry sequences for four other peptides, including one for a diapause hormone.

The females of the corn earworm often mate on the first night after their emergence, and continue to mate throughout their short life, but only once each night. Pheromone production is terminated after mating and resumes during the following night. Continued production of pheromone after mating is a waste of resources and may cause disruption in egg laying, as the males will continue to be attracted to the female. A pheromonostatic peptide (PSP) which is transferred by the male to the female during mating, has been identified. Together with neural signals generated as a result of mating, PSP causes termination of pheromone production. In the corn earworm, pheromonostasis is temporary, and the female can produce pheromone on subsequent nights. However, termination of pheromone production is often permanent in species in which the female mates only once. An example of this is the gypsy moth. In this species, it is the presence of eupyrene sperm in the spermatheca of the female that is responsible for achieving pheromonostasis.

Another feature in the regulation of pheromone production is the role of host plants. First suggested almost 35 years ago, it was unequivocally demonstrated in 1988 in the corn earworm. Although the corn earworm is a polyphagous insect, it feeds primarily on fruiting parts of all of its hosts. The plant hormone ethylene, associated with fruit ripening, together with other volatile factors from host plants, were shown to induce pheromone production in females of wild or recently colonized corn earworms. This host-factor requirement is not



Regulation of Sex Pheromone Production in Moths, Figure 12 **Extrinsic and intrinsic factors regulating sex pheromone production in a female moth.**

very common among other species of moths, and in the corn earworm it was lost after prolonged laboratory rearing on artificial diet. In addition, temperature has been shown to play a modulating role in control of pheromone production. Thus, pheromone is not produced at very low or very high temperatures.

► Sex Attractant Pheromones
► Pheromones
► Juvenile Hormone

References

Cardé RT, Minks AK (1997) Insect pheromone research. New directions. Chapman & Hall, New York, NY, 684 pp
Prestwich GD, Blomquist GJ (1987) Pheromone biochemistry. Academic Press, Orlando, FL, 565 pp
Raina AK (1993) Neuroendocrine control of sex pheromone biosynthesis in Lepidoptera. Annu Rev Entomol 38:329–349

Regulations Affecting the Implementation of Regulatory Entomology Practices

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Regulatory entomology is a specialized area within the scientific field of entomology dealing with laws, regulations and requirements aimed at protecting agriculture and the natural environment from pests. Such laws, regulations and requirements may be implemented at all levels of government including local, state, national and international levels. In the United States, the federal government agency that is primarily responsible for implementing such regulations and requirements is the United States Department of Agriculture (USDA) Animal and Plant Health Inspection Service (APHIS) Plant Protection and Quarantine (PPQ). PPQ "safeguards agriculture and natural resources from the risks associated with the entry, establishment, or spread of animal and plant pests and noxious weeds to ensure an abundant, high-quality, and varied food supply.... Fulfilment of its safeguarding role ensures an abundant, high-quality, and varied food supply, strengthens the marketability of American agriculture in domestic and international commerce, and contributes to the preservation of the global environment." In addition, each state has a department of agriculture that includes a regulatory function.

Regulatory entomology had its start in the United States with the Federal Plant Quarantine Act (1912). The act provided the legal basis for implementing quarantines against non-native pests through preventing their introduction on plant material imported into the United States. The law was revised in 1957 (Federal Plant Pest Act). In 1971, APHIS was formed, integrating animal health and plant health protection into one agency. Noxious weeds were included in legislation under the Federal Noxious Weed Act (1974). Over almost 60 years, the legal and regulatory authority of the USDA remained largely unchanged in spite of new laws being added. It was eventually recognized that the legal and regulatory authority of APHIS and PPQ had to be revised and expanded to address new challenges in plant protection. In 2000, the Plant Protection Act was enacted by Congress, providing for a wider authority and greater enforcement of plant protection regulations. The Plant Protection Act consolidated and replaced 10 laws and acts in total, including the Federal Plant Pest Act and Federal Noxious Weed Act.

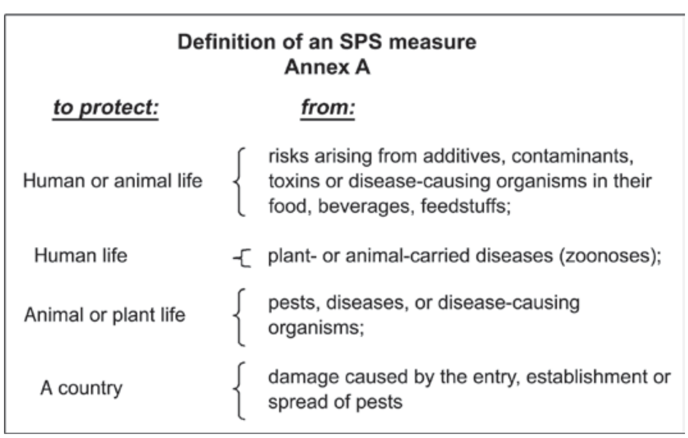
The need for the Plant Protection Act, and for increasing the role of regulatory entomology, is the result of ever increasing pressure on agriculture and the environment from threats arising from the unintentional introduction of plant pests. Increased movement of goods and people increase the risk of moving pests to new areas. Agricultural trade has increased steadily since the World Trade Organization (WTO) provided for a global, liberalized trade framework in the 1990s. As of 2000, the global value of agricultural trade exports was

~US$275 billion. Developed countries such as the United States, the European Community, Canada, Australia and Japan account for the majority of trade, while developing countries have had mixed results taking advantage of the liberalized trade environment. Nonetheless, there is a greater variety of products being transported from a wider range of countries. Along with increased trade, there is an increased possibility of moving pests.

The WTO and its agreements liberalized global trade, beginning in 1995. At the time the agreements were negotiated, it was also recognized that countries would need a means of implementing measures to protect their people, animals, plants and environments from the introduction and spread of pests and diseases. Members of the WTO therefore negotiated the Agreement on the Application of Sanitary and Phytosanitary Measures, or SPS Agreement as a subsidiary agreement of the WTO. It is a legally binding international agreement, and all Members of the WTO (including the United States) should follow its requirements. It sets out rights and obligations for Members of the WTO with respect to sanitary and phytosanitary measures that may be implemented for protecting human, animal or plant life and health. The SPS Agreement provides a framework to ensure that measures at the national level (e.g., laws, regulations or other requirements) are applied only to the extent necessary to protect health and that the measures are technically justified. In the same vein, the Agreement maintains that such measures should not be implemented arbitrarily or as disguised barriers to trade. Annex A of the SPS Agreement defines the scope of SPS measures (Fig. 13).

The SPS Agreement contains several key provisions that define rights, obligations and responsibilities of Members in designating SPS measures at the national level, several of which highlight the role and importance of scientific information. Article 2 (Basic Rights and Obligations) of the SPS Agreement states that “Members shall ensure that any sanitary or phytosanitary measure is applied only to the extent necessary to protect human, animal or plant life or health, is based on scientific principles and is not maintained without sufficient scientific evidence… .” This means that measures should be technically justified and based on available scientific information (see also Articles 3 and 5).

Article 5 (Assessment of Risk and Determination of the Appropriate Level of Sanitary or Phytosanitary Protection) addresses the application of risk assessment in determining appropriate SPS measures. Importantly, it states that risk assessments used for determining SPS measures should be based on methods developed by relevant international organizations and take into account available scientific evidence. It is also important to note that measures that deviate from standards, as



Regulations Affecting the Implementation of Regulatory Entomology Practices, Figure 13 **Definition of an SPS measure from Annex A of the SPS Agreement (WTO, 1994).**

defined in Article 3, should be based on risk assessment. Furthermore, Article 5 states that Members should implement measures only to achieve an appropriate level of protection, and that these measures should be the "least trade restrictive" possible. The Agreement allows for measures that are more stringent than those defined by standards, but these measures should be fully justified by a risk assessment.

Article 3 (Harmonization) of the SPS states that measures (laws, regulations and other requirements) should be based on international standards or that measures that deviate from standards should be technically justified. Members can use international standards as the basis for their national regulations and know that those measures cannot be challenged under the SPS Agreement. The Agreement identifies the internationally recognized standard-setting bodies as:

- The Codex Alimentarius Commission for food safety and human health
- The World Animal Health Organization (formerly Office Internationale des Epizooties or OIE) for animal health; and
- The International Plant Protection Convention for plant health

International standards developed by these organizations incorporate available scientific information and assess the risks associated with a given situation. As such, any measure based on a standard is by default considered to be scientifically and technically justified.

As stated above, the SPS Agreement identifies the International Plant Protection Convention (IPPC) as the international standard setting body for plant health. The IPPC is an international treaty with its own signatories, or Contracting Parties (member countries). It originally entered into force in 1952; it was amended in 1979 and the 1979 text entered into force in 1991. More recently, in 1997, the text was revised again largely to meet new expectations set forth in the SPS Agreement. The 1997 amendments created a Secretariat, the Commission on Phytosanitary Measures (CPM, comprised of all Contracting Parties, including the United States) and formalized standard-setting as part of the IPPC's mission.

The purpose of the IPPC is to secure common and effective action to prevent the spread of plant pests and to promote measures for their control. Although the IPPC has a clear relationship to the SPS Agreement and to trade, its scope is not limited to trade. The scope of the IPPC applies to protecting all plants including wild flora from plant pests. Plant pests include any organism that may affect plant health, including diseases and weeds. To achieve this goal of protecting plant health, the text of the IPPC sets forth rights, obligations and responsibilities of Contracting Parties, including pest risk analysis, harmonization, equivalence, minimal impact, regionalization, pest free areas and areas of low pest prevalence. According to the IPPC, Contracting Parties should make provision for a national plant protection organization (NPPO) that is responsible for performing certain key functions including:

- Phytosanitary certification
- Surveillance
- Implementation of appropriate phytosanitary measures
- Conducting quarantine treatments and certify exports
- Exchanging scientific and technical information
- Developing and observing standards
- Conducting eradication programs and other pest control programs, and
- Recognition of pest free areas and areas of low pest prevalence (IPPC, 1997a)

In the United States, the NPPO is APHIS-PPQ.

Contracting parties receive guidance on meeting these provisions through the use of international standards developed under the auspices of the IPPC. International Standards for Phytosanitary Measures (ISPMs) are developed under the guidance of the CPM. The CPM decides which ISPMs should be developed as part of the work program.

An expert panel is formed to draft the standard, ensuring that the best scientific expertise is incorporated into the standard. The Standards Committee (SC) reviews and revises the draft standard, which is then sent to all Members of the CPM for comment. After another review by the SC, the draft standard can be submitted to the CPM for adoption. To date there have been ~30 ISPMs adopted.

There are three general types of standards: reference, concept and specific. Reference standards include the ISPM No. 5 Glossary of Phytosanitary Terms and ISPM No. 1 Phytosanitary Principles fort the Protection of Plants and the Application of Phytosanitary Measures in International Trade. Concept standards include ISPMs such as ISPM No. 4 Requirements for the Establishment of Pest Free Areas and ISPM No. 6 Guidelines for Surveillance. The pest risk analysis standards (ISPMs No. 2 (revised) Framework for Pest Risk Analysis, and No. 11 Guidelines for Pest Risk Analysis for Quarantine Pests Including Analysis of Environmental Risks and Living Modified Organisms) are also concept standards.

Specific standards address specific pests or commodities. ISPM No. 15 Guidelines for Regulating Wood Packaging Material in International Trade is a specific standard; the only other specific standard at this time is ISPM No. 26 (2006) Establishment of Pest Free Areas for Fruit Flies (Tephritidae). Other pest or commodity specific standards are under various stages of development. Importantly, entomological expertise played a critical role in the development of ISPM Nos. 15 and 26; likewise, expert working groups for other pest specific standards are comprised largely of subject matter experts (e.g., fruit fly experts, forest entomologists, etc.). The role of entomological science is therefore essential to the development of international standards and, subsequently, national regulations.

Other ISPMs that rely heavily on entomological expertise include:

- ISPM No. 3 Guidelines for the Export, Shipment, Import and Release of Biological Control Agents and Other Beneficial Organisms
- ISPM No. 6 Guidelines for Surveillance
- ISPM No. 4 Requirements for the Establishment of Pest Free Areas
- ISPM No. 22 Requirements for the Establishment of Areas of Low Pest Prevalence
- ISPM No. 9 Guidelines for Pest Eradication Programmes
- ISPM No. 10 Guidelines for Pest Free Places of Production and Pest Free Production Sites
- ISPM No. 2 Guidelines for Pest Risk Analysis
- ISPM No. 11 Guidelines for Pest Risk Analysis for Quarantine Pests Including Analysis of Environmental Risks and Living Modified Organisms
- ISPM No. 14 The Use of Integrated Measures in a Systems Approach for Pest Risk Management

These standards are based on scientific (including entomological) and technical information and, as such, they provide scientific and technical guidance for the design and operation of key components of national regulatory plant protection programs. For example, ISPM No. 6 (Guidelines for Surveillance) provides valuable information on how surveillance programs for pests should be designed and executed, and covers basic sampling techniques. The PRA standards address how biological information on pests should be gathered and analyzed. Although the design of pest management programs does not necessarily include a risk assessment component, there is considerable overlap in the type of information needed to make accurate judgments. ISPM No. 14 provides extensive guidance on the integrated use of different types of pest risk management options to reduce pest risk. Finally, several standards discuss eradication, pest freedom and low pest prevalence from a regulatory standpoint. They provide both scientific and technical guidance as to how such programs may be developed, the types of information that should be gathered and analyzed, the requirements for certain procedures (e.g., surveillance) and how pest freedom can be officially recognized by other countries.

Other international agreements and protocols affect regulatory plant protection and regulatory entomology at the national level. The adoption of the Montreal Protocol, requiring the reduction in use or elimination of ozone depleting substances, may lead to reduced availability of methyl bromide, an important quarantine treatment, in the future. Although the use of methyl bromide for quarantine purposes is exempted from the Protocol, there is still a desire on the part of many countries to scale back their use of methyl bromide due to its ozone depleting effects. In the absence of suitable alternatives, the role of entomological expertise in finding pest management solutions (including the development of alternative quarantine treatments) has become increasingly important for regulators. Likewise, market forces and food safety standards are leading to acceptance of lower and lower levels of pesticide residues (maximum residue limits or MRLs) in food, with a concomitant reduction in the reliance on certain pesticides in the field.

Concurrently, it is becoming widely recognized that the operational standard of "Probit 9" for quarantine treatments is not a technically justifiable requirement for many, if not most, pests. Probit 9 security refers to the level of efficacy of a phytosanitary treatment and converts to 32 surviving individuals for every one million individuals treated. For more than 50 years, it has been assumed that this level of security was sufficiently protective, especially for fruit fly pests. However, as pest risk analysis continues to evolve, it has become evident that for many pests, Probit 9 may be too stringent a requirement; in some cases, Probit 9 may not afford enough security. In either case, NPPOs are re-evaluating the need for Probit 9 security and are seeking suitable alternatives (including pest management options) to long used point of origin-, in transit- or post-entry quarantine treatments. The need for entomological expertise in the regulatory arena is thus becoming ever more critical as NPPOs, including PPQ, seek new solutions to existing and newly arising pest problems.

It should also be understood that regulatory entomology is fundamentally different from other fields of entomology due to its legal and regulatory functions. In general, NPPOs are not concerned with common agricultural pests and their management within their respective territories, except in circumstances where those pests may readily move in agricultural trade. In a few instances, some established pests may be subject to regulatory measures or localized quarantines to prevent further spread (e.g., red imported fire ant, gypsy moth, Japanese beetle, pink hibiscus mealybug). NPPOs and regulatory entomologists are largely concerned with preventing the introduction and spread of quarantine pests (as defined by the IPPC, a pest of potential economic importance to the area endangered thereby and not yet present there, or present but not widely distributed and being officially controlled). In instances where a quarantine pest may become introduced, the NPPO may undertake an eradication, suppression or other quarantine program to either eradicate or prevent further spread of the pest.

Similarly, the role of scientific information in regulatory programs must be considered in relation to the role of *official* information. Scientific information, including taxonomic identity, geographic distribution and host range of pests can have serious impacts on regulatory processes, both domestically and internationally. Variability in scientific information as well as differing interpretations can lead to disagreements between NPPOs and cause serious disruptions to international trade. Official information would be information communicated between and among NPPOs regarding such issues as pest status in an area (distribution), issues related to biotypes or strains (taxonomic identity) and host status. Scientific information, for instance, may be used in developing a pest risk analysis (PRA); however, the PRA would be means of communicating official information between governments. It is thus important for there to be a clear connection between scientists and regulators while recognizing the respective roles of scientific and official information.

In short, regulatory entomology is concerned with preventing the introduction and spread of pests to new areas. This is accomplished through the implementation of laws (internationally and nationally), regulations and requirements at international, national and local/state levels. These laws, regulations and requirements are necessarily based on entomological science. Entomological expertise in regulatory plant protection is therefore essential; entomologists working in the regulatory arena provide a critical service in helping to protect both agricultural and natural resources.

► Regulatory Entomology
► Costs and Benefits of Insects
► Invasive Pests

References

Devorshak C, Griffin RL (2002) Role and relationship of official and scientific information concerning pest status. In: Hallman GJ Schwalbe CP (eds) Invasive arthropods in agriculture. Problems and solutions. Science, Enfield, NH, 462 pp

Follett PA, Neven LG (2006) Current trends in quarantine entomology. Annu Rev Entomol 51:359–385

Henstridge P (2002) History of regulatory plant health in the United States. In: Hallman GJ, Schwalbe CP (eds) Invasive arthropods in agriculture. Problems and solutions. Science, Enfield, NH, 462 pp

IPPC (1996) ISPM No. 4 – requirements for the establishment of pest free areas. FAO, Rome

IPPC (1997) New revised text of the international plant protection convention. FAO, Rome

IPPC (1997) ISPM No. 6 – guidelines for surveillance. FAO, Rome

IPPC (1998) ISPM No. 9 – guidelines for pest eradication programmes. FAO, Rome

IPPC (1999) ISPM No. 10 – guidelines for pest free places of production and pest free production sites. FAO, Rome

IPPC (2001) ISPM No. 5 – glossary of phytosanitary terms. FAO, Rome

IPPC (2002) ISPM No. 14 – the use of integrated measures in a systems approach for pest risk management. FAO, Rome

IPPC (2002) ISPM No. 15 – guidelines for regulating wood packaging material in international trade. FAO, Rome

IPPC (2004) ISPM No. 11 – guidelines for pest risk analysis for quarantine pests including analysis of environmental risks and living modified organisms. FAO, Rome

IPPC (2005) ISPM No. 3 – guidelines for the export, shipment, import and release of biological control agents and other beneficial organisms. FAO, Rome

IPPC (2005) ISPM Guidelines for areas of low pest prevalence. FAO, Rome

IPPC (2006) ISPM No. 1 – phytosanitary principles for the protection of plants and the application of phytosanitary measures in international trade. FAO, Rome

IPPC (2007) ISPM No. 2 – (revised) framework for pest risk analysis. FAO, Rome

Mumford J (2002) Economic issues related to quarantine in international trade. Eur Rev Agric Econ 29:329–348

UNEP (2000) The Montreal protocol on substances that deplete the ozone layer. United Nations Environment Program, Nairobi, Kenya

USDA (1997) Quarantine security for commodities: current approaches and potential strategies. In: Liquido NJ, Griffin RL, Vick KW (eds) Proceedings of joint workshops of the agricultural research service and the animal and plant health inspection service, Beltsville, MD

Regulations Affecting Use of Pesticides in the USA

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The intent of regulations affecting pesticides and their use in the USA has evolved over the years. Beginning in 1906, the Federal Food, Drug, and Cosmetic Act required that canned, fresh, or frozen foods in interstate commerce be pure and wholesome. This law was also known as the Pure Food Law. There was no provision that specifically regarded pesticides. In 1910, the Federal Insecticide Act was signed, but it pertained to only fungicides and insecticides, and its main intent was consumer protection of farmers from falsely acclaimed pesticides. The original Pure Food Law was amended in 1938 to include coverage of pesticides on foods and pertained mainly to the arsenical class of pesticides. At that time, the first two arsenical pesticides were widely used – Paris Green and lead arsenate. The Pure Food Law contained provisions that required manufacturers to include coloring agents in pesticides that were originally white materials. The intent was to prevent the accidental use of foodstuffs that had a similar appearance, such as flour. Through the evolution of pesticide regulation, the intent of pesticide laws today include protection of pesticide applicators, the environment, consumers of treated products, pets, and domestic animals. Other countries have adopted similar regulations, though the policies may be more or less stringent.

Federal Insecticide, Fungicide and Rodenticide Act (FIFRA)

A more encompassing law, the original Federal Insecticide, Fungicide and Rodenticide Act, known as FIFRA, was passed in 1947. Its intent was for the United States Department of Agriculture to register all pesticides prior to their interstate commerce. This law remained in place until 1964, when it was amended to allow refusal of products that were determined to be unsafe or ineffective and their removal from the market.

Since pesticides have become an integral part of controlling pests, a succession of federal and state laws has addressed their changing role and regulation. In 1970, the United States Environmental Protection Agency (EPA) was formed and was charged with enforcing FIFRA, which was again amended in 1972. Pesticide laws and regulations were refocused with the basic goals of:

- Requiring EPA registration of all pesticides, each use of the pesticide, and product label approval
- Classifying all registered pesticides as either "general use" which can be used by anyone, or "restricted use" which requires licensing
- Establishing certification and licensing programs carried out by individual states that must meet at least minimal FIFRA requirements, although individual states are allowed to be more stringent. Licensed applicators are considered to be either "private" or "commercial" applicators
- Establishing tolerances for pesticide residues which may legally remain on raw agricultural products or in processed food
- Penalizing pesticide users for "use inconsistent with the labeling" of a pesticide
- Making it illegal to store or dispose of pesticides or containers other than as directed by regulations and penalizing for illegal handling of containers
- Providing civil penalties when there is an unintentional violation of a regulation. Fines can be $1,000 for private applicators and others, and as much as $5,000 for each offense by commercial applicators
- Providing criminal penalties when the law is knowingly violated. The maximum penalty for private applicators and others is $1,000 and/or 30 days in prison. Commercial applicators may be fined up to $25,000 or 1 year in prison, or both

Certification of Applicators

FIFRA distinguishes between commercial and private applicators. Private applicators use or supervise the use of pesticides on property owned or leased by them or their employee for the purpose of producing an agricultural commodity. Commercial applicators include all other certified applicators. The EPA has established rules and procedures to be followed by individual states for certifying both groups.

Private applicators may be required by states to demonstrate their competency to apply pesticides through a written or oral examination. This generally involves testing their ability to read and understand directions on pesticide labels and their general comprehension of safety and environmental problems potentially arising from pesticide use.

Restrictions on commercial applicators are more stringent, requiring persons seeking certification to demonstrate competency by taking a written examination and, if required by law, to attend certification programs and take performance tests. Topics covered by the examinations may include a person's ability to read and understand a pesticide label, knowledge of application equipment and techniques, knowledge of potential pesticide harmful effects on human health and the environment, and basic knowledge of pesticide laws.

The EPA regulations also divide commercial applicators into categories based on types and sites of pesticide use. For example, some categories are: agriculture, ornamental and turf, rights-of-way, and aquatic pest control. Persons seeking certification as commercial applicators must demonstrate knowledge of the use and handling of pesticides generally, and knowledge of the particular standards applicable to their respective area or areas. Individual states determine when certification must be renewed.

Recall of Suspended Pesticides

The 1988 amendments to FIFRA require the recall of pesticides if their registration is suspended, or if the EPA determines that a recall of the pesticide is necessary to protect health or the environment. If a pesticide is recalled, the registrant must take reasonable steps to inform users of the recall and must provide storage facilities to persons in possession of the pesticide and, if requested, transportation of the pesticide. Users of the recalled pesticide are entitled to an indemnity from the EPA for the price of the pesticide. An indemnity cannot be made unless there is a specific line item appropriation of funds made in advance by the U.S. Congress.

The Federal Food, Drug, and Cosmetic Act (FFDCA)

The FFDCA of 1938 has been amended several times in its history. It is administered by the Food and Drug Administration (FDA) of the Department of Health and Human Welfare. Whenever pesticides are applied, their residues will remain on treated surfaces for a time. The chemical properties, frequency of application, rate applied, and environmental factors determine how much residue will be present. Residues are undesirable when they expose people, domestic animals, or wildlife to unsafe levels of pesticides. Pesticide residues on agricultural commodities are regulated under both FIFRA and FFDCA. FIFRA regulates residues by forbidding the use of a pesticide in a manner inconsistent with its label, and by denying registration to pesticides found to cause unreasonable adverse effects to people or the environment. Because FFDCA prohibits the distribution of agricultural commodities that contain levels of pesticides that exceed federally determined maximum tolerances, it is interrelated with FIFRA. In order for EPA to register a pesticide under FIFRA, a tolerance must be established under FFDCA. Information on a tolerance is useful in determining to register a pesticide and, if so, how the label will be composed. This takes into account that if the label's directions are followed correctly, then the tolerance will not be exceeded. If a pesticide is used on a crop not listed on the label, the crop may be determined to be unfit and destroyed by the government.

Pesticide Record Keeping Requirements

The Food, Agriculture, Conservation and Trade Act of 1990 (FACT Act, Farm Bill) contains regulations that require certified applicators of restricted use pesticides to keep records of applications. Certified applicators are determined to include both commercial and private applicators. The USDA Agricultural Marketing Service is responsible for implementing the record keeping provisions of the FACT Act. FACT further requires that certified applicators adhere to individual state record keeping requirements. If there is no state record keeping regulations, then certified applicators must include the following items as outlined by FACT:

- The pesticide's product name
- The amount of pesticide applied
- The date that the pesticide was applied
- The location of the pesticide application
- The size of the treated area

FACT requires that all pesticide records be kept for at least two years after each application. Also, the application must be recorded within 14 days after the pesticide was applied.

Endangered Species Act (ESA)

The Endangered Species Act is a Federal law administered by the Fish and Wildlife Service (FWS) of the Department of the Interior. The ESA makes it illegal to kill, harm, or collect endangered or threatened wildlife or fish or to remove endangered or threatened plants from areas under Federal jurisdiction. It also requires other Federal agencies to ensure that any action they carry out or authorize is not likely to jeopardize the continued existence of any endangered or threatened species, or to destroy or adversely modify its critical habitat. As a result, EPA must ensure that no registered pesticide use is likely to jeopardize the survival of any endangered or threatened species.

The FWS has the authority to designate land and freshwater species as endangered or threatened and to identify their current habitat or range. The National Marine Fisheries Service has the same authority for marine species.

The FWS has the authority to prosecute persons, including pesticide users, who harm endangered or threatened species. In addition, EPA enforcement personnel have the authority to ensure that pesticide users observe labeling restrictions.

Occupational Safety and Health Act of 1970 (OSHA)

The OSHA of 1970 is administered by the Occupational Safety and Health Administration of the Department of Labor. This law:

- Requires any employer with eleven or more employees to keep records of all work-related deaths, injuries and illness and to make periodic reports. Minor injuries needing only first aid treatment need not be recorded. Records must be made if the injury involved medical treatment, loss of consciousness, restriction of work or motion, or transfer to another job
- Requires investigation of employee complaints that may be related to pesticide use, reentry or accidents

Written and administered by OSHA, the Hazard Communication Standard (HCS), provides protection for employees exposed to hazardous chemicals. Pesticides are considered hazardous chemicals. An employee is defined as a worker who may be exposed to hazardous chemicals under normal operating conditions or in foreseeable emergencies. Exposure or exposed means that an employee is subjected to a hazardous chemical in the course of employment through any route of entry (inhalation, ingestion, skin contact, or absorption), and includes potential (accidental or possible) exposure. This law requires:

- Employers to read the Standard and understand the provisions and responsibilities of an employer
- A list of the hazardous chemicals in the work place be made
- Employers to obtain material safety data sheets (MSDS) for all hazardous substances on their list
- All containers to be labeled
- A written communication program be developed and implemented
- That employee training be conducted based upon the chemical list, MSDS, and labeling information
- Employers must create a hazard communication file, and make it available to any employee upon request in a reasonable period of time

Superfund Amendments and Reauthorization Act of 1986 (SARA Title III)

SARA Title III is a Federal right-to-know law that affects those that produce or store hazardous chemicals. Pesticide producers, distributors, retailers, and some pesticide applicators are among those that must comply with this law. It is designed to inform communities regarding hazardous chemicals located in the vicinity and addresses the need for community emergency response plans in the event of an accident.

Title III has many sections, however, the areas that affect pesticide applicators, applicator businesses, or dealers are confined to:

- Emergency planning and notification: under certain conditions, the law requires notification of state and local officials about the location and amount of hazardous chemicals at a site. EPA has designed a Threshold Planning Quantity (TPQ) for a number of active ingredients, not the formulated product. When the product in storage is at or above the TPQ, the State Emergency Response Commission (SERC) must be notified in writing. Each facility is also required to designate a coordinator to work with the Local Emergency Planning Committee (LEPC). The state will notify the LEPC that the operation is covered under SARA. This is a one time notification.
- Emergency release reporting: describes the safety measures when an accidental release, such as a spill, of any extremely hazardous substance occurs. If all of the following occur:
  - The pesticide was spilled.
  - Is covered under SARA Title III.
  - The spill quantity was greater than the Reportable Quantity (RQ).
- The spill created off-site exposure.
- If those conditions exist, then one is required to notify the SERC, LEPC, and the National Response Center. If a pesticide is applied according to the label, the use is exempt from emergency release reporting.
  - Material Safety Data Sheet (MSDS) reporting: employers are required to obtain and keep material safety data sheets. They must submit copies of each MSDS, or a listing of MSDSs that must be maintained, to their local fire department, the LEPC, and the SERC. There is one exclusion: if a chemical is used solely for household, consumer, or agricultural purposes, notification is not required.
  - Annual inventory reporting: all regulated facilities must submit an annual inventory to their local fire department, LEPC, and SERC. The inventory must include:
    - All hazardous chemicals stored at the facility in quantities of 10,000 pounds or more, and
    - All extremely hazardous chemicals stored in quantities of 500 pounds, or 55 gallons, or more, or in a quantity that exceeds the TPQ, whichever is less

Agricultural producers are exempt from this section.

Resource Conservation and Recovery Act of 1976 (RCRA)

The EPA regulates wastes under the RCRA. EPA issues a list of materials that are considered hazardous. Under RCRA:

- Private applicators (farmers) who properly dispose of pesticide wastes, excess pesticides, and triple rinsed empty containers on their own property are generally exempt from the requirements of this law (states and tribes often have more strict laws)
- "Wastes" include unrinsed containers, excess pesticides and pesticide dilutions, and rinse and wash water that contain a listed chemical and cannot be used
- Those who accumulate wastes of acutely toxic pesticides totaling 2.2 pounds or more per month or wastes of any RCRA-regulated pesticides totaling 2,200 pounds per month are regulated. Such users must register as a generator of hazardous waste, obtain an identification number from EPA, state, or tribe and follow certain disposal requirements

The EPA RCRA telephone hotline can be contacted for determining if a pesticide is listed.

Food Quality Protection Act (FQPA)

The FQPA was signed into law in 1996 and was the first significant amendment to FIFRA since 1988. The following are some of the major provisions of FQPA:

- Periodic review of pesticide registrations. FQPA requires EPA to establish a system for periodic review of all pesticide registrations on a 15-year cycle using new food safety standards mandated under the act.
- Emergency suspension authority. EPA may suspend a pesticide registration immediately. A notice of intent to cancel must be issued within 90 days, or the emergency suspension would expire.
- Minor use pesticides. FQPA enhances incentives for the development and maintenance of minor use registrations through extensions for exclusive use of data, flexibility to waive certain data requirements, and requiring EPA to expedite review of minor-use applications.
- Time-limited tolerances. FQPA requires the establishment of a time-limited tolerance for pesticides that have received registration under Section 18 of FIFRA.

Worker Protection Standard (WPS)

In 1992, EPA announced its final rule revising its regulations regarding protection of workers from exposure to agricultural pesticides. It is directed toward the working conditions of the following two types of employees:

- Pesticide handlers. Those who handle agricultural pesticides, including mixing, loading, applying, cleaning or repairing equipment, flagging application equipment, etc.
- Agricultural workers. Those who perform tasks related to cultivation and harvesting.

The provisions are intended to accomplish the following:

- Eliminate or reduce exposure to pesticides. Exposure is limited by establishing restricted entry intervals (REIs) for all pesticide products used in the production of agricultural plants and for which REIs have not been set according to current standards.
- Mitigate exposures that occur.
- Inform employees about the hazards of pesticides.

Products affected by the WPS are, with some exceptions, those products registered for use in the production of agricultural plants. It includes any product registered for use in the production of agricultural plants on farms, forests, nurseries, and greenhouses. Facility owners and operators are ultimately responsible to ensure compliance within the WPS.

Safe Drinking Water Act (SDWA)

EPA establishes national drinking water standards, called Maximum Contaminant Levels (MCLs), for protecting the quality of drinking water for both underground and above ground sources. Public water systems may not deliver water exceeding the MCLs. Congress amended the law to require the development of a screening and testing program for chemicals, including pesticides, for possible endocrine disrupting effects. EPA has the same requirement within the FQPA.

Hazardous Materials Transportation Act (HMTA)

The HMTA was enacted over the concern for spills of unknown substances on public highways. It is under the jurisdiction of the Department of Transportation (DOT) since it is the agency responsible for the safe transportation of all materials on public highways. HMTA authorizes the Secretary of Transportation broad authority to designate any material shipped in commerce as hazardous if it poses an unreasonable risk to health, safety, and property. Hazardous materials can include radioactive materials, disease-causing agents, flammable and combustible liquids or solids, oxidizing or corrosive materials, compressed gases, poisons, and explosives. The list of materials does not include certain chemicals used in pesticides; however, pesticides fall within the materials characterized as hazardous under the regulations issued by DOT.

The regulations apply to common, contract, or private carriers of hazardous materials. A commercial pesticide applicator transporting pesticides for application under contract would constitute either a contractor or private carrier and be subject to the regulations. Under certain circumstances, a private applicator transporting pesticides may be subject to the regulations. Generally, the carriers subject to HMTA:

- Operate across state lines and transport materials listed in the Hazardous Material Table; or
- Transport materials above the reportable quantities for various chemicals listed in the Hazardous Substance Table; or
- Do not meet the above requirements, but operate in a state that requires compliance with DOT regulations

Most states have adopted the DOT requirements for intrastate commerce. It is important to note that one should always follow the DOT regulations if there are no state requirements and there is no interstate commerce.

To avoid liability, manufacturers and distributors of hazardous materials often provide the information needed to follow HMTA regulations. However, it is the responsibility of anyone handling hazardous chemicals to ensure that the information is correct. Anyone who falls under the jurisdiction of the DOT and HMTA should know how to use the Hazardous Materials Table and Hazardous Substance Table.

Private carriers transporting only within the borders of a single state are exempted from this requirement provided the transport vehicle has a gross vehicle weight of less than 10,000 pounds. If the vehicle is a tank truck, it must have a tank of less than 3,500 water gallons capacity to be exempted.

Pesticide Use in the USA

In terms of actual pounds of pesticides used in the USA, volumes have actually decreased, from 1.2 billion pounds in 1981 to 975 million pounds in 1997. At least partly responsible for this trend is technology in formulation manufacturing. Many of the newer generation pesticides are applied at much lower rates than older compounds, yet are just as or more effective in the achieved results.

Of the pesticides used in the USA, the majority sold was for agricultural purposes, followed by industrial, government and commercial use, and home and garden use accounted for the least amounts sold. By class, herbicides were sold in the largest amounts (Table 5).

A Global Perspective of Pesticide Regulation

During the 1960s, the Food and Agriculture Organization (FAO) and World Health Organization (WHO) created the Codex Alimentarius Commission for the purpose of developing international food standards. Its ultimate goal is health protection of consumers and ensuring fair food trade practices. A major impetus in its formation was the differing food safety standards among nations. Because of a lack of standardization, trade barriers were created. As a result of barriers, various trade associations pressured their governments into establishing food safety standards to facilitate safe trade practices. The standards developed encompass various factors affecting food safety; pesticide residues are but one aspect of its intent. Pesticide residue analysis methods have been developed by the Commission to ensure

Regulations Affecting Use of Pesticides in the USA, Table 5 Volumes of pesticide active ingredients used by sector (millions of pounds) in the USA

Sector	Herbicides[a]	Insecticides[b]	Fungicides[c]	Miscellaneous[d]	Total
Agriculture	470	82	53	165	770
Industry and government	49	30	20	30	129
Home and garden	49	17	8	2	76
Total	568	128	81	197	975

From Aspelin and Grube, 1998
[a]Includes plant growth regulators
[b]Includes miticides and contact nematicides
[c]Does not include wood preservatives
[d]Includes rodenticides, fumigants, and molluscicides, but does not include wood preservatives, disinfectants, and sulfur, which account for 1.6 billion pounds

standardization in the international community. For practically any commodity and every pesticide, maximum residue levels have been set by the Codex Alimentarius Commission.

References

Aerts M, Nesheim ON, Fishel FM (2005) Pesticide recordkeeping. University of Florida/IFAS EDIS Extension Document PI-20. Available at http://edis.ifas.ufl.edu/PI012

Aspelin AL, Grube AH (1998) Pesticides industry sales and usage – 1996 and 1997 market estimates. Office of Prevention, Pesticides and Toxic Substances, U.S. Environmental Protection Agency, 733-R-98-0001, Washington, DC, 37 pp

Dean TW, Nesheim ON, Fishel FM (2005) Pesticide container rinsing. University of Florida/IFAS EDIS Extension Document PI-3. Available at http://edis.ifas.ufl.edu/PI003

Fishel FM (2005) Interpreting pesticide label wording. University of Florida/IFAS EDIS Extension Document PI-34. Available at http://edis.ifas.ufl.edu/PI071

Fishel FM (2005) Pesticide residues. University of Florida/IFAS EDIS Extension Document PI-69. Available at http://edis.ifas.ufl.edu/PI106

Fishel FM (2006) Restricted use pesticides. University of Florida/IFAS EDIS Extension Document PI-36. Available at http://edis.ifas.ufl.edu/PI073

Fishel FM (2005) Understanding material safety data sheet language. University of Florida/IFAS EDIS Extension Document PI-35. Available at http://edis.ifas.ufl.edu/PI072

Gardner RD (1990) Pesticide applicator training manual, 2nd edn. Cornell University, Ithaca, New York

Mossler MA, Fishel FM (2006) Pesticide tolerances and exemptions. University of Florida/IFAS EDIS Extension Document PI-118. Available at http://edis.ifas.ufl.edu/PI155

Nesheim ON, Fishel FM (2005) Proper disposal of pesticide waste. University of Florida/IFAS EDIS Document PI-18. Available at http://edis.ifas.ufl.edu/PI010

Olexa MT, Kubar S, Cunningham T, Meriwether P (1995) Laws governing use and impact of agricultural chemicals: an overview. University of Florida/IFAS Extension Bulletin 311

United States EPA (2005) How to comply with the worker protection standard for agricultural pesticides: what employers need to know. Available at http://www.epa.gov/agriculture/htc.html

United States EPA (1998) Laws affecting EPA's pesticide programs. Available at http://www.epa.gov/pesticides/factsheets/legisfac.htm

Regulatory Entomology

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Regulatory entomology entails the detection, management and study of non-native or geographically displaced insects in the public interest, principally by governmental agencies and institutions. This branch of entomology began in the 1800s, as governments around the world became aware of the detrimental effects to agriculture and to the public from the unrestricted movement of insect pests associated with trade goods. The United States government's first attempt to intervene in the control of a non-indigenous insect pest occurred in California in 1888. At this time, the vedalia beetle, *Rodolina cardinalis* (Mulsant), and a dipteran parasite, *Cryptochaetum iceryae* (Williston), were imported from Australia to control an accidentally introduced pest, the cottony cushion scale (*Icerya purchasi* Maskell). R. V. Riley, Entomologist to the U.S. Department of Agriculture, coordinated this classical biological control program. Following this successful control effort, interest in an expanded governmental role increased and, in 1904, the Bureau of Entomology was created within the U.S. Department of Agriculture. Other countries, and political subdivisions such as states and provinces, have similarly passed legislation to address the problem of invasion by exotic pests.

A principal role of regulatory entomologists is to prevent the entry of insects to new geographical areas where they may become established as pests. Border inspections of plants began in the U.S. in 1906 to intercept harmful organisms associated with trade goods (agricultural plants and plant products). Inspections have expanded in scope since then to keep pace with increases in trade and travel. In conjunction with border inspections, analyses of future pest status, termed Pest Risk Assessments, associated with the introduction of specific foreign insects are conducted to investigate the potential concerns subsequent to an introduction and to determine appropriate detection and control techniques. Introduction pathways are then examined and targeted for survey. Taxonomic support is critical to the correct targeting and implementation of mitigating measures.

The authority for the U.S. government to establish quarantines was legislated in the Plant Quarantine Act of 1912. Their purpose is to monitor and regulate the movement and spread, both interstate and internationally, of insect pests and trade goods that may harbor them. Regulatory entomologists are responsible for the implementation and enforcement of this act. Early quarantines for insects such as the gypsy moth and the Japanese beetle were effective in limiting the spread of these pests and formed the basis for future efforts. Control measures are also established as components of quarantine programs and can include insecticide treatments, foreign exploration for biological control agents and restrictions on the movement of regulated items such as nursery stock.

Regulatory entomologists also are responsible for determining if exports meet the insect pest requirements of state and foreign governments by certifying that products are free of injurious pests. To assist domestic producers, regulatory entomologists develop protocols designed to limit or prevent the movement of insect pests in or on trade goods. The protocols permit producers to fulfill quarantine regulatory requirements to control insects and to provide shippers with greater flexibility and efficiency in shipping pest-free products. Protocols can include various measures such as heat treatments, fumigation, isolation of production or transit areas, irradiation, insecticide applications, and/or changes in production and handling methods. With increased trade and speed of travel, the likelihood that insects will survive and become established in new geographic areas is increasing. It is the responsibility of regulatory entomologists to identify creative means to limit the number of introductions and to mitigate the impacts of newly established insect pests.

References

Essig EO (1931) A history of entomology. Macmillan, New York, NY, 1,029 pp

Metcalf CL, Flint WP, Metcalf RL (1993) Destructive and useful insects, their habits and control, 5th edn. McGraw-Hill, New York, NY, 1,087 pp

Smith IM, McNamara DG, Scott PR, Holderness M (1996) Quarantine pests for Europe, 2nd edn. CABI/EPPO, CAB International, Wallingford, UK, 1,425 pp

USDA, Animal and plant health inspection service web site for APHIS history. Available at http://www.aphis.usda.gov/oa/history.html

Regulatory Sequence

A DNA sequence involved in regulating the expression of a gene. A promoter or operator.

Rehn, James Abram Garfield

James Rehn was born at Philadelphia, Pennsylvania, USA, in 1881. As a child be became associated with the Academy of Natural Sciences, and then became a staff member and fell under the influence of prominent entomologists. By 1900 he was publishing on Orthoptera, which soon became his life's work. He made collecting trips to Africa and South America, as well as throughout the United States. He worked closely with Morgan Hebard on a great number of projects, and they both became renowned orthopterists. Rehn published over 300 papers on Orthoptera, and several books. Among his most important publications are "The grasshoppers and locusts of Australia" (in three volumes, begun in 1949) and "A monograph of the Orthoptera of North America (north of Mexico), Vol. 1" (with H. J. Grant, Jr.) (1961). He edited the "Transactions of the American Entomological Society" from 1917 to 1924, and served on many important committees of the American Entomological Society. Rehn received many honors, and served as president of the Entomological Society of America. He died on January 25, 1965.

References

Mallis A. (1971)American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Roback SS (1984) James A. G. Rehn and the American Entomological Society. Entomol News 95:163–165

Reitter, Edmund

Edmund Reitter was born at Mohelnice in Moravia (Czech Republic) on October 22, 1845. He initially worked as a farm manager, and was responsible for fish pond management on an estate. However, insects were his passion, and he moved to Vienna in 1879 and started a business selling insects. He moved to Mödling, near Vienna in 1881 and expanded his business to include entomological equipment and literature. Mödling became a favorite meeting place for entomologists, but Reitter's wife insisted that they move to Paskov, which was accomplished in 1891. Reitter's house again became a favorite meeting place for entomologists. Reitter is considered a genius among coleopterists because he had an uncanny ability to find useful diagnostic characters, even among species studied extensively by others. He was a prolific publisher, with over one thousand papers to his credit. He worked extensively across the various taxa of the Coleoptera. He also authored "Fauna Germanica" a 5-volume treatise that was the most important book on Coleoptera of Europe for decades. He is credited with describing a phenomenal 1,062 genera and 6,411 species! His personal collection contained 250,000 specimens, including 4,500 types; it is now housed in the Hungarian Natural history Museum. He died at Paskov, Moravia, on March 15, 1920.

Reference

Herman LH (2001) Reitter, Edmund. Bull Am Mus Nat Hist 265:126–128

Relapsing Fever

Several tick-transmitted spirochetes cause disease symptoms called "relapsing fever".

► Ticks

Relative Humidity

The percentage saturation of the air with water vapor.

Relative Methods of Sampling

Techniques used to sample insect populations that provide an estimate of abundance relative to other times or places (e.g., per trap or per unit time of visual search). Types of relative sampling include sex pheromone, blacklight and sticky traps, and amount of plant damage. (contrast with absolute methods of sampling).

► Sampling Arthropods

Releaser Pheromone

A pheromone that stimulated the nervous system to produce a quick behavioral response (contrast with primer pheromone).

► Pheromones

Remigium

The rigid anterior portion of the wing, which is directly affected by the wing muscles and is very important in flight.

Remington, Charles Lee

Charles Remington was an important force in modern American lepidopterology. He was born in Reedville, Virginia, USA, on January 19, 1922, but raised in St. Louis, Missouri, where his father was a prep school teacher with an interest in butterflies. He attended Principia College in Elsah, Illinois, where an emergence of periodical cicadas occurred, triggering a lifelong interest in insects. After military service in the Pacific region as a medical entomologist during World War II, he attended Harvard University. There, as a graduate student he co-founded the Lepidopterists' Society, which came to produce the "Journal of the Lepidopterists' Society." Remington graduated in 1948 and joined the faculty at Yale University, where he remained for his entire career.

Remington served as curator at the Peabody Museum of Natural History at Yale, where he began the Yale insect collection, which now numbers about 2.5 million specimens, and contains an unusually large number of extinct species and unusual (gynandromorph) specimens. He was well known for the breadth of his knowledge of entomology, not just his expertise in Lepidoptera. Remington's evolutionary research suggested that there were geographic regions where species tended to hybridize. In these areas, which he called suture zones, he suggested that species of all different sorts – plants, insects, mammals and so on – might be found hybridizing with close relatives. This evolutionary concept fell into disfavor for many years, but has recently been revived by others. Among other achievements was his involvement in the founding of "Zero Population Growth," an organization dedicated to controlling overpopulation. He died on May 31, 2007, in Hamden, Connecticut.

Remote Sensing

Examination of a site from a distance, typically from an airplane but also by satellite.

Removal Trapping for Population Estimation

An absolute method of insect sampling that involves repeated collection and removal of insects from an area. The rate of decline in abundance as the population is depleted is used to estimate the initial population size.

► Sampling of Arthropods

Reniform

Kidney- or bean-shaped. Noctuid (Lepidoptera) moths often bear a reniform spot in the center of the front wings.

Reoviruses (Cypoviruses)

The family Reoviridae contains members in nine genera that infect animals, plants and fungi.

The name of this group is derived from its association with respiratory enteric orphans. All reoviruses are characterized by a segmented dsRNA genome encapsidated within 50–70 mm icosahedral particles. Each of the dsRNA segments contains one or two open reading frames. Members of two genera, *Orbivirus* (referred to previously as arboviruses) and *Phytoreovirus*, cause disease in vertebrates and plants, respectively, but are capable of limited replication in their insect vector. In nature, the majority of reoviruses associated with animals cause asymptomatic diseases. Likewise, most of the non-occluded insect reoviruses (unassigned genera) are characterized as being weakly invasive and non-lethal.

A series of reoviruses have been detected in various *Drosophila melanogaster* cell lines and has been reported to contain 10–13 segments of dsRNA. These viruses may establish persistent infections and do not appear to adversely affect the host cell. In nature, the reovirus *Drosophila* S virus (DSV) has been isolated from malformed *D. simulins* populations. In *D. simulins*, this virus is maternally transmitted to the epidermal or mesodermal cells of progeny flies. The virus possesses reduced invasive powers; electron microscopy of infected tissues has revealed no evidence of cell lysis, release of the virus, or viral penetration. Infection of the cuticle epidermis results in the S-phenotype characterized by the loss of varying numbers of thoracic bristles. Interestingly, a reovirus of a terrestrial isopod, similar in several respects to DSV, is the causal agent of an inter-sex phenotype. Infection of female isopods by this reovirus induces external pseudohermaphroditism via inhibition of the feminizing endosymbionts affiliated with this isopod host. Other reoviruses related to DSV include the *D. melanogaster* F virus, *Ceratitis capitata* reovirus, and the housefly *Musca domestica* (HSV) reovirus. Unlike DSV, the HSV is virulent to its host, adult houseflies. The virus replicates in the cytoplasm of hemocytes and appears to undergo partially defective replication in the midgut tissue. In addition to dipteran hosts, reoviruses also have been detected in several hymenopteran parasitoids. The reovirus of the wasp *Diadromus pulchellus* (DpRV) has been well-characterized and is believed to be related to the *Orthoreoviruses*. The DpRV is considered to have a commensal relationship with its wasp host. This virus is distinct in that it produces ploidy-specific genotypes. In haploid male wasps, the DpRV contains 10 dsRNA segments, whereas in diploid female wasps the DpRV contains an additional 3.3 kb supernumerary dsRNA segment.

Members of the genus *Cypovirus* (cytoplasmic polyhedrosis viruses, CPVs) are the best-characterized insect reoviruses. CPVs have been isolated from over two hundred insect species and several non-insect invertebrates. The majority of CPVs have been isolated from the larval stages of Lepidoptera (moths, butterflies). CPVs, like the occluded baculoviruses and entomopoxviruses, are characterized by their ability to produce proteinaceous occlusion bodies. The size and shape of these occlusions may vary according to the viral isolate, the degree of maturation, and the type of host cell. For example, the silkworm *Bombyx mori* is host to a variety of different CPV strains that either produce cuboidal, hexagonal, or tetragonal shaped inclusions. In some cases, more than 10^4 viruses may be occluded within a single occlusion. Cypoviruses produce icosahedral virus particles (65 nm diameter) which encapsidate 10–12 dsRNA monocistronic segments (total size 14 to 15×10^6 Da), an RNA-dependent RNA polymerase, and various enzymes involved in the production of 5′ capped, methylated viral mRNAs. The electrophoretic patterns of extracted dsRNA segments have been used to cluster CPVs into twelve electrophenotype groups. Northern blots employing cDNA probes constructed from selected dsRNA segments have demonstrated no homology between the *Cypovirus* and non-occluded reoviruses. Furthermore, little homology was demonstrated among CPV isolates having similar dsRNA electrophenotypes.

In host insects, these viruses preferentially replicate in the midgut columnar epithelium and do not appear to spread to other tissues. However, it has been reported that a CPV of a chironomid is capable of replicating in the fat tissue. The occlusions, ingested by susceptible insects, are disrupted by the conditions in the alimentary tract and release the icosahedral virus particles. These non-enveloped particles contain surface projections that mediate attachment to the microvilli. Within the midgut columnar cells, the virus undergoes replication in a manner similar to that outlined for non-occluded reoviruses. As the name implies, the replication of the CPVs occurs in the cell cytoplasm. During the early phase of the disease, dissected midguts contain regions or zones of infected columnar cells. As the disease progresses, the virus spreads to adjacent cells in a fashion reminiscent of the expansion of viral plaques in cell monolayers. Additional infected cells may undergo extensive hypertrophy and become dislodged from the basement membranes. The sloughing of these cells into the lumen release inocula that can spread the infection to new regions in the midgut. In heavily infected hosts, the large numbers of progeny occlusion bodies generated in columnar cells produce milky colored midgut tissue. The occlusions produced in the midgut cells are released in the feces, aiding in the transmission of this disease. In nature, epizootics of CPV are uncommon. This disease causes problems in insect colonies, especially when insects are mass-reared. The cypovirus disease has several characteristics that make it ideally suited for spread within insectaries. Firstly, these viruses do not cause acute infections; their in vivo development is often described as a chronic, debilitating disease that may take weeks to kill infected hosts. During this period, the virus is continuously shed via the feces from infected insects. Secondly, slightly infected hosts may survive and produce chronically infected adults. During both mating and oviposition, the virus can be released from infected alimentary tracts and be passively transmitted to other adults or to the egg surface. At the population level, the presence of a cypovirus may result in reduced food intake, retarded development, and a gradual die-off, resulting in the collapse of the colony.

References

Aruga H, Tanada Y (1971) The cytoplasmic polyhedroses virus of the silkworm. University of Tokyo Press, Tokyo, Japan, 234 pp

Bellonick S (1989) Cytoplasmic polyhedrosis viruses-Reoviridae. Adv Virus Res 37:173–206

Nibert ML, Schiff LA, Fields BN (1996) Reoviruses and their replication. In: Fields BN, Knipe DM, Howley PM (eds) Fundamental virology, 4th edn. Lippencott-Raven, Philadelphia, PA, pp 691–730 Pennsylvania

Repellents

Chemicals that cause insects to make an oriented movement away from the source of the chemicals.

Repellents of Biting Flies

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The first use of a repellent was probably by prehistoric humans, sitting in the smoke of a fire to avoid biting flies. This method is still used in many places by remote populations. Some individuals resorted to covering themselves with mud, or grease from the animals they killed, to reduce fly biting. Repellents against insects were first mentioned in classical Roman literature by Pliny, the Naturalist (23–79 AD). The Greek physician and pharmacologist, Dioscorides (40–90 AD) described the use of wormwood, *Artemisia absinthium*, to repel gnats and fleas. Most of the early repellents consisted of parts of plants or animals, and some were associated with religious beliefs. Native Americans rubbed cedar tree needles, *Juniperus virginiana*, on their bodies to repel insects. Some people wore herbs or plant extracts around their necks or rubbed them on their skins.

Oil of citronella was one of the most widely used early repellents. It was used for human application to repel adult gnats and mosquitoes since 1882, and was initially registered in the U.S. in 1948 as McKesson's Oil of Citronella. Citronella was the standard repellent for many years. Other essential oils that were used as repellents were anise, bay laurel, bergamot, cassia, cedarwood, eucalyptus and wintergreen.

In 1929, dimethyl phthalate was reported as a fly repellent. At Rutgers University, a number of compounds were synthesized, including ethyl hexandiol, and reproducible methods of evaluating repellents were developed. Indalone (dimethyl carbate) was reported as a repellent in 1937.

At the U.S. Department of Agriculture laboratory at Orlando, Florida, and later at Gainesville, Florida, thousands of compounds were tested for repellency. During World War II, the standard military repellent was 6-2-2, a mixture of 6 parts dimethyl phthalate, and 2 parts each of ethyl hexandiol and indalone.

After World War II, the standard military repellent was M-2020, which was a mixture of 40% dimethyl phthalate, 30% ethyl hexandiol and 30% dimethyl carbate. The standard clothing repellent was M-1960, a mixture of 30% benzyl benzoate, 30% n-butylacetanilide, 30% 2-butyl-2-ethyl-1,3 propanediol, and 10% Tween 80.

Diethyl toluamide (DEET) was developed in 1954. DEET was by far the best repellent developed, and is the repellent of choice for the military. Military forces may have to deploy in areas where vector-borne diseases are rampant, and other methods of protection cannot be employed. Pest mosquitoes may exist in such large numbers as to interfere with military operations. A long lasting repellent was required and a new extended duration repellent formulation was developed. However, these sorts of conditions normally do not occur in the backyard of suburbia, or on the sunny beaches of the coast. Therefore for normal civilian use, shorter duration repellents may be satisfactory.

In recent years there has been a tendency towards the use of "natural agents" or phytochemicals. Among the so called "natural" products, or better described as "herbal" products, are the following:

Citronella

Oil of citronella is the volatile oil obtained from the steam distillation of freshly cut or partially dried grass of the genus *Cymbopogon*. Oil of citronella is an essential oil made up of more than 80 compounds of closely related terpenic hydrocarbons, alcohol, and aldehydes.

Geraniol

Geraniol is a component of citronella. Geraniol coeur is a mixture of geraniol, nerol and citronellol.

Quwenling

Quwenling is derived from the waste distillation after extraction of lemon eucalyptus (*Eucalyptus maculata citriodon*) and used in China as a mosquito repellent. The principal active ingredient is p-methane-3,8-diol.

Neem

Neem is a compound found in the leaves, seeds and seed oil of the neem tree (*Azadirachta indica*). The neem tree is a tropical tree, native to East India and Myanmar.

Soy Bean Oil

Soy bean oil is composed of a lecithin base plus other derivatives from soy oil.

Oil of Palmarosa

The oil from *Cymbopogon m. martinii* var. *sofia* provides 12 h of protection against *An. culicifacies*, *An. annularis* and *An. subpictus*.

Castor Seed Oil

A distillation fraction of castor seed oil was reported as a mosquito repellent.

Thujic Acid

Diethylamide of thujic acid distilled from the wood of western red cedar, *Thuja plicata*, was reported as a repellent of *Aedes aegypti*.

Indian Privet

The steam distillate of leaves of Indian Privet (*Vitex negundo*) provided 1–3 h of protection against Aedes aegypti.

Lemon Oil

Lemon oil was similar to DEET in repellency against the sand fly *Lutzomyia youngi*.

Tarweed

An extract of tarweed (*Hemizonia fitchii*) containing 1,8-cineole (eucalyptol) repelled *Aedes aegypti*.

Eucalyptus *camaldulensis*

Various extracts from this plant, including eucamol, 4-isopropylbenzyl alcohol, *p*-methane 3,8-diol were reported to be repellents to *Aedes aegypti* and *Ae. albopictus*.

(+)-Eucamolol

Eucamolol and its 1-epimer showed significant repellent activity against *Aedes albopictus*.

There are numerous reports in the literature of repellency of phytochemicals, but most of these phytochemicals have not been developed commercially. Three repellents have recently come to the market, and may be the trend of the future.

Merck 3535

3-(N-butylacetamino)-propionate has shown strong repellent action against biting flies.

KBR 3023

KBR 3023 is a Bayer product, a piperidine derivative, 1-Piperidinecarboxylic acid, 2-(2-hyroxyethyo) 1-methylpropylester.

PMD

PMD is similar to Quwenling, but is derived by a different extraction process. The active ingredient is p-methane-3,8-diol with additional isopulegol and citronellol. The product provided 5 h of complete protection time against *Anopheles funestus* and *An. gambiae*.

Though Permethrin, a pyrethroid, is not technically a repellent, it is used in a manner similar to repellents, to protect a person against biting insects. It is used to impregnate uniforms, clothing and bed nets.

The future repellents may be systemic repellents, or compounds masking the attractiveness of humans. Compounds may be developed to shield or block the body from bites.

Development of new repellents with increased protection time and effectiveness will likely come from a better understanding of host-finding. Attraction compounds combined with an insecticide may be developed to apply to clothing.

Despite recommendations that repellents be used to prevent mosquito-borne disease transmission, there is very little scientific evidence that repellents can be used to reduce the transmission of vector-borne diseases. It should be recognized that people use repellents to prevent annoyance from mosquito bites, and it would be inappropriate to recommend the use of repellents to prevent disease transmission by biting vectors.

References

Carlson DA (1997) Insect repellents. In: Rosen D, Bennett FD, Capinera JL (eds) Pest management in the subtropics. Integrated pest management – a Florida perspective. Intercept, Andover, UK, pp 283–297

Granett P (1940) Studies of mosquito repellents. II. Relative performance of certain chemicals and commercially available mixtures as mosquito repellents. J Econ Entomol 33:566–572

Gupta RK, Rutledge LC (1994) Role of repellents in vector control and disease prevention. Am J Trop Med Hyg 50 Suppl:82–86

Gupta RK, Sweeney AW, Rutledge LC, Cooper RD, Frances SP, Westrom DR (1987) Effectiveness of controlled-release personal-use arthropod repellents and permethrin-impregnated clothing in the field. J Am Mosquito Control Assoc 3:556–560

Replete

Individual ants whose crops are greatly distended with liquid food. Repletes serve as living reservoirs, and will regurgitate on demand to supply the colony with food.

Reproduction

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As in nearly every other aspect of their lives, insects display great diversity in modes of reproduction. Most insects reproduce in the adult stage by laying eggs, but a few reproduce during an immature stage, a process known as paedogenesis. Some, such as aphids and certain flies, for example, give birth to live young. Although sexual reproduction by union of male and female gametes is typical, certain insects reproduce some or all of the time by laying unfertilized eggs (parthenogenesis).

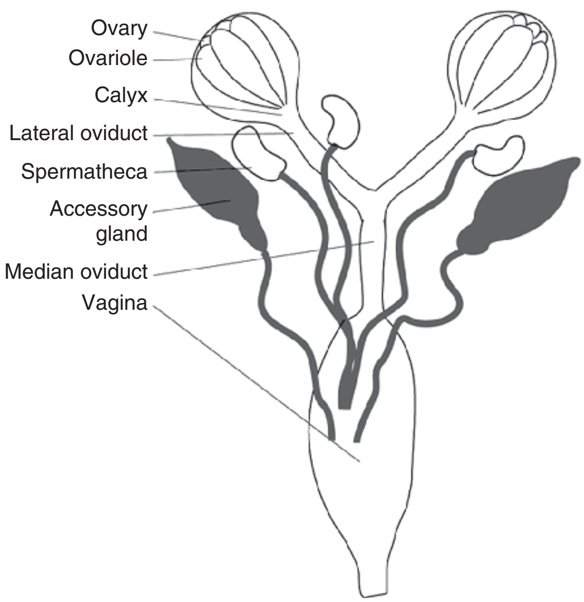
Oocytes accumulate yolk and cytoplasm and develop in egg chambers or follicles in the ovarioles within the ovary. Follicles are surrounded by a single layer of epithelial cells, the follicular epithelium. The presence or absence of nurse cells associated with ovarioles divides ovaries into two major groups; meroistic ovaries have nurse cells and panoistic ovaries do not. Nurse cells provide nutrients and gene products for the developing oocyte. In panoistic ovaries, similar components probably are provided by other cells, possibly the follicular epithelium. Insects typically produce eggs with a large amount of yolk relative to the cytoplasm, and the yolk is rich in proteins and lipids to be used in forming the new embryo and for energy, respectively. In most insects the yolk is formed from large glycolipoproteins called vitellogenins that are synthesized in fat body cells and transported to the ovaries by hemolymph. In contrast, small molecules called yolk proteins, to distinguish them from large vitellogenins, are incorporated into the yolk by the higher Diptera, such as tephritid fruit flies, drosophilid flies, house flies and related dipterans (but not in mosquitoes, which have vitellogenins). Two different sets of genes are required for the synthesis of yolk proteins and vitellogenins. Some parasitic insects produce small (20–200 μm), almost yolkless eggs that are deposited in a host (another insect) where the developing embryo absorbs nutrients from the host through a thin egg shell. In most insects several hormones regulate oogenesis, synthesis of yolk proteins, and additional aspects of reproduction such as pheromone production, mating, and oviposition. Not surprisingly, the complement of hormones is not the same for all groups of insects. When maturation of the oocyte is nearly complete, a vitelline membrane is secreted, followed by secretion of the egg shell, or chorion. After the chorion is secreted onto the egg, it is ready to pass down the oviduct and, in most insects, be fertilized by sperm released from the spermatheca. Hymenoptera and some coccids (Hemiptera) produce haploid males without fertilization and diploid females when the egg is fertilized. The ratio of sex chromosome to autosomes and/or the presence of sex-determining genes are two mechanisms known to determine gender in most insects.

The Ovary and Egg Production

The typical internal reproductive system of females consists of paired ovaries, lateral oviducts, a common oviduct, one or more spermatheca and accessory glands. These structures are located dorsally to the alimentary tract. Generally, several to many ovarioles make up an ovary. Each ovariole contains a string of egg chambers called follicles. The tsetse fly *Glossina* spp. has one ovariole, two other dipterans (*Melophagus* spp. and *Hippobosca* spp.) have two, *Drosophila melanogaster* has from 10 to 30, the blowfly *Calliphora erythrocephala* has about 100, the American cockroach *Periplaneta americana* has eight, and termite queens (Isoptera) may have up to 2,000. The nymphalid butterfly, *Phyciodes phaon*, commonly known as the phaon crescent, has four ovarioles in each ovary and about 50 immature oocytes that look like a string of pearls in each ovariole when the adult female emerges from the pupal stage. Just one ovary containing one ovariole occurs in some aphids, and Collembola have sac-like ovaries that do not contain ovarioles. Typically, oocytes in various stages of development occur in each ovariole in many insects, but generally, the most terminal set of oocytes is matured and laid before the other oocytes grow very large, and in some insects at least, the growth of secondary oocytes is under hormonal control. It makes sense that one set of eggs is matured and laid, making room in the abdomen for maturation of the next set (Fig. 14).

Nurse cells are associated with developing eggs in meroistic ovaries that occur in most of the Holometabola (except Siphonaptera), and in Hemiptera, Dermaptera, Psocoptera, Siphunculata, and Mallophaga among the Hemimetabola. Panoistic ovaries that do not have special nurse cells likely evolved first, and occur in present-day Thysanura, Odonata, Plecoptera, Blattodea, and Isoptera. Panoistic ovaries evolved secondarily in Ephemeroptera, Orthoptera, and Siphonaptera.

In meroistic ovaries, nurse cells may occur in the same follicle with the developing oocyte (*Drosophila*), in an adjacent follicle (Hymenoptera), or be located in the germarial region with long cytoplasmic strands projecting to the developing oocyte (some beetles and Hemiptera). Nurse cells



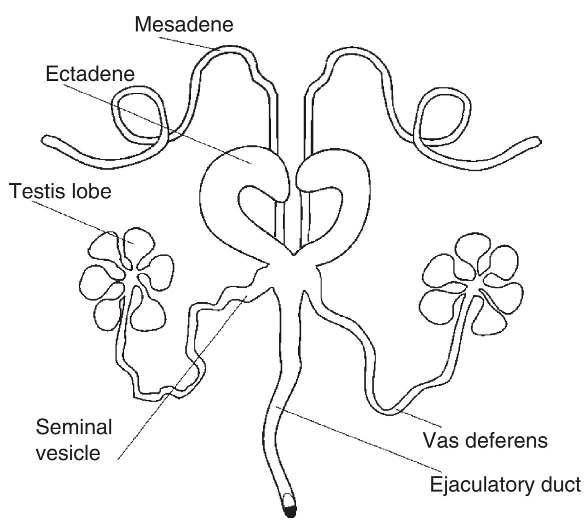
Reproduction, Figure 14 Diagram of a female reproductive system as found in *Rhagoletis* (Coleoptera) (adapted from Chapman, 1998, The insects: structure and function).

transfer nutrients and gene transcripts (mRNA) to developing eggs, and finally are used up in the process. Presumably follicular cells that surround all follicles provide nutrients and gene transcripts in those insects with panoistic ovaries.

Hormones control ovary growth, synthesis of yolk proteins and vitellogenins and their assimilation by the developing oocytes. Juvenile hormone seems to control all reproductive functions in some insects (Orthoptera, for instance), but in others juvenile hormone and ecdysone are important, and in still other groups juvenile hormone, ecdysone, and additional neuropeptide hormones are required. Juvenile hormone is synthesized by the corpora allata in adult insects, as in larvae, but ecdysone is synthesized by the ovaries in adult females. Near the termination of egg growth, the follicular epithelium secretes a thin protein sheet, the vitelline membrane, around the yolk and cytoplasm. Then the follicular epithelium secretes a laminar meshwork of cross-linked proteins, the egg shell or chorion. The follicular epithelial cells, now on the outside of the egg shell, die and are sloughed off the egg. The chorion contains no chitin, and with a few exceptions, it is not mineralized like the egg shell of birds. Sperm, which are released from the spermatheca as the egg passes down the common oviduct, traverse the chorion by passing through a small, usually twisted channel, the micropyle. More than one micropyle channel may be present. Although most Diptera have only one, the migratory locust *Locusta migratoria* has 35–43 openings.

The Male Internal System and Sperm Production

Typically, sperm are produced in paired testes in males, although in some Lepidoptera the testes are fused into a single structure. From the testes they pass into the short vas efferens that leads into the longer vas deferens and finally into the ejaculatory duct. Accessory glands are often, but not universally, part of the male system and when present they are attached by a duct to the vas deferens or to the ejaculatory duct (Fig. 15). Secretions from the accessory glands form the spermatophore in some insects, or if no spermatophore is formed, the secretions are added to the sperm prior to transfer to the female. Some of the secretory products provide nutrients and stimulate contractions in the reproductive tract of females, aiding movement of sperm into the spermathecae of the female. Each testis generally consists of a number of tubes or follicles in which spermatozoa are matured. Follicles may vary from one to more than 100 follicles, and may be incompletely separated from each other, as in Lepidoptera, or the testes may consist of several lobes, each with several follicles. In Diptera the testes consist of an elongated and undivided sac. Typically, sperm progress through several developmental stages. Sperm begin as diploid cells secreted by mitotic divisions of cells in the germarium. These initial diploid cells, called spermatogonia, further divide by mitosis into numerous diploid spermatocytes that become enclosed within a cyst or capsule of somatic cells (also diploid). Spermatocytes within a sac or cyst generally arise from the same spermatogonial cell



Reproduction, Figure 15 **Diagram of a male reproductive system as found in *Tenebrio* (Coleoptera) (adapted from Chapman, 1998, The insects: structure and function).**

and have synchronized development. Spermatocytes may undergo still more mitotic divisions; there are five to eight divisions in Acrididae and seven in *Melanoplus*, but eventually in a maturation zone they divide by meiosis and produce haploid spermatids. Spermatids undergo some further maturation in the transformation zone, and usually are bundled together by a thin membrane in this stage, or may be enclosed within a spermatophore. Insect spermatozoa tend to be long and have a slender head region, probably an evolutionary adaptation to navigate the micropyle.

Many males mature sperm during the pupal stage, while others may require several days as an adult to mature sperm. In contrast to the situation in most vertebrates, sperm can survive in the spermatheca of a female for weeks, months, or even years. Honeybee queens have been known to lay fertilized eggs after several years (8–9 years in one reported case), and queen ants were reported to contain viable sperm after 15 years.

During most of the twentieth century, various experiments failed to show hormonal control of spermatogenesis, but beginning in the 1970s ecdysteroids were found in the testes of flies, crickets, mosquitoes, and various lepidopterans, and experiments showed that they were synthesized there and stimulated spermatogenesis. Neuropeptides also may be involved in a cascade of reactions leading to ecdysteroid synthesis in testes; physiological levels (~10^{-13} to 10^{-15} M concentrations) of an ecdysiotropic peptide from gypsy moth brain stimulates synthesis of ecdysteroids in testes of larval and pupal gypsy moth males. These observations bring spermatogenesis in insects more in line with well known hormonal control of spermatogenesis in other animals.

An unusual situation evolved in male Lepidoptera. They produce both apyrene sperm without a nucleus and nucleated eupyrene sperm. Only the latter type can fertilize an egg. The two types of sperm are present in some of the earliest families of Lepidoptera that evolved, but one of the most primitive families, the Micropterigidae, do not produce apyrene sperm. Male Lepidoptera form a spermatophore in the female bursa copulatrix during mating, and both types of sperm are incorporated. As sperm pass down the ejaculatory duct, male silkmoths (*Bombyx mori*) secrete an enzyme, an endopeptidase called initiatorin, from cells in the ejaculatory duct. In the spermatophore, initiatorin begins to act upon the surface coat of both types of sperm, but the coat of the apyrene sperm is more quickly digested, releasing them. Motile apyrene sperm agitate the viscous contents of the spermatophore and aid liberation of the eupyrene sperm. Initiatorin also activates a carboxypeptidase that digests proteins in the seminal secretions and liberates arginine and other amino acids. Arginine is readily converted to glutamate, which sperm metabolize to provide energy for motility.

Pheromones in Reproduction

Many insects secrete pheromones, a special class of semiochemicals, to attract mates. Sometimes both sexes produce a pheromone that functions in some aspect of mating. Alternatively, only the female or the male may produce an attractant pheromone, commonly called a sex pheromone. The term "pheromone" is derived from two Greek words, pherein, meaning to carry, and *horman*, meaning to excite. The sex pheromone is usually composed of several chemical components secreted in a particular ratio or blend. Typically, glands at or near the surface of the body secrete the pheromone blend into the air. The total blend generally is considered to be the pheromone. The blend or ratio of components allows more information to be encoded, and allows greater discrimination among closely related species, which often use the same, or some of the same, components. Pheromones have been identified from more than 1,600 species of insects in 90+ families from 9 orders. Lists of Lepidoptera and the chemical nature of their sex pheromones are available on the Internet (Arn et al. 1999). Sex pheromones are sometimes used by predators and parasites to locate a potential host. The sex pheromone of

Dendroctonus frontalis, a bark beetle, not only attracts a potential mate, but may attract a clerid predator, *Thanasimus dubius*.

Most moths find each other and mate in low light intensity during some part of the evening or night. Perhaps because of activity at low-light intensity, their ability to detect chemicals in the air has evolved to a very high degree of sensitivity. In most Lepidoptera, the female produces the sex pheromone, and males fly to it. The antennae of many male Lepidoptera are plumose, with thousands of small hairs containing pheromone sensitive sensory neurons. The female silkworm moth contains about 1×10^{-8} g pheromone in her body. If this amount of pheromone were released instantly and uniformly distributed into slightly moving air, theoretically a male should be able to sense the pheromone about 4,560 m (2.8 miles) downwind. Any male within that active space, or wandering into its periphery, should be excited to fly upwind. The possibility of a male detecting a single female up to 4,500 m distant stretches the imagination. Several factors probably preclude this theoretical example from being achieved. First of all, females do not release their pheromone instantly, but do so slowly over some period of time each evening. Neither is there uniform distribution of pheromone in the air because of changes in wind current and direction, and buildings, trees, and other objects between the female and the male that disrupt the air flow and create turbulence. In addition, pheromones are adsorbed to the surface of plants and other objects, reducing the amount in the air. Nevertheless, the success of moths in locating each other under semi-dark conditions is impressive and attests to the effectiveness of pheromone in their success.

It is not always the female, however, that produces a sex pheromone. Some male Lepidoptera also produce pheromones, and in most bark beetles (family Scolytidae) both sexes typically produce pheromones. In true fruit flies (family Tephritidae), the male produces the attractant pheromone (with one known exception: the female olive fruit fly, *Bactrocera oleae*).

Sex pheromone synthesis and secretion seem to be under hormonal control in many, perhaps even most, insects, but few specific details have been elucidated. The most thoroughly studied examples of hormonal control of sex pheromone come from moths and cockroaches. A polypeptide hormone that controls the synthesis of the sex pheromone in moths has been named PBAN (Pheromone Biosynthesis Activating Neuropeptide). PBAN is now known from several different moths, and it may have slightly different roles in different moths. For example, in the redbanded leafroller, *Argyrotaenia velutinana*, PBAN regulates pheromone biosynthesis by increasing the supply of octadecanoyl and hexadecanoyl fatty acids needed for pheromone biosynthesis. In several moths, PBAN appears to regulate an enzyme, a Δ 11 desaturase, that is necessary to introduce a double bond into the pheromone precursors. In still others, it influences the reduction of fatty acids to the alcohol precursor of acetate pheromones.

Determination of Gender

At least three chromosomal systems, with variations, control sex in insects. Probably the earliest to evolve was one in which male sex chromosomes are XY and female XX. This system exists in many different groups today, including *D. melanogaster* and other Diptera. In some insects the Y chromosome has been lost, and those males are XO. Males in the orders Odonata, Orthoptera, and some groups in other orders are XO males. In Lepidoptera and Trichoptera, the female is the heterogametic sex, usually designated as ZW while males are ZZ. In the third system, found in Hymenoptera and some Hemiptera, females are diploid and males are haploid. If an egg is fertilized by a sperm, it becomes a female, and if no fertilization occurs, the egg develops into a haploid male. In honeybees and probably other Hymenoptera, the female can control the release of sperm from the spermatheca, and thus can control the sex of the individuals that will develop from the eggs she lays. In a few insects the sex of individuals is determined by prevailing temperature, as in subarctic mosquitoes, and in some gall midges by available nutrition.

Exactly how the different chromosomal patterns described above lead to sex determination is variable and poorly known for all except a few insects. The ratio of X chromosomes to autosomes (A) in determining sex of offspring has been characterized in *Drosophila melanogaster*. Although the Y chromosome carries genes for factors necessary for the production of motile sperm, it does not carry gender-determining genes in *Drosophila*. The ratio 2X:2A = 1 (one set of autosomes with an X from each parent) results in normal females, and the ratio of 3X:2A in aneuploids also results in female phenotype. A sex chromosome:autosome ratio of 0.5 (1X:2A, an autosome set from both parents, but an X from the female parent and a Y from the male parent) results in a normal male, and even a smaller ratio (1X:3A) produces a male phenotype. Intermediate ratios can result in mosaic intersexes in which the individual contains both male and female cells. Chromosomal ratios are ultimately expressed in specific gene actions. Since males have only one X chromosome, genes on it that control important functions or synthesis of critical molecules must be twice as active in males as in females, a process known as dosage compensation, but few details are known. Specific sex determining genes control the phenotype of some insects, including the housefly *Musca domestica*, the silkworm moth *Bombyx mori*, and some mosquitoes.

► Juvenile Hormone
► Ecdysteroids
► Oogenesis
► Vitellogenesis
► Endocrine Regulation of Insect Reproduction
► Sex Attractant Pheromones
► Pheromones
► Sex Ratio Modification by Cytoplasmic Agents
► Sterile Insect Technique

References

Arn H, Tóth M, Preisner E (1999) The pherolist. Available at www.nysaes.cornell.edu/pheronet

Chapman RF (1998) The insects: structure and function. Cambridge University Press, Cambridge, UK, 770 pp

Klowden MJ (2002) Physiological systems in insects. Academic Press, New York, NY, 415 pp

Nation JL (2002) Insect physiology and biochemistry. CRC Press, Boca Raton, FL, 485 pp

Reproductive Rate

The number of offspring produced per unit of time.

Reservoir

A site where organisms can survive, usually in relatively small numbers, and then invade or repopulate an area.

Resilience

An expression of the ability of some species to recover from disturbance. Persistence of a particular level or density despite perturbations (contrast with stability).

Resilin

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Resilin is a colorless, transparent structural protein of cuticle that has even better elastic properties than natural rubber. A rubber band elongates upon prolonged stretching, but experiments have shown that resilin retains about 97% of its original length even after extended periods of stretching. Resilin is not appreciably sclerotized, or else it could not retain its elasticity. Only small patches of resilin occur in the cuticle, and it mainly occurs at joints where wings or legs are hinged to the thorax. The prealar arm connecting the mesotergum to the first basalar sclerite of the thoracic wall in the wings of the migratory locust *Schistocerca gregaria* contains about 50 μg resilin and 15 μg chitin, and a similar hinge in large *Aeshna* spp. of dragonflies contains 5–7 μg resilin. A pad of resilin located near the coxal attachment to the pleural arch is compressed when a jumping flea crouches and prepares for a jump, and as the compressed resilin springs back to its original shape when the leap begins, it helps propel the flea into the air. Resilin is rich in the amino acids glycine and proline, as are some other structural proteins such as collagen, elastin, and silk fibroin. Resilin contains no hydroxyproline, hydroxylysine, tryptophan, or sulfur-containing amino acids, but does contain two unusual amino acids, dityrosine and trityrosine. These latter two amino acids may be involved in light cross-linking of resilin protein chains, enabling them to hold their shape. Studies of resilin biosynthesis are sparce, possibly because of the rather small areas in which it occurs and the difficulty of getting it out of the cuticle since it is insoluble in aqueous solvents. Resilin may be secreted by specialized epidermal cells.

► Integument: Structure and Function
► Locomotion

Resistance of Solanaceous Vegetables to Insects

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Tomato (*Lycopersicon esculentum*), potato (*Solanum tuberosum*) and pepper (*Capsicum annuum*) are “new world” crops. Tomato and potato originated in the northern regions of South America, and pepper in the tropical regions of Latin America. These crops are thought to be relatively new under cultivation, perhaps 200–300 years. Eggplants (*S. melongena*), however, originated in India and have been cultivated for hundreds of years. Wild eggplant species are not known.

The Pests and Their Geographical Origin

Almost all the pests are insects belonging to the following orders: Thysanoptera (thrips), Hemiptera (bugs, leaf-hoppers, whiteflies and aphids), Orthoptera (mole-crickets and grasshoppers), Coleoptera (beetles), Lepidoptera (moths and butterflies), and Diptera (flies). Out of the known pest species, only about one-fifth are major pests of primary importance. These may cause severe damage during almost every season and in many countries on different continents. All others are considered as minor pests, restricted to a rather limited area. Within this area, however, they might be severe pests of primary importance. Booklice or psocids (Psocoptera) and the wingless Collembola (springtails) are considered nuisance pests.

The pests affecting these crops either originated from South America, like the crop, and were accidentally reintroduced to the crop in other countries, or are local pests of other plants, which have adapted to the newly introduced crops. The greenhouse whitefly (*Trialeurodes vaporariorum*) and the potato tubermoth (*Phthorimaea operculella*) originated in Central America. The Colorado potato beetle (*Leptinotarsa decemlineata*) originated in North or Central America. The serpentine leafminer (*Liriomyza trifolii*) and the western flower thrips (*Frankliniella occidentalis*) originated in North America. Some other pests, such as the sweet potato (tobacco) whitefly (*Bemisia tabaci*) and the onion thrips (*Thrips tabaci*), are from Central Asia. The tomato fruitworm (*Keiferia lycopersicella*), the Egyptian cotton leafworm (*Spodoptera littoralis*), the beet armyworm (*Spodoptera exigua*), the *Phytometra* (*Plusia*) *chalcites*, the tomato fruitworm (*Helicoverpa zea*) and the African cotton bollworm (*Heliothis armigera*) seem to be local pests that have adapted to the newly introduced tomato, potato, pepper, and eggplants. Knowing the origin of the pests can assist with the search for resistant plants for breeding.

Mechanisms of Resistance

In solanaceous plants, resistance mechanisms are based on exterior and/or interior plant features. The most pronounced are the exterior mechanisms, based on physical means: trichomes or glandular-trichomes and their sticky exudate, which interferes with any small insect like thrips, whiteflies, aphids, leafminer flies or the younger stages of various larvae of other insects. These trichomes cover the plant's surface, leaves and twigs, and provide an exterior defense mechanism. The glandular hair exudate, when dislodged from cell walls, adheres to the legs and mouthparts of the insects and rapidly hardens, entrapping small insects or causing them to fall off the plant. Stuck insects rarely feed, quickly die, and thus are unable to transmit viruses. The interior mechanisms provide resistance that is based on secondary plant substances, which impose repellent, toxic, or hormonal effects, mainly on biting and chewing insects.

Trichomes occur in a multitude of forms in many wild tomatoes. In numerous species, there is a negative correlation between trichome density, and insect feeding and oviposition responses, and the nutrition of larvae. Specialized hooked trichomes may impale adults or larvae as well. Trichomes may also complement the chemical defense of a plant by possessing glands that exude terpenes, phenolics, alkaloids or other substances, which are olfactory or gustatory repellents. In essence, glandular trichomes afford an outer line of chemical defense by advertising the presence of "noxious" compounds. These features make them good sources for breeding resistance to virus transmission by insects. This is hereditary in the hybrids of the wild plants with cultivated varieties.

Resistant plants may possess both exterior and interior mechanisms, which then provide simultaneously resistance to a variety of pests. For example, *Lycopersicon* (*Solanum*) *pennellii* (e.g., LA 716) is resistant to a number of insect pests due to the accumulation of acylsugars exuded from type IV trichomes. Thus, it is resistant to *B. tabaci* adults, both causing direct damage and transmitting virus diseases. At the same time, it is also resistant to *S. littoralis*. The small larvae (L_I and L_{II}) become entangled in the sticky exudate of the leaf trichomes, like any small insect. Bigger larvae (L_{III}) generally overcome the stickiness, but they are then confronted with a juvenile hormone mimic in the leaves, which causes high larval mortality, adult morphological deformation, and male sterility. The survivors pupate earlier, and the emerging adults are smaller and less fertile than usual. The large larvae (L_{IV}) are not affected by these mechanisms.

The secondary plant chemicals, present in the ancestors of the domesticated cultivar, provided them with natural resistance to pests. Unfortunately, these chemicals may also be unpalatable or even toxic to people so such plant chemicals were deleted during the breeding process. In this way, the susceptibility to pests of the solanaceous crops was inadvertently increased during their domestication. As a result, the modern cultivars need to be continuously protected by the grower against pests. The reintroduction of resistance, or partial resistance, to pests into the modern cultivars is an invaluable component of integrated pest management programs.

Vector Resistance

Virus diseases are transmitted to these crops by various insect pests (e.g., aphids mainly to potatoes and pepper, and whiteflies and thrips mainly to tomatoes). Because viruses cannot be controlled, and infected plants cannot be cured, the only way (other than by eliminating vector insects) to combat viruses is by preventing their transmission, mainly by promoting resistance.

Hypothetically, two expressions of plant resistance are recognized: resistance, or tolerance, to the virus itself, distinguished as "virus resistance," and resistance to the virus-transmitter, distinguished as "vector resistance." These types of resistance are complementary and can be integrated into the same plant. The advantage of the combined vector-, and virus-resistance is due to the fact that plant resistance to insects is expected to be of greater durability than plant resistance to viruses, and the combination of the two resistance mechanisms will even prolong the durability of plant resistance to virus infection.

Breeding for Pest Resistance

Tomatoes are attacked by various pests, but within cultivated tomato varieties no sufficient pest resistance has been detected. Wild types such as *L. pimpinellifolium*, *L. peruvianum*, *L. chilense*, and *L. glandulosum* express some resistance to various pests. Nevertheless, adequate levels of resistance were detected mainly in accessions (ecotypes) of *L. pennellii*, *L. hirsutum* (also known as *L. hirsutum* f. *typicum*), and *L. hirsutum* f. *glabratum*. These sources of resistance had been intensively exploited. Some are resistant enough to prevent direct damage, and some, although virus-susceptible themselves, even prevent virus transmission. Glandular trichomes of these plants exude a sticky material and protect the plants by physically trapping and immobilizing of the pests. Others also exude chemicals that are toxic or repellent to the pests. The resistant accessions usually show resistance to various insects.

The potato pests are generally similar to those attacking tomatoes, but most of the sources of resistance had been chosen among wild *Solanum* species, some of which bear tubers. Some of the source plants, e.g., *S. berthaultii*, *S. polyadenium* and *S. tarijense*, possess glandular trichomes on the foliage that protect the plants by physically trapping and immobilizing the attacking insects. Other *Solanum* spp. possess a variable degree of secondary plant substances such as glycoalkaloids (e.g., tomatin, demissin, α- and β-solamarie, α- and β-chacinine, and α-solanine), which may have a toxic effect or inhibit feeding. *Solanum berthaultii* releases an aphid alarm pheromone that repels aphids such as *Myzus persicae*.

Aphids

The most severe aphid problem is the transmission of virus diseases in potato. Most of these aphid-borne viruses are non-persistent, or stylet-borne viruses. The agricultural means to prevent this virus transmission are very limited. One of the more efficient ways is the use of aphid vector-resistant plants. Naturally, most breeding efforts in potato have been devoted to aphid resistance. The potato crop is commonly infested by *Myzus persicae*, *Macrosiphum euphorbiae*, and *Aulacorthum solani*. Glandular hairs are quite effective in limiting aphid damage to the potato crop. They occur abundantly on *S. polyadenium*, *S. tarijense* and *S. berthaultii*. The sticky exudate, which is discharged from the trichome glands, precipitates on the aphid's limbs, impedes the aphid's movements and immobilizes it; the aphid finally starves to death. This trait of glandular trichomes is hereditary and expressed in the hybrid progenies of wild and cultivated plants. *Solanum polyadenium* and *S. berthaultii* are adequate sources for breeding potatoes resistant to aphids. The resistance of *S. chacoense*, *S. stolomfenerum* and *S. demissum*, to *M. persicae*, *A. solani* and *M. euphorbiae* depends on the species of the aphid and on the physiological condition of the leaves. This shortcoming must be considered while using them as sources of resistance.

Resistance in the wild tomato, *L. hirsutum* f. *glabratum* (PI 134417), is due primarily to the presence of the toxic factor that is exuded by the trichomes. A concentrated chloroform extract from the foliage is toxic to *Aphis craccivora*, *A. gossypii* and *M. persicae*.

Tomatoes, to which Mi-1, a *L. peruvianum* gene conferring resistance to the root-knot nematode (*Meloidogyne incognita*) was introgressed, also confer resistance to *M. euphorbiae*. Furthermore, tomatoes that bear the *Mi-1.2* gene, which also provides resistance to nematodes, express resistance to *M. euphorbiae* and to the Q-biotype of *B. tabaci* as well. The incidence of tomato yellow leaf curl virus, expressed in cumulative percent of infected plants, in tomato and in wild *Lycopersicon* spp. in the field. (The most resistant known accessions of the wild species were selected to demonstrate the potential of host plant resistance).

Whiteflies

High levels of resistance to the greenhouse (or glasshouse) whitefly, *T. vaporariorum*, are well known in *L. pennellii*, *L. hirsutum* and *L. hirsutum* f. *glabratum* accessions, whereas *L. chilense*, *L. minutum*, and *L. peruvianum* express moderate levels of resistance.

Tomato resistance to direct damage, and to the transmission of the tomato yellow leaf curl virus (TYLCV), by the cotton (or sweet potato) whitefly, *B. tabaci*, and resistance to *B. argentifollii*, is known in *L. pennellii*, and to some extent also in *L. hirsutum* and *L. hirsutum* f. *glabratum*, though they are susceptible to the virus itself. The incidence of natural virus infection seems generally to reflect the level of resistance of the plants to *B. tabaci* (Table 6).

Lycopersicon pennellii accessions LA 716 and PI 79659 are highly resistant to *Bemisia*, whereas the resistance of LA 1277 depends on light intensity and day length. The primary mechanism of resistance is the sticky exudate of the glandular trichomes. Whiteflies that land on these plants become entangled in this sticky exudate and die within a short time. In some accessions, the sticky exudate does not appear on the first three to four true leaves. These leaves are then unprotected and the whiteflies feed and develop on them readily. When artificially removed exudate is applied on cotton leaves, it protects them from whitefly attack for a long time. A toxic effect, browning and death of whiteflies, can be observed even when the sticky effect of the extracted exudate is neutralized by applying it on filter paper.

Among several *L. hirsutum* accessions, two are known to be rather resistant in respect to population build-up parameters, in comparison to the cultivated tomato: LA 1777 and IVT 771498; however, LA 1363 is rather susceptible. The main mechanisms of resistance are due to the physical interference of the glandular trichomes, and to toxic factors that occur in the trichomes and in the leaf tissues. Among

Resistance of Solanaceous Vegetables to Insects, Table 6 The incidence of tomato leaf curl virus, expressed in the cumulative percent of infected plants, in tomato and wild *Lycopersicon* spp. in the field. (The most resistant known accessions of the wild species were selected to demonstrate the potential of host plant resistance.)

Weeks from planting	Tomato cv. "Allround"	*L. hirsutum* f. *glabratum*		*L. hirsutum*		*L. pennellii*	
		(1*)	(2*)	(3*)	(4*)	(5*)	(6*)
2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
3	50.0	14.2	5.0	0.0	0.0	0.0	0.0
4	100.0	47.6	35.7	0.0	0.0	0.0	0.0
5	100.0	57.1	75.5	0.0	0.0	0.0	0.0
6	100.0	92.5	59.3	4.0	0.0	0.0	0.0
7	100.0	92.5	59.3	4.0	0.0	0.0	0.0
8	100.0	100.0	59.3	45.0	46.6	5.0	0.0

L. hirsutum f. *glabratum* (1*) PI 134418 (2*) PI 129157
L. hirsutum (3*) LA 1777 (4*) IVT 771498
L. pennellii (5*) LA 716 (6*) PI 79659

L. hirsutum f. *glabratum*, accessions PI 134418, PI 129157 and LA 407 are relatively resistant, and some others are not. In PI 365907, resistance depends on day length and light intensity and probably on some additional environmental factors. The main mechanism of resistance seems to be physical interference of the leaf trichomes and their exudate, which cause immobilization of the insects. It appeared that the exudate also has a repellent effect and, most likely, toxic factors that occur on the leaf surface or within the leaf are involved in plant resistance.

Leafhoppers

Total glycoalkaloid fractions, especially tomatine, provide resistance to the leafhopper in potatoes. *S. hougasii* and *S. bulbocastanum* are among the exploited sources of resistance. *S. berthaultii* (PI 218215) and *S. chacoense* (WRF 888) show less resistance than expected, probably because of their relatively low tomatine content.

Leafminer Flies

Lycopersicon pennellii accessions (LA 1735 and LA 716) possess a very high level of resistance to the leafminer *L. trifollii*. Adequate resistance is also found in *L. cheesmanii* (LA 1401) and in *L. hirsutum* f. *glabratum* (PI 126449). Larval antibiosis also occurs in F_1 hybrids. For breeding purposes, the resistance in *L. cheesmanii* has the most immediate value because it can be reciprocally hybridized with *L. esculentum*, and it produces orange fruit. Oviposition and adult feeding of *L. trifolii* on *L. pennellii* is significantly less than that on the cultivated tomato. This resistance is reduced when the foliage is rinsed with ethanol. Resistant attributes of *L. pennellii* can be transferred to *L. esculentum* through mechanical appression of *L. pennellii* foliage onto *L. esculentum* leaflets. Application of purified 2,3,4-tri-O-acylglucoses (the principal component of type IV glandular trichome exudate of *L. pennellii*) to *L. esculentum* significantly decreased feeding and oviposition on *L. esculentum*. Hence, the principal mechanism of resistance in *L. pennellii* to the leafminer is due to the secretion of acyiglucoses.

Lycopersicon hirsutum (PI 126445 and PI 127826) and *L. hirsutum* f. *glabratum* (PI 126449) possess a high level of resistance to the vegetable leafminer, *L. sativae* and *L. munda*.

Moths and Butterflies

Breeding resistance to moths and butterflies has been conducted mainly in tomatoes. The moths and butterflies belong mainly to three families. Members of the Gelechiidae are the tomato pinworm and the potato tuber moth. Both are oligophagous insects, which feed exclusively on Solanaceae under field conditions. High resistance expressed in delayed larval development, high mortality, and reduced leaf consumption to *K. lycopersicella* has been derived from *L. hirsutum* accessions (PI 126445, PI 127826 and LA 361) and from *L. hirsutum* f. *glabratum* accessions (PI 126449 and PI 134417). On these plants, basal cells of type VI trichomes and other epidermal cells as well as most of the palisade mesophyll are not consumed by *K. lycopersicella* larvae. It seems that these structures also contain deterrent chemicals. The resistance of other wild tomatoes – e.g., *L. peruvianum*, *L. peruvianum* var. *humifusum*, *L. cheesmanii* f. *minor* and *L. glandulosum* – varies in its intensity. *L. hirsutum* (LA 1777) is highly resistant to *P. operculella*.

Resistance to the tobacco hornworm, *Manduca sexta* (Sphingidae) is expressed in several of the *L. hirsutum* f. *glabratum* accessions (PI 134417 and LA 407).

Several of the moths that attack tomato crops belong to Noctuidae. Resistance of tomato cultivars to the tomato fruitworm *Heliothis zea* varies greatly, indicating that much of the variability can be used to develop less susceptible cultivars. Higher levels of resistance can be obtained from *L. hirsutum* (PI 127826) and *L. hirsutum* f. *glabratum* (PI 126449, PI 129157, PI 134417, PI 134418, PI 251304, PI 251305), whereas the resistance of

L. pimpinellifolium and *L. peruvianum* is insufficient. The antibiotic factor, which affects *H. zea*, appears to be inherited recessively. *H. armigera* larvae are strongly affected by feeding on leaves of the resistant *L. hirsutum* (LA 1777), *L. hirsutum* f. *glabratum* (LA 407), and *L. pennellii* (LA 716). Highest levels of resistance to *Phytometra chalcites* are found in *L. hirsutum* (LA 1777), *L. hirsutum* f. *glabratum* (LA 407 and LA 1625), and *L. pennellii* (LA 716). Resistance to *S. littoralis* larvae occurs in *L. hirsutum* (LA 1777), *L. hirsutum* f. *glabratum* (LA 407 and LA 1625), and *L. pennellii* (LA 1277). In conclusion, many sources of resistance are common to a various noctuid larvae, and their resistance is based mainly on toxic or antifeedant repellents.

Beetles

Tobacco flea beetle, *Epitrix hirtipennis*, adults are strongly repelled by *L. hirsutum* and *L. hirsutum* f. *glabratum* due to the exudate of their glandular trichomes. Removing this exudate by rinsing the leaves with 75% ethanol eliminates the resistance.

Colorado potato beetle, *Leptinotarsa decemlineata* resistance is due to the four-lobed glandular hairs on the leaves and stems of the wild potato *S. polyadenium*. Sticky material is discharged from these hairs on contact, trapping larvae or encasing their feet. Larvae with encased feet fall off the plants and die.

Feeding rates of *L. decemlineata* are negatively correlated with the occurrence of tomatine, a steroidal glycoalkaloid, in the tomato and in wild tomatoes such as *L. hirsutum*. High tomatine content in leaves virtually inhibits beetle feeding.

References

Berlinger MJ (1986) Host-plant resistance to *Bemisia tabaci*. Agric, Ecosyst Environ 17:69–82

Berlinger MJ, Dahan R (1987) Breeding for resistance to virus transmission by whiteflies in tomato. Insect Sci Appl 8:783–784

Berlinger MJ, Tamim M, Tal M, Miller AR (1997) Resistance mechanisms of *Lycopersicon pennellii* (Corr.) D'Arcy accessions to the *Spodoptera littoralis* (Boisduval) (Lepidoptera: Noctuidae). J Econ Entomol 90:1690–1696

Juvik JA, Berlinger MJ, Ben-David T, Rudich J (1982) Resistance among accessions of the genera *Lycopersicon* and *Solanum* to four of the main insect pests of the tomato in Israel. Phytoparasitica 10:145–156

Smith CM (1989) Plant resistance to insects: a fundamental approach. Wiley, New York, NY, 286 pp

Resistance to Insecticides

One of the principal (but not only) reasons for difficulty with controlling insects and other arthropods. Resistance is usually metabolic, but can also have a behavioral or physical basis. Other causes of control failure commonly ascribed to resistance include incorrect mixing or formulation, incorrect application, weather-related interference, and the presence of microbes in the soil that biodegrade pesticides. Finally, the movement or emergence of insects post-application can sometimes give the appearance of resistance.

► Insecticide Resistance
► Pesticide Resistance Management
► Detoxification Mechanisms in Insects
► Enhanced Biodegradation of Soil-Applied Pesticides
► Insecticide Application: The Dose Transfer Process

Resistant

Organisms that are tolerant of conditions that are deleterious to other strains of the same species. In entomology this term usually is applied to plant tolerance of pest damage, or arthropod tolerance of pesticides or pathogens.

Resource Concentration Hypothesis

The concept that the lack of diversity resulting from a homogeneous plant population limits community stability because herbivores have a ready food supply, favoring herbivore population increase.

Resource Partitioning

The differential use of resources by organisms.

Respiratory Horns

Elongate projections of the egg chorion that form a plastron on the egg, facilitating gas exchange but minimizing water loss. Respiratory horns are found on the eggs of several taxa, including Diptera, Hymenoptera, and some Hemiptera.

Respiratory Siphon

A tube found in larvae of certain insects, and used for breathing.

Respiratory Trumpet

Protuberances associated with the prothorax of the pupal stage in certain aquatic Diptera.

Restricted-Use Pesticide

This terminology was developed by the US Environmental Protection Agency to describe pesticides that are considered to be unsafe for use by the public without special training. Pesticides in this class cannot be purchased and used without license or permit. In contrast, less toxic or less hazardous materials are classified as "general-use pesticides" and can be purchased and used by anyone.

► Insecticides
► Regulations Affecting Use of Pesticides

Restriction Endonuclease

An enzyme that cuts DNA only at a limited number of specific nucleotide sequences. It is also known as a restriction enzyme.

Restriction Fragment Length Polymorphism (RFLP)

A polymorphism in an individual, population or species defined by restriction fragments of a distinctive length. Usually caused by gain or loss of a restriction site but could result from an insertion or deletion of DNA between two conserved restriction sites. Differences in DNA RFLPs are visualized by gel electrophoresis.

Resurgence of Pests

Increase in abundance of pests, rapidly and sometimes to higher than previous levels, following actions made to suppress them.

Reticulations

A netlike structure, usually referring to the pigmented pattern on eyes of Lepidoptera.

Reticulated Beetles

Members of the family Cupedidae (order Coleoptera).

► Beetles

Retina

The light receptive apparatus of an eye.

Retournement and Deversement of the Aedeagus in Coleoptera

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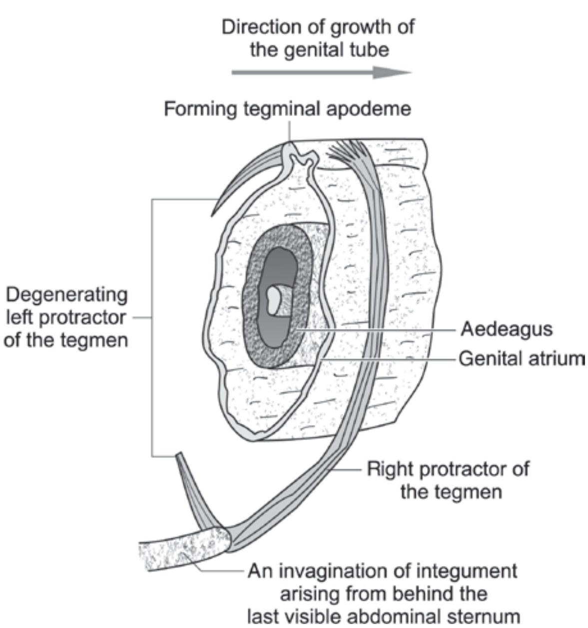
Seemingly coupled with the riding mode of copulation (that is the male riding on the back of the female, with both the participants of copulation facing the same direction) are two special features of the male copulatory apparatus in many Coleoptera, namely "retournement" and "deversement" (Fig. 16). Retournement refers to the turning or rotation of the aedeagus through 180° about its longitudinal axis during development (Fig. 17). Deversement refers to a sideway inclined asymmetric orientation of the deeply ventrally curved aedeagus, when in repose within the abdomen. Every time the intromittent organ is protruded for copulation, it returns to a symmetrical orientation, which is undone when the organ is withdrawn after coitus. In contrast retournement is an irreversible and permanent change in the orientation of the organ.

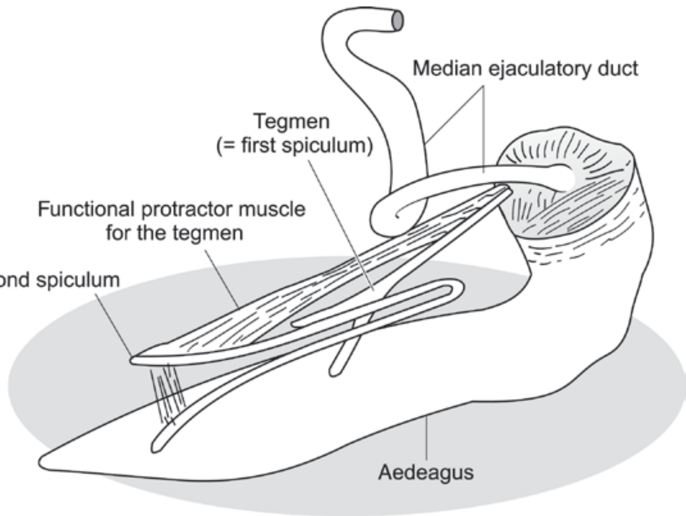


Retournement and Deversement of the Aedeagus in Coleoptera, Figure 16 Copulatory apparatus of *Aulacophora foveicollis*, ventrolateral view. Note the asymmetric origin of the protractor of the tegmen (=first spiculum) and the coiled course of the median ejaculatory duct (From Verma, 1994).

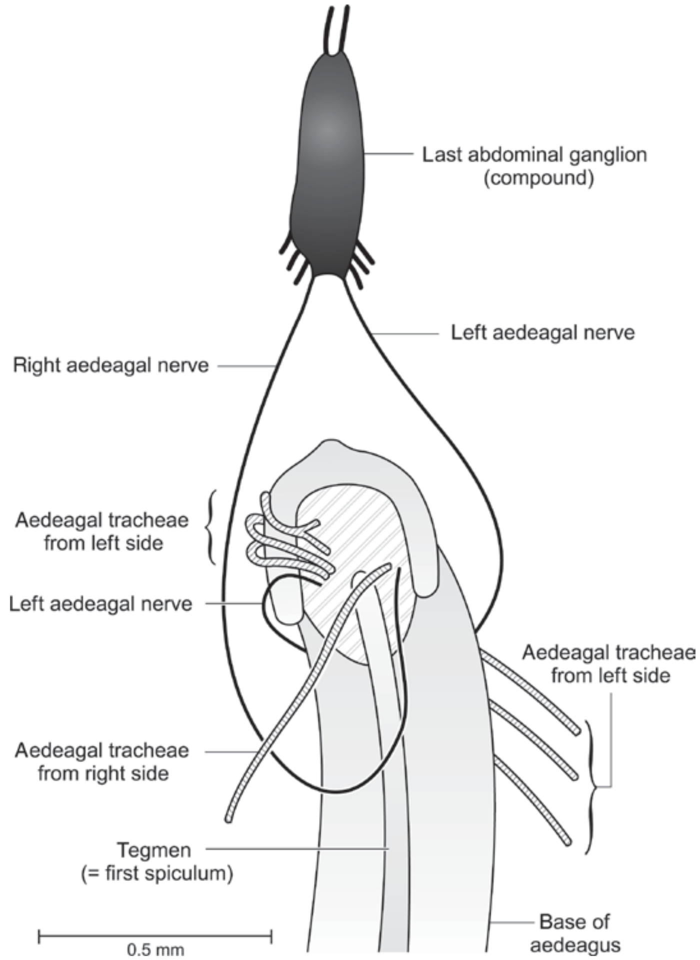
Heberdey has recorded retournement in the dytiscid *Hydroporus*. Jeannel has mentioned this phenomenon in some Silphidae, Staphylinidae and with probability also in Oedemeridae. Verma and his coworkers have noted retournement in many Chrysomelidae and in some other Phytophaga. In at least two chrysomelids, *Galerucella birmanica* and *Aspidomorpha miliaris*, the progress of retournement in development could be traced (Fig. 18). Retournement takes place in late pupal life in the former species, and soon after eclosion from the pupal skin in the latter. In two paropsine chrysomelids (*Chrysophtharta* species) from Tasmania, retournement could be inferred by comparing the orientation of the aedeagus in just-ecloded adults with that in reproductive males.

Retournement leaves behind certain anatomical effects, which help in inferring occurrence of the developmental turning of the copulatory organ. Such effects include: (i) the aedeagal nerve and tracheae, arising on the left side, enter the basal foramen of the aedeagus on the right side, and similarly the nerve and tracheae of right origin approach the foramen on the left side, (ii) the median ejaculatory duct, if not very long and winding, presents a coiled course, and (iii) the protractor muscle of the tegmen may present an asymmetry at its attachment on the tegmen and/or at its origin, as in the chrysomelids *Aulacophora* and *Colasposoma*, in the cerambycid *Aeolesthes*, and in the bruchid *Caryedon gonagra*.

Asymmetry of the protractor of the tegmen is due to involvement of this muscle in the mechanism of retournement during development. As has been observed in *Galerucella* and *Aspidomorpha*, this muscle is paired in development. The protractors arise on a pocket like invagination of the integument at the hind end of the abdomen behind the last visible sternum, or on



Retournement and Deversement of the Aedeagus in Coleoptera, Figure 17 **Diagram to illustrate mechanism of "retournement" of the aedeagus in Phytophaga (Coleoptera).**



Retournement and Deversement of the Aedeagus in Coleoptera, Figure 18 **Nervous and tracheal supply for the aedeagus in *Galerucella birmanica*, ventral view (From Verma, 1994).**

the second speculum, formed by sclerotization of the integumental pocket. (Note: the author of these lines chooses to refer to the apodemal part of the tegmen as the first speculum for reasons explained elsewhere.) Beyond the origin, the paired muscles extend forward and upward to find attachment on the dorsal surface of a longitudinal rod-like evagination of the genital atrium, which encloses the aedeagal rudiment. This outpocketing of the genital atrium is the forming apodemal part of the tegmen. Subsequently one muscle of the pair degenerates, and the surviving member exerts a downward unilateral pull on the genital tube (=aedeagus + the genital atrium). The pull is partly due to the genital tube growing in length anteriorly. As a result of this pull, the genital tube rotates, and the aedeagus turns through about 180°.

In most cases the right protractor of the tegmen survives, while the left one degenerates. Hence rotation of the aedeagus is clockwise, if looked at from behind. But occasionally the right one degenerates and the left one survives, and this results in anticlockwise retournement. The direction of retournement has been found connected with polymorphism in stored legume bruchids.

The mechanism of retournement also involves the role of a hormone, the juvenile hormone or JH. It has been found that in *Aspidomorpha miliaris*, if in a freshly ecloded adult male 22 h after the eclosion a ligature is put on the neck, connecting the head with the thorax, and thus availability of JH to the postcephalic body is denied, retournement fails to occur. If, however, the neck ligature is removed 30–32 h after the eclosion, anticlockwise retournement occurs, though in untreated males clockwise retournement is a rule in this species. This involvement of JH in the occurrence and direction of retournement has been experimentally inferred in a bruchid, too.

Diptera also show a phenomenon comparable to the retournement in Coleoptera. They show formation of “hypopygium inversum” and “hypopygium circumversum,” in development of which some terminal abdominal segments rotate through varying degrees, and this results in a rotation of the aedeagus. In beetles, however, retournement of the aedeagus is independent of the terminal segments of the abdomen, and these segments retain their bilateral symmetry undisturbed. Obviously, rotation of the male copulatory organ has evolved independently among Diptera and Coleoptera.

Jeannel has hypothesized that the riding mode of copulation, seen among Coleoptera, has evolved from the more primitive mode, the end-to-end method, in which the male and female, resting on the same substratum with their heads pointed in opposite directions, achieve intromission through their abdominal ends coming in contact. This primitive mode is seen among Hemiptera and also in some primitive Coleoptera. In the female the spermathecal opening is located in the sternal wall of the copulatory bursa. Hence, for successful sperm transfer in end-to-end copulation the ostium of the aedeagus, through which the internal sac is everted, is on the ventral face of the organ. When the primitive copulatory mode was replaced in evolution by the riding mode, the aedeagus has become ventrally curved to achieve intromission. When such a curved aedeagus enters the female bursa, its apical portion gets inverted; hence the ventrally placed ostium becomes dorsal, a position unsuitable for successful sperm transfer to the spermatheca. According to Jeannel this difficulty could be solved in some different ways, one of which is retournement. The retournement makes the ostium dorsal in the resting aedeagus, the apical part of which becomes inverted on intromission. Two other ways for achieving this end, as per Jeannel: (i) “l’inversion de l’aedeagus,” i.e., transposition in development of ventral features of the aedeagus to the dorsal surface and vice versa (e.g., in Carabidae and Psephalidae); and (ii) “la migration de l’orifice apical,” in which the apical region of the aedeagus is twisted, so that the ostium gets shifted to a dorsal position (e.g., in *Ptomaphagus* belonging to Catopidae). The terms “retournement” and “deversement” have been retained by authors, writing their communications in English, as they have been well defined, though they are French terms.

Jeannel has asked a question: Why a functional need, produced by the riding mode of copulation replacing the end-to-end mode, has not produced changes in the female organs? There is no satisfactory answer to this question as yet.

Deversement, or the laterally inclined orientation of the aedeagus in repose among internal organs, is obviously due to its ventral curvature and the need to accommodate the curved organ among other viscera. The asymmetry of the functional protractor muscle of the tegmen (vide supra) may also help in bringing the retracting aedeagus to an inclined orientation. The undoing of the deversement during protrusion of the organ for copulation seems to be due to the terminal part of the aedeagus being dorsoventrally depressed and the opening of the anogenital vestibule, bordered by the last visible abdominal tergum and sternum, being shaped like a horizontal slit.

References

George J, Verma KK (1994) Polymorphism in *Callosobruchus maculates* (F.) (Coleoptera, Bruchidae) – new dimensions. Russian Entomol J 3:93–107

Heberdey RF (1928) Ein Beitrag zur Entwicklungsgeschichte der mannlichen Geschlechtsapparates des Coleopteren. Z Morphol Okol Tiere 10:533–575

Jeannel R (1955) L’Edeage. Museum National d’Histoire Naturelle, Paris, 1–155 pp

Kumar D, Verma KK (1971) “Retournement” of the aedeagus in Chrysomelidae (Coleoptera, Phytophaga). J Nat Hist 5:635–642

Kumar D, Verma KK (1978) An endocrine control of “retournement” of the aedeagus in the tortoise beetle *Aspidomorpha miliaris* (F.). Indian J Exp Biol 16:639–641

Kumar D, Verma KK (1980) Aedeagal musculature in Phytophaga (Coleoptera). J Nat Hist 14:237–270

Nahrung H, Reid C (2002) Reproductive development of the Tasmanian eucalypt-defoliating beetles *Chrysophtharta agricola* (Chapuis) and *C. bimaculata* (Olivier) (Coleoptera, Chrysomelidae, Paropsini). Coleopt Bull 56:84–95

Verma KK (1969) Functional and developmental anatomy of the reproductive system in the male of *Galerucella birmanica* (Jac.). Ann Sci Naturelles Zool, Paris 12e ser, 11:139–234

Verma KK (1994) “Retournement” of the aedeagus in Chrysomelidae (Coleoptera). In: Jolivet P, Cox ML, Petitpierre E (eds) Novel aspects of the biology of Chrysomelidae. Kluwer Academic, Dorsdrecht, The Netherlands, pp 355–362

Verma KK, Kumar D (1972) The aedeagus, its musculature and “retournement” in *Aspidomorpha miliaris* (Coleoptera, Chrysomelidae). J Nat Hist 6:699–719

Rey, Claudius

Claudius Rey, was born at Lyon, France, on September 8, 1817. He was a noted French entomologist who is remembered for his collaborations with Etienne Mulsant on Coleoptera and Hemiptera. Initially he was financially independent due to a family-owned printing business, which allowed him to direct most of his energies to the study of beetles. Though the business went bankrupt in 1847, his uncle offered him a job at a vineyard in southern France. While working at the vineyard he began a collaboration with Mulsant. Together they published almost continuously from 1850 until Rey’s death in 1895. He was an honorary member of the Entomological Society of France, and served as president of the Société Francaise d’ Entomologie from 1882 until his death.

References

Anonymous (1895) Obituaries, Claudius Rey. Entomol Mon Mag 31:122–123

Herman LH (2001) Rey, Caludius. Bull Am Mus Nat Hist 265:129

RFLP

See restriction fragment length polymorphism.

Rhabdom

The site of the light-absorbing rhodopsin in an ommatidium. The rhabdom typically consists of several rhabdomeres and is situated in the center of the ommatidium.

Rhabdomere

The part of a retinular cell in an ommatidium that contains the light-sensitive rhodopsin. The rhabdomere membrane is formed into microvilli. The electrical impulses generated by light absorption are transmitted to the optic lobe of the brain.

Rhabdoviruses

The rhabdoviruses are a diverse group of more than 200 viruses which can cause disease in both plant and animal hosts. The animal rhabdoviruses are characterized by a bullet-shaped morphology, whereas certain plant rhabdoviruses have bacilliform morphology. The best-known rhabdovirus is the rabies virus, one of the many diseases studied by L. Pasteur in the 1880s. Many of the vertebrate viruses within the genera *Vesiculovirus* (vesicular stomatitis virus, VSV) and *Lyssavirus* (rabies-like viruses) are insect-transmitted and are capable of replicating in mosquitoes, blackflies, midges, sandflies and houseflies, as well as in select insect cell lines. The vesicular stomatitis virus, a relative of the rabies virus, has served as a model for studying the structure and function of rhabdoviruses. The animal rhabdoviruses are composed of a nucleocapsid protein (N) and a matrix protein (M) which form a helical structure encasing the (–) ssRNA. The resulting nucleocapsid or ribonucleic protein core is enveloped by a lipid-bilayer membrane. This envelope contains a viral glycoprotein (G) that anchors the membrane to the M-protein of the ribonucleic protein core. The M-protein (about 220 aa, pI = 9.07) is multifunctional, serving various structural roles as well as modulating viral transcription/replication and suppressing certain host cell functions. Extracted (–) ssRNA is non-infectious and requires encapsidated RNA transcriptase activity. RNA transcription is dependent upon three proteins, the N protein which complexes to the RNA to form a template, the L-protein which acts as the polymerase, and the polymerase-associated P (or Ns) protein responsible for RNA chain elongation.

The only well-characterized insect rhabdovirus is the Sigma virus of *Drosophila melanogaster*. This virus, discovered in 1937 by L' Heretier and Teissier, is characterized by its ability to induce CO_2 sensitivity (anoxia) and to be vertically transmitted to progeny flies via an extrachromosomal route. Unlike the polydnavirus, the Sigma virus does not integrate its genome into the host chromosome but undergoes limited replication in the cytoplasm of male and female gametes. Interestingly, the CO_2 anoxia, which is temperature dependent, also can be induced in fly and mosquito species that have been challenged with various lassa- and vesiculoviruses. The sensitivity to CO_2 is believed to be due to the presence of virus in the insect nerve ganglia and more specifically to the expression of the viral membrane proteins (G protein). The Sigma virus, unlike other rhabdoviruses, is not cytopathogenic and usually is considered to be harmless to *Drosophila*. This virus, unable to replicate in alternate hosts, undergoes a restrictive replication within *Drosophila* cells. In addition to the Sigma virus, several rhabdovirus-like particles have been detected in other invertebrates. In certain insects, such as the house cricket, *Acheta domestica*, the rhabdovirus VLP is polytropic, causing trembling symptoms and over 80% mortality. In other insects, such as the hymenopteran parasitoid *Biosteres longicaudatus*, a rhabdovirus VLP has been detected in venom apparatus. In this case, the virus does not appear to cause any pathology but may be involved in the suppression of the immune response of the host, the Caribbean fruit fly, *Anastrepha suspensa*. Like the polydnaviruses, this entomopoxvirus virus is associated with the lumen of the venom apparatus of the parasitoid.

References

Coll JM (1995) The glycoprotein G of rhabdoviruses. Arch Virol 140:827–851

Fleuriet A (1994) Female characteristics in the *Drosophila melanogaster*-sigma virus system in natural populations from Languedoc (southern France). Arch Virol 135:29–42

Teninges D, Bras F, Dezelee S (1993) Genome organization of the sigma: six genes and a gene overlap. Virology 193:1018–1023

Rhagionidae

A family of flies (order Diptera). They commonly are known as snipe flies.

► Flies

Rhammatocerus schistocercoides, a Swarm-Forming Grasshopper from South America

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The grasshopper *Rhammatocerus schistocercoides* (Orthoptera: Acrididae: Gomphocerinae) causes severe damages in rice, soybeans, maize, sugar cane, and native pastures in Brazil. This species is mainly concentrated between the parallels 12° and 15° south and meridians 52°–61° west (Fig. 19). This area partially occupies the states of Rondonia, Mato Grosso, and Goiás, where since 1983 there have been severe outbreaks (mainly in 1984–1988 and 1992–1993). This insect also is present in Colombia and Venezuela, where it is reported as one of the main problems in the local agriculture.

***Rhammatocerus* schistocercoides, a Swarm-Forming Grasshopper from South America, Figure 19** Seventh (penultimate) instar of *Rhammatocerus schistocercoides*.

Biology

This is a univoltine species. Biological cycles in Brazil and Colombia are approximately the same, with one generation per year, nymphal development during the rainy season and adults during the dry season. In Brazil, females lay their eggs at the beginning of the rainy season, from September to late October. Nymphs (eight to nine instars) develop during the rainy season, from late October to mid-April. Adults appear in mid-April and remain in the immature state through most of the dry season (May–September). Breeding activity begins in late August, apparently regardless of the rains, followed by the first egg laying in late September. In Colombia, *R. schistocercoides* lays its eggs from February to March. Nymphs are present from March to August, and adults from August to March (Fig. 20).

Behavior

Rhammatocerus schistocercoides has a remarkable gregarious behavior, similar to the behavior of other gregarious acridians, e.g., the desert locust, *Schistocerca gregaria* (Forskål), and the migratory locust, *Locusta migratoria* (L.). To this date, no phase transformation has been demonstrated. Its gregarious behavior is very close to that of the Moroccan locust, *Dociostaurus maroccanus* Thunberg. Hopper bands are formed, spreading over a few hundred to a few thousand square meters, with densities frequently ranging from 5,000 to 10,000/m^2 for the first nymphal instars to 250–500/m^2 for the last instars. Hopper bands have a very standard shape, i.e., generally a frontal formation which is common in many gregarious species. They move from a few ten to a few hundred meters per day. Swarms are generally small-sized, of a few thousand square meters to a few hectares on the ground (Fig. 21). When flying, during the day, these swarms can be much larger, frequently one km or more in length. Density on the ground is around 500–1,500/m^2 and 2–3 insects/m^3 when flying. The height of flight is low and does not exceed 5–10 m. Swarms display a typical "rolling" behavior. Flight activity seems maximal during sexual maturation; it stops temporarily during oviposition. The direction of swarms is mainly determined by the wind. In general, the swarms present a low mobility and move only locally. Distance covered per day is low, even in good conditions, a few hundred meters to 2–3 km a day only.

***Rhammatocerus* schistocercoides, a Swarm-Forming Grasshopper from South America, Figure 20** **Adult of *R. schistocercoides*.**

Habitat

In Brazil, *R. schistocercoides* outbreaks occur in the "cerrado" area of Central Brazil (Mato Grosso) and in the "llanos" of Colombia and Venezuela. In Brazil, the vegetation of outbreak areas is mainly pure or bushy savannas (Fig. 22). Two main habitats have been recognized: breeding biotopes usually on sandy soils, and dry season dispersion/wandering biotopes on heavier sand-clay soils.

Recent studies revealed that *R. schistocercoides* outbreaks in Mato Grosso cannot be explained by the accelerated agricultural development that has occurred in the affected areas since the early 1980s. Evidence clearly indicates that *R. schistocercoides* outbreaks are a long-standing phenomenon, both

***Rhammatocerus* schistocercoides, a Swarm-Forming Grasshopper from South America, Figure 21** **Swarm of *R. schistocercoides* in Mato Grosso, Brazil.**

***Rhammatocerus* schistocercoides, a Swarm-Forming Grasshopper from South America, Figure 22** **Typical savanna-like habitat of *R. schistocercoides*.**

in terms of their extent and nature. In fact, the newly cropped and previously uninhabited areas have long been conventional outbreak areas for this species. Much evidence suggests that the outbreaks surely have been the result of irregular interannual rainfall, particularly marked during the dry season and at the onset of the rainy season, just when the grasshopper populations are achieving sexual maturation.

References

Ebratt EE, Correal CE, Gómez MI, Villamizar LF, Cotes AM, Gutiérrez JC, Triana NB, Granja EM, León G (2000) La langosta llanera en Colombia. In: Ramirez N (ed) Boletín técnico. CORPOICA, Ministerio de Agricultura y Desarrollo Rural, Bogotá, Colombia, 103 pp

Lecoq M, Assis-Pujol CV (1998) Identity of *Rhammatocerus schistocercoides* (Rehn, 1906) forms south and north of the Amazonian rain forest and new hypotheses on the outbreak determinism and dynamics (Acrididae, Gomphocerinae, Scyllinini). Trans Am Entomol Soc 124:13–23

Lecoq M, Foucart A, Balanca G (1999) Behaviour of *Rhammatocerus schistocercoides* (Rehn, 1906) hopper bands in Mato Grosso, Brazil (Orthoptera: Acrididae, Gomphocerinae). Ann Soc Entomol France 35:217–228

Lecoq M, Pierozzi I Jr (1995) *Rhammatocerus schistocercoides* locust outbreaks in Mato Grosso (Brazil): a long-standing phenomenon. Int J Sustain Dev World Ecol 2:45–53

Lecoq M, Pierozzi I Jr (1996) Chromatic polymorphism and geophagy: two outstanding characteristics of *Rhammatocerus schistocercoides* (Rehn 1906) grasshoppers in Brazil (Orthoptera, Acrididae, Gomphocerinae). J Orthoptera Res 5:13–17

Lecoq M, Pierozzi I Jr (1996) Comportement de vol des essaims de *Rhammatocerus schistocercoides* (Rehn, 1906) au Mato Grosso, Brésil (Orthoptera, Acrididae, Gomphocerinae). Annales Soc Entomol France 32:265–283

Miranda E, de E, Lecoq M, Pierozzi I Jr, Duranton J-F, Batistella M (1996) Le criquet du Mato Grosso. Bilan et perspectives de 4 années de recherches, 1992–1996. EMBRAPA-NMA, Campinas, Brésil/CIRAD-GERDAT-PRIFAS, Montpellier, France, 146 pp

Rhaphidiporidae

A family of crickets (order Orthoptera). They commonly are known as camel crickets.

► Grasshoppers, Katydids and Crickets

Rheotaxis

Taxis response with respect to water currents.

Rhinophorid Flies

Members of the family Rhinophoridae (order Diptera).

► Flies

Rhinophoridae

A family of flies (order Diptera). They commonly are known as rhinophorid flies.

► Flies

Rhinotermitidae

A family of termites (order Isoptera). They also are called lower subterranean termites.

► Termites

Rhipiceridae

A family of beetles (order Coleoptera). They commonly are known as cicada parasite beetles.

► Beetles

Rhipiphoridae

A family of beetles (order Coleoptera). They commonly are known as wedge-shaped beetles.

► Beetles

Rhopalidae

A family of bugs (order Hemiptera). They sometimes are called scentless plant bugs.

► Bugs
► Coreid Bugs and Relatives

Rhopalopsyllidae

A family of fleas (order Siphonaptera). They sometimes are known as club fleas.

► Fleas

Rhopalosomatidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees, Sawflies

Rhyacophilidae

A family of caddisflies (order Trichoptera). They commonly are known as primitive caddisflies.

► Caddisflies

Rhypharochromidae

A family of bugs (order Hemiptera, suborder Pentamorpha).

► Bugs

Rhysodidae

A family of beetles (order Coleoptera). They commonly are known as wrinkled bark beetles.

► Beetles

Rhythms of Insects

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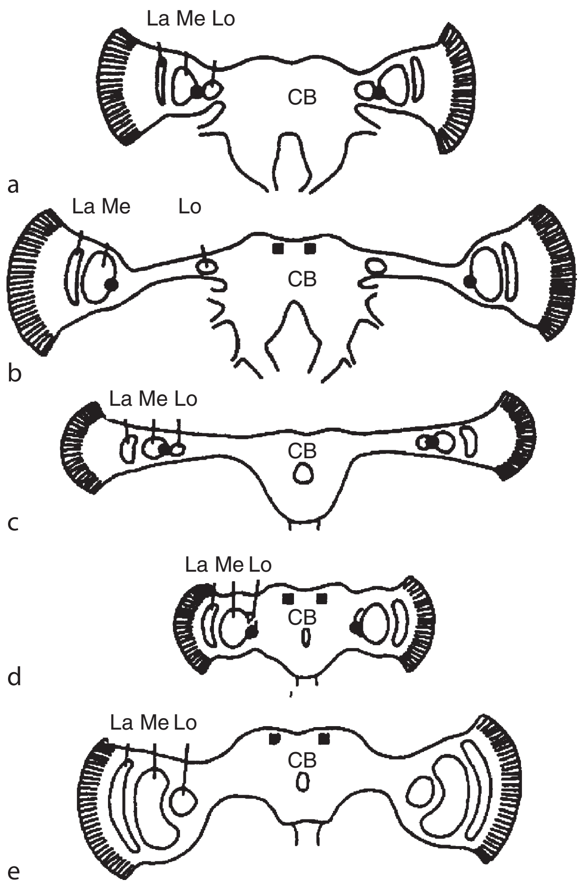
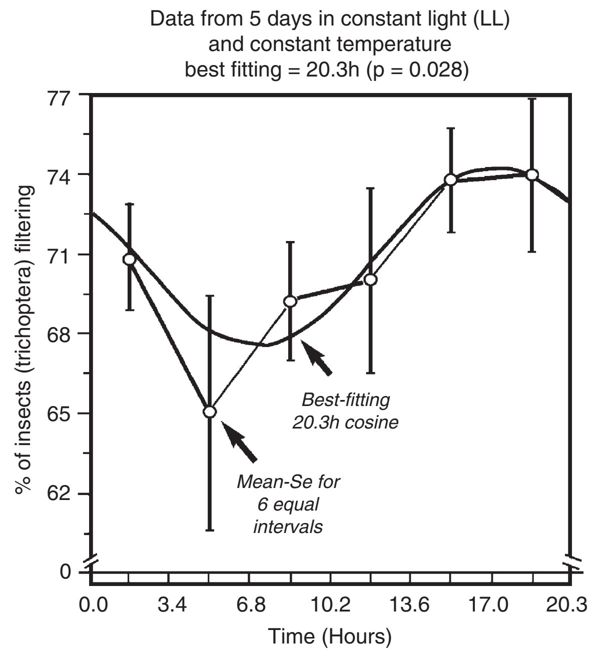
Chronobiology is an academic discipline that includes the rhythms of insects. There are several types of rhythms. The most common and prominent are "circadian rhythms," which oscillate with a period close to the astronomical (usually between 23 and 25 h, but an acceptable range is 20–28 h). Furthermore, such a rhythm is evident in every living organism studied. Other rhythms with different frequencies have been determined. The two other major groups are the "ultradian rhythms" (period of less than 20 h) and the "infradian" (greater than 28 h). They will be presented following the discussion of circadian rhythms. Plants and animals possess accurate time-measuring machinery termed "circadian clocks." The circadian system, studied extensively in insects, indicates that a central oscillator is located in the optic lobes serving as a pacemaker, but with neurons associated with neuroendocrine functions (Fig. 23). This information is based primarily on studies of *Drosophila*, especially the species *D. melanogaster*. Using larger insects, notably the cockroaches *Periplaneta americana* and *Leucophaea maderae*, it was shown that locomotion was controlled by the clocks in the optic lobes and was entrained solely through compound eyes.

Recent biochemical studies describe the organization of the circadian system. One component is termed the period protein (PER). This appears to colocalize with a peptide pigment dispersing hormone (PDH) in about half of the fruit fly's presumptive neurons. The period protein (PER) is also found in the pacemaker neurons of beetles and moths, but it may have different functions. In moths, the pacemakers are situated in the central brain and are associated with neuroendocrine functions. In other insects, the neurons associated with neuroendocrine functions appear to be closely coupled to optic lobe pacemakers. In some crickets and flies, central brain pacemakers are present in addition to optic lobe pacemakers.

Reliable documentation of a circadian rhythm utilizes the application of a statistically appropriate treatment using the cosine model. This permits one to verify the rhythm and detect possible masking effects when insects have been in unusual environments, or encounter interfering agents. An example illustrating this is shown in a comprehensive study with the caddis fly larvae, *Brachycentrus occidentalis* (Trichoptera), in



Rhythms of Insects, Figure 23 **Schematic of brains of (a) cockroach, (b) cricket, (c) beetle, (d) fly, (e) moth; Within optic lobes are lamina (La), medulla (Me) and lobula (Lo) which process and transfer visual signals from the compound eyes to the central brain (CB). Location of circadian pacemaker centers are indicated by filled circles in the optic lobes and by squares in the central brain (after Helfrich-Forster et al. (1998) Chronobiol Int 15:567–594).**



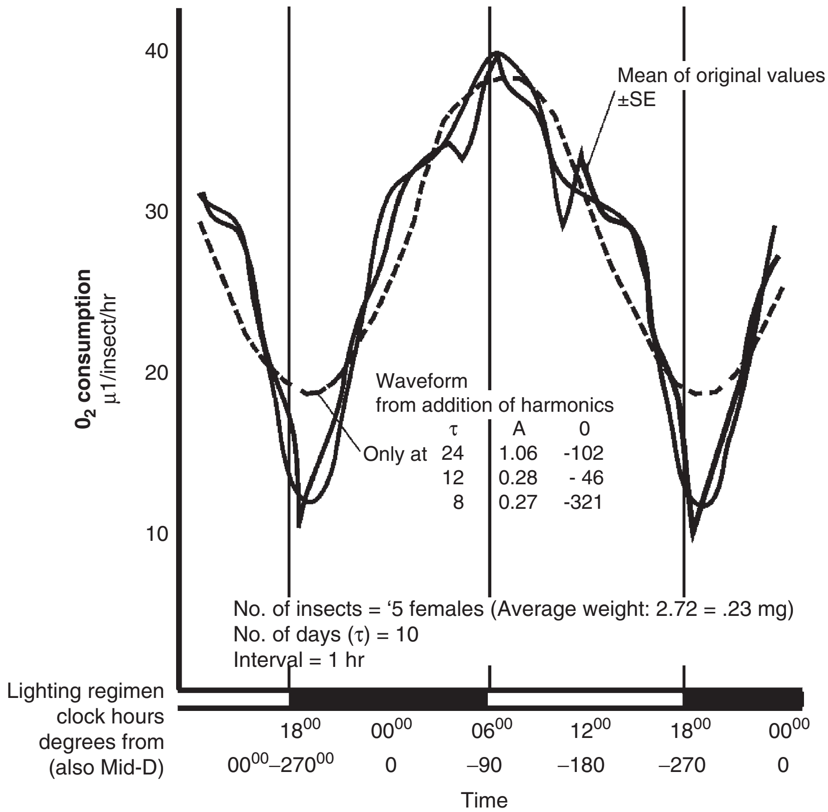
Rhythms of Insects, Figure 24 **Circadian waveform of filtering activity of caddis fly larvae (200 larvae) showing best fitting cosine (20.3 h) (after Sothern et al. (1998) Chronobiol Int 15:595–606).**

which an 8-h feeding schedule in water masked a circadian rhythm determined at 20.3 h (Fig. 24).

Examples of Behavioral Circadian Rhythms

Prominent circadian rhythms include locomotion and flight, foraging, biting habits (especially mosquitoes and other Diptera, cat fleas, among others). Other circadian rhythms include oviposition, hatching, pheromone emission, molting (eclosion in immatures), as well as spermatophore formation and the release of sperm, the secretion of ecdysteroids from prothoracic glands, and cuticle deposition. Oxygen consumption also shows a circadian rhythm as studied in the flour beetle, *Tribolium confusum*, using sterilized adults (Fig. 25). Circadian rhythms of oxygen consumption and heart rate have been discovered in the American cockroach. Additional biochemical rhythmic events, described as diurnal, were found with the neuroactive chemicals, acetylcholine and acetylcholinesterase in the cockroach, *Periplaneta americana*.

In summarizing the important role of circadian rhythms, it is evident that insects are best adapted to periodic environments in which the cycle of light and temperature is close to that of a solar day. Cycles with an unnatural period usually



Rhythms of Insects, Figure 25 **Oxygen consumption of flour beetles during a 24-h span using mean values of original data to show fit with a cosine function and a waveform using harmonics (after Chiba Y et al. (1973) J Insect Physiol 19:2163–2172).**

result in reduced longevity or impaired physiological function.

"Exogenous" rhythms are those that occur as a direct response to the environmental cycle of light and darkness and temperature. In the absence of these variables, the rhythm does not persist. In contrast, an "endogenous" rhythm is a periodic system that is a part of the temporal organization of the organism that is self-sustaining, i.e., it "free runs" in the absence of temporal cues such as the daily cycles of light and temperature.

Developmental Processes in Insects

Most insects, especially those living at higher latitudes, show seasonally appropriate cycles as indicated by activity, feeding and reproduction during the long days of summer. The winter is passed in a state of dormancy or diapause. Recent experimental studies designed to explain the circadian rhythms and photoperiodism in a diapausing insect have been conducted with the blow fly, *Calliphora vicina*. Both the locomotor activity rhythm and the rhythm system underlying photoperiodic timing are part of a circadian system and are dependent upon the environmental light cycle for entrainment and/or photoinduction. They appear to be brain-centered. Research on the blow fly indicates some differences, however. The locomotor activity in the adult fly shows an average circadian period of 22.5 h, whereas the photoperiod timing is much closer to 24 h. The suggestion made is that the locomotor activity is neural, while the photoperiod may have a humoral output, perhaps arising from the ovaries.

The conclusion is that circadian rhythms overall are an integral component of insect developmental processes, including diapause.

Studies carried out with the European corn borer, *Ostrinia nubilalis*, led to the conclusion that thermoperiodic and photoperiodic responses involved identical biological clock systems. Similar conclusions have been made with other insects, notably the cockroach, *Leucophaea maderae*, even though the latter insect does not undergo diapause (Fig. 24).

Spectrum of Rhythms

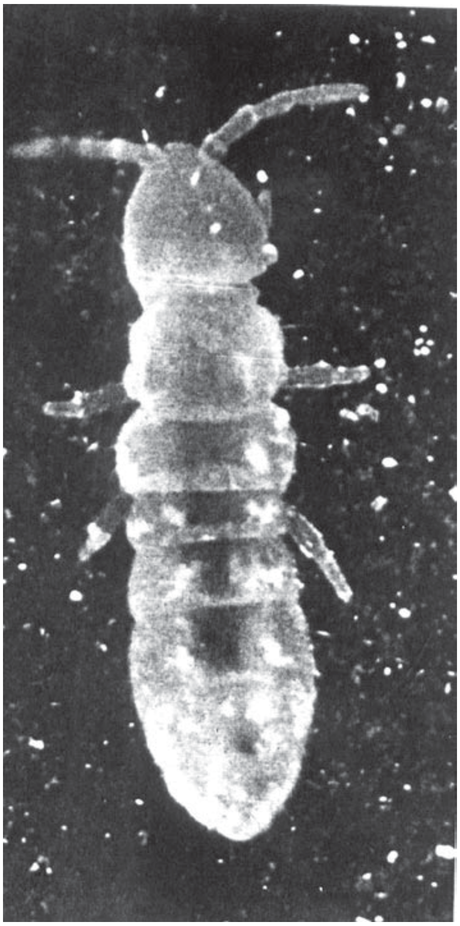
Rhythm frequencies include ultradian (0.5–20 h), circadian (20–28 h), and infradian (28 h to 6 days); those with low frequencies include circaseptan (about 7 days), circavigintan (about 20 days), circatrigintan (about 30 days), and circannual (about 1 year).

Circaseptan rhythm deserves a more complete discussion as it was discovered in a primitive insect (springtails, Order Collembola), namely *Folsomia candida*, and can be considered as a model for the study of infradian rhythmicity (Fig. 27). This insect is parthenogenetic. Insects were studied in the dark under humid conditions; daily counts of egg laying determined that egg deposition recurred at 7 days, the average number being 46.6, at a constant temperature of 15°C. With higher temperatures (not optimum), the interval between oviposition became circasemiseptan (about 3 days). The lengthening of the egg-laying interval also occurred with aging of the insects. The infradian rhythm of oviposition does not have any obvious environmental counterpart. A study of molting (ecdysis) determined that an infradian rhythm (about 3 days periodicity) occurred at 23°C.

Further studies with *Folsomia candida* determined that life spans could be varied by shifting from an optimal environmental temperature (20°C.) to a nonoptimal environmental temperature of 25°C. The temperatures were alternated every 12 h. The greatest longevity was found to be when the shift intervals were 7 days (circaseptan). A separate study with a Dipteran, the face fly, *Musca autumnalis*, revealed that shifts of the lighting regime every 2 or 9 days shifted at intervals of 7 days apart, had relatively short survival times, whereas some groups that were shifted at intermediate intervals did as well, or better, than the controls. One other documented circaseptan frequency response to the shifts of the lighting regimen of growth was found in an algal species, *Acetabularia mediterranea* (Fig. 26).

Lunar Rhythms

Lunar rhythms (circatrigintan) occur at about 30 days. Documented examples of lunar rhythms

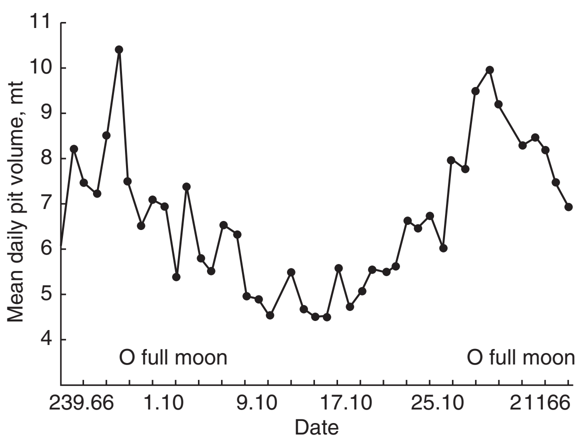


Rhythms of Insects, Figure 26 ***Folsomia candida*** **adult (Collembola: Isotomidae).**

have been found in a limited number of insects. Studies on the mayfly, *Povilla adusta* (Ephemeroptera), showed a periodicity of emergence from Lake Victoria in West Africa and in a crater lake, Barombi Mbo, with the emergence of adults occurring in greatest numbers after the full moon.

The ant-lion *Myrmeleon obscurus* (Myrmeleontidae), builds pits to capture prey. Using the volume of pits as a measure, it was found that maximum pit-building activity occurred at the full moon (about 28 days). This species also has a solar day activity (Fig. 27).

Experiments with a midge, *Clunio marinus* (Chironomidae), living in the intertidal zones of the Atlantic and the Pacific oceans have demonstrated semilunar rhythms. Adult emergence was governed by the superposition of a circadian rhythm that controlled pupal eclosion, and a semilunar rhythm that determined the beginning of pupation. The best documentation was done with the midge population from Normandy, France. The same species showed greater variation of the rhythm in other oceanic areas. In northern latitudes, the brightness of the moon may influence the behavior of the midge.



Rhythms of Insects, Figure 27 Daily pit volume of fifty ant lion (*Myrmeleon obscurus*) larvae subjected to normal daylight conditions and each larva fed one ant per day. Times of full moon shown by circles (after Youthed G J, Moran V C (1969) Insect Physiol 15:1259–1271).

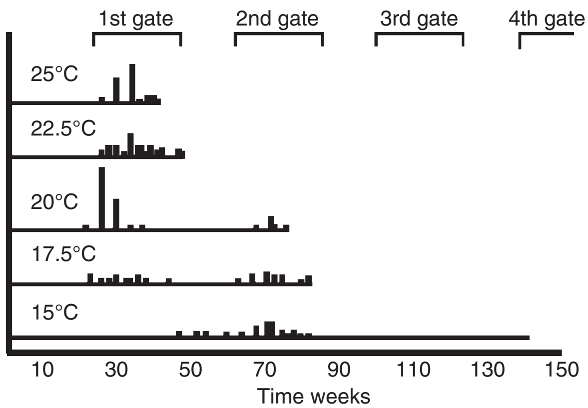
Circannual Rhythms

Circannual rhythms are uncommon. The best documented case is with a carpet beetle, *Anthrenus verbasci* (Dermestidae), which commonly has a life cycle of 2 years, termed "semi-voltine." It feeds on material of animal origin and is often found in house sparrow nests. The first winter is spent in diapause as a young larva, and the second winter as a full-grown larva. These larvae pupate and emerge the following spring. The period of the rhythm was between 41 and 44 weeks. When larvae were reared at cooler temperatures, 15–20°C, the larvae underwent two cycles of development and did not pupate until about 41 weeks after the first group reared at 25°C. This delay by the group reared at cooler temperatures indicated a phenomenon called "gated" rather than a continual or gradual sequence of pupation. This "gated" phenomenon had been previously shown by several workers investigating pupal eclosion in the fruit fly *Drosophila pseudoobscura*. Thus, the circannual rhythm in the carpet beetle was the result of the natural seasonal change, attributed primarily to day length (Fig. 28).

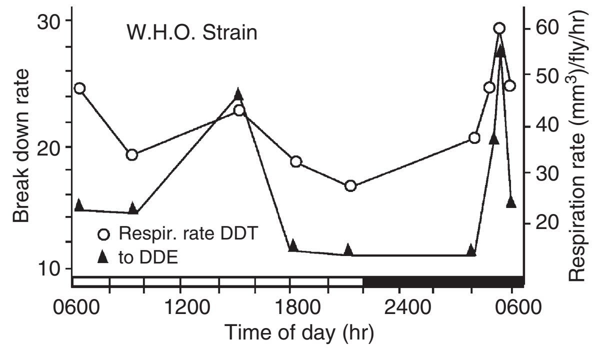
Some experiments with short-lived aphids (Hemiptera) showed that they appear to distinguish spring from autumn. Experiments with *Megoura viciae*, for example, indicated a non-rhythmic interval timer that prevents the aphids from responding prematurely to short days in the spring. No sexual forms were produced for as long as 90 days in a short photoperiod (at 15°C). After this duration, the photoperiod response was restored and reproducing oviparae were produced under the short-day treatment.

Interrelationships of Circadian Rhythms and Insecticide Sensitivity

A number of studies have explored the possibility that toxicity to an insecticide or toxin could be



Rhythms of Insects, Figure 28 **Circannual rhythm of pupation in *Anthrenus verbasci* (Oermestidae) using constant conditions of temperature, humidity and darkness. A black square represents the time of pupation to the nearest week, of an individual. Those at higher temperatures utilize the first gate; at lower temperatures an increasing number are required to wait (after Blake G M (1959) Nature (London) 183:126–127).**



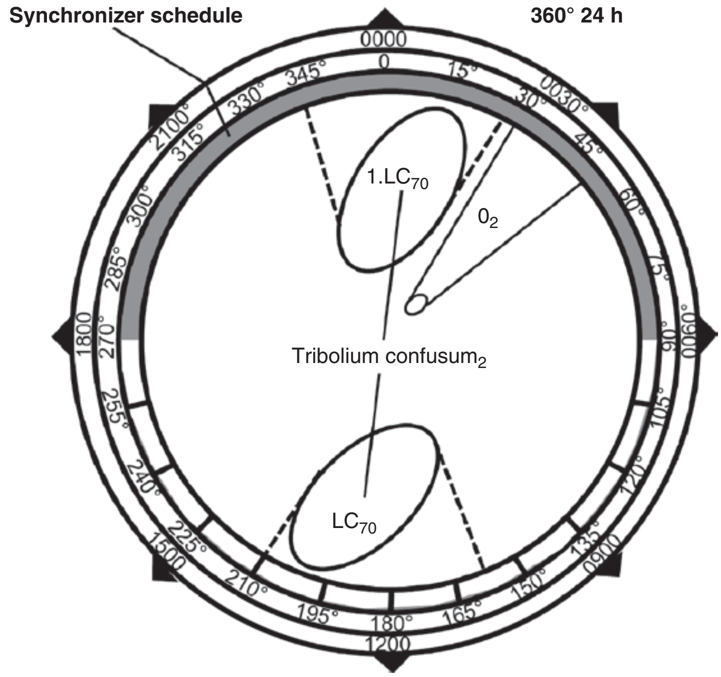
Rhythms of Insects, Figure 29 **The effect of time on the treatment of adult flies, *Musca domestica*, with DDT on rate of respiration (open circles) and conversion of DDT to its metabolite, DDE (after Shipp E, Otton J (1976) Ent Exp et Appl 19:235–242).**

related to a critical time in the insect rhythm, particularly with respect to lighting or photoperiod ("photophase" or daylight and "scotophase" or a dark period). In house flies, the respiratory rate correlated with the conversion of DDT (dichlorodiphenyltrichloroethane) to DDE (a metabolite). Both occurred in the mid-light period (Fig. 29). In a separate study, using the flour beetle, *Tribolium confusum*, measurements of their oxygen consumption were related to the sensitivity to a rapid acting organophosphate insecticide, dichlorvos. This species, normally feeding on flour, showed the greatest sensitivity in the middle of the dark period, while the peak in oxygen consumption occurred 2 h later (Fig. 30). Nocturnal species, such as German cockroaches and house crickets, showed the greatest sensitivity a few hours after the onset of a daily dark span. Several diurnal species, including the boll weevil, the pink bollworm and the two-spotted mite, showed the greatest sensitivity shortly after the onset of the light span.

The larvae and adults of the mosquito, *Aedes aegypti*, showed the greatest sensitivity to insecticides at the beginning of the dark period. Biting habits of mosquitoes reveal their greatest occurrence in the early evening, although a second period may occur before dawn, or late in the dark period. Noteworthy is the fact that both the larvae and the adults had maximum sensitivity to an insecticide at approximately the same time. The insecticides evaluated were dichlorvos on the adult mosquitoes and chlorpyrifos on the mosquito larvae.

Rhythmic events using locomotory activity in relation to sensitivity to an insecticide were studied in the American cockroach. The greatest sensitivity to dichlorvos occurred near the onset of the dark span, with locomotory activity occurring about 3 h later. In a separate study using house crickets, *Acheta domestica*, a positive relationship occurred with maximum locomotor activity and sensitivity to three anesthetics, namely ether, chloroform and carbon tetrachloride. The peaks occurred during early scotophase. The cricket can be considered to be nocturnal.

A study of the circadian rhythm of the nerve enzyme acetylcholine esterase showed synchronization with sensitivity to two insecticides,



Rhythms of Insects, Figure 30 **The lethal concentration (LC 70) of an insecticide, dichlorvos, expressed as a reciprocal to flour beetles, *T. confusum*, indicating a 2-h earlier lethal effect than peak oxygen consumption. The peak or acrophase of oxygen consumption occurred about 3 h after the middle of the daily dark span (after Vea HH et al. (1977) Chronobiologia 4:313–323).**

carbaryl and malathion. The test insect was the rice grasshopper, *Aiolopus thalassinus*, a diurnal species. The peak or acrophases of both rhythms occurred during the photophase at about the same time. A study conducted much earlier revealed a trimodel (8-h period) rhythm in the larvae of the mosquito, *Aedes aegypti*. The enzyme Mg^{2+} ATPase was measured in relation to its inhibition by the insecticide gamma chlordane.

Exceptions to the generalization that insecticide sensitivity has circadian rhythm peaks at or near the time of circadian peaks of insect metabolism were found in studies with a nocturnal insect, the cockroach, *Leucophaea madeira*, and the house fly, *Musca domestica*, a diurnal species. Similar peaks were found in sensitivity to pyrethrum, whereas peak activity and metabolism were distinctly different times in a 24-h period.

The practical application of the circadian sensitivity to toxins has had limited study. Perhaps it deserves greater attention to refine insecticide usage and insect sensitivity.

References

Blake GM (1959) Control of diapause by an "internal clock" in *Anthrenus verbasci* (L.) (Col. Dermestidae). Nature (London) 183:126–127

Cole CL, Adkisson PL (1965) A circadian rhythm in the susceptibility to an insecticide. In: Aschoff J (ed) Circadian clocks. North-Holland Publishers, Amsterdam, The Netherlands, pp 39–313

Cutkomp LK, Marques MD, Snider R, Cornelissen G, Wu J, Halberg F (1987) Chronobiologic view of molt and longevity of *Folsomia candida* (Collembola) at different ambient temperatures. Adv Chronobiol 227A:257–264

Giebultowicz JM (2000) Molecular mechanism and cellular distribution of insect circadian clocks. Annu Rev Entomol 45:760–793

Saunders DS (1982) Insect clocks, 2nd edn. Pergamon, Oxford, UK, 409 pp

Ribbed-Cocoon Maker Moths (Lepidoptera: Bucculatricidae)

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Florida State Collection of Arthropods,
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Ribbed-cocoon maker moths, family Bucculatricidae, total 247 species worldwide, with most species being Nearctic (103 sp.) or Palearctic (86 sp.). Most species are in the genus *Bucculatrix*. The family is part of the superfamily Tineoidea, in the section Tineina, subsection Tineina, of the division Ditrysia. Adults minute to small (5–16 mm wingspan), with rough-scaled oblique head and an eye-cap on the antennal bases; haustellum naked; labial palpi short and porrect; maxillary palpi minute, one-segmented or absent. Maculation variable and spotted, often with iridescent markings; venation reduced (especially on hindwings) and long fringes on hindwings. Adults are mostly diurnal. Larvae are leafminers, with some changing to external leaf skeletonizing in later instars, but a few are gall makers or stem miners. Pupation is in a white spindle-shaped cocoon with a ribbed surface, unique to the family. Numerous different host plants are known but many are in Compositae. Some species are economic.

References

Braun AF (1963) The genus *Bucculatrix* in America north of Mexico (Microlepidoptera). Mem Am Entomol Soc 18:1–208, 45 pl

Friend RB (1927) The biology of the birch leaf skeletonizer *Bucculatrix canadensisella* Chambers. Bull Connecticut Agric Exp Stn (New Haven) 288:395–406

Needham HB (1948) A bucculatricid gall maker and its hypermetamorphosis. J NY Entomol Soc 56:43–50

Scoble MJ, Scholtz CH (1984) A new, gall-feeding moth (Lyonetiidae: Bucculatricinae): from South Africa with comments on larval habits and phylogenetic relationships. Syst Entomol 9:83–94

Seksjeva SV (1981) Bucculatricidae. In: Identification keys to insects of European Russia. IV. Lepidoptera, vol 2. Academie Nauk, St. Petersburg, pp 137–148 (in Russian)

Selsjeva SV (1994) Review of the mining moths (Lepidoptera, Bucculatricidae) of the fauna of Russia. In: Proceedings of the Zoological Institute, Russian Academy of Sciences, vol 255, pp 99–120, 1993 (in Russian)

Ribosomal RNA

Ribosomal RNA genes (rRNA genes) are found as tandem repeating units in the nucleolus organizer regions of eukaryotic chromosomes. Each unit is separated from the next by a nontranscribed spacer. Each unit contains three regions coding for the 28S, 18S, and 5.8S rRNAs.

Ribosome

A self-assembling cellular organelle comprised of proteins and RNA in which translation of mRNA occurs. Ribosomes consist of two subunits, each composed of RNA and proteins. In eukaryotes, ribosome subunits sediment as 40S and 60S particles.

Ricaniidae

A family of bugs (order Hemiptera, suborder Fulgoromorpha). All members of the suborder are referred to as planthoppers.

► Bugs

Rice Weevil, *Sitophilus oryzae* (L.) (Coleoptera: Curculionidae)

This is one of the key pests of stored grain.

► Stored Grain and Flour Insects

Richardiid Flies

Members of the family Richardiidae (order Diptera).

► Flies

Richariidae

A family of flies (order Diptera). They commonly are known as richardiid flies.

► Flies

Richards, Owain Westmacott

O.W. Richards was born on December 31, 1901, and educated at Oxford University, Oxford, England. In 1927 he moved to Imperial College, and worked at the College Field Station at Slough on stored products pests until 1947. He remained at Imperial College until his retirement in 1967, and served as head of the Zoology and Applied Entomology Department for many years. Richards was principally interested in taxonomy, ecology and the theory of evolution. He had considerable expertise with various groups of flies, but was particularly interested in Aculeate Hymenoptera. His books entitled "Social insects" (1953) and "The social wasps of the Americas" (1978) reflect this latter interest. Over the course of his career, Richards published over 180 papers and six books, including two revisions (with Gareth Davies) of "Imms' general textbook of entomology" (1957, 1977). He served as president of the British Ecological Society and editor of its journal "Journal of Animal Ecology," and was considered one of the most distinguished entomologists of his generation. He died on November 10, 1984.

Reference

Davies RG, Waloff N, Southwood R (1985) O. W. Richards. Antenna 9:60–62

Ricinidae

A family of chewing lice (order Phthiraptera). They sometimes are called hummingbird lice.

► Chewing and Sucking Lice

Rickettsia

Bacteria-like, gram-negative organisms. Insect rickettsia are obligate intracellular pathogens with cell walls, but lack flagella. Some, such as *Wolbachia*, are seldom pathogenic, whereas others, such as *Rickettsiella*, are commonly insect pathogens.

Riffle Beetles (Coleoptera: Elmidae)

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The family Elmidae is divided into two subfamilies: Elminae and Larainae. The Elminae are far more abundant and diverse than the Larainae, with about 100 genera and over 1,000 species worldwide, of which 26 genera and about 100 species occur in the United States. This subfamily is represented in every American state but Hawaii and in every bordering province of Canada and state of Mexico.

Order: Coleoptera
Suborder: Polypleaga
Superfamily: Dryopiidea
Family: Elmidae

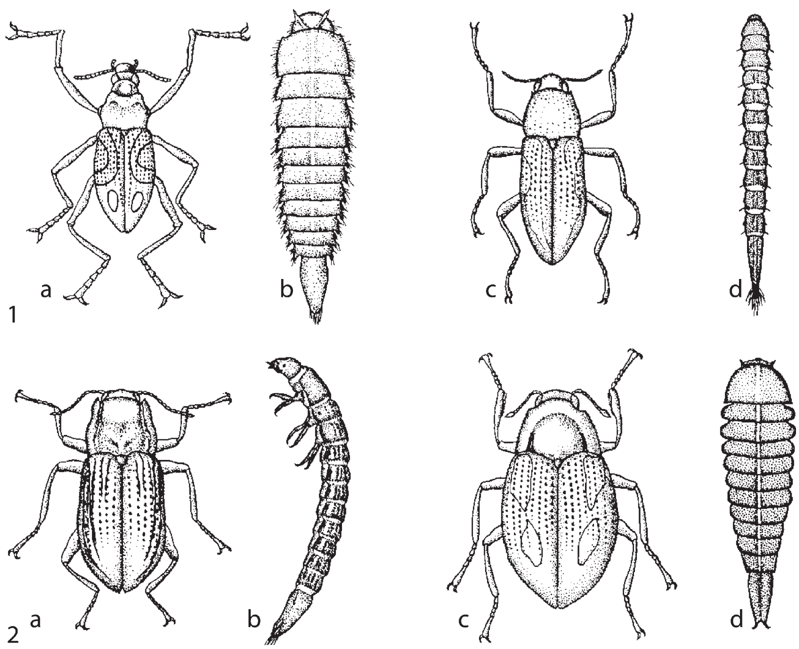
The Larainae, however, have only about 20 genera and 110 species world wide, with only two genera and no more than four species in the United States. Adult Laraines are usually found near or at the water's edge, sometimes partially submerged. When disturbed, they may fly rapidly. Some tropical species occur in swarms around cataracts or waterfall spray zones. (Big black adults of *Potamophilops* are conspicuous flying about in the spray of the world-famous Iguassu Falls shared by Brazil, Argentina, and Paraguay.) The bodies of Laraines are rather soft, and their lives as adults are much briefer than as larvae. In size, the adults range from about 3–9 mm.

Elmines are more completely aquatic, adults entering the water soon after pupation and usually never again emerging. They commonly share the habitat and food of their larvae and are rather long-lived (months or years). Although members of a few genera are quite sizable (e.g., some species of *Macrelmis* exceed 5 mm in length), most Elmines are small (1–3 mm) and some are tiny (under 1 mm) (Fig. 31).

Of the four genera illustrated, *Ancyronyx* is the most unusual. It is represented in the Western Hemisphere only by this one species. Its few known relatives occur in southeastern Asia. The other three genera are represented by a number of species in various regions of the U.S.A. *Microcylloepus*, though abundant in much of the U.S.A., is primarily Neotropical, with many species in South America. *Dubiraphia* is unusual among elmids in that the microhabitat of the larva is so different from that of the adult. *Optioservus* might well be termed the most typical elmid of American and Canadian brooks.

Ecology

Riffles are rippling streams, usually shallows across streambeds where water flows swiftly and is well aerated. In such habitats, elmids are the most typical and abundant beetles, but usually



Riffle Beetles (Coleoptera: Elmidae), Figure 31 **Riffle beetles: (i) *Ancyronyx variegates*: (a) adult, 2.1–2.6 mm long, conspicuously colored with black and yellow or orange, on or in waterlogged wood in streams of eastern North America; (b) larva, commonly with adults. (ii) *Dubiraphia vittata*: (a) adult, 1.8–2.5 mm long, brown or tan, with a broad yellowish longitudinal stripe on each elytron, clings to submerged plants in streams of eastern North America; (b) larva, usually in sediment on the bottom of streams. (iii) *Microcylloepus pusillus*: (a) adult, 1.65–2.2 mm long, reddish brown to black, often with reddish lengthwise stripe or spot on each elytron, common on many different substrates in streams of central and eastern North America; (b) larva, side view, often with adults. (iv) *Optioservus ovalis*: (a) adult, 2.4–2.6 mm long, plump, brown to black with two elongate yellowish or reddish spots on each elytron, in gravel or among mossy stones in spring-fed streams of eastern states; (b) larva, often with adults.**

quite inconspicuous. They are mostly bottom dwellers or clinging to submerged wood or debris, and do not swim or come up for fresh air.

The respiratory mechanism of adult Elmines is noteworthy because it enables them to remain permanently underwater without having to come up for fresh air. The key feature, termed a plastron, consists of a thin layer or film of air held by a dense coating of hydrofuge pubescence, or tomentum, on various parts of the legs and body. The plastron is in contact with the air reservoir beneath the elytra, into which the spiracles open. There is normally plenty of dissolved oxygen in the water of stream riffles, and oxygen can readily diffuse into the plastron, and then into the tracheal system and to all body tissues.

Since wetting agents such as soap and detergents destroy plastrons, riffle beetles do not thrive downstream from sites where people bathe and do their laundry. Other types of pollution such as sewage promote excessive bacterial growth and consequent oxygen depletion, and industrial wastes often include toxic substances. Because some species require water of great purity, whereas other species are tolerant of one or another type or quantity of pollutant, riffle beetles are useful as indicators of water quality.

In streams with high mineral content, all sorts of objects may become coated: wood, pebbles, boulders, and riffle beetles. Some elderly Elmines get covered by thick encrustations that outweigh the beetles. Other things than mineral armor often occur on riffle beetles: diatoms and sessile protozoans such as *Vorticella* are common.

Elmids range in color from tan to black, but many exhibit patterns of longitudinal or diagonal stripes or transverse bands, yellow to red. Some have prominent spots and patterns. Such aposematic coloration is probably related to the fact that elmids are not prey for most predators.

All known elmid larvae are aquatic, creeping on, or burrowing in, the substrate – some in mud, sand or gravel, some on, or under rocks, and others on, or in waterlogged wood, leaf-packs or detritus. Their respiratory mechanism employs a three-branched tuft of tracheal gill filaments that may be extruded from a cavity in the last abdominal segment, or withdrawn and covered by a trap-door-like operculum. They feed chiefly on diatoms and decaying plant materials.

When ready to pupate, mature larvae leave the water to find a suitable place in moist sand, humus, moss, or in a crevice, or beneath a rock, or under loose bark. Some larvae are able to just crawl out of the water in search of pupation sites. Drifting enables mature larvae to get from midstream to snags or boulders that they use to crawl out. Others, in streams with fluctuating water levels, simply wait in shallow water until the level drops so they can pupate in situ. In temperate regions, pupation occurs from late spring through summer, but in humid tropics, it may occur throughout the year. Pupation usually requires a week or two, though a bit longer for larger species.

Most kinds of insects use membranous wings as an important means of dispersal. Beetles are no exception, but their front wings (elytra) are relatively stiff and protective. However, the membranous hind wings are neatly folded beneath the elytra, and can pop out and unfold to serve in flight. Among Elminae, many of the newly emerged adults fly before they enter the water. Other adults never fly because their hind wings do not develop adequately. Usually, neither alates (fliers), nor non-fliers ever leave the water once they have entered it. At relatively low elevations, collecting at lights, or the use of light traps may yield hundreds of elmids. Collectors prefer light-collected specimens because they require so much less cleaning than those taken from streams.

References

Barr CB, Chapin JB (1988) The aquatic Dryopoidea of Louisiana (Cleoptera: Psephenidae, Dryopidae, Elmidae). Tulane Stud Zool Bot 26:89–164

Brown HP (1976) Aquatic drypoid beetles (Coleoptera) of the United States. Biota of freshwater ecosystems identification manual no. 6. Water Pollution Control Research Series, USEPA, Cincinnati, OH, 82 pp

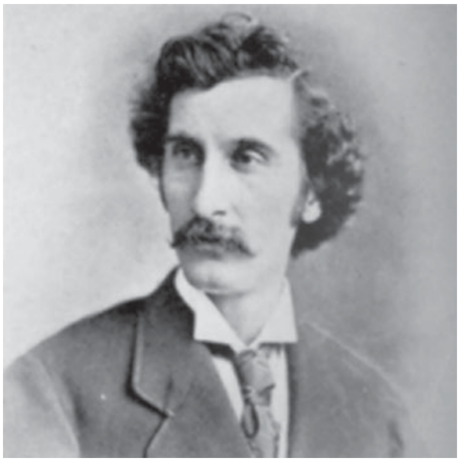
Brown HP (1981) A distributional survey of the world genera of aquatic dryopoid beetles (Coleoptera: Dryopidae, Elmidae, and Psephenidae sens. lat.). Pan-Pacific Entomol 57:133–148
Brown HP (1983) A catalog of the Coleoptera of America North of Mexico, family: Elmidae. U.S. Department of Agriculture, agriculture handbook #529-50. Agriculture Research Service, Washington, DC, i-x, pp 1–23
Brown HP (1987) Biology of riffle beetles. Annu Rev Entomol 32:253–273
Leech HB, Chandler HP (1956) Aquatic Coleoptera. In: Usinger RL (ed) Aquatic insects of California. University of California Press, Berkeley, CA, pp 293–371

Riker Mount

A thin glass-topped exhibition case.

Riley, Charles Valentine

C. V. Riley was born at Chelsea, England, on September 18, 1843. One of the foremost American economic entomologists, he was educated in England, France, and Germany, but at the age of 17 moved to a farm in Illinois, USA (Fig. 32). He soon developed an interest in entomology and in 1864 moved to Chicago and began his career in entomology as a reporter for the "Prairie Farmer." In 1868 he was appointed State Entomologist for Missouri. Over the next 9 years he devoted much of his energy to the production of the annual reports on "Noxious, beneficial and other insects of Missouri" for the years 1868–1877. These were landmark publications in the field of economic entomology, and firmly established his reputation. Interestingly, it is not so much the information content of the reports that made such a positive impression at the time, but their appearance. Unlike earlier reports, Riley's were printed in large type and were quite readable, and they had excellent illustrations. Also, he endeavored to keep the reports readable by farmers by keeping the language within the understanding of the readers. During this period Riley also lectured weekly at the University of Missouri. He and B. D. Walsh started the "American Entomologist" in 1868, and Riley became sole editor for volumes 2–3. Between 1870 and 1872 Riley lectured at Kansas State University. In 1887 the US Entomological Commission was organized, and consisted of Riley, A. S. Packard, and Cyrus Thomas. He was involved in production of 4 of the 5 reports, and also several bulletins issued between 1877 and 1881. Soon after Riley was appointed to the Entomological commission, the "locust" plague affecting much of the central and western United States collapsed. Though it was nature, not the Entomological Commission, that caused the disappearance of the grasshoppers, Riley and the Commission received accolades. In 1887, Riley was appointed Entomologist by the United States Department of Agriculture, which led to creation of the Division of Entomology and then the Bureau of Entomology. Riley was adept at identifying qualified entomologists, and soon had a nationwide effort organized. It is largely due to Riley's efforts that the United States Department of Agriculture had such a prominent entomological component, and it is due to his organizational ability that federal entomology was so successful. He founded the entomological collections of the US National Museum with a donation of his own collection of 115,000 specimens. Riley promoted the idea of state experiment stations, which eventually had a profound effect on American agriculture by



Riley, Charles Valentine, Figure 32 **C. V. Riley.**

introducing scientific discipline to the farming process. He also promoted the idea of a federal branch of economic ornithology, which brought great attention to the importance of birds as friends of farmers, and which evolved into the Bureau of Biological Survey and eventually into the Fish and Wildlife Service. Riley also was involved in the formation of the Entomological Society of Washington, in 1884, and the Association of Economic Entomologists, in 1889. Riley edited a six-volume series called "Insect life" between 1888 and 1894. Riley played a prominent role in the introduction of natural enemies of cottony cushion scale from Australia into California, and the eventual solution of the grape phylloxera problem on grapes in France. Over the course of his extremely productive career, Riley authored nearly 3,000 papers, and he was a member of nearly all the American and European entomological societies. He died at Washington, DC, on September 14, 1895, after a bicycle accident.

References

Anonymous (1895) Prof CV Riley, M.A., Ph.D. Entomol News 6:241–243

Essig EO (1931) A history of entomology. Macmillan, New York, NY, 1,029 pp

Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Ring Gland

A composite structure encircling the esophagus, and found in some Diptera, that contains both ecdysone-secreting and juvenile hormone-secreting cells.

Ring-Legged Earwigs

Some of the earwigs in the family Carcinophoridae (order Dermaptera).

► Earwigs

Riodinidae

A family of butterflies (order Lepidoptera). They commonly are known as metalmark butterflies.

► Metalmark Butterflies and Moths

Ripicolous

Use to refer to organisms associated with riverbanks.

RNA

Ribonucleic acid, one of the two forms of nucleic acids.

RNA Interference (RNAi)

RNA interference is known by other names such as gene silencing, post-transcriptional gene silencing, transgene silencing, and quelling. In RNAi, the expression of genes is inhibited. The RNAi pathway, which occurs in most eukaryotic organisms, is thought to have evolved to prevent the invasion of exogenous genetic elements such as those of viruses; thus, it is effectively an immune response, but perhaps also is involved in genome maintenance. Transposable elements, for example, introduce a lot of "chaos" into genomes because they replicate like viruses and produce foreign proteins.

DNA in the cell nucleus produces messenger RNA (mRNA), which is exported from the nucleus to the cell cytoplasm. In the cytoplasm, ribosomes translate the mRNA, creating proteins as directed by the nuclear DNA. When foreign double-stranded RNA (dsRNA) from a virus is detected in the cytoplasm, the cell's immune system is initiated, starting with activation of an enzyme called "dicer." Dicer severs the foreign dsRNA into short units of 20–25 bp called "small interfering RNAs" (siRNAs). Then, proteins in the cytoplasm called the RNA-Induced Silencing Complex (RISC) cleave the siRNAs, leaving only single strands. RISC incorporates a single strand, then searches for matching sequences in the cell. If it locates a long strand of foreign RNA containing a matching sequence it binds to it, preventing it from being used as a translation template, and effectively eliminating its capacity to damage the cell.

It is possible to introduce synthetic double-stranded RNA into cells, much like an invading virus might do naturally. In doing this, the RNAi process can be induced, tricking the cell into attacking selected genes, repressing expression or function of the gene or a region of the gene. The process is highly specific, allowing highly targeted activities. RNAi is transferable in plants, moving from one region to another, and can be transferred by grafting. RNAi activities can be induced in nematodes by feeding them bacteria carrying the dsRNA. Delivery of dsRNA to other organism is more complicated, but in some cases it has proved possible to provide delivery to insects through feeding as well as by injection. This presents the possibility that plants could be engineered with insect-specific resistance, and that other insects could be affected by feeding them baits containing dsRNA. The effects of RNAi are heritable in plants, but heritability in insects and mammals is uncertain.

RNA Polymerase

An enzyme capable of synthesizing an RNA copy of a DNA template.

Roach Stoneflies

Members of the stonefly family Peitoperlidae (order Plecoptera).

► Stoneflies

Robber Flies (Diptera: Asilidae)

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The Asilidae are a family of voracious predatory dipterans commonly known as robber flies. Distinctive features of robber flies include a hollowed-out region between the eyes, bearded facial appearance, large, strong legs for grabbing and subduing prey, and a tube-like proboscis that houses a needle-like structure (Fig. 34). This latter structure is used to stab prey and inject proteolytic saliva. Robber flies range in length from about 0.5–3 cm. They often are dull gray or brown, and generally lack bright coloration or striking patterns. However, striking metallic coloration is found in the southern Asian and South Pacific genus *Maira*, as well as in *Lampria* of the New World tropics. In addition, some robber flies are impressive bee mimics, a feature that may allow these flies to get closer to the bees they prey on, or may serve to protect these flies against vertebrate predators that have learned to associate bee color and shape with stinging ability.

The Asilidae includes roughly 7,000 known species worldwide. Based on the fossil record, the group dates back at least 35 million years. Robber flies are found on all continents except Antarctica, with the Eurasian and Australian regions having the greatest diversity. Robber flies are generally most abundant and diverse in dry and sandy areas, and in arid and semiarid regions. Apparently, relatively few species prefer woodlands, and those that do often tend to concentrate along the forest/grassland edges, perhaps because of the clearer field of view associated with these locations. Robber flies are generally quite diverse in grasslands, but shrubby grasslands tend to have the greatest robber fly diversity. This may be because the shrubs provide perching sites which are critical for finding prey and potential mates. Habitats with clay soils are generally associated with low robber fly numbers. These soils seem to provide poor habitat for the soil-dwelling larvae, probably because the texture of these soils makes movement difficult. These soils also provide relatively little vegetation for adult perches.

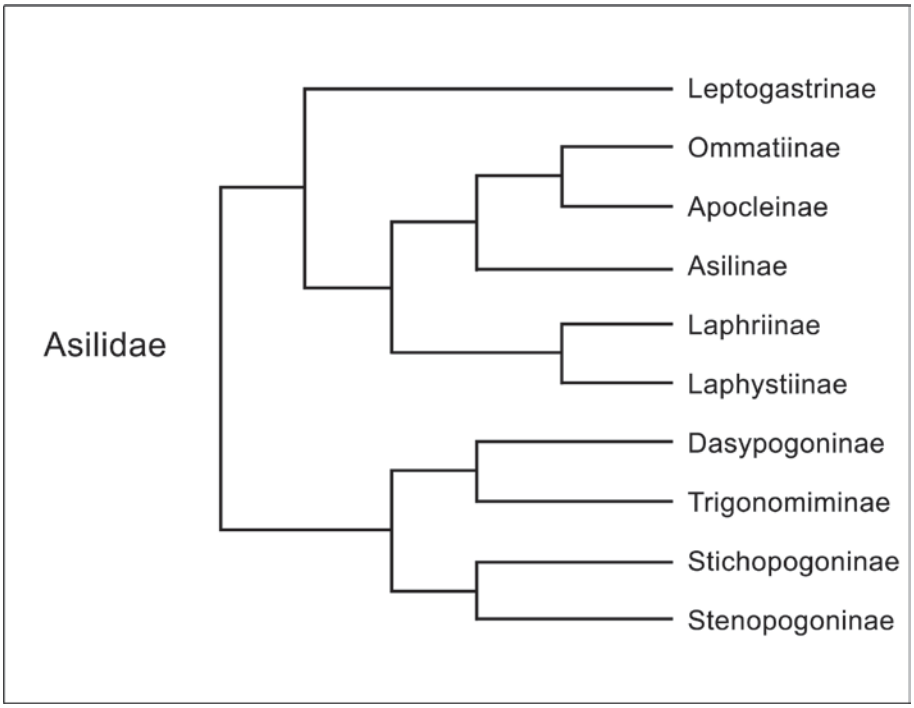
Classification and Relationships

The following is intended to put the robber fly family Asilidae into taxonomic perspective:

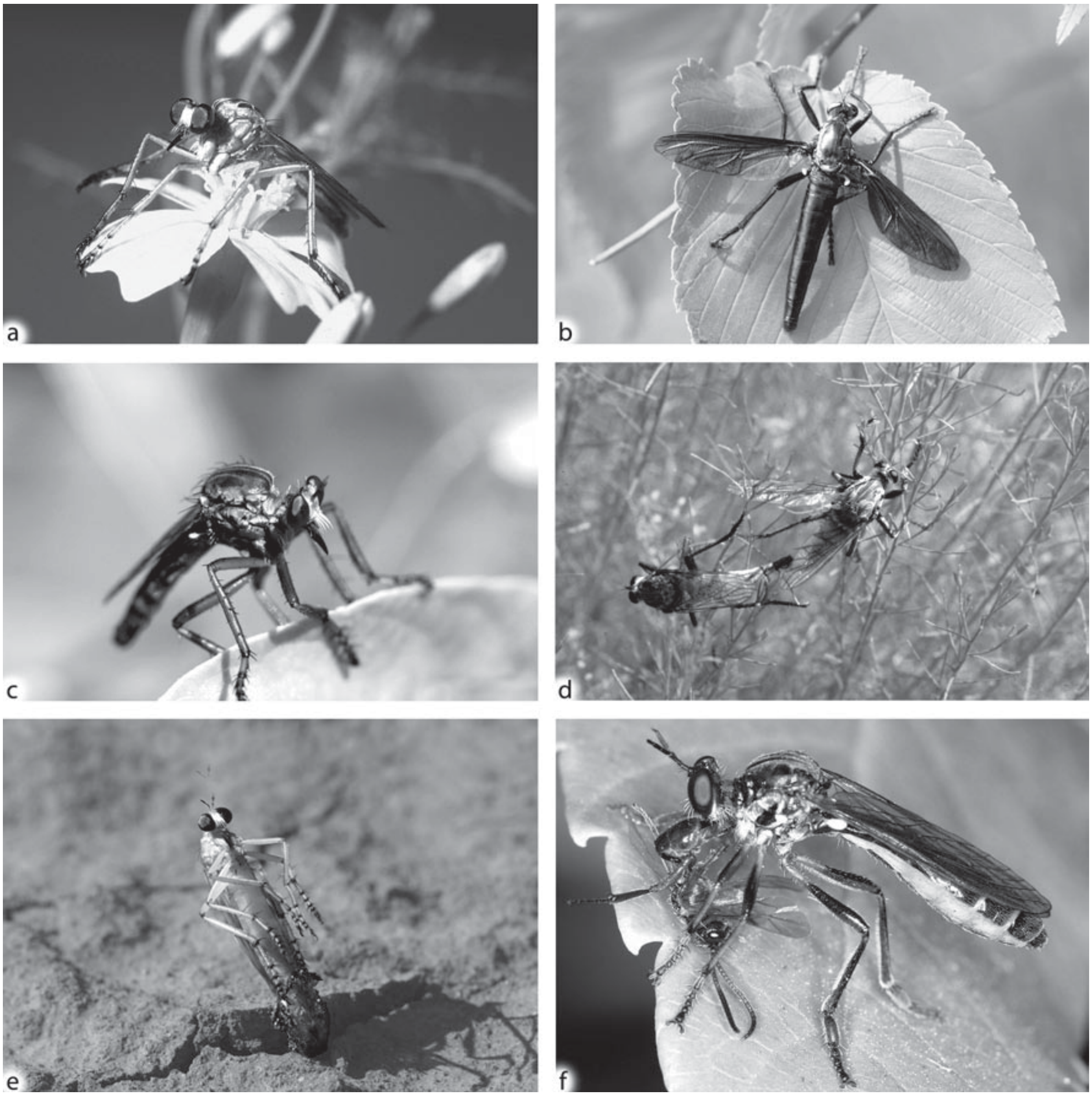
Order: Diptera (true flies)
  Suborder: Brachycera (short-horned flies)
    Superfamily: Asiloidea (robber flies and closely related families)
      Family: Asilidae (robber flies)

Some other common families that are close relatives of robber flies, and are also contained in the Superfamily Asiloidea, include the Bombyliidae (bee flies), Mydidae (mydas flies), and Therevidae (stiletto flies).

Recent classifications generally organize the Family Asilidae into 5–12 subfamilies. A hypothetical phylogeny of the subfamilies of Asilidae is shown (Fig. 33). The Leptogastrinae are commonly referred to as "grass flies." This is a relatively small subfamily, but does contain the widespread genus *Leptogaster*. *Leptogaster* is quite diverse in southern Asia, the South Pacific, and North America, but less so in Europe. The "Asilinae group" contains a trio of closely related families, the Ommatiinae, Apocleinae, and Asilinae. The first two subfamilies are sometimes included as tribes within the Asilinae. The Ommatiinae includes the widespread genus *Ommatius*, which appears to reach its greatest abundance in Asia, Africa, and Australia. In the subfamily Asilinae, the genus *Asilus* has been the subject of much uncertainty regarding the taxonomic status of many species. The subfamilies Laphriinae and Laphystiinae ("Laphriinae group") are likewise considered to be closely related. Both are widespread. The former includes the dominant northern hemisphere genus *Laphria*, as well as the primarily neotropical genus *Atomosia*. The Laphystiinae appear to achieve their greatest diversity in the Holarctic and African regions.



Robber Flies (Diptera: Asilidae), Figure 33 **Hypothetical phylogeny of the Asilidae (from the Geller-Grimm and Dikow website: http://www.geller-grimm.de/asilidae.htm).**



Robber Flies (Diptera: Asilidae), Figure 34 Some robber flies: (a) *Erax barbatus*, (b) *Microstylum morosum*, (c) *Diogmites angustipennis*, (d) mating robber flies in the genus *Proctacanthus*, (e) adult eclosion in *Diogmites angustipennis*, (f) *Dioctria* sp. with prey. (Photo credits: (a) courtesy of Edward L. Manigault, Clemson University Donated Collection; (b–e) courtesy of Whitney Cranshaw, Colorado State University; (f) courtesy of David Cappaert, Michigan State University.)

The "Dasypogoninae group" includes the remaining four subfamilies. The subfamily Dasypogoninae is a diverse and widespread subfamily that includes the large New World genus *Diogmites* as well as the tribe Megapodini, which is confined to the Neotropical region. The Stichopogoninae includes pale colored flies that are often associated with sandy areas or mud flats. The Stenopogoninae is a large subfamily that includes the very diverse genera *Stenopogon*, *Cyrtopogon*, and *Microstylum*. The first two genera are very well represented in the northern hemisphere, whereas *Microstylum* is particularly diverse in South Africa.

Recent molecular evidence suggests that the family Asilidae is monophyletic, with the Leptogastrinae as the basal group. The monophyly of the

Asilinae group is likewise supported, but the Laphriinae and Dasypogoninae groups are each paraphyletic.

Reproduction and Immatures

Robber flies exhibit a variety of mating behaviors. In many species, the male simply chases down a female, captures her in midair and copulates with her. But in some species, more complex courtship behaviors have evolved. These may involve relatively simple behaviors by the male such as primitive dances and hovering performed for the female. But in many species, more complex courtship rituals have evolved. In *Nannocyrtopogon neoculatus*, for instance, the male places his foretarsi underneath those of the female, almost as if the two were "holding hands." The male then rhythmically lifts the female's legs. Males of some species have even evolved elaborate structures, such as very long or strikingly colored bristles, that serve as display signals for the female. Mating in robber flies can take place tail-to-tail, or male over female with both facing the same direction. In some species, mating actually takes place in the air, whereas in others mating occurs on vegetation.

In many robber fly species, egg-laying involves simply randomly dropping the eggs. However, other species oviposit in soil or vegetation. In these latter species, the abdomen of females generally has an elongated terminal segment or blade-like structure that serves as an ovipositor, allowing placement of the egg in crevices and holes of plant tissue or under loose soil. Likewise, egg shape often reflects the female's egg-laying habits. Random-dropper eggs are generally spherical. But eggs of ovipositioning species are usually more elongate, probably so they will be more likely to stay put in the particular location the female has chosen. As in most insects, parental care is lacking. Once laid, the eggs and larvae that hatch from them are on their own.

Robber fly larvae are maggot-like, and live in soil, decaying wood or old stumps, or beneath bark. The larval stage can last from one to several years, depending on the species. It was once thought that robber fly larvae were primarily phytophagous. However, it is now well established that, like the adults, larval robber flies are predaceous, although some scavenging may occur as well. Robber fly larvae generally feed on other immature insects, such as the eggs and immature stages of beetles, grasshoppers, and flies. Larvae of some species may provide biological control of pest species. Larvae of the robber fly *Promachus yesonicus*, for instance, commonly feed on beetle larvae. This fly has been shown to be a potentially effective biological control agent of white grubs that attack the roots of various crops in China. In field experiments, the addition of *P. yesonicus* larvae reduced grub populations by up to 99% and reduced damage to wheat seedlings by up to 96%.

Robber fly pupae are generally somewhat elongate, usually with strong thorny structures on the head and/or abdomen. Pupation generally takes place in the soil. When the adult is ready to emerge, it uses muscular contractions to work its way to the surface, then breaks through the pupal case.

Predatory Habits of Adults

It was once thought that robber fly adults were bloodsuckers that fed on cattle and other large mammals. However, it is now known that adult robber flies are rapacious predators of other arthropods. Unlike many predators which specialize on relatively defenseless prey, many robber flies will attack formidable opponents such as bees and wasps, and larger species of robber flies can overcome large dragonflies and horse flies.

Some robber flies are fairly specific in their predatory habits, but most are probably opportunistic generalists. There is some evidence that interspecific competition for prey among overlapping robber fly species may be reduced by behavioral differences. For instance, three species of robber flies in the genus *Efferia* coexist in the same habitat (oak brush savannah), but perch at different heights in the vegetation, feed on different sized prey, and are active at different times of the day. Little is known regarding potential biological control impacts of adult robber flies. Studies of the grassland robber fly *Proctacanthus milbertii* estimated that these flies kill from 0.5 to 2% of the adult grasshopper population per day. However, experimental removal of robber flies from a Montana grassland resulted in increased parasitism of grasshoppers by parasitic flies. Effects of robber fly predation on pest populations probably vary depending on species, habitat, prey availability, and other factors.

Robber flies are generally daytime predators. When prey is detected, the robber fly quickly darts out, grabbing the prey with its powerful legs, well equipped with large spines for holding the prey. Once the prey is captured, the robber fly quickly subdues it by stabbing it with its short, stout beak in the neck region, between the thorax and abdomen, at the end of the abdomen, or even through an eye. Although robber flies generally dispatch their prey with little problem, struggles sometimes occur. It has been suggested that the bristles which give robber flies their fierce, bearded appearance may serve to protect the eyes when the prey does struggle. After stabbing the prey, the robber fly injects neurotoxic saliva which immobilizes the prey. The saliva also contains proteolytic enzymes that begin the process of external digestion, liquefying the tissues. The contents of the prey are then sucked out.

Robber flies typically establish a perch in open, sunny locations, where they command a good view of passing prey. The robber fly's well-developed eyes and correspondingly acute vision allow it to detect even subtle movements. The eyes are so large that most of the head appears to be composed of these two compound eyes separated only by a deep depression. It has been suggested that robber flies have stereoscopic vision. This is a useful adaptation for predators that need to locate moving prey in a complex spatial environment and accurately determine distance to the prey. The robber fly's mobile head allows it to increase its field of view.

Robber flies generally capture their prey in flight. The three pairs of large, powerful legs are often used to form a net or basket. The prey is seized primarily with the front and middle legs, with support from the remaining legs. The legs have large, strong bristles to help in seizing and holding prey. However, not all robber flies capture their prey in flight. *Stenopogon coyote* has been observed leaving their perches to attack grasshoppers on the ground. Members of the subfamily Leptogastrinae are also notable exceptions to the "perch and intercept" behaviors of most robber flies. Leptogastrines are slender, elegant flies that superficially resemble damselflies, and are known by the common name "grass flies." Instead of perching and waiting for moving prey, these flies make "patrol flights" in search of stationary prey on vegetation. When a potential victim is located, the fly pounces, seizing the prey with its two front pairs of legs.

Among the perching robber flies, some species are particular in the type of perch they use, and will change position with changing microclimate. Studies of robber flies in the genus *Efferia* have shown that the flies tend to perch on the ground early in the day when temperatures are low. The body is held low to the ground, and is oriented with the axis perpendicular to the sun. This position maximizes heat absorption from the ground and the sun. As surface temperatures increase, the flies move to perches above the ground. At the highest temperatures, the flies perch with the body axis toward the sun, reducing heat absorption by minimizing the surface area exposed to the sun. The behavior of an assemblage of desert grassland robber flies has also been found to correlate with climatic conditions. Species active during late winter to late spring tend to perch on shrubs, and thus avoid hot soil surfaces. They also thermoregulate by moving between the soil surface and the vegetation. But species active from autumn through early winter include primarily ground perching species. Behavioral thermoregulation is probably of great importance in robber fly predatory success. Insect muscle performance, and therefore flight speed and quickness of take-off, is to a great extent dependent on body temperature.

The robber flies are an important group of insects that are exquisitely well adapted for their predatory lifestyle. Their distinctive appearance and interesting behaviors make them fascinating subjects for study by both professional and amateur entomologists.

References

Bybee SM, Taylor SD, Nelson CR, Whiting MF (2004) A phylogeny of robber flies (Diptera: Asilidae) at the subfamilial level: molecular evidence. Mol Phylogenet Evol 30:789–797

Geller-Grimm F, Dikow T. Robber Flies (Asilidae). Available at http://www.geller-grimm.de/asilidae.htm. Last accessed 13 April 2008

Hespenheide HH (1978) Prey, predatory and courtship behavior of *Nannocyrtopogon neoculatus* Wilcox and Martin (Diptera: Asilidae). J Kansas Entomol Soc 51:449–456

Hull FM (1962) Robber flies of the world. Bull US Nat Mus 224:1–907

Joern A, Rudd NT (1982) Impact of predation by the robber fly *Proctacanthus milberti* (Diptera: Asilidae) on grasshopper (Orthoptera: Acrididae) populations. Oecologia 55:42–56

Lavigne RJ (1963) Notes on the behavior of *Stenopogon coyote* Bromley with a description of the eggs. Pan-Pacific Entomol 39:103–107

Lavigne RJ (2003) Evolution of courtship behaviour among the Asilidae (Diptera), with a review of courtship and mating. Stud Dipterol 9:703–742

Lavigne RJ, Dennis DS (1985) Ethology of three coexisting species of *Efferia* (Diptera: Asilidae) in Mexico. Proc Entomol Soc Washington 87:146–160

Londt JGH (1994) Afrotropical Asilidae (Diptera) 26. Ethological observations, and a possible ecological classification based on habits. Ann Natal Mus 35:97–122

Oldroyd H (1964) The natural history of flies. Weidenfeld and Nicolson, London, UK

O'Neill KM, Kemp WP, Johnson KA (1990) Behavioral thermoregulation in three species of robber flies (Diptera: Asilidae: *Efferia*). Anim Behav 39:181–191

Rees NE, Onsager JO (1985) Parasitism and survival among rangeland grasshoppers in response to suppression of robber fly (Diptera: Asilidae) predators. Environ Entomol 14:20–23

Wei X, Xu X, DeLoach CJ (1995) Biological control of white grubs (Coleoptera: Scarabaeidae) by larvae of *Promachus yesonicus* (Diptera: Asilidae) in China. Biol Control 5:290–296

Whitford WG, Forbes GS, Kerley GI (1995) Diversity, spatial variability, and functional roles of invertebrates in desert grassland ecosystems. In: McClaran MP, Van Devender TR (eds) The desert grassland. University of Arizona Press, Tucson, pp 152–195

Wood GC (1981) Asilidae. In: McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR, Wood DM (eds) Manual of Nearctic Diptera, vol 1. Monograph No. 27. Research Branch, Agricultural Canada, Ottawa, pp 549–573

Robineau-Desvoidy, Jean Baptiste

Jean Baptiste Robineau-Desvoidy was born at St. Sauveur in Puisaye, Department of Yonne, France, on January 1, 1799. He studied in Paris and obtained his doctorate in 1822, and then returned to his native town where he divided his time between medical duties and the study of natural history. Robineau-Desvoidy lived in a marshy area, a generally unhealthy environment. His death in 1857 at the age of 57 is attributed to this environment. At his death, a colleague took on the posthumous publication of Robineau-Desvoidy's work, "Diptères des environs de Paris." He published a large and important work in 1830 that was controversial and not well received. His basic thesis was that the classification of the adults could be based on the mode of life of the immature stage. As an indication of the disapproval by some of his colleagues, Macquart, in his "Histoire Naturelle des Diptères" ignores Robineau-Desvoidy. However, in his 1830 publication "Essai sur les Diptères" Robineau-Desvoidy described many exotic Diptera from South America and the West Indies.

Reference

Papavero N (1971–1973) Essays on the history of Neotropical dipterology with special reference to collectors (1750–1905). Museu de Zoologia, Universidade de São Paulo, Brazil

Robust

Within statistics and sampling, the quality of being widely applicable. For example, a sampling plan is robust if it can be used to precisely estimate the density of an arthropod under many different environmental conditions.

► Sampling Arthropods

Robust Marsh-Loving Beetles

Members of the family Lutrochidae (order Coleoptera).

► Beetles

Rock Crawlers (Grylloblattodea)

Rock crawlers are a small order of primitive orthopteroid insects known only from Siberia, Japan, and North America. The order name is based on the Latin words *gryllus* (cricket) and *blatta* (cockroach). Sometimes this order is called Notoptera. The number of described species numbers about 20 in a single family, Grylloblattidae.

Characteristics

Rock crawlers are elongate, wingless insects. As the name "Grylloblattodea" implies, they resemble crickets and cockroaches, though the similarity with *Timema* walkingsticks also is apparent. As with other orthopteroids, the mouthparts are of the chewing type. Rock crawlers measure 14–30 mm in length, and are elongate and cylindrical. Eyes are small or absent. The head is large, consistent with orthopteroids. The antennae are filiform, moderate in length, and shorter than many crickets and cockroaches. The legs are unspecialized, and the tarsi have five segments ending with a pair of claws. The body segments are clearly differentiated, and the abdomen consists of ten segments. The tip of the abdomen bears a pair of segmented cerci, and in the case of the female, the ovipositor is of nearly equivalent length. The nymphs resemble the adults except for size. There are nine nymphal instars.

Biology

Rock crawlers are found among rocks, often in association with glaciers. Some dwell in caves. They are nocturnal, and apparently feed principally upon organic matter such as dead insects found on snow fields and glaciers. The adult deposits eggs singly in the soil or among moss, and the egg requires an incubation period of about a year. A protracted period of time, probably 5 years, is required to attain maturity. Rock crawlers are rarely observed, and their biology is poorly known.

References

Arnett RH Jr (2000) American insects 2nd edn. CRC Press, Boca Raton, FL, 1003 pp

Gurney AB (1953) Recent advances in the taxonomy and distribution of Grylloblatta (Orthoptera: Grylloblattidae). J Washington Acad Sci 43:325–332

Kamp JW (1970) The cavernicolous Grylloblattodea of the western United States. Ann Speleol 25:223–230

Nickle DA (1987) Order Grylloblattodea (Notoptera). In: Stehr FW (ed) Immature insects, vol 1. Kendall/Hunt Publishing, Dubuque, Iowa, pp 143–144

Rocky Mountain Spotted Fever

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Rocky Mountain spotted fever (RMSF) is caused by the bacterium *Rickettsia rickettsii*, a member of the spotted fever group of Rickettsiae, and transmitted by several species of ticks belonging to the family Ixodidae. Rickettsiae are intracellular parasites of eukaryotic cells. RMSF is a zoonosis that is cycled in small rodents, rabbits, dogs and other domestic mammals. Humans are accidental hosts and are not part of the natural transmission cycle. The maintenance and persistence of RMSF in domestic and wild animals is complicated. Serological tests have shown that antibodies to *R. rickettsii* exist in many species of ground feeding birds and at least 31 species of mammals. Not all these animals are of equal importance in maintaining the disease in nature. Meadow voles and chipmunks can develop high rickettsemias sufficient to infect more than 50% of ticks feeding on them. Dogs show symptoms of RMSF and often have a high seropositivity in areas where RMSF occurs. They have a low level of rickettsemia which is transitory in nature, and consequently dogs are not believed to be important as a reservoir potential of RMSF. However, dogs are important in bringing infected ticks into contact with humans.

RMSF occurs in most of the continental states of the USA, some parts of Canada, in Mexico, and in some parts of Central America, Brazil and Colombia. The disease is endemic in most of these areas. RMSF, also known as tick-borne typhus, has several local names, including the black measles in the Rocky Mountain region, Mexican spotted fever or fiebre manchada in Mexico, tobia fever in Colombia, and Sao Paulo fever or fiebre maculosa in Brazil. Six species of ixodid ticks are known to harbor and transmit *R. rickettsii* in nature, the Rocky Mountain wood tick *Dermacentor andersoni*, the American dog tick *Dermacentor variabilis*, the lone star tick *Amblyomma americanum*, the brown dog tick, *Rhipicephalus sanguineus*, the cayenne tick *Amblyomma cajennense*, and the rabbit tick, *Haemaphysalis leporispalustris*. The principal vectors of RMSF to humans are the Rocky Mountain wood tick in the western USA and Canada, the American dog tick in the rest of the USA, the brown dog tick in Mexico, and the Cayenne tick in Central and South America. Several species of Ixodes from the eastern and southern states of the USA as well as *Dermacentor occidentalis* and *Ixodes pacificus* in California are known to have natural infections of *R. rickettsii*, but their role in the transmission of RMSF is not understood. It is not yet clear what role the lone star tick plays in transmission of RMSF, although it can transmit the disease to humans. The rabbit tick rarely bites man, but it is important in maintaining the rickettsia in animal populations because it is the only vector of *R. rickettsii* found in all regions of the continental USA where the disease occurs. RMSF accounts for over 95% of the reported human rickettsial disease in the United States. Almost all human infections occur through tick bites although infection can occur through the fingers during tick removal, and laboratory workers handling infected ticks or *R. rickettsii* are at special risk.

History of Rocky Mountain Spotted Fever

RMSF has an important history among the annals of arthropod-borne diseases studied by scientists. It was first described as a disease in 1896 in the Snake River Valley of Idaho, although RMSF is known to have infected pioneers in the Rocky Mountain region since at least 1872. The disease was serious and often fatal. It had a mortality rate of over 90% in the Bitter Root Valley of Montana. The United States Public Health Service sent a physician and scientist, Dr. Howard Taylor Ricketts, to Hamilton, Montana, in the center of the Bitter Root Valley. Here, he started a laboratory in the most primitive of conditions where he carried out classic experiments in vector biology. First he established that the unknown pathogen of RMSF could be transmitted directly to guinea pigs which showed symptoms of the disease after inoculation. Other workers had previously theorized that a tick was the natural transmitter of the disease, but it was Ricketts who experimentally established their role as vectors of RMSF. In his laboratory, he fed a male tick on the ear of a guinea pig previously inoculated with the pathogen and then fed this tick on two other healthy guinea pigs which came down with the disease. Healthy guinea pigs did not contract the disease when placed in close contact with infected guinea pigs, eliminating the possibility of the aerosol route of infection. Ricketts then used infected field-collected ticks to transmit the disease to a guinea pig in his laboratory. He established that any stage of a tick can transmit the pathogen and that the pathogen is transferred from stage to stage in a given tick (transstadial transfer) and to eggs of the infected females (transovarial transmission). It was subsequently found by other scientists that the pathogen was a bacterium which was named *Rickettsia rickettsii* in his honor. Ricketts died in Mexico in 1910 from typhus, a non-tick borne rickettsial disease, shortly after completing his pioneering studies on RMSF.

The laboratory Dr. Ricketts started in Hamilton, Montana, is now the Rocky Mountain Laboratory which is part of the United States National Institute of Allergy and Infectious Diseases of the National Institutes of Health. The laboratory has grown considerably and today is an internationally renowned center for the study of infectious diseases, including RMSF.

Epidemiology

A dramatic shift in the geographical distribution of human cases of RMSF has occurred in the USA. Before the 1930s, most human cases were in the Rocky Mountain region although the disease occurred sporadically throughout the continental USA. Thereafter, human cases of RMSF declined in the Rocky Mountain region, but increased greatly in the southeastern and south-central states. Over 97% of all human cases of RMSF now occur outside the Rocky Mountain region, with some 48% of all cases reported from Oklahoma, Tennessee, North and South Carolina. Why this disease underwent a dramatic decline in the Rocky Mountain region is not known. Its increase in other regions coincides with the expansion of humans from urban areas into suburban and rural areas where people have a greater chance of being bitten by infected ticks. Associated with the change in the distribution of RMSF is a change in who is likely to be infected. In the Rocky Mountain States most infected persons were males who worked farms and ranches and frequented the woods to hunt, but in the southwestern and eastern USA, females and children as well as males contract the disease. The frequency of reported cases of RMSF in the USA is greatest among males, Caucasians and children. Two thirds of the reported cases occur in children less than 15 years old. The number of RMSF cases reported in the USA has varied from about 250–1200 cases per year over the last 50 years. RMSF occurs throughout the year but over 90% of cases occur in the spring and early fall, from April to September with the peak number occurring in June and July.

Ticks can acquire *R. rickettsii* by feeding on a rickettsemic host, or through transovarial or transstadial transmission, and by venereal transmission between ticks. Ticks thus function both as a reservoir and vector of *R. rickettsii*. Venereal transmission is not deemed important in the transmission of *R. rickettsii*. Ticks feeding on an infected host must ingest a "threshold" number of *R. rickettsii* to become infected. After ingestion, rickettsiae disperse out of the midgut, usually within 5 days, to the cells of all tissues and organs of the tick including the ovaries and salivary glands. Feeding has been shown to be a stimulus for rapid multiplication of the pathogen within cells of the infected tick, increasing the chance of passage into an animal host. This rapid multiplication, known as the reactivation phenomenon, greatly increases the chances of transstadial transmission to the next life stage and transovarial transmission to eggs. Transovarial transmission can be as high as 100% of offspring, and offspring are capable of continuing the transmission through as many as 12 generations of ticks. However, in later generations, many infected ticks die soon after completion of feeding, and those ticks that survive lay a smaller clutch of eggs. Transovarial transmission is more effective in females that acquire the pathogen transstadially since *R. rickettsii* cannot penetrate tick eggs after the vitelline membrane develops. *R. rickettsii* are pathogenic to ticks, especially the more virulent strains. The actual percentage of ticks infected with *R. rickettsii* usually varies from 2 to 10% in areas of endemic RMSF but may be less than 1%.

Rocky Mountain Spotted Fever, Figure 35
Photograph of a patient with Rocky Mountain spotted fever showing the entire body and extremities covered with the rash typical of RMSF (from Sonenshine, 1993, used with permission of Oxford University Press).

Symptomology

In humans, RMSF has a variable incubation period depending on the severity of the infection. In mild cases, the incubation period is about 3–14 days, in severe infections 2–5 days. Three symptoms are common in RMSF: a sudden onset of fever, a severe frontal headache, and a rash. Often these three symptoms are accompanied by muscle and joint aches. Patients may also experience vertigo, ringing in the ears and later photophobia. The rash is present in most but not all cases of the disease, but only a little over half of patients have a rash on the palms or soles. Much less common is the additional report of a tick bite. Temperatures can rise to over 40°C. The rash usually appears between the 2nd and 6th day after onset of symptoms, and begins on the wrists and ankles and less commonly on the back then spreads to all parts of the body including the face (Fig. 35). The rash starts as small surface spots that later become raised bumps. The spots may form large discolored areas similar to a bruise, which may leave a slight scar after healing. The rash is the result of blood leakage from injured endothelium of small blood vessels. The rash is often delayed in adults for up to 7 days.

Acute cases of RMSF can result in severe damage to vital organs. The heart may suffer from muscle damage, or the patient may become deaf, or develop impaired vision, or partial paralysis. Gangrene can also occur during the disease causing loss of toes or fingers. In fatal cases, death from RMSF usually occurs 9–15 days following onset of symptoms. Death is commonly the result of encephalitis, but may also be caused by renal failure. Strains of *R. rickettsii* with different virulence occur, and several different strains can occur in the same area. Mortality rates have declined from 20 to 30% in the 1940s to anywhere from 3 to 10% presently, no doubt due to the advent of antibiotics effective against the disease and a more educated public. If untreated, recovery from RMSF is slow. Physicians are also now more skilled in early diagnosis of RMSF. Mortality from RMSF is greater when there is a delay in treatment with antibiotics, or when older people are infected, or when people with genetic deficiency of glucose 6-phosphate dehydrogenase are infected. This deficiency can result in a greater hemolysis during the course of the disease.

Treatment

It is important not to delay treatment if RMSF is suspected, and the initial diagnosis and treatment should be made on clinical grounds and must not wait for the result of laboratory tests. Most people who die from the disease have not received prompt treatment after the onset of symptoms. Tetracycline and chloramphenicol are the only antibiotics approved for treatment. The disease can be confused with meningococcemia and human ehrlichiosis. Mortality of untreated RMSF varies from 20 to 80% with an average of 25%. Commercial vaccines have been withdrawn as ineffectual.

Prevention

RMSF is best controlled by avoiding tick-infested areas, or by wearing clothing that covers the ankles and wrists and wrapping the ankles with tape when in tick infested areas. The clothing should be light colored in order to see any crawling ticks. Use of a repellent or acaricide increases protection. Daily examination of the body, especially in areas where ticks are likely to be embedded, should be a routine preventive measure. Proper removal of ticks is important, especially because transmission of the disease can occur during tick removal. For proper examination of the body for ticks and a description of how to properly remove them see the entry on "Ticks." Save the tick for species determination by a physician or scientist. Put it in a plastic bag for storage. Removal of ticks early in feeding lessens the chance of transmission of *R. rickettsii*. Education about symptoms of RMSF is very important.

► Ticks

References

Burdorfer W (1975) A review of Rocky Mountain spotted fever (tick-borne typhus), its agent, and its tick vectors in the United States. J Med Entomol 12:269–278

Dumler JS (1994) Rocky Mountain spotted fever. In: Beran GW, Steele JH (eds) Handbook of zoonoses, Section A: bacterial, rickettsial, chlamydial, and mycotic diseases, 2nd edn. CRC Press, Boca Raton, FL, pp 417–427

Sexton DJ, Breitschwerdt EB (1998) Rocky Mountain spotted fever. In: Palmer SR, Lord Soulsby, Simpson DIH (eds) Zoonoses: biology, clinical practice and public health control. Oxford University Press, Oxford, England, pp 207–215

Sonenshine DE (1993) Biology of ticks, vol 2. Oxford University Press, New York, NY, 465 pp

Sonenshine DE, Mather TN (eds) (1994) Ecological dynamics of tick-borne zoonoses. Oxford University Press, New York, NY, 447 pp

Rocky Mountain Wood Tick, *Dermacentor andersoni* Stiles (Acari: Ixodidae)

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The Rocky Mountain Wood Tick, *Dermacentor andersoni* Stiles, is distributed in western Canada east of the Coast Mountains in British Columbia, through Alberta, and Saskatchewan to 105° longitude and north to the 53rd parallel. The tick occurs in the northwestern United States including western Washington, Oregon and eastern California, Nevada, Colorado, Wyoming, Idaho and Montana. The southern limit of its range is northern New Mexico and Arizona, and the eastern limit includes western portions of North Dakota, South Dakota, and Nebraska. Preferred tick habitat in mountainous areas includes rocky slopes, clearing, outcrops and ecotones between grasslands and forest. South-facing slopes are preferred at higher elevations and in northern parts of its range. In drier, prairie habitats, the tick tends to localize in river bottoms and coulees. The presence of shrubby vegetation such as Saskatoon (*Amalanchier*) and rose (*Rosa*) are positive indicators of tick habitat, while the presence of aspen (*Populus*) is a negative indicator of tick habitat.

Rocky Mountain wood tick is a three-host tick and completes its life cycle in 1–3 years depending on latitude, elevation, and local environmental conditions. Longer life cycles occur in cooler areas such as higher elevations and more northerly latitudes. Adult ticks are brown with grey patterns and are ~3–4 mm long and 2–4 mm broad. Wood ticks have a rectangular basis capitulum and short, broad palps. The spiracle has a dorsal prolongation and numerous small goblets that distinguish it from the related species *Dermacentor albipictus* and *D. variabilis*. Adult ticks feed on various moderate to large hosts including cattle, sheep, horses, dogs, porcupines, goats, deer and humans. Adults are active in the early spring and quest when temperatures are above 10°C. In the interior of British Columbia, adults are active from mid-March through mid-May, with peak activity in early April. Ticks in prairie regions are active somewhat later, with peak activity in May through June. Adults seek hosts by climbing grasses or low shrubs and waiting for a host to approach. The adults sense carbon dioxide emanations from a potential host, become active, and attach to the host as it passes. Ticks will crawl on the host until they find a suitable site for attachment and feeding. Montane ticks tend to attach and feed on the upper surfaces of cattle near the withers while prairie ticks tend to attach to the undersides of cattle. This may be to avoid excessive exposure to increased solar radiation and host temperatures due to the later periods of activity in prairie regions. Both sexes feed on blood, although male ticks take smaller meals and may redistribute themselves on the host. Ticks that do not find a host in the spring may enter a behavioral diapause, and a small proportion of these can successfully overwinter to seek a host the following spring. Feeding females gain weight slowly during the first few days of feeding, but greatly increase the rate of engorgement after mating. Females require 7–10 days to become fully engorged, and can increase their weight from 4 to 700 mg (Fig. 36). Once engorgement is complete, the females detach, fall to the ground, and seek sheltered areas to oviposit.

The preoviposition period is dependent on temperature, ranging from 5 days at 25°C to

Rocky Mountain Wood Tick, *Dermacentor andersoni* Stiles (Acari: Ixodidae), Figure 36 Wood ticks, unfed and well fed.

20–40 days at 15°C. Females produce from 5,000 to 10,000 eggs over a period of several weeks, and die once oviposition is completed. Eggs hatch in about 4 weeks, depending on temperature. The larvae are six-legged and will attach to smaller mammals such as mice, ground squirrels, and chipmunks. Larval engorgement requires 5–10 days, and the fully engorged larvae drop from the host. Molting to the nymphal stage requires 1–4 weeks depending on temperature. Larvae are most abundant on hosts during July to August in the interior of British Columbia. Newly molted nymphs may attach to a small mammal host, engorge in 5–10 days, drop from the host, and molt to adults in 2–4 weeks depending on temperature. Nymphs that are unable to find a host may overwinter, and seek hosts the next spring. Nymphal activity thus occurs over a broader period time than do larvae, from April though August in the interior of British Columbia. Nymphs that are active early in the season are likely those that overwintered, while nymphs active later in the season likely originate from larvae produced the current year. Adults that are produced in the fall do not seek hosts but enter a behavioral diapause that must be terminated by chilling before they will resume normal feeding.

Feeding activity of adult wood ticks on cattle probably does not result in appreciable economic losses due to reduced weight gains of cattle. Adult activity occurs early enough in the season for compensatory weight gain to occur.

However, feeding ticks can cause paralysis in cattle in the interior of British Columbia south through Idaho. Paralysis can also affect sheep and humans, as well as dogs and horses. The economic effect of paralysis is difficult to estimate, but results from animal death, underuse of native pasture, and increased costs for surveillance. Currently, tick paralysis is prevented by early season application of synthetic acaricides such as Lindane. However, the availability of such compounds is increasingly limited. Other potential methods for managing ticks based on rangeland management practices have been proposed but not fully investigated.

Rocky Mountain wood ticks can vector several of diseases of humans and livestock. These include anaplasmosis in cattle, and Rocky Mountain spotted fever, Tularemia, and Colorado tick fever to humans. Disease prevention is achieved by removing ticks before feeding, and requires careful inspection after engaging in outdoor pursuits during the season of adult activity. Precautions to prevent ticks from attaching include wearing long pants outdoors, and pulling socks up over the pant legs. Repellents can also be used.

References

Gregson JD (1956) The Ixodoidea of Canada. Canadian Department of Agriculture Science Serial Publication No. 930

Rich GB (1971) Disease transmission by the Rocky Mountain wood tick, *Dermacentor andersoni* Stiles, with particular reference to tick paralysis in Canada. Vet Med Rev 1:3–26

Schaalje GB, Wilkinson PR (1985) Discriminant analysis of vegetational and topographical factors associated with the focal distribution of Rocky Mountain wood ticks, *Dermacentor andersoni* (Acari: Ixodidae), on cattle range. J Med Entomol 22:315–320

Wilkinson PR (1967) The distribution of *Dermacentor* ticks in Canada in relation to bioclimatic zones. Can J Zool 45:517–537

Wilkinson PR (1968) Pest-management concepts and control of tick paralysis in British Columbia. J Entomol Soc Br Columbia 65:3–9

Rodent Fleas

Members of the family Hystrichopsyllidae (order Siphonaptera).

► Fleas

Rodent Trypanosomiasis: A Comparison Between *Trypanosoma lewisi* and *Trypanosoma musculi*

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Trypanosoma lewisi and *Trypanosoma musculi* are protozoans that belong to the Phylum Sarcomastigophora and Subphylum Mastigophora. The Mastigophora, commonly known as flagellates, typically possess one or more flagella. Although they reproduce asexually by binary fission, sexual reproduction is known to occur. Both *T. musculi* and *T. lewisi* are assigned to the class Zoomastigophorea, family Trypanosomatidae, and order Kinetoplastida because they have flagella, typically with a paraxial rod and an axoneme. In addition, they contain a single mitochondrial kinetoplast located near the flagellar kinetosomes and a Golgi apparatus located close to the flagellar depression.

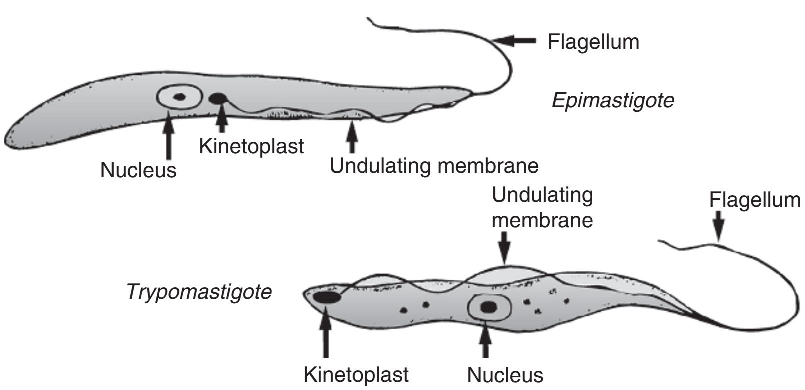
T. lewisi, a cosmopolitan parasite in the blood of rats (*Rattus* sp.), is transmitted by several species of rat fleas (*Ceratophyllus fasciatus*, *Nosopsyllus fasciatus*, and *Xenopsylla cheopis*). On the other hand, *T. musculi*, also a cosmopolitan blood parasite, is found in mice and is transmitted primarily by the rat flea, *Nosopsyllus fasciatus*. Both trypanosomes are highly specific for their vertebrate hosts where they live extracellularly, primarily in the bloodstream.

Fleas become infected with these trypanosomes upon ingesting a blood meal from an infected rodent. In the fleas, however, the trypanosomes are present in the alimentary tract, where they undergo morphological changes and then move posteriorly towards the rectum and anus. The trypanosomes are then voided in the feces of the insect vector ("posterior station transmission") and can be ingested by the rodent during grooming. Within the rodent, the trypanosomes now enter the bloodstream by way of the oral mucous membranes. Once in the bloodstream, they undergo further development and are now infective to the adult flea during a blood meal. Rosettes, which usually consist of eight daughter cells, have been found in both *T. lewisi* and *T. musculi* during in vitro cultivation. Rodents stressed by starvation, low temperature, multiple infections, or intraspecies fighting do not show an increase in the prevalence of the rosette forms.

Although *T. lewisi* was believed to be primarily monomorphic in appearance with lengths varying from 21 to 36.5 μm and an average of 30.6 μm, two additional forms (type II and III) have been observed. Type II is a morphological variation of the original type and it has a total length of 35.3–39.3 μm. The posterior end of this form is extremely elongated. The distance between the posterior end and the kinetoplast (P-K) is 11.9–15.0 μm. The average length of type III of *T. lewisi* is 26.7 μm (19.8–30.9 μm) and the distance between the posterior end and the kinetoplast is 2.9–6.3 μm. The size of *T. musculi* varied from 23 to 30 μm, with an average of 26.5 μm. This parasite has a diameter of 3–5 μm. Electron microscopic studies have shown that the kinetoplast of *T. lewisi* appears as a mass of DNA-containing fibrils, about 25 Å in diameter, lying in parallel array and situated within an enlarged portion of the mitochondrion. There are no studies on the kinetoplastic DNA replication of *T. musculi*.

The two developmental stages of *T. musculi* and *T. lewisi* differ by the position of the kinetoplast. In the epimastigote form, the kinetoplast is anterior to the nucleus, whereas in the trypomastigote form, the kinetoplast is posterior to the nucleus. Epimastigotes have been characterized as dividing, sausage shaped and juvenile forms while trypomastigotes are sometimes referred to as the adult, leaf-shaped stage. During the conversion of the epimastigote stage to the trypomastigote stage, there is a shift in the kinetoplast. The epimastigote form requires iron for its cytochrome oxidase system. When the epimastigote changes to the trypomastigote form, the trypanosomes are believed to utilize the iron from the host (Fig. 37).

Both *T. musculi* and *T. lewisi* parasites produce a self-limiting infection comprising of a growth phase, a plateau phase, and an elimination phase during a 2–4 week period. In *T. musculi* and *T. lewisi*, upon infection of their specific hosts, there is a latent period which is determined by the size of the parasitic inoculum. Following the latent period, there is a phase of rapidly increasing parasitemia in



Rodent Trypanosomiasis: A Comparison Between *Trypanosoma lewisi* and *Trypanosoma musculi*, Figure 37 **Epimastigote and trypomastigote forms of mouse trypanosomes.**

the infected blood that becomes stabilized after 6–7 days in *T. musculi* and 4–5 days in *T. lewisi*. This period is followed by a plateau phase in *T. musculi* that lasts about 7–10 days. The onset of the plateau phase with the elimination from the blood of all reproductive forms of the parasites is called the first crisis. The antibody ablastin is responsible for this elimination in *T. lewisi*-infected rats. A trypanocidal antibody is responsible for the elimination of reproductive trypanosomes in *T. musculi*-infected mice. A second crisis, at the end of the plateau phase, produces an abrupt fall in the parasitemia, and the parasites disappear from the blood within a few days. An IgM antibody is involved during this second crisis in *T. lewisi* and *T. musculi* infections. *T. lewisi* neither divides in the peritoneal cavity after the first crisis nor remains in the vasa recta of the kidneys after blood recovery from the infection. As opposed to *T. lewisi*, *T. musculi*-infected mice showed both continuous parasitic division in the peritoneal cavity and persistence of dividing forms in the vasa recta of the kidneys of the immune mice. These mice with chronic or latent infections are immune to re-infection and do not experience relapses, although isolated kidney forms and homogenates of kidneys from these animals are infective when inoculated into naive mice.

Trypanosoma musculi and *T. lewisi* infections, although referred to as non-pathogenic, can produce profound changes in the size, cellularity, and histoarchitecture of spleen, liver, lymph nodes, and thymus of the respective hosts. There are obvious pathological changes associated with the elimination of these parasites. They involve splenomegaly, marked enlargement of the lymph nodes, hepatomegaly to a lesser degree, and immunodepression, that are clinical features of the pathogenic trypanosomes in man and animal host.

Life Cycle and Control of Rodent Fleas

Fleas are holometabolous insects with an egg, several larval instars, and a pupal stage. Eggs of adult fleas are typically laid in the rodent's nest or bedding, where they hatch within a few days into larvae. The larvae feed on a variety of organic material in the nest or bedding materials of the host. Food of the larvae also may include feces of the adults which contain partially digested blood. The larvae eventually change into a pupa and then either a female or adult male emerges. Both sexes feed on blood.

Because rodent trypanosomiasis generally produces a benign infection in rats and mice, the *T. lewisi*-rat flea system (also *T. musculi*-mouse-flea system) has been used as a laboratory model for studying more virulent trypanosomes that are pathogenic to man and domestic animals. However, it is imperative that flea control strategies (e.g., improved garbage sanitation near homes where rodent populations may build up, as well as interrupting the flea development cycle, or chemicals) be used to reduce the threat or possibility of fleas vectoring the etiological agents of more serious man and animal diseases (e.g., plague, murine typhus, Q fever, etc.).

References

Ashraf M, Nesbitt RA, Gugssa A, Lee CM (1999) Development and proliferation of *Trypanosoma musculi* in the presence of adherent splenic cells. J Parasitol 85:129–132

Bogitsh BJ, Cheng TC (1990) Human parasitology. Saunders College Publishing, Philadelphia, PA

D'Alesandro PA, Clarkson AB (1980) *Trypanosoma*: avidity and adsorbability of ablastin, the rat antibody inhibiting parasite reproduction. Exp Parasitol 50:384–396

Shapiro TA, Englund PT (1995) The structure and replication of kinetoplast DNA. Annu Rev Microbiol 49:117–143

Simpson L (1987) The mitochondrial genome of kinetoplastid protozoa: genomic organization, transcription replication, and evolution. Annu Rev Microbiol 41:363–382

Vincendeau P, Guilleman B, Daulouede S, Ripert C (1986) In vitro growth of *Trypanosoma musculi*: requirements of cells and serum free culture medium. Int J Parasitol 16:387–390

Wechsler DS, Kongshavn PAL (1988) Further characterization of the curative antibodies in *Trypanosoma musculi* infection. Infect Immun 56:2379–2384

Rolled-Wing Stoneflies

Members of the stonefly family Leuctridae (order Plecoptera).

► Stoneflies

Romaleidae

A family of grasshoppers (order Orthoptera). They commonly are known as lubber grasshoppers.

► Grasshoppers, Katydids and Crickets

Romaña's Sign

This is an indication of acute infection with Chagas disease, and includes swelling of the eyelids on the side of the face near the bite wound or where the bug feces were deposited or accidentally rubbed into the eye. Other more general indications of infection, if present, may include fever, fatigue, aches of the head or body, rash, loss of appetite, diarrhea, vomiting, mild enlargement of the liver or spleen, swollen glands, and local swelling. Symptoms usually fade away after a few weeks or months. However, if untreated, the disease persists.

► Chagas

► Chagas Disease or American Trypanosomiasis

► Chagas Disease: Biochemistry of the Vector

► Assassin Bugs (Hemiptera: Reduviidae)

Rondani, Camillo

Camillo Rondani was an eminent Italian entomologist, and a renowned dipterist (Fig. 38). A native of Parma, Italy, he was born on November 23, 1803. After study in France, Rondani served as a professor of natural history at the Royal College, and served as director of the "Instituto Tecnico." An author of many publications on Diptera, his great work "Dipterologiae Italicae Prondromus," of which eight volumes were published from 1856 to 1877, was unfortunately unfinished at the time of

Rondani, Camillo, Figure 38 **Camillo Rondani.**

his death at the age of 72, on September 18, 1879. Other significant achievements include his "Degli insetti parassiti" and numerous other bulletins, and service to the Italian Entomological Society. He also published on Lepidoptera and Hymenoptera, and described numerous aphids.

References

Anonymous (1880) Obituaries, Camillo Rondani. Entomologist 13:120

Meade RH (1879) Professor Camillo Rondani. Entomol Mon Mag 15:138–139

Papavero N (1971–1973) Essays on the history of Neotropical Dipterology with special reference to collectors (1750–1905). Museu de Zoologia, Universidade de São Paulo, Brazil

Root Maggots

Some members of the family Anthomyiidae (order Diptera).

► Flies

Root-Eating Beetles

Members of the family Monotomidae (order Coleoptera).

► Beetles

Root-Infecting Fungi

Some fungi that attack roots of plants are found by the feeding activities of insects.

► Transmission of Plant Diseases by Insects

Ropalomerid Flies

Members of the family Ropalomeridae (order Diptera).

► Flies

Ropalomeridae

A family of flies (order Diptera). They commonly are known as ropalomeric flies.

► Flies

Roproniidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees, Sawflies

Rose-Grain Aphid, *Metopolophium dirhodum* (Walker) (Hemiptera: Aphididae)

This is an important direct pest of grains, but also vectors plant viruses.

► Wheat Pests and their Management

Rosen, David

David Rosen was born on April 20, 1936, in Tel-Aviv, Israel. He received his education at the Hebrew University of Jerusalem (M.S., 1959; Ph.D., 1965). His thesis research, entitled "Parasites of the Coccoidea, Aphidoidea and Aleurodidea of citrus in Israel" earned him the Jacobsen Prize in 1965. He obtained a postdoctoral appointment with Paul DeBach at the University of California at Riverside, and together they published "Species of Aphytis of the world" (1979). For this important project they received a gold medal from the Filippo Silvestri Foundation in 1980. In 1991 they published a second edition of "Biological Control by natural enemies." David also edited two volumes of "Armored scale insects: their biology, natural enemies and control" (1990), and coedited two volumes of "Pest management in the subtropics" (1994, 1996). Rosen was a powerful voice for practical implementation of biological control, and had a productive career emphasizing population dynamics of pests, particularly biological control of pests, and including the systematics of parasitoids. He served as chairman of the Department of Entomology at Hebrew University of Jerusalem, and was named Vegevani Chair of Agriculture in 1990. He served on the editorial board of several journals, and was well-known and highly respected in international biological control circles. Rosen's career included publication of 140 technical papers, 33 book chapters, and 8 books. He died on January 8, 1997.

Referencesw

Hoy MA (2000) The David Rosen lecture: biological control in citrus. Crop Prot 19:657–664

Gerson U, Applebaum SW (1997) David Rosen (1936–1997) in memorium. Phytoparasitica 25:171–174

Ross, Herbert Holdsworth

Herbert Ross was born in 1908 at Leeds, England, educated in British Columbia, Canada, and received his Ph.D. from the University of Illinois in 1933. Ross began work with the Illinois Natural History Survey in 1927 and was named head of the survey and identification section in 1935. He also held the rank of professor of entomology at the University of Illinois. Ross retired from the University of Illinois in 1969 but then worked for the University of Georgia until 1976. Herbert Ross was an authority on caddisflies (Trichoptera) and published over 200 technical publications, as well as several books. He is best known for a popular introductory text, "A textbook of entomology" (1948 and followed by several editions), but also authored "Understanding evolution" (1966), "Evolution and classification of the mountain caddisflies" (1956), and "Synthesis of evolutionary theory" (1962). Herbert Ross died November 2, 1978, at Athens, Georgia.

Reference

Anonymous (1979) Herbert Holdsworth Ross, 1908–1978. Entomol News 90:62

Rostrum

In weevils, the snout-like prolongation of the head containing the mouthparts distally. In Hemiptera, this sometimes refers to the beak or piercing-sucking mouthparts.

Rosy Apple Aphid, *Dysaphis plantaginea* (Passerini) (Hemiptera: Aphididae)

This is likely the most important of the apple-attacking aphids.

► Apple Pests and their Management

Rotation

In agriculture, purposeful alternation of crops grown on the same plot of land. In pest control, purposeful alternation of insecticides used to control a pest population.

Rotenone

This insecticide is derived from the roots of *Derris* and *Lonchocarpus*.

► Botanical Insecticides

Rothschild, Miriam

Born into a famous and wealthy banking family on August 5, 1908, Miriam Rothschild might well have pursued a leisurely, less scholarly lifestyle more typical of her class and gender during that era. Instead, she followed the lead of her father, Charles, who was a naturalist as well as a financier. Her father had obtained the world's best collection of fleas and had studied the role of fleas in the transmission of bubonic plague. So Miriam spent many years preparing a six-volume illustrated catalogue of the Rothschild Collection of Fleas, earning her the honorary title of "Queen of Fleas."

Miriam Rothschild was married, and raised six children, but also pursued her scientific enterprises actively, publishing more that 300 papers in scientific journals. She was awarded eight honorary doctorates from institutions in three countries. In addition to the aforementioned taxonomic interests, she studied flea behavior, producing now-classic studies on the synchronization of the sexual cycle of the rabbit flea and its host. Later in life she became fascinated with chemical ecology, particularly the role of secondary plant compounds on caterpillar feeding behavior. Rothschild's interests also extended to butterflies, snails, trematodes, and birds, and she became a well-known naturalist in Britain, and elsewhere, as her public appearances on radio and television were broadcast. In 1991, she published the book "Butterfly Cooing Like a Dove," which helped to popularize insects. Eventually she turned her attention to wildflower habitat preservation and became an ardent conservationist. She died February 20, 2005.

Reference

Ewing SA (2005) Miriam Rothschild 1908–2005. J Parasitol 91:1293

Rotoitidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Rottenwood Termites

Members of the termite family Termopsidae.

► Termites

Roubal, Jan

Jan Roubal was born at Chudenice, Czech Republic, on August 10, 1880. He was educated at the university in Prague, and in 1905 left the university as a high school teacher. He continued as a gymnasium teacher and director until he retired in 1940, when he directed his entire energy to the study of entomology. Roubal is reputed to have had an encyclopedic knowledge of Coleoptera. This, combined with an outgoing and unselfish personality, made him an important and influential coleopterist in middle Europe. He preferred the Staphylinidae, and influenced many others to work with this large group. He published over 300 papers, mostly on beetles but also on Hemiptera/Heteroptera. His "Katalog Coleoper (brouků) Slovenska a Parkarpatska" was published in three volumes (1930–1941) and set a new standard for catalogs because it contained extensive habitat data and comments. Roubal died at Prague on October 23, 1971.

Reference

Herman LH (2001) Roubal, Jan. Bull Am Mus Nat Hist 265:129–131

Round Fungus Beetles

Members of the family Leiodidae (order Coleoptera).

► Beetles

Roundheaded Pine Beetle, *Dendroctonus adjunctus* Blandford (Coleoptera: Curculionidae, Scolytinae)

JOSE F. NEGRON
USDA Forest Service, Ft. Collins, CO, USA

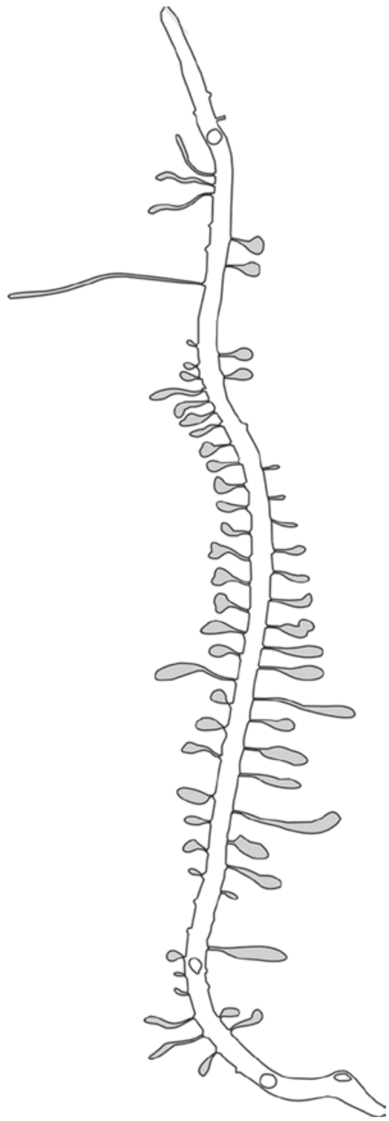
The roundheaded pine beetle, *Dendroctonus adjunctus*, is an important bark beetle that attacks and kills various species of pines from Nevada, Utah, and Colorado south to Guatemala. In the Southwestern United States its primary host is ponderosa pine, *Pinus ponderosa*. It often occurs in trees in conjunction with the western pine beetle, *Dendroctonus brevicomis*, and pine engravers of the genus *Ips*. Like other tree-killing bark beetles, the roundheaded pine beetle causes tree mortality by feeding and developing in the phloem of the tree. Utilization of the phloem for habitat and nourishment results in girdling of the tree so that translocation of nutrients is impeded. The insect also inoculates attacked trees with blue-stain fungi *Ophiostoma adjuncti* and *Leptographium pyrinum*, but the ecological role of these in helping the insect kill the tree or providing nutritional benefits to the insect is unclear.

Patterns of tree mortality range from a single tree to groups of tens to hundreds of trees. Occasionally, only a portion of the tree is attacked, commonly referred to as a strip attack, and the tree usually survives. Initial symptoms of attack include an accumulation of brown-reddish boring dust at the base of the tree and in bark crevices. As the insect enters the tree, resin canals, which are the primary defensive mechanism of the tree, are severed and resin exuded. The resin then solidifies on the outer surface of the bark forming a pitch tube. As the tree dies, the foliage changes in color from green to a light yellow and then bright orange within the first year of attack.

In the Southwest, the roundheaded pine beetle has generally a 1-year life cycle. The primary emergence and dispersal flight of the insect occurs in late October and early November, with some variation observed among geographical locations. Soon after emergence females seek suitable hosts for attack. Colonization of new hosts involves a complex chemical communication system of pheromones and host chemicals.

Once the adult beetles enter the tree, a small chamber is excavated and then the main egg gallery begins either to the right or left of the chamber for the first 2.5–5 cm. The egg gallery then turns vertically moving upward with the grain of the wood and gently meandering to the right or left (Fig. 39). The gallery is constructed by the female and packed with frass by the male behind. Galleries as long as 122 cm have been observed but they are normally about 31 cm and located in the inner bark but do score the wood. Ventilation holes are excavated about every 4–8 cm. Females oviposit single eggs in niches alternately on both sides of the gallery. Egg niches are about 1.5 mm across and about 1 mm deep and are covered with frass and other debris. Egg niches are about 4–8 mm apart. Oviposition begins after the tree is invaded, ceases through the winter, and then resumes in the spring, usually March, and continues into April.

The eggs are pearly white, oblong, and about 1 mm in length and 0.6 mm in width. Some eggs may begin hatching in the fall, but the majority will hatch in the spring. The eggs and egg-laying adults are the primary overwintering stage. The larvae are legless, grublike, mostly translucent but with light reddish-brown coloration. Each larva constructs its own larval gallery, which are most commonly 4–15 mm in length. There are four larval instars. Average head capsule width for instars 1–4 is 0.5, 0.7, 1.0, and 1.2 mm, respectively. Average body length for the fourth instar is about 6.3 mm. Larval development through the third instar is rather fast and rather slow in the fourth instar. Pupation occurs at the end of the larval gallery usually between June and August. Average length of the pupae is 5.2 mm. The beetles will usually complete development and become adults by the middle of August but will remain on the tree until the flight period begins again in the fall.



Roundheaded Pine Beetle, *Dendroctonus adjunctus* Blandford (Coleoptera: Curculionidae, Scolytinae), Figure 39 **Roundheaded pine beetle egg gallery (drawing by Joyce VanDeWater).**

Newly emerged adult beetles are shiny black with a reddish tint in the elytra; parent adults are shiny black. Males exhibit heavy pigmentation along the angular rear margin of the seventh abdominal tergite while females have a transverse elevated ridge on the anterior area of the pronotum, which is lacking in the males. Adult beetles vary widely in total length from 2.9 to 6.9 mm but the majority are 4.5–6.0 mm. Females tend to be slightly larger than the males.

The roundheaded pine beetle can kill trees in all crown and diameter classes. Studies have indicated average diameter at breast height of beetle-killed of 29 cm in the Sacramento Mountains of south-central New Mexico, 43 cm in the Pinaleno Mountains of Arizona, 48 cm in the Pine Valley Mountain of Utah with dominant, co-dominant, and intermediate trees being killed. In these areas, tree mortality was more common in areas with high stocking and poor tree growth. In an outbreak in Nevada, tree mortality was most common in trees at least 50 cm in diameter at breast height.

Various natural enemies attack the roundheaded pine beetle but little is known about their ecology and impact. The most important appears to be the red-bellied clerid, *Enoclerus sphegeus*. The roundheaded pine beetle is probably the only species in the genus in North America that overwinters mostly in the egg stage and that has a flight period predominantly in the fall.

► Bark Beetles in the Genus *Dendroctonus*

References

Chansler JF (1967) Biology and life history of *Dendroctonus adjunctus* (Coleoptera: Scolytidae). Ann Entomol Soc Am 60:760–767

Lucht DD, Frye RH, Schmid JM (1974) Emergence and attack behavior of *Dendroctonus adjunctus* Blandford near Cloudcroft, New Mexico. Ann Entomol Soc Am 67:610–612

Massey CL, Lucht DD, Schmid JM (1977) Roundheaded pine beetle. U.S. Department of Agriculture, Forest Service, Forest Insect and Disease Leaflet 155

Negrón J (1997) Estimating probabilities of infestation and extent of damage by the roundheaded pine beetle in ponderosa pine in the Sacramento Mountains, New Mexico. Can J Forest Res 27:1936–1945

Negrón JF, Wilson JL, Anhold JA (2000) Stand conditions associated with roundheaded pine beetle (Coleoptera: Scolytidae) infestations in Arizona and Utah. Environ Entomol 29:20–27

Six DL, Paine TD (1996) *Leptographium pyrinum* is a mycangial fungus of *Dendroctonus adjunctus*. Mycologia 88:739–744

Rove Beetle Dermatitis

A term used by some authors for dermatitis linearis.

► Dermatitis Linearis

Row Cover

A covering, usually consisting of spun-bonded polyester, that is placed over crops to protect them from adverse weather or pests.

Royal Cell

In honey bees, a large wax cell constructed by workers and used to rear the queen larvae. In some termites, a cell in which the queen is housed.

Royal Jelly

A high-quality food produced by the hypopharyngeal gland of worker honey bees that, if fed to larvae throughout their development, can cause them to develop into queens. Royal jelly also is known as "bee milk."

Royal Moths

Some members of the family Saturniidae (order Lepidoptera).

► Emperor Moths
► Butterflies and Moths

Royal Palm Bugs

Members of the family Thaumastocoridae (order Hemiptera).

► Bugs

R-Strategists

Species with life history characteristics making them well suited for exploiting transient environments ("r" is an expression denoting the intrinsic rate of increase). r-selected species represent an extreme on a continuum of life history characteristics, with K-selected species at the other end of the continuum. r-selected species can also be said to conform to the "ruderal strategy" (Table 7).

Ruderal

A type of organism, especially plants, found in sites associated with humans and human disturbance. This term is also used with respect to insects that display the characteristics of r-Strategists.

► r-Strategists

Rudimentary

Poorly developed, very small in size, or embryonic.

Rufous

Pale red in color.

Rugose

Wrinkled or roughened.

Runoff

The liquid spray material that drips off the target after a heavy pesticide application is made. The surface water that leaves a field after irrigation.

Rupicolous

This describes organisms that dwell among rocks and stones.

Russian Wheat Aphid, *Diuraphis noxia* (Mordvilko) (Hemiptera: Aphididae)

An Asian pest of wheat, this species has become very important in southern Africa and North America.

► Wheat Pests and their Management

R-Strategists, Table 7 A comparison of the characteristics of r-selected and K-selected species

	r-Selected	K-selected
Habitat type	Unstable, not permanent	More stable
Reproduction	Rapid under favorable conditions; many offspring produced	Usually slower; fewer offspring produced
Development	Rapid; often multivoltine	Slower; often univoltine
Mortality	Often density independent and catastrophic	Often density dependent and more gradual
Population size	Extremely variable in time	Less variable in time
Dispersal capacity and mode	High and random	Lower and oriented
Brood care	Absent	Sometimes present
Body size	Often quite small	Often larger
Competition	Variable, but often low	Often very keen
Ultimate effect	High productivity	Efficient use of resources

Rust Diseases

Rust diseases of plants do not require insects to be pathogenic, but benefit from transport by insects.

► Transmission of Plant Diseases by Insects

Rust Flies

Members of the family Psilidae (order Diptera).

► Flies

Rusty Grain Beetle, *Cryptolestes ferrugineus* (Stephens) (Coleoptera: Laemophloeidae)

This is an important grain-infesting beetle in colder climates.

► Stored Grain and Flour Insects

Ryania

An extract of *Ryania speciosa* (Flacurtiaceae) plants that is used as a botanical insecticide. The active ingredients are alkaloids, and extracted from the roots and stems. There are several active ingredients, the most important of which is ryanodine. It is regarded as a slow-acting stomach poison, and is more stable than some other botanical insecticides.

► Botanical Insecticides

Rove Beetles (Coleoptera: Staphylinidae)

J. HOWARD FRANK[1], M. C. THOMAS[2]
[1]University of Florida, Gainsville, FL, USA
[2]Florida State Collection of Arthropods, Gainsville, FL, USA

The family Staphylinidae belongs to the suborder Polyphaga of the order Coleoptera (beetles). The superfamily Staphylinoidea includes the small families Hydraenidae, Ptiliidae, Agyrtidae, Leiodidae, Scydmaenidae, and Silphidae, and the huge family Staphylinidae.

Order: Coleoptera
Suborder: Polyphaga
Superfamily: Staphylinoidea
Family: Staphylinidae

Four phyletic lines are now (Lawrence and Newton 1995) included in Staphylinidae:

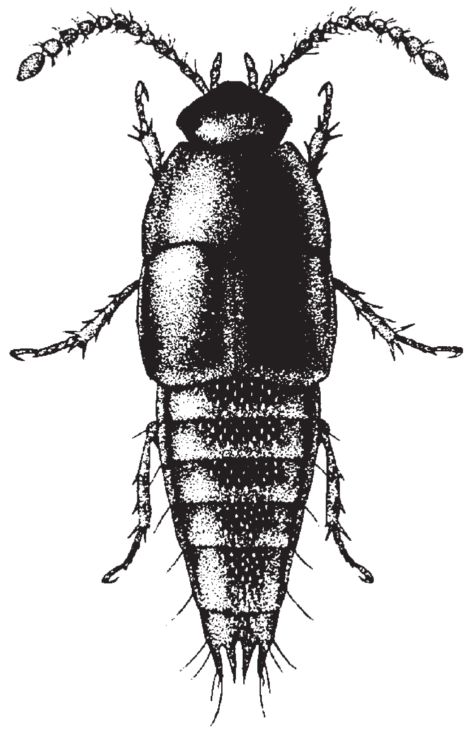
1. Subfamilies Glypholomatinae, Microsilphinae, Omaliinae, Empelinae, Proteininae, Micropeplinae, Neophoninae, Dasycerinae, Protopselaphinae, and Pselaphinae
2. Subfamilies Phloeocharinae, Olisthaerinae, Tachyporinae, Trichophyinae, Habrocerinae, and Aleocharinae
3. Subfamilies Trigonurinae, Apateticinae, Scaphidiinae, Piestinae, Osoriinae, and Oxytelinae
4. Subfamilies Oxyporinae, Megalopsidiinae, Steninae, Euaesthetinae, Solieriinae, Leptotyphlinae, Pseudopsinae, Paederinae, and Staphylininae

The former taxa Brathinidae (now just part of subfamily Omaliinae), Dasyceridae (now subfamily Dasycerinae), Empelidae (now subfamily Empelinae), Glypholomatini (formerly a tribe of Silphidae), Microsilphinae (formerly a subfamily of Silphidae), Pselaphidae (now subfamily Pselaphinae), and Scaphidiidae (now subfamily Scaphidiinae) of earlier authors are here included within the family Staphylinidae. As now constituted, this is one of the largest families of beetles, with over 45,000 species known worldwide and probably over 75% of tropical species still undescribed. In the future, systematists may, however, choose to split the family into the four phyletic lines to form four families.

Adults

The length of adult Staphylinidae ranges from less than 1 mm to almost 30 mm. Most are under 7 mm long. Most have short elytra, exposing several abdominal segments – but it would be an error to imagine that all have short elytra, or that all beetles with short elytra are Staphylinidae. Typically, they are slender with short elytra and abdominal musculature that renders them very flexible, thus able to enter narrow crevices. Those that have short elytra trade flexibility for exposure, rendering them subject to desiccation and dependent upon humid habitats. Typically, abdominal segments are bounded by tergites, one or two sets of paratergites, and sternites, with membranous connections, but in some genera (e.g., of Paederinae and Osoriinae, and partially so in Steninae) the tergites-paratergites-sternites are fused into rings around each segment, probably limiting water loss. The length of adults, which is nevertheless normally used to express size, is an inaccurate determinant of size because abdominal segments typically can be telescoped – making the body appear longer when under moist conditions and alive, but shorter when dried and dead. Eyelessness has evolved in some soil-inhabiting (Leptotyphlinae) and cave-inhabiting species, and winglessness in species occupying environments including mountains, the soil, caves, and seashores (Figs. 40–43).

Non-entomologists sometimes confuse Staphylinidae with Dermaptera. However, the non-opposable valvulae (appendages of the ninth abdominal segment) are not the opposable forcipes of Dermaptera, and the radial wing-folding pattern of Dermaptera is unlike that of Staphylinidae.



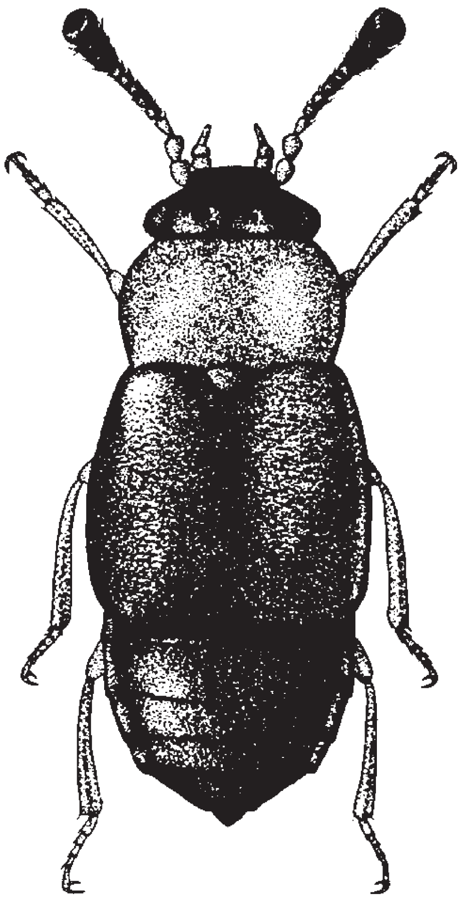
Rove Beetles (Coleoptera: Staphylinidae), Figure 40 Adult *Coproprorus rutilus*, subfamily Tachyporinae, 3.8 mm long, West Indies.

Immature Stages

Staphylinid eggs typically are white, spherical, spheroidal, or pyriform. Eggs of some genera within the Staphylininae (e.g., *Philonthus*) have pronounced surface sculpture, allowing identification at least to the species-group level. Larvae are campodeiform (sometimes called staphyliniform). In some subfamilies (Paederinae, Staphylininae, and to a lesser extent in their immediate relatives) the head is relatively more heavily sclerotized and there is a distinct "neck" (nuchal constriction of the head). Prepupae of Aleocharinae, Steninae, and one genus (*Astenus*) of Paederinae spin a silken cocoon in which they pupate. Pupae are obtect, pigmented, and sclerotized in the subfamily Staphylininae, but exarate, white, and unsclerotized in all the other subfamilies. In general, the immature stages develop rapidly, in a few days to a few weeks, and the adults are long-lived.

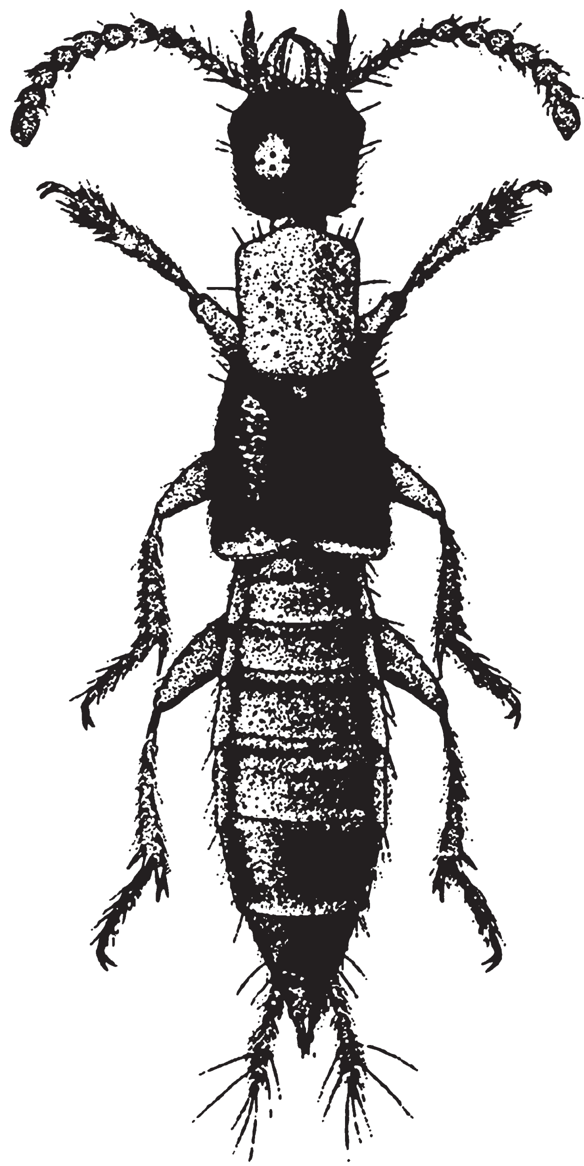
Habitats

Staphylinidae occupy almost all moist environments throughout the world. Because none of them is truly aquatic, they do not live in open waters; although winged adults may be skimmed from the sea surface far from land, their presence is due to misadventure but attests to their dispersive ability. They live in leaf litter of woodland and forest floors and grasslands. They concentrate in



Rove Beetles (Coleoptera: Staphylinidae), Figure 41 **Adult *Proteinus thomasi*, subfamily Proteininae, 1.5 mm long, North America.**

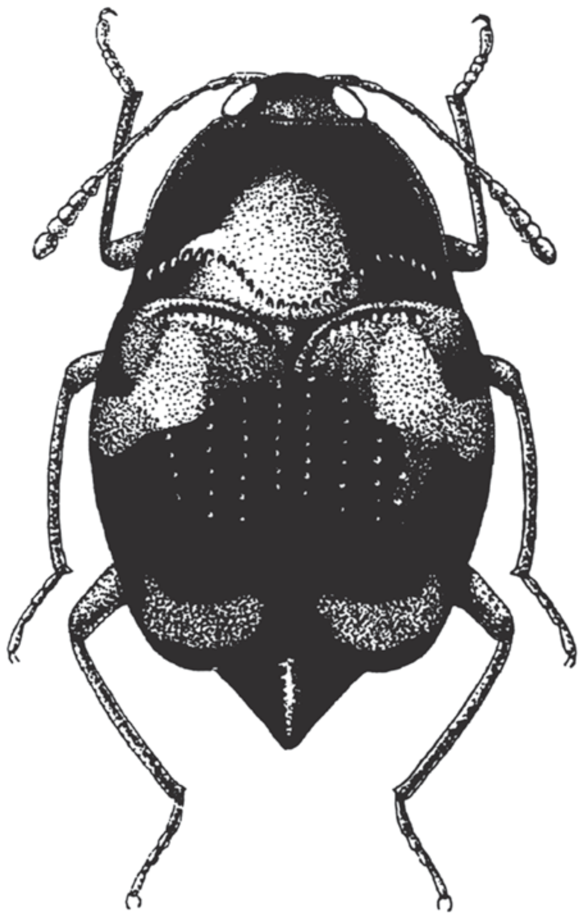
fallen decomposing fruits, subcortical cavities of fallen trees, drifted plant materials on banks of rivers and lakes, and dung, carrion, and nests of vertebrate animals. Several hundred species live only on seashores. Large numbers of species are specialized to existence in nests of social insects. Many inhabit caves, underground burrows of vertebrate animals, and smaller soil cavities, even of burrows that they (a few of them) excavate. Many live in mushrooms. Adults and even larvae of a few are associated with living flowers. Others climb on plants, especially at night, and hunt for prey. A few seem to live with terrestrial snails, although their role is not understood. Their distribution in arid environments is restricted to moist microhabitats.



Rove Beetles (Coleoptera: Staphylinidae), Figure 42 **Adult *Neobisnius occidentoides*, subfamily Staphylininae, 4 mm long, North America.**

Food

A little about the feeding habits of Staphylinidae has been deduced from casual observations by many observers, and from dissections of alimentary canals and from feeding trials and examination of mouthparts by a few. Archetypal



Rove Beetles (Coleoptera: Staphylinidae), Figure 43 Adult *Scaphisoma quadriguttatum*, subfamily Scaphidiinae, 4.3 mm long, North America.

staphylinids probably were saprophagous. Saprophagy is still a major feeding mode in Piestinae, Osoriinae, and Proteininae, perhaps with some adaptation to mycophagy. Mycophagy has evolved in Oxyporinae, Scaphidiinae, some Tachyporinae, and a few Aleocharinae. Phytophagy has evolved in some Oxytelinae, to the point where the diet of adults and larvae of *Bledius* consists of diatoms, and at least one species of *Apocellus* has been accused of damaging flowers, one species of *Carpelimus* has (probably wrongly) been accused of damaging cucumbers, and one species of *Osorius* (Osoriinae) has been accused of damaging turf grass. Saprophagy has evolved toward carnivory in other subfamilies (many Tachyporinae, most Aleocharinae, Pselaphinae, Euaesthetinae, Steninae, Paederinae, and Staphylininae), representing the bulk of species in the family, so that it may be said that most Staphylinidae – tens of thousands of species – are facultative predators. Some have specialized, for example *Oligota* (Aleocharinae) as predators of mites, *Erichsonius* (Staphylininae) as predators of soil-inhabiting nematodes, *Odontolinus* (Staphylininae) as predators of mosquito larvae in water-filled flower bracts of *Heliconia* (Heliconiaceae), and *Eulissus* (Staphylininae) on adult dung-inhabiting scarab beetles. One line of Aleocharinae (*Aleochara*) has evolved to become parasitoids in fly puparia.

Presocial or Subsocial Behavior

This behavior is known in *Bledius* and *Platystethus* (Oxytelinae) and *Eumicrota* (Aleocharinae). Adults construct chambers in which they deposit and guard their eggs, *Bledius* in sandy or muddy shores, *Platystethus* in the dung of ungulates, and *Eumicrota* in mushrooms. Another dimension of social behavior has arisen in interactions with termites and ants – thousands of species of Aleocharinae, and numerous species of several other subfamilies, are inquilines in the nests of these social insects, with attendant structural and behavioral adaptation. *Emus* (Staphylininae) invades bee nests in Europe, and a species of *Euvira* (Aleocharinae) develops in communal nests of a butterfly in Central America.

Obligate Relationships with Higher Plants

Among those species attracted to flowers, *Pelecomalium testaceum* (Omaliinae) pollinates *Lysichiton americanum* (Araceae) in the mountains of the Pacific coast of the USA and Canada. It is conceivable that *Polyobus* spp. do the same for

Espeletia (Asteraceae) in the northern Andes of South America. *Charoxus* spp. (Aleocharinae) also have an obligate relationship with plants – the adults are attracted in the Neotropical region to the syconia of *Ficus* spp. (Moraceae) within which they oviposit, but the adults and larvae feed on pollinating wasps (Agaonidae) of those fig flowers.

Relationships with Fungi

There are three forms of relationships with fungi. Adults and larvae of many species eat fungi. Others find prey items (fly larvae and other organisms) in fungi. A major association with fungi is that adults of many species are infected by Laboulbeniales (Ascomycetes), and some other fungi, many of which specialize at the level of host genus, tribe, or subfamily.

Relationships with Decomposing Plants, Dung, and Carrion

The frequent presence of many staphylinids at decaying plant materials raises the question of whether they arrived there by random movement – and then remained there – or whether they are attracted in much the same way that adults of their prey (fly larvae, etc.) arrived there. Thus, adults and larvae of *Cafius* (Staphylininae) inhabit decaying brown algae (Fucales) on sea beaches and eat fly larvae; adults and larvae of some *Philonthus* (Staphylininae) occur in the dung of ungulates and eat fly eggs and larvae; adults of some *Eulissus* (Staphylininae) are found in the dung of ungulates and there maim and then eat adult scarab beetles; adults and larvae of some *Belonuchus* and *Philothalpus* (Staphylininae) are found in decaying fruits, and eat fly larvae; adults of some *Platydracus* (Staphylininae) are found in carrion and eat fly larvae and adults.

Nests of Vertebrates

Some staphylinid species have specialized to live in the nests of vertebrates, especially tortoises, birds, and rodents. Their prey seems to be mainly the larvae of fleas and flies. Thus, in central Asia, where sylvatic plague is endemic, some are credited with suppressing flea populations – and thus help to suppress transmission of plague. Adults of *Amblyopinus* and its close relatives (tribe Amblyopini, subfamily Staphylininae) occur in the fur of some rodents in Central and South America. For years they were suspected of being parasites of these rodents, and taking blood from them. Now, however, they are believed to be phoretic on the rodents, thus being transported from nest to nest. They oviposit in the nests, and larvae feed as predators there of other arthropods.

Secretions and Glands

Glandular systems of Staphylinidae are mainly implicated in the production of defensive secretions, of which there is a remarkable array. However, glands of some species that are inquilines in nests of social insects produce substances that appease rather than repel the nest-builders. Further, glands of adult *Stenus* (Steninae) produce a surfactant, stenusin, that enables these beetles to skim over the surface of fresh water into which they have fallen, to regain dry land.

Pederin is a powerful toxin and DNA inhibitor circulating in the hemolymph of all devel opmental stages of some species of *Paederus* (Paederinae) and close allies in the subtribe Paederina. It is produced by endosymbionts in some, but not all, adult females. Is transferred to eggs at oviposition, and thus to larvae and pupae. Males may obtain it by eating eggs. It is a defensive secretion active against spiders, but seems to have no insecticidal effect. It is a contender for the title of most powerful animal toxin.

Pheromones

A female sex pheromone has been identified in *Aleochara curtula*, but pheromones in 45,000 other species remain unidentified.

Prey Capture and Pre-Oral Digestion

The mandibles are the mouthparts typically associated with prey capture by predatory adults and larvae. However, adult *Stenus* (Steninae) use a prey-catching apparatus in which the labium (with its palpi) can be protruded by hemolymph pressure to grip small prey such as Collembola. Oxyporinae, Steininae, Euaesthetinae, Paederinae and Staphylininae have pre-oral digestion. They use mandibles to hold their food, secrete digestive fluids, and imbibe partially-digested food. A consequence is that their digestive systems contain much liquid and few solids, so visual identification of food is difficult. Drops of anal secretions of Neotropical *Leistotrophus* (Staphylininae) adults placed on leaves attract their prey.

Natural Enemies

Scattered evidence – needing analysis – suggests that spiders, various insects (including Reduviidae, Carabidae, Asilidae, Formicidae, etc.) amphibia, reptiles, birds, and bats, include Staphylinidae among their diets. Among the parasites, fungi play a major role, and hymenopterous parasitoids, nematodes, and nemata, a relatively minor role. Non-target effects of chemical pesticides and habitat destruction kill many Staphylinidae.

Biological Control

Biological control practitioners have observed predation by various non-specialist Staphylinidae on fly larvae and other invertebrates and have imported various Staphylinidae into Italy, Hawaii, mainland USA, and Easter Island, to capitalize on the perceived benefits – without evident success. Species of *Belonuchus*, *Creophilus*, *Ocypus*, *Philonthus*, *Philothalpus*, and *Thyreocephalus* (Staphylininae) and *Paederus* (Paederinae) have been moved. Other attempts have involved more specialist *Oligota* (Aleocharinae) against tetranychid mites in East Africa, and *Aleochara* against horn fly in mainland USA, but again with little success. Current attempts in Europe involve conservation of native staphylinids, including *Tachyporus* (Tachyporinae) as predators of cereal aphids, and *Aleochara* as predators of root maggots (including augmentative use).

Fossils

Pleistocene fossil Staphylinidae have been reported from northeastern North America from peat bogs, and from Europe. They seem to be of extant species and help to show former distribution of some of these species. Oligocene fossils are amber from the Baltic, the Dominican Republic, and elsewhere, and from shales in the USA (Colorado), France, Germany, and elsewhere. Most of these are recognizably members of modern genera. Deposits from the mid-Cretaceous to lower Jurassic in Eurasia have also yielded fossils. Most of these resemble members of modern subfamilies. The oldest recorded staphylinid, more than 200 million years old, is from the upper Triassic of the USA (Virginia). Species-level identification of present-day staphylinids normally requires dissection, at least of the genitalia – when this cannot be done with fossil specimens they have limited value.

Importance to Humans

The importance of staphylinid predation on pests has been demonstrated repeatedly in the literature. They suppress populations of pest insects and mites in numerous crops (agricultural, horticultural and forest entomology), and of biting flies and fleas (medical and veterinary entomology). Their presence in carrion gives them a role in forensic entomology. With one exception (*Paederus* and its close allies) they have trivial importance as pests; but although contact of humans with *Paederus* may cause dermatitis on human skin, the toxin pederin may be harnessed for its therapeutic effects, and some *Paederus* species are valuable predators of crop pests. Finally, Staphylinidae form a substantial part of the world's biodiversity.

References

Frank JH (1991) Staphylinidae. In: Stehr FW (ed) Immature insects, vol 2. Kendall-Hunt, Dubuque, IA, pp 341–352

Frank JH, Thomas MC (1999) Staphylinidae. "Featured Creatures." Available at http://creatures.ifas.ufl.edu/misc/beetles/rove_beetles.htm. Accessed April 27, 2001

Herman LH (2001) Catalog of the Staphylinidae (Insecta: Coleoptera). 1758 to the end of the second millennium. Bull Am Mus Nat Hist 265:1–4218 (note: this enormous scholarly work includes a bibliography to taxonomic works, together with a catalog of species belonging to most of the subfamilies (excepting only the subfamilies Aleocharinae, Paederinae, Pselaphinae, and Scaphidiinae))

Lawrence JF, Newton AF (1995) Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). In: Pakaluk J, Slipinski SA (eds) Biology, phylogeny, and classification of Coleoptera. Museum i Instytut Zoologii PAN, Warsaw, Poland, pp 779–1006

Newton AF, Thayer MK, Ashe JS, Chandler DS (2000) Staphylinidae. In: Arnett RH, Thomas MC (eds) American beetles, vol 1. CRC Press, Boca Raton, FL, pp 272–418

S

Sabrosky, Curtis

Curtis Sabrosky was born on April 3, 1910, at Sturgis, Michigan, USA. He graduated from Kalamazoo College in 1931, and obtained a M.S. from Kansas State University in 1933. He taught at Michigan State University from 1936 to 1944, and after military service joined the United States Department of Agriculture at the Systematic Entomology Laboratory. He served in this capacity for 35 years, until retiring in 1980. Widely recognized as an authority on Diptera, Sabrosky published on several families, but considered Chloropidae to be his favorite. He worked diligently on the International Code of Zoological Nomenclature, and served as the president of the Society of Systematic Zoology and the president of the Entomological Society of America. He died on October 5, 1997.

Reference

Crosskey R (1998) Curtis Sabrosky (1910–1997). Antenna 22:58–61

Sackbearer Moths (Lepidoptera: Mimallonidae)

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Sackbearer moths, family Mimallonidae, total 254 species, all New World and primarily Neotropical (250 sp.). The family is in the superfamily Bombycoidea (series Bombyciformes), in the section Cossina, subsection Bombycina, of the division Ditrysia (some researchers maintain the family in its own monobasic superfamily, Mimallonoidea). Adults medium size (22–60 mm wingspan), with head scaling roughened; haustellum short or vestigial; labial palpi short (rarely 2-segmented); maxillary palpi vestigial; antennae bipectinate; body robust. Wings broad (Fig. 1) and triangular, usually with a falcate of acute forewing; hindwing rounded. Maculation mostly somber shades of brown or gray, to nearly black, but some more colorful, and with various markings or striae. Adults are nocturnal. Larvae are leaf feeders, with cases having openings that can be plugged by the head and a plate-like structure on the posterior of the body. Host plants are recorded in a number of plant families, including Anacardiaceae,

Sackbearer Moths (Lepidoptera: Mimallonidae), Figure 1 **Example of sackbearer moths (Mimallonidae), *Mimallo amilia* (Cramer) from Peru.**

Combretaceae, Fagaceae, Melastomaceae, Myrtaceae, and Rubiaceae, among others. A few can be economic.

References

D'Almeida RF (1943) Algunas tipos de generos de orden Lepidoptera. Quarta Nota: Heterocera, Fam. Mimallonidae. Boletim do Museu Nacional (n.s.) (Zoologie) 10:1–6

Franclemont JG (1973) Mimallonoidea, Mimallonidae. In: Dominick RB (eds) The moths of America north of Mexico including Greenland, Fasc. 20.1. Bombycoidea [part]. E. W. Classey, London, 86 pp, 11 pl

Gaede M (1931) Mimallonidae. In: Lepidopterorum catalogus, vol 50. W. Junk, Berlin, pp 1–21

Seitz A (ed) (1928–1929) Familie: Mimallonidae. In: Die Gross-Schmetterlinge der Erde, 6:635–672 (1928); 673, pl 86–87 (1929). A. Kernen, Stuttgart

Sacbrood

A disease of honey bee larvae caused by a nonoccluded RNA virus.

► Sacbrood Disease

Sacbrood Disease

This is a viral disease of honey bees, and is characterized by the diseased-infected larva being encased in a tough fluid-filled sac formed from the larval cuticle. The presence of dead or dying brood is the first symptom of infection. The brood dies soon after being capped but before changing to pupae. Affected capped cells often contain a small puncture, usually about the size of a pinhead. If a large proportion of brood becomes affected, the colony is weakened. Bees appear reluctant to remove dead material from the cells and the queen is forced to deposit eggs elsewhere in the hive. The dead larvae are discolored, usually dark, with the head curled and darkened. Older larvae typically are affected, and the disease can persist in dead insects for several months. Acquisition of the virus is via ingestion. The spread of sacbrood in a hive is believed to be caused by feeding young larvae contaminated pollen, nectar or water. Nurse bees become infected with the virus while cleaning out cells containing infected larvae. The spread of sacbrood from hive to hive is due to the exchange of contaminated equipment or bees, or robbing. Sacbrood disease may appear at any time during the year, but more often during the brood rearing season. Colonies showing symptoms of sacbrood disease will often recover if moved to environments with good nutrition. Requeening the hive also is recommended. Apparently the virus affects the ability of the larva to molt. It is found on several continents, but not much is known about it.

► Honey Bees
► Apiculture

Sac Spiders (Class Arachnida, Order Araneae, Families Tengellidae, Zorocratidae, Miturgidae, Anyphaenidae, Clubionidae, Liocranidae, and Corinnidae)

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The sac spiders are a varied group that at one time was included mostly in one family, the Clubionidae. Now, after some extensive taxonomic analysis, the nominate family is down to two genera in the United States, *Clubiona* and *Elaver* (formerly *Clubionoides*); all the rest have been transferred to new families. In retrospect it is obvious that these disparate groups should have family status. In the case of the Tengellidae and Miturgidae, the genera are more closely related to the three-clawed spiders than the two-clawed spider families into which the other "clubionoid" families fall. The characters used to separate the original family Clubionidae (including Anyphaenidae and the other clubionoid families) from the related Gnaphosidae (ground spiders) included conical, contiguous spinnerets (Gnaphosids, except for the ant-like genus *Micaria*, have cylindrical spinnerets that are usually separated by at least one spinneret diameter), endites (lateral mouthparts) lacking a depression (*Micaria* is often said to lack a depression, but Platnick considers it to have a small median one), and eyes homogeneous in size and shape (the eyes of most gnaphosids are heterogeneous in size and shape).

The Tengellidae, Zorocratidae and Miturgidae are unusual because of their current placement within the three-clawed spiders, although many (but not all) are actually two-clawed. The loss of the third claw (used primarily for web walking) apparently started to occur among non-web builders fairly early and appears to have occurred more than once.

Based on genitalic characters these spiders are not closely related to the other "clubionoid" families and Griswold has suggested that the tengellids actually are a sister group of the lycosoids. He also implies that the tengellids may turn out to be only a subfamily of the Miturgidae.

The North American genera now placed in the Tengellidae include *Lauricius* and at least four other genera. At least 50 species may be in this family, with about half of them described. *Lauricius hooki* is a flattened, crab spider-like, and fast moving representative of the family that is commonly found clinging to the underside of rocks in the southwestern USA. Another North American genus in this family is *Liocranoides*. The cribellate genus *Zorocrates* is now given a separate family, the Zorocratidae, along with the Madagascar genus *Uduba*. *Zorocrates karli* is a wolf spider-like species commonly found in desert scrub in the southwestern USA.

The Miturgidae, as now defined, include several common and also less-known genera. Some (such as *Calamistrula* in Africa) are cribellate and these, plus a few others (such as *Griswoldia*) are three-clawed. All of the members of the North American fauna are ecribellate and two-clawed. Several miturgids, such as *Syspira*, resemble wolf spiders. The common sac spider genus *Cheiracanthium* was recently removed from the remains of the Clubionidae and placed in this family. This spider is one of the most studied of the sac spiders in regard to economic impact in agricultural crops. They are predators of a number of pest species and, like several of the anyphaenids, are known to recognize and eat insect eggs.

The rest of the "clubionoids" are all two-clawed spiders, apparently more or less related to each other. The first family to be separated from the Clubionidae in most publications was the Anyphaenidae. The members of this family have tracheal spiracles that are from one third to over half the distance from the spinnerets to the epigastric furrow (in most spiders this spiracle is just anterior to the base of the anterior spinnerets). Another characteristic of the family is the possession of claw tufts of flattened hairs. These are classic sac-building spiders that are probably important members of the natural enemies complex in agroecosystems, especially in tree crops, such as citrus and pecans. They are known to feed on insect eggs and also at extrafloral nectaries, as well as on moving insect prey, including aphids and other pests. The most numerous anyphaenids in the United States are in the genera *Anyphaena* and *Hibana* (formally *Aysha*).

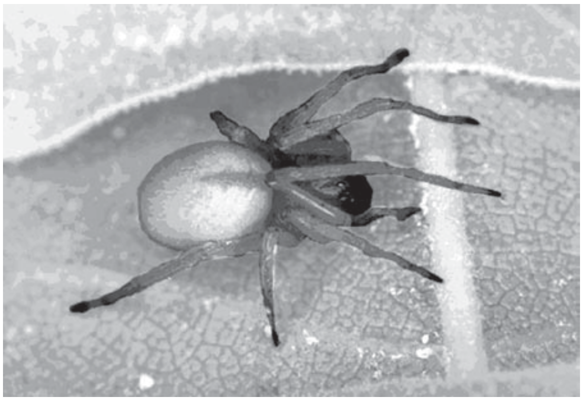
As noted earlier, the Clubionidae s.s. are now represented in the United States by only two genera, *Clubiona* and *Elaver*. These common sac spiders are found under rocks and bark, and in sacs inside folded leaves. They have prominent claw tufts on their tarsi.

The Liocranidae are two-clawed, like most of the "clubionoid" families. This family has been drastically altered recently. Many of those currently recognized as liocranids were referred to as phrurolithines in the literature, but these have now been transferred to the Corinnidae, leaving only a handful of genera, including *Neoanagraphis* and *Agroeca* in North America.

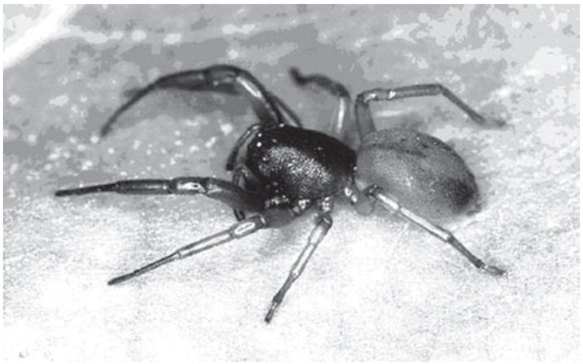
The Corinnidae are now the largest of the clubionoid families in the world, with nearly a thousand species, and contains some ant or velvet ant-like species, as well as many common typical "sac" spiders in the genera *Trachelas* and *Meriola*. One of the most abundant genera is *Castianeira*. These typically run over the ground much like large ants or female mutillid wasps. Other North American genera in this family are *Mazax* and *Corinna*, with the latter not occurring north of Mexico. All of the phrurolithines (now transferred from Liocranidae) have multiple macrosetae (spines) on the ventral first tibiae. Phrurolithines are abundant in leaf litter at high elevations in the southwestern USA.

It is sometimes rather disconcerting to the non-specialist to see so many drastic changes in classification in a common group of organisms. Unfortunately, classification schemes are imperfect because they are based on the data at hand. Whales were once classified with the fishes because it was obvious that, like fishes, they were aquatic, had fins, and were good to eat. The characters of warm-bloodedness, presence of air-breathing lungs, suckling of young, and complicated social interactions resulting from a very unfish-like nervous system were overlooked. Similarly, any "sac" spider with the eyes in two rows was dumped into the Clubionidae (or even earlier the Drassidae, which also included anyphaenids and gnaphosids). It must be kept in mind that, while more stable than the multitude of common names and classifications, scientific names and classifications are approximations that become (we hope) more accurate as information is added.

Despite the taxonomic muddle of the sac spiders, these creatures are well worth investigating. The probable important roles of sac spiders in the natural enemies complex in agricultural cropping systems is among the best documented of the spiders, although much remains to be done. *Cheiracanthium*, *Hibana*, *Anyphaena* and *Trachelas* are all probably of interest in this regard, as other genera may prove to be in future studies. Several species of *Cheiracanthium*, for example, are common in Egyptian cotton fields, and may be important in controlling various cotton pests. *Hibana velox* has been observed eating the eggs of the sugar cane root stalk borer weevil, *Diaprepes abbreviatus*, and *Cheiracanthium inclusum* is known to feed on the eggs of soybean looper, *Pseudoplusia includens* (Figs. 2 and 3).



Sac Spiders (Class Arachnida, Order Araneae, Families Tengellidae, Zorocratidae, Miturgidae, Anyphaenidae, Clubionidae, Liocranidae, and Corinnidae), Figure 2 ***Cheiracanthium inclusum*** **female from New Mexico. Photo by D. Richman.**



Sac Spiders (Class Arachnida, Order Araneae, Families Tengellidae, Zorocratidae, Miturgidae, Anyphaenidae, Clubionidae, Liocranidae, and Corinnidae), Figure 3 ***Trachelas mexicana*** **female from New Mexico. Photo by D. Richman.**

The life cycle of the miturgid *Cheiracanthium inclusum* (as noted earlier, this species is usually placed in the Clubionidae in the literature) is perhaps the best known of all the sac spiders, primarily because of its agriculture importance. As may be presumed for many, if not most, other sac spiders the cycle is annual, with adults being prominent in the late summer. Adults of the anyphaenid *Hibana incursa*, a common spider in pecan groves in the southwestern USA, are also found only for a short time in late summer, with immature spiders found throughout the year. During winter they usually are found in silken sacs under bark or in pecan nut hulls. They invade understory plants in the spring, before the pecans leaf out, apparently seeking prey insects such as aphids.

Of the spiders in these families, only a few are known to have venom that can cause notable effects in humans. All of these are in the genus *Cheiracanthium* and include both *C. inclusum* and the European species, *C. mildei*. The latter apparently was introduced into the United States a number of years ago. Mild necrotic arachnidism has been reported for both species. North Africa has even larger species of *Cheiracanthium*, but almost nothing is known about their venoms.

► Spiders
► Spider Behavior and Value in Agricultural Landscapes

References

Dippenaar-Schoeman AS, Jocqué R (1997) African spiders. ARC-Plant Protection Research Institute, Pretoria, South Africa

Griswold CE (1993) Investigations into the phylogeny of the Lycosoid spiders and their kin (Arachnida: Araneae: Lycosoidea). Smithson Contrib Zool 539:1–39

Kaston BJ (1978) How to know the spiders, 3rd edn. McGraw-Hill, Boston

Platnick NI (1993) Advances in spider taxonomy 1988–1991. New York Entomological Society/American Museum of Natural History, New York, 846 pp

Ubick D, Paquin P, Cushing PE, Roth V (eds) (2004) Spiders of North America. American Arachnological Society, Stockton, CA, 377 pp

Saddle

A chitinous plate on the anal siphon of mosquito larvae.

Saddle-Case Makers

Members of the family Glossosomatidae (order Trichoptera).

► Caddisflies

Sagittal

This has two different meanings, depending on use: (i) sagittal or sagittate describes things that are arrowhead-shaped or elongate triangular; (ii) sagittal is also used to designate something situated along the longitudinal plane (“sagittal plane”) of the body. The sagittal plane is the longitudinal, vertical axis that divides a bilateral symmetrical animal in half, resulting in right and left halves.

Sahlberg, Carl Reinhold

Carl Sahlberg was born at Eura, Finland, on January 22, 1779. He entered the Academy in Turku in 1795, and in 1802 obtained the degree of “magister,” followed by being appointed the docent of natural history in 1804. In 1810 he obtained a medical license. In 1816 he was named the professor of natural history and economy. After a devastating fire, the University was transferred to Helsinki, and in 1828 he was named professor of zoology and botany. He retired in 1841. Sahlberg did not publish extensively, though the two-volume series “Dissertatio entomologica Fennica enumerans” is noteworthy. He died on October 18, 1860, at Uusinkartano, Finland.

Reference

Herman LH (2001) Sahlberg, Carl Reinhold. Bull Am Mus Nat Hist 265:132–133

Sailer, Reece I

Reece Sailer was born on November 8, 1915, near Roseville, Illinois, USA. He studied biology at Western Illinois State College from 1934 to 1936, but transferred to the University of Kansas where he obtained his bachelor’s degree in entomology in 1938, followed by a Ph.D. in 1942. He worked for a short time as assistant state entomologist in

Kansas, then moved to the United States Department of Agriculture, Bureau of Entomology and Plant Quarantine. His principal duties involved identification and research on Hemiptera. A special interest was stink bugs. He also was involved in an extensive and comprehensive assessment of forest fauna treated with DDT, a study that anticipated the eventual problems associated with this popular and widely used insecticide. In 1957 he became Assistant Chief of the Insect Identification Branch. Throughout the 1950s he taught insect ecology at the University of Maryland. He developed a strong interest in biological control, and in 1960 he moved to France to serve as Director of the USDA European Parasite Laboratory. During this time period the laboratory introduced parasitoids of alfalfa weevil, cereal leaf beetle, and European elm bark beetle, as well as predators of balsam woolly adelgid and face fly. In 1966 he returned to Beltsville, Maryland, as Chief of the Insect Identification and Parasite Identification Branch. He retired in 1973 and accepted a graduate research professorship at the University of Florida where he taught biological control and conducted research on citrus whitefly, mole crickets, and other invading pests. Sailer was author of over 100 publications and received numerous honors for his dedicated and effective research and service, including being elected president of the Entomological Society of America. He died on September 8, 1986, while vacationing in Delaware.

Reference

Buckingham GR, Bennett FD, Frank JH, Wirth WW (1987) Reece I. Sailer 1915 to 1986. Bull Entomol Soc Am 33:1222–1223

Saldidae

A family of bugs (order Hemiptera). They sometimes are called shore bugs.

► Bugs

Saliva

This generally is a liquid secretion of the salivary glands (= labial glands), but sometimes apparently originating from the crop, into the buccal cavity (mouth) of the insect. The saliva consists of water, salts, proteins, and enzymes, though sometimes it contains plant growth regulators or is contaminated with plant disease organisms such as viruses. Although digestion is an important aspect of saliva, it also serves to lubricate the mouthparts and aids in swallowing. In piercing-sucking insects that penetrate plants, saliva also may harden to form tubes or "sheaths" that hold the mouthparts (stylets) firmly in place and help prevent leakage while the insect sucks up liquids from the phloem or xylem. The saliva also hinders the plants' response to injury and feeding, to the benefit of the insect. Piercing-sucking insects normally have a salivary canal for secretion of saliva plus a food canal for food uptake, but thrips (Thysanoptera) have only a single canal, the food canal, that is used both for secretion of saliva and uptake of food.

► Alimentary Canal and Digestion
► Plant Viruses and Insects
► Transmission of Plant Diseases by Insects

Salivary Glands

Glands (sometimes called labial glands) that produce saliva. They are found in the head, but may be large and extend into the abdomen in some insects. The glands are connected by ducts to the insect's mouth. Some salivary glands are modified for production of silk. Some persistent plant viruses pass into the salivary glands and then are secreted into plants when the insects feed. A few viruses (persistent propagative viruses) replicate in the salivary glands.

► Saliva
► Silk
► Alimentary Canal And Digestion

Salpingidae

A family of beetles (order Coleoptera). They commonly are known as narrow-waisted bark beetles.

► Beetles

Sample

A collection of sample units from a sampling universe. (contrast with census).

► Sampling Arthropods

Sample Size

The number of sample units collected from the sample universe for a given sampling effort. Ideally, sample size is based on prior information about dispersion and the desired level of precision or accuracy. Sometimes referred to as average sample size, abbreviated ASN.

Sample Unit

A proportion of the habitable sample universe from which counts of individuals are taken. The sample unit is based on a specific sampling method, should be representative of the behavior and size of the organism, and should strike a balance between cost and variability. Examples include whole leaves, branches or plants, a set number of sweeps along a row, a sticky trap set at canopy height, 10-min timed count, a 1 m^2 quadrat, etc.

Sample Universe

The physical area that contains the population of interest. Typical examples include a single crop field, an orchard, a section of stream, the cows in a pasture or barn, etc. Synonymous with the management unit in agricultural production systems.

Sampling Arthropods

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Sampling is a fundamental component of any experimentally based research program in the discipline of entomology, whether conducted in the laboratory, greenhouse or field. It also is an essential element for describing, measuring and quantifying arthropod population dynamics, whether the goal is to understand the population or community ecology of a given species or group of species, or to develop decision aids for integrated pest management (IPM). Although a population census may be highly desirable for many reasons, rarely does one have the time and resources to exhaustively count every insect, spider or mite within a defined area even if that area is relatively small, say, a small greenhouse or field plot. Instead we must resort to drawing a sample from the population and using the information gained from this sample to estimate variables such as population density or size and to draw inferences that can be applied to the entire population. Fortunately, there is a large body of theory and practical knowledge to guide our efforts in sampling. This short review will attempt to provide a broadly-based, non- mathematical overview of sampling, from discussion of the goals of sampling, to the basic tools for gathering data, to the basic components and mechanics of developing a useful sampling plan.

Samples and sampling are terms with which most entomologists are intuitively familiar. However, as with any field of study, there is a specific vocabulary associated with the study of sampling that may not be as well understood. Thus, brief definitions of some of the more commonly used terms in sampling are provided (Table 1).

Goals of Sampling

The first, and perhaps most important, element in the development of a useful sampling plan or

Sampling Arthropods, Table 1 **Definitions of some common terms associated with arthropod sampling**

Absolute method	A sampling method that allows the estimation of numbers per unit of habitat, generally per unit of ground area.
Accuracy	A measure of the closeness of an estimate to the true mean or variance of a population.
Bias	An unidirectional deviation of an estimate from the true mean or variance of a population.
Binomial sampling (presence/absence sampling)	Sampling based on determining the presence or absence of one or more individuals in the sample unit in lieu of complete counting of all organisms. Commonly used for pest management decision-making application. Contrast with enumeration sampling.
Census	Complete enumeration of every individual within a defined sample universe. Contrast with sample.
Classification	A sampling plan that classifies population density as being either above or below some predetermined level (e.g., economic threshold), or belonging within some density class (e.g., low, medium, high). Commonly used in pest management decision making application. Contrast with estimation.
Dispersion/distribution	The spatial patterning of individuals in a population in their habitat. This pattern can be broadly described as uniform, random or, most commonly, aggregated. Dispersion can be quantified by explicit spatial indices, or more typically by probability models (e.g., Poisson, Negative-binomial) or empirical models (e.g., Taylor's power law). The measurement of dispersion is dependent on the sample unit size and population density. Most often the term is used to denote the sampling dispersion/distribution and not true spatial patterning. Dispersion is an important element in the development of a sampling plan.
Double sampling	A sampling approach in which an initial sample (usually small) is drawn and used to determined the necessary sample size for a subsequent sample within the same time period.
Efficiency	A measure of the level of precision or accuracy per unit of cost (time or currency).
Enumeration sampling	Sampling based on the complete counting of all individuals in the sample unit. Contrast with binomial sampling.
Estimation	A sampling plan that numerically estimates population density or intensity. Commonly used for detailed population dynamic and experimental studies. Contrast with classification. The term can also denote the process of calculating various statistical parameters such as variance.
Fixed-sample size sampling plan	A sampling plan in which a predetermined number of sample units is collected based on a prescribed level of desired precision, classification accuracy, or level of confidence. Contrast with sequential sampling.

Sampling Arthropods, Table 1 **Definitions of some common terms associated with arthropod sampling (Continued)**

Mean-variance model	A model, generally a regression model, which predicts the variance of a sample from an estimate of the sample mean. Such models can characterize dispersion over a large range of population densities and are commonly used in developing sampling plans. Common examples are Taylor's power law and Iwao's patchiness regression.
Operating characteristic	A measure of the accuracy of a classification sample. An operating characteristic curve shows the probability of classifying density below a critical value (e.g., economic threshold) as a function of true mean density. Ideally, probabilities should be near 1 at densities far below the critical value, near 0.5 at densities very near the critical value and near 0 at densities far above the critical value. Often abbreviated as OC.
Population index	A sampling method that attempts to provide an indirect estimate of population density based on an associated product (e.g., frass) or effect (e.g., defoliation).
Precision	A statistical measure of the repeatability of an estimate relative to a group of estimates from the same population at the same time. Typically measured as the quotient of the standard error of the mean over the mean. Low numerical values indicate high precision, high numerical values indicate low precision. Precision is a key element in developing and evaluating the performance of sampling plans.
Probability model	A mathematical description of the dispersion or distribution of individuals in a population based on numbers per sample unit. Common models include Poisson, Negative-binomial, Binomial, Normal, and Neyman Type A. Such models can form the foundation of a sampling plan.
Random sampling	A method of allocating sampling units within a sampling universe in which each sample unit has an equal chance of being selected. Random sampling ensures an unbiased estimate, but is rarely used in the practice of arthropod sampling due to time and cost constraints.
Relative method	A sampling method that results in numbers per unit effort. Generally much faster and easier than absolute methods. Sometimes possible to convert counts to absolute density. Common examples are sweep nets and sticky traps.
Robust	Within statistics and sampling, the quality of being widely applicable. For example, a sampling plan is robust if it can be used to precisely estimate the density of an arthropod under many different environmental conditions.
Sample	A collection of sample units from a sampling universe. Contrast with census.
Sampling method/technique	A particular tool or technique used to gather information on population density from the sample universe. Examples include sweep nets, beat clothes, visual counts, suction devices, and various kinds of attractive and passive traps.

Sampling Arthropods, Table 1 Definitions of some common terms associated with arthropod sampling (Continued)

Sampling plan/program	A structured set of rules for collecting a sample that is based on delineation of the sample universe, knowledge of dispersion, a specific sample unit, a predetermined sample size (but see sequential sampling), time of sampling, and a given allocation of sample units throughout the sample universe (e.g., random, stratified, systematic).
Sample size	The number of sample units collected from the sample universe for a given sampling effort. Ideally, sample size is based on prior information about dispersion and the desired level of precision or accuracy. Sometimes referred to as average sample size, abbreviated ASN.
Sample unit	A proportion of the habitable sample universe from which counts of individuals are taken. The sample unit is based on a specific sampling method, should be representative of the behavior and size of the organism, and should strike a balance between cost and variability. Examples include whole leaves, branches or plants, a set number of sweeps along a row, a sticky trap set at canopy height, 10-min timed count, a 1 m^2 quadrat, etc.
Sample universe	The physical area that contains the population of interest. Typical examples include a single crop field, an orchard, a section of stream, the cows in a pasture or barn, etc. Synonymous with the management unit in agricultural production systems.
Sequential sampling plan	A sampling plan in which "stop-lines."continually assess the need for additional sample units during the sampling effort on a given day or time interval. These stop lines are typically based on a prescribed level of desired precision or classification accuracy. Sequential sampling is efficient because no prior knowledge of density is required and no more sample units than necessary are collected. Contrast with fixed-sample size sampling.
Stratified sampling	A method of allocating sampling units in which the sample universe is subdivided into two or more sections and sample units are randomly collected from each subdivision in proportion to their size or relative variability. Examples include the subdivision of a crop field into border and interior sections, the subdivision of a plant along vertical strata, or different rooms within a structure.
Systematic sampling	A method of allocating sample units within a sample universe in which sample units are collected at fixed intervals along a predetermined pattern. Examples include sampling along transects or along V or X shaped patterns in crop fields. Often, the starting point of the pattern is determined randomly. Systematic sampling is probably the most common method for allocating sample units in most agricultural systems because it is simple and time-efficient.
Tally threshold	In binomial sampling, the number of individuals required to be present per sample unit to consider the sample unit infested. Proper selection of the tally threshold can improve the accuracy of classification sampling.

Sampling Arthropods, Table 1 Definitions of some common terms associated with arthropod sampling (Continued)

Variable-intensity sampling plan	A sampling plan that shares the characteristics of fixed-sample size and sequential sampling plans in which prior sampling information is used to evaluate the number and allocation of subsequent sample units, but ensures that sample units are collected throughout the sample universe.

program is to clearly define the goal(s) of sampling. Is the goal to survey for the abundance or presence of one or more insect species over a large geographical region? Or is the goal to intensively study the temporal dynamics and examine rates of mortality of a single insect species in a relatively small area? Perhaps the goal is to develop a simple procedure that a field scout can use to determine the need for remedial pest control in a field crop. A researcher may be interested in testing the effect of a control tactic on populations of a pest insect using replicated field plots. Although some of the information that will be necessary to devise sampling plans is shared among all these and other applications, as we will see below, there are also differences in the sampling methods that may be used and the levels of accuracy and precision that may be required to provide useful data. For example, a quick and simple relative sampling method such as a sweep net or a colored sticky trap may be sufficient for survey detection or for monitoring the relative abundance of one or more insect species over a large region. Here the premium would generally be placed on extensive spatial coverage at the expense of precise estimation of density, which may not be necessary. In contrast, detailed population studies involving the construction of life tables would require an absolute sampling method, such as quadrat or whole plant counts, and fairly large sample sizes so that mortality factors and recruitment to subsequent life stages could be precisely estimated. The development of a decision-aid for pest scouting could use either an absolute or a relative method of sampling depending on the pest and would likely involve the use of a sequential sampling plan that would allow the classification of pest density as either above or below an established economic threshold.

The time and resources that one has to devote to the activity of sampling are almost always in short supply, even in well-funded research programs. Thus, clear delineation of the goal(s) of sampling is the first step towards ensuring that available time and resources will be put to the best use to answer the questions that are being asked of the sample data.

Sampling Methods

Many sampling methods have been devised by entomologists for sampling all types of insects, mites and spiders. Each arthropod poses its own unique challenges. In fact, there are probably as many sampling methods as there are entomologists using them. It would be impractical to try and cover all of the available techniques that have been developed. Instead, focus will be placed on relatively few methods that have been widely used to provide a flavor of the diversity. Readers are referred to the excellent and comprehensive treatment of all aspects of sampling provided by Southwood (1978).

For purposes of organizing this discussion, it is convenient to classify sampling methods according to the type of information that they can potentially provide the sampler. These include absolute methods, relative methods, and population indices. Sometimes the difference between an absolute and a relative method is not distinct and a technique that provides an absolute method for one insect will not do so for another in the same habitat. Absolute sampling methods attempt to provide an estimate of density from a specific and quantifiable fraction of the habitat in which the arthropod lives. Generally, these counts have the unit of numbers per square meter or some other unit of ground area or space within structures. Common examples include quadrat sampling in which a square, rectangle or circle of known area is placed on the ground and all arthropods of interest falling within that area are counted in situ or the vegetation is collected and later examined in the laboratory. In agricultural, horticultural or rangeland situations the quadrat delineates a volume that may be relatively small if dealing with low-growing grasses or forbs, or relatively large if dealing with corn plants or fruit trees. Quadrats may also be used to sample arthropods within barns, houses or other structures. Often, the quadrat is placed the day before sampling to minimize disturbance. For arthropods that are found only on the plant surface, absolute counts can be made by counting all individuals on a single plant, groups of plants, or even specific parts of plants such as whole leaves, stems, or branches. Sometimes these efforts are aided by the use of various sorts of enclosure devices (e.g., cages or sacks) to confine the arthropods until they can be counted. In many cases, conversion to unit ground area can be accomplished by knowing the number of habitable plants, leaves or branches per unit area. For certain arthropods that are readily dislodged from plants, various kinds of beat cloths and buckets can be used (Fig. 4). Suction samplers may provide absolute counts for certain arthropods depending on plant size and growth characteristics. Absolute sampling of soil-dwelling arthropods can be achieved by taking soil cores or digging trenches of a known volume. Surface-dwelling arthropods can be counted directly or collected from the litter within a quadrat. Arthropods can be extracted from collected soil, plant or litter material using a variety of approaches including simple inspection, dry and wet sieving, flotation in concentrated salt solutions, leaf brushing machines, and other methods. Live arthropods can be extracted by chemical fumigation or heat (e.g., Berlese funnel). Emergence traps can be used in some instances to measure the absolute density of adult stages of insects that pupate in or on the soil. Suction traps or aerial nets towed by an airplane or vehicle can be used to obtain absolute samples of flying insects (Fig. 5). In this instance the unit is a given volume of air that can be calculated by knowing the volume of air drawn by the motor per unit time (or speed of the vehicle) and other environmental factors such as wind speed.

Relative methods are so named because they generally provide estimates of density that are comparable in relation to other estimates made in the same way in the same type of habitat. Relative sampling results in counts per unit of effort and it is not always possible to define the physical units of a method. In contrast with absolute methods, relative methods are generally less costly, easier to perform, and tend to concentrate arthropods. As such they are well-suited to extensive detection and survey work and as components of decision aids in IPM. Relative methods are also widely used in experimental field work where it is often necessary to sample a large number of plots in a short period of time, and only comparative results are sought. In some cases relative estimates can be converted to absolute estimates, but this depends on the specific arthropod and the nature of the sampling method. Common examples of relative methods include the ubiquitous sweep net which is almost the *de facto* standard for estimating densities of arthropods associated with many field crops (e.g., cotton, soybean, small grains, alfalfa). The sweep net can cover a large area of habitat in a short period of time and the particular pattern and number of swings can be standardized across samplers. However, it also samples only a proportion of the population (that inhabiting the tops of plants) and this proportion can change with plant growth, environmental conditions, and time of day. Various methods involve the dislodgement of arthropods from plants into buckets, cloths, nets, trays

Sampling Arthropods, Figure 4 **Examples of various kinds of sampling methods: (a) beat-bucket in which a plant is shaken against the sides of a bucket to dislodge arthropods; (b) beat-cloth in which a piece of white cloth is placed on the ground and plants are shaken or beaten to dislodge arthropods; (c) beat-net (or cloth) in which arthropods are dislodged into a net with a beating stick; (d) plant cage that encloses a specific portion of habitat; arthropods are dislodged from the enclosed plant material; (e) example of a Berlese funnel in which arthropods are driven from litter or soil into a collection bucket by the application of heat and light from above; (f) sweep net; (g) D-vac suction sampler; (h) high powered suction sampler designed for field row crops; (i) trench for sampling soil-dwelling arthropods; (j) quadrat; (k) visual inspection of a leaf, (l) visual inspection of a whole plant. All photographs by the author unless otherwise noted.**

Sampling Arthropods, Figure 5 **Examples of various kinds of traps for sampling arthropods: (a) canopy trap for sampling insects flying vertically out of a crop field; (b) emergence trap for sampling adult stages of insects that pupate in the soil; (c) window-pane trap for assessing the movement patterns of flying insects; (d) modified malaise trap for assessing the movement patterns of flying insects; (e) one of a large number of sizes and types of sticky traps; (f) suction trap for aerial sampling of flying insects. All photographs by the author unless otherwise noted.**

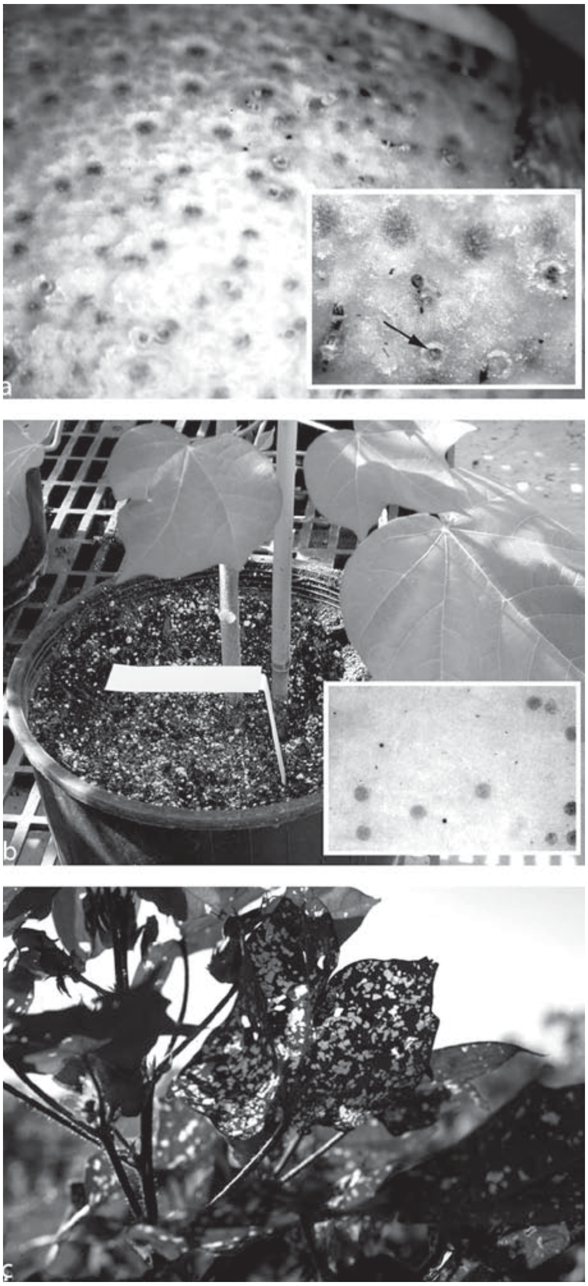
or other surfaces. Depending on the behavior and biology of the arthropod and the portion of the plant sampled, this may provide either absolute or relative sampling information. In most cases only a small portion of the plant is sampled. The same is true of various suction sampling devices such as the well-known D-vac, modified leaf blowers, or high-powered vacuums attached to carts or tractors. Visual inspections of various plant parts such as leaves or branches are generally considered relative methods, although in many cases, counts on these parts can be related to counts per plant or tree. Timed-counts, which simply involves enumerating all the arthropods that can be counted in a specified period of time are commonly used, especially when the goal it to compare densities of a specific arthropod in a number of different habitats.

By far, traps of various kinds represent the broadest diversity of relative methods. Traps and trapping are the subject of an entry in this volume and so will only be briefly discussed here. Traps can be delineated into those that passively intercept and those that attract actively moving arthropods. Examples of the former include canopy traps, window-pane traps, malaise traps, pitfall traps, and white or clear sticky traps. Examples of the latter include semiochemical- or food-baited traps, traps of various colors (yellow is most common) generally coated with a sticky material, light traps, and sound traps. Mammals and birds also may be used as baits to trap arthropods of medical and veterinary importance. In general, trap counts are very difficult or impossible to convert to absolute counts because they rely on behavior that can be influenced by an array of biological and environmental factors.

Finally, the product or effect of an arthropod population rather than counts of individuals can be used to gauge relative abundance. Common examples of products include the collection of insect frass underneath plants or trees, the collection of larval or pupal exuviae, or the counting of spider webs. Examples of arthropod effects include the assessment of defoliation by foliage-feeding insects, tunneling by stalk-boring insects, or root pruning soil-dwelling insects (Fig. 6). Acoustic monitoring can be used to detect the presence and relative abundance of insects inside fruit, grain bins or within the walls of structures. Both products and effects can sometimes be related to more quantitative measures of population density. The examination of arthropod effects can be important in their own right in terms of assessing economic damage.

Development of a Sampling Plan/ Program

A sampling plan or program is a structured set of rules that guide sampling activities. The sampling plan includes delineation of the sample universe, timing of sampling, the size and nature of the sample unit, how many sample units need to be collected, and how these sample units are spatially allocated among potential sample units in the population. Thus, a sampling plan is distinct from a sampling method or technique (a component of a plan) with which it is sometimes mistakenly confused in the entomological literature. Not all sampling activities in entomology require a sampling plan; for example, collections for systematic or taxonomic purposes. However, if the goal includes the estimation or classification of the density or size of an arthropod population, then the user would be best served by considering, at the very least, selected components of a sample plan to ensure that the sample data are trustworthy. Binns et al. (2000) suggest that a trustworthy sampling plan should adhere to four criteria. First, estimates generated by the plan should be representative of actual pest density thereby avoiding or at least being able to account for any bias. Second, sample estimates should be largely independent of the sampler and of uncontrollable environmental variables such as weather. Third, sample information should be relevant to the questions being asked. For example, estimates of pest density in a management context should be have an identifiable



Sampling Arthropods, Figure 6 Examples of methods for estimating population indices: (a) counting entrance holes of neonate pink bollworm larvae on the surface of a cotton boll; (b) counting honeydew droplets from whiteflies or aphids on water-sensitive paper; (c) assessing caterpillar abundance from defoliation. All photographs by the author.

relationship to crop damage. Finally, the sampling plan must be practical for its intended purpose. For example, it would do little good to develop an elaborate and expensive sampling plan for IPM decision-making that scouts would be unable to implement due to time and resource constraints. These criteria can be met by careful attention to the building blocks of a sample plan.

Sample Plan Components

Delineation of the sample universe is often dictated directly by the goals of the sampling plan. For example, the population of interest for IPM of a particular pest species is generally a single crop field or perhaps a set of crop fields on a single farm that share a similar cultivar and planting date. In a rangeland setting the sample universe might be an entire ranch or perhaps sections or partial sections of the operation. The population of interest in an experimental research program would be a replicate plot representing a given treatment. If the population of interest occurs in an area where physical portions of the habitat are distinct and vary in their suitability for the organism under investigation, several sampling universes might be identified or a stratified sampling approach might be employed. This situation will be discussed below.

Likewise, the timing of sampling is often largely dictated by the goals of sampling. Each arthropod species has a distinct phenology and seasonality that will determine the appropriate time to gather samples on the life stage or stages of interest. The timing of occurrence of particular species might be estimated by phenological models, the presence of indicator plants, or historical records. In instances where the timing of occurrence is not well-characterized or highly variable, the use of detection traps may help to determine the need for more intensive sampling by other methods.

Of all the components of a sampling plan, the sample unit is perhaps the most important yet most frequently overlooked element. The sample unit defines the unit of habitat represented by the sample and is the foundation for all further development of an efficient sampling plan. Each sample unit should have an equal chance of being selected from the sample universe. It should contain a consistent fraction of the population over time. Thus, definition of the sample unit may include a time component. For example, arthropods may inhabit different parts of a plant over the course of a day due to changes in temperature, light and other factors. The sample unit should be easy to delineate in the sample universe. The sample unit should be appropriately sized relative to the size and behavior of the species in question. For example, a small disk from a leaf may be suitable for spider mites or aphids, but not for large and mobile insects such as assassin bugs or grasshoppers. Finally, the sample unit should strike a balance between variability of counts and the cost of sampling that unit. Using these criteria helps to ensure that the sample unit is representative of the population and help to minimize or eliminate bias.

The sample unit is based on the sampling method from which it is derived. Examples of sample units include 25 sweeps with a sweep net along a single crop row between 0800 and 1000 h, the lower surface of a leaf five nodes below the terminal apex of a plant, the silks at the tip of one ear of corn, a 8 × 8 cm yellow sticky card oriented horizontally at the top of the crop canopy and exposed for 24 h, five beats to a tree branch one meter above the ground with a stick over an open 38 cm diameter net, 0.001 m^3 of soil dug from within a 100 cm^2 frame, the head or leg of a single cow, or 2 min of suction from a D-vac placed over the top third of a crop plant. Very often the sample unit is selected *a priori* based on knowledge of the biology and behavior of the organism and experience, and is not the subject of further investigation. However, careful attention to the size and nature of the sample unit can greatly increase the efficiency of the overall sampling program by minimizing both variability and cost. Established methods are available for comparing various candidate sample units (see Southwood 1978) based on consideration of precision and cost. However, as a guideline, smaller sample units are generally more efficient than larger units. This generalization is based on the typical aggregated dispersion of many arthropod populations and the lower cost of counting individuals on smaller sample units even when a comparatively larger sample size may be required.

Dispersion, or spatial distribution, is a characteristic of populations and can be influenced by a host of biological, behavioral, ecological and environmental factors. Patterns of dispersion are typically categorized as uniform, in which individuals are evenly spaced throughout a habitat, random, in which the location of one individual bears no relation to the location of others, or aggregated (contagious), in which individuals are found in clumps of varying sizes. Many arthropod populations are described as having an aggregated dispersion. Knowledge of dispersion is an important element in the development of sampling plans, influencing both the determination of sample size and the allocation of sample units. The measurement of dispersion is spatially contextual. That is, patterns of dispersion depend on the spatial scale under which they are observed. As a result, the dispersion of a population is greatly influenced by the size of the sample unit. For example a population could be aggregated at the level of a whole plant, but randomly distributed at the level of a single leaf. Thus, in sampling work, dispersion generally refers to the sampling distribution rather than the true spatial distribution. A number of methods are available to explicitly measure dispersion or to provide indices of dispersion. A common index is to simply divide the sample variance by the sample mean. Values <1, ~ 1 or >1 indicate uniform, random or aggregated distributions, respectively. For sample plan development it is more typical to characterize dispersion with probability models or empirical mean-variance models. Common probability models include the Poisson for random distributions, and the

Negative-binomial for aggregated distributions. The primary limitation of using probability models is that sampling distributions typically vary with changing arthropod density and it is not always possible to account for these changes in the model. Empirical regression models offer a solution to this problem by permitting prediction of sample variance from the sample mean. Such models can provide useful information over a wide range of densities. Common examples include Taylor's power law and Iwao's patchiness regression, both of which can be parameterized with simple linear regression.

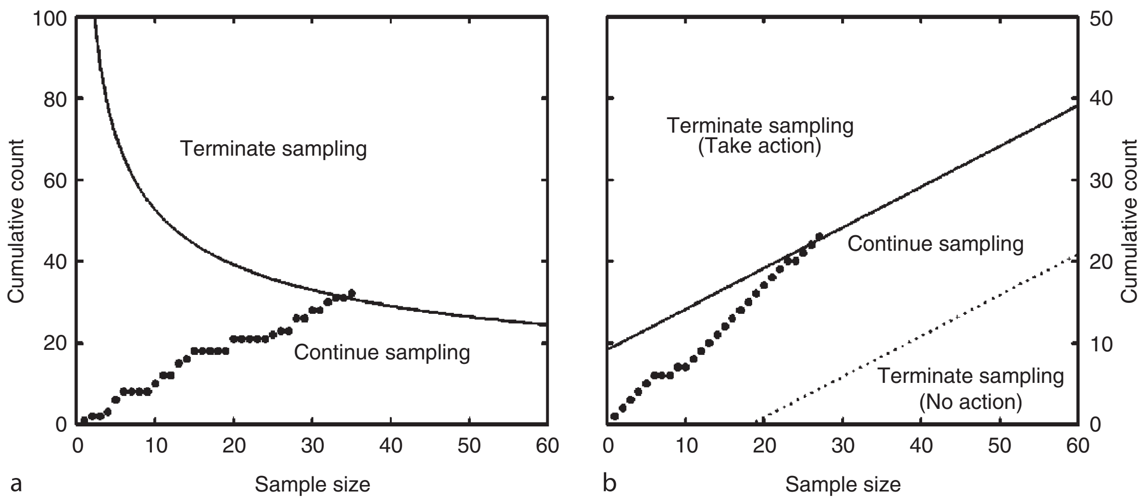
Once the sample unit has been selected and the sampling distribution has been characterized by either a probability or empirical model, the sample size can be calculated. How this is done depends on the goals of sampling, the criteria for determining the adequacy of the population estimate or classification, and the resources that can be devoted to sampling activities.

Types of Sampling Plans

Fixed-sample-size sampling plans, as the name implies, are based on the collection of a set number of sample units. The optimum sample size is the minimum number of sample units that achieves a desired level of performance. Fixed-sample-size sampling can be applied to density classification as well as estimation; however, it is more commonly used for the latter and so consideration will be restricted to estimation here. Several approaches can be used depending on how dispersion is characterized and how precision is quantified. The simplest approach is to calculate the optimum sample size such that the standard error is within a specified proportion of the mean, or that the mean falls within a certain confidence interval of the true mean with a specified probability. Variations on this approach explicitly account for sampling distribution (e.g., Poisson, Negative binomial). A slightly more complicated and robust approach uses a mean-variance model such as Taylor's power law to solve for sample size using the same measures of precision. The main advantage of this approach is that the optimum sample size is dependent on the mean density of the population. Typically, sample size decreases exponentially with increasing density. The reader is referred to Southwood (1978) and Pedigo and Buntin (1994) for mathematical details.

One of the main advantages of a fixed sample size is that sample allocation (see below) can be structured so that sample units are collected from throughout the sample universe. The main disadvantage is that the mean density is unknown for the population under study at any given point in time. One solution would be to calculate sample size for the lowest expected density or the average expected density and then apply that in all cases. This would clearly be inefficient at high densities, or require too many or too few sample units depending on density at any point in time, respectively. The use of double sampling would be an alternative solution. Here a small sample would be collected and used to solve for the required sample size at that point in time.

Sequential sampling is another alternative that solves the problem of unknown density and generally maximizes sampling efficiency. Sequential sampling was developed for military application during World War II and has since become the most widely applied approach for developing sampling plans for arthropods based on both density estimation and density classification. Efficiency is optimized because in sequential sampling the need for further sample information is assessed following the collection of each individual sample unit. Regardless of the mean density, sequential sampling ensures that no more sample units are collected than necessary in order to achieve a predetermined level of precision or classification accuracy (Fig. 7). Sequential sampling for estimation of mean density operates by accumulating counts over subsequent sample units and then consulting a "stop-line." This stop-line represents the cumulative count as a function of sample size and the desired precision. It can be plotted or presented



Sampling Arthropods, Figure 7 **Hypothetical examples of (a) sequential sampling plan for estimating mean density with a fixed precision and (b) sequential sampling plan for classifying mean density relative to an economic threshold. The lines denote the stop-lines and the data points represent a hypothetical sample that terminates after crossing the stop-line.**

in table form. Matching the current cumulative count and sample size relative to the stop-line determines whether more sample units are need or whether sampling should be terminated. Once sampling is terminated the mean is calculated by simply dividing the cumulative count by the number of sample units collected. Sequential sampling plans for mean estimation can be developed on the basis of probability or mean-variance models. Frequently, a minimum and maximum sample size is specified as part of the sequential plan. The reader is referred to Nyrop and Binns (1991) and Pedigo and Buntin (1994) for mathematical details.

A second application of sequential sampling involves the classification of population density. Most often this approach is applied to the development of decision-aids for IPM where one simply wants to know whether pest density is above or below the economic threshold. Operationally, sequential sampling for classification is similar to that described above for mean estimation except that a critical density (e.g., economic threshold) and upper and lower decision boundaries must be specified. The calculation of the stop-lines is also more complex. Several approaches have been developed. One goes by the daunting name of the sequential probability ratio test (abbreviated SPRT) and can be based on various probability models including the Poisson, negative-binomial, normal or binomial. A second technique termed Iwao's confidence interval method is based on the normal distribution, and a third called the sequential interval procedure is based on the binomial distribution. All three approaches result in pairs of stop lines rather than a single one, delineating three distinct decision zones. More complex plans can be developed involving multiple stop lines designating even finer decision zones. Such sampling plans are popular for use in IPM because of their high degree of efficiency. Very few sample units are required when densities are much smaller or larger than the critical density and the maximum number of sample units is required only when the density is very near the critical density. Sequential sampling plans for classification are developed and evaluated on the basis of two criteria, the operating characteristic (OC) and the average sample number (ASN). The OC estimates the probability of classifying density below the critical density as a function of the true mean density. Various parameters of the sequential plan can be adjusted to increase or decrease the level of classification accuracy and the associated sample size.

Up to this point the discussion has focused on enumerative sampling in which all individuals inhabiting a sample unit are counted. However, depending on program goals, the general efficiency of sampling can be potentially improved by determining only the presence or absence of individuals in the sample unit. This approach, referred to as binomial sampling has been widely used in the development of decision aids for IPM and is typically implemented as a sequential classification sampling plan as described above. Generally, the foundation for this approach is the development of a relationship between mean density and the proportion of sample units containing at least T individuals. T is known as the tally threshold and traditionally has a value of 1 (true presence/absence); however, it can take on any value and proper selection of T can often improve the accuracy of classification. This mean density-presence/absence relationship can be determined using various probability models or it can be represented by one of several empirical models. In some instances it is more convenient to base the economic threshold simply on binomial counts and, thus, there is no need to develop a relationship with mean density. A well-devised and tested binomial sampling plan can significantly reduce the cost of sampling without sacrificing accuracy of density classification in IPM decision-making. Binomial sampling can also be an efficient approach for estimating population density, although its application for this purpose has been limited. The reader is referred to Nyrop and Binns (1991), Pedigo and Buntin (1994), and Binns et al. (2000) for mathematical details on sequential sampling for classification using both enumerative and binomial sampling.

A final sampling approach, termed variable-intensity sampling, is a classification method that shares some of the attributes of both fixed-sample-size and sequential sampling plans. It was developed primarily to address a potential deficiency in sequential sampling having to do with adequate coverage of the sample universe. As a result of its high efficiency, sequential sampling often terminates sampling after only a small portion of the sampling universe is observed. Variable intensity sampling solves this problem by delineating a transect (see allocation below) across the sample universe, dividing that transect into equal lengths, and requiring at least one sample unit in each section. Thus, the sample is more representative, especially in situations where pest density might be highly variable across a field. The overall number of sample units taken in each transect section ultimately depends on prior sampling information much as in a traditional sequential sampling plan. Variable intensity sampling can be based on enumerative or binomial counts.

Allocation of Sampling Units

The final element of a sampling plan is the collection of sample units from the sample universe. Random sampling assumes that every possible sample unit within the sample universe has an equal chance of being selected. As such, random sampling ensures that the sample will provide unbiased estimates (assuming that the proper sample unit is used and sample size is adequate). Random sampling can be accomplished by enumerating every sample unit and then selecting them using a random number table, drawing numbers from a hat, or using a computer random-number generator. This assumes that the spatial location of each sample unit can be correctly identified which may be extremely difficult. In field crops, orchards or greenhouses with evenly spaced plants, sample unit location can be simplified somewhat by defining a coordinate system and randomly selecting a random row and a random number of steps or plants along the row from the edge. A variation of random sampling is stratified sampling. This approach may be used if there is some a priori knowledge that the population being sampled is heterogeneously distributed. Common examples are the differential distribution of insects in border rows compared with interior rows of a crop field, the differential distribution of insects within the vertical strata of a plant, or differences in distributions of arthropods within structures. In instances such as these a more precise estimate may be achieved by allocating sample units to different strata in proportion to the size of each strata, or in relation to variability within each strata. More sample units would be collected in strata that are known to be more variable and vice versa. The allocation of sample units within a stratum is random, preserving the benefits of random sampling, but different formulae are needed to estimate mean density and variance.

Despite the desirable qualities of random sampling, it is rarely used in practice mainly because proper implementation is costly. It is much more common for sampling plans to be implemented using some sort of systematic sampling. In systematic sampling, some predetermined path is chosen and sample units are collected at fixed intervals along this path. Typical examples are diagonal transects, or X-, V-, or Z-shaped patterns laid out across the sample universe. Aside from being easy and inexpensive to implement, systematic sampling generally allows sample units to be collected from throughout the entire sample universe, resulting in a more representative sample. A degree of randomness can be added by randomly selecting the starting point of the transect and the interval between sample units. A disadvantage to systematic sampling is that it can produce biased estimates if there is some underlying pattern in the population that closely mimics the pattern of sample unit collection. Further, there are no exact formulae for calculation of variance and so estimates based on random sampling are often assumed. The overall effect of these limitations is not well-known, however, proper testing and evaluation (see below) can help to ensure that the sample obtained is reliable and provides the necessary levels of precision and accuracy.

Testing and Evaluation of Sample Plans

Ideally, sampling plans should be developed from observations that encompass the geographic area and range of environmental conditions that future users of the sampling plan are likely to encounter. In reality, however, sampling plans are often developed from a more restricted range of observations and then applied to similar or novel situations. In addition, regardless of the extent of data collection, any sampling plan is based on observations that are measured with some amount of error. Thus, it is important that the performance of a sampling plan be evaluated so that its limitations and strengths can be better defined. This evaluation process is known as validation. In the past, generally little attention was paid to sample plan validation, however, this situation is changing and several validation approaches have been formalized in the last 10–15 years. The simplest involves the use of Monte Carlo simulation. In this method the sampling plan is applied to sample units counts that are randomly drawn on a computer from a probability distribution (e.g., Poisson, Normal, Negative binomial) that is representative of the sampling distribution of the arthropod in question. This procedure is repeated a large number of times (usually 500 or more) to represent a large number of possible sampling outcomes and average precision or classification accuracy (and their variances) are calculated. An alternative approach uses real sample data independently collected at the time of sample plan development or collected from an area where the sample plan is to be implemented. These real data are then resampled on a computer much as in the Monte Carlo approach. The advantage of the resampling method is that the data rather than a probability distribution are used to represent the sampling distribution. The result is a more robust test of the sampling plan and the assumed probability model upon which it may be based. A disadvantage is that larger amounts of data collection are required. With both approaches, the validation data can have an explicit spatial arrangement so that issues of sample unit allocation can be tested as well. The reader is referred to Naranjo and Hutchison

(1997) and Binns et al. (2000) for further detail and available computer software.

References

Binns MR, Nyrop JP, van der Werf W (2000) Sampling and monitoring in crop protection: the theoretical basis for developing practical decision guides. CABI Publishing, Wallingford, UK

Cochran WG (1977) Sampling techniques, 3rd edn. Wiley, New York, NY

Flint ML, Gouveia P (2001) IPM in practice: principles and methods of integrated pest management. University of California, Statewide Integrated Pest Management Project, Agriculture and Natural Resources Publication 3418, 344 pp

Morris RF (1960) Sampling insect populations. Ann Rev Entomol 5:243–264

Naranjo SE, Hutchison WD (1997) Validation of arthropod sampling plans using a resampling approach: software and analysis. Am Entomol 43:48–57

Nyrop JP, Binns M (1991) Quantitative methods for designing and analyzing sampling programs for use in pest management. In: Pimentel D (ed) Integrated pest management. CRC Press, Boca Raton, FL, pp 67–132

Pedigo LP, Buntin GD (eds) (1994) Handbook of sampling methods for arthropods in agriculture. CRC Press, Boca Raton, FL

Southwood TRE (1978) Ecological methods: with particular reference to the study of insect populations, 2nd edn. Chapman and Hall, London, UK

Sampling Plan

A structured set of rules for collecting a sample that is based on delineation of the sample universe, knowledge of dispersion, a specific sample unit, a predetermined sample size (but see sequential sampling), time of sampling, and a given allocation of sample units throughout the sample universe (e.g., random, stratified, systematic).

► Sampling Arthropods

Sanderson, Dwight

Dwight Sanderson was born at Clio, Michigan, on September 25, 1878. He earned B.S. degrees from both Michigan State University and Cornell University. He then worked in entomology in Maryland, Delaware, and at Texas A&M and the University of New Hampshire. At New Hampshire he became Director of the Agricultural Experiment Station and was elected president of the American Association of Economic Entomologists. In 1910 he became dean of the College of Agriculture at West Virginia University and then director of the experiment station. He was awarded a doctorate in sociology from the University of Chicago in 1921. Sanderson was interested in insect development and in insect pest control. He authored "Insects injurious to staple crops" (1902), and "Insect pests of farm, garden, and orchard" (1911). He was a founder of the Journal of Economic Entomology and was instrumental in getting the Federal Insecticide Act of 1910 passed by the United States Congress. He also wrote four books on rural sociology. He died at Ithaca, New York, on September 27, 1944.

Reference

Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Sandfly Fever

This is an influenza-like viral disease caused by several bunyaviridae and transmitted by *Phlebotomus* flies (Diptera: Psychodidae), especially *Phlebotomus papatasii*. Hence, it is also called phlebotomus fever. The vectors feed on vertebrate blood, often being found in rodent burrows and other animal shelters. Symptoms of human infections are flu-like, and include headache, fever, chills, shivering, muscle and joint pain, and eye and vision problems. The flies bite at night and in the early morning hours. The disease is endemic to the Mediterranean region, and has been known to incapacitate large numbers of military personnel during regional conflicts. It is not fatal. Prevention includes sleeping under bed nets, and use of insect repellent.

Reference

Tesh RB (1989) The epidemiology of *Phlebotomus* (sandfly) fever. Isr J Med Sci 25:214–217

Sand Fly

A name applied to various small biting flies (Diptera), including members of the family Psychodidae, Simuliidae, and Ceratopogonidae, though this name refers most correctly to members of the family Psychodidae.

► Flies
► Biting Midges, *Culicoides* spp.

Sanitation

The practice of eliminating pests by removal or destruction of materials or sites that might harbor pests.

Sap Beetles (Coleoptera: Nitidulidae)

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The family Nitidulidae belongs to the superfamily Cucujoidea in the suborder Polyphaga of the order Coleoptera (beetles).

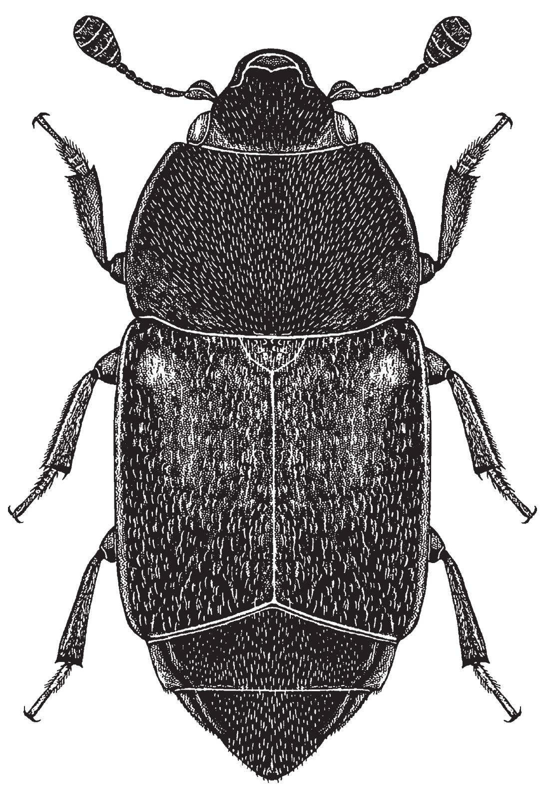
Order: Coleoptera
Suborder: Polyphaga
Superfamily: Cucujoidea
Family: Nitidulidae

Six subfamilies of Nitidulidae are recognized, although the classification at both the generic and subfamily levels is still in a state of flux. One subfamily, Brachypterinae, was recently elevated to family status. The subfamily Cybocephalinae is often placed in its own family Cybocephalidae, and sometimes Cateretidae, Brachypteridae, Cybocephalidae and Smicripidae are included in the Nitidulidae.

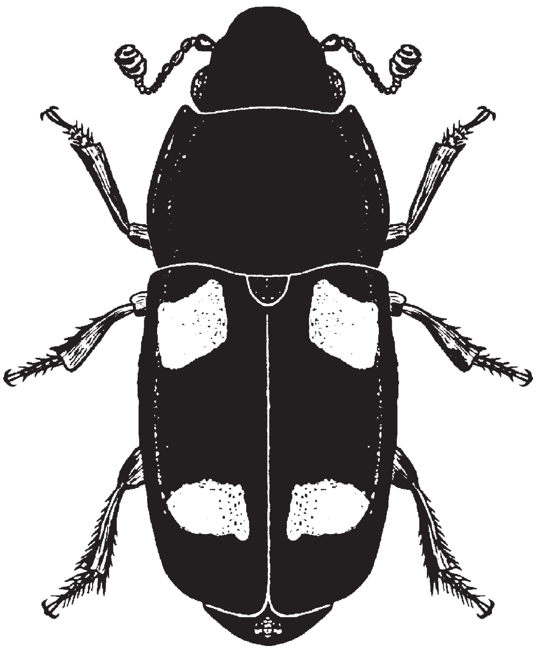
The Nitidulidae are a small family of mostly small beetles. There are 165 species in North America and about 3,000 described worldwide, although many more remain undescribed.

Adults

The length of adult Nitidulidae ranges from about 1 to 12 mm. Bodies are often depressed, usually oval shaped, but some elongate. The adults often bear red or yellow spots. The head is prognathous. The antennae are 11-segmented, with the apical three segments forming a club (Figs. 8 and 9). The antenna is often received in a groove on the underside of the head. The tarsi are 5-segmented on all legs, but with only four segments in the Cybocephalinae.



Sap Beetles (Coleoptera: Nitidulidae), Figure 8 Adult dusky sap beetle, *Carpophilus lugubris*.



Sap Beetles (Coleoptera: Nitidulidae), Figure 9 **Adult fourspotted sap beetle, *Glischrochilus quadrisignatus*.**

Larvae

The larvae are elongate, and 2–20 mm long, but most <12 mm, parallel sided and frequently flattened. In many larvae, the mandibles bear a well-developed prostheca. Most larvae with paired, fixed appendages (urogomphi), but they are lacking in the Meligethinae and Cybocephalinae. The spiracles are two openings at the end of tubes (except in Cybocephalinae). The pupae are exarate.

Food

Nitidulidae display a wide range of feeding habits, though they are generally considered to be saprophagous and mycetophagous. As the common name (sap beetles) implies, many (especially *Carpophilus* and *Glischrochilus*) are found at sap flows on injured trees. Cybocephalinae are predatory on scale insects, and Glischrochilus have been reported to be predators of wood-boring larvae. Many species (e.g., *Pallodes*, *Pocadius*, *Thalycra*, *Cychramus*, *Aphenolia*) feed on fungi. Pollen and nectar-feeding occur in the *Meligethes*, most *Conotelus* and some *Carpophilus*. *Nitidula* and *Omosita* are carrion feeders and *Amphotis* are associated with ant colonies at least part of the year.

Economic Importance

Aethina tumida is a serious pest in bee hives. *Carpophilus dimidiatus* is a minor pest of stored grains, and *C. lugubris* is a pest of sweet corn. Several species in the genera *Carpophilus*, *Glischrochilus*, *Epuraea* and *Colopterus* are involved in transmitting the pathogenic fungus causing oak wilt.

► Beetles
► Small Hive Beetle, *Aethina tumida*

References

Habeck DH (2002) Nitidulidae. In: Arnett RH, Thomas MC (eds) American beetles, vol 2. CRC Press, Boca Raton, FL, pp 311–315

Lawrence JF (1991) Nitidulidae (Cucujoidea) including Brachypteridae, Cateretidae, Cybocephalidae, Smicripidae. In: Stehr FW (ed) Immature insects, vol 2. Kendall/Hunt, Dubuque, IA, pp 456–460

Lawrence JF, Newton Jr (1995) Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). In: Pakaluk J, Slipinski SA (eds) Biology, phylogeny, and classification of Coleoptera. Museum: Instytut zoologii PAN, Warsaw, Poland, pp 779–1006

Parson CT (1943) A revision of Nearctic Nitidulidae (Coleoptera). Bull Museum of Comp Zool 92:121–278

Saprophagous

Feeding on dead or dying plant or animal tissue.

Sapygidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Sarcophagidae

A family of flies (order Diptera). They commonly are known as dung flies.

► Flies

Sarcoptic Mange

A disease caused by mites of the genus *Sarcoptes*; scabies.

► Mites

Sarcosomes

Large mitochondria found in muscle, especially thoracic muscle.

Saturniidae

A family of moths (order Lepidoptera). They commonly are known as giant silkworm moths, emperor moths, or royal moths.

► Emperor Moths
► Butterflies and Moths

Satyrs

Some members of the family Nymphalidae, subfamily Satyrinae (order Lepidoptera).

► Brush-Footed Butterflies
► Butterflies and Moths

Saucer Bugs

Members of the family Naucoridae (order Hemiptera).

► Bugs

Saunders, William

William Saunders was born in England in 1820, and moved from Devonshire to Canada in 1832, where he became known as a pioneer in horticulture and entomology, and Canada's first economic entomologist. Though lacking much formal education he received some technical training in chemistry and became a druggist in London, Ontario. However, he loved nature and took to the study of plants and insects. He became a specialist in medicinal plants, and became well-known as a supplier of quality products to the medical profession. He also became a professor at the University of Western Ontario (Fig. 10). Saunders was co-founder (with C.J.S. Bethune) of the Entomological Society of Canada in 1863, and also co-founder of the Canadian Entomologist, in 1868. Interestingly, the co-founders were also the only two authors of the first two editions of this journal! Saunders managed the journal for 5 years, ending in 1886 when he moved to Ottawa. In 1883 he published an important treatise, "Insects injurious to fruit." He was also appointed Director of Experimental Farms of the Dominion in Ottawa, in 1886, and helped establish the first experimental farm. He died on September 13, 1914, in London, Ontario.

Saunders, William, Figure 10 **William Saunders.**

Reference

Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Saussure, Henri Louis Frederic De

Henri Saussure was born at Geneva, Switzerland, on November 27, 1829. A noted specialist in Hymenoptera and Orthoptera, Saussure initially studied social wasps, but is best known for work on the grasshoppers. He received his education in Switzerland and Paris, and also studied with the entomologist François Jules Pictet de la Rive. Saussure traveled to the West Indies, Mexico and the United States, returning to Europe with valuable collections of animals. His interests were quite broad, and in 1858 he founded the Geographical Society of Geneva. In Geneva, he was also associated with the Natural History Museum of Geneva. Saussure died at Geneva on February 20, 1905.

Reference

Essig EO (1931) A history of entomology. Macmillan, New York, 1029 pp

Sawflies (Hymenoptera: Symphyta)

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Sawflies are members of the order Hymenoptera, suborder Symphyta. Adult sawflies can be distinguished from the other members of that order (Suborder Apocrita: the parasitic Hymenoptera, wasps, bees, and ants) by their saw-like ovipositor, lack of constriction at the base of the abdomen, fly-like appearance and more extensive wing venation. Sawfly larvae are eruciform (caterpillar-like) and phytophagous (except members of the family Orussidae) rather than grub-like and parasitic or predatory. They are often confused with lepidopteran larvae, but have numerous distinguishing characteristics, including six or more pairs of abdominal prolegs, a lack of chrochets on the abdominal prolegs, one lateral ocellus on each side of the head, and distinctly segmented maxillary and labial palpi. Furthermore, sawfly larvae generally lack long hairs, spines, or tubercules, common characteristics of many lepidopteran larvae.

There are approximately 8,000 species of sawflies worldwide, with most of the diversity found in the Northern Hemisphere. Diversity appears to be relatively low in the tropics. However, this may reflect a lack of significant sampling and study of sawflies in this region. Most sawflies, whose hosts are woody plants, are external leaf or needle feeders, and are relatively monophagous. In northern forest ecosystems, sawflies are the second most dominant group of defoliators behind the Lepidoptera. A number of introduced species have major pest status and many can periodically cause severe localized damage. Because studies of this group have not been extensive, they are not as well known to the public and it is likely that sawfly damage has often been attributed to other groups, particularly the Lepidoptera.

There are thirteen families within the Symphyta (Table 2). The Diprionidae and the Tenthredinidae contain most of the economically important species, with the latter family being by far the most speciose group. The table describes the species diversity, distribution, major hosts, and feeding habits of each sawfly family.

Adult sawflies are sexually mature upon emergence. Following mating, females of most species use their saw-like ovipositor to create a slit in the host plant tissue, into which they insert their eggs. Like other Hymenoptera, sawflies have haplodiploid sex determination, in which unfertilized eggs become males and fertilized eggs become females. Larvae of many species feed gregariously, particularly during the early instars. In most species, male larvae pass through five instars, females six. Mature larvae that have finished feeding usually drop off from the host plant, burrow into leaf litter or soil, and enter dormancy as a pre-pupae,

Sawflies (Hymenoptera: Symphyta), Table 2 Families of sawflies

Family	Approximate No. of species	Distribution	Hosts/feeding habits
Xyelidae	75	Holarctic	Pollen of *Pinus*, bud and twig borers of *Abies*, external leaf feeders on *Ulmus* and *Carya*.
Pamphiliidae	300	Holarctic	Web-spinning and leaf-rolling species on hardwoods, conifers, and shrubs.
Megalodontidae	50	Palearctic	Web spinners on herbaceous plants only.
Pergidae	500	Worldwide, most abundant in neotropics, dominant in Australia	Known hosts include species of *Eucalyptus*, *Quercus*, *Carya*, and *Nothofagus*. Hosts and habits are unknown for most species.
Argidae	800	Worldwide, most abundant in neotropics, dominant in Africa	All genera but one feed on angiospermous trees, shrubs, and herbaceous plants. One Australian genus feeds on *Cupressus*.
Diprionidae	125	Holarctic, with extensions into the northern tropics	Feed exclusively on conifers, primarily *Pinus*.
Cimbicidae	150	Holarctic	Defolators of woody plants.
Blasticotomidae	6	Palearctic	Stem borers of ferns.
Tenthredinidae	5000	Worldwide, rare in Australia	Many subfamilies, feed on a variety of plants including horsetails, ferns, grasses, sedges, hardwoods, and conifers.
Xiphydriidae	100	Worldwide, most diverse in sub-tropical Asia	Wood borers of hardwoods.
Siricidae	100	Mostly holarctic, some tropical	Wood borers of conifers and hardwoods.
Cephidae	100	Holarctic	Twig and stem borers of grasses, serious grain crop pests.
Orussidae	75	Worldwide, most diverse in tropics and subtropics	Only non-phytophagous group of Symphyta, parasitic on wood borers, especially Coleoptera.

often within a cocoon. For most species, the pre-pupae is the overwintering stage, and pupation occurs in the spring.

There is considerable variation in life history and voltinism (number of generations per year) within the Symphyta. Voltinism can even vary within a species depending on latitude and within a population depending on local microclimate. Most species in the Northern Hemisphere are univoltine (one generation per year), with an increase in multivoltinism towards the tropics and semivoltinism (more than 1 year required to complete life cycle) towards the poles. The red-headed pine sawfly, for example, has one to five generations per year throughout its range from Ontario, Canada to Florida, respectively.

A handful of sawfly species have major economic importance, particularly those that have been introduced from other regions. Some important conifer pests that were introduced into North America from Europe include the European pine sawfly, *Neodiprion sertifer*, the introduced pine sawfly, *Diprion similis*, the European spruce sawfly, *Gilpinia hercyniae*, and two European strains of the larch sawfly, *Pristiphora erichsonii*. Other native species in North America that frequently plague conifer plantations are the red-headed pine sawfly, *Neodiprion lecontei*, and the yellow-headed spruce sawfly, *Pikonema alaskensis*. The European woodwasp, *Sirex noctilio*, along with a symbiotic fungus, has been a substantial problem in the Southern Hemisphere where it was introduced into the highly profitable radiata pine plantations of Australia. It poses a similar threat to pine plantations in other regions such as South America. It is likely that new sawfly pests will emerge as species continue to be introduced into new areas in the absence of their natural enemies.

► Wasps, Ants, Bees and Sawflies
► Sawflies (Hymenoptera: Tenthredinidae)

References

Coulson RN, Witter JA (1984) Forest entomology: ecology and management. Wiley, New York, NY

Drooz AT (1985) Insects of eastern forests. Forest Service Miscellaneous Publication No. 1426, US Department of Agriculture, Washington, DC, 608 pp

Furniss RL, Carolin VM (1977) Western forest insects. Forest Service Miscellaneous Publication No. 1339, US Department of Agriculture, Washington, DC, 654 pp

Smith DR (1993) Systematics, life history, and distribution of sawflies. In: Wagner MR, Raffa KF (eds) Sawfly life history adaptations to woody plants. Academic Press, San Diego, CA, pp 3–32

Wilson LF, Wilkinson RC, Averill RC (1992) Redheaded pine sawfly: its ecology and management. USDA, Forest Service, Agriculture Handbook No. 694

Sawflies (Hymenoptera: Tenthredinidae)

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The Tenthredinidae belong to the Hymenoptera, suborder Symphyta. “Sawflies” is a generic term generally designating the superfamily Tenthredinoidea. In this section, the term “tenthredinid” will be used for clarity.

Systematics and Geographic Distribution

The superfamily comprises the Argidae, Blasticotomidae, Cimbicidae, Diprionidae, Pergidae and Tenthredinidae. The oldest fossil record of the tenthredinids is from the Early Cretaceous, whereas the other families evolved much later, namely from the Middle Tertiary.

Class: Insecta
Order: Hymenoptera
Superfamily: Tenthredinoidea
Family: Tenthredinidae

Over 5,000 tenthredinid species are described worldwide and distributed approximately in 430 genera. Major genera that contain over 50 species are *Amauronematus* (approximately 170 species described), *Athalia* (80), *Dolerus* (200), *Nematus* (240), *Macrophya* (170), *Pachyprotasis* (110), *Pristiphora* (180), *Tenthredo* (700), *Tenthredopsis* (60). Today, seven or sometimes eight subfamilies are recognized, as follows: Allantinae (represented approximately by 110 genera; e.g., *Athalia*, *Eriocampa*), Blennocampinae (105; e.g., *Blennocampa*, *Monophadnus*, *Periclista*), Heterarthrinae (40; e.g., *Caliroa*, *Fenusa*, *Profenusa*), Nematinae (55; e.g., *Cladius, Euura*, *Hemichroa*, *Hoplocampa*, *Nematus*, *Phyllocolpa*, *Pontania*, *Priophorus*, *Pristiphora*, *Trichiocampus*), Selandriinae (including Dolerinae; 75; e.g., *Dolerus*), Susaninae (1), and

Tenthredininae (50; e.g., *Macrophya*, *Pachyprotasis*, *Tenthredo*, *Tenthredopsis*).

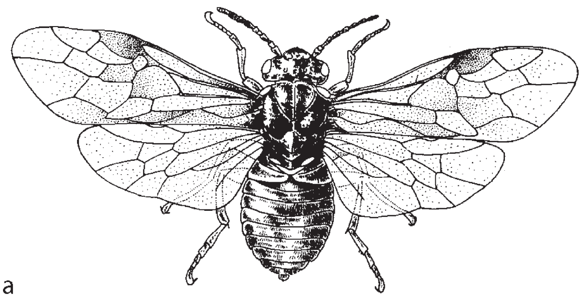
Tenthredinids occur as native species on almost all continents, being absent in Antarctica and New Zealand, and rare in Australia and smaller islands. They are the most diverse and abundant in the temperate zones of the northern hemisphere, preferring humid biotopes. However, some subfamilies are the most diverse in (sub) tropical zones (Selandriinae, Tenthredininae), while the Nematinae are virtually the only sawflies in the subarctic zone. The geographic distribution of tenthredinids is limited by the fact that adults are not strong fliers and by the distribution of the larval host plant. In contrast, the distribution of some species has been expanded in the last centuries by accidental introductions, mainly from Europe to North America.

The monophyly of the tenthredinids remains under debate since no unambiguous apomorphies could be found so far.

Morphology

Adults vary in size from 2.5 to 15 mm. Their color pattern consists of black as well as pale orange, yellow or green (that fade to straw coloration in dead specimens). Most tenthredinids can be identified by a combination of the following characters: antennae filiform and composed of nine flagellomeres; thorax with mesoscutellar appendage distinct; pronotum markedly concave along the posterior margin; fore-tibiae with two apical spurs, hind tibiae without subapical spurs; forewing with subcosta absent or as cross-vein; ovipositor saw-shaped (and that gave the name "sawflies" to the group). The subfamilies are separated mainly on the basis of wing morphology (Fig. 11).

Tenthredinid larvae are eruciform, meaning subcylindrical in shape and resembling caterpillars. The body is depressed only in some species. The larva possesses seven or eight pairs of pseudopods, or prolegs, on abdominal segments 2–8 and 10 (in most subfamilies), 2–7 and 10 (Nematinae), or 2–8 (e.g., *Caliroa*), except in the mining taxa where pseudopods are reduced or absent. A tenthredinid larva can be distinguished easily from that of a lepidopteran since the latter never possess more than five pairs of pseudopods, and never a pair on the second abdominal segment. The abdomen of tenthredinid larvae consists of ten segments, each one composed of 3–7 annulets. The head capsule is well developed and antennae are short with 3–5 segments. The nervous, tracheal, muscular, circulatory and reproductive systems are roughly similar and comparable to other insects, whereas the digestive and excretory systems, fat body and integument show interspecific differences of systematic interest.



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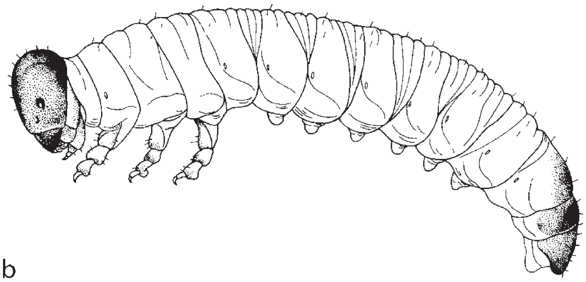

b

Sawflies (Hymenoptera: Tenthredinidae), Figure 11
Adult (a) and larva (b) of the tenthredinid *Hoplocampa flava* (drawings by Marylise Leclercq).

Life History and Habits

The biology of the Tenthredinidae is highly diversified, of course by comparing one species with another. However, all species of a genus or subfamily can show a similar biological trait. Examples of such taxa are given in brackets from now on throughout the text. Another preliminary remark is that general characteristics are given, while exceptions usually are omitted.

The emergence of adults is strongly linked in non-(sub)tropical regions to the phenology of the host plant (of the larvae, see later). In holarctic regions, Dolerinae and many *Amauronematus* emerge early, at the very beginning of the spring, but most tenthredinid species occur as adults in May and June.

After its molt from pupal to adult stage, the tenthredinid will remain during 1–7 days in the cocoon. Newly emerged sawflies will drink rain or dew droplets. Later, they can feed on honeydew, but they feed most typically on pollen and nectar, thus helping somewhat in pollination, whereas several species are carnivorous (*Tenthredo*) and some others do not feed at all. On a still, sunny day, one might commonly find adults, especially on flowers of the Apiaceae, Ranunculaceae, Rosaceae, Saxifragaceae, Compositae, and on catkins of Salicaceae, Betulaceae, etc. Tenthredinid adults generally do not fly very much, and usually only for a short distance.

In captivity, females live 1–2 weeks, males only a few days. The effective occurrence of adults in the field might spread over weeks or months. Male emerge somewhat earlier than females. Individuals of both sexes will find each other by optical and chemical cues. During copulation, lasting generally 1–2 min, the two bodies point in opposite directions, facing away from each other (i.e., stophandry).

Tenthredinids reproduce sexually or asexually. Parthenogenesis is a typical and frequent feature. It is generally either facultative (arrhenotokous, i.e., unfertilized eggs produce males, whereas fertilized eggs produce females), or obligatory (thelytokous, i.e., eggs always produce females, males being unknown). For arrhenotokous species, males can be obviously absent or rare in given populations and geographic areas. In most tenthredinid species, the number of chromosomes is $n = 7–10$, extreme values being $n = 5–22$. A trend seems to be that the chromosomes become more numerous during evolution.

Normally a female possesses from 40 to 250 eggs. Eggs that will be laid are generally already mature in the emerging female. Egg sizes range from 0.4 to 3.9 mm in length, and from 0.2 to 0.9 mm in width. The female cuts with a saw-like ovipositor such plant tissue as a petiole, leaf vein, or fertilized flower. Then, eggs are deposited in the created slit, more often singly than in small clusters. In the particular case of leaf galling species, the female will lay eggs and concurrently a secretion that will start the development of the leaf gall (later on, the larva will continue to stimulate this process). In a few other species, it has been observed that females lay their eggs on plants different from the larval host plant. Once deposited, the egg will mature (into an embryo) by which its volume will increase, swelling, thereby, the surrounding tissue. Egg eclosion will occur 1–3 weeks after eggs are laid, depending on temperature; eggs also are particularly sensitive to a moisture deficiency.

All tenthredinid larvae feed on plant material. Their host plants are horsetails and ferns (Pteridophyta), resinous trees (Coniferae) as well as flowering plants (Angiosperms), namely herbs, shrubs and deciduous trees, but mosses, Compositae, Lamiaceae and Apiaceae are rarely attacked. Compared to other herbivorous insects, tenthredinid larvae have a relatively narrow diet breadth; most species are "specialists" feeding on one given plant genus or even one plant species. Exceptions to this rule are found among the Tenthredininae. The host range observed today in tenthredinid species suggests, to some extent, a radiation of the insects parallel to the evolution of their host-plants.

Larvae generally feed freely on leaves, but some species groups are leaf miners (Heterarthrinae), leaf rollers (*Phyllocolpa*, *Blennocampa*), leaf gallers (*Pontania*), shoot gallers (some *Euura*), fruit borers (*Hoplocampa*), etc. Within the Nematinae, it is likely that from free-feeding larvae evolved the habit to live more and more deeply in the plant (tissue), namely from leaf rollers through leaf gallers to shoot gallers.

There are four to eight larval instars, males showing often one instar fewer than females. Larval growth can be best followed, beside weight, by measuring the head capsule width. This will allow the instar to be determined. The feeding larval stages together require approximately 10–30 days. This period and the feeding rhythm are influenced by species, sex, climatic conditions, etc.

The location of a larva feeding freely on a leaf can be the leaf edge (Nematinae). The leaf edge generally corresponds to the external border of the leaf, but it can be an internal border when a larva makes a hole on the edge of which the larva will continue to feed. Furthermore, the location of a larva can be on one of both sides of a leaf. The larva then either only feeds on the parenchyma (*Caliroa*) or from the edge of the leaf while it remains with its body on the underside of the leaf (*Trichiocampus*). A case of acoustic communication has been reported in the gregarious species *Hemichroa crocea*. By scratching the leaf surface with the abdomen, the larvae of a group remain together and are informed on food quality.

The last larval molt leads to a so-called prepupa. This instar either feeds (most Nematinae), or not (Blennocampinae). The prepupa can be different in color and external morphology compared to the previous instars (Blennocampinae, Tenthredininae). It will drop off and crawl into the soil (litter) in order to build a cocoon. Some species not going into the soil will bore into a fruit or bark of a plant that is, generally, not the food plant, and some species (in the Tenthredininae, Selandriinae) do not spin a cocoon. The prepupa undergoes an apolysis leading (without a molt) to a form that is somewhat retracted. This is generally the resting, overwintering stage. Then, at the end of the winter the prepupa molts into the pupa that is an instar lasting only a few weeks.

Most species have one generation per year (univoltine), but they can have up to three or four. Conversely, within one species, a part of a population can overwinter more than one winter. Most northern species enter diapause that then needs to be broken by a specific temperature and by light.

The influence of abiotic parameters on the life cycle of sawflies can be listed as follows: light (photoperiod) on diapause; light, relative humidity and air pressure on emergence timing and on activity of adults; temperature on development time of eggs and larvae as well as on larval and pupal weight. Moreover, larva and pupa are highly sensitive to dryness, but a very moist soil will enhance risk for the (pre)pupa to be attacked by fungi and micro-organisms.

Natural Enemies and Defense Strategies

Numerous arthropods are known to prey upon tenthredinids, as follows: Acari (on the egg stage); Insecta: Hemiptera, Pentatomidae (larva); Cimicidae (egg); Thysanoptera (egg, larva); Dermaptera (larva); Coleoptera, Elateridae (prepupa and pupa); Mecoptera (adult); Diptera, Asilidae (adult); Hymenoptera, Tenthredinidae (adult), Vespidae (larva), Formicidae (larva). Spiders seem to avoid tenthredinids due to the occurrence of chemical defenses (see later).

Birds such as tits, woodpeckers, cuckoos, partridges, chaffinches and starlings have been observed preying sometimes heavily on tenthredinid larvae. Avian predation seems to be especially important in the regulation of prey populations when these populations are at low densities. Mammals such as shrews and voles are well known to destroy overwintering prepupae and pupae, and are important as well in the regulation of populations. Deleterious compounds originating from a toxic host plant and which the feeding larva previously sequestered can deter shrews from attacking tenthredinid cocoons. Amphibians and reptiles, which can feed on tenthredinid adults and larvae, are probably less important predators than birds and mammals.

Many tenthredinid adults drop off when disturbed. Then they feign death for a few seconds with the antennae and legs pressed to the body as at the pupal stage. On the contrary, other species are rather aggressive, and can use their strong mandibles to bite an aggressor (for instance, your finger) as well as predators. Most tenthredinid adults are cryptic in appearance, but some species do mimic dangerous insects (e.g., *Tenthredo vespa* resembling a wasp).

Deposition within the plant tissue protects tenthredinid eggs. One tenthredinid species is known to defend the eggs after oviposition: the female of *Pachynematus itoi* remains with stretched wings upon her cluster of eggs until their hatch.

Larvae living within plant tissue are protected mechanically against some predators, but when attacked, their escape capabilities are of course reduced. In contrast, some free-feeding larvae can drop off the plant when disturbed. The stimuli eliciting this escape behavior are visual or mechanical (by vibration, touching). On the ground, they will often curl their body so that the abdomen protects the head. A regurgitated droplet can be emitted simultaneously (*Dolerus*).

The visual appearance of the larvae is generally one of the following patterns. Most free-living larvae are greenish (cryptic), resembling the leaf color, whereas others are brightly colored (e.g., black head and black spots and lines on a yellowish background of the body). To these opposite trends are linked a different level of gregariousness, larvae being solitary or gregarious, respectively.

The integument of tenthredinid larvae often presents adaptations acting as a form of protection (that is passive) and/or a defense (that is linked to a given behavior). The larvae of most Nematinae species raise up their abdomen once disturbed. Gregarious larvae can perform such movements of the body simultaneously, which can visually frighten birds at distance. The movement of a single larva can deter an approaching parasitoid. Larvae can also dislodge, using their abdomen, an attacking predator. If Nematinae larvae with an already raised up abdomen are continued to be disturbed, then ventral glands of the abdomen can be evaginated. The glandular secretion will evaporate and will be able to repel arthropods such as ants. In some Nematinae species, the ventral glands are developed enough to allow a chemical protection against birds. Larvae can be covered by developed setae (*Cladius*) or spines (*Periclista*), by a wax secretion (*Eriocampa*) or a slimy liquid (*Caliroa*). The hemolymph of many tenthredinid species is distasteful to ants. Larvae can sequester in their hemolymph toxins originating from plants. The hemolymph can be released by bleeding, spitting, or upon wounding.

A majority of tenthredinid parasitoids belong to the Ichneumonidae (Hymenoptera), which are believed to be often specialized on one host species. Tenthredinids are also frequently parasitized by Chalcidoidea (Hymenoptera) and Tachinidae (Diptera). Most parasitoid species attack the tenthredinid at the larval stage, but some species are either egg, or cocoon (i.e., prepupa) parasitoids. The parasitoid female lays one or several egg(s) per tenthredinid individual. The egg is laid either on the body surface or directly in the body of the larva. When a parasitoid egg is in the body of a larva, hemolymph cells of the latter can encapsulate the parasitoid egg, killing it. This is a form of counter-adaptation of the sawflies that become, consequently, resistant to a parasitoid.

Tenthredinids can be attacked by Nematodes (Mermetidae) as well as by fungal, bacterial, protozoan and viral agents. Pathogenic micro-organisms are unknown from the galling sawflies *Pontania* and *Euura*, so that inhabiting the plant tissue might constitute a protection towards diseases (and more generally to natural enemies such as parasitoids).

Economic Importance

Tenthredinid pests are especially important as forest defoliators. Pests are known on deciduous trees (e.g., *Fenusa* on birch, Nematinae species on willow, poplar, birch), their economic effect being probably stronger on conifers (e.g., *Pristiphora abietina* on spruce, *P. erichsonii* on larch). However, there exist only a few real outbreak species among tenthredinids. On the other hand, tenthredinid species are sometimes regional pests in orchards (*Hoplocampa* spp. on apple, plum and pear; *Nematus ribesii* and *Pristiphora appendiculata* (= *pallipes*) on red-current and gooseberry), in agriculture (e.g., *Athalia rosae* on several Brassicaceae such as turnip) and on ornamental plants (e.g., *Blennocampa phyllocolpa* (= *pusilla*) on rose, *Pristiphora rufipes* (= *aquilegiae*) on columbine).

Tenthredinids can be beneficial. Monophagous species are used sometimes as biological control agents of weeds (e.g., *Monophadnus spinolae* introduced in New Zealand and feeding on *Clematis recta* that is invasive there; *Priophorus brullei* (= *morio*) in Hawaii on *Rubus*). At a local level, tenthredinid richness and/or the occurrence of given "indicator" species can inform us on the biodiversity of a studied biotope.

► Wasps, Ants, Bees and Sawflies
► Sawflies (Hymenoptera: Symphyta)

References

Benson RB (1950) An introduction to the natural history of British sawflies (Hymenoptera Symphyta). Trans Soc Brit Entomol 10:45–142

Goulet H (1992) The insects and arachnids of Canada. Part 20. The genera and subgenera of the sawflies of Canada and Alaska: Hymenoptera: Symphyta. Agriculture Canada Publication 1876, 235 pp

Lacourt J (1999) Répertoire des Tenthredinidae ouest-paléarctiques (Hymenoptera, Symphyta). Mémoires de la Société Entomologique de France no. 3. Paris, France. 432 pp

Lorenz H, Kraus M (1957) Die Larvalsystematik der Blattwespen (Tenthredinoidea und Megalodontoidea). Akademie Verlag, Berlin, Germany, 339 pp

Schedl W (1991) Hymenoptera Unterordnung Symphyta. Handbuch der Zoologie. Band IV Arthropoda: Insecta. Walter de Gruyter, Berlin, Germany, 136 pp

Smith DR (1979) Suborder Symphyta. In: Krombein KV, Hurd PD, Jr, Smith DR, Burks BD (eds) Catalog of Hymenoptera in America North of Mexico, vol 1. Smithsonian Institution Press, Washington, DC, pp 3–137

Taeger A, Blank SM (eds) (1998) Pflanzenwespen Deutschlands (Hymenoptera, Symphyta) Kommentierte Bestandsaufnahme. Verlag Goecke & Evers, Keltern, Germany, 364 pp

Viitasaari M (2002) Sawflies (Hymenoptera, Symphyta). I. A review of the suborder, the Western Palearctic taxa of Xyeloidea and Pamphilioidea. Tremex Press, Helsinki, Finland, 516 pp

Wagner M, Raffa KF (eds) (1993) Sawfly life history adaptations to woody plants. Academic Press, New York, 581 pp

Sawtoothed Grain Beetle, *Oryzaephilus surinamensis* (Linnaeus) (Coleoptera: Silvanidae)

This species is a common stored-products pest, affecting grain products.

► Stored Grain and Flour Insects

Say Stink Bug, *Chlorochroa sayi* Stål (Hemiptera: Pentatomidae)

This is an occasional pest of wheat in western North America.

► Wheat Pests and their Management

Say, Thomas

Thomas Say was born at Philadelphia, Pennsylvania, USA, on July 27, 1787, and is considered by most to be the "father of American entomology," and the first great American systematist. Others argue that F. V. Melsheimer was the father of American entomology, but none dispute that Say was the first American of equal stature with the European entomologists of the era. He was educated as a pharmacist in Philadelphia, where his father was an apothecary and physician. He lacked interest in medicine, however, favoring natural history. In 1812 he became a member of the Academy of Natural Sciences of Philadelphia, and became influenced by this enthusiastic group of naturalists who were in the very early stages of building a fabulous museum collection. The Academy became his home as well after a business failure, and he slept and ate at the Academy. Say began to publish in 1817. He participated in collecting trips to the Georgia and Florida coasts, the Rocky Mountain region, and western Canada, eventually taking up residence at a utopian Quaker commune in New

Harmony, Indiana. At New Harmony, Say became superintendent for literature, science and education for the community. Say is well known to economic entomologists because he described many of the economically important pests found in the United States. He published a three-volume treatise, "American Entomology," during the period of 1817–1828, as well as numerous papers. He was a member of all the important entomological societies. Say is also credited with being the "father of American conchology," publishing six papers on the subject while living at New Harmony. Say died in New Harmony, Indiana, on October 10, 1834.

References

Essig EO (1931) A history of entomology. Macmillan, New York. 1029 pp

Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Scabies

A disease caused by mites of the genus *Sarcoptes*; sarcoptic mange.

► Mites

Scale

A modified, flattened seta on the surface of an insect.

Scale and Hierarchy in Integrated Pest Management

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Integrated pest management (IPM) has been defined as a control system that, in the context of the associated environment and the population dynamics of the pest species, utilizes all suitable techniques and methods in the most compatible manner possible and maintains pest populations at levels below those causing economic injury. Conceptually, IPM operates at the interface of two multidimensional systems: the ecological and the socioeconomic systems, which are hierarchically ordered in ascending levels of complexity and expanding spatial scales.

From a socioeconomic standpoint, IPM schemes are designed to maximize the benefits from control measures, minimize adverse environmental impact and maximize social benefits. Presumably, these objectives are easier to meet on industrialized agricultural holdings than on subsistence farms. African agriculture is characterized by a large majority of small-scale farmers who cultivate small landholdings of less than one hectare to a few hectares and practice intercropping in horticulture-based production systems. Often, farmers do not have titles to the land, and ownership of the harvest is not restricted to the ones cultivating it, which is important when it comes to implementing IPM.

From an ecological standpoint, IPM schemes integrate compatible pest control methods by considering the population dynamics of a pest and its interaction with the commodity. Even the most basic level of population dynamics involves the problem of multiple scales. The problem of multiple scales permeates the study of ecological process and pattern, uniting aspects of space, time and organizational complexity.

Concepts of Scale and Hierarchy

Scale has numerous definitions in the ecological literature. One common definition is that it denotes the resolution within the range of a measured quantity. Scale, therefore, is the unit measure (resolution) relative to the largest multiple (range). This definition applies to space, time and mass. Scale differs from hierarchical levels in that it is recorded as a quantity and involves (or at least implies) measurements and measurement units. Scale-dependent patterns can be defined as a change in some measure of pattern with change in either the resolution or the range of measurement. Scale also refers to power law relations between variables. Specifically, a quantity Q scales with another measured quantity Y (e.g., area, duration, mass) as follows.

$$\frac{Q}{Q_{ref}} = \left(\frac{Y}{Y_{ref}}\right)^{\beta} \qquad [1a]$$

Hence

$$Q = (Q_{ref}\, Y_{ref}^{-\beta})\, Y^{\beta} \qquad [1b]$$

The exponent of these power laws can sometimes be obtained by dimensional analysis. In ecology, power laws are typically obtained empirically, by regressing the logarithm of Q against the logarithm of Y. Examples of power law scaling in ecology include body size allometry (Y = mass), species area curves (Y = area), and Taylor's Power Law (Y = mean density).

Like the word "scale," hierarchy has multiple meanings in ecology. One common definition is that it refers to discrete levels in hierarchically organized systems, where levels are distinguished by rates that differ by one or more orders and magnitude. Rate differences cause structural differences among levels. Hierarchical organization means that higher level processes can steer and constrain lower level processes, while, at the same time, higher level features might emerge from lower level dynamics. Hierarchical organization can be described a two step procedure: top-down across two or three levels of organization at a time by analysis, then bottom up across the same levels by synthesis. Also, natural laws do not apply equally at all scales, but are formulated at particular levels of space, time and complexity. At each level of organization phenomena exist that require new laws and principles which still cannot be predicted from those at more fundamental levels. As one proceeds away from those levels at which a law was cast, the explanatory capability wanes. Hierarchy theory takes into account the problem of aggregation errors by identifying levels of nested systems within larger systems. From this perspective, it is natural to analyze data across multiple scales to seek discontinuities that define changes in the levels. Translating hierarchical concepts into equations that can be used in applied ecology has proven difficult. Hierarchical levels are useful in labeling different levels of human organization as it affects ecosystems including agroecosystems where IPM applies.

Application of Scale and Hierarchy Concepts to IPM

Human institutions and their economic activities introduce levels of field, farm and village and beyond. Clearly, the hierarchy levels are identified on organizational rather than observational ground. Often, the IPM literature refers to the hierarchical organization of decision-making in IPM ranging from farmers to extension agents and policy makers. To simplify the treatment of the topic, this discussion is restricted to a single-species pest population and does not elaborate on its interaction with the commodity or with social institutions and policy. Recognize that there is a connection between temporal and spatial scales. Nevertheless, for the sake of simplicity, they are treated separately.

An adequate understanding of spatio-temporal dynamics is a prerequisite for planning and undertaking control measures within an IPM framework. This understanding is often obtained by the analysis of age-structured populations changing in time and space, via statistical inference or mathematical modeling. Both methods require scale considerations. Statistical inference in IPM relies on spatial design considerations of plot size and layout, which introduce considerations of spatial scale. As shown below, changes in the sample unit size and in the distribution of the samples in the sampling universe also require scaling considerations. Inference from a sample to a larger area introduces questions of scale that bear on population density estimation used for decision-making in threshold-based IPM.

Spatial Scales

In homogenous fields, there is no standing pattern in underlying physio-chemical environment, individual sites may vary from one another at any particular time due to history, but will exhibit similar statistical features over long periods of time. For example, the overall dynamics of an acarine predator-prey system in a greenhouse is composed of local dynamics. Homogeneous sampling universes enable the use of simple random sampling procedures, i.e., a method of selecting units so that every one of the samples has an equal chance of being drawn. In heterogeneous sampling universes it is advantageous to use stratified sampling procedures and work with subpopulations having known sampling probabilities.

The design of a sampling plan requires the definition of the physical size of the sampling unit and recommends cost-benefit procedures. There are significant advantages of a large number of samples with small units over a small number with large units. Also, sample size should be chosen according to the nature of the organisms, and with consideration of the objective of the study.

Homogeneous Sampling Universe

The range of measurement, or sampling universe, is given by the dimension of a field. In weed control, there is no doubt of the importance of field-level management, while this is not always true for other pests. Many invertebrates show few differences between field and farms, and seemed to be changing evenly across the whole area in response to factors operating at higher levels.

The design of efficient agricultural experiments requires minimizing residual variability in order to detect small effects with the least effort. To overcome spatial heterogeneity, the efficiency of many small plots versus a few big plots needs to be assessed. The number of samples required to meet reliability criteria depends on the spatial distribution of the pest population. Frequency distributions, or variance δ^2 to mean μ relationships, are generally used for the design of sampling plans. Selected here as an example is Taylor's power law even though other descriptions as well as frequency distributions could be used with equal justification. According to this law, the variance in density of organisms $\delta^2(\mu)$ scales as a power law of the mean μ.

$$\delta^2\,(\mu) = a\mu^{\mathrm{b}} \qquad [2]$$

The parameter a be definition depends on the units of μ and is thus largely, possibly wholly, a sampling or computing factor. The scaling exponent b ranges typically from 2 to 4 and was interpreted as an index of aggregation. There are publications with the explicit or implicit assumption of a constant species-specific b. In simulation studies, however, b varies with the sample unit size. This result has important implications both for the design of sampling plans and for the interpretation of spatial distributions. Namely, b describes a consistent relationship between sample variance and sample mean over a range of densities, on a spatial scale connected to the sample unit size. This is consistent with observation that different sampling unit sizes detect different spatial patterns.

The dependence of Taylor's Power law on sample unit size can be estimated from data or by deriving it from assumptions regarding population processes and models as well as frequency distributions. A diffusion-limited aggregation model to derive [3] and yields:

$$\delta^2\,(q) = \delta^2\,(1)q^b \qquad [3]$$

That is, the variance for a unit size quadrate q is scaled up by a factor q^b when the quadrate size is increased by the factor q. Similar scaling relations describe fractal symmetry, then from this proposes that the exponent b can be interpreted as a fractal dimension.

Heterogeneous Sampling Universe

Consider the case of an inhomogeneous field and the extension of the range of measurement to neighboring fields. In statistical terminology, the measurement is strata and, therefore, reliance is on stratified sampling procedures for population estimation. Sawyer and Haynes use [1] to represent the spatial distribution of cereal leaf beetle trap catches in each stratum (field) and for the region, with mean density v

$$\delta^2 (v) = a_s v^b \qquad [4]$$

These authors recognize that the intercept contains strata-specific information. However, Sawyer and Haynes stress the need to validate the assumption of constant proportions, e.g., density invariant, distribution of individuals in the different strata. Stratification addresses discontinuities in the sampling universe. To the degree that it is effective, it indicates a shift from the homogeneous to heterogeneous distributions. Stratification can be based on physical conditions (e.g., soil moisture). It also can be based on imposed levels of organization of land use practice at the scale of the field, farm and village.

Spatial Range Extension

A wide spatial range is addressed when pest movements and control operations require that density estimates are done on village levels. Mass trapping is an efficient technique for the control of the savannah tsetse flies *Glossina pallidipes* and *G. morsitans* submorsitans. The minimum range for control operations covers an area of several km^2, and typically includes many farms and villages. The scale is related to the area of attraction of an odor-baited trap that may attract flies within a 50–100 m radius. For monitoring purposes, traps are deployed on a $0.25 \times 1.0\ km^2$ grid. Control operations are carried out with 4–12 traps per km^2, depending on the fly density. In both cases, the sampling universe is assumed to be homogeneous.

In a highly structured sampling universe, subsampling procedures may be appropriate for density estimation. Thereby, a relatively small scale sample is cast over two or more levels or stages. Subsampling refers to the fact that a unit on a given level is not measured completely but is itself sampled.

Temporal Scale

A temporal range covering a crop growing period may often be too short for a complete pest generation to develop. Often, however, the crop may be exposed to either single generation or even multi-generation infestation patterns. In any case, the infestation patterns influence the temporal scale for density estimates.

Models on the dynamics of physiologically structured populations often represent infestation patterns adequately. For example, the outcome of weed-crop plant interactions and thus, yield loss, is determined by temporal coincidence: a scale of 12 h may affect yield.

Temporal Range Extension

The temporal range is extended to cover a series of growing periods at the field, or at higher levels. For example, the immature life stages of the European cockchafer *Melolontha melolontha*, develop in one or more crops during an often 3-year period, and soil samples with surface of $0.5 \times 0.5\ m^2$ and adequate depths are taken at the field level. The adults operate in areas of several km^2, hence, adult flight patterns are studied during the time of adult occurrence, at the level of villages.

In general, the extension of the temporal range and frequent measurements allow the use of spectral analyses, where the measure of association, plotted against the frequency of measurement, depends on the time scale used. Hence, the results obtained by spectral analyses are specific to the time scale used, and for generalization purposes, should be completed by scaling up work.

Mass Scale

In many cases, the amount of food consumed by a pest can be linked to yield losses. In a small range of pest organism masses, it may be considered as proportional to the body mass, while scaling up for higher body mass may require nonlinear functions. Likewise, respiration costs do not increase proportionally to an increase in individual body mass. Often, the relationship

$$r(m) = r(1)m^c \qquad [5]$$

is used. That is, the respiration r for a unit mass organism is scaled up by a factor m^c. This is important when explaining the population dynamics on the basis of the supply-demand theory.

Concluding Remarks

The IPM literature often refers to concepts of hierarchy and scale, but does not rely on a coherent terminology adopted in this paper. Often, the IPM literature refers to spatial levels of fields, farms and villages and beyond as well as to levels in hierarchical decision-making organization, ranging from farmers to policy makers. Presumably, this is because human institutions and economic considerations allow a convenient organizational identification of levels. There are strong indications, however, that these levels may not have the same importance in pest population dynamics, hence their relevance for studies and management should be supported by data. Scale related problems including the implications of scale selection have received little attention in IPM, but we expect an increasing interest in the treatment of scaling and in the design of field experiments. These studies might confirm that, from an ecological standpoint, scaling functions (variants of equation [1]) are easier to define from data than hierarchies.

IPM schemes remain often narrowly designed for field-specific measures and do not appear to fully consider the ecological knowledge obtained in the past decade. When addressing hierarchies, bottom-up approaches receive more attention than top-down approaches. This could be corrected by putting IPM into a landscape context. This approach could complement field- and species-specific IPM programs and become useful when designing IPM schemes at the community and ecosystem level. When dealing with landscape concepts, however, the distinction between the level of organization and the level of observation should be taken into account.

References

Allen TFH, Starr TB (1982) Hierarchy. University of Chicago Press, Chicago, IL

Kogan M, Croft BA, Sutherst RF (1999) Applications of ecology for integrated pest management. In: Huffaker CB, Gutierrez AP (eds) Ecological entomology, 2nd edn. Wiley, New York, NY, pp 681–736

Levin SA (2000) Multiple scales and the maintenance of biodiversity. Ecosystems 3: 498–506

Sawyer AJ, Haynes DL (1978) Allocating limited sampling resources for estimating regional populations of overwintering cereal leaf beetles. Environ Entomol 7:63–66

Schneider DC (1994) Quantitative ecology, spatial and temporal scaling. Academic Press, San Diego, CA

Schneider DC (1998) Applied scaling theory. In: Peterson DL, Parker VT (eds) Ecological scale: theory and applications. Columbia University Press, New York, NY, pp 253–269

Schneider DC (2001) Scale, concept and effects. In: Levin SA (ed) Encyclopaedia of biodiversity. Academic Press, San Diego, CA, pp 245–254

Scaled Fleas

Members of the family Leptopsyllidae (order Siphonaptera).

► Fleas

Scale Insects and Mealybugs (Hemiptera: Coccoidea)

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Scale insects, including mealybugs, comprise a diverse group of insects within the superfamily Coccoidea in the suborder Sternorrhyncha containing more than 7,500 species worldwide. Scale insects initially were called coccids, a name derived from *Coccus* meaning berry. These small, often cryptic plant-feeding insects are considered pests with several species capable of inflicting substantial economic damage. Scale insects are distinguished from other hemipterans by several morphological and behavioral traits. The adult females are always wingless and usually have a powdery covering or waxy test protecting their body. Their mouthparts arise between the front coxae. When legs are present, they have 1 (rarely 2) segmented tarsi with a claw. The first instars always are mobile, while later instars often are sedentary. Most females deposit their eggs either beneath their tests or in ovisacs. The adult males may be winged or wingless. When present, a pair of wings is located on the mesothorax and a pair of hamulohalteres often occurs on the metathorax. The head of the male is distinguished by two or more pairs of various types of eyes and non-functional mouthparts. Because females are present longer throughout the year, the taxonomy of the group is based on their morphology.

The scale insects usually are arranged in 22 families worldwide that include: the Aclerdidae (grass scales), Asterolecaniidae (pit scales), Beesoniidae, Carayonemidae, Cerococcidae (ornate pit scales), Coccidae (soft scales or coccids), Conchaspididae (false armored scales), Cryptococcidae (bark crevice scales), Dactylopiidae (cochineal scales), Diaspididae (armored scales), Eriococcidae (felted scales), Halimococcidae, Kermesidae (gall-like scales), Kerriidae (lac scales), Lecanodiaspididae (false pit scales), Margarodidae (giant scales), Micrococcidae, Ortheziidae (ensign scales), Phenacoleachiidae, Phoenicococcidae (date scales), Pseudococcidae (mealybugs), and Stictococcidae. Six families (Electrococcidae, Grimaldiellidae, Inkaidae, Jersicoccidae, Kukaspididae, and Labiococcidae) are represented by extinct species found in amber. In the U.S., 856 species are known representing 16 families. The families Diaspididae, Pseudococcidae, Coccidae, and Asterolecaniidae, respectively, contain the highest numbers of species. Adult females in the more primitive families often have well-developed legs providing them more mobility than adult females in the more advanced families that often are sessile.

Economic Impact of Scale Insects

Many species are important pests of fruit, nut, forest and ornamental trees, greenhouse and house plants, as well as several agricultural crops. Losses due to plant death and increased production costs are estimated to exceed five billion dollars annually worldwide with losses in North America approaching 500 million dollars annually. The most economically important infestations of scale insects are in cultivated plantings, nurseries, greenhouses, and other urbanized areas where ecological disturbances have occurred. These minute scale insects often go unnoticed on the branches and leaves until a heavy infestation is present, which results in loss of plant vigor, dieback, leaf drop, fruit damage, or eventual death of the host plant. Over an extended period, the tests or scale covers from successive generations encrust the stems and limbs that not only damage the plant, but diminish their aesthetic appeal. Some scale insects can injure the plant surface by injecting their needle-like stylets into the tissue, producing open wounds, which may allow plant pathogens to enter into the plant. For example, damage caused from feeding by the beech scale is believed to be responsible for the outbreak of beech bark disease that now threatens the beech groves in the Great Smoky Mountains National Park. In addition, several species of mealybugs are known vectors of pathogens that may lead to the death of the plant.

In some instances, the saliva injected during feeding may be toxic to the host plant resulting in gall formation, deformed areas, or discoloration around the feeding site. Species of several families (e.g., Eriococcidae, Asterolecaniidae, and Beesoniidae) induce gall formation on their hosts. Where the mouthparts are inserted, normal growth of the host is disrupted and eventually the tissue forms a closed or open gall around the scale. Some scales (mostly in the Australian region) develop inside these galls on leaves, stems, and twigs. Those species that develop within closed galls often exhibit morphological changes that may include an enlarged head and more posteriorly located thoracic spiracles, with the spiracles in Beesoniidae positioned near the anal opening. Species of the gall-forming genus *Apiomorpha* develop an elongated and constricted abdomen. Open galls in the form of slight depressions or pits are induced by species of Asterolecaniidae and Lecanodiaspididae. While golden oak scales produce distinctive open galls on oaks, galls formed by sweetgum scales appear as reddish to whitish specks on the ventral surface of the leaf of sweetgum. Damage around the feeding sites often is manifested in the formation of chlorotic spots. The feeding activity by San Jose scales may produce discolorations in the form of red rings on apples, while Florida red scales produce light circular areas on citrus. The birch margarodid is found embedded within the bark of birch with only a hollow, waxy tube-like filament linking it to the external environment.

Secondary injury to the plant host by most soft scales and mealybugs results from exuding a liquid excretion (often referred to as honeydew), which is a by-product of the large volume of sap they ingest. The excreted honeydew that falls onto the lower leaves and branches serves as a substrate for the development of sooty mold, which inhibits growth, lowers fruit yields and sugar content, and reduces the aesthetic value of the host plant. Honeydew also attracts ants that collect and feed on the sugary residue. In return, the ants often protect the scales from natural enemies.

Several species have been beneficial to cultures over the past centuries. Species of *Kermes* and cochineal scales were used as a dye source from antiquity to the present. Carminic acid is a natural red dye from the cochineal scale (*Dactylopius* spp.), a family of scale insects that feed on cacti. This dye has been used commercially worldwide since the sixteenth century and was the dominant dye source used in cosmetics, food, medicine, and textile products until its replacement by aniline dyes. The white waxy tests of the Chinese wax scale were used to make wax candles and figurines in China. Also, candles made from the tests of this species were used in religious ceremonies as a symbol of purity. Ground-dwelling margarodids, known as ground pearls, are collected and strung into bracelets and necklaces in several South American countries. For centuries, the secretions from lac scales have been processed into shellac and used to protect a variety of items including furniture, machinery, etc. Also, adult females of the giant scale, *Llaveia axin*, are processed for their "fat" content that is used as a lacquer coating on wood products, especially art and sculpture creations, in Mexico and Central America. The ornate pit scale, *Cerococcus quercus*, was used as a glue source and as a chewing gum by native American Indians of the southwestern U.S. In addition, a few species are effective in suppressing invasive weeds, such as some species of cochineal scales on cacti.

General Morphology

Dramatic sexual dimorphism is particularly exhibited within the scale insects. The adult male's appearance is so different from the adult female that pairing them as a species can be difficult. Because of the diverse differences between the males and females, taxonomists use a different morphological nomenclature to describe the two sexes.

Female development in the more primitive species consists of the egg, first instar (crawler), second instar, third instar, in some species, and adult stage. Although exceptions occur (e.g., Pseudococcidae), females of the more advanced species differ by having the egg, first instar (crawler), second instar, and adult. Adult females are pyriform, subcircular or elliptical, wingless, and usually without any constriction between the head and thoracic regions. Ocelli often are present in species of the more primitive families (e.g., Margarodidae, Ortheziidae, and Phenacoleachiidae). However, the ocelli may be reduced to a slight protuberance, pigmented spots, or completely absent in adult females in the remaining families.

Antennal segments range from zero in Beesoniidae, 1-segmented in several families (e.g., Aclerdidae, Asterolecaniidae, Cerococcidae, Diaspididae, and Phoenicococcidae), to as many as 13 segments in some species of Margarodidae (except Margarodinae) and Phenacoleachiidae. Mouthparts consist of a clypeolabral shield and a labium with species within scale insect families exhibiting a 1- to 4-segmented labium. Two pairs of thoracic spiracles are present in all families; however, species of Margarodidae and Ortheziidae also have submarginal abdominal spiracles. Legs are absent in adult females of several families (e.g., Aclerdidae, Asterolecaniidae, Beesoniidae, Phoenicococcidae, and Diaspididae), but range from 1-segmented stubs (e.g., most Cerococcidae, species of Cryptococcidae with metathoracic plate) to 5-segmented with a tarsal claw in other families. Leg development may be variable among species within some families ranging from absent to 5-segmented legs (e.g., Lecanodiaspididae and Pseudococcidae). When present, the leg types vary from digging in Margarodidae to walking or running in most other families.

Body segmentation is pronounced in the more primitive families (e.g., Margarodidae and Ortheziidae) and in some species of a few advanced families (e.g., Pseudococcidae and Eriococcidae). Segmentation of the cephalothorax is indistinct in most species, but the presence of marginal setae often is used to distinguish segments. Ventrally, the thoracic segments are demarcated by the attachment of the legs, when present, and the location of the spiracles on the mesothorax and metathorax. Segmentation is more visible on the ventral surface of the abdomen than on the dorsum. Segments often are delineated by transverse creases and marginal setae. However, the number of discernible segments often varies among species with two to three segments visible in Phoenicococcidae to eight or nine in Cerococcidae. In diaspidids, the last four segments of the abdomen are fused into one pygidial structure with plates and small lobes on the margin. Apparent segmentation also is reduced in Aclerdidae, Asterolecaniidae, Conchaspididae, Crytococcidae, Kermesidae, and Kerriidae. The vulva is located on the eighth segment, and an anal ring often denotes the terminal segment. The anal ring is covered and protected by a pair of anal plates in Coccidae, while a single plate occurs in Aclerdidae and Cerococcidae. A pair of anal plates with an associated arched anal plate surrounds the anal ring in Lecanodiaspidae and some species of Asterolecaniidae.

Male development consists of the egg, first and second instars, prepupa, pupa, and adult stages. Males are nearly always linear in appearance, possessing prominent cephalic, thoracic, and abdominal regions. Adult males have 9- to 10-segmented antennae, a non-functional mouth, a pair of compound eyes is present in Margarodidae and Ortheziidae, and dorsal and ventral ocelli occur in most species in other families. The thorax of most species contains a pair of mesothoracic wings, metathoracic hamulohalterae (except Aclerdidae), and 5-segmented legs. In some species, wings may be present in one generation and reduced or absent in others. On the abdomen, the aedeagus is distinguished by a distinctive penile sheath with 0–3 pairs of caudal filaments. Adult males do not feed and live only 1–3 days. Adult males resemble aphids and small flies.

First instar nymphs (crawlers) are mobile with well-developed 5-segmented legs, 5- to 6-segmented antennae, and a variety of wax pores and ducts. Each anal lobe terminates with a long anal lobe seta. Sexual dimorphism is visible in the first instar nymphs of several species (e.g., Kuno scale and flat grass scales) representing various families. These differences are evident by the number and arrangement of setae and wax-secreting pores and ducts. Sexual differences in the second instars are generally more pronounced than in crawlers with males being more elliptical than the more ovoid females. The presence or absence of legs among scale insect species is variable. In some species, legs may be present in the males, but absent in the sedentary females. Males often are distinguished by the presence of various ducts and glands, which are usually absent or reduced in the females or appear later in the adult stage.

Protective Test or Scale Cover

One of the more prominent features of the scale insects, including mealybugs, is the development of a protective covering over their bodies. The covering may vary from a powdery secretion to a complete soft or hard waxy coating over the body. The wax is produced by an assortment of pores and ducts on the derm, and the covering is often referred to as a test or scale cover. In some families (e.g., Pseudococcidae), a variety of protective coverings occur ranging from a coating of white waxy powder to long wax strands. In species of Ortheziidae, the body is covered by a series of waxy plates. The Kerriidae aggregate and secrete a flexible lac compound for protection. Members of the genus *Cerococcus* also tend to aggregate close together resulting in wax production completely covering their bodies and sections of adjacent scales. The species within the families Asterolecaniidae and Lecanodiaspididae secrete a papery to waxy test with the individual located in a pit or depression on its host. Many species of Eriococcidae secrete a felt-like sac completely enclosing the female. The Coccidae have a variety of test forms ranging from felt-like in *Eriopeltis*, papery in *Lecanium*, waxy in *Ceroplastes*, to cottony in *Pulvinaria*. Females of Beesoniidae develop within galls and no longer produce tests to cover their bodies. In several species of Margarodidae, the waxy excretions that flow over and cover the body aid in the development of a cyst-like covering.

The protective test or waxy covering over the body allows most species to maintain a favorable humidity level, while preventing rapid temperature changes. The test also functions as a protective barrier against predators and parasitoids. The tests of several species provide protection by blending in with the color and texture of the bark on the plant host and are most often in shades of gray or brown. However, some species display ornate shapes and colors. A stellate appearance is common with waxy extensions projecting from the margins or from the complete test. A number of species in various families are covered by individual wax strands presenting the appearance of a cotton ball. The colors of the waxy scale covers range from hues of brown to a brilliant white to rosy pink to vibrant yellows. The tests of several species display a disruptive pattern. For example, some soft scale species are vivid red to crimson with white zebra-like markings (e.g., calico scale), and others have dark backgrounds with series of irregular white spots to break up the outline of the body, perhaps making them less conspicuous to parasitoids and predators. Some mealybugs aggregate in small groups and appear berry-like, while species of Kermesidae resemble galls or plant buds.

Life Cycle and Behavior

The life cycle is quite varied among the Coccoidea depending upon the family and species. Development also differs between the female and the male. Most species have one or two generations per year, but some have multiple generations. A number of polyphagous species have two or more overlapping generations outdoors, but reproduce continuously in greenhouses. Generally, all stages of development are present throughout the year in species with multiple generations. Developmental time for the various stages is usually influenced by temperature and humidity. However, the development time for a number of species may take several years. For example, the spruce mealybug has a 4-year life cycle that involves multiple migrations annually from the foliage to bark crevices or the duff at the base of the tree. The Chilean margarodid *Margarodes vitium* may remain in a cyst-like state for 7 or 8 years and only after heavy rains emerges as adult females. This adaptation may provide this species the ability to survive periods of extended droughts.

Although most scale species reproduce bisexually, some Coccoidea exhibit parthenogenetic and hermaphroditic reproduction. Adult females that possess protective tests covering their bodies usually have a sedentary nature and a limited active courtship. Some species (e.g., San Jose scale) are known to produce sex pheromones to attract males. The mobile males must locate and mate with females on the host plant. Upon finding a receptive female, the male of Diaspididae inserts the stylus under the pygidial region with the hind legs assisting in the insertion. Although adult males are ephemeral, living only about 1–3 days upon emergence, they can fertilize several females during this period. Virgin females of the San Jose scale are known to exert their pygidia from beneath their tests and slowly move it back and forth in a short arc. During this activity, females probably release sex pheromones to attract males.

Some females (e.g., Pseudococcidae and Dactylopiidae) actively seek out males for mating. In a species of *Pseudococcus*, the two sexes live apart during the winter with the female inhabiting the smaller branches and the males, still in the pupal stage, on the trunk of the host tree. The adult females become active during early spring and travel down the branches to the trunk where they continue their search for males. Adult females usually precede the emergence of males by several days. After mating, females return to the branches, construct their ovisacs, and lay their eggs. In the fall, the nymphs separate and the males descend to the tree trunks to pupate. A similar behavior is found in northern red oak kermes. Males travel down to the lower levels of the tree trunk, and occasionally leave the tree to pupate, while females remain on branches in the canopy. Upon adult emergence, males fly into the tree canopy to locate and mate with females.

Females protect the eggs during embryonic development, and also the newly hatched crawlers, by laying them under the scale cover or in an ovisac. During the course of egg deposition, the bodies of females in several families (e.g., Asterolecaniidae and Diaspididae) shrivel up to eventually occupy only the anterior one-third of the waxy test. In several species of Coccidae and Kermesidae, the female's exoskeleton hardens providing protection for the eggs against adverse environmental changes and many natural enemies. Most species lay eggs, producing from less than a few dozen to over five thousand eggs. A variety of species in several families (e.g., Margarodidae, Ortheziidae, and Coccidae) deposit their eggs in an ovisac. The type of ovisac and the number of eggs produced vary with the species. The ovisac may completely cover the insect's body, be reduced to cover only part of the abdomen, or be positioned ventrally. Females of Ortheziidae produce a long, cylindrical ovisac for egg deposition. Several species of Eriococcidae and some Coccidae make a fine structured felted sac to retain the eggs until hatching. One of the strangest means of protecting the eggs in some species (e.g., Margarodidae) is the development of a deep invagination of the integument forming a cavity. Females that produce eggs that hatch within their bodies, such as the pineapple mealybug, hairy mealybug, and tuliptree scale, shield the crawlers for a short period by covering them with their abdomens and tests. Most species overwinter in the egg stage (e.g., oystershell scale), while others overwinter as second instars (e.g., European fruit lecanium), or in the adult stage (e.g., golden oak scale).

Parthenogenesis has been documented in several species (e.g., golden oak scale and brown soft scale). It has been speculated that parthenogenesis favors a higher reproductive potential for sedentary species in harsh environments. Some species exhibit life cycles that include a combination of bisexual and parthenogenetic reproduction (e.g., oleander scale and oystershell scale). One of the rarest forms of reproduction is hermaphroditism that occurs in a few species, such as the cottony cushion scale.

A mutualistic relationship exists among species of several scale insects and ants. In exchange for honeydew, a soft scale or mealybug population may be attended and protected by ants, or physically taken within the ant's tent or nest where they are not only protected from parasitoids and predators, but also against adverse environmental changes and fungal infestations. For example, tuliptree scales often are found in association with ants that construct a paper-like tent over a group of adult females protecting them from parasitoids and predators. When leaving the nest on the nuptial flights, females of the ant *Acropyga paramaribensis* always carry a fertilized rhizoecus coffee mealybug female in their mandibles. These mealybugs are maintained within a special chamber in the nest where they are cared for, and in return, provide honeydew to the ants when stroked. Another remarkable way of dispersal occurs in species of *Hippeococcus* that have long raptorial legs and digitules for clinging to attending *Dolichoderus* ants. When disturbed, they cling to the ants and are carried into their nests. The presence and active associations of ants with scale insects and mealybugs result in an increase in their numbers, and a subsequent reduction in the scale insect populations following the removal of the ants. Because ants are so protective, some predators have adapted by mimicking the appearance of their prey to move freely about and feed on mealybugs, such as the larvae of the lady beetle, *Cryptolaemus montrouzieri*.

Host Selection and Distribution

The age of the Coccoidea is placed in the Cretaceous Period which basically coincides with the time angiosperms became the dominant plant form. This adaptation to the angiosperms was so successful that the majority of present day species cannot leave the host plant and survive. Only a few species are found on gymnosperms. Species may be monophagous (e.g., sweetgum scale), oligophagous feeding on plants in one genus (e.g., kermes oak scales on *Quercus*) or one plant family (e.g., flat grass scales primarily on Gramineae grasses), or polyphagous (e.g., juniper scale on Cupressaceae and Taxodiaceae). Members of some families (e.g., Pseudococcidae) feed on both deciduous and conifer hosts with some being polyphagous, while others are oligophagous or monophagous. Most species feed on a variety of plant species within a given generic or family level. Although most coccid species are polyphagous, members of several families have specific plant associations. These include members of Dactylopiidae on cacti, Halimococcidae on palms, most Kermesidae that feed on oaks, and Phoenicococcidae on palms. Also, most species of Aclerdidae, some Coccidae and Pseudococcidae feed on grasses, while the eriococcid genus *Apiomorpha* feeds exclusively on *Eucalyptus*. A number of species prefer particular habitats. Several members of Ortheziidae are found in wet meadows, mosses, and in the soil of slopes and forest areas, while the boreal ensign scale commonly is found in leaf litter.

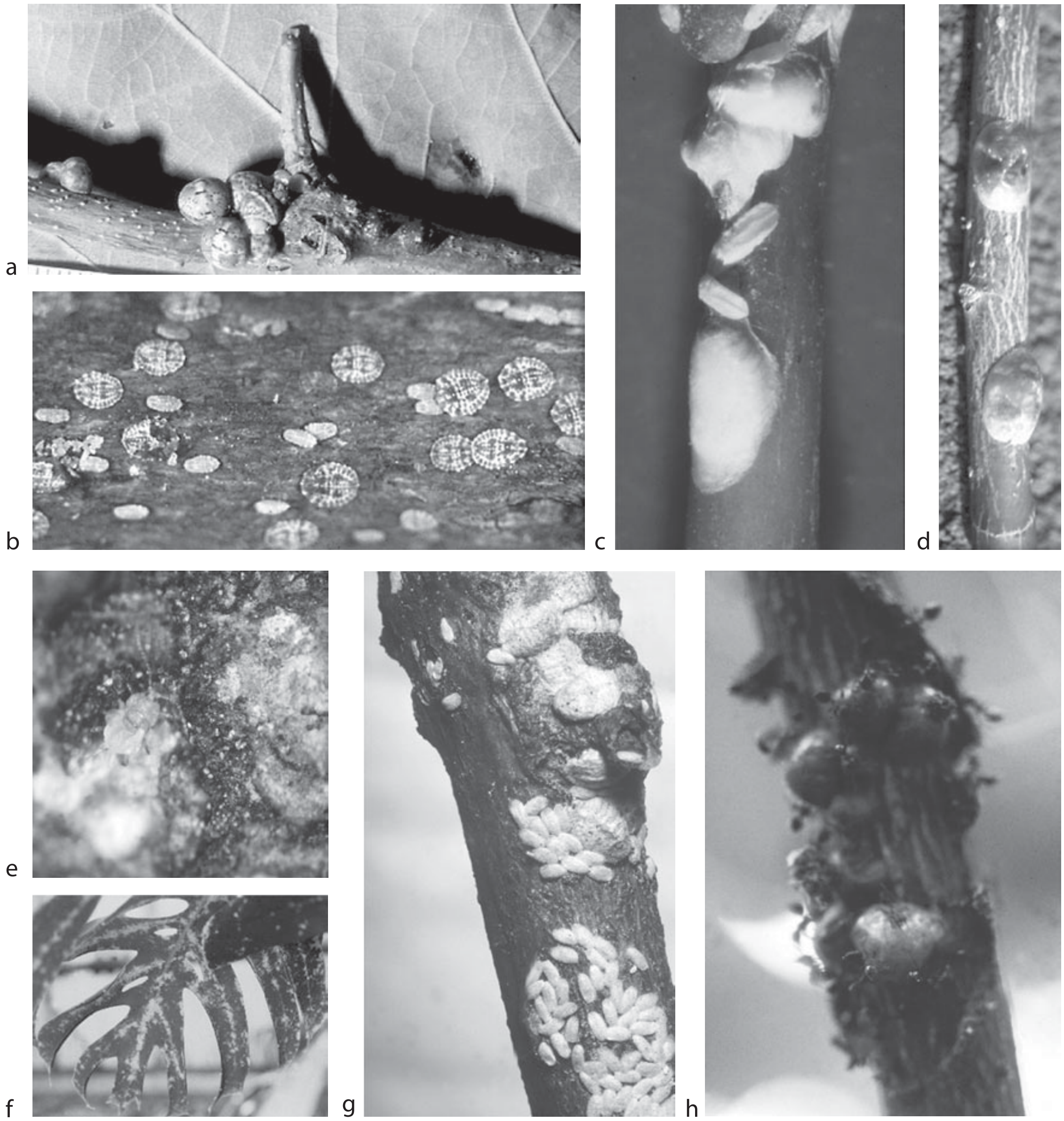
Species of several families actively seek out the host in many instances. For example, species of Margarodidae, Ortheziidae, and Pseudococcidae are mobile throughout their various life stages, and are able to walk from area to area on a given host or even to different hosts. Several species overwinter in the detritus or in cracks on the trunk of a tree and migrate the following spring to the stems and fruits to feed. For those sedentary adult females, the problem of finding food is resolved by the female ovipositing on the host plant.

The mobile crawler is the usual stage that finds a suitable host and feeding site. Dispersal takes place primarily through the movement of the crawlers from tree to tree, by wind, or on the bodies of other insects, spiders, mites, birds, and mammals. Within a day or two after hatching, crawlers migrate, either by walking or with the aid of wind, to new feeding sites on the host plant or adjacent plants. Upon locating a suitable site, crawlers settle, insert their stylets, begin to feed, and continue to mature. Once they establish their position on the host, an adequate food supply is available throughout their development. Species that infest annual plants are unique because their hosts are present for only a short period of the year. Several species have adapted some unusual development patterns. For example, the male crawlers often settle on the leaves, while females tend to settle more often on the twigs (e.g., black willow scale). A common habit exhibited by species in a number of families is for a cluster of male crawlers to settle and develop around a female or group of females increasing the potential of finding a mate upon maturity (e.g., walnut scale). In those species where the crawler settles and develops on the leaves, the leaf veins often are the preferred sites. There is usually a progressive migration back to the stems or twigs by members of the overwintering generation in species with multiple generations. The distance covered on the host plant may vary from species to species depending upon the number of generations per year. While some species settle on specific areas of the host, others (e.g., euonymus scale) do not appear to differentiate between the leaves or stems as preferred sites. Many species commonly infest the underside of limbs and stems of host plants that may protect them from adverse weather conditions, exposure to direct sunlight, and predators. Successive generations force specimens to disperse to other areas to obtain feeding sites that eventually result in a heavy encrustation of the branches.

Several species are known to select multiple locations on the host. The position depends upon the time of year, available space, and their stage of development. The solenopsis mealybugs feed in the crown of their host in the summer, but migrate onto the roots before winter. Members of Eriococcidae may be found on the upper or lower leaf surfaces of one or several hosts, in the axils of leaves and smaller stems, on the surface of smaller stems, on the bark of larger branches, or on the main tree trunk. Sugarcane mealybug crawlers actively walk to the tops of stalks where the developing new tissue allows for easy insertion of their stylets. The females aggregate around the nodes of the stalk. In early spring, they may go to the leaf axil, but development time is slow until they later migrate to the stalks. Orientation of first instars on the underside of leaves and on stems does not appear to be at random; for instance, cottony cushion scales position themselves with their heads upward on the stems. Aside from the numerous species that feed above ground, an enormous fauna of subterranean species exists that feed on the roots of plants. These under-explored niches hold the potential for the discovery of new species, even in North America.

Morphological changes in body shape and size often are influenced by population density and site location. In crowded conditions, the tests usually develop abnormally around other females or around projections of their host (oystershell scale). The position and location on the host often have an effect on the shape of the individual. Species that settle on or between the leaf sheaths and stems of grasses exhibit a dorso-ventrally flattened appearance (e.g., *Aclerda*, *Antonina*, and *Chaetococcus*). The immature azalea bark scale, *Acanthococcus azaleae*, often settles between the petiole and branch at the axillary bud, and frequently acquires a wedge-shaped appearance (Fig. 12). Kermesids that reside on the limbs of their host are gall-like or spherical. Host-induced variation results in shape, size, and color variations among populations (e.g., European fruit scale).

Population density is affected by several biotic and abiotic factors. Seasonal abundance is highest in the summer and fall, and declines during the winter months. Mortality is attributed to adverse weather conditions, such as heavy rains washing crawlers off the host, high relative humidity, fungal development on the test and insect, or hot and dry conditions. In some instances, drier environments produce more females, while more moist environments produce more males (e.g., citrus mealybug). Distributional patterns of species in several families imply macroenvironmental preferences as to the elevation, regions inhabited, and climatic conditions. The number of species and family taxa tend to be fewer as the elevation increases. Microenvironmental preferences are demonstrated by the host plants selected and the area and position taken by the species on the host. It is postulated those increases in the population size of endemic species



Scale Insects and Mealybugs (Hemiptera: Coccoidea), Figure 12 Some scale insects: (a) *Allokermes kingi* (Cockerell) on *Quercus rubra* L. (Kermesidae); (b) *Lecanodiaspis prosopidis* (Maskell) on *Aescules* sp. (Lecanodiaspididae); (c) *Chionaspis salicisnigrae* (Walsh) on *Salix nigra* Marsh. (Diaspididae); (d) *Neolecanium cornuparvum* (Thro) on *Magnolia acuminata* L. (Coccidae); (e) *Quadraspidiotus juglansregiae* (Comstock) on *Cornus floridensis* L.: male and female (Diaspididae); (f) *Pseudococcus longispinus* (Targioni Tozzetti) on *Dieffenbachia* sp. (Pseudococcidae); (g) *Acanthococcus quercus* (Comstock) male and female clusters on *Quercus borcalis maxima* Ashe. (Eriococcidae); (h) *Toumeyella liriodendri* (Gmelin) attended by ants on *Liriodendron tulipfera* L. (Coccidae).

in disturbed habitats are in part due to air pollution and lower levels of natural enemies.

For many species, favorable environmental conditions often result in several generations of scales within one season. The movement of the crawlers is directly affected by temperature with increased activity as the temperature rises. The length of time the crawlers remain under the female ranges from a few hours to 2–3 days depending on the temperature. Newly emerged crawlers remain under the test on cool, cloudy days, but leave immediately during warmer days. The ephemeral adult males are feeble fliers and more often rely on walking over the host plant for a successful encounter with a female. Their range is generally believed to be restricted to that of the population; however, some males in flight are carried to other parts of the host plant or to other plants. In those sessile stages where individuals retain their legs, a short mobile period may occur between molts. The degree of mobility is dependent on the flexibility of the test that extremely limits the distance they can travel.

Control

The transport of exotic species from one country to another is enhanced by the international trade in plants and fruits. As a result, several exotic species have entered the United States on imported plants. Many of these species are destructive and pose substantial threats to native trees and shrubs, as well as plants grown in commercial greenhouses. Monitoring plants for ant activity, sooty mold growth, or abnormalities in color and structure of stems and leaves can help locate scale insect infestations in landscape and plant production systems. Several chemicals are available for use against pest populations with the most effective results obtained when applied against the emerging and unprotected first instars (i.e., crawlers). Infestations of house plants and shrubs around the house may be controlled by handpicking or spraying with soapy water, insecticidal soaps, or oils. Several natural enemies including parasitic wasps primarily in the families Encyrtidae and Eulophidae, and predators in the families Coccinellidae, Anthribidae, and Nitidulidae, also are effective at maintaining pest populations at low levels. To obtain the most effective control of pest species, identification of the species or family groups is essential. A key to identify the families in the U.S. is provided.

Key to Families of Coccoidea in the U.S. (Modified from Kosztarab, 1996)

1 Abdominal spiracles present 2

– Abdominal spiracles absent 3

2(1) Anal ring distinct, with band of pores and 6 setae; eyes usually stalked; antennae 3- to 8-segmented ....Ortheziidae

– Anal ring reduced, with no pores or setae; eyes rarely stalked; antennae 1- to –13-segmented ....Margarodidae

3(1) Anal opening covered by 2 two triangular anal plates (except *Physokermes* with one plate); abdomen with a well-developed anal cleft … ……………………........................... Coccidae

– If anal plate present, only one cover over anal opening (although sclerotized plates lat eral of anal opening may be present); anal cleft, if present, not as well developed, as in Coccidae.. 4

4(3) Caudal margin with furrows; usually under leaf sheaths of grasses and reeds… Aclerdidae

– Caudal margin without furrows and ridges; habitat and host variable 5

5(4) Cluster pore plate present below each posterior thoracic spiracle; anal ring surrounded by short and stout setae.......................Cryptococcidae

– Cluster pore plate absent; anal ring not surrounded by setae 6

6(5) Dorsal spine on abdomen; with dorsal brachial plate and tube; anterior spiracle larger than posterior .... Kerriidae

– Dorsal spine on abdomen absent; without dorsal brachial plate and tube; spiracles similar in size 7

7(6) 8-shaped pores present on dorsum 8

– 8-shaped pores absent from dorsum.........11

8(7) 8-shaped pores on dorsum and in a submarginal band on venter; ventral tubular ducts scattered over entire body; antennae 1- to 9-segmented; on various hosts..................... 9

– 8-saped pores restricted to dorsum; ventral tubular ducts form a submarginal band around body margin; antennae 5-segmented; on Fagaceae only .... Kermesidae

9(8) Tubular ducts with inner filaments; antennae 1- to 9-segmented; with cribiform plates.... 10

– Tubular ducts without inner filaments; antennae 1-segmented; without cribiform plates ....Asterolecaniidae

10(9) Antennae 1-segmented, with an associated cluster of 5- to 7-locular pores; with sclerotized triangular plate lying over anal opening; tubular ducts without constriction on outer ductile .... Cerococcidae

– Antennae 7- to 9-segmented, without associated 5- to 7-locular pore cluster; with arched and anal plates around anal opening; tubular ducts with constriction on outer ductile .... Lecanodiaspididae

11(7) Usually with dorsal ostioles, cerarii, ventral circuli, and trilocular pores; anal ring with inner and outer rows of pores.. .... Pseudococcidae

– Without dorsal ostioles, cerarii, ventral circuli, and trilocular pores; anal ring variable; tubular ducts invaginated 12

12(11) Terminal abdominal segments fused into a pygidium; anal opening simple; body covered with thin, hard shieldlike test, with exuviae of previous instars 13

– Terminal abdominal segments not fused to form a pygidium; anal opening often setiferous; test not as above or body covered by waxy powder or strands 4

13(12) Antennae 1-segmented; labium 1-segmented; legs absent; without dermal slits on venter ....Diaspididae

– Antennae 3- or 4-segmented; labium 2-segmented; legs present; with dermal slits on venter .... Conchaspididae

14(12) 8-shaped tubular ducts on dorsum and ventrum; anal ring reduced, without pores but with 2 minute setae; antennae 1-segmented; legs absent .... Phoenicococcidae

– 8-shaped tubular ducts absent; anal ring normally with pores and setae; antennae well developed; legs present 15

15(14) Without dorsal clusters of 3- to 5-locular pores; cruciform pores usually present; on hosts other than Cactaceae .... Eriococcidae

– With dorsal clusters of 3- to 5-locular pores; cruciform pores absent; only found on Cactaceae .... Dactylopiidae

References

Ben-Dov Y, Miller D (2001) ScaleNet. Avilable at http://www.sel.barc.usda.gov/scalenet/scalenet.htm

Borror DJ, Triplehorn CA, Johnson NF (1989) An introduction to the study of insects, 6th edn. Saunders College Publishers, New York, NY, 875 pp

Kosztarab M (1996) Scale insects of northeastern North America: identification, biology, and distribution (Special Publication No 3). Virginia Museum of Natural History, Martinsville, VA, 650 pp

McKenzie HL (1967) Mealybugs of California, with taxonomy, biology and control of North American species (Homoptera: Coccoidea: Pseudococcoidae). University of California Press, Berkeley, CA, 526 pp

Poole RW, Gentili P (eds) (1996) Nomina Insecta Nearctica: a check-list of the insects of North America, vol 4: Non-holometabolous orders. Entomological Information Service, Rockville, MD, 731 pp

Scaly Crickets

A subfamily of crickets (Mogopistinae) in the order Orthoptera: Gryllidae.

► Grasshoppers, Katydids and Crickets

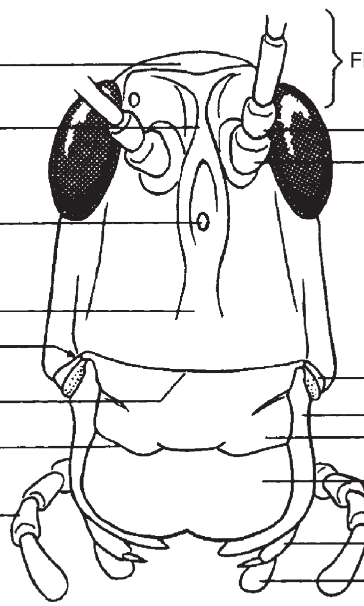
Scape

The basal segment of the antenna (Fig. 13).

► Antennae of Hexapods

Scarabaeiform Larva

A larval body form resembling a scarab beetle larva (white grub). Characteristics include hairy,



Scape, Figure 13 **Front view of the head of an adult grasshopper, showing some major elements.**

thick bodied, well-developed thoracic legs, the absence of prolegs, and C-shaped in overall body form. This also is known as scarabaeoid. It is found in the beetle families of the superfamily Scarabaeoidea.

Scarabaeidae

A family of beetles (order Coleoptera). They commonly are known as scarab beetles.

► Beetles

Scarab Beetles (Coleoptera: Scarabaeoidea)

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The superfamily Scarabaeoidea is one of the largest and most diverse superfamilies of Coleoptera, including over 35,000 described species and 2,500 genera worldwide. Based on studies of insect diversity, it is estimated that the Scarabaeoidea may include up to 50,000 species. Some of the most beautiful and largest insects on Earth belong to this superfamily of beetles. Of all the beetles, scarabaeoids are among the best known because of their beauty, fascinating life histories, and economic importance. In the Nearctic region, the taxonomy of most scarabaeoids is now fairly well known although there remain a few areas of uncertainty.

Scarab beetles are adapted to most habitats, and they can be fungivores, herbivores, necrophages, coprophages, saprophages, and sometimes carnivores. They are widely distributed around the globe, even living in the Arctic in animal burrows. Some scarabs exhibit parental care and sociality. Some species live in close association with ants (myrmecophiles) or termites (termitophiles). Many possess extravagant horns, others are able to roll into a compact ball, and still others are highly armored for inquiline life. A very few are occasionally agricultural pests that may destroy crops and turf, while others are used in the biological control of dung and dung flies.

Morphology and Development

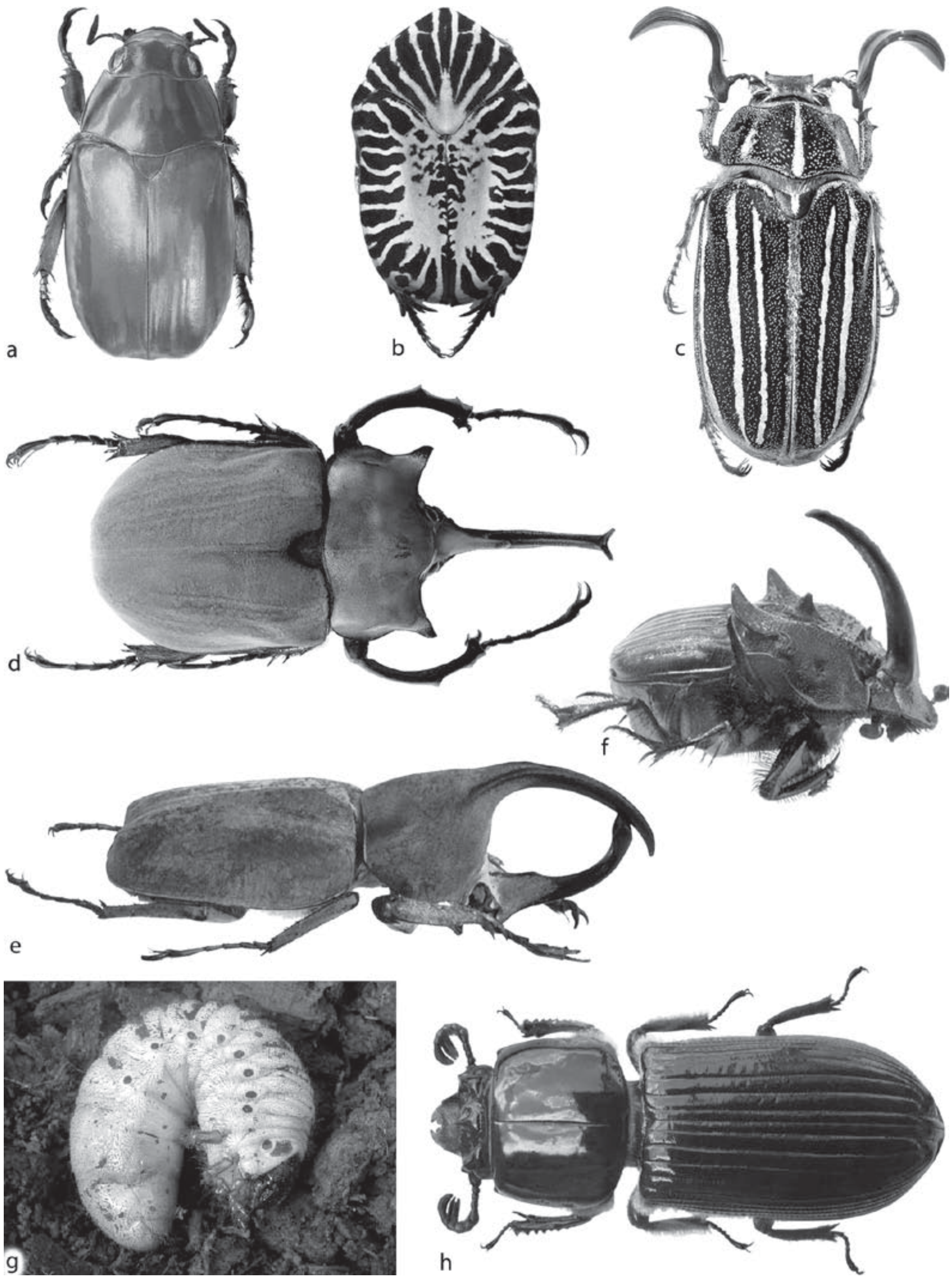
Adult scarabs range from 2 to 160 mm in length. The robust body form may be ovate, obovate, quadrate or cylindrical (Figs. 14 and 15). Color varies from dull brown to black to brightly metallic green, blue, gold, or silver (e.g., *Chrysina strasseni*); many species have bright color patterns of yellow, red, or orange (e.g., *Gymnetosoma stellata*). Coloration is due to pigments present in the cuticle and/or the cuticle's microstructure that absorbs and reflects different light waves. The integument may be wholly glabrous or covered with dense hairs or scales. Antennae are 7- to 12-segmented with a 3- to 8-segmented, asymmetrical, usually lamellate club (e.g., *Polyphylla petiti*). The head is not covered by the prothorax which is often highly modified for burrowing (with large coxae that are strongly transverse or conical and projecting below the prosternum). The head and/or pronotum may have horns (e.g., *Megasoma elephas*, *Spodistes mniszechi*, *Phanaeus eximius*), usually present only in males. The protibia has 2–3 teeth or is serrate on the outer margin. The tarsal formula is 5–5–5; rarely, the anterior tarsi are absent. The hind wings have reduced venation, but are well developed with a strong intrinsic spring mechanism for folding. Tergite 8 forms a true pygidium not concealed by tergite 7.

Larvae are C-shaped, with a distinct head capsule (e.g., *Dynastes maya*). Antennae are 4-segmented and ocelli are present or absent. Six thoracic legs are present and are 2 or 4-segmented, but in the Passalidae the hind legs are reduced to a stub with apical teeth that rub against the mesothoracic coxae for stridulating. Abdominal segments 1–6 or 7 usually have three annuli, each with one or more transverse rows of setae. Body color varies from pale yellow to white, thus giving them the name white grubs. Larvae usually pass through three instars and completion of development may take 1–3 years. A short period of pupation follows during which the larva transforms to the adult insect. Emergence from the pupa occurs after a specified time or in reaction to environmental cues such as rainfall or temperature.

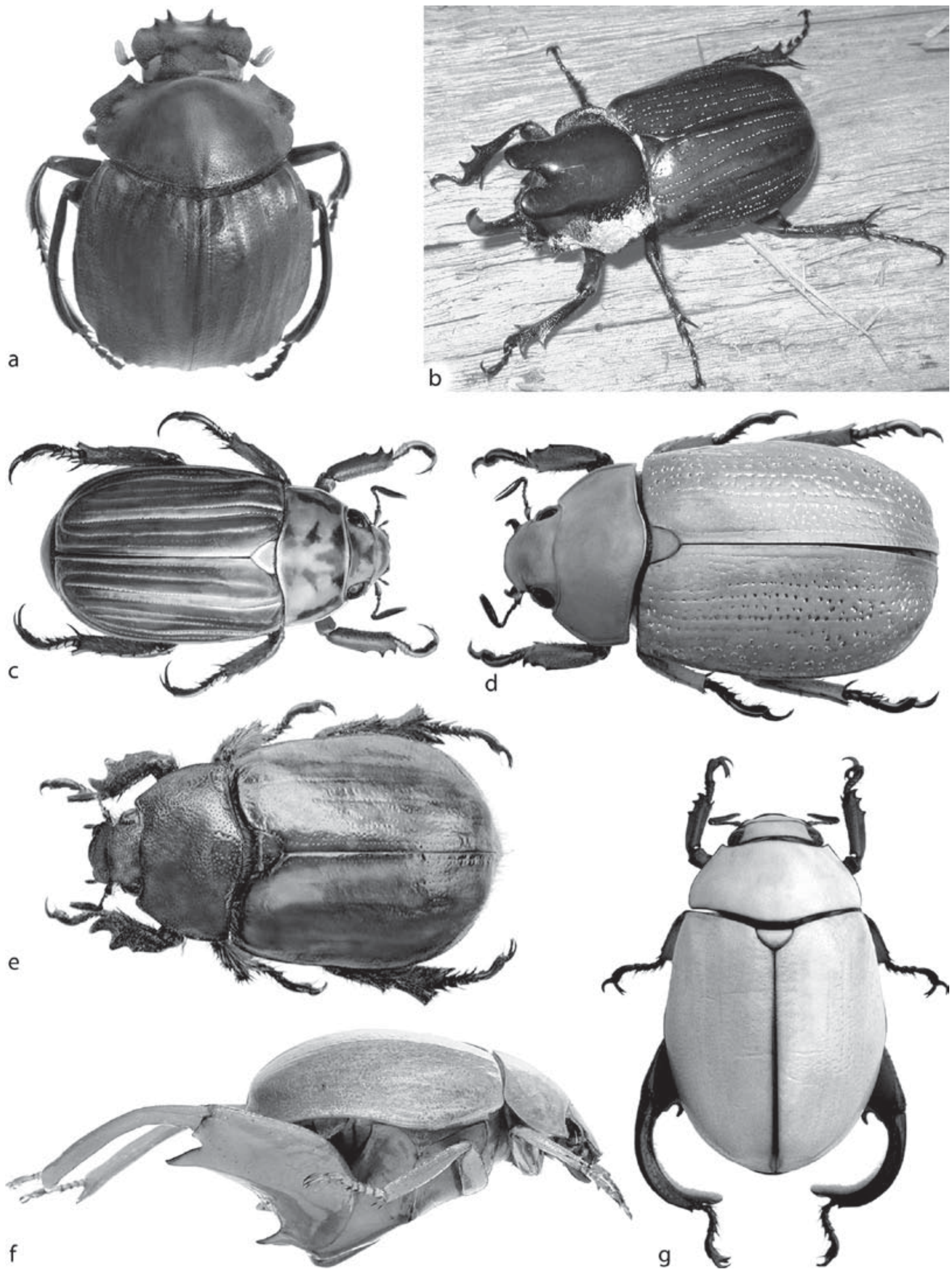
Taxonomic Composition

Significant changes have occurred in the classification of the Scarabaeoidea during the last 20 years. These changes are a result of intensified study of the family groups using traditional morphological evidence combined with increasingly insightful molecular studies. Monophyly of the superfamily Scarabaeoidea is well founded and undisputed. However, the hierarchical level of families and subfamilies within the Scarabaeoidea is in disarray and remains unresolved. Underlying the classification problem is the fact that our classification constructs are 200 years old and pre-date evolutionary theory. Thus, some groups within the superfamily are not monophyletic lineages; instead, they are groups that were created historically because they superficially resembled each other. In most US literature prior to the 1970s, the Scarabaeoidea included three families: Passalidae, Lucanidae, and Scarabaeidae. Phylogenetic research indicates, however, that the family Scarabaeidae (in the traditional sense) is not a monophyletic group. Accordingly, most workers now follow the 12-family system that places emphasis on the differences that separate taxa rather than the similarities that unite them. The classification of Scarabaeoidea is summarized as:

- Order: Coleoptera
  - Suborder: Polyphaga
    - Series: Scarabaeiformia
      - Superfamily: Scarabaeoidea
        - Family: Lucanidae
        - Family: Diphyllostomatidae
        - Family: Passalidae
        - Family: Glaresidae
        - Family: Trogidae
        - Family: Pleocomidae



Scarab Beetles (Coleoptera: Scarabaeoidea), Figure 14 **Representative scarab beetles: (a) *Chrysina strasseni* (Rutelinae) from Central America; (b) *Gymnetosoma stellata* (Cetoniinae) from Central America; (c) male *Polyphylla petiti* (Melolonthinae) with enlarged lamellate antennal club; (d) male *Megasoma elephas* (Dynastinae) with two acute pronotal protuberances and a large bifurcate head horn; (e) male *Spodistes mniszechi* (Dynastinae) with large, curved head and pronotal horns; (f) male *Phanaeus eximius* (Scarabaeinae) with a large, curved head horn and a number of small, acute pronotal protuberances; (g) larva of *Dynastes maya* (Dynastinae); (h) *Passalus punctiger* (Passalidae) from Central America.**



Scarab Beetles (Coleoptera: Scarabaeoidea), Figure 15 **Additional scarab beetles: (a) *Deltochilum lobipes* (Scarabaeinae) from Central America; (b) male *Coelosis biloba* (Dynastinae) with two large, rounded pronotal horns and a large up-curving head horn; (c) *Chrysina quetzalcoatli* (Rutelinae) from Central America; (d) *Chrysina spectabilis* (Rutelinae) from Central America; (e) *Viridimicus omoaensis* (Rutelinae) from Central America; (f) male *Macropoidelimus mniszechi* (Rutelinae) with enlarged, spinose hind legs for grasping the female during mating; (g) male *Macropoides crassipes* (Rutelinae) with enlarged, curved hind legs for grasping the female during mating.**

Family: Geotrupidae
Family: Belohinidae
Family: Ochodaeidae
Family: Hybosoridae
Family: Glaphyridae
Family: Scarabaeidae

Lucanidae

Commonly called stag beetles, the species of this family number about 1,000 worldwide. Most species occur in Asia. They are associated with decaying wood and logs in coniferous and deciduous forests. Adults vary from <1 to 9 cm in length. Males of several species, e.g., *cyclommatus imperator*, possess greatly enlarged, curving mandibles that are used in combat with male rivals.

Diphyllostomatidae

This is a small family of only three species in one genus, all occurring in California. Females have reduced eyes and wings.

Passalidae

This family of insects commonly called bess beetles (e.g., *Passalus punctiger*) is found on all continents except Antarctica but is most speciose in the tropics. There are over 500 described species divided between two subfamilies. All life stages live in well decayed logs and stumps. Adults excavate galleries in which eggs are laid and larvae develop. Larvae and adults form subsocial groups and communicate by stridulation. Adults feed the larvae chewed wood mixed with saliva, and both stages consume adult feces to enhance the microflora in their digestive system. The elongate and dorsoventrally flattened body, sublamellate antennal club, and deeply emarginate mentum distinguish adult passalids from all other scarabaeoids.

Glaresidae

Fifty species in a single genus constitute this family found worldwide except Australia. Adults are small (2.5–6.0 mm) and inhabit arid and sandy regions. Nothing is known about the larval biology.

Trogidae

This worldwide family consists of approximately 300 species in four genera. Excellent revisionary, larval, and phylogenetic studies are available for this group. The pronotum and elytra of adults is warty, and brown to gray to black in color but usually heavily encrusted with dirt. Adults and larvae live in the dried remains of dead animals or in nests of birds and mammals, where they feed on hair, feathers and skin. For this reason they have been given the common name of hide beetles. Adults will also feed on dung.

Pleocomidae

This family of large (16–45 mm) and ventrally pubescent beetles is geographically restricted to western North America from Washington to Baja California. It consists of a single extant genus encompassing 26 species. Larvae are subterranean and feed on tree roots. Adults emerge during fall or winter rains to mate and disperse. Only males are fully winged and capable of flying. Due to their propensity for increased activity during precipitation, these scarabs are referred to as rain beetles.

Geotrupidae

Excellent monographs are available for identifying the approximately 620 species and 68 genera of Geotrupidae, and these provide the foundation for addressing relationships within this group. However, the classification of the family has been the topic of debate. Diversity of larval and adult morphology provides evidence that the group includes two distinct lineages. Some taxonomists separate one lineage as a distinct family, Bolboceratidae. Food resources for adults and larvae include decomposing plant or animal material, dung, and fungi. Adults will provision subterranean burrows with food for larvae, but do not tend the larvae. Their excavating behavior has earned them the common name earth-boring scarab beetles.

Belohinidae

This family consists of a single species, *Belohina inexpectata*, which lives in southern Madagascar. This rare species is known by only a few specimens.

Ochodaeidae

This small but widespread family contains ten extant genera and about 80 species. Adults are small (3–10 mm), capable of stridulating, and primarily active at night. Sandy areas are the preferred habitat, so these beetles are commonly called sand-loving scarab beetles. One species has been found in association with detritus deposits of harvester ants. Nothing else is known about the biology of adults and larvae.

Hybosoridae

This family is divided into five subfamilies represented by more than 220 species placed in 35 genera. Adults of Anaidinae, Hybosorine, Liparochrinae, and Pachyplectrinae feed on vertebrate and invertebrate carrion, dung, fungi, or turf, thus they are called scavenger scarab beetles. *Hybosorus illigeri* is known to be predaceous. Larvae are found in decomposing plant material and are capable of stridulation. Adults of Ceratocanthinae are able to roll themselves into a ball by deflexing their head and pronotum ventrally, and are therefore called pill scarab beetles. Adults and larvae occur on bark and branches of dead trees and vines, on fungi, in passalid burrows, in wet tree holes, and in association with termites and ants.

Glaphyridae

Adults of this family are active day fliers, many of which are brightly colored and hairy, thus resembling bees and bumblebees. Larvae live in riparian and coastal dunes, feeding on decaying leaf litter and detritus in the sand. *Lichnanthe vulpina* is a pest of cranberry bogs in North America. The family includes six genera and about 70 species worldwide.

Scarabaeidae

Members of this, the sixth largest family in the order Coleoptera, are popular beetles due to their large size, bright colors, and interesting natural histories. Early Egyptians revered the scarab as a god, Jean Henri Fabre studied their behavior, and Charles Darwin used observations of scarabs in his theory of sexual selection. Species of scarabs are important agricultural pests, are used in the biological control of dung and dung flies, are pollinators, and have been used as bioindicators of high-quality forest habitat. Classification of the family is variably resolved. The classification of the world Dynastinae is fairly well established. Most Melolonthinae, Rutelinae, and Cetoniinae remain relatively poorly known taxonomically, and many Neotropical genera cannot be reliably identified. Classification of the Scarabaeinae and Aphodiinae is fairly well established, although the Aphodiinae in particular have recently been the subject of extensive taxonomic inflation. The taxonomy of the North American scarab beetles is relatively stable, although no one volume is available for identification to species. Regional works are sometimes the best sources for identification of scarabs.

There are currently about 2,000 known genera and over 31,000 described species of Scarabaeidae. Aphodiinae and Scarabaeinae are widepread, with approximately 6,850 species representing about 22% of scarabaeoids and 25% of Scarabaeidae. The worldwide subfamilies Orphninae, Melolonthinae, Dynastinae, Rutelinae, and Cetoniinae include approximately 20,950 species (about 69% of scarabaeoids and 75% of Scarabaeidae). Three subfamilies (Cretoscarabaeinae, Lithoscarabaeinae, and Prototroginae) are known only from fossils.

Aclopinae

This subfamily contains four genera with 19 known species distributed in Australia, Borneo, and southern South America. Little is known of their ecology and biology. In Australia, adults may be taken at lights, but morphological characters suggest that females may be flightless. No larval stages are described.

Allidiostomatinae

This group contains a single genus with 11 species, all restricted to South America. The ecology, biology, and immature stages of this subfamily are unknown.

Aphodiinae

There are more than 300 genera and at least 3,000 species divided among 11 or 12 tribes comprising this worldwide subfamily. Many species are highly specialized dung feeders (e.g., feces in nests of pocket gophers, prairie dogs, and gopher tortoises), while many others are generalist dung feeders. Some species feed on decaying plant material, often in riparian or littoral habitats. A few species live as inquilines in ant colonies.

Cetoniinae

Twelve tribes containing 510 genera and approximately 4,000 species constitute this subfamily. The adults are referred to as fruit chafers or fruit beetles because they usually feed on ripe or decomposing fruits, but they will feed also on pollen or slime flux. Many species are very brightly colored with metallic reflections or multicolored patterns. The goliath beetles (genus *Goliathus*) of Africa are among the largest insects known.

Dynamopodinae

This group contains a single genus with three species found in central Asia and northern Africa.

Dynastinae

This subfamily is divided into eight tribes containing more than 1,500 known species in 196 genera. It occurs in all major biogeographic regions, but most species live in the tropics, particularly the New World tropics. The adults are herbivores, feeding on fruits, pollen and leaves, while the larvae are consumers of decomposing wood and roots. Larvae of a few species of *Tomarus* and *Cyclocephala* are pests of turf grass and crops. In English they are called white grubs, but in Spanish they are referred to as "gallina ciega" or "joboto." The males of several species have prominent and spectacular horns on the head and/or prothorax, which have earned them the vernacular names "hercules," "rhinoceros," "elephant," "unicorn," and "atlas" beetles.

Euchirinae

This subfamily contains three genera and 16 species of mostly Asian distribution; a single species each are found in Turkey and Cyprus. Their common name is long-armed chafers due to the very long front legs of the males.

Melolonthinae

The members of this large and diverse subfamily are divided into 26 tribes encompassing approximately 750 genera and nearly 11,000 species. Adults are usually leaf or pollen feeders, but some will consume flowers and ripe fruits. The larvae live in the soil feeding on roots and other organic matter. In North America the adults are referred to as May beetles or June bugs and the larvae as white grubs. In Mesoamerica, the adult is called "ronrón" and the larva "gallina ciega" or "joboto". The larvae of several species of *Phyllophaga* are serious pests in crops and nurseries.

Orphninae

This subfamily includes about 80 species divided into two tribes: the New World Aegidiini with four genera and the Old World Orphnini with ten genera. Adults of some species were found feeding on decaying banana stems in coffee-cacao plantations. The larva of one species was found under rotten logs.

Pachypodinae

This is a small subfamily of only one genus and three species occurring in Europe.

Phaenomeridinae

This is an African subfamily of only 12 species split between two genera.

Rutelinae

Six tribes containing 200 genera and approximately 5,000 species worldwide constitute this subfamily. The adults are phytophagous, feeding on leaves, flowers, and pollen; larvae feed on roots and decomposing plant material. A few species are pests of turf grass and crops. The males of some species have enlarged hind legs with robust teeth for grasping the female during copulation. The genus *Anomala*, with over 1,000 known species, is one of the largest genera of animals. The jewel scarabs, members of the genus *Chrysina*, are a favorite among collectors because of their bright colors.

Scarabaeinae

This subfamily is divided into 12 tribes with 234 genera and more than 5,000 species. Members of this group are for the most part coprophagous, but several species also consume carrion, mushrooms, rotting fruit, and other decomposing plant material. The males of some species have long cephalic horns and other ornate protuberances arising from the pronotum.

Ecology

Scarab beetles live in a diverse array of microhabitats and consume a wide range of food. Adults and larvae of many species feed on dung, carrion, hides, feathers, or decaying plant material, but several species have evolved the ability to utilize unique resources. A great number of species feeding on dung are specialists, feeding only on one type of vertebrate dung (e.g., deer dung, elephant dung, sloth dung), whereas many other species are generalist dung feeders. Some species will feed on both dung and carrion. Many species of *Aphodius* (Aphodiinae) live in the nests of prairie dogs and pocket gophers. *Auperia denominata* (Aphodiinae) in Florida lives in tree squirrel nests. In the southeastern USA, *Onthophagus polyphemi* (Scarabaeinae) inhabits the subterranean tunnels of gopher tortoises. A number of species have developed the habit of feeding on fungi. Species of *Scarabaeus*, *Sceliages*, *Onthophagus*, and *Canthon* (all Scarabaeinae) have been observed using injured or dead millipedes for food whereas at least two species of *Deltochilum* (Scarabaeinae) (e.g., *Deltochilum lobipes*) are known to actively prey on live millipedes. A few species of Hybosoridae will feed on earthworms. Myrmecophilous scarabs are not uncommon. Adults and larvae of *Coelosis biloba* (Dynastinae) and *Ptichopus angulatus* (Passalidae) occur in leaf-cutter ant nests, where the larvae eat not only the decaying leaf material accumulated by the ants but also the fungus cultivated by the ants. Species of *Cremastocheilus*, *Genuchinus* (both Cetoniinae) and *Euparia* (Aphodiinae) also live in ant nests. Less common are the termitophilous scarabs, e.g., *Afroharoldius ennearthrus* from the Congo and *Scarabatermes amazonensis* (both Scarabaeinae) from Colombia. Adults of the South American genus *Zonocopris* (Scarabaeinae) feed on the mucosal secretions from terrestrial snails.

The feeding habits of phytophagous species are quite variable. Most adults of Dynastinae, Melolonthinae, Rutelinae, and Cetoniinae are herbivores consuming leaves, flowers, fruits, and pollen. *Chrysina quetzalcoatli* (Rutelinae) and *Polyphylla decemlineata* (Melolonthinae) feed on fresh pine needles. Species of *Podischnus* (Dynastinae) excavate burrows in the stalks of sugarcane and bamboo. Adults of many *Cyclocephala* (Dynastinae) species are often found within the spathe of aroids where they feed on the spadix. Some species readily feed on rotting fruits or the slime flux emanating from tree wounds. The larvae of these herbivorous adult scarabs feed, for the most part, on roots, decaying wood, or other organic matter accumulated in the soil, in tree holes, or in epiphytic plants. Their digestive system holds symbiotic microbes which aid in the digestion and assimilation of nutrients from cellulose and lignin.

Behavior

The adults of most species of scarab beetles are nocturnal or crepuscular and are readily attracted to lights. Some species, such as those of *Heterogomphus* and *Strategus* (Dynastinae), are active soon after dusk then are no longer seen at lights. On the other hand, *Golofa pizarro* (Dynastinae) will have a peak flight activity for only an hour around midnight, whereas species of *Dynastes* (Dynastinae) and *Amithao* (Cetoniinae) are most frequently active in the hour or two before dawn. Some species of *Chrysina* (Rutelinae) have dual flight activity periods, one in early evening and another during the pre-dawn hours. *Chrysina spectabilis* (Rutelinae) and species of *Viridimicus* (Rutelinae) and *Pleocoma* (Pleocomidae) fly more actively during a rain shower. The colorful cetoniine species and some scarabaeines are diurnal in their activity.

Feeding behavior of dung beetles is classified into four types. Feeding without burial is done by dwellers (Type 1) and is practiced by coprophagous species of Aphodiinae. Tunnelers bury dung without overland transportation (Type 2) but dig their tunnels before provisioning them. Tunnels are excavated below or very near the primary dung source. Dung is removed from the primary source and carried or dragged into the tunnel by backing into the entrance. In overland transportation without formation of a ball (Type 3), tunnels are excavated separate from the primary dung source and dung is carried or dragged to the burrow by either grasping it with the front legs and walking backwards, rolling the food source by walking forward and pushing with the head and front legs, or grasping the dung with the front tibiae and running forward using only the middle and hind legs. Overland transportation with formation of a ball (Type 4) consists of forming a portion of dung into a round mass, rolling it a distance from the primary dung source by pushing backwards with the middle and hind legs or front and hind legs, then burying it intact. Practitioners of Types 2–4 are all members of the Scarabaeinae. Females lay an egg in the provisioned food source where the larvae feed and develop until pupation.

A number of dung beetle adults attach themselves to mammalian animals to be close to dung nutrients leaving the host. Examples are *Canthon quadriguttatus* (Scarabaeinae) residing near the anus of *Callicebus brunneus* (Titi monkey) in Peru, *Macropocopris parvus* (Scarabaeinae) on the anal hairs of the Australian wallaby, and *Trichillum adisi* and *Uroxys besti* (Scarabaeinae) on the pelage of three-toed sloths (*Brachypus* sp.) in Brazil.

The males of several species of Dynastinae (e.g., *Megasoma elephas* and *Spodistes mniszechi*) and Scarabaeinae (e.g., *Phanaeus eximius*) are endowed with elaborate head and/or pronotal horns, the uses of which provide interesting lessons in intraspecific behavioral interactions and natural selection. The extravagant armaments serve as effective tools in contests between members of the same species over critical resources such as mating privileges with females, feeding sites, and dung provisions for oviposition. They may be employed as a crowbar for prying a rival from a substrate so that it may be pushed away from the contested resource, or as forceps for lifting rivals and dropping them from a tree or log to the ground. Head horns and pronotal protuberances are prevalent in tunneling male dung beetles, who employ them to effectively block tunnel entrances or push opponents out of tunnels. Horns are often serrated or hairy to increase prying or gripping.

Males of some species of Rutelinae have greatly enlarged hind legs (e.g., *Macropoidelimus mniszechi* and *Macropoides crassipes*), often with strong, sharp protuberances that they use to grasp the female firmly during mating. Males of Euchirinae and Dynastinae often have very long front legs for the same purpose. Many male dynastines in the tribe Cyclocephalini have enlarged front tarsi that they use to grasp the elytral margins of the female during copulation; the female's elytral margins will often have small, rounded protuberances to accommodate the grasp of the male. These marginal protuberances are also evident on the elytra of female jewel scarabs (*Chrysina* spp.).

Ecological Importance

The larvae of scarab beetles play a crucial role in recycling nutrients from decaying plant material, dung, and carrion. The consumption of stumps and fallen logs by saprophagous scarab larvae, with assistance from symbiotic intestinal microflora, decomposes cellulose and lignin and returns carbon and nitrogen to the soil so that these elements can be utilized by plants. Likewise, vertebrate animal feces and carrion are incorporated into the soil by dung beetles and necrophagous scarabs, which maintains ecosystem health and contributes to soil fertility.

Dung-feeding scarab beetles have been useful in classical biological control. In 1968, several species of dung beetles were introduced into Australia to aid in the decomposition of cattle feces which is utilized as a breeding resource by noxious flies. Domesticated cattle produce feces different from native Australian herbivores. Native Australian dung beetles were not adapted to feed on the dung of domesticated cattle. As a result, cattle feces accumulated at such a rate that grasses and forbes were smothered and killed and noxious fly populations erupted. Dung beetles, such as *Onthophagus gazella* (Scarabaeinae), were introduced from Africa, and these scarabs readily feed on cattle dung, thus enriching the soil with dung, allowing grasses and forbs to thrive, and eliminating a resource which led to a reduction in noxious fly populations.

Diurnal species of Cetoniinae are frequent visitors to flowers and as such are important agents in cross-pollination. The adults of *Erioscelis* spp. and *Cyclocephala* spp. (both Dynastinae) are also recognized as important pollinators of palms and aroids. After visiting male stage flowers of *Philodendron selloum* and exiting with their bodies laden with pollen, adults of *Erioscelis emarginata* are attracted to female stage inflorescences at dusk by a mixture of visual and olfactory stimuli. Odoriferous inflorescences in the female stage of flowering induce adult beetles to remain within the inflorescence during this stage. *Cyclocephala atripes* and *Cyclocephala conspicua* are frequent pollinators of *Cyclanthus bipartitus* in Costa Rica. The beetles arrive during the pistillate phase, feed on pollen and specialized tissue on the bracts of the inflorescence, and remain in the flower until the end of staminate anthesis. The inflorescence also serves as an aggregation site for mating.

Species diversity and endemism in faunal assemblages of Passalidae and Scarabaeidae (particularly Dynastinae, *Chrysina* spp., and *Phyllophaga* spp.) have been used to prioritize the conservation of cloud forests in Guatemala. Faunal similarity indices have been used to compare these high montane forest habitats where endemism can be high. Advantages to using these beetles as bioindicators for prioritizing conservation efforts and analyzing relationships among cloud forest areas are (i) they are continually present year-round, (ii) they are easy to collect in a short period of time, and (iii) they are relatively well known taxonomically. Other potentially useful scarabaeoid groups are Geotrupidae and Scarabaeinae. The patterns of endemism in scarab beetles are similar to those observed with longhorn beetles (Cerambycidae), salamanders, birds, small mammals, and trees, thus making them good indicators. The methodology using scarab beetles, as developed in Guatemala, may be adapted for use in understanding areas of endemism and high species diversity for better conservation efforts in other countries.

Agricultural and Medical-Veterinary Importance

The following table (Table 3) presents a partial list of scarab beetles known to be pests of annual and perennial crops, ornamental plants, turf, and forests. The larvae of at least 27 species of *Phyllophaga* (Melolonthinae) are documented as pests of maize, potatoes, sugarcane, wheat, sunflower, cranberry, and beans in North and Central America. Adults of *Phyllophaga falsa* are capable of defoliating pine trees in nurseries. Not <15 species in 13 genera are recognized as pests of turf grass in the United States. Adults of the Japanese beetle, *Popillia japonica* (Rutelinae), feed on over 300 host plants in eastern North America.

Scarab beetle have also played a significant role in medical and veterinary entomology. Several species, mostly in the subfamily Scarabaeinae, whose larvae develop in dung, carrion, or compost, are known to serve as intermediary hosts of parasitic nematodes and cestodes whose definitive hosts are mammals. The excrement of the definitive hosts contains eggs of the parasitic worms, which are then ingested by the larval scarabs. The larval stages of the parasites develop within the larval beetle hosts. The infective scarab grubs, and the pupae and adults that develop from them, are then ingested by uninfected definitive hosts (e.g., pigs, sheep, goats, cattle, dogs, rodents) to complete the cycle.

Chickens and other domestic birds that eat the adults of the rose chafer, *Macrodactylus subspinosa* (Melolonthinae), take on a drowsy appearance, droopy wings, closed eyes, and a slightly trembling body. Death may occur 5–24 h after consumption. Beetles removed from the crop of a killed chicken and fed to a second chicken will cause the death of the second chicken, indicating that the beetles need not be alive to cause death. A toxic substance is suspected since mashed bodies of dead beetles fed to chickens killed the birds and filtered solutions prepared from crushed beetles and intravenously injected into rabbits killed the mammalian subjects.

In July 1957, a bizarre case of ear invasions by *Cyclocephala borealis* (Dynastinae) and *Maladera castanea* (Melolonthinae) occurred in 186 Boy Scouts at Valley Forge State Park, Pennsylvania, USA. All but two boys were sleeping on the ground at the level at which the beetles are known to fly looking for mating and oviposition sites; no cases were reported in persons sleeping on cots. So deep were the intrusions that the beetles could not be seen without an otoscope. The presence of a beetle in the ear canal was extremely painful because the tibial spines pierced the delicate skin as the insect forced its way in. Cotton ear plugs or neckerchiefs provided mechanical barriers preventing additional invasions.

Scarab Beetles (Coleoptera: Scarabaeoidea), Table 3 Partial list of scarab beetles known as pests of crops, ornamental plants, turf, and forests

Pest scarab	Affected plants
Scarabaeidae	
Aphodiinae	
Aphodius granarius	turf
Aphodius tasmaniae	many host plants
Ataenius spretulus	turf
Cetoniinae	
Cotinis nitida	vegetables, turf
Euphoria sepulcralis	many host plants
Protaetia pryeri	many host plants
Dynastinae	
Adoryphorus couloni	pasture
Cyclocephala spp.	maize, sugarcane, guava, turf
Diloboderus abderus	pastures, cereals
Dyscinetus morator	carrots, radishes, caladium bulbs
Euetheola spp.	rice, sugarcane
Heterogomphus chevrolati	coconut
Heteronychus arator	cereals
Oryctes rhinoceros	coconut
Podischnus spp.	bamboo, maize, sugarcane
Strategus aloeus	dates
Strategus antaeus	turf
Tomarus spp.	carrots, sugarcane, turf
Melolonthinae	
Amphimallon majale	turf
Apogonia spp.	cacao
Costelytra zealandica	pasture
Holotrichia spp.	groundnuts, beans, cereals
Hoplia callipyge	roses
Hoplia modesta	cranberry
Macrodactylus subspinosa	many host plants
Maladera matrida	many host plants
Melolontha spp.	fruit trees, forests
Phyllophaga spp.	many host plants
Diplotaxis spp.	ornamental trees
Serica spp.	avocado
Rutelinae	
Adoretus sinicus	many host plants

Scarab Beetles (Coleoptera: Scarabaeoidea), Table 3 Partial list of scarab beetles known as pests of crops, ornamental plants, turf, and forests (Continued)

Pest scarab	Affected plants
Anomala spp.	bamboo, turf
Exomala orientalis	many host plants
Popillia japonica	many host plants
Strigoderma arbicola	various ornamental plants
Geotrupidae	
Peltotrupes sp.	turf
Glaphyridae	
Lichnanthe vulpina	cranberry
Hybosoridae	
Hybosorus illigeri	turf

Cultural Importance

Scarab beetles, because of their size, numbers, and beauty, have played various roles in their interactions with humankind, especially religion and folklore, folk medicine, food, and ornamentation of regalia. Scarabs are often used in modern cultures for art (painting, sculpture, baskets, wood, and lacquer ware), toys (plastic), and as entertainment in the form of betting on fights between adult rhinoceros beetles.

The first documented use of scarab beetles by humankind was a small alabaster case made in the shape of a dung beetle by the ancient Egyptians (3000 B.C.). Historically, dung beetles played a prominent role in the mythology of ancient Egypt. Collectively known as the sacred scarab, these insects and their ball-rolling behavior symbolized certain parts of the Egyptian polytheistic theory of the universe. Ra, in Egyptian theology, was the Sun God responsible for the daily shepherding of the sun across the sky. Ra, in this belief system, was also the first ruler of Egypt. A cult developed whereby Ra was symbolized by the scarab and the sun was represented by the dung ball. The scarab pushing its ball was an earthly manifestation of Ra escorting the sun on its daily journey across the sky.

After 200 B.C., during the Middle Kingdom, older interpretations of the role of scarabs changed so that the beetle was credited with the supernatural power of insuring rebirth after death. The scarab's likeness was fashioned into amulets, jewelry, and seals that were used as good luck charms by many cultures, including the later rulers of Egypt and Persians, Macedonians, Romans, and Phoenicians. The Romans especially had great faith in the scarab's protective powers, particularly in battle, and many artificial scarabs have been found in Roman graves dating from before 400 A.D.

The larvae and adults of many scarabs were (and are) used as food by peoples in Europe, Africa, Asia, and Latin America. Insects are consumed because they have a high nutritive value and are abundant. Many Indian tribes in South America routinely use insects in their diets. The larvae constitute a rich source of proteins and fats. Some Australian aboriginals used scarab beetles both as totems and as food. The aversion to insects as food is a recently established custom and prejudice of western civilization.

The use of scarabs in folk medicine was once widespread in Europe and remains so in Asia, especially China. Roasted, pureed, or pulverized scarabs are used as a medicine for diarrhea, stomach cramps, dysentery, and even cancer.

The use of scarabs in regalia decoration and as ornaments occurs in South America. The Jivaro, of the eastern lowlands of Ecuador, make beautiful headdresses and necklaces using the brilliant, metallic green bodies of *Chrysophora chrysochlora* (Rutelinae). The horns of large rhinoceros beetles are fashioned into necklaces in Brazil, Venezuela, and Colombia.

Some South American Indians eat large rhinoceros beetles in the belief that the special powers associated with the size of these animals (150 mm) could be acquired by eating them (imitative magic). To the Aymara of the Lake Titicaca Plateau in Bolivia, a certain scarab beetle was believed to cause madness, and occasionally, in referring to an insane person, they would say "someone has given him a scarab to drink."

Collecting beetles is a very popular hobby practiced by many worldwide, and scarab beetles are avidly sought after by collectors. There are a number of companies that advertise scarabs for trade or sale on the Internet. The more common species sell for only a few dollars per individual, whereas rare or extravagant species may sell for a few hundred dollars for an individual or several hundred dollars for a mated pair. Jewel scarabs (*Chrysina*) and other colorful Rutelinae, horned species of Dynastinae and Scarabaeinae, and Lucanidae are the more popular, and expensive, scarab beetles in the marketplace.

► Beetles

References

Arrow G (1951) Horned beetles. Dr. W. Junk, The Hague, The Netherlands, 154 pp

Halffter G, Edmonds WD (1982) The nesting behavior of dung beetles (Scarabaeidae): an ecological and evolutive approach. Instituto de Ecología. Mexico City, México, 312 pp

Hanski I, Cambefort Y (1991) Dung beetle ecology. Princeton University Press, Princeton, NJ, 481 pp

Howden HF (1964) The Geotrupinae of North and Central America. Mem Entomol Soc Can 39:1–91

Howden HF (1968) A review of the Trichiinae of North and Central America (Coleoptera: Scarabaeidae). Mem Entomol Soc Can 54:1–77

Jameson ML, Ratcliffe B.C (2002) Series Scarabaeiformia Crowson 1960, Superfamily Scarabaeoidea Latreille 1802. In: Arnett RH, Thomas M, Skelley PE, Frank JH (eds) American beetles Polyphaga: Scarabaeoidea through Curculionoidea, vol 2. CRC Press, Boca Raton, FL, pp 1–5

Mizunuma T, Nagai S (1994) The lucanid beetles of the world. Mushi-Sha, Tokyo, Japan, 337 pp

Morón MA (ed) (2003) Atlas de los Escarabajos de México (Coleoptera:Lamellicornia), vol 2: Familias Scarabaeidae, Trogidae, Passalidae y Lucanidae. Argania Editio, Barcelona, Spain, 227 pp

Morón MA (2004) Escarabajos, 200 millones de años de evolución. Instituto de Ecología, A.C. y Sociedad Entomológica Aragonesa. Zaragoza, Spain, 204 pp

Morón MA, Ratcliffe BC, Deloya C (1997) Atlas de los escarabajos de México (Coleoptera: Lamellicornia), vol 1: Familia Melolonthidae. Comisión Nacional parael Conocimiento y Uso de la Biodiversidad (CONABIO) and Sociedad Mexicana de Entomología, Mexico, 280 pp

Ratcliffe BC, Cave RD (2006) The Dynastine scarab beetles of Honduras, Nicaragua and El Salvador (Coleoptera: Scarabaeidae: Dynastinae). Bulletin of the University of Nebraska State Museum, vol 21. Lincoln, Nebraska. 424 pp

Ratcliffe BC, Jameson ML, Smith ABT (2002) Scarabaeidae Latreille 1802. In: Arnett RH, Thomas M, Skelley PE, Frank JH (eds) American beetles Polyphaga: Scarabaeoidea through Curculionoidea, vol 2. CRC Press, Boca Raton, FL, pp 39–81

Ritcher PO (1958) Biology of Scarabaeidae. Ann Rev Entomol 3:311–334

Ritcher PO (1966) White grubs and their allies. Oregon State University Press, Corvallis, Oregon, 219 pp

Sakai K, Nagai S (1998) The cetoniine beetles of the world. Mushi-Sha, Tokyo, Japan, 421 pp

Scholtz CH (1990) Phylogenetic trends in the Scarabaeoidea (Coleoptera). J Nat Hist 24:1027–1066

Scatophile

An organism that is attracted to or lives on animal waste or excrement (sometimes called "scat"). Such animals are said to scatophilous.

Scarabaeidae

A family of beetles (order Coleoptera). They commonly are known as scarab beetles.

► Beetles
► Scarab Beetles

Scatopsidae

A family of flies (order Diptera). They commonly are known as minute black scavenger flies.

► Flies

Scavenger Moths (Lepidoptera: Blastobasidae)

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Scavenger moths, family Blastobasidae, total over 296 species worldwide, with many known from North America and Europe, in three subfamilies; actual fauna probably exceeds 600 species. There are two subfamilies: Holcocerinae and Blastobasinae (Symmocinae have been included as well but now are a tribe of Autostichinae, Oecophoridae). The family is part of the superfamily Gelechioidea in the section Tineina, subsection Tineina, of the division Ditrysia. Adults small (5–35 mm wingspan), with head smooth-scaled; haustellum scaled; maxillary palpi 4-segmented. Maculation mostly somber shades of gray with few markings. Adults nocturnal as far as is known. Larvae are scavengers or detritus feeders, sometimes feeding on plant fruits, flowers, or seeds, among a number of plant families, but few are known biologically. At least one species lives with coccids (Hemiptera) but predation on the coccids has not been confirmed (Fig. 16).

References

Adamski D (1995) Review of the Blastobasidae of the Republic of the Seychelles (Lepidoptera: Gelechioidea). Proc Entomol Soc Washington 97:489–499

Scavenger Moths (Lepidoptera: Blastobasidae), Figure 16 **Example of scavenger moths (Blastobasidae), (Sinev) from Italy.**

Adamski D (2002) A synopsis of described neotropical Blastobasinae (Lepidoptera: Gelechioidea; Coleophoridae). Entomological Society of America, Lanham, MD (Thomas Say Monograph), 150 pp
Adamski D, Brown RL (1989) Morphology and systematics of North American Blastobasidae (Lepidoptera: Gelechioidea). Mississippi Agr Forest Exp Stat Tech Bull 165:1–70
Adamski D, Hodges RW (1996) An annotated list of North American Blastobasinae (Lepidoptera: Gelechioidea: Coleophoridae). Proc Entomol Soc Washington 98:708–740
Buszko J (1978) Blastobasidae. In Klucze do Oznaczania Owadów Polski. 27. Motyle & Lepidoptera, 36:22–32. Polskie Towardzystwo Entomologiczne [in Polish]

Scelionidae

A family of wasps (order Hymenoptera).
► Wasps, Ants, Bees and Sawflies

Scenopinidae

A family of flies (order Diptera). They commonly are known as window flies.
► Flies

Scent Gland

A gland producing an odor.

Scentless Plant Bugs

Members of the family Rhopalidae (order Hemiptera).
► Bugs

Scheerpeltz, Otto

Otto Scheerpeltz was born near Olomouc, Czech Republic, on July 16, 1888. He enrolled in the Technische Hochschule, in Vienna, to become an engineer, but instead became a teacher. He continued at this profession until his retirement in 1945. In 1922, while still employed as a teacher, he entered the University of Vienna to study zoology and botany, and graduated in 1930. There he became interested in the Staphylinidae. Scheerpeltz amassed one of the largest collections of Staphylinidae, containing 300,000 specimens and 10,000 types. He authored 286 papers describing 1,405 species and 181 genera, and is considered to be an important contributor to our knowledge of this family. He died at Vienna, Austria, on November 10, 1975.

Reference

Herman LH (2001) Scheerpeltz, Otto. Bull Am Mus Nat Hist 265:137–139

Schizopteridae

A family of bugs (order Hemiptera).
► Bugs

Schmidt's Layer

A zone of new cuticle deposition within the procuticle.
► Cuticle

Schneiderman, Howard Allen

Howard Schneiderman was born at New York, NY, USA, on February 9, 1927. He received a bachelor's degree from Swarthmore College in 1948, and a M.S. and Ph.D. from Harvard University in 1949 and 1952, respectively. Early in his career he became recognized as an authority on juvenile hormone chemistry. He was a member of the faculty at Cornell University from 1953 to 1961. Schneiderman helped found the Developmental Biology Center at Case-Western Reserve University, where he also served a chairman of the Biology Department. During this period he was co-discoverer of JH II. In 1969 Schneiderman moved to the University of California at Irvine, where he chaired the Department of Developmental and Cell Biology, and later became dean of the School of Biological Sciences. During this period Schneiderman's focus shifted from the developmental biology of Lepidoptera to *Drosophila*. In 1979 he joined the Monsanto Company, and eventually was chief scientist and senior vice president of research and development. His activities with Monsanto and collaborative arrangements with universities earned him national prominence as one of the architects of industrial biotechnology research, and one of the leading figures in physiology, development, and genetics of insects. Schneiderman published over 200 papers during his career, and was awarded many honors, including election to the National Academy of Sciences. He died on December 5, 1990, in St. Louis, Missouri.

Reference

Oberlander H (1991) Howard Allen Schneiderman. Am Entomol 37:124

Schizopodid Beetles

Members of the family Schizopodidae (order Coleoptera).
► Beetles

Schizopodidae

A family of beetles (order Coleoptera). They commonly are known as schizopodid beetles.
► Beetles

School IPM, or Pest Management on School Grounds

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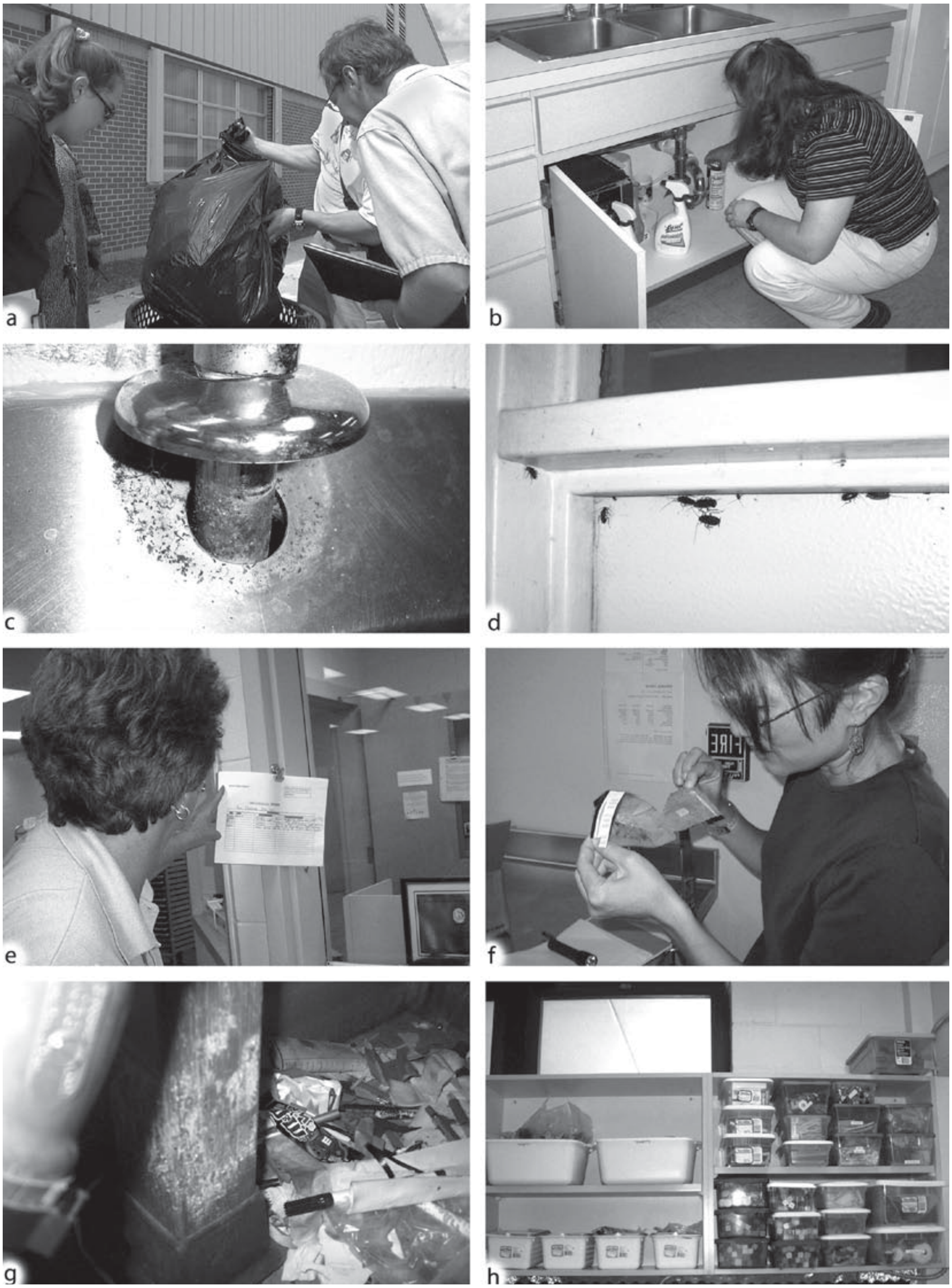
The purpose of school IPM (integrated pest management) is to reduce the risk to students from pests, to eliminate unnecessary pesticide use by promoting IPM in schools, and to provide the support, resources and training needed to accomplish these tasks. To be very clear, IPM is a process. This effort has developed in response to concerns surrounding the potential hazards of pests and pesticide use in schools. The school environment is an important element in the life of nearly every child, a place where he or she spends a great deal of time. This is not an environment where students should be at risk from either pests or pesticides, but sometimes this has occurred due to lack of knowledge by administrators, parents, and others. School IPM is a community-wide approach involving education of school administrators, parents, students, building maintenance people, food service personnel and pest management professionals (PMP), as well as the application of appropriate pest control technologies.

A number of pests and pest-related problems are encountered in the school environment (Fig. 17). The pests occurring in school buildings are typically ants, cockroaches, head lice, fleas, flies, spiders, termites, bedbugs, rats, mice, and bats. Pests affecting the school outdoor environment include grasshoppers, house flies, deer flies, midges, mosquitoes, honey bees inc luding Africanized bees, yellow jackets and hornets. Some schools have butterfly gardens or demonstration vegetable gardens, which introduce another group of plant pests such as caterpillars, aphids, whiteflies, and beetles. The most common pest situations involve head lice on young students, cockroach contamination of cafeterias and classrooms, termites affecting the structural integrity of the building, rodents infesting food storage and preparation areas, nuisance ants and flies in classrooms, and stinging and biting insects in the schoolyard. To address these pest threats, pesticides are sometimes used. For both pest and pesticide issues, there is particular risk associated with hypersensitive children that have a physiological reaction to these stimuli, requiring emergency medical treatment.

The Role of Parents

Often parents can provide the most influential voice on issues regarding school policies. Getting integrated pest management (IPM) into a school or even the entire school district can begin at the grass roots level by organizing concerned parents. Parental involvement requires that parents become knowledgeable about what is and isn't being done in the schools. The involvement of the parent-teachers organization (PTA) is helpful. PTA officers likely are among the decision-makers at the school. The more informed they are about IPM, the better equipped they will be to lobby the local school board. The school's principal should be kept fully informed of parents concerns about pests or about excessive pesticide use in the school, and that alternatives such as IPM exist. One of the most important steps in getting IPM into a school is to get the local school board to approve an IPM policy statement district-wide. Often a trial period is desirable, because any change involves discomfort for someone, and even small adjustments can seem difficult to implement if it involves changing well-established procedures or protocols. A trial could consist of switching several schools over to IPM, switching just one entire school, or just a few isolated structures (e.g., the media center or administration wing) at one school. Usually it is desirable to have a school IPM committee made up of concerned parents, pest managers, administrators, etc. Establishment of such a committee will increase sustainability of a school IPM program. The role of this committee is to review the IPM program periodically and incorporate feedback from the schools into possible policy changes.



School IPM, or Pest Management on School Grounds, Figure 17 **Key elements of implementing school IPM programs: inspection of trash (a) and under-sink harborages (b) favored by cockroaches; cockroaches commonly follow plumbing (c) to gain entry, resulting in high population densities (d); record-keeping (e) helps assess the abundance of pests, as does trapping (f); trash accumulations beneath or within desks and cupboards (g) provides shelter for pests, but neatly organized and covered containers (h) can eliminate harborage, making detection easier and survival more difficult for pests.**

The Role of Administrators

It is important that administrators understand the IPM concept and the implementation process. The faculty, staff, students, and parents will expect the administrator to be knowledgeable about IPM.

If pest management is handled by in-house staff, the administrator should contact the supervisor of pest management to convey an interest in IPM. If the pest management supervisor is unfamiliar with IPM, the pest management supervisor should be advised of the benefits of IPM, including the reduced health risks associated with IPM implementation, and allowed time to become familiar with the concept and procedures.

If pest management is handled by a private pest management firm, the administrator should contact the person listed in the school's pest management contract as the supervisor or "contact" person. This information usually can be found by contacting the school district's purchasing agent. It is important to let the supervisor know that you are interested in getting IPM implemented. The supervisor should be willing to cooperate with your efforts depending upon certain contractual obligations. Keep in mind that you are the customer, and that the pest management industry is customer driven.

There is no sense in "re-inventing the wheel." Contacting school administrators from neighboring schools or neighboring districts can be extremely helpful. Other schools in the district may have already gone through the process of converting to an IPM program and might be able to offer valuable suggestions. If they haven't, they may become interested in IPM and be willing to combine their efforts with yours.

It probably will be important for you to make a brief presentation to the local school board and initiate the process of establishing an official school IPM policy statement. Adoption of an official policy statement is important because it gives school officials the authority to make decisions regarding pest management. In the case of an IPM policy, it provides administrators the foundation from which to implement IPM.

Your local county extension agent should have considerable expertise in insect pest identification and pest management. The extension agent may also be able to provide assistance in developing and supporting an IPM program. Because the Cooperative Extension Service is also a governmental resource, the extension agent has the ability to contact outside IPM experts and bring considerable information to the local level. There may also be individuals within the county administration that could provide expertise. Many local resources such as the county health department or environmental services employ professionals who possess experience in pest related health risks, pest management, and sanitation. All of these individuals can provide support for an IPM program in schools.

It is important to create a mechanism through which the IPM program can be maintained. The best method of accomplishing this is to create a school IPM advisory committee. This committee should have representatives from pest management (whether in-house or contracted), teachers, school administration, sanitation staff, and concerned parents (PTA). Because IPM is a process, it will be important for this committee to help make decisions on pest management that may be unique to your school or school district. Additionally, periodic feedback from these individuals will help improve the IPM program.

The Role of School Faculty and Staff

Faculty and staff frequent classrooms and food service areas. As a result, teachers and staff are exposed to all the same risks as the students. However, faculty and staff are often expected to "take charge" of unpleasant situations such as the occurrence of pests. It is important not to introduce "bug sprays" into the classroom. Commonly used "over-the-counter" products available at local stores can contain the same ingredients as those products used by licensed PMPs. When used in the classroom, these sprays are potentially dangerous to chemically sensitive children. Also, these products can make some pest problems worse because they may interfere with or even reduce the effectiveness of treatments made previously by the pest management staff. Finally, using pesticides sets a precedent that this is the way to deal with pest problems, and students will imitate this behavior at home. In an effective school IPM program, a mechanism exists whereby the faculty and staff can notify the pest management technician (by telephone, email, or written report) of any pest problems so they can quickly treat the problem.

Food or beverage items are a major source of pest problems, and should not be introduced into the classroom except in sealed containers (e.g., lunch boxes). It is very important to continually remind children that food and snacks are to be eaten in the cafeteria, not the classroom. Even a few crumbs are a full meal for rodents, cockroaches or ants. If food incentives are used in the classroom, they should be stored in plastic, sealable containers. If items are small, freezer bags are recommended because they are made of a thicker material that is more pest resistant than the less expensive food storage bags. If food is consumed in the classroom, remove food trash from the classroom once the meal is over; don't wait for the custodial staff to deal with it hours later. Also, remember that serving utensils need to be thoroughly cleaned and rinsed before storage.

Sanitation, not pesticides, makes the biggest impact on many pest populations. Cleaning up after any pets in the classroom and after parties is an absolute must. Empty soda cans, used paper plates, food wrappings, etc. should be placed in the trash can and then taken to an outside disposal area before the end of the day. Trash containers full of this type of food-contaminated debris left overnight in the classroom are often sources of pest problems. Indoor recycle bins should also be emptied daily.

Whether pest management is handled in-house or is contracted out, the faculty and staff should interact with the pest management technicians as often as possible. The more communication that occurs between the faculty/staff and the pest control technician, the more effective pest control will be. It is very important for teachers/school staff to communicate with the pest control technicians about the kind of pest problems that exist. Specifics such as where the pests are (e.g., near the sink in the rear of the classroom), what kind of pests exist (e.g., cockroaches, ants, wasps, rodents), and when they are a problem (e.g., only in the morning or all the time) is valuable information to the pest control technician. The technician will be better prepared to treat the pest problem with this sort of information.

A great way to communicate pest problems to the pest control technician is by using a "pest sighting log." Pest sighting logs are used by school employees to communicate pest problems to the pest control technician. The log is a record of when the pests were seen, by whom, where, and what kind of pests were present. The pest control technician checks the log and then uses the information provided to treat the problem. The pest control technician also records what action was taken to treat the pest problem on the pest sighting log. It is important to record such information such as what pests were identified, what the cause of the pest problem was, and what action was taken (including exclusion, sanitation, or pesticides, if any). The pest control technician also makes recommendations to building maintenance staff about what changes in maintenance might help prevent future pest problems (installation of proper door sweeps, turning off unnecessary lights at night, installing proper window screening). A pest sighting log should be kept in an accessible area such as the main office, cafeteria manager's office, or teacher's lounge area.

Faculty should consider IPM as a topic at a school PTA and/or faculty meeting. Faculty can help build support for the idea of switching to a school-wide IPM program by distributing IPM materials to others. A knowledgeable *group* of people who support an issue is often more effective than a single voice of concern.

The Role of Pest Management Personnel

Integrated Pest Management (IPM) is a viable alternative to traditional pest control. There are many sources available to pest management personnel if they are not familiar with IPM practices. Most professional pest management professionals have such knowledge, but sometimes schools entrust pest management to maintenance or janitorial staff, who may lack proper knowledge of pest management. Local regulatory agencies and the Cooperative Extension Service are good sources for additional information. In addition, many manufacturers also supply technical bulletins and documents with their products which describe IPM techniques and application methods. Lastly, many WWW sites contain pertinent information.

To reduce pests in schools, you must reduce pest-conducive conditions. These conditions are found most often in "pest vulnerable areas." These are areas that have food, water and harborage available to pests. In order to identify these pest vulnerable areas, it is important for pest managers to monitor the school for pests. There are many pest monitoring methods including the use of monitoring stations. This is done through monitoring stations placed throughout the school. Typically, the pest vulnerable areas consist of:

- Offices
- Food service areas
- Dry food storage
- Custodial closets
- Classrooms
- Storage areas
- Gyms and locker rooms
- Teachers' lounge
- Landscape

Not only do pest managers monitor for pests, but they look for pest harborage sites as well. Once an infestation is identified, measures are taken to reduce the infestation including exclusion, reduction of food, water and harborage, and the careful use of pesticides, usually in a targeted bait application. By using integrated pest management principles, schools can reduce the numbers of pests as well as maintain a healthy learning environment.

Successful Out-Sourcing of IPM

When discussing the issue of IPM with the purchasing agent it is important to alert the agent that an IPM program can be quite a different method of controlling pests than traditional pest control and therefore requires different contract language. If pest management is to be conducted by a private pest management firm, it is very important that recommendations from the IPM advisory committee and others associated with the school be passed on to both the purchasing agent and the PMP. Ideally, a mechanism for regular feedback from the school (perhaps including the pest sighting log) be part of the contract. If recommendations from the advisory committee are viewed as outside of the scope of service provided by the PMP, these recommendations should be adequately detailed and given to the purchasing agent to consider incorporating into the next pest management contract when contract bids are solicited. Following are definitions and important elements of a model school IPM contract for interior services [lice and termite control are excluded], although they may be adjusted according to needs (e.g., inclusion of outdoor IPM services):

- *Integrated pest management (IPM)*
  IPM is a process through which pest risk is minimized while simultaneously minimizing risk associated with pest treatment such as pesticide exposure. IPM involves several decision-making steps based on all available information to ensure the most appropriate treatment method is employed and students, staff, and faculty are protected from the potential dangers of pests and pesticides.
- *Risk of pest exposure*
  It is recognized that pests present health hazards to the occupants of school buildings. These hazards

exist in the form of insect stings or bites, allergens generated and/or dispersed by insects, or human pathogens mechanically vectored by insects.

- *Risk of pesticide exposure*
  It is recognized that pesticides can present a potential health risk. Depending on toxicity of the pesticide and exposure, pesticides can cause severe harmful effects to humans if misused.
- *Thinking (decision-making process) versus applying pesticides*
  Integrated pest management stands as a contrast to traditional regularly scheduled pesticide applications to structures. Integrated pest management involves preventing pest problems, treating only documented pest problems, treating pest problems through precision targeting with the most appropriate material (least toxic while still being effective) and technique. This process requires decisions to be made at every step. Integrated pest management requires a high level of communication between the pest manager and the school official supervising pest management (IPM Coordinator). Communication between pest managers and school officials should be well documented.
- *Pest prevention and exclusion*
  Exclusion is a method of keeping pests out of structures and therefore preventing pests from becoming an indoor pest problem. Techniques used in exclusion include but are not limited to installing door sweeps to exterior doors to prevent pests from entering the structure under the door, installing hardware cloth to any appropriate opening in structures such as air vents and sealing of exterior windows with appropriate caulking material.
- *Sanitation*
  Sanitation is critical in pest management because food debris left behind by humans often attracts pests. Sanitation improvements that help prevent pests include but are not limited to placing plastic liners in trash cans and removing them daily, placing trash away from any entrance to the structure, keeping trash receptacle lids closed, proper cleaning of the food handling and preparation area daily, and eliminating water sources available to pests in all structures.
- *As-needed application of treatments*
  Only after a pest infestation has been documented through inspection and/or monitoring should a treatment be initiated.

Inspection involves a thorough examination of structures to assess pest identification, pest infestation levels, evidence of pest activity, and identification of potential pest encouraging circumstances. Monitoring is a technique to evaluate the presence/absence of pests, the identification of pests, and the location of pest infestations.

Treatment includes any action that serves to reduce or exclude pest populations.

- *Least toxic methods and non-chemical treatments*
  Several treatments for pest management do not include the use of pesticides. Examples of such treatments include vacuum devices or mechanical traps. Additionally, non-chemical treatments can include structural modifications and sanitation measures.
- *Non-use of space sprays*
  Use of space sprays is not typically considered part of an IPM program. Only on the rarest occasion would this method be considered. Space spraying is the technique of applying liquid pesticides to entire surfaces within a structure including baseboards, floors, and walls.
- *Crack and crevice treatments*
  Crack and crevice treatments intentionally apply pesticides in areas difficult for children to contact. Crack and crevice treatments might include treatment of wall voids, behind electrical outlets, or behind stationary equipment or furniture.
- *Baits*
  Baits are pesticide formulations which contain a pest attractant, a toxicant, and a carrier substance. Baits are generally considered a choice treatment method because they contain relatively small amounts of toxicant and generally are applied such that it is difficult for children to contact any residue. Baits are formulated as granules, gels, liquids, and in containerized stations.
- *EPA hazard categories*
  The use of a Category I pesticide in a school is considered unnecessary and is not part of an IPM

program. Use of a Category II pesticide is considered for use in only those unusual circumstances where alternative treatments have failed. The vast majority of pest management strategies within an IPM program should be adequate utilizing either category III or IV pesticides.

- *Banned products*
  Use of any product being phased out or banned by state or federal agencies is prohibited under this contract.
- *Precision targeting*
  Precision targeting treatments is essential in attaining the most efficient pest management without increasing risk. Precision targeting is placing treatments only where the pests are present and where children are not present. Precision targeting is using the least amount of pesticide necessary to solve the pest problem.
- *Indoor pest control (contract does not include "outdoor"/landscape turf)*
  This contract is for in-door pest control. This contract covers those pests which may occur in classrooms, cafeterias, offices, bathrooms, gymnasiums, locker rooms, and other in-door areas of the school. This contract does not include landscape pest management or turf pest management including athletic fields, playgrounds, and other out-door areas.
- *Service call*
  A service call is that service provided by the contractor outside of regularly scheduled visits generated by contact.
- *Integrated pest management (IPM) coordinator*
  The IPM coordinator is a school official designated to communicate with contractor on school's behalf and supervise contractor's service.
- *Service list*
  The service list identifies all buildings and/or areas to be serviced by the contractor by number or name.
- *Necessary qualifications of service provider*
  Contractor shall possess a certified pest control operator's license. Contractor employees servicing the school must have completed extensive training in Integrated Pest Management. All employees of service provider must possess proper identification and proof of credentials while on school premises.
- *Areas of service*
  This contract for pest management includes all buildings and immediate perimeters of buildings (approximately 5 ft. from exterior walls) on school grounds except those identified by IPM Coordinators as not requiring pest management service. The area of service does not include those areas generally regarded as athletic fields or other outdoor turf areas not associated with buildings. (In some cases the IPM coordinator may wish to include areas designated as "playgrounds" under this contract. This "model" contract should be amended appropriately in those cases). The contractor and IPM coordinator shall agree prior to contract initiation which buildings on school grounds will be under service and which will not. Each building should be identified by number or name and this shall be known as the service list.
- *Specified services*
  The primary service rendered by the contractor in an IPM program is the contractor's knowledge about pests and their management; not the contractor's ability to apply pesticides. The service provided by the contractor will include (i) regularly scheduled inspections, (ii) regular monitoring for pests, (iii) proper identification and treatment of pests consistent with IPM principles and (iv) recommendations to IPM coordinator to reduce future infestations of pests.

Regularly scheduled inspections will consist of examining the entire inside and outside of all buildings on the service list for pests or evidence of pest activity not less than once per month. During inspection, the contractor will complete an inspection form for each building. On the inspection form the contractor will report the date and time of the inspection and any pests observed or evidence of pest activity. The contractor will report any structural features that could be improved to prevent current or future pest problems. The contractor will report on the inspection form specifically where within the building any pests were observed and specifically where the structural improvements should be made. In addition, the contractor will report results of monitoring devices placed within the building. Copies of all inspection forms will be made available to IPM coordinator upon completion of inspection and signed by the contractor and IPM coordinator documenting communication. The IPM coordinator will maintain these records at a central location for a minimum of 1 year. It is recommended that the contractor maintain records of all inspections as well. As a part of the inspection service, the contractor will also inspect the Pest Sighting Form for each location where a Pest Sighting Form exists. The contractor will use the information provided on the Pest Sighting Form to aid in locating pest infestations. The contractor will initial his/her name next to each pest sighting recorded in the Pest Sighting Form upon completing investigation of that pest sighting.

Regular monitoring for pests will provide documentation of where and when pests occur and will help to focus treatment efforts to only those areas which are infested. Monitoring may include the use of devices known as "sticky traps" or "trap monitors." These devices contain no pesticides but have sticky surfaces such that pests are retained within the device. The types of monitors and the number of monitors placed in each building on the service list should be agreed upon by the contractor and IPM coordinator at the time of contract "signing." As a default setting, no fewer than ten monitors should be used in school cafeterias or lunchrooms (including food storage areas) and all other rooms (classrooms, teacher's lounges, offices, vending machine areas, custodial closets,) etc. monitored with no fewer than two monitors each. The number of monitors placed in each room and the exact location of each monitor within each room can be modified by the contractor as deemed appropriate. Monitors are to be inspected not less than monthly by the contractor and results of monitors reported on the inspection form. The type and number of pests observed through the monitoring program should be reported on the inspection form. The specific location of the monitors with pests should be noted on the inspection form. Monitors should be in good working condition at all times. Any change in overall monitoring program should be communicated to the IPM coordinator on the inspection form.

Correct identification of pests and proper treatment is crucial. Upon properly identifying the pest, the contractor will determine the most effective method of treating the pest problem considering specific pest behavior, biology, location within structure, and potential health hazards of the pest and treatment. The first consideration for solving the pest problem will always be a treatment without using pesticides. Such treatments are sanitation, the use of vacuum devices, mechanical traps, or mechanisms for exclusion. If the contractor determines that a pesticide treatment will be necessary, the contractor should evaluate the various products labeled for use in the specific circumstance and make a decision on which product and treatment method is most appropriate considering potential health hazards of the pest and the treatment.

If a treatment will include the use of a pesticide not formulated as a bait or in a containerized bait station, a consideration may be to have the contractor notify the IPM coordinator prior to application. If the treatment will include only a pesticide formulated as a bait or in a containerized bait station the contractor does not have to notify the IPM coordinator prior to application.

All treatments, whether including a pesticide or not, must be reported on the Record of Treatment form. Copies of the Record of Treatment form should be made available to the IPM coordinator immediately upon completion of the treatment.

The contractor shall make recommendations to the IPM coordinator regarding unsatisfactory structural features which unnecessarily attract, encourage, support, provide entry to, or otherwise increase the levels of pest infestation. These features are termed conducive conditions. The contractor will report such recommendations to the IPM coordinator using the Pest Proofing form. The contractor shall complete this form as necessary during regular inspection periods. The contractor should record which building and a specific location within the building where the pest conducive condition(s) exists and provide details on what kind of pest(s) may be influenced and why.

- *Inspection form*
  Inspection forms should be used by the contractor to record any pest activity or evidence of pest activity during inspection periods. The inspection form should indicate the date and time of the inspection, building number, specific location within the building, type of pest observed, and an assessment of the level of infestation. Copies of all inspection forms should be made available to the IPM Coordinator immediately upon completion of all inspections. Any treatments performed by the contractor upon completion of an inspection should be justified by reported sightings of pests on the Inspection Form.
- *Pest Sighting Form*
  A Pest Sighting Form shall be placed in a central location within each school, building, or room as determined most appropriate by the contractor and IPM coordinator. A Pest Sighting Form is to be the responsibility of a predetermined individual for each location where a Pest Sighting Form exists. All employees of the school working within that area are to be notified of the existence of the Pest Sighting Form and report any pest sightings to this individual. When pest sightings are reported this individual should then enter the date, time, specific location, and estimated type of pest sighted on the Pest Sighting Form. The Pest Sighting Form must be made available to the contractor during treatments or scheduled inspections.
- *Pest Proofing Form*
  A Pest Proofing Form should be used by the contractor to communicate possible structural modifications which would improve pest management. During regular inspections the contractor should identify specific locations and conditions within buildings which require attention by IPM coordinators. Copies of the Pest Proofing Form should be made available to the IPM coordinator upon completion of inspections.
- *Record of treatment*
  A Record of Treatment form should be completed by the contractor whenever treatment is enacted to correct a pest problem. Details of the treatment such as date, time, building, location, type of pest, method of treatment, and any materials used should be reported on the Record of Treatment Form. Copies of this form should be made available to the IPM coordinator immediately upon completion of the treatment.
- *Notification of pesticide applications*
  The IPM coordinator may want to be notified prior to insecticide applications. If targeted applications are used, such as crack and crevice bait applications, the need for prior notification may be unnecessary. Notification shall include type of material used, building, location, and time of treatment. It is the responsibility of the IPM coordinator and the Contractor to ensure that all treatments are in compliance with local, state, and federal law regarding notification requirements to parents and students. A well-structured mechanism should be in place, regarding proper notification guidelines, prior to contract initiation.
- *Materials used for service/treatment*
  No Category I pesticides shall be used on school grounds. EPA Category II pesticides shall be used only after consideration of less toxic alternatives. If pesticides are regarded as being a necessary component of the treatment then the contractor shall use primarily EPA Category III or IV products.
  Monitoring devices include those devices which

contain no pesticides but collect samples of pests. These are commonly known as sticky traps, capture devices, or pheromone traps.

Any device or product, not excluded above, which has been registered by appropriate regulatory agencies which the contractor has determined is a proper component of an integrated pest management program.

- *Methods of service/treatment*
  Contractor's first consideration in all treatments should include non-pesticidal solutions. If the treatment requires use of pesticides, the contractor shall evaluate the most appropriate method considering potential health hazards of the pest problem and those associated with the treatment. All methods of service and/or treatment shall be in accordance with Integrated Pest Management.
- *Timing of inspections/monitoring*
  Inspections by the contractor shall be conducted during regular business hours to facilitate access to buildings and communication between school employees. Additional inspections deemed necessary by the contractor outside of regular business hours should be arranged through the IPM Coordinator.
- *Timing of treatments*
  No pesticide, with the exception of crack and crevice gels, containerized baits, or in an emergency situation, is to be applied in any room or area while in use or occupied by faculty, staff, or students. Contractor will make attempts at conducting pesticidal treatments at times such that the potential of faculty, staff, or students being contacted by treatment residues are minimized. Contractor will follow all requirements present on product labels regarding re-entry periods. Contractor should make every effort to treat areas when not occupied.
- *Service calls*
  Service calls will be conducted after IPM Coordinator has contacted the contractor regarding a pest problem that requires immediate attention. The contractor will address service calls using the same procedure as described under "Specified Services."
- *Pests included/excluded under this contract*
  Contractor shall adequately suppress the following pests:

Indoor populations of cockroaches, ants, flies, silverfish, wasps, spiders, rodents, or other arthropods not excluded below. Also, insects such as red imported fire ants that may nest primarily outdoors but forage around building perimeters and indoors should be managed.

Pests excluded in this contract

- Vertebrate pests other than rodents
- Termites or other wood destroying organisms
- Head lice
- Pests that primarily feed on outdoor vegetation

- *Evaluation and Review*
  Periodic evaluation of contractor's service by IPM coordinator shall occur no less than three times per year and consist of a review of (i) materials/methods used, (ii) level of communication, and (iii) pest sightings by school staff.

IPM Coordinator shall review the methods of pest management being utilized based on records that appear on Inspection Forms, Treatment Forms, Pest Proofing Forms, and Record of Treatment Forms. Any concerns regarding contractor's treatment strategies should be communicated to the contractor at this time. IPM Coordinator shall review all records and forms provided by the contractor for the previous service period and confirm adequate details exist describing the types of service being provided by the contractor. Any changes to documentation forms deemed necessary by the IPM Coordinator should be communicated to the contractor at this time. The IPM Coordinator shall review Pest Sighting forms and anecdotal records to evaluate contractor's ability to address pest sightings by school staff.

► Urban Entomology
► Cockroaches
► Ants
► Human Lice
► Integrated Pest Management (IPM)

References

IPM Strategies in Institutional Settings CD. http://ifasbooks.ufl.edu
US Environmental Protection Agency, School IPM Website: http://www.eps.gov/pesticides/ipm/
Mallis A (2004) Handbook of pest control: the behavior, life history, and control of household pests. GIE Media, Cleveland, OH, USA, 1397 pp
National Pest Management Association (NPMA) (1998) Urban IPM Handbook: An Integrated Approach to Management of Pests In and Around Structures. Dunn Loring, VA, USA, 149 pp
National School IPM information source website: http://schoolipm.ifas.ufl.edu/
Texas A&M University (1997) The ABCs of IPM. Integrated pest management for schools, DVD

Schreckensteiniidae

A family of moths (order Lepidoptera). They are commonly known as bristle-legged moths.

► Bristle-Legged Moths
► Butterflies and Moths

Schwarz, Eugene Amandus

Eugene Schwarz was born in Liegnitz, Germany, on April 21, 1844. He was educated at the University of Breslau and University of Leipzig. He moved to the United States in December of 1872. He left Germany because he had deceived his father, who expected his son to study philosophy when, in fact, he studied zoology and entomology. Schwarz joined the Museum of Comparative Zoology at Harvard University in 1872, and initially worked as a preparator. He moved to Detroit where he co-founded the Detroit Scientific Association and helped initiate the Hubbard-Schwarz collection of Coleoptera. In association with this effort many collecting trips were made in the Great Lakes region and to Florida. Beginning in 1878 he was employed by the Division of Entomology of the United States Department of Agriculture, and he remained in this capacity for most of the period of employment, which ended with retirement in 1926. During the early years of his employment he studied cotton pests in the southern United States, and fig pests in California. His principal interest, however, remained the systematics of Coleoptera, and he amassed a large collection in the U.S. National Museum, where he was named curator of Coleoptera. He was one of the founders of the Entomological Society of Washington and reportedly had significant influence in the Department of Agriculture and National Museum. Schwarz published 395 papers over the course of his career. He died at Washington, DC, on October 15, 1928.

References

Essig EO (1931) A history of entomology. Macmillan, New York, 1029 pp
Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Sciadoceridae

A family of flies (order Diptera).

► Flies

Sciaridae

A family of flies (order Diptera). They commonly are known as dark-winged fungus gnats.

► Flies

Scientific Name

A Latin or Latinized name given to all biological organisms and consisting of two parts, a genus and species. The first of the two names is the genus and is capitalized. The second is the species and is not capitalized. Both words are italicized. The author's name (the person who first provided a technical description of the species) often follows the scientific name. If the genus name has been changed since the organism was named by the author, then the author's name is placed in parentheses to indicate that a change has been made. When several species in the same species are discussed together, then "species" may be abbreviated spp. For example, in discussing the genus *Spodoptera*, we might refer to the members as *Spodoptera* spp. On the other hand, a single species is indicated as "sp."

► Scientific Names and Other Words from Latin and Greek

Scientific Names and Other Words from Latin and Greek

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These words are often misused by people who do not understand the rules governing them. The rules are explained here simply.

Words from Latin and Greek Adopted into English & Singular and Plural Forms

Words such as larva, sensillum, and elytron appear to be Latin or Greek. Many of them were invented by scientists and were never part of classical Latin or Greek. They were invented because new words were needed to name newly described structures. For hundreds of years they had to be in Latin (or Greek) because books about biology and medicine were written in Latin (with a few entries in Greek), which was the international language of science. When such books began to be written in English, those invented words were not changed. Instead they were adopted into English. More were added later, also with a Latin or Greek origin, because by then the tradition was to use words of that form.

Most English nouns form the plural by adding -s (or -es) to the singular. There are exceptions (man, ox, goose, mouse, etc.) but these are relatively few.

However, almost all words adopted from Latin or Greek still form their plural in the way this is done in Latin or Greek, not by adding -s. Exceptions are the words abdomen and trochanter, whose English plurals are now spelled by adding -s.

If you have studied Latin you will know that you need to remember only a small subset of that grammar to use the correct singular or plural form of each word. Some of those words are shown in the table below, in two columns, giving the singular and plural forms that may be memorized. They are grouped (by their last letters) according to their placement in Latin grammar, which helps to place others of similar form.

The form of these words is not fixed because poorly trained news writers commonly use the plural forms algae, bacteria, data, larvae and media as if they were singular. This misuse confuses a large audience and may influence the future direction of English.

Words that are Considered to be Latin (Not English)

Scientific (Latin) names of insects and other animals are either singular or plural, not both. Whether they are singular or plural depends upon the rank (species, genus, tribe, family, etc.).

Names of species are singular

Danaus plexippus is (not are) a species of butterfly

The name of each and every species consists of two words. These two words are conventionally printed in italic font. When written by hand or typed on a typewriter, they are underlined, which indicates to a publishing company that they should be set in italics. The two words are normally written or printed using upper and lower case (large and small letters), and then the first letter of the first word should be capitalized, and the first letter of the second word should not be capitalized. In titles, all letters of both words may be capitalized.

When upper and lower case letters are used, it is incorrect to capitalize the first letter of the

Scientific Names and Other Words from Latin and Greek, Table 4 Singular and plural forms of some words from Latin

Singular (is)	Plural (are)
alumnus	alumni
circus	cerci
fungus	fungi
ocellus	ocelli
palpus	palpi
tarsus	tarsi
alga	algae
alumna	alumnae
coxa	coxae
[a]	exuviae
lamella	lamellae
larva	larvae
maxilla	maxillae
pupa	pupae
seta	setae
tibia	tibiae
agendum[b]	agenda
bacterium	bacteria
cilium	cilia
datum[b]	data
flagellum	flagella
labium	labia
medium	media
labrum	labra
ommatidium	ommatidia
operculum	opercula
ovum	ova
sensillum	sensilla
sternum	sterna
tergum	terga
tympanum	tympana
foramen	foramina
corpus	corpora
femur	femora
genus	genera
[c]	faeces

Scientific Names and Other Words from Latin and Greek, Table 4 Singular and plural forms of some words from latin (Continued)

Singular (is)	Plural (are)
	feces (american)
axis	axes
penis	penes
species	species

[a]the singular does not exist
[b]the singular is rarely used in English
[c]the singular is not used in English

Scientific Names and Other Words from Latin and Greek, Table 5 Singular and plural forms of some words from Greek

Singular (is)	Plural (are)
chrysalis	chrysalids
	(or chrysalides)
proboscis	proboscides
criterion	criteria
elytron	elytra
ganglion	ganglia
protozoon[a]	protozoa
stemma	stemmata
stigma	stigmata
stoma	stomata
thorax	thoraces
	thoraxes (American)

[a]protozoan is an English word formed from Protozoa

second word of the name of a species of insect or any other animal (according to current and recent editions of the International Code of Zoological Nomenclature). The rules of botanical nomenclature differ, so that it is permitted for names of certain plants, and it once was permitted to do the same for some animals.

The convention of putting these words into italics came about to indicate that these words are

Latin, not English. Neither of the two words may have any diacritical mark (accent) because Latin has none.

The first word of a species name is the name of the genus to which it belongs. The second word of a species name has variously been called the specific epithet, the trivial epithet, or even the "specific name" although this last is a confusing term (because it is not the name of a species).

Most if not all scientific journals require that the name of a species be spelled out in full at its first mention in a text. In subsequent uses of the name in the same text, it may be abbreviated by reducing the generic name to a single capital letter followed by a period (full stop), as in:

D. plexippus

Some entomologists have adopted other conventions for abbreviating generic names of insects (for example, mosquitoes) in the names of species.

Names of genera, too, are considered to be Latin, are conventionally italicized, and are singular:

Names of genera are singular

Danaus is (not are) a genus of butterfly

Names of all Higher Categories are Plural:

The Latin (or Greek) terminations of these scientific names make it plain that they must be treated as singular (species and genera) or plural (all higher categories). Article 11.7 of ICZN (1999) declares that "family-group names" (names of tribes to families) must be in the nominative plural (see a Latin grammar for further explanation), so cannot be construed as singular.

To follow the rules, we must write "Coleoptera are a huge order" and "Culicidae have many species that transmit disease." Why, then, do some people write "Coleoptera is a huge order" or "Culicidae has many species that transmit disease?"

Scientific Names and Other Words from Latin and Greek, Table 6 Names of tribes, families, orders, classes and phyla are plural

Tribe:
Brachinini are (not is) the bombardier beetles
Subfamily:
Cicindelinae are (not is) the tiger beetles
Family:
Culicidae are (not is) the mosquitoes
Order:
Plecoptera are (not is) the stone flies
Class:
Insecta are (not is) the insects
Phylum:
Arthropoda are (not is) a phylum of invertebrates

There seem to be three reasons why some writers treat these words as singular:

1. They have not learned that the words are plural. This is quite common among students. Even some more experienced writers thoughtlessly copy the erroneous style of earlier writers.
2. They argue that when they write "Coleoptera is speciose," what they really mean is "the order Coleoptera is speciose," but scientific writing should have no hidden meanings, so this excuse is not valid.
3. They perversely refuse to accept what they are told are the established rules, or want to flaunt their ignorance of Latin and Greek and disdain for the International Code of Zoological Nomenclature, and want to make their own rules.

It is of course acceptable to write "the order Coleoptera is speciose."

Another error is made by students in such expressions as "A Culicidae was seen feeding" by which they mean a mosquito (not the whole family!) was seen feeding. This may be written as "a culicid was…" or "a mosquito was…" or "an individual of the family Culicidae was…" or "individuals of a species of Culicidae were…"

Although the names of higher categories (tribe and above) are considered to be Latin, they are not conventionally printed in italic font. Each must have a capital initial letter.

References

Brown RW (1956) Composition of scientific words, 2nd edn. Published by the author, Baltimore, MD, 882 pp

International Commission on Zoological Nomenclature (ICNZ) (1999) International code of zoological nomenclature. International Trust for Zoological Nomenclature, London, UK, xxix + 306 pp

Sciomyziidae

A family of flies (order Diptera). They commonly are known as marxh flies.

► Flies

Scirtidae

A family of beetles (order Coleoptera). They commonly are known as marsh beetles.

► Beetles

Sclerite

A rigid section or plate of cuticle forming a component of the insect's body wall, and bounded by sutures or membranous areas.

Sclerogibbidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Sclerotin

Cuticular protein that has been irreversibly hardened and darkened by chemical cross-linking of the molecules.

Sclerotization

The process of sclerotization, or tanning, results in the hardening of the cuticle after an insect molts. Sclerotization involves the cross-linking of proteins, aided by quinones, which typically contribute to the darkening of the cuticle.

Scolebythidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Scoliidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Scolopidium (pl., scolopidia)

A mechanoreceptor sensillium located beneath the cuticle that perceives vibration, stretch or pressure.

Scolus (pl., scolli)

An extension of the integument, in the form of a projection or tubercle, that bears stout setae. These are found on some highly spinose insects, such as the caterpillars of Saturniidae.

Scolytidae

Considered by some to be a family of beetles (order Coleoptera). They commonly are known as bark beetles or ambrosia beetles. Here they are treated as a subfamily (Scolytinae) of Curculionidae.

► Beetles

► Weevils, Billbugs, Bark Beetles and Others

Scopa

Patches of branched hairs occurring on the body of bees, and used to collect and hold pollen. The location of the scopa varies among bees.

Scopuridae

A family of stoneflies (order Plecoptera).

► Stoneflies

Scorpionflies (Mecoptera)

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This is a small, primitive order of holometabolous insects. Some scorpionflies are known as hangingflies or earwigflies. Mecoptera are small to moderately large in size, ranging in body length from 2 to 35 mm. The order name is derived from the Greek words *mecos* (= length) and *pteron* (= wing). At present there are approximately 600 known, extant species arranged in 34 genera and 9 families worldwide. Two families, Panorpidae and Bittacidae, comprise most of the species. During recent decades, increasing taxonomic information on extant Mecoptera has necessitated a reevaluation of the systematics and evolution of this group. Traditional "Mecoptera" lack defining, unifying characters, thus they may not represent a monophyletic grouping. Recent DNA and older morphological data suggests that Mecoptera (particularly Boreidae) are closely related to fleas (Siphonaptera). It is also likely that Nannochoristidae, and perhaps Boreidae, typically hypothesized to represent basal mecopteran taxa, may be part of a distinct order. Molecular support for a monophyletic grouping known as the Antiliophora (Diptera and (Mecoptera + Siphonaptera)) is strong. The Antiliophora in turn share a common ancestry with Amphiesmenoptera (Trichoptera and Lepidoptera).

The origin of Mecoptera may still be in doubt and fossil evidence of "Protomecoptera" is confusing, but the earliest fossils originate in the lower Permian geological period (approximately 270 million years ago). Mecoptera are well represented in sedimentary rocks of the lower Permian, and based on additional fossil records, were relatively abundant insects during the Mesozoic Era. The extant family Meropeidae, has been hypothesized to have arisen in the Paleozoic Era, and was once thought to represent living Protomecoptera, but currently only thought to be basal to more derived Mecoptera. There are nearly 400 known fossil species in approximately 87 genera and as many as 34 families (although researchers disagree on the exact number of extinct families) exhibiting a greater diversity than extant mecopteran taxa.

Worldwide, Mecoptera distributions presently show two divergent trends: greater diversities of families and genera exist in the Australian, Nearctic, and Neotropical regions, with relatively few species (approximately 30% of all of the known mecopteran species); slightly less diversity at the familial and generic levels occurs in the Ethiopian, Oriental, and Palearctic regions, with a greater diversity at the species level. Mecoptera are largely absent on islands; for example, no species are known from Madagascar, and they are known only from Trinidad in the Caribbean. In most island areas where Mecoptera are represented (e.g., Japan, Taiwan, Trinidad), there is a geological history of relatively recent land connection to the adjacent continent, suggesting that Mecoptera are poor dispersers.

Carl Linnaeus described and named the first mecopterans in the eighteenth century, and at that time he placed these European taxa (i.e., *Panorpa communis*, *P. germanica*, *Boreus hyemalis*) in the order Neuroptera. North American Mecoptera were first described by N. Swederus, and since that time several prominent American and European entomologists have worked within the order. Nathan Banks, J.S. Hine, and

P. Esben-Petersen published catalogs and described several species, F.M. Carpenter revised the Nearctic Mecoptera fauna and published several papers on their distributions, and G.W. Byers has published numerous papers on world-wide mecopteran fauna covering a wide variety of topics and has described many species. Comprehensive, regional studies on Mecoptera have been published by Byers (Africa and Southeast Asia), C.-S.H. Chau and Byers (Indonesia), T. Miyaké (Japan), and E.F. Riek and C.N. Smithers (Australia). The morphology of Mecoptera has been fairly well described (Fig. 18), and research completed by G.C. Crampton on genitalia, E. Potter on reproductive and digestive tracts, H.R. Hepburn on the adult skeletomuscular system, and R. Willmann on several internal and external structures has provided useful taxonomic information pertinent to present day mecopteran systematics.

The ancient origin of Mecoptera has allowed for the evolution of diverse life histories and morphologies. Approximately one-fifth of the genera have acquired flightlessness (e.g., Apteropanorpidae [*Apteropanorpa*], Boreidae [including *Boreus*], Bittacidae [*Apterobittacus*], and Panorpodidae [some species of female *Brachypanorpa*]), two families have adapted to cold climates (Boreidae and Apteropanorpidae), two others are cockroach-like (Meropeidae and Eomeropidae), and some have predaceous life stages (Bittacidae and Nannochoristidae) while most are saprophagous or herbivorous. The diversity of forms and behaviors in this small insect order may indicate that these taxa are the remnants of a nearly extinct group.

Extant Mecopteran Families and their Continental Distributions

Order Mecoptera

- Family Nannochoristidae – southeastern Australia, Tasmania, New Zealand, and southern South America
- Family Bittacidae (hangingflies) – North America, South America, Europe, Africa, Asia, and Australia
- Family Boreidae (snow scorpionflies, "snow fleas") – mostly boreal and montane North America, Europe, and parts of Asia
- Family Meropeidae (earwigflies) – eastern North America and southwest Western Australia
- Family Eomeropidae – southern South America
- Family Apteropanorpidae (wingless scorpionflies) – Tasmania, Australia
- Family Choristidae – southeastern Australia
- Family Panorpodidae (short-faced scorpionflies) – Appalachian region and Pacific Northwest of North America, eastern Asia
- Family Panorpidae (scorpionflies) – North America, Europe, Asia

Characteristics and Life History

Eggs are generally ovoid and smooth to finely reticulate. At oviposition, the chorion is smooth, only lightly sclerotized, and usually whitish to yellowish-brown in many groups. Eggs vary in size between and within species and are deposited in a variety of ways. Some are placed in loose cavities in the soil (*Panorpa* spp.), dropped randomly to the ground (*Bittacus* spp.), or are deposited in rows on leaf litter near water (*Nannochorista* spp.). *Boreus* place their eggs singly or in small clusters near the stem bases of mosses on which the larvae will feed. The duration of the egg stage varies greatly, depending on the species and environmental conditions. In *Panorpa*, duration can range from 5 to 10 days for many species. In contrast, the eggs of *Boreus* laid in early winter may not hatch until the following spring.

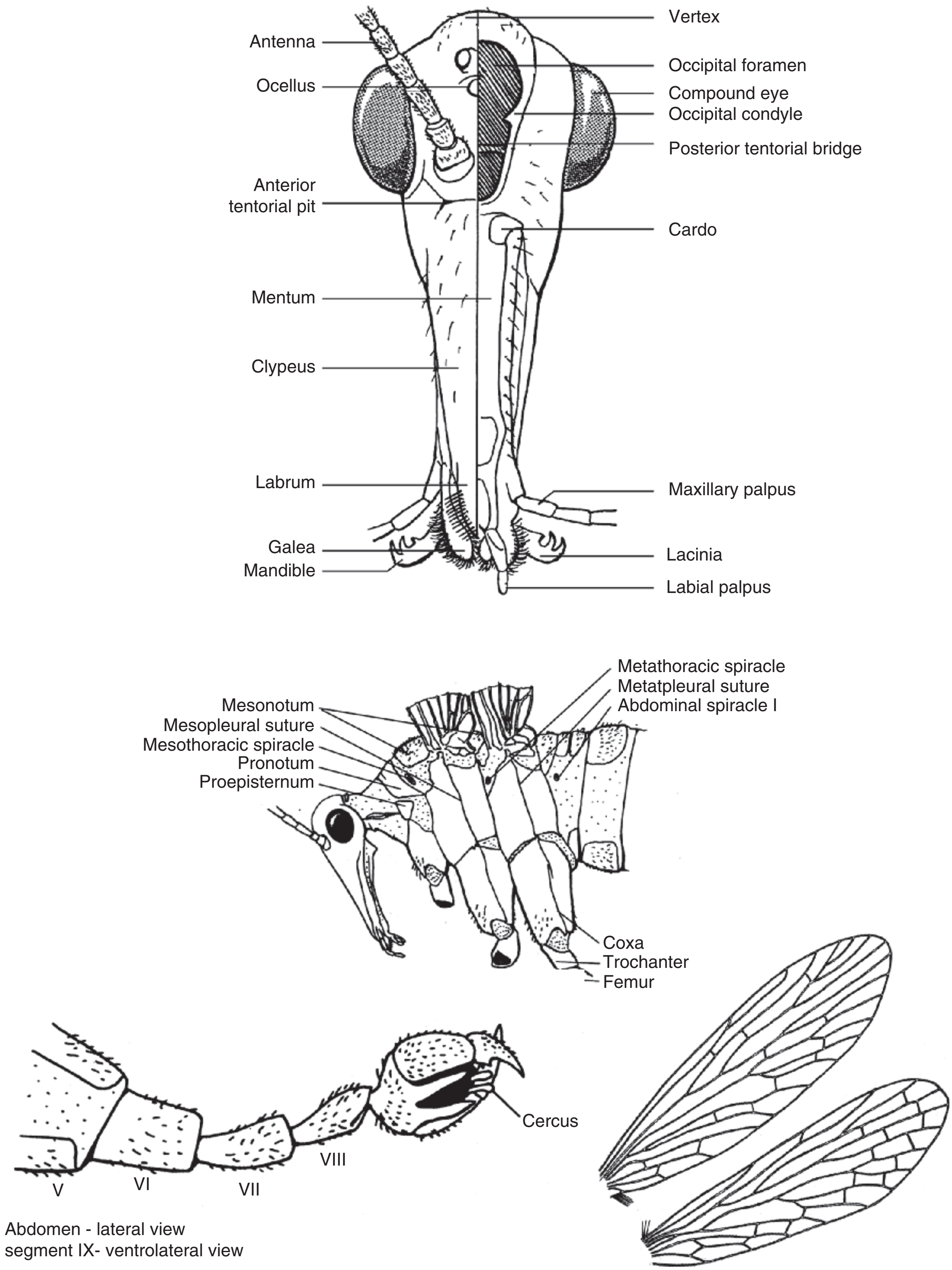
Larval Mecoptera are generally eruciform or caterpillar-like (e.g., Panorpidae, Bittacidae), while a few groups are grub-like in form (e.g., Boreidae, Panorpodidae). There are fleshy or setiform projections on the larvae in many groups and these may be used taxonomically. Larvae bear a well-sclerotized head capsule with compound eyes comprised of 3–30 ommatidia, or eyes may be absent (e.g., Panorpodidae: *Brachypanorpa* and *Panorpodes* spp.). Many groups have thoracic legs and fleshy prolegs on the first eight abdominal segments, or in some taxa the prolegs are absent (e.g., Nannochoristidae). *Panorpa* larvae pass through four instars and will remain in a prepupal diapause for as long as 7 months to overwinter. The larvae of Meropeidae (*Merope tuber* and *Austromerope poultoni*) and Eomeropidae (monotypic: *Notiothauma reedi*) are unknown.

The pupal stage is exarate in form (adult-like and capable of abdominal movement) with the wings compactly folded in sheaths. The mandibles are decticous (able to move) and are larger, and more larval-like than adult-like. Pupation typically occurs in a cell or burrow prepared by a fourth instar larva. Some bittacids cover their dorsal parts in fecal and soil particles. The time from pupal ecdysis to adult emergence varies between groups; it ranges from 10 to 21 days in *Panorpa*, 15–24 days in *Bittacus*, 14–50 days in *Harpobittacus*, or 37–40 days in *Boreus*.

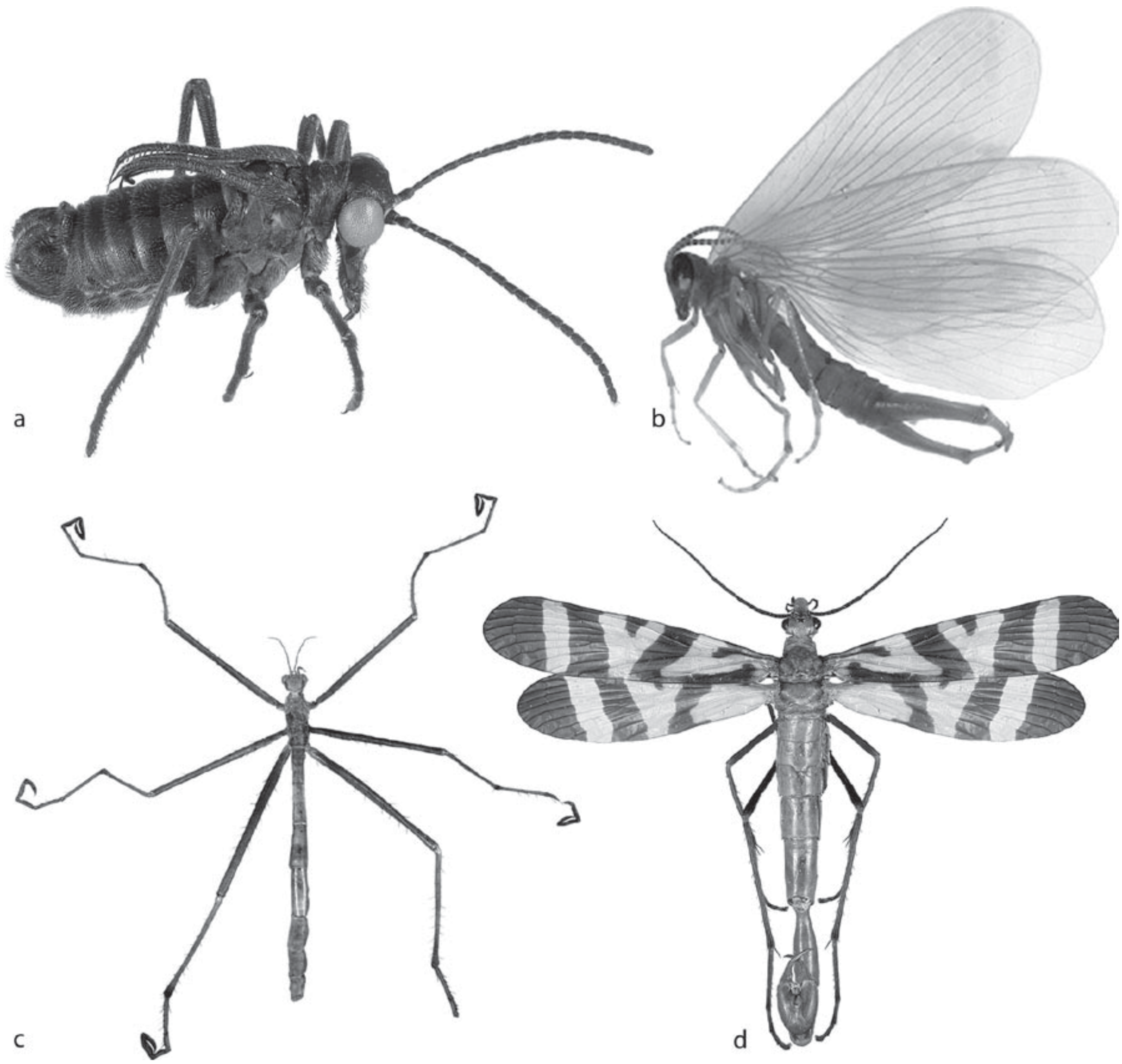
Adult Mecoptera are largely defined on the basis of wing venation and tarsal structure, but have undergone relatively few structural changes since their first appearance geologically (Fig. 18). At the family level, extant Mecoptera are significantly diversified. *Boreus*, *Panorpa*, and *Neopanorpa* possess a distinct rostrum or "beak," but the heads of *Panorpodes* are comparatively less specialized and orthopteran-like in form. Compound eyes are typically large and many species bear three ocelli (these reduced or absent in *Boreus*, Meropeidae, and Apteropanorpidae). In general, Mecoptera have chewing mouthparts with short mandibles in phytophagous taxa, longer mandibles in saprophagous taxa, and elongate and blade-like mandibles in carnivorous groups such as bittacids. The nannochoristids have short but sharp mandibles that may be functionless. Antennae are typically filiform with the scape and pedicel enlarged, and depending on the taxon, range from 14 to 60 flagellar segments (Fig. 19).

The thorax is elongate in some groups (i.e., Panorpidae, Bittacidae, Choristidae) with the pronotum generally saddle-like, wider than long, and often with transverse ridges. Adult legs bear 5-segemeted tarsi with the basitarsus usually the longest. The pretarsus has two claws, except in Bittacidae, where a single, large claw is located at the end of each tarsus. Mecoptera have four membranous wings with several crossveins, and many species bear spots or transverse, colored bands. Hindwings are slightly shorter than the forewings and usually have similar markings. A few species are apterous (e.g., *Apteropanorpa*, *Apterobittacus*, and some female *Brachypanorpa* spp.) or brachypterous (e.g., *Boreus* spp.). The forewings and hindwings are not effectively coupled in flight, but there is a jugal lobe located on the forewing and stout setae at the base of the costal margin of the hindwing. *Merope tuber* has an enlarged jugal lobe that is utilized for stridulating against ridges located on the thorax (Fig. 20), hypothetically for communication between the sexes.

The abdomen is 11-segmented and is often slightly constricted at the attachment of the thorax. A genital bulb, resembling that of a scorpion "stinger," is located on the ninth abdominal segment of male panorpids, giving rise to the vernacular name "scorpionflies." Similar but less pronounced male genital morphology can be found in apteropanorpids, panorpodids, and boreids. Adult longevity depends in large part to reproductive biology, as males in certain groups may engage in risky activities associated with mating. For example, male meropeids have clasper-like terminal abdominal segments (see also, Earwigflies) that hypothetically may be used in male-to-male combat for females. Adult longevity in *Panorpa nuptialis* rarely exceeds a month, while adult *Hesperoboreus notoperates* in southern California can be observed from November to March. Under laboratory conditions, adults of various Mecoptera species are reported to live for 2–3 months.



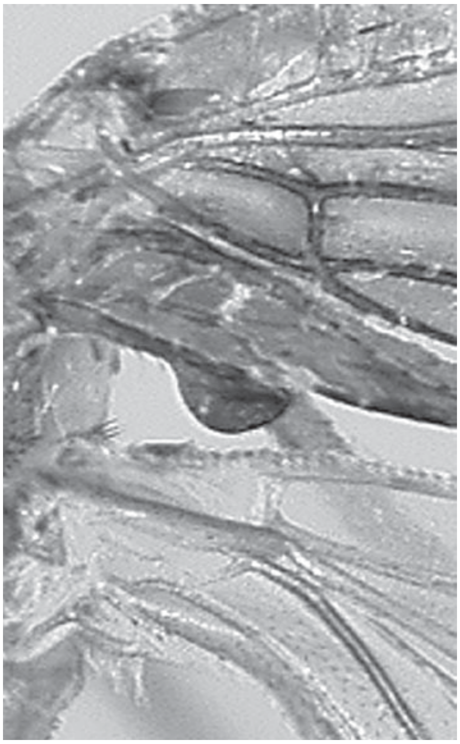
Scorpionflies (Mecoptera), Figure 18 **Morphology of adult scorpionfly (Mecoptera: Panorpidae): *above*, the head, showing anterior aspect on left, and posterior aspect on right; *center*, lateral view of the thoracic region; *lower left*, lateral view of the tip of the male abdomen; *lower right*, the front and hind wings.**



Scorpionflies (Mecoptera), Figure 19 **Scorpionflies: (a) *Boreus coloradensis* (Boreidae), male; Montana, USA (image by James C. Dunford); (b) *Merope tuber* (Meropeidae), male; Wisconsin, USA (image by Steven J. Krauth); (c) *Apterobittacus apterus* (Bittacidae), female; California, USA (image by James C. Dunford); (d) *Panorpa nuptialis* (Panorpidae), male; Missouri, USA (image by James C. Dunford).**

Biology

Most Mecoptera inhabit moist environments, although a few species inhabit semidesert environments. Adults are frequently associated with broad-leaved plants, and can be occasionally observed in open, sunny areas. Scorpionflies (Panorpidae) are likely to be encountered in wooded habitats where there are deciduous trees growing in rich, shaded soils. Boreid adults occur in the winter months, and in montane habitats are often seen on the surface of snow or on mosses in which the larvae feed and can jump like fleas. Bittacids are known to inhabit grasslands, forests, and caves where high moisture levels occur. Since most mecopterans inhabit moist forests, any disturbance reducing moisture levels (i.e., deforestation) could adversely affect or extirpate the Mecoptera present. In general, Mecoptera are weak fliers, and dispersal can be severely limited if suitable habitat is reduced.



Scorpionflies (Mecoptera), Figure 20 Jugal lobe located on base of *Merope tuber* forewing (image by David Serrano).

The larval stage is often difficult to locate and unknown in some families, but they typically occur in mosses, dead leaves, and in soil cover in wooded areas. At least one species of nannochoristid, *Nannochorista philpotti*, has aquatic larvae. Many mecopteran species feed on decaying vegetation, or dead or dying soft bodied arthropods as larvae and/or adults; some groups are reported to feed on nectar, pollen, carrion, mosses, and larval midges, or less often dead mice and frogs. Bittacidae bear modified legs for grasping and holding prey such as Diptera, Hymenoptera and Lepidoptera. Kleptoparasitic *Panorpa* scorpionflies are known to feed on dead or dying insects captured in spider webs as well as the spiders inhabiting the web.

The males in many genera (e.g., *Panorpa*, *Bittacus*) emit pheromones to attract females, in some cases from several meters in distance. Mating behavior usually involves an offering of food from the male, and this is often a dead insect or a brown salivary secretion. The males of many boreid species bear slender, hook-like wings that are used to carry females on their backs during mating. Males are reported to run alongside the female for a short distance and then grapple with and grasp the female at the base of the abdomen with their modified wings, placing the female upon their backs during copulation. Male *Panorpa* vibrate their wings rapidly, and some species may stridulate as they approach the female and seize them just before copulation takes place.

A few natural enemies of Mecoptera have been reported in the literature, such as web-building spiders, damselflies, reduviid bugs, and asilid flies. Hymenopterous parasitoids are reported in some *Boreus* larvae. Although no economic importance is associated with Mecoptera, predatory *Harpobittacus nigriceps* (Bittacidae) adults have reportedly interfered with the biological control of ragwort by feeding on the cinnabar moth in Australia, and Bittacidae may be regarded as beneficial as they are known to feed on adult mosquitoes. Although Mecoptera are of little apparent economic significance, they represent a systematically and biologically important, ancient insect lineage.

► Earwigflies

References

Byers GW (1994) Mecoptera (scorpion-flies, hanging-flies). In: Naumann ID (ed) Systematic and applied entomology: an introduction. Melbourne University Press, Carlton, Australia, pp 365–368

Byers GW, Thornhill R (1983) Biology of the Mecoptera. Ann Rev Entomol 28:203–228

Cooper KW (1940) The genital anatomy and mating behavior of *Boreus brumalis* Fitch (Mecoptera). Am Midland Nat 23:354–367

Grimaldi D[A], Engel MS (2005) Evolution of the insects. Cambridge University Press, Cambridge, UK, 755 pp

Kaltenbach A (1978) Mecoptera (Schnabelhafte, Schnabelfliegen). Handbuch der Zoologie 4(2) (2/28):1–111

Novokschonov VG (2002). Order Panorpida Latreille, 1802. The scorpionflies. In: Rasnitsyn AP, Quicke DLJ (eds) History of insects. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 194–199

Palmer CM, Yeates DK (2005) Diet and feeding behavior in adults of the Apteropanorpidae (Mecoptera). J Insect Behav 18:209–231

Penny ND (1975) Evolution of the extant Mecoptera. J Kans Entomol Soc 48:331–350
Penny ND (1977) A systematic study of the Boreidae (Mecoptera). Univ Kans Sci Bull 51:141–217
Penny ND, Byers GW (1979) A check-list of the Mecoptera of the World. Acta Amazon 9:365–388
Whiting MF (2002) Mecoptera is paraphyletic: Multiple genes and phylogeny of Mecoptera and Siphonaptera. Zool Scripta 31:93–104
Willmann R (1989) Evolution und phylogenetisches System der Mecoptera (Insecta: Holometabola). Abhandl Senckenberg Naturforsch Gesellsch (544):1–153

Scorpions (Class Arachnida, Order Scorpiones)

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The scorpions are an ancient group of arachnids that date back at least as far as the Silurian, over 400 million years ago. They probably began as aquatic arthropods, as evidenced by the lack of tarsal claws on the earliest fossil scorpion such as *Palaeophonus*. Some of the earliest forms may have had gills, although this is not firmly established. While scorpions had certainly invaded the land by the Devonian, at least some were probably terrestrial by the Silurian (ca. 420 million years ago). By the Carboniferous (350 million years ago) many were almost indistinguishable from modern scorpions. At least some (including the earliest) appear to have had compound eyes, but these have been lost except for a small cluster of "simple eyes" at the front corners of the carapace. Scorpions are now considered to be closely related either to the harvestmen (Opiliones) or to the extinct Eurypterida (often placed with the horseshoe crabs in the Class Merostomata). The exact relationships are still being worked out and both claims are found in the literature.

Scorpions are primarily nocturnal and have adapted to live in very dry deserts, as well as tropical and subtropical forests and scrub, high mountains, grasslands, caves, intertidal zones of the oceans and other habitats. In deserts they survive largely by living in deep burrows or under rocks and only coming out at night to feed and mate. Like most arachnids, scorpions are predators and use their claw-like pedipalps to capture and hold prey while stinging it with the stinger at the end of their long curved postabdomen.

The anatomy of scorpions is unusual among the Arachnida. In addition to the claw-like pedipalps, 5-segmented postabdomen (metasoma) and stinger segment (telson), scorpions also have four pairs of walking legs, a pair of jointed and claw-like chelicerae, a pentagonal (most), triangular (Buthidae and Microcharmidae) or elongated split (Bothriuridae) sternum, a genital plate, and a pair of odd comb-like sensory structures called pectines. The exact function of the pectines is still debated, but they seem to function in habitat scanning and in chemoreception. Other important sense organs include the eyes (both median and lateral), which function in vision, light level perception and entrainment of daily biological rhythms, and the trichobothria, which are primarily air-borne vibration and touch receptors.

The biology of scorpions is much better known now than in J. Henri Fabre's time. Fabre, working in the latter half of the nineteenth century, did not discover the male's production of a spermatophore toward the end of the "promenade a deux" of scorpion courtship. He was under the mistaken impression that the mating actually took place under a rock or other object, after which the female ate the male. In reality, the walk or dance of the scorpions starts when male and female contact each other and the male grasps the female's pedipalps. The spermatophore is produced and the male pulls the female over the package of sperm, which is then picked up in her genital opening. Then he either escapes (probably in most cases in the wild) or gets caught and eaten (as Fabre observed in the close confines of his scorpion cages). A few species, notably a few *Tityus* from northern South America, reproduce parthenogenetically and have few or no males.

Young scorpions are produced alive by viviparity. The young of some species actually are attached to the mother at their mouth, forming a sort of placenta. At birth the baby scorpions clamber onto the mother's back and ride until the first molt, after which they typically disperse. Scorpions may live for at least several years, even after reaching adulthood. Some, such as *Hadrurus*, as well as some of the diplocentrids, ischnurids, and scorpionids have been reported to live as long as 20 years, about the same at that reported for some tarantulas.

The taxonomy of scorpions has been undergoing great changes in the last few years. Sissom recognized nine families in 1990 (Bothriuridae, Buthidae, Chactidae, Chaerilidae, Diplocentridae, Ischnuridae, Iuridae, Scorpionidae and Vaejovidae). By 2000 this had nearly doubled to 16 families (Bothriuridae, Buthidae, Chactidae, Chaerilidae, Diplocentridae, Euscorpiidae, Heteroscorpionidae, Ischnuridae, Iuridae, Microcharmidae, Pseudochactidae, Scorpionidae, Scorpiopidae, Superstitioniidae, Troglotayosicidae and Vaejovidae). Two more families, the Hemiscorpiidae and the Urodacidae, have been proposed by Prendini, the new families being separated from the Ischnuridae and the Scorpionidae, respectively. A cladistic analysis published by Soleglad & Sissom (2001) has now placed the Scorpiopidae as a subfamily under the Euscorpiidae. More recent proposals have become quite controversial and until a consensus is reached it seems wise to retain the classification of 2000–2001, while keeping in mind that this will probably change.

The North American species of scorpions are primarily in the families Buthidae, Chactidae, Diplocentridae, Iuridae and Vaejovidae. The family Superstitioniidae is represented in the United States by the southwestern species *Superstitionia donensis*. The family Euscorpiidae includes several species in tropical Mexico and Guatemala and South America, but is otherwise all Old World, including Asia. Most scorpion species in the United States are found in the southern tier of states, with the largest number in Texas, New Mexico, Arizona and California. One species reaches British Columbia in the west and another reaches Virginia in the east. There are no scorpions in the northeastern United States and most of Canada.

Of the buthids, only the genus *Centruroides* is found in the United States. There are five known species, with three (*C. gracilis*, *C. hentzi* and *C. guanensis*) occurring in Florida and two (*C. exilicauda* and *C. vittatus*) in the midwestern and southwestern United States (Fig. 21). The genus *Centruroides* is more complex in Mexico, where it contains a number of dangerous species, such as *C. noxious*, *C. limpidus*, *C. infamatus, C. elegans*, and *C. suffusus* (the so-called Durango scorpion). All are very slender scorpions, with the metasoma especially elongate in the male, and most have a subacular tubercle just anterior to the stinger on the ventral side of the telson. Most are straw-colored, except for *C. gracilis*, which is dark and gets as large at 11 cm in total length, and a similar large and dark-colored species, *C. margaritatus*, found in Mexico and Central America, south into South America. *Centruroides gracilis* has also been introduced to the Canary Islands and *C. margaritatus* is known from the Cape Verde Islands, Sierra Leone and Gambia. These are the only members of the genus found outside the New World.

In the rest of the world there are a number of buthid genera. In South America and nearby islands the genus *Tityus* includes several

Scorpions (Class Arachnida, Order Scorpiones), Figure 21 ***Centruroides vittatus*** **male from New Mexico. Photo by D. Richman**

dangerous species. In the Middle East and North Africa there are several genera including dangerously venomous species. These include *Leiurus* and *Androctonus*. These scorpions are large (8–10 cm) in length and possess highly potent neurotoxins. There is a record of a healthy adult dying in 4 h after being stung by *Androctonus australis*. Oddly, the effects of the venom differ from population to population and some local populations are "hotter" than others. In the rest of Africa there are other genera that may be dangerous, such as *Hottentotta*. Some members of *Buthus*, which is widespread from southern Europe into Asia and Africa, can also be dangerous. Common, but apparently much less dangerous and widely ranging genera include *Isometrus* and *Lychas*. *Isometrus maculatus* is common in Hawaii, where it is likely introduced. Although readily available through the exotic pet trade, live specimens of the more venomous buthids, such as *Androctonus australis*, should only be kept by experienced researchers.

Chactids occur from Mexico south into Central and South America. Only the genus *Nullibrotheas* is known from North America. The family is closely allied to the Vaejovidae and was initially difficult to separate from it. All chactids are known now to have many accessory trichobothria (slender sensory hairs), while almost all vaejovids have the basic trichobothrial pattern without accessories.

Diplocentrids are represented in the United States by the genus *Diplocentrus*, which ranges south into Mexico. This genus consists of chunky, highly polished rock-dwelling scorpions with large pedipalps and pronounced subacular tubercles. None are known to be dangerous. Other genera occur in Mexico, Central America, South America, the Caribbean and parts of Asia.

Iurids include the largest of North American scorpions in the genus *Hadrurus*. These desert dwelling scorpions can reach over 12 cm and make an impressive sight when out foraging after dusk. The genus *Anuroctonus* (only recently removed from the Vaejovidae) contains only one species, which is distinguished from all other scorpions by the male having a bead-like swelling on the stinger (Fig. 22). It lives primarily in burrows under rocks in desert and coastal mountains from Utah and northern Arizona through California. Of the remaining four genera, *Hadruroides* is known from Ecuador and Peru, including the Galapagos Islands, and *Iurus* (the type genus for the family) is found in Turkey. None are known to be dangerous.

Scorpions (Class Arachnida, Order Scorpiones), Figure 22 ***Anuroctonus phaiodactylus*** **male from California. Photo by D. Richman.**

Vaejovids make up the largest part of the North American fauna. The genus *Vaejovis* is by far the largest, with over 60 species known from the United States and Mexico. *Vaejovis spinigerus* is the common "devil scorpion" of the Southwest United States. *Vaejovis coahuilae* replaces it in the Chihuahuan Desert (Fig. 23). *Vaejovis carolinianus* is found in the Southeast, north of Florida. A number of other species are known from Arizona, New Mexico and Texas, with many more in Mexico. Other common genera include *Paruroctonus*, *Serradigitus*, *Smeringurus* and *Uroctonus*. Most of these were in the old genus *Vaejovis*, which is still huge despite the deletions.

Recognized families (until 2003) not found in North America include Bothriuridae (South America,

Scorpions (Class Arachnida, Order Scorpiones), Figure 23 ***Vaejovis coahuilae*** **from New Mexico. Photo by D. Richman**

Scorpions (Class Arachnida, Order Scorpiones), Figure 24 ***Hadogenes troglodytes*****, the flat rock scorpion from South Africa. Photo by D. Richman**

Africa, India and Australia), Chaerilidae (one genus from southern and southwest Asia), Heteroscorpionidae (all from Madagascar), Ischnuridae (Europe, Asia, Africa, South America, and Australia), Microcharmidae (Africa), Pseudochactidae (Asia), Scorpionidae (Africa and Asia), Urodacidae (Australia), and Hemiscorpiidae (Asia and northeastern Africa). Some of the Ischnuridae and Scorpionidae genera are commonly sold in the exotic pet trade, especially *Scorpio* and *Pandinus*.

Scorpions (Class Arachnida, Order Scorpiones), Figure 25 ***Pandinus imperator*** **from West Africa. Photo by D. Richman.**

The latter and the Ischnurid genus *Hadogenes* include the largest living scorpions known, reaching around 20 cm in length (Figs. 24 and 25). These giants have venoms with very low toxicity and thus are not really dangerous. Several species of *Pandinus* are now on the CITES list and so trade in these giant scorpions is monitored for wild-caught individuals.

References

Dunlop JA, Webster M (1999) Fossil evidence, terrestrialization and arachnid phylogeny. J Arachnol 27:86–93

Fet V, Sissom WD, Lowe G, Braunwalder ME (2000) Catalog of the scorpions of the world (1758–1998). New York Entomological Society, New York, NY

Keegan HL (1980) Scorpions of medical importance. University Press of Mississippi, Jackson, MS

Polis GA (ed) (1990) The biology of scorpions. Stanford University Press, Stanford, CA

Prendini L (2000) Phylogeny and classification of the superfamily Scorpionoidea Latreille 1802 (Chelicerata, Scorpiones): An exemplar approach. Cladistics 16:1–78

Rein JO (2005) The scorpion files. http://www.ub.ntnu.no/scorpion-files/

Soleglad ME, Sissom WD (2001) Phylogeny of the family Euscorpiidae Laurie 1896 (Scorpiones): a major revision. In: Fet V, Selden PA (eds) Scorpions 2001. In Memoriam Gary A. Polis. British Arachnological Society, pp 25–111

Scouting

Systematic, regular monitoring of plants or animals, normally as part of an effort to determine the need for suppression.

► Sampling of Arthropods

Scramble Competition

Competition for limited resources, often intraspecific competition, wherein all individuals have equal access and a free-for-all occurs, with resources being dissipated among the many individuals, and in some cases inadequate supply for any individuals. This also is known as exploitation competition.

Scraper

In some Orthoptera (katydids and crickets), the anal angle of the tegmen, which rubs against a file; part of the stridulatory apparatus.

Scrapers

Insects in aquatic communities that feed by grazing on algae growing on rocks.

Scraptiidae

A family of beetles (order Coleoptera). They commonly are known as false flower beetles.

► Beetles

Screwworms, *Cochliomyia* spp. (Diptera: Calliphoridae)

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American screwworms, the larvae of *Cochliomyia hominivorax* (Coquerel 1858) (Diptera: Calliphoridae), are obligate parasites that cause wound myiasis in mammals. Also called "primary" screwworms, American screwworms are now referred to as "New World Screwworms," or "NWS," to distinguish them from the unrelated "Old World screwworm" *Chrysomya bezziana*. The epithet "screwworm" is derived from the screw-like appearance of a larva and its vertical orientation, head down, in the wound of a host animal. Picture a hole in the skin in which a tightly packed cluster of woodscrews wiggle and squirm in a soup of blood and lymph. An infestation often attracts additional females to lay their eggs, leading to an growing infestation, increased tissue loss and death of the host if untreated.

New World screwworms are indigenous in tropical and subtropical region of the Americas and they can extend their range to temperate regions during warm seasons. In North America, screwworm outbreaks have been recorded as far north as Nebraska, South Dakota, Iowa, Illinois, Wisconsin, and Minnesota in the upper midwestern states of the USA, and North Carolina in the east. They have occurred also in California, Nevada, and Colorado. Screwworms were unknown in eastern North America until 1933, when they introduced via infested livestock imported from the southwestern USA. NWS became established and overwintering successfully in southern Florida. In 1934, they spread in a devastating epizootic to Mississippi, Alabama, Georgia, and the Carolinas. Screwworms east of Texas were eradicated by using the sterile insect technique in 1959. New World screwworms also became established in 1988 in Libya, via infested sheep imported from South America. They have since been eliminated from Libya as well as North and Central America, as reviewed below.

Morphologically similar and easily confused with screwworm flies is the saprophagic blow fly, *Cochliomyia macellaria* (Fabricius 1775), now referred to as the "secondary screwworm." In 1933, Cushing and Patton recognized the differences between *C. americana* and *C. macellaria*, with which it had been confused Later it was determined that *hominivorax* (Coquerel 1858) had priority over *americana* (C & P). The median mesonotal stripe of screwworm flies is shorter than the two lateral stripes (Fig. 26). In *C. macellaria*, the three mesonotal stripes are of equal length. Although rarely found in wounds of living animals, larvae of *C. macellaria* feed only on dead or necrotic tissue whereas screwworm larvae invade and feed on healthy, living tissue. New World screwworm larvae show two dark posterodorsal tracheal trunks but the tracheal trunks of secondary screwworm larvae are not darkly pigmented. Even before screwworms were eliminated from North America, *C. macellaria* was far more common than *C. hominivorax*.

Economic Importance

Female screwworm flies are attracted to wounds of cattle caused by dehorning, castration, branding, and tick infestations, especially those of the Gulf Coast tick, *Ambylomma maculatum* Koch. Shearing wounds in sheep and goats also are attractive. Animals are at particular risk during parturition, as are their newborns, via screwworm oviposition on the vulva and the umbilical cord, respectively. Screwworm infestations usually lead to death in untreated animals. Screwworms cost the animal industry in several ways. Damaged hides and dead animals are important losses. Also costly is continuous inspection and treatment, and restriction of certain husbandry practices to times of predictably least risk. Apart from their economic importance to livestock production, screwworm infestation of humans is an important health consideration.

The total financial cost of screwworm eradication over the 45 year effort, including appropriations from Mexico and the Central American countries, was about $1.3 billion. The annually recurring benefits of screwworm eradication were estimated to be $1.312 billion in a 1996 study.

Screwworms no longer occur in North America, but remain in South America (except Chile) and some Caribbean islands, including Cuba, Hispaniola, Trinidad, Tobago, and Jamaica. The disappearance of screwworms from North America and Central America can be attributed to application of the sterile insect technique, together with extension and quarantine measures carried out by the United States Department of Agriculture, the Mexico-American Commission, and national agencies of Belize, Nicaragua, Guatemala, El Salvador, Honduras, and Panama. Eradication programs are reviewed briefly after a discussion of relevant screwworm biology.

Screwworm Biology

To understand the epizootiology of screwworm infestations, we must consider the fly's reproductive biology and ecology. Ovarian development in screwworms is, of course, temperature dependent. Females are autogenous so they do not require a protein meal to initiate the first ovarian cycle. They do, however, require exogenous protein to support subsequent ovarian cycles. Females can be seen feeding on serous fluids in mammalian wounds. The number of eggs produced in a clutch varies with the size of the fly. The range is about 250–425 eggs and some or all may be oviposited on a single wound (Fig. 26). At summer temperatures, second and subsequent cycles of ovarian development occur at about 3-day intervals. Females usually become inseminated by day five after eclosion and single matings are the rule. Screwworm demography suggests a mean adult female expectation of life of about 7 days at summer temperatures. Expectation of life is longer at cooler temperatures, but oviposition intervals become greater.

Screwworms do not exhibit diapause or a quiescent period that allow them to survive winter or dry seasons. Generations continuously overlap. Early studies indicated that screwworms die out completely when daily mean temperatures drop below 10°C for 3 months. Adults become inactive when temperatures drop below 21°C but the threshold temperature for ovarian

Screwworms, *Cochliomyia* spp. (Diptera: Calliphoridae), Figure 26 Screwworm fly ovipositing at wound.

development is only ca. 9°C. In most winters, screwworm overwintering in USA was confined to southern Texas and southern Florida, but overwintering also occurred in Arizona, New Mexico, and southern California in mild winters. Because pupal development and ovarian development are temperature dependent, generation times can require up to 2 months or more in the cooler months. Eggs and larvae are insulated from diurnal temperature fluctuations because they are on or in their mammalian hosts.

The chief limiting factor in screwworm abundance is thought to be the availability of suitable oviposition sites. Indeed, before screwworms were eliminated from North America, control and inspection of wounds on domestic animals was the chief method of preventing screwworm infestation. Other limiting factors have been shown to include high summer temperatures and low winter temperatures. Extensive studies in Texas do not support the contention that wet weather *per se* favored screwworms.

Screwworm fly densities, averaged over time and space, often are quite low, but sampling distributions are highly aggregated. A typical distribution shows the most frequent daily sample is zero, a large number of ones, and progressively fewer samples showing multiple flies or ovipositions or cases. Thus, most screwworms tend to occur in a small fraction of sampling units. This means that densities can be quite high locally, but transiently so, whereas most sampling units experience comparatively low risk most of the time. Such clumped distributions have an important bearing in planning sterile fly releases because a local screwworm outbreak is begun by fertile flies that cannot later be made sterile. Sterile males must be distributed in such a way as to be present when wild virgin females eclose. Thus, sterile fly dispersions must be made continuously wherever screwworms may occur.

The Sterile Insect Technique and Screwworm Eradication

Biological Considerations

Essentially, the sterile insect technique (SIT) is applied birth control. Sterility via dominant lethal mutations is induced in factory produced males (and females) which are continuously released into a wild, target population. Sterile matings result in no progeny. In theory, as a target population declines, the ratio of sterile to fertile increases, leading to higher frequencies of sterile matings and decreasing natural population size until it is no longer self-sustaining.

A number of key advances in our knowledge of screwworm biology led to the development and practical application of the SIT. First was the finding by Emory Cushing and colleagues at the Liverpool School of Tropical Medicine that the erstwhile screwworm, *Cochliomyia macellaria* (Fabricius 1775), as it was then known, was a complex consisting of *C. americana* (now *hominivorax*), an obligate parasite, and the saprophagic *C. macellaria*. The second key advance was learning how to rear screwworms and maintain them in continuous laboratory culture. This eventually led to mass rearing, an endeavor that continues to develop incremental improvements. The third advance was learning to sterilize flies with ionizing radiation – in the first instance, with x-rays. Mass production of sterile flies eventually depended on Cobalt-60 and more recently Cesium-137. It is now planned to return to using X-rays to induce sterility in the new Panama screwworm production plant. Rather high doses are administered (80 Gy) in efforts to inhibit ovarian development in the females. This causes an incremental loss of male competitiveness. Another advance was to falsify the assumption that sterile male flies behaved as the females in dispersal behavior. Recapturing sterile females after aerially or ground releasing large numbers suggested screwworm flies dispersed over wide distances. Released male flies, however, were recaptured in very low numbers but it was assumed erroneously that they demonstrated the same dispersal behavior as females. It was shown in 1976 that males did not actively disperse, but perched on vegetation awaiting opportunities to mate with screwworm females in the immediate area. Appropriate modifications to program release tactics as practices in the southwestern USA program greatly improved sterile mating rates beginning in 1977. The improvements included maximizing the chances of placing sterile males at potential breeding sites by packaging sterile flies in smaller boxes and releasing them from flight lanes set two miles apart instead of five or ten miles apart, as had been the practice in the southwestern eradication program.

Monitoring Screwworm Abundance and Program Effectiveness

Screwworm adult populations were sampled by using Bishopp traps baited with rotting liver. Beginning in 1975, a chemical attractant called "swarmlure" was developed and replaced liver as the bait. Trap catches consist mostly of *C. macellaria* and other blow flies, but include female screwworm flies as well. Wherever sterile fly dispersions are made, traps rapidly accumulate large numbers of released females. But trapping is inefficient for monitoring fertile screwworm distribution and abundance because labor requirements are great, and visually distinguishing wild from released flies is highly uncertain.

Screwworm infestations were monitored by animal inspection and laboratory identification of larvae from wounds. In the USA, stockmen removed larvae from infested animals, placed them in tubes containing ethanol, and submitted them postpaid to the responsible USDA laboratory where specific diagnosis was made. Each confirmed submission was termed a "case" and these were summed by month, county, and state. The efficiency of the procedure depended on the willingness and timeliness of stockmen to submit larvae. Case incidence was used to plan sterile fly releases and monitor program effectiveness.

Historical Aspects of Screwworm Eradication

The first trials of the SIT were carried out on Sanibel Island, offshore from Ft. Myers, Florida, USA, in 1951–1953. Sterile screwworm flies (both sexes) were ground released in small packets. Native screwworm fertilities approached zero, as measured by egg hatch on artificially wounded, sentinel animals, and case incidence dropped to low levels. Remaining cases were attributed to immigrating flies from the mainland, some 3.2 km distant. Plans were then made to attempt eradication in an environment at no detectable risk of immigration. The location chosen was Curaçao, an island of 444 km^2 in the Netherlands Antilles, one of the Leeward Islands in the southern Caribbean, 65 km north of Venezuela. Here, in a classic experiment carried out in 1954, sterile flies were released from aircraft over the entire island. Pens of artificially wounded, sentinel sheep were used to monitor sterile mating rates and simultaneously provide estimates of wild population density. The island was declared free of screwworms after 6 months. The next SIT trial was in Florida, where screwworms could overwinter in the southern half of the state. This experiment developed into an eradication program, a massive undertaking compared with the Curaçao project. The Florida program became operational in 1958, producing and distributing up to 60 million sterile flies weekly (half males) over areas up to 226,00 km^2, and was successfully concluded in 1959.

A far more extensive program than Florida's was established in the southwestern USA in 1962. Screwworms were known to overwinter in Texas south of San Antonio and in small areas of southern New Mexico, Arizona, and California, but all the border states, from Texas west to California, were subject to annual invasion from Mexico. Given screwworm propensity to disperse rapidly and widely, a containment strategy instead of eradication was necessary. For this reason, arrangements were made with the Mexican government in 1962 jointly to carry out extension, inspection, and sterile fly releases in a "barrier zone" on the USA-Mexico frontier that extended 160 km into Mexico. The area to be treated rapidly expanded northward during the warm season, April to October. As monthly screwworm cases increased in the USA, sterile fly dispersions were withdrawn from Mexico. It was decided, therefore, to attempt eradication in Mexico north of the Isthmus of Tehuantepec, where a much smaller barrier could be established and maintained. A joint Mexico-American Commission for the Eradication of Screwworms was then established in 1972. The agreement included provision to construct a factory for screwworm production in Tuxtla Gutierrez, Chiapas State, Mexico, with weekly production capacity of up to 550 million sterile flies. The factory went into production in 1976 and is still operational as of this writing (March 2007).

An unexpected epizootic in the southwestern USA occurred in 1972 and continued with varying intensity through 1976. The epizootic attracted international attention from scientists and generated a rich literature in which climatic and genetic hypotheses to explain the epizootic and concomitant control failures were advocated and later falsified.

The last autochthonous screwworm cases in North America were detected in 1982. The course of eradication in Central America included Mexico north of the Isthmus of Tehuantepec in 1984, but movements of livestock from untreated Yucatan Peninsula to eradicated areas north of the isthmus were a constant risk and divided Mexico's livestock industry into two regions. A barrier further to the south was necessary. The Darien Gap in Panama is the smallest area that could serve as a barrier. It was estimated that such a barrier would require for its maintenance only 50 million sterile flies (half males) weekly. That goal was reached in 2004 and no self-sustaining screwworm populations have been detected in the barrier since then. The barrier, which includes proximal portions of Colombia, is now treated with 40 million sterile flies weekly.

Sterile fly production for the Central American and Libyan eradication programs was carried out at the Tuxtla Gutierrez plant in Mexico. Pupae were shipped by air to dispersal centers in participating countries, placed in boxes, and the boxes dispersed from aircraft. Further progress in elimination of screwworms includes the Yucatan and Quintana Roo states of Mexico in 1991, Belize and Guatemala in 1994, and Central America south to the Darien Gap in Panama in 1999. Screwworms have also been eliminated from Puerto Rico and the Virgin Islands.

An effort to eradicate screwworms in Jamaica by using SIT was begun in 1997 and terminated in 2006 when it became clear that program management and administration was inadequate, unresponsive, and unchanging.

A new screwworm production factory has been built in Panama and it is scheduled go into production in 2007. It will have the capacity to produce 150 million sterile flies weekly.

New World Screwworms in Libya

The first Libyan collections of American screwworm larvae were made in March 1988, from humans, and specific diagnosis was confirmed the next December. A total of 234 human cases was diagnosed in 1988. It was clear that screwworms were well established and an epidemic/epizootic encompassing 26,500 km^2 was recorded in Northwest Libya that continued until 1990. Intensive efforts by the International Atomic Energy Agency, the United Nations Food and Agriculture Organization, and Libyan authorities began in December 1990 and involved the aerial dispersal of up to 40 million flies weekly. Equally important, 70 teams of livestock inspectors traveled throughout the infested region helping stockmen to locate, treat, and report screwworm cases. All detected wounds were treated prophylactically, and active cases were treated definitively. The last infestation was detected in early April 1991, but intensive surveillance continued until July 1992 when eradication was declared complete.

Risks of Screwworm Incursion

The Libya infestation highlights a risk of modern commerce and travel, that of unknowingly distributing dangerous plants, animals, disease agents, and pests. Introduction of New World Screwworms to old and new habitats is a clear and present danger, given the increasingly heavy volume of commercial and international transport including pets and livestock on the hoof. There have been numerous recent detections of screwworm-infested livestock, pets, and humans in North America, Europe, New Zealand, and Australia. In all instances, the infestations originated in countries where screwworm remain enzootic. There have been no autochthonous cases in the USA, but two instances of screwworm outbreaks in Mexico were traced to sabotage from workers worried about becoming unemployed when eradication was achieved, thus illustrating the danger of accidental or intentional introductions.

Screwworm Detection and Treatment

Detection can be difficult because close, detailed inspection for wounds is required. Ideally, animals from screwworm endogenous regions should be quarantined, with inspection for up to 7 days to detect maturing larvae before they drop out of the wounds and pupate.

Chloriform, benzol, or ethyl ether can kill most larvae and cause others to exit wounds. Insecticidal treatments include brushing 5% coumaphos powder in cooking oil on wounds, and application of puffed fenchlorophos or coumaphos powders or aerosols of dichlorofenthion. Infesting larvae can be killed by using ivermectin applied topically or subcutaneously by injection. For human cases, oral administration of ivermectin at 200 μg/kg or a topical application of 1% in propylene glycol are recommended.

Larvae from myiasis cases should be preserved in ethanol solution and submitted to animal health authorities for specific identification. In the USA samples should be sent to the US Department of Agriculture, Animal and Plant Health Inspection Service, Veterinary Services, National Veterinary Services Laboratories, 1800 Dayton Avenue, Ames, IA 50010. Important information can be found on their website: http://www.aphis.usda.gov/vs/nvsl.

► Myiasis
► Area-Wide Insect Pest Management
► Sterile Insect Technique

References

Klassen W, Curtis CF (2005) History of the sterile insect technique. In: Dyck VA, Hendrichs J, Robinson AS (eds) Sterile insect technique. Principles and practice in area-wide integrated pest management. IAEA/Springer, pp 3–36

Krafsur ES, Whitten CJ, Novy JE (1987) Screwworm eradication in North and Central America. Parasitol Today 2:131–137

Laake EW, Cushing EC, Parish HE (1936) Biology of the primary screw worm fly, *Cochliomyia americana*, and a comparison of its stages with those of *C. macellaria*. USDA Technical Bulletin 500, color plate. General Collection, National Agricultural Library, 24 pp

Meyer NL (1994) History of the Mexico-United States screwworm eradication program. Vantage Press, New York. 367 pp

Vargas-Teran M, Hofmann HC, Tweddle NE (2005) Impact of screwworm eradication programmes using the sterile insect technique. In: Dyck VA, Hendrichs J, Robinson AS (eds) Sterile insect technique. Principles and practice in area-wide integrated pest management. IAEA/Springer, pp 629–650

Scrub Typhus

A rickettsial disease transmitted by some chigger mites.

► Mites
► Typhus
► History and Insects

Scudder, Samuel Hubbard

Samuel Scudder was born at Boston, Massachusetts, USA, on April 13, 1837. He is known for his pioneering work in the Orthoptera and Lepidoptera, but especially in insect paleontology, and is considered to be the founder of insect paleontology in the United States. He was educated at Williams College and Harvard University, in Massachusetts. He was appointed custodian of the Boston Society of Natural History in 1864, and assistant librarian of Harvard University in 1879. Scudder was one of the founders of the Cambridge Entomological Club, founder of the journal Psyche, and editor of Psyche from 1883 to 1885. He served as president of the Boston Society of Natural History from 1882 to 1887, and was employed as paleontologist with the United States Geological Survey from 1886 to 1892. Scudder described over 2,000 fossil insects and published the "Index to the known fossil insects of the world, including myriapods and arachnids," in 1891. Scudder's interest in Orthoptera began in 1862 and continued until about 1900; during this period he developed the reputation as being America's foremost orthopterist. He described about 630 species and 106 genera of grasshoppers. Among his important publications on Orthoptera were "Catalogue of the Orthoptera of North America described previous to 1867," and "Catalogue of described Orthoptera of the U.S. and Canada." Scudder's work on Lepidoptera began in 1889 when he published a 3-volume treatise "Butterflies of the Eastern United States and Canada." Over the course of his career, Scudder published 791 papers and was a member of numerous scientific societies. He died in Cambridge, Massachusetts, on May 17, 1911.

References

Essig EO (1931) A history of entomology. Macmillan, NY, 1029 pp
Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Scutelleridae

A family of bugs (order Hemiptera). They sometimes are called shield-backed bugs.

► Bugs

Sculpture

The insect integument and insect chorion possess various ridges, grooves, and depressions that collectively are called sculpture or ornamentation. They may be obvious, but often require magnification. They usually serve some function, though their purpose may not be immediately apparent. Often the sculpture proves to be an aid in identification of the insect.

Scutate

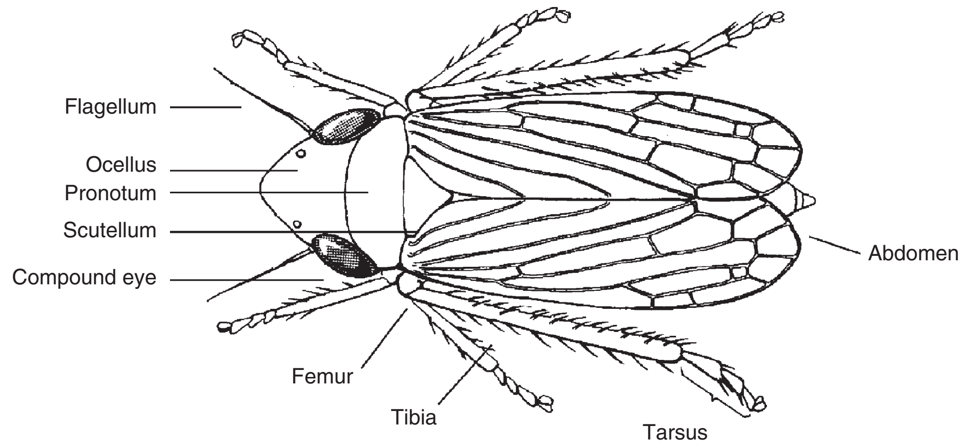
This has two meanings: (i) it is used to describe a structure that is covered with large plate or scales, and (ii) it is sometimes used to describe a structure that is shield-shaped.

► Scutellum
► Scutum

Scutellum

In Hemiptera, the triangular mesothoracic region between the base of the wings; in other winged insects, a small posterior section of the meso- and metanotum, separated from the scutum by a suture (Fig. 27).

► Thorax of Hexapods



Scutellum, Figure 27 **Adult leafhopper (Hemiptera: Cicadellidae).**

Scutum

The middle region of the meso- and metanotum, set off from the scutellum by a suture.

► Thorax of Hexapods

Scuttle Flies, (Diptera: Phoridae)

Members of the fly family Phoridae are sometimes called scuttle flies or coffin flies.

► Myiasis
► Flies
► Decomposition by Insects

Scydmaenidae

A family of beetles (order Coleoptera). They commonly are known as antlike stone beetles.

► Beetles

Scythrididae

A family of moths (order Lepidoptera). They commonly are known as flower moths.

► Flower Moths
► Butterflies and Moths

Seal Lice

Members of the family Echinophthiriidae (order Phthiraptera).

► Chewing and Sucking Lice

Seaside Earwigs

Some of the earwigs in the family Carcinophoridae (order Dermaptera).

► Earwigs

Sea Spiders (Pycnogonida)

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The Pycnogonida (Gr. *pyknos*, thick, dense + Gr. *gony*, knee) are a class of small, primarily benthic marine arthropods often called sea spiders because they superficially resemble the true, terrestrial spiders. Like true spiders, pycnogonids possess an anterior pair of chelicerae followed by a pair of pedipalps and four pairs of long, slender legs. However, unlike spiders or any other arthropod, pycnogonids possess an unsegmented anterior proboscis, special brooding appendages (ovigers) in the male, male brooding behavior, an unusual body form with poorly-defined regions, a unique body-coxa joint, multiple gonopores, and polymerous species with 10 or 12 walking legs instead of the usual eight. The cephalothorax is more slender and the abdomen is much smaller than that of true spiders. Unlike true spiders, sea spiders do not possess a specialized respiratory system. Much of the body cavity is filled with the digestive and reproductive systems, both of which extend far into the legs – an unusual feature for any arthropod. The legs of pycnogonids may be two or three times longer than the cephalothorax. The long legs give this group a second name, Pantopoda (Gr. *pantos*, all + Gr. *pous* (gen. *podos*), foot). Sea spiders are classified as follows:

Phylum: Arthropoda
Subphylum: Cheliceriformes or Chelicerata
Class: Pycnogonida

Pycnogonids inhabit all oceans and can be found from the littoral (intertidal) zone to the abyssal and hadal zones at depths of nearly 7,000 m. Most pycnogonids belong to the epifauna and walk slowly about on the substrate; some species can swim. There are a few planktonic and bathypelagic pycnogonids and a few are members of the infauna. Pycnogonids obtain their nutrition by using the proboscis as a piercing-sucking organ to extract fluids and/or tissues from other marine invertebrates such as hydroids, bryozoans (ectoprocts or polyzoans), anemones, soft corals, sponges, and molluscs. Some, possibly many, pycnogonids are scavengers. A few pycnogonids are herbivores of algae that grow on the surface of sessile organisms and a few are detritivores.

Although sea spiders are cosmopolitan, they are easily overlooked because they are not usually numerous and because they are often small and cryptic. Most pycnogonids have a body length of 2–10 mm and a leg span of 5 mm to 3 or 4 cm. However, some species of *Austrodecus* and *Rhynchothorax* have a body length <1 mm and a leg span of 3 mm, while some species of *Colossendeis* regularly attain a body length of 6–10 cm and a leg span of 30–40 cm. The largest leg span reported for a pycnogonid is 70 cm for *C. colossea*; the smallest leg span is 2 mm for *Austrodecus palauense*. Coloration and encrusting organisms on the body of sea spiders contribute to their crypsis. Pycnogonids are often transparent or a translucent cream or white, or they may be an opaque pale brown or pale yellow. Some species, however, are green, purple, orange, bright red or even multicolored. The body may be covered with detritus or encrusting organisms such as hydroids.

There are approximately 1200 living species of pycnogonids in 87 genera and 8–10 families. Living species of the class Pycnogonida are assigned to the order Pantopoda; fossil specimens are placed in the order Paleopantopoda. The poor fossil record of this archaic group includes only a few species that date back to the Lower Devonian of Germany, the Silurian of England, and the Upper Cambrian of Sweden.

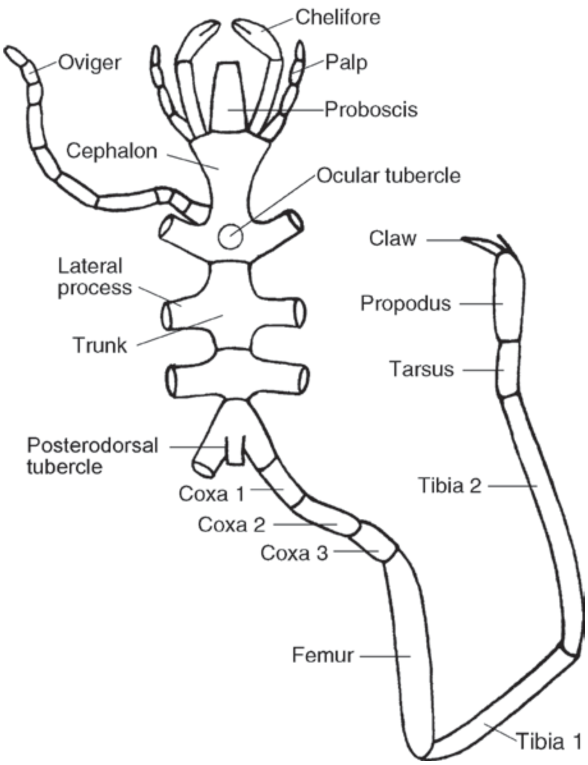
External Anatomy

The body is divided externally into the appendages and a central region that includes a narrow tubular cephalothorax (prosoma) and a short conical abdomen (opisthosoma).

Cephalothorax

The cephalothorax can be divided into the anterior cephalon (head) and the more posterior thorax (trunk) (Fig. 28). The cephalon is comprised of four segments that appear to be one while the thorax possesses three segments that are not always distinct. The cephalon and each of the thoracic segments possess one pair of walking legs.

The cephalon may be compact or elongate and possesses the proboscis anteriorly, the eyes dorsally, and up to four pairs of appendages (one pair each of chelifores, pedipalps, ovigerous legs, and walking legs). The proboscis is a prominent tubular structure that articulates proximally with the cephalon by way of a flexible cuticle (arthrodial



Sea Spiders (Pycnogonida), Figure 28 External features of a long-legged pycnogonid, dorsal view. One walking leg and one oviger are shown.

membrane) similar to that found in the leg joints. The proboscis is triradiate in cross-section and varies considerably in size and shape from relatively short and slender to elongate and bulbous. In some species, the proboscis may be half the length of the cephalothorax. The distal end of the proboscis possesses an opening, sometimes called the mouth, surrounded by three lip-like lobes. The surface of the proboscis cuticle may be smooth, or it may be covered with tubercles or an occasional spine. Setae are present on the proboscis and these may be mechanosensory or chemosensory. Four simple eyes are usually present on a tubercle located mid-dorsally on the cephalon. Species in the genus *Stylopallene* have eight eyes while in some pycnogonids the four eyes may be fused into two. The ocular tubercle may be anterior or posterior on the cephalon and may be small or prominent; in some abyssal forms the tubercle and the eyes are lacking. The posterior portion of the cephalon, with its lateral processes and single pair of legs, is regarded as a trunk segment that has fused with the head to form the cephalon.

The trunk segments possess prominent bilateral processes (pedestals or crurigers) that are often longer than the associated body segments. The walking legs articulate with these processes.

Abdomen

Pycnogonids lack the large abdomen characteristic of most chelicerates. Traditionally, the unsegmented projection (often called the posterodorsal tubercle, Fig. 28) borne distally on the last trunk segment has been called the abdomen (opisthosoma). However, recent evidence indicates that the abdomen includes the tubercle plus the last limb-bearing segment. The posterodorsal tubercle is often truncate and conically shaped or tapering, though it may also be clavate or cuboid, and possesses the terminal anus. Spines or tubercles similar to those often found on other regions of the body may be present on the abdomen.

Appendages

The first pair of appendages, the chelifores (called chelicerae in other chelate arthropods), is present anteriorly on each side of the cephalon at the base of the proboscis (Fig. 28). The chelifores comprise three or four articles (segments), with one or two basal articles forming the scape and two distal articles forming the chelae. Primitively, the fourth article is a terminal moveable digit that opposes the fixed distal portion of the third article. The moveable and fixed digits vary in length among the species and may be curved or straight; they are often toothed on the opposing surfaces. These appendages exhibit varying degrees of reduction such as being present but non-functional in the Ammotheidae, or they may be completely absent as in the Pycnogonidae, Colossendeidae, and Endeidae. The chelifores are used to tear off pieces of host tissue and pass it to the proboscis during feeding. Pycnogonids with reduced or absent chelifores often have a well-developed proboscis that is thrust into the host tissue for feeding. Chelifores are present and functional in all immatures.

The leg-like pedipalps (palps) are located just posterior and lateral to the chelifores. These appendages are primarily sensory; however, in some species they also function in feeding and cleaning. The number of articles comprising the palps is variable and usually ranges from 1 to 11. Palps are absent in some pycnogonids.

Many pycnogonids possess modified legs called ovigers or ovigerous legs. These appendages comprise 5–10 articles inserted ventrally on stout projections located between the pedipalps and the first pair of walking legs. Ovigers are usually well-developed in the male and shorter or less robust in the female; however, they may be well-developed in both sexes, absent in the female, or minute or absent in both sexes. The male uses the ovigerous legs to carry fertilized eggs received from the female; the embryos develop while attached to these legs. In pycnogonids without ovigers, males carry eggs on the ventral surface of the cephalothorax. In some sea spiders, such as *Nymphon* and *Colossendeis*, the ovigers are used to clean other appendages, especially the legs. Cleaning is done by wrapping an oviger around an appendage and then drawing the oviger along the appendage.

Most pycnogonids have four pairs of well-developed legs with an internal volume greater than that of the cephalothorax and abdomen. Each leg comprises nine articles (segments or podomeres); the names given to the articles do not parallel those used in other arthropod groups (Fig. 28). From proximal to distal the articles are: three coxae, a single femur, two tibiae, a tarsus, propodus, and terminal claw. The terminology used to describe the leg articles varies. The most common variations (given in parentheses) are coxa 1, coxa 2 (trochanter 1), coxa 3 (trochanter 2), femur, tibia 1 (patella), tibia 2 (tibia), tarsus 1 (tarsus, basitarsus), tarsus 2 (tarsus, propodus) and claw or dactyl. Auxiliary claws often flank the claw and terminal spines may be present. Leg length varies, resulting in short-legged, compact forms such as *Pycnogonum* or long-legged, elongate forms such as *Nymphon* and *Colossendeis*. Compact forms with stout legs and strong claws are often found in the turbulent littoral or shallow sublittoral zones and are adapted to clinging to the substrate or a host. The long-legged forms are found in somewhat deeper water and are adapted to walking slowly on a substrate of hydroids, bryozoans, or algae. The very large species with elongate bodies and long legs are characteristic of polar and deep water where the long legs may help to keep them from sinking into fine bottom debris.

Polymerous species with either five or six pairs of legs instead of the usual four pairs have one additional trunk segment for each additional pair of legs. This variation in trunk segment and leg number within a group is not found in any other arthropod. There are nine polymerous species in four families of pycnogonids that include the genera *Pentanymphon* (Nymphonidae, two species), *Pentapycnon* (Pycnogonidae, two species), *Decolopoda* (Colossendeidae, two species), and *Pentacolossendeis* (Ammotheidae, one species) with five segments and five pairs of legs and *Hexanymphon* (= *Sexanymphon*) (Nymphonidae, one species) and *Dodecolopoda* (Colossendeidae, one species) with six segments and six pairs of legs.

Integument

Pycnogonids and other arthropods possess an integument consisting of the cuticle (exoskeleton) and the underlying epidermis (= hypodermis) that secretes it. The cuticle is the visible, outer portion of the integument that covers the entire organism; it also lines the foregut (pharynx, esophagus) and hindgut. The cuticle is acellular, hard, and rigid, and comprises the thin outer epicuticle and a procuticle consisting of the exocuticle and the innermost soft endocuticle. In many arthropods the exocuticle is tanned or sclerotized resulting in a hard cuticle; however, in pycnogonids the exocuticle appears to be untanned. The untanned cuticle of pycnogonids provides flexibility at appendage joints and the base of the proboscis; the untanned cuticle also makes growth in length possible during intermolt periods and following the last molt to adult. With the exception of the joints, the endocuticle consists of cross-banded fibrils of chitin similar to that found in the lower crustacea. The ordered structure of the endocuticle may provide rigidity to the cuticle. Epidermal cells beneath the endocuticle possess the extensive rough endoplasmic reticulum and numerous Golgi complexes needed to produce and secrete cuticle as well as the lysosomes needed to digest endocuticle during molting. Integumental glands are remarkably numerous in many regions of the body. The function of many of these glands is unknown, however; some glands apparently secrete mucus or defensive secretions while others may be excretory.

The surface of the integument may be smooth or it may possess spines and/or tubercles. Sensory filaments and setae are distributed over the cuticular surface and may vary among species from few to numerous and from short to long. Many regions of the cuticle are penetrated by a remarkable number of canals that permit the epidermal cells and integumental glands to pass their secretions. The pore canals of the epidermal cells terminate just inferior to the epicuticle while the integumental glands open onto the cuticular surface by way of bilobed valves. Often, the exterior surface of pycnogonids is covered with varying amounts of detritus and may be decorated with small encrusting organisms such as algae, foraminifera, sponges, hydroids and anemones, bryozoans, barnacles, molluscs, or tunicates. The encrusting organisms and detritus are temporarily lost at the molt.

Articulations and Movement

Articulations or joints permit one part of the exoskeleton to move relative to another. The movements possible at a joint are related to joint structure, musculature, and in some cases, hydrostatic mechanisms. Most pycnogonid joints are dicondylic (having two points of articulation) and eudesmatic (powered by muscles). Dicondylic joints possess two condyles on the distal margin of an article that engage acetabula on the proximal margin of a succeeding article. The orientation and location of the condyles and acetabula limit movement to a single plane perpendicular to a line connecting the two points of articulation. Thus, the joints are hinge joints. A flexible membrane (articular corium) associated with the condyles permits the joint to bend. Antagonistic pairs of striated skeletal muscle inserted near the plane of motion of a joint control movement; the origins of these muscles are usually in the preceding article or body structure. In pycnogonids, all muscles are intrinsic to the leg except those of the body-coxa 1 joint which is spanned by extrinsic muscles originating in the bilateral processes. The joint between the second tibia and the tarsus (which lacks an extensor muscle) and the joint between the tarsus and propodus (which has no muscles) may rely on hydrostatic pressure; however, pressure-isolating mechanisms that would permit the use of hydrostatic pressure in limb movement have proven difficult to demonstrate.

Muscles are attached to the cuticle in a fashion similar to that described for other arthropods. Desmosomes ("spot welds") join muscles cells to the base of modified epidermal cells called tendonal cells and to microtubules that run through the tendonal cells. In turn, hemidesmosomes in the apical region of the tendonal cell join the microtubules to muscle attachment fibers (tonofilaments) secreted by the tendonal cells. The muscle attachment fibers pass into the cuticle to complete the link between muscles and the cuticle.

The leg joints of pycnogonids have features that appear to be oriented toward feeding and swaying in currents in addition to locomotion. The body-coxa 1 joint is a hinge with a horizontal axis that provides levator-depressor movements, a condition unique among the arthropods. The levator-depressor movements permit the body to be raised or lowered or swayed side-to-side, especially in long-legged pycnogonids (Fig. 28). Because the leg bases are oriented in different directions, the body can be shifted forward or backward, sideways, or up or down, thus enabling the pycnogonid to move the proboscis from polyp to polyp during feeding while the tarsi remain in a fixed position. This same levator-depressor movement of the body-coxa joint allows the sea spider to sway in the current along with prey such as hydroids, resulting in motion camouflage for the pycnogonid.

The coxa 1-coxa 2 joint of pycnogonids is a hinge joint with a vertical axis and large flexor and extensor muscles originating laterally in coxa 1. This joint has a considerable range of motion and is the only leg joint capable of promotion (lifting, a forward motion made without ground contact) and remotion (pulling or pushing depending on the angle of the joint to the body). In other arthropods, promotion-remotion of the leg is accomplished at other joints. For example, in spiders promotion-remotion occurs at the coxa-trochanter joint, insects utilize the body-coxa joint and harvestmen accomplish promotion-remotion at the articulation between the trochanter and femur. Joints distal to the coxa 1-coxa 2 articulation of pycnogonids are hinge joints that have levator-depressor movements.

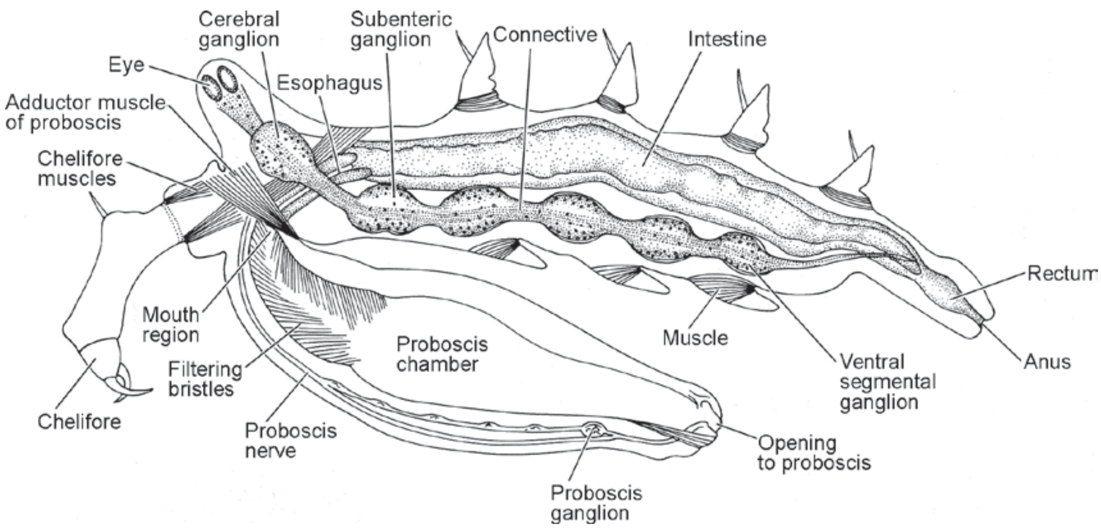
Coordinated movements of leg articles result in an extremely slow walk in pycnogonids. The limb movements are angular with one part of a limb being bent relative to the body or another portion of the same limb. During the movement of a single leg, there is both a promotion and remotion phase. The stepping pattern is diagonal as is commonly observed in arthropods. In the stepping cycle, there is a 0.5 phase difference between successive legs on a side that results in legs one and three on the left side being active together while legs two and four on the right side are also active. The movements of the different legs are not perfectly synchronized, however, resulting in an irregular stepping pattern similar to that of arachnids.

Pycnogonids can use the walking legs to swim. Swimming occurs in genera with short bodies and long slender legs such as *Nymphon*, *Colossendeis*, *Callipallene* and *Anoplodactylus*. Swimming depends on the levator-depressor movements of the leg base to enable the legs to beat dorso-ventrally. The power stroke occurs when the legs beat downward in an extended position; the legs are flexed toward the body during the upward recovery stroke. The locomotory rhythm is such that when one pair of legs performs the downstroke, the adjacent pair performs the upstroke. The legs therefore exhibit the same 0.5 phase difference as in walking. The resulting motion is continuous swimming that pycnogonids can further enhance with slight promotor–remotor movements of the coxa 1-coxa 2 joint.

Some pycnogonids exhibit modifications of the basic swimming rhythm. The large *Colossendeis* has been observed swimming by rapidly bringing its legs together under the body to propel the animal upward, then extending its legs horizontally to slow the sinking rate. *Nymphon* can also control its vertical position in the water column by extending its legs horizontally, and in addition, can move forward or backward. Because of the levator-depressor movements possible at the basal leg joints, both *Nymphon* and *Colossendeis* can assume a "plummeting" posture with legs folded vertically over the body to achieve a rapid descent.

Alimentary Canal, Feeding, and Digestion

The arthropod alimentary canal is an elongate tube that extends from the mouth to the anus (Fig. 29). The canal is differentiated into three main regions: the foregut, midgut, and hindgut. Both the foregut and hindgut are lined with cuticle that is shed at the molt along with the outer exoskeleton. In pycnogonids, the foregut opens at the tip of the proboscis and extends the length of the proboscis to the midgut; the midgut extends through the cephalothorax and is connected to a short hindgut



Sea Spiders (Pycnogonida), Figure 29 **Mid-sagittal view of the pycnogonid *Ascorhynchus castelli* (Ammotheidae) showing the major internal organs. The dorsal blood vessel/heart and gonad, not shown, are superior to the intestine. (From Brusca RC, Brusca GJ (2003) Invertebrates, 2nd edn. Reproduced by permission of Sinauer Associates, Sunderland, MA, USA.)**

(rectum) that passes through the posterodorsal tubercle to open at the terminal anus.

The terminology used to describe the pycnogonid alimentary canal varies. The most common differences involve the location of the mouth and midgut. Some authorities believe the mouth is located at the tip of the proboscis and call the canal in the proboscis a pharynx (the canal has also been called an esophagus); the pharynx extends to a short esophagus that leads into the midgut. Others have termed the canal in the proboscis a proboscis chamber and have placed the mouth between the chamber and the esophagus. In either case, the canal within the proboscis is lined with a cuticle that is shed during the molt. The midgut of pycogonids is sometimes called an intestine, whereas in many other arthropods the term intestine is used for a subdivision of the hindgut.

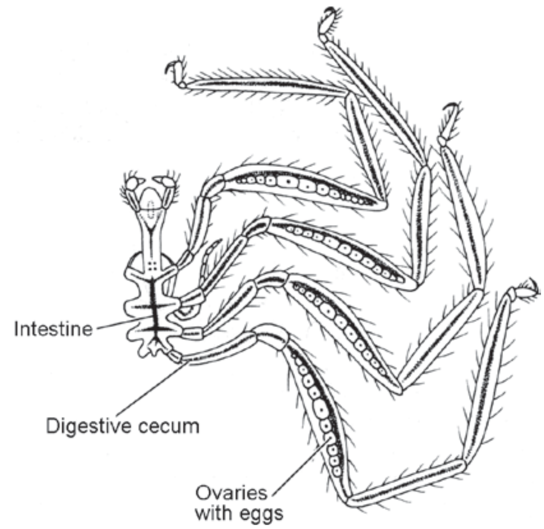
The principal food-gathering organ is the proboscis, a prominent anterior feature of all pycnogonids. The proboscis is attached to the cephalon by a ring of flexible cuticle and is positioned for feeding by extrinsic muscles. There are usually two pairs of well-developed extrinsic muscles originating on a cuticular apophysis behind the ocular tubercle; one pair inserts on the dorsolateral wall of the proboscis, the other on the ventrolateral wall. Some pycnogonids have a smaller, third pair of extrinsic muscles. In conjunction with hydrostatic pressure, muscular action raises or lowers the proboscis. Although the proboscis is non-retractable, it may be protracted or retracted slightly by the extrinsic muscles.

The proboscis opening is encircled by three lip-like lobes; these lobes help regulate the size of the opening and also act as a rasp during feeding. The rasping action of the proboscis helps to pull food off the substrate or gain entrance to a soft-bodied host when the proboscis is used as a piercing-sucking organ. In some species, the chelifores aid the feeding process by tearing off bits of tissue and passing them to the proboscis. The claws and terminal spines of the walking legs, and sometimes the entire leg of clinging species, help anchor the sea spider during feeding.

Most pycnogonids feed on soft-bodied invertebrates such as hydroids, anemones, soft corals, sponges, bryozoans, or polychaetes by piercing the body and ingesting body fluids and tissue fragments. This feeding behavior has been variously described as carnivorous, predaceous, or parasitic depending on the degree of damage inflicted upon the prey or host. Some pycnogonids are herbivores of algae and a few are detritivores. Some adults, perhaps many, are scavengers.

The proboscis opening leads into a cuticle-lined foregut that is triradiate in cross-section and extends the length of the proboscis. Intrinsic proboscis muscles, the radial and interradial muscles, control the diameter of the foregut. These muscles originate on the inner proboscis wall and insert on the outer wall of the foregut. When the muscles contract, the foregut enlarges sufficiently to create a slight suction that brings food into the lumen. A short esophagus at the distal end of the foregut bears several rings of setae, the so-called "oyster basket," that may help to break up particulate food and filter out large particles. The esophagus extends into the cephalon and opens into the midgut near the base of the ocular tubercle by way of the tripartite esophageal valve.

The midgut is the largest part of the alimentary canal and extends throughout the cephalon and trunk. Remarkably, the midgut has diverticulae (digestive caecae) that extend into the legs (Fig. 30), often as far as the tarsi, where diverticulae narrow and attach to the appendage walls by way of connective tissue. In some species, diverticulae extend into the base of the proboscis, chelifores, pedipalps and/or ovigers. Such extensive diverticulae are found in no other arthropod group (spiders come the closest with midgut branches that surround many of the internal organs and diverticulae that extend into the coxae of the walking legs). The unusual diverticulae of pycnogonids are probably a consequence of the small size of the cephalothorax and abdomen. Diverticulae provide a large surface area for digestion and absorption and may partially explain why at least some sea spiders, e.g., *Pycnogonum litorale*, can withstand starvation for several months. A tripartite valve at the end of the midgut leads into a short hindgut (rectum) that passes undigested food to the anal opening at the tip of the posterodorsal tubercle.



Sea Spiders (Pycnogonida), Figure 30 ***Pallene brevirostris*** **female showing egg storage in the femoral portions of the gonad diverticulae. Note also the digestive caecae extending far into the legs. (From Brusca RC, Brusca GJ (2003) Invertebrates, 2nd edn. Reproduced by permission of Sinauer Associates, Sunderland, MA, USA.)**

Digestion in pycnogonids is intracellular; however, details of this process are not well known. Specific mucosal cells take up food from the midgut lumen and later detach from the midgut wall to float freely in the lumen. Other mucosal cells absorb nutritive materials from the floating cells until this material is exhausted and the floating cells are eliminated from the anus.

Circulatory System

The circulatory system of pycnogonids is of the open type typical of arthropods. In this system, there is no pressurized, closed system of blood vessels as seen in vertebrates, nor is there a lymphatic system to return fluid to the circulatory system. Instead, the blood (hemolymph) circulates freely around the internal organs. The hemocoel is the major body cavity through which the hemolymph circulates and a muscular mid-dorsal blood vessel serves as the heart.

The hemocoel of sea spiders extends throughout the cephalothorax and appendages and possesses several septa that help direct hemolymph flow. The largest septum is a horizontal partition in the cephalothorax between the midgut and the overlying dorsal vessel (heart); this septum forms a dorsal chamber (pericardial sinus) and a ventral chamber (perivisceral sinus) in the cephalothorax and also extends into the legs as a partition above the lateral diverticulae of the midgut to create dorsal and ventral sinuses. The septum has slits near the lateral processes that permit communication between the dorsal and ventral chambers. The mid-dorsal heart extends nearly the length of the cephalothorax and is often v-shaped or reduced to muscular lateral walls with two pairs of openings (ostia) near the bases of the second and third walking legs that permit hemolymph entry. The roof of the heart is formed by epidermis of the dorsal body wall and the floor of the heart is formed by the horizontal septum. In some species there is an unpaired posterior ostium.

The general pattern of hemolymph circulation is away from the heart in the ventral chambers and toward the heart in the dorsal chambers. Hemolymph flows in the anterior direction within the heart and is pumped from the anterior end of the heart into dorsal chambers in the proboscis and chelifores. Hemolymph then flows posteriorly in the perivisceral sinus and into the ventral sinuses of the legs. The partition dividing the legs into dorsal and ventral sinuses does not reach the end of the appendages. At the tips of the legs the hemolymph enters the dorsal sinus and flows back toward the cephalothorax to enter the pericardial sinus where it passes through the ostia into the heart. Hemolymph flow is aided by leg movement and by peristaltic contractions of the midgut diverticulae.

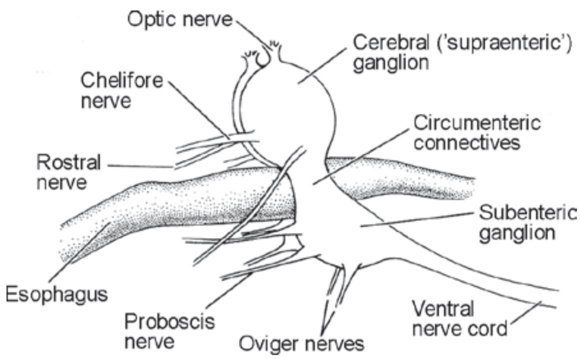
The hemolymph is a colorless fluid that contains several morphological types of hemocytes such as granulocytes and ameboid cells; however, the lineage and function of the different types of hemocytes is poorly known. The hemolymph transports nutrients throughout the body and there is some evidence that it may have a respiratory function.

Respiratory and Excretory Systems

Organs dedicated to respiration have not been found in pycnogonids. Presumably, the small body with its relatively large surface area-to-volume ratio is sufficient for gas exchange. Excretion and osmoregulation are poorly known and may occur by one or more pathways: the body surface, gut, and/or nephridia. The body surface appears to be used by some larvae during the molt to eliminate wastes stored in epidermal cells; adults may also pass wastes from or through the epidermis. Internal routes of excretion may involve passage of materials across the gut epithelium or detachment of waste-laden epithelial cells from the gut wall into the lumen. Nephridia are present in the scape of the chelifores of at least one species, *Nymphopsis spinosissima*, and it seems likely that the examination of additional species will lead to similar findings. The nephridia consist of podocytes that form an ultrafiltration end sac connected to a nephridiopore by a tubule and cuticle-lined duct.

Nervous System

The nervous system can be divided into two principal parts, the central nervous system and the peripheral nervous system. The central nervous system comprises cerebral ganglia (supraesophageal ganglia or "brain") above the esophagus, a subesophageal (subenteric) ganglion connected to the cerebral ganglia by a pair of connectives that encircle the esophagus (Fig. 31), and a ventral nerve cord that extends posteriorly from the subesophageal ganglion. The ventral nerve cord is double and has paired segmental ganglia that are often fused to form bilobed masses (Fig. 29). The peripheral nervous system consists of the many nerves arising from the central nervous system that innervate the eyes, appendage and trunk



Sea Spiders (Pycnogonida), Figure 31 Lateral view of the anterior portion of the nervous system of *Nymphon* (Nymphonidae) showing the cerebral (supraesophageal) and subesophageal (subenteric) ganglia and associated nerves. The unlabeled nerve just dorsal to the esophagus is the stomodeal nerve; the unlabeled nerve just ventral to the esophagus is the palp nerve. Only one pair of proboscis nerves is shown. (From Brusca RC, Brusca GJ (2003) Invertebrates, 2nd edn. Reproduced by permission of Sinauer Associates, Sunderland, MA, USA)

musculature, and peripheral sense organs such as the setae and sensilla.

The cerebral ganglia are located anterodorsally in the cephalon ventral to the eye tubercle and represent a syncerebrum comprising a protocerebrum and tritocerebrum. Pycnogonids, as well as other chelicerates, lack the deutocerebrum that in other arthropods innervates the antennae. The cerebral ganglia give off two pairs of optic nerves that innervate the eyes, paired cheliforal nerves that innervate the chelifores, and a median rostral nerve that, along with paired stomodael nerves, extend forward to innervate the proboscis. Within the proboscis, the rostral and stomodael nerves may be linked by several transverse connectives. The subesophageal ganglion supplies the paired dorsal and ventral proboscis nerves that innervate the dorsal and ventral proboscis muscles and paired nerves that innervate the pedipalps and ovigers. Posterior to the subesophageal ganglion, ganglia of the ventral nerve cord correspond to the legs in number and position and are responsible for innervation of their respective segments. Each ganglion is connected to the adjacent ganglion by two interganglionic connectives of varying length, and each ganglion gives rise to two nerves to each leg as well as a paired nerve that innervates the ventral segmental muscles. In addition to innervating the legs and ventral segmental muscles, the terminal ganglion innervates the posterodorsal tubercle via three short, paired nerves.

Sensory perception is accomplished by exteroceptors such as the eyes, setae and sensilla. The four eyes (ocelli or so-called simple eyes) located on the lateral surfaces of the ocular tubercles are the most studied sensory organs of pycnogonids. These receptors can detect blue and red wavelengths of light, but presumably cannot form images. Cells of the ocelli are contained in a hemispherical depression covered by a biconvex cuticular lens that is thicker than the surrounding cuticle. From superficial to deep, these cells are the hypodermal cells that secrete the lens, translucent vitreous cells, elongate neurons that are the photoreceptive retinal cells, reflective tapetal cells, and the innermost layer of anucleate pigment cells. Light reaches the retinula cells through the vitreous cells. A large number of retinula cells are packed close together without any regular arrangement. On at least one side of a retinula cell a rhabdomere is formed; rhabdomeres of several adjacent cells combine to form a rhabdom. The light sensitive rhabdomeres point away from the lens and incoming light and are therefore of the "inverted" type similar to the secondary eyes of spiders and similar in principle to that of the vertebrate retina. The axon of each retinal neuron passes through the basal portion of the ocellus where they group together to form the optic nerve.

The sensory setae and sensilla widely distributed over the body have a structure similar to that found in other arthropods and are believed to be mechanoreceptors or chemoreceptors. Structural, behavioral and physiological information support this belief.

Neurosecretory cells are found throughout the nervous system; however, little is known about their function. A possible neuroendocrine organ, Sokolow's organ, is present lateral to the optic lobes of the brain in some pycnogonids.

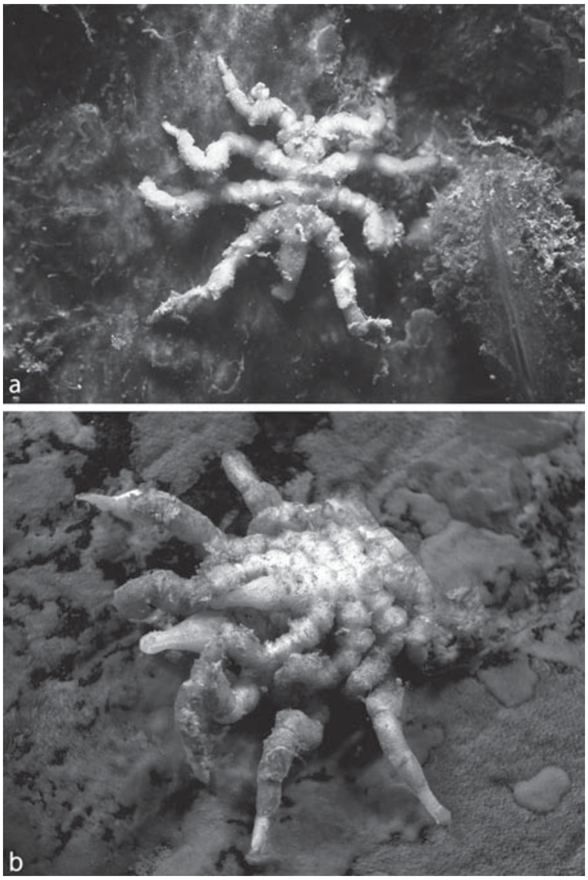
Reproductive System and Development

Except for one hermaphroditic species, *Ascorhynchus corderoi*, sea spiders are gonochoric or dioecious (having separate sexes). Females can often be told from males by examination of the femora which in gravid females become distended with developing ova. Sexual dimorphism may also be evident in the well-developed ovigerous legs of the male and the female's larger size. In both sexes, the gonad is a single, well-developed, bilaterally symmetrical, u-shaped organ located in the trunk above the alimentary canal. Portions of the gonad extend into the leg, a condition likely related to the small size of the cephalothorax. Frequently, diverticula of the testis reach as far as the third joint of the leg and those of the ovary to the fourth. In most species, vitellogenesis is confined to the lateral diverticulae of the ovary; however, ova also develop in the trunk of some *Austrodecus* and in the well-known *Pycnogonum litorale*. Ova are often stored in the dilated femurs prior to egg-laying. A duct connects the genital diverticulae with multiple reproductive openings (gonopores). The position and number of gonopores varies by species and sex; however, gonopores are often located on the anteroventral surface of the second coxae of the last one or two pairs of legs in males and of all legs in females. The female orifice is usually larger to allow egg passage and the orifice often has an operculum. The extension of the gonads into the legs and the possession of multiple gonopores is unusual in arthropods and represents another of the unique features of pycnogonids.

Fertilization is external with the gonopores of the male and female held in close proximity to each other during mating. In some species the male suspends himself beneath the female so their ventral surfaces are opposed. In other species, such as *Pycnogonum litorale*, the male clings to the female's back. Males fertilize the eggs as they are emitted from the gonopores of the female. Mating is usually a quick process in pycnogonids; however, in *P. litorale* the process may last from several days to a month or more, with much of the time being spent by the male in mate guarding (Fig. 32). Depending on the species, females release the eggs from one or more legs (sometimes all legs) at the time of mating. The male gathers the eggs, either singly or in bracelets or balls, onto his ovigerous legs. The eggs are cemented to the ovigers, typically several balls per leg, with the aid of an adhesive produced by femoral cement glands. Males brood the eggs until hatching; some species also brood the young for varying periods of time. Pycnogonids are one of the few animal groups in which the males exclusively brood the offspring.

Embryonic Development

The basic processes that occur during embryonic development are cleavage, blastula formation, gastrulation, and organogenesis. Cleavage of pycnogonid eggs is complete (total or holoblastic cleavage). If the eggs are small and contain a small to moderate amount of yolk, such as in *Pycnogonum*, the resulting cells (blastomeres) are of equal size and the resulting ball of cells (blastula) has a small blastocoele. Larger eggs that are rich in yolk, such as those of *Nymphon*, cleave to produce a blastula with cells of unequal size (micromeres and macromeres). In the small eggs, gastrulation occurs by the inward growth of cells. A superficial blastomere grows into the blastocoele and forms the endoderm; cells adjacent to this blastomere move into the blastocoele to form the mesoderm. The gastrula consists of the outer ectoderm underlain by the mesoderm and the central endoderm. In the larger eggs with more yolk, gastrulation occurs when the macromeres are overgrown by the smaller micromeres in a process sometimes called epiboly. Macromeres in the region of the blastopore become isolated and move to a position under the micromeres to form the mesoderm.



Sea Spiders (Pycnogonida), Figure 32 The North Atlantic *Pycnogonum litorale*, family Pycnogonidae, a short-legged compact form. (a) Dorsal view of adult. The anterior proboscis, between the first pair of legs, is oriented toward the bottom of the photograph. Note the minute posterodorsal tubercle between the fourth pair of legs. Detritus is beginning to accumulate on this newly molted individual. (b) Mate guarding and external fertilization. The male climbs onto the back of the female with his genital openings opposed to those of the female. The genital openings, located on the second coxae of the last pair of legs of both sexes, are on the dorsal surface in the female and on the ventral surface in the male. Both animals may remain in this position for days or weeks before the female releases her eggs. (Photograph (b) courtesy of David Whittemore.)

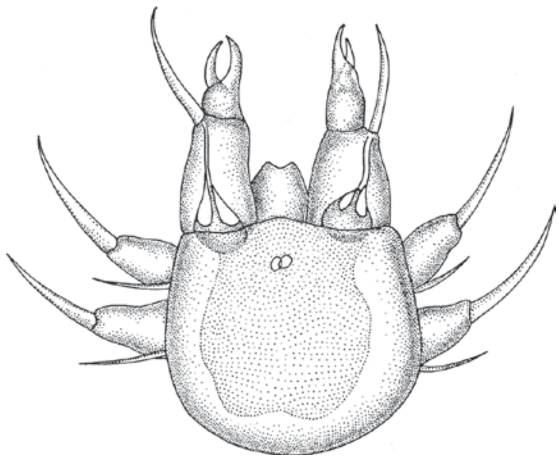
The endoderm is formed of macromeres below the mesoderm. Thus, the gastrula consists of a central mesoderm that is surrounded dorsally by the ectoderm and ventrally by the endoderm. In both small eggs and large eggs, cells of the endoderm fuse to form a syncytium.

The appendage buds and stomodeum (foregut) form early in development. The midgut forms within the endodermal syncytium and then connects to the stomodeum; the proctodeum (hindgut) forms later, a short time before hatching. The cells that line the foregut and hindgut secrete cuticle and are of ectodermal origin. The ectoderm also gives rise to the nervous system as five paired ganglia. The first pair fuse to form the protocerebrum; the second pair are associated with the chelifores and are initially postoral and ventral, but later move anterior to fuse with the protocerebrum. The third and fourth pairs of ganglia are associated with the larval legs and fuse to form the subesophageal ganglion. The fifth pair of ganglia appear later than the others and divide to innervate the adult limbs as the limbs develop.

Duration of the embryonic period varies among and within species and is known for only a few pycnogonids. For *Pycnogonum litorale* reared in the laboratory, the length of time from oviposition to hatching ranges from approximately 1 month to over 3 months.

Post-Embryonic Development

Most pycnogonids undergo indirect development and hatch from the egg at an early stage as a larva bearing little resemblance to the adult. This larva is often called a protonymphon (Fig. 33), a term sometimes used for all pycnogonid larvae. However, there is a second distinct larval type known as the attaching larva, which also exhibits indirect development. Direct development has been observed in some species of *Pallene* and *Nymphon* where the embryos leave the egg with a full complement of adult appendages.



Sea Spiders (Pycnogonida), Figure 33 Dorsal view of the six-legged protonymphon larva. (From Brusca RC, Brusca GJ (2003) Invertebrates, 2nd edn. Reproduced by permission of Sinauer Associates, Sunderland, MA, USA.)

The protonymphon is square to ovoid and appears to be unsegmented externally. Internally, however, a pre-oral region and four post-oral segments can be discerned; there is an unsegmented abdomen. This larva has three pairs of uniramous appendages and superficially resembles a crustacean nauplius larva except that the first pair of appendages is chelate. The appendages are associated with the first three post-oral segments and are the chelifores (whether or not these are present in the adult) and larval legs that correspond in position to the pedipalps and ovigers. Each appendage has three articles and very often possesses either an elongate spine or a filamentous seta on the proximal segment. These spines and setae, along with adhesive produced by cheliforal cement glands (not present in the adult) and muscular grasping by the appendages, help keep the larvae in a cohesive group on the adult. The chelifores terminate with a pair of pincers and the larval legs terminate in a single claw. Eyes are present dorsally and there is a short proboscis.

Most protonymphon larvae leave the male's ovigers by swimming or crawling away or by simply latching onto something nearby; others remain with the male for a species-specific time before dispersing to become free-living, parasitic or commensal in or on an invertebrate host. Hosts include hydroids, coral, jellyfish, anemones, echinoderms, bivalves, and gastropods; the initial host may be different from the host fed upon as an adult. Larvae from eggs with little yolk tend to leave the male's ovigers earlier than those hatched from eggs with more yolk. Most pycnogonids carry the eggs only until they hatch; however, some species have a prolonged association with the male. The longest duration of male parental care has been observed in some arctic species of *Nymphon* and *Boreonymphon* that carry young until they are approximately one-half the adult size.

Recent work indicates that the protonymphon follows one of three developmental pathways after it leaves the male: the encysted larva, typical protonymphon, or atypical protonymphon. The encysted larva burrows into a cnidarian host and remains encysted in the gastric cavity through several molts, the typical protonymphon remains free-living, often in association with another invertebrate, and the atypical protonymphon becomes associated with the interior of a clam or the surface of a nudibranch or polychaete for several molts. Development in the typical protonymphon, encysted larva and attaching larva (next paragraph) involves an anamorphosis in which the larva undergoes a series of molts to add new segments and legs sequentially behind existing ones. During this time, appendages such as the palps, ovigers and legs increase in length and number of articles. Appendages may also be lost during metamorphosis such as when *Pycnogonum litorale* loses the chelifores during transformation from the last larval to the first juvenile stage. The atypical protonymphon acquires all of its limb buds at once at the first molt. In subsequent molts, the size and segment number of the leg articles increase.

The attaching larva is a form that undergoes the first molt in the egg, then hatches and attaches to the male's ovigerous legs. This larva is filled with yolk and does not feed for several molts before swimming away to take up a free-living existence.

The number of post-embryonic stages and duration of the post-embryonic period is variable and is known wholly or in part for about 20 species. In the laboratory, development through nine stages in nine molts from hatching to the adult stage in the Eastern Pacific *Propallene longiceps*, which has an attaching larva, takes about 5 months. The North Atlantic *Pycnogonum litorale*, with a protonymphon larva, passes through five larval stages followed by six (occasionally seven or eight) juvenile stages within a year in nature and slightly longer than a year in the lab. Variation in development time in *P. litorale* can be remarkable in water of different temperature and because these small organisms, like some other pycnogonids, can withstand starvation for several months.

Size increases in pycnogonids are associated with the molt as they are in other arthropods. However, unlike most other arthropods, juvenile pycnogonids increase in size not only when they molt, but also during intermolt periods. Size increases during the intermolt period have been attributed to the stretching of thin flexible membranes at the joints, or to lack of tanning in the exocuticle, so that as the tissue mass increases, the size can also increase.

Adult longevity is poorly known. Adults of *Pycnogonum litorale* reared in the lab have lived for more than 6 years (9 years for one individual) and have undergone repeated mating without further molts.

Classification and Taxonomic Affinity

The unique features of Pycnogonida have long presented difficulties in determining the taxonomic relationship of this group to other arthropods. The proboscis, multiple prosomal gonopores, segmented trunk and lack of distinct tagmata, male ovigers and male brooding behavior, the body-coxa joint, size increases during intermolt periods, digestive system and gonads that extend into the legs, and the additional pairs of walking legs in some genera have no counterpart among the chelicerates nor among other arthropods. Pycnogonids also lack, at any stage of their life cycle, the large abdomen characteristic of the chelicerates. At one time or another, pycnogonids have been associated with most major arthropod groups as well as with the polychaete worms and onychophorans (velvet worms).

Pycnogonids possess many features of the chelicerates – horseshoe crabs, terrestrial spiders, scorpions, and mites. Chelicerate features include the pedipalps, chelicerae (called chelifores in pycnogonids), lack of antennae, body divided into cephalothorax (prosoma) and abdomen (opisthosoma), and the four pairs of slender, multiarticulate uniramous legs. Other chelicerate features are the similar structure of sense organs and brain (including the lack of a deutocerebrum), the suctorial method of feeding, the gut with two to six pairs of digestive caecae, and the four postoral segments in the earliest embryonic stages. Thus, pycnogonids are often classified as chelicerates in the subphylum Chelicerata or as a sister taxon of the chelicerata in the subphylum Cheliceriformes.

The uncertainty of the relationships of Pycnogonida to other arthropods is reflected in multiple classification schemes. Indeed, classification among the pycnogonids themselves is in a state of flux. One common classification places pycnogonids in two orders, Paleopantopoda (fossil sea spiders) and Pantopoda (recent or living sea spiders).

The names Pycnogonida (Latreille, 1810) and Pantopoda (Gerstaecker, 1863) can be a source of confusion. Originally proposed to represent the same taxon, the terms are used in both a linguistic sense and in a systematic-taxonomic context. Linguistically, Pycnogonida is often used in the English and French literature, whereas Pantopoda frequently appears in German works. Systematically, there are several classification schemes involving the terms Pycnogonida and Pantopoda. Most commonly, the Pycnogonida has been divided into the orders Paleopantopoda and Pantopoda, or three orders, Palesoisopoda, Paleopantopoda and Pantopoda.

The Pantopoda are further subdivided into eight to ten families including Ammotheidae, Austrodecidae, Callipallenidae, Colossendeidae (includes the largest known pycnogonids in the genus *Colossendeis*), Endeidae (with one genus, *Endeis*), Nymphonidae (the genus *Nymphon* has nearly 200 species), Phoxichilidiidae, Pycnogonidae (*Pycnogonum* is one of the most common and widely studied genera), Rhynchothoracidae (with one genus, *Rhynchothorax*) and Tanystilidae. Family names and the number of families recognized vary among pycnogonid workers. There are at least 87 genera containing approximately 1200 described species. It is likely that many more species await description.

Much more remains to be learned about the anatomy and physiology, ecology, general biology, and taxonomic affinities of these fascinating creatures.

References

Arnaud F, Bamber RN (1987) The biology of Pycnogonida. Adv Marine Biol 24:1–96

Bain BA (2003) Larval types and a summary of postembryonic development within the pycnogonids. Invertebr Reprod Dev 43:193–222

Brusca RC, Brusca GJ (2003) Invertebrates, 2nd edn. Sinauer Associates, Sunderland, MA, USA

Fahrenbach WH (1994) Microscopic anatomy of pycnogonida. I. Cuticle, epidermis, and muscle. J Morphol 222:33–48

Fry WG, Stock JH (1978) A pycnogonid bibliography. Zool J Linn Soc 63:197–238

King PE (1973) Pycnogonids. St. Martin's Press, New York, NY, 144 pp

Tomaschko K-H, Wilhelm E, Buckmann D (1997) Growth and reproduction of *Pycnogonum litorale* (Pycnogonida) under laboratory conditions. Marine Biol 129:595–600

Vilpoux K, Waloszek D (2003) Larval development and morphogenesis of the sea spider *Pycnogonum litorale* (Strom, 1762) and the tagmosis of the body of Pantopoda. Arthropod Struct Dev 32:349–383

Wilhelm E, Buckmann D, Tomaschko K-H (1997) Life cycle and population dynamics of *Pycnogonum litorale* (Pycnogonida) in a natural habitat. Marine Biol 129:601–606

Seaweed Flies

Members of the family Coelopidae (order Diptera).

► Flies

Secondary Pests

Pests that normally are not considered to be important, but which become important after a change in pest control or cropping practices.

Secondary Plant Substance

Material found in plants that has no apparent role in basic plant metabolism, but which functions to deter herbivory or herbivore survival in some manner.

Secondary Production

Production by herbivores, carnivores and detritus feeders. (contrast with primary production)

Secondary Vector

Arthropods that can transmit disease organisms to animals or humans but which cannot sustain the occurrence of the disease without the presence of a primary (usually more efficient or with a different host range) vector.

Sectorial Cross Vein

Cross veins that connect radius veins at the base of the branches.

► Wings of Insects

Sedge Moths (Lepidoptera: Glyphipterigidae)

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Sedge moths, family Glyphipterigidae, total 431 species from all regions, mostly in the genus *Glyphipterix* (in the past often misspelled as

Glyphipteryx), with the largest number from the Australian-New Zealand region; actual world fauna probably exceeds 800 species. There are two subfamilies: Orthoteliinae (only a single species from Europe) and Glyphipteriginae. The family is part of the superfamily Yponomeutoidea in the section Tineina, subsection Tineina, of the division Ditrysia. Adults small (5–35 mm wingspan), with head smooth-scaled; haustellum naked; labial palpi tufted and somewhat flattened; maxillary palpi 2 -to 4-segmented. Wings elongated and forewings typically with a somewhat falcate apex in many species. Maculation generally dark with various white and metallic-iridescent spots and markings. Adults are diurnal, usually in proximity of the host plants. Larvae are mostly borers in seeds, stems, or leaf axils, and a few are leafminers, but most tropical species are unknown biologically. Host plants are mostly sedges (Cyperaceae), rushes (Juncaceae), and grasses (Gramineae), plus a few other plant families.

References

Arita Y (1987) Taxonomic studies of the Glyphipterigidae and Choreutidae (Lepidoptera) of Japan. Trans Shikoku Entomol Soc 18:1–244

Arita Y, Heppner JB (1992) Sedge moths of Taiwan (Lepidoptera: Glyphipterigidae). Tropical Lepidoptera, 3 (Suppl 2):1–40

Diakonoff AN (1986) Glyphipterigidae auct. sensu lata (sensu Meyrick, 1913). In: Amsel HG et al. (eds) Microlepidoptera Palaearctica, vol 7. G. Braun, Karlsruhe, 436 pp, 175 pl

Heppner JB (1982) Synopsis of the Glyphipterigidae (Lepidoptera: Copromorphoidea) of the world. Proc Entomol Soc Washington 84:38–66

Heppner JB (1985) The sedge moths of North America (Lepidoptera: Glyphipterigidae). Flora & Fauna Publishing, Gainesville, FL, 254 pp

Kyrki J, Itämies J (1986) Immature stages and the systematic position of *Orthotaelia* [sic] *sparganella* (Thunberg) (Lepidoptera: Yponomeutidae). Syst Entomol 11:93–105

Seed Beetles

Members of the family Bruchidae (order Coleoptera).

► Beetles

Seed Bugs

Members of the family Lygaeidae (order Hemiptera).

► Bugs

Seed Chalcids

Members of the family Eurytomidae (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Seedcorn Maggot or Bean Seed Fly, *Delia platura* (Meigen) (Diptera: Anthomyiidae)

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Seedcorn maggot was first described in Germany, but attained North America by the mid 1800s. Now it is found in temperate areas throughout the world, but usually is absent from tropical environments. Seedcorn maggot is very difficult to distinguish from turnip maggot, *Delia floralis* (Fallen), so some reports of occurrence and damage are suspect.

Life History

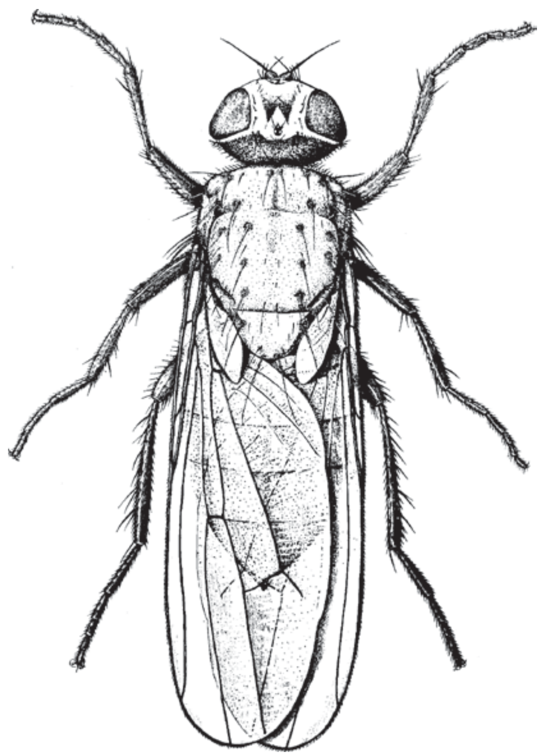
A complete life cycle requires 15–77 days, but during the warm periods of the year 16–21 days is adequate. However, due to aestivation of larvae in the summer and diapause of pupae in the winter, there usually are only 2–4 generations annually. The exact number of generations in a location is often uncertain due to asynchronous emergence, generations that are divided into diapausing and nondiapausing populations, and variable weather. The threshold temperature for egg-adult development is estimated at 3.9°C, but unlike some other *Delia* spp., it has proven difficult to predict accurately the development of seedcorn maggot from temperature accumulations.

The eggs are elongate and ovoid, with one end tapering to a blunt point and the other more bluntly rounded. The egg is slightly curved, with one side being decidedly convex and the opposite being slightly concave. The pearly white eggs are about 0.92 mm long (0.90–0.95 mm range) and 0.3 mm wide. Eggs are usually placed at the soil surface, singly or in clusters of up to 10 eggs. Oviposition occurs readily at 10–27°C. Favorite oviposition sites are sprouting or decaying seeds, decaying plant material, and organic fertilizer such as fish meal or cottonseed meal. Moist, freshly turned soil is quite favorable for egg laying; females avoid both dry and very moist soil. Duration of the egg stage is a function of temperature. It may hatch in as little as 1 day when held at 28°C, but at a more spring-like temperature of 15°C egg hatch requires 2–3 days, and at cool temperatures of 5–7°C about 7–9 days are required. Larvae dig down upon hatching, often burrowing to a depth of 6–8 cm to locate suitable food.

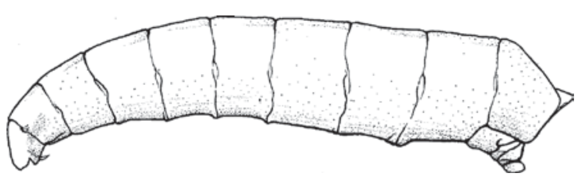
Larvae are white in color, and have three instars. They increase in length from about 0.7 mm at hatch to about 7 mm at maturity. The length of the mouthparts (cephalopharyngeal skeleton) is 0.33, 0.65, and 0.89 mm for the three instars, respectively. Larvae are reported to feed gregariously. First instar larvae cannot successfully attack food such as freshly cut or healed (corked) potato seed pieces; they survive and grow better if they locate food that is decaying. Larvae may develop at rather low temperatures, 4–7°C, but optimal growth occurs at 21–23°C. Larval development time is 20–30 days at temperatures of about 10°C, but 7–12 days under more optimal temperatures of 21–30°C. At about 14–17°C duration of the first instar is 1–3 days, second instar is 3–5 days, and third instar is 5–16 days. The anterior spiracles, a character with some diagnostic value, bears 5–8 lobes (Fig. 35).

The oval puparium is light reddish brown initially, but becomes quite dark prior to emergence of the adult. It is about 4–5 mm long and 1.5 mm wide Following a prepupal period of about 2 days pupation occurs in the soil, often at the site of feeding. When larvae have burrowed into their food, as occurs with potato seed pieces, they leave the food source prior to pupation. Duration of the pupal period is 7–14 days at 18–24°C.

The adults are grayish brown, with few distinctive markings. The male tends to bear stripes on the thorax and a mid-dorsal stripe on the abdomen, but stripes are usually lacking in females (Fig. 34). Flies measure 4–5 mm in length. The legs are black and the wings are unmarked but bear dark veins. Adults seek



Seedcorn Maggot or Bean Seed Fly, *Delia platura* (Meigen) (Diptera: Anthomyiidae), Figure 34 Adult of seedcorn maggot or bean seed fly, *Delia platura* (Meigen).



Seedcorn Maggot or Bean Seed Fly, *Delia platura* (Meigen) (Diptera: Anthomyiidae), Figure 35 Mature larva of seedcorn maggot or bean seed fly, *Delia platura* (Meigen).

food and moisture soon after emerging, and feed on the flowers of a large number of plants. Fish meal, cottonseed meal, and other materials commonly used as fertilizer are quite attractive to ovipositing adults. The duration of the preoviposition period in seedcorn maggot is 7–14 days. Mated adults live 30–40 days, with longevity increased during cool weather and shortened during the heat of summer. There are some reports that temperatures of 28–30°C are fatal to adults. Egg production is estimated at 100 per female, but this may not reflect field conditions.

A number of plants are reported to be attacked. Most vegetables plus alfalfa, cotton, strawberry, tobacco, and wheat are damaged. Seedcorn maggot also has been reported to feed on grasshopper eggs. Seedcorn maggot attacks seeds and seedlings, but there is some question about its status as a primary pest. It is often regarded as saprophagous, associated with plants that have already been damaged by other insects or plant disease.

The natural enemies of seedcorn maggot seem to be largely the same as those attacking the closely related onion maggot, *Delia antiqua* (Meigen). Among the most important are the parasitoids *Aleochara bilineata* (Gyllenhal) (Coleoptera: Staphylinidae) and *Aphaereta pallipes* (Say) (Hymenoptera: Braconidae). General predators such as ants, and the fungus *Entomophthora muscae* (Entomophthoraceae), affect the seedcorn maggot.

Damage

Damage to seeds and developing embryos may occur before the seedling breaks through the soil. Larvae are able to penetrate seeds as the seed coat splits. Rot often develops as they burrow in the cotyledon. Attack by several maggots may completely inhibit seed germination, but seedlings may suffer only deformity, or recover completely, from attack by a single insect. Despite the fact that flies are able to locate emerging seedlings readily, and oviposit freely on seedlings, larval performance is superior on freshly planted seeds. Severe damage characteristically occurs during periods of cool, wet weather, when insect activity is favored but plant growth is inhibited.

There is a strong association between seedcorn maggot and plant disease, and it is believed that some microorganisms secrete attractive volatiles. It is often argued that seedcorn maggot is primarily saprophagous. For example, research conducted in Colorado, USA, showed that seedcorn maggots were associated with *Fusarium*-infected onions, and that, in choice tests, 78% of eggs were deposited on *Fusarium*-infected bulbs. Not all microbial organisms are attractive to seedcorn maggots, however. Also, this association does not mean that crops will not be damaged by seedcorn maggot in the absence of disease, because damage by these insects is reported in the absence of apparent plant disease.

Seedcorn maggot may also be important in transmission of plant disease. They apparently assist in the overwintering and transmission of bacterial soft rot, *Erwinia carotovora*.

Management

Seedcorn maggot flies are attracted to volatiles given off by microbial organisms associated with decay and to other volatiles. Cone traps can be baited for adult monitoring with alcohol, odors of fermentation from honey-yeast or molasses solution, or oviposition stimulants such as meat and bonemeal. Enzymatic yeast hydrolyzate also is an attractive bait. If sticky traps are used, the most attractive color is gray, followed by yellow, white, blue, and other colors. Some success has been reported with yellow water pan traps.

The use of insecticides for control of seedcorn maggot is similar to onion and cabbage maggot, except that usually it is only the period of plant germination and early growth that is of concern. Therefore, there is less need for long-term protection, and for highly residual insecticides. Nevertheless, residual materials have been used, and insecticide resistance has resulted. Granular in-furrow and over-the-row applications are common. Seed treatment is often adequate.

Beans with a dark seed coat are less susceptible to injury than are white varieties, possibly due to the hardness of the seed coat and speed of germination. Seedling response to injury varies greatly among plants, with cantaloupe and watermelon being severely injured, snap bean and lima bean being intermediate, and corn most resistant.

Cultural practices that normally are considered favorable for crop growth are, unfortunately, also sometimes suitable for seedcorn maggot. There are numerous observations suggesting that freshly tilled soil is attractive to ovipositing seedcorn maggots. Buried crop residues and rotting manure also are attractive, and reduced or no-tillage systems exacerbate fly problems due to the abundance of organic material. Egg and larval survival is enhanced when plants are frequently watered. Planting in warm soil, however, favors seedling growth more than it does maggot feeding, so delayed planting is advantageous if it can be timed to avoid the large (usually June) flight. If cover crops or other sources of organic matter are present, it should be disked at least 4 weeks before planting to allow adequate time for decomposition to occur.

Growers can sometimes manipulate planting dates and escape the principal flights of seedcorn maggot, because there is often a mid-season depression in maggot abundance.

Screens and row covers are effective protectants against a wide range of insect pests, but they can be ineffective against seedcorn maggot. Because pupae overwinter in the soil, even early spring placement of a covering will not protect against attack; rather, the insects emerge beneath the covering. This is especially true with seedcorn maggot, which feeds freely on manure and rotting plant material as well as a large number of crops.

► Vegetable Pests and their Management

References

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, CA, 729 pp

Finch S (1989) Ecological considerations in the management of *Delia* pest species in vegetable crops. Ann Rev Entomol 34:117–137

Miles M (1948) Field observations on the bean seed fly (seed corn maggot), *Chortophila cilicrura* Rond., and *C. trichodactyla* Rond. Bull Entomol Res 38:559–574

Miles M (1952) Studies of British anthomyiid flies. III. Immature stages of *Delia cilicrura* (Rond.), *D. trichodactyla* (Rond.), *Erioischia brassicae* (Bch.), *E. floralis* (Fall.) and *Pegohylemyia fugax* (Mg.). Bull Entomol Res 43:83–90

Seed Predation by Insects

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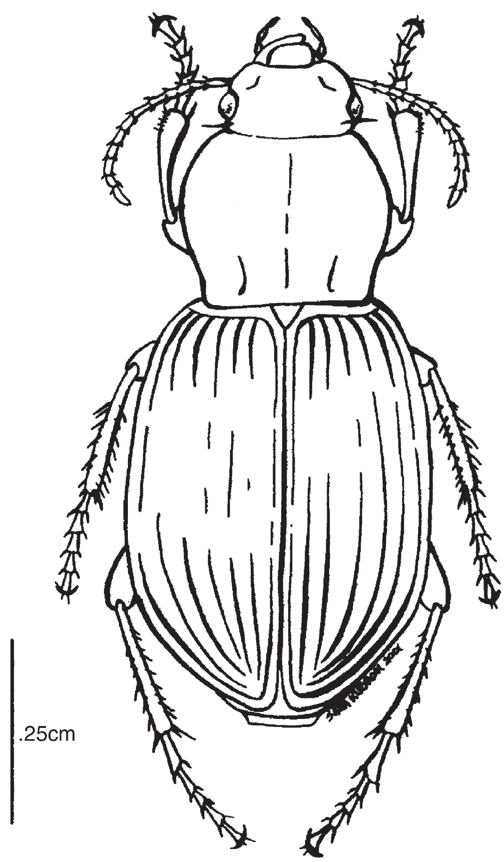
Seeds represent an important food resource. Nearly 70% of all human food comes from seeds or their products, and a large portion of the remainder is produced from animals fed on seeds. Insects also consume large quantities of seeds. Seed predation, also referred to as granivory, represents a particular type of herbivory in which a mobile predator consumes a sessile prey (the seed). This prey constitutes a high food quality, but is usually too small to allow full development of the predator with the consumption of only a single prey item. Because of its magnitude and ubiquity, entomologists and plant ecologists have long recognized the important role that seed predation plays in population and community dynamics, and in evolution. Impacts of seed predation can be found in natural habitats including temperate and tropical forests, grasslands, wetlands, mangroves, prairies, and deserts. Insect seed predation has also been documented in human dominated ecosystems such as forest plantations, orchards, and herbaceous annual crop fields.

Conceptually, and due to differences in mechanisms, seed predation can be divided into predispersal and postdispersal phenomena. Predispersal seed predation refers to the consumption of seeds on the parent plant prior to being shed. These seeds represent a spatially and temporally aggregated resource with defense mechanisms provided by the parent plant. Small and sedentary specialist feeders belonging to the insect orders of Diptera, Lepidoptera, Coleoptera, and Hymenoptera are mostly responsible for predispersal seed predation.

Despite the wide occurrence of predispersal seed predation, it is difficult to generalize about the impact that feeding on flowers, ovules, and seeds has on plant recruitment and population dynamics. Several studies have shown that compensatory flowering or seed development may reduce any consequence of predispersal predation. Nevertheless, insect feeding on flowers and developing seeds has been found to be a key factor determining the spatial distribution and density of certain plant species. For example, experimental exclusion of Diptera, Lepidoptera, Hymenoptera, and Thysanoptera has shown that interactions between insect herbivory and seedling survival could determine variation in plant density along a 100-km gradient from the coast to the inland mountains of San Diego County, California, USA.

Although relatively little is known about the extent and impact of predispersal seed predation by insect in herbaceous crop systems, several researchers have reported its occurrence. For example, in soybean fields, the joint effect of *Niesthrea louisianica*, a scentless plant bug that feeds on seeds, and fungi of the genera *Fusarium* and *Alternaria*, has been proposed as a tool to control velvetleaf (*Abutilon theophrasti*), a common weed of agricultural systems. The combined effect of seed predation and fungal infection significantly reduced the density of viable velvetleaf seeds. Other examples of predispersal seed predation of agricultural weeds include *Orellia ruficauda* (Diptera: Tephritidae) eating large quantities of seeds of Canada thistle (*Cirsium arvense*), as well as fruit fly, weevils, and moths eating giant ragweed (*Ambrosia trifida*) seeds. Glassy

Seeds are inconspicuous once they have been dispersed from the parent plant. These seeds are primarily fed upon by mobile and generalist herbivores in a process referred as postdispersal seed predation. Postdispersal seed predators include vertebrates such as birds and rodents, as well as insects of the order Hymenoptera and Coleoptera. In particular, carabid beetles of the genera *Amara*, *Zabrus*, and *Harpalus* (Fig. 36) are conspicuous seed-eaters. Because of this, considerable research has been conducted on the physiological, behavioral, and morphological adaptation of carabid beetles to seed predation. Carabid beetle larvae consume seeds on the soil surface and accumulate them in below-ground burrows, but seed predation by adult beetles occurs mostly on the soil surface. Seed predation habits of carabids are related to the shape of the mandibles. Specialist granivores of subfamily Carabinae have squat, slender and pointed mandibles, whereas true granivores of Amarini and Harpalini have short, stout, quadrate mandibles with large mandibular muscles, and generalist granivores have intermediate shapes.



Seed Predation by Insects, Figure 36 ***Harpalus pensylvanicus*, a common carabid beetles of many agricultural and natural habitats known to eat large number of seeds (Drawing by S. Kudrom).**

Ants are another important group of seed predators found in many ecosystems. In the Sonoran and Chihuahuan deserts of Arizona, USA, colonies of the specialized genera *Pogonomyrmex*, *Veromessor*, and *Pheidole*, as well as the omnivorous genera *Novomessor* and *Solenopsis* contain thousands of foraging workers. During periods of warm temperature, high humidity, and food availability these workers collect large quantities of seeds and store them in underground galleries. Similarly, in tropical agroecosystems of Mexico the native fire ant, *Solenopsis geminata*, harvests large amounts of weed and stores them underground. Despite the large number of seeds attacked by ants, the implications of this behavior for plant population and community dynamics are not straightforward. On one hand, ant nests may provide microsites rich in essential nutrients such as phosphorus and nitrogen that may boost seed germination and seedling growth. On the other hand, seeds captured by ants suffer high rates of destruction and are buried several centimeters below ground, which reduces seedling establishment and growth.

Much less is known about the seed feeding habits of the field cricket, *Gryllus pennsylvanicus*. This species is one of the most abundant and widely distributed field crickets in the northeastern United States, occurring in various grassy habitats, such as crop fields, pastures, weedy areas, roadsides, and lawns. Recent laboratory and greenhouse studies indicated that *G. pennsylvanicus* actively locates and feeds on seeds of several weed species. In a 24-h period under laboratory conditions, a female cricket ate an average of 223 redroot pigweed (*Amaranthus retroflexus*) seeds.

In contrast with predispersal seed predation, the parent plant can not respond to seed death once seeds have been shed. The lack of a physiological feedback implies that the mother plant cannot compensate for an increase in postdispersal seed predation by producing more seeds. Therefore, changes in the intensity of postdispersal seed predation generate responses that occur at the evolutionary level. Defense strategies against postdispersal seed predation include physical mechanisms (e.g., thorns, hard seed covers), camouflage, toxicity through high concentrations of a variety of chemicals, and mast seeding, i.e., the production of seeds in a bimodal distribution with years of large seed outputs and years of small seed outputs.

In recent years, there as been a growing interest in the potential of pre- and postdispersal invertebrate seed predators to act as biological control agents of invasive plants and agricultural weeds. The probability of success of seed-feeding insects in reducing plant abundance depends not just on the establishment and reproduction of large insect populations, but also on characteristics of plant populations. If seed production is high, seedbank density is large, and there are few "safe sites" for germination and establishment, then the density of these sites, not the number of seeds in the soil, determines seedling densities. It is also necessary to consider the number of seedling plants that reach adult stages of development. Nonetheless, there are several cases in which successful control of invasive plants has been achieved through seed feeding insects. For example, the apionid *Trichapion lativentre* and the weevil *Ryssomatus marginatus* feed on seeds prior to their dispersal. These two insects have been successfully employed in South Africa to reduce the abundance of *Sesbania punicea*, an invasive shrub from South America. Also, two seed-head attacking flies, *Urophora affinis* and *U. quadrifasciata*, are promising biological control agents for control of spotted knapweed (*Centaurea maculosa*), which is a serious problem in rangelands, meadows, and roadsides, especially in sandy soils. Under experimental conditions, the joint effect of these two flies can reduce spotted knapweed seed production up to 95%.

Despite the importance of seed feeding insects as biological control agents, non-target effects may be serious potential problems. For example, the Eurasian weevil *Rhinocyllus conicus* has been released in Canada and the United States since 1968 for the biological control of introduced thistle species. This weevil feeds on thistle seedheads and attacks not just the targeted invasive species, but several species of native thistles.

In herbaceous crop systems, invertebrate seed predation appears to be a relatively safe strategy to control agricultural weeds. The relatively large size that crop seeds have in comparison with agricultural weeds, the short time span between crop planting and emergence, the tendency of invertebrate seed predator populations to peak when crops are harvested rather than when they are planted, the ground-dwelling habits of invertebrate seed predators, and their inability to fed on buried seeds suggest that invertebrate crop seed predation should not be a concern to farmers.

In conclusion, insect seed predation is a particular type of plant/insect interaction occurring in both natural habitats as well as agricultural systems. Because of the extremely diverse nature of insect-seed relations, it is difficult to make generalizations about the dynamics and consequences of insect seed predation. However, several patterns emerge: (i) seed predation involves plant-insect interactions that have coevolved in chemical, spatial, and temporal dimensions; (ii) invertebrate seed predation involves processes spanning from the individual energy budget to dynamics of entire communities; (iii) due to several biotic and abiotic factors, seed predation by insects is highly variable in time and space, (iv) because insects predators are usually selective, seed predation has a strong potential to affect plant population and community dynamics; and (v) the cumulative effects of insect seed predation coupled with other sources of plant mortality, such as seedling herbivory and seed decay, can determine spatial patterns of plant abundance. Finally, entomologists interested in developing a weed biological control program based on pre- or postdispersal seed predation should carefully study the potential for non-target effects prior to the release of natural enemies.

► Food Habits of Arthropods
► Ground Beetle Feeding Ecology

References

Crawley MJ (1992) Seed predators and plant population dynamics. In: Fenner M (ed) Seeds: the ecology of regeneration in plant communities. CAB International, Wallingford, Oxon, UK, pp 157–191

Janzen DH (1971) Seed predation by animals. Ann Rev Ecol Syst 2:465–492

Louda SM (1989) Predation in the dynamics of seed regeneration. In: Leck MA, Parker VT, Simpson RL (eds) Ecology of soil seed banks. Academic Press, New York, NY, pp 25–51

Menalled F, Liebman M, Renner K (2006) The ecology of weed seed predation in herbaceous cropping systems. In Batish D (ed) Handbook of sustainable weed management. Food Products Press, Binghamton, NY, pp 297–328

Seed Treatment

A pesticide application to the seed prior to planting to protect the seed, and sometimes the seedling, from injury.

► Insecticides
► Insecticide Formulations

Segment

A major subdivision of the body or appendage, separated from other segments by areas of flexibility.

Selective Pesticide

Pesticides that are toxic principally to the target pest. Pesticides having few adverse effects on non-target (beneficial) organisms.

Selective Pressure

A force acting on populations that results in some individuals leaving more progeny (descendents, genes) than others, contributing to natural selection.

Self-Regulation

The concept that deterioration in the intrinsic quality of individuals regulates populations rather than some external factor such as predators or weather.

Selys-Longchamps, Michel Edmond De

Michel Selys-Longchamps was born at Paris, France, on May 25, 1813. Though lacking formal education, he was a man of wealth, rank, and political influence. He represented various communities in the Belgium parliament and later served as senator and then president of the senate. In addition to such public service, Selys-Longchamps was interested in Odonata, as well as neuropteroid and orthopteroid insects, and in ornithology. His wealth and influence allowed him to amass one of the great insect collections of Neuroptera and Orthoptera. He is now considered to be the father of the study of Odonata. Selys-Longchamps authored about 250 publications, including "Revue des odonates ou libellules d' Europe" in 1850, "Catalogue des insectes Lépidoptères de la Belgique," (1857) and "Memoirs of Odonata from New Guinea, Philippines, Japan, palearctic regions, Europe, Sumatra, and Burma" (1878–1891). He died at Luttich, Belgium, on December 11, 1900.

Reference

Essig EO (1931) A history of entomology. Macmillan, New York, 1029 pp

Sematuridae

A family of moths (order Lepidoptera). They commonly are known as American swallowtail moths.

► American Swallowtail Moths

► Butterflies and Moths

Semelparity

When organisms produce all their progeny in a single reproductive event, or over a short period of time.

Semelparous

This is used to describe insects that are short-lived as adults, and that lay eggs in a short period of time. This is used in the context of mosquito biology.

► Iteroparous

Semilooper

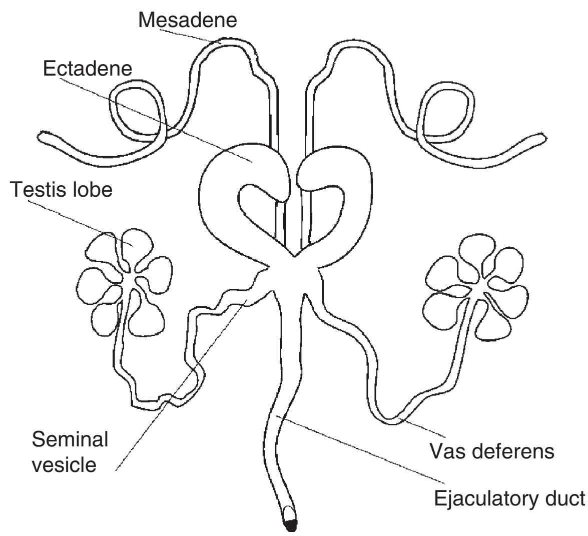
Caterpillars, usually of the order Lepidoptera, family Noctuidae, with a reduced number of prolegs, usually one or two pairs fewer than normal. These loopers move in a looping motion, but the looping movements are small. (contrast with looper)

Seminal Vesicle

An expansion of the vas deferens of the male which stores sperm (Fig. 37).

Semiochemical

Any chemical involved in the chemical interaction between organisms, particularly signaling



Seminal Vesicle, Figure 37 **Diagram of a male reproductive system as found in *Tenebrio* (Coleoptera) (adapted from Chapman, The insects: structure and function).**

chemicals that allow transfer of a message. These also sometimes are called "infochemicals." They may be intraspecific or interspecific. Examples include pheromones, kairomones, allomones, and synomones.

► Chemical Ecology
► Allelochemicals
► Pheromones

Semiochemical Parsimony

The natural products produced by insect exocrine glands (external secretions) serve multiple functions. Many exocrine secretions that have been identified with a single function (e.g., alarm and sex pheromones) often possess additional functions that are highly adaptive for their producers. Thus, insects may exploit the secretions of a single gland for unrelated diverse roles that can include defense, sexual attraction, and communication. The multifunctional compounds secreted by insects are termed "semiochemicals" and primarily include pheromones (communication chemicals) and allomones (defensive chemicals). These compounds, which have been identified in insect species in at least six orders, had often been assigned single functions, but it is now evident that they possess a variety of unsuspected – and vital – additional functions as chemical regulators of a large diversity of behaviors. This phenomenon has been described as "semiochemical parsimony" as a reflection of the great adaptiveness of insects manipulating their exocrine products.

► Multifunctional Semiochemicals
► Allelochemicals
► Chemical Ecology

Semisocial Behavior

A level of sociality less than eusocial behavior. A type of presocial behavior. As in quasisocial behavior, semisocial behavior involves individuals of the same generation sharing a nest and cooperating in brood care. However, it also includes division of reproductive behavior, with a worker caste caring for the young of the reproductive caste.

► Presocial
► Solitary
► Communal
► Subsocial
► Quasisocial
► Eusocial Behavior

Senescence

The process of aging in organisms.

Senescent

The period of life after maturity.

Sensillum (pl., sensilla)

A simple sense organ associated with the integument, often taking the form of a hair or bristle.

Sensorium (pl., sensoria)

A transparent sensory pit on the antennae, usually near the tip.

Sensory Neuron

Nerves that connect a peripheral sensory location with the insect's central nervous system. Types of sensory neurons include: mechanoreceptors (for touch, position and sound), chemoreceptors (for taste and smell), hygroreceptors (for humidity), photoreceptors (for light), and thermoreceptors (for heat).

► Nervous System

Sentinel Host

A method of early detection of viruses transmitted by mosquitoes. Various birds, most often chickens, are caged in areas where mosquitoes are active.

Blood from the birds is sampled periodically and tested for antibodies specific to arboviruses of interest. Antibody presence can trigger warning of mosquito transmitted disease in human and animal populations.

► Mosquitoes

Sepsidae

A family of flies (order Diptera). They commonly are known as black scavenger flies.

► Flies

Septicemia

A morbid condition caused by the multiplication of bacteria in the blood, and accompanied by production of toxins. *Serratia* and *Streptococcus* species commonly are implicated.

Septobasidium

Septobasidium (Order: Septobasidiales, Phylum: Basidiomycota, anamorph: *Harpographium*) is parasitic on colonies of scale insects. *Basidiospores* germinate on the host insect, and hyphae penetrate the cuticle and underlying tissues. Additionally, an extensive hyphal mat forms over the insect as it adheres to the host plants. In *Septobasidium*, this hyphal mat may encase an entire colony of insects with each insect located in an individual chamber. Hyphal mats are often easily recognizable and range in color from brown to yellow, red, or purple. These fungi usually do not kill host scales, but do cause sterility in infected individuals. They cannot survive in nature without the host insects, depending upon them for nutrients and dispersal. In turn, the fungi form an umbrella-like structure that provides a protective environment for any uninfected scales that exist under the mycelial umbrella. At the level of the colony, the relationship between Septobasidiales and scale insects may therefore be considered to be mutualistic.

Reference

Couch JN (1938) The genus *Septobasidium*. University of North Carolina Press, Chapel Hill, NC

Sequential Sampling

A sampling plan in which “stop-lines” continually assess the need for additional sample units during the sampling effort on a given day or time interval. These stop lines are typically based on a prescribed level of desired precision or classification accuracy. Sequential sampling is efficient because no prior knowledge of density is required and no more sample units than necessary are collected. (contrast with fixed-sample size sampling).

► Sampling Arthropods

Sericostomatidae

A family of caddisflies (order Trichoptera).

► Caddisflies

Sericulture

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The production of silk is known as sericulture. Normally, silk is produced from the cocoons of the mulberry or Chinese silkworm, *Bombyx mori* (L.), though other species may be used. For example, in India most silk is produced by *B. mori* fed on mulberry, but smaller quantities of tasar silk, muga silk, and eri silk are also produced, contributing importantly to the rural economy. Some of the species that have been used for silk production, and area of occurrence, include:

Bombycidae (silkworm moths)
- *Bombyx mori* (silkworm) (Asia, Europe)
- *Bombyx* spp. (India)

Lasiocampidae (tent caterpillars, lappets, etc.)

Gonomera postica (Africa)

Trabala vishnou (Oriental lappet moth) (Southeast Asia)

Notodontidae (prominent moths)

Anaphe infracta (African wild silkworm) (Africa)

Saturniidae (emperor moths, giant silkmoths)

Actias selene (moon moth) (India)

Antheraea mylitta (India)

Antheraea paphia (tussor silkworm) (Southeast Asia)

Antheraea pernyi (Chinese oak silkworm) (China)

Antheraea yamamai (Japanese oak silkworm) (Japan)

Attacus atlas (atlas moth) (New and Old World tropics)

Eriogyna pyretorum (giant silkworm moth) (Southeast Asia)

Naudaurelia spp. (silkworms) (Africa)

Samia cynthia (Ailanthus silkworm moth) (formerly India to China, now also Europe, North America, South America)

Philosamia ricini (Eri silkworm) (India, Southeast Asia)

History of Silk Production

Bombyx mori has been domesticated since about 2700 BC, and probably no longer survives in the wild. According to Chinese history, China's third emperor Huang-ti directed his wife Hsi-ling-chi to examine the silkworm, and to assess its potential for making thread. According to legend, she not only discovered how to rear silkworms, but also how to unravel the silk from the cocoon and to make garments from the silken threads. Initially, only members of the royal family were allowed to wear garments of silk. The usefulness and beauty of the resultant garments eventually led to construction of the "silk road" from China to the Mediterranean region, along which not only silk but also jade, gold, and new ideas spread. The Chinese guarded the secret of silk production closely, but according to legend the Roman Emperor objected to the exorbitant prices he was required to pay to obtain silk, and he recruited spies to discover how silk was cultured. Eventually the secrets spread both eastward to Japan and Korea, and westward to India and to eastern Europe. By the eighteenth and nineteenth centuries, Europe was producing great quantities of silk. The great French scientist Louis Pasteur is remembered for many achievements, but one of the most notable is the rescue of the French silk industry in 1870 through discovery of a disease of silkworms (pebrine) and ways to manage the disease.

It is interesting to note that attempts were made to establish sericulture in America beginning in the 1600s. Unlike introduction of sericulture to Europe, however, it was unsuccessful. Particularly in the early and mid-1800s, the idea of silk culture became very popular in the United States. Promotion of silk culture can be traced to the promotional practices of the agricultural newspapers and journals of the 1820s, a time when sericulture was also being promoted by governments in Europe. Silk production was viewed as attractive because it would be another cash crop, as well as being a crop could be harvested in as little as 6 weeks, one that required little initial cash outlay, and one that would use land that otherwise was unusable for mulberry propagation. It was advanced as a suitable enterprise for anyone who could grow mulberry plants, and coincides with the introduction from China of Asian mulberry (although native mulberry is suitable), and a time when industrialization/mechanization was freeing up labor that was seeking alternative employment. It was also a suitable occupation for women, children, and others not readily employed in occupations requiring heavy labor. Inhabitants of northern states imagined that silk would compete with southern cotton as a wealth-generating commodity. Lastly, silk production challenged America's self-image of being populated by exceptionally creative, ingenious people who could solve any problem if they invented and applied appropriate technology. By 1939 many Americans were actively involved in silkworm culture as a "cottage industry," and some made a profit, but the cold winter of 1939–1940 devastated the Asian mulberry trees, and the industry never recovered. In hindsight, it seems that the principal promoters of sericulture in

America were individuals who benefited from the sale of mulberry plants. Indeed, the principal profits were made by tree speculators who made their profits before the weather-induced collapse.

The reduced availability of cotton following the American Civil War led to further, but more modest, interest in sericulture. Reportedly this led to the introduction of gypsy moth, *Lymantria dispar* (L.), to America from Europe by E. Leopold Trouvelot, an American naturalist. Trouvelot believed that gypsy moth could be a useful source of silk. However, not only did it not prove to be a practical source of silk but it developed into one of North America's worst forest pests. Other attempts to establish silk production in the western hemisphere were made in the late 1800s and early 1900s, but none succeeded. Now, production of silk using *B. mori* is dominated by China and Japan. Considerable quantities of silk are also produced in India, including silk produced using other species. In India, *Antheraea mylitta*, *A. perniyi*, and *A. royeli* are used to produce tasar silk by rearing them on *Terminalia* spp. trees. Also, *Antheraea assama* is reared on *Machilus bombycina* and *Litsaea polyantha* trees to produce munga silk, and *Philosamia ricini* is cultured on castor for eri silk.

Silkworm Culture

Silkworms typically are reared at about 24°C. The egg stage of *B. mori* requires about 10 days, followed by 25–30 days for the larval stage, and 10 days for the pupal stage. There are four instars during the larval stage, with about 95% of food consumption occurring in the terminal two instars. Fresh foliage is provided continuously to the growing larvae, usually spread on paper. Cleanliness and good air-flow are essential to prevent disease. When they are ready to pupate, however, they must be provided with brush or straw on which to construct their cocoons, which are made from silk. Some adults are allowed to emerge from the cocoon to mate and produce eggs, of course, but most are killed by heat to prevent adult emergence because escape of the moth from the cocoon breaks the silk thread. The female moth produces about 400 eggs.

Different strains of *B. mori* are used in silk production. Univoltine and bivoltine strains naturally produce only one or two generations per year, respectively, but by treating the eggs with hydrochloric acid and high temperature it is possible to disrupt diapause and obtain up to four generations. Other, multivoltine strains produce up to six generations per year, but these insects are smaller than the univoltine and bivoltine strains, so they produce less silk per cocoon.

Silk Production

The mature silkworm spins its cocoon from one continuous filament of silk, which makes harvest of the silk possible. The process starts with softening of the cocoon, which is done in hot water. The individual strand can then be unwound from the cocoon; a good-quality cocoon may produce 350–750 m of filament. The individual filament of silk is very fine, so several must be wound together (reeled) to form a thread strong enough to handle. Not all silk can be unwound successfully, but other processes use the waste silk. Once the silk filaments are reeled (this product is called "raw silk") it can be dyed or twisted in several ways to give it unique character. The silk processing can be done by hand, or on machines called "filatures." Once assembled, the raw silk is twisted with other silk to give it further strength and thickness, a process called "throwing." This latter step is typically done by machine in factories. The silk can then be woven into various textiles using standard processes, but using special machinery better suited for the delicate nature of silk.

Silk production is an important enterprise. The leading producers are China, Japan, India, South Korea, and some of the former Soviet republics. In China, mulberry and silkworm cultivation has been fully integrated with fish farming. Pond mud, rich in organic material and nutrients, is used to fertilize mulberry plants. The mulberry leaves are harvested to feed to silkworms, resulting in production of silk. Remnants of the mulberry harvest, caterpillar feces, and other remnants of silkworms are fed to fish in ponds. The fish are harvested for food, but their wastes enrich the pond bottoms, producing fertile mulch to re-initiate the plant and silkworm production processes. Thus, the "mulberry plot-fish pond" concept represents integrated farming with complete recycling of wastes, and spawns affiliated enterprises such as silk reeling.

► Silkworms
► Eri Silkworm
► Gypsy Moth
► Costs and Benefits of Insects

References

Creek AB (1986) *Bombyx mori* and Americans; or, here we go round the mulberry bush. University of Rochester Library Bulletin 39
Ganga G (2003) Comprehensive sericulture. Science Publishers, Enfield, NH, USA
Hamamura Y (ed) (2001) Silkworm rearing on artificial diet. Science Publishers, Enfield, New Hampshire, USA, 311 pp
Hisao A (1994) Principles of sericulture. A.A. Balkema, New Delhi, India, 376 p
King BM (2005) Silk and empire. Manchester University Press, New York, 195 pp
Molà L (2000) The silk industry of Renaissance Venice. Johns Hopkins University Press, Baltimore, MD, USA, 457 pp

Serosa

The membrane that separates the egg shell (chorion) from the developing embryo and other components of the egg.

► Embryogenesis
► Eggs of Insects

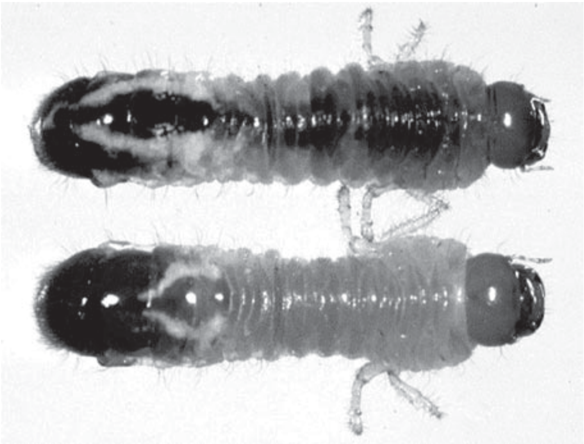
Serrate

Notched, like the teeth of a saw.

Serratia entomophila

Several species within the genus *Serratia*, including *Serratia marcescens*, *S. entomophila* and *S. proteamaculans*, have been identified as entomopathogenic. These species can be isolated using the selective caprylate thallous agar. Many *S. marcescens* strains produce characteristic bright red colonies. Insects infected with *S. marcesens* succumb within 1–3 days and often exhibit a reddish tinge. Whether or not *S. marcesens* is able to actively invade healthy insects is unclear. In many cases, this disease has been associated with poor sanitation and crowded rearing conditions. Certain parasitic hymenoptera have been reported to vector this bacterium on contaminated ovipositors. Very likely, both the pigmented and non-pigmented *S. marcescens* strains are opportunistic pathogens.

Strains of *S. entomophila* and *S. proteamaculans* are true pathogens of the New Zealand grass grub, *Costelytra zealandica*, and are the causal agents of amber disease. *Serratia* strains that induce amber disease possess a common large 140 kb plasmid (pADAP) which, when removed by heat-curing cells, resulted in loss of virulence. These pADAP plasmid bearing strains of *Serratia* exhibit a high degree of host specificity and have been found to infect only *C. zealandica*. Larvae infected with pathogenic *S. entomophilia* and *S. proteamaculans* rapidly cease feeding. It has been shown that infection by pathogenic *Serratia* strains causes a reduction in the trypsin activity in the gut, disrupting the normal digestive process. The gut contents, which are normally black, are clarified, conferring an amber coloration to infected larvae (Fig. 38). The amber larvae are unable to feed and assimilate nutrients and undergo a starvation period that may last from 1 to 4 months. During this period, the bacteria colonize the gut and become attached to cuticular surfaces including the external cuticle. Late in infection, bacteria may penetrate the hemocoel and cause a generalized septicemia. Alternatively, the colonizing population of this pathogen may be displaced by secondary bacteria prior to



Serratia entomophila, **Figure 38 Healthy (*top*) and infected (*bottom*) *Costelytra zealandica* grubs. Note the absence of the dark underlying midgut in the grub infected with *Serratia entomophila*. These amber grubs have voided their guts and have ceased feeding.**

host death. Interestingly, the pathology induced by *S. entomophila* is similar to that caused by *S. proteamaculans*.

References

Jackson TA, Huger AM, Glare TR (1993) Pathology of amber disease in the New Zealand grass grub *Costelytra zealandica* (Coleoptera: Scarabaeidae). J Invertebr Pathol 61:123–130

Jackson TA, Boucias DG, Thaler J-O (2001) Pathobiology of amber disease caused by *Serratia* spp. in the New Zealand grass grub *Costelytra zealandica*. J Invertebr Pathol 48:232–243

Serritermitidae

A family of termites (order Isoptera).

► Termites

Sesiidae

A family of moths (order Lepidoptera). They commonly are known as clearwing moths.

► Clearwing Moths

► Butterflies and Moths

Sessile

Immobile; incapable of moving.

Seta (pl., setae)

A hair or bristle.

Setaceous

Bristle-like. This term usually is used to describe antennae.

► Antennae of Hexapods

Setal Map

A diagrammatic representation of the setae found on the body of larvae.

Setose

The occurrence of large numbers of setae or bristles on the surface of a structure.

Sex Attractant Pheromones

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Pheromones are chemicals emitted and secreted by an individual and received by another individual of the same species, in which they induce a species specific reaction. By far the greatest variety of pheromone-mediated systems occurs among insects. Sex pheromones (chemicals, or blends of chemicals, emitted by an individual of one sex for the purpose of inducing sexual behaviors by members of the opposite sex) are the only pheromone mediated system in common usage by members of all insect orders. This undoubtedly stems from the universal need to reproduce and the development of chemosensory organs early in the evolutionary history of Hexapoda, perhaps even before the development of light-sensitive organs. In general, sex pheromones act as sexual attractants when they induce the receiving sex to move toward the releasing sex or as copulatory stimulants, or aphrodisiacs, when released or perceived in close proximity to the receiving sex to induce a receptivity or copulatory behaviors. However, it should be noted that attractant pheromones also may act as copulatory stimulants at close range. Although known sex pheromones act to induce a behavioral change in the receiving sex (releaser pheromones) there is no reason not to assume that sex pheromones could have primer effects and induce physiological changes associated with sex. Indeed, it is quite conceivable that volatile pheromones could induce release of neuropeptides or other rapidly dispersed hormones or cause nervous signals that would induce physiological changes required for effective mating. Quite simply, we have not looked extensively for such effects.

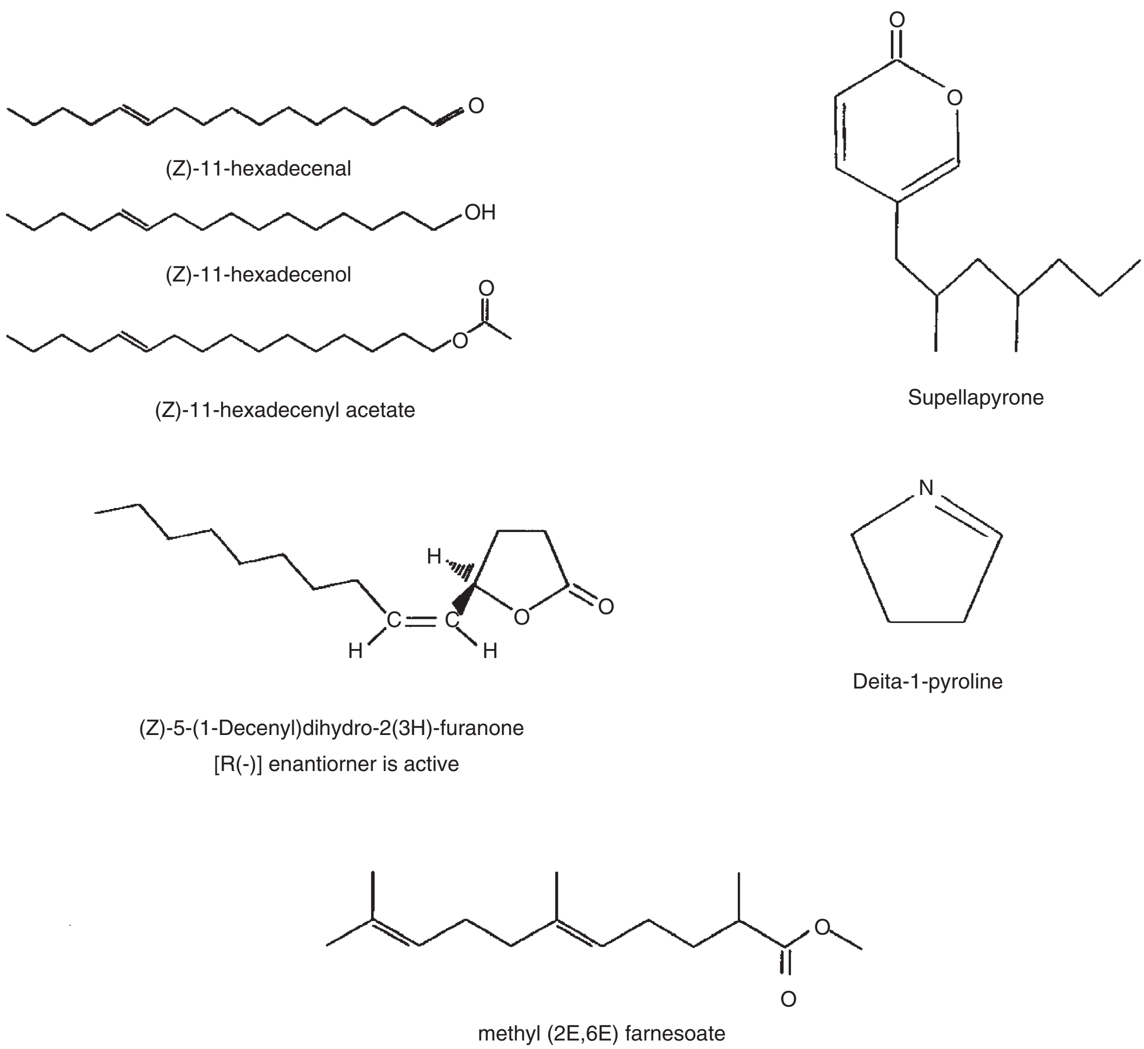
Historically, the use of conspecific attractant pheromones by insects was documented as early as 1690 when John Ray reported several male *Biston betularia* (Lepidoptera) flying around a caged female. This knowledge of the attractive capacity of female Lepidoptera was used by such great naturalists as Fabré for collection of rare specimens; the procedure used was essentially the same as that of Ray. The use of live females, and naturally produced sex pheromones for population monitoring of the gypsy moth, *Lymantria dispar* (L.), began as early as 1914, but by 1920 females had been replaced by organic solvent extracts of abdomen tips, which remained attractive for longer periods of time than did females. Attempts to isolate the chemicals responsible for induction of sexual attraction and behavior also were begun in the 1920s. However, the methods available for chemical analysis were inadequate to obtain concrete identifications and required such tremendous amounts of sample that little headway was made. Butenandt and his colleagues identified the first sex pheromone, produced by females of the silkworm moth, *Bombyx mori* (L.), in 1959. The elucidation of this pheromone, bombykol ((*E*,*Z*)-10,12-hexadecadiene-1-ol), had taken 20 years and required sacrifice of 500,000 females. With the development of improved analytical chemistry techniques, methods for collection of volatile chemicals released by insects, highly sensitive electrophysiological techniques like the electroantennogram detector and sophisticated bioassay techniques, the isolation and identification of sex pheromone components has become much easier, rapid and requires far fewer insects than those used for earlier work. In fact, sex pheromones have now been identified for at least 2,000 species representing more than 90 families of insects, and the list grows every day.

Chemistry

Sex pheromones used by insects are all lipidic in nature, and most are composed of acetogenins and mevalogeninsins. Apart from this, there is no general theme associated with the types of lipids that act as pheromones. However, relatively low molecular weight compounds (20 carbons or less) generally serve as long distance attractants because of their volatility. Most of these contain oxygenated functional groups like alcohols, esters, ketones, aldehydes, epoxides, and lactones, but non-oxygenated monoterpenes, sesquiterpenes and hydrocarbons also serve as long distance attractants. Long chain wax esters and hydrocarbons that are not volatile serve as close range stimulants and require contact by the receiver in order to induce sexual behavior. Often, closely related groups of insects use pheromones synthesized in a similar fashion, as is evidenced by the use of long chain cuticular hydrocarbons as contact sex pheromones by muscid flies, the acetates and propionates of monoterpene and sesquiterpene alcohols used by scale insects, and the blends of 12–16 carbon saturated, and unsaturated alcohols, aldehydes and acetates used by noctuid moths. These moth sex pheromones are formed by δ-11-desaturation of palmitic (or octadecanoic) acid followed by varying degrees of chain shortening via β-oxidation and subsequent modification of the acid moiety to form the oxygenated functional group. Nonetheless, there are many insects that use blends of compounds that are structurally unrelated for sexual signaling. For example, males of the Mediterranean fruit fly release a blend of compounds containing straight chain alcohols, monoterpenes, sesquiterpenes, lactones, and nitrogen containing compounds including 1-pyrroline and 2-ethyl-3,5-dimethyl pyrazine (Fig. 39).

Pheromone Function

The key to effective sexual signaling with pheromones is the use of chemicals, or chemical blends, that are species specific because it is metabolically



Sex Attractant Pheromones, Figure 39 **Examples of insect sex pheromones. Sex pheromones common to noctuid moths include (*Z*)-11-hexadecenal, (*Z*)-11-hexadecenol and (*Z*)-11-hexadecenyl acetate. That of the Japanese beetle is (*Z*)-5-(1-decenyl)dihydro-2(3H)-furanone. Supellapyrone is the pheromone of the brown banded cockroach, *Delta*-1-pyroline is from the Mediterranean fruit fly and methyl (2*E*,6*E*)-farnesoate is produced by male stink bugs.**

very expensive to produce or respond to pheromones if no mating reward results. In fact, sex pheromones of insects are the primary means by which many closely related species achieve reproductive isolation. Although there are instances in which insects use a single component for sexual communication, these cases are rare and, more often than not, involve the use of chiral compounds in which one enantiomer is active and the other inhibitory. For example, the sex pheromone of the Japanese beetle is (*R,Z*)-5-(1-decenyl)-dihydro-2(3H)-furanone and the (*S,Z*) enantiomer is inhibitory. Thus, a significant decline in trap capture has been documented when as little as 1% of the (*S,Z*) enantiomer is incorporated into lures containing the (*R,Z*) enantiomer. The most common method for imparting species specificity is the use of blends of chemical compounds. As such these pheromones are best equated with perfumes because, as with perfumes used by humans, very minor differences in the blend of chemicals results in significant differences in the attractive odor of the pheromone. Blend specificity can be imparted by a number of simple changes in chemistry of the compounds including the use of: (i) compounds having different oxygenated functional groups (aldehydes, acetates, alcohols or ketones); (ii) compounds having different numbers of carbons in the skeleton; (iii) compounds having different degrees of unsaturation; (iv) compounds having different geometries of double bonds; (v) blends of compounds having different ratios of the same components; (vi) blends of compounds containing different numbers of components.

Despite the fact that sex pheromones have been identified from a large number of insect species, detailed studies on perception and signal processing have been conducted on surprisingly few insect species. Thus, we are just beginning to understand the mechanisms involved in peripheral perception and central signal processing. Peripheral perception of pheromones occurs at the antenna, where specialized sensilla act to filter out pheromone molecules from the air. The cuticular wall of the sensilla contains numerous pore tubules through which odorant molecules diffuse into the lumen of the sensilla. Once in the lumen, the pheromone molecules are bound to pheromone binding proteins that solublize the pheromone in the aqueous receptor lymph and carry them to specialized receptors on the surface of dendrites in the sensillum. Binding of pheromone molecules with receptors on the dendrites leads to a G-protein-mediated activation of phospholipase C and generation of inositol triphosphate, which activates inositol triphosphate-gated Ca^{++} channels in the dendritic membrane, and results in electrochemical signal transduction. After release from the dendritic receptor, pheromone molecules must be degraded rapidly. This is accomplished by aggressive pheromone degrading enzymes in the receptor lymph. These degrading enzymes do not distinguish between pheromone molecules that have bound with receptors, or those that have not, so there is competition between pheromone binding proteins and degrading enzymes in the receptor lymph. Pheromone-responsive axons exit the antenna and enter specialized structures in the antennal lobe of the brain called the macroglomerular complex. The macroglomerular complex is sex specific, being found only in the sex that perceives and responds to sex pheromone, and it is here that efferent axons form synapses between interneurons and afferent neurons. The actual mechanisms that translate electrical signals generated by pheromone responsive neurons in the macroglomerular complex into behavioral events associated with response to sex pheromones are, as yet, not known.

Use of Sex Pheromones for Insect Management

Sex pheromones have been targets for development of strategies for insect control because of their species specificity. Initially, sex pheromones were primarily used as monitoring tools to determine population densities of pests in agricultural crops or storage facilities and this is still the major use of sex pheromones. When deployed in traps, sex pheromones can be used as detection tools to provide: (i) an early warning system about the presence of a pest, (ii) a survey tool to determine the population distribution of insects, and (iii) a way to determine if quarantine pests have been introduced to an area. Sex pheromone trapping systems are also effective for determining a population threshold for: (i) the timing of control treatments, (ii) timing of other sampling methods, for example, searching for larvae, and (iii) risk assessment. Population monitoring also provides ways to assess population trends, the effects of control programs and dispersion of pests. Additionally, sex pheromones of insects can be effectively used to determine the distribution and spread of entomophagous insects released as biological control agents.

Sex pheromones also are used for direct control of insect pest populations. Direct control using sex pheromones can be achieved by mass trapping, attraction of pest insects to baits containing pesticide (attract-and-kill protocols) and disruption of mating. Although mass trapping is conceivably possible with sex pheromones alone, the fact that mated females are not normally captured in sex pheromone baited traps significantly reduces the efficacy of this technique. However, sex pheromones are used in combination with other attractants for mass trapping. For example, mass trapping of the Japanese beetle with lures containing the female produced sex pheromone along with the feeding attractants phenethyl propionate, eugenol and geraniol has been shown to be effective. Males are attracted to the sex pheromone in large numbers and inclusion of the feeding lure results in capture of great numbers of females. Additionally, the use of pheromones that act in dual roles has been shown to be effective for mass trapping. For example, the pheromone of the boll weevil acts as an aggregation pheromone in the spring and fall, which results in capture of both sexes, but in summer only females are attracted. Capture of both sexes in spring and fall reduces the populations significantly prior to infesting cotton, and capture of females in the summer keeps the population in check during the growing season.

A second method of population suppression with sex pheromones is the attract-and-kill system in which pheromone dispensers also contain a conventional pesticide. The key to such systems is the use of a pheromone system that is as effective, or preferably more effective, in attracting insects than is the releasing sex.

Mating disruption has become the most successful method for direct control of insect pests using sex pheromones. In this technique, large amounts of pheromone are released throughout control areas, either by strategic distribution of a relatively small number of pheromone dispensers, each of which releases substantial amounts of pheromone, or by broadcasting large numbers of small dispensers which release relatively small amounts of pheromone throughout the entire control area. Although the exact mechanisms responsible for mating disruption with pheromones are not well understood, five mechanisms have been proposed to account for mating disruption. These mechanisms include: (i) sensory fatigue in which constant exposure to high levels of pheromone causes sensory adaptation of pheromone receptors on the antenna or an habituation to pheromone in the central nervous system which, in either case, inhibits the receiving sex from responding to natural pheromone; (ii) competition between natural and synthetic sources (false trail following) in which the number of pheromone plumes in a field generated from synthetic sources is far greater than the number of the signaling sex and, thus, the receivers spend all of their time finding synthetic sources; (iii) camouflage of natural sex pheromone plumes could occur when the amount of pheromone released is so great that it forms a fog permeating the entire atmosphere which does not allow the receiver to track down a natural point source of sex pheromone (i.e., the emitter); (iv) sensory imbalance can occur when an "off blend," not so different from the natural blend that insects fail to respond to it, is completely superimposed over the natural point sources of pheromone and results in the disorientation of the insect; and (v) mating disruption also occurs when compounds that inhibit the response of insects to the natural pheromone blend are included in the synthetic disruptant, as is evidenced by disruption of

Eupoecilia ambiguella using technical grade pheromone which contains the pheromone (*Z*)-9-dodecenyl acetate plus as little as 0.1% of the inhibitory isomer (*E*)-9-dodecenyl acetate.

► Reproduction
► Pheromones
► Regulation of Sex Pheromone Production in Moths

References

Cardé RT, Minks AK (eds) (1997) Insect pheromone research new directions. Chapman and Hall, New York, NY

Millar JG, Haynes KF (eds) (1998) Methods in chemical ecology, vol.1. chemical methods. Chapman and Hall, New York, NY

Prestwich GD, Blomquist GJ (eds) (1987) Pheromone biochemistry. Academic Press, Orlando, FL

Ridgeway RL, Silverstein RM, Inscoe MN (eds) (1990) Behavior-modifying chemicals for insect management. Marcel Dekker, New York, NY

Sex Chromosome

A chromosome which is involved in sex determination.

Sex Pheromone

Pheromones that attract the opposite sex for mating. These are often used, in conjunction with traps, to monitor abundance of insects.

► Chemical Ecology
► Sex Attractant Pheromones

Sex Ratio Modification by Cytoplasmic Agents

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The normal sex ratio of progeny produced by mated diploid insects is one female to one male (1:1); typically, unmated diploid females cannot produce progeny. That normal 1:1 sex ratio is modified when unmated insects reproduce by parthenogenesis (called arrhenotoky or thelytoky). With arrhenotokous (haplo-diploid) species, such as bees and wasps in which both haploid males and diploid females occur, the sex ratio of progeny produced by mated females commonly is biased towards females, often with 2 or 3 females for each male. Unmated arrhenotokous females can produce only haploid male progeny. Thelytokous species commonly have only females, although sometimes rare males are produced. These sex-determining systems are based on the chromosomes in the nuclear genome of insects. However, normal sex ratios in insects can be modified by a number of organisms (bacteria, viruses, protozoans) and by genetic elements called meiotic drive elements, which are genes on the chromosomes that modify the normal distribution of chromosomes to egg and sperm during meiosis.

► Meiotic Drive in Insects

Cytoplasmic Agents Distort Normal Sex Ratios

Most cytoplasmic agents (bacteria, viruses, spiroplasmas) are inherited primarily through the mother and thus are cytoplasmically or maternally inherited. Cytoplasmic agents that can manipulate their insect host's sex ratio (usually increasing the proportion of females) and promote their own spread are called cytoplasmic sex ratio distorters. The spread of a cytoplasmic sex ratio distorter often reduces the fitness of its host and can drive insect populations to extinction. Sex ratio distorters are usually suspected if single-pair crosses produce a heavily biased sex ratio in the progeny, although meiotic drive agents are also possible mechanisms.

At least 50 cases have been identified in which cytoplasmic agents alter sex ratios in insects or mites. Examples are found in the Diptera, Heteroptera, Coleoptera, Lepidoptera or

Acari (mites). Cytoplasmic sex ratio distorters may be widespread, but undetected, in other arthropods. Maternal transmission rates of these agents typically are high, although a few daughters may fail to become infected. The altered sex-ratio conditions are found in natural populations at frequencies ranging from low to high. The infections may reduce fitness of the hosts, with egg hatch or larval survival reduced in the progeny of infected females. Specific examples are described below.

Spiroplasmas

The sex ratio condition of *Drosophila willistoni*, and related neotropical *willistoni* group species, is due to a spiroplasma. Spiroplasmas are maternally inherited and transovarially (transmitted in the egg) transmitted. The spiroplasmas are lethal to male embryos. Spiroplasmas can be transmitted between species by injecting hemolymph containing them. Spiroplasmas from different species are different and a virus associated with the spiroplasmas also is different for each spiroplasma. When spiroplasmas from different species are mixed, they clump because the viruses lyse the spiroplasmas of the other species.

L-Form Bacteria

The *Drosophila paulistorum* complex contains six semispecies (subgroups derived from a single species that are thought to be in the process of speciation) that do not normally interbreed in the field. When they are crossed in the laboratory, fertile daughters and sterile sons are produced. Streptococcal L-form bacteria that are associated with the male sterility have been isolated and cultured in artificial media. The L-forms are transferred through the egg cytoplasm and each semispecies is associated with a different L-form bacterium. The L-forms can be microinjected into females and can produce the expected male sterility in the progeny.

Wolbachia

These rickettsia-like organisms are one of the most commonly described microorganisms found in arthropods. *Wolbachia* are intracellular and found in the reproductive tissues, as well as in the somatic cells of some species. *Wolbachia* have different effects on their arthropod hosts, but one that is relevant to this entry is their ability to alter sex ratio. The role of *Wolbachia* as endosymbionts was discussed in the section on Symbionts of Arthropods.

Wolbachia are gram-negative rods that cannot be cultured easily outside their hosts and they are widespread, having been found in up to 76% of all insect species surveyed. In addition to insects and mites, *Wolbachia* have been found in Crustacea and nematodes. Knowledge of the physiological and phenotypic effects of *Wolbachia* on most of their hosts remains limited.

In the Crustacea, *Wolbachia* infect isopods, including *Armadillidium album*, *Ligia oceanica*, *A. nasatum*, *Porcellionides pruinosus*, *Chaetophiloscia elongata* and *Spaeroma rugicauda*. Some *Wolbachia*-infected isopods regularly produce female-biased broods because the *Wolbachia* change genetic males (homogametic ZZ individuals) into functional females. Such individuals are chromosomally male (ZZ) but phenotypically appear and function as females. These "daughters" of infected mothers produce all-female or highly female-biased progeny, resulting in isopod lineages that are chromosomally males but are functional females. Interestingly, there has been speculation that some *Wolbachia* genes have been transferred to the isopod nuclear genome—reminiscent of the movement of genes over evolutionary time from the mitochondria (originally a microbial symbiont) to the nuclear genome of eukaryotes.

Wolbachia can cause thelytoky (production of all females), male killing, and female mortality in insects and mites. Some *Wolbachia* improve fertility or vigor while others appear to decrease these traits in their hosts. Some species appear to have *Wolbachia* only in their germ line (ovaries and testes) while others have *Wolbachia* in somatic tissues, as well. *Wolbachia*-induced thelytoky (production of females only) in the Hymenoptera has been found in the Tenthredinoidea, Signiforidae and Cynipoidea, as well as at least 70 species of parasitoids (Aphelinidae, Encyrtidae, Eulophidae, Pteromalidae, Torymidae, Trichogrammatidae, Cynipidae, Eucoilidae, Braconidae, Ichneumonidae, Proctotrupoidae). Many hymenopteran parasitoids have both arrhenotokous and thelytokous strains, with thelytoky associated with the presence of *Wolbachia*.

In thelytokous populations of parasitoids, unfertilized eggs give rise to females. A number of thelytokous parasitoids (*Ooencyrtus submetallicus*, *Pauridia peregrina*, *Trichogramma* sp., *Ooencyrtus fecundus*) produce a few males, usually less than 5%, when reared at temperatures over 30°C. Heat treatments are known to reduce or eliminate *Wolbachia* infections in some species, so it is thought that the low rates of male production are due to reduction or elimination of *Wolbachia* from some females. Sometimes, the rare males produced by cured females have been shown to mate and transfer sperm, indicating that these males have normal vigor and fertility. In other cases, the rare males are infertile, suggesting that the *Wolbachia* infection had existed for a long time in the population, which could have allowed selection for essential fertility genes to be relaxed over evolutionary time. In addition to heat treatments, several antibiotics (tetracycline hydrochloride, sulphamethoxazole and rifampin) can induce the production of males in some thelytokous parasitoid populations.

The cytogenetic changes that occur during meiosis to restore an unfertilized haploid egg to diploidy (thus permitting thelytoky) has been studied in *Trichogramma*. In the eggs of *Wolbachia*-infected *Trichogramma* females, meiosis progresses to the stage of a single haploid pronucleus but the diploid chromosome number is restored during the first mitotic division. This happens because, during anaphase, the two identical sets of chromosomes do not separate and the result is a single nucleus containing two copies of the same set of chromosomes, resulting in a female that is completely homozygous at all loci.

Wolbachia infection can influence mating behavior of insects, as well as kill males. For example, populations of the butterfly *Acraea encedon* are found across Africa. In many populations, females produce only female progeny while other populations produce both males and females in a normal 1:1 sex ratio. The production of all female progeny is caused by a *Wolbachia* strain that kills males. *A. encedon* typically deposit clutches of 50–300 eggs and newly hatched larvae often cannibalize unhatched eggs, only gradually dispersing into smaller groups.

The evolution of male-killing by *Wolbachia* may be favored when the behavior and ecology of a species makes antagonistic interactions between host siblings or sib cannibalism likely. Under field conditions, the *Wolbachia* infection rates in *A. encedon* females may result in populations with a serious shortage of males. As a consequence, the mating behavior of *Wolbachia*-infected *A. encedon* has been altered. Normally males seek out and compete for individual females that are located near larval food plants. However, when male-killing *Wolbachia* are present in high frequency in a population, *A. encedon* females instead form dense aggregations in grassy areas near trees, perhaps to attract rare males as mates.

B Chromosomes and Cytoplasmic Factors

Sex ratio in the haplo-diploid (arrhenotokous) parasitoid wasp *Nasonia vitripennis* can be altered by at least two different mechanisms. Some natural populations of *N. vitripennis* carry a supernumerary or B chromosome that causes a condition called paternal sex ratio (PSR). B chromosomes are found in many plant and animal species and are small non-vital chromosomes mostly consisting of heterochromatin (DNA that is noncoding for proteins). Most B chromosomes have few genes but they often cause a small fitness cost to their host, making them selfish genetic elements. Some B chromosomes are thought to be derived from normal chromosomes and are transmitted at higher rates than expected, thus exhibiting "drive."

The PSR chromosome is carried only by haploid male *N. vitripennis* and is transmitted via sperm to fertilized eggs. After an egg is fertilized by a PSR-bearing sperm, all normal paternally derived chromosomes condense into a chromatin mass and are lost, leaving only the maternal chromosomes. The PSR chromosome itself survives. Thus, the PSR chromosome changes fertilized diploid (female) eggs into haploid males that carry the PSR chromosome.

Where did the PSR chromosome come from? Molecular analyses suggest the PSR chromosome has sequences that are homologous with sequences found in *Nasonia giraulti*, *N. longicornis* and *Trichomalopsis dubius*, but not with *N. vitripennis*. Thus, the PSR chromosome could have been present prior to the divergence of the genera *Trichomalopsis* and *Nasonia*. Alternatively, PSR may have crossed the species barrier more recently (horizontal transfer) through a series of transfers between species capable of mating. Experimental interspecific transfer of PSR was successful after these species were cured of *Wolbachia* which causes cytoplasmic incompatibility between them. The transferred PSR chromosome continued to function in both recipient species.

The sex ratio of *Nasonia vitripennis* can be modified by cytoplasmic factors, including "Son-killer," a maternally transmitted bacterium that prevents development of unfertilized male eggs and "Maternal Sex Ratio," a cytoplasmically inherited agent that causes female wasps to produce nearly 100% daughters.

Male Killing in Coccinellidae

The Coccinellidae appear particularly prone to invasion by male-killing organisms, with four different groups (*Rickettsia*, *Spiroplasma*, Flavobacteria and *Wolbachia*) having been associated with this phenomenon. Coccinellids may be especially susceptible to invasion by male-killing microbes due to their behavior; coccinellids typically feed on aphid populations that are patchy and deposit eggs in tight batches. This behavior could promote egg cannibalism by newly hatched larvae when normal prey populations are low. Such cannibalism could provide an additional mechanism by which the bacteria are transmitted to new individuals.

The evolution of the male killing ability may have evolved in the bacteria because they are almost exclusively transmitted vertically from mother to eggs; thus, bacteria in male hosts are at an evolutionary dead end, so male-killing has a fitness cost of zero from the bacterial point of view. Furthermore, the death of male embryos could augment the fitness of the remaining female brood members by providing food to those females carrying the relatives of the male-killing bacteria. A full understanding of the evolutionary dynamics of male-killers and their hosts remains elusive.

► Reproduction

Relevant Website

The European Wolbachia Project: Towards Novel Biotechnological Approaches for Control of Arthropod Pests and Modification of Beneficial Arthropod Species by Endosymbiotic Bacteria.

► http://wit.integratedgenomics.com/GOLD/Wolbachia.html

► http://www.ncbi.nim.nih.gov

References

Bourtzis K, O'Neill S (1998) *Wolbachia* infections and arthropod reproduction. Bioscience 48:287–293

Cook JM, Butcher RDJ (1999) The transmission and effects of *Wolbachia* bacteria in parasitoids. Res Popul Ecol 41:15–28

Hurst GDD, Jiggins FM (2000) Male-killing bacteria in insects: mechanisms, incidence and implications. Emerg Infect Dis 6:329–336

Jiggins FM, Hurst GDD, Majerus MEN (1998) Sex ratio distortion in *Acraea encedon* (Lepidoptera: Nymphalidae) is caused by a male-killing bacterium. Heredity 81:87–91
O'Neill SL, Hoffmann AA, Werren JH (eds) (1997) Influential passengers: inherited microorganisms and arthropod reproduction. Oxford University Press, Oxford, UK, 214 pp
Wrensch DL, Ebbert MA (eds) (1993) Evolution and diversity of sex ratio in insects and mites. Chapman and Hall, New York, NY

Sexual Recombination

The process by which DNA is exchanged by homologous chromosomes by pairing and crossing over during meiosis.

Sexual Reproduction

Reproduction involving the union of gametes (contrast with parthenogenetic reproduction).

Sexuales

In aphids, the sexual forms of male and females.

Sexual Selection

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Sexual selection is the class (i.e., form, section, axis) of natural selection that is associated with genetic differences among individuals in their ability to (i) compete for, or (ii) select, fertile partners in reproduction (i.e., mates). The former is typically associated with males, and the latter, with the female sexual role, but such distinction is continually eroded as ever more is learned of the details of mating behavior in different kinds of organisms.

Competition and mate attraction on the one hand, and mate choice on the other, can involve: direct physical combat among rivals; physical appearance reflecting health (e.g., symmetry or conformity to "type," as these reflect nutritional and disease history); vigor or strength as demonstrated via "ritualized" displays; the ability to provide or defend resources for partners, and many other comparative and competitive categories and situations.

It can be useful to think of natural selection and sexual selection as the agents of genetic changes that promote individual adaptation (any genetically controlled attribute and e.g., structure, physiological process, or behavior and that increases an organism's probable genetic contribution to succeeding generations; a characteristic that enhances an organism's chances of perpetuating its genes, usually by leaving descendants) in genetic lineages along two axes: the first axis, ecological/somatic adaptation is that connected with growth, development, maintenance, and survival; and the second, reproductive/genetic adaptation is that directly connected with procreation, the successful production of competitive, fertile offspring. Such a separation in a thought experiment quickly reveals the strong connection yet important distinction that exists between natural and sexual selections, and that must be recognized by entomologists in a number of fields and taxonomy, behavioral ecology, ecology, and pest control and management, to mention a few. For example, a taxonomist who wishes to understand the process of speciation and the genetic divergence of populations needs to give special attention to the mate choice aspects of sexual selection and its connection with classical "reproductive isolation" theory.

Examples of sexual selection phenomena in insects include weapons used by males to control resources and gain access to females. If a resource, something that females lay their eggs into or eat is relatively rare, then males that wait on or near the resource are likely to encounter potential mates among the females that come to oviposit or feed. If this resource is relatively small, then a male may be able to keep it and its associated females to himself by defeating intruding males. Under these circumstances males may have evolved weapons that intimidate or help physically remove sexual rivals. In certain wood and dung-feeding beetles (Scarabaeidae), males sometimes have enormous horns arising from the head and prothorax that are used as levers or pinchers to fling or carry other males from branches, logs, and feces.

Examples of male display and female choice are seen when resources are relatively common, and males cannot profitably wait by an oviposition or feeding site to encounter females. In such situations, should females encounter male interference at a resource site they can easily find another, one without males, where they are not forced to fend off or submit to sexual advances. Under these circumstances males tend to evolve courtship displays that persuade females that they are suitable mates. For example, certain Tephritidae, such as *Ceratitis capitata* Wiedemann (the Mediterranean fruit fly), are among the most serious pests of fruits and limit exports wherever they occur. Males produce a buzzing sound (song) with their wings as they attempt to mate, and within limits, females select as mates those with louder songs, even when a male's effort is artificially amplified by playing a recorded song at a higher volume than one could otherwise produce. The "meaning" of (i.e., relevant information within) such displays is often difficult to decipher, but it may be that the song is a display of vigor that advertises an underlying genetic quality.

Sex role reversals sometimes occur in species with male "nuptial gifts." Males sometimes provide females with a food item before mating, and in these circumstances females appear to choose mates based on the quality of the gift presented. It may be that females are primarily interested in the food, but they may also judge the ability of the male, i.e., his underlying genetic quality, by his capacity to find and capture or produce certain items. In a number of katydids (Tettigoniidae), including the agricultural pest the Mormon cricket (*Anabrus simplex* Haldeman), males produce a very large spermatophylax. This protein-containing wad of cheese-like material is associated with the ejaculate and can constitute as much as 30% of a male's body weight. Females use this substance as food and those that receive larger "gifts" have greater fecundity (achieved reproduction). When other foods are scarce, and in species where males produce an exceptionally large gift, there sometimes occurs a sex-role reversal. That is, it is the females that seek out and display toward choosy males. Male Mormon crickets estimate the weight of a potential mate, hence the numbers of eggs she is likely to produce in the future as she mounts him (orthoptera fashion) prior to copulation. Males reject light-weight females in favor heavier ones, and in this way promote the favored outcome, that their resources will be used in the production of greater numbers of offspring.

► Visual Mating Signals

References

Blum M, Blum N (1979) Sexual selection and reproductive competition in insects. Academic Press, New York, NY

Choe JC, Crespi BJ (1997) Mating systems in insects and arachnids. Cambridge University Press, Cambridge, UK

Gwynne D (2001) Katydids and bush-crickets: reproductive behavior and evolution of the Tettigoniidae. Cornell University Press, Ithaca, NY

Lloyd JE (1979) Mating behavior and natural selection. Fla Entomol 62:17–34

Sirot L (2006) The evolution of insect mating structures through sexual selection. Fla Entomol 86:124–133

Sivinski J, Aluja M, Dodson G, Freidberg A, Headrick D, Kaneshiro K, Landolti P (2000) Topics in the evolution of sexual behavior in the Tephritidae. In: Aluja M, Norrbom A (eds) Fruit flies (Tephritidae): phylogeny and evolution of behavior. CRC Press, Boca Raton, FL, pp 751–792

Thornhill R, Alcock J (1983) The evolution of insect mating systems. Harvard University Press, Cambridge, MA

Sexupara (pl., sexuparae)

In aphids of the family Pemphigidae, winged viviparous parthenogenetic females that produce both males and females.

► Aphids

Shade Tree Arthropods and Their Management

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There are unique issues associated with arthropod management of shade trees. These include: the high value of the plant material, including replacement costs; the siting of plants in areas of high human traffic; the unique management considerations associated with the above; and the aesthetic issues that can be important in management decisions.

Almost invariably, shade trees are a blend of native species and, increasingly, exotic species that have desirable features for the site. Concurrently, associated arthropod pests are also a mixture of native and exotic species and in many areas, the latter predominate. For example, among the more serious exotic shade tree pest species present in the United States are the gypsy moth, *Lymantria dispar* (L.), oystershell scale, *Lepidosaphes ulmi* (L.), the European elm bark beetle, *Scolytus multistriatus* (Marsham), the twospotted spider mite, *Tetranychus urticae* (Koch), and the Japanese beetle, *Popillia japonica* (Newman).

Hundreds of species of insects and mites seriously affect shade trees worldwide. These are often differentiated using a combination of taxa and feeding habits.

Arthropods with Sucking Mouthparts

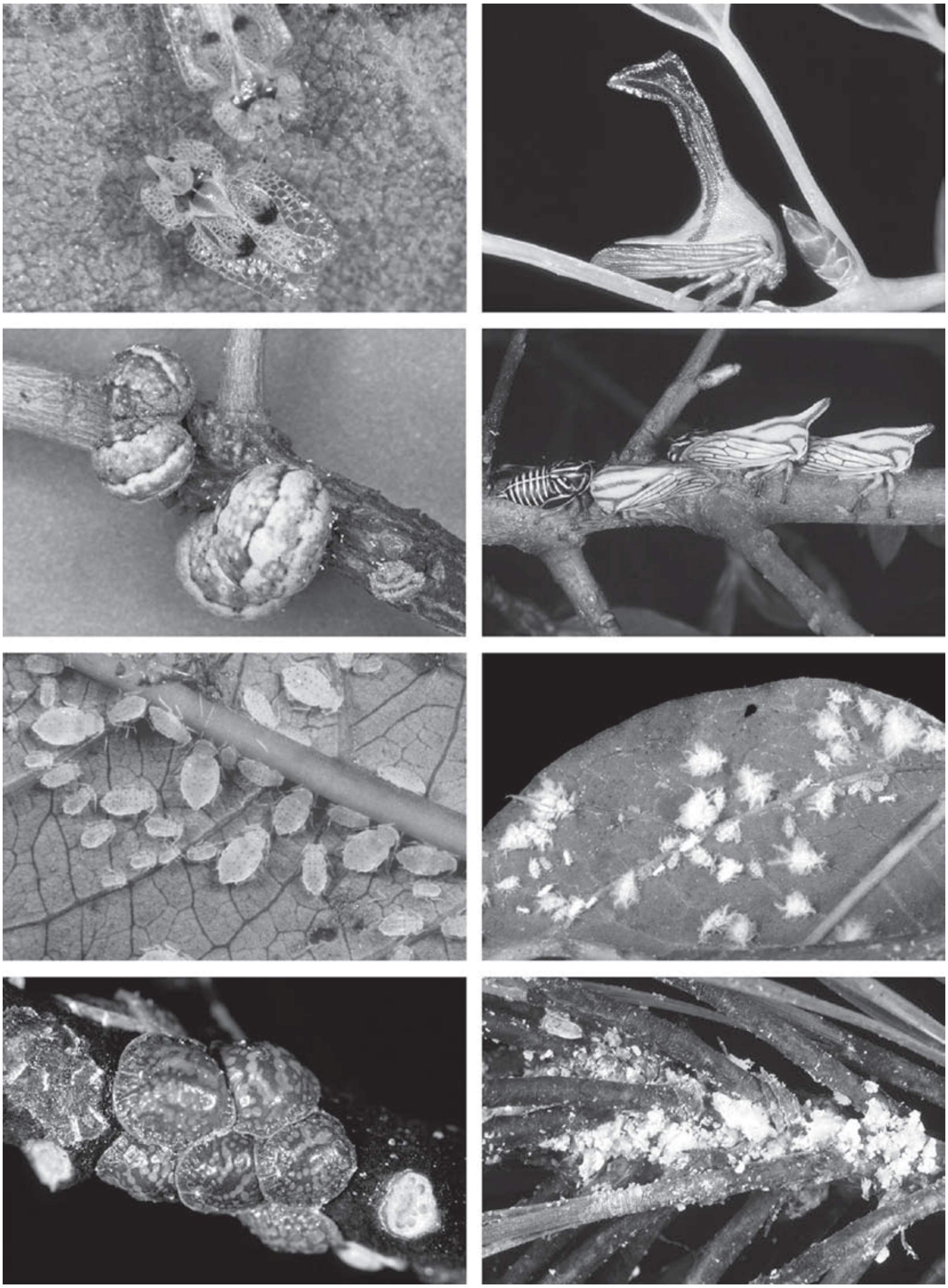
Aphids

These may be considered in a broad sense to include "true aphids" (Aphididae), as well as "woolly aphids" associated with deciduous plants (Aphididae: Eriosomatinae) and adelgids (Adelgidae). Aphids primarily extract sap from the phloem. This injury is often well tolerated by healthy plants, but may be a serious stress. Species that colonize branches and trunks, such as the hemlock woolly adelgid (*Adelges tsugae* Annand), can be particularly damaging. On some plants, aphids colonize during periods of new growth and produce serious curling distortions of leaves or needles that can adversely affect the growth and form of plants. Aphids (Aphididae) also excrete honeydew, a significant aesthetic problem with shade trees. Among the more important aphids associated with North American shade trees are the tuliptree aphid, *Illinoia liriodendri* (Monell), the apple aphid, *Aphis pomi* De Geer, the giant willow aphid, *Tuberolachnus salignus* (Gmelin), the Norway maple aphid, *Periphyllus lyropictus* (Kessler), the leafcurl ash aphid, *Prociphilus fraxinifolii* (Riley), and the woolly apple aphid, *Eriosoma lanigerum* (Hausmann).

Soft Scales

Several families of scales within the superfamily Coccoidea are associated with shade trees. Most share habits that include: phloem feeding with associated honeydew production; mobility after the first instar (crawler stage), often involving migration with early instars on foliage and later stages on small branches and twigs; and the production of hundreds or even a couple thousand eggs. Damage can include loss of vigor, dieback of branches and nuisance problems associated with honeydew.

The most important family is Coccidae, the soft scales. Among the more damaging species in North America are the cottony maple scale, *Pulvinaria innumerabilis* (Rathvon), the striped pine scale, *Toumeyella pini* (King), the European fruit lecanium, *Parthenolecanium corni* (Bouché) and the calico scale, *Eulecanium cerasorum* (Cockerell). Related families of scales of importance to shade trees include giant scales or the margarodids (Margarodidae), gall-like scales (Kermesidae), eriococcids (Eriococcidae), false pit scales (Lecanodiaspididae) and pit scales (Asterolecaniidae) (Fig. 40).



Shade Tree Arthropods and Their Management, Figure 40 **Some shade tree insects: *top left*, sycamore lace bug, *Coryuthuca ciliata*; *top right*, a thorn bug, *Umbonia crassicornis*; second row, *left*, kermes scale, *Kermes* sp.; second row, *right*, a treehopper, *Platycotis vittata*; third row, *left*, crapemyrtle aphid, *Tinocallis kahawaluokalani*; third row, *right*, Asian woolly hackberry aphid, *Shivaphis celti*; *bottom left*, tuliptree scale, *Toumeyela liriodendri*; *bottom right*, acute mealybug, *Oracella acuta* (photo credits: left column by James Castner, right column by Lyle Buss).**

Armored Scales

Armored scales (Diaspididae) include some of the most damaging scale insects associated with shade trees. Unlike the soft scales, armored scales do not feed on the phloem, but confine feeding to the mesophyll and parenchyma cells. Honeydew is not produced, but cells around the feeding site are often killed and sustained infestations can cause foliage loss, branch dieback, and increased susceptibility to canker producing fungi. Typically, armored scales produce no more than 2–3 dozen eggs that hatch within the cover (test) of the female. The first instar nymphs (crawlers) are active for only a few days and then they lose their legs at the first molt. Some important armored scales in North America include the obscure scale, *Melanaspis obscura* (Comstock), the walnut scale, *Quadraspidiotus juglansregiae* (Comstock), the pine needle scale, *Chionaspis pinifoliae* (Fitch) and the California red scale, *Aonidiella aurantii* (Maskell).

Leafhoppers

Many leafhoppers (Cicadellidae) are associated with shade trees. Most feed on the phloem, typically producing minor injuries in the form, loss of vigor and honeydew production. Others feed on the parenchyma, causing white flecking (stippling) injuries. A leafhopper of particular concern in much of eastern North America is the potato leafhopper, *Empoasca fabae* (Harris), that seriously damages the phloem when it feeds, disrupting photosynthesis and producing an injury known as "hopperburn."

One subfamily of leafhoppers (Cicidellinae), known as the sharpshooters, feed on the xylem. Some of these are capable of transmitting certain xylem-inhabiting bacteria that produce diseases of shade trees. Lethal yellowing of coconut, Pierce's disease (bacterial scorch) and ash yellows are shade tree diseases spread by leafhoppers.

Minor Insect Families

Bugs (Hemiptera)

Several families of true bugs can be damaging to shade trees. Plant bugs (Miridae) are primarily important when they feed on new growth, killing the area around the feeding site. This produces distortions of new growth and necrotic spotting; in heavy infestation, some plant bugs may temporarily kill emergent growth. Lacebugs (Tingidae) often produce pale-colored spotting of leaves, caused by the destruction of the mesophyll, which can adversely affect the appearance and vigor of plants.

Some true bugs associated with shade trees are most important not for the injuries they produce to plants, but because of the subsequent nuisance problems they produce when they move to adjacent buildings for winter shelter. The boxelder bug, *Boisea trivittata* (Say), and the western conifer seed bug, *Leptoglossus occidentalis* Heidemann, are notorious for this habit in parts of North America.

Several additional families of Hemiptera suck sap from the foliage and/or woody parts of shade trees including certain whiteflies (Aleyrodidae), mealybugs (Pseudococcidae) and psyllids (Psyllidae). These insects tend to be more important on shrubs and ornamental plants.

Spider Mites

Several species of spider mites (Tetranychidae) are important pests of shade trees. Feeding damage is caused by breaking into the surface cell layers and removing the sap. This results in small, pale colored or necrotic spots that may coalesce and produce a generalized yellowing or bronzing, often with associated premature leaf drop.

Spider mite problems can sometimes be aggravated due to pesticide use practices unfavorable to natural enemies. Most species also thrive under relatively dry conditions. Many spider mites tend to be most abundant during warmer periods of the year, such as the twospotted spider mite, *Tetranychus urticae* (Koch) and the honey locust spider mite, *Platytetranychus multidigituli* (Ewing). Others attain peak population during cooler periods of spring and fall, such as the spruce spider mite, *Oligonychus ununguis* (Jacobi) and the European red mite, *Panonychus ulmi* (Koch).

Eriophyid Mites

Eriophyid mites are commonly associated with the foliage of most shade trees, but few cause visible injury. A few, known as "rust mites," can cause bronzing of the foliage often associated with increased thickening and brittleness of the foliage. Other eriophyid mites, discussed below, produce galls.

Gall-Making Arthropods

Galls are some of the most conspicuous injuries associated with shade trees. Galls are abnormal growths caused by feeding and other activities of insects and mites. Galls on shade trees can range from being fairly simple swellings to bizarre alterations of plant tissue. Galls frequently attract considerable attention and concern, but few are damaging to the health of shade trees. Several families of arthropods produce galls on shade trees with the primary ones summarized below.

Gall-Making Aphids

Some aphids (Aphididae, subfamily Eriosomatidae) produce galls that usually take the form of a simple swelling of the leaves. These insects have complex life cycles that typically involve a spring form that produce galls on the twigs, petioles or leaves of trees followed by a summer form that develops on the roots of a different host plant. The most important gall-making aphids found on shade trees in North America are found in the genus *Pemphigus*.

Adelgids

Adelgids (Adelgidae) are associated with conifers and may produce galls that involve stunting and/or thickening of terminal growth. Typical are the Cooley spruce gall adelgid, *Adelges cooleyi* (Gillette) and the eastern spruce gall adelgid, *Adelges abietis* (L.). Most gall-producing adelgids show alternation of hosts and do not produce galls on the primary host plant.

Phylloxerans

Phylloxerans (Phylloxeridae) are uncommon pests of shade trees, limited to certain leaf and petiole gall-forming species that attack *Carya* spp. (pecan). However, other phylloxerans can be seriously damaging to other woody plants, notably the grape phylloxera, *Daktulosphaira vitifoliae* (Fitch), that produces, alternately, leaf galls and root galls on grape vines.

Psyllids

Several genera of psyllids (Psyllidae) produce galls on the foliage or on the woody parts of plants. Leaf galls on foliage take the form of blisters, pouches, or nipples. Slight swellings are produced on twigs and small branches. A very common genera in North America is *Pachypsylla*, which includes over a half dozen species all of which are associated with *Celtis* spp.

Eriophyid Mites

The eriophyid mites (Eriophyidae) associated with shade trees make an extremely diverse range of gall forms on shade trees. Simple eruptions of blisters on leaf surfaces (blistergalls) are common on some Rosaceae. Other eriophyid mites make more elaborate galls in the form of pouchgalls, or are further extended into elongate fingergalls. A proliferation of plant hairs producing small, felt-like mats is characteristic of other eriophyid mites. These are known as an erineum (erinea, pl.). Other eriophyid mites produce gross disorganization and cell proliferation of buds and flowers.

Gall Midges

Hundreds of species of gall midges (Cecidomyiidae) are associated with woody plants. Galls typically are fairly simple, involving stunting and/or swelling of foliage. Leaves and needles that are galled usually shed prematurely.

Gall-Making Sawflies

Some sawflies in the family Tenthredinidae make galls in the form of simple balls or swellings in leaves or stems, primarily of willow.

Gall Wasps

The largest family of gall making insects are gall wasps (Cynipidae). Hundreds of species produce galls of very determinate form on leaves and stems. These galls may involve ball like growths (Fig. 42), sometimes with bizarre projections and spines, that have a very different appearance from the tissues from which they are differentiated. Some galls produced by gall wasps exude honeydew.

Life cycles of many gall wasps can involve alternating forms that produce different types of galls at different periods in the life cycle. Despite their abundance, essentially, all galls produced are limited to *Quercus* spp. and *Rosa* spp. Only a very few, limited to gall production on stems and twigs, cause significant plant injury.

Defoliators

Leaf feeding on shade trees is a habit widespread among the orders Lepidoptera, Coleoptera and Hymenoptera. Phasmida and Orthoptera are minor orders associated with shade tree defoliation.

Defoliation injuries to established shade trees are often well tolerated in terms of plant health. Usually only sustained, high levels of defoliation over several years significantly increases risks to plant health. However, defoliation stresses can favor increased incidence of wood borers, bark beetles and certain fungal pathogens that act more aggressively in weakened plants.

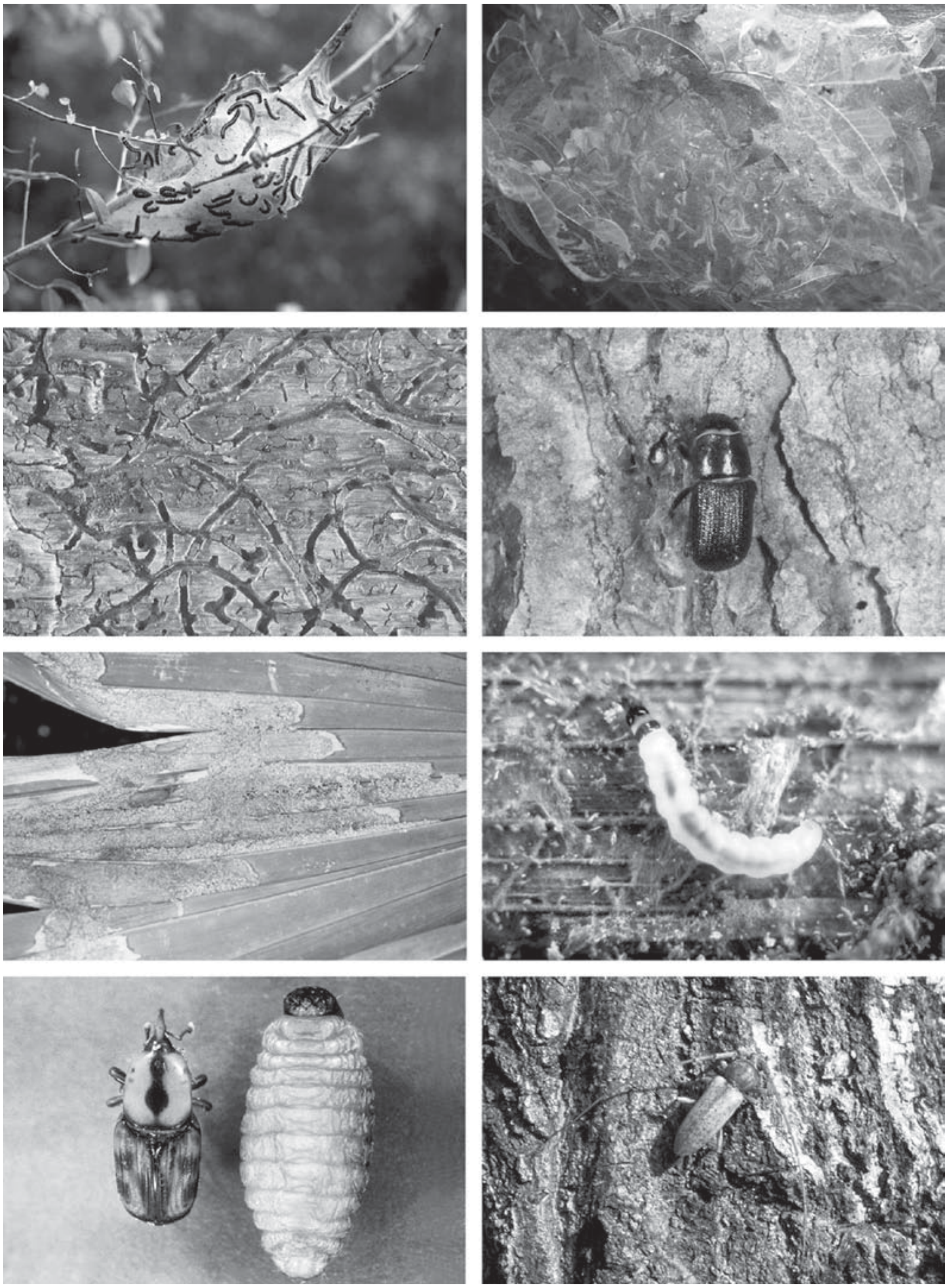
Defoliation of shade trees can have serious aesthetic effects. In addition to leaf injuries and loss, some defoliating insects may also produce large amounts of silk, a habit particularly common among some Lepidoptera in the families Lasiocampidae and Arctiidae. Dropping excrement can also be a nuisance issue with defoliating insects of shade trees.

Leafminers

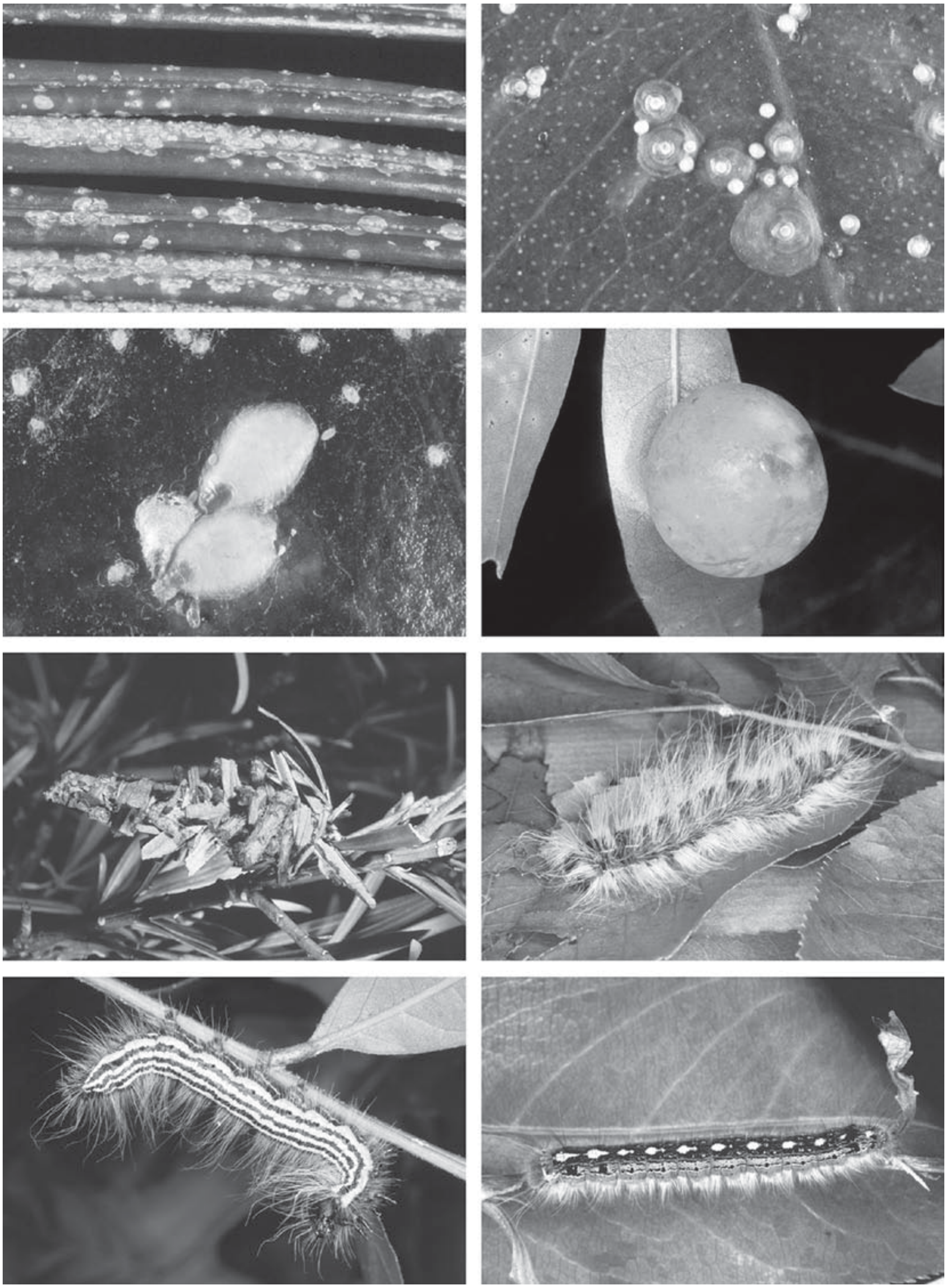
Insects that develop between the leaf surfaces are known as leafminers; species with this habit that are associated with conifers are known as needleminers. Common leafminers that are associated with shade trees are found in three orders: Coleoptera (primarily Chrysomelidae), Hymenoptera (primarily Tenthredinidae) and Lepidoptera (several families). Some Diptera, primarily Agromyzidae, are occasionally associated with shade trees, although they are more important on shrubs and ornamentals. Leafminers tend to be classified by the pattern of the mine that they produce; blotch, serpentine, or tentiform are terms commonly used in their description. Leafminers on shade trees can seriously affect the aesthetic appearance of foliage, but are very rarely significantly damaging to the health of established shade trees.

Bark Beetles

Bark beetles (Scolytidae or Curculionidae: Scolytinae) develop under the bark, scoring the cambium during their production of larval galleries and producing girdling wounds (Fig. 41). Although bark



Shade Tree Arthropods and Their Management, Figure 41 **Additional shadetree insects and damage: *top left*, eastern tent caterpillar, *Malacosoma americanum*; *top right*, fall webworm, *Hyphantria cunea*; second row, *left*, galleries caused by southern pine beetle, *Dendroctonus frontalis*; second row, *right*, black turpentine beetle, *Dendroctonus terebrans*; third row, *left*, damage caused by palm leafskeletonizer, *Homaledra sabella*; third row, *right*, palm leafskeletonizer, *Homaledra sabella*; *bottom left*, giant palm weevil, *Rhynchophorus cruentatus*, adult (*left*) and larva (*right*); *bottom right*, red oak borer, *Enaphalodes rufulum* (photo credits: left column and top right, James Castner; others by Lyle Buss).**



Shade Tree Arthropods and Their Management, Figure 42 **Additional shade tree insects and damage: *top left*, oriental scale, *Aonidiella orientalis*; *top right*, dictospermum scale, *Chrysomphalus dictyospermi*; second row, *left*, magnolia white scale, *Pseudaulacaspsis cockerelli*; second row, *right*, an oak gall, insect species unknown; third row, *left*, a bagworm, insect species unknown; third row, *right*, walnut caterpillar, *Datana intergerrima*; *bottom left*, yellow-necked caterpillar, *Datana ministra*; *bottom right*, forest tent caterpillar, *Malacosoma disstria* (photo credits: top row and second row, left, by Lyle Buss; others by James Castner).**

beetles sometime can kill shade trees, they often are considered secondary pests that largely limit infestations to trees that are wounded, diseased, recently transplanted or otherwise weakened. Almost all bark beetles have an association with fungi, primarily in the genera *Ceratocystis* or *Ophiostoma*. The transmission of fungi can greatly increase the importance of bark beetles. The most spectacular example of this involves Dutch elm disease. This devastating disease of the American elm has largely eliminated this formerly very popular shade tree in much of North America. Dutch elm disease is produced by infection with *Ophiostoma ulmi*, which is primarily spread by the smaller European elm bark beetle.

Wood Borers

Most insects that develop within wood are collectively known as wood borers. This general term includes several families from three insect orders.

In the Coleoptera, the metallic wood borers (Buprestidae), known as flathead borers in the larval stage, are particularly damaging to shade trees. The larvae make meandering tunnels beneath the bark, sometimes causing girdling of the plants. Members of the genus *Agrilus* are particularly important as shade tree pests in North America. Many longhorned beetles (Cerambycidae), known as roundhead borers in the larval stage, are also important. Larval injuries tend to involve tunneling of the interior of the trunks and branches, sometimes producing significant weakening and predisposing plants to breakage. A few species of weevils (Curculionidae), also develop as wood borers.

The most aggressively damaging wood boring insects are found in the order Lepidoptera. The clearwing borers (Sesiidae), include dozens of important species of woody plants. Larvae make irregular gouging wounds under the bark, with most species concentrating feeding around the crown of the trunk. In the Pyralidae, the genus *Dioryctria* includes several species that tunnel the trunks and branches of pines. Carpenterworms (Cossidae), is quite a large species that is associated with a wide variety of trees and shrubs.

Relatively few Hymenoptera develop as borers in shade trees. Most prominent are the horntails (Siricidae). Although they primarily limit attacks to trees that are in serious decline or recently killed, the ability of some to transmit white rot fungi can cause premature tree death.

Tip and Terminal Borers

Several insects develop by tunneling tips and terminals. This habit is particularly common among certain families of Lepidoptera and Coleoptera; Hymenoptera are a minor order with species of this habit. A particularly common group that girdles the twigs and the new growth of pines are known as "tip moths," primarily found in the lepidopteran genera *Rhyacionia* and *Eucosoma*. Some insects, such as the weevils in the genus *Pissodes*, only develop within the terminal growth of conifers.

Root Damaging Species

Roots are consumed by the larval stages of several families of Coleoptera and some Lepidoptera. The adults of many root-feeding species typically feed above ground on leaves and twigs and may be important in both stages. For example, several root-feeding weevils (Curculionidae) in the genus *Otioryhnchus*, consume roots as larvae and later chew on foliage as adults. The larvae of root-feeding species in the family Scarabaeidae also commonly feed on foliage as adults.

References

Howard FW, Moore D, Giblin-Davis RM, Abad RG (2001) Insects on palms. CABI Publishing, Wallingford, UK, 400 pp

Johnson WT, Lyon HH (1988) Insects that feed on trees and shrubs, 2nd edn. Cornell University Press, Ithaca, NY, p 556

Pirone PP (1978) Diseases and pests of ornamental plants, 5th edn. Wiley, New York, NY, 556 pp

Soma (pl., somata)

The cell body of a nerve cell. Also known as the perikaryon.

▶ Nervous System

Skiff Beetles

Members of the family Hydroscaphidae (order Coleoptera).

▶ Beetles

Sharp, David

David Sharp was born at Towcester, England, on October 18, 1840. He studied at St. Bartholomew's Hospital and the University of Edinburgh, and received a medical degree in 1866. He was torn between his interest in insects and his career as a physician, and sought positions that would allow him the leisure to also study insects. In 1885 he moved to Cambridge to serve as Curator of the University Museum, effectively ending his medical career. Sharp made many important contributions to our knowledge of Coleoptera, including "Fauna Hawaiiensis" (1899, 1908), "Beetles of Central America" (1894), "Insecta" (1895, 1899), a large portion of the Cambridge Natural History (1895 and 1899), and many other voluminous works. He authored more than 250 publications. He also worked tirelessly on behalf of "Entomologist's Monthly Magazine," "The Entomologist," and "Zoological Record." Sharp served as president of the Entomological Society of London, and was fellow of several societies. He died August 26, 1922, at Brockenhurst, England.

Reference

Lucas WJ (1922) David Sharp, M.A., M.B., F.R.S. etc., 1840–1922. Entomologist 55:217–121

Sharpshooters

Some members of the family Cicadellidae (order Hemiptera).

▶ Leafhoppers

▶ Bugs

Sheath

A structure enclosing others cells or structures.

Shelf Life

The period of time that a pesticide can be stored without losing its effectiveness.

Shelford, Victor Ernest

Victor Shelford was born at Chemung, New York, USA, on September 22, 1877. He received his bachelor's degree in 1903 and his Ph.D. in 1907, both from the University of Chicago. He remained on the staff of the University of Chicago until 1914 when he moved to the University of Illinois at Urbana. Although he retired in 1946, he remained active and continued to publish for many years. Shelford's contributions to entomology included several important and long-term studies on the relationship of insect abundance to weather and climate. However, he also worked with vertebrate populations, and made major contributions to characterization of ecosystems in North America. Some of his important publications included "Animal communities in temperate America" (1913), "Laboratory and field ecology" (1929), "Bio-Ecology" (with F.E. Clements, 1939), and "The ecology of North America" (1963). Shelford was a pioneer in the ecological sciences, was named Eminent Ecologist by the Ecological Society of America in 1968, and has been called the "father of animal ecology in the United States." He died on December 27, 1968.

Reference

Buffington JD (1970) Victor Ernest Shelford. 1877–1968. Ann Entomol Soc Am 63:347

Shellac

Several scale insects (Hemiptera: Kerriidae) can be grown on trees in Southeast Asia and used as a source of lac, a resin that is the principal ingredient of shellac. *Laccifer lacca* Kerr is the species most commonly cultured for this purpose. In Bangladesh, lac producers use ber (*Zizyphus mauritiana*) as a host plant, whereas in India they use ber, dhak (*Butea monosperma*), and kusum (*Schleichera oleosa*), in Thailand they use rain tree (*Samanea saman*) and pigeon pea (*Cajanus cajan*), and in China, pigeon pea and *Hibiscus* spp. are used. Lac culture probably dates back at least 4,000 years in China, though cultivation in India and Bangladesh has been practiced for only a few hundred years, and it is a recent introduction to Thailand.

For production of lac, the eggs of the scale insects on branches (called "broodlac") are attached to trees without insects. There they hatch, and the young scales disperse, settle and feed on the plant sap. Like most scale insects, they exude a covering that protects their bodies as they grow, but in this case the covering is a resinous secretion. After a few months, branches covered with resin are harvested as "sticklac." The resin is scraped off the twigs and dried before it is crushed, sieved, and washed to remove impurities. The resultant material is called "seedlac." Its quality varies according to the host plant, weather, and harvesting procedures. Seedlac is then processed by heat and filtering, or solvent (ethyl alcohol) extraction to produce shellac. Traditionally, shellac was used as wood finish, but it also has been incorporated into cosmetics, pharmaceuticals, and phonographs, and in the production of textiles and in printing. India produces the largest proportion of shellac on the world market, though production has fallen greatly due to the availability of synthetic resins.

Shelter Tubes

Earthen tubes constructed by termites on exposed surfaces such as brick or concrete surfaces. These tubes allow the workers and soldiers to move between the food supply and colony with minimal risk of predation and with elevated humidity.

Shield-Backed Bugs

Members of the family Scutelleridae (order Hemiptera).

► Bugs

Shield-Backed Katydids

A subfamily of katydids (Tettigoniinae) in the order Orthoptera: Tettigoniidae.

► Grasshoppers, Katydids and Crickets

Shield Bugs

Members of the family Pentatomidae (order Hemiptera).

► Bugs

Shield Bearer Moths (Lepidoptera: Heliozelidae)

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Shield bearer moths, family Heliozelidae, total 106 species from all regions, with more than half the species split between North America (31 sp.) and Australia (36 sp.); actual fauna probably exceeds 200 species. The family is in the superfamily Incurvarioidea, in the section Incurvariina, of division Monotrysia, infraorder Heteroneura.

Adults minute to small (3–9 mm wingspan), with very smooth head scaling (one sp. has roughened head scales in the Neotropics); haustellum scaled and scales usually merging with head scaling to form a triangular-appearing face; labial palpi porrect; maxillary palpi minute, 5-segmented. Maculation usually dark with shining metallic-iridescence, plus some light markings. Adults are diurnal. Larvae make serpentine leaf mines at first, then make blotch mines in later instars. Host plants include a variety of hardwood trees and bushes.

References

Kuroko H (1961) The genus *Antispila* from Japan, with descriptions of seven new species (Lepidoptera, Heliozelidae) Esakia 3:11–24, pl. 4–9

Lafontaine JD (1973) Eastern North American species of *Antispila* (Lepidoptera: Heliozelidae) feeding on *Nyssa* and *Cornus*. Can Entomol 105:991–994

Snodgrass RE (1922) The resplendent shield-bearer and the ribbed-cocoon-maker: two insect inhabitants of the orchard. Smithsonian Reports 1920, 485–509, 3 pl

Wojtusiak J (1976) Heliozelidae. In Klucze do Oznaczania Owadów Polski. 27. Motyle & Lepidoptera 94:1–18. Polskie Towardzystwo Entomologiczne [in Polish], Warsaw

Shining Flower Beetles

Members of the family Phalacridae (order Coleoptera).

► Beetles

Shining Leaf Chafers

Members of the subfamily Rutelinae, family Scarabaeidae (order Coleoptera).

► Beetles
► Scarab Beetles

Shining or Shiny

These terms are best avoided in the sciences (see glossy in contrast with luminescent).

Shiny Head-Standing Moths (Lepidoptera: Argyresthiidae)

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Shiny head-standing moths, family Argyresthiidae, include 160 species, mostly from Holarctic regions; actual fauna probably exceeds 450 species. The family is part of the superfamily Yponomeutoidea in the section Tineina, subsection Tineina, of the division Ditrysia. The family is placed as a subfamily of Yponomeutidae by some researchers. Adults small (6–15 mm wingspan), with head slightly roughened; haustellum naked; labial palpi upcurved; maxillary palpi minute, 1-segmented. Wings elongated and hindwings usually more linear and with long fringes. Maculation various shades of tan with white and darker spots, often with forewings lustrous. Adults mostly crepuscular, but many may be diurnal. Larvae are leafminers and needleminers, and some mine in various plant parts. Numerous plants are recorded as hosts, with many records in Cupressaceae, Ericaceae, Fagaceae, Pinaceae, and Rosaceae, among others. Adults typically angle their bodies with the head down when at rest, with the wings held tightly onto the body. Several species are economic in the genus *Argyresthia*.

References

Busck A (1907) Revision of the American moths of the genus *Argyresthia*. Proc US Natl Mus 32:5–24, pl. 4–5

Freeman TN (1972) The coniferous feeding species of *Argyresthia* in Canada (Lepidoptera: Yponomeutidae). Can Entomol 104:687–697

Friese G (1969) Beiträge zur Insekten-Fauna der DDR: Lepidoptera & Argyresthiidae. Beiträge zur Entomologie 19:693–752, pl. 1–2

Gershenson ZS (1974) *Moli gornostajevi* (Yponomeutidae, Argyresthiidae). In Fauna Ukraine 15:1–129. Kiev

Moriuti S (1969) Argyresthiidae (Lepidoptera) of Japan. Bull Osaka Prefect Univ, Ser B 21:1–50

Ship-Timber Beetles

Members of the family Lymexylidae (order Coleoptera).
► Beetles

Shore Bugs

Members of the family Saldidae (order Hemiptera).
► Bugs

Shore Flies

Members of the family Ephydridae (order Diptera).
► Flies

Short-Faced Scorpionflies

Members of the family Panorpodidae (order Mecoptera).
► Scorpionflies

Shorthorned Grasshoppers

A family of grasshoppers (Acrididae) in the order Orthoptera.
► Grasshoppers, Katydids and Crickets

Short-Horned Springtails

A family of springtails (Neelidae) in the order Collembola.
► Springtails

Short-Winged Flower Beetles

Members of the family Brachypteridae (order Coleoptera).
► Beetles

Shredders

Insects living in aquatic communities that feed by chewing up large particles such as leaves.

Sialidae

A family of insects in the order Megaloptera. they commonly are known as alderflies.
► Alderflies and Dobsonflies

Sibling Species

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Two or more species that are nearly identical in their appearance, yet reproductively isolated, are referred to as sibling or cryptic species. Although they have been discovered in organisms from protozoans to elephants, they are probably best known and abundantly documented among the insects. As small organisms, insects can exploit a multitude of niches, changing physiologically and behaviorally during speciation while retaining their structural similarity. Two or more sibling species constitute a species complex, and in some groups of insects, the existence of five or more sibling species is common.

Differences in habitat, host preferences, reproductive behavior, pheromones, seasonality, or other attributes within a so-called species may first suggest the presence of sibling species. What appears to be a generalist species using a broad range of hosts or occupying a diversity of habitats is often a group of sibling species, each a specialist. For example, the treehopper *Enchenopa binotata* originally was considered a single polyphagous species, but is actually a group of at least six species, each developing on a different species of plant.

Confirmation, or even discovery, of sibling species often comes from detailed behavioral, chromosomal, ecological, or molecular studies.

These studies demonstrate conclusively that populations on different hosts or in different habitats are not merely host races or varieties. Once sibling species are revealed and studied, they can be formally named. With appropriate scrutiny of pure material, they often can be distinguished morphologically from one another. Often, however, only one or two life stages offer distinguishing morphological characters. In some species complexes of mosquitoes, for instance, only the eggs are morphologically distinct.

The frequency of sibling species is unknown for most insect groups because many are still being discovered. Perhaps half of the crickets in North America have been discovered by the sounds that they make. Among North American black flies, more than one quarter was first discovered through studies of the giant polytene chromosomes in their larval salivary glands.

Sibling species often overlap broadly in their distributions and have been used to illustrate probable examples of sympatric speciation. In the *Rhagoletis pomonella* species complex, sympatric speciation might have produced the various sibling species when these fruit flies shifted and adapted to new host plants in the same geographic area.

The recognition of sibling species is critical to meaningful biological research and effective pest management. The *Simulium damnosum* (black fly) species complex consists of as many as 40 sibling species, each biologically distinct but only some of which actually transmit the filarial nematode that causes human onchocerciasis, or river blindness. Many sibling species of mosquitoes also differ in their ability to transmit agents of disease. Successful management of pest species, many of which are members of species complexes, relies on precisely targeting them in the appropriate habitats. Natural enemies, especially parasitoids, used in biological control are often complexes of sibling species. The success or failure of biological control programs can rest on the recognition of sibling species because parasitoids are often highly host specific.

References

Adler PH (1988) Ecology of black fly sibling species. In: Kim KC, Merritt RW (eds) Black flies: ecology, population management, and annotated world list. Pennsylvania State University Press, University Park, PA, pp 63–76

Bush GL (1993) Host race formation and sympatric speciation in *Rhagoletis* fruit flies (Diptera: Tephritidae). Psyche 99:335–357

Henry CS (1985) The proliferation of cryptic species in *Chrysoperla* green lacewings through song divergence. Fla Entomol 68:18–38

Mayr E (1999) Systematics and the origin of species from the viewpoint of a zoologist. Harvard University Press, Cambridge, MA, 368 pp

Rosen D (1977) The importance of cryptic species and specific identifications as related to biological control. In: Romberger JA (general ed) Biosystematics in agriculture. Beltsville Symposia in Agricultural Research, vol 2. Allanheld, Osmun, Montclair, NJ, pp 23–35

Wood TK, Guttman SI (1983) *Enchenopa binotata* complex: sympatric speciation? Science 220:310–312

Sidedressing

Application of an agricultural chemical to a growing crop, often in a strip or band along the side of a row of plants.

Sierolomorphidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Sieve Plate

A perforated covering over, or just inside, the opening of a spiracle.

Sigmoid Curve

An S-shaped curve (e.g., the logistic curve).

Sign

Any aberration or manifestation of disease indicated by a change in structure (contrast with symptom).

Signal Word

Words required to appear on most pesticide labels that denote its toxicity: "danger-poison" for highly toxic materials, "warning" for moderately toxic materials, and "caution" for slightly toxic or nontoxic.

Signiphoridae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Sign of Romaña

This is an indication of acute infection with Chagas disease, and includes swelling of the eyelids on the side of the face near the bite wound or where the bug feces were deposited or accidentally rubbed into the eye. Other more general indications of infection, if present, may include fever, fatigue, aches of the head or body, rash, loss of appetite, diarrhea, vomiting, mild enlargement of the liver or spleen, swollen glands, and local swelling. Symptoms usually fade away after a few weeks or months. However, if untreated, the disease persists.

► Chagas
► Chagas Disease or American Trypanosomiasis
► Chagas Disease: Biochemistry of the Vector
► Assassin Bugs (Hemiptera: Reduviidae)

Signoret, Victor Antoine

Victor Signoret was born at Paris, France, on April 6, 1816. This distinguished French entomologist is known as one of the first great authorities on Hemiptera, with particular expertise on Coccidae. He conducted important work on Phylloxera, and several scales are named after him. He died at Paris, France, on April 3, 1889.

Reference

Essig EO (1931) A history of entomology. The Macmillan Company, New York, 1029 pp

Silent Slantfaced Grasshoppers

A subfamily (Acridinae) of grasshoppers in the order Orthoptera: Acrididae.

► Grasshoppers, Katydids and Crickets

Silken Fungus Beetles

Members of the family Cryptophagidae (order Coleoptera).

► Beetles

Silken-Tube Spiners

Members of the family Philopotamidae (order Trichoptera).

► Caddisflies

Silk

Silk is produced only by arthropods, and specifically by members of the classes Arachnida, Insecta, and Myriapoda. Silk is produced to provide shelter, as in cocoons in Lepidoptera (insects) or retreat silks (spiders). Silk is produced to provide structural support, as in egg stalks in Neuroptera (insects) or egg sac suspension threads (spiders). Silk is produced to aid in reproduction, as in restriction of female movement during mating by Thysanoptera (insects) or production of sperm webs by males (spiders). Silk is used in foraging, as in underwater nets for prey capture by Trichoptera (insects) or aerial nets (spiders). Silk is used to aid dispersal of neonate larvae in Lepidoptera (insects) or neonate spiderlings (spiders).

Silks are fibrous proteins that are stored as a liquid and formed into fibers when "spun" at secretion. Insects produce many types of silk proteins, though each species produces only one type. In contrast, spiders produce a number of types of silk, and each individual is capable of producing several types. Following are the common proteinaceous silks found in insects:

- Alpha-helical silks are produced by Siphonaptera, Hymenoptera, Mantodea, Isoptera, and Blattodea using their colleterial glands. Structures produced by these insects include reinforcement of wax combs (Hymenoptera), cocoons (Siphonaptera), and ootheca (Mantodea).
- Parallel-beta pleated sheet silks are the most common type of silks, and are found in the typical silks of Lepidoptera cocoons, and created by their labial glands.
- Cross-beta pleated sheet silks are created by larval Malpighian tubules or derived from the peritrophic membrane, and though uncommon, are found in Neuroptera, Coleoptera, and Diptera. These silks are especially resilient, tolerating considerable stretching.

Other fibrous proteins are produced by insects, such as collagen-like silk produced by perigid sawflies (Hymenoptera). They are created by a dedicated silk gland derived from a salivary gland. Chitin is a nitrogenous polysaccharide, and found in cocoon threads of certain beetles. It is produced in the peritrophic membrane.

Thus, most insect orders produce silk in some form and in some manner, though in most cases it comes from organs that evolved primarily for some other purpose. The best known silk is a product of silk moths, *Bombyx* spp. The cocoon filament is spun by the fifth instar larva of *Bombyx mori* and other silk moths. The cocoon filament contains two cylinders of fibroin, each surrounded by three layers of sericin. Fibroin is secreted by the cells of the posterior region of the silk gland. The fibroin gene is present in only one copy per haploid genome, but these silk gland cells undergo 18–19 cycles of endomitotic DNA replication before they begin transcribing fibroin mRNAs. The sericin proteins are so named because they contain abundant serines (over 30% of the total amino acids). Sericins are secreted by the cells from the middle region of the silk gland.

► Silkworms
► Eri Silkworm
► Sericulture

Reference

Craig CL (1997) Evolution of arthropod silks. Annu Rev Entomol 42:231–267

Silkworms

This name refers to the family Bombycidae of the order Lepidoptera, but more commonly is used to designate the Chinese silkworm, *Bombyx mori* L. Chinese silkworm is the most important of the silkworms because it is the principal source of silk used by humans to construct silken cloth. With the possible exception of the European honey bee, *Apis mellifera*, it is the most beneficial insect to humans. For centuries, Chinese silkworm has been the basis of large industries in both Asian and European countries, where raw silk is produced. In turn, it is manufactured into articles of clothing in many countries. The production of silk, called sericulture, is very labor intensive, so increasingly it is concentrated in Asian countries where labor costs are lower. A single cocoon produces a single thread measuring from 300 to

900 m in length. About 3,000 cocoons are required to manufacture a pound of silk.

A by-product of silk production is the silkworm pupae. The pupae are used as animal feed. Production is estimated at 50,000–100,000 tons annually in India and China, and is fed to pigs, chickens, rats and fish. In addition, ground silkworm pupae sometimes are used as a bait in food-based baits for pest ants.

As the common name suggests, *Bombyx mori* is native of Asia, where it has been domesticated for so many centuries (approximately 5,000 years) that, like many domestic animals, it has lost the ability to survive without human intervention, and cannot fly. Selective breeding has resulted in races that differ in the quality, quantity, and color of silk produced by the insect. It apparently no longer occurs in the wild.

The adult moth has a wing span of 4–6 cm. They are heavy bodied and creamy white, with dark wing veins and sometimes several weak dark transverse lines crossing the wings. Adults do not feed. Each adult female produces about 300 nearly spherical eggs. The eggs are white initially but soon darken to bluish gray. Larvae normally feed on white or black mulberry leaves (*Morus* sp.), though they will accept other foliage. They are whitish in color, and bear a pronounced anal horn similar to that found in the hornworms of the Sphingidae. There are five instars. Larvae complete their development in about 45 days, attaining a length of 45–55 mm. At pupation, they spin a large, oval, white or yellow cocoon. If allowed to complete their development, the adult will emerge from the cocoon in 12–16 days, and they can produce up to 16 generations per year. If allowed to emerge, however, the silk is damaged, so in silk production systems the silkworm pupae are killed in hot water. Silkworms are readily reared in containers if mulberry foliage or artificial diet is provided. Because they are easy to culture, they are popular for use in schools. However, silkworms are quite susceptible to disease.

► Eri Silkworm
► Silkworm Moths
► Sericulture

Silkworm Moths (Lepidoptera: Bombycidae)

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Silkworm moths, family Bombycidae, total 166 described species, all Old World and primarily Oriental (146 sp.), with only five species known for Africa. Two subfamilies are involved: Bombycinae and Prismostictinae. The family is in the superfamily Bombycoidea (series Bombyciformes), in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults medium size (19–64 mm wingspan), with head scaling roughened; haustellum absent; labial palpi reduced, 1-segmented; maxillary palpi absent; antennae bipectinate (serrate or filiform in females); body robust. Wings broadly triangular (Fig. 43), usually with acute and falcate forewings; hindwings rounded. Maculation is mostly subdued browns and grays, with various striae or other markings; or white as in the domesticated silkworm moth. Adults are nocturnal. Larvae are leaf feeders. Host plants predominate in Moraceae. The silkworm (*Bombyx mori*), used for silk production, is related to other native species in China (probably *Bombyx mandarina*), but is now completely white after centuries of breeding in culture.

Silkworm Moths (Lepidoptera: Bombycidae), Figure 43 Example of silkworm moths (Bombycidae), *Bombyx mandarina* (Moore) from Taiwan.

References

Holloway JD (1987) Family: Bombycidae. In The moths of Borneo, vol 3. Malayan Nature Society (Malayan Nat J 41), pp 74–90, pl. 9

Jost B, Schmid J, Wymann H-P (2000) Bombycidae & Seidenspinner. In Schmetterlinge und ihre Lebensräume: Arten-Gefährdung-Schutz. Schweiz und angrenzenden Gebiete, 3:399–402, pl. 17. Pro Natura-Schweizerische Bund fuer Naturschutz, Basel

Mell R (1951) Der Seidenspinner. In Die Neue Brehm-Bücherei, 34. A. Ziemsen, Wittenberg, 45 pp

Rougeot PC (1971) Bombycidae. In Les Bombycides (Lepidoptera-Bombycoidea) de l'europe et du Bassin Méditerranéen. In Faune de l' Europe et du Bassin Méditerranéen, 5:42–46. Masson, Paris

Seitz A (ed) (1910–1927) Familie: Bombycidae. In Die Gross-Schmetterlinge der Erde, 2:189–192, pl. 29–30, 35 (1911); 10:433–442, pl. 57 (1910); 14:283–285, pl. 41 (1927). A. Kernen, Stuttgart

Silphidae

A family of beetles (order Coleoptera). They commonly are known as carrion beetles.

► Beetles

Silvanid Flat Bark Beetles

Members of the family Silvanidae (order Coleoptera).

► Beetles

Silvanidae

A family of beetles (order Coleoptera). They commonly are known as silvanid flat bark beetles.

► Beetles

Silverfish (Zygentoma)

This is a primitive order of insects known as Zygentoma or Thysanura. The order name is derived from the Greek words *zyg* (bridge) + *entoma* (insect) because when Carl Börner first introduced the name in 1904 he believed that this group represented an evolutionary link or "bridge" between the wingless (subclass Apterygota) and winged (subclass Pterygota) insects. Alternatively, if the more traditional "Thysanura" is used, the derivation is *thysanos* (bristle) + and *oura* (tail). Because these insects are wingless and none of their ancestors appear to be winged, this order is placed (with the order Archeognatha) in the subclass Apterygota; in this regard apterygotes differ from all other insects. In the past, these two orders were united into a single order, the Thysanura.

Classification

There are about 320 species found throughout the world, grouped into three families:

- Class Insecta
  - Subclass Apterygota
    - Order Zygentoma
      - Family Lepidotrichidae
      - Family Nicoletiidae
      - Family Lepismatidae
      - Family Ateluridae
      - Family Maindroniide

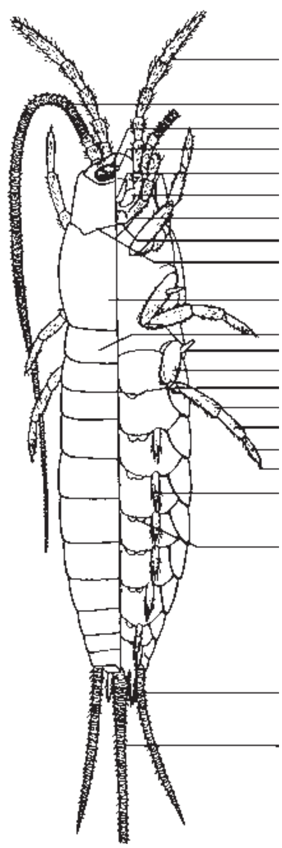
Characteristics

Silverfish are small, measuring 2– 20 mm. They are elongate and somewhat flattened, with three tail-like appendages. The body is soft, and may or may not bear scales. They are whitish, gray, or brownish. The median appendage is only slightly longer than the lateral cerci. The antennae are variable in length, but often long. The compound eyes are small and separate, or absent, and ocelli are absent. The more advanced form of the mouthparts (mandibles) is the basis for separation of the Zygentoma from the Archeognatha. They tend to be more flattened and lack the distinctive "humped" shape of Archeognatha. Most have two or three-segmented tarsi. There is no evidence of external metamorphosis; the immatures and adults differ only in size.

The number of molts is considerable; 20–70 have been reported. They can live from 1 to 4 years.

Ecology

Silverfish are found in cryptic (beneath bark) and subterranean (animal burrows, caves, ant and termite nests) habitats. Some are inquilines; some reproduce parthenogenetically. Often they require high humidity, though some can survive within buildings, where they are minor pests. Silverfish feed on plant materials, and those that inhabit buildings feed on starchy material such as book bindings and wall paper glue (Fig. 44).



Silverfish (Zygentoma), Figure 44 A diagram of a silverfish showing a dorsal view (*left*) and a ventral view (*right*). Note that the medial caudal filament is abbreviated, and normally is about twice the length of the lateral caudal filaments.

References

Arnett RH Jr (2000) American insects, 2nd edn. CRC Press, Boca Raton, FL, 1003 pp

Grimaldi D, Engel MS (2005) Evolution of the insects. Cambridge University Press, Cambridge, UK, 755 pp

Paclt J (1963) Thysanura fam. Nicoletiidae. Genera *Insectorum de P. Wytsman*, Fasicle 216e. 58 pp

Paclt J (1967) Thysanura fam Lepidotrichidae, Maindroniidae, Lepismatidae. Genera *Insectorum de P. Waytsman*, Fasicle 218e. 86 pp

Remington CL (1954) The suprageneric classification of the order Thysanura (Insecta). Ann Entomol Soc Am 47:277–286

Wygodzinsky P (1987) Order Thysanura. In: Stehr FW (ed) Immature insects, vol 1. Kendall/Hunt Publishing, Dubuque, IA, pp 71–747

Silverleaf Whitefly, *Bemisia argentifolii* Bellows and Perring (Hemiptera: Aleyrodidae)

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The silverleaf whitefly, *Bemisia argentifolii* Bellows and Perring, is also known as B-type of *B. tabaci* Gennadius. *B. tabaci* is commonly known as the cotton, sweetpotato or tobacco whitefly, and is believed to have originated in the Orient. To date there are over 1,100 species of whiteflies recognized worldwide. Among these, only three (*B. tabaci*, *Trialeurodes vaporariorum* (Westwood), and *T. abutilonea* [Hald].) are known as vectors of plant viruses. *B. tabaci* is the most common and important whitefly vector of plant viruses. This species is multivoltine and polyphagous, attacking at least 506 dicot and monocot species in 74 families. However, host specialization is commonly observed for certain *B. tabaci* populations. It is commonplace that populations raised on one host species may be difficult to establish on another, although the populations may eventually become well adapted to the new host. In the last decade, *B. argentifolii* has become prominent because of its ability to cause silverleaf symptom on squash and other

Cucurbita spp.; irregular ripening in tomato and stem whitening in *Brassica* spp., and to transmit numerous plant viruses. The etiology of silverleaf of squash and irregular ripening of tomato is not known. It is believed that this disorder is toxicogenic derived from the whitefly saliva, because symptoms increase in severity with increasing whitefly numbers, and removal of whiteflies after silverleaf development results in non-symptomatic new growth. The whitefly-transmitted plant viruses are divided into three categories based on their particle morphology, and nucleic composition: carlavirus-like virus, closterovirus, and geminivirus. The latter is the largest group, and all geminiviruses have a paired particle morphology. They either have a monopartite DNA genome of 2.6 kb or bipartite DNA genome of 5.2 kb. Transmission of geminiviruses by whitefly vectors are similar to that of leafhoppers and aphids; virus acquisition and inoculation efficiency increases with increasing aquisition access times, a minimum of several hours latent period is required, and the virus persists after molting and for life. The acquisition efficiencies of a Florida isolate of bean golden mosaic virus (BGMV) (a geminivirus) are 27.1, 27.3, 38.7, 48.8, 67.1, and 72.9% after 2, 4, 8, 24, 48 and 72-h acquisition access periods, respectively. The respective inoculation efficiencies by single adults after 1, 4, 8, 24 and 48-h inoculation access periods are 4.3, 3.3, 21.9, 38.2 and 67.6%. The minimum inoculation time by individual adults is 15 min. Viruliferous adults can retain BGMV until the death of insect.

Morphological similarities (Fig. 45) between *B. tabaci* A and B types are evident. *Bemisia argentifolii* was described as a distinct species in 1993 based on pupal cases, PCR-based DNA analysis, allozymicfrequency, crossing experiments and mating behavior differences. In retrospect, it is quite possible that many plant viruses reported to be transmitted by *B. tabaci* prior to 1993 might well be transmitted by *B. argentifolii*.

The length of the life cycle of *B. argentifolii* varies with temperature, host plant and whitefly

Silverleaf Whitefly, *Bemisia argentifolii* Bellows and Perring (Hemiptera: Aleyrodidae), Figure 45 Adult and immature silverleaf whitefly, *Bemisia argentifolii* (photo J. Tsai).

population. The average egg incubation period decreases as temperature increases from 15 to 30°C, ranging from 4 to 26 days. Within 15–30°C, the developmental time for four instars decreases significantly as temperature increases, ranging from 79 to 9 days. However, the average nymphal development time at 35°C is significantly longer than that at 25–30°C.

The adult longevity of females averages from 44 days at 20°C, to 22 days at 35°C. The oviposition of *B. argentifolii* averages 324 eggs at 20°C, to 22 eggs at 35°C. The average generation time ranges from 46 days at 20°C, to 18 days at 30°C.

Host plants affect nymphal development times. At 25°C, there is a uniform egg incubation period of 6 days when *B. argentifolii* are reared on eggplant, tomato, sweet potato, cucumber and garden bean. The average developmental time from egg to adult emergence on these host plants varies significantly, ranging from 20 days on garden bean, to 17 days on eggplant. The body lengths of second, third and fourth instars are not different when reared on these different hosts, but the males are always smaller than females, regardless of their rearing hosts. The average female longevity on these plants is 24, 21, 17, 10, and 13 days, respectively. The average number of eggs laid per female on these host plants are 234, 168, 78, 66 and 84 eggs, respectively. The mean generation time of *B. argentifolii* on these hosts ranges from 23 to 27 days.

Whiteflies are difficult to control with insecticides, and frequently they develop resistance to pesticides. Barriers such as row covers and reflective mulches have been effective in reducing disease incidence when the vector populations are low. Biological controls, and cultural controls such as removing volunteer crops and weeds within and around the field, planting trap crops, and practicing crop free periods, are commonly used with various degrees of success. However, the classical plant breeding technique incorporating engineered types of resistance into a single cultivar or variety would probably have a greater potential for a long term control strategy.

► Sweetpotato and Silverleaf Whiteflies
► Whiteflies

References

Harrison BD (1985) Advances in geminivirus research. Annu Rev Phytopathol 23:55–82

Perring TM, Cooper AD, Rodriguez RJ, Farrar CA, Bellows TS Jr (1993) Identification of a whitefly species by genomic and behavioral studies. Science 259:74–77

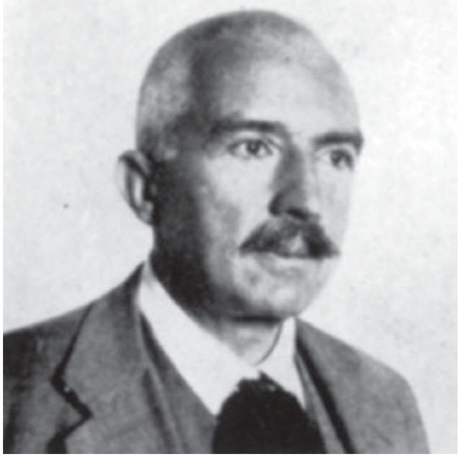
Tsai JH, Wang KH (1996) Development and reproduction of *Bemisa argentifolii* (Homoptera: Aleyrodidae) on five host plants. Environ Entomol 25:810–816

Wang K, Tsai JH (1996) Temperature effect on development and reproduction of silverleaf whitefly (Homoptera: Aleyrodidae). Ann Entomol Soc Am 89:375–384

Yokomi RK, Hoelmer KA, Osborne LS (1990) Relationship between the sweetpotato whitefly and the squash silverleaf disorder. Phytopathology 80:895–900

Silvestri, Filippo

Filippo Silvestri was born at Bevagna, Italy, on June 22, 1873. He was educated at the University of Palermo, and worked at the University of Rome and the Buenos Aires Museum. In 1904 he was appointed director of the Zoological Station



Silvestri, Filippo, Figure 46 Filippo Silvestri.

at Portici, and he held this position until his death. Silvestri was a remarkable entomologist, publishing 470 papers, of which 320 were on systematics. He established the orders Protura and Zoraptera, and had considerable interest in myrmecophilous and termitophilous insects. He died at Bevagna, Italy, on June 1, 1949 (Fig. 46).

Reference

Herman LH (2001) Silvestri, Filippo. Bull Am Mus Nat Hist 265:143–144

Simple Eyes

The eyes of insects other than compound eyes: stemmata and ocelli.

► Ocelli
► Stemmata

Simple Metamorphosis

A type of metamorphosis characterized by slight changes in body form during the developmental period, and the presence of the egg, nymphal and adult stages. The pupal stage is lacking. This is also known as incomplete metamorphosis or hemimetabolous development. Some of the aquatic insects displaying simple development (Odonata, Ephemeroptera, Plecoptera) differ in the degree of difference between the mature and immature stages, and so are sometimes said to have gradual metamorphosis or paurometabolous development.

► Metamorphosis
► Complete Metamorphosis
► Gradual Metamorphosis

Simulidae

A family of flies (order Diptera). They commonly are known as black flies or buffalo gnats.

► Black Flies
► Black Flies Affecting Livestock
► Flies

Simulium spp., Vectors of *Onchocerca volvulus*: Life Cycle and Control

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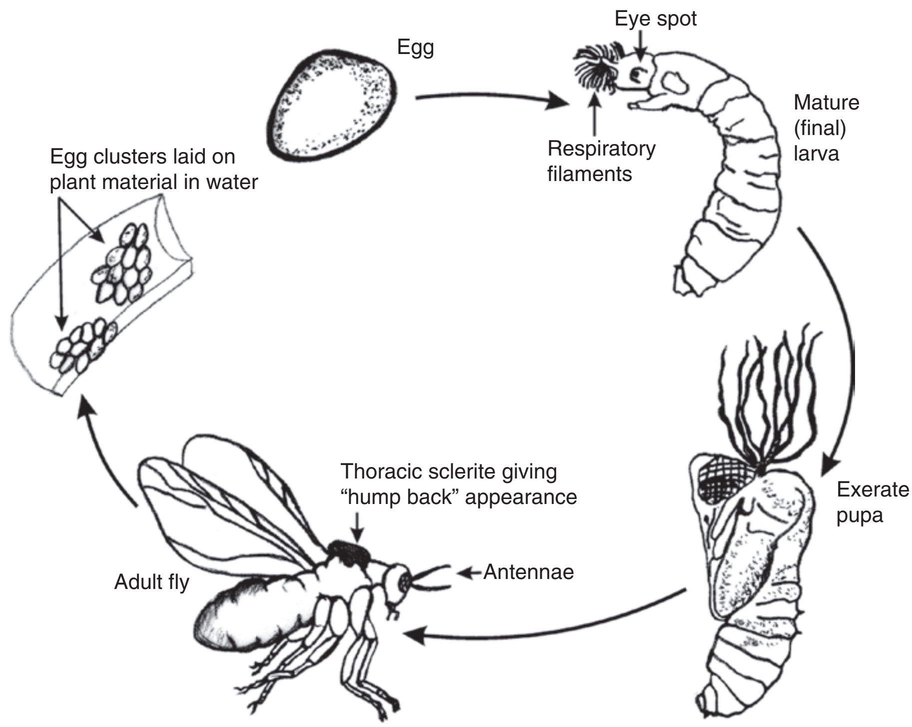
Members of the dipteran genus *Simulium* are of significant medical and veterinary importance. They belong to the suborder Nematocera and family Simuliidae, usually called black flies. These flies have long segmented antennae of about 11 segments, and all immature stages are aquatic, or at least live in very moist environments. Members of the family have a reduced mesothoracic segment giving them the appearance of having a humped back hence their alternate name humped back flies. Some members are also called buffalo gnats. Most of the species belong to the genera *Cnephia*, *Simulium*, and *Prosimulium*.

Simulium damnosum (the most widely known), and *S. neavei* vector the filarial parasite *Onchocerca volvulus* that causes human onchocerciasis (oncho) or river blindness in several East and West African countries. *S. ochraceum*, a smaller species, is the most common vector of the parasite in Mexico and several Central and South American countries. Other species of *Simulium*, and those of *Cnephia* and *Prosimulium*, attack livestock and birds worldwide and in some cases cause toxemia and anaphylactic shock. Their bites also are irritating to man. *S. meridionale* are irritating pests of poultry, while *S. vittatum* and *S. articum* in the United States and *S. colombaschense* in Canada attack cattle. In Australia, several other species of *Simulium* transmit the filarial worm *Onchocerca gibsoni* to cattle.

The female is haematophagous, using the protein from the blood meal for egg development, but feeds on plant juices at other times while the male feeds only on plant juices. When the short piercing-sucking mouthparts of a female fly previously infected with the *O. volvulus* parasite is inserted into the skin of the victim, the infective L3 (third instar) nematode enters the wound. Molting, maturation and offspring production of *O. volvulus* occur in the connective tissues of the host, inducing symptoms of onchocerciasis.

Simulium damnosum is actually a complex of different strains, and are known to use aggregation and oviposition pheromones to mate in swarms followed by mass oviposition in riverine habitats. A female may oviposit up to 800 eggs in her lifetime. Eggs are attached to rocks or plant material just below the water surface. The larva is elongate, with a distinct head, and adheres itself by means of a hook on its abdominal segment to a silken pad spun from its salivary glands on a rock, stick, or other submerged vegetation. The larva is thereby suspended in the fast running water from which it extracts microscopic organisms using a special filtering apparatus around its mouth. Fast running, well-oxygenated water is necessary for larval development (Fig. 47).

There are 6–7 instars if conditions are favorable. Prior to pupation, the last instar spins a silken cocoon around itself. Long filaments that serve as gills facilitate respiration. The pupal stage may last up to 4 weeks but *S. damnosum* adults usually emerge after 8–12 days and live for up to 4 weeks.



Simulium spp., Vectors of *Onchocerca volvulus*: Life Cycle and Control, Figure 47 **Life cycle of *Simulium* spp. Eggs are deposited in clusters on plant debris in or near fast-running rivers. Each egg is ovoid to wedge-shaped. There are three larval instars and the third stage (mature) larva has two well-defined eye spots and a delineated head, thorax, and abdomen. The pupa is exerate with well-developed eyes and elongate cephalic respiratory filaments. Adult flies have a characteristic "hump back" because of the modified thoracic sclerite.**

Chromosomal variation and morphological keys have been used to identify adults, larvae, and pupae of the Simuliidae in various European, African, and South American countries.

A major *Simulium* and onchocerciasis control effort was successfully initiated in West Africa by the Onchocerciasis Control Programme (OCP) in 1974 by the World Health Organization, the Food and Agricultural Organization (FAO), the United Nations Development Program, and other international and non-governmental agencies. The OCP employed several strategies to decrease the incidence of "oncho" and improve economic conditions in the affected regions. In addition to educating local people and administering chemotherapy with the antifungal drug ivermectin against the nematode infection, the OCP significantly reduced the *Simulium* population with aerial spraying of the large riverine habitats. They used a mixture of several larvicides, at minimum concentrations, and biological control agents including *Bacillus thuringiensis* and mermithid nematodes that parasitize the insects. The OCP utilized computers and satellites at hydrological stations to predict the flow of the river and estimate the appropriate dose of larvicides needed. Thus, the program successfully controlled black fly populations with minimal negative effects on the environment.

In Central America as in Africa, in addition to the spraying of breeding habitats, the *Simulium* populations have been controlled by clearing vegetation around housing, and decreasing irrigation that causes fast flowing water.

References

Anonymous (1994) Onchocerciasis in a nutshell. OCP, World Health Organization. Onchocerciasis Control Programme, 1974–1994

Cheng TC (1986) General Parasitology, 2nd edn. Academic Press, New York, NY, 827 pp

Davies JB, Oskam L, Lujan R, Schoone GJ, Kroon CCM, Lopez-Martinez LA, Paniagua-Alvarez AJ (1998) Detection of *Onchocerca volvulus* DNA in pools of wild-caught *Simulium ochraceum* by use of the polymerase chain reaction. Ann Trop Med Parasitol 92:295–304

McCall PJ (1995) Oviposition/aggregation pheromones in the *Simulium damnosum* complex. Med Vet Entomol 9:101–108

Schmidt GD, Roberts LS (1989) Foundations of parasitology, 4th edn. Times Mirror/Mosby Publishers, St. Louis, MO, 750 pp

Wigg D (1993) And then forgot to tell us why. A look at the campaign against river blindness in West Africa. World Band Development Essays. The World Bank, Washington, DC, 44 pp

Siphlaenigmatidae

A family of mayflies (order Ephemeroptera).

► Mayflies

Siphlonuridae

A family of mayflies (order Ephemeroptera).

► Mayflies

Siphon

The breathing apparatus of a mosquito larva. Less often, this term is used to describe the tube-like mouthparts of certain insects, particularly Hemiptera.

Siphonaptera

An order of insects. They commonly are known as fleas.

► Fleas

Siphunculata

An order name sometimes applied to the sucking lice or Anoplura. More generally, it is now treated as a suborder in the order Phthiraptera.

► Chewing and Sucking Lice

Siphunculus (pl., siphunculi)

The paired tubular structures on the back of an aphid; cornicles.

► Aphids
► Cornicles
► Abdomen of Hexapods

Siricidae

A family of wood wasps (order Hymenoptera, suborder Symphyta). They commonly are known as horntails.

► Wasps, Ants, Bees and Sawflies

Sisyridae

A family of insects in the order Neuroptera. They commonly are known as spongillaflies.

► Lacewings, Antlions and Mantidflies

Sixspotted Spider Mite, *Eotetranychus sexmaculatus* (Riley) (Acari: Phytoseiidae)

This is an occasional pest of citrus, particularly grapefruit.

► Citrus Pests and their Management

Skeletonize

To remove the tissue of a leaf except for the veins, leaving a “skeleton.”

Skin Beetles

Members of the family Trogidae (order Coleoptera).
► Beetles

Skin Beetles

Members of the family Dermestidae (order Coleoptera).
► Beetles

Skin-Piercing and Blood-Feeding Moths, *Calyptra* spp. (Lepidoptera: Noctuidae: Calpinae)

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Blood feeding is an ordinary way of life for many insects, but within Lepidoptera, the ability to pierce mammalian skin and take a blood meal is restricted to the moth genus *Calyptra* Ochsenheimer (Lepidoptera: Noctuidae: Calpinae). *Calyptra* consists of seventeen described species and two subspecies. These are medium-sized moths with wingspans ranging from 35 to 72 mm in size. *Calyptra* species have modified proboscides equipped with strongly sclerotized tearing hooks used for piercing the skin of hard fruits such as peaches and citrus, and of mammals. The number of apical tearing hooks of the proboscis varies between species and among specimens, but this variation does not appear to be in any way associated with one piercing behavior or the other (e.g., sucking fruit juices versus sucking blood). The tearing hooks are unique to a tribe of apparently closely related fruit-piercing moths consisting of at least six genera: *Calyptra*, *Eudocima*, *Gonodonta*, *Oraesia*, *Plusiodonta*, and *Phyllodes*. The tearing structures observed in these genera arise from a socket and thus are not homologous with other forms of modified sensilla of the proboscis found among fruit-sucking and tear-drinking moths within the Lepidoptera (Fig. 48).

The first species recorded piercing the skin of a mammal and feeding on its blood was *Calyptra eustrigata*, and was discovered feeding on water buffalo, deer, tapir, and antelope in Malaysia by Hans Bänziger in 1968. The moths were described as feeding on all parts of the animals for up to 10 min. Human blood feeding behavior under laboratory conditions by this species was also observed and documented by Hans Bänziger in his 1968 article. The moths inserted the tip of the proboscis into the subject's hand and began sucking blood. Blood-feeding moths are subcutaneous pool-feeders, severing the capillaries below the surface of the skin in order to form a pool of blood from which they can feed. The moths cut the tissues by moving the two straw-like tubes, or galae, of their proboscis back and forth in opposing directions; this movement has been termed by several authors as "antiparallel motion of the proboscis." This saw-like movement is often performed at short intervals followed by intermittent uptake of the blood meal. Penetration of the host skin by the moth's barbed proboscis can be quite painful, and the resulting wound(s) are large in diameter when compared to the wound of a mosquito bite or bee sting. Since the description of the first blood feeding *Calyptra* species, males of nine additional *Calyptra* species have been observed piercing mammalian skin and feeding on blood under both laboratory and natural conditions.

Calyptra species are distributed throughout the Old World, but blood-feeding species have primarily been recorded from tropical and subtropical South and Southeast Asia. Recently, the first record of a species in the genus feeding on mammalian blood was reported from a temperate region in Far Eastern Russia (Table 7).

Blood feeding in these moths is considered to be facultative and they have been recorded feeding on a broad range of hosts such as cattle, deer, tapirs,

Skin-Piercing and Blood-Feeding Moths, *Calyptra* spp. (Lepidoptera: Noctuidae: Calpinae), Figure 48 **(a) Scanning electron microscope (SEM) image of *Calyptra thalictri* (Borkhausen) proboscis: *TH* = tearing hooks; *EB* = erectile barbs; *DG* = dorsal galeal cross linkage; *SS* = sensilla styloconica (terminology follows Büttiker et al. (1996)); (b) *Oraesia rectistria* Guenée piercing plum (Godavari, Nepal); (c) image of *Calyptra thalictri* (Borkhausen) feeding on human thumb.**

and zebu. Occasionally elephants and humans are attacked; female *Calyptra* adults have not been documented to feed on blood. It has been hypothesized that the skin piercing and blood feeding habit in these moths evolved from the fruit-piercing habit, a likely scenario given fruit-piercing and blood-feeding moths share the proboscis and behavioral modifications observed in both feeding types. In both cases, the male moths appear to be in search of sugars, proteins, and salts in order to increase longevity. It is possible that the occurrence of blood feeding in these moths is dependent on the availability of fruit hosts; thus, when the typical fruit hosts are unavailable, the moths seek out mammalian hosts to obtain the nutrients essential to survival. It is known that many fruit-piercing *Calyptra* species and those of related genera are of great economic importance in many countries, but their potential as vectors of human or animal disease remains unknown.

An alternative hypothesis regarding the evolution of feeding in *Calyptra* has been proposed and suggests the skin-piercing and blood feeding behavior is derived from other animal-associated feeding behaviors such as dung, urine, or tear feeding. Although one *Calyptra* species, *C. minuticornis* (Guenée), has been recorded feeding on tears, this evolutionary trajectory is an unlikely one given the proboscis structures of fruit piercers and blood feeders are not homologous with those of tear-feeding moths, and such lachrophagous moths do not pierce fruit. This hypothesis is also problematic given the shared behavioral modifications found in both fruit piercing and blood feeding moths. The actual piercing of fruits or mammalian skin is restricted to a small group of taxonomically associated genera of Noctuidae,

Skin-Piercing and Blood-Feeding Moths, *Calyptra* spp. (Lepidoptera: Noctuidae: Calpinae), Table 7
Summary of feeding behaviors for species recorded as blood feeders in the genus *Calyptra* (after Bänziger (1989), Zaspel et al. (2007))

Species	Location	Blood feeding habit	Fruit piercer	Mammalian hosts
C. bicolor	Nepal	Natural conditions	Yes	Zebu, humans
C. eustrigata	Thailand, Malaysia	Natural conditions	Yes	Tapir, rhinoceros, zebu, deer, antelope, Indian elephant, water buffalo
C. fasciata	N Thailand, NW India	Natural conditions	Yes	Indian elephant, pig, mule, zebu
C. fletcheri	China, Tibet	Laboratory conditions	Yes	Humans
C. minuticornis	Thailand, Malaysia	Natural conditions	Yes	Indian elephant, mule
C. ophideroides	NW India	Natural conditions	Yes	Zebu, humans
C. orthograpta	N Thailand	Natural conditions	Yes	Indian elephant
C. parva	N Thailand	Natural conditions	Yes	Horse, humans
C. pseudobicolor	Nepal	Natural conditions	Yes	Zebu, humans
C. thalictri	Russia	Experimental and semi-natural conditions	Yes	Human

whereas animal-associated feeding behaviors, including the imbibing of blood droplets found on the bodies of mammals, are widespread within Lepidoptera.

References

Bänziger H (1968) Preliminary observations on a skin-piercing blood-sucking moth, *Calyptra eustrigata* (Hampson) (Lepidoptera: Noctuidae) in Malaya. Bull Entomol Res 58:159–165

Bänziger H (1982) Fruit-piercing moths in Thailand: a general survey and some new perspectives. Mittellungen der Schweizerischen Entomologischen Gesellschaft 55:213–240

Bänziger H (1983) A taxonomic revision of the fruit-piercing and blood-sucking moth genus *Calyptra* Ochsenheimer = Calpe Treitschke (Lepidoptera: Noctuidae). Entomol Scand 14:467–491

Bänziger H (1989) Skin-piercing blood-sucking moths V: attacks on man by 5 *Calyptra* spp. (Lepidoptera: Noctuidae) in S. and S.E. Asia. Mittellungen der Schweizerischen Entomologischen Gesellschaft 62:215–233

Fay HAC (2002) Fruit piercing moths and fruit spotting bugs: intractable pests of tree fruits in a reduced-insecticide environment. ISHS Acta Horticulturae 575 International Symposium on Tropical and Subtropical Fruits

Fay HAC, Halfpaff KH (2006) Fruit maturity and soundness relevant to feeding choice by fruit-piercing moths (Lepidoptera: Noctuidae) in citrus crops in northeast Australia. Int J Pest Manag 52:317–324

Hilgartner R, Raoilison M, Büttiker W, Lees DC, Krenn HW (2007) Malagasy birds as hosts for eye-frequenting moths. Biol Lett (doi: 10.1098/rsbl.2006.0581)

Huber P, Fay H, Sands D, Seymour J (1998) Seasonality of fruit-piercing moths in northern Queensland with special reference to the principal pest species, *Eudocima fullonia* (Clerk) (Lepidoptera: Noctuidae). Sixth Australian Applied Entomological Research Conference

Sands DPA, Leibregts WJMM, Broe RJ (1993) Biological control of the fruit-piercing moth, *Othreis fullonia* (Clerck) (Lepidoptera: Noctuidae) in the Pacific. Micronesica (suppl 4):25–31

Scoble MJ (1992) The Lepidoptera: form, function and diversity. Natural History Museum Publications, Oxford University Press, New York

Todd EL (1959) The fruit-piercing moths of the genus *Gonodonta* Hübner (Lepidoptera: Noctuidae). USDA-ARS Technical Bulletin No. 1201. Washington, DC

Zaspel JM, Kononenko VK, Goldstein PZ (2007) Another blood feeder? Experimental feeding of a vampire moth on human blood in the Primorye Region of Far Eastern Russia. J Insect Behav 20:437–451

Skipper Butterflies (Lepidoptera: Hesperiidae)

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Skipper butterflies, family Hesperiidae, include about 4,100 species from all faunal regions; most are Neotropical, with 2,338 species. The actual world fauna probably exceeds 4,500 species. Seven skipper subfamilies are recognized: Megathyminae, Coeliadinae, Pyrrhopyginae, Pyrginae, Trapezitinae, Heteropterinae, and Hesperiinae. The family is in the superfamily Papilionoidea (series Hesperiiformes), in the section Cossina, subsection Bombycina, of the division Ditrysia. Adult small to medium size (16–82 mm wingspan); antennae with clubs mostly elongated and hooked distally (club more compact in Megathyminae). Wings mostly triangular with somewhat acute forewing apexes; hindwings mostly rounded (rarely with tails); body robust. Maculation is primarily subdued shades of brown, often with various pale or hyaline spotting; rarely very colorful. Adults are diurnal, usually with very rapid flight, but a few tropical species are crepuscular. Larvae are leafrollers or borers, and typically have a large head capsule followed by a narrow prothorax (or "neck"). Host plants are primarily grasses (Gramineae) and other monocots, but some other hosts are also utilized; the primitive Nearctic Megathyminae are borers in Agavaceae. A few economic species are known, particularly on rice (Fig. 49).

Skipper Butterflies (Lepidoptera: Hesperiidae), Figure 49 Example of skipper butterflies (Hesperiidae), *Hesperia leonardus* Harris from Florida, USA.

References

Evans WH (1937–1953) A catalogue of the Hesperiidae, 5 volumes. British Museum, London
Freeman HA (1970) Systematic review of the Megathymidae. J Lepidopterists´ Soc 23(suppl 1):1–59
Hayward KJ (1948–1950) Genera and species animalium Argentinarum.insects, Lepidoptera. familia Hesperiidarum, 2 volumes. G. Kraft, Buenos Aires
Lindsey AW, Bell EL, Williams RC Jr (1931) The Hesperioidea of North America. J Sci Lab Denison Univ Bull 26:1–142
Seitz A (ed) (1909–1931) Familie: Hesperiidae. In Die Gross-Schmetterlinge der Erde, 1:330–355, pl. 84–89 (1909); 1(suppl):307–326, 353; pl. 16 (1931); 5:833–1056, pl. 160–193 (1921–24); 9:1027–1107, pl. 163–175 (1927); 13:505–588, pl. 75–80 (1925). A. Kernen, Stuttgart
Sonderegger P (1997) Hesperiidae & Dickkopffalter. In Schmetterlinge und ihre Lebensräume: Arten-Gefährdung-Schutz. Schweiz und angrenzenden Gebiete, 2:69–164, pl. 1–3. Pro Natura-Schweizerische Bund fuer Naturschutz, Basel

Skipper Flies

Members of the family Piophilidae (order Diptera).

► Flies

Slavery

A phenomenon among ants wherein slave-making ants capture larvae and pupae of another ant species and take them (the future slaves) to their nest where they are raised and become part of the slave-making ant colony, carrying out their normal functions but for the benefit of the slave-making ant species.

Sleeping Sickness or African Trypanosomiasis

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Sleeping sickness is a vector-borne parasitic disease of humans in sub-Saharan Africa. The parasites causing the disease are transmitted to humans principally by the bite of tsetse fly, *Glossina* spp. (Diptera: Glossinidae). The parasites may be acquired by the flies from either humans or animals. The parasites are in the genus *Trypanosoma* (flagellated protozoa in the family Trypanosomatidae), and there are two forms (species or subspecies, depending on the author). *Trypanosoma gambiense* or *T. brucei gambiense* is found in central and western Africa. It is named after the country of Gambia in western Africa. *Trypanosoma rhodesiense* or *T. brucei rhodesiense* is found is southern and eastern Africa. It is named after the former country of Rhodesia, now Zimbabwe, in eastern Africa. Not only are the two trypanosome forms separated geographically (Fig. 50), but they differ in their hosts and in symptoms of infection. Morphologically, however, they are indistinguishable.

Trypanosoma gambiense or West African trypanosomiasis is the more common of the two diseases, representing over 90% of the known cases in humans. It also tends to cause a chronic infection, and a person can be infected for months or years without seeing symptom expression. However, once the disease is expressed, the disease is far advanced, and the nervous system is adversely affected. Humans are the only important reservoir for this disease. Tsetse of the *palpalis* group are the vectors, often *Glossina palpalis*, *G. tachinoides*, and *G. fuscipes*. These flies inhabit riverine areas and attack people when they collect water, wash clothing or bathe in the rivers, or collect firewood in these areas.

Trypanosoma rhodesiense or East African trypanosomiasis is much less frequent in

Sleeping Sickness or African Trypanosomiasis, Figure 50 **The distribution of sleeping sickness in Africa. The *shaded area* represents the regions generally affected. Areas west (*left*) of the *broken line* are affected by the West African form, and areas east (*right*) of the *line* are affected by the East African form.**

humans, but occurs in an acute form, with symptoms expressed in weeks or months. As in the case of the *gambiense* form, it affects the central nervous system but, of course, the disease progresses more rapidly. Tsetse of the *morsitans* group are the principal vectors, including *G. morsitans*, *G. pallidipes*, and *G. swynnertoni*. Cattle and wild animals are the principal reservoir of *rhodesiense*. Among the wild animals serving as hosts for East African trypanosomiasis are antelopes (bushbuck, duiker, impala, hartebeest, situtunga, wildebeest), buffalo, bushpig, elephant, giraffe, hyena, lion, warthog, and zebra.

Sleeping sickness occurs only in sub-Saharan Africa in regions where there are tsetse flies that can transmit the disease. For reasons that are not yet understood, there are many regions where tsetse flies are found, but sleeping sickness is not. Only certain species transmit the disease.

They are mainly found in vegetation by rivers and lakes, in forests, and in the savannah, but the different species have different habitat preferences.

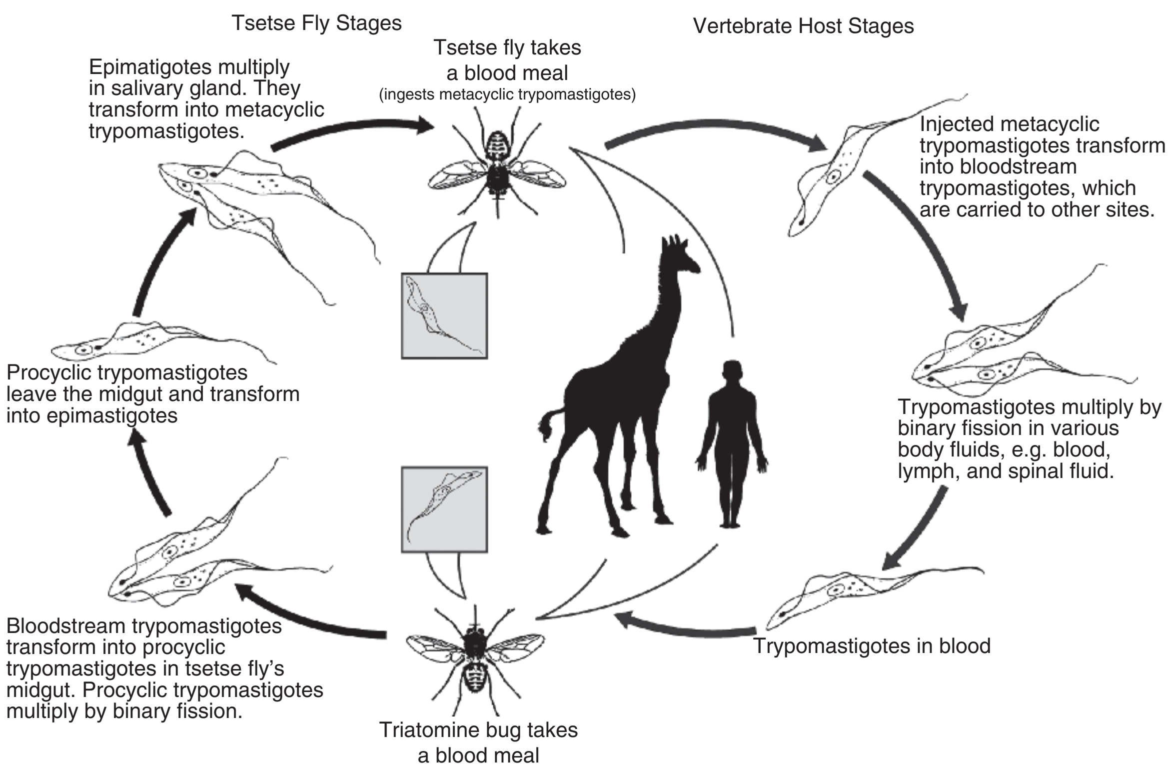
When the disease occurs in animals it is called nagana instead of sleeping sickness. Unlike the human form of the disease, which is not found everywhere tsetse flies occur, nagana occurs throughout the range of tsetse flies. Nagana is much more common than sleeping sickness, but sleeping sickness occurs frequently even today. The disease in domestic animals, and particularly the effects on cattle, has been a major obstacle to the economic development of rural central and southern Africa. It is estimated that three million cattle die annually due to this disease. For thousands of years, the ability of tsetse to transmit trypanosomes has denied the people of central and southern Africa the use of large domestic animals such as oxen and horses in their agriculture. Also, it has led to shortage of animal protein in the diet of many Africans. Offsetting this, perhaps, is the benefit of tsetse-borne disease in preventing the southward migration of Arab invaders because their horses and camels were susceptible. Also, the presence of tsetse-borne diseases probably has helped preserve the natural environment of Africa, particularly the rich wildlife. There is also evidence that some other flies play a minor role in mechanical transmission of the protozoan. Flies in the families Tabanidae and Muscidae also may transmit the disease to animals, and perhaps to humans, though this is of minor importance compared to tsetse transmission.

Typically, 40,000–50,000 cases are reported annually in humans, but this is likely a serious underestimate of the total number of people affected. It is more commonly a problem where public health services are inadequate, in rural habitats and among poor people, and in these situations accurate reporting is infrequent. Rural populations usually depend on agriculture, fishing, animal husbandry or hunting, and in these pursuits they are often exposed to the bite of the tsetse fly and therefore to the disease. Displacement of people following war or famine can exacerbate the problem. Sometimes the trypanosomes cross the placenta and infect the fetus, resulting in mother-to-child infection. Blood transfusions can be a source of the disease.

A tsetse fly bite is often painful and can develop into a red sore, called a chancre. Upon transmission of the disease by the bite of a fly, the trypanosomes multiply in the subcutaneous tissues, blood and lymph of the host. This first stage of the disease is known as the hemolymphatic phase. Associated with this phase are periods of fever and sweating, headache, swelling of the lymph nodes, joint pain and itching. With time, the typanosomes cross the blood-brain barrier and infect the central nervous system. This second stage, or neurological phase, has associated with it confusion, mood swings, sensory disturbances, weakness and poor coordination. As the “sleeping sickness” designation suggests, another symptom of the disease is disturbance of sleep. Ultimately, without treatment, sleeping sickness often leads to coma or convulsions, and death. The long asymptomatic first stage of the West African form of the disease (Fig. 50), and the generalized symptoms that occur when any ailment is noticed, make diagnosis difficult. Serological and cerebro-spinal tests usually are required. The drugs used to treat the disease during the first stage of the disease are not too toxic, easy to administer, and fairly effective. Unfortunately, if early diagnosis is not made, the drugs used to treat the second stage are toxic and difficult to administer.

Development of this trypanosome is similar but not the same as that of *Trypanosoma cruzi*, the causative agent of Chagas disease or American trypanosomiasis. Trypomastigotes (one major form of the trypanosome) circulate in the blood and the tsetse fly becomes infected with bloodstream trypomastigotes when taking a blood meal on an infected mammalian host. In the fly’s midgut, the parasites transform into procyclic trypomastigotes, multiply by binary fission, and leave the midgut. Eventually they migrate to the proboscis and attach to the epithelium of the salivary glands where they transform into epimastigotes (the other major form of the trypanosome). The epimastigotes continue multiplication by binary fission. The cycle in the fly takes approximately 3 weeks to progress, and then the trypanosomes transform back to trypomastigotes; at this point they are called metacyclic trypomastigotes and are infective to humans and animals. Once infected, the fly remains infective during its entire 6- to 12-month life span. An infected tsetse fly injects metacyclic trypomastigotes into skin tissue when taking a blood meal, and the parasites enter the host's lymphatic system and pass into the blood. There, they transform into bloodstream trypomastigotes and are carried to other sites throughout the body, reach other blood fluids (e.g., lymph, spinal fluid), and continue the replication by binary fission (Fig. 51).

Prevention and control of the disease tends to focus on elimination of the vector, tsetse flies. Clearing of brush, which favors persistence of flies by providing them cover, is an important management technique. The flies do not disperse long distances, so it is possible to create barriers around inhabited areas by removing such cover. Land used for crop culture or grazed periodically by livestock similarly is not very suitable for survival of tsetse. Insecticide application, both ground and aerial applications, has long been used for tsetse suppression. Area-wide management approaches can be implemented using release of sterile insects, but presently is too costly. Use of traps (blue or black cloth sprayed with insecticide, or cattle sprayed with insecticides) has had some success, as has traps baited with chemical attractants. Care should be taken to avoid being bitten. Bed netting and thick, long-sleeved clothing are helpful. Avoidance of brushy



Sleeping Sickness or African Trypanosomiasis, Figure 51 **The sleeping sickness disease cycle in tsetse flies and their hosts (adapted from CDC).**

habitats is helpful. Vaccines and preventative drugs are not available. It also is desirable to screen communities for occurrence of sleeping sickness to identify foci of disease outbreak and to apply curative medications to affected individuals. Certain breeds of cattle such as N'dama are tolerant of trypanosome infection, so this is an active area of research.

There are other forms of trypanosomiasis in Africa and elsewhere. For example, the aforementioned African sleeping sickness is perhaps better called African human trypanosomiasis to differentiate it from African animal trypanosomiasis (nagana). This latter disease is basically the same as the tsetse fly-transmitted disease transmitted to humans, but is caused by other trypanosomes such as *Trypanosoma congolense*, *T. suis*, *T. simiae*, *T. uniforme* and *T. vivax* in addition to *T. brucei*.

► Tsetse Flies
► *Glossina* spp. (Diptera: Glossinidae)
► Trypanosomes
► Chagas Disease or American Trypanosomiasis
► Area-Wide Pest Management
► Veterinary Pests and their Management

References

Leek SGA (1998) Tsetse biology and ecology: their role in the epidemiology and control of trypanosomosis. CABI, New York, NY, 592 pp

Marquardt WC, Demaree RS, Grieve RB (eds) (2000) Parasitology and vector biology. Academic Press, San Diego, CA, 702 pp

Mullen G, Durden L (2002) Medical and veterinary entomology. Academic Press/Elsevier, Amsterdam, The Netherlands, 597 pp

Seed JR, Black SJ (eds) (2001) The African trypanosomes. Kluwer Academic Press, Dordrecht, The Netherlands, 179 pp

Slender Springtails

A family of springtails (Entomobryidae) in the order Collembola.

► Springtails

Slug Caterpillar Moths (Lepidoptera: Limacodidae)

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Slug caterpillar moths, family Limacodidae, total 1,104 known species worldwide, the largest family of Cossoidea, mostly tropical and especially biodiverse in the Oriental tropics; likely world total is near 1,600 species or more. There is no established subfamily classification thus far. The family is in the superfamily Cossoidea (series Limacodiformes) in the section Cossina, subsection Cossina, of the division Ditrysia. Adults small to medium size (9–80 mm wingspan) (typically 20–30 mm), with head small and relatively rough-scaled; haustellum and maxillary palpi vestigial or reduced; labial palpi short; antennae short, usually bipectinate in males (typically becoming filiform near apex). Body robust. Wings usually quadrate and rounded, although some with forewings more pointed and elongated; hindwings usually ovoid. Maculation mostly various shades of brown, but some are colorful (rarely hyaline or with hyaline patches or spots), with few markings but for many with diagonal lines, various markings (some with bright green patches); hindwings usually unicolorous to match forewings or lighter (rarely hyaline). Adults perhaps only nocturnal; many with unique resting postures. Larvae slug-like (often colorfully marked over green base color) and mostly polyphagous leaf feeders, with vestigial prolegs and usually an extensive array of poisonous stinging spines dorsally. Large numbers of host plants utilized. Few species are economic, other than medically as stinging caterpillars, but palm defoliators can be a problem in the tropics (Fig. 52).

References

Cock MJW, Godfray HCJ, Holloway JD (eds) (1987) Slug and nettle caterpillars: the biology, taxonomy and control of

Slug Caterpillar Moths (Lepidoptera: Limacodidae), Figure 52 Example of slug caterpillar moths (Limacodidae), *Monoleuca erectifascia* Dyar from Florida, USA.

the Limacodidae of economic importance on palms in South-East Asia. CABI, Wallingford, 270 pp, 36 pl
Guenin R (1997) Limacodidae & Schneckenspinner (Asselspinner, Schildmotten). In Schmetterlinge und ihre Lebensräume: Arten-Gefährdung-Schutz. Schweiz und angrenzenden Gebiete, 2:441–446, pl. 11. Pro Natura-Schweizerische Bund fuer Naturschutz. Basel
Holloway JD (1986) Family: Limacodidae. In Moths of Borneo, vol 1. Malayan Nature Society (Malayan Nature Journal 40:47–150, pl. 5–9), pp 47–150, pl. 5–4
Holloway JD (1990) The Limacodidae of Sumatra. In Heterocera Sumatrana. Heterocera Sumatrana Society, Göttingen, pp 9–77
Janse AJT (1964) Limacodidae. In The moths of South Africa, pp 71–136, pl. 1–44. Pretoria
Seitz A (ed) (1912–1937) Familie: Limacodidae. In Die Gross-Schmetterlinge der Erde, 2:339–347, pl. 49–50 (1912); 2(suppl):201–209, pl. 15 (1933); 6:1104–1136, pl. 164–167 (1935–1937); 10:665–728, pl. 85–89 (1931); 14:447–472, pl. 73–75 (1928). A. Kernen: Stuttgart

Small Dung Flies

Members of the family Sphaeroceridae (order Diptera).

► Flies

Small Fruit Flies

Members of the family Drosophilidae (order Diptera).

► Flies

Small Fruit Pests and Their Management

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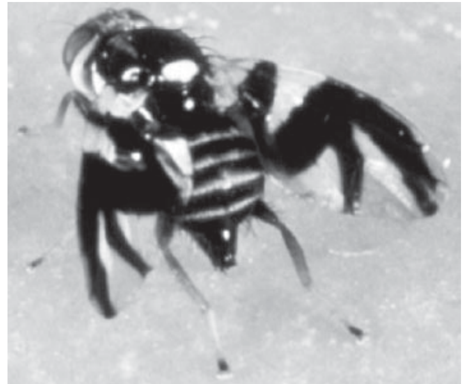
In the United States, the production of small fruit is becoming increasingly important as growers diversify from traditional staple crops to specialty fruits. Blueberries, cranberries, strawberries, and grapes comprise the major small fruit crops with combined annual sales exceeding $3 billion dollars. Despite these figures, further growth and development of small fruit industries will depend on producers' ability to develop effective pest management programs that specifically target key pests within these systems. The passage of the 1996 Food Quality Protection Act (FQPA) and public concern over food safety, as well as pressure from environmentalists, are forcing producers and pest management specialists to develop programs aimed at reducing pesticide residues in food and improving agricultural worker safety.

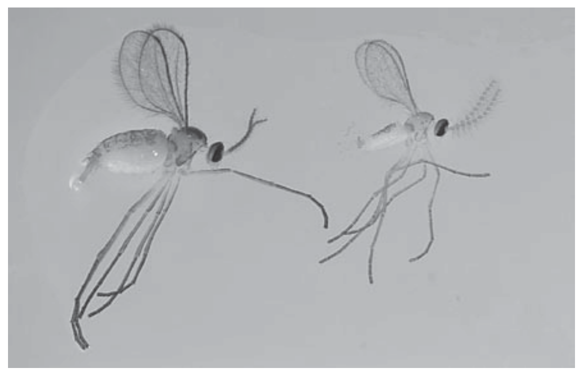
The goal of this section is to provide biological information on some of the major pests within small fruit systems in the United States. It is difficult to cover all of the economic pests that affect small fruit crops in a single section; therefore, a special effort has been made to highlight key insect pests that cause serious economic damage within the various small fruit systems. We attempted to provide up-to-date information on distribution, biology, and damage symptoms and focused our management efforts on effective monitoring and cultural techniques. A special effort was made to provide useful IPM strategies that can be adopted to minimize the use of pesticides. The information that is provided can be used as a basis to provide growers, consultants, and pest management specialists' options for managing key pests in these systems. Although there is substantial information in the literature on the use of reduced-risk pesticides, we did not make any spray recommendations because pesticide information changes frequently as more research becomes available.

Blueberries

In the USA, commercial blueberries are grown on approximately 109,000 acres of land with a total market value of 411 million USD. Michigan leads the US in producing over 40% of the northern highbush blueberries, *Vaccinium corymbosum* L., while Maine produces more than 90% of the lowbush blueberries, *V. agustifolium* Aiton. Rabbiteye blueberries, *V. ashei* Reade, are grown mostly in the southeastern United States, with the highest production coming from Georgia. The recently developed southern highbush blueberries, *V. corymbosum* X *V. darrowi* Camp are grown primarily in Florida, although Georgia and some areas in the western US, including Oregon and California also produce small quantities of southern highbush blueberries. Blueberries are a rich source of antioxidants as well as other nutrients that are associated with lowering the risk of cardiovascular diseases and cancer. Blueberries are attacked by several pests including blueberry maggot, *Rhagoletis mendax* Curran, cranberry fruitworm, *Acrobasis vaccinii* Riley, blueberry gall midge, *Dasineura oxycoccana* (Johnson) and flower thrips, *Frankliniella* spp.



Small Fruit Pests and Their Management, Figure 53 Adult blueberry maggot.



Small Fruit Pests and Their Management, Figure 54 Blueberry gall midge female (*left*) and male (*right*).

Pests of Blueberries, *Vaccinium* spp. (Family Ericaceae)

Blueberry Maggot, *Rhagoletis mendax* Curran (Diptera: Tephritidae)

Distribution

Blueberry maggot, *Rhagoletis mendax* Curran, is an important pest of commercially grown blueberries, *Vaccinium* L. spp., in the eastern and Midwestern United States. Only one generation per year has been reported throughout its distribution. Temperature, soil type, moisture and the presence of wild host plants may affect rate of emergence. Deerberry, *V. stamineum* L., and huckleberries, *Gaylussacia* Humboldt, Bonpland, and *Kunth* spp., have been identified as principal host species in the southeast (Fig. 53).

Biology

Adults emerge from overwintering puparia when berries begin to ripen, and flies will continue to emerge until all cultivars have fully ripened. Adults are black with a white spot on the thorax and are approximately 3–4 mm in length. The abdomen of females is black and pointed with four white cross bands. Males are slightly smaller than females and have only three white cross bands on their abdomen. Both males and females have a characteristic F-shaped marking on their wings. Mature females oviposit eggs singly into maturing berries. The larva is a creamy white, legless maggot approximately 4–6 mm in length. Larval development requires 18–20 days, at which time mature larvae drop to the ground to pupate in the soil. Puparia are smooth brown colored capsules and usually are located about 2–3 cm below ground level.

Damage

Larvae feed on the internal tissues of the fruit causing major destruction of the tissues. There is a low tolerance for maggots in fruit, and *R. mendax* infestations may render shipments of blueberries unmarketable.

IPM Strategies. Blueberry maggot can be controlled effectively with insecticides if applications are properly timed. Three principle types of traps should be considered when monitoring blueberry maggot: (i) yellow sticky boards, (ii) green sticky spheres and (iii) sticky red spheres. Baiting traps with ammonium acetate can increase monitoring efficiency. In highbush blueberries, a minimum of two sticky boards or spheres is needed for every two hectares (about 5 acres). One trap should be placed near (10–20 m) the border of the planting adjacent to wild host plants and the other trap should be placed in the center of the two-hectare block. Yellow sticky boards should be hung 15 cm (6 in.) above the bush and positioned in a "V" orientation with the sticky surface facing downward. Traps should be monitored weekly and recoated or replaced after 3 weeks of exposure to maintain efficiency. Spraying for blueberry maggot should commence when two or more flies are found on any one trap during a sampling period, or when the total number of flies over all traps in a field equals or exceeds five in 1 week. In the field, *Daichasma alloeum*, an opiine parasitoid, is known to attack third instar blueberry maggot larvae.

References

Gaul SO, McRae KB, Estabrooks EN (2002) Integrated pest management of *Rhagoletis mendax* (Diptera: Teohritidae) in lowbush blueberry using vegetative field management. J Econ Entomol 95:958–965

Liburd OE, Alm SR, Casagrande RA, Polavarpu S (1998) Effect of trap color, bait, shape, and orientation in attraction of blueberry maggot (Diptera: Tephritidae) flies. J Econ Entomol 91:243–249

Cranberry Fruitworm, *Acrobasis vaccinii* Riley (Lepidoptera: Pyralidae)

Distribution

Cranberry fruitworm is a pest of *Vaccinium* spp. throughout the eastern United States and Canada, from Nova Scotia southward to Florida. Typically, cranberry fruitworm is a univoltine pest, although a second generation is possible under favorable climatic conditions.

Biology

Cranberry fruitworm adults are brownish-gray moths with a blend of light and dark coloration. Adult wingspan is approximately 18 mm, with females having a slightly larger and more orange-colored abdomen. Adult moths are nocturnal, with female activity preceding that of males at dusk/after sunset. Mated females lay eggs near the calyx-cup of expanding cranberries and blueberries. Females often lay eggs in berries located near bog or planting edges. Cranberry fruitworm eggs are white and slightly elliptical, approximately 1 mm in diameter. Newly hatched larvae exit the fruit near the oviposition site and crawl over the berry surface before reentering the same berry at either the stem end or the calyx to begin feeding. Mature larvae are pale green with a darkened head capsule, approximately 15 mm in length. Larvae pupate in hibernacula composed of sand, leaves and debris, and emerge as adults the following spring.

Damage

Damage caused by cranberry fruitworm is characterized by internal feeding. Larvae consume the pulp of approximately 5–8 berries, webbing berries together at their point of contact. Infested berries may exhibit premature color change, and larval frass often becomes entangled in the webbed cluster. Early instar larvae sometimes construct a silken enclosure over the entry site. Webbed fruit containing frass is a characteristic of *A. vaccinii* damage that is useful for differentiating between damage caused by cherry fruitworm and sparganothis fruitworm.

IPM Strategies

Current IPM strategies employ the use of pheromone-baited, (*E,Z*)-8,10-pentadecadien-1-ol and (*E*)-9-pentadecen-1-ol acetate, winged traps to monitor male *A. vaccinii* activity. Traps are available commercially, although their effectiveness may depend on several factors, including height with respect to host plant and geographic position within a bog or planting. Traps placed in adjacent habitats or within close proximity to blueberry or cranberry fields may provide additional information regarding male moth flight throughout the season. Monitoring for cranberry fruitworm also can be accomplished by examining individual clusters or plants for the presence of eggs. This strategy requires the aid of a hand lens, and since infestations of cranberry fruitworm may be aggregated, an accurate assessment may require a large sample size. Monitoring tactics will be useful for predicting peak oviposition and for timing insecticide applications. One cultural technique for managing cranberry fruitworm in cranberries involves late-water flooding because hibernacula cannot survive in water exceeding 16°C for more than 2 weeks.

References

Sarzynski EM, Liburd OE (2004) Effect of trap height and within-planting location on captures of cranberry fruitworm (Lepidoptera: Pyralidae) in highbush blueberries. Agric For Entomol 6:199–204

Mallampalli N, Isaacs R (2002) Distribution of egg and larval populations of cranberry fruitworm (Lepidoptera: Pyralidae) and cherry fruitworm (Lepidoptera: Tortricidae) in highbush blueberries. Environ Entomol 31:852–858

Blueberry Gall Midge, *Dasineura oxycoccana* (Johnson) (Diptera: Cecidomyiidae)

Distribution

Blueberry gall midge is distributed throughout the eastern, mid-western and north western United States. In the south, blueberry gall midge infests rabbiteye and southern highbush blueberries (Table 8).

Biology

Blueberry gall midges are small insects, approximately 2 mm in size with long, slender legs, delicate wings (with microtrichia) and globular antennae. Female gall midges are slightly larger than males and have a distinctively orange-colored abdomen. A single female is capable of ovipositing more than 20 eggs into the developing buds. Eggs hatch within 2–3 days, and the emerging larvae develop through three or four instars that are characterized by color: transparent (first instar), white (second instar), and orange (third instar), respectively. Larvae drop to the ground and pupate in the upper layers of the soil. There are several generations per year. Climatic conditions and latitude influence the number of generations within a particular region.

Damage

The larvae of blueberry gall midge feed within the buds, which ultimately kill the developing tissues and terminates growth of the affected shoot. Vegetative buds also may be affected after fruits are harvested. Curled, cupped leaves characterize blueberry gall midge damage in a blueberry planting. In general, blueberry gall midge prefers young shoots rather than older growth. The injury is often misdiagnosed as frost damage. In blueberries post-harvest injury may limit flowering potential for subsequent seasons.

IPM Strategies

Monitoring for blueberry gull midge can be accomplished by destructively sampling floral and vegetative buds during and after bud swell, when scales have begun to separate. A dissecting microscope is necessary to view eggs and early larval instars. In blueberries, applications of reduced-risk insecticides may be most effective if targeted during the egg-hatching stage of the first generation. Cultural control practices include the use of bed sanding and alteration in pruning and fertilization practices.

Small Fruit Pests and Their Management, Table 8 Selected list of arthropods that affect blueberries, *Vaccinium* spp., in the United States

Common name(s)	Scientific name	Order	Family
Blueberry bud mite	*Acalitus vaccinii* (Keifer)	Acari	Eriophyidae
Japanese beetle[a]	*Popillia japonica* Newman	Coleoptera	Scarabaeidae
Blueberry flea beetle	*Altica sylvia* Malloch	Coleoptera	Chrysomelidae
Blueberry leaf beetle	*Pyrrhalta vaccinii* Fall	Coleoptera	Chrysomelidae
Plum curculio[a]	*Conotrachelus nenuphar* (Herbst)	Coleoptera	Curculionidae
Blueberry stem borer	*Oberea myops* Hald	Coleoptera	Cerambycidae
Cranberry weevil[b]	*Anthonomus musculus* Say	Coleoptera	Curculionidae
Blueberry gall midge[b]	*Dasineura oxycoccana* (Johnson)	Diptera	Cecidomyiidae
Blueberry maggot	*Rhagoletis mendax* Curran	Diptera	Tephritidae
Blueberry aphid	*Illinoia pepperi* McGillivray	Hemiptera	Aphididae
Terrapin scale	*Mesolecanium nigrofasciatum* (Pergande)	Hemiptera	Coccidae
Sharpnosed leafhopper	*Scaphytopius magdalensis* Provancher	Hemiptera	Cicadellidae
Blueberry stem gall wasp	*Hemadas nubilipennis* Ashmead	Hymenoptera	Pteromalidae
Blueberry leafminer	*Gracilaria vacciniella* Ely	Lepidoptera	Gracillariidae
Blueberry tip borer	*Hendecaneura shawiana* Kearfott	Lepidoptera	Tortricidae
Read-banded leafroller	*Argyrotaenia velutinana* Walker	Lepidoptera	Tortricidae
Fruittree leafroller	*Archips argyrospilus* Walker	Lepidoptera	Tortricidae
Oblique-banded leafroller	*Choristoneura rosaceana* Harris	Lepidoptera	Tortricidae
Blueberry spanworm	*Itame argillacearia* Packard	Lepidoptera	Geometidae
Fall webworm	*Hyphantria cunea* (Drury)	Lepidoptera	Arctiidae
Yellow-necked caterpillar	*Datana ministra* (Drury)	Lepidoptera	Notodontidae
Cranberry fruitworm[b]	*Acrobasis vaccinii* Riley	Lepidoptera	Pyralidae
Cherry fruitworm[b]	*Grapholita packardi* (Zeller)	Lepidoptera	Tortricidae
Blueberry thrips	*Frankliniella vaccinii* Morgan	Thysanoptera	Thripidae
Blueberry thrips	*Catinathrips kainos* O'Neill	Thysanoptera	Thripidae

[a]also infest grapes
[b]also infest cranberries

References

Sampson BJ, Rinehart TA, Liburd OE, Stringer SJ (2006) Ecology of endoparasitods (hymenoptera) attacking cranberry and blueberry tipworms, *Dasineura oxycoccana* and *Prodiplosis vaccinii* (Diptera: Cecidomyiidae). Ann Entomol Soc Am 99: 113–120

Sarzynski EM, Liburd OE (2003) Techniques for monitoring blueberry gall midge (Diptera: Cecidomyidae) in rabbiteye and southern highbush blueberries. J For Entomol 96:1821–1827

Cranberries

Cranberries are produced mainly in Wisconsin, Massachusetts and New Jersey. In 2001, the US produced 500 million pounds of cranberries valued at $115 million dollars. Wisconsin leads the country in producing 60% of the nation's cranberries, followed by Massachusetts and New Jersey, which produced 142 and 57 million pounds, respectively. Cranberries are a rich source of vitamins, potassium and fiber, and have been reported to play a significant role in lowering the incidence of cystitis and other urinary tract infections. Recent studies also have indicated that cranberries are a good source of antioxidants. Like other plants belonging to the genus *Vaccinium*, cranberries are susceptible to several pests including Sparganothis fruitworm, *Sparganothis sulfureana* (Clemens) Riley, black-headed fireworm, *Rhopobota naevena* (Hübner) and cranberry fruitworm, *Acrobasis vaccinii* Riley (discussed under blueberry section).

Pests of Cranberries, *Vaccinium macrocarpon* Aiton (family Ericaceae)

Sparganothis fruitworm, *Sparganothis sulfureana* (Clemens) (Lepidoptera: Tortricidae)

Distribution

Sparganothis fruitworm is a major pest of cranberries throughout the eastern United States and Wisconsin. This species is not known to affect production of *Vaccinium* spp. on the west coast of the United States. Sparganothis fruitworm also has been reported on strawberry (Table 9).

Biology

Sparganothis fruitworm has no approved common name. Adults are approximately 15 mm in length and are characterized by having yellowish wings with a distinctly brownish "X" marking on the dorsal surface. Larvae have a yellow-green body with paired white spots on the dorsal surface and a yellow head. Sparganothis fruitworm has two generations per year. The first generation larvae are indirect pests, feeding on young foliage and webbing together terminal vine tips. Second generation larvae feed internally, causing direct damage to the fruit. Sparganothis fruitworm overwinter as larvae.

Damage

Fruit entry sites are generally larger and more tattered compared with cranberry fruitworm. Direct injury result from internal feeding and consumption of fruit pulp, with no evidence of frass inside affected berries.

IPM Strategies

Sparganothis fruitworm may be difficult to manage due to organophosphate resistance. There may be some promise for mating disruption with sprayable micro-encapsulated pheromones. The pheromone (E)-11-tetradecenyl acetate (E11–14: Ac) has been known to significantly reduce mating among virgin females in cranberry plots.

References

Polavarapu S, Lonergan GC, Peng H, Neilsen K (2001) Potential for mating disruption of *Sparganothis sulfureana* Clemens (Lepidoptera:Tortricidae) in cramberries. J Econ Entomol 94:658–665

Teixeira LAF, Averill AL (2006) Evaluation of flooding for cultural control of *sparganothis sulfureana* (Lepidoptera) in cranberry bogs Environ Entomol 35: 670-675

Cranberry Girdler, *Chrysoteuchia topiaraia* (Zeller) (Lepidoptera: Pyralidae)

Distribution

Cranberry girdler, classified as a sod webworm because of the characteristic webbing at the feeding site, is a pest of cranberries throughout the United States and Canada. This species also

Small Fruit Pests and Their Management, Table 9 Selected list of arthropods that affect cranberries, *Vaccinium macrocarpon* Aiton, in the United States

Common name(s)	Scientific name	Order	Family
Cranberry weevil[a]	*Anthonomus musculus* Say	Coleoptera	Curculionidae
Cranberry rootworm[a]	*Rhabdopterus picipes* (Oliver)	Coleoptera	Chrysomelidae
Cranberry white grub	*Phyllophaga anxia* LeConte	Coleoptera	Scarabaeidae
Black vine weevil	*Otiorhynchus ovatus* L.	Coleoptera	Curculionidae
Blueberry gall midge[a]	*Dasineura oxycoccana* (Johnson)	Diptera	Cecidomyiidae
Cranberry aphid	*Ericaphis scammelli* Mason	Hemiptera	Aphidae
Cranberry girdler	*Chrysoteuchia topiaraia* (Zeller)	Lepidoptera	Pyralidae
Blackheaded fireworm	*Rhopobota naevena* (Hübner)	Lepidoptera	Tortricidae
Cranberry fruitworm[a]	*Acrobasis vaccinii* Riley	Lepidoptera	Pyralidae
Green spanworm	*Itame sulphurea* Packard	Lepidoptera	Geometridae
Brown spanworm	*Ematurga amitaria* Guenée	Lepidoptera	Geometridae
Sparganothis fruitworm[b]	*Sparganothis sulfureana* (Clemens)	Lepidoptera	Tortricidae
Gypsy moth	*Lymantria dispar* L.	Lepidoptera	Lymantriidae
Spotted fireworm[b]	*Choristoneura parallela* (Robinson)	Lepidoptera	Tortricidae
Cranberry blossomworm	*Epiglacea apiata* Graote	Lepidoptera	Noctuidae
False armyworm	*Xylena nupera* Lintner	Lepidoptera	Noctuidae

[a]also infest blueberries
[b]also infest strawberries

affects grasses that are common to many cranberry bogs.

Biology

Adult moths are approximately 9 mm in length and silvery, with light brown coloration on the outer edge of the forewing. Small black dots also may be visible on the outer margin of the forewing, although adults lose their coloration soon after emerging. Females lay eggs randomly within the bog floor. Eggs (0.5 mm) appear white when laid and attain a pinkish color when mature prior to hatching. Larvae have a dark brown head and cream-colored abdomen with fine hairs. Girdler larvae are concealed largely in the leaf litter on the bog floor and feed on the bark and internal vascular system of low-lying cranberry vines. Mature larva is approximately 13 mm in length. Prior to pupation, larva prepares a cocoon made from leaf litter for overwintering in the soil. Pupation occurs in the spring and there is one generation per year.

Damage

Larval feeding results in "girdled" or completely severed vines, which interrupts water and nutrient transfer in affected plants. Damage symptoms (including foliage browning) may appear in the late fall, although more extensive damage may not be visible until the spring. The occasional appearance of many dead or dying uprights in late summer and early fall could be a sign of girdler damage. Damage may be more abundant in bogs with accumulated trash.

IPM Strategies

Commercially available pheromone traps are useful for monitoring adult populations. There are some indications that certain plant species, including foxtail, *Alopecurus pratensis* L., can be used as monitoring tools in cranberry bogs. Cultural control practices include sanding and flooding. Parasitic wasps, spiders, and ground beetles may offer some degree of control in some areas.

References

Cockfield SD, Mahr DL (1994) Prediction models for flight activity of the cranberry girdler (Lepitera: Pyralidae) in Wisconsin. Great Lakes Entomol 27:107–109

Simard L, Belair G, Brodeur J (2002) Susceptibility of cranberry girdler to entomopathogenic nematodes. Can Entomol 134:329–330

Blackheaded Fireworm, *Rhopobota naevena* (Hübner) (Lepidoptera: Tortricidae)

Distribution

Blackheaded fireworm is a major pest of cranberry production in North America.

Biology

Adults are darkly colored small moths, approximately 7 mm, with light and dark brown-banded forewings. Mature larvae have shiny black heads with greenish-yellow abdomens and measure approximately 8 mm in length. Young larvae burrow into the green tissue of developing leaves eventually moving to the growing tips. Larvae often tunnel into swollen buds and web terminal leaves together with silk. Larvae feed for about 3–5 weeks, during which time a single larva can construct more than five silken tents. Blackheaded fireworm overwinters in the egg stage on the underside of cranberry leaves. Overwintering eggs are yellow, disc-shaped, and approximately 0.5 mm in length. There are two or three generations per year. First generation egg hatch begins in the spring. Pupation occurs either within tents or in the trash layer on the bog floor. Females lay eggs on the underside of cranberry leaves in the late spring/early summer. Development of the second generation proceeds similarly to the first except that second generation larvae cause direct damage to blossoms and berries. In addition, second generation adults fly in mid/late summer. A third generation is possible under favorable conditions.

Damage

Damage symptoms caused by first generation larvae appear similar to leafminer damage. First generation larvae also mine terminal buds, which may reduce fruit set. Second generation larvae cause direct damage to the flowers and fruit, often hollowing the fruit. Affected bogs exhibit a scorched appearance.

IPM Strategies

Monitoring for larvae often is conducted by viewing runner tips or sweepnet sampling. Particular attention should be paid to areas of previous infestation and bed edges. Pheromone traps are commercially available for monitoring adults. Regional recommendations for trap maintenance and spacing may vary.

References

Fitzpatrick SM (2006) Delayed mating reduces fecundity of blackheaded fireworm, *Rhopobota naevana*, on cranberry. Entomol Exp Appl 120:245–250

Ilze A, Cinitis R (2006) Major pests in cranberry plantations in Latria. J Fruit Ornamental Plant Res14:133–136

Grapes

Among the small fruit crops, grapes have the highest market value in the US, averaging more than 2 billion dollars in annual sales. Grapes are produced on almost a million acres of land in the US. About 85% of the grapes produced are processed for wine production. A small amount of grapes is dried for raisins, or processed for jams and jellies, and less than 10% are used for juice production.

California leads the US in grape production, generating more than 90% of total sales, followed by Washington and New York, which produce 4 and 2%, respectively. Most American grape cultivars are hybrids of native American species and European grapes, *Vitis vinifera* L. Hybridization combines the excellent wine quality of European grapes with the insect and disease resistance qualities of the wild American grape species. American hybrids were used during the latter part of the nineteenth century to combat a major pest, grape phylloxera, *Daktulosphaira vitifoliae* (Fitch). A few European cultivars are grown in the colder regions of the American Muscadine grapes, *Vitis rotundifolia* Michx., are grown on small acreage in the southeastern regions of the USA. Muscadine grapes have a long history in commercial and backyard culture in eastern USA and were the first American grape to be cultivated. Muscadine grapes usually are sold in groceries as fresh pack. Like other small fruits, grapes are susceptible to many insect and disease pests. The glassy-winged sharpshooter, *Homalodisca coagulata* (Say), recently has become established in California and is a major threat to the state wine industry because it vectors the bacterium *Xylella fastidiosa*, which causes Pierce's disease in grapes.

Pests of Grapes, *Vitis* spp. (Family Vitaceae)

Grape Berry Moth, *Endopiza vitana* Clemens (Lepidoptera: Tortricidae)

Distribution

Grape berry moth is a key pest of grapes throughout the United States and Canada east of the Rocky Mountains. Prior to grape cultivation in this region, the grape berry moth infested wild grapes.

Biology

Adults are brown moths with grayish markings, with a 9–12 mm wingspan. There are two or three generations per year. First generation adults emerge from pupation in late spring. Females lay eggs singly on buds or stems, while the later generation(s) lay eggs directly on the fruit. Eggs, which are approximately 0.7 mm, must be viewed using a hand lens. Eggs hatch into creamy white larvae within a week in most regions. Larvae have a brown head and dark thoracic shield. The abdomen changes color from white to green to purple as the larvae mature. Full grown larvae measure about 10 mm in length. Larvae generally construct cocoons from leaves and leaf litter, although some larvae pupate within the fruit cluster in which they once fed. Pupae are light brown to green in color and are 5 mm long.

Damage

First generation larvae feed on tender stems, blossom buds, and berries. Later generations cause direct damage to the fruit, often boring into several grape berries at their point of contact and webbing the cluster together. Up to seven berries may be damaged by a single larva.

IPM Strategies

Pheromone lures are available commercially for monitoring the emergence of male moths within vineyards and in adjacent locations. These pheromone baited traps are useful for properly timing insecticide applications where grape berry moth is an annual pest. Cultural control methods include removing infested clusters, generally when infestations are mild. Leaf litter containing cocoons can be destroyed after harvest. In the spring, applying a layer of compact soil on top of the leaf litter may reduce adult emergence.

References

Jerkins PE, Isaacs R (2007) Reduced-risk insecticides for control of grape berry moth (Lepidotera: Tortricidae) and conservation of natural enemies. J Econ Entomol 100:855–865

Williamson JR, Johnson DT (2005) Effects of grape berry moth management practices and landscape on arthropod diversity in grape vineyards in southern United States. Horttechnology 15:232–238

Grape Root Borer, *Vitacea polistiformes* (Harris) (Lepidoptera: Sesiidae)

Distribution

The grape root borer is a major pest of grapes in the south eastern United States. The life cycle of grape root borer requires 2–3 years in states north of Georgia. However, in Florida the lifecycle could be completed 1 year (Fig. 55).

Biology

Adults are dark brown with thin yellow bands across the abdomen and resemble paper wasps. The forewings are dark brown, while the hind wings are transparent. Adult moths are daytime fliers and live for approximately 7 days. Females lay up to 500 dark brown eggs in clusters on the soil surface, on grape leaves, or on nearby weeds. Eggs hatch in about 2 weeks, and first instar larvae drop to the ground and tunnel into vine roots. Larvae are cream colored with a brown head. Studies suggest that only 3% of neonate larvae survive threats of parasitism, predation and desiccation. However, once larvae become established in the vine roots, mortality is very low. Mature larvae can be up to 40 mm in length. Second year larvae leave the vine roots to pupate in cocoons near the soil surface. The pupal stage lasts approximately 35–40 days.

Small Fruit Pests and Their Management, Figure 55 Grape root borer.

Damage

Grape root borer damage is often difficult to diagnose since the damaging larvae are hidden within the vine roots. However, evidence such as protruding pupal skins left by emerging adults may indicate that an infestation is present. Larval feeding results in reduced vine vigor and a reduction in grape yield. Only two or three larvae are necessary to destroy an entire plant.

IPM Strategies

Cultural methods for control of grape root borer include mounding soil under vines just after pupation in order to reduce adult emergence. Proper weed management is also important for reducing potential egg laying sites and to increase larval mortality due to desiccation. Two species of *Heterorhabditis* nematodes have shown promise as biological control agents against grape root borer larvae. Pheromone-baited traps are recommended for monitoring adult moths. These traps should be placed about 100 m apart inside the vineyard and along adjacent woodland boundaries. Monitoring information may be useful for timing insecticide applications, although contact insecticides are ineffective once larvae reach the root system.

Reference

Weihman SW, Liburd OE (2006) Mating disruption and attack-and-kill as reduced-risk strategies for control of grape root borer, *Vitacea polistiformis* (Lepidoptera: Sesiidae) in Florida vineyards. Fla Entomol 89:245–250

Weihman SW, Liburd OE (2007) Seasonal distribution and evaluation of two trap types for monitoring grape root borer *Vitacea polistiformis* (Lepidoptera: Sesiidae) in Florida vineyards. Fla Entomol 90:480–487

Glassy-Winged Sharpshooter, *Homalodisca coagulata* (Say) (Hemiptera: Cicadellidae)

Distribution

The glassy-winged sharpshooter, *Homalodisca coagulata* (Say), is native to the southeastern

United States. Glassy-winged sharpshooter recently has become established in California where it vectors the bacterium *Xylella fastidiosa*, which causes Pierce's disease in grapes.

Biology

Adults measure up to 2 cm in length and have large membranous wings with red markings. There are distinguishing small yellow dots on the head and thorax. The glassy-winged sharpshooter overwinters as an adult and emerges under favorable climatic conditions. Generally, there are two generations per year in semi-tropical climates. Females lay eggs in groups of 10–20 on the underside of leaves, just under the epidermis. After oviposition, females protect their eggs with "brochosomes," which are white hydrophobic particles produced in specialized locations within the Malphigian tubules.

Damage

The glassy-winged sharpshooter feeds on vines, not leaves. Early symptoms of Pierce's disease include wilting, the appearance of water loss, which is caused by bacterial growth that blocks the flow of xylem in affected plants. Subsequent damage includes discolored leaf margins, shriveled fruit, leaf drop, and irregular maturation of new canes. Several other sucking insects may transmit the *X. fastidiosa* bacterium, including the blue-green leafhopper, *Graphocephala atropunctata* (Signoret), although the common grape leafhoppers (discussed later) are not known to be vectors.

IPM Strategies

Host plant resistance methods, which focus on planting vines resistant to *X. fastidiosa* may reduce the incidence of Pierce's disease. In general, muscadine grapes are resistant to *X. fastidiosa*, which may be responsible for the absence of Pierce's disease in some places, including Florida.

References

Phillips PA (2001) Protecting vineyards from Pierce's disease. Calif Agric 25:19–20

Vickerman DB, Hoodle SM, Triapitsyn S, Stouthamer R (2004) Species identity of geographically distinct populations of the glassy-winged sharpshooter parasitoid. Biol Control 31:338–345

Grape Leafhoppers, *Erythroneura* spp. (Hemiptera: Cicadellidae)

Distribution

There are several species of Cicadellidae that are referred to as grape leafhoppers. In general, members of the genus *Erythroneura* cause the most serious damage to grapes. The grape leafhopper, *Erythroneura comes* (Say), is the most abundant species in the northeastern United States. In Florida, *E. vulneurata* is the most important species, while *E. elegantula* and the variegated leafhopper, *E. variabilis*, occur in California. These species are also believed to vector Pierce's disease (Table 10).

Biology

Leafhoppers of the genus *Erythroneura* overwinter as adults, emerging from nearby hibernation sites when temperatures exceed 16°C. Adults are approximately 3 mm in length and are pale yellow in the beginning of the season. As the season progresses, adults obtain a deeper color, often with distinct markings or spot. Eggs are laid singly on the underside of the leaf just below the epidermis. Nymphs hatch within 7–10 days. Newly hatched nymphs are nearly transparent and have distinct red eyes. There are five nymphal instars, and with each molt thorax markings and wing pads become more prominent. Both nymphs and adults are very active.

Damage

Adults and nymphs bore small holes into the underside of leaves and extract cell sap and chlorophyll, generally when plant nutrients are

Small Fruit Pests and Their Management, Table 10 Selected list of arthropods that affect grape production in the United States

Common Name	Scientific Name	Order	Family
Grape erineum mite	*Colomerus vitis* (Pagenstecher)	Acari	Eriophyidae
Two-spotted spider mite[a]	*Tetranychus urticae* Koch	Acari	Tetranychidae
Pacific spider mite	*Tetranychus pacificus* McGregor	Acari	Tetranychidae
Willamette spider mite	*Eotetranychus willamettei*	Acari	Tetranychidae
Branch and twig borer	*Melalqus confertus* LeConte	Coleoptera	Bostrichidae
Grape curculio	*Craponius inaequalis* (Say)	Coleoptera	Curculionidae
Plum curculio[b]	*Conotrachelus nenuphar* (Herbst)	Coleoptera	Curculionidae
Grape bud beetle	*Glyptoscelis squamulata* Crotch	Coleoptera	Chrysomelidae
Grape flea beetle	*Altica chalybea* (Illiger)	Coleoptera	Chrysomelidae
Grape colaspis	*Colaspsis brunnea* (Fabricius)	Coleoptera	Chrysomelidae
Southern grape rootworm	*Fidia longipes* (Melsheimer)	Coleoptera	Chrysomelidae
Grape cane girdler	*Ampeloglypter ater* LeConte	Coleoptera	Curculionidae
Grape cane gallmaker	*Ampeloglypter sesostris* LeConte	Coleoptera	Curculionidae
Japanese beetle[b]	*Popillia japonica* Newman	Coleoptera	Scarabaeidae
Grape trunk borer	*Clytoleptus albofasciatus* (Laporte & Gory)	Coleoptera	Cerambycidae
Grape blossom midge	*Contarinia johnsoni* Felt	Diptera	Cecidomyiidae
Grape sawfly	*Erythraspides vitis* (Harris)	Hymenoptera	Tenthredinidae
Grape seed chalcid	*Eroxysoma vitis* (Saunders)	Hymenoptera	Eurytomidae
Grape whitefly	*Trialeurodes vittata* (Quaintance)	Hemiptera	Aleyrodidae
Sharpshooters	*Homalodisca coagulata* (Say)	Hemiptera	Cicadellidae
Grape mealybug	*Pseudococcus maritimus* (Ehrhorn)	Hemiptera	Pseudococcidae
Grapevine aphid	*Aphis illinoisensis* (Shimer)	Hemiptera	Aphididae
Grape leafhopper[a]	*Erythroneura comes* (Say)	Hemiptera	Cicadellidae
Grape leafhopper[a]	*Erythroneura elegantula* Osborn	Hemiptera	Cicadellidae
Variegated grape leafhopper	*Erythroneura variabilis* Beamer	Hemiptera	Cicadellidae
Grape phylloxera	*Daktulosphaira vitifoliae* (Fitch)	Hemiptera	Phylloxeridae
Grape scale	*Diaspidiotus uvae* (Comstock)	Hemiptera	Diaspididae
Grape berry moth	*Endopiza vitana* Clemens	Lepidoptera	Tortricidae
Omnivorous leafroller	*Platynota stultana* Walshingham	Lepidoptera	Tortricidae
Orange tortrix	*Argyrotaenia citrana* (Fernald)	Lepidoptera	Tortricidae
Grape leaffolder	*Desmia funeralis* (Hübner)	Lepidoptera	Pyralidae
Grapevine looper	*Eulythis diversilineata* (Hübner)	Lepidoptera	Geometidae
Brassy cutworm	*Orthodes rufula* Grote	Lepidoptera	Noctuidae
Spotted cutworm	*Amathes c-nigrum* (L.)	Lepidoptera	Noctuidae
Variegated cutworm	*Peridroma saucia* (Hübner)	Lepidoptera	Noctuidae

Small Fruit Pests and Their Management, Table 10 Selected list of arthropods that affect grape production in the United States (Continued)

Common Name	Scientific Name	Order	Family
Grape plume moth	*Pterophorus periscelidactylus* Fitch	Lepidoptera	Pterophoridae
Grape root borer	*Vitacea polistiformes* (Harris)	Lepidoptera	Sesiidae
Grapeleaf skeletonizer	*Harrisina americana* (Guérin-Méneville)	Lepidoptera	Zygaenidae
Western grapeleaf skeletonizer	*Harrisina brillians* Barnes & McDunnough	Lepidoptera	Zygaenidae
Western flower thrips[a,b]	*Frankliniella occidentalis* (Pergande)	Thysanoptera	Thripidae
Eastern flower thrips[a,b]	*Frankliniella tritici* (Fitch)	Thysanoptera	Thripidae
Florida flower thrips[a,b]	*Frankliniella bispinosa* (Morgan)	Thysanoptera	Thripidae

[a]also infest raspberries and strawberries
[b]also infest blueberries

abundant. Affected leaves have a mottled appearance and may lose their color. Severe injury to the leaf tissue may result in leaf drop and reduced fruit quality. Excreta (honeydew) from leafhoppers may accumulate on the foliage and berries making them susceptible to fungal attack, particularly sooty molds.

IPM Strategies

Monitoring strategies for leafhoppers include the use of yellow sticky boards or counting the number of nymphs and adults relative to the number of leaves. Removal of alternate host plants and weed management in areas adjacent to vineyards may reduce food sources and potential overwintering sites. Coverage on the undersides of leaves is important when insecticide treatments are warranted for leafhopper control.

References

Böll S, Herrmann JV (2004) A long-term study on the population dynamics of the grape leafhopper antagonistic mymarid species. J Pest Sci 77:33–42

Böll S, Schmitt T, Burschka C, Schreier P, Schwappach P, Herrmann JV (2005) Calcium tartrate crystals in the midgut of the grape leafhopper. J Chem Ecol 31:2847–2856

Grape Leaffolder, *Desmia funeralis* (Hübner) (Lepidoptera: Pyralidae)

Distribution

The grape leaffolder is a common pest of grapes throughout the United States. It is native to eastern North America but it is now distributed from southern Canada to northern Mexico. Although damage is typically minor, outbreaks of grape leaffolder have been occurred occasionally in both California and Florida. There are several generations per year in the southeastern United States and California, although damage appears to be most problematic during the second and third generations.

Biology

Adult moths are nearly black and have slightly iridescent wings. Wingspan varies from 2 to 2.5 cm. There are two white, oval-shaped spots on the forewings of both sexes. Males have a white band on the hindwings, while a similar band may be partitioned into two spots in females. Mated females lay elliptical-shaped eggs singly on the underside of leaves, often near the veins. Emerging larvae feed on the leaves of grapevines. At maturity, larvae are 15–20 mm long and nearly transparent; larvae also may appear green as a result of consuming leaf material. The head of the larva is light brown and the abdominal segments have fine yellow hairs. If larvae are disturbed, they wriggle from their silken enclosure and drop to the ground. Pupation generally occurs within the leaf-roll.

Damage

Larvae feed for about 2 weeks before rolling the edge of a leaf to complete development. The leaf folds are constructed with silk threads. Rolled leaves have their undersides exposed, and often the upper surface is skeletonized. Third generation larvae may completely defoliate a vineyard, resulting in sun-scorched berries. In some instances, larvae may feed directly on the berries.

IPM Strategies

In general, populations of grape leaffolder are balanced by the presence of several larval parasites, including *Bracon cushmani* (Muesebeck). However, growers could monitor vineyards with a history of leaffolder outbreaks. Adult moths can be monitored with tent-shaped traps baited with terpinyl acetate or by using blacklight traps. If insecticide treatment becomes necessary, sprays are generally most effective against early instars.

References

Aliniazee MT, Stafford EM (1973) Sex pheromone of the grape leaffolder, *Desmia funeralis* (Lepidoptera: Pyralidae): laboratory and field evaluation. Ann Entomol Soc Am 66:909–911

Millar J, McElfresh JS, de Assis Marques F (2002) Unusual acetylenic sex pheromone of grape leaffolder (Lepidoptera: Pyralidae). J Econ Entomol 95:692–705

Strawberries

In the USA, California is the largest producer of strawberries, generating more than 50% of the nation's strawberries on over 25,000 acres of land. Florida ranks second in the country in terms of quantity of strawberries produced, followed by Oregon and the state of Washington. During 2001, the total value of strawberries produced in the USA exceeded $1 billion dollars. In the south, strawberries are grown as an annual crop and are cultivated between October and May. In the northeast, strawberries are grown as a perennial crop. Some of the cultivars commonly grown in the north include Kent, Annapolis and Honeoye. In the south and western US, Camarosa, Sweet Charlie, Chandler, and Aromas are fairly common cultivars. Each variety has its own unique characteristics with distinct advantages and disadvantages. Strawberries are a rich source of vitamin C and folic acid. They are relatively low in calories and some varieties are rich in antioxidants. Strawberries are susceptible to several mite and insect pests including the two-spotted spider mite, *Tetranychus urticae* Koch, plant bugs belonging to the genus *Lygus*, tarnished plant bug, *Lygus lineolaris* (Palisot de Beauvois), in the east, and the western plant bug, *L. hesperus* Knight. The strawberry clipper, *Anthonomus signatus* (Say), once was considered a major pest of strawberries, but recent reports have indicated that the floral buds removed early in the season by strawberry clipper are compensated with more vigorous bud growth later in the season, resulting in larger more dense fruit.

Pests of Strawberries, *Fragaria* spp. (Family Rosaceae)

Twospotted Spider Mite, *Tetranychus urticae* Koch (Acari: Tetranychidae)

Distribution

The two-spotted spider mite is distributed widely across North America, and is known to feed on more than 180 species of plants in both greenhouse and outdoor environments. The two-spotted spider mite occurs year-round in the greenhouse, but its presence in the field requires warm temperatures (Fig. 56).

Small Fruit Pests and Their Management, Figure 56 **Twospotted spider mite.**

Biology

The two-spotted spider mite develops through five phases: egg, larvae, proto-nymph, deuto-nymph and adult. The larva can be distinguished from the other stages because it has only six legs and is the size of the egg. The protonymph and deutonymph resemble the adult. Adults are approximately 0.5 mm long and range in color from light green to dark red, usually with two dark spots on the dorsal surface of the abdomen. Adults overwinter under vegetative cover, and mated females begin feeding and laying eggs when temperatures increase. Maturity from egg to adult requires at least 5 days, but may approach 1 month, depending on environmental conditions. Dispersal of two-spotted spider mites can occur by either ambulatory or aerial means. The vast majority of dispersal takes place aerially due to the small size of mites and the amount of time it would take for a spider mite to travel from one plant to another. There are several generations per year.

Damage

Two-spotted spider mite feeds on the underside of strawberry leaves by inserting their mouthparts into the leaf cells and extracting cellular fluid from the plant. The result is chlorosis, which leads to a decrease in photosynthetic activity by the plant and a subsequent reduction in fruit yield. Infested leaves are often mottled brown and the leaf surfaces may be covered with fine webbing. Mite colonies tend to be localized rather than evenly distributed and are more abundant when the weather is dry.

IPM Strategies

Sampling for two-spotted spider mite can be accomplished by collecting leaves from the field and counting the number of mites on individual leaves, generally with the aid of a microscope. Heavy infestations can be treated with reduced-risk miticide. An alternative to treatment with miticides is the inoculative release of predatory mites, primarily in the family Phytoseiidae (Fig. 58). Monitoring for the persistence of Phytoseiidae mites in the fields should be conducted in conjunction with two-spotted spider mite sampling.

References

Rhodes EM, Liburd OE (2006) Evaluation of predatory mites and acramite for control of twospotted spider mites in strawberries in north central Florida. J Econ Entomol 99:1291–1298

White JC, Liburd OE (2005) Effects of soil moisture and temperature on reproduction and development of twospotted spider mite (Acari: Tetranychidae) in strawberries. J Econ Entomol 98:154–158

Strawberry Sap Beetle, *Stelidota geminata* (Say) (Coleoptera: Nitidulidae)

Distribution

There are several species of sap beetles that affect strawberries throughout the United States, including the strawberry sap beetle, *Stelidota geminata* (Say). Other sap beetles, including the picnic beetle, *Glischrochilus quadrisignatus* (Say), and the dusky sap beetle, *Carpophilus lugubris* Murray, also may be problematic in many areas.

Biology

Adult beetles are brown and somewhat mottled, approximately 3 mm in length with capitate antennae. The elytra are shortened, leaving the terminal abdominal segments exposed. Larvae range in color from white (early instar) to pale yellow (mature) and have a light brown head. The body is elongate and the mouthparts are exposed. Larval development is much shorter compared with the adult lifestage. *Stelidota geminata* pupae are tan colored prior to adult emergence and are about 4 mm in length. Adults emerge in the spring from decaying vegetation and mate and lay eggs near decomposing plant material. Larvae develop in decomposing material in or near the soil before pupating. The cycle from egg to adult takes about 30–35 days.

Damage

The sap beetle is also a contaminant of strawberries, which may cause large batches of fruit to be rejected by processors. In some cases the adults bore into the strawberry fruit, rendering it unmarketable.

IPM Strategies

The sap beetle may be monitored with traps baited with synthetic volatile compounds. Since the beetles are attracted to ripe fruits, insecticide treatments are usually not recommended. One cultural tactic is to harvest berries before they become over-ripe. In addition, damaged, decaying or diseased fruit should be removed from the field.

References

Peng C, Williams RN (1991) Effect of trap design, trap height, and habitat on the capture of sap beetles (Coleoptera: Nitidulidae) using whole-wheat bread dough. J Econ Entomol 84:1515–1519

Williams RN, Ellis MS, Fickle DS, Bloom ST (1996) A migration study of *Sterlidota germinata* (Coleopteran: Nitidulidae). Great Lakes Entomol 29:31–36

Strawberry Bud Weevil (Clipper), *Anthonomus signatus* (Say) (Coleoptera: Curculionidae)

Distribution

Strawberry bud weevil is a pest of several small fruits in the northeastern United States and Canada, including strawberries, blueberries, and brambles. This species often is called the "strawberry clipper" because clipped buds are characteristic damage resulting from weevil infestation (Table 11).

Biology

Strawberry bud weevil overwinters as an adult, emerging from protected areas such as mulch and fence lines when temperatures become favorable. Adults are approximately 3 mm in length. They are reddish brown beetles with a pronounced snout. Mated females lay eggs singly inside flower buds and then partially clip the blossom below the bud. The infested bud may remain on the plant or drop to the ground, where egg and larval development occurs. Eggs hatch within 1 week. The larvae are white and develop within the bud, reaching maturity after 3–4 weeks. Adults emerge in early to mid-summer, depending on region.

Damage

The major damage caused by strawberry bud weevil occurs during egg lay, as infested buds wilt and fail to produce fruit. Prior to egg lay, adults also may feed on pollen from unopened buds. Brownish-purple holes in the sepals may indicate pollen feeding, although this type of damage does not necessarily disrupt normal fruit development.

IPM Strategies

Monitoring tactics for strawberry bud weevil should focus on counting the number of clipped buds in a particular area. One method involves placing a 30 × 60-cm frame over plants

Small Fruit Pests and Their Management, Table 11 Selected list of arthropods that affect strawberry production in the United States

Common name	Scientific name	Order	Family
Strawberry spider mite	*Tetranychus turkestani* Ugarov & Nikolski	Acari	Tetranychidae
Two-spotted spider mite[a,b]	*Tetranychus urticae* Koch	Acari	Tetranychidae
Cyclamen mite	*Phytonemus pallidus* (Banks)	Acari	Tarsonemidae
Strawberry bud weevil[a]	*Anthonomus signatus* (Say)	Coleoptera	Curculionidae
Strawberry root weevil[a]	*Otiorhynchus ovatus* L.	Coleoptera	Curculionidae
Strawberry rootworm	*Paria fragariae* Wilcox	Coleoptera	Chrysomelidae
Strawberry crown borer	*Tyloderma fragariae* (Riley)	Coleoptera	Curculionidae
Black vine weevil[a]	*Otiorhynchus sulcatus* (Fabricius)	Coleoptera	Curculionidae
Rough strawberry root weevil[a]	*Otiorhynchus rugosostriatus* (Goeze)	Coleoptera	Curculionidae
Strawberry sap beetle	*Stelidota geminata* (Say)	Coleoptera	Nitidulidae
Tarnished plant bug[a]	*Lygus lineolaris* (Palisot de Beauvois)	Hemiptera	Miridae
Strawberry aphid	*Chaetosiphon fragaefolii* (Cockerell)	Hemiptera	Aphididae
Strawberry root aphid	*Aphis forbesi* Weed	Hemiptera	Aphididae
Strawberry whitefly	*Trialeurodes packardi* (Morrill)	Hemiptera	Aleyrodidae
Meadow spittle bug	*Philaenus spumarius* (L.)	Hemiptera	Cercopidae
Potato leafhopper[a,b]	*Empoasca fabae* (Harris)	Hemiptera	Cicadellidae
Strawberry leafroller	*Ancylis comptana* (Froelich)	Lepidoptera	Tortricidae
Strawberry crown miner	*Aristotelia fragariae* Busck	Lepidoptera	Gelechiidae
Strawberry crown moth	*Synanthedon bibionipennis* (Boisduval)	Lepidoptera	Sesiidae
Western flower thrips[c]	*Frankliniella occidentalis* (Pergande)	Thysanoptera	Thripidae
Eastern flower thrips[c]	*Frankliniella tritici* (Fitch)	Thysanoptera	Thripidae
Florida flower thrips[c]	*Frankliniella bispinosa* (Morgan)	Thysanoptera	Thripidae

[a]also infest brambles
[b]also infest grapes
[c]also infest blueberries and grapes

and counting the number of clipped buds. Growers should pay particular attention to rows located near potential overwintering sites. Insecticide applications may be warranted if the number of clipped buds exceeds 13 per sampling area (30 × 60 cm). Sampling should continue after insecticide applications are made in order to assess the need for further applications.

References

English-Loeb G, Pritts M, Kovach J, Rieckenberg R, Kelly MJ (1999) Compensatory ability of strawberries to bud and flower removal: implications for managing the strawberry bud weevil (Coleoptera: Curculionidae). J Econ Entomol 92:915–921

Mailloux G, Bostanian NJ (1993) Development of the strawberry bud weevil (Coleoptera: Curculionidae) in strawberry fields. Ann Entomol Soc Am 86:384–393

Tarnished Plant Bug, *Lygus lineolaris* (Palisot de Beauvois) (Hemiptera: Miridae)

Distribution

Tarnished plant bug feeds on wild and cultivated plants throughout North America, although it is a pest primarily in temperate regions. Regarding small fruit production, tarnished plant bug often affects strawberries and brambles (raspberry and blackberry) (Fig. 57).

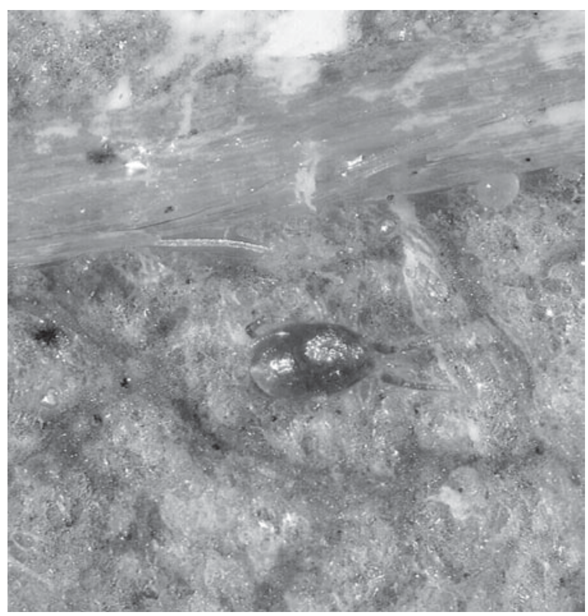
Small Fruit Pests and Their Management, Figure 57 **Tarnished plant bug.**

Biology

Tarnished plant bug adults exhibit a greenish-brown coloration that is mottled with red. Adults are approximately 6 mm in length and are identified by a characteristic yellow triangle at the junction of the wings anteriorly. Tarnished plant bugs overwinter as adults under bark, leaves, and other ground covers that offer protection. Adults become active during the blossoming period of fruit production and feed on nutritive plant juices. Females lay 1 mm long, cream-colored eggs in the plant tissue, either directly on the fruit crop or within adjacent ground cover. There are five nymphal stages, characterized by a progressive color change from green to brown. The entire lifecycle requires 25–40 days, yielding a varying number of generations, depending on seasonal weather conditions.

Damage

Fruit affected by tarnished plant bug feeding exhibits "catfacing," which is the result of tissue development around a centralized wound. Damage caused by egg lay may cause more intense fruit distortion and may be accompanied by one or more blemishes (scabs). The severity of damage resulting from tarnished plant bug injury may vary with cultivars.



Small Fruit Pests and Their Management, Figure 58 ***Phytoseiulus persimilis*, a predatory mite.**

IPM Strategies

There are several techniques that can be used for monitoring tarnished plant bug populations. Direct plant examinations or visual inspections, sticky traps, sweep sampling, and fruit injury counts are only some of the techniques used for monitoring tarnished plant bug activity in the field. Any one of these tactics may be preferred in one setting over another. Sweep netting is a simple way to sample for nymphs in nearby vegetation. Visual examination is a direct method for visualizing insect activity, although adults may fly if disturbed, and this method may vary considerably with weather conditions. Ground cover management, including mowing and tilling, may be useful for reducing migrating tarnished plant bug populations.

References

Handley DT, Pollard JE (1993) Tarnished plant bug (*Lygus lineolaris*) behavior on cultivated strawberries. Acta Hortic Aug:463–468

Panneton B, Belanger A, Vincent C, Piche M, Khelifi M (2000) Effect of water volume rates on spray deposition and control of tarnished plant bug (Hemiptera: Miridae) in strawberry crops. Phytoprotection 81:115–122

Brambles

Brambles are defined as plants belonging to the genus *Rubus* and include blackberries and raspberries. Tayberries are brambles resulting from a cross between blackberry and raspberry. Blackberries and raspberries are the two most common bramble crops grown in the US. In 2001, more than 6,000 acres of blackberries were produced in the US with an estimated value exceeding $14 million dollars. Oregon leads the country in blackberry production with more than 90% of the US sales. Among the brambles, raspberries are cultivated on the largest acreage. The three most commonly types of raspberry grown in the US are red, black and purple. In 2001, approximately 16,000 acres of raspberries were produced in the US with more than 50% of the production coming from the state of Washington. Brambles are susceptible to several key pests including raspberry cane borer, *Oberea bimaculata* (Olivier), rednecked cane borer, *Agrilus ruficollis* (F.), and blackberry psyllid, *Trioza tripunctata* (Fitch).

Pests of Raspberries and Blackberries (Brambles), *Rubus* spp. (Family Rosaceae)

Raspberry Cane Borer, *Oberea bimaculara* (Olivier) (Coleoptera: Cerambicidae)

Distribution

The raspberry cane borer is native to North America and it is found throughout the northeastern United States and Canada (Table 12).

Biology

The posterior region of the head (pro-thorax) is bright yellow with two or three black dots. Raspberry cane borer requires a 2-year cycle to complete its development. Females lays eggs on the canes and then girdle a hole approximately 6 mm in diameter around the eggs. After eggs hatch, larvae bore further into the cane to overwinter into the soil. During the following season, larvae continue to bore into the canes until they reach the raspberry crown. During the second spring mature larvae continue to feed, eventually pupating in the hollow surface of the cane. Adults begin to emerge in early summer and produce eggs shortly after.

Damage

Heavy infestation results in wilted shoots and toppled canes.

IPM Strategies

Canes should be examined weekly for hollow stems and signs of wilting. One cultural technique, which may reduce total infestation of raspberry cane borer, involves the removal of hollow canes and wilted shoots that show signs of injury. After canes are removed, end surfaces should be re-inspected to ensure that no hollow surfaces remain in the existing canes.

Small Fruit Pests and Their Management, Table 12 **Selected list of arthropods that affect brambles (raspberry and blackberry) production in the United States**

Common name	Scientific name	Order	Family
Raspberry cane borer	*Oberea bimaculara* (Olivier)	Coleoptera	Cerambicidae
Rednecked cane borer	*Agrilus ruficollis* (F.)	Coleoptera	Buprestidae
Raspberry fruitworm	*Byturus unicolor* (Say)	Coleoptera	Byturidae
Eastern raspberry fruitworm	*Byturus rubi* Barber	Coleoptera	Byturidae
Western raspberry fruitworm	*Byturus bakeri* Barber	Coleoptera	Byturidae
Raspberry cane maggot	*Pegomya rubivora* (Coquillett)	Diptera	Anthomyiidae
Blackberry psyllid	*Trioza tripunctata* (Fitch)	Hemiptera	Psyllidae
Blackberry leafhopper	*Dikrella californica* (Lawson)	Hemiptera	Cicadellidae
Blackberry gallmaker	*Diastrophus nebulosis* (O.S)	Hymenoptera	Cynipidae
Raspberry sawfly	*Monophadnoides geniculatus* (Hartig)	Hymenoptera	Tenthredinidae
Blackberry leafminer	*Metallus rubi* Forbes	Hymenoptera	Tenthredinidae
Blackberry skeletonizer	*Schreckensteinia festaliella* (Hübner)	Lepidoptera	Heliodinidae
Raspberry bud moth	*Lampronia rubiella* (Bjerkander)	Lepidoptera	Incurvariidae
Raspberry crown borer	*Pennisetia marginata* (Harris)	Lepidoptera	Sesiidae
Raspberry leafroller	*Olethreutes permundana* (Clemens)	Lepidoptera	Tortricidae

References

Bessin R (2001) Rednecked and raspberry cane borers. Extension Publication, College of Agriculture. University of Kentucky. Available at http://www.uky.edu/ Agriculture/Entomology/entfacts/fruit/ef209.htm (accessed 3 April 2008)

Eaton A (1994) Raspberry cane borer, small fruit pest. Extension fact sheet #53, Cooperative Extension Unit. University of New Hampshire, Durham, New Hampshire

Raspberry Fruitworm, *Byturus unicolor* (Say) (Coleoptera: Byturidae)

Distribution

Raspberry fruitworm is distributed throughout the eastern United States wherever raspberries are grown.

Biology

Adult beetles are yellowish brown, hairy and about 8 mm long. Adults lay grayish-white eggs on swollen, unopened blossom buds, which may be deposited at the base of the developing fruit. Eggs hatch into larvae within a few days, and the emerging larvae feed on the developing fruit for 5–6 weeks. Larvae pupate in the soil inside of a cocoon. Raspberry fruitworm overwinters as an adult, and emerges the following year when blossoms begin to develop.

Damage

Raspberry fruitworm larvae feed on raspberry receptacles, causing berries to dislodge from the plant stems. In some cases, larvae feed on internal tissues of immature berries. Adults feed on blossom and foliage but rarely cause significant damage. High populations of adult fruitworm may result in characteristic longitudinal holes in the foliage.

IPM Strategies

Collecting and inspecting known numbers of blossoms and looking for eggs can be used as a strategy for monitoring populations of raspberry fruitworm. Developing berries also should be examined for larvae. Cultural strategies include cultivating the soil to bury raspberry fruitworm pupae and exposing pupae to natural predators. Infested plant debris also should be removed from the soil. The use of some selected reduced-risk insecticides also may play a role in regulating raspberry fruitworm populations.

Reference

Baker W (1949) Biology and control of the western raspberry fruit worm in western Washington. Bull State Coll Wash Agric Exp Stn 497:63

Occasional Pests of Small Fruits

Japanese Beetle, *Popillia japonica* Newman (Coleoptera: Scarabaeidae)

Distribution

The Japanese beetle is native to Japan and was first detected in the United States in New Jersey in 1916. Since then, the Japanese beetle has migrated southward into Alabama and Georgia. Specimens also have been collected in Florida, although the Japanese beetle is not considered a pest in that region. High populations of Japanese beetles have been recorded in Michigan and Ohio, whereas isolated populations have been detected in some western states (Table 13).

Biology

Japanese beetle adults are metallic green with an amber hue on their forewings. Adults are about 10 mm long and 7 mm wide with characteristic rows of hair along each side of the abdomen. Adults are active by day and spend the nighttime hours within tunnels in the soil. Within 10 days of emergence females begin to lay eggs in the soil of short grasses and continue to lay eggs for several weeks. Larvae (grubs) are usually cream colored just after hatching. Larvae develop through three instars and turn darker with age as they mature. During the winter, larvae move downward into the soil to hibernate when temperatures are cool. After hibernation, grubs tunnel up through the soil to feed on grasses to complete their development. There is usually one generation per year.

Damage

Adult beetles are generalist feeders that skeletonize the leaves of more than 400 broadleaf plants. Feeding damage is characterized by brown lacy leaves. However, adults also may attack flower buds and fruit, including blueberries and grapes. When populations are high, the adult becomes a contaminant in the harvest of blueberries and grapes, thus interfering with the marketability of the fruit. Larvae generally are not injurious to fruit crops but their existence in the ground cover serves as inoculum for next year's adult population.

IPM Strategies

The strategies for controlling adults and grubs are quite different. Traps baited with a combination of sex and aggregation pheromones are available commercially for monitoring adult populations of Japanese beetle. However, traps may attract adults from adjacent areas, which may increase the potential for damage to fruit crops. When chemical control is warranted, several applications of insecticide may be necessary to provide adequate control since adults continue to emerge all season long. In the past, grubs have been controlled using the bacterial milky diseases *Bacillus popilliae* Dutky and *B. lentimorbus* Dutky. This method has been relatively successful in the eastern United States. Recently, certain species of entomophagous nematodes have been shown to be effective in suppressing larval populations.

Small Fruit Pests and Their Management, Table 13 Selected list of arthropods that affect small fruit production in the United States

Common name	Scientific name	Order	Family
Plum curculio[a]	*Conotrachelus nenuphar* (Herbst)	Coleoptera	Curculionidae
Picnic beetle[b]	*Glischrochilus* spp.	Coleoptera	Nitidulidae
Japanese beetle[a]	*Popillia japonica* Newman	Coleoptera	Scarabaeidae
Rose chafer[c]	*Macrodactylus subspinosus* (Fabricius)	Coleoptera	Scarabaeidae
Green June beetle[b]	*Cotinis nitida* (L.)	Coleoptera	Scarabaeidae
Leaffooted bugs[c]	*Leptoglossus* spp.	Hemiptera	Coreidae
Stink bugs[c]	*Acrosternum hilare* (Say)	Hempiptera	Pentatomidae
Gypsy moth	*Lymantria dispar* L.	Lepidoptera	Lymantriidae
Oblique-banded leafroller[b]	*Choristoneura rosaceana* (Harris)	Lepidoptera	Tortricidae
Redbanded leafroller[c]	*Argyrotaenia velutinana* Walker	Lepidoptera	Tortricidae
Western flower thrips[c]	*Frankliniella occidentalis* (Pergande)	Thysanoptera	Thripidae
Eastern flower thrips[c]	*Frankliniella tritici* (Fitch)	Thysanoptera	Thripidae
Florida flower thrips[c]	*Frankliniella bispinosa* (Morgan)	Thysanoptera	Thripidae

[a]also infest blueberries and grapes
[b]also infest strawberry and brambles
[c]also infest blueberries, grapes, strawberries and brambles

Cultural methods of controlling Japanese beetle include decreasing irrigation to young grasses between rows and mowing of ground cover.

References

Cappaert DL, Smitley DR (2002) Parasitoids and pathogens of Japanese beetle (Coleoptera: Scarabaeidae) in southern Michigan. Environ Entomol 31:573–580

Stewart CD, Braman SK, Sparks BL, Williams-Woodward JL, Wade GL, Latimer JG (2002) Comparing an IPM pilot program to a traditional cover spray program in commercial landscapes. J Econ Entomol 95:789–796

Flower Thrips, *Frankliniella* spp. (Thysanoptera: Thripidae)

Distribution

There are several species of flower thrips that affect small fruit production throughout the United States. The eastern flower thrips, *Frankliniella tritici* (Fitch), is found east of the Rocky Mountains, and western flower thrips, *F. occidentalis* (Pergande), occurs throughout the United States and Canada. In the northeast, the blueberry thrips *F. vaccinii* Morgan and *Catinathrips kainos* O' Neil are minor pests in lowbush and highbush blueberries, causing leaf distortion and discoloration in small isolated patches in fields. In Florida, a species of flower thrips, *F. bispinosa* (Morgan), locally called Florida flower thrips, causes significant damage to southern highbush and rabbiteye blueberries. *Frankliniella bispinosa* also has been detected as far north as Georgia (Fig. 59).

Biology

In the absence of microscopic examination, flower thrips species are difficult to distinguish. Members of the genus *Frankliniella* are approximately 1–1.3 mm in length and yellow to brown in color, often

Small Fruit Pests and Their Management, Figure 59 ***Frankliniella bispinosa* thrips.**

with gray blotching across the abdomen. Males are generally smaller and paler than females. Eggs are cylindrical and are laid within the plant tissue, making them difficult to see. Thrips development progresses through several nymphal instars (latter stages sometimes are referred to as prepupae and pupae), each of which resembles the adult morph without wings. Adults and nymphs have rasping mouthparts. Most flower thrips migrate over long distances and are known to have an extensive host range.

Damage

Thrips are capable of causing damage in at least two different stages of fruit development. During the blooming period, thrips feed within the flowers by inserting their mouthparts into developing tissue and remove fluids. The resulting effect can be either aborted or distorted fruits. Thrips also may feed on pollen, causing additional floral abortion. Thrips also may feed on foliage, removing cell sap from plant tissues. If populations of thrips are high during the fruiting period, significant damage to the fruit can be observed, particularly in areas where the fruits are touching or closely clustered. This may result in silvery blemishes resembling a halo. Some species of thrips may be of particular concern for their potential to vector various plant viruses.

IPM Strategies

Because thrips are very mobile, their management can be very difficult. There are several methods available for monitoring flower thrips populations, including the use of sticky traps (white or blue), tapping infested flowers over a hard surface, and dipping infested flowers into alcohol. Grower preference and crop specifics may dictate which monitoring method works best in a particular area. It is also helpful to know which species is being targeted. Several predatory insects may be successful for suppressing flower thrips populations, including the minute pirate bug, *Orius insidiosus* (Say). The fungal pathogen *Beauveria bassiana* has shown potential for control of *F. occidentalis*, and may be a potential agent for control of other thrips species in the future. Cultural methods for control of thrips species include elimination of alternate hosts near the main crop, particularly if the blooming periods overlap.

References

Arévalo HA, Liburd OE (2007) Horizontal and vertical distribution of flower thrips in southern highbush and rabbiteye blueberry fields, with notes on a new sampling method for thrips inside the flowers. J Econ Entomol 100:1622–1632

Moritz G, Morris D, Mound L (2001) Thrips ID: pest thrips of the world. CSIRO Publishing, Collingwood, Victoria, Australia

Small Green Stink Bug, *Piezodorus guildinii* (Westwood) (Hemiptera: Heteroptera: Pentatomidae)

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The small green stink bug, *Piezodorus guildinii* (Westwood), is a Neotropical pentatomid found from the southern U.S. to Argentina. It first was described from the island of St. Vincent, and frequently has been reported from Central and South

America. It is a major pest of soybean in South America. In Brazil, this stink bug was seldom found on soybean until the early 1970s. Subsequently, it has become more common, ranging from Rio Grande do Sul (32° S latitude) to Piau (5° S latitude). With the expansion of soybean production to the central, west, and northeast regions of the country, *P. guildinii* is, perhaps, the most important pest of soybean in Brazil.

The list of food plants includes some economically important plants in addition to soybean, mostly legumes such as common bean, pea, and alfalfa. It is reported occasionally on sunflower, cotton, and guava, but it is not believed to be a serious pest of these crops. Native host plants include species of indigo legumes, *Indigofera* spp., in the southern U.S., Colombia, and Brazil. It also feeds on legumes of *Sesbania* and on *Crotalaria*.

Eggs are blackish and laid in two parallel rows. First, second, third, fourth, and fifth instars are 1.30, 2.25, 2.58, 4.60, and 7.87 mm long, respectively. Adults are light green to yellowish, with a red-band at the base of the scutellum, particularly on females (Fig. 60).

Small Green Stink Bug, *Piezodorus guildinii* (Westwood) (Hemiptera: Heteroptera: Pentatomidae), Figure 60 Adult of small green stink bug.

The number of egg masses per female will vary from approximately 3 on soybean up to 37 in some indigo species. Total number of eggs per female will vary from approximately 28 on soybean to approximately 200 on *Indigofera hirsuta* to approximately 500 on *I. truxillensis*. Adults will have a total longevity of approximately 50 days on soybean (mean of female and male) up to approximately 90 days on some of the indigo legumes. Despite its relatively low performance on soybean compared to native legumes, *P. guildinii* is highly detrimental to this crop, as noted previously.

Piezodorus guildinii, like most of the phytophagous pentatomids associated with soybean, feeds primarily on pods. The nature and extent of the damage to this crop is similar to that reported for southern green stink bug, *Nezara viridula*. *Piezodorus guildinii* usually is the first species to appear in soybean fields during flowering or even earlier. Apparently, *P. guildinii* is better adapted to feeding on flowering plants than other pentatomid species. However, it does have to feed on reproductive structures to thrive.

Chemical insecticides, such as monocrotophos and endosulfan, are the major weapons used to control *P. guildinii*. Natural enemies include several species of egg parasitoids such as *Telenomus mormideae* Lima, *Telenomus* sp., *Trissolcus basalis* (Wollaston), *T. scuticarinatus* Lima, *Ooencyrtus submetallicus* (Howard), and *Ooencyrtus* sp. Nymphs and adults of the pentatomid *Tynacantha marginata* Dallas were reported as predators of fifth instars, and adults are reported to be a substantial part of the diet of some birds in Argentina.

► Stink Bugs
► Hemiptera

References

McPherson JE, McPherson RM (2000) Stink bugs of economic importance in America North of Mexico. CRC Press, Boca Raton, FL, 253 pp

Panizzi AR (1997) Wild hosts of pentatomids: ecological significance and role in their pest status on crops. Ann Rev Entomol 2:99–122
Panizzi AR, Slansky F Jr (1985) Review of phytophagous pentatomids associated with soybean in the Americas. Fla Entomol 8:184–214
Panizzi AR, Smith JG (1977) Biology of *Piezodorus guildinii*: oviposition, development time, adult sex ratio, and longevity. Ann Entomol Soc Am 70:35–39
Schaefer CW, Panizzi AR (eds) (2000) Heteroptera of economic importance. CRC Press, Boca Raton, FL, 828 pp

Small Hive Beetle, *Aethina tumida* Murray (Nitidulidae: Coleoptera)

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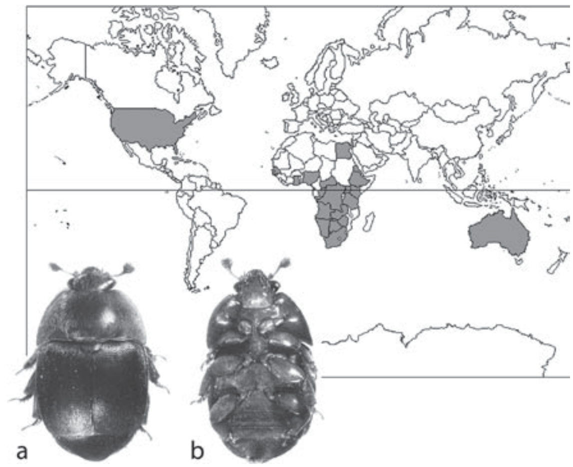
The small hive beetle, *Aethina tumida* Murray, is native to sub-Saharan Africa where it is an occasional pest in colonies of African subspecies of western honey bees (Hymenoptera: Apidae, *Apis mellifera* L.). However, the beetle has been found outside of its native range where it can cause considerable damage to colonies of European subspecies of honey bees. Because of its spread, the SHB is studied increasingly, both for its economic importance and biological significance (Fig. 61).

The small hive beetle was confirmed in the southeastern USA in 1998 in a commercial apiary in Florida, but previously unidentified specimens indicate its presence in the USA since at least 1996. The small hive beetle initially occurred in port cities such as Charleston, South Carolina, and Savannah, Georgia, as well as parts of Florida. However, it has spread throughout the entire eastern half of the US and is now reported in western states.

Small hive beetles were found in Australia in the early 2000s. They initially were found in Sydney and Brisbane; both are port cities. From there, small hive beetles have spread in Australia, being firmly established there. The small hive beetle was found in Portugal, but it was eradicated quickly after its detection.



Small Hive Beetle, *Aethina tumida* Murray (Nitidulidae: Coleoptera), Figure 61 **An adult small hive beetle, viewed dorsally (a) and ventrally (b) (photo by James Ellis, University of Florida), and its worldwide distribution (from Ellis and Munn (2005) Bee World 86:88–101).**

Description

Newly emerged small hive beetles are light brown, becoming progressively darker (almost black) as their exoskeleton hardens. These color changes may occur in the pupal cell before the adult emerges. Adult female (5.7 ± 0.02 mm) small hive beetles are generally longer than males (5.5 ± 0.01 mm) but both are nearly identical in width (about 3.2 mm). Adult females (14.2 ± 0.2 mg) are also heavier than males (12.3 ± 0.2 mg) and occur in greater proportions of the population. Naturally occurring small hive beetles can vary greatly in size, possibly depending on diet, climate, etc.

Small hive beetle eggs are 1.4 × 0.26 mm (l × w) and pearly white in appearance. Newly emerged small hive beetle larvae have relatively large heads and numerous protuberances covering their bodies. Larval growth rate varies depending on diet, but the majority mature in 10–14 days. Upon full maturation, larvae will have reached a length and width of 9.5 mm and 1.6 mm respectively. Early-stage pupae of small hive beetles are pearly white, having characteristic projections on the thorax and abdomen. Later-stage pupae darken as their exoskeleton develops and hardens.

Life Cycle

Although not fully known, small hive beetle biology is becoming better understood. Upon emerging from the ground (where they pupate), adult small hive beetles search for honey bee colonies, probably identifying the host colony by a suite of olfactory cues. Studies have shown that small hive beetles fly before or just after dusk and that odors from adult bees and various hive products (honey, pollen) are attractive to flying small hive beetles. Some studies have suggested that small hive beetles also may find host colonies by detecting honey bee alarm pheromone. Additionally, small hive beetles carry a symbiotic yeast that produces honey bee alarm pheromone when deposited on pollen reserves in the hive.

Upon locating and entering the host colony, adult small hive beetles seek out cracks and crevices where they hide from bee aggression. Remarkably, honey bees station guards around the cracks where small hive beetles hide. The "prison" guards keep the small hive beetles confined to the cracks and out of the brood combs where there is an ample supply of honey, pollen, and brood on which small hive beetles reproduce. Small hive beetles do not starve in these prisons as they are able to solicit food trophallactically from their bee captors. In this behavior, small hive beetles use their antennae to rub the bees' mandibles and induce the bees to regurgitate. Small hive beetles then feed on the regurgitated substance.

Mating behavior of small hive beetles (including whether female small hive beetles mate once or multiple times) is not understood, but adult small hive beetles do not appear to be sexually mature until about 1 week post-emergence from the soil. If allowed to reproduce, female small hive beetles will oviposit directly onto food sources such as pollen or brood combs. Alternatively, female small hive beetles may deposit irregular masses of eggs in crevices or cavities away from the bees as female ovipositors are long and flexible, being perfectly designed to lay eggs in tiny, concealed places. A female small hive beetle may lay 1,000 eggs in her lifetime, although data suggests that the number of eggs produced in one female's lifetime might be upwards of 2,000. The majority of these eggs hatch within 3 days; however, some eggs are still viable and hatch after 5 days. Humidity appears to be a crucial factor influencing hatch rates as small hive beetle eggs are prone to desiccation if exposed to circulating air and relative humidity below 50%.

Newly hatched larvae immediately begin feeding on whatever food source is available, including honey, pollen, and bee brood, yet they have demonstrated a preference for bee brood. Maturation time for larvae is generally 10–14 days although some may feed longer than a month. Once the larvae finish feeding, a "wandering" phase is initiated where larvae leave the food source and migrate out of the colony to find suitable soil in which to pupate. It is believed that the bulk of larvae do this at night in the cover of darkness.

Larvae in the wandering stage may wander great distances from the hive to find suitable soil. Despite this, most larvae pupate within 90 cm of the hive. Nearly 80% of the larvae burrow down into the soil less than 10 cm from the soil surface but generally not more than 20 cm. Once larvae cease burrowing, they construct a smooth-walled, earthen cell in which they pupate. The period of time spent in the ground pupating can vary greatly depending on factors such as soil temperature, etc. However, the majority of adults emerge after being in the soil 3–4 weeks. Upon adult emergence, the entire life cycle begins again. The turnover rate from egg to adult can be as little as 4–6 weeks; consequently, there may be as many as six generations in a 12-month period under moderate climatic conditions.

Damage

In its native range, the small hive beetle regularly occurs in honey bee colonies but it does not cause damage in strong, healthy ones. In the USA and Australia though, small hive beetle damage in European colonies follows a characteristic pattern: (i) adult invasion into colonies; (ii) population build-up of small hive beetles; (iii) reproduction of small hive beetles; (iv) significant damage to brood, pollen, and honey stores by feeding small hive beetle larvae; (v) mass exodus of larvae from the colony; (vi) pupation in the soil; and (vii) emergence as adults and subsequent re-infestation of colonies. There is fermentation of hive products (particularly honey) associated with feeding larvae. This likely occurs due to specific yeasts associated with the small hive beetle. Honey damaged by small hive beetles is rendered foul and unfit for human consumption. Colonies heavily infested with adult small hive beetles may abscond (entirely leave the nest) although the number of adults needed to elicit this behavior often must be high (>1,000 small hive beetle adults per colony).

Small hive beetle damage to living colonies is not the only loss experienced by beekeepers. Adult and larval small hive beetles can be a significant problem in unprocessed honey crops stored in the honey house. As a result, beekeepers realize the necessity of extracting honey quickly and moving the equipment out of honey houses to discourage the ensuing build-up of small hive beetle larvae. Further, stored supers of honey or supers containing pollen residues are prime targets for small hive beetle reproduction and subsequent damage.

Despite the fact that small hive beetles may cause considerable damage in bee colonies in the USA, they increasingly are considered a secondary pest of bee colonies, much like the greater (*Galleria mellonella* Linnaeus) and lesser (*Achroia grisella* Fabricius) wax moths. Colonies hosting other bee diseases/pests are more likely to suffer small hive beetle damage than are healthy colonies. It appears that small hive beetles rarely kill a colony. They usually complete the job started by another colony malady, whether disease/pathogen or management-related.

Control

Since the introduction of small hive beetles into the United States, little progress toward developing chemical control methods has been made. As such, more attention has focused on cultural, biological, and genetic controls. Cultural/mechanical controls result from a change in practice with the intention of limiting, but not eradicating, a pest. Practices such as removing honey, bits of comb, and cappings from around the honey house will minimize foodstuffs to which small hive beetles may be attracted. It is also important to extract supers of honey quickly to reduce the damage that small hive beetle adults and larvae do to standing, unprotected crops. Reducing the relative humidity to 50% in honey houses and other places where honey is stored inhibits small hive beetle eggs from hatching. In the apiary, one should eliminate, requeen, or strengthen weak colonies to reduce colony stress and to make the colony better able to deal with small hive beetles. One should avoid other conditions that might lead to colony stress such as brood diseases, mite problems, wax moth activity, failing queens, excessive swarming and over-supering.

Two effective in-hive trapping devices have been developed for small hive beetle control. The first, the Hood beetle trap, fits in a standard hive frame. It can be filled with apple cider vinegar to attract and drown adult small hive beetles. A second trap, the West beetle trap, is designed to rest on the bottom board of a colony. It is covered with a lid containing small holes through which small hive beetles can move but through which bees cannot follow. The idea is that small hive beetles run from bee aggression through the holes in the lid of the trap, and into a tray filled with vegetable oil. The small hive beetle then becomes coated with oil and presumably suffocates.

Other control measures are being developed. First, a symbiotic yeast associated with the small hive beetle has been discovered. This yeast, when mixed with pollen, attracts other small hive beetles to weakened colonies. Researchers are taking advantage of this relationship and are developing traps using the yeast mixed with pollen as bait for adult small hive beetles. Secondly, two species of soil-dwelling nematodes have demonstrated activity against pupating small hive beetles. Finally, researchers have shown that some honey bee colonies are able to detect and remove brood that has been oviposited on by small hive beetles. This behavior, called hygienic behavior, can be selected for in-breeding programs and can help reduce small hive beetle problems. Research in these areas, as well as in others, is ongoing.

References

Ellis JD (2005) Reviewing the confinement of small hive beetles (*Aethina tumida*) by western honey bees (*Apis mellifera*). Bee World 86:56–62

Ellis JD, Hepburn HR (2006) An ecological digest of the small hive beetle (*Aethina tumida*), a symbiont in honey bee colonies (*Apis mellifera*). Insectes Soc 53:8–19

Elzen PJ, Neuman P (2004) The biology of the small hive beetle (*Aethina tumida* Murray): gaps in our knowledge of an invasive species. Apidologie 35:229–247

Hood WM (2004) The small hive beetle, *Aethina tumida*: a review. Bee World 85:51–59

Small Honey Ant, *Prenolepis imparis* (Say) (Hymenoptera: Formicidae)

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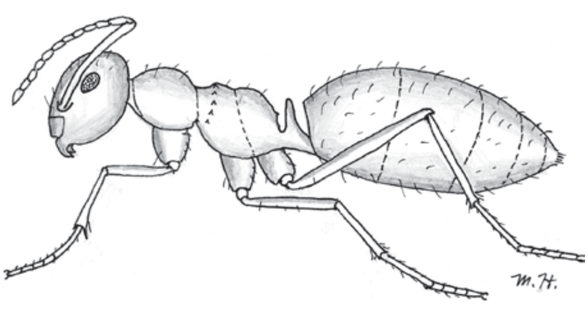
The small honey ant, *Prenolepis imparis*, is also sometimes referred to as the false or winter honey ant. The term "false honey ant" is used to distinguish it from the true honey ants, and the term "winter honey ant" describes its characteristic of remaining active even during cold weather. This ant species is reported to be widely found in areas across the continental USA.

Description

The worker ant is approximately 3 mm in length and has a light to dark brown color and the queen is approximately 7 mm in length. When the ant becomes filled with food, however, it may appear larger due to enlargement of the gaster (abdomen). Other identifying characteristics of the ant are: (i) the scape (basal segment) of the 12-segmented antennae is longer than the ant head, (ii) the thorax is hour-glass shaped, (iii) there is only one node on the petiole, (iv) the abdomen is triangular in shape and wider than the head when viewed from above, (v) there is a small tight circle of hairs on the tip of the abdomen, (vi) the ant appears rather shiny, and (vii) it has no foul odor when crushed (Fig. 62). Ants are social insects and therefore share food with other members of the colony. This species has a large abdomen relative to overall body size, which thereby accommodates carrying a larger amount of food per foraging trip. Replete ants serve as honey containers, which may comprise up to 80% of the workers prior to aestivation; however, it was observed that by end of summer



Small Honey Ant, *Prenolepis imparis* (Say) (Hymenoptera: Formicidae), Figure 62 **Small honey ant, *Prenolepis imparis* (Say).**

in Missouri, numbers had fallen to about 67%. This drop occurred during the period when workers were not foraging and larvae were being fed. During this sequence in the life cycle of the small honey ant, eggs are laid around mid-July, larvae pupate around mid-August and pupae emerge around mid-September. Length of development time from egg to adult may, however, be dependent on temperature. New male and female ants produced are kept in the nest over winter until their nuptial flights in early April. During the winter months no brood is retained in the nests.

Behavior

Small honey ant, *P. imparis*, is a cold-temperate ant species. It initiates ground surface activity (foraging) when temperatures reach just above freezing and discontinue such activity at about 20°C. The optimal humidity for ground surface activity ranges from 80 to 100%. In fact, this ant does not hibernate during the cold season of the year, as many ant species do, although, during the warmer season of the year, it may exhibit aestivation for a period of 1–2 months in areas such as Ohio and up to 7–8 months in climatic conditions of Florida. In Missouri, *P. imparis* was primarily active above-ground during the day in early March due to optimum temperatures occurring at midday, whereas, in early April the ants were primarily nocturnal due to elevated daytime temperatures. Ants, being social insects, exhibit behaviors that are designed to benefit the entire colony, whether it be gathering food, caring for immature members, or defending the colony and its food sources. Ant species vary in the intensity of their defensive behavior. Workers in the genus *Myrmecia*, for example, defend only the colony nest area. In contrast, workers of *P. imparis* have been observed defending rotting fruit as far as 1.5 m from the nest entrances. This is expressed by exhibiting aggressiveness towards other insects approaching the food source and by also emitting a highly repellent chemical from the posterior end of the abdomen. An extreme example is the case of wood ants, *Formica rufa*, which travel on pathways 200 m in length leading to trees where they forage and aggressively protect their food sources from other insects.

Colonies

It has been observed in one study in Florida that the number of ants per colony ranged from 600 to 10,300, and nesting sites were generally found in soil in open shaded areas. The typical nesting site has a small mound surrounding the single nest entrance which leads to a vertical tunnel extending to depths of 2.4–3.6 m (where $n = 8$ and mean = 2.83 m) with horizontal chambers positioned at intervals along the tunnel. Nest tunnels are thought to be only about one-third or less as deep in more northern states such as Ohio and Missouri. Likewise, the upper nest chambers may only be a few cm below the surface of the ground compared to 60 cm in Florida. It is suggested that soil type and temperature could be factors related to chamber depth and distribution. However, the small honey ant may also be found nesting in or around homes, especially during the colder season of the year. Winged males and females typically begin their mating flights during the first warm days of spring, in April or May, in more northern states. This is earlier than many other ant species, which are just completing their winter dormancy by that time. Most mating likely occurs on the surface of the ground. Following mating, the inseminated queen breaks off her wings and then attempts to establish a new colony in the soil. Twenty nests of *P. imparis* were excavated in Missouri and no queens were seen in three nests, one queen in each of 15 nests and two queens in each of two nests. Eight nests examined in northern Florida revealed that two nests had one queen each and the rest were polygynous, with up to six queens per nest (mean = 4.14). It has been suggested that in Florida, worker ants may live for 2 years or more and that a colony may continue to function for over 9 years.

Nutrition Sources

During aestivation, honey from replete workers is also used for larval development. It has been observed in Florida that brood rearing during aestivation is highly dependent upon large amounts of fat and other nutrients stored in the replete workers. The weight of corpulent (obese) workers ranged up to 8 mg (average of 5.4 mg) and the weight of foragers was 2.0–2.2 mg. Elsewhere the mean dry weight of *P. imparis* has been recorded as being 0.7 mg (where $n = 20$), with substantial within-colony variation. Emergence from aestivation seems to coincide with time of fruit maturation in Missouri. The small honey ant is in great need of nutrition at that time and readily feeds upon fruit available. In general, this species feeds upon sweet substances from certain honeydew-producing insects (aphids, scales, and treehoppers; order Hemiptera), extrafloral nectar produced by plants, and upon tender plant tissues such as flower buds. It has been reported, however, that in baiting trials, *P. imparis* demonstrated a preference for protein-fat food (tuna over sugar baits). They have been observed to feed upon certain other insects as well as dead earthworms. In addition, these ants may be found feeding upon sweetened foods and beverages in house kitchens where ant foraging traffic appears to flow along trails as a result of laying down scent markers (pheromones) as they travel.

This species may be considered a nuisance when it is active in or around homes, especially when feeding on fruits, baked goods, meats, and sugar products. They have also been known to cause some plant damage as a result of chewing into soft tissues of certain flower buds to feed upon sugar sweetened plant sap. In such cases, the use of an insecticide may be warranted.

► Ants (Hymenoptera: Formicidae)
► Ant-Plant Interactions
► Plant Extrafloral Nectaries

References

Holldobler B, Wilson R (1990) The ants. The Belknap Press of Harvard University Press, Cambridge, MA, 732 pp

Lynch JF, Balinsky EC, Vail SG (1980) Foraging patterns in three sympatric forest ant species, *Prenolepis imparis*, *Paratrechina melanderi* and *Aphaenogaster rudis* (Hymenoptera: Formicidae). Ecol Entomol 5:353–371

Talbot M (1943) Response of the ant, *Prenolepis imparis* (Say) to temperatures and humidity changes. Ecology 24:345–352

Tschinkel WR (1987) Seasonal life history and nest architecture of a winter-active ant, *Prenolepis imparis*. Insectes Soc 34(3):143–164

Wesson LG Jr, Wesson RG (1940) A collection of ants from South-central Ohio. Am Midl Nat 24:89–103

Wheeler WM (1930) The ant, *Prenolepis imparis* (Say). Ann Entomol Soc Am 23:1–26

Wilson EO (1971) The insect societies. The Belknap Press of Harvard University Press, Cambridge, MA, 548 pp

Small Rice Stink Bug, *Oebalus poecilus* (Dallas) (Hemiptera: Heteroptera: Pentatomidae)

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The small rice stink bug, *Oebalus poecilus* (Dallas), also known as *Solubea poecila* (Dallas), is perhaps the most important pest of rice in South America. Although showing preference for Gramineae such as rice, barley, oat, corn and wheat, it also is associated with soybean, cotton, and guava. There are about 42 species of host plants for this pest within the state of Rio Grande do Sul, Brazil.

Adults are rust to black dorsally, with yellowish spots; the venter usually is darker in females than males. Males are 6.9–8.3 mm long and females are 7.4–9.5 mm long. The small rice stink bug has distinctive morphs that distinguish non-diapausing and diapausing adults. The adult key characters are the pronotal shape and color of the body (Fig. 63). In the non-diapausing summer morph, the lateral angles of the pronotum are spinose and the predominant dorsal

Small Rice Stink Bug, *Oebalus poecilus* (Dallas) (Hemiptera: Heteroptera: Pentatomidae), Figure 63 **Small rice stink bug.**

coloration is dark brown, almost black; in the overwintering diapausing morph, the lateral angles are rounded and the predominant dorsal coloration is light brown.

Despite the importance of *O. poecilus* as a pest, little has been published on its biology. The egg color changed due to the embryonic development, which allowed the age of the egg to be estimated. *Oebalus poecilus* is reared successfully in the laboratory using panicles of the weed *Polygonum punctatum*.

Nymphs and adults fed on the developing grains of rice, and the nature and extent of damage depend on the stage of grain development at the time of attack. Florets fed upon during early endosperm formation (milk stage) resulted in either empty glumes or severely atrophied kernels. Feeding during later stages of endosperm development (dough and hard stages) resulted in a chalky discoloration around the feeding site. Rice with this damage, known as "pecky rice," is weakened structurally and often breaks under mechanical stress during milling. Furthermore, the pecky rice that escapes breakage is of inferior quality as a finished product because of the discoloration. Other types of damage include withering of young plants, reduction of tillers, and grain emptiness due to feeding activity.

In spite of being a major pest, no effective method to manage *O. poecilus* on rice fields has been developed. However, a pest management strategy for *O. poecilus* in southern Brazil based on planting time has been recommended. This method consists of delaying and restricting the time of rice planting. Planting the crop in the first half of December results in a synchrony between the pest and the crop because the developing grain is available in March when bugs entering the adult stage are diapausing morphs that migrate to hibernating sites instead of remaining in the crop. The result is that damage is considerably reduced.

Natural enemies of *O. poecilus* include the egg parasitoid *Telenomus mormideae* Lima, and the nymph and adult parasite *Beskia cornuta* Brauer & Bergenstan (Diptera: Tachinidae).

► Stink Bugs
► Hemiptera

References

Albuquerque GS (1993) Planting time as a tactic to manage the small rice stink bug, *Oebalus poecilus* (Hemiptera, Pentatomidae), in Rio Grande do Sul, Brazil. Crop Prot 12:627–630

van Halteren P (1972) Some aspects of the biology of the paddy bug, *Oebalus poecilus* (Dallas), in Surinam. Surinaam Landb 2:23–33

Schaefer CW, Panizzi AR (eds) (2000) Heteroptera of economic importance. CRC Press, Boca Raton, FL, 828 pp

Silva CP (1992) Aspectos biológicos básicos de *Oebalus poecilus* (Dallas, 1851) (Heteroptera: Pentatomidae) por ataque de parasitóides de ovos na cultura de arroz. Anais da Sociedade Entomológica do Brasil 21:225–231

Silva CP (1992) Mortalidade de *Oebalus poecilus* (Dallas, 1851) (Heteroptera:) Pentatomidae) por ataque de parasitóides de ovos na cultura de arroz. Anais da Sociedade Entomológica do Brasil 21:289–296

Small RNA Viruses of Invertebrates

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Baculoviruses are the best-known viruses associated with insects. They have large, rod-shaped particles that measure around 30–60 nm by 250–300 nm which contain double-stranded DNA genomes. Baculovirus particles are most often embedded in large proteinaceous occlusion bodies that usually measure between 0.5 and 2 μm and thus are visible by light microscopy. However, during the last 30–40 years a large number of non-occluded, small (25–40 nm in diameter), icosahedral viruses have been reported in a variety of insects and other invertebrates. With their small size, spherical appearance, and genomes comprised of RNA, they have frequently received the general epithet picornaviruses. This name derives from the combination of terms pico (=small) + RNA + viruses. However, to avoid confusion with the recognized taxonomic group of vertebrate viruses known as the Picornaviridae, the insect viruses are best referred to by the more general term small RNA viruses (SRVs). Wherever possible we have used the terminology and nomenclature recognized by the International Committee for Taxonomy of Viruses (ICTV) in their VIIth report.

There are three recognized families of invertebrate SRVs: Nodaviridae, Tetraviridae and Dicistroviridae (previously termed the "cricket paralysis-like viruses"). In addition, there is an emerging grouping of picorna-like viruses that show superficial similarity to the Picornaviridae. The basic characteristics of these four groups are presented below. Moreover, while a large number of SRVs still remain unclassified and show no affinities with other recognized groups of viruses, we also provide a brief description of some of the more novel virus-types to be found among this more ad hoc assemblage. In the final sections of this chapter, we also provide a brief summary of the general pathology of insect SRVs and of their potential for use as biocontrol agents and biopesticides.

Nodaviridae

This is a unique and well-studied group with virus representatives from both vertebrate and invertebrate hosts. The members of the family from the genus *Alphanodavirus* generally infect insects while those from the genus *Betanodavirus* are those isolated from fish species. The nodavirus genome is comprised of two separate single-stranded RNAs: RNA1 (approximately 3,100 nucleotides long) and RNA2 (approximately 1,400 nucleotides long). The 30 nm diameter virus particles are primarily assembled from a single protein of 40,000–45,000 molecular weight (MW) whose precursor is coded by RNA2. The protein(s) that form the structural shell (the capsid) which surrounds the viral nucleic acid generally are referred to as the capsid proteins. The type virus of the family, Nodamura virus (NV), was isolated from *Culex* mosquitoes but is able to replicate in other invertebrate hosts (e.g., *Galleria melonella* larvae and honey bees, *Apis mellifera*) as well as in suckling mice. There are also nodavirus isolates from Lepidoptera (Boolara virus (BoV) from the hepialid, *Oncopera inticoides* and gypsy moth virus from *Lymantria ninayi*), and from Coleoptera (black beetle virus (BBV) from *Heteronychus arator;* Flock House virus (FHV) and Manawatu virus (MwV) from *Costelytra zealandica*). Surprisingly, FHV has been shown to replicate and assemble infectious virus particles in some plants, although these infections only occur if the viral genome is introduced directly into the plant cells (by a process known as transfection). Some of the alphanodaviruses (e.g., FHV, BBV) generate extraordinarily large yields (milligram quantities of virus) during laboratory infections of two *Drosophila* cell lines (i.e., Schneider's Line 1 and Line 2 cells). They also are capable of establishing persistent infections in these cell lines under certain conditions and one nodavirus, New Zealand virus (NZV; also known as *Drosophila* line 1 virus, DLV) is most likely to have resulted from a chance laboratory infection of this continuously cultured cell line.

Tetraviridae

Tetraviruses have been isolated so far only from, or shown to infect, Lepidoptera, mainly saturniid, limacodid and noctuid moths. The particles of tetraviruses are relatively large (38–40 nm in diameter) and exhibit a lower density than most of the other SRVs of insects (i.e., approximately 1.30 g/ml in caesium chloride cf. 1.34–1.43 g/ml for the dicistroviruses and picorna-like viruses). The group name is derived from the unusual $T = 4$ (tetra) symmetry of their particles which contrasts to the $T = 1$ or $T = 3$ symmetry common to most other small RNA viruses. The major tetravirus capsid protein is large, around 60,000 MW, although a minor protein of 7,000–8,000 MW can also be present in some types. The tetraviruses are divided into two genera: Betatetravirus (the *Nudaurelia* β-like viruses) and Omegatetravirus (the *Nudaurelia* ω-like viruses), although the majority of isolates have yet to be assigned to either group. Members of both genera contain a major single-stranded RNA approximately 5,300–6,500 nucleotides long. However, Omegatetraviruses also contain a second, smaller strand of RNA approximately 2,500 nucleotides long that has been shown to code for the capsid protein. The betatetraviruses *Darna trima* virus (DtV) and *Setothosea asigna* virus (SaV) (*Thosea asigna* virus) have been successfully used in biological control programs directed against their primary limacodid hosts, which are pests of oil palms. Field trials with an Omegatetravirus, *Heliothis armigera* stunt virus (HaSV), have indicated that it has potential for the control of the cotton bollworm (*Helicoverpa armigera*) even though no natural epizootic of the virus has been recorded.

Picorna-Like Viruses

The vertebrate Picornaviridae include such well-known members as poliovirus, hepatitis A virus (HAV) and foot-and-mouth disease virus (FMDV), as well as the plethora of viruses whose infections result in the common cold (rhinoviruses). Although the derivation of the family name simply alludes to being small RNA viruses, the true picornaviruses all have three major capsid proteins which encase a ssRNA genome around 7,500 nucleotides long. Many picornaviruses also have a fourth, internal capsid protein. During infection, the genomic RNA is translated to produce a single, long polypeptide (greater than 200,000 MW). This is cleaved to produce the various non-structural proteins (involved in RNA replication and protein processing) observed during the replication cycle as well as the capsid proteins which eventually are assembled into mature virions which contain the RNA genome.

Although a number of the invertebrate small RNA viruses are remarkably similar to picornaviruses with respect to their particle diameters, densities and protein compositions, it is at the molecular level of the genome where important differences have recently become apparent. Thus, while these recent genomic studies have produced evidence that some insect SRVs produce a single polypeptide from the genomic RNA and have their genomes organized like the picornaviruses with their structural proteins at the 5′ end of the genome, the specific arrangement of the capsid proteins is more like the discistroviruses (see below). Three viruses have, to date, been found to have such characteristics, namely Infectious flacherie virus (IFV) of silkworms, sacbrood virus (SBV) of honeybees and *Perina nuda* picorna-like virus (PnPV) from the ficus transparent wing moth, *Perina nuda*.

Other picorna-like SRVs are either insufficiently characterized or, like the type member, Cricket paralysis virus (CrPV), have been shown to have a genome structure and replication characteristics that warrant them being placed in a separate group, the so-called Cricket paralysis-like viruses or Dicistroviridae.

Dicistroviridae (Cricket Paralysis-Like Viruses)

A number of other insect SRVs originally isolated in the 1960s and 1970s, such as CrPV, *Drosophila* C virus (DCV) and IFV, also were thought to be picornaviruses since they produced large precursor polypeptides which were then post-translationally cleaved to produce three major capsid proteins and the non-structural proteins. However, there were a number of discrepancies which suggested that these well-studied insect viruses, as well as others, represented a novel category of SRVs. The proteins observed during infection, for example, were produced in unequal amounts, i.e., some were present at significant molar excess whereas equivalent amounts would be expected from the true picornavirus strategy. Also, partial sequence analysis indicated that the 3′ end of the genome (where picornaviruses code for the non-structural proteins) appeared to be directing the synthesis of the virus capsid proteins. The sequencing and analyses of the complete genomes of DCV and several other viruses, including CrPV, has since revealed that these viruses actually translate their RNA in two separate parts in stark contrast to the true picornaviruses. The existence of two separate cistrons (or Open-Reading Frames, ORFs) is the derivation of the name, Dicistroviridae. Interestingly, these viruses also use a novel method of translating the polyprotein; the more 3′ of the two ORFs has dispensed with the initiation codon used for starting the translation, of virtually every other eukaryotic protein. Other confirmed dicistroviruses are the lepidopteran *Plautia stali* intestine virus (PSIV); several viruses isolated from hemipterans (*Triatoma* virus, TrV; *Rhopalosiphum padi* virus, RhPV; Himetobi P virus, HiPV); and the hymenopteran isolates Acute bee paralysis virus (ABPV) and Black queen cell virus (BQCV). As more viruses are sequenced, the Dicistroviridae will undoubtedly accumulate more members. Recently, a virus that infects penaid shrimp (Taura syndrome virus) has been found to have all of the characteristics of a discistrovirus, demonstrating that these viruses are not restricted to the Insecta.

Unclassified Viruses

Most of the insect SRVs isolated to date remain unclassified. These include observations made of presumably RNA-containing virus-like particles in insect extracts examined by electron microscopy or crystalline arrays noted in thin sections. There are also virus isolates which are reasonably well characterized biophysically but which still defy classification because they do not easily fit into pre-established taxonomic categories. Some have unique features, like the lemon-shaped particles of Chronic bee paralysis virus (CBPV) and *Drosophila* RS virus or the knobbed capsid structure of kelp fly virus (KFV). At present, there is insufficient data to confidently classify these viruses. Other unclassified examples include the icosahedral *Acyrthosiphum pisum* virus, which produces a single major capsid protein and several smaller capsid proteins from an array of overlapping ORFs, and Bee virus X and Bee virus Y that have only single capsid proteins of around 50,000 MW.

Pathology of SRVs

Despite the size of their single-stranded RNA genomes, which comprise only about 3–15 genes, SRVs often are capable of rapidly killing or severely debilitating their host. In other instances the SRVs appear to be benign, existing as latent or unapparent infections in their hosts who show no obvious symptoms of infection. Thus, the presence of SRVs may remain undetected for years until their hosts display obvious symptoms which in many instances seem to be associated with increased stress in the host. For example, during studies on the Australian field cricket, *Teleogryllus commodus*, in the 1960s, apparently healthy young crickets were collected and brought into the laboratory. Subsequently, in these large overcrowded laboratory colonies some crickets became paralyzed and died. The paralytic disease, which spread rapidly and devastated the colony, was found to be caused by the now well-known Cricket paralysis virus.

Similar outbreaks of other virus diseases in laboratory colonies of insects are not unheard of even in the best-maintained rearing facilities. However, the symptoms of disease often are difficult to define. They may range from reduced longevity of the host insect (*Drosophila* A virus and *Drosophila* C virus), general lethargy (*Setothosea asigna* virus), through to the more obvious symptoms of paralytic disease (CrPV and Aphid lethal paralysis virus) and inability to molt or developmental stunting (*Helicoverpa armigera* stunt virus). Many insect SRVs are readily transmitted from individual to individual but many also are transmitted through the germ-line to the progeny of infected individuals. In the latter case, surface sterilization of eggs using low concentrations of hypochlorite often can eliminate the offending SRV but re-infection from laboratory sources can occur readily.

Potential for Insect SRVs as Biocontrol Agents and Biopesticides

SRVs replicate in the cytoplasm of infected cells and may produce on the order of 250,000–1 million particles within each infected cell during their 12–24 h replication cycle. Thus, their capacity to increase in number and spread to uninfected individuals is enormous. This, coupled with the often severe pathological effects of infection, makes them candidates for use as biological control agents or biopesticides of insect pests. There are several examples of their successful use in the field. In the 1960s in Uganda, the lasciocampid moth *Gonometa podocarpi* was a serious pest of pine plantations. Some larval cadavers were found to contain a small RNA virus and a crude extract of these, applied in areas where no diseased larvae had been detected, resulted in effective control of the pest. Other examples are in the Indonesian states of Sabah and Sarawak in the early 1970s with the control of *Darna trima*, a pest of oil palms and in the 1990s with *Epicerura perigrisea*, a lepidopteran defoliator of two economically important tree species in the Ivory Coast.

There has been some reluctance to seriously consider the insect SRVs as biocontrol agents/biopesticides primarily because of similarities to the vertebrate picornaviruses. Safety testing, as with any biological agent, would be required. Host range considerations also would be important since some of the SRVs can affect a wide range of insect hosts. CrPV, for example, has been shown to multiply in a large number of species from five different insect orders (Lepidoptera, Orthoptera, Diptera, Hymenoptera and Heteroptera) and arguably has the widest host range of all known viruses. Some SRVs (e.g., the tetraviruses) have a highly restricted host range and may infect only a few lepidopteran species. Others, like kelp fly virus (KFV), may infect only a few species but from different orders (Diptera and Lepidoptera). The SRVs are particularly attractive control agents for pests where no baculoviruses are available.

The host range of any SRV contemplated as a biological control agent would require specific tests with reference to the ecological considerations of the areas in which their use was contemplated. The use of selective application strategies or baits may be advantageous. Economic concerns may limit commercial production of SRVs although large quantities, in some cases, can be produced directly in insect hosts or in available insect cell lines. However, local cottage industry production and application as in the cases in Uganda, Sabah and Sarawak, and the Ivory Coast may be the most feasible alternative in many situations.

References

Granoff A, Webster R (eds) (1999) The encyclopaedia of virology, 2nd edn. Academic Press, New York, NY, 2000 pp
Longworth JF (1978) Small isometric viruses of invertebrates. Adv Virus Res 23:103–157
Miller LK, Ball LA (eds) (1998) The insect viruses. Plenum Press, New York, NY, 413 pp

Small Winter Stoneflies

Members of the stonefly family Capniidae (order Plecoptera).

► Stoneflies

Small-Headed Flies

Members of the family Acroceridae (order Diptera).

► Flies

Smicripidae

A family of beetles (order Coleoptera). They commonly are known as palmetto beetles.

► Beetles

Sminthuridae

A family of springtails in the order Collembola. They commonly are known as globular springtails.

► Springtails

Smirnoff, Vladimir A.

Vladimir Smirnoff was born on 1 September, 1917 in St. Petersburg, Russia, and he completed a degree at the Forest Institute of the Soviet Union and then attained his Ph.D. from the Forestry Academy. Early in his career he became interested in forest pests. He left the USSR near the end of World War II and became a research entomologist with INRA in Morocco, studying scale insects of palms. He completed another Ph.D. at the Sorbonne in France.

In 1957, Smirnoff moved to Quebec, Canada, and became an insect pathologist with the Canadian Forest Service. This led to important work on several insect pathogens of forest insects, and he became a leading voice for biological control in Canada. He is best known for his effective and pioneering work on the use of the bacterium *Bacillus thuringiensis* for control of spruce budworm outbreaks. This led to general use of *B. thuringiensis* for control of lepidopterous pests in forests and agriculture.

Smirnoff earned many recognitions, including the Parizeau Award of the French Canadian Association for the Advancement of Science, a medal from the Chemical Institute of Canada, and an award of merit from the Quebec Order of Engineers. He was a prolific publisher, authoring more than 300 publications. He retired in 1984 and died on 1 November, 2000.

Reference

Valéro José (2001) Vladimir A. Smirnoff, 1917–2000. Bull Entomol Soc Can 33:36–37

Smith, John Bernhardt

John B. Smith was born at New York City, New York, USA, on November 21, 1858. Though admitted to the bar in 1879, after practicing for a few years he abandoned the legal profession to pursue a career in entomology. He had many interests and proficiencies, and became known as both an economic entomologist and a taxonomist. The members of the Brooklyn Entomological Society were likely responsible for switching Smith from a legal to an entomological career. Initially he worked for the United States Department of Agriculture, but in 1886 he became assistant curator in entomology at the U.S. National Museum. There he published some excellent works including "Monograph of the Sphingidae of America North of Mexico," "A preliminary catalogue of the Arctiidae of temperate North America," "A revision of the lepidopterous family Saturniidae," and "Contributions toward a monograph of the family Noctuidae." In addition to this work on Lepidoptera he also studied Coleoptera while at the Museum, and in 1889 moved to Rutgers University. In 1894 he became state entomologist for New Jersey. Though taxonomy was Smith's first interest, he applied his considerable energy and enthusiasm to solving the state's pest problems, and so became involved in insecticide studies aimed at vegetable, fruit, shade tree, livestock and medical pests. A particular success was demonstration of the effectiveness of fish-oil soap for suppression of San Jose scale. However, he is best known for the development of mosquito management techniques for the New Jersey salt marshes, which emphasized ditching and draining. His vision of ridding New Jersey of salt marsh breeding mosquitoes was met with ridicule by the state legislature, but Smith was both intelligent and persistent, so he persevered and eventually the legislature appropriated funds to support this project. One of the important concepts that he promoted was that mosquitoes did not honor municipal boundaries, and that mosquito control had to be handled on a large geographic scale. Smith's approach was quite effective at reducing salt marsh mosquitoes, and eventually became adopted all along the Atlantic coast of the United States. Smith authored more than 600 titles, including several important books, including "Mosquitoes occurring within New Jersey, their habits, life history, etc.," "Catalogue of the Lepidopterous superfamily Noctuidae found in boreal America," "Explanation of terms used in entomology," and "Economic Entomology." Smith belonged to many societies, often serving in a leadership role, and was a fellow of the American Association for the Advancement of Sciences, and the New York Academy of Sciences. He died March 12, 1912.

References

Crans WJ (2002) John B. Smith, Pioneer for organized mosquito control in New Jersey. Wing Beats 13(2):6–7, 13

Grosbeck JA (1912) Professor John Bernhardt Smith, Sc.D. Entomol News 23:193–196

Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Smith, Harry Scott

Harry Smith was born at Aurora, Nebraska, on November 29, 1883. He obtained his A.B. (1907) and M.S. (1908) degrees from the University of Nebraska. From 1909 to 1913 he worked for the United States Bureau of Entomology, studying natural enemies of important pests. In 1913 Smith was appointed superintendent of the California State Insectary in Sacramento, and in 1923 was transferred to the University of California at Riverside where he was put in charge of the Department of Biological Control. He remained in this capacity until his retirement in 1951, and did much to foster implementation of biological control in California and the western United States. Smith was largely responsible for the large-scale use of the coccinellid *Cryptolaemus moutrouzieri* for citrus mealybug suppression, and the wasp *Macrocentrus ancylivorus* for Oriental fruit moth suppression. He also pioneered the use of biological suppression of Klamath weed with insect herbivores. Smith was elected president of the American Association of Economic Entomologists, and received an honorary doctorate from the University of Nebraska. He died at Riverside on November 28, 1957.

Reference

Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Smith, Ray F.

Ray Smith was born at Los Angeles, California, USA, on January 20, 1919. He received all his degrees at the University of California-Berkeley. He joined the faculty there in 1946, and became Department Chairman in 1959. Smith authored over 300 publications, and championed the ecological approach to pest management, and the minimization of pesticides in agricultural ecosystems through integration of pesticides with other approaches to pest suppression. A paper he co-authored on integrated control was cited as one of the most important publications on crop protection, and Smith is considered by some to be the "father of pest management." Among his many honors and awards are the C.W. Woodworth Award, Fellow and President of the Entomological Society of America, and member of the National Academy of Sciences. He also was co-recipient of the 1977 World Peace Prize. He died August 23, 1999, in Lafayette, California.

Reference

Scalise K (1999) UC Berkeley pest control scientist Ray F. Smith has died at age 80. University of California, Berkeley, news release, 9/30/99. Available at http://www.berkeley.edu/news/media/releases/99legacy/9–3–99.html. Accessed Aug 2002

Smoky Moths

Some members of the family Zygaenidae (order Lepidoptera).

► Burnet Moths
► Butterflies and Moths

Smooth Springtails

A family of springtails (Isotomidae) in the order Collembola.

► Springtails

Snakeflies (Raphidioptera)

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The Raphidioptera, or snakeflies, are virtually restricted to the Holarctic region. They are easily identified by their general appearance, have an elongate head and prothorax, with the legs arising posteriorly (Fig. 64). The females have a long ovipositor. There are two families which have similar biologies. The larvae usually live in the crevices in the bark of trees or shrubs, or in the superficial stratum of the soil around the roots of shrubs. The pupae are strange in that they can move about in their environment. Most of the taxonomy is based on the male and female terminalia.

The family Inocelliidae is a small family of about 20 species in about five genera. They differ from the Raphidiidae in lacking ocelli. Two genera occur in the New World, *Negha* Navás (also in Spain) and the endemic *Indianoinocellia* Aspöck & Aspöck.

The family Raphidiidae consists of about 168 species in 26 genera. The majority of genera and species are found in the Palaearctic Region. There are only two genera found in North America, *Alena* Navás, which is the southernmost occurring genus in the world with two species living in the pine forests of Oaxaca,

Snakeflies (Raphidioptera), Figure 64 **A snakefly, *Agulla bicolor* (Albarda) (Raphidioptera: Raphidiidae) (photo L. Buss).**

Mexico, and *Agulla* Navás which is restricted to the western half of North America. Larvae of *Alena* were found under pine bark.

Reference

Aspöck H, Aspöck U, Rausch H (1991) Die Raphidiopteren der Erde. Eine monographische Darstellung der Systematik, Taxonomie, Biologie, ökologie und Chorologie der rezenten Raphidiopteren der Erde, mit einer zusammenfassenden übersicht der fossilen Raphidiopteren (Insecta:Neuropteroidea), 2 volumes. Goecke & Evrs, Krefeld. 730 and 550 pp

Snipe Flies

Members of the family Rhagionidae (order Diptera).

► Flies

Snodgrass, Robert Evans

Robert Snodgrass was born at St. Louis, Missouri, on July 5, 1875. His family relocated to Kansas and then California, and Robert entered Stanford University in 1895. He majored in zoology, and due to his interest in birds he was encouraged by V.L. Kellogg, the entomology instructor, to study bird lice. This culminated in two publications on louse morphology. He accepted a teaching position at Washington State University when he graduated in 1901, but his practical jokes were not fully appreciated and he returned to Stanford. There he caused problems by stripping the mulberry trees to feed his silkworms, so he moved on to San Francisco and eventually Washington, DC, where he commenced work for the Bureau of Entomology. Not satisfied with that employment, Snodgrass moved to New York to study art. He work in entomology off and on for brief periods, then settled in with the Bureau of Entomology in 1917 and taught entomology at the University of Maryland from 1924 to 1947. Snodgrass authored over 80 publications, but is best known for his expertise in morphology, exemplified by his books: "Anatomy and physiology of the honeybee" (1925), "The principles of insect morphology" (1935), and "Textbook of arthropod anatomy" (1952). After nearly 70 years, his "principles" book remains the definitive work on the subject. He died in Washington, DC, on September 4, 1962.

References

Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Schmidt JB (1963) Robert Evans Snodgrass (1875–1962). Entomol News 74:141–142

Snout Beetles

Members of the family Curculionidae (order Coleoptera).

► Beetles

► Weevils, Billbugs, Bark Beetles and Others

Snout Butterflies (Lepidoptera: Libytheidae)

JOHN B. HEPPNER

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Snout butterflies, family Libytheidae (also called beaks), are a small family of only 12 species but with at least one species in each faunal region. Alternate classifications, either as a separate family, or as a subfamily within Nymphalidae, continue to plague specialist views on the group, but the family basically represents the lineage to Nymphalidae and are very unique if included within the latter family. The family is in the superfamily Papilionoidea (series Papilioniformes), in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults medium size (25–55 mm wingspan), with very long porrect labial palpi; forelegs somewhat reduced and not used for walking. Wings triangular, typically with a falcate forewing apex, often somewhat truncated; hindwing relatively rounded with emarginate

Snout Butterflies (Lepidoptera: Libytheidae), Figure 65 Example of snout butterflies (Libytheidae), *Libytheana bachmanii* (Kirtland) from Pennsylvania, USA.

margin. Maculation mostly shades of brown with orange or red suffusion and some light and dark spotting. Adults are diurnal. Larvae are leaf feeders. Host plants are in Ulmaceae (Fig. 65).

References

Heppner JB (2003) Libytheidae. In Lepidopterorum Catalogus, (n.s.). Fasc. 99. Association for Tropical Lepidoptera, Gainesville, 12 pp

Hering EM (1921) Die geographische Verbreitung der Libytheiden. Archiv der Naturgeschichte (Berlin), 87A(4):248–296, 2 pl

Pagenstecher A (1901) Libytheidae. In Das Tierreich 14:1–18

Seitz A (ed) (1908–1919) Unterfamilie: Libytheini. In Die Gross-Schmetterlinge der Erde, 1:251–252, pl. 71 (1908); 5:622–623, pl. 120D (1916); 9:767–771, pl. 139 (1914); 13:293–294, pl. 61 (1919). A. Kernen, Stuttgart

Shields AO (1979) Zoogeography of the Libytheidae (snouts or breaks [sic]). Tokurana 9:1–58

Snout Moths (Lepidoptera: Pyralidae)

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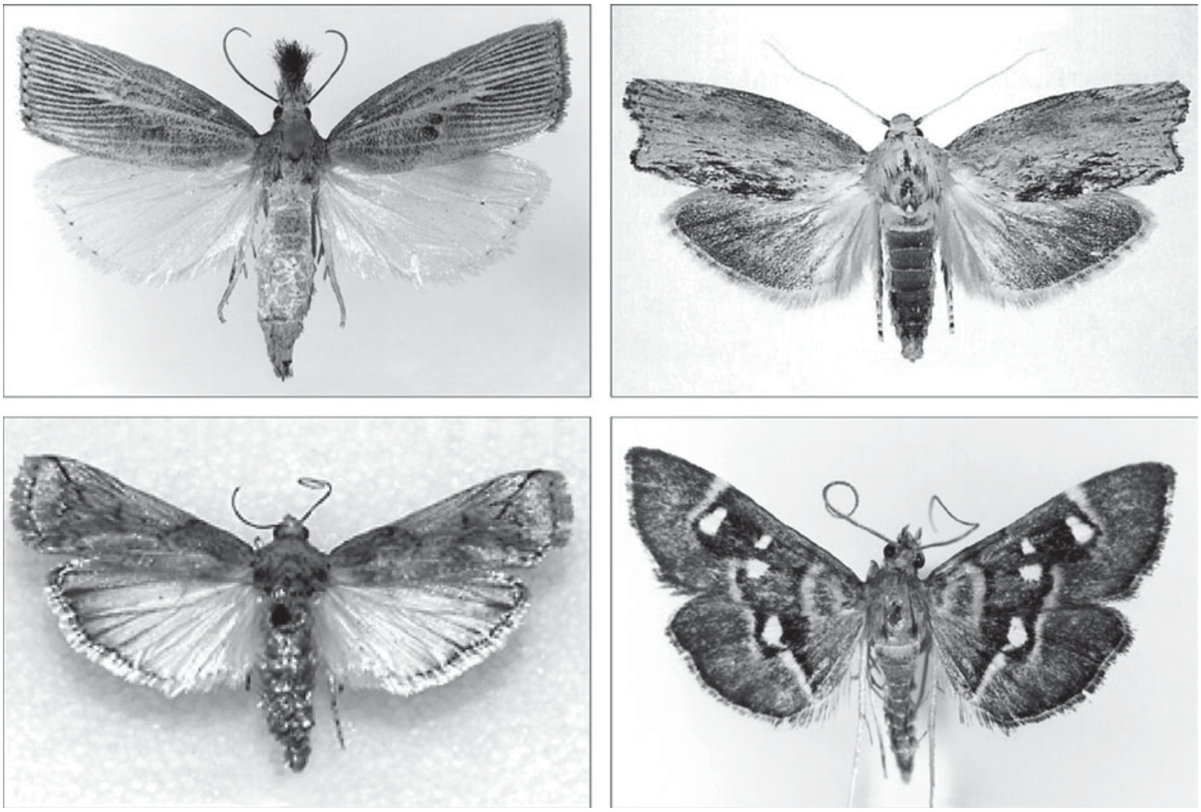
Snout moths, family Pyralidae, comprise the third largest family of Lepidoptera, with about 16,500 described species, but a probable fauna of at least 25,000 species worldwide. There are 19 subfamilies in the classification, divided into two groups: group Crambinina, with 14 subfamilies (Crambinae, Schoenobiinae, Cybalomiinae, Linostinae, Scopariinae, Musotiminae, Midilinae, Nymphulinae, Odontiinae, Noordinae, Wurthiinae, Evergestinae, Glaphyriinae, and Pyraustinae), and group Pyralinina, with five subfamilies (Pyralinae, Chrysauginae, Galleriinae, Epipaschiinae, and Phycitinae). The group names are sometimes elevated to separate families, as was already done over 100 years ago, but they can equally be maintained within the single family Pyralidae as has long been the practice. By far the largest subfamily is the Pyraustinae, with about 7,500 species worldwide. The family is in the superfamily Pyraloidea in the section Tineina, subsection Tineina, of the division Ditrysia. Adults small to large (6–95 mm wingspan), with head mostly rather smooth-scaled; haustellum scaled; labial palpi usually porrect and prominent; maxillary palpi 4-segmented (rarely 2- to 3-segmented). Wing shape (Fig. 66) usually has rather elongated and pointed forewings. Maculation extremely varied, often subdued and with various markings, but also many very colorful species; hindwings usually unicolorous and pale. Adults mostly nocturnal, but some are crepuscular and a few are diurnal. Larvae are mostly leafrollers or leaf webbers, but many are borers, root feeders, detritus feeders (including stored products pests), and a few are leafminers, plus rare myrmecophilous species, and even some aquatic groups making cases (Nymphulinae). Host plants are in a large number of plant families. A large number of economic species are in this family, including pests on virtually all crops and forest trees. Most Crambinae and Schoenobiinae larvae feed on grasses, including crops such as rice and other grains. Pyralinae and Phycitinae include a number of stored products pests, now mostly worldwide in distribution due to their association with dry stored foods. Galleriinae have beehive pests.



Snout Moths (Lepidoptera: Pyralidae), Figure 66 **Examples of snout moths (Pyralidae): *top left* (subfamily Crambinae), *Diatraea crambidoides* (Groe) from Florida, USA; *top right* (subfamily Galleriinae), *Galleria mellonella* (Linnaeus) from Italy; *bottom left* (subfamily Phycitinae), *Cactoblastis cactorum* (Berg) from Florida, USA; *bottom right* (subfamily Pyraustinae), *Diathrausta harlequinalis* Dyar from Florida, USA.**

References

Balinsky BI (1994) A study of African Phycitinae in the Transvaal Museum. Johannesburg, 208 pp

Bleszynski S (1965) Crambinae. In: Amsel HG, Reisser H, Gregor F (eds) Microlepidoptera Palaearctica, vol 1. G. Fromme, Vienna, 533 pp, 133 pl. [in German]

Goater B (1986) British pyralid moths: a guide to their identification. Harley Books, Colchester, 175 pp, 8 pl

Heinrich C (1956) American moths of the subfamily Phycitinae. Bull U S Natl Mus 207:1–581

Munroe EG (1972–1976) Fasc.13.1, Pyraloidea (in part). In: Dominick RB et al. (eds) The moths of America north of Mexico, 13.1:1–304, 9 pl. (1972–1973); 13.2:1–150, 8 pl. (1976). E. W. Classey and R. B. D. Publishing, London

Neunzig HH (1986–1997) Pyraloidea, Pyralidae (part). Phycitinae (part). In: Dominick RB et al. (eds) The moths of America north of Mexico, 15.2:1–113, 6 pl. (1986); 15.3:1–165, 5 pl. (1990); 15.4:1–157, 4 pl. (1997). Wedge Entomological Research Foundation, Washington

Roesler RU (1973–1993) Phycitinae [part]. In Microlepidoptera Palaearctica, 4(1):1–752, 4(2):1–137, 170 pl. (1973); 8:305, 82 pl. (1993)

Slamka F (1997) Die Zünslerartigen (Pyraloidea) Mitteleuropas: Bestimmen & Verbreitung & Flugstandort & Lebensweise der Raupen, 2nd edn. Bratislava, 112 pp, 13 pl

Zimmerman EC (1958) Lepidoptera, Pyraloidea: insects of Hawaii, vol 8. University of Hawaii Press, Honolulu, pp 1–456

Snow Pool Mosquitoes

These are *Aedes* mosquitoes that breed early in the spring in pools of water formed from melting snow. In the northernmost northern hemisphere they breed in tremendous numbers, causing great suffering to animals such as caribou that have little option but to try to get away from these blood sucking insects.

► Mosquitoes

Snow, Francis Huntington

Francis Snow was born at Fitchburg, Massachusetts, on June 29, 1840. He was an industrious young man from the start, and in the course of his life developed an astounding number of interests and competencies, among them ornithology, botany, geology, paleontology, mineralogy, and entomology. Professionally, he was at various times a minister, teacher, and chancellor of the University of Kansas. He grew up in the exciting days just before the American Civil War, and the antislavery views of his father strongly influenced young Francis Snow. He excelled at Williams College, from which he graduated in 1862, and was most interested in natural history. He taught high school briefly, then entered Andover Theological Seminary. An avowed pacifist, he assisted chaplains and aided the wounded during the war. In 1866 Snow moved to Kansas to accept a professorship in mathematics and natural science. Snow quickly gained a reputation for being a knowledgeable, sincere, and patient teacher, greatly admired by the students at the University of Kansas. Snow was quite impressed with the grasshoppers in Kansas; at times they were so numerous that the train could not move because the crushed bodies of the grasshoppers prevented traction of the wheels on the tracks. A swing of an insect net would collect up to 190 grasshoppers. However, Snow was interested in everything, and he and his students collected insects, birds, plants, minerals and other elements of natural history earnestly, an activity that would eventually result in a fine museum. Williams College bestowed on Snow an honorary Ph.D. in 1881. In 1882 he was named State entomologist, and in 1885 the legislature named the Snow Hall of Natural History in his honor. In 1890 he accepted the position as chancellor. Though Snow was a collector, he was not a taxonomist. He devoted much of his energies to economic entomology, a fact that encouraged the practical farmers of Kansas to support him as chancellor. As chancellor he strengthened the faculty of both science and humanities. In 1889 Snow's son died an accidental death, and in the wake of this unfortunate event Snow suffered nervous disorders. He never completely recovered, and he died on September 20, 1907, while visiting Wisconsin (Fig. 67).

Snow, Francis Huntington, Figure 67
Francis Snow.

Reference

Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Snow Scorpionflies

Members of the family Boreidae (order Mecoptera).

► Scorpionflies

Soaps as Insecticides

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Soaps were used as insecticides in Europe as long ago as 1787, and there are several thousand references in the literature on the use of soaps as insecticides. Prior to 1900, fish or whale oil soaps were the most commonly used insecticidal soaps. Soaps have changed a lot since then, yet they still prove to be an effective control of certain insect pests. Currently, numerous soap salts are registered as insecticides with the US Environmental Protection Agency (EPA). There are three documented active ingredients of soluble soap salts: sodium, ammonium and potassium. It is principally potassium salts that are used as insecticides, acaricides, herbicides, and algaecides.

Because of their chemical structure, soap salts precipitate out of hard water, resulting in an insoluble residue known as soap scum. To combat this, synthetic soap substitutes, or detergents, are available as cleaning products. Detergents share the cleansing and emulsifying properties of soap, and they are not separately listed as pesticides by the EPA.

Toxicity of Soaps

Soaps are salts of fatty acids. Fatty acids are long hydrocarbon chains that are naturally derived from plant oils and animal tallow. Plants and animals have differing amounts and combinations of fatty acids. For example, caprylic, capric, lauric and myristic acids are all constituents of coconut oil. Some plant oils have a large proportion of one fatty acid. Peanut oil is 51% oleic acid, coconut oil is 48% lauric acid, while palm oil is 47% palmitic acid. Corn, sunflower and safflower oil are made mainly of linoleic acid. Animal fat such as lard contains 44% oleic acid, while beef tallow is 44% linoleic acid. Tallow also contains 29% palmitic and 19% stearic acid. These insoluble fatty oils are distilled or pressed from their source and are exposed to a metal radical or organic base to produce soap.

Not all commercially available insecticidal soaps are pure fatty acid salts; some contain other active ingredients such as pyrethrum or neem. These combination insecticidal soaps must be registered for each active ingredient. The majority of the registered fatty acid salts include C_8–C_{18} potassium laurate, potassium myristate, potassium oleate, and potassium ricinoleate. These salts may be used singly or as mixtures because the EPA considers all potassium fatty acid salts to be the same active ingredient. Potassium fatty acid salts are generally recognized as safe by the Food and Drug Administration (FDA), and the EPA has exempted them from tolerance levels for all raw agricultural commodities. These soft soaps, such as oleic acid, have an oral LD_{50} of 74,000 mg/kg which places them in the lowest toxicity category, Category IV. These potassium fatty acid salts also have low to very low dermal toxicity, and may cause mild irritation if applied directly to the eyes. These salts have a half-life of less than a day and are readily broken down by soil microbes. While they may cause vomiting if ingested, these fatty acids pose no known health risks and are not toxic to birds.

Chemical Structure of Fatty Acids

Fatty acids are carboxylic acids. They are made of long unbranched hydrocarbon chains ending with a carboxyl group. Most naturally occurring fatty acids contain an even number of carbons in their chain, with C_{16} and C_{18} being the most common. These chains are building blocks for more complex fatty acids that are used as energy stores in many organisms. Fatty acids may be saturated or unsaturated, with unsaturated fatty acids being the most abundant in living organisms.

Shorter fatty acid chains are water soluble but become less so as the chain lengthens. The longer chains are viscous and form a gel in water. To increase solubility of fatty acids, a cation in the form of a mineral salt, potassium, sodium, or ammonium, must be added (e.g., potassium caprylate CH_3–CH_2–CH_2–CH_2–CH_2–CH_2–CH_2–COO–K^+). The addition of the salt causes hydrolysis of the carboxyl end of the fatty acid, resulting in a bond with the salt. This formation of the fatty acid chain and mineral salt is commonly called a fatty acid salt or soap salt.

Chemical Structure of Potassium Fatty Acid Salts

The fatty acids that are most commonly used in soap production are saturated, straight chain, monocarboxylic groups with even numbered carbon members. After the fatty acid is saponified with potassium hydroxide, a potassium fatty acid salt is precipitated. In some studies, the toxicity of the saturated fatty acids increases as the chain length increases peaking at C_{10} and then decreases until another peak at both the saturated and unsaturated C_{18} chains (Table 14).

The carboxyl end of the potassium soap salt is hydrophilic and carries a negative charge. The soap has a pH of 10 and is generally used as a cleaner. When in water, the negatively charged hydrophilic ends of the soap salts repel each other forming a spherical structure called a micelle. Non-polar soil or oil particles become suspended in the micelle and are held in solution. This action is known as surface active, or surfactant. Although the mode of action is unclear when used as an insecticide, fatty acids and their salts have been shown to have insecticidal properties.

Insecticidal Uses of Potassium Fatty Acid Salts

As noted previously, there is documented use of soaps as insecticides from as early as 1787. From the 1880s through the early 1900s, cottonseed oil soaps and fish oil soaps were used to control scale insects. In 1925, research documented that between 90 and 99% of *Anuraphis sanburni* Gill, black chrysanthemum aphid, were killed with caproic, capric, and lauric fatty acid sprays. Myristic acid, however, demonstrated significantly less toxicity. It was noted that soap salts, potassium, sodium, and ammonium, required higher concentrations to meet the same mortality as the fatty acids plus additives. It was later shown that fatty acid salts could produce mortality rates as high or higher than the fatty acids alone. Researchers noted that aphid exposure to the soap salts resulted in paralysis, with the dead insects remaining attached to the plant by their inserted mouthparts. After comparing fatty acids to fatty acid salts, the authors

Soaps as Insecticides, Table 14 **Common potassium salts**

Technical name	Structural name	Chemical formula	Molecular weight
K^+ caprylate	Octanoic acid	$C_8H_{15}KO_2$	182
K^+capryate	Decanoic acid	$C_{10}H_{19}KO_2$	210
K^+ laurate	Dodecanoic acid	$C_{12}H_{23}KO_2$	238
K^+ myristate	Tetradecanoic acid	$C_{14}H_{27}KO_2$	266
K^+ palmitate	Hexadecanoic acid	$C_{16}H_{31}KO_2$	294
K^+ stearate	Octadecanoic acid	$C_{18}H_{35}KO_2$	322
K^+ oleate	9-Octadecanoic acid	$C_{18}H_{33}KO_2$	320
K^+ ricinoleate	Ricinoleic acid	$C_{18}H_{33}KO_3$	336

All examples are saturated except for K^+ oleate (unsaturated) and K^+ ricinoleate (unsaturated alcohol) surmised that the free fatty acids were the toxic agents and were absorbed through the insect membranes and tracheae. Other studies on sodium and potassium soap salts from an assortment of animal and plant sources produced various levels of mortality to the Japanese beetle, *Popillia japonica* Newman. The highest mortalities were found from palm oil, beef tallow, and coconut oil (65–85% mortality).

In 1930, the efficacy of resin fish oil soap (6%) and a commercial soap, Crystal Cocoa (2%), on the harlequin bugs, *Murgantia histrionica* (Hahn), Colorado potato beetle, *Leptinotarsa decemlineata* (Say), and an aphid species was tested by dipping or spraying the insects. The investigator theorized that the soap solution covered the spiracles with a film that blocked the air supply to the insects. In order to test this hypothesis, *Murgantia histrionica* (Hahn) were submerged in water for 25 min. All insects fully recovered and had no ill effects from the submersion treatment. In comparison, after a five second soap exposure, 92% of the insects were killed. To further investigate the hypothesis, India ink, as a dye marker, was added to the soap solution to visualize the penetration of the soap solution into the insect. Insects that died after soap exposure had ink that penetrated deep into the thoracic spiracles. Thus, the investigator concluded that soap did not cause mortality by blockage.

One of the most thorough studies of fatty acids and their soaps was conducted in 1935 in New York. Instead of evaluating commercial soaps, this study evaluated fatty acids and their potassium salts against the rose aphid, *Macrosiphum rosae* L., and the bean aphid, *Aphis rumicus* L. Because fatty acids have low solubility in water, sulphonated cod oil was added to the solution as an emulsifier. Aphids exposed to cod oil (0.5%) alone resulted in 9% mortality. Aphids exposed to capric acid (0.17%) and cod oil (0.5%) or lauric acid (0.17%) and cod oil (0.5%) resulted in the highest mortality at 45% and 42% respectively; however, there was some phytotoxicity. The fatty acids that were the most toxic to the insects, lauric and capric acids, also caused plant injury to tomato, *Lycopersicon esculentum* Mill.; tobacco, *Nicotiana tabacum* L.; potato, *Solanum tuberosum* L.; bean, *Phaseolus vulgaris* L.; cabbage, *Brassica oleracea* L.; and nasturtium, *Tropaeolum minus* L. Aphids exposed to 0.5% potassium oleate and 0.5% potassium laurate resulted in 89 and 67% mortality, respectively. The authors also compared potassium oleate with sodium oleate at concentrations from 0.125 to 1%. Mortality of 98% was reached with concentrations ≥0.5%. The order of toxicity of the potassium soaps at 0.5%: oleate > laurate > caprate > caprylate > myristate > palmitiae. There was no significant mortality of aphids exposed to potassium caproate and potassium stearate when compared to controls.

Other research used various solvents, including kerosenes, mineral oils, hexane, pentane, and others, to trace penetration of substances into the nervous system of mosquito larvae. Detergents including Tergitol #7, and a fatty acid, oleic acid, were introduced into the respiratory siphon. None of the detergents migrated to the nervous tissue of the insect. The oleic acid had good diffusion into the tracheae but had less, or erratic, penetration into the nervous tissue.

The creation of the Environmental Protection Agency in 1970 prompted new research on soaps as insecticides. After an application of a 0.1% coconut oil soap spray, *Aphis gossypii* Glover was reduced by 79% and *A. spiraecola* Pagenstecher by 72% on roadside plantings in California. One study found that 1% solutions of C_{10} capric and $C_{18:1}$ oleic acid were most effective on balsam woolly aphid, *Adelges piceae* (Ratzburg). To increase solubility of the fatty acids, 0.1% Tween, a non-ionic surfactant, was added to the solutions. In this case, the potassium soaps performed better than the fatty acids alone.

Interestingly, some research demonstrated that immersions of yellow mealworm (*Tenebrio molitor* L.) pupae in 5% solutions of oleic acid, linoleic acid, potassium oleate, and potassium linoleate caused early death. The growth inhibition resulting from the treatment was described as "juvenile hormone-like." In 1979, Ivory® dishwashing liquid (Proctor and Gamble, Cincinnati, OH), Acco Highway Plant Spray® soap (38.5% coconut oil soap) (Acme Chemical Co., Blue Bell, PA), Shaklee's Basic® laundry bar soap (Shaklee, Pleasantville, CA) and Tide® detergent (Proctor and Gamble, Cincinnati, OH) were tested on the thrips *Heliothrips haemorrhoidalis* (Bouche); mites, *Panonychus citri* (McGregor); psyllids, *Psylla uncatoides* (Ferris and Klyver); and aphids, *Myzus persicae* (Sulzer), *Aphis citricola* (van der Goot), and *A. fabae* in the home landscape. Ivory® dishwashing liquid at 1–2% provided the most consistent results. It was noted that soaps do not provide any residual activity and must be applied often.

The majority of the early studies involving the use of fatty acids and their salts as insecticides used them against soft-bodied insects. However, a few studies tested soaps on hard-bodied insects such as harlequin bugs, Colorado potato beetles and Japanese beetles. More recently, when soaps were used as a contact insecticide by splashing, a 0.5% solution of the Chandrika® or Surf® soaps achieved 100% mortality of crickets, and a 2% solution achieved 100% mortality in cockroaches. The authors theorized that the soaps cause spiracle blockage, and they noted that a soap-water spray may prove a safe and economical solution to insect pests. For all cockroach stages, exposure to concentrations of 3% soap solution resulted in 100% mortality within 72 h. The researcher suggested that the mode of action was asphyxiation due to spiracle or tracheae blockage. In another study, American, *Periplaneta americana*, and German, *Blattella germanica*, cockroaches were exposed by 30 s immersion to even-numbered fatty acid salts, C_8–C_{18}. A 2% solution of potassium oleate (C_{18}) was the most toxic to both German (LC_{50} = 0.36%) and American (LC_{50} = 0.17%) cockroaches.

Potential Mode of Action of Potassium Fatty Acid Salts

The traditional explanations for the mode of action of soaps are cuticle disruption and spiracle blockage, but there is a third possibility. In contrast to this uncertainty, everyone agrees that fatty acids and their salts are contact-only insecticides and that they provide no residual activity.

Cuticle Disruption

It is sometimes stated that the mode of action of insecticidal soaps is dehydration after contact. The fatty acid purportedly penetrates the cuticle and disrupts the cellular integrity, causing leakage and collapse. The Olympic® Horticultural Products Insecticidal Soap 49.52 CF label states that the mode of action is a disruption of the outer waxy layer that causes damage to the cuticle.

Spiracle Blockage and Asphyxiation

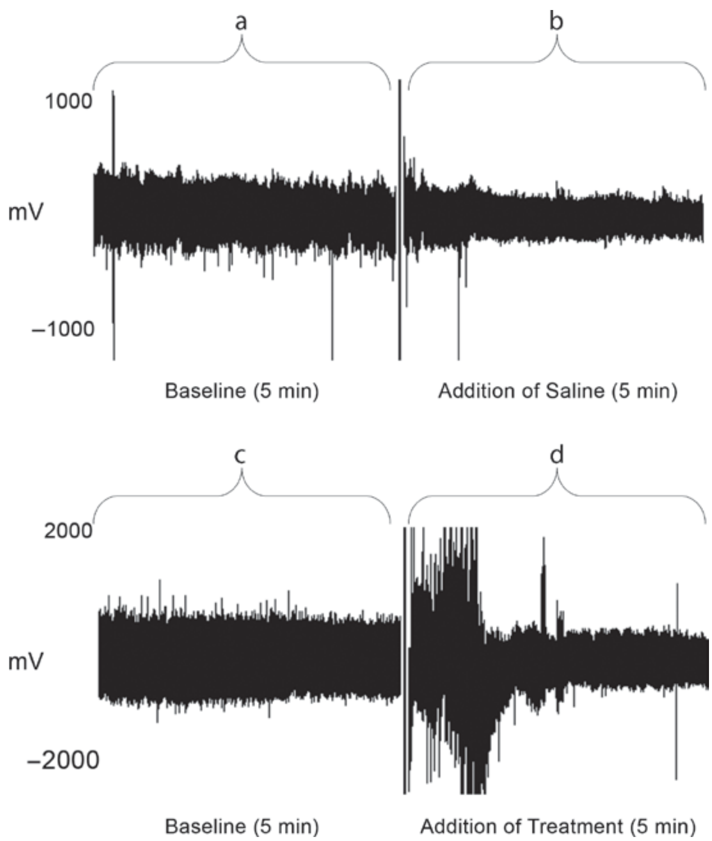
The majority of researchers believe that blockage of the spiracles or tracheae is the source of mortality in insects. This theory seems plausible because soap is able to enter and may be actively pumped in through the respiratory system of the insect. Water has a high surface tension so cannot enter the tracheal system of insects. When the surface tension is reduced to half of that of water by an emulsion, the solution may enter the tracheae. A soap solution would be an example of this. Once inside, the liquid can spread along the walls of the tracheal tubes. Rapid paralysis occurs after soap solutions enter the tracheal system. This has been attributed to hemolytic action.

Neurotoxins

It has also been suggested that soaps act as nerve toxicants. Supporting this hypothesis is the rapid paralysis and death of the insect after contacting soap solutions. Asphyxiation and dehydration could not account for the almost immediate response of insects to soap treatments; these modes of action would not result in such rapid death. Neurophysiological recordings of cockroaches exposed to soaps (Fig. 68) support the hypothesis that the soaps act, at least partially, via a neurological mode of action.

The Future of Soaps for Pest Control

Soap solutions, due to their low mammalian toxicity, have potential for use as a pest management option in sensitive environments such as occupied hospital rooms, in classrooms with children, and in daycare centers while children are present. Dishwashing liquid and household cleaners are readily available and are common



Soaps as Insecticides, Figure 68 **Spontaneous electrical activity from representative *Periplaneta americana* neural preparations were recorded with a threshold of 500 baseline counts per minute. Baseline electrical activity from an untreated neural preparation in physiological saline is seen in (a). After a 5 min recording, a saline control (1 ml) was added to the neural preparation as seen in (b). Baseline electrical activity in physiological saline was recorded in a separate neural preparation (c) before the addition of potassium laurate (1 ml at 0.75%) in physiological saline (d). As seen, the addition of the potassium laurate caused an increase in electrical activity followed by a quieting of spontaneous electrical activity. The decrease in electrical activity corresponded with paralysis, without recovery, of the specimen. (From R. Baldwin, unpublished Ph.D. Dissertation, University of Florida.)**

Soaps as Insecticides, Table 15 **Potassium fatty acid salts currently registered in the USA (source is http://ppis.ceris.purdue.edu/htbin/cnamlist.com)**

Woodstream Corporation
36488-31 Ringer Aphid-Mite Attack Concentrate
36488-33 Ringer Aphid-Mite Attack For Roses And Flowers
36488-36 Ringer Aphid Mite Attack/Fruit And Vegetable
36488-45 Ringer Attack Soap Concentrate
36488-46 Woodstream Ant & Cockroach Killer Aerosol
36488-47 Woodstream Flying Insect Killer Aerosol
36488-49 Woodstream Ant & Cockroach Killer
50932-3 Concern Insect Killing Soap Concentrate
50932-4 Concern Insect Killing Soap Ready To Use
Safer, Inc.
42697-1 Safer Insecticidal Soap Concentrate
42697-2 Safer Insect Killer
42697-7 Safer Moss And Algae Attack Concentrate
42697-10 Safer Agro-Chem's De-Moss-Ready To Use
42697-22 Safer Sharpshooter Weed And Grass Killer Ready To Use Spray (Rtu)
42697-33 Safer Soap And Pyrethrum Ready-To-Use
42697-34 Safer Brand Entire Insect Killer Concentrate
42697-35 Safer Sharpshooter Weed & Grass Killer Concentrate
42697-36 Safer (Tm) Sharpshooter V Ready To Use
42697-58 Safer Brand Garden Fungicide, Insecticide, & Miticide Rtu Spray
42697-59 Safer Brand O-Insect Killer
42697-60 Safer Brand O-Insecticidal Soap Concentrate
59913-2 Safer Brand Rose & Flower Insect Killer
59913-3 Safer Brand Fruit & Vegetable Insect Killer
59913-4 Safer Brand Moss & Algae Killer & Surface Cleaner Concentrate
59913-5 Safer Brand Moss & Algae Killer & Surface Cleaner Ready-To-Use
59913-9 Safer Brand O-Sap Concentrate II
59913-10 Safer Brand O-Sap Ready-To-Use Spray II
59913-12 Safer Brand 3-In-1 Rtu II
59913-13 Safer Brand 3-In-1 Concentrate
Agro-K Corp.
48222-5 Super Insecticidal Soap Concentrate
Miracle-Gro Lawn Products Inc.
62355-2 Secta Spray Vegetable Oil Soap Insecticide Concentrate
62355-3 Secta Ready To Use Vegetable Oil Soap Insecticide
Dow Agrosciences LLC
62719-515 M-Pede Insecticide/Fungicide

Soaps as Insecticides, Table 15 Potassium fatty acid salts currently registered in the USA (source is http://ppis.ceris.purdue.edu/htbin/cnamlist.com) (Continued)

Arysta Lifescience North America Corporation
66330-253 40% Insecticidal Soap
W. Neudorff Gmbh Kg
67702-11 Neu 1128
67702-12 Ho2 Moss Killer
67702-13 Neu1128 Rtu
67702-21 Neudorff's Insecticidal Soap Rtu
67702-22 Neudorff's Insecticidal Soap Concentrate
67702-23 Ho2 Moss Killer Rtu
Organica Biotech, Inc.
70191-1 Organica Neem Oil Insecticidal Soap Concentrate

items already found in these environments and in the home (Table 15). Many different brands and formulations provide rapid knock-down and kill ants, cockroaches and other insects effectively. Not only are soaps effective against different stages of the insect, but there is little if any recovery of insects after the initial knock-down. Soaps are inexpensive and concentrations of soap needed to knockdown or kill pest cockroaches are very low. This results in not only an effective, but also and economic pest management option.

Soaps also have a place for plant feeding insect management. Commercial products developed for use on plants generally are safe to use. Some people like to make their own soap sprays from household soaps and detergents, and certain brands of hand soaps and liquid dishwashing detergents can be effective for this purpose. They are also substantially less expensive. However, there is increased risk of plant injury with these products, as they are not designed for use on plants. Dry dish soaps and all clothes-washing detergents are likely too harsh to be used on plants safely. Regardless of the product selected, soap and detergent sprays are always applied diluted with water, typically at a concentration of around 2–3%. A test area should be sprayed with the soap solution to test for phytotoxicity before making a full application.

References

Butler GD, Henneberry TJ, Stansly PA, Schuster DJ (1993) Insecticidal effects of selected soaps, oils and detergents on the sweetpotato whitefly (Homoptera: Aleyrodidae). Fla Entomol 76:161–167

Koehler CS, Barclay LW, Kretchun TM (1983) Soaps as insecticides. Calif Agric 37(9/10):11–13

Oetting RD, Latimer JG (1995) Effects of soaps, oils, and plant growth regulators (PGRs) on *Neoseiulus cucumeris* (Oudemans) and PGRs on *Orius insidious* (Say). J Agric Entomol 12:101–109

Osborne LS (1984) Soap spray: an alternative to a conventional acaricide for controlling the two-spotted spider mite (Acari: Tetranychidae) in greenhouses. J Econ Entomol 77:734–737

Patrican LA, Allan SA (1995) Laboratory evaluation of desiccants and insecticidal soap applied to various substrates to control the deer tick *Ixodes scapularis*. J Med Vet Entomol 9:293–299

Pinnock DE, Brand RJ, Milstead JE, Coe NF (1974) Suppression of populations of *Aphis gossypii* and *A. spiraecola* by soap sprays. J Econ Entomol 67:783–784

Puritch GS (1975) The toxic effects of fatty acids and their salts on the balsam woolly aphid, *Adelges picese* (Ratz). Can J For Res 5:515–522

Szumlas DE (2002) Behavioral responses and mortality in German cockroaches (Blattodea: Blattellidae) after exposure to dishwashing liquid. J Econ Entomol 95:390–398

Social Insect Pheromones

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Social insects are unique in that they have overlapping generations in which adult workers (normally sterile) assist their mother in rearing sisters and brothers. In addition, there are reproductive and non-reproductive castes constituting a division of labor. Our discussion of social insect pheromones will be restricted to the social Hymenoptera (Formicidae, ants; Apidae, bees; Vespidae, wasps) and Isoptera (Termitidae, termites), although there are examples of social thrips and cockroaches.

Regardless of the size of the social insect colony, which can range from tens of individuals to millions, social interactions are required for effective food retrieval, brood and queen care, regulation of caste (sexuals/workers), recognition and exclusion of non-nestmates, and other tasks. There are several sensory mechanisms available to social insects for communication, e.g., tactile and vibratory, however, chemical communication has evolved to a high level of complexity in these insects.

There are advantages to the use of chemical signals as a means of information transfer. The chemicals are relatively small, volatile structures that are energetically inexpensive to biosynthesize and easy to release into the surrounding airspace. In addition, because the signal is detected through space by the sense of smell, it is functional under various environmental conditions. Some disadvantages are that it is difficult to direct the signal at a single recipient unless detection is through direct contact. Also, once released, the signal cannot be changed rapidly or in some cases the signal dissipates before the information has been transferred to all intended recipients. Specific terminology has been developed to define chemical interactions between organisms. We will restrict ourselves to intraspecific chemical communication.

Pheromones are chemicals released by an individual that have an effect on members of the same species. The word pheromone is derived from the Greek "pheran" meaning to transfer and "horman" meaning to excite. There are two pheromone subcategories, (i) releaser pheromones and produce an immediate response in the recipient individual, e.g., a male moth orienting toward the sex pheromone released by the female moth; and (ii) primer pheromones and perception triggers the initiation of a complex physiological response that is not immediately observable. Both pheromone types are extremely important in maintaining colony social structure.

Unlike hormones, pheromones must be secreted outside the insect's body via exocrine glands. It is a testament to the importance of pheromones to the success of social insects that they have evolved a very diverse repertoire of exocrine glandsand over 70, with 45, 21, 14, and 11 in ants, bees, wasps, and termites, respectively. Some of these glands function to produce wax, other types of building materials, or defensive compounds; however, many exocrine glands have become specialized for the production of pheromones that play major roles in communication and the maintenance of colony social structure. Pheromone-producing glands can be found anywhere on the social insect and from the pretarsal glands of bees to the frontal and labial glands of termites. In addition, the ovipositor of solitary insects evolved into the sting in the aculeate Hymenoptera, bees, wasps, and ants. Most important for this discussion is that the accessory glands associated with the ovipositor evolved into the Dufour's and poison glands. Both of these glands have become very important in pheromone communication in social insects.

The pheromone products have diverse uses among social insects. Recruitment pheromones help guide workers to food materials and in a different context can lead the entire colony to new nesting sites. When a worker ant, wasp, bee, or termite detects an intruder it will release an alarm pheromone that acts to excite and attract nearby workers, which then respond aggressively toward the intruder. Other compounds act as sex pheromones, queen recognition pheromones, territory markers, and brood pheromones, among others. Additional layers of complexity are added because pheromone structure and function varies within the morphological/functional caste system in social insects. Not only is there variability between queens and workers different, but also between the different worker castes as well. Sometimes, a single chemical plays different pheromonal roles, depending on the caste releasing it and the context of the situation. With such a plethora of glandular sources and elicited behaviors there appears to be no pattern in pheromone chemical structure or the glandular source relative to behavior elicited. To illustrate the unpredictability of glandular source versus function, trail pheromones in ants have been reported from the Dufour's gland, venom gland, hindgut, pygidial gland, Pavan's gland, and the postpygidial gland. Thus, the glandular source of a pheromone that elicits a particular biological behavior must be determined through bioassay.

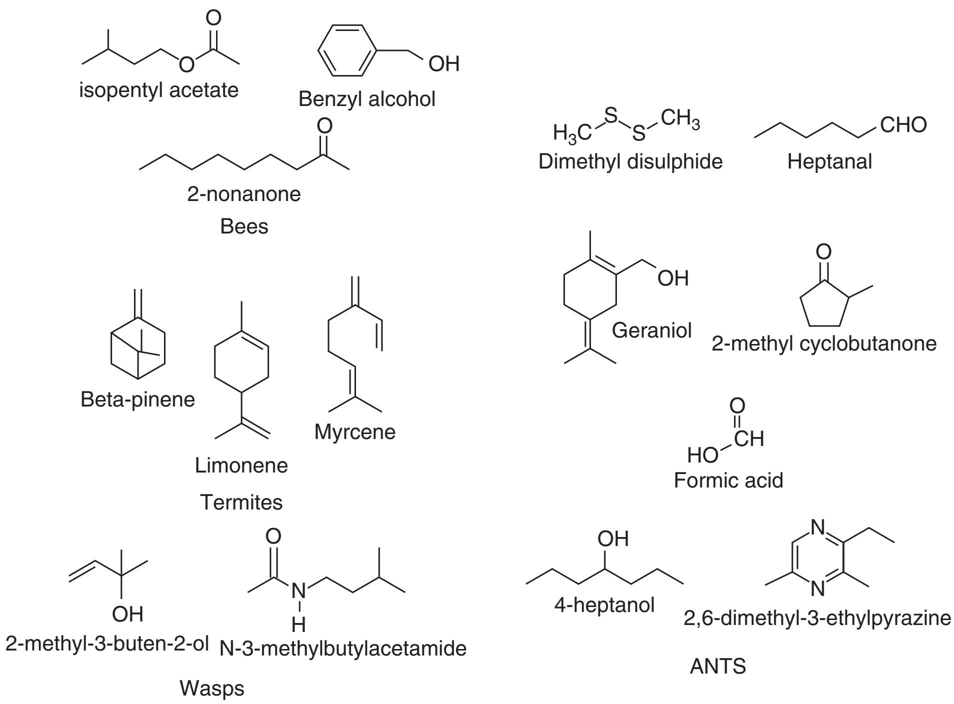
Pheromone Glands

Pheromone-producing glands are specialized for the distribution of their secretory products. Besides the biosynthesis of the active pheromone components, the glands must be able to regulate the release of the secretion. The mechanisms of release are not well understood; however, glands that have reservoirs may have specialized musculature at the reservoir opening that controls the release of the gland contents. Interestingly, the act of opening the mandibles initiates the release of alarm pheromones from mandibular glands of some ant species. Where there is no reservoir, glandular products may be released directly to the outside as they are produced. Release may be continuous or synthesis and release could be triggered by exogenous stimuli.

The chemistry of social insect pheromones is very diverse. Releaser pheromones elicit an immediate response in the recipient and are generally detected by the antennae in the air and therefore must be volatile. Primer pheromones elicit physiological change and may or may not be volatile, because they can be distributed to colony members by grooming and/or trophallaxis (passage of regurgitated material from one individual to another). We will briefly go through the major pheromone behavioral categories and their associated chemistry.

Alarm Pheromones

Alarm pheromones represent an important evolutionary development for eusocial insects because they enable colony worker resources to be focused at specific colony needs, e.g., nest or food defense. The alarm signals only act to alert other members of the colony. If the alerted workers subsequently find an intruder they will likely respond aggressively by attacking. If they find food they may be stimulated to ingest the food. So, while the alarm reaction is usually associated with defensive behavior, it is subsequent stimuli that often dictate what happens next. The release of alarm pheromones may be initiated by the physical disturbance of an individual worker or by the chemical recognition of an intruder. Once the alarm response is initiated, its release may be "telegraphed" to other nearby workers. This helps explain anecdotal accounts that hundreds of nestmate bees or wasps respond to the accidental disturbance of a single bee or wasp. Similarly with fire ants, people report that worker ants will sneak up their leg, then when in position all of them will sting in unison. Actually the ants simply go undetected for a period of time, until a movement disturbs one ant that then releases an alarm pheromone, quickly activating nestmates in the area. While the mandibular gland is the most common source of alarm pheromones they have also been reported from the pygidial gland, Dufour's gland, Koschevnikov's gland (associated with the sting apparatus of bees), and other glands (Fig. 69).



Social Insect Pheromones, Figure 69 **Representative alarm pheromones identified from bees, termites, wasps and ants, illustrating the diversity of structural types.**

There are many reported behaviors associated with alarm pheromones. In ants for example, attraction to the alarm pheromone source, increased speed of movement, frenzied running, aggression, raised head and more have all been reported as alarm behaviors. More complicating is that the context in which the alarm pheromone is released can affect worker response, e.g., colony disturbance, an encountered intruder, age of the colony, etc. Consequently, it is important for the researcher to clearly define the alarm behavior being investigated.

The requirement for a quick response to the alarm pheromone, as well as for its rapid dissipation after the perceived need has passed suggests that alarm pheromones should be small volatile compounds. While in some instances only one component is reported, e.g., 2-methyl-3-buten-2-ol for the hornet (*Vespa crabro*), it is expected that many more potentially active compounds will be isolated and identified. For example, initially only isopentyl acetate was isolated from Koschevnikov's gland in honey bees (alarm pheromone source); however, subsequent analysis has identified at least 22 additional compounds. Many ant alarm pheromones have been isolated and identified. Considering the necessity that alarm pheromones must be highly volatile, the variety of structural types pays homage to the biosynthetic versatility of the social insects and ants in particular.

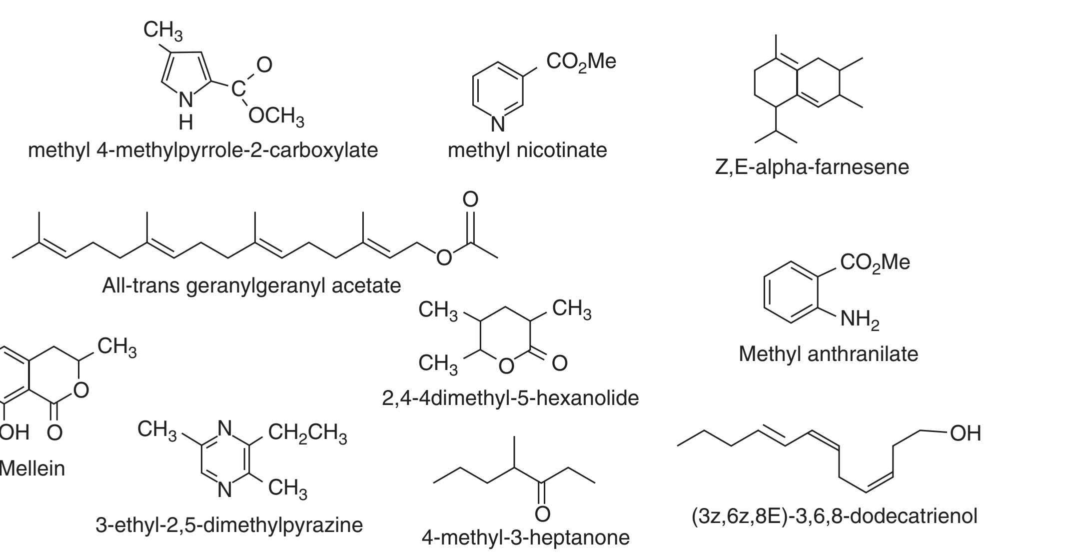
Future work in this area should focus on the precise definition of the alarm behavior, development of a behavior-specific bioassay, and then the bioassay-driven isolation of the active compounds.

Recruitment Pheromones

Recruitment pheromones are compounds involved in bringing colony workers to a particular location where they are needed. An ant trail between the colony's nest to a dead insect or other food material is a familiar sight to most people. The trail is the end result of a complex process; but since it is easily observed this pheromone system is sometimes referred to as the trail pheromone. Nestmates may be recruited to gather food resources, or to defend their territory against invasion, or recruitment pheromones may be used to guide the migration of the colony to a better nest site (Fig. 70).

The terrestrial ants, of necessity, have evolved a wide variety of recruitment mechanisms and glandular sources of recruitment pheromones. In ants the Dufour's gland, poison gland, the pygidial glands, and sternal glands, hindgut, and rectal gland have been reported as sources of recruitment pheromones. Pheromones from these sources can be readily envisioned being deposited on a solid substrate. Similarly the sternal gland is used in several genera of termites as a source of trail pheromones. Thus far this gland is the only known source of termite trail pheromones. The flying social insects also have a need to recruit a worker force to food supplies and/or to guide colony members to new nesting sites and hence recruitment pheromones can also play a role. Social wasps do not commonly recruit to food sources but do recruit to new nest sites. During this process workers drag their gasters on a substrate to deposit sternal gland secretions, which then guides the migrating colony to a new nest site. Stingless meliponine bees deposit mandibular gland products at intervals on the ground while the Nasanov gland in honeybees is a source of marking pheromones. Most investigations of recruitment pheromones have focused on ants, primarily because they form readily observed trails on the surface and bioassays have been relatively easy to develop.

The red imported fire ant, *Solenopsis invicta*, is a good model to illustrate the behavioral components of the recruitment process. The process begins when a foraging scout worker discovers a food source too large for it to carry back to the colony. During the foraging process the scout keeps track of its position relative to a light source (sun, street light, etc.) and is able to navigate pretty much straight back to the colony. As it makes its way back, it periodically deposits minute amounts of Dufour's gland products to the substrate. The Dufour's gland is attached to the base of the sting apparatus and the products exit through the sting. Thus, in this case, the sting is periodically extended to touch the substrate. When the scout returns to the nest Dufour's gland products are used to attract other workers toward the scout and activate them to follow the very weak initial trail. The attracted and activated workers detect and respond to the trail by following it to the food source. The movement back



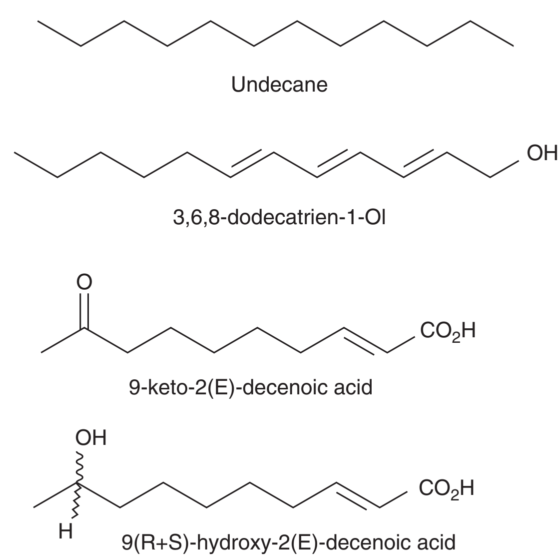
Social Insect Pheromones, Figure 70 Representative recruitment pheromone structures illustrating the diversity of structural types.

and forth along the trail is called orientation. The newly recruited workers ingest some food, stimulating them to reinforce the trail with additional recruitment pheromone as they return to the nest. More workers are recruited until the food source is covered with fire ants and additional workers cannot get to the food and do not reinforce the trail. As the food source diminishes fewer workers reinforce the trail and because of its volatility, the concentration of the deposited recruitment pheromone weakens until the food is gone and the trail evaporates completely. The recruitment process can be broken down into several sub-categories. (i) Initial trail laying by the scout ant; (ii) attraction of additional workers to the scout ant; (iii) activation (induction) of the workers to follow the trail; (iv) trail orientation. Separate behavioral bioassays were developed for each of the categories and used to guide the isolation of the responsible pheromone components. Z,E-α -farnesene appears to be solely responsible for orientation, but does not attract worker fire ants. A mixture of Z,E-α-farnesene and a bicyclic homofarnesene account for 100% of the Dufour's gland activity in an olfactometer (attraction) bioassay. Remarkably, when this mixture is presented to foraging ants as a trail they do not orient along the artificial trail! This illustrates that the workers first need to be activated or put into a more alert state. In some ant species the scout worker will physically agitate perspective recruits, whereas the fire ant can do the same job with Dufour's gland products. This activation requires virtually a reconstitution of the complete chemical profile of the Dufour's gland.

The fire ant provides one example; however, in some ant species the scout attracts and escorts a single nestmate back to the food source and in others the scout physically activates nestmates who are then able to independently follow the trail. Social insects occupy virtually all ecological niches and have evolved a myriad of mechanisms to accomplish tasks such as recruitment to bring nestmates to a point in space where extra legs and mandibles are needed. The chemistry of many recruitment pheromones has been determined.

Sex Pheromones

Sex pheromones are substances that are emitted by males or females that function to attract the opposite sex for the purpose of mating. Most commonly the female attracts the male(s) to her. There are many examples among solitary insects, especially lepidopteran species, of both the associated behaviors and the chemistry of the pheromones involved. However, few sex pheromones have been reported in social insects, probably because of the difficulty in developing appropriate bioassays. Most social insects, including the terrestrial variety (ants and termites), mate during "mating flights." The mating flights are usually triggered by specific environmental conditions, so laboratory assays are difficult to establish and observations of the natural phenomenon have been rare. For example, the red imported fire ant, Solenopsis invicta, may send off hundreds of thousands of male and female winged sexuals, with males taking flight approximately 30 min before the females. The males and females find each other, presumably through sex pheromones, and mate about 100–200 m in the air, then the females come down to attempt to start a colony (Fig. 71). No one has



Social Insect Pheromones, Figure 71 The structures of known social insect sex pheromones.

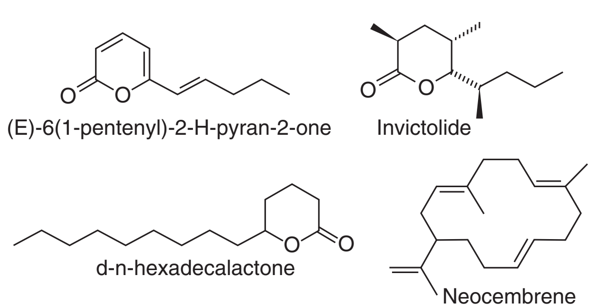
yet seen a mating pair of fire ants and no one has been able to get them to mate successfully in the laboratory!

The honey bee "queen substance" produced by the mandibular glands is used in the context of an established colony to control the production of female sexuals. These same glandular products are used by virgin queens to attract male drones for mating. While there are many compounds produced by the mandibular glands, only two compounds appear to play a sex pheromone role: (E)-9-oxodec-2-enoic acid and (E)-9-hydroxydec-2-enoic acid. The other two examples of sex pheromones in social insects are also pheromones that have different behavioral effects depending on the context of their use. In termites 3,6,8-dodecatrien-1-ol is a trail pheromone, but has also been implicated as a sexual attractant for two termite species: *Pseudacanthotermes spiniger* and *Reticulitermes santonensis*. The one and only sex pheromone from an ant species was isolated from Formica lugubris. The pheromone undecane was isolated from the mandibular glands and accounted for 100% of the sex pheromone bioassay activity. This compound is also used by workers as an alarm pheromone.

Queen Pheromones

Queen recognition pheromones or more simply "queen pheromones" are exocrine gland products released by the queen that usually attract workers to her, eliciting care and protection. Most queens of social insects have the ability to attract workers, so the behavior is well documented. Again, various glands serve as sources for the queen pheromone, from the mandibular glands in the head of honey bees to the poison sac in the abdomen of fire ants. The queen benefits from the attention of the workers, and the workers may also use the pheromone signal to gain information about the queen. For example, the release of poison sac contents is directly linked to queen egg laying, thus workers may be able to assess the fecundity of their queen based on the amount of pheromone released into the colony (Fig. 72).

The chemistry of these pheromone systems has been elucidated in only a few systems. In the fire ant *Solenopsis invicta* the source of attractant pheromones was found to be the queen's poison sac. Two lactones have been identified as the active pheromones. The pharoah's ant, *Monomorium pharaonis*, produces a macrocyclic compound, cembrene A, in its Dufour's gland that elicits worker attraction. Ejection of the sting and possible deposition of Dufour's gland products on the eggs has also been reported for this species. The honey bee queen pheromone is produced by the mandibular gland and has turned out to be a very complex mixture of compounds that by themselves are only slightly active but when taken together act as synergists, reproducing the activity from the mandibular gland itself. Unusual for pheromones, most of the compounds are found in tens of μgs. In spite of the large quantity of pheromones produced, the synergistic effects of the components complicated the isolation of the active compounds. No queen pheromones have been isolated and identified yet from termite species. Only one compound, δ -n-hexadecalactone, has been isolated as a queen pheromone from a wasp species. It was isolated from head extracts and affect worker behavior.



Social Insect Pheromones, Figure 72 The structures of queen recognition pheromones.

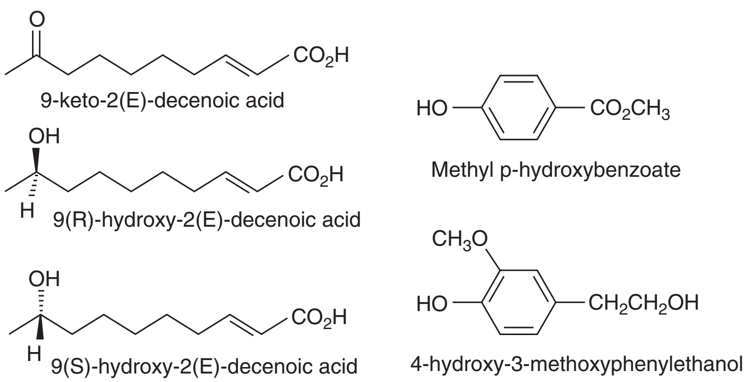
Releaser and Primer Pheromones

As mentioned earlier there are two broad categories of pheromones, releaser and primer pheromones. The above discussion centers around releaser pheromones whose detection yields an immediate observable behavioral change. Thus, bioassay development is easier and results can be obtained quickly. This area of social insect pheromone communication has foraged ahead rapidly, while primer pheromones have lagged far behind. This is because they trigger the initiation of complex physiological responses that are not immediately observable. It may take days or more to obtain results. Bioassays have been developed that demonstrate the existence of primer pheromones, but the chemistry has not been forthcoming, except for the honey bee (Fig. 73).

The honey bee, *Apis mellifera*, is one of the most extensively studied social insects, in part because of its economic importance and the ready availability of colonies. Interestingly, the queen's mandibular pheromone blend of five components acts as both releaser and primer pheromones. The blend attracts workers to the queen as in "queen recognition" and therefore has releaser pheromone effects. It acts as a primer pheromone by inhibiting queen rearing by workers. Additionally, it retards the build up of juvenile hormone titer in worker bees, which effectively acts to slow the developmental progression of workers from brood tending to foraging. These effects clearly represent changes in the physiology of honey bee workers.

Most, if not all, social insect primer pheromones are produced by the queen and function in some way to prevent reproductive competition. Another example comes from the fire ant. The fire ant queen has been demonstrated to produce several primer pheromones that function to: (i) inhibit ovary development in female sexuals; (ii) suppress egg production by mature queens in polygyne colonies; (iii) inhibit the production of female sexuals; (iv) regulate nestmate recognition sensitivity, such that newly mated queens are executed by workers. Unfortunately, the structures of these interesting primer pheromones are still unknown.

We have discussed the main behavioral categories of pheromones in social insects; however, there are other categories, such as territorial marking and brood pheromones, a discussion of which can be found in the references. In addition, there are nestmate recognition cues that are on the surface of individuals that allow members of one colony to distinguish members of another colony of the same species. While the effect is conspecific, the behavioral response is different for nestmate and non-nestmate; acceptance or attack, respectively. Nestmate recognition cues may be acquired from the environment, inherited, or derived from a combination of the two sources. Thus, nestmate recognition cues do not quite fit into the realm of pheromones.



Social Insect Pheromones, Figure 73 **The five components that constitute the queen produced honey bee primer pheromone.**

We have demonstrated the complexity of social insect pheromones and their sources, associated behaviors, and chemistry and hope that readers will be stimulated to delve deeper into the literature to further uncover the beauty and intricacies of this fascinating subject.

► Pheromones
► Sociality in Insects

References

Hölldobler B, Wilson EO (1990) The ants. Harvard University Press, Cambridge, MA

Traniello JFA, Robson SK (1995) Trail and territorial communication in social insects. In: Cardé R, Bell WJ (eds) The chemical ecology of insects 2. Chapman & Hall, New York, NY, pp 241–286

Vander Meer RK, Morel L (1988) Brood pheromones in ants. In: Trager JC (ed) Advances in myrmecology. E.J. Brill, New York, NY, pp 491–513

Vander Meer RK, Breed M, Winston ML (1998) Pheromone communication in social insects: ants, wasps, bees, and termites. Westview Press, Boulder, CO

Winston ML (1992) Semiochemicals and insect sociality. In: Roitberg BD, Isman MB (eds) Insect chemical ecology. Chapman & Hall, New York, NY, pp 315–333

Social Insects

Insects that live in groups or colonies and cooperate among themselves. The degree of sociality varies among insects, and even among social insects, but most insects show no evidence of sociality.

► Sociality in Insects
► Castes

Sociality of Insects

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The social insects represent a major evolutionary success story. Their cooperative nest-building, prey capture, and recruitment for food have captured the attention and fueled the imaginations of humans. This cooperation also has contributed to the numerical abundance and ecological dominance of social insects in many habitats. For example, in tropical forests and savannahs, ants and termites outweigh the impressive and very conspicuous mammalian fauna. In all but the coldest environments, ants are the predominant predators of other insects, and they are also major dispersers of seeds of numerous plant species. Social bees pollinate a large proportion of the flora throughout the world, both because they are abundant and because many of them have efficient recruitment tactics such as the remarkably complex dance language of honey bees. Termites are the primary decomposers of wood and other materials containing cellulose in the tropics. Termites and ants together move more soil than earthworms in all tropical habitats, and even in temperate regions, have a major role in mixing nutrients in the soil and creating topsoil. From these examples, it is evident that the social insects figure prominently in nutrient cycles and energy flow in the biosphere.

The majority of all insects are solitary. For solitary species, the most social point in their life cycle is often the interaction between mates, after which females go about their business of reproduction without cooperating with other members of their species. Parasitic wasps lay eggs in their hosts, grasshoppers oviposit in the soil, and butterflies seek out larval host plants on which to lay their eggs. The common thread among these diverse solitary groups of insects is that their offspring develop into adults without interaction with their mothers.

Eusocial Insects

At the other extreme are the eusocial insects. Eusociality is a term that refers to a set of three very specific criteria: overlap of generations (i.e., mothers live sufficiently long to interact with their adult offspring); cooperative brood care (i.e., females provide some care to offspring that are not their own, and individual larvae are provisioned by more than one female); reproductive division of labor (i.e., some individuals of a group leave behind more offspring than others).

Most of the insects we think of as highly social and honey bees, yellowjacket wasps and hornets, ants, and termites and meet the criteria of eusociality. In fact, most eusocial species belong to the order Hymenoptera, with all the species of ants (about 9,000 species), about ten percent of bees (more than 2,000 species), and some wasps (about 1,000 species) being eusocial. The other main group of eusocial insects contains the termites, order Isoptera, with all 2,200 species being eusocial. There are only a handful of other eusocial organisms by the above set of criteria: a bark beetle in Australia, various gall-forming aphids and thrips, sponge-inhabiting snapping shrimp, and naked mole rats in Africa.

Between the extremes of solitary and eusocial insects are numerous species in many different taxa that exhibit some, but not all, of the criteria for eusociality. These insect species often are described by the nonspecific term, presocial. Because eusociality evolved from presocial societies, considerable attention has been directed at presocial insects in an attempt to elucidate those factors that favor the evolution of more complex social systems. Presociality can be further divided into parasociality and subsociality. The definitions and examples of these two major categories of subsocial species will be discussed here, and their central role in the evolution of sociality will be considered later in this article.

Parasocial Insects

Parasocial species are those in which the colonies are comprised of individuals of the same generation, and are usually groups of sisters that nest together. Thus, in parasociality, the first criterion of eusociality (overlap in generations) is not met. For example, females of the carpenter bee (*Xylocopa virginica*), that is common over much of eastern North America, construct galleries in wood. The young adult bees emerge after their mother has died and often they remain in the gallery in a communal society over winter. Once spring arrives, they disperse and initiate nests individually. Although the offspring share the nest for a period of time, there is little or no cooperation between individuals. In some parasocial colonies (e.g., some neotropical orchid bees, *Euglossa* spp.), although all adult females have developed ovaries and apparently are equally capable of laying eggs (i.e., no reproductive division of labor), there are more adult bees than cells with larvae being provisioned at any point in time. This is suggestive of cooperative brood care. There also may be some slight specialization in nest guarding, but overall cooperation in such parasocial bee societies usually is rudimentary. Tropical parasocial spiders (e.g., *Anelosimus eximus*, *Agelena consociata*) are able to construct huge webs in clearings and thereby encounter more and larger prey than their solitary relatives can. Within their societies, these spiders exhibit a variety of relatively complex behaviors, but they lack reproductive division of labor.

Subsocial Insects

The other broad category of presociality is subsociality. Subsocial insects are those in which females show extended care of their offspring that enhances offspring survival. The specific selective forces that favor subsociality vary widely, but generally are linked to either very harsh conditions or very favorable but ephemeral conditions. The European rove beetle, *Bledius spectabilis*, provides an example of a species that lives under extremely unfavorable conditions. Adult females construct vertical burrows in tidal mudflats. After feeding on algae on the mud at low tide, the beetles retreat to their burrows and plug the entrances. Without the adult beetle present when the burrows are submerged at high tide, the younger immatures are unable to maintain the tunnels and they die from lack of oxygen. At the opposite extreme, burying beetles (*Nicrophorus* spp.) reproduce on small rodents that represent abundant, high quality, ephemeral resources. In order to reproduce successfully they must find, then defend, a dead rodent from potential competitors such as fly larvae, fungi and bacteria, and even other *Nicrophorus* beetles. Consequently, a reproductive pair of beetles usually fights other *Nicrophorus* to gain control of the rodent, after which they shave it and treat it with mandibular secretions. The female, and sometimes the male, remain with the larvae, protecting and even directly feeding them, until they pupate in the soil. At that time, the continued presence of the adults cannot enhance offspring survival, and the beetle(s) disperse to seek new cadavers upon which they can reproduce.

The evolutionary "breakthrough" that enabled some presocial species to evolve more complex eusocial societies is reproductive division of labor. In most cases, that translates into morphologically distinct queen and worker castes, with queens doing most or all of the reproduction. "On the Origin of Species", Darwin wrote that the sterile workers and soldiers of social insects presented "one special difficulty, which at first appeared to me insuperable, and actually fatal to my whole theory." Why should some individuals "give up" their own reproduction in order to assist the queen of their colony? The evolution of sterile individuals seems contrary to the principles of natural selection, in which those individuals with the highest fitness as measured by number of offspring contribute most to succeeding generations. Darwin believed he solved this puzzle by treating the colony as the unit of selection. If specialization into distinct worker and soldier castes enhances colony survival and functioning, then the colony will be able to invest greater energy into the rearing of reproductives (new gynes [potential queens] and males) and as a result will experience enhanced reproductive success. As a consequence, colonies could evolve various specializations of queens, workers, and soldiers that contribute to colony-level fitness. This view of social insect colonies probably helped to usher in the early-1900s view of social insect societies as "superorganisms," in which colonies were seen to have attributes or abilities that were distinct from the sum of the behaviors of the individuals that comprise those colonies.

In 1964, W.D. Hamilton III proposed a different view of sociality based on kinship. He pointed out that in the Hymenoptera (bees, wasps and ants), males arise from unfertilized eggs. A consequence of this is that all sperm from a single male are identical. Female nestmates (sisters) that have the same father share three quarters of their genes in common, more than they share with their own offspring (one half). Hamilton pointed out that in hymenopteran colonies in which the queen has mated only once, it is genetically beneficial for females to remain in their nest to cooperate in rearing sisters rather than to risk leaving to start a new nest and raise daughters with which she would be less closely related and would share fewer genes. Hamilton extended his theory of "inclusive fitness" to all kin, both direct offspring and others that share some genes through shared ancestry (e.g., sisters, cousins, etc.).

Hamilton's theory of inclusive fitness ushered in a new wave of research on the role of kinship (i.e., the proportion of genes shared through common ancestry) on social systems, a field termed "sociobiology." One of the first steps was to determine whether organisms could recognize kin. Now, four decades later, there is ample evidence that within all the taxa of social insects, kin recognition abilities have been demonstrated. Recognition is mediated by chemical "signatures," both intrinsic, or genetically determined, and environmentally influenced, on the surface of the insect that are learned by nestmates. But simply having the ability to recognize kin does not mean that social insects also choose to direct aid towards individuals that are more closely related to them. Again, after numerous contributions from many researchers, the evidence has mounted that proves that, in most cases, social insects can act in ways to enhance their inclusive fitness. A classic demonstration of the operation of kin recognition comes from "worker policing" in honey bees. Worker bees have the ability to lay unfertilized eggs that develop into males, but when the queen is present in a normally functioning colony, worker-laid eggs usually are cannibalized by other workers. One can predict mathematically that it is in the workers' best interests to attempt to reproduce, because they are more closely related to their own sons (relatedness = 1/2) than to their brothers (i.e., queen-derived unfertilized eggs; r = 1/4). However, because queens naturally mate with about ten males, when a worker in the colony encounters a worker-laid egg, roughly nine times out of ten it will share only 1/8 of its genes with it as a result of common ancestry. When faced with eggs laid by workers (the majority of which are related by 1/8) and queen-laid male eggs (r = 1/4), it is in the best interests of worker bees to destroy the eggs laid by other workers. In fact, when tested empirically, it was found that after 24 h all worker-laid eggs had disappeared from colonies, whereas approximately 50% of queen-laid male eggs remained. As another example, paper wasps (*Polistes* spp.) have been shown to preferentially join with nestmates (e.g., sisters) rather than non-nestmates when more than one foundress wasp cooperate to initiate nests in spring.

On the surface it seemed that W.D. Hamilton had discovered the major factor leading to insect sociality, namely the genetic asymmetry resulting from the haplodiploid sex determination system (females diploid, males haploid) of Hymenoptera. The simple fact that females could gain more inclusive fitness by staying in their nest to cooperate in rearing sisters rather than leaving to initiate new nests to rear daughters seemed to answer the question. However, several pieces of information suggest that the situation is not so simple. As early as 1976, Robert Trivers and Hope Hare pointed out that the inclusive fitness gained by rearing their sisters (r = 3/4) is lost in rearing brothers (r = 1/4) rather than sons (r = 1/2) if colonies rear equal numbers of queens and males. Secondly, there are many haplodiploid taxa that have failed to evolve eusociality. Even most taxa in which offspring are produced clonally by their mothers, so that sisters and brothers share all of their genes in common, are not eusocial. Thirdly, the termites are an extremely diverse and successful group of insects, but their males derive from fertilized eggs and there is no genetic asymmetry between daughters and sisters, or sons and brothers. Although Hamilton's ideas have dramatically changed the perspective of biologists with respect to the concept of fitness and the role of kin in animal sociality, other considerations have eliminated the 3/4 relatedness hypothesis as the sole factor favoring the evolution of sociality.

In place of a unifying theory, most scientists now recognize that each taxonomic group of insects has its own set of conditions that have influenced the evolution of sociality. As an example, paper wasp (*Polistes*) larvae have the ability to eat proteinaceous prey, while adults with the narrow petiole connecting their head and thorax to the abdomen are restricted to a liquid diet. In times of inclement weather and the ensuing food shortages that regularly occur early in the nesting cycle, the adults solicit and receive food from the larvae to prevent their own starvation. While this behavior allows the queens and their brood to survive into warmer, less threatening times of year, it results in the offspring produced early in the nesting cycle receiving suboptimal nutrition. It has been suggested that these nutritionally compromised adults gain higher inclusive fitness by remaining on their natal nest rather than initiating new nests on their own. In the case of sweat bees (family Halictidae) that nest in aggregations in soil, brood parasitism often is reduced by sharing of the nest with another female. When either of the females is away foraging, the other is usually in the nest defending it from intruders. This mutualism enhances the overall reproductive success of both females and has played a significant role in the repeated evolution of sociality in sweat bees. In termites, symbiotic gut microorganisms are passed between colony members. When nymphs molt, they must become re-inoculated with these symbionts from their nestmates. The exchange of these symbionts has undoubtedly been a factor in the evolution of termites from their closest relatives, the cockroaches. However, Hamilton's work made it clear that no matter what the specific set of circumstances surrounding a particular taxonomic group, loss of reproductive capacity will not evolve unless the interactions involve related individuals (i.e., kin).

Bernard Crespi has examined in detail the life history traits of the less typical eusocial organisms, as a way to elucidate the suite of traits that are most likely to enable eusociality to evolve. He has suggested that three conditions are necessary for the evolution of eusociality: coincidence of food and shelter, strong selection pressure for defense of nests, and the ability to defend nests. In this context, the occurrence of the sting in Hymenoptera probably has played a large role in the evolution of sociality in bees, wasps, and ants. Crespi suggests that additional eusocial insect taxa may be found among long-lived bark beetles that have substantial cohabitation of adults and their offspring, book lice (order Psocoptera) and webspinners (order Embiidina) that occupy long-lived webs, and other gall-inhabiting taxa.

Because evolution cannot be viewed directly, we must infer the evolutionary pathways to eusociality followed by various groups of social insects. In the past, this was achieved by logical reconstruction of the stepwise changes that could have led to eusociality using the biologies of living species. An excellent example involves the evolution of sociality in wasps. Howard Evans used the comparative approach to relate social systems of various wasp species to each other. He developed a widely accepted framework, from solitary species to primitive mother-offspring (subsocial) associations, to more complex subsociality, and finally eusociality with reproductive division of labor as seen in temperate hornets and yellowjackets (subfamily Vespinae). With the advent of cladistic methods to construct phylogenies (evolutionary histories), and statistical analyses that allow the certainty of those phylogenies to be tested, we have made important advances in the understanding of the evolution of sociality. Returning to wasp evolution, by "mapping" behavioral states onto the phylogeny of the subfamilies of vespid wasps, it has been discovered that the most basal wasp subfamily in the phylogeny that exhibits sociality contains only parasocial associations of sisters, not subsocial mother-daughter associations. The sweat bees provide another example of the approach of combining phylogenetic analyses with behavioral data. It has long been recognized that parasocial associations of females have been involved in the repeated evolution (and loss) of eusociality within the family. By mapping states of sociality onto phylogenies, it is possible to identify those species for which further study will best illuminate the factors affecting the evolution of sociality, by finding closely related species that differ in their degree of social complexity. In a similar way, this approach of combining behavioral traits with phylogenies has enhanced our understanding of the evolution of sociality in termites.

The superorganism concept was mentioned earlier. Early in the twentieth century, the concept that insect colonies were analogous to whole organisms complete with "germ plasm" (queens and males) and "soma" (workers and soldiers) gained enormous popularity. Despite the importance of the superorganism concept as a paradigm for studying the biology of social insects for a significant period of time, it had largely disappeared by the 1960s. As ethological approaches to the study of animal behavior gained in force, so too did the application of the scientific method to field studies. Modern scientists entered an era of hypothesis formulation and testing. While the superorganism concept provided interesting analogies to other organisms, it failed to provide concrete hypotheses that could be tested empirically. Interestingly, the concept has seen a revival since the development of powerful personal computers. Researchers can quantify simple rules of behavior by observing individual insects, then combine them through computer simulations to recreate behavioral patterns of self-organized behavior with remarkable accuracy. This approach has been used to model, among other behaviors, pattern formation on honey bee combs, nest construction by termites, and army ant raids.

The study of insect sociality has led to many profound discoveries about insects. Some areas of research that should provide new insights in the future include the study of molecular and genetic changes that occur as complex societies evolve, the specific conditions that favor sociality, the relative importance of parasocial and subsocial routes to eusociality, more complex integration of systems of self-organized behavior, and enhanced understanding of the role of social insects in ecosystem functioning.

References

Brockmann HJ (1984) The evolution of social behaviour in insects. In: Krebs JR, Davies NB (eds) Behavioural ecology: an evolutionary approach, 2nd edn. Sinauer Associates, Sunderland, MA, pp 340–361
Crespi BJ (1994) Three conditions for the evolution of eusociality: are they sufficient? Insectes Soc 41:395–400
Hamilton WD (1964) The genetical evolution of social behaviour, I and II. J Theor Biol 7:1–52
Hölldobler B, Wilson EO (1990) The ants. Belknap Press of Harvard University Press, Cambridge, MA
Michener CD (1974) The social behavior of the bees. Belknap Press of Harvard University Press, Cambridge, MA
Ross KG, Matthews RW (1991) The social biology of wasps. Comstock Publishing Associates, Ithaca, NY
Trivers RL, Hare H (1976) Haplodiploidy and the evolution of the social insects. Science 191:249–263
Wilson EO (1971) The insect societies. Belknap Press of Harvard University Press, Cambridge, MA

Social Parasites

Insects that obtain their sustenance at the expense of a colony of insects from another species, without destroying the colony.

Sociobiology (in Insects)

The study of social behavior, and population characteristics among social insects.

Sod Webworm

Several species of moths (Lepidoptera: Pyralidae) affect the roots of turfgrasses, and are called sod webworms.

► Turfgrass Insects and their Management

Soft-Bodied Plant Beetles

Members of the family Artematopididae (order Coleoptera).

► Beetles

Soft Scales

Some members of the family Coccidae, superfamily Coccoidae (order Hemiptera).

► Bugs
► Scale Insects and Mealybugs

Soft-Winged Flower Beetles

Members of the family Melyridae (order Coleoptera).

► Beetles

Soil Fumigation

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Soil fumigation is a preplant chemical treatment of soil, using a pesticide product that converts to form a volatile gas. The gas is able to diffuse through open pore space throughout the soil to provide soil-borne pest and disease control. All of the fumigants are phytotoxic to plants and the fumigant gases must dissipate from soil, usually from a few days to a month, before seeding or transplanting can occur without risk of crop injury. They are used globally on a wide range of annual and perennial crops, and can be used alone or in combination to control a wide range of soil inhabiting pest species including insects, nematodes, fungi, and weeds. Because of their wide range ofpesticidal activity, they are often called "multipurpose" or "broad-spectrum" fumigants.

Fumigants are commonly used in high value cropping systems to protect investment in crops where pest pressure is so high that it would be technically or economically unfeasible to grow a crop without the use of fumigant. As such, preplant soil fumigants have had a profound influence on production agriculture, and have catalyzed the worldwide development of many different high-value cropping systems. In some cases, fumigants have been adopted almost to the exclusion of all other soil pest management strategies because of their superior broad-spectrum pest control efficacy and consistent enhancement of crop growth, development, yield, and quality.

Historical Background

Discovered in 1869, the first fumigant pesticide to become available for agricultural use was carbon bisulfide. Because of its flammability, high rates of application, cost, and pest control inconsistency, carbon bisulfide was never extensively used in agriculture. In 1919, soil treatment with chloropicrin was demonstrated to provide excellent control of the root-knot nematode (*Meloidogyne* spp.), while in other studies, use of chloropicrin was shown to cure problems of "soil sickness" that restored the soil to a higher productivity than could be obtained from years of crop rotation or fallow. After considerable delay, chloropicrin was commercially introduced in the USA as a soil fumigant in 1937. It was first used on a limited basis by nurserymen and greenhouse operators as a substitute for soil steaming. In 1943, D-D (1,3-dichloropropene, 1,2,-dichloropropane and related C3 hydrocarbons) was shown in field trials to be an effective nematicide. By 1945, Shell Chemical Corporation had developed specialized field application equipment for D-D, including a tractor-drawn cart, complete with applicator, shanks, pumps, and tank for the fumigant, and even offered the first custom soil fumigation service. As a result, D-D was commercially introduced in 1945 as the first really effective and inexpensive soil fumigant for general field use.

In 1945, after demonstrating excellent control of root-knot nematode, ethylene dibromide (EDB) was commercially introduced by Dow Chemical Company as a low cost fumigant. Within a few years, the use of D-D and EDB increased tremendously due to the dramatic improvements in plant growth that were often observed following their use. Because use of these soil fumigants made the difference between an excellent yield and no yield, many growers adopted soil fumigation as a general practice. By 1949, soil fumigation with D-D and EDB has expanded to such an extent in many areas of the west and southeast, that the first mass production of field application equipment was undertaken.

Methyl bromide was first reported to be effective as a soil fumigant in 1940. In 1953, the synergistic effect of methyl bromide-chloropicrin mixtures for improved disease control was reported in California. Because specialized equipment required for methyl bromide field application was expensive, it was not extensively used, being employed only by large farming enterprises.

Soil fumigation in the USA really began in earnest during the early 1950s with in-furrow applications of D-D and EDB to control nematodes that became economic problems in re-cropped fields. In 1954, DBCP (1,2-dibromo-3-chloropropane) was determined to be a highly effective nematicide. Sodium methyldithiocarbamate (metam sodium) was introduced about 1956 and methyl isothiocyanate (MITC) mixed with D-D and released as DD-MENCS about 1960. By the mid 1960s, soil fumigation had become a common practice for controlling nematode and disease pests. In 1965, an integrated approach to soil pest management was introduced which combined broad spectrum soil fumigation using methyl bromide and chloropicrin with plastic film mulch to cover a raised plant bed for crop production. Soil fumigation with methyl bromide was quickly adopted and for over 40 years, preplant soil fumigation with methyl bromide and chloropicrin has been the principal fumigant used for soil-borne pest and disease control for many fruit and vegetable crops around the world.

As indicated previously, many different soil fumigant compounds have been field evaluated for soil-borne pest and disease control. Six soil fumigants have been used at one time or another for crop production including methyl bromide-chloropicrin; DD-MENCS (chlorinated C3 hydrocarbons (80% D-D) + 20% methyl isothiocyanate [Vorlex]); sodium methyl dithiocarbamate (Vapam); 1,3-d (1,3-dichloropropenes [D-D, Telone]); EDB (ethylene dibromide) (Dowfume, Soilfume, W85); and DBCP (1,2-dibromo-3-chloropropane [Nemagon, Fumazone]). Unfortunately, many of these fumigants have been found to leave toxic residues in the soil and/or pose potentially serious risks to humans and/or to the environment. For example, in 1977, a high incidence of male sterility was reported among workers at the Occidental Petroleum plant in Lathrop, California, USA, where DBCP was manufactured. In May 1979, DBCP was discovered in groundwater in California, and was shortly thereafter withdrawn from most of the global marketplace. In 1984, EDB was similarly banned for environmental contamination. In 1990, 1,3-d was restricted from use in California due to potentially harmful air quality concerns resulting from high soil emissions during spring fumigations. It was restored for use in 1994 after improved application and soil containment methods were tested and implemented. Most recently, methyl bromide was implicated as a significant contributor to ozone depletion. In 1993, it was mandated for phase-out of production and use by January 1, 2005, in developed countries and a phase-out deadline of 2015 in developing countries. Recent actions by state and federal regulatory agencies suggest that additional restrictions, including buffer zones that will restrict places of fumigant use, and added forms of personal protective equipment worn by field workers, will serve to limit use of any of the remaining fumigants in the USA, and perhaps elsewhere.

Fumigant Spectrum of Activity

Since their introduction to agriculture, many different soil fumigants have been evaluated in field research trials to characterize pest control efficacy and crop yield response. The results from many of these research trials have provided the basis for overall generalization of pesticidal activity for the various fumigant chemicals. In general, this research has repeatedly demonstrated methyl bromide or methyl iodide to be very effective against a wide range of soil-borne pests including nematodes, diseases, and weeds. Chloropicrin has proved very effective against diseases but seldom nematodes or weeds. Although with some suppression, bacterial pathogens have not been satisfactorily controlled by any of the soil fumigants. Historically, most of the research conducted to evaluate 1,3-dichloropropene (Telone™; Dow AgroSciences) has repeatedly demonstrated consistently effective nematode control with little or no control provided for soil-borne disease or weeds. Metam sodium, metam potassium, and dazomet are all non-selective preplant soil fumigants which provide measures of fungicidal, herbicidal, insecticidal, and nematicidal activity. Pest control efficacy of metam sodium and metam potassium have proved inconsistent, performing good to excellent in some trials, while poor in others. Field research continues to evaluate modification of rate, placement, and improved application technology to resolve problems of fumigant inconsistency with these compounds.

Because of their target pest specificity, many of the soil fumigants are formulated together or co-applied to increase their overall level and spectrum of pest control. For example, chloropicrin is used both as a stand-alone soil fumigant, as a chemical warning agent in formulation with methyl bromide, and in formulation with 1,3-d to increase its disease control effectiveness. Examples of co-formulated or sequential application include 1,3-dichloropropene plus chloropicrin formulated together as Telone C17 or Telone C35, or sequential applications involving a broadcast application of 1,3-dichloropropene, followed later by chloropicrin and/or metam sodium in separate soil applications. Given the general lack of herbicidal activity associated with many of the fumigants, separate application of one or more herbicides may be required to achieve effective weed control (Table 16).

Physical and Chemical Properties

After application to soil, the fumigants penetrate into the soil and quickly become partitioned in liquid, gas, and adsorbed soil phases. Initially, and immediately after soil injection, fumigant movement in soil is driven by density and pressure gradients from a narrow, linear band of concentrate product deposited directly below the chisel path. As the fumigant's partial pressure falls, soil movement via mass flow becomes less important than by simple gas diffusion processes. Fumigant persistence, volatility, and degradation are influenced by many factors, including chemical properties, soil properties, and environmental conditions. A listing of the physical and chemical properties of the primary soil fumigants is provided (Table 17).

Volatilization continues as long as the fumigant remains in soil and upward movement of the fumigant occurs as long as a concentration difference exists between the soil surface and soil atmosphere. Henry's Law Constant characterizes the equilibrium distribution of dilute concentrations of volatile, soluble chemicals between gas and liquid phases, and is used to describe the mobility potential of volatile organic compounds through soil as a gas. High soil mobility in soil is due to vapor diffusion, large Henry's constant and low soil sorption. Vapor pressure is a measure of the tendency of a fumigant compound to change into the gaseous or vapor state. The temperature at which the vapor pressure at the surface of a liquid becomes equal to the pressure exerted by the surroundings is called the boiling point of the liquid. The lower the boiling point, the more volatile the fumigant compound. Hot and dry soil conditions favor more rapid escape of fumigants like methyl bromide, methyl iodide, and chloropicrin, particularly within surface soil horizons.

Methyl bromide is a colorless, odorless, liquid under certain conditions of pressure and temperature. At temperatures below the boiling point of 3.6°C, or within the confines of a pressurized cylinder, methyl bromide exists as a liquid. At temperatures typical of field application (26–32°C), methyl bromides rapidly volatilizes to a gas once

Soil Fumigation, Table 16 Generalized summary of the effectiveness of various soil fumigants for nematode, soil-borne disease, and weed control (L = liquid; G = Microgranule)

Fumigant	Nematode	Disease	Weed
Methyl bromide (L)	Excellent	Excellent	Good to excellent
Chloropicrin (L)	None to poor	Excellent	None to poor
Methyl iodide (L)	Good to excellent	Good to excellent	Good to excellent
Metam sodium (L)	Poor to excellent	Poor to good	Poor to good
Dazomet (G)	Poor to good	Poor to good	Poor to good
1,3 Dichloropropene (Telone II) (L)	Good to excellent	None to poor	Poor
1,3 Dichloropropene + chloropicrin (17%) (Telone C17) (L)	Good to excellent	Good	Poor
1,3 Dichloropropene + chloropicrin (35%) (Telone C35) (L)	Good to excellent	Good to excellent	Poor
Metam potassium (L)	Poor to good	Poor to good	Poor to good

Soil Fumigation, Table 17 **Physical and chemical properties of various soil fumigants (physical state: L = liquid; G = Microgranule)**

Fumigant compound and physical state	Boiling point (°C)	Molecular weight	Density (g cm^{-3})	Vapor pressure (mmHg)	Henry's constant	Specific gravity	Soil degradation half-life (d)	Solubility (mg L^{-1})
1,3-Dichloropropene (L)	120	111	1.22	28	0.06	1.218	3–5	2,250
Chloropicrin (L)	112.4	164	1.69	18	0.07	1.692	1–2	2,270
Methyl bromide (L)	3.6	95	1.73	1,420	0.25	1.732	12–20	13,400
Methyl iodide (L)	42	142	2.28	400	0.22		20–40	14,200
Metam sodium (L)	112	129	1.21	0.4	0.01		25 min	578,290
Metam potassium (L)	114	145	1.27	24				
Dazomet (MG)	–	284		–	–	–		30
Methyl isothiocyanate	112	73	1.05	20	0.01	–	4–5	89,400

released from the pressurized cylinder into the ambient pressure of air or soil. With such a high vapor pressure (1,420 mmHg), methyl bromide is capable of very high mobility through open air passages among soil particles. Water may effectively block efficient diffusion in soil. Without impediment, methyl bromide can quickly move to the soil surface and escape into the atmosphere. With such rapid soil diffusion, some form of containment is usually necessary to hold highly volatile gases like methyl bromide, chloropicrin, and methyl iodide in soil for sufficient time and concentration to achieve satisfactory pest and disease control. Factors which affect containment include use of plastic mulch, thickness and permeability properties of the mulch, soil injection depth, soil bulk density, and soil water content.

Chloropicrin is a small, colorless, single-carbon molecule (mw 164.4) with a moderate vapor pressure (18.3 mmHg) and high boiling point (112°C). Chloropicrin diffuses readily through soil, but the diffusion and dissipation process is slower than that of methyl bromide. Chloropicrin is also a strong lacrimator (tear producer), which makes it useful as a warning agent to field workers if it escapes from the soil. Released to the atmosphere, chloropicrin photodegrades at a half-life of 20 days. Like chloropicrin, 1,3-d has an intermediate vapor pressure of 28 mmHg and water solubility of 2,250 mg/L. In general, the entire soil fumigant process for 1,3-d (volatilization, diffusion, dissipation) is about three to five times slower than that of methyl bromide, and all phases of the process can be significantly delayed by rainfall or irrigation events that saturate soil air spaces with water. Under conditions of low soil temperature and/or high soil moisture, outward diffusive movement is retarded and soil dissipation is protracted if soils remain cold and wet. In some instances, it may be necessary to disturb the soil to encourage soil fumes of 1,3-d to escape before transplanting or seeding.

Dazomet is a granular product that must be mixed mechanically with the soil and activated with water to release the bioactive degradation product, MITC. Metam sodium and metam potassium are both very water soluble compounds with low vapor pressure. Both become activated in water and also quickly degrade to MITC at rates determined by soil moisture and temperature conditions. Metam sodium and metam potassium differ from other soil fumigants like 1,3-d, methyl iodide, methyl bromide, and chloropicrin that principally move through open air passages within soil. Both metam compounds are not as volatile and move in the soil profile with soil moisture. In general, movement in soil is most efficient in the water phase than gas phase.

Mode of Action and Lethal Dose

Fumigant mode of action refers to the lethal action of a chemical on specific and vital life processes of an organism. For example, a broad-spectrum fumigant can penetrate the body wall of a nematode directly and does not have to be eaten to be effective. Once inside the body cavity of the nematode, different internal organs are affected since they are bathed by body fluids containing the fumigant compound. Metam sodium and potassium are very soluble compounds which become activated in water. The fumigants and their products interfere with many different vital processes, including enzymatic, nervous, and respiratory systems. Death of the nematode is rapid under these conditions, and development of tolerant or resistant populations to the chemical are unlikely because so many integral bodily functions are simultaneously affected. In general, fumigant concentration in internal body fluid frequently reaches equilibrium with soil concentrations within about 30 min to 4 h. In some cases fumigant concentration may accumulate to much greater levels within the nematode than in soil.

In general, the lethal effect of a fumigant is determined by two components. The first is concentration (C) of the fumigant in soil air or soil solution, usually expressed as parts per million (PPM). The second is the length of time (T) the pest organism is exposed, expressed in minutes, hours or days. The level of pest control is then related to dosage, the amount of fumigant pesticide placed in the environment of the soil-borne pest for a known length of exposure time (concentration X time). Total exposure is the sum of CT products. Computed in this way, the cumulative dosage or concentration-time index (CT), is often used as a criterion with which to evaluate the effectiveness of soil fumigation. For most organisms, there is a concentration level below which kill is not obtained regardless of the length of exposure. For most nematodes, long exposures to low concentrations of fumigant nematicides above the minimum concentration appears to be more effective than short exposures to higher concentration.

Fumigants move through soil air, dissolve in the soil water and kill in the soil water. Fumigants are volatile substances and change into gases upon injection into the soil as liquids. The vapors can only move through the continuous soil air space. Pest and disease organisms normally exist within surface films of water surrounding soil particle grains. Even as fumigants move through open air passages, fumigant molecules dissolve into these surface water films and establish a dynamic equilibrium, moving back and forth from the air to the water phase as the fumigant diffuses through the soil mass. That portion of the fumigant dissolved in the soil water establishes the concentrations responsible for the kill of most soil-borne organisms.

In practice, fumigants are commonly injected through a series of uniformly spaced shanks into soil. As the liquid volatilizes, gases begin moving in mass flow, diffusing outward in all directions from the point of injection. Because diffusion is greater in air above the soil surface, upward mass flow and diffusion is usually greater than downward movement, and much of the gas may escape the soil and enter the atmosphere. As the fumigant front moves through soil, gaseous molecules are adsorbed to soil particle surfaces, redissolve into soil solution, and fill empty air spaces between soil particles. Maximum fumigant concentration decreases as do the sums of CT products with distance from the point of injection. Eventually, with time and distance, concentrations fall below an immediate killing level. The number of pests or disease propagules killed by fumigant treatment within these areas depends on the number of CT units which develop within the fumigant treated zone. The relationship between fumigant application rate and pest control efficacy is therefore not only a measure of fumigant toxicity but chemical dispersion as well. If dispersal is good, increases in fumigant application rates will result in higher CT values and provide control to a greater soil volume. If dispersal is poor, increases in application rates will not provide control to a larger soil volume. Reducing volatilization losses from soil is an effective way in which to increase CT values and improve fumigant pest control efficacy. It is for this reason that water seals and impermeable plastic mulches are used to increase fumigant diffusion resistance near the soil surface. This serves to promote both downward diffusion of the fumigant and to enhance residence time and gas phase persistence in soil.

Factors Affecting Efficacy

Various edaphic, environmental, biological, and cultural factors are known to directly influence fumigant treatment performance and consistency. Regardless of application method, fumigant efficacy is highly dependent upon dosage, uniform delivery, and soil distribution. Prevailing soil and climatic conditions are also very important determinants of gas phase movement in soil, and thus pest control efficacy and crop response.

Soil Moisture

Once injected into soil and at temperatures above 15°C, most fumigants vaporize readily into a gas and diffuse through open soil pore space. Soil moisture content is important in this regard, primarily as it relates to the availability of continuous pore space. Soils that are too moist inhibit extensive diffusion through soil. Fumigants can move as much as 10,000–30,000 times faster in soil air than they do in the soil water. Soils that are too dry promote the rapid escape of gases from soil into the atmosphere. As a soil changes from dry to field capacity, the amount of fumigant in the soil water increases and the amount in the soil air decreases. In the case of a saturated or wet soil, the fumigant will not move through the soil as a gas. Soils with a high water table effectively block downward diffusion and limit depth of pest control. In general, good fumigation conditions exist when the soil can be compressed in the palm of a hand to form a ball that breaks apart with slight finger pressure. If the soil ball does not break apart easily, it is likely too wet for fumigant treatment.

Some fumigants, like 1,3-d, are more vulnerable to high soil moisture conditions. As a soil-injected liquid, 1,3-d slowly volatilizes into a gas that then moves through unrestricted air space. It is the unrestricted movement of 1,3-d through soil air spaces three dimensionally that defines treated soil volume and the overall zone of pest control. Any soil zone in which water fills open pore spaces between soil particles, or where soil particles are compressed and closely compacted, will inhibit 1,3-D diffusion. High levels of rainfall or irrigation can thus potentially reduce 1,3-d treatment efficacy by filling open pore air space before, during, or even after fumigation has been completed. This reduced efficacy can occur via containment (trapping the liquid, preventing further volatilization, movement and degrading the product via hydrolysis), or by inhibiting unrestricted movement from the chisel stream flow of injected product. Because of its differences in vapor pressure compared to other fumigants, 1,3-d requires much more consideration of appropriate soil preparation and moisture condition to ensure satisfactory performance in the field.

Soil Temperature

Temperature is also important as it relates to soil moisture, because it directly influences the fumigant vaporization rate in soil. As temperature increases, so then does the vaporization rate of the fumigant. The importance of soil moisture and temperature to product efficacy cannot be overemphasized. For example, when applied to dry, sandy soil under conditions of high air and soil temperatures, substantial losses of fumigants from soil can occur. A change in soil temperature also changes the solubility of the soil fumigants in air and water. More fumigant is dissolved in the soil water at 4°C than at 26°C; the solubility of a fumigant in the water increases at lower temperatures, whereas the percent of the fumigant in soil air decreases. The decrease in the amount of fumigant in the soil air occurs because the cold soil results in slower movement of the fumigant s compared with warm soil. It is important, therefore, that appropriate conditions of soil moisture, temperature, and land preparation are present at the time of fumigation to optimize outward diffusion and soil retention of any soil fumigant. In general, moist (not wet) soils of a temperature between 15 and 26°C are usually considered ideal for soil fumigation.

Soil Texture

The ability of a fumigant to move throughout the soil profile, and therefore its efficacy, also varies with soil type. Diffusion of a fumigant through fine textured soils such as silt or clay is a slower and much more difficult process than diffusion through a coarse textured soil like sand. As a result, a clay or silty loam soil should be quite dry prior to treatment, whereas a very sandy soil can be quite wet. Any soil condition that restricts fumigant diffusion or favors rapid escape will affect the overall performance of soil fumigation.

Plow, rip or otherwise till the soil to the depth to which effective treatment is required. The soil should be worked until free of clods or large lumps. Residue from previous crops should be worked into the soil to allow for decomposition prior to fumigation. Soil moisture should be adequate for seed germination. Coarse textured soils can be fumigated with higher moisture content than fine textured soils. For best results, soil should be kept moist for at least 4 days prior to treatment. Do not fumigate if the soil temperature is below 10°C. For best results, fumigate when soil temperature is 15–26°C at a depth of 15 cm.

Compaction, Clods, Organic Matter

After the fumigant is injected into the soil, it vaporizes and a portion of it moves upward. As it approaches the soil surface, it tends to move more rapidly because of the drier conditions and increased porosity. If the surface is sealed by compaction or with some type of sealing device, loss through the surface will be reduced. A clod represents two problems in control. A compacted soil clod will not allow the fumigant to penetrate and control the organisms within the clod, and the soil surface is very difficult to seal if there are large clods on the surface. Organic matter in the soil also affects the mobility of the fumigant in the soil. Soil fumigants are readily absorbed by organic matter. Also, undecayed plant remains can foul application equipment and puncture plastic film. If possible, organic matter should be allowed to decay before application. Fumigant rates should be increased where soils contain large amounts of organic matter. Weed control is greatly influenced by soil conditions. Soil too wet, too dry or cloddy will reduce the level of control achieved.

The presence of a compacted zone, hard pan, or traffic layer can impede downward diffusion and overall performance of fumigant treatment. As the soil becomes more and more compacted, the particles make physical contact, and the water films bridge over resulting in an impermeable condition. Thus, compacted soil layers cannot be effectively penetrated with fumigants. However, this same principle can be utilized to hold fumigants in the soil by compaction of soil particles near the surface, providing a type of seal by closing off the soil air spaces. To resolve problems of compaction, deep tillage is recommended.

Phytotoxicity

All of the fumigants, including the gas and water phases of these fumigants, are toxic to plants. Soil dissipation and the persistence of toxic residues are strongly influenced by environmental conditions. Any change in soil condition that promotes a cooling and/or wetter soil condition will typically delay dissipation of a fumigant compound. As a result, soil applications must always be made well in advance of a seeding or planting date to ensure sufficient time for dissipation of fumigant residues from soil. The problem is usually most severe with fumigants of low vapor pressure, where longer term planning horizons must be adopted to avoid problems of phytoxicity or to avoid long unscheduled delays in planting after the plants have arrived from the nursery. Growers that use fumigants, typically adopt planning horizons that consider beginning field preparation and soil application 2–3 weeks earlier than normal to avoid problems of potential phytotoxicity that may result from use of impermeable mulches, or unexpected cold fronts or storm(s) producing abundant rainfall.

Fumigant Containment

Historically, most of the field research conducted to evaluate the use of soil fumigation has repeatedly demonstrated effective soil-borne pest and disease control when applications were made under optimal soil conditions, uniformly applied at the appropriate dosage and depth, and using containment systems that prevented rapid escape of gases from soil. Any system designed to provide containment of fumigant gases must first insure immediate closure and seal of chisel traces as they are produced behind the tractor moving across the field. Left undisturbed, the chisel traces act as chimney vents for volatilizing fumigant gases. This can be accomplished with press wheels behind the chisel or chisel injections immediately in front of bed forming equipment. The treated field area may also be rolled to compact surface soil, so as to increase soil density and reduce air passage size and volume. Irrigation is also often applied over the top of the treated area or rolled surface to form a surface water seal to further inhibit fumigant outgassing from soil. In some instances, repeated irrigations may be necessary to manage fumigant containment and offsite movement of fumigant gases.

After a fumigant is applied, the treated soil may also be tarped with a plastic polyethylene mulch to provide an additional measure of fumigant containment to soil. The plastic mulches, often a prerequisite for fumigant use, are not only a barrier in themselves but act as a condensation surface for the formation of water droplets that redeposit to soil as a water layer, adding another barrier to soil volatilization loss. There are a range of different mulches which can be used to reduce fumigant emissions from soil. Low density polyethylene (LDPE) or high density polyethylene (HDPE) tarps have been extensively used in combination with soil fumigation as a soil covering to reduce fumigant emissions from soil. Unfortunately, the barrier properties of LDPE and HDPE to fumigant gases are quite poor and, depending on the fumigant, much of it may quickly escape the soil. In general, the permeability of plastic mulch to a fumigant gas is directly related to its thickness, density, and chemical composition. Significant resistance to fumigant outgassing has been achieved with use of virtually impermeable mulch films (VIF). VIF mulches are typically manufactured as multi-layer films composed of barrier polymers such as ethylene vinyl alcohol (EVOH) or polyamide (nylon) sandwiched between other polymer layers (typically LDPE) or have metalized coatings to reduce the amount of fumigant that can move through the film and into the atmosphere.

Compared to LDPE, certain VIF films are over 20,000 times less permeable to fumigant compounds and, as a result, significantly increase the residence time of fumigants in soil. Because of their excellent barrier properties, fumigant application rates can often be reduced as much as 50% without loss of pest control activity or crop yield. The mulch, although not completely impervious to fumigant gases, reduces the dissipation rate of gases into the air that increases the overall efficacy of the treatment by subjecting soil pests to greater cumulative dosages levels of the fumigant.

Due to increased environmental and regulatory scrutiny, use of VIF or high barrier plastic mulch films are likely to become mandated for use of any soil fumigant in the future. Use of these more gas-retentive mulches will, however, require changes in field application and soil injection equipment to insure accurate and uniform dispensing of such reduced volumes and application rates of the fumigants. These required changes include reduced rate flow meters, smaller delivery tubing size, installation of sight gauges to monitor flow uniformity among chisel streams, and installation of low pressure gauges upstream of flow divider to monitor and insure adequate system back pressure.

Field Application Equipment

Soil fumigants are applied using several methods. Liquid fumigants can be applied by directly injecting them into the soil using shanks or chisels, and in some cases by injection into the irrigation system (chemigation). Fumigants are formulated and applied to soil in a number of ways. The portion of the field that is fumigated can also vary. For example, in the production of some crops, the entire field is treated, and this represents an overall or broadcast treatment. In other situations, fumigants are only applied in the plant row or raised plant bed. In this situation, only a portion of the field is treated and this is termed a strip, band, or in-row treatment. Most liquid fumigants with high vapor pressure are shanked or knifed into the soil. Narrow knifelike shanks are tractor-drawn through the soil at the required depth to inject the fumigant into soil. Metal delivery tubes attached to the trailing edges of the shanks provide the conduit for injection to soil. Delivery tubes release the fumigant in the bottom of the furrow made when pulling the shank thorough the soil. Fumigant flow rate to the soil shanks is regulated using various combinations of pressure, metering valves, nozzle orifices, shank spacing, and speed of travel.

Metam sodium, metam potassium, and emulsified concentrate formulations of 1,3-dichloropropene, chloropicrin, and methyl iodide can also be metered into irrigation systems and applied through a low volume trickle or drip irrigation system. Metam sodium and potassium have also been broadcast applied by overhead sprinklers. The other fumigants are liquids with high vapor pressure, so they are usually stored and applied as liquids (under pressure) and begin to vaporize shortly after injection in the soil. It may also be applied to field or row crops during preplant stages via chemigation, soil broadcast treatment, soil band treatment, soil-incorporated treatment, and soil-injection treatment. Chemigation is the most common method of application for some fumigants like metam sodium or metam potassium.

Because of the slow diffusion of MITC as a gas and high affinity for the water phase, continuous delivery in irrigation water following premixing has generally resulted in more uniform soil distribution with enhanced nematode control and crop yield when compared with conventional chisel injection methods. The proximity of the plant to the drip tube has also been demonstrated to be very important in terms of defining pest control efficacy and plant growth response with a chemigated fumigant. Given the sandy nature of some soils, narrower bed widths, drip tubes with closer drip emitter spacing (likely in the range of 8–12 in.), and planting practices that place plants closer to the drip tube may need to be adopted to more effectively utilize the drip tape for chemigational purposes. Soils and grower production practices differ markedly, and these differences in soil type, compaction, and depth to restrictive layers can all affect water movement and the final distribution of chemicals. The presence of a shallow compacted traffic layer severely restricts downward penetration of drip water. In general, the average depth, width, and cross sectional area wetted by drip irrigation water increases with total water volume applied. For a given water volume, the use of two tapes per bed increases spatial distribution of irrigation water simply because of the spacing between drip tubes and the increased number of emission points along the bed.

As a microgranule formulation, dazomet is typically applied to the soil surface using a Gandy type drop spreader, and then watered into or mechanically incorporated into soil. New soil application technologies are capable of multiple operations, including drop spreading, rotovator incorporation via L-shaped tines, followed immediately by a power-driven roller to optimize containment of methyl isothiocyanate (MITC) gases after soil incorporation. Power rolling serves to compress, smooth, and seal the soil surface to minimize escape of MITC gases. After application, incorporation, and rolling, irrigation is applied to provide another form of surface water seal to escaping gases, as well as to convert (activate) dazomet to the bioactive compound, MITC. Because of typical tractor power requirements, incorporation depths are often limited to 15 cm or less. In general, biocidal activity derived from conversion of dazomet to MITC is directly related to Dazomet application rate and limited by incorporation depth. Dazomet's physical characteristics (ultra-fine powder) also impose application limitations because it is extremely corrosive to equipment, vulnerable to drift, and application equipment must be tightly sealed to limit spillage to areas of application.

Other fumigants, like methyl bromide, chloropicrin, and 1,3-dichloropropene, are premixed and sold in compressed gas cylinders. In most cases, these fumigants are shank-injected into the soil 20–60 cm deep using a positive pressure-closed system in which the fumigant cylinders are pressurized with nitrogen. With this system, an inert gas is used to propel liquid flow from the cylinder through the metering systems and through armored lines to the rear shanks or chisels, exiting through a steel delivery tube welded to the back side of the shank or chisel. Deep placement is not only a requirement of the fumigant label but is essential for prolonged fumigant retention in soil. In general, the closer to the soil surface a fumigant is applied, the faster the outgassing or escape from soil and, in general, the poorer the pest control response. A plastic, polyethylene tarp may be laid down over the soil immediately behind the shanks of the injection equipment to provide a diffusion barrier for containment of the fumigant.

Application

As indicated previously, an inert gas (nitrogen) is used to maintain constant pressure to the fumigant cylinder to ensure a constant flow of the fumigant from the cylinder to the metering device during fumigant application. In-line valves downstream of the fumigant cylinder are then used to actually control the delivery rate of the fumigant to and through the flow meter. The sole function of the meter is to act as a simple gauge to indicate the percentage of maximum flow (0–100%) discharging from the meter. Many factors affect the actual flow rate of a liquid through the flow meter. For example, all soil fumigants have different densities (specific weights) and are heavier than water. In general, the denser a liquid, the higher its specific gravity, and the more slowly it will flow through a flow meter compared to water. Because of these differences in specific gravity, the actual capacity of the flow meter will change, and thus must be corrected to insure application accuracy with the different fumigants. Miscalibration of the flow meter and determination of field application rate are two of the most common causes of fumigation failure. Other causes of inconsistency are due to inappropriate soil conditions, application procedures, or equipment. In general, uniform delivery and distribution among soil chisels can only be achieved with proper fumigant metering, delivery tube sizing, and maintenance of manifold back-pressure at the flow divider.

Risks to Environment and Human Health

A considerable amount of research has been conducted to evaluate food and worker safety and risks to the environment. For example, the results of numerous plant metabolism studies generally confirm that there is no reason to expect unhealthful residues in or on any raw agricultural commodity when any of the fumigant compounds are applied as a preplant soil treatment according to label directions. As a result, none of the fumigants have required the establishment of food tolerances for US federal pesticide registration. There are, however, other key concerns that have been consistently expressed by state and federal regulatory agencies. These concerns generally involve both dermal and inhalation exposure by field workers. Also, those people in the general population living and working in close proximity to fumigant treated fields are susceptible to inhalation exposure.

Methyl bromide is colorless, tasteless, and odorless except at extremely high concentrations. Because methyl bromide is a gas at room temperature, respiratory problems through inhalation are the most common and serious injury. Methyl bromide is poorly absorbed through the skin, although direct contact with the liquid phase of methyl bromide can cause skin blisters and diffuse through the skin to enter the circulatory system. In the body, it may cause severe lung irritation and cumulative damage to the heart, kidneys, and nervous system. Accidental overexposure to methyl bromide may result in acute (short term) or chronic (long term) poisoning.

Chloropicrin is a colorless oily liquid, alternatively identified as tear gas. Concentrations of 0.1 ppm or greater generally result in painful irritation to the eyes in three to 30 s. Since chloropicrin causes so much irritation of the eyes and upper respiratory tract, exposed individuals are unlikely to inhale a quantity of fumigant capable of damaging the lungs. Methyl bromide is not so irritating to the nose, eyes, throat, and bronchi, but causes serious injury to the cells lining the fine air sacs of the lung. The onset of symptoms of methyl bromide poisoning may be delayed several hours or days following exposure. Thus, it is more likely than other fumigants to induce pulmonary edema (fluids in lungs), a major cause of death from overexposure. In practical terms, mixtures with chloropicrin are always used in commercial agriculture to minimize the insidious effects of methyl bromide.

For both metam sodium and potassium, the principal routes of entry include skin and eye contact and inhalation. In general, the principal signs of dermal exposure include moderate to severe skin irritation depending on solution concentration and length of exposure. As with all MITC-generating fumigants, overexposure to MITC may cause irritation of mucous membranes of the lungs, bronchitis or pneumonia or other symptoms of respiratory distress. Because of this, various types of eye, skin and respiratory protection may be required for field workers.

All of the fumigants continue to be closely scrutinized by local, state and federal regulatory agencies for worker safety and risk of exposure. Following application, many of these fumigants can volatilize into the atmosphere and be transported off-site. This can lead to inhalation hazards and exposures to the fumigants in the general public and to workers following application. New rules and regulations governing use of fumigants within the USA continue to change. Currently, the US EPA is considering new requirements for personal protective equipment to mitigate possible contact and inhalation exposures. These new changes may require field workers to wear NIOSH-approved respirators, and to mitigate dermal exposures, workers may be required to wear adequate protective clothing, which, dependent upon the fumigant, may include coveralls, impervious gloves, boots, face sealing goggles, and/or other protective headgear.

Reference

Anon (2004) Proceedings of the Sixth International Symposium on Chemical and Non-Chemical Soil and Substrate Disinfestation. ISHS Working Group on Soil Borne Pathogens, Corfu, Greece.

Soil Mites (Acari: Oribatida and Others)

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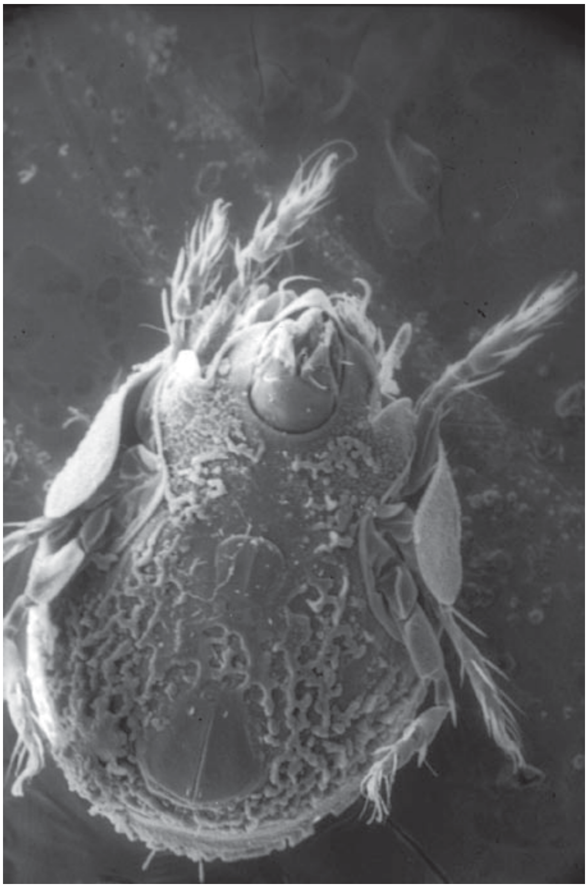
Soil is a complex of living and non-living components which are present in different combinations. Small arthropods, including several groups of mites, contribute to the humus fraction and permit complexes of soil organisms to exist. Even though the role of mites in soil mixing may be small in comparison with that of larger invertebrates such as earthworms, insects, crustaceans and millipedes, mites exercise an important function in mineral turnover, vegetation succession and as decomposers of organic matter. Densities of 50,000–250,000 or more mites per square meter may be found in the upper layers of soil. Dozens of species may be found in a small area when soil is rich in organic material such as decaying vegetation, dung or animal remains. In combination with microflora, which the mites may disperse, soil mites help in decomposing organic matter which they cannot digest. Much of the work on soil mite taxonomy, biology and ecology, including their role in nutrient cycling and fertility-humification processes, has been carried out in Europe.

Mites in the Suborder Oribatida (=Cryptostigmata), also called moss mites or beetle mites (Figs. 74–75), are distinctive soil mites, ranging in size from 200 to 1,400 μm. They are common in soils that are relatively undisturbed and have a high organic content. Some species of Oribatida may be found on the trunks of trees or on low-growing vegetation. Oribatida species can even be found associated with roots of plants very deep in the soil. There are an estimated 150 families in the Oribatida in 10,000 species in 1,100 genera. The name “beetle mites” is a result of the fact that many have hard, dark brown exoskeletons and somewhat resemble miniature beetles. The term moss mites is due to the fact that they are often found in mosses.

A summary of their biology is as follows: Sperm transfer is indirect, and mating takes place when males deposit spermatophores that are taken up by the female (indirect sperm transfer). Spermatophores are stalked and often deposited in groups. Many are destroyed by being eaten. Copulation has never been observed in oribatids and parthenogenesis (reproduction without mating) is known in some families. Females typically deposit one to twelve eggs at a time. After mating, females deposit oval eggs singly or in small clumps in old exuviae, the axils of moss bracts, under detritus, and in the soil pores. Often the female retains a number of eggs until all are mature and she deposits them at once. There is a prelarva, larva, three nymphal stages and the adult. The length of time to reach adulthood depends on temperature, but is relatively slower than that of other mite suborders; smaller oribatid species have a shorter development time and life span than larger species. Rate of development also is influenced by whether the diet is adequate and whether the mites are crowded. In general, small species may have several generations a year (compared to one generation a week for the two-spotted spider mite, a plant-feeding pest in the suborder Prostigmata). Larger species may have one generation per year and some oribatid species may require several years to complete their life cycle in cool climates.

Soil Mites (Acari: Oribatida and Others), Figure 74 A soil-dwelling oribatid mite, *Galumna* sp. (Galumnoidea), viewed from below.

Soil Mites (Acari: Oribatida and Others), Figure 75 **A soil-swelling oribatid mite, *Haplophorella cucullata* (Ewing), side view (photo by Roy Norton, SUNY, Syracuse).**



Soil Mites (Acari: Oribatida and Others), Figure 76 **A soil-dwelling oribatid mite, *Ceratozetoidea pteromorphae*, viewed from below.**

Oribatids chose optimal temperatures (or at least avoid unfavorable temperatures). Humidity requirements are species specific; some are able to survive for days at low relative humidities while others need higher relative humidities to survive. Salinity and soil pH are important; soils rich in organic matter have a high pH.

Oribatid mites are microphytophages, feeding on pollen, small pieces of algae, lichens, highly decomposed humus, and fungal hyphae. They can also be macrophytophagous, feeding on dead plant tissues, parenchyma of needles, or directly on dead wood. Some are nonspecialized, feeding on leaf tissue and on fungal mycelia. The larger species are generally macrophytophagous or nonspecialized and thus play the main role in litter decomposition. Some oribatids prefer animal food and can be maintained on cricket powder in the laboratory. Some oribatids feed on the numerous nematodes in the soil. Laboratory rearing of some species can be accomplished with dried mushrooms, chopped lichens, decomposing leaves, or an artificial diet of dextrose and casein or brewer's yeast.

Only a few soil mite species have a direct role in altering soil morphology. Most exercise indirect effects through stimulation of microbial activity and distribution of spores. Pesticides can have a negative effect on nutrient cycling by permitting energy to remain bound up in undecomposed plant debris. Pesticides can positively affect nutrient cycling by killing predators of saprophagous arthropods, thus releasing detritus-feeding populations.

Species in the Oribatida are thought to be especially important decomposers of plant debris. On mulched plots, they make up 60% of the total arthropod species, compared to 8.5% on mowed or fallow plots. Distribution of microarthropods is irregular under annual crops, in part due to the effects of cultivation. Fewer mites are found in grasslands than in forest communities. Microarthropod distribution is influenced by water, pore space, oxygen saturation deficits, temperature variations, ground cover, fungi, flooding, cropping, cultivation, organic matter, disturbance, soil compaction, soil type and texture, predation, and feeding habits.

Oribatida serve as food for centipedes, symphyla, diplurans, spiders, pseudoscorpions, opilionids, ground beetles, and ants. The Oribatida also are fed on by beetles in the families Pselaphidae and Ptiliidae. Some birds, salamanders, frogs, skinks and other small lizards also may feed on oribatid mites. Oribatid mites may function as vectors of anoplocephaline tapeworms; moss mites are intermediate hosts for the transmission of cysticercoids of these tapeworms and 12 families, 25 genera and 32 species are confirmed vectors.

Mites other than species in the Oribatida also are found in the soil; Actinedida, Gamasida and Acaridida are present, although are not as numerous. Much remains to be learned about the role of the Oribatida, and other mite groups, in soil biology and ecology.

► Mites

References

Balogh J (1972) The Oribatid genera of the world. Akademiai Kiado, Budapest, Hungary

Evans GO, Sheals JG, MacFarlane D (1961) The terrestrial Acari of the British Isles. An introduction to their morphology, biology and classification. British Museum of Natural History Press, London, UK

Walter D, Proctor H (1999) Mites. Ecology, evolution and behavior. CABI Publishing, Wallingford, UK

Soldier Beetles

Members of the family Cantharidae (order Coleoptera).

► Beetles

Soldier Flies

Members of the family Stratiomyidae (order Diptera).

► Flies

Solenophages

Arthropods that feed at blood vessels, and specifically from small veins (contrast with telmohages).

Solitary Behavior

Showing none of the following traits of sociality: individuals of the same species cooperate in caring for the young; there is division of reproductive behavior, with more or less sterile individuals working on behalf of the fecund individuals; overlap of at least two generations in life stages contributing to colony labor, so that offspring can assist parents during some period of their life.

► Presocial
► Subsocial
► Communal
► Quasisocial
► Semisocial
► Eusocial Behavior

Solitary Midges

Members of the family Thaumaleidae (order Diptera).

► Flies

Solitary Parasitoid

A parasitoid that has nutritional requirements limiting the ability of the host insect to support but a single parasitoid.

Soma (pl., somata)

The cell body of a nerve cell. Also known as the perikaryan.

► Nervous system

Soldier

A member of the nonreproductive caste in social insects that contributes to the welfare of the colony through defense of the colony. Soldiers often bear an enlarged head and mandibles.

► Ants

► Termites

Somabrachyidae

A family of moths (order Lepidoptera) also known as Mediterranean flannel moths.

► Mediterranean Flannel Moths

► Butterflies and Moths

Somatic Cells

All the eukaryotic body cells except the germ line cells and the gametes they produce.

Somatiidae

A family of flies (order Diptera).

► Flies

Sooty Mold

A dark-colored fungus growing on the honeydew secreted by hemipterous insects, usually aphids or scales.

► Transmission of Plant Diseases by Insects

Sorosporella

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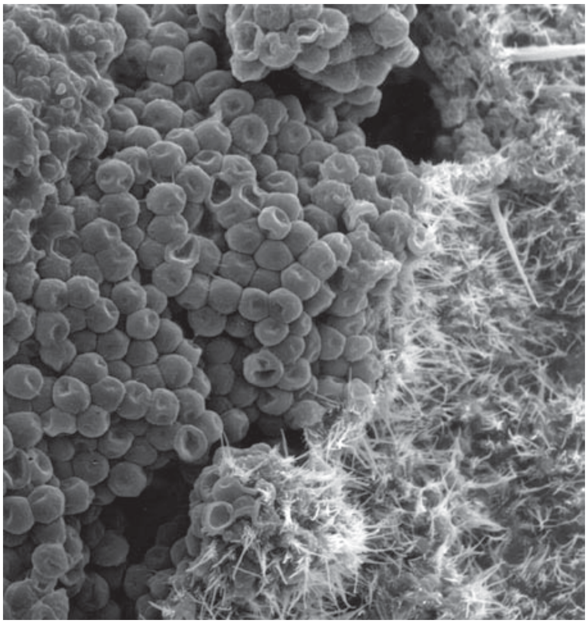
Sorosporella was first described from a coleopteran, *Cleonus punctiventris*, in 1886 by Krassilstschik, and then 2 years later from a lepidopteran by Sorokin. Krassilstschik named the fungus *Tarichium uvella*, while Sorokin called it *Sorosporella agrotidis*. In 1889, Giard suggested that these two genera were the same and combined the two names into *Sorosporella* uvella. Speare, in the early 1900s, wrote the only detailed descriptions of Sorosporella to date; included were his observations on phagocytosis of the hyphal bodies by hemocytes in cutworms, which constitute one of the first reports of cellular defense response in insects invaded by a fungal pathogen.

Sorosporella exists endogenously as globose, brick-red, thick-wall chlamydospores (Fig. 77) which are 6–10 μm in diameter. These structures form within the insect hemocoel from the yeast-like vegetative hyphal bodies and cohere into solid masses that, at maturity, may become dry and powdery, and then separate. *Sorosporella* germinates on water or various types of media. On Sabouraud maltose agar, the germinating chlamydospores produce a white mycelial mat with a synnematous-type growth sometimes evident. The mycelia generate conidiophores and phialides, which produce hyaline, ellipsoidal conidia approximately 1–1.5 μm in diameter. This conidial stage is known as the alternate state of *Sorosporella* and was identified as Syngliocladium. This is not a teleomorph-anamorph association since both genera represent asexual states. The laboratory-produced conidia were infectious to several different insects, but *Sorosporella-Syngliocladium* has never been seriously targeted as a biocontrol agent, especially in comparison to other more promising Hyphomycetes.



Sorosporella, Figure 77 **Scanning electron micrograph of chlamydospores produced in mole crickets infected with *Sorosporella*. The cuticle of the mole cricket has been peeled away exposing internal chlamydospores.**

References

Pendland JC, Boucias DG (1987) The hyphomycete *Sorosporella-Syngliocladium* from mole cricket, *Scapteriscus vicinus*. Mycopathologia 99:25–30

Petch T (1942) Notes on entomogenous fungi. Trans Br Mycol Soc 25:250–265

Speare AT (1920) Further studies of *Sorosporella uvella*, a fungous parasite of noctuid larvae. J Agric Res 18:399–451

Sound Production in the Cicadoidea

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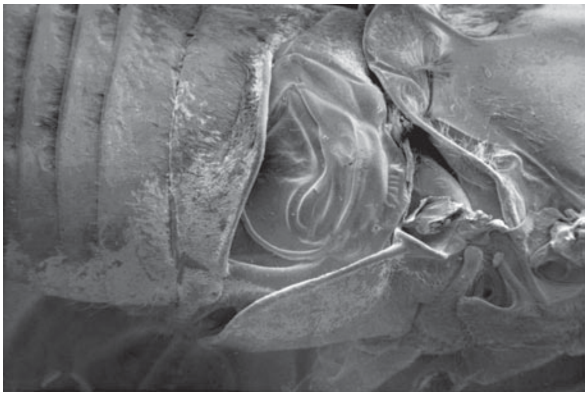
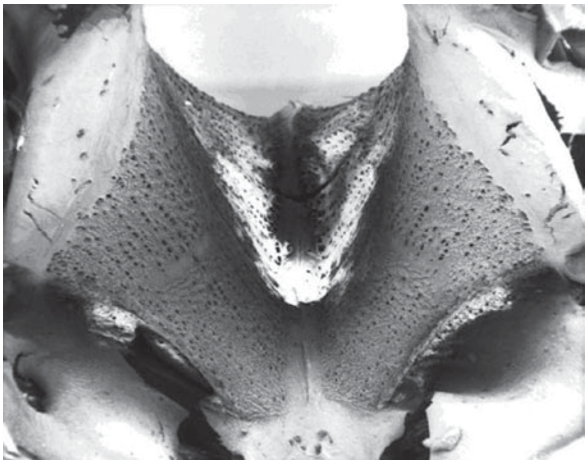
One of the characteristic sounds of summer is the calling of cicadas. The sounds cicadas produce are used in the attraction of mates, courtship, and as an alarm to startle potential predators. These sounds can be as intense as 109 dB at 50 cm, and choruses can be heard for more than a mile. Each species has a unique calling song and there are significant differences between the frequency and temporal patterns of species that share the same environment. Cicadas use three main mechanisms to produce sound.

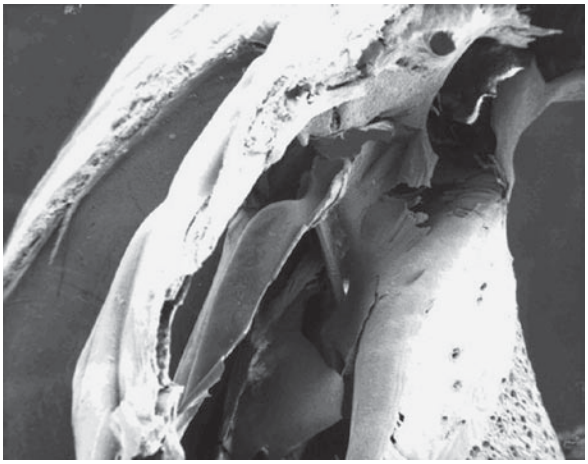


Sound Production in the Cicadoidea, Figure 78 **Right timbal of *Beameria venosa* (Uhler). The operculum can be seen extending under the ventral surface of the abdomen. The wings have been removed for clarity.**

The primary sound production mechanism in cicadas is the timbal organ (Fig. 78). The timbal is a chitinous membrane located on the dorso-lateral surface of the first abdominal segment of most male cicadas. The timbal contains a flattened area, termed the timbal plate, and several ribs that help to strengthen the timbal. The timbal produces sound pulses when it is deformed by a timbal muscle. The timbal muscles are located within the abdomen attached to a support structure (the chitinous V) on the ventral side and is attached dorsally to the timbal plate by an apodeme. To produce sound, the timbal muscle contracts, pulling on the timbal. Eventually the muscle force is sufficient to buckle the timbal plate and continued muscle force leads to buckling of the timbal ribs. Sound pulses are produced when the timbal plate and ribs buckle. In addition, some timbals will produce sound when they return to their resting position as the timbal muscle relaxes. Rebound of the buckled timbal to a resting state is facilitated by the rubber-like protein resilin that is incorporated into the timbal. The rate of timbal muscle contraction determines the sound pulse repetition rate for each species. The frequency of the sound that is produced by a particular species is primarily determined by the resonance of the timbal organ. There is a good inverse correlation between body size and the frequency of the song produced in cicadas, where larger species have lower frequency calls. However, there are several body structures that can alter the frequency of the sound produced (Figs. 79 and 80).



Sound Production in the Cicadoidea, Figure 79 **Timbal muscles of *Tibicen winnemanna* (Davis). The ventral attachment is to the chitinous V in the lower center of the micrograph.**



Sound Production in the Cicadoidea, Figure 80 **The timbal is attached to the timbal muscle by an apodeme. A timbal cover can be seen lying over the surface of the timbal.**

Multiple accessory structures have been shown to affect the sound produced by the timbal organs. The timbal covers protect the timbals from damage in members of the Family Cicadidae but they also can act as resonating structures to increase the amplitude of the cicada call. The opercula are plate-like structures on the ventral surface of the abdomen that can also resonate or modify the frequency of the timbal. The abdominal air sacs transform the abdomen into an amplifier to increase the intensity of the call. The tympana are thin membranes at the base of the dorsal abdomen that can dampen the sound produced and also act as the main site of sound radiation so cicadas radiate sound through their eardrums. The timbal tensor muscle acts to put tension on the timbal that increases the amplitude of the emitted sound. The dorsal and ventral abdominal muscles act to elevate and depress the abdomen. The changes in abdominal position can bring the abdomen into resonance with the timbals and also produces frequency and amplitude modulations in more complex calls.

Stridulation is a second method of sound production in cicadas. A stridulatory apparatus has been described in various cicada genera from around the world. A typical stridulatory apparatus is composed of a file and scraper similar to the system found in crickets, grasshoppers, and some heteropterans. The cicada stridulatory apparatus is normally found associated with the tegmina and the mesonotum. However, one stridulatory apparatus has been described as a modification of the genitalia, although it has not been seen being used in the field. Stridulation is used primarily as a secondary acoustic system in cicadas. The stridulating cicadas that have been studied use stridulation in addition to the timbal call. In addition, stridulation has permitted some females to respond to male timbal calls (Fig. 81).

A final method of sound production in cicadas is crepitation. The North American genera *Platypedia* and *Neoplatypedia* have replaced timbal songs with crepitation but other genera use crepitation in addition to timbal song production. A crepitating cicada will snap the wings together or

Sound Production in the Cicadoidea, Figure 81 The mesonotal stridulatory apparatus of *Tettigades undata* Torres.

bang the wings on vegetation to produce a sound pulse. Individual sound pulses are produced when the wings are snapped against the body. There does not appear to be a cost in terms of the sound intensity to the cicadas that use a crepitation signal. It has been found that a crepitating species does not differ from the expected sound intensity based on the relationship between body size and timbal song intensity. A benefit to crepitation appears to be the two-way communication between males and females that it permits. The two-way communication between males and females in crepitating and stridulating species can ensure proper species identification when it comes to selecting a mate.

It should be noted that the mechanisms described above are used by members of the family Cicadidae. The primitive Tettigarctidae of Australia have been shown to communicate through vibrational rather than acoustic signals.

► Acoustic Communication

References

Bennet-Clark HC (1997) Tymbal mechanics and the control of song frequency in the cicada *Cyclochila australasiae*. J Exp Biol 200:1681–1694

Bennet-Clark HC, Young D (1992) A model of the mechanism of sound production in cicadas. J Exp Biol 202:3347–3357

Boulard M (2005) Acoustic signals, diversity and behaviour of cicadas (Cicadidae, Hemiptera). In: Drosopoulos S, Claridge MF (eds) Insect sounds and communication: physiology, behaviour, ecology and evolution. CRC Press, Boca Raton, FL, pp 331–349

Claridge MF, Morgan JC, Moulds MS (1999) Substrate-transmitted acoustic signals of the primitive cicada, *Tettigarcta crinita* Distant (Hemiptera Cicadoidea, Tettigarctidae). J Nat Hist 33:1831–1834

Moore TE (1993) Acoustic signals and speciation in cicadas (Insecta: Homoptera: Cicadidae). In: Lees DR, Edwards D (eds) Evolutionary patterns and processes. Linnean Society Symposium Series 14. Academic Press, London, UK, pp 269–284

Pringle JWS (1954) The physiological analysis of cicada song. J Exp Biol 31:525–560

Sanborn AF, Phillips PK (1999) Analysis of acoustic signals produced by the cicada *Platypedia putnami* variety *lutea* (Homoptera: Tibicinidae). Ann Entomol Soc Am 92:451–455

Southern Bacterial Wilt

This bacterial disease is more of a problem where insects or other wound-producing organisms occur.

► Transmission of Plant Diseases by Insects

Southern Blotting

A technique developed by E. M. Southern for transferring DNA fragments isolated electrophoretically in an agarose gel to a nitrocellulose filter paper sheet by capillary action. The DNA fragment of interest is then probed with a radioactive nucleic acid probe that is complementary to the fragment of interest. The position on the filter is determined by autoradiography. The related techniques for RNA and proteins have been dubbed “Northern” and “Western” blots, respectively.

Southern Chinch Bug, *Blissus insularis* Barber (Hemiptera: Blissidae)

This is an important pest of southern turf, particularly St. Augustinegrass.

► Turfgrass Insects and their Management

Southern Green Stink Bug, *Nezara viridula* (L.) (Hemiptera: Heteroptera: Pentatomidae)

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The southern green stink bug, *Nezara viridula* (L.), has a worldwide distribution, occurring throughout the tropical and subtropical regions of Europe, Asia, Africa, and the Americas. To this distribution should be added California in the United States and some areas in South America, wherein the bug is expanding its distribution, in particular in Paraguay, south Argentina, and central-west toward the north-east of Brazil. The expansion in South America is the result of increased acreage for soybean production.

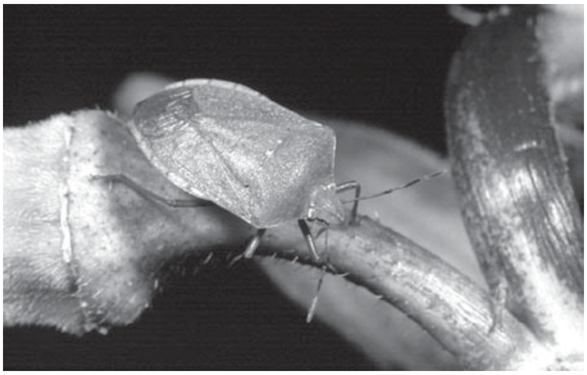
Nezara viridula is highly polyphagous, and more than 150 species of plants of over 40 families have been recorded as hosts. Despite its polyphagy, this stink bug shows preference for leguminous and brassicaceous plants.

This bug completes several generations per year, depending on the favorability of the environment. For instance, in the United States, adults leave overwintering shelters during spring and begin feeding and ovipositing in clover, small grains, early spring vegetables, corn, tobacco, and weed hosts, where they complete the first generation. A second generation is completed on leguminous weeds, vegetables and row crops, cruciferous, and okra, which are typical midsummer hosts. Third generation adults move into soybean where they complete the fourth and fifth generations. Another example of host plant sequence for *N. viridula* was studied in Paraná state, southern Brazil. The bug concentrates on soybean during the summer, which is very abundant at this time; two to three generations are completed on this crop. During fall, adults move to wild hosts, which include the star bristle, *Acanthospermum hispidum*, and the castor bean, *Ricinus communis*, where they feed but do not reproduce. They also move to wild legumes, such as the beggar weed, *Desmodium tortuosum* and *Crotalaria* spp., where they feed and reproduce, with its resulting offspring completing a fourth generation. During late fall and early winter, *N. viridula* completes a fifth generation on radish, *Raphanus raphanistrum*, and mustards, *Brassica* spp. During winter, it may feed but will not reproduce on wheat, *Triticum aestivum*. During spring, a sixth generation is completed on Siberian motherwort, *Leonurus sibiricus*. Many other cases of *N. viridula* host plant sequences have been studied elsewhere, indicating the importance of knowing these sequences to manage this pest species better. Both pods and seeds of legumes generally provide a suitable food source for nymphs, whereas survival is poor on leaves and stems.

Adults are (Fig. 82) green and 12 mm long. Eggs are firmly glued together in rows within compact polygonal clusters. At the time of deposition, eggs are cream colored, turning pinkish or reddish as development progresses. Nymphs in the early instars are strongly gregarious, and this behavior tends to disappear as the nymphs grow older.

Significant reductions in seed yield, quality, and germination can result from feeding by this pest; damaged seeds can have an increased incidence of pathogenic organisms. The feeding punctures (flanges) on seeds cause minute darkish spots, and generally chalky-appearing air spaces are produced when the cell contents are withdrawn.

The effects of *N. viridula* on corn are more severe on younger plants, and yield reductions are



Southern Green Stink Bug, *Nezara viridula* (L.) (Hemiptera: Heteroptera: Pentatomidae), Figure 82 **Adult southern green stink bug.**

attributed to total ear loss rather than reduction in kernel weight. On tomato, its feeding is associated mostly with reduced quality of the fruit. *N. viridula* also can attack nut crops. It is one of the most damaging pests of macadamia, causing nut abortion in small nuts and quality damage in larger nuts in the trees or on the ground. In recent years, *N. viridula* has been reported as a pest of flue-cured tobacco. Both adults and nymphs extract plant fluids from younger tender growth, causing the leaves to wilt and flop over due to loss of turgor pressure.

Several tactics have been studied and implemented to manage *N. viridula* attacking many crops. The use of chemical control still is the major tool used by growers, but many other tactics within the context of cultural practices and biological control have been investigated and used. For chemical control, chlorinated hydrocarbon, organophosphates and organochlorophosphate insecticides, such as methyl parathion, monocrotophos, trichlorphon, dimethoate, and endosulfan have been recommended. Some of these insecticides are recommended to control *N. viridula* on soybean using reduced dosages mixed with sodium chloride, which increase their efficacy. Also, the use of a natural insecticide, such as an extract of neem seed, has been reported to decrease the scars on pecan nuts caused by *N. viridula* feeding.

Trap cropping has been utilized to suppress *N. viridula* and other pentatomid species on soybean. It takes advantage of the fact that stink bugs colonize soybeans during the pod-set and pod-filling stages of plant development. Thus, early maturing or early planted soybeans are highly attractive to stink bugs and can be used to exploit this behavioral response by attracting large populations of the bugs into small areas containing these trap crops (usually less than 10% of the total area). The concentration of ovipositing females and the subsequent nymphal population can be controlled effectively with insecticides before the next generation of adults disperses to the surrounding fields. The key to success of this cultural practice is to control nymphs before they become adults and disperse to adjacent fields. If insecticide controls are not timed properly, then this management strategy is useless and, in fact, actually intensifies the stink bug problem in the main crop. Inoculative releases of the egg parasitoid Trissolcus basalis (Wollaston) (Hymenoptera: Scelionidae) in early-maturing soybean, used as trap crops, caused a reduction and delay in the population peak of this stink bug.

Some progress has been made in the development of host plant resistance to *N. viridula* feeding on some crops. But, so far, cultivars with variable levels of resistance have been little used, mainly because the potential production of these cultivars is usually lower than other commercial cultivars.

Nezara viridula is attacked by numerous natural enemies including parasitoids, predators, and entomopathogens. As many as 57 parasitoid species are recorded for *N. viridula*. The most important of these are the egg parasitoid *Trissolcus basalis* (Wollaston) and, in the New World, the adult parasitoid *Trichopoda pennipes* (F.) in North America, and *Trichopoda nitens* (Blanchard) in South America.

Several arthropod predators have been reported to feed on *N. viridula*. There is a complex of nonspecific predators, and the fire ant, *Solenopsis invicta* Buren, is mentioned as an effective predator of eggs and early instars in the United States.

References

Jones WA (1988) World review of the parasitoids of the southern green stink bug, *Nezara viridula* (L.) (Heteroptera: Pentatomidae). Ann Entomol Soc Am 81:262–273

McPherson JE, McPherson RM (2000) Stink bugs of economic importance in America North of Mexico. CRC Press, Boca Raton, FL, 253 pp

Panizzi AR (1997) Wild hosts of pentatomids: ecological significance and role in their pest status on crops. Annu Rev Entomol 42:99–122

Panizzi AR, Slansky F Jr (1985) Review of phytophagous pentatomids associated with soybean in the Americas. Fla Entomol 68:184–214

Schaefer CW, Panizzi AR (eds) (2000) Heteroptera of economic importance. CRC Press, Boca Raton, FL, 828 pp

Todd JW (1989) Ecology and behavior of *Nezara viridula*. Annu Rev Entomol 34:273–292

Soybean Aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae)

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This insect is native to Asia where it is only an occasional pest of soybean, *Glycine max* (L.) Merr. In addition to cultivated soybean, *A. glycines* has been collected from wild relatives of cultivated soybean, e.g., *Glycine soja* Sieb. & Zucc. In North America, soybean aphid was first found in the summer of 2000 nearly simultaneously in ten north central states. By 2007, soybean aphid was reported from 22 states and 3 Canadian provinces. Economic infestations of soybean aphid have occurred primarily in the north central USA and Canada. It appears that high summer temperatures are limiting the expansion of the soybean aphid's range to the south with only occasional records of soybean aphids collected from soybean in Mississippi and Georgia.

It is likely that soybean aphid was present in the USA prior to 2000, but until populations reached damaging levels, it went unnoticed. Interestingly, soybean aphid was also discovered infesting soybean in Australia in the 1999–2000 growing season. Since 2000 there has been little research published regarding soybean aphid in Australia, suggesting that its pest status is more limited in Australia. However, in North America soybean aphid has become one of the most serious pests of soybean, capable of causing annual yield losses in excess of $100 million.

Life History of Soybean Aphid

In temperate parts of Asia, soybean aphid has a heteroecious and holocyclic life cycle, meaning that it alternates between an asexual form of reproduction (parthenogenesis) in the summer and sexual reproduction in the fall, and it uses two unrelated host plants during its seasonal cycle. Sexual reproduction occurs in the fall when winged sexual forms (gynoparae and androparae) fly from soybean (secondary host) to a woody perennial, in this case buckthorn, *Rhamnus* spp. (primary host) where mating occurs and overwintering eggs are laid. Beginning in the spring through late summer, reproduction is by parthenogenic, viviparous females. In Asia, soybean aphid uses *R. davurica* Pallus and *R. japonica* Maxim as primary hosts. In early spring, females hatch from overwintering eggs and several parthenogenic generations are completed on the primary host. During late spring winged forms are produced and soybean aphid migrates from the primary host to the secondary host, which in North America is restricted to soybean.

In the USA, neither of the recorded primary hosts is present, but an invasive buckthorn species from Europe, *R. cathartica* L., common buckthorn, is widespread in the north central US and Canada. Soybean aphid uses *R. cathartica* as its principal primary host in North America. Another native species of *Rhamnus*, alderleaf buckthorn, *R. alnifolia* L'Hér, can also serve as a primary host for soybean aphid, but its distribution is far less extensive than *R. cathartica*. It is noteworthy that an exotic aphid from Asia survives in North America by using a primary host introduced from northern Europe and a secondary host (soybean) from Asia. There are no other members of the genus *Glycines* native or introduced to North America except soybean. In the laboratory, soybean aphid will accept and reproduce on red clover, *Trifolium pratense* L., but soybean aphid has only rarely been observed colonizing this plant in the field. In other parts of the world other secondary hosts of soybean aphid include kudzu, *Pueraria thunbergiana* (Sieb. & Zucc.) Benth., tropical kudzu, *P. phaseoloides* (Roxb.) Benth., *Desmodium intortum* (P. Mill.) Urban, and scarlet runner bean, *Phaseolus coccineus* L. (= *multiflorus*).

Aphis glycines is a small yellow aphid similar in size to a closely related species, *A. gossyppii*, the cotton or melon aphid. Winged morphs are required to distinguish *A. glycines* from other *Aphis* spp. On *R. cathartica*, the buckthorn aphid, *A. nasturtii* Kaltenbach, coexists with soybean aphid. There are several unique characteristics used to distinguish between winged morphs of *A. nasturtii* and *A. glycines* including the following characters unique to soybean aphid: pale cauda, a sclerotized patch on the abdomen at the base of the dark cornicles, and antennal segment IV without rhinaria.

Damage to Soybean

In North America, *A. glycines* begins colonizing soybean as soon as the crop emerges (late May to early June). During the vegetative growth stage, soybean aphid colonies are typically found on the growing point including the stem, petioles and the partially expanded trifolioates. In North America it is uncommon to find soybean aphid colonies tended by ants, but in China and Japan ant-tended aphid colonies are common. Multiple studies conducted in North America and Asia show that aphid colonization of young vegetative plants rarely results in a yield loss. Yield loss is mostly attributed to heavy aphid infestation during reproductive plant growth stages. In response to high aphid density during the beginning of the reproductive growth stage, R1 (first flower) through R5 (pod elongation and beginning seed set) plants often abort pods. Once pods abort, yield potential is substantially reduced so, even if aphids were controlled following pod abscission and plants remained aphid-free the remainder of the season, a significant yield loss would still occur. Yield losses in excess of 50% have been reported during aphid outbreaks.

Once soybeans reach terminal height aphids are no longer found on the upper portion of the plant. Aphids move lower in the canopy and can be found on secondary growing points (lateral shoots), expanding pods, and on mature leaves. Aphids found on fully expanded mature leaves are often smaller and are pale white. These "white dwarfs" are less fecund and shorter lived than the large pale green soybean aphids found on the growing points. As the plant enters R6 (pod filling) these mature leaves become an excellent resource equal in quality to the growing point during vegetative growth as photosynthate stored in mature leaves is mobilized for pod filling.

Environmental conditions that favor soybean aphid development are cool temperatures ranging from 20 to 28°C, low humidity which suppresses entomopathogenic fungi, and lower than average rainfall because heavy rainfall can dislodge soybean aphid from the growing points. The optimal temperature for growth and reproduction is 28°C and in laboratory studies under optimal conditions, population doubling times are as low as 1.3 days. In the field doubling times of 2.4 days have been measured but average doubling time during reproductive growth stage R1 to R5 in a 6-state study over 19 locations was 6.8 days. During a growing season as many as 18 generations can occur.

Currently, in North America soybean aphid is not commonly found in the southern soybean production areas. It is unknown why this is the case, whether it is a lack of overwintering hosts since *R. cathartica* is not present in the deep south, or if high summer temperatures are detrimental to soybean aphid population growth. Soybean aphid is known from subtropical areas of Asia, so there may be biotypes adapted to the warm humid conditions of the south central US and soybean aphid may continue to expand its range in the future.

Natural Enemies

As an exotic invasive insect, soybean aphid arrived in North America without its full complement of natural enemies. Since 2000, numerous native predators and fungal pathogens have been documented as being important mortality factors of soybean aphid. Predators such as *Orius insidiosus* (Say), insidious flower bug (Hemiptera: Anthocoridae), and several species of ladybird beetles are recognized as key predators of soybean aphid. One predator in particular, the exotic multi-colored Asian ladybird beetle, *Harmonia axyridis* (Pallas), has proven to be an important predator of soybean aphid. Throughout North America, one guild of natural enemies that is largely missing is the parasitoids (Hymenoptera). Only rarely are parasitized soybean aphids observed in North America, but in Asia parasitoids appear to be the principal natural enemy guild keeping soybean aphid populations under control. It is not uncommon to find more than 40% of soybean aphids parasitized in China.

Management

Soybean aphid is currently the most damaging insect pest of soybean in the north central region. Tens of millions of acres of soybean have been treated with insecticide since 2001, costing producers more than a billion dollars in lost yield and additional production costs.

Economic Threshold and Economic Injury Level

An economic threshold (ET) has been developed that is applicable for the entire north central region. The current ET is 250 aphids per plant when more than 80% of the plants are aphid infested. The ET assumes the aphid population is doubling in less than 7 days, and the corresponding economic injury level is 674 aphids per plant. The ET is valid from plant growth stage R1 through R5. An ET during growth stage R6 (full-size green seed) is not yet available, but the limited number of replicated trials where aphid populations peaked during R6 suggests the ET during R6 will be substantially higher. Soybean aphid populations often naturally decline during late R6, due in part to environmental cues (shortened day length and lower nighttime temperatures) resulting in development of sexual morphs. Sexual morphs begin leaving soybean and migrate back to buckthorn where a fertilized female will deposit overwintering eggs on the primary host instead of producing live young.

Sampling

One of the key elements of any IPM program is an effective sampling program. Counting aphids on a per plant basis is time consuming and tedious, often taking more than 1 h to sample a single field. Using whole plant counts for the ET requires a minimum of 30 plants per field to make a treatment decision. To reduce sampling time and to encourage adoption of an ET for making treatment decisions, a bionomial sequential sampling plan (presence or absence) was developed. This binomial sampling plan termed "Speed Scouting" allows a producer to make a treatment decision faster and is as accurate as whole plant counting. Speed Scouting uses a tally threshold of 40, so if a plant has 40 or more soybean aphids it is tallied as "infested." It is important to note that the Speed Scouting tally threshold of 40 is not a lower economic threshold. If you took every plant that exceeded the tally threshold of 40 and took the time to count every aphid, the average aphid density per plant would be 250. Speed Scouting is most effective when aphid populations are very low or when aphid populations are high, and a decision to treat or to leave the field untreated can be made by sampling as few as 11 plants and requires <15 min to make a treatment decision. In validation studies, 79% of the time Speed Scouting made the correct "treat" decision compared to whole plant sampling using the ET of 250 aphids per plant. In the remaining 21% of the cases, Speed Scouting and whole plant counts did not arrive at the same decision, and Speed Scouting was always more conservative, i.e., arriving at a "treat" decision when in fact the aphid population was lower than 250 aphids per plant. To overcome this bias, a "treat" decision via Speed Scouting needs to be confirmed by a second sample taken 3–4 days later, to assure that the aphid population is indeed increasing.

Biological Control

A classical biological control program began in 2001 with the first collection of parasitic hymenoptera from China, followed by subsequent collection in different regions of China, and in Japan and Korea. In 2007, host range testing was completed for one parasitic wasp, *Binodoxys communis* (Galan) (Hymenoptera: Braconidae), and this parasitoid was released in at least five midwestern states in the summer of 2007. Whether this classical biological control program will succeed in permanently reducing soybean aphid densities below damaging levels is yet to be determined.

Insecticides

The most common foliar-applied insecticides used to control soybean aphid are the pyrethroids. However, if twospotted spider mites, *Tetranychus urticae* Koch, are also found, the organophosphate insecticide clorpyriphos is recommended instead of pyrethroids because the latter tends to flare twospotted spider mites under drought conditions. Insecticide application for soybean aphid is most typically applied to full canopy soybeans. Application of insecticide by airplane is as effective as application by ground equipment, but application costs are typically double of that by grower-owned, tractor-drawn spray equipment. Using ground equipment in full canopy soybeans causes mechanical damage to soybean and research shows that such losses often exceed 1 bu/ac (67 kg/ha).

Insecticides in a new chemical group, the neonicotinoids, are being used more frequently to control soybean aphid. As foliar-applied materials, the neonicotinoids are highly effective. Neonicotinoids are also used as seed treatments for use at planting. Efficacy of seed treatments is relatively short lived with mortality no different from untreated controls by 35 days after planting (V3 to V5). Although aphids do colonize young vegetative soybean, it isn't until much later in the growing season that aphids build to damaging densities that exceed the ET and long after seed treatments remain effective. The inability to predict when and where soybean aphid will reach damaging densities, coupled with the ability of young vegetative plants to withstand substantial aphid feeding without a concomitant yield loss, all suggest that seed treatment is a poor method of aphid control.

Host Plant Resistance

Soon after the discovery of the soybean aphid, aphid resistant soybean cultivars were identified. The cultivars Dowling and Jackson (Maturity Group VII and VIII, respectively) were shown to be nearly immune to soybean aphids in greenhouse and field cage studies which suggested antibiosis as the mechanism of resistance. However, these maturity groups can only be grown in the southern-most soybean production area in the US where soybean aphid has not yet been found. Markers for the soybean aphid resistance gene, *RagI*, were identified through conventional breeding. *RagI* was transferred into cultivars typically grown in the north central region (Maturity Group III and 0). However, in the summer of 2006, even before these resistant cultivars were released to the public, a variant of soybean aphid that overcomes *RagI* mediated resistance was discovered in Ohio. Release of cultivars with only a single gene for soybean aphid resistance would appear to be only a short term benefit and, if widely planted, soybean aphid biotypes that overcome *RagI* mediated host plant resistance are already present in the population.

Altogether, soybean aphid represents a major constraint to profitable soybean production in the north central USA and Canada. Long term strategies of host plant resistance and biological control offer promise but until those tactics are widely available growers must rely on sampling, economic thresholds and conventional means of crop protection.

References

Costamagna AC, Landis DA (2006) Predators exert top-down control of soybean aphid across a gradient of agricultural management systems. Ecol Appl 16:1619–1628

Desneux N, O'Neil RJ, Yoo HJS (2006) Suppression of population growth of the soybean aphid, *Aphis glycines* Matsumura, by predators: the identification of a key predator and the effects of prey dispersion, predator abundance, and temperature. Environ Entomol 35:1342–1349

Hill CB, Li Y, Hartman GL (2004) Resistance to the soybean aphid in soybean germplasm. Crop Sci 44:98–106

Hodgson EW, McCornack BP, Koch KA, Ragsdale DW, Johnson KD, O'Neal ME, Cullen EM, Kraiss HJ, DiFonzo CD, Behnken LM (2007) Field validation of Speed Scouting for soybean aphid. Crop Management. Available at http://dx.doi.org/10.1094/CM-2007-0511-01-RS)

McCornack B, Ragsdale DW, Venette RC (2004) Demography of soybean aphid (Homoptera: Aphididae) at summer temperatures. J Econ Entomol 97:854–861

Voegtlin DJ, Halbert SE, Qiao G (2004) A guide to separating *Aphis glycines* Matsumura and morphologically similar species that share its hosts. Ann Entomol Soc Am 97:227–232

Sparganothis Fruitworm, *Sparganothis sulphureana* (Clemens) (Lepidoptera: Tortricidae)

This is a small fruit pest, affecting cranberry and blueberry.

► Small Fruit Pests and their Management

Sparkling Archaic Sun Moths (Lepidoptera: Eriocraniidae)

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Sparkling archaic sun moths, family Eriocraniidae, are a Holarctic family of 25 species, of which about half the species are in Europe and half in North America. The family, plus the related Acanthopteroctetidae, are the only members of the superfamily Eriocranioidea, which form the infraorder Dacnonypha of the suborder Glossata. Adults small (6–13 mm wingspan), with roughened head scaling; haustellum reduced; mandibles present but vestigial (haustellum absent); labial palpi 3-segmented; maxillary palpi 5-segmented and folded. Maculation rather colorful with various iridescent spots of gold on darker forewings. Adults are diurnally active. Hosts are mostly in Betulaceae and Fagaceae, and the egg is inserted by the female into tender host leaves in early spring, whereupon the young larvae feed before the leaves turn hard. Larvae are leafminers with serpentine mines that become blotch mines as the larvae grow.

References

Busck A, Böving A (1914) On *Mnenonica auricyanea* Walsingham. Proc Entomol Soc Wash 16:151–163

Davis DR (1978) A revision of the North American moths of the superfamily Eriocranioidea with the proposal of a new family, Acanthopteroctetidae (Lepidoptera). Smithson Contrib Zool 251:1–131

Heath J (1976) Eriocraniidae. In: Heath J. (ed) The moths and butterflies of Great Britain and Ireland, vol 1. Harley Books, London, pp 156–165

Sutter R (2000) Beiträge zur Insektenfauna Ostdeutschlands: Lepidoptera-Eriocraniidae (Insecta). Faunistische Abhandlungen 22:49–67

Spatulate

Broad at the tip and narrow at the base. The tip is flattened or sometimes recessed and spoon-like.

Spear-Winged Flies

Members of the family Lonchopteridae (order Diptera).

► Flies

Specialist

Insect occupying a narrow niche, or consuming a narrow range of food.

Speciation Processes Among Insects

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The development of molecular genetics has led to a renewed attempt to define the concept of the species. Originally, "species" was defined by Ernst Mayr as an interbreeding group of organisms (= population) that is reproductively isolated from other such groups (typically referred to as the biological species concept or BSC). However, the increasing frequency of reported viable hybrids produced by crosses of "parental species" in natural systems (often recognized as distinct species until molecular analyses revealed that they are intermediate crosses of various degrees between the parentals and/or hybrids), suggests that Mayr's definition was inadequate. As a result, other species concepts were developed such as the phylogenetic species concept (PSC), which identifies species (and other taxonomic categories) based on the presence of shared derived characters. In other words, taxa that share recently derived morphological or genetic characters are assumed to be more closely related than lineages that do not share these derived traits. While this definition circumvented the reproductive isolation requirement imposed by the BSC, it has its own unique set of problems. For instance, the phylogenetic (i.e., evolutionary) relationships inferred from a cladistic analysis can be affected by the choice of characters used in the assessment (this is also true for studies that rely on the use of shared derived genetic sequences).

Regardless of the functional definition of the term, the evolution of new species is traditionally believed to occur through allopatry or, less frequently, through the more controversial pathway of sympatry. Allopatric speciation, which involves a geographic separation and isolation of segments of a formerly contiguous population, is firmly established as the primary mechanism by which new species evolve. Sympatric speciation also predicts the development of new species under certain restrictive conditions, but this mechanism does not require speciating subpopulations to be geographically isolated from one another. It is precisely this lack of geographic isolation that has rendered sympatric speciation so contentious because, without spatial isolation among speciating subpopulations, it is difficult to imagine a scenario in which interbreeding (i.e., gene flow) among diverging groups can be greatly reduced or eliminated (a requirement for speciation).

Insects in general, and phytophagous insects in particular, provide some of the strongest evidence for the sympatric pathway of speciation. Several recent studies have found evidence suggesting that host range expansion by phytophagous insects may result in the development of new species without geographical isolation of host-specific subpopulations. The tenability of this mechanism is directly tied to the problem of fitness trade-offs and potential gene flow among diverging subpopulations. According to the generalized model, females mistakenly oviposit on an atypical (i.e., outside its normal host range) plant species and, if progeny survive on this novel host (to which they are, by definition, non-adapted), temporal or seasonal differences in host plant phenology may effectively isolate this subpopulation from conspecifics on the natal host species. However, for this scenario to be feasible, insects from the atypical host species must show a high degree of fidelity for this novel host even though they are likely to suffer decreased survival, fitness and performance compared to insects from the original host.

How can such a paradox be resolved? Many phytophagous insects are specialists on one or a few hosts and they often exhibit host-specific assortative mating. Although the reasons for this behavior are unclear, plant-feeding insects, especially endophages such as leafminers or gallers, may become chemically marked by the host plant during development. As adults, they may rely on these chemical cues when searching for mates and/or oviposition sites. Additionally, host-specific mating behavior may simply provide the most reliable source for locating a potential mate, a likely possibility if the host shift is to a plant with a different phenology than the ancestral host species. For instance, in one of the best-documented cases of nascent speciation, host-associated races of the apple maggot fly (*Rhagoletis pomonella*) complex, undergo courtship and mating on their individual host plants, often on the fruits. This is also true for the tephritid sawfly (*Eurosta solidagginis*), which consists of two host-associated races that attack the goldenrods, *Solidago altissima* and *S. gigantea*, in which mating and oviposition occur on the natal host plant. Mating of the soapberry bug, *Jadera haematoloma*, which has expanded its host range to include several introduced species, is also limited to the host plant.

Host-specific associative mating is likely to result in reduced gene flow between subpopulations or races that utilize different host species if insect development time is variable and host fidelity among subpopulations is high. For example, spring-summer gall persistence (measured as LD_{90} and correlated with larval development time) of host-associated populations of the gall midge, *Asphondylia borrichiae*, which galls the terminals of three plants in the aster family, ranges from approximately 29 days on *Iva imbricata* to 70 days on *Borrichia frutescens*. Since these midges only live for a couple of days as adults after emergence from the gall, it is very likely that host shifts have resulted in semi-isolated subpopulations of *A. borrichiae* because adults may be limited to mating with conspecifics from the same host species owing to different host-specific emergence times. Host-associated populations of *A. borrichiae* also exhibit a high degree of host fidelity (at the level of plant genus). Midges that emerged from sea oxeye daisy (*Borrichia frutescens*) attacked the natal host approximately 97% of the time, whereas midges that emerged from the other two hosts (*Iva* spp.) attacked these hosts exclusively. Similar allochronic isolation owing to variable host plant phenology occurs among host-specific races of *R. pomonella* that feed on the fruits of several plants including blueberry, domestic apple and hawthorn. Prior to pupation, larvae emerge from the fruit of the host plant and drop to the ground where they pupate in the soil. Larvae from blueberry pupate 1–2 weeks earlier than those from apple and approximately 4 weeks earlier than those from hawthorn. Synchronization of adult eclosion also mirrors differences in host-specific fruit phenology; adults from the blueberry race eclose first, followed by those from apple and hawthorn, respectively. Gene flow among the ancestral host, hawthorn, and the derived host, domestic apple, has been estimated at 4–6% per generation.

Moreover, larvae that find themselves on a novel host plant may experience reduced levels of attack by natural enemies such as parasitoids. For the apple maggot fly, which has apparently expanded its host range numerous times from its ancestral host, hawthorn (*Crataegus* spp.), including expansion to the commercially important domestic apple (*Malus pumila*) introduced from Europe, both interspecific competition and parasitism are greatly reduced on the derived host. Asphondylia borrichiae also appears to experience lower levels of parasitism on two species of *Iva* compared midges on *B. frutescens*. Indeed, reduced levels of parasitism and/or competition on derived hosts may offset lower rates of survival and fitness on sub-optimal hosts, thereby aiding the establishment and maintenance of host-choice polymorphisms.

Although phytophagous insects provide some of the best evidence for the sympatric pathway of speciation, it does not appear to be limited to herbivorous insects. For instance, the predatory lacewings *Chrysoperla carnea* and *C. downesi*, which differ in color, are believed to have originated in sympatry relatively recently. Most likely a color polymorphism arose in the ancestral population, which lead to habitat-specific assortative mating among subpopulations. *Chrysoperla carnea* is light green-brown and prefers deciduous woodlands, while *C. downesi* is dark green and prefers coniferous forests. Differences in habitat-specific survivorship/fitness and habitat preference has favored fixation of different color morphs and asynchronous breeding seasons among the subpopulations that would eventually become *C. carnea* and *C. downesi*.

While phytophagous insects provide model systems for investigating sympatric speciation, some plant-feeding insect guilds such as leafminers and gallers, which are intimately associated with their hosts, may possess characteristics that facilitate the formation of host-associated races or species in sympatry including: (i) sessile larvae that are restricted to feed on the host plant selected by the ovipositing female; (ii) endophagous larvae that feed exclusively within the tissue of the host plant; (iii) significant host-specific variation in larval survival and performance (including differential attack by natural enemies); (iv) differences in host plant phenology (and host-specific insect development) that result in allochronic isolation of host-specific subpopulations (i.e., plant-mediated reduction in gene flow); and (v) host fidelity of ovipositing females. While many biologists still harbor doubts about sympatric speciation, several recent studies provided strong evidence for this evolutionary pathway. After all, Charles Darwin clearly stated in Chap. 4 of his magnum opus, "On the Origin of Species": "I can see no means to agree…that migration and isolation are necessary elements for the formation of new species."

► Species Concepts

References

Berlocher SH, Feder JL (2002) Sympatric speciation in phytophagous insects: moving beyond controversy? Annu Rev Entomol 47:773–815

Darwin C (1859) On the origin of species by natural selection or the preservation of favored races in the struggle for life. Mentor, New York, NY, 479 pp (reprinted 1958)

Jaenike J (1990) Host specialization in phytophagous insects. Annu Rev Ecol Syst 21:243–273

Mopper S, Strauss SY (eds) (1998) Genetic structure and local adaptation in natural insect populations. Chapman and Hall, New York, NY, 449 pp

Rossi AM, Stiling P, Cattell MV, Bowdish TI (1999) Evidence for host-associated races in a gall-forming midge: trade-offs in potential fecundity. Ecol Entomol 24:95–102

Thompson J (1988) Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. Exp Appl 47:3–14

Via S (1990) Ecological genetics and host adaptation in herbivorous insects: the experimental study of evolution in natural and agricultural systems. Annu Rev Entomol 35:421–446

Wheeler QD, Meier R (eds) (2000) Species concepts and phylogenetic theory: a debate. Columbia University Press, New York, NY, 230 pp

Species

Populations with individuals that are similar in structure and behavior, and capable of mating and producing fertile offspring.

► Speciation Processes Among Insects

Species Areas-Relationship

The concept that the number of herbivore species associated with a plant is positively related to the area occupied by the plant. This is an outgrowth of island biogeography theory, in which larger islands support larger faunas; alternative explanations include the length of time a plant has been available for colonization (with more insects accumulating over time) and habitat heterogeneity (with plants living over a wider range being exposed to greater environmental and faunistic diversity).

Species Complex

A group of closely related species, or a species that appears to be variable, and is thought to consist of more than one undefined species.

Species Concepts

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Species concepts are not new to biology. Biologists today are using more species concepts than ever before, concepts which convey how they think about and define species. The notion of species is central to biology in that it provides a formal connection between biological research and the organisms being studied. This connection is in no way trivial and needs to be made in a careful and systematic manner. With an increasing number of species concepts to choose from, opinions differ about the importance of the various processes which shape species and how species should be diagnosed. Much debate has also focused on the applicability and limitations of these various concepts. Obviously, species concepts vary greatly depending on their purpose.

Theoretical Versus Operational Species Concepts

Species concepts can generally be divided into two main categories on the basis of whether they are theoretical (process-oriented) or operational (descriptive) concepts.

Theoretical Species Concepts

These focus on defining what a species is as it relates to our understanding of evolutionary processes. The focus of this type of concept is the process of evolution within species. This concept usually incorporates processes related to reproduction, competition and distribution. A common criticism of these concepts is that because the mode of reproduction (e.g., sexual vs. asexual) is so narrowly defined, the concept is not widely applicable to other organisms (see below.) In addition, a great deal of information about specific biological process remains unknown for most taxa.

Operational Species Concepts

These focus on specific criteria used to identify species. These concepts serve the practical purpose of diagnosing species based on specific criteria. A common criticism of this type of concept is that it is so narrowly restricted to specific measurable features that its implementation could subdivide species. Even though theoretical concepts are often impractical for application to most taxa, they provide information about processes that shape species. Even though operational concepts prove practical for identifying species, they usually do not provide much insight into how species are formed and maintained. Theoretical and operational species concepts can correspond, but they do not always.

Species Concepts in Use Today

Some 22 different species concepts have been identified as being in use in the modern literature on species. These 22 species concepts vary considerably in their focus, depth and applicability to various taxa. While many of these concepts have not been widely adopted or discussed, several are routinely juxtaposed in discussions of species concepts (Table 18).

Biological Species Concept [sensu Mayr and Ashlock] – (theoretical) "A species is a group of interbreeding natural populations that is reproductively isolated from other such groups." The use of this concept requires knowledge of population distributions in time and space. Criticisms of this concept include:

1. Excludes uniparental species.
2. Indiscriminate use of a reproductive isolation criterion.
3. Its relational nature: *A* is a species in relation to *B* and *C* because it is reproductively isolated from them.

Evolutionary Species Concept [sensu Wiley and Mayden] – (theoretical) "… an entity composed of organisms which maintains its identity from other such entities through time and over space, and which has its own independent evolutionary fate and historical tendencies." It has been proposed

Species Concepts, Table 18 Species concepts proposed by various authors (after Mayden, 1997)

Agamospecies Concept
Biological Species Concept
Cladistic Species Concept
Cohension Species Concepts
Composite Species Concept
Ecological Species Concept
Evolutionary Significant Unit
Evolutionary Species Concept
Genealogical Concordance Concept
Genetic Species Concept
Genotypic Cluster Concept
Hennigian Species Concept
Internodal Species Concept
Morphological Species Concept
Non-Dimensional Species Concept
Phenetic Species Concept
Phylogenetic Species Concept (Diagnosable Version)
Phylogenetic Species Concept (Monophyly Version)
Phylogenetic Species Concept (Diagnosable And Monophyly Version)
Polythetic Species Concept
Recognition Species Concept
Reproductive Species Concept
Successional Species Concept

that this species concept could possibly accommodate all known types of biological diversity. As such, it is important as a theoretical species concept for structuring ideas about species. Criticisms include:

1. It is not as helpful in the operational or practical sense.
2. It cannot be used to identify species.

Phylogenetic Species Concept [sensu Wheeler and Platnick] – (operational) "…the smallest aggregation of (sexual) populations or (asexual) lineages diagnosable by a unique combination of character states." Phylogenetic species are basal taxonomic units that can be broadly compared. This concept is also operational, i.e., can be applied to diagnosing species, even from dead museum specimens labeled with little more than date and locality information. Criticisms include:

1. Could potentially over-estimate species diversity if the characters of choice do not accurately diagnose real "species."

Recognition Species Concept [sensu Paterson] – (theoretical) "A species is then most inclusive population of individual, biparental organisms which share a common fertilization system." This concept emphasizes mating adaptations that become fixed in the population; individuals "recognize" certain characteristics of suitable mates. Criticisms include:

1. Impossible to apply without knowledge of the specific mate recognition system of the organism.
2. Excludes uniparental species.

Issues of Special Concern to Entomologists

There are several issues that might be of concern to entomologists when choosing a species concept. Parthenogenesis is known to occur in a variety of insect orders. This asexual form of reproduction occurs persistently in clonal populations or in alternating generations in other populations. While it is generally agreed that populations of persistent clonal organisms appear to constitute a unique species, it is appropriate to distinguish them as such by using a species concept that accommodates uniparental organisms. However, some authors recommend that when a parthenogenetic lineage is derived from a known bisexual species, it should not be designated as a new species, but as a parthenogenetic form of the original species.

In many insect groups, specimens can be readily identified to species on the basis of the morphological variation associated with the male reproductive organ, the aedeagus. However, not all groups possess enough variation in this structure to prove useful for delineation. Because some insect groups are host specific they may be very diverse yet morphologically indistinguishable from other closely related taxa. Modern molecular methods are showing promise in identifying genetic sequence variation in addition to traditional morphological suites of characters. Currently there is much debate about which molecular marker is the most informative at the level of species and how much variation needs to be present to justify raising a population to species status.

The Importance of Selecting Appropriate Species Concepts

The importance of species concepts directly relates not only to processes associated with speciation but also to studies of conservation biology, the Endangered Species Act and the current biodiversity crisis. Identifying species requires an operational concept, which once selected will affect the accuracy of the total estimated number of species for a particular region, or the planet. It is also important for biologists to explicitly state which species concept they have adopted for a particular study, as the concept conveys the particular view of species used as well as the particular assumptions associated with it.

► Species Processes Among Insects

References

Enghoff H (1976) Taxonomic problems in parthenogenetic animals. Zool Scr 5:103–104

Foottit RG (1997) Recognition of parthenogenetic insect species. In: Claridge MF, Dawah HA, Wilson MR (eds) Species: the units of biodiversity. Chapman & Hall, New York, NY, pp 291–307

Mayden RL (1997) A hierarchy of species concepts: the denouement in the saga of the species problem. In: Claridge MF, Dawah HA, Wilson MR (eds) Species: the units of biodiversity. Chapman & Hall, New York, NY, pp 381–424

Mayden RL, Wood RM (1995) Systematics, species concepts, and the evolutionarily significant unit in biodiversity and conservation biology. Am Fish Soc Symp 17:58–113

Mayr E, Ashlock PD (1991) Principles of systematic zoology. McGraw-Hill, New York, NY, 475 pp

Paterson HEH (1993) Evolution and the recognition concept of species, collected writings of H.E.H. Paterson. (McEvey SF, ed). Johns Hopkins University Press, Baltimore, MD, 234 pp

Suomalainen E, Saura A, Lokki J (1987) Cytology and evolution in parthenogenesis. CRC Press, Boca Raton, FL

Wheeler QD, Platnick NI (2000) The phylogenetic species concept (sensu Wheeler and Platnick). In: Wheeler QD, Meier R (eds) Species concepts and phylogenetic theory: a debate. Columbia University Press, New York, NY, pp 55–69

Wiley EO, Mayden RL (2000) The evolutionary species concept. In: Wheeler QD, Meier R (eds) Species concepts and phylogenetic theory: a debate. Columbia University Press, New York, NY, pp 70–89

Species Diversity

An index of community diversity that considers both species richness and the relative abundance of species.

Species Inquirenda

A questionable species; there is some doubt about its status.

Species Novum

A species that is about to be described in the accompanying text; a species new to science.

Species Odor

The odor associated with the body of social insects It is unique to a species, though it may be a component of the colony odor.

Species Richness

The number of species present in an assemblage, community, or other defined ecological unit.

Specific Name

The name applied to a species, accompanying the genus name; the second portion of the scientific name. It must be an original combination, and must agree grammatically with the generic name according to Latin grammar.

Sperm Precedence

In insects with multiple matings, the sperm of the last male to copulate with the female is most likely to father the offspring. The last sperm to be stored in the spermatheca are the first to be released.

Spermatheca

A small cuticular storage chamber that stores sperm and is associated with the median oviduct of females. Impregnated females can store sperm for weeks, months or even years depending on the species, and release sperm as an egg passes through the oviduct, resulting in fertilization (Fig. 83).

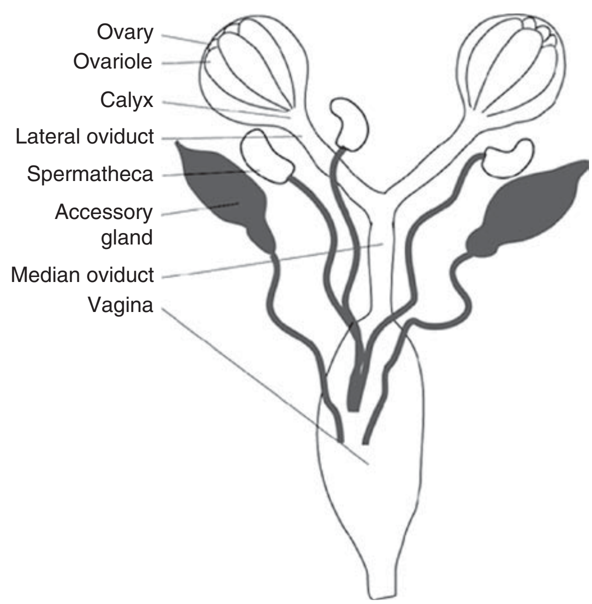
Spermatid (pl., spermatozoa)

A germ cell in the testis that eventually becomes sperm. Developmentally, the spermatid develops from the spermatocytes by mitosis, and mature into sperm.

Spermatocyte

A cell in the testis that divides, eventually forming the sperm. Developmentally, spermatocytes occur in multicellular cysts created by mitosis of spermatogonia, and develop into spermatids.

► Reproduction
► Endocrine Regulation of Reproduction



Spermatheca, Figure 83 **Diagram of the female reproductive system, as found in *Rhagoletis* (Diptera) (adapted from Chapman, The insects: structure and function).**

Spermatogenesis

The production of sperm cells in the testis.

► Sterile Insect Technique

► Reproduction

Spermatogonia

Cells developing in the testis and forming spermatocytes mitotically. The first step in the production of sperm.

► Reproduction

► Endocrine Regulation of Reproduction

Spermatophore

A covering or capsule around the sperm.

Spermatophylax

A portion of the spermatophore that does not include the sperm. It is produced by the male and consumed by the female after copulation as a nutritive supplement.

► Nuptial Gift

► Cannibalism

► Mormon Cricket

Sphaeritidae

A family of beetles (order Coleoptera). They commonly are known as false clown beetles.

► Beetles

Sphaeroceridae

A family of flies (order Diptera). They commonly are known as small dung flies.

► Flies

Sphaeropsocidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice or Psocids

Sphecidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Sphecology

The scientific study of wasps.

Sphecophile

An organism that spends part of its live cycle in wasp colonies.

Spherulocyte

A type of hemocyte of intermediate size.

► Hemocytes of Insects: Their Morphology and Function

Sphindidae

A family of beetles (order Coleoptera). They commonly are known as dry-fungus beetles.

► Beetles

Sphragis

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In many species, mating is preceded by complex courtship rituals, in which females have a choice of mate. However, the male sometimes places a plug or "chastity belt" on the female after mating, limiting her ability to choose other mates. This structure is called a sphragis, from the Greek word for "seal." These sphragis devices can range from a simple plug secreted by a male into female's mating tube at the end of copulation, to elaborate shell-shaped structures attached to the outside of the female's abdomen that prevent the male's claspers from holding onto the female and positioning his genitalia for mating.

In African *Acraea* butterflies, a male can grab a flying female in the air and take her down onto the ground to mate with her. Other males might later attempt a similar strategy with the same female, but they will not be able to attach themselves to the female's abdomen, whose mating tube is blocked by a waxy plug, and pairing will not take place. In the Holarctic genus of primitive tailless swallowtail butterflies, *Parnassius*, the sphragis is external and gives a strong visual cue to an approaching male that the female has been mated. One large species of these butterflies, *Parnassius clodius*, can be observed in the mountains of northern California in late summer. By making the sphragis so noticeable to other males, the successful male not only protects the female from subsequent intercourse by means of a physical barrier, but saves her and his competitors a great deal of energy that would be lost in the redundant hopeless sexual pursuit. Research has shown that males of *Parnassius* invest up to 10% of their body weight during mating by transferring not only sperm into the female, but also nutrients used for building the egg mass.

Reference

Drummond BA III (1984) Multiple mating and sperm competition in the Lepidoptera. In: Smith RL (ed) Sperm competition and the evolution of animal mating systems. Academic Press, New York, pp 291–370

Spicula, Spicule, or Spiculum

Any small, pointed or needle-like process or spine.

Spider Behavior and Value in Agricultural Landcapes

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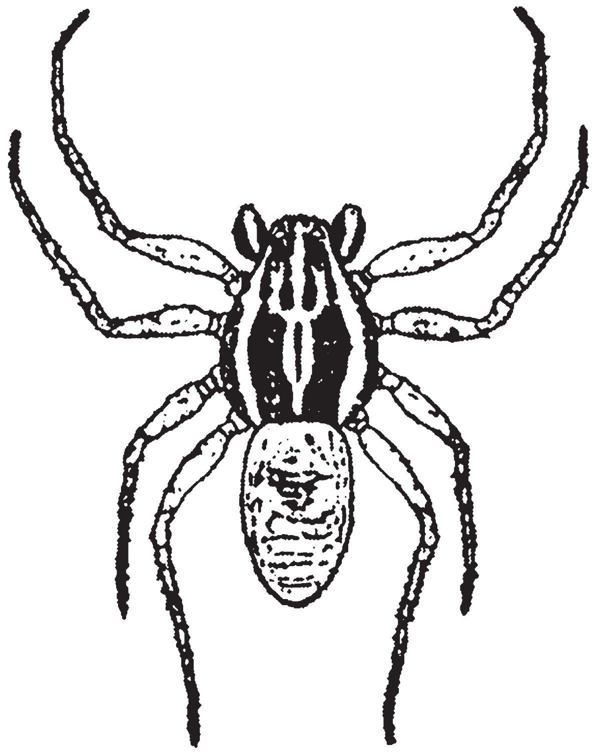
Spiders are one of the largest groups of predatory organisms in the animal kingdom with more than 39,000 species distributed over 108 families worldwide. They are so diverse they are found almost everywhere on earth, from arctic islands to dry desert regions. They are particularly abundant in areas of rich vegetation. It is no exaggeration to say that spiders have conquered all possible ecological niches on land.

Even though spiders are found in abundance all over the world, they have not been fully used in pest management programs. The widespread, undeserved reputation of spiders as being dangerous to people and their animals is one reason why they are not given proper credit as important natural pest control agents. With the exception of one group under the family *Uloboridae*, all spiders have poison glands. However, not all spiders have venom of medical importance to humans. There are many more useful spider species than harmful ones. Of over 39,000 known species, only about 160 are considered to be of any medical hazard to humans. The venom produced by spiders is intended to affect insects and the effect of the venom on humans is usually only slight. Spider venom was not designed to kill humans. Human death by spider venom is an unfortunate reaction, much the same as adverse human reaction to some wasp and bee stings.

Some of the most well known spider species in the world that can cause medical problems when they bite include black widow spiders in the genus *Latrodectus* (Theridiidae). Species of *Latrodectus* can be found throughout the world. The venom is considered a neurotoxin and can cause systemic pain. Recluse spiders in the genus *Loxosceles* (Sicariidae) are distributed worldwide, but most species are found in tropical regions or regions with relatively high humidity. Bites of these spiders cause necrotic lesions surrounding the bite site. Yellow sac spiders in the genus *Cheiracanthium* (Miturgidae) are found worldwide and some species are particularly common in homes. Bites from species of *Cheiracanthium* can be painful and can result in minor necrotic lesions. Banana spiders in the genus *Phoneutria* (Ctenidae) are found in Central and South America. These spiders can be aggressive and their venom is neurotoxic, causing similar symptoms as a black widow bite. The Sydney funnel web spider, *Atrax robustus* is found in Australia. This notorious spider is aggressive and has dangerous venom that can and has caused deaths in humans. Reliable information about spiders with venom of medical importance can be found at http://spiders.ucr.edu/dermatol.html.

Most of the dangerous spiders are shy and only become aggressive and bite when provoked. Overall, spiders receive an undeserved reputation for causing bites. Generally, they are friends of farmers, not foes to be avoided or eliminated.



Spider Behaviour and Value in Agricultural Landcapes, Figure 84 **Beneficial spider, *Lycosa pseudoannulata*.**

Importance of Spiders in Agriculture

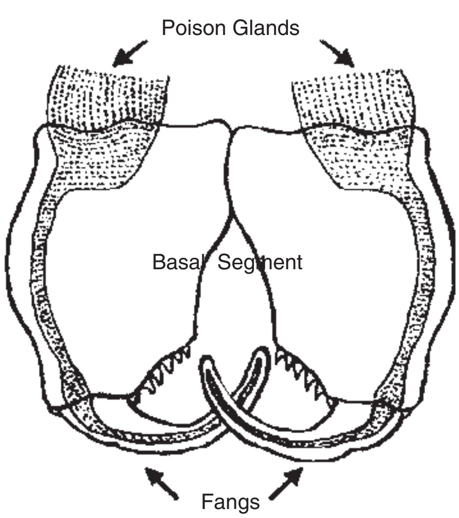
In reality, spiders are a component of the natural enemy complex in nearly all agricultural landscapes. To date, over 300 studies on spiders in different agricultural crops are documented. In general, spiders are extremely beneficial because they are important predators of pests such as thrips, caterpillars, aphids, plant bugs, leafhoppers, flies, and other arthropod pests in home gardens and crop fields. Spiders, along with other predators, are important in agriculture because they regulate and balance arthropod pest populations. They are beneficial in keeping insect populations in check, which far outweighs the hazard posed by the few spiders that occasionally bite humans and pets.

The importance of spiders as pest control agents (Fig. 84) is not a recent discovery. Several ancient books in agriculture mention their importance. In China, the use of spiders for pest control dates back 2,000 years and even today, many elderly people in Chinese villages consider the number of spiders in a field as a measure of its potential agricultural productivity. The scientific literature amply demonstrates the biological control potential of spiders. A classic example of a successful biological control system using spiders was reported on rice. A wolf spider, *Pardosa pseudoannulata* (Lycosidae), successfully controlled the brown planthopper, *Nilaparvata lugens*, which is the major pest of rice in Southeast Asia. In Britain, comb-footed spiders (Theridiidae) and dwarf spiders (Linyphiidae) suppress orchard mites. In Australia, another species of small theridiid, *Achaearanea veruculata*, successfully controls the tortricid moth. A study in an unsprayed peach orchard in the Niagara Peninsula of Canada shows another species of theridiid, *Theridion murarium* and a species of Philodromidae crab spider *Philodromus praelustris*, regulate the density of phytophagous mites.

Feeding Behavior

Great differences exist among spiders concerning the ways in which they capture their prey. While some spiders stalk their prey and others ambush it, most spiders trap their prey by snares and a few live by eating the prey captured by other spiders (these are called kleptoparasites). Spiders paralyze their prey by injecting poison secreted by a pair of venom glands in the chelicerae (front jaws). The ducts from these glands open on each side through a minute pore located near the tip of the fang (Fig. 85).

Prey catching strategies have been thoroughly studied in web-building spiders. For instance, the sheet web spider (family Agelenidae) hides in its funnel-shaped web and rushes out only when the prey has been trapped in the web. Members of the family Linyphiidae construct a horizontal sheet web with vertical threads that serve as trapping lines for insects. Once the prey is trapped by the threads, the spider shakes the web until the victim falls onto the sheet, then bites through the web and pulls down the victim. Some web-building spiders (e.g., theridiids) produce threads with glue droplets that trap and glue insects to the broken threads. The insects become progressively more entangled while attempting to escape. The alerted spider quickly climbs down and throws more sticky threads over the victims before biting them. Some orb weaving spiders bite prey caught in the web, then wrap the prey in silk; others throw silk over the prey first to subdue it, then bite through the silken shroud.



Spider Behaviour and Value in Agricultural Landcapes, Figure 85 **Front jaws (chelicerae of spider).**

The wandering spiders do not rely on snares. Most locate and overpower their prey directly. Among the more familiar examples of wandering spiders are the wolf spiders (Lycosidae), the jumping spiders (Salticidae), most of the crab spiders (Thomisidae), and the two-clawed foliage spiders (Clubionidae, Anyphaenidae). These spiders run in search of their prey and pounce upon it when an opportunity arises. Wandering spiders, exemplified by lycosids or wolf spiders, actively hunt for their prey. Wandering spiders spend some of their time stationary adopting a sit and wait strategy. Wandering spiders catch their prey in a different manner than web-builders. First, they locate the prey. Then they turn toward the victim and grasp it with the tips of the front legs, pulling it to the chelicerae and then biting (venom injection). Next, they release their grasp with the legs and hold the prey with the chelicerae instead, fastening some silk thread over the immobilized victim, and then commence feeding. Wandering spiders may locate their prey either by visual cues or by vibration, depending on the species. Classical examples of visually guided predators are the jumping spiders. They have highly developed main eyes that can analyze shapes, and can even recognize motionless prey. Spiders with poor eyesight, like the clubionids and related species, rely on the vibration of the substrate, or immediate contact with a victim to elicit direct catching movements.

Three species of sac spiders, *Chiracanthium inclusum* (Clubionidae), *Hibana velox* (Anyphaenidae), and *Trachelas volutus* (Corrinnidae), belong to the wandering spider group. Studies show they do not capture prey in webs, but actively hunt their prey, usually at night. During the day, they hide in tubular silken capsules that they construct, which give them the common name sac spiders. They are important in agriculture because they feed on the larvae and prepupae stages of citrus leafminer (*Phyllocnistis citrella* Stainton), one of the major pests of citrus. These spiders belong to the group of spiders with poor vision and they are nocturnally active hunters. Their prey capture depends greatly on substrate vibration. They detect their prey through the vibration of the substrate where the prey is concealed. Movement of citrus leafminer larvae and prepupae creates vibrations on the leaf substrate, which serves as a cue for the spiders to locate the positions of the prey. The prey capture sequence for these three species of spiders follows a similar pattern. During the searching period, the spider moves around and then stops for a while to locate sources of vibration. Once the spider touches the prey with its legs, the spider turns rapidly toward the prey and grasps it.

Two methods of prey attack are exhibited by the three species of sac spiders. In one method, the spider punctures the mine, immobilizes the larva then it bites and sucks the larval body fluid. In the second behavioral pattern, the spider makes a slit on the mine, and then pulls the larva or prepupa out of the mine using its forelegs. The first gentle touch of the forelegs quickly changes into a powerful grip aided by the special hairs on the spider's forelegs. For *Cuppiennius*, another genus of wandering spider, the forelegs are able to improve their secure hold by means of the adhesive hairs or scopulae on the tarsi. This may also be true for *Chiracanthium inclusum*, *Hibana velox*, and *Trachelas volutus* since these species possess tarsal scopulae and dense claw tufts. After securing a hold, the prey is pulled quickly toward the spider's body, then the chelicerae of their fangs move apart and are inserted rapidly into the nearest part of the victim's body. Immediately after the bite, the tips of the legs release their grip and the prey is held in the air only with the chelicerae, thereby minimizing any danger to the spider from the prey. This is advantageous because the victim has no contact with the substrate and therefore cannot apply any direct force to free itself. Only after the prey has become immobilized by the venom does actual feeding (the chewing and the exuding of digestive juice) begin.

Studies show that *Chiracanthium inclusum*, *Hibana velox*, and *Trachelas volutus* start to feed on citrus leafminer larvae at their first nymphal stage. This is not surprising, since spiders in general, after their first nymphal molt, are self-sufficient. At this stage, they have developed their sensory hairs, their legs are equipped with the typical claws, the eyes have the bulging lenses, and the mouthparts are already differentiated for hunting and feeding. The percent of citrus leafminer consumption for all the species of hunting spiders varies among the different nymphal stages and the adult stage. Consumption increases as they develop to later nymphal stages, especially for *H. velox*. Consumption peaks at the third nymphal stage for all of the species, halfway to the adult stage. For all of the species, feeding slows down and sometimes stops for 1 or 2 days before molting and then resumes right after molting. Most spiders that are preparing to molt withdraw into their retreat for several days and stop feeding. This phenomenon occurs naturally in all spiders.

Conservation

The diversity and voracious appetite of spiders in almost all agricultural systems suggests the importance of spiders as predators of insect pests and other arthropods. Thus, they should be considered as an important component of integrated pest control programs. Conservation and augmentation of spiders in fields is a simple and efficient method of pest control. There are several ways to conserve and augment the populations of spiders in the field. One way is to avoid the use of harmful pesticides. Studies show that there are more spiders and fewer insect pests in unsprayed fields than in sprayed ones. Another way is to manipulate their habitat by providing natural mulches (ground cover), which serve as refuge areas for spider breeding or by naturally increasing habitat diversity in the field. A more diverse agroecosystem in terms of habitat structure results in increased environmental opportunities for biological control agents like spiders, and consequently improved biological control. One way to enrich the vegetation structure of cropping systems is through weed management. The impact of weed diversity in the form of weed borders, alternate rows, or by providing weeds in certain periods of the crop growth is important in keeping the populations of the existing beneficial natural control agents, including spiders.

References

Bristowe WS (1971) The world of spiders. New Naturalist, London, UK

Chant DA (1956) Predaceous spiders in orchards in southeastern England. J Hortic Sci 31:35–46

Foelix RF (1996) Biology of spiders, 2nd edn. Oxford University Press, Oxford, UK

Jackson RR (1996) Predatory behavior of jumping spiders. Annu Rev Entomol 41:287–308

Spiders (Arachnida: Araneae)

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Spiders differ from insects, crustaceans and other members of the phylum Arthropoda by having two body parts rather than the three of insects and crustaceans, and the multiple body parts of other arthropods. They also completely lack antennae, the only arthropod group to lack these sensory organs. Spiders use structures called chelicerae in feeding rather than the mandibles found in other arthropod groups.

Evolution and Taxonomy

Spiders, in the order Araneae, share the class Arachnida with other organisms such as scorpions (order Scorpiones), pseudoscorpions (order Pseudoscorpiones), camel spiders (order Solifugae), vinegaroons (order Thelyphonida), tailless whipscorpions (order Amblypygi), daddy long-legs (order Opiliones), and mites and ticks (order Acari). All these arachnid groups are thought to have evolved from an ancestor similar to eurypterids (order Eurypterida). These marine chelicerates were common in the seas from 500 to 245 million years ago (Ordovician to the Permian). Some eurypterids grew to two meters long. These giant aquatic arthropods were formidable predators of the ancient seas and had similar morphological characteristics as extant scorpions. In fact, some of the earliest scorpion fossils resemble more recent eurypterid fossils. Scorpion fossils from the Silurian period probably were aquatic because gills are apparent on these fossils. The arachnids that evolved from a eurypterid-like ancestor moved from the marine environment to the terrestrial environment, but largely maintained their predatory nature.

The earliest fossil arachnids include certain scorpions that date back to the Silurian period between 440 and 410 million years ago. The earliest true spiders appear in the fossil record in the Devonian Period about 380 million years ago. Early terrestrial arthropods had certain adaptations that gave them an advantage in the transition from an aquatic to a terrestrial environment including jointed legs to support the body against the pull of gravity and an exoskeleton to protect them from the desiccating effects of the air. The respiratory structures of the early aquatic chelicerates were probably similar to the book gills found on horseshoe crabs. These book gills are, in turn, similar in structure to the internal book lungs of extant terrestrial arachnids. It is tempting to imagine that as the early chelicerates were making the evolutionary transition from an aquatic to a terrestrial existence, the external respiratory structures became internalized as the book lungs.

The order Araneae currently includes over 40,000 species. This number includes only those species known to science. New species are being discovered every year, and the true species diversity is probably closer to 80,000, according to Dr. Norman Platnick of the American Museum of Natural History. Spiders are found in 108 families and over 3,600 genera. Following is a current taxonomic classification system for spiders, and the currently accepted families. Detailed information about spider taxonomy can be found in The World Spider Catalog at http://research.amnh.org/entomology/spiders/catalog/INTRO1.html.

Kingdom Animalia
Phylum Arthropoda
Subphylum Chelicerata
Class Arachnida
Order Araneae
Suborder Mesothelae
Family Liphistiidae
Suborder Opisthothelae
Infraorder Mygalomorphae
Family Atypidae
Family Antrodiaetidae
Family Mecicobothriidae
Family Hexathelidae
Family Dipluridae
Family Cyrtaucheniidae
Family Ctenizidae
Family Idiopidae
Famiy Actinopodidae
Family Migidae
Family Nemesiidae
Family Microstigmatidae
Family Barychelidae
Family Theraphosidae
Family Paratropididae
Infraorder Araneomorphae
Family Hypochilidae
Family Austrochilidae
Family Gradungulidae
Family Filistatidae
Family Sicariidae
Family Scytodidae
Family Periegopidae
Family Drymusidae
Family Leptonetidae
Family Telemidae
Family Ochyroceratidae
Family Pholcidae
Family Plectreuridae
Family Diguetidae
Family Caponiidae
Family Tetrablemmidae
Family Segestriidae
Family Dysderidae
Family Oonopidae
Family Orsolobidae
Family Archaeidae
Family Mecysmaucheniidae
Family Pararchaeidae
Family Holarchaeidae
Family Micropholcommatidae
Family Huttoniidae
Family Stenochilidae
Family Palpimanidae
Family Malkaridae
Family Mimetidae
Family Eresidae
Family Oecobiidae
Family Hersiliidae
Family Deinopidae
Family Ulobridae
Family Cyatholipidae
Family Synotaxidae
Family Nesticidae
Family Theridiidae
Family Theridiosomatidae
Family Symphytognathidae
Family Anapidae
Family Mysmenidae
Family Synaphridae
Family Pimoidae
Family Linyphiidae
Family Tetragnathidae
Family Nephilidae

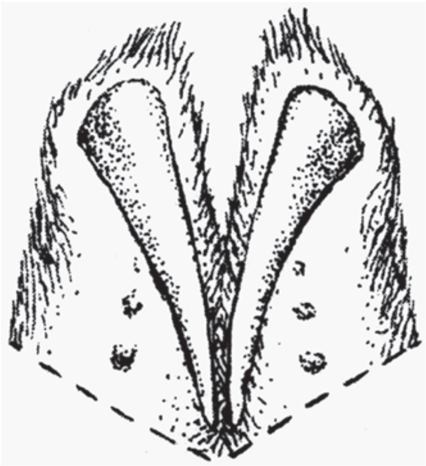
Family Araneidae
Family Lycosidae
Family Trechaleidae
Family Pisauridae
Family Oxyopidae
Family Senoculidae
Family Stiphidiidae
Family Zorocratidae
Family Psechridae
Family Zoropsidae
Family Ctenidae
Family Agelenidae
Family Cybaeidae
Family Desidae
Family Amphinectidae
Family Cycloctenidae
Family Hahniidae
Family Dictynidae
Family Amaurobiidae
Family Phyxelididae
Family Titanoecidae
Family Nicodamidae
Family Tengellidae
Family Miturgidae
Family Anyphaenidae
Family Liocranidae
Family Clubionidae
Family Corinnidae
Family Zodariidae
Family Chummidae
Family Homalonychidae
Family Ammoxenidae
Family Cithaeronidae
Family Gallieniellidae
Family Trochanteriidae
Family Lamponidae
Family Prodidomidae
Family Gnaphosidae
Family Zoridae
Family Selenopidae
Family Sparassidae
Family Philodromidae
Family Thomisidae
Family Salticidae

Spider Phylogeny

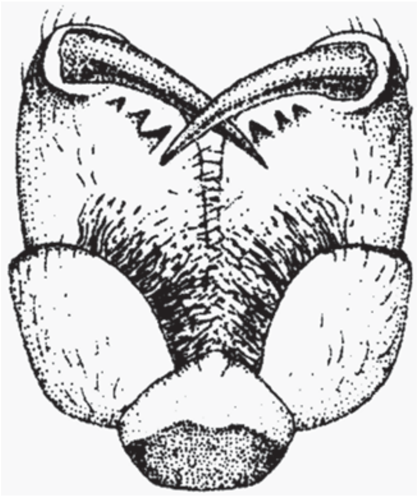
The order Araneae is considered a monophyletic lineage. Characters that unite spiders include venom glands in the chelicerae, male pedipalpi modified for sperm storage, and abdominal silk glands. The suborder Mesothelae is considered a plesiomorphic lineage. Liphistiids are the only spiders that have a segmented abdomen, a character that has been lost in all more recently evolved lineages. Liphistiids also have four distinct pairs of spinnerets instead of the three pairs found in all other spiders. This suborder contains only the single family Liphistiidae, species of which are found only in China, Japan, southeast Asia, and Sumatra.

The suborder Opisthothelae contain all remaining spider families which are divided into two infraorders: the Mygalomorphae and the Araneomorphae. In North America, the mygalomorphs are commonly called tarantulas and, elsewhere, are referred to as baboon spiders. This infraorder includes the quintessential large, hairy pet store spiders. The mygalomorphs are united as a single lineage based largely on spinneret and male genitalic characters. They have only two functional pairs of spinnerets and the bulb of the male pedipalp is fused in most families of mygalomorphs. Most mygalomorphs also are characterized as having paraxial chelicerae that are positioned more or less parallel to one another like the tongs of a garden rake (Fig. 86) These robust spiders also are characterized as having two pairs of book lungs. They also lack a key character present in the infraorder Araneomorphae, the piriform silk gland. Piriform glands allow araneomorphs to cement their silk to a substrate. Piriform silk has enabled araneomorphs to substantially diversify their use of silk, including in the construction of elaborate prey capture webs.

The infraorder Araneomorphae contains the majority of spider species worldwide. This infraorder is sometimes referred to as the "true" spiders even though liphistiids and mygalo-

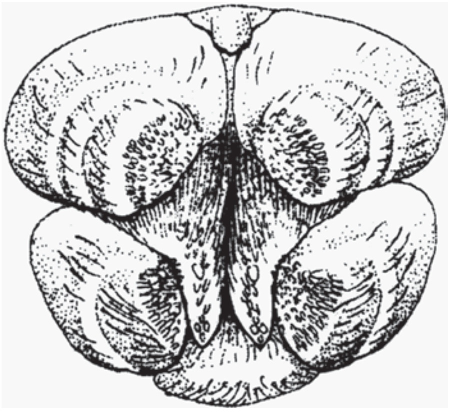


Spiders (Arachnida: Araneae), **Figure 86** **Chelicerae of a spider in the infraorder Mygalomorphae (drawing by Eric Parrish, University of Colorado).**



Spiders (Arachnida: Araneae), **Figure 87** **Chelicerae of a spider in the infraorder Araneomorphae (drawing by Eric Parrish, University of Colorado).**

morphs are as true as they come! This infraorder contains the best known and most familiar spiders, such as the orb weavers in the family Araneidae, the wolf spiders in the family Lycosidae, the jumping spiders in the family Salticidae, and the crab spiders in the family Thomisidae. Araneomorphs typically have opposing chelicerae that move somewhat like the blades of scissors (Fig. 87), and they typically have either one pair of book lungs or lack book lungs altogether. They also have three pairs of spinnerets, although some families of araneomorphs have a residual pair of anterior spinnerets that has evolved into a flattened spinning plate called the cribellum. Ecribellate spiders have a non-functional structure called the colulus (see "Silk production" section for information on the cribellum and its function; Figs. 88 and 89).



Spiders (Arachnida: Araneae), **Figure 88** **Spinnerets of a spider. The colulus is the nipple-shaped structure anterior to the spinnerets (drawing by Eric Parrish, University of Colorado).**

The majority of araneomorph spiders are further divided into two groups known as the Haplogynae and Entelegynae. In the haplogyne araneomorphs, the terminal part of the female's genitalia – that portion that opens to the outside – serves as both a copulatory duct and a fertilization duct. In other words, the external portion of the genitalia connects directly with the seminal receptacles, or spermathecae. Haplogyne females have no complex sclerotized structures associated with their genital opening. The entelegyne spiders, on the other hand, have females with very complex structures associated with their genital openings. These sclerotized structures are collectively referred to as the epigynum. In the entelegyne spiders, side ducts lead from the fertilization duct to the spermathecae. Sixteen families make up the Haplogynae branch of araneomorph spiders and 71 families make up the Entelegynae branch. Three araneomorph families – the Hypochilidae, the Gradungulidae, and the Austrochilidae – are not considered either haplogynes or entelegynes. Hypochilidae form a sister group to all the other Araneomorphae taxa. The hypochilids, like the Mesothelae and Mygalomorphae, are considered a more "primitive" (i.e., earlier evolved) group. Remnants of abdominal segmentation are present in hypochilids and hypochilids have a cribellum (see "Silk production" section). The Gradungulidae and Austrochilidae together form a sister group to the entelegyne/haplogyne branch of the evolutionary tree. The species in these two families are found primarily in South America and Australia, probably due to a Gondwana distribution.

Arachnid Characteristics

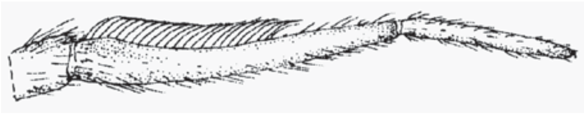
Most arachnids share certain characteristics including: (i) a body divided into two parts, the cephalothorax or prosoma and the abdomen or opisthosoma; (ii) no antennae; (iii) chelicerae; (iv) a unique pair of appendages in the front of their bodies called pedipalps involved in feeding and/or mating; (v) four pairs of walking legs; (vi) external digestion; (vii) indirect sperm transfer; (viii) elaborate courtship behaviors; and (ix) a strict predatory lifestyle. However, not all arachnids share all these characteristics. For example, the cephalothorax and abdomen of opilionids and acarines have become fused giving them the appearance of having only a single body part rather than the two characteristic of the other arachnid groups. Some species in these two orders also differ in having direct sperm transfer. Opilionid males have a penis that delivers the sperm directly into the female's body. Some opilionids can digest solid particulate food and, therefore, do not rely solely on pre-digested, or externally digested, material. Opilionids and acarines also differ in that neither group is a strict predator. Opilionids are, for the most part, scavengers, whereas acarines can be predators, ectoparasites, or plant feeders.

Silk Production

Silk is characteristic of all spiders. Spider silk emerges from structures at the posterior end of the spider's abdomen called spinnerets. The proteinaceous material is produced in silk glands in the abdomen. As the silk protein is exuded through the tiny opening of the silk spigot on the surface of the spinneret, most of the water is re-absorbed. The protein configuration completes its transformation from liquid to solid as the droplet of silk is stretched or put under tension. This can occur as the spider pulls the silk out of the spinnerets with a rear leg, or as the spider attaches the droplet to the substrate and walks away – these movements create enough tension to change the protein structure from liquid to solid.

Most spiders have three pairs of spinnerets – the anterior, the median, and the posterior pairs. However, it is thought that ancestral spiders had four pairs: an anterior lateral pair, an anterior median pair, a median pair, and a posterior pair. Spiders in the suborder Mesothelae still have four pairs of spinnerets, but one pair (the anterior median) is nonfunctional and residual. Many mygalomorph spiders have only two pairs of functional spinnerets having lost the anterior pairs (i.e., the pairs closest to the cephalothorax). Among araneomorph spiders, most species have three pairs of functional spinnerets. The anterior median pair has been lost and a rudimentary, non-functional structure called the colulus remains, positioned between the anterior lateral pair of spinnerets. Other species of araneomorphs, called cribellate spiders, have a flattened spinning plate, called the cribellum, positioned between the anterior lateral pair of spinnerets (Fig. 89). It is thought that the cribellum and the colulus are homologous structures and both are thought to be evolutionary derivatives of the anterior median pair of spinnerets. The cribellum is also thought to be an ancestral, or plesiomorphic, characteristic among the araneomorph spiders. The cribellum is covered with hundreds to thousands of individual silk spigots. In some cribellate species, the cribellum is divided into two small plates; in others, it is a single continuous plate. Cribellate spiders also have a specialized comb, called a calamistrum (Fig. 90), on the metatarsal segment of the last leg. The calamistrum is used to comb the cribellate silk out of the cribellum. Both cribellate and ecribellate spiders are found in the Haplogynae and in the Entelegynae. Therefore, it is currently thought that the cribellum is a polyphyletic characteristic.

Spiders (Arachnida: Araneae), Figure 89 Cribellum located anterior to the spinnerets (drawing by Eric Parrish, University of Colorado).



Spiders (Arachnida: Araneae), Figure 90 Calamistrum located on the metatarsal segment of the last leg of a cribellate spider. Used to comb the silk out of the cribellum (drawing by Eric Parrish, University of Colorado).

On the surface of each spinneret are different types of silk spigots each of which leads to a silk gland in the abdomen of the spider. Spiders can possess up to six different types of silk glands, each secreting a different kind of silk for different functions. These glands include ampullate glands, aciniform glands, tubuliform glands, piriform glands, aggregate glands, and flagelliform glands. Ampullate glands produce dragline silk and spider web frame threads. Draglines are continually produced by spiders as they move around in the environment and serve as safety lines. Aciniform glands produce the silk used to wrap prey as well as silk used by male spiders to construct sperm webs and silk used by females in constructing the outer walls of the silken egg sacs. Tubuliform glands are only found in female spiders and are also involved in the construction of the egg sacs. Piriform glands are used in the production of prey capture silk and in fastening silk lines to the substrate. Flagelliform and aggregate glands are found only in orb weaving spiders. Aggregate glands produce the glue that covers the prey capture silk of ecribellate spiders' webs. Flagelliform glands produce the axial thread of the sticky spiral. Adult male spiders lose their aggregate and flagelliform glands when they mature and, thus, lose the ability to build prey capture webs.

Spider silk is remarkable for its strength and elasticity. In terms of tensile strength, it is about as strong as the best steel. In terms of its tenacity and elasticity, dragline silk would have to be 80 km long before it broke under its own weight and it is more elastic than the stretchiest nylon. Many spiders recycle silk proteins by eating their webs. Scientists have radioactively labeled silk to determine how the silk proteins are used by such spiders. The results of these studies indicate that the silk proteins appear again as new silk in just 30 min;

spiders are clearly the masters of recycling. In World War II, spider silk was used for the cross hairs in gun sights because of its strength and durability. Natives of New Guinea used spider webs as fishing nets. The real Dr. Thomas Muffet of Little Miss Muffet fame was an actual practicing physician who had a fondness for spiders. One of Dr. Muffet's treatments for cuts or abrasions was to wrap the wound in fresh spider webs. Some spider silk has an acidic pH (around pH 4) and is, therefore, resistant to bacterial decomposition. Because of this, there seems to be some benefit to Dr. Muffet's treatment of wounds.

Spiders use silk for a variety of purposes. Dragline silk protects the spider walking around the habitat from plummeting to its death when a sudden gust of wind knocks it off a leaf; egg sac silk provides the spider eggs some protection from desiccation and from egg parasites and predators; non-sticky silk provides the framework for webs and serves to line burrows and retreats of non-web building spiders; sticky silk allows ecribellate web building spiders to capture prey by gluing the prey to the web; cribellate silk allows cribellate web building spiders to capture prey by tangling the hairs of the prey in the fine sheaths of silk combed from the cribellum by the calamistrum. Cribellate silk has also been found to be quite adhesive. Silk production is at the core of a spider's day-to-day existence.

Prey Capture

When spiders encounter prey, most either bite the prey, injecting it with venom and then wrap the prey in silk, or they wrap the prey to immobilize it and then inject the wrapped prey with venom. Whatever immobilization technique is used, venom plays a crucial role. Venom is produced by all families of spiders except those in the family Uloboridae. All other spiders have venom glands in the cephalothorax that are linked to the fangs by ducts running through the chelicerae. One of the common misconceptions about spiders is that the venom of spiders acts not only to immobilize the prey, but also to digest the prey. This is incorrect. The venom is not involved in digestion and contains only trace amounts of digestive enzymes if any at all.

Spider Venoms of Medical Importance

Another common misconception about spiders is that the venom of many spiders is harmful to humans. Of the over 40,000 species of described spiders worldwide, only 160 or fewer have venom harmful to humans, not even 1% of the species. In the United States, the most common spiders with venom of medical importance are the black widow species in the genus *Latrodectus* (family Theridiidae) and the recluse spiders in the genus *Loxosceles* (family Sicariidae). These spiders have proteinaceous toxins in their venom. Both black widows and recluse spiders are fairly timid and only bite when severely provoked. People get bitten by black widows primarily when they accidentally press down on a resting spider hidden beneath a stone, under a log, or under the seat of a privy in an outhouse. In areas where *Loxosceles* is common inside homes, people usually get bitten when the spider seeks shelter in clothing dropped on the floor. As a person puts on the clothing, the spider is threatened and may bite in defense.

The venom of black widows is neurotoxic and can cause severe systemic pain by disrupting the transmitter substances at the neural synapses. Toxicity of *Latrodectus* venom varies between different vertebrates. Rabbits and sheep, for example, are little affected by bites from black widows, whereas horses and camels are very susceptible to injections of the venom. The effect of black widow bites on humans varies between individuals depending on the amount of venom injected, and the age and health of the individual. Rarely do bites from black widows cause death, but they can cause severe abdominal pain, cramps, pain in the joints, and other systemic effects. Antivenin is now readily available in areas where black widows are common. However, because the antivenin is in horse serum and because many people have allergic reactions to the serum, other treatments may be attempted first to ease the pain caused by the bite. Injection of calcium salts may be beneficial. Treatment with pain medications may temporarily ease the symptoms as well, although administration of the antivenin is most effective.

Loxosceles (or recluse) venom is proteolytic and hemolytic, primarily affecting tissues at the bite site. A substance in the recluse venom triggers an immune response that causes the body to cut off blood supply to the affected area. This is what causes the lysis of the cells surrounding the bite site. Bites from these spiders can cause deep, ulcerous wounds that heal very slowly, sometimes taking up to 3 weeks. These lesions can become extensive. They are typically treated topically with corticosteroids. Antibiotics often are given to prevent secondary bacterial infection of the wound site. In extreme cases, surgical excision of necrotic tissue is necessary, often followed by skin grafts. Although antivenin is being developed, it is not yet readily available.

One of the more infamous spiders with medically significant venom is the Sydney funnel web spider, *Atrax robustus* (Mygalomorphae, family Hexathelidae). This spider is found only in Australia. The venom of male *A. robustus* acts upon neuromuscular endings, stimulating the release of acetylcholine, adrenaline and noradrenaline from the autonomic nervous system. Males are much more venomous than females and much more likely to be encountered. Females tend to remain in the funnel webs, whereas adult males are found wandering in search of females and may, in their wanderings, have a face-to-face encounter with a human. When only a little venom is injected, the bite site is very painful for hours to days but, otherwise, only mild reactions to the venom are evident. A more serious bite can result in nausea, vomiting, abdominal pain, arrhythmia and other systemic symptoms. In severe cases, confusion, coma and death by asphyxiation can result from an *A. robustus* bite. Antivenin is now readily available in areas of Australia where the Sydney funnel web spider is found. This antivenin is extremely effective.

Digestion of Prey

Once the prey has been immobilized using venom, the spider regurgitates digestive enzymes onto the prey through the mouth. The mouth is located between three plates situated on the ventral side of the cephalothorax: a central plate called the labium and two lateral plates called the endites. These enzymes that are regurgitated onto the prey break down, or pre-digest the body of the prey until the body has been completely liquefied. When a spider bites its prey, the fangs create holes in the exoskeleton of the prey that serve as entryways for the digestive enzymes. Some spiders create further holes in the body of the prey using teeth lining the fang furrows on the chelicerae. Spiders without such teeth on the chelicerae rely on the holes created by the fangs to digest and suck up the pre-digested prey. With these spiders, all that is left when they are done is the intact exoskeleton of the prey, a hollow husk of its former self.

A spider's stomach is the main organ used to imbibe the pre-digested food. The stomach is located in the dorsal portion of the cephalothorax. It is connected to the spider's exoskeleton by a series of muscle bands. The apodeme, or muscle attachment, of the dorsal band can be seen clearly on the cephalothorax of a tarantula as a median indentation, somewhat like a dimple. Circular muscle bands surround the stomach. When the muscle bands connecting the stomach to the body wall contract, the stomach lumen expands; when these muscles relax, the circular bands reduce the volume of the stomach. The spider's stomach thus acts as a pump, drawing fluid into the body when the long bands contract, or pumping fluid out of the stomach and either forward as regurgitant, or laterally and backward into the remaining tubes of the digestive system. The stomach of spiders, appropriately, is called a sucking stomach.

A spider cannot ingest solid particulate matter; it can only suck into its body pre-digested liquids. Setae are often found on the lateral borders of the endites and on the anterior border of the labium. These setae function to filter out particulate material. The pharynx is lined with downward pointing ridges that also act to filter out larger particles. These larger particles are spit out of the mouth by an anti-peristaltic stream of digestive fluid and are concentrated as a solid pellet, which is then cleared away from the mouthparts using the pedipalps. While feeding, the spider continually vomits digestive fluid and sucks up the resulting liquefied prey until all that is left is the empty exoskeleton, or bits of exoskeleton. When larger spiders feed on vertebrate prey, the pre-digestive process is readily apparent as the mouse or small bird becomes a glistening, liquefied ball of material. All that is left when a vertebrate is eaten is a collection of bones, cartilage, feathers and other indigestible material.

Extensions of the digestive system, called diverticula, extend out into all areas of the spider's body including the legs, the eyes and the abdomen. These extensions create an incredibly efficient and effective transport system for the pre-digested food. Partly because of these extensive diverticula and partly because of the low metabolism of spiders, these animals can go a very long time without eating. Pet tarantulas can be fed once a month or less and be perfectly content (or so it seems).

Excretion

The posterior portion of the digestive system ends in a stercoral pocket, or cloacal chamber. The excretory products of the main excretory organs, the Malpighian tubules, empty into this sac-like stercoral pocket. The main excretory products secreted by spiders are guanine, adenine, hypoxanthine and uric acid, all of which are largely insoluble in water. Therefore, spiders lose very little water through excretion. These excretory products are stored in the stercoral pocket until the pocket is periodically emptied and the material excreted through the anus. In some spiders, waste products from digestion are stored as crystals of guanine just below the transparent cuticle where they are seen as white markings on the abdomen.

Respiratory and Circulatory Systems

When talking about the circulatory system of spiders, it makes sense to talk about the respiratory system as well because the primary function of the circulatory system is oxygen transport. Oxygen enters the body of a spider through openings in the body called spiracles. For mygalomorph spiders, these spiracles lead to two pairs of book lungs. Araneomorph spiders have either one pair or no book lungs. The posterior pair of book lungs in most araneomorph spiders is thought to have evolved into a pair of tubular tracheae.

The spiracle opening into the book lung is a passive opening; in other words, it cannot be closed. The air flows between thin plates of tissue called lamellae. In between these lamellae are evaginations of the body cavity filled with hemolymph, or blood. Oxygen diffuses through the lamellae into the hemolymph. The tubular tracheae of spiders are similar to the tracheae of insects, except that insects have multiple spiracular openings into the tracheae, whereas spiders have either one or two spiracles opening into their tracheae. As with insect tracheae, spiders' tracheae branch into ever smaller tubes. Passive diffusion of oxygen into the hemolymph occurs across the tiny walls of the smallest tracheoles.

For both the book lungs and tracheae, oxygen enters the body passively with little help from muscular contractions. The tracheal system varies in different araneomorph families. In some, the tubes branch out only into the abdomen; in others, the tubes branch all over the spider's body including into the cephalothorax. In some very tiny spiders, they have lost the book lungs completely and rely on an extensive system of tracheal tubes to get their oxygen.

The hemolymph of spiders contains oxygen-carrying molecules called hemocyanin. This molecule functions very similarly to hemoglobin found in mammals. However, hemoglobin has iron atoms as part of its structure and is contained in blood cells, whereas spider hemocyanin has copper atoms and is not contained within blood cells. Whereas the iron atoms give mammalian blood its red color when it becomes oxygenated, the copper atoms gives spiders' blood a blue-green color. Hemocyanin is nearly as effective as hemoglobin in binding to oxygen molecules. The hemolymph of spiders also contains cells that are involved in blood clotting, wound healing, fighting off infections, and storing different types of compounds for transport throughout the body.

After the hemocyanin molecules pick up the oxygen from the book lungs and from the tracheae, this oxygenated blood is carried throughout the body. This transport is carried out via the circulatory system. As with all arthropods, spiders have an open circulatory system; the hemolymph bathes the internal organs and tissues and is not contained in blood vessels. Nevertheless, a circulatory pathway does exist. A spider's heart is located in the dorsal portion of the abdomen. As the heart muscle relaxes, holes in the sides of the heart, called ostia, open and the oxygenated blood is sucked into the heart. The heart then contracts, which causes the ostia to close and forces the blood anteriorly and posteriorly into a system of open-ended arteries. The oxygenated blood thus gets circulated throughout the body in a directional manner such that as the hemolymph loses its oxygen, it flows back toward the abdomen and the respiratory organs before returning to the heart. The circulation of the hemolymph follows a gradient of decreasing blood pressure. This carries the deoxygenated blood back to the abdomen and over the book lungs or tracheal.

In addition to its other functions, the hemolymph of spiders also serves another very important function. Spiders have both flexor and extensor muscles in all their leg joints except the femur-patella joint and the tibia-metatarsal joint, which both lack extensor muscles. Spiders extend their legs at these joints by increasing the blood pressure in their limbs. This increased pressure is caused by a contraction of muscles connecting the carapace (or top of the cephalothorax) with the sternum (or bottom plate of the cephalothorax) thus reducing the volume of the first body segment and increasing blood flow into the extremities. If spiders lose too much water, they can no longer increase hemolymph pressure sufficiently to extend the legs. Spiders caught inside homes away from any source of free water are often found with their legs curled up underneath them. If found in time, a droplet of water can revive such a hapless spider. Although spiders can survive long periods without food, most cannot survive long without some source of moisture.

Sensory Setae and Pits

Setae on a spider's body serve as mechanoreceptors, responding to touch, vibrations, air currents, and positions of the spider's joints. In some mygalomorph species, the setae on the abdomen also serve for defense. These setae are often barbed and, when provoked, the spider brushes them off using a rear leg. Some wandering spiders, such as mygalomorphs and jumping spiders, spiders that hunt without a web, have scopula and claw tufts on the tarsi and metatarsi (Fig. 91). These setae are more structural than sensory. They are very fine setal fringes that allow these spiders to climb and keep a foothold on very smooth surfaces. Any smooth surface is covered by a fine film of water. The thousands of small setae making up the claw tufts and scopula allow these spiders to walk across these surfaces surefootedly due to capillary forces.

Spiders (Arachnida: Araneae), Figure 91 Scopula and claw tufts of a mygalomorph spider (drawing by Eric Parrish, University of Colorado).

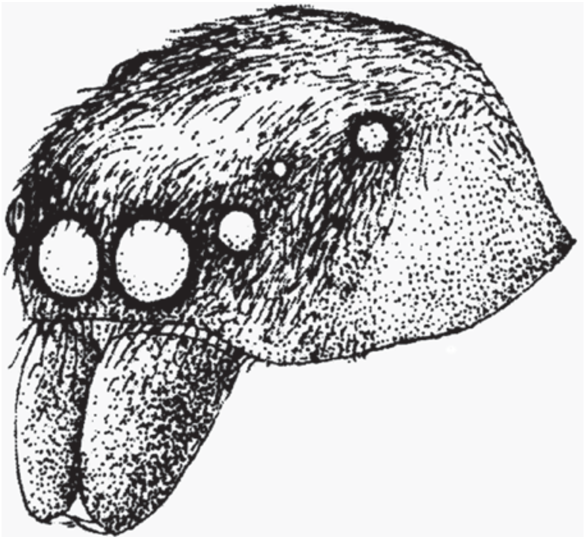
On the leg segments of spiders are long, fine hair-like sensillae called trichobothria. These sensillae are sunk into sockets with multiple dendritic nerve endings at the base. They are found on the legs and are extremely sensitive to air currents, even those produced by the wings of an insect flying nearby. They probably serve in localizing prey or enemies. Patterns of trichobothria are often diagnostic of certain families. Sensory structures called slit sense organs are located near the leg joints. These slits are also connected to dendrites. Clusters of slit sense organs are called lyriform organs because they look like a stringed instrument called a lyre. Slit sense organs, or slit sensilla, serve multiple functions. Some slit sensilla are sensitive to airborne sounds, some probably serve as gravity receptors, some respond to vibrations within a certain frequency, others respond to movements of the spider's own extremities.

Open-ended hair-like setae at the ends of the legs and pedipalps serve as taste receptors. Spiders will avoid pungent or acidic substances upon contact. An adult spider can have over 1,000 contact chemoreceptors, or taste hairs, on the tarsal segments of its legs. These contact chemoreceptors probably enable the spider to tell good-tasting prey from bad and enable males to detect female pheromones that may be deposited in their silk. It is clear that spiders can also respond to airborne odors or smells. It is thought that the "noses" of a spider are small, open pits on the dorsal side of each tarsus. These pits are called tarsal organs. Spiders use these tarsal organs to respond to airborne cues from prey and mates. Although the majority of spiders are solitary predators often living and hunting far away from conspecifics, when a female matures, males are able to quickly locate her. This localization is almost certainly done via airborne pheromones or chemical cues that females deposit either on the substrate or in their silk.

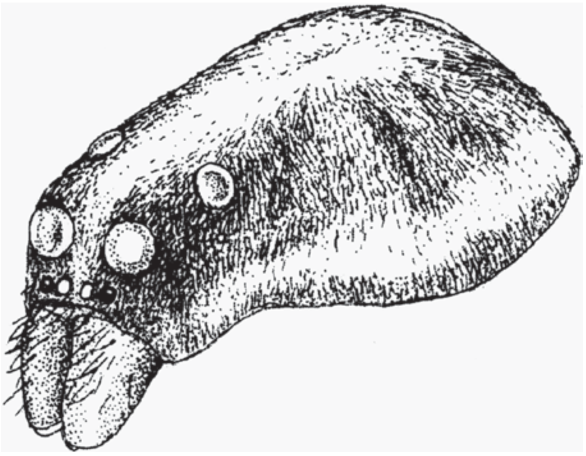
Vision

Most spiders have eight eyes arranged as two rows, although some families are characterized by spiders with only six or two eyes and some cave dwelling species have lost their eyes altogether. Often, the eye arrangement is diagnostic for a particular family. For example, jumping spiders (Salticidae) and wolf spiders (Lycosidae) can be identified to the family level solely by their eye pattern. The structure of a spider's eyes is similar to the ocelli of insects. Spiders have simple eyes with a single outer lens, an inner cellular vitreous body and a layer of visual and pigment cells which together make up the retina. For the vast majority of spiders, vision is not the primary sense they rely upon in their daily lives. Most spiders are nocturnal and, in the low light levels of the night, they rely primarily on tactile and chemical cues. Web building spiders, in particular, have what, by vertebrate standards, would be considered poor vision. They respond to changes in light intensity, or to changes in the polarization of incoming light, but probably cannot see fully formed images of objects. However, wandering spiders or cursorial hunters, such as wolf spiders, jumping spiders and crab spiders are much more reliant on vision both to catch prey and to court mates (Figs. 92 and 93).

Jumping spiders, in particular, have exceptional eyesight. They can probably see in color and can perceive images of objects 8–10 cm from them. A jumping spider will respond to movement of objects up to 40 cm away. These spiders are diurnal and can often be found hunting on the sides of houses, fences, barns or other structures. When a human moves close to a jumping spider, the spider often responds to the movement and orients its body in order to face the person. Their large main eyes, or anterior median eyes, and their



Spiders (Arachnida: Araneae), Figure 92 Eye pattern of a jumping spider in the family Salticidae (drawing by Eric Parrish, University of Colorado).



Spiders (Arachnida: Araneae), Figure 93 Eye pattern of a wolf spider in the family Lycosidae (drawing by Eric Parrish, University of Colorado).

responsiveness to the slightest movement give these spiders a very personable countenance (at least to arachnophiles). Salticids have elaborate courtship behaviors involving zigzag dances and specific movements of the front legs and pedipalps. The bright colors of many salticids probably serve a role in mate choice.

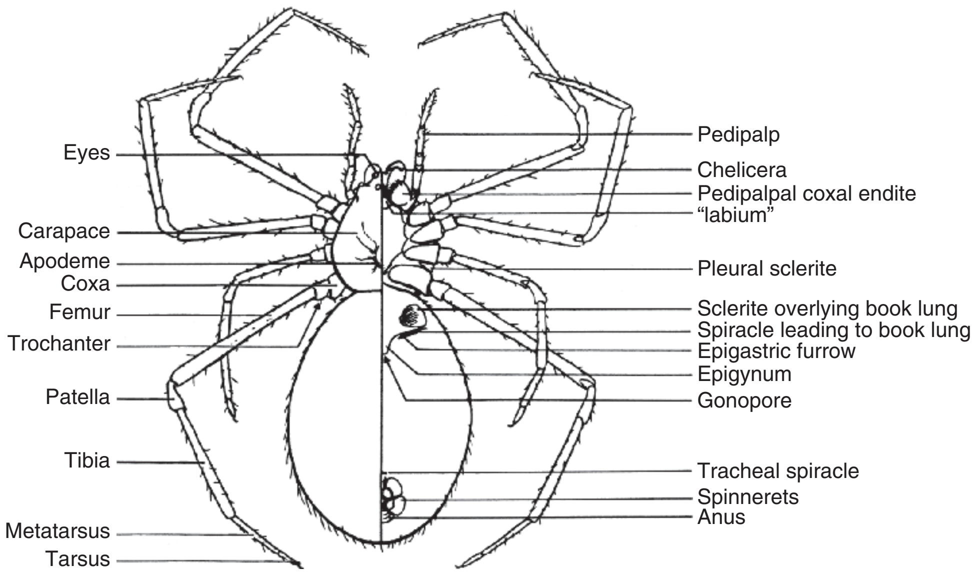
Wolf spiders also have keen vision. Most wolf spiders are crepuscular, or nocturnal. These spiders have a light-reflecting crystalline structure called a tapetum behind the retinal cells of the secondary eyes (secondary eyes include all eyes except the anterior median eyes). It is thought that the tapetum functions to gather incidental light in low light conditions. The tapetum also allows arachnologists to hunt wolf spiders at night using headlamps. The light from the headlamp reflects off the tapetum so spider hunters can find wolf spiders by their eyeshine. Diurnal hunters, such as salticids, lack tapeta. Wolf spiders also have keen vision and actively pursue their prey and their mates. They also have elaborate courtship behaviors involving visual signals. In addition, some wolf spiders incorporate vibratory cues in their courtship rituals by tapping their legs and pedipalps against the substrate.

Central Nervous System

Whereas insects have interconnected ganglia throughout their bodies, spiders have only two major ganglia. Both nerve centers are located in the cephalothorax: the supra- and the subesophageal ganglia. The subesophageal ganglion consists of nerves controlling the legs and pedipalps. A nerve bundle called the cauda equina arises from the subesophageal ganglion and enters the abdomen. The supraesophageal ganglion, located, as the name implies, above the spider's esophagus, includes the nerves to the chelicerae, the pharynx, the poison glands and the eyes. The supraesophageal ganglion is considered the spider's "brain." (Figure 94 shows an overview of a spider's body.)

Although some aspects of a spider's behavior are "pre-programmed" or instinctive, in many respects spiders show a wide range of behavioral plasticity in their response to environmental cues; spiders, in other words, can think. Perhaps they do not think in the way that humans define that term, but they certainly show more behavioral flexibility than one would expect of an animal showing purely instinctive responses to cues.

A good example of this behavioral plasticity is seen with the jumping spiders in the genus *Portia*



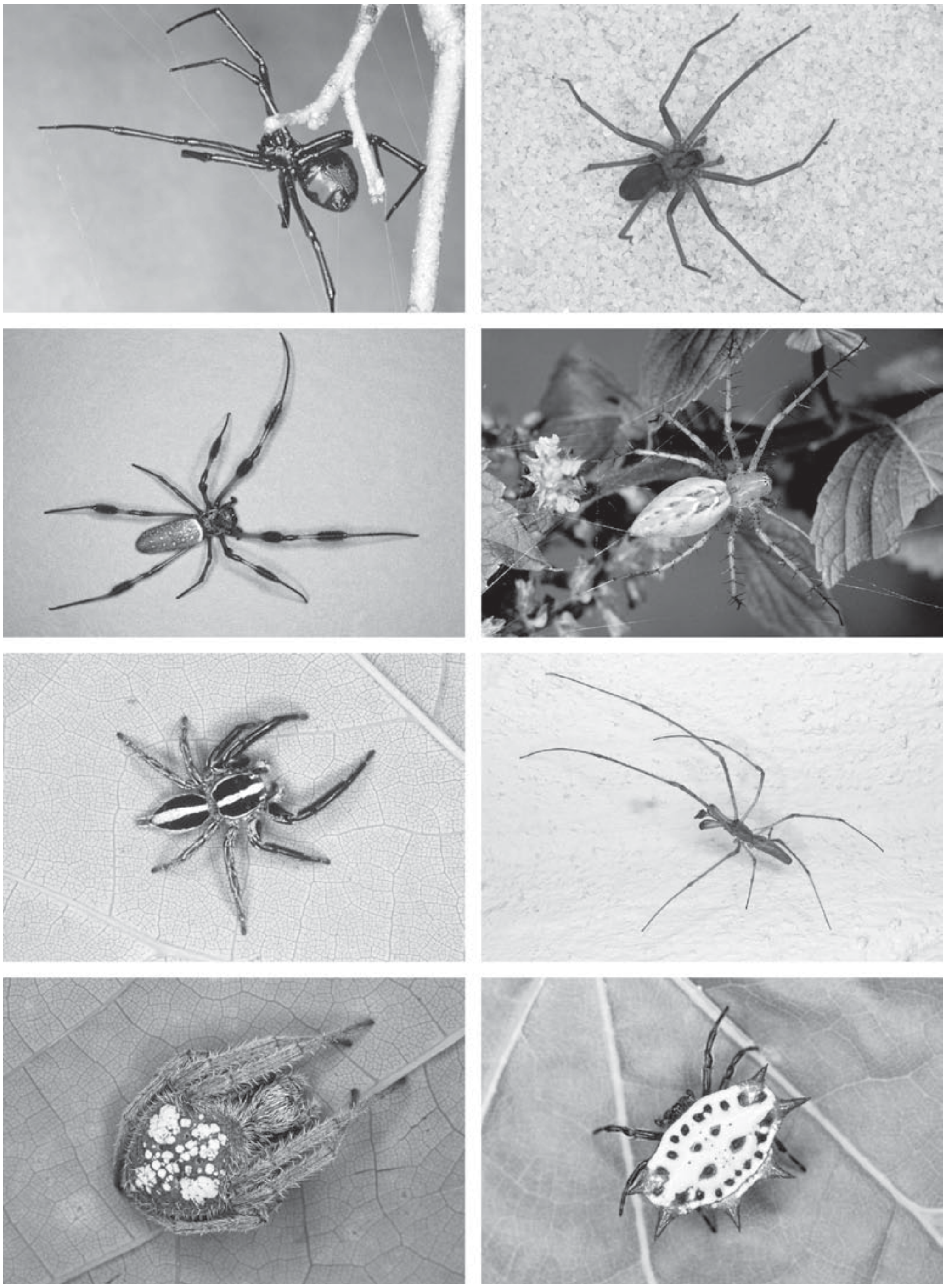
Spiders (Arachnida: Araneae), Figure 94 Composite drawing of a typical spider with principal body parts labeled. *Left half* is dorsal view; *right half* is ventral view.

found in New Zealand. Although most jumping spiders hunt primarily insects, *Portia* specializes in hunting other species of spiders as well as spider egg sacs and insects. *Portia*, as do all jumping spiders, has very keen vision. If it is stalking an insect, its behavioral hunting strategy is similar to that of any other jumping spider. Most insects that *Portia* hunts cannot fight back very effectively so the spider uses stealth, but not caution, in its hunt. However, if *Portia* is stalking another spider, the tables can turn quickly, and hunter can become hunted. *Portia*'s hunting strategy changes commensurate with the type of prey. If the prey is a web building spider, *Portia* will approach the web and pluck it to mimic an insect caught in the silk. If the web builder responds by approaching the vibrations, *Portia* pounces. However, if the web builder does not respond, or if the web builder is larger than *Portia*, the jumping spider will try different vibratory cues or different hunting tactics until its behavior is effective in luring the web builder close enough to kill. *Portia* is even known to detour around a particularly dangerous prey in order to approach from a direction from which *Portia* itself cannot be attacked. A spider's brain may only be the size of a pinhead, but the integration of electrical signals from the spider's appendages and eyes can result in extraordinarily complex behaviors (Figs. 95 and 96).

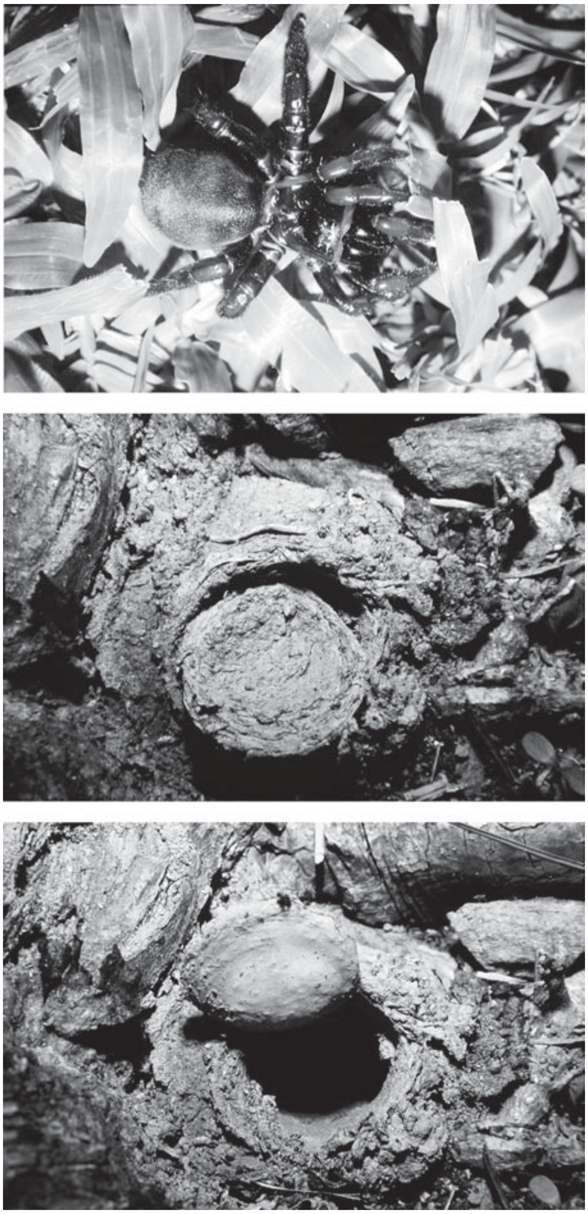
Sex Among the Spiders

The internal sexual organs of spiders, the testes and ovaries, are located in the abdomen. However, male spiders have no intromittent organs associated with the genital opening. As with most arachnids, spiders have indirect sperm transfer. With primitive groups of arachnids, such as scorpions, the male deposits a stalked sperm packet, or spermatophore, on the substrate and, using complex courtship behaviors, manipulates the female over the spermatophore. Male spiders have evolved a more direct strategy for ensuring that their spermatophore makes it into the female.

Male spiders can be distinguished from females by the shape of their pedipalps. Male spiders look like they are wearing boxing gloves on the end of their pedipalps. When a male spider matures, he builds a small platform of silk called a sperm web. In some groups, the sperm web consists of just a few lines of silk. Onto this sperm web,



Spiders (Arachnida: Araneae), Figure 95 **Some common spiders: *top row left*, black widow, *Latrodectus mactans* (family Theridiidae); *top row right*, brown recluse, *Loxosceles reclusa* (family Sicariidae); *second row left*, golden silk spider, *Nephila clavipes* (family Nephilidae); *second row right*, green lynx, *Peucetia viridans* (family Oxyopidae); *third row left*, a jumping spider, *Plexippus paykulli* (family Salticidae); *third row right*, a long-jawed spider, *Tetragnathus* sp. (family Tetragnathidae); *bottom row left*, a tropical orb-weaver, *Eriophora ravilla* (family Araneidae); *bottom row right*, a spiny orb-weaver, *Gasteracantha cancriformis* (family Araneidae) (all photos by James Castner, University of Florida).**



Spiders (Arachnida: Araneae), Figure 96 **Trapdoor spider (family Ctenizidae) (*above*) and burrow with door closed (*middle*) and open (*below*) (photos by author).**

the male deposits a droplet of sperm from his genital opening. He then presses a tube associated with the pedipalp called the embolus into this droplet of sperm and sucks the sperm into the bulb of the pedipalp where it is stored until the male mates. The pedipalps of entelegyne spiders are much more complex than those of haplogynes. However, mating in all groups of spiders requires the expulsion of the sperm stored in the pedipalp into the female's genital opening. In entelegyne spiders, complex structures on the male pedipalp correspond to structures located on the female's epigynum.

The majority of spiders are solitary predators and will opportunistically feed on whatever prey is available, even if the prey is of its own species. A male spider must, therefore, be cautious when approaching a female and must effectively communicate to her that he is a mate and not a meal. This is particularly important among web building spiders because there is often dramatic dimorphism between males and females with males being considerably smaller than their female conspecifics. When a male web building spider locates a female, probably via airborne pheromones, he sings a silk song to her communicating that he is a mate and not a hapless insect caught in the web. If the female is mature and is willing, she will respond to his vibrations in a species specific manner. If she is not responsive to mating, she may try to attack the male.

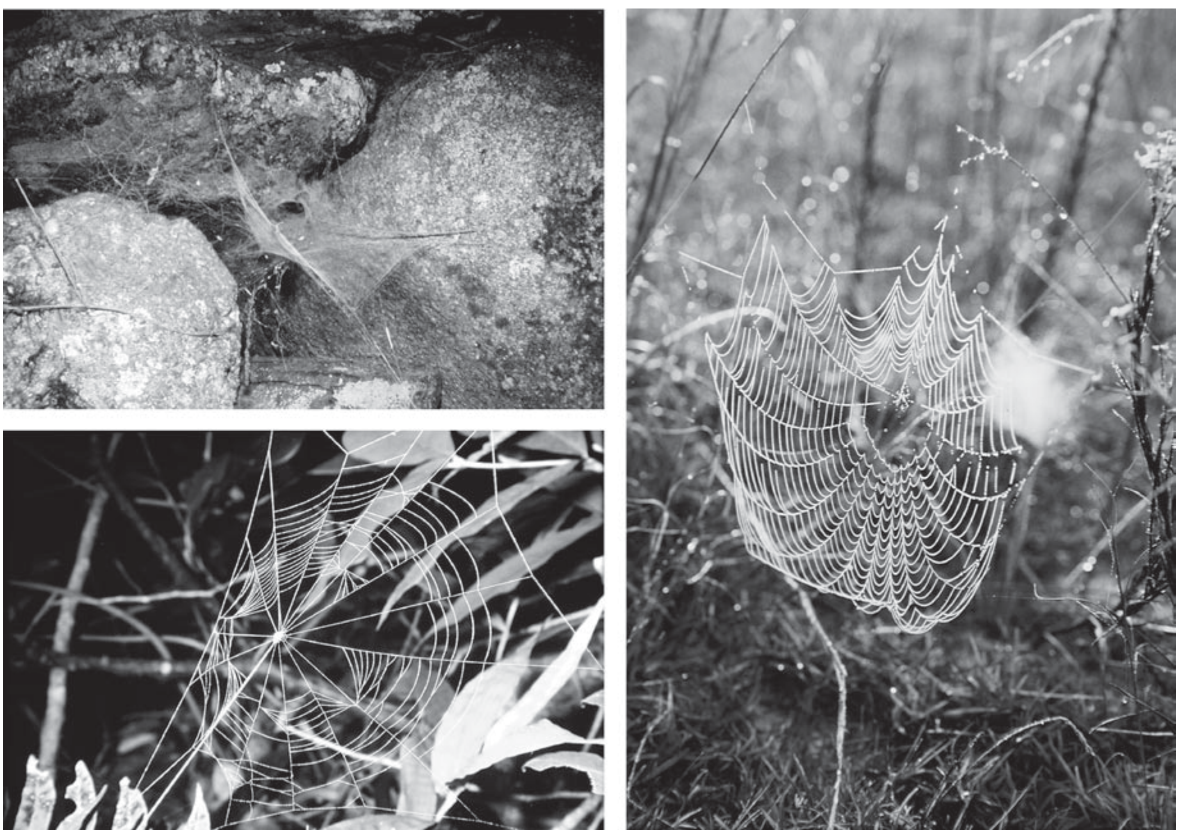
Male wandering spiders, such as wolf spiders or jumping spiders, dance for their lady loves. The courtship behaviors of male jumping spiders are particularly striking in that they often involve zigzag dances, and waving of the legs and pedipalps. Wolf spiders may add a vibratory component by tapping their pedipalps on the ground. Some male spiders have stridulatory structures on their bodies that are probably involved in courtship.

When a male's courtship behaviors have been accepted by a female, he will approach her cautiously and may stroke her. Finally, he will insert his embolus into her genital opening to inject the sperm. The female has seminal receptacles where the male's sperm is stored. Some females will mate multiple times with the same or with different males. In some species, depending on the location of the seminal receptacles in relation to the oviducts, the first male to mate with the female fertilizes most of her eggs, whereas in other species, the last male's sperm takes precedence. In some species, the male will deposit a mating plug into the female's genital opening in an attempt to prevent her from mating with other males. Sometimes, the mating plug is the broken tip of the male's embolus.

When male web building spiders mature, the silk glands responsible for creating prey capture silk become non-functional. In other words, the aggregate and flagelliform glands of male ecribellate spiders become non-functional and the glands associated with the cribellum of cribellate spiders become non-functional. When male web building spiders mature, they are no longer thinking about food, but only of true love. Partly as a consequence of this, male web building spiders have shorter life spans then their conspecific females. This difference in life span holds true for the majority of spiders including mygalomorphs (Fig. 97).

Brood Care, Hatching and Dispersal

Within a few weeks after copulating, female spiders are ready to lay their eggs. The stored sperm is released and fertilization occurs in the oviduct just prior to egg emergence from the genital opening. The female builds a silken egg sac to protect the eggs. In some spiders, the egg sac is an elaborate structure with thick walls of silk. However, some spiders, such as those in the daddy longlegs or cellar spiders family (Pholcidae) (which share a common name with the arachnids in the order Opiliones) attach the eggs together with just a few silk strands. Most females can produce multiple egg sacs, each containing from a few to over 1,000 eggs depending on the species. In many species, the female guards the



Spiders (Arachnida: Araneae), Figure 97 Some spider webs: funnel web (Agelenidae) (*upper left*), theridiosomatid web (Theridiosomatidae) (*lower left*), and orb web (Araneidae) (*right*) (photos by author).

egg sac against egg sac parasitoids and predators until hatching. Female spiders in the family Uloboridae, for instance, remain in contact with the suspended egg sac, brushing off any insect that might land or walk on it. Female wolf spiders (Lycosidae) attach the silken, disc-shaped egg sacs to their spinnerets and carry them around until the egg sacs hatch. Female fishing spiders (Pisauridae) carry their egg sacs in front, holding onto the silk with their chelicerae. Female jumping spiders (Salticidae) remain in silken retreats with their egg sacs until they have hatched.

Within a few weeks, the egg sacs hatch except in those species that overwinter. In some cases, as with wolf spiders, the mother assists her young by cutting a hole in the egg sac to facilitate emergence. In most cases, the offspring cut their own way out of the silken structure. After hatching, some females will continue to guard and care for their young. For example, upon hatching, wolf spiderlings crawl up onto their mother's back. Wolf spider females have specialized knobbed setae on the back of the abdomen to which the babies cling. The female carries her offspring on her back until the yolk supply from the egg stage is depleted and they are old enough to hunt for themselves. In a very few species, the mother actually provides food for her newly hatched offspring either in the form of prey the mother has killed, or in the form of regurgitated food.

After 1 or 2 weeks, the spiderlings of most species are ready to disperse. Ballooning is one common method of dispersal seen among araneomorph spiderlings. These spiderlings crawl to the top of a blade of grass, a twig, a branch or some other structure and release a strand of silk. Air currents catch the silk, often called gossamer, and lift the tiny spider up, up and away. Although some of these "flying spiders" may land only a meter or two away from the take-off point when their silk gets tangled in the branches of a nearby tree, others can travel truly extraordinary distances by this means of aerial dispersal. Some ballooning spiders have been found on ships far out at sea and have been collected from airplanes. Because of this ability to travel long distances by ballooning, spiders are often one of the first pioneer species to establish themselves on distant oceanic islands. However, lack of food and water probably makes life difficult if not impossible for these pioneer predators. In a few families of very tiny spiders, even the adults will sometimes move to a new habitat by means of ballooning. In other spider families, including some mygalomorphs, dispersal mechanisms are much more mundane. The spiderlings, when they are old enough to hunt, simply wander away from natal ground and establish themselves in a new area.

Spiderlings look much like the adult stages except that they are often paler and have no fully developed sexual organs. The complex structures of the male pedipalp do not appear until the final molt, nor do the structures associated with the female's epigynum. The palpal and epigynal characters are the structures used by arachnologists to identify spiders to species. Tiny spiders require about five molts to reach maturity, whereas larger species can require up to 10 molts. Araneomorph spiders do not undergo any further molts after reaching maturity; mygalomorph females, however, continue to molt all their lives. The molting process in spiders is similar to that in insects. As with insects, all chitinous structures, including such internal structures as the trachea, the book lungs and, with mygalomorph females, the linings of the seminal receptacles, are molted. For adult mygalomorph females, this means that any sperm stored in the seminal receptacles when they molt is lost and the female becomes newly virginal (the one group of animals that can actually regain its virginity!).

Most araneomorph spiders either drop down on a silken thread, or enter a silken retreat or burrow when they are getting ready to molt. Mygalomorphs turn over onto their backs prior to molting. Many a pet tarantula owner has thrown away their pet thinking it was dead when it was just getting ready to put on a new skin. As with all arthropods, molting is a dangerous time for the spider. The spider is vulnerable to predators during the molting process and just after completing the molt when the new exoskeleton is not completely sclerotized.

Most male spiders, araneomorphs and mygalomorphs, die shortly after maturation. In temperate regions, most species live only 1 or 2 years. The majority of adults die soon after the first hard frost. In tropical regions, lifespans can vary and there can be multiple generations of one species at any time. The longest lived spiders are some mygalomorph species that have recorded lifespans in the laboratory of up to 30 years for females and up to about 10 years for males. In temperate regions, some spiders overwinter in the egg sac stage, the development arrested until warmer temperatures in the spring. In other species, the spiderlings overwinter by seeking protection in warmer microhabitats in cracks, crevices, or in the leaf litter layer.

Spiders as Predators

Spiders are found in every terrestrial ecosystem on earth except Antarctica. Although a few spiders can obtain some nutritional value from pollen on occasion, all species of spiders, including the occasional pollen eater, are overwhelmingly predatory in their lifestyle. They are one of the top invertebrate predators in terrestrial communities. An arachnologist, William S. Bristowe, once estimated that a one acre field (0.4 hectare) in England could be home to over two million spiders. Although no volunteers have been found to empirically verify this extraordinary number, spiders are in high enough numbers to affect the populations of their prey species. Most spiders are generalist predators and, because of their euryphagous diet, have not been considered useful biocontrol agents in agroecosystems. However, more and more studies have indicated that spiders can, in fact, suppress pest populations. Exploring the usefulness of spiders as biocontrol agents in integrated pest management is a burgeoning field of research.

► Spider Behavior and Value in Agricultural Landscapes
► Predation: The Role of Generalist Predators in Biodiversity and Biological Control
► Conservation Biological Control

References

Barth FG (2002) A spider's world: senses and behavior. Springer-Verlag, Berlin, Germany, 394 pp

Coddington JA (2005) Phylogeny and classification of spiders. In: Ubic D, Paquin P, Cushing PE, Roth V (eds) Spiders of North America: an identification manual. Am Arachnol Soc, pp 18–24

Coddington JA, Levi HW (1991) Systematics and evolution of spiders (Araneae). Annu Rev Ecol Syst 22:565–592

Foelix RF (1996) Biology of spiders, 2nd edn. Harvard University Press, Cambridge, MA

Hillyard P (1994) The book of the spider: a compendium of arachno-facts and eight-legged lore. Avon Books, New York, NY

Nentwig W (ed) (1987) Ecophysiology of spiders. Springer-Verlag, Berlin, Germany

Platnick NI (2002) The world spider catalog, version 8.5. Am Mus Nat Hist. Available at http://research.amnh.org/entomology/spiders/ catalogs/intro1.html (accessed 3 April 2008)

Shear WA (1986) Spiders: webs, behavior, and evolution. Stanford University Press, Stanford, CA

Wise DH (1993) Spiders in ecological webs. Cambridge University Press, Cambridge, MA

Spielman, Andrew

Spielman is recognized for his contributions to public health entomology. Born in 1930 in Brooklyn, New York, USA, he graduated from Colorado College in 1952 before enrolling at Johns Hopkins University where he received a Sc.D. in 1956 in pathobiology. While studying for his doctorate, Spielman worked with the Tennessee Valley Authority in Alabama as a malariologist, and after graduating worked for the U.S. Navy at Guantanamo Bay, Cuba. In 1959, he moved to Harvard University, eventually rising to become a professor of tropical public health in the department of immunology and infectious diseases. His areas of study included malaria, dengue, encephalitis, Lyme disease, West Nile virus, and babesiosis. He worked actively in both the USA and in Africa. Spielman made notable contributions by working in both the field and laboratory. He is probably best remembered for pioneering work on Lyme disease, and the role of deer ticks in transmitting this ailment to humans. He was a proponent of reducing the deer population as a way of managing the disease, but also developed methods to curtail infection in small rodents, and worked on development of a vaccine. Among his nearly 350 publications was a book coauthored with Michael D'Antonio, "Mosquito: a natural history of our most persistent and deadly foe." He died suddenly on December 20, 2006.

Spindle-Shaped

Elongate, cylindrical, thickened at the middle and tapering at the ends.

Spine

A large, stout seta or thorn-like process extending from the integument.

Spinose

Spined, spiny, covered with spines.

Spiny-Headed Worms

A phylum of invertebrates called Acanthocephala. They are usually slightly flattened, and bear an evertable proboscis with hooks or spines (hence the name spiny-headed worms) that are used to pierce and hold the gut wall of its host. They live in the intestinal tracts of vertebrates, but insects sometimes serve as intermediate hosts.

Spined Soldier Bug, *Podisus maculiventris* (Say) (Hemiptera: Pentatomidae, Asopinae)

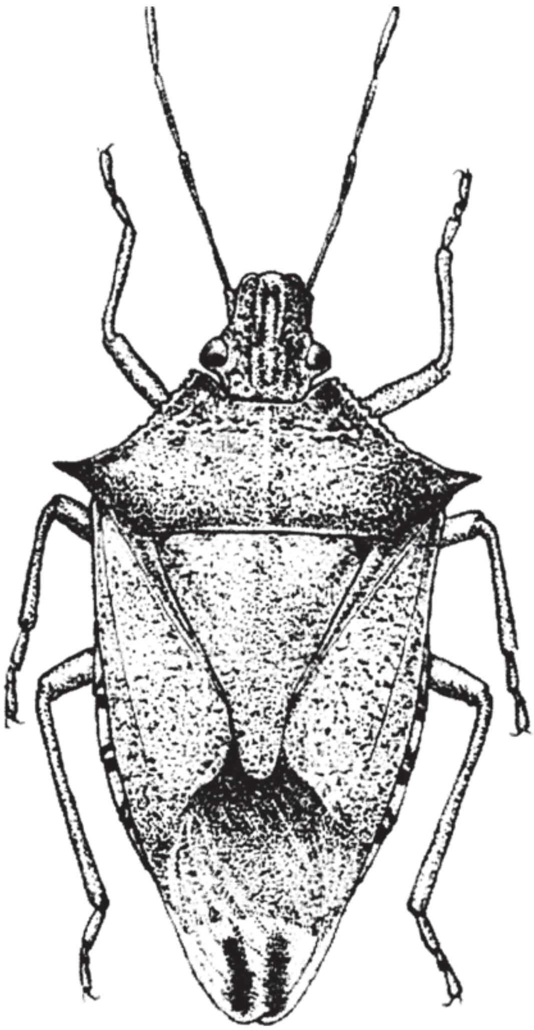
PATRICK DE CLERCQ
Ghent University, Ghent, Belgium

The spined soldier bug, *Podisus maculiventris*, is the most common predatory stink bug in North America. It is naturally distributed from Mexico, the Bahamas and parts of the West Indies into Canada. The insect occurs in a variety of natural and agricultural ecosystems, such as shrubs, woods, streambanks, orchards and several field crops.

Adult spined soldier bugs (Fig. 98) are pale brown to tan in color and are 10–14 mm long, with the females somewhat larger than the males. They are shield-shaped and have a prominent spine on each "shoulder." The adults have a distinct dark spot on the membranous tip of each forewing. The adults, as well as the nymphs, have a thickened rostrum or beak which they can extend fully forward to feed on prey, and which they keep folded under their body when not feeding. The females start ovipositing about 1 week after emerging and usually lay eggs throughout their entire lifetime. The adults are long-lived, with reported longevities ranging from 1 to 4 months under laboratory conditions. Fecundities measured in the laboratory range from 300 to over 1,000 eggs per female, mainly depending on the prey supplied.

The eggs are deposited in loose oval clusters, each containing on average 15–30 eggs. The eggs are about 1 mm in diameter and 1 mm long, are cream-colored to black in color and have a ring of about 15 long micropylar processes around the operculum on top. The duration of the egg stage is 5–8 days, depending on the temperature.

There are five nymphal instars. The nymphs are round to oval rather than shield-shaped. Young nymphs are red and black in color, whereas older nymphs are marked with black, red, yellow-orange and cream bands and patches. The wing pads become clearly visible from the fourth instar on. The length of the respective instars averages 1.3–1.5, 2.5–3, 3.5–4, 5–6, and 7–9 mm. First instars



Spined Soldier Bug, *Podisus maculiventris* (Say) (Hemiptera: Pentatomidae, Asopinae), Figure 98 ***Podisus maculiventris*.**

are highly gregarious and hardly move about. In later instars, the nymphs become progressively more solitary with each molt. First instars are not predaceous and usually only take up moisture, although they have been observed feeding on unhatched eggs from the same mass. The nymphs start actively searching for insect prey shortly after molting to the second instar. The nymphs (and adults) become cannibalistic when food is short. The nymphal stage requires 20–30 days for complete development, depending on the temperature and on the availability and quality of food.

Development from the egg to the adult stage typically takes 4–5 weeks at 20–25°C. A lower threshold temperature for immature development is approximately 12°C. In Canada and in central and northern parts of the United States, the spined soldier bug usually has 2–3 generations per year and hibernates as an adult from October to April. Overwintering takes place in litter, under tree bark, under stones, etc. In warmer climates, like in the southern United States, the insect is active all year.

Although in natural habitats it is primarily found in association with soft-bodied larvae of plant-feeding Lepidoptera, Coleoptera and Hymenoptera, the spined soldier bug is a strongly generalist predator, reportedly attacking more than 90 insect species from 8 orders. Nonetheless, there may be important differences in developmental and reproductive success depending on the prey species or stage supplied. The nymphs and the adults of the spined soldier bug have frequently been observed feeding on plant juices. This plant-feeding habit appears to be particularly important when prey is scarce. Plant-feeding primarily provides moisture, but it may also furnish certain nutrients to the bugs at critical times. Plant-feeding by spined soldier bugs has not been reported to cause plant damage.

Several studies have favorably assessed the predation capacity of the spined soldier bug on various insect pests, including the Colorado potato beetle, *Leptinotarsa decemlineata*, the Mexican bean beetle, *Epilachna varivestis*, the pine sawfly, *Diprion similis*, the fall webworm, *Hyphantria cunea*, the cotton leafworm, *Alabama argillacea*, the cotton bollworm, *Helicoverpa zea*, the tobacco budworm, *Heliothis virescens*, and the beet armyworm, *Spodoptera exigua*. From the 1930s up to the 1980s, numerous attempts have been made to introduce the spined soldier bug into different parts of Europe for the control of the Colorado potato beetle, but the predator never became established, probably because of its inability to overwinter. The predator has been used in augmentative biological control of leaf-feeding caterpillars (mainly belonging to Noctuidae) in

European and North American greenhouse crops. For augmentative releases, the nymphs are preferred to the adults, because the latter tend to fly quickly from the treated plots. Two releases of 0.5 fourth-instars per square meter in commercial glasshouses proved to be effective in keeping noctuid caterpillars in check on sweet peppers, eggplants and some ornamentals. Hot spots of aggregating caterpillars have been treated successfully at densities of 5–10 nymphs per square meter. In field crops in North America, natural populations of the spined soldier bug are often too low to effectively suppress outbreaks of pests like the Colorado potato beetle, particularly early in the season. Natural populations may be augmented by releasing laboratory-reared individuals. In small field plots, releases of about three second- to third-instars per potato plant reduced high densities of Colorado potato beetle eggs and larvae and provided good foliage protection. However, the cost of rearing and releasing the predator on a large scale may be prohibitive. Alternatively, a synthetic pheromone can be used to lure spined soldier bugs to target areas in early spring, as adults emerge from overwintering. The pheromone can also be employed to capture large numbers of predators that can be used to establish mass cultures.

Podisus maculiventris is easily reared in the laboratory on different factitious prey, including larvae of the yellow mealworm, *Tenebrio molitor*, and the greater wax moth, *Galleria mellonella*. Wax moth larvae appear to be a particularly good food, yielding good survival, rapid development and high fecundity. However, given the great voracity of the predator, extensive parallel cultures of prey insects are needed, rendering its mass production less economical. An artificial diet based on beef is available to support the production of consecutive generations of the bug, but development is somewhat prolonged and fecundity is about half of that obtained when wax moth larvae are the primary food.

Although the spined soldier bug has been commercially available in Europe and North America since the 1990s, wider adoption of this beneficial in augmentative biological control is hindered mainly by its high production cost. In Europe, there is also some concern that releases of this and other exotic generalist predators may have detrimental effects on nontarget, native fauna.

► Stink Bugs (Hemiptera: Pentatomidae) Emphasizing Economic Importance
► Predatory Stink Bugs (Hemiptera: Pentatomidae, Asopinae)
► Bugs (Hemiptera)

References

Couturier A (1938) Contribution à l'étude biologique de *Podisus maculiventris* Say, prédateur américain du Doryphore. Annales Epiphyties Phytogénétique 4:95–165

De Clercq P (2005) *Podisus*. Available at http://users.ugent.be/~padclerc/(accessed 3 April 2008)

De Clercq P (2000) Predaceous stinkbugs (Pentatomidae: Asopinae). In: Schaefer CW, Panizzi AR (eds) Heteroptera of economic importance. CRC Press, Boca Raton, FL, pp 737–789

O'Neil RJ (1995) Know your friends: spined soldier bug. Midwest Biological Control News, vol II, no. 8. Available at http://www.entomology.wisc.edu/mbcn/kyf208.html

Weeden CR, Shelton AM, Hoffmann MP (1998) Biological control: a guide to natural enemies in North America. *Podisus maculiventris* (Hemiptera: Pentatomidae). Available at http://www.nysaes.cornell.edu/ent/biocontrol/predators/podisus.html

Spiny Shore Bugs

Members of the family Leptopodidae (order Hemiptera).

► Bugs

Sphingidae

A family of moths (order Lepidoptera). They commonly are known as sphinx, hawk or hummingbird moths, or hornworms.

► Hawk Moths
► Butterflies and Moths

Spinneret

A structure that produces silk in immature insects. The spinneret is often a finger-like structure.

Sphinx Moths

Some members of the family Sphingidae (order Lepidoptera).

► Hawk Moths
► Butterflies and Moths

Spider Beetles

Members of the family Ptinidae (order Coleoptera).

► Beetles

Spider Mites

Mites (Acari) in the family Tetranychidae are often called spider mites.

► Mites
► Acaricides or Miticides

Spider Wasps

Members of the family Pompilidae (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Spine-Tailed Earwigs

Members of the earwig family Forficulidae (order Dermaptera).

► Earwigs

Spinose Ear Tick, *Otobius megnini* (Duges) (Acari: Ixodidae)

This is a livestock pest in western North America.

► Ticks

Spiny Rat Lice

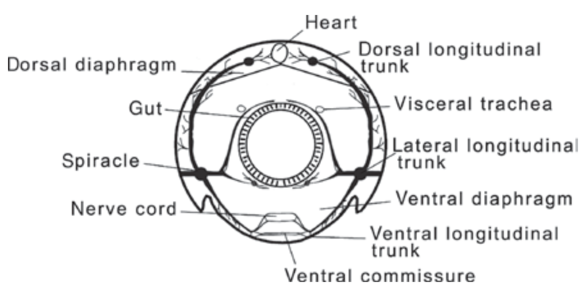
Members of the family Polyplacidae (order Phthiraptera).

► Chewing and Sucking Lice

Spiracle (pl., spiracles or spiraculae)

An external opening of the system of ducts (trachea) used to transfer atmospheric gases into, and out of, the body of arthropods. They are commonly found along each side of the body (Fig. 99).

► Tracheal System and Respiratory Gas Exchange



Spiracle (pl. Spiracles or Spiraculae), Figure 99 **Cross section of the abdomen of an insect, showing the principal trachea and tracheal connections (adapted from Chapman, The insects: structure and function).**

Spiracular Bristles

Bristles found in close proximity to a spiracle.

Spiracular Gill

A gill formed by an extension of a spiracle, or a plastron around a spiracle.

► Tracheal System and Respiratory Gas Exchange

Spiracular Plate

A plate found adjacent to or surrounding a spiracle.

Spirea Aphid, *Aphis spiraecola* Patch (Hemiptera: Aphididae)

This aphid affects citrus and other trees and shrubs.

► Citrus Pests and their Management

Spittlebugs (Hemiptera: Cercopoidea)

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The superfamily Cercopoidea belongs to the suborder Auchenorrhyncha of the order Hemiptera. It includes four taxa, the family Cercopidae, Aphrophoridae, Clastopteridae and Machaerotidae, which encompass the spittlebugs proper and the tube-dwelling machaerotids. Some taxonomists still include all four groups as subfamilies within the traditional unified family Cercopidae.

The Clastopteridae (about 85 described species in one genus) and Machaerotidae (about 105 species in 27 genera) are sister groups, limited to the New and Old World, respectively. The Machaerotidae are predominantly tropical, with a handful of temperate species in China and Japan. The Clastopteridae are abundant from Canada to Argentina, all in the single speciose genus *Clastoptera* (the status of an additional isolated Philippine genus is problematic). The Aphrophoridae (about 820 species in 150 genera) probably represent a polyphyletic group, in which the Cercopidae constitute one monophyletic branch. The Aphrophoridae are best represented in north temperate habitats, but also occur widely in the tropics. There are approximately 1,360 described species in the Cercopidae in 140 genera, and a recent revision lists 416 of those species distributed in the New World. This group is predominately tropical. Only two species, *Prosapia bicincta* and *P. ignipectus*, occur north of Mexico in the Americas, and only two genera, *Cercopis* and *Haematoloma*, occur in Europe.

Adult spittlebugs, known as froghoppers for their quick jumps and putative resemblance to tiny frogs, are named in parallel to other Auchenorrhyncha such as the leafhoppers, planthoppers and treehoppers. They are distinguished from these groups by 1 or 2 strong spines on the metatibia, a crown of spines at the distal end of the tibia, and nymphs that live in spittle masses or calcareous tubes filled with liquid.

Biology and Behavior

Nymphs and adults of the Cercopoidea have sucking mouthparts and feed on the xylem sap of host plants. Compared to phloem sap, xylem sap is a challenging food resource because it is normally under negative pressure and offers a very dilute source of organic nutrients. Special adaptations to this resource include a filter chamber shunt to manage high volumes of fluid and an inflated clypeus and reinforced apodemes to support the enlarged sucking muscles. Other consequences include a relatively long life cycle and unique defensive opportunities for the nymphs compared to phloem-feeding Auchenorrhyncha.

The Cercopoidea have five nymphal instars. Nymphs in the Clastopteridae, Aphrophoridae and Cercopidae construct spittle masses at their feeding sites and gain protection from desiccation and most natural enemies. The spittle is composed of bubbles added to excreted, attenuated xylem sap fortified with mucopolysaccharides that are secreted by the Malphigian tubules. Nymphs form the bubbles one-by-one with repeated thrusts of the tip of the abdomen out of the excreted liquid to pick up air in a special pocket formed by the ventral abdominal plates. The Clastoptera tend to have very aqueous spittle masses, while those of the Aphrophoridae are frothy and those of the Cercopidae intermediate. Typically there is a single nymph per spittle mass, but sometimes two or more nymphs cohabit one mass. On occasion, nymphs of two species share a common spittle mass. The widespread Neotropical aphrophorid species *Cephisus siccifolius* forms large communal spittle masses with dozens of nymphs. Machaerotid nymphs live in liquid-filled calcareous tubes constructed at the feeding site. They form a spittle mass, at the mouth of the tube, only in conjunction with the adult molt.

Adult spittlebugs do not make spittle masses. Like nymphs, they excrete large volumes of sap, but flick it away in small drops, so it does not accumulate. Large species may drip like faucets when actively feeding. In Africa, species of the aphrophorid genus *Ptyelus* drip so copiously that it appears to be raining beneath their dry season "raintree" hosts.

Adult Aphrophoridae, Clastopteridae and Machaerotidae depend on camouflage or disruptive coloration and jumping as defensive mechanisms. The Cercopidae exhibit a unique shared character, reflex bleeding. When threatened, adult Cercopidae emit odoriferous orange hemolymph from the tips of their feet, helping to repel attackers. This defense is accompanied by warning coloration in a large proportion of taxa. Many species exhibit striking red, yellow, orange or black markings, making them conspicuous in their natural surroundings.

Substrate communication plays an important role in courtship and other behaviors among adult Cercopoidea. Tymbals located on the first abdominal segment produce vibrations that are transmitted through the host plant. In the Cercopidae, male courtship calls vary in pulse structure (simple to compound), duration, peak frequency and pulse repetition frequency. A receptive female transmits her response via the substrate to guide males to copulation. There is also evidence for other classes of vibrational communication, such as distress calls.

Most temperate spittlebugs are univoltine. A few have two generations per year. Most tropical spittlebugs are multivoltine, with life cycles tied to seasonal rainfall patterns.

Ecology

Spittlebugs feed on an unusually wide range of plants. Very generally speaking, the Cercopidae tend to feed on herbaceous monocots, the Clastopteridae and Machaerotidae on flowering trees and shrubs, and the Aphrophoridae on conifers and herbaceous dicots. There are many exceptions to these generalizations, however, and some species feed on an extraordinarily wide range of hosts. Philaenus spumarius, the aphrophorid meadow spittlebug, may have more recorded hosts than any other phytophagous insect. Presumably, wide host range is a consequence of xylem feeding, xylem sap being chemically less defended and rather similar in composition across plant groups. Within this diversity of hosts, many spittlebugs have an affinity for nitrogen-fixing plants that may provide a richer and more constant source of xylem sap nutrition. The Cercopidae, for instance, have a predilection for plants that have associative nitrogen fixation through root zone bacteria, while many Aphrophoridae prefer legumes, and many Clastoptera prefer actinorhizal hosts. Other factors that influence host plant or feeding site selection include concentration of amino acids, tissue toughness, depth of xylem elements, presence of trichomes and growth habit or architecture.

Two species of the genus *Mahanarva* in Central America have aquatic nymphs that live in the flowers of Heliconia plants, the only known truly aquatic spittlebugs. Nymphs of several species of Aphrophoridae and Clastoptera as well as one machaerotid have associated Diptera (Drosophilidae: Cladochaeta, Leucophenga, Paraleucophenga) larvae that share their spittle masses. The precise nature of these associations, whether parasitic or commensal, is not fully understood.

In the temperate zone several aphrophorid species (primarily of the genera *Aphrophora* and *Peuceptyelus*) are serious pests of conifers. Philaenus spumarius is a pest of alfalfa and other legume forage crops, as well as strawberries. Clastoptera species attack cacao, pecans and citrus but are only rarely of serious concern. The cercopid species Haematoloma dorsatum is a pest of pines in Southern Europe and, as elaborated below, the grass-feeding Cercopidae as a group are serious pests in Latin America.

As xylem feeders, spittlebugs are infrequent disease vectors, but all tested species transmit the xylem-limited bacterium *Xylella fastidiosa*, which causes Pierce's disease of grape and diseases of several other plants. *Xylella fastidiosa* is a serious concern in California and other areas where this bacterium poses a threat to commercially important crops. Spittlebugs also transmit the bacterium that causes Sumatra disease of cloves and the mycoplasma that causes stunt disease of *Rubus*.

Grass-Feeding Neotropical Spittlebugs

As pests, the Neotropical grass-feeding spittlebugs of the cercopid subfamily Ischnorhininae are by far the most important Cercopoidea. This economically critical subset includes dozens of species from at least 11 genera (*Aeneolamia*, *Deois*, *Isozulia*, *Kanaima*, *Mahanarva*, *Maxantonia*, *Notozulia*, *Prosapia*, *Sphenorhina*, *Tunaima*, *Zulia*). These insects are destructive pests of forage grasses and sugar cane, and occasionally other cultivated graminoids, such as turfgrass and rice. The following sections relate specifically to this well-studied group.

Life Cycle

Eggs go through four generalized developmental stages, completing development in 2–3 weeks. In the case of diapause and quiescence, time to hatching can be prolonged up to 530 days. Although soil is the most common oviposition site, litter and plant stem surfaces are used by some species and favored in preference to soil by others.

The five nymphal instars can be reliably differentiated by morphological measurements, particularly the width of the head capsule. Recently emerged first instar nymphs usually establish spittle masses on roots at the soil surface or in cracks and pores of the upper layer of soil. While the nymphs of most species remain near the soil, others migrate upwards into leaf axils on more erect hosts. In sugar cane, for instance, *Aeneolamia postica* nymphs emerge from eggs in the soil and complete development on surface roots, while *Mahanarva andigena* nymphs emerge from eggs on litter or the base of old leaf sheaths and favor aerial spittle masses in leaf whorls. Development time varies with species and climate, ranging from 4 to 9 weeks. Duration of the adult phase ranges from 1 to 3 weeks.

Adults usually exhibit sexual dimorphism, with males smaller and often more brightly colored than females. Some species also exhibit multiple color forms within one or both sexes, while unrelated species often share common color patterns, complicating species identification. The styles, plates and aedeagus of the male genitalia are the most diagnostic taxonomic features.

Agricultural Ecology

Nymphs and adults of grass-feeding spittlebugs occur during the wet season. Most species pass the dry season as drought tolerant diapause eggs. Depending on species, habitat and duration of the wet season, they achieve 1–6 generations per year. In highly seasonal sites, the return of the wet season promotes synchronous hatching and damaging early season outbreaks. Population dynamics are characterized by high population fluctuations and population synchrony. In continuously humid sites, all life stages are present throughout the year, fluctuations and synchrony are reduced, and yield loss can be less severe.

The most widely reported natural enemies are fungal entomopathogens, predaceous larvae of the pan-Neotropical syrphid fly *Salpingogaster nigra* that attack nymphs in their spittle masses, parasitic nematodes (Mermithidae), and generalist robber flies (Asilidae). Egg parasites (Eulophidae, Mymaridae, Trichogrammatidae), parasitic flies (Pipunculidae) and parasitic mites (Erythraeidae) also have been reported.

Economic Impact

Grass-feeding spittlebugs are widely distributed in the Neotropics and are economically important in lowlands and highlands from the southeastern U.S. to northern Argentina. They attack all economically important genera of tropical forage grasses, particularly species of African origin. Adult feeding causes a phytotoxemia identified by a chlorosis that spreads from the feeding site. Nymphs cause damage similar to water stress, identified by browning spreading from the leaf tip. Severe outbreaks result in the yellowing off of the entire aboveground portion of the plant. This damage lowers forage production, quality, and palatability, reduces milk and beef production, inhibits the establishment and persistence of improved pastures, and increases soil degradation.

Pest Management

Management of spittlebugs in forage grasses and sugar cane is still haphazard, given the challenges posed by the diverse situations in which they occur. Due in part to incomplete information on the biology and habits of the specific pest species, there has been a tendency to overgeneralize the spittlebug/host/habitat interactions to the detriment of control efforts. In pastures, controlled grazing, effective fertilization, burning, host plant selection and diversification of forage species offer possibilities for control. A long-term breeding program is achieving successes for spittlebug resistance in *Brachiaria* grasses, the most widely planted forage grasses in South America and the most susceptible to spittlebug attack. In sugar cane, control measures include cultural control tactics and applications of commercial fungal entomopathogens. Management successes in both systems are limited by poorly developed IPM decision tools such as yield loss assessments, sampling schemes and thresholds, in addition to the fundamental challenges inherent to IPM in extensive and low value agroecosystems such as rangelands.

In systems with highly seasonal precipitation, the recommended management strategy is temporal and spatial identification of the early season nymph outbreaks to target control tactics that will suppress population development before the invasion of uninfested areas and the propagation of future generations. In less seasonal systems, the recommended management strategy will depend on cultural control techniques such as host plant selection and controlled grazing, and there will be more options for biological control.

References

Carvalho GS, Webb M (2005) Cercopid Spittle Bugs of the New World: Hemiptera, Auchenorrhyncha, Cercopidae. Pensoft Publishers, Sofia-Moscow. 280 pp

Hamilton KGA (1982) The spittlebugs of Canada (Homoptera: Cercopidae). The insects and arachnids of Canada, Part 10, 102 pp
Peck DC (1999) Seasonal fluctuations and phenology of *Prosapia* spittlebugs (Homoptera: Cercopidae) in upland dairy pastures of Costa Rica. Environ Entomol 28:372–386
Thompson V (1994) Spittlebug indicators of nitrogen-fixing plants. Ecol Entomol 19:391–398
Valério JR, Lapointe SL, Kelemu S, Fernandes CD, Morales SJ (1996) Pests and diseases of *Brachiaria* species. In: Miles JW, Maass BL, do Valle CB (eds) *Brachiaria*: biology, agronomy and improvement. CIAT, Cali, Colombia, pp 87–105

Splenetic Fever

This tick-borne illness of cattle is also known as Texas cattle fever.

► Piroplasmosis

Spongillaflies (Neuroptera: Sisyridae)

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The insect order Neuroptera is primarily a terrestrial group. Unique among the neuropterans, however, is the family Sisyridae that have aquatic larvae. The common name of this family is spongillaflies and is derived from the predaceous, and arguably parasitic, feeding of the larvae on freshwater sponges (Porifera: Spongillidae). Spongillafly larvae occur in various types of freshwater habitats including streams, lakes and impoundments. Comparatively little is known about the biology of sisyrids in relation to other aquatic insect groups largely due to their unique larval habitats and their relative rarity. The classification is as follows:

Order: Neuroptera
Suborder: Planipennia
Superfamily: Hemerobioidea
Family: Sisyridae

Taxonomy and Distribution

The known genera of spongillaflies include *Climacia*, *Sisyra*, *Sisyrina* and *Sisyborina*. The genus *Climacia* is distributed primarily in the New World tropics although three species are represented in temperate regions. The genera *Sisyrina* and *Sisyborina* consist of only three described species and is restricted to India and Asia, respectively. *Sisyra* occurs throughout the world from boreal to tropical environments. Only about 60 described species of spongillaflies among all genera occur worldwide.

Adult spongillaflies superficially resemble brown lacewings (Family Hemerobiidae). However, because of the branching pattern of the forewing venation, brown lacewings appear to have two radial sector veins while the spongillaflies have only one clearly defined radial sector vein. In addition, most of the coastal crossveins of brown lacewings are branched, but those of sisyrids are not branched. Most spongillaflies are uniformly brown in color, but some species in the genus *Climacia* have colorless wings marked with black and brown patches or streaks (Figs. 100–101).

Sisyrid larvae (Fig. 102) are robust, odd-looking insects having fairly long antennae, and slender legs each bearing a single tarsal claw. Their bodies bear numerous stout setae, and they are variably colored ranging from yellowish-brown to green. In addition, the second and third instar larvae bear two-or three segmented, transparent ventral gills that are folded beneath the abdominal segments. The mouthparts of larval spongillaflies are modified into elongate, unsegmented styles used for sucking fluids from their sponge hosts.

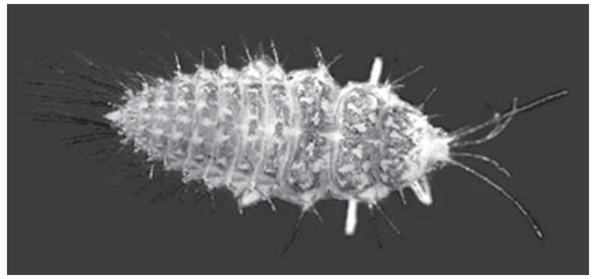
Natural History

Spongillafly larvae most often are found crawling about the surface of their host sponge, but occasionally they may be found within the cavities and recesses of the sponge. Several genera of freshwater sponge are parasitized by spongillaflies

Spongillaflies (Neuroptera: Sisyridae), Figure 100 ***Sisyra vicaria*** **(Walker). Female, lateral view.**
Sisyrid larvae are robust, odd-looking insects having fairly long antennae, and slender legs each bearing a single tarsal claw. Their bodies bear numerous stout setae, and they are variably colored ranging from yellowish-brown to green. In addition, the second and third instar larvae bear two- or three segmented, transparent ventral gills that are folded beneath the abdominal segments. The mouthparts of larval spongillaflies are modified into elongate, unsegmented stylets used for sucking fluids from their sponge hosts.

Spongillaflies (Neuroptera: Sisyridae), Figure 101 ***Climacia areolaris*** **(Hagen). Female, lateral view.**

and all are widely distributed in North America. These genera include *Anheteroeyenia*, *Dosilia*, *Ephydatia*, *Eunapius*, *Heteromeyenia*, *Radiospongilla*, *Spongilla* and *Trochospongilla*. Some

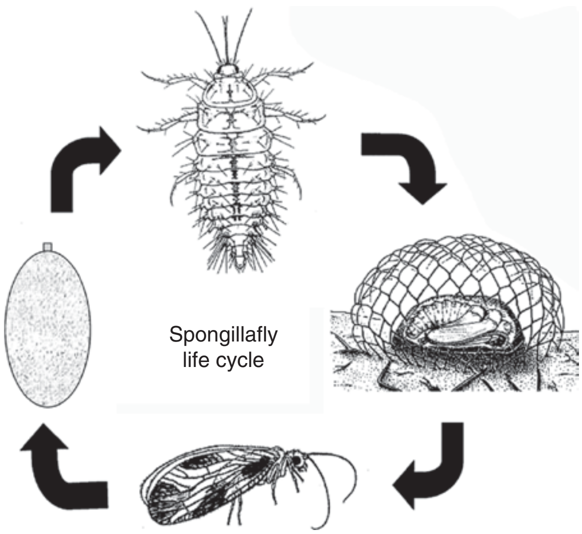


Spongillaflies (Neuroptera: Sisyridae), Figure 102 ***Climacia chapini*** **Parfin & Garneg. Larva, dorsal view.**

sponges do not form large, robust colonies and may appear only as a thin encrustation on woody debris or stones. The latter forms are more difficult to locate and collect than the former, but they still can support spongillaflies. Rarely, spongillaflies have been reported feeding on bryazoans and algae. Adult spongillaflies often can be found on flowering plants and other riparian vegetation during daylight. The feeding habits of adult spongillaflies are not well known, but they have been observed feeding on insect eggs, and nectar also may be a food source.

Spongillaflies have complete life cycles similar to that of other neuropterans. Female spongillaflies typically lay eggs in masses of 2–5 on emergent vegetation or other objects overhanging the water. The eggs are oval, whitish to yellowish in color, and covered with a web of white silk. The eggs hatch in about 1 week and the first instar larvae fall into the water and immediately proceed to search for a host sponge. First instar larvae "jump about" presumably to aid in their distribution. Jumping is accomplished by tucking the various appendages underneath the body and then rapidly straightening them out causing the body to lift off the substrate and move forward. Mature larvae swim in a vertical position and gain forward movement by snapping the body. There are three larval instars in the life cycle with the final instar larvae ranging from 4 to 8 mm in length (Fig. 103).

Prior to pupation, final instar larvae leave the water and climb onto objects along the bank such



Spongillaflies (Neuroptera: Sisyridae), Figure 103 **Generalized life cycle of a spongillafly. The pupal cocoon is cut-away to show the pupa inside. Illustrations are redrawn and modified from those of Brown (1952) and Pupedis (1987).**

as plants, tree limbs and other solid structures often some distance from the water. Pupae are housed in hemispherical, usually double-walled, silken cocoons. The inner wall of the pupal cocoon consists of tightly woven mesh and the outer wall is more loosely constructed.

Spongillafly larvae in North America occasionally are attacked by the parasitoid wasp *Sisyridivora cavigena* Gahan (Hymennoptera: Chalcidoidea: Pteromalidae). The female wasp pierces the pupal cocoon of the spongillafly using a long ovipositor, stings the pupa, and lays its eggs. In some instances, the female wasp may use a feeding tube constructed from their own ovipositors to feed on the body fluids of the host. The extent and effects of such parasitism on spongillafly populations are unknown.

Collecting Methods

Adult spongillaflies are strongly attracted to a variety of lights including incandescent, ultraviolet, and mercury-vapor. Such lights provide an excellent means by which to collect adult spongillaflies. Adult spongillaflies also can be collected by sweeping the vegetation bordering aquatic habitats. Larvae can be collected by hand from freshwater sponges, and by using a variety of benthic collecting devices and techniques such as kick-nets, Surber and Hess samplers, and Eckman and Ponar grabs.

Preservation

Larval and pupal spongillaflies ideally should be fixed in Kahle's solution (parts by volume: 15–95% ethyl alcohol, 6–10% formalin, 1-glacial acetic acid, 30-distilled water) for approximately 24-h when possible, and then permanently stored in 70% ethyl or isopropyl alcohol. However, 80% ethyl or isopropyl alcohol will serve this purpose satisfactorily when Kahle's solution is unavailable. Adult specimens ideally should be pinned or pointed, but preservation in 70% ethanol or isopropyl also is suitable.

► Lacewings
► Antlions
► Mantidflies

References

Brown HP (1951) *Climacia areolaris* (Hagen) parasitized by a new pteromalid (Hym.: Chalcidoidea). Ann Entomol Soc Am 44:103–110

Brown HP (1952) The life history of *Climacia areolaris* (Hagen), a neuropterous "parasite" of freshwater sponges. Am Midl Nat 47:130–160

Parfin SI, Gurney AB (1956) The spongilla-flies, with special reference to those of the Western Hemisphere (Sisyridae, Neuroptera). Proc U S Natl Mus 105:421–529

Pupedis RJ (1978) Tube feeding by *Sisyridivora cavigena* (Hymenoptera: Pteromalidae) on *Climacia areolaris* (Neuroptera: Sisyridae). Ann Entomol Soc Am 71:773–775

Pupedis RJ (1980) Generic differences among new world spongilla-fly larvae and a description of the female of *Climacia striata* (Neuroptera: Sisyridae). Psyche 87:305–314

Pupedis RJ (1987) Foraging behavior and foods of adult spongilla-flies (Neuroptera: Sisyridae). Ann Entomol Soc Am 80:758–760

Spore

A reproductive stage of fungi, usually somewhat resistant to adverse environmental conditions, that is capable of growing into a new organism.

Spotted Cucumber Beetle or Southern Corn Rootworm, *Diabrotica undecimpunctata* Mannerheim (Coleoptera: Chrysomelidae)

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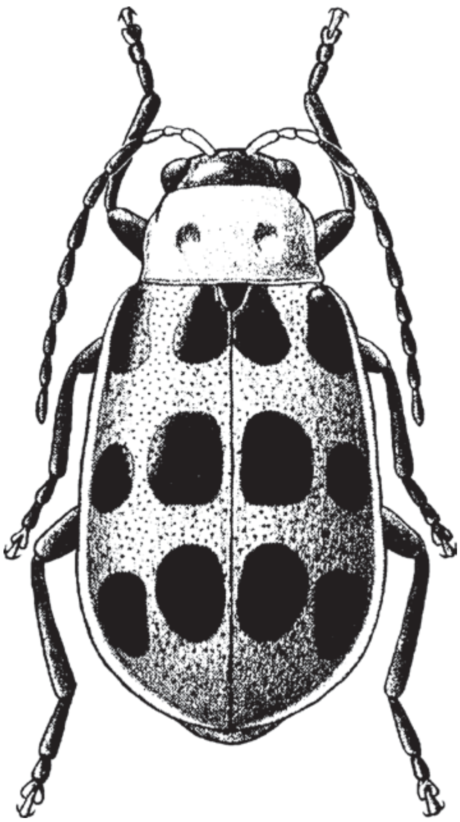
This species is found throughout the United States and southern Canada, although two races are recognized. In the Rocky Mountain region and westward a variant designated as *Diabrotica undecimpunctata undecimpunctata* Mannerheim is recognized, and called the western spotted cucumber beetle. The eastern form of the spotted cucumber beetle is found east of the Rocky Mountains, including eastern Canada as far west as Alberta, and is designated *Diabrotica undecimpunctata howardi* Barber. Spotted cucumber beetle is also found in Mexico, and consists mostly of the eastern race.

In the USA, spotted cucumber beetle is often found in the same areas occupied by other cucumber beetles. However, in the north the striped cucumber beetle, *Acalymma vittatum* (Fabricius), is dominant; in most southern areas spotted cucumber beetle is most abundant, and in the southernmost areas of Florida and Texas the banded cucumber beetle, *Diabrotica balteata* LeConte, predominates. Spotted cucumber beetle is highly dispersive, overwintering in southern states and dispersing northward annually.

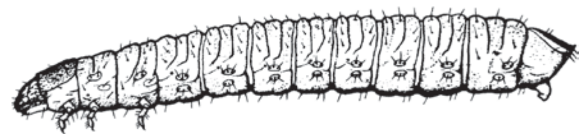
Life History

The spotted cucumber beetle normally completes its life cycle in 4–6 weeks. The number of generations per year seems to be unusually variable, possibly because there is no true diapause in these insects and they continue to reproduce as long as the weather allows, and because they annually re-invade northern areas. Often there are two generations per year, but a single generation is reported in Oregon, and three in Alabama and southern California. Because the generations overlap considerably, and adults can be found continuously during warm weather, field observations could lead to an underestimate of generation number. The adult is the overwintering stage. Overwintering beetles hide in plant debris and become active when the temperature reaches about 15–20°C. In the mild weather areas of the northwestern USA, aggregation of beetles in protected locations may occur during the winter, but this is the exception, not the rule, and beetles generally overwinter only in areas with mild winters, principally the southern states, dispersing northward annually. Northward dispersants in the spring can consist of a mixture of insects that had dispersed southward during the preceding autumn, and new adults produced at southern latitudes (Fig. 104).

Normally, about 40 eggs are produced at each oviposition. Beetles prefer coarse soil or soil with cracks to fine, smooth soil; they also prefer wet over dry soil for oviposition. A female will deposit, on average, six egg clusters during her life, for a total of 200–300 eggs. All values related to egg production are quite variable, with the values decreasing as the beetles progress from generation 1, to 2, to 3. The yellow egg is oval, and measures about 0.7 mm long and 0.5 mm wide. Egg incubation time varies with temperature, from as little as a week to up to a month. The three instars generally require about 7, 5, and 4 days, respectively, or about 14–24 days for complete larval development. The larva grows from about 1.8 mm long at hatching to about 12 mm long at maturity. Head capsule widths measure 0.3, 0.4, and 0.6 mm, respectively. The larva is yellowish white, with the head and the dorsal plate at the tip of the abdomen colored brown. The mature larva



Spotted Cucumber Beetle or Southern Corn Rootworm, *Diabrotica undecimpunctata* Mannerheim (Coleoptera: Chrysomelidae), Figure 104 Adult of spotted cucumber beetle or southern corn rootworm, *Diabrotica undecimpunctata* Mannerheim.



Spotted Cucumber Beetle or Southern Corn Rootworm, *Diabrotica undecimpunctata* Mannerheim (Coleoptera: Chrysomelidae), Figure 105 Mature larva of spotted cucumber beetle or southern corn rootworm, *Diabrotica undecimpunctata* Mannerheim.

constructs a small chamber in the soil and pupates within (Fig. 105).

The pupa is white initially, but turns yellow with age. It measures about 7.5 mm long and 4.5 mm wide. The tip of the abdomen bears a pair of stout spines, and smaller spines are found dorsally on the remaining abdominal segments. Duration of pupation is about 7 days, with a range of 4–10 days. After completion of the pupal period the beetle digs to the soil surface.

The adult is long-lived; 60 days is common during the summer but longevity is extended considerably, up to 200 days, during the winter. The adult is about 6–7.5 mm long. It is generally colored yellowish green with 12 black spots on the elytra and a black head. The western form of spotted cucumber beetle has black legs and abdomen, whereas the eastern form has a pale abdomen and the legs are at least partly pale. Adults usually do not begin oviposition until 2–3 weeks after emergence.

This insect has a very wide host range; more than 200 plants are known to be fed upon. Beetles fly considerable distances regularly in search of suitable food. Adults are especially fond of pollen and flower petals. Although the adult will feed on the flowers of almost any plant, they prefer cucurbits, legumes, tomato, ornamental plants, and fruit crops. Adults also feed readily on sweet substances, such as fruits and aphid honeydew, and the foliage of some plants. The larvae, however, are largely restricted to feeding on the roots of cucurbits, legumes, and grains (including corn) and grasses. Winter cover crops and weeds, especially broadleaf species, often are attractive to ovipositing females.

Several natural enemies of spotted cucumber beetles are known, the most important being *Celatoria diabroticae* (Shimer) (Diptera: Tachinidae). This fly deposits her larva within the abdomen of the adult beetle, which soon perishes. Cucumber beetles also are fed upon by many bird species and attacked by mermithid nematodes and the fungus *Beauveria*. The nematode *Howardula benigna* (Cobb) (Nematoda: Allantonematidae) can sometimes parasitize a high proportion of beetles. *Howardula*-infected female beetles have poorly developed ovaries.

Environmental conditions, and particularly soil moisture, have been implicated in the abundance of spotted cucumber beetle. High soil moisture is a requisite for larval survival. In dry years it is only the clay soils or low spots that successfully produce beetles, whereas during moist years sandy soils are more suitable.

Damage

Adults eat small holes in the leaves and flower petals of many plants. If provided a choice, vegetable crops rather than grain crops are usually attacked by adults. Fruit of smooth-skinned melons is susceptible to damage, especially before the skin hardens. In a study of adult feeding on seedlings of zucchini squash in Louisiana, densities of ten beetles per plant caused significant levels of plant mortality, but their effect diminished greatly once the seedlings attained the two or three leaf stage. While beetle damage may result in complete defoliation, sometimes the feeding is limited to the pollen or fruit. Because beetles often avoid heat, the shaded portions of the fruit may be especially damaged.

The beetles also transmit cucumber mosaic virus and muskmelon necrotic spot virus, and bacterial wilt of cucurbits and of corn. Transmission of cucurbit bacterial wilt by spotted cucumber beetles is a secondary, late-season spread, so these insects are considered to be less important vectors than striped cucumber beetles.

The larvae feed on the roots of plants and also bore into the base of the stems. Root pruning may result in only a discolored and stunted plant, whereas when larvae burrow into the stem they may cause the plant's death. Larval feeding may increase the incidence and severity of Fusarium wilt. Some injury to the surface, or rind, of fruit may occur as larvae burrow up from the soil and feed on fruit in contact with soil, and larvae are sometimes called "rindworms." Grain seedlings, particularly corn, are often damaged by larval feeding. Older plants are less susceptible to death following feeding.

Management

Planting time application of granular insecticides, applied in a band over the row, is often recommended for protection of plant roots if a field is expected to be heavily infested by larvae. Foliar and blossom injury is prevented by timely application of insecticides, especially to the seedling stage because they are more susceptible to injury. There is risk of foliar insecticides interfering with pollination in insect pollinated crops such as cucurbits, though this is not a consideration in wind pollinated crops such as corn. Insecticide applications made late in the day minimize damage to pollinators. Waiting at least 1 day after insecticide treatment before introducing beehives is also advisable. Control of beetles helps reduce spread of cucurbit wilt, but the concern over this disease diminishes as the plants mature.

Feeding stimulants and lures have considerable potential for increasing both the effectiveness and selectivity of insecticide applications. Cucurbitacins are arrestants and feeding stimulants for spotted cucumber beetle, although they have low volatility and therefore are not valuable as lures. Volatile components of blossoms, attractive to beetles, have been identified and evaluated as lures. Various mixtures attract beetles, but phenyl acetaldehyde was found to be more attractive to spotted cucumber beetle than to the other common squash blossom-infesting *Diabrotica* beetles. Cinnamaldehyde alone or in a mixture with trimethoxybenzene and indole also were very attractive kairomones, and have been used experimentally in the field to capture beetles. These lures are especially good for detecting beetles when they are at low densities, and otherwise difficult to locate. Combinations of volatile attractants, cucurbitacins, and low rates of insecticides have been applied to corn cob grits to make lethal baits. The need for insecticides can be reduced if the timing of planting can be manipulated so that the beetles have already dispersed and deposited most of their eggs before planting.

Because there is such a wide range of suitable hosts and the insects are so mobile, crop rotation is usually not considered to be a practical management approach. There are some crops, however, such as cotton, that seem to be immune to injury. When corn is planted immediately after legumes, the larvae cause severe injury because the legumes are attractive to adults. Grass weeds growing in a field immediately before planting may also predispose a crop to injury, so clean cultivation is important. Broadleaf cover crops, especially hairy vetch, induces greater insect problems than grain crops such as wheat. Fallow, weed-free fields have a low incidence of problems.

Soil moisture conditions affect the insects and their damage. Crops grown in moist soil, due either to a high water table or abnormally heavy rainfall, are more likely to be damaged by larvae, probably due to enhanced larval survival. In contrast, water-stressed, wilted cucurbit plants are more attractive to beetles, and experience more foliar damage than turgid plants.

There are some varietal differences among cucurbits with respect to susceptibility to injury. Bitter cultivars, which have higher cucurbitacin content, are reported to be more attractive and injured; however, non-bitter cultivars have less bacterial wilt disease.

► Vegetable Pests and Their Management

References

Arant FS (1929) Life history and control of the southern corn rootworm. Ala Agric Exp Stn Bull 230:1–46

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, CA, 729 pp

Krysan JL (1986) Introduction: biology, distribution, and identification of pest *Diabrotica*. In: Krysan JL, Miller TA (eds) Methods for the study of pest *Diabrotica*. Springer-Verlag, New York, pp 1–23

Krysan JL, Branson TF (1983) Biology, ecology, and distribution of *Diabrotica*. In: Gordon DT, Knoke JK, Knoke LR, Nault LR, Ritter RM (eds) Proceedings of the international maize virus disease colloquium and workshop, 2–6 August 1982. Ohio State University, Ohio Agricultural Research and Development Center, Wooster, pp 144–150

Spotted Tentiform Leafminer, *Phyllonorycter blancardella* (Fabricius) (Lepidoptera: Gracillariidae)

This European insect was accidentally introduced to North America, where it has caused significant loss to apple production.

► Apple Pests and Their Management

Spot Treatment

The application of pesticides to the area where pests actually are found rather than to the entire field.

Spreader

An adjuvant added to a pesticide to enhance the ability of the pesticide to spread over a larger area of the foliage, and often combined with another adjuvant to produce a combined "spreader-sticker."

► Insecticides
► Insecticide Formulations

Spread-Winged Damselflies

A family of damselflies in the order Odonata: Lestidae.

► Dragonflies and Damselflies

Spring Stoneflies

Members of the stonefly family Nemouridae (order Plecoptera).

► Stoneflies

Springtails (Collembola)

Springtails are a primitive entognathous order of hexapods that sometimes (along with Protura and Diplura) are considered to be insects. They are among the most widespread and abundant terrestrial arthropods, and are found in Antarctica, where arthropods are scarce. Generally they are considered to be useful as they assist in the decomposition of organic materials, and few are pests.

Classification

There are over 6,000 species of springtails, and they are found throughout the world, including Antarctica. The order generally is subdivided into two suborders: Arthropleona, the elongate-shaped species, and Symphypleona, the globular species.

Class: Entognatha
- Order: Collembola
  - Suborder: Arthropleona
    - Family: Neanuridae
    - Family: Odontellidae
    - Family: Brachystomellidae
    - Family: Poduridae and water springtails
    - Family: Hypogasturidae and elongate and bodied springtails
    - Family: Onychiuridae and blind springtails
    - Family: Isotomidae and smooth springtails
    - Family: Entomobryidae and slender springtails
    - Family: Cyphoderidae
    - Family: Paronellidae
    - Family: Oncopoduridae
    - Family: Tomoceridae
    - Family: Coenaletidae
    - Family: Actoletidae
    - Family: Microfalculidae
    - Family: Protentomobryidae
  - Suborder Symphypleona
    - Family: Neelidae and short and horned springtails
    - Family: Sminthuridae and globular springtails
    - Family: Mackenziellidae and Mackenzie globular springtails
    - Family: Dicyrtomidae

Characteristics

These are small animals, measuring only 0.25–10 mm in length, and usually less than 5 mm long. They are either elongate or globular in body form. Their color varies greatly, and though often obscure, some are brightly colored. The antennae are short to medium in length, and consist of 4–6 segments. The compound eyes are small, with only a few facets per eye. The mouthparts are basically the biting (chewing) type, but sometime extensively modified, and somewhat enclosed by the head. The legs are small, and lack extensive modifications. Wings always are absent. The abdomen consists of 5 or 6 segments, though some may be obscure. Springtails often are equipped with a jumping apparatus that serves as the basis for the common name. This apparatus consists of a fork-like furcula originating near the tip of the abdomen that is flexed ventrally and held by a catch, the tenaculum. When the tenaculum releases, the furcula springs with a snap that propels the insect forward. In addition, springtails possess a small ventral tube-like structure on the first abdominal segment, called a collophore or ventral tube. The collophore has various functions, including water absorption and excretion, and possibly adhesion to smooth surfaces. They lack cerci. Metamorphosis may be lacking or incomplete. Collembolans often display 6–8 molts during their life, with sexual maturity attained after the fifth molt. Thus, unlike insects, they continue to molt as adults. The immatures usually resemble the adults in external morphology.

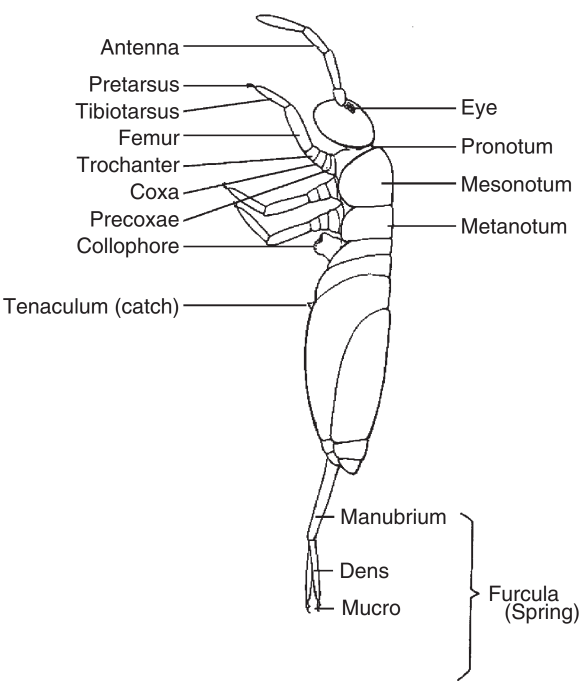
There are three major body types found among springtails: globular, elongate, and grub-like. In globular species, the abdominal segments are fused to form a globe-shaped abdomen. Such species typically inhabit open, grassy habitats. In elongate species, the first thoracic segment is reduced in size relative to the other thoracic segments, producing a "neck" -like structure. Also, the legs and antennae, and furcula are elongate, and the eyes well developed. Sometimes these insects are will marked with patterns or colors, and the body is covered with scales or hairs that help reduce the rate of drying when the springtails forage over the surface of the soil. This body form is called entomobryomorphoid. The grub-like springtails have short legs, antennae, and furcula, and poorly developed eyes.

The first thoracic segment is the same size as the other thoracic segments. Such springtails typically lived deep in the litter or soil, and the body form is called podomorphoid (Fig. 106).

Biology

Springtails occur in numerous habitats, including the water surface of fresh water, the tidal region of salt water, in soil, leaf debris, bird nests, beneath bark, and occasionally on foliage. They feed primarily on lichens, pollen, fungi, bacteria, and carrion, though a few feed on seedling plants or are carnivorous. In general, the above-ground species are in the suborder Arthropleona, are slender in shape, brightly colored, relatively large, and have long antennae and legs, and relatively well-developed eyes. The below-ground species are small, pale colored, with short antennae and legs, and with reduced eyes and the jumping apparatus. The species in the suborder Symphypleona, which are globular in shape, dwell in moist habitats or caves, and are active jumpers. Like the other above-ground species, their eyes are well developed, and their body pigmented. Springtails generally lack trachea, with gas exchange occurring through the integument. Springtails often aggregate in large groups, and this can be observed on the surface of water, snow, or on organic material. The purpose or cause of aggregations is unknown.

The reproductive behavior of springtails is consistent with other entognathous insects. Sperm transfer is indirect, with sperm deposited in stalked droplets on the ground. In most cases, sperm uptake by the female is a passive process, but in some of the more advance species, the male guides the female to his sperm.



Springtails (Collembola), Figure 106 **A diagram of a springtail showing a lateral view.**

References

Arnett RH Jr (2000) American insects, 2nd edn. CRC Press, Boca Raton, FL, 1003 pp
Christiansen K (1964) Bionomics of Collembola. Annu Rev Entomol 9:147–178
Christiansen K, Bellinger PF (1998) The Collembola of North America north of the Rio Grande, a taxonomic analysis. Grinnell College, Grinnell, IA, 1520 pp
Hopkin SP (1997) The biology of the springtails. Oxford university Press, Oxford, UK, 330 pp
Snider RJ (1987) Class and order Collembola. In: Stehr FW (ed) Immature insects, vol. 1. Kendall/Hunt Publishing, Dubuque, IA, pp 55–65

Spruce Budworms, *Choristoneura* Lederer (Lepidoptera: Tortricidae)

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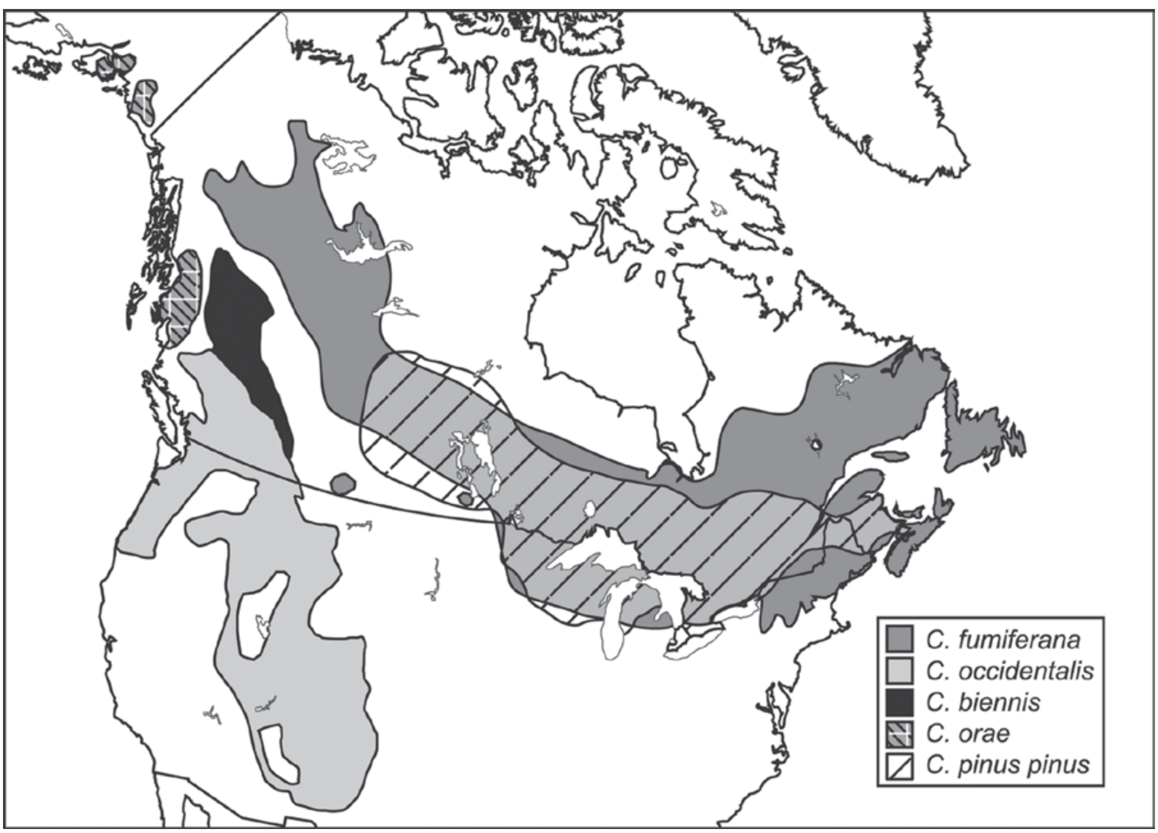
Spruce budworms in the genus *Choristoneura* display cyclical dynamics in several major northern conifer forest ecozones in North America. Periodic outbreaks cause defoliation over extensive areas and are characteristic ecological disturbances in these forest ecosystems. Tree mortality may be extensive in severe outbreaks, especially in understory or suppressed trees, and growth rates are significantly affected even in moderate outbreaks.

At least 12 taxa of conifer-feeding *Choristoneura* are currently recognized in North America, with the greatest diversity west of the Rocky Mountains. Five closely related species, the (eastern) spruce budworm, *C. fumiferana* (Clem.), the jack pine budworm, *C. pinus pinus* Free., the western spruce budworm, *C. occidentalis* Free., the 2-year-cycle spruce budworm, *C. biennis* Free., and the coastal spruce budworm, *C. orae* Free., are notable for causing significant damage and consequently attracting the attention of forest entomologists (Fig. 107).

There are few consistent, conventional taxonomic characters to distinguish these budworm species. Polymorphisms are common and isozyme studies have been equivocal. Major pheromone components are similar especially among the geographically disjunct spruce-feeding species. All species tested to date hybridize freely in captivity and produce fertile offspring, suggesting a relatively recent phylogenetic divergence. The most reliable means of distinguishing these species is by their principal host trees and associated geographical distributions. The (eastern) spruce budworm feeds primarily on spruces (*Picea* spp.) and balsam fir [*Abies balsamea* (L.) Mill.] from the Atlantic coast to the continental divide and possibly into Alaska. The jack pine budworm has a similar, although more restricted, sub-boreal geographic range reflecting the distribution of its preferred host, jack pine (*Pinus banksiana* Lamb.). The western spruce budworm occurs west of the continental divide where it is most commonly associated



Spruce Budworms, *Choristoneura* Lederer (Lepidoptera: Tortricidae), Figure 107 Distribution of spruce budworm species in North America. (Map by Mark Lindal, Natural Resources Canada-Canadian Forest Service.)

with Douglas fir [*Pseudotsuga menziesii* (Mirb.) Fanco]. True firs (*Abies* spp.) are also important hosts, especially in the central portion of this budworm's extensive latitudinal range. The coastal spruce budworm occurs in coastal Alaska and British Columbia north of 52° and feeds on sitka spruce [*P. sitchensis* (Bong.) Carr.] and on amabilis fir [*A. amabilis* (Dougl.) Forbes]. The 2-year-cycle spruce budworm has an allopatric distribution to all of these other species, occurring in the submontane forest zones of north-central British Columbia, Canada, and in the Rocky Mountains, where it feeds on spruces (*Picea* spp.) and subalpine fir [*A. lasiocarpa* (Hook.) Nutt.]. Although other tree species such as larch (*Larix* spp.) and hemlock (*Tsuga* spp.) have been reported as occasional hosts for spruce budworms, the identities and distributions of the budworm species considered here are largely defined by the biogeography of their principal hosts.

Life History

All of these budworm species have nearly identical life histories. Eggs are laid in masses of 15 (*C. fumiferana*) to 60 (*C. pinus pinus*) overlapping eggs on host foliage in mid-summer and hatch within 2 weeks. Neonates do not feed but seek sheltered locations throughout the tree where they establish a hibernaculum, molt to a second instar and pass the winter in obligatory diapause. In this dormant phase, larvae are cold-hardy to at least −30°C. Diapause development requires approximately 4 months at cool to moderate temperatures (0° to about 10°C). Once diapause is complete, larvae are maintained in a quiescent state until temperatures exceed about 15°C.

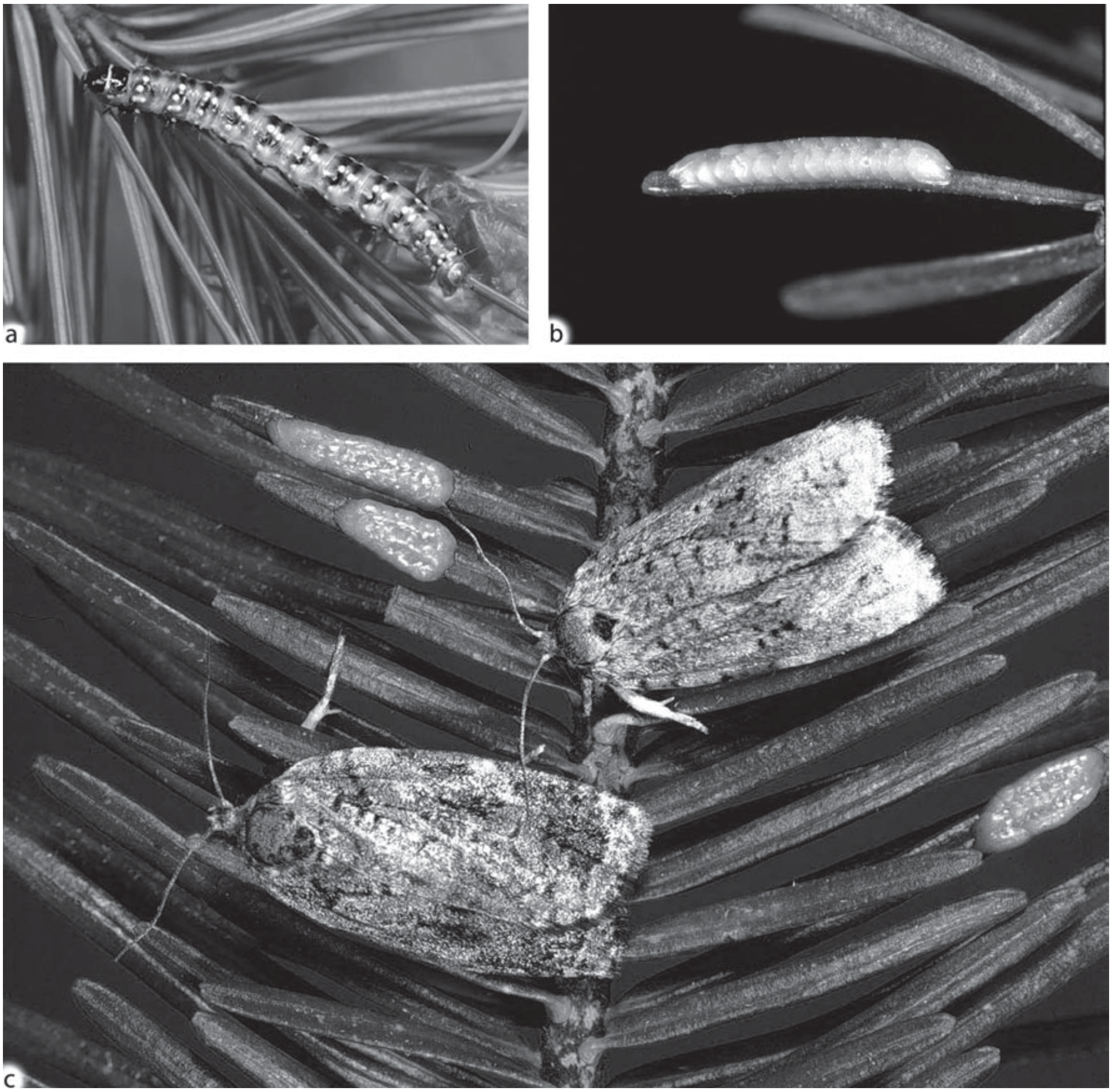
Larvae emerge on warm days in early spring and forage for feeding sites both within and between tree crowns by ballooning on silk threads. Spring emergence of these budworms is typically in advance of bud flush, so early-stage larvae often occupy pollen cones or mine needles of previous years' growth before finally constructing a feeding shelter in expanding, current-year shoots. A second diapause event in which budworms completing the first diapause feed for a brief period and enter a second diapause at the end of the third larval stage has been observed in all spruce budworm species. The frequency ranges from rare (<2%) in eastern spruce budworm and jack pine budworm to more than 50% in the coastal spruce budworm to nearly 100% in the aptly named 2-year-cycle spruce budworm. The frequency in western spruce budworm can be manipulated to a relatively high level (>40%) by rearing at short photoperiods but in nature is likely much lower. Diapause-free strains can also be obtained in this species using artificial conditions.

Spring foraging activities result in frequent movement and re-distribution of early-stage larvae whereas later feeding stages seldom move from their shelters unless disturbed. All budworms prefer current-year foliage and only feed on previous years' growth if forced by severe defoliation. The number of larval instars among this complex of species varies between five and eight and can be polymorphic within a species. Pupation occurs on the foliage near the ultimate feeding shelter. Moths emerge in mid-summer of the same year. Males are attracted to females by a sex pheromone and mating occurs within the tree crown. Fecundity varies with the size of the female and usually exceeds 150 eggs in a well-nourished adult. Moths are capable of long-distance flight and migrations of more than 200 km have been documented (Fig. 108).

Outbreaks and Damage

The population dynamics of all four budworm species is characterized by fluctuation of population densities over several orders of magnitude. The periodicity, duration and extent of these outbreaks vary in ways that are significant to understanding damage and other impacts.

The most damaging outbreaks are those of the eastern spruce budworm. Historical data reveal a somewhat regular periodicity of outbreaks



Spruce Budworms, *Choristoneura* Lederer (Lepidoptera: Tortricidae), Figure 108 Some life stages of spruce budworms: (a) mature larva of *Choristoneura occidentalis*, (b) egg mass of *C. occidentalis*, (c), adults and egg masses of *C. fumiferana*. (Photos by Bob Duncan, Natural Resources Canada-Canadian Forest Service.)

(35 years on average). These outbreaks are relatively long in duration; usually more than six and often more than 10 years in any one location, and may be synchronized over very large areas. During the mid-1970s, severe defoliation was mapped in over 50 million ha of forest. The intensity and duration of these outbreaks frequently results in severe, even catastrophic, mortality especially in stands dominated by mature balsam fir. Spruce species are more tolerant of defoliation and larger trees often survive prolonged outbreaks albeit with marked reductions in growth rates. Even severely affected stands appear to regenerate to a similar forest type. Thus, despite the significant economic impacts of spruce budworm outbreaks over large areas in the short-term, the spruce-fir forest appears resilient to this ecological disturbance.

In contrast to the spruce budworm, the periodicity of jack pine budworm outbreaks is highly variable and apparently associated with fire history and edaphic conditions. Nonetheless, periods of outbreak can coincide over large areas. In the late 1980s and early 1990s, defoliation of jack pine forests peaked at four million ha in the forests surrounding the Great Lakes. The return time of outbreaks can range from 10 years to several decades. Outbreaks rarely last more than 4 years in any one location and individual trees are usually damaged for only a few years in each outbreak event. The result is that widespread tree mortality is the exception; top-kill and reduction in growth rates are more typical. Most mortality occurs in suppressed, understory trees.

Outbreak characteristics of the western spruce budworm appear intermediate to those of spruce and jack pine budworms with evidence of regular periodicity exceeding 10 years within some regions and no large-scale spatial synchrony. These patterns may be a function of the complex topography that fragments the host forest throughout the range of the western spruce budworm. Recent increases in the local dominance of Douglas fir because of fire suppression may be changing these patterns. Defoliation has been chronic, for example, in the southern interior of British Columbia since the mid-1980s, and is extending further north than previously observed. The duration of damaging outbreaks varies greatly at the local level from a few to as many as 8 years. Effects are equally variable, with intermediate and understory trees most vulnerable to damage.

The outbreak behavior of the coastal and 2-year-cycle spruce budworms is the least known of this species complex. Available evidence indicates a periodicity of outbreaks of approximately 35 years for *C. biennis*. When outbreaks occur, they extend over most of this insect's relatively restricted range, including isolated alpine populations. Interestingly, populations of 2-year-cycle spruce budworm are not synchronized across their range with respect to their life cycle: populations. In the northern and western portions of the range, populations reach the adult stage in odd-numbered years (e.g., in 2005) while those in the southern and eastern portions do so in even-numbered years (e.g., 2006). The alternating years of severe, then light, defoliation associated with the 2-year life cycle gives trees a reprieve during outbreaks so damage is reduced.

Population Dynamics

Our understanding of population dynamics of spruce budworms is based largely on detailed studies of *C. fumiferana* populations in the 1950s and 1980s in eastern Canada. The expansion of the forest industry north and west into the boreal forest and from the Pacific coast eastward to interior forests, as well as the increased commercial value of species such as balsam fir and jack pine, have increased the need to understand the causes and potential management of budworm outbreaks. Given the variable nature of outbreak behavior among the five budworm species considered here, there is unlikely a single driver of population behavior. The following considers the role of major mechanisms of population change common to all of these budworm species.

Weather

Early investigators sought a direct connection between weather and outbreak behavior, and identified correlations between successive years of warm, dry weather during the larval feeding stage and the initiation of outbreaks. Although there is little doubt that extreme weather events and average climatic conditions can influence local mean population densities, it is more likely that the effect of weather on population rates of change is via biological processes rather than by directly causing multi-season trends.

For example, the association of outbreaks with successive years of warm, dry spring weather in both spruce and jack pine budworm may be because these same conditions promote the production of pollen cones in host species which, in turn, provide a critical food source to foraging larvae. Or, the differential, temperature-dependent developmental responses of the host tree and budworm result in both spatial and temporal variability in the degree of synchrony between the budworm and its food source, with significant effects on survival. Weather conditions during the adult period clearly influence reproductive success and long-distance dispersal of moths, with potential repercussions on local rates of change in population density and the large-scale synchrony of outbreaks.

Host Plants

The most damaging outbreaks are associated with contiguous stands of mature, preferred host species. Severe defoliation and catastrophic tree mortality in these same stands has been invoked as the major determinant of population collapse. However, populations rise and fall without widespread mortality of host trees. Exhaustive study of foliage quality over the course of outbreaks has returned little convincing evidence that variation in nutritional quality of the trees plays a major role in budworm survival. Quantitative changes in foliage, however, may well influence population levels. Moth fecundity is reduced significantly during periods of moderate to severe defoliation, and cumulative defoliation reduces needle density and may increase emigration of moths and reduce survival of foraging larvae, both of which can influence local population densities.

There is increasing evidence that host tree phenology and structural changes associated with defoliation affect budworm survival in important ways. For example, jack pine budworm depends on the production of pollen cones by its host to bridge the period between spring emergence of the larvae and the availability of fresh foliage. Defoliation, however, reduces the trees' propensity to produce these cones with commensurate negative effects on jack pine budworm survival. This host plant relationship is especially significant to population dynamics because the reduction in pollen cones, and thus host suitability, is the direct result of previous budworm densities. Such a lagged, density-dependent relationship has the capacity to drive cyclical population behavior.

Natural Enemies

Natural enemies include predators, parasitoids and diseases that attack directly any life stage of the budworm. Birds are the most prominent vertebrate predators of budworms. Several species of migratory warblers can specialize on budworm larvae, and larger birds such as grosbeaks have been observed flocking to high-density budworm populations. The importance of bird predation, however, is restricted to lower-density budworm populations due to the limited numerical response and territorial behavior that characterize bird populations. The importance of invertebrate predators is more enigmatic. Spiders are very common on spruce and ants have been observed commonly feeding on western spruce budworms, but the link between their effects and population rates of change has not been established.

Insect parasitoids have received the most attention in terms of their influence on populations of budworms. More than 75 species of insect parasitoids have been recorded attacking budworms and there is a rich and complex guild of hyper- and secondary parasitoids to complicate the system further. There appear to be few parasitoid species that are specialists of the *Choristoneura*. In fact, many of the same species of parasitoids attack all budworm species throughout their ranges. Moreover, the relative abundance of these species also appears consistent during outbreak declines.

The most common species found in outbreak populations include parasitoids of the eggs, *Trichogramma minutum* Riley (Hymenoptera: Trichogrammatidae), early-larval stages, *Apanteles fumiferanae*

Viereck (Hymenoptera: Braconidae) and *Glypta fumiferanae* (Viereck) (Hymenoptera: Ichneumonidae), late-larval stages, *Meteorus trachynotus* Viereck (Hymenoptera: Braconidae) and *Smidtia fumiferanae* (Tothill) (Diptera: Tachinidae) and pupae, *Itoplectis conquisitor* (Say) (Hymenoptera: Ichneumonidae) and *Phaeogenes hariolus* (Cresson) (Hymenoptera: Ichneumonidae). The generalist parasitoids attacking the late-larval and pupal stages of the budworm have received the most attention as it is mortality in these latter stages that is most strongly correlated to generation rates of change in budworm density and therefore trends in population change. Recent evidence suggests that as outbreaks collapse, the impact of these generalist parasitoids is reduced and a distinct suite of more specialized parasitoids becomes prominent.

More than 15 species of pathogenic microorganisms (viruses, bacteria, fungi and protozoans) have been isolated from populations of spruce budworms. As with parasitoids, these pathogens appear common to all budworm species considered here. Interestingly, epizootics are uncommon and localized in spruce budworm populations compared to other eruptive forest Lepidoptera such as tussock moths and tent caterpillars. Viruses appear to play a minor role in natural mortality. Most natural epizootics have been caused by mycopathogens such as *Entomophaga aulicae*. A chronic and ubiquitous microsporidian, *Nosema fumiferanae* Thomson, has clear debilitating effects on heavily infected budworms. It has been difficult, however, to link the varied and insidious impacts of infections by *Nosema* to clear trends in population behavior of the budworm.

Management

Control of budworm populations has occupied forest managers for the past 60 years, especially in eastern North America. The emphasis has been on suppression of populations to save trees and protect growth of infested stands until harvest. The outbreaks of eastern spruce budworm in the late 1940s coincided with development of aerial application of effective pesticides such as DDT. A succession of synthetic products combined with advances in spray technology characterized successful operations into the 1970s when pesticides fell into public disfavor. The on-going need to protect the highly vulnerable forests stimulated research into alternative controls including use of parasitoids, pathogens, and so-called bio-rationals such as pheromones and hormonal analogs which disrupt biological processes such as mating and moulting. From this suite of products, the bacterial insecticide, *Bacillus thuringiensis* Berliner (*Bt*), has emerged as the most widely used operational alternative to chemical pesticides.

The singular reliance on *Bt* for forest protection and the sheer potential magnitude of outbreaks has stimulated forest managers to seek new approaches to prevent or at least mitigate severe damage through either novel strategies using existing products or through application of silvicultural practices that reduce risk. Novel strategies include moving away from the conventional reactive approach to reduction of risk through purposeful management of forests toward stand types less vulnerable to budworms. For example, it is well known that spruces are better able to withstand budworm damage than firs so the move toward planting and favoring spruce over fir in eastern forests could reduce losses. Tolerating a hardwood component also tends to reduce impacts. Management of pollen-cone production in jack pine stands by removing large, open-crown trees would reduce susceptibility to jack pine budworm while commercial thinning of Douglas fir could reduce the vulnerability of multi-stage stands to damage by the western spruce budworm. Combining these silvicultural approaches with effective control products when needed probably offers the most pragmatic approach to stand-level management.

At the landscape level, forest managers may just have to concede that occasional disturbance to growth of native trees by native defoliators is not only inevitable but perhaps necessary to sustain northern forest ecosystems. Accommodating more mixed-species forests in timber management, maintaining flexible supply areas, and developing diverse forest product options could help mitigate the negative economic impacts of these outbreaks.

References

MacLean DA (1985) Effects of spruce budworm outbreaks on forest growth and yield. In: Sanders CJ, Stark RW, Mullins EJ, Murphy J (eds) Recent advances in spruce budworms research. Catalogue No. Fo18–5/1984. Ottawa, Canada, pp 148–175

McCullough DG (2000) A review of factors affecting the population dynamics of jack pine budworm (*Choristoneura pinus pinus* Freeman). Popul Ecol 42:243–256

Nealis VG (2005) Diapause and voltinism in western and 2-year-cycle spruce budworms (Lepidoptera: Tortricidae) and their hybrid progeny. Can Entomol 137:584–597

Régnière J, Lysyk TJ (1995) Population dynamics of the spruce budworm, *Choristoneura fumiferana*. In: Armstrong JA, Ives WGH (eds) Forest Insect Pests in Canada. Catalogue No. Fo24–235/1995E, Ottawa, Canada, pp 95–105

Sanders CJ (1991) Biology of North America spruce budworms. In: Geest LPS, van der Evenhuis HH (eds) Tortricid pests, their biology, natural enemies and control. Elsevier Science Publishers B.V., Amsterdam, The Netherlands, pp 579–620

Shepherd RF, Gray TG, Harvey GT (1995) Geographical distribution of *Choristoneura* species (Lepidoptera: Tortricidae) feeding on *Abies, Picea*, and *Pseudotsuga* in western Canada and Alaska. Can Entomol 127:813–830

van Frankenhuyzen K (1990) Development and current status of *Bacillus thuringiensis* for control of defoliating forest insects. For Chron 67:498–507

Volney WJA (1989) Biology and dynamics of North American coniferophagous *Choristoneura* populations. Agric Zool Rev 3:133–156

Williams DW, Liebhold AM (2000) Spatial synchrony of spruce budworm outbreaks in eastern North America. Ecology 81:2753–2766

Spur

A moveable spine. Spurs are often located on a leg segment, usually at the tip of the segment.

Spurious Vein

A vein-like thickening of the wing membrane. The presence of a spurious vein is an important diagnostic feature in Syrphidae (Diptera).

► Wings of Insects

Spurthroated Grasshoppers

Subfamilies of grasshoppers in the old world (Catantopinae) and new world (Melanoplinae) in the order Orthoptera: Acrididae.

► Grasshoppers, Katydids and Crickets

Squash Bug, *Anasa tristis* (Degeer) (Hemiptera: Coreidae)

The squash bug attacks cucurbits (squash and relatives) throughout Central America, the United States, and southern Canada. In some areas of North America it is the most serious pest of cucurbits.

Description and Life Cycle

The complete life cycle of squash bug commonly requires 6–8 weeks. Squash bugs have one generation per year in northern climates and 2–3 generations per year in warmer regions. In intermediate latitudes the early-emerging adults from the first generation produce a second generation whereas the late-emerging adults go into diapause. Both sexes overwinter as adults. The preferred overwintering site seems to be in cucurbit fields under crop debris, clods of soil, or stones but sometimes adults also are found in adjacent wood piles or buildings.

Eggs

Eggs usually are deposited on the lower surface of leaves. The elliptical egg is somewhat flattened and bronze in color. The average egg length is about 1.5 mm and the width about 1.1 mm. Females deposit about 20 eggs in each egg cluster. Eggs may be tightly clustered or spread a considerable distance apart, but an equidistant spacing arrangement is commonly observed. Duration of the egg stage is about 7–9 days.

Nymph

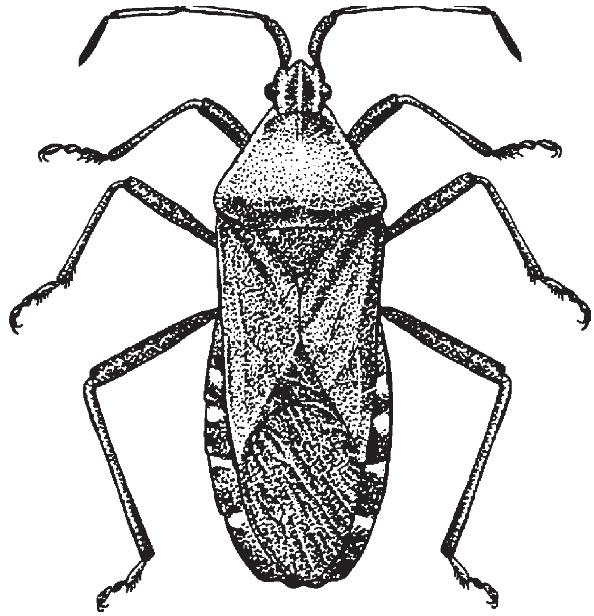
There are five nymphal instars, collectively requiring about 33 days for complete development. The nymph is about 2.5 mm in length when it hatches, and light green in color. The second instar is initially about 3 mm long, and its color is light gray. The third, fourth, and fifth instars initially are about 4, 6–7, and 9–10 mm in length, respectively, and darker gray. The youngest nymphs are rather hairy, but this decreases with each subsequent molt. In contrast, the thorax and wing pads are barely noticeable at hatch, but get more pronounced with each molt. Young nymphs are strongly gregarious, a behavior that dissipates slightly as the nymphs mature.

Adult

The adult measures 1.4–1.6 cm in length and is dark grayish brown in color. In many cases the edge of the abdomen is marked with alternating gold and brown spots (Fig. 109). Adults are long-lived, surviving an average of about 75–130 days, depending on availability and quality of food.

Host Plants

Squash bug has been reported to attack nearly all cucurbits, but squash and pumpkin are preferred for oviposition and support high rates of reproduction and survival. There is considerable variation among species and cultivars of squash with respect to susceptibility to damage and ability to support growth of squash bugs. New World varieties are preferred. Studies conducted in the United States



Squash Bug, *Anasa tristis* (Degeer) (Hemiptera: Coreidae), Figure 109 **Adult of squash bug, *Anasa tristis*.**

reported survival of squash bug to be 70, 49, 14, 0.3, and 0% when nymphs were reared to the adult stage on pumpkin, squash, watermelon, cucumber, and muskmelon (cantaloupe), respectively.

Damage

The squash bug causes severe damage to cucurbits because it secrets highly toxic saliva into the plant. The foliage is the primary site of feeding but the fruit is also fed upon. The foliage wilts, becomes blackened, and dies following feeding. Often an entire plant or section of plant perishes while nearby plants remain healthy. The amount of damage occurring on a plant is directly proportional to the density of squash bugs.

Natural Enemies

Several natural enemies of squash bug are known, principally wasp egg parasitoids (Hymenoptera: Encyrtidae and Scelionidae). Up to 30% parasitism among eggs collected in Florida, USA has been reported. The best known natural enemy is a common parasitoid of several hemipterans, *Trichopoda pennipes* (Fabricius) (Diptera: Tachinidae). The brightly colored adult fly is easy to recognize, having a gold and black thorax and an orange abdomen, with a prominent fringe of feather-like hairs on the outer side of the hind tibia. Flies develop principally in the adult bug, initially castrating the female, and then killing her when the fly emerges. In Connectcut, USA about 20% on the squash bugs have been found to be parasitized in late summer.

Management

Squash bug adults are unusually difficult to kill with insecticides. Although adult control can be accomplished if the correct material is selected, it is advisable to target the more susceptible nymphs. Squash bugs are not often considered a severe pest of large-scale cucurbit production, probably due to the absence of suitable overwintering sites in well managed crop fields and because the bug's effects are diluted by the vast acreage. However, small fields and home gardens are commonly damaged.

Pollinators, particularly honeybees, are very important in cucurbit production, and insecticide application can interfere with pollination by killing honeybees. If insecticides are to be applied when blossoms are present, it is advisable to use insecticides with little residual activity, and to apply insecticides late in the day, when honeybee activity is minimal.

Adult squash bugs preferentially colonize larger, more mature plants. Thus, early-planted crops may be especially prone to attack. Numbers are also highest on plants during bloom and fruit set. Use of early-planted crops as a trap crop has been proposed, but due to the high value of early season fruit most growers try to get their main crop to mature as early as possible. The use of squash or pumpkin as a trap crop to protect less preferred host plants such as melons and cucumbers is reported to be effective.

The tendency of squash bugs to aggregate in sheltered locations can be used to advantage by home gardeners. Placement of boards, large cabbage leaves, or other shelter for squash bugs induces the bugs to congregate there during the day where they are easily found and crushed. Row covers and netting delay colonization of squash, but bugs quickly invade protected plantings when covers are removed to allow pollination.

Removal of crop debris in a timely manner is very important. Squash bugs will often be found feeding on old fruit or in abandoned plantings, so clean cultivation is essential to reduce the overwintering population.

► Vegetable Pests and Their Management

References

Beard RL (1940) The biology of *Anasa tristis* DeGeer with particular reference to the tachinid parasite, *Trichopoda pennipes* Fabr. Conn Agric Exp Stn Bull 440:597–679

Bonjour EL, Fargo WS (1989) Host effects on the survival and development of *Anasa tristis* (Heteroptera: Coreidae). Environ Entomol 18:1083–1085

Bonjour EL, Fargo WS, Rensner PE (1990) Ovipositional preference of squash bugs (Heteroptera: Coreidae) among cucurbits in Oklahoma. J Econ Entomol 83:943–947

Bonjour EL, Fargo WS, Al-Obaidi AA, Payton ME (1993) Host effects on reproduction and adult longevity of squash bugs (Heteroptera: Coreidae). Environ Entomol 22:1344–1348

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, CA, 729 pp

Squash Vine Borer, *Melittia cucurbitae* (Harris) (Lepidoptera: Sesiidaae)

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Squash vine borer, *M. cucurbitae*, is found in most of North and Central America, though infrequent in Canada. Though rarely a pest of commercial crops due to frequent application of insecticides, it is a severe pest in home gardens and elsewhere where insecticides are not used.

Life History

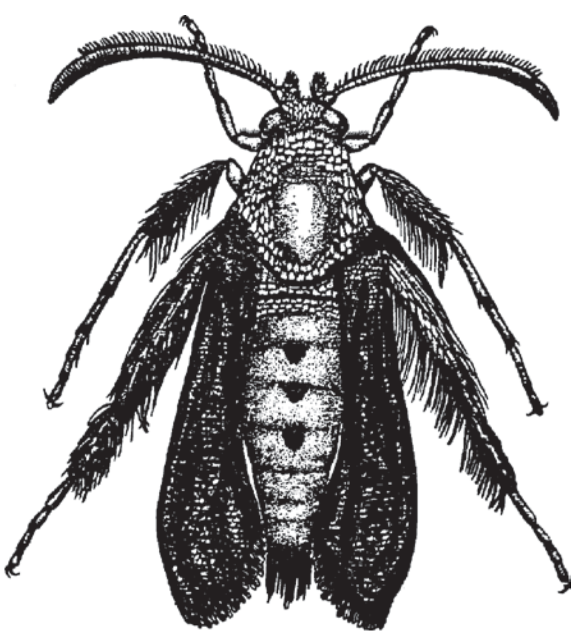
The squash vine borer completes its life cycle in about 60 days. In the southern areas of the USA it displays two generations annually, but in cooler climates only a single generation occurs regularly. In intermediate areas such as Ohio, USA, most borers diapause after the first generation, but some go on to complete a second generation. There has been considerable confusion concerning the number of generations, because in the field it is difficult to discern a single protracted generation from two overlapping generations. Each generation may remain active for 2 or 3 months.

Oval eggs, reddish brown in color, are glued to the plant tissue and are slightly flattened at the point of attachment. Eggs measure about 1.1 mm in length and 0.85 mm in width. Each female is capable of producing 150–200 eggs. Eggs are distributed singly on all portions of the plant except the upper surface of the leaves; most appear to be attached to the basal region of the vine, probably because this tissue is oldest and therefore exposed longer. The basal portion of leaf petioles receives a moderate number of eggs. Some eggs are deposited in cracks in the soil near the base of the plant. Eggs hatch in 10–15 days and larvae soon bore into the plant. Those that hatch on the vine usually remain in this location to feed, whereas those hatching on leaf petioles eventually work their way to the base and enter the vine.

Larvae are white in color with a dark brown or black head. Initially the larval body is markedly tapered posteriorly and equipped with numerous large hairs. As the larva matures it loses its tapered shape and hairy appearance and acquires a dark thoracic shield. There are four instars, with head capsule widths of about 0.4, 0.7, 1.3, and 2.0 mm, respectively. The larva requires 4–6 weeks to complete its development, and eventually attains a length of about 2.5 cm (Fig. 110). The mature larva exits the plant tissue and burrows into the soil to a depth of 4–5 cm where pupation and formation of a black cocoon occurs.

The pupa is mahogany brown in color and the anterior end is equipped with a short but sharply pointed cocoon breaker, a structure used to cut a hole in the cocoon when the moth is ready to emerge. There is some disagreement whether squash vine borer always pupates soon after producing the cocoon. In cooler areas it is reported that the fully grown larva overwinters in the cocoon, pupating in the spring prior to producing the single northern generation. However, in two-generation warmer areas the pupa is reported to overwinter. In any event, a distinctive, heavy-bodied moth eventually emerges from the cocoon.

The wingspan of the moth is about 3 cm. The front wings are blackish and tinged with olive-green while the hind wings are colorless. The abdomen is usually dull orange and marked with black dots dorsally (Fig. 110), although on some specimens the abdomen is entirely black. The hind



Squash Vine Borer, *Melittia cucurbitae* (Harris) (Lepidoptera: Sesiidaae), Figure 110 **Adult of squash vine borer, *Melittia cucurbitae* (Harris).**

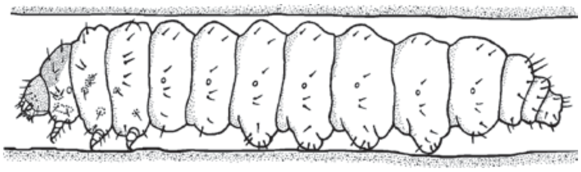
legs are prominently tufted and are colored orange and black. Adults are capable of oviposition about 3 days after emergence. Moths are active during the daylight hours (Fig. 111).

Squash vine borer feeds on wild and cultivated species of *Cucurbita*. Summer squash, *Cucurbita pepo*, and some winter squash, *C. maxima*, are most preferred for oviposition by adults, and most suitable for larval development. Some pumpkin, *C. mixta*, are intermediate in suitability. Winter squash derived from *C. moschata* does not support complete larval development. The weeds *C. texana* and *C. andreana* are very suitable hosts, while *C. okeechobeensis* is intermediate and several cucurbit weed species are unsuitable. Other cucurbit crops such as cucumber and melon may be attacked, but this occurs mostly when the more favored hosts are not present.

The natural enemies of squash vine borer are not well studied. General predators such as robber flies (Diptera: Asilidae) are reported to prey upon adults, and a wasp egg parasitoid, *Telenomus* sp. (Hymenoptera: Scelionidae) is known. Larvae seem to be relatively free of natural enemies.

Damage

The damage caused by these insects is accurately described by the common name: squash vine borer. The larva spends almost its entire life feeding within the plant stem. Because larvae feed within plant tissues they are hidden from view and easily overlooked. However, upon close examination frass can be found accumulating beneath small entrance holes. The presence of one, or even several, larvae is not always deadly to the plant. However, up to 142 larvae have been removed from a single plant, and obviously such large numbers of insects will disrupt the physiology of the plant beyond its ability to compensate successfully for the feeding injury. Often the first sign of infestation is wilting of the plant in the heat of the day while other plants remain turgid. If the vine is thin or heavily infested the portion beyond the feeding site of the larva(e) may be killed. Infestation of fruit is unusual. Commercial cucurbit production rarely suffers significant damage by squash vine borer. These borers seem to plague small plots especially severely; almost all home gardeners have had some unpleasant experience with this pest.



Squash Vine Borer, *Melittia cucurbitae* (Harris) (Lepidoptera: Sesiidae), Figure 111 Larva of squash vine borer, *Melittia cucurbitae* (Harris).

Management

A sex pheromone produced by females has been identified, and male moths of *M. cucurbitae* may be attracted to traps baited with the insect's sex pheromone, but thus far pheromone technology has not been demonstrated to improve management practices. In fact, one study reported increased injury of squash plantings when pheromone was released; the biological basis for this is uncertain.

Squash vine borer can be difficult to control with chemical insecticides because it is protected from contact with most insecticides by its burrowing activity. Therefore, it is imperative that insecticide residues be in place during oviposition so that when the larva hatches from the egg it has an opportunity to make contact with a lethal dose.

Pollinators, particularly honeybees, are very important in cucurbit production, and insecticide application can interfere with pollination by killing honeybees. If insecticides are to be applied when blossoms are present, it is advisable to apply insecticides late in the day, when honeybee activity is minimal.

It has long been known that early-planted crops experience minimal injury, so early planting is recommended. Also, the moths preferentially attack certain species such as summer squash; this can be used as a trap crop if the plants are then destroyed or sprayed, thereby protecting less preferred cucurbit species.

Cucurbit plants are very resilient, recovering well from injury. If accumulated frass can be located adjacent to vine tissue, indicating the presence of active feeding, larvae can be killed or removed with a knife without severely affecting growth of the remaining tissue. Vines also develop additional roots if covered with soil, which can compensate for damage by borers. Covering the vines near the base of the plant discourages oviposition near critically important tissue. Dying vines should be removed and destroyed.

Using a medicine dropper or similar device, the bacterium *Bacillus thuringiensis* and the entomopathogenic nematode *Steinernema carpocapsae* can be injected into squash vines to kill existing larvae or to prevent their establishment. The hollow, moist vines are especially conducive to the spread and survival of nematodes. Obviously this approach is not applicable to commercial crop production.

References

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, CA, 729 pp

Friend RB (1931) The squash vine borer, *Melittia satyriniformis* Hübner. Conn Agric Exp Stn Bull 328:587–608

Squirrel Lice

Members of the family Enderleinellidae (order Phthiraptera).

► Chewing and Sucking Lice

ssDNA

Single-stranded DNA.

Stabilimentum

Some orb-weaving spiders created a zig-zag shaped band of silk at or near the center of the web; this structure is called a stabilimentum.

Stability

An expression of constancy. In population biology it refers to population densities and age structures that remain fairly constant over long periods of time (contrast with resilience).

Stable Fly, *Stomoxys calcitrans* (Diptera: Muscidae)

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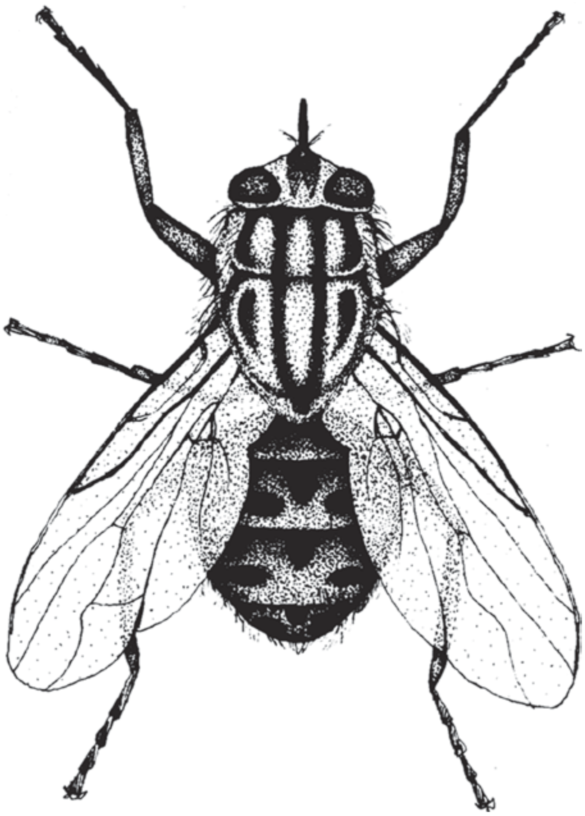
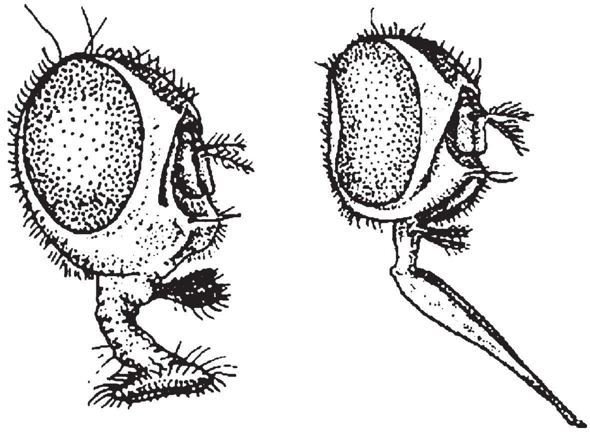
The stable fly (*Stomoxys calcitrans* L.), sometimes referred to as the dog fly or the biting house fly, is primarily a pest of cattle. This species closely resembles a house fly, but possesses piercing-sucking instead of sponging mouthparts (Fig. 113). Both sexes of the stable fly feed on blood 2–3 times per day from a variety of warm-blooded animals including humans. The act of feeding by several flies can produce quite an annoyance to cattle. Fly avoidance behavior often includes constant stomping of feet, tail switching, and "bunching," whereby the herd gathers or "bunches" together in a tight circle with heads facing inward to protect their front legs from feeding flies. When fly avoidance behavior takes up most of an animal's daily activity, it is not eating. Stable flies have been reported to reduce weight gain in beef cattle and lower milk production in dairy cattle. Research has estimated an economic threshold of less than 1–5 feeding flies per front leg depending on animal size, age, breed and production system. Because stable flies feed on blood, they are capable of transmitting pathogenic organisms that cause anthrax, brucellosis, swine erysipelas and equine infectious anemia to a variety of their animal hosts.



Stable Fly, *Stomoxys calcitrans* (Diptera: Muscidae), Figure 112 Adult stable fly (source: University of Florida).



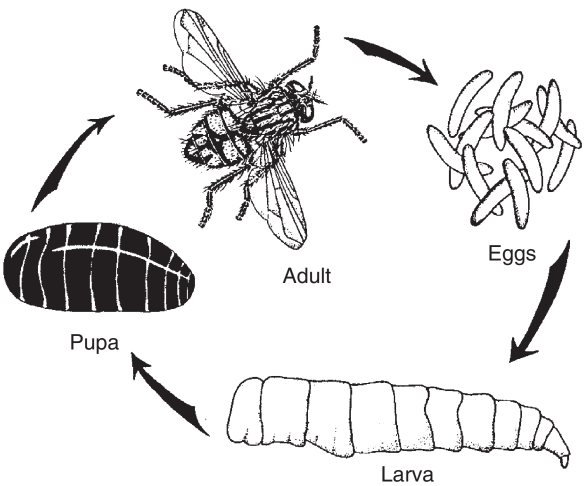
Stable Fly, *Stomoxys calcitrans* (Diptera: Muscidae), Figure 113 Comparison of nonbiting and biting mouthparts: left, sponging mouthparts of the adult house fly (source: Novartis Corporation); right, piercing-sucking mouthparts of the adult stable fly (source: Axtell, R. C. 1986. Fly control in confined livestock and poultry production. CIBA-GEIGY Agric. Div., Greensboro, NC).

Blood-seeking stable flies can also affect recreational areas. In some areas of the U.S. (e.g., Florida panhandle beaches, coastal areas of New Jersey, Great Lakes Region and Tennessee Valley Authority lakeshores) stable flies often disperse from cattle producing areas and congregate along the shorelines. Weather systems associated with the passage of cold fronts often move the flies to these areas. It is currently unknown how or why this happens.

Although most stable flies (Fig. 112) seldom disperse farther than needed to obtain a blood meal, studies have shown that this pest can routinely travel distances up to 8 km and as far as 225 km on storm fronts to Florida panhandle beaches. Suburban areas that have expanded into rural cattle production areas have experienced problems with stable flies. Oftentimes, this phenomenon occurs when stable fly populations are not adequately controlled on surrounding farms and they disperse into the surrounding environs. However, a study in Kansas indicated that a suburban stable fly problem was not the result of nearby rural livestock operations. Rather, local developmental areas for stable flies, such as numerous compost heaps located within the suburban landscape, contributed greatly to the problem. In any event, legal issues have arisen with many livestock operations going out of business.

Biology

Stable flies go through complete metamorphosis (Fig. 114). The eggs are laid on decayed vegetation, or vegetation mixed with cattle feces and/or urine. Improperly composted vegetative material, or decomposing grass clippings that remain wet can provide adequate developmental medium for stable flies in residential areas.



Stable Fly, *Stomoxys calcitrans* (Diptera: Muscidae), Figure 114 **Generalized fly life cycle (source: University of California Cooperative Extension).**

After oviposition, the eggs hatch in 1–5 h and the larvae go through three successive molts called instars. When the larva is mature (i.e., third instar), it ceases to feed and often migrates from the developmental area to pupate in drier conditions. Sometimes larvae will enter the ground to the depth of about 2–4 cm to pupate. At the time of pupation, the exoskeleton from the last larval instar will harden. This "shell" forms the puparium in which the pupa will reside. The pupa is the transitional stage from larva to adult fly. Depending upon temperature and other environmental parameters, the cycle from egg to adult can take as little as 10 days, but can be extended to 2 months or longer under unfavorable conditions. Several generations are produced annually and tremendous numbers of biting adults can develop if not held in check.

Adult flies can live about 20 days under favorable conditions. Adult stable fly seasonal peaks appear to change with climatic zone in the U.S. Populations in the more temperate areas (e.g., Minnesota, Michigan, and New York) primarily peak in mid-summer, whereas further south (e.g., Texas and Florida) the population peak is bimodal, occurring in late spring and again in late summer to early fall.

Control

The most effective method of reducing stable flies is to eliminate the habitat for fly development. The removal of accumulated feed, silage, manure, grass clippings, etc., in a timely manner (e.g., weekly) will help to reduce the fly population. If removal is not feasible, then it should be piled in rows and turned at least once a week to facilitate drying. In lieu of this, heavy black plastic can be placed over the piles (especially compost heaps). Oftentimes, the temperature produced by anaerobic decomposition of the pile will be high enough to kill any fly larvae present. Edges of the plastic should be covered with soil to create firm contact with the ground and prevent adult flies from ovipositing underneath the plastic.

Stable fly pupae have a variety of minute wasp parasitoids that parasitize them as a form of natural control. The most common parasitoids are referred to as microhymenoptera, and belong to the family Pteromalidae. These tiny wasps (about 2.0 mm in length) parasitize stable flies by ovipositing one or many eggs (depending on species) into a pupa. The egg(s) hatch and the larva(e) consume the developing fly, eventually killing it. The immature wasp then pupates and emerges from the stable fly puparium as an adult. As a result, wasps in this family are considered to be of potential use for the control of stable flies in animal facilities. Research has shown that native wasp parasitoids have the best potential for colonizing and impacting native stable fly populations. Currently, knowledge on how many parasitoids should be released, and the optimum number of releases to obtain control is poorly understood.

Application of insecticides to organic materials is not recommended because the quantity needed would be greater than the labeled rate to achieve any degree of control. Also, organic substrates often bind up insecticides making them ineffective against the targeted pest. Stable fly control on animals usually involves spraying labeled insecticides onto the animal's legs.

Because stable flies often rest on the sides of buildings, a residual insecticide applied to such surfaces may provide short-term control of adult flies. Currently, repellents do not give long-term relief for animals or humans against stable fly biting annoyance.

References

Foil LD, Hogsette JA (1994) Biology and control of tabanids, stable flies and horn flies. Revue Scientifique et Technique. Office International des Epizooties, Paris 13:1125–1158

Petersen JJ, Greene GL (1989) Current status of stable fly (Diptera: Muscidae) research. Misc Publ Entomol Soc Am 74:1–53

Scholl PJ, Petersen JJ (1985) Biting flies. pp 49–63 In: Williams RE, Hall RD, Broce AB, Williams RE (eds) Livestock entomology. Wiley, New York, NY, 335 pp

Steelman CD (1976) Effects of external and internal arthropod parasites on domestic livestock production. Annu Rev Entomol 21:155–178

Thomas GD, Skoda SR (eds) (1993) Rural flies in the urban environment. Agricultural Research Division, Institute of Agriculture and Natural Resources, University of Nebraska-Lincoln Research Bulletin 317, 97 pp

Stable Transformation

Transformation that alters the germplasm of an organism so that the progeny transmit the trait through subsequent generations.

Stag Beetles

Members of the family Lucanidae (order Coleoptera).

► Beetles

Stadium

The time interval between molts in a developing arthropod.

Stål, Carl

Carl Stål was born at the castle of Carlberg, in Sweden, on March 21, 1833. He was the greatest Swedish hemipterist and orthopterist, and one of the world's greatest authorities on Hemiptera. He began his education at Uppsala, Sweden, including medical studies, and obtained further education at Stockholm and Jena. Stål became an assistant to the Swedish coleopterist C.H. Boheman at the National Zoological Museum, and eventually supervised the entomological section of the Museum. Although he favored Hemiptera, Stål was an authority on Coleoptera, Orthoptera and Hymenoptera. Some of his noteworthy publications include "Hemiptera Fabriciana" (two volumes: 1868, 1869), "Enumeratio Hemipterorum" (five volumes: 1870–1876), "Revisio Pentatomidarum, Coreidarum, Lygaeidarum, Reduviidarum et Tingitidarum Europae," and "Recensio Orthopterorkum" (1873–1876). At his death, Stål was the world's authority on Hemiptera, and he left the Museum with the finest collection of Hemiptera in the world. He died at Trösundavik, Sweden, on June 13, 1878.

References

Anonymous (1878) Obituary, Carl Stål. Entomol Monthly Mag 15:94–96

Essig EO (1931) A history of entomology. The Macmillan Company, New York, 1029 pp

Stalk or Stem-Infecting Fungi

Insects are sometimes implicated in the transmission of stalk or stem fungi to plants.

► Transmission of Plant Diseases by Insects

Stalk-Eyed Flies

Members of the family Diopsidae (order Diptera).

► Flies

Staphylinidae

A family of beetles (order Coleoptera). They commonly are known as rove beetles.

► Beetles

Staphylinidae Dermatitis

A term used by a few authors for dermatitis linearis.

► Dermatitis Linearis

Steinhaus, Edward Arthur

Edward Steinhaus was born at Max, North Dakota, USA, on November 7, 1914. H graduated from North Dakota State University in 1936 with a degree in bacteriology, and then moved to Ohio State University where he received a Ph.D. in 1939. In 1940 he joined the staff of the U.S. Public Health Service Rocky Mountain Laboratory, and then moved to the University of California at Berkeley in 1944. He organized and chaired the Laboratory of insect pathology in 1945, which became the Department of insect pathology in 1960, and then the Division of invertebrate pathology in 1963. Later he moved to the University of California at Irvine as dean of Biological Science. Edward Steinhaus was the most distinguished insect pathologist of his era, and created the world's foremost program in insect pathology at Berekeley. He authored 200 publications on insect pathology and the first comprehensive publications on the subject: "Insect microbiology" (1946), "Principles of insect pathology" (1949), and "Laboratory exercises in insect microbiology and insect pathology" (1961). In addition, he edited a two-volume treatise "Insect pathology, an advanced treatise" (1963). Steinhaus founded and edited an important scientific journal, "Journal of invertebrate pathology," and founded the Society for Invertebrate Pathology. He was honored by the Entomological Society of America by being selected to present a Founders Memorial Lecture, and also served as president of the Society. He died at Newport Beach, California, on October 20, 1969.

References

Linsley EG, Smith RF (1970) Edward Arthur Steinhaus (1914–1969). J Econ Entomol 63:689–691

Pristavko VP (1970) In memory of Professor E. A. Steinhaus (1914–1969). Entomol Rev 49:306–307

Stem Cells

Stem cells are able to self-renew and generate cell populations that differentiate to maintain adult tissues. There are about two stem cells in the ovary of *Drosophila* that maintain oocyte production.

Stemmata

The small, simple eyes found on the side of the head of larvae in holometabolous insects. The number of stemmata varies from one to six in different taxa. They are similar to ommatidia of compound eyes in structure and function. A single simple eye of this type is called a stemma.

Stemmocryptidae

A family of bugs (order Hemiptera).

► Bugs

Stem Sawflies

Members of the family Cephidae (order Hymenoptera, suborder Symphyta).

► Wasps, Ants, Bees and Sawflies

Stenocephalidae

A family of bugs (order Hemiptera, suborder Pentamorpha).

► Bugs

Stenopelmatidae

A family of crickets (order Orthoptera). They commonly are known as Jerusalem crickets.

► Grasshoppers, Katydids and Crickets

Stenophagous

Feeding on a small number of hosts. Also called oligophagous.

Stenopsocidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice or, Psocids

Stenostritidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Stenotrachelidae

A family of beetles (order Coleoptera). They commonly are known as false long-horned beetles.

► Beetles

Stephanidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Stephanocircidae

A family of fleas (order Siphonaptera).

► Fleas

Stereokinesis

Kinesis response with respect to contact with surfaces.

Sterile Insect Control

A pest control method using sterilized insects to interfere with normal mating behavior in a wild population, thereby disrupting reproduction of the wild (non-sterile) insects.

Sterile Insect Release Method (SIRM)

A technique used to control pest insects. Large numbers of mass produced males are given nonlethal but sterilizing doses of radiation or chemical mutagens and then released in nature. The natural populations are so overwhelmed by releases of large numbers of these males, that females are almost always fertilized by them. The resultant matings produce inviable progeny and a new generation is not produced. Used to eradicate the screwworm from the USA.

► Sterile Insect Technique

Sterile Insect Technique

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The sterile insect technique (SIT) is a form of birth control imposed on a population of an insect pest to reduce its numbers. Thus far, this has involved rearing large numbers of the target insect pest species, exposing them to gamma rays to induce sexual sterility and releasing them into the target population of the pest on an ecosystem-wide or area-wide basis. The concept of releasing insects of pest species to introduce sterility into wild populations, and thus to control them, was independently conceived by three scientists on three different continents. The first scientist to propose genetic control of insect species was A.S. Serebrovskii, a geneticist in the Institute of Zoology, Moscow State University, who proposed the use of chromosomal translocations for population suppression. The second was Dr. F. L. Vanderplank at a British Overseas Service tsetse research field station in rural Tanganyika (now Tanzania). He showed that the sterility of interspecific hybrids of two tsetse species could strongly suppress a field population of one of the species. The third was E.F. Knipling, a scientist with the U.S. Department of Agriculture. The sterile insect technique was conceived by Knipling in 1937 and first developed for use against the screwworm, *Cochliomyia hominivorax* (Coquerel), a deadly parasite of warm-blooded animals and man in the Americas. This article is limited to a discussion of the latter technique.

Sterile Insect Technique, Figure 115 **Edward F. Knipling in 1946.**

General Overview

The sterile insect technique harnesses the sex drive of insects. The idea of doing this first occurred in 1937 to Edward F. Knipling (Fig. 115), an entomologist with the U.S. Department of Agriculture at Menard, Texas. Knipling did not know of a method to induce sexual sterility. However, in 1926 Herman Müller at the University of Texas had found that X-rays cause numerous changes or mutations in the genes of the vinegar fly, *Drosophila melanogaster* Meigen, and that at high radiation doses, dominant lethal mutations are induced in the sperm or the eggs, which cause the embryos to die. After World War II, both the United States and the Soviet Union were testing hundreds of atomic weapons in the atmosphere. Müller was concerned that the radioactive fallout would induce numerous deleterious mutations in people, so in 1950 Müller publicized his findings that ionizing radiation induces mutations in the vinegar fly, and at high radiation doses, the insects are completely sterilized. Immediately thereafter, under Knipling's leadership, the sterile insect technique was developed and used against the screwworm fly, a major insect parasite of warm-blooded animals and man. Over a period of 43 years, this technique was used to eradicate the screwworm from the United States, Mexico, and Central America to Panama.

Considerable research has been conducted to develop the use of the sterile insect technique against a variety of major pests. For example, Dr. M.D. Proverbs initiated such research on the codling moth, *Cydia pomonella* (L.), in 1955 at Summerland, British Columbia, Canada, but more than two decades lapsed before a practical program was launched against this major pest of temperate tree fruits. Since radiation affects the chromosomes of moths quite differently than those of flies, and since the large scale rearing of moths also is more difficult, the work on moths has lagged behind similar work with flies.

The sterile insect technique has been used with great success against various species of tropical fruit flies. The Japanese used the sterile insect technique to eradicate the melon fly, *Bactrocera cucurbitae* Coquillett, from Okinawa and all of Japan's southern islands, and this has opened the main markets in Japan to fruits and vegetables produced on Okinawa and the islands.

Chile used the sterile insect technique to rid the entire country of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann). By 1980 the entire country of Chile had become a medfly-free zone, and since then Chilean fruits in huge volumes have entered the U.S. market without the need for any quarantine treatments. This has dramatically strengthened the economy of Chile. Now Argentina, Peru and other countries have sterile insect technique programs that they hope will enable them to become fly-free zones with free access to markets in southern Europe, Japan and the United States.

Also, Mexico has used the sterile insect technique to get rid of the Mediterranean fruit fly. Indeed Mexico is ridding large sections of its territory of all fruit fly species of economic importance. The Mexican states of Baja California, Chihuahua and Sonora have been freed of all economically important species of fruit flies, so that citrus, stone fruits, apples and vegetables are being exported from these states without any postharvest treatment. In other parts of Mexico, low prevalence fruit fly areas are being established by means of a systems approach.

To prevent the establishment of medflies that enter the United States with smuggled fruit, sterile medfly males are being released continuously over the Los Angeles Basin and over Tampa and Miami. This has obviated the need to spray these urban areas with the insecticide malathion to suppress outbreaks.

Tsetse flies, which transmit trypanosomes to people and to livestock, are regarded as the root cause of rural poverty in Sub-Saharan Africa because they prevent mixed farming. Food is produced with hoes and spades because African sleeping sickness kills draft animals. Milk cannot be produced and manure is not available to fertilize the worn-out soils. The conquest of sleeping sickness would allow the use of cattle for draft and for milk production, and this is key to facilitating rural development and well being in Sub-Saharan Africa. In 2001 the African Heads of State committed their countries to a campaign to rid Africa of sleeping sickness. This undertaking is known as the "Pan African Tsetse and Trypanosomosis Eradication Campaign." Eradication of the tsetse fly, *Glossina austeni* Newstead, and sleeping sickness from Zanzibar Island was completed in 1997 by means of the sterile insect technique. Previously tsetse populations had been eradicated by this means in small areas in Nigeria and Burkina Faso. Obviously the conquest of African sleeping sickness will require decades of concerted effort.

The sterile insect program against the codling moth is of great global significance, since it is pioneering the practical application of this technique against a species of moth. There are a number of very damaging moth species, and these include the gypsy moth, various cutworm moths, the corn earworm, the European corn borer, the diamondback moth which plagues vegetable production and is resistant to almost all chemical insecticides, rice stem borers, a number of species that destroy stored products, and many others. For a number of years, sterile pink bollworm moths, *Pectinophora gossypiella* Saunders, have been released over the cotton fields in the San Joaquin Valley of California to prevent the establishment of pink bollworms that migrate from southern California. However, the prevention of incipient infestations is not nearly as demanding as coping with a well-entrenched pest population, such as the codling moth in the Okanagan Valley of British Columbia, Canada. Success against the codling moth in the

Okanagan is likely to provide the confidence needed to initiate SIT programs against moth pests in other countries.

Clearly over the past four decades the SIT has come to play a progressively greater role in overcoming poverty, and in expanding free, fair and safe trade between countries, and this is being accomplished with minimal pollution and ecological disruption.

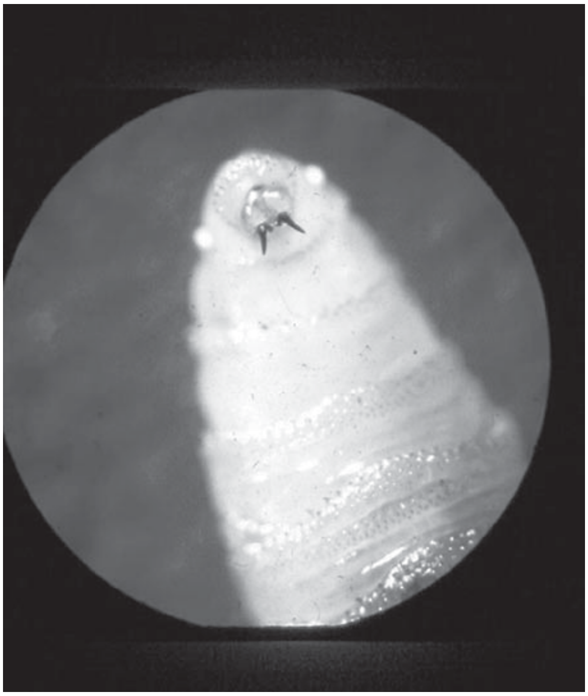
The Theoretical Basis of the SIT and Screwworm Eradication

The New World screwworm is adapted to range throughout the tropics and subtropics. Before it was eradicated from the USA, the parasite survived the winters in southern Arizona, California, Florida and Texas, and ranged far to the north during the summers. The conceptualization of the SIT arose out of the tremendous difficulty of coping with infestations of wounds of livestock by what was believed to be the carrion-feeding blow fly, then known as *Calitroga macellaria* (Fabricius). (The common name of this species was later changed to the secondary screwworm.) However, Emory Cushing, an employee of the Bureau of Entomology and Plant Quarantine, U.S. Department of Agriculture (USDA) at Menard, Texas, suspected that a complex of species was involved. Consequently, Cushing took specimens of the various life stages collected from wounds, carcasses and traps to the Liverpool School of Tropical Medicine for investigation under the guidance of Professor Walter S. Patton, an expert on the taxonomy of Diptera. Cushing and Patton discovered that in addition to *C. macellaria*, a second species was involved in wound infestations, which they named *Calitroga americana* Cushing and Patton. This second species, an obligate parasite, proved to be the major species involved in causing wound infestations, but its identity had been mistaken for *C. macellaria*, which feeds on necrotic tissue and not on living flesh. Thus, it was said that Cushing and Patton had "unmasked the great insect imposter." Clearly, efforts to suppress screwworm attack through the practices of burying carcasses and mass trapping *C. macellaria* adults had been utterly futile. The name of this New World screwworm was later changed to *Cochliomyia hominivorax* (Coquerel), since the screwworm (Figs. 116 and 117) had first been described by Coquerel, a French naval physician, who in 1854 described this parasite as the cause of the deaths of prisoners held on Devil's Island, French Guyana.

Of course, the biology and ecology of this new species needed to be elucidated, and this was facilitated by an unfortunate development. In 1933 a drought visited the Great Plains, and ranchers sought to rescue cattle by shipping them to Georgia and Florida where water and grass were plentiful. This program inadvertently introduced the screwworm to the southeastern USA, whereas previously it had not existed east of the Mississippi. The climate in Florida permitted the pest to reproduce year round, and its population grew explosively. The USDA sought to ameliorate the problem by establishing a small facility at Valdosta, Georgia, with the goal of educating cattle owners on ways of managing their herds in order to minimize the number of screwworm cases.

One of the scientists assigned to the Valdosta laboratory was Edward F. Knipling, who had grown up on a farm at Port Lavaca, Texas, where coping with screwworm-infested wounds

Sterile Insect Technique, Figure 116 **Female screwworm laying a mass of eggs on the edge of a wound.**



Sterile Insect Technique, Figure 117 **Anterior end of a screwworm larva showing the mouth hooks used to tear living flesh.**

in farm animals was an unrelenting chore. The USDA scientists at Valdosta taught cattle owners to control the insemination of cows so that they would calve only during the winter, and also to restrict any operations that result in wounds (branding, castration, dehorning) to the winter when the screwworm populations were depressed. Knipling found time to investigate the biology of the newly described screwworm. Unlike the common blowfly, which can complete its development on carcasses, the screwworm proved to be an obligate parasite of warm-blooded mammals. The female fed on the serum oozing from wounds and laid her eggs at the edges of wounds, and not on carcasses. In addition, the density of screwworms per square mile was quite low. These and later studies led Knipling to estimate the number of screwworms that survive the winter to be roughly 10–20 per square mile, and that peak densities rarely exceeded 1,000 screwworms per square mile.

Meanwhile, Raymond C. Bushland, a young scientist at Menard, Texas, had the duty of rearing the screwworm species on rabbits in order to provide screwworm larvae for evaluating candidate toxicants for inclusion in wound treatments. Bushland devised an economical method of rearing the screwworm on a mixture of hamburger meat, citrated blood and formalin. Bushland was readily able to rear about 5,000 screwworms on one pound of hamburger meat.

In 1937, Knipling was transferred to Menard, Texas, and for the first time he was able to observe the mating behavior of screwworms in the cages of adults maintained by Bushland. Knipling noted that the flies mated on the second and third day of adult life, and that the females mated only once, but that the males remained highly aggressive sexually. Thus, the great idea was born in Knipling's mind that if sexual sterility could be induced in the males, and if vast numbers could be reared, sterilized and released into nature, then the screwworm population could be suppressed strongly. Knipling reasoned that if a natural population could be over-flooded overwhelmingly with sexually sterile males for several successive generations, then most of the wild females would be mated with sterile males and the population would decline towards extinction. Knipling developed very simple mathematical models to simulate the dynamics of screwworm populations, and to assess the effects of the sterile male method and of insecticides on the dynamics of screwworm populations.

Knipling recognized that the level of suppression that is required to prevent further growth (stabilize) a population depends on its actual rate of increase (Table 19). This can be summarized as follows:

Knipling estimated that the overwintering screwworm population typically increases at roughly fivefold between generations, and that this same rate of increase is likely to occur for the next two or three generations. For example, in an area of 100,000 square miles, if 1,000,000 screwworms overwinter, this population will increase

Sterile Insect Technique, Table 19 Rates of mortality and survival required to prevent population growth and decline in relation to various intrinsic rates of increase

			To prevent population increase			
Intrinsic rate of increase	Progeny per female	Number that must survive to prevent population from declining (fraction)	Number that must die	Fraction that must die	Percent that must die	Percent that may survive
2-fold	4	2 (1/2)	2	2/4 = 1/2	50	50
3-fold	6	2 (1/3)	4	4/6 = 2/3	67	33
4-fold	8	2 (1/4)	6	6/8 = 3/4	75	25
5-fold	10	2 (1/5)	8	8/10 = 4/5	80	20
10-fold	20	2 (1/10)	18	18/20 = 9/10	90	10
20-fold	40	2 (1/20)	38	38/40 = 19/20	95	5

to 5,000,000, 25,000,000 and 125,000,000 in the F_1, F_2 and F_3 generations, respectively. In any subsequent generations, the rate of increase would be less than fivefold so that the population would not greatly exceed 1,000 per square mile. In order to calculate the consequences of releasing sterile screwworms into a population of fertile screwworms, Knipling listed the various types of matings, calculated the frequency of each type of mating and assigned ten progeny to each mating of a normal (fertile) female (NF) with a normal (fertile) male (NM). When both sterile males (SM) and sterile females (SF) are released, there are four types of matings. Thus, the above wild population has 500,000 normal males (NM) and 500,000 normal females (NF), and 4,500,000 sterile males (SM) and 4,500,000 sterile females (SF) are released. The frequencies of the various matings and the progeny produced are shown in the following table (Table 20).

Using this method, Knipling constructed a model showing the trend of this hypothetical screwworm population subjected to sterile insect releases when the normal increase rate is fivefold (Table 21).

Knipling's model indicated that if we assume a given insect has a net capacity to increase fivefold each generation, the ratio of fully competitive sterile to fertile insects will have to be 4:1 in order to keep the natural population stable. However, when the increase rate is fivefold, a sustained release rate sufficient to achieve an initial sterile to fertile ratio of 9:1 will have the effect shown in the table above. The first column of figures in that table shows the relative trend of an uncontrolled population increasing at a fivefold rate. Theoretically, an initial ratio as low as five sterile to one fertile will be adequate to start a downward trend in the natural population when the net increase rate is only fivefold. Actually, starting with this lower over-flooding ratio, theoretical elimination of the population will be achieved with fewer insects than will be required with a 9:1 ratio. However, in these models we are concerned with the overall population. In actual practice, the density of insects will vary in different parts of the environment. Moreover, the distribution of sterile insects will never be uniform. Therefore, in control operations, the initial ratio should be sufficiently high to be certain that an overall reduction in the population will occur in all parts of the environment from the start. In some instances, the sterility procedures might reduce the vigor and competitiveness of the organism. Allowance must be made for this factor.

The ratio of sterile to fertile insects increases asymptotically as the density of the wild population

Sterile Insect Technique, Table 20 Method of calculating frequencies of various types of matings and resultant progeny when sterile males (SM) and females (SF) are released in to a population of normal males (NM) and females (NF)

Type of mating	Number of matings	Progeny per mating	Number of progeny
NF×NM	$\frac{500{,}000 \times 500{,}000}{5{,}000{,}000} = 50{,}000$	10	500,000
NF×SM	$\frac{500{,}000 \times 4{,}500{,}000}{5{,}000{,}000} = 450{,}000$	0	0
SF×NM	$\frac{500{,}000 \times 4{,}500{,}000}{5{,}000{,}000} = 450{,}000$	0	0
SF×SM	$\frac{4{,}500{,}000 \times 4{,}500{,}000}{5{,}000{,}000} = 4{,}050{,}000$	0	0

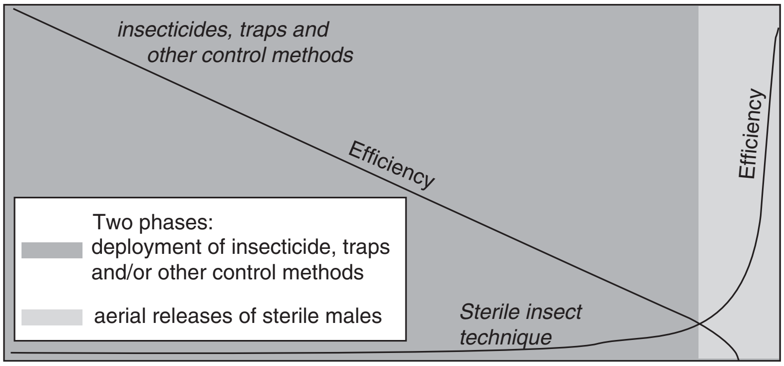
Sterile Insect Technique, Table 21 Trend of an insect population subjected to sterile insect releases when the normal increase rate is fivefold

Generation	Uncontrolled natural population (5X increase rate)	Controlled population		Ratio sterile to fertile
		Natural population	Sterile population	
1	1,000,000	1,000,000	9,000,000	9:1
2	5,000,000	5,00,000	9,000,000	18:1
3	25,000,000	1,31,625	9,000,000	68:1
4	125,000,000	9,535	9,000,000	942:1
5	625,000,000	50	9,000,000	180,000:1

declines to low levels. Thus, in order to take advantage of the tremendous power of the SIT against sparse populations of pests, Knipling advocated that releases of sterile insects should be initiated when the wild population was at a seasonal low, or immediately after adverse weather events, such as freezes and hurricanes, had decimated it. In addition, Knipling designed pest management systems in which insecticides, biocontrol agents, etc., were used to reduce the density of the target population to a level at which the SIT could manifest its great suppressive power (Fig. 118).

Over a period of several years, Knipling and Bushland continued to delve into screwworm behavior and to discuss Knipling's notion on finding a way to harness the sex drive of the screwworm to combat the parasite in a preventive manner rather than making rescue wound treatments after the livestock had become infested. However, neither Knipling nor Bushland knew of a method of inducing sexual sterility in insects. The quest to harness the screwworm's sex drive was interrupted in 1940 with Knipling's transfer to Portland, Oregon, to conduct investigations on mosquitoes and then by World War II when in 1942 both Knipling and Bushland were assigned to Orlando, Florida, to develop methods to combat insect vectors of diseases of concern to military personnel.

In 1946, Knipling was appointed Chief of the USDA's research on insects affecting livestock, man, households, and stored products. Knipling again turned his attention to the possibility of eliminating the deadly screwworm by means of the production and release of sterile flies. An absolutely essential technology was needed to induce sexual sterility in insects. However, such a method had



Sterile Insect Technique, Figure 118 Schematic representation of the sequential use of methods of suppression that efficiently decimate a dense population followed by use of the sterile insect technique, which becomes progressively more suppressive as the pest population declines. Source: FAO/IAEA.

already been discovered in 1926 at the University of Texas by Herman J. Müller, who used X-rays to induce mutations in the vinegar fly, *Drosophila melanogaster*. In 1950, Müller, now a Nobel laureate, published a popular article in the American Scientist with the intent of explaining to the scientific community that radioactive fallout from atmospheric testing of atomic bombs produced both lethal and non-lethal mutations in the sperm and eggs of living organisms. Müller had found that at elevated doses, X-rays caused complete sterility in both male and female flies. In correspondence between Müller and Knipling, Müller assured Knipling that X-rays and gamma rays would probably be effective in sexually sterilizing the screwworm. Accordingly, Knipling assigned Bushland to investigate the effects of X-rays on the screwworm. In brilliantly executed laboratory experiments, Bushland and Hopkins identified doses of X-rays that completely sterilized both sexes of the screwworm. They found that somatic damage did not occur when pupae were irradiated shortly before the adults emerged, because at this late stage all divisions of somatic cell required to form the adult had been completed. Also, Bushland showed that in laboratory cages, sexually sterile males, in competition with normal males, reduced the number of progeny of normal females, in accordance with Knipling's theoretical calculations.

Next, in 1953 Bushland's team evaluated the sterile male release concept on Sanibel Island, two miles off the coast of Florida. By over-flooding the native population with sexually sterile flies, the numbers of screwworm cases were, at times, reduced to zero. However, the continuous influx of flies from the Florida peninsula prevented the total elimination of the screwworm.

It was Knipling's incredibly good fortune that in 1953, B. A. Bitter, an animal health officer on the Dutch island of Curaçao, contacted him about screwworm control forty miles off the coast of Venezuela. Bitter requested the assistance of the USDA in dealing with a major screwworm infestation that was taking a major toll on goats and dairy cows. The USDA negotiated a cooperative agreement with the Government of The Netherlands to conduct a pilot eradication experiment on this island of 176 square miles. Bushland's team at Orlando produced sterile flies, and A. H. Baumhover and W. D. New were dispatched to conduct the operational program on Curaçao. In 1954, about 150,000 sterile screwworm flies per week were released over Curaçao, and within 3 months and the time needed for four generations to mature and the screwworm had been eradicated from the island. The Curaçao venture entailed considerable political risk, since failure surely would have resulted in severe criticism from the Congress for wasting money on such an unheard-of scheme.

The Florida livestock industry soon demanded that the USDA conduct an eradication program in the southeastern United States, and a plan to do so was developed. However, Knipling was hesitant to take this giant step, and he argued for an additional 2 years to develop more robust technologies, which could reduce program costs by $2 million. However, Florida Governor Thomas Leroy Collins asked Knipling, "Why wait 2 years to save $2 million when losses are $10 million per year?" Knipling often cited the Governor's astute reasoning in encouraging subordinates to take well thought out risks. The Florida Legislature appropriated $3 million for the program and the U.S. Congress matched this. The program started late in 1957 when a cold air mass invaded Florida and killed all screwworms southward to a line running from Tampa to Vero Beach, Florida. The program took advantage of this development by initially releasing sterile flies over the northern half of Florida to prevent reinfestation. An aircraft hangar in Sebring, Florida, was converted quickly into a giant "fly factory" and, by the fall of 1958, it produced 50 million sterile flies per week. A fleet of 20 aircraft dropped sterile flies over the infested area, while livestock owners treated all wounds with insecticide smears. The University of Florida Cooperative Extension Service trained cattle producers in management practices needed to minimize opportunities for screwworms to infest animals, to report all cases of infestations, to collect samples of larvae from infested wounds and submit them for identification at the program's headquarters in Sebring. No screwworms could be found in Florida after the end of June 1959.

Cattle producers in the states bordering on Mexico insisted on a program to eradicate the pest from the entire southwest. The Southwest Animal Health Research Foundation raised $3 million from producers to initiate the program. The Texas Legislature had appropriated $2.8 million to match the federal appropriation. A mass rearing facility was built by the Foundation at an air base in Mission, Texas. The plan was to let the cold weather destroy the screwworms to the north of the overwintering area, and to release sterile flies only on the overwintering area. As soon as screwworms had been eradicated from the overwintering area, the sterile flies would be deployed to create a barrier zone along the U.S.-Mexico border to protect against reproduction by invading flies. In this way, the parasite was eliminated from Texas, New Mexico, Arizona and California, but the parasite population in the adjacent area of northern Mexico was managed to minimize the number of flies that would enter the United States.

During 1966 no screwworms could be found in the United States for several months, and the state governors persuaded the U.S. Secretary of Agriculture to declare that the parasite had been eradicated from the United States. This declaration caused the screwworm to be considered a foreign pest, and thus the federal government became solely responsible for costs incurred when screwworms reappeared in the United States.

Eradication of the screwworm to the Isthmus of Tehuantepec was the long-range goal, but the program could not be moved into Mexico because the Governments of Mexico and the United States took 6 years and until 1972 and to negotiate an agreement. The strategy of eradication was replaced with area-wide population management as a static holding action along the entire border with Mexico. During this static decade many difficulties arose. The sterile fly barrier proved to be narrower than the flight range of the screwworm, so that infestations occurred north of the international boundary. The deer population in Texas exploded, and many ranchers reduced the number of cowboys needed to treat wounds. Screwworm cases began to arise as far as 300 miles north of the Mexican border. Serious difficulties were encountered in 1968 when almost 10,000 cases were recorded in the United States, and 1972 was a disaster with more than 95,000 cases. Prestigious scientists criticized the program and decried the strategy of eradication.

The Mexico-American Screwworm Eradication Agreement was signed in 1972 by the two Secretaries of Agriculture with the purpose of removing the parasite to the north of the Isthmus of Tehuantepec and then establish there a sterile fly barrier. For this purpose, a Joint Mexico-U.S. Screwworm Eradication Commission was created. Field operations began in 1974 and a newly constructed screwworm factory near Tuxtla Gutierrez came into full production in January 1977 with a capacity of 500 million flies per week. By 1982, the Commission employed 2,031 people.

The approaches and technologies employed were the latest versions of those that had been pioneered in the U.S. campaigns with the addition of SWASS (Screwworm Adult Suppression System), and a pelletized form of attractants and toxicant developed under the leadership of Wendell Snow for broadcast application. SWASS was effective in attacking high population densities, a necessity to obtain an overwhelming ratio of sterile to wild flies.

The initial deployment of sterile flies was in the Mexican states bordering the U.S., Baja California, and regions of Tamaulipas and Vera Cruz, which provide very favorable screwworm habitat and propitious routes for flies migrating toward Texas. Heavy emphasis was placed on examining and, if it was necessary, treating every animal. Some livestock inspectors traveled routes by horseback that required 15 days to traverse. About 11% of the larvae recovered from wounds were secondary species. By 1984, the Commission had achieved the goal of eradicating to the Isthmus of Tehuantepec.

Dr. Peneda-Vargas, who served as the Mexican Director of the Commission during this period, wrote, "I feel compelled to state that this accomplishment, eradication, was the result of hard work by thousands of people both in the Commission and outside of it, but it would be impossible to overstate the contribution of the Mexican rancher. It was the livestock owner who first saw the need for the program, who initiated and supported it for a period of almost 25 years, and who was in the final analysis most responsible for its success. It was his attention to his animals and his cooperation that made it possible to locate and eliminate every infestation from this large country with all its extremes of terrain and ecology."

In 1986, operations were extended to the Yucatan Peninsula and the countries bordering Mexico. Mexico was declared free of screwworm in February 1991. In order to further reduce the threat of the screwworm to the United States, the decision was made to move the sterile fly barrier to Panama. Thus, agreements were signed between the U.S. Department of Agriculture and the various Central American governments. By 2001, the screwworm had been cleared from Central America north of Panama and a barrier of sterile flies was established across Panama from the Atlantic to the Pacific Ocean (Fig. 119).

It is important to keep in mind that with modern travel and transportation, *C. hominivorax* could easily be re-introduced into areas that have been cleared of this plague. The defenses against this parasite would be improved if all of the Caribbean countries could be freed of the parasite, and eventually the problem in South America must be addressed. However, sufficient progress has been made to enable us to recognize the triumph of an original idea and the benefits nuclear science can add to our quest to assure a reliable and adequate food supply.

Physiological and Cytogenetic Bases of Sterility

Reproductive Physiology of Male Insects

To understand the physiological nature of sexual sterility in insects, familiarity with fertility and reproduction in insects is important. The insect male's mating drive is scarcely affected by castration, and spermatogenesis is under the control of the frontal ganglion and the prothoracic gland. The paired testes become visible in the early instars,

Sterile Insect Technique, Figure 119 **Progress in eradication of the screwworm.**

and in many species sperm are produced before adult emergence. Nevertheless, the development of the germ cells is not correlated closely enough with morphogenesis to estimate the degree of sex-cell maturation based on the individual's life stage. In many species, all types of germ cells are present in the late immature instars and in adults. However, in other species, most notably those belonging to the Lepidoptera, only one or two types of germ cells are present at a given life stage. The spermatozoa pass from the testis through the vasa deferentia into paired seminal vesicles for temporary storage. Typically, a pair of accessory glands flanks the seminal vesicles, and their secretions are transferred with sperm during copulation (Table 22).

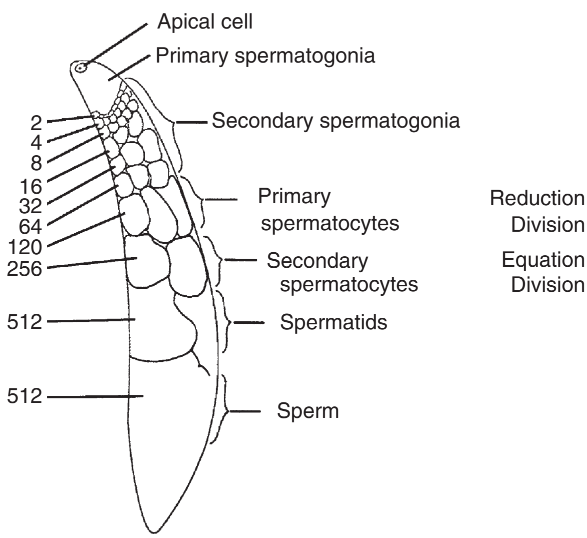
Each testis consists of tubules or follicles, and each tubule is divided into a number of zones. Most distal in the tubule lies the germarium comprised of the primary spermatogonia. Usually, each spermatogonium detaches from the germarium and becomes enveloped by cyst cells (Fig. 120). The spermatogonium then undergoes mitotic divisions to form 256 primary spermatocytes. Next, in the zone of maturation and reduction, each of these primary spermatocytes divides into two haploid secondary spermatocytes, and then each secondary spermatocyte divides to produce two spermatids. In the zone of transformation, the spermatids (still enclosed in the cyst) elongate to form sperm. Finally the sperm rupture the cyst and accumulate in the seminal vesicles as densely packed bundles. In Diptera, during mating the sperm are transferred in semen from the seminal vesicles to the female's spermatheca, while in Lepidoptera the male synthesizes a spermatophore, fills it with sperm bundles, and positions the opening of spermatophore to allow the sperm bundles to pass down the seminal duct to the spermatheca (Table 23).

The amount of time required for a spermatogonium to develop into a bundle of mature sperm varies from species to species, but in most species this time period probably ranges from 5 to 15 days. In *Drosophila melanogaster*, this period is roughly 5–6 days, and another 2 days of maturation are required before the sperm are transferred during mating. Newly formed sperm bundles continuously enter the elastic seminal vesicle to increase its volume and to mix with sperm that had matured previously (Table 24).

Male insects produce much less sperm than do male mammals. An inseminated *Drosophila* female stores 500–700 sperm in her spermatheca, and all of these sperm may be utilized, because a female may lay more than 500 eggs. When the

Sterile Insect Technique, Table 22 Types of germ cells present in the testes of many species of male insects at a given life stage

Life stage	Cell stage in testes
Hatching to penultimate level	Spermatogonia
Pupa	Spermatogonia, primary and secondary spermatocytes
Pupa and adult	Spermatogonia, primary and secondary spermatocytes, spermatids and mature sperm



Sterile Insect Technique, Figure 120 Schematic diagram of a testis tubule as found in Diptera and Coleoptera. The numbers on the left indicate the number of cells in a cyst or sperm bundle.

Drosophila female remates, the sperm of the second mating may displace the majority of the stored sperm. In contrast, when the female boll weevil remates, the sperm received from the second mating are used much more frequently than the sperm from the first mating.

The frequency of copulation by males, and their ability to transfer sperm in successive matings, varies between species. Habrobracon males can mate 14 times in rapid succession and transfer sperm in every mating. Boll weevil males mate 2.55 ± 1.50 times per day. Male *Aedes aegypti* have been observed to mate 30 times in 30 min, however, sperm is transferred only to the first 3 or 4 females. Also, in *Drosophila*, few sperm are transferred after the third closely spaced mating. In *Drosophila* this inability to transfer sperm is not caused by the lack of sperm, but by the exhaustion of the accessory gland secretion, without which sperm transfer is impossible. Regeneration and replenishment of accessory gland secretion in *Drosophila* requires more than 2 h, and 24 h in *Aedes aegypti*.

Reproductive Physiology of Female Insects

Each female possesses a pair of ovaries for egg production. Each ovary consists of ovarioles varying in number from one to several hundred depending on the species. Primitive orders such as Odonata and Orthoptera have panoistic ovarioles without special cells for yolk production. In such insects, nutrients absorbed from the hemolymph are converted into yolk by an enlarged oocytes nucleus or germinal vesicle.

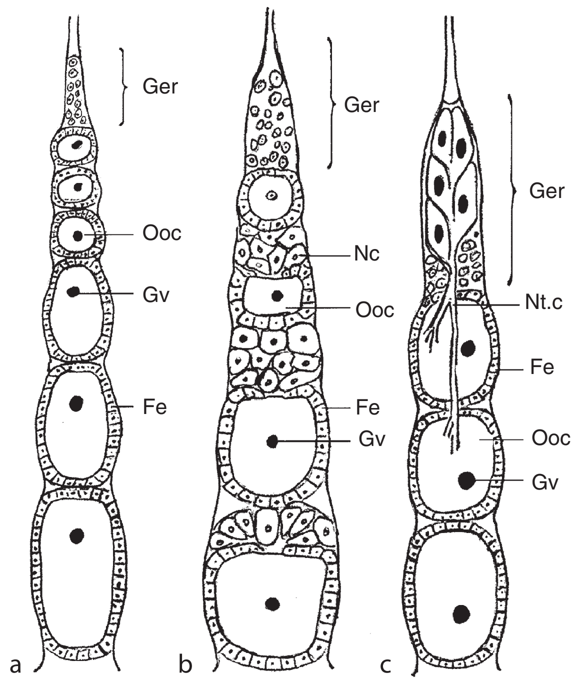
In other orders, special nutritive cells or trophocytes for yolk production are present in the meroistic ovarioles. Depending on the location of the nurse cells in relation to the oocytes, meroistic ovarioles are categorized as either telotrophic or polytrophic. In telotrophic ovarioles the trophocytes are distant from the oocytes, and they deliver yolk via cytoplasmic strands. In polytrophic ovarioles, the trophocytes lie adjacent to the oocytes and form part of the egg follicle. Telotrophic ovarioles are characteristic of Coleoptera, while polytrophic ovarioles are characteristic of Diptera and Hymenoptera.

Sterile Insect Technique, Table 23 **Types of germ cells present at given life stages of the silkworm (Sado, 1961)**

Life stage	Cell stage in testis
Hatching to first instar	Primary spermatogonia
Second to third instar	Secondary spermatogonia
Third to fourth instar	Spermatocytes in early meiotic prophase
Fourth to fifth instar	Spermatocytes in early and late meiotic prophase
Fifth instar to spinning	Same as fourth instar plus a few early spermatids
Pupa	Spermatids and fully formed spermatozoa
Emerged adult	Only fully formed spermatozoa

Sterile Insect Technique, Table 24 **Schedule of spermatogenesis in *Drosophila melanogaster* (Martin, 1965)**

Late spermatogonia	Primary spermatocytes	Secondary spermatocytes	Spermatids		Sperm
0 h	24 h	48 h	72 h	96 h	120 hs



Sterile Insect Technique, Figure 121 **Diagrams of the principal types of ovarioles based on R.E. Snodgrass (1935): (a) panoistic (Odonata and Orthoptera); (b) meroistic and polytrophic (Diptera and Hymenoptera); and (c) meroistic and telotrophic (Coleoptera). fe = folicular epithelium, ger = germarium, gv = germinal vesicle, nc = nurse cell, nt.c = nutritive chord, ooc = oocyte.**

The following description pertains to species with polytrophic ovarioles (Fig. 121).

Egg production depends on mitotic division of oogonial cells. These oogonial divisions produce a cyst of interconnected cells. Depending on the species, each oogonium gives rise to one oocyte and 1, 7, 15, 31 or more trophocytes. For egg maturation to commence, important changes first must occur in the nuclei of the trophocytes. These cells must nurse the growing oocytes. In preparation for this, the nurse-cell chromosomes undergo endomitosis, which entails the repeated replication of trophocyte chromosomes without cell division.

During oogenesis, the volume of a trophocyte cell nucleus increases an estimated 2,000-fold. Thereafter, the oocyte proceeds to grow rapidly. In *Drosophila*, the volume of the oocytes increases by over 100,000-fold in 3 days. After the oocytes have matured, the trophocytes degenerate and disappear. After vitellogenesis has been completed, the follicle cells secrete the chorion, but leave an opening, the micropyle, to facilitate entry of sperm. Finally, the egg ruptures through the follicle, passes down the vagina, receives sperm from the spermatheca, and is deposited. The presence of the sperm in the egg stimulates its nucleus to divide into four haploid nuclei. One nucleus becomes the female pronucleus and unites with the sperm (syngamy) to form the zygote.

Causes of Sterility

Sterility is defined as the inability to produce offspring. Conversely, fertility is the ability to reproduce. Fecundity is the number of progeny produced per female. Thus, only females can be infecund. Sterility may be caused by (i) inability of females to lay eggs (infecundity), (ii) inability of males to produce sperm (aspermia), or inability of sperm to function (sperm inactivation), (iii) inability to mate or (iv) dominant lethal mutations in the reproductive cells of either the male or the female. All of these mechanisms may be induced by exposure of insects to gamma rays or X-rays or to certain chemicals. In addition, sterility may be induced by insect growth regulators, which can be transferred from a treated male to an untreated female during mating, and subsequently disrupt the development of the embryo by interfering with endocrine mechanisms.

Dominant lethal mutations are of foremost importance in the effective use of sterility by means of the sterile insect technique (SIT). In many instances, the successful use of the SIT also requires that infecundity has been induced. For example, in the use of the SIT against the New World screwworm, both males and females are irradiated in the late pupal stage with a dose of gamma rays that induces dominant lethal mutations in all of the sperm of the male and that induces infecundity in all females. In addition, this dose must destroy the spermatogonia of the male so that the male cannot recover fertility.

Infecundity

A reduction in fecundity is expressed as a depression of egg production. Depressed egg production is almost always observed following the treatment of female insects with certain chemicals (antimetabolites and alkylating chemicals), various forms of ionizing radiation (X-rays, gamma rays, and neutrons), ingestion of radioisotopes and intense ultraviolet radiation.

Egg production is dependent on the differentiation and development of oocytes from oogonia and their supply of nutrients from properly functioning nurse cells (trophocytes). Both the oogonia and the trophocytes are readily impaired by the above treatments. Severe damage to these two cell types results in permanent infecundity. In Diptera, the trophocytes attain a high degree of polyploidy during development. Before the trophocytes have fully differentiated (during endomitosis), they are extremely sensitive to the effects of ionizing radiation and to antimetabolites and alkylating agents. On the other hand, after the trophocytes have differentiated they are extremely resistant to impairment by these agents. For example, when the yellow fever mosquito, *Aedes aegypti*, females are irradiated 4 h after ingesting a blood meal, only 10 krad are required to induce infecundity, yet 100 krad are required to induce the same effect when the irradiation occurs 42 h after the blood meal.

Inability or Failure to Mate

Irradiation of either male of female insects with very high doses of ionizing radiation or of chemosterilant, or the application of these mutagenic agents when many somatic cells are dividing, can prevent the treated insects from mating, or at least from mating readily. For example, weevils are debilitated at substerilizing doses of ionizing radiation or by most alkylating chemosterilants. This phenomenon was studied in detail in the boll weevil, *Anthonomus grandis* Boheman. In the midgut of the adult boll weevil, the secretory cells are sloughed to release the digestive enzymes into the lumen of the gut, and these secretory cells are continuously replaced by dividing cells. The latter are destroyed with doses of ionizing radiation or alkylating agents that are only a fraction of the doses required to induce dominant lethal mutations in the sperm. The damage to the midgut prevents the boll weevil from digesting food, and also makes the gut vulnerable to penetration by microorganisms. The capacity of male weevils to mate falls off sharply several days after exposure to ionizing radiation or most alkylating agents.

In the Lepidoptera, the large doses required to induce sterility in the males may impair the transfer of sperm from the male to the spermatheca of the female. During coitus, lepidopteran males enclose their sperm in a spermatophore and position the opening of the spermatophore against the opening of the seminal duct so that the sperm can traverse from the spermatophore down the seminal duct to the spermatheca. Irradiated males in some species experience difficulty in placing the spermatophore opening against the seminal duct opening. Consequently the females from such pairings do not lay eggs, and they call for another mate.

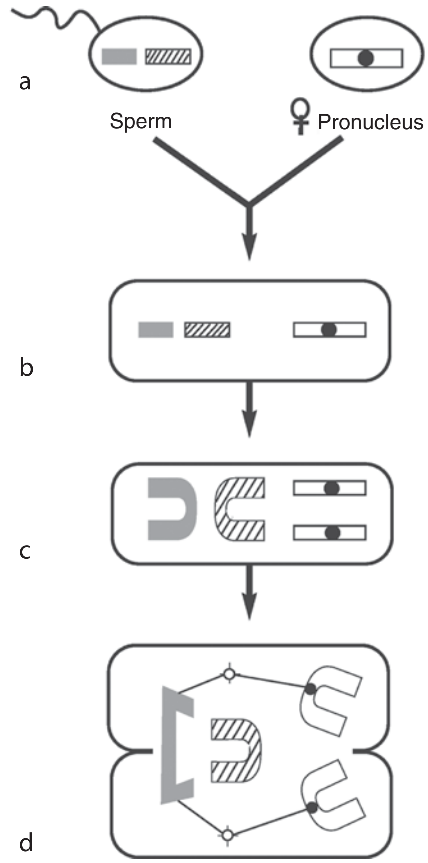
Sperm Inactivation

In most insects of economic importance, the frequency of sperm inactivation is not easily ascertained because lack of egg hatch can be the result of dominant lethal mutations, aspermia or sperm inactivation. However, sperm inactivation by mutagenic agents is studied most readily in the Hymenoptera in which fertilized eggs develop into females, and nonfertilized eggs develop into males. Any egg fertilized with a sperm in which a dominant lethal mutation has been induced will not hatch because the mutation will cause the embryo to die. Generally, inactivation of a significant portion of the sperm requires higher doses than are needed to induce dominant lethal mutations. Careful studies have shown that in some species, some sperm are inactivated at fairly low doses of radiation. However, sperm inactivation has not been found to be an important factor affecting applications of the sterile insect technique.

Dominant Lethal Mutations

Ionizing radiation induces dominant lethal mutations. A dominant lethal mutation is a change in the nucleus of the sperm or the egg that usually causes the death of the zygote, even when such mutation is introduced by only one of the two germ cells that unite at fertilization. (Of course there are also dominant lethal mutations that are expressed at later stages of development and they prevent reproduction of the bearer of the mutation.) A dominant lethal mutation does not impede the maturation of the treated germ cell into a gamete or the subsequent participation of the gamete in fertilization to form the zygote. However, the dominant lethal mutation prevents the zygote from developing into a reproducing adult. Lethal mutations are not lethal to the treated cell. Rather, lethal mutations are lethal to a descendant of the treated cell. Because only one dose of a dominant allele is needed for expression, dominant lethal mutations are expressed in the first generation of the treated cell. However, recessive lethal mutations may be passed on to many generations before they appear in homozygous form required for expression.

Numerous studies that involved insect species in diverse orders and families have shown that dominant lethal mutations are characterized by the presence of chromosome fragments and bridges between dividing nuclei in the zygote or young embryo. The vast majority of dominant lethal mutations induced by ionizing radiation are the result of chromosome breaks (Fig. 123). A broken chromosome, in which the two segments do not rejoin and heal prior to cell division, is the simplest kind of dominant lethal mutation. The chromosome fragment, which lacks a centromere, may not be included in the daughter nucleus, and this would be a lethal deficiency. Moreover, the broken end of a chromosome is sticky and readily joins with any other broken end of a chromosome. Chromosome breaks that rejoin, but not in the original fashion, invariably have a lethal effect. Such asymmetrical exchanges result in acentric fragments (fragments without a centromere) and dicentric chromosomes. Dicentric chromosomes form bridges between the two daughter nuclei formed during cell division. Such a bridge may block cell division or the bridge may break to form genetically unbalanced chromosome fragments that are lethal. In the eggs of the screwworm formed in matings of irradiated males and untreated females, numerous chromosome aberrations occur in the first two cleavage divisions, and that embryonic development seldom progressed beyond the second cleavage division. However, when an irradiated female was mated to an untreated male, numerous chromosome aberrations were found during the first two meiotic divisions. These meiotic divisions occur after the egg is laid and before the cleavage divisions can occur. Again, numerous chromosome aberrations occurred during the cleavage divisions and the embryos invariably died before blastoderm formation (Fig. 122).



Sterile Insect Technique, Figure 122 Schematic representation of the effects of a broken chromosome in a sperm on cell division in the zygote or early cleavage stage. (a) Irradiated sperm with broken chromosome unites with normal oocyte pronucleus; (b) and (c) after syngamy, each chromosome produces sister chromatids. Broken ends of chromatids stick together and heal to form acentric and dicentric isochromosomes. (d) At the cleavage division, a chromosome bridge is formed and the acentric fragment is lost. The bridge may terminate cell division or it may break. In any case the daughter cells will be genetically unbalanced.

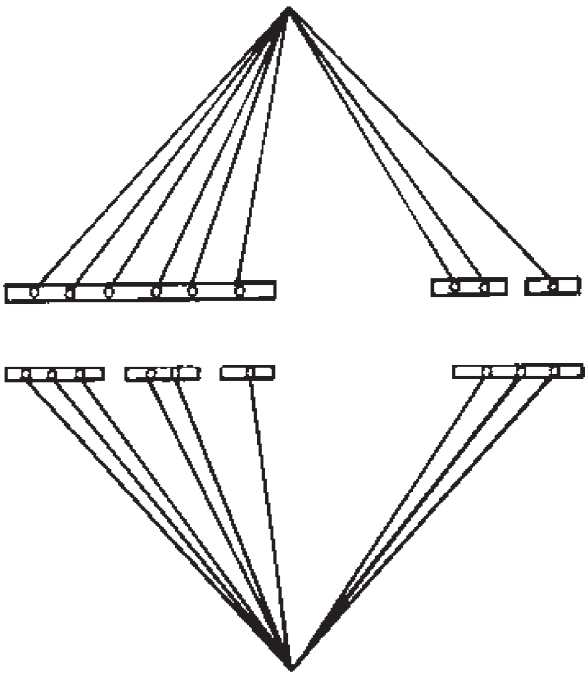
Aspermia

Aspermia is the lack of a supply of sperm. Either mature sperm are not produced or their supply becomes exhausted and their replenishment is prevented. Aspermia can be induced by exposure of immature insects to a dose of a mutagenic agent sufficiently high to inhibit the spermatogenic cycle (kill the spermatogonia). Irradiation of an immature whose testes contains only spermatogonia may destroy them, so the resulting adult is devoid of sperm. Irradiation of the adult male also can result in aspermia because the spermatogonia are killed at substerilizing doses. Thus, such an adult male may exhaust his supply of sperm after several matings.

In order to achieve permanent sterility by means of irradiation, it is necessary to kill all of the spermatogonia. Any spermatogonia that survive irradiation will continue to divide and to repopulate the germarium. Sperm derived from such surviving spermatogonia lack chromosome breaks, and hence they largely lack dominant lethal mutations.

Transfer of a Chemosterilant During Mating

A compound with hormonal effects can be transferred to females by treated males in the process of mating in sufficient amounts to prevent the



Sterile Insect Technique, Figure 123
Diagrammatic representation of a one holokinetic chromosome at late metaphase in a dividing nucleus. The breaks have been induced with ionizing radiation. In the F_1, broken ends of chromosomes join to form a variety of translocations between chromosomes. These translocations cause lethal genetic imbalances in the gametes, and are the primary cause of sterility in the F_1 generation.

development of progeny. This was first shown by Massner et al. with *Pyrrocoris apterus* (L.). As pointed out by Knipling, such a chemical sterilant, when applied to individuals in the wild populations has the following two effects: (i) it prevents the treated insect from reproducing and (ii) it converts the treated insect into a biological agent that can nullify the biological potential of untreated individuals with which it mates. For example, if 90% of a population of 1,000,000 were simply killed, the 100,000 survivors would reproduce normally. However, if 90% of the population was effectively treated with the sterilant, then the 900,000 treated insects would compete for mates with the 100,000 untreated insects. Thus only 10,000 insects would succeed in reproducing. Clearly, if this level of treatment were continued for several more generations, the population would become extinct. Pheromone-baited traps fitted with contaminating devices were developed to dispense the mutagenic chemosterilant bisazir to flies. Subsequently, an insect growth regulator was used as the sterilant, and it provided encouraging results in a field trial. The latter compound arrests development during the pupal stage. More recently, this approach was used against tsetse on the Buvuma Islands, Uganda. Unfortunately, only 25–30% of wild tsetse populations are attracted into the contaminating devices, though models indicate that the effect of this level of sterilization of untreated individuals by mating with chemosterilant-contaminated individuals is considerable. This autosterilization approach is entirely compatible with the release of sterile insects, and is especially applicable as a component of barriers to reinvasion of zones from which the pest has been completely eliminated.

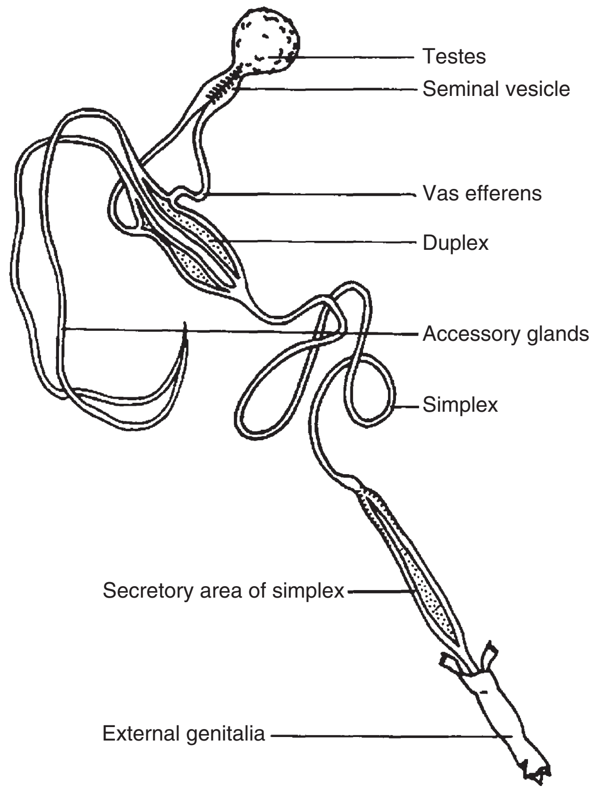
Inherited Sterility in Lepidoptera

Because the very high doses of gamma rays (40,000 krads) required to induce complete sterility in codling moth males is quite debilitating in most species, the effects of partially sterilizing doses of radiation on the competitiveness of the codling moth were investigated. When the treated males were crossed to untreated females, most of the progeny were males. Further, F_1 males crossed to untreated females produced F_1 males with a higher level of sterility than their irradiated fathers. Also, the F_1 females had a high level of sterility. Simulation models showed that released males with inherited sterility would suppress the wild population to a greater extent than the release of equal numbers of fully sterile males.

The phenomenon of inherited sterility was found to occur in species whose chromosomes have a "diffuse centromere" with multiple spindle fiber attachments that are characteristic of the Lepidoptera, Hemiptera and Acari. Such chromosomes have a diffuse centromere and have been referred to as holokinetic or holocentric. Some have argued that these terms are not appropriate, since the kinetochore plates do not extend the full length of the chromosome, but only about 70% of the length, as in the milkweed bug, *Oncopeltus fasciatus* (Dallas). In any case, these multiple spindle fiber attachments insure that most radiation-induced chromosome breaks will not lead to the immediate loss of chromosome fragments. Indeed, these fragments persist and are transmitted through the germ cells to the next generations. The chromosome fragments may unite and form various types of chromosomal translocations, which result in genetically unbalanced gametes in the F_1, and serve as the primary cause of the enhanced level of sterility.

In spite of the existence of inherited sterility, its application for suppressing lepidopteran pests has been slow to develop because ionizing radiation harshly affects (i) the formation and functioning of the two types of sperm, eupyrene and apyrene, and (ii) the ability of the male to properly position the spermatophore opening adjacent to the opening of the seminal duct and thus facilitate the transfer sperm to the spermatheca (Fig. 124).

Eupyrene sperm occur in bundles and possess nuclei and large mitochrondrial derivatives. These nucleate sperm are needed to fertilize the egg. Apyrene sperm do not occur in bundles after they leave the testis, and they lack nuclei. Apyrene sperm appear to be necessary for the transport of the eupyrene sperm from the spermatophore down the seminal duct into the spermatheca, and to prevent the inseminated female from calling for another mate. Eupyrene sperm are susceptible to damage by irradiation, and damage to the flagellum and apex of the sperm cell are frequent. Moreover, in the F_1 male progeny, the number of eupyrene sperm per sperm bundle appears to be reduced, and the many sperm exhibit ultrastructural abnormalities. However, only normal appearing sperm are found in the spermathecae of females that mated with an F_1 male (Fig. 125).

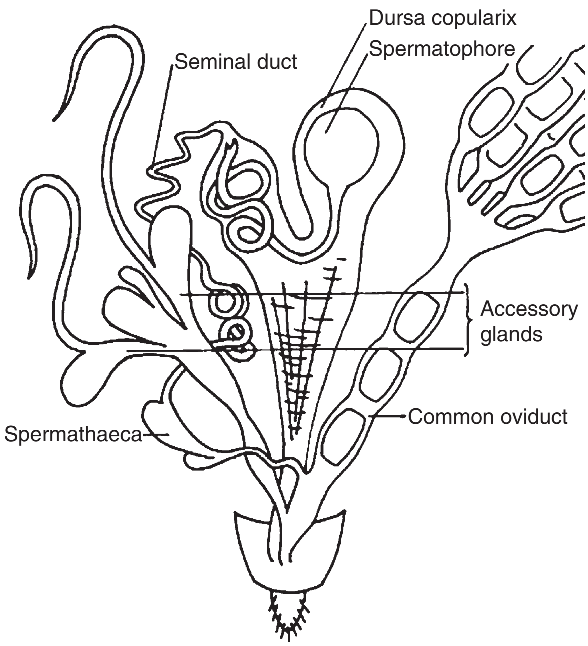


Sterile Insect Technique, Figure 124 Diagram of the male reproductive system of the tobacco budworm, *Heliothis virescens* (Fabricius). Courtesy of H. M. Flint.

Even though F_1 males have not been irradiated, they often fail to transfer sperm to the spermathecae of females. For example, when P_1 adult *Anagasta kuehniella* (Zeller) males received 15–20 krads of gamma rays, roughly 50% of F_1 males failed to transfer eupyrene sperm. Nevertheless, season-long releases of partially sterile males, which resulted in production of F_1 progeny on the field, strongly suppressed wild populations of *Heliothis virescens* in North Carolina and of *Cydia pomonella* in Washington.

Appropriate Applications and Some Limitations of the SIT

The sterile insect technique is a tactic almost always used in association with other control tactics as part



Sterile Insect Technique, Figure 125 Diagram of the female reproductive system of the tobacco budworm, *Heliothis virescens* (Fabricius). Note the position of the open end of the spermatophore at the entrance of the seminal duct. Courtesy of H. M. Flint.

of a pest management system designed to accomplish a certain strategy of pest management. Thus, a "tactic" is a method for detecting, monitoring or controlling a pest. A "system" is an assemblage of tactics that are applied simultaneously or sequentially so that the effects on the pest population of individual tactics are either additive or mutually potentiating, and so that counter-productive (negative) interactions are avoided or minimized. A pest management "strategy" is a broad overall plan for employing pest control tactics to minimize negative ecological, economic, sociological and/or political impacts of a pest problem, both in the short term and in the longer term. Successful strategies should strongly protect agriculture on a sustained basis.

Pest management strategies include (i) prevention or containment, (ii) temporary alleviation, (iii) management of local populations, (iv) management of total populations in an ecosystem or area-wide pest management, and (v) eradication of a pest, i.e., the destruction of every individual of a species in an area surrounded by natural or man-made barriers sufficiently effective to prevent re-invasion except through the intervention of man.

Each control tactic has characteristics that need to be considered in the design of a system to implement a strategy effectively and efficiently. Ecological selectivity is important to avoid the destruction of natural enemies needed to prevent the resurgence of the pest population following a control operation. Most conventional insecticides are relatively nonselective. Highly selective tactics include the SIT and other genetic techniques, resistant crop varieties, certain insect pathogens, parasitoids and predators and certain artificial and naturally occurring attractants. Light traps, some attractant baits, "general" predators, parasitoids and pathogens, and certain insecticides are only moderately selective. These characteristics are displayed in Table 25.

Ideally pest management systems are based on an appreciation of the selectivity and efficiency of the available tactic. Whenever possible, highly selective measures should be chosen. When suppression of populations to very low levels is required, methods that are effective against high populations, and methods that are effective against low populations, should be integrated in such a way that the former potentiate the latter. When the economic threshold of the pest is moderately high, several tactics that are effective against dense populations often may be combined to give much more reliable suppression than a single method.

Because the SIT is not efficient in combating dense pest populations, it is almost always used in concert with a method that is effective against dense populations. Conversely, since the SIT is extremely efficient in suppressing or eradicating low density pest populations, it is used to eradicate incipient infestations of major pests. By analogy, the SIT is useless against the "roaring blaze" but extremely effective in extinguishing the sparks. Thus, the SIT is used effectively as a preventive measure to prevent the establishment of immigrant

Sterile Insect Technique, Table 25 Characteristics of control tactics and their efficiencies

	Constant efficiency at all pest densities	Efficient at high pest densities	Efficient at low pest densities
Highly selective ecologically	Resistant varieties; sex pheromones used to confuse; synthetic attractants	Selective insect pathogens, parasitoids and predators	SIT and other genetic techniques; sex pheromone baited traps
Moderately selective ecologically	Light traps; food baits; systemic insecticides	General predators, parasitoids and pathogens	
Nonselective ecologically	Most chemical insecticides; cultural measures; harsh weather events		

populations of the Mediterranean fruit fly in the vicinities of Los Angeles, Tampa and Miami, and of the pink bollworm in cotton growing areas of California. Similarly, the SIT was used to prevent the spread of the screwworm throughout Africa and to eradicate it from its foothold along the Mediterranean coast of Libya.

The SIT is extremely useful for combating the leading edge of a pest population invading uninfested territory. To be effective, the width of the sterile insect barrier must be greater than the range of dispersal of the wild females. Thus, the MOSCAMED Program has used the SIT as an important component of the barrier to contain the Mediterranean fruit fly in Guatemala and prevent its movement into Mexico. Since 1957 the SIT has been used in barriers to contain populations of the screwworm.

Pest-free zones and pest-free fields of production are area-wide approaches to facilitating exports of agricultural commodities without the need for postharvest or quarantine treatments. Both the International Plant Protection Convention and the Sanitary and Phytosanitary Agreement are structured to accept and encourage area-wide pest management as a tool for promoting safe trade and contributing as much as possible to the complementary goals of food security and economic security for all countries. In Florida, sterile Caribbean fruit flies, *Anastrepha suspensa* Loew, are part of a system used each year to create fly-free fields of citrus production as required to permit the export of fresh citrus to Japan.

The effectiveness of the SIT is affected by many variables. For pest species, which have contagious or clustered distributions, it is the overflooding ratio in the clusters that determines the effectiveness of the SIT. Seasonal patterns of abundance must be taken into account, since a high overflooding ratio can be established most easily when the wild population is low, and since the SIT has tremendous impact when imposed on a wild population with a low or negative intrinsic rate of increase. The longevity of gravid females is important, because they tend not to mate. Thus, it is often cost effective to make one blanket treatment with an insecticide to kill gravid females. The overlapping of generations prolongs the period during which sterile insects must be released. Advantage should be taken of climatic events that synchronize insect development. For example, in the program to eradicate the screwworm from Libya, releases of the sterile flies were begun on December 18, 1990, when the cold rainy weather had halted all reproduction and the wild population consisted entirely of pupae in the soil. Thus, early in February 1991, when wild flies emerged synchronously from beneath the soil, they encountered numerous sterile males. Consequently, the wild population was decimated, and no wild flies could be found after the end of April 1991. The induction of close to 100% sterility is critically important in combating pest species with high intrinsic rates of increase. Also, rearing, sterilization, and release procedures may diminish the quality of the released flies. Clearly no other method of pest suppression is influenced by as many factors as is the SIT.

The SIT is an underutilized and widely misunderstood technology. There is a need for additional data to correlate the frequencies of matings of sterile males with wild females with the dynamics of the pest population.

Economic Analysis of SIT Programs

Apart from clearly objective measures such as technical effectiveness or cost efficiency, there are several subjective measures that come into the evaluation of SIT and other area-wide programs. These include risk of failure of containment or eradication, the boundaries of externalities (for example, variable probabilities of pesticide drift under different conditions, or concerns of people who feel they have no economic stake in a program, as is usually the case when an agricultural pest must be combated in an urban setting), and time preferences for returns on capital investments (such as insect rearing facilities). Such subjective issues may cause great difficulties in reaching agreed decisions, even with a consensus on the data used. It is useful to analyze three general classes of economic problems: (i) annual comparisons of costs and benefits, (ii) initial capital costs with delayed projected benefits, and (iii) initial costs with delayed and uncertain future benefits.

The two basic principles governing the selection of area-wide management over individual local pest management are effectiveness and efficiency. Containment and eradication can be achieved only on an area-wide basis, and total effectiveness is required. Questions of efficiency subsequently arise in deciding which area-wide techniques to employ, not in comparing them to uncoordinated local control. Nevertheless, economic efficiency must be considered at an early stage to decide whether containment and eradication are affordable goals, and if so, whether the resources can be assembled.

The SIT also may be applied on an area-wide basis for population suppression and not for eradication, and this is certainly the case when the SIT is used to create pest-free fields of production. Suppression may or may not be more effective by area-wide management than by management on a local basis, but the main issue is one of cost efficiency. Is area-wide pest suppression more cost efficient than the sum of local pest management? This is a challenge, because local pest management often yields private returns of 4:1.

Size, Coordination and Economies of Scale

Legal authority to conduct a coordinated SIT program may be based on existing laws, or it may require a referendum of all affected parties. Usually, in the USA such referenda must pass with a majority of two thirds.

The optimal size of an area or a sub area for a SIT program depends on the mobility of the pests, the uniformity of their densities and the costs of coordination, and whether pre-existing decision-making and administrative institutions exist. Total detection plus suppression costs per hectare of crop usually will decline as the size of the area increases. However, suppression costs usually decline with increasing size, but they may increase in very large programs if expensive items as helicopters or airplanes must be purchased. Per hectare organizational costs (management, meetings, solving financial problems, etc.) tend to rise sharply with project size.

Approaches to dealing with problems of coordination and economies of scales include: centralized handling of area-wide surveillance with suppression left to individual producers, and division of the area into zones and sub-zones. For example, a zone may correspond to a political subdivision, and sub-zones may be established for areas of uniform pest density. In some eradication programs, growers in areas where the pest is only a minor problem are unwilling to pay as much per hectare as growers in areas were the pest is devastating.

Benefit-Cost Assessment and Discounting Net Returns

Investment in large-scale SIT programs usually is made with the expectation that program benefits will accrue over a multi-year time horizon. Therefore, we must discount future benefits to balance them against present or near term expenditures. The stream of discounted annual benefits and costs for many years of an undertaking can be summed up and expressed as a single value, known as the present value net benefits (PVNB). The formula for calculating the PVNB for a 15-year project is as follows:

$$\text{PNVB} = \text{NB}_1 + w_2\,\text{NB}_2 + w_3\,\text{NB}_3 + w_4\,\text{NB}_4 + \ldots\, w_t\text{NB}_t \ldots\, w_{15}\text{NB}_{15},$$

where NB_t represents the net benefits in year t, and w_t represents the weighting factor for year t. The weighting factors are a function of a discount rate (r):

$$w_t = \frac{1}{(1+r)^t}$$

The discount rate is the "opportunity cost" of the money, or the interest value that money could earn if allocated to the best alternative use. This rate may be established by subtracting the national inflation rate from the bank interest rate for savings. In normal times, this procedure generally will produce a figure around 4 or 5% in developed countries. This represents the "reasonable" person's discount on the future, since people put their money in the bank to gain this premium, and otherwise they would spend it now. So, the benefit of eradication next year is worth 5% less if it is brought back to the present. Benefits in 20 years are only worth 37% of their face value when brought back to the present. In riskier economic environments, discount rates will be much greater, so the calculated net present value of future benefits may be insignificant. However, for SIT programs involving vectors of human diseases, the futures of groups of people are at stake, and it does not seem appropriate to discount benefits in the manner appropriate for private investments. The health of the human population 30 years in the future seems just as important as the health of the population at present. Nevertheless, investments in vector control programs must be subjected to critical analysis in the interest of efficient and sound management. However, if high discount rates (e.g., 25%) are selected commensurate with economic risk in many developing countries, then it seems unlikely that vector control programs in these countries would ever be launched.

With respect to the screwworm eradication in Jamaica, discount of the benefits and costs at 11% and produce the following data (Table 26).

The benefit-cost ratio for screwworm eradication in Mexico was in the order of 10:1.

Who Should Pay for SIT Programs? Or How Much Does Each Group of Beneficiaries Gain?

In developing a concept of how the cost of an area-wide project should be partitioned between producers and consumers, it is helpful to consider the market effects on the market price of the commodity produced. An effective area-wide program will have the immediate effect of increasing supply of the commodity. The relative benefit to producers and consumers can be determined easily by analyzing the relationship of unit price to quantity of production.

If producers profit significantly from the SIT program (increased yield and lowered costs), they may be expected to expand the area under production. If the price of the commodity is elastic (because extra production is easily stored and exported), then an increase in supply will not

Sterile Insect Technique, Table 26 **Benefits and costs of screwworm eradication**

Discounted value	After year 3		After year 10	
	Scenario 1 (US$ million)	Scenario 2 (US$ million)	Scenario 1 (US$ million)	Scenario 2 (US$ million)
Benefits	18.3	18.3	48.0	48.0
Program costs	4.5	8.2	4.5	8.2
Net savings	13.8	10.1	43.5	39.8
Benefit-cost ratio	4.1:1	2.2:1	10.7:1	5.9:1

greatly reduce the market price. In this case, consumers are likely to benefit more than producers, and they should shoulder part of the program cost. On the other hand, for a commodity with an inelastic demand any program that greatly stimulates production will cause the unit price to fall, and this could be damaging to producers.

SIT programs have good potential for capturing returns through commercial sales or privatized management. Privatization is likely to become common for SIT where it is used for suppression rather than eradication. In eradication programs, the period in which sterile insects are used may be too short to recover the cost of private investment in a rearing facility. However, in suppression programs, profits realized over a much longer period can repay private investment in facilities and avoid the need for publicly initiated or coordinated control programs. In particular, the easy and efficient intercontinental transport of sterile insects by air can be expected to allow commercial competition based on price and quality and opportunities for specialization and economies of scale in production facilities.

References

Bloem S, Bloem KA, Carpenter JE, Calkins CO (2001) Season-long releases of partially sterile males for control of the codling moth, *Cydia pomonella* (Lepidoptera: Tortricidae) in Washington apples. Environ Entomol 30:763–769

Graham OH (1985) Symposium on eradication of the screwworm from the United States and Mexico. Misc Publ Entomol Soc Am 62:1–68

Klassen W (1989) Eradication of introduced arthropod pests: theory and historical practice. Misc Publ Entomol Soc Am 73:1–29

Klassen W, Lindquist DA, Buyckx EJ (1994) Overview of the Joint FAO/IAEA Division's involvement in fruit fly sterile insect technique programs. In: Calkins CO, Klassen W, Liedo P (eds) Fruit flies and the sterile insect technique. CRC Press, Boca Raton, FL, pp 3–26

Krafsur ES (1998) Sterile insect technique for suppressing and eradicating insect population: 55 years and counting. J Agric Entomol 15:303–317

LaChance LE, North DT, Klassen W (1968) Cytogenetic and cellular basis of chemically induced sterility in insects. In: LaBrecque GC, Smith CE (eds) Principles of insect chemosterilization. Appleton-Century-Crofts, New York, NY, pp 99–157

Stern, Vernon M

Vern Stern was born in 1923 and died in 2006 after a long and illustrious career with the University of California, Riverside. He is remembered principally for his promotion of aspects fundamental to the integrated pest management (IPM) concept. Important aspects included restricting the use of insecticides to only when natural mortality agents were not functioning adequately, the economic threshold concept (treating with insecticides only when treatment was economically justified), and the recognition of the deleterious aspects of pesticide use. Vern Stern (along with Ray Smith, Robert van den Bosch and Ken Hagen) published a landmark paper on the concept of integrated control in Hilgardia in 1959 that laid out many of the key elements of IPM, and became a citation classic. This was followed by numerous papers on economic thresholds, strip cropping, and natural control, and he was also recognized as a leader in the field of biological control. A "colorful" individual who gave interesting and unpredictable talks, Stern was an effective mentor for numerous graduate students who spread around the globe and greatly enhanced the reputation of the University of California, where he served on the faculty from 1956 to 1991.

Reference

Trumble JT (2006) Vernon M. Stern. Am Entomol 52:204–205

Sternite

The lower or ventral plate of a body segment, or a portion of this region.

Sternum

The ventral portion of any segment, often used to describe the ventral portion of the thorax.

Stick Insects

Members of an order of insects (order Phasmatodea).

► Stick and Leaf Insects

Stick and Leaf Insects (Phasmida)

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Phasmida are terrestrial, nocturnal, phytophagous insects found in nearly all temperate and tropical ecosystems. Scientists have described over 3,000 species, yet this figure is uncertain since some taxon names are synonyms, and many new species have not been formally described.

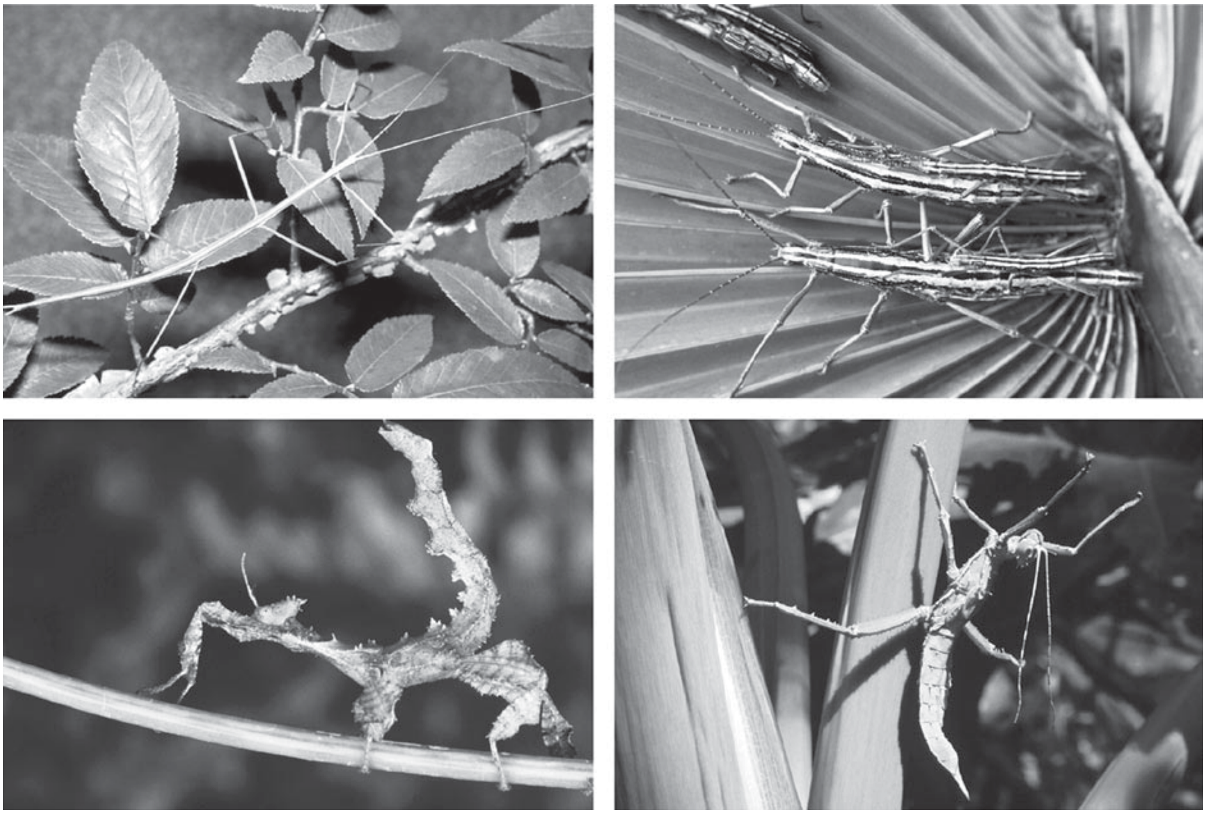
They are variable in appearance, ranging from relatively plain forms, to some that are wonderful mimics of sticks and/or leaves (Fig. 126). They display varying degrees of brachyptery, and can be winged or wingless. The tarsi have three articles in *Timema* Scudder and five in other Phasmida. Cerci are composed of one article, except for adult males of *Timema* which have a lobe on the right cercus.

Sexual dimorphism is usually extreme: the males are smaller and more gracile than the females. Reproduction is typically sexual, but parthenogenesis occurs frequently. The egg capsule is distinctively shaped, possessing a lid called the operculum and a micropylar plate. Eggs are large and oftentimes highly sculptured resembling plant seeds. They are laid singly, and are either dropped, flicked, buried, glued to a surface, or riveted to a leaf. Some species that drop the eggs rely on ants to disperse them in a process analogous to myrmecocory. The entire life cycle from egg to adult can take from several months to several years, depending on the species.

The order consists of two extant monophyletic groups: the genus *Timema* and the remaining species of Phasmida termed the Euphasmida. These two clades diverged at least 50 million years ago and are phenotypically distinct.

Timema are small, wingless Phasmida that lack elongation of the body segments. They have three tarsal articles, unlike other Phasmida which have five. Using her large paddle-shaped cerci, the female coats each egg with defecated soil before oviposition. This forms a coating that may protect the egg from fire.

Timema are found only in the mountains of the western United States and are primarily associated with the Chaparral biome. They live on their host plants and are highly cryptic due to their coloration and habits while resting. When disturbed they release a spray from the prothoracic exocrine glands, but it has not been demonstrated to have a defensive function. They are unusual in that they feed on a variety of plants, including both Gymnosperms and Angiosperms.



Stick and Leaf Insects (Phasmida), Figure 126 **Some stick insects: *top left*, *Diapheroma femorata*; *top right*, *Anisomorpha buprestoides* (Stoll); *lower left*, *Exactosoma tiaratum*; lower left, *Heteropteryx dilatata* (top photos by Lyle Buss, lower photos by Mike Turco).**

Euphasmida are commonly referred to as stick and leaf insects. Exquisitely camouflaged, many species look like twigs and may have the appearance of being covered by lichens, mold, bird feces, or moss. The leaf-like forms usually bear a striking resemblance to foliage, exhibiting leaf veins, mildew spots and even apparent insect feeding damage.

Their primary means of avoiding predators is crypsis. If discovered, they either play dead (catalepsy), or they try to scare the predator with a startle display which can include wing flashing, leg kicking, or spastic motion. Some species also release an irritating "tear gas-like" spray when disturbed. In addition, many Euphasmida can purposely lose some of their legs to help free them from a predator's grasp, or free them from the exuvia while molting. If this occurs during the immature stages, they can regenerate the lost limbs during successive molts.

Compared to other insects, Euphasmida are large, and a few are gigantic. Several species measure over 200 mm in length and the world's largest extant insect is the Euphasmida *Phobaeticus serratipes*, with one documented female measuring 555 mm.

Since Euphasmida are wonderful looking insects, and are relatively easy to rear in captivity, they are popular as pets and for displays at zoological gardens.

References

Bragg PE (1995) The phasmid database version 1.5. Phasmid Studies 3:41–42

Crespi BJ, Sandoval C (2000) Phylogenetic evidence for the evolution of ecological specialization in *Timema* walking-sticks. J Evol Biol 13:249–262
Seow-Choen F (1995) The longest insect in the world. Malay Nat 48:12
Tilgner E (2001) Fossil record of Phasmida (Insecta: Neoptera). Insect Syst Evol 31:473–480
Tilgner EH, Kiselyova TG, McHugh JV (1999) A morphological study of *Timema cristinae* Vickery with implications for the phylogenetics of Phasmida. Deutsche Entomologische Zeitschrift 46:149–162

Stick Katydids

A subfamily of katydids (Saginae) in the order Orthoptera: Tettigoniidae.

► Grasshoppers, Katydids and Crickets

Sticky Trap

A method of insect sampling that uses an adhesive material to capture insects. Sticky traps normally use visual attraction based on color, or chemical attraction based on sex pheromone, to attract the insect to the trap. Some sticky traps depend instead on interception of flying insects with transparent material such as glass to obtain an unbiased assessment of population density because they do not concentrate the insects, as do lures.

► Traps for Capturing Insects

Stictococcidae

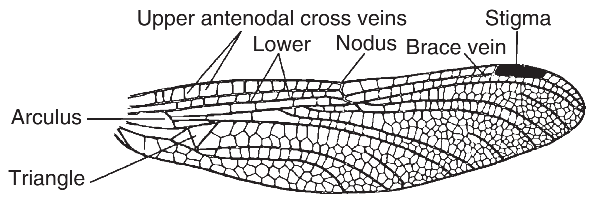
A family of insects in the superfamily Coccoidae (order Hemiptera). They are sometimes called false soft scales.

► Scales and Mealybugs
► Bugs

Stigma

The dense, often discolored portion of the costal margin of a wing, usually at the end of the radius. This is also known as the pterostigma (Fig. 127).

► Wings of Insects



Stigma, Figure 127 Front wing of a dragonfly (Odonata).

Stiletto Flies

Members of the family Therevidae (order Diptera).

► Flies

Stilt Bugs (Hemiptera: Berytidae)

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Berytids are characterized by a slender and elongate body, with long four-segmented antennae and very elongated and slender legs. The first antennal segments as well as the femora are thicker apically. They have a pair of ocelli in the head, three-segmented tarsi and a limited number of veins in the hemelytra. Some have long spines on the pronotum and scutellum. The suture between the clavus and corium is very conspicuous.

The family Berytidae was established by Fieber in 1851, in order to cluster seven genera. Traditionally, authors have divided this family in two subfamilies Berytinae and Metacanthinae, and this classification was maintained until 1995. Following cladistical analysis by Henry in 1997, which included all the genera in the world, this family was divided into three subfamilies, each with two tribes. The subfamily Berytinae with Berytini and Berytinini, Gampsocorinae with Gampsocorini and Hoplinini, and Metacanthinae with Metacanthini and Metatropini. Henry's phylogenetic analysis clarifies the monophyletic character of this family, as well as the relationships between this taxon and the rest of families that are part of the superfamily Lygaeoidea.

There are 170 species known worldwide, segregated in 35 genera. In the Paleartic Region there are 54 species in 35 genera, but only five tribes, because the tribe Hoplinini is not represented in the Paleartic fauna.

In general, the berytids present univoltine biological cycles with hibernating adults that seek refuge in leaf litter and mosses. Almost all species are polyphagous and there are some reports of facultative predaceous species, such as *Berytinus minor* attacking aphids. In general, the berytids of temperate regions do not represent a threat to crops. However, in Peru, *Jalysus wickhami* Van Duzee and *Parajalysus spinosus* Distant are pests in tomato and cacao crops respectively.

References

Henry TJ (1997) Cladistic analysis and revision of the stilt bug genera of the world (Heteroptera: Berytidae). Contr Am Entomol Inst 30:1–100

Henry TJ (1997) Phylogenetic analysis of family groups within the infraorder Pentatomomorpha (Hemiptera: Heteroptera), with emphasis on the Lygaeoidea. Ann Entomol Soc Am 90:275–304

Henry TJ (2000) Stilt bugs (Berytidae). In: Schaefer CW, Panizzi AR (eds) Heteroptera of economic importance. CRC Press, Boca Raton, FL, pp 725–735

Henry TJ, Froeschner RC (1998) Catalog of the stilt bugs, or Berytidae, of the world (Insecta: Hemiptera: Heteroptera). Contr Am Entomol Inst 30:1–72

Henry TJ, Froeschner RC (2000) Corrections and additions to the "Catalog of the stilt bugs or Berytidae of the world (Insecta: Hemiptera: Heteroptera)." Proc Entomol Soc Washington 101:1003–1009

Péricart J (2001) Pentatomomorpha I. Lygaeidae. In: Aukema B, Rieger C (eds) Catalogue of the Heteroptera of the Palaeartic region, vol 4. Netherlands Entomological Society, pp 35–22

Schuh RT, Slater JA (1995) True bugs of the world (Hemiptera:Heteroptera). Classification and Natural History. Cornell University Press, 336 pp

Wheeler AG Jr, Schaeffer CW (1982) Review of stilt-bug (Hemiptera: Berytidae) host-plants. Ann Entomol Soc Am 75:498–506

Stilt-Legged Flies

Members of the family Micropezidae (order Diptera).

► Flies

Stink Bugs

Members of the family Pentatomidae (order Hemiptera).

► Bugs

Stink Bugs (Hemiptera: Pentatomidae), Emphasizing Economic Importance

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This is one of the largest groups within the suborder Heteroptera, the so-called true bugs. This family is the third largest of the suborder; it is surpassed by the Reduviidae, the predatory assassin bugs, and the Miridae, the plant bugs or capsids, which is by far the largest family of Heteroptera. Of over 36,000 described species of true bugs, more than 4,000 species belong to the family Pentatomidae. The classification of the family is as follows:

Order: Hemiptera
  Suborder: Heteroptera
    Superfamily: Pentatomorpha
      Family: Pentatomidae

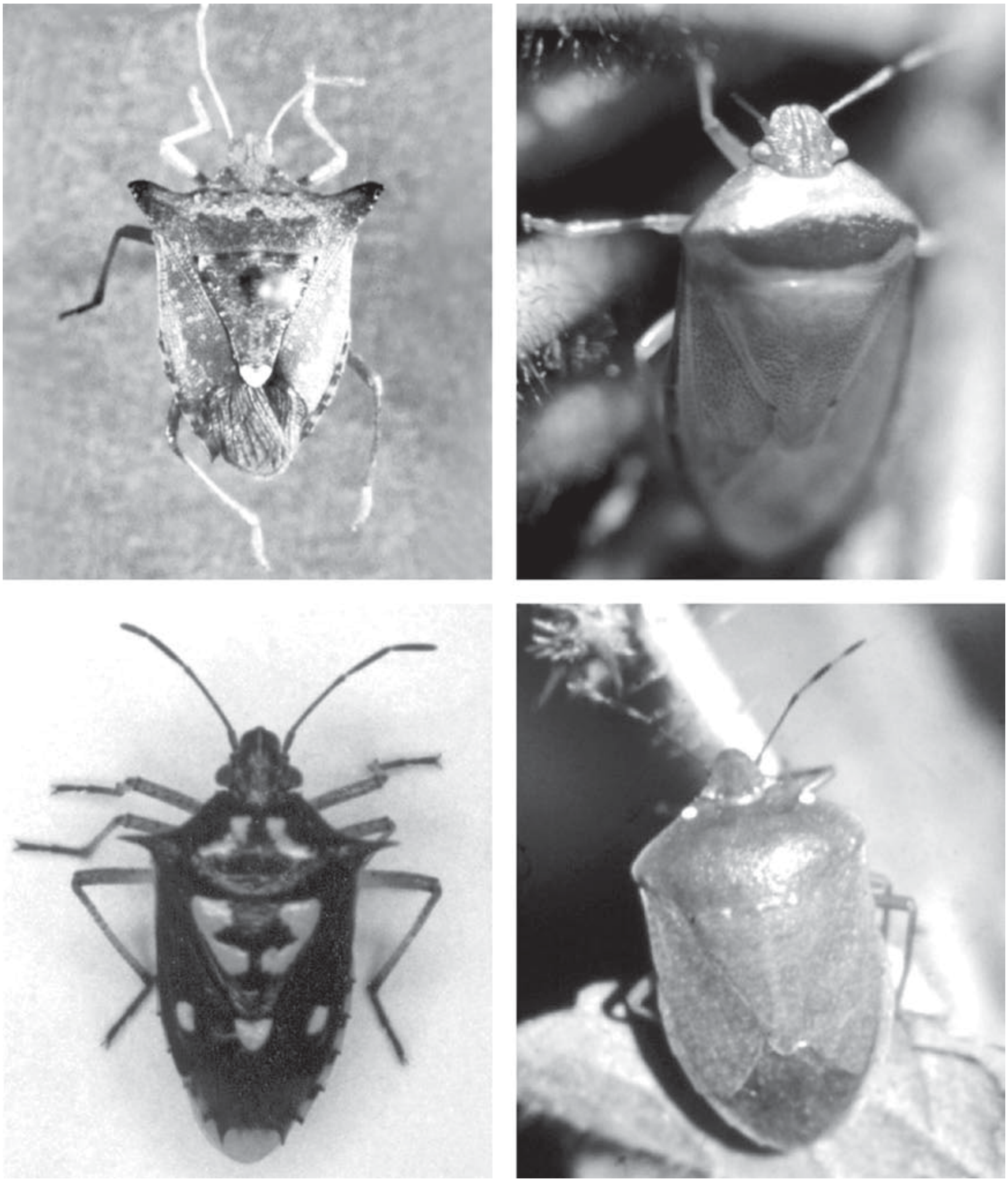
Within the family pentatomidae there are eight subfamilies: Asopinae, Cyrtocorynae, Discocephalinae, Edessinae, Pentatominae, Phyllocephalinae, Podopinae, and Serbaninae. Members of the subfamily Asopinae are distributed worldwide, and are predatory. Because of their feeding habits they are important biological control agents, particularly those of the genera *Podisus* and *Perillus*. Members of the subfamily Cyrtocorinae are found only in the Neotropical Region, and are cryptically colored, resembling tree bark. They are of minor economic importance, feeding on branches of weeds, shrubs or trees. Eventually they may be found feeding on soybean. The Discocephalinae are flat and colored dark, typical from the Neotropics and of no economic importance. The Edessinae are large stink bugs, being abundant in the Neotropics. They are pests of several crops, including Leguminosae and Solanaceae. The Pentatominae contains most of the species in the family and are plant feeders. They are cosmopolitan. These phytophagous pentatomids are characterized by being round or ovoid, with five-segmented antennae, three-segmented tarsi, and a scutellum that is short, usually narrowed posteriorly, and more or less triangular. Several species are pests of major crops, feeding mostly on legumes and brassicas, but by being extremely polyphagous, also damage fruit trees, nut trees, palms, etc. Members of the subfamilies Phyllocephalinae, Podopinae, and Serbaninae are, in general, flat, feeding on bark of trees. They are mostly present in the Neotropics. With very few exceptions, they are of no economic importance (Fig. 128).

Pentatomids are called stink bugs because they produce a disagreeable odor by means of scent glands which open in the region of the metacoxae. Some nymphs have scent glands located on the dorsum of the abdomen.

Stink bugs feed by inserting their stylets into the food source to suck up the nutrients. By doing this, they cause injury to plant tissues, resulting in plant wilt and, in many cases, abortion of fruits and seeds. During the feeding process, they also may transmit plant pathogens, which increase their damage potential. Because they feed on several plant species of economic importance, they are regarded as major pests.

The economic importance of these insects varies greatly from species to species and within a species depending on the plant attacked. From the subfamily Edessinae, the species *Edessa meditabunda* (F.) is a pest of many vegetable crops, particularly Solanaceae such as tomato and potato, and Leguminosae, such as peas, soybean, and alfalfa. It also feeds on cotton, eggplant, tobacco, sunflower, papaya, and grapes. Of the many host plants, soybean is perhaps the most important. Among the Pentatominae, the pest species injure a wide range of plants, from vegetables to trees. The generalist southern green stink bug, *Nezara viridula* (L.), is a pest of grain, legumes and vegetables worldwide; *Piezodorus* spp. feed mostly on legumes, being a severe pest of soybean in South America, in Africa, and in the Orient. Members of the genus *Euschistus* are major pests of several crops, mostly damaging legumes such as soybean in the New World; *Eurydema* spp. in the Orient also attack grain legumes and vegetables. Members of the genera *Oebalus*, *Mormidea*, and *Aelia* are major pests of Gramineae, particularly on rice and wheat. Pests of trees include the spined citrus bug, *Biprorulus bibax* Breddin, on *Citrus* spp. in Australia; *Lincus* spp. on coconut in South America; *Bathycoelia thalassina* (Herrich-Schaeffer) on cocoa in Africa; and *Plautia* spp. on orchard plants in the Orient. The wide ranges of bug species and the host plants fed upon, with frequently detrimental effects to plant production, make this perhaps the most economically important group of insects among the Heteroptera. As an example of this, total losses from Hemiptera during 1985, including stink bugs, were estimated at 3.5 million dollars for the pecan industry in Georgia. In addition, pentatomids may disturb human beings by invading houses in large numbers for overwintering. Finally, because they are polyphagous, pentatomids feed on an array of wild plants.

After copulating, which may last for several hours in an end-to-end position, stink bugs lay eggs in clusters. First instars remain on the top of egg shells, apparently acquiring symbionts, and do not feed. During the second and third stadia, they are gregarious and feed, in general, on immature seeds of their host plants. As nymphs develop through the fourth and fifth stadia, the gregarious behavior decreases, and



Stink Bugs (Hemiptera: Pentatomidae), Emphasizing Economic Importance, Figure 128 **Some stink bugs (Pentatomidae) of economic importance: *top left*, Neotropical brown stink bug, *Euschistus heros*; *top right*, small green stink bug, *Piezodorus guildinii*; *lower left*, small rice stink bug, *Oebalus poecilus*; *lower right*, southern green stink bug, *Nezara viridula*.**

nymphs disperse. Fifth instars molt into adults, which usually disperse further to colonize other host plants. Several generations (1–7) are produced per year, depending on the favorability of abiotic (e.g., temperature, photoperiod, humidity) and biotic (e.g., food availability) factors.

Stink bugs have several natural enemies, the most common being the egg parasitoids

(Hymenoptera) and tachinid flies (Diptera: Tachinidae), which are parasites of adults. Birds also prey on stink bugs.

► Southern Green Stink Bug
► Small Green Stink Bug
► Neotropical Brown Stink Bug
► Spined Soldier Bug
► Predatory Stink Bugs
► Hemiptera

References

McPherson JE, McPherson RM (2000) Stink bugs of economic importance in America north of Mexico. CRC Press, Boca Raton, FL, 253 pp

Panizzi AR (1997) Wild hosts of pentatomids: ecological significance and role in their pest status on crops. Annu Rev Entomol 42:99–122

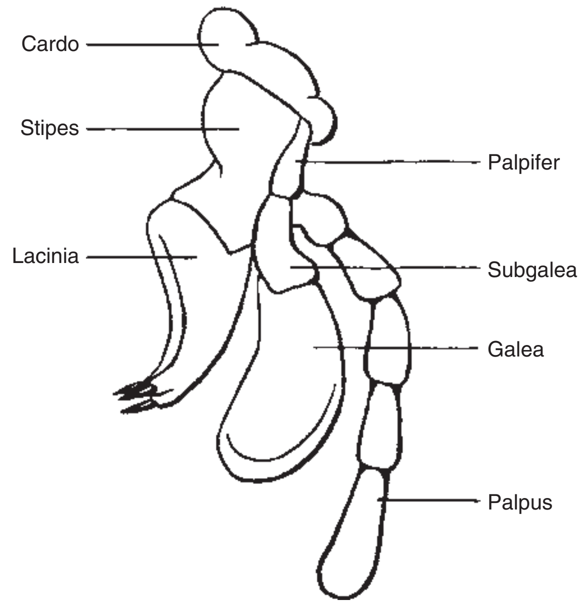
Schaefer CW, Panizzi AR (eds) (2000) Heteroptera of economic importance. CRC Press, Boca Raton, FL, 828 pp

Schuh RT, Slater JA (1995) True bugs of the world (Hemiptera: Heteroptera). Classification and natural history. Cornell University Press, Ithaca, NY, 336 pp

Stipes

A portion of the maxilla. In Diptera, it is sometimes modified into a piercing structure or a lever for flexing the proboscis (Fig. 129).

► Mouthparts of Hexapods



Stipes, Figure 129 External lateral aspect of the left maxilla in an adult grasshopper, showing some major elements.

Scarab Beetles

Members of the family Scarabaeidae (order Coleoptera).

► Beetles

Scenopinidae

A family of flies (order Diptera). They commonly are known as window flies.

► Flies

Schmidt's Layer

A zone of new cuticle deposition within the procuticle (Fig. 130).

► Cuticle

St. Louis Encephalitis

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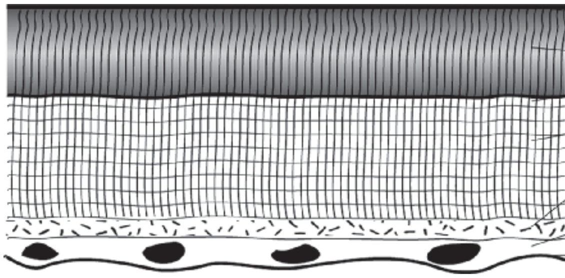
St. Louis encephalitis is the most important mosquito-transmitted disease in the United States. It was first detected in the city after which it is named in 1939 where it claimed 220 lives. It is distributed throughout most of the continental United States although epidemics have only occurred in the Midwest and Southeast. The Centers for Disease Control (CDC) report more than 4,000 confirmed cases in the United States since 1964. The disease is also found in parts of Central and South America and the Caribbean. The pathogen that can cause the disease is an arbovirus (arthropod-borne virus). These viruses are maintained in nature



Schmidt's Layer, Figure 130 **Cross section of the insect cuticle and epidermis (adapted from Chapman, The insects: structure and function).**

through transmission between vertebrate hosts and blood-feeding arthropods (mosquitoes, flies, ticks, etc.). The St. Louis encephalitis virus belongs to the family Flaviviridae and is related to the Japanese encephalitis virus.

The Virus Transmission Cycle

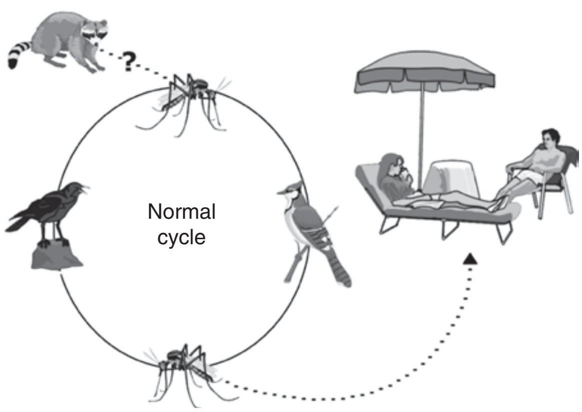
The transmission cycle of St. Louis encephalitis is not completely known, but we know that wild bird populations are of paramount importance in the cycle. When a wild bird is infected by the bite of a carrier mosquito, it produces large amounts of the virus in its bloodstream that can then infect other mosquitoes that subsequently bite the bird. This process is known as "amplification" and is essential for virus transmission. The hosts, in this case wild birds, are known as "amplification hosts." Birds do not show any symptoms of the disease and become immune after infection. In an infected mosquito, the virus replicates and invades other parts of the body, including the salivary glands. From there, the virus can be transferred to other hosts because when mosquitoes bite they inject a small amount of saliva to act as an anti-coagulant.

Mosquitoes remain infective for life, but the virus disappears from the amplification host in a few days. As more and more birds become immune after recovering from the infection, transmission to uninfected mosquitoes diminishes. Therefore, as infected mosquitoes die off (they usually live a week or two) the epidemic subsides. It is unclear what roles other vertebrates such as raccoons and squirrels play in the transmission cycle of St. Louis encephalitis. Mosquitoes known to play a role in transmission of the St. Louis encephalitis virus include *Culex nigripalpus* in Florida, *Culex pipiens* and *Culex quinquefasciatus* in the Midwest and Gulf Coast, and *Culex tarsalis* in western states.

Although humans are not part of the natural transmission cycle, they can become infected by the bite of a vector mosquito. However, humans are "dead-end hosts," meaning that sufficient amplification of the virus does not occur in humans and therefore, uninfected mosquitoes cannot acquire the virus from a human. Also, St. Louis encephalitis is not transmitted directly from human to human (Fig. 131).

Symptomology and Treatment

There have been more than 4,000 human cases of St. Louis encephalitis reported in the United States since 1964. However, less than 1% of St. Louis encephalitis infections are clinically apparent and the vast majority of cases go unreported. Symptoms of infection range from mild headaches and low fever to full meningoencephalitis symptoms including severe headaches and high fever, impaired motor skills, drowsiness, seizures, and central nervous system malfunction. Neurological symptoms may persist for some time after the disease has subsided. Symptoms are usually milder in children than in adults and are most severe in the elderly. Mortality rates for the disease range from 5 to 15%.



St. Louis Encephalitis, Figure 131 Transmission cycle of St. Louis encephalitis.

All resident of areas where active cases of the disease have been confirmed are considered at risk of contracting the disease. Disease risk increases in those persons that are frequently exposed to mosquito bites. The elderly are particularly prone to exhibit severe symptoms and death. Diagnosis of the disease is confirmed by a fourfold rise in antibody titer, or detectable immunoglobular M antibody in sera or cerebrospinal fluid, or by isolation of the viral agent from the patient. Other techniques such as enzyme-linked immunosorbent assay (ELISA) and polymerase chain reaction techniques can increase the speed and accuracy of diagnosis, and are increasingly being used in clinical settings. There is no specific treatment for the disease and no vaccines are available for humans. Affected persons are given supportive treatment for the symptoms and after-effects.

Preventing Infection

As in most arthropod-transmitted diseases, prevention involves personal protection and control of the vector populations to break the transmission cycle in nature. Personal protection includes the use of clothes that protect against mosquito bites (long-sleeved shirts and long pants), the use of repellents containing DEET, and avoidance of areas where mosquitoes are present, particularly after dark, when the *Culex* mosquitoes are most active. Vector population control includes the use of approved pesticides to kill adult and/or immature mosquitoes, and reduction or elimination of sites known to breed mosquitoes.

Surveillance programs are important parts of disease prevention. An effective surveillance program can provide an early warning of when the risk of disease transmission to humans is high. During those times, local health departments may alert the public that personal protection measures against mosquito bites are advisable. It can also trigger increased mosquito control efforts in the affected area. Surveillance programs monitor virus activity in nature, usually by monitoring virus activity in captive chicken flocks ("sentinel chickens"). Weather, particularly rainfall, is an important factor in prediction of vector abundance and is thus an integral part of successful surveillance programs. Direct monitoring of mosquito abundance, behavior, and movement is obviously of paramount importance in predicting risk for human populations, and a variety of techniques are routinely used by mosquito control and health agencies to monitor these vector-related variables. Finally, if disease transmission to humans does occur, it is important to monitor the distribution of cases in time and space, to determine the demographic characteristics of infected persons, and to try to determine the likely place of exposure for each case.

References

Chamberlain RW (1988) History of St. Louis encephalitis. In: Monath TP (ed) The arboviruses: epidemiology and ecology. CRC Press, Boca Raton, FL

Eldridge BF (1987) Strategies for surveillance, prevention and control of arbovirus diseases in western North America. Am J Trop Med Hyg 37:775–885

Lazoff M (1998) Encephalitis. In Emergency medicine-an online reference. http://emedicine.com/EMERG/topic163.htm

Tsai TF, Mitchell, CJ (1988) St. Louis encephalitis. In: TP (ed) The arboviruses: epidemiology and ecology. CRC Press, Boca Raton, FL

Stochastic Model

A mathematical model that is based on probabilities. Thus, the prediction of the model is based not on fixed numbers, but a range of possible numbers. (contrast with deterministic model)

Stoma (pl., stomata)

A pore in the epidermis of plants through which gas exchange occurs. They are most abundant on leaves.

Stomach Poison

A toxicant that acts only after it has been eaten.

► Insecticides

► Insecticide Formulations

Stomatogastric Nervous System

Several small ganglia, including the frontal ganglion and hypocerebral ganglion, that control the foregut muscles.

Stomodeum

The foregut of insects.

► Alimentary System

► Alimentary Canal and Digestion

Stonebrood

Aspergillus spp. fungi cause a disease in honeybees called stonebrood. Several species may be involved, although *A. flavus* and *A. fumigatus* are most commonly implicated. Larvae and pupae are transformed into stone-like mummies, which is the basis for the name of this disease. The disease is known from Europe, North and South America.

These fungi are ubiquitous, and found widely in the soil. They affect other insects, not just honey bees, and also other organisms. Both larval and adult bees are susceptible to infection. Infection occurs by ingestion of spores. Eventually the fungus sporulates on the surface of the insect, imparting a greenish color. These fungi are not highly infectious, and normally only a small part of the colony is affected. Some have suggested that the disease only appears when colonies are stressed. There is no good treatment, but colonies are commonly burned if the beekeeper is concerned about spread of the disease.

► Honey Bees

► Apiculture

Reference

Morse RA, Nowogrodzki R (1990) Honey bee pests, predators and diseases, 2nd ed. Cornell University Press, Ithaca, NY, 474 pp

Stoneflies (Plecoptera)

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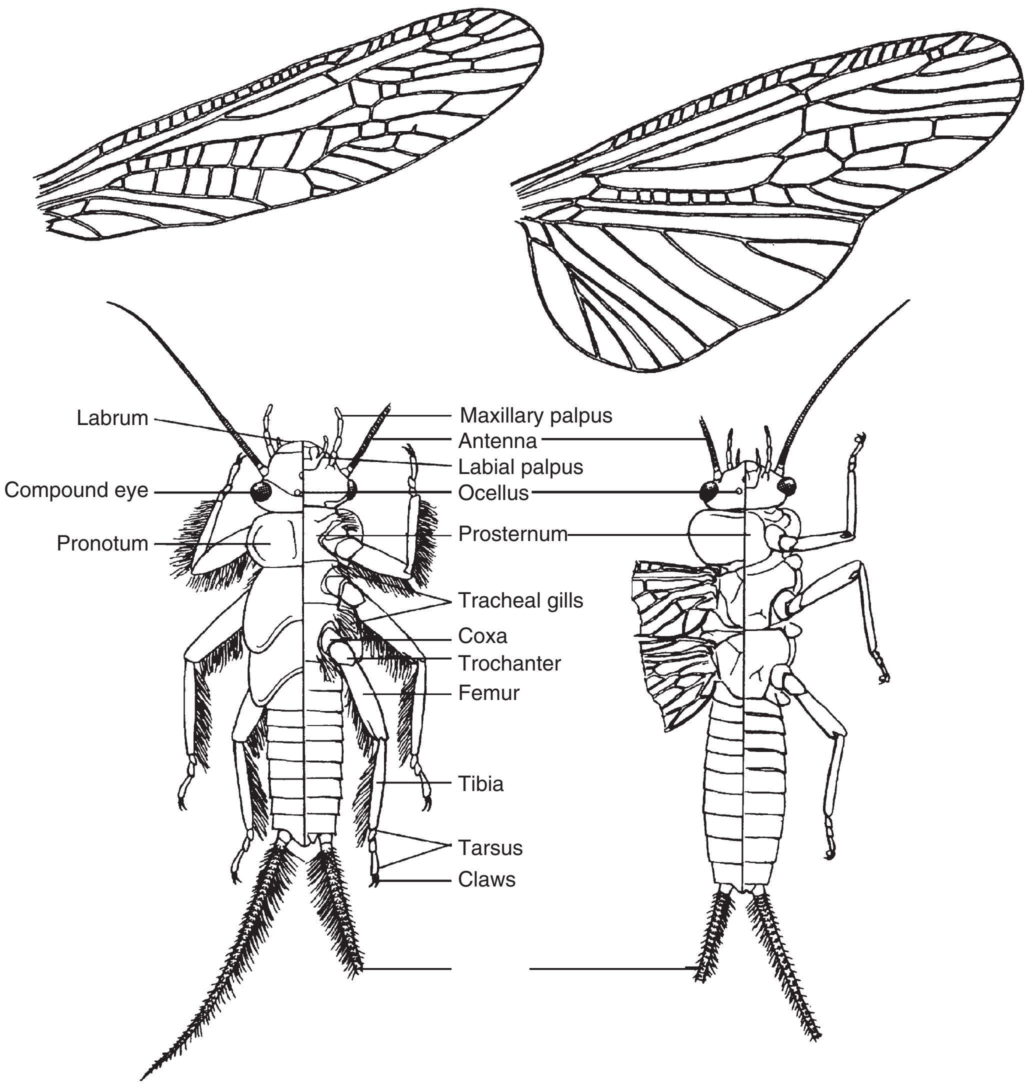
The order name Plecoptera is derived from the Greek "pleco" or folded and "ptera" or wings. More than any other order of insects, stoneflies are typical inhabitants of running waters. Nearly all species occur exclusively in streams, and many are restricted to running water habitats of mountainous regions of the world. Usually water temperatures of these streams are below 25°C and have high dissolved oxygen levels. These requirements make them excellent indicators of water quality.

Stoneflies display incomplete metamorphosis (hemimetabolous development), though it is sometimes called gradual metamorphosis (paurometabolous development). Adult stoneflies can be distinguished from other insects that undergo hemimetabolous development by the long, thin antennae; membranous wings, when not used, lying flat over the abdomen; and the front wings straight and about the same length as the body. The front wings usually have a "fish skeleton-like" venation pattern. The hind wings usually have an expanded posterior area that folds like a fan. Some adult stoneflies have reduced wings or even lack wings. All stonefly adults have two tails or cerci that project from the end of the abdomen; however, in some species these are reduced to a single segment. In addition, all stoneflies have three tarsal segments and two tarsal claws on each leg (Fig. 132).

The nymphs have either cylindrical or flattened bodies; the head has long, thin antennae and wings pads are usually present on the thorax in more mature individuals. Three pairs of segmented legs are present bearing three-segmented tarsi with two terminal claws, and two long, thin tails or cerci occur at the end of the abdomen. Some species have single or branched gills on the thorax or abdomen.

Most stonefly nymphs are herbivores, feeding principally on plant detritus. Even the young nymphs of many carnivorous species feed on fine detritus before switching to animal prey. The Perlodidae, Perlidae, and Chloroperlidae are predominantly predators as older instars. Mature nymphs range in length from a few millimeters (some



Stoneflies (Plecoptera), Figure 132 **Diagram of stonefly wings (*above*); adult female stonefly (*lower right*); immature (*lower left*). Note that the adult and immature are divided into a dorsal perspective (*left portion* of each diagram) and ventral perspective (*right portion*).**

capniids) to over 5 cm (Pteronarcyidae). Although some species emerge in autumn, most stoneflies transform to adults in spring or early summer. Mature nymphs often congregate at emergence sites such as piles of rocks, bridge abutments, and woody debris. The cast skins or exuviae of the nymphs are often abundant at these sites.

Stonefly nymphs occur most commonly in lotic habitats with rocky bottoms and with high dissolved oxygen concentrations, but some species are restricted to seeps and springs, and others to high gradient coldwater streams. One species is known only in both nymphal and adult stages from the depths of Lake Tahoe. Many stonefly nymphs, when subjected to low dissolved oxygen concentrations, will exhibit a "push up" behavior that apparently increases the rate of water movement over the body and gills.

A remarkable behavior of adult stoneflies is the two-way communication between sexes called drumming. Males tap, rub or scrap their elongated abdomens upon various substrates such as branches and leaves. The female adult detects this vibration and she will answer, allowing for an eventual location of each other. The drumming pattern in amplitude, frequency, or duration is species specific.

Numerous "winter stoneflies" occur in North America. These species typically emerge as soon as openings appear in the ice (late winter, early spring); the dark-colored adults are seen on snow-covered stream banks, bridges, fence posts or tree trunks. The remarkable aspect of these stoneflies is the reversal of the typical development pattern of aquatic insects, in that growth and maturity occur during the coldest part of the year. Eggs laid by adult females during the winter or early spring hatch quickly, and the nymphs migrate into the interstitial spaces of the loose, rocky streambed (known as the hyporheic zone) and begin a state of inactivity or diapause throughout the warmer months. As water temperatures begin to cool in the fall and early winter, nymphs move back to the substrate surface and complete development.

The classification of the order is relatively well established, with over 2,000 species in the world placed in 16 families. Nine of these families occur in North America, including about 626 species. The following web site, maintained by R.E. DeWalt, provides a listing of all North American species by province or state: http://plsa.inhs.uiuc.edu/plecoptera/.

- Order: Plecoptera
  - Suborder: Arctoperlaria
    - "group" Euholognatha
      - Family: Capniidae
      - Family: Leuctridae
      - Family: Nemouridae
      - Family: Notonemouridae
      - Family: Taeniopterygidae
      - Family: Scopuridae
    - "group" Systellognatha
      - Family: Chloroperlidae
      - Family: Peltoperlidae
      - Family: Perlidae
      - Family: Perlodidae
      - Family: Pteronarcyidae
      - Family: Styloperlidae
  - Suborder: Antarctoperlaria
      - Family: Austroperlidae
      - Family: Diamphipnoidae
      - Family: Eustheniidae
      - Family: Gripopterygidae

A short synopsis of the families found in North America follows:

Family Capniidae (Small Winter Stoneflies)

This family is composed primarily of small species. It contains many "winter stoneflies," with adults typically emerging from January to April. The numerous species are most common in small streams, including seeps and springs. Nymphs are usually found in leaf packs, accumulations of woody debris, and develop during the coldest water temperatures of winter. The early instars diapause in the hyporheic zone of the stream. Most species of capniids are detritivore shredders. Common genera include the eastern *Allocapnia* and the western *Capnia*.

Family Leuctridae (Rolledwinged Stoneflies)

Nymphs occur in lotic habitats from intermittent streams, springs to small rivers, and are associated primarily with leaf packs, woody debris or mineral substrates. Nymphs are considered shredder-detritivores. Adults of some species emerge during late winter to early spring (*Paraleuctra*), some during the entire summer (*Leuctra*), and others in the fall (*Despaxia*). Some species are very tolerant of low pH.

Family Nemouridae (Nemourid Stoneflies)

Nymphs occur in a wide range of aquatic habitats, from seeps and springs to lakes. Some species also are found in large rivers. Nymphs typically occur in leaf packs, woody debris, but also rocky areas. Most species are restricted to higher elevations. Most adults are recognized by one-segmented cerci and the X-pattern of veins of the front wing. The life cycles vary from 1 to 2 years for completion. Emergence of adults occurs typically in the spring, but some species emerge in the winter, and others in the fall. Several genera are common, *Amphinemura* in eastern North America and *Malenka* in western North America.

Family Taeniopterygidae (Winter Stoneflies)

This family is another well-known group of "winter stoneflies." Adults in warm-weather regions emerge during the winter, and in cool climates and at high elevations they emerge through the spring and early summer. The nymphs, characterized by their stout, robust habitus with divergent wing pads, can be found in almost all sizes of permanent streams. Nymphs usually are associated with leaf packs, wood debris, but also coarse mineral substrates. They are primarily detritivore shredders. The common genera in the east are *Strophopteryx* and *Taeniopteryx*, and *Taenionema* in the west.

Family Chloroperlidae (Green Stoneflies)

Chloroperlid nymphs are small, elongate, gill-less inhabitants of the hyporheic zone, the interstitial spaces between substrate particles in the streambed. Some species reside at considerable depths in the substrate and laterally under the banks. Most species are found only in clean, cool streams of mountainous areas. Adults are recognized by slender bodies and yellow or green coloration. The western genus *Paraperla* is a collector-gatherer and scraper. Other genera are predaceous on other aquatic insects (often chironomid midges), but also act as collector-gatherers. The genus *Sweltsa* is one of the most common genera.

Family Perlidae (Common Stoneflies)

The distinctively patterned yellow and brown nymphs can be found in all types of streams from intermittent to large rivers, and some species occur along wave-swept shores of lakes. Members of this family inhabit warmer waters than most other stoneflies. Nymphs are usually associated with large loose rocks, but also leaf packs, woody debris, and submerged logs.

Several genera, *Hesperoperla* and *Claassenia* in the western USA and *Acroneuria* and *Paragnetina* in the eastern USA, are relatively large and conspicuous stoneflies. The nymphs are predatory, feeding largely on other aquatic insects. The life history varies from 1 to 3 years, with most adults emerging from May to August. Adults often can be found attracted to lights near streams.

Family Perlodidae (Perlodid Stoneflies)

Perlodid nymphs are medium to moderately large-sized and predatory. If gills are present, they are simple (unbranched) and are restricted to the thorax or neck region, except in the rare California genus *Oroperla*, which has lateral gills on abdominal segments. Nymphs of most species are restricted to cool, swift, mountain streams with rocky bottoms. Some species are found only at splash zones of seeps. Others are restricted to large silty western rivers. All species apparently have a single generation per year. Emergence is generally in the spring, but some species are active as adults in the fall. Several species have egg diapause as long as 5–7 months. *Isoperla* is the most common and widespread genus in North America.

Peltoperlidae (Roach-Like Stoneflies)

The "roach-like" appearance of the nymphs makes them one of the most recognizable of all North American stoneflies. Nymphs can be abundant in leaf packs of small woodland streams of the southern Appalachians. Some species are restricted to splash zones of seeps, springs, and even intermittent streams. All species are shredders-detritivores and are important in the breakdown of leaves. Adults generally emerge in the spring and early summer.

Family Pteronarcyidae (Giant Stoneflies)

Nymphs of this family are usually found in cool steams and rivers of small to medium size. Nymphs can be especially abundant in accumulations of woody debris, or among large rocks in the swifter reaches. They are shredders that typically feed on submerged leaf material, but sometimes take in animal material. The life cycle requires 1–4 years to complete, depending on geographic location. Adult emergence typically occurs in May or June for most species. The adults are the largest stoneflies found in North America, reaching 5–6 cm.

Members of the genus *Pteronarcys* are known as salmonfly to anglers, and are widespread over most of North America, whereas the other genus, *Pteronarcella*, is restricted to the west. Adults and nymphs use reflex bleeding to repel potential predators.

References

Baumann RW, Gaufin AR, Surdick RF (1977) The stoneflies (Plecoptera) of the Rocky Mountains. Mem Am Entomol Soc 31:1–207

Stark BP, Armitage BJ (eds) (2000) Stoneflies (Plecoptera) of Eastern North America. Volume I. Bull Ohio Biol Surv New Ser 14:1–98

Stark BP, Armitage BJ (eds) (2004) Stoneflies (Plecoptera) of Eastern North America. Volume II. Bull Ohio Biol Surv New Ser 14:1–192

Stewart KW, Harper PP (1996) Plecoptera. Pp 217–266 In: Merritt RW, Cummins KW (eds) An introduction to the aquatic insects of North America, 3rd edn. Kendall/Hunt Publishing Company, Dubuque, Iowa, 862 pp

Stewart KW, Stark BP (2002) Nymphs of North American stonefly genera (Plecoptera), 2nd edn. The Caddis Press, Columbus, OH, 510 pp

Zwick P (2000) Phylogenetic system and zoogeography of the Plecoptera. Annu Rev Entomol 45:709–746

Stop Codon

One of the three mRNA codons (UAG, UAA, and UGA) that prevents further polypeptide synthesis.

Storage Protein Receptors

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During metamorphosis of holometabolous insects, most larval structures are broken down, while adult tissues are formed. Many new proteins need to be synthesized, requiring vast mounts of amino acid precursors. These amino acid resources, however, must be present prior to pupation, because pupae are not able to feed and take up nutrients from external sources. Specific larval serum proteins, often called "storage proteins," provide these amino acid resources. These proteins accumulate in the hemolymph of last instar larvae, and move shortly before pupation into the fat body, where most new proteins are synthesized. Storage proteins enter the fat body in small vesicles, which fuse with one another to form larger, often crystalline protein granules. As development progresses, these granules are hydrolyzed to provide the needed amino acids.

Most storage proteins are members of the hexamerin family; these proteins are composed of six subunits of 80 kDa each, and are evolutionarily related to hemocyanin. The most common storage protein is arylphorin, a protein rich in aromatic amino acids, but most species contain other storage proteins as well. In one lepidopteran family (Noctuidae), an additional, structurally unrelated storage protein has been found: a very high density lipoprotein (VHDL) composed of four 150 kDa subunits. VHDL is colored brightly blue, due to biliverdin that is bound non-covalently to the protein.

The uptake of storage proteins into fat body cells is selective. Storage proteins are present at very high concentrations in the hemolymph of last instar larvae in both lepidopteran and dipteran species, but prior to pupation they are efficiently removed from the hemolymph, and sequestered by the fat body. Other hemolymph proteins, such as lipophorin, remain in the hemolymph. Storage proteins enter the fat body via endocytosis; to be selective, the uptake is mediated by specific endocytotic receptors, proteins that are associated with the fat body membrane. Such receptors have been found in Diptera and Lepidoptera.

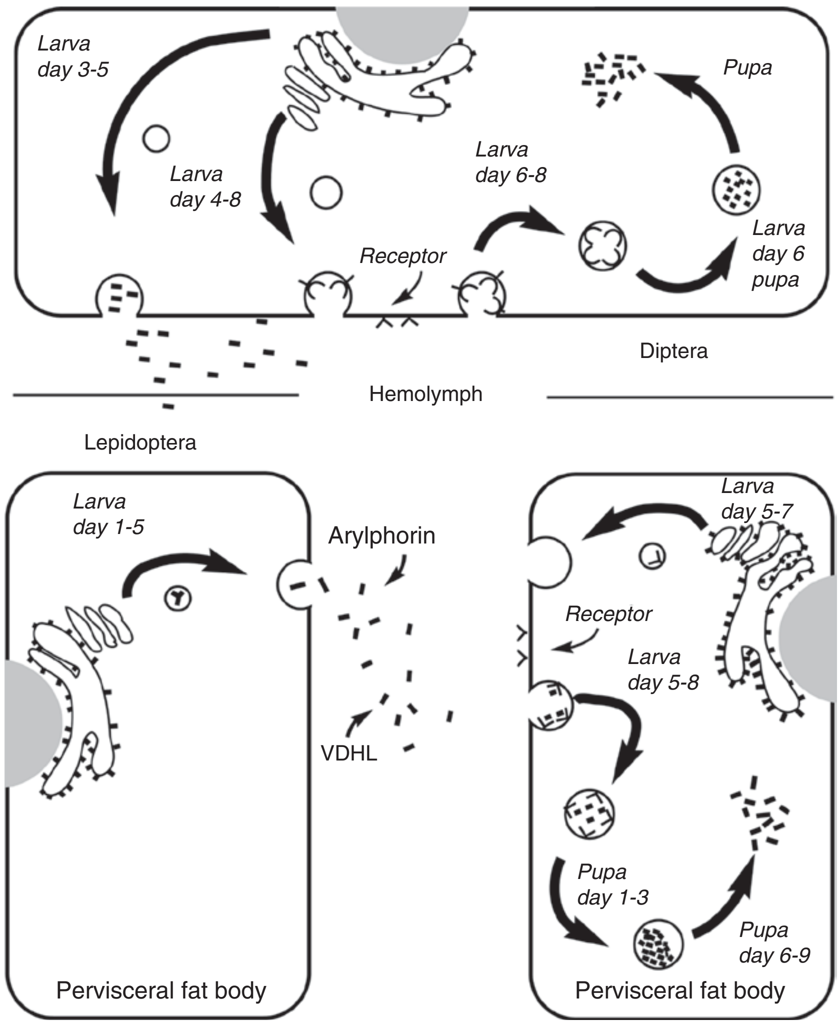
Dipteran Storage Protein Receptors

Storage proteins receptors have been identified in two dipteran species, namely the fleshfly *Sarcophaga peregrina* and the blue bottle fly *Calliphora vicina*. These proteins bind arylphorin in a saturable manner, with dissociation constants between 2 and 800 nM. Binding generally requires Ca^{2+} ions and is pH dependent, with optimal binding at the slightly acidic pH of the hemolymph (pH 6.5). While the reported molecular weights for the arylphorin receptor vary between 50 and 140 kDa, it is now clear that the observed variability is the result of the cleavage of an initial protein of around 140 kDa. The protein is encoded by a gene that is evolutionary related to its own ligand, arylphorin, and other members of the hexamerin superfamily. The genes of the arylphorin (or storage protein) receptors of *Calliphora vicina* (Genbank ID 630903) and *Sarcophaga bullata* (Genbank ID 984655) show high sequence homology with the previously identified fat body P1 protein from *Drosophila melanogaster* (Genbank ID 544281) which appears to be the storage protein receptor in that insect species. The transcription of the latter gene is under the control of the hormone 20-hydroxy ecdysone. While the exact mechanism of action of the receptor remains unclear, proteolytic cleavage of the initial gene product is necessary for the formation of the active receptor. Following the removal of the signal peptide, a protease removes a C-terminal fragment of approximately 50 kDa. The remaining receptor protein is then moved to the outside of the cell, where it can bind to its ligand. The uptake of the bound arylphorin, however, cannot occur until the receptor is further processed by another protease, which appears to be under the control of the hormone 20-hydroxy ecdysone, however at the post-translational level.

Interestingly, the active receptor does not contain a typical membrane spanning domain, and is likely a peripheral membrane protein that is attached to the membrane through another transmembrane protein (Fig. 133).

Lepidopteran Storage Protein Receptors

In contrast to the activation of the dipteran storage proteins receptor, the receptor identified in Lepidoptera does not seem to be regulated by



Storage Protein Receptors, Figure 133 **Model of storage protein uptake and use. The times of the various events are indicated as days after hatching for the dipteran species, and as days after the preceding molt for Lepidoptera.**

proteolytic cleavage. The apparent receptor is a basic 80 kDa protein that is glycosylated. In *Helicoverpa zea*, the protein binds arylphorin as well as VHDL, with similar binding constants (Kd approximately 100 nM). Binding of its ligands occurs between pH 6.5 and 7.5, and requires at least 4 mM Ca^{2+}. The receptor protein can be found only during the second half of the last larval instar, and only in those regions of the fat body that take up storage proteins, located centrally surrounding the gut (perivisceral fat body). In contrast, the storage proteins themselves are synthesized in different regions of the fat body (peripheral fat body). Electron microscopy revealed that the uptake process occurs through classical receptor mediated endocytosis, via coated pits that are internalized as coated vesicles into the perivisceral fat body, where they fuse to form endosomes. Fusion with primary lysosomes leads to the digestion of membrane components and of the receptor protein, so that the electron dense protein granules containing arylphorin and VHDL can be formed.

The receptor protein is generally associated with the cell membrane fraction, and cannot be found in the hemolymph. It does not bind to antibodies against arylphorin or VHDL, and antibodies raised against the receptor do not cross-react with these or other cytosolic proteins. Its sequence was recently reported; the receptor appears to be also related to members of the hexamerin superfamily, namely to the basic juvenile hormone suppressible proteins identified in another noctuid species. It is not entirely clear how it is associated with the fat body cell membrane. Although it contains one potential transmembrane region, it lacks other motifs typically found in endocytotic receptors, like adaptin binding sites that link the receptor to the coat protein clathrin. Hence, another integral membrane protein may be required to serve as an intermediary of the uptake process, as it has been suggested for dipteran species.

► Metamorphosis
► Storage Proteins

References

Burmester T, Scheller, K (1999) Ligands and receptors: common theme in insect storage protein transport. Naturwissenschaften 86:468–474

Burmester T, Scheller, K (1997) Developmentally controlled cleavage of the *Calliphora arylphorin* receptor and post-translational action of the steroid hormone 20-hydroxy ecdysone. Eur J Biochem 247:695–702

Haunerland NH (1996) Insect storage proteins: gene families and receptors. Insect Biochem Mol Biol 26:755–765

Haunerland NH, Shirk PD (1995) Regional and functional differentiation in the insect fat body. Annu Rev Entomol 40:121–145

Wang Z, Haunerland NH (1994) Receptor mediated endocytosis of storage proteins by the fat body of *Helicoverpa zea*. Cell Tissue Res 278:107–115

Storage Proteins

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Insect life cycles are characterized by periods of feast and famine, wherein times of high nutrient demand are not always associated with high nutrient intake. This is evident in molting and metamorphosis, a time when insects require substantial nutrients for fueling metabolism and body building but are not feeding. Therefore, raw materials for molting and metamorphosis must come from nutrient reserves accumulated during prior larval feeding. Nutrient storage is a critical trait for insect physiology and life cycles because it decouples times of nutrient need from times of availability, and numerous insect life history traits such as holometabolous development, long-distance migration, diapause, and reduced adult feeding would not be possible without extensive nutrient reserves. In addition to storing fat and carbohydrates, insects are capable of storing large quantities of amino acids in specialized storage proteins. Storage proteins are functionally defined as proteins that are synthesized during feeding, when amino acid availability is in excess of demand, and depleted to provide substrates during periods of high demand, such as molting. The best characterized and most common storage proteins are the hexamerins, which have been found in all insects that have been investigated. However, non-hexamerin proteins that appear to function as storage proteins have been identified in Lepidoptera, Hymenoptera, and Coleoptera, suggesting that proteins with amino acid storage functions have evolved multiple times within the insects.

Hexamerins: Structures and Evolutionary Relationships

The hexamerins are a family of proteins consisting of six identical or similar subunits with molecular weights between 70 and 90 kD each. These proteins are synthesized by the fat body during feeding and secreted into the hemolymph where they can accumulate to very high concentrations. An amazing diversity of protein storage strategies exists among insect species, wherein any single species can synthesize between one and five different hexamerins. Furthermore, patterns of hexamerin synthesis, accumulation, and utilization throughout the lifecycle can differ both among the various proteins within a species and among homologous proteins between species. For example, the hexamerins in three grasshopper species have been well studied and all three species show a different pattern of storage protein accumulation and utilization: (i) the American locust *Schistocerca americana* contains a single abundant storage hexamerin during both nymphal development and in adulthood; (ii) the migratory locust *Locusta migratoria* contains two storage hexamerins, including one that accumulates to high levels in nymphs but is not present in adults, and one that occurs in only low levels in nymphs but is present in high levels in adults; (iii) the lubber grasshopper *Romalea microptera* contains three different hexamerins that are synthesized and utilized in both the larval and adult stages.

Much of the early efforts to characterize hexamerins were based on biochemical properties of the proteins. Across all organisms most proteins differ little in total amino acid composition. Therefore, elevated contents of particular amino acids within a protein suggest a specific function. Two groups of insect hexamerins immediately stood out based on their amino acid composition. Hexamerins in many insect species were termed arylphorins because they contained high quantities of the aromatic amino acids phenylalanine and tyrosine, up to twice as much as in the average protein. Similarly, some hexamerins identified in Lepidoptera contained almost twice as much methionine than the average protein and were termed methionine-rich hexamerins. Other hexamerins were initially characterized by functional observations, such as the riboflavin-binding hexamerins and the juvenile hormone-suppressible hexamerins of Lepidoptera. Some hexamerins were also named by their occurrence during the insect life cycle. For example, the larval storage hexamerin of the migratory locust, *Locusta migratoria*, is found only in larvae whereas the persistent storage hexamerin occurs in larvae and persists into adulthood. Antibody cross-reactivity was also frequently used to assess homology between hexamerins within and between species. Due to their hexameric shape and similar-sized subunits, it was hypothesized that hexamerins were derived from the hemocyanins, respiratory proteins found in other arthropods that form hexamerins or multi-hexamer aggregations and utilize two copper ions in each subunit to bind and transport oxygen in the blood.

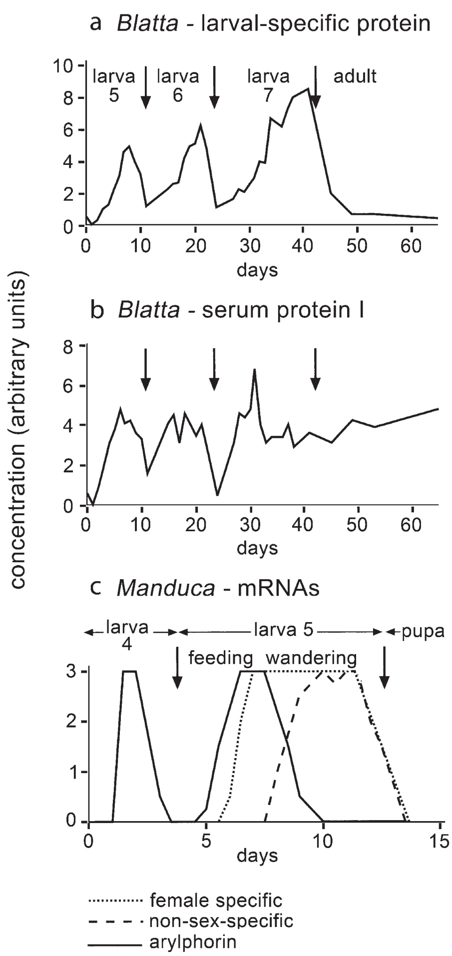
Accumulation of nucleotide sequence data followed by phylogenetic analysis has established that the hexamerins are part of the larger arthropod phenyloxidase-hemocyanin-hexamerin protein family (Fig. 137). While the majority of insects exchange gases directly with the environment via the tracheal system, some basal groups also contain hemocyanins that facilitate oxygen transport and storage in the blood like those observed in crustaceans. Insect hemocyanins have been best studied in the stonefly *Perla marginata* (Plecoptera) which has retained a functional hemocyanin composed of two different subunits containing copper-binding sites. Interestingly, phylogenetic analysis of the two subunits suggests that one is more basal and the other is sister to the insect hexamerins. Therefore, it is thought that the insect hexamerins evolved early during the hexapod radiation, likely due to the duplication of basal insect hemocyanin genes that secondarily lost their copper-based oxygen binding sites. The high efficiency of tracheal gas exchange may have later facilitated the loss of hemocyanin-based oxygen transport in the blood of higher insects. In support of this hypothesis, putative hemocyanins have been identified in many hemimetabolous orders, but appear to be absent from the holometabola. This scenario for the evolution of storage hexamerins from functional hemocyanins after the insects diverged from crustaceans is bolstered by a convergent evolutionary event in crustaceans wherein the Dungeness crab, *Cancer magister*, contains both hemocyanin for oxygen transport and a hexameric protein called cryptocyanin, which has lost its copper-oxygen binding sites. Like insect hexamerins, cyrptocyanin is accumulated during the intermolt feeding period and utilized during molting. Similarly, the American lobster, *Homarus americanus*, contains both a functional hemocyanin and a cryprocyanin-like molecule that has lost its copper-oxygen binding sites and may play a role in molting.

Within hexapods, divergence of the hexamerins largely follows that of the insects themselves (Fig. 136). All hemimetabolous groups appear to contain a single lineage of hexamerins, while the Diptera and Lepidoptera each contain more than one distinct clade of hexamerins. In Diptera the two hexamerin clades, the LSP-1 and LSP-2 protein groups, are sister to each other. In contrast, among the three clades of Lepidopteran hexamerins the arylphorins and methionine-rich hexamerins are sister to each other, but the riboflavin-binding hexamerins appear to have evolved earlier and are basal to the rest of the hexamerins in holometabola. Both the Dipteran LSP-1 group and the lepidopteran arylphorins have very high contents of the aromatic amino acids phenylalanine and tyrosine (>15%) that play a key role in cuticular growth and sclerotization. Prior to phylogenetic analysis of hexamerin nucleotide sequences these two groups were thought to be homologous. However, it is now clear that one lineage in each group has converged on the disproportionate accumulation of aromatic amino acids. Interestingly, hexamerins of some basal clades such as grasshoppers and cockroaches are also higher in aromatic amino acids than the typical protein suggesting that the functional demand for aromatic amino acids for producing cuticle proteins and sclerotization during molting may have affected amino acid composition independently several times within the hexamerins.

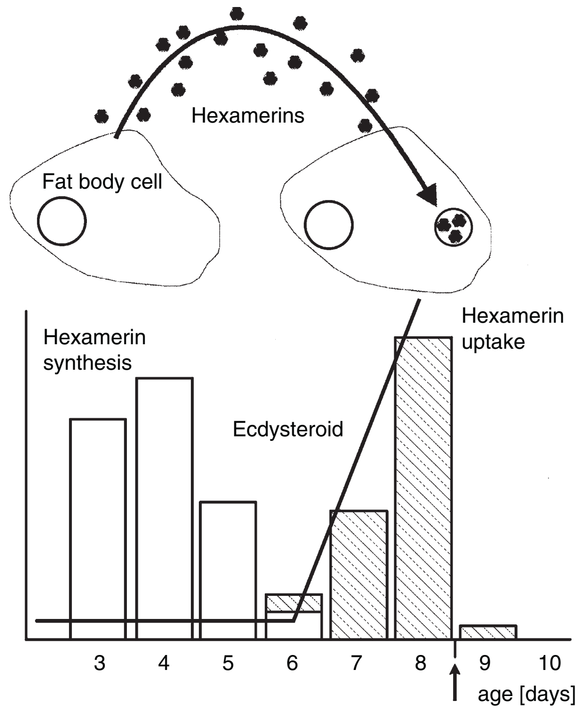
Hexamerins in Nymphs and Larvae

Hexamerins are synthesized during juvenile feeding and can accumulate in large quantities in the hemolymph during the intermolt period. Hexamerin transcripts have been found expressed in a variety of tissues including the epidermis, gut, brain, and ovaries, but the majority of hexamerin expression and protein synthesis occurs in the fat body. Hexamerins synthesized in the fat body are secreted into the hemolymph where they accumulate. The timing and extent of hexamerin synthesis can differ dramatically among species and between different hexamerins within a species (Fig. 134). For example, larvae of the tobacco hornworm, *Manduca sexta*, synthesize three different hexamerins. The *Manduca* arylphorin is expressed in the penultimate larval instar and again at the beginning of the final larval instar prior to wandering, whereas the *Manduca* female-specific hexamerin and methionine-rich hexamerin are not produced until after wandering in the last instar. Because insects do not feed during molting, hexamerins provide a critical pool of amino acids for the large pulse of protein synthesis that occurs during the molt. In hemimetabolous insects such as the cockroach *Blatella orientalis*, hexamerins accumulated in the hemolymph during inter-molt feeding are largely depleted at the time of molting, although some can also be carried into adulthood. During the molting event, storage hexamerins are taken up from the hemolymph and hydrolyzed and their constituent amino acids are incorporated into a vast array of tissues, such as cuticle and muscle. Although hexamerins are largely broken down, some evidence exists for the incorporation of intact hexamerins or large peptide fragments directly into structures such as cuticle.

Holometabolous larvae tend to accumulate even greater quantities of hexamerins in their blood during larval feeding than hemimetabolous nymphs. These hexamerins are transiently stored in the hemolymph, as in hemimetabola, but are largely taken up out of the hemolymph into the fat body prior to metamorphosis (Fig. 135). Hexamerin uptake is mediated by a specific receptor-mediated endocytotic process induced by ecdysteroids during the larval wandering period just prior to pupation, after which hexamerins are concentrated in distinctive protein granules in the fat body cells. Amino acids can be subsequently mobilized from protein granules to support both energy metabolism and catabolic building reactions during metamorphosis.



Storage Proteins, Figure 134 **The timing of expression and accumulation of particular storage proteins can differ within a species lifecycle. For example, the larval specific storage protein of *Blatta orientalis* is only accumulated by larvae and is utilized prior to adulthood (a), whereas the persistent storage protein accumulates in both larvae and adults (b) (modified from Duhamel and Kunkel, 1978). The three storage proteins expressed by larvae of *Manduca sexta* differ slightly in the timing of their transcription during the last instar (c) (modified from Riddiford and Hice, 1985).**

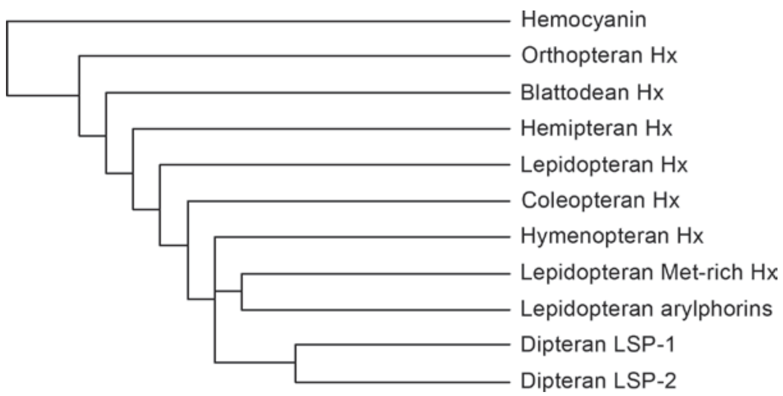


Storage Proteins, Figure 135 **Hexameric storage proteins are synthesized by the fat body and secreted into the blood during the feeding period in the last instar larvae of the blowfly, *Calliphora vicina*, age days 3–5 after laying on the x-axis. Once the larvae wander from the food, synthesis ceases and storage proteins are taken back up by the fat body cells via specific receptor-mediated endocytosis (days 6–8), clearing storage proteins from the blood (taken from Burmester and Scheller, 1999).**

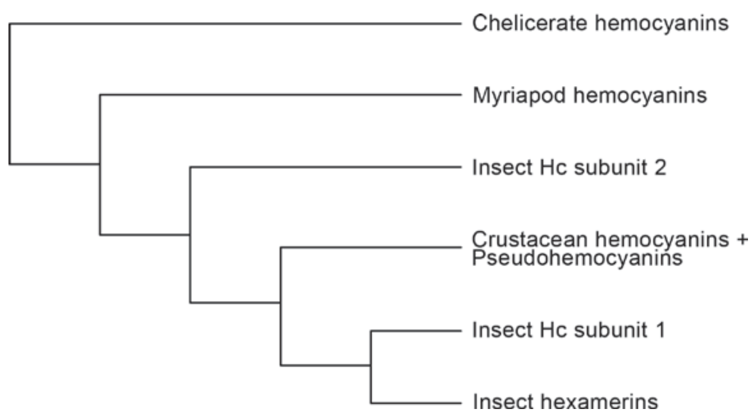
Among species that express multiple types of hexamerins, their distinct amino acid profiles, patterns of uptake from the hemolymph, localization within the fat body, and incorporation into different tissues or substrates is evidence for specialization of hexamerins for distinct roles in metamorphosis and post-metamorphic development. For example, larvae of the monarch butterfly, *Danaus plexippus*, produce an arylphorin that is used to support metamorphosis and adult development and two methionine-rich hexamerins that are used to support egg development later during adulthood.

Hexamerins in Adults

While hexamerins were initially characterized as larval-specific proteins, it is clear that they also



Storage Proteins, Figure 136 **This phylogenetic tree showing the relationships among the insect hexamerins, supports the hypothesis that the hexamerins were present in the most basal insects and diversified along with the insects (modified from Burmester, 2002).**



Storage Proteins, Figure 137 **This Bayesian phylogenetic tree shows the relative relationships of the two subunits of the insect hemocyanin to the crustacean hemocyanins and the insect storage hexamerins and crustacean pseudohemocyanin storage proteins, supporting the hypothesis that the storage hexamerins are derived from hemocyanins (modified from Burmester and Hankelen, 2007).**

play important roles in adult insects. Although hexamerins are used during molting and metamorphosis, some species carry significant quantities of hexamerins over from larval life into adulthood. This is particularly apparent in the Lepidoptera wherein most species do not feed on significant quantities of protein as adults and therefore rely on larva-derived protein reserves to support egg production. Females of many Lepidoptera species will store greater quantities of hexamerins or will contain a different complement of hexamerins than males, and amino acids from these hexamerins have been shown to be utilized for vitellogenesis. Similarly, larvae of autogenous mosquitoes that can reproduce without taking a blood meal have been shown to accumulate greater quantities of hexamerins than their anautogenous counterparts, which must feed on blood to obtain the amino acids necessary to reproduce. The importance of larva-derived amino acid reserves is readily apparent in species with adults that do not protein feed, however, larva-derived protein reserves may also play important roles in insects that continue to feed on protein as adults. For example, lines of *Drosophila melanogaster* that were genetically manipulated to eliminate or drastically reduce the production of the larva-expressed LSP-1 hexamerin did not show any significant developmental or metamorphic defects, but had significant reproductive deficiencies in both males and females.

Many insect species have also been shown to synthesize and accumulate hexamerins during adult feeding. Accumulation of hexamerins in adults is often greater in females with hexamerin depletion occurring to support vitellogenesis. An extreme example of adult hexamerin accumulation occurs in claustral-founding ant queens that accumulate substantial hexamerin stores in their natal colonies prior to mating flights. After the mating flight, these queens seclude themselves in a nest chamber and use stored fat and hexamerins to rear their first brood without foraging; semi-claustral queens that will forage during founding and queens of parasitic species do not accumulate substantial hexamerin stores prior to the mating flight.

Other Hexamerin Functions

Many species of diapausing insects accumulate greater nutritional reserves than their non-diapausing counterparts, including the accumulation of hexamerins which lead to their initial characterization as "diapause proteins." For example, diapause-destined adults of the Colorado potato beetle, *Leptinotarsa decemlineata*, accumulate more than twice the quantity of DP-1 hexamerin prior to burrowing into the soil and entering diapause than equivalently-aged, non-diapausing individuals. This hexamerin pool is utilized to support metabolism during the non-feeding diapause period and to support post-diapause functions, such as rebuilding the thoracic flight muscles. Interestingly, the wax moth, *Galleria mellonella*, continues to actively synthesize hexamerins during the non-feeding larval diapause period. In addition to serving as amino acid reservoirs, it has been suggested that hexamerins play other roles during diapause, such as altering blood osmolarity to prevent cold-induced damage or acting as part of the humoral immune defense.

Hexamerins may also have other important physiological functions aside from nutrient storage in non-diapausing insects. Hexamerins from many species have been shown to bind organic molecules in the hemolymph including juvenile hormone, ecdysone, pesticides, and vitamins such as riboflavin. The low binding coefficients of hexamerins for many of these organic molecules has prompted some authors to suggest that this binding role is accidental due to the presence of hydrophobic residues in the hexamerins. However, hexamerins can occur in great abundance, as much as 60% of hemolymph protein, so despite low binding coefficients the sheer numbers of hexamerins available for binding molecules hexamerins may still have a physiologically important role in organic molecule binding. One of the most intriguing current topics is whether hexamerins can act as signaling molecules during juvenile and adult development. For example, the peak of hexamerin accumulation in adult females of the lubber grasshopper, *Romalea microptera*, is directly associated with the timing of juvenile hormone release that initiates vitellogenesis. This has prompted the suggestion that hexamerin accumulation may serve as an internal signal that the animal has reached an appropriate nutritional condition to successfully reproduce, triggering the endocrine cascade leading to egg production. In addition to diapause and reproduction, differences in hexamerin titers have been associated with developmental polyphenisms, such as the solitary and migratory phases of locusts or the castes of bees, ants, and termites. A recent study on the development of the soldier caste in the termite, *Reticulitermes flavipes*, has shown that manipulating the titer of storage hexamerins affects whether nymphs differentiate into soldiers or remain as nymphal workers. Whether this dramatic effect of decreased hexamerin titer on development was due to a shift in the nutritional milieu of the nymphs or was due to alteration some other function of the hexamerins, such as binding juvenile hormone or other organic molecules, is currently unknown.

Other Storage Proteins

In addition to the hexamerins, unrelated proteins that appear to perform a similar storage function have been identified in several species. A very high density lipophorin (VHDL) has been shown to play a storage role in several species of noctuid moths. In the corn earworm, *Helicoverpa zea*, VHDL occurs as a dimeric protein that contains approximately 10% lipid, far less than typical lipid-transport proteins but much more than the hexamerins. VHDL is synthesized by the fat body of feeding larvae, secreted into the blood, and taken back up into the fat body at pupation, after which it is broken down and used to support metamorphosis. Dimeric VHDL-like proteins have also been identified in honeybees, wasps, and ants where they have been associated with seasonal cycles and colony founding. Lepidopteran and Hymenopteran species that contain VHDL also contain hexamerins and the patterns of accumulation and utilization appear to be similar in the two groups of proteins, begging the question of whether there are functional differences between VHDL and hexamerins. In addition, a group of tyrosine-rich storage proteins has been identified in several beetle species. Two major characteristics differentiate these tyrosine-rich storage proteins from the hexamerins and VHDL: (i) they are composed of much smaller subunits ranging in size from 20 to 50 kDa, and (ii) while they are synthesized in the fat body and utilized during metamorphosis, these tyrosine-rich storage proteins are never released into the hemolymph. However, like other known storage proteins they accumulate during feeding and are depleted at metamorphosis. Considering the diversity of form, function, and phenology of the known storage proteins, there may also be other groups of proteins that serve storage functions during juvenile or adult reproductive development that remain to be identified.

References

Burmester T (1999) Evolution and function of the insect hexamerins. Eur J Entomol 96:213–225

Burmester T, Hankelen, T (2007) The respiratory proteins of insects. J Insect Physiol 53:285–294

Delobel B, Rahbé Y, Nardon C, Guillaud J, Nardon P (1993) Biochemical and cytological survey of tyrosine storage proteins in Coleoptera: diversity of strategies. Insect Biochem Mol Biol 23:355–365

Hagner-Holler S, Schoen A, Erker W, Marden JH, Rupprecht R, Decker H, Burmester T (2004) A respiratory hemocyanin from an insect. Proc Natl Acad Sci USA 101:871–874

Hatle JD, Borst DW, Juliano SJ (2004) Plasticity and canalization in the control of reproduction in the lubber grasshopper. Integr Comp Biol 43:635–645

Haunerland NH (1996) Insect storage proteins: gene families and receptors. Insect Biochem Mol Biol 26:755–765

Telfer WH, Kunkel JG (1991) The function and evolution of insect storage hexamerins. Annu Rev Entomol 36:205–228

Terwilliger NB, Dangott L, Ryan M (1999) Cryptocyanin, a crustacean molting protein: Evolutionary link with arthropod hemocyanins and insect hexamerins. Proc Natl Acad Sci USA 96:2013–2018

Wheeler DE, Martinez T (1995) Storage proteins in ants (Hymenoptera: Formicidae). Comp Biochem Physiol B 112:15–19

Zhou X, Oi FM, Scharf ME (2006) Social exploitation of hexamerin: RNAi reveals a major caste-regulatory factor in termites. Proc Natl Acad Sci USA 103:4499–4504

Stored Grain and Flour Insects and Their Management

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Hundreds of insects are found in stores of grain and milled cereal, but only a few species cause direct damage to products that are in sound condition. Most pest species can feed only on processed or damaged grain and mold, and their presence results in food contamination with their waste, caste skins, webbing, and body parts. Insects may also contribute to the conditions that cause grain to heat and mold. Approximately fifty species are deemed pests of economic concern. Nearly all of them are beetles or moths.

Environmental Factors

Insect infestation in stored grain is fostered by moisture, moderate heat, and damaged kernels. Not only does high moisture content in grain and processed food provide a favorable physical environment for development of many pest species, it also fosters the development of the molds on which some insects feed. The most favorable grain moisture range for stored grain insects is from 12 to 18%. In many instances, insect infestation amplifies mold problems in grain by exposing otherwise hidden endosperm surfaces to molds, transporting mold spores to new areas and encouraging mold germination in microhabitats made moist by insect metabolic activity. Indeed, insect and mold metabolic activity can raise grain temperatures.

At grain temperatures below 60°F (15°C) insect development and activity are minimal and pest populations can be expected to remain static. Temperatures a few degrees above 35°F (90°C) are detrimental or lethal to stored-product insects, and brief treatments of 122°F (50°C) are used for stored-product pest control.

Grain insects move within the grain mass at a rate that is determined by the season and grain temperature. During the summer and fall, insect infestations are usually on the surface of the grain. In cold weather, insects congregate at the center and lower portions of the grain and may escape detection until high population numbers are reached.

The presence of damaged grain, dust, and chaff, collectively known as dockage, is quite beneficial to the survival and reproduction of insects that feed externally. For example, flour beetles are reportedly unable to maintain populations in dockage-free wheat. Accordingly, grain stored without cleaning is subject to more severe insect infestation than is cleaned grain.

Damage

Some insects, designated primary pests, damage grain by developing inside kernels (egg, larvae, pupae), feeding on the inner endosperm, and chewing holes in the kernels through which the adult insects exit. The five primary pests of stored grain in the U.S.A. are the lesser grain borer, *Rhyzopertha dominica* (Fabricius), the rice weevil, *Sitophilus oryzae* (L.), the granary weevil, *Sitophilus granarius* (L.), the maize weevil, *Sitophilus zeamais* Motschulsky, and the Angoumois grain moth, *Sitotroga cerealella* (Olivier) (Gelechiidae), all of which deposit eggs in undamaged kernels. Other insect species, designated secondary pests, do not develop within the kernels, although they may hide inside cracked grain, making detection very difficult. Some secondary pests, including most of those designated as grain beetles, feed primarily on mold. Other species such as the sawtoothed grain beetle, *Oryzaephilus surinamensis* (L.), the flour beetles, and moth larvae feed on damaged grain or fines.

Insect damage can reduce grain quality through loss of weight or nutritional quality, spreading and encouraging mold germination, adding to the fatty acid content of the grain, and leaving quantities of uric acid that cause grain rancidity. Insects also create fines and broken kernels when feeding that reduce air flow through grain and prevent proper aeration. In addition, the presence of insects in a grain sample can cause price discounts and shipping restrictions.

In the U.S.A., the presence of two insects of any kind in 1 kg of wheat, rye, or triticale causes the grain to be graded the lowest quality category, sample grade. Insect tolerances in finished commodities such as flour or cornmeal are stricter.

Perhaps the most difficult problems associated with insect infestation of grain are quarantine and export restrictions. Many nations require the fumigation or return of grain shipments that harbor the Khapra beetle, *Trogoderma granarium* Everts. Under the most restrictive export laws, detection of a single insect in grain precludes its shipment.

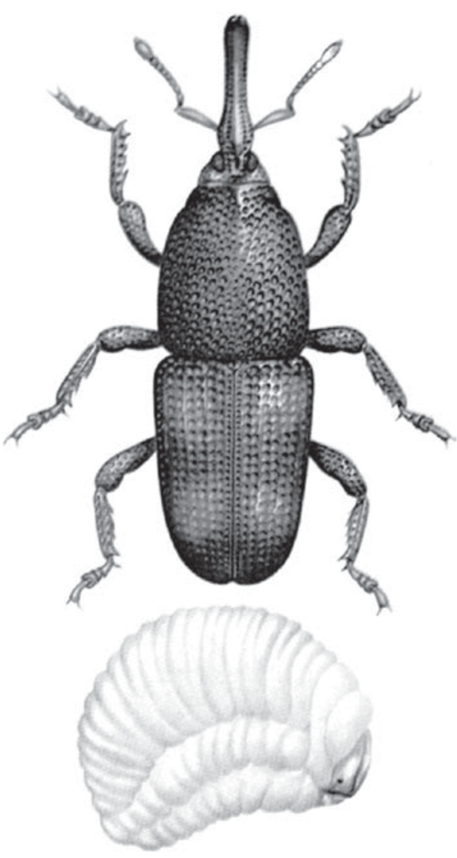
Monitoring and Control

Grain processing facilities are monitored by light or pheromone traps and by visual inspections. In stored grain, plastic pitfall traps are the dominant method, but sticky traps are useful for headspaces. Also, grain can be inspected by screening or sieving and searching in the screenings for insects, examining kernels for damage, checking grain for webbing, and investigating off-odors. Monitoring is especially important in summer and early fall when temperatures are optimum for rapid development. Grain temperature should be monitored as an indicator of grain condition and to locate areas of bulk grain in which conditions are favorable for insects. The number of insects found in traps is recorded and charts constructed so that changes in population size can be easily noticed and management tactics can be implemented as needed. Traps are used following control interventions to determine whether the treatments are effective.

The first defense against stored-grain insects is exclusion by means of pest-resistant construction, protective packaging, and sanitation. Empty storage and processing facilities can be treated with chemical insecticide sprays. Residual grain protectants are sometimes added directly to grain at the beginning of storage. These are usually organophosphates, but synergized pyrethrum or diatomaceous earth may be used. The dominant method for control of insects in stored grain is fumigation with phosphine. Non-chemical controls include temperature modification, either by heat treatment or lowering temperature through aeration. Atmosphere modifications to reduce oxygen are used primarily outside the U.S.A.

Grain Weevils

The three economically important species of the weevil family Curculionidae that infest cereal grains in storage are the rice weevil, *S. oryzae* (Fig. 138), the maize weevil, *S. zeamais*, and the granary weevil, *S. granarius* (L.). Adult weevils can be distinguished from other grain-infesting insects by their long snouts with chewing mouth parts at the tip and elbowed antennae. Both the rice and maize weevils have two light areas on each elytron and dense small, nearly round pits on the pronotum, giving a rough appearance. The granary



Stored Grain and Flour Insects and Their Management, Figure 138 **Rice weevil, *Sitophilus oryzae* (L.): adult above, larva below.**

weevil is uniformly colored and has less dense elliptical pits on the pronotum, giving the prothorax a glossier appearance than that of the other two species. Adults of all three species are dark brown, with the rice and maize weevils being slightly darker than granary weevils. Adult maize and granary weevils are 3–4.5 mm long, and the slightly smaller rice weevils are about 3 mm long. Egg, larval, and pupal stages are spent within the grain kernel. The larvae of all three species are nearly identical, being legless and crescent shaped. As with the adults, larvae of maize and granary weevils are slightly larger than larvae of rice weevils.

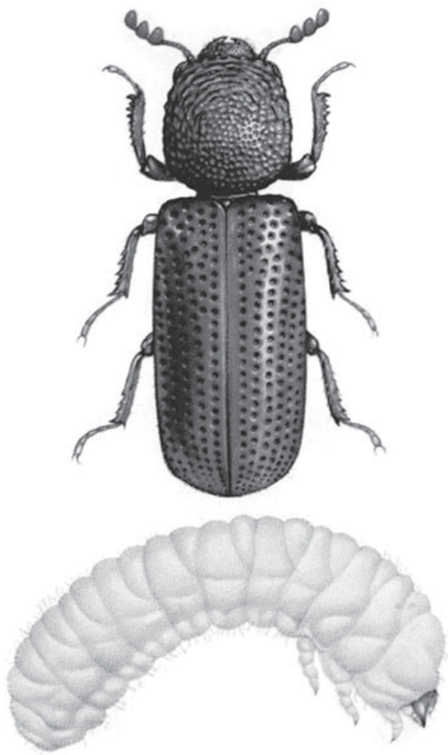
After mating, a female weevil uses her long snout to chew a small cavity in a grain kernel into which she places an egg. She then seals the hole with a gelatinous egg plug. From this time until the new adult chews its way out of the kernel, the infestation is inapparent. Each female can lay as many as 300–400 eggs in her lifetime. Under similar conditions, rice weevils generally lay more eggs than maize or granary weevils. Two rice weevils may develop in a wheat kernel, one on either side of the crease, but usually only one maize or granary weevil develops in a kernel. The four larval instars feed on the endosperm of the grain kernel. Pupation and adult emergence take place within the kernel. The adult chews its way out of the kernel, leaving visible damage behind. About one third of a wheat kernel is consumed by rice weevils and over half by maize or granary weevils. Under favorable conditions, granary weevils require about 40 days to complete their development and maize and rice weevils about 35 days. Almost immediately after emerging as adults, the females are mated and the developmental cycle is repeated. The adult weevils live as long as 5–8 months.

The rice weevil is the most destructive pest of stored grain. It is found in all parts of the world where grain is used and is particularly abundant in warm climates where it breeds continuously. Although wings are present some question the ability of the rice weevil to fly. Infestations of grain field origin lend credibility to the presumption of flight ability. The rice weevil's habitat is almost identical to that of the granary weevil. The granary weevil is one of the oldest known insect pests. It has been carried to all parts of the world by commerce. It prefers temperate climates and, in the US is more frequently found in the northern states than the southern states. The granary weevil cannot fly and must reside in accumulations of grain or be carried from place to place in infested lots of grain. Maize weevils are capable of flight, and in warm areas, they commonly fly to fields and infest corn before it is harvested. They can easily move from one lot of stored grain to another.

Grain Borers

The family Bostrichidae, which comprises mainly wood-boring beetles, has two species that are important primary pests of grain. The lesser grain borer, *R. dominica* (Fig. 139), is one of the most damaging insects found in grain, especially in wheat. The larger grain borer *Prostephanus truncatus* (Horn) is a more serious pest of maize in warm tropical areas, especially where maize is stored on the cob.

Adults of the lesser grain borer are cylindrical and about 3 mm long. The prothorax forms a hood over the head, which is directed downward. The hood has distinct, sharp tubercles on the top and near the front margin of the prothorax. The wing covers have rows of indentations, but they are glossy. Each antenna has a distinctive loose, three-segmented club at the end. Individual segments of the club are frequently found in flour milled from wheat that has been infested with the lesser grain borer. The adult has functional flight wings and is a strong flyer. Most larvae develop inside whole grain kernels and thus are rarely visible. The larvae have three pairs of small legs located on the segments immediately behind the head. The head is a partially withdrawn into the thorax. The body of the larva is grub-like with the thorax and last segments of the abdomen enlarged.



Stored Grain and Flour Insects and Their Management, Figure 139 **Lesser grain borer, *Rhyzopertha dominica* (F.): adult above, larva below.**

The female lays as many as 300–400 eggs, placing them among, but not inside the grain kernels, sometimes in clusters of up to 45. Larvae chew into kernels or penetrate through cracks in the pericarp. Inside the kernel, the borers pass through three to five larval instars and a pupal stage and emerge as adults. In some instances, where broken kernels and much dust are present, larvae may feed and develop externally. Adult insects live an average of 7–8 months and often return to kernels from which insects have emerged to feed and more extensively damage the grain.

Lesser grain borer infestations are characterized by the presence of grain dust and a characteristic sweetish, musty odor. The dust is mostly fecal matter. In localized heavy infestations, the dust and heavily damaged kernels form compacted areas that can cause uneven aeration or fumigant penetration.

The lesser grain borer is better able to survive in drier grain than the weevils, which probably accounts for its being a more serious pest of farm-stored wheat in the central and southern plains areas of the United States.

Larger grain borers are similar to lesser grain borer in development, habits, and appearance. The adults also have the typical cylindrical borer shape, but they are somewhat larger than the lesser grain borer, measuring 3–4 mm in length. In contrast to those of the lesser grain borer, the posterior portions of the elytra are steeply flattened with many small tubercles on the surface. The head is turned under and covered by the prothorax. The antennae terminate in flattened, three-segmented clubs similar in appearance to those of the lesser grain borer. The larvae are similar in appearance to the lesser grain borer larvae, but larger.

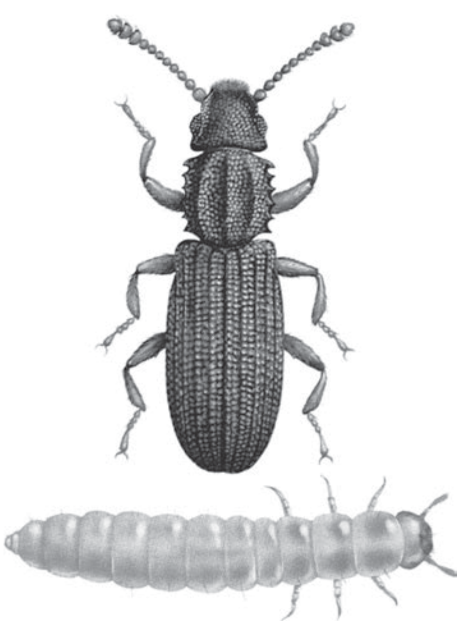
The larger grain borer is a serious pest of corn, as well as dried cassava. It is seldom found in the United States but is common in Central and South America. It was introduced into Kenya in the 1970s and has rapidly spread across sub-Saharan Africa, where it has become an extremely serious pest. The climate and the prevalence of farm storage corn on the cob in parts of Africa are particularly favorable for larger grain borer infestations. Adult borers infest corn shortly before and after storage. Shelled corn is a marginal medium for development, but unhusked corn is particularly vulnerable to infestation. Females bore into the attached kernels and lay eggs in side tunnels. Larvae feed mainly on dust, much of which is created by adult feeding. The developmental cycle can be completed in about 27 days under optimum conditions and about a week longer in dry grain.

Grain Beetles

Often the most abundant insects in stored grain are those belonging to a guild of dorso-ventrally-flattened beetles that feed on damaged grain, dust and mold. None of these grain beetles attack undamaged grain. The larvae of grain beetles do not stay within a single grain, but crawl about actively to feed. The development times are typically about a month under favorable conditions, and populations often build up rapidly.

The family Laemophloeidae includes eight species in the genus *Cryptolestes* that are secondary pests of cereals and cereal products. Two are prominent, particularly in moist environments. The rusty grain beetle, *Cryptolestes ferrugineus* (Stephens), is a cold-tolerant species and is often the most abundant insect in stored grain in temperate climates. The flat grain beetle *Cryptolestes pusillus* (Schönherr) is a minute beetle of about 1.5 mm in adult length. It is cosmopolitan, but less tolerant of low temperature and humidity than the rusty grain beetle and is more common in warm moist climates such as Southeast Asia.

The members of the family Silvanidae are generally larger (2–4 mm adults) and more active than *Cryptolestes* species, but they lack the flying ability of *Cryptolestes*. The sawtoothed grain beetle, *O. surinamensis* (Fig. 140), derives its common name from the tooth-like projections on the sides of its thorax. It is among the best-known cosmopolitan pests in stored grain and grain products and is considered the most serious stored grain pest in the United Kingdom. The merchant grain beetle, *Oryzaephilus mercator* (Fauvel), is often confused with the sawtoothed grain beetle, but it prefers oilseed products, including nuts. Several other Silvanidae can infest cereals but are of minor importance.



Stored Grain and Flour Insects and Their Management, Figure 140 **Sawtoothed grain beetle, *Oryzaephilus surinamensis* (L.): adult above, larva below.**

Flour Beetles

In the family Tenebrionidae, *Tribolium castaneum* (Herbst), the red flour beetle, and *Tribolium confusum* Jacquelin du Val, the confused flour beetle, are the most intractable insect pests of grain and flour processing areas. They are notoriously difficult to control with chemical insecticides. The adults are 3–4 mm long, reddish brown to brown and rather glossy. The light, honey-colored larvae have darkened heads and darkened forked processes at the tips of their abdomens that distinguish them from other grain-infesting larvae. Like other grain insects that feed externally, the larvae develop best in the presence of grain dust and broken kernels. Where such material is abundant, flour beetles can develop in grain with as little as 8% moisture content. The larvae will pass through 5–11 larval instars depending on growing conditions, and pass from egg to adult in less than a month under ideal conditions. The adults are known to live for up to 5 years.

Stressed or agitated flour beetles secrete quinones that have a pungent odor and can give a pink hue to heavily infested flour. There is concern that the quinones may be carcinogenic.

Mealworms

The mealworms comprise several large members of the family Tenebrionidae that are nocturnal and frequent dark, damp places. Three species are common, the yellow mealworm *Tenebrio molitor* L., the dark mealworm *Tenebrio obscurus* Fabricius, and the lesser mealworm, *Aphitobius diaperinus* Panzer. The yellow and dark mealworms are the largest insects found in grain and grain products. The larvae are 26–30 mm long and resemble wireworms. Under natural conditions, the yellow and dark mealworms complete only one generation per year and, consequently, are not serious pests. The lesser mealworm is similar to the yellow and dark mealworms, but reaches only 5.5–7 mm in length. All three species prefer damp, out of condition grains and grain products, but they also feed on various deteriorating food materials. Lesser mealworms are especially common in poultry feed.

Dermestid Beetles

Dermestidae is a small but important family whose members scavenge and feed on animal matter. It includes some 55 species that have been reported as stored-product pests. The black carpet beetle, *Attagenus megatoma* (Fabricius), is a cosmopolitan species that is often found in cracks in warehouses, but most of the dermestid pests are *Trogoderma* species. *Trogoderma* adults are reddish-brown to black, ovoid and convex, mainly 2–4 mm in length, and covered with scales. The larvae are very hairy, with setae of various characteristic shapes. *Trogoderma inclusum* LeConte, *T. glabrum* (Herbst), and *T. variable* Ballion are common pests of grain, seed, and other stored products. The adults of these beetles live only 1–3 weeks, but development from egg to adult can take from 1 month to as long as a few years. The ability of the larvae to remain in a quiescent state for several months in the absence of food makes *Trogoderma* species especially dangerous pests.

The Khapra beetle is the only truly phytophagous dermestid beetle. It feeds on many stored foodstuffs in addition to grain. Worldwide, it is the most destructive member of this group. The Khapra beetle is believed to have been eradicated from the U.S. in 1961 and has been a quarantine target since that time.

Other Beetles

The cadelle, *Tenebroides mauritanicus* (L.), is a member of the family Trogositidae that infests flour, meal, and grain worldwide. Larvae and adults have the destructive habit of moving from kernel to kernel, devouring the germs. Both stages are omnivorous and will eat other insects.

The cigarette beetle, *Lasioderma serricorne* (Fabricius) and the drugstore beetle, *Stegobium paniceum* (L.) are in the family Anobiidae. Both are found in all temperate and subtropical regions. As its common name indicates, the cigarette beetle infests tobacco, but it also attacks various food products, including grain. Its ability to penetrate packaging materials makes it a threat to high value stored products. The drugstore beetle has an extremely diverse diet, and takes its name from its ability to feed on pharmaceutical drugs.

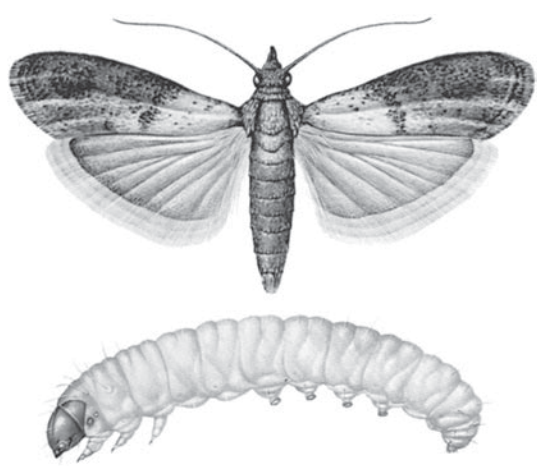
Lepidoptera

Among the Lepidoptera, there is only one important primary feeder in grain, the Angoumois grain moth. It is a pest of stored grain throughout the tropics and subtropics, primarily in on-farm stores. Each larva eats out the inside of a single grain and remains in the grain through pupation, leaving no visible signs of infestation. The complete life cycle requires approximately 1 month at 30°C. Adults are 5–7 mm long, pale brown moths with fringed wings and long up-turned labial palpi. The female adult lives only 5–12 days, during which time she lays about 200 eggs. Angoumois grain moths are thought to compete with *Sitophilus* spp. for larval habitat and may dominate in drier habitats that are stressful for the weevils.

In the family Pyralidae, the subfamily Phycitinae or knot-horn moths, comprises the most important secondary lepidopterous pests of stored grains. Among them, the Indianmeal moth *Plodia interpunctella* (Hübner) (Fig. 141) is the most important pest of stored foodstuffs worldwide. It is especially common on corn, hence its common name.

In grains the larvae feed primarily on embryos. During the development of the 5–7 instars, Indianmeal moth larvae spin webs that are often dense enough to attract attention. The last instar spins a silken cocoon. Adults are 5–10 mm in length and about 16 mm in wingspan. They are easily recognized by the distinctive appearance of the forewing, which is light gray basally and bright copper red distally. The females lay up to 400 eggs that can develop into adults in as few as 28 days under optimal conditions. In the tropics, there may be 6–8 generations; in temperate zones 1–2 generations are usual.

In addition to the Indianmeal moth, several other pyralids are pests in stored grain. The Mediterranean flour moth, *Ephestia kuhniella* Zeller, a native of Europe, is a general feeder that was once the most troublesome pest in US flour mills. Its pest status was primarily due to the particle matting created by the larva-produced silken thread. Other occasional pyralid pests include the meal moth, *Pyralis farinalis* (L.), the tobacco moth *Ephestia elutella* (Hübner), the raisin moth, *Cadra figulilella* (Gregson), and the almond moth, *Cadra cautella* (Walker). Among these the almond moth is the most serious pest especially in rice and sorghum grain in tropical and subtropical climates.



Stored Grain and Flour Insects and Their Management, Figure 141 **Indian meal moth, *Plodia interpunctella* (Hübner): adult above, larva below.**

References

Cotton RT (1963) Pests of stored grain and grain products. Burgess Publishing Co., Minneapolis, MN

Mueller DK (1998) Stored product protection… a period of transition. Insects Limited, Inc., Indianapolis, Indiana

Pederson JR (1992) Insects: identification, damage and detection. pp 435–489 In: Sauer DB (ed) Storage of cereal grains and their products. American Association of Cereal Chemists, St. Paul, MN

Subramanyam BH, Hagstrum DW (1996) Integrated pest management of insects in stored products. Marcel Dekker, New York, NY

Straight-Snouted Weevils

Members of the family Brentidae (order Coleoptera)

► Beetles

► Weevils, Billbugs, Bark Beetles and Others

Stratified Sampling

A method of allocating sampling units in which the sample universe is subdivided into two or more sections and sample units are randomly collected from each subdivision in proportion to their size or relative variability. Examples include the subdivision of a crop field into border and interior sections, the subdivision of a plant along vertical strata, or different rooms within a structure.

► Sampling Arthropods

Stratiomyidae

A family of flies (order Diptera). They commonly are known as soldier flies.

► Flies

Strawberry Bud Weevil, *Anthonomus signatus* (Say) (Coleoptera: Curculionidae)

In some areas, this is an important pest, affecting the fruit of strawberries.

► Small Fruit Pests and Their Management

Strawberry Sap Beetle, *Stelidnota geminata* (Say) (Coleoptera: Nitidulidae)

This can be an important fruit pest, damaging ripe strawberry fruits.

► Small Fruit Pests and Their Management

Streblidae

Formerly a family of flies (order Diptera). They (and Nycteribiidae) were commonly known as bat flies, but are now included in the family Hippoboscidae.

► Flies

Strepsiptera

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The order name is derived from the Greek *Strepsi-* (twisted) and *pteron* (wing). The term "twisted wing" refers to the free-living male, which, when in flight, gives the impression that its hind wings have a "twisted" motion.

Strepsiptera are unique, bizarre, obligate entomophagous parasites of cosmopolitan distribution and exhibit extreme sexual dimorphism. There are only two free-living stages: the adult male, and the first instar host-seeking larva, except in the family Mengenillidae, where both male and female emerge to pupate externally from the host. The neotenic adult female in all the other families remains endoparasitic, except for the anterior region, the cephalothorax, which is extruded through the host cuticle. The number of species described worldwide so far is about 600, but recent studies suggest that many of these are cryptic species. If so, the true estimate might be nearer double that number.

Strepsipteran genomes are among one of the smallest insect genomes reported and are associated with their unique morphology and life history.

Several fossil Strepsiptera have been discovered and described, of which the families Protoxenidae and Mengeidae from the Baltic amber, and the genus *Cretostylops* from the Cretaceous Burmese amber, are extinct. Until further fossils are described, and on-going studies on DNA sequence data are analyzed, the two extinct families and genus are placed under the suborder Mengenillidia and the rest of the seven extant families in the suborder Stylopidia.

- Suborder Mengenillidia
  - Family Protoxenidae (extinct)
  - Family Incerta Sedis
    - Genus *Cretostylops* (extinct)
  - Family Mengeidae (extinct)
  - Family Mengenillidae
- Suborder Stylopidia
  - Family Corioxenidae
  - Family Myrmecolacidae
  - Family Xenidae
  - Family Stylopidae
  - Family Elenchidae
  - Family Halictophagidae
  - Family Bohartillidae

Strepsiptera parasitize Aptery-, Exo- and Endopterygota insects belonging to seven orders and 28 families. The hosts are Thysanura: Lepismatidae; Blattodea: Blattidae; Mantodea: Mantidae; Orthoptera: Gryllidae, Tettigoniidae, Tridactylidae; Hemiptera (Homoptera): Cercopidae, Cicadellidae, Delphacidae, Dictyopharidae, Eurybrachyidae, Flatidae, Fulgoridae, Issidae, Membracidae, Ricaniidae, Tettigometridae; Hemiptera (Heteroptera): Coreidae, Cydnidae, Lygaeidae, Pentatomidae; Diptera: Tephritidae and Hymenoptera: Formicidae

[Dolichoderinae, Ecitoninae, Formicinae, Myrmicinae, Ponerinae, Pseudomyrmecinae], Vespidae [Eumininae, Masarinae, Polistinae, Stenogastrinae, Vespinane], Sphecidae [Bembicinae, Larrinae, Sphecinae], Colletidae [Hylaeinae, Panurginae], Halictidae [Rophitinae], Andrenidae [Andreninae]).

In one family, the Myrmecolacidae, the males and females parasitize different hosts: males parasitize ants, whereas females parasitize grasshoppers, crickets and mantids. The dual host nature of this family is unusual not only in Strepsiptera but also among parasites.

Some of these hosts are pests of economic crops, or are nuisance pests. *Nilaparvata lugens* Stål and *Sogatella furcifera* Hováth (Hemiptera: Delphacidae) spread viruses in rice, causing "hopper burn" in South and Southeast Asia, and *Javesella pellucida* (F.) (Delphacidae), which is a vector of oats in the Palaearctic region, is parasitized by *Elenchus* sp. (Elenchidae); *Nephotettix* sp. (Hemiptera: Cicadellidae) is a vector on rice in Southeast Asia and is parasitized by *Halictophagus* sp. (Halictophagidae); the corn leafhopper *Dalbulus maidis* (Delong & Wolcott) (Cicadellidae) is a vector of three pathogens on corn and is parasitized by *Halictophagus naulti* Kathirithamby & Moya-Raygoza (Halictophagidae) in Mexico; *Proutista moesta* (Westwood) (Hemiptera: Derbidae), a pest of coconuts, and araca nuts and oil palm in southern India, is parasitized by *Halictophagus palmi* Kathirithamby & Ponnamma; fruit flies *Dacus* sp., that damage fruits in Australia, the South Pacific, and Southeast Asia, are parasitized by *Dipterophagus daci* Drew & Allwood (Halictophagidae); *Segestes decoratus* Redtenbacher, *Sexava nubila* (Stål), *Segestidea defoliaria defoliaria* Uravov and *Segestidea novaeguineae* Brancsik (all Orthoptera: Tettigoniidae), which feed on palm fronds and cause severe defoliation of oil palm, coconut and *Pandanus*, are parasitized by *Stichotrema dallatorreanum* Hofeneder in Papua New Guinea; *Solenopsis invicta* Buren (Hymenoptera: Formicidae), a nuisance pest in the southern Nearctic region, is parasitized by *Caenocholax fenyesi texensis* Kathirithamby & Johnston.

Morphology

Male

The adult free-living male is most conspicuous because of its flabellate antennae, raspberry-like eyes, and large hind wings. The antennae have 4–7 segments with sensorium (Fig. 143). The eyes have 15–150 ommatidia, which are separated by strips of cuticle or setae. Except in the family Corioxenidae, all males have mandibles. Maxillae vary in size, with a shorter basal segment and longer palpi. In the Bohartillidae, however, the basal segment is six times longer than the palpi.

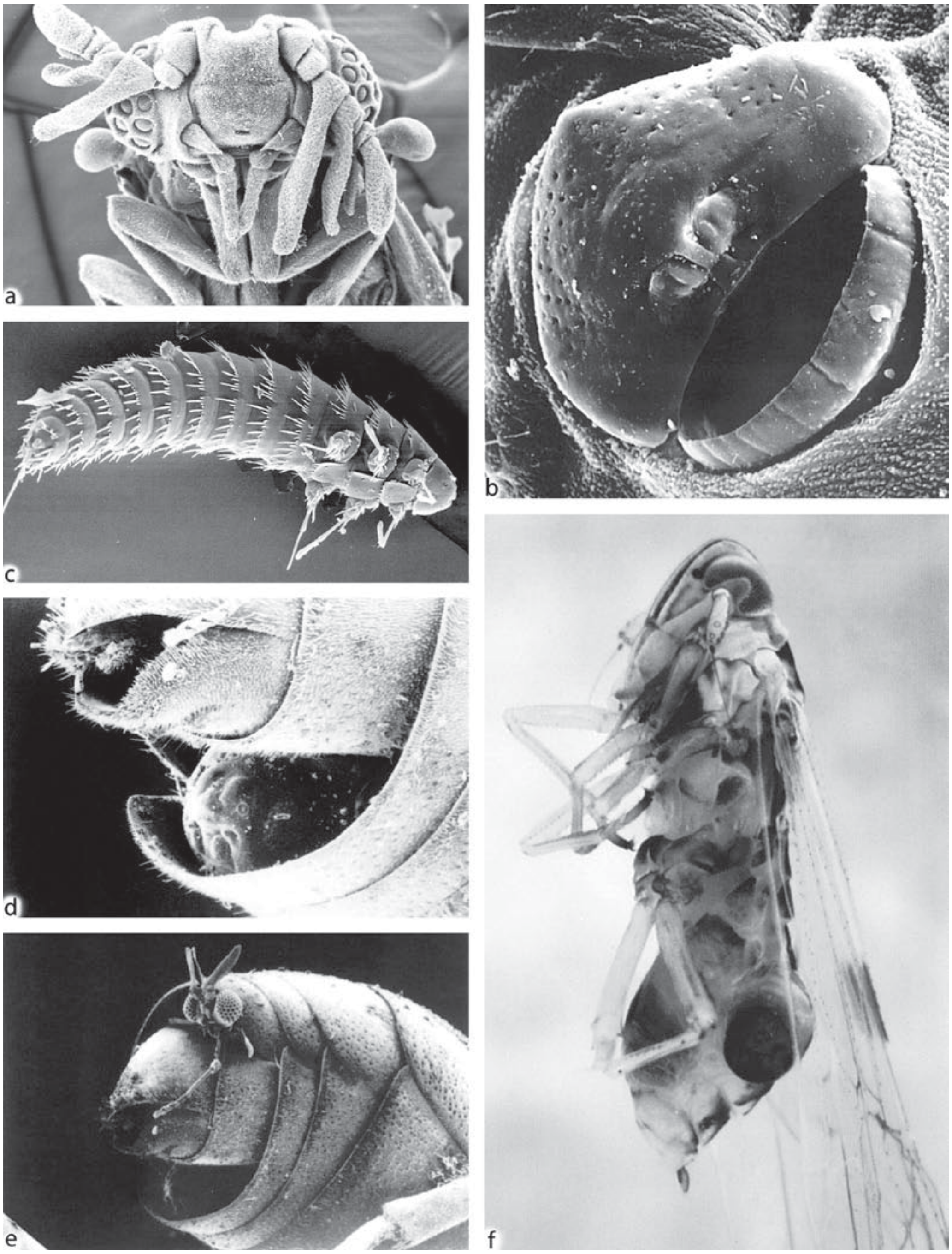
The pro- and mesothorax are reduced; the latter has a pair of reduced wings which are analogous to the halteres of Diptera. The metathorax is large, and bears the flight muscles that power the large hind wings, which have reduced veins.

The legs have 2–5 segmented tarsi, with absence of trochanter in the fore- and midlegs. Claws may either be present or absent.

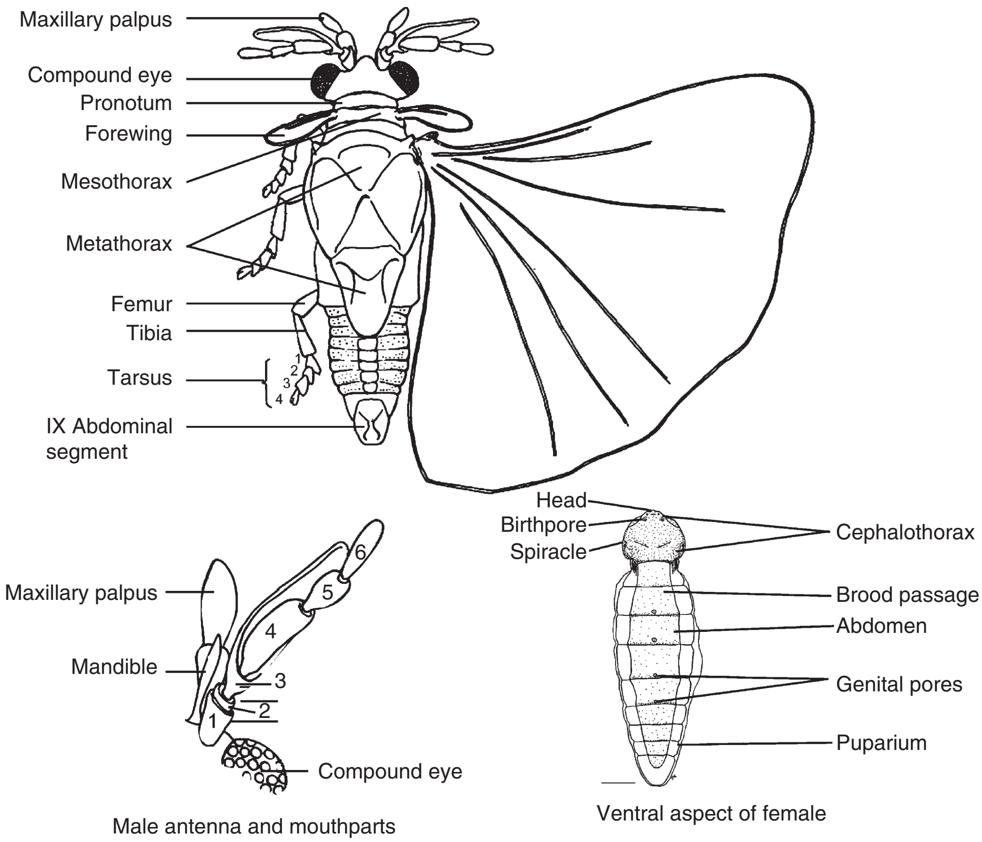
There are ten abdominal segments. The ninth abdominal segment has a simple aedeagus, except in *Caenocholax fenyesi sensu lato*, which has a large shield-shaped plate dorsally. There are no parameres. The tenth abdominal segment varies in size, and overhangs the ninth segment.

Female

Only the females of the family Mengenillidae are free-living as pupae and adults. They emerge to pupate externally from the host and, as both pupae and neotenic adults, have a head which bears eyes and antennae, and legs. The neotenic adult also has a genital orifice, but is wingless. The females of the suborder Stylopidia remain endoparasitic in the host, except for their cephalothorax, which is extruded at the neotenic adult stage. They do not possess any adult insect characters, and are viviparous. The brood canal opening in the cephalothorax is used both for the insemination of the female by the male and for



Strepsiptera, Figure 142 (a) *Halictophagus australensis* Perkins, male. SEM of head, ventral view; (b) *Elenchus varleyi* Kathirithamby, SEM of female cephalothorax. x630; (c) *Stylops* sp. first instar larva; (d) *Pseudoxenos* sp. Male pupa extruded between sternites of host *Odynerus bicolour* Saussure (Hymenoptera). SEM. x50; (e) Adult male *Pseudoxenos* sp. male free-living adult emerging from host *Odynerus bicolour* Saussure (Hymenoptera). SEM. x20; (f) *Sogatella furcifera* Hováth (Delphacidae) with pupa of male *Elenchus japonicus* Esaki & Hashimoto. Note extremely reduced external genitalia. x66. (From Kathirithamby J (1992) Invertebrate Taxonomy 6(1): 159–196. Reprinted with permission from CSIRO PUBLISHING, Melbourne Australia.)



Strepsiptera, Figure 143 A diagram of a male Strepsiptera (above) showing a dorsal view with the left wing removed. The lower diagrams show a close-up of the male antenna and mouthparts (left) and a ventral view of a neotenic endoparasitic female (right) (scale bar = 0.8 mm).

the emergence of the first instar larvae. The brood canal opening leads into the brood canal, which in turn leads to the genital ducts which open into the body cavity of the female. The entire body is filled with developing oocytes/first instar larvae.

Immature Stages

The first instar larva is free-living and is about 0.08–0.30 mm in length. The head has stemma, antennae, mandibles, and labium. The ventral region of the head is made up of microtrichia with serrated edges containing fringes. The thoracic and abdominal sternites and tergites and intercoxal sternites are serrated. The abdomen bears long caudal setae (Fig. 142). Entry of the first instar larva into the host occurs when the host is at the nymph or larva stage, and parasitization at the egg stage has also been reported. The point of entry of the first instar larva is usually via the abdomen and thorax (in nymphal hosts), or the head, thorax and abdomen (in larval hosts). In *Stichotrema dallatorreanum* Hofeneder in Papua New Guinea, which parasitizes tettigoniids, the first instars have been observed to enter the host via the tarsi.

On entry into the host, the first instar moults to an apodous second instar, and there are three endoparasitic stages which undergo apolysis without ecdysis, whereby the larva sheds the cuticle but does not emerge from it. Instead, it retains the cuticles as layers. At the late fourth instar, the male and female of the suborder Stylopidia extrude their cephalotheca and cephalothorax, respectively. In the Mengenillidae, the male and female at the end of the fourth instar emerge to pupate externally.

The male pupates within the puparium which is formed by the last instar cuticle. During the pupation of the male Stylopidia, the host remains mobile, and the strepsipteran male emerges as a free-living adult by breaking the cap of the cephalotheca. On extrusion of the cephalothorax, the fourth instar female Stylopidia becomes a neotenic adult, and awaits fertilization by the male. The females are viviparous, and after fertilization the larvae begin development. The first instars emerge via the brood canal opening of the female Stylopidia or the genital orifice of Mengenillidae, and seek new host nymphs or larvae to parasitize.

Host Associations

Species of Strepsiptera have been found not to be host specific, and may parasitize several genera (up to 23) and several species (up to 42). Recent studies show that this superficial polyphagous nature may by due to cryptic speciation.

Parasitization by Strepsiptera (stylopization) may affect morphology and behavior of the host. The reduction in the secondary sexual characters is marked in Delphacidae (Hemiptera), where the male and female genitalia are extremely reduced when stylopized (Fig. 142f). Abnormal facial coloration and foveae, proportions of the antennal segments, reduction in the pollen-basket on the leg, anal fimbria, ovipositor and male genitalia, have been reported in stylopized Hymenoptera.

Stylopization also affects hymenopteran host behavior such as loss in the power of flight, less savage when stinging, unbalanced flight and a lack of pollen-collecting instinct. Studies on the paper wasp, *Polistes dominulus* (Christ), showed that stylopized wasps desert the nest before the extrusion of the male cephalotheca and female cephalothorax, and form summer aggregations consisting of castrated wasps, in order to facilitate mating of the strepsipteran.

The behavior of stylopized ants is different from the behavior of stylopized wasps described above. It has been suggested that, when ants are stylopized, they abandon the nest, ramble about, and climb high on grass and bushes. However, when whole nests were dissected, a large proportion of ants with extruded cephalotheca containing fully developed male myrmecolacids that were ready to emerge were found. The pupal instar of the male strepsipteran is long, and it is most likely that the stylopized ants only leave the nest when the male strepsipteran is ready to emerge from the host. When the stylopized ant leaves the nest, it climbs onto grass stems or a bush in order to release the male myrmecolacid. Stylopized ants, unlike stylopized wasps, only leave the nests when the male strepsipteran is ready to emerge, because the worker ant is safer from predators in the nest than outside, and this could be adaptive for the strepsipteran.

References

Grimaldi D, Kathirithamby J, Schawaroch V (2005) Strepsiptera and triungula in Cretaceous amber. Insect Syst Evol 36:1–20

Kathirithamby J (1989) Review of the order Strepsiptera. Syst Entomol 14:41–92

Kathirithamby J (1991) Strepsiptera. In: Naumann ID, Carne PB, Lawrence JF, Nielson ES, Spradberry JP, Taylor RW, Whitten MJ, Littlejohn MJ (eds) Insects of Australia, A textbook for students and research workers, 2nd edn. CSIRO, Melbourne University Press, Carlton, Victoria, Australia, pp 684–695

Kathirithamby J (1992) Strepsiptera of Panama and Mesoamerica. In: Diomedes Q, Aiello A (eds) Insects of Panama and Mesoamerica: selected studies. Oxford University Press, Oxford, UK, pp 421–431

Kathirithamby J (2005) Further homage to Santa Rosalia: discovery at last of the elusive females of a species of Myrmecolacidae (Strepsiptera: Insecta). In: Ridley M (ed) Narrow roads of Gene Land. Collected papers by W. D. Hamilton, vol III. Oxford University Press, Oxford, UK, pp 117–134

Kinzelbach RK (1971) Morphologische Befunde an Fächerflügler und ihre Phylogenetische Bedeutung (Insecta: St repsiptera).Schweizerbart'sche Verlangsbuchhandlung, Stuttgart, Germany

Kinzelbach RK (1978) Insecta, Fächerflügler (Strepsiptera). Series: Die Tierwelt Deutschlands, vol. 65. V. G. Fischer Verlag, Jena, 166 pp

Kinzelbach RK (1990) The systematic position of Strepsiptera. Am Entomol 35:59–70

Pohl H, Beutrl RG, Kinzelbach RK (2005) Protoxenidae fa,. Nov. (Insecta, Strepsiptera) from the Baltic amber – a "missing link" in strepsipteran phylogeny. Zool Scripta 34:57–69

Strepsiptera

An order of insects. They commonly are known as twisted-wing parasites or stylopids.

► Stylopids

Stress-Induced Host Plant Free Amino Acids and Insects

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Various researchers have demonstrated that individual amino acids differ in their effects on insect growth and development. Subsets of amino acids are the mechanistic bases of relationships between total plant nitrogen and insect vitality. For example, artificial diets with the amino acid distribution found in anthers were found to be successful for rearing tobacco budworms, *Heliothis virescens* F. At least to some extent, nutritional strength has been linked with insect preference for host plants and higher levels of readily available (unbound) amino acids presumably improve insect development. Similarly, plants with accumulations of certain free amino acids (FAAs) are, in some cases, preferred by some herbivorous insects.

Abiotic Plant Stress Factors and FAAs

Higher levels of some FAAs, especially free proline, in association with water deficit stress occur in many plants, including cotton, *Gossypium hirsutum* L.; soybeans, *Glycine max* (L.) Merr.; wheat, *Triticum aestivum* L. Pers.; cowpea, *Vigna unguiculata* L.; tomato, *Lycopersicon esculentum* Mill.; and jack pine, *Pinus banksiana* Lamb. In corn, *Zea mays* L., seedlings, drought treatment caused an increase in total FAA content and a consistent rearrangement of the amino acid pool with increased accumulation of free alanine, arginine, valine, aspartate, serine, threonine, and tyrosine. Lower amounts of free glutamic acid, glycine, and methionine likely resulted from a strong decrease in glutamate. In cotton, increasing degrees of water deficit stress increased foliar free alanine, arginine, glycine, histidine, isoleucine, phenylalanine, proline, and valine, but associations between the weekly volume of water provided and the quantity of individual FAAs were not always linear.

Researchers have most often focussed on the relationship between water deficit stress to plants and free proline accumulations. Suspension culture cells of water deficit adapted tomatoes to polyethylene glycol had a 300-fold bigger free proline pool than untreated cells, the result of a tenfold rise in proline synthesis via the glutamate pathway. Use of N-15 labels in tomato plants determined that ornithine was an unlikely precursor to proline, and it has been suggested that the rate of proline synthesis in unstressed cells only slightly exceeds the rate required to sustain both protein synthesis and free proline pool maintenance. Mechanisms restricting free proline oxidation, and oxidation of other FAAs, can operate at different rates governed by the degree to which water deficit stress is imposed. Some researchers have interpreted the accumulation of large pools of free proline and other FAAs in water deficit stressed rice as being an indication of protein synthesis pathway disruption, or an increase in protein degradation. Others concluded that the higher free proline levels in *Arabidopsis thaliana* (L.) Heynh tissues with low water content resulted from increased biosynthesis. Osmotic stress in *A. thaliana* induced a rapid accumulation of free proline through *de novo* synthesis from glutamate, and during recovery from osmotic stress, accumulated free proline is oxidized to glutamate and the first step of this process is catalyzed by proline oxidase. A study using water deficit stressed bermudagrass, *Cynodon dactylon* (L.) Pers., showed that 10–100 times more free proline accumulated than in controls and it was suggested that, because proline turns over more slowly than other FAAs during water deficit stress, free proline might function primarily as a nitrogen storage compound.

Alternatively, in hydroponic potatoes, *Solanum tuberosum* L., subjected to water deficit stress induced by polyethylene glycol, plants were able to grow in "dry" conditions by accumulating organic solutes for use in osmoregulation. Osmoregulation in the tubers occurred in two phases: (i) during the first 2 days hexoses were accumulated, and (ii) after 7 days osmotic adjustment was mostly due to the accumulation of FAAs, especially proline (150 times the amount found in unstressed controls). Free proline might act as a compatible solute, a readily utilizable source of energy, and a sink for soluble nitrogen. Plants originating in dry climates were found to have higher levels of free proline than plants in wetter climates, and it has been postulated that the high free proline levels accompany survival and growth rather than being a result of damage. One study demonstrated that free proline sprayed on cotton plants counteracted the effects of water deficit stress. Leaf relative water content, dry matter content, and chlorophyll content and stability to heat increased. FAA accumulations associated with disease and nematode infections of plants might result from osmotic disruption, but also from other reasons, including xylem injury repair, syncytial wall formation in nematode-induced root galls, cell wall formation, and blockage of protein synthesis. Other abiotic stresses that have been associated with significantly increased foliar free amino acids accumulation include high soil salinity and soil nitrogen levels (each results in increased free proline in particular), and shade (particularly free arginine).

Biotic Plant Stress Factors and FAAs

Weed Competition

Competition with weeds has been associated with increased free arginine accumulations, but not proline, in sugarcane and cotton. In cotton, shade from weeds was attributed to be the cause of the stress. Sugarcane canopy closure shaded out weed growth after weeds had already caused a significant sugarcane stand reduction, and the higher free arginine levels in weed-free sugarcane habitats were attributed to shade caused by denser stands of the crop itself.

Fungi and Bacteria

Plants infected with various pathogens have been found in association with increased accumulations of FAAs. *Fusarium solani* (Mart.) altered host plant metabolic activity in citrus, and it was suggested that the higher levels of free arginine, asparagine, glutamic acid, glycine, and proline were caused by a fungal toxin that enhanced xylem membrane permeability. Pecan trees, *Carya illinoinensis* (Wangenh.) K. Koch, are more susceptible to fungal leaf scorch, *Phomopsis* sp. and *Glomerella cingulata* (Ston.), when under water deficit stress, and FAAs were more abundant in scorch-infected tree leaves. It was suggested that foliage with higher FAA levels might favor the growth and development of leaf scorch. Tobacco, *Nicotinia tabacum* L., infected with crown gall, caused by the bacteria *Agrobacterium tumefasciens*, had 70-fold higher accumulations of free proline than healthy controls. Similarly, crown gall infected tomatoes, *Lycopersicon esculentum* Mill., had 22 times more free proline as compared to healthy controls. Non-pathogenic fungi can also influence FAA accumulations in plants. For example, the vesicular-arbuscular mycorrhizal fungus, *Glomus faciculatum* (Thax. Sensu Gerd.) caused ammonia-fed corn to accumulate more FAAs than control plants. Major components of the FAA pool were glycine, glutamine, alanine, serine, asparagine, and GABA. These FAAs were between two and threefold more concentrated in *Glomus*-colonized roots.

Viruses

Tomato plants infected with tomato leaf curl virus had higher concentrations of soluble amino acids than controls, and it was suggested that virus infection stimulates nitrogen metabolism and mobilization of proteins. The rate of turn-over of FAAs into bound amino acids is enhanced by virus infection. FAAs are not directly converted to amino acids in viral protein, but they are incorporated into viral protein by way of bound amino acids. Aspartic acid, glutamic acid, serine, alanine, phenylalanine, and other amino acids are actively turned over and used for the synthesis of viral protein (these amino acids comprise much of the viral protein). FAAs have also been shown to increase in association with a variety of viruses infecting different plants, including barley yellow dwarf virus infection of barley, *Hordeum vulgare* L., and wheat, *Triticum aestivum* L.; cassava mosaic virus infection of cassava, *Manihot esculenta* Crantz; pigweed mosaic virus infection of pigweed, *Amaranthus* sp.; southern bean mosaic virus infection of cowpea, *Vigna* sp.; common bean mosaic virus infection of mung bean, *Vigna radiata* (L.) Wilczek; and soybean mosaic virus and bean pod mottle virus infection of soybean, *Glycine max* (L.) E. Merill.

Plant Stress, FAAs, and Phytophagous Nematodes

Some phytophagous nematodes have been shown to be associated with higher host plant FAA levels than healthy controls, including *Radopholus similis* (Cobb) Thorne infected grapefruit, *Citrus* x *paradisi* Mcfad., seedlings; reniform nematode, *Rotylenchulus reniformis* Linford & Oliveira, in cotton, *Gossypium barbadense* L.; green gram, *Phaseolus aureus* Roxb.; black gram, *P. mungo* (L.); and cowpea; and stem nematode, *Ditylenchus dipsaci* (Kuhn) Filipjev, infecting alfalfa, *Medicago sativa* L. Augmentation of root knot nematodes, *Meloidogyne* spp., was associated with lower levels of free cysteine, histidine, proline, and serine concentrations in sugarcane, *Saccharum officinarum* L. Shading in dense stands of sugarcane elevated levels of some FAAs compared to less dense stands of sugarcane, and the increases were correlated to populations of stunt nematodes, *Tylencorhynchus annulatus* Cobb. Concentrations of FAAs were unchanged when roots of *Beta patellaris* (Moq.), a resistant species of beet, were infected with cyst nematodes, *Heterodera schactii* (Schmidt). However, in the susceptible sugar beet, *B. vulgaris* L., concentrations of aspartic acid, glutamic acid, and glutamine, and total FAAs were significantly higher when infected with cyst nematodes. Another study determined that infection of tomato plants by *Meloidogyne javanica* (Treub) Chitwood resulted in accumulation of free proline in galls. The concentration of free proline increased with increasing density of nematodes, but the highest concentration occurred at the time of egg production, and the concentration of free proline was highest in *M. javanica* eggs and egg sacs compared to portions of the plant. Proline is reported as being a major constituent of the egg shells of phytophagous nematodes, including *M. javanica* and *Heterodera rostochiensis* Wellenweber. Other researchers have suggested that proline might stimulate xylem production following injury induced by phytophagous nematodes.

Although the previous examples of research have indicated an association between nematode feeding and elevated accumulations of FAAs in the host plant, other studies have shown that host plant resistance to nematodes is conferred through high levels of FAAs. For example, quantities of FAAs in segments of cotton roots resistant and susceptible to *Meloidogyne incognita* (Kofoid and White) were compared. Following infection, the susceptible cultivar had greater percentage increases in certain FAAs than a resistant cultivar, but the sum total of FAAs was greatest in the resistant cultivar. Another study, using ring nematode, *Criconemella xenoplax* (Raski) Luc & Raski, showed that nematode resistant cultivar peach, *Prunus persica* (L.) Batsch, seedlings accumulated significantly more FAAs in the root tissue in association with phytophagous nematode populations.

Virus infected host plants, presumably with greater accumulations of FAAs, have been shown to be associated with higher numbers of certain phytophagous nematodes than healthy control plants. *Meloidogyne javanica* juveniles entered bean, *Phaseolus* sp., plant roots, infected with tobacco ring spot virus more than uninfected plants, though the growth of the nematodes was unaffected. The root knot nematode grew more rapidly on tobacco mosaic virus-infected beans than on controls, but the virus did not affect the number of nematodes entering the root. Root exudates can attract nematodes, and it is possible that the exudates are attractive at least in part because they contain FAAs or other constituents of the exudate signal high FAA levels in the host plant.

Plant Stress, FAAs, and Phytophagous Insects

One study demonstrated that mildly water deficit stressed soybean plants were preferred by Mexican bean beetle, *Epilachna varivestris* Mulsant, larvae, possibly as a result of higher levels of FAAs in the foliage. Beet armyworm, *Spodoptera exigua* (Hübner), eggs have been reported as being most concentrated on water deficit stressed cotton in fields and this observation might be because water deficit stressed cotton plant foliage has greater accumulations of FAAs. However, water deficit stress has been shown to decrease aphid populations because the insects are more dependent on water pressure in the plant than other insects.

Insects that depend on host plant water pressure for efficient ingestion of nutrients have been shown, in some cases, to prefer virus infected host plants over non-infected plants, presumably because the nutritional value of the plant is enhanced by higher accumulations of FAAs. Pigeon pea, *Cajanus cajan* (L.) Millsp., plants infected with a mosaic virus were infested with more potato leafhoppers, *Empoasca kerri* Pruthi, than healthy plants. The virus-infected leaves had higher accumulations of total nitrogen, peptides, and FAAs than the controls. Sweetpotato whitefly, *Bemisia tabaci* (Gennadius), populations were higher on pumpkin, *Cucurbita pepo* L., infected with squash leaf curl virus than healthy pumpkin plants. Sugar beet, *Beta vulgaris* L., leaves with a mosaic virus were more suitable food for aphids than uninfected leaves. Grasshopper, *Melanoplus* sp., preferred to feed on leaves of sunflower, *Helianthus* sp., infected with rust, *Puccinia* sp. Cotton aphids, *Aphis gossypii* Glover, lived longer and produced more offspring on pumpkin plants infected with zucchini yellow mosaic virus than non-infected plants. Aphids, *Rhopalosiphum padi* (L.) and *Sitobion avenae* (F.), reared on oats, *Avena byzantina* (Koch), infected by various isolates of barley yellow dwarf virus were much more likely to mature as winged adults than were aphids reared on healthy oats. However, sweetpotato whitefly populations were lower on squash, *Cucurbita* sp.; tomato; and cotton plants infected with squash leaf curl virus, chino del tomate virus, and cotton leaf crumple virus, respectively, than non-infected controls. In some studies, no significant differences were observed between herbivorous insect populations and virus-infected host plants.

Insects absorb nitrogen through the gut primarily in the form of FAAs or small peptides. Thus, the initial cost of proteolysis is saved if amino acids are ingested in this form. The distinction between FAAs and those bound in proteins may be important for insects such as aphids that cannot ingest large molecules or are not exposed to large molecules because of the composition of the plant's phloem sap on which insects like aphids feed, but this is separate from the costs of proteolysis. In terms of optimizing insect development, it is probable that the balance between different amino acids is particularly important. For example, pink bollworm, *Gossypiella pectinophora* (Saunders), larvae raised on a diet in which one of the essential amino acids was omitted grew slowly and failed to survive beyond the second instar. Increased glutamic acid caused growth stimulation. In some cases, amino acids such as glycine have been shown to be essential. Beet armyworms prefer to oviposit on pigweed, *Amaranthus hybridus* L., over cotton, *G. hirsutum*, and third instars prefer to feed on pigweed foliage over cotton foliage. Beet armyworm larvae also grow and develop better on pigweed than on cotton, and it has been suggested that the lack of gossypol and other deterrent or toxic compounds found in cotton leaves, and the higher accumulations and greater diversity of FAAs in pigweed leaves make pigweed the superior host. However, in some insect-plant relationships, preferences for the plant host that most favors phytophagous insect growth and development is not always evident.

At least in some cases, the increased availability of readily available nitrogen appears to not only improve the chances of some disease organisms becoming established, but might also increase the likelihood of survival of insects feeding on the infected plants. Environmental stresses, whether biotic or abiotic, seem to affect the survival, fecundity, morphology, and vitality of some phytophagous insects through physiochemical processes mediated by corresponding changes of FAA accumulations in the host plant.

References

Brodbeck B, Strong D (1987) Amino acid nutrition of herbivorous insects and stress to host plants. In: Barbosa P, Schultz JC (eds) Insect outbreaks. Academic Press, London, UK, pp 346–364

Costa HS, Brown JK, Byrne DN (1991) Life history traits of the whitefly, *Bemisia tabaci* (Homoptera: Aleyrodidae) on six virus-infected or healthy plant species. Environ Entomol 29:1102–1107

Dadd RH (1968) Dietary amino acids and wing determination in the aphid, *Myzus persicae*. Ann Entomol Soc Am 61:1201–1210

Helms JA, Cobb FW Jr, Whitney HS (1971) Effect of infection by *Verticicladiella wagenerii* on the physiology of *Pinus ponderosa*. Phytopathology 61:920–925

Kennedy JS (1951) Benefits to aphids from feeding on galled and virus-infected leaves. Nature 168:825–826

Showler AT (2002) Effects of water-deficit stress, shade, weed competition, and kaolin particle film on selected foliar free amino acid accumulations in cotton, *Gossypium hirsutum* L. J Chem Ecol 28:615–635

Showler AT, Reagan TE, Shao KP (1990) Nematode interaction with weeds and sugarcane mosaic virus in Louisiana sugarcane. J Nematol 22:31–38

Stria

Grooves or indented lines.

Striate

The occurrence of fine, parallel grooves or impressions of the surface of the integument.

Stridulate

To produce a noise by rubbing together two surfaces.

Stridulating Slantfaced Grasshoppers

A subfamily (Gomphocerinae) of grasshoppers in the order Orthoptera: Acrididae.

► Grasshoppers, Katydids and Crickets

Strigilation

The oral removal of secretions by one insect from another.

Strip Cropping

Cultivation or harvesting crops in strips rather than in large expansive fields, with the strips sometimes following the natural contours of the land.

► Cover, Border and Trap Crops for Pest and Disease Management

Stripe

A line that runs horizontally or lengthwise on an insect. This term often is confused with a “band” or transverse line.

Striped Earwigs

Members of the earwig family Labiduridae (order Dermaptera).

► Earwigs

Striped Walkingsticks

A family of walkingsticks (Pseudophasmatidae) in the order Phasmatodea.

► Walkingsticks and Leaf Insects

Structural Gene

A gene that codes for an RNA molecule or protein other than a regulatory gene.

Structural Genomics

The study of protein structure based on DNA sequences.

Structural Fumigation

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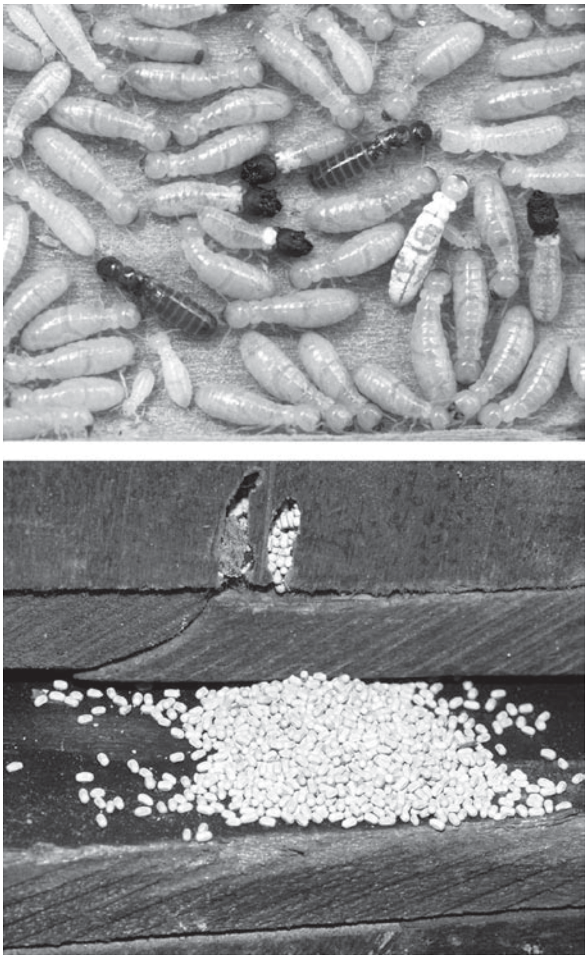
Fumigation is a category of pest control in which a gaseous pesticide (fumigant) is applied within a measured volume of space that is enclosed by tarpaulins or otherwise sealed. The fumigant must be confined in this space for a time and at a concentration sufficient to kill the target organism. A fumigant is a chemical that, at a required temperature and pressure, can exist in the gaseous state in sufficient concentration to be lethal to a given organism. Fumigation should not be confused with the Spanish word "fumigación" which has a broader definition that includes spraying of liquid pesticides. Structural, soil, and commodity fumigation are named for the material type which harbors the target pest(s). Quarantine fumigation is usually ordered by governmental regulators to prevent the transportation of exotic pests, usually infesting a commodity, into a jurisdiction which is free of that pest. Structures most commonly fumigated include residential and commercial buildings, however, boats, railcars, and truck trailers may also require fumigation.

Structural fumigation is unlike any other category of modern pest control. It demands that a sequence of procedures be conducted in varying, and often difficult, physical environments using toxic gases and an assortment of heavy, costly, and specialized equipment. Fumigation is the only method of pest control that allows for complete and rapid eradication of a target organism within a defined space. The great advantage of structural fumigation over other methods of pest control is that all target pests are killed within the fumigated space, regardless of their location. Fumigants follow all the physical laws of gases; therefore, their molecules diffuse freely through air and infiltrate the minutest of spaces. The disadvantage of fumigation is the lack of residual activity to protect the fumigated space from subsequent reinfestation.

Target Pests

Drywood termites (Family Kalotermitidae) are by far the most important target pests of structural fumigations (Fig. 144) while wood-boring beetles (families Lyctidae, Bostrichidae, Anobiidae, and Cerambycidae) and aerial infestations (including boats) of subterranean termites (families Rhinotermitidae and Termitidae) account for the other wood-destroying insects controlled by fumigation. Although most structural fumigations in the United States are for wood-destroying insects, infestations of other pests may arise



Structural Fumigation, Figure 144 **Termites are the most common target pests of structural fumigation: (*top*) the West Indian drywood termite, *Cryptotermes brevis*, a widespread target of structural fumigation, (*bottom*) drywood termite pellets are a common sign of infestation.**

that require fumigation. Among such insect pests are cockroaches, carpet beetles, stored-product beetles and moths, clothes moths, bedbugs, and spiders. Rodents such as rats and mice are common vertebrate pests for which fumigation might be prescribed. Large or severe infestations, infestations in difficult to treat or sensitive locations, or when standard methods of non-fumigant control are not working are potential candidates for structural fumigation.

Fumigants

Numerous volatile solvents and gases have been used in the past as structural fumigants. Over the last 15 years, methyl bromide, once a widely used structural fumigant, has been phased out for this use because of its reactivity with atmospheric ozone. The only viable structural fumigant for the foreseeable future is sulfuryl fluoride which is sold under the trade names Vikane® and Zythor®. Chloropicrin (nitrochloromethane) must be released simultaneously with sulfuryl fluoride because the latter is relatively odorless. Chloropicrin is a potent teargas that prevents unauthorized entry into the fumigated airspace.

It remains unlikely that any new fumigant will be discovered but the mixture of fumigants with carbon dioxide or other synergistic gases may be developed to increase the efficacy of currently available fumigants. The relatively small pool of candidate chemicals does not include a single gas with some, or even a few, of the many desirable properties needed for a structural fumigant. In late 2001, chlorine dioxide was the first new structural fumigant to be used since sulfuryl fluoride was introduced over 40 years ago. Chlorine dioxide gas was implemented under a strict USEPA emergency exemption to decontaminate anthrax spores from several federal government buildings at the cost of hundreds of millions of dollars. Although chlorine dioxide has antibacterial properties, it is very short-lived, unstable, and explosive. In addition, this gas cannot be containerized, is highly corrosive, and is effective only in a narrow temperature and humidity range.

Transport Equipment

Equipment and chemicals must be transported to the fumigation site using vehicles specially designed for this purpose. Vehicles carrying hazardous materials (sulfuryl fluoride or chloropicrin) must also have warning signage and a secure chemical storage area separate from that of the driver and passengers. Some companies choose to carry all needed material on a single truck (Fig. 145). Other companies use one vehicle for transporting chemicals and another for sealing materials.

Inspection and Measurement

The target pest, volume of the structure, building design, and sealing conditions must be determined in order to deliver the proper equipment to the site. A graph of the structure, in aerial view and marked with linear dimensions, is required to calculate the volume under seal. A measuring wheel, tape measure, and graduated pole can be used to determine dimensions. Several photographs are also useful for considering any special procedures or equipment for the job.

Exterior and Interior Preparation and Sealing

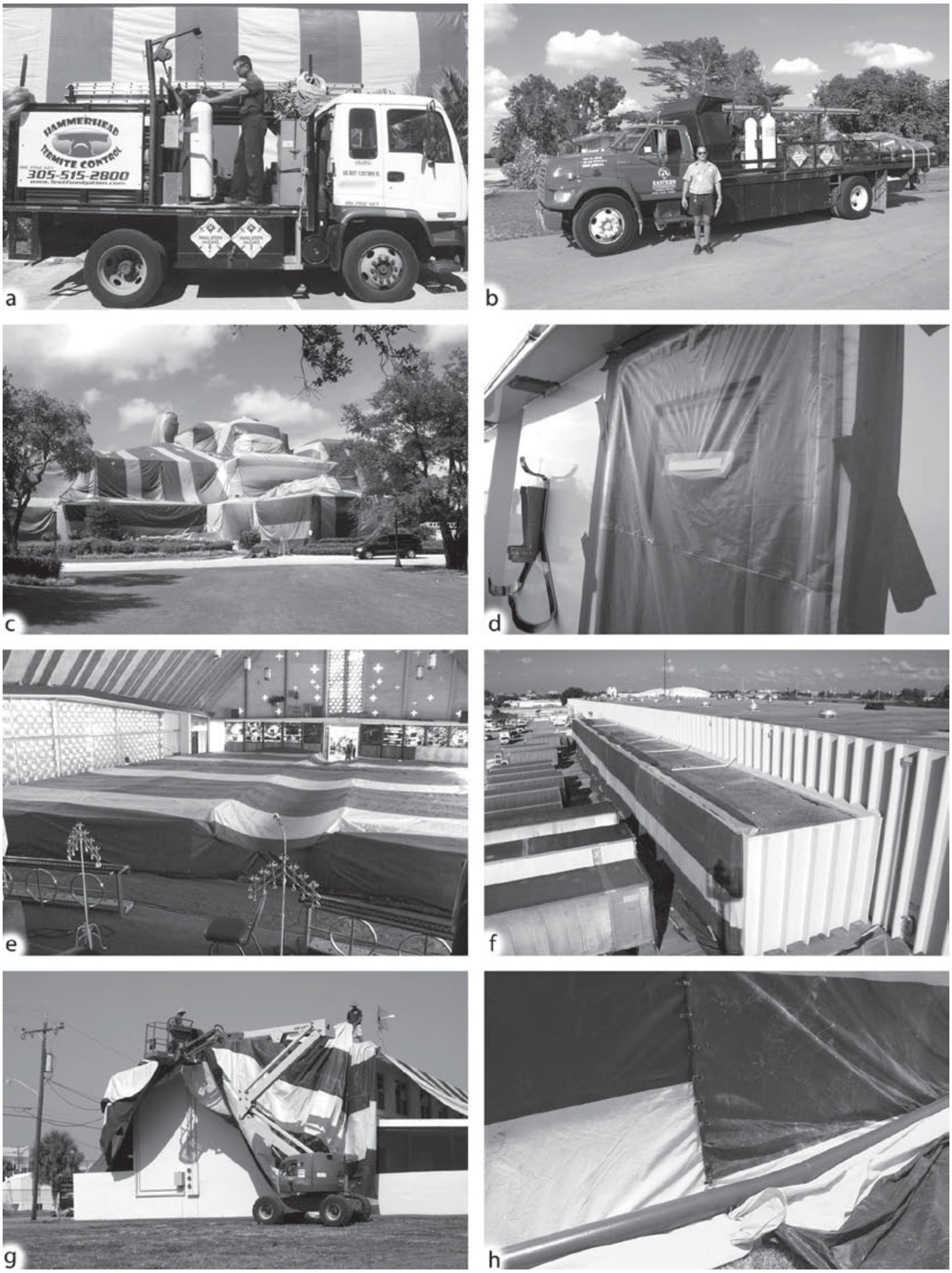
There are three basic categories of sealing a structure for fumigation: (i) tarpaulin sealing of the entire structure, (ii) "tape and seal" using polyethylene sheeting and tape to seal windows and doorways of a structure with an otherwise impermeable exterior structure (e.g., concrete, steel, fiberglass), and (iii) compartmental fumigation in which only the infested portion of a larger structure is sealed.

In a typical fumigation, exterior and interior preparations are done simultaneously. Exterior preparation in tarpaulin fumigations involves the removal or repositioning of fragile components such as antennas, awnings, and patio screening. The ground around the structure must be freed of porous substrata, curbs, and roots by removing, raking, or placing a layer of sand over the area. The tarpaulin apron can then be secured at ground level using sand or water "snakes" to weigh down and seal the tarpaulin to the smooth substrate. The tarpaulins are then positioned on the roof of the structure, dropped to the ground, and adjoining seams are sealed with hand clamps. Warning signs must be placed on all sides of the structure and must have contact information to reach the fumigator in case of an emergency.

Interior preparation includes the sealing of food and medicinal items inside special nylon bags, removal of all plants and animals, opening all possible indoor enclosures (e.g., windows, cabinets, closets, attic access doors, etc.), placement of high output fans to facilitate fumigant diffusion, securing the sulfuryl fluoride introduction hose location(s), and the chloropicrin evaporation pan site(s). All flames and exposed hot elements must be turned off. All operable doors must be locked using secondary locking devices that only the fumigator can open.

Introduction of Chloropicrin and Sulfuryl Fluoride

The target pest, volume, exposure time, seal quality, and weather conditions will determine the total quantity (and concentration) of fumigant and warning agent to be applied. Seal quality includes the condition of tarps, the quality of the ground seal (tarp apron on ground), and underseal (concrete slab or soil type). Special handheld calculators or programs supplied by the manufacturers are used to calculate fumigant dosage based on quantitative or qualitative value for each of the variables listed above. Colder temperature, strong wind, and small total volume contribute to higher calculated dosages. Efficacious rates for sulfuryl fluoride against drywood termites are up to 10 times lower than rates for some solitary insects like wood boring beetles because egg kill is not needed to eradicate termite colonies. Rodents and other vertebrate



Structural Fumigation, Figure 145 **Fumigation of structures: (a) a compact truck for narrow streets, (b) a full size truck provisioned to transport equipment, chemicals, and crew members to a fumigation site, (c) tarpaulin fumigation of a mansion, (d) "tape and seal" fumigation of a boat (exterior door shown), (e) compartmental fumigation of church pews, (f) a combination tarpaulin and "tape and seal" fumigation of a warehouse (g) mechanical lift to raise tarpaulins onto building, (h) water "snake" for proper ground seal.**

vermin are killed at half the rate required for drywood termites at 80°F (25°C).

After the structure has been sealed, the interior preparation completed (Fig. 146), and a final walk-through inspection is made to insure that no people or pets are in the structure, fumigation can proceed. The fumigator enters an open seam (tarpaulin fumigation) or doorway (tape and seal fumigation) with a measured quantity of chloropicrin which is poured into one or more evaporation pans (1 pan and up to 3 fluid ounces per 45,000 cubic feet). After pouring the chloropicrin into the pan, the fumigator exits the structure and the entrance opening is sealed. After allowing at least 5 min for the chloropicrin to begin evaporating, the sulfuryl fluoride can be introduced. Cylinders containing 125 lbs. of fumigant when full are hoisted onto a balance, a release hose is connected, and the cylinder valve is opened. When the appropriate quantity of fumigant has been released (typically 4–8 ounces per 1,000 cubic feet (= 4–8 g/m3) for drywood termites), the cylinder valve is closed. Typical fumigation exposure periods range from 18 to 48 h. Depending on urgency to reoccupy building, exposure periods can be shortened by the addition of a higher initial fumigant concentration.

Monitoring, Aeration and Clearance

During a fumigation, the concentration of sulfuryl fluoride can be measured using a Fumiscope® thermal conductivity detector. Monitoring is not typically required but may be an important procedure if seal conditions are uncertain or a very large structure is fumigated. By monitoring the concentration, the fumigator can add additional fumigant if needed and will thus insure that the fumigation is successful. If the fumigator is only concerned with detecting overt leaks in the seal, he/she can use a halogen leak detector to locate leaks and correct them.

Upon completion of the predetermined exposure period, the aeration process begins. The seal is first broken and the fumigator enters the structure wearing a self contained breathing apparatus. The fumigator opens all operable doors (and windows in a tape and seal fumigation). At this time the structure must be aerated with doors open for a minimum of one hour. During this period, the crew removes all sealing materials from the structure and after 1 h, the doors can be relocked. Six to eight hours after the beginning of initial aeration, the fumigator returns to the structure to test the concentration of residual sulfuryl fluoride before reoccupancy can take place. Using an Interscan® pyrolytic fluoride detector or an ExplorIR® infrared analyzer, the fumigator walks throughout all rooms of the structure. If all readings are equal to or less than one part per million, the structure is deemed safe for reentry and clearance notices are affixed to all doors allowing for people to reenter and restore the structure to its original state.

Hazards and Limitations of Structural Fumigation

Structural fumigation produces sufficient concentration of sulfuryl fluoride to be toxic to humans upon relatively short exposure. With the proper building inspection procedures, secondary locks, warning signs, and chloropicrin release, accidents involving human exposure have been greatly minimized in recent years. Because sulfuryl fluoride diffuses readily between structural walls, the entire building must be evacuated, typically for two nights, even if only part of the building needs fumigation treatment. Occasionally, vegetation is planted so close to a building that it must be covered by the fumigation tarpaulin. Dowsing soil around roots with water reduces sulfuryl fluoride exposure but temporary leaf-drop will often occur in many plant species.

Structural Fumigation, Figure 146 **Fumigation, continued: (a) warning signs should be placed on all sides of the structure, (b) liquid chloropicrin is poured into an evaporation pan placed next to a fan and the outlet of the sulfuryl fluoride release hose, (c) sulfuryl fluoride is released as a liquid. Upon exiting the end of the release hose, the liquid boils and spontaneously turns into a gas at atmospheric temperature and pressure, (d) Fumiscope® used to measure working concentrations of fumigant, (e) halogen leak detector is useful for finding leaks in the seal of a fumigated structure, (f) initial aeration requires that the fumigator enters the building to open doors wearing a self-contained breathing apparatus, (g) gn Explorer IR clearance detector can measure down to 1 ppm sulfuryl fluoride.**

References

Anon (2003) Vikane gas fumigant structural fumigation manual. Dow AgroSciences LLC, Indianapolis, Indiana
Bennett GW, Owens JM, Corrigan RM (2003) Truman's scientific guide to pest management operations, 6th edn. Advanstar Communications, Cleveland, OH
Scheffrahn RH, Cabrera BJ, Kern WH Jr (2004) Florida fumigation manual. IFAS Extension Publication No. SP-340, November 2004
Thoms E, Phillips T (2004) Fumigation. In: Mallis A (ed) Handbook of pest control, 9th edn. GIE Media, Cleveland, OH

Structural Pest

A pest that affects the structural wood in buildings.
► Urban Entomology

Stylet

The elongated needle-like portions of the piercing-sucking type of insect mouthparts in Hemiptera.
► Mouthparts of Hexapods

Stylet-Borne Virus

A virus that does not persist in the vector, but which is a mechanical contaminant of the insect's mouthparts (stylets). Also known as nonpersistent virus.

Stylopidae

A family of insects in the order Strepsiptera.
► Stylopids

Stylopization

The occurrence of parasitism by stylopids (Strepsiptera).

Stylus

A finger-like process; a simple, primitive ovipositor.

Subalare

A small, upper portion of the pleuron, posterior to the wing, to which wing muscles are inserted.

Subcosta

The longitudinal vein running parallel to the costa. It usually turns and connects to the anterior margin of the wing before reaching the wing apex, and usually is unbranched.
► Wings of Insects

Subcosta Fold

The depression between the costa and the radius.

Subcuticular Space

The space created between the epidermal cells and the endocuticle during molting.

Subdorsal

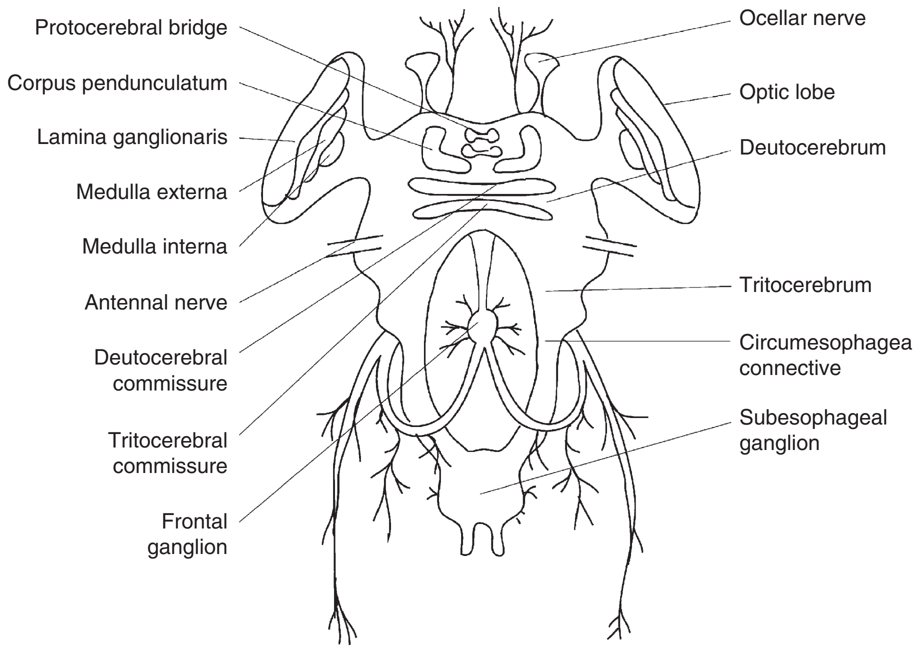
A region between the dorsal and lateral areas.

Subesophageal Ganglion

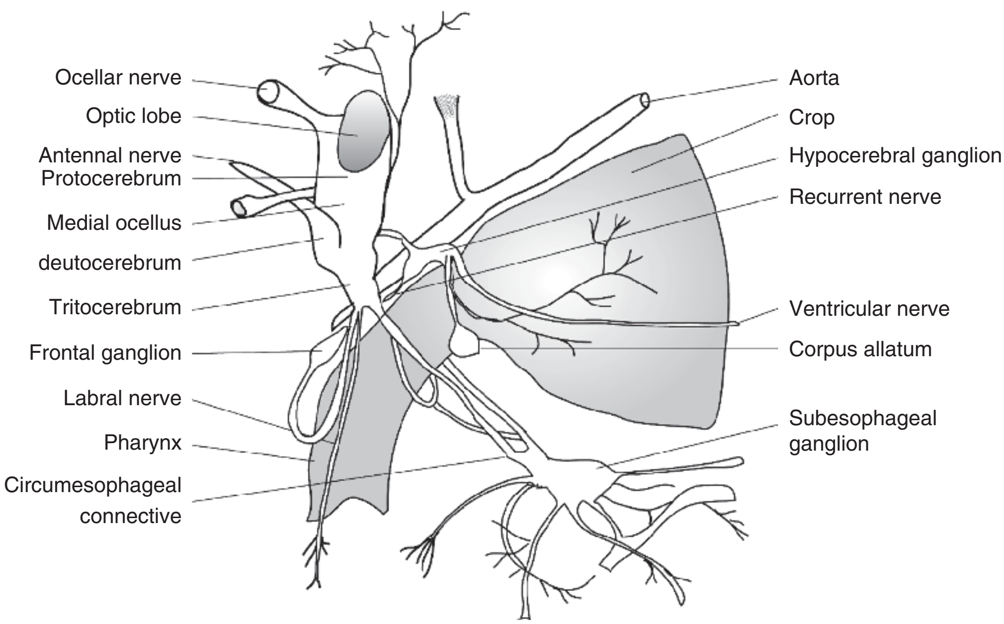
A ganglion located in the head that is found beneath the digestive tract (Figs. 147 and 148), and which innervates the mouthparts.
► Endocrine Regulation of Insect Reproduction
► Nervous System

Subfamily

In classification, a major division of the family unit consisting of related tribes or genera. Subfamily names end in -inae. Although not one of the major taxonomic units, subfamilies sometimes are quite useful in describing clusters of like taxa.



Subesophageal Ganglion, Figure 147 **Cross section showing the relationships of the principal endocrine glands with the brain (adapted from Chapman, The insects: structure and function).**



Subesophageal Ganglion, Figure 148 **Lateral view of the insect brain (adapted from Snodgrass, Insect morphology).**

Subgalea

A maxillary segment associated with the stipes.

Subgenital Plate

A plate covering the gonopore from below.

Subimago

The first of two winged instars of mayflies (Ephermeroptera) after they emerge from the water.

Submedial Arc

Pigmentation in the form of an arc occurring on the face or top of the head in caterpillars.

Submentum

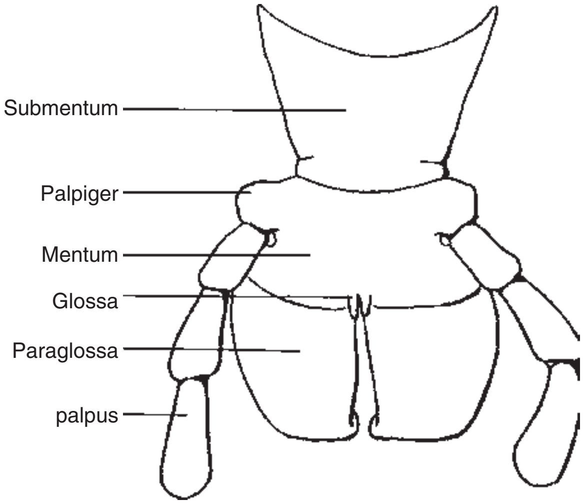
The basal portion of the insect labium (Fig. 149), by means of which it attaches to the head.

► Mouthparts of Hexapods

Subsocial Behavior

A level of sociality less than eusocial behavior. A type of presocial behavior. It involves cooperation within a family, usually expressed as a mother caring for her offspring. However, the cooperation does not extend to include to cooperation between sisters.

► Presocial
► Solitary



Submentum, Figure 149 External aspect of the labium in an adult grasshopper, showing some major elements.

► Communal
► Quasisocial
► Semisocial
► Eusocial Behavior
► Sociality in Insects

Subspecies

A subdivision of species, usually a geographic race and differing slightly or greatly in appearance but capable of interbreeding. Subspecies generally carry little importance, but may be indicative of speciation in progress. In some taxa, particularly with butterflies (Lepidoptera, in part) subspecies are widely recognized.

Subspiracular

The area immediately below the spiracles.

Subterranean Termites

A group of termites in the family Rhinotermitidae that maintain contact with the soil as they attack wood.

► Termites
► Termites in South America

Succession

A progressive series of changes in the vegetation of a site, starting with colonization and ending with establishment of a climax community. Also called ecological succession.

Sucking Lice

This suborder of wingless ectoparasitic insects is also called Anoplura, and usually is grouped together with the chewing lice (Mallophaga) into a single order, Phthiraptera, though sometimes they are treated as separate orders. The name is based on the Greek word *sipho* (tube) and the Latin *cula* (little).

Sugarcane Rootstock Borer Weevil, *Diaprepes abbreviatus* (Linnaeus) (Coleoptera: Curculionidae)

This insect, also known as *Diaprepes* weevil, attacks numerous crops in tropical regions of the Americas.

► Citrus Pests and Their Management

Sugarcane Pests and Their Management

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Sugarcane is a tropical, perennial grass that evolved in Asia, most likely the South Pacific, probably the island of New Guinea. It is composed of six species in the genus *Saccharum* L. Two species are wild, *S. spontaneum* and *S. robustum*, and four species are cultivated, *S. officinarum*, *S. barberi*, *S. sinese*, and *S. edule*. All commercial sugarcane cultivars grown today are interspecific hybrids of *Saccharum*.

History of Sugarcane

Humans have cultivated sugarcane for at least the last two millennia. Traders and migrating populations hybridized and moved sugarcane from southeastern Asia through India and China, through the Middle East and northern Africa, and into the Mediterranean. Europeans introduced sugarcane into the islands off the west coast of Africa, and Columbus transported sugarcane from the Canary Islands to the Dominican Republic on his second voyage in 1493. Sugarcane plantings and production spread during the next century into the other Caribbean islands and into Mexico, Central America, and South America.

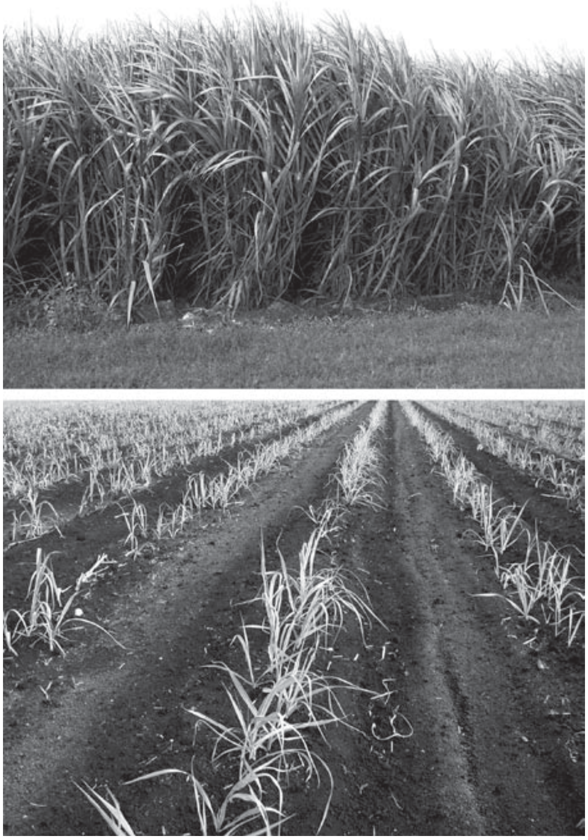
Sugarcane Production in the USA

Sugarcane is grown commercially in four states in the USA, with over 900,000 acres harvested and a value of $754 million. Jesuit priests brought sugarcane into New Orleans, Louisiana, in 1751. Commercial-scale production in New Orleans began in 1795. Sugarcane is now grown on 435,000 acres in 24 parishes in southern Louisiana. The value of sugarcane production in Louisiana in 2005 was over $282 million.

Sugarcane has been grown in many locations in Florida since the arrival of the French and Spanish. Commercial production today is centered south, east, and west of Lake Okeechobee in the southern part of the state (Fig. 150). The sugarcane industry expanded in Florida during the 1960s and harvested acres in 2006 reached 405,000. The value of sugarcane production in Florida in 2005 was almost $357 million.

Sugarcane has been grown in several locations in Texas, from the Houston area south to the Rio Grande Valley. Sugarcane was introduced into the Rio Grande Valley in the early 1800s and by 1913 there were five sugar mills. However, due to economic hardships, the last mill closed in 1921. Research was conducted in the 1960s to determine the economic feasibility of growing the crop again and in 1973 a new sugar mill was completed in south Texas. In 2006 the harvest was 46,500 acres. The value of sugarcane production in Texas in 2005 was over $54 million.

Commercial sugarcane production started in Hawaii in 1837. However, because of increasing land values and poor economic returns, production



Sugarcane Pests and Their Management, Figure 150 **Sugarcane: a mature field of sugarcane (*above*), and recently planted (*below*).**

has declined steeply since the mid-1980s. Final sugarcane harvests occurred in 1996 on the islands of Oahu and Hawaii, and in 2006, there were 22,300 acres harvested on Kauai and Maui. The value of sugarcane production in Hawaii in 2005 was over $61 million.

Sugarcane Botany

Commercial sugarcane is vegetatively propagated by planting seed pieces. Seed pieces are sections of stalks that contain two or more nodes and internodes. A node is where the leaf attaches to the stalk but is also where the buds and root primordia are located. After planting, a primary shoot and two different types of roots emerge from the bud. Secondary shoots (tillering) emerge after the primary shoot and each shoot develops their own root system. Above ground, the sugarcane leaf is composed of a leaf sheath which surrounds the stalk and a leaf blade. Sugarcane stores sucrose in the stalks with decreasing concentrations as you move up the stalk. Commercial production involves the use of plant cane fields and ratoon or stubble fields. Stubble fields have been harvested and the plants are allowed to regrow. The number of stubble crops depends on various factors such as sugarcane variety, plant diseases, soil type, and soil insect pressure.

Pest Descriptions

This section includes the important mite and insect species that attack sugarcane in the USA (Florida, Hawaii, Louisiana and Texas). Sugarcane insect pests are generally local insects that have adopted this plant as a host after its cultivation; however the movement of sugarcane has provided new geographical areas for these adopted pests. Many other insects inhabit sugarcane fields and act as predators or parasitoids. These insects are not mentioned here. Pest management considerations are discussed at the end of this section.

Acari

Although sugarcane may be infested by many different mite species, few are economic pests. Species within the genus *Oligonychus* (Tetranychidae) are occasional pests. *Oligonychus stickneyi* (McGregor) occurs in Hawaii and Florida and *O. pratensis* (Banks) is known to attack Florida sugarcane. A new mite, *O. grypus* Baker & Pritchard, was found infesting sugarcane in Florida greenhouses in 2002. This species, originally from Africa, was previously found in Cuba and

Brazil. The mite *Steneotarsonemus bancrofti* (Michael) (Tarsonemidae) is rarely found in Hawaii and Florida.

Collembola

During the 1950s in Louisiana, control measures were taken against "small soil arthropods" although there was little evidence that they caused damage. *Lepidocyrtus cyaneus* Tullberg, *Onychiurus armatus* (Tullberg), *Proisotoma minuta* (Tullberg) and *Pseudosinella violentus* (Folsom) are soil-dwelling, whereas *Salina beta* Christiansen & Bellinger have been found on the underside of leaves in Florida.

Orthoptera

In other regions of the world where sugarcane is grown, grasshoppers can be serious pests. In the USA, several species of grasshoppers and field crickets may inhabit but usually don't economically damage sugarcane. These include the grasshopper *Schistocerca obscura* (F.) and the field crickets *Gryllus assimilis* (F.) and *G. firmus* Scudder. Two species of mole crickets, *Scapteriscus borellii* Giglio-Tos and *S. vicinus* Scudder, sometimes attack young sugarcane plants.

Isoptera

Termites can be major pests of sugarcane, especially in parts of Australia, China, and India. In the USA, *Coptotermes formosanus* Shiraki in Hawaii and *Reticulitermes flavipes* (Kollar) in Florida are considered minor pests.

Psocoptera

Few species of Psocoptera have been identified in sugarcane. *Ectopsocopsis cryptomeriae* (Enderlein) was found in Florida and perhaps consumes sugarcane rust fungus (*Puccinia melanocephala* H. & P. Syd).

Hemiptera

At least 11 families have been documented to cause plant injury to sugarcane. Injury is caused by feeding from xylem or phloem tissues or by vectoring a plant pathogen which causes disease. Results of these types of injury can cause economic damage through a reduction in sugar production or plant death. Management tactics for hemipteran species include varietal resistance and the use of natural enemies.

Acleridae

This very small family of scale insects has two representatives from Louisiana, *Aclerda holci* Teague and *A. sacchari* Teague. Neither species is important economically.

Aphididae

Several aphid species are considered serious pests of sugarcane, while several other species are probably incidental inhabitants. Aphids cause injury by direct feeding and by vectoring plant diseases.

The sugarcane aphid, *Melanaphis sacchari* (Zehntner) is a widely distributed species. It was reported in Hawaii in 1896, Florida in 1977, and Louisiana in 1989. It was not found in Texas in a survey conducted in 1990. Large populations can sometimes be present and it is known to vector sugarcane yellow leaf virus (SCYLV). Although large numbers of aphids can be present, natural enemies can keep the aphids under economic control.

The yellow sugarcane aphid, *Sipha flava* (Forbes), occurs in Florida, Louisiana, and Texas. In 1989, it was found to be established in Hawaii. It is a serious pest of sugarcane and can cause premature yellowing and death of sugarcane leaves. Young plants are sometimes killed by large populations, and if the plant survives, there is a reduction in sugar yield. Natural enemies, such as predators, and varietal resistance are the two strategies used for control, although in Florida chemical control is common in some years.

Five aphid species are known vectors of the potyvirus mosaic virus: *Acyrthosiphon pisum* (Harris), *Hyperomyzus* (= *Nasonovia*) *lactucae* (L.), *Hysteroneura setariae* (Thomas), *Rhopalosiphum maidis* (Fitch), and *Uroleucon* (= *Dactynotus*) *ambrosiae* (Thomas). *Rhopalosiphum maidis* also transmits SCYLV and the phytoplasma causal organism of grassy shoot disease, which is not currently in the Western Hemisphere.

Cercopidae

Froghoppers or spittlebugs are serious pests of sugarcane in many areas of Mexico, Central and South America. These insects can attack sugarcane roots and also feed from leaf or stem tissues. Important genera include *Aeneolamia*, *Mahanarva*, *Sphenoclypeana*, *Sphenorhina*, and *Tomaspis*. Only one species, *Prosapia bicincta* (Say), is present in Louisiana and Florida. Surveys taken in Texas failed to find this species.

Cicadellidae

Many species of leafhopper can be found in sugarcane but it is doubtful that they cause economic damage. *Draeculacephala portola* Ball is a common species found in sugarcane and was once thought to be a vector of the sugarcane disease chlorotic streak. Other species collected in USA sugarcane include *D. mollipes* (Say) (Hawaii, Louisiana), *Balclutha caldwelli* Blocker (Florida), *B. rosea* (Scott) (Texas), *Graminella nigrifrons* (Forbes) (Florida, Texas), *G. plana* (DeLong) (Texas), *G. sonora* (Ball), *Homalodisca insolita* (Walker) (Florida, Texas), and *Oncometopia lateralis* F. (Louisiana).

Cixiidae

Two cixiid planthopper species have been found in USA sugarcane and have been reported in other sugarcane-producing areas of the New World. *Myndus crudus* Van Duzee, the American palm cixiid, is a serious pest of palms and is known to vector the palm disease lethal yellowing. Nymphs develop on the roots of grasses and adults feed on the foliage of palms. *Oliarus texanus* Metcalf is a species found in Texas and is not considered to be an economic pest.

Coccidae

One species of soft scale, *Pulvinaria elongata* Newstead, has been found in Florida, Hawaii, Louisiana, and Texas. It is a serious pest of sugarcane through its feeding, but also has been shown to vector a disease called sugarcane yellow leaf luteovirus. Natural enemies, including parasitoids and predators, can be effective in controlling populations.

Cydnidae

Burrower bugs attacking sugarcane are found in several areas in South America (Brazil and Venezuela) and southeastern Asia (Indonesia, Myanmar, Philippines, and Taiwan). In Florida, *Cyrtomenus ciliatus* (Palisot de Beauvois) and *Pangaeus bilineatus* (Say) are sometimes found at low populations levels, and in Louisiana, *P. bilineatus* and *Sehirus cinctus* (Palisot) can be abundant during spring and early summer.

Delphacidae

Two species of delphacid planthopper are potentially important pests to sugarcane in the USA. *Perkinsiella saccharicida* Kirkaldy, the sugarcane delphacid, was found in Florida in 1985, Texas in

1991, Louisiana in 1994, and Hawaii in the early 1900s. This pest can cause severe economic damage and is a vector of *Fijivirus* sp., causal agent of Fiji disease of sugarcane. Currently the disease is restricted to southeastern Asia, Madagascar, and the southern Pacific. *Saccharosydne saccharivora* (Westwood) is found in Florida, Louisiana, and Texas. This species has the potential to build up large populations on some varieties, but it usually doesn't cause economic damage in the USA. However, reports from Cuba have recently (2005) identified this species as a vector of sugarcane yellow leaf phytoplasma, a plant pathogen that inhabits the phloem sieve tubes of infected plants. Surveys in Florida and Texas have documented several other delphacid species on sugarcane, but it is not believed that they are breeding on the host plant.

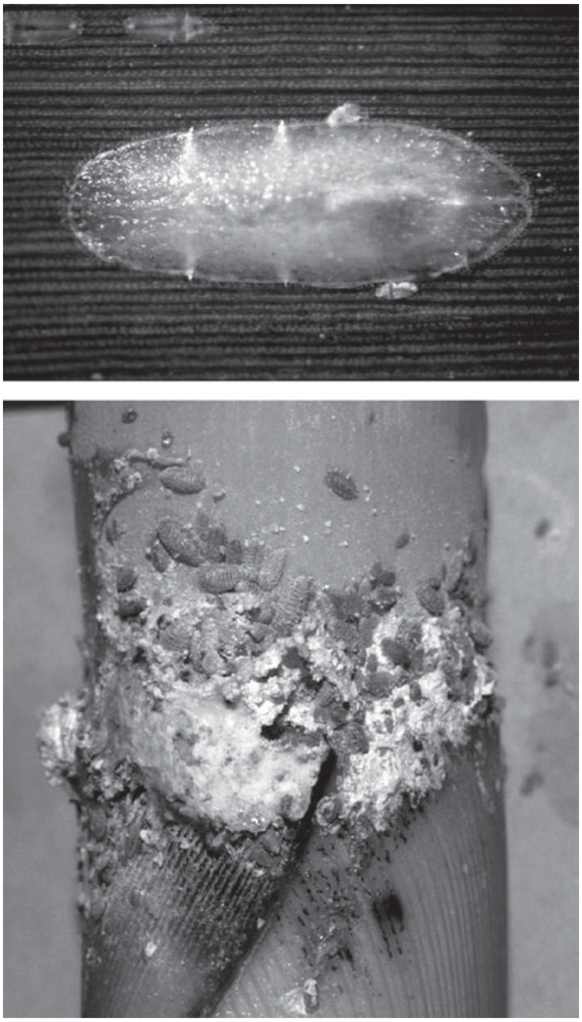
Diaspididae

Several species of armored scales are important pests of sugarcane. They congregate on the stalks under the leaf sheaths and can produce several generations during a season. Large populations can reduce sugar production. Two species, *Aulacaspis tegalensis* (Zehntner) and *Melanaspis glomerata* (Green), are not present in the USA, but are serious pests in other sugarcane areas.

Several species do occur in the USA but are not considered serious pests. *Aspidiella sacchari* (Cockerell) and *Odonaspis saccharicaulis* (Zehntner) are found in Florida, Hawaii, and Texas. *Aspidiotus destructor* Signoret is a serious pest of coconuts but is only casually found in sugarcane. *Duplachionaspis divergens* (Green) was discovered on *Miscanthus* sp. in Florida in 2000 and on sugarcane in a greenhouse in 2003. It has been reported as a minor sugarcane pest but as of yet has not been found infesting Florida sugarcane in the field. Sugarcane is noted as being a host plant for three other species, *Diaspis bromeliae* (Kerner), *Hemiberlesia cyanophylli* (Signoret), and *Selenaspidus articulatus* (Morgan).

Pseudococcidae

Mealybugs infest sugarcane in all production areas of the world. In the USA, several common species are found, although none are considered economic pests. *Dysmicoccus boninsis* (Kuwana), the gray sugarcane mealybug, is a common species found in all sugarcane-producing states. *Saccharicoccus sacchari* (Cockerell), the pink sugarcane mealybug (Fig. 151), is present in Florida, Hawaii, and Texas. It was found in Florida in



Sugarcane Pests and Their Management, Figure 151 **A sugarcane-feeding soft scale, *Pulvinaria elongata* Newstead (*above*), and pink sugarcane mealybug, *Saccharicoccus sacchari* (Cockerell) (*below*).**

1944 but was not found in sugarcane until 1995. Both species attack sugarcane by feeding on the stalks behind leaf sheaths. *Dysmicoccus brevipes* (Cockerell), the pineapple mealybug, is found in Florida and Hawaii and attacks roots and stalks near the ground. The Rhodesgrass mealybug, *Antonina graminis* (Maskell), is a pest of rangeland grasses along the USA Gulf Coast and is seldom found in sugarcane. *Birendracoccus* (= *Pseudococcus*) *saccharifolii* (Green) was noted to be in Florida and is a disease vector. It has not been found in surveys. Two other species, *Chorizococcus rostellum* (Lobdell) and *Pseudococcus longispinus* (Targioni-Tozzetti), have been noted as attacking sugarcane in Hawaii. Natural enemies and healthy seedcane programs (using uninfested cane for planting) appear to keep populations managed.

Tingidae

The sugarcane lacebug, *Leptodictya tabida* (Herrich-Schaeffer) was documented in Texas sugarcane as early as 1910, being known as a common species in Mexico, Venezuela, and the Caribbean. When the sugarcane mills shut down in the 1920s, sugarcane lacebug disappeared until its rediscovery in 1989. This species was discovered on Maui in 1985 and in Florida in 1990. Although having the potential to produce large populations, it has not yet created economic damage.

Thysanoptera

Several thrips species have been documented in Hawaiian sugarcane but few have been noted in sugarcane in the continental USA. However, many of the species listed from Hawaii are cosmopolitan in distribution and have been reported from other plants in Florida, Louisiana, and Texas. Therefore, the species listed below is where there is a historical reference to being found in sugarcane. Thrips appear not to cause economic damage to sugarcane.

One species from the family Phlaeothripidae, *Haplothrips halophilus* Hood, has been documented in Louisiana sugarcane. Eight species from the family Thripidae have been documented either from Florida, Hawaii, or Louisiana. Most of these species are cosmopolitan in distribution and probably occur in Texas. The grass thrips, *Anaphothrips obscurus* (Müller), and the Hawaiian grass thrips, *A. swezeyi* Moulton, are pests in turf grasses but also can be found in sugarcane. Four species, *Arorathrips* (= *Chirothrips*) *mexicanus* (Crawford), *A.* (= *Chirothrips*) *spiniceps* (Hood), *Chirothrips sacchari* Moulton, and *Thrips saccharoni* Moulton, have only been documented in sugarcane in Hawaii. *Hercinothrips femoralis* (Reuter), the banded greenhouse thrips, has a world-wide distribution both in greenhouses and in the field in subtropical and tropical areas. It is probably present in all USA sugarcane areas, but has only been documented in Hawaii and Florida. *Bregmatothrips venustus* Hood has been found in Louisiana sugarcane.

Coleoptera

Beetle pests of sugarcane either tunnel within the stalks or infest the roots and seed pieces. There are a couple of families where only a few species are found in association with sugarcane in the USA. These include Alleculidae (*Lobopoda* sp.), Cerambycidae [*Prionus* sp. and *Prosoplus bankii* (F.)], Nitidulidae [*Carpophilus humeralis* (F.)], and Tenebrionidae (*Eutochia lateralis* Boheman). Most of these species are only casually associated with sugarcane and may not feed on any plant tissue.

Buprestidae

One species, *Aphanisticus cochinchinae seminulum* Obenberger, was found in Florida sugarcane in 2000. This species is a leafmining insect, as larvae tunnel between the upper and lower leaf epidermal layers. This feeding injury results in dead tissue. Adults are small and elongated in shape and feed on leaf tissue. This beetle is native to Malaysia and southeastern Asia and was reported in Hawaii in 1984 and Texas in 1994. It is not considered an economic pest.

Chrysomelidae

Two flea beetle species, the desert corn flea beetle *Chaetocnema ectypa* Horn and *C. pulicaria* Melsheimer, can be found feeding on sugarcane leaves. The desert corn flea beetle was found injuring sugarcane leaves in Florida in 2000 and is a common species being recorded from a variety of grass hosts. It is probably not an economic pest in sugarcane. *Diabrotica* spp. (rootworms) have been reported in Florida sugarcane and are probably present in Louisiana and Texas.

Curculionidae

The Diaprepes root weevil, *Diaprepes abbreviatus* (L.), is native to the Caribbean and is an important pest of sugarcane on some of the islands. It was found in central Florida near Apopka in a nursery in 1964. Populations have moved south and adults were found in sugarcane in 2002. These weevils were associated with alternate host plants such as hemp sesbania [*Sesbania exaltata* (Raf.) Rydb. Ex A.W. Hill] and sicklepod (*Cassia obtusifolia* L.). Thus far it has not been a problem in sugarcane but is a major concern to the citrus industry.

The silky cane weevil, *Metamasius hemipterous sericeus* (Olivier), is a subspecies of the West Indian cane weevil, *Metamasius hemipterous* (L.). It was first reported in southern Florida in 1984 but not reported infesting sugarcane until the mid-1990s. It is distributed throughout the Caribbean, Central, and South America. Females are attracted to sugarcane stalks that are cracked or have other types of injury. Larvae tunnel in the stalks and cause damage so severe that stalks may lodge or break. Pheromone trapping technology is available for monitoring, and varietal resistance (especially varieties that don't produce growth cracks) appears to be the best management approach. This insect is also an important pest of nursery palms and banana plantings.

Southern blue-green citrus root weevil adults, *Pachnaeus litus* (Germar), have been found in sugarcane fields but there has been no observed injury to sugarcane leaves or roots. It is not known if they can complete development on sugarcane host plants.

The New Guinea sugarcane weevil or sugarcane weevil borer, *Rhabdoscelus obscurus* (Boisduval), is currently one of the three most important pests to sugarcane in Hawaii. This species has a wide distribution throughout the western Pacific, including Australia, and was documented in Hawaii in the 1880s. Females lay eggs either into bored holes or into stalks previously injured by insects or rodents. Larvae tunnel extensively in the stalks. A tachinid fly, [*Lixophaga sphenophori* (Villeneuve)], was imported from New Guinea into Hawaii in the early 1910s and again in the early 1970s. This parasitoid appears to be an important mortality agent.

Xyleborus kraatzi Eichhoff is only casually associated with sugarcane and is not thought to cause damage.

A complex of billbug species are occasionally found associated with sugarcane. These include *Sphenophorus cariosus* (Olivier), *S. coesifrons* Gyllenhal, *S. maidis* Chittenden, and *S. venatus vestitus* Chittenden. These insects are pests of forage and turf grasses and are not generally considered to be economic pests of sugarcane.

Elateridae

Wireworms, the larval stage of click beetles, are considered one of the most important pest groups attacking sugarcane. Many species are found in the sugarcane growing regions of the USA, but *Melanotus communis* (Gyllenhal) and various species of *Conoderus* are the most serious pests.

Wireworms feed on the buds and root primordia of newly planted seed pieces and on the young shoots and roots after germination. Wireworms are seldom pests of stubble sugarcane. The death of buds or young shoots leads to stand reductions. Chemical control is the most common management technique, although cultural controls such as change in planting date (Louisiana) or flooding (Florida) have had some success. Sampling for larvae is tedious and difficult; therefore, researchers in Florida have developed baits composed of rolled oats as a monitoring tool.

Scarabaeidae

This is a large family of beetles that are serious pests of sugarcane in many parts of the world, especially India and Australia. Scarabaeidae is separated into several subfamilies which in the literature may be given family status, including Cetoniinae (flower beetles), Dynastinae, Melolonthinae (May or June beetles), and Rutelinae (shining leaf chafers). Most scarab species damage sugarcane by feeding on roots and underground stems of stubble crops, especially around field edges. Some species will attack buds and root primordia of newly planted sugarcane and the apical meristem of growing plants [sugarcane beetle, *Euetheola humilis rugiceps* (LeConte)]. In Louisiana the white grub *Phyllophaga latifrons* (LeConte) is a pest, while in Florida *Tomarus* (= *Ligyrus*) *subtropicus* (Blatchley) is the most serious (Fig. 152) grub pest. Studies in Florida have shown that high infestations of *T. subtropicus* caused yield reductions in tonnage of 39%. Chemical control tactics are not always effective against white grubs in the USA, but are successful in other sugarcane areas. Biological controls (parasitoids, milky disease *Bacillus popilliae*, and the fungal disease *Metarhizium anisopliae*) occur naturally and may have positive benefits to lowering populations. Cultural practices such as disking, reducing the number of stubble crops, and flooding are also used against these pests, and have reduced the impact of *T. subtropicus* in Florida.

Sugarcane Pests and Their Management, Figure 152 **An important sugarcane-feeding white grub species, *Tomarus* (= *Ligyrus*) *subtropicus* (Blatchley): larva (above) and adults (below).**

Diptera

Few fly species are noted as pests in sugarcane. In Florida adults of the otitid *Euxesta stigmatias* Loew (cornsilk fly) are found in sugarcane fields but no injury has been recorded.

Lepidoptera

Moth species attack both above- and belowground portions of the sugarcane plant. Many of the families we have listed (Elachistidae, Noctuidae, and Oecophoridae) contain species that are only casual occupants in sugarcane. One exception is fall armyworm (FAW) [*Spodoptera frugiperda* (J.E. Smith)], a sporadic pest that can, under certain conditions, defoliate a field of newly planted sugarcane.

Crambidae and Pyralidae

The most important group of moth pests is the crambid and pyralid stalkborers. Species in these groups are found everywhere that sugarcane is grown, and in many locations, a stalkborer species is the most important insect pest in that region. In the USA, sugarcane borer (SCB) [*Diatraea saccharalis* (F.)] is the species of concern in Florida and Louisiana. In Texas, the Mexican rice borer (MRB) [*Eoreuma loftini* (Dyar)] surpassed SCB as primary pest (Fig. 153). In Hawaii few stalkboring species are present but the lesser cornstalk borer [*Elasmopalpus lignosellus* (Zeller)] has invaded and is a serious pest.

Stalkborers lay eggs on sugarcane leaves (SCB) or in dried leaf material at the base of plants (MRB). The first few instar larvae feed or mine in the leaves, midribs, and leaf sheaths. The resulting injury appears as "pinholes" or "window-panes." In young plants, feeding within the inner whorl of leaves can cause "deadhearts," where the central growing shoot is killed. Older instar larvae enter and tunnel within stalks, creating injury defined as a "bored internode." Tunnels constructed by SCB larvae are cleaner and more linear than tunnels created by MRB larvae. Sugarcane borer larvae may tunnel in stalk sections between internodes, whereas MRB larvae generally meander within one internode. Pupation is completed within the stalk and adults emerge through their tunnels. Stalkborer feeding weakens the stalks so that they break or lodge more easily. Also, feeding allows entry for saprophytic red rot fungi [*Glomerella tucumanensis* (Speq.) Arx & E. Müller (= *Colletotrichum falcatum* Went.) and various secondary insect pests (Nitidulidae).

Chemical, biological, and plant resistance techniques are used to manage stalkborer populations. Insecticides applied that are targeted to the adult and young larval stages can be effective, but once larvae enter the stalks control is difficult. *Cotesia flavipes* Cameron, a parasitoid of *Chilo* spp. in India and Pakistan, was initially brought to the Caribbean for SCB control. It is now the main natural enemy of SCB in Florida and Texas. In Florida, augmentative releases of this parasitoid are made in some areas. In Louisiana, predation by the red imported fire ant, *Solenopsis invicta* Buren, provides good biological control. The search for effective natural enemies of MRB continues in several states of western Mexico. Certain varieties of sugarcane have natural tolerance (ability to produce high sugar yields under stalkborer pressure) or confer resistant characters (tough leaves or rind hardness) that reduce populations. New techniques such as the production of plants with insecticidal proteins are showing positive results.

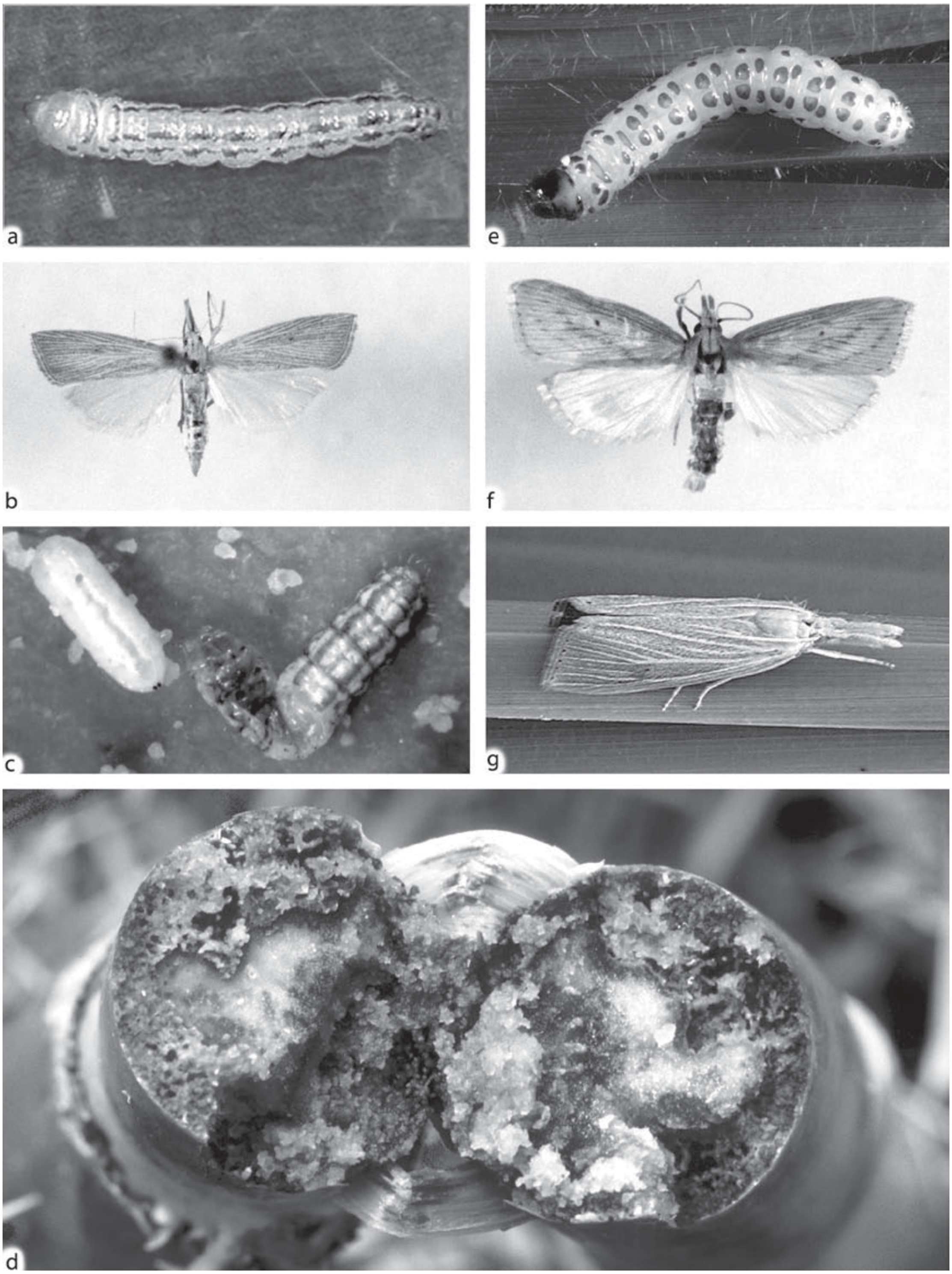
The lesser cornstalk borer (LCB) is native to the southeastern USA and is a pest of sugarcane on sandy soils. It is a relatively new pest in Hawaii, being first recorded in 1986. Lesser cornstalk borer is a more serious pest to young sugarcane plants under dry conditions. Eggs are laid just below the soil surface and larvae feed from silken tunnels at or below the soil level. Larvae kill the primary shoots causing deadhearts. Cultural controls, such as regulating irrigation, insecticides, introduction and conservation of parasitoids, and varietal resistance are some of the management techniques that are used for control.

Sugarcane Pest Management

Management Strategies

Growers use a variety of approaches to control insect and mite pests of sugarcane. Cultural control is defined as using agronomic techniques to reduce the likelihood of pest problems. These techniques include planting clean seed pieces (i.e., planting uninfested cane pieces), the use of irrigation or flooding, disking or tillage of fields, reduction of the number of ratoon crops, and sanitation of infested plant material.

Biological control is another management strategy that has been very successful with some sugarcane pests. The introduction of insect pathogens (for beetle and stalkborer pests) and predators (for aphid, scale insect, and mealybug pests) has



Sugarcane Pests and Their Management, Figure 153 **Some important Lepidoptera affecting sugarcane: Mexican rice borer, *Eoreuma loftini* (Dyar) larva (a), adult (b), larva from which a tachinid parasitoid has emerged (d), and tunneling damage in cane stalks; and sugarcane borer, *Diatraea saccharalis* (F.) larva (e) and adults (f, g).**

had varying degrees of success. However the introduction and conservation of parasitoids has had the most success in controlling insect pests. Insect species within families of Diptera (Tachinidae) and Hymenoptera (Bethylidae, Braconidae, Eulophidae, Ichneumonidae, Scelionidae, and Trichogrammatidae) have been released in large numbers to control various hemipteran and lepidopteran pests. For example, 17 species in six parasitoid families have been introduced into Texas sugarcane for biological control of the crambid pest MRB. Continued research into the requirements of these parasitoids and the conditions which promote their establishment and population growth will guarantee success of biological control.

Chemical control, especially against soil pests, is used in USA sugarcane production. In Florida and Louisiana, two materials are registered for wireworm and other soil insect control. Insecticides are also labeled for SCB, LCB, and aphid control in Florida and Louisiana. To maintain the presence of biological control agents, insecticide applications are made to <1% of the sugarcane acreage in Hawaii and Texas.

Varietal resistance through classical breeding has been an important management strategy against stalkborers. There is variability in the number of bored internodes among the commercial and non-commercial sugarcane clones when tested against SCB and MRB. Resistance can be separated into leaf and stalk components. Young larvae must be able to become established within the leaves, midribs, and leaf sheaths and obtain sufficient nutrients before entering stalks. Leaf sheath appression and leaf midrib hardness have been shown to be resistant characters. Stalk resistance involves the ability of larvae to enter and tunnel. Rind hardness (an interior section of the stalk), stem

Sugarcane Pests and Their Management, Table 27 **Sugarcane arthropod pests, geographical area affected, and site of injury**

Taxa scientific/Common name	USA geographic area	Site of injury
Acari		
Tetranychidae		
Oligonychus stickneyi (McGregor)	Hawaii, Florida	leaves
O. grypus Baker & Pritchard	Florida	leaves
O. pratensis (Banks)	Florida	leaves
Tarsonemidae		
Steneotarsonemus bancrofti (Michael)	Hawaii, Florida	leaves
Collembola		
Entomobryidae		
Lepidocyrtus cyaneus Tullberg	Florida	
Pseudosinella violentus (Folsom)	Florida, Louisiana	roots
Salina beta Christiansen & Bellinger	Florida	leaves
Isotomidae		
Proisotoma minuta (Tullberg)	Louisiana	roots
Onychiuridae		
Onychiurus armatus (Tullberg)	Florida, Louisiana	roots
Orthoptera		
Acrididae		
Schistocerca obscura (F.)	Florida	leaves

Sugarcane Pests and Their Management, Table 27 **Sugarcane arthropod pests, geographical area affected, and site of injury (Continued)**

Taxa scientific/Common name	USA geographic area	Site of injury
Gryllidae		
Gryllus assimilis (F.) – Jamaican field cricket	Florida	leaves
G. firmus Scudder – sand field cricket	Florida	leaves
Gryllotalpidae		
Scapteriscus borellii Giglio-Tos – southern mole cricket	Florida	roots, shoots
S. vicinus Scudder – tawny mole cricket	Florida	roots, shoots
Isoptera		
Rhinotermididae		
Coptotermes formosanus Shiraki – Formosan subterranean termite	Hawaii	roots
Reticulitermes flavipes (Kollar) – eastern subterranean termite	Florida	roots
Psocoptera		
Ectopsocidae		
Ectopsocopsis cryptomeriae (Enderlein)	Florida	leaves
Hemiptera		
Acleridae		
Aclerda holci Teague	Louisiana	leaves
A. sacchari Teague	Louisiana	leaves
Aphididae		
Acyrthosiphon pisum (Harris) – pea aphid	cosmopolitan	leaves
Hyperomyzus lactucae (L.) – sowthistle aphid	cosmopolitan	leaves
Hysteroneura setariae (Thomas) – rusty plum aphid	all sugarcane-producing states	leaves
Melanaphis sacchari (Zehntner) – sugarcane aphid	Florida, Hawaii, Louisiana	leaves
Rhopalosiphum maidis (Fitch) – corn leaf aphid	cosmopolitan	leaves
Sipha flava (Forbes) – yellow sugarcane aphid	all sugarcane-producing states	leaves
Uroleucon ambrosiae (Thomas) – brown ambrosia aphid	Louisiana	leaves
Cercopidae		
Prosapia bicincta (Say)	Florida, Louisiana	roots, leaves
Cicadellidae		
Balclutha caldwelli Blocker	Florida	leaves
B. rosea (Scott)	Texas	leaves
Draeculacephala mollipes (Say)	Hawaii, Louisiana	leaves

Sugarcane Pests and Their Management, Table 27 Sugarcane arthropod pests, geographical area affected, and site of injury (Continued)

Taxa scientific/Common name	USA geographic area	Site of injury
D. portola Ball	Florida, Louisiana, Texas	leaves
Graminella nigrifrons (Forbes) – blackfaced leafhopper	Florida, Texas	leaves
G. plana (DeLong)	Texas	leaves
G. sonora (Ball)	Texas	leaves
Homalodisca insolita (Walker)	Florida, Texas	leaves
Oncometopia lateralis F.	Louisiana	leaves
Cixiidae		
Myndus crudus Van Duzee – American palm cixiid	Florida	roots, leaves
Oliarus texanus Metcalf	Texas	leaves
Coccidae		
Pulvinaria elongata Newstead	all sugarcane-producing states	leaves
Cydnidae		
Cyrtomenus ciliatus (Palisot de Beauvois)	Florida	roots
Pangaeus bilineatus (Say)	Florida, Louisiana	roots
Sehirus cinctus (Palisot)	Louisiana	roots
Delphacidae		
Perkinsiella saccharicida Kirkaldy – sugarcane delphacid	all sugarcane-producing states	leaves
Saccharosydne saccharivora (Westwood)	Florida, Louisiana, Texas	leaves
Diaspididae		
Aspidiella sacchari (Cockerell)	Florida, Hawaii, Texas	stalks
Aspidiotus destructor Signoret	Florida, Hawaii	stalks
Diaspis bromeliae (Kerner) – pineapple scale	Florida, Hawaii	stalks
Duplachionaspis divergens (Green)	Florida in USA; cosmopolitan	stalks
Hemiberlesia cyanophylli (Signoret)	Florida, Hawaii	stalks
Odonaspis saccharicaulis (Zehntner)	Florida, Hawaii, Texas	stalks
Selenaspidus articulatus (Morgan)	Florida	stalks
Pseudococcidae		
Antonina graminis (Maskell) – Rhodesgrass mealybug	all sugarcane-producing states	stalks
Birendracoccus saccharifolii (Green)	Florida?	leaves
Chorizococcus rostellum (Lobdell)	Hawaii	stalks
Dysmicoccus boninsis (Kuwana) – gray sugarcane mealybug	all sugarcane-producing states	stalks
D. brevipes (Cockerell) – pineapple mealybug	Florida, Hawaii	roots/stalks

Sugarcane Pests and Their Management, Table 27 **Sugarcane arthropod pests, geographical area affected, and site of injury (Continued)**

Taxa scientific/Common name	USA geographic area	Site of injury
Pseudococcus longispinus (Targioni-Tozzetti) – longtailed mealybug	Hawaii	stalks
Saccharicoccus sacchari (Cockerell) – pink sugarcane mealybug	Florida, Hawaii, Texas	stalks
Tingidae		
Leptodictya tabida (Herrich-Schaeffer) – sugarcane lacebug	Florida, Hawaii, Texas	leaves
Thysanoptera		
Phlaeothripidae		
Haplothrips halophilus Hood	Louisiana	leaves
Thripidae		
Anaphothrips obscurus (Müller) – grass thrips	Hawaii	leaves
A. swezeyi Moulton – Hawaiian grass thrips	Hawaii	leaves
Arorathrips (= *Chirothrips*) *mexicanus* (Crawford)	Hawaii	leaves
A. (= Chirothrips) spiniceps (Hood)	Hawaii	leaves
Bregmatothrips venustus Hood	Louisiana	leaves
Chirothrips sacchari Moulton	Hawaii	leaves
Hercinothrips femoralis (Reuter) – banded greenhouse thrips	Florida, Hawaii	leaves
Thrips saccharoni Moulton	Hawaii	leaves
Coleoptera		
Alleculidae		
Lobopoda sp.	Florida	roots?
Buprestidae		
Aphanisticus cochinchinae seminulum Obenberger	Florida, Hawaii, Texas	leaves
Cerambycidae		
Prionus sp.	Florida	stalks?
Prosoplus bankii (F.)	Hawaii	stalks?
Chrysomelidae		
Chaetocnema ectypa Horn – desert corn flea beetle	Florida, Louisiana, Texas	roots, leaves
C. pulicaria Melsheimer	Florida, Louisiana	roots, leaves
Diabrotica spp.	Florida	roots, leaves
Curculionidae		
Diaprepes abbreviatus (L.) – Diaprepes root weevil	Florida, Texas	roots

Sugarcane Pests and Their Management, Table 27 Sugarcane arthropod pests, geographical area affected, and site of injury (Continued)

Taxa scientific/Common name	USA geographic area	Site of injury
Metamasius hemipterous sericeus (Olivier) – silky cane weevil	Florida	stalks
Pachnaeus litus (Germar) – southern blue-green citrus root weevil	Florida	roots
Rhabdoscelus obscurus (Boisduval) – New Guinea sugarcane weevil; sugarcane weevil borer	Hawaii	stalks
Sphenophorus cariosus (Olivier) – nutgrass billbug	Hawaii, Louisiana, Florida?, Texas?	roots
S. coesifrons Gyllenhal	Florida	roots
S. maidis Chittenden – maize billbug	Louisiana	roots
S. venatus vestitus Chittenden – hunting billbug	Florida, Louisiana	roots
Xyleborus kraatzi Eichhoff	Hawaii	stalks
Elateridae		
Aeolus dorsalis (Say)	Florida	buds, roots
Conoderus amplicollis (Gyllenhal) – gulf wireworm	Florida, Hawaii, Texas	buds, roots
C. exsul Sharp	Hawaii	buds, roots
C. falli Lane – southern potato wireworm	Florida	buds, roots
C. lividus (De Geer)	Florida, Louisiana, Texas	buds, roots
C. (= Aeolus) perversus Brown	Florida	buds, roots
C. rudis Brown	Florida	buds, roots
C. scissus (Schaeffer)	Florida	buds, roots
Glyphonyx bimarginatus Schaeffer	Florida	buds, roots
Ischiodontus sp	Florida	buds, roots
Melanotus communis (Gyllenhal) – corn wireworm	Florida	buds, roots
Neotrichophorus carolinensis (Schaeffer)	Florida	buds, roots
Orthostethus infuscatus (Germar)	Florida	buds, roots
Simodactylus cinnamomeus (Boisduval)	Hawaii	buds, roots
Nitidulidae		
Carpophilus humeralis (F.)	Florida	seed pieces
Scarabaeidae		
Cetoniinae		
Euphoria sepulcralis (F.)	Florida, Texas	roots
Dynastinae		
Cyclocephala borealis Arrow	listed as USA	roots
C. parallela (Casey)	Florida	roots
Dyscinetus morator (F.)	Florida, Texas	roots

Sugarcane Pests and Their Management, Table 27 **Sugarcane arthropod pests, geographical area affected, and site of injury (Continued)**

Taxa scientific/Common name	USA geographic area	Site of injury
Euetheola humilis rugiceps (LeConte) – sugarcane beetle	Louisiana	roots, buds
Tomarus (= Ligyrus) subtropicus (Blatchley)	Florida	roots
T. gibbosus (DeGeer)	Louisiana	roots
Melolonthinae		
Phyllophaga antennata (Smith)	listed as USA	roots
P. clypeata (Horn)	listed as USA	roots
P. congrua (LeConte)	listed as USA	roots
P. crassissima (Blanchard)	listed as USA	roots
P. latifrons (LeConte)	Louisiana, Florida	roots
Rutelinae		
Anomola marginata (F.)	Florida	roots
A. orientalis (Waterhouse)	Hawaii	roots
Tenebrionidae		
Eutochia lateralis Boheman	Hawaii	roots
Diptera		
Otitidae		
Euxesta stigmatias Loew – cornsilk fly	Florida	?
Lepidoptera		
Crambidae		
Diatraea crambidoides (Grote) – southern corn stalk borer	Florida, Louisiana, Texas	stalks
D. evanescens Dyar	Florida, Louisiana?	stalks
D. saccharalis (F.) – sugarcane borer	Florida, Louisiana, Texas	stalks
D. lineolata Walker	Texas	stalks
Eoreuma loftini (Dyar) – Mexican rice borer	Texas	stalks
Herpetogramma bipunctalis (F.) – southern beet webworm	Florida, Louisiana, Texas	leaves
Elachistidae		
Elachista saccharella (Busck)	Louisiana	leaves
Elachista (= Dicranoctetes) sp.	Florida	leaves
Noctuidae		
Agrotis crinigera (Butler)	Hawaii	leaves
A. dislocata (Walker)	Hawaii	leaves
A. ipsilon (Hufnagel) – black cutworm	all sugarcane-producing states	leaves, shoots

Sugarcane Pests and Their Management, Table 27 Sugarcane arthropod pests, geographical area affected, and site of injury (Continued)

Taxa scientific/Common name	USA geographic area	Site of injury
A. malefida Guenée – pale-sided cutworm	Florida, Louisiana, Texas	leaves, shoots
A. subterranea (F.) – granulated cutworm	Florida, Louisiana, Texas	leaves, shoots
Anicla infecta (Ochsenheimer) – green cutworm moth	Florida, Louisiana, Texas	leaves
Elaphria chalcedonia (Hübner)	Florida, Louisiana, Texas	leaves
E. nucicolora (Guenée)	Florida, Louisiana, Texas	leaves
Leucania latiuscula Herrich-Schaffer	Florida, Louisiana, Texas	leaves
L. scirpicola Guenée – scirpus wainscot	Florida, Louisiana, Texas	leaves
Meropleon cosmion Dyar	Florida, Louisiana, Texas	leaves
Mocis latipes (Guenée) – small mocis	Florida, Louisiana, Texas	leaves
Pseudaletia amblycasis (Meyrick)	Hawaii	leaves
P. pyrrhias (Meyrick)	Hawaii	leaves
P. unipuncta (Haworth) – armyworm	all sugarcane-producing states	leaves
Spodoptera dolichos (F.)	Florida (greenhouse)	leaves
S. frugiperda (J.E. Smith) – fall armyworm	Florida, Louisiana, Texas	leaves
S. eridania (Stoll) – southern armyworm	Florida, Louisiana, Texas	leaves
S. latifascia (Walker)	Florida (greenhouse)	leaves
Oecophoridae		
Autosticha pelodes (Meyrick)	Hawaii	leaves
Pyralidae		
Cryptoblabes aliena Swezey	Hawaii	stalks
Elasmopalpus lignosellus (Zeller) – lesser cornstalk borer	all sugarcane-producing states	tillers, shoots
Marasmia trapezalis (Guenée)	Florida	stalks
Tineidae		
Opogona apicalis Swezey	Hawaii	stalks, buds
O. aurisquamosa (Butler)	Hawaii	stalks, buds
O. omoscopa (Meyrick)	Hawaii	stalks, buds
O. purpuriella Swezey	Hawaii	stalks, buds
O. sacchari (Bojer) – banana moth	Florida, Hawaii	stalks, buds

diameter, and physical attributes of the interior part of the stalk are mentioned as possible resistant characters.

However, classical breeding for sugarcane improvement is labor intensive as well as time consuming, and is often limited by genetic complexity and low fertility. Unlike many other grasses, sugarcane tissue culture and transformation is, for the most part, genotype independent. Consequently, elite sugarcane cultivars can be genetically engineered for improved traits like insect resistance.

Sugarcane plants have been genetically engineered through the biolistic method of transformation (using a "gene gun" to insert genes into the tissue) using embryogenic callus as the target tissue derived from young plant tissue. Additionally, *Agrobacterium*-mediated transformation has been successful using meristematic sections and axillary buds of the sugarcane plant. A lectin-encoding gene (*Galanthus nivalis* agglutinin) from the snowdrop lily was used to transform sugarcane, and experimental results showed less feeding by larvae and fewer eggs placed on these plants by MRB and SCB. Partial resistance to SCB was also observed in transgenic sugarcane plants expressing genes encoding soybean proteinase inhibitors. However, the most common genes used for insect resistance in sugarcane have been modified *Bacillus thuringiensis* (Bt) endotoxin protein genes. Transgenic sugarcane plants expressing these Bt genes have displayed resistance to the LCB, SCB, and FAW.

References

Box HE (1953) List of sugar-cane insects – a synonymic catalogue of the sugar-cane insects and mites of the world, and of their insect parasites and predators, arranged systematically. Commonwealth Institute of Entomology, London, UK, 101 pp

Hall DG (1988) Insects and mites associated with sugarcane in Florida. Fla Entomol 71:138–150

Ingram JW, Bynum EK, Mathes R, Haley WE, Charpentier LJ (1951) Pests of sugarcane and their control. USDA Circular 878, 38 pp

Long WH, Hensley SD (1972) Insect pests of sugar cane. Ann Rev Entomol 17:149–176

Williams JR, Metcalfe JR, Mungomery RW, Mathes R (eds) (1969) Pests of sugar cane. Elsevier, Amsterdam, The Netherlands

Sugar-Feeding in Blood-Feeding Flies

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In the order Diptera, there are several groups of haematophagous (blood-feeding) flies that also feed on carbohydrates. Many a hiker can attest to the fact that when you get swarmed by black flies and accidentally crush a few between your teeth, the black flies taste quite sweet. This is due to the presence of sugars within the crop, the sugar-storage organ.

In contrast to some blood-sucking flies (e.g., stable fly, family Muscidae; tsetse fly, family Glossinidae), in which both sexes feed on blood, it is only the females that blood-feed in the following dipteran families: Simuliidae (black flies); Culicidae (mosquitoes); Tabanidae (deer flies, horse flies); and Ceratopogonidae (biting midges). Depending on the species, sugars are required by both sexes for increased longevity and/or flight. Females benefit from the blood meal because they use the extra protein for egg development; however, in certain species fecundity is increased following sugar feeding.

Sugar Meal Sources

The major sources of sugar meals are floral nectar, extrafloral nectaries, and hemipteran honeydew; minor sources include tree sap, rotting or damaged fruit, and leaf wounds. Floral nectar contains three major sugars, namely fructose, glucose and sucrose. A few floral nectars also contain maltose, melebiose and/or raffinose. Most studies on the sugar-feeding biology of biting flies have used the cold-anthrone test to detect fructose and fructose-containing sugars, under the assumption that most biting flies use floral nectar as their main source of sugar. Recently, several studies have employed other techniques such as gas chromatography, high performance liquid chromatography and thin layer chromatography in which the trisaccharide melezitose (and in some instances, the trisaccharide erlose or the tetrasaccharide stachyose) is used as an indicator sugar to show when flies have fed on honeydew. Using these techniques, the incidence of honeydew feeding in biting Diptera has been reported to be from approximately 5–55% in mosquitoes (with most species <15%), 0–5% in biting midges, 20–50% in black flies (with an average of 35%), 45–85% in deer flies (with an average of 65%) and 50% in horse flies.

Black Flies and Sugar Sources

A long-held view has been that black flies preferentially take nectar from plants with small white, yellow or green flowers. There have been several records of black flies feeding on ivy and willow. Folklore has it that on the Canadian Shield black flies are a major pollinator of lowbush blueberries (*Vaccinium angustifolium* and *V. myrtilloides*), but it has been shown experimentally that although they will enter the flowers and feed avidly on blueberry nectar, black flies do not assist in pollination. The exact plants on which black flies nectar-feed can sometimes be determined by examining the crop contents for pollen grains and identifying the pollen microscopically. They have been observed feeding directly on the honeydew produced by adelgids found on tamarack.

Mosquitoes and Sugar Sources

Depending on the species, early spring *Aedes* mosquitoes have been recorded nectar-feeding on Canada plum, pin cherry and a variety of woodland plants. Even in the high Arctic, mosquitoes have been observed feeding on floral nectar from the flower *Dryas integrifolia*. A relatively high incidence of crops tested positive for honeydew sugars in *Anopheles* mosquitoes (about 55%) but other genera seem less inclined to feed on hemipteran honeydew (Fig. 154).

Sugar-Feeding in Blood-Feeding Flies, Figure 154 Mosquito feeding on nectar from plant nectary. (Photo by Doug Burkett, University of Florida.)

Tabanids and Sugar Sources

There have been only a few observations of tabanids feeding on floral nectar, whereas several researchers have observed tabanid flies feeding on aphid honeydew (e.g., on the leaves of marsh elder, *Iva frutescens*). For salt marsh horse flies it has even been suggested that honeydew represents a more important source of sugar than floral nectar.

Role and Timing of Sugar-Feeding

The role of the sugars in the biology of biting flies varies according to the species. For example, it is known that a mosquito species that feeds almost exclusively on human blood, *Aedes aegypti*, does not feed often on sugars in the wild although it will nectar-feed when flowering plants are abundant. In fact, in *Aedes aegypti*, feeding on sugars results in a decrease in longevity and fecundity.

Most other biting Diptera (including most mosquitoes) are thought to sugar-feed soon after emergence for it is from sugar-meals that energy from general maintenance and for flight is acquired. Most haematophagous Diptera will also sugar-feed before mating, host-seeking and oviposition. As a result, it is generally thought that sugar-feeding occurs more often than blood-feeding.

Almost all mosquitoes, black flies, biting midges and tabanids survive significantly longer in captivity when provided with sugar-meals (such as 10% sucrose) as opposed to water alone.

The composition of the sugar-meal can affect fly longevity as well as other traits such as flight distance and duration, parasite transmission and/or egg development. The optimal sugar-feeding regime (i.e., source and frequency of sugar-feeding) for a given species and gender will depend on a number of factors including the amount of larval fat body reserves carried forward into the adult stage, the amount of flying to be done, the parasite load, and the parous state (for females).

Following sugar-feeding and digestion, circulating monosaccharides are removed from the hemolymph, assembled into large macromolecules of glycogen and stored in the fat bodies. When sugars are required, there is hydrolysis of individual glucose molecules from the glycogen reserves. The non-reducing disaccharide, trehalose, is then synthesized and released into the hemolymph. Subsequently, when flight energy is required, the trehalose is transported to the flight muscles (where it is broken back down into monosaccharides which fuel the actual flight).

In the females of some *Culex* mosquitoes lipids accumulate in the fat body after sugar-feeding. This is correlated indirectly with a behavioral switch to host-seeking (i.e., becoming attracted to blood-host odors over floral odors). Furthermore, it has been shown that the switch to host-seeking mode following a sugar-meal is mediated by juvenile hormone (JH) activity (caused by follicular development that, itself, can be triggered by a sugar-meal). Diapausing females in the genus *Culex* sugar-feed more frequently and for longer periods than do non-diapausing mosquitoes in order to build up adequate fat reserves. Nocturnal sugar-feeding behavior is also greater in diapausing vs. non-diapausing mosquitoes.

Historical Considerations

Hemiptera appear in the fossil record in the Permian, Diptera in the Triassic and flowering plants (angiosperms) in the Cretaceous. There are three ancestral traits among Diptera that facilitate honeydew usage. First, the presence of a pseudotracheate labellum allows flies to secrete saliva onto dried sugars and then suck up the liquefied sugars. This type of labellum seals off the dissolved sugars from the air, thereby reducing evaporative water loss. Second, the presence of tarsal sensilla sensitive to sugars allows the flies to "taste" sugars with their feet. This is convenient for testing the surface of leaves for honeydew (but less convenient for tasting sugars within floral nectaries). Third, flies tend to be attracted to glossy spots on leaf surfaces; this helps foraging flies flying over vegetation to locate honeydew droplets.

It is not surprising, therefore, that black flies (which appeared in the Jurassic) are capable of using honeydew sugars; effectively, nectar-feeding was a more recent development in this family. Interestingly, tabanids appeared in the fossil record at about the same time as the flowering plants and apparently maintained an ancestral preference for honeydew over floral nectar. Mosquitoes, in contrast, did not appear in the fossil record until the late Cretaceous (Senonian) or the Paleocene of the Tertiary, long after the angiosperm radiation had begun; this probably explains why mosquitoes seem to preferentially exploit nectar sources. In addition, mosquitoes have olfactory chemosensilla on their palps which respond to nectar odors and their long mouthparts are well adapted for probing flowers for nectar.

References

Clements AN (1992) The biology of mosquitoes, vol 1: Development, nutrition and reproduction. Chapman & Hall, London, UK, 509 pp
Crosskey RW (1990) The natural history of blackflies. Wiley, London, UK, 711 pp
Foster WA (1995) Mosquito sugar feeding and reproductive energetics. Ann Rev Entomol 40:443–473

Sulcate

Used to describe a surface that is furrowed or grooved.

Sulcus (pl., sulci)

A groove or furrow formed by the infolding of the body wall.

Sulfurs

Some members of the family Pieridae (order Lepidoptera).

► Yellow-White Butterflies
► Butterflies and Moths

Summit Disease

A disease of grasshoppers caused by the fungus *Entomphaga grylli*. Not all grasshoppers are equally susceptible, and different pathotypes of the fungus are known. Those that are infected typically die at the top of plants (the basis for the name), and are found clinging to the substrate as if alive. In arid environments, the disease is associated with the margins of water bodies such as the vegetation surrounding ponds, presumably because the humidity is higher, favoring the sporulation of this fungus.

► Diseases of Grasshoppers and Locusts
► Fungal Pathogens of Insects
► Entomophthorales

Sun Moths (Lepidoptera: Heliodinidae)

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Sun moths, family Heliodinidae, are a small family of 56 species, mostly Neotropical (31 sp.); actual fauna probably exceeds 100 species. The family is part of the superfamily Yponomeutoidea in the section Tineina, subsection Tineina, of the division Ditrysia. Adults small (7–15 mm wingspan), with head smooth-scaled; haustellum naked; labial palpi porrect; maxillary palpi minute, 1-segmented. Wings elongated (Fig. 155), with lanceolate hindwings with long fringes. Maculation usually brilliantly colored, with metallic-iridescent markings and sometimes raised scale tufts. Adults are diurnal. Larvae are mostly leaf skeletonizers, but some are borers in fruit racemes. Several plant families are used as hosts, particularly Chenopodiaceae, Nyctaginaceae, Portulacaceae, and Scrophulariaceae, among others.

Sun Moths (Lepidoptera: Heliodinidae), Figure 155 Example of sun moths (Heliodinidae), *Heliodines galapogoensis* Heppner & Landry from Galapagos Islands.

References

Emmet AM (1985) Heliodinidae. In: Heath J, Emmet AM (eds) The moths and butterflies of Great Britain and Ireland, vol 2. Harley Books, Colchester, pp 410–411, pl 11

Falkovitsh MI (1981) Heliodinidae. In identification keys to insects of European Russia 4. Lepidoptera, vol 2. Academie Nauk, St. Petersburg [in Russian], pp 529–531

Le Marchand S (1937) Les Heliodinidae. Amateur de Papillon 8:217–221

Powell JA (1991) A review of Lithariapteryx (Heliodinidae), with description of an elegant new species from coastal sand dunes in California. J Lepid Soc 45:89–104

Wester C (1956) Comparative bionomics of two species of Heliodines on *Mirabilis* (Lepidoptera, Heliodinidae). Proc Entomol Soc Washington 58:43–46

Sunn Pest

This term applies to several scutellerid pests of wheat (Hemiptera: Scutelleridae). The species *Eurygaster integriceps* is most important.

► Wheat Pests and Their Management

Supergene

Mutually advantageous genes clustered together on the same chromosome by selection for this beneficial association. Separation of the genes is so infrequent that they function as if they were a single gene.

Supernumerary

From a developmental perspective, this is the occurrence of extra instars (more than the "normal") in immature stages of insects. The presence of additional juvenile hormone apparently stimulates this effect, although it is correlated with environmental stress. From a morphological perspective, this refers to the occurrence of extra or added structures on an insect.

Superorder

Closely related orders, sharing common traits and thought to have evolved from one another or from a common ancestor. This level of classification is not often used, but is useful in understanding phylogeny.

► Classification

Superorganism Concept

In ecology, the concept that communities consist of some species that are tightly linked together now and in their evolutionary history. In social insects, the concept that the different castes perform functions equivalent to the physiological properties of a single organism.

Superparasitism

When more parasites (parasitoids) are developing on or in a host insect than can survive to maturity.

Supersedure

The replacement of an old or sickly queen by a new one reared by the workers.

Supplementary Reproductive

A queen or male termite that takes over the reproductive functions of the colony after removal of the primary reproductive.

Supraspiracular

The area immediately above the spiracles.

Surfactant

A pesticide adjuvant that affects surface tension of the pesticide, and enhances penetration and retention. An abbreviated form of "surface active agent."

► Insecticides

► Insecticide Formulations

Survivorship

The probability of a newly born individual surviving to a particular age, usually to maturity or reproduction.

Survivorship Curve

A plot of the declining numbers of a cohort or population as the individuals die over time.

Survivorship is usually expressed as a percentage of the initial population.

Suture

A seam or impressed line that indicates the juncture of two body plates.

Swallowtail Butterflies (Lepidoptera: Papilionidae)

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Swallowtail butterflies, family Papilionidae (including birdwings, parnassians, and kites), total about 589 species worldwide, with about 250 species being Indo-Australian. Three subfamilies are recognized: Baroniinae (a single relict species in Mexico), Parnassiinae, and Papilioninae. The family is in the superfamily Papilionoidea (series Papilioniformes), in the section Cossina, subsection Bombycina, of the division Ditrysia. Hundreds of local races have been given subspecies names, and form names without validity, for European *Parnassius* (Parnassiinae). Adults large (35–285 mm wingspan); head sometimes roughened (Parnassiinae); antennae mostly with elongated clubs (more compact in Baroniinae and Parnassiinae). Wings triangular (Fig. 156) and mostly with relatively acute apexes (rounded in Baroniinae and most Parnassiinae; hindwings usually with tails (some species tailless, including Baroniinae and most Parnassiinae); body mostly robust. Maculation very varied, with many color combinations and sometimes with iridescence, but Parnassiinae mostly pale (even hyaline) with various spotting on both fore- and hindwings. Adults diurnal; usually slow and gliding fliers. Larvae leaf feeders; with an osmeterium defensive gland behind head. Host plants include many plant groups, especially Crassulaceae, Lauraceae, Leguminosae, Rutaceae,

Swallowtail Butterflies (Lepidoptera: Papilionidae), Figure 156 Example of swallowtail butterflies (Papilionidae), *Byasa polyeuctes* (Doubleday) from India.

and Saxifragaceae, among others. Birdwings use various Aristolochiaceae vines. Some economic species are known, mainly citrus feeders.

References

D'Abrera B (1975) Birdwing butterflies of the world. Hill House, Melbourne, 216 pp
Igarashi S (1979) Papilionidae and their early stages, 2 vols. Kodansha, Tokyo
Rothschild W (1895) A revision of the Papilios of the Eastern Hemisphere, exclusive of Africa. Novitates Zoologicae 2:167–463, pl 6
Scriber JM, Tsubaki Y, Lederhouse RL (eds) (1995) Swallowtail butterflies: their ecology and evolutionary biology. Scientific Publishing, Gainesville, FL, 459 pp (32 pl)
Seitz A, Stichel H (1906–1931) Familie: Papilionidae. In: Die Gross-Schmetter linge der Erde, 1:7–38, pl. 1–16 (1906); 1(suppl): 7–91, 327–332, pl 1–6 (1929–31); 5:11–51, 1012–1014, pl 1–17 (1907–24); 9: 11–118, pl 1–50 (1908–1909); 13:11–28, pl 1–9 (1908–10). A. Kernen, Stuttgart
Tsukuda E, Nishiyama, Y (1980)Butterflies of the South East Asian islands. I. Papilionidae. Plapac, Tokyo, 459 pp, 166 pl
Tyler HA, Brown KS Jr, Wilson KA (1994) Swallowtail butterflies of the Americas. A study in biological dynamics, ecological diversity, biosystematics and conservation. Scientific Publishers, Gainesville, FL, 376 pp, 157 pl
Weiss J-C (1992–1994) The Parnassiinae of the world. Venette: Sci Nat 3

Swallowtail Moths (Lepidoptera: Uraniidae)

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Swallowtail moths, family Uraniidae, comprise about 120 species from all tropical regions, mostly Indo-Australian (85 sp.); one species strays into the United States-Mexican border region (mainly in Texas). Two subfamilies are known: Microniinae, for the smaller mostly white species with very short tails (all Old World), and Uraniinae for the more well known larger and long-tailed species. The family is in the superfamily Uranioidea, in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults medium to large (31–160 mm), with head somewhat roughened; haustellum naked; labial palpi often long with short apical segment; maxillary palpi small, 1-segmented; antennae often serrate and thickened. Wings triangular, with acute forewings (Fig. 157) and mostly tailed hindwings (margins of hindwings usually with some emarginations). Maculation usually dark browns to black, with green or pale striae, but some smaller species mostly white with very short tails on hindwings; one colorful African species (*Chrysiridia*) has three tails on each hindwing. Adults nocturnal or diurnal, with some of the larger diurnal species known to migrate (*Urania*). Larvae are leaf feeders. Host plants are known in Asclepiadaceae and Myrtaceae for the larvae in Microniinae, and Euphorbiaceae for the larvae in Uraniinae.

Swallowtail Moths (Lepidoptera: Uraniidae), Figure 157 Example of swallowtail moths (Uraniidae), *Urania leilus* (Linnaeus) from South America.

References

Dalla Torre KW von (1924) Uraniidae. In: Lepidopterorum catalogus, vol 30 [part]. W. Junk, Berlin, pp 1–57

Holloway JD (1998)Family Uraniidae. In: The moths of Borneo, vol 8. Malayan Nature Society (Malayan Nature Journal, 52), Kuala Lumpur, Malaysia, pp 77–78, 82–92, pl 5–6

Regteren Altena CO van (1953) A revision of the genus *Nyctalemon* Dalman (Lepidoptera, Uraniidae) with notes on the biology, distribution, and evolution of its species. Zool Verhandlingen 19:1–57, 4 pl

Seitz A (ed) (1912–33) Familie: Uraniidae. In: Die Gross-Schmetterlinge der Erde. 2. Die palaearktischen Spinner und Schwärmer, 2:275–276, pl 22, 48 (1912); 2(suppl):171–172, pl 15 (1933); 6:829–837, pl 67, 138 (1930); 10:93–103, pl 69–72 (1929); 14:387–394, pl 67, 48 (1928). A. Kernen, Stuttgart

Smith NG (1992) Reproductive behaviour and ecology of *Urania* (Lepidoptera: Uraniidae) moths and their larval food plants, *Omphalea* spp. (Euphorbiaceae). In: Quintero D, Aiello A (eds) Insects of Panama and Mesoamerica: selected studies. Oxford University Press, Oxford, pp 576–593

Swammerdam, Jan

This Dutch naturalist played an important role in the development of biology during the 1660s and 1670s. This was an important period in the development of science because it marked the re-ascendency (dormant since the Greek scholars) of scientific observation and experimentation, and the consequent diminution of divine interpretation. Swammerdam was born in Amsterdam on February 12, 1637; his father was an affluent apothecary who, though frustrated by Jan's lack of a "proper" vocation (medicine), apparently provided support to Jan throughout his life. Indeed, the elder Swammerdam is likely responsible for the younger Swammerdam's interest in insects, as he had a notable insect collection. Jan enrolled in the medical program at the University of Leiden at the age of 24 and received his M.D. in 1667, though there is no evidence that he ever practiced medicine. Jan Swammerdam made several important anatomical discoveries, including the presence of valves in lymph ducts, respiration and nerve-muscle function; the presence of human ovarian follicles; and the mechanism of penile erection. In 1669 he published a book: "Historia Generalis Insectorum," in which he put forth a revolutionary classification of insects based on their mode of development. His work supported that of Francesco Redi, who maintained (contrary to popular belief) that insects were not the product of spontaneous generation, but originated from eggs deposited by females. Stimulated by the work of the physiologist Marcello Malpighi, in 1670 Swammerdam began to study insects under a microscope. In this effort, he greatly advanced our knowledge of insect anatomy, particularly that of the honey bee. Unfortunately, Swammerdam fell under the influence of the religious mystic Antoinette Bourignon, and abandoned his scientific activities for several years, only to become disillusioned with Bourignon and return to science in 1676. The result of his latter work, particularly his magnificent drawings, were published much later by the Dutch physician Herman Boerhaave in 1737–1738 as "Bibliae Naturae," revealing a wealth of detail about insects and insect anatomy. Swammerdam died prematurely at the age of 43 in Amsterdam on February 17, 1680.

References

Cobb M (2002) Eric Weisstein's world of biography. Available at http://scienceworld.wolfram.com/biography/Swammerdam.html. Accessed Aug 2002

Pellett KL (1929) Lives of famous beekeepers, John Swammerdam. Am Bee J 69:130–131

Westfall RS (2002) Catalog of the scientific community. Available at http://es.rice.edu/ES/humsoc/Galileo/Catalog/Files/swamrdam.html. Accessed Aug 2002

Swarming

The exodus of the reproductive (or reproductives) from the original nest, with the intent to form a new colony. In bees, this is normally accomplished by a single female accompanied by a large number of workers, whereas in ants and termites, usually large numbers of reproductives disperse but new colonies are founded by only a pair of individuals.

Sweetpotato and Silverleaf Whiteflies (Hemiptera: Aleyrodidae)

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The whitefly (Hemiptera: Aleyrodidae) species *Bemisia tabaci* (sweetpotato whitefly or cotton whitefly) was described by Gennadius infesting tobacco in Greece in 1889. In the mid 1980s, following outbreaks of a similar, but not identical, insect (initially called *B. tabaci* biotype B) was recognized and in 1994, Bellows and Perring described it as *B. argentifolii* (silverleaf whitefly). To date, the validity of the "B" biotype as a separate species is still disputed. In addition, about ten biotypes have since been recognized using molecular and biochemical methods. They differ in host plant relationships and their capacities to transmit plant disorders and/or viral diseases. In the present discussion, the whole *B. tabaci* complex will be treated under the name *B. tabaci*.

Following its description in 1889, *B. tabaci* was recorded from the United States in 1894, and shortly thereafter in several African and Asian countries. It was considered to have originated in India or Pakistan until recently, when molecular studies pointed to an African origin. Moreover, some of the different biotypes probably arose locally; e.g., the "B" and the "Q" biotypes originated in the Mediterranean basin, E is from Benin, H from India and K from Pakistan. *Bemisia tabaci* was first reported as a pest from India, The Sudan, and several mideastern countries. In the United States, damage was first noted when cotton leaf crumple virus was found to be transmitted by *B. tabaci* in 1954. During the last 20 years, with the spread of the B biotype, *B. tabaci* became a cosmopolitan pest. It attacks vegetable, ornamental and field crops in tropical and subtropical regions, and greenhouse crops in colder climates.

Plant Injury

Bemisia tabaci damages plants through direct removal of plant assimilates, honeydew contamination, virus transmission and the induction of physiological plant disorders. Direct damage may range from slight plant injury to plant death. The honeydew of both nymphs and adults, and the sooty mold fungi that develop on the honeydew, contaminate plant leaf surfaces, thereby reducing their photosynthetic efficiency. The insects also contaminate the produce, reducing its market value. The most severe contamination-related economic damage is caused to cotton, where stickiness may sharply reduce lint value. The transmission of more than 70 different kinds of viral plant diseases by *B. tabaci* is a major agricultural problem. Most viruses belong to the Begomoviruses (Geminiviridae), but recently Carlaviruses, Closteroviruses, Criniviruses, Luteoviruses, Nepoviruses and Potyviruses also were recorded. Some Begomoviruses, such as the Tomato Yellow Leaf Curl Virus (TYLCV) and the East African Cassava Mosaic Virus (EACMV), drastically curtail crop production and raise great difficulty in devising an integrated or biological control program for the pest. Physiological plant disorders have mainly been associated with type B of the pest The best known disorder is leaf silvering of squash, in which the plant cuticle separates from the underlying cells giving the leaf a silvery appearance, and providing a basis for its new name (silverleaf whitefly or *B. argentifolii*). Another disorder, "uneven tomato ripening" appears when heavy whitefly populations are present during tomato ripening season.

Biology

Like all whiteflies, the *B. tabaci* female inserts its eggs into the leaf tissue by means of a pedicel. On most plants, development occurs on the underside of the leaves. They hatch into crawlers that settle close to the point of hatching, insert their mouth parts into the phloem, molt into the second instar, and loose their ability to walk on the leaf. The second to fourth instars are spent in the same location, with the developing nymphs growing from ca. 0.2–0.8 mm in length depending upon growing conditions and plant species. The nymphs may have a glabrous or spiny dorsum, in direct correspondence to the degree of pubescence of the leaf upon which they develop. The nymphs feed by inserting their 100–300 μm long mouthparts (stylets) into medium to small phloem tubes and imbibing the exuded fluid. The fourth instar includes a developing stage during which it continues to grow, and a later sessile stage that can be distinguished through appearance of larger, red eye spots. This sessile stage corresponds to the pupal stage of the Holometabola when larvae undergo metamorphosis to adults. Therefore, the red-eyed stage of the fourth instar is often referred to as a "pupa." The adults emerge through the dorsum of the "pupal" case, leaving a T-shaped split behind. The body of the emerging adults is covered with wax and is completely white. Both sexes are winged, and their body is about 12 mm long, with males somewhat shorter than the females.

Bemisia tabaci is arrhenotokous, having haploid males and diploid females. Their longevity, fecundity and developmental duration may vary greatly depending the temperature, the host plant and the whitefly biotype. Typically, females live 20–30 days in outdoor conditions during which they often lay 50–150 eggs per female. However, the number of eggs may vary, and as many as 500 eggs per female have been recorded. Developmental duration from egg to adult ranges between 2 weeks in the summer and over 2 months in the winter, in subtropical and temperate regions.

Emerging adults may stay on the leaf of emergence, mate there and lay their eggs near the point of emergence. Often, however, they migrate to the top of the canopy where they settle on younger leaves of the same or of neighboring plants. In addition to trivial, short-distance flight, long distance migration (up to 7 km) has been recorded. Individuals that migrate have somewhat different body proportions, a smaller egg load and less investment in vitellogenins than the trivial flyers.

Host Range

The full host plant range of *B. tabaci* is probably not known. Recent reports record over 500 different plant species with some reports reaching as many as 900 hosts. Given the ease at which this pest adopts new host plants, it is useful to consider any plant, especially of the dicotyledons, as a potential host, rather than to adhere to a fixed host plant list. Host plant finding is a random process until the plant itself is reached and selection takes place following a short probing. *B. tabaci* interacts with plant physiology, and plant nutrition, including nitrogen levels, influences the insect's developmental success. Feeding by *B. tabaci* can change the source-sink relationships in young melon plants, redirecting the flow of amino acids and thus enriching its feeding sites. Induced plant resistance, in which previously infected plants are relatively less suitable for insect growth than unifested plants, does not seem to affect *B. tabaci*, thus differing from other phytophagous insects such as the leaf miner *Liriomyza trifolii* or from several noctuid larvae.

Bemisia tabaci adults produce several compounds that apparently render them better adapted to the high summer temperatures in which they live and to the variation in osmotic pressures they may experience while feeding on a wide variety of plants. In addition to the presence of heat-shock proteins, which are produced in response to short-term heat stress, diurnal increases in environmental temperature induce *B. tabaci* adults to accumulate a high level of sorbitol (15–27-fold increase to ca. 0.5 M) in their body fluids which apparently protect the insect's proteins from heat damage. The presence of the recently discovered \ isobemisiose in the adult's body fluids, and its absence from the excreted honeydew, have led to the conclusion that the creation of this trisaccharide and/or it decomposition into smaller moieties facilitates adjustment of the osmotic pressure in the hemolymph, enabling the insect to withstand the relatively wide fluctuations in sugar concentration of the imbibed phloem.

Management

Because it is a very serious pest of both greenhouse and outdoor field crops, this whitefly is often treated with insecticides. This brought about widespread insecticide resistance that ranges from five to tenfold, to over 1000-fold, to both conventional materials such as organophosphates and pyrethroids, and to the newer insect growth regulators (IGRs) such as buprofezin and pyriproxyfen. IPM programs, including the insecticide resistance management (IRM) strategies recently established in Israel and the southwestern USA, depend on alternating key insecticides and limiting the numbers of yearly applications of IGRs, thus reducing the buildup of resistance. The use of insect pollinators such as bumblebees in tomatoes and in peppers, and the high incidence of resistance, brought about a widespread search for other control solutions. These include plant varieties that are resistant to the transmitted viruses or to the whitefly, the use of cultural methods such as enclosing the crop in 50-mesh screenhouses, the use of UV absorbent sheets plastic (that apparently affect the insect's orientation) and screens in greenhouses and the utilization of natural enemies: parasitoids, predators and fungal diseases. Many of the natural enemies appear spontaneously in the field crops, but may not do so early enough or in large enough numbers to control the pest by themselves. Therefore, their augmentation through timely releases in concert with utilization of other control measures, are often recommended.

Natural Enemies

The principal species of *B. tabaci* parasitoids belong to the genera *Eretmocerus* and *Encarsia*, whereas the predators may belong to numerous families and vary greatly according to the geographic location. In recent years, predators that invaded Spanish greenhouses in the spring, mainly Miridae and Anthocoridae, were found to be effective and are artificially reared and sold as control in agents in addition to the parasitoids. The use of fungal diseases to control *B. tabaci* is not widespread, mainly due to their cost and their lack of efficacy under low humidity conditions.

Organizations, Literature and Web Sites

A *Bemisia* website is available: http://rsru2.tamu.edu/BIRU/sweetpot.html. It directs readers to the various United States-based agencies that work and publish on this insect. In addition several international organizations are devoted to the study and application of *Bemisia* control. The main ones are:

European Whitefly Studies Network (EWSN) at http://www.jic.bbsrc.ac.uk/hosting/eu/ewsn/What.html

Sustainable Integrated Management of Whiteflies as Pests and Vectors of Plant Viruses in the Tropics, an SP-IPM Task Force led by CIAT at http://www.cigar.org/spipm/tf/wgv.html

Action Network for Whitefly and Geminivirus Management in Ibero America and the Caribbean, at http://www.catie.ac.cr/moscablanca

The quarterly newsletter *Mosca Blanca al Dïa* (*Whitefly Update*), which has been published since 1993, is included in this site.

In addition, over 300 publications about *B. tabaci* appear each year, listed by Dr. S. Naranjo, T. Henneberry and colleagues (Western Cotton Research Laboratory of the USDA, Phoenix, AZ) at http://www.wcrl.ars.usda.gov

Until the end of 2000 a *Bemisia Newsletter* was published and can be obtained at http://207.43.217.12/biru/BEMISIA13.htm

From 2001 on, it has been united with the EWSN newsletter that appears about every 3 months since 1998 and can be seen at http://www.jic.bbsrc.ac.uk/hosting/eu/ewsn/EWSN_ News04.htm

► Whiteflies (Hemiptera: Aleyrodidae)

References

Ohnesorge B, Gerling D (1986) *Bemisia tabaci*-ecology and control. Agric Ecosyst Environ 17:1–152 (Special issue)

Gerling D, Mayer RT (1996) *Bemisia* 1995: taxonomy, biology, damage, control and management. Intercept Ltd, Andover, UK, 702 pp

Naranjo SE, Oliveira MRV, Ellsworth PC, Fernandes OA (eds) (2001) Challenges and opportunities for pest management of *Bemisia tabaci* in the new century. Crop Protect 20:707–869 (Special issue)

Sweetpotato Flea Beetle, *Chaetocnema confinis* (Coleoptera: Chrysomelidae: Alticinae)

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Chaetocnema (*Tlanoma*) *confinis* Crotch, 1873 is a very small (1.4–1.8 mm) and light species.

Although thought to have originated in North America (USA), it has become ubiquitous in the tropics of the Old and New World. It is becoming the most widely spread species of leaf-beetle. It has two known synonyms: *C. flavicornis* J. LeConte and *C. etiennei* Jolivet. *Chaetocnema perplexa* Blake from Central America is probably also a junior synonym.

Morphology

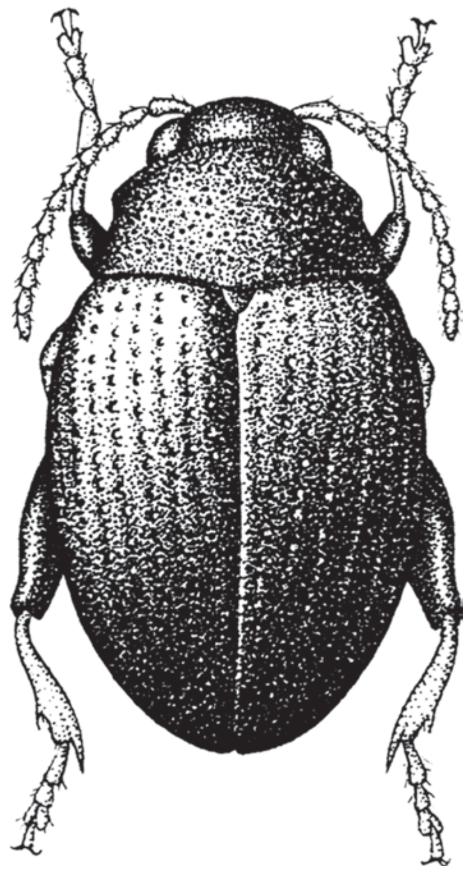
Chaetocnema confinis is a very small species; even the female is <2 mm. The adult is black to dark bronze, moderately glossy, with the antennae pale brown, the ventral surface black to dark brown, the femora brown to dark brown, the tibiae brown to pale brown, the tarsi pale brown. The striae on the elytra are parallel and the punctures moderate. The punctures are deep on the pronotum (Fig. 158).

The male has the fore and middle tarsus with the first segment somewhat enlarged. The aedeagus relatively small and sinuate. *Chaetocnema perplexa* Blake seems to differ by only a small variation of the shape of the aedeagus. The eggs are deposited in small groups and do not differ from those of related species (0.8 × 0.2 mm). The larvae are eruciform, straight, cylindrical, legged and measure 6 mm at the final stage. They live on plant roots.

Biology

Normally, *C. confinis* larvae feed inside Convolvulaceae roots, but they also attack the collar at the limit between stem and root. Long narrow grooves are eaten in the leaves, especially on the upper surface along the veins, during May and early June in North America, and throughout the year in the tropics. When these channels are numerous, the leaf may wilt. In the tropics there are many generations per year and no winter diapause. Otherwise in the US the species is univoltine.

In the US, *C. confinis* overwinters as adult under trash and various sheltered places. When they come out of hibernation, adults attack the plants when they are set out from seedbeds. By the end of June, they leave the sweet potatoes, migrating to bindweed where they lay their eggs and die. The larvae hatch after 3 weeks incubation. The new generation of beetles will feed and enter diapause in the fall. In the US and Canada, both sexes are present. In the Old World tropics only thelytokous parthenogenetic females are present, and so far as is known this is the condition in Central and South America.



Sweetpotato Flea Beetle, *Chaetocnema confinis* (Coleoptera: Chrysomelidae: Alticinae), Figure 158 ***Chaetocnema confinis*** **Crotch.**

Distribution

Chaetocnoma confinis originated in the US and Canada where both sexes are present. The beetle walks, flies and jump easily. Its recent dispersal in Africa and Asia-Pacific is probably due to typhoons and hurricanes because the beetle is light, small and winged. The first specimen was discovered on *Ipomoea aquatica*, a vegetable grown in Reunion, in 1976. It was then described under the name of *C. etiennei* Jolivet and 10 years later M. L. Cox synonymized it with *C. confinis*. Having only females in the tropics makes identification rather difficult.

Then the beetle invaded Madagascar, Mauritius and spread over most of tropical and southern Africa. *C. confinis* is also known from Brazil and Galapagos, Central America, Oceania (Palau), New Caledonia, Asia (India, Vietnam, Thailand, Ryukyu islands, etc.). At the speed that it spreads, New Guinea, Indonesia and Australia are the next targets. It is very probable that the species is already in New Guinea and several Indonesian islands. Probably it will soon cover all the tropical lands of Indian Ocean and Pacific.

Food Plants

The beetle feeds on Convolvulaceae. It feeds on *Convolvulus arvensis* (bindweed) in the US and Canada, but it has adapted to many other Convolvulaceae: sweet potato, *Ipomoea aquatica*, *I. pandurata*, *Calystegia sepium*, *Pharbitis purpurea*, *P. cathartica*, etc.

The beetle has become secondarily polyphagous, and adapted mostly in North America to corn (*Zea mays*), sugarbeet, tomato, and many other crops and weeds. In the tropics, so far it remains a major pest of sweet potato and related plants.

Conclusion

Few parasites have been recorded on this beetle and related species: fungi (Laboulbeniales, *Beauveria*), nematodes (*Howardula*), bacteria (*Xanthomonas*) and one parasitoid (Ichneumonidae).

Except in the US, where the beetle can become a serious pest on various crops, sweet potato seems to be the only host in the tropics. Several other *Chaetocnema* species and other alticines are also parthenogenetic and that seems to help in the expansion of the species. *Chaetocnoma confinis* is invading the whole of the tropics, mainland and islands together, and is becoming the most ubiquitous chrysomelid. Exchanges between Europe and the US have been common in the past (Colorado Potato Beetle, *Plagiodera* and many others) but only due to passive importations. This time the beetle seems to have dispersed by wind. Strict quarantine measures are certainly necessary in places like Australia when importing sweet potatoes, but aerial dispersion is very probable in the near future.

References

Biondi M (2002) Checklist of Afrotropical species of the genus *Chaetocnema* Stephens (Col. Chrys.: Alticinae): synonymies and geographical distribution. Afr Entomol10:265–284

Cox ML (1996) Parthenogenesis in the Chrysomeloidea. In: Jolivet P, Cox ML (eds) Chrysomelidae biology, vol 3: General studies. SPB Academic Publishing, Amsterdam, The Netherlands, pp 133–151

Jolivet P (1979) Réflexions sur l'écologie, l'origine et la distribution des chrysomélides (Col.) des îles Mascareignes, avec la description de deux espe`ces nouvelles. Bull Soc Linn Lyon 48:524–528; 48:606–608, 641–649

Jolivet P (1998) Les nouveaux envahisseurs ou les chrysomélides voyageurs (Col.). L'Entomologiste, Paris 54:33–44

White RE (1996) A revision of the genus *Chaetocnema* of America, north of Mexico (Col. Chrys.). Contrib Am Entomol Inst 29:1–156

Sweetpotato Weevil, *Cylas formicarius* (Fabricius) (Coleoptera: Brentidae)

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Sweetpotato weevil presently is found in tropical regions of Africa, Asia, and North and South

America. Its origin is believed to be Africa or India despite the fact that the sweet potato plant likely evolved in northwestern South America. Thus, the association between this crop and its principal pest is relatively recent.

Life History

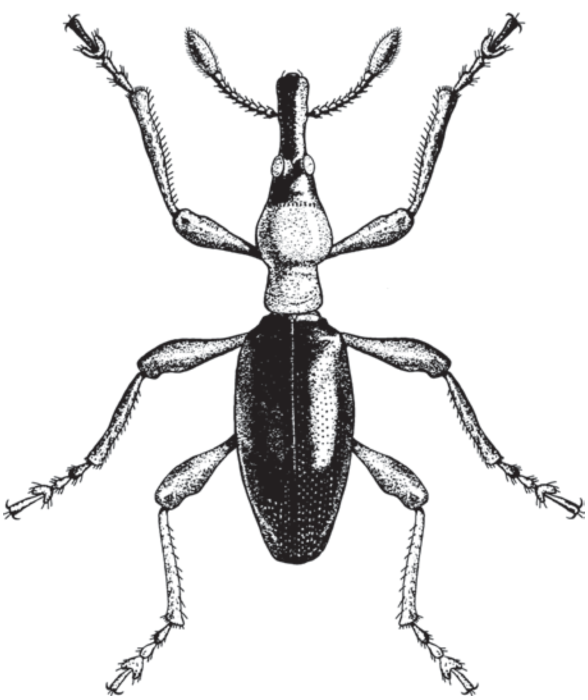
A complete life cycle requires 1–2 months, with 35–40 days common during the summer months. The generations are indistinct. In the USA, the number of generations occurring annually is estimated to be five in Texas, and about eight in Louisiana. Adults do not undergo a period of diapause in the winter, but seek shelter and remain inactive until the weather is favorable. All stages can be found throughout the year if suitable host material is available.

Eggs are deposited in small cavities created by the female with her mouthparts in the sweet potato root or stem. The female deposits a single egg, and seals the egg within the oviposition cavity with a plug of fecal material, making it difficult to observe. Most eggs tend to be deposited near the juncture of the stem and root (tuber). Sometimes the adult will crawl down cracks in the soil to access tubers for oviposition, in preference to depositing eggs in stem tissue. The egg is oval and creamy white. Its size is reported to average 0.65–0.79 mm in length and 0.41–0.50 mm in width. There is little distinct sculpturing on the surface of the egg. Duration of the egg stage varies from about 5–6 days during the summer to about 11–12 days during colder weather. Females apparently produce 2–4 eggs per day, or 75–90 eggs during their life span of about 30 days. Under laboratory conditions, however, mean fecundity has been reported to be 50–250 eggs per female.

When the egg hatches, the larva usually burrows directly into the tuber or stem of the plant. Those hatching in the stem usually burrow down into the tuber. The larva is legless, white in color, and displays three instars. The mean head capsule widths of the instars are 0.29–0.32 mm, 0.43–0.49 mm, and 0.75–0.78 mm for instars 1–3, respectively. Duration of each instar is 8–16, 12–21, and 35–56 days, respectively. Temperature is the principal factor affecting larval development rate, with larval development (not including the prepupal period) occurring in about 10 and 35 days at 30 and 24°C, respectively. The larva creates winding tunnels packed with fecal material as it feeds and grows.

The mature larva (Fig. 160) creates a small pupal chamber in the tuber or stem. The pupa is similar to the adult in appearance although the head and elytra are bent ventrally. The pupa measures about 6.5 mm in length. Initially the pupa is white, but with time this stage becomes grayish in color with darker eyes and legs. Duration of the pupal stage averages 7–10 days, but in cool weather it may be extended to up to 28 days.

Normally the adult (Fig. 159) emerges from the pupation site by chewing a hole through the exterior of the plant tissue, but sometimes it remains for a considerable period and feeds within the tuber. The adult is striking in form and color. The body, legs, and head are long and thin,



Sweetpotato Weevil, *Cylas formicarius* (Fabricius) (Coleoptera: Brentidae), Figure 159 Adult of sweetpotato weevil, *Cylas formicarius* (Fabricius).

Sweetpotato Weevil, *Cylas formicarius* (Fabricius) (Coleoptera: Brentidae), Figure 160 **Mature larva of sweetpotato weevil, *Cylas formicarius* (Fabricius).**

giving it an ant-like appearance. The head is black, the antennae, thorax and legs orange to reddish brown, and the abdomen and elytra are metallic blue. The snout is slightly curved and about as long as the thorax; the antennae are attached at about the mid-point on the snout. The beetle appears smooth and shiny, but close examination shows a layer of short hairs. The adult measures 5.5–8.0 mm in length. Under laboratory conditions at 15°C, adults can live over 200 days if provided with food and about 30 days if starved. In contrast, their longevity decreases to about 3 months if held at 30°C with food, and 8 days without food. Adults are secretive, often feeding on the lower surface of leaves, and are not readily noticed. The adult is quick to feign death if disturbed. Adults can fly, but seem to do so rarely and in short, low flights. However, because they are active mostly at night, their dispersive abilities are probably underestimated. Females feed for a day or more before becoming sexually active, but commence oviposition shortly after mating; the average preoviposition period is 7 days. A sex pheromone produced by females has been identified and synthesized.

This weevil feeds only on plants in the plant family Convolvulaceae. Although it has been found associated with several genera, its primary hosts are in the genus *Ipomoea*. Among vegetable crops only sweet potato, *I. batatas*, is a suitable host. Some cultivars of sweet potato are called yams, and these are susceptible to sweetpotato weevil. True yam, *Dioscorea* spp., belongs to the plant family Dioscoreaceae. Wild plants can be important hosts of sweetpotato weevil. Railroad vine, *Ipomoea pes-caprae*, and morningglory, *I. panduratea*, are among the suitable wild hosts.

Several natural enemies are known. Wasps such as *Bracon mellitor* Say, *B. punctatus* (Muesebeck), *Metapelma spectabile* Westwood (all Hymenoptera: Braconidae) and *Euderus purpureas* Yoshimoto (Hymenoptera: Eulophidae) have been reared from sweetpotato weevil larvae in the southeastern United States. There have been no studies of parasitoid effectiveness, but these species seem to be infrequent. Among predators, ants (Hymenoptera: Formicidae) seem to be most important. Diseases, especially the fungus *Beauveria bassiana*, have been observed to inflict high levels of mortality under conditions of high humidity and high insect density, but field conditions are rarely conducive for disease epizootics.

Damage

Sweetpotato weevil is often considered to be the most serious pest of sweet potato, with reports of losses ranging from 5–97% in areas where the weevil occurs. There is a positive relationship between vine damage or weevil density, and tuber damage. However, the plants exhibit some compensatory ability, with the relationship between vine damage and yield nonlinear.

A symptom of infestation by sweetpotato weevil is yellowing of the vines, but a heavy infestation is usually necessary before this is apparent. Thus, incipient problems are easily overlooked, and damage not apparent until tubers are harvested. The principal form of damage to sweet potato is mining of the tubers by larvae. The infested tuber is often riddled with cavities, spongy in appearance, and dark in color. In addition to damage caused directly by tunneling, larvae cause damage indirectly by facilitating entry of soil-borne pathogens. Even low levels of feeding induce a chemical reaction that imparts a bitter taste and terpene odor to the tubers. Larvae also mine the vine of the plant, causing it to darken, crack, or collapse. The adult may feed on the tubers, creating numerous small holes that measure about the length of its head. The adult generally has limited access to the tubers, however, so damage by this stage is less severe than by larvae. Adult feeding on the foliage seldom is of consequence.

Management

Planting time applications of insecticides are commonly made to the soil to prevent injury to the slips or cuttings. Either granular or liquid formulations are used, and systemic insecticides are preferred. Postplant applications are sometimes made to the foliage for adult control, especially if fields are likely to be invaded from adjacent areas, but if systemic insecticide is applied some suppression of larvae developing in the vine may also occur. Due to the long duration of the plant growth period, it is not uncommon for preplant or planting time applications to be followed by one or more insecticide applications to the plant or soil at mid season. Insecticides are also applied to tubers being placed into storage to prevent reinfestation and inoculation of nearby fields.

Cultural practices are sometimes recommended to alleviate weevil problem. Isolation is frequently recommended, and it is advisable to locate new fields away from previous crops and distant from sweet potato storage facilities, because both can be a source of new infestations. However, despite the infrequency of flight by adults, dispersal can occur over considerable distances. Dispersal rates of 150 m per day have been documented, with dispersal more rapid in the absence of suitable hosts.

Sanitation is particularly important for weevil population management. Discarded tubers and unharvested tubers can support large populations, and every effort should be made to remove such host material. Related to this, of course, is the destruction of alternate hosts; control of *Ipomoea* weeds is recommended.

Soil conditions affect weevil damage potential. Because adults crawl into cracks in the soil to gain access to tubers, efforts are made to reduce soil cracking. Irrigation, mulching, and hilling are common approaches, and planting in sandy soil is preferable to soil with high clay content because cracking is less likely.

Considerable research has been conducted on host plant resistance in sweet potato, and several commercially available varieties exhibit low levels of resistance. Unfortunately, resistance is not adequate when plants are exposed to high weevil population densities, and severe damage results.

Entomopathogenic nematodes seem to be the organisms with the greatest potential for practical biological suppression of sweetpotato weevil. Several strains of *Steinernema carpocapsae* (Nematoda: Steinernematidae) and *Heterorhabditis bacteriophora* (Nematoda: Heterorhabditidae) penetrate the soil and tubers, killing weevil larvae. In some soils, the infective nematodes are persistent, remaining active for up to 4 months. In some cases nematodes are more effective than insecticides at reducing damage.

Other methods of suppression are sometimes used, especially for postharvest treatment of tubers. Postharvest treatment not only prevents damage in storage, but allows shipment of tubers to areas where sweetpotato weevil is not found but might survive. Traditionally, postharvest treatment has been accomplished with chemical fumigants, but they have fallen from favor. Irradiation is potentially effective, although older stages of insects are less susceptible to destruction. Storage in controlled atmospheres, principally low oxygen and high carbon dioxide, is very effective for destruction of weevils, but requires good storage conditions.

► Sweetpotato Weevils and Their Eradication Programs in Japan
► Vegetable Pests and Their Management

References

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, CA, 729 pp
Cockerham KL, Deen OT, Christian MB, Newsom LD (1954) The biology of the sweet-potato weevil. Louisiana Agricultural Experiment Station Bulletin 483, 30 pp
Sherman M, Tamashiro M (1954) The sweetpotato weevils in Hawaii, their biology and control. University of Hawaii Technical Bulletin 23, 36 pp

Sweetpotato Weevils and their Eradication Programs in Japan

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The sweetpotato weevil, *Cylas formicarius* (Fabricius) (Coleoptera: Brentidae), is the most destructive pest of the sweet potato, *Ipomoea batatus* (Linnaeus). The insect occurs circumglobally in tropical and sub-tropical regions of Asia, the Pacific, Africa, the Caribbean and the United States. *Cylas* spp. are believed to have originated in Africa and/or Madagascar; only *C. formicarius* (Fig. 161) occurs world-wide as a pest species. Larvae and adults damage fleshy roots and stems of sweet potatoes. Larvae cause serious damage because they tunnel through the roots. Furthermore, the roots respond to weevil larvae feeding by producing ipomeamarone, a toxic furanoterpenoid with an unpleasant odor. The entire roots are rendered inedible, even though they are damaged in part, and because of their bitter taste, they cannot be eaten by livestock such as pigs, either. Because most of the larvae are cryptic in the roots below the soil surface, it is difficult to control the weevil populations effectively by the application of chemical insecticides. In 1986, the sex pheromone of *C. formicarius* was isolated, identified and synthesized in the United States. The synthesized pheromone strongly attracts the male adults of the weevil. Pheromone-trap monitoring systems have been developed in the field, and the monitoring trap is also used as a regulatory tool to detect an invasive organism in quarantined areas.

The West Indian sweetpotato weevil, *Euscepes postfasciatus* (Fairmaire) (Coleoptera: Curculionidae), is another major pest of sweet potato (Fig. 162) in the tropical and sub-tropical islands of the Pacific and the Caribbean and a part of Central and South America. The range of its distribution is narrower than that of *C. formicarius*

Sweetpotato Weevils and their Eradication Programs in Japan, Figure 161 Adult sweetpotato weevil 7 mm (photo by S. Moriya).

Sweetpotato Weevils and their Eradication Programs in Japan, Figure 162 Adult West Indian sweetpotato weevil. 3–4 mm (photo by S. Moriya).

as a whole, but the two species coexist in some places such as the Pacific and the Caribbean regions. The adults of both species are quite different in shape; that is, *Cylas* is a snout beetle of ant-like appearance, while *Euscepes* is inconspicuous and looks like a soil particle, especially when it feigns death. However, their immature stages are indistinguishable by the naked eye, as is the damage they do to sweet potato roots. Unlike *C. formicarius*, no sex pheromone has been found in *E. postfasciatus* up to now, and no evidence has been obtained either in the laboratory or the field that this weevil can actually fly, even though the adults possess well-developed hind wings. These facts may limit available information on the management of *E. postfasciatus*.

In Japan, these two weevil pests are exotic and distributed only in the Ryukyu Islands and Bonin Islands, the southernmost part of Japan. Because the weevils are not found on the main islands of Japan, transporting host plants from infested areas to uninfested areas is prohibited by quarantine regulations, as with quarantine programs for *C. formicarius* in the United States and *E. postfasciatus* in the islands of the South Pacific. To solve the problems caused by this restriction, eradication programs were initiated by the Kagoshima and Okinawa Prefectural Governments in 1988 and 1990, respectively, under the supervision of the National Government of Japan.

A combination of two unique methods was adopted on *C. formicarius* to eradicate it from the target areas. One is to use sex pheromone traps to annihilate males; the other is to release into the field masses of laboratory-reared males sterilized by gamma irradiation, thereby depriving wild females of their chance to mate with wild males. Because of the absence of effective attractants for *E. postfasciatus*, only the sterile insect technique (SIT) could be applied to their case.

There are three steps in the course of the eradication programs, as there were with the melon fly, *Bactrocera cucurbitae* (Coquillett), which was successfully eradicated from the same area of the Ryukyu Islands in 1993. The first step was essentially a research phase to develop basic techniques required for the procedures, including mass rearing, a sterilization and marking method, and pilot eradication experiments started on two small islands (21–35 ha) in 1988 and 1990. The second step was to confirm the feasibility of the programs; thus, in 1994, experimental eradication projects were initiated on two "medium sized" islands of about 57 and 63 km^2. The sweetpotato weevil populations were almost eradicated in the target areas of both islands. The final step of the programs was put into practice in 2001 to eradicate the two weevil pests from all the distribution areas (ca. 3,500 km^2) in the Ryukyu Islands. Since this program constitutes the first attempt at area-wide eradication of sweetpotato weevils in the world, it might take longer for it to reach its goals than the melon fly eradication project, which took 22 years.

References

Chalfant RB, Jansson RK, Seal DR, Schalk JM (1990) Ecology and management of sweet potato insects. Ann Rev Entomol 35:157–180

Jansson RK, Raman KV (eds) (1991) Sweet potato pest management: a global perspective. Westview Press, Boulder, Colorado, 458 pp

Moriya S (1995) The possibility of eradicating two sweet potato pests, *Cylas formicarius* and *Euscepes postfasciatus*, in Japan. Food & Fertilizer Technology Center (FFTC) Extension Bulletin 403, pp 1–7

Moriya S, Miyatake T (2001) Eradication programs of two sweetpotato pests, *Cylas formicarius* and *Euscepes postfasciatus*, in Japan with special reference to their dispersal ability. Jpn Agric Res Q (JARQ) 35:227–234

Sutherland JA (1986) A review of the biology and control of the sweetpotato weevil *Cylas formicarius* (Fab). Trop Pest Manag 32:304–315

Swezey, Otto Herman

Otto Swezey (Fig. 163) was born near Rockford, Illinois, USA, on June 7, 1869. He attended Lake Forest College (B.A. 1896) and then obtained an M.A. from Northwestern University in 1897. He taught biology at Northwestern until 1903. He

Swezey, Otto Herman, Figure 163 Otto Swezey.

gained employment with the Hawaiian Sugarcane Planters Association in 1904, apparently the first American entomologist to be employed by a private company. In Hawaii, Swezey was instrumental in establishing biological control for sugarcane pests. He was a founder of the entomological section of the Bishop Museum in Honolulu, and pursued his interest in Lepidoptera, though he was more interested in describing life histories than in describing insects. Nevertheless, he described over 100 Lepidoptera. Swezey was editor of the Proceedings of the Hawaiian Entomological Society for 39 years, and also served as president of that society. A major publication was "Forest insects in Hawaii" (1954). Swezey died at San Jose, California, on November 3, 1959.

Reference

Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Swifts

Members of the family Hepialidae (order Lepidoptera). They also are known as ghost moths.

► Ghost Moths
►Butterflies and Moths

Swimmeret

Paired gill-like or plate-like abdominal or thoracic appendages on the aquatic larvae of some Neuroptera. They can serve as oar-like appendages to facilitate locomotion.

Sword-Tail Crickets

A subfamily of crickets (Trigonidiinae) in the order Orthoptera: Gryllidae.

► Grasshoppers, Katydids and Crickets

Sylvatic

A disease that is found in, or acquired in, a wooded or other undeveloped natural habitat.

Sylveira Caldeira, João Da

João da Sylveira Caldeira was born at Rio de Janeiro, Brazil, on June 28, 1800. After studying medicine at the University of Edinburgh, Scotland he worked for a time as a preparator at the "Jardin des Plantes" in Paris. Returning to Rio de Janeiro, he and others were commissioned to revise and publish the "Flora Brasiliensis." He also served as professor of chemistry and director of the National Museum. Following the proclamation of Brazilian independence in 1822, the holdings of the National Museum were greatly increased. He also established exchanges with European museums. Sylveira contributed materially to the collections of Macquart, and many species described by the latter are attributed to Sylveira, and several species were named after him. He died in Rio de Janeiro on July 4, 1854.

References

Papavero N (1971) Essays on the history of neotropical dipterology with special reference to collectors (1750–1905),

Vol 1. Museu de Zoologia, Universidade de São Paulo, São Paulo
Papavero N (1973) Essays on the history of neotropical dipterology with special reference to collectors (1750–1905), Vol 2. Museu de Zoologia, Universidade de São Paulo, São Paulo

Symbiont

An organism living symbiotically with another organism.

Symbionts of Insects

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Symbiosis has been defined as mutualism (a beneficial interdependence of different species), and as parasitism (a form of interaction that is beneficial only to one partner and detrimental to the other). Today, symbiosis is sometimes equated with the concept of mutualism, in which one partner is considered the host and the other the symbiont. A difficulty with this definition is that it can be difficult to resolve relationships because the boundary between symbiosis and parasitism may be fluid. Symbionts may be intracellular or extracellular.

Mitochondria are Intracellular Symbionts

All arthropods have a nuclear genome with chromosomes consisting of DNA and proteins. In addition, insect cells also contain multiple copies of mitochondria, which are involved in basic functions of the cell. Mitochondria are generally accepted to be microbial symbionts that were modified after a long process of evolution within eukaryotic cells. Mitochondria retain a distinctive genome that is replicated and expressed, but all mitochondria are incapable of independent existence. Most of the genes in mitochondrial DNA were transferred from the mitochondrion to the nuclear genome of its eukaryotic host over the course of evolution. Only a few genes are left in the mitochondria which are located in the cytoplasm.

Multiple Symbionts May be Present

In addition to mitochondria, insects have intimate relationships with a diverse array of other symbionts, including viruses, bacteria, yeasts, and rickettsia. The details of the relationship between the host and the microorganism usually are unknown. There are intracellular symbionts (such as viruses and bacteria) as well as the extracellular symbionts.

The rice weevil *Sitophilus oryzae* (Rhynchophoridae), for example, has four genomes important to the weevil's biology. These are: nuclear, mitochondrial, principal gut endosymbiont, and *Wolbachia*. The principal gut endosymbiont is found (3×10^3 bacteria/cell) in specialized cells called bacteriocytes. A total of 3×10^6 of these bacteria are found in each weevil. The principal symbionts induce the specific differentiation of the bacteriocytes and increase mitochondrial oxidative phosphorylation. Their elimination impairs many physiological traits.

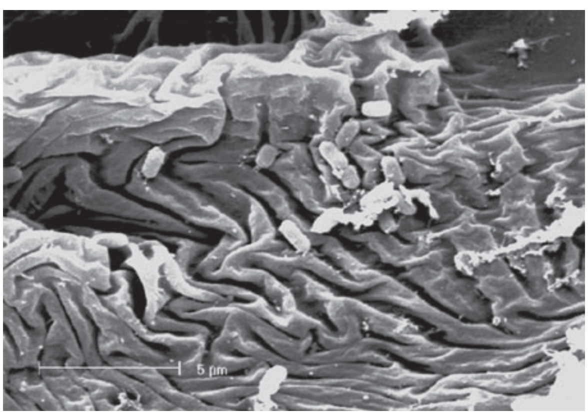
The multiple genomes found in this weevil support the serial endosymbiotic theory, which states that endosymbiosis did not occur just once in eukaryotic evolution with the origin of a nucleus, or even twice, when an anaerobic single-celled organism acquired a respiring bacterium which ultimately became the mitochondrion. Molecular data suggest the gut symbiont of *Sitophilis* was established prior to acquisition of *Wolbachia*. One scenario suggests that the colonization of cereal plants by *Sitophilus* was facilitated by the acquisition of the gut symbiont, a vitamin supplier.

Symbiont Function(s)

In many cases, symbionts possess metabolic capabilities that the insect host lacks and the insects use these capabilities to survive on poor or unbalanced diets. The insect and its microbes often require their mutual association. Many insects freed of symbionts grow slowly and produce few progeny; many symbionts cannot grow outside their insect host. The amazing diversity of relationships and organisms involved in symbiotic relationships with insects has raised many questions, but provided few clear cut answers because many symbionts cannot be cultured outside their hosts. Many symbionts are contained in special structures and transmitted by a highly-specific method, including transovarial transmission (transmission through the egg), to progeny. Transmission also can occur when larvae feed on contaminated egg shells or feces.

Some insect species contain several different types of symbionts in different tissues, including the gut, malpighian tubules, salivary gland, fat body, or gonads (Figs. 164 and 165). Usually these symbionts are neutral or beneficial to their hosts. For example, symbionts of some aphids (Hemiptera) synthesize essential amino acids, sterols, and vitamins and may function as genetic elements distinct from the host nuclear genome. Symbionts found in scale insects (Hemiptera) are particularly diverse, with almost twenty different types of associations described so far.

Antlions (Myrmeleontidae) prey on other insects by sucking out the body fluid after first paralyzing their prey with a toxin produced by salivary gland secretions produced by salivary bacteria. The paralyzing toxin produced by the bacterial endosymbionts is a homologue of GroEL, a protective heat-shock protein that functions as a molecular chaperone in the common bacterium *Escherichia coli*. In the antlion, the GroEL protein may act on receptors in insects to induce paralysis, perhaps having evolved this non-chaperone function to establish a mutually



Symbionts of Insects, Figure 164 Gut symbionts: scanning electron micrograph (magnification 6000X) of bacteria attached to the convolutions of the peritropic membrane in a *Ceratitis capitata* intestine (photo provided by Carol Lauzon, University of California, Hayward).

Symbionts of Insects, Figure 165 Gut symbionts: transmission electron micrograph (magnification 12,000X) of bacterial cells attached directly to the peritrophic membrane in the gut of *Anastrepha ludens*. Data bar 500 nm (photo provided by Carol Lauzon, University of California, Hayward).

beneficial antlion-bacterium relationship. It is unknown if such insecticidal proteins are produced by endosymbionts to help other fluid-feeding predatory insects.

Insects lacking some symbionts are apparently completely normal. For example, in the beetle family Cerambycidae, all of which live in wood, some species have symbionts while others lack them. Thus, the hypothesis that symbionts always supply a deficiency in the insect's diet appears to be simplistic.

Gut Symbionts

The primary habitat for the majority of microorganisms associated with insects is the digestive tract, especially the hind gut. The termite gut is one of the better studied examples of symbiosis, and molecular tools are improving our ability to resolve the taxonomy of these complex relationships.

The hindguts of termites can be compared to small bioreactors where wood and litter is degraded, with the help of symbiotic microorganisms, to provide nutrients. The hindgut of termites is a structured environment with distinct microhabitats. The dense gut microbiota includes such organisms as Bacteria, Archaea, Eukaryotes, and yeasts. These organisms do not occur randomly within the gut, but may be suspended in the gut contents, located within or on the surface of flagellates, or attached to the gut wall. The identity, exact number, and location of most is inadequately known because these organisms are difficult to culture outside their hosts.

Molecular tools will provide significant new information. For example, the microbiota of termites includes spirochaetes, which account for as many as 50% of the organisms present in some termite species. Spirochaetes are a distinct phylum within the bacterial domain, but relatively little is known about them. One molecular analysis of spirochaetes in the termite *Reticulitermes flavipes* suggested there are at least 21 previously unknown species of *Treponema*, suggesting that the long-recognized and striking morphological diversity of termite gut spirochaetes is paralleled by their genetic diversity, which may reflect substantial physiological diversity.

Omnivorous cockroaches also have microbial communities within their guts, but the associations are less interdependent than those of termites. The gut microbial communities in cockroaches anaerobically degrade plant polymers and include hydrogen-consuming bacteria, especially methanogens (bacteria that produce methane gas). The densities of these microorganisms can be enormous; for example 5×10^{12} bacteria per ml were found in the hindgut of the cockroach *Periplaneta americana*.

Tsetse flies (Glossinidae) are vectors of African sleeping sickness disease in humans and animals. Microorganisms associated with these flies, that are blood feeders, are responsible for nutrients that the flies are unable to synthesize. Different microorganisms have been found in midgut, hemolymph, fat body and ovaries. Until molecular techniques were used, their taxonomic status was unresolved. Now we know that at least three different microorganisms are present: the primary (P) symbiont *Wigglesworthia glossinidia* is an intracellular symbiont residing in specialized epithelial cells that form a U-shaped organ (bacteriome) in the anterior gut. The secondary gut symbiont *Sodalis glossinidius* is present in midgut cells. The third, *Wolbachia*, is found in reproductive tissues.

Tsetse flies are viviparous, with females retaining each egg within her uterus, where it hatches. One young larva matures at a time and is born as a fully developed third instar larva. During its intrauterine life, the larva receives nutrients and both of the gut symbionts from its mother via milk-gland secretions. The *Wolbachia* are transmitted transovarially. Efforts to eliminate tsetse symbionts with antibiotics result in retarded growth and a decrease in egg production; because it is impossible to eliminate only one gut symbiont at a time, it is difficult to decipher the role each plays. However, they play a role in metabolism, supplying B-complex vitamins. *Sodalis* also produces a chitinase, which appears responsible for increasing the susceptibility of its host to the sleeping sickness trypanosome. An analysis of the *Wigglesworthia* and *Sodalis* genomes indicate that they each form a distinct lineage in the Proteobacteria. The phylogenetic data suggest that a tsetse ancestor was infected with a *Wigglesworthia* and from this ancestral pair tsetse species evolved along with the different *Wigglesworthia* strains existing today. No evidence exists that horizontal transfer of *Wigglesworthia* symbionts occurred between tsetse species. However, the *Sodalis* symbiont might have been acquired recently by each tsetse species or there may have been multiple horizontal transfers between tsetse species.

Perhaps the best studied gut endosymbiont of insects is *Buchnera aphidicola*, an associate of aphids. The complete genome of this symbiont has been sequenced. Buchnera is found in huge cells (bacteriocytes) in most of the 4,400 aphid species, supplying its host with essential amino acids. In return, *Buchnera* is given a stable and nutrient-rich environment. Aphids become sterile or die if their symbionts are eliminated. This relationship has been stable for 200–250 million years and *Buchnera* and aphids have co-evolved over a long period. About 9% of the *Buchnera* genome is devoted to producing essential amino acids for use by the aphid. Genes for nonessential amino acids are absent in *Buchnera* and thus this symbiont depends on its host for these, making Buchnera and the aphid co-dependent.

Analyses of different aphid species and their *Buchnera* symbionts indicate that vertical transmission of the symbionts has occurred from the time of the common ancestor of aphids, approximately 150–250 million years ago. Thus, the aphids and their symbionts appear to have co-speciated and there is no evidence of horizontal transfer, even within a single aphid species. In many *Buchnera* lineages, genes involved in tryptophan and leucine biosynthesis are present on plasmids rather than in the *Buchnera* genome. The location of these genes on plasmids would allow increased expression and, thus, increased benefit to their hosts. The number of copies of the plasmids appear to vary across *Buchnera* in different aphid lineages, perhaps reflecting coordinated, adaptive adjustment to the nutritional needs of the different aphid hosts. The genome of *Buchnera* is unusual when compared to the free-living bacterium *E. coli*. First the sequences are very AT-biased (about 28% GC) and second, DNA sequences evolve faster in *Buchnera* than in free-living relatives. Finally the genome of *Buchnera* from *A. pisum* is reduced, consisting of only about 650 kb (about one-seventh of the genome size of *E. coli*). It appears to contain only a subset of about 600 of the 4,500 genes present in an *E. coli*-like ancestor.

Remarkably, it appears that each *Buchnera* contains 50–200 chromosomal copies, with the number of copies varying with the life cycle stage of the host, suggesting chromosome amplification is used to vary the contribution of the symbiont to its host's nutrition. The amplification of genome copy number to 200 copies/cell is very unusual in the microbial world; *E. coli* typically has one or two chromosomes per cell. The dramatic reduction in genome size of *Buchnera* and the extraordinary increase in genome copy number make this intracellular symbiont resemble eukaryotic cell organelles such as mitochondria and chloroplasts—which are considered to be evolutionary descendants of symbiotic bacteria. *Buchnera* resemble these organelles also in that they are transmitted maternally between host generations.

A less intimate relationship between gut microbes and insects is that between *Enterobacter agglomerans*, found in the gut of the apple maggot *Rhagoletis pomonella*. Enterobacteriaceae are the most common microorganisms associated with the apple maggot in the gut and female reproductive organs, and there are suggestions the flies use the bacteria for some vital function(s). In addition to *E. agglomerans*, *Klebsiella oxytoca* is found in the gut of *R. pomonella* and both are most abundant in the esophageal bulb, crop and midgut.

These bacteria are found on host plants and other substrates in the environment. It appears that the bacteria provide usable nitrogen for *R. pomonella* and other tephritids by degrading purines and purine derivatives, making them facultative symbionts. The relationship between the *Enterobacter* and *Klebsiella* species is probably complex. *Rhagoletis* gut symbionts exist as a biofilm in the gut. A biofilm is a complex, structured community of microbes attached to surfaces. Biofilms function as a cooperative consortium in a complex and coordinated manner.

A full understanding of the genetic and evolutionary roles played by symbionts remains to be determined. In the few cases that have been well studied, a genetic interplay between insect host and symbiont occurs, factors are supplied to each from the other, and the microorganism has specific means of movement and relocation within the insect. Insects commonly control movement and multiplication of the symbiont, and the symbiont often influences growth and reproduction of the insect. A symbiont must not be subject to suppression or elimination by the insect immune system. Our understanding of how microorganisms were incorporated into insect tissues and cells and have evolved remains fragmentary, but advancing with the use of molecular tools.

Bugs Within Bugs Within Mealybugs

Perhaps most amazing is the recent discovery that there are bugs within bugs within mealybugs. Mealybugs (Pseudococcidae) have endosymbionts that live within the cytoplasm of large, polyploid host cells of a specialized bacteriome. The symbionts provide nutrients to their hosts and the relationship between hemipteran insects and these primary endosymbionts is ancient, perhaps dating to the origins of the families or superfamilies 100–250 million years ago.

The mealybug *Planococcus citri* packages its intracellular endosymbionts into mucus-filled spheres which surround the host cell nucleus and occupy most of the cytoplasm. These spheres are structurally unlike eukaryotic cell vesicles, and it was recently demonstrated that the mealybug cells actually harbor two types of Proteobacteria. The bacteria are not co-inhabitants of the spheres. Rather, the spheres themselves are β-proteobacteria with γ-proteobacteria living inside. This is the first report of an intracellular symbiosis involving two species of bacteria and the authors hypothesized that the internalization of the γ-proteobacterium by the β-proteobacterium may facilitate the exchange of genes and gene products to slow or reverse the genetic degradation that is common to long-term intracellular symbionts over evolutionary time.

Wolbachia

The genus *Wolbachia* is found in the α-proteobacteria. These bacteria are one of the most commonly found intracellular microorganisms found in arthropods. *Wolbachia* are gram-negative rods that cannot be cultured easily outside their hosts and are widespread, with estimates of infection frequency ranging to as many as 76% of all arthropod species.

Wolbachia have been implicated as both the cause of alterations in sex ratio (resulting in thelytoky and male killing), and cytoplasmic incompatibility in arthropods. Some *Wolbachia* improve fertility or vigor in their hosts, while other strains of *Wolbachia* appear to decrease these traits in their hosts.

The molecular mechanism(s) by which reproductive incompatibility are induced by *Wolbachia* are hypothesized to be due to *Wolbachia*'s ability to modify sperm. This hypothesis suggests that paternal chromosomes are modified during spermatogenesis by *Wolbachia* and this modification is "rescued" in eggs of females infected with the same strain of *Wolbachia* during fertilization. If, however, the female is not infected with *Wolbachia* and mates with an uninfected male or male infected with a different strain of *Wolbachia*, then the embryos die. Some *Wolbachia* strains have been identified that fail to modify sperm but can rescue the modification in eggs of other *Wolbachia* strains.

Species in which *Wolbachia*-induced cytoplasmic incompatibility has been documented include mosquitoes (*Culex pipiens*, *Aedes scutellaris*, *A. albopictus*), flies (*Drosophila similans*, *D. melanogaster*), the moth *Ephestia cautella*; beetles (*Tribolium confusum* and *Hypera postica*), the parasitoid *Nasonia*; and the hemipteran *Laodelphax striatellus*. Mites in the families Tetranychidae and Phytoseiidae also exhibit cytoplasmic incompatibility due to infection with *Wolbachia*.

Cytoplasmic incompatibility caused by *Wolbachia* may be partial or complete. Sometimes incompatibility is found in both reciprocal crosses (A × B and B × A, bidirectional incompatibility), perhaps due to the presence of different strains of *Wolbachia* in each population. Incompatibility more often is found in one reciprocal cross (A × B or B × A, unidirectional incompatibility). Cytoplasmic incompatibility typically is incomplete (<100%), perhaps due to inefficient transfer of *Wolbachia* to all progeny or to differences in the titer of *Wolbachia*. Such differences in titer could occur naturally if the infected insects encounter antibiotics in their environment or if they experience high temperatures (typically >30°C).

Some insects appear to have *Wolbachia* only in their germ line tissues (ovaries and testes) while others have *Wolbachia* in somatic tissues. Large numbers of *Wolbachia* have been found in ovaries and testes of populations with cytoplasmic incompatibilities. Incompatible strains have been converted to compatible by treating the colonies with heat or antibiotics to eliminate (or reduce the titer of) the *Wolbachia*.

Wolbachia can be transferred to new populations experimentally by microinjecting infected egg cytoplasm into uninfected eggs. Transinfected strains of *D. simulans* and *D. melanogaster* with high titers of *Wolbachia* exhibited cytoplasmic incompatibilities at high levels, but those with low titers exhibited low levels of incompatibility, suggesting that a threshold level of infection is required and that host factors may determine the density of the *Wolbachia* in the host.

Wolbachia have been identified in at least 70 species of parasitic Hymenoptera, including species in the Aphelinidae, Encyrtidae, Eulophidae, Pteromalidae, Torymidae, Trichogrammatidae, Cynipidae, Eucoilidae, Braconidae, Ichneumonidae, Proctotrupoidae and in three dipteran parasitoids (Tachinidae). Both cytoplasmic incompatibility and induction of parthenogenesis occur in these parasitoids. Many hymenopteran parasitoids have both bisexual (arrhenotokous) and unisexual strains consisting only of females (thelytoky), probably due to the presence of *Wolbachia*.

Phylogenetic analysis suggests that the *Wolbachia* common ancestor evolved between 80 and 100 million years ago, whereas the arthropod common ancestor occurred at least 200 million years earlier. Thus, *Wolbachia* probably invaded arthropods through horizontal transmission. In fact, the molecular phylogenies of *Wolbachia* and arthropods do not match, supporting the hypothesis that horizontal transmission is important in the distribution of different strains of *Wolbachia* among arthropods.

Several methods have been proposed as mechanisms for horizontal transfer, including the movement of *Wolbachia* from host arthropods to their parasitoids and vice versa. Experimental microinjection (artificial horizontal transfer) of *Wolbachia* from the parasitoid *Muscidifurax uniraptor* into its host *D. simulans* resulted in a temporary infection, but no specific phenotypic effects were observed. These results suggest that host-symbiont interactions are important for successful establishment of a *Wolbachia* infection in a new host. The reasons for failure to experimentally transfer *Wolbachia* remain unknown, but it is clear that *Wolbachia* has successfully bridged large phylogenetic distances in its horizontal movements over evolutionary time. Some arthropods have been found to have double or even triple infections of

Wolbachia. The effects of these multiple infections are diverse, but usually are unknown.

The availability of genetic information about *Wolbachia* has fostered increased knowledge of *Wolbachia*. The molecular technique called the polymerase chain reaction (PCR) allows scientists to study *Wolbachia* even though *Wolbachia* cannot be cultured outside their arthropod hosts. The availability of PCR primers for *Wolbachia* genes revolutionized the study of the distribution and evolution of *Wolbachia*. The *Wolbachia* genome project will further revolutionize such studies. Based on a phylogeny developed using DNA sequences from the *fts*Z gene, *Wolbachia* infecting arthropods have been divided into Groups A and B, which are estimated to have diverged from each other 58–67 million years ago. Phylogenies based on the *wsp* gene sequences have yielded more groups, indicating considerable genetic variation exists among different *Wolbachia* strains.

Wolbachia may have a role in the speciation of arthropods by generating reproductive isolation, although some argue that the role of *Wolbachia*'s in this important process remains unproved. Typically, *Wolbachia* cause unidirectional cytoplasmic incompatibility when a *Wolbachia*-infected male mates with an uninfected female. The eggs or embryos of such matings die, resulting in a fitness cost to uninfected females, which over time results in the infected cytotype becoming fixed in the population. A problem with this speciation hypothesis is that *Wolbachia* females transmit <100% of the time to progeny, so some progeny will be produced that are compatible. Secondly, incompatibility is not completely expressed (incomplete penetrance of the trait) when infected males and uninfected females mate in natural populations, perhaps due to differences in the titer of the *Wolbachia* within the different individuals. Furthermore, selection on both the host and *Wolbachia* may favor reduced penetrance of the incompatibility phenotype or loss of *Wolbachia*. This could lead to a situation in which there is no gene flow to some gene flow, reducing reproductive isolation. Thus, unidirectional incompatibility caused by *Wolbachia* may be insufficient to cause the reproductive barriers that could lead to speciation, although such reproductive isolation could assist in the process of speciation. Additional factors, such as hybrid sterility (sterility of the hybrid when crossed with either of the parental species) and hybrid breakdown (the inviability or sterility of progeny resulting from a backcross of hybrid progeny with either of the parental species) may also be involved in the speciation process.

A second speciation mechanism possibly associated with *Wolbachia* may be by the induction of thelytoky (reproduction by females only), as has been found in the hymenopteran *Encarsia formosa*. Some populations of *Encarsia* no longer have males, so that they essentially become clonal and over time could differentiate genetically. A third potential *Wolbachia* speciation mechanism is by bidirectional incompatibility; if a population is infected with two different strains of *Wolbachia* that are incompatible with each other, then the incompatibility could act as a post-zygotic reproductive barrier.

How *Wolbachia* are maintained in populations has considerable theoretical and practical importance. *Wolbachia* have been proposed as vectors for genetically transforming their host arthropod, as well as mechanisms for driving genes into arthropod populations in genetic manipulation projects for improved pest control.

The interest in the biology and evolution of *Wolbachia*, with its fascinating effects on reproductive isolation (thus potentially having effects on speciation), sex ratio, feminization, and male killing, has led to the development of a *Wolbachia* genome project, with four different groups of *Wolbachia* as targets.

Despite the wealth of information obtained about *Wolbachia* within the past few years, our understanding of the role of *Wolbachia* in arthropod biology and evolution probably remains fragmentary. For example, some *Wolbachia* in arthropods were recently shown to contain bacteriophages named WO. A phylogenetic analysis of different WOs from several *Wolbachia* strains yielded a tree that was not congruent with the phylogeny of the *Wolbachia*, suggesting that the phages were active and horizontally transmitted among the various *Wolbachia*. Because all *Wolbachia* strains examined had WO, the phage might have been associated with Wolbachia for a very long time, conferring some benefit to its microbial hosts.

Polydnaviruses as Symbionts

A particularly interesting example of an intimate relationship between insects and symbionts is illustrated by the relationship between polydnaviruses and some parasitoids. Polydnaviruses are relatively newly-recognized viruses that are found only in the Braconidae and Ichneumonidae among the parasitic Hymenoptera. Polydnaviruses are symbiotic proviruses that have double-stranded circular DNA genomes; they are literally poly-DNA-viruses, having segmented genomes composed of several circular DNA molecules. For example, the genome of the virus within the parasitic wasp *Campoletis sonorensis* consists of 28 DNA molecules ranging in size from approximately 5.5–21 kb, with the total genome size approximately 150 kb.

Polydnaviruses are important in ensuring that some species of braconids and ichneumonids are able to successfully parasitize their insect hosts. At least fifty species of parasitic wasps have been shown to contain polydnaviruses and over 30,000 species are thought to carry polydnaviruses. Polydnaviruses alter the host insect's neuroendocrine and immune responses, prevent encapsulation of wasp eggs and larvae by host hemocytes, and influence development of the host to benefit the wasp. Genera of parasitoids containing polydnaviruses appear to have more species and have broader host ranges than sibling groups lacking them, suggesting the viruses contribute to the evolutionary success of their hosts. The two polydnaviral groups, Ichnoviridae and Brachoviridae, are phylogenetically and morphologically distinct and use different mechanisms to inhibit host immunity and development. The association between braconid parasitoids and their viruses appears to have lasted at least 60 million years. Thus, the viruses and braconid parasitoids appear to have a long association and have evolved a variety of interactions with their lepidopteran hosts.

Polydnaviruses replicate only in braconid or ichneumonid wasp ovaries and are secreted into the oviducts from where, during oviposition, they are injected into host lepidopteran larvae. The viruses appear to be vertically transmitted and integrated into the chromosome of the wasp. Each wasp species appears to carry a polydnavirus characteristic of that species. If one species within a particular genus carries a polydnavirus, they all are likely to do so.

Insects possess immune mechanisms that protect them from microorganisms, other invertebrates, and abiotic materials. Protection occurs through constitutive factors or by inducible humoral and cellular responses. Many parasitoid wasps are internal parasites and spend part of their lives in the bodies of other insects. Many behavioral, morphological, nutritional, and endocrine factors determine whether the interactions between a host and a parasitoid will lead to development of the parasitoid or to its destruction. The polydnavirus influences the immune system of the insect host, which allows the parasitoid eggs and larvae to survive. The virus replicates asymptomatically in the parasitoid but causes a pathogenic virus infection in the wasp's lepidopteran host. The virus alone can induce altered immune responses in some hosts, but in other hosts the venom injected by the wasp also must be present for the full effect of the virus to occur. Parasitoid wasps thus appear to benefit significantly from the polydnaviruses that replicate in their reproductive tracts. The virus also clearly benefits if the wasp is able to reproduce, because polydnaviruses are known to replicate only within their wasp hosts.

The polydnavirus-parasitoid-lepidopteran host system provides an unusual example of an obligate mutualistic association between a virus and a parasitoid that functions to the detriment of the parasitoid's lepidopteran host. The origin of polydnaviruses is unknown, as is how they became established in the parasitoid genome. It has been speculated that polydnaviruses may have potential value in agricultural pest management programs if genetically engineered pathogens (viruses, bacteria, fungi) containing polydnavirus genes could produce products that immunosuppressed the target pest, making the pathogens more effective. Alternatively, genetically engineered parasitoids could be developed that exhibit a modified host range, making them more effective in controlling pests.

► Symbiosis Between Planthoppers and Microorganisms
► Symbiotic Viruses of Parasitic Wasps

References

Aksoy S (2000) Tsetse-a haven for microorganisms. Parasitol Today 16:114–118

Bandi C, Slatko B, O'Neill SL (1999) *Wolbachia* genomes and the many faces of symbiosis. Parasitol Today 15:428–429

Baumann P, Moran NA, Baumann L (1997) The evolution and genetics of aphid endosymbionts. BioScience 47:12–20

Beckage, NE (1998) Parasitoids and polydnaviruses. BioScience 48:305–310

Brune A, Friedrich M (2000) Microecology of the termite gut: structure and function on a microscale. Curr Opin Microbiol 3:263–269

Cazemier AE, Hackstein JHP, Op den Camp HJM, Rosenberg J, Drift C, van der (1997) Bacteria in the intestinal tract of different species of arthropods. Microb Ecol 33:189–197

Cook JM, Butcher RDJ (1999) The transmission and effects of *Wolbachia* bacteria in parasitoids. Res Popul Ecol 41:15–28

Douglas AE (1992) Symbiotic microorganisms in insects. In: Encyclopedia of Microbiology, Academic Press/Elsevier, San Diego, CA, USA. vol 4, pp 165–178

Gray MW (1989) Origin and evolution of mitochondrial DNA. Ann Rev Cell Biol 5:25–50

Hales DF, Tomiuk J, Wohrmann K, Sunnucks, P (1997) Evolutionary and genetic aspects of aphid biology: a review. Eur J Entomol 94:1–55

Heddi A, Grenier AM, Khatchadourian C, Charles H, Nardon P (1999) Four intracellular genomes direct weevil biology: nuclear mitochondrial, principal endosymbiont, and *Wolbachia*. Proc Natl Acad Sci USA 95:6814–6819

Hurst GDD, Schilthuizen M (1998) Selfish genetic elements and speciation. Heredity 80:2–8

Jeyaprakash A, Hoy MA (2000) Long PCR improves *Wolbachia* DNA amplification: wsp sequences found in 76% of 63 arthropod species. Insect Mol Biol 9:393–405

Kaufman MG, Walker ED, Odelson DA, Klug MJ (2000) Microbial community ecology and insect nutrition. Am Entomol 46:173–184

Krell PJ (1991) The polydnaviruses: multipartite DNA viruses from parasitic Hymenoptera. In: Kurstak E (ed) Viruses of invertebrates. Marcel Dekker, New York, NY, pp 141–177

Lauzon CR, Sjogren RE, Wright SE, Prokopy RJ (1998) Attraction of *Rhagoletis pomonella* (Diptera: Tephritidae) flies to odor of bacteria: apparent confinement to specialized members of Enterobacteriaceae. Environ Entomol 27:853–857

Lilburn TG, Schmidt TM, Breznak JA (1999) Phylogenetic diversity of termite gut spirochaetes. Environ Microbiol 1:331–345

Moran NA, Baumann P (2000) Bacterial endosymbionts in animals. Curr Opin Microbiol 3:270–275

O'Neill SL, Hoffmann AA, Werren JH (eds) (1997) Influential passengers: Inherited microorganisms and arthropod reproduction. Oxford University Press, Oxford, UK, 214 pp

Schwemmler W, Gassner G (eds) (1989) Insect endocytobiosis: morphology, physiology, genetics, evolution. CRC Press, Boca Raton, FL

Webb BA (1998) Polydnavirus biology, genome structure and evolution. In: Miller LK, Ball A (eds) The insect viruses. Plenum, New York, pp 105–139

Werren JH (1997) Biology of *Wolbachia*. Ann Rev Entomol 42:587–609

Symbiosis

A close association of two different organisms in which some benefit is derived from the association. A special type of symbiosis is mutualism, in which both organisms benefit.

Symbiosis Between Planthoppers and Microorganisms

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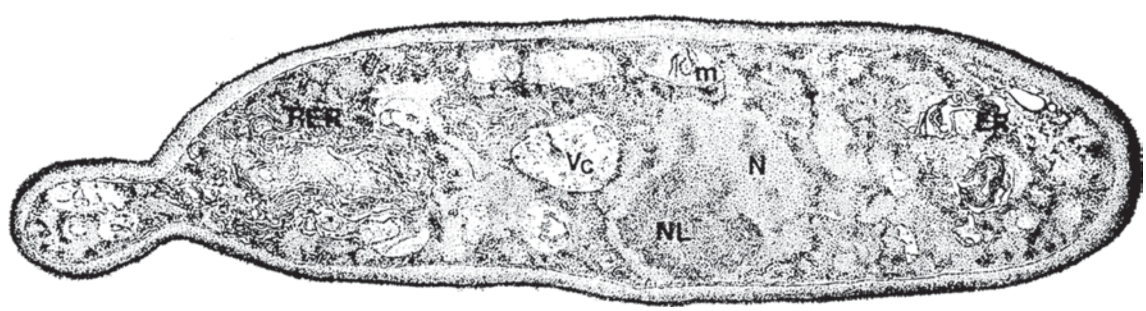
Symbiosis is a rather common biological phenomenon and is defined as living together intimately between two or more dissimilar organisms. At least nine orders of insects possess symbiotes, which may be different in forms and are located in various organs (mycetoms) or cells (mycetocytes). Many plant-sucking hemipterans harbor intracellular symbiotes. For example, aphids have symbiotic bacteroids, leafhoppers have rickettsia-like organisms in addition to bacteroids, and planthoppers harbor mostly the yeast-like symbiote. The brown planthopper, *Nilaparvata lugens* Stål, is one of the most destructive pests of rice in Asia, and is extensively studied on its symbiotic association with microorganisms.

The yeast-like symbiote of *N. lugens* is located in fat body cells of the abdomen, but never in the head or thorax. It measures 2.5 × 8–10 μm in size. This symbiote is bacilliform and unicellular, has a two-layered cell wall, and reproduces by budding, forming a convexity at the budding site. The fat body in the abdomen (Fig. 166) is full of yeast-like symbiote, as observed by histological sectioning. Ultrastructural observations showed that the yeast-like symbiote has a large nucleus, ribosomes, rough endoplasmic reticulum, Golgi apparatus, and many mitochondria in cytoplasm. Its morphology resembles cellular structure of the yeast. Because it is not cultured in vitro, this microorganism is named the yeast-like symbiote. However, a phylogenetic study based on direct sequencing of its 18S rRNA genes showed that the yeast-like symbiote in three planthoppers (*N. lugens*, *Sogatella furcifera*, and *Laodelphax striatellus*) is placed in the class Pyrenomycetes of the subphylum Ascomycotina. Therefore, the taxonomic position of the yeast-like symbiote is at present uncertain.

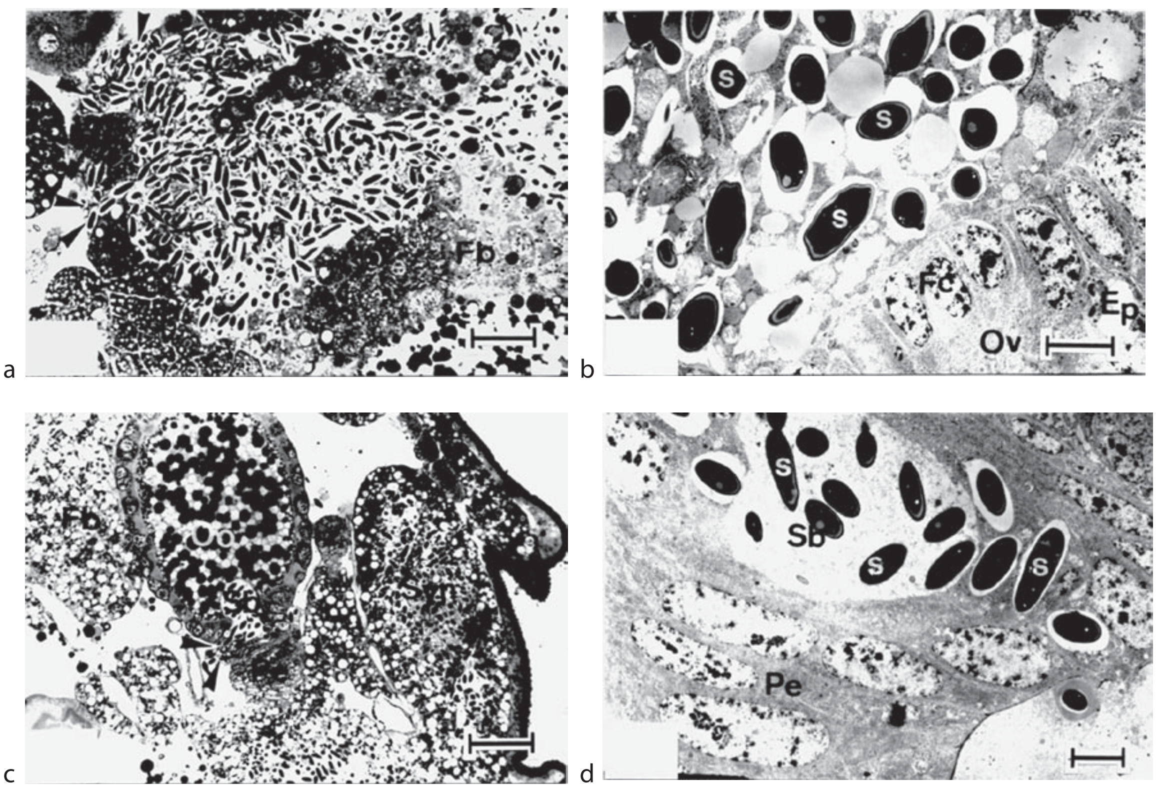
The population of yeast-like symbiote increases through nymphal development of *N. lugens*. The total number reaches a peak before oviposition in female adults and then declines, while the maximal number in males is at the fifth nymphal instar. The females harbor more yeast-like symbiote than the males, especially at the fifth nymphal and adult stages. The population declines drastically by incubating the neonate nymphs at 32°C, or above, for 3 days or longer, resulting in subsymbiotic or aposymbiotic insects (insects with less symbiotes or without symbiotes). Incubation at 32°C causes some cellular changes, such as disintegration of its cell wall, degeneration of nucleus, and loss of cytoplasm. The reduction in yeast-like symbiote number caused by high-temperature treatment (at 32°C) could be due to these cellular changes. In addition, treatment of yeast-like symbiote with some antibiotics also may result in lowering the symbiote number. For example, 0.3% Polyoxin S and 0.1% chlamphenicol as well as 0.1% cycloheximide may reduce yeast-like symbiote number, and thus kill the insects due to loss of the symbiotes.

The physiological roles of yeast-like symbiote can be studied by comparing normal with subsymbiotic or aposymbiotic insects. The brown planthopper eggs treated with high temperature



Symbiosis Between Planthoppers and Microorganisms, Figure 166 **Schematic diagram of a yeast-like symbiote in the brown planthopper, *Nilaparvata lugens* (after Cheng and Hou, 1996). Abbreviations: N, nucleus; NL, nucleolus; m, mitochondrium; r, ribosome; RER, rough endoplasmic reticulum.**

on day 1, 4 or 7 after oviposition display reduced hatchability only on day 7, indicating that the symbiote is more significant in the late embryonic development than the earlier stages. The eggs within the high-temperature treatment harbor only a few of the symbiotes, and their symbiote ball in eggs through embryonic development is free of symbiotes. The embryos of subsymbiotic eggs cannot undergo blastokinesis and dorsal closure, and fail to hatch due to lack of differentiation of the abdominal segments. Electrophoretic profile of the eggs laid by the subsymbiotic females showed the absence of several minor proteins, which are usually found in the fat body of normal females. A protein of 131 kDa is barely detectable in the subsymbiotic insects, and is not found in the ligated eggs in which the symbiote ball is completely separated from the developing germ band. Therefore, the symbiote seems to supply its host with proteins for normal embryonic and postembryonic development. The yeast-like symbiote number in females may be reduced after injection with lysozyme solution, and some of the eggs are unable to hatch due to failure in blastokinesis. The embryos of ligated eggs could complete segmentation and differentiation normally before 110 h of embryonic development, but the abdominal segments fail to



Symbiosis Between Planthoppers and Microorganisms, Figure 167 Histological micrographs showing transovarial transmission of yeast-like symbiote in *Nilaparvata lugens* (rearranged from Cheng and Hou, 2001). (a) The yeast-like symbiote moves out of the syncytium by exocytosis. Bar = 10 μm; (b) The free yeast-like symbiote in hemolymph approaches to the ovarioles near pedicel. Bar = 10 μm; (c) The yeast-like symbiote enters follicle cell around the primary oocyte by endocytosis (arrow heads) at epithelial plug. Bar = 10 μm; (d) The yeast-like symbiote aggregates at the posterior end of the mature egg after entering, forming a symbiote ball. Bar = 10 μm. Abbreviations: Ep, epithelial plug; Fb, fat body; Fc, follicle cell; Oo, oocyte; Ov, ovariole; Pe, pedicel; S, symbiote; Sb, symbiote ball.

differentiate after dorsal closure, forming the head embryos. Partially ligated eggs harbor some symbiotes and may produce normal larvae. Hence, the yeast-like symbiote is significant in abdominal segmentation and differentiation of the planthopper embryo.

The yeast-like symbiote of *N. lugens* passes to progeny by transovarial transmission. The symbiotes in mycetocytes move out of the syncytium, which is formed from a layer of fat body cells, by exocytosis, and are released (Fig. 167) into hemocoel in females. Then, the free yeast-like symbiote in hemolymph approach to the ovarioles near the pedicel and are enclosed by follicle cells. They enter the follicle cells around the primary oocyte by endocytosis at epithelial plug of the ovariole. The yeast-like symbiote aggregates at the posterior end of the mature egg after entering, forming a symbiote ball, and finally complete the transovarial transmission. Therefore, the yeast-like symbiote is intimately associated with the brown planthopper through generations and is indispensable for its host life.

References

Chen CC, Cheng LL, Hou RF (1981) Studies on the intracellular yeast-like symbiote in the brown planthopper, *Nilaparvata lugens* Stål. II. Effects of antibiotics and elevated temperature on the symbiotes and their host. Zeitschrift fur angnewandte Entomologie 92:440–449

Chen CC, Cheng LL, Kuan CC, Hou RF (1981) Studies on the intracellular yeast-like symbiote in the brown planthopper, *Nilaparvata lugens* Stål. I. Histological observations and population changes of the symbiote. Zeitschrift fur angnewandte Entomologie 91:321–327

Cheng DJ, Hou RF (1996) Ultrastructure of the yeast-like endocytobiont in the brown planthopper, *Nilaparvata lugens* (Stål) (Homoptera: Delphacidae). Entocytobiosis Cell Res 11:107–117

Cheng DJ, Hou RF (1998) Cellular changes of the yeast-like endocytobiont in the brown planthopper, *Nilaparvata lugens* (Stål), after high-temperature treatment. Endocytobiosis Cell Res 12:177–183

Cheng DJ, Hou RF (2001) Histological observations on transovarial transmission of a yeast-like symbiote in *Nilaparvata lugens* Stål (Homoptera, Delphacidae). Tissue Cell 33:273–279

Hou RF, Lee YH (1984) Effect of high-temperature treatment on the brown planthopper, *Nilaparvata lugens*, with reference to physiological roles of its yeast-like symbiote. Chin J Entomol 4:107–116

Lee YH, Hou RF (1987) Physiological roles of a yeast-like symbiote in reproduction and embryonic development of the brown planthopper, *Nilaparvata lugens* Stål. J Insect Physiol 33:851–860

Noda H, Nakashima N, Koizumi M (1995) Phylogenetic position of yeast-like symbiotes of rice planthoppers based on partial 18S rDNA sequences. Insect Biochemistry and Molecular Biology 25:639–646

Symbiotic Viruses of Parasitic Wasps

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Parasitic wasps (parasitoids) have been extensively used as biological control agents against veterinary and agricultural pests. Over the past several years, it has become increasingly evident that many of these parasitoids, particularly members of the Ichneumonoidea, have silent partners that play a major role in their success as biological control agents. These third party entities consist mainly of viruses and virus-like particles (VLPs, lacking nucleic acid or for which the nucleic acid composition is not yet known) that are presumed or determined empirically, to enhance the survival of the parasitoid within its host.

More than 80% of the Hymenoptera consist of parasitic species but little is known about their viral or VLP symbionts. It has been suggested that symbiotic viruses and VLPs influence the host range of their wasp, influencing the types of hosts they infect. Nevertheless, very little is known about the distribution and types of viruses and VLPs that occur in different species and families of the parasitic Hymenoptera. An understanding of the distribution of symbiotic viruses within parasitic wasps would provide valuable insights into which wasps may be most effectively utilized as biological control agents of insect pests. It would also further our understanding of the co-evolutionary relationships that may have arisen between hymenopteran families and particular genera of viruses.

Several factors influence the successful development of the immature wasp within its host. These include the fluctuations in the host's endocrine system, the biochemical and nutritional status of the host, as well as its physiological ecology. An equally important but more immediate factor that influences the wasp's developmental success is its ability to avoid or circumvent the host's cellular defense responses, particularly during the wasp's egg development. Substances from the venom gland of the wasp, proteins and other secretions from extra-embryonic membranes of wasp first instars, as well as ovarian proteins injected with the wasp egg play various roles in enhancing development/survival of the wasp egg and larva. The VLP of the ichneumonid wasp *Venturia canescens* was one of the first to be identified as protecting the oviposited wasp egg. However, the subsequent discovery and characterization of polydnaviruses (PDVs), double stranded DNA viruses with unusual segmented circular genomes, followed by discoveries of even more PDVs, RNA and unipartite DNA viruses, and VLPs, brought into focus the widespread distribution of wasp-associated viruses and their impact on the host's immune response and survival of the developing wasp.

The availability of molecular tools has facilitated the sequencing and comparative analyses of the genes and/or genomes of several PDVs, as well as their phylogenetic relationships within the Ichneumonoidea. Consequently, PDVs are the best studied wasp-associated third party entities. PDVs belong to the genera *Ichnovirus* and *Bracovirus* from the Ichneumonidae and Braconidae wasps, respectively. Bracoviruses appear to share one evolutionary origin but apparently are distinct from ichnoviruses. Nevertheless, the genomes of both groups are integrated into their wasp genomes as a provirus and are transmitted as such to the next wasp generation. These PDVs replicate as virions within the epithelium of the ovarian calyx (swollen base of the ovary) but not in the host. Over 30 bracoviruses and more than 20 ichnoviruses have been described from different wasp species. Their genome organization is complex and thought to be more eukaryotic than viral, and is considered to be highly evolved packages of wasp genes.

The major focus of this overview is on viruses other than PDVs, with emphasis on those that belong to recognized/established taxonomic virus families, based on characteristic morphology and/or empirical molecular data. The overview will address basic characteristics of the family of viruses and will discuss reported findings on the biology, location, and putative role of the virus in wasp survival within the host. Where available, aspects of the molecular characterization of genes from relevant viruses will be addressed.

While PDVs are more widely studied, several types of RNA viruses and unipartite double stranded DNA viruses and VLPs have been described from parasitic wasps and are known or presumed to be transmitted to their hosts during oviposition. Some of these belong to six known virus families (Ascoviridae, Baculoviridae, Picarnoviridae, Poxviridae, Reoviridae, and Rhabdoviridae) but fewer than 20% of these viruses have been characterized, in whole or in part, at the molecular level. Most VLPs have been described only by their shape and size, with no demonstrated relationship to known virus families. No nucleic acids have been detected in some of these, suggesting that VLPs vary in their evolution from true viruses to other entities that have co-evolved with the parasitic wasp. All viruses and VLPs described to date were reported from either the epithelium of the ovarian calyx or the lumen of the poison gland apparatus of the female wasp, but most are presumed to be transmitted to the host during oviposition since these sites are confluent with the oviducal canal. Fewer, however, have been traced to the parasitized hosts as well, providing direct evidence of transmission from the wasp. Following is an overview of wasp-associated viruses from recognized virus families excluding the PDVs and unclassified VLPs that lack morphological or molecular relationship to recognized virus families.

Ascoviridae

Ascoviruses are a recently established group of large (400 × 130 nm), double-stranded, enveloped DNA viruses with an electron dense core and are all presumed to have a circular genome of about 100–180 kb. The virions vary in shape from allantoid to reniform and bacilliform and infect primarily noctuid larvae. The noctuid-attacking ascoviruses of *Spodoptera frugiperda* (SfAV1), *Trichoplusia ni* (TnAV2), and *Heliothis virescens* (HvAV3) are mechanically transmitted by ovipositing wasps and are highly pathogenic to their hosts. They presumably retard and even kill developing parasitoid larvae within infected hosts, are therefore not beneficial to the parasitoid and are not considered here among the symbiotic viruses.

The *Diadromus pulchellus* ascovirus (DpAV4) is 220 × 150 nm and replicates in both the ichneumonid wasp vector *D. pulchellus* and its noctuid host *Acrolepiopsis assectella* and enhances the development of the wasp larva. DpAV4 is the first unipartite DNA symbiotic virus to be characterized, in whole or in part, at the molecular level. It has a 116 kb circular genome and replicates extra chromosomally in the nuclei of the ovarian calyx of the wasp and of various somatic tissues of male and female wasps, suggesting that the virus is transmitted as an episome. This is in contrast to the PDV proviruses within the wasp's chromosomal DNA. The DpAV4 genome contains several highly conserved (77%) repeats of 494 bp containing sequences similar to the DNA-binding motifs of baculoviruses, herpesviruses, and adenoviruses, although the same viral replication functionality of those motifs cannot be ascribed with certainty. Phylogenetic analysis of the d-DNA polymerases of DpAV4 with those of the noctuid ascoviruses and other DNA viruses, suggested that DpAV4 belongs to a different clade, and likely a different family, from the noctuid ascoviruses and are close relatives of iridoviruses. It is also interesting that motifs known to be conserved within the d-DNA polymerases of baculoviruses, herpesviruses, adenoviruses, and entomopoxviruses also occur in DpAV4 and the other noctuid Ascoviridae. The presence of such motifs may either be a result of viral acquisition of housekeeping genes from their hosts, conservation of original genes from a common ancestral virus, or convergent evolution. Given the paucity of information on the origin and/or evolution of viral symbionts, these and other molecular similarities to known viruses are potentially fruitful avenues of inquiry in the future.

The DpAV4 ascovirus is presumed to have either no effect on, be pathogenic to, or mutualistic with, its host, depending on the species of *Diadromus* wasp that carries it, and this variable relationship is presumed to be regulated by some suppressive/permissive factor found in the wasp females. There is limited evidence of similarities between ichnoviruses and DpAV4, leading to speculation that they may constitute an intermediate in the evolution from the pathogenic ascoviruses to symbiotic form and further, to ichnoviruses.

DpAV4 replicates within host hemocytes and disrupts their encapsulation response, presumably by destroying their intercellular communication and inducing hemocyte segregation. This mechanism, no doubt, enhances the survival of the developing parasite within the host. However, DpAV4 does not benefit all parasitoids that co-occur in the *A. assectella* host. Indeed, it enhanced the development of *D. pulchellus* and its close relative *D. collaris* but retarded and sometimes killed larvae of another but unrelated ichneumonid *Itoplectis tunetana*. In the latter wasp, developmental retardation and death were concomitant with fast replication of DpAV4. The authors therefore hypothesized that the *D. pulchella* and *collaris* female wasps regulate the rate of viral replication to the benefit of the wasp. It is presumed that these wasp females express virus controlling/regulating factors without which viral replication is unchecked, and thereby induce premature death of the host before the wasp completes its development. If this is the case, what is this female factor? Do parasitic wasps that lack this presumed factor also lack symbiotic viruses and if so, what mechanisms do they use to overcome host defenses? Studies on the relationship between

DpAV4 and the three ichneumonid parasitoids raise interesting questions about the biochemical basis of virus acquisition by and compatibility with parasitic wasps and should form the basis for related studies in other host-parasitoid systems.

Baculoviridae

Baculoviruses characteristically have large circular double stranded DNA genomes of 90–160 bp. The enveloped nucleocapsid is rod-shaped and has occluded and non-occluded (budded) forms. The two main members of the group include the granulovirus genus (GVs), distinguished by its granular appearance, and the nucleopolyhedrovirus genus (NPVs) which has a more crystalline structure. GVs only contain a single virion per inclusion body. Prior to the establishment of the Polydnaviridae, VLPs were described from several parasitoid and lepidopteran species as baculoviruses or baculovirus-like. However, most of these have since been reclassified as PDVs. Similarities (multiple nucleocapsides within a viral envelope and virus localization within the host nucleus and replication in the ovarian calyx) between baculoviruses and bracoviruses raise the question of whether PDVs arose from baculoviruses. Baculoviruses in parasitoids are poorly studied, but molecular analyses and other experimental studies could shed further light on the relationships between these two groups.

Poxviridae

Entomopoxviruses (EPVs) represent a subfamily of the Family Poxviridae that are large (200–400 nm in diameter), enveloped, double stranded DNA viruses with unipartite linear genomes of 130–380 kilobase pairs (kbp). EPVs are characterized by a biconcave central core and two lateral bodies and the mature virion is included in a large crystalline proteinaceous matrix called spheroidin, that surrounds and protects the virions from UV damage in the external environment.

The *Diachasmimorpha longicaudata* entomopoxvirus (DlEPV) is the first symbiotic EPV from a parasitoid to be described and for which genes have been sequenced. This virus was first described as an entomopoxvirus-like particle (Fig. 168) in hemocytes of the parasitized tephritid host *Anastrepha suspensa* and was subsequently traced back to the poison gland of the *D. longicaudata* braconid wasp female where they were first shown to undergo morphogenesis and assembly in the gland filaments and the mature virions stored in the gland reservoir. A similar 200 nm membrane-bound particle reported from the poison gland reservoir of the same wasp species was referred to as "irregular" but not described as a virus. The "irregular" description was likely based on the biconcave core, typical of dipteran entomopoxviruses and is most likely DlEPV.

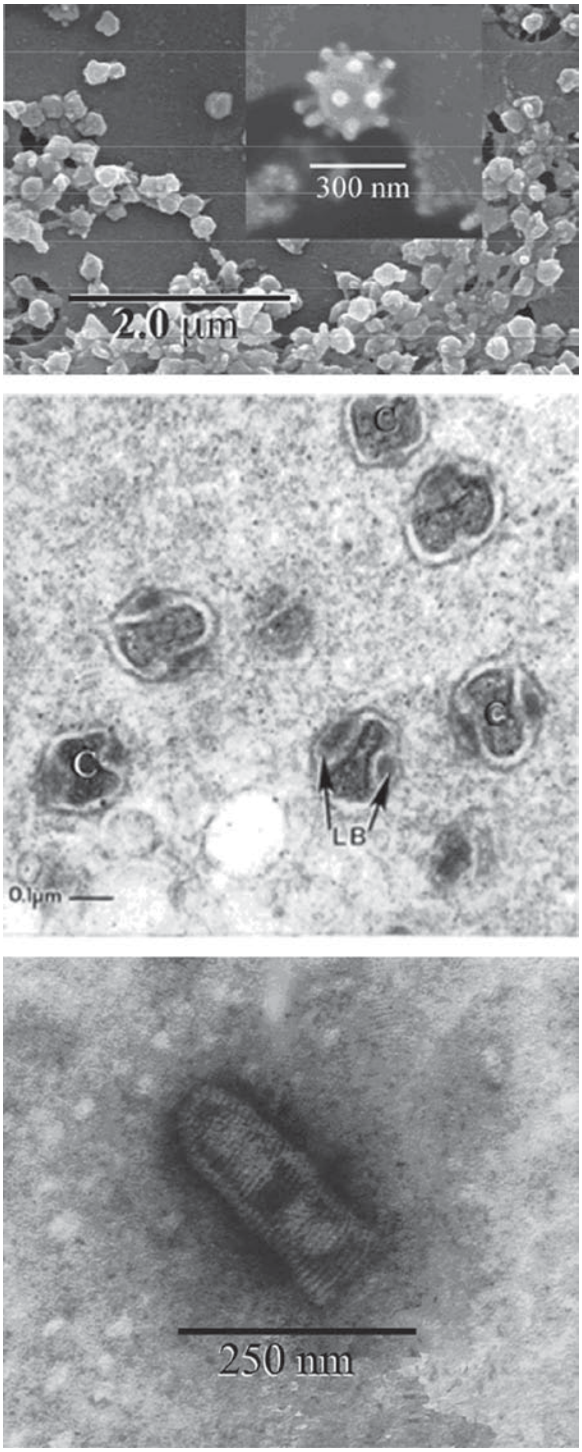
DlEPV has a large (250–300 kb) unipartite DNA genome. Nucleic acid and deduced amino acid sequences of several open reading frames (ORFs) from a DlEPV EcoRI genomic library have facilitated comparisons with other members of the Poxviridae and confirmed its position within the Entomopoxvirinae subfamily. Indeed, DlEPV genes encoding putative proteins such as DNA-directed RNA polymerase, DNA helicase, transcription factors, membrane proteins and RNA polymerase, and a poxvirus rifampicin resistance proteins, have been identified and share up to 60% sequence homology with those of other poxviruses. Thus, DlEPV is included in the subfamily Entomopoxvirinae (ICTVdB, 2002). While it is believed to be the first member of the Group C (Dipteran) EPVs to be characterized, DlEPV genes must first be compared with those from gammaentomopoxviruses. Unfortunately, none have as yet been sequenced.

DlEPV infection inhibits encapsulation of wasp ovarian eggs by inhibiting the cellular encapsulation response of the host. The virus also induces the expression of a host-encoded parasitism-specific protein (PSP24) when the purified virus is injected into healthy fruit flies. DlEPV proteins and DNA also occur in male wasps, suggesting that the virus is transmitted vertically. It remains to be determined whether transmission is as an intact virion or episome within the egg or whether it is eaten by the developing larvae with the virus-infected host hemolymph.

Picornaviridae and Picornalike Viruses

Picornaviruses are isometric/icosahedral virions that lack an envelope and are among a group of small RNA-containing viruses (SRVs) of <40 nm that occur in insects. They have a non-segmented, linear positive-sense, single-stranded RNA genome of about 10 kb. The 5´-end of the negative-sense strand has a covalently attached terminal protein. The 3′-terminus has a poly (A) tract. Some insect viruses with similar characteristics have been described but their fidelity to true Picornaviridae of mammals remains in doubt and as a consequence, are referred to as Picornalike.

Recently, a picornalike virus was found in the *V. canescens* parasitoid and confers protection on the developing parasitoid egg within their lepidopteran host *Ephestia kuehniella*. This small RNA-containing virus was designated VcSRV and co-occurs with the *V. canescens* VLPs (VcVLP) in the lumen of the wasp's ovarian calyx. Upon injection into the larval host, VcSRV invades the hemocytes of the host. The virus induces no obvious pathology to the host but a beneficial role in parasitoid development has not yet been identified.



Symbiotic Viruses of Parasitic Wasps, Figure 168 **(*top*) Electron microscopy (EM) of the *Diachasmimorpha longicaudata* entomopoxvirus (DlEPV). Scanning EM of virion purified from the poison glands of female wasps by sucrose density gradient centrifugation and processed for SEM as previously described (Lawrence and Matos, 2005). The virions are 250–300 nm in diameter from the base of the spikes. (*center*) Transmission EM of DlEPV showing the characteristic biconcave core and two lateral bodies (arrowheads) of poxviruses. (*bottom*) Negative stain of the *Diachasmimorpha longicaudata* rhabdovirus (DlRhV) purified by sucrose density gradient centrifugation. Virions are 60–70 nm in diameter and 250–300 nm long. Note cross striations typical of rhabdoviruses.**

Analysis of the RNA-dependent RNA polymerase protein sequence of VcSRV indicated that the virus is probably related to the infectious flacherie virus [Iflavirus (IFV)] genus and is now recognized as an unassigned member of the Iflavirus genus within the Picornavirales superfamily. Members of the genus Iflavirus have similarities to other picornaviruses but appear to occur primarily in insects.

Picornalike viruses in insects have been reported from dipterans, particularly from *Drosophila* and tephritid fruit flies such as the Mediterranean fruit fly, *Ceratitis capitata*, Queensland fruit fly, *Bactrocera* (*Dacus*) *tryoni*, and the olive fruit fly, *B. olea* and still others occur in Hemiptera and Lepidoptera. Since dipterans, hemipterans, and lepidopterans represent the largest insect orders that contain agricultural pest species, and given the large numbers of parasitoids known to attack them, we should anticipate that many more small RNA viruses will be found in parasitoids. Careful molecular characterization of these viruses should elucidate the possible evolutionary pathways from plant-infesting viruses (of which many picornalike viruses are known), to viruses of plant feeding insects, and ultimately to being beneficial viruses of parasitoids.

Reoviridae

Members of the Reoviridae characteristically have icosahedral virions of 60–80 nm in diameter and lack an envelope. The 2–3 layered nucleocapsid contains a linear genome of 10–12 segments of double-stranded RNA varying from about 18 to 31 kb. Each segment has a duplexed positive and negative strand. The termini of the negative strands are phosphorylated while the 5′ end of the positive strand is capped. Particles matching the description of reoviruses (RV) that appear to be symbiotic to parasitoids include DpRV-1 and DpRV-2 found in *D. pulchellus*. DpRV-1 occurs along with the ascovirus DpAV-4a (see above) and is hypothesized as benefiting the developing wasp indirectly by slowing down the rate of the ascovirus replication within the host. DpRV-2 is beneficial to certain *D. pulchellus* wasp populations by being immunosuppressive to their lepidopteran host.

The reovirus McRVLP found in the braconid *Microplitis croceipes*, and HeRV from the ichneumonid *Hyposoter exiguae*, are morphologically distinct and are regarded as "non pathogenic commensals" of the wasps. This is because they are not only found in reproductive tissues of female wasps but also in non-reproductive tissues of both sexes (though not in all strains of the parasitoid) and cause no pathology or obvious benefit to the parasitoid. A reovirus-like particle (OpRVLP) also occurs in the poison gland apparatus of *Opius* (now *Psyttalia*) *concolor*, a braconid parasitoid of tephritids. The uncharacterized OpRVLP is a double enveloped icosahedral particle, 72 nm in diameter, and possesses an "inner shell" with "hollow spikes at the vertices" and occurs in the poison gland lumen in association with secretory vesicles. There is no direct evidence that this VLP is transmitted to the tephritid host or what role, if any, it plays in the survival of the *O. concolor* immatures within the tephritid host. However, its presence within the lumen of the poison gland suggests that it is injected into the host during oviposition. As has been observed with most of the viruses and VLPs reported to date, OpRVLP co-occurs in the poison gland with a second, slightly smaller VLP, presumably a coronavirus-like particle. No nucleic acid characterization of these particles has been done. However, reoviruses have been found in the gut of one of the hosts, *C. capitata*, of *O. concolor*. This system could be a candidate for studies on the evolution of symbiotic wasp viruses through initial contamination by pathogenic viruses of their hosts. It is apparent that molecular characterizations of these reoviruses are needed along with a detailed analysis of their replication in wasp and host. The results could provide meaningful insights into the potential of these viruses as microbial control agents against tephritid pests.

Rhabdoviridae

Rhabdoviruses are enveloped, negative sense, non-segmented single stranded RNA viruses. They replicate in the cell cytoplasm of numerous plants, insects, and vertebrates. Several are vectored by insects. Virions are usually bullet-shaped and are about 180 nm × 70 nm, with some phyto rhabdoviruses being bacilliform and more than 300 nm long. Virions characteristically have spike-like projections arising from the major membrane glycoprotein that are apparent in negatively stained virions.

The *D. longicaudata* rhabdovirus originally described as a rod-shaped particle has been shown to replicate in the cytoplasm of accessory gland filament cells of the poison gland apparatus of the parasitoid and in vesicles of the epithelium of parasitized *A. suspensa* puparia, an indication of direct transmission from wasp to host. While the nucleic acid of this virus (called DlRhV) has not yet been characterized, negative stain and transmission electron microscopy reveal typical rhabdovirus morphology and replication within both the wasp and the *A. suspensa* tephritid host. DlRhV morphogenesis is evidenced by the presence of paracrystalline arrays of the immature particles. The replication and aggregation of mature virions are associated with secretory vesicles, as has been reported for other rhabdoviruses.

Within 24 h of injection into its host, DlRhV particles affix to cells associated with the tracheae and invade hemocytes where they replicate but after 30–40 h post infection, disappear from the hemolymph and migrate to the epidermal cells where they traverse the basement membrane and aggregate in the epidermal cell vesicles from which they bud to invade new cells. In superparasitized hosts, virus overload of vesicles is presumed to inhibit the migration of vesicles containing molting fluid, and hence inhibit apolysis. DlRhV is the first rhabdovirus reported from a parasitic wasp but its specific role in the virus-wasp relationship needs to be clarified.

DlRhV is transmitted vertically as intact virions in the subchorionic spaces of postvitellogenic eggs in the ovary. Although virions are observed in the midgut of first instars of the wasps during feeding on infected host hemolymph, it is not clear whether these virions are able to penetrate the midgut and enter the hemocele and ultimately, enter the poison gland as a secondary avenue of virus transmission to wasp offspring.

Summary and Conclusion

There is either direct or reasonable circumstantial evidence that several types of viruses enhance the survival of the immature wasp within their insect hosts. Here are discussed the wasp viruses that, on the basis of either characteristic virion morphology and/or molecular characterization of one or more viral genes, can be placed in established/recognized virus families and, as such, are regarded as true viruses. Because PDVs are the best studied parasitoid-associated "viruses," a synopsis of the group is provided here but the reader is encouraged to consult recent reviews as well as other papers describing more detailed molecular characterization of the many PDVs that have been described. PDVs are regarded either as viruses that are so highly co-evolved with their parasitoids that they no longer exhibit true viral characteristics (e.g., virions do not replicate within the host insect) or are packaged wasp genes that have evolved to manipulate the host and enhance the survival of the wasp's offspring. Numerous other viruses and VLPs reported from parasitoids remain unclassified due to lack of molecular characterization of their nucleic acids or the absence of nucleic acids, as in the case of *V. canescens*.

This overview of parasitoid viruses from six established virus families (Ascoviridae, Baculoviridae, Poxviridae, Picornaviridae, Reoviridae, and Rhabdoviridae) demonstrates that much remains to be done to better characterize these viruses at the molecular level. There is preliminary evidence that parasitoids of the same host or faunistic complex of hosts probably contain the same or closely related viruses and lend support to the hypothesis that symbiotic viruses of wasps may have arisen through contamination by viral pathogens from insect hosts. The presence of viruses from taxonomically established virus families, with relatives in plants or in non-parasitoid insects, provides an exciting opportunity for developmental and molecular studies on the evolution of virus-wasp-pest host relationships. This is especially true with RNA viruses that have wide distribution among plant, insect, and vertebrate hosts. It is hoped that this overview will stimulate further study of this topic as it is also likely to lead to novel approaches to agricultural pest control either through use of the viruses directly, or through molecular manipulation that would render parasitoids more effective biological control agents. Some parasitoids may lack VLPs or viruses altogether. Nevertheless, they are able to circumvent the host's immune system and develop successfully.

References

Bigot Y, Rabouille A, Doury G, Sizaret PY, Delbost F, Hamelin MH, Periquet G (1997) Biological and molecular features of the relationships between *Diadromus pulchellus* ascovirus, a parasitoid hymenopteran wasp (*Diadromus pulchellus*) and its lepidopteran host, *Acrolepiopsis assectella*. J Gen Virol 78:1149–1163

Federici BA, Bigot Y (2003) Origin and evolution of polydnaviruses by symbiogenesis of insect DNA viruses in endoparasitic wasps. J Insect Physiol 49:419–432

Fleming J (1992) Polydnaviruses: Mutualists and pathogens. Ann Rev Entomol 37:401–425

Lawrence P (2005) Non-poly-DNA viruses, their parasitic wasps, and hosts. J Insect Physiol 51:99–101

Lawrence P (2005) Morphogenesis and cytopathic effects of the *Diachasmimorpha longicaudata* entomopoxvirus in host haemocytes. J Insect Physiol 51:221–233

Lawrence PO, Akin A (1990) Virus-like particles from the poison gland of the parasitic wasp *Biosteres longicaudatus* (Hymenoptera: Braconidae). Can J Zool 68:539–546

Prevost G, Eslin P, Doury G, Moreau S, Guillot S (2005) *Asobara*, braconid parasitoids of *Drosophila* larvae: unusual strategies to avoid encapsulation without VLPs. J Insect Physiol 51:171–179

Schmidt O, Schuchmann-Feddersen I (1989) Role of virus-like particles in parasitoid-host interaction of insects. In: Harris JR (ed) Subcellular biochemistry: virally infected-cells, vol 15. Plenum Press, New York, NY, pp 91–119

Stoltz D, Whitfield J (1992) Viruses and virus-like entities in the parasitic Hymenoptera. J Hymenopt Res 1:125–139

Whitfield J, Asgari S (2003) Virus or not? Phylogenetics of polydnaviruses and their wasp carriers. J Insect Physiol 49:397–405

Sympatric

Possessing the same geographic range as a related organism without loss of genetic identity (contrast with allopatric)

Sympatric Speciation

Speciation that occurs in the same place, due to such factors as consumption of different food (allophagic speciation) or occurrence at different times (allochronic speciation).

► Species Concepts
► Species Processes Among Insects

Symphylans (Class Symphyla)

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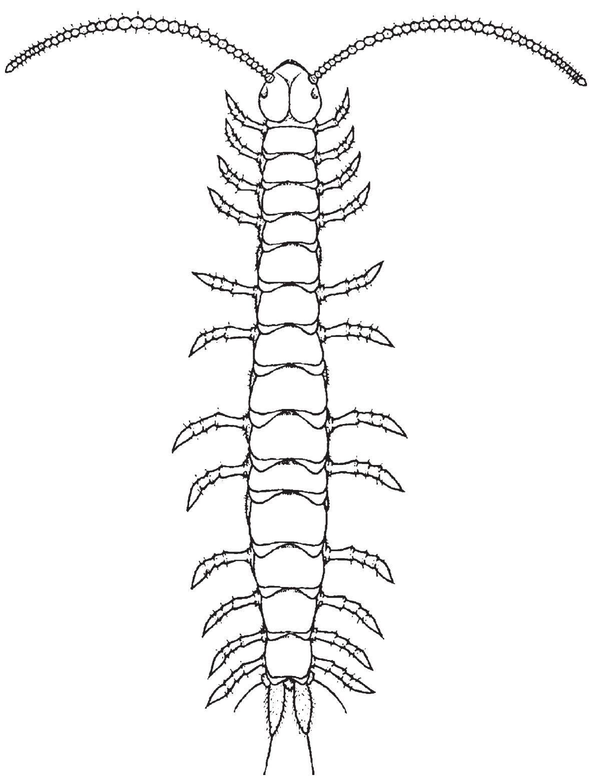
Symphylans are insect relatives in the subphylum Atelocerata (Myriapoda), and are related to centipedes (Chilopoda) and millipedes (Diplopoda). They possess a single pair of Malpighian tubules, no median simple eyes, and have tomosvary organs (humidity and/or chemoreceptors). They also have musculated antenna and diffuse nervous systems. There are approximately 160 species within the single order.

Phylum: Arthropoda
Subphylum: Atelocerata
Class: Symphyla
Order: Scolopendrellida

The apterygotes (wingless insects) may be derived from ancestral symphylans via paedomorphosis (juvenile characteristics are retained in the adult.).

Symphyla are <10 mm long, slightly dorsoventrally compressed, and white or colorless with a slender, soft body. They resemble small centipedes without the fangs found in Chilopoda. The head is distinct and well-developed, and the mouthparts are endognathous (mouthparts are concealed by the labium or cranial folds). Symphylans resemble the apterygotes with a single pair of long antenna with many segments and a single pair of spiracles are open on the head. They lack eyes and are blind. There are 15–22 body segments present, with an average of 15. Each body segment has one pair of hook-like legs. Immatures begin with 6–7 pairs of legs. All legs on one side move simultaneously, alternating side to side (Fig. 169).



Symphylans (Class Symphyla), Figure 169 An adult symphylan (original by M. L. Baker, Louisiana State University-Shreveport).

There are two legless caudal segments at the tip of the body, which may posses a pair of spinnerets for silk production. The number of dorsal tergites (14–24) exceeds the number of true segments. The fourth segment has a gonopore. In an unusual fertilization ritual, the egg is taken from the gonopore and stored in the mouth, where it is exposed to sperm from a spermatophore. Spermatophores are generally deposited on the ground. Ten to twenty eggs are laid in clusters on the soil. Symphylans do not dig tunnels, but take advantage of naturally occurring cracks and worm burrows for shelter. Symphylans inhabit soil that is rich in organic material, particularly humus and decaying wood. They feed on plant material, especially the roots. They can become a pest in greenhouses and in the field. They are cosmopolitan, yet concentrated in the tropics. Garden symphylan, *Scutigerella immaculata* (Newport), is the best known of the pests species, and has a wide host range. Though likely originating in Europe, it is now widely distributed.

References

Barnes RSK (ed) (1998) The diversity of living organisms. Blackwell, Oxford, UK, 345 pp

Borror DJ, Triplehorn CA, Johnson NF (1989) An introduction to the study of insects, 6th edn. Harcourt Brace College Publishers, Stamford, Connecticut

Michelbacher AE (1938) The biology of the garden centipede, *Scutigerella immaculata*. Hilgardia 11:55–148

Symptom

Any aberration in function (including behavior), indicating disease. (contrast with sign)

Synanthropic

Living in association with humans, without actually feeding on humans.

Synapse, pl., synapses

The narrow gap between two nerves, or between a nerve and a muscle, that is bridged by a chemical neurotransmitter. Acetylcholine is a major synaptic transmitter in the insect central nervous system.

► Nervous System

Synchroa Beetles

Members of the family Synchroidae (order Coleoptera).

► Beetles

Synchroidae

A family of beetles (order Coleoptera). They commonly are known as synchroa beetles.

► Beetles

Synchronous Muscle

Muscle in which the frequency of contraction is controlled directly by nervous impulses, with each contraction caused by nervous stimulation. (contrast with asynchronous muscle)

Syndrome

A group of signs and symptoms characteristic of a particular disease.

Synecology

Study of groups of organisms in relation to their environment (population, community, and ecosystem ecology).

Synergism

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Chemical interactions may occur when two or more toxic chemicals are given to a living organism simultaneously or sequentially. Such interactions may result in a toxicity that is additive of individual toxicities of the chemicals or that is greater or less than the additive toxicity of these chemicals if administrated separately. Generally, the effects of chemical interactions can be divided into four types, including additive effects, synergism, potentiation and antagonism (Table 28).

Both synergism and potentiation refer to the action or phenomenon in which two or more chemicals (e.g., insecticides) administered simultaneously

Synergism, Table 28 Effects of chemical interactions on chemical toxicity

Chemical effect	Characteristics of chemical effect
Additive toxicity	The combined toxicity of two chemicals administered together is equal to the sum of the toxicities of the chemicals administered separately.
Synergism	The combined toxicity of two chemicals administered together is greater than the sum of the toxicities of these chemicals, one of which has little or no intrinsic toxicity, if administered separately.
Potentiation	The combined toxicity of two chemicals administered together is greater than the sum of the toxicities of these chemicals; both have appreciable toxicities if administered separately.
Antagonism	The combined toxicity of two chemicals administered together is less than the sum of the toxicities of these chemicals administered separately.

or sequentially achieve a greater toxicity than the sum of the individual toxicities of the chemicals administered separately. However, the term synergism is reserved for the case in which one chemical has little or no toxicity if administered alone, whereas in the case of potentiation both chemicals have appreciable toxicities.

A relatively non-toxic chemical substance applied with an insecticide to increase the toxicity of the insecticide against insect pests is known as a synergist. Different synergists may confer their synergistic effects on an insecticide through different mechanisms. They may inhibit the metabolic detoxification of the insecticide, increase the penetration of the insecticide through the insect cuticle, or act at the binding site(s) of the insecticide on the receptor proteins in target insects.

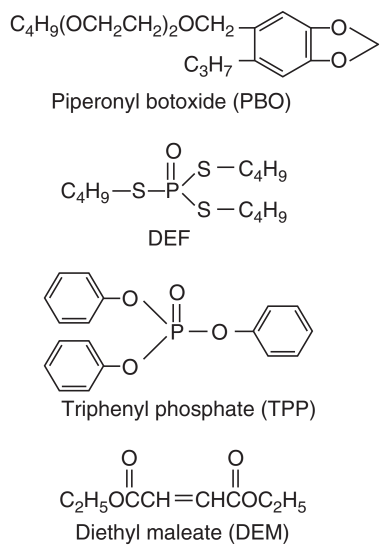
The most commonly used insecticide synergists are metabolic inhibitors that block certain detoxification enzymes so that insecticide detoxification in target insects is abolished or significantly reduced. Such synergists may serve as research tools to help determine the mechanisms of insecticide detoxification in a living organism and as control agents to increase the efficacy of insecticides in a pest management program. For example, the insecticide synergist piperonyl butoxide (PB or PBO) is a rather potent inhibitor of cytochrome P450-dependent polysubstrate monooxygenases (PSMOs, formerly known as mixed-function oxidases or MFOs), a major group of detoxification enzymes in living organisms. Both DEF (*S,S,S*-tributyl phosphorotrithioate) and triphenyl phosphate (TPP) inhibit various esterases that may be involved in detoxification of various insecticides including organophosphates, carbamates and pyrethroids. Currently, there is no specific inhibitor available for glutathione *S*-transferases (GSTs). However, diethyl maleate (DEM), which conjugates with and rapidly depletes glutathione, has been commonly used as a synergist to suppress the GST activity (Fig. 170).

The degree of synergism is often determined by two parallel but separate bioassays for an insecticide. One bioassay treats insects with mixtures of the insecticide and synergist or pretreats the insects with synergist and then with insecticide. The other bioassay treats the insects with insecticide only. If both bioassays determine the LD_{50} (lethal dose for 50% of the target insect population) values for the insecticide with and without the synergist, the level of synergism, which often is presented as the synergism ratio (SR), can be calculated:

$$SR = LD_{50}\text{ (Without synergist)}/LD_{50}\text{ (With synergist)}$$

Insecticide bioassays with synergists can help researchers learn possible detoxification mechanisms for a particular insecticide in a target population. For example, Yang et al. (2001) evaluated the susceptibility and possible detoxification mechanisms of the Banks grass mite (BGM), *Oligonychus pratensis* (Banks), and the two-spotted spider mite (TSM), *Tetranychus urticae* Koch, to three selected insecticides with three synergists (TPP, DEM and PBO) (Table 29). Their study suggests that esterases, GSTs, and PSMOs all play important roles in the detoxification of the pyrethroid bifenthrin in the two-spotted spider mite because TPP, DEM and PBO enhanced the toxicity of bifenthrin by 6.2-, 4.1- and 4.5-fold, respectively.

► Synergist



Synergism, Figure 170 Chemical structure of some commonly used insecticide synergists.

Synergism, Table 29 Effect of three synergists (TPP, DEM, and PBO) on bifenthrin toxicity against the two-spotted spider mite using glass vial residual contact bioassay

Chemical	LC50 (95% CI) (μg/ml)	DF	Slope + SE	P(x^2)	SR
Bifenthrin	114.0 (92.3–144.0)	5	0.42 ± 0.03	0.35	—
Bifenthrin + TPP	18.5 (13.9–23.6)	5	0.37 ± 0.03	0.32	6.2
Bifenthrin + DEM	27.5 (20–5–36.8)	4	0.34 ± 0.03	0.45	4.1
Bifenthrin + PBO	25.1 (19.8–31.0)	5	0.42 ± 0.03	0.20	4.5

Data adapted from Yang et al. (2001)

References

B-Bernard C, Philogène JR (1993)Insecticide synergists: role, importance, and perspectives. J Toxicol Environ Health 38:199–223

Eaton DL, Klaassen CD (2001) Principles of toxicology. In: Klaassen CD (ed) Cassarett and Doull's toxicology: the basic science of poisons, 6th edn. McGraw-Hill, New York, NY, pp 11–34

Gordh G, Headrick DH (2001) A dictionary of entomology. CABI Publishing, New York, NY, 1032 pp

Hodgson E (1994) Chemical and environmental factors affecting metabolism of xenobiotics. In: Hodgson E, Levi PE (eds) Introduction to biochemical toxicology. Appleton & Lange, Norwalk, Connecticut, pp 154–175

Parkinson A (2001) Biotransformation of xenobiotics. In: Klaassen CD (ed) Cassarett and Doull's toxicology: the basic science of poisons, 6th edn. McGraw-Hill, New York, NY, pp 133–224

Raffa KF, Priester TM (1985) Synergists as research tools and control agents in agriculture. J Agric Entomol 2:27–45

Yang X, Zhu KY, Buschman LL, Margolies DC (2001) Comparative susceptibility and possible detoxification mechanisms for selected miticides in banks grass mite and two-spotted spider mite (Acari: Tetranychidae). Exp Appl Acarol 25:293–299

Synergist

Synergists are chemicals that lack pesticidal properties on their own but increase the toxicity of pesticides (other chemicals). They inhibit degradative enzymes (mixed function oxidase, or MFO) such as P450 monooxygenases. Examples of synergists include sesamex, *n*-propyl isome, sulfoxide, piperonyl butoxide, and MGK 264. Initially used extensively to increase the toxicity of pyrethrum, and used to some degree with other pesticides (the effectiveness varies among insecticides), synergists have become of increased importance in recent years as pyrethroid insecticides have increased in use.

The most common synergist is piperonyl butoxide, which was developed in 1947. It functions by inhibiting the breakdown of pesticides by insects. Without piperonyl butoxide, insects may degrade the insecticide before mortality can occur, and recover from the poisoning. In addition to reducing the ability of insects to recover from insecticide poisoning, addition of piperonyl butoxide to insecticide formulations usually reduces the amount of active ingredient needed in the formulation, thus reducing pesticide load in the environment and potentially reducing cost. It is applied to all types of insecticide formulations, especially household pesticides and livestock treatments. Piperonyl butoxide alone has very little toxicity. It is not persistent in the environment. Long-term exposure may have effects on the liver, however.

► Synergism

Reference

Jones DG (ed) (1998) Piperonly butoxide – the insecticide synergist. Academic Press, San Diego, CA, 336 pp

Synlestidae

A family of damselflies (order Odonata).

► Dragonflies and Damselflies

Synomone

A chemical produced by one organism and perceived by another that benefits both organisms. An example is the release of chemical elicitors by plants that attract entomophagous insects when they are attacked by herbivores.

► Chemical Ecology
► Allelochemicals
► Semiochemical Parsimony
► Multifunctional Semiochemicals

Syringogastridae

A family of flies (order Diptera).

► Flies

Syrphid Flies

Members of the family Syrphidae (order Diptera).

► Flies

Syrphidae

A family of flies (order Diptera). They commonly are known as flower flies, hover flies, or syrphid flies.

► Flies

Systematics

In entomology, an abbreviated form of "biosystematics," the relationships of taxa based on study of their genetics and evolutionary history.

Systematic Sampling

A method of allocating sample units within a sample universe in which sample units are collected at fixed intervals along a predetermined pattern. Examples include sampling along transects or along V or X shaped patterns in crop fields. Often, the starting point of the pattern is determined randomly. Systematic sampling is probably the most common method for allocating sample units in most agricultural systems because it is simple and time-efficient.

► Sampling Insects

Systemic

Absorbed and translocated through the vascular system of plants or animals.

► Insecticides
► Insecticide Formulations

Szent-Ivány, József Gyula Hubertus

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József Szent-Ivány was born on the 3rd of November 1910 in Budapest, Hungary. He matriculated in Rimaszombat and from 1928 he continued his studies in Vienna, Austria. Between 1933 and 1936, he was a student at the Budapest University of Science, where he completed his studies and received his doctoral degree of zoology, geography and mineralogy. In 1936, he joined the staff of the Hungarian Natural History Museum, where he primarily worked on Lepidoptera. In 1938, he established Fragmenta Faunistica Hungarica, a zoological journal, and from 1937 until 1944 he was the editor of Folia Entomologica, the official publication of the Hungarian Entomological Society. He collected huge numbers of Lepidoptera for the museum and during World War II, at his own cost, he translocated the entire collection from Budapest to Tihany, a small town where it was safe from bombing raids. The war disrupted his scientific work and as the Russians occupied the country, he fled to the West. In 1950, he migrated to Australia but it took another 4 years before he could continue with his entomological work. He gained employment as government entomologist in Papua New Guinea. He spent 12 years there, building an insect collection of more than 100,000 specimens, which formed the basis of the Papua New Guinea Entomological Institute. His entomological activities were not restricted to collecting and taxonomy alone. He took active part in running the Institute and conducting numerous studies in the field of crop protection against insect pests, projects of medical and forest entomology, environmental studies and a whole host of other scientific activities. He published a great number of papers, mostly in English, German and Hungarian. After his retirement in 1966, he remained active as an entomologist, taking on many assigments, consultation projects and honorary positions. From 1972–74 he was the president of the committee which investigated and found the lost grave of Sámuel Fenichel at Stephansort. In 1975, the newly established entomological research station in Wau was named Szent-Ivány Laboratory. In 1985, he received from Queen Elizabeth II the Order of Australia. In 1988, he was admitted into the Hungarian Academy of Science. A few days after this honor, on the 8th of June 1988, József Szent-Ivány passed away.

References

Gressitt JI (1968) Szent-Ivány, J. Bibliography of New Guinea entomology. Honolulu, Hawaii

Balázs D (1989) Búcsú Szent-Ivány Józseftő l. Földrajzi Múzeum Tan, 6

T

Tabanidae

A family of flies (order Diptera). They commonly are known as horse flies or deer flies, and some are called yellow flies or greenheads.

► Flies

Tachinidae

A family of flies (order Diptera). They commonly are known as tachinid flies.

► Flies
► Tachinid Flies

Tachinid Flies (Diptera: Tachinidae)

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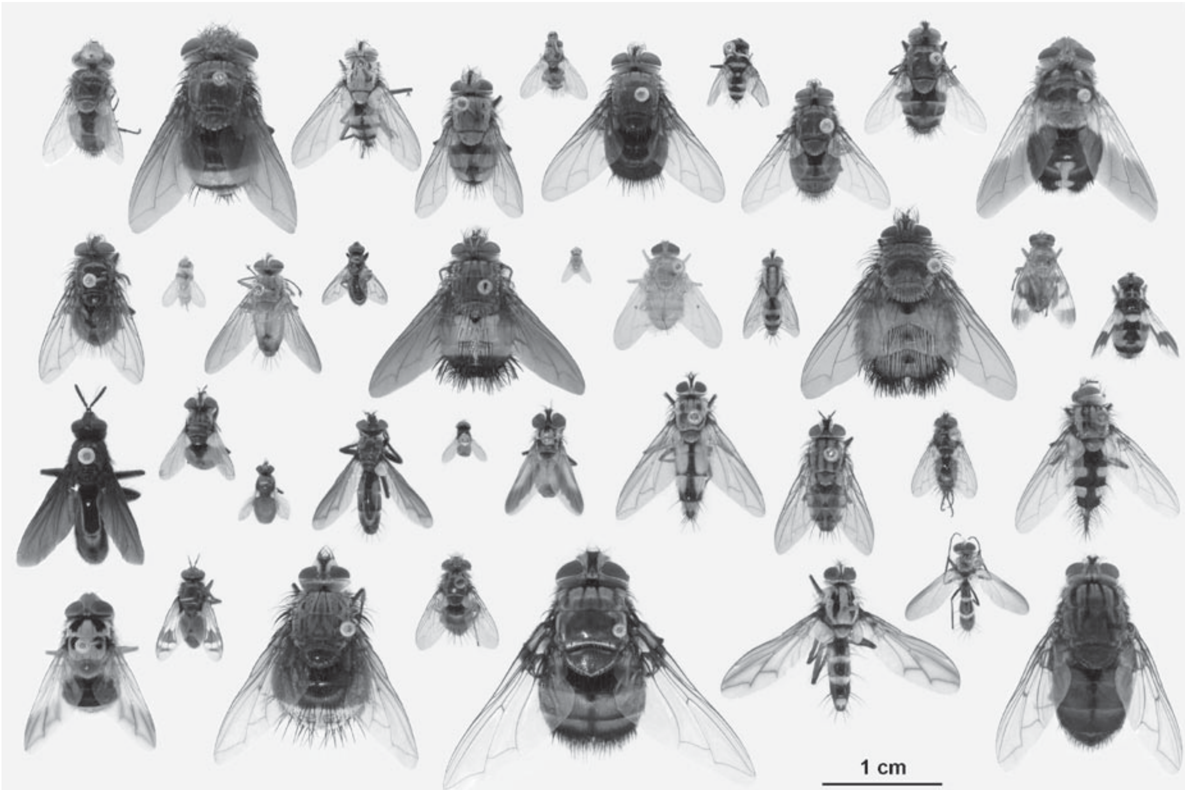
There are well over 100 families in the order Diptera, or true flies, and most of them are comprised entirely of species with free-living larvae. There are, however, about 20 families with at least some species classed as parasitoids, species that live within other animals as larvae and kill their hosts before progressing on to the adult stage. It is estimated that this type of parasitic life style evolved over 100 times in the Diptera and multiple times within certain families. About 16,000 of the approximately 120,000 described species of Diptera are parasitoids, and about 10,000 of them belong to a single family, the Tachinidae. All tachinid flies are parasitoids in their larval stage and their hosts all belong to the Arthropoda, almost exclusively the Insecta. The true diversity of the Tachinidae is likely many thousands of species higher than the 10,000 currently described, making this family a good candidate for the most speciose family of Diptera and without question the most successful with a parasitic way of life.

Most tachinid flies are larger than a house fly and noticeably more bristly, but they range in size from 2–20 mm and across the family there is a tremendous variety of shapes, colors and degree of bristling. The features upon which the family is founded and that support its monophyly (descent from a common ancestor) are rather subtle. In addition to features shared with other families of the Oestroidea (Rhinophoridae, Sarcophagidae, Calliphoridae, and Oestridae), adult tachinids possess a well developed postscutellum (a rounded bulge below the hind part of the thoracic dorsum) and the labrum (or mouth hook) of the first instar larva is fused with the cephalopharyngeal skeleton. The family is cosmopolitan in distribution and most diverse in the subtropics and tropics.

Classification

The Tachinidae are currently divided into four subfamilies, the Phasiinae, Dexiinae, Exoristinae and Tachininae (see Fig. 1 for representatives of each). The smallest of these in terms of species,



Tachinid Flies (Diptera: Tachinidae), Figure 1 **Representative Tachinidae. Row 1 (top), left to right: Exoristinae, *Gonia porca*, *Belvosia bifasciata*, *Calolydella lathami*, *Chrysoexorista ochracea*, *Cyzenis browni*, *Leschenaultia fusca*, *Trigonospila* sp., *Lespesia stonei*, *Winthemia vesiculata*; Tachininae, *Microtropesa* sp. Row 2: Tachininae, *Chrysotachina* sp., *Siphona (Siphona) lutea*, *Genea* sp., *Euscopolia dacotensis*, *Xanthoepalpus bicolor*, *Siphona (Baeomyia) xanthogaster*, *Ormia reinhardi*, *Vanderwulpia sequens*, *Paradejeania rutilioides*, *Oestrophasia* sp., *Neximyia* sp. Row 3: Phasiinae, *Penthosia satanica*, *Gymnosoma par*, *Besseria brevipennis*, *Cylindromyia (Cylindromyia) euchenor*, *Phasia aldrichi*, *Trichopoda* sp.; Dexiinae, *Zelia vertebrata*, *Billaea* sp., *Periscepsia (Ramonda) clesides*, *Uramya halisidotae*. Row 4: Dexiinae, *Amphitropesa* sp., *Euthera tentatrix*, *Euchaetogyne roederi*, *Voria aurifrons*, *Rutilia (Donovanius) regalis*, *Euantha litturata*, *Cordyligaster septentrianalis*, *Trixodes obesus*.**

the Phasiinae, is possibly but not demonstrably a monophyletic lineage in which all species are parasitoids of Hemiptera-Heteroptera, or true bugs. The Phasiinae are morphologically diverse and include most of the tachinid species that lack strong bristling. The Dexiinae are the next largest subfamily and the only one widely regarded as monophyletic, a belief based on shared derived features of the male terminalia. In particular, male dexiines possess a hinged connection between the basiphallus and distiphallus of the phallus (or aedeagus) that is not found in other tachinids. Some of the most visually stunning tachinids belong to the dexiine tribe Rutiliini, an Oriental and Australasian group of mostly large and metallic-colored flies. The Exoristinae and Tachininae are the most speciose subfamilies. The former is more homogeneous in appearance, with many species grayish black in color and moderately bristly. Given this combination of homogeneity and diversity, the Exoristinae are, as a group, the most taxonomically difficult of all Tachinidae. The Tachininae are more morphologically diverse and include some of the largest, most colorful, and most bristly of tachinids. The subfamily also includes some of the smallest and least conspicuous tachinids.

The phylogenetic relationships within the Tachinidae are unclear at the higher levels. There are currently about 40 tribes recognized, but not all are monophyletic and the relationships within and between them are poorly known. Many of the main characters used to distinguish tachinid species are not unique to particular lineages, thus inhibiting attempts to infer relationships through parsimony analysis of external morphological traits. It is possible that more detailed study of male and female terminalia and immature stages will provide better, less homoplastic, characters for phylogenetic analysis. Molecular systematics is beginning to show promise in the elucidation of tachinid relationships but there have been few studies to date.

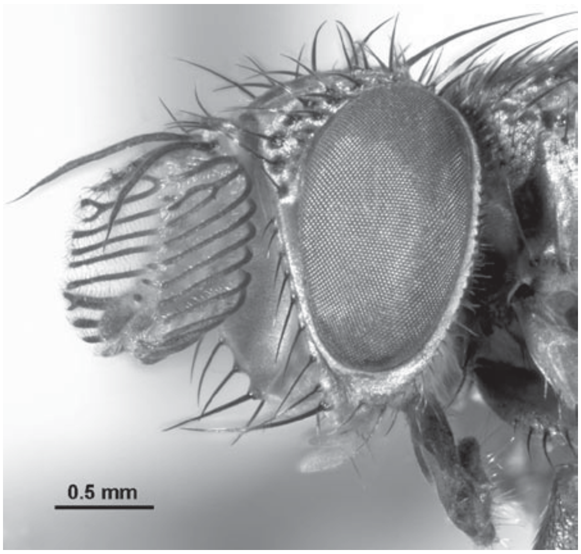
The classification at the generic level is relatively stable in the Nearctic and Palearctic regions where the tachinid faunas are fairly well known. There are literally thousands of undescribed species in the other regions, and until those species have been better studied the genera of those regions will remain poorly characterized. Certain authors in the first half of the 1900s had a tendency to oversplit the Tachinidae to the extent that each genus would often comprise only one or two species, and this legacy is still in evidence today in less studied parts of the world. For example, the Neotropical Region has nearly 30% of all described tachinid species but over 50% of all genera.

Life Stages

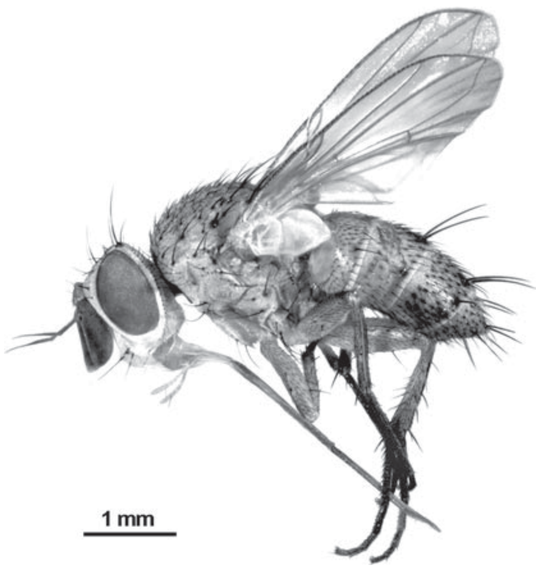
Adult

The variation in size and shape of adult tachinids has been mentioned above and is evident in the specimens shown in Figure 1. Tachinids range in color from pale yellow to jet black, with some species shiny metallic blue or purple (e.g., *Gymnocheta*), or brilliantly metallic and multicolored (many Rutiliini). Wings are usually clear but are darkened or patterned in some species, or even bicolored. Despite the huge range in size, shape and color within the family, the majority of tachinids are grayish black and 5–10 mm in length. Many species have four black longitudinal stripes on the thorax, in contrast to members of the closely related family Sarcophagidae that usually have three stripes.

The head is about the width of the thorax, with compound eyes that vary in size from about half head height to almost head height. Eyes are only rarely holoptic (meeting above) and range from bare to densely haired. Antennae range from tiny to enlarged and in certain species (males only) are bifid, trifid, or elaborately branched (Fig. 2). Mouthparts are present and functional, apically padlike for feeding on liquids (e.g., nectar and honey dew), and occasionally greatly elongated (up to length of body) (Fig. 3). Chaetotaxy (arrangement of setae) on the head is greatly varied and very useful for the identification of species.



Tachinid Flies (Diptera: Tachinidae), Figure 2
Head of male *Borgmeiermyia* sp., illustrating elaborately branched antenna.



Tachinid Flies (Diptera: Tachinidae), Figure 3
***Siphona pisinnia*, illustrating unusually long proboscis.**

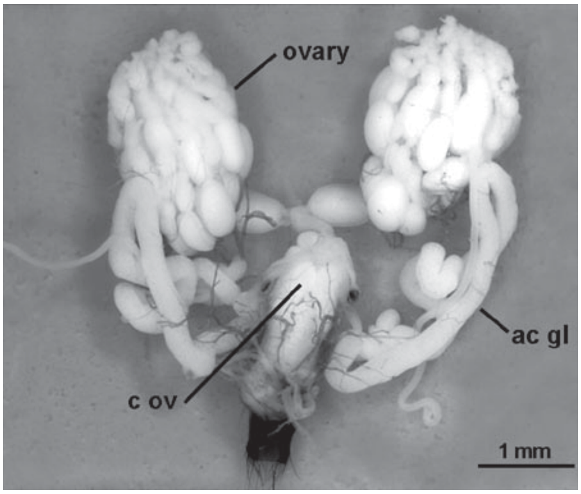
The thorax is slender to broad, typically setose but almost bare dorsally in many Phasiinae. The prosternum between the fore legs is typically haired in Exoristinae, bare in Phasiinae and Dexiinae, and varied in Tachininae. Legs are setose and in some groups elongated, without elaborate modifications except for the flattened, feather-like setae on the hind tibia of *Trichopoda*. Wings are well developed, haired along several veins in a few species, and show some variation in venation. Vein *M* in the center of the wing has a bend near the wing margin (bend rarely absent, e.g., *Cinochira*) and the vein may terminate in vein R_{4+5} or the wing margin. Very rarely, vein *M* fades out at about the usual location of the bend. Chaetotaxy of the thorax, especially the arrangement of setae on the upper surface (i.e., scutum and scutellum), is taxonomically and diagnostically very important.

The abdomen is greatly varied from narrow and long to short and round, and from nearly bare to thickly setose. A few species are very good wasp mimics (e.g., *Cylindromyia* (*Ichneumonops*) *mirabilis*) with a wasp-like abdomen. Males of some *Uramya* species have the tip of tergite 5 constricted and lengthened posteriorly into an almost cone-like appendage that can be nearly as long as the rest of the abdomen (slightly developed in *Uramya halisidotae,* see Fig. 1). Segments 6–11 comprise the terminalia and are highly varied morphologically in both sexes. The female terminalia show obvious modifications related to oviposition: short unspecialized ovipositors in most species that lay eggs on foliage, tubular telescopic ovipositors in some species that lay eggs with great precision on their hosts, and piercers of varied shapes and sizes derived from different sternites in different lineages. The terminalia, particularly those of the male, provide some of the best characters for interpreting the phylogenetic relationships within the Tachinidae and are helpful for identifications at the species and genus levels.

Egg

Modifications to the female reproductive system, egg, and ovipositor permit tachinids to parasitize hosts in a wide variety of ways. In the primitive condition, an unembryonated egg is deposited directly on a host by means of an extensible ovipositor. The egg is typically thick and convex on its upper surface and thinner and flatter on its under surface, and is attached to a host with a glue-like substance. Tachinids employing this mode of attack are termed oviparous because the egg is undeveloped when laid and the first instar is not fully formed for several days. The first instar may then burrow directly through the underside of the egg and through the host's integument, or may exit the egg through an operculum and then burrow into the host. Certain oviparous tachinids, including most Phasiinae, inject an egg directly into a host by means of a piercing ovipositor. Oviparous tachinids comprise the Phasiinae and some Exoristinae (Exoristiini, Winthemiini, and a few species of Blondeliini and Eryciini). The female reproductive system of an oviparous tachinid is shown in Fig. 4.

The majority of tachinids are ovolarviparous, depositing eggs that contain fully developed first



Tachinid Flies (Diptera: Tachinidae), Figure 4 **Female reproductive system of an oviparous tachinid, *Smidtia fumiferanae*. Not more than one fertilized egg is retained in the common oviduct at a time. Abbreviations: ac gl, accessory gland; c ov, common oviduct.**

Tachinid Flies (Diptera: Tachinidae), Figure 5 **Female reproductive system of an ovolarviparous tachinid, *Lypha fumipennis*. Fertilized eggs form tightly packed rows within a coiled ovisac.**

instars. The female reproductive system of these flies is modified to retain fertilized eggs in an ovisac or uterus until they are ready to hatch. The ovisac stretches and forms a coil as hundreds to thousands of fertilized eggs are added to it (Fig. 5). The females of numerous ovolarviparous species still deposit eggs directly on a host, but other strategies, some quite ingenious, are used as well. In most cases the eggs have a thin chorion and hatch almost immediately after deposition. The eggs of many species are laid near a host or are broadcast on its food plant and the motile first instar either crawls to a host or waits for one to pass by. The eggs of Dexiini and most Rutiliini (Dexiinae) are deposited on the ground and the first instar burrows into the soil in search of a beetle host. A few ovolarviparous species have the unusual habit of ovipositing an egg into the mouth of a host. Members of the Goniini (Exoristinae) have tiny "microtype" eggs that they scatter on the food plant of a host, usually in the vicinity of feeding damage, and these eggs hatch only after being ingested by a host. Various types of piercers have evolved in different lineages of ovolarviparous tachinids to inject an egg into a host.

The number of eggs produced by a tachinid is roughly proportional to the likelihood of a first instar infecting a host. Species that oviposit directly on or in a host have a high success rate and low fecundity, generally less than a few hundred eggs. Species that oviposit in the vicinity of a host often produce many hundreds of eggs, and species with microtype eggs or that oviposit rather indiscriminately on a host's food plant have the highest fecundity of all, with the number of eggs produced numbering into the thousands.

Some tachinids are cited in the literature as larviparous, meaning in the strict sense of the term that their eggs hatch internally and first instars are oviposited instead of eggs. However, the term larviparous has also been used in a looser sense to describe tachinids that deposit fully developed eggs that hatch immediately after deposition (i.e., ovolarviparous tachinids). The eggs are frequently so thin and membranous as to be almost invisible. In some cases, first instars inside a freshly killed female will break free of their thin-walled eggs and escape through the ovipositor, giving the impression that the species is normally larviparous. Dissections of killed females may also reveal first instars free in the ovisac that would, under normal circumstances, remain in the egg until after oviposition. Although there may be species that are truly larviparous, they have yet to be reliably documented.

The eggs of tachinid flies are not intended to provide long term protection for a first instar. Tachinids do not overwinter in the egg stage or as free-living first instars.

Larval instars

Tachinids, like other cyclorrhaphan flies, have three larval instars. The first instar is remarkably varied externally, adapted to cope with the different circumstances under which eggs are placed in the environment. First instars that must search for hosts on their own have evolved a number of specializations to aid movement and avoid desiccation. Their bodies are often adorned with bands of small spines or sclerotized plates, in some instances displaying more morphological variation between species than the bodies of their adults. First instars of ovolarviparous species can be removed from pinned adult females in museum collections and rehydrated for morphological study. Research into the diversity of first instars is expected to contribute valuable characters for tachinid taxonomy and for phylogenetic analyses of tachinid relationships.

First instars that enter a host on their own do so with the cutting action of a sharp labrum that is varied apically from pointed to axe-like. The labrum is scraped against the host's integument with a back-and-forth motion until a hole is created, likely aided by an enzymatic substance in the saliva. Once inside the host, the first instar may attach itself posteriorly to its entrance hole or to the host's tracheal system, or it may remain free in the host's body. First instars that remain free usually attach themselves to the tracheal system when they become second instars to provide an adequate supply of oxygen for developmental needs. A first instar may start to feed immediately and can pass through all three instars in as little as a few days, but in most species the larval stage lasts a few weeks. Not uncommonly, the first instar delays development until the host reaches a particular stage. It might migrate to specific places within the host during its period of inactivity, such as the salivary glands, ganglia or muscles, where it is able to evade the host's immune system. It is generally hormonal signals within the host that trigger the first instar to relocate and continue development. Some tachinid species overwinter as first instars within their hosts.

A first instar feeds on host hemolymph and carefully avoids damaging any vital organs, living more like a parasite than a host-killing parasitoid. This changes during the second instar when rapid feeding and growth begin. If a larva did not form a connection to tracheal or outside air during its first instar, then it typically does so as an early second instar. At the same time as the tachinid larva is attempting to feed and obtain oxygen, the host is attempting to kill it through an immune response termed encapsulation. In the early stages of encapsulation, a thin membrane forms around the larva. A first instar can be almost completely encased, but if this happens then it can usually still feed on hemolymph that filters through to it. The larger second instar frees itself anteriorly and begins to feed more aggressively on non-vital tissues, at the same time continuing to stay attached to an air supply posteriorly. The capsule that forms around the larva is termed a respiratory funnel and it becomes larger and thicker as time passes. The ability of the Tachinidae to thwart the encapsulation process is one of the keys to their success. This ability does not afford total protection and some larvae are killed by encapsulation even in suitable hosts. Other potential hosts that are seldom successfully parasitized may have immune systems that are more effective at combating tachinid invaders or there may be other incompatibilities between parasitoid and host.

The primary cutting structure in the first instar, the labrum, is replaced in later instars by paired mandibles. The second instar is a voracious feeder that selectively consumes non-vital tissues, especially fat stores. The host may appear normal or somewhat lethargic, or may display atypical behavior induced in some way by the parasitoid.

The third instar leaves the respiratory funnel and feeds less discriminately. Except in rare cases, the host is killed and the third instar continues to feed until fully grown or until the food supply is exhausted. The latter situation is not uncommon among tachinids that develop gregariously within a single host and the tachinid adults that develop from under-fed third instars can be half or less the size of typical adults.

Puparium

Pupation in tachinid flies takes place within a puparium, the hardened shell of the third instar. Most commonly the third instar crawls away from the host and pupariates in the soil or ground litter, but in some species pupariation takes place within the host. A few species that pupariate within adult beetles strategically cut openings in the host's integument to facilitate respiration and the eventual exit of the adult (Fig. 6). Quite a few tachinids overwinter in the pupal stage.

The puparium is roughly cylindrical with two small anterior spiracles and generally two conspicuous and darkened posterior spiracular discs, for respiration. The posterior spiracular discs can be flush with the surface of the puparium or raised above it, and directly level with the midline or above or below it. In a few species the spiracular discs are fused into one. Quite often there are three or four spiracular slits on the upper surface of each spiracular disc. The morphology of the spiracular discs is highly varied and provides useful characters for the identification of species. An adult tachinid emerges from its puparium by inflating a balloon-like ptilinum from behind its face to force open the anterior end of the puparium along a circular line of weakness.

Tachinid Flies (Diptera: Tachinidae), Figure 6
Puparium of *Myiopharus neilli* within remains of its host, an adult sunflower beetle (*Zygogramma exclamationis*). Anterior and posterior ends of puparium are visible. The beetle is typically decapitated between the prothorax and mesothorax. Underside of beetle is shown with legs removed. Abbreviations: a spr, anterior spiracle; p spr ds, posterior spiracular disc.

Distribution and Evolution

The Tachinidae are well distributed throughout all zoogeographic regions of the world (see Table 1), although poorly represented on smaller islands that are distant from larger land masses (e.g., Hawaiian Islands, Galapagos Islands). The total number of described species is about 10,000, but this number is misleading because only the Nearctic and Palearctic faunas are relatively well known. The Neotropical Region has the largest number of described species at about 3,000, almost twice that of any other region and representing 30% of the world's fauna, yet there are so many undescribed species and the region is so vast and under-collected that the actual number is probably well over 5,000. Similarly, Australia has a described fauna

Tachinid Flies (Diptera: Tachinidae), Table 1
Number of tachinid species and genera in each biogeographic region and the world

Biogeographic region	Genera	Described species
Neotropical	822	2,864
Nearctic	304	1,345
Palearctic	405	>1,600
Afrotropical	213	1,006
Oriental	264	725
Australasian	230	808
World	1,523	about 10,000

Numbers for genera follow O'Hara (2007) and for described species follow the most recent regional catalogues. Actual number of tachinid species (described + undescribed) in the world is likely greater than 15,000. Some species and many genera are found in more than one region so the values for the world are not the sums of the regional numbers.

numbering about 500 species but the actual fauna has been estimated at 3,500–4,000 species. The tachinid faunas of the Afrotropical and Oriental regions have not been well studied and also contain many undescribed species. Given these circumstances, it is likely that the total number of tachinid species in the world is in excess of 15,000.

Some older insect groups show an interesting pattern of distribution that links the faunal elements in South America, Australia and sometimes southern Africa. These relationships are thought to date back to Gondwanaland when the southern continents were fused into a single land mass. By the end of the Cretaceous Period about 65 million years ago, Africa was drifting northward and the connection between South America and Australia (via Antarctica) was becoming cooler and more tenuous. If the Tachinidae began their radiation in the Cretaceous then evidence of this might be sought in the fossil record and modern distribution patterns. However, no fossil Tachinidae are known from the Cretaceous and there is no clear evidence of southern relationships, so the family is assumed to be of Tertiary origin.

The sister group to the Tachinidae has not been determined but is to be found among the families Sarcophagidae, Calliphoridae, Rhinophoridae and Oestridae. These five families are united by their possession of a row of setae on the meron (a sclerite above the hind leg) and together comprise the superfamily Oestroidea.

Hosts

The evolutionary success of the Tachinidae is closely tied to their exploitation of arthropods as a source of hosts. The family is a difficult one taxonomically and a relatively young one, suggesting that it is still undergoing rapid radiation within its specialized niche. The life of an endoparasitoid is a complex one with strong selective pressures centered around finding and parasitizing a host. In some cases selection has produced generalists that attack many species of hosts, in others selection has produced specialists that attack only one or a very few host species.

Hosts of Tachinidae are all arthropods, almost exclusively insects. For many tachinid species the hosts are unknown. The non-insect hosts comprise only a few species in the Chilopoda (centipedes), Scorpiones (scorpions), and Araneae (a single record from a spider). These hosts are attacked by a few species of Tachininae, mostly within the Polideini.

The majority of hosts of tachinids are Lepidoptera, mostly caterpillars that feed on foliage in exposed situations but also others that are concealed, such as leafrollers and stem borers. Lepidoptera represent the main hosts of the two largest tachinid subfamilies, Exoristinae and Tachininae, and are also significantly attacked by the third largest subfamily, the Dexiinae. The smallest subfamily, the Phasiinae, attacks only Heteroptera and there is only one genus outside the Phasiinae (*Euthera* in the Dexiinae) that also attacks heteropteran bugs.

Larval and adult Coleoptera of about 20 families are attacked by a small number of species in the Exoristinae and Tachininae and by the majority of species in the Dexiinae. The greatest number of beetle hosts belong to the Scarabaeidae, larvae of which are parasitized by nearly all members of the sizable dexiine tribes Dexiini and Rutillini; adult scarabs are parasitized by members of the small dexiine tribe Palpostomatini.

Hymenopteran hosts are chiefly larval Symphyta, many of which are exposed defoliators like larval Lepidoptera. A small number of wasps (Vespoidea) and ants (Formicidae) also serve as hosts. Hymenopteran parasitoids belong to the Exoristinae and Tachininae. The remaining hosts of tachinids are also parasitized by members of these two tachinid subfamilies and include the Orthoptera (crickets, grasshoppers, katydids), Blattaria (cockroaches), Mantodea (mantids), Phasmatodea (leaf and stick insects), Dermaptera (earwigs), Diptera (flies), and Embioptera (webspinners).

Some tachinids are solitary endoparasitoids and will fight one another within a host until a single larva remains alive. Other species, especially those that parasitize larger hosts, are not aggressive toward one another and numerous individuals can successfully develop into adults. If conditions are crowded, then some maggots may die and the rest may produce stunted adults. Multiparasitism, the development of more than one larva within a host, also can result in more than one tachinid species successfully parasitizing a single host.

There are a variety of factors that determine how many host species a tachinid species will parasitize. The adult female plays a large role in host range by deciding where to oviposit. If eggs are laid on or near a host or injected into it, then the host range is determined by the specificity of the ovipositing female and the ability of the larva to develop in the selected host. Females of some species search for a particular microhabitat and once in it (e.g., a particular plant species) will oviposit on different potential host species encountered there. One tachinid species, *Compsilura concinnata*, has become well known because it is highly indiscriminate in its selection of hosts and its larvae are capable of developing in many different species. The female fly injects an incubated egg into a host and the larva escapes the defenses of its varied hosts by living and feeding in the midgut between the peritrophic membrane and gut wall. *Compsilura concinnata* has almost 200 recorded hosts in numerous families of Lepidoptera and also parasitizes sawflies and a species of weevil.

Host Location

The ancestral mode of host finding in Tachinidae likely involved a series of cues, olfactory and visual, that guided a searching female to the right microhabitat and host plant and then to an exposed host, where perhaps tactile stimuli initiated oviposition behavior. This method of host location is still common, but there are many sophisticated behaviors that have evolved to aid the searching tachinid. For example, oviposition in numerous tachinids does not involve the visual sighting of a host. In the case of Goniini, microtype eggs are deposited on the food plant of a host, usually in response to plant volatiles released at the site of feeding damage, and the eggs do not hatch until ingested by a host. Many other tachinids also oviposit on the food plant of a host or in a specific microhabitat (e.g., those that parasitize litter insects like cockroaches and earwigs), not necessarily within sight of a host, and the first instar locates a host on its own or lies in wait for one to pass by. Certain tachinids (e.g., *Lixophaga diatraeae*) are stimulated to oviposit near the burrow of a concealed host by the odor of the frass that has accumulated at the entrance. Members of the Dexiini oviposit on the ground, leaving the task of finding a soil-dwelling scarab host to their first instars.

The importance of visual cues varies in different tachinids. Those that search for hosts at night must rely mostly on other sensory cues to find an acceptable place to oviposit. Some tachinids that lay eggs on exposed caterpillars not only select hosts of a particular size, presumably by sight, but may also place the eggs near the front of the host where they cannot be reached by the host's mandibles. A few species that parasitize adult beetles assist their first instars by ovipositing near natural openings such as the mouth, anus and spiracles. Not uncommonly, females that oviposit on a specific part of a moving host have a telescopic ovipositor that can be brought forward under the body and in front of the head to permit egg placement to be visually guided. Some tachinids attack their hosts on the wing, requiring acute vision as well as maneuverable flight.

In most instances where olfaction is involved, the chemical cues that attract a female tachinid to an oviposition site are the standard odors of a host or host plant, or odors (volatiles) given off by a damaged plant that is being fed upon. More unusual are the cues that attract certain Phasiinae to their hosts; these species use the pheromones of their heteropteran hosts as host-finding kairomones. The antennae of these tachinids are up to 10 times more sensitive to the bug pheromones than are those of the bugs.

The vast majority of Tachinidae are incapable of hearing, but members of the tribe Ormiini have evolved an inflated prosternum between the front legs that functions as a tympanal organ. This structure allows these tachinids to locate their orthopteran hosts at night by homing in on their mating calls. So effective are these parasitoids in finding their calling hosts that some hosts have evolved strategies to reduce their susceptibility. The tympanal organs are different in male and female ormiines, with those of the female very receptive to the low frequency calls of hosts and to sounds in the ultrasonic range, whereas males are only sensitive to ultrasonic sound. It has been suggested that the sensitivity of these nocturnally active flies to high frequency sound helps them avoid predators such as insectivorous bats.

Mate Finding

Male and female tachinids that are commonly found in meadows and along roadways, particularly on wildflowers, probably mate in those places, e.g., Phasiinae, larger Tachinini, most Siphonini. There are other tachinids that go to species-specific aggregation sites to find a mate. The most noteworthy of all aggregation phenomena is "hilltopping," where males of certain tachinid species fly to the tops of hills or mountains to await the arrival of females. Each species has its own predetermined time of day during which it will hilltop, with some species preferring the morning, others the afternoon, and the night-active *Ormia* hilltopping at dusk. On hot days the activity begins earlier than on cool days, and on cloudy days there are fewer flies. A good hilltop on a hot and sunny day is a frantic place, with anywhere from a few tachinid species to 75 or more (in exceptional habitats) visiting the hilltop by mid afternoon, after which fly activity drops off considerably. Virtually all the observable individuals are males, presumably because they remain on the hilltop for some time whereas females stay only long enough to find a mate. Males of each species are guided by instinct to a particular place on a hilltop and successive generations will return to the same spot year after year. One species may prefer a sunlit spot on the ground at the base of a bush, another will alight on tree trunks, and others will sit on foliage to one side of the hilltop or buzz around the topmost branches of a bush at the hilltop's center, etc. Males of some species spend most of their time perched at preferred locations, darting out frequently to inspect passing insects. Males of other species are in almost constant motion as they fly from point to point but seldom alight.

Aggregation sites for male tachinids are not always on hilltops. The branches of an isolated tree, or shrubs alongside a stream, or a patch of ground below a bush, are a few of the places where males of one or more species may congregate to await a potential mate, nearly always in sunlit situations. Tree trunks also serve as aggregation sites for a number of species. Often several males will occupy the same tree trunk, but the males of some species (e.g., *Trixodes obesus*) are always found singly. Generally only one or a few trees in an area are attractive to aggregating males and these trees will be frequented by the same species year after year. Some species do not alight on a tree but instead fly in a zig-zag pattern up the trunk for a few moments before flying to another tree to repeat the behavior.

It is not uncommon for the antennae of male tachinids to be larger than those of females, but usually this difference is slight. Rarely, the difference is dramatic with the first flagellomere greatly enlarged over that in its conspecific female, or even bifid or multi-branched. Since antennae serve a mostly olfactory function, it is presumed that such antennae help in the location and/or courtship of females. Very little is known about courtship and mating in tachinids, especially under natural conditions.

Ecology

The vast majority of hosts of tachinid flies are plant-feeding insects. As a result, parasitism by tachinids has two major effects at the community level: a reduction of host populations, and an indirect reduction in feeding damage to plants used by hosts. The level of parasitism can vary greatly, from less than 1% to approaching 100%, depending on such factors as the size of a host population, size of the parasitoid population, and environmental conditions. Parasitism levels usually vary locally from one portion of a host's range to another. Parasitism rates are quite dynamic and rise and fall through the generations and from area to area in cycles that both influence, and are influenced by, host populations. The net effect is generally low rates of parasitism (under 5%) with occasional generations where parasitism is significantly higher. Most of the studies into parasitism rates by tachinid flies have involved pest insects, some of which cause damage to crops or forests on an annual basis and some of which are only of economic concern during outbreaks. How quickly a tachinid population can take advantage of an increase in host numbers is dependent on a number of factors but is influenced in part by the oviposition strategy and fecundity of the tachinid species involved.

Tachinid species can be broadly divided into two types, specialists and generalists. As the names imply, specialists attack one or a few host species and generalists attack multiple hosts. On the whole, tachinids tend to be less host specific than hymenopteran parasitoids. Factors affecting tachinid host range include, but are not limited to, habitat choice, host searching strategy, oviposition strategy, method for coping with physiological defenses of host, and developmental synchrony. There is recent evidence from large scale, long term rearings of Tachinidae from Lepidoptera in Costa Rica that some supposedly generalist tachinid species actually comprise a group of specialist cryptic species (species that are difficult to separate morphologically). Although it is likely true that cryptic species are more common in the Tachinidae than previously thought and these species may have narrow host ranges, there are still many tachinid species that are clearly generalists. Most generalists have fewer than 20 recorded hosts, but some have over 50 and a very few have over 100. The hosts of many tachinid species are either unknown or poorly known and are not completely known for the vast majority of species.

Tachinid flies and other parasitoids exert selection pressures on their hosts to evolve ways in which to minimize parasitism. The more obvious may involve the evolution of cryptic coloration, specialized feeding strategies such as concealed feeding or feeding at night, or evasive maneuvers that are evoked when a host is attacked. Less obvious, but quite important at the community level, are the effects of tachinid parasitism on host and host-plant interactions (i.e., tritrophic interactions). Insect herbivores do not always feed preferentially on plant species that provide the highest nutrition. Certain insect herbivores will feed on less preferred host plants if such feeding reduces their level of mortality due to parasitism. The investigation of enemy-free space as an important component of tritrophic interactions is an active area of research.

Biological Control

Potential insect pests are kept largely in check by their natural enemies in their native habitats, but the spread of agriculture and the introduction of insects into new areas has resulted in a steady increase in the number of economically important insect pests attacking crops and forests. Control measures continue to be largely chemical-based, but the benefits of biological control or integrated pest control (control by chemical, biological and other means) have long been recognized. By the early 1900s there was an increasing realization that some insects unwittingly transported to new places by sea vessels were causing considerable damage in their new locations. An early example concerns the gypsy moth (*Lymantria dispar*) and browntail moth (*Euproctis chrysorrhoea*), two forest pests introduced into eastern North America from Europe prior to 1900. In one of the earliest cases of a classical biological control program, several tachinid parasitoids of these pests were imported into eastern USA from Europe in huge numbers in the early 1900s. Although the program was not a complete success, it laid the groundwork for future studies of tachinids as biological control agents. In recent years, one of the tachinid species introduced against those forest pests, *Compsilura concinnata*, has been implicated in the decline of giant silk moths (Saturniidae) in northeastern United States.

Some of the best known success stories of tachinid biological control programs have been reviewed many times. They include: the release of *Cyzenis albicans* from Europe against the winter moth (*Operophtera brumata*) in Canada; release of *Lixophaga diatraeae* from Cuba and elsewhere and *Lydella minense* from Brazil against sugarcane borers (*Diatraea* spp.) in the Caribbean; release of *Bessa remota* from Malaysia against the coconut moth (*Levuana iridescens*) in Fiji; and release of *Ceromasia sphenophori* from Papua New Guinea against the New Guinea sugarcane weevil (*Rhabdoscelus obscurus*). More recently, *Ormia depleta* from Brazil has been implicated in the control of pest mole crickets (*Scapteriscus* spp.) in Florida, USA. Similarly, several species of *Trichopoda* from the southern United States and South America have been introduced recently into Hawaii, Australia, Italy (accidentally), South Africa, and other places for control of the southern green stink bug (*Nezara viridula*), with mixed results.

Some tachinid species have been successfully mass-produced for biological control programs whereas others have proved difficult or expensive to rear under laboratory conditions. The in vitro propagation of tachinids on artificial diets has been achieved for a very few species in laboratory experiments but has yet to be employed in a biological control program.

► Flies
► Natural Enemies Important in Biological Control

References

Belshaw R (1994) Life history characteristics of Tachinidae (Diptera) and their effect on polyphagy. In: Hawkins BA, Sheehan W (eds) Parasitoid community ecology. Oxford, Oxford University Press, pp 145–162

Grenier S (1988) Applied biological control with tachinid flies (Diptera, Tachinidae): a review. Anz Schadlingskd Pfl 61:49–56

O'Hara JE (2007) World genera of the Tachinidae (Diptera) and their regional occurrence. Version 3. 71 pp. http://www.nadsdiptera.org/Tach/Genera/Gentach ver3.pdf

Stireman JO, O'Hara JE, Wood DM (2006) Tachinidae: evolution, behavior, and ecology. Annu Rev Entomol 51:525–555

Tschorsnig H-P, Richter VA (1998). Family Tachinidae. In: Papp L, Darvas B (eds) Contributions to a manual of Palaearctic Diptera (with special reference to flies of economic importance). Higher Brachycera, vol. 3. Science Herald, Budapest, Hungary, pp 691–827

Wood DM (1987) Tachinidae. In: McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR, Wood DM (eds) Manual of Nearctic Diptera, vol. 2. Agriculture Canada Monograph 28: i–vi, 675–1332, pp 1193–1269

Tachiniscidae

A family of flies (order Diptera).

► Flies

Taenidium (pl., Taenidia)

Cuticular ridges that strengthen and support the walls of the trachae.

Taeniopterygidae

A family of stoneflies (order Plecoptera). They sometimes are called winter stoneflies.

► Stoneflies

Tagma (pl., Tagmata)

One of the major body regions. In insects, this is the head, thorax and abdomen. In many other arthropods it is the cephalothorax and abdomen.

Taiga Tick, *Ixodes persulcatus* Schulze (Acari: Ixodida: Ixodidae)

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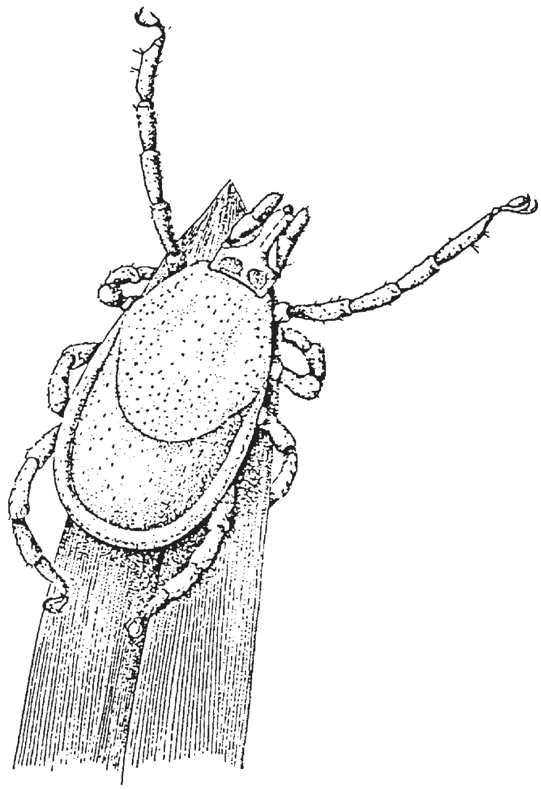
This is one of the most well-studied species among hard ticks. Intensive study of *Ixodes persulcatus* was initiated in the late 1930s when this tick was found to be the main vector and reservoir of a virus causing a severe human disease, tick-borne encephalitis (Russian spring-summer encephalitis, Far Eastern encephalitis), that occurs throughout the range of the tick. Two other viruses responsible for human pathogenicity were isolated from the taiga tick: Powassan virus in the southern Russian Far East, and Kemerovo virus in Western Siberia and the European part of Russia. Later, *I. persulcatus* was found to be the main vector of Lyme borrelioses, caused by *Borrelia garinii* and *B. afzelii*, over the entire range of the tick. Recently, *I. persulcatus* was found to be a vector of a number of agents of human and animal diseases: babesiosis (*Babesia microti*), human monocytic ehrlichiosis (*Ehrlichia muris*) and human granulocytic anaplasmosis (*Anaplasma phagocytophilum*). Also, two new agents were isolated from *I. persulcatus* in Siberia: *Bartonella henselae* responsible for cat-scratch disease, and a new rickettsia of unclear pathogenicity (*Rickettsia tarasevichiae*). This tick plays some role in mechanical or biological transmission and maintenance of agents of some other human diseases (salmonellosis, tularemia, Omsk hemorrhagic fever, Q-fever). Transovarial and/or transstadial passage of many pathogens has been proved. Thus, this tick is one of the most important vectors and reservoirs of human pathogens from various groups. Mixed infections in the same populations of ticks, as well as in the same individuals, were documented. A double infection of humans was recorded, and this event may dramatically change the clinical course of human illness.

The range of *I. persulcatus* covers a huge territory of boreal coniferous (taiga) forests, from the Baltic Sea to the Pacific Ocean, extending as a large strip through Estonia, Latvia and the entire Russian Federation. In the west, the tick range includes the eastern parts of Lithuania and some spots in Finland, Poland, Belorussia and in Ukrainian and Hungarian parts of the Carpathians. In the east, the range includes the northern part of Mongolia, the northwestern and northeastern parts of China, North and partly South Korea, as well as a part of Hokkaido Island and several smaller nearby islands in Japan. In the south, there are findings of the taiga tick in limited areas of Kazakhstan, Uzbekistan and Kyrgyzstan. The spread of *I. persulcatus* to the north of its reproductive range is limited by low temperature, and to the south by low humidity. The single findings of the tick to the north of its reproductive range are explained by its introduction by birds during spring migrations from their overwintering areas to the breeding sites. Thus, cases of tick findings on humans and animals even within the Arctic Circle have been documented. The routes of bird migrations are influenced by various geomorphological formations including the valleys of large rivers. Evolutionarily, the taiga tick is one of the youngest representatives of the closely related species in the subgenus *Ixodes* that are united in the *I. persulcatus* group or *I. ricinus* complex, but its range is the largest one among all ticks of this group.

As is the case with most species of ticks living in the temperate zone, *I. persulcatus* has a well-defined seasonality. The unfed ticks search for hosts (questing or host seeking) during the spring-summer season of the year. They use a so-called "ambush strategy" for seeking hosts: unfed ticks are positioned on the vegetation, from the litter layer to the tips of stems or branches, scanning nearby spaces with their chemoreceptors (part of Haller's organs, located on the dorsal surface of tarsus I). They spend from several hours to several days in questing position (Fig. 7) depending on particular environmental conditions. Adult ticks sense the host stimuli from a distance of 5 to 10 m. They can also detect paths of regular host migration, which explains their high concentration nearby. Questing ticks either catch onto a passing host or, sensing it from a distance, move in its direction. Ticks cannot constantly be in a questing position because their water reserves would become depleted. To maintain their water balance, ticks must regularly migrate down to the litter and soil where the temperature is lower and humidity higher. During the day, unfed adults have two peaks of activity: in the morning (8–10 a.m.) and in the late afternoon (after 4 p.m.). Nymphal activity is maximal at dusk and the beginning of the night. Cloudy weather, rain or warm nights may significantly change this pattern. However, if a host appears close to an unfed tick, it may be attacked at any time.

The capacity of *I. persulcatus* for active migration is limited. The questing larvae usually can move up to 20 cm, nymphs up to 40–50 cm, and adults up to 1.0 m. The height of vertical movement is directly correlated with the air humidity. Ticks also are unable to carry out long horizontal migrations: mean 5 m (up to 10 m) for adults and 0.5 m (up to 1.5 m) for larvae. The rate of adult movement may be as high as 30 cm/min at 23°C but generally is lower, decreasing with decreasing



Taiga Tick, *Ixodes persulcatus* Schulze (Acari: Ixodida: Ixodidae), Figure 7 **Unfed adult female of the taiga tick on foliage, seeking a host (after B. I. Pomerantsev and G. V. Serdyukova 1947).**

temperatures. The taiga tick has no eyes, though it can distinguish between more or less illuminated areas, preferring the latter. Photosensitive cells were found approximately in the same area where eyes might be, and their response to light is no less pronounced than in some species of ticks having eyes.

The season of adult activity lasts for 3–6 months, from the time of snow melt (April–May) until July-September, depending on the conditions of a particular region. The season of activity for unfed subadults (larvae and nymphs) principally corresponds to that for adult ticks, though it may be longer. The activity period does not correspond to the life span of individual ticks. After hatching or molting, unfed subadults live about 14–15 months and unfed adults live about 12 months, including post-molting development and behavioral diapause during hibernation, when ticks do not seek hosts. The life of active (host-seeking) ticks is much shorter, from 1 day to about 75 days for unfed adults. The unfed ticks do not become active immediately after post-molting development or diapause but gradually, during the main part of the activity season. Most adults become active during the first 15–30 days of the season. The adults that become active earlier in the season live longer than ticks that become active later. The abundance of active adults sharply increases during the first third of the season (often during a shorter period) and then gradually diminishes until the end of the season. Unfed ticks that do not find a host and cannot feed during the activity period die due to complete expenditure of their nutritional reserves.

The taiga tick is a typical exophilic three-host tick. Each parasitic stage feeds on a vertebrate host only once: the larva feeds for 3–5 days, the nymph for 3–6 days and an adult female for 6–10 days. The duration of feeding strongly depends on the host species. Males feed several times during their active life for 15–30 min each time, and even these brief periods are sufficient for infection of hosts with viruses. The obligatory condition for normal female engorgement is its insemination. The female *I. persulcatus* can be inseminated not only on a host, but also in nature before finding a host. In some populations, about 50% of unfed females collected from vegetation are inseminated. The larvae and nymphs increase their weight during feeding 15- to 30-fold, while engorged females are heavier than unfed females 100- to 150-fold. The mass of an unfed larva is 0.03–0.045 mg, whereas the mass of fully engorged females reaches 250–470 mg. Females lay from 2,000 to 4,000 eggs. The minimal weight of engorgement, after which females are capable of laying single eggs, is about 20–35 mg. The heavier the engorged female becomes, the greater the ratio of the number of laid eggs/mg of the female's weight, until the female weight reaches 140–200 mg, after which the dependence of egg number/mg of engorged female becomes linear and equals approximately 8.5–9.5 eggs/mg of the female weight. Values of all these parameters differ for tick populations from different parts of the range of *I. persulcatus*.

The engorged ticks drop off the host into the litter where they develop before molting, or where the females oviposit and the eggs develop. The engorged subadults feeding in the late summer have no time to undergo the necessary metamorphosis by the autumn; they enter the morphogenetic diapause and molt into the next stage only in the second part of the summer of the following year. The possibility of nymphal diapause during 2 years is rather questionable and needs further study. The molted unfed individuals hibernate, being in behavioral diapause, and become active next season. Only eggs and engorged adults cannot hibernate. The general duration of the entire life cycle (from eggs to eggs) may fluctuate from 2 years under most favorable conditions (the southern part of the Russian Far East) to 5 years. In most cases, the tick populations consist of ticks of different cohorts (having life cycles of different durations). These two factors make *I. persulcatus* a unique reservoir for pathogenic agents.

The taiga tick is one of the most opportunistic (generalist) tick species, using as hosts nearly 300 species of different vertebrates (about 100 species of mammals, more than 175 species of birds and a few species of reptiles). Larvae principally feed on small mammals (rodents and insectivores), nymphs on medium-sized mammals (rodents, lagomorphs, some carnivores) and birds, and adults on large mammals. The questing height of ticks of each stage coincides with the size and location of their main hosts. In years of depression of the abundance of small mammals, or under specific environmental conditions, subadults may change their hosts for larger ones or for hosts less typical for them under normal conditions. Adults actively attack people and are the main source of human infection by different pathogens; nymphal attacks toward humans have been recorded extremely rarely. *Ixodes persulcatus* adults are more aggressive than adults of the closest relative, the sheep tick *I. ricinus*. Their efficient attachment to the host body is enhanced by a long hypostome covered with numerous recurved teeth, preventing tick removal.

A number of parasites and predators of the taiga tick are known. However, the prospects of their use for tick control are rather slim. The taiga tick is a member of some rather complicated forest communities formed long ago, and there is little chance of destroying a well developed balance of such communities by introducing new agents. The high stability of adult tick abundance from year to year (the difference is not more than one order of magnitude) indicates the extreme fitness of this species. This stability is provided for by a number of factors, such as a complicated life cycle, existence of different types of diapause, numerous hosts from various groups, and a high level of aggressiveness of adults toward potential hosts.

The simplest mode of human protection from taiga tick attacks and bites is proper clothing when in forested areas, and regular self- and cross-inspections followed by tick removal. A wide-scale educational program (lectures, leaflets, articles in newspapers, etc.) just before and during the season of tick activity may increase public awareness of tick attacks and personal motivation for self-protection. There are data on the protective effect of some repellents which can be used on clothing or applied directly to the skin to reduce tick infestation. Large-scale treatment of tick-populated forest areas by persistent acaricides, which were used in the 1950s to 1970s, is now banned. The only target for treatment with non-persistent acaricides might be the popular sites of human relaxation during the summer months.

► Ticks

References

Filippova NA (ed) (1985) The taiga tick, *Ixodes persulcatus* Schulze (Acarina, Ixodidae). Nauka, Leningrad, 416 pp (in Russian)

Goodman JL, Dennis DT, Sonenshine DE (eds) (2005) Tick-borne diseases of humans. American Society for Microbiology, Washington, DC, 402 pp

Korenberg EI (2000) Seasonal population dynamics of *Ixodes* ticks and tick-borne encephalitis virus. Exp Appl Acarol 24:665–681

Uspensky I (1993) Ability of successful attack in two species of ixodid ticks (Acari: Ixodidae) as a manifestation of their aggressiveness. Exp Appl Acarol 17:673–683

Uspensky I (1995) Physiological age of ixodid ticks: aspects of its determination and application. J Med Entomol 32:651–664

Uspensky I (1996) Tick-borne encephalitis prevention through vector control in Russia: an historical review. Rev Med Vet Entomol 84:679–689

Uspensky I, Ioffe-Uspensky I (1999) The relationship between engorged female weight and egg number in ixodid ticks: a biological interpretation of linear regression parameters. Acarologia 40:9–17

Uspensky I, Garuto RM, Goldfarb L (2003) The taiga tick *Ixodes persulcatus* (Acari: Ixodidae) in the Sakha Republic (Yakutia): distributional and reproductive ranges. J Med Entomol 40:119–122

Tally Threshold

In binomial sampling, the number of individuals required to be present per sample unit to consider the sample unit infested. Proper selection of the tally threshold can improve the accuracy of classification sampling.

► Sampling Arthropods

Tanaostigmatidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees, and Sawflies

Tandem Running

A from of communication among some ants, wherein ants trail one another, with each ant maintaining contact with the preceding individual by means of its antennae.

Tangle-Veined Flies

Members of the family Nemestrinidae (order Diptera).

► Flies

Tanning

The process of sclerotization (hardening) of the cuticle after an insect molts; tanning involves the cross-linking of proteins, aided by quinones. Darkening may accompany tanning. Transparent cuticle can be tanned (hardened), as occurs over the compound eye, though in the absence of darkening.

Tanoceridae

A family of grasshoppers (order Orthoptera). They commonly are known as desert longhorned grasshoppers.

► Grasshoppers, Katydids and Crickets

Tanyderidae

A family of flies (order Diptera). They commonly are known as primitive crane flies.

► Flies

Tanypezid Flies

Members of the family Tanypezidae (order Diptera).

► Flies

Tanypezidae

A family of flies (order Diptera). They commonly are known as tanypezid flies.

► Flies

Tanzaniophasmatidae

A family of gladiators (order Mantophasmatodea).

► Gladiators (Mantophasmatodea)

Tarnished Plant Bug, *Lygus lineolaris* Palisot De Beauvois (Hemiptera: Miridae)

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The tarnished plant bug, *Lygus lineolaris* (Palisot de Beauvois) is a widely distributed mirid, known from Alaska to southern Mexico. It is a pest of a wide range of seed, vegetable, fruit, fiber and forage crops. More than 600 different plant species have been reported as potential hosts for this insect. Its ability to cause economic losses is often related to the migratory behavior of the adult and the phenology of the host plant. Depending on the host plant species, feeding may cause any of the following injuries: malformation of fruit, abnormal growth habits, necrosis, abscission of fruiting structures, or production of shriveled or embryoless seeds.

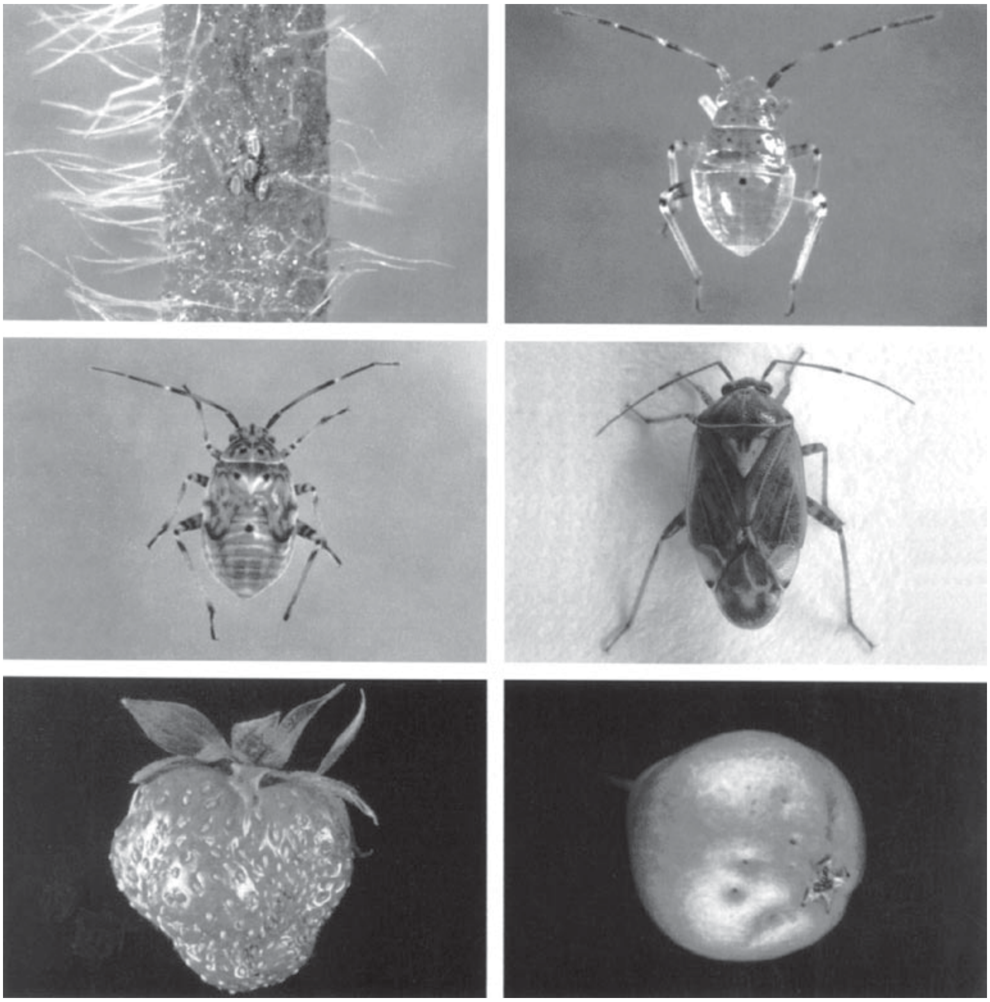
Life Stages

Egg

A freshly laid egg is translucent. Later it is yellowish. It is oval and slightly curved on one side. One end is obtuse and broadly rounded, whereas the other end is almost squarely truncated. The hardened egg shell (chorium) is smooth. Each is 0.85–1.6 mm long and 0.22–0.28 mm wide.

Nymphs

The five instars (Fig. 8) are very similar in form and all are yellowish-green. They walk rapidly and drop readily when disturbed.



Tarnished Plant Bug, *Lygus lineolaris* Palisot De Beauvois (Hemiptera: Miridae), Figure 8 Tarnished plant bug, *Lygus lineolaris*: *upper left*, eggs; *upper right*, third-instar nymph. Note the black spot of the abdominal gland; *second row left*, fifth-instar nymph. Note the four black spots on the thorax. The wing pads are yellowish with irregularly marked brown lines and extend to the fifth and sixth abdominal segments; *second row right*, the adult, dark brownish; *lower left*, a berry injured by tarnished plant bug nymphs. Note the closeness of the achenes where the bug has fed; *lower right*, a pear injured by tarnished plant bug. Note the "pit."

First Instar

The yellowish-green body has a pale orange spot in the middle of the caudal margin of the third abdominal segment. The body length is 0.85–1.10 mm and the body width is around 0.40 mm. The width of the head at the eyes is 0.34–0.36 mm.

Second Instar

The body is yellowish to yellowish pea-green. The third abdominal segment exhibits a bright orange-yellow spot with a slightly smaller spot at the posterior margin. The body length is 1.30–1.65 mm and the body width is about 0.60 mm. The width of the head at the eyes is 0.45–0.52 mm.

Third Instar

The body is green. The abdominal gland is indicated by a black spot. Toward the end of this stage, four dark thoracic spots begin to appear. Wing pads also appear and extend on to the second abdominal segment. The body length is 1.7–2.2 mm and the body width is about 1 mm. The width of the head at the eyes is 0.58–0.60 mm.

Fourth Instar

A great variation of color exists and green, red, white and black predominate. The four black thoracic spots are more prominent. The caudal margin of the third abdominal segment bears a large black spot. Two prominent reddish bands appear on each femur. The wing pads extend to the third abdominal segment. The body length is 2.1–2.7 mm and the body width is about 1.5 mm. The width of the head at the eyes is 0.78–0.80 mm.

Fifth Instar

The color is variable, but greenish in general. The yellowish head has five longitudinal brownish stripes converging behind, but not attaining, the posterior margin of the vertex. The thorax and wing pads are yellowish with irregularly marked brown lines. The abdomen is yellowish or greenish yellow. The wing pads extend onto the fifth or sixth abdominal segment. The veins begin to appear in the pads. Four black spots are conspicuous on the thorax. The dorsal abdominal gland is indicated by a conspicuous black spot on the caudal margin of the third abdominal segment. The legs are variable in color. The body length is 3.2–4.2 mm and the body width is about 2 mm. The width of the head at the eyes is 0.94–0.96 mm.

Adult

The color is variable, usually greenish or brownish, with reddish brown markings on the wings. The thorax has five longitudinal dark stripes. The scutellum has two medium and two lateral black or reddish lines. Eleven segments comprise the abdomen, although some of these are considerably modified. The first ventral segment is reduced to an elastic membrane that joins the abdomen to the thorax. In the female, the seventh segment is named the subgenital plate, as it extends posteriorly in the midventral region to cover the base of the ovipositor. The body length is 4.9–5.7 mm for males and 5.2–6.0 mm for females. The body width is 2.4–2.8 mm for males and 2.4–3.0 mm for females. Moreover, around the base of the ovipositor on the ventral surface of the abdomen, there is usually a dark brown patch that may extend to the thorax.

Life Cycle

Tarnished plant bugs overwinter as diapausing adults either beneath plant litter or duff ground cover, or between the leaves of plants and long dry grasses. In piled leaves and rubbish, winter survival is about 29%, whereas in orchard sod it is only 6%. Overwintering adults start emerging in mid-April at temperatures as low as 8°C. These adults feed first on the opening buds of trees such as apple, peach and shrubs. A little later they migrate to early appearing annual plants. The favorite spring food plants include black current (*Ribes nigrum* L.), wild currents (*Ribes* spp.), common mullein (*Verbascum thapsus* L.), sheep sorrel (*Rumex acetosella* L.), yellow rocket (*Barbarea vulgaris* R.Br.), and strawberries (*Fragaria* spp.) (Table 2).

Overwintering adults gradually disperse on these spring plants as the temperature increases and then migrate to other favorable emerging weeds or cultivated plants. The bugs usually feed on the sap of growing tips or the reproductive parts of a plant, such as the buds of flowers, or the

Tarnished Plant Bug, *Lygus lineolaris* Palisot De Beauvois (Hemiptera: Miridae), Table 2 Annotated list of crop plants attacked by the tarnished plant bug

Forest trees (nurseries)			
Bare-root pine and container nurseries	Conifers	Douglas-fir	Larch
Fruit trees			
Apple	Cherry	Prune	Grape
Peach	Pear	Pecan	Plum
Quince			
Small fruits			
Blackberry	Currant	Grape	Raspberry
Strawberry			
Commercially Grown Flowers			
Aster	Bachelor's button	Bleeding heart	Calendula
Carnation	Chrysanthemum	Cosmos	Dahlia
Garden balsam	Geranium	Gladiolus	Golden glow
Hollyhock	Impatiens	Iris	Marigold
Nasturtium	Peony	Poppy	Rose
Sage	Salvia	Shasta daisy	Snapdragon
Stock	Strawflower	Sunflower	Sweet pea
Verbena	Zinnia		
Garden crops			
Asparagus	Beet	Broccoli	Cabbage
Carrot	Celery	Cucumber	Eggplant
Endive	Escarole	Horseradish	Lettuce
Lima beans	Mustard	Onion	Pea
Pepper	Potato	Radish	Snap beans
Spinach	Squash	Swiss chard	Tomato
Turnip			
Forage crops			
Alfalfa	Birdsfoot trefoil	Clover	Soybeans
Other crops			
Oilseed rape	Tobacco	Sunflower	Sweet corn
Seed heads of wheat and other grasses			

rapidly growing meristematic tissue of such plants as asparagus, alfalfa and other forage crops.

Tarnished plant bugs generally migrate to a host only when the plant enters its reproductive growth stage. There is a seasonal succession of hosts as the bugs feed on different plants from spring to fall (Table 3). Nymphs can disperse long distances (15–20 m) within a short time and adults

Tarnished Plant Bug, *Lygus lineolaris* Palisot De Beauvois (Hemiptera: Miridae), Table 3 Annotated list of weeds attacked by the tarnished plant bug

Spring	
Annual fleabane	*Erigeron annuus* (L.) Pers.
Common mullein	*Verbascum thapsus* L.
Common ragweed	*Ambrosia artemisiifolia* L.
Garden sorrel	*Rumex acetosa* L.
Wild strawberries	*Fragaria* spp.
Yellow rocket	*Barbarea vulgaris* R. Br.
Summer	
Black mustard	*Brassica nigra* (L.) Koch
Boneset	*Eupatorium perfoliatum* L.
Brown knapweed	*Centaurea jacea* L.
Lamb's-quarters	*Chenopodium album* L.
Narrow-leaved hawk's beard	*Crepis tectorum* L.
Ox-eye daisy	*Chrysanthemum leucanthemum* L.
Pineappleweed	*Matricaria matricarioides* (Less.)
Redroot pigweed	*Amaranthus retroflexus* L.
Shepherd's-purse	*Capsella bursa-pastoris* (L.)
St. John's-wort	*Hypericum perforatum* L.
Tansy	*Tanacetum vulgare* L.
White mustard	*Sinapsis alla* L.
White sweet-clover	*Melilotus alba* Desr.
Yellow sweet-clover	*Melilotus officinalis* (L.) Lam.
Wild carrot	*Daucus carota* L.
Wild mustard	*Sinapsis arvensis* L.
Autumn	
Canada fleabane	*Erigeron canadensis* L. (=*Conyza canadensis* (L.) Crong)
Canada goldenrod	*Solidago canadensis* L.
Canada thistle	*Cirsium arvense* (L.) Scop.
Common ragweed	*Ambrosia artemisiifolia* L.
European stinging nettle	*Urtica dioica* L. subsp. *Dioica*
False ragweed	*Iva xanthifolia* Nutt.
Narrow-leaved goldenrod	*Solidago graminifolia* (L.) Salisb.
Red-stemmed aster	*Aster puniceus* L.
Rough goldenrod	*Solidago rugosa* Mill.
Tall white aster	*Aster simplex* Willd.

can travel at least 5.1 km in sustained flight. Most adults fly no higher than 1 m from the ground, although some adults have been collected at elevations as high as 1,500 m. Multiple matings occur, but a single mating is sufficient for a female to lay viable eggs throughout her entire life. In Canada, overwintering females oviposit from the first week of May to the third week of June (about 50 days). Optimal oviposition occurs between 21°C and 27°C and oviposition does not take place below 16°C. Eggs can sustain low temperatures of 10°C for 15 days without adverse effect. Eggs are embedded in the stem, in the petioles, or in the midribs of leaves. They may be deposited singly or sometimes in groups of two or three in close proximity.

Following eclosion, the nymphs feed immediately on the succulent parts of the host plant and molt five times. The choice of the host plant dictates significantly the duration of each stage. Laboratory studies, with the temperature fluctuating irregularly between 17°C and 30°C, showed that female longevity ranged from 31 to 68 days, whereas male longevity ranged from 19 to 41 days. In southern Quebec, Canada, adults of the first generation appear about mid-June and reach maximum abundance around mid-July. During this time, adults migrate in great numbers from early season hosts, e.g., June bearing strawberries toward other host plants such as the following: raspberry (*Rubus* spp.), garden beans (*Phaseolus vulgaris* L.), potato (*Solanum tuberosum* L.), pepper (*Capsicum annuum* L.), turnip (*Brassica napus* L.), sugar beet (*Beta vulgaris* L.), red clover (*Trifolium pratense* L.), celery (*Apium graveolens* L.), wild mustard (*Sinapsis arvensis* L.), brown knapweed (*Centaura jacea* L.), and lamb's-quarters (*Chenopodium album* L.). This list is by no means complete. Eggs laid by summer adults produce adults 20–25 days later. For a given area, the seasonal sequential presence of tarnished plant bugs on wild plant hosts is practically the same year after year. The first generation adults mate when they are 4–6 days old. The pre-oviposition period varies between 9 and 13 days, with individual ranges from 5 to 29 days. The fecundity may reach up to 140 eggs per female with an average oviposition of 0–3.4 eggs per female per day. The population dynamics of the second generation nymphs is a function of the immigration time of the adults, the oviposition period of each individual and the nutritive quality of the different host plants. With the season progressing, more and more overlapping occurs between the developmental stages and the different generations of the tarnished plant bug. The overlap results in a smooth exponential growth pattern as opposed to a stepwise pattern. From the end of July to the second week of September, all stages of the bug can generally be found in the field. First generation adults that emerge in mid-June oviposit on several hosts and lead to a continuous emergence of second generation summer adults from the beginning to the end of August. A third generation of nymphs could occur on some cultivated hosts such as alfalfa and asparagus, and on wild plants such as common ragweed (*Ambrosia artemisiifolia* L.), Canada goldenrod (*Solidago canadensis* L.), rough goldenrod (*Solidago rugosa* Mill.), tall white aster (*Aster simplex* Willd.), stinging nettle (*Urtica dioica* L.), Canada fleabane (*Erigeron canadensis* L.), and the red-stemmed aster (*Aster puniceus* L.). In the fall, 25–30 days are needed for the tarnished plant bug to complete its life cycle. In southeastern Canada there are two generations per season whereas in the cotton belt in the southern USA, there are four to seven generations. Past the second generation, it is difficult to distinguish the generations. For example, on lamb's quarters characterized by continuous germination, second and third generation adults and larvae are found on the same plant. Therefore, the extended vegetative and flowering period of this weed contributes to the build-up of tarnished plant bugs in adjacent fields.

Despite some variations, the sex ratio is 1:1 irrespective of the host plant. The bugs are mainly phytophagous; however, they can sometimes feed as facultative predators on soft-bodied arthropods such as aphids and mites, or as scavengers on dead nymphs and adults of their own species.

As fall progresses, the testes and ovaries atrophy and the adults enter diapause. Exposure of nymphs of the first four stages (the photosensitive stages) to photoperiods of 12.5 h or less induces diapause in the adult stage. Rearing these nymphs to a photoperiod of 13.5 h or more will prevent the adults to enter diapause. Continuous light prevents diapause in young adults and terminates diapause in diapausing adults. Fifth-instar nymphs and adults are not sensitive to diapause-inducing photoperiods.

Attractants

There is now some evidence that virgin female tarnished plant bugs release an attractant to males. However, the attractant has not yet been isolated and identified. The presence of an aggregation pheromone that attracts both sexes also has been suggested. In any case, there are still no practical applications for these findings.

Pest Host Relationships

In southeastern Canada and northeastern United States, adults are subject to late fall temperatures that induce the tarnished plant bug to hibernate until the following spring. Management practices to control this bug in fields must consider plant hosts as reservoirs for the build-up of adults and nymphs in the vicinity of cultivated fields. Any flowering plant seems to attract the tarnished plant bug. Nevertheless, there are a few exceptions such as dandelions, sowthistle, milkweed and dogbane, which are all sap latex-type plants. Goldenrod is one of the rare latex-type sap plants which is very attractive in the fall to field populations of this bug.

Plant hosts range from highly attractive to highly resistant to the tarnished plant bug. Resistance to *Lygus* has been reported in some cultivars of celery, alfalfa, cotton, beans and carrots. Some plants do not attract the bug at all. For example, outbreaks have never been reported on wheat, rye and turf grass.

Although the tarnished plant bug is able to develop on a wide range of hosts, field observations show that some plants consistently support much higher populations than others. Management on selected hosts at particular growth stages over a short time, e.g., before the nymphs become adults, may result in lowering bug populations in crop agro-ecosystems. Sites with ephemeral, lush growth that dries out quickly provide a release of tarnished plant bugs and are of immediate concern during the cropping season. In uncultivated fields, weeds growing in sequence that are acceptable to tarnished plant bug development will retain their bug populations throughout the year without any activity of dispersion toward the surrounding crop lands, as long as the site is not disturbed or dried up.

Natural Enemies

Presently, it seems that natural enemies (Table 4), other than a few species of insect parasitoids, are not capable of checking a *L. lineolaris* population once it begins to build up. Endemic populations of *L. lineolaris* are under tremendous environmental pressure that checks their populations. In such instances, natural enemies play an important role. We do not yet have quantitative analyses of the intricate relationships between prey (*L. lineolaris*) and their natural enemies. In addition to parasitic Diptera and Hymenoptera, an identified species of nematode has been reported to rarely parasitize *L. lineolaris* adults in Quebec. Several predators are known to attack *L. lineolaris*, including damsel bugs (*Orius* spp., Anthocoridae), leaffooted bugs (Coreidae), stink bugs (Pentatomidae), lacewings (Chrysopidae), solitary wasps (Sphecidae), robberflies (Asilidae), lady beetle larvae (Cocinellidae), and spiders (Oxyopidae, Tetragnathidae and Thomisidae).

Damage

In southeastern Canada and northern United States, overwintering adults are pests of fruits such as apple, peach and pear. The adults injure the buds causing a circular depression referred to as "pit" in apples and pears (Fig. 8). In peaches, the fruit

Tarnished Plant Bug, *Lygus lineolaris* Palisot De Beauvois (Hemiptera: Miridae), Table 4 Known parasitoids of *Lygus* bugs

Parasitoid name	Family	Target	Comments
Indigenous species			
Polynema pratensiphagum Walley	Mymaridae	Egg	72% *Lygus* mortality in Quebec
Anaphes iole Girault	Mymaridae	Egg	
Anaphes ovijentanus Crosby Leonard	Mymaridae	Egg	50–85% *Lygus* mortality widespread
Erythmelus miridiphagus Dozier	Mymaridae	Egg	
Telenomus spp.	Scelionidae	Egg	
Peristenus pallipes (Curtis)	Braconidae	Larvae adults	First generation May–June; second generation Aug.–Sept. combined 15–20% *Lygus* mortality in Quebec; 38% in Ontario and 22% in Saskatchewan-Alberta
Alophora opaca (Coquillett)	Tachinidae	Adults	7% *Lygus* mortality in Quebec
Alophorella sp.	Tachinidae	Adults	0.8% *Lygus* mortality in Ontario
Imported species			
Peristenus stygicus Loan (USA, Sask., Alta.)	Braconidae	Larvae	Diapausing race from France and a nondiapausing race from Turkey; polyvoltine
Peristenus rubricollis (Thomson) (USA)	Braconidae	Larvae	From Poland; univoltine
Peristenus digoneutis Loan	Braconidae	Larvae	From France (potato, alfalfa rye fields) released in alfalfa field in New Jersey 1979–1988; 36% parasitism of first generation and 29% parasitism of second generation; released in seed alfalfa, Saskatchewan, and strawberries, Quebec, in 1991, 1992; Currently, descendents from the New Jersey releases are collected at St. Clothilde Qc. It is bivoltine; population at maximum abundance about same time as Lygus populations; attacks early stage nymphs of *Lygus*.

appears as if it has been gouged when small and the injury is called "cat facing." Furthermore, a certain percentage of fruit drop occurs following *Lygus* attack. The nymphs that will comprise the first generation attack strawberries causing malformed berries where the achenes are very close to each other and straw-colored. Similar to peaches, the injury is called "cat facing." Several vegetables such as celery, tomato, eggplant and pepper are also attacked by first generation adults and second generation nymphs and adults, causing flower abscission, which reduces yield in some years. In celery, early injuries to the stalk are of no economic consequence. However, near harvest, injury to petioles and necrosis of leaflets leads to secondary infections by bacteria. The damage is called black joint. It is serious and causes unacceptable economic losses. Though cotton is not its preferred host, the tarnished plant bug is a serious pest of cotton. Migration occurs when the wild hosts have dried along cotton fields. Following the completion of the second generation, the bugs enter the cotton fields and damage all fruiting forms of cotton. Early to mid-June pinhead squares (immature flower buds) are attacked and turn yellowish, dry up and eventually drop off the plant. In addition to feeding on pinhead squares, tarnished plant bugs also feed on terminal shoots. This activity results in several physiological changes caused by the toxins injected into the meristematic tissue of the plant terminal. The tall, fruitless plant is characterized by shortened internodes, swollen nodes and excessive lateral branches. This condition is often referred to as "crazy cotton." Later, damage to larger squares shows up as darkened anthers in white blooms resulting in poor pollination and deformed bolls. These are called "dirty blooms." Eventually, the tarnished plant bugs even attack the bolls causing small, dark, sunken spots on the outside of the boll and brownish discoloration inside the boll.

► Small Fruit Pests and their Management
► Vegetable Pests and their Management

References

Bostanian NJ (1994) The tarnished plant bug and strawberry production. Technical Bulletin 1994-1E. Agriculture and Agri-Food Canada, St. Jean-sur-Richelieu, Canada

Day WH (1987) Biological control efforts against *Lygus* and *Anthocoris* spp. infesting alfalfa, in the United States, with notes on other associated mirid species. In: Hedlund RC, Graham HM (eds) Economic importance and biological control of *Lygus* and *Adelphocoris* in North America. U.S. Department of Agriculture, Washington, DC, ARS-64, pp 20–39

Tingey WM, Pillemer EA (1977) *Lygus* bugs: crop resistance and physiological nature of feeding injury. Bull Entomol Soc Am 23:277–287

Young OP (1986) Host plants of the tarnished plant bug, *Lygus lineolaris* (Heteroptera: Miridae). Ann Entomol Soc Am 79:747–762

Taro Caterpillar or Rice Cutworm, *Spodoptera litura* (Fabricius)

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This insect occurs in Asia, Australia, and Oceania. There are reports that it invaded many locations outside its natural range and was eradicated, but it is not certain that such eradications involved this species. A very similar but allopatric insect, *Spodoptera littoralis* (Boisduval) (cotton cutworm), is found in Africa, Madagascar, Europe and the Middle East. For many years these two species were thought to be the same, and although they have been considered to be separate species by most authorities since 1962, confusion lingers. Other common names applied to *S. litura* include rice cutworm, tobacco budworm and common cutworm.

Life History

The number of generations displayed by this species depends on temperature. A generation can be completed in less than a month, and 12 generations have been reported annually in India, though 8–10 generations is more common in the wet tropics. Development ceases when temperatures are less than about 8°C, and the upper limit for development is about 37°C.

Eggs are spherical, somewhat flattened, and measure about 0.4–0.6 mm in diameter. They are deposited in clusters of 200–300 eggs, in fairly regular rows comprising three layers, and covered with whitish scales from the abdomen of the female moth. The eggs are orange or pink initially, but turn black before hatching. Eggs persist for 2–3 days in the summer, but considerably longer under cooler conditions, up to 25 days. Females have been shown to produce 2,000–2,500 eggs.

Larvae initially are blackish green with black heads. The older larvae are more variable, often appearing gray, brown or almost black and with dark markings. The latter instars bear triangular spots laterally on each body segment, and a yellow dorsal stripe. They attain a length of 40–50 mm. Young larvae feed in groups, but as they mature they become more solitary. However, at high densities they may disperse in large groups from field to field. Normally there are six instars. Larvae are inactive during the day, with the older instars seeking shelter in the soil but the younger larvae remaining motionless on the foliage. Larval development may require only 12–18 days under hot conditions.

Larvae burrow into the soil to a depth of 3–5 cm in preparation for pupation. Pupae are dark red to reddish brown, and are found in cells buried in the soil. The pupae are 15–22 mm in length, and the last segment bears two hooks. Pupal development time is only 7–10 days under warm conditions, but requires up to 30 days under cool conditions.

The appearance of adults are typical of *Spodoptera* moths, with the forewings bearing gray, brown, yellow and white markings, and the hind wings whitish with a brown or gray margin and dark veins. The wing span is about 30–38 mm. It is nearly identical to the yellowstriped armyworm, *S. ornithogalli* (Guenée), of North America. Adults are active at dusk and during the evening. They mate immediately upon emergence and can begin to deposit eggs within 2 days of mating, though sometimes several days elapse before egg deposition. The adults are short-lived, rarely surviving 7 days under warm conditions, though persisting for 3 weeks under cool conditions. Sex pheromones are produced and have been identified for use in traps.

Damage

This is one of the most serious crop pests in the Asian tropics. It is highly polyphagous, feeding on numerous vegetables, herbs, flowers, and field crops including soybean, cotton, maize, sunflower, rice, and grasses. Plants are often entirely defoliated, and bolls or flower buds can be eaten. Young plants may be severed at the soil surface.

Management

This species is often heavily parasitized by wasps and tachinid flies. Both eggs and larvae are affected. Numerous diseases also are known. However, management generally depends on use of chemical insecticides. Insecticide resistance is an increasing problem, however. In India, integrated management is promoted using trap crops (sunflower and castor plants) around crop fields, clean cultivation, prediction of egg laying by using pheromone traps for capture of moths, and application of neem and nuclear polyhedrosis virus for suppression of larvae. Resistance has been identified in some varieties of peanuts.

References

CABI and EPPO (1997) *Spodoptera littoralis* and *Spodoptera litura*. In: Quarantine pests for Europe, 2nd edn. CABI International, Wallingford, United Kingdom, pp 518–525

Etman AAM, Hooper GH (1979) Developmental and reproductive biology of *Spodoptera litura* (F.) (Lepidoptera: Noctuidae). J Aust Entomol Soc 18:363–372

Rao GVR, Wightman JA, Rao DVR (1989) Threshold temperatures and thermal requirements for the development of *Spodoptera litura* (Lepidoptera: Noctuidae). Environ Entomol 18:548–551

Rao GVR, Wightman JA, Rao DVR (1993) World review of the natural enemies and diseases of *Spodoptera litura* (Lepidoptera: Noctuidae). Insect Sci Appl 14:273–284

Tarsal Claw

The claws at the tip of the tarsus.

► Legs of Hexapods

Tarsomeres

The major subdivisions of the tarsus (the foot), the distal segment of which is called the pretarsus, and bears claws and sometimes a pad or arolium.

► Legs of Hexapods

Tarsus (pl., Tarsi)

The jointed portion of the insect leg distal to the tibia, consisting of tarsomeres and often bearing claws on the distal segment (pretarsus). The "foot" of an insect (Fig. 9).

► Legs of Hexapods

Taste and Contact Chemoreception

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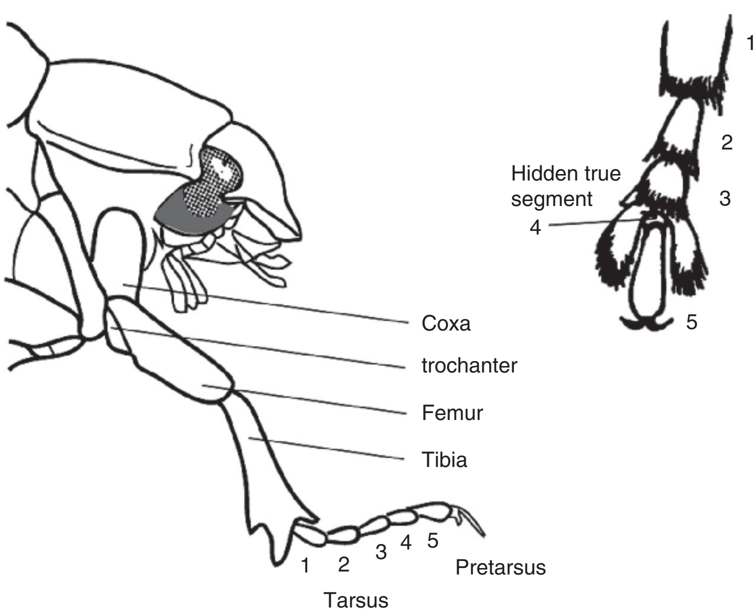
The sense of taste provides animals with the ability to identify potential food by the perception of certain nutrients, and also to detect potentially toxic materials. Insects are no exception, but unlike most other animals their taste receptors are not restricted to the region around the mouth and they may be able to recognize oviposition cues, and, occasionally, intraspecific signals as well as food. In addition, whereas in vertebrates the taste receptors are stimulated by chemicals in solution, insects have the capacity to perceive chemicals on dry surfaces. For this reason, it is referred to as "gustation" or "contact chemoreception" rather than "taste."

Insect contact chemoreceptors are usually in the form of hairs, or conical projections from the cuticle, with a pore at the tip. The pore permits chemicals to pass through the cuticle to the sense cells beneath. Each hair, or cone, contains the sensitive endings (dendrites) of (commonly) four sensory cells, and each of these responds to a different range of chemicals. The ranges of chemicals reflect the habits of the insect and also the position and specific function of a particular hair.

Very little is known about why an insect chemosensory cell responds to one, or some chemicals and not to others, but it is probable that, as in other animals, this is determined by receptor molecules in the cell membrane of the dendrite just inside the pore in the cuticle. A taste receptor cell may have only one type of receptor molecule, in which case, its response is limited to one, or a few, structurally similar chemicals that interact with the receptor. Other cells have more than one type of receptor molecule, and so have the capacity



Tarsus (pl., Tarsi), Figure 9 Leg of a beetle (Coleoptera: Scarabaeidae) leg showing its component parts, and a close-up of one type of beetle tarsus (foot).

to respond to a range of structurally different chemicals. Some cells that are presumed to have these different characteristics are described below.

The interaction of the appropriate chemical with a receptor molecule leads to changes in the electrical potential across the cell membrane and an electrical signal is sent along the axon that connects each sensory cell to the central nervous system. Connections within the central nervous system determine whether the insect responds positively or negatively to the stimulating chemical, that is, whether it accepts or rejects food, or an oviposition site. In practice, how the insect responds nearly always depends on the integration of signals from a number of receptors.

Contact chemoreceptors are found primarily on the mouthparts, the labrum, maxillae, labium, and hypopharynx, and they may be especially abundant on the maxillary and labial palps when these are present. A small number are present on the epipharynx (the inside surface of the labrum) just outside the mouth in all insects that have been investigated. Many insects also have contact chemoreceptors on the tarsi, and on the antennae, although most of the chemoreceptors on the antennae are olfactory receptors. Females of some Orthoptera, Diptera, Hymenoptera and Lepidoptera have contact chemoreceptors on their ovipositor, but this is not a general characteristic of females even within a group.

The numbers of contact chemoreceptors associated with the mouthparts is very large in cockroaches, grasshoppers and related insects. An adult of the migratory locust, *Locusta migratoria*, for example, has about 3,000 contact chemoreceptors on the mouthparts. In these insects, additional receptors are produced at each molt. By contrast, much smaller numbers are present in sucking bugs. Aphids have no contact chemoreceptors on the exposed parts of the proboscis, but they have a few on the epipharynx. As a result, aphids must draw fluid into the cibarial cavity before they are able to taste it. This is not true of all sucking bugs, however, many of which have contact chemoreceptors on the tip of the labium, which is the first mouthpart structure to contact the food prior to feeding. Holometabolous insects also generally have few mouthpart contact chemoreceptors, especially in larvae. Caterpillars have only 16–20 contact chemoreceptors and this number does not change throughout development. In grasshoppers, species with more restricted diets tend to have smaller numbers of contact chemoreceptors on the mouthparts than polyphagous species. Among caterpillars, however, this is not true. The numbers are similar irrespective of feeding habit.

Feeding

The primary function of contact chemoreceptors on the mouthparts is the selection of food. Once the insect bites into food, some receptors become immersed in the juices released from the food and so function very much like taste receptors in vertebrates by detecting compounds in solution. However, the receptors on the maxillary and labial palps often come into contact with food before the insect bites. They can detect compounds on the dry surface of a leaf, for example. In grasshoppers, crickets and cockroaches, the palps are vibrated rapidly so that the contact chemoreceptors at their tips are brought into a rapid series of brief contacts with the surface. As many as 15 contacts per second may be made, and each period of contact probably lasts less than 20 ms. This behavior, known as palpation, probably serves two functions. It allows the insect to receive a more sustained flow of information from the receptors than would be possible if contact were maintained because the receptors become adapted (as our taste receptors do after the first mouthful of a sweet drink), and it also allows the insect to sample a larger surface area than if the palps remained stationary. The information provided by palpation before an insect starts to feed enables it to make feeding decisions more rapidly and also, perhaps, to avoid the possible intake of noxious compounds if the food contains toxins.

Insects, like other animals, can taste the major nutrients essential for their development, survival and reproduction: sugars (as a source of energy), amino acids (the building blocks for protein), and inorganic salts and water. There is no direct evidence that insects are able to taste proteins. The specific chemicals to which an insect's taste receptors respond, however, vary with the feeding behavior of the insect. It is common for one of the sense cells in a contact chemoreceptor to be sensitive to some sugars, and another to be sensitive to some amino acids. Some insects have also been shown to possess a "water cell," that is, a cell that responds to water and very dilute salt solutions, and it is possible that this type of cell is of widespread occurrence. All insects appear to have a cell responding to inorganic salts, but this cell exhibits increased activity as the salt concentration increases (unlike the "water cell" whose activity declines with increased salt concentration), and it is probably a cell that inhibits further feeding, ensuring that the insect does not ingest excessive amounts of salt. The other nutrients such as sterols, fatty acids and vitamins appear to be acquired as a result of their widespread occurrence in the insect's food and do not require specific taste receptors.

A cell responding to sugars does not necessarily respond to all sugars, nor does an amino acid-sensitive cell respond to all amino acids. In the woolly bear caterpillar of the moth, *Grammia geneura*, for example, a sugar-sensitive cell in one hair only responds to the fruit sugar, fructose. This cell probably has only one type of receptor molecule that only reacts with fructose. However, a cell in another hair close by responds to sucrose and glucose although not to fructose. This cell probably also has a single type of receptor molecule that reacts with both sucrose and glucose because of similarities in their molecular structure. In the same way, cells in different hairs may respond to different ranges of amino acids. This probably allows an insect to detect food of different qualities. Even so, not all different types of sugar or amino acids are tasted by any one insect even though some of them are essential for its development. It obtains a balanced diet mainly because a food with some nutrients, which it can taste, will generally contain most of the others, which it cannot taste.

In addition to nerve cells that respond to nutrient compounds, many plant-feeding insects possess sensory cells that respond to plant secondary compounds. These compounds, alkaloids, terpenoids, and many others, are produced by plants outside the normal primary metabolic pathways (hence "secondary") and are important in the plant's ecology. Many of them inhibit feeding by herbivorous animals, including insects, and the human interpretation is that they taste "bitter." Sometimes they are also toxic. In a majority of plant-feeding insects, stimulation of a cell by these secondary compounds inhibits, or deters feeding, and the cells are usually called "deterrent cells." A deterrent cell usually responds to several different secondary compounds, but by no means all the different types. This almost certainly reflects that fact that it has several different types of receptor molecules.

Because all plants contain secondary compounds, whether or not an insect feeds on a particular plant and the amount it eats is dependent on the balance between information received from taste cells signaling the presence of nutrients, and deterrent cells signaling the presence of secondary compounds. However, in some insect species that feed only on particular plant species or groups of plants, characterized by a specific chemical, it is common for the deterrent cells to have lost any sensitivity to that chemical so the plant is no longer "distasteful." Correspondingly, some now have a sensory cell that responds only to that compound or class of compounds and which indicates "acceptability" rather than "distastefulness" to the insect. The best-known example of this is the response to glucosinolates. These are sulfur-containing compounds characteristic of the cabbage family. For most plant-feeding insect species, these compounds stimulate deterrent cells and inhibit feeding, but in many species that feed habitually on plants in the cabbage family, the deterrent cells are not affected. Instead, another sensory cell responds to the glucosinolates, indicating acceptability so that the insects are stimulated to feed or oviposit.

In species that feed on vertebrate blood, the contact chemoreceptors have a sense cell that responds to adenine nucleotides such as ATP and ADP. These compounds are released when the insect probes into the host's blood vessels and damages blood cells. They provide the insect with an unequivocal signal that appropriate food is available.

Not only the chemoreceptors on the mouthparts are involved in feeding decisions, however. This is most obvious in fluid feeding insects like flies and bees, where extension of the proboscis, which is necessary before the insect can feed, is induced if chemoreceptors on the tarsi are stimulated with sucrose. In the tsetse fly, *Glossina fuscipes*, similar receptors respond to some of the common components of human sweat, such as uric acid and the amino acids leucine and valine. Stimulation with these compounds causes the insect to probe with its proboscis and is presumably part of the normal host recognition process. Tarsal receptors are also involved in host recognition by plant-feeding insects.

Oviposition

It is common for contact chemoreceptors to be involved in oviposition, although attraction to the oviposition site often depends on the sense of smell. Contact chemoreception in this context has been most thoroughly investigated in some flies such as the cabbage fly, *Delia radicum*. The tarsal receptors on this fly respond to glucosinolates on the leaf surface of the host plant. Other insects, like the imported cabbage butterfly, *Pieris brassicae*, and the cabbage looper, *Trichoplusia ni*, that lay their eggs on cabbage plants also have tarsal receptors responding to glucosinolates. Contact with these compounds induces the insects to lay eggs. A number of butterflies drum on the leaf surface with their fore tarsi when selecting a leaf for oviposition. This appears to be a process analogous to palpation, bringing the contact chemoreceptors on the tarsi into a series of brief contacts with the leaf surface. There is no evidence that the leaf surface is broken by these activities, so the insect does perceive chemicals on the surface, not from within the plant.

Although contact chemoreceptors do occur on the ovipositors of some insects, there is not yet clear evidence of their roles in oviposition.

Pheromone Detection

Contact chemoreceptors are sometimes important in the perception of pheromones involved in sexual recognition, prevention of oviposition, and trail following. In the tsetse flies, *Glossina* species, the male recognizes a female by touching her with contact chemoreceptors on his fore tarsi. This contact also enables him to determine whether or not she has mated through the perception of specific molecules in the wax on the surface of the female's cuticle. Changes in the proportions of some components occur at the time of mating because wax from the male contaminates the female, and the male is able to detect the difference with his tarsal receptors. A similar process occurs in *Drosophila* fruit flies, except that in this case, the female wax alters as a result of changes in synthesis in the female following mating. Females of the German cockroach, *Blattella germanica*, also have sex specific compounds in their cuticular wax which function as a sex recognition pheromone. At the start of courtship, the male touches the female with his antennae, presumably detecting the compounds with contact chemoreceptors on the antennae.

Contact chemoreceptors are used by the adults of some flies to detect oviposition deterrent pheromones laid down by previously ovipositing females to reduce the likelihood of competition with their larvae. This is known to be the case in adults of the apple maggot fly, *Rhagoletis pomonella*, and the cabbage butterfly. The cabbage seed weevil, *Ceutorhynchus assimilis*, however, detects its oviposition deterrent pheromone with contact chemoreceptors on the club of the antenna. Although contact chemoreceptors are common on insects' antennae, this is one of the few instances where their function is known. Many insects are known to make rapid vibrations of the antennae when they encounter a potential food or prey item. This process is known as antennation, and it is probably analogous to palpation with the insect bringing contact chemoreceptors at the tip of the antenna into brief contacts with the substrate. Parasitic Hymenoptera, for example, are commonly seen doing this when they encounter a potential host.

Tent caterpillars follow chemical trails deposited by conspecifics. The trails are detected by contact chemoreceptors on their maxillary palps.

It is almost certain that there are many situations in which insects use contact chemoreceptors on their antennae or tarsi for the perception of intraspecific signals.

► Ultrastructure of Insect Sensilla

References

Chapman RF (1995) Chemosensory regulation of feeding. In: Chapman RF, de Boer G (eds) Regulatory mechanisms in insect feeding. Chapman and Hall, New York, 101–136 pp

Glendinning JI, Chaudhuri N, Kinnamon SC (2000) Taste transduction and molecular biology. In: Finger TE, Silver WL, Restrepo D (eds) The neurobiology of taste and smell. Wiley-Liss, New York, 315–351 pp

Taxis (pl., Taxes)

A directional movement in response to an environmental stimulus, directed toward or away from a stimulus. A movement toward the stimulus is considered to be a positive taxis, a movement away is a negative taxis. Types of taxes include anemotaxis, astrotaxis, chemotaxis, geotaxis, hygrotaxis, phonotaxis, phototaxis, rheotaxis, and thermotaxis.

Taxon (pl., Taxa)

A group of organisms, populations or taxonomic groups considered to be sufficiently different from other groups to be treated as a unique group from the perspective of classification or taxonomy. For example, a species is a taxon when it is compared to another species; likewise, higher level groups such as families and orders can be referred to as taxa.

► Classification

Taxonomy

The principles and procedures according to which species are named and assigned to taxonomic groups.

► Classification

Teaching and Training Entomology: Institutional Models

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Research on insects, whether to understand basic biology or to provide management strategies, most often occurs within thef context of an institutional paradigm. Precisely the same is true for teaching/training programs and extension. The structure of an organization in which researchers, trainers or extension specialists work is crucial to understanding the goals, motivations and successes of those human resources. Understanding the institutional framework within which programs are developed and delivered is therefore an important consideration when evaluating program effectiveness.

There are five principal models of institutional and procedural frameworks within which research, teaching and/or extension programs associated with entomology occur. Three are fairly widely used and two have the potential to become global.

The very framework chosen within which to pursue entomology may well affect the types and quality of information developed. Evaluating the effectiveness of entomological programs cannot be complete without recognizing the institutions within which such programs are developed and reside.

The degree to which entomological programs developed under one paradigm can function successfully when transferred to another is therefore an important and an intriguing issue, but one that has been virtually ignored on a global basis. Each of the five major models currently used has advocates and critics, and each has relative strengths and weaknesses. However, discussion of program strengths and weaknesses most often fails to consider the institutional context in which they have developed historically, and thus fails to provide a comprehensive analysis of when, how and why these programs succeed or fail.

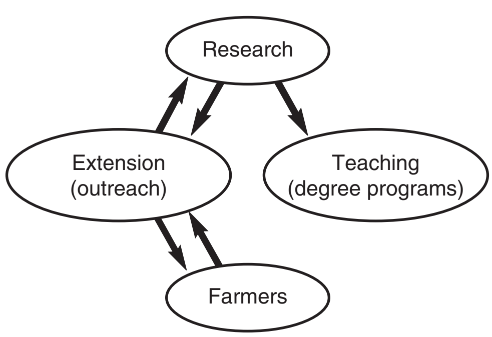
The Land Grant System: USA

During Abraham Lincoln's presidency, the United States Congress was moved to provide legislation directly aimed at assisting farmers. This made both practical and political sense, as some 65% of the U.S. population was involved in agriculture in one way or another. Under Lincoln's guidance, the United States Department of Agriculture was established in 1861. Then, four successive Federal Acts (Morrill Land Grant Act, Hatch Act, second Morrill Act and Smith-Lever Act), dating from 1862 to 1914, set aside lands for agricultural research and put the infrastructure and human resources in place to conduct that research. The second Morrill Act (1890) set aside a second set of lands and infrastructure for the development of what are often termed Historically Black Colleges and Universities (HBCUs), and the Smith-Lever Act (1914) created the Federal Extension System.

The Land-Grant system is based on the concept of combining teaching, research, and extension within a single institution, and it took about 50 years to establish all three functions. All 50 states and U.S. protectorates and territories employ the system. America has led the world in agricultural production since the Land Grant system was established.

Proponents of the Land-Grant model point to the productivity of American agriculture and the associated research infrastructure. Indeed, due in part to the Federal and state investment in this institutional model, the USA is today the world's leading producer of food with only about 1.8% of the population involved in food production. The USA grants more graduate degrees in the agriculture-related disciplines than any other nation, and more international students seeking advanced degrees in agriculture choose to study in the United States than anywhere else. Including extension in the model indicates the importance of a forward and backward link between farmers and researchers. Finally, this model ensures that advances in agricultural technology to find their way into the classroom very quickly, ensuring that future generations of agricultural professionals and farmers are able to apply the new technologies (Fig. 10).

Not everyone agrees that this model is ideal. Critics of the Land-Grant model point out several weaknesses in the system:



Teaching and Training Entomology: Institutional Models, Figure 10 **Basic structure and flow of information in a Land-Grant Institution as originally conceived.**

1. Over the years, extra-mural grants have supplanted Federal and state direct support for agricultural research and extension. Grants programs are fickle and trendy. Land-grant institutions have a long history of "following" extra mural priorities (integrated pest management in the 70s, sustainable agriculture in the 80s, and genetic engineering now). The wholesale commitment to these types of trends by significant percentages of land-grant scientists is indicative of how susceptible this model is to abrupt shifts in priorities in the quest to acquire funds and publish. Research is driven more by granting agency priorities than by farmer needs.
2. Due in part to the emphasis on extra-mural funding, Land-Grant institutions tend to recruit faculty with ever-narrowing expertise so they can compete successfully for grants. As a result, the system lacks scientists who have either the skills or the incentives to integrate knowledge across disciplines. Individuals who are capable of critically analyzing the potential impacts of new technologies in a broader social, economic and ecological framework are rare.
3. The departmental and college management structure of Land-Grant institutions is, in many ways, the antithesis of the type of holistic program structure needed to resolve real problems. University units are rewarded for their individual productivity, not for their collective cooperation. While universities constantly discuss the need for inter-disciplinary approaches, their very structure often prevents them from implementing effective cross-disciplinary solutions.
4. The ability of the USA to capitalize on the high productivity of Green Revolution agriculture is as much attributable to good fortune as to agricultural research, and it is likely not sustainable. Green Revolution agriculture depends on high levels of off-farm inputs that make successful farmers more dependent on a few transnational corporations that supply seed, fertilizers, equipment, and chemicals while also increasing the farmers' debt. Other farmers simply cannot obtain these inputs. There appears to be an internal conflict of priorities in the Land-Grant Model. One priority is to feed the masses at any cost. The other is to keep small farmers in business for the social good.
5. Teaching in Land-Grant institutions often is the single least rewarded activity. Reward and professional advancement depend largely on the amount of grant dollars obtained and the number of publications produced. Relevance to real farm problems may not rank high among the factors taken into consideration for faculty promotion.
6. Extension often does not work as it was conceptualized. The fundamental idea was for extension to serve as the voice of the farmers and to vocalize the research needs seen by farmers as priorities. That extension voice would then explain those priorities to university researchers who, using their research expertise, would investigate the issues, develop solutions and have the extension voice deliver those solutions back to the farmers. In reality, researchers are driven by grant priorities, rather than extension-relayed farmer needs.
7. Finally, critics point out that the USA has moved from an original farm policy designed to keep farmers on the farm and farming profitable, to a "cheap food" policy designed to feed urban populations who, by and large, elect Federal officials. The Land-Grant infrastructure evolved to pay little attention to the promotion of agricultural procedures that would make farming sustainable and conserve natural resources.

While the debate continues, the sheer volume of output from Land-Grant programs is impressive. In the USA, the Land-Grant system encompasses a wide range of farming enterprises. Large scale, corporate farming often becomes a source of information for Land-Grant scientists as corporations have the capital to invest in staff and research on their crops and pests that tax-based Land-Grant institutions do not. Small farmers often cannot afford to adopt the technologies proposed by Land-Grant scientists and tend to utilize a mix of modern science and traditional farming practices.

The system has not gained acceptance outside the U.S. and, in fact, has really not ever been replicated elsewhere, although components of the system have been implemented in other places. This model depends greatly on a collaborative relationship among peers for its success. Peer review, for example, is a major factor in evaluating the quality of teaching, research and extension. Similarly, funding for the system involves Federal, state and local support, and farmers must be empowered to ensure that their problems and priorities are imposed on the entire structure. All of these characteristics are typical of the social and political structure in the United States. The poor "transportability" of the U.S. system, especially to non-European based cultures and to nations where democracy is not the norm, may be due, in large part, to the absence of an appropriate social, cultural and political context for the system. The Land-Grant model may be culturally insensitive, but not necessarily wrong. Agricultural productivity appears to be like every other increasingly globalized activity: one cannot compete if one doesn't play the top-level game. This, of course, is not highly acceptable to politically sensitive people who want to maintain local culture and merely improve agricultural productivity. Global competition likely will demand local cultural changes in the way farmers and governments spend their time and money.

Training and Visit (T&V): World Bank

T&V is a child of the World Bank, and this model was conceptualized and first utilized in Asia in the 1970s. This hierarchical system began in India, Turkey, Burma, Nepal, Sri Lanka and Thailand, and today exists in more than 40 nations. The basic premise of the T&V system is that much more information and technologies exist than are used by farmers, and the principal reason for this is the ineffectiveness of extension delivery systems. T&V thus places major emphasis on training and outreach. Research is most often limited to site-specific adaptive research of existing technologies. While more recent T&V programs have tended to re-emphasize the research component, the approach continues to focus heavily on outreach.

T&V is a top-down approach. A subject matter specialist trains a limited number of regional extension agents who, in turn, provide training to local extension agents who, in turn, train farmers. This approach emphasizes the timeliness of actions, and the progress of agricultural productivity at the farm and regional levels is "tracked" by the training process. For example, training on improved seedbed preparation will be delivered just before the time when seedbed preparation is to occur. Frequent, regular reporting from the bottom up is a key feature of the T&V model. The Land-Grant system has "field days" and "demonstration plots" where farmers can come to witness innovations. While not hierarchical in nature, as is T&V, the idea is somewhat the same.

Proponents of T&V argue that the system is ideal because it focuses on those human resources that are native to indigenous cultures, provides a "filter" to take existing technology and adapt it to local conditions, and it is both relevant and timely. T&V takes complete advantage of cultural and social hierarchies already in place. The fact that T&V is currently utilized in over 40 nations, so say the proponents, is indicative of its relevance. Simply put, it works.

Critics of T&V point to several shortcomings:

1. Methods are geared to the top, best-educated, most articulate facilitators (regional extension personnel). Most T&V programs end up with a paltry number of highly capable facilitators. The methods that are emphasized both confuse and leave behind the other participants in the system. One result is that the less capable extension agents train their local agents poorly, and the farmers who rely on them, in essence, receive poor advice.
2. In the same vein, T&V historically has not sanctioned facilitators for not attending all training sessions. One result is poorly equipped facilitators, and the problem progresses down the hierarchy.

3. This approach, in many ways, "force fits" the T&V timetable into an often-unreceptive farmer schedule resulting in poor adoption of advice.
4. T&V programs historically are narrow in perspective and not linked to broader, yet relevant, issues of great concern to farmers. Timely seedbed technology is useless if not linked to socially relevant local schedules and to lending periods and priorities of local banks.
5. T&V programs were developed for irrigated systems where water was controlled and never attempted to develop procedures exportable to rain fed agriculture.
6. Many analyses have shown T&V approaches to be overly costly and non-sustainable.

T&V differs from the Land-Grant system in its almost sole focus on a hierarchical extension-training approach. An interesting note is that virtually all the countries where T&V is employed are in World Bank-funded efforts in Asia. T&V does not appear to have been widely adopted elsewhere. However, the essence of T&V sometimes is practiced in other countries like Jamaica despite no formal funding of projects actually called T&V.

Once again, cultural and social factors may play an important role in determining how well this system "travels" from its Asian heartland to other parts of the world. The very hierarchical model that assumes that knowledge flows "downward" from more educated and knowledgeable experts to practitioners (farmers) would not, for example, be very acceptable to many farmers in the United States or perhaps in most societies where egalitarian norms are strong.

Farming Systems: United States Agency for International Development

The farming systems model originated from programs in Latin America and, over the last two decades, has been promoted by a variety of international development agencies. The single largest advocate of this model in the 1980s was the United States Agency for International Development (USAID). Many of the CGIAR centers (notably CIP, CIMMYT and IITA) also have used this model.

The farming systems model differs widely from T&V in that farming systems primarily emphasizes research, not extension. Underlying the farming systems model is the assumption that most existing technology has not been adapted to specific regional or local conditions. Farmers are, therefore, unable to adopt and utilize what would be useful methods. The major emphasis of farming systems is on site-specific, adaptive research. While there is episodic invention of "new technology," the major emphasis focuses on local tests of existing technologies. Proponents of this model argue that there are major differences between the farming systems model and the Land-Grant model. In practice, those differences are often hard to discern. Both models depend on strong linkages between research and extension and are difficult to implement in places where the two functions are not housed in the same institution. Further, many advocates of the Land-Grant system argue that both models emphasize features such as on-farm research, site-specific testing and multidisciplinary research teams. There is, in practice, one major difference between the two models. The farming systems model emphasizes research much more than extension, and farming systems projects that demonstrate mass dissemination of information are rare.

A basic tenet of the farming systems model is that many global farmers have been by-passed by the Green Revolution. Their land holdings or their economies were too poor to take advantage of high-yielding agriculture and its associated inputs. Thus, the advocates say the most relevant approach is the use of a multidisciplinary "rapid rural appraisal" team to ask farmers' opinions, followed by research aimed at tailoring existing technology to individual farmers' fields (Figs. 11 and 12).

Critics of the farming systems model point to a number of constraints on its effectiveness:

Teaching and Training Entomology: Institutional Models, Figure 11 **Farming systems training effort in The Gambia, West Africa.**

Teaching and Training Entomology: Institutional Models, Figure 12 **Farming systems project to teach proper goat-dipping techniques for tick control in Kenya. Slide provided by Dr. Sandra Russo, International Programs, University of Florida.**

1. The disciplinary make-up of the initial rapid rural appraisal team can severely bias what the team determines is pertinent research.
2. Farming systems teams have often been unable to define their tasks and, consequently, served only to "spread the gospel" of farming systems rather than to provide holistic solutions for real problems. Farming systems failed in Africa for precisely this reason.
3. Many farming systems projects to date have focused on crop variety and/or fertilizer trials – the very things that these farmers supposedly could not afford, thus giving rise to the farming systems model in the first place.
4. To date, adherents of the farming systems model have been primarily economists, anthropologists and a few agronomists. The broad spectrum of agricultural disciplines apparently has not b ought into the basic premise of farming systems.
5. It is an expensive system, relying on a highly trained and educated body of researchers becoming very familiar with local conditions, problems and farmers. The central role of the multi-disciplinary team, along with the emphasis on the site-specificity of knowledge, means that any institution using this approach must make a relatively large investment in the local farming systems team and cannot spread the effect of that investment across a very large geographic area. Not surprisingly, like T&V, most places using the farming systems model also have been the recipients of funding from the principal donor advocating the model.

The basic argument for the origination of the farming system model would seem pertinent, and the approach has been tried in a number of locations with mixed results. Like the Land-Grant model, which it resembles in many other aspects, the farming systems model depends on mutual respect among peers and between agricultural professionals and farmers. In societies where there are strong biases against effective communication between individuals of differing social, economic or cultural status, the all-important communication between researcher and farmer is likely to fail. Again, the success of this system may well depend on the social and cultural context in which it exists, and its distinct lack of success in some parts of the world may reflect cultural and social realities rather than simply the ineffectiveness of the system itself in solving farmers' problems.

Interestingly, the World Bank funded both T&V and Farming Systems projects in Africa. T&V came first as an extension effort and was followed by farming systems as a research effort (Malawi, Tanzania, Ethiopia). World Bank saw these two models as complementary. Yet, African successes at solving real problems in a cost effective manner are hard to find.

Training-Driven Research: Indonesian Integrated Pest Management

This model is relatively new and has not been implemented in many places. Basically, it has been developed as part of an Asia-wide integrated pest management effort funded originally by the Australian government and is now managed by the Global Integrated Pest Management Group within FAO in Rome, Italy. It offers exciting possibilities to overcome many of the flaws inherent in the other three models.

Training-driven research is based on two fundamental premises (i) do not conduct research unless it is needed and (ii) use training as the tool to identify what research is needed. This model is like T&V in that it trains personnel who, in turn, train others and farmers. It is like farming systems in that it focuses only on "relevant" research, and it is like the Land-Grant model in that it combines training, extension and, when needed, research.

Farmers and those who assist and advise them need to be trained. Thus, experts establish a rigorous, field-based training program for the farmer support system, then for the farmers. Beginning with field preparation, each and every step in the agricultural production annual cycle is demonstrated to the trainees, both in the field and on site. Experience of the trainers, literature and formal knowledge possessed by the trainers are incorporated into the training course. As long as the information exists to proceed in relevant fashion through all the steps of production (from field preparation, to fertilization, to pest management, to harvesting, to marketing), there is no need for research (Fig. 13).

If, at any step, the trainer recognizes that the information to train appropriately does not exist, there is a call for "research." This may take the form, however, of a demonstration rather than a full-blown, randomized experiment. In any case, the product of this research is not a journal article, but rather feedback provided directly to the training program. This is an iterative process resulting, sooner or later, in an ability to appropriately train farmers and their assistants without conducting research until a new, unknown situation arises.

Teaching and Training Entomology: Institutional Models, Figure 13 In-field training for rice farmers and support staff at a farmer field school, Indonesia.

This model differs markedly from the Land-Grant model where funded research is the top priority. Further, the first priority of Land-Grant research is not training, but publication and the volume of such publications produced is germane to continued employment in the Land-Grant system. Training-driven research also offers a paradigm to regiment discipline expertise. Often, Land-Grant multidisciplinary teams attacking some aspect of agriculture will find, once the problem is truly understood, they have the wrong expertise on the team (e.g., hiring a bacteriologist when a virologist was needed). Training-driven research avoids this issue by first identifying the particular need, then seeking the appropriate expert.

Training-driven research, to date, has not been attempted in enough places to have many proponents or critics. One criticism to date focuses on TDR's inability to demonstrate any significant research accomplished after identification of the problem in training. Indonesian rice has been the principal target to date. As it expands and is attempted, similar to the first three models, inherent strengths and weakness will be identified.

Farmer Participatory Research: CGIAR Network

Concerns over the lack of appropriate technology transfer have given rise to a more recent institutional paradigm. Farmer participatory research (FPR) has its origins within the CGIAR system and, from all appearances, has had its greatest impact to date in Asia. The conceptual foundation for FPR is a belated appreciation of mainstream agricultural scientists for the importance of indigenous knowledge to agricultural systems management, especially with resource-poor, marginal farmers.

Operationally, FPR begins with four fundamental steps (i) community-based dialogue with individuals or small groups used to identify local changes in agriculture over a generation or two; (ii) community-based analysis used to identify high-priority problems that need resolution; (iii) community-based inventory of local methods attempted to solve the key agricultural problems; and (iv) community-based assessment of how well methods tried in (iii) have performed. The purpose of FPR is to initially learn how farmers think and assess agricultural productivity and damage. Only then can new technology be injected in a socially and culturally relevant fashion.

A recent FPR project in Viet Nam illustrates how the approach functions. Vietnamese farmers were invited to test the heuristic, "We do not need to spray insecticides in the first 30 days after transplanting [rice]." Volunteer rice farmers were invited to participate, and each reported results based on individual assessment of perceived damage. Analytical variables used to determine success or failure of the project included farmers' beliefs, intentions, spray frequencies, timing and targets, yields, inputs and other management practices (Fig. 14).

Teaching and Training Entomology: Institutional Models, Figure 14 **Viet Nam farmer participatory training session on evaluation of insecticides during first 30 days after sowing. Photo provided by Dr. Kong Luen Heong, International Rice Research Institute, Los Baños, Philippines.**

Such experiments, if managed properly, usually are inexpensive and easy to conduct, and they facilitate farmer learning by pragmatically "testing" a new idea. The process provides researchers the opportunity to learn how farmers think and perceive success or failure. The FPR approach can be quite expensive if attempted over large areas. The presence of well-educated scientists will affect farmers differentially, and care must be taken to minimize this influence by including farmers at all levels of planning and decision-making. Reductionist scientists often view FRP as scientifically "weak," however, those using this approach must remember that the idea is to evaluate farmer responses and learn how they perceive success and failure. The idea is not to conduct well-controlled, reductionist experiments. Adoption rates for new varieties of plants and improved technology are well-documented in the literature, however, much less is known about the adoption or adaptation of information into farmer decision-making.

Fundamental to FPR is a concerted effort to train local agriculturists to proceed through the above four steps so that, after a few iterations, local farmers and their support network work independently of outside influence. Unlike reductionist science, FPR begins by assuming that indigenous peoples have usable solutions to many agricultural problems or they would not have survived. The effort is to extract those solutions up front and, by doing so, convince local farmers that they will not be treated simply as passive recipients of modern, science-based information. Rather, they will be partners in the experimentation and delivery phases of agricultural development. There is growing evidence that the most effective extension programs in Land-Grant models also operate this way. Unfortunately, this is not yet the norm.

FPR is a unique approach and quite different from station-based research and traditional extension-delivery systems. It is, in many ways, the antithesis of the Land-Grant model. Unlike farming systems, FPR does not have to "adapt" station-based research because the blend of indigenous knowledge and modern science is inherent in FPR. Unlike the T&V approach, there is no hierarchy involved and no loss of information between tiers. FPR most closely resembles the training-driven research model, but has been tried in more places to date than TDR. There are on-going efforts in Asia, Africa and Latin America that use FPR as the paradigm. In Ecuador, small groups of farmers form committees and decide on a theme they want to research and then conduct that research under the guidance of an extension specialist. Colombia, under the auspices of CIAT, has adopted the same approach. There is increasing awareness that talking with farmers is an improvement over talking at farmers.

Unlike the Land-Grant, T&V and farming systems models, FPR is a new approach. In essence, it has been developed out of the perception that the other models have failed to resolve real problems with marginal farmers. The concept of formalized farmer field schools appears unique to TDR and FPR, although, Land-Grant extension experts would argue their "turn row conversations" with farmers serve precisely the same purpose. As TDR and FPR gain maturity, the global agricultural community can begin to assess their real impact and their relative value as compared to the other three institutional paradigms.

In agricultural societies of relative wealth where individuals, not social groups, make decisions, and where egalitarian norms prevail, systems resembling, at least in part, the Land-Grant system have prevailed. Land holdings and economies conducive to high-yielding agriculture seem to be requirements for the success of Land-Grant style entomological programs, probably because of the emphasis on the ability of individual farmers to make critical decisions about how they will manage their resources. The other four models have both been conceptualized and implemented with farmer groups who have virtually none of these characteristics. The latter groups consist of farmers that are relatively poor, often make group or community decisions, typically have poor access to credit and are labor intensive. These models appear to be more successful in places where cultural norms play a stronger role in determining acceptance of new practices than in places where decisions about technological innovation are less subject to social and political control.

By far, the Land-Grant system is the model that adheres most rigorously to reductionist experimentation. Large numbers of farmers under the Land-Grant, T&V, and farming systems approaches are today still treated as passive recipients of information, not as active participants in the identification and generation of new information. The farming systems approach does ask farmers what they think is important as a way to initiate the model. Training-driven research and Farmer Participatory Research truly involve the farmer and the associated support system as active participants in the process. Both these latter paradigms make use of indigenous knowledge systems and thus strive to have as end products agricultural programs that are blends of traditional approaches and modern science.

All five models (Table 5) have inherent strengths and weaknesses, but only three have been attempted to date on a fairly broad scale.

Teaching and Training Entomology: Institutional Models, Table 5 Characteristics of five institutional models of agricultural (including entomology) research, training and extension

Characteristic	Land-Grant	T&V	Farming systems	Training driven research	Farmer participatory research
Major focus on research	Yes	No	Yes	No	Yes (with an altered definition of research)
Major focus on publication	Yes				
Major focus on extension	Yes	Yes	No	Yes	No
Focus on use of indigenous knowledge	No	No	No	Yes	Yes
Major focus on farmer training	No	Yes	No	Yes	Yes
Targets users with relatively good resources	Yes	No	No	No	No
Targets marginal users	No	Yes	Yes	Yes	Yes
Regiments technical expertise	No	No	No	Yes	Yes
Puts farmers in active role	No	No	No	Yes	Yes
Combines research, training and extension	Yes	No	No	Some	Inherently
Sufficiently tested outside area(s) of origin	No	No	No	No	No
Area(s) targeted to date	USA	Asia; some Africa; some Latin America	Latin America; some Africa	Asia	Asia; some Latin America; some Africa

Clearly, the questions asked about insects, the methods chosen for investigation, the methods used in training and the consequences of entomological programs can vary markedly from one model to the next. Recognition of which model predominates in any effort is fundamental to success, and global entomologists need to address, perhaps in a side-by-side comparative fashion, just how transportable information developed under one model is to farmers living under another. This could be one of the reasons that "technology cannot be simply exported." International donor organizations clearly need to be attentive to matching the institutional model being promoted with appropriate cultural, social and economic norms.

An Example

How might the use of an exotic biological control agent in a particular crop be implemented under each of the five models? For argument, the crop is soybean and, among its insect pests, is one that pesticides have failed to control. It is the key pest and it limits yield annually. The idea is to try a biological control approach.

Under the Land-Grant Model

Entomologists with biological control expertise, either individually or in small groups, would survey the literature for what is known about biological control of the target pest. Two avenues would be explored initially: the potential use of indigenous natural enemies and the importation of exotic ones. As the indigenous complex was not maintaining the pest's population density below acceptable levels, the choice might be made to search for exotic natural enemies. The USDA/APHIS protocol would be utilized for permits, and travel likely would be to China, the indigenous home of the soybean plant. If the pest has been subjected to biocontrol previously through the efforts of others and the results were published, travel to China might not be necessary.

Collections of potential natural enemies would likely result in the importation of each and every one found to inflict mortality on the pest in China. In quarantine, each potential natural enemy would be checked for hyperparasites, and then reared to sufficient densities to test any deleterious effects a release might have. Later, progeny of the imports would be released and evaluated for effectiveness. Results would be published in the refereed journal literature. At this point, extension agents and farmers would best get access to the information if they had been working in teams of individuals from the various agencies involved. Otherwise, those responsible for implementation would need to be keenly aware of the refereed journal literature.

Practical use of the new imported natural enemy(ies) might demand a mass rearing facility. Thus, further development could occur if, and only if, someone procured the resources for that facility and dedicated it to the rearing and release of natural enemies in soybean. If inoculative releases worked, the problem would be less costly. A key point here is the fragile relationship between research and extension. Researchers perceive that they get "rewarded" for publishing the results, not implementing them. Extension specialists have to be alert to know the new technology has been developed, especially if they have not been included as part of the overall team. Viewed as too simplistic a solution by some, one way around this dilemma is to have scientists who have formal, evaluated appointments in both research and extension.

Under the T&V Model

Once someone else did the research, experts who understood biological control could bring the imported biocontrol agents to a regional training session where extension specialists were being trained. Those extension agents could be shown how to identify the natural enemies, what they did to the pests and how to tell if the biological control worked. They also could be taught how to establish a cottage rearing operation. This process would continue down the training hierarchy, provided there were enough natural enemies to go around and provided the extension specialists had enough formal education to grasp some basic entomology and the concept of biological control. A lot of useful information likely would get lost between training tiers, leaving the ultimate farmer user wondering what all the fuss was about.

Under the Farming Systems Model

The entire issue would likely never even come up unless there was an entomologist or other biological scientist on the rapid rural appraisal team who was aware of the biological control agents that might be tested on local farms. Given the presence of the expertise, biocontrol agents could be imported, released on the farm and evaluated, with the farmers observing. If the biological control was effective, farmers would of course want to adopt it and the entire farming systems effort would have to become more akin to a T&V effort to train the farmers about the conservation of natural enemies and perhaps a cottage rearing and release operation.

Under the Training-Driven Research Model

Like farming systems, this model would demand that trainers be up to date on the latest research literature and recent progress to even know there was a new biological control agent that might be used locally. If so, use of the agent in field training exercises would be quick and would not have to pass through as many tiers of training as with the T&V model. The same problem outlined above exists in this model, too. It does little good to educate farmers about a new technique and entice them to adopt it if nobody teaches them how to implement it in a self-sufficient fashion.

Under the Farmer Participatory Research Model

If the CGIAR or other staff working with local farmers were able to identify the indigenous knowledge including experiences with natural enemies, there likely would be receptivity to the importation and use of an exotic biocontrol agent. In fact, such indigenous knowledge might even identify a better candidate for use than the one potentially coming from China. If there was no evidence that indigenous knowledge systems reflected previous exposure to natural enemies, training in the concepts and uses of natural enemies would, in essence, have to occur. Techniques to sustain the biocontrol effort, if accepted in local culture, would become part of the training.

Some General Conclusions

Institutional models for the research–extension–training activities would appear to best serve and reflect the societies in which they originate. The Land-Grant model likely could never develop in a strong hierarchical society. Much of the success of T&V in Asia and Israel comes from the fact that the organization of T&V "fits" those societies. The farming systems approach or Land-Grant approach do not work well in places where people are simply afraid of, or are unused to, expressing their opinions (e.g., Haiti and Cameroon).

There does appear to be a single model potentially usable in the wide array of situations that exist in today's world: farmer participatory research. All farmers and farming communities, save large industry systems, have an indigenous culture. This is especially true for resource poor farmers anywhere in the world. They have survived to date with, to one extent or another, a blend of traditional approaches and modern science. FPR and, to almost as great an extent, TDR offer what appear to be extremely high probabilities for solutions to agricultural problems that are acceptable to farmers almost by definition, that include farmers in the process and that avoid the inherent loss of information quality that occurs in the transfer of information.

There is debate over the extent to which the Land-Grant system involves farmers as active participants. No doubt, the better extension systems do just that, however, the extent to which farmer involvement permeates the breadth of Land-Grant efforts has not, to our knowledge, been gauged. FPR has been harder to implement in relatively wealthy nations like the USA where farmers see their tax revenues as providing agricultural services and resources they can tap "free of charge" without having to participate themselves.

Very few people outside the USA really understand the role of the extension specialists in the Land-Grant Model. To make this model work as designed, this is a key position, yet, some Land-Grant universities only recently have begun to employ individuals with formal, evaluated appointments in BOTH extension and research. Others utilize the inter-agency committee approach, and still others do not address the problem in any overt fashion. Joint appointments are still the exception, not the rule. The whole idea of state specialists grew up informally in the Land-Grant model as a need, but has over time become detached from formal research. Europeans do not employ extension advisory groups at all.

Three of the aforementioned systems have a rather disappointing track record on environmental issues. The reason is that all three fail to really focus on the farmer and long-term sustainability. It is hard to think of the off-site impacts of items like synthetic, organic pesticides if the farm is not viewed as part of a larger ecological and cultural system. Farming Systems appears to have the worst track record of the group on environmental and pest issues, with T&V a close second. The Land-Grant model is a classic example of how the system can derail on environmental issues (e.g., total commitment to pesticides for almost 25 years). FPR and TDR try overtly to avoid this problem by beginning their paradigm with farmer knowledge. Many modern Land-Grant extension personnel argue that current extension programs involve farmers in active decision-making more now than at any time in history.

Relationships among research, extension and training, independent of institutional models, demand choices be made on various levels. Some cultural, social, and economic systems clearly are more amenable to one choice versus another:

- Public versus private
- Government versus non-government
- Top-down (bureaucratic) versus bottom-up participatory)
- Profit versus nonprofit
- Free versus cost-recovery
- General versus targeted sector
- Multipurpose versus single purpose
- Technology-driven versus need-oriented

The role of publicly funded research and extension is changing. In the U.S., large-scale farmers depend less and less upon information generated and delivered through Land-Grant models. Part of the reason is that more and more of total agricultural productivity comes from corporate, rather than individual farmer, sources. Corporations have their own staff. The agricultural chemical companies provide all sorts of information and technical advice, but are single-minded in approach and profit motivated. Even in developing nations, where farming systems, T&V, FPR and TDR have predominated, they have been sponsored mostly by international donors and have regressed once funding ceased. So, just what is the role for public sponsored research-extension-training? There is a role if such programs will re-define their clientele base from richer corporate-industrial programs to poorer, smaller farming enterprises and beginning producers. With this new clientele definition must come a commitment to long-term sustainability of both the farmer and the farm.

References

Barfield CS, Swisher ME (1994) Integrated pest management: ready for export? Historical context and internationalization of IPM. Food Rev Int 10:215–267

Benor D, Baxter M (1984) Training and visit extension. World Bank, Washington, DC, 199 pp

Shaner WW, Phillips PF, Schmehi WR (1982) Farming systems research and development: guidelines for developing countries. Westview, Boulder, 405 pp

Teaching Entomology: A Review of Techniques

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Both positive and negative interactions with insects have long been a part of the human experience. However, people have not always had an opportunity to study insects in any formal, systematic fashion. Insects as biological organisms and various institutions where they can be studied are both part of the discussion on teaching entomology.

With the Neolithic Revolution (ca. 8,000 BCE), humans began the process of sedentary agriculture and civil development. Social scientists have provided us with at least anecdotal information on some of the roles played by insects in the human quest for survival and expansion. Early in human existence, insects vectored diseases, competed for food, consumed structures and were general irritants. They also were subjects of curiosity and sources of food and food products like honey.

Insects are the single largest and most diverse group of living organisms on Earth, and humans begin noticing and interacting with them almost from birth. Insects are among the first living organisms that children notice, and today's elementary education includes a host of activities that center on insects – butterfly gardens, games, music and use of the Internet being but a few examples. Students can choose to study entomology formally as part of their college education. A bit of historical context on the university as an institution where entomology is taught is relevant.

Entomology and Higher Education

Virtually none of the biological sciences existed as logical, written disciplines until Aristotle, and not until the ancient Greeks did the study of insects become characterized by the delight in observational opportunity insects provided. The 11th Book of the Roman Pliny's Historia Naturalis (AD 77) was the most comprehensive treatise on insects to date; however, it contained almost no original observations. Pliny's time and writings marked the beginning of a body of knowledge that would allow university degree programs to arise in the ninteenth century.

Higher education in Europe, from antiquity until the end of the middle ages, was maintained in the monastic and cathedral schools, enriched by a huge influx of knowledge from the Islamic world. These institutions eventually developed into universities as products of cross-cultural influence. Modern universities thus treasure a multi-cultural faculty and student body and a plethora of teaching styles. Those early European institutions were places where ideas spread, and where local and national authority was engaged. Entomology was not an area of formal study in these early institutions. Insects were engaged as plentiful examples of the biological world and, fairly often, as "pests." Indeed, the first real concerns about insects as a group were more in the context of "sources of products" (e.g., honey) and "competitors" (e.g., agricultural pests) than just for the need to understand their biology and history. The Catholic Church would often put "bad" insects on trial and hire them defense attorneys, ultimately "banishing" them from select provinces. These practices occurred fairly frequently from the middle ages right up to the start of the nineteenth century. Both the Bible and the Torah refer frequently to insects, paying special attention to the parables that can be extracted from insect life and to whether or not select insects are kosher. Entomology was important because most everyone had personal experiences with insects, not because it was a recognized area of study.

The study of entomology was nested within the general biological sciences in Europe and America throughout the seventeenth and most of the eighteenth centuries. Things began to change toward the start of the American Civil War. In 1862, President Abraham Lincoln established the United States Department of Agriculture and set in motion what would ultimately be three key Federal Acts to institutionalize the research and teaching (Morrill Land Grant Act and Hatch Act) and extension (Smith-Lever Act) functions by which all Land-Grant Universities are recognized today. While entomology is taught at many higher education institutions, the vast majority of American entomology majors are housed within colleges of agriculture and life sciences at Land-Grant institutions. Part of the reason for this situation is that, to many in the general public, insects are viewed as pests and colleges of agriculture were developed, at least in part, to help solve the public's pest problems.

After WWII, departments of entomology grew at almost every Land-Grant institution. Today, many of these institutions offer undergraduate degrees in entomology, and most offer graduate degrees. An undergraduate major in entomology, depending on the institution, will take 18–30 h of entomology courses offered in sequence. Graduate entomology degrees take 30–90 additional hours, the majority of which are insect-related. Graduate degrees usually include a research experience.

Teaching Entomology at the University Level

The present treatise will focus very little on the content of entomology courses; rather, the focus will be aimed at the style and methods through which any given content may be delivered. Clearly, different styles are applicable to different audiences, and the professor of any single course must understand the background and motivation of his/her audience before the most appropriate style can be selected. Interestingly, this is not how it usually works. Most often, any professor has his/her long-adopted style, and it is left to the clientele (students) to make the adjustments. There are possible consequences of this long-adopted practice, as illustrated in Table 6.

These various professor roles translate in myriad ways to an individual style used in the professor-student classroom experience. The entire point is that there is not a single best way to teach. The capabilities of both professor and students are basic ingredients in the choice of teaching style. An assessment of the students' optimum learning style early in the term is ideal if the professor has both the desire and the capability to shift teaching styles to align with learning styles. Here are a few possibilities (Table 7).

The Socratic, Discussion Approach

This approach to teaching entomology is used most often in small classes and can be applicable to either entomology students or general students simply curious about insects. It is commonly used in undergraduate honors classes at large universities, and small colleges and universities often use this approach throughout their curriculum. Students who take these classes typically are interested, motivated, and engaging. They are willing to read and discuss a plethora of historical, social and current issues related to insects and then perhaps, via a series of essays, analyze and critique what they have read. In this context, entomology becomes merely the biological medium in which to have students develop their interpersonal, analytical, critical thinking, oral presentation, and English grammar skills. Such students may become enticed to explore entomology as a major and an ultimate career, but most often these students, if they are interested in the biological sciences at all, are focused on medicine or veterinary medicine.

Success in this approach demands specific criteria on the part of both students and professor. The professor must be knowledgeable of a wide array of entomological issues and literature. Even more important, he/she must be charismatic, engaging and able to entice bright students to develop curiosity about entomology. The professor must be able to write and speak well, as these students will discern quickly between what is said and what is done in critique of written and oral presentation performances. The students must be engaging and willing to participate in class discussions. The Socratic Approach is, in many ways, the antithesis of more traditional presentation of copious facts about insect morphology, physiology, behavior and control. The idea is to entice students to explore, on their own, issues presented incompletely in discussion periods, thus developing skills that will serve them well during their university tenure. This approach will simply not work if either the students or the professor are not engaging or if the class resorts to a host of information-laden

Teaching Entomology: A Review of Techniques, Table 6 **Five models for the presence of an instructor in the classroom (summarized from Grasha 1966)**

	Expert	Formal authority	Personal model	Facilitator	Delegator
Professor role	Source of knowledge; status as expert; gets students prepared	Status symbol; reinforces correct, acceptable and standard methods; establishes learning goals	Role model; teaches students to emulate him as model	Emphasizes personal student–professor interactions; guides learning; creates independent students; supports and encourages	Focuses on student independence; serves as a resource
Advantages	Copious information; development of skills	Clear expectations; identification of acceptable approaches	Emphasis on direct observation and following the role model	Personal flexibility; focus on students' needs and goals; open-mindedness	Students become independent learners
Disadvantages	Volume of information; students may be intimidated; lack of focus on underlying processes that led to information	Rigidity in approach to students	Feeling of inadequacy if students feel they cannot live up to model	Time-consuming; often lacks positive reinforcement	Student anxiety; student may be misperceived as ready for independent work

Teaching Entomology: A Review of Techniques, Table 7 Comparison of five entomology teaching styles

	Socratic	Lecture/lab	Land lab	FFS	Internship
Experientially based	No	No	Yes	Yes	Yes
Focus on insect facts	No	Yes	Yes (limited)	Yes (limited)	Yes (limited)
Focus on student analytical skills	Yes	No	Yes	Yes	Yes
Demands large resources	No	No	Yes	Yes	No
Teacher focused	No	Yes	No	No	No
Student focused	Yes	No	Yes	Yes	Yes
Ideally requires supplemental funding	No	No	Yes	Yes	Yes

slides, films, blackboard text or, more frequently now, Power Point or Internet presentations.

Topics typical of this style of teaching may include many that do not appear, on the surface, to have anything to do with entomology. However, discovering their links to entomology is part of the desired outcome. For example:

1. Pliny's Historia naturalis
2. The Idea of "Food Insurance"
3. Social attitudes on pesticides versus pharmaceuticals
4. What was The Green Revolution?
5. In your supermarket, what foods are indigenous to the contiguous 48 states?
6. Medieval higher education?
7. Colonial American living?
8. What is social Darwinism?
9. Who is Norman Borlaug and what did he do?
10. What is the role of empiricism in science?

For example, in a classroom of 20 or so students, the professor initiates a discussion about the diet of Colonial Americans. Initially, the professor seeks to understand what the students already know about this subject. He discovers this by asking them and expecting them to engage in dialogue with him and with each other. The conversation expands to include the crops grown and the problems the colonists had with food production. Analogies are drawn periodically to modern agriculture and its problems. As some of the problems were insect related, the dialogue eventually permits the students to discover the linkages between Colonial American diet and the study of insects, as well as the various means of controlling those insects under social and technological conditions existing in colonial times. The result is a group of students who are better able to place insects and entomology into appropriate historical context and then draw inferences to the importance of entomology today.

This teaching style assuredly contributes to the student's knowledge of biological science and thus meets both professorial and student objectives in this context. There is a decent chance this approach will entice such students to become interested in entomology as a major and a career – something the vast majority of them have never before considered. Many will not even know it is possible to major in entomology.

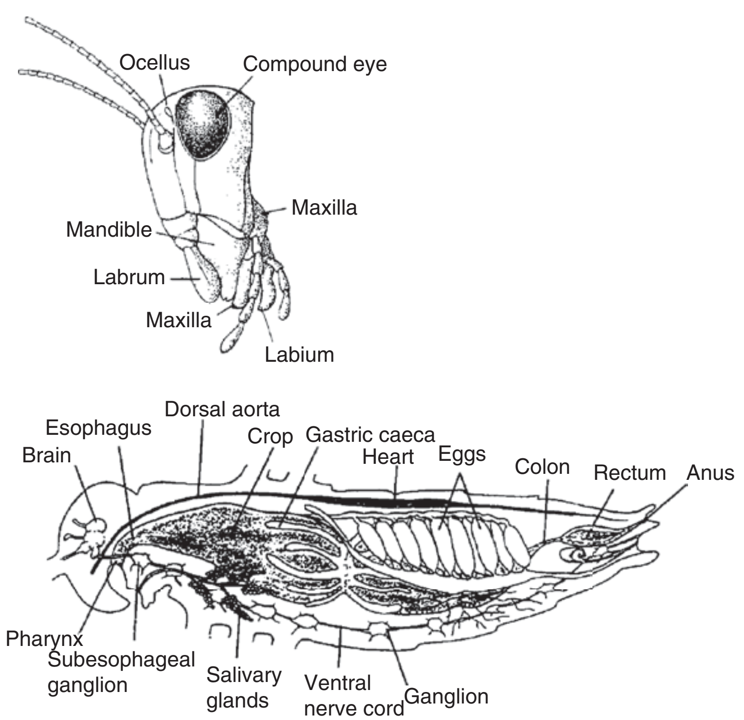
The Lecture/Lab Approach

By far, the most common way entomology is taught in modern universities is as a 3- or 4-credit hour course. This involves a series of lectures (2–3 per week) and 1–2 laboratory sessions per week. Lectures are used to present facts about entomology, and the lab is experientially based and involves dissection and study of the various physical and physiological features of insects. Interestingly, what actually occurs during the lecture period can follow any of the teaching styles presented in this paper; however, by far the most common is using the professor as the expert whose role it is to pass entomological facts and knowledge on to the students. The labs, if scheduled as typically desired, mirror the lecture periods and provide visual, hands-on experience for the topics discussed that week during lecture.

Lecture approaches vary from professor to professor, but there is concern under this model to ensure sufficient information is imparted to justify the student moving on to the next course in the sequence. General undergraduates who simply want biological science credits do take these type courses just because they want to learn about organisms they have experienced daily. It is the entomology majors, however, who professors feel the need to get ready for continued study of entomology. Lectures are replete with facts, drawings, information; labs follow suit. Figure 15 illustrate typical information presented under this style.

The emphasis is often on learning facts about insects. Professors pursue these facts in various ways. Some choose a systematic approach that focuses on the principal orders and a comparison of their morphologies, physiologies, behaviors and control. Others use a type of comparative biology approach that may compare insect adaptations with those of other animals (Fig. 16). While various entomological issues may be discussed, students spend time hearing the expert impart expertise, then committing that expertise to memory. Labs will have students dissecting, searching for, and identifying these morphological structures, and a test may include a lab practical where students must identify parts labeled. This is precisely the approach used in Colleges of Medicine.

Entomology lecture/lab courses do not have to unfold in any pre-determined fashion, and many professors use creativity in what they impart as entomological knowledge. The point here,



Teaching Entomology: A Review of Techniques, Figure 15 Elements of insect morphology and anatomy.

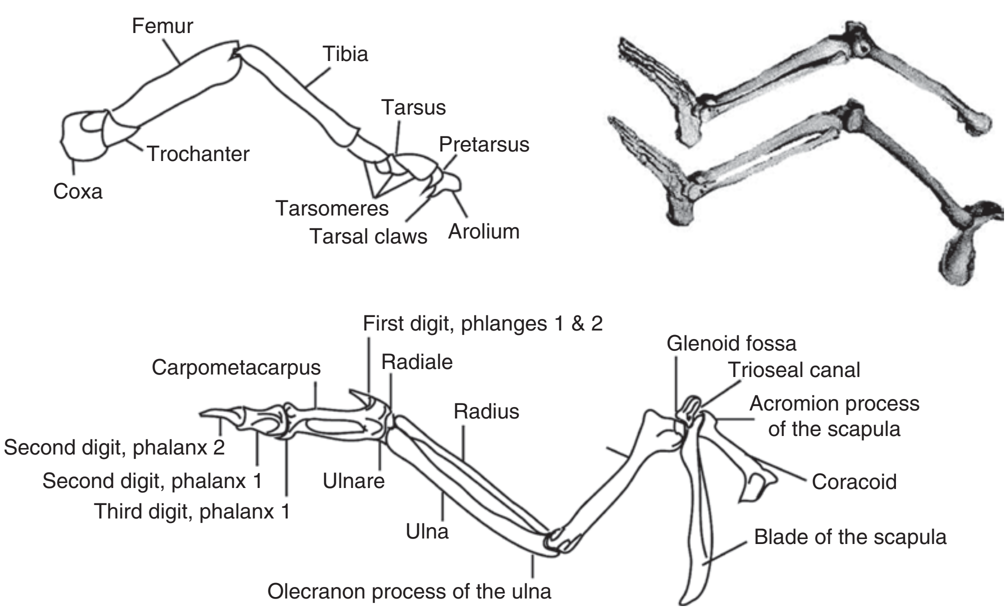
however, is that introductory entomology courses are typically taught for entomology majors or at least biological science majors, not for non-science students, despite the fact that diverse students often enroll. Under this approach, more emphasis is placed on facts about insects than on issues associated with insects. This is not a criticism, but rather an observation.

Introductory entomology textbooks offer a range of approaches to teaching the subject. Most will begin with chapters that discuss the general importance of insects to science and to humans. From there, the authors' approaches vary greatly. Likely, the most common approach is to begin immediately with external and internal anatomy and physiology. Sensory systems, reproduction, development, life history, and systematics follow. Then, insects as part of special habitats (e.g., aquatic and terrestrial systems) are presented, followed by subjects like insect societies, insects and plants, predation, parasitism, medically important insects, insect pest management and collection/preservation methods. Several texts will place collection and preservation methods, plus insect systematics, immediately following introductory chapters. In any case, most existing entomology texts will cover the above subjects, independent of which order of presentation is chosen.

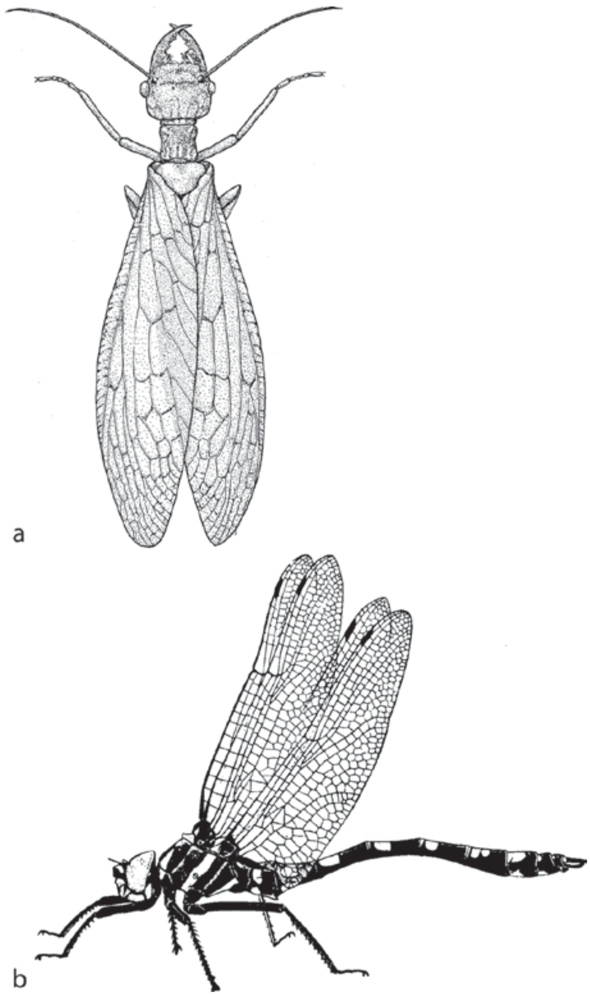
The teaching approach used is tied more to the bent and capability of the individual professor than to the subject matter. One teaching strategy is more of a comparative biology approach that might compare, for example, the insect leg and locomotion to analogous structures and functions in mammals, birds, reptiles, etc. This approach is effective in placing insects and their adaptations in perspective among all animals and is depicted in Fig. 16.

Another strategic approach is to compare insects among the various orders and explore metamorphosis, wing type, locomotion, habitat, life history, etc., as a means to compare-and-contrast the different orders of insects. This approach is illustrated in Fig. 17.

There is no shortage of information (journals, books, Internet sources) from which to supplement the basic text to expand student knowledge



Teaching Entomology: A Review of Techniques, Figure 16 Comparative biology approach to teaching insect leg morphology and its analogous structure and function in other animals. Human leg unlabeled; an exercise might be for students to locate analogous structures on human anatomy.



Teaching Entomology: A Review of Techniques, Figure 17 Neopterous (a) versus Paleopterous (b) wing types characteristic of different orders of insects.

of insects both as biological organisms and as social entities interacting with humans. Indeed, social scientists (especially anthropologists) often use insects to illustrate daily life, problems and indigenous approaches indicative of specific cultures. Some instructors of basic entomology will include sections on indigenous cultures and the role insects played therein.

Increasingly, entomology departments are offering courses to non-science majors. This is both as a way to educate undergraduates to the possibility of entomology as a major and as a mechanism to capitalize on the general student's previous experience with insects and their required enrollment in a specific number of science courses. Perusal of university catalogs usually will reveal courses such as: The Insects, Bugs and People, Pesticides and Pills, Ecology and Human Intervention, Insects and Society, The Insect World and You. These type courses typically are taught in one of two diverse formats. First, they frequently appear as honors courses taught to small-sized classes consisting of very intelligent students. In this context, the aforementioned Socratic style is most prevalent. Such students are often searching for creative majors, as their academic credentials permit them to select most any major they desire. The second prevalent delivery format is a lecture, replete with detailed syllabus and copious illustrations, to a large class. This delivery style is the aforementioned lecture/lab, but without the lab portion in most cases. Most every academic unit, including entomology, in a large university now offers such courses for non-majors. Strategically, these courses expose searching students to possibilities of a major they had not theretofore considered. Further, these courses allow students more flexibility in fulfilling general education requirements.

Internships

Most professional disciplines in the biological sciences require extensive internship experiences prior to certification. One cannot imagine a licensed Medical Doctor or Veterinarian without such experiences before they are sanctioned to ply their trade. The basic biological sciences in general, and entomology as one example therein, do not typically make such requirements. However, those parts of entomology related to agricultural plant protection often do require internships as part of graduation requirements. While wonderful in their intent and educational possibilities, internships are not without their potential problems.

An internship typically occurs toward the end of an undergraduate degree program. The idea is to match a student's need for hands on experience with a public or private sector business. The student would typically leave the university and locate at the business site for 1–2 semesters. Under the supervision of the business contact, the student would work daily in several of the tasks in which the business is involved. This might include plot preparation, fumigation, sampling, pest control, assessment of pest damage, interaction with the public, identification of insect pests, bookkeeping, and seminars. The entire experience would be aimed at permitting the student to translate academic knowledge obtained to marketplace demands. The university professor in charge of internships would make periodic visits to assess the student's progress and to witness first-hand the range of activities in which the student was involved. The student would register for a university course and pay associated tuition, and he/she may or may not receive salary compensation for the work.

Matching undergraduates with appropriate public or private internship opportunities often means asking them to relocate or commute for 1–2 semesters during their undergraduate studies. Many students are reticent to encumber the additional travel and per diem costs. Parents express similar concerns. If an internship is a requisite for graduation, care must be taken to ensure the intern's experience does not resort to a more trivial exercise based on student economics rather than on learning needs. Care also must be taken to ensure the business contact understands the needs of the student intern and is not simply looking for a short-term source of cheap labor. Medical and Veterinary interns accept the requisite; however, they are older, graduate students, away from parental influence and knowledgeable that the economic pay-offs of certification are potentially great. Often, none of these issues are the same for undergraduates. The more successful undergraduate intern programs provide financial support, if justified, to offset additional costs to students.

Field-Based Courses

This section refers to courses taught totally in the field, not to courses where sporadic field trips are part of a lecture/lab style. If field-based courses are targeting agricultural entomology, they require facilities: land, equipment, etc. There is debate over the cost needs for such facilities. Some feel adequate field-based courses are limited only by the creative imagination of professors teaching them. Others feel adequate land, equipment and staff are crucial to the success of such courses. As universities often do not consider such teaching resources high-priorities, these courses often piggyback onto research efforts, using plots developed for some professor's research. This can work, but often encounters problems as the timing associated with teaching conflicts with the timing of needed research activities.

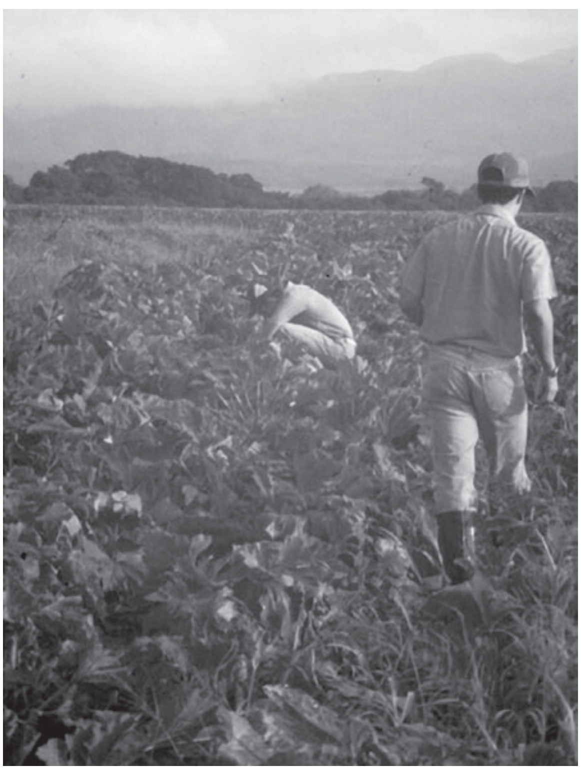
Many universities have natural areas that can, within certain guidelines, be used to teach various aspects of entomology. In any case, the fundamental idea in a field-based course is to provide students with experiential learning. Under ideal conditions, such a course would be offered on facilities set aside exclusively for teaching and would be under the control of teachers so that the timing of activities could occur in an orderly fashion consistent with educational paradigms.

Also known as the Land-Laboratory Approach, this style is somewhat analogous to a teaching hospital where doctors and nurses get experiential learning under real situations – all supervised by professorial experts. Where else is it possible to give developing professionals the opportunity to gain practical experience in a supervised learning environment? Many educators feel such practical experience should be a mandatory part of science education.

Joliet Junior College in Joliet, Illinois, exemplifies the intent and structure of the Land-Laboratory concept. As stated in their advertisements, they exist to "serve as a teaching tool for instructors to use hands-on learning as a means to reinforce classroom instruction." The Land-Laboratory exists as

101 acres of land donated for the exclusive purpose of teaching. The Pennsylvania State University has a similar facility dedicated to land analysis. In most cases, Land-Laboratories exist because the land and perhaps the infrastructure needed to make it operational were donated. Rarely do universities encumber the costs of a Land-Laboratory from their operational budgets.

The Escuela Agrícola Panamericana (Pan American School of Agriculture, EAP) in Honduras, Central America, provides an example of both experiential learning and the Land-Laboratory style (Fig. 18). Students attend from throughout the Caribbean Basin and beyond and spend 0.5 day in class and 0.5 day in the field in a wide array of agricultural experiential learning activities including land preparation, planting, harvesting, processing, marketing, plant protection, outreach and with both plant and animal systems. Entomology plays a prominent role in the experiences of the "Zamoranos."



Teaching Entomology: A Review of Techniques, Figure 18 **Zamorano students in land-laboratory exercise, Pan American School of Agriculture, Honduras, Central America.**

Teaching at the International Rice Research Institute (Philippines) exemplifies the same approach and has been in place much longer than the EAP. The general trend is for international research institutes that also teach to place a higher premium on Land-Laboratory approaches than do U.S. universities. This is true likely because they have the land and labor to make this approach work and because they understand that hands-on experience for their student clientele is of maximum importance.

Extra-University Models

The international arena offers a variety of teaching approaches aimed directly at farmers and professionals who provide technical support to farmers. In this context, the stakes (possible food self-sufficiency) are much higher than the pursuit of an undergraduate college degree. These programs offer both challenge and opportunity to university-based degree programs in entomology.

The Farmer Field School Approach

The principal sponsor and promoter of this approach is the United Nations Food and Agriculture Organization, Rome, Italy. Principally, the Global Integrated Pest Management Group within the UN/FAO developed this model based on experiences in Rice Integrated Pest Management programs in Indonesia. This approach serves as a model that universities might want to emulate in those aspects of entomological education that demand experiential learning.

The FFS was established to provide training to farmers and their support network (researchers and extension specialists) on the problems and opportunities associated with specific crops (Fig. 19). The idea is to follow crop development

Teaching Entomology: A Review of Techniques, Figure 19 **Farmer field school training in corn-based agriculture, Honduras.**

from land preparation to marketing of the harvest, teaching at every step the techniques demanded, the pests encountered, the sampling needed, the pest management approaches needed, etc. Those same trained people obtain the multiplier effect by training others. The idea is to teach, in a hands-on fashion, the details for any specific crop. As the crops change, so do the issues and thus additional training may be needed. In 2002, FAO is assisting Korea in the establishment of a junior college level curriculum of study based exactly on the FFS concepts. Students would hold night sessions on the more general aspects of, say, entomology. Unlike the lecture/lab approach typical of American Universities, the FFS approach begins with the field and then moves to general classroom experience (Fig. 20).

The FFS approach served as the basis for development of The Farmer Centered Agricultural Resources Management (FARM) Program that, until funding declined, consisted of the member countries of China, India, Indonesia, Nepal, Philippines, Sri Lanka, Thailand and Viet Nam. The entire FARM program was supported by the UNDP and implemented by FAO. In 2002, there were 19 sites in eight nations covering some 10,000 Asian households (Figs. 21 and 22). FARM, and its parent idea, the FFS, was one of the most rapidly expanding teaching resources in the world.

Teaching Entomology: A Review of Techniques, Figure 20 **Farmer field school classroom training, Indonesia.**

It offered practical hands-on training that could be supplemented with more traditional academic education in a wide array of subjects, including entomology. Sadly, politics overtook needs and funding was cut to the point the program vanished in its original form.

The purpose of the FFS is not pursuit of academic degrees. Training is focused on the specificities of individual crops or cropping systems and is increasingly supplemented with "after hours" academic work on subjects like entomology. Students are adults, not undergraduates in pursuit of degree requirements. Results of this educational style are improved chances of food self-sufficiency, not a B.S. degree and employment. However, in the few places where the fundamental

Teaching Entomology: A Review of Techniques, Figure 21 Farmer field school plot facilities for rice-based agriculture, Indonesia.

Teaching Entomology: A Review of Techniques, Figure 22 In-field training on rice insects, Indonesia.

concepts of the FFS or its close relative, the Land-Laboratory, have been directly combined with academic programs, the results have been astonishing. These are the rare situations that make agricultural and entomological education the most analogous to professional school education in the USA.

Cross Style Comparisons

Three things limit what style is used to teach entomology (i) imagination, (ii) budget, and (iii) either professor or student capability. The most appropriate criterion for a comparison among styles is whether or not students achieved course objectives. The reality is that various styles have different intents and expected outcomes. The problem occurs when a style of teaching is used that has a low probability of generating the desired outcomes.

Use of the lecture/lab approach where the lecture is used to present copious facts about insects which are to be memorized and repeated on a multiple choice exam may not be the most appropriate for a group of students who have selected beginning entomology for its general education function and who are simply curious about insects. Not providing the future field practitioner of agricultural entomology a field-based experience will not achieve desired outcomes in the most efficient manner.

If the professor desires students to become independent thinkers, capable of analysis and presentation, playing the role of "expert" who imparts facts about insects that are to be learned and demonstrated on an exam is probably not the most ideal approach. Tailoring teaching style to a particular student audience is hard, not easy. It takes effort and does not occur automatically. Just like any other aspect of the human experience, some professors can do it and others cannot. This is not a criticism, but a fact. Ideal learning experiences tend to occur in entomology or any other subject when care is taken to match the style of teaching to the needs and learning styles of students in that class that term. Adoption of a single teaching style to be used throughout one's tenure is, quite literally, a "hit and miss" proposition where desirable and less desirable outcomes will occur among semesters.

The key to any professor adjusting to dynamic learning styles of students is an ability to gauge quickly their response to a variety of styles. Literally, what works well one term and gets students involved and responsive is not automatically what will work best next term, given a new group of students. Many, if not most, university professors of basic entomology courses offered to entomology or science majors, do not attempt to adjust to perceived student learning styles. Such adjustments are much more common in entomology courses offered to non-science majors.

► Teaching and Training Entomology: Institutional Models

References

Evans EP (1998) The criminal prosecution and capital punishment of animals. Richard Clay, Bungay, Suffolk, United Kingdom, 336 pp

Grasha A (1996) Teaching with style. Alliance, Pittsburgh, Pennsylvania

Smith RF, Mittler TE, Smith CN (eds) (1973) History of entomology. Annual Reviews, Palo Alto, California, 517 pp

Teak Moths (Lepidoptera: Hyblaeidae)

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Teak moths, family Hyblaeidae, are a small tropical family of 18 species, mostly Indo-Australian and in the genus *Hyblaea* (one pantropical species is also established in southern Florida). The family is in the superfamily Pyraloidea in the section Tineina, subsection Tineina, of the division Ditrysia (sometimes placed in its own superfamily, Hyblaeoidea). Adults medium size (25–49 mm wingspan), with head relatively smooth-scaled; haustellum naked; labial palpi porrect and prominent; maxillary palpi 3- to 4-segmented. Maculation mostly shades of brown, with colorful spotted hindwings. Bodies are usually robust. Adults are diurnal or perhaps crepuscular. Larvae are leaf rollers. Host plants are in Bignoniaceae and Verbenaceae. One economic species: the teak leafroller. Due to their robust form, these moths were often associated with Noctuidae in the past (Fig. 23).

Teak Moths (Lepidoptera: Hyblaeidae), Figure 23
Example of teak moths (Hyblaeidae), *Hyblaea puera* (Cramer) from Taiwan.

References

Common IFB (1990) Superfamily Hyblaeoidea. In: Common IFB, Moths of Australia. Melbourne University Press, Melbourne, pp 334–337

Dalla Torre KW von (1928) Die Hyblaeinen (Noktuiden). Entomol Jahrb 37:162–164

Koning HS de, Roepke W (1949) Remarks on the morphology of the teak moth, *Hyblaea puera* Cr. (Lep. Hyblaeidae). Treubia 20:25–30

Singh B (1956) Description and systematic position of larvae and pupa of the teak defoliator, *Hyblaea puera* Cramer (Insecta, Lepidoptera, Hyblaeidae) Indian Forest Records (n.s.). Entomology 9:1–16

Viette PEL (1962) Les Noctuidae Hyblaeinae de Madagascar (Lep.). Bull Mens Soc Linn Lyon 30:191–194

Technical Grade

A chemically pure preparation. This is often used to describe research-grade pesticides as opposed to commercial formulations.

► Insecticides

Tegmen (pl., Tegmina)

The thickened front wing of Orthoptera and related insects.

► Wings of Insects

Tegula

A small flap or lobe at the anterior edge of the forewing of some insects. It is also known as the patagium.

Telegeusidae

A family of beetles (order Coleoptera). They commonly are known as long-lipped beetles.

► Beetles

Telephone-Pole Beetles

Members of the family Micromalthidae (order Coleoptera).

► Beetles

Teloganellidae

A family of mayflies (order Ephemeroptera).

► Mayflies

Teloganodidae

A family of mayflies (order Ephemeroptera).

► Mayflies

Telomere

Telomeres are the physical ends of eukaryotic chromosomes. They protect the ends of chromosomes and confer stability. Telomeres consist of DNA repeats and the non-histone proteins that bind specifically to those sequences.

Telopodite

The portion of the limb beyond the base; the shaft.

Telmophages

Arthropods that feed at blood vessels, and specifically from pools of blood created by lacerating vessels (contrast with solenophages).

Telson

The terminal portion of the abdomen bearing the anus. In insects the telson is usually found only in the embryonic stage. It is not normally recognized as a body segment in insects, but it is in some other invertebrates.

Template

A macromolecular mold for synthesis of another macromolecule. Duplication of the template takes two steps; a single strand of DNA serves as the template for a complementary strand of DNA or mRNA.

Tenaculum

In Collembola, a small structure on the third abdominal segment that serves as a clasp for the furcula (Fig. 24).

► Abdomen of Hexapods

Tenebrionidae

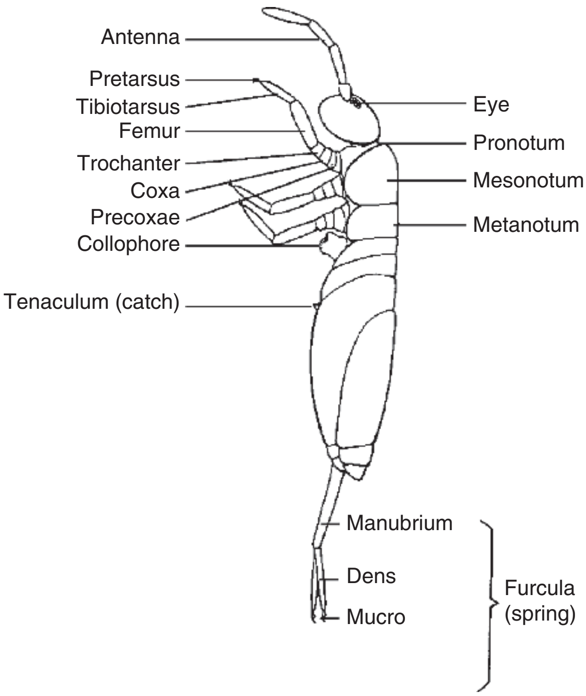
A family of beetles (order Coleoptera). They commonly are known as darkling beetles.

► Beetles

► Darkling Beetles

Teneral

The condition of an insect after molting but before the new cuticle has hardened.



Tenaculum, Figure 24 Lateral view of a springtail (Collembola).

Tent Caterpillars

Some members of the family Lasiocampidae (order Lepidoptera).

► Tent caterpillars, *Malacosoma* spp.
► Lappet Moths
► Butterflies and Moths

Tent Caterpillars, *Malacosoma* spp. (Lepidoptera: Lasiocampidae)

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Tent caterpillars occur in the family Lasiocampidae and are related to silk moths in the families Bombycidae and Saturniidae. Tent caterpillars are placed in the genus *Malacosoma* established by Hübner in 1820. The name *Malacosoma* derives from the Latin for *malakos* (soft) and *soma* (body). In the earlier literature, tent caterpillars were referred to the genus *Clisiocampa* which was erected by Curtis in 1828, unaware that Hübner had already named the group.

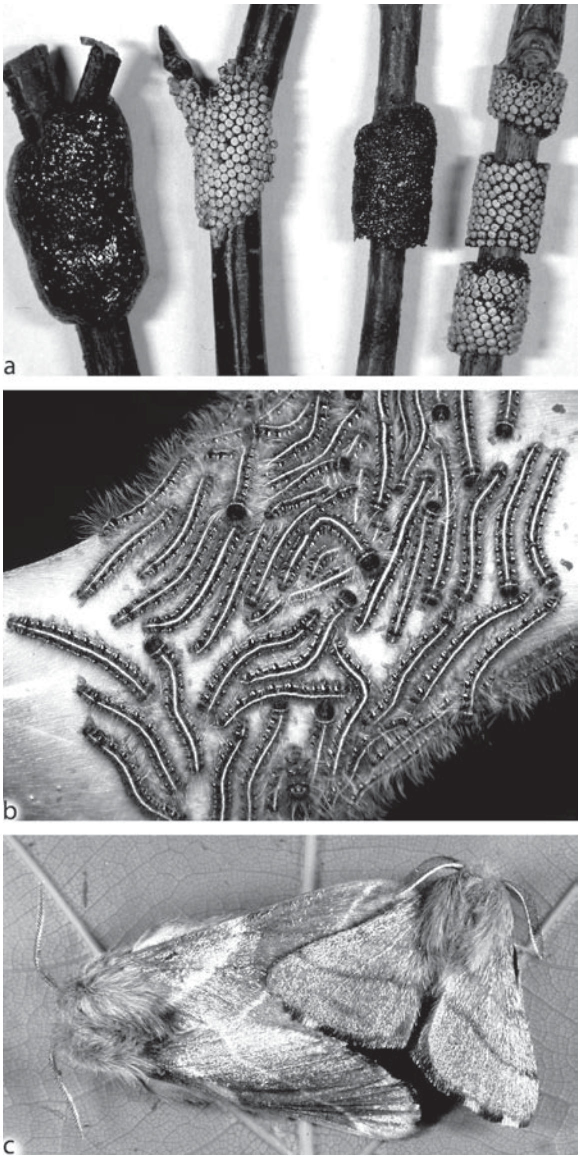
Species of *Malacosoma* occur throughout the Holarctic region. Although the taxonomy of the group is far from settled, currently there are 26 valid species. Six of these occur in North America and the rest in Eurasia. A number of these species are also further divided into subspecies. The best-known of the tent caterpillars are the North American species, particularly the eastern tent caterpillar, *M americanum* (Fig. 25), the western tent caterpillar, *M. californicum* and the forest tent caterpillar, *M. disstria* (Fig. 26). Of the Eurasian species, *M. neustrium* is the best known and has the broadest geographical range.

Life Cycle and Behavioral Ecology

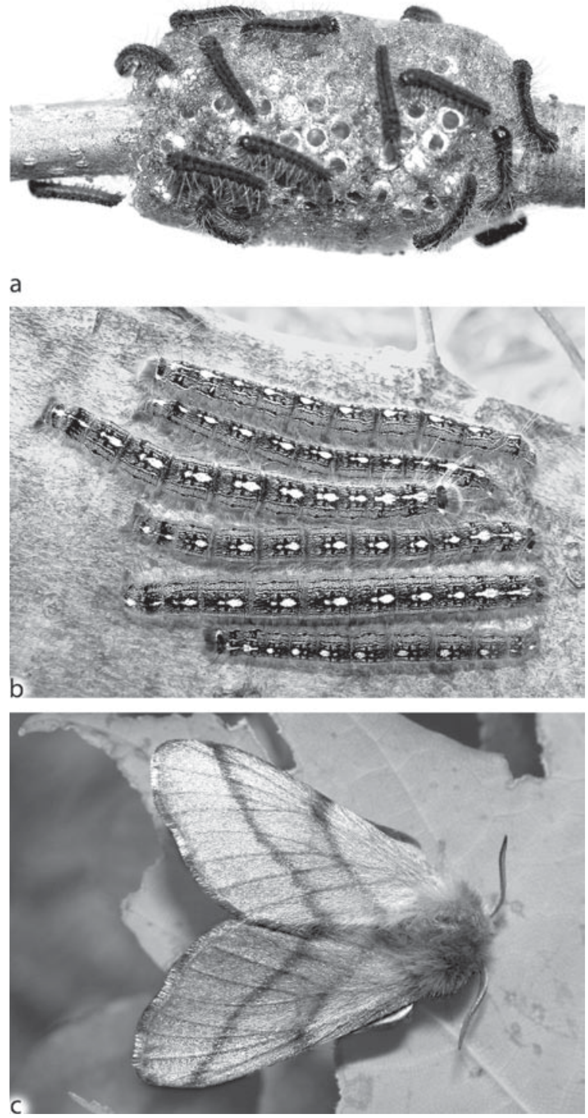
Little detailed information is available for many of the species of *Malacosoma*, but the evidence we have suggests that their life history features are similar to those of the eastern tent caterpillar, the most studied of the group. The seasonal history and behavioral ecology of this species is described here.

The eastern tent caterpillar obtains all the energy required for its adult life while still a larva and reproductively mature moths emerge from their cocoons in late spring. Females secrete sex pheromones to attract males. Mating typically takes place soon after eclosion and the female may oviposit the evening of the same day she emerges.

The moth produces a single egg mass, typically containing 150–250 eggs, though larger egg masses are not uncommon. The egg mass is attached to a branch of the host plant and is covered with a foamy substance termed spumaline. The material serves to protect the eggs from desiccation and may also prevent parasitoids from reaching the larvae inside the eggs. Embryogenesis proceeds rapidly and fully formed larvae can be found within the shells of their eggs several weeks following oviposition. The sequestered caterpillars undergo an obligatory



Tent Caterpillars, *Malacosoma* spp. (Lepidoptera: Lasiocampidae), Figure 25 Eastern tent caterpillar, *Malacosoma americanum*: (a) egg masses of the eastern tent caterpillar with and without spumaline (left) and of the forest tent caterpillar (right) (b) mature larvae, (c) adults. (Photos by Terrence Fitzgerald.)



Tent Caterpillars, *Malacosoma* spp. (Lepidoptera: Lasiocampidae), Figure 26 Forest tent caterpillar, *Malacosoma disstria*: (a) larvae hatching on egg mass, (b) mature larvae, (c) adult. (Photos by Terrence Fitzgerald.)

diapause which is broken only after exposure to cold temperatures over the winter. Eclosion of the caterpillars in the spring is closely synchronized with the flushing of leaves of the host tree but if eclosion occurs before leaves have flushed the young larvae may obtain food by mining buds. Development occurs rapidly and most species finish the active larval stage of their life cycle in 6–8 weeks. The last of the six larval instars spins a cocoon in a protected place and the moth emerges about 2 weeks later.

All tent caterpillars are social species that live in sibling groups. Although they are commonly viewed as pests because of their habit of defoliating forest and ornamental trees, they are among the most social of all caterpillars and exhibit many noteworthy behaviors. Their life histories are highlighted by four collective behaviors: shelter building, thermal regulation, cooperative foraging, and predator defense.

For those species that make large, permanent tents such as the eastern tent caterpillar, the tent site is selected by the first instar caterpillar, typically in a part of the tree that receives the early morning sun. In the eastern tent caterpillar, the parent moth may facilitate this process by selecting an oviposition site on the south side of a tree. The tent is expanded daily to accommodate the growing colony, allowing the caterpillars to rest, molt, and thermoregulate in synchrony. Silk is added to the structure during episodes of spinning which precede bouts of foraging. The colony expands their tent until they enter the last stadia of their lives as caterpillars; the last instar retains its silk to construct its cocoon.

The tent is multi-functional. It serves primarily as a secure mat, providing the caterpillars with purchase during their extended periods of rest. The tent also serves as a staging area from which colonies launch intermittent forays in search of food. It may also serve as a communication center where successful foragers alert their hungry tent mates to food discoveries as detailed below. The extent to which the tent protects the caterpillars from predators and parasitoids is unclear. When the caterpillars rest within the tent they may be secure from certain predators and parasitoids that cannot enter the structure. However, the caterpillars often rest on the outside where they are more vulnerable but not defenseless. Caterpillars assembled on the surface of the tent respond to predators with a defensive body-flicking display. The display may serve to alert tent mates to danger.

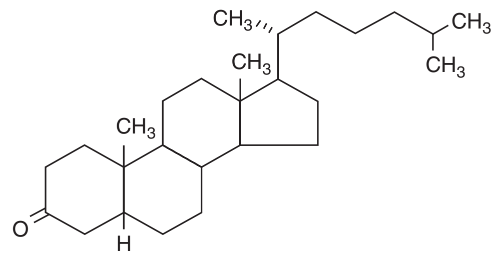
Tent caterpillars are active during the time of the year when the days are typical cool and the tent serves the important function of facilitating thermoregulation. Although eastern tent caterpillars are capable of locomotion at temperatures as low as 3–5°C, they cannot process food at temperatures much below 15°C. The caterpillars can achieve temperatures in excess of ambient only by basking in the sun, and on cool and cloudy days they grow little if at all. The caterpillars have dark bodies and are effective behavioral thermal regulators but the tent enables the caterpillars to elevate their body temperatures far above ambient. They aggregate on the surface of the tent or within the structure. When basking on the surface, the caterpillars arrange themselves in a tight cluster, minimizing heat loss due to wind currents. The tents act like greenhouses, trapping the heat of the morning sun. Because of its layered structure, the tent is thermally heterogeneous and the caterpillars can adjust their temperature by moving from layer to layer. One study showed that a cluster of models simulating an aggregation of caterpillars basking in the sun on the tent surface achieved temperatures as great as 44°C in excess of ambient temperature. Indeed, the tent may become so hot by midday that the caterpillars overheat and take evasive action to avoid the sun. They do this by moving to the shaded side of the tent and by hanging suspended in the air, attached to the tent only by the posterior ends of their bodies. This minimizes the amount of heat that is conducted to their bodies from the hot tent surface and maximizes the cooling effect of convective air currents.

Eastern tent caterpillars secrete a chemical trail marker as they move over the branches of the host tree. The marker is secreted from the ventral surface of the tip of the abdomen and caterpillars actively mark trails by lowering and dragging the tips of their abdomens against the substrate. Although eastern tent caterpillars also lay silk strands as they move over branches, silk does not elicit trail following; the elicitation of trail following is dependent on the trail pheromone.

The eastern tent caterpillar utilizes a bilevel trail system consisting of exploratory and recruitment components. Hungry foragers in search of food mark *exploratory* trails with a pheromone as they move over the bark surface. The caterpillars show great reluctance to move over surfaces not already marked with the exploratory trail pheromone, advancing slowly in close proximity to others. Exploratory trails enable foraging columns to stay together without necessitating direct physical contact among the caterpillars. Larvae that locate food and feed to repletion lay down *recruitment* trails as they follow their exploratory trails back to the tent. Recruitment trails are more effective in eliciting trail following than exploratory trails; they function to lead hungry tent mates to food finds in a manner similar to the recruitment trails of ants and termites. It is presently not known whether the difference between exploratory and recruitment trails is qualitative or quantitative, but recent studies of the related genus *Eriogaster* suggest that the difference may be quantitative.

The foraging system of the forest tent caterpillar differs from that of the eastern tent caterpillar in that the larvae range widely in search of food and do not establish a nest or other permanent resting site. The caterpillars travel between feeding sites en masse, laying down an exploratory trail marker as they proceed. After feeding, the caterpillars move to a temporary resting site or bivouac. Trails marked by the caterpillars immediately after feeding are more stimulating than exploratory trails and serve to recruit fed colony mates to the new bivouac where they rest en masse.

Studies undertaken to identify the trail pheromone of the eastern tent caterpillar showed that the chemical 5β-cholestane-3,24-dione, isolated from the tips of the abdomens of eastern tent caterpillars, elicited trail following when applied to paper cards at rates as low as 10^{-10} g/mm trail. Bioassays, however, showed that while the chemical was competitive with the exploratory trails of the caterpillar, it was not competitive with authentic recruitment trails. A number of compounds with similar structure were subsequently obtained and bioassayed for activity. Of these, the steroid 5β-cholestane-3-one (Fig. 27) proved more effective in eliciting trail following than



Tent Caterpillars, *Malacosoma* spp. (Lepidoptera: Lasiocampidae), Figure 27 5β-cholestane-3-one, a chemical that elicits trail following in caterpillars.

5β-cholestane-3,24-dione and was shown to be fully competitive with the authentic recruitment trails of the caterpillar.

Tent caterpillar larvae are highly sensitive to the amount of pheromone present in trails and carefully compare trails at branch junctures by sweeping their maxillary chemoreceptors from trail to trail. Caterpillars choose stronger over weaker trails and newer over older trails when foraging allowing them to move efficiently between feeding and resting sites.

Economic Importance and Caterpillar Outbreaks

Gregarious caterpillars are among the most economically important of forest and shade tree insects. Studies indicate that about 70% of the lepidopterous pests of trees capable of achieving outbreak proportions deposit eggs in batches and over half of these form social larval aggregates. The ability of social species of caterpillars to reach outbreak numbers has been attributed to enhanced predator defense, collective thermoregulation, and foraging efficiency. Although all species of North American tent caterpillars may be capable of achieving outbreak numbers, the most significant are the forest tent caterpillar, the eastern tent caterpillar, the western tent caterpillar (*M. californicum*), and the southwestern tent caterpillar (*M. incurvum*). *Malacosoma disstria* is the best-known of these species, causing considerable damage during its periodic outbreaks. Surveys conducted by the U.S. Department of Agriculture showed that between 1953 and 1983, the forest tent caterpillar achieved outbreak status on 70 occasions. The Eurasian species *M. neustrium* is an economically important defoliator of oak and other forest and shade trees.

It is commonly reported that outbreaks of tent caterpillars occur at ten-year intervals but the historical record shows that the actual interval between successive outbreaks varies widely. The most complete records of forest tent caterpillar outbreaks are from Ontario, Canada. From 1867 to 1987, province-wide outbreaks occurred at intervals of 9–16 years. Caterpillars remained in outbreak numbers for 1–8 years (average = 3 years). In Manitoba and Saskatchewan, outbreaks occurred at 6–16 year intervals from 1923 to 1957 but some areas in these provinces experienced only one outbreak in the 34-year period.

Density dependent mortality factors that bring population explosions of the tent caterpillar to a close are fungal, viral, and to a lesser extent bacterial diseases, starvation, and predators and parasitoids. The primary density independent factors are elements of the weather. Cool and cloudy springs can be lethal for tent caterpillars. As noted above, studies of the eastern tent caterpillar show that when a tent caterpillar's body temperature drops below about 15°C, the insect cannot digest food. Although air temperature in the spring is often less than this threshold temperature, caterpillars bask in the sun to raise their core temperatures. However, basking is not possible if there is dense cloud cover, and a prolonged episode of cool, cloudy weather can lead to the death of the caterpillars due to starvation. A combination of density dependent and density independent mortality factors may interact to bring a population explosion to a close. Thus, disease may sweep through a population of forest tent caterpillars, precipitated by the cool and wet weather that favors the pathogen *Furia*.

In addition to its importance as a defoliator, the eastern tent caterpillar has been implicated in the death of horses. During the spring of 2001 and 2002 horse breeders in central Kentucky experienced an unprecedented loss of foals, a phenomenon now known as Mare Reproductive Loss Syndrome or MRLS. In 2001 alone, more than 3,000 mares aborted, causing an estimated loss of over $330 million. At the time of the abortions there was an outbreak of tent caterpillars, and studies showed that pregnant mares fed the caterpillars aborted their foals. The exact cause of MRLS is not known but one possibility is that irritation of the mare's gut by setal fragments facilitates the invasion of bacteria which infect the placenta and induce abortion. Apparent instances of MRLS have also been reported from other areas experiencing outbreaks of tent caterpillars including New York, New Jersey, Florida, and Washington State.

References

Bernard B, Webb B, LeBlanc M (2003) Gastric administration of eastern tent caterpillars causes early fetal loss in pregnant mares. In: Proceedings of the First Workshop on Mare Reproductive Loss Syndrome. University of Kentucky Agricultural Experiment Station Publication SR-2003-1, p 79

Casey TM, Joos B, Fitzgerald TD, Yurlona M, Young P (1988) Group foraging, thermoregulation, and growth of eastern tent caterpillars in relation to microclimate. Physiol Zool 61:372–377

Crump D, Silverstein RM, Williams HJ, Fitzgerald TD (1987) Identification of the trail pheromone of the eastern tent caterpillar *Malacosoma americanum* (Lepidoptera: Lasiocampidae). J Chem Ecol 13:397–402

Dirikolu L, Hughes C, Harkins D, Boyles J, Bosken J, Lehner F, Troppmann A, McDowell K, Tobin T, Sebastian M, Harrison L, Crutchfield J, Baskin SI, Fitzgerald TD (2003) The toxicokinetics of cyanide and mandelonitrile in the horse and their relevance to the mare reproductive loss syndrome. Toxicol Mech Methods 13:199–211

Filotas MJ, Hajek AE, Humber RA (2003) Prevalence and biology of *Furia gastropachae* (Zygomycetes: Entomophthorales) in populations of the forest tent caterpillar (Lepidoptera: Lymantriidae). Can Entomol 135:359–378

Filotas MJ, Hajek AE (2004) Influence of temperature and moisture on infection of forest tent caterpillars (Lepidoptera: Lasiocampidae) by the entomopathogenic fungus *Furia gastropachae* (Zygomycetes: Entomophthorales). Environ Entomol 33:1127–1136

Fitzgerald TD, Costa JT (1986) Trail-based communication and foraging behavior of young colonies of the forest tent caterpillar *Malacosoma disstria* Hubn. (Lepidoptera: Lasiocampidae). Ann Entomol Soc America 79:999–1007
Fitzgerald TD (1995) The Tent Caterpillars. Cornell University Press, Ithaca, New York
Fitzgerald TD, Jeffers PM, Mantella D (2002) Depletion of host derived cyanide in the gut of the eastern tent caterpillar, *Malacosoma americanum*. J Chem Ecol 28:257–268
Joos B, Casey TM, Fitzgerald TD (1988) Roles of the tent in behavioral thermoregulation of eastern tent caterpillars. Ecology 69:2004–2011
Kane E, Kirby E (2001) Death in the bluegrass. Equus 287:60–68
Nothnagle PJ, Schultz JC (1987) What is a forest pest? In: Barbosa P, Schultz JC (eds) Insect outbreaks. Academic, New York, pp 59–80
Roessingh P, Peterson SC, Fitzgerald TD (1988) The sensory basis of trail following in some lepidopterous larvae: contact chemoreception. Physiol Entomol 13:219–224
Ruf C (2002) Social life-styles in caterpillars: behavioral mechanisms and ecological consequences. Ph.D. dissertation, University of Bayreuth, Bayreuth, Germany
Stehr FW, Cook EF (1968) A revision of the genus *Malacosoma* Hübner in North America (Lepidoptera: Lasiocampidae): systematics, biology, immatures, and parasites. Smithsonian Institution, U.S. National Museum Bulletin, p 276
Webb BA, Barney WE, Dahlman DL, DeBorde SN, Weer C, Williams NM, Donahue JM, McDowell KJ (2004) Eastern tent caterpillars (*Malacosoma americanum*) cause mare reproductive loss syndrome. J Insect Physiol 50:185–193

Tenthredinidae

A family of sawflies (order Hymenoptera, suborder Symphyta). They commonly are known as common sawflies.

► Wasps, Ants, Bees, and Sawflies

Tentorium

The internal invaginations of the exoskeleton occurring in the head tergite.

► Head of Hexapods

Tephritidae

A family of flies (order Diptera). They commonly are known as fruit flies (but not to be confused with small fruit flies, Drosophilidae)

► Flies

Teratembiidae

A family of web-spinners (order Embiidina).

► Web-Spinners

Teratomyzidae

A family of flies (order Diptera).

► Flies

Tergum

The dorsal section of a body segment. Also called tergite. They sometimes are named after their body segment (e.g., mesotergum is the tergum of the mesothoracic segment) (Fig. 28).

Termen

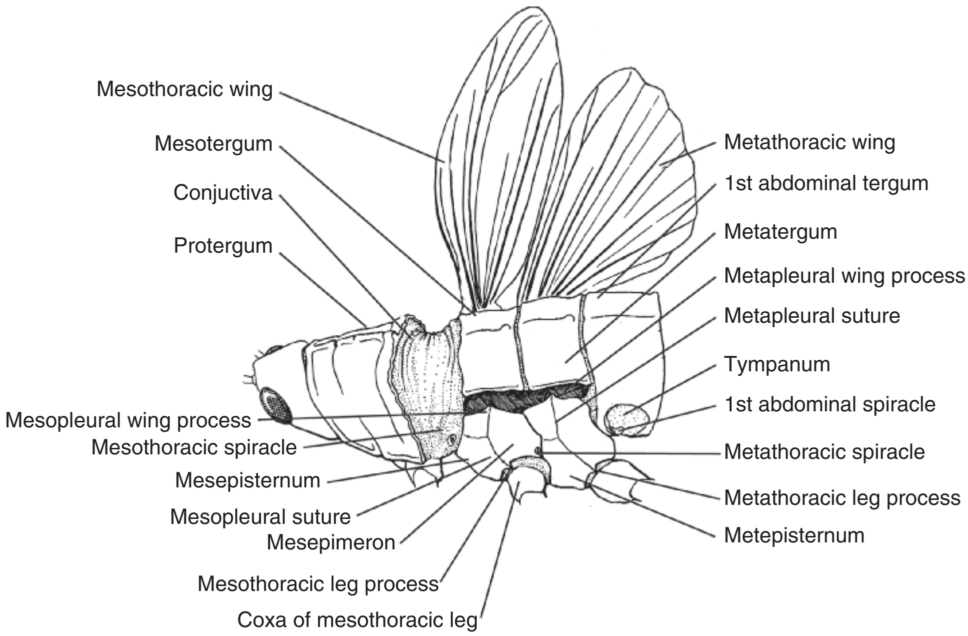
In Lepidoptera, the edge of the wing in the distal (lateral) area.

Terminal Arborization

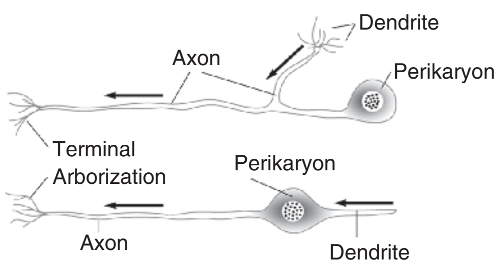
An extensive branching of the dendrites at the end of a nerve cell (Fig. 29).

Terminal Filament

Long, slender projections from the last abdominal segment.



Tergum, Figure 28 **Head and thorax of a grasshopper (Orthoptera).**



Terminal Arborization, Figure 29 **Diagrams of insect nerve cells showing direction of nervous impulse (adapted from Chapman 1998, The insects: structure and function).**

Termitaphididae

A family of bugs (order Hemiptera, suborder Pentamorpha).

► Bugs

Termitarium

A termite nest, or the artificial net used to house termites in a laboratory.

Termites (Isoptera)

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Termites are small to medium-sized orthopteroid insects that are cryptic in habit. All species live in eusocial colonies and feed primarily on cellulose. Although referred to in older literature as "white ants," termites are unrelated to ants. The name of the order is derived from the Greek words "iso" (equal) and "ptero" (wing) that describe the similar length and shape of both the fore and hind wings of the reproductive alates. Mature colonies are composed of task-specific castes that typically include one or more pairs of reproductives, about 0–25% soldiers, and a majority of immature or sterile workers. During part of the year, colonies may also contain some maturing or fully winged reproductives (alates, imagos) destined to leave their colony in brief, but often intense, dispersal flights. The order Isoptera is divided into seven families. The family Rhinotermitidae is divided into seven small and closely allied subfamilies and the Termitidae into four large

Termites (Isoptera), Table 8

Order: Isoptera, the termites	No. genera	No. species
Family: Hodotermitidae, Old World Harvester Termites	3	19
Family: Kalotermitidae, Drywood and Dampwood Termites	21	452
Family: Mastotermitidae, Giant Northern Australian Termite	1	1
Family: Rhinotermitidae, Lower Subterranean Termites	14	350
Subfamily: Coptotermitinae	1	79
Subfamily: Heterotermitinae	3	143
Subfamily: Prorhinotermitinae	1	18
Subfamily: Psammotermitinae	1	8
Subfamily: Rhinotermitinae	7	56
Subfamily: Stylotermitinae	1	43
Subfamily: Termitogetoninae	1	3
Family: Serritermitidae	2	2
Family: Termitidae, Higher Termites	240	2,021
Subfamily: Apicotermitinae, Soldierless Termites	42	215
Subfamily: Macrotermitinae, Fungus-Growing Termites	14	365
Subfamily: Nasutitermitinae, Nasutiform Termites	93	674
Subfamily: Termitinae	91	771
Family: Termopsidae, Primitive Dampwood or Rottenwood Termites	5	21
Total	286	2,870

and diverse subfamilies (Table 8). By historical convention, all but 2% of termite genera end in the suffix "*termes*," the Latin word for termite.

Phylogeny and Fossils

Termites are closely related to cockroaches and mantids. Based on molecular and morphological characters, the Mastotermitidae are the most primitive termite family, followed by the Termopsidae, Hodotermitidae, Kalotermitidae, Serritermitidae, Rhinotermitidae, and finally the "higher" termites of the family Termitidae. The earliest fossil records of termites are from the Cretaceous period (144–65 million years before present, YBP) and include the families Mastotermitidae, Hodotermitidae, and Termopsidae. Cretaceous fossils consist of wings or imago bodies in sedimentary deposits or amber. Excellent soldier and alate fossils have been found for the Mastotermitidae, Kalotermitidae, Rhinotermitidae, and Nasutitermitinae in Dominican amber from the Oligocene to early Miocene (20–30 million YBP). Over one hundred extinct termite species have been identified worldwide except from Africa.

Description of Important Taxa

The family Mastotermitidae consists of a single primitive species, *Mastotermes darwiniensis*, a large subterranean nester that attacks sound wood in northern Australia. The alates of *M. darwiniensis* have some roach-like characters and queens lay eggs in batches that resemble cockroach ootheca. The Termopsidae are large to very large primitive wood-nesting termites found in damp logs in temperate forests of both hemispheres. The Hodotermitidae are an Old World family consisting of large termites that nest in the soil and openly forage in grasslands and savannas for herbaceous growth. Unlike other termites, the eyes of Hodotermitidae workers are rather well developed. The Kalotermitidae include wood-dwelling species found throughout the tropics and subtropics. Although some species require wood with moderate to high moisture content, other kalotermitids thrive in low moisture conditions and are called drywood termites. Drywood termites produce characteristic six-sided fecal pellets that are stored in galleries and periodically ejected from the wood through surface holes. One drywood species in particular, *Cryptotermes brevis*, is a worldwide pest known only from structural lumber and furniture.

The family Rhinotermitidae is worldwide in distribution and contains primarily wood-feeding subterranean nesters and includes some of the most important pest genera attacking buildings: *Coptotermes* (Coptotermitinae), *Heterotermes*, and *Reticulitermes* (Heterotermitinae). A few *Coptotermes* are known to build mounds in Australia. The Prorhinotermitinae (*Prorhinotermes*) typically locate their nests inside and under damp logs near oceanic coastlines. The Psammotermitinae constitute one genus (*Psammotermes*) of subterranean termites that occurs in arid lands of Africa and the Middle East. Some genera of the Rhinotermitinae, such as the neotropical *Rhinotermes* and the paleotropical *Schedorhinotermes* have dimorphic soldiers, one with large mandibles and the other with an extended labrum, that bear little or no resemblance to one another. The monogeneric subfamilies Stylotermitinae and Termitogetoninae are limited to central and Southeast Asia, respectively. The Serritermitidae are an obscure family known only from a few collections of two species in Brazil.

By far the largest termite family is the Termitidae inclusive of all evolutionarily advanced or "higher termites." The soldierless subfamily Apicotermitinae includes grass feeders and humivores. Most apicotermitine species live in diffuse underground gallery systems but some African genera, such as *Apicotermes*, build elaborate geometrically proportioned nests. The Macrotermitinae are an Old World subfamily of large mound-building termites. These medium to very large termites eat fungus grown on special combs in their nest. Many species provision the fungus with herbaceous vegetation that is gathered by workers from forests, grasslands, and agroecosystems. The massive 8 m high chimney mounds of *Macrotermes* have classically defined the landscape of the African savanna. The Macrotermitinae, which also include the diverse genera *Microtermes* and *Odontotermes*, range east to the Philippines. The Nasutitermitinae are a tropicopolitan subfamily of arboreal, mound, and subterranean nesting termites that are characterized by long-snouted soldiers. The snout, or nasus, is the armature from which a volatile and sticky secretion is exuded as a defensive mechanism. Some Nasutitermitinae, primarily in the genus *Nasutitermes*, feed on wood and can be serious pests of structures, while others are humivores. In some Neotropical genera, e.g., *Armitermes*, the soldiers have both a nasus and long sickle-shaped mandibles. The subfamily Termitinae is the most diverse of all the termitid subfamilies. Included is the genus *Cubitermes* of sub-Saharan Africa which is characterized by mushroom-shaped mounds. The pantropical *Termes* and related genera have soldiers with snapping mandibles and arboreal or rotten log nests. The *Amitermes* and related genera like *Microcerotermes* occur in the tropics and subtropics worldwide where they feed on wood, grasses, and cellulosic debris. *Amitermes* is subterranean nester in the Nearctic Region while species from northern Australia build large epigeal mounds. *Microcerotermes* tend to be arboreal or subterranean in nesting habit.

Diversity and Distribution

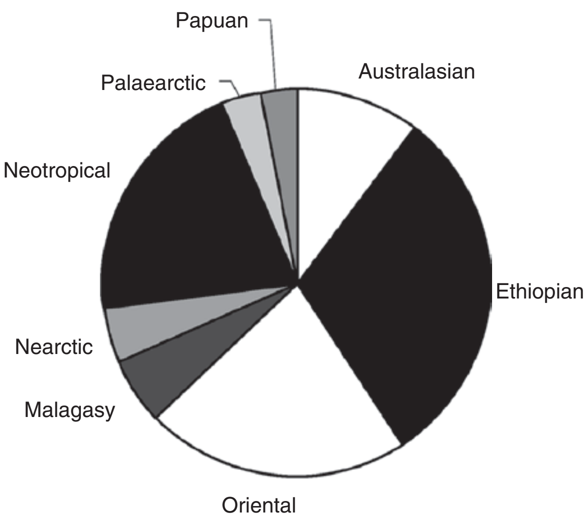
Almost 2,900 termite species in 286 genera have been described and it is likely that more than 4,000 species may ultimately be recorded. Termites are found in all zoogeographic regions of the world and many oceanic islands between latitudes of about 50°N (southern British Columbia) and 45°S (southern Chile and South Island, New Zealand) (Table 9, Figs. 30 and 31). The greatest diversity, measured by numbers of genera and species, occurs in the tropical non-arid regions of Africa, Asia, and the Americas. Some regions show remarkable speciation by single genera such as the *Cryptotermes* from the circum-Caribbean with 25 species, the *Amitermes* of Australia with 61 species, the *Nasutitermes* of the Neotropics with 72 species, and the *Odontotermes* of tropical Asia with nearly 100 species. Certain genera, such as *Reticulitermes* (Rhinotermitidae) and all those of the Termopsidae are characteristic elements of more temperate climates. In turn, *Heterotermes* and *Neotermes*, respectively, occupy similar niches in the tropics. Numerous genera are found in all tropical regions of the world. These include the *Neotermes*, *Glyptotermes*, *Kalotermes*, *Procryptotermes*, *Cryptotermes* (Kalotermitidae), *Coptotermes*, *Heterotermes*, and *Prorhinotermes* (Rhinotermitidae), and *Anoplotermes*, *Microcerotermes*, *Amitermes*, *Termes*, and *Nasutitermes* (Termitidae).

International trade has facilitated the spread of "weedy" species from native habitats across natural barriers to non-native locations worldwide. Human transport, especially by boat, has facilitated the spread and establishment of about a dozen major pest species. Among them are the drywood termites (Kalotermitidae) *Cr. brevis* (West Indian drywood termite), *Cr. havilandi*, *Cr. dudleyi*, *Cr. domesticus*, *Cr. cynocephalus*, and *Incisitermes minor* (Western drywood termite). Invasive species among the lower subterranean termites include *Coptotermes formosanus* (Formosan subterranean

Termites (Isoptera), Table 9 **Occurrence of termite families and subfamilies of termitidae by zoogeographic region**

Family	Region							
	Australasian	Ethiopian	Oriental	Malagasy	Nearctic	Neotropical	Palaearctic	Papuan
Hodotermitidae		X					X	
Kalotermitidae	X	X	X	X	X	X	X	X
Mastotermidae	X							
Rhinotermitidae	X	X	X	X	X	X	X	X
Serritermitidae						X		
Termopsidae	X	X	X		X	X	X	
Termitidae	X	X	X	X	X	X	X	X
Subfamily								
Apicotermitinae		X	X	X	X	X		
Macrotermitinae		X	X	X				
Nasutitermitinae	X	X	X	X	X	X		X

Termites (Isoptera), Figure 30 **Worldwide occurrence of termites in the major zoogeographic regions. Unshaded areas (northernmost North America, Eurasia, southernmost South America) do not support termites.**



Termites (Isoptera), Figure 31 **Proportion of termite genera found in the eight zoogeographic regions.**

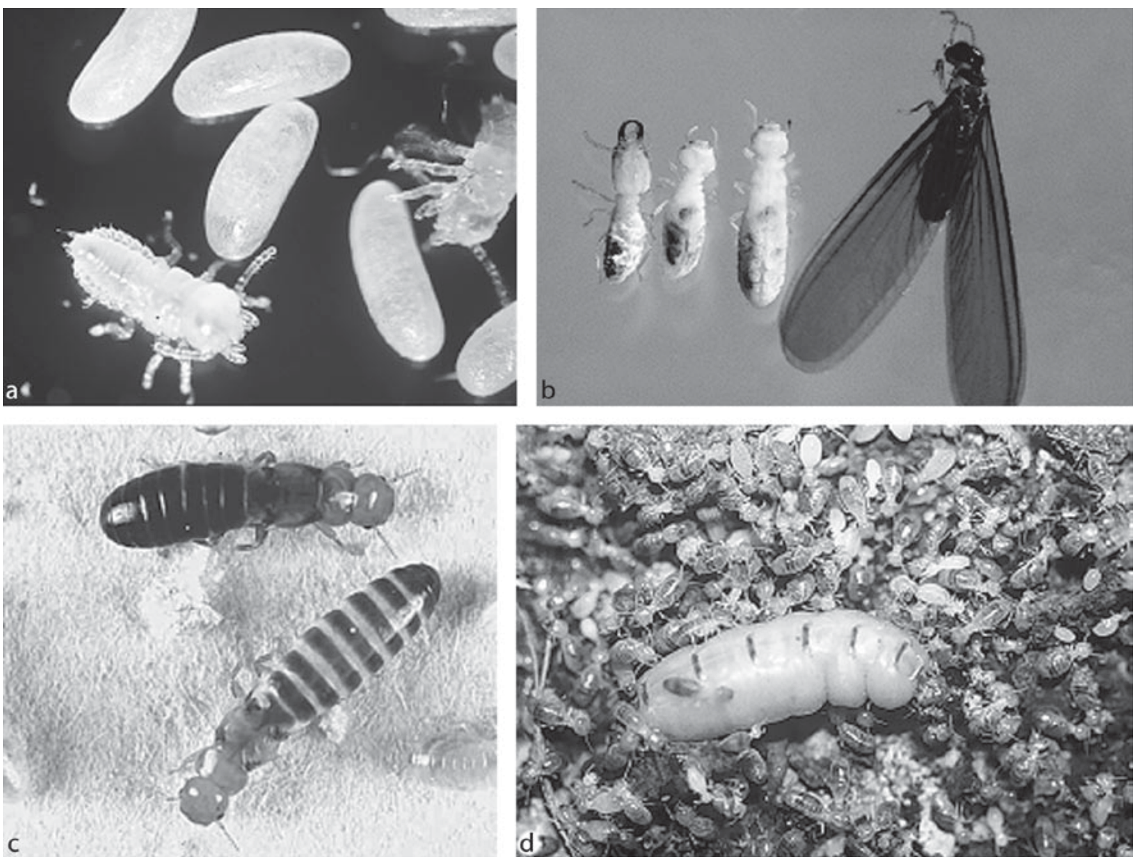
termite), *Co. gestroi*, and *Reticulitermes flavipes* (Eastern subterranean termite). Among the Termitidae, only one species, *Nasutitermes costalis*, has become established in a non-native habitat.

Morphology

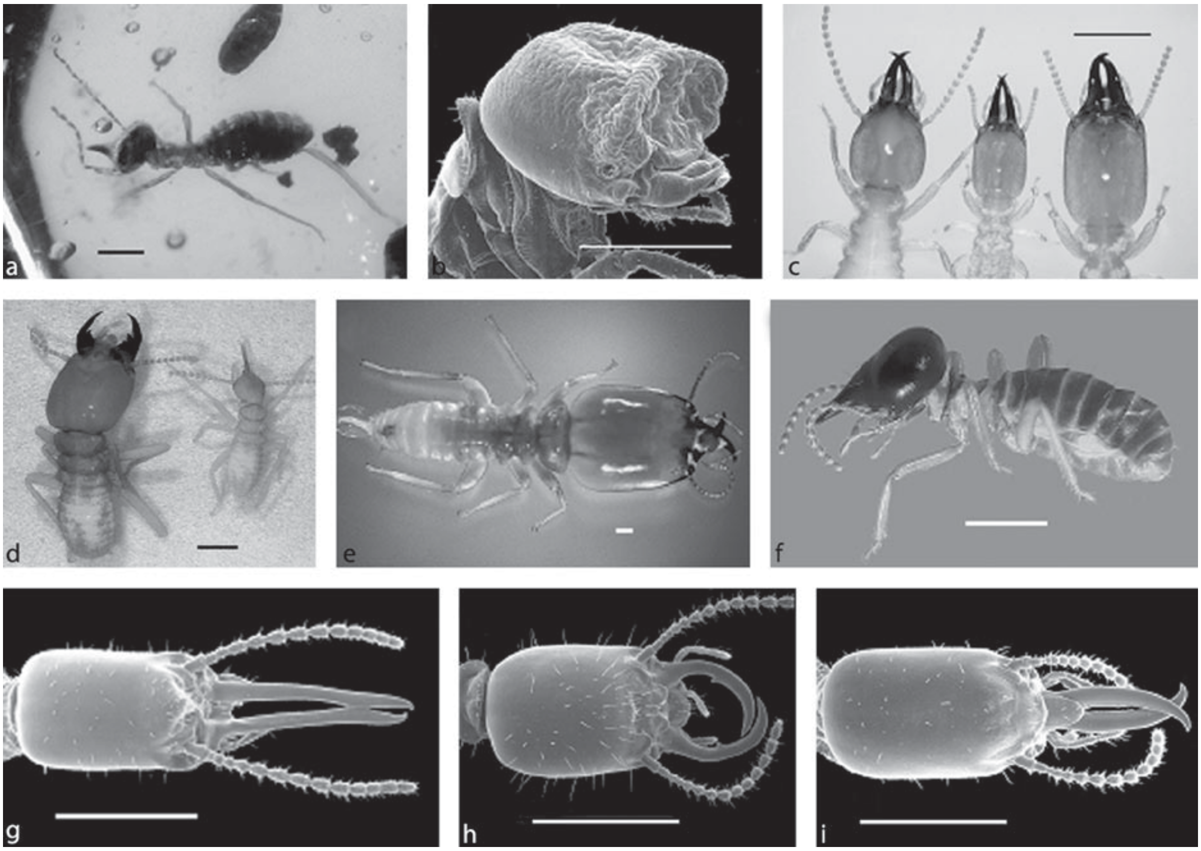
All termite castes are soft-bodied. Only the soldier head-capsules, the heads and bodies of some imagos, and the mandibles of all castes have moderate to heavy sclerotization. Termite workers and imagos have chewing mouthparts, filiform or moniliform antennae, and a shield-like pronotum behind the head. Soldier mandibles are highly developed to atrophied and variable in shape depending on the defenses employed. Important morphological characters used to classify termites include wing venation and mandible dentition in imagos, head capsule and mandible shape in soldiers, and gut configuration and mandible dentition in workers. Alates have compound eyes and ocelli while eyes of other castes are reduced to spots or are completely absent. The tarsi of most termites are not well suited for climbing smooth surfaces. Worker and soldier bodies are usually light colored but some have darker pigmentation. Alate bodies and wings range in color from pale yellow to black. Soldier head capsules range in color from light yellowish to orange, reddish-brown, or black. Among the smallest of termite soldiers is *Atlantitermes snyderi* (Nasutitermitinae) from Trinidad and Guyana with a total length of 2.5 mm while one of the largest is *Zootermopsis laticeps* (Termopsidae) from Arizona and Mexico at 22 mm long. The largest termite alates are the African *Macrotermes* measuring up to 45 mm in length with wings while the smallest is *Serritermes serrifer* (Serritermitidae) at 6 mm with wings. Alates of some *Incisitermes* and *Glyptotermes* (Kalotermitidae) and Apicotermitinae are less than 7 mm long with wings (Figs. 32 and 33).

Life Cycle and Behavior

The inception of a termite colony occurs when a male and female alate pair after a dispersal flight. Flights are typically associated with weather conditions superimposed over annual cycles. Rainfall is a prerequisite for flights by many subterranean species. The beginning of a rainy season coincides with flights by many species. After separation from their wings along specialized suture lines, the reproductive pair runs in tandem until a suitable nesting site is encountered and selected. Once in the protected site, e.g., a crevice in a branch, a tree hole, or underneath a log or stone, the new king and queen build a small nuptial chamber in which the first eggs are deposited and hatch into larvae. The first batch of developing workers and first soldier are cared for by the reproductives. The workers, usually blind and composed of both sexes, in turn begin to forage and feed the royal pair, soldiers, and younger sibling larvae. Feeding is accomplished by trophallaxis in which food is passed mouth-to-mouth from workers to their dependent nestmates. As foraging and food resources increase, the size and reproductive output of the queen grow accordingly. The abdomens of mature queens in the Rhinotermitidae and Termitidae, filled with egg-swollen ovaries, reach a state of near immobility



Termites (Isoptera), Figure 32 **Termite castes. (a) Eggs and larvae of *Cryptotermes brevis* (Kalotermitidae), Florida. (b) Soldier (L), worker, nymph, and alate of *Amitermes floridensis* (Termitinae), Florida. (c) King (top) and queen of *Incisitermes minor* (Kalotermitidae), California. (d) Queen (center) of *Nasutitermes rippertii* (Nasutitermitinae), Bahamas.**

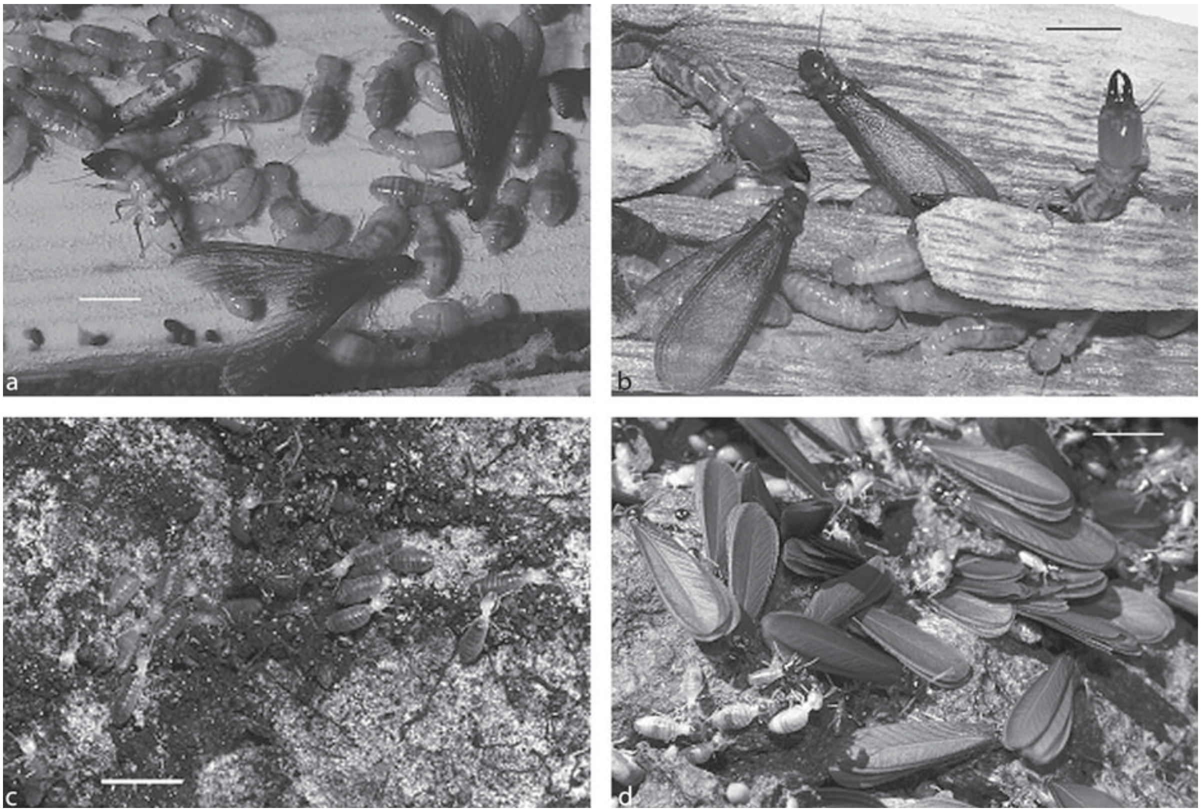


Termites (Isoptera), Figure 33 **Termite soldiers. (a) A. *Constrictotermes* sp. in amber, Dominican Republic. (b) *Cryptotermes brevis* (Kalotermitidae), Florida. (c) Rhinotermitidae: *Coptotermes formosanus* (L), *Heterotermes* sp., and *Reticulitermes flavipes*, Florida. (d) *Rhinotermes marginalis* (Rhinotermitidae) major (L) and minor, Dominican Rep. (e) *Macrotermes* sp. (Macrotermitinae) major, Kenya. (f) *Nasutitermes costalis* (Nasutitermitinae), Trinindad. (g) *Termes hispaniolae* (Termitinae), St. Croix. (h) *Amitermes amicki* (Termitinae), Aruba. (i) *Microcerotermes arboreus* (Termitinae), Trinidad. Scale bars = 1 mm.**

called physogastry. In the Kalotermitidae, castes develop along a single line with both soldiers and alates molting from the immature worker (pseudergate) line. In the higher termites, each caste differentiates along separate developmental pathways after hatching with the workers becoming sterile adults. Unlike social Hymenoptera, the king is retained and periodically fertilizes the queen. After a number of years when a large crop of workers and soldiers are present, the colony matures to produce its first batch of alates, completing the reproductive cycle. Colonies will produce alates for many years after maturation. Termites have some complex symbiotic relationships with a community gut-inhabiting microorganisms. Various bacteria (prokaryotes) and protists (eukaryotes) are important for cellulose digestion, nitrogen fixation, and metabolism. Protists are absent from the Termitidae. Termites also produce their own cellulytic enzymes. Proctodeal feeding, the transfer of gut contents via anus to mouth, facilitates the exchange of gut biota to freshly molted nestmates (Fig. 34).

Defense Mechanisms and Natural Enemies

Termites are an ideal food source for other animals. They are relatively slow moving, soft-bodied, and rich in fat and protein. Termites passively



Termites (Isoptera), Figure 34 **Termite colonies. (a)** ***Zootermopsis angusticollis*** **(Termopsidae), California. (b)** ***Neotermes castaneus*** **(Kalotermitidae), Florida. (c)** ***Anoplotermes*** **n. sp. (Apicotermitinae), Bahamas. (d)** ***Nasutitermes costalis*****, (Nasutitermitinae), Florida. Scale bar = 5 mm.**

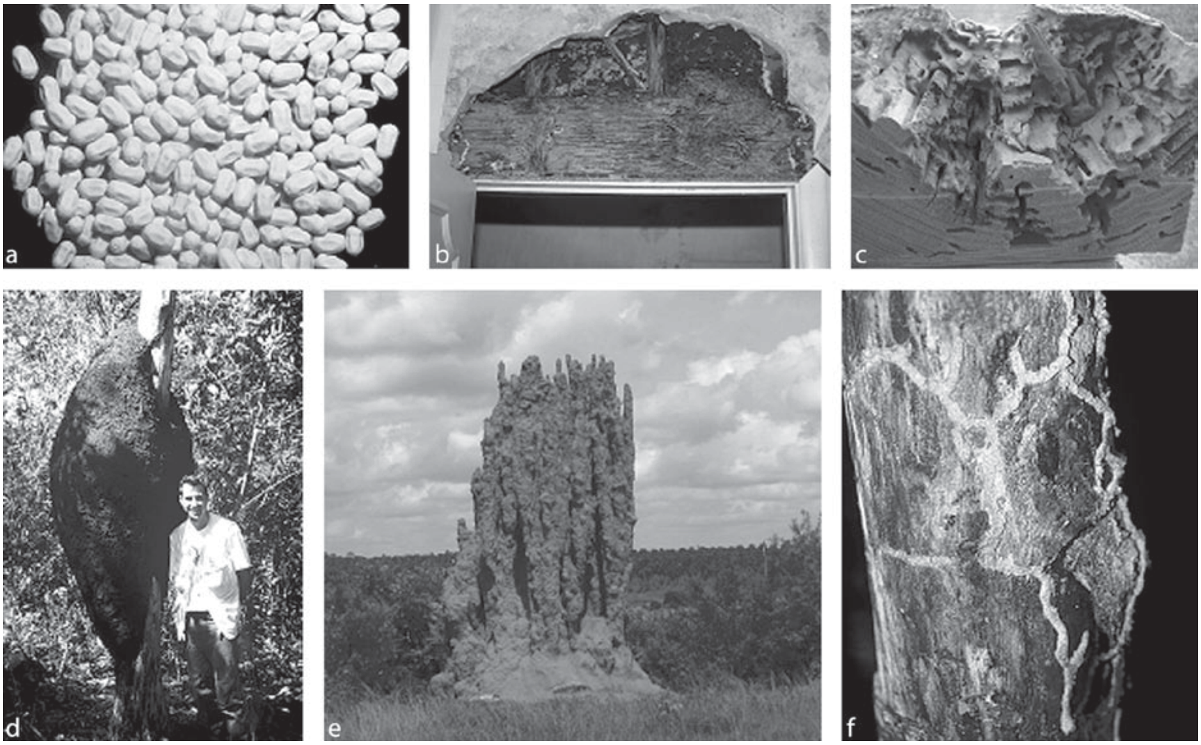
avoid casual predation because of their cryptic habits of living in nests, feeding mostly under cover, and foraging in narrow galleries constructed in soil or wood. Most termite species, however, have a highly specialized soldier force to defend the colony from specialized invaders, especially ants. Soldiers of the Kalotermitidae, Termopsidae, and Hodotermitidae rely solely on mechanical defenses including powerful crushing mandibles. Some kalotermitid genera, e.g., *Cryptotermes* and *Calcaritermes*, have soldiers with plug-shaped or phragmotic heads used to seal off nest galleries in wood from ants. Termites in other families use various combinations of biting, piercing, or slashing mandibles and repellent, sticky, and/or toxic chemical secretions which they exude, brush, or squirt onto ants. In most species of Nasutitermitinae, soldier mandibles are altogether lacking and instead, the soldiers use their conical nasi to squirt repellent secretions over several body lengths.

Many animals, especially birds, bats, rodents, reptiles, and amphibians opportunistically gorge themselves on termite alates during dispersal flights. Some large mammals, such as the aardvark and aardwolf of Africa, pangolins of the paleotropics, anteaters of the neotropics, the echidna of Australia, and the sloth bear of Asia are specialized predators of termites and use claws and long tongues to excavate and feed inside hard nest structures. Humans, especially in Africa, trap and eat *Macrotermes* alates during seasonal dispersal flights from their mounds.

Some arthropods have evolved an association with termites that includes living in termite nests. Those arthropods that have an obligate relationship with the termite colony are called termitophiles. Usually the termitophiles rely on termites for both food and shelter. The great majority of termitophiles are beetles. Some staphylinid beetles even resemble their hosts. Other termitophile taxa include isopods, millipedes, phorid flies, and silverfish.

Ecology

Termite nests consist of a network of galleries that interconnect all colony members and foraging sites. Nest types include single-piece wood nests, (Termopsidae, Kalotermitidae), diffuse subterranean nests (Mastotermitidae, Rhinotermitidae, Termitidae), hollow tree, log, and stump nests connected to other food resources via subterranean galleries (Rhinotermitidae, Termitidae), on-soil (epigeal) mounds (Hodotermitidae, Rhinotermitidae, Termitidae), and arboreal nests (Termitidae). Arboreal nests are constructed of feces while epigeal nests are composed mostly of soil (Fig. 35). Foraging is the means by which termite colonies locate and exploit new food resources. If such resources are abundant, secondary nest structures may be constructed nearby. Usually workers, but in some cases soldiers, follow specific search patterns to locate food. If food is encountered, the foragers will recruit additional nestmates to exploit the food source for the colony. When on exposed surfaces, foraging trails are usually protected from predators by tube or sheet-like enclosures made of feces or soil. Recruitment to food locations is enforced and oriented by chemical trails released from the sternal gland located on the ventral surface of the abdomen. Large immovable food sources may be covered with a protective fecal or soil sheeting. Smaller food items such as leaves and grasses are either covered with soil sheeting or



Termites (Isoptera), Figure 35 **Termite workings. (a) Fecal pellets of *Cryptotermes brevis* (Kalotermitidae), Florida. (b) Exposed damage and aerial nest of *Coptotermes formosanus* (Rhinotermitidae), Florida. (c) Nest galleries of *Neotermes jouteli* (Kalotermitidae) in structural lumber, Florida. (d) Arboreal nest of *Nasutitermes rippertii* (Nasutitermitinae), Bahamas. (e) Soil mound of *Macrotermes* sp. (Macrotermitinae), Ivory Coast. (f) Foraging tubes of *Microcerotermes arboreus* (Termitinae), Trinidad.**

are subdivided and carried back to the nest for consumption, storage, or fungal gardens. Foraging territories for single termite colonies may extend 100 m or more from the nest. Water, either in food or substrata, can have a profound influence on foraging. Most termites forage in the direction of moisture gradients and prefer moist foods and nesting sites. In savannas and arid lands, surface objects caste heat shadows that are often investigated by termites foraging near the soil surface.

Although cryptic for the most part, the absolute numbers of termites in most tropical and semitropical forests, deserts, and savannas ranges from several hundred to thousands of individual termites per square meter. Colony populations of termites vary from several hundred (Kalotermitidae) to several million (Rhinotermitidae, Termitidae) individuals.

The biomass of termites often rivals that of terrestrial vertebrates and ranges from less than 1 g/m^3 to over 10 g/m^3. Food consumption by termites can be greater than that of large ungulates. Termite foods include dry, moist, wet wood, bark, live wood, leaf litter, soil (humus), live and dried grasses and herbs, and leaves, lichens, fungi, and algae. Termites are also significant, albeit, relatively minor sources of global atmospheric methane and carbon dioxide. Termites, along with earthworms, create large turnover and aeration of organic and mineral content in soil and thus benefit plant growth and nutrient cycling.

Termites as Pests

About 10% of the termite species worldwide attack structural lumber, wood products of a broad array including paper, and agricultural and forage crops. About 1–2% of all species are major pests and account for the bulk of the untold billions of dollars in damage caused by termites around the world each year. The vast majority of termites is a cryptic and essential component of the environment but has very little direct impact on humans. Termite control in developed countries relies on chemical applications in the form of specialized residual soil termiticides, wood preservatives, baits, dusts, and fumigants often applied by professional pest control operators. People in developing countries may treat termite infestations with unsafe or unproven methods or simply replace damaged and infested wood.

Collecting

Because termites are delicate and can desiccate rapidly, they should be preserved in alcohol (85% ethanol is best) while still alive. A hatchet, trowel, and aspirator are essential collecting tools. Obvious places to collect termites include nests, foraging tubes, and dead limbs and logs. Subterranean species also congregate under boulders, stones, and other surface debris. Herbivore dung, under which some subterranean termites forage, is another surface feature to collect from. Small dried twigs on trees, tree holes, leaf litter, and disturbed areas such as road, trail sides, or even garbage dumps are good collecting places. A few species even infest branches, stems, and roots of live trees and shrubs. Termite alates that fly at dusk or at night are attracted to lights where they can be collected by aspirator or net. Because identification relies heavily on characters of soldiers or imagos, one should take multiple samples of each caste present. When alates are not found, one might be lucky to find a queen, king, or both. Nestmates from one colony should be combined as a single sample to confirm their relationship.

► Wood-Attacking Insects
► Termites (Isoptera) in South America

References

Abe T, Bignell DE, Higashi M (eds) (2000) Termites: evolution, sociality, symbiosis, ecology. Kluwer, Dordrecht, 466 pp

Edwards R, Mill AE (1986) Termites in buildings. Their biology and control. Rentokil, East Grinstead, 261 pp

Krishna K, Weesner FM (eds) (1969) Biology of termites, vol. 1. Academic, New York, 598 pp

Krishna K, Weesner FM (eds) (1970) Biology of termites, vol. 2. Academic, New York, 643 pp

Pearce MJ (1997) Termites: biology and pest management. CAB International, New York, 172 pp

Termites (Isoptera) in South America

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Termites are abundant in most parts of South America, especially in tropical lowland forests, savannas and grasslands. In many places, termitaria comprise a conspicuous element of the landscape. Early European naturalists who traveled in South America often mentioned termite damage or termite constructions in their writings. The South American fauna contains representatives of the termite families Kalotermitidae, Rhinotermitidae, Serritermidae, Termitidae, and Termopsidae (Figs. 36 and 37). This fauna comprises 76 genera (54% endemic) and 422 known species (90% endemic). Family Serritermitidae, which includes two genera and three species, is restricted to South America. Table 10 summarizes the number of genera and species recorded in each country. The termite faunas of Brazil, Argentina, Guyana, Chile and Trinidad are relatively better studied, while the faunas of Colombia, Ecuador, Paraguay and Suriname remain very poorly known. The knowledge in the remaining countries is intermediate.

Taxonomy

Family Kalotermitidae

This family is represented in South America by 67 species and 11 genera. Genera *Eucryptotermes* and *Tauritermes* are endemic and genus *Comatermes* occurs only in South America and Panama. The most diverse genera of Kalotermitidae in this region are *Neotermes* (16 species), *Cryptotermes* (11 native species) and *Glyptotermes* (10 species). Four species of *Cryptotermes* have been introduced from other regions as urban pests: *C. brevis*, *C. domesticus*, *C. dudleyi* and *C. havilandi*. However, only *C. brevis* is widespread and there is a single unconfirmed record of *C. domesticus* from Trinidad. In general, this family has been little studied in South America, and there are still many undescribed species.

Family Rhinotermitidae

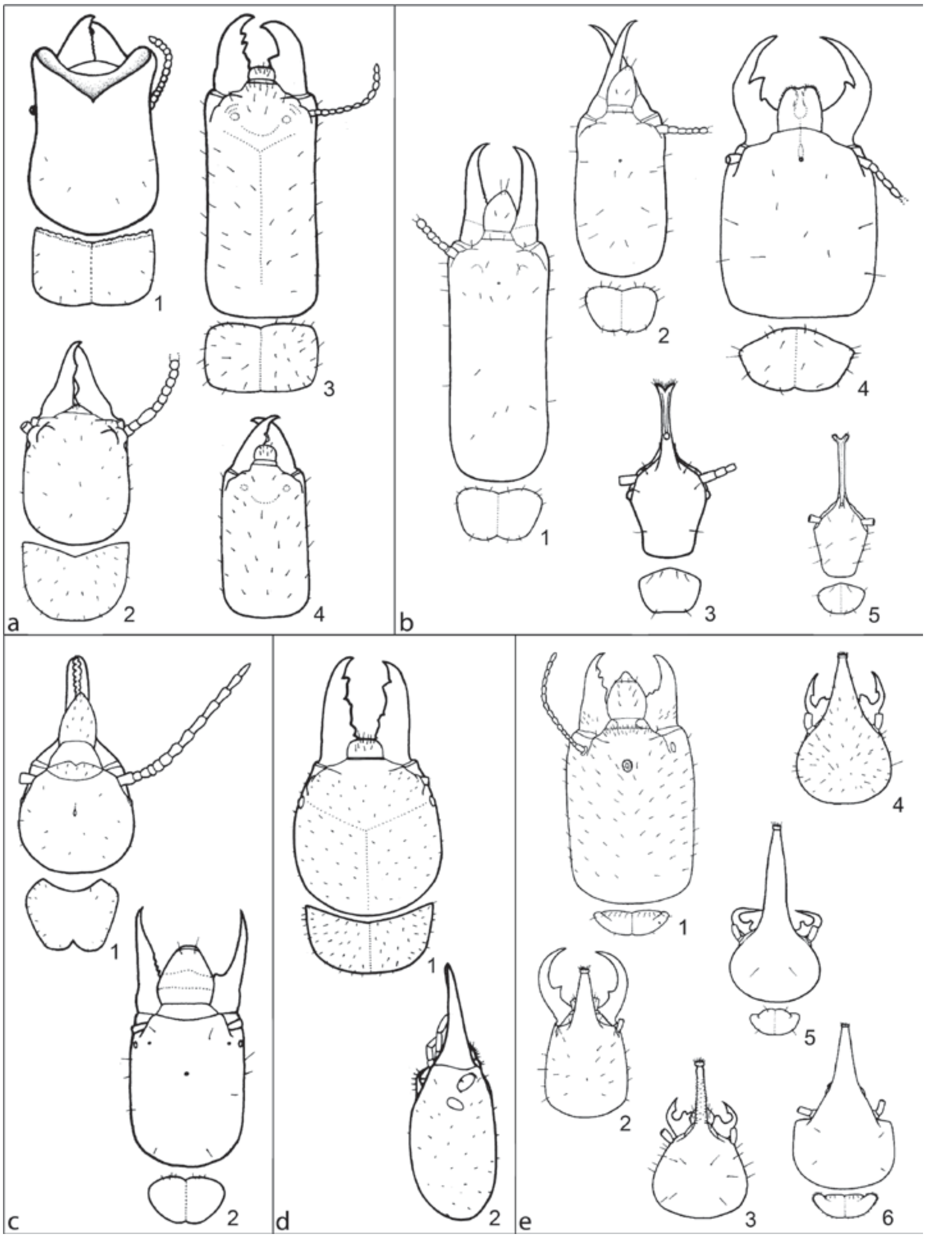
There are 21 species of rhinotermitids reported from South America, belonging to six genera: *Acorhinotermes*, *Coptotermes*, *Dolichorhinotermes*, *Heterotermes*, *Reticulitermes* and *Rhinotermes*. *Acorhinotermes* is endemic, with only one species, and *Dolichorhinotermes* is mostly endemic, with five species in South America and one in Panama. *Heterotermes* is the most important genus, with six species. *Heterotermes tenuis* is the most common species and an important agricultural pest. Despite the low diversity, this is a very important family including several major pests. Two species of Rhinotermitidae were introduced into South America and became major urban pests: *Coptotermes gestroi* in Brazil and *Reticulitermes flavipes* in Chile and Uruguay.

Family Serritermitidae

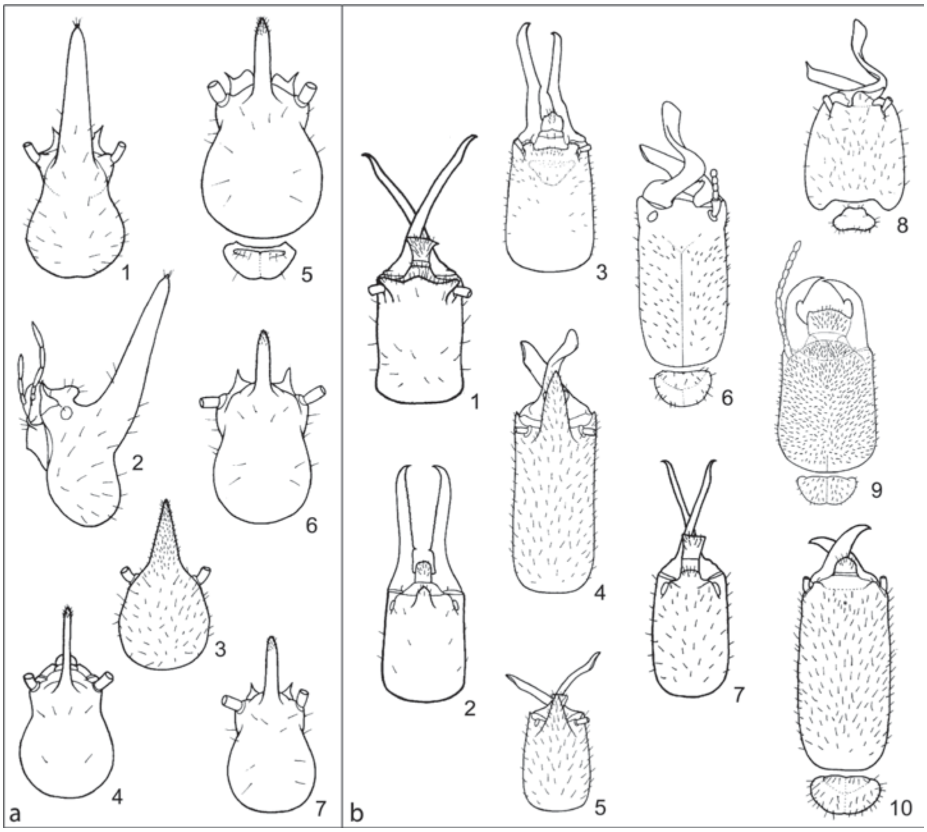
This family is endemic to South America and includes two genera and three species. *Serritermes serrifer* is endemic to the Cerrado and lives in nests built by *Cornitermes* spp., where it feeds on the dark organic matter of the nest walls. The genus *Glossotermes* includes two species, *G. oculatus* from Guyana, and *G. sulcatus* from Brazilian Amazonia. *Glossotermes* feeds on decayed wood.

Family Termitidae

This the largest family and comprises 76% of the South American species. The so-called nasute



Termites (Isoptera) in South America, Figure 36 **(a) South American Kalotermitidae (soldiers) (1)** ***Eucryptotermes wheeleri*****; (2)** ***Tauritermes vitulus*****; (3)** ***Comatermes perfectus*****, major soldier; (4)** ***C. perfectus*****, minor soldier. (b) South American Rhinotermitidae (soldiers) (1)** ***Heterotermes longiceps*****, major soldier; (2)** ***H. longiceps*****, minor soldier; (3)** ***Acorhinotermes subfusciceps*****, soldier; (4)** ***Rhinotermes marginalis*****, major soldier; (5)** ***R. marginalis*****, minor soldier. (c) Serritermitidae (soldiers) (1)** ***Serritermes serrifer*****; (2)** ***Glossotermes oculatus*****. (d) South American Termopsidae,** ***Porotermes quadricollis*** **(Termopsidae), (1) dorsal and (2) lateral views. (e) Soldiers of South American mandibulate nasutes (Termitidae: Nasutitermitinae) (1)** ***Labiotermes emersoni*****; (2)** ***Embiratermes neotenicus*****; (3)** ***Cyrilliotermes cashassa*****; (4)** ***Curvitermes odonthognathus*****; (5)** ***Rhynchotermes nasutissimus*****; (6)** ***Macuxitermes triceratops (drawings previously published in Zootaxa and used with permission)*****.**



Termites (Isoptera) in South America, Figure 37 (a) Soldiers of South American nasute termites (Termitidae: Nasutitermitinae). (1–2) *Angularitermes clypeatus*; (3) *Caetetermes taquarussu*; (4) *Coatitermes clevelandi*; (5–7) *Velocitermes heteropterus*, major, intermediate and minor soldiers. (b) Soldiers of South American Termitinae (Termitidae) (1) *Cavitermes tuberosus*; (2) *Genuotermes spinifer*; (3) *Orthognathotermes humilis*; (4) *Dihoplotermes inusitatus*, major soldier; (5) *D. inusitatus*, minor soldier (6) *Neocapritermes pumilis*; (7) *Crepititermes verruculosus*; (8) *Planicapritermes planiceps*; (9) *Onkotermes brevicorniger*; (10) *Cylindrotermes parvignathus* (drawings previously published in Zootaxa and used with permission).

termites (subfamily Nasutitermitinae) are the dominant group, with more than 50% of the species. Genus *Nasutitermes* alone includes 65 South American species. Most species of this genus are wood-feeders and live in arboreal carton nests, but some are subterranean or mound builders. The other 35 genera of Nasutitermitinae occur in South America, 22 of them endemic. Among them, *Syntermes* is the most diverse, with 23 species, including some of the largest known termites. They are mostly subterranean and feed on leaf or grass litter. Another important genus is *Cornitermes*, with 14 species, most of them mound-builders. Some species of *Cornitermes*, such as *C. cumulans*, occur in high densities and dominate the landscape of some grasslands. Other common and diverse genera of Nasutitermitinae are *Armitermes*, *Embiratermes*, *Labiotermes* and *Velocitermes*. Subfamily Termitinae is the second in diversity, with 16 genera (10 endemic) and 72 species in South America. The most important genus is *Neocapritermes*, with 16 species. Other common genera are *Termes*, *Microcerotermes*, *Spinitermes*, and *Orthognathotermes*. Very few South American Termitinae are strict wood-feeders and many are soil-feeders. A few

Termites (Isoptera) in South America, Table 10 **Number of termite genera and species recorded in South America**

Country	Kalotermitidae		Rhinotermitidae		Serritermitidae		Termitidae		Termopsidae		Total	
	gen.	sp.	gen.	sp.	gen.	sp.	gen.	sp.	gen.	sp.	gen.	sp.
Argentina	5	10	1	2	–	–	23	43	1	1	30	56
Bolivia	3	3	4	6	–	–	24	87	–	–	31	96
Brazil	7	26	4	12	2	2	54	268	–	–	67	308
Chile	3	4	1	1	–	–	–	–	1	1	5	6
Colombia	5	8	3	4	–	–	13	26	–	–	21	38
Ecuador	2	6	–	–	–	–	8	19	–	–	10	27
French Guiana	–	–	5	6	–	–	27	52	–	–	32	58
Guyana	5	14	5	10	1	1	30	69	–	–	41	94
Paraguay	–	–	1	1	–	–	21	36	–	–	22	37
Peru	3	3	3	4	–	–	18	48	–	–	24	55
Suriname	1	1	–	–	–	–	6	15	–	–	7	16
Trinidad & Tobago	6	16	3	4	–	–	15	25	–	–	24	45
Uruguay	2	2	1	1	–	–	5	6	–	–	8	9
Venezuela	7	11	4	8	–	–	20	50	–	–	31	69
Total	11	67	6	21	2	3	56	330	1	1	76	422

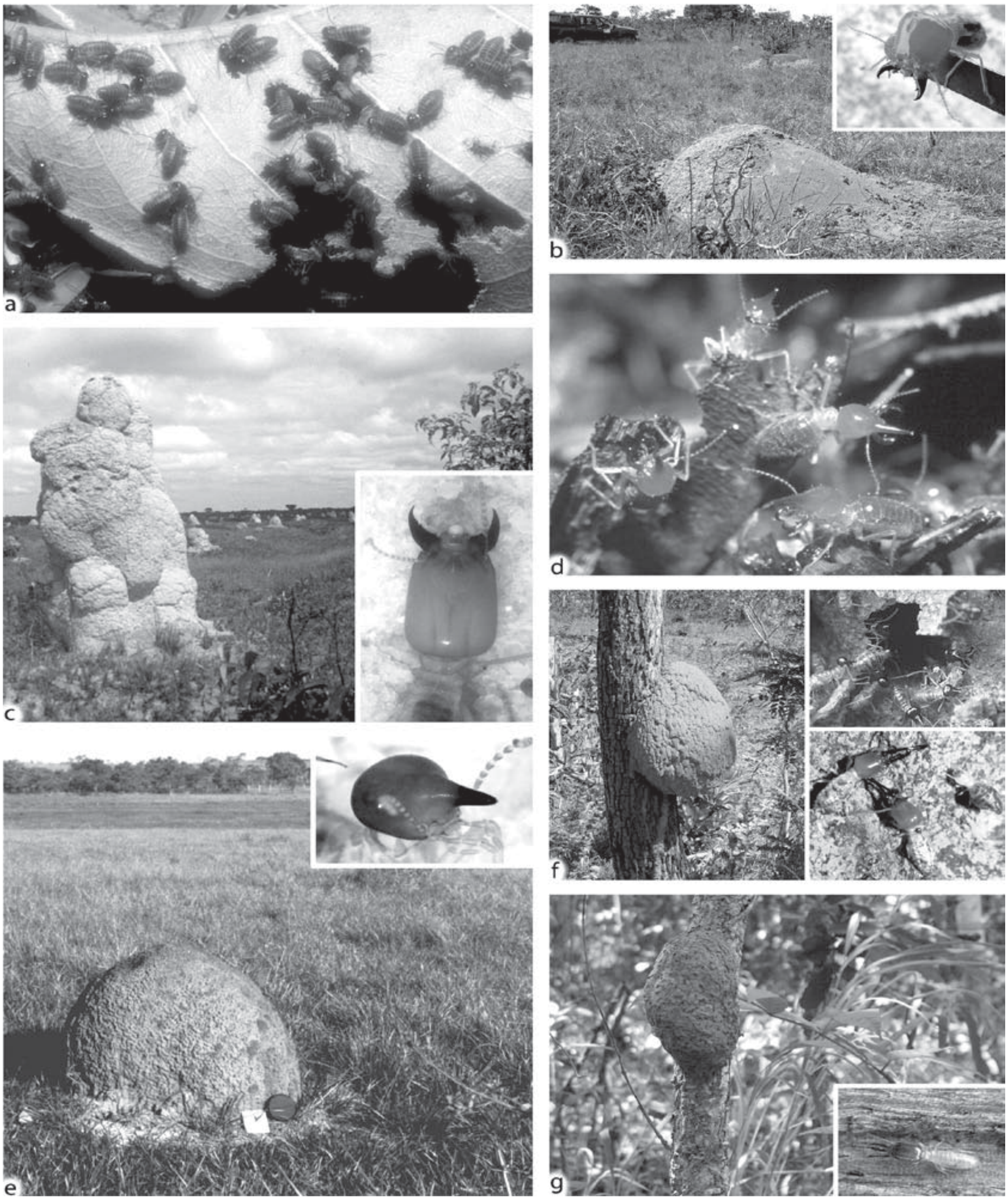
species have been reported damaging living plants, but in general they are of little economic importance. Subfamily Apicotermitinae is also important and diverse, but has been very little studied. All New World species of this subfamily are soldierless and most are subterranean, soil-feeders, and live in diffuse nests in the soil. They are difficult to collect and identify and have been neglected by termitologists. The South American species are classified in five genera: *Anoplotermes*, *Aparatermes*, *Grigiotermes*, *Ruptitermes* and *Tetimatermes*. *Anoplotermes* is the most common and diverse, with more than 25 South American species, and also occurs in North and Central America. The other four genera are endemic to South America and have a few species each. *Ruptitermes* feed on leaf litter. These termites are important in the soil fauna, but are not pests (Fig. 37 and 38).

Family Termopsidae

Porotermes quadricollis is the only representative of this family in South America. It occurs only in the Valdivian forests of Chile and Argentina, living in humid places. *Porotermes quadricollis* may damage structural wood, but it is not an important pest.

Vegetation Zones of South America and Their Termite Fauna

South America can be divided into distinct vegetation zones or biomes, each with a more or less typical termite fauna (Fig. 39). These zones are not homogeneous and the limits between them are not precise. There are no termites at higher elevation in the Andean region.



Termites (Isoptera) in South America, Figure 38 **(a) Workers of *Ruptitermes reconditus* (Termitidae: Apicotermitinae) feeding on leaf-litter. (b) Nest of *Syntermes wheeleri* (Termitidae: Nasutitermitinae) in a pasture. *Top right*: soldier. (c) Nests of *Cornitermes cumulans* (Termitidae: Nasutitermitinae) in a grassland in the Cerrado region. *Bottom right*: soldier. (d) *Armitermes teevani* (Termitidae: Nasutitermitinae) in the Amazon forest. (e) Nest of *Nasutitermes* sp. (Termitidae: Nasutitermitinae) in a grassland in the Amazon region. *Top right*: soldier. (f) Arboreal nest of *Constrictotermes cyphergaster* (Termitidae: Nasutitermitinae). *Top right*: *C. cyphergaster*. *Bottom right*: *Inquilinitermes fur* (Termitinae), an obligatory inquiline termite which feeds on the organic matter of the nest wall. (g) Nest of *Microcerotermes* sp. (Termitidae: Nasutitermitinae) in a dry forest ("cerradão"). *Bottom right*: soldier.**

The largest and most diverse zone is Amazonia, with nearly 6 million km^2, mostly covered by tropical rain forest. About 250 termite species have been recorded in Amazonia. Termite biomass in Amazon forests has been estimated as about 2 g/m^2, which corresponds to nearly 20% of the total animal biomass. As many as 60–70 species can be found in a single hectare of upland Amazon forest. The genus *Nasutitermes* is dominant, and their arboreal nests are conspicuous in the forest. Mound builders are also common, but most mounds are relatively small. Many termite genera are endemic to the Amazon region, including *Glossotermes*, *Anhangatermes*, *Caetetermes*, *Coendutermes*, *Macuxitermes*, *Rotunditermes*, *Triangularitermes*, *Cornicapritermes*, and *Planicapritermes*.

The second largest zone is the Cerrado, a kind of savanna vegetation which covers almost 2 million km^2. Termites are extremely abundant in the Cerrado and their mounds comprise a conspicuous element of the landscape, reaching densities between 300 and 750 nests/ha. There are about 150 species recorded in this region, almost half of them endemic. Litter-feeding termites are abundant in the Cerrado, and forage on the surface at night in large numbers. Mound-building *Cornitermes* can reach impressive densities in some places and are considered keystone species.

The Atlantic forest originally covered 1.2 million km^2, but has mostly been destroyed and only about 8% remains. There are approximately 70 termite species recorded from the Atlantic forest. The dominant termites are arboreal nesting *Nasutitermes* spp. Dry-wood termites (Kalotermitidae) are also abundant. Mounds are much less common in this region than in Amazonia and the Cerrado. The termite fauna is more diverse in the northern part, which shares many species with the Amazon forests.

The termite fauna of the Caatinga vegetation, a xerophytic open forest or savanna of northeastern Brazil, is poorly known. There are little more than 20 species recorded for the entire region, but some recent surveys indicate the presence of many undescribed species. Mounds and arboreal nests are rare, just a few per hectare. The most common genera are *Heterotermes*, *Nasutitermes*, *Constrictotermes* and *Amitermes*.

The Chaco region is a large extension of xerophytic open forest of Bolivia, Paraguay and northern Argentina. Its termite fauna is still little known, but it seems to be similar to that of the Cerrado. There are only about 20 termite species recorded in this region, but it is likely that the total number is considerably higher, probably including undescribed taxa.

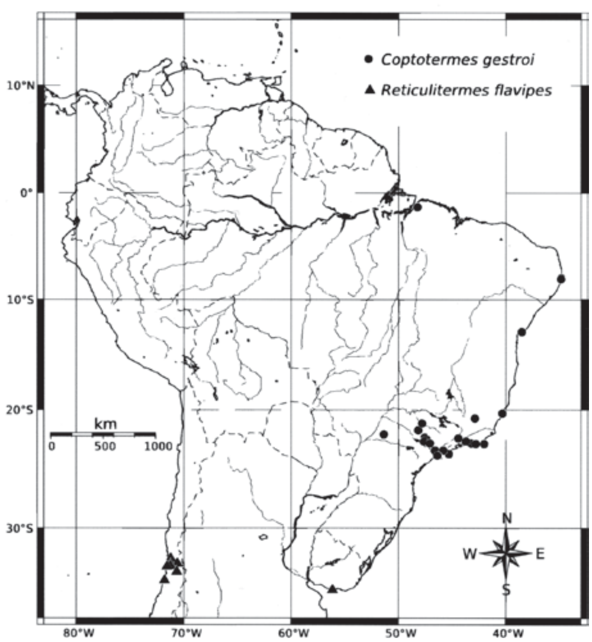
The Pampa region of Argentina, Uruguay and southern Brazil is mostly covered by open grassland, which is often used as pasture. There are about 32 species recorded for this region, but many seem to be restricted to patches of forest. Most of these species are also present in the Atlantic forest, Chaco or Cerrado. Typical species of the Pampa grassland are *Cortaritermes fulviceps* (=*Nasutitermes fulviceps*), *Procornitermes striatus* and *Termes saltans*.

The Llanos of Venezuela and Colombia is a tropical grassland situated in the Orinoco basin. Its termite fauna is poorly known, but it seems to be composed mainly of mound-building *Nasutitermes* and *Velocitermes*, which may reach high densities and feed on grass litter.

The Caribbean zone of Colombia and Venezuela includes tropical forest and xerophitic vegetation. Its termite fauna shares many species with Central America and the Antilles. The forests are dominated by arboreal nesting *Nasutitermes*, especially *N. corniger*, *N. ephratae* and *N. acajutlae*. *Amitermes foreli*, *Heterotermes convexinotatus*, *Microcerotermes* sp., and *Obtusitermes* sp. are also common.

The North Pacific region, which includes part of Colombia and Ecuador, is mostly covered by tropical forests connected to Central America. Its termite fauna is little known, but it is also dominated by *Nasutitermes* spp. and includes at least one endemic species, *Cornitermes acignathus*.

Patagonia is the southernmost portion of South America, including part of Argentina and Chile. The vegetation of this region is mostly



Termites (Isoptera) in South America, Figure 39
Main vegetation zones of South America (*above*), and current distribution of two introduced termite species (Rhinotermitidae) in South America (*below*).

grassland. The only termite that occurs in the lowland of Patagonia is *Onkotermes brevicorniger*, with a southern limit near 43°S.

The Valdivian forest zone is located in Chile and a small part of Argentina. The dominant vegetation is temperate rain forest. There are only two termite species native to this region, both also endemic: *Porotermes quadricollis* and *Neotermes chilensis*.

Termites as Urban and Structural Pests in South America

Many termite species live in urban spaces in South America. More than 20 species have been reported in some cities. However, few of them can be considered pests and most live in green spaces such as gardens and urban parks. The most important pest species have been introduced from other regions: *Cryptotermes brevis*, *Cryptotermes dudleyi*, *Cryptotermes havilandi*, *Coptotermes gestroi*, and *Reticulitermes flavipes*. *Crytotermes brevis* is an ubiquitous house termite present in most cities except in cold places. The southernmost record for this species is Montevideo (34°51′S). *Cryptotermes dudley* and *C. havilandi* have been reported in a few cities in Brazil and Trinidad. *Coptotermes gestroi* (previously also referred to as *Coptotermes havilandi*, a synonym), is a very destructive species native of Southeast Asia, which was introduced in Brazil in the 1920s. It was first recorded in Rio de Janeiro in 1923, and today it is present in many large and important cities. *Reticulitermes flavipes*, which is native of North America, was introduced into Uruguay (Montevideo) in the 1960s and into Chile in the 1980s, where it became an important urban pest. Before the introduction of *Reticulitermes*, these regions were relatively free of termite problems. Among native species, the most important urban pests are *Nasutitermes* spp. and *Heterotermes* spp., which occur in most cities north of 30°S. *Nasutitermes corniger* is a wood-feeder, arboreal nesting termite, which occurs from Mexico to northern Argentina and is a major pest in many cities. *Nasutitermes macrocephalus* is also present in many cities and has a similar biology. *Heterotermes* ssp. are subterranean wood-feeders which are widespread and may damage wood. There are six species in South America, the most common of which is *H. tenuis*.

Termites as Agricultural Pests in South America

Several cultivated plants are significantly damaged by termites in South America, especially sugarcane, upland rice, and eucalyptus. Other plants affected include maize, cotton, peanuts, soybean, coffee, cassava, fruit trees and vegetables. Termites may cause injury to plants by feeding on roots, leaves, stems, and woody tissue. The most important pests belong to genera *Heterotermes*, *Nasutitermes*, *Cornitermes*, *Procornitermes*, and *Syntermes*. Besides injuring living plants, some termites also build large mounds, which may be a problem for the use of machinery and reduce the useful soil surface. Some species of mound-building *Cornitermes* are present at high densities in pastures, but their effect is controversial. Farmers dislike their presence but they do not seem to cause real loss of production. These are all native species and, unlike the urban pests, they are associated with their natural biomes. Therefore, a plant species may be damaged by different termite species in different regions. The following conditions favor termite damage in agriculture: (i) use of exotic crops, which are not resistant nor tolerant to termites; (ii) no-tillage systems, because subterranean termite colonies develop better in undisturbed soil; (iii) non-irrigated crops or crops that are under stress, because vigorous crops are more tolerant to termites.

► Termites (Isoptera)

References

Araujo RL (1970) Termites of the Neotropical Region. In: Krishna K, Weesner FM (eds) Biology of termites, vol. 2. Academic, New York, 527–576 pp

Constantino R (1998) Catalog of the living termites of the New World (Insecta: Isoptera). Arq Zool 35:135–231. Updated online version available at http://www.unb.br/ib/zoo/docente/constant/catal/

Constantino R (2002) The pest termites of South America: taxonomy, distribution and status. J Appl Entomol 126:355–365

Constantino R (2002) An illustrated key to Neotropical termite genera (Insecta: Isoptera) based primarily on soldiers. Zootaxa 67:1–40

Termitidae

A family of termites (order Isoptera).

► Termites (Isoptera)

Termitology

The scientific study of termites.

► Termites (Isoptera)

Termitophile

An organism that spends at least part of its life cycle with termites.

Termopsidae

A family of termites (order Isoptera). They also are called primitive dampwood termites or rotten-wood termites.

► Termites

Territorial Pheromone

Pheromones that serve as markers, delineating territory used by an insect and causing others of the same species to avoid that space.

► Pheromones

Tertiary Period

A geologic period extending from about 65 to 2 million years ago. The beginning of the Cenozoic era.

► Geological Time

Tessaratomidae

A family of bugs (order Hemiptera, suborder Pentamorpha).

► Bugs

Test

The covering of scale insects (Hemiptera: various families). The test is a glandular secretion consisting of wax, polyphenols and proteins. It provides protection for the nymph and adult that secrete it, and then for the eggs which the female deposits within it.

Testicular Follicles

Tubules in the testes that form sperm.

► Testis

► Reproduction

Testis (pl., Testes)

An assemblage of testicular follicles, each of which produces sperm (spermatozoa). Each testis empties into a tube called the vas deferens, the seminal vesicles, and then into the ejaculatory duct. The seminal vesicles may be simply an extension of the vas deferens, or may be expanded for sperm storage. Associated with the ejaculatory duct is the accessory gland, which produces secretions that aid in sperm transfer. Most noteworthy of the secretions is the spermatophore, a sac containing sperm (Fig. 40).

► Reproduction

Tethinid Flies

Members of the family Tethinidae (order Diptera).

► Flies

Tethinidae

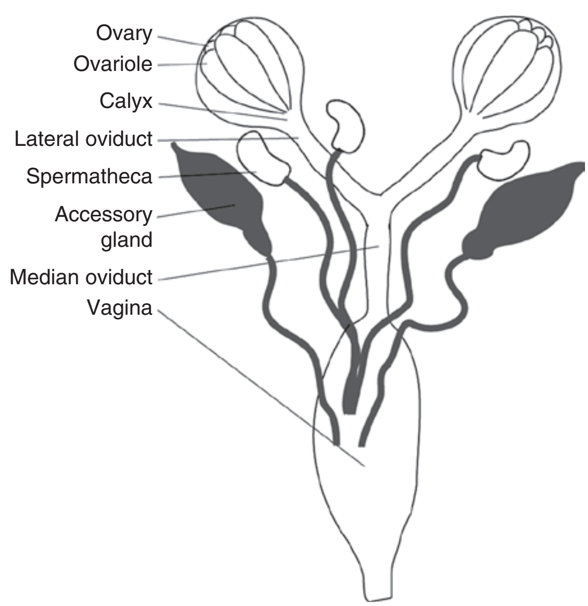
A family of flies (order Diptera). They commonly are known as tethinid flies.

► Flies

Tetracampidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees, and Sawflies



Testis (pl., Testes), Figure 40 **Diagram of a male reproductive system as found in *Tenebrio* (Coleoptera) (adapted from Chapman 1998, The insects: structure and function).**

Tetratomidae

A family of beetles (order Coleoptera). They commonly are known as polypore fungus beetles.

► Beetles

Tetrigidae

A family of grasshoppers (order Orthoptera). They commonly are known as pygmy grasshoppers or grouse locusts.

► Grasshoppers, Katydids and Crickets

Tettigarctidae

A family of bugs (order Hemiptera, suborder Cicadomorpha).

► Bugs

Tettigometridae

A family of bugs (order Hemiptera, suborder Fulgoromorpha). All members of the suborder are referred to as planthoppers

► Bugs

Tettigoniidae

A family of katydids (order Orthoptera). They commonly are known as longhorned grasshoppers.

► Grasshoppers, Katydids and Crickets

Texas Beetles

Members of the family Brachypsectridae (order Coleoptera).

►Beetles

Texas Cattle Fever

This ailment is caused by a tick-transmitted protozoan.

► Piroplasmosis

Texas Citrus Mite, *Eutetranychus banksi* McGregor (Acari: Tetranychidae)

These mites are citrus pests in North America.

Thanatosis

This behavior is also called death-feigning, a response to disturbance displayed by some insects that may help them escape predation. For example, when disturbed, beetles may release their hold on a plant, retract their legs, and drop to the ground. Likewise, chrysidid wasps may roll into a ball and drop. Thanatosis may be displayed in addition to or instead of other defensive reactions such as stridulation, dodging, flight or reflex bleeding. For example, *Crioceris asparagi* (Coleoptera: Chrysomelidae) displays severe thanatosis, dropping at even minor disturbance, whereas its sibling species *C. duodecimpunctata* displays only mild thanatosis but readily stridulates.

Thaumaleidae

A family of flies (order Diptera). They commonly are known as solitary midges.

► Flies

Thaumastellidae

A family of bugs (order Hemiptera, suborder Pentamorpha).

► Bugs

Thaumastocoridae

A family of bugs (order Hemiptera). They sometimes are called royal palm bugs.

► Bugs

Theileria

An important genus of protozoans causing disease in animals, and transmitted by ticks.

► Piroplasmosis

Theileriosis

Several related diseases caused by infection with *Theileria* protozoans, and transmitted by ticks.

► Piroplasmosis

Thelytokous Parthenogenesis

A type of parthenogenesis wherein females produce only diploid females from unfertilized eggs.

Theochodaeid Scarab Beetles

Members of the family Ochodaeidae (order Coleoptera).

► Beetles

Therevidae

A family of flies (order Diptera). They commonly are known as stiletto flies.

► Flies

Thermoregulation in Insects

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Temperature is a physical component of the environment that affects animals from the subcellular to the population level. Because cells are units of chemical reactions and chemical reactions are temperature dependent, animal activity is determined by temperature. Temperature has been shown to be an important influence on all aspects of insect life. Numerous studies have shown that temperature influences cellular activity by changing the efficiency of enzymes, changes the physiological responses of tissues such as nerves and muscles, alters the rate of development, determines when species emerge, limits the biogeography of species, and determines when a species can be active. There are two strategies for any animal to deal with temperature: they can be a thermoconformer or a thermoregulator.

A thermoconformer is an animal that permits its body temperature to fluctuate with, and is about equal to, environmental temperature. For many insects, being a thermoconformer is determined by the size or activity patterns of a species. For example, a very small insect will exchange heat with the environment so rapidly that its body temperature will always approximate ambient temperature, or a nocturnal insect with a low metabolism may not be able to elevate body temperature above ambient conditions. The major problem with being a thermoconformer is that enzymes must be able to work over a greater temperature range than the enzymes of a thermoregulator. This means that the enzymes are less efficient at any particular temperature in the thermoconformer. The benefit to being a thermoconformer is that an animal spends no time or metabolic energy attempting to regulate body temperature.

A thermoregulator is an animal that maintains body temperature within a limited range regardless of changes in ambient temperature. A thermoregulator has the benefit of keeping its enzymes and physiological systems within the temperature range where they operate most efficiently. The cost to a thermoregulator is the use of time or metabolic energy needed to maintain their body temperature within a specific temperature range. Thermoregulators can be classified as either ectotherms or endotherms based on the source of the energy used in the regulation of body temperature (the terms poikilotherm or cold-blooded and homeotherm or warm-blooded are no longer used due to ambiguities).

An ectotherm is an animal that uses energy from the environment to regulate body temperature. These animals generally are heliotherms, using the radiant energy of the sun to regulate body temperature, but there are also thigmotherms, animals that use the energy of the substrate to regulate body temperature. Ectothermy is a metabolically inexpensive form of thermoregulation. The major metabolic expense is the cost of transporting the animal from sun to shade. The problem with ectothermy is the animal is still dependent on the environment for a heat source and thus activity. This problem was solved by the evolution of endothermy.

An endotherm is an animal that produces metabolic heat specifically for thermoregulation. Endotherms have been identified in a wide variety of insects orders. The source of heat in endothermic insects is the flight musculature. Endothermic insects will increase heat generation through muscular activity to elevate body temperature to the range necessary for activity. The heating can occur without flight or wing movements but shivering can be observed in many night flying moths or bees at flowers on cool days prior to take-off. The body temperatures of endothermic insects have been recorded more than 35°C above ambient temperature. The use of metabolic energy for thermoregulation frees the endotherm from possible environmental constraints on activity.

Behavior

Thermoregulation can occur through behavioral and/or physiological mechanisms. The first option used by any organism to thermoregulate is behavior. Behavioral mechanisms are metabolically inexpensive and produce immediate results. Very simple forms of behavioral thermoregulation are changing body orientations and shuttling between the sun and shade. Changing body orientation to the sun is a common behavior that alters the heat exchange of an insect. When an insect has a low body temperature, it will sit in an exposed position to gain radiant heat from the sun. Often they will orient their body axis perpendicular to the sun to maximize radiant heating. Conversely, when an insect has an elevated body temperature, it will seek a shaded location to decrease the radiant gain and lose heat to the environment. Also, insects will orient their body parallel to the sun's rays when they have an elevated body temperature, which minimizes the exposed surface area and radiant heat uptake. One benefit an insect has in thermoregulating is its small size. The high surface to volume ratio means that heat exchanges quickly with the environment and it can take advantage of small microclimates within the habitat.

Microhabitat selection is another important behavioral mechanism of thermoregulation. For example, a desert insect can change the ambient temperature to which it is exposed by more than 30°C simply by selecting a particular microhabitat within the environment. Insects will also employ vertical migration as a means to optimize the ambient conditions in which they are found. Desert animals will move away from the ground as ground temperature (and the boundary layer above the earth) becomes warmer. Similarly, if it is cool and windy, insects will move toward the ground in an effort to find a warmer microclimate. Stilting is a similar behavior seen in some beetles and grasshoppers. When their body temperature is low, the insects will press their body against the ground to increase the rate of heat uptake by conduction and keep their body in the warm boundary layer next to the ground. When their body temperature becomes elevated, they will extend their legs, lifting their body as high as possible above the ground. These types of behavioral mechanisms are used by endotherms as well as ectotherms.

Physiology

Physiological mechanisms of thermoregulation can occur through endothermy, evaporative cooling, or thermal adaptation. Endothermic insects generally use the heat generated by the flight musculature to raise body temperature. The flight musculature is a good source of heat because it makes up a significant portion of body mass and it is a highly aerobic tissue. Electrical recordings from the muscles of moths and bees show that the moths shiver (simultaneously activating wing elevator and depressor muscles) to elevate heat production. As the body temperature of the insect increases, the activity of the wing elevator and wing depressor muscles become more out of phase and flight is then initiated. Overheating is prevented by varying the rate of heat production, through circulatory adaptations that increase heat loss, or through the cessation of activity. The functional significance of endothermy has been described for many insect species and represents the diversity of insect behavior. Endothermy permits such diverse behaviors as flight, foraging, acoustic activity, dung ball rolling, maintenance and defense of territories, the use of habitats unavailable to ectothermic species, predator avoidance, defense, brood incubation, and hive temperature regulation.

Evaporative cooling represents a significant avenue of potential heat loss for animals. The problem with using evaporative cooling is that there must be a water source for the animal to replace water used for cooling. The small size of insects means they have a relatively small water reservoir in their bodies, but several evaporative cooling mechanisms have evolved in insects. Evaporative cooling by extruding a bubble from the mouth has been described in moths and bees. A bubble of saliva is extended, heat is lost as water evaporates, the bubble is withdrawn back into the mouth to pick up more heat, and the process is repeated until the animal is sufficiently cool. This system is very good at cooling the head but is limited in its ability to cool the entire body. Locusts evaporatively cool through an abdominal pumping mechanism while some caterpillars will spread rectal fluid on their ventral surface to cool through evaporation.

Another group of insects in which evaporative cooling has been studied extensively is cicadas. Cicadas can avoid the potential water balance problems because they feed on xylem fluid. Thus, the desert cicadas that evaporatively cool have access to a water source that other animals cannot use. As a result, desert species like *Diceroprocta apache* (Davis) and *Okanagodes gracilis* Davis can continue their activity while other animals in the environment have sought shelter from the extreme desert heat. In addition, these animals can survive water loss of over 40% of their total body mass. Water is evaporated through pores in the cuticle of the thorax and abdomen of cicadas. The evaporative response of cicadas appears to be energy dependent, as toxins can eliminate the response and the response can change dramatically by altering ambient temperature. Evaporative cooling responses are not universal in insects and appear to be restricted to desert species or species whose metabolism may cause dangerous increases in body temperature.

A final physiological mechanism of thermoregulation is thermal adaptation. Insects will adapt their enzymes to work best under particular thermal conditions. The enzymes will show optimal activity temperatures that are related to their environment. In addition, the membrane composition of insects will change dependent upon where the insect lives and even with the daily fluctuations in ambient temperature. These changes in membrane composition are necessary to maintain the fluidity of the membrane and, thus, the integrity of the cell.

Finally, there have been several morphological adaptations that assist insects in thermoregulating. Light coloration in hot environments or dark coloration in cool environments changes the rate of heating and the maximum temperature that can be attained by an insect which increases the time a species can be active in their particular environment. In fact, some dragonflies undergo a temperature dependent color change to alter the amount of radiation uptake. Animals from warmer climates may also reflect more infrared radiation. There are desert beetles that have highly convex elytra forming a large subelytral space that acts to decrease heat transfer to the body while the animal is active in the sun. Some desert tenebrionid beetles have legs that are much longer than their forest relatives. These long legs elevate the animal above the boundary layer and significantly increase the time of activity for the species. Many endothermic and ectothermic species that live in cool habitats are covered with pile. The pile acts as insulation to help conserve heat within the body.

References

Heinrich B (ed) (1981) Insect thermoregulation. Wiley, New York, 328 pp

Heinrich B (1993) The hot-blooded insects: strategies and mechanisms of thermoregulation. Harvard University Press, Cambridge, MA, 601 pp

May ML (1979) Insect thermoregulation. Annu Rev Entomol 24:313–349

May ML (1985) Thermoregulation. In: Kerkut GA, Gilbert LI (eds) Comprehensive insect physiology, biochemistry, and pharmacology. New York, Pergamon, pp 507–552

Sanborn AF (1998) Thermal biology of cicadas (Homoptera: Cicadoidea). Trends Entomol 1:89–104

Sanborn AF, Villet MH, Phillips PK (2004) Endothermy in African platypleurine cicadas: the influence of body size and habitat (Hemiptera: Cicadidae: *Platypleura* spp.). Physiol Biochem Zool 77:816–823

Thermotaxis

Taxis response with respect to temperature.

Thick-Headed Flies

Members of the family Conopidae (order Diptera).

► Flies

Third Generation Insecticide

Organic insecticides derived from knowledge of insect's hormones. By mimicking hormones, the insecticides provide great selectivity, and are less disruptive to nontarget organisms.

Thomas, Cyrus

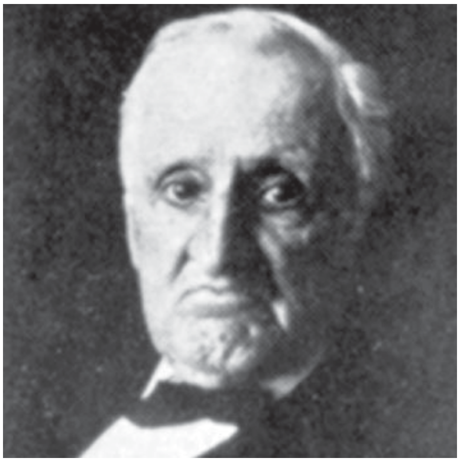
Cyrus Thomas was born at Kingsport, Tennessee, USA, on July 27, 1825. A lawyer and Lutheran minister by training, he became one of America's foremost systematists and economic entomologists. Thomas had little formal education and did not attend college; nevertheless, he learned science, mathematics, and practiced law. He sought an area of science where he could be recognized, and which could be mastered with little expense and the materials at hand; entomology met those needs. While still practicing law, he began to publish entomology papers. Thomas served with the Hayden Geological Survey of the territories of the West and Southwest from 1869 to 1874. From 1874 to 1876 he taught natural history at the University of Illinois, and was state entomologist for Illinois, publishing six annual reports. Thomas served on the United States Entomological Commission for 5 years. One of his most significant achievements was to author a comprehensive treatment of Aphididae, included in the "Third annual report of the state entomologist of Illinois on noxious and beneficial insects," published in 1879. He is also remembered for authorship of the "Synopsis of the Acrididae of North America," published in 1873. In his taxonomic work he named chiefly aphids and grasshoppers. Despite a successful career in entomology, he devoted the last 25 years of his life to archaeological and ethnological studies, and became an authority on the Cherokee, Shawnee, and Maya people. Thomas died at Washington, DC, on June 27, 1910 (Fig. 41).

References

Anonymous (1910) Obituary, Cyrus Thomas, Ph.D. Entomol News 21:387–388

Essig EO (1931) A history of entomology. Macmillan, New York, 1029 pp

Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp



Thomas, Cyrus, Figure 41 **Cyrus Thomas.**

Thomson, Carl Gustav

Carl Gustav Thomson was born at Skaane, Sweden, on October 13, 1824. He became a student at Lund in 1843, and attained his Ph.D. in 1850. Beginning in 1850 he worked in various capacities at the Lund Zoological Museum. Thomson tackled difficult taxonomic problems successfully. He studied principally Hemiptera, Hymenoptera, and Coleoptera, but also Diptera. A prolific author, he published nearly 9,000 pages during his lifetime, though his work on Diptera is not highly regarded. He died on September 20, 1899, in Lund, Sweden.

References

Papavero N (1971, 1973) Essays on the history of Neotropical Dipterology with special reference to collectors (1750–1905). Museu de Zoologia, Universidade de São Paulo

Herman LH (2001) Thomson, Carl Gustav. Bull Am Mus Nat Hist 265:150–151

Thoracic Plate

In caterpillars, the shield-like dorsal covering or plate on the body segment immediately behind the head, usually dark in color. Also known as the cervical shield.

Thorax

The second or middle of the three major body regions of insects, and the section bearing wings (if present) and jointed (true) legs.

► Thorax of Hexapods

Thorax of Hexapods

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The arthropods, and particularly the insects, present a basic model of body organization constructed on a metameric base, about which is produced the process of tagmosis. This process consists of the grouping of a variable number of segments to form a suprasegmentary unit called the tagma.

Tagmosis is probably produced to establish a more operative model in the development of certain functions important to the life of those animals. In this case, in the hexapods, the thoracic tagmata have come about by the grouping of three segments, called the prothorax, mesothorax and metathorax, which have developed principally for locomotion.

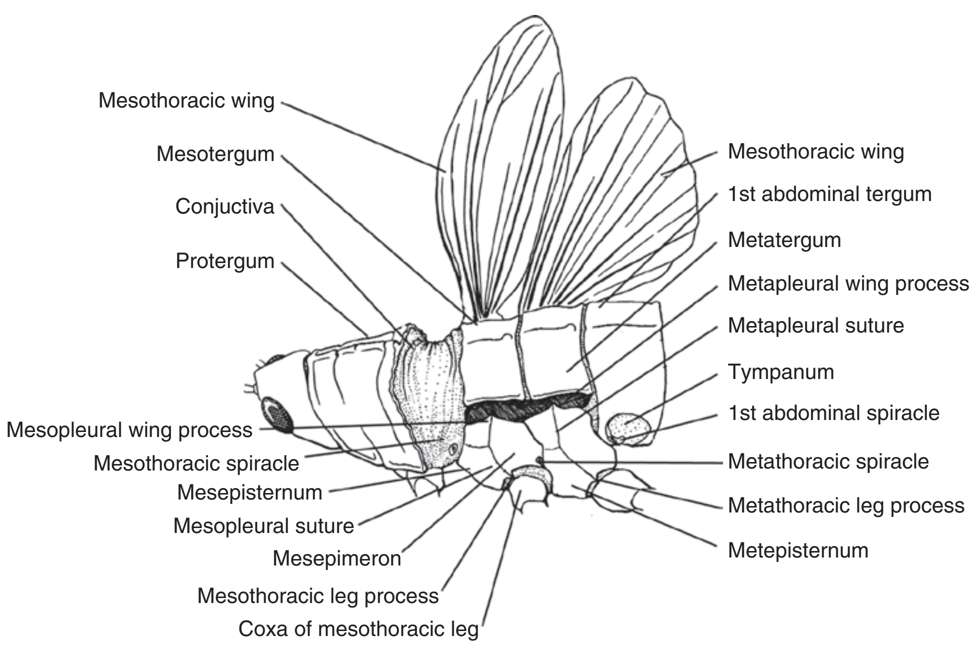
The formation of the thorax by three segments was pointed out in the nineteenth century by Adouin and later recognized by the majority of authorities, except by some like Verhoeff, who at the beginning of the twentieth century considered that the intersegmentary regions were authentic segments, whereby five segments would form the thorax. This theory was rapidly rejected, as it was demonstrated through comparative studies of morphology and embryology that the hexapod thorax consists of only three segments.

Except in the apodous larvae of certain orders, each thoracic segment carries a pair of legs, and in addition the winged forms present a pair of wings on the mesothorax and on the metathorax, with both segments constituting a functional "subtagma" called the pterothorax. The presence of legs and wings on the thorax demonstrates that it is a tagma specialized for locomotory function, developed and controlled by muscles and ganglia situated in the thorax itself. It is probable that this locomotory function originated the differentiation of the thoracic tagma from the other two that form the body of the hexapods: the head and the abdomen (Figs. 42–47). The fact that the thorax is found basically formed in the most primitive hexapod groups and that it appears perfectly individualized in the first stages of ontogenetic development makes one think that the differentiation of this tagma ought to have occurred in early periods of insect evolution. As much from the structural as functional point of view, the hexapod thorax is the most specialized and centralized tagma if we compare it with analogous tagmata of other arthropods.

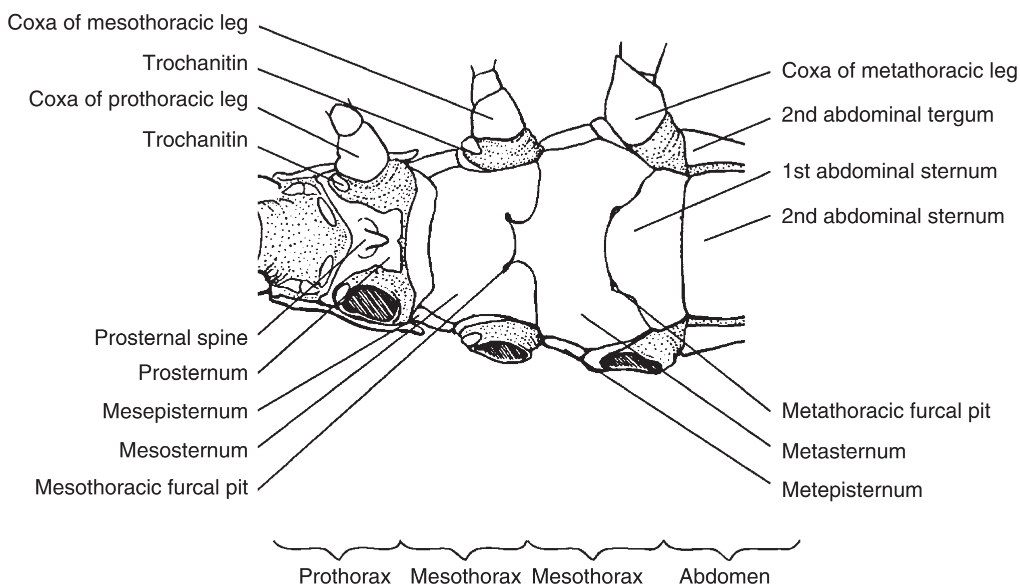
Before beginning a description of the thorax itself, it is necessary to emphasize the existence of an anterior region of the body called the neck or cervical region (Fig. 42), which is of mixed origin: labial and prothoracic. The morphological, embryological, musculature and neurological data demonstrate that the neck results from the fusion of the dorsal and ventral parts of the labial and prothoracic segments, respectively. The cervical sclerites can be found in the dorsal position (dorsal cervical or dorso-cervical sclerites), lateral (lateral cervical or latero-cervical sclerites) and ventral (ventral cervical or ventro-cervical sclerites) (Figs. 42 and 43). The lateral cervical sclerites can originate from the anterior part of the propleura [some Thysanura (Zygentoma) and the majority of holometabolous insects] or from the presternal region (hemimetabolous insects and Coleoptera). The dorsal cervical sclerites are considered structures of secondary formation and are united anteriorly to the dorsal posterior margin of the occiput. The same occurs with the ventral ones.

Modern studies of the hexapod thorax began with the decade of the 1940s, particularly such authors such as Snodgrass, Weber, Barlet, Carpentier, Francois, La Greca, and Matsuda. As in each arthropod segment, each hexapod segment presents a dorsal region called the notum or tergum, another ventral region named the sternum, and between the two, a zone that constitutes the pleuron.

The tergal region presents variations in the number of sclerites and sutures, whose interpretation in Pterygota should be analyzed with a previous



Thorax of Hexapods, Figure 42 **Lateral view of a grasshopper head and thorax (Orthoptera: Romaleidae).**



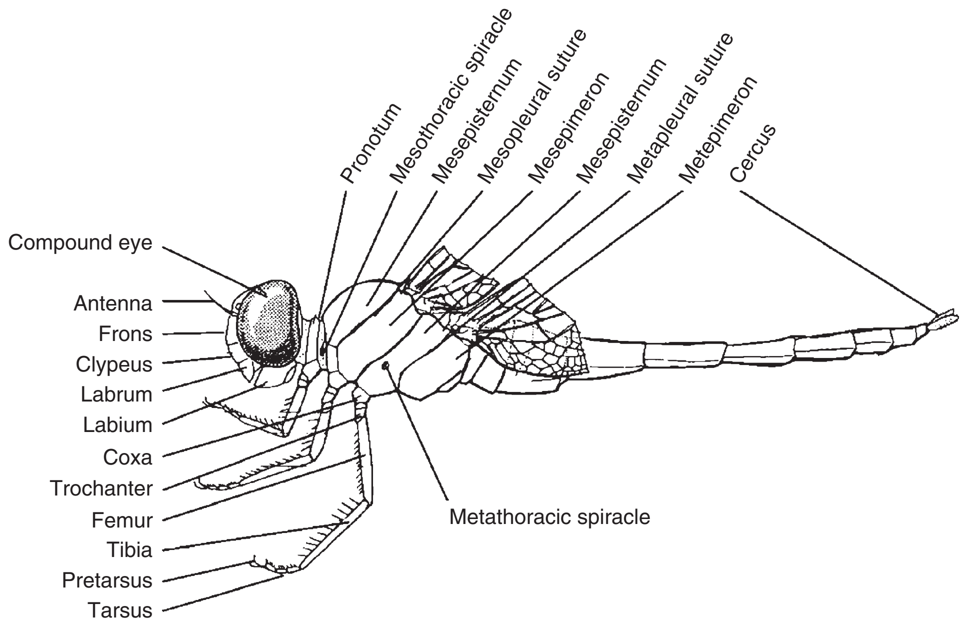
Thorax of Hexapods, Figure 43 **Ventral view of a grasshopper thorax (Orthoptera: Romaleidae).**

understanding of what occurs in the Apterygota. The Protura display a more elaborate tergum whose homologization with the rest of the hexapods is difficult. In Diplura, Archaeognatha and primitive Thysanura, an anterior zone exists, which, according to Matsuda, is named the pseudoprescutum. It is separated from the rest of the tergum by a pseudoprescutoscutal suture that produces toward the interior a suture named the pseudophragma. The study of *Nicoletia* is interesting in that it explains the passage of a primitive tergum to another evolved in the Pterygota by the loss of the pseudophragma, which would have no functional significance on developing a phragma with the incorporation of an acrotergite; the pseudoprescutoscutal suture would be transformed into the prescutoscutal suture and the pseudoprescutum into the prescutum. In the case of *Lepisma*, a narrow antenotum (delimited by an antecosta), a prescutum and a scutum (separated by a prescutoscutal suture) and a postnotum united laterally to the pleuron are differentiated; these sclerites are already homologous to those of the Pterygota.

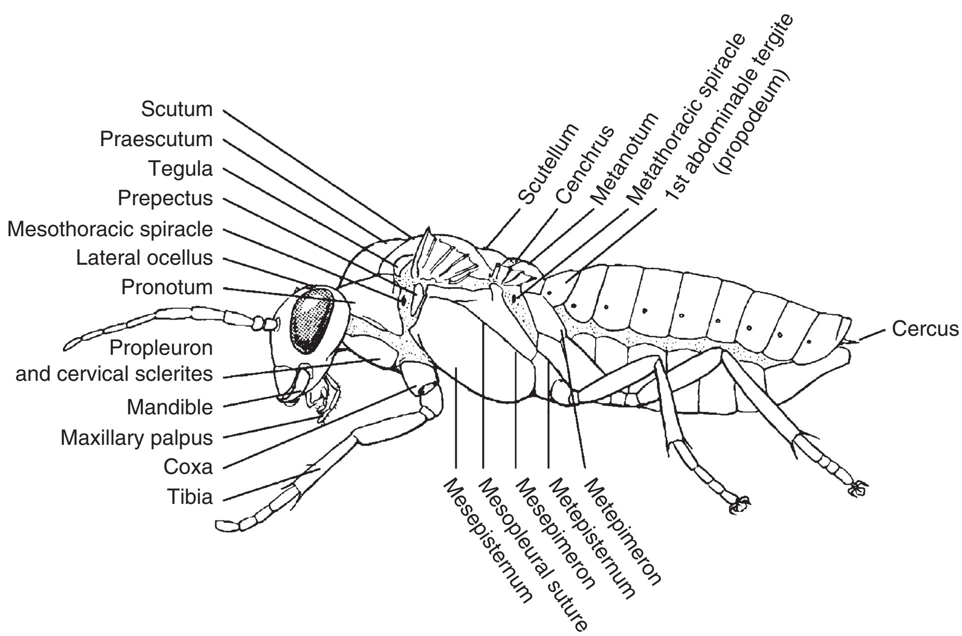
The tergal region of the pterothorax of Pterygota (meso and metathorax of winged insects), presents sclerites delimited by two types of sutures: some homologous to those of the Apterygota and other, new ones that appear by the wings. The wings, in addition, produce modifications in the zone of insertion that fundamentally affect the lateral margins of the tergum (Fig. 44).

Among the sutures homologous to those of the Apterygota are the antecosta, which delimited anteriorly a zone that corresponds to the acrotergite and gives rise to a phragma toward the interior. The prescutoscutal suture is situated behind the antecosta, delimiting a sclerite named the prescutum, whose lateral zones form the prealar arms.

Among the sutures not homologous to those of the "Apterygota" stands out the scutoscutellar suture, which has a sinuous form and reaches the axillary ligament. This suture separates two sclerites, an anterior (scutum) from another posterior (scutellum). The proper parapsidal lines and the lateral parapsidal lines are differentiated as intrascutal formations; both arising from the prescutoscutal suture, the first in a more or less median position and the second lateral. Two marginal lines exist within the scutum, one that delimits the anterolateral angle of the scutum, forming the suralare, a sclerite that includes the anterior and antemedian notal wing processes. The other marginal

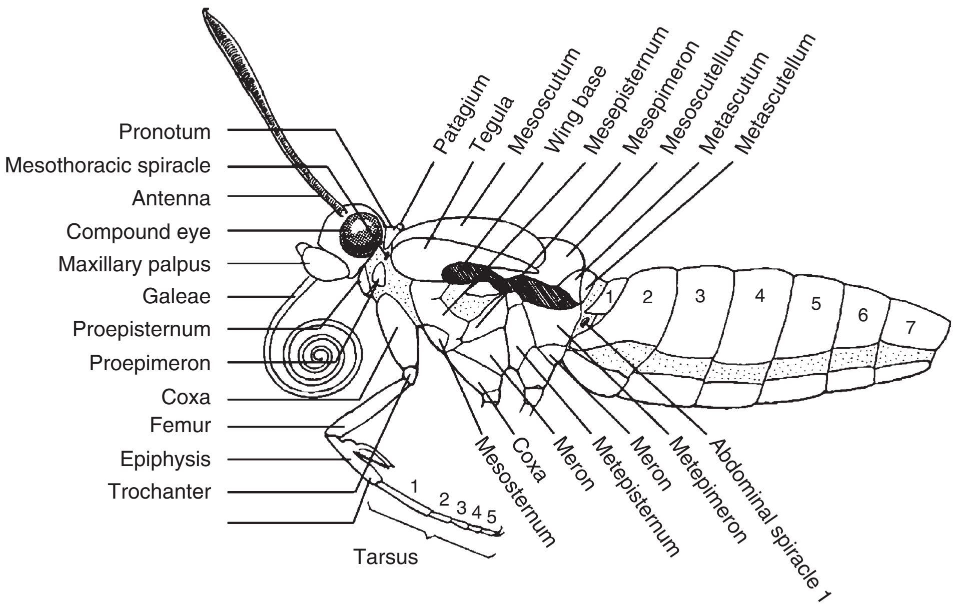


Thorax of Hexapods, Figure 44 **Lateral view of a dragonfly (Odonata: Libellulidae).**

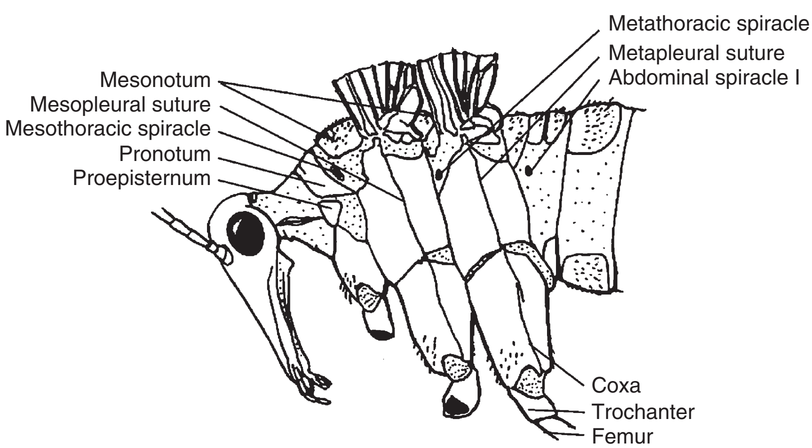


Thorax of Hexapods, Figure 45 **Lateral view of a sawfly (Hymenoptera: Tenthredinidae).**

suture delimits the posterolateral angle of the scutum, which includes the posterior notal wing process. In primitive forms of certain orders a tergal fissure is differentiated, which transversally unites the sides of the scutum at the level of the anterior or antemedian notal wing process. The recurrent scutoscutellar suture originates from or near the center of the posterior margin of the scutellum, diverging toward the anterior part. The last sclerite is the postnotum.



Thorax of Hexapods, Figure 46 **Lateral view of a moth (Lepidoptera: Sphingidae).**



Thorax of Hexapods, Figure 47 **Lateral view of a scorpion fly (Mecoptera: Panorpidae).**

The presence of the wings brings with it a series of modifications in the lateral margins of the tergum, differentiating a series of processes, some of which have been mentioned previously. Thus, the most anterior process is called the prealar arm or branch, which in the majority of orders is a prolongation of the prescutum, although in others like the Hymenoptera it does not exist. Posteriorly, five points of articulation with the wings are differentiated, which are called notal wing processes. From the anterior part to the posterior, they are the anterior and antemedian (already mentioned), median, postmedian, and posterior (also mentioned). In the case where the five processes are evident, the first four are joined with the first axillary sclerite and the last with the third axillary sclerite.

The notal region of the thorax can present different modifications. Among the most customary and conspicuous is the prolongation of the mesothoracic scutellum, which in certain cases projects toward the back, on top of the metanotum (for example, Hemiptera: Scutelleridae), and in other cases adapts to its conformation.

The sternum, as already mentioned, corresponds to the ventral zone. In generalized Diplura, Archaeognatha and some Thysanura, five parts or apotomes are distinguished, which from the anterior to the posterior part are: the presternum, the basisternum, the furcasternum, the spinasternum and the poststernum. In principle, the question is posed of whether the poststernum, instead of representing the final portion of the sternum, constitutes the more anterior of the following sternum that would have been incorporated. In any case, the different apotomes of the sternum of Aptergygota have a relatively well-defined position, with the poststernum being a posterior segmentary structure, although it does not appear in Ptergygota.

The association of the mentioned sclerites to the sternum, and the reductions that occur during evolution toward advanced hexapod groups, are justified through the study of endosternal formations. In the Apterygota, a non-cuticular endoskeletal complex is distinguished, in addition to spinasternal processes in Diplura and pleural apodemes in Archaeognatha. Cuticular formations are well defined in Ptergygota, corresponding to the furca and the spina.

As a consequence of losses, modifications and fusions of certain zones, the original division of the sternum in Pterygota has suffered changes that do not permit delimiting a clear position from its apotomes. Thus, the lack of a presterno-basisternal suture makes the differentiation of a presternum very difficult. The posternum is lost in the Pterygota, with this loss affecting the two anterior apotomes (spinasternum and furcasternum). The reduction affects, in the first place, the most posterior apotome, which is the spinasternum, being reduced in certain cases to the spine, as occurs in the mesosternum of the Orthoptera. The spine is also lost in more evolved groups like Coleoptera, Diptera and Hymenoptera, causing reductions to the furcasternum, which can reach the point of disappearing. The anterior part of the metasternum then occupies its place, shifting toward the front and situating itself close to the furcal bases. When this occurs, obliteration is produced on the ventral border between the meso and metathorax. This obliteration, which exists in different levels of development in advanced insects, appears to directly affect the formation of a functional subtagma, the pterothorax, to which reference has already been made. In this process, a tendency for the reduction of the anterior and posterior parts of the sternum can be observed, always leaving a well-developed apotome, the basisternum.

All the studies carried out on the origin of the pleuron demonstrate that this zone of the thorax, situated between the tergum (or notum) and the sternum in Archeognatha, Thysanura (Zygentoma) and Pterygota, consists of a ventral subcoxal area and another dorsal or pleural area, which have become indistinguishable because of the sclerotization. In this sense, an evolutionary sequence can be established from the pleuron of Archaeognatha to that of the pterothorax, considering the increase in sclerotization tied to the development of the wings. In primitive Pterygota like Blattodea, the sclerotization is not very pronounced, and the sclerites that surround the base of the coxa have not been obliterated, so clear homologies can be established with Archaeognatha.

If one considers the pleural formations existing in the segments of the pterothorax, there are distinguished, in the first place, a pleural suture and its corresponding internal costa. In principle, this suture ought to present a vertical path as is observed in certain orders like Neuroptera, with a tendency to present an oblique path toward the front. The most dorsal part constitutes the pleural wing process. This suture has been obliterated in some orders of advanced hemimetabolous insects like Hemiptera (Heteroptera) while conserved in secondarily apterous orders like Siphunculata, Mallophaga and Siphonaptera, and in orders like Psocoptera. Internally, it is distinguished by way of a pleural branch that is united to the furca through a tendinous structure or a muscle. This pleural suture divides the pleuron into two regions: an anterior one (episternal region or episternum) and a posterior one (epimeral region or epimeron).

Another important suture is the paracoxal, which divides the pleuron into two rings, an external anapleural ring, or anapleurite, and an internal ketapleural ring, or katapleurite. Its presence in Archaoegnatha indicates that it is a primitive suture.

Considering the two pleural sutures mentioned up to now, the pleuron remains divided into four regions: anepisternum, katepisternum, anepimeron and katepimeron. In species of certain orders like Neuroptera, Hemiptera and Hymenoptera, another suture exists, named the transepimeral, which is a continuation of the paracoxal suture in the episternal part. The anepisternum remains divided by the anapleural suture in one part dorsally (the anepisternum proper), and another part ventrally (the preepisternum). In species of some orders like Psocoptera, the anapleural suture is situated more ventrally, with another suture being differentiated in those cases named the transepimeral suture, which divides the anepisternum proper into two portions (dorsal and ventral). In primitive orders, beginning from the anepisternum a small sclerite called the basalare is differentiated, situated just in front of the pleural wing process. When the area that surrounds the basalare is membranous, it can extend posteriorly, originating a basalar incision that in some orders like Dermaptera forms the episternal suture. Behind the pleural wing process the subalar sclerite is differentiated, which in reality is a sclerite differentiated from the tergum.

Three bridges exist. The prealar bridge or prealare, which has already been mentioned in the section dedicated to the tergum. The precoxal bridge or precoxale, which is formed by the preepisternum uniting with the basisternum and, are separated by the pleurosternal suture. This suture is obvious in Apterygota and in the majority of hemimetabolous Pterygota but does not exist in certain holometabolous insects, in those in which the preepisternum and basisternum are fused. This fusion is not produced in other holometabolous insects, since the preepisternum extends forward, forming the lateral cervical sclerite. The third bridge is the postalar bridge or postalare, a structure similar to the prealare, but formed by the connection between the dorsal margin of the anepimeron and the lateral extension of the postnotum.

The trochantin is a sclerite differentiated from the katepisternum, which can present four points of articulation in Thysanura, one dorsal with the katapleuron and three ventral with the coxa. In Pterygota, only the anterior coxal-trocantinal articulation is conserved, with various modifications of the trochantin being observed. It can be isolated (prothorax of Psocoptera), partially fused to the katepisternum, conserving the anterior coxal-trocantinal articulation (eutrochantin), and it can even be undifferentiated due to the strong sclerotization of the katepisternum, as occurs in advanced orders.

In the more primitive groups, in the posterior zone of the katepisternum the sternopleurite is found, which appears to correspond, according to Matsuda (1970) to a part of the ventral zone of the katapleuron. This ventral pleurite in holometabolous insects is not appreciated, and it is possible that it has been transformed in the ventral articulation process of the coxa.

It can be concluded that the evolution of the hexapod thorax has been a continual process, between the thorax of the groups of Apterygota and that of the Pterygota, a process based on the loss and modifications of different structural elements.

► Wings of Insects

References

Bitsch J (1994) The morphological groundplan of Hexapoda: critical review of recent concepts. Ann Soc Entomol Fr 30:103–129

Kristensen NP (1998) The groundplan and basal diversification of hexapods. In: Fortney RA, Thomas RH (eds) Arthropod relationships. Systematics Association, Special Volume Series 55. Chapman and Hall, London, 281–293 pp

Manton SM (1977) The arthropoda. Habits, functional morphology and evolution. Clarendon, Oxford

Matsuda R (1970) Morphology and evolution of the insect thorax. Mem Entomol Soc Can 76:1–431

Snodgrass RE (1952) A textbook of arthropod anatomy. Comstock, Ithaca, New York

Thripidae

A family of thrips (order Thysanoptera). They commonly are known as common thrips.

► Thrips

Thrips-Parasitic Nematodes

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Several species of nematodes belonging to the genus *Thripinema* (=*Howardula*) (Tylenchida: Allantonematidae) are known to naturally parasitize thrips (Thysanoptera).

Taxonomy, Host Range and Distribution

The genus *Thripinema* was erected by Siddiqi in 1986 during a taxonomic revision of the species. To date, there are five described species of *Thripinema*: *T. reniraoi*, *T. aptini*, *T. nicklewoodi*, *T. khrustalevi* and *T. fuscum*. Together these nematodes have been recovered from twelve species among eight genera of thrips: *Thrips physapus* L., *T. trehernei* Prisner, *T. physopus* L., *Aptinothrips rufus* Gmelin, *Frankliniella vaccinii* Morgan, *F. occidentalis* Pergade, *F. fusca* Hinds, *Taeniothrips vaccinophilus*, *Stenothrips graminium*, *Catinathrips vaccinophilus*, *Heliothrips* sp., *Megaluriothrips* sp. The biogeographical range of thrips parasitic nematodes is known to include the UK, Germany, USA, Canada, Russia and India. However, the extent of this distribution probably reflects where surveys have been made. Given *Thripinema* spp. hosts include introduced agricultural pest species found worldwide, thrips-parasitic nematodes are probably widely distributed.

Biology and Life Cycle

Unlike soil-dwelling nematodes of the family Rhabditidae, *Thripinema* spp. are not mutually associated with pathogenic bacteria and do not appear to kill their host. Rather, *Thripinema* spp. have evolved a parasitic lifestyle and develop through a single heterosexual generation in the live host. Although infected thrips show no obvious physical signs of the internal parasite, a consequence of infection is that embryos do not develop and adult female thrips are effectively sterile. The cause of host sterility is unknown, but nematodes may deprive the host of the protein required for oogenesis or secrete a toxin, which damages the reproductive organs. Male thrips are similarly parasitized, although the effect of infection on male fertility is unknown. During the infection stage, parasitic female nematodes penetrate a thrips host through intersegmental membranes. Following infection, the female nematode swells to a sac-like organism in which her reproductive organs become the only visible structure. Nematode eggs are laid into the host hemocoel. Upon hatching, the resulting vermiform juveniles feed on fluids within the thrips' abdominal cavity. When mature, both male and female nematode progeny penetrate into the lumen of the hosts' gut, and are continually released for the lifetime of infective thrips via the anus in the frass or via the ovipositor. Relatively little is known about the biology of *Thripinema* spp. following its emergence from the host. However, an intriguing aspect of the life cycle of the free-living stage is that they appear to attack their hosts in the above-ground parts of the plant. While all free-living nematodes require high humidity, *Thripinema* spp. appears to exploit the moist microclimate found within a leaf gall, flower perianth or developing foliage terminal. Since mature thrips nematodes exit the host via the anus or ovipositor, these free-living forms naturally accumulate in and around thrips foraging sites where defecation and oviposition are pronounced and where susceptible hosts may be found. Fertilization of parasitic female nematodes is thought to occur outside the host despite the fact that survival of this "free-living" stage may only be a few hours; thus the cycle is complete.

Thripinema spp. are not currently mass produced commercially. However, the ability of these nematodes to attack thrips in their preferred feeding sites, areas that are often impenetrable to insecticides and natural enemies, have led several investigators to speculate that thrips parasitic nematodes have potential for thrips management in agriculture.

► Thrips (Thysanoptera)
► Nematode Parasites of Insects

Reference

Loomans AJM, Murai T, Greene ID (1997) Interactions with hymenopterous parasitoids and parasitic nematodes. In: Lewis T (ed) Thrips as crop pests. CAB International, Wallingford, United Kingdom, 355–397 pp

Thrips (Thysanoptera)

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The Thysanoptera, thrips, are a diverse insect order with worldwide distribution (Table 11). There are approximately 5,800 species described from nine families. The order is divided into two distinct suborders: Tubulifera and Terebrantia. These two suborders can be distinguished by the shape of the last abdominal segment of the adult stage which is short and pointed in the Terebrantia, or long and tubular in the Tubulifera. Nearly all described species are less than 5 mm in length, and can be yellow, green, black, or red colored. The name Thysanoptera, derived from the Greek words, "thysanos" meaning fringe and "ptera" meaning wings, refers to the two pairs of slender wings which have few or no veins and bear a dense fringe of long hairs (Figs. 48 and 49). These hairs allow for greater wing area and increased flight efficiency. Thrips are thought to be closely related to Hemiptera and Psocoptera.

Order: Thysanoptera
- Suborder: Tubilifera
  - Family: Phlaeothripidae
- Suborder: Terebrantia
  - Family: Aeolothripidae
  - Family: Merothripidae
  - Family: Heterothripidae
  - Family: Thripidae
  - Family: Melanthripidae
  - Family: Uzelothripidae
  - Family: Adeheterothripidae
  - Family: Fauriellidae

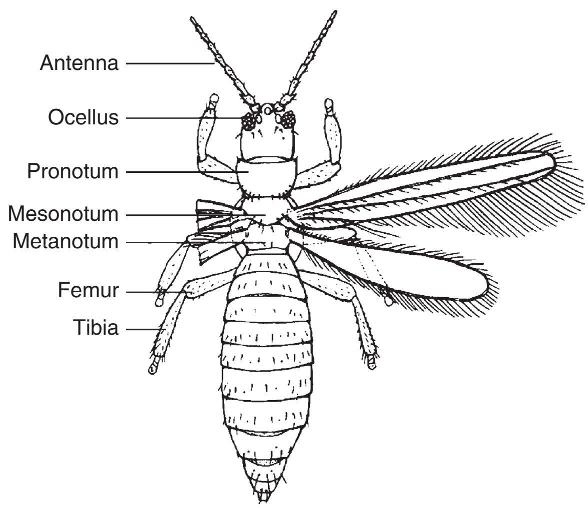
Thrips are holometabolous insects with complete metamorphosis. Development includes the egg, 2 larval instars, 2–3 pupal stages and the adult. The pupal stages do not feed but are capable of limited movement. Females of terebrantia have a curved ovipositor which is used to insert eggs into

Thrips (Thysanoptera), Table 11 Some economically important thrips and their distribution

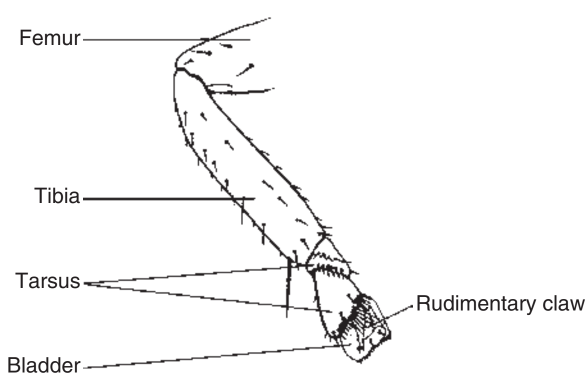
Common and species name	Present geographic distribution	Native range
Western flower thrips *Frankliniella occidentalis* (Pergande)	World-wide; Mediterranean climates, greenhouses in coolerclimates	Central California
Tobacco thrips *Frankliniella fusca* (Hinds)	North America, Mexico, and Puerto Rico	North America, Mexico, and Puerto Rico
Flower thrips *Frankliniella tritici* (Fitch)	Eastern temperate North America and Mexico	Eastern temperate North America and Mexico
Melon thrips *Thrips palmi* Karney	Tropics, southern Florida	Southeast Asia
Onion thrips *Thrips tabaci* (Lindeman)	World-wide	Mediterranean climates

Thrips (Thysanoptera), Table 11 Some economically important thrips and their distribution (Continued)

Common and species name	Present geographic distribution	Native range
Cotton bud thrips *Frankliniella schultzei* (Trybom)	World-wide	Africa
Florida flower thrips *Frankliniella bispinosa* (Morgan)	Southeastern U.S.	Southeastern U.S.
Yellow tea thrips or chillie thrips *Scirtothrips dorsalis* Hood	Southeast Asia, India, Africa, Australia	Southeast Asia
Thrips setosus Moulton No common name	Japan	Japan
Frankliniella intonsa (Trybom) No common name	Europe, Russia, Britain, Spain, Mongolia, Japan, British Columbia, USA (Washington state).	Europe, Russia, Britain, Spain, Mongolia, Japan,



Thrips (Thysanoptera), Figure 48 Diagram of a thrips, showing fringed wings.

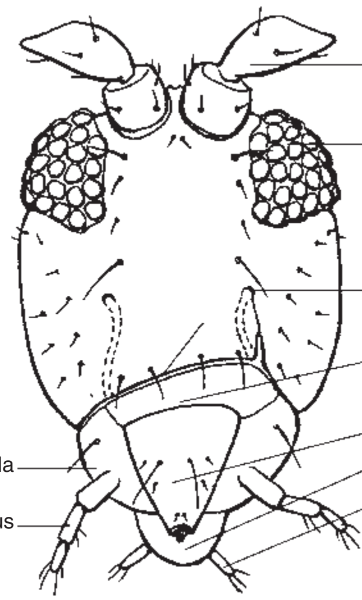


Thrips (Thysanoptera), Figure 49 Leg of a thrips; note that claws are not apparent.

plant tissue. The antenna are short with 6–10 segments. Thrips have asymmetrical sucking mouthparts, possessing only the left mandible (Fig. 50). Thrips are weak flyers and short directed flights are called thripping. Longer range dispersal is dependent on wind currents. Within the same species, populations may have individuals with reduced wings (brachypterous) or no wings (apterous) depending on environmental conditions such as density, food quality, and season.

Thrips are important members of the ecosystem as both herbivores and predators. Many species live in leaf litter or dead wood and feed nearly exclusively on fungus and will often supplement their diet with plant pollen. Other thrips species are gall formers and display primitive eusocial behavior. Predatory thrips are often beneficial species in agronomic situations and can help regulate populations of mites and other small insect pests including other thrips. Thrips are often associated with disturbed growth areas where large numbers can occur quickly on new plant growth.

The vast majority of the described species of thrips are herbivorous, with several being destructive pests of grain crops, fruits, vegetables and ornamentals. Certain species are important pests of plants grown in greenhouses. Feeding activities can result in plant deformities, scarring, loss



Thrips (Thysanoptera), Figure 50 Head of a thrips; note lack of symmetry due to absence of the right mandible.

of yield, and in some cases, transmission of plant pathogens. Plant-feeding thrips pierce and suck juices from the outer layer of cells, causing stippling, or small scars, on leaves, flowers and fruit. This feeding damage may result in stunting of the plant, premature leaf drop and aborted fruit. Flowers that have been damaged by thrips feeding may be deformed and fail to open properly. As many as 90 species of thrips are of economic importance, including nine species capable of vectoring plant viruses in the genus *Tospovirus*. These viruses are the most important disease of agronomic crops in many regions of the world today.

References

Lewis T (1998) Thrips as crop pests. Oxford University Press, Oxford

Moritz G, Mound L (2001) Thrips ID: pest thrips of the world. Interactive CD. ACIAR, CSIRO, Collingwood, VIC, Australia

Stannard LJ (1968) The thrips, or Thysanoptera of Illinois. Illinois Natural History Survey, Urbana, IL

Throscidae

A family of beetles (order Coleoptera). They commonly are known as false metallic wood-boring beetles.

► Beetles

Thunberg, Carl Peter

Carl Thunberg was born at Joenkoepping, Province of Smaaland, Sweden, on November 11, 1743. He studied at the University of Uppsala under Linnaeus, and served as a medical doctor in South Africa for several years before returning to Sweden. While in South Africa, he also visited the Dutch colonies of the Far East, and was able to investigate the fauna of Ceylon, Java and Japan. He replaced Carl Linnaeus, Jr., at the University of Uppsala, and transformed the Royal Gardens into botanical gardens to honor Linnaeus. Though known principally as a botanist, Thunberg published numerous entomological papers, including some descriptions. A prolific publisher, he authored over 150 scientific publications. He died August 8, 1828.

Reference

Papavero N (1971, 1973) Essays on the history of Neotropical Dipterology with special reference to collectors (1750–1905). Museu de Zoologia, Universidade de São Paulo

Thuringiensin

A soluble, heat-stable beta-exotoxin produced by *Bacillus thuringiensis* during the vegetative growth stage of the bacteria. It has several properties, including insecticidal, feeding deterrent, and teratological effects.

► *Bacillus thuringiensis*

Thyatiridae

A family of moths (order Lepidoptera). They commonly are known as false owlet moths.

► False Owlet Moths
► Butterflies and Moths

Thyreocoridae

A family of bugs (order Hemiptera). They sometimes are called negro bugs.

► Bugs

Thyretidae

A family of moths (order Lepidoptera) also known as African maiden moths.

► African Maiden Moths
► Butterflies and Moths

Thyrididae

A family of moths (order Lepidoptera). They commonly are known as picture-winged leaf moths.

► Picture-Winged Leaf Moths
► Butterflies and Moths

Thysanoptera

An order of insects commonly are known as thrips.

► Thrips

Thysanura

An apterygote order of insects. They commonly are known as silverfish. This order is also known as Zygentoma.

► Silverfish

Thysanuriform Larva

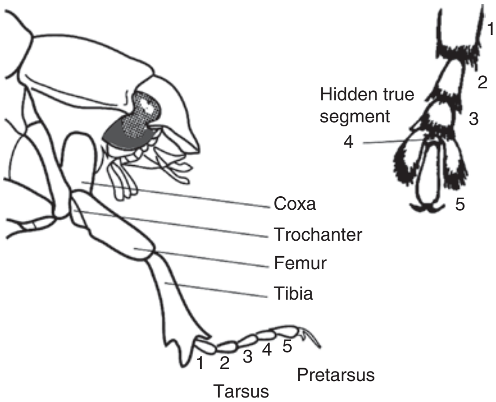
These are active, flattened, chitinous, free living, and principally predaceous larvae. Subcategories of thysanuriform larvae include campodeiform, caraboid, triunguloid, naupliiform and planidiiform.

► Campodeiform
► Caraboid
► Triunguloid
► Naupliiform
► Planidiiform

Tibia (pl., Tibiae)

The section of the insect leg between the femur and the tarsus, usually one of the largest sections and often bearing spines or spurs (Fig. 51).

► Legs of Hexapods



Tibia (pl., Tibiae), Figure 51 Leg of a beetle (Coleoptera: Scarabaeidae) leg showing its component parts, and a close-up of one type of beetle tarsus (foot).

Tick-Borne Encephalitis

Although encephalitis viruses usually are transmitted by mosquitoes, ticks also can transmit some types.

► Ticks

Tick Paralysis

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Adult ticks inject considerable quantities of saliva into the hosts during feeding. In some species of ticks, proteins in the saliva can paralyze the vertebrate host. At leas t 43 species of ticks have been reported to cause paralysis, but some records are doubtful. Paralysis caused by *Dermacentor andersoni* Stiles in North America and *Ixodes holocyclus* Neumann in Australia have been studied most extensively. *Dermacentor andersoni*, the Rocky Mountain Wood Tick, causes paralysis in a variety of hosts including sheep, cattle, horses, dogs and humans. Paralysis has been reported in various wildlife species, but this is rare and may be because affected animals are not readily visible. Wood ticks can paralyze cattle at doses of 25–83 mg tick per kg host body weight, and in sheep at doses of 37–70 mg tick per kg host. Increasing numbers of ticks per host may increase the incidence of paralysis, but this has only been demonstrated for laboratory animals. Humans may be paralyzed by a single tick. There are at least 10 cases of human paralysis in children aged 3–8 years that were caused by single ticks ranging in weight from 60 to 300 mg.

Although *D. andersoni* is widely distributed in western North America, paralysis is mainly associated with tick populations in a relatively small portion of its range. Paralysis occurs in the interior of British Columbia, and extends into Idaho, Oregon and Montana. Paralysis is relatively rare in the prairie regions of its distribution. Even though paralysis is associated with a particular geographic location, the ability of individual ticks to cause paralysis varies considerably within areas that paralysis occurs. Only a small proportion of ticks may be capable of causing paralysis when placed singly on susceptible laboratory animals.

Paralysis is typically associated with unmated female ticks that have fed for at least 4–5 days on the host. Males do not cause paralysis as they do not engorge to the extent that females do, and not inject the copious amounts of saliva into the host that females do. Female ticks are most likely to cause paralysis after they have attained a minimum weight of 40 mg. Although paralysis will occur in humans of all ages, it is less common in adults compared with young children as adult humans are more likely to detect and remove feeding ticks. In cattle, yearlings are the most susceptible age class as older cattle may develop immunity, and calves can have ticks removed by maternal grooming. Paralysis typically occurs in the early spring when adult ticks are actively searching for hosts. Cattle placed on pasture in the early spring are most at risk for paralysis (Fig. 52).

Tick paralysis is a progressive condition and worsens the longer that ticks are attached. Regardless of the host, paralysis begins with loss of hind limb function (posterior ataxia), proceeding to full ataxia. The victims lose the ability to stand or sit. Cattle will become sternally recumbent, and as paralysis proceeds, will become laterally recumbent.

Tick Paralysis, Figure 52 **Cow immobilized by tick feeding.**

If ticks are not removed, death due to respiratory failure will occur. Prompt removal of ticks from paralyzed animals can result in rapid recovery, even as the ticks are being removed. The earlier ticks are removed, the more rapid is the recovery. Paralysis is most common in cattle. Several thousand cattle have been reported paralyzed, with some occurrences involving entire herds of over 100 head. Death rates vary, but may range upwards of over 20–25% of an affected herd. Several hundred cases of human paralysis have occurred in the interior of British Columbia since the early 1900s.

Tick paralysis is believed to be caused by a toxin produced in the salivary glands and released during feeding. Injection of artificially collected saliva can cause paralysis. The rapid recovery of the host following tick removal suggests that infectious agents are not directly involved. Increasing incidence of paralysis with increasing doses of ticks further suggests that a toxin is involved. To date, the nature and identity of the toxin has not been identified. The mode of action of the toxin is not well understood, but is associated with reduced nerve conduction, possibly by attacking the nerve membrane. It is thought to involve motor polyneuropathies, with only limited participation of the afferent pathways.

Paralysis caused by *Ixodes holocyclus* is similar in some respects to that caused by *D. andersoni*, and markedly different in others. *Ixodes holocyclus* is among the most virulent of paralyzing ticks, and is common in moist areas along the eastern coast of Australia. Approximately 10 females can paralyze young calves 30–40 kg in weight, and 20–25 can paralyze calves 80–160 kg. The main hosts of the tick are various species of bandicoots, but the tick will cause paralysis in dogs, cats, domestic livestock and humans. Paralysis is associated with feeding by the adult females, and these are active from June through December. Toxins are secreted by the tick after the third day of attachment, and paralysis occurs after feeding for 4–5 days. Variation in virulence has not been found as has with *D. andersoni*. Symptoms are similar to those caused by *D. andersoni*, including an ascending flaccid paralysis, however, the victim may become acutely ill, and vomiting may occur. The symptoms may worsen following removal of the tick, and symptomatic treatment or administration of a canine hyperimmune antiserum. Immunity to paralysis can develop through previous exposure, through mother's milk, or by immunization.

The toxin produced by *Ixodes holocyclus* appears to have a different mode of action compared to other tick paralysis toxins, and may act to inhibit acetylcholine release at the neuromuscular junction. Considerable research has been conducted to isolate and identify the toxin produced by *Ixodes holocyclus*. Initial work suggested the toxin was a 40–80 kDa protein, but more recent studies suggest the toxin is of a lower molecular weight and related to scorpion neurotoxins. Toxins from other tick species, such as *Rhipicephalus evertsi evertsi*, are approximately 68 kDa.

The evolutionary significance of the toxins remains unclear. Toxins may have evolved to reduce mortality caused by host grooming, may have been con-served from an ancestor that used venom to immobilize prey, or may have other functions associated with tick-host interactions and paralysis is accidental.

► Ticks

References

Gothe R (1981) Tick toxicoses of cattle. In: Ristic M, McIntyre I (eds) Diseases of cattle in the tropics. Current topics in veterinary medicine and animal science, vol. 6. Martinus Nijhoff, The Hague, 587–598 pp

Gothe R, Kunze K, Hoogstraal H (1979) The mechanisms of pathogenicity in the tick paralyses. J Med Entomol 16:357–369

Gregson JD (1973) Tick paralysis: an appraisal of natural and experimental data. Monograph No. 9. Agriculture Canada

Stone BF, Doube BM, Binnington KC (1979) Toxins of the Australian paralysis tick *Ixodes holocyclus*. In: Rodriguez JG (ed) Recent advances in acarology, vol. 1. Academic, New York, 347–356 pp

Wilkinson PR (1982) Tick paralysis. In: Steele JH, Hillyer GV, Hopla CE (eds) CRC handbook series in zoonoses. CRC, Boca Raton, 275–282 pp

Ticks (Acari: Ixodida)

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Ticks are obligatory blood-feeding ectoparasites of reptiles, birds and mammals. They belong to the subclass Acari, order Ixodida. Ticks are the largest mites, ranging in length from about 2 mm to 30 mm depending on the species and life stage. All ticks pass through an egg and three active stages, a six-legged larva also known as a "seed tick," an eight-legged nymph and an adult. Each active stage molts into the next and, with few exceptions, each requires a blood meal before molting. The complex relationship of the tick to its vertebrate host that may date back to the dinosaurs, and the need for the tick to obtain a blood meal, have been the principle driving forces for their evolution.

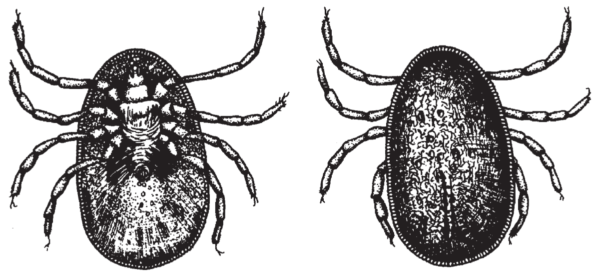
Classification of Ticks: The Order Ixodida

About 850 species of ticks are arranged in three families:

- Class: Arachnida
  - Order: Ixodida
    - Family: Argasidae
      - Subfamily: Argasinae
      - Subfamily: Ornithodorinae
      - Subfamily: Otobinae
      - Subfamily: Antricolinae
      - Subfamily: Nothoaspinae
    - Family: Nuttallielinae
    - Family: Ixodidae
      - Subfamily: Ixodinae
      - Subfamily: Rhipicephalinae
      - Subfamily: Amblyomminae
      - Subfamily: Haemaphysalinae
      - Subfamily: Hyalomminae

Argasidae

The Argasidae with some 159 species is divided into five subfamilies, each with one genus: Argasinae (*Argas* with seven subgenera and 56 species), Ornithodorinae (*Ornithodoros* with 100 species), Otobinae (*Otobius* with two species), Antricolinae (*Antricola* with about eight species), and Nothoaspinae (*Nothoaspis* with one species) (Fig. 53).



Ticks (Acari: Ixodida), Figure 53 **Adult of *Argas persicus*, the blue bug. The *left side* is a ventral view and the *right side* is a dorsal view (from Marquardt et al. 2000, used with permission of Harcourt Academic Press).**

Nuttallielidae

The Nuttallielidae has a single species *Nuttalliella namaqua* known only from females and nymphs. It is found in South Africa and Tanzania where it is believed to be a parasite on small mammals such as rodents and the rock hyrax. What little is known about this species suggests that it has many characteristics in common with both of the other two tick families.

Ixodidae

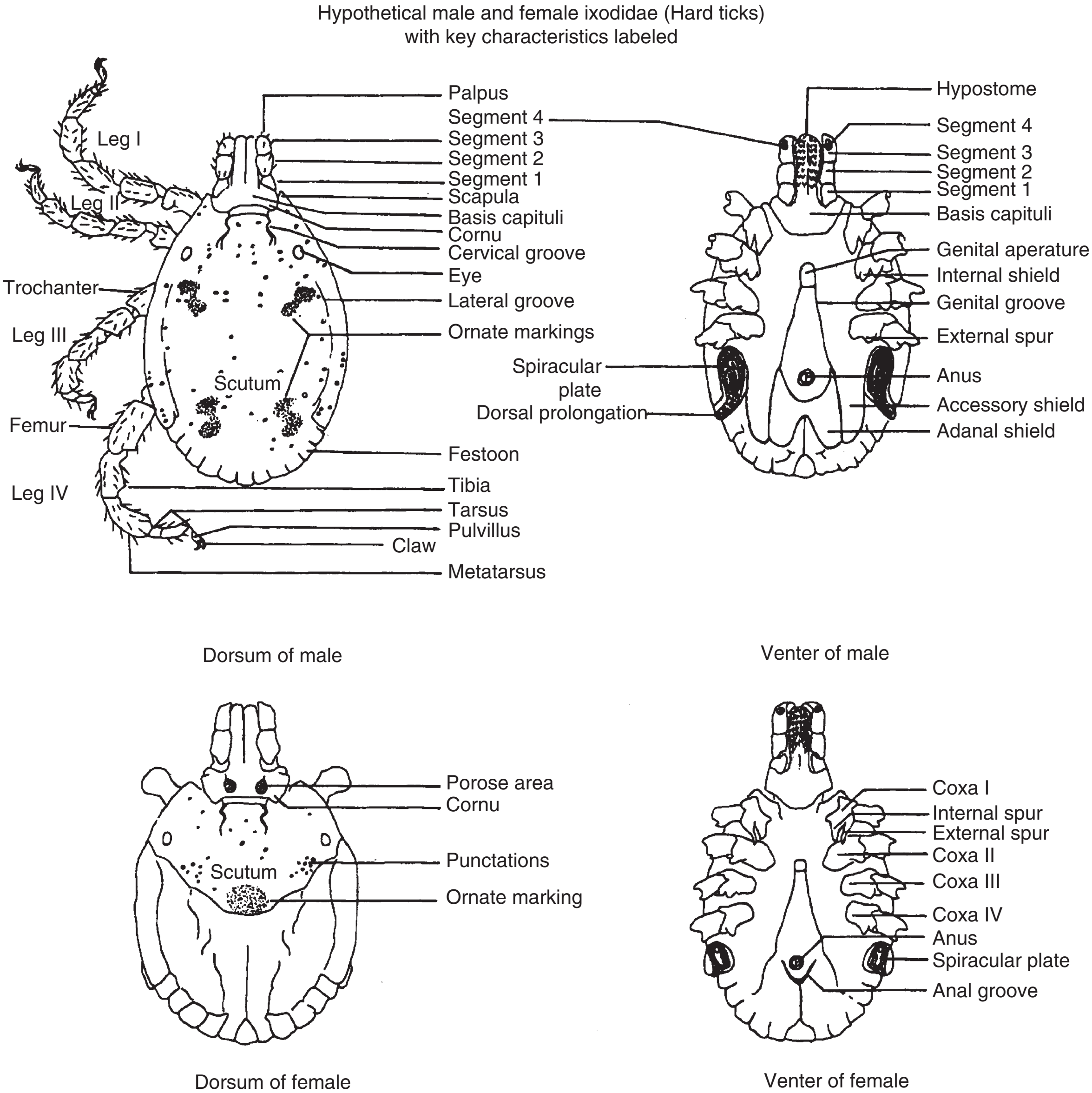
The Ixodidae, with some 650 species, is divided into five subfamilies. The subfamilies are grouped into two divisions, the Prostriatia and the Metastriata. The Prostriata has a single subfamily, the Ixodinae, with one genus, *Ixodes*, and some 245 species. The Metastriata contains four subfamilies. The largest of these, the Rhipicephalinae, has eight genera, *Dermacentor* with 30 species, *Cosmiomma* with one species, *Nosomma* with one species, *Rhipicephalus* with 70 species, *Anomalohimalaya* with three species, *Rhipicentor* with two species, *Boophilus* with five species, and *Margaropus* with five species. The other three subfamilies are smaller: Amblyomminae with two genera, *Amblyomma* with 102 species, and *Aponomma* with 24 species; Haemaphysalinae has one genus, *Haemaphysalis* with 155 species, and Hyalomminae has one genus, *Hyalomma* with 30 species.

External Morphology of Ticks

Ticks have a typical acarine body, but one that has been adapted to an ectoparasitic life. The body is divided into a movable head region, the capitulum or gnathosoma and the idiosoma, which makes up the rest of the body. There is no visible segmentation. The small dorso-ventrally flattened body of unfed ticks makes it difficult for the host to remove them (Fig. 54).

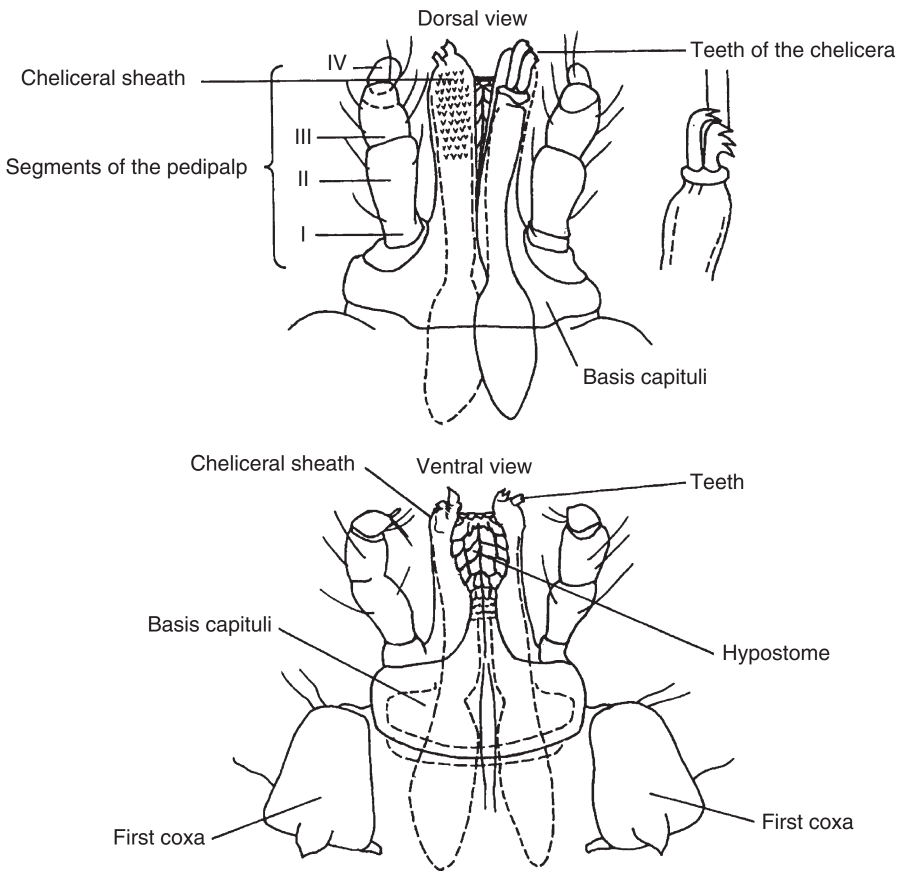
The capitulum, or gnathosoma, consists of the basis capituli, the palps, and the chelicerae, and the hypostome. The gnathosoma is anteriorly situated in the larvae of soft ticks and in all instars of hard ticks. In postlarval instars of soft ticks, it is not visible from above, being mostly hidden by the overlapping anterior part of the idiosoma. The gnathosoma is connected with the idiosoma by a cavity, the emargination in hard ticks, or the camerostome in soft ticks. The connection is via a soft articulation membrane that allows the gnathosoma to be flexed or extended (Figs. 55 and 56).

The basis capituli, an integumental ring that encircles the mouthparts, contains the shafts of the chelicerae, the salivary ducts and the pharynx. Its dorsum bears the area porosa in female hard ticks. The paired palps have four segments, and resemble legs in soft ticks, but have a more flattened shape than legs in hard ticks. In soft ticks, the terminal segment is normal in appearance but, in hard ticks, it is much shorter and can be retracted or protruded. The palps bear several types of setiform sensilla.



Ticks (Acari: Ixodida), Figure 54 **Diagrams illustrating the external anatomy of a hypothetical male and female ixodid tick with key characteristics labeled. Note that the chelicerae have been removed (compare to following figure) (from Marquardt et al. 2000, used with permission of Harcourt Academic Press).**

The paired two-segmented chelicerae have been modified as cutting organs that are unique among the mites. Chelicerae consist of a bulbous base, an elongated shaft, and the cutting digits, or articles. In many species, a cheliceral hood covers the articles. The cutting edges of the internal and external articles are laterally oriented. The internal article is moved from side to side by the tendons attached to the powerful muscle masses in the bulbous cheliceral bases. The external article moves with it. This movement is used by the tick to tear into the hosts skin prior to embedding its mouthparts. Sensory structures occur on the external and internal articles.



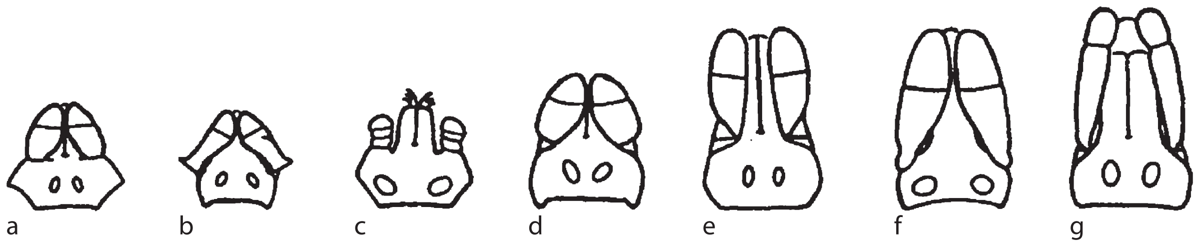
Ticks (Acari: Ixodida), Figure 55 **Capitulum and mouthparts of a tick (from Marquardt et al. 2000, used with permission of Harcourt Academic Press).**

The hyopostome, located on the ventral gnathosoma, is a dorso-ventrally flattened protrusion with recurved teeth on its ventral side, and a preoral canal on its dorsal side. The preoral canal leads to the mouth and the muscular pharynx. The action of the pharynx sucks up blood through the preoral canal. The preoral canal and the space between the dorsal surface of the hypostome and the ventral surfaces of the chelicerae are the common channels for blood intake and saliva outflow. In hard ticks, the intake of blood alternates with saliva flow with some pauses between the two events. At the junction of the preoral canal with the pharyngeal valve, a short and pointed flap-like labrum exists.

The mouthparts of hard ticks vary in length. Those species with longer mouthparts are referred to as longirostrate, and those with smaller mouthparts as brevirostrate.

The idiosoma is divided into the podosoma which bears the walking legs and, in adults, the genital opening, and the opisthosoma that lies posterior to legs IV and bears the spiracular plate and the anal opening. Some hard ticks have patterns in the cuticle, usually in the scutum or the dorum of the basis capituli, which are referred to as markings or ornamentations.

The idiosoma of soft ticks is tough and leathery and, with the exception of some larval forms, has no sclerotized plates or shields. Eyes, when present, are found laterally above the fourth pair of legs in soft ticks and, in hard ticks, on the lateral surface of the scutum. The cuticle of all Argasidae, but *Argas*, have tiny ridges (mammillae) and



Ticks (Acari: Ixodida), Figure 56 **Capituli of the genera of hard ticks, family Ixodidae. (a) *Rhipicephalus*; (b) *Haemaphysalis*; (c) *Boophilus*; (d) *Dermacentor*; (e) *Ixodes*; (f) *Hyalomma*; (g) *Amblyomma* (from Marquardt et al. 2000, used with permission of Harcourt Academic Press).**

depressions (discs) to which muscles attach. Some hard ticks have grooves, or festoons, along portions of the ventral posterior body margin.

The idiosoma of hard ticks bears several sclerotized plates or shields. In female hard ticks, an anterior shield, the scutum, occurs on the dorsum. The alloscutum covers the remainder of the idiosoma. The alloscutum is not sclerotized and is folded in unfed ticks. This allows the alloscutum to greatly enlarge during feeding to accommodate the large blood meal. Male hard ticks take small blood meals, the alloscutum is lacking, and the scutum covers the whole dorsum. Various shields such as the accessory shield and adanal shield occur only in male hard ticks. Sexual dimorphism is well developed in hard ticks. Soft ticks are so-called because they lack the scutum. There is little visible external difference between males and females in soft ticks, except the shape of the genital opening.

The podosoma contains the walking legs. Each leg is divided into six segments or podomeres, from proximal to distal: the coxa, trochanter, femur, tibia, metatarsus and tarsus. Muscles, hydrostatic pressure from hemolymph and bending stresses are used to produce movement. Muscles and tendons run between the joints. Joints between the body and the legs, between the podomeres, and between the tarsus and the apotele allow movement of the legs. The direction of movement is determined by the type of articulation, the extent of the flexible arthrodial membranes, and the insertion points of the muscles and the position of the tendons. The tarsus of each leg has an apotele, or pretarsus, which includes the claws and, in hard ticks, only the pulvillus. The pulvillus is a flap-like structure with a central lumen containing lipid compounds that are secreted onto the surface and may act as an adhesive that allows the tick to walk on almost any surface and to move vertically.

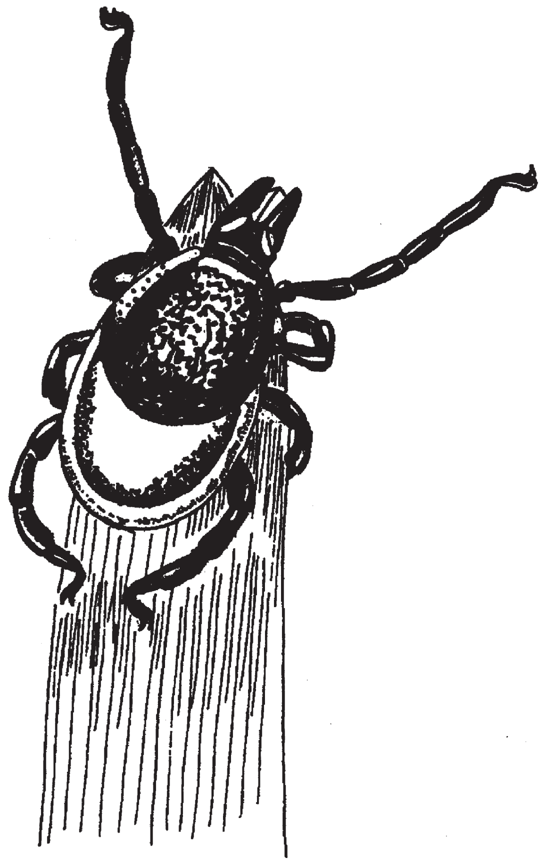
The opisthosoma contains the opening of the respiratory tract and the anus. Adult and nymphal ticks respire through tracheae, most larvae and all eggs respire through their integument. However, the larvae of some species of *Argas* and *Ornithodoros* have a simple tracheal system that opens through minute apertures between coxae I and II. Tracheae in other ticks open to the outside through a complex structure, the stigmata (or spiracle). This is associated with a sclerotized elevated region of the cuticle, the spiracular plate. A pair of spiracular plates occur near coxae IV in all adult and nymphal ticks. The spiracles of soft and hard ticks are similar, although the spiracular plate is often less conspicuous in the Argasidae. The exchange of gases occur through pores that perforate the spiracular plate and lead to a labyrinth of chambers that in turn lead to the trachea. Spiracular pores help prevent dust and other debris from entering the trachea. Pillars of cuticle (pedicles) run from the floor to the top of these chambers. A valve-like structure, the atrial valve, occurs beneath the spiracular plate. High carbon dioxide concentrations stimulate the atrial valve to open.

The tick respiratory system is designed, in part, to conserve water. Ticks that live in arid habitats have the most efficient spiracles to reduce water loss. The pores and the elaborate labyrinth system beneath the sieve plate function to reduce water transpiration during respiration. When stigmata remain open, loss of water increases, which explains why a discontinuous ventilation cycle exists in hard ticks. A discontinuous ventilation cycle coupled with a low metabolic rate is probably the reason unfed adults can survive long periods of starvation and desiccation off the host. Engorged hard ticks ventilate continuously with little spiracular control.

Host Seeking and Tick Feeding

Most ticks are ambushers, seeking their hosts in a passive manner. The exceptions are some species of *Hyalomma*, which are active hunters that will crawl several meters toward a host after perceiving their odors and movements. Ticks have evolved specialized structures to sense the presence of a host. The most important of these is Haller's organ, a specialized area of the dorsal surface of the first pair of legs found on all ticks. Haller's organ, along with other setae, can sense CO_2, ammonia found in sweat and urine, hydrogen sulfide found in the breath, belches or flatulence, nearby movement, and a rapid rise in temperature. When seeking a host ticks extend their first pair of legs and assume a questing position (Fig. 57). Ticks process sensory information through their central nervous system, or synganglion, which is described in the section on mites. Host seeking behavior is rhythmic in some ticks. *Rhipicephalus appendiculatus*, which mostly infests cattle, has a bimodal diurnal periodicity, that is, a peak of host seeking that occurs twice during each day. The peaks shift depending on the time of year.

Once on the host, a tick selects a feeding site then embeds its mouthparts into the skin. First, the tick uses its legs to elevate the body to a sharp angle, then it cuts the skin with its chelicerae and inserts the hypostome and chelicerae into the wound using a rocking motion of the body.

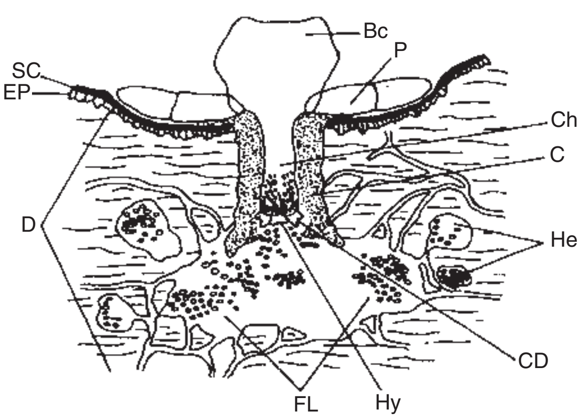


Ticks (Acari: Ixodida), Figure 57 **Female *Ixodes persulcatus* in questing posture, waving its first pair of legs (from Marquardt et al. 2000, used with permission of Harcourt Academic Press).**

The palps are splayed out on the surface of the hosts skin. Ticks are pool feeders, that is, they feed on blood that flows into a wound site in the case of soft ticks, or a feeding lesion in the case of hard ticks. Soft ticks create wounds by using their chelicerae to tear into small blood vessels and capillaries. Soft ticks are rapid feeders compared to hard ticks, finishing their blood meal in 20–60 min depending on the species. Exceptions to this rapid feeding are the larvae of many species of *Argas* and *Ornithodoros*, which require several days to complete a blood meal.

After insertion of the hypostome, all hard ticks, with the exception of some species of *Ixodes*, secrete a substance from their salivary glands that hardens into a cone-like structure. This "cement" cone covers the mouthparts but not the palps. This cone has multiple functions. It cements the tick onto the host. It creates a feeding tube that make the mouthparts more effective at taking up blood. It limits contact with the host to a small opening at the apex of the cone. Hard ticks do not create a wound at the feeding site similar to that of soft ticks. Instead, a specialized feeding lesion develops beneath the cement cone. This lesion does not develop without the host's initial inflammatory reaction. Both the bite wound of soft ticks, and the feeding lesion of hard ticks are maintained by saliva from the tick's salivary glands (Fig. 58).

The paired salivary glands of ticks are complex, multifunctional organs that are very important in off-host physiology as well as feeding. Salivary glands consist of grape-like acini connected to a system of salivary ducts. The ducts lead to a preoral cavity, the salivarium, which is isolated by a trap door mechanism. When the salivarium is opened, saliva flows into the host; when it is closed, blood is sucked into the digestive system by the



Ticks (Acari: Ixodida), Figure 58 Diagram of the feeding lesion that develops beneath the attached female ixodid. The lesion is filled with blood and inflammatory infiltrates. BC, basis capituli; C, cement cone; CD, cheliceral digit; Ch, outer cheliceral sheath; D, dermis of host skin; EP, epidermis of host skin; FL, feeding lesion; He, hemorrhage; Hy, hypostome; P, palps; SC, stratum corneum of host skin (from Coons and Alberti 1999, used with permission of Wiley).

action of the muscular pharynx. Both soft and hard ticks alternate blood sucking with saliva production. Acini contain specialized cells that produce the many bioactive compounds found in the saliva. One type of acini produces a salt that takes up atmospheric water when secreted on the mouthparts of nonfeeding ticks. This is used to replenish the water lost during the off host part of the tick life cycle. The salivary glands of hard ticks undergo a great developmental change during feeding to become organs of osmoregulation that return excess water and ions from the bloodmeal back into the host via the saliva. Tick salivary glands are innervated with a catecholaminergic-like synapse.

Tick saliva compounds have anti-hemostatic, anti-inflammatory and immunosuppressant properties. These compounds help the tick to obtain an adequate bloodmeal and avoid rejection by the host.

Antihemostatic compounds in tick saliva inhibit platelet adhesion, activation and aggregation, blood coagulation, and vasoconstriction. Some compounds promote vasodilation. The importance of preventing platelet activation at the tick feeding site is apparent by the number of compounds that *Ornithodoros moubata* has evolved to prevent platelet activation that include at least five different compounds. Moubatin, a 17 kDa polypeptide, Tick Adhesion Inhibitor, a 15 kDa polypeptide, and disagregin, a 6 kDA peptide, prevent exposed collagen on damaged blood vessel walls from activating platelets. Disagregin also prevents the formation of fibrinogen and ADP. Apyrase, an enzyme that hydrolyzes adenosine diphosphate (ADP) is also present in the saliva of *Ornithodoros moubata*. ADP can activate platelets and is released from injured cells and activated platelets. Apyrase is found in the saliva of a wide variety of ticks in addition to *O. moubata*. An exception is *Amblyomma americanum*, which has no apyrase. In this tick, inhibition of platelet aggregation is carried out by high concentrations of prostaglandins (PGE_2 PGD_2). *Ixodes scapularis* saliva also contains high levels of prostaglandins (PGI_2, PGE_2).

The prostaglandins are the most powerful known inhibitor of platelet aggregation known and can actually cause desegregation of aggregated platelets. Prostaglandins, PGI_2, PGE_2 and PG_2, are also potent vasodilators that can help increase blood flow during feeding.

Blood coagulation is initiated by either the extrinsic system or the intrinsic system. The extrinsic system is initiated by exposure of blood to subendothelial components such as collagen, which then activates tissue factor. The intrinsic system is initiated by the release of tissue thromboplastin from injured cells. Each system leads to a common reaction that involves factor Xa (the Stuart factor), catalyzing prothrombin to thrombin. Thrombin catalyzes the conversion of soluble fibrinogen to an insoluble fibrin mesh that forms a blood clot. Most tick anticoagulants inhibit either the serine protease factor Xa, or thrombin. An exception to this is a compound from *Dermacentor andersoni* saliva that inhibits the serine protease VIIa, and a compound from *Dermacentor variabilis* salivary glands that inhibits tissue factor.

The vertebrate host's inflammatory and immune systems are closely linked and many anti-inflammatory compounds of tick saliva also inhibit or suppress the host's immune system. Compounds in tick saliva can inhibit both the innate and the acquired immune response of the vertebrate host. Innate immune responses include those mounted by the host immediately without the requirement of previous contact with the foreign invader. These include the process of inflammation and a series of soluble proteins (complement) that can destroy or damage foreign objects. Other components of the innate response are natural killer cells and the interferons. Studies have shown that some factors in tick saliva can inhibit complement, suppress the activity of natural killer cells and also suppress the anti-viral action of some interferons. This includes the production of nitric oxide by host macrophages, which is used to destroy foreign objects. The acquired immune response is highly specific and requires prior exposure to the foreign object which must be antigenic. Acquired immunity can be divided into humoral immunity carried out by antibodies, which are bloodborne proteins of the Immunogloblin superfamily manufactured by B lymphocytes or B cells, and cell-mediated immunity, which is carried out by T lymphocytes or T cells. Compounds in tick saliva suppress antibody production and responses of host T lymphocytes. The cement cone, which is known to be antigenic, binds host immune response factor IgG. This may act as a molecular mask to prevent recognition of the cement cone as a foreign object by the host's acquired immune response. A novel family of immunoglobulin-binding proteins (IGBPs) may also play an important role in evading the host's acquired immune response. IGBPs have been found in all ixodid species studied to date, and have been isolated from both saliva and hemolymph. IGBPs secreted by males co-feeding with their mates have been shown to enhance the female's ability to complete her blood meal and lay a larger clutch of eggs.

After formation of the feeding lesion early in feeding, hard ticks suppress the host's inflammatory response. The high levels of prostaglandins in tick saliva inhibit neutrophil function and suppress the release of inflammatory mediators from mast cells. Bradykinin, an inflammatory mediator of vertebrates that potentiates pain, is deactivated by the saliva of *Ixodes scapularis*. Histamine binding compounds and host immunoglobulin binding compounds have been identified in tick saliva. Histamine is an important mediator of the inflammatory response, and immunoglobulins mediate the host's immune response.

Tick drop-off from the host after feeding is not uniform with respect to day/night cycles. Completion of feeding at certain times has evolved to ensure that ticks drop off into habitats that are the most advantageous for their reproduction and for the availability of hosts for the next life stage. Photoperiod is the most common external factor that affects drop-off timing. Individual ticks of the same species feeding on the same host may finish at different times.

Physiology of Ticks

Digestive System

Ticks have a typical acarine digestive system consisting of a foregut, midgut and hindgut. The foregut is divided into a mouth, a muscular pharynx that is designed to suck up blood, and an esophagus. The midgut is divided into a ventriculus, or stomach, and several ceaca. Digestion takes place in the midgut, which is the largest division of the digestive system. A peritrophic membrane occurs in several species of ticks. A short hindgut leads from the midgut to the anal opening. Digestion starts when the bloodmeal is taken up by the midgut cells using receptor-mediated endocytosis into coated vesicles. These are sorted into endosomes that fuse with lysosomes. The bloodmeal is digested in the lysosomal system in a process termed heterophagy. The end products are residual bodies that accumulate in the cell as digestion proceeds. The products of digestion are released into the hemolymph. A pulsating organ, the heart, is located dorsally and helps circulate the hemolymph throughout the body cavity. Soft ticks digest only a portion of the bloodmeal as needed. This probably contributes to their ability to live for relatively long periods without an additional bloodmeal. Hard ticks digest the entire bloodmeal, but do so in stages. The first stage occurs before rapid engorgement. Cells in the epithelial lining of the midgut fill up with residual bodies during the digestive process and are sloughed off into the midgut lumen. They are replaced by new cells that repeat the digestive process, slough off and are replaced. The second stage of digestion occurs during rapid engorgement. To enter rapid engorgement, a female must be inseminated. During rapid engorgement, midgut cells become greatly distended and are filled with endosomes containing the bloodmeal. At this time, digestion is minimal. Following completion of the bloodmeal, the female drops off the host and the third stage of digestion occurs. During this time, all the bloodmeal is utilized and the midgut cells fill up with residual bodies. Cells do not slough off during second or third stage of digestion.

Osmoregulatory and Excretory Organs

Osmoregulatory organs are used to eliminate the excess water and ions of the blood meal. In hard ticks, salivary glands develop into osmoregulatory organs and return water and ions to the host as saliva. In soft ticks, coxal glands are the osmoregulatory organs and eliminate excess water and ions to the outside through the coxal fluid, which appears as a colorless drop between the base of legs I and II during, or shortly after, feeding. Coxal glands are absent in hard ticks. In hard and soft ticks, paired Malpighian tubes accumulate guanine, the end product of nitrogenous metabolism. Malpighian tubes empty into the lower digestive tract near the junction of the midgut and hindgut. Guanine is then expelled through the anus as a white paste-like substance along with the undigested portion of the bloodmeal, which appears as small red pellets.

Water Loss

Unfed ticks must prevent desiccation to survive. This is accomplished by physical barriers and physiological and behavioral adaptations. The most important physical barriers are the impermeable cuticle and a discontinuous respiratory cycle in which the spiracle remains closed except during gas exchange. Physiological adaptations include the excretion of guanine which is a dry waste product, and dry fecal material. An important behavioral adaptation is that ticks move down close to the ground into microenvironments with increased humidity following questing. Here, the tick can actively reabsorb water from the environment using a salt solution secreted onto its mouthparts by the salivary glands.

Reproduction

Male ticks inseminate their mates by transferring packets of sperm in a structure termed a spermatophore. Parthenogenesis is rare, but occurs in both hard and soft ticks and involves thelytoky where females produce only females. In female ticks, a large amount of the blood meal is converted to the female-specific glycolipoheme protein vitellogenin, which is secreted into the hemolymph and taken up by the eggs to become vitellin. Vitellin is the yolk of the tick egg and is the main energy source of the developing embryo.

Soft and hard ticks wax their eggs using Gene's organ which is located in the anterior body cavity. The Gene's organ turns inside out during oviposition. Unwaxed eggs dehydrate and do not develop. In female hard ticks, secretions from the porous area on the dorsal surface of the basis capituli are also added to the eggs during waxing.

Semiochemicals

Semiochemicals are informational chemicals. Two types of semiochemicals have been identified in ticks. Pheromones regulate beneficial functions between the same species, and allomones repel predators. Four different types of pheromones occur in ticks: assembly pheromones, aggregation-attachment pheromones, sex pheromones and a primer pheromone.

Assembly pheromones are common in many species of soft and hard ticks and induce clustering of ticks. These pheromones are interspecific and effect all life stages. Perception of assembly pheromones cause free living ticks to cluster. Guanine, the major excretory product of nitrogenous metabolism in ticks, acts by contact as a non-specific assembly pheromone in the species of *Argas*, *Ornithodoros*, *Amblyomma*, and *Rhipicephalus*.

Aggregation-attachment pheromones induce attachment of ticks to areas where males are feeding. They are produced by males of *Amblyomma* and affect the behavior of adults and, in some cases, nymphs. Females of *A. maculatum*, *A. hebraeum*, *A. variegatum*, and *A. marmoreum* will not embed in hosts unless feeding males are present.

Sex pheromones elicit behavior patterns that lead to copulation. A pheromone in the coxal fluid of female *Ornithodoros*, which is most active a few days following feeding, elicits courtship behavior in sexually active males. In all hard ticks except *Ixodes*, there is a complex, but similar, courtship behavior. Three different types of sex pheromones are involved. A volatile attractant sex pheromone, 2,6-dichlorophenol, is produced by the foveal glands in most of these species. These glands are located on the dorsal alloscutum just posterior to the scutum in all metastriate ticks. After contact with the female, males must identify a second pheromone, the mounting sex pheromone, or they will abandon the female. A third sex pheromone, the genital sex pheromone, must be recognized by males of some species before a spermatophore is formed and copulation completed.

A primer pheromone, in this case the fecundity reducing pheromone, has been identified in *Argas arboreus*, where its effect is most noticeable when ticks are crowded. The large wax glands of *Dermacent variabilis* and *Amblyomma americanum* secrete an allomone that repels predators.

Life Cycles and Habitats of Ticks

Many aspects of the life cycles and habitats of soft and hard ticks differ. Differences also occur between two divisions of hard ticks, the Prostriata and Metastriata.

Postembryonic Development

The Argasidae have multiple nymphal stages with different species having different numbers of nymphal molts. Following a final blood meal, the last instar nymph molts into the adult stage. The Ixodidae have a single nymphal stage.

Feeding

Depending on the species, soft ticks feed on the host once to many times in a given life stage.

Feeding is much shorter for soft ticks (15 min to several hours) than for hard ticks, although some larvae require several days to complete feeding. Soft ticks ingest a relatively small amount of blood compared to hard ticks. In a few species of soft ticks, the larval stage molts to a nymph without feeding. Hard ticks take a much larger blood meal (up to or greater than 100 times their unfed body weight in some species) than soft ticks, and feed for a long time (9–13 days depending on the species). Hard ticks feed only once in a given life stage. Larvae complete feeding in the shortest time, adult females in the longest time. Females pass through a feeding stage known as rapid engorgement, while the males do not. It is during this feeding stage, which occurs 24–48 h prior to the completion of feeding that most of the blood meal is taken up. Depending on the species, each ixodid tick can consume up to 15 ml of blood during feeding. This is made possible by the tick returning excess water and ions from the blood meal to the host through its saliva. Compared to females, males produce only about one-twentieth the amount of saliva.

Mating and Reproductive Cycles

Ticks either mate on, or off, the host. Almost all soft ticks mate off the host. Two exceptions are *Argas (Microargas) transversus*, and *Otobius megnini*. The former is a small tick that spends its entire life on the Galapagos giant tortoise, and is the only known tick to oviposit on its host. The latter tick is the spinose ear tick, an economically important species. A blood meal is not necessary to initiate gametogenesis in species of Prostriata. They can mate before feeding, and can mate on, or off, the host depending on the species. In many of the nidicolous (nest or burrow dwelling) species of *Ixodes*, males cannot feed and do not occur on hosts. Instead, they seek out females and usually mate off the host. This life cycle may have evolved in nidicolous, or nest dwelling species, to ensure that females can survive long periods without feeding and still oviposit. An exception occurs in the subgenus *Ixodiopsis* where, despite a nidicolous life, males feed. All species of Metastriata mate on the host.

Soft and hard ticks have different reproductive cycles. Soft ticks go through multiple egg laying (gonotrophic) cycles. Females lay a clutch of eggs during each cycle. Each clutch of eggs is usually progressively smaller. Autogeny, the ability to lay eggs without a bloodmeal, is obligatory in genera where females have nonfunctional mouthparts, i.e., *Otobius*, *Antricola*, and possibly *Nothoaspis*; and facultative in *Argas persicus*, and several species of *Ornithodoros*, including *O. lahorensis*. Female hard ticks go through one gonotrophic cycle, lay a single clutch of eggs, then die.

Hosts

Ticks either have multiple hosts, or have a one-, two-, or three-host life cycle. Almost all soft ticks have multiple hosts although the hosts may be the same species. Two exceptions are *Argas transversus*, and *Otobius megnini*.

All species of ixodids have either a one, a two- or a three-host life cycle. In a one-host life cycle, ticks infest the host as larvae then remain on the same host as nymphs and adults. Adults mate following a blood meal. Mated females drop off the host and lay eggs in a protected niche such as a crack in the ground, or under vegetation litter. About 12 species of metastriate ticks have a one-host life cycle. In a two-host life cycle, the larvae infest a host then remain on the host to feed as nymphs after molting. Following completion of feeding, the replete nymph drops off to molt into an adult. The adult then infests a second host to feed and mate, after which the female drops off to oviposit. Only a dozen or so species of metastriate ticks have a two-host life cycle. Two examples are *Hyalomma anatolicum excavatum* and *Rhipicephalus evertsi*. By far the majority of metastriate ticks have a three-host life cycle where each life stage infests a host. Usually, each host is a different species and each is larger than the previous host. Molting from one stage to another occurs off the host, and mating occurs on the penultimate host then the replete female drops off to oviposit.

In their preference of hosts, ticks are categorized as either host-specific or opportunistic. Host-specific ticks are less common, and are considered specialists. An example is the cattle tick *B. microplus*. These ticks respond dramatically to the odors of cattle, but not to human odors. Opportunist ticks are generalists and have a wide range of hosts. Two examples are *Ixodes scapularis*, whose hosts include a number of species of birds and mammals, and *Amblyomma americanum*, whose host list includes reptiles, birds and mammals.

Many species of ticks have repeated feeding success on their natural hosts, but not on unnatural laboratory hosts. Repeated infestations of *Dermacentor variabilis* on their natural hosts, such as deer mice, results in successful feeding, but when larvae and nymphs are fed on guinea-pigs, feeding success is reduced. Successful molting to the next stage by ticks that have completed feeding is also reduced.

Habitats

Ticks can be divided into nidicolous and non-nidicolous. Nidicolous ticks either live in, or in close association with, the host's dwelling. That is, the host's nest, burrow, cave or shelter. Non-nidicolous ticks live throughout the host's range. Almost all species of Argasidae and many Prostriata are nidicolous. Most Metastriata are non-nidicolous. The behavior of nidicolous ticks is adapted to specialized niches. Such behavior can include (i) the ability to survive for years in the absence of a host, (ii) negative phototropism, an avoidance of light, (iii) thigmotropism, a positive reaction to contact with a solid object, so these ticks prefer small cracks or crevices in their environments that contact both surfaces of their body, (iv) a narrow tolerance of temperature and humidity, often the optima is that of the host's residence.

Non-nidicolous ticks live throughout the host's range, but most are not distributed in a uniform fashion throughout this range. Some are found in several different habitats of their host's range, while others have a single preferred type of habitat, for example a deciduous forest, where most of their population is found. Important factors that determine this non-uniform type of distribution are climate, vegetation, availability of hosts, presence or absence of diapause, and the ability of the tick species to withstand adverse environmental conditions. No single ecological factor can account for this non-uniform type of distribution.

The presence of diapause enables many tick species to synchronize their populations with the presence of hosts or with favorable climatic conditions. Diapause is a state of low metabolic activity in an arthropod that is mediated by neurohomone(s). Two types exist in ticks, behavioral diapause, or developmental diapause. Ticks in behavioral diapause will not feed when offered hosts and often fail to quest for hosts. Behavioral diapause is the most common type. Developmental diapause involves delayed completion of development in an egg, or fed immature. Developmental diapause is often an important regulator of the developmental cycle in nidicolous ticks that use migratory birds or bats for hosts. Usually this diapause occurs as delayed oviposition, which ensures that expansion of the tick population is related to the presence of the host. Great numbers of nidicolous ticks can occur in a given nest or burrow. Bird nests can contain up to 20,000 ticks per square foot, and warthog burrows have contained 250,000 ticks per burrow. In some cases, seabirds have abandoned their nests and fledglings due to the presence of large numbers of ticks. Diapause has not been reported in nidicolous ticks that have non-migratory hosts. Diapause is widespread in non-nidicolous ticks. In *Ixodes rincinus*, developmental diapause exists in the egg and all active stages, which results in separate spring and fall feeding populations. Delayed oviposition (developmental diapause) occurs in *Dermacentor marginatus*. Behavioral diapause occurs in *Dermacentor albipictus*, *Dermacentor andersoni* and *Dermacentor variabilis* to name a few species.

Dispersion

Ticks move slowly over short distances and must rely on their hosts for dispersal. Most widespread tick species have hosts that, in turn, are widely dispersed, or are migratory. An example is the brown or red dog tick, *Rhipicephalus sanguineus*, which is found throughout the world. Many ticks have at least one life stage that infests migratory birds that can carry them between continents. Using hosts as mechanisms of dispersal has resulted in the spread of tick transmitted diseases through large distances, and has made many of the diseases transmitted by ticks multifocal.

Ticks of Medical and Veterinary Importance

Three genera of soft ticks, *Argas*, *Ornithodoros* and *Otobius* have species that are medical or veterinary pests. The other genera, *Antricola* and *Nothoaspis*, are parasites on bats.

The genus *Argas* is divided into seven subgenera, two of which, *Argas* and *Persicargas* infest birds. The other subgenera are parasites on bats and small mammals. Almost all species in the genus *Argas* are nocturnal and occur in arid habitats with long dry seasons. *Argas (Persicargas) persicus*, the fowl tick or blue bug, is the most widespread soft tick on poultry. Larvae of this tick feed on the host for 2–10 days depending on the situation. Fed larvae drop off and molt in 4–16 days. Nymphs seek hosts and complete feeding within 30 min. There are three nymphal stages. Adults complete feeding within 45 min. Females feed before laying each clutch of eggs, and this cycle may occur daily. Several hundred eggs are laid in the early clutches, and only a couple of dozen in the later ones. *Argas (Persicargas) persicus* originated in the Palearctic region but, following domestic poultry, this tick has spread throughout the world with the possible exception of the Neotropical region. In addition to domestic poultry, it is found on wild birds. The fowl tick transmits two diseases to poultry, fowl spirochetosis and a rickettsial disease caused by *Aegyptianella pullorum*. Three other closely related ticks, *Argas (Persicargas) walkerae*, *Argas (Persicargas) persicus*, and *Argas (Persicargas) arboreus*, are also parasites on birds. In the southern U.S.A., *Argas persicus*, *Argas sanchezi*, and *Argas radiatus* are parasites on poultry, but are not problems in large commercial poultry houses.

Three species of *Ornithodoros*, *Ornithodoros moubata*, *Ornithodoros savignyi*, and *Ornithodoros lahorensis*, are important parasites of man and domestic animals. The African tampan, or eyeless tampan, *Ornithodoros moubata*, is a complex of at least four species. *Ornithodoros moubata* sensu strictu (in the narrow sense) occurs throughout semi arid, or arid Africa from Kenya southward to South Africa. The life cycle is relatively short, about 4 months from egg to adult. The larvae are nonfeeding and molt directly into a nymph. There are three or more nymphal stages. Females deposit several hundred eggs per batch. More than seven clutches are laid, which can total over 2,500 eggs. Large infestations of this tick can kill pigs. The tick can become a parasite of humans that live in huts or in dwellings with cracks. *Ornithodoros moubata* is the vector of *Borrelia duttoni*, which causes endemic relapsing fever. Other species in this complex include *Ornithodoros moubata porcinus*, found in Africa, *Ornithodoros tholozani* and *Ornithodoros erraticus*, found in the Middle East. *Ornithodoros moubata porcinus*, the African warthog tick, and *Ornithodoros erraticus*, transmit the causative agent of African swine fever. The eyed tampan, *Ornithodoros savignyi*, occurs in the arid regions of Africa, the Middle East, India and Sri Lanka where it is a parasite on domestic stock and humans. It does not transmit disease, but heavy infestations can cause severe damage. *Ornithodoros* *lahorensis* is a parasite of domestic stock throughout its range in Asia and the southern republics of the former Soviet Union. *Ornithodoros hermsi*, *Ornithodoros turicata* and *Ornithodoros parkeri*, feed on humans along with other hosts, and can vector *Borrelia* species that cause relapsing fever.

The spinose ear tick, *Otobius megnini*, is a parasite on cattle, horses and companion animals. It occurs mostly in stables and in other animal shelters. The spinose ear tick has spread from America to southern Africa and India, and has been reported from humans in the later region. The larvae have a capitulum that is over one-third its body length. Larvae invade the ear and feed for 5–10 days then molt to a nymph. Nymphs reattach within the ear. The integument of the nymph has numerous spines from which the tick gets its common name. The second stage nymph drops off the host and seeks small, hidden areas such as cracks where they molt to a fiddle-shaped adult. The adult does not feed. Its hypostome is small and has no teeth. Mated females lay up to 1,500 eggs in cracks in the walls of the shelters at a height suitable for transfer to a large host. Larval spinose ear ticks die within 4 months, but adults can live up to 2 years without hosts.

In the Ixodidae, the genus *Ixodes* has the largest number of species. All are three-host ticks without eyes and festoons. The capitulum is much longer in the female than in the male. The most important species group is the *Ixodes ricinus-persulcatus* complex which has a wide distribution from North America south into Mexico, and in Europe south to the Sahara, and in Asia south to the Himalayas. This complex is important in vectoring pathogenic viruses of man, the *Borrelia* that causes Lyme disease, and the protozoa that cause piroplasmosis. Important species of this group are the blacklegged tick, or American deer tick, *Ixodes scapularis* (=*dammini*), found in North America, the European sheep tick, or European castor bean tick, *Ixodes ricinus*, and the tiaga tick, *Ixodes persulcatus*. *Ixodes scapularis* occurs in North America. *Ixodes ricinus* is found along the western parts of the British Isles, and Norway southward to Iran and Turkey, Bulgaria, Italy and the Pyrenes. *Ixodes persulcatus* has a wide distribution from Japan westward into Germany. All three are vectors of the causative agent of Lyme disease. *Ixodes persulcatus* is also the main vector of the virus that causes Russian spring-summer encephalitis. This tick is more tolerant of temperatures and is more cold hardy than *Ixodes ricinus*. Two other species, the Karoo paralysis tick *Ixodes rubicundus* in southern Africa, and *Ixodes holocyclus* in Australia, cause paralysis in mammals. Lyme disease is transmitted by *Ixodes rincinus* in Europe, *Ixodes scapularis* in the Eastern U.S. and *Ixodes pacificus* in the Pacific coast states and intermountain west of the U.S. *Ixodes pacificus* is a major cause of tick paralysis.

The European sheep tick, *Ixodes ricinus,* is a three-host tick with a 2- to 6-year life cycle depending on location. Immatures attack birds, but sheep can be the hosts for all three life stages. This tick has separate spring and fall feeding populations. The larvae, seek a host in the spring or fall, feed for 3–6 days, then drop off and molt. After molting, the larvae ascend grass and twigs to assume a questing position but, here, they tend to lose body water causing them to descend to a microclimate on or near the ground where water is at or near saturation. They rehydrate in this microclimate. The nymphs seek a host the next spring or fall, engorge for 3–5 days, then drop off the host and molt. The adults seek a host the next spring or fall. Females take from 5 to 14 days to complete feeding. Fertilized females lay from 500 to 2,000 eggs that hatch by late spring or late fall, but the larvae usually do not feed until the following spring or fall.

Ixodes scapularis is found from Maine south to Florida and west into central Texas and possibly Mexico, and from Maine west into Minnesota and Iowa. It is a small three-host tick that attacks a wide variety of birds and mammals including man. Larvae and nymphs attack small rodents especially the white footed mouse *Peromyscus leucopus*. Adults occur on larger animals with the white-tailed deer *Odocoileus virginianus* being the most common. A large population of deer is an important factor in the presence of large populations of *Ixodes scapularis*. Changes in agriculture and patterns of human use in the eastern U.S. have resulted in humans coming more into contact with areas supporting populations of *Ixodes scapularis*. The tick population in these areas has increased dramatically due to the increase in the deer population. This tick is an important vector of the causative agent of Lyme disease, human babesiosis and human granulocytic ehrlichiosis. The Western black legged tick, *Ixodes pacificus*, is found on the pacific coast states and British Columbia. It is closely related to *Ixodes scapularis*. Immatures of *Ixodes pacificus* feed on small rodents and lizards, the adults feed on deer, horses and man. Throughout its range, this tick occurs in regions of higher mositure. *Ixodes pacificus* transmits the causative agent of Lyme disease and equine granulocytic ehrlichiosis.

Species of *Dermacentor* are mostly large, ornate, brevirostrate ticks with eyes and festoons. This genus is most common in the New World. *Dermacentor marginatus* transmits Siberian tick typhus and *Dermacentor reticulatus* infests livestock. Both occur throughout Europe and Asia. *Dermacentor albipictus*, the winter tick, occurs from the west coast to the east coast of Canada and far north to almost 60°N latitude. This one-host tick does not feed during the summer. Heavy infestations on large horned animals such as moose can result in death. The Pacific Coast tick, *Dermacentor occidentalis*, is found from Oregon to California where it transmits anaplasmosis. This species also causes paralysis in livestock and deer.

The American dog-tick, *D. variabilis,* occurs in the central and eastern United States (U.S.) northward into southern Canada and Nova Scotia. The American dog tick vectors the *Rickettsia* bacteria that causes Rocky Mountain spotted fever, the bacterium that causes tularemia and anaplasmosis. *D. variabilis* is an important pest of domestic animals and man throughout its range. It can cause canine paralysis. In the southern U.S., a life cycle can be completed in 3 months under favorable conditions. However, in the northern regions of its distribution, a life cycle can take 2 years. *D. variabilis* has expanded its range in recent years. It is found in the mid-western U.S. and Pacific states where local populations have been established, mostly along river valleys. Northward expansion is probably limited by cold temperature because the tick has not established breeding populations beyond the mean winter (December–February) 0°C isotherm. Westward expansion is probably limited by the lack of rainfall and deciduous forests or brushy habitats. The American dog-tick prefers field-forest ecotones. *D. variabilis* is a three-host tick. Replete females drop from the host and, within 4–10 days, lay a clutch of 4,000–6,500 eggs preferably in cracks and crevices on the ground. In the summer, the eggs begin to hatch in about 35 days depending on the temperature. The larvae feed mostly on wild mice and voles for 3–12 days then drop off and molt to nymphs. The nymphs also prefer wild mice and voles as hosts. They feed for 3–11 days then drop off to molt on the ground and emerge as adults. The adults prefer dogs and other larger mammals including man. The females engorge in 6–13 days. Mating takes place on the host. Unfed adults may live for more than 2 years.

The Rocky Mountain wood tick, *D. andersoni*, occurs in the western U.S. and British Columbia. It is a three-host tick with a similar life cycle to that of *D. variabilis*. The adults prefer large mammals, the nymphs smaller mammals and the larvae feed mostly on wild mice. *D. andersoni* transmits the causative agents of Rocky Mountain spotted fever, Colorado tick fever and anaplasmosis. The tick causes paralysis in mammals.

The genus *Anocentor* has a single species, the Neotropical ear tick of horses, *A. nitens*, found in the southern U.S. westward to Texas and southward to Brazil. This one-host tick has no ornamentation and the eyes are obsolescent. Some workers place this tick in the genus *Dermacentor*.

Nosomma has a single species, *N. monstrosum*, which has a wide range of hosts including cattle, buffalo, humans, boar, bear, horses and dogs, with the larvae infesting rodents. This three-host tick occurs in India and Southeast Asia.

Species of *Rhipicephalus* are brevirostrate, small, mostly inornate ticks. This genus is found in the Old World, mainly in Africa south of the Sahara and southern Arabia. One species, the brown or red dog tick *R. sanguineus*, is now cosmopolitan with a greater geographical distribution than any other species of tick. *R. sanguineus* has a wide host range preferring dogs and other carnivores, some large herbivores, lagamorphs, rodents, bats, reptiles, and some primates including humans. This tick is a warm-climate species that probably originated in Africa. Its ability to colonize shelters in cold climates has significantly contributed to its distribution. The brown dog tick vectors *Babesia canis* and *Rickettsia conorii*. The latter pathogen causes boutonneuse fever. In some areas of Mexico, this tick transmits *Rickettsia rickettsii* that causes Rocky Mountain spotted fever.

Other important species of *Rhipicephalus* on domestic animals are the brown ear tick *R. appendiculatus*, *R. evertsi* and *R. simus*. *R. appendiculatus* is a three-host tick that occurs in the eastern and southern parts of Africa south of the equator. This tick is found on goats and sheep but is mostly a parasite of cattle. Its distribution reflects an interaction between climate, vegetation and hosts. It is thought that the presence of cattle is necessary for the tick to become established. Temperatures around 4°C will kill all stages of engorged *R. appendiculatus*. A dry climate prevents eggs from hatching through desiccation. Under ideal conditions, a life cycle in this tick can be completed in 3–4 months. The number of cycles per year depend on the local conditions. In southern Africa, there is one generation per year, but in Tanzania, two generations per year can occur under optimal conditions. *R. appendiculatus* vectors *Theileria parva* which causes east coast fever in cattle, the Nanovirus that causes Nairobi sheep disease, and *Babesia bigemina* that causes babesiosis in cattle.

The two-host African red tick, *R. evertsi*, infests domestic cattle, goats, sheep and wild ungulates. The eggs of this tick hatch on the ground and the larvae seek a host animal where they attach to the inner surface of the ear. After feeding to repletion, larvae detach and molt into nymphs that attach in the same area of the ear and feed to repletion then drop off the host to molt on the ground. The adults seek a second host, attaching mostly in the perianal region under the base of the tail or less commonly on the teats, the base of the legs, or the scrotum. Here they mate and females feed to repletion then drop off to lay eggs on the ground.

All five species of *Boophilus* are brevostriate, one-host ticks and all are parasites on large hoofed mammals, especially cattle. No festoons, or eyes are present. Three species are important vectors of babesiosis to cattle: *B. microplus*, the cattle tick, is found in the Neotropical, Afrotropical and Australian regions; *B. decoloratus* occurs in tropical Africa; and *B. annulatus* is found in North America. The life cycle of *B. microplus* is completed in about 5 weeks under favorable conditions and can require up to several months under less favorable conditions. Females lay a single clutch of 2,000–3,000 eggs that hatch in about 2 weeks at 70% humidity. Larvae quest on the tips of grass and twigs but do not move down to rehydrate in a microenivronment. Larvae feed for about 4 days on the host then molt into a nymph after a quiescent period of about 2 days. The nymphs may move about the host before attaching. They feed for about a week and then molt into an adult. This molt is also preceded by a short quiescent period. The adults mate on the host. The females take about 3 weeks to feed to repletion, then drop off to lay eggs. The oviposition period lasts some 10 days and is preceded by a short preoviposition period of several days. *B. microplus* must have a high rainfall, and cannot be found in dry areas with a low humidity. This tick is widespread throughout the warmer climates of the world. In the tropics, *B. microplus* are found on cattle throughout the year. In subtropical regions, it has a seasonal cycle. A commercial vaccine has been developed against "concealed antigens" of the tick midgut. This vaccine has reduced tick fertility by as much as 70% in some cases. Booster shots are necessary.

Some species of *Margaropus*, infest giraffes in the Sudan and East Africa, but *M. winthemi*, the winter horse tick, is a parasite on horses in southern Africa. *Margaropus* are one-host ticks that are considered relic boophilids.

Amblyomma are mostly large, highly ornamented, longirostrate ticks with eyes and festoons. Most species occur in the tropics. All have a three-host life cycle. Their long mouthparts are especially damaging to cattle hides. Species from the southern U.S. are the only members of this genus from the temperate region, although some nymphs occur on migratory birds from Africa northward through Europe and Asia. The African brown ear tick, *A. appendiculatus*, and the tropical bont tick, *A. variegatum*, transmit *Cowdria ruminantium*, the causative agent of heartwater fever in cattle. *A. nuttali* has the distinction of producing the largest clutch of eggs ever recorded from a single tick, over 22,000.

The lone star tick, *Amblyomma americanum*, is found across the southeastern U.S. from central Texas to the Atlantic coast and north to New York. It prefers a forested habitat. The questing activity of this tick is most active from sundown to the late evening hours when its principle host, white-tail deer, forage. Large numbers of ticks occur in, or near, the bedding of hosts. Active stages have no host preference. Immatures are found on birds and all sizes of mammals, but adults occur mostly on medium to large mammals. All stages of this tick attack man. *Amblyomma americanum* is well adapted to forest communities. Two factors that must be present to support large populations of *Amblyomma americanum* are suitable hosts, and a moist microenvironment to protect the ticks from desiccation. An area with a forest canopy and lots of vegetative ground cover is ideal habitat for *Amblyomma americanum*. Male ticks are found on deer all year. Engorgement of the females may be a photoperiod response as there is a small drop-off period that begins in May, and is over in late August. The larvae first occur on deer in late June and continue until mid-November. The nymphal activity, which occurs from March to October, is the longest of any stage. The lone star tick is a vector of Rocky Mountain spotted fever and Q fever.

The Cayenne tick, *Amblyomma cajennense*, is also found in the southwestern U.S. south through Mexico and Central and South America and the West Indies. It commonly attacks man and many other animals. It transmits Rocky Mountain spotted fever from Mexico south to Brazil. The Gulf Coast tick, *A. maculatum*, is a parasite on deer and cattle. The deer population has dramatically increased, and this has resulted in an increase in the population of *A. maculatum*.

Some or all species of *Hyalomma* are longirostrate, medium-sized ticks with eyes that may or may not have festoons and scutal ornamentations. This genus most likely originated in the dry deserts of Kazakhstan and Iran in the Palaearctic. Some or all species of *Hyalomma* are hardy ticks. Several economically important species exist. The *H. marginatum* complex and *H. anatolicum anatolicum* are major vectors of the arbovirus that causes Crimean-Congo haemorrhagic fever. The *H. marginatum* complex extends from India and Indochina westward throughout southern and southeastern Europe into the Near East and North Africa. Populations are scattered throughout the drier areas of Africa south of the Sahara from the Red Sea to the Atlantic Ocean. Hosts of immature ticks in this complex include wild birds, small mammals, hedgehogs and hares. The adults attack any domestic animal especially cattle, horses and camels. Migrating birds are important in spreading these ticks. A typical *H. marginatum* life cycle is completed in 116 days at 18–19°C. All stages of this tick complete feeding in about 6 days. The females lay from 4,300 to 15,500 eggs in a single clutch. Unfed adults can live for over a year.

Species of *Haemaphysalis* are small, inornate, brevirostrate ticks. The genus is most common in the tropics where it probably originated. *H. punctata* in the Australian region, and *H. longicornis* in the Oriental region, are important parasites of cattle. The latter tick is also found on red deer in New Zealand. *H. leachi*, the yellow dog tick of Africa, is a common parasite of dogs and carnivores throughout the tropics and subtropics of Asia and Africa. It transmits the protozoan pathogen of malignant jaundice in dogs. In the Oriental region, *H. spinigera* transmits the arbovirus that causes Kyasanur Forest Disease. Two species of *Haemaphysalis* occur in North America. The rabbit tick, *H. leporispalustris*, occurs in the New World from Alaska south to Argentina. It has a large host list that includes horses, cats, dogs and birds. It rarely attacks man, but is responsible for the transmission of Rocky Mountain spotted fever and tularemia among wild animals. The bird tick *H. chordelis*, is common on upland game birds in North America and is an important parasite of turkeys. *H. mageshimaensis* is found in Japan, and is rare in that it has both bisexual and parthenogenetic reproduction.

Economic Importance of Ticks

Ticks are of great economic importance. Many disorders are caused directly by the interaction of the host to the tick. These can occur locally at the tick bite area, but some are systemic such as toxic reactions, or toxicoses and host paralysis produced by tick toxins. Ticks have a high vector potential and transmit more varieties of serious diseases to vertebrates than any other blood feeding arthropod. They are second behind mosquitoes in transmitting diseases to humans, and first in veterinary importance. Some species of ticks have a toxin in their saliva that can cause death through paralysis. Another of the many afflictions imposed on their host has to do with blood loss through heavy tick burdens. Large mammals can harbor enormous numbers of ticks. A moose can have more than 50,000 ticks feeding on it at any given time, as can a small giraffe. The record is probably a single caribou found with more than 400,000 ticks. Heavy tick infestations also occur in livestock and companion animals where loss of blood can result in the development of anemia, or in extreme cases, death.

Several superficial local disorders such as dermatosis, inflammation, itching, swelling and ulceration can occur at the tick feeding site. In some individuals, tick feeding can produce a hypersensitivity reaction that can be local, or in severe cases, systemic, and can even result in anaphylactic shock. These reactions usually occur early in the course of tick feeding. The feeding site can become a means of secondary infections from pathogens not transmitted by the tick. The infestation of the auditory canal by ticks, otocariasis, can cause serious secondary infections. Proper removal of ticks is important to minimize secondary infections because skin ulceration and lesions can result from improper or partial removal of tick mouth parts.

Tick toxins introduced into the host through the saliva cause paralysis or death in domestic animals, some wildlife, and humans. Tick paralysis manifests itself as a motor paralysis that spreads from the lower limbs to the upper limbs and head region within hours. Paralysis rescinds following removal of the tick, or ticks, except in the case of *Ixodes holocyclus*, which is discussed below. Paralysis is most likely to occur when a tick embeds on the neck, especially near the base of the skull. Many different ticks can cause paralysis, but five species are notorious. These are *Dermacentor andersoni* and *Dermacentor variabilis* in North America; *Ixodes rubicundus*, *Rhipicephalus evertsi evertsi* and *Argas walkerae* in South Africa; and the Australian paralysis, or scrub tick, *I. holocyclus* in Australia. The toxin of the latter tick, known as holocyclotoxin, has been isolated, characterized and an antitoxin developed. The scrub tick is the most virulent paralysis tick in the world. Most cases of paralysis are caused by females because larvae and nymphs have much less toxin, and the adult males feed only by inserting their mouthparts into females. Removal of *I. holocyclus* does not rescind the paralysis, which must be treated by an antitoxin given intravenously.

The high vector potential of ticks is a direct result of the following characteristics: (i) Ticks are persistent blood feeders that stay attached to the host for long periods allowing ample time for the transfer of pathogens. Hard ticks feed for 5–14 days depending on the species. (ii) Ticks have great longevity that enhances the chances of acquiring and transmitting pathogens. (iii) Ticks have a high reproductive potential. Hard ticks lay a single clutch of eggs that can number over 20,000 depending on the species. (iv) Ticks have few natural enemies due to heavy body sclerotization. (v) Pathogens in ticks can persist through transovarial transmission to the next generation, and from one life stage to another through transstadial transmission. (vi) Ticks transmit pathogens through several routes. Most are transmitted through the saliva, but some *Borrelia* are transmitted through the coxal fluid. Stercoral transmission occurs through the feces and requires pathogens that can survive in the dry excrement of ticks, so this route is uncommon. However, *Coxiella burnetti* and *Rickettsia conori* are transmitted in this fashion. (vii) Some pathogens are transmitted directly from an infected tick to a non-infected tick while both are feeding on the same host. This phenomena is termed co-feeding and may be an important means of maintaining tick-borne pathogens. Anti-hemostatic, anti-inflammatory and immnuosuppresant actions of tick saliva facilitate blood-feeding and may indirectly enhance pathogen transmission. This is termed saliva-activated transmission (SAT). In some diseases, such as tick-borne encephalitis, uninfected ticks can acquire the pathogen when co-feeding with infected ticks on hosts that do not exhibit a viremia, or systematic infection. This phenomenon is known as non-viremic transmission and may be due to SAT. Bacterial pathogens may be acquired by continuing to feed at a localized site where previously infected ticks have fed.

Tick transmitted pathogens include arboviruses (arthropod-borne viruses), rickettsiae, other bacteria, and protozoans. Most tick-borne diseases are zoonoses, that is they occur in wild and or domestic animals that act as a natural reservoir of infection. Man is only an incidental host in many of these diseases. Some zoonotic diseases are transmitted within their natural reservoirs by a species of tick that does not attack man. A different tick species then transmits the disease to man. If the zoonoses includes a large wild animal reservoir with multiple vector species of ticks it becomes difficult to control.

Tick-borne arboviruses are members of three families, the Flaviviridae, the Bunyaviridae and the Reoviridae. The Flaviviridae includes the genus *Flavivirus* whose virons are spherical, about 40–50 nm in diameter with a lipoprotein envelope, and a genome that consists of a single molecule of single-stranded RNA. The Bunyaviridae includes the genus *Nairovirus* in which all species are transmitted by ticks. The *Nairovirus* are spherical in shape, 80–100 nm in diameter, with a lipid envelope that has glycoprotein projections. Their genome consists of three molecules of single-stranded RNA. The Reoviridae contain the genus *Orbivirus* which causes Colorado tick fever. This virus is icosahedral in shape, 60–80 nm in diameter, with an outer protein coat and a genome of 12 pieces of RNA. All tick-borne arboviruses replicate in intermediate vertebrate hosts as well as in the tick. The major arboviral diseases transmitted by ticks include Tick-Borne Encephalitis, Louping Ill, Omsk Hemorrhagic Fever, Kyasanur Forest Disease, Powassan Encephalitis, Crimean-Congo Hemorrhagic Fever, Nairobi Sheep Disease, Colorado Tick Fever and African Swine Fever. Other lesser known tick-borne arboviral diseases occur in birds, especially seabirds. Treatment for human arbovirus diseases is often relegated to supportive measures. Hospitalization can help especially if a high fever or other symptoms can be treated.

Tick-Borne Encephalitis (TBE) is caused by a *Flavivirus* and can affect humans, sheep, monkeys, mice and hamsters. It is transmitted by species of *Ixodes*. In Europe and Northern Asia, it is transmitted mostly by *Ixodes ricinus*, and in areas of the Far East by *I. persulcatus*. TBE can also be transmitted through fresh milk or cheese from infected goats or sheep. TBE is most common during spring and summer. The disease is maintained in nature by infections of small mammals such as rodents. Agricultural and forest workers are most at risk of infection, but urban residents that spend time in the forests and countryside are also at risk.

Two subtypes of TBE are recognized, Russian Spring-Summer encephalitis (RSSE), which is found in Siberia, the southern republics of the former Soviet Union and in north-eastern China; and Central European Encephalitis (CEE), which occurs in Russia west of the Ural mountains and Europe. RSEE is more serious than CEE. RSSE is a life-threatening disease with a mortality rate of from 8% to 54%. However, an effective vaccine exists. RSSE is characterized by high fever, headache, nausea followed by the symptoms of developing encephalitis, which include paralysis especially in the upper body regions. Paralysis may persist in some patients that have recovered. The milder European form is biphasic with a brief remission after 4–6 days of illness followed by renewed fever. Brain dysfunction and meningeal irritation are common. Mortality in the milder CEE subtype is from 1% to 5%.

Louping Ill (LI) is caused by a *Flavivirus* and is found in Great Britain where it has been known for centuries among sheepherders in Scotland and Ireland. LI infects a variety of mammals including man, and some birds, especially upland game birds. The virus is transmitted by *I. ricinus*. Transstadial, but not transovarian, transmission occurs. The disease is so named because it causes an erratic "louping" gait in sheep. The mortality in sheep is severe, often as high as 60%, and has been known to reach 100%. LI causes a severe, fatal encephalitis that often results in permanent neurologic damage in animals that recover. In humans, LI also produces an encephalitis that can be severe and even result in death. Those at risk include farmers, veterinarians, and animal husbandry workers. A vaccine for sheep exists, but sick animals are destroyed. Lambs are protected by a maternal antibody that disappears after weaning.

Omsk Hemorrhagic Fever (OHF) is caused by a *Flavivirus* and affects humans, rats, mice, muskrats and wild rodents. OHF occurs in Siberia and is transmitted by *D. reticulatus* and *I. apronophorus*. Immature *D. reticulatus* ticks bite mostly water voles, which are found in a forest-steppe habitat. The cyclic nature of the vole population can produce a huge population of ticks, many of whom are infected with the virus. Adult *D. reticulatus* ticks infect several different large mammals and humans. The tick is the reservoir, which is maintained by transovarial transmission. *I. apronophorus* does not transmit the virus to humans, but is thought to help maintain the virus in nature by feeding on many different small mammals especially voles and muskrats. Muskrats have a high incidence of infection (up to 30% of the population). Transmission of OHF to humans can occur through handling infected muskrat carcasses, or by drinking infected water contaminated by muskrats or voles. Muskrats are amplifying hosts for the disease. Hunters of muskrats are at severe risk. The disease occurs during the spring and summer seasons. OHF is characterized by hemorrhagic symptoms. Mortality is less than 5%. No vaccine is available, but some cross-protection occurs with the Tick-Borne Encephalitis vaccine.

Kyasanur Forest Disease (KFD), caused by a *Flavivirus* affects humans and monkeys. KFD occurs in the Kyasanur State Forest and a surrounding area in India where it is transmitted by *H. spinigera*. Increased human activity in the forest has increased the opportunity of this tick to attack humans. The pathogen is maintained within a given tick by the transstadial route, but is not transmitted transovarially. KFD has a sudden onset after a short incubation period (2–7 days). Symptoms include coughing, diarrhea, vomiting, a severe fever for up to 12 days and muscle pain. Mortality is 8–10%. Monkeys are very susceptible to KFD. They are viremic for days, during which time they have many ticks feeding on them. In this fashion, monkeys act as an amplifying host for the disease. Human cases of this disease are increasing. Individuals working in the forest are especially at risk, however, an effective vaccine exists.

Powassan Encephalitis (PE) is caused by a *Flavivirus*. It occurs in Canada, Russia and northeastern parts of the U.S. where it has been isolated from a variety of vertebrates and causes a sickness in humans, horses, and foxes. PE is transmitted by several species of *Ixodes*, *Dermacentor* and *Haemaphysalis*. *I. cookei* is an important vector of PE in North America. No vaccine for PE exists.

Crimean-Congo Hemorrhagic Fever (CCHF) is caused by a *Nairovirus* that is transmitted by a wide range of tick species. It was first described in ad 1100. CCHF is widely distributed throughout Europe, Asia and Africa, and is most common in arid or semiarid regions of these areas. CCHF is transmitted mostly by ticks of the genus *Hyalomma*, or by contact with blood or tissues from human patients or infected livestock. Person to person spread can occur through respiratory secretions and excreta, which can cause serious outbreaks of the disease in hospitals. In Eurasia, *Hyalomma marginatum marginatum* and *D. marginatus* are the principal vectors. The clinical disease has been found only in humans, but the virus occurs in a wide variety of mammals. CCHF is found in isolated enzootic foci throughout its range. An enzootic disease occurs in a population of animals at all times. Ground-feeding birds are important in maintaining the disease and migratory birds are important in its spread. Incubation of CCHF takes from 3 to 7 days. The disease has a sudden onset with fever, chills, photophobia and severe headache. Muscle pain occurs mostly in the legs and back. The hemorrhagic state of the disease involves bleeding from the mucous membranes and the appearance of a round red spot, which is due to intradermal hemorrhage. Mortality is from 10% to 50%. Ticks are the reservoirs of CCHF. The rate of infection in ticks is amplified by feeding on infected mammalian hosts, and by transstadial and transovarial transmission. A vaccine exists in Russia and parts of Eastern Europe. Controlling this disease is very difficult due to its widespread distribution and the large number of different tick species involved.

Nairobi Sheep Disease (NSD), also known as Ganjam virus disease, is caused by a *Nairovirus*. NSD is found in sheep, goats, and wild ruminants in East Africa. The principle tick vector is *R. appendiculatus*. There is no evidence for a wildlife reservoir. Onset of the disease is sudden with a dramatic rise in temperature as high as 41°C. A nasal discharge and diarrhea is common, along with abdominal pain. Mortality is high. Humans exposed to the virus develop an antibody, but no symptoms, with the exception of one case. Treatment of NSD involves destroying sick animals. In areas of enzootic NSD, sheep are protected by a maternal antibody. Epizootics, diseases that spread rapidly through an animal population, are related to large increases in the vector populations and require the use of acaricides.

Colorado Tick Fever (CTF) is caused by an *Orbivirus*, and is found in the Western U.S. where it infects humans and many other mammals. The principle vector to humans is *Dermacentor andersoni*. Transovarian transmission does not occur. The disease is enzootic in wild rodents. Wherever the principle vector occurs with infected reservoirs of wild rodents and humans, local outbreaks will occur. CTF has a short incubation period in humans of 1–4 days. A biphasic fever occurs in about 50% of the cases. Symptoms include chills, nausea, sore throat and retroorbital pain. Sometimes meningitis occurs, and leukopenia is common. However, mortality is low, less than 0.2%. The peak incidence of CTF occurs from April to July. Treatment is supportive and no vaccine exists. Prevention of tick infestation in focal areas of the disease is the best method of control.

African Swine Fever (ASF) occurs in Europe, Africa, South America and the Caribbean. This icosahedral-shaped virus is about 200 nm in diameter with a lipoprotein coat and a single molecule of double-stranded DNA. It is the only known DNA virus to be transmitted by an arthropod. Originally, it was placed in the family Iridoviridae, but is now unassigned to any family. Wild swine, including warthogs, harbor the virus. Domestic pigs are at risk with the mortality being as high as 100% in herds. Several species of *Ornithodoros* have been shown to be vector-competent in the laboratory, but the only natural vectors are

O. erraticus and *O. m. porcinus*. Transstadial, transovarial and sexual transmission of ASF has been shown to exist in *O. moubata*. Many of the vector-competent species exist outside the known distribution of ASF suggesting that the disease has a good possibility of spreading. ASF is characterized by sporadic epizootics. Ticks are not the only way of spreading the disease, direct contact with animals is also a factor. Three forms of the disease are known in domestic pigs – acute ASF, subacute ASF and chronic ASF. Acute ASF causes a high fever (up to 41°C) about 3 days following infection. Then the fever subsides and the animal dies. In the subacute form of ASF, the fever follows an irregular course for 3–4 weeks, then the sick pigs either die, or recover and become carriers of the virus. In chronic ASF, the main symptoms are stunted growth and emaciation. In chronic ASF, sick pigs often remain carriers and can live for a long time. They eventually die from a secondary illness.

The *Rickettsia* are bacteria that are obligate, intracellular parasites of vertebrates. Unlike viruses, they have both DNA, RNA and bacterial cell walls. During evolution, the *Rickettsia* have lost several enzymes and cell components necessary to live outside the cell. Some 15 genera of *Rickettsia* are recognized, seven of which are transmitted by ticks: *Rickettsia*, *Coxiella*, *Ehrlichia*, *Cowdria*, *Anaplasma*, *Aegyptianella*, and *Haemobartonella*.

Rickettsia are divided into three groups, each containing serologically related species. Two groups, the Spotted Fever Group (SFG), and the Typhus Group (TG) are transmitted by ticks. The third group, the Scrub Typhus Group, is transmitted by a mite. The only species of TG transmitted by ticks is *R. canada*, which was first isolated from rabbit ticks in Ontario. *R. canada* has not yet been shown to cause a human disease despite a single case of possible human infection where the patient presented with Rocky Mountain Fever-like symptoms. The SFG is made up of the following species: *R. rickettsii*, *R. montana*, *R. belii*, *R. rhipicephali*, *R. parkeri*, *R. conorii*, *R. australis*, *R. sibirica*, *R. slovaca*, *R. helvetica*, and *R. akari*. In general, species of the SFG cause severe diseases characterized by headache, chills and fever. These rickettsiae grow mainly in the cytoplasm of the host's cells, but can also grow in the nucleus. Infected host cells are seldom killed by SFG rickettsiae. They have an optimal growth temperature of 32–34°C. They do not cause hemolysis. The associated rash in humans is the result of damage to capillaries that causes blood to leak out. SFG rickettsia can cause collapse of the cardiovascular system.

Several SFG rickettsiae are not associated with human disease. *Rickettsia parkeri* occurs in *A. maculatum* and *Amblyomma americanum*, from Texas through Mississippi and Georgia. The principle hosts are domestic animals. *Rickettsia montana* is found in *D. andersoni* and *D. variabilis* in at least 13 states in the U.S. and is maintained naturally by small mammals. *Rickettsia rhipicephali* is found in *R. sanguineus*, *D. andersoni*, *D. variabilis*, and *D. occidentalis* in the southeastern U.S., and is maintained by small mammals. It is not pathogenic in dogs. *Rickettsia belii* is found in *D. andersoni*, *D. variabilis*, *D. occidentalis*, *D. albipictus*, *H. leporispalustris*, *A. cooleyi*, and *O. concanensis* in eight states in the U.S. Again, it is maintained in nature by small mammals.

A species of tick can harbor more than one serotype of *Rickettsia*. However, experimental evidence shows that a serotype present in a given tick interferes with the establishment of another serotype of *Rickettsia*. This phenomena is termed rickettsial interference. Ticks are considered the reservoir of infection in rickettsial diseases. This is due to the fact that infected animals remain rickettsemic for just several days and horizontal transmission of rickettsiae from an infected animal to a feeding tick is not as efficient as transstadial and transovarial transmission. Venereal transmission of rickettsiae in ticks during mating does not occur.

Treatment of rickettesial diseases is greatly dependent on the proper early diagnosis of the disease. Several effective antibiotics exist including tetracyclines, doxycyclines, chloramphenical, chloromycetin and cotrimexazol.

The most severe disease caused by SFG rickettsiae is Rocky Mountain Spotted fever (RMSF) caused by *R. rickettsii*. This disease is covered in a separate entry. The other human diseases caused by SFG rickettsiae are discussed below.

Boutonneuse Fever (BF) (=Mediterranean spotted fever, Fievre Boutonneuse, Marseilles fever, Kenya tick typhus, South African tick bite fever, Indian tick typhus) is caused by *Rickettsia conorii*, which is closely related to *R. rickettsii*. BF is widely distributed in Southern Europe, Africa, Western and Central Asia and India. It can be transmitted by many species of hard ticks. The principle vector in the Mediterranean is *R. sanguineus*, while in southern Africa, *R. evertsi*, *A. hebraeum*, *H. leachi* and *R. sanguineus* transmit the disease. In India, *I. ricinus*, *H. leachi* and *R. sanguineus* are vectors. BF is maintained in nature by a wide variety of smaller mammals. It is principally a seasonal disease. Endemic areas exist in Israel and throughout Africa. The disease is characterized by chills, fever, lymphadenitis, headaches and joint and muscle aches following a 5- to 7-day incubation period. Fever can reach 40°C. A distinctive ulcer, known as a tache noire, is covered with a black crust and appears at the site of the tick bite. Untreated cases recover, but some virulent strains can result in death. The pathology is similar to RMSF, but milder. Vaccines are not available. Control of ticks on dogs is the most effective method of preventing the disease.

North Asian Tick Typhus (NATT), is caused by *Rickettsia siberia*, and is transmitted by species of *Dermacentor*, *Hyalomma* and *Haemaphysalis*. The most common are *D. marginatus*, *D. silvarum*, *D. reticulatus*, *D. nuttalli*, *Hy. asiaticum*, *Hy. japonicum*, *H. punctata* and *H. concina*. NATT occurs from Siberia to Mongolia, and from Central Asia to Eastern Europe. Natural foci of this diseases exist in populations of small mammals. Ticks can harbor *R. siberia* for long periods of time. The pathogen is moved through the tick's life cycle by transstadial and transovarial transmission. In the former Soviet Union, NATT most commonly occurs in farm workers. It occurs from spring to fall. After an incubation period that lasts about a week, the disease manifests as chills and a fever that becomes intermittent after about a week. A small lesion may develop at the tick bite. A rash appears on the extremities and spreads to the trunk.

Queensland Tick Typhus (QTT) is caused by *Rickettsia australis* and transmitted by *I. holocyclus*, and possibly other species of this genus. The disease occurs in Queensland, Australia, mostly in a savanna habitat with intermittent rain forest. A large population of rodents and marsupials is necessary to support the tick population. QTT is a mild disease. The incubation period varies from a few days to over a week. QTT manifests as a general malaise, headache and a mild fever pattern that is often remittent. The tick bite site shows an eschar, a lesion similar to that of the tache noire seen in Boutenneuse fever. Nearby lymph nodes are enlarged and painful. A variable rash appears.

Q-Fever (QF), also known as nine mile fever or the Balkan grippe, is caused by the rickettsiae *Coxiella burnetii*, and is transmitted by many species of hard and soft ticks. The disease was first recognized in Australia in 1936, where the Q in Q-fever came from the word "Query." The disease is world wide in distribution, except in Antarctica. The pathogen is found in small mammals, reptiles, birds and domestic animals. *Rickettsia* are shed in the feces of infected animals. Unlike other members of the *Rickettsia*, *C. burnetii* can survive long period outside the host cells. It is believed to be able to survive up to 6 years in tick feces. This hardiness may be due to the presence of a spore-like cell in its life cycle. *Coxiella burnetii* is only secondarily transmitted by ticks. Most commonly, it is transmitted through airborne transmission, consumption of infected milk, handling of contaminated wool or hides, infected animal feces, animal bedding and contaminated clothing. The most susceptible people are agriculture and laboratory workers where sheep and goats are used for scientific experiments. The pathogen can enter the body through abrasions in the skin, inhalation in the lungs, mucous membranes, the gastrointestinal tract and possibly placental transfer. The disease has an incubation period of about 20 days. It starts with a sudden fever of 38–40°C which may last for up to 2 weeks and can have a biphasic pattern. Headache, diarrhea, sore throat, sweats and chills also occur. A rash is usually absent, but when it occurs, is found on the trunk and shoulders. Pneumonia can occur in some areas with acute Q-fever. Mortality rates usually are less than 1%, and a vaccine exists.

Ehrlichia are obligate, intracellular parasites of white blood cells, especially monocytes. They cause ehrlichiosis, a serious and sometimes fatal blood disease in animals and humans. Canine ehrlichiosis, caused by *Ehrlichia canis*, and transmitted by *R. sanguineus*, is found world wide. Following an incubation period of about 2 weeks, the infected dog has a fever that can reach 40.5°C, edema, anorexia, conjunctivitis and pancytopenia. Dogs lose weight. In most breeds, the disease has a mild form, but in German shepherds, it may produce a severe hemorrhagic condition known as tropical canine pancytopenia. Ehrlichiosis can persist in dogs for years without clinical symptoms. *E. ewingii* causes canine granulocytic ehrlichiosis, a similar but less severe disease. *E. (=Cytoecetes) phagocytophila*, is transmitted to cattle and to sheep by *I. ricinus*. The disease, known as tickborne fever, manifests itself in weight loss, reduced milk production and sometimes abortion. It occurs in Ireland, Great Britain and is widely distributed in Europe. This disease can make young animals, especially lambs, susceptible to other more serious diseases. *E. chaffeensis* causes human ehrlichiosis. The pathogen is believed to be transmitted by *Amblyomma americanum* and *D. variabilis*, but the vector has not been proven. The disease in man is similar to RMSF. However, in human ehrlichiosis, a rash occurs in less than a 33% of patients, and a rash on the palms and feet occurs in less than 5% of patients, which differs from the rash found in RMSF. *E. equi*, which is transmitted by *I. pacificus*, causes equine granulocytic ehrlichiosis in horses and a wide variety of other mammals in California. Several *Ehrlichia* have unknown vectors, but all are assumed to be transmitted by ticks. Examples are *E. risticii*, which causes equine monocytic ehrlichiosis (=Potomac horse fever); *E. bovis*, from cattle; *E. platys*, which infects canine blood platelets; and *E. senetsu*, which causes ehrlichiosis in humans in Japan.

Two important livestock diseases are heartwater, which is caused by *Cowdria ruminantium*, and anaplasmosis, which is caused by three species of *Anaplasma*. Two other species of rickettsiae are transmitted by ticks. *Aegyptianella pullorumn* is transmitted by species of *Argas*, especially *A. persicus*, and causes a disease of fowl that can be severe in young chickens. *Haemobartonella canis*, transmitted by *R. sanguineus*, is found in the red blood cells of dogs, but is not associated with any pathology. *H. canis* is widely distributed throughout the world. It is transmitted by *R. sanguineus*.

Ticks transmit pathogens from four genera of bacteria other than *Rickettsia*. These are *Borrelia*, *Francisella*, *Klebsiella* and *Staphylococcus*. *Borrelia* are helically coiled, Gram-negative, motile spirochetes that cause Lyme disease, several types of relapsing fever, epizootic bovine abortion, bovine borreliosis and fowl (avian) spirochetosis. *Borrelia* are similar to the spirochetes that cause syphilis and Leptospirosis. Lyme disease is covered in a separate entry.

Several species of *Borrelia* cause tick borne relapsing fever, a disease known since ancient times. Each of these species of *Borrelia* is transmitted by a given species of soft tick. Some species of *Borrelia* are transmitted in the coxal fluid of their vectors, but other vector species do not produce coxal fluid until they leave the host and, therefore, transmission must follow a different route. Some vectors, such as *O. hermsi* and *O. turicata*, transmit the spirochetes in their saliva. In Africa south of the Sahara, *B. duttoni* is transmitted by *Ornithodoros moubata*. In Spain, Portugal and northern Africa exclusive of Egypt, *B. hispanica* is transmitted by *O. erraticus* and causes Hispano-African relapsing fever. In Morocco and Libya, *B. crocidurae* is transmitted by *O. erraticus*, and causes North African relapsing fever. *O. erraticus* also transmits *B. merionesi* in Egypt and Senegal, *B. microti* in Kenya and Turkey, and *B. dipodilli* in Iran. All cause relapsing fever. *B. persica* is transmitted by *O. tholozani*, from China through India and Iran to areas of the former USSR into Egypt. It causes Asiatic-African relapsing fever. *B. caucasica* is transmitted by *O. verrucosus* from the Caucasus to Iraq, and causes Caucasian relapsing fever. *B. latyschewii* is transmitted by *O. tartakovskyi* in Iran and central Asia, and causes relapsing fever. American tickborne relapsing fever is caused by at least six different species of *Borrelia*: *B. hermsii* is transmitted by *O. hermsi* in the Western U.S.; *B. turicatae* is transmitted by *O. turicata* in the southwestern U.S.; *B. parkeri* is transmitted by *O. parkeri* in the western U.S.; *B. mazzotti* is transmitted by *O. talaje* in the southern U.S.; and *B. venezuelensis* is transmitted by *O. rudis* in Central and South America. Relapsing fevers are zoonoses that involve the circulation of the *Borrelia* between reservoir hosts and vector species of *Ornithodoros*. With one exception, the primary reservoir hosts of all species of *Borrelia* that cause tick borne relapsing fevers are species of rodents, chipmunks and squirrels. The exception is *B. duttoni*, which has humans as its primary reservoir host. This form of relapsing fever is endemic in Kenya and other East African countries because the vector *O. moubata* has adapted to human dwellings, especially the huts made of mud or straw. Studies on the DNA of the relapsing fever *Borrelia* suggest that all species are closely related.

All tick-borne relapsing fevers have similar clinical features and pathology. Relapsing fever spirochetes migrate rapidly from the bite site into the hosts circulatory system. An incubation period lasts from 2 to 18 days. Symptoms appear abruptly and include headache, fatigue, chills and fever that can be as high as 41°C. Subsequent periods of fever are relapses. The first attack lasts about 3 days, followed by another after 7 days, and one or more attacks after that. The virulence of the disease abates with secondary relapses, which tend to be shorter and milder. Relapses are probably due to the pathogen's change in its antigenicity thus evading the host's immune system. Relapsing fevers are treated with antibiotics. Because all *Ornithodoros* that transmit relapsing fever *Borrelia* are nidicolous, humans are incidental hosts and are not involved in the zoonotic cycle. Relapsing fevers are enzootic and occur in humans as scattered local outbreaks.

Epizootic bovine abortion is caused by *B. coriacease*, and is transmitted by *O. coriaceus*. It is a serious problem in the western U.S. *Bovine borreliosis*, caused by *B. theleri*, is transmitted by the *Boophilis* species and *R. evertsi*. Fowl or avian spirochetosis is caused by *B. anserine*, and is transmitted by *A. persicus*, *A. reflexus*, and *A. miniatus*. All are species of the *Argas* subgenus *Persicargas*. The disease is pathogenic for most domestic fowl, but less so for guinea fowl and pigeons. It occurs world wide mostly as an endemic disease.

Francisella tularensis causes tularemia, which has a worldwide distribution. The most common mammals with the disease are cottontail rabbits, muskrats and rodents. Many species of ticks can transmit the disease. The pathogen undergoes transovarial transmission in ticks. In the U.S., the disease is most commonly associated with rabbit hunting. Transmission can occur in three ways: through the skin, through inhalation of the pathogen and through contaminated water or meat. Each method of transmission produces a distinct form of the disease. Entry of the pathogen through the skin from the bite of a tick results in the ulceroglandular form of tularemia. Following a 2-day incubation period, the patient has a fever of up to 41°C, accompanied by chills and shaking. The fever plus enlarged lymph nodes (buboes) and severe headache can last up to a month in untreated patients. A vaccine exists, but must be administered every 3 years and is not always protective. Streptomycin is effective. *Klebsiella paralytica*, transmitted by *D. albipictus*, causes moose disease in North America. The disease is of limited importance. *Staphylococcus aureus*, transmitted by *I. ricinus*, causes tick pyaemia in sheep in Britain. This disease is not widespread or very pathogenic, and ticks may not be necessary for its transmission.

The protozoan class Piroplasmea contains the genera *Babesia* and *Theileria*. All of whose species are transmitted by ticks. These are parasites of vertebrate blood cells and cause piroplasmosis such as human babesiosis and east coast fever in cattle.

Control of Ticks

The high reproductive rate, host variability, wide dispersion, secretive habits and longevity of many ticks make control difficult. Strategies for tick control involve the reduction of transmitted diseases and the reduction of numbers of ticks on animals to an acceptable economic level. Surveillance of ticks in a given area, which involves determining the species, their population density and any pathogens present, is an important part of any control strategy. Control measures have included one or more of the following: use of pesticides, vaccination of susceptible animals, environmental management, and protection of individual humans. The latter, coupled with education about the species of tick present and its life cycle, is probably the most effective measure to prevent transmission of tick-borne diseases to humans. Biological control, which has proven valuable in controlling many insect pests, has so far not been of much use in controlling ticks. Some parasitic wasps have been released in an attempt to control *D. variabilis* in the northeastern U.S., but this has not proven effective. Oxpeckers are natural agents of biological control and, in Africa, consume large numbers of ticks from ungulates. Likewise, fire ants will eat ticks. How these natural enemies can be used by man to control ticks is unclear.

Pesticides

Pesticides (=acaricides) are applied by spraying a given area, or more commonly, by dipping or spraying individual domestic animals. Other methods of application use a systemic acaricide, or involve controlled delivery systems such as collars impregnated with a slow releasing acaricide. The use of acaricide impregnated cotton fibers that are taken by wild mice to their nests has been successful in reducing populations of *Ixodes scapularis*; or the use of baited stations that dispense the acaricide to the animal when it takes food from the device has been successful in controlling tick populations on domestic livestock in some regions and on deer in the southwestern U.S. The development of resistance to acaricides in recent years and their adverse environmental effects have prompted the use of other means such as vaccines and environmental management to control ticks. Other strategies use pheromones or CO_2 to attract ticks to stations containing pesticides.

Vaccines

Several commercial vaccines against ticks now exist. These all take advantage of the fact that host IgG in the midgut of the tick is immunologically competent, and is transported through the midgut as such into the hemolymph of the tick. The most effective vaccines use concealed antigens. These are antigens from the tick that the host has never been exposed to before being vaccinated. Concealed antigens usually require booster shots of the vaccine.

Environmental Management

Ticks need a suitable habitat and suitable hosts for an abundant population to develop. Habitat modification involves controlled burning, use of herbicides, mowing to destroy vegetation, and plastering to seal cracks and crevices in human dwellings. The latter is an effective control on some species of nidicolous ticks such as *Ornithodoros moubata*. Indigenous herdsman in Africa have used controlled burning for centuries to limit ticks that attack cattle. In some cases, removal of vegetative litter and opening up the ground to intense sunlight by altering the forest canopy has been effective. Reducing or denying hosts is most effective when the target area is isolated and has little possibility of their reintroduction. If a wildlife host exists, control of ticks in an area is very difficult, although fencing has been used with some success to exclude large wildlife hosts such as the Cervidae. It is possible to keep domestic animals out of tick infested areas by rotating pastures.

Protecting Humans

Protecting humans against ticks involves prevention of infestation, and proper removal of attached ticks. Within the urban environment, measures to prevent infestation include strategies to kill and repel ticks inside the home and on companion animals. In the home, foggers and sprays for the house and yard are important. Topical repellants and sprays, anti-tick collars and shampoos are effective means of killing and repelling ticks on dogs and other companion animals. Measures that prevent infestation outside the urban environment involve avoidance of heavily infested areas, especially during high tick activity. If this is not possible, then tucking trousers into exposed socks using some sticky tape and the use of repellents to clothes and or exposed skin (follow the directions on the label). Complete inspection of one's person immediately after leaving the area is essential. Ticks prefer the area around the waist, the axillary region, the genital and perianal region, the neck and the head. It is important to know how to remove ticks because improper removal can result in secondary infections and, in some cases, the transmission of pathogens from the tick to the person removing the tick. Attached ticks should be removed by placing tweezers between the tick and the skin of the host and pulling slowly and gently up until the tick is removed. Once removed, the tick should be examined to make certain that the mouthparts are not still in the host. Once removed, the tick should be saved. Preserve the tick in a container with 70% ethanol or rubbing alcohol. Preserved in this manner, a physician or scientist can identify the tick, and also determine if it is capable of transmitting a disease. Following removal, the bite area should be cleaned, an antiseptic applied and the area covered with a small dressing.

► Mites
► Acaricides or Miticides
► Ticks as Vectors of Pathogens
► Tick Paralysis

References

Coons LB, Alberti G (1999) The Acari-ticks. In: Harrison FW, Foelix R (eds) Microscopic anatomy of invertebrates. Chelicerate Arthropoda, vol. 8B. Wiley-Liss, New York, pp 267–514

Sonenshine DE (1991) Biology of ticks, vol. 1. Oxford University Press, New York, 447 pp

Sonenshine DE (1993) Biology of ticks, vol. 2. Oxford University Press, New York, 465 pp

Sonenshine DE, Mather TN (eds) (1994) Ecological dynamics of tick-borne zoonoses. Oxford Unversity Press, New York, 447 pp

Marquardt WC, Demaree RS, Grieve RB (2000) Parasitology and vector biology, 2nd edn. Harcourt, New York, 702 pp

Ticks as Vectors of Pathogens

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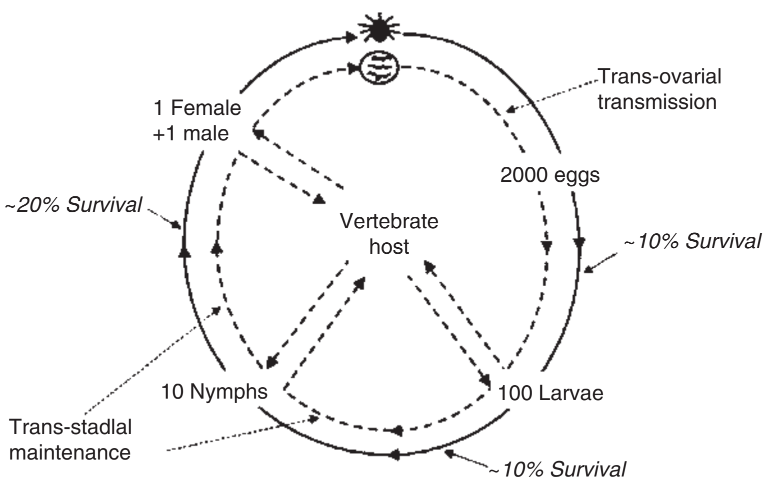
Worldwide, ticks transmit an exceptional number and diversity of micro-parasites (viruses, bacteria, rickettsia, protozoan parasites, even filarial worms) that cause disease in humans and their livestock. In temperate regions, ticks surpass insects in importance as vectors, and a number of "new" tick-borne pathogens recently have been recognized as causing human disease in the northern hemisphere. These include the spirochete bacteria (*Borrelia burgdorferi* s.l.) that cause Lyme disease and the rickettsia *Erhlichia* spp. In reality, however, the burden of these infections pales into insignificance beside the medical and veterinary impact of ticks in the tropics. Added to the ticks' role as vectors, the direct damage they do as parasites is a major brake on livestock productivity. Together, this imposes huge economic burdens where they can least be afforded.

Like most true vectors, ticks are blood feeders, for which they are superbly designed; they cut through the host's skin with a pair of toothed chelicerae and suck up body fluids from the sub-dermal lesion through a hypostome. Yet as vectors, ticks appear to rather poorly designed, lacking the high mobility and frequent feeding habits characteristic of most insect vectors. Ticks have no wings, nor do they jump. Nidiculous (nest-dwelling) Argasid (soft) ticks live in semi-permanent, or seasonally repeated, close association with their hosts. Most Ixodid (hard) ticks are not nidiculous; typically they climb to some vantage point on the vegetation from where they contact a passing host, a procedure that exposes them to considerable moisture stress. Intermittently, they must return to the ground where they can absorb water from the moist air, but this is energetically expensive.

Ticks minimize the costs of achieving contact with their host by taking very few, very large meals. This is taken to extreme by Ixodid ticks, which feed once per life stage, as larvae, nymphs and adults, and reproduce once after the adult meal. Most ticks drop to the ground after each meal, where they develop to the next stage. Some species take both the larval and nymphal meals from the same host, and *Boophilus* ticks, worldwide vectors of cattle babesias, take all three meals from the same individual host before dropping back to the ground. Each meal is enormous; even after concentrating the blood by returning 30–70% of the imbibed fluid to the host via salivary secretions, on average immature tick stages increase their body weight by about one order of magnitude, and adult females by two orders of magnitude. To accommodate such a large volume of blood, ticks secrete new endocuticle during a long phase of very slow blood intake, before engorging rapidly toward the end of the meal that typically takes from about 4 (immature stages) to 14 (adult females) days to complete. This prolonged feeding itself incurs a cost as hosts mount strong hemostatic and immunological defenses; in response, tick saliva contains an impressive cocktail of pharmacologically active components. At the same time, the large volume of saliva can transport large numbers of infective parasites, whose infectivity is enhanced by their entering the host at an immuno-modulated site (Fig. 59).

To exploit as a vector an hematophage that feeds only once per life stage, a parasite must survive trans-stadially. It is acquired from an infected host by a tick of one stage, maintained through the tick's development and moulting processes, and transmitted to a new host by the following tick stage.



Ticks as Vectors of Pathogens, Figure 59 ***Ixodes ricinus*** **life cycle with typical reproduction and mortality rates and pathogen transmission cycle.**

The parasite's transmission cycles are thus determined by the tick's stage-specific host relationships (larvae that acquire infections from one host species may later feed as nymphs on hosts of a different species) and rates of development, survival and reproduction. An infection in one host acquired by many feeding larvae may be retained and transmitted to several new hosts by individuals of one or both of the succeeding stages, nymphs and adults. This achieves horizontal amplification between vertebrate hosts, but as only about 10% of ticks survive from one stage to the next, this route is more limited than it may at first appear. On the other hand, those parasites that are passed trans-ovarially, from females via the eggs to larvae of the next generation, can exploit the tick's impressive fecundity (several thousand eggs) to achieve considerable potential for vertical amplification of prevalence in addition to any horizontal amplification. Even though trans-ovarial transmission is usually inefficient, with less than 20% of an infected tick's larval progeny being infected, nevertheless the abundance of larvae (typically 100 times more numerous than adult ticks and 10 times more than nymphs) can make this route quantitatively significant.

Due to these biological peculiarities of ticks, the quantitative framework (i.e., model) for estimating the transmission potential of tick-borne pathogens differs from that for insect-borne pathogens. The tick's feeding pattern makes the concept of an individual's daily biting rate inappropriate, but, most importantly, it introduces a long delay between acquisition and transmission of an infection. The off-host inter-stadial period, comprising both post-engorgement development and questing for the next host, is functionally equivalent to a very long extrinsic incubation period as the tick is not infective until it is ready to feed again. This period is specific to the vector rather than to the transmitted parasite, and may last from one month to more than a year depending on the tick stage, the temperature-dependent rate of development and whether diapause occurs.

Ticks are renowned for their longevity. Engorged ticks must survive the long, temperature-dependent inter-stadial development periods, and unfed ticks must survive the long period while they quest for hosts, which may not always be available just when and where the tick needs them. Unlike insect vectors, however, a tick's vectorial capacity does not increase proportionally with a prolonged life-span. This is because however long an individual tick survives, it does not feed on and infect more than one host per life stage. Although tick longevity (which may exceed that of smaller host species such as rodents) ensures an enduring reservoir of infection, it slows the pace of transmission, because long survival as any one life stage increases the delay between acquisition and transmission of infection.

An important limiting factor on the transmission potential of any parasite is the period of host infectivity, determined by rates of host mortality and recovery from infection. If the transmitted parasites are highly virulent, high daily mortality rates of infected hosts may significantly reduce transmission potential. If a host dies prematurely, the feeding ticks will not complete their blood meals. The risk of killing their hosts is avoided by those tick-borne viruses that limit their infection to a non-lethal, non-systemic form (i.e., limited to certain parts of the host's body) that is, nevertheless, highly transmissible to ticks over short periods of time. The quantitative impact of this transmission route arises from the large numbers of infectible ticks that co-feed with an infected tick at sites of localized infection. This is a natural feature of tick-host interactions, as prolonged meals taken on certain preferred parts of the host's body result in very large aggregations of ticks feeding close together on some host individuals. The immuno-modulatory effects of saliva secreted by so many co-feeding ticks further facilitate this transmission route. Although first recognized for tick-borne viruses, this route has now been identified for *B. burgdorferi* s.l., and shown to be sufficient to allow sheep to support natural cycles of Lyme borreliosis in the absence of other, systemically infected hosts.

Whereas insect vectors are viewed as the bridge between reservoir vertebrate hosts, the identity of reservoir host and bridge is reversed for the many parasites that survive in their long-lived tick vectors rather than in vertebrates. A multitude of specific parasite-vector-host interactions have clearly evolved to allow many micro-parasites to exploit the transmission potential offered by ticks, even though ticks are not endowed with the features we normally associate with insect vectors.

► Ticks

References

Nuttall PA (1998) Displaced tick-parasite interactions at the host interface. Parasitology 116:S65–S72

Randolph SE (1998) Ticks are not insects: consequences of contrasting vector biology for transmission potential. Parasitol Today 14:186–192

Randolph SE, Gern L, Nuttall PA (1996) Co-feeding ticks: epidemiological significance for tick-borne pathogen transmission. Parasitol Today 12:472–479

Sonenshine DE, Mather TN (eds) (1994) Ecological dynamics of tick-borne diseases. Oxford University Press, Oxford, 447 pp

Tiger Beetles (Coleoptera: Carabidae: Collyrinae and Cicindelinae)

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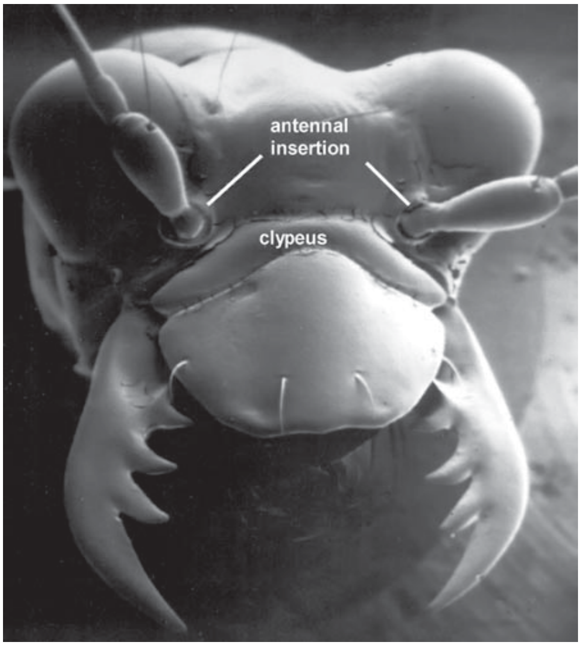
Tiger beetles are very active, predaceous beetles. Often brilliantly colored, they derive their common name from the fierce appearance of their large mandibles and protruding eyes. Their popularity among scientists and the general public stems from their relatively large size, accessibility for observation and study, available literature for many parts of the world, and a reasonably stable classification system. An entire journal, CICINDELA, is devoted to this group of beetles. Many web sites are devoted to various aspects of these insects, and many colorful photographs have been posted for internet viewing. Conservationists are using species of tiger beetles as bio-indicators, and more than a few species are now included on endangered species lists.

Taxonomy

Most modern taxonomists believe that tiger beetles should be considered a subfamily of the beetle family Carabidae (ground beetles). Historically they have been considered a family (Cicindelidae) separate from other ground beetles, due largely to their easily recognizable features and appeal with collectors. Many workers have now accepted the close relationship of this group to the ground beetle subfamily Carabinae. This is in agreement with many larval and adult structural characters. Throughout the history of the classification of the group, this close association has been maintained. It is more a matter of personal opinion whether this group should or shouldn't be recognized as a separate family. As there are no set rules for the determination of family rank, their status remains a matter of opinion pending further cladistic analyses (Fig. 60).

Tiger beetles are usually placed in the family Cicindelidae Latreille, 1804, or as a subfamily of the ground beetles, as Cicindelinae. Historically,



Tiger Beetles (Coleoptera: Carabidae: Collyrinae and Cicindelinae), Figure 60 **Head of *Cicindela* illustrating characters used to separate tiger beetles from other ground beetles.**

the following families were also proposed to incorporate new taxa (currently considered tribes): Collyridae Hope, 1838; Ctenostomidae Castelnau, 1835; Mantichoridae Castelnau, 1835; and Megacephalidae Castelnau, 1835.

Tiger beetle suprageneric classification is reasonably stable (tribes). Generic classification is very unstable, however, due primarily to the 1954 splitting of *Cicindela* into many genera, based solely on male genitalia characteristics. Thus, many genera are not readily identifiable. Species definition within each genus is oftentimes also problematic. There are a great many subspecies and color variants, most of which are named. Their status and synonymy is confusing. Much work must be done before all species can be properly understood. However, in spite of the complexity of their classification, many species groups and regional faunas have been sufficiently studied so that now it is possible to place names on most forms (Fig. 61). As for generic identification, there is no modern identification key that incorporates all of the currently accepted genera. There is presently only Willis' 1969 translation of Horn's outdated key to the world genera of tiger beetles, which does not reflect modern supraspecific classification.

In 2002, K. Werner published the only complete world checklist of tiger beetles. His classification scheme is reproduced here. Tiger beetles are divided into two subfamilies, Collyrinae and Cicindelinae. Subfamily Collyrinae is divided into two tribes, Ctenostomini with two genera and Collyrini with six genera. The subfamily Cicindelinae is divided into three tribes, Manticorini (two genera, African only), Megacephalini (nine genera), and Cicindelini with many ill-defined genera resulting from the splitting of *Cicindela*. The approximate geographical distribution for many genera is given here. Genera are listed in phylogenetic order (related genera close together) according to J. Wiesner's 1992 checklist, along with their approximate world distribution.

Tiger Beetles (Coleoptera: Carabidae: Collyrinae and Cicindelinae), Figure 61 **Males of *Cicindela scutellaris unicolor* (*left*) and *C. nigrior* (*right*), once considered to be the same species.**

Modern Classification of Tiger Beetles

Order Coleoptera
Family Carabidae
Subfamily Collyrinae
Tribe Ctenostomini
Pogonostoma Klug (Madagascar)
Ctenostoma Klug (Mexico, Central America, South America)
Tribe Collyrini
Derocrania Chaudoir (India, Sri Lanka)
Tricondyla Latreille (India, Sri Lanka, China, SE Asia, Indonesia, Malaysia, Borneo, Philippines)
Collyris Fabricius (India, Sri Lanka, SE Asia, Indonesia, Borneo)
Taiwanocollyris Mandl (Taiwan)
Protocollyris Mandl (Burma, Indonesia, Philippines)
Neocollyris W. Horn (India, Indonesia, SE Asia, Japan, Philippines, Thailand, Taiwan, Vietnam, China, Nepal, Malaysia)
Subfamily Cicindelinae
Tribe Manticorini (Africa only)
Mantica Kolbe (Namibia)
Manticora Fabricius (Namibia, S Africa, Angola, Botswana, Zaire)
Tribe Megacephalini
Platychile Macleay (Namibia, South Africa)
Picnochile Motschulsky (Chile)
Amblycheila Say (Mexico, SW USA)
Omus Eschscholtz (Canada, W USA)
Aniara Hope (Trinidad, S America)
Megacephala Latreille (widespread throughout world)
Oxycheila Dejean (Mexico, S America)
Pseudoxycheila Guerin (S America, Central America)
Cheiloxya Guerin (S America)
Tribe Cicindelini
Prothyma W. Horn (Africa, Madagascar, India, Indonesia, SE Asia, Philippines, China, Taiwan)
Neochila Basilewsky (Tanzania, Africa)
Euryarthron Guerin (Africa)
Dromica Dejean (Africa)
Heptodonta Hope (SE Asia, Philippines, China, Nepal, India, Malaysia, Indonesia)
Dilatotarsa Dokhtouroff (Indonesia, Malaysia, Philippines, Borneo)
Pronyssa Bates (India)
Pronyssiformia W. Horn (China)
Calyptoglossa Jeannel (Madagascar)
Peridexia Chaudoir (Madagascar)
Physodeutera Lacordaire (Madagascar)
Walthornia Olsoufieff (Madagascar)
Stenocosmia Rivalier (Madagascar)
Oxygoniola W. Horn (Indonesia)
Darlingtonica Cassola (Papua New Guinea)
Caledonomorpha W. Horn (Papua New Guinea)
Vata Fauvel (New Caledonia)
Caledonica Chaudoir (New Caledonia)
Odontocheila Castelnau (S America, Central America)
Cenothyla Rivalier (S America)
Pentacomia Bates (S America, Mexico)
Phyllodroma Lacordaire (Brazil)
Cheilonycha Lacordaire (Brazil, Argentina)
Prepusa Chaudoir (Paraguay, Brazil)
Opisthencentrus W. Horn (Brazil)
Oxygonia Mannerheim (S America, Central America)
Metopon Fleutiaux (Brazil)
Eucallia Guerin (Ecuador, Colombia)
Euprosopus Dejean (Brazil)
Iresia Dejean (S America, Central America)
Distipsidera Westwood (Australia, Papua New Guinea, Indonesia)
Rhysopleura Sloane (Australia)
Megalomma Westwood (Mauritius, Reunion)
Diastrophella Rivalier (Reunion)
Rhytidophaena Bates (Bangladesh, India, Burma)
Langea W. Horn (S America)
Nickerlea W. Horn (Australia)
Baloghiella Mandl (New Caledonia)
Therates Latreille (Indonesia, SE Asia, India, Burma, Japan, Taiwan, China, Malaysia, Philippines)
Bennigsenium W. Horn (Tanzania, Africa)
Prothymidia Rivalier (Africa)
Chaetotaxis Jeannel (Madagascar)

Ambalia Jeannel (Madagascar)
Cicindelina Jeannel (Madagascar)
Trichodela Rivalier (Africa)
Epitrichodes Rivalier (Africa)
Trichotaenia Rivalier (Africa)
Ophryodera Chaudoir (S Africa, Angola, Zaire, Mozambique)
Bostrichophorus Thomson (Mozambique)
Elliptica Fairmaire (Africa)
Ropaloteres Guerin (Africa, China)
Hipparidium Jeannel (Africa, Indonesia, Madagascar)
Calochroa Hope (Nepal, India, Burma, SE Asia, Philippines, Nepal, Sri Lanka)
Cicindela Linnaeus (worldwide distribution)
Lophyridia Jeannel (Turkey, Iran, Iraq, China, Afghanistan, Syria, Africa, Japan, India)
Cosmodela Rivalier (Afghanistan, India, Nepal, China, SE Asia, Borneo)
Plutacia Rivalier (India)
Platydela Rivalier (Morocco, S Africa)
Lophyra Motschulsky (Africa, Iran, Pakistan, Sri Lanka, Pakistan, India, Madagascar, Italy, Turkey, SE Asia)
Habrodera Motschulsky (Madagascar, Africa)
Chaetodera Jeannel (Madagascar, Africa)
Neolaphyra Bedel (N Africa)
Jansenia Chaudoir (India, Sri Lanka)
Thopeutica Schaum (Indonesia, Philippines)
Wallacedeala Cassola (Indonesia)
Cephalota Dokhtouroff (Central Asia, Morocco, Spain, Greece)
Cassolaia Wiesner (Algeria, Tunesia)
Homodela Rivalier (Turkey)
Naviauxella Cassola (Burma, Thailand)
Glomera Acciavatti & Pearson (India)
Setinteridenta Acciavatti (India)
Cylindera Westwood (Japan, China, Taiwan, Europe, Central Asia, Korea, India)
Brasiella Rivalier* (Cuba, Mexico, Central America, S. America)
Ellipsoptera Dokhtouroff*
Dromochorus Guerin*
Myriochile Motschulsky*
Cratohaerea Chaudoir*
Microthylax Rivalier*
Eunota Rivalier*
Habroscelimorpha Dokhtouroff*
Opilidia Rivalier*
Salpingophora Rivalier (Iran, Pakistan)
Hypaetha LeConte (Iran, Yemen, India, Somalia, Australia)
Abroscelis Hope (China, SE Asia, Indonesia, Philippines, Taiwan)
Callytron Gistl (Pakistan, India, Iran, S Korea, Taiwan, Japan, Malaysia, Burma, Philippines)
Enantiola Rivalier (Indonesia, Malaysia)
Notospira Rivalier (Burma)
Neocicindela Rivalier (New Zealand)
Euzona Rivalier (Australia)
Antennaria Dokhtouroff (Australia)
Marcfarlandia Sumlin (Australia)
Micromentignatha Sumlin (Australia)
Archidela Rivalier (Australia, Papua New Guinea)
Grandopronotalia W. Horn (Australia)
Rivacindela Nidek (Australia)
Parapolyrhanis Rivalier (Fiji)
Polyrhanis Rivalier (Indonesia, Papua New Guinea)
Oceanella Rivalier (Fiji)
Orthocindela Rivalier (Indonesia, Papua New Guinea)
Guineica Rivalier (Indonesia)
Leptognatha Rivalier (Indonesia, Papua New Guinea)
Eurymorpha Hope (Angola, Namibia, S Africa)
Apteroessa Hope (India)

(*genus treated as a subgenus of *Cicindela* by many authors)

Description

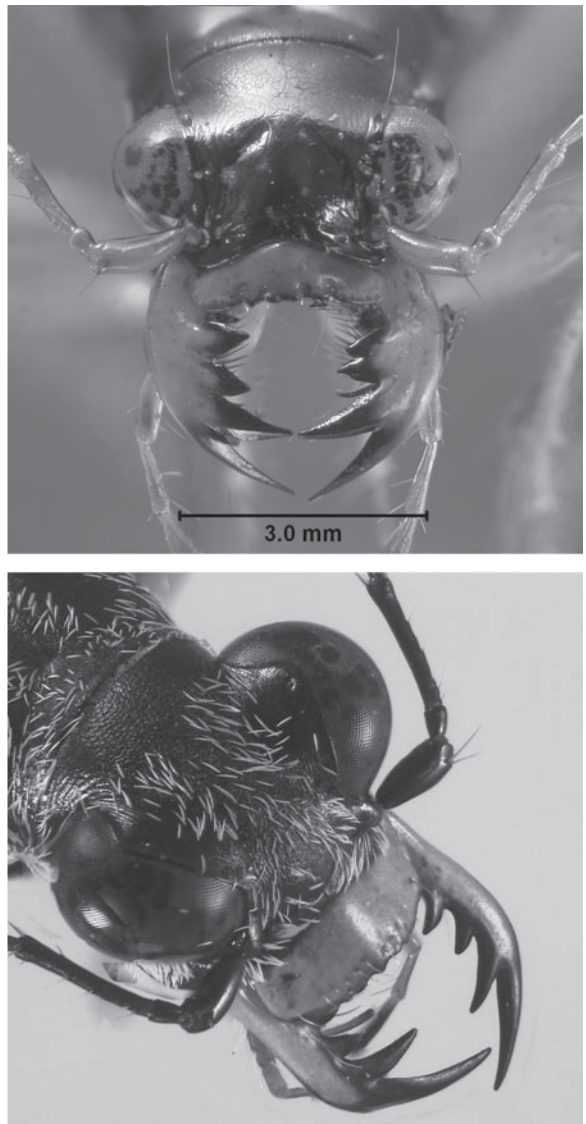
Most species have conspicuous eyes, long legs, and frequently display brilliant colors, a characteristic shape, rapid locomotion, and nervous behavior. The body is elongate or round, with a large head and prominent eyes. Their size ranges from 6 mm to over 70 mm (*Manticora latipennis* – South Africa) in length (Fig. 62). Their color often includes iridescent markings, though some genera are uniformly brown or black (*Omus*, *Amblycheila*, *Mantica*, *Manticora*). Body hair is usually sparse, though sometimes with long, stout setae, especially on legs and mouthparts.

The head is variously shaped, prominent, but not elongate. The antennae are filiform, long and slender, with eleven segments (Fig. 63). The mandibles are stout, toothed, sometimes very large and prominent, much larger than the head, and other mouthparts also are large (Fig. 64). The eyes vary from very small to very large and prominent.

The pronotum is variously shaped, but is narrower than the elytra, usually cylindrical, and without lateral margins or (rarely) with lateral margins. The legs are long and slender, and

Tiger Beetles (Coleoptera: Carabidae: Collyrinae and Cicindelinae), Figure 62 **Intrapopulation variation in *Cicindela dorsalis saulcyi* from Carabelle Beach, Florida, USA.**

Tiger Beetles (Coleoptera: Carabidae: Collyrinae and Cicindelinae), Figure 63 **Head of male *Manticora latipennis*.**



Tiger Beetles (Coleoptera: Carabidae: Collyrinae and Cicindelinae), Figure 64 **Face of adult tiger beetles showing prominent toothed mandibles: (*above*) *Megacephala carolina*; (*below*) *Cicindela marginata*.**

well suited for running. The tarsal segment formula is 5–5–5. Tiger beetles display typical carabid-type wings; the elytra cover the abdomen, and sometimes are connate, rounded behind, and sometimes possess lateral margins. The wings may be present or absent.

The abdomen of tiger beetles is sometimes narrow, with elytra covering the sides, with four to six visible ventral sternites. Male genitalia are highly modified, carabid-like tri-lobed parameres with a separate *pars basalis* (unlike that found in other ground beetles) entirely separate from the base of the penis and forming a lateral connection between the parameres at a mid-point. Larvae are distinguished by two or three pairs of hooks present on the tergum (top) of the fifth abdominal segment (Fig. 65).

Tiger Beetles (Coleoptera: Carabidae: Collyrinae and Cicindelinae), Figure 65 **Tiger beetle larva.**

Members of Cicindelinae are separated from other Carabidae by a combination of the following characters: clypeus laterally extending beyond antennal insertion, both spurs of protibiae apical, and larvae with dorsal hooks on fifth abdominal tergite (dorsal plate). Consistent treatment of the families of beetles requires that these beetles be placed within the rest of the ground beetles.

Species Numbers and Distribution

There are approximately 2,100 described species found in all regions of the world except Hawaii, Antarctica, Maldives Islands off the southern tip of India, and Tasmania (Table 12). They occur at elevations from −60 m to over 4,000 m. The Indian subcontinent is home to the largest number of species of tiger beetles.

Fossil Records

There are very few tiger beetle fossil records. Some published records are suspect; their identity may not be correct, and there is even evidence that more than one record may be a fraud. The oldest known tiger beetle fossil (*Oxycheilopsis cretacicus* Cassola and Werner) was described in 2003 from the Santana Formation of Nova Olinda, Brazil, Mesozoic formation, dating from the Lower Cretaceous, ca. 120 million years ago. Other fossil records include Oligocene Baltic Amber, Quaternary from USSR and Trinidad, Pleistocene (California, Minnesota, and Washington, USA) United Kingdom (Europe), and Ontario, Canada.

Reproduction

Males visually locate potential mates. It is not uncommon to see males attempt to mount other males, as well as other species trying to mate. Frequent encounters between conspecific

Tiger Beetles (Coleoptera: Carabidae: Collyrinae and Cicindelinae), Table 12 **Number of species of tiger beetles known from many countries of the world, as reported in 1992 by Pearson and Cassola**

Country	No. species
Algeria	15
Angola	69
Argentina	64
Australia	81
Bangladesh	53
Bolivia	86
Botswana	27
Brazil	184
Burma (Myanmar)	93
Cameroon	43
Central African Republic	46
Chile	6
China	94
Colombia	42
Costa Rica	38
Cuba	11
Ecuador	74
El Salvador	17
Ethiopia	51
Fiji	2
Guatemala	23
Guinea-Bissau	34
Guyanas	29
Hispaniola	9
Honduras	7
India	193
Indonesia	217
Iran	30
Italy	17
Ivory Coast	21
Japan	22
Kenya	53
Laos	59
Libya	6
Madagascar	176

Tiger Beetles (Coleoptera: Carabidae: Collyrinae and Cicindelinae), Table 12 **Number of species of tiger beetles known from many countries of the world, as reported in 1992 by Pearson and Cassola (Continued)**

Country	No. species
Malaysia	95
Mali	16
Mauritius Island	3
Mexico	116
Mongolia	23
Morocco	14
Mozambique	47
Namibia	31
Nepal	64
New Caledonia	17
New Zealand	14
Pakistan	33
Panama	28
Papua New Guinea	72
Paraguay	38
Peru	79
Philippines	94
Réunion Island	4
Solomon Islands	20
Somalia	31
South Africa	94
Spain	16
Sri Lanka	55
Taiwan	26
Tanzania	68
Thailand	102
Togo	24
Trinidad & Tobago	4
Tunisia	14
Turkey	25
U.S.S.R. (C.I.S.)	49
Uganda	33
USA	111
Venezuela	51
Vietnam	93

Tiger Beetles (Coleoptera: Carabidae: Collyrinae and Cicindelinae), Table 12 Number of species of tiger beetles known from many countries of the world, as reported in 1992 by Pearson and Cassola (Continued)

Country	No. species
Western Samoa	2
Yemen	10
Zaire	134
Zambia	53
Zimbabwe	53

Tiger Beetles (Coleoptera: Carabidae: Collyrinae and Cicindelinae), Figure 66 Mating pair of *Cicindela dorsalis*.

males result in brief wrestling/aggressive behavior. Once a male is successful at mating, he will frequently be seen riding on the back of a female after mating has occurred. This is called mate guarding, and this behavior is believed to be used to prevent other males from mating the same female. There also are morphological differences between species that act as interspecific barriers. A mandible coupling sulcus occurs in many species. A combination of male mandible shape and thoracic sulcus on females is believed to be a selection mechanism to prevent interspecific breeding. The mandible of conspecific males fits into the sulcus on the female. Males of other species have mandibles that are not fitted for female sulci (Fig. 66).

Karyology

Karyotypes are known for fewer than 100 species of tiger beetles, which are among the organisms with two to four multiple X sex chromosomes. These multiple X chromosomes are unique among insects because they do not form chiasmata, crossover points which allow recombination during meiosis. Another characteristic of male chromosomes is that they do not align in parallel during meiosis, but rather form a conspicuous sex particle, chromosomes linked at their ends, forming a circle.

Development

Tiger beetles undergo complete metamorphosis, passing through the egg, larval, and pupal stages before emerging as adults. Eggs are laid singly by females. Hatching occurs from 9 to 38 days after oviposition. Larvae undergo three instars. The newly hatched larva forms a vertical burrow in which it will remain through pupation. Larvae for most known species live in vertical tunnels, holding themselves with the aid of dorsal hooks on the fifth abdominal segment. If suitable prey comes within range of a tunnel entrance, the larva seizes it and drops down into the burrow to feed. The abdominal hooks also serve to anchor the larva in its tunnel if a prey is too large to subdue. Larvae of the Ctenostomatini (*Neocollyris* and *Ctenostoma*) are unusual in that they develop in rotting logs and branches or standing vegetation rather than in burrows in the ground.

Larvae of many species have been described. A list and key to all known tiger beetle larvae was published by Putchkov and Arndt. The entire life cycle from egg to adult may take as long as 4 years. Food availability seems to be a major factor in the rate of larval development. Many species appear to be able to endure long periods of fasting, entering into a quiescent stage which may last for months. Adults normally live from 8 to 10 weeks, but some may live for several years (*Manticora*).

Survival from Heat and Flooding

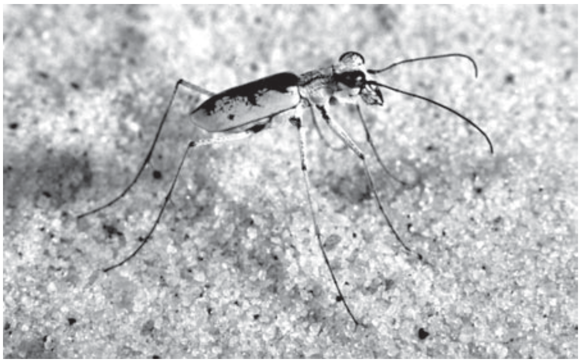
Many species inhabit extremely hot regions, where air temperatures during the day may easily exceed 37°C. Those species that are active during hot times of the day may exhibit a behavior known as "stilting," where the individual stands with legs fully extended, keeping the insect as far away as possible from the hot soil (Fig. 67). They may also seek out shaded structures, or hide under debris, or hide in leaf litter. Larvae of riparian species are able to survive long periods of anoxia (lack of oxygen) during seasonal flooding of their sandbar and bank habitats (Fig. 68). Larval burrows may contain sufficient oxygen to allow their inhabitants to survive weeks under flood waters. The salt marsh-inhabiting species *Cicindela togata* is reported to have larvae that can survive 5 days of burrow immersion in salt water.

Activity

Tiger beetles often run very rapidly over the ground, frequenting sandy banks of streams, along roadways and paths and other such sunny places. Many species are rapid flyers. In spite of their often brilliant metallic colors they are often difficult to see because of their quick movements. Unlike most beetles, a net is often necessary to collect these insects. Some desert-inhabiting species can be collected in abundance by hand. Pitfall trapping has also proven a successful technique for some species. Many species are more easily collected at night with such attractors as UV black-light or mercury vapor lights. The use of lights to collect many of the more elusive species has led to the demise of some populations due to overzealous collecting. Several species are on the verge of extinction, with over-collecting appearing to be as responsible as habitat destruction.

The genera *Manticha* and *Manticora* inhabit deserts and steppes of southern Africa. A few species of *Cicindela* live in termite nests. The tropical tribes Ctenostomini and Collyrini are arboreal, searching out their prey among the branches of trees and bushes.

Adults of *Megacephala*, *Amblycheila*, and *Omus* are crepuscular/nocturnal and are most effectively collected with pitfall traps. Some species



Tiger Beetles (Coleoptera: Carabidae: Collyrinae and Cicindelinae), Figure 67 ***Cicindela hirtilabris*** **displaying "stilting" behavior.**

Tiger Beetles (Coleoptera: Carabidae: Collyrinae and Cicindelinae), Figure 68 ***Cicindela blanda*****, a river sandbar species from the southeastern USA.**

of *Megacephala* have been reported to be attracted to electric lights, but are usually found beneath stones, hiding in crevices in the earth, or under almost any debris. *Megacephala affinis* was reported to prey on dung beetles in Panama. *Megacephala fulgida* was reported to appear at sound traps being used to attract *Scapteriscus* mole crickets. Individuals of *Amblycheila* have been reported to become active soon after sunset. Adult *Omus* have been reported to be predators on millipedes.

Species of *Cicindela* are both diurnal and nocturnal. Many species prefer dry sunny areas, but others are known to prefer semi-aquatic sites. Some species, while active both during daytime and night, appear to accomplish most of their mating at night. Many species are strong flyers, but some have fused elytra and are incapable of flight. Others appear reluctant to fly even though flight wings are present.

Tiger Beetles (Coleoptera: Carabidae: Collyrinae and Cicindelinae), Figure 69 **Clay bank at Thomasville, Georgia, USA, with holes marking entrances to larval burrows.**

Predators and Parasites

Larvae have only a few methods of escaping predation and parasitism. They will either drop to the bottom of their burrow when danger approaches, or they may even leave the burrow and run to another location. Since they are restricted to the one vertical burrow during their development, parasites are able to locate and attack larvae with a fair amount of success. Members of the hymenopteran family Tiphiidae (*Methoca*, *Karlissa*, and *Pterombus*) hunt for larvae, sting them, then deposit an egg on the paralyzed larva. The burrow is then closed by the wasp. The parasite larva develops, killing the tiger beetle larva. A fly family (Bombyliidae) also is a parasite of tiger beetle larvae. These flies flip eggs near or into the larval burrow. Eggs fall to the bottom of the burrow, hatch, and the new larva attaches to the tiger beetle larva, remaining attached until the larva pupates (Fig. 69).

Adult tiger beetles will defend against such predators as bats, mites, lizards, other tiger beetles, flies (Asilidae), birds, dragonflies, and, of course, collectors (Fig. 70). Defensive strategies

Tiger Beetles (Coleoptera: Carabidae: Collyrinae and Cicindelinae), Figure 70 **Natural enemies of tiger beetles: (*above*) robber fly (Asilidae) predator; (*below*) bee fly (Bombylidae) parasitoid.**

include running, hiding (camouflage and cryptic coloration), flying (quick short flight or long sustained flight), dropping from the canopy (arboreal species), displaying a warning coloration such as bright orange abdomen, and chemical defenses. Many (but not all) species of tiger beetles produce the chemical benzaldehyde, a chemical known to be an effective predator deterrent.

Sound Production

Some species of tiger beetles have been found to produce sounds through stridulation. The mechanisms behind sound production are being investigated, and only a few species have been analyzed. Sound production may be useful in predator avoidance, or it may be part of intraspecific communication. Two different types of sound production have been found in tiger beetles. One method is the scraping of a *pars stridens* found on the dorsal side of costal and subcostal veins upon a plectrum on the ventral apical area of the elytra. Others have rings on the elytra which are rubbed by either the hind tibia (*Manticora*) or hind femur (*Oxycheila* and *Cheiloxya*).

Sound Detection

Tiger beetles are capable of detecting sound. It is believed that some species have evolved a hearing organ (tympanum) to detect the hunting sounds of bats. Not all species of tiger beetles have tympana. When present the tympanum has been found to be located on the dorsal-lateral side of the first abdominal segment. It is believed that some species use night dispersal flights to avoid daytime predators such as robber flies, dragonflies, and birds. This exposed them to predatory bats. Detection of the ultrasound cries of bats results in the tiger beetle dropping out of the air to the ground.

Defensive Behavior

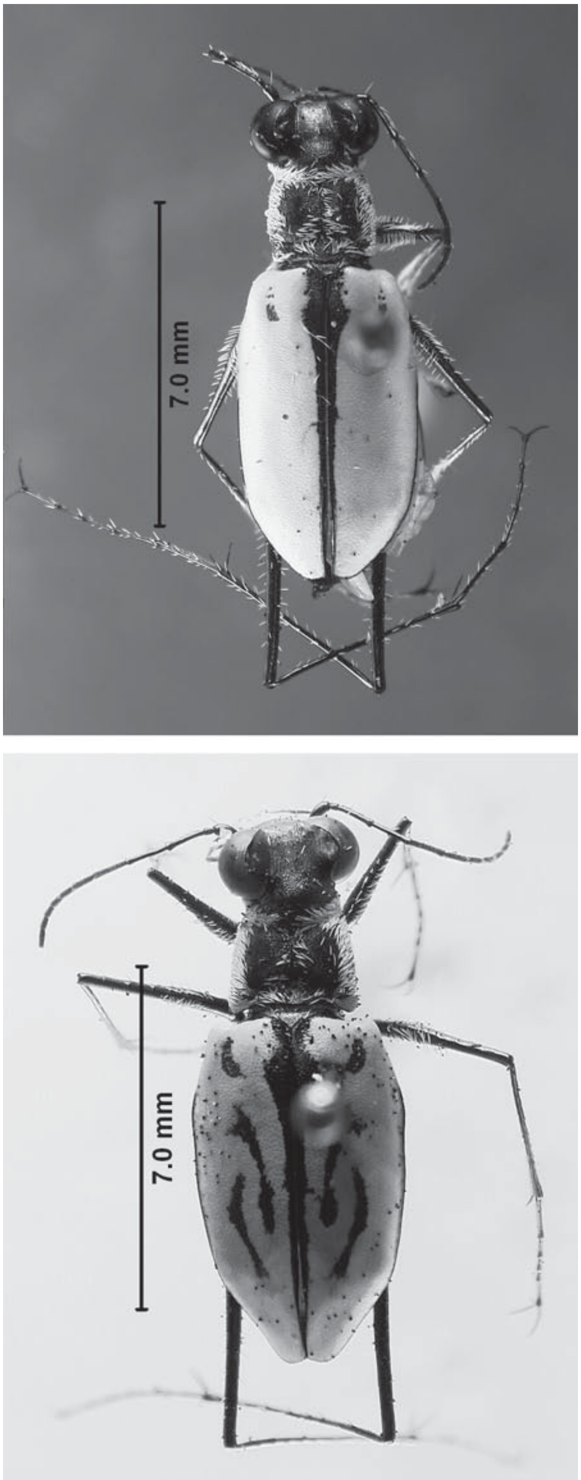
Benzaldehyde and cyanide have been identified as defensive secretions in *M. virginica*. Other species are reported to have similar defensive secretions, but of 89 species investigated, only 39 produced these compounds. Other defensive behavior includes crypsis, aposematism, evasive running, evasive flight, deception, roosting aggregations, and release of noxious chemicals from pygidial glands. While the principal predators of tiger beetles are believed to be birds, lizards, spiders, robber flies, and bats, birds are believed to be the major force behind selection for defensive coloration.

Phenotypic Variation

Intrapopulation color and extent of maculation is common among tiger beetles. This variation has resulted in many named subspecies. The taxonomic validity of many of these names has not been resolved, and many of these most likely represent variation of little taxonomic value (Fig. 71).

Sexual Dimorphism

Many species exhibit sexual dimorphism in extent of maculation, degree of hairiness of the head, number of labrum teeth, overall color, protarsal pads, shape of the elytral apex, overall body shape and size (Fig. 72). Females tend to be larger and wider, while males are often smaller and narrower. Males have many more erect setae between their eyes, and the first four segments of their protarsi have dilated pads that are used to hold onto females during mating. In species that have dimorphic coloring to their labrum, males usually have a white or pale labrum, while females may have a totally black or dark labrum. This may aid in mate recognition, and reduce the number of male/male encounters (Fig. 73).



Tiger Beetles (Coleoptera: Carabidae: Collyrinae and Cicindelinae), Figure 71 **Male *Manticora latipennis*, 70 mm long, from South Africa. Members of this genus contain the largest species of tiger beetles.**

Tiger Beetles in Folklore and Religion

Though there are relatively few references to tiger beetles in religious literature, the African genus *Manticora* is one that has been a part of local legends and folklore. A recent revision of *Manticora* described the folklore concerning the derivation of the name *Manticora*, and the beliefs surrounding the insects by native populations. The name *Manticora* was derived from the mythological beast, the Manticore. The Manticore was a beast that had the head of a lion, the body of a serpent, and the tail of a scorpion. The genus *Manticora* was proposed for these beetles in 1792 by Johann Fabricius. This name was taken from the Persian for a man-eating monster. This may have been the result of reports of these beetles feeding on cadavers of warriors killed in native conflicts, or from sighting of these beetles occasionally emerging from skulls, presumably used as hiding places to avoid the midday heat. According to native legend in southern Africa, manticoras cannot die, and are believed to be personification of the Grim Reaper. They are thought to bring nothing but ruin and destruction to native tribes. They are so feared that it is believed that if a manticora points its mandibles in the direction of a person, that person will die within 3 days. The natives try to sneak up behind any manticora and crush it with their feet before it can point its mandibles in their direction. If a person is so unfortunate as to see a manticora, that person must undergo a lengthy religious purge ceremony to be saved from this demon.

Tiger Beetles on Stamps

A few countries have used images of tiger beetles on their stamps. Examples of these are shown here, with insect species name and country where used (Fig. 74):

Tiger Beetles (Coleoptera: Carabidae: Collyrinae and Cicindelinae), Figure 72 ***Cicindela hirticollis*** **(*left*, male; *right*, female) showing increased maculation in female and narrower body shape of male.**

Tiger Beetles (Coleoptera: Carabidae: Collyrinae and Cicindelinae), Figure 73 **Female *Cicindela unicolor*. Note the elongate middle tooth and unicolorous black color of the labrum.**

- Vietnam – *Cicindela aunulenta*, *Cicindela tennipes*, *Cicindela japonica*
- Senegal – *Cicindela lunulata*
- Ethiopia – *Cicindela petiti*
- North Korea – *Cicindela chinensis*
- Albania – *Cicindela hybrida*
- Portuguese Guinea – *Cicindela brunet*
- East Germany – *Cicindela campestris*
- Madagascar – *Cicindela andriana*
- Republic of Equatorial Guinea – *Cicindela purpurea*
- Democratic Republic of Congo – *Cicindela regalis*
- Niger – *Cicindela cicindela*
- Vietnam – *Collyris collyris*
- Republic of South Africa – *Cicindela regalis*
- Japan – *Cicindela japonica*

Conservation

The attractive appearance of many tiger beetles has been one of the reasons that collectors have sought out specimens, sometimes to the detriment of populations from over-zealous collecting.

Tiger Beetles (Coleoptera: Carabidae: Collyrinae and Cicindelinae), Figure 74 **Examples of stamps displaying tiger beetles: (*top row, left* to *right* – *Cicindela japonica*, *Cicindela aunulenta*, *Cicindela petiti*, *Cicindela cicindela*; *bottom row, left* to *right* – *Cicindela regalis*, *Cicindela purpurea*, *Cicindela andriana*).**

The biology of many species is sufficiently well known to permit estimates of their survival status. As a result, several species of North American tiger beetles have been elevated for protection under the Endangered Species Act. Among USA endangered species are *Cicindela highlandensis* Choate (central Florida), *Cicindela puritana* G.H. Horn (Maryland, Connecticut), *C. ohlone* Freitag and Kavanaugh (California), *C. dorsalis dorsalis* Say (northeastern seacoast), *Cicindela nevadica lincolniana* Casey (Nebraska), and *Cicindela limbata albissima* Rumpp (Utah). Many other species are listed as "species of concern," meaning that they are potential candidates for endangered species status in the future as their habitats disappear. The following list (by state) includes most of the U.S. species that are being monitored:

- Minnesota – (Endangered) *Cicindela fulgida fulgida* Say, *Cicindela limbata nympha* Casey; (Threatened) *Cicindela denikei* W.J. Brown, *Cicindela fulgida westbournei* Calder, *Cicindela lepida* Dejean; (Special concern) *Cicindela hirticollis rhodensis* Calder, *Cicindela macra macra* Leconte, *Cicindela patruela patruela* Dejean, *Cicindela splendida cyanocephalata* Eckhoff;
- Washington – *Cicindela columbica* Hatch;
- South Dakota – *Amblycheila cylindriformis* (Say);
- Texas – *Cicindela chlorocephala smythi* E.D. Harris; *Cicindela cazieri* Vogt, *Cicindela hornii* Schaupp, *Cicindela nevadica olmosa* Vaurie, *Cicindela nigrocoerulea subtropica* Vogt, *Cicindela obsoleta neojuvenilis* Vogt, *Cicindela politula barbarannae* Sumlin; *Cicindela politula petrophila* Sumlin;
- Nebraska – *Cicindela nevadica lincolniana* Casey;
- Vermont, New Hampshire – *Cicindela marginipennis* Dejean;
- California, Santa Cruz Co. – *Cicindela ohlone* Freitag and Kavanaugh;
- Massachusetts – *Cicindela rufiventris hentzii* Dejean, *Cicindela dorsalis dorsalis* Say, *C. marginipennis* Dejean, *C. patruela* Dejean, *C. puritana* G.H. Horn;
- Utah – *Cicindela limbata albissima* Rumpp, confined to the Coral Pink Sand Dunes formation in southern Utah;

- Ohio – *C. hirticollis* Say, *C. marginipennis* Dejean.
- While less well-studied, a few species elsewhere are also candidates for protection. Among those are the following:
- Canada, British Columbia – *Cicindela parowana* Wickham;
- Spain – *Cicindela* (*Cephalota*) *deserticoloides* (Codina), endemic to the few remaining salt steppes of southeastern Spain;
- South Africa – *Dromica* spp., all species; *Manticora* spp., all species; *Megacephala asperata* Waterhouse, *Megacephala regalis* Boheman, *Platychile pallida* (Fabricius), *Prothyma guttipennis* Boheman;
- Japan – *Lophyridia angulata* (Fabricius), *Abroscelis anchoralis* (Chevrolat), *Cicindela lewisii* Bates, and *Chaetodera laetescripta* Motschulsky.

Habitat destruction from encroachment by recreational vehicles, housing construction, damming of rivers, and forest harvesting are risk factors that may eventually lead to species extinction. Even night-lights have been investigated as potential risk factors in the life cycle of some tiger beetles because they draw adults from their habitat and interrupt their mating behavior.

► Ground Beetles (Coleoptera) Taxonomy
► Beetles

References

Freitag R (1999) Catalogue of the tiger beetles of Canada and the United States. NRC Research Press, Ottawa, 195 pp

Mares J (2002) A monograph of the genus *Manticora* (Coleoptera, Cicindelidae, Manticorini). Taita, Hradec Kralove, 208 pp

Naviaux R, Pinratana A (2004) The tiger beetles of Thailand (Coleoptera, Cicindelidae). Sunprinting, Bangkok, 177 pp

Pearson DL, Cassola F (1992) World-wide species richness patterns of tiger beetles (Coleoptera: Cicindelidae). Indicator taxon for biodiversity and conservation studies. Conserv Biol 6:376–391

Pearson DL, Knisley CB, Kazilek CJ (2006) A field guide to the tiger beetles of the United States and Canada. Identification, natural history, and distribution of the Cicindelidae. Oxford University Press, New York, 227 pp

Pearson DL, Vogler AP (2001) Tiger beetles. The evolution, ecology, and diversity of the Cicindelids. Cornell University Press, Ithaca, NY, 333 pp

Putchkov AV, Arndt E (1994) Preliminary list and key of known tiger beetle larvae (Coleoptera, Cicindelidae) of the world. Mitt Schweiz Entomol Ges 67:411–420

Werner K, (1999)The tiger beetles of Africa (Coleoptera: Cicindelidae), vol. 1. Taita, Hradec Kralove, 191 pp

Werner K (2000) The tiger beetles of Africa (Coleoptera: Cicindelidae), vol. 2. Taita, Hradec Kralove, 208 pp

Wiesner J (1992) Verzeichnis der Sandlaukäfer der Welt [Checklist of the tiger beetles of the world (Coleoptera: Cicindelidae)]. Erna Bauer, Keltern, 364 pp

Tiger Moths (Lepidoptera: Arctiidae)

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Tiger moths, family Arctiidae (including flag moths and wasp moths), total 11,155 species worldwide, primarily Neotropical (about 6,000 sp.); actual world fauna likely exceeds 14,000 species. The family is in the superfamily Noctuoidea, in the section Cossina, subsection Bombycina, of the division Ditrysia. There are five subfamilies among three groups: group Pericopinina (with Pericopinae), group Arctiinina (for Lithosiinae and Arctiinae), and group Ctenuchinina (for Ctenuchinae and Syntominae). Various specialists use other classifications. Adults small to large (8–115 mm wingspan); tympanal organs absent or vestigial in Syntominae; hindwings greatly reduced in some groups (wasp moths). Maculation extremely varied, but mostly very colorful, especially among the wasp moths (Ctenuchinae and the Old World Syntominae) which mimic wasps in many cases. Adults mostly nocturnal but many are crepuscular or diurnal (Pericopinae, Ctenuchinae, and Syntominae). Larvae are leaf feeders. Host plants are varied among numerous plant families, including mosses and lichens. A few are economic. Among the largest adults are females of *Aglaomorpha histrio*, from China, while the smallest are some of the Lithosiinae (Fig. 75).

Tiger Moths (Lepidoptera: Arctiidae), Figure 75 **Example of tiger moths (Arctiidae), *Grammia virgo* (Linnaeus) from USA.**

References

Bryk F, Strand E, Zerny H (1912–37) Arctiidae. Lepidopterorum Catalogus, 7:1–179 (1912); 22:1–416 (1912); 26:501–900 (1922); 45:1–57 (1931); 82:1–126 (1937). W. Junk, Berlin

Fang CL (2000) Lepidoptera Arctiidae. In: Fauna Sinica (Insecta), 19. Science, Beijing, 589 pp, 20 pl. (in Chinese)

Holloway JD (1998) Family Arctiidae. In: The moths of Borneo, 6. Malayan Nature Society, Kuala Lumpur, 101 pp, 19 + 6 pl.; Malayan Nat J 42

Jacobson NL, Weller SJ (2001) A cladistic study of the Arctiidae (Lepidoptera) using characters of immatures and adults. Thomas Say Monograph. Entomological Society of America, Lanham, 130 pp

Marmet P, Schmid J (2000) Arctiidae-Bärenspinner. In: Schmetterlinge und ihre Lebensräume: Arten-Gefährdung-Schutz. Schweiz und angrenzenden Gebiete, 3: 581–744, pl. 26–34. Pro Natura-Schweizerische Bund fuer Naturschutz, Basel

Seitz A (1909–34) Familie: Arctiidae. Die Gross-Schmetterlinge der Erde, 2: 37–108, pl. 9–18 (1909–10); 2(suppl.): 53–94, 278–290, pl. 1–8 (1931–34); 6: 33–230, 293–455, 469–497, pl. 9–31, 38–67 (1915–25); 10: 61–92, 105–290, pl. 10–30 (1912–15); 14: 41–122, pl. 3–5, 8–19 (1926). A. Kernen, Stuttgart

Watson A, Goodger DT (1986) Catalogue of the Neotropical tiger-moths. Occas Pap Syst Entomol 1:1–71 (4 pl.)

Tillyard, Robin John

Tillyard, Robin John, Figure 76 **Robin Tillyard.**

Robin Tillyard was born January 31, 1881, at Norwich, England. He was educated at Dover College and Queen's College, University of Cambridge, and received a Sc.D. in 1920. He taught math and science in Sydney, Australia, from 1905 to 1913, and began publishing on dragonflies in 1905. He was named a lecturer in zoology at the University of Sydney in 1917, and received several honors from that University and from the Linnean Society of London. He also served as Chief of the Biological Department of Cawthron Institute in New Zealand, and Chief of the Division of Economic Entomology, CSIRO, Canberra, Australia. Tillyard published nearly 100 scientific papers, on many aspects of entomology and most orders of insects, but was especially interested in their evolution, in fossil insects, and in dragonflies. He also provided numerous contributions to "The illustrated Australian encyclopedia" (1925) and "The insects of Australia and New Zealand" (1926). Tillyard died in 1937 (Fig. 76).

Reference

Musgrave A (1932) Bibliography of Australian Entomology, 1775–1930. Royal Zoological Society of New South Wales, Sydney, pp 316–321

Timema Walkingsticks

A family of walkingsticks (Timemidae) in the order Phasmatodea.

► Stick and Leaf Insects

Timemidae

A family of walkingsticks (order Phasmatodea). They commonly are known as Timema walkingsticks.

► Stick and Leaf Insects

Timarcha latreille (Coleoptera: Chrysomelidae, Chrysomelinae)

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The leaf-beetle genus *Timarcha* Latreille comprises about four subgenera, 125 species and 30 subspecies, spread in eastern North America and around the Mediterranean basin. They are absent from Syria, Lebanon, Israel, and Egypt, where very probably European and African species once met, but were eradicated during the Pleistocene desertification. In Libya, it survives along the coast on the western side and in Cyrenaica, but also survives on some oases, 80 km south. *Timarcha* does not reach or survive in the central Sahara (Hoggar, 2,918 m) where some *Chrysolina* live.

Fossil *Timarcha*, before the Pleistocene, are unknown, but *Timarcha* is a very old genus, perhaps related to the Upper Jurassic Timarchopsis, a Siberian fossil. The genus *Timarcha* combines plesiomorphic characters (very primitive nervous system, primitive aedeagus and tegmen, etc.) with apomorphic ones, like the welding of the elytra in tenon and mortise and a complete aptery. How long has the beetle been apterous? Probably very early, during the Cretaceous, because it is found with Meloe (Meloidae), one of the rare beetles that is apterous at the pupal stage. Aptery and a subelytral cavity are forms of protection against heat and water loss in many tenebrionids living in desert and semidesert areas. Such structures reduce transpiration, act as a thermal buffer for heat flow and allows the beetle to store the maximum amount of water possible to compensate for the loss of liquid through reflex bleeding. Lack of flight muscles and shortening and widening of metasternum are a direct consequence of aptery. *Pimelia* spp. (Tenebrionidae), also totally apterous, often mimic the *Timarcha* spp. and there seems to be a certain concordance in northern Africa between the local *Timarcha* and *Pimelia* species. It could be more Müllerian mimicry than Batesian, however, because Pimelia regurgitates liquid when disturbed.

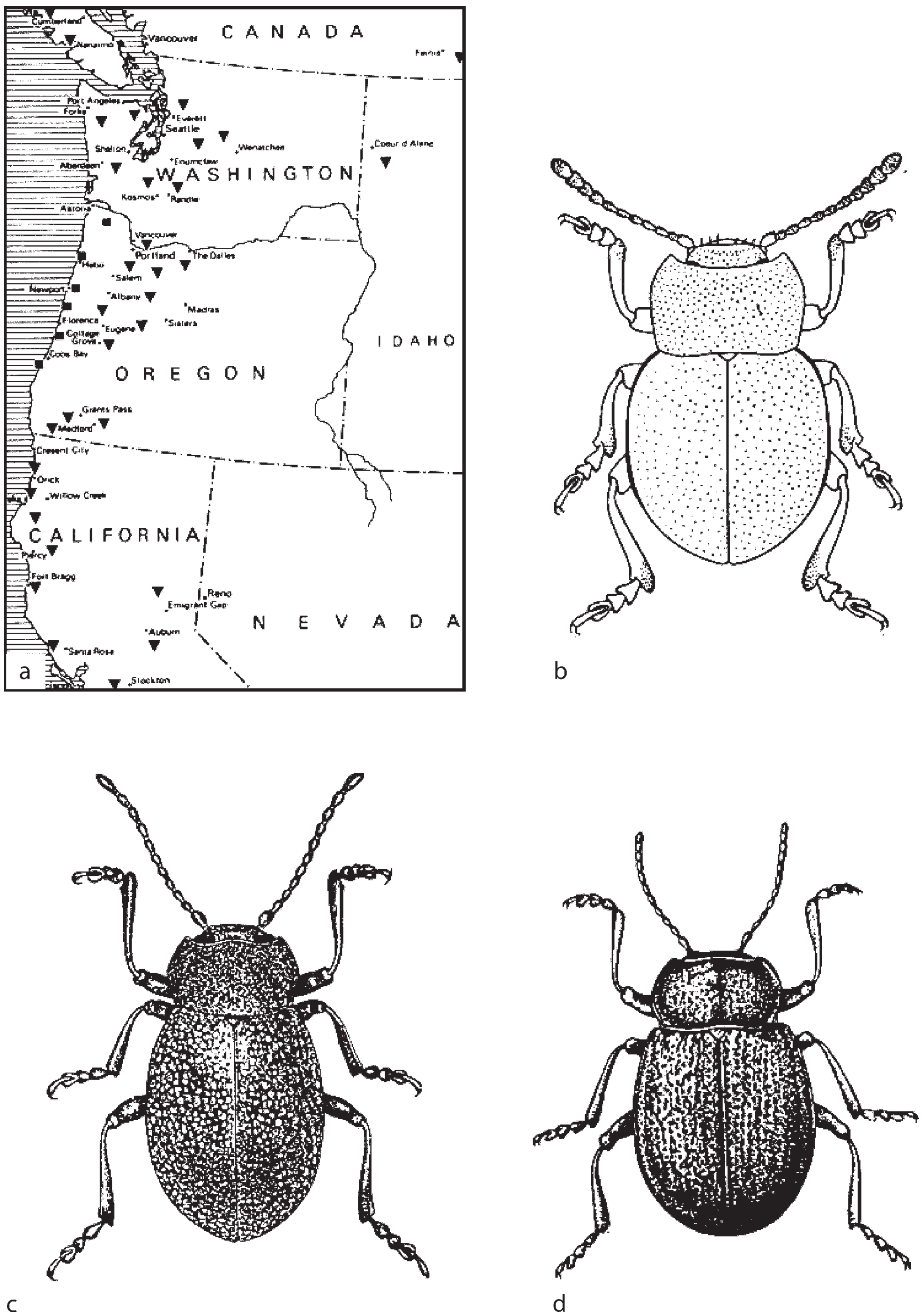
The archaic characteristics of the adult, and morphological structures of the larvae, probably warrant for *Timarcha* a subfamily of its own, the Timarchinae, situated between primitive ones (Aulacoscelinae, Sagrinae) and more evolved ones (Chrysomelinae). That status has already been proposed by various authors, but many others remain hesitant and prefer the status of tribe (Timarchini) at the beginning of the Chrysomelinae. Timarchini would be a monogeneric tribe with four subgenera. All other genera formerly included among the Timarchini are now listed among the Entomoscelina, a subtribe. No other Chrysomelinae has a ring piece around the aedeagus, divided at its base, with a ciliated cap-piece on the top. Several rare chrysomeline genera show a ring piece (tegmen) devoid of any cap piece on the top. Normally Chrysomelinae genera and species have a V or Y-shaped tegmen, a more evolved form of aedeagus. Farrell's molecular analysis of the Chrysomelinae unfortunately missed *Timarcha*, a key genus.

The genus *Timarcha* probably originated in the steppes of Central Asia, from where it has been eliminated by the Pleistocene glaciations. It adapted through a complicated system of egg or adult diapause to Middle Europe and North America, including middle-sized mountains. It still does not occupy areas that were glaciated in the Pleistocene in the U.S. and Canada (except Vancouver island) and in Europe (below Scotland, the Baltic States and Denmark). Species of *Timarcha* can survive moderate cold, but in Normandy, for instance, one species (*T. goettingensis* (Linné)) becomes active in February when the sun shines. Most of the species are diurnal, but some can be crepuscular or entirely nocturnal. *Timarcha punctella* Marseul in Tunisia and Libya, and *T. laevigata* (L.) in Morocco, are active during the day when other species in the North African mountains are mostly crepuscular. Through the Middle European mountains, adults of the subgenus *Metallotimarcha* Motschulsky (*T. metallica* Laicharting, *T. hummeli* Faldeman, etc.) seem to be mostly crepuscular or nocturnal in activity. In the United States and southern Canada, adults of the subgenus *Americanotimarcha* Jolivet are entirely nocturnal. During the summer, they climb over *Rubus* plants at around 9 p.m. and start to go down around 5 a.m. to hide under the trash, fallen leaves, and near the roots of brambles. They do the same on strawberry plants. European and African *Timarcha* show abundant reflex bleeding (haemorrhage) around the mouth and between femur and tibia. American species, being nocturnal and in this way being protected from most of the predators, show a very discrete bleeding. Not only does *Timarcha* blood taste bitter, but it is toxic in its contents (anthraquinones). Also, the purely nocturnal species of *Timarcha* (the American species, and also some of the *Metallotimarcha*) do not have the elytra fused. Probably, problems of water loss are not acute during the night.

Timarcha species fed originally on *Plantago* species (*P. albicans* L., *P. maritima* L., etc.) and this choice is maintained with most of the African and southern European species (no data are known on Asian *Timarcha*). This host selection behavior is absent among north European and North American species. However, the dual choice (Rubiaceae/Plantaginaceae) is still shown along the French Atlantic coast with *Timarcha maritima* Perris which feeds alternatively on *Galium arenarium* Lois and *Plantago maritima* L. Many Iberian or Moroccan species have adapted to the same diet, Rubiaceae/Plantaginaceae, related taxonomically and chemically, but they eventually switch to other related plant families: *Veronica* (Scrophulariaceae), *Scabiosa* (Dipsacaceae) or not related: *Launaea* (Asteraceae), *Carrichtera*, *Iberis*, *Alyssum* (Brassicaceae). Southern species (Sicily, Spain, Morocco) display such adaptations, but generally Rubiaceae (*Galium*, *Rubia*, *Crucianella*, *Asperula*, *Sherardia*) along with various species of *Plantago* form part of the diet. There are also reports of *Timarcha metallica* feeding on *Vaccinium* spp. (Ericaceae) and other Ericaceae. The difference in food plants between Old and New World stocks of *Timarcha*, and the big difference in chromosome formula between the two groups, indicate a long isolation, probably since the separation of the northern land masses of the Atlantic in the early Eocene period. American *Timarcha* feed on Ericaceae and Rosaceae.

Timarcha is a K-strategist and lays few big eggs protected by a primitive ootheca mostly made of buccal secretions. Aptery and suppression of flight muscles likely allows the female to increase its egg production. Aptery is a serious handicap in case of fragmentation of the habitat. Once *Timarcha* is eliminated from a habitat, repopulation is unlikely.

Timarcha is distributed in middle and southern Europe, northern Africa and western North America, and new species are described from time to time in Turkey, Italy and Corsica. However, *Timarcha* has completely disappeared from central Asia, and its ephemeral and possible existence in Teneriffe, Japan and elsewhere (Iceland) seems to be due to accidental introduction with forage not followed by survival. *Timarcha* has survived in some big islands (Corsica, Sardinia, Sicily, Mallorca, Minorca) and small ones (Channel Islands, Chausey archipelago, Aegades, small islands off the coast of eastern Spain, etc.), but has disappeared or has never existed in the eastern Mediterranean islands, including Cyprus and Crete. Malta remains *Timarcha* free, but probably lost the beetle due to intense urbanization since the Greek and Roman times. It was connected with Sicily during the Cenozoic. Stranger is the lack of *Timarcha* in three small Balearic islands, perhaps due to geological history. *Timarcha* has disappeared completely from the eastern and central USA (Fig. 77), probably during



Timarcha latreille (Coleoptera: Chrysomelidae, Chrysomelinae), Figure 77 ***Timarcha*: (a) Distribution of the genus *Timarcha* in the USA and Canada. Localities in Montana are not visible on the map; (b) *Timarcha (Metallotimarcha) metallica* Laicharting from Belgium; (c) *Timarcha (Americanotimarcha) intricata* Haldeman, Oregon, USA; (d) *Timarcha (Americanotimarcha) cerdo* Stål, Oregon, USA.**

the Pleistocene, though host plants are present in the Apalachian Mountains and elsewhere. It is also difficult to understand why the *Timarcha* did not cross the Sahara when it was vegetated, and did not colonize the Hoggar and the East African mountains as *Chrysolina* did. In some ways, the original distribution of *Timarcha* could have been similar to that of *Pimelia* and Pimeliinae in the West before the desertification of the Middle East, with a wider distribution toward Mauritania and the western Sahara, plus Egypt, Sudan, eastern Mediterranean and western Asia.

Being protected by their toxic fluid (by regurgitation) and prebuccal and tibio-femoral reflex bleeding (by anthraquinones) and eventually also by a nocturnal life, *Timarcha* spp. have few parasites and parasitoids (Ichneumonidae and Braconidae), mites under the subelytral cavity (Canestriniidae) and microbial commensals: gregarines. Practically no predators (birds, lizards) feed on them. When resting during the cold season in the Mediterranean, adults of *Timarcha* often gather together under tufts of plants, showing a tendency to gregarism.

American and European species of *Timarcha* differ in number of chromosomes, the American species having a much greater number. The basic formula in Europe is: $2n = 12$ and in America: $2n = 44$.

The black body color of *Timarcha* and the red blood extruded abundantly likely have an aposematic effect because of the contrast with the green background of the food plant. However, aposematism is of no use for nocturnal species.

The size of *Timarcha* adults varies from 5–8 mm (*T. cerdo*) to 18–23 mm (*T. tangeriana* Bechyne). Generally a size of 10–12 mm (*T. goettingensis* (L.)) is common.

Conclusions

The genus *Timarcha* remains rather enigmatic. In certain areas it seems to be evolving very quickly. Isolated valleys and mountains, acting as islands, like the Pyrenees in France and Spain, and the Atlas in Morocco, seem to be the focus of strong variation. Along the Moroccan coast and in the Pyrenees, small morphological differences, probably linked with interbreeding, sometimes show small variations in food habits. In the Pyrenees, each river, each valley seems to have a small variation.

Separation of the genus between America and the Old World has always puzzled entomologists. Very few other cases are similar among the arthropods. Transpacific migration remains a possibility, but the genus is absent in the Far East.

Extinction is caused by urbanization, fragmentation of the habitat, use of insecticides and herbicides, general pollution and many other reasons. The survival of many species is actually in jeopardy in Europe and in the USA. Probably several species will soon be extinct, and many more are endangered.

References

Farrell BD (1998) “Inordinate fondness” explained: why are there so many beetles? Science 281:555–559

Gomez-Zurita J, Juan C, Petitpierre E (2000) The evolutionary history of the genus *Timarcha* (Col Chrys.). Inferred from mitochondrial COII gene and partial 16S rDNA sequences. Mol Phylogenet Evol 14:304–317

Jolivet P (1994) Remarks on the biology and biogeography of *Timarcha* (Chrysomelidae Chrysomelinae). In: Furth DG (ed) Proceedings 3rd International Symposium on Chrysomelidae, Beijing, 1992. Backhuys, Leiden, 85–97 pp

Jolivet P (1995) A status report on the species of *Timarcha* (Col. Chrys.). Insecta Mundi 9:153–154

Jolivet P, Petitpierre E (1973) lantes-hôtes connues des *Timarcha* Latreille (Col. Chrys.). Quelques considérations sur les raisons possibles du trophisme sélectif. Bull Soc Entomol Fr 78:9–25

Tineid Moths

Members of the family Tineidae (order Lepidoptera).

► Fungus Moths

► Butterflies and Moths

Tineidae

A family of moths (order Lepidoptera). They commonly are known as tineid moths, fungus moths, or clothes moths.

▶ Fungus Moths
▶ Butterflies and Moths

Tineodidae

A family of moths (order Lepidoptera) also known as false plume moths.

▶ False Plume Moths
▶ Butterflies and Moths

Tingidae

A family of bugs (order Hemiptera). They sometimes are called lace bugs.

▶ Lacebugs
▶ Bugs

Tiphiidae

A family of wasps (order Hymenoptera).

▶ Wasps, Ants, Bees, and Sawflies (Hymenoptera)
▶ Tiphiid Wasps (Hymenoptera: Tiphiidae)

Tiphiid Wasps (Hymenoptera: Tiphiidae)

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The family Tiphiidae belongs to the informal group (series) Aculeata, which includes all stinging wasps, of the order Hymenoptera (ants, wasps and bees). The Tiphiidae were previously placed in the superfamily Scolioidea and later Tiphioidea. The current classification of the Hymenoptera which recognizes only three aculeate superfamilies, Chrysidoidea, Apoidea and Vespoidea, places the Tiphiidae in the superfamily Vespoidea.

Order: Hymenoptera
Suborder: Apocrita
Informal Group: Aculeata
Superfamily: Vespoidea
Family: Tiphiidae

Most members of the Tiphiidae are believed to be parasitoids of the edaphic (soil inhabiting) larval stage of certain beetles (Coleoptera). Primarily a tropical family, the Tiphiidae are represented worldwide by seven subfamilies containing about 1,500 species. These subfamilies are the Anthoboscinae (six genera), Diamminae (one genus), Thynninae (50 genera), Tiphiinae (nine genera), Brachycistidinae (13 genera), Myzininae (12 genera) and Methochinae (two genera). The Thynninae is the largest subfamily of the Tiphiidae, present mainly in the Neotropical regions and Australia. The five subfamilies represented in North America include the Tiphiinae, Myzininae, Methochinae, Anthoboscinae and Brachycistidinae. Of these subfamilies, the Tiphiinae is the largest containing about 140 species in North America. The most common group of Tiphiinae are the members of the genus *Tiphia*, represented by about 100 North American species.

External Morphology

The adult Tiphiidae range from 5 to 30 mm in length. The wasps are typically black but may have red, yellow or white markings. The antennae are 12-segmented in females and 13-segmented in males. The pronotum and mesonotum are separated by a suture and not fused. The middle and hind legs are often heavily spined. Sexual dimorphism ranges from slight to pronounced and in some species, the wings of the female are reduced or absent. Males often have a modification of the eighth sternite (or hypopygidium) forming an upward curved spine that may be mistaken for a sting. Two morphological features which help to distinguish the Tiphiidae from other families are a mesosternum with two posterior lobes and the separation of abdominal segments by well-defined constrictions.

Life History and Habits

The Tiphiidae are all solitary wasps and develop as ectoparasitoids on their soil-dwelling hosts. Most tiphiids are parasitoids of larval Scarabaeidae, commonly referred to as white grubs. The Thynninae, Tiphiinae and Myzininae contain species that, for the most part, are parasitoids of white grubs. The exception is the Myzininae, in which a few of the species parasitize larval Tenebrionidae, Cicindellidae or Cerambycidae (all Coleoptera). The biology of the Anthoboscinae and Brachycistidinae has not been studied but it is believed that members of these two subfamilies are also parasitoids of scarabaeid larvae. The Diamminae, an Australian group, parasitizes mole crickets (Orthoptera: Gryllotalpidae) and the Methochinae parasitize the larvae of tiger-beetles (Coleoptera: Cicindellidae).

Adult Tiphiidae feed primarily either on honeydew produced by other insects, or on the nectar of flowering plants. Female wasps may also feed by biting a paralyzed host during an oviposition event and then imbibing the hemolymph exuding from the wound. Females lay about 50 eggs over their 3- to 4-week lifespan, but in a few species may lay as many as 100 eggs. As in most members of Hymenoptera, fertilized eggs become females and males are produced with unfertilized eggs. Females control the sex of their offspring, with male eggs placed on smaller hosts and female eggs placed on larger hosts (Fig. 78).

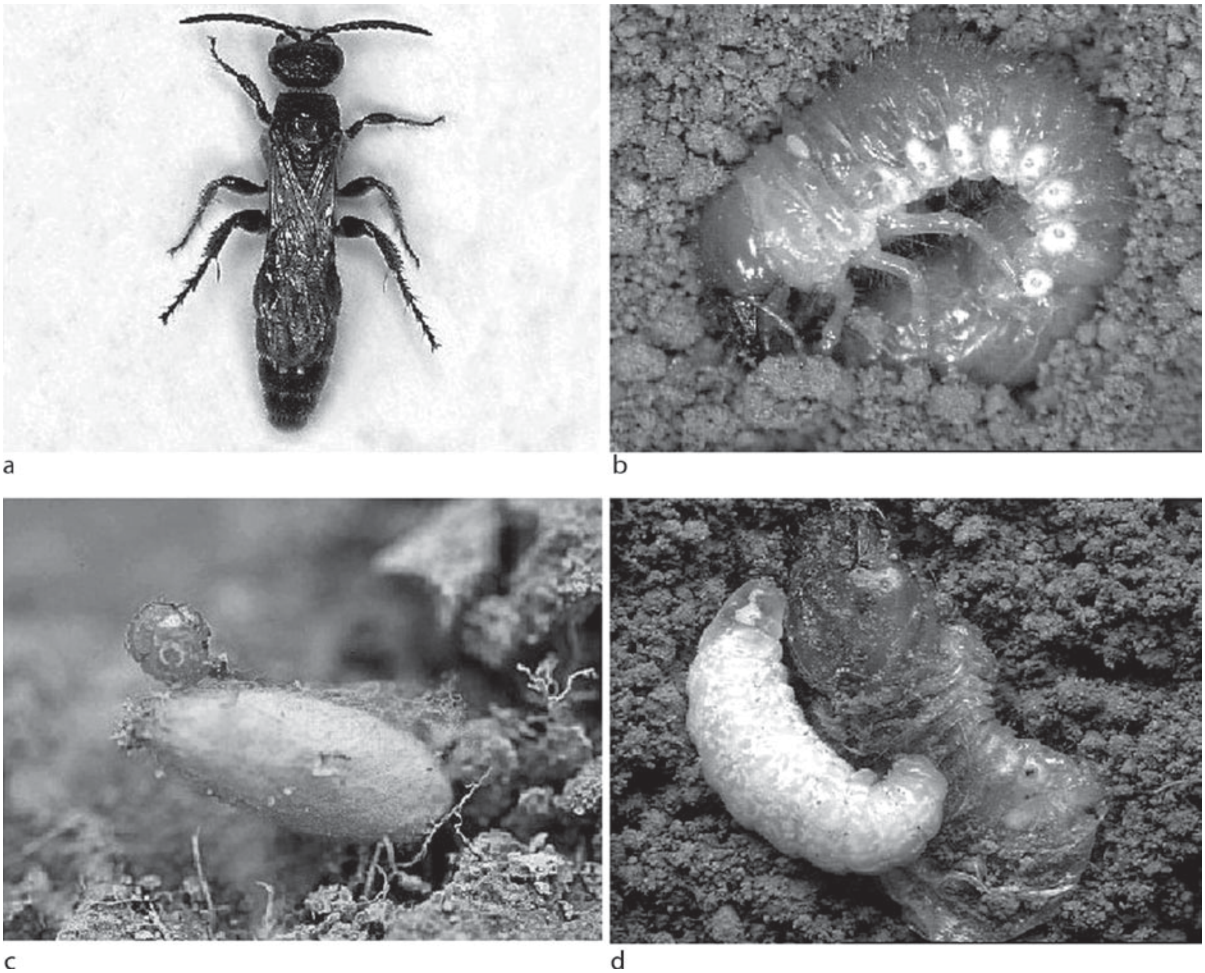
The best-studied group of Tiphiidae is the genus *Tiphia*. *Tiphia* are mostly host specific, i.e., each wasp species parasitizes larvae of only one species of grub. In cases where more than one grub species is parasitized, all host grub species are usually of the same genus. The emergence of adult wasps is synchronized with the presence of the third instar of grubs with a 1-year life cycle or the second instar of grubs with a 2- or 3-year life cycle. After mating, the female burrows into the soil and uses kairomones from grub frass (feces) and body odor trails to locate a host. Once a host is found, the wasp stings the grub ventrally between the first and second thoracic segments causing temporary paralysis. An egg is then laid on the host. The position of the egg on the host differs among the species of *Tiphia*. The larval *Tiphia* hatches from the egg in 3–7 days. Upon hatching, the wasp larva pierces its host's cuticle with its mouthparts and feeds on its body fluids. After a period of about 21 days, the fifth instar *Tiphia* devours the remaining non-sclerotized body parts of its host and then spins a silken cocoon. In temperate regions, *Tiphia* have one generation per year and will overwinter in the cocoon. Tropical species of *Tiphia* have multiple generations each year.

Predators and Parasites

The impact that natural enemies have on tiphiid populations is not known. Bombyliid flies (Diptera) and rhipiphorid beetles (Coleoptera) are common parasites reared from the cocoons of various Tiphiidae. Sphecid and mutillid wasps (Hymenoptera) and nematodes are less commonly observed as natural enemies of tiphiids.

Importance in Biological Control

During the 1920s and 1930s, 14 species of *Tiphia* were introduced into the U.S. from Japan and China to control the spread of the Japanese beetle, *Popillia japonica* (Coleoptera: Scarabaeidae). Only two of them, *Tiphia popilliavora* and *T. vernalis*, became established. Only *T. vernalis* is known to still be established throughout much of the range of the Japanese beetle. Currently, efforts are under way to move *Tiphia vernalis* to areas of the U.S. where the Japanese beetle has recently spread but *Tiphia vernalis* is not yet established. Of the native Tiphiidae, *Tiphia pygidialis* and *T. relativa* are common parasitoids of masked chafer,



Tiphiid Wasps (Hymenoptera: Tiphiidae), Figure 78 **Tiphiid wasps: (a) Adult female *Tiphia pygidialis*, subfamily Tiphiinae, 12 mm long, North America. (b) Masked chafer, *Cyclocephala* sp. with egg of *T. pygidialis*. (c) Fifth instar *T. pygidialis* devouring *Cyclocephala* sp. host. (d) *Cocoon* of *T. pygidialis*.**

Cyclocephala spp., grubs and *T. berbereti*, *T. intermedia*, *T. tegulina*, *T. transversa* and *T. vulgaris* parasitize June beetle, *Phyllophaga* spp., grubs.

► Wasps, Ants, Bees, and Sawflies (Hymenoptera)

References

Brothers DJ (1999) Phylogeny and evolution of wasps, ants and bees (Hymenoptera, Chrysidoidea, Vespoidea and Apoidea). Zool Scr 28:233–249

Clausen CP (1940) Entomophagous insects. McGraw-Hill, London, 688 pp

Clausen CP, Jaynes HA, Gardner TR (1933) Further investigations of the parasites of *Popillia japonica* in the far east. Technical Bulletin *No. 366* United States Department of Agriculture, Washington, DC

Kimsey LS (1991) Relationships among the tiphiid subfamilies (Hymenoptera). Syst Entomol 16:427–438

King JL, Holloway JK (1930) *Tiphia popilliavora* Rohwer, a parasite of the Japanese beetle. Circular No. 145. United States Department of Agriculture, Washington, DC

Rogers ME, Potter DA (2002) Kairomones from scarabaeid grubs and their frass as cues in below-ground host location by the parasitoids *Tiphia vernalis* and *Tiphia pygidialis*. Entomol Exp Appl 102:307–314

Tipulidae

A family of flies (order Diptera). They commonly are known as crane flies.

► Flies

► Crane Flies (Tipulidae and Others)

Tischeriidae

A family of moths (order Lepidoptera). They commonly are known as trumpet leafminer moths.

► Trumpet Leafminer Moths
► Butterflies and Moths

Toad Bugs

Members of the family Gelastocoridae (order Hemiptera).

► Bugs

Tobacco

The source of nicotine, a natural product having insecticidal properties.

► Botanical Insecticides

Toe Biters

Members of the family Belostomatidae (order Hemiptera).

► Bugs
► Giant Water Bugs

Togossitidae

A family of beetles (order Coleoptera). They commonly are known as bark-gnawing beetles.

► Beetles

Tolerance

The ability of a host to grow and reproduce normally while supporting an insect population that would normally be damaging.

Tomato Big Bud

A bacterial disease transmitted by leafhoppers.

► Transmission of Plant Diseases by Insects

Tomato Hornworm, *Manduca quinquemaculata* (Haworth) and Tobacco Hornworm, *Manduca sexta* (Linnaeus) (Lepidoptera: Sphingidae)

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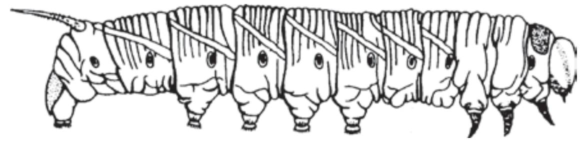
These species occur in North, Central and South America, and the Caribbean Islands. The tobacco and tomato hornworms are very similar in appearance, biology, and distribution, and are commonly confused. However, the tobacco hornworm is more common in warmer climates, such as the Gulf Coast States of the USA, whereas the tomato hornworm is more common in cooler regions such as the northern USA and Canada.

Life History

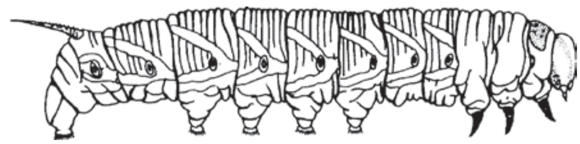
The number of annual generations ranges from one in cool locations such as Canada to perhaps four in warmer locations such as Florida, USA. The proportion of insects that enter diapause increases from about 5% in June to 95% in mid August, as day length decreases. In northern Florida, the insects are active from April to November, but they are abundant only for the first two generations because many pupae enter diapause. In North Carolina they occur from mid May to October, and evidence of a third generation is weak. Throughout their range, hornworms overwinter in the pupal stage, and in the northernmost portions of their range may not overwinter successfully, occurring only after dispersal northward during the summer. The life cycle can be completed in 30–50 days, but often is considerably protracted.

The eggs are spherical to oval in shape, and measure 1.25–1.50 mm in diameter. Eggs are smooth and vary in color from light green or yellow when they are early in development, to white at maturity. Eggs are deposited principally on the lower surface of foliage, but also on the upper surface. Mean fecundity is about 250–350 eggs, with seasonal fluctuations and maximum egg production at mid-season. However, with adequate adult nutrition, fecundity of nearly 1,400 eggs per female could be attained. Duration of the egg stage is 2–8 days, but averages 5 days.

The larva is cylindrical in form and bears five pairs of prolegs in addition to three pairs of thoracic legs. The most striking feature of the larva is a thick pointed structure or "horn" located dorsally on the terminal abdominal segment. The horn is as long as the body in newly hatched larvae, but becomes relatively smaller as the larva matures. Young larvae are yellowish white but during the second instar become green with white lines laterally. The tobacco hornworm develops seven straight oblique whitish lines laterally. The white lines are edged with black on the upper borders, and the horn is usually red in color. The tomato hornworm is superficially similar, but instead of the seven oblique lateral bands it bears eight whitish or yellowish "V"-shaped marks laterally, and pointing anteriorly. The V-shaped marks are not edged in black (Figs. 79 and 80). Also, in tomato hornworm the horn tends to be black in color. The body of both species is usually light green in color, but occasionally dark brown or blackish forms occur; the larvae blend in very well with the foliage on which they feed. There normally are five instars, but occasionally six are observed. The mean head capsule width is 0.8, 1.2, 2.0, 3.0, and 5.0 mm for instars 1–5, respectively. Corresponding mean larval body lengths are 6.7, 11.2, 23.4, 49.0, and 81.3 mm, respectively. Larval development time averages about 20 days, but ranges from 13 to 44 days depending on temperature. Mean development time for larvae reared under insectary conditions in northern Florida is 3.4, 2.9, 3.0, 3.9, and 6.6 days for instars 1–5, respectively.



Tomato Hornworm, *Manduca quinquemaculata* (Haworth) and Tobacco Hornworm, *Manduca sexta* (Linnaeus) (Lepidoptera: Sphingidae), Figure 79 Tomato hornworm larva.

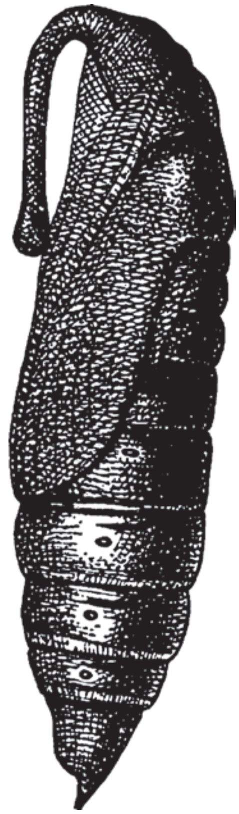


Tomato Hornworm, *Manduca quinquemaculata* (Haworth) and Tobacco Hornworm, *Manduca sexta* (Linnaeus) (Lepidoptera: Sphingidae), Figure 80 Tobacco hornworm larva.

Mature larvae drop to the soil at maturity and burrow to a depth of 10–15 cm. There they form a pupal cell measuring about 7 cm long and 4 cm wide, and pupate within. The interval between entering the soil and pupation is usually 4–8 days. The pupa is large and elongate-oval in form, but pointed at the posterior end. It measures 45–60 mm in length and 13–14 mm in width. The pupa bears a pronounced maxillary loop, a structure that encases the mouthparts. The maxillary loop in tobacco hornworm extends back about one-fourth the length of the body, whereas in tomato hornworm it is longer, usually extending for about one-third the length of the body (Figs. 81 and 82). The color of the pupa is brown or reddish brown. Duration of the pupal stage is protracted and variable. Pupal duration often exceeds 100 days, even in the summer generations, but may be as short as 15 days, and 21 days is about average. Overwintering pupae do not emerge synchronously, with emergence spread from May to early August; a few even diapause through two winters.

The adults of both species are large moths with stout, narrow wings, and a wing span of 80–130 mm. The forewings are much longer than

Tomato Hornworm, *Manduca quinquemaculata* (Haworth) and Tobacco Hornworm, *Manduca sexta* (Linnaeus) (Lepidoptera: Sphingidae), Figure 81 Tomato hornworm pupa.



Tomato Hornworm, *Manduca quinquemaculata* (Haworth) and Tobacco Hornworm, *Manduca sexta* (Linnaeus) (Lepidoptera: Sphingidae), Figure 82 Tobacco hornworm pupa.

the hind wings. The females are larger than the males and can be differentiated from them by the narrower antennae. Both species are dull grayish or grayish brown in color, though the sides of the abdomen usually are marked with six orange-yellow spots in tobacco hornworm and five spots in tomato hornworm. The hind wings of both species bear alternating light and dark bands (Figs. 83 and 84). Adults become active at sunset, when they can be observed feeding at flowers. Though some adults remain active throughout the night, most activity occurs early in the evening and just before dawn. Both hornworm species likely produce sex pheromone, but only that of the tobacco hornworm has been identified. The preoviposition period of moths is about 2 days, and eggs are deposited for about 4–8 days.

Tomato Hornworm, *Manduca quinquemaculata* (Haworth) and Tobacco Hornworm, *Manduca sexta* (Linnaeus) (Lepidoptera: Sphingidae), Figure 83 Tomato hornworm adult.

These insects feed only on solanaceous plants, particularly tomato and tobacco. They are recorded from other vegetables such as eggplant, pepper, and potato, but such feeding is unusual. Several

Tomato Hornworm, *Manduca quinquemaculata* (Haworth) and Tobacco Hornworm, *Manduca sexta* (Linnaeus) (Lepidoptera: Sphingidae), Figure 84 Tobacco hornworm adult.

solanaceous weeds are reported to serve as hosts, including groundcherry, *Physalis* spp.; horsenettle, *Solanum carolinense*; jimsonweed, *Datura stramonium*; and nightshade, *Solanum* spp.; but wild hosts are unimportant larval food sources relative to crops. Adults imbibe nectar from flowers of a number of plants such as catalpa, *Catalpa speciosa*; daylily, *Hemerocallis* sp.; hollyhock, *Althaea rosea*; jimsonweed; four o'clock, *Mirabilis jalapa*; mallow, *Hibiscus lasiocarpus*; mimosa, *Albissia julibrissin*; and tobacco.

A large number of natural enemies is known from tobacco and tomato hornworm. Natural enemies of the egg stage include *Trichogramma* sp. (Hymenoptera: Trichogrammatidae) and *Telenomus* sp. (Hymenoptera: Scelionidae), but these are thought to be of little importance. Of greater importance is the stilt bug *Jalysus spinosus* (Say) (Hemiptera: Berytidae) and other general predators such as bigeyed bugs (Hemiptera: Lygaeidae) and lacewings (Neuroptera: Chrysopidae).

Larvae often are parasitized by *Apanteles congregatus* (Say) (Hymenoptera: Braconidae), and larvae are sometimes seen bearing clusters of white pupal cases formed by this wasp, attached to their bodies. In North Carolina, 30–40% of hornworms may be parasitized by this wasp. In contrast to this one species of wasp accounting for most of the parasitism by Hymenoptera, a number of insects in the order Diptera, particularly the Tachinidae, attack tobacco and tomato hornworm. Records of tachinid parasitism from tomato hornworm include *Compsilura concinnata* (Meigen), *Drino incompta* (Wulp), *D. rhoeo* (Walker), *Lespesia frenchii* (Williston), *Winthemia leucanae* (Kirkpatrick), and *W. quadripustulata* (Fabricius). Records of tachinids from tobacco hornworm include *Carcelia* spp., *Drino incompta*, *D. rhoeo*, *Lespesia* spp., *Metavoria orientalis* Townsend, and *Winthemia quadripustulata*. In North Carolina, the proportion of hornworm larvae parasitized by tachinids increases during the season, sometimes attaining 100%. The number of tachinid eggs per hornworm larva also increases seasonally, indicating a greater abundance of flies. Also of great significance as a mortality agent of larvae is *Polistes* spp. (Hymenoptera: Vespidae). These wasps kill and consume, or sometimes carry away to provision their nest, a very high proportion of larvae. Apparently *Polistes* spp. is the most important larval mortality factor in North Carolina.

Pathogens sometimes affect hornworms. A bacterial disease that causes the larva to blacken and droop is sometimes reported to kill larvae, but this does not occur regularly, and is observed mostly at very high larval densities. Larvae also are susceptible to infection by the fungus *Entomophaga aulicae*, but this disease also does not occur widely.

Vertebrates may prey on the pupae. Skunks and moles are particularly important. Tachinids emerge from the prepupal and pupal stages, but attack only the larvae.

Damage

Although these insects are common, they are not serious pests in commercial agriculture because they are easily killed by insecticides. In home gardens they often cause considerable damage to tomato.

Larvae are defoliators, usually attacking the upper portion of plants initially. Rather than chewing holes in the leaf, they usually consume the entire leaf. Sometimes they attack green fruit. Because the larvae of hornworms attain such a large size, they are capable of high levels of defoliation. The consumption of tobacco foliage by larvae is 5.2, 9.7, 33.5, 175.4, and 1,941.4 cm^2 by instars 1–5, respectively, for a total of 2,165 cm^2. Note that about 90% of the foliage consumption occurs during the final instar, and although the exact value of foliage consumption would differ on tomato, the pattern would be the same. Larvae blend in with the foliage and are not easy to detect. Thus, it is not surprising that they often are not observed until they cause considerable damage at the end of the larval period.

Management

Moths are attracted to light and can be captured in light traps. Light traps have also been used to attempt suppression of hornworm populations, and although some reduction was noted, this approach has not proved practical. Isoamyl salicylate is attractive to both species of hornworms. Visual examination of foliage usually is recommended for monitoring of larval populations. Young larvae of tobacco hornworm tend to be found in the upper regions of the plant, whereas larvae of tomato hornworm tend to be lower; differential flight and oviposition behavior between the species is implicated.

Chemical insecticides or *Bacillus thuringiensis* are applied to the foliage for larval suppression. The mature caterpillars are more difficult to kill, so young larvae should be targeted. The pupae are large and not buried very deeply in the soil, so greater than 90% mortality is caused by normal soil tillage practices. Hand picking and destruction of larvae is often practical in the home garden.

To take advantage of the preference of *Polistes* wasps for hornworm larvae, wasp shelters or nesting boxes have been placed in tobacco fields to encourage the wasps, and wasp colonies were relocated into tobacco. Although wasp predation was inadequate to prevent damage to tobacco, this approach might be satisfactory for tomato.

Tobacco and tomato hornworm thrive on tobacco plants that are allowed to revegetate after harvest of the leaves, leading to high populations during the next year. Destruction of tobacco stalks, or inhibition of sprouting by application of plant growth regulators, greatly reduces hornworm populations in subsequent seasons. Though not documented, timely destruction of tomato crop residue likely would have similar beneficial effects.

References

Bell RA, Joachim FG (1976) Techniques for rearing laboratory colonies of tobacco hornworms and pink bollworms. Ann Entomol Soc Am 69:365–373

Capinera JL (2001) Handbook of vegetable pests. Academic, San Diego, 729 pp

Chamberlin FS, Tenhet JN (1926) The seasonal history and food habits of the tobacco budworm, *Heliothis virescens* Fab., in the southern tobacco-growing region. J Econ Entomol 19:611–614

Madden AH, Chamberlin FS (1945) Biology of the tobacco hornworm in the southern cigar-tobacco district. USDA Technical Bulletin 896, 51 pp

Rabb RL (1969) Environmental manipulations as influencing populations of tobacco hornworms. Proc Tall Timbers Conf Ecol Anim Cont Habitat Manage 1:175–191

Tomato Rust Mite, *Aculops lycopersici* (Massee) (Acari: Eriophyidae)

This is a pest of solanaceus crops, especially tomato.

Tomoceridae

A family of springtails in the order Collembola.

► Springtails

Tonic Receptors

Sensory neurons that are slow to adapt to continuing steady stimuli, with the receptor potential remaining elevated (contrast with phasic receptors).

Tooth-Necked Beetles

Members of the family Derodontidae (order Coleoptera).

► Beetles

Tormogen Cell

An epidermal cell that forms a depression in the integument and which contains a seta, often is a flexible socket. It typically is innervated and has sensory capabilities.

Torre-Bueno, José Rollin De La

José de la Torre-Bueno was born at Lima, Peru, on October 6, 1871. At the age of 14 he and his family moved to the United States. He attended Columbia University and graduated in 1894. He obtained employment with the General Chemical Company of New York, where some of his principal responsibilities involved editorial work. He was an active member of the Brooklyn Entomological Society, and helped revive the society's publications as the Bulletin of the Brooklyn Entomological Society, New Series, and of Entomologica Americana, New Series. He served as editor of both until he died. Torre-Bueno was a hemipterist, and published "Synopsis of the North American Hemiptera Heteroptera" in three parts (1939, 1941, 1946). In 1937 the Brooklyn Entomological Society published Torre-Bueno's "Glossary of Entomology." Though the "Glossary" was a revision of J.B Smith's "An explanation of the terms used in entomology," it became a classic publication. It was updated in 1989 by S.W. Nichols. Torre-Bueno died in Tucson, Arizona, on May 3, 1948.

Reference

Mallis A (1971) American Entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Tortoise Beetles

Members of the subfamily Cassidinae of the beetle family Chrysomelidae. The lateral expansion of the pronotum and elytra hide the legs and head, giving a tortoise-like appearance to the insect.

► Beetles

Tortoise Scales

Some members of the family Coccidae, superfamily Coccoidae (order Hemiptera).

► Scale Insects and Mealybugs

► Bugs

Tortricid Moths

Members of the family Tortricidae (order Lepidoptera).

► Leafroller Moths

► Butterflies and Moths

Tortricidae

A family of moths (order Lepidoptera). They commonly are known as leafroller moths or tortricid moths.

► Leafroller Moths

► Butterflies and Moths

Torymidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees, and Sawflies

Townes, Jr., Henry K

Henry Townes was born at Greenville, South Carolina, USA, on January 20, 1913. He received B.S. and B.A. degrees from Furman University in

1933, and then attended Cornell University where he attained the Ph.D. in 1937. He taught at Cornell and Syracuse Universities until receiving a fellowship in 1940 to work at the Philadelphia Academy of Natural Sciences in Philadelphia, where he prepared a catalog on the Nearctic Ichneumonidae. He also worked at the U.S. National Museum, where he was employed by the United States Department of Agriculture as a taxonomist. In 1949 he moved to North Carolina State University, where he worked on tobacco pests, and traveled to the Philippines to advise the government on pests of rice and corn. In 1956 he moved to the University of Michigan to work on Ichneumonidae. Henry and his wife Marjorie founded the American Entomological Institute in Ann Arbor, Michigan, in 1962 as an independent, nonprofit research institute. Henry also worked briefly at Michigan State University and Carleton University during the early stages of the institute, but it soon became a mecca for parasitic hymenopterists, and a full-time job. The Institute relocated to Gainesville, Florida, in 1985. Henry was passionate about the study of Ichneumonidae, became known as the world's foremost authority, and amassed the world's best collection. He published nearly 140 articles or books during his career, of which nine were at least 500 pages long. Along with colleagues, he established a firm knowledge of this group, one of the largest families of insects known. Henry Townes died at Gainesville, Florida, on May 2, 1990.

Reference

Buckingham GR, Gupta VK, Townes MC (1991) Henry K. Townes, Jr. Am Entomol 37:252–253

Toxemia

A condition produced by the dissemination of toxins in the blood, though the bacteria are confined to the gut (e.g., brachytosis).

Toxicant

A toxic substance, often the active ingredient in pesticide formulations.

► Insecticides
► Acaricides or Miticides

Toxicity

The ability of a toxin to harm or kill an organism.

► Insecticide toxicity

Toxicogenic Insects

Insects capable of producing disease in plants due to injection of saliva or other secretions, and in the absence of microbial pathogens.

Trachea (pl., Tracheae)

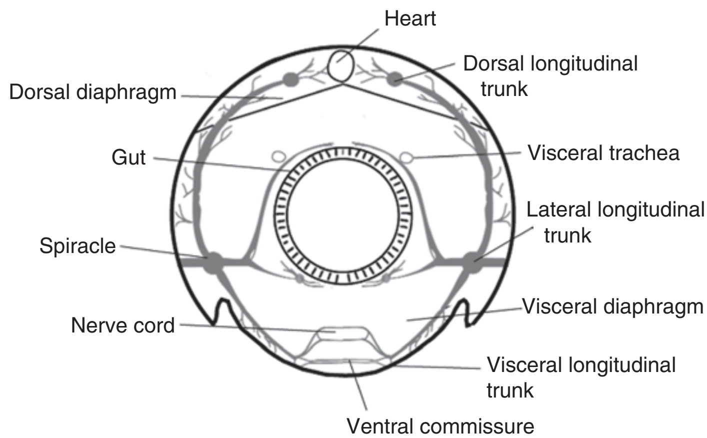
An internal tube that delivers air to tissues, and part of a system of large and small tubes. The external openings of the system are called spiracles, and the smaller tubes are called tracheoles. Air sacs, or dilated areas of trachea, are often found in the system (Fig. 85).

► Tracheal System and Respiratory Gas Exchange

Tracheal Gill

An extension of the insect's body that contains numerous tracheae and serves as a site for oxygen extraction from water. The heavily tracheated flaps or filaments of the body wall are usually lateral or ventral expansions of the thorax or abdomen, and gas exchange occurs across the body surface.

► Tracheal System and Respiratory Gas Exchange



Trachea (pl., Tracheae), Figure 85 Cross section of the abdomen of an insect, showing the principal trachea and tracheal connections (adapted from Chapman 1998, The insects: structure and function).

Tracheal Mite, *Acarapis woodi* (Rennie) (Acariformes: Tarsonemidae)

THOMAS C. WEBSTER
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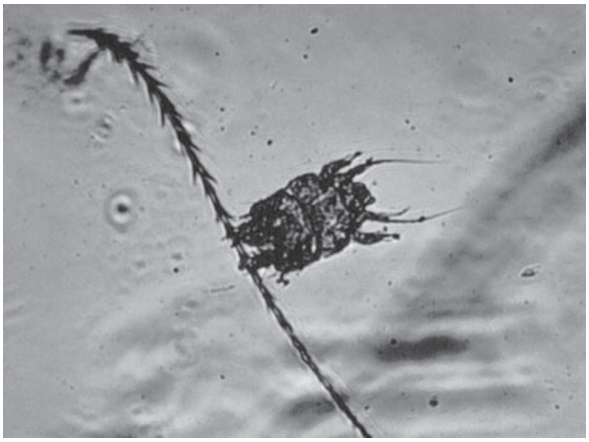
The tracheal mite is an internal parasite of honey bees. It feeds and reproduces inside the prothoracic tracheae of the adult bee. If a bee is heavily infested, its tracheae become scarred and filled with mites. Bees from heavily infested colonies may be seen crawling on the ground nearby, unable to fly.

Young bees are more susceptible to infestation than older bees. The female mite enters the tracheal tube at the spiracle, and lays eggs within several days of entry. The egg is followed by a larval and a pharate nymphal stage. The immature stages last 11–12 days for males and 14–15 days for the larger females. Immature and mature mites feed by piercing the host bee's tracheal wall with stylet mouthparts, and consuming the hemolymph. Male and female offspring mate in the trachea. Only mated females exit the spiracle to find another host bee (Fig. 86).

The means by which tracheal mites kill bees is not entirely clear. Some bees found crawling near infested hives have no mites or any apparent damage to their tracheae. Possibly, pathogen outbreaks in a bee colony are stimulated or mediated by the mite.



Tracheal Mite, *Acarapis woodi* (Rennie) (Acariformes: Tarsonemidae), Figure 86 Female tracheal mite clinging to a bee hair, in wait for a new host bee.

Dispersal from bee to bee is most rapid in winter when the bees cluster tightly. Since no bees are reared during winter, the proportion of bees which are infested rises considerably in winter. Consequently, a heavy infestation is often discovered on the first warm days of early spring, when many bees are found crawling on the ground near the hive. Tracheal mites spread from hive to hive when infested bees drift to, or rob honey from, other hives nearby.

An earlier name, the acarine mite, has been abandoned because it is meaningless and redundant. Two closely related mites, *A. externus* and *A. dorsalis*, live externally on the bees. They are not known to be harmful to their hosts.

History

The tracheal mite was first identified in 1919, when it was found in Scotland. Originally the mite was implicated in the "Isle of Wight disease," which had plagued the British Isles earlier in the century. However, more recent studies suggest that the disease was not caused simply by mite infestations.

Since then, the mite has been discovered in many other parts of the world. It is very well adapted to life as a honey bee parasite and is not found on hosts other than *Apis* species. Consequently, the host-parasite relationship must be very old.

Mexico was found to have the mite around 1980. In 1984 it was discovered in the United States, having apparently entered Texas from Mexico. Infestations were confirmed in Canada in 1986. By the late 1980s many thousands of hives in the United States and Canada were dying yearly. This parasite was rapidly dispersed by the shipment of queen and package bees, and migratory beekeeping operations. By the late 1990s, however, tracheal mite infestations had declined dramatically. Now the mite continues to be endemic in North America, as it is elsewhere. The decline of tracheal mite infestations is still not well understood.

Diagnosis and Control

Tracheal mites are identified by removing the prothoracic tracheae alone, or within the anterior portion of the bee's thorax. Thoracic muscle tissue is cleared with potassium hydroxide solution. Tracheal mites and scarring of the tracheae are easily seen by low power microscopy. Positive identification is not possible for those without a microscope.

Menthol, formic acid and chlorobenzilate have been used effectively as fumigants to control the mites inside the hive. Vegetable oil also has been used with success, mixed with sugar and placed inside the hive. Bees that walk over the oil preparation acquire a fine coating which seems to inhibit mite dispersal among bees in the hive.

Some bees groom themselves of mites. This trait is heritable, so selection for grooming behavior can be part of a breeding program for tracheal mite resistance.

► Mites
► Apiculture
► Honey Bee

References

Bailey L, Ball BV (1991) Honey bee pathology, 2nd edn. Academic, New York

Webster TC, Delaplane KS (eds) (2001) Mites of the honey bee. Dadant, Hamilton, IL

Wilson WT, Pettis JS, Henderson CE, Morse RA (1997) Tracheal mites. In: Morse RA, Flottum K (eds) Honey bee pests, predators and diseases, 3rd edn. A.I. Root, Medina, OH

Tracheal System and Respiratory Gas Exchange

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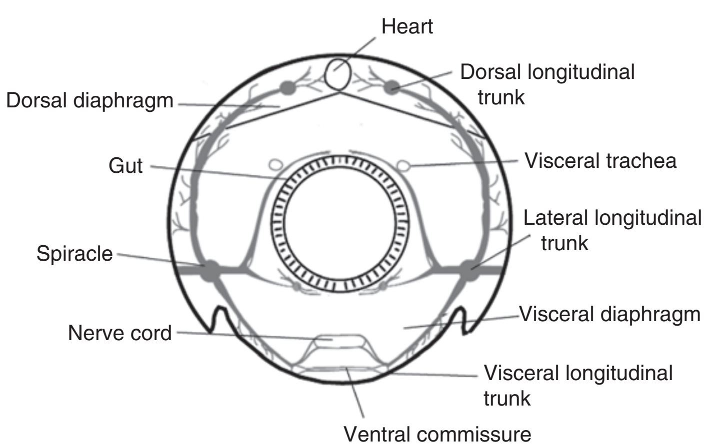
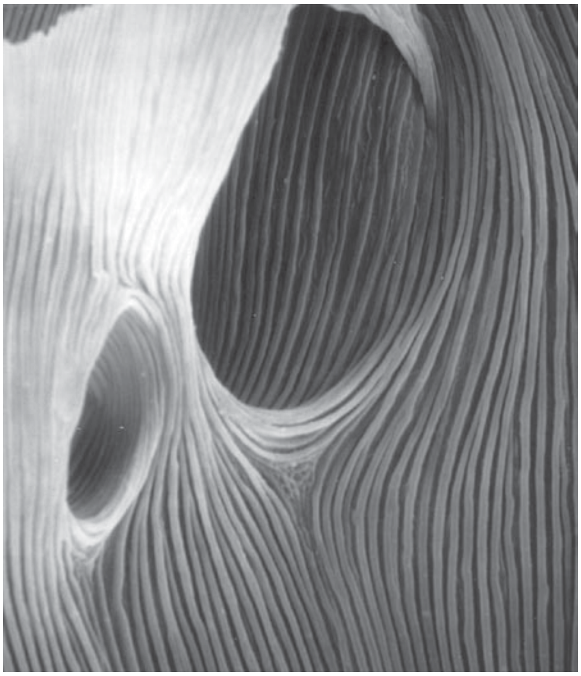
Insects breathe through a complex network of tubules, the tracheae. Large tracheae connect to spiracles opening at the surface of the body, where air enters and carbon dioxide exits. Spiracles usually occur on the pleural surface of the body, typically one on each side of each segment, but numerous variations have evolved. Airflow may be tidal, in and out of the same spiracles, or directed flow with inflow through anterior spiracles and outflow through posterior abdominal ones. Interconnecting longitudinal and transverse tracheal trunks make directed flow possible and more efficient than tidal flow because the system is constantly flushed and incoming air is not mixed with used air. Larger tracheal tubes send off branches that become smaller in diameter as they ramify to all tissues. The smallest diameter tracheoles (tubes 1 μm diameter or less) end blindly on the surface of most cells and even indenting some cells, like pushing a finger into a soft balloon, until they terminate within a few μm of mitochondria that actually use the oxygen. Tracheoles indented into a cell are said to be intracellular, although in reality they are not really within the interior of the cell, for the tracheal epithelium cell layer and the cell membrane separate the tracheole from the cytoplasm of the cell. The chitinous lining of tracheae are shed at each molt, but the lining of tracheoles is not molted. Spiracular valves at the body surface often can be closed to reduce water loss from the system. Although all parts of the tracheal system allow oxygen to diffuse out to the tissues and carbon dioxide to enter, most of the gas exchange occurs across the smaller tracheae and tracheoles because they are the parts of the system in intimate contact with cells. The extensive ramification of tracheae and tracheoles and their relationship to all cells are similar to the pattern of the vertebrate circulatory system, with the exception that tracheoles end blindly and vertebrate capillaries do not. The tracheal system is remarkably efficient for insects. Insects do not accumulate an oxygen debt during vigorous activity, such as flight. In some very small insects (smaller than a *Drosophila* fly), simple diffusion of gases through the tracheae may suffice, but most insects, large or small, actively ventilate the system by rhythmic compression of the abdomen. Muscular movements during flight or other vigorous muscular and body movements compress the tracheal system and act like a pump to ventilate the system (Figs. 87, 88, and 89).

Tracheae develop from embryonic ectodermal tissue, and all parts, including the smallest tracheoles, have an epicuticular lining or intima that is continuous with the external cuticle. In some larger insects one can see larger tracheal trunks that are pulled out and still attached to the old exoskeleton at a molt. Larger tracheae may contain a thicker endocuticle layer that gives more strength to the tubular structure. The internal surface of tracheae contains a hydrophobic substance that helps prevent water from entering the tracheae, and reduces evaporative water loss from the internal tracheal surfaces. Thickened, tight spirals of the cuticular intima, the taenidia, strengthen tracheae, provide elasticity, and help the tubes resist compression and collapse. Even tracheoles and air sacs show some evidence of taenidial reinforcements, but thickenings usually



Tracheal System and Respiratory Gas Exchange, Figure 87 Cross section of the abdomen of an insect, showing the principal tracheae and tracheal connections (adapted from Chapman 1998, The insects: structure and function).



Tracheal System and Respiratory Gas Exchange, Figure 88 **A view from inside a large trachea in a mole cricket. This scanning electron micrograph shows the branching of two smaller tracheae and the taenidial windings that strengthen all tracheae and keep them from collapsing.**

Tracheal System and Respiratory Gas Exchange, Figure 89 **A scanning electron micrograph view of a trachea (about 2 μm diameter) that branches several times into smaller tracheae and tracheoles that penetrate the salivary gland tissue of a male Caribbean fruit fly, *Anastrepha suspensa*.**

are widely spaced apart so that these parts of the system are more flexible.

Tracheae are not simply tubes and tubules; every part of the system contains living cells. Tracheal epithelial cells are thin and flattened, like many small pieces of ribbon glued together and wrapped around the tracheae. A tracheal epithelial cell encloses a tracheole. New tracheae and tracheoles develop as the insect grows. A new tracheole develops as a tubule or cavity within a tracheal epithelial cell that grows out, often in multiple finger-like shapes, from the surface of a larger trachea. The tracheole unites with the larger tracheal branch to which the parent tracheal cell is still attached.

Air sacs, dilated portions of tracheae, occur in many insects. They are variable in size, but frequently are large in flying insects such as honeybees, cicadas, many adult Diptera, and some scarab and buprestid beetles. The rhythmical squeezing action of working flight muscles pumps air sacs like a bellows and increases the flow of air through the system. Air sacs may collapse as growing tissues fill the body space, and by collapsing they make room for the new tissue, with little change in the general body shape. Air sacs serve a hydrostatic function in some aquatic insects, and allow more freedom in vibration of the tympanic membrane in some sound-producing insects. By taking up space and restricting hemolymph volume, air sacs increase solute concentration in the hemolymph without increasing total solute.

Hemocytes, the circulating blood cells, are the only cells in the body that do not have direct tracheal connections. Recently, it was shown that hemocytes tend to accumulate on very thin-walled tufts of tracheae near the last pair of abdominal spiracles and in the compartment at the tip of the abdomen called the tokus. It seems as if the highly branched tracheal system of the last segment and the tokus are sites where the hemocytes can become oxygenated; they probably pass their carbon dioxide directly into the hemolymph.

Discontinuous Breathing

Some insects regulate spiracle closing and opening, and keep the spiracles tightly closed and/or apparently closed for a high percentage of the time. Gas exchange occurs in three periods named the open, flutter, and closed periods (often designated as O, F, and C, respectively) because of the action of spiracles over the duration of a cycle. This functional pattern, variously known as discontinuous release of CO_2, passive suction ventilation, discontinuous ventilation cycle, and as the discontinuous gas exchange cycle (DGC) has been known in some insects for more than half a century. The earliest studies were in diapausing pupae of Lepidoptera, and initially DGC was thought to be limited to quiescent insects in a depressed state of metabolism. DGC patterns, however, have been observed in a number of different insects in various states of activity, including ants, the cockroach *Periplaneta americana*, a number of adult tenebrionid beetles, the locust *Schistocerca gregaria*, the lubber grasshopper *Romalea guttata*, and adults of additional species. DGC behavior also occurs in some arthropods other than insects. During DGC, accumulated CO_2 is discharged periodically in bursts during brief intervals when spiracles are open. After a burst, the spiracles are closed for some period of time that varies from species to species. During the closed interval, tissues use oxygen and intratracheal oxygen tension falls. Most insects that exhibit discontinuous gas exchange allow the spiracular valve to flutter with imperceptible amplitude to the unaided eye during a portion of a cycle. The fluttering (F) phase allows small amounts of O_2 to be sucked into the tracheal system by the slight negative pressure arising from O_2 consumption by the tissues. The F phase usually is considered to involve convective transfer of O_2. This has given rise to the name "passive suction ventilation" that sometimes is applied to the process. The slight internal vacuum retards the outward loss of water vapor and CO_2 during the fluttering phase, and the low influx of O_2 lengthens the time to full opening or "burst" of spiracles. Tissues produce CO_2 even when the spiracles are closed. The high solubility of CO_2 in aqueous solutions enables insects to accumulate bicarbonate ion, HCO_3^-, in the hemolymph. Buffering capacity of hemolymph aids in solubilizing CO_2 as bicarbonate, and this keeps gaseous CO_2 from building up rapidly in the tracheal system. At some point, probably different for different insects, the relationship between gaseous O_2 and CO_2, and HCO_3^- in solution reaches an equilibrium at which tracheal tension of CO_2 and O_2, and/or pH change in the hemolymph, trigger spiracle opening and release of CO_2 from the hemolymph as a gas. It often has been assumed, but not proven, that the functional benefit of discontinuous ventilation is conservation of water. In diapausing pupae that must pass a long winter under the soil, leaf litter, or other pupation site, water conservation seems quite necessary and a reasonable driving mechanism for the evolution of discontinuous ventilation, since the pupa is a closed (to food/water intake) system. Most adult insects that exhibit discontinuous ventilation do so only intermittently, and the rest of the time they ventilate the system continuously. Surprisingly, some insects do not show DGC respiration under conditions that might be expected (based upon assumptions) to promote the behavior. For example, the lubber grasshopper *Romalea guttata*, which discontinuously ventilates at times, tends to ventilate continuously when dehydrated, a physiological condition in when it presumably has a great need to conserve water. No good explanation has been provided for such behavior. The ant *Camponotus vicinus*, which exhibits discontinuous gas exchange, actually loses more water than CO_2 during the period when the spiracles are open. The harvester ant, *Pogonomyrmex rugosus*, and similar desert ants have a relatively high percentage (up to 13%) of body water loss through the tracheal system, even though they exhibit discontinuous ventilation at times. Whether the higher rate of water loss from the tracheal system in these ants is a significant stress for them may depend upon how much of the time the ants exhibit discontinuous gas exchange, how much access they have to food with high water content, and duration of exposure to environmental extremes. Although it seems somewhat intuitive that water loss might be high from the tracheal system, actual measurements in some insects indicate that more than 90% of total body water loss occurs through the cuticle, with only 2–5% typically lost from the tracheal system. In summary, a definitive selection mechanism for evolution of discontinuous gas exchange cycling is not evident, but the mechanism is fairly widespread in many insects including larvae, pupae, and large and small adults. Water conservation, ecological niche occupied by insects, and interactions of sensory components may be important factors.

Gas Exchange in Aquatic Insects

The tracheal system of most aquatic insects is structurally the same as that of terrestrial insects, i.e., with open spiracles and an extensive network of tracheae and tracheoles. These aquatic insects breathe air by coming to the surface. Water is prevented from entering the system by the hydrophobic surface of the tracheae, and in some cases, by spiracles that can be closed. Many aquatic larvae have a tracheal system with only one functional pair of spiracles near the tip of the abdomen. When the insect comes to the surface, it does so with the posterior end uppermost and only the tip of the abdomen bearing the spiracles is held above the surface. A large number of aquatic insects submerge with a bubble or film of air around a spiracle. These gas bubbles or films of air are called gas gills, and they may be temporary or permanent. Temporary ones must be replenished periodically as the oxygen is used. Permanent gas gills are called plastrons. They do not collapse and oxygen can be extracted from water into the gill (if the water is well aerated), allowing the insect to live underwater. A plastron consists of an extensive physical meshwork, either of fine hairs or setae, or a meshwork of small pores and channels that can hold a volume of air and can present a large water-air interface. Plastrons are common in aquatic insects and can take many physical forms. Some aquatic insects are able to capture and utilize gas bubbles of oxygen released by aquatic plants. Certain species of Diptera, Coleoptera, and Lepidoptera independently evolved modifications for piercing aquatic plants for air.

Some aquatic insects have a closed tracheal system without functional spiracles. The lack of functional spiracles eliminates any chance that water will enter the system, but oxygen must diffuse into the tracheal system through the cuticle, a breathing mechanism called cutaneous respiration. Some aquatic insects have tracheal gills, thin flaps of cuticle with many tracheoles just under the cuticle. Larvae of Trichoptera, Plecoptera, Odonata, and some Lepidoptera utilize cutaneous respiration, facilitated by extensive elaboration of thin hair-like or flap-like tracheal gills from the body surface. Internally these insects still have an extensive tracheal system, and gas transport through the tracheae and tracheoles to internal body tissues is the same as in terrestrial insects. Movement of water over the gill and body surface of aquatic insects is important in maintaining a fresh supply of oxygenated water in contact with the body, and most use undulations of the body and/or movements of the gills themselves to create ventilatory currents of water. Larvae of some dragonflies (Anisoptera) draw water into the rectum by elastic expansion of the body as dorso-ventral compressor muscles relax. Typically there are six main gill folds of the cuticular intima in the anterior part of the rectum with extensive tracheoles just beneath the intima that extract O_2 from the water. The water is pumped out by dorso-ventral compression of the abdomen. The rate of ventilation varies with several factors including the O_2 content of the water. About 85% of the water in the rectum is renewed during each pumping cycle, and 25–50 cycles/min have been recorded. Larvae also will come to the surface and ventilate the rectum with air when oxygen content of the water is very low.

Many hymenopterans and dipterans are parasitic on other insects, and have been little studied with respect to respiration, perhaps for the obvious reasons that they are usually small and hidden in the body of the host. Cutaneous respiration is probably very important. Many chalcid wasps and tachinid flies hatch from eggs laid on the surface of the host insect and they eat their way into the host. They orient the posterior pair of spiracles at the body surface of the host so that they breathe air directly. Bot fly larvae, *Hypoderma* spp., migrate to the skin of the vertebrate host where they bore a tiny opening to the surface through which gas exchange occurs. Respiration is cutaneous in earlier instars that are migrating through the body of the host.

Respiratory pigments occur in only a few insects. *Chironomus* spp. larvae have a small hemoglobin molecule composed of two chains with a MW of 31,400. The hemoglobin is not in the cells, but occurs as a circulating hemolymph protein. The molecule has extraordinarily high affinity for oxygen and is 50% saturated at a pO_2 of 0.6 mmHg at 17°C. This means that it will not give up its oxygen to tissues except under extremely low oxygen tension. Its principal function may be to aid recovery from anaerobic conditions and to provide limited O_2 to some critical tissues, such as the nervous system. Hemoglobin occurs in certain cells of *Gastrophilus* spp. (horse bots) and in larvae and adults of some beetles (Family Notonectidae, certain species of the genera *Anisops* and *Buenoa*). In contrast to the situation in *Chironomus* larvae, the hemoglobin of the beetle *Anisops pellucens* is only 50% saturation at a pO_2 of 28 mmHg at 24°C (i.e., it will give up half of its oxygen at 28 mmHg, a pressure that might occur in actively metabolizing tissues), giving it much more functional potential. The beetle may get up to 75% of the O_2 consumed during a normal dive from its hemoglobin. Increased temperature also causes the hemoglobin to release more oxygen, which could be important to actively working tissues such as muscles.

The embryo developing inside the egg must obtain sufficient oxygen for development. The majority of aquatic and semi-aquatic insects lay eggs with no special respiratory structures incorporated into the shell, while eggs of a majority of terrestrial insects contain special structures for respiration, including an extensive, inner chorionic meshwork that can function as a plastron when the egg is submerged in well aerated water. Gas exchange in eggs with no special respiratory structure occurs by simple diffusion through the egg shell.

Non-Respiratory Functions of the Tracheal System

Tracheae serve some important functions other than gaseous transport. Tracheae act as the connective tissue of insects, helping to tie cells and tissues together. Tracheae are important as a structural base for at least two important endocrine tissues (i) the prothoracic glands whose cells are attached to the tracheae near the prothoracic spiracle in larvae of Lepidoptera, and (ii) cells of the epitracheal glands attached to the surface of the major ventrolateral tracheal trunk to each spiracle in lepidopterous larvae. Air sacs lie behind sound producing organs in insects and are important to sound modulation. A large air sac backs up to the tymbal located on each side of the first abdominal segment of male cicadas. The size of the air sac varies with different species, and its size and tuning are partly responsible for the species-specific quality of the sound produced by male cicadas. The interconnected prothoracic tracheae extending across the prothorax and into the prothoracic legs of crickets act as a resonator of sounds. They aid the cricket in discriminating direction of sounds reaching the tympanal membrane located just below the joint of the femur with the tibia (i.e., the knee joint) on each prothoracic leg. Hissing cockroaches produce a hissing sound by expelling air forcefully from certain spiracles when they are disturbed. Lubber grasshoppers, *R. guttata*, release quinones from the tracheal system on the side of the attack when an ant attacks, or when stimulated by probing.

References

Chapman RF (1998) The insects: structure and function. Cambridge University Press, Cambridge, 770 pp

Klowden MJ (2002) Physiological systems in insects. Academic, New York, 415 pp

Nation JL (2002) Insect physiology and biochemistry. CRC, Boca Raton, 485 pp

Tracheole

A very narrow trachea (1 µm or less in diameter) that serves as the actual site of gas exchange between the tracheal system and the body tissues because they penetrate organs and lie so close to the cells.

► Tracheal System and Respiratory Gas Exchange

Trachypachidae

A family of beetles (order Coleoptera). They commonly are known as false ground beetles.

► Beetles

Trade Name

The name given a product that is marketed by a company. The same product may be marketed by more than one company using different names.

Trail Pheromone

A pheromone that is deposited along the ground or other substrate that allows insects to maintain the group or to communicate to others in their group (usually nest- or tent-mates) directionality, often to a feeding location.

► Pheromones
► Sociality of Insects

Transcript

A mRNA copy of a gene.

Transcription

The process of producing a mRNA copy of a gene.

Transformation

The process of changing the genetic makeup of an organism by introducing foreign DNA. Transformation may be transient or stable (transferred to succeeding generations.)

Transgene

The DNA that is inserted into the genome of a cell or organism by recombinant DNA methods.

Transgenic Arthropods for Pest Management Programs

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Transgenic organisms contain genes that have been introduced into the genome using biotechnology (recombinant DNA) methods. Transgenic plants (including corn, rice, cotton and squash) have been developed using recombinant DNA methods and currently are grown commercially. Development of the tools to develop transgenic insects and mites has lagged behind that of plants and microorganisms, but genetic modification using recombinant DNA methods have been used to transform a number of pest and beneficial insects and mites. The successful transformation of the fruit fly *Drosophila melanogaster* by a genetically modified transposable element called the P element in 1982 stimulated subsequent research to genetically modify other insects (and mites) using similar methods. (See the entry on Transformation of *Drosophila melanogaster* by P elements for details of this method.)

Domesticated and semidomesticated insects have been modified by traditional breeding methods for hundreds of years. Genetic manipulation has improved disease resistance and silk production in silk moths, and disease resistance and pollination attributes in honey bees. More recently, natural enemies of insects and mites used in biological control programs in agriculture and forestry have been modified by traditional breeding methods and by hybridization of different strains to achieve hybrid vigor. A pesticide-resistant predatory mite (*Metaseiulus occidentalis*), developed with traditional breeding methods, was incorporated into a integrated mite management program in almonds in California. These predators provided effective control of spider mites, reduced the need for costly pesticides, reduced production costs and saved almond growers approximately $22 million per year, most of which was due to fewer applications of pesticides to control the spider mites. This project demonstrated that genetic improvement of natural enemies could result in improved pest management programs. Genetic improvement of natural enemies for biological control of pest insects and mites by traditional genetic methods has involved selecting for resistance to pesticides, lack of diapause, and increased tolerance to temperature extremes, although modification of other traits, such as sex ratio, theoretically could result in improved biological control.

During the past 40 years, a number of pest insects have been sterilized by irradiation or chemicals for use in genetic control programs. This approach to pest management has been called the sterile insect release method (SIRM) or the sterile insect technique (SIT). Male insects are mass reared and sterilized, usually by irradiation, and released in to control a number of serious pests, including the Mediterranean and Caribbean fruit flies, mosquitoes and the New World screwworm *Cochliomyia hominivorax*. The SIRM has been used to eradicate pests or to reduce pest populations.

Sex and the Sorted Insects: A Case Study

Genetic control of pest insects represents an attractive alternative to chemical control of some pests in terms of safety, specificity and the limited negative effect this control tactic has upon the environment. The screwworm (*Cochliomyia hominivorax*) eradication campaign demonstrates what can be achieved with mass releases of males sterilized by irradiation.

The genetic control method used to eradicate the screwworm was called the "sterile insect release method" (SIRM) or "sterile insect technique" (SIT), and involves mass rearing, sterilization of males by chemicals or irradiation, and their subsequent release to mate with wild females. Because females of the screwworm mate only once, any wild female mating with a sterile male fails to contribute progeny to the next generation. By releasing an excess of sterile males (compared to the number of wild males), populations decline in a predictable manner, ultimately becoming extinct. Because absolute population densities were often low in the USA, the number of sterile males that had to be released could be produced in "fly factories."

The screwworm eradication program in the USA was initiated in Florida with small scale trials on Sanibel Island in 1951. The results were promising and the project was geared up to cover the state of Florida and then the southeastern USA. The screwworm was declared eradicated from the southeastern USA in 1959, one year ahead of schedule. Eradication was achieved in a surprisingly short time due to the combined effects of a severe winter in Florida during 1957–1958, which greatly reduced the overwintering screwworm population, and a 17-month eradication program beginning in July 1958 that cost approximately $7 million and involved the release of almost nine billion sterile screwworm flies over an area of approximately 56,000 square miles.

Since 1959, the livestock industry of Florida and adjacent states have saved at least $20 million each year because the screwworm is no longer present; actual benefits are even greater in today's dollars. Furthermore, the elimination of losses due to the deaths of livestock and labor and control costs are only part of the benefits; loss of wildlife to screwworm attack also was eliminated.

The success of the SIRM program in the southeastern USA led the cattle growers of Texas to mount, in collaboration with the state and the USDA, a similar but much more ambitious program in the southwestern USA in the 1960s. This program required more time and effort because the area in which the screwworm was to be eradicated bordered on a front 2,400 km long, stretching from the Gulf of Mexico to the Pacific Ocean. Despite this challenge, and some setbacks with quality control and reinvasion of flies from Mexico, both Texas and New Mexico were declared "screwworm free" in 1964.

The SIRM program was moved into Arizona and California in 1965, and in 1966 the entire USA was declared free of screwworms. To reduce the likelihood that the screwworm would reinvade the USA from Mexico, the program was expanded into Mexico in 1972, with the goal of eradicating the screwworm all the way south to the Isthmus of Tehuantepec.

After successfully eliminating the pest in Mexico, the SIRM program was expanded to cover all of Central America. Screwworms were eliminated from Guatemala between 1988 and 1994, from Belize between 1988 and 1994, from El Salvador between 1991 and 1995, from Honduras between 1991 and 1996, from Nicaragua between 1992 and 1998, from Costa Rica between 1995 and 1999, and from Panama between 1997 and 2000. These eradication programs were carried out so that a barrier zone could be set up at the Isthmus of Panama, which is only 190 km wide as compared to the 2,400 km border that the USA and Mexico share. This barrier zone has been maintained by a combination of quarantines and mass releases of sterile screwworms.

Benefits of this massive, and expensive, screwworm eradication program are large. In 1996, the annual producer benefits in the USA, Mexico and Central America were estimated to be $796 million, $292 million and $77.9 million, respectively. These benefits were due to decreases in deaths of livestock, reduced veterinary services, medicines, insecticides, inspections, handling costs, and increases in meat and milk production. The estimated benefit to cost ratios for the eradication programs average 12.2:1 for Central America to 18:1 for the USA and Mexico.

The principle of sterile insect releases has been applied to other pest insect species, including the Mediterranean fruit fly (*Ceratitis capitata*), tsetse flies (*Glossina palpalis* and *G. morsitans*), mosquitoes (*Anopheles albimanus*), codling moth (*Cydia pomonella*) and ticks.

Sterile insect release programs usually require only males, but both sexes must be reared. Not only is it expensive to rear large numbers of "useless" females, but, in the case of species that vector disease or annoy or bite humans or domestic animals, it is undesirable to release any females, sterile or not! As a result, various genetic methods have been used to develop "genetic sexing strains." Slight differences in size or color of pupae have been used to sort out undesirable females during mass rearing. Most genetic sexing strains are based on maintaining the desired genes (such as *white pupa* or a temperature sensitive lethal) within translocations. However, because translocations can undergo recombination in the region between the translocation breakpoint and the sexing gene, the strains are not completely stable. As a result, if no practical means exist to remove the recombinants, an increasing number of the undesirable females will be reared and released.

Ideally, a genetic sexing method using recombinant DNA methods will become available that could produce only males of high quality and vigor to compete with wild males for female mates. Since an all-male colony will be difficult to maintain (!), this character ideally would be a conditional trait, perhaps dependent upon temperature or some other environmental cue. Because the released males would be sterile they could not persist in the environment, which could reduce potential risks. Other potential improvements using recombinant DNA methods could result in insects containing a marker gene, such as green fluorescent protein, that would allow the released sterile males to be identified readily in the traps used to monitor progress in the program; because such males would be sterile, risks associated with their release would also be low. Finally, recombinant DNA methods might be developed that would allow the insects to be sterilized without radiation; this could reduce the damage produced by irradiation to the entire body and allow fewer insects to be reared and released, resulting in considerable cost savings.

Why Use Transgenic Methods?

Traditional genetic methods have limitations, and recombinant DNA methods offer new opportunities for improving pest management programs (Table 13). For example, significant benefits could accrue if recombinant DNA methods allowed sterile insects to be produced without incurring the negative effects of irradiation. During the sterilization process, the insect's whole body is irradiated, which damages all tissues. As a result, the SIRM requires rearing very large numbers of males for release because the irradiated males are damaged by the sterilization process. Commonly, pest populations are first reduced by pesticide applications or through natural seasonal (winter) mortality to reduce the number of insects that have to be released. The number of males released is usually a

Transgenic Arthropods for Pest Management Programs, Table 13 Pest management goals that might be achieved with transgenic methods

Project type	Objective(s)
Biological control of insect and mite pests	
• Improve survival of natural enemies in environment	Enhance ability to control pests by introducing resistance genes; modify diapause or temperature tolerance traits
• Improve effectiveness of natural enemies	Alter traits such as sex ratio (more females), host/prey specificity; restrict ability to fly
Disease control method	
• Develop insects that introduce a vaccine into their hosts when taking a blood meal	Provide low cost vaccination against widespread, serious diseases such as malaria
Improve domesticated and semi-domesticated insects	
• Improve silk production in silkworms (*Bombyx mori, Philosamia, Anthaerea*)	Improve quantity, quality or type of silk, introduce disease resistance genes, introduce silk genes from spiders or other silk producing arthropods into moths to produce special types of silk
• Improve honey bees, *Apis mellifera*	Insert genes for resistance to bacterial, viral and fungal pest resistance; introduce resistance to mite (*Varroa*) pests; modify pollination behaviors, modify aggressive behaviors

Transgenic Arthropods for Pest Management Programs, Table 13 Pest management goals that might be achieved with transgenic methods (Continued)

Project type	Objective(s)
Population control methods	
• Population replacement	Eliminate traits that make a pest, such as make a pest unable to transmit diseases such as malaria, dengue, sleeping sickness or yellow fever, by altering ability of the pathogen to pass gut or salivary gland barriers; eliminate the need for a blood meal by vector mosquitoes; alter behavior so the vector feeds on only one host. Release altered strain to replace the pest population. Replacement will require some type of drive mechanism or a way to select for the released population in the field.
• Insert useful/deleterious genes	Release genetically modified individuals to mate with a "driver" such as wild individuals in correct ratio to insert genes transposable elements or *Wolbachia* into populations. Proposals include releasing (introgression model) insects with active transposable elements, lethal genes or genes that cause sterility, with the goal of causing so much genetic damage that the pest population crashes (as laboratory populations can do when a new transposable element invades)
Sterile insect release method (SIRM)	
• Sterilize males by recombinant DNA methods to reduce damage from radiation/chemosterilization	Introduce genes and regulatory sequences to cause sterility that can be stimulated by light, diet or other environmental cues during mass rearing, as needed, allowing colony to be reared normally until the transgene(s) is activated
• Mark released males with molecular such as green fluorescent protein, that can be detected in trapped dead males so that the effectiveness of the SIRM program can be assessed	Insert benign marker gene that is expressed or visible in dead insects
• Develop genetic sexing method so that females do not have to be reared, reducing program costs	Introduce a conditional lethal gene so that females can be killed during the mass rearing program when a particular cue is provided

multiple of the estimated density of wild males, with a 100:1 ratio of sterile to wild males commonly used. Rearing such huge numbers of insects is costly and difficult.

Recombinant DNA methods also could allow unique molecular markers to be inserted into the sterile insects, which would allow SIRM program managers to more easily discriminate between released sterile males and wild fertile males caught in the traps used in monitoring the progress of the program. Current marking methods using fluorescent dusts are unsatisfactory because they can reduce fitness of the insects and the dyes do not always adhere, which could falsely indicate that the program is not working well. Other significant benefits could be obtained if recombinant DNA methods make it possible to control the sex of insects being reared in SIRM programs, to introduce lethal genes or genetic loads into pest populations, or to produce vectors of human and animal diseases that are unable to transmit diseases such as malaria, dengue, yellow fever and sleeping sickness.

Recombinant DNA techniques could make genetic improvement of beneficial insects, such as silkworms (*Bombyx mori*), honey bees (*Apis mellifera*) or biological control agents, more efficient and less expensive. Once a useful gene has been cloned, it could be inserted into a number of beneficial species in a relatively short time. Furthermore, recombinant DNA methods broaden the number and type of genes potentially available for use; no longer is a project dependent upon the intrinsic genetic variability of the species under study.

Many have speculated about the role that recombinant DNA methods could play in the genetic control of insects that serve as the vectors of human and animal diseases or pests of agricultural crops. Some consider transgenic technology to be a new and vitally important pest management tool for the control of serious pests that cannot be controlled by any other means. Others have expressed reservations about the goals and methods suggested.

There are limitations to transgenic methods at present. For example, traits primarily determined by single major genes are most appropriate for manipulating insects by recombinant DNA techniques. Methods for manipulating and stabilizing traits that are determined by complex genetic mechanisms are not yet feasible with insects, although such methods could be developed using procedures similar to those developed by plant molecular geneticists.

Components of a Genetic Manipulation Project

Genetic manipulation with recombinant DNA methods requires methods for efficient and stable insertion of foreign genes into the genome of the target insect or mite, and the availability of useful genes and appropriate promoters and other regulatory elements to obtain effective expression of the inserted gene in the appropriate tissue at the appropriate time. Inserting cloned DNA into insects can be accomplished using several different techniques. If the inserted DNA is incorporated into the chromosomes in the cells that give rise to the ovaries and testes, the foreign gene(s) or transgenes could be transmitted faithfully and indefinitely to successive generations (stable germline transformation).

Initial research on stable transformation methods was accomplished with *Drosophila melanogaster* when it was discovered that the P element could be genetically manipulated to serve as a vector to carry foreign genes into the chromosomes of germ line cells. In molecular genetics, vectors are self-replicating DNA molecules that transfer a DNA segment between host cells. P-element vectors were investigated as possible gene vectors for insects other than *Drosophila*, but failed to function in other insects. Other transposable element vectors such as *mariner*, *piggy*-Bac, *Hermes* and *hobo* have been isolated from insects and genetically modified for use as vectors to transform insects other than *D. melanogaster*. Another approach to genetic modification involves the genetic engineering of insect gut symbionts. For example, a bacterial symbiont of the Chagas disease vector *Rhodnius prolixus* lives in the insect's gut lumen and is transmitted from adult to progeny by contamination of egg shells or of food with infected feces. The symbionts have been genetically engineered and transmitted to hosts lacking any symbionts. The goal is to reduce the ability of *Rhodnius* to transmit pathogens when it takes a blood meal, perhaps by infecting the bugs with gut bacteria that produce antibiotics that kill the Chagas disease agent. Likewise, gut symbionts of tsetse flies (*Glossina* species), which are vectors of both animal and human African sleeping sickness, also have been transformed. Proposals have been made to release tsetse flies carrying transgenic symbionts so the released flies could replace or out-compete native populations, but fail to transmit the disease.

The ability to introduce cloned genes into the germ line at a predictable chromosomal site is especially desirable, as it reduces the likelihood of "position effects" on gene expression. Genes introduced by transposable element and viral vectors insert more or less randomly into the chromosomes, making it difficult to predict how well the transgene will be expressed. One method for accomplishing precise insertion is based on a system found in the yeast *Saccharomyces cerevisiae*. A gene for yeast recombinase, called FLP recombinase, and two inverted recombination target sites (FRTs) that are specifically recognized by the FLP enzyme have been cloned. The FLP-FRT system has been modified to insert DNA into a specific site in a *Drosophila* chromosome. If the FRT sites can be inserted into other insects, the system could reduce concerns about unstable transformation that may be elicited by the use of transposable element vectors.

A few experiments have delivered linear or circular plasmid DNA into the genome of insects without using a specific vector. This approach has the advantage of eliminating potential risks of introducing vector sequences into the insect genome, which could result in increased stability of the inserted genes in the genome. This approach assumes that the inserted gene is no more likely than any other gene to be moved by "wild" transposable elements or viruses.

A variety of methods have been evaluated for delivering genes into insects in order to achieve transformation. These include microinjection of transposable element vectors and other vectors into dechorionated insect eggs, microinjection of plasmids directly into the abdomen of female mites or insects (maternal microinjection), soaking eggs in DNA, using sperm to carry foreign DNA into eggs of the honey bee, using microprojectiles (gene gun technology) to insert DNA into insect eggs, electroporation of DNA into insect eggs, transplanting nuclei and cells, and transformation of an insect microbial gut symbiont (which has been called paratransgenesis because the insect genome has not been modified).

What Genes are Available to Insert?

Cloned DNA can be isolated from the same or other species. It is technically feasible to insert genes from microorganisms into arthropods and have the DNA transcribed and translated, although coding sequences isolated from microorganisms must be attached to promoters (controlling elements) and other regulatory sequences derived from a higher organism so that the gene can be expressed in insects. The regulatory sequences determine when a gene will be transcribed, at what level, in what tissues, and how long the messenger RNA can be used for translation. Considerable research is under way to identify regulatory sequences that regulate genes in specific insect tissues, such as the salivary glands and gut. It also may be possible to isolate a gene from the species being manipulated, alter it, and reinsert it into the germ line, although this approach has not yet been attempted in insects other than *Drosophila* to date.

Project goals will dictate what type of regulatory sequences might be most useful to regulate transgene expression. In some cases, a low level constitutive production of transgenic proteins will be useful, while in other cases high levels of protein production will be required after inducement by a specific cue. Researchers may have to evaluate the trade-offs between high levels of protein production and the subsequent negative effects these could have on fitness of the transgenic arthropod strain based on the specific goals of each program.

After inserting the desired genes and regulatory elements, the next issue is how to detect whether the gene has in fact been incorporated into the germ line. Because transformation methods are relatively inefficient, a screening method is needed to identify transformed individuals. This process is relatively simple in *Drosophila*, where there is a wealth of genetic information and visible markers can be used to identify transgenic individuals. Most pest or beneficial arthropods lack such extensive genetic information or markers. Identifying transformed individuals could be achieved using a pesticide resistance gene as the selectable marker. However, the release of pesticide-resistant pests into the environment would create concerns about risk. Another option is to use antibiotic resistance genes as selectable markers to identify transgenic insects. However, horizontal movement of resistance genes into microbes in the environment could result in increased levels of antibiotic resistance; the likelihood of this potential risk has not been quantified. Antibiotic resistance gene markers are no longer considered safe for release into the environment in transgenic crops, and methods have been developed for their removal. Another potential marker is the β-galactosidase gene (*lacZ*) isolated from *E. coli*, which can be detected by an assay that produces a blue color in the transformed insects and mites. This construct has been present in a number of released organisms and it has been concluded that risks associated with their release are low. Eye color and green fluorescent protein (GFP) genes also are considered to be safe selectable markers if transgenic insects are to released into the environment. Unfortunately, transgenic insects with mutant eye colors may exhibit abnormal behavior, which could reduce their effectiveness in the field. The effects of GFP on vision could be important when the GFP gene is expressed in the eyes of insects. Normal behavior often is crucial to the function of released insects in pest management programs. It is probably desirable to eliminate unneeded marker genes from transgenic insect strains prior to their release into the environment.

Once transgenic strains have been produced, they should be contained in the laboratory using effective procedures and containment facilities until permits have been obtained from the appropriate governmental agencies that would allow the transgenic arthropods to be released into the environment in a pest management program. Transgenic strains must be evaluated for fitness and the expression of the desired traits should be stable in the laboratory. However, efficacy of the transgenic strain for the intended purpose will have to be evaluated eventually under field conditions. At present, transgenic strains are first evaluated in greenhouses, field cages, or some other contained environment to be sure that they perform as expected and do not exhibit unintended traits. Purposeful permanent releases of transgenic insects or mites have, as of winter 2004, not been requested.

Risk Assessments of Transgenic Arthropods

Risk equals the potential for damage and the likelihood of its occurrence. Risk estimates may be different for pest versus beneficial insects and may depend on whether the insect is expected to persist in the environment or is unable to reproduce and cannot persist. Risks also will vary with the specific transgene(s) inserted. At present, it is easier to identify potential types of harm than to quantify the likelihood of its occurrence.

Relative Risks

The least risky transgenic insects could be the domesticated silkworm (*B. mori*), which is unable to survive on its own in the wild. Transgenic *B. mori* are unlikely to have a negative effect on the environment because they should not be able to persist even if they were accidentally released. Also, transgenic pest or beneficial insects that are sterile and unable to reproduce should pose lower risk than insects that are able to reproduce and persist in the environment. Transgenic pest or beneficial insects that are unable to persist because the environment is unsuitable during a portion of the year also are likely to pose a lower risk. Honey bees, *Apis mellifera*, are only semi-domesticated and thus can escape human management to survive in the wild. Transgenic honey bees could pose a greater environmental risk than the domesticated silkworm for this reason.

Evaluating the risks associated with releasing insects and mites that have been manipulated with recombinant DNA techniques will likely change as we learn more about risk assessment procedures and gain experience. Current concerns can be summarized as:

- Is the transgenic population stable?
- Has its host or prey range has been altered?
- Does it have the potential to persist in the environment?
- Will the transgenic strain will have unintended effects on other species or environmental processes?

Another question we may need to ask is how far and how quickly can the transgenic strain disperse from the experimental release site? Less is known about dispersal behavior of many insects than might be needed. The first three questions are relatively easy to answer with a variety of laboratory experiments. The last issue is much more difficult to answer. For the near future, releases of transgenic arthropods in the USA will be evaluated by regulatory agencies on a case-by-case basis. Initial permits for releases will be for short term releases in controlled situations so that unexpected outcomes might be mitigated.

Horizontal Gene Transfer

One risk issue that is unusually difficult to quantify is the risk of horizontal transfer of transgenes or transposable elements, or of drive elements such as *Wolbachia*, to other organisms. Our knowledge of horizontal transfer and transposable elements only began in the 1950s when Barbara McClintock discovered transposable elements in maize. Horizontal gene transfer results in the movement of genes or transposable elements or drive elements from one insect population to another of the same species, from one insect species to another, or to other organisms in the environment. It is difficult to quantify this risk because we lack fundamental information on the frequencies and mechanisms of horizontal gene transfer; furthermore, the specific genes transferred will be important in determining potential harm as will the site into which the transgene or transposable element inserts. If the insertion is into noncoding DNA in the chromosome, no harm may occur to the recipient. If the insertion is into functional and essential gene(s), then the recipient may be harmed or killed. If the insertion is into somatic cells the effect, if any, may be minimal but if the insertion is into germ line cells then the unintended genetic modification could be transmitted to future generations. The whole topic of horizontal gene transfer in insects has received limited scientific attention until relatively recently.

We do know that horizontal transfer of genes may occur between insect species by movement of naturally occurring transposable elements. Horizontal transfer is thought to be rare, yet more than one such transfer has been observed within historical times in *D. melanogaster* and may have been missed in other species because no one was looking. The P element appears to have invaded *D. melanogaster* populations within the last 50 years, perhaps from a species in the *D. willistoni* group. Controversy exists as to whether P elements were transferred between *Drosophila* species by the semiparasitic mite *Proctolaelaps regalis*. Another transposable element, *hobo*, appears to have invaded natural populations of *D. melanogaster* around the 1960s, representing the second invasion of this well-studied insect in the past 40–50 years.

Transfer of transposable element vectors from insects to other organisms, including humans, is potentially feasible, although these transfers would be expected to occur very rarely. Recall that risk is determined by frequency of occurrence and the damage that might occur. In this case, the frequency is expected to be very low if natural invasions represent a realistic estimate of frequency in the case of purposeful releases of active transposable elements as drive mechanisms or of conversion of inactive transposable element vectors into active ones.

We are still discovering new aspects of the biology and ecology of transposable elements and this lack of knowledge makes it difficult to predict what would happen if insects were released that contained either active or inactive transposable element vectors. The safest course might be to remove any introduced transposable element vector sequences from a transgenic insect strain prior to its permanent release into the environment to reduce the probability that the transgene will move, either within the strain or horizontally between different populations or species.

Some questions to answer: When developing a genetic manipulation project if it is to be deployed successfully

PHASE I. Defining the problem and planning the project:

- What genetic trait(s) limit effectiveness of beneficial species or might reduce damage caused by the pest?
  - Do we know enough about the biology, behavior, genetics and ecology of the target species to answer this question?
  - Is the potential trait determined by single or multiple genes?
- Can alternative control tactics be made to work more effectively and inexpensively than genetic manipulation projects, and are they more environmentally friendly?
  - The costs of genetic manipulation projects are high and the time to develop a functional program can be quite long
  - Transgenic technology may not be appropriate if traditional genetic or other control methods can be used because issues surrounding risk assessment of releasing transgenic arthropods into the environment for permanent establishment have not been resolved.
- How will the genetically-manipulated strain be deployed?
  - Will releases be inoculative and some type of selection or drive system used to replace the wild strain?
  - Will the desired genes be introgressed (introduced) into the wild population?
  - What selection mechanism will be used?
  - Will augmentative releases of very large numbers be required?
  - Will multiple releases be required over many years?
- What risk issues, especially of transgenic strains, should be considered in planning?
  - If pesticide resistance genes are used as a selectable marker for beneficial species is there a possibility of the resistance gene moving to a pest?
  - What is known about the potential for horizontal gene transfer?
  - If transposable element or viral vectors are used in the transformation process, what risks might they pose if the transgenic strain is released into the environment?
  - What health or other hazards might be imposed on human subjects if the transgenic strain were released?
- What advice do the relevant regulatory authorities give regarding your plans to develop a transgenic strain?
  - Which agencies are relevent to consult for your project?

PHASE II. Developing the genetically-manipulated strain and evaluating it in the laboratory:

- Where will you get your gene(s)?
  - Should the transgene(s) sequence be modified to optimize expression in the target species if it is from a species with a different codon bias?
- Is it important to obtain a high level of expression in particular tissues or life stages?
  - Where can you get the appropriate regulatory sequences?
- How can you maintain or restore genetic variability in your transgenic strain?
  - Because both artificial selection and transgenic methods typically involve substantial inbreeding to obtain pure lines, how will you

outcross the manipulated strain with a field population to improve its adaptation to the field or otherwise increase genetic variability.

- What methods can you use to evaluate "fitness" in artificial laboratory conditions that will best predict effectiveness in the field?
  - Have life table analyses and laboratory studies of the stability of the trait under no selection been correlated with efficacy in the field?
  - Is it possible to carry out competitive population cage studies?
- Do you have adequate containment methods to prevent premature release of the transgenic strain into the environment?
  - Have these containment methods been reviewed by appropriate regulatory authorities?
- Do you have adequate rearing methods developed for carrying out field tests?
  - Are artificial diets available to reduce rearing costs?
  - Are quality control methods available to maintain quality during mass rearing?
- What release rate will be required to obtain the goals you have set?
  - Do you have an estimate of the absolute population density of the target species in your field test?
  - What release model are you applying: inundative, inoculative, introgressioin, complete population replacement?
- Have you tested for mating biases, partial reproductive incompatibilities or other population genetic problems?
- If the strain is transgenic, have you obtained approval from the appropriate regulatory authorities to release the strain into the greenhouse or small plot?
  - Can you contain it in the release site?
  - Can you retrieve it from the release site at the end of the experiment?
  - Can you mitigate if unexpected problems arise?
- How will you measure effectiveness of the modified strain in the field trials?

PHASE III. Field evaluation and eventual deployment in practical pest management project:

- If the small-scale field trial results were promising, what questions remain to be asked prior to the deployment of the manipulated strain?
  - Are mass rearing methods adequate?
  - Is the quality control program in place?
  - Is the release model feasible?
  - Were there unexpected reproductive incompatibilities between the released and wild populations?
- If permanent releases are planned, have relevant risk issues been evaluated?
- How will the program be evaluated for effectiveness?
- Will the program be implemented by the public or private secto?
- What did the program cost and what are the benefits?
- What inputs will be required to maintain the effectiveness of the program over time?

(Modified from Hoy 2000.)

Steps in Developing a Transgenic Arthropod

The above description indicates that a number of steps are involved in a program designed to control pest insects through transgenic methods. The target species probably should be identified as a significant pest for which conventional control tactics are ineffective because genetic manipulation is usually more expensive and difficult than other pest management approaches. Furthermore, genetic manipulation with recombinant DNA techniques may generate concerns about risk, requiring additional time and resources.

How best might our knowledge about the pest species' physiology, ecology, or behavior be used against it? How will the transgenic strain be deployed in a pest management program?

Once a target trait has been identified, it must be genetically altered using appropriate genes and genetic regulatory sequences to ensure that the new trait is expressed at the appropriate time and in appropriate tissues. After a modified strain has been developed, it must be evaluated in the laboratory for fitness and stability. If ultimate deployment requires mass rearing of very large numbers of high quality insects, mass rearing and release models will need to be developed. Eventually the manipulated strain must be released into greenhouses or small field plots in the field for evaluation.

Permission to release a transgenic insect will have to be obtained from (several) regulatory agencies. Short term releases initially will be made into small plots, perhaps in cages. Initial releases of transgenic insects into the environment in the USA are intended to be short term experiments, and current regulation of such releases by the U.S. Department of Agriculture require the researcher to retrieve all transgenic insects from the environment at the end of the experiment.

If the transgenic insect strain(s) perform well and risk assessments are completed satisfactorily, permanent releases into the environment may be allowed, but the guidelines for such releases are lacking as of spring 2002. Many pest management programs, especially those involving replacement of pest populations by the transgenic population, will require permanent establishment in the environment. The use of several "drive mechanisms" have been proposed for replacement. Analysis of the potential risks of such drive mechanisms has not been carried out.

Could "Gene Silencing" Reduce Program Effectiveness?

There is always the risk that a transgenic insect population could be released into the field and fail to function as expected due to a phenomenon called "gene silencing." Transgenic plants and mammals have been shown to be able to inactivate (silence) transgenes that overexpress proteins or are otherwise novel. Gene silencing is thought to be due to genetic systems that evolved as a means to prevent high levels of expression of transposable elements or viruses that can cause genetic damage when they invade new hosts. In fungi and plants, gene silencing is associated with several mechanisms, including methylation of the DNA or posttranscriptional or transcriptional processes. Multiple mechanisms of transgene silencing also occurs in *Drosophila melanogaster*. Thus, methods may have to be developed to eliminate transgene silencing in insects or this phenomenon could reduce the effectiveness of a pest management program. The use of genetic sequences called insulators or boundary elements may limit gene silencing.

Gene silencing might be turned into a positive attribute if specific genes in insects could be turned off. Gene silencing has purposefully induced in *D. melanogaster* by introducing a sequence that codes for an extended hairpin-loop RNA by P-mediated transformation. Perhaps endogenous gene expression and developmental processes could be modified in other insects by a similar genetic process.

The ultimate utility of transgenic insects and mites for pest management programs remains to be resolved in the coming years. Research on improved transformation methods, isolation of additional useful genes and regulatory elements and development of improved risk assessment methods based on an international consensus must be achieved before transgenic arthropods are widely used in pest management programs.

► Genetic Modification of *Drosophila melanogaster* by P Elements
► Sterile Insect Technique

References

Atkinson PW, Pinkerton AC, O'Brochta DA (2001) Genetic transformation systems in insects. Annu Rev Entomol 46:317–346

Handler AM, James AA (eds) (2000) Insect transgenesis methods and applications. CRC, Boca Raton

Hoy MA (2000) Transgenic arthropods for pest management programs: risks and realities. Exp Appl Acarol 24:463–495

Letourneau DK, Burrows BE (eds) (2002) Genetically engineered organisms. Assessing environmental and human health effects. CRC, Boca Raton

U.S. Department of Agriculture, Animal and Plant Health Inspection Service (2001) The regulation of transgenic arthropods. http://www.aphis.usda.gov:80/bbep/bp/arthropod/#tgenadoc

Transgenic Organism

An organism whose genome contains genetic material originally derived from an organism (not its parents) or from a different species. The transgene(s) can be transmitted to subsequent generations (stable transformation) or can be lost subsequently (unstable transformation).

Translocation

A type of mutation in which a section of a chromosome breaks off and moves to a new position in that or a different chromosome.

Transmission of Plant Diseases by Insects

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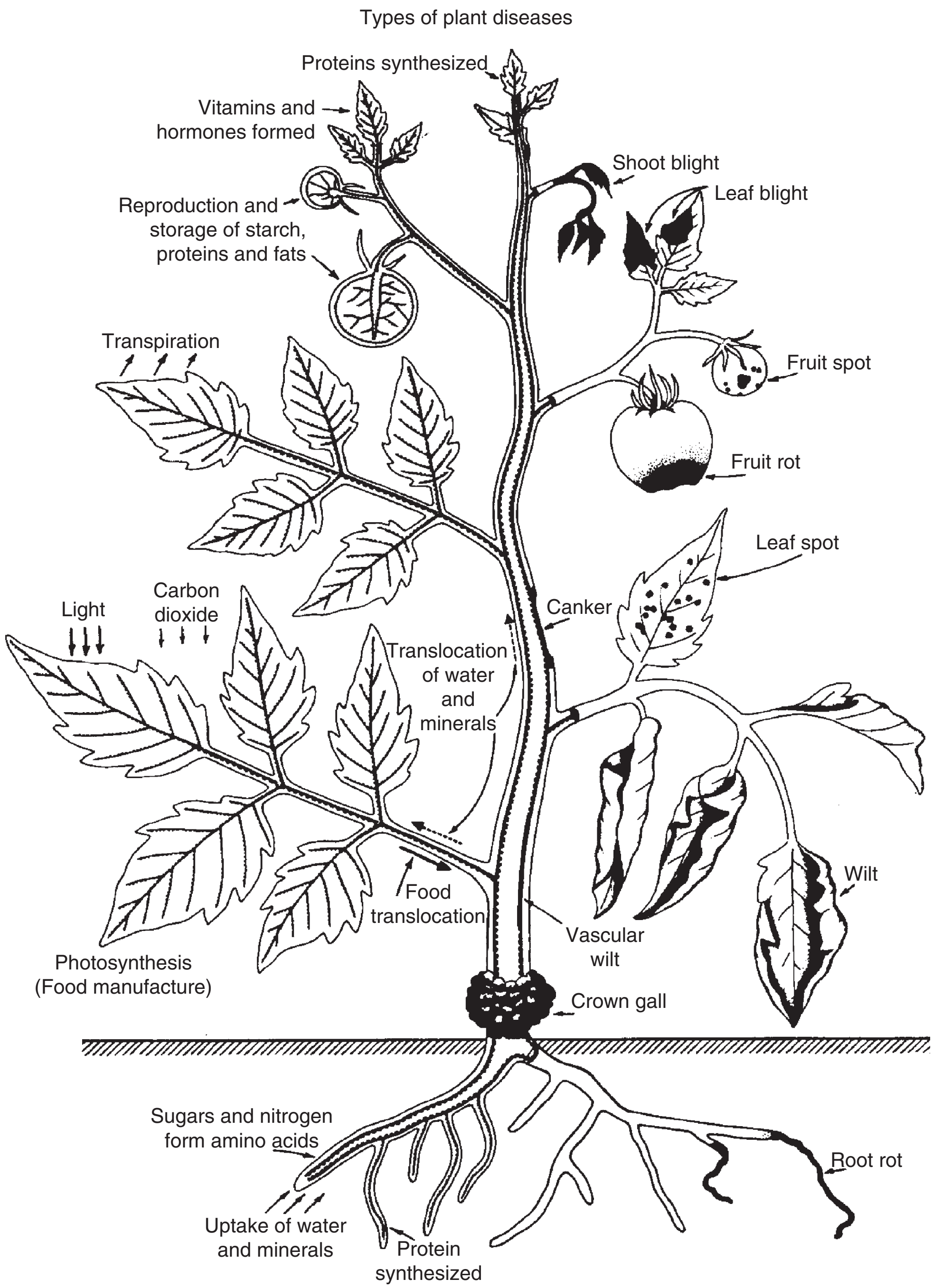
Plant diseases appear as necrotic areas, usually spots of various shapes and sizes on leaves, shoots, and fruit; as cankers on stems; as blights, wilts, and necrosis of shoots, branches and entire plants; as discolorations, malformations, galls, and root rots, etc. Regardless of their appearance, plant diseases interfere with one or more of the physiological functions of the plant (absorption and translocation of water and nutrients from the soil, photosynthesis, etc.), and thereby reduce the ability of the plant to grow and produce the product for which it is cultivated. Plant diseases are generally caused by microscopic organisms such as fungi, bacteria, nematodes, protozoa, and parasitic green algae, that penetrate, infect, and feed off one or more types of host plants; submicroscopic organisms such as viruses and viroids that enter, infect, spread systemically and affect the growth of their host plants; parasitic higher plants which range from about an inch to several feet in size and penetrate and feed off their host plants. Plant diseases are also caused by abiotic, environmental factors such as nutrient deficiencies, extremes in temperature and soil moisture, etc. that affect the normal growth and survival of affected plants.

Of the aforementioned causes of disease, many of the microscopic organisms and of the viruses are transmitted by insects either accidentally (several fungi and bacteria) or by a specific insect vector on which the pathogenic organism (some fungi, some bacteria, some nematodes, all protozoa causing disease in plants, and many viruses) depends on for transmission from one plant to another, and on which some pathogens depend on for survival (Fig. 90).

The importance of insect transmission of plant diseases has generally been overlooked and greatly underestimated. Many plant diseases in the field or in harvested plant produce become much more serious and damaging in the presence of specific or non-specific insect vectors that spread the pathogen to new hosts. Many insects facilitate the entry of a pathogen into its host through the wounds the insects make on aboveground or belowground plant organs. In some cases, insects help the survival of the pathogen by allowing it to overseason in the body of the insect. Finally, in many cases, insects make possible the existence of a plant disease by obtaining, carrying, and delivering into host plants pathogens that, in the absence of the insect, would have been unable to spread, and thereby unable to cause disease. It is offered as a guess that 30–40% of the damage and losses caused by plant diseases is due to the direct or indirect effects of transmission and facilitation of pathogens by insects.

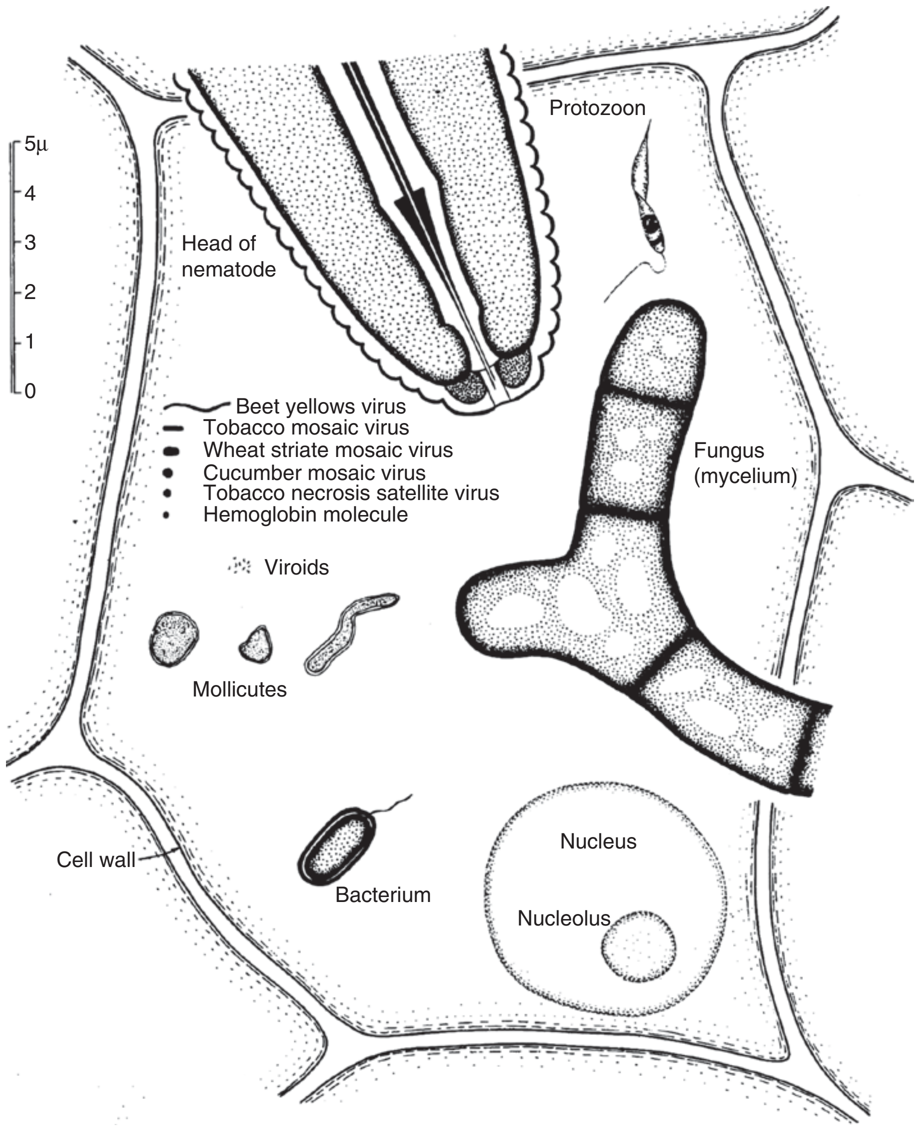
Insects and related organisms, such as mites, are frequently involved in the transmission of plant pathogens from one plant organ, or one plant, to another on which then the pathogens cause disease. Equally important is that insects can and do transmit pathogens among plants from one field to another, in many cases even when the fields are several to



Transmission of Plant Diseases by Insects, Figure 90 **Schematic representation of the basic functions in a plant (*left*) and the interference with these functions (*right*) caused by some common types of plant diseases (from Agrios 1997).**

many miles apart. Almost all types of pathogens, that is, fungi, bacteria, viruses, nematodes, and protozoa, can be transmitted by insects. Insects transmit pathogens, such as many fungi and bacteria, mostly externally on their legs, mouthparts, and bodies. Almost all plant pathogenic viruses, all phytoplasmas, xylem- and phloem-inhabiting fungi and bacteria, some protozoa, and some nematodes are also transmitted by insects, and they are usually carried by the insect internally. The insects that transmit fungi and bacteria externally on their bodies and legs belong to many orders of insects. On the contrary, the insects that transmit the other pathogens listed above internally are very specialized and specific for the pathogen they transmit and belong to a certain species or genus of insects (Fig. 91).

Insects transmit pathogens in three main ways. (i) Many insects transmit bacteria and fungal spores passively by feeding in or walking through an infected plant area that has on its surface plant pathogenic bacteria or fungal spores as a result of the infection. The bacteria and spores are often sticky, cling to the insect as it moves about, and are carried by it to other plants or parts of the same plant where they may start a new infection. (ii) Some insects transmit certain bacteria, fungi, and viruses by feeding on infected plant tissues and carrying the pathogen on their mouthparts as they

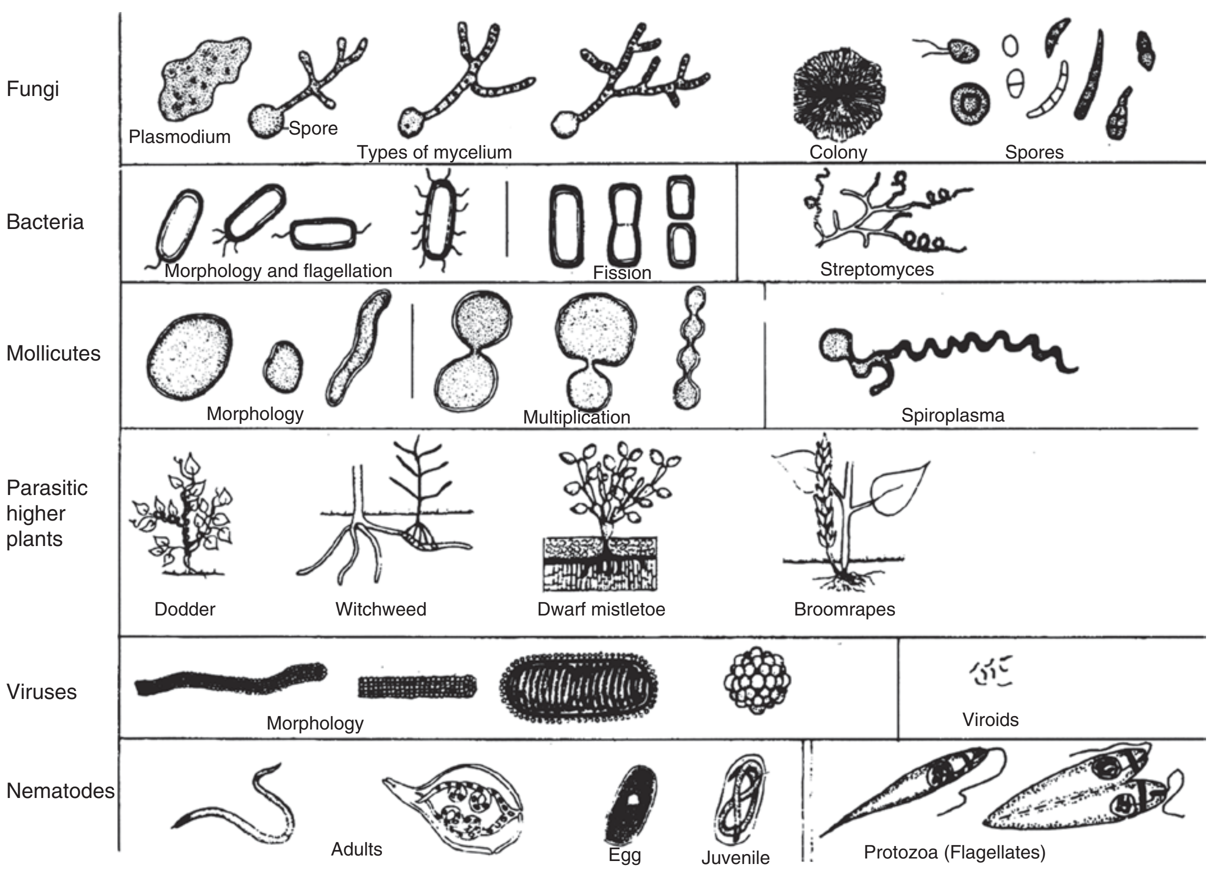


Transmission of Plant Diseases by Insects, Figure 91 **Schematic diagram of the shapes and sizes of certain plant pathogens in relation to a plant cell (from Agrios 1997).**

visit and feed on other plants or plant parts. (iii) Several insects transmit specific viruses, phytoplasmas, protozoa, nematodes, and xylem- and phloem-inhabiting bacteria by ingesting (sucking) the pathogen with the plant sap they eat. Subsequently, the pathogen circulates through the body of the insect until, with or without further multiplication in the insect, the pathogen reaches the salivary glands and the mouthparts of the insect through which it is injected into the next plant on which the insect feeds (Fig. 92).

Role of Insects in Bacterial Diseases of Plants

In most plant diseases caused by plant pathogenic bacteria (especially in those that cause spots, cankers, blights, galls, or soft rots, bacteria), which are produced within or between plant cells, escape to the surface of their host plants as droplets or masses of sticky exudates (ooze). The bacteria exudates are released through cracks or wounds in the infected area, or through natural openings such as stomata, nectarthodes, hydathodes, and sometimes through lenticells, present in the infected area. Such bacteria are then likely to stick on the legs and bodies of all sorts of insects, such as flies, aphids, ants, beetles, whiteflies, etc., that land on the plant and come in contact with the bacterial exudates. Many of these insects are actually attracted by the sugars contained in the bacterial exudate and feed on it, thereby further smearing their body and mouthparts with the bacteria-containing exudate. When such bacteria-smeared insects move to other parts of the plant or to other susceptible host plants, they



Transmission of Plant Diseases by Insects, Figure 92 **Morphology and multiplication of some of the groups of plant pathogens (from Agrios 1997).**

carry on their body numerous bacteria. If the insects happen to land on a fresh wound or on an open natural opening, and there is enough moisture on the plant surface, the bacteria may multiply, move into the plant, and begin a new infection. The same happens if the insects happen to create a fresh wound on the plant.

The type of insect transmission of bacteria is probably quite common and widespread among bacterial diseases of plants, but it is passive and haphazard, depending a great deal on the availability of wounds or moisture on the plant surface. In any case, there are few data on how frequently such transmission occurs, and many conclusions about it are the result of conjecture. A further point that has been made is that insects which, whether above or below ground, wound the host plant organs (roots, shoots, fruit, etc.) by feeding or by ovipositing in them, increase the probability of transmission of plant pathogenic bacteria. This occurs because such insects place the bacteria, with their mouthparts or the ovipositor, in or around wounded plant cells, where they are surrounded by a suspension of nutrients (plant cell sap) in the absence of active host defenses and where they can multiply rapidly and subsequently infect adjacent healthy tissues.

Numerous plant diseases could be listed among those in which bacteria are spread by insects passively as described above, for example, the bacterial bean blights, fire blight of apple and pear, citrus canker, cotton boll rot, crown gal, bacterial spot and canker of stone fruits, etc. In several bacterial diseases, however, the causal bacterium has developed a special symbiotic relationship with one or a few specific types of insects and depends a great deal on these insects for its spread from infected to healthy host plants. Some of the better known bacterium – insect associations are described briefly below.

Bacterial Soft Rots

Bacterial soft rots cause tremendous losses worldwide, particularly in the warmer climates and the tropics. They are caused primarily by the bacterium *Erwinia carotovora* pv. *carotovora*, to some extent by *Pseudomonas fluorescens* and *Ps. chrysanthemi*, and, occasionally, by species of *Bacillus* and *Clostridium*. The last two genera of bacteria cause rotting of potatoes and of cut fleshy leaves in storage while *Pseudomonas fluorescens* and *Ps. chrysanthemi* cause soft rots of many fleshy fruits and fleshy vegetables. The species *E. c.* pv. *carotovora* causes the vast majority of soft rots on fleshy plant organs of any type (leave, blossoms, fruit, stems, or roots), especially in storage and under cover or in plastic bags. Affected fleshy fruits are, for example, strawberries and other berries, cantaloupes, peaches, pears, etc.; vegetables, for example, tomatoes, potatoes, spinach, celery, onions, cabbage, etc.; and ornamentals, for example, cyclamen, iris, lily, etc. Nearly all fleshy vegetables are subject to bacterial soft rots. The soft rot bacteria enter the plant organ through a wound, sometimes in the field but more commonly during storage, and there they multiply rapidly, secrete enzymes that separate the cells from each other and macerate the plant cell walls, which causes the tissues to become soft and to rot. In many cases, these bacteria are accompanied in the rotting tissues by other saprophytic bacteria that further degrade the softened plant tissue and cause it to give off a foul odor. In all cases, rotting tissues become soft and watery, and slimy masses of bacteria ooze out from cracks in the tissues.

The soft rotting bacteria survive in infected fleshy organs in storage and in the field, in plant debris, in infected roots and other plant parts of their hosts, in ponds and streams from where irrigation water is obtained, and to some extent in the soil and in the pupae of several insects. The seedcorn maggot, *Delia platura* (Meigen) (Diptera: Anthomyiidae), was shown to play an important role in the dissemination and development of bacterial soft rot in potatoes both in storage and in the field. The soft rot bacteria are usually introduced into a potato field on infected or contaminated seed pieces but they can also live in all stages of the insect, including the pupae, and there they may survive cold or dry weather conditions. The insect larvae become contaminated with the bacteria as they feed in, or crawl about on, infected seed pieces; they also carry the bacteria to healthy plants and there they deposit them into wounds they create. Even when the plants or storage organs are resistant to soft rot bacteria and can normally stop the advance of the bacteria by developing a barrier of cork layers, the maggots destroy the cork layers as fast as they are formed and the soft rot continues to spread. Some other related flies, for example, the bean seed maggot *Delia florilega* (Zetterstedt), *Drosophila busckii* Coquillett (Diptera: Drosophilidae), and probably others, seem to have analogous relationship to the soft rot of potato and other fleshy organs. It has also been shown that several other flies have similar relationships with soft rot bacteria and the host plants on which they prefer to feed. Such relationships, for example, exist between the cabbage maggot, *Delia radicium* (Linnaeus) and soft rot in the Brassicaceae; the onion maggot, *Delia antiqua* (Meigen), the onion black fly, *Tritoxa flexa* (Weidman) (Diptera: Otitidae), the seedcorn maggot, and the onion bulb fly, *Eumerus strigatus* (Fallen) (Diptera: Syrphidae) and the soft rot of onion; and the iris borer, *Macronoctua onusta* (Grote) (Lepidoptera: Noctuidae) and soft rot of iris.

The exact relationship between soft rot in each host and each specific insect found to possibly be involved in the transmission of soft rot bacteria from one organ or plant to another is not clear. There is little doubt, however, that insect transmission of soft rot bacteria does occur, that insects help introduce the bacteria into wounds they open, and that the presence of insects in soft-rotting tissues inhibits the defense reaction of the plants against the bacteria. The insects also, by carrying the soft rot bacteria internally in their bodies, help the bacteria survive adverse environmental conditions. On the other hand, the bacteria seem to help their insect vectors by preparing for them a more nutritive substrate through partial maceration of the host plant tissues.

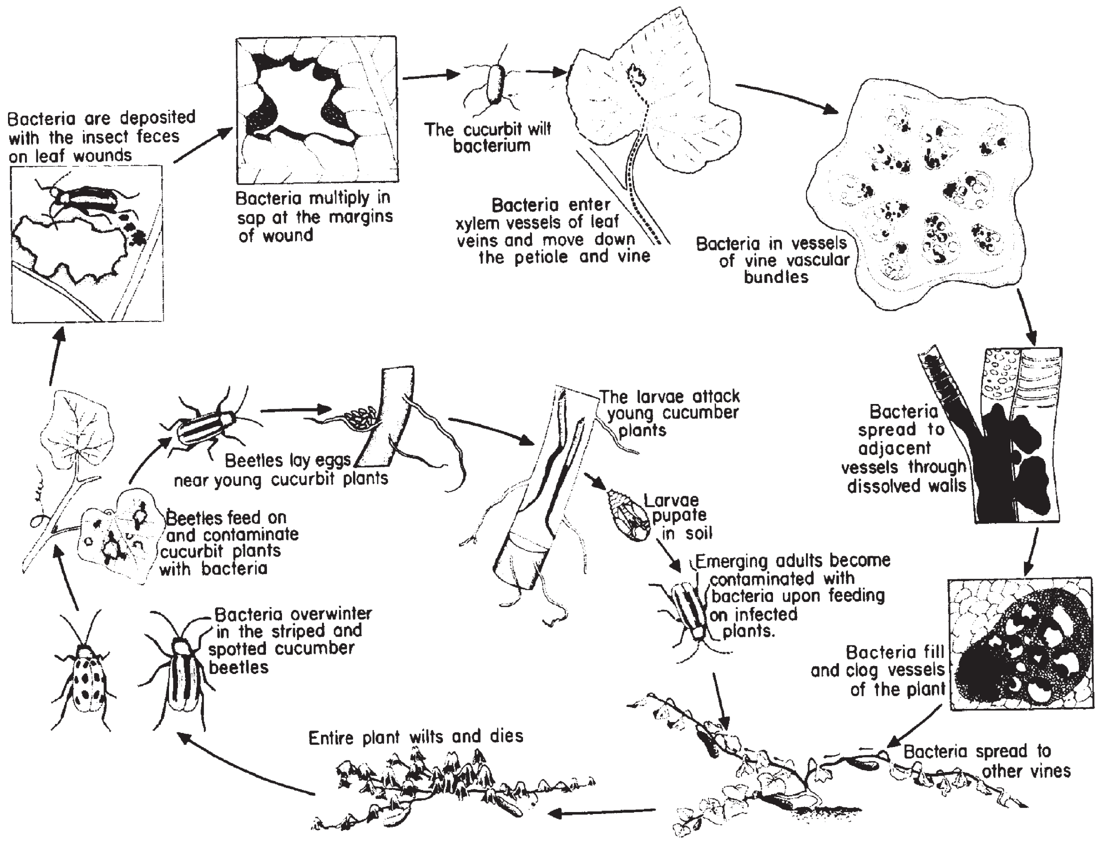
Bacterial Wilts of Plants

In several bacterial diseases of plants, the bacteria enter the xylem conductive system of the plant and there they move, multiply, and clog up the vessels. The clogging of the xylem vessels is further increased by substances released from cell walls by bacterial enzymes and interferes with the translocation of water through the stems to the shoots of the plant. As a result of insufficient water, the leaves and shoots loose turgor, wilt, and eventually turn brown and die. In some bacterial wilts, the bacteria destroy and dissolve parts of the xylem walls and move into the adjacent tissues where they form pockets full of bacteria from which the bacteria ooze out onto the plant surface through cracks or natural openings. In other bacterial wilts, the bacteria remain confined in the xylem and do not reach the plant surface until the plant is killed by the disease.

The wilt-causing bacteria overwinter in plant debris in the soil, in the seed, in vegetative propagative material, and in some cases, in their insect vector. They enter plants through wounds, and they spread from plant to plant through the soil, through tools and direct handling of plants, or through insect vectors. The most important bacterial wilts in which insects play a significant role in the transmission of the bacteria from plant to plant are described briefly below.

Bacterial Wilt of Cucurbits

Bacterial wilt of cucurbits has been reported from most developed countries but it probably occurs throughout the world. It affects many species of cucurbits, including cucumber, muskmelon, squash, and pumpkin. Watermelon is resistant or immune to bacterial wilt. Diseased plants develop a sudden wilting of their foliage and vines and eventually die. Diseased squash fruit develops a slimy rot in storage. Losses from bacterial wilt vary from an occasional wilted plant to destruction of 75–95% of the crop (Fig. 93).



Transmission of Plant Diseases by Insects, Figure 93 **Disease cycle of bacterial wilt of cucurbits caused by *Erwinia tracheiphila* and transmitted by the striped cucumber beetle (*Acalymma vittatum*) (from Agrios 1997).**

Bacterial wilt of cucurbits is caused by the bacterium *Erwinia tracheiphila*. The bacterium survives in infected plant debris for a few weeks but it survives over winter in the intestines of its two insect vectors, the striped cucumber beetle (*Acalymma vittatum* [Fabricius]) and the spotted cucumber beetle (*Diabrotica undecimpunctata* Mannerheim [Coleoptera: Chrysomelidae]). The bacterium depends on these two vectors for its transmission to and inoculation of new plants. In the spring, striped cucumber beetles and, to a lesser extent, spotted cucumber beetles, that carry bacteria, feed and cause wounds on the leaves of cucurbit plants. The insects deposit bacteria in the wounds through their feces and the bacteria enter the wounded xylem vessels in which they multiply rapidly and through which they move to all parts of the plant. In the xylem, the bacteria excrete polysaccharides, secrete enzymes that break down some of the cell wall substances, and induce xylem parenchyma cells to produce tyloses in the xylem. All of them together form gels or gums that clog the vessels, especially at their end walls, thereby reducing the upward flow of water in the xylem by up to 80% and causing the leaves and vines to wilt. Beetles feeding on infected cucurbit plants pick up bacteria on their mouthparts and when they feed onto healthy plants they deposit the bacteria in the new wounds they have made. Thus, the bacteria start a new infection. Each contaminated beetle can infect several healthy plants after one feeding on an infected plant. It appears that a relatively small percentage of beetles become carriers of the bacteria through the winter. Spotted cucumber beetles transmit the wilt bacteria rather late in the season, therefore they are considered less important vectors of this disease than the striped cucumber beetles.

Bacterial Wilt of Corn

This disease is also known as Stewart's wilt of corn. It is caused by the bacterium *Pantoea* (formerly *Erwinia*) *stewartii*. It occurs in North and Central America and also in Europe and China. It is more severe in the northern states. The bacterium invades the vascular tissues but it also spreads into other tissues. When sweet corn plants are affected at the seedling stage they may wilt rapidly and may die, or they develop pale green wavy streaks on the leaves, become stunted, wilt, and may also die. If infected plants survive, they often tassel prematurely, the tassels become bleached and may die, and produce deformed ears. Bacteria also enter the stalk pith, which they macerate in places near the soil line and form cavities. From there the bacteria invade all vascular tissues and spread throughout the plant. Field corn is more resistant to early infection but becomes more severely infected later in the season. Some hybrids are susceptible and their symptoms parallel those of sweet corn. Later infections, after tasseling, produce irregular streaks on the leaves that originate at feeding points of the corn flea beetle, *Chaetocnema pulicaria* Melsheimer. The corn wilt bacteria are also transmitted by the toothed flea beetle (*Chaetocnema denticulata* Illiger), the spotted cucumber beetle (*Diabrotica undecimpunctata howardi* Barber), and by the larvae of the seed corn maggot (*Delia platura* Meigen), wheat wireworm (*Agriotes mancus* Say), and the May beetle (*Phyllophaga* sp.). It appears, however, that overwintering and spread of the bacteria in the field is carried out primarily by the corn flea beetle.

These beetles cause direct damage to corn leaves and seedlings but their main damage comes from harboring and transmitting the bacteria from plant to plant. The beetles pick up the bacteria when they feed on infected corn plants. The bacteria survive in the digestive tract of the insect as long as the latter lives. The insects are also the main place where the bacteria overwinter. The corn flea beetles overwinter as adults in the upper 2–3 cm of soil in grass sod. They are rather sensitive to low temperatures, however. In mild winters, when the sums of mean temperatures for December, January, and February are above 3–4°C, large numbers of beetles survive. When the soil warms up to about 17–20°C, they begin to feed on corn seedlings, which they infect with bacteria. Following mild winters, bacterial wilt of corn is spread rapidly by corn flea beetles, and corn losses can be quite severe. During cold winters that average temperatures below 0°C, many of the beetles do not survive and the incidence and spread of bacterial wilt of corn the following spring and summer are quite limited.

Southern Bacterial Wilt of Solanaceous and Other Crops

This vascular wilt is caused by the bacterium *Ralstonia solanacearum*. It occurs in the warmer regions around the world and is particularly severe in the tropics. It is known by different names in different hosts, for example, southern wilt or brown rot in potato and tomato, Granville wilt in tobacco, and Moko disease in banana. Insects, primarily bees (*Trigona corvine* Cockerell, Hymenoptera: Apidae), wasps (*Polybia* spp., Hymenoptera: Vespidae), and flies (*Drosophila* spp., Diptera: Drosophilidae) have been implicated as vectors. Because these and other insects visit infected stem wounds and natural abscission sites oozing out bacteria, they are considered as playing a role in the transmission of the bacteria to natural infection courts and in providing wounds for bacterial entry, but their importance as vectors has not been documented.

Fire Blight of Pears, Apples and Other Rosaceous Plants

The disease is caused by the bacterium *Erwinia amylovora*. Fire blight occurs in North America, Europe and countries surrounding the Mediterranean Sea, and in New Zealand. It continues, however, to spread into new countries. Fire blight is the most devastating diseases affecting rosaceous plants. The symptoms consist of infected blossoms and young shoots becoming discolored and water-soaked, then being killed rapidly and appearing brown to black as though scorched by fire. The disease spreads rapidly into larger twigs and branches, which it also kills, and parts of or entire trees may be killed. At the base of twig or branch infections, cankers develop at the margins of which the bacteria overwinter. Fruit also become infected and ooze droplets of bacteria. The bacteria kill and macerate the contents of primarily parenchyma cells on flowers and in the bark of young shoots and twigs, but as they destroy these cells they move on mass in the bark. The bacteria also enter the phloem and xylem vessels through which they may move over relatively short distances.

The fire blight bacteria overwinter at the margins of cankers of twigs and branches. In the spring, the bacteria around cankers multiply and their byproducts absorb water and build up internal pressure. This results in droplets of liquid containing masses of fire blight bacteria oozing out of the cankers. The bacteria in the ooze are disseminated by splashing rain and also by flying and crawling insects, several of which are attracted to the bacterial ooze, and their legs, bodies, and mouthparts become smeared with bacteria. More than 200 species belonging to many insect groups, including aphids, leafhoppers, psyllids, beetles, flies, and ants, have been shown to visit oozing cankers and healthy blossoms, although bees and wasps seem not to visit oozing cankers routinely. Insects smeared with bacteria oozing out at cankers carry the bacteria to young shoots where they deposit them in existing wounds or in fresh wounds they make upon feeding, or in the nectar of the flowers. Once the fire blight bacteria are transmitted to blossoms by rain or insects, they enter the flower tissues through nectarthodes or wounds, multiply rapidly in them, and ooze out of them and commingle with the nectar in the flower. The same kinds of insects apparently can transmit fire blight bacteria from infected to healthy flowers but flower to flower transmission of fire blight bacteria is carried out so much more efficiently by pollinating insects, namely bees, that the contribution of other insects to that type of transmission seems to be relatively insignificant. As honeybees, wild bees, bumblebees, wasps, and other insects visit pear, apple, and other flowers infected with fire blight bacteria, their mouthparts, legs, and other body parts become smeared with the bacteria in the nectar. The insects then carry the bacteria and deposit them in the nectar of healthy flowers they visit and there the bacteria start new infections. The bacteria, however, do not survive on or in the insects for more than a few days and do not appear to overwinter in association with the insects.

Olive Knot

Olive knot is caused by the bacterium *Pseudomonas savastanoi*. It occurs in the Mediterranean region, in California, and probably the other parts of the world where olive trees grow. The disease occurs as rough galls of varying sizes developing on leaves, branches, roots, on leaf and fruit petioles, and on wounds in tree branches and trunks. Sometimes the galls are so numerous on twigs that the twigs decline and may die back. The galls are the result of growth regulators being produced by the bacteria, which grow and multiply in the intercellular spaces of the outer cells of the galls. In California, the bacteria are spread by running and splashing rain water that carries the bacteria to existing wounds, pruning wounds, and leaf scars. In other parts of the world, however, such as the Mediterranean region, the olive knot bacteria are also spread by the olive fly or olive fruit fly, *Bactrocera* (formerly *Dacus*) *oleae* (Gmelin) (Diptera: Tephritidae), which is the most destructive pest of olive in its own right.

The bacterium and the olive fly have developed a close symbiotic relationship that contributes to the transmission of the olive knot bacteria from tree to tree. The bacteria are carried by all stages (larvae, pupae, and adults) of the olive fly. The adult olive flies, and related fly species, have specialized structures along their digestive tract that are filled with bacteria. There is even a connection of the digestive tract with the oviduct that insures contamination of the eggs before oviposition. Transmission of the bacteria by the insect takes place during feeding and oviposition into olive tissues. The bacteria actually penetrate the egg through the micropyle, thereby ensuring that when the larvae hatch they are contaminated with the bacteria. It appears that while the olive fly plays a significant role in the transmission of the olive knot bacteria, the bacteria contribute to the insect by hydrolyzing proteins and making available to the insect certain amino acids needed by the insect for survival of the larvae and for development of adults.

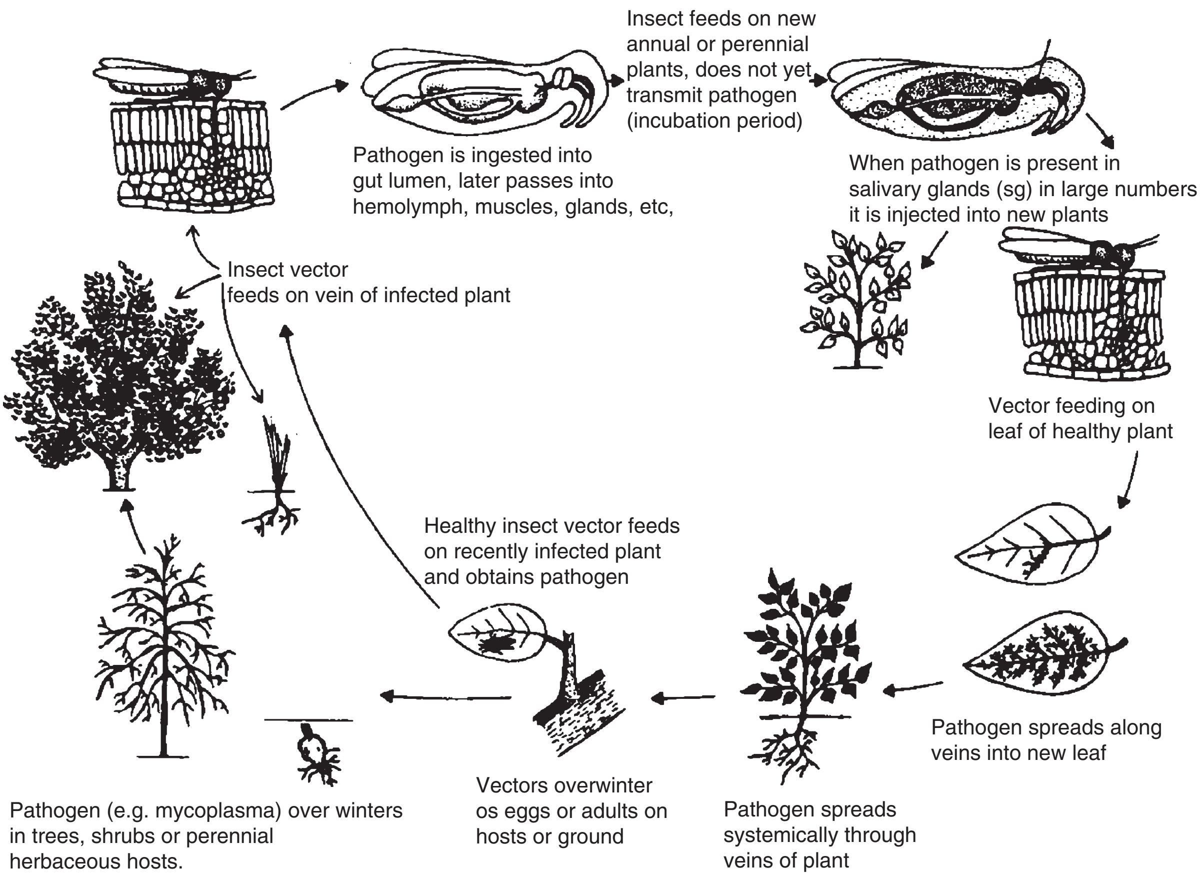
Insect Transmission of Xylem-Inhabiting Bacteria

Quite a few important bacterial diseases of plants, primarily trees, are caused by the fastidious bacterium *Xylella fastidiosa*. These bacteria inhabit the xylem of their host plants and are rather difficult to isolate and to grow on the usual culture media. The diseases they cause differ from the vascular wilts caused by conventional bacteria in that instead of wilt they cause infected plants to decline, some of their twigs to die back, and in some cases the whole plant to die. The xylem-inhabiting fastidious bacteria are transmitted in nature only by xylem-feeding insects, such as sharpshooter leafhoppers (Cicadellidae: Cicadellinae) and spittlebugs (Cercopidae). *Xylella* bacteria seem to be distributed in tropical and semitropical areas worldwide. Among the most important diseases caused by *Xylella* are Pierce's disease of grape and citrus variegated chlorosis. Other diseases caused by xylem-inhabiting bacteria include phony peach, plum leaf scald, almond leaf scorch, bacterial leaf scorch of coffee, oak leaf scorch, and leaf scorch diseases of oleander, pear, maple, mulberry, elm, sycamore, and miscellaneous ornamentals, as well as the alfalfa dwarf disease (Fig. 94).

Pierce's Disease of Grape

Pierce's disease is a devastating disease of European-type grapevines (*Vitis vinifera*). It is caused by the xylem-inhabiting bacterium *Xylella fastidiosa*. It occurs in the Southern United States and in California, in Central America, and parts of northwestern South America. The presence of Pierce's disease in an area precludes the production of European-type grapes in that area but some muscadine grapes and hybrids of European grapes with American wild grapes are tolerant or resistant to Pierce's disease. The Pierce's disease bacterium moves and multiplies in the water-conducting (xylem) vessels of shoots and leaves, some of which become filled with bacteria and reduce the flow of water through them. Leaves beyond such blocked vessels become stressed from lack of sufficient water and develop yellowing and then drying or scorching along their margins. During the summer, the scorching continues to expand toward the center of the leaf, while some or the entire grape clusters begin to wilt and dry up. Scorched leaves fall off leaving their petioles still attached to the vine, while the vines mature unevenly and have patches of brown (mature) and green bark. In the following season(s), affected grapevines show delayed growth and stunting. The leaves and vines repeat the symptoms of the first year and both, the top of the plant as well as the root system, decline and die back.

The bacterium that causes Pierce's disease of grape is *Xylella fastidiosa*. The bacterium apparently consists of various host specific strains. The strain that causes Pierce's disease of grape also causes alfalfa dwarf disease and almond leaf scorch. Apparently related but different strains of the bacterium cause citrus variegation chlorosis, the other related leaf scorch diseases of fruit and forest trees and of ornamental trees and



Transmission of Plant Diseases by Insects, Figure 94 **Sequence of events in the overwintering, acquisition, and transmission of plant viruses, mollicutes, and fastidious bacteria by leafhoppers (from Agrios 1997).**

shrubs. The identity and taxonomy, as well as the host range and vector preference of the possible strains of *Xylella fastidiosa*, are unknown. In all cases, the bacterium is transmitted from plant to plant through vegetative propagation, such as cuttings, budding, and grafting, and by one or more of several closely related insects. The known vectors of *Xylella fastidiosa* are sharpshooter leafhoppers (family Cicadellidae, subfamily Cicadellinae) or spittlebugs (family Cercopidae). It is possible that other or all sucking insects that feed on xylem sap, for example, the cicadas (family Cicadidae), are also vectors of *Xylella fastidiosa*. In California, there are at least four important sharpshooter leafhopper vectors of *Xylella*: The blue-green (*Graphocephala atropunctata*), the green (*Draeculacephala minerva*), the red-headed (*Carneocephala fulgida*), and the glassy-winged (*Homalodisca coagulata*) sharpshooters. The vectors may be different in other parts of the world. All vector insects acquire the bacteria when they feed on infected plants. Ingested bacteria seem to adhere to the walls of the foregut of the insect and when the insect moves to and feeds on the next healthy plant, the insect transmits the bacteria into the xylem vessels of that plant where they multiply and cause a new infection. Once a vector acquires bacteria from a diseased plant, it remains infective indefinitely. When, however, infective insects shed their external skeleton by molting, they loose the bacteria and must feed on a diseased plant again before they can transmit the bacteria to healthy plants.

Insect Transmission of Phloem-Inhabiting Bacteria

At least four plant diseases are caused by bacteria that inhabit only the phloem of their host plants. These diseases include the destructive citrus greening disease, the severe papaya bunchy top disease, the cucurbit yellow vine disease, and the infrequent clover club leaf disease. The bacteria causing these diseases have not yet been grown on nutrient media and so far many of their properties remain unknown. All of them, however, are transmitted from plant to plant only by specific insect vectors. The citrus greening bacterium is transmitted by a psyllid, while the papaya bunchy top disease bacterium and the clover club leaf bacterium are transmitted by leafhoppers, and the cucurbit yellow vine disease bacterium is transmitted by the squash bug. In the psyllid and leafhopper vectors, the bacterium also multiplies in and is passed from the mother insect to its offspring through the eggs (transovarial transmission). It is not known what happens to the bacteria transmitted by the squash bug.

Citrus Greening Disease

Citrus greening is a very destructive disease of all types of citrus. It occurs in most citrus producing areas of Asia, including the Arabian Peninsula, and in Africa. The disease is caused by the bacterium *Liberobacter asiaticum* in Asia, and *L. africanum* in Africa. Both bacteria are limited to the phloem of the host plants, and have yet to be cultured. The disease first appears as a chlorosis and leaf mottling on one shoot or branch, which it has given it the name "huanglongbing," or "yellow shoot," in Chinese. Later on, entire trees become chlorotic as though they are suffering from zinc deficiency, their twigs die back, and the trees decline rapidly and become non-productive. Fruit on diseased trees is small, lopsided, and does not color uniformly as it ripens but large parts of it remain green even when mature, thereby the "greening" name of the disease. Diseased fruit is also quite bitter.

Citrus greening is spread by vegetative propagation with buds and grafts, and by at least two citrus psyllids: *Diaphorina citri* Kuwayama, which is the principal vector of the more severe and more destructive Asian form of the citrus greening bacterium that occurs at higher temperatures (30–35°C), commonly found at lower elevations; and *Trioza erytreae* Del Guercio, which is the principal vector of the milder, less severe, lower temperature (27°C) African form of the bacterium, which is normally found at higher elevations. Both vectors, however, can transmit both forms of the bacterium. Asian psyllids acquire the bacterium within 30 min of feeding while African psyllids require 24 h. The bacterium apparently multiplies in the vector and can be transmitted within 8–12 days from acquisition.

Infected plants and vectors have been introduced into several citrus-producing countries but in most cases it was eradicated before it could become established. The vector of the greening bacterium *Diaphorina citri* was introduced in Brazil in the early 1980s and in Florida in 1998 but, so far, the causal bacteria apparently have not been introduced and no trees have been found in either place to be infected with citrus greening.

Bunchy Top of Papaya Disease

Bunchy top is a devastating disease of papaya. It occurs in most or all islands of the Caribbean Basin and, probably, also in Central America and in the northern part of South America. Young leaves of infected plants show mottling, then chlorosis and marginal necrosis, and become rigid. Internodes become progressively shorter, further apical growth stops, and the plant develops a "bunchy" top. Older leaves may fall off, any fruits that are set are bitter, and the entire plant may die.

Bunchy top of papaya is caused by a rickettsia-like phloem-limited bacterium that moves and multiplies in the phloem elements of the plant. The bunchy top bacteria are transmitted from diseased to healthy papaya plants by the leafhoppers *Empoasca papayae* Oman and *E. stevensi* Young. Symptoms appear 30–45 days after inoculation.

Cucurbit Yellow Vine Disease

Yellow vine disease affects watermelon, melon, squash, and pumpkin. It was first reported in the Texas–Oklahoma area and has since been found in Massachusetts, New York, and Tennessee. Affected plants show vines with yellow leaves, the phloem of leaves and vines becomes discolored, and the leaves and vines collapse and die. The disease has been severe in the Texas and Oklahoma areas where it annually destroys thousands of acres of cucurbits costing millions of dollars.

Cucurbit yellow vine disease is caused by a phloem-limited bacterium that has been placed in the species *Serratia marcescens* and its properties are still being characterized. The bacterium is most probably transmitted by insect vectors. The squash bug, *Anasa tristis*, is considered to be a vector of this bacterium, but its involvement in transmitting this bacterium has been questioned.

Insect Transmission of Plant Diseases Caused by Mollicutes

Mollicutes are prokaryotes (bacteria) that lack cell walls. In nature, plant pathogenic mollicutes are limited to the phloem of their host plants. Plant pathogenic mollicutes are generally classified as belonging to the genus *Phytoplasma*. Most phytoplasmas have an irregular spherical to elongated shape and have been obtained and maintained on complex nutrient media, although they do not readily grow or multiply on them. A few plant pathogenic mollicutes typically have spiral morphology and belong to the genus *Spiroplasma*. Spiroplasmas grow and multiply readily on specialized nutrient media. Plant diseases caused by mollicutes appear as yellowing of leaves, proliferation of shoots (witches' brooms) and of roots, stunting of shoots and whole plants, greening of flowers, abortion of flowers and fruit, dieback of twigs, and decline and death of trees. Numerous important diseases of annual crops are caused by mollicutes, mostly phytoplasmas, for example, aster yellows of vegetables and ornamentals, tomato big bud (stolbur), corn stunt, etc. Phytoplasmas cause even more, and more severe, diseases on trees, including X-disease of peach, peach yellows, apple proliferation, elm yellows, pear decline, and lethal yellowing of coconut palms. Spiroplasmas also cause severe diseases, for example, corn stunt, and citrus stubborn disease.

All mollicutes, that is, phytoplasmas and spiroplasmas, are spread from plant to plant through vegetative propagation and, in nature, these pathogens depend for their transmission on phloem-feeding, sap-sucking insects, mainly leafhoppers, planthoppers, and psyllids. These insects can acquire the pathogen after feeding on appropriate infected plants for several hours or days, or if they are artificially injected with extracts from infected plants or insects. More insects become vectors when they feed on young leaves and stems of infected plants than on older ones. The insect vector cannot transmit the pathogen immediately after feeding on the infected plant but it begins to transmit it after an incubation period of 10–45 days, depending on the temperature. The quickest transmission (10 days) occurs at about 30°C, while the slowest (45 days) takes place at about 10°C.

The reason for the incubation period is that the acquired phytoplasmas or spiroplasmas must first multiply in the intestinal cells of the insect vector and then move through the insect by passing into the hemolymph, then infect internal organs and the brain, and finally reach and multiply in the salivary glands. When the concentration of the pathogen in the salivary glands reaches a certain level, the insect begins to transmit the pathogen to new plants and continues to transmit it with more or less the same efficiency for the rest of its life. Insect vectors are not generally affected adversely by the phytoplasmas or spiroplasmas multiplying in their cells, but in some cases they show severe pathological symptoms. Phytoplasmas and spiroplasmas can be acquired as readily or better by nymphs than by adult leafhoppers, etc., and they survive through subsequent molts of the insect. The pathogens, however, are not passed from the adults to the eggs and to the next generation. For this reason, young insects of any stage must feed on infected plants in order to become infective vectors.

Some of the most important plant diseases caused by mollicutes and their insect vectors are described briefly below.

Aster Yellows

Aster yellows is caused by phytoplasmas and occurs worldwide. It affects numerous annual crops, mostly vegetables and ornamentals, for example, tomato, lettuce, carrot, onion, potato, chrysanthemum, aster, and many others, on which it causes severe symptoms and serious losses, in some crops amounting to 10–25% of the crop and occasionally up to 80–90% of the crop. Plants infected with aster yellows develop general chlorosis (yellowing) and dwarfing of the whole plant, abnormal production of shoots and, sometimes, roots, sterility of flowers, malformation of organs, and a general reduction in the quantity and quality of yield. The aster yellows phytoplasma is transmitted by several leafhoppers, one of which is the aster leafhopper *Macrosteles fascifrons*. The various leafhopper vectors have a wide host range, as does the aster yellows phytoplasma. The phytoplasmas survive in perennial ornamental, vegetable, and weed plants. The vector leafhopper acquires the phytoplasmas while feeding by inserting its stylet into the phloem of infected plants and withdrawing the phytoplasmas with the plant sap. After an incubation period, when the insect feeds on healthy plants it injects the phytoplasmas through the stylet into the phloem of the healthy plants where they establish a new infection and multiply. The phytoplasmas move out of the leaf and spread throughout the plant causing the symptoms characteristic of the host plant.

Tomato Big Bud

The disease occurs in many parts of the world but except for a few areas, it is of little economic importance. It affects most Solanaceous vegetables and lettuce. The symptoms include small, distorted, yellowish green leaves and production of numerous thickened, stiff, and erect apical stems that have short internodes. The flower buds are excessively big, green, and abnormal looking, and fail to set fruit. Fruit present when infection takes place becomes deformed.

Tomato big bud is caused by a phytoplasma that is transmitted by several leafhoppers, the main one of which is the common brown leafhopper *Orosius argentatus*. The insect feeds and breeds on infected weed hosts and when they become undesirable the insects move into tomato or other crops bringing with them the big bud phytoplasmas.

Apple Proliferation

It is the most important insect transmitted disease of apple in most of Europe. It may also occur in South Asia and South Africa. Depending on prevalence in an orchard, apple proliferation may cause economic losses of 10–80% due to reduction in fruit size, total yield, and vigor of trees. The most conspicuous symptoms of apple proliferation are the production of witches' brooms or of leaf rosettes, and of enlarged stipules at the base of leaves. Affected trees leaf out earlier in the spring but flowering is delayed. The leaves, fruit, and entire trees are smaller, and fruit color and taste are also poor. Proliferating shoots are often infected with powdery mildew.

Apple proliferation is caused by a phytoplasma that also infects other wild and ornamental apple species, and possibly pear and apricot.

The phytoplasma is spread in nature by several leafhoppers, including *Philaenus spumarius*, *Aphrophora alni*, *Lepyronia coleoptrata*, *Artianus interstitialis*, and *Fieberiella florii*. The leafhopper vectors acquire the phytoplasmas when they feed on the phloem elements of young leaves and shoots of infected apple trees and, after an incubation period, transmit the phytoplasmas into healthy apple trees. The time between inoculation and appearance of symptoms varies with the size of the inoculated tree. Young nursery trees may develop symptoms within a year while large established trees may do so 2 or 3 years after inoculation.

Pear Decline

It is a serious disease of pear resulting in significant crop losses and also in stunting and death of affected pear trees grown on certain rootstocks. The disease, which is caused by a phytoplasma, occurs in North America and in Europe, and probably in many other parts of the world where pears are grown. The symptoms of pear decline may develop as a quick decline, that is, sudden wilt and death of a tree within a few days or weeks, with or without first showing reddening of leaves, or a slow decline. Quick decline usually develops on trees propagated on certain hypersensitive rootstocks in which a brown necrotic line develops at the graft union of the tree. Slow decline also occurs on trees grafted on the same or other rootstocks, and appears as a progressive weakening of the tree of varying severity. Slow declining trees have reduced or no terminal growth, have few, small, leathery, light green leaves whose margins are slightly rolled up and may be yellow or red in the autumn. Such trees may or may not die a few years after infection. Some infected pear trees, however, show primarily a reddening of the leaves in late summer or early autumn, and mild reduction in vigor.

The pear decline phytoplasma is transmitted from tree to tree by grafting and by the pear psylla (*Psylla pyricola* Forster) and in Europe, probably by *P. pyri* and *P. pyrisuga*. Pear psylla acquires the phytoplasma after feeding on infected trees for a few hours and remains infective for several weeks. Young trees inoculated with phytoplasma by the insect show symptoms the same or the next year, while older trees may take longer. The phytoplasma is sensitive to low temperatures and dies out in the above-ground parts of the tree but survives in the tree roots. In the spring, the phytoplasma recolonizes the stem, branches and shoots and from the latter it can be acquired and transmitted again by the insect vectors.

Lethal Yellowing of Coconut Palms

Lethal yellowing is a blight that kills coconut and some other palm trees within 3–6 months from the time the trees show the first symptoms. It occurs in Florida, Texas, Mexico, most Caribbean islands, in West Africa, and elsewhere. The disease appeared for the first time in Florida in 1971 and killed 15,000 coconut palm trees the first two years, 40,000 by the third year, and by the fourth year (1975), 75% of the coconut palms in the Miami area were dead or dying from lethal yellowing. The disease appears as a premature drop of coconuts followed by blackening and death of the male flowers. Subsequently, first the lower and then the other leaves turn yellow and then brown and die, as does the vegetative bud, and the entire top of the tree falls off leaving the palm trunk looking like a telephone pole.

Lethal yellowing is caused by a phytoplasma that lives and multiplies in the phloem elements of the plant. The main means of spread of lethal yellowing from tree to tree is through the planthopper *Myndus crudus*, although other vectors are also possible. As with the other phytoplasma diseases, the vector acquires the phytoplasma while sucking juice off the phloem of palm leaf veins, the phytoplasma multiplies in the vector during an incubation period, and the insect then transmits the phytoplasma when it visits and feeds on leaf veins of healthy palm trees.

Corn Stunt

Corn stunt causes severe losses where it occurs although losses vary from year to year. It occurs in the southern United States, Central America, and northern South America. Symptoms consist of yellow streaks in young leaves followed by yellowing and reddening of leaves, shortening of internodes, stunting of the whole plant, and sterile tassels and ears.

Corn stunt is caused by the spiroplasma *Spiroplasma kunkelii*. The spiroplasma invades phloem cells from where it is acquired by its leafhopper vectors *Dalbulus maidis*, *Dalbulus eliminatus*, and other leafhoppers after feeding on infected plants for several days. The vectors transmit the spiroplasma after an incubation period of 2–3 weeks, during which the spiroplasma moves and multiplies in the insect.

Citrus Stubborn Disease

It is present and severe in hot and dry areas such as the Mediterranean countries, the southwestern United States, Brazil, Australia, and elsewhere. It is one of the most serious diseases of sweet orange and grapefruit. It is hard to diagnose but reduces yield, quality, and marketability of fruit dramatically. Infected trees grow upright but are stunted. There is less fruit and it is smaller, lopsided, green, and sour, bitter, and unpleasant.

Citrus stubborn disease is caused by the spiroplasma *Spiroplasma citri*, which is found in the phloem of affected orange trees. It is transmitted by budding and grafting and, in nature, by several leafhoppers such as *Circulifer tenellus*, *Scaphytopius nitrides*, and *Neoaliturus haemoceps*. Role of insects on fungal diseases of plants.

Insect Transmission of Fungi

As with bacteria, many insects are involved in the transmission of numerous plant pathogenic fungi from diseased to healthy plants. Insects are also involved in plant diseases by breaking the epidermis and other protective tissues of plants with their mouthparts or with their ovipositor and thereby allowing the fungus to enter. Most of the insect transmissions of fungi are accidental, that is, they occur because the insects happen to become externally or internally contaminated with the fungus or its spores when they visit infected plants and then carry the spores with them to the plants or plant parts they visit next. In some cases, insect transmission of a fungus occurs as the insect visits blossoms during pollination, in others it occurs while wounding plants during oviposition, and in other and most frequent cases, transmission occurs while wounding the plant during feeding. In relatively few cases, the insect and the fungus it transmits develop a symbiotic relationship in which each benefit from its association with the other.

Root-Infecting Fungi

It should be pointed out that there are innumerable cases for which there is circumstantial evidence that insects are apparently involved in the transmission of many plant pathogenic fungi and in the development of disease by them, but this has not been proven experimentally. In this category belong, for example, root infections by fungi such as *Pythium*, *Fusarium*, and *Sclerotium*, being facilitated by billbugs such as *Calendra parvula* and *Anacentrus deplanatus*, by the Hessian fly *Phytophaga destructor*, and by the southern and northern corn root worms *Diabrotica undecimpunctata howardi* and *Diabrotica longicornis*, respectively. In the black stain root disease of pines, hemlock, and Douglas fir is caused by the fungus *Leptographium wageneri*, the teliomorph of which is *Ophiostoma wageneri*, and is transmitted by the root-feeding bark beetle *Hilastes nigrinus* and two root and crown weevils, *Steremnius carinatus* and *Pissodes fasciatus*.

Stalk or Stem-Infecting Fungi

Many fungi infecting stalks or stems, for example *Gibberella*, *Fusarium*, and *Diplodia* in corn, are apparently aided by various insects, for example, the widespread European corn borer, *Pyrausta nubilalis*.

Trunk and Branch Canker-Causing Fungi

Many fungi, such as species of *Neofabrea*, *Nectria*, *Leucostoma* (*Cytospora*), *Ceratocystis*, and *Leptosphaeria*, causing tree cankers, are apparently also often associated with and assisted by insects in the initiation and development of the cankers. The insects involved vary with the particular host and fungus. For example, the fungus *Neofabrea perennans* (Gloeosporium perennans), the cause of the perennial canker of apple, is transmitted by the wooly aphid *Eriosoma lanigerum*. The woolly aphids feed on the bark at the base of the trunk where they cause the formation of galls within which they multiply. In early spring the galls burst, the aphids come out and the fungus attacks the injured tissue and from it advances into healthy tissue and produces a canker. In the summer, the apple tree produces callus tissue and seals off the fungus and the spread of the canker stops. The aphids, however, grow into the callus tissue and form a new gall, and the process is repeated.

The spittlebug *Aphrophora saratogensis* seems to be involved in the *Nectria* canker of pines, the nitidulid beetle *Carpophilus freemani* and the drosophilid fly *Chymomyza procnemoides* in the *Ceratocystis* cankers of stone fruit trees, while the tree cricket *Oecanthus niveus* and the raspberry midge *Thomasianna theobaldi* are involved in the tree cricket canker of apple and the midge canker of raspberry, respectively. Many more such insect-pathogen associations could be mentioned.

In the beech bark canker, caused by the fungus *Nectria coccinea* var. *faginata*, the fungus is transmitted to some extent by the scale insect *Cryptococcus fagi* but the main effect of the insect is in weakening the tree and reducing its defenses to the fungus. Thus, after beech trees have been heavily infested by scale insects for about 3–5 years, the fungus invades and kills the bark and the tree forms a canker that may girdle the tree partially or completely and may kill it.

In the birch constriction disease, the lower parts of shoots become constricted at the point where the apical birch woodwasp (*Pseudoxiphydria betulae* Ensl.) feeds on the shoots. The leaves above the constriction wither and die but cling to the twigs past the autumn. Almost all (92%) of the constrictions are also infected with the anthracnose fungus *Melanconium bicolor*.

A similar case in which twig canker initiation and development are facilitated by insects is the cacao dieback disease in which the fungi *Calonectria* (*Fusarium*) *rigidiuscula* and/or *Botryodiplodia theobromae* enter the twigs through wounds created by the feeding of the capsid insects *Sahlbergella singularis* and *Distantiella theobroma*. In isolated infections the tree defenses take over, isolate the fungus, and its further spread stops. In trees massively infested with the insect, however, the fungus develops unchecked in the insect-infested tissues and causes a chronic dieback of twigs. Control of the insects also halts the invasion by the fungus and the tree recovers.

In mango malformation disease, presumably caused by the fungus *Fusarium moniliforme*, the fungus is transmitted by the eriophyid mite *Aceria mangifera*, while other fungi seem to be carried in the digestive tract of certain termites.

Sooty Molds

These are black-colored fungi that grow on the surfaces of mostly leaves of plants, especially in the tropics and subtropics. Sooty mold fungi do not penetrate and infect plants but cause disease by blocking the light from reaching the leaves. Sooty mold fungi do not parasitize plants but feed off the honeydew excreted by insects such as whiteflies, scales, mealybugs, aphids, etc. The sooty mold fungi are disseminated through their spores being blown about by wind. However, they are also spread by the honeydew-producing insects and, also, by several other types of insects such as flies, wasps, bees, and ladybug beetles, all of which seek honeydew as a source of food and in the process become smeared with fungus spores which they carry about.

Wood Rots

Rotting of wood is carried out primarily by wood-rotting basidiomycete fungi. The shelf or conk-shaped fruiting bodies of many of these fungi are visited routinely by many types of insects and it is believed that many of these insects act as vectors of the wood-rotting fungi. Insects and mites have also been implicated in the spread of some pine rust diseases, while at least three common scolytid beetles have been shown to be involved in the transmission of the scleroderis canker of pine and spruce.

Wood-Stain Diseases

Wood stain or wood discoloration diseases occur in conifer trees and felled timber. They are caused by the so-called blue-stain fungi, of which the most common are species of *Ceratocystis* and *Ophiostoma*. The blue-stain fungi are associated with several species of bark beetles, such as *Dendroctonus ponderosae*, *Ips pini*, etc., which serve as vectors of the fungi and provide them with wounds for penetration. On the other hand, the fungi reduce the water content of the tree and otherwise improve the microenvironment for the developing brood of insects. Such a fungus-insect relationship is described as true mutualistic symbiosis. In other blue-stain diseases, like the ones caused by the fungi *Trachosporium tingens* and *T. t.* var. *macrosporum*, the fungi are constantly associated with their bark-beetle vectors *Myelophilus* (*Blastophagus*) *minor* and *Ips acuminatus*, respectively, and are found regularly in the breeding places of the insects in pine stems. Such fungal-insect associations are known as symbiotic ambrosia cultures.

In the Southern United States, attacks of short-leaf pines by beetles like *Dendroctonus frontalis* are quickly followed by heavy fungus infection soon after the beetles tunnel through the bark and outer wood. Several fungi, including *Ceratocystis pini*, *Saccharomyces pini*, *Dacryomyces* sp. and *Monilia* sp. can be isolated from the infected wood and are carried by the same insects both externally and internally. A similarly complex association seems to occur in spruce attacked by *Dendroctonus engelmani*, followed by the fungi *Leptographium* sp., *Endoconidiophora* sp., or *Ophiostoma* sp. infecting the wood and causing a gray stain in the sapwood of the infected trees.

Vascular Wilts

Several vascular wilts affect trees and some of them cause extensive death of trees, because the fungus responsible for the disease is transmitted from diseased to healthy trees by specific insect vectors. The spores produced by the causal fungi are sticky and are produced primarily inside the tree, therefore, they can be spread by no other means but only by certain insects closely associated with the disease. These vascular wilts include (i) persimmon wilt, a devastating disease caused by the fungus *Cephalosporium diospyri* which enters through all kinds of wounds but is also transmitted by the powder-post beetle. *Xylobiops basilaris* and the twig girdler beetle *Oncider cingulatus*, and (ii) mango wilts, one caused by the fungus *Diplodia recifensis* and transmitted by the beetle *Xyleborus affinis*, and another caused by the fungus *Ceratocystis fimbriata* and transmitted by the scolytid beetle *Hypocryphalus mangiferae*. The other two vascular wilts are oak wilt and the Dutch elm disease and will be discussed in some detail below.

Oak Wilt

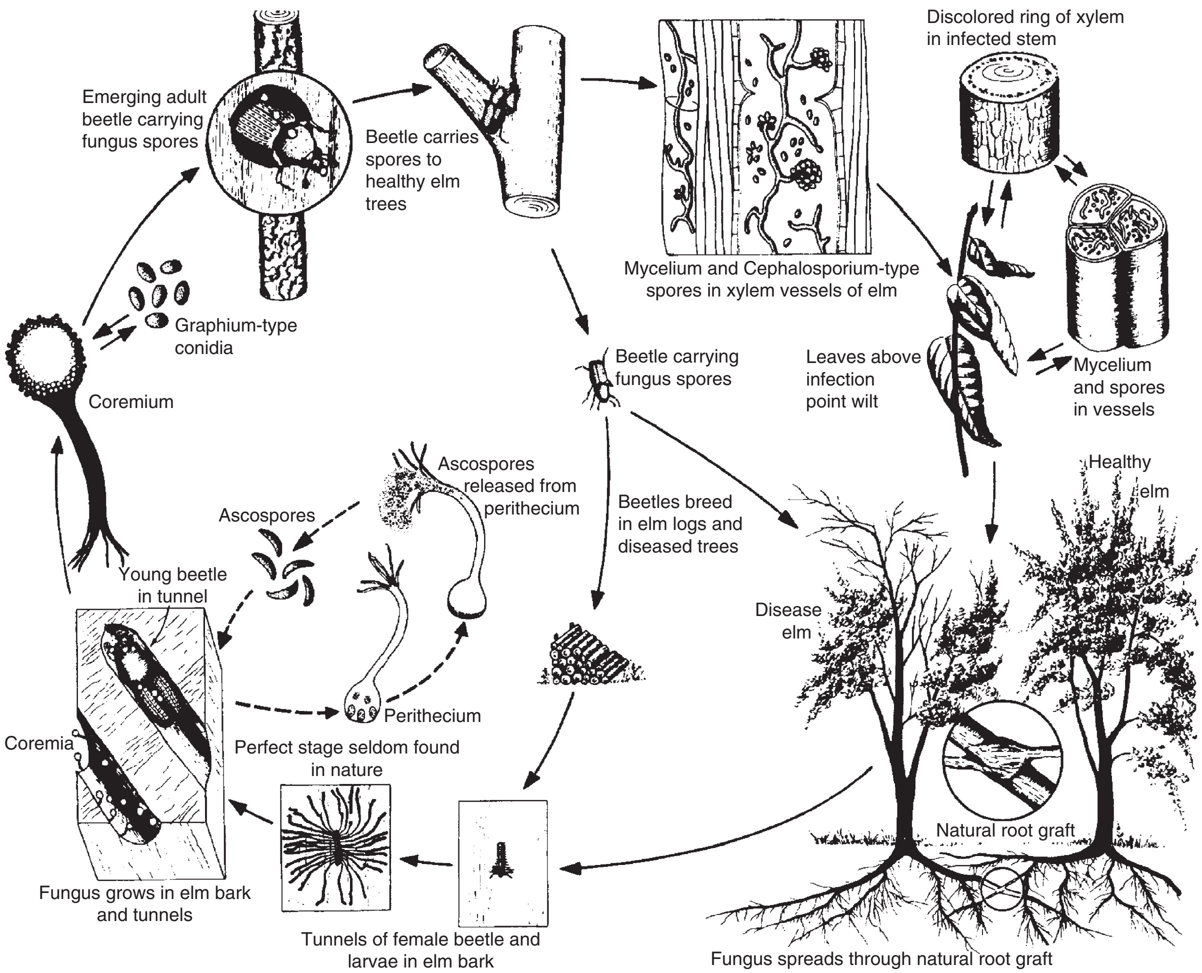
It is caused by the fungus *Ceratocystis fimbriata* and is one of the most important diseases of forest trees. The fungus enters the xylem vessels of trees through fresh wounds to which it is carried by air or insects, and through natural root grafts. Tree parts beyond the point of infection wilt, turn brown and die while newly infected wood shows dark streaks. The fungus is spread to healthy trees by nitidulid beetles such as *Carpophilus lugubris*, *Colopterus niger*, *Cryptarcha ample*, and several species of *Glischrochilus*. These fungi breed in the mycelial mats of the fungus between the bark and wood and carry the fungus both externally on their bodies and internally through their digestive tract. In addition to the nitidulid beetles, several scolytid beetles, such as *Monarthrum fasciatum* and *Pseudopityophthorus minutissimus*, the brentid beetle *Arrhenodes minuta*, the buprestid *Agrillus bilineatus*, the flat-headed borer *Chrysobothrys femorata*, and others, have been shown to carry the spores of the fungus, both externally and internally, when they emerge from the tunnels in diseased trees in which they breed and overwinter and to carry them to susceptible trees in the spring. Transmission of the oak wilt fungus by insects not only spreads the fungus and the disease to new trees and into new areas, it also increases the ability of the fungus to produce new variants and new races more virulent than the existing ones. This is accomplished by the insects bringing together in the same tree the compatible self-sterile mating types which results in the production of perithecia containing the sexual spores ascospores. The latter express any new characteristics brought together during the formation of the spores, some of the characteristics possibly being increased virulence.

Dutch Elm Disease

It is caused by the fungus *Ophiostoma ulmi* and the most recent variant *Ophiostoma novo-ulmi*, which is replacing the earlier species. The disease was first described in the Netherlands in 1921, found in Ohio and New York in the 1930s, and has since spread throughout the United States and much of the rest of the world. It kills elm tree twigs, branches and whole trees by clogging their xylem vessels and blocking movement of water from the roots to these parts. Dutch elm disease has been particularly devastating in the United States where the native elm tree *Ulmus americana* is extremely susceptible to the pathogen. The disease has killed almost all trees in its path, especially elm trees planted along streets and parks. Elm trees in forests have also been killed but many of them have escaped infection so far (Fig. 95).

The fungus causing Dutch elm disease is spread from diseased to healthy trees by the European elm bark beetle *Scolytus multistriatus* and the native elm bark beetle *Hylurgopinus rufipes*, and by natural root grafts. The fungus overwinters in the bark of dying or dead elm trees and logs as mycelium and spores. The elm bark beetles lay their eggs in galleries they make in the intersurface between bark and wood of weakened or dead elm trees. If the tree is already infected with the Dutch elm disease or if the insects carry with them spores of the fungus, the fungus grows and produces new spores in the tunnels. After the eggs hatch, the larvae make tunnels perpendicular to that made by the adult female and pupate. The adults emerge, carrying thousands of fungal spores on their body. The emerging adults prefer to feed on young twigs of trees and the crotch of small branches. As the beetles burrow into the bark and wood for sap, the spores they carry on their body are deposited in the wounded moist tissues of the tree. There the spores germinate and grow into the injured bark and wood and the fungus reaches the xylem vessels of the tree in which it grows producing mycelium and spores. The latter are carried upward by the sap stream where they can start new infections. Shoots beyond the infected areas turn brown, wilt, and die, and as their number increases the tree shows more browning and more wilted branches. Eventually large parts of or entire trees wilt and die, while the fungus continues to grow and spread in the dead tree. Such trees are then visited by adult female beetles that lay their eggs in them and the cycle is repeated.

In Dutch elm disease there is a clear dependency of each organism, the fungus and the insect, on the other. Probably more than 99% of the elm



Transmission of Plant Diseases by Insects, Figure 95 **Disease cycle of Dutch elm disease caused by the fungus *Ophiostoma ulmi* and transmitted by the European and the American elm bark beetles (from Agrios 1997).**

tree infections are caused by the fungus being carried to the elm trees by the elm bark beetles. On the other hand, the elm bark beetles depend on the fungus for causing many elm trees to weaken and die, thereby becoming available as breeding grounds for the two species of elm bark beetles that transmit the fungus. The interdependence of the two organisms has provided the most effective means of managing the Dutch elm disease by burning or debarking dead elm trees and logs, thereby denying the insects the breeding ground they need and, through the reduced number of insects produced, reducing the number of elm trees to which they spread the disease.

Foliar Diseases

Many foliar diseases are probably spread by various insects visiting and moving about on leaf surfaces that are exhibiting infections by spore-producing fungi. Spores or the spore containers of many such fungi are sticky or have appendages that cling to the legs or other body parts of such insects and are carried by them to other plants or plant parts they visit next. A few examples of foliar diseases in which insect transmission of the fungal pathogen has been shown to occur are described briefly below.

Powdery Mildews

These are diseases that affect most annual and perennial plants. They are characterized by white superficial mycelial growth and sporulation by a small group of fungi that cause symptoms on leaves, shoots, blossoms and fruit of their host plants. Powdery mildews serve as food for many mycophagous fungi and produce large numbers of loosely attached spores. Such spores become attached to, and are disseminated by, insects with which they come in contact. Examples include the feeding of thrips on and the transmission of spores of the fungi *Sphaerotheca panosa* and *Uncinula necator* that cause powdery mildew on rose and grape, respectively. Although these fungi are disseminated readily by wind, it is likely that transmission is aided by insects.

Rust Diseases

Most rust diseases produce several types of superficial spores on their host plants that, like those of the powdery mildews, are easily disseminated by air currents but are also visited, eaten, and transported by a wide variety of insects. Furthermore, many rust fungi produce spermatia and receptive hyphae in the same spermagonium but they are self-sterile. Many insects, when visiting such spermagonia become smeared with sticky spermatia. When the insects visit successive spermagonia, they transfer to the receptive hyphae spermatia from the opposite, compatible type. These spermatia can fertilize the receptive hypha which then produces dikaryotic mycelium and spores that contain two nuclei. These dikaryotic spores have entirely different properties. For example, they can infect an entirely different host plant from the plant on which they were produced. The involvement of insects in rust diseases is, therefore, important in both the dissemination of the spores to new hosts and, more importantly, in the fertilization of the fungus and, thereby, in increasing the potential of the fungus to produce more new and possibly more virulent races.

Some other examples of foliar diseases in which insects have been shown to play a role in their transmission include: red pine needle blight caused by the fungus *Pullularia pullulans* and transmitted and aided in penetration of pine needles by a cecidomyiid midge; cucurbit anthracnose, caused by the fungus *Colletotrichum lagenarium* and transmitted and aided in penetration by the spotted cucumber beetle *Diabrotica undecimpunctata*; oil palm leaf spot, caused by the fungus *Pestalotiopsis palmarum* and transmitted and aided in penetration by the oviposition punctures of a tinged of the genus *Gargaphia*.

Diseases of Buds and Blossoms

Insects often overwinter in buds of plants and many also visit blossoms to feed on the nectar they produce. Buds also often contain mycelium and spores of plant pathogenic fungi, and blossoms are often the first plant organ such fungi attack in the spring. Examples of bud infections in which insects have been implicated to play a role include: bud-blast disease of rhododendron, caused by the fungus *Pycnostyamus azalea* and aided by the leafhopper *Graphocephala coccinea*; bud rot disease of carnations caused by the fungus *Fusarium poae* and aided by the mite *Siteroptes graminum*.

Several diseases of blossoms have been associated with insect vectors. In most cases, transmission of the fungus by the insect is related to the activities of the insect during pollination. Some of the better-known examples include:

Anther Smut of Carnations

This is caused by the fungus *Ustilago violacea*. In this disease, the pollen is replaced by the teliospores of the fungus but the petals remain unaffected and continue to attract insects. The visiting insects become smeared with the smut spores, which they transfer to previously healthy flowers.

Blossom Blight of Red Clover

This is caused by the fungus *Botrytis anthophila* and is transmitted primarily by pollinating bees.

Ergot of Cereals and Grasses

This is caused by the fungus *Claviceps purpurea*, which develops in the flowers and produces spores that are contained in a sweet and sticky substance. That substance is attractive to many insects, particularly flies and beetles. The insects feed on the spores and also become smeared with them externally and carry them, externally and through their feces, to healthy flowers. Although primary infections by the ergot fungus are primarily from ascospores produced by sclerotia overwintering on the ground and carried via air currents, insect transmission of conidia is important for secondary transmission of the disease and for transmission over long distances. Some beetles, however, feed on ergot sclerotia on the ground and may carry mycelium and ascospores on their bodies to healthy plants and through them may cause primary infections.

Anthracnose Disease of Musa Balsamiana

This is caused by the fungus *Gloeosporium musarum* and is transmitted by the hymenopterans *Polybia occidentalis*, *Synoeca surinama*, and *Trigona* sp. The fungus infects the floral parts of the plant but these are dropped while still producing conidia and sweet exudate. The insects are attracted to the exudate on the fallen flowers and there they become smeared with conidia, which they subsequently carry to healthy flowers, which the spores infect.

Flower Spot of Azalea

This is caused by the fungus *Ovulina azaleae* and is transmitted by several species of bees, thrips, and ants. The insects carry spores on their bodies and drop them off on healthy flowers they visit which, in addition, may injure directly and facilitate penetration and infection by the fungus.

Diseases of Fruit and Seeds in the Field

Fruits and seeds are the source of food and the breeding grounds of many insects. Insects puncture fruit and seeds to obtain food and to lay their eggs in them. Although insects often cause direct damage to fruits and seeds that make them unsalable, the damage increases manifold when the insects also carry to the fruits and seeds fungi that infect and cause these organs to rot or to develop other symptoms. Numerous examples of fruit-insect-pathogen interactions could be cited, although in many cases no hard data of such interactions exist. Some of the better-studied cases are described briefly below.

Rots of Fleshy Fruits

Fig Rots

Several kinds of fungi attack figs and cause rotting of fruits in the field. In most such cases, certain types of insects play a more or less important role in the transmission and introduction of the fungus into the fig.

Endosepsis of Figs

This is caused by the fungus *Fusarium moniliforme*, and results in the entire fruit content turning into a pulp. The fungus is transmitted from fruit to fruit by the fig wasp *Blastophaga psenes*, which also plays a crucial role in the pollination of figs. Fig trees, being dioecious, have male trees that produce staminate flowers around the opening and gall flowers in the cavity, and female trees that produce only pistilate flowers. The fig wasp lays its eggs in the ovules of the gall flowers of male plants, which are thereby stimulated to grow. The eggs hatch and the larvae parasitize the galls until they pupate. The adults emerge from the pupae and the females are fertilized while still in the male fig. When they come out of the fig, the females brush against the staminate flowers that surround the opening and become smeared with pollen. The female wasps carry the pollen to male and female flowers they subsequently visit for oviposition. In female flowers, however, because of the length of styles, oviposition fails but pollination is nevertheless successful and the fruit develop into edible figs. If, however, as the female wasp visits some infected figs it becomes smeared with spores of the fungus, it transmits the spores to male and female figs it visits, and the fungus then causes endosepsis of the female figs.

Souring of Figs

This is caused by yeast fungi that cause fermentation, and appears as discoloration and wateriness of the fig contents which then exude from the fig opening. Such figs shrivel, dry, and cling to the tree. The fermenting yeasts are transmitted to figs externally and internally on the bodies of the two most common visitors of figs still in the tree, the sap beetle *Carpophilus hemipterus* and the fruit fly *Drosophila melanogaster*.

Fig Smuts and Molds

These are caused by the black mycelium and spores of *Aspergillus niger* and the variously colored growths of other fungi. These fungi are carried into green figs on the bodies of predatory mites and, to a lesser extent, by thrips.

Brown Rot of Stone and Pome Fruits

This is caused by the three related fungi *Monilinia fructicola*, *M. fructigena*, and *M. laxa* and affects all the stone fruits and, to a lesser extent, the pome fruits. The fungi are aided in their penetration of the fruit by the feeding and oviposition wounds made by the insects plum curculio (*Conotrachelus nenuphar*) and the oriental fruit moth (*Grapholitha molesta*), and the feeding wounds of the dried fruit beetle (*Carpophilus hemipterus*) and two nitidulid beetles (*Carpophilus mutilatus* and *Haptonchus luteolus*). The insects also become smeared with spores of the brown rot fungi which they carry on their bodies and deposit at the wounds they make on the fruits they visit. In pome fruits, the fungus is facilitated in penetrating the fruit by the feeding holes made by the earwig *Forficula auricularia* at the beginning of ripening of the fruit, at which time they are susceptible to brown rot.

Gray Mold of Grapes

This is caused by the fungus *Botrytis cinerea*. The fungus spores are generally spread by air currents. Penetration of the grapes and shoots, however, seem to be increased by the wounds made on them by the larvae of the lepidopterans *Argyrotaenia pulchellana* and *Lobesia botrana*.

Black Pod of Cacao

This is caused by the fungus *Phytophthora palmivora* and results in devastating losses of yield. Insects of several different families play a role in the transmission of this disease. At least 10 species of ants, especially *Crematogaster striatula* and to a lesser extent *Camponotus acvapimensis* and *Pheidole megacephala*, appear to spread the fungus vertically within the tree, especially during the rainy season, when they carry spore-containing soil particles up the cacao tree for nesting purposes. Certain coleoptera, such as the nitidulid beetle *Brachypeplus pilosellus*, and certain dipterans, such as the fly *Chaetonarius latifemur*, colonize black pods in the field and may carry the fungus internally or externally on their bodies to healthy pods. Because of their large numbers on cocoa trees, their habit of visiting wounded pods, and their proven efficiency to transmit the fungus, these insects are considered the main vectors of the fungus locally and over long distance.

Boll Rots of Cotton

These are caused by several fungi including *Fusarium moniliforme*, *Alternaria tenuis*, *Aspergillus flavus*, and *Rhizopus nigricans*. Various insects are apparently involved in the transmission of these fungi and they seem to use different mechanisms of transmission. Thus, in boll rot due to *Fusarium* and *Alternaria*, the fungi penetrate cotton bolls through feeding and oviposition wounds made by the boll weevil (*Anthonomus grandis*), the cotton bollworm (*Heliothis zeae*), and the tarnished plant bug, *Lygus lineolaris*, or they are brought to and penetrate through the nectarines by nectar feeding flies such as *Drosophila* and cabbage looper, *Trichoplusia ni.* In boll rots caused by *Aspergillus flavus* and other aflatoxin-producing species, the fungus is primarily wind disseminated but is also carried internally and externally by insects, such as the lygus bug *Lygus hesperus* and the stink bug *Chlorochroa sayi*, that frequently visit cotton bolls. The latter fungus, however, seems to depend for entrance on the presence of large wounds like the large exit holes made by the mature larvae of the pink bollworm, *Pectinophora gossypiella*. On the other hand, boll rots by *Rhizopus stolonifer* occur when wounds made by the bollworm *Earias insulana* and by the pink bollworm are available. In the lint rot of cotton, caused by the fungus *Nigrospora oryzae*, the fungus is transmitted very efficiently by the mite *Siteroptes reniformis*. In Stigmatomycosis or internal boll disease, caused by the fungus *Nematospora gossypol*, the cotton fibers are stained in the absence of external symptoms. This disease is associated with the feeding of several species of plant bugs primarily of the genus *Dysdercus*, often referred to as cotton stainers. The insects carry the fungus spores externally on the mouthparts and internally in their deep stylet pouches and introduce it via their proboscis through the wall of young cotton bolls.

Coffee Bean Rot

This is caused by the related fungi *Nematospora corylii* and *N. gossypii*, which cause berries to turn black and subsequently to rot. The fungi are introduced into the berries through the feeding wounds made by the insects *Antestia lineaticolis* and *A. faceta*. The insects feed on small and large berries and if they carry the fungus the latter causes infection of the bean. The number of infected berries is proportional to the number of insects, approximately 300 insects per tree resulting in infection of all the berries on the tree.

Molds and Decays of Grains and Legumes

Numerous decays and molds affect the various grains and legumes while still in the field and their frequency and severity increase as the number of insects infesting the crops, and feeding on the seeds, increases. In corn, for example, seed rots can be caused by species of the fungi *Fusarium*, *Gibberella*, *Diplodia*, *Cephalosporium*, *Nigrospora*, *Physalospora*, *Cladosporium*, *Penicillium*, *Aspergillus*, *Rhizopus*, *Trichoderma*, and others. The insects most commonly involved in transmitting and facilitating infection of corn kernels by these fungi are the corn earworm, *Heliothis zea*, and the European corn borer, *Pyrausta nubilalis*, but other borers and other insects also play important roles as vectors and, most importantly, as facilitators of infection by these fungi by creating wounds that allow the fungus to enter the seed. In seed infections by *Aspergillus* and by *Fusarium* there is the added adverse effect of production of debilitating mycotoxins. Similar, although less studied situations have been reported for rice infections by fungi, e.g., *Nematospora corylii*, transmitted and facilitated by wounds made by the rice stinkbug *Oebalus pugnax*; wheat and corn infections by *Nigrospora* sp. and *Fusarium poae*, transmitted by large numbers of *Peliculopsis* mites feeding on and transporting spores of the fungus in their abdominal sacs; and in various legume infections by the fungi *Nematospora*, *Cladosporium*, *Aureobasidium*, etc., transmitted and facilitated in their penetration and infection of the seeds by the stinkbugs

Acrosternum hilare and *Thyanta custator*, the lygaeid *Spilostethus pandurus*, by thrips, aphids, and other insects.

Molds and Decays of Harvested Fruits and Seeds

Generally little is known definitively about the roles of specific insects on the transmission and facilitation of rots of specific fruits and vegetables, and of molds and decays of seeds of specific grains, legumes, or nuts by specific fungi. It is generally accepted, however, that postharvest infections of plant products are greatly increased in numbers and in severity if insects are also present in the same or adjacent containers. There is agreement that insects moving about among stored fruits, seeds, etc., transport externally and internally on their bodies spores of fungi infecting such fruits and seeds and deposit such spores on the next fruit or seed they feed on. There is also agreement that by creating feeding or oviposition wounds on harvested fruit and seeds, the insects create openings through which the fungi can penetrate and release sap and additional nutrients. The fungi then can grow and build momentum to eventually infect and rot the entire fruit or seed.

The fungi that cause most rots of fleshy fruits and vegetable after harvest include *Penicillium*, *Fusarium*, *Botrytis*, *Rhizopus*, *Alternaria*, *Sclerotinia*, *Monilinia*, and *Colletotrichum*, while the molds and decays of grains and legumes involve primarily *Aspergillus*, *Fusarium*, and *Penicillium*. The insects involved in transmission and facilitation of infection of fleshy organs after harvest include larvae and adults of various Lepidoptera such as the oriental fruit moth, *Grapholitha molesta*, Diptera such as the apple maggot, *Rhagoletis pomonella*, the Mediterranean fruit fly, *Ceratitis capitata*, the house fly, and others. The insects involved in the transmission and facilitation of infection by fungi causing molds and decays of grains and legumes are the larvae and adults of various Coleoptera such as the rice weevil *Sitophilus oryzae*, the granary weevil *Sitophilus granarius*, and the confused grain beetle, *Tribolium confusum*, and also Lepidoptera such as the Angoumois grain moth, *Sitotroga cerealella*, the European corn borer, *Pyrausta nubilalis*, the ear cornworm, *Heliothis zea*, and other insects.

Insect Transmission of Plant Pathogenic Nematodes

Two very serious plant diseases caused by nematodes of the genus *Bursaphelenchus* are transmitted by insects. In both diseases there is a symbiotic relationship between the fungal pathogen and the insect vector.

Pine Wilt

This is a lethal disease of many species of pines and other conifers. It is caused by the nematode *Bursaphelenchus xylophilus*, known as the pinewood nematode. The nematode is about 800 μm long by 22 μm in diameter and it develops and multiplies rapidly, each female laying about 80 eggs and completing a life cycle in as short as 4 days. The nematode produces the four juvenile stages and the adults. The juvenile stages develop in the resin canals of infected pine trees, feeding at first on plant cells and later on fungi that invade the dying or dead tree. Later, the nematode produces special fourth-stage dispersal juveniles that are adapted to survive in the respiratory system of the cerambycid beetles *Monochamus carolinensis* and *M. alternatus* by which they are transmitted to healthy pine trees.

The pinewood nematode overwinters in the wood of infected dead trees, which also contain larvae of the beetle vectors of the nematode. Early in the spring, the larvae dig small cavities in the wood in which they pupate. As the adult beetles emerge from the pupae later in the spring, large numbers of fourth-stage juvenile nematodes enter the beetles and almost fill the tracheae of the respiratory system of each insect with about 15,000–20,000 juveniles. These nematode-carrying adult beetles emerge and fly to young branch tips of healthy pine trees where they feed for several weeks. As the beetles strip the bark and reach the cambium, the nematode juveniles emerge from the insect and enter the pine tree through the wound. The juveniles in the tree then undergo the final molt and produce adult nematodes. The latter migrate to the resin canals, feed on their cells and cause their death, and then they move in the xylem and in the cortex where thy reproduce quickly and build enormous populations of nematodes and kill twigs, branches and entire trees.

After the adult *Monochamus* beetles, the vector of the pine wilt nematode, have fed on young twigs for about a month, they are ready to breed and look for stressed and dead pine trees, including trees showing symptoms or dying from infection by the pinewood nematode. The female beetles deposit their eggs under the bark of such trees where the first two instars develop and feed. The third instar penetrates the wood where it undergoes the next molt and produces the fourth instar, which overwinters there. In early spring, the fourth instar digs a cavity in the wood where it pupates and to which numerous third-stage nematode juveniles are attracted and congregate. The juvenile nematodes undergo the next molt and produce the fourth-stage dispersal juveniles, which by the thousands infect the tracheae of the adult insects as soon as they emerge from the pupae and are carried by them to healthy pine trees, thus completing the cycle.

Red Ring of Coconut Palms

This disease kills coconut palm trees from Mexico to Brazil and in the Caribbean islands. It is caused by the nematode *Bursaphelenchus cocophilus*, which is transmitted from palm to palm by the American palm weevil, *Rhynchophorus palmarum*, the sugarcane weevil, *Metamasius* sp., and probably other weevils. The nematodes infect, discolor, and kill the palm tissues in a ring 3–5 cm wide about 5 cm inside the stem periphery over the length of the stem.

The nematode pathogen lays its eggs and produces all its juvenile stages and the adults inside infected palm trees, completing a life cycle in about 9–10 days. Female weevil vectors are attracted to red ring-diseased trees but they also lay eggs on healthy or wounded palm trees. If the female carries red ring nematodes, it deposits them in its feeding wounds at bases of leaves or at internodes. The nematodes then enter the palm tissues and undergo repeated life cycles and spread intercellularly in the parenchyma cells of the petioles, stem, and roots, where the cells break down and form a flaky, orange to red discolored tissue with cavities. Red ring nematodes do not invade xylem and phloem tissues but cause tyloses to develop in xylem vessels within the red ring that block the upward movement of water and nutrients. In the meantime, the weevil larvae of the insect vector feed on the red ring tissue and swallow several hundred thousand nematode third-stage juveniles. Of these, however, only a few hundred of the nematodes survive and pass through the molt, internally or externally, to the next stage weevil larvae and to the adult weevil. As weevil females emerge from rotted palms, a small percentage of them carry with them third-stage juveniles of the nematodes. Nematode populations increase rapidly at first but later they decline and about 3–5 months after infection there are hardly any red ring nematodes or their eggs left in decomposed stem tissue of infected, dead palm trees. The nematodes, however, survive in newly infected palm trees and, briefly, in their insect vector.

Insect Transmission of Plant Pathogenic Protozoa

Three plant diseases: phloem necrosis of coffee, heartrot of coconut palms, and sudden wilt of oil palms, are caused by flagellate protozoa of the genus *Phytomonas*. In all three diseases, protozoa invade the phloem elements of infected plants and multiply in them, reaching populations of varying densities. Some of the sieve tubes become plugged by protozoa. Generally, the more severe the symptoms of infected plants, the higher the populations of protozoa in their phloem. The pathogen is transmitted from infected to healthy plants occasionally through natural root grafts, and primarily by stink bugs (Pentatomidae) such as the genera *Lincus* and *Oclenus*, and possibly others.

Insect Transmission of Plant Pathogenic Viruses

Plant viruses cause many and severe diseases of plants, their number and importance being second only to fungal diseases of plants. Most viruses infect their host plants systemically, that is, the virus multiplies internally throughout the plant. Almost all viruses enter and multiply in phloem and in parenchyma cells. Viruses do not produce spores, nor do they come to the surface of the plant. All plant viruses are transmitted to new plants that are propagated from infected plants vegetatively (that is, by grafting or budding, by cuttings, by bulbs, corms, roots, tubers, etc.), and many can be transmitted artificially by mechanical inoculation, that is, by rubbing sap from infected plants onto leaves of healthy plants. Some plant viruses can be transmitted from diseased to healthy plants by pollen or seed produced by infected plants, some by the parasitic higher plant dodder when it is infecting both virus-infected and healthy plants, and some plant viruses are transmitted from plant to plant by certain plant pathogenic fungi, nematodes, or certain mites. More than half of the plant viruses, numbering more than 400, are transmitted from diseased to healthy plants by insects.

The number of insect groups that are vectors of plant viruses is relatively small. The most important vector groups, with the number of vector species and viruses transmitted, are listed below. Hemiptera, which includes the aphids (Aphididae, 192 species, 275 viruses), leafhoppers (Cicadellidae, 49 species, 31 viruses), the planthoppers (Fulgoroidea, 28 species, 24 viruses), the whiteflies (Aleurodidae, 3 species, 43 viruses), the mealybugs (Pseudococcidae, 19 species, 10 viruses), and some treehoppers (Membracidae, 1 species, 1 virus), contain by far the largest number and the most important insect vectors of plant viruses, but the true bugs (Hemiptera, 4 species), the thrips (Thysanoptera, 10 species, 11 viruses) and the beetles (Coleoptera, 60 species, 42 viruses) also are implicated. Grasshoppers (Orthoptera, 27 species) seem to occasionally carry and transmit a few viruses. Unquestionably, the most important virus vectors are the aphids, leafhoppers, whiteflies, and thrips. These and the other groups of Hemiptera have piercing and sucking mouthparts, although several thrips have rasping, sucking ones. Beetles and grasshoppers have chewing mouthparts, but many beetles are quite effective vectors of certain viruses. Generally, viruses transmitted by one type of vector are not transmitted by any other type of vector.

Aphids and Aphid-Transmitted Viruses

Aphids have evolved as the most successful exploiters of plants as a food source, particularly in the temperate regions. Many species of aphids alternate between a primary and a secondary host, although there are many variations of aphid life cycles depending on the aphid species and on climate. Some aphids overwinter as parthenogenetic viviparous forms while others go through their life cycle on one host species or on several related species. On the other hand, there are several aphid species, such as *Myzus persicae*, that have as many as 50 primary and alternate species of host plants.

Aphids have mouthparts that consist of two pairs of flexible stylets held within a groove of the labium. During feeding, the stylets are extended from the labium and, through a drop of gelling saliva, the stylets rapidly penetrate the epidermis. Penetration may stop at the epidermis or it may continue into the middle layers of leaf cells with a sheath of saliva forming around the stylets. The stylets move between the cells until they reach and enter a phloem sieve tube from which the aphids obtain their food. Individual aphids vary in their ability to transmit the virus to individual plants. Infection of a plant with a virus often makes the plant more attractive for aphids to grow on and to reproduce. Both acquisition and transmission of virus by aphids are affected by temperature, humidity and light.

Virus–Vector Relationships

Insect vectors that have sucking mouthparts carry plant viruses on their stylets, and such viruses are known as stylet-borne, externally borne, or non-circulative, because they do not pass to the vector's interior. The remaining viruses are taken up internally within the vector and are called internally borne persistent circulative or persistent propagative viruses.

Stylet-Borne Non-Persistent Transmission

Most externally borne viruses can be transmitted in the typical stylet-borne non-persistent manner. In such a transmission the virus is assisted in its transmission by a specific configuration of its coat protein or by a non-structural virus-encoded protein. The insect acquires the virus from the plant by feeding on it for only seconds or, at most, minutes. The insect can transmit the virus immediately after the acquisition feeding, that is, without any incubation period required for transmission. The insect retains the virus and is usually able to transmit it for only a few minutes after it acquired it. Most of the nearly 300 known aphid-borne plant viruses are stylet-borne non-persistent. Some of the most important groups of plant viruses, such as those in the genera *Potyvirus*, *Cucumovirus*, *Alfamovirus*, and the *Caulimovirus* transmitted by *Myzus persicae* are stylet-borne non-persistent viruses. In the few seconds in which aphids acquire the virus, the aphid stylet usually penetrates only the epidermal cell. Actually, deeper penetration of the stylet into leaf tissues reduces the ability of aphids to transmit the virus. Aphids vary greatly in their ability to transmit viruses, each particular virus being transmitted by one or a few species of aphids. Sometimes, certain virus strains are transmitted by distinct aphid species. Also, even individual aphids in a population vary in their ability to transmit the same virus, some of them being incapable of transmitting the virus.

All non-persistently transmitted viruses have simple structures of elongated or isometric particles with the nucleic acid encapsidated by one or more kinds of coat proteins. In some viruses, the coat protein interacts directly with the binding site of virus retention in the aphid. In other viruses, the virus encodes a non-structural protein which interacts with the aphid-virus retention binding site and forms a bridge between the virus and the aphid stylet. However viruses are bound to the aphid stylet, there must also be a mechanism for release of the virus when the aphid feeds on the next plant. It appears that saliva alone may carry out this function.

Semi-Persistent Viruses

Some externally borne non-persistent viruses are known as semi-persistent because they reach but do not seem to go past the foregut of the vector; the vector must feed on an infected plant (acquisition period) for several minutes or hours before it can transmit the virus; and the vector can then retain (retention time) and transmit the virus to healthy plants for several hours. Semi-persistent viruses are also assisted in their transmission by a transmission helper protein or coat protein configuration. The best known semi-persistent viruses are caulimoviruses, which occur in most cell types, and the closteroviruses beet yellows virus and curly top virus, which are found primarily in phloem cells. In several of the semi-persistent viruses, a helper component seems to be involved in their transmission. In cauliflower mosaic virus, the helper component consists of two non-capsid proteins, one of which is associated with the virus particles and the other has two binding domains that interact strongly with microtubules. In some cases, certain viruses can be transmitted only in the presence of a second virus which acts as the helper virus.

Persistent Viruses

Internally borne viruses are either persistent circulative or persistent propagative. Persistent circulative viruses are acquired from the plant by the vector after an acquisition feeding period of several hours to several days, and then they are retained by the insect vector and can be transmitted by it for several days or weeks. Persistent circulative viruses require a latent period of several hours to several days beyond the acquisition time before they can be transmitted by the insect vector, they reach the hemolymph of the vector, and pass through the various stages of the insect, but not through the ovaries to the egg. Persistent propagative viruses are acquired by the insect after a feeding period of several hours to several days, are retained by the vector for several weeks to several months, they multiply in the vector, they have a latent period of a few to several weeks, and can pass through the various stages of the insect, including transovarial passage to the egg. Persistent viruses are generally transmitted by one or a few species of aphids and cause symptoms characterized by leaf yellowing and leaf rolling.

Persistent Circulative Viruses

These include primarily the luteoviruses, such as barley yellow dwarf virus, and the nanoviruses, such as banana bunchy top virus. The luteoviruses are acquired after a feeding period as short as 5 min but it usually takes 12 h. After an incubation period of an additional 12 h, the vector can transmit the virus within a 10–30 min inoculation feeding and can continue transmitting it for several days or a few weeks. In the vector, the virus particles seem to associate only with the hind gut of the aphid, entering its cells by endocytosis into coated pits and vesicles and accumulating in tubular vesicles and lysosomes. Virus particles are then released into the hemolymph by fusion of the vesicles with the plasmodesmata and enter the salivary glands of the aphid via invaginations with two plasma membranes on the hemocoel side of the salivary gland accessory cells. It appears that persistent circulative viruses do not require a non-capsid protein for helper component but they require a protein produced via a read-through of the coat protein stop code if they are to advance beyond the hemocoel. Some persistent circulative viruses also require a helper virus to be present for them to be transmitted by their aphid vector.

Persistent Propagative Viruses

Propagative viruses are transmitted primarily by leafhoppers and planthoppers but several members of the Rhabdoviridae multiply in and are transmitted by their aphid vector. These bacilliform viruses replicate in the nucleus and the cytoplasm of cells in the brain, salivary glands, ovaries, and muscle of the insect vector. The virus goes through the egg to about 1% of the nymphs. Infection of aphids with rhabdoviruses results in increased mortality of the aphids.

Leafhoppers and Planthoppers, and Transmission of Plant Viruses

Leafhoppers lay eggs that hatch to nymphs which pass through several molts before becoming adults. Some of them overwinter as eggs, some as adults, and some as immature forms. They all feed by sucking sap from phloem elements of plants. Their feeding behavior is similar to that of aphids in that the mouthparts, surrounded by the salivary sheath, penetrate the phloem of host plants.

Virus–Vector Relationships

All hopper-transmitted viruses are persistent circulative or persistent propagative, and are transmitted by only one or by a few closely related species of the hopper vectors. Only two of the 60 sub-families of leafhoppers (Cicadellidae) contain species that are vectors of viruses: the Agalliinae feed on herbaceous dicotyledonous hosts and the Deltocephalinae that feed on monocots. Of the 20 planthopper families (Fulgoroidea), only one, the Delphacidae, have species that are vectors of viruses all of which infect monocotyledonous plants and many of them cause severe diseases on cereal crops such as rice, wheat, and corn.

Semi-Persistent Transmission

Two viruses, maize chlorotic dwarf virus (MCDV) and rice tungro spherical virus (RTSV), are acquired by their vectors (*Graminella nigrifrons* and *Nephotettix virescens*, respectively) from their hosts within about 15 min and are retained by their vectors for one to a few days. MCDV particles have been seen in the foregut and a few other tissues but not beyond. Hoppers egest material from the foregut once in a while during feeding and it is thought that transmission occurs during this ingestion-egestion process.

Persistent Transmission

This involves the internal movement of the virus obtained from the plant to the salivary glands of the insect vector. Some of these viruses are circulative while others are propagative.

Circulative Viruses

Only two genera of geminiviruses (*Mastrevirus* and *Curtovirus*) are transmitted by leafhoppers in the persistent circular manner. The viruses are acquired by the vector after feeding for a few seconds to an hour. There is a latent period of about a day, presumably for the virus to reach the salivary glands. The internal movement of these viruses is determined by the viral coat protein and by receptor-mediated endocytosis.

Propagative Viruses

There are four families and genera of plant viruses that replicate within the cells of their insect vectors as well as the cells of their host plants. Two of these families, Rhabdoviridae and Reoviridae, contain viruses that infect animals, and their virus members that infect plants have been considered as animal viruses that infect plants. The propagative viruses have a latent period of about 2 weeks. During this period the virus replicates and invades most tissues of the insect vector. When the virus reaches the salivary glands of the vector, the latter can transmit the virus to new plants and can continue to transmit it for the rest of their life. Only a small percentage of the hoppers feeding on infected plants become vectors and of these only about 1% pass the virus through their eggs to the next generation. Various capsid proteins seem to be necessary for passage of viruses through the organs of the vector and are required for transmission.

The two genera that have propagative viruses are Tenuivirus, members of which are transmitted by delphacid planthoppers, and Marafivirus, which is vectored by the leafhopper *Dalbulus maydis*. These viruses have an acquisition feeding period of 15 min to 4 h, a latent period of 4–31 days, inoculation periods as short as 30 s, and can transmit the virus for as long as they live. Almost all of these viruses are transmitted transovarially to the egg.

Whitefly Transmission of Plant Viruses

Whiteflies transmit the viruses in the genus *Begomovirus* of the family Geminiviridae, and all the viruses in the genus *Crinivirus* and some in the genus *Closterovirus* of the family Closteroviridae. Whitefly adults are winged but only the first instar among the larvae is mobile. Whiteflies produce many generations in a year and reach high populations. Only a few species of whiteflies transmit viruses, mostly in the tropics and subtropics, but the viruses they transmit cause very severe diseases. Begomoviruses are transmitted by *Bemisia tabaci* whiteflies, while the criniviruses and the whitefly-transmitted closteroviruses are vectored by the whiteflies *Trialeuroides vaporariorum*, *T. abutilonea*, *B. tabaci*, and the type B of *B. tabaci* (also referred to as *B. argentifolii*). Whitefly mouthparts and feeding behavior resemble those of aphids.

Begomoviruses are bipartite geminiviruses and are transmitted by whiteflies in the persistent circulative manner. A helper factor coded by the virus seems to be involved in the transmission. The whitefly-transmitted monopartite closteroviruses and the bipartite criniviruses reach only the foregut of the vector and are transmitted in the semi-persistent manner. These viruses are retained in the vector for about 3–9 days. Two capsid proteins help the virus in its transmission by the vector.

Thrips Transmission of Plant Viruses

About 10 species of thrips of the family Thripidae are the vectors of about a dozen viruses belonging to four genera (*Carmovirus*, *Ilarvirus*, *Sobemovirus*, and *Tospovirus*) of four families. Thrips are polyphagous insects that have many hosts. Some of the vector species reproduce mainly parthenogenetically. The larvae are rather inactive but the adults have wings and are very active. Thrips adults feed by sucking the contents of subepidermal cells. Adults live up to 3 weeks and there may be as many as 20 generations per year. The tospoviruses are transmitted in the persistent propagative manner, while the viruses of the other genera are transmitted in the pollen carried by the thrips vectors and by mechanical damage during feeding of the vector.

By far the most important thrips-transmitted viruses are the tospoviruses, which include the widespread and severe tomato spotted wilt virus and the impatience necrotic spot virus. In tospoviruses, only the larvae but not the adults can acquire the virus, and their ability to acquire it decreases with age. Larvae sometimes acquire the virus after feeding on a diseased plant for as little as 5 min, but usually they must feed for more than an hour both in acquiring and in inoculating the virus. There is a latent period of 3–4 days before the larvae can transmit the virus. The virus is passed from the larvae to the adults which can transmit it, although erratically, for as long as they live. These viruses appear to multiply in the vector but are not passed through the egg. Several structural proteins of the virus seam to be associated with the acquisition, passage through, and inoculation of the virus by its larval and adult insect vector.

Mealybug and Other Bug Transmission of Plant Viruses

Mealybugs are important as virus vectors primarily on some perennial plants in the tropics and subtropics. They move slowly on plants and therefore are not as efficient virus vectors as those discussed previously. They move from plant to plant, mostly as crawling nymphs, through leaves of adjacent plants being in contact with each other; by ants tending the mealybugs and moving them from one plant to the other; and occasionally by wind.

Mealybugs feed on the phloem and they are vectors of the badnaviruses, such as the cacao swollen shoot virus (CSSV), several closteroviruses, such as grapevine leafroll associated viruses and the pineapple mealybug wilt associated virus, and the trichoviruses, such as grape viruses

A and B. Mealybugs acquire the viruses after feeding on diseased plants for only a few, about 20 min and retain the virus for a few, up to 24 h, so the transmission resembles the non-persistent or semi-persistent mechanism of transmission by aphids.

Other bugs that transmit plant viruses include the mirid bugs, which transmit some sobemoviruses in manners that have characteristics of non-persistent, semi-persistent, and beetle-like transmission, and the piesmatid bugs, which transmit beet leaf curl virus in a persistent propagative manner.

Virus Transmission by Insects That Have Biting/Chewing Mouthparts

Although there are a few vectors in the orders Orthoptera and Dermaptera, there are more than 60 vector species in the order Coleoptera (beetles), 30 of them in the family Chrysomelidae. Most beetle vectors tend to eat plant cells between the leaf veins and regurgitate during feeding, thereby bathing their mouthparts with sap and virus. Virus transmission by beetles, however, is specific between each virus and its vector. Beetle-transmitted viruses belong to the genera *Tymovirus*, *Comovirus*, *Bromovirus*, and *Sobemovirus*. Most of these viruses are small (25–30 nm in diameter), stable, reach high concentrations, and are easily transmitted by sap. These viruses can also be translocated through the xylem of the plant. Beetles can acquire and can transmit the virus after feeding for a few seconds and they can retain the virus from 1 to 10 days.

Virus Transmission by Mites

Several members of the mite family Eriophyidae transmit viruses of the genus *Rymovirus* which cause many serious diseases in grain crops. Two mite species of the family Tetranychidae transmit two plant viruses, one of them transmitting the peach mosaic virus. All mites in these families feed by piercing plant cells and sucking their contents.

Eriophyid mites are small (0.2 mm long), move little by themselves and, instead, they are spread by wind. They have two nymphal instars followed by a resting pseudopupa. They complete a life cycle within 2 weeks. Mites can acquire virus from infected host plants within 15 min from the start of feeding and can transmit it to healthy plant within a similar duration. Mites acquire the virus as nymphs but not as adults. They carry the virus through molts and remain infective for 6–9 days.

Tetranychid mites are larger (0.8 mm long). Pre-adult mites readily acquire the virus and they, as well as the adults, transmit the virus efficiently.

Virus Transmission by Pollinating Insects

Honey bees and other pollinating insects seem to play a role in distributing virus-infected pollen from infected plants to healthy ones. It appears, however, that no special mechanisms or involvement of the insect are present in such virus transmission.

Summary

Insects play various roles in the transmission of plant pathogens, and in the initiation and development of disease in plants. In some diseases, the insects incidentally carry pathogens on their bodies or in their feces and deposit them on healthy plants where they cause disease, without developing any special relationships with the pathogens. In several cases, the insects weaken the plants on which they feed and make them much more susceptible to attack by pathogens. In other cases, the pathogens depend on the insects to carry them to healthy plants and to deposit them on fresh wounds through which they penetrate and infect the plants. While pathogens seem to be the beneficiaries of these actions, insects also derive advantages by the pathogen making the diseased plant more attractive to the insect for feeding or breeding purposes, and in some cases, by the insect feeding on the

pathogen growing in the cavities made by its insect vector. Also, while in most cases the pathogen does not affect its insect vector directly, there are several plant viruses and mollicutes that multiply in the insect vector as well as in their plant host, and such vector insects often show histopathological symptoms, reduced reproduction, and shorter life span. Most of the insect/pathogen associations are highly specific and involve sophisticated molecular mechanisms that regulate the uptake, retention, and transmission of the pathogen by its insect vector.

► Plant Viruses and Insects
► Management of Insect-Vectored Pathogens of Plants
► Transmission of *Xylella fastidiosa* Bateria by Xylem-Feeding Insects
► Vectors of Phytoplasmas

References

Agrios GN (1997) Plant pathology, 4th edn. Academic, San Diego
Anonymous. Compendium of Diseases of…A series of books on diseases of individual crops published periodically by APS, St. Paul, MN
Capinera JL (2001) Handbook of vegetable pests. Academic, San Diego
Hull R (2001) Matthews' plant virology, 4th edn. Academic, San Diego
Harris KF, Maramorosch K (1980) Vectors of plant pathogens. Academic, San Diego
Hiruki C (ed) (1988) Tree mycoplasmas and mycoplasma diseases. University of Alberta Press, Edmonton
Nault LR (1997) Arthropod transmission of plant viruses: a new synthesis. Ann Entomol Soc Am 90:521–541
Schowalter TD, Filip GM (eds) (1993) Beetle-pathogen interactions in conifer forests. Academic, San Diego

Transmission of *Xylella fastidiosa* Bacteria by Xylem-Feeding Insects

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Insects that feed predominantly on the sap of plants' water-conducting systems (xylem) can transmit bacteria that are specific parasites of the plant xylem. Most xylem sap-feeders are spittlebugs (families Cercopidae and Machaerotidae) or sharpshooters (subfamily Cicadellinae) belonging to the leafhopper family (Cicadellidae) in the order Hemiptera (Fig. 96). Xylem sap is extremely low in nutrition, and xylem sap-feeders have the highest feeding rates of any terrestrial animals, consuming up to 1,000 times their body weight per day.

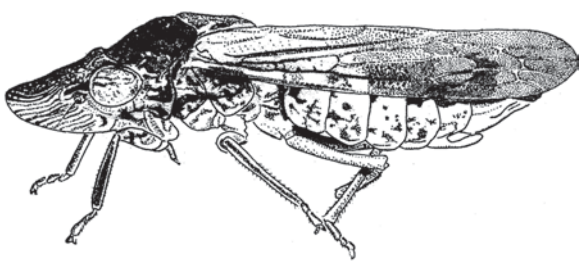
The best known xylem-limited bacterium that causes plant diseases is *Xylella fastidiosa*. Various strains of *X. fastidiosa* cause disease in grape, peach, almond, orange, alfalfa, and numerous tree species (Table 14). The bacteria and associated gums plug the xylem system, leading to discoloration and killing or stunting of leaves and fruits. Pierce's disease of grape, phony disease of peach, and citrus variegated chlorosis are among the best known and most economically damaging of these diseases. For example, Pierce's disease is so severe and widespread in the southeastern United States that it has prevented commercial viticulture there using susceptible European grapes. Less appreciated, but economically and ecologically important, are the numerous and more widespread leaf scorch diseases caused by *X. fastidiosa* in numerous forest trees such as oak, sycamore, maple, and elm. This bacterial species has an enormously wide range of plant species – about 75–90% of all plant species tested – in which it can multiply, but it causes symptoms in relatively few. Except for a leaf scorch disease of pear in Taiwan, these diseases appear to be limited to the Americas. However, in 1996, Pierce's disease was confirmed to occur in southeastern Europe. Numerous other bacterial pathogens invade the xylem system, but not exclusively. The widespread *Leifsonia (Clavibacter) xyli*, a xylem-limited bacterium that causes ratoon stunt disease of sugar cane, is not transmitted by insects.

The great majority of insect species that are xylem sap-feeding specialists that have been tested as vectors (transmitters) of *X. fastidiosa* have been shown to be able to transmit this bacterium to plants. Only a small fraction of the species that are xylem sap-feeding specialists have been tested as

Transmission of *Xylella fastidiosa* Bacteria by Xylem-Feeding Insects, Table 14 Examples of plant diseases caused by strains of the bacterium *Xylella fastidiosa*

Crop	Disease	Where found
Grape (*Vitis vinifera* and other *Vitis* species)	Pierce's disease	Southern North America, Central America (northern South America?)
Citrus	Variegated chlorosis	South America
Peach	Phony disease (dwarfing)	Southeastern United States
Oak, sycamore, elm, others	Leaf scorch diseases	Southeastern United States
Pear	Leaf scorch	Taiwan
Alfalfa	Dwarf	California, probably other locations in North and Central America
Coffee	Leaf scorch	South America, possibly Central America

See Purcell (1997) for a more complete list



Transmission of *Xylella fastidiosa* Bacteria by Xylem-Feeding Insects, Figure 96 The glassy-winged sharpshooter (*Homalodisca coagulata*) a vector of the xylem-limited bacterium *Xylella fastidiosa*. Drawing by and with permission of Rosser Garrison.

vectors, so several thousand species are probably vectors of *X. fastidiosa*. This broad degree of vector specificity, as well as other characteristics of vector transmission point to the method by which insects transmit the bacterium. There is no time delay (latent period) between a vector's acquiring the bacterium by feeding on infected plants and its introducing the bacterium to other plants. Once infective, a vector can transmit for the rest of its life, but immature vectors lose the ability to transmit when they shed their skin. All of these characteristics can be best explained if the bacteria are transmitted from the foregut of the vector. The exact location in the foregut from which the bacteria are transmitted is not yet known. The lack of a latent period and the persistence of infectivity in vectors makes control of diseases caused by *X. fastidiosa* especially difficult. Because a few infective insects can quickly transmit the bacterium to susceptible plants, insecticides to kill vectors within vineyards has not proven to be effective.

References

Goodwin P, Purcell AH (1992) Pierce's disease. In: Grape pest management, 2nd edn. University of California, Division of Agriculture and Natural Resources, Oakland, pp 76–84

Purcell AH (1989) Homopteran transmission of xylem-inhabiting bacteria. In: Harris KF (ed) Advances in disease vector research, vol. 6. Springer, Berlin Heidelberg New York, pp 243–266

Purcell AH (1997) *Xylella fastidiosa*, a regional problem or global threat? J Plant Pathol 79:99–105

Purcell AH, Finlay AH, McClean DL (1979) Pierce's disease bacterium: mechanism of transmission by leafhopper vectors. Science 206:839–841

Purcell AH, Hopkins DL (1996) Fastidious xylem-limited bacterial plant pathogens. Annu Rev Phytopathol 34:131–151

Raven JA (1984) Phytophages of xylem and phloem: a comparison of animal and plant sap-feeders. Adv Ecol Res 13:135–234

Transmission Threshold

The level of abundance of a parasite, or the abundance of its vector, that is necessary for disease to spread.

Transovarial Transmission

Passage of a material through the ovariole and within the egg.

Transovum Transmission

Passage of a material on the surface of the egg.

Transpiration

The evaporation of water from the surface of plant foliage.

Transposable Element

An element that can move from one site to another in the genome. Transposable elements have been divided into two classes, those that transpose with an RNA intermediate, and those that transpose as DNA.

Transposon

A transposable element carrying several genes including at least one coding for a transposase enzyme. Many elements are flanked by inverted repeats. *Drosophila melanogaster* contains multiple copies of 50–100 different kinds of transposons.

Transstadial Transmission

The transmission of pathogens or parasites through successive stages of the host's life cycle, as from the egg to the larva, pupa and adult.

Trap Crop

A crop or portion of a crop that is intended to lure insects away from the main crop.

► Cover, Border and Trap Crops for Insect and Disease Management

Traps for Capturing Insects

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Traps developed for capturing insects are as varied as the purpose for the trapping, the insects targeted, and the habitats in which they are used. Traps are used for general survey of insect diversity, and these usually are simple interception devices that capture insects moving through an area. Traps also are used for detection of new invasions of insect pests in time and/or space, for delimitation of area of infestation, and for monitoring population levels of established pests. This information is used to make decisions on the initiation of control measures or to measure effectiveness of a pest management program. Traps may be used as direct control measures, for example, by mass trapping (use of a high density of traps throughout the infested area) or by perimeter trapping (use of traps as a barrier around a pest-free area to intercept insects moving into the area) to remove a large number of individuals, with the goal of preventing or suppressing population buildup. Traps can be used as direct control measures if they are highly effective, if they capture a high percentage of females (especially if they capture them before they have a chance to lay eggs), and if they are integrated with other pest management approaches. Factors such as cost per trap, the need to service the traps frequently and the high reproductive rate of individuals that escape capture, however, prevent widespread use of traps as a stand-alone pest control measure (Figs. 97 and 98).

Traps for specific insect species or pest groups may use combinations of cues to lure the target insect and exploit aspects of the insect's behavior to facilitate movement of insects into the trap. Several factors influence the effectiveness of a specific trap. The ability of the trap to mimic and present those cues to the insect, the strength of those cues in influencing the insect's behavior, and the proper placement of the trap in the habitat are important.

Following is an overview of the basic trap types, and variations of those basic trap types for specific uses. Traps may be used with or without attractant cues, and may use a combination of cues, including visual (color, light, shape), chemical (food/host, pheromone, parapheromone, oviposition) and acoustic stimuli to make them more specific and/or more effective. Automated monitoring systems exist that will transmit information on trap capture to an offsite station. Insect traps are an important part of insect pest management programs. Although a number of trapping systems are discussed, the intent is to provide a general framework of types of traps that are used with some representative examples. It is not intended to be a complete listing of all traps that have been developed or are in use. Representative literature is presented at the end of the section that will provide additional information on insect traps and specific uses.

Trap Types

There are a few basic designs that describe almost all insect traps. They may be a surface that is presented flat or is formed into baffles or cylinders; containers with holes on the sides, top or bottom; and funnels leading up or placed over the container to hold captured insects. However, different types of traps are used for insects moving through air (that is, flying or wind-borne insects), ground-dwelling or walking insects, subterranean insects, or aquatic insects. A number of these are described below.

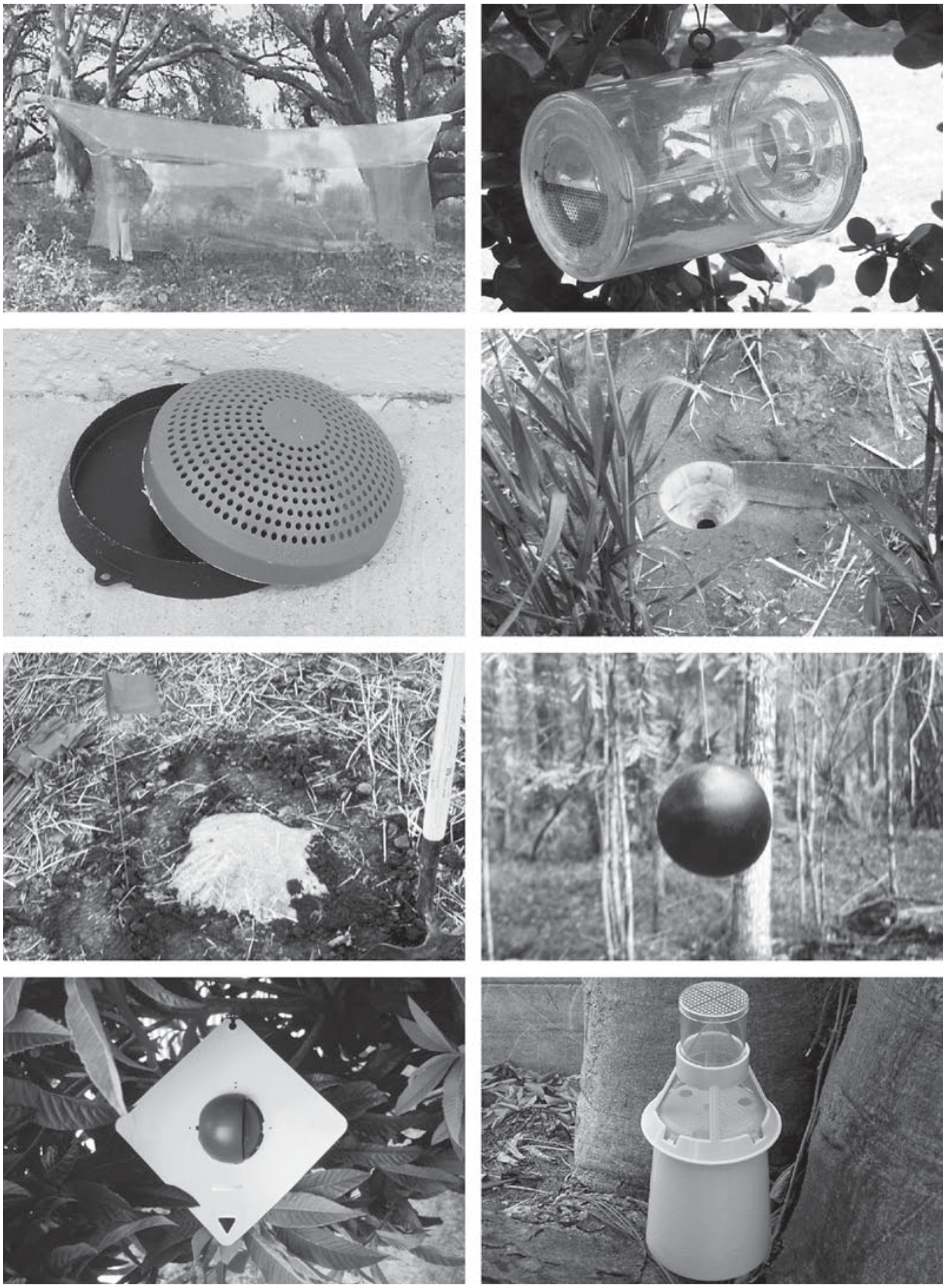
Traps for Flying Insects and Wind-Blown Insects

Interception Traps

Interception traps are commonly used for faunal surveys in ecological studies, although they can also have pest management applications. In its simplest form, it is a suspended net with an invagination along the top that leads to a collecting tube. The Malaise trap is an example of an interception trap. Fixed interception traps have been used to study insect migration, with separate collecting tubes for north-bound versus south-bound insects. Or, the trap may be used with a wind vane attachment so that the flat surface of the net swivels to face into the wind. Large, funnel-shaped nets have been mounted on moving trucks for sampling flying insects such as biting midges (Ceratopogonidae) or attached to a suction device to sample Russian wheat aphids, *Diuraphis noxia* (Mordvilko).

Sticky Traps

Panels, cylinders or spheres covered with sticky material are probably the most commonly used traps for faunal surveys in agricultural studies. In the simplest form, they may be clear panels that are coated with a material that will retain insects that are blown onto the panel or fly into it. Panels may also be used with a color and/or a shape and a chemical attractant. Very small insects will be retained by a thin coating of motor oil, but larger insects may escape this substance. To capture both small and



Traps for Capturing Insects, Figure 97 **Some insect traps: *top left*, Malaise trap, an interception trap for capture of flying insects; *top right*, Steiner trap, a lure-based trap used for capturing fruit flies; *second row left*, PC floor trap, a lure-based trap for stored product insects; *second row right*, pitfall trap for capture of insects walking on the soil surface; *third row left*, solar bait station for early detection of wireworms; *third row right*, suspended black ball coated with adhesive for capture of tabanid flies; *bottom left*, red sphere on yellow panel coated with adhesive for detection of apple maggot flies; *bottom right*, boll weevil trap.**

Traps for Capturing Insects, Figure 98 **Additional insect traps: *top left*, grain probe traps for detection of stored grain insects; *top right*, blacklight trap for detection of nocturnal flying insects; *second row left*, wing trap, a lure-based trap with a sticky interior for sampling flying insects; *second row right*, wasp trap, a food lure-based trap; *third row left*, unitrap, a popular pheromone-based trap for capture of moths; *third row right*, a bucket trap baited with pineapple and pheromone for capture of palm-infesting weevils; *bottom left*, a cylindrical yellow panel coated with adhesive for detection of flying insects; *bottom second from left*, New Jersey light trap for capturing mosquitoes; *bottom third from left*, mosquito emergence trap; *bottom right*, McPhail trap, a food lure-based trap for capture of fruit flies.**

large insects, sticky material such as Tangle-trap is applied to the surface. The traps can be serviced by using a small tool to scoop insects of interest off the trap and onto a card, or the entire trap can be replaced. For transport, the panel with sticky material can be covered with clear plastic wrap or the panel can be placed in a box with spacers to keep panels from touching other surfaces. To reuse the trap, a paint scraper or thinner can be used to remove sticky material from the surface so that new material can be applied. The advantage of this trap is that it is inexpensive and will capture a variety of insects that are moving through the area. The surface area and trap orientation can be increased by using two panels that are crossed into baffles. The primary disadvantage is the trap can be very messy, can become coated with dirt or debris and will no longer capture insects, and the sticky material is difficult to remove from the captured insects. These traps, as well as other traps for flying insects described below, are usually placed above the ground at the height of the vegetative growth. When used in row crops, the traps usually are attached to a wooden or metal stake, and the traps are moved higher as the plants grow over the season. When used in trees, traps are normally hung within the canopy. Trap placement and orientation within the canopy, as well as amount of vegetation near the trap, will vary among the trap types and target species.

Three-Dimensional Triangular Traps, Diamond Traps and Wing Traps

This group is another set of fairly inexpensive traps that are used with an attractant. These are basically sticky traps with the sticky surface protected on the interior of the trap and are either disposable or used with a sticky component that is replaced at servicing. Delta traps are small and light-weight triangular (tent-shaped) traps that are easy to hang in trees and to transport. The Jackson trap is a delta trap used for a number of tropical tephritid fruit flies. It has a removable base coated with sticky material that can be replaced at time of sampling. Diamond-shaped (in profile) traps are used to monitor indoor pests in public areas, such as stores and supermarkets. Wing traps composed of a roof and a floor are used for pest Lepidoptera. These are larger and more cumbersome than delta traps, but the larger surface is more suitable for larger pest moths. Because the sticky surface is enclosed, these traps are less susceptible to dirt and dust and capture fewer non-target insects than sticky traps, but the surface still may be coated with dust or debris that gets blown into the trap.

Water Pan Traps

A simple collection method for aphids and other small flying insects is a water pan trap. Insects flying over the trap are attracted to the reflective surface of the water and are captured. The traps are made from rectangular baking pans, storage containers, or dish-washing pans partially filled with aqueous solutions of soap or car antifreeze. Care should be used in selecting soap to be used so that it does not contain odors that may be repellent to target insects or that the antifreeze is environmentally safe. (Most antifreeze solutions are poisonous, and traps containing antifreeze should be placed so that animals are unable to gain access to them.) These traps are open containers, so there may be problems with movement in wind, evaporation during dry periods or overflowing during periods of heavy rain.

Bucket Traps

Another simple and inexpensive trap is a bucket trap. The bucket trap may be used without a lid, or as a closed container with holes on either the top or sides for insects to enter. Small drainage holes may be placed near the bottom of the trap to allow trapped water to drain out. The Nadel trap and Mission trap are examples of bucket traps that are translucent closed containers with entrance holes around the periphery. The corn rootworm trap has a large dome-shaped top and a gap between the top and the container. Size of the container and placement, diameter and number of entry holes is dictated by the targeted insect. These usually are used with a chemical lure of some type. These may be used without a killing agent so that live insects can be recovered, however captured insects may escape through the entrance openings. A variety of retention devices can be used with bucket-type traps. A pesticide such as dimethyl 2,2-dichlorovinyl phosphate (DDVP, mothballs) can be used inside, but if the concentration is too high it may prevent insects from entering. Aqueous solutions of soap or car antifreeze or surfactants such as triton may also be used. Again, care should be used in selecting soap that does not contain odors that may repel target insects and/or environmentally safe antifreeze should be used. Sticky material may also be used on either the interior or exterior surface. When used on the exterior, this may increase effectiveness of lure-baited traps because usually only a proportion of the insects attracted to the trap will proceed to enter the trap. However, the same problems outlined above for sticky panels will apply to sticky-coated bucket traps. Open-bottom cylindrical traps are essentially bucket traps used upside down. The Phase 4 trap is a green cylinder that uses a yellow panel as a sticky insert to retain captured insects. Clear versions of the trap have also been used. In addition to the opening on the bottom of the trap, entrance openings also are located around the periphery of the cylinder.

Bucket Traps with Funnels

Probably the most common traps for agricultural use are combinations of bucket traps with funnels. They are more costly than simple bucket traps and they are often used with some type of odor attractant. The funnel essentially provides an enlarged hole that directs movement of the attracted insect into the bucket. There are differences among this group of traps in orientation of the funnel and size of the funnel in relation to size of the bucket. The Steiner trap is a clear plastic horizontally oriented cylinder with small funnels centered on the flat sides of the cylinder. For insects that approach from the underside of the trap and move upward, the funnel is used with the large opening facing downward and the small opening leading up into a bucket or other container. Because it is difficult for the insect to find the top of the funnel for exiting, and these insects tend to move upward, they can be used with or without a pesticide or liquid to retain the insects. A well-known example of the downward facing trap is the McPhail trap, which is a bell-shaped invaginated trap that is used for tephritid and drosophilid fruit flies. The original trap was made from glass and there are several plastic versions of McPhail-type traps available including dome fruit fly traps, International Pheromones McPhail traps and Multilure traps available that typically have a clear top and a yellow base. Another example is a wasp trap, such as the Victor yellowjacket trap. This trap has holes around the sides of the base for wasps to enter, and then a funnel that leads to a separate upper container that retains the wasps.

Other insects approach from the top and either move or fall downward. For these insects, bucket traps with funnels that have the large opening facing upward and the small opening leading down into the bucket are appropriate. The universal moth trap (unitrap) and Multipher trap are examples of this trap and they commonly are used for Lepidoptera adults. These traps have lids held above the funnel opening to shelter the contents from rain and are available in a variety of colors. A trap developed for the Japanese beetle, *Popillia japonica* Newman, uses a funnel with the large opening facing upward and the small opening over a container, but the funnel is topped by two panels crossed to form a baffle. Insects are intercepted by the baffles, fall into the funnel and are captured in the container. The boll weevil trap is a version of a bucket trap that contains a funnel mounted on a cylinder. Insects land on the cylinder and move up the sides of the trap, enter the funnel and move into the small collection bucket above the small funnel top. The Lindgren funnel trap consists of 4, 8 or 12 plastic funnels stacked vertically over the container. It is used for ambrosia beetles and bark beetles. Fast-flying beetles hit a funnel and are deflected down into the collection container.

Cone Traps

Cone traps are essentially bucket traps with funnels, but the funnel is very large in relation to the size of the bucket or collecting tube. These are used with the large opening of the funnel oriented toward the ground and the top of the funnel leading up to a container. Examples of these traps include *Heliothis* traps and butterfly bait traps. These traps are made from a light cloth or mesh material and the design takes advantage of the moth or butterfly's tendency to move upward. The butterfly bait traps have a large container for the butterfly to move into so that the insect is undamaged.

Traps for Walking Arthropods and Soil-Dwelling Insects

Pitfall Traps

Pitfall traps are useful for collecting insects and other arthropods that are walking across a surface. This surface is usually a soil surface, for capturing beetles, spiders and other ground-dwelling organisms, although they also may catch flying insects that are walking across the soil surface. Pitfall traps placed into the top of stored grain also have been used to sample stored product insects. Pitfall traps consist of a container that is buried in the substrate, and into which insects and arthropods fall and are captured. The traps used in soil consist of an upper funnel, a collecting container, and perhaps a liner that makes servicing easier. Upper funnels can be made from disposable plastic funnels with the bottoms removed to enlarge the hole. Collecting containers can be made from plastic cups, and can be designed for dry catches with screens in the bottom to permit rain water to flow through, or can be made to hold a glycol (antifreeze)/water/detergent solution. Dry containers need to be serviced several times a week to minimize destruction of the sampled insects from other insects entering the trap. They have the advantage of providing live specimens for further studies. Wet containers can be serviced at longer intervals, but have the disadvantage of filling with rain water. Traps should be designed to produce minimal impact on the nearby soil, because insects may be repelled or attracted to the disturbance. To do this, holes can initially be cut with golf-hole cutters and lined with 4″diameter polyvinylchloride (PVC) pipe. The top of the pipe should be carefully leveled with the soil, and the traps serviced without disturbing the soil. Covers can be installed over the top to prevent rainfall from entering. Enhancement-fences or guides can be installed to guide insects to the trap. A cone with a gradual slope and smooth edge is necessary because insects may back away from the void of a direct hole. Captured insects should be removed at least weekly (wet) or twice weekly (dry).

Grain Probe Traps

Grain probe traps are a special modification of a pitfall trap for use in stored grain. Grain probe traps consist of an elongated cylinder with holes drilled into the sides that are above a funnel and insect receptacle. An early version of the trap was machined from solid brass and included a hollow cylinder made from 14 gauge brass sheet. Subsequently, probe traps have been made from clear polycarbonate (Lexan) plastic and from a perforated section of tubular polyethylene. The receptacle is coated with liquid Teflon (polytetrafluoroethylene) to prevent captured insects from escaping, however, insects remain alive for a while and may damage previously captured insects. These traps may be used at any depth within the grain mass, with long rods used to push the traps into place. A rope connected to the trap is affixed to the roof of the grain bin to allow removal of the grain probe trap and to prevent loss of the trap during grain bin filling and emptying operations. Traps should be inspected at 1–2 week intervals to remove the trapped insects. The PC trap is a cone-shaped trap that usually is used on grain mass surface, although it too can be pushed into the grain mass as long as it remains in an upright position. The top is covered by a convex lid that is covered with concentric circles of small holes to allow insects to enter the trap. When used at the grain surface, the traps are easy to remove for servicing, but webbing produced by larvae of lepidopteran grain pests, such as the Indianmeal moth, may block the openings into the trap and render them ineffective.

Shelter Traps

Shelter traps are used for insects that prefer a dark harborage and are useful in areas where it is preferred that the trap be inconspicuous. These are usually used to intercept insects as they walk over a surface and have small openings that encourage insects to enter the trap. Roach motels are the most well-known examples of such traps. They usually have a sticky material inside to trap insects that have entered or contain an oil or other substance to retain attracted insects. Shelter traps are used for stored product insects, and designs include dome traps, stealth traps and corner traps. The PC floor trap has been modified from the PC trap for use as a shelter trap by replacing the cone-shaped bottom with a flat container, which allows the trap to be placed on the ground or hung on a wall. Swarm traps are shelter traps that are used to capture unwanted swarms of domestic honey bees and to detect invading swarms of Africanized honey bees. These traps are fairly large bucket-shaped traps made of molded fiber material, have a single entrance hole, and are hung at least one meter above the ground. They provide a nesting site for bees, and the captured bees can be kept alive and moved to standard bee hives for honey production or pest bees can be identified and destroyed.

Emergence Traps

Emergence traps are a type of cone trap used for capturing adults that have subterranean larval and/or pupal stages. These traps are made from aluminum screening shaped into a funnel, with the top opening leading to a collecting tube or vial. The trap is placed flush with the ground and soil is pushed up around the edges to seal the trap to the ground. Adults emerging from below-ground stages move up into the trap and are captured in the collecting tube. The number of insects per unit area can be determined and the source of infestations can be identified. However, these traps may interfere with ground maintenance activities that prevent use in certain situations. Circle traps are another type of emergence trap. They are wire cone traps that are attached to the trunk or branch of a tree. Insects moving up a tree are captured, and because the traps are off of the ground, they do not interfere with ground maintenance activities.

Solar Bait Stations

The above traps can be used to capture the above-ground stages of subterranean insects, however the below-ground stages of wireworms (Elateridae), and false wireworms (Tenebrionidae) can be captured with solar bait stations. These are used to estimate wireworm populations and to make decisions on seed treatment/non-treatment. Larvae of these insect groups can be concentrated by creating microenvironments that have favorable moisture, temperatures, and food. A handful of grain (wheat, etc.) is buried a few inches below the surface of the soil. The bait is covered with a mound of soil, about 18″ high, and is covered with clear plastic. Edges of the plastic should be covered with soil to prevent them from blowing away. Stations should be constructed in the fall before soil freezes, and they can be examined in the spring before planting time. Surveyors' flags can be used to mark sites for easy location.

Traps for Aquatic Insects

Interception Traps

Interception traps capture aquatic insects moving through the water and are generally similar to interception traps used for wind-borne insects. Often, these traps are tapered nets with either round or rectangular openings which can be fixed in place to sample insects in moving water or pulled through the water manually. The size of the mesh governs the size of insects retained, but use of too fine a mesh may impede movement of water through the trap and retain too much debris.

Emergence Traps

Floating emergence traps are used to capture insects with aquatic larval stages when they emerge as adults. Construction and use is similar to that for emergence traps used for soil-dwelling insects.

Attractant Cues

Attractant cues are signals that are used by insects to locate resources for feeding, members of the opposite sex for mating, and oviposition sites for egg laying. Cues are added to traps to increase insect specificity and effectiveness of the traps. Attractive cues from natural substrates may be perceived by one or several of the senses including sight, sound, and smell. Semiochemicals are naturally occurring, message-bearing chemicals that are used by insects (and other organisms) for communication and for perception of their environment. Semiochemicals that have a behavioral effect on insect orientation, that is, chemicals that cause an insect to move toward the source, are used in insect traps. Of specific interest are kairomones, which are signals emitted and received by members of different species (interspecific) that give an advantage to the receiving species, and pheromones, which are signals emitted and received by members of the same species (intraspecific). Traps may use single cues to lure insects, but often a combination of cues is used to improve insect capture. For each cue and each insect species being targeted, there is usually an optimal range of stimulus intensity, below which attraction is minimal and above which attraction is reduced. Control of the stimulus level is particularly important for semiochemical cues, and considerable research has been conducted to optimize emission rates and ratios of semiochemical blends. This effect seems less important for acoustic cues, where it has usually been determined that the greatest capture rates are found for traps with the highest sound levels.

Visual Cues

Color

Color can serve as a strong attractant for use in a trap. Insects may use a specific color to locate host fruit or plant material, with both hue and intensity affecting insect response. Contrasts between light and dark can also play a role, with either the trap in contrast with the background color or through the use of lines with insects orienting to an edge between a light and dark area on a trap. Most sticky traps use a color to target certain insects. Yellow is the most commonly used attractant color, and is used to capture hemipterans such as whiteflies and aphids, but is also used for almost every order of flying insects. The Rebell trap is constructed from two yellow panels as baffles, and is used for walnut husk flies, *Rhagoletis completa* Cresson, and cherry fruit flies, *Rhagoletis cingulata* (Loew). A disadvantage of using yellow for sticky traps is that it also attracts beneficial insects such as hymenopteran parasitoids, and the traps may fill up with these and other non-target insects. Yellow-colored pan traps are used to capture Hymenoptera, especially the parasitoid species. Orange sticky traps are used for carrot rust fly, *Psila rosae* (Fabricius), and blue sticky traps for western flower thrips, *Frankliniella occidentalis* (Pergande). Blue is also highly attractive to tsetse flies (Glossinidae). White sticky traps are used as panels and as trunk wraps for capture of tarnished plant bug, *Lygus lineolaris* (Palisot de Beauvois), and eastern apple sawfly, *Hoplocampa testudinea* (Klug), and red trunk wraps for apple blotch leafminer, *Phyllonorcycter crataegella* (Clemens). Use of contrasts may increase insect capture, such as the use of insect silhouettes added to the surface of white sticky panels to increase capture of house flies, *Musca domestica* L.

Shape

Shape can be used as an attractant, although it is combined with appropriate color for the target insect. Spheres commonly are used as traps for tephritid fruit flies. Red spheres are used for apple maggot flies, *Rhagoletis pomonella* (Walsh), small green spheres for blueberry maggot flies, *Rhagoletis mendax* Curran, and large green spheres for papaya fruit flies, *Toxotrypana curvicauda* Gerstaecker. A Ladd trap is a red sphere that is mounted on a yellow panel and is used for apple maggot flies and cherry fruit flies, *Rhagoletis cingulata* (Loew). Black spheres have been used to capture biting flies in the family Tabanidae, which are attracted to the movement of the black ball hanging in a tree. A tree silhouette is mimicked by a Tedders trap, which is a baffle constructed from two dark isosceles triangles, with the unequal side forming the base. The size of the Tedders trap can be adjusted to optimize capture of tree-dwelling beetles. Root-infesting weevils, such as pecan weevils, *Curculio caryae* (Horn) and several citrus root weevils, as well as wood-boring beetles, may be captured by these traps. Beetles emerging from soil or moving along the soil surface respond to the trap as if it were the trunk of a tree. The insect moves up the baffles and is captured in a small collection container at the top of the trap.

Light

Attraction of insects to light is easily observed by standing next to a porch light or street light during the night. A commonly accepted explanation of this phenomenon is that insects have evolved mechanisms to travel straight paths at night by orienting at a constant angle to the light of the moon. Artificial light produced by man-made devices interferes with this response. Moving at a constant angle to a light source always directs the insect toward the source of the light, once it comes within a few meters. Lights that include ultraviolet (UV) frequencies may also be attractive because insects in a confined area can use UV light as a cue to the direction of an opening into a clear area. A variety of insect traps have been developed and used that are based on a light as the attractant. Lights used include mercury lamps and black lights (UV) for moths, incandescent lights for flies and mosquitoes, green lights for stored product insects and cyalume lightsticks for aquatic light traps. Light traps, also called electric traps, are typically bucket traps with funnels. When used with fluorescent bulbs, the traps have baffles alongside the bulb that knock insects attracted to the light down into the trap. The Pennsylvanian light trap is an example of this design. Rothamsted and Robinson-type traps use incandescent bulbs with a reverse funnel over the light bulb. The New Jersey trap and the CDC trap are light traps developed for mosquito surveillance. They use incandescent bulbs, a fan that creates a suction to draws attracted mosquitoes down into the bucket and a filter to prevent larger insects from entering the trap. Lights may also be used with sticky traps to retain attracted insects. These more commonly are used for control of indoor pests such as house flies, stored product insects and fleas. A LED-CC trap for whiteflies uses a green light-emitting diode (LED) to attract insects into an open-bottom clear cylindrical trap with a yellow ring on the bottom.

Chemical Cues

Food/Host Lures

Volatile chemicals emitted from host plants, animals and other materials are used by insects to locate food sources. These chemicals are referred to as kairomones, that is, chemicals produced by a plant or animal that are advantageous to the receiving individual of a different species. Host material can be used to bait traps for insect capture, and the spectrum of use of food-based baits for insect control and pest management are covered in separate chapters. Examples of use of host material in a trap include use of carrion in pitfall traps or fruit in butterfly bait traps as survey tools, or fruit and meat in traps for yellowjackets (Hymenoptera). Grain or grain products (e.g., wheat germ, wheat germ oil, corn oil, etc.) are used for stored product insect pests, and grain oils used in shelter traps provide both an attractant and a method to kill attracted insects. However, host material may rapidly decay or may release attractive chemicals for only a short time period after initial placement. The insect may be using only a few of the sometimes numerous volatile chemicals emitted by a host and traps baited with synthetic chemical versions of the host can be used to lure an insect into a trap. The quality and quantity of the chemical can be controlled by the method of formulation, providing a standard release rate for a known time period, which improves trap performance. Carbon dioxide is used by mosquitoes to locate vertebrate hosts, and addition of dry ice to a trap can be used to survey blood-feeding mosquitoes. Octenol (1-octen-3-ol) is a naturally occurring chemical emitted by oxen and cows because they ingest large amounts of vegetable matter, and combinations of octenol and carbon dioxide are used to bait traps for mosquitoes, biting midges and no-see-ums (Ceratopogonidae). To make these chemicals more attractive, they can be combined with heat and moisture in a trap such as the Mosquito Magnet. Host kairomones are used with blue sticky traps to capture tsetse flies and in rootworm traps for corn rootworm adults. Floral cues are used in traps for Japanese beetles, and for nectar-feeding female moths (Lepidoptera). These are used in bucket traps with funnels. Fruit lures that provide volatile chemicals emitted from apples and plums are used in traps for apple maggot flies and for plum curculio, *Conotrachelus nenuphar* (Herbst). Fruit lures for apple maggot flies are hung near red sphere traps; fruit lures for plum curculio are used in a variety of traps, including Tedders, circle and boll weevil traps. McPhail-type traps can be used with a variety of liquid baits. They have been used with fermenting sugar solutions to capture small fruit flies (Drosophilidae) and moths (Lepidoptera), and with aqueous protein solutions for fruit-infesting fruit flies (Tephritidae). Ammonia has been found to be the primary chemical responsible for attraction of tephritid fruit flies to protein solutions, and ammonia alone or in combination with other synthetic volatile chemicals emitted from protein baits are used in sticky panels, sticky spheres or McPhail traps to catch these fruit flies.

Pheromone Lures

There are two main types of pheromones that are used with insect traps. Sex pheromones are produced by one sex to attract the opposite sex. The sex pheromones most commonly used in traps are ones that are produced by females. These are used in either wing traps or bucket with funnel traps, and there are lures available for numerous species of pest Lepidoptera and for sweetpotato weevils, *Cylas formicarius elegantulus* (Summers). The moths tend to be active at night, so visual cue is less important, however, the contrast of a white or light colored trap versus the dark background often increases capture. The advantage of traps baited with these sex pheromones is that they are highly specific and very effective, however, they capture only males and so no information on or samples of females are obtained. Some male tephritid fruit flies produce a sex pheromone that is attractive to female flies, and the papaya fruit fly pheromone increases capture of both male and female flies on green sticky sphere traps.

Aggregation pheromones are used with insect traps also. These are attractive to both sexes and are used to bring both sexes to a common location for both feeding and mating. Although both males and females can be captured in traps baited with aggregation pheromones, they tend to be less effective lures than sex pheromones or they need to be presented with other cues. Exceptions are the pheromone produced by boll weevils (Grandlure), *Anthonomus grandis grandis* Boheman, and the lesser and larger grain borers, *Rhyzopertha dominica* (Fabricius) and *Prostephanus truncatus* (Horn). Sticky, shelter and wing traps baited with these pheromone lures capture both sexes of these borers. Aggregation pheromones are often produced by males in conjunction with feeding, thus since both insect pheromone and host kairomones are emitted as signals, both are needed to elicit attraction. Combinations of synthetic aggregation pheromone and host material as source of kairomones are used in shelter traps for stored product beetles and cockroaches, in Lindgren or panel traps for bark beetles, and in bucket traps for palm weevils. A combination of honey bee pheromones is used in swarm traps to increase bee capture. This includes honey bee queen mandibular pheromone (BeeBoost) and an orientation pheromone produced by worker bees (Nasonov).

Parapheromone Lures

Parapheromones are a special group of lures that are used to trap some species of tephritid fruit flies. They act as sex pheromones because they are highly attractive to male fruit flies, similar to female-produced sex pheromones. However, these are not insect-produced compounds and do not appear to play a dominant role in the biology of the responding species. They may be synthetic kairomones, as they are similar in structure to some plant compounds, and access to the synthetic or natural versions of these compounds have been shown to increase sexual competitiveness of males. These compounds include trimedlure for Mediterranean fruit flies, *Ceratitis capitata* (Wiedemann), cuelure for melon flies, *Bactrocera cucurbitae* (Coquillett), and methyl eugenol for oriental fruit flies, *Bactrocera dorsalis* (Hendel). These lures are most commonly deployed in white Jackson traps (triangle traps) or on yellow sticky panels.

Oviposition Lures

Oviposition lures are chemicals that attract egg-laying (gravid) females. A gravid mosquito trap uses a baited water solution to attract and capture the adult females. A trap and bait also has been developed for navel orangeworms, *Amelyois transitella* (Walker), on which the female moth lays eggs.

Acoustic Cues

Just as many insect species produce volatile chemicals to attract members of the opposite sex, some species use sound alone or in combination with chemicals for this purpose. Such cues have been incorporated successfully into panel or bucket traps of several different shapes. The different sounds broadcast as attraction cues have included songs recorded from conspecifics of the targeted insect and synthetic mimics of the songs. A variety of different speaker systems have been used, including standard loudspeakers, piezoelectric boards with extensive surface areas, and piezoelectric cylinders.

The most successful use of acoustic traps has been for mole cricket (Gryllotalpidae). Sound traps have been developed that produce highly amplified synthetic or recorded calls of male mole crickets. A bucket or bucket with funnel trap is placed under the sound emitter to capture responding crickets. These traps also capture tachinid flies that parasitize adult crickets and that locate them by responding to the call. Sticky traps broadcasting the recorded male lesser wax moth, *Achroia grisella* (Fabricius), calling song have been used to attract virgin females. Many tephritid fruit flies perform wing-vibration behaviors during courtship, and there have been a few attempts to attract female fruit flies by broadcasting songs recorded from courting males. Such songs have been demonstrated to be attractive to Mediterranean fruit flies over distances of 50 cm or less, but the traps are noisy and require electric power. Jackson traps broadcasting the recorded male Caribbean fruit fly, *Anastrepha suspensa* (Loew), calling song have been demonstrated to attract virgin females.

Another use of acoustic cues is as an attractant for males of some midge and mosquito species that form swarms to attract females. When females fly into a swarm, the males are attracted by their wingbeats, which are of distinctly lower frequencies than those of the males in the swarm. Consequently, males can be attracted in great numbers by placing a black cloth or other swarm marker on the ground and broadcasting recorded or synthetically generated female wingbeats from a speaker inside or at the edge of a sticky panel, cylinder, or cup hung about 1 m above the swarm marker. Acoustic traps can greatly reduce male populations of sedentary mosquito species, and also have been used to chemosterilize and re-release males rather than killing them. However, they are not yet in common use in isolated field environments because they require electricity and some technical skill to operate, and the sound that must be broadcast at high amplification for optimal trap catch can be a nuisance.

Automated Monitoring Systems

Advances in information technology, computer technology, and remote sensing are adding to the field of precision agriculture; that is, use of computers to aid in management decisions. The ability to rapidly move data from traps into computer databases or spreadsheets is an integral component of precision agriculture, and will facilitate making pest management decisions in a timely manner. Bar codes can be added to traps and a bar code scanner can be taken to the field to expedite data entry on trap type, trap location, etc., so that only insect counts need to be entered manually. In addition, data can now be transmitted by cable or wireless devices directly to a local computer for later downloading, or data can be transmitted to an off-site computer. Ideally, the tasks of species identification and counting would be automated to eliminate expensive, time consuming labor. This ideal has not yet been realized to any practical extent, although it is a goal of considerable interest to agricultural engineers and entrepreneurs.

A potential method for automating the insect identification process is to analyze the wingbeats of insects coming into a trap or flying overhead. Fourier transforms, nearest neighbor classification, and artificial neural network classification schemes have been tested in feasibility studies with aphids and mosquitoes, and species classification accuracies of up to 70–90% have been reported. If the costs of hardware needed to detect and transmit wingbeat sounds continue to decrease, automated identification will soon emerge from the laboratory as a practical option in environments where traps are difficult to service or labor costs are prohibitive. An example of counting insects where traps might be difficult or dangerous to service is a device to evaluate the intensity of honey bee defensive attacks near a hive. The device includes a microphone set inside a plastic target, connected to a datalogger with an amplifier, tone decoder, and a microcontroller that times and stores information from the decoder continuously, and later transfers data to a personal computer. For operation, the target is moved next to the hive and the hive is disturbed. The bees attack the target with sharp blows that are counted and saved for downloading after the attack is over.

Another already existing approach to automated off-site monitoring is the use of gravimetric analysis of flight trap captures of red flour beetles, *Tribolium castaneum* (Herbst). Beetles responding to cone-shaped flight traps fall into a small container coated with liquid Teflon which rests on the weighing pan of a digital pan balance. Signals from the balance are sent over a cable to a personal computer, and the weight, which is recorded at sequential intervals, is used to estimate the numbers of insects captured over time. Insect movements that interrupt an infrared light beam can be counted by a computer that monitors fluctuations in the beam intensity. Infrared beams can be used in actigraphs to monitor insect movement in activity chambers. Infrared beams also are used in a recently developed electronic grain probe insect counter system. The beams are located below the bottom of the funnel in a cylindrical grain probe trap. Insects falling through the funnel are counted electronically and time-stamped data is transmitted to off-site computers. Counts from electronic traps along with information from automated temperature and relative humidity probes can be collected together and used for management decisions.

Trap Uses in Integrated Pest Management (IPM)

The goals of trapping are highly variable. Traps may be used for general survey of biota, for detecting the start of population increase in infested areas, for identifying the source of stored product pest infestation in a store or warehouse, or for detecting invasion by exotic invasive insect pests in previously uninfested areas. Trapping systems for insects are important components in integrated pest management programs. Trapping data can be used to make decisions on the initiation or termination of control measures, as well as to assess efficacy of control approaches that have been implemented. Detection trapping is used to alert personnel to the presence of a new insect pest in a previously pest-free area so that control measures can be implemented in a timely manner. Early detection and targeting the locations of small infestations will facilitate pest management strategies such as biological control or sterile insect technique that are most effective when pest populations are low. With the availability of sufficiently effective traps that capture both female and male pest insects, trapping systems may be used as control measures, and thus could be added to the growing list of biologically based technologies for insect control. Traps can be used as toxicant delivery systems, with insects that visit the trap taking a slow-acting poison back to the rest of the population. This approach is used with social or gregarious insects such as termites, ants and cockroaches. Mass-trapping is the use of large numbers of traps in an effort to suppress the population. Sticky traps are usually used in this approach as a high percentage of responding insects are captured. This approach has been used to suppress populations of a pest such as apple maggot flies and papaya fruit flies, which spend part of their life cycle away from the host and can be intercepted by traps placed around the periphery of the orchard. However, these traps require frequent servicing to maintain activity. An alternate approach is the development of attract-and-kill systems, sometimes called attracticides. In this approach, insects responding to traps consume or contact a toxicant, but then exit the trap and die away from the trap. Examples include addition of insecticide to artificial cows for control of tsetse flies, methyl eugenol mixed with insecticide for control of oriental fruit flies, addition of insecticide to pheromone to control codling moth in apples, and addition of insecticide to feeding stimulant in corn rootworm traps. All of these control approaches should be combined with other pest management strategies to be fully successful.

References

Hienton TE (1974) Summary of investigations of electric insect traps. Technical Bulletin 1498. Agricultural Research Service, USDA, 136 pp
Mayer MS, McLaughlin JR (1991) Handbook of insect pheromones and sex attractants. CRC, Boca Raton, 1083 pp
Muirhead-Thomson RC (1991) Trap responses of flying insects. Academic, San Diego, 287 pp
Pedigo LP, Buntin GD (1993) Handbook of sampling methods for arthropods in agriculture. CRC, Boca Raton, 714 pp
Southwood TRE (1966) Ecological methods. Chapman and Hall, New York, 524 pp

Traumatic Insemination

A form of insemination practiced by bed bugs (Hemiptera: Cimicidae) and some other bugs wherein the male punctures the female's abdomen with his needle-like penis and deposits sperm within her hemolymph; they then migrate to her ovary to fertilize the eggs. This is also called "hemocoelic insemination."

► Bed Bugs

Tree Crickets

A subfamily of crickets (Oecanthinae) in the order Orthoptera: Gryllidae.

► Grasshoppers, Katydids and Crickets

Trehalose

A polysaccharide found in insects that is one of the two most common carbohydrate stored reserves (the other is glycogen) for insect flight. It occurs principally in the hemolymph, fat body, and gut tissues. Trehalose is usually the first metabolite used when energy is needed. Each molecule of trehalose is hydrolyzed into two molecules of glucose. Trehalose also is rapidly synthesized from glucose as it is absorbed in the midgut. Glucose is not usually present in high concentrations in the hemolymph because of this synthesis, so glucose absorption is easily accomplished.

Treherne, John E

John Treherne was born on May 15, 1929, near Swindon, England. He was educated at Bristol University. After military service he was invited by Vincent Wigglesworth the join the Unit of Insect Physiology at Cambridge. Treherne did so, and also served as lecturer and reader at the University. Upon Wiggleworth's retirement, Treherne headed up a new Unit of Invertebrate Chemistry and Physiology at Cambridge. Treherne's reputation was based on research of insect neurobiology, the blood-brain barrier of insects, gut physiology, circadian rhythms, hormones, cuticle permeability, osmoregulation, and other physiological subjects. His subjects were not just insects, as he worked on molluscs and annelids. Indeed, he was a physiologist first and foremost, and never pretended to be an entomologist in the classic sense. Nevertheless, he enjoyed field entomology, especially marine and salt marsh insects, and made insightful behavioral and evolutionary contributions in this area. Treherne served as editor of "The Journal of Experimental Biology," and edited "University Reviews of Biology," "Advances in Insect Physiology," and others. He served as president of Downing College from 1985 to 1988. Treherne also wrote popular novels, some of which included entomological elements. He died on September 23, 1989.

Reference

Foster W (1990) John E Treherne (1929–1989). Antenna 14:6–9

Treehoppers (Hemiptera: Membracidae)

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Most treehoppers are readily distinguished from their close relatives, the leafhoppers, by their enlarged pronotum, which extends posteriorly over the remaining thoracic segments and often bears horns, spines, bulbs, or other projections. A few treehoppers have a pronotum that is more modest in size; these differ from leafhoppers in that the scutellum is enlarged with either a median longitudinal keel, or a distinct median longitudinal groove or notch (Fig. 99).

Order: Hemiptera
Infraorder: Cicadomorpha
Superfamily: Membracoidea
Family: Membracidae

Membracidae, a large and diverse family of plant-feeding insects, comprises approximately 3,100 described species in 400 genera. Their closest living relatives are Melizoderidae (a small group of treehopper-like insects endemic to Chile) and Aetalionidae (a small, mostly neotropical family with one endemic southeast Asian genus). Aetalionidae, Melizoderidae and Membracidae together constitute a specialized lineage apparently derived from leafhoppers (Cicadellidae). Treehoppers are mainly a tropical group, but a sizeable fauna of mostly oak-feeding species occurs in temperate North America. Most of the subfamilies of Membracidae are endemic to the new world. Centrotinae, the only treehopper subfamily that occurs worldwide, is well represented in tropical and subtropical regions of Africa, Asia and Australia, but the palearctic fauna is extremely depauperate. The oldest fossil treehoppers are known from Tertiary-age Dominican and Mexican amber.

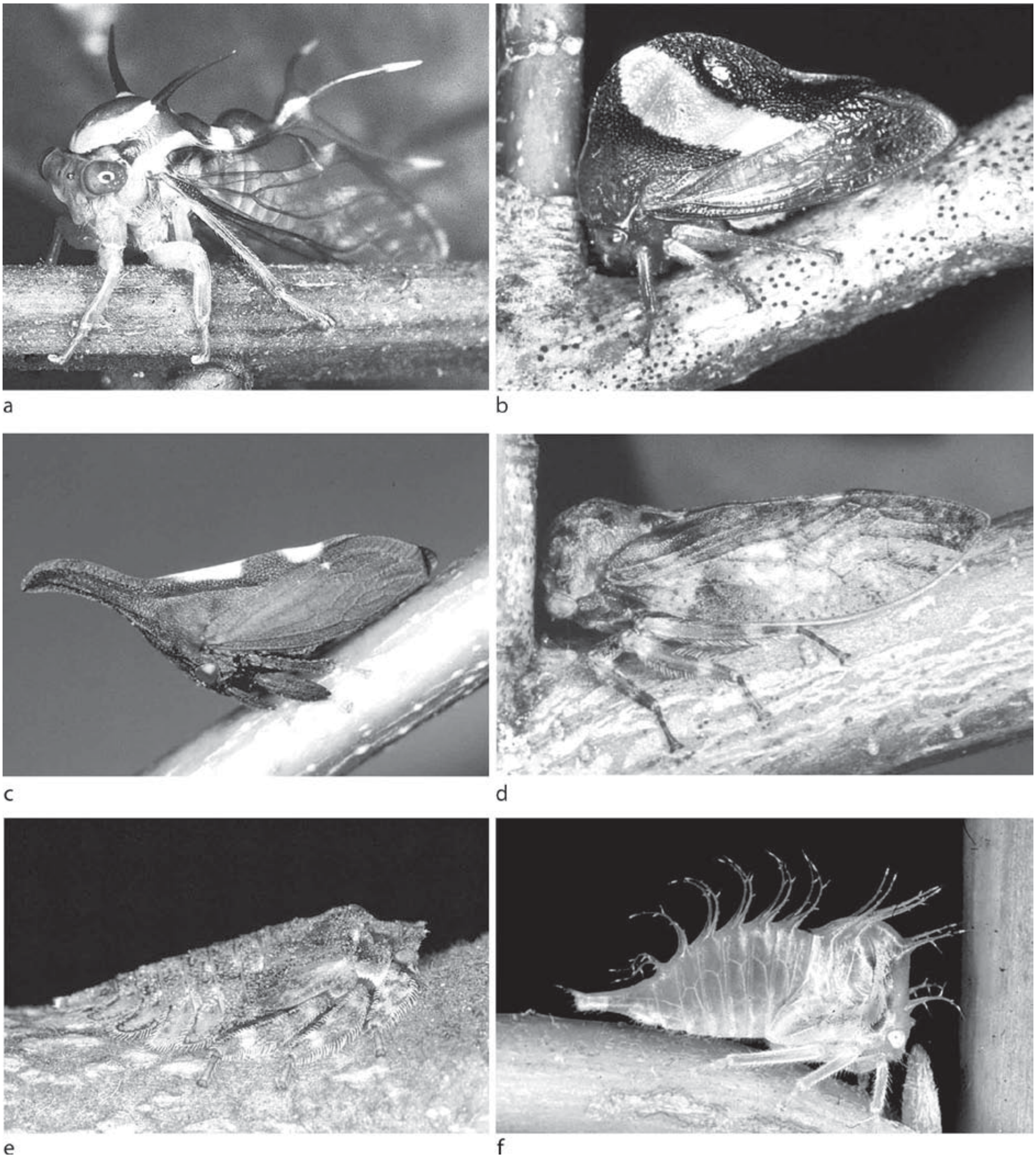
External Morphology

Adult treehoppers range from 3 to 30 mm in length. In addition to differences in coloration and the shape of the pronotum, genera and species of treehoppers differ in the shape and proportions of the head, the wing venation, the arrangement of setae on the legs (particularly the hind tibia), the shape of the female ovipositor and the male genitalia. Sexual and seasonal dimorphism in pronotal shape and color is common in many species. Treehopper nymphs are often even more bizarre than the adults. some species have large spines on the head, thorax and abdomen; others are well adapted for crypsis, being strongly depressed with the flattened tibiae fitting like puzzle pieces into notches in the sides of the thorax.

Life History and Habits

Details of the life cycle vary from species to species. The female deposits several eggs on the bark or into the living tissue of a woody host plant and may cover the eggs with a frothy substance that hardens when dry. The eggs either remain dormant for a period ranging from a month to over a year, or they develop and hatch within a few weeks. The young, known as nymphs, feed on plant sap by inserting their mouthparts into the phloem vessels of the host plant and go through a series of five molts reaching the adult stage after a period of several weeks. The adult males and females seek each other out for mating, locating each other through vibrational signals made by sound producing organs at the base of the abdomen called tymbals. These signals are transmitted through the substrate and are usually too faint to be heard by human ears. Some treehoppers exhibit anointing behavior similar to that of their relatives, the leafhoppers, but, unlike leafhoppers, treehoppers do not produce brochosomes (a hydrophobic, granulated coating).

As implied by their name, most treehoppers are strong jumpers as adults. However, treehopper nymphs cannot jump and avoid predation through crypsis, ant-mutualism, or parental care. Although many species are solitary as nymphs and adults, numerous treehopper species are gregarious and exhibit various degrees of parental care (or presocial) behavior. In the most advanced form of parental care, females guard their eggs and remain with the nymphs throughout their development, repelling invertebrate predators by kicking with the legs or buzzing the wings.



Treehoppers (Hemiptera: Membracidae), Figure 99 **Treehoppers (Membracidae). (a) *Heteronotus* sp. adult; (b) *Smilia fasciata* Amyot & Serville adult; (c) *Enchenopa binotata* (Say) adult; (d) *Microcentrus caryae* (Fitch) adult; (e) *Microcentrus caryae* nymph; (f) *Stictocephala taurina* (Fitch) nymph. (Photos by C. H. Dietrich.)**

Predators and Parasites

Treehoppers are a food source for vertebrate predators such as birds and lizards, as well as invertebrate predators such as spiders, assassin bugs, wasps and robber flies. Treehoppers also are attacked by various parasitoids such as dryinid and mymarid wasps, epipyropid moths, pipunculid flies and strepsipterans. They also are attacked frequently by entomopathogenic fungi.

Economic Importance

Several treehopper species are minor pests, particularly of tropical fruit trees such as papaya, cacao and palm. A few species are known to transmit plant pathogens. The buffalo treehopper (*Stictocephala bisonia* Kopp & Yonke), a North American species that injures apple and related fruit trees, was introduced accidentally into Europe and now is well established in the temperate zone of the palearctic region as far east as central Asia.

Control

Treehoppers rarely inflict economic damage on crops, but when they do, control usually involves the use of conventional contact insecticides.

► Bugs

References

Deitz LL (1975) Classification of the higher categories of the New World treehoppers (Homoptera: Membracidae). North Carolina Agricultural Experiment Station Technical Bulletin 225:1–177

Deitz LL, Dietrich CH (1993) Superfamily Membracoidea (Homoptera: Auchenorrhyncha). I. Introduction and revised classification with new family-group taxa. Syst Entomol 18:287–296

Dietrich CH, Deitz LL (1993) Superfamily Membracoidea (Homoptera: Auchenorrhyncha). II. Cladistic analysis and conclusions. Syst Entomol 18:297–312

Dietrich CH, Mckamey SH, Deitz LL (2001) Morphology-based phylogeny of the treehopper family Membracidae (Hemiptera: Cicadomorpha: Membracoidea). Syst Entomol 26:213–239

Mckamey SH (1998) Taxonomic catalogue of the Membracoidea (exclusive of leafhoppers). Second supplement to fascicle I – Membracidae of the general catalogue of the Hemiptera. Mem Am Entomol Inst 60:1–37

Trench Fever

A bacterial disease of humans transmitted by the body louse, *Pediculus humanus*. The disease agent is *Bartonella* (*Rochalimaea*) *quintana*. The organism does not affect lice, and is defecated after a few days within the louse. Humans contract the disease primarily by scratching and rubbing the organism into wounds (bites, scratches) but possibly also through inhalation. Formerly known mostly as a war-related illness, particularly among soldiers lacking in sanitation, it has also appeared in modern times within urban settings among the homeless, drug abusers, political refugees, and others lacking adequate access to shelter and sanitation. Recovery may require a few days to over a month. It is treated with antibiotics. Symptoms include rash, malaise, headache and bone pain; mortality is not attributed to trench fever. Only humans are known to host this malady.

► Chewing and Sucking Lice

Triassic Period

A geological period at the beginning of the Mesozoic era, extending from about 250 to 213 million years ago.

► Geological Time

Trichobothrium (pl., Trichobothria)

Small spots or depressions on the cuticle that bear setae or bristles. The number and location is often used for identification of immature insects.

Trichoceridae

A family of flies (order Diptera). They commonly are known as winter crane flies.

► Flies

Trichodectidae

A family of chewing lice (order Phthiraptera). They sometimes are called mammal chewing lice.

► Chewing and Sucking Lice

Trichogrammatidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees, and Sawflies

Trichomes

Hairs or small spines on the surface of a plant, and an important morphological defense against attack by insects.

► Trichomes and Insects

Trichomes and Insects

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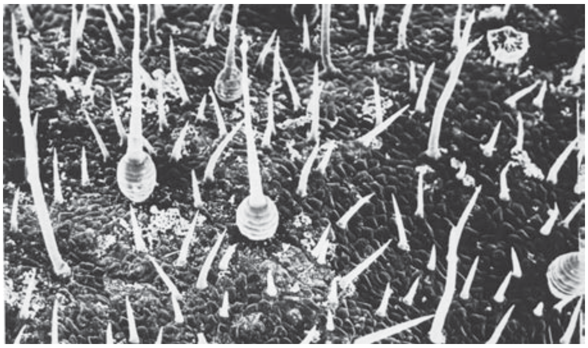
Trichomes, also called plant hairs, are found on vegetative and reproductive structures in all higher plant families. They have evolved independently in a number of plant families. In general, monocotyledons are less pubescent (hairy) than dicotyledons, but trichome production can be induced in many glabrous (hairless or smooth) plant species. Several factors, including various light and temperature regimes, moisture availability and soil conditions affect the development and expression of trichomes. Trichomes are the first structure an insect encounters when landing on a plant, and provide the initial arena for complex and varied plant-insect interactions.

Types and Functions of Trichomes

The structure and function of trichomes are highly variably within and among plant species. There are two general types of trichomes: glandular, which produce, secrete or contain chemicals, and non-glandular, which are simple hairs and do not produce or contain chemicals. Trichomes have also been classified morphologically. Various morpho-types have been observed including: simple unicellular, multicellular uniseriate, multicellular multiseriate, two to five branched, stellate, dendritic or arboriform, and peltate. Several different classifications have been proposed and there is much variation and overlap in the description of trichome types. Developing a generalized classification system based on trichome morphology has not been possible because of their highly polymorphic nature (Fig. 100).

Trichomes may have either or both physiological and defensive functions for the plant, though may be utilized for a different purpose by an insect. For example, a dense covering of hairs on a leaf may have a physiological role for the plant but may provide a preferred ovipositional surface for an insect. The following physiological functions have been identified for trichomes: altering optical properties of the leaf surface, deflecting solar radiation and thus reducing leaf



Trichomes and Insects, Figure 100 Trichomes on the surface of a pigeonpea (*Cajanus cajan*) pod. Three types of trichomes are visible: short and long non-glandular (simple hairs), and a multicellular glandular trichome with a bulb-like base. Photo credit: International Crops Research Institute for the Semi-Arid Tropics, Patancheru, A.P., India.

temperature, maintaining water balance, acquiring nutrients and water from the atmosphere, and excreting excess salts. The focus of this discussion is insect/trichome interactions; therefore, the physiological functions of trichomes will not be considered further. Trichomes can affect both primary (herbivores) and secondary (predators and parasitoids) consumers.

The impact of trichome density, length, and orientation on insect behavior and performance has been well documented. Trichome density is perhaps more important than length or orientation but all three characteristics have been shown to impact insect behavior and/or performance. Wild relatives are often good sources of pubescence and have been utilized to develop insect resistant crop cultivars.

Trichomes as an Ovipositional Substrate

Oviposition has been positively correlated with increasing trichome density in many herbivorous species. For example, more eggs have been observed on trichome-dense cotton cultivars compared to smooth cotton cultivars for several insects including *Lygus hesperus*, *Helicoverpa* spp., *Earias fabia* and *E. vitella*. A similar situation has been noted for *Laspeyresia glycinivorella* and *Ophiomyia phaseoli* on soybean pods and leaves, respectively. Hairy surfaces can also positively alter egg and larval development and survival by ameliorating environmental factors such as increasing humidity levels. Conversely, trichomes inhibit oviposition in some insect species. At least one species of bruchid, *Callosobruchus chinensis*, prefers smooth as opposed to hairy pigeonpea (a tropical legume) pods for laying eggs. The cereal leaf beetle, *Oulema melanopus*, lays fewer eggs on wheat genotypes with highly pubescent leaves compared to genotypes with glabrous leaves. Both egg laying and larval survival are lower on cultivars with relatively longer and/or denser trichomes.

Impact of Trichomes on Herbivores

Trichomes interact with insect herbivores in many ways. The role of trichomes in providing defense against insect herbivores has been well documented and has been the topic of considerable investigation. Trichomes provide protection to the plant by acting as a physical barrier limiting an insect herbivore's contact with the plant, or as a chemical barrier by producing toxic compounds that poison the insect or by producing gummy, sticky or polymerizing chemical exudates which impede the insect. The effectiveness of the first mechanism, as a simple physical barrier to reaching the plant surface, is dependant on the length, density, and orientation of the trichomes, and on the insect's size, mode of locomotion, and type of mouthparts. In general, longer, denser and/or more erect hairs provide a better barrier to insect herbivores than shorter, sparser or recumbent hairs. As a purely physical phenomena, trichomes may also interfere with the insect digestion.

Wild relatives of cultivated plant species often have higher densities of trichomes than the cultivated relatives. A wild relative of pigeonpea possesses twice the density of small, non-glandular trichomes on pods as cultivated pigeonpea pods. When newly emerged pod borer (Helicoverpa armigera) larvae are placed on pods of both species, mortality is increased by 85% relative to the cultivated pigeonpea. The high density of non-glandular trichomes prevent the larvae from reaching the pod surface and they starve or desiccate before feeding.

Trichomes have been used to develop soybean cultivars with resistance to several insect pests. Soybean leaves possess simple non-glandular trichomes and cultivars vary in their degree of pubescence. Feeding and survival of at least four different caterpillars and two species of beetles were lower on pubescent leaves than on smooth leaves. Trichome length and shape are also important, especially for small-bodied insects such as the potato leafhopper. Potato leafhopper populations decreased with increasing trichome length, regardless of trichome density. The irregular shape produced by the highly pubescent accessions prevents potato leafhopper from attaching normally for feeding and oviposition.

Reduced movement of first instar larvae of pink bollworm on cotton has been observed on highly pubescent versus glabrous leaves. Larvae pause regularly to swing their heads and sample the substrate while moving. This resulted in higher larval mortality due to starvation or desiccation. The larvae of *Heliothis virescens* are also more likely to die from biotic (predators and parasites) and abiotic (high temperature and insecticides) factors because of slower movement on pubescent genotypes.

In contrast to non-glandular trichomes, glandular trichomes can act as both physical and chemical barriers to insect herbivores. The fluidity and volume of the exudates, whether toxic or sticky, may vary with weather, time of day and age of the plant. There is also tremendous diversity in the structure of glandular trichomes and the composition of glandular exudates.

Glandular trichomes confer resistance to several phytophagous insects and, because of the toxic and deterrent properties of their exudates, are often more effective than non-glandular trichomes in providing resistance to insect pests. Glandular trichomes secrete and/or accumulate a variety of compounds that generally act either as insect repellents or immobilize insects by entrapment. In addition to protecting plants by deterring herbivores, glandular trichomes may also attract pollinators; these structures contribute to the flavor and aroma of many plants.

The commercial potato, *Solanum tuberosum*, and its wild relatives, *Solanum* spp., possess two types of glandular trichomes. Type A is short, globular, and releases exudates after rupturing; Type B is longer, more hair-like, and continuously exudes a viscous fluid. After landing, an insect first encounters Type B exudates. In struggling to escape from the sticky coating, the insect disturbs and ruptures Type A trichomes. The exudates in Type A trichomes combine with the Type B exudates to harden the sticky exudate. Thus, small bodied insects such as aphids and leafhoppers are trapped and starve to death. The Type B exudates also increase the mortality rate and inhibit settling and probing behavior of some aphids. These trichomes provide greater resistance to wild *Solanum* spp. than in the cultivated *S. tuberosum*. In general, wild species are more pubescent and have more glandular trichomes, and are hence more resistant to insect pests than the cultivated relatives.

Another type of glandular trichome are those found on chickpea. They secrete highly acidic (pH = 1) exudates, containing primarily malic and oxalic acids. The quantity of malic acid in the exudate reportedly confers resistance to the leafminer, *Liriomyza cicerina*, and the pod borer, *H. armigera*, though others have reported an antibiotic effect of oxalic acid, but not malic acid.

Impact of Trichomes on Parasitoids and Predators

Trichomes can have a direct negative impact on the predators and parasitoids that attack insect herbivores. The efficacy of these natural enemies can be impaired by (i) increasing search time, (ii) decreasing residence time in the host/prey habitat, (iii) chemical and/or physical entrapment, and (iv) chemical repellents. As with herbivores, small bodied natural enemies are generally more affected by trichomes than larger ones.

The time parasitoids and predators spend searching for hosts/prey is directly related to their walking speed; more hosts/prey are encountered when parasitoids and predators walk faster. Trichomes, even simple non-glandular hairs, interfere with movement and reduce walking speed. Faster walking speeds of several egg parasitoids (*Trichogramma* spp.) have been measured on smooth versus hairy cotton leaves and pigeonpea pods. In addition, parasitoids which walk on the plant surface can be slowed by exudates secreted by glandular trichomes. Predators are similarly hindered by glandular and non-glandular trichomes. The walking speed of coccinellid larvae are inversely related to the density of trichomes on potato and tomato.

On pigeonpea, eggs of an important pest (*Helicoverpa armigera*) are readily parasitized (>55%) by an egg parasitoid (*Trichogramma chilonis*) when placed on leaves but are rarely attacked (<1%) when placed on pigeonpea pods. Parasitoids walked significantly faster on leaves than on pods, where their movement was inhibited by long trichomes. The higher density of glandular trichomes on pods compared to leaves resulted in the parasitoids being trapped by glandular exudates. The same pest (*H. armigera*) feeds on chickpea, but is never attacked by the egg parasitoid, *T. chilonis*. The highly acidic trichome exudates secreted by vegetative and reproductive parts of chickpea deter, and may entrap, the egg parasitoid. Other examples of *Trichogramma* spp. being trapped by sticky trichome exudates have been reported from tomato and potato.

The negative effects of glandular trichomes on natural enemies may not be as strong under field conditions as often observed in greenhouse or laboratory experiments. Glandular trichome exudates may be dried by the sun or wind, washed off by rain, or even be rendered ineffective by dust under field conditions.

Conclusions

Trichomes are found on vegetative and reproductive structures in many plant species. There are two types, non-glandular and glandular; both are found in a variety of shapes and forms. Trichomes and insects interact in numerous ways. Trichomes on a number of plants have evolved a defensive function and may protect plants from insect herbivores. Plants are protected from insect feeding when trichomes form a chemical or physical barrier, preventing herbivores from reaching the surface. Trichomes may also provide a preferred oviposition site and/or may interfere with an insect's movement on the plant surface. Both positive and negative interactions, from the insect's point of view, have been documented. Generalizing about the role and function of trichomes and how these structures interact with insects is difficult because trichomes vary greatly across plant species and because the interactions may be specific or unique to the plant-insect association.

► Plant Resistance to Insects

References

Gutschick VP (1999) Biotic and abiotic consequences of differences in leaf structure. New Phytol 143:3–18

Juniper BE, Southwood R (eds) (1986) Insects and the plant surface. Edward Arnold, London, 360 pp

Levin DA (1973) The role of trichomes in plant defense. Q Rev Biol 48:3–15

Peter AJ, Shanower TG (2001) Role of plant surface in resistance to insect herbivores. In: Ananthakrishnan TN (ed) Insects and plant defense dynamics. Science, Enfield, NH, pp 107–132

Romeis J, Shanower TG, Peter AJ (1999) Trichomes on pigeonpea (*Cajanus cajan*) and two wild *Cajanus* spp. Crop Sci 39:564–569

Trichomycetes

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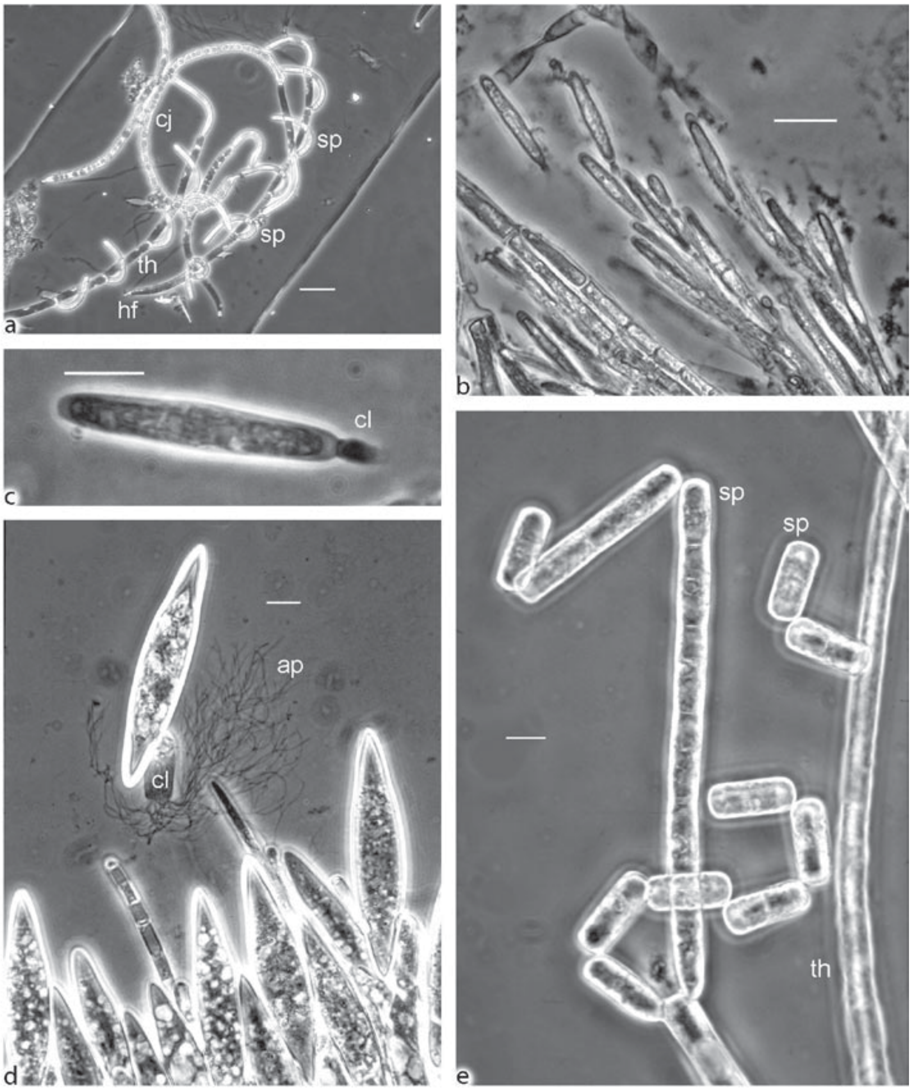
Trichomycetes are obligate symbiotic organisms that typically live in the guts of arthropods. They are generally viewed as commensals, having little effect on the host, but in stressful environments they might confer an advantage to colonized hosts; in some cases they act as pathogens. In the broad sense, trichomycetes (designated by a lower case t) includes the fungal class Trichomycetes (designated by an upper case T) and some historically similar protists that were earlier considered fungi. Most trichomycetes colonize freshwater and marine arthropods, but some colonize terrestrial arthropods. Hosts are filter feeders, detritus feeders, or aquatic grazers, but not predators or fluid feeders (e.g., Brachycera) (Fig. 101).



Trichomycetes, Figure 101 **Trichomycetes: (a) Fresh dissection of *Harpella melusinae* from *Simulium innoxium*. Asexual spores and conjugating thalli are shown. cj = conjugating thalli, hf = holdfast, sp = asexual spore, th = vegetative thallus. Scale bar is 30 μm. Phase contrast. (b) Preserved *Smittium* sp. from *Blepharicera similans*. Scale bar = 20 μm. (c) Asexual spore showing collar. cl = collar. Scale bar is 10 μm. (d) Zygospore of *Trichozygospora chironomidarum* showing thickened end walls, collar, and multiple appendages. ap = appendages, cl = collar. Scale bar is 20 μm. Photo courtesy of R. W. Lichtwardt. (e) *Asellaria ligiae* with asexual spores produced inside thallus (endogenous). sp = spore, th = vegetative thallus. Scale bar is 20 μm. Photo courtesy of R. W. Lichtwardt.**

Non-Fungal Trichomycetes

The first trichomycetes were described by Joseph Leidy in 1849 from millipedes. Initially, Leidy thought trichomycetes were colorless algae. Later, trichomycetes were placed in various fungal groups. Because of similar lifestyles, all trichomycetes were placed in the fungal class Trichomycetes until the 1990s. The non-fungal trichomycetes constitute the orders Amoebidiales and Eccrinales. Recent molecular analysis has shown that these trichomycetes are protists in the Mesomycetozoa group.

Order Amoebidiales

The thalli of these trichomycetes are coenocytic (one large multinucleate cell not divided into cells by septae or cross walls) and unbranched. They are usually associated with freshwater larval Diptera or Crustacea. They are most common with filter feeders and grazers, but might occur externally on predatory insects. A secreted holdfast is usually evident. Many workers had suspected that organisms in the order Amoebidiales were not fungi, because they produce amoeboid dispersal cells and lack chitin (or have very little). This order includes two genera: *Amoebidium* and *Paramoebidium*.

Amoebidium parasiticum attaches to the external cuticle of freshwater arthropods (e.g., Diptera, Ephemeroptera, and Crustacea). *Amoebidium* spp. are usually restricted to still-water (lentic) environments. Although not pathogenic, this fungus has a life cycle that is closely coordinated with that of the host. During the intermolt period of the host, the thallus produces asexual spores that can attach to other areas of the cuticle. Prior to molting or at host death, production of amoeboid cells rather than spores begins. The amoebae swarm from the thallus, encyst, and produce spores. These then form new thalli upon external contact with hosts. Sexual reproduction has not been verified.

Paramoebidium species live in the hindgut of aquatic insect larvae, usually hosts from the orders Diptera, Ephemeroptera, and Plecoptera. They do not produce spores directly, as do *Amoebidium* spp., but produce amoebae upon molting or death of the host. The amoebae swarm and then produce cysts that produce spores. Spores in this genus are presumed to germinate in the gut after ingestion. Sexual reproduction is unknown.

Order Eccrinales

The thalli are coenocytic and unbranched; however, in some species (e.g., *Leidyomyces attenuatus* in passalid beetles), multiple thalli share a common attachment point and appear branched at the base. The holdfast is a secreted material and can be large. These trichomycetes are found in the foregut or hindgut of Crustacea, Diplopoda, Insecta and Isopods. Eccrinales is the only trichomycete group in terrestrial insects (Passalidae and Scarabaeidae), other than *Orchesellaria* (see Asellariales below) in Collembola. Various asexual spore types are formed depending on taxon. The spores are usually formed by division within the tips of vegetative thalli. Fusion of adjacent cells has been reported, but confirmation of subsequent sexual spores is lacking.

Fungal Trichomycetes (Class Trichomycetes)

Trichomycetes are a class in the fungal division Zygomycota and include the trichomycetes most encountered in insects. Sexual zygospores are produced in many of the taxa.

Order Asellariales

Thalli of these fungi are branched and septate. The septation produces endogenous (inside the thallus) spores. The holdfast area (basal cell) often appears bulbous or branched (digitate). The order consists of two genera. The genus *Asellaria* inhabits isopods (Crustacea) and the genus *Orchesellaria* inhabits springtails (Collembola). Zygospore production following conjugation of thalli has been reported in this order.

Order Harpellales

The thalli produce large cells with septa. The spores are produced exogenously. Many spores have nonmotile appendages that are usually longer than the spore proper. The length and number of appendages have taxonomic value. Harpellales in the midgut are unbranched (Harpellaceae), whereas the species in the hindgut (Legeriomycetaceae) have a branched growth pattern. These Trichomycetes are common in aquatic insect larvae, especially Diptera. No Trichomycetes have been found in predatory insects, and most occur in filter-feeding or grazing insects.

Harpellales exhibit three reproduction types in their life cycle. The most common type is the production of asexual spores that are shed in the feces and ingested by hosts. When in the proper gut environment, asexual spores quickly germinate. Germination is a complex process involving extrusion of the spore protoplast from the spore wall and attachment to the host gut. The second type of spore is the sexual zygospore, which is produced by fusion of nuclei from adjacent cells of the same thallus or of neighboring thalli. Conjugation tubes between thalli are sometimes detected in the latter, whereas the sexual apparatus might not be evident in the former. The zygospores are usually characterized by a thickened end wall on one or both poles of the spore. The role of the zygospore in the natural history has not been determined, but because of the biomass investment, it presumably plays an important survival role. A third type of spore is the pathogenic spore, often referred to as a cyst (not to be confused with the cysts of Amoebidiales). These spores proliferate in the ovaries of adult females and are deposited as if they were eggs. The cysts produce spores (smaller than other asexual spores) that presumably colonize new larvae from adjacent eggs as the clutch hatches. This cycle helps explain how trichomycetes can colonize upstream hosts as the spores in feces are washed downstream, because infected females can carry the cysts upstream. The cyst stage is documented in a few locations (due to insufficient geographic sampling) (e.g., eastern Canada), but is expected to be common at a site on a temporal basis.

Harpellales are the Trichomycetes most likely to be encountered by entomologists; therefore, a few specific examples are presented. *Harpella melusinae* is common in larval black flies (Diptera: Simuliidae) on all continents except South America and Antarctica. Different species of *Harpella* are found in South America and black flies are not known from Antarctica. *Harpella melusinae* inhabits the midgut of the larva, where the pH is very high (up to pH 11.3) in Diptera. The fungal thalli attach to the peritrophic matrix and grow in this seemingly hostile environment. Asexual spores form on the unbranched thalli, usually absorbing the protoplast from the vegetative thallus and leaving empty cell walls. These spores continue through the hindgut unaltered and exit with the wastes. Sexual conjugations between adjacent vegetative thalli occur in some populations. When conjugations are occurring, large numbers of thalli in a locality might be sexual. Zygospores are seldom seen in fresh dissections, but in nature zygospores likely are produced by these conjugations. Other larval Diptera have Trichomycetes in the midgut. Species of *Stachylina* are common in chironomids and occasionally in Blephariceridae. No Trichomycetes have been reported from mosquito midguts.

Smittium species are the most commonly cultured Trichomycetes. These branched hindgut-dwelling species are known from larval Diptera such as Chironomidae, Culicidae, Simuliidae, and Tipulidae. Often, a species can inhabit larvae of different host families, a degree of host plasticity not seen in most Harpellales. Asexual spores are produced on branched thalli and have one hair-like appendage. When ingested, the spores react to gut pH changes and potassium levels to avoid germinating in the midgut (high pH) where they do not grow, but delay germination until until they pass to the hindgut with its lower pH. Zygospores are formed after conjugation of thalli and can be quite large. Zygospores of *Smittium megazygosporum* can be up to 150 μm long. Pathogenesis has been reported in the species *Smittium morbosum*. This species appears to mechanically interfere with molting of the hindgut lining and thus leads to mortality.

Stoneflies are hosts of several genera, including *Capniomyces*, *Ejectosporus*, *Genistelloides*, *Orphella*, and *Paramoebidium*. The stonefly genus

Allocapnia has been of particular interest because of its hypothesized biogeography and use in dating symbiotic associations. Two of the species of Trichomycetes (*Genistelloides hibernus* and *Ejectosporus spica*) that colonize *Allocapnia* have a wide distribution. Based on hypothesized host origins, the association is dated from the Pleistocene, and must have been in the host from this time (early in its evolution) and before dispersal. One trichomycete species (*Capniomyces stellatus*) had restricted distribution and was hypothesized to have evolved after *Allocapnia* dispersal.

Organisms that Might Resemble Trichomycetes

Insects host a variety of organisms that can be confused with trichomycetes. Among the nonfungal forms is a bacterium called *Arthromitus*. This bacterium forms chains of cells attached at a common point, so they appear as tufts or clusters. Molecular evidence has shown that many of these are an alternate growth form of the soil bacterium *Bacillus cereus*.

External fungi that resemble Amoebidiales include chytrid fungi and Laboulbeniales. The chytrid fungi resemble *Amoebidium*, but they produce flagellated zoospores for reproduction. The names *Harpochytrium* and *Oedogoniomyces* have been associated with these fungi. These fungi are probably incidentals, and are usually expected on other substrates. The Laboulbeniales can be distinguished by thick cell walls and septate thalli that are often branched. Also, Laboulbeniales are usually restricted to terrestrial insects and often have a tan color. Trichomycetes are usually colorless or white.

Passalid beetles host an ascomycete fungus that grows in a trichomycete-like form in the gut. The septate filaments form tufts on the hindgut lining. These fungi have a yeast-growth form in culture. They belong to the genus *Pichia* or *Enteroramus* (synonym). They have the ability to digest xylose, which can be beneficial to wood-feeding organisms.

References

Leidy J (1849) *Enterobrus*, a new genus of Confervaceae. Proc Acad Nat Sci Philadelphia 4:225–233

Lichtwardt RW (1986) The Trichomycetes: fungal associates of arthropods. Springer, Berlin Heidelberg New York, 343 pp

Lichtwardt RW (1996) Trichomycetes and the arthropod gut. In: Howard D, Miller D (eds) The Mycota, animal and human relations. Springer, Berlin Heidelberg New York, pp 315–330

Lichtwardt RW, White MM, Cafaro MJ (2003) Freshwater trichomycetes and their arthropod hosts. In: Tsui CKM, Hyde KD (eds) Freshwater mycology. Fungal Diversity Research Series 10. Fungal Diversity, Hong Kong, pp 81–100

Misra JK (1998) Trichomycetes-fungi associated with arthropods. Symbiosis 24:179–220

Nelder MP, Beard CE, Adler PH, Kim S-K, McCreadie JW (2006) Harpellales (Zygomycota: Trichomycetes) associated with black flies (Diptera: Simuliidae): world review and synthesis of their ecology and taxonomy. Fungal Diversity 22:121–169

Trichopsocidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice, or Psocids

Trichoptera

An order of insects. They commonly are known as caddisflies.

► Caddisflies

Tricorythidae

A family of mayflies (order Ephemeroptera).

► Mayflies

Tridactylidae

A family of grasshoppers (order Orthoptera). They commonly are known as pygmy mole crickets.

► Grasshoppers, Katydids and Crickets

Trigonalyidae

A family of wasps (order Hymenoptera).
► Wasps, Ants, Bees, and Sawflies

Trimenoponidae

A family of chewing lice (order Phthiraptera). They sometimes are called marsupial lice.
► Chewing and Sucking Lice

Trinotonidae

A family of chewing lice (order Phthiraptera).
► Chewing and Sucking Lice

Triozidae

A family of bugs (order Hemiptera, superfamily Psylloidea).
► Bugs

Tritocerebrum

The portion of the brain that innervates the labrum and stomatogastric nervous system, and the most posterior portion of the brain (Fig. 102).
► Nervous System

Tritrophic Interactions

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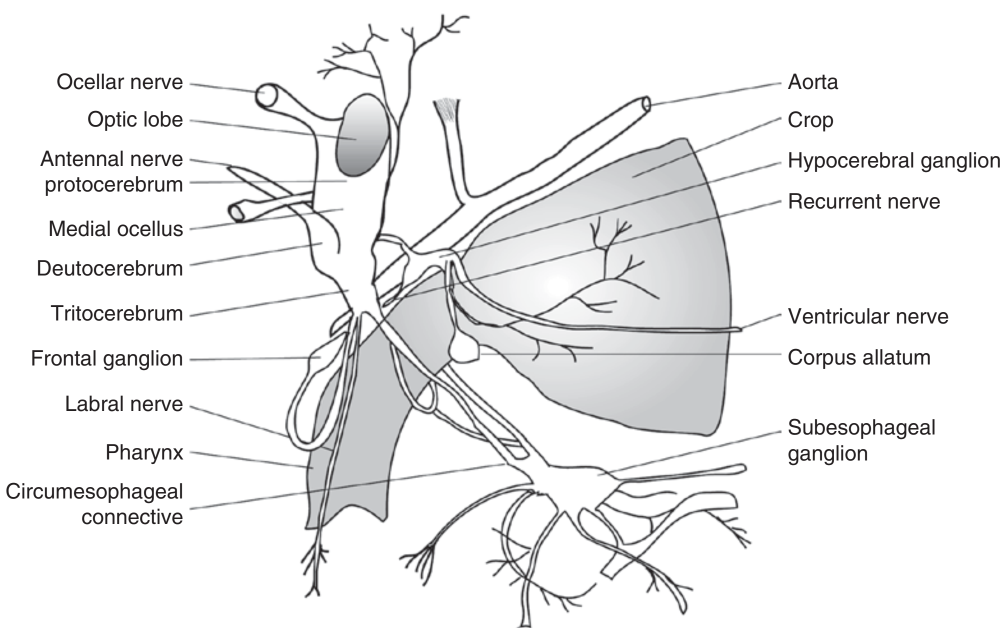
Two central issues in ecology are (i) how do organisms interact with their environment, and (ii) what interactions determine the composition and dynamics of communities. Ecologists have long debated the relative importance of bottom-up and top-down effects on communities. An example of a bottom-up effect is that nutrient availability to plants can affect the composition of insect communities and this can subsequently influence top-down forces. Top-down



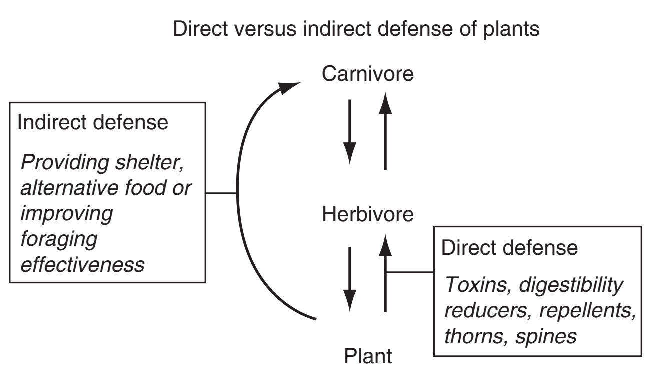
Tritocerebrum, Figure 102 **Diagram of the insect brain, lateral view (adapted from Snodgrass, Insect morphology).**

effects comprise, for instance, the effects of carnivores on herbivore populations with consequences for plant population biology. However, it is becoming more and more clear that this is not an either/or issue, but rather one of the degree to which bottom-up and top-down forces are integrated. Bottom-up forces, such as nutrient availability to plants, can affect the composition of animal communities and this can subsequently influence top-down forces. Furthermore, plants have many characteristics that influence the effectiveness of carnivores in reducing herbivore numbers, i.e., bottom-up and top-down forces can be linked.

Although it is long-known that food webs are composed of more than two trophic levels, it was Price and coworkers who, in 1980, pointed to the important effects of plants on interactions between herbivores and carnivores, and of carnivores on herbivore-plant interactions. They introduced the term "three-trophic level interactions" or "tritrophic interactions." With this term, they indicated that apart from food web considerations where one trophic level feeds on another (lower) level, there are interactions between alternate trophic levels that can be of decisive importance to the outcome of interactions between two subsequent trophic levels. Thus, within a tritrophic context, indirect interactions in a community are considered in addition to direct interactions.

To obtain a sound ecological understanding of each bitrophic interaction (one between plants and herbivores and the other between herbivores and carnivores), it is essential to consider at least three trophic levels and all their interrelationships. For instance, plant defense may be aimed directly against herbivores, but, in addition, carnivores may be a component of the plant's battery of defense. Thus, there are two distinct kinds of plant defense (i) direct defense where plant characteristics have a negative effect on herbivores, and (ii) indirect defense that affects herbivores by promoting the effectiveness of their carnivorous enemies. Direct defense may consist of such elements as repellents, toxins or digestibility reducers, while indirect defense may consist of the provision of shelter, alternative food, or chemical information that promotes the abundance and/or activity of carnivores (Fig. 103).

The majority of research has been done on plants and arthropods and, therefore, this discussion concentrates on these organisms. The arthropods involved are herbivorous arthropods and carnivorous arthropods, i.e., predators and parasitoids (parasitic wasps). Tritrophic interactions between plants, herbivores and carnivores will be addressed. However, tritrophic interactions are not restricted to these three trophic levels; they may also encompass interactions between, for example, herbivores, first order carnivores and second order carnivores.



Tritrophic Interactions, Figure 103 **Direct and indirect defenses of plants in a tritrophic context.**

Plant Characteristics that Affect Herbivores and Indirectly Affect Natural Enemies of the Herbivores

Any plant condition that reduces the growth rate of an herbivore makes the herbivore available to natural enemies for a longer period of time and, thus, raises the probability of mortality. This is especially true for mortality from parasitoid attack, because parasitoids are usually stage-specific and, thus, prolongation of the vulnerable growth stage may be essential for the parasitoid to find that stage. For instance, digestibility reducers have growth-retarding effects. This theory was tested using several soybean varieties, the Mexican bean beetle (*Epilachna varivestis* Mulsant) as the herbivore and some predatory pentatomid bugs. It was found that the herbivores that grew more slowly were more effectively regulated by the predator than those on the soybean variety that was more favorable for herbivore growth. In addition, it was found that the reduced growth rate of the herbivore also affects the functional response of the predator (the relationship between predation rate and prey density) because more small prey are needed for satiation than large prey, and small prey are usually easier to handle by the predator.

Digestibility reducers produced by plants may affect herbivore-natural enemy interactions in several ways:

1. Prolonged developmental time of herbivores and, thus, prolonged risks of attack by carnivores.
2. Reduced resistance of herbivores to pathogens and natural enemies.
3. Reduced herbivore body size and, thus, fecundity, resulting in a lower rate of population increase. This may determine the ability of natural enemies to exterminate the herbivore population.

The influence on enemy effectiveness through a direct influence on herbivores is not limited to digestibility reducers. Any plant characteristic that can affect growth, resistance to disease, or fecundity can have an influence. Variation in plant nutrient composition is probably important in this regard. While such variation probably seldom involves complete presence or absence of essential nutrients, changes in their proportions appear to be commonplace. Effects that are sublethal should, therefore, also be commonplace. Negative effects of imbalanced diets on insect survivorship, growth, and development, not surprisingly, have been demonstrated in controlled artificial diets for a number of insects and nutrients.

On the other hand, retardation of herbivore growth may hamper some predators or parasitoids. For instance, some predators do not take small prey because of a low energetic (nutritional) reward in combination with high capture costs. For example, an insectivorous bird, the European Great Tit, rejects small insect prey when large prey are available.

Another effect of growth rate and size results from the minimum size of an herbivore that is acceptable to its natural enemies; however, this critical size is different for different natural enemy species. Luck and colleagues at the University of California showed that host size is a very important factor in the coexistence of *Aphytis* parasitoid species attacking Californian red scale, *Aonidiella aurantii* (Maskell). *Aphytis lignanensis* needs larger hosts for female progeny than *Aphytis melinus* DeBach. Thus, *A. melinus* can attack hosts before they become available to *Aphytis lignanensis* Compere. In addition, host size depends on plant part. Host size is smallest on wood, largest on fruits and intermediate on leaves. Thus, many more scales are available to *A. melinus* than to *A. lignanensis*, and the degree of this difference is dependent on the location in the tree. As a consequence, *A. melinus* can effectively replace *A. lignanensis* in many citrus areas where red scale is a problem. It is simple to imagine that the three plant parts (wood, leaves and fruits), actually represent different "cultivars" of a species with different levels of defense, and their different impacts on host-parasitoid interactions.

Retardation of growth can also result from induced resistance in plants. In many cases, plant defense is not active prior to herbivore infestation. The damage inflicted by herbivores may induce the defensive actions of plants. Thus, the production of phytoalexins in response to infestation by pathogens is well known. Such induced responses also may occur after an herbivore attack. For instance, tomato plants that are damaged, either by herbivores or by mechanical means, produce proteinase inhibitors that reduce the digestibility of the plant material. These proteinase inhibitors are produced systemically throughout the damaged plant. Induced resistance (or induced direct defense) appears to be rather nonspecific. Infestation with one species of herbivore often affects the performance of other herbivore species as well. Induced resistance lasts for some time after the herbivores are gone. It may last for hours or days, but in some cases (e.g., for perennial plants such as trees), induced resistance has been reported to last for one to several years. Thus, previous and current herbivory may affect the growth rate of other herbivores and, thus, their vulnerability to parasitoids and predators. In addition, mechanical characteristics of plants can be subject to induction also (e.g., trichomes of nettles).

Plant Characteristics that Directly Affect the Effectiveness of Natural Enemies of Herbivores

Mutualisms between plants and animals have been known for a long time but, until the 1980s, the focus had been almost exclusively on mutualisms between plants and herbivores, e.g., involving pollination or seed dispersal. The best and longest (more than 100 years) known mutualism between plants and members of the third trophic level is that between *Acacia* plants and protective ants. The *Acacia* plant provides sugar-containing secretions from extrafloral nectaries and other macronutrients from food bodies on their stems, leaves, or buds. Some *Acacia* species even provide hollow stems, thorns, or bulbs that the ants penetrate to use as shelter for their colonies. The ants guard the source of nutrients and simultaneously defend the plant against herbivorous insects or even encroaching vegetation. Recently, it was shown that ants may even reduce the feeding by large herbivores such as giraffes. Also, less conspicuous structures, such as pits and pouches at vein cross-sections, can function as shelter for carnivorous enemies of herbivores. Such structures are called "domatia" (Greek for "little rooms") and are usually inhabited by predatory or fungivorous mites, whose activities can be important in reducing the abundance of plant attackers.

The protection of plants by ants is far more general than the well-known example of *Acacia* suggests. Many plant species have well-developed nectaries on stems, stipules, or leaves, or they secrete sugar-rich liquid from unopened flower or leaf buds. Such nectaries attract virtually any sugar-loving ants, most of which also eat insects. In temperate climates, seedlings and developing buds often secrete nectar, and are defended by ants. For example, seedlings of cherry trees (*Prunus* sp.) secrete nectar that encourages their defense by a variety of opportunistic ants.

Ants are generalist protectors that can defend a plant against a wide variety of herbivores. However, recent evidence shows that mutualisms between plants and members of the third trophic level also involve much more specialized predators and parasitoids. When a plant is attacked by an herbivore, the plant starts to produce and emit volatiles that attract natural enemies of the herbivore. This appears to be a common phenomenon among plants and many different herbivore species have been shown to induce carnivore attractants in plants (Fig. 104). Herbivory is not always necessary. Hilker and colleagues of the Free University of Berlin showed that even the deposition of herbivore eggs can induce a plant to emit induced volatiles that attract egg parasitoids. It has been shown for several tritrophic systems that the natural enemy discriminates between different plant species infested by the same herbivore species and between different herbivore species on individuals of one plant species. Chemical analyses have shown this specificity on

Herbivore-induced carnivore attractants:
a *common* phenomenon

Plants	Herbivores	Carnivores
• 8 families	• 13 families	• 8 families
• 23 species	• 27 species	• 28 species
Monocots and dicots mostly agricultural plants	e.g. mites, thrips, aphids, butterflies and months	e.g. parasitic wasps and predatory mites and bugs

Tritrophic Interactions, Figure 104 The induction of carnivore attractants by herbivory has been reported for a wide variety of tritrophic systems.

the molecular level. The composition of the blend is determined to the greatest extent by the plant species/cultivar. Not only natural enemies of the herbivore seem to use the herbivore-induced synomone, herbivores may respond also; spider mites avoid locations with high concentrations of induced plant volatiles that are related to conspecific damage. In addition, for a tritrophic system consisting of lima bean or cotton plants, spider mites and predatory mites, it was recorded that downwind, uninfested neighbors of infested plants are more attractive to predatory mites than upwind neighbors or other control plants.

Apart from mutualistic interactions, plants also may hamper the performance of natural enemies. For instance, a thick bark hinders parasitoids that attack herbivores that forage under the bark. The same holds true for the effect of gall thickness on parasitoids of gall-forming herbivores. Hairs on stems and leaves may affect the locomotion and the survival of natural enemies of herbivores (in addition to adverse effects on herbivore performance). For instance, cucumber leaves have many long, non-flexible hairs that interfere with parasitoid movement. In addition, herbivore products, such as honeydew, may adhere to these hairs, which enhances the adverse effects on parasitoid performance. The capability of the parasitoid *Encarsia formosa* Gahan to reduce populations of the greenhouse whitefly (*Trialeurodes vaporariorum*) on cucumbers depends on the density of these hairs. Also, trichomes that hamper herbivore survival may have strong adverse effects on the survival of natural enemies. Hairs, usually seen as a component of direct defense against herbivores thus may be incompatible with natural enemies that are a component of indirect defense.

Effect of Dietary Specialization

An animal's degree of dietary specialization is an important characteristic frequently used in comparative ecological and evolutionary studies. This concept also has been applied to herbivores and their natural enemies, although knowledge on herbivore range used by natural enemies is generally sparse. Dietary specialization of herbivores is assigned to the plant level, while dietary specialization of natural enemies can be assigned to both the herbivore and the plant level.

Specialist herbivores are usually better adapted to plant defenses, such as toxins, than are generalized herbivores. Specialist herbivores can usually tolerate higher levels of toxins and can sequester the defensive plant chemicals. As a result, they usually are much better protected against their natural enemies such as pathogens, predators and parasitoids. For example, consider the interactions between the nicotine in tobacco, the specialist herbivore *Manduca sexta* L. (tobacco hornworm), the generalist herbivore *Trichoplusia ni* (Hübner) (cabbage looper), and a pathogenic bacterium, *Bacillus thuringiensis*. The generalist herbivore is adversely affected by the nicotine in the plant, while the nicotine has only minor effects on the fitness components of the specialist herbivore. Higher nicotine concentrations in the plant are actually beneficial to the specialist herbivore because infection by the pathogen *B. thuringiensis* is reduced. Among predators and parasitoids, the specialists also are better adapted to the defenses of their prey/host. Thus, specialist herbivores are better protected against generalist natural enemies than against specialist natural enemies. This example shows that tritrophic interactions also may extend to pathogens of herbivores. The following example relates to the dietary specialization of parasitoids. Nicotine may be sequestered by *Spodoptera frugiperda* (J. E. Smith) (the fall armyworm), and adversely affects the development and survival of the polyphagous wasp parasitoid, *Hyposoter annulipes* (Cresson). In contrast, the specialist wasp parasitoid, *Cotesia congregata* (Say), is much less affected by the sequestered nicotine.

The first step in the chain of events leading to interactions between an herbivore and its predators or parasitoids is the location of an herbivore-containing habitat from a distance by its natural enemies. Predators and parasitoids are faced with a great variety of stimuli they may use to locate their victim, even when considering only one sensory modality, i.e., chemoreception. Both plants and herbivores produce odors and, thus, potential information. The appropriateness and usability of information ultimately depends on two factors (i) its reliability in indicating herbivore presence, accessibility and suitability, and (ii) the degree to which stimuli can be detected. It is assumed that the use of information that is both reliable and easy-to-detect enhances searching efficiency and consequently, Darwinian fitness.

Stimuli derived from the herbivore itself are generally the most reliable source of information. Ideally, the infochemicals should reliably tell natural enemies whether a herbivore is present, to which species it belongs, whether there is more than one individual and, if so, how many, whether it is suitable to be parasitized or eaten, and whether it is readily accessible or hidden. For parasitoids, whose host continues to develop, and for predators that search for an oviposition site, there is the additional need to know whether the food plant is suitable for the development of their offspring. In fact, the more intimate the herbivore-carnivore interaction, the more specific the information that the carnivore needs.

However, the use of herbivore-derived stimuli often is limited by low detectability, especially at longer distances. Stimuli from plants, on the other hand, are usually more readily available because of the plants' relatively larger biomass, but are less reliable predictors of herbivore presence. Reliability of plant cues depends on the predictability of plant infestation over space and time. So, natural enemies are challenged to combine the advantageous characteristics of information from both trophic levels. It has been hypothesized that detectability of stimuli from the second trophic level puts a major constraint on the evolution of herbivore location by their natural enemies. Natural enemies may approach the reliability-detectability problem in three ways (i) by resorting to the use of infochemicals from herbivore stages different from the one under attack, that are more conspicuous in their infochemical release (infochemical detour), (ii) by focusing their responses to herbivore-induced plant volatiles (HIPV) that originate from specific interactions of the herbivore and its food, and (iii) by learning to link easy-to-detect stimuli (plant cues) to reliable but hard-to-detect stimuli (herbivore cues). Which of these options is/are employed is dependent on the ecological context in which the parasitoid has evolved, and the degree of dietary specialization is an essential aspect of this.

By using the comparative approach, one can speculate whether and, if so, how the natural enemy species' use of herbivore-induced synomones correlates with their dietary specialization. The more natural enemies are specialized at a certain trophic level, the more they innately use infochemicals from that trophic level. In contrast, polyphagy at a trophic level is expected to result in more plastic responses to infochemicals from that trophic level. Thus, it is hypothesized that (i) natural enemies that are specialists on specialist herbivores have strong fixed responses to kairomones from their victims, to uninduced plant volatiles and to HIPV, (ii) natural enemies that attack several herbivore species on one host plant species have fixed responses to general kairomone components shared by the different herbivores and strong fixed responses to uninduced plant volatiles and HIPV, (iii) natural enemies that are specialists on a polyphagous herbivore have strong fixed responses to kairomones and have to learn to respond to plant volatiles and HIPV, and (iv) natural enemies that are extremely polyphagous on polyphagous herbivores are not expected to use infochemicals in finding their prey or hosts. These four categories are extremes in a continuum. The ecological settings of many natural enemies are intermediates along the continuum. The way these species use infochemicals will depend on the relative importance of the diet breadth at each trophic level.

Relative Importance of Plant and Natural Enemies to Herbivore Fitness

Herbivorous arthropods are affected by both their food plants and by predators and parasitoids. They have to deal with plant defenses such as toxins and digestibility reducers, but also with predator attacks. In general, it seems that there is a wide variation in effects of plants and natural enemies on the fitness of herbivores. This has led to speculation on which effects are the most important: "top-down effects" (effects of natural enemies) or "bottom-up effects" (effects of plants). The answer to this question is not likely to receive a general answer. It seems that the relative importance of the two effects is dependent on system-specific characteristics and the two effects are integrated, rather than alternatives.

The discussion about top-down and bottom-up effects is remarkable with respect to herbivore specialization. Two main selective forces have been mentioned: plant secondary chemicals have long been assumed to be the selective force determining the high degree of specialization among herbivores. More recently, natural enemies of herbivores have been mentioned as another important selective.

The role of toxic plant secondary chemicals has centered on the so-called "arms race" of plants and herbivores. Less than 10% of all herbivorous insects are polyphagous species that feed on plants in more than three different plant families. The high degree of specialization of insect herbivores usually is explained by the existence of secondary plant chemicals. However, this has received criticism by L. Bernays and colleagues at the University of Arizona who argue that generalist natural enemies, especially predators of the herbivores, may be an important factor in the evolution of narrow host range. Bernays and colleagues argue that oviposition choice and/or host utilization ability can be significantly altered within only 10–16 generations, which implies that current patterns of host use should probably be seen as ecologically dynamic, and not as an end result of co-evolutionary processes over millennia. Moreover, host shifts by insects with a restricted host range often are to unrelated plant species, suggesting that behavioral barriers do not simply reflect a need to avoid toxins. Plant secondary chemicals tend to provide the proximate, mechanistic bases for narrow host range, but do not necessarily provide the ultimate, functional basis for the patterns presently seen. An important aspect in their arguments is the concept of "enemy-free space," which indicates that, on some plants, an herbivore is not, or is less, affected by natural enemies compared to other plant species. Within a given place and time, preference for a plant less likely to be visited by natural enemies could evolve rapidly. Specializations for continued avoidance of predators also may then be rapidly selected and established. For example, it is self-evident that the most effective insect crypsis is developed on specific substrates, and the most celebrated instances of sequestration of compounds toxic to vertebrates from plants are reported for insects with specialized feeding habits. Both of these specializations are predator related. Because many parasitoids are relatively restricted in host range, or restricted in the ranges of plants searched, they might be more important in causing host switches or broadening herbivore host range. This could leave the predator element as the most important factor in pushing insect herbivores toward narrow host range and the specializations that can then follow.

The Plant's Perspective: A Paradox in Its Defense Against Herbivores and the Answer in a Tritrophic Context

The previous section considered the herbivore's viewpoint of being in between plant defense and natural enemy attack. When taking the plant's perspective of defense against herbivores, a bitrophic view may yield a paradox. If plants affect herbivore fitness by reducing the food quality through digestibility reducers or nutrient composition (e.g., low nitrogen content), the herbivores will respond by inflicting more damage to compensate (e.g., by prolonged feeding, or more intense feeding). Natural enemy attack may be the essential factor needed to turn digestibility reducers into a positive trait. Digestibility reducers result in longer duration of herbivore stages. This may affect attacks by parasitoids that are usually rather restrictive as to the herbivore instar they attack, or attacks by (insect) predators that consume more small prey than large prey. However, experimental evidence for this often-mentioned scenario is still limited.

Plants also may face another dilemma. If the secondary chemicals the plants produce are sequestered by specialist herbivores, that means the herbivores exploit the plant's defense for their own protection against carnivores, and the plant faces a net ecological cost. Many plants only start the (increased) production of these secondary metabolites in response to herbivory. A recent example shows that the induction can be dependent on the herbivore that feeds on the plant. Wild tobacco plants initiate nicotine production in response to wounding by such factors as rabbit feeding or mechanical wounding. However, Kahl and colleagues at the Max Planck Institute for Chemical Ecology showed that when caterpillars of a specialist herbivore, i.e., tobacco hornworm (*M. sexta*), feed on the plant, the plant does not initiate a high nicotine biosynthesis, but rather, initiates the production of volatiles that attract carnivorous enemies of the specialist herbivore.

Hidden Players

Currently, tritrophic interactions are mostly considered for above-ground interactions of plants, and herbivorous and carnivorous arthropods. However, it is increasingly apparent that microorganisms play an important role in communities in general, and in plant-insect communities in particular. Microorganisms may compete with insects for food, and microorganisms may be symbionts or pathogens of insects. Therefore, all interactions in tritrophic systems can be affected by microorganisms. Research in this area is rapidly increasing.

Moreover, most knowledge on tritrophic interactions relates to above-ground systems, especially because they are more easily investigated than below-ground interactions. However, above-ground and below-ground interactions cannot be considered individually because they are intimately linked. Intensified research on below-ground interactions, as well as their link to above-ground interactions, is foreseen for the near future.

Theories on Plant Defense

Classical plant defense theory describes the evolution of secondary plant substances in direct defense against herbivores as the result of an arms race between plants and herbivores: plants evolve secondary metabolites in response to attacks by insects, while insects meet the challenge by evolving new detoxification systems. In the 1970s, P. Feeny of Cornell University, and D. Rhoades and R. Cates at the University of Washington, developed a theory that centers on plant "apparency," which emphasizes the herbivore's perspective. A third plant defense theory is the "resource availability theory," developed by P. Coley and colleagues at the University of Utah. This theory emphasizes the plant's perspective and centers around the possibilities of defense as affected by the availability of nutrients and energy.

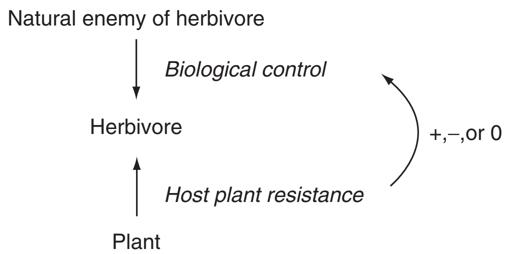
The relatively young field of three-trophic-level interactions has not been the subject of many theoretical considerations. Yet, Price at Northern Arizona University has integrated the plant apparency theory with the actions of natural enemies (indirect defense). He argues that many of the broad patterns relating to natural enemies discovered to date relate to gradients from herbs to shrubs to trees, from unstable to stable environments, and from herbivores with external to concealed feeding habits. When using plant succession as a starting point, and concentrating on parasitoids as natural enemies, Price notes five patterns:

1. With plant succession, the number of parasitoid species per host species increases.
2. With plant succession, the prevalent parasitoid species becomes more generalistic.
3. With an increase in the number of parasitoid species per host species, host mortality increases; this has not been well-studied.
4. With an increase of the number of parasitoid species per host species, the probability increases that herbivore populations are regulated.
5. Host-specific parasitoids (that are more often present in early succession stages) have innate and strong responses to kairomones and plant volatiles, whereas generalistic species (more frequently present in later successional stages) have more plastic responses that are subject to learning.

Price then theorizes on the differences in plant defenses in early and late succession. In early succession, plants are unapparent to herbivores and defend themselves through specific toxins. Thus, host location by parasitoids is constrained and the parasitoids need specialized enzymes to cope with the sequestered toxins in the herbivores. Thus, selection will favor specificity of the parasitoids. It is exactly host-specific parasitoids that are predicted to use specific synomones and kairomones in host location in a genetically fixed pattern. In late succession, plants are apparent and defend themselves in similar ways (convergence) through digestibility reducers. This increases the chance that an herbivore will include a new plant species in its diet; herbivores are less plant-specific. Parasitoid species may be more generalistic than in early successional stages. For these parasitoids, the recognition of, and innate response to, a large number of specific synomones and kairomones is less likely (physiological constraint) and, thus, learning will be more important.

Applied Aspects

The importance of considering interactions between insects and their food and enemies in a multitrophic context has been realized since the beginning of the 1980s. Thus, the field of tritrophic interactions is a relatively young one. However, developments in this field are quick and the knowledge gained is not only important from a scientific point of view, but also from an applied point of view. For instance, in environmentally benign pest control, herbivores can be controlled through plant breeding for resistance and through biological control (Fig. 105). The combination of these two methods may be explicitly exploited, or may occur without special intervention, because naturally occurring, carnivorous arthropods often play an important, but unnoticed, role in the reduction of pest populations. Therefore, it is important that these two methods are synergistic rather than antagonistic. However, synergistic interaction between host plant resistance and biological control is by no means self-evident. If certain plant characteristics are selected because they have a negative influence on herbivores in the absence of biological control agents, this does not automatically mean that the plant contributes to pest control in the presence of biological control agents. A remarkable example was recorded for cabbage plants. Two cabbage varieties differed in resistance against the cabbage aphid, *Brevicoryne brassicae* (L.), which resulted in reduced aphid populations when parasitoids had been excluded. However, the susceptible cultivar emitted larger quantities of a parasitoid-attracting volatile and, therefore, under conditions where biological control was applied, aphid densities were lower on the susceptible variety than on the resistant variety.



Tritrophic Interactions, Figure 105 Durable and environmentally benign pest management can incorporate host plant resistance and biological control. Host plant characteristics may affect biological control positively, negatively, or not at all. Which of these interactions between host plant resistance and biological control occurs can be important for the success of environmentally benign pest control.

Along similar lines, current developments should be considered in the field of transgenic insect-resistant plants. So far, the main emphasis is on the effects of the transgenic plants on pest insects, without much emphasis on tritrophic effects. However, an important question is: Do plants that have been engineered to express certain toxins affect non-target organisms, including non-target herbivores and carnivorous arthropods that attack target and/or non-target herbivores?

Agricultural plants have to produce under conditions where they are members of a community. Agroecosystems harbor a diverse community – even when they are usually less diverse than the community in a natural ecosystem – and if important carnivores are eliminated or hampered by introducing crop plants that have different characteristics, the result may be that pest control is hampered rather than improved. This is a lesson that is older than the research on tritrophic interactions. The dusting of crop plants with broad-spectrum pesticides in the 1960s and 1970s can be seen as an artificial alteration of plant characteristics that had severe impacts on pest control, where even novel pests were induced as a result of the elimination of carnivorous arthropods.

Conclusion

Interactions in communities comprise direct and indirect interactions. Characteristics of community members can have effects on interactions with their direct enemies or resources, but also on non-producer/consumer interactions. Indirect interactions are by no means less important than direct interactions between producers and consumers. Indirect interactions can decisively influence producer-consumer interactions. Tritrophic interactions show that the debate on the role of bottom-up versus top-down forces in shaping communities is not an either/or debate, but rather one of the degree of integration of the two forces. Considering tritrophic interactions is not only interesting from a basic point of view, it is also important from an applied point of view (for example, in developing novel methods of environmentally benign pest control). Finally, the study of tritrophic interactions is not an endpoint but only a beginning. After initiating studies on interactions among plants, herbivores and carnivores (not exclusively insects), it is now clear that microorganisms can play important roles in these interactions. Moreover, second-order carnivores and interactions with organisms that cannot be exclusively linked to a single trophic level, such as omnivores, should be included as well. Therefore, the study of tritrophic interactions is evolving into the research area of multitrophic interactions.

References

Barbosa P (1988) Natural enemies and herbivore-plant interactions: influence of plant allelochemicals and host specificity. In: Barbosa P, Letourneau DK (eds) Novel aspects of insect–plant interactions. Wiley, New York, pp 201–229

Bernays E, Graham M (1988) On the evolution of host specificity in phytophagous arthropods. Ecology 69:888–892
Chadwick DJ, Goode JA (eds) (1999) Insect–plant interactions and induced plant defense. Novartis Found Symp 223. Wiley, Chichester
Dicke M (1999) Direct and indirect effects of plants on performance of beneficial organisms. In: Ruberson JR (ed) Handbook of pest management. Marcel Dekker, New York, pp 105–153
Dicke M (1999) Evolution of induced indirect defense of plants. In: Tollrian R, Harvell CD (eds) The ecology and evolution of inducible defenses. Princeton University Press, Princeton, NJ, pp 62–88
Groot AT, Dicke M (2002) Insect-resistant transgenic plants in a multitrophic context. Plant J 31:387–406
Hilker M, Meiners T (2002) Induction of plant responses towards oviposition and feeding of herbivorous arthropods: a comparison. Entomol Exp Appl 104:181–192
Karban R, Baldwin IT (1997) Induced responses to herbivory. Chicago University Press, Chicago
Price PW, Bouton CE, Gross P, McPheron BA, Thompson JN, Weis AE (1980) Interactions among three trophic levels: influence of plant on interactions between insect herbivores and natural enemies. Annu Rev Ecol Syst 11:41–65
Price PW (1991) Evolutionary theory of host and parasitoid interactions. Biol Control 1:83–93
Turlings TCJ, Loughrin JH, McCall PJ, Rose USR, Lewis WJ, Tumlinson JH (1995) How caterpillar-damaged plants protect themselves by attracting parasitic wasps. Proc Natl Acad Sci USA 92:4169–4174
Van der Putten WH, Vet LEM, Harvey JA, Wackers FL (2001) Linking above-and belowground multitrophic interactions of plants, herbivores, pathogens, and their antagonists. Trends Ecol Evol 16:547–554
van Emden HF (1986) The interaction of plant resistance and natural enemies: effects on populations of sucking insects. In: Boethel DJ, Eikenbary RD (eds) Interactions of plant resistance and parasitoids and predators of insects. Ellis Horwood, Chichester, pp 138–150
Vet LEM, Dicke M (1992) Ecology of infochemical use by natural enemies in a tritrophic context. Annu Rev Entomol 37:141–172

Triungulin

The active first instar of stylopids (Strepsiptera) and certain beetles (Coleoptera) that undergo hypermetamorphosis, becoming less active after they find a host and commence feeding (contrast with planidium).

Triunguloid Larva

A larval body form with minute, active, spiny first instars, and found in certain predaceous beetles and stylopids.

► Triungulin

Trochanter

A small leg segment found between the coxa and femur. The second segment of the leg (Fig. 106).

► Legs of Hexapods

Trochantin

The basal part of the trochanter when it is subdivided. In Coleoptera and some other groups, it refers to a structure present on the outer side of the coxa.

Trochiliphagidae

A family of chewing lice (order Phthiraptera).

► Chewing and Sucking Lice

Troctopsocidae

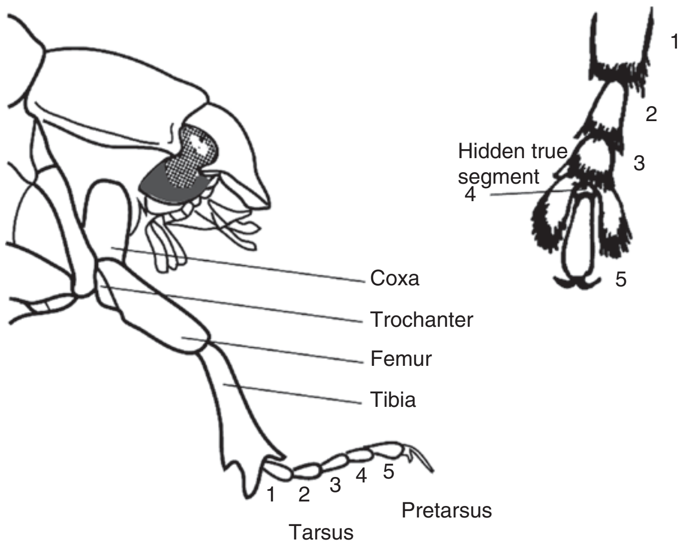
A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice and Psocids

Trogidae

A family of beetles (order Coleoptera). They commonly are known as skin beetles.

► Beetles



Trochanter, Figure 106 **Leg of a beetle (Coleoptera: Scarabaeidae) leg showing its component parts, and a close-up of one type of beetle tarsus (foot).**

Trogiidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice and Psocids

Trophallaxis

A behavior found in social insects involving the exchange of food between members of the colony, or among colony members and guests. The food may originate from the mouth (stomodeal trophallaxis) or from the anus (proctodeal trophallaxis).

Trophic Egg

A degenerate egg that is inviable, and used to feed other members of the colony.

Trophic Level

The classification of organisms in a community according to their feeding relationships. The first trophic level usually is green plants. The second tropic level includes herbivores, and insects are a principal component. However, insects also are carnivores, parasites, and detritivores, so they appear in various tropic levels (Table 15).

Trophic Structure

Organization of a community in terms of energy flow through the constituent trophic levels.

Trophobiosis

The indirect stimulation of reproduction through plant conditioning following the host plant's exposure to insecticides. Normally the insecticide affects the nutrient condition in a favorable manner. This phenomenon is best documented in aphids.

Trophogenic Polymorphism

Polymorphism in social insects due to differential feeding of the larvae, or different sized eggs.

Trophic Level, Table 15 Trophic relationships of some insect orders

Primary consumers (herbivores)	Secondary consumers (insectivores and carnivores)	Decomposers
Coleoptera (some)	Coleoptera (some)	Coleoptera (some)
Diptera (some)	Diptera (some)	Diptera (some)
Embiidina	Ephemeroptera (some)	Ephemeroptera (some)
Grylloblattodea	Hemiptera (some)	Isoptera
Hemiptera (some)	Hymenoptera (SimpleParasitic and provisioning wasps)	Plecoptera (some)
Hymenoptera (sawflies, horn-tails, some bees)	Mallophaga	
Mecoptera	Mantodea	
Lepidoptera	Megaloptera	
Orthoptera	Neuroptera	
Phasmatodea	Odonata	
Thysanoptera (most)	Plecoptera (some)	
	Raphidioptera	
	Siphunculata	
	Thysanoptera (some)	
	Trichoptera	

Tropical Burnet Moths (Lepidoptera: Lacturidae)

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Tropical burnet moths, family Lacturidae, total 138 species, mostly Indo-Australian but with a few in the southern United States; actual world fauna probably exceeds 250 species. The family is in the superfamily Sesioidea in the section Tineina, subsection Sesiina, of the division Ditrysia. Adults small to medium size (11–65 mm wingspan), with head scaling average; haustellum naked; labial palpi upcurved; maxillary palpi small, 1- to 2-segmented; antennae filiform. Wings elongated. Maculation usually colorful, especially with orange, red and yellow colors, and with various bands or spots, and with darker hindwings. Adults nocturnal but some may be crepuscular. Larvae are leaf skeletonizers and are colorful, but most are not known biologically; somewhat slug-like, with concealed head. Host plants include families Celastraceae, Moraceae, and Sapotaceae.

References

Busck A (1913) Notes on the genus *Mieza* Walker, with descriptions of three new species from Costa Rica. Insecutor Inscitiae Menstruus 1:70–73
Common IFB (1990) Family Zygaenidae (burnets, foresters) [part]. In: Common IFB, Moths of Australia. Melbourne University Press, Carlton, pp 294–299
Heppner JB (1995) Lacturidae, new family (Lepidoptera: Zygaenoidea). Trop Lepidoptera 6:146–148

Tropical Carpenterworm Moths (Lepidoptera: Metarbelidae)

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Tropical carpenterworm moths, family Metarbelidae, include 103 species, mainly Afrotropical and

Oriental, with one species in the Palearctic region; actual world fauna likely exceeds 150 species. The family is in the superfamily Cossoidea (series Cossiformes) in the section Cossina, subsection Cossina, of the division Ditrysia. Some recent views place the group as a subfamily of Cossidae. Adults small to medium size (21–48 mm), with head small and rough scaled; labial palpi upcurved; maxillary palpi minute; antennae short and bipectinate; legs short. Body robust. Wings elongated and rounded (frenulum-retinaculum usually absent). Maculation mostly shades of brown and gray, even nearly white background, with dark spotting (often also with a preapical darker forewing discal spot); hindwings darker. Adults may be crepuscular. Larvae nocturnal borers on tree bark or in tree trunks, but most species remain unknown biologically. Host plants include various trees in Anacardiaceae, Guttiferae, Lauraceae, Leguminosae, Myrtaceae, Rhamnaceae, Rutaceae, Sapindaceae, and Sterculiaceae. A few have minor economic status.

References

Dalla Torre KW, von Strand E (1923) Lepidarbelidae. Lepidopterorum Catalogus, 28:1–14 [part]. W. Junk, Berlin

Holloway JD (1986) Family Metarbelidae. In: Moths of Borneo, 1:42–46, pl. 4. Malayan Nature Society, Kuala Lumpur (Malayan Nat J 40:42–46, pl. 4)

Janse AJT (1925) A revision of the South African Metarbelidae. S Afr J Nat Hist 5:61–100, pl. 4–8

Seitz A (1929) Familie: Indarbelidae. Die Gross-Schmetterlinge der Erde, 10:803–806, pl. 93 (1933); 14:501–513, pl. 78 (1929). A. Kernen, Stuttgart

Srivastava AS (1962) A preliminary study of the life-history and control of *Indarbela quadrinotata* Wlk. (Metarbelidae: Lepidoptera). Proc Natl Acad Sci India 328:265–270

Tropical Ermine Moths (Lepidoptera: Attevidae)

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Tropical ermine moths, family Attevidae, include 48 species, mostly tropical and in the genus *Atteva* (the single partially non-tropical species known occurs across the southern United States and into the Caribbean and Mexico); actual fauna probably at least 60 species. The family is part of the superfamily Yponomeutoidea in the section Tineina, subsection Tineina, of the division Ditrysia. Adults small to medium size (20–34 mm wingspan), with head smooth-scaled; haustellum naked; labial palpi upcurved; maxillary palpi 1- to 2-segmented. Wings elongated with termens rather rounded. Maculation usually colorful (many with red or orange forewings), with various spots on the forewings (Fig. 107). Adults diurnal or crepuscular. Larvae are leaf webbers and leaf skeletonizers on Araliaceae and Simaroubaceae. Minor economic species occur on *Ailanthus* trees in India and the United States.

References

Clarke JFG (1965) Atteva Walker. In: Clarke JFG, Hyponomeutidae [sic], in Catalogue of the type specimens of Microlepidoptera in the British Museum (Natural History) described by Edward Meyrick, 5: 292–293. British Museum (Natural History), London

Mathur RN (1960) Setal arrangement of *Atteva fabriciella* Swederus (Yponomeutidae, Lepidoptera). Indian J Entomol 21:1–5

Powell JA, Comstock JA, Harbison CF (1973) Biology, geographical distribution, and status of *Atteva exquisita* (Lepidoptera: Yponomeutidae). Trans San Diego Soc Nat Hist 17:175–186

Taylor OR (1967) Relationship of multiple mating in *Atteva punctella* (Lepidoptera: Yponomeutidae). Ann Entomol Soc Am 60:583–590

Tropical Fruit Pests and their Management

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Tropical fruits are important in several production areas of south and southeast Asia, Australia,

Tropical Ermine Moths (Lepidoptera: Attevidae), Figure 107 Example of tropical ermine moths (Attevidae), *Atteva niveigutta* Walker from India.

Africa, the Mediterranean, the Americas and the Caribbean region. Tropical fruits are regularly grown in different climates from latitude 23°27″N to 23°27″S of the equator, while some are grown to approximately 37°N in Spain. Proximity to the sea, sea currents, altitude, direction of prevailing winds, rainfall and air humidity all have modifying effects on these crops. Most tropical fruits are perennial plants which persist for several years without abrupt, major changes other than seasonal leaf formation, flowering, and fruit development. However, pineapple, papaya, and passion fruit are grown for shorter periods of time and their arthropod management is influenced by their persistence in the field.

In general, tropical fruit crops provide a relatively stable environment over many years, offering continuing habitats for both pests and natural enemies and providing opportunities for biological control and effective pest management programs. Avocado, mango, pineapple, banana, passion fruit, litchi, guava, *Annona* spp., durian, mangosteen, rambutan, acerola and carambola, and their most common pests are included here.

Annona Fruits (Annonaceae Family)

The genus *Annona* embraces several valuable fruit trees and is centered in the Neotropics, with about 110 species. The most common species are *A. muricata* L., *A. montana* McFadden, *A. glabra* L., *A. cherimola* P. Miller, *A. squamosa* L., *A. reticulata* L., and *A. longiflora* Watts. Fruits of Annona are fleshy aggregates that arise from coalesced carpels and contain large seeds with reticulate endosperm.

Most species of Annona have specific climatic requirements for growth, flowering, and fruit maturation. The origins of the tropical species, such as the sugar apple (*A. squamosa*), are the warm lowland regions of Brazil, Guyana, Venezuela, Mexico, and the West Indies. A distinctly subtropical species is the cherimoya (*A. cherimola*), which originates from the cool Andean valleys of Peru and Ecuador at elevations of around 2,000 m. The hybrid atemoya (*A. cherimola* × *A. squamosa*), which appeared spontaneously when parent trees were cultivated side by side and also through manual pollination, exhibits intermediate climatic requirements for growth and fruiting.

Within the family Annonaceae, fruits of the cherimoya, sugar apple, atemoya, and soursop (*A. muricata*) have the greatest potential for utilization and export in the American, Caribbean, Asian and Australian countries. Much of the production of commercially grown species has spread from their indigenous areas to tropical and subtropical parts of Australia, New Zealand, Asia and around the Mediterranean. Thus, production methods vary from more sophisticated systems to less intensive, small farm or backyard type production. The key pests are the annona seed borers, *Bephratelloides* spp., *B. cubensis* (Ashmead), *B. pomorum*, *B. paraguayensis* (Crawford), and *B. petiolatus* Grissell and Schauff (Hymenoptera: Eurytomidae), destroying seeds and pulp; fruit borers, *Cerconota anonella* Sepp (Lepidoptera: Oecophoridae), *Talponia batesi* Heinrich (Lepidoptera: Tortricidae) and *Thecla ortyginus* (Lepidoptera: Lycaenidae); fruit flies, the Queensland fruit fly, *Bactrocera tryoni* (Froggatt), *Anastrepha* spp., and *Ceratitis capitata* (Diptera: Tephritidae); and recently, the pink hibiscus mealybug, *Maconellicoccus hirsutus* (Green), causing defoliation.

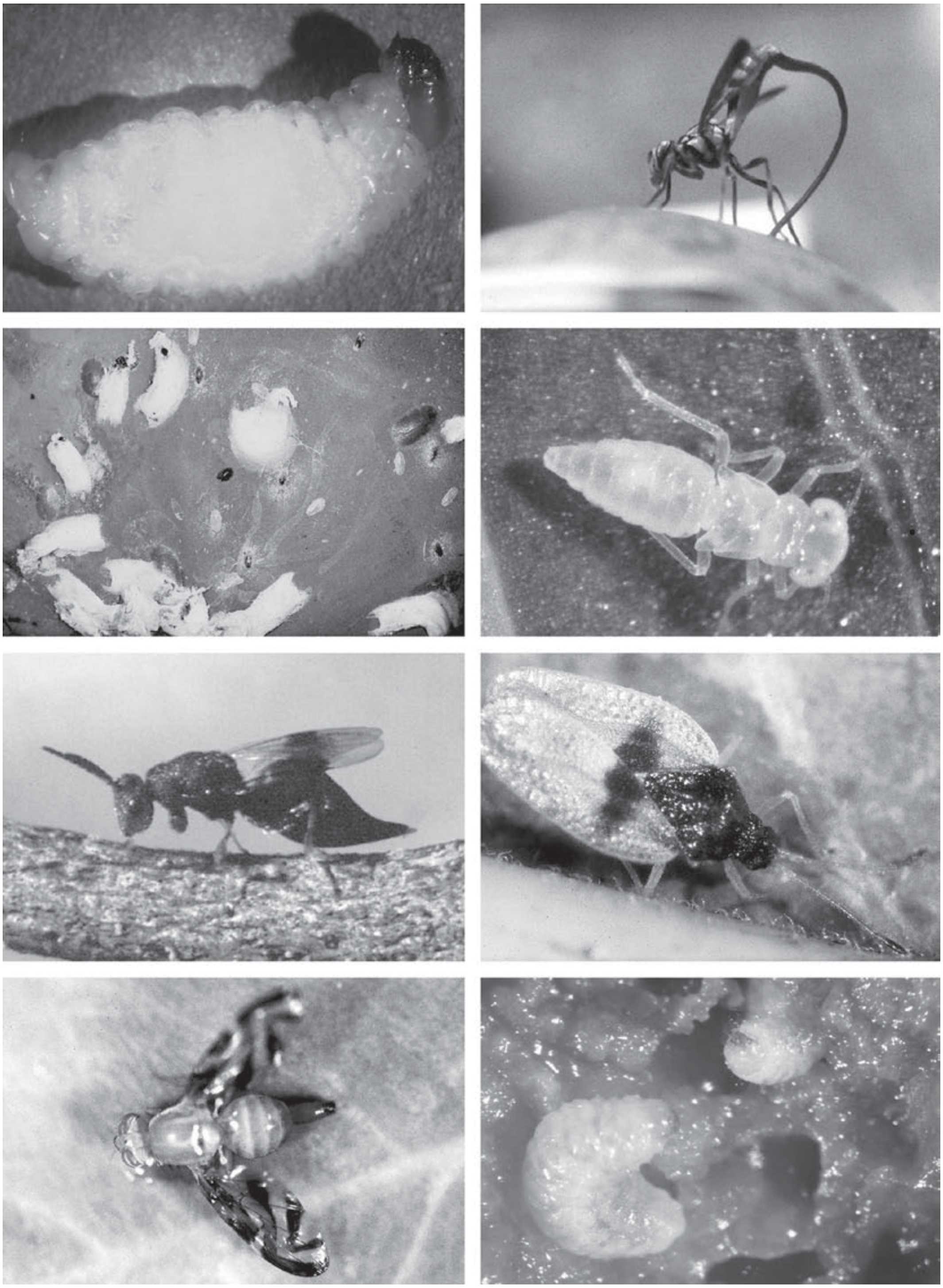
Avocado, *Persea americana* Mill. (Lauraceae family)

The avocado, *Persea americana* Mill. (Lauraceae), is of Central American origin and well known to the native inhabitants of Mexico, Central America and northern South America. Today, avocado is grown commercially not only in North America and throughout tropical America and the larger islands of the Caribbean, but also in Polynesia, the Philippines, Australia, New Zealand, Madagascar, Mauritius, Madeira, the Canary Islands, Algeria, tropical Africa, South Africa, southern Spain, southern France, Sicily, Crete, Israel and Egypt. The most important pests include the tea red mite, *Oligonychus coffeae* (Nietner), avocado brown mite, *Oligonychus punicae* (Hirst), the persea mite, *Oligonychus perseae* (Tuttle, Baker and Abbatiello), and the avocado red mite, *Oligonychus yothersi* (McGregor) (Acari: Tetranychidae), as well as the eriophyid mite *Tegolophus perseaeflorae* (Keifer) (Acari: Eriophyidae). Severe damage to the leaves can be produced by the psyllids *Trioza anceps* Tuthil and *Trioza perseae* Tuthill (Hemiptera: Psyllidae), and by the large blacktip wilter, *Anoplocnemis curvipes* F., injuring new flush, and by the leaffooted bugs, *Amblypelta nitida* Stål and *A. lutescens* lutescens (Distant) (Hemiptera: Coreidae), attacking fruits. Other important species are the avocado lace bug, *Pseudacysta perseae* (Heidemann) (Hemiptera: Tingidae) (Fig. 108), causing leaf chlorosis and necrosis, the mirids, *Dagbertus fasciatus* (Reuter), *D. olivaceous* (Reuter), and *Rhinacloa* sp. (Heteroptera: Miridae), affecting flowers and fruitlets, the thrips, *Scirtothrips aguacatae* Johansen and Mojica and *Scirtothrips kupae* Johansen and Mojica, *Scirtothrips perseae* Nakahara, the red-banded thrips, *Selenothrips rubrocinctus* (Giard) (Thysanoptera: Thripidae), affecting leaves and sometimes fruits. Among lepidopterans, several species affect production, including the avocado seed moth, *Stenoma catenifer* Walsingham (Lepidoptera: Oecophoridae), the western avocado leaf roller, *Amorbia cuneana* Walsingham (Lepidoptera: Tortricidae), and the avocado loopers *Anacamptodes defectaria* (Guenée), *Epimeces detexta* (Walker), *Epimeces matronaria* (Guenée), *Oxydia vesulia transponens* (Walker), and *Sabulodes aegrotata* Guenée (Lepidoptera: Geometridae), which consume foliage and eventually chewing on small fruit.

Other important pests are the weevils, *Conotrachelus perseae* Barber, *Conotrachelus aguacatae* Barber, *Conotrachelus serpentinas* (Klug) and *Heilipus lauri* Bohemann (Coleoptera: Curculionidae), boring into fruits and seeds.

Banana and Plantain, *Musa* spp. (Musaceae Family)

Bananas and plantains (*Musa* spp.) are among the most important crops in tropical and subtropical climates. The genus *Musa* evolved in Southeast Asia where numerous undomesticated *Musa* species still grow as opportunistic weeds. Edible bananas (*Musa* spp., *Eumusa* series) originated within this region from two wild progenitors, *Musa acuminata* and *M. balbisiana*, producing a series of diploids, triploids and tetraploids through natural hybridization. Additionally, man has selected for parthenocarpy (development of fruit without pollination or seeds). Hybridized bananas may be divided into six genome groups (i.e., AA, AAA, AAB, AB, ABB, ABBB) based on the relative contributions of *M. acuminata* and *M. balbisiana*. Domesticated bananas include a wide range of dessert, cooking and brewing cultivars. The most extensively grown bananas are triploids. In terms of gross value of production, bananas and plantains are the fourth most important global food crop. Bananas grown for export are almost exclusively of one variety, "Cavendish"; this cultivar accounts for slightly more than 10% of global production. Bananas are rhizomatous herbaceous plants ranging in height from 0.8 to 15 m. A mat (=banana stool) consists of an underground corm (rhizome) from which one or more plants (shoots) emerge. Adventitious roots spread extensively 4–5 m from the parent and downward 75 cm or more; however,



Tropical Fruit Pests and their Management, Figure 108 Some tropical fruit pests: *upper left*, banana weevil larva (photo Rita Duncan); *upper right*, papaya fruit fly (photo R. Swanson); *second row left*, papaya scale (photo M. Shepard); *second row right*, papaya leafhopper (photo Rita Duncan); *third row left*, Annona seed borer (photo H. Nadel); *third row right*, avocado lacebug (photo J. Peña); *bottom left*, Caribbean fruit fly (photo Rita Duncan); *bottom right*, Acerola weevil larva (photo Rita Duncan).

most roots are near the soil surface. Plants represent a single shoot (pseudostem, stem, leaves, flower and bunch). Yield is normally expressed in kg/area/year reflecting both number and size of bunches harvested.

Pests of the corm and pseudostem include the banana weevil, *Cosmopolites sordidus* (Germar), banana pseudostem borer, *Odoiporous longicollis* (Olivier) and the West Indian sugarcane borer, *Metamasius hemipterus sericeus* (Olivier) (Coleoptera: Curculionidae). The following are pests of flowers and fruits: banana thrips *Hercinothrips bicinctus* (Bagnall), *Caliothrips bicinctus* Bagnall, *Chaetanaphothrips orchidii* (Moulton), *C. signipennis* (Bagnall), *Thrips hawaiiensis* (Morgan) and *Tryphactothrips lineatus* Hood (Thysanoptera: Thripidae), while the banana fruit scarring beetles, *Colaspis hypochlora* Lefebre (Coleoptera: Chrysomelidae) and the "Irapua" bee, *Trigona spinipes* Fabricius (Hymenoptera: Apidae), are considered troublesome in some areas in the Neotropics. The banana moths, *Opogona sacchari* Bojer, *Opogona glyciphaga* (Meyrick) (Lepidoptera: Tineidae), the banana scab moth, *Nacoleia (Notarcha, Lamprosema) octasema* (Lepidoptera: Pyralidae) damage flowers and sometimes bunches. Important pests of foliage include the bagworm, *Oiketikus kirbyi* Guilding (Lepidoptera: Psychidae), *Caligo* spp., *Opsiphanes* spp. (Lepidoptera: Nymphalidae). The banana aphid, *Pentalonia nigronervosa* Coquerel. (Heteroptera: Aphidae) is important as the sole vector of the bunchy-top disease.

Barbados Cherry or Acerola, *Malpighia glabra* (L.) (Malpighiaceae Family)

Barbados cherry is a tropical fruit native to the West Indies, Central America, and South America. Recently, the Barbados cherry has received attention because its fruits are exceptionally high natural source of ascorbic acid (vitamin C). Its cultivation has extended throughout the subtropics and tropics and some of the largest plantings are in Brazil. Estimated commercial acreage in the Caribbean region is more than 400 acres with a potential crop value of several million U.S. dollars. Flowering and fruit set occurs almost continuously from April through November in Florida, and fruits mature in approximately 30 days. Acerola's most important pests are the acerola weevil, *Anthonomus macromalus* Gyllenhal (=*A. flavus*, =*A. bidentatus*, =*A. malpighia*) (Coleoptera: Curculionidae), injuring fruits and flowers; fruit flies, *Anastrepha* spp., and the Mediterranean fruit fly, *Ceratitis capitata* Wiedemann (Diptera: Tephritidae), and the coreids, *Leptoglossus* spp., *Crinocerus* spp. (Hemiptera: Coreidae), and the stink bug, *Nezara viridula* L (Hemiptera: Pentatomidae), causing fruit deformation.

Carambola, *Averrhoa carambola* L. (Oxalidaceae Family)

Known as carambola, star apple, or five corner, this fruit tree is a 5–12 m high evergreen tree native to southern Asia. Leaves imparipinnate, flowers in axillary or cauliflorous panicles, pentamerous. The fruit is a large berry, ovoid to ellipsoid in outline, with five pronounced ribs, stelate in cross section. The tree grows well in tropical or subtropical lowland conditions and flowers abundantly. Most of the information on pests of carambola comes from southeastern Asia and Australia. Important arthropods include the carambola fruit fly, *Bactrocera carambolae* Drew and Hancock (Diptera: Tephritidae), whose larvae feed on the fruit and make tunnels in the fruit; fruit piercing moths, *Gonodonta* spp. and *Eudocima* spp. (Lepidoptera: Noctuidae), pierce the skin of the ripe or ripening fruit with their strong proboscis, the damage resulting in crop loss or unmarketable fruit; the armored scale, *Morganella longispina* (Morgan) (Hemiptera: Diaspididae), feeds on buds and bark causing severe die back; the stink bug, *Nezara viridula* (L.), extracts fruit fluids leaving a small puncture and eventual fruit deformation; and the false spider mite, *Brevivalpus phoenicis* (Geijskes) (Acarina: Tenuipalpidae), causes bronzing of the fruit.

Durian, *Durio zibethinus* Murray (Bombacaceae Family)

Durian, a common fruit in Southeast Asia, originated in Borneo and Sumatra, and is held in high esteem from Sri Lanka and southern India to New Guinea. The ripe fruits, or rather the arils which form the edible part, are generally eaten fresh. Its strong and unmistakable smell is present in every market and street stall during the fruiting season. The fruit also can be preserved, deep frozen or consumed in ice creams, cakes and cookies. The fruit is a globose, ovoid or ellipsoid capsule, up to 25 cm long and 20 cm diameter, green to brownish, covered with numerous broadly pyramidal, sharp, up to 1-cm-long spines; usually with five thick, fibrous valves. Seeds are up to 4 cm long and completely covered by a white or yellowish, soft, very sweet aril. The tree is propagated by seeds, or superior cultivars by budding on seeding stock. Thailand is the largest producer with 444,500 tons in 1987, followed by Indonesia.

The key pests of durian are *Hypomeces squamosus* F. (Coleoptera: Curculionidae), a polyphagous weevil in which the adult stage feeds on leaves, causing extensive defoliation of young plants; the durian psyllid, *Allocaridara malayensis* (Crawford) (Hemiptera: Psyllidae), inserts eggs into young leaves, and both nymphs and adults feed on the underside of the leaf; the durian borer, *Conogethes punctiferalis* (Guenée) (Lepidoptera: Pyralidae), damages both young and mature fruits by boring into the pulp. The newly hatched larva of the durian seed borer, *Mudaria luteileprosa* Holloway (Lepidoptera: Noctuidae), feeds initially on the skin of the fruit and later bores into the husk and then into the seeds. The mite *Eutetranychus africanus* (Tucker) (Acari: Tetranychidae) feeds on the upper side of the leaf, especially along the mid-vein, causing withering spots that later spread over the whole leaf.

Guava, *Psidium guajava* L. (Myrtaceae Family)

The guava, *Psidium guajava* L., occurs naturally from southern Mexico to South America and the Caribbean. The guava is a small tree that is grown worldwide in the tropics and warm subtropics for its edible fruit. Guavas can flower and bear fruit continuously in the tropics, however, there are normally two crops a year. In Florida and Puerto Rico, there is a large crop in early to mid-summer (June and July), and a smaller crop in late winter (February). In Hawaii, the small harvest peak occurs in April to May and the heavy peak in September and November. In India and Malaysia, the main crop is in mid-winter and the lesser crop during the rainy season (July–September). Fruits mature 90–150 days after flowering depending on the variety or clone of the fruit and cultural and weather conditions. The large white flowers attract a large variety of pollinating insects including many species of bees. In many tropical regions the honey bee, *Apis mellifera* L., is the most important pollinator species.

Guavas are either eaten fresh, or used in juice, ice cream, jellies, pastes or preserves. Key pests involve fruit flies of the genera *Anastrepha* and *Bactrocera*, and several species of fruit boring weevils, such as *Conotrachelus psidii* Marshall. Fruit flies injure the fruit by ovipositing eggs and the developing larvae consume the pulp, leaving the fruit unmarketable. A secondary pest is *Heliopeltis theobromae* Miller (Miridae), which feeds on many parts of the plant, including the fruit. Damage to the fruit results in necrotic lesions which render the fruit unmarketable. Many species of mealybugs, including *Ferrisia virgata* (Cockerell), *Planococcus citri* (Risso), *Planococcus pacificus* Cox, *Pseudococcus citriculus* Cox, *Pseudococcus nipae*, *Planococcus minor* (Maskell), and *Pseudococcus* *lilacinus* Cockerell affect guava. Normally these insects do not damage the host severely, but large populations cause the fruit to become misshapen and deformed. For instance, honeydew produced by mealybugs often results in sooty mold, which lowers the fruit's market value. The red-banded thrips, *Selenothrips rubrocinctus* (Giard) and *Scirtothrips dorsalis* Hood, also attack guavas by feeding on the leaves and fruit and cause russetting or bronzing of the plant surface.

Mites can cause serious damage, and they include *Oligonychus yothersi* (McGregor), *Panonychus* sp., *Eotetranychus* sp., and *Oligonychus biharensis* (Hirst). These mites are reported to feed on leaves, causing leaves to become dull green, and then bronzed. The mites, *Tegolophus guavae* and *Brevipalpus* spp., cause damage to fruits and tender leaves.

Litchi and Longan (Sapindaceae Family)

The litchi (*Litchi chinensis* Sonn.) and longan (*Dimocarpus longan* Lour.) are closely related species belonging to the family Sapindaceae. Of Southeast Asian origin, they thrive in subtropical areas with cool dry winters and warm wet summers, but may be grown in tropical areas at high elevation. Around the world, litchis have been successfully grown commercially in latitudes from 15° to 35°. The litchi is a traditional fruit in China, and it occupies a special place in Chinese culture. Indo–China is the center of origin for this species and many old specimen trees have been identified. Litchi and longan fruits are best when eaten fresh, but they also can be processed by canning, juicing or drying into litchi nuts. In Asia they are usually harvested as whole panicles in order to maintain freshness, and are sold in street markets or at roadside stalls within a few days of harvest.

Apart from China and India, large litchi industries have been developed in Taiwan, Thailand, Vietnam, Madagascar, South Africa and Réunion. Smaller but expanding industries exist in Australia, Bangladesh, Mauritius, Mexico, the Seychelles, Spain and the USA (California, Florida and Hawaii).

In general, longans can be grown successfully wherever litchis are cultivated. Although both species flower at about the same time, longans take longer than litchis to mature. Major world producers are China (400,000 tons), Thailand (150,000 tons) and Vietnam (20,000 tons).

Litchi and longan are adapted to the warm subtropics and produce the best crops when winters are short, dry and cool, but frost-free. Such climatic conditions initiate the development of flower panicles. The inflorescences emerge during late winter and the flowers open in early spring. Most cultivars set fruit far in excess of what an individual tree can carry through to maturity and will shed the excess at various times during fruit development. Longan flowers about 2–3 weeks later than litchi, and matures 4–8 weeks later. Harvesting fruit as whole panicles has the effect of pruning and stimulates new leaf growth after harvest. It also reduces tree size. Ideally, trees should produce one or two vegetative flushes after harvest. The aim is to have the second or third flush commence in winter. If conditions are cool during the early part of the flush, development of the new growth will be floral. However, if warm weather is encountered, the new growth will produce leaves. Litchi and longan often are cultivated in the same geographical areas, and many pests are common to both crops.

Pests include the fruit borers *Conopomorpha sinensis* Bradley, *Conopomorpha litchiella* Bradley (Lepidoptera: Gracillariidae), *Cryptophlebia peltastica* Meyr., *Cryptophlebia leucotreta* Meyr., *Cryptophlebia bactrachopa* Meyr. (Lepidoptera: Tortricidae), and in the New World, *Crocidosema* n. sp. (Lepidoptera: Tortricidae). These insects lay new eggs on the fruit anytime after fruit set, as well as on new leaves and shoots. Larvae can bore into leaf buds and fruits. Fruit-piercing moths (Lepidoptera: Noctuidae) attack a range of fruits throughout Southeast Asia, the South Pacific and Australia. The larvae of fruit-piercing moths develop on a variety of host plants. In the Pacific Islands, *Eudocima (Othreis) fullonia* (Clerck), *Eudocima salaminia* (Cramer) and *Eudocima jordani* (Holland) are primary feeders on litchi fruit on the wet tropical coast of Queensland in Australia. Unlike most lepidopterous pests, of which the larva is the damaging stage, in this case it is the adult that causes the damage through its feeding on the fruit. The loopers *Oxyodes scrobiculata* F. and *Oxyodes tricolor* Guen. (Lepidoptera: Noctuidae) occupy similar niches in Thailand and Australia, respectively. The caterpillars feed on the foliage of litchi trees and can cause severe defoliation. Although they will eat leaves of any age, they prefer the younger ones. The litchi longicorn beetle, *Aristobia testudo* (Voet), is a serious pest of both litchi and longan in Guangdong Province in China. In Taiwan, the white spotted longicorn beetle, *Anoplophora maculata* (Thomson), has a one year life cycle. These beetles girdle branches by chewing 10 mm strips of bark. The larvae bore into the xylem and create tunnels up to 60 cm long in the wood. Several bugs belonging to the family Tessaritomidae attack litchis and longans throughout China, Southeast Asia and Australia. *Tessaritoma papillosa* Drury occurs in southern China, Vietnam, Thailand, Burma, the Philippines and India, although there are reports that *Tessaritoma javanica* Thunberg and *Tessaritoma quadrata* Distant are the species found on litchi in India. In litchis and longans, adults and nymphs feed on terminals, which may be killed, and also on flowers and fruit, causing these to fall.

The litchi erinose mite, *Aceria litchii* (Keiffer), also known in China as litchi hairy mite, hairy spider, or dog ear mite, occurs throughout China and Taiwan, India, Pakistan, Hawaii and Australia. The litchi erinose mite attacks new growth, causing a felt-like erineum to be produced on the leaflets. This may form as several blisters, but if the infestation is severe, it may eventually cover the entire leaflet, causing it to curl. Whole terminals may be deformed. The erineum is at first silver-white, changing as it ages to light brown and then dark reddish brown. The longan erinose mite, *Aceria longana* Boczek and Knihinicki, is a sporadic but major pest of longan in Thailand. *A. longana* is specific to longan, severely affecting the terminals and flowers. The longan gall mite, *Aceria dimocarpi* (Kuang), is associated with longans in China where it is recorded as causing erineum on leaves and also witches' broom symptoms. The litchi leaf midge, *Dasyneura* sp., is regarded as one of the major pests of litchi in China, and *Litchiomyia chinensis* Yang and Luo has been reared from galls collected on litchi leaves in Guangdong.

Mango, *Mangifera indica* L. (Anacardiaceae Family)

The mango most likely originated in Southeast Asia, particularly in the Malay Archipelago. However, it was probably first grown as a food crop in India, where its cultivation is thought to have commenced at least 4,000 years ago. Mangoes are now grown as an important crop all over the world, in both tropical and subtropical areas. Mangoes may be eaten ripe or green, or the fruit is juiced or processed into preserves, chutney, frozen puree, or dried. World production of mangoes in 2000 was estimated to be about 24.5 million tons. Worldwide, mango is affected by many pests. For instance, mango flowers are attacked by a variety of insects such as midges, leafhoppers, caterpillars and thrips. These include leafhoppers (Hemiptera: Cicadellidae) infesting mango flowers throughout Asia, such as *Idioscopus clypealis* Lethierry, *Idioscopus niveosparsus* Lethierry, *Idioscopus magpurensis* Pruthi and *Amritodius atkinsoni* Lethierry. The mango blister midge or mango gall midge (Diptera: Cecidomyiidae), *Erosomyia mangiferae* Felt, infests mangoes in the West Indies. Five cecidomyiid species, including *Erosomyia indica* Grover and Prasad, are reported to attack mango flowers and to cause severe damage in India, while *Dasyneura mangiferae* (Felt) does the same in Hawaii.

Numerous species of lepidoptera have been found to infest mango flower panicles in all production areas, but in few cases have the species involved been identified. In Florida, *Pococera atramentalis* Lederer (Pyralidae) and *Platynota rostrana* (Walker) (Tortricidae) are the two most damaging species of a complex that also includes *Pleuroprucha insulsaria* (Guenée) (Geometridae), *Tallula* spp. (Pyralidae) and *Racheospilla gerularia* (Hübner). In the Philippines, the tip borer, *Chlumetia transversa* Walker (Noctuidae), is second only to mango hoppers as a pest of flowers. The geometrids, *Eupithecia* sp., *Chloropteryx glauciptera* Hampson and *Oxydia vesulia* (Cramer), as well as *Penicillaria jocosatrix* Guenée (Noctuidae), also can be found feeding on mango panicles. Other blossom pests are *Frankliniella bispinosa* (Morgan) and *Frankliniella kelliae* (Sakimura) in Florida, the western flower thrips, *Frankliniella occidentalis* (Pergande), in Israel, and the chili thrips, *Scirtothrips dorsalis* Hood, in Thailand.

Because of the high price paid for unblemished fruit, fruits need to be protected from a range of insects that may cause physical damage or loss, or merely affect its outward appearance. Flies of the Tephritidae are pests of mango in many parts of the world. In the Neotropics, *Anastrepha* spp., *A. obliqua* (Macquart), the Mexican fruit fly, *A. ludens* (Loew), *A. serpentina* (Wiedemann), *A. striata* Schiner, *A. suspensa* (Loew), *A. ocresia* Walker, *A. distincta* Greene, *A. fraterculus* Wiedemann, and *A. chiclayae* Greene are considered important pests. *Bactrocera tryoni* (Frogatt), *B. neohumeralis* (Hardy), *B. jarvisi* (Tryon), *B. zonata* (Saunders), *B. frauenfeldi* Schiner and *B. dorsalis* (Hendel) are all reported to attack mango. The Mediterranean fruit fly, *Ceratitis capitata*, is reported to attack mango throughout the world, whereas the marula fruit fly, *Ceratitis cosyra* (Walker), and the Natal fruit fly, *Ceratitis rosa* Karsch, are important in Africa.

The mango seed weevils, *Sternochetus mangiferae* (F.) (Coleoptera: Curculionidae), are widely distributed in Africa, Asia, Australia, the Pacific Islands and in some Caribbean islands, whereas *Sternochetus gravis* (F.) and *Sternochetus frigidus* (F.) occur in India and Bangladesh. Seed weevils generally lay eggs in small green fruit, and the larvae tunnel to the seed, where they feed and develop. *Deanolis sublimbalis* Snellen (Lepidoptera: Pyralidae), the mango seed borer, is also an important pest of mango fruits in the Philippines, Vietnam, China, Thailand, Indonesia and Papua New Guinea. The distinctive red-banded larvae feed on and bore through the pulp to the seed.

Fruitspotting coreid bugs, such as the yellowish-green coreid bugs *Amblypelta lutescens lutescens* (Distant) and *Amblypelta nitida* Stål, and the tip wilter, *Anoplocnemis curvipes* (Fabricius), can be serious pests of young mango trees in South Africa. *Amblypelta lutescens* feeds on the young fruit, causing black lesions to develop and the fruit to fall.

Pest of leaves and buds include gall midges (Diptera: Cecidomyiidae) such as *Protocontarinia matteiana* Kieffer and Cecconi, *Erosomyia* spp., *Procontarinia schreineri* Harris, *Amradiplosis echinogalliperada* Mabi and *P. matteiana*. The galls dry up and fall out, leaving a typical "shot-hole" effect. Red-banded thrips, *Selenothrips rubrocinctus* (Giard), and the Mediterranean mango thrips, *Scirtothrips mangiferae* Priesner, feed on the leaf, especially adjacent to the midrib, where they cause a silvering that develops into necrosis, eventually leading to leaf drop. The mango bud mite, *Aceria mangiferae* Sayed is reported to attack the buds of terminals, and spider mites belonging to the genus *Oligonychus* (*O. mangiferae* Rahman and Sapra, *O. punicae* (Hirst), and *O. yothersi* McGregor) feed on the upper surface of mango leaves.

The mango scale, *Aulacaspis tubercularis* (Newstead), is regarded as a key pest mostly because it infests the fruit. Among the mealybugs, *Rastrococcus invadens* Williams, and the margarodid *Drosicha stebbingii* (Green) (Margarodidae) remain as important pests of leaves in different mango growing areas.

Mangosteen, *Garcinia mangostana* L. (Guttiferae Family)

Mangosteen is known only as a cultivated species, although there have been occasional observations of wild specimens in Malaysia. The scarcity of mangosteen orchards, limited fruit supply and the fruit's short shelf life are major marketing problems. The long juvenile period of 10–15 years, which discourages commercial production, contributes to much of the limited fruit supply. The mangosteen fruit is a globose and smooth berry, turning dark purple at ripening. It is a crop of the humid tropics, often found in association with durian. The fruit has a diameter of 4–7 cm. The edible part is the sweet white aril that envelops the seeds within the pericarp.

Floral initiation to anthesis takes about 25 days and the fruit ripens 100–120 days later. The most serious pests are *Hyposidra talaca* (Walker) (Lepidoptera: Geometridae), a highly polyphagous insect. *Hyposidra talaca* is a typical looper, causing defoliation in tropical lowlands and highlands. The citrus leafminer, *Phyllocnistis citrella* (Lepidoptera: Phyllocnistidae), mines leaves of mangosteen, causing leaf deformation and often leading to early fall. *Sictoptera cuculloides* Guenée (Lepidoptera: Noctuidae) is reported to feed voraciously on young flushes of mangosteen.

Papaya, *Carica papaya* L. (Caricaceae Family)

Papaya, *Carica papaya* L., is a major tropical fruit cultivated through the tropical and Neotropical regions of the world between 32°N and 32°S. Although papaya was probably cultivated by early civilizations in the New World, no botanical records are available prior to the arrival of Columbus to America. This herbaceous plant is also known as papaw, paw paw, kapaya, kepaya, lapaya, tapaya, papayao, papaya, papaia, papita, lechosa, fruta bomba, mamon, mamona, mamao, and tree melon. Papaya is cultivated mainly for its edible fruit, but medicinal and industrial uses also have been documented.

Fruit flies (Diptera: Tephritidae) are the only group of insects that actually penetrate the pulp or seeds. Twenty-six species from seven genera, *Anastrepha* (two species), *Bactrocera* (17 species), *Ceratitis* (three species), *Dacus*, *Euphranta*, *Myoleja*, and *Toxotrypana* (one species each) attack papaya fruits. *Toxotrypana curvicauda* Gerstaecker is the most important fruit fly species attacking papaya in the Americas and Caribbean Basin, whereas *Bactrocera papayae* (Drew and Hancock) is one of the most threatening pests to papaya in Australia. *Anastrepha* spp., *C. capitata* (Wiedemann), *C. catoirii* Guerin-Meneville, and *C. rosa* Karsch also are known to attack papaya.

Arthropods affecting the foliage and trunk of papaya include the white peach scale, *Pseudaulacaspis pentagona* (Targioni-Tozetti), the papaya scale, *Philephedra tuberculosa* Nakahara and Gill, and the papaya mealybug, *Paracoccus marginatus* Williams and Granara de Willink. Several species of mites feed on papaya. They include the carmine mite, *Tetranychus cinnabarinus* (a key pest), the red and black flat mite, *Brevipalpus phoenicis* (an occasional pest), and the papaya leaf edge roller mite, *Calacarus brionese*. Damage by the broad mite, *Polyphagotarsonemus latus* (Banks) (Tarsonemidae), is confused with virus-like symptoms. Nine cicadellid species from three genera (*Empoasca*, *Poeciloscarta* and *Sanctanus*) can affect papaya, such as *Empoasca papayae* Oman, which transmits bunchy-top, *E. stevensi* Young, and *E. insularis* Oman. Aphids do not colonize papaya plants and are considered minor pests, but several species, *Aphis coreopsidis* (Thomas), *Aphis nerii* Boyer de Fonscolombe, *Aphis gossypii* Glover, *Aphis spiraecola* Patch, *Myzus persicae* (Sulzer), and *Toxoptera aurantii* (Boyer de Fonscolombe), can be found on papaya plants. Several aphid species [*M. persicae*, *M. euphorbiae*, *A. spiraecola* (=*A. citricola*), *A. gossypii*, *A. craccivora*, *A. nerii*, *R. maidis*, and *T. auranti* (Boyer de Fosc)] are capable of transmitting papaya ringspot virus. Among the defoliators, hornworms (Lepidoptera: Sphingidae), *Eryinnis alope* (Drury), *E. ello*, and *E. lassuxi merianae* Grote, are considered important.

Passion Fruit (Passifloraceae Family)

Passion fruits belong to the genus *Passiflora* (family Passifloraceae), which has a wide genetic base. While some species are undomesticated, others are cultivated as ornamental plants, for nourishment and for medicinal purposes. The majority of Passiflora are indigenous to the tropical and subtropical regions of South America. Of the 400 known species of Passiflora, about 50 or 60 bear edible fruits. A few species are economically important, e.g., *Passiflora edulis* Sims., botanical form *flavicarpa* Deneger, the yellow passion fruit, whose juice and pulp are used extensively as ingredients of beverages, salads, fruit cocktails and desserts. The major producers of passion fruits are found in South America, mainly Brazil, Colombia, Peru and Ecuador. Commercial plantations of passion fruits are found also in Australia, Hawaii, India, New Guinea, Kenya, South Africa, Sri Lanka and Costa Rica. *Passiflora edulis f. flavicarpa*, *P. edulis* (purple passion fruit), and *P. alata* (sweet passion fruit) are the main species cultivated in the world. *Passiflora ligularis* (granadilla) and *P. quadrangularis* (badea) are cultivated in the Andean region of South America and in Central America.

Although the passion fruit crop has great economic potential, its establishment and expansion have been hindered by various problems. For example, passion fruit is attacked by a wide host range of diseases, insects and mites. Some pest species cause significant losses, reaching the status of key pests or secondary pests. They include lepidopterous defoliators such as three heliconiine species, *Dione juno juno* Cramer, *Agraulis vanillae vanillae* Linnaeus, and *Eueides isabella huebneri* Ménétries (Nymphalidae). Many species of bugs attack passion fruit; the majority belong to the Coreidae (leaf-footed bugs), such as *Diactor bilineatus* Fabricius, *Leptoglossus* spp., and *Holhymenia* spp. *Diactor bilineatus* is the most common species in Brazil and Venezuela, and is known as the passion fruit bug because it feeds only on fruit of *Passiflora* spp. Among the *Holhymenia*, *Holhymenia clavigera* (Herbst.) and *H. histrio* (Fabricius) are reported attacking passion fruit. *Leptoglossus gonagra* Fabricius and *L. australis* Fabricius are reported from several passion fruit producing regions.

Flies of the genera *Anastrepha* Schiner (Tephritidae) and *Lonchaea* Fallén (Lonchaeidae) cause economic losses. *Anastrepha consobrina* (Loew), *A. ethalea* (Walker), *A. grandis* (Macquart), *A. kuhlmenni* Lima, *A. lutzi* Lima and *A. pseudoparallela* (Loew) are the most frequent species followed by *Anastrepha pallidipennis* Guerne on yellow passion fruit. The oriental fruit fly, *Bactrocera dorsalis* (Hendel), melon fly, *Dacus cucurbitae* Coquillett, and the Mediterranean fruit fly, *Ceratitis capitata* Wiedemann, are known to attack passion fruit in Hawaii. The Queensland fruit fly, *Dacus tryoni* (Froggatt), is the most important insect pest of passion fruit in Australia.

Neosilba pendula (Bezzi) and *Dasiops* sp. (Lonchaeidae) attack flowers and buds of passion fruit. The species of *Dasiops* include *D. curubae* Steykal, *D. inedulis* Steykal and *D. passifloris* McAlpine. Other flies that may also feed upon flower and buds are *Lonchaea cristula* McAlpine (Lonchaeidae) and *Zapriothrica salebrosa* Wheeler (Drosophilidae).

Several species of mites have been reported from passion fruit including *Brevipalpus phoenicis* (Geijskes) (Tenuipalpidae) and the red spider mites, *Tetranychus mexicanus* (McGregor) and *T. desertorum* Banks (Tetranychidae), causing general discoloration of the leaves and necrosis, culminating in leaf drop. The broad mite, *Polyphagotarsonemus latus* (Banks), induces malformations in developing leaves, which later dry and drop. It may attack flowering buds, causing a reduction in the number of flowers.

Pineapple, *Ananas comosus* (L.) Merr. (Bromeliaceae Family)

The pineapple, *Ananas comosus* (L.) Merr., is a self-sterile herbaceous, perennial, monocotyledonous plant originating in the New World. The commercial cultivars are placed in five distinct groups, i.e., "Cayenne," "Spanish," "Queen," "Pernambuco" and "Perolera." It is currently grown in many countries with tropical and subtropical climates. Most pineapple pests are endemic to the new countries and adapted to utilize the pineapple to support their life-cycles.

More than 100 species of plant-parasitic nematodes have been recorded in association with pineapple roots, and between three and five species are usually found in most pineapple fields. The key nematode pests include the root-knot nematode (*Meloidogyne javanica* and *M. incognita*), the reniform nematode (*Rotylenchulus reniformis*) and the lesion nematode (*Pratylenchus brachyurus*). The key nematode pests of pineapple are all endoparasites. They either establish a permanent feeding site within the root and become sedentary, e.g., root-knot and reniform nematodes, or they live inside roots but remain migratory, e.g., lesion nematodes. Key arthropod pests are the pineapple leathery pocket mite/pineapple fruit mite, *Steneotarsonemus ananas* (Tryon), *Dolichotetranychus floridanus* (Banks), and the symphylids *Hanseniella* (Symphyla: Scutigerellidae), e.g., *H. unguiculata*, *H. ivorensis*, and *Scutigerella sakimurai* (Symphyla: Scolopendrellidae). *Steneotarsonemus ananas* is important because of its association with the fruit diseases, interfruitlet corking, leathery pocket and fruitlet core rot/black spot. The pineapple flat mite, *D. floridanus*, attacks plants of all ages. Damage is primarily to the whitish leaf bases, which develop brown/black necrotic lesions and appear progressively dehydrated, with feeding mites around lesion peripheries, or as orange patches on leaf bases.

The symphylids *H. unguiculata*, *H. ivorensis* and *S. sakimurai* feed on young meristematic tissues causing newly established plants to stop root development and causing severe witches' broom symptoms. Other important pests are the onion thrips or yellow spot thrips, *Thrips tabaci* Lindeman, responsible for yellow spot disease of pineapples, the pink pineapple mealybug, *Dysmicoccus brevipes* (Cockerell), associated with the devastating disease, pineapple mealybug wilt, the pineapple scale, *Diaspis bromeliae* (Kerner), infesting the lower pineapple leaves, the pineapple caterpillar, *Thecla basilides* (Geyer), causing larval galleries and rendering the fruit unmarketable, and the white grubs, *Lepidiota grata*, *Rhopaea magnicornis*, *Adoretus ictericus*, and the melolonthids, *Macrophylla ciliata* and *Asthenopholis subfasciata*, destroying the root system.

Rambutan, *Nephelium lappaceum* Blume (Sapindaceae Family)

Rambutan is a tropical relative of litchi, with a distribution that ranges from southern China through the Indo-Chinese region, Malaysia, and Indonesia to the Philippines. As the name suggests (the Malay word "rambut" meaning hair), the fruit is glabrous, resembling a burr. Rambutan, while highly prized in its region of origin, remains a minor fruit internationally. The fruits are consumed fresh or canned. The rambutan fruit is an ellipsoid to subglobular schizocarp, up to 7 cm × 5 cm, usually consisting of one nutlet. The skin color varies from yellow to purplish red. The seed usually is covered by a thick, sweet, juicy, white to yellow, translucent sarcotesta, which is the edible part.

The main flowering period occurs during the dry season. Fruits ripen about 110 days after bloom. The most important pests are the durian borer, *Conopomorpha* (=*Acrocercops*) *cramerella* (Snellen) (Lepidoptera: Gracillariidae). This insect tends to damage only the part of the fruit next to the fruit stalk. The cockchafer beetle, *Adoretus* (=*Lepadoretus*) *compressus* (Weber) (Coleoptera: Scarabaeidae), feeds on the interveinal areas close to the center of the leaf. Adults of *Apogonia cribricollis* Burmeister (Coleoptera: Scarabaeidae) are active at night, feeding on foliage from the leaf margin inwards. *Chalcocelis albiguttatus* (Snellen) and *Parasa lepida* (Cramer) (Lepidoptera: Limacodidae) cause severe defoliation of rambutan trees.

Integrated Pest Management (IPM) for Tropical Fruit

Tropical fruit crops provide a relatively stable environment over many years, offering continuing habitats for both pests and natural enemies, and providing opportunities for biological control and effective pest management programs. Any attempt to develop integrated control programs in fruit crops must take into account the following: (i) knowledge of native or resident arthropod fauna; (ii) arthropod fauna affecting the tree crop in its area of origin or domestication; and (iii) presence of natural enemies. The basis for integrated pest management includes the pest's biology and ecology, sampling and monitoring techniques, economic thresholds and the application of management tactics, i.e., chemical, biological, autocidal, plant resistance, etc.

Sampling and Monitoring

Sampling and monitoring methods for tropical fruits are well established for some direct pests such as fruit flies and fruit borers, as well as for some indirect pests (i.e., banana weevil) and defoliators. However, the inability to relate results of sampling to infestation of the fruit at the time of harvest is still a problem. Attempts have been made to develop sampling techniques for several pests of mango, avocado and banana; however for some pests and crops, adequate sampling techniques are not available. This, of course, may be a reflection of the place where the crop is grown, the purpose of tree cultivation (export vs. internal consumption) and grower economic solvency (Australia, USA, South Africa, Israel) vs. growers from other regions of the world.

Economic Thresholds

As export commodities, tropical fruit crops have a consistently high value, with highest prices for undamaged fruit of high quality; thus, the lack of knowledge of economic thresholds, or the low existent economic thresholds, requires control programs to focus on preventing damage by these pests.

Chemical Control

Pesticides have been significant for protecting tropical fruit from insect attack and increasing tropical fruit productivity, therefore the control of fruit and foliar insect pests tends to be heavily dependent on chemical insecticides/acaricides. Information regarding proper timing, spray volumes, and knowledge of the pest complex is available for some crops such as pineapple, and scarce for others such as papaya. Regular, heavy sprays for controlling fruit flies and leafhoppers in papaya can cause heavy outbreaks of mites and other pests. Widespread use of nonselective pesticides continues to be the rule, but currently there is a trend toward evaluating a new generation of pesticides, adoption of selective spraying, timing of spray applications, and determining the effect of pesticides on predators and parasitoids. In contrast, there is minimal to nonexistent information on the effect of pesticides on pollinators. For instance, the deleterious effects on pollinators can be reduced by timing spray applications in passion fruit, according to the cultivar. Purple passion, whose flowers open during the morning hours, should be sprayed during late afternoon, while the yellow cultivar, whose flowers open in the afternoon, should be sprayed in the morning.

Attractants (Pheromones)

Use of sexual attractants (pheromones) is mostly limited to fruit flies, while little information is available for other insect groups, such as curculionids and Lepidoptera.

Crop Sanitation

Crop sanitation is an important factor for maintaining low banana weevil densities in banana farms, and is used as a tentative effort to control important pests of avocados (i.e., weevils), annona (annona seed borer) and mango (mango seed weevil).

Biological Control

Biological control has great potential as a major tactic for regulating pest populations in fruit orchards. The ability to apply biological control effectively has increased in recent decades because of greater knowledge of the arthropod fauna of some tropical fruits (citrus, avocado, pineapple and mango). While biocontrol agents are recorded for most pests of other tropical fruit crops, concentrated efforts to use bio-regulators are rarely observed. For instance, efforts toward developing systems for biocontrol of pink mealybug, *Maconellicoccus hirsutus*, and carambola fruit fly, *Bactrocera carambolae*, in the Caribbean were not initiated until these pests were major threats to crops such as citrus. If a stenophagous insect (i.e., avocado weevils, papaya fruit fly, avocado thrips and annona fruit moths) is the major constraint to a single commodity, efforts for biological control are half-hearted. The exception to this rule is the current strong effort toward biocontrol of banana weevil and the search for natural enemies of avocado thrips. With time, it is likely that more extensive use will be made of biological agents to control pests of tropical fruit crops.

Host Plant Resistance

Host plant resistance offers considerable promise as a tactic in pest management. Even though it appears that most efforts are concentrated toward plant pathogens, use of this tactic merits attention for some crops and some pest species. Resistance to arthropods in tropical fruit germplasm collections should be a high priority. Most efforts are directed at insect vectors (papaya and pineapple) and pests of avocado, mango and guava. Several fruits, i.e., durian and acerola, continue to be largely unnaturalized, and improved selections are rare.

Cultural Practices

Untreated backyard trees and neglected plantings are considered to be major sources of pests, such as fruit flies. For instance, in Australia, hygiene and attention to alternative host plants that can increase pest pressure on the custard apple orchard are important. Mature fruit infested with yellow peach moth or with fruit fly should be collected and destroyed. Preferred fruit fly hosts like guava and loquat should not be planted in or near the orchard. Cultural practices generally do not offer a direct means for controlling pests, but used properly they can enhance natural enemy activity or retard pest population growth to a degree that is important in integrated control programs.

References

Aguiar-Menezes E, Menezes EB, Cassino PCR, Soares M (2002) Passion fruit. In: Peña JE, Sharp JL, Wysoki M (eds) Tropical fruit pests and pollinators. CABI, Wallingford, pp 361–390

Gold CS, Pinese B, Peña JE (2002) Pests of banana. In: Peña JE, Sharp JL, Wysoki M (eds) Tropical fruit pests and pollinators. CABI, Wallingford, pp 13–56

Gould WP, Raga A (2002) Pests of guava. In: Peña JE, Sharp JL, Wysoki M (eds) Tropical fruit pests and pollinators. CABI, Wallingford, pp 295–314

Ooi PAC, Winotai A, Peña JE (2002) Pests of minor tropical fruit. In: Peña JE, Sharp JL, Wysoki M (eds) Tropical fruit pests and pollinators. CABI, Wallingford, pp 315–330

Pantoja A, Follett PA, Villanueva J (2002) Pests of papaya. In: Peña JE, Sharp JL, Wysoki M (eds) Tropical fruit pests and pollinators. CABI, Wallingford, pp 131–156

Peña JE, Nadel H, Barbosa-Pereira M, Smith D (2002) Pollinators and pests of Annona. In: Peña JE, Sharp JL, Wysoki M (eds) Tropical fruit pests and pollinators. CABI, Wallingford, pp 197–222

Petty G, Stirling G, Bartholomew DP (2002) Pests of pineapple. In: Peña JE, Sharp JL, Wysoki M (eds) Tropical fruit pests and pollinators. CABI, Wallingford, pp 157–196

Waite GK (2002) Pests and pollinators of mango. In: Peña JE, Sharp JL, Wysoki M (eds) Tropical fruit pests and pollinators. CABI, Wallingford, pp 103–130

Waite G, Hwang JS (2002) Pests of litchi and longan. In: Peña JE, Sharp JL, Wysoki M (eds) Tropical fruit pests and pollinators. CABI, Wallingford, pp 331–360

Wysoki M, van den Berg MA, Ish-Am G, Gazit S, Peña JE, Waite G (2002) Pests and pollinators of avocado. In: Peña JE, Sharp JL, Wysoki M (eds) Tropical fruit pests and pollinators. CABI, Wallingford, United Kingdom, 223–294

Tropical Fruitworm Moths (Lepidoptera: Copromorphidae)

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Tropical fruitworm moths, family Copormorphidae, are a small family of 58 species, mostly tropical; actual fauna probably exceeds 100 species. The family is part of the superfamily Copromorphoidea in the section Tineina, subsection Tineina, of the division Ditrysia. Adults small to medium size (12–37 mm wingspan), with head somewhat smooth-scaled; haustellum naked; labial palpi prominent and porrect; maxilary palpi 3- to 4-segmented (rarely 1-segmented). Wing venation with forewing veins long and typically equidistant near the termen; wings typically rounded along forewing termen. Maculation mostly dull gray with dark markings, and many have forewing scale tufts. Adults nocturnal. Larvae are leaf feeders using a leaf web, or are borers (one feeds beneath bark), but few biologies are known. Host plants include Berberidaceae, Ericaceae, Moraceae, Podocarpaceae, and Rubiaceae.

References

Clarke JFG (1955) Copromorphidae. In JFG Clarke, Catalogue of the type specimens of Microlepidoptera in the British Museum (Natural History) described by Edward Meyrick, 2: 509–531. British Museum (Natural History), London

DeBenedictis JA (1984) On the taxonomic position of Ellabella Busck, with descriptions of the larva and pupa of *E. bayensis* (Lepidoptera: Copromorphidae). Journal of Research on the Lepidoptera 23:74–82

DeBenedictis JA (1985) The pupa of *Lotisma trigonana* and some characteristics of the Copromorphidae (Lepidoptera). Journal of Research on the Lepidoptera 24:132–135

Heppner JB (1984) Revision of the Oriental and Nearctic genus *Ellabella* (Lepidoptera: Copromorphidae). Journal of Research on the Lepidoptera 23:50–73

Heppner JB (1986) Revision of the New World genus *Lotisma* (Lepidoptera: Copromorphidae). Pan-Pacific Entomologist 62:273–288

Tropical Lattice Moths (Lepidoptera: Arrhenophanidae)

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Tropical lattice moths, family Arrhenophanidae, total 30 species, mostly Neotropical but recently with some Southeast Asian additions; actual fauna probably exceeds 50 species. The family is part of the superfamily Tineoidea, in the section Tineina, subsection Tineina, of the division Ditrysia. Adults small to medium size (12–69 mm wingspan), with robust bodies and roughened head scaling; haustellum reduced or absent; maxillary palpi absent; antennae serrate to bipectinate. Maculation varies from light colored (often yellow) with translucent and colored wing marks, to dark and somber colored. Adult activity nocturnal but some are diurnal (e.g., species in Taiwan). Biologies are unknown except for one Neotropical species with casebearing larvae that feed on fungi.

References

Bradley JD (1951) Notes on the family Arrhenophanidae (Lepidoptera: Heteroneura), with special reference to the

morphology of the genitalia, and descriptions of one new genus and two new species. Entomologist 84:178–185
Davis DR (1984) Arrhenophanidae. In: Heppner JB (ed) Atlas of Neotropical Lepidoptera. 2. Checklist: Part 1 (Micropterigoidea-Immoidea) 6. W. Junk, The Hague
Davis DR (1991) First Old World record of Arrhenophanidae. Trop Lepidoptera 2:41–42

Tropical Longhorned Moths (Lepidoptera: Lecithoceridae)

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Tropical longhorned moths, family Lecithoceridae, total about 1,038 described species, mostly tropical Oriental, but also with one group in the Palearctic; actual fauna probably exceeds 1,500 species. There are four subfamilies: Ceuthomadarinae, Oditinae, Lecithocerinae, and Torodorinae. The family (previously known as Timyridae) is part of the superfamily Gelechioidea in the section Tineina, subsection Tineina, of the division Ditrysia. Most species are in Lecithocerinae (475 sp.). The most colorful and largest species are in the tropical subfamily Torodorinae. Adults small (5–30 mm wingspan), with head mostly smooth-scaled, and antennae mostly long; haustellum scaled; labial palpi long; maxillary palpi 4-segmented and folded over haustellum base (rarely reduced to one segment). Maculation varies from dull to brightly colored and variously marked. Adults are mostly diurnal and many have the habit of holding the antennae together to the front when at rest. Larvae may mostly be leaf litter feeders or leaf tiers, but few species are known biologically. A few varied host plants are recorded, such as Fagaceae, Myrtaceae, Rosaceae, and Rubiaceae (Fig. 109).

Tropical Longhorned Moths (Lepidoptera: Lecithoceridae), Figure 109 **Example of tropical longhorned moths (Lecithoceridae), *Lysipatha diaxantha* Meyrick from Taiwan.**

References

Clarke JFG (1965) Timyridae. In: Clarke JFG, Catalogue of the type specimens of Microlepidoptera in the British Museum (Natural History) described by Edward Meyrick, 5:1–255. London: Br. Mus. (Nat. Hist.)
Gozmány LA (1978) Lecithoceridae. In: Amsel HG, Gregor F, Reisser H (eds) Microlepidoptera Palaearctica, 5:1–306, 93 pl. G. Fromme, Vienna (in German)
Wu C-S (1997) Lepidoptera. Lecithoceridae. In: Fauna Sinica. Insecta, vol. 7. Science, Beijing, 302 pp
Wu C-S, Park K-T (1999) A taxonomic review of the family Lecithoceridae (Lepidoptera) in Sri Lanka. Tinea 16:61–72; Korean J Syst Zool 15:1–9, 205–220; Insecta Koreana 16:1–14, 131–142

Tropical Plume Moths (Lepidoptera: Oxychirotidae)

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Tropical plume moths, family Oxychitoridae, include only six species, all Indo-Australian and South Pacific. Some specialists include this family as part of the Tineodidae. The family is in the superfamily Pterophoroidea in the section Tineina, subsection Tineina, of the division Ditrysia. Adults small (10–12 mm wingspan), with head scaling average; haustellum naked; labial palpi porrect; maxillary palpi 4-segmented. Wings extremely linear, with long fringes, or wider and with both wings split into two plumes each. Maculation shades of brown or gray, with coordinated spotting or banding in the split-wing species. Adults may be crepuscular. Larva of one species feeds on seeds of white mangrove (Avicenniaceae); the remainder are unknown biologically.

References

Clarke JFG (1986) Family Oxychirotidae. In: Pyralidae and Microlepidoptera of the Marquesas Archipelago. Smithson Contrib Zool 416:14–16

Common IFB (1970) Oxychirotidae. In: Insects of Australia. Melbourne University Press, Melbourne, p 835

Common IFB (1990) Family Tineodidae. In: Moths of Australia, [part]. Melbourne University Press, Melbourne, pp 322–325

Heppner JB (1997) Oxychirotidae. Lepidopterorum Catalogus, (n.s.). Fasc. 62. Association for Tropical Lepidoptera, Gainesville, 8 pp

Tropical Slug Caterpillar Moths (Lepidoptera: Dalceridae)

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Tropical slug caterpillar moths, family Dalceridae, include 84 Neotropical species (only one sp. occurs north of Mexico, in southern Arizona). Two subfamilies are known: Acraginae and Dalcerinae. The family is in the superfamily Cossoidea (series Limacodiformes) in the section Cossina, subsection Cossina, of the division Ditrysia. Adults small to medium size (11–50 mm wingspan), with head small and scaling roughened; labial palpi 2-segmented and very short; maxillary palpi vestigial; antennae short and bipectinate. Body robust. Wings quadratic and rounded; hindwings notably ovoid (Fig. 110); frenulum sometimes absent. Maculation mostly brown hues with few markings but can be colorful, with yellow, orange, or pink, or lustrous white and silvery. Adult activity uncertain; possibly only nocturnal or crepuscular. Larvae slug-like, often with translucent gelatinous wart-like surface; feeding as leaf feeders (early instars as leaf skeletonizers), but few are known biologically. Various host plants are used and some larvae are polyphagous. Few have any economic status.

References

Epstein ME (1996) Dalceridae Dyar, 1898. pp 79–81 In: Revision and phylogeny of the limacodid-group families, with evolutionary studies on slug caterpillars (Lepidoptera: Zygaenoidea). Smithson Contrib Zool 582: 1–102

Hopp W (1928) Beitrag zur Kenntnis der Dalceriden. Dtsch Entomol Z Iris 42:283–287

Miller SE (1994) Systematics of the Neotropical moth family Dalceridae (Lepidoptera). Bull Mus Comp Zool 153:301–495

Orfila RN (1961) Las Dalceridae (Lep. Zygaenoidea) argentinas. Rev Invest Agric 15:249–264, 1 pl

Seitz A (ed) (1938–39) Familie: Dalceridae. Die Gross-Schmetterlinge der Erde 6:1303–1304 (1938); 1305–1312, pl. 168, 185 (1939). A. Kernen, Stuttgart

Tropical Theileriosis

A tick-transmitted disease caused by the protozoan *Theileria annulata*.

► Piroplasmosis

Tropical Slug Caterpillar Moths (Lepidoptera: Dalceridae), Figure 110 **Example of tropical slug caterpillar moths (Dalceridae), *Acraga coa* (Schaus) from Mexico.**

Tropiduchidae

A family of insects in the superfamily Fulgoroidae (order Hemiptera). They sometimes are called planthoppers.

► Bugs

Trout Stream Beetles

Members of the family Amphizoidae (order Coleoptera).

► Beetles

True Katydids

A subfamily (Pseudophyllinae) of katydids in the order Orthoptera: Tettigoniidae.

► Grasshoppers, Katydids and Crickets

Trumpet

The respiratory horn or tube of the mosquito pupa.

Trumpet Leafminer Moths (Lepidoptera: Tischeriidae)

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Trumpet leafminer moths, family Tischeriidae, total 81 known species from all regions except Australia, but the Nearctic has most of the known species (48 sp.). The family forms a monobasic superfamily, Tischerioidea, in the section Nepticulina, of the division Monotrysia, infraorder Heteroneura. Adults small (6–11 mm wingspan), with head rough-scaled, with very large head tuft (no eye-caps on the antennal bases); haustellum is short, scaled basally; labial palpi 3-segmented, short and porrect; maxillary palpi minute and 1-segmented. Wing venation is very reduced, with frenular bristles as the wing coupling. Maculation is generally somber but often with iridescences. Adults are diurnally active. The few larvae known are leafminers, usually trumpet-shaped mines or blotch mines, on a variety of host plants.

References

Braun AF (1972) Tischeriidae of America north of Mexico (Microlepidoptera). Mem Am Entomol Soc 28:1–148

Diskus A (1998) Review of the Tischeriidae (Lepidoptera) of Central Asia. Acta Zool Lituanica 8:(3)23–33

Grandi G (1929) Contributo alla conoscenza della *Tischeria gaunacella* Dup. ed appunti sulla *Tischeria complanella* Hbn. (Lepidoptera – Tischeriidae). Boll Lab Entomol Bologna 2:192–243, 5 pl

Hering O (1926) Die Blattminierer-Gattung *Tischeria* in ihren palaearktischen Arten. Entomol Jahrb 35:99–106, 1 pl

Sato H (1993) *Tischeria leafminers* (Lepidoptera, Tischeriidae) on deciduous oaks from Japan Jpn J Entomol 61:547–556

Trumpet-Net Caddisflies

Members of the families Polycentropodidae and Psychomyiidae (order Trichoptera).

► Caddisflies

Truncate

Cut off squarely.

Trunk and Canker-Causing Fungi

Fungi transmitted to plants by insects

► Transmission of Plant Diseases by Insects

Trypanosomes

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Trypanosomes are microscopic unicellular protozoa that are ubiquitous parasites of plants, invertebrates, and vertebrates. These parasites have existed for more than 300 million years and have evolved with their natural hosts. Most of the trypanosomes cause no harm to their hosts and are found in locations throughout the world. Some, however, cause serious diseases in their hosts and are of major medical and veterinary significance. Only a few species of trypanosomes are pathogenic to man. These trypanosomes are not only found in sub-Saharan Africa, where they infect both man and livestock, but also occur in Canada, Latin America, and extend to the southern borders of the United States.

The pathogenic trypanosomes of mammals are called hemoflagellates. These trypanosomes require the blood of their host (human, livestock, etc.) in order to undergo changes pertaining to their life cycles. In addition, the parasite may be transmitted to its host by various techniques, depending on the species of the parasite. For example, *Trypanosoma equiperdum*, a trypanosome known to infect horses, is transmitted via venereal contact. However, the vast majority of the different species of trypanosomes affecting mammals are transmitted via an insect vector.

The most important insect vectors associated with trypanosomiasis (disease caused by protozoa belonging to the genus *Trypanosoma*) in vertebrates are the tsetse flies belonging to the genus *Glossina*. There are 33 known and recognized species of this genus. These vectors can be further divided ecologically into three major groups: the riverine flies of the *palpalis* group; the savanna flies of the *morsitans* group; and the forest flies of the *fusca* group.

Tsetse flies can be distinguished from other flies by the presence of a needle-like forward projecting proboscis, a hatchet-like cell in the middle of the wings and a lateral plumose like arista on the antennae. They are closely related to the muscoid (i.e., house flies, stable flies) flies but may be given their own family name, Glossinidae.

Unlike most flies that are oviparous, the female tsetse fly retains the larva in the uterus and gives birth to one 3rd instar larva at a time. During gestation, the larva is fed from so-called uterine milk-like glands found in the body. When the female larviposits, the larva burrows quickly in the soil and transforms quickly into a pupa. Adult emergence is dependent on the soil temperature and moisture conditions. Adult tsetse flies mate only once and a female produces about 10 offspring during her life span. Both sexes are active bloodsuckers.

Rarely are tsetse flies found in open country because all need some tree/vegetation cover. They are mostly confined to a specific type of habitat and the physical conditions prevailing therein. The flies feed on those animals most readily available in their specific habitat, and therefore carry trypanosomes harbored by their preferred hosts. As a result, infection rates and kinds of trypanosomes vary from one fly habitat to another.

Another important insect vector associated with trypanosomiasis in vertebrates is the assassin bug, cone-nose bug, or kissing-bugs belonging to the family Reduviidae of the order Hemiptera (true bugs). They are characterized by having two pairs of wings; the forewings have leathery basal portions and a membranous distal portion. The second pair of wings is membranous. Hemiptera belonging to this family have piercing sucking mouthparts adapted for feeding on other arthropods or blood. The most important genera of reduviid bugs with some medical importance are *Triatoma*, *Panstrongylus*, and *Rhodnius* which serve as vectors of *Trypanosoma cruzi*, the causative agent for Chagas' disease.

General Life Stages of Trypanosomes

Trypanosomes appear in four basic forms or stages as they undergo changes in the life cycle. These forms or stages differ from species to species, in that some species may exhibit only 2 of the four forms and others may exhibit all four forms. Each form has specific structures that enable it to adapt to its environment. One form is the amastigote or leishmanial stage. This stage has a kinetoplast, which is a structure that is always located at the place of entry into the cell of the flagellum and is opposed to the basal body of the later. The kinetoplast is further composed of a blepharoplast and parabasal body. This structure is analogically similar to the structure of the mitochondria, which is the powerhouse of most types of cells. In addition to a kinetoplast, the amastigote stage has a nucleus. Although the orientation of the kinetoplast can be detected by using the flagellum as a landmark, the leishmanial stage does not have a flagellum. A second stage is the promastigote or leptomonad stage. This stage is found within the tissues of the infected host. In this stage, a flagellum is present. From this stage, the parasite can and does change back and forth between the amastigote and the leptomonad stage in a phenomenon known as transition or morphogenesis. A third stage is the epimastigote or the crithidial stage. The unique characteristic or defining feature of this stage in the history of hemoflagellates is that its undulating membrane or flagellum originates anteriorly to the nucleus. Finally, the last stage is the trypomastigote or trypanosomal stage. The unique or defining feature of this stage is that its undulating membrane originates posterior to the nucleus.

In addition to the morphological differences, these stages can also show metabolic differences. For example, another interesting aspect to the life cycle of the trypanosomes involves the cytochrome oxidase system. The cytochrome oxidase system is one that requires the presence of the metal iron (Fe) in order to work. The only stage that uses this system (i.e., the cytochrome oxidase system) is the epimastigote stage or form. Once the epimastigote stage is placed in a culture that contains other sources of nutrients apart from iron, there is an immediate change or transformation that occurs. The epimastigote form of the parasite immediately changes to the trypomastigote stage, which does not use the cytochrome oxidase system. The trypomastigote stage then use the other forms of nutrients in the culture in order to survive.

Pathogenic Trypanosomes in Humans

The three major species of this parasite that are extremely pathogenic to humans are *Trypanosoma rhodesiense*, *Trypanosoma gambiense*, and *Trypanosoma cruzi*. These parasites were named based on, or according to, either the region they were first found or by the person who first found them. All are hemoflagellates, and thus require the blood of their host in order to undergo their life cycles. Furthermore, the three species also have one or two of the same life cycle stages or forms present. Notwithstanding, different vectors transmit them and all three parasites run a totally different course of infection in man.

T. rhodesiense and *T. gambiense* are found primarily in Africa while *T. cruzi* is located throughout Latin America and extends to the southern borders of the United States of America.

Trypanosoma rhodesiense

Trypanosoma rhodesiense is the causative agent for East African sleeping sickness or *Rhodesian trypanosomiasis* and is found primarily in the eastern region of Africa. It produces a virulent form of sleeping sickness and often results in death within a matter of weeks if not treated.

The principal insect vectors (tsetse flies) responsible for the transmissions of *T. rhodesiense* are *Glossina morsitans*, *Glossina pallidipes* and *Glossina swynnertoni*. When feeding on an infected host, the flies obtain the trypanosomal stage of the protozoa, which undergoes a period of development in the midgut region and eventually transforms into the epimastigote stage. The epimastigote stage then migrates to the insect's salivary glands and then changes to the elongated infective (metacyclic) trypanosomal stage. This stage can now be passed to another host during a blood meal and can initiate infection or disease. The transformations usually are completed in about 3 weeks.

Once in the human blood, the parasite multiplies rapidly. In most infected individuals, there is an enlargement of the lymph nodes (Winterbottom's sign) in the post-cervical region. Irregular fever, headache, joint and muscle pains, and a rash characterize the disease. *T. rhodesiense* may be found in is the blood, lymph nodes and tissues of humans.

Trypanosoma gambiense

Trypanosoma gambiense is the causative agent of the disease known as West African sleeping sickness and is found in the western part of Africa. *T. gambiense* is essentially transmitted between humans and tsetse flies sharing riverine vegetation habitats. In the case of *T. gambiense*, two tsetse flies (*Glossina palpalis* and *Glossina tachinoides*) serve as the primary vectors and are capable of transmitting the trypanosome.

West African sleeping sickness runs a more chronic course of infection in humans. In the first or early phase of the disease, infected individuals show similar clinical and pathological symptoms when infected with *T. rhodesiense*. However, the second or late phase of the disease is unique to *T. gambiense*. This phase involves severe damage to the central nervous system, and may be accompanied by other physical and mental impairment (mental retardation, speech impediments, swelling of the brains, etc.). At this time, the terminal sleeping stage develops and gradually the patient becomes more and more lethargic.

A person can be infected for months or even years without expressing obvious symptoms of the disease. When symptoms do appear, the disease is already at an advanced stage and, without treatment can lead to death. During the early or febrile stage of the sleeping sickness caused by *T. gambiense*, the organism occurs in the blood and lymph node of the infected individual. In the late stages where there is a development of cerebral symptoms, and the organisms can be found in the cerebrospinal fluid.

In infections with *T. rhodesiense* or *T. gambiense*, the presence of trypanosomes in chancre fluid, lymph node aspirates, blood, bone marrow, or, in the late stages of infection, cerebrospinal fluid (in the case of *T. gambiense*), using microscopic examination and other assays (such as testing for specific antibodies in the blood) are helpful in diagnosing trypanosomiasis.

In trypanosomiasis with *T. rhodesiense* or *T. gambiense*, treatment should be started as soon as possible and is based on the infected person's symptoms and laboratory results. The drug regimen depends on the infecting species and the stage of infection. Pentamidine isethionate and suramin (under an investigational New Drug Protocol from the CDC Drug Service) are the drugs of choice to treat the hemolymphatic stage of West and East African Trypanosomiasis, respectively. Melarsoprol is the drug of choice for late disease of *T. gambiense* with central nervous system involvement.

Tsetse flies do not normally fly far from their breeding sites (i.e., streams, lakeshores, lowland forests with dense growth of shrubs and trees, etc.) and are attracted to moving objects during the day. Control methods for the tsetse flies have included the removal of breeding sources, the use of a variety of insecticides, and well as traps.

Trypanosoma cruzi

Trypanosoma cruzi was first discovered in 1909 in Brazil by the scientist Carlos Chagas, in the midgut of its insect vector the kissing bug (*Triatoma infestans*). It is known to infect man and a wide range of domestic and wild species, including dogs, cats and rodents.

Chagas disease (named after Dr. Chagas) or American Trypanosomiasis is caused by *Trypanosoma cruzi* and is mostly prevalent in Brazil, Argentina, Uruguay, Chile, Venezuela, Central America and the Caribbean and afflicts approximately 15–20 million people. It is a disease primarily affecting low-income people living in rural areas. Chagas disease is also the leading cause of cardiac failure for men age 20–40 years in Brazil due to population and workforce movements into area infested with the insect vector. Houses built of adobe, mud, or thatch with cracks in the walls provides a suitable habitat and breeding habitat for the insect vectors.

Transmission of the trypanosomes depends on the presence of the parasite, vectors, reservoirs, and the host being present in the same location. Important reservoir animals in the United States are raccoons, opossums and armadillos. Also, in addition to animal reservoirs, insect vectors (*Triatoma infestans*, *Panstrongylus megistus*, *Rhodnius prolixus*) belonging to the family Reduviidae may also transmit the parasite. These bugs tend to inhabit cool, dark and damp areas, which makes underdeveloped communities with dilapidated, inadequate or simply unsanitary housing especially at risk for the infection.

Transmission of the parasite occurs when reduviids or kissing bugs that live in the cracks and crevices of substandard housing ingest the parasite in the blood from infected humans or animals. The protozoan *Trypanosoma cruzi* multiplies in the digestive tract of the insect and is eliminated in the feces on a person's skin, usually while the individual is sleeping at night. The individual often rubs the contaminated feces into a bite wound, an open cut, the conjunctiva or other mucous membranes. In addition, transmission through blood transfusion and the placenta have been reported. Animals may also become infected with the protozoa via similar methods, or by actually eating infected bugs. Transmission does not occur through the bite of the insect vector.

Some individuals may be infected and not show any symptoms of the disease until many years after infection (chronic form). The most recognized symptom of acute Chagas disease (especially in children) is the Romana's sign, or the swelling of the eye on one side of the face. Other symptoms may include fever, fatigue, enlarged liver and spleen and swollen lymph nodes, followed by convulsions and cardiac involvement. In infants and very young children with acute Chagas disease, cardiac arrest and death may result.

Beside the Romana's sign, and because many individuals do not show symptoms of the disease, xenodiagnosis (process whereby a small sample is injected into the body of an animal and after a period of time, the animal is tested for the amastigote form) may be able to determine the presence of the protozoan. Another form of laboratory diagnosis involves the culture of tissue aspirates especially from the lymph nodes on culture plates (N.N.N. culture plates).

No vaccination or drug is both safe and effective in the prevention and treatment of Chagas disease. Some drugs (anti-inflammatory doses of glucocorticoids and other supportive measures) may help to alleviate the symptoms associated with Chagas disease.

The usual method of insect control is the application of residual insecticides to the interior surfaces and roofs of the houses. In rural areas where the bugs may live and breed in substandard housing, plastering the walls to cover up cracks and crevices, or replacing homes with bricks and cement blocks can significantly contribute to the elimination of the insects inside of the home. The use of bed nets while sleeping has also shown to be effective in preventing bites from the bug. Outside, removal of the breeding sites of animals where the insects are found may also help to reduce the population of the insect vector, thereby reducing possible contact with the human host.

Trypanosomes in Animals

Some trypanosome species have been reported from wild and domesticated animals. These trypanosomes may be transmitted biologically or mechanically by various biting insects. *Glossina* or tsetse fly have been shown to transmit *Trypanosoma rhodesiense*, *T. gambiense*, *T. brucei*, *T. congolense*, *T. vivax*, *T. evansi* and *T. suis*. While insects such as tabanids have been shown to mechanically transmit *T. evansi* in animals, *T. equiperdum* in horses and camels is transmitted by direct blood contact during copulation. Some other trypanosomes, such as *T. thelieri* and *T. cervi*, are found in animals in the United States, but these species of the parasite are not pathogenic.

Of the various diseases associated with trypanosomes in which wild and domesticated animals are involved, *T. brucei* produces a disease called nagana which infects a wide range of animals, especially cattle. This trypanosome normally produces chronic infections in animals and may also produce different clinical signs. A severe acute case may be seen in horses, donkeys, dogs, goats and camels. In cattle, a chronic but sometimes fatal form of infection exists when the animals are infected by *T. brucei*.

When livestock are infected with *T. brucei*, they are mass-treated with drugs such as ethidium, isomethamidium or berenil. These drugs are effective, both for treatment and for prophylaxis, but may also be mutagenic. Slaughtered cattle fed these drugs may only be used for human consumption several months after drug treatment in order to avoid any residual effect of the drugs.

Recent Findings and Issues Associated with the Trypanosomes

Despite some progress with the trypanosomes, resurgence of the parasite remains a concern. During the nineteenth and twentieth centuries, trypanosomiasis was among the vector-borne diseases that prevented the development of large areas in the tropics, especially Africa. Fortunately, by 1910, it was shown that trypanosomes require blood sucking insect vectors, and over the next 50 years prevention and control programs were applied to curb the vectors. These programs placed emphasis on the elimination of the vector breeding sites, environmental hygiene and the limited use of chemical insecticides. However, the success of curbing the vectors was short lived, because by 1970 a reemergence of the vectors was seen and later intensified, over the next 20 years. Trypanosomes now infect over two million people each year.

Several factors have been implicated for the increase and reemergence of trypanosome related diseases. These factors include the following:

Civil and Political Unrest

Many of the affected African countries are currently experiencing wars, leading to the disruption of the available forms of controlling both the spread of the vector, and the parasite. War has also aided in the disruption of the ecosystem, and the displacement of the vectors from their native breeding grounds. In addition, many of the citizens of the affected countries have also been displaced, and are affected by the ongoing poverty.

Competing National Health Priorities

Currently, most of the available local resources are being put into research involving the prevention and cure of AIDS and malaria. Due to the efforts to solve the problems related to these diseases, funding for trypanosomiasis is limited.

Lack of Funding Support to Aid in the Availability of New Drugs, Vector Control and Diagnostic Tests

There has been very limited funding to support new drugs, vector control, and diagnostic tests. Due to the high level of poverty in most of the affected countries, most individuals cannot afford to buy the drugs to treat their illnesses. It is estimated that less than 10% of the infected individual are treated. Furthermore, there are no vaccines to protect the uninfected population from the parasite, because the parasite is able to mutate in order to evade the immune system.

Recently, several organizations including the World Health organization, the World Bank and some pharmaceutical companies have decided to look into the problem of the reemergence of trypanosomiasis. They have decided to employ the following methods to control the disease: increase research on vaccines, provide environmentally safe insecticides, educate the masses on the parasite and how to deal with it, and increase the availability of drugs to the infected areas so that people can afford them. Only by these concerted efforts will we be able to have a significant affect on trypanosomiasis.

► Tsetse Flies
► *Glossina* spp. (Diptera: Glossinidae)
► Chagas Disease or American Trypanosomiasis
► Sleeping Sickness or African Trypanosomiasis

References

Barrett MP (1999) The fall and rise of sleeping sickness. Lancet 353:1113–1114

Beaty B, Marquardt WC (1966) The biology of disease vectors. University Press of Colorado, Boulder, 632 pp

Bogitsh BJ, Cheng TC (1990) Human parasitology. Saunders College, Philadelphia, 435 pp

Lambrecht FL (1985) Trypanosomes and hominid evolution. Bioscience 35:640–646

Mulligan HW (1970) The African trypanosomiasis. Wiley, New York, 950 pp

Welburn SC, Fevre E, Coleman P (1999) Sleeping sickness rediscovered. Parasitol Today 15:303–305

Trypanosomiasis

A disease of vertebrate animals caused by trypanosomes.

► Trypanosomes
► Chagas Disease or American Trypanosomiasis
► Sleeping Sickness or African Trypanosomiasis

Trypsin Modulating Oostatic Factor

(TMOF) In female mosquitoes, the decapeptide hormone TMOF is synthesized by the ovarian follicle after a blood meal, affects the midgut cells, and regulates digestion.

Tsetse Flies, *Glossina* spp. (Diptera: Glossinidae)

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Tsetse flies (*Glossina* spp.), pronounced "set-see" or "tet-see," are found only in Africa where they range discontinuously from coast to coast, limited primarily by environmental and ecological factors. They infest 37 countries and about 10 million km^2 of sub-Saharan Africa. Their negative impact on the potential for economic development is immense, and they often have been blamed for the widespread poverty that exists in tropical and sub-tropical Africa.

Tsetse flies have a significant impact on human activities because they are obligatory blood feeders (Fig. 111) and they transmit blood parasites of the genus *Trypanosoma*, which cause sleeping sickness. When untreated or treated too late, sleeping sickness is a fatal disease. Because many tsetse species feed on humans and domestic animals, as well as on the wild animals that serve as immune reservoirs of the parasites, the potential for transmission can be very high. The incidence in fly populations of trypanosomes that cause animal trypanosomosis (trypanosomiasis), for example, often exceeds 20% and sometimes is as high as 90%.

Animal Sleeping Sickness

The major impact of animal sleeping sickness, nagana, is to preclude maintenance of domestic animals. Thus, this disease has restricted cattle

Tsetse Flies, *Glossina* spp. (Diptera: Glossinidae), Figure 111 Adult tsetse fly, *Glossina morsitans*, engorged with blood. (Photo by D.F. Lovemore.)

production in the tsetse-infested areas to less than 15% of the carrying capacity of the land. Without draught animals, inhabitants have been limited to subsistence level farming because it is necessary to till the land by hand. Without cattle and other domestic animals, severe protein deficiency is widespread. The estimated annual cost and losses in potential animal and crop production is $4 billion.

Preventive or curative drugs for control of nagana in livestock are only partially effective and often uneconomical due to the development of resistance. Trypanotolerant livestock, such as the N' Dama cattle in western Africa, have provided partial relief, but under heavy fly challenge these small cattle also succumb to the parasite. Immunization against trypanosomes has not as yet been successful due to the antigenic plasticity of the parasites. Thus, the primary means of preventing transmission is by elimination of contact between vectors and hosts by control of the vectors. Tsetse flies are the only significant vectors of trypanosomosis, although some limited mechanical transmission results from the feeding activities of other biting flies (*Stomoxys, Tabanus,* etc.).

Human Sleeping Sickness

Human sleeping sickness, transmitted by tsetse flies from man to man in western and central Africa (*Trypanosoma gambiense*) and from animal reservoirs to man in eastern and southern Africa (*Trypanosoma rhodesiense*), has a lower incidence than animal trypanosomiasis. This is because of the relatively fewer encounters between flies and humans than between flies and livestock, and also because of the much lower rate of *T. gambiense* and *T. rhodesiense* infections in fly populations. In 1999, over 45,000 new human cases were reported, but due to incomplete reporting it is estimated that the actual human incidence was probably closer to 300,000–500,000. Historically, millions have been killed by trypanosomosis. Curative drugs are harsh, but can be effective with early diagnosis. Neurological disorders are common following recovery from infection. Due to civil unrest and disruption, combined with reduced control effort in many infested regions, the 60 million individuals estimated to be at risk of infection are subject to increased likelihood of severe disease outbreaks.

Tsetse Biology

Vector control is complicated by such a wide distribution of the flies, which usually are found in broad belts that are more or less continuous and often cross international boundaries. They can be difficult to detect in areas where the fly populations are advancing or at low density. Furthermore, there are over 20 distinct vector species, although not all are important vectors and often several species co-exist in the same areas (Table 16).

Members of the *morsitans* group, which inhabits savannah grasslands, and the palpalis group, which is generally found in lacustrine and riverine situations, are the primary vectors of both human and animal trypanosomosis. Because of ecological requirements, the palpalis group is generally restricted to areas near the dense vegetative cover found in aquatic situations, whereas species of the *morsitans* group have a wider range of ecological niches and are more widely dispersed.

Tsetse Flies, *Glossina* spp. (Diptera: Glossinidae), Table 16 Habitat relationships of *Glossina* spp.: savannah (morsitans), riverine (palpalis), and forest (fusca) group tsetse flies

Morsitans	*Palpali*	*Fusca*
austeni	*calignea*	*brevipalpis*
longipalpis	*fuscipes fuscipes*	*fusca congolensis*
morsitans centralis	*fuscipes martini*	*fusca fusca*
morsitans morsitans	*fuscipes quanzensis*	*fuscipleuris*
morsitans submorsitans	*pallicera pallicera*	*haningtoni*
pallidipes	*pallicera newsteadi*	*longipennis*
swynnertoni	*palpalis gambiensis*	*medicorum*
	palpalis palpalis	*nashi*
	tachinoides	*nigrofusca hopkinsi*
		nigrofusca nigrofusca
		schwetzi
		severini
		tabaniformis
		vanhoofi

All species are larviparous, not laying eggs but producing living young that have been nurtured in the uterus of the female fly for several days. They deposit only one offspring at a time and, even though the adults occasionally survive for as long as 90–100 days in nature, their biotic potential is quite low compared to that of other dipteran species (Fig. 112). The larvae usually burrow into the soil or other suitable substrate, where they pupate and develop for 3–4 weeks or more before emerging as adults. Thus, at any given time a significant portion of the fly population is underground, a fact that plays an important role in control strategy.

The adults move about in a diurnal pattern, governed to a great extent by temperature. For example, in the summer in southern Africa, *G. m. morsitans* feeds in the mornings when the temperature is moderate, seeks shelter during midday when the temperature is high and the insect exhibits negative phototaxis, and resumes feeding as the temperature declines in the latter part of the day. At night the flies rest. Nutritional requirements cause the flies to seek blood meals about every third day, and the males also actively visit host animals in search of mates feeding there. In this process, the sexually appetitive males move about several times daily, often resting on host animals grazing or traversing the bush. In the course of these activities, the flies alight on numerous resting sites in their preferred habitat. The preferred resting sites vary somewhat for the different species.

Tsetse Behavior and Ecology in Relation to Control

The association of tsetse flies with particular vegetation types has played a major role in determining control practices. Riverine species of the palpalis group are generally found within a short distance of their breeding sites, in or close to the riverine vegetation canopy that provides protection from sunlight, high temperature, and lower humidity of the surrounding, more open

Tsetse Flies, *Glossina* spp. (Diptera: Glossinidae), Figure 112 Adult female tsetse fly depositing fully developed larva.

vegetation. This habitat affords the fly an environment replete with a variety of hosts, and incidentally provides direct contact with humans and domestic animals when they come to the water. Partial or complete removal of the riverine vegetation results in the reduction or elimination of these tsetse flies. However, in more humid areas, species of the *palpalis* group may be found well away from surface water. *Glossina tachinoides*, for example, has been observed to breed in peridomestic habitats, where bush encroachments around villages have allowed flies to find suitable resting and larviposition sites well away from the typical riverine situation. Similar observations with species of the morsitans group have revealed their preferences for selected resting sites and their dependence upon certain characteristics of the habitat for survival. Ruthless removal or discriminative clearing of selected portions of the habitat results in major reductions of fly density because the flies cannot then find suitable protective cover when environmental stresses are maximal.

Similarly, feeding behavior characteristics of the tsetse fly have provided a means for reducing population density with a corresponding reduction in the risk of trypanosomosis. Most tsetse species feed on a variety of animals but prefer certain hosts, sometimes riverine. For example, in Zimbabwe, *G. m. morsitans* feeds on numerous hosts, but prefers bushpig, warthog, bushbuck, and kudu. Thus, by selective reduction of these four species, the fly density could be reduced along with the incidence of trypanosomosis.

However, for economic, environmental and aesthetic reasons, game reduction and wide-scale bush clearing are no longer acceptable control measures.

Awareness of specific tsetse resting niches spurred the development of selective application methods for the organic insecticides that first became readily available in the 1940s. Because most species have well defined resting site preferences, such as the lower boles of trees of certain diameters, application of persistent insecticides to these sites provided excellent control without resort to broadspread applications. Furthermore, since the flies have a long life span, during which the majority probably move less than 1,000 m from their origin, not all resting sites needed to be sprayed to achieve a high level of control. Flies below ground in the pupal stage eventually emerge and sooner or later come to rest on a treated surface. Treatment of 10–20% of the preferred resting sites in some tsetse habitats was sufficient to eliminate or substantially reduce the fly population when the toxicant persisted for several months.

Approaches to Fly Management

Glossina spp. are extremely susceptible to insecticides. Aerial applications of very low rates of nonpersistent aerosols repeated at 2–3 week intervals have been used to initially control the ambient fly population and then the flies that have recently (0–15 days) emerged, thereby precluding reproduction and eliminating the fly population after six or seven spray cycles. Alternatively, selectively placed helicopter applications of persistent insecticides have been used with dramatic results. These applications were discriminative in that they included only those habitats that offer refuge for the fly in the dry season, when tsetse fly distribution typically is more restricted. Most of the application was deposited on the leaves of the upper canopy, where tsetse rest at night. These residual types of application were particularly effective in areas with discrete wet and dry seasons.

But the broadspread application of pesticides has given way to the use of attractants and trapping to expose the flies to spot treatments of pesticides. Both visual and olfactory components are involved in tsetse host-seeking behavior. In the 1970s, animal emanations attractive to tsetse flies were found to be highly effective for trapping several species of tsetse, especially when combined with suitable visual attractants. By utilizing a persistent insecticide in conjunction with attractant devices, significant population reductions can be achieved in a matter of months. Such trapping provides a relatively inexpensive method of control, and because the pesticide is incorporated into the attracting device the probability of environmental contamination is low.

However, the attractant approach does not guarantee elimination of the vector, and thus the disease, even though fly population density in most situations can be reduced to well below the threshold level necessary to maintain regular transmission. Extensive study and operational level trials of the sterile insect technique have demonstrated the feasibility of this approach for area-wide elimination of tsetse where geographically isolated fly populations already have been reduced to low density. Used to eliminate *Glossina austeni* from the main island in Zanzibar, the inhibition of natural reproduction with sterile fly releases after reducing fly density by trapping is an environmentally friendly method of control that has potential application for most of Africa.

► Trypanosomes
► Sleeping Sickness or African Trypanosomiasis
► Histroy of Insects

References

Buxton PA (1955) The natural history of tsetse flies. H. K. Lewis, London, +47 plates, 816 pp

Food and Agriculture Organization (1992) Programs for the control of African animal trypanosomiasis and related development. FAO Animal Production and Health paper 100. In: Proceedings of Symposium, Harare, Zimbabwe. www.fao.org/docrep/004/to559e/to599e00.htm

Leak SGA (1998) Tsetse biology and ecology: their role in the epidemiology and control of trypanosomosis. CABI, Wallingford, 592 pp

Mulligan HW (ed) (1970) The African trypanosomiases. George Allen and Unwin, London, 950 pp

World Health Organization (1998) Control and Surveillance of African trypanosomiasis. Technical Report Series No. 881, vi + 113 pp. www.who.int/health-topics

Tube-Making Caddisflies

Members of the families Polycentropodidae and Psychomyiidae (order Trichoptera).

► Caddisflies

Tubercle

A small raised area or extension of the integument. In caterpillars, a hair often originates from these raised areas.

Tube Moths (Lepidoptera: Acrolophidae)

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Tube moths, family Acrolophidae, total 270 species in the New world, mostly in the large genus

Acrolophus; actual fauna likely exceeds 350 species. The family is part of the superfamily Tineoidea, in the section Tineina, subsection Tineina, of the division Ditrysia. Two subfamilies are used: Amydriinae and Acrolophinae (formerly included in Tineidae). Adults small to medium size (9–60 mm wingspan), with rather robust bodies and roughened head scaling and usually large recurved labial palpi; haustellum naked (unscaled); maxillary palpi minute, 2-segmented. Maculation is mostly somber hues of brown or black, sometimes with some spotting and other markings. Adults are mostly nocturnal, but some may be crepuscular. Larvae are root feeders, mostly of grasses, and construct long silken tubes to feed on host-plant roots. A few are economic, mainly as turf grass pests (Fig. 113).

Tube Moths (lepidoptera: Acrolophidae), Figure 113 Example of tube moths (Acrolophidae), *Acrolophus plumifrontellus* (Clemens) from Florida, USA.

References

Becker VO, Robinson GS (1981) Neotropical taxa referable to *Acrolophus* (Lepidoptera: Tineidae). Syst Entomol 6:143–148

Davis DR, Milstrey EG (1988) Description and biology of *Acrolophus pholeter* (Lepidoptera: Tineidae), a new moth commensal from gopher tortoise burrows in Florida. Proc Entomol Soc Washington 90:164–178

Hasbrouck FF (1964) Moths of the family Acrolophidae in America north of Mexico (Microlepidoptera). Proc US Natl Mus 114:487–706

Hinton HE (1955) On the taxonomic position of the Acrolophinae, with a description of the larva of *Acrolophus rupestris* Walsingham (Lepidoptera: Tineidae). Trans R Entomol Soc London 107:227–231

Turgor

The distension of living tissue, usually plant tissue, due to internal pressures (hydration).

Tullgren Funnel

An extraction devise used to separate and extract small arthropods from leaf litter or similar material. A Tullgren funnel normally consists of a funnel with a wire mesh insert that supports the plant material above a reservoir containing alcohol or another preservative. An incandescent light bulb is suspended above the funnel to provide a source of heat and drying, encouraging the movement of the arthropods. As the arthropods move about, particularly as they move deeper into the funnel to escape drying of the plant material, they slip down the funnel into the reservoir containing liquid, where they are retained for identification. This technique is useful for many arthropods, but not for those that may fly to escape, or those that are very fragile and perish from desiccation before they can escape the plant material. A cover is often provided to eliminate escape by insects capable of flight, and to more efficiently direct the heat generated by the light bulb. A Tullgren funnel is a modified Berlese funnel, with the difference being the light bulb, but the distinction is not usually appreciated and most Tullgren funnels are called Berlese funnels.

Tularemia

Also known as rabbit fever, this is a serious infectious disease caused by the bacterium *Francisella* *tularensis*. The disease is endemic in North America, and parts of Europe and Asia. The primary vectors are ticks and deer flies, but occasionally the disease can also be spread through other arthropods. Animals such as rabbits and muskrats serve as reservoir hosts. The disease is named after Tulare County, California, where in 1911 the disease was studied in squirrel and human populations.

► Ticks

Tumbling Flower Beetles

Members of the family Mordellidae (order Coleoptera).

► Beetles

Tungidae

A family of fleas (order Siphonaptera).

► Fleas

Turfgrass Insects of the United States: Biology and Management

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Turfgrasses are grown throughout the United States, covering over 30 million acres (12.2 million hectares). As urban environments have grown, the use of turfgrass in the U.S. has increased over the past several decades. Subsequently, large areas of land have been developed with dense, dark green, uniform turf providing numerous practical, recreational, and ornamental uses. Uses for turfgrass include dense turf for soil stabilization and erosion prevention; runways for rural airports; cemeteries; parks and recreational facilities for relaxation, picnics and general family activities; sports facilities and complexes including baseball, cricket, football, lawn bowling, polo, soccer, tennis and, especially, golf courses. Turfgrasses often are considered the most intensively managed plantings in urban landscapes. It is estimated that $45 billion is spent per year in the U.S. for turfgrass culture in its many forms.

Turfgrass can be designated as either cool-season or warm-season grasses depending on their climatic adaptations. These two categorical designations can be further divided into four distinct turfgrass adaptation zones in the U.S. including (i) cool, humid; (ii) cool, arid or semi-arid; (iii) warm, humid; and (iv) warm, arid or semiarid. Despite these partitioned zones, there is considerable overlap of the species of turfgrass grown in various regions of the U.S. As a result, it is rather difficult to effectively provide an accurate description for the boundaries of specific insect pests and nearly impossible to give a comprehensive classification for all turfgrass pests including disease pathogens, insects and weeds.

Some insect pests are host specific, feeding only on certain turfgrass species or types, while others are non-discriminate, infesting a diversity of grass and broadleaf plant materials. An insect pest such as the European chafer typically only infests cool-season areas, whereas mole crickets and fire ants infest warm-season turfgrasses. Preference of an insect pest can be either for a host (e.g., turf-type or species) or it may be a reflection of the geographic range of the pest. Destructive turfgrass insects can be divided into three primary groups according to the habitat in which the destructive life stage spends its life in the turfgrass ecosystem. They include (i) leaf and stem, (ii) thatch, and (iii) root zone/soil. This method of grouping is highly valuable because specific control tactics or strategies implemented for each group have a direct bearing on the effectiveness or satisfaction of control for the respective insect pest. Some insects are capable of occupying more than one habitat during its development, and may even occupy all three habitats during its various life stages. Thus, a modified designation of turf habitats has been suggested including (i) foliage and stem, (ii) crown and thatch, and (iii) soil.

Effective control of any pest (plant pathogen, insect or weed) can be accomplished successfully only with a comprehensive understanding of both the host and the pest. Factors such as growth habits and cultural requirements of the host (turfgrass) must be understood. Knowledge of the biology, behavior, ecology, life history for the host and pest are critical for making decisions. Symptomology or type of damage caused by the pest(s), accurate identification of the pest, information regarding the time of year, growth stage of the host and the pest, and environmental conditions under which pest damage is most likely to occur are all important factors that also should be understood. This information is the foundation for the Integrated Pest Management (IPM) philosophy. IPM is a commonsense approach to pest management that is effective and environmentally responsible. IPM relies on a combination of preventative and corrective measures to keep pest densities below levels that would cause unacceptable damage. IPM includes sampling and monitoring, accurate pest identification, decision-making, appropriate intervention, follow-up, and detailed record keeping. In terms of the appropriate intervention tactic, several control options are available including biological, chemical, cultural, and plant resistance. IPM is a decision-making process that does not preclude the use of pesticides, however, it does not rely upon chemical control as its first line of defense. The ultimate goal of IPM is to manage pests effectively, economically, and with minimal risks to people and the environment. For this reason, turfgrass managers must constantly be aware of potential pest problems that they may experience. The listing that follows provides vital information for the major insect and mite pests affecting turfgrass in the US (Figs. 114 and 115).

Foliar and Stem Inhabitants: Surface Chewing and Sucking Insects

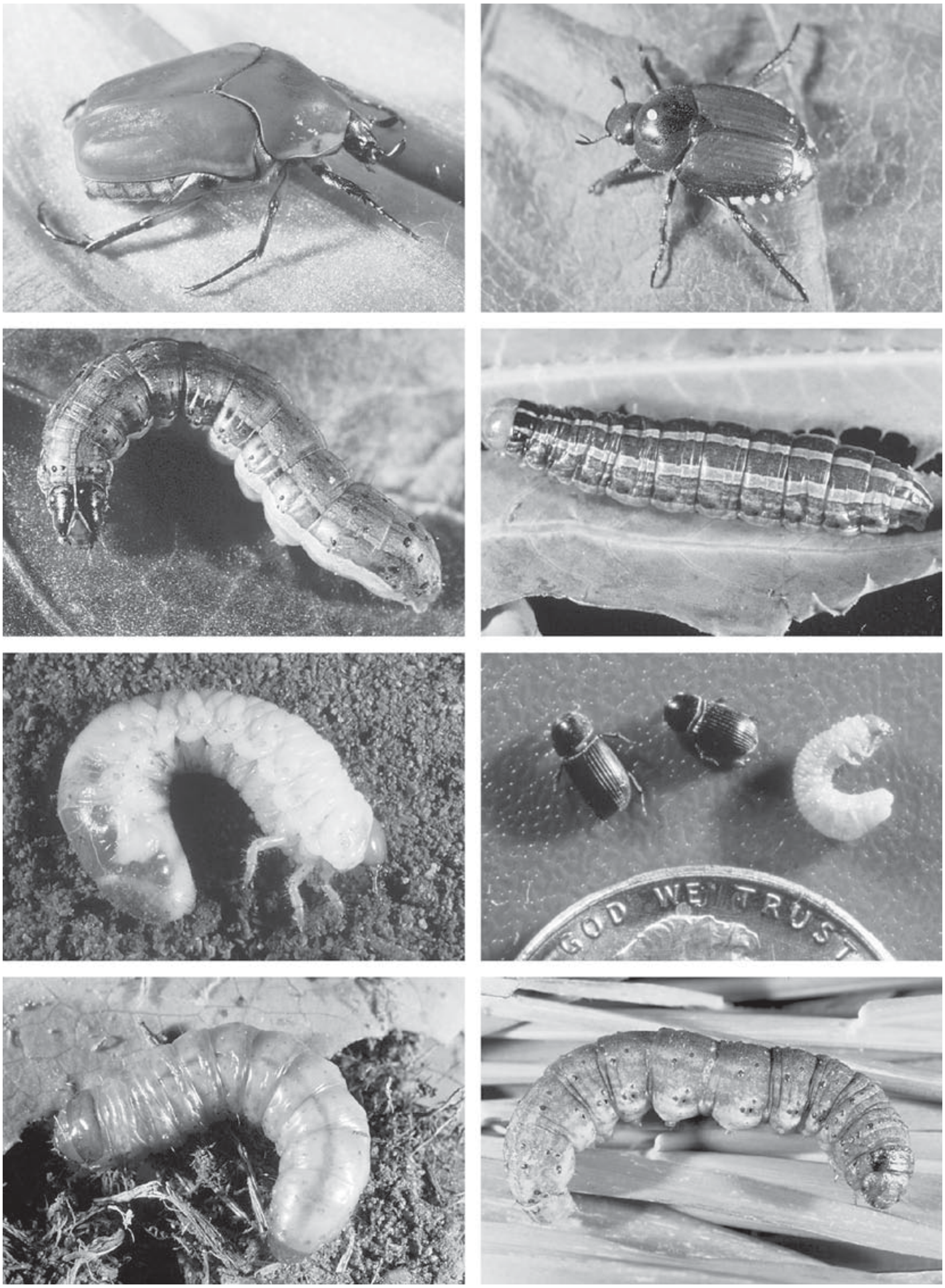
Armyworms (Lepidoptera: Noctuidae)

Armyworms get their name because of their gregarious nature of crawling in large numbers from one field or feeding site to another after they have exhausted their food supply. Although these pests are often sporadic, they do have the potential for outbreaks. Most armyworm larvae are thick-bodied, hairless, striped caterpillars that chew on the foliage of turfgrass. There is one armyworm species that frequently attacks turfgrasses in both the northern and southern United States, the “common” or “true” armyworm.

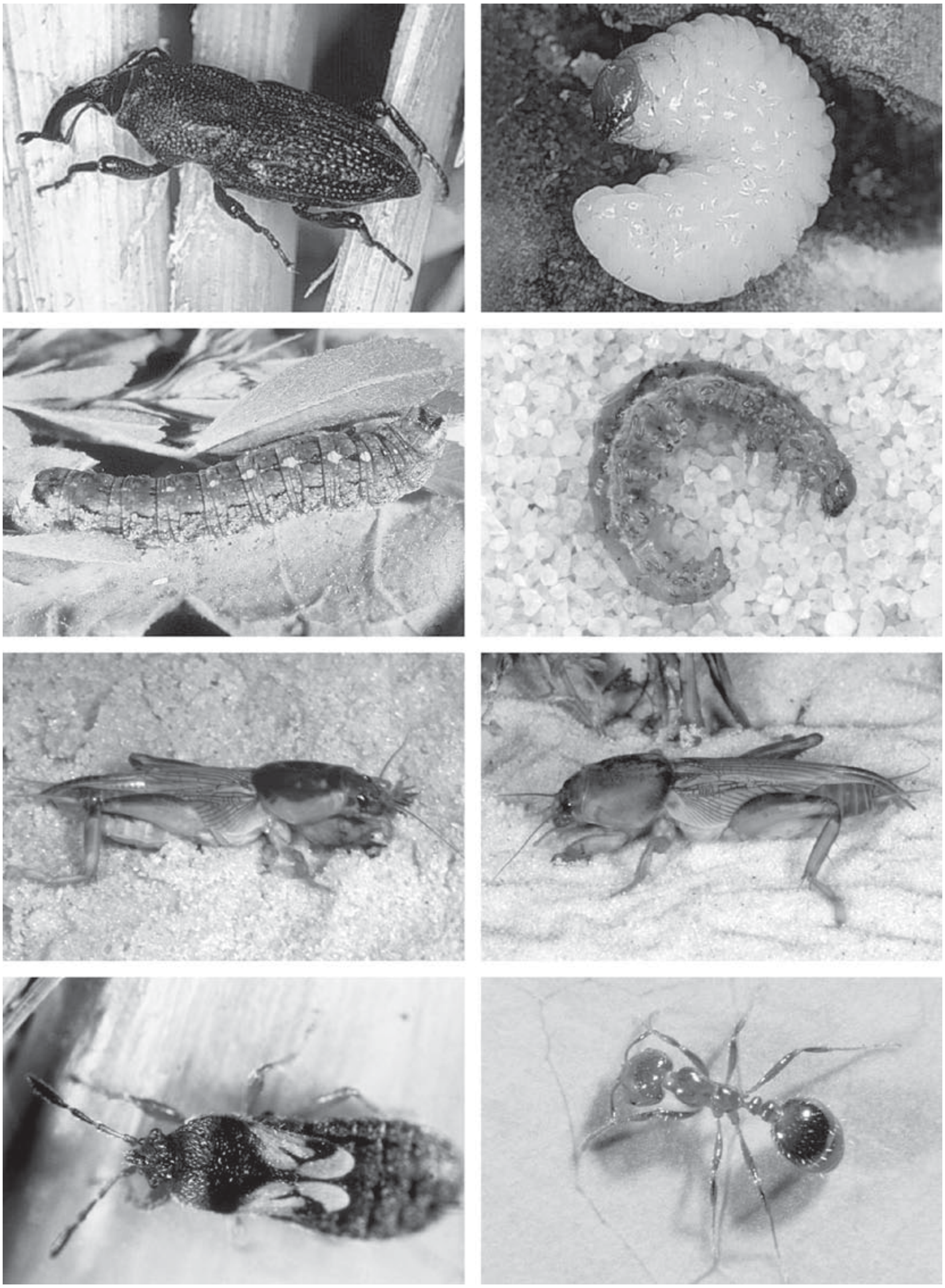
Armyworm, *Pseudaletia unipuncta* (Hawthorn)

Frequently referred to as the “common” or “true” armyworm in order to differentiate it from other armyworm species, the armyworm is a native species that is distributed throughout the United States and southern Canada east of the Rockies.

Armyworm adults are evenly pale-brown to grayish-brown moths with a wingspan of approximately 38–40 mm. The distinct white spot in the center of their front wings readily identifies them. The hind wing is dirty white. The female adult moths lay pearly white eggs, 0.5 mm diameter, in masses containing 20 to several hundreds of eggs. Young larvae, more than 2 mm long, are pale green. Mature larvae range from 35 to 50 mm in length, grayish to greenish-brown, with two pale-orange stripes along each side of the body and another pale-colored, broken stripe down the middle of the back. The head capsule is honeycombed with dark lines. Pupae are reddish-brown, about 16–19 mm long and shaped like a football.



Turfgrass Insects of the United States: Biology and Management, Figure 114 **Some important turfgrass pests: *top left*, green June beetle; *top right*, Japanese beetle; *second row left*, fall armyworm; *second row right*, bronzed cutworm; *third row left*, a June beetle larva (white grub); *third row right*, black turfgrass ataenius adults and larva; *bottom row left*, glassy cutworm; *bottom row right*, black cutworm.**



Turfgrass Insects of the United States: Biology and Management, Figure 115 **Additional important turfgrass pests: *top row left*, billbug adult; *top row right*, billbug larva; *second row left*, variegated cutworm; *second row right*, tropical sod webworm; *third row left*, tawny mole cricket adult; *third row right*, southern mole cricket adult; *bottom row left*, immature chinch bug; *bottom row right*, red imported fire ant.**

Armyworm caterpillars feed on a wide range of grasses. They especially like barley, corn, millet, oats, rice, rye and wheat. When such food supplies are depleted, they will attack nearby turfgrass. Young larvae initially feed on tender foliage resulting in a skeletonized appearance. Third instar and older larvae are primarily nocturnal and consume all or part of the leaf.

Armyworms overwinter as partially grown larvae or pupae in the southern half of the U.S. and possibly as partially grown larvae in the northern half. Infestation in the North may also be the result of spring migration flights of adults. In the temperate United States, there are typically two generations (broods) per year. The number of annual broods depends primarily on latitude. The first generation is a result of annual moth migration in the spring (i.e., late April through May). Once the eggs are laid, they typically hatch in as few as 3 days. Larvae usually go through six instars over a period ranging from 20 to 48 days. Pupation occurs in the soil and the duration of the pupal stage averages 15 days. Adult armyworm moths are nocturnal, with most flight activity occurring within 2 hours after sunset. A second generation occurs during June and July. In the southern regions, four to five generations may occur. Infestations in turfgrass are often most severe following drought conditions. Populations have a tendency to fluctuate widely from generation to generation and year to year.

Fall Armyworm, *Spodoptera frugiperda* (J. E. Smith)

The fall armyworm is found throughout much of the South and is a frequent problem in turfgrass, especially in the Southeast westward into Texas, New Mexico, Arizona and southern California. It does not overwinter outside of Florida and the immediate Gulf Coast area, and must disperse to reinfest areas each year. Populations usually do not reach the more northern areas until very late summer or fall.

Fall armyworm moths have a wingspan of about 38 mm and the forewings are generally a dark gray and mottled in appearance. There is a white spot near the tip of the forewing and a light diagonal mark in the middle of each wing. The back wings are white. The eggs are laid in clusters of 50–100 and are initially greenish white, but soon turn dark. The egg clusters often look gray and fuzzy from the scales of the female's wings. The caterpillars are green to brown, to almost black. The head is marked by a typical inverted "Y" on the "face" or front. There is a longitudinal dark stripe that runs the length of the body and a fainter, pale mid-dorsal stripe. Each abdominal segment has four small black dots. The fully grown larvae are 35–50 mm long. The pupa is 13 mm long and is found in the soil. It is reddish-brown, somewhat football shaped, and becomes black prior to emergence of the moth.

Fall armyworms feed on a wide range of plants, but prefer grasses of all types. However, this pest is most commonly associated with bermudagrasses in the southern U.S. They can and do feed on both cool and warm season turfgrasses and are often most likely to attack lush, green, dense areas of turf. Fall armyworms are very common problems in areas that have recently been sodded or sprigged. The small larvae skeletonize the leaf blades while larger larvae may consume all above-ground plant parts. The turf also may turn brown and look dead from drought stress. The larvae often move from heavily damaged areas into new food sources. Warm season turf usually recovers from such feeding, but if it occurs late in the season, the turfgrass may be stressed going into the winter.

Fall armyworm moths are active at night and may be attracted to lights. They lay eggs on a wide range of objects, usually light-colored, that are adjacent to turf areas. These sites may include fence posts, metal buildings, flagpoles, the underside of leaves of various landscape plants, gutters, etc. Eggs hatch quickly in warm temperatures and the small larvae spin down on silken thread to the turf surface and begin feeding. Small caterpillars feed at any time of the day, but larger ones feed more at night to avoid predation by birds. The fall armyworms will feed for 2–3 weeks and then burrow into the soil to pupate. New moths emerge 2 weeks later and the cycle starts again. Multiple infestations can occur in the same location and population as high as 100 per square meter have been observed. The number of generations per year depends upon location and migration of the moths. Migration varies each year depending upon weather conditions, which are responsible for enhancing the migration of the moths. In the extreme South, four or more generations may occur and the damage from the larvae may begin in the spring. In locations further north, only one generation will occur and it may not be seen until August or September. Wet springs sometimes increase the likelihood of fall armyworm outbreaks.

Chinch Bugs (Hemiptera: Lygaeidae)

Chinch bugs damage turfgrass by sucking plant juices from stems (i.e., leaf sheaths) and crowns, causing gradual yellowing and eventual dead patches of turf. Damage occurs predominantly during hot, dry periods of time in mid- to late summer. Sunny areas are often most heavily infested. There are four chinch bug species that are important turfgrass pests in the United States (i) the hairy chinch bug, (ii) the common chinch bug, (iii) the "buffalograss" chinch bug, and (iv) the southern chinch bug.

Hairy Chinch Bug, *Blissus leucopterus hirtus* Montandon

The hairy chinch bug occurs across the eastern Canadian provinces and from the northeastern United States to the Middle Atlantic states south to Virginia and west to Minnesota.

Chinch bugs have gradual metamorphosis, thus the immature (nymph) life stage is similar in physical appearance and feeding habits to the adult, however, there is variation in size, color and wing development. There are five nymphal stages; the first instar nymphs are tiny, approximately 2.5 mm long, bright red with a white band across the abdomen. As the nymphs develop and mature, their color changes from bright red to orangish-brown and ultimately black once they reach the fifth instar. Hairy chinch bug adults are approximately 6.0–6.4 mm long and 1.0 mm wide, and females typically are slightly larger than males. Adults range in color from grayish-black to black and white and often are covered with fine hairs and the legs are typically a dark, burnt-orange tint. There is a triangular-shaped marking in the middle of the outer edge of each wing. Populations of hairy chinch bugs may consist of mostly long-winged (macropterous) or short-winged (brachypterous) individuals, or contain both wing forms. The long-winged chinch bugs have wings that extend to the tip of the abdomen, and short-winged chinch bugs have wings that extend only halfway to the tip. The adults lay eggs that are tiny, elongate, and bean-shaped; initially they are white, but become orange-red within a few days prior to hatching.

The hairy chinch bug is one of the most important insect pests of northern turfgrasses, especially home lawns. It prefers cool-season turfgrasses including creeping bentgrass, fine fescues, Kentucky bluegrass, and perennial ryegrass. However, hairy chinch bugs will feed also on zoysiagrass, a warm-season turfgrass species that occasionally occurs where cool-season turfgrasses dominate. Both the adults and nymphs cause damage to turfgrass plants by inserting their piercing-sucking mouthparts into stems and crowns, extracting plant juices while pumping toxic salivary fluids into the plant. Subsequently, turfgrass plants are damaged by the loss of plant fluids as well as the clogging of the conducting tissues within the stems. Generally, hairy chinch bug occurs sporadically in scattered aggregations rather than uniformly distributed across the turf. Damage typically occurs during hot, dry periods in mid- to late summer when turf is commonly experiencing drought stress symptomology. Additionally, hairy chinch bug prefers open, sunny areas of turf that have heavy thatch accumulation as well as high percentages of perennial ryegrass and fine-leaf fescue. Initial damage often appears as irregular patches of wilted, yellowish-brown turf that frequently is mistaken for drought stress. As populations grow, often reaching 200–300 bugs per 0.1 m^2, feeding damage intensifies and damaged patches of turf begin to coalesce into large areas of dead or dying turf that does not recover regardless of irrigation or rainfall.

Typically there are two generations per year in the temperate United States; however, in the most northern portion, as well as Canada, there is only one generation per year. The adults overwinter in the turfgrass thatch, leaf litter, and similar sites. They become active in the early spring as temperatures reach 10°C. Thereafter, the adults feed and mate for approximately 2 weeks before females begin laying eggs in mid-April to May. In areas where there is only one generation per year, egg-laying may be delayed by several weeks and occurs over an extended period. Females lay as many as 20 eggs per day for a period of about 2–3 weeks. Eggs typically are laid in leaf sheaths or in the thatch. Because insects are cold-blooded animals, they are dependent on temperature, thus the developmental rate of eggs and nymphs varies within species and geographic range. Eggs that are laid during April may require as long as a month to hatch, and eggs laid in midsummer may hatch in as few as 7–10 days. Where two generations occur, the first generation typically matures in 4–6 weeks, usually by mid-July. The second-generation adults then begin laying eggs from mid-July through late August. These eggs hatch soon thereafter, and the nymphs complete development by September or October. As cooler temperatures prevail, the adults seek out protected sites to overwinter. The most extensive damage to turf commonly occurs during periods of heat and drought stress, typically in late July and August when the first generation adults are actively feeding and laying eggs.

Common Chinch Bug, *Blissus leucopterus leucopterus* (Say)

The common chinch bug is an occasional pest of turf, especially in the Great Plains region. It feeds primarily on small grains and other field crops, however, sometimes it damages turfgrass, especially when located in close proximity to maturing small grain fields. Several turfgrass species that are likely to be attacked by the common chinch bug include creeping bentgrass, fescues, Kentucky bluegrass, perennial ryegrass, and zoysiagrass. This species closely resembles the hairy and the buffalograss chinch bugs both in appearance and damage.

Buffalograss Chinch Bug, *Blissus occiduus*

The buffalograss chinch bug was first identified in Nebraska feeding and causing damage on buffalograss. Upon its discovery, it was understood that the buffalograss chinch bug was limited to buffalograss as a host. However, it has recently been reported damaging zoysiagrass, and may have the potential also to feed on and damage several other turfgrasses and small grain crops. This species closely resembles other chinch bugs species in appearance and damage.

Southern Chinch Bug, *Blissus insularis* Barber

The southern chinch bug is a major pest throughout the range of its primary host, St. Augustinegrass.

Distribution is generally from the Carolinas down through all of Florida and west to Texas. They also can be found in California, Mexico and throughout the Caribbean. Like other chinch bugs, they damage the turfgrass by sucking out plant juices.

Southern chinch bugs are similar to other chinch bugs, but slightly smaller than the hairy chinch bug. The adults are about 1 mm wide and 3–3.5 mm long and are black with shiny white wings. Most characteristics are similar to other chinch bugs including the presence of long- and short-winged adults.

The southern chinch bug is one of the most important insect pests of home lawns in the deep South. Virtually all St. Augustinegrass will be infested with southern chinch bugs, but not necessarily at damaging population levels. Southern chinch bugs will feed also on bermudagrass, centipedegrass, bahiagrass, and zoysiagrass. As with the other species of chinch bugs, their feeding on stems, crowns, and stolons removes plant juices, but also injects a toxin. This causes the grass to turn yellow and often die. Populations often are aggregated and damage appears in patches. Drought or heat-stressed areas of lawns are areas that usually are attacked first and most severely.

There are probably two to three generations in the most northern areas of the southern chinch bug range. Further south in northern Florida and the Gulf Coast area, three to four generations are common. In south Florida, seven or more generations can occur. Overwintering in the most northern areas is primarily as adults while all stages are present in the more southern areas.

Cutworms (Lepidoptera*:* Noctuidae)

Cutworms are plump, smooth, dull-colored caterpillars that hide in the turf profile in burrows or aerification holes during the day, emerging at night to feed on the foliage and leaf sheaths of turfgrass plants.

Black Cutworm, *Agrotis ipsilon* (Hufnagel)

The black cutworm is considered the most destructive cutworm that attacks turfgrasses. It is a major pest of creeping bentgrass putting greens, tees, and occasionally fairways throughout the United States and worldwide. Black cutworm larval feeding damage typically results in small, irregular sunken patches or pockmarks that often are mistaken for golf ball marks. Subsequently, black cutworm damage reduces the smoothness and uniformity of the putting green surface. Because aesthetics and playability are high priorities for golf course superintendents, multiple insecticide applications are done each growing season to control this important turfgrass insect pest.

Adult black cutworm are robust, hairy (scaly) moths with a wingspan of approximately 35–45 mm. The forewings are dull-brown to grayish-black, and slightly lighter in color or pale toward the tip of the wings. A distinctive, black, dagger-shaped marking is located in the center of each forewing, approximately 6 mm from the tip. The hindwings are considerably lighter, uniformly cream to dirty white, with darker veins. Black cutworm adult moths typically hold their wings flat over the back in a triangular position when resting. Males can be differentiated easily from females by their comb or feather-like antennae, whereby female moth antennae are filiform or slender and thread-like.

Black cutworm females lay eggs predominantly singly near the tip of grass blades. Eggs are approximately 0.5 mm in diameter. They are cream colored initially, later becoming darker as the embryo develops. Larvae are hairless with the exception of a few scattered bristles. The dorsal side, above the spiracles, ranges in color from gray to black, and the ventral side is typically lighter gray. Spiracles are typically black and extend from the prothorax to the terminal abdominal segment. As a whole, the body of a black cutworm larva is without distinct stripes or marking except for an indistinct, pale stripe down the middle of the dorsal side. Under magnification, the cuticle (skin) has a pebble-like surface, and is generally greasy in appearance. Like many other caterpillars, there are three pairs of true legs on the thorax and five pairs of fleshy prolegs on the abdomen. Neonate larvae, less than 24 h old, are approximately 3.5 mm long whereas mature larvae range from 30 to 45 mm long and are approximately 7 mm wide. Black cutworm larvae typically have six instars, however, they sometimes have seven. Upon maturity, black cutworm larvae pupate in the turf profile predominantly in the soil, and occasionally in the thatch associated with the turf. Pupae are reddish-brown to dark brown in color and are about 19 mm long.

The black cutworm is distributed throughout most of North America, as well as in Europe, Asia, Africa and elsewhere. Depending on geographic location, latitude and temperature, there can be two to six generations per year. In the southern U.S., in states such as Louisiana and Alabama, there are five to six overlapping generations, whereas in the northern U.S., in states such as Minnesota and Wisconsin, there may be only one or two generations per year. The black cutworm has difficulty surviving subfreezing soil temperatures, thus, it may be unable to overwinter in some years north of the transition zone (a narrow range between the cool-season temperate region and warm-season zone, extending from southern Illinois, Missouri and Ohio to Tennessee and North Carolina). As a result, spring infestations in northern areas begin with the arrival of migratory adults from southern states. Black cutworm moths can be carried several hundred miles in a few days by strong southerly winds. In Wisconsin, the first spring migrants typically arrive in late April to early May; damage from their offspring begins appearing in early to mid-June. Damage from the second generation (brood) starts appearing late July through early August. Occasionally a third generation will appear in late summer or early fall if temperatures are conducive, otherwise it is understood that third generation adults will migrate south as temperatures are less favorable. Multiple larval sizes (instars) may be present at a given time because black cutworm populations tend to spread out their emergence and egg-laying as the season progresses. In addition, the first generation appearance of black cutworm in states located in the northernmost temperate U.S. may have a later arrival of migrating adults than states in the southernmost location of the temperate U.S. In the southernmost states (e.g., Alabama, Louisiana, Mississippi and Georgia), first generation larvae may be present as early as February and March and cutworm problems may persist into November and December. In North Carolina, adults have been captured in pheromone traps every month of the year except January. Turfgrass in Florida and Gulf Coast areas may experience problems with cutworms all year. Areas with warm season turfgrass that are closer to the transition zone may experience cutworms as early as March and April through late October.

Both black cutworm moths and larvae are nocturnal. Adults do not cause any turf damage, however, they do feed by sucking nectar from flowers. Soon after emergence, adult females call (attract) males by releasing a sex pheromone (chemical sex attractant). Once fertilized, female moths begin laying eggs. Individual females can lay as many as 1,200–1,600 eggs over a 5- to 10-day period. Eggs are predominantly attached to the tips of grass blades singly. Eggs typically hatch in 3–6 days depending on temperature. Once hatched, the young larvae (first and second instars) begin feeding on leaf blades, both day and night. Young larvae feed on both the top and bottom sides of the of leaf blades in a skeletonizing manner. As larvae develop and mature, older larvae (third to sixth instars), they become nocturnal (feeding only during the scotophase) as well as developing a subterranean habit, forming silk-lined burrows in the turf thatch or soil. On golf course turf, the larvae will commonly occupy aerification holes, spike marks, or golf ball injury sites. Black cutworm larvae hide in the aforementioned burrows during the daylight, and venture out to feed at night. The larvae typically pass through six molts, maturing in 20–40 days. Young larvae do not cause measurable damage, however, large larvae are highly destructive, consuming relatively large amounts of turfgrass foliage in a single night. Once black cutworm larvae reach maturity, pupation occurs within the larval burrow or the turfgrass profile. After approximately 14–21 days, the adult moth emerges.

Most black cutworm larvae feeding occurs from around midnight until just before dawn. On golf course putting greens, wandering larvae can move approximately 20 m or more in a single night. This ability to move helps explain why golf course putting greens and tees are sometimes reinfested soon after being treated with a short-residual insecticide. It is likely that black cutworm larvae are moving onto putting greens from the surrounding area.

Bronzed Cutworm, *Nephelodes mimians* Guenée

The bronzed cutworm is only an occasional pest of home lawns and golf course turf, and unlike the black cutworm, they rarely damage golf course putting greens and tees. Bronzed cutworm is distributed across the northern half of the U.S. east of the Rocky Mountains, as far south as Tennessee.

Adult bronzed cutworms are similar in size to black cutworm, however, they lack the black dagger-shaped mark on the wings. The forewings are highly variable in color ranging from brown to purplish-gray to maroon, and there is a wide, darker-brown band across the middle of each forewing. The hindwings are buff-colored similar to the black cutworm. Bronzed cutworm eggs resemble black cutworm eggs. Larvae are fat-bodied, light to dark brown dorsally and lighter ventrally, and they have a distinctive bronze sheen. Larvae also have a light-yellow stripe that extends longitudinally the entire length of the body on the center of the dorsal side, with another pale longitudinal stripe on each side of the body. Spiracles are black and are located on each thoracic and abdominal segment. Fully developed, mature larvae are 35–45 mm long. Bronzed cutworm and black cutworm pupae look similar in color and size.

Although the bronzed cutworm has been well studied in field crops, little is understood about its biology in turf. Unlike most turf-infesting cutworm species, the bronzed cutworm has only one generation per year. Adult moths emerge, mate, and lay eggs in late summer or early fall. The eggs, however, do not hatch until the following spring. After eggs hatch in April, larvae begin feeding and developing until fully developed in mid- to late May, when most damage occurs. As bronzed cutworm larvae reach maturity, they burrow into the soil and form pupal cells where they remain until pupation in mid-August. Thereafter, new adult moths emerge in approximately 30 days.

Variegated Cutworm, *Peridroma saucia* (Hübner)

The variegated cutworm is an occasional pest in lawns and golf course roughs, especially in rural areas where turfgrass areas are bordered by field crops where infestations may originate. It occurs throughout both North and South America.

Variegated cutworm moths have yellowish to brownish forewings that frequently have a row of small black dashes on the leading edge of the wing. Similar to the bronzed cutworm, they lack the black dagger-shaped marking present on black cutworm moths. Variegated cutworm moth hindwings are whitish, with dark-shaded veins. Variegated cutworm eggs are similar in size and color to black cutworm eggs. However, variegated cutworm eggs are laid in groups of several hundred eggs in a single layer on foliage. Mature larvae are approximately 35–46 mm long and vary in color from pale gray to dark brownish-gray. A row of pale yellow dots and dashes extend longitudinally on the dorsal side of the body, and a distinct brownish W-shaped marking is apparent on the eighth abdominal segment, as well as a yellowish or orange area near the terminal abdominal segment. The larvae also have a rather indistinct, black, yellowish or orange marking that extends longitudinally on both sides. Pupae are similar to both bronzed and black cutworm.

The variegated cutworm has from three to six generations per year depending on geographic location. Adult moths emerge from overwintered pupae in March and April. Larvae from eggs deposited by the first generation moths are typically fully developed by late May. The subsequent generations occur from June to November, with the last generation producing overwintering pupae. A complete generation, egg to adult, typically requires 8–9 weeks. Compared to other cutworm species, the variegated cutworm is less subterranean and nocturnal, thus is sometimes feeds fully exposed during daylight, especially on cloudy days.

Sod Webworms

There are more than 20 species of sod webworms that feed on turfgrasses in North America, however, only about three or four species are pests in specific geographical regions. Among the more common sod webworm species that attack turfgrasses in the northern U.S. are the bluegrass webworm, *Parapediasia teterrella* (Zincken); the larger sod webworm, *Pediasia trisecta* (Walker); and the western lawn moth, *Tehama bonifatella* (Hulst). All of the aforementioned sod webworms species at one time were grouped together in the genus *Crambus*. Because their biology is similar, they can be discussed together. The tropical sod webworm, *Hertopetogramma phaeopteralis* (Guenée), has a wide distribution only in the southeastern U.S. and will be discussed separately.

In general, sod webworms are relatively small larvae that live in silk-lined tunnels in the turf canopy, specifically in the thatch and soil, hence the name "webworms."

Adult sod webworms are small, buff-colored moths that have wingspans that range in size from 19 to 25 mm. The forewings are primarily whitish, dull gray to tan, with longitudinal stripes as well as other indistinct markings of brown, black, gold, silver, and even yellow. Such markings are used to identify individual species. Hindwings are typically lighter, whitish to light-gray, with delicate fringes on the outer margins of the wing. When resting, the wings are usually folded over the body. Possibly the most distinguishing characteristic of sod webworm moths is the presence of two small, snout-like projections that extend forward from the front of the head. These snout-like projections are merely mouthparts, but are the reason why sod webworm moths are frequently referred to as "snout moths." Moreover, the combination of folded wings and the snout enable sod webworm adults to be distinguished from other turfgrass moths. Sod webworm eggs are extremely tiny, oval to barrel-shaped, with fine, longitudinal ribbing on the surface. Ribbing is distinctive for each species. Sod webworm larvae range in color from beige to gray to brown to greenish, depending on species. Nearly all sod webworm species have characteristic dark, circular spots and coarse hairs scattered randomly over the body. Fully developed larvae are typically 16–25 mm long. Pupae are "torpedo-shaped," approximately 10–13 mm long, and vary in color from tan to dark brown.

Several species of sod webworms are distributed throughout the temperate U.S., however, damage appears to be greatest in the Midwest and the eastern U.S. Sod webworms attack and damage several turfgrass species including creeping bentgrass, Kentucky bluegrass, perennial ryegrass, as well as fine-leaf and tall fescues, however, they will also feed and cause damage on other grasses that are considered weeds. Certain turfgrasses, such as perennial ryegrass and fescues that contain endophytes, are relatively resistant to sod webworms. Sod webworm larvae hide in silk-lined burrows in the turf canopy, emerging at night to feed on turfgrass foliage. Feeding damage results in leaves and stems being chewed off just above the crown; thereafter, the plant material is pulled into the burrow where it is consumed. Initial signs of sod webworm feeding damage typically appears as general thinning of the turf, followed by small irregular patches of brown, closely cropped grass. Close inspection of the damaged area reveals silk-lined tunnels and clumps of green insect frass (fecal pellets) near or around the burrow. When infestations are high and damage escalates, the small irregular patches begin coalescing into large irregular patches of brown, closely cropped grass. Early symptoms of sod webworm damage are typically masked, especially when the turf is dormant from drought stress, and as a result the damage rapidly becomes apparent after the turf recovers from the environmental stress and the sod webworm damaged area fails to recover. Moreover, sod webworm damage frequently is mistaken for several fungal diseases, golf ball damage, golf shoe (spikes) damage, as well as black cutworm damage.

Sod webworms in the northern U.S. overwinter as partially grown larvae in silk-lined chambers in the turf canopy. In the early spring when soil temperatures become conducive, sod webworm larvae resume feeding and growing, eventually pupating. Thereafter, adults typically emerge in 10–20 days, depending on species and temperature. Immediately after adult emergence, mating occurs, and females typically begin laying eggs by the following night. The adults are nocturnal, active at dusk or after dark. Adult females are rather unique in their oviposition behavior. They fly rather close to the turf surface (30–60 cm above), erratically for short distances, fluttering or hovering over the turf dropping approximately 60 eggs like bombs from a military aircraft. Each female lives for about 2 weeks or less, laying several hundred eggs during her lifetime. The dropped eggs do not contain any sticky substrate for adhesion, therefore, they tend to settle into the turf canopy where they are rarely seen. Eggs typically hatch in about seven days, and there are usually six to eight instars. Newly hatched and early instar larvae feed by scraping surface tissues from leaf blades. Soon thereafter, larvae drop to the ground to form the silk-lined burrows or tunnels. As larvae develop and mature, they feed predominately at night. A complete life cycle, egg to adult, requires 6–10 weeks, and depending on geographic location, most temperate region sod webworm species have two to three generations per year.

Adult tropical sod webworms do not roll their wings around their bodies when they are at rest. Instead they hold them in more of a delta-winged fighter plane configuration. The dingy brown moths have a wingspread of about 20 mm. The larvae is a dingy cream color, but will take on a green appearance when the larvae are feeding. They develop through seven or eight instars, reaching a maximum length of 19 mm. The head is yellowish brown. The larvae feed only at night and require about 25–45 days to complete development. Tropical sod webworms attack and damage all species of warm season turfgrass. Highly maintained bermudagrass is attacked most often and damaged most severely. The larvae give the turf a ragged, notch appearance from their feeding and eventually the turf will take on a close-cropped appearance and turn yellow. Damage is often first noticed near flower beds and shrubs. Damage is common in southern Florida in the spring and throughout the rest of its range in the Southeast by late summer. Generations may continue well into the fall and damage often is mistaken for fall armyworm feeding.

Crown and Thatch Inhabitants: Burrowing Insects

The larval stage of numerous types of billbugs and weevils damage turfgrasses by burrowing into the stems (leaf sheath) or by damaging the crowns (apical meristems). The apical meristem is the most vulnerable part of the plant because it is the source that contains the growing points whereby roots, shoots, and leaves originate. Subsequently, when burrowing insects attack turfgrasses, plant death often results.

Annual Bluegrass Weevil, *Listronotus maculicollis* (Dietz)

The annual bluegrass weevil, formerly called the hyperodes weevil, is a serious pest of closely cut annual bluegrass (*Poa annua*) on golf courses, bowling greens, and tennis courts in the northeastern U.S. Although both the adults and larvae cause damage to turfgrasses, adult damage is minor compared to larval damage.

Annual bluegrass weevil adults are small, 3.5–4.0 mm long, generally black or dark charcoal-gray beetles. The body is covered with fine, yellowish hairs and scales that typically wear off as the beetle ages. Thus, older adults often appear shiny black. Newly emerged adults are light reddish-brown, and often do not darken for several days. The thorax is approximately one-third as long as the abdomen, and the head is prolonged into a blunt (broad and short) snout. As a result, the annual bluegrass weevil is regularly confused with other turf-infesting billbugs that are similar in morphological characteristics. However, annual bluegrass weevil can be accurately differentiated by its shorter and broader snout; billbugs have a longer, narrower snout. Annual bluegrass weevil antennae are attached at the tip of the snout and can be folded back along the side of the snout in a compact groove. Annual bluegrass weevil eggs are rice-shaped, approximately 1 mm long, rounded at both ends, yellow initially but eventually becoming smoky gray to black before hatching. Eggs are laid between leaf sheaths of annual bluegrass. Females typically lay two to three eggs end to end within the leaf sheath. Larvae are creamy white, legless, with a distinct sclerotized brown head capsule. Larvae are approximately 1 mm long when newly hatched, and about 5 mm long when fully grown. There are five instars, and all are similar in appearance, differing only in size. Pupae are approximately 3.5 mm long, whitish at first, but later become reddish brown before the adults emerge. The snout, legs and wing pads are visible on the pupa, but are folded close to the body.

The only host that annual bluegrass weevil attacks is closely cut annual bluegrass. Although damage is only minor, the adults chew notches or holes in grass blades. The larva is the primary damaging life stage. Young larvae feed and tunnel within the plant stems. As larvae develop and become too large to feed within plant stems, they burrow out and feed externally on the crown of the plant. One larva can kill several plants during its lifetime. Damage typically begins along the edges of golf course fairways, especially those bordering wooded areas or other overwintering sites, as well as around the edges of putting greens and tees. Damage first appears as yellowish-brown, wilting or scattered dead patches of turf that eventually coalesce into larger dead areas as larvae develop and mature. The tunneled stems easily break off near the crown of the plant. Large infestations have the potential to cause severe damage to golf course putting greens, tees and fairways, especially where annual bluegrass is prevalent.

The annual bluegrass weevil has one to two generations per year depending on geographical locations; in more northern areas of its range it has only one generation per year. Adults overwinter in refuges such as leaf litter under trees, tufts of tall fescue, or other sheltered sites including golf course roughs where the turf is typically higher. Adults become active in the spring (mid-April), when they begin to crawl or fly to closely cut annual bluegrass hosts to begin feeding. Adult annual bluegrass weevil typically hide in the foliage during daylight, and later climb up turfgrass plants to feed at night. In early May, adults begin laying eggs. The eggs typically hatch in 4–5 days, depending on temperature. Immediately thereafter, the newly hatched larvae begin burrowing within the grass stems until they reach the third instar. Older larvae, third to fifth instars, burrow out of the plant to feed along the exterior, primarily on the plant crown. Upon maturation, annual bluegrass weevil larvae pupate sometime in mid- to late June in earthen cells just under the soil surface. The second generation adults emerge in late June or early July to feed, mate, and lay eggs.

In areas where there are two generations per year, most populations pupate by late August and adults emerge sometime in September, and migrate back to overwintering sites.

Billbugs (Coleoptera: Curculionidae)

Billbugs are one of the most misdiagnosed pests of turfgrass. Turfgrass managers often confuse billbug damage with symptoms of drought stress, disease or other insect damage such as chinch bugs and white grubs. There are four species of billbugs that are considered major insect pests within their range in the U.S. These species include the bluegrass billbug, Denver billbug, Phoenician billbug, and the hunting billbug. Billbug damage is similar to that of weevil damage. Both the adults and larvae feed and cause damage to turf, however, adult damage is minor compared to larval damage.

Bluegrass Billbug, *Sphenophorus parvulus* Gyllenhal

The bluegrass billbug is among the most serious pests of Kentucky bluegrass and perennial ryegrass in the temperate U.S. It is distributed throughout most of the U.S. and southern Canada where cool-season turfgrasses are grown. Damage frequently results in areas of brown, dead turf.

Adult bluegrass billbugs are characteristic billbugs that have a long, slender, beak-like snout. They are approximately 7–8 mm long, excluding the length of the snout. Adults are hard-bodied, sclerotized, usually slate gray to black in color, and may sometimes appear brownish from dried soil adhering to their body. Newly emerged adults are initially reddish-brown, but eventually become dark after a few days. Bluegrass billbug eggs are elongate, bean-shaped, translucent white eggs approximately 1.6 mm long. Larvae are plump, legless, creamy white grubs with a sclerotized brown head capsule. All larval instars are similar except for size; early instars (first and second) range in size from 1.3 to 2.4 mm long and mature larvae (fifth instar) are approximately 6–10 mm long. Pupae are approximately 8.5 mm long, creamy colored, gradually changing to reddish brown prior to adult emergence. The pupa has several morphological characteristics of the adult, the snout and legs are tucked under the thorax, and the wings are folded along the side of the abdomen.

Kentucky bluegrass is the preferred host of the bluegrass billbug, but it also will feed on and cause damage to perennial ryegrass as well as occasionally fine-leaf and tall fescues, especially when they are near heavily infested Kentucky bluegrass sites. Damage is usually worst from late June to early August, especially when turf is undergoing heat and drought stress. Although damage is only minor, the adults chew notches or holes in grass blades. The larva is the primary damaging life stage. Young larvae feed and tunnel within the plant stems. As larvae develop and become too large to feed within plant stems, they burrow out and feed externally on the crown of the plant. One larva can kill several plants during its lifetime. Damage first appears as yellowish-brown, wilting or scattered dead patches of turf that eventually coalesce into larger dead areas as larvae develop and mature. The tunneled stems easily break off near the crown of the plant. Lower populations of bluegrass billbugs typically produce scattered brown patches of turf, whereas heavier infestations can completely destroy areas of turf.

Adult bluegrass billbugs overwinter practically everywhere, in areas including thatch, soil crevices, under bark mulch or leaf litter, as well as other sheltered locations. However, it has been reported that crevices between the sidewalks and lawns is a preferred winter refuge. Adults become active in late April to mid-May when soil temperatures reach approximately 18°C. Once active, they are frequently seen crawling over sidewalks, curbs and driveways on warm spring days as they are seeking out suitable turfgrass in which to feed and lay eggs. After mating, adult female bluegrass billbugs begin laying eggs into small crevices created by adult feeding, chewed in grass stems just above plant crowns. Eggs typically are laid singly, and occasionally in groups of two or three. Each female can lay up to 2–5 eggs per day, and as many as 200 in her lifetime. Nearly all eggs are laid by early July, however, some females may continue laying eggs as late as August. Eggs usually hatch in approximately 6 days, and young larvae begin feeding within the grass stems, later burrowing down to feed on the plant crown as they mature. Infested turfgrass plants are hollowed out and packed with a powdery frass. As the bluegrass billbug larvae become too large (second or third instar) to feed within the turfgrass stems, they burrow out and move to the soil to feed externally on both the crowns and roots. An accurate indicator of bluegrass billbug activity is the presence of fine, whitish, sawdust-like frass near the feeding site. Larvae are most abundant in the soil from early June to early August, and they typically require 35–55 days to mature, depending on temperature. Thereafter, they pupate in small earthen cells in the soil. The adults emerge in approximately 8–10 days. Thus, adults are abundant in late summer and fall, briefly feeding before seeking out overwintering sites as cooler temperatures prevail. Occasionally, some early emerging adults may begin to lay eggs for a second generation, however, resulting larvae do not develop fast enough to mature before the onset of winter.

Denver Billbug, *Sphenophorus cicatristriatus* Fahraeus

Compared to other billbug species, little is known about the biology and life history of the Denver billbug. However, damage from this insect pest has been reported in Colorado, Kansas, and central and western Nebraska. It is considered the most serious pests of Kentucky bluegrass in Colorado. Damage frequently results in areas of brown, dead turf.

Adult Denver billbugs are considerably larger than either the bluegrass or hunting billbug, reaching 8–12.5 mm long. The Denver billbug adult is differentiated from the other two species by its larger size and the presence of distinctive, double-lobed markings on the wing covers. The Denver billbug may overwinter as an adult, but is more likely to spend the winter as a mid-to-late stage larva. After a spring feeding period by the larvae, eggs are laid by adults, and subsequent larvae develop over the summer. Larvae are plump, legless, creamy white grubs with a sclerotized brown head capsule. All larval instars are similar except for size, early instars (first and second) range in size from 1.3 to 2.4 mm long and mature larvae (fifth instar) are approximately 6–10 mm long. Pupae are approximately 9.0 mm long, creamy colored, gradually changing to reddish brown prior to adult emergence. The pupa has several morphological characteristics of the adult, the snout and legs are tucked under the thorax, and the wings are folded along the side of the abdomen.

Kentucky bluegrass is the preferred host of the Denver billbug, but it will also feed on and cause damage to perennial ryegrass. Damage typically occurs in the fall and early spring. Damage symptoms of the Denver billbug are comparable to that of the bluegrass and hunting billbug. The larva is the primary damaging life stage. Young larvae feed and tunnel within the plant stems. As larvae develop and become too large to feed within plant stems, they burrow out and feed externally on the crown of the plant. One larva can kill several plants during its lifetime. Damage first appears as yellowish-brown, wilting or scattered dead patches of turf that eventually coalesce into larger dead areas as larvae develop and mature. The tunneled stems easily break off near the crown of the plant. Lower populations of bluegrass billbugs typically produce scattered brown patches of turf, whereas heavier infestations can completely destroy areas of turf.

Phoenician Billbug, *Sphenophorus phoeniciensis* Chittenden

The Phoenician (or Phoenix) billbug occurs primarily in southern California and Arizona. The adults and larvae have a typical billbug appearance. The adult Phoenician billbug has an M-shaped raised area on the pronotum. It is primarily a pest of bermudagrass and zoysiagrass, particularly in those areas that are stressed or poorly maintained.

The injury from Phoenician billbug feeding is greatest during the summer months, at times of maximum temperatures and drought stress. The larval stage is the principal stage that causes damage. The small larvae usually feed inside the plant stems. The larvae continue to feed and once they become larger, they feed outside the stem around the crown and stolons of the plant. Larvae can kill a plant (or several plants) but usually the bermudagrass is growing quite rapidly during the summer and damage goes unnoticed until fall. Damage usually appears as stressed turf that turns yellowish-brown and wilts, which is easily mistaken for drought stress. Scattered dead patches may occur later in the season or be observed the following spring as the bermudagrass fails to grow. The damaged stems break off easily at the crown of the plant. Populations often are highest and damage most severe in sunny, drought-prone locations.

Hunting Billbug, *Sphenophorus venatus vestitus* Chittenden

The hunting billbug closely resembles the bluegrass billbug but is slightly larger and has parenthesis-like markings on the back of the thorax. This billbug species prefers warm season turfgrass species including but not limited to bermudagrass and zoysiagrass. On occasion, hunting billbug will damage Kentucky bluegrass. The hunting billbug is primarily a pest of the southeastern U.S., however, it is also found in the mid-Atlantic states as well as further west and north into Missouri, Kansas and southeast Nebraska.

Adult hunting billbugs are characteristic billbugs that have a long, slender, beak-like snout. They are approximately 6–11 mm long, excluding the length of the snout. Adults are hard-bodied, sclerotized, usually slate gray to black in color, and may sometimes appear brownish from dried soil adhering to their body. Hunting billbug eggs are elongate, bean-shaped, translucent white eggs approximately 1.6 mm long. Larvae are plump, legless, creamy white grubs with a sclerotized brown head capsule. All instars are similar except for size; early instars (first and second) range in size from 1.3 to 2.4 mm long and mature larvae (fifth instar) are approximately 7–10 mm long. Pupae are approximately 8.5 mm long, creamy colored, gradually changing to reddish brown prior to adult emergence. The pupa has several morphological characteristics of the adult; the snout and legs are tucked under the thorax, and the wings are folded along the side of the abdomen.

Damage is usually greatest from mid-June through early August during the period of maximum heat and drought stress. The larva is the principal damaging life stage. Young larvae feed and tunnel within the plant stems. As larvae develop and become too large to feed within plant stems, they burrow out and feed externally on the crown of the plant. One larva can kill several plants during its lifetime. Damage first appears as yellowish-brown, wilting or scattered dead patches of turf that eventually coalesce into larger dead areas as larvae develop and mature. The tunneled stems easily break off near the crown of the plant. Lower populations of hunting billbugs typically produce scattered brown patches of turf, whereas heavier infestations can completely destroy areas of turf.

As is the case with the Denver billbug, little is known about the biology of this pest. The hunting billbug has been reported to overwinter as dormant adults in the soil. Adults become active in late April to mid-May when soil temperatures reach approximately 18°C. Once active, they are seen frequently crawling over sidewalks, curbs, and driveways on warm spring day as they are seeking out suitable turfgrass in which to feed and lay eggs. After mating, adult female bluegrass billbugs begin laying eggs into small crevices created by adult feeding, chewed in grass stems just above plant crowns. Eggs typically are laid singly, and occasionally in groups of two or three. Each female can lay up to 2–5 eggs per day, and as many as 200 in her lifetime. Nearly all eggs are laid by early July, however, some females may continue laying eggs as late as August. Eggs usually hatch in approximately 3–10 days, and young larvae begin feeding within the grass stems, later burrowing down to feed on the plant crown as they mature. Infested turfgrass plants are hollowed out and packed with a powdery frass. As the bluegrass billbug larvae become too large (second or third instar) to feed within the turfgrass stems, they burrow out and move to the soil to feed externally on both the crowns and roots. An accurate indicator of bluegrass billbug activity is the presence of fine, whitish, sawdust-like frass near the feeding site. Larvae are most abundant in the soil from early June to early August, and they typically require 35–55 days to mature, depending on temperature. Thereafter, they pupate in small earthen cells in the soil. The adults emerge in approximately 8–10 days, thus adults are abundant in late summer and fall, briefly feeding before seeking out overwintering sites as cooler temperatures prevail.

Soil Inhabitants: Root-Infesting Insects

White Grubs (Coleoptera: Scarabaeidae)

White grubs are the most widespread, and considered the most destructive, insect pests of turfgrasses in the continental U.S. Most species of white grubs damage turfgrass by chewing off the roots near the soil surface. Most often, white grub damage occurs during periods of hot and dry weather. Subsequently, turf loss can be relatively abrupt and severe. To compound this problem, vertebrate predators such as armadillos, badgers, birds, moles, raccoons, skunks and various other animals may dig up infested areas of turf in search of grubs. In many cases these animals cause more damage than the grubs themselves.

Because white grubs feed on the roots below ground, they often go undetected until measurable loss to the root system has occurred. Moreover, grubs can be relatively difficult to control because soil insecticides must penetrate the turf canopy and thatch layer in order to effectively make contact with the grubs located in the soil. To achieve maximum control, turfgrass managers, through appropriate application equipment, adjuvants or surfactants, gravity, and irrigation or natural rainfall, must effectively place respective insecticides into the target zone where the grubs are located.

The larval stage (grub) typically is the damaging life stage to turfgrass, however, some species of beetles cause damage to ornamental plant materials as adults. White grubs are stout-bodied beetle larvae. About 15 species are pests of turfgrasses in North America, with about 10 species considered to be important: Aphodius grubs, Asiatic garden beetle, black turfgrass ataenius, European chafer, green June beetle, Japanese beetle, May beetles, northern and southern masked chafers, and Oriental beetle. These species of white grubs are generally similar in appearance, habits, and the damage they cause. An overview of the biology of individual species follows.

Aphodius Grubs, *Aphodius granaries* (L.) and *Aphodius paradalis* Le Conte

Two species that belong to the genus *Aphodius* are occasional pests of turfgrass, especially golf course fairways. *Aphodius* grubs are relatively small grubs compared to most other white grubs. They closely resemble black turfgrass ataenius grubs, and because they are frequently found in association with black turfgrass ataenius, often they are confused or misidentified. Although they seem to be less frequently associated with turf than black turfgrass ataenius, they are capable of causing serious damage to turf.

Adults are typically black with a reddish tinge, reddish-brown legs, and pale antennae. The adults have two triangular projections on the outer edge of the tibia and hind leg, whereas black turfgrass ataenius lack these projections. *Aphodius* eggs are tiny (less than 0.7 mm when fully hydrated), and pearly white. Larvae are typically white grubs, however, they are considerably smaller than most other common turf-infesting species. Newly hatched first instars are approximately 2.4 mm long, and are difficult to see. Second instar larvae are about 5 mm long and third instars are approximately 7.0 mm long. Fully mature third instars often are mistaken for young grubs of other species such as European chafers, Japanese beetles, and masked chafers. A distinguishing morphological characteristic that differentiates the two species of Aphodius larvae, as well as black turfgrass ataenius and other white grubs, is the raster pattern. The raster pattern is a distinctive pattern of hairs, spines, and bare spaces on the raster located on the ventral side of the last abdominal segment, anterior of the anus. The raster of Aphodius grubs has two rows of short spines forming a distinctive V-shaped pattern, whereas black turfgrass ataenius grubs have a random arrangement of spines as well as two distinctive, pad-like structures at the tip of the abdomen, anterior of the anal slit.

Both the adults and larvae of *Aphodius* feed primarily on decaying organic matter, especially animal manure. However, occasionally they will feed on living roots of cool-season turfgrasses such as annual bluegrass, creeping bentgrass, and Kentucky bluegrass. *Aphodius* grubs cause sporadic, severe damage predominantly to golf courses in the temperate U.S. Damage to home lawns is uncommon. The initial symptoms of *Aphodius* larval damage are patches of thin or wilted turfgrass that resemble drought stress, however, the turf does not respond or recover with the application of irrigation. As turfgrass root loss continues, the turf typically dies in irregular patches that eventually coalesce into larger dead areas. Heavily infested areas of turf can be rolled up similar to a loose piece of carpet. Upon close inspection or sampling, the grubs, pupae, and adults can be found under the dead patches of turf in the soil. Irrigated turfgrass with a high proportion of annual bluegrass are especially susceptible. Populations of as many as 200–300 m^{-2} are not uncommon. In addition, vertebrate predators frequently forage for grubs, resulting in additional turf damage.

The life history of *Aphodius* is poorly understood. Observations from Ohio, Michigan and Ontario, Canada suggest that there is only one generation per year with adults becoming active during the first warm days of spring; egg-laying apparently begins 2–3 weeks earlier than that of black turfgrass ataenius. However, other published reports indicate the possibility that two annual generations may be possible, especially in the more southern parts of the species range. Nonetheless, because *Aphodius* species are frequently associated with black turfgrass ataenius, similar biological attributes may be extrapolated to effectively manage *Aphodius*.

Asiatic Garden Beetle, *Maladera castanea* (Arrow)

The Asiatic garden beetle is a relatively minor pest of turfgrass, however, it can be locally abundant and damaging, especially in the temperate northeastern U.S.

Asiatic garden beetle adults are dull chestnut-brown, with a velvety appearance and a slight iridescent sheen. The beetles range in size from 8 to 11 mm long and 5–6.4 mm wide. The elytra (wing covers) do not quite reach the tip of the abdomen, leaving the terminal two segments of the abdomen exposed. The ventral side of the Asiatic garden beetle adult is partially covered with yellow hairs, and each visible segment of the abdomen has a row of backward-pointing yellow hairs that extend across the width of the body. The dorsal side of the elytra is bald with the exception of a row of fine hairs on the outer margins. Another distinctive morphological characteristic is the presence of scattered, small hairs on the dorsal (top) side of the head. Asiatic garden beetle eggs are pearly white, oval and are approximately 1 mm in diameter. After becoming hydrated from soil moisture, they become almost spherical. The eggs are typically laid in clusters of 3–19 eggs that are loosely held together by a gelatinous secretion. Newly hatched first instars are approximately 1.4 mm long and reach 19 mm long when fully mature. They are like most other white grubs, having a C-shaped body, a brown head capsule, and six jointed legs. However, the body color of Asiatic garden beetle larvae typically remains somewhat lighter than in other white grub species. The important distinguishing feature is the single, transverse curved row of spines on the raster, together with a Y-shaped anal opening. The hind legs have tufts of hairs, and extremely small claws relative to those on the pro- and meso-legs (front and middle legs, respectively). The presence of a whitish, enlarged, bulbous morphological structure (the stipes) on each maxilla beside the jaws is another distinctive feature of Asiatic garden beetle grubs. The pupa is approximately 7–10 mm long, and appears white initially but turns tan as it matures. Initially the pupa is enclosed in the final instar skin, which soon splits and is pushed back over the terminal portion of the abdomen; thus, it lies exposed in an earthen cell created by the larva. This characteristic is common also in the European chafer and May beetles.

Asiatic garden beetle grubs feed on the roots of all cool-season turfgrasses as well as weeds, woody ornamentals, herbaceous perennials, and vegetables. Adult Asiatic garden beetles prefer box elder, butterfly bush, cherry, Devil's walkingstick, Japanese barberry, oriental cherry, peach, rose, strawberry, sumac, and viburnum. Asiatic garden beetle larvae feed on the roots of various turfgrass species, causing typical white grub injury resulting in thinning, wilting, irregular dead patches of turf. Well or highly maintained turf that is irrigated regularly and is located near weedy areas containing adult Asiatic garden beetles' preferred food sources is more likely to be infested. Compared to other white grub species such as Japanese beetles, an equal number of Asiatic garden beetle grubs is typically less destructive. It is likely that this is a result of the fact that Asiatic garden beetle grubs typically feed deeper in the soil profile, thus leaving more of the turfgrass root system intact. Where Asiatic garden beetle infestations are heavy, it is not uncommon to observe more than 100 grubs/m^2, resulting in severe damage. Not only do Asiatic garden beetle grubs cause damage, but the adults feed on more than 100 species of woody and herbaceous ornamental plant material. When beetles are abundant, preferred plants can be stripped of foliage and flowers.

Asiatic garden beetle has a univoltine (one life cycle per year) life cycle similar to the Japanese beetle. Adults are most abundant from mid-July to mid-August. Adult females burrow into the turf canopy to lay eggs in the soil at about 2.5–5 cm in depth. Each female is capable of laying up to 60 eggs in her approximately 30-day lifetime. Once laid, eggs typically hatch in about 10 days; immediately thereafter the young larvae commence feeding on the tender, succulent roots of turfgrass and decaying organic matter until sometime in the fall when the first measurable frost occurs. The majority of Asiatic garden beetle grubs will have attained the final instar (third) by the first frost, however, approximately 25% will overwinter as second instars. As the soil temperatures continue to decline, the grubs will continue to burrow deeper into the soil profile, ultimately overwintering approximately 20–43 cm below the turf surface in a semi-dormant, nonfeeding state. Sometime in mid- to late April, the grubs will move slowly back up to the root zone where they will begin feeding until mid-June. Thereafter, mature grubs will begin preparing earthen cells or cavities 4–10 cm below the turf surface where they will pupate. Pupation occurs mainly from mid-June through mid-July, and typically lasts for approximately 10 days. New adults remain in the pupal cell for a few days until they become fully sclerotized (hardened) and their color changes from whitish to chestnut-brown. Soon after, the adults burrow upward and emerge from the soil to feed, mate, and lay eggs in susceptible areas of turf.

Black Turfgrass Ataenius, *Ataenius spretulus* Haldeman

Although sporadic in occurrence, the black turfgrass ataenius causes severe damage to golf courses in the temperate U.S., especially where cool-season turfgrasses are grown. They are also occasional pests where bentgrass greens are utilized in warm season turfgrass areas of the U.S. Black turfgrass ataenius has many of the same biological characteristics as several other white grub species, however, its season life cycle differs in that there are typically two generations per year throughout much of its range. In the more southern areas of the U.S., its life cycle is poorly understood, but more than two generations may occur in some areas.

Adult black turfgrass ataenius are relatively small, shiny black beetles ranging in size from 3.6 to 5.5 mm long and approximately half as wide. There are distinct longitudinal grooves on the elytra. Newly emerged adults are reddish-brown initially, and darken in a few days. Eggs are minute, less than 0.7 mm in diameter after absorbing water from the soil, and pearly white. Larvae are typical white grubs in appearance, however, they are considerably smaller than other turfgrass-infesting species. Newly hatched larvae are quite small, approximately 2.4 mm long, thus they are relatively difficult to see. Second and third instars are about 5 mm and 7.0 mm long, respectively. Fully mature black turfgrass ataenius grubs are mistaken frequently for young grubs (first instars) of several other white grub species such as European chafer, Japanese beetle, and both northern and southern masked chafers. However, black turfgrass ataenius larvae can be distinguished easily by the two distinctive, pad-like structures located at the terminal end on the ventral side of the abdomen anterior to the anal slit. Upon maturation, black turfgrass ataenius grubs pupate into small, approximately 4.2–5.7 mm long, pupae that are initially cream colored, but eventually become reddish-brown before the adult beetle emerges. A distinctive characteristic of black turfgrass ataenius pupae is that the wings and legs are folded close to the body.

Black turfgrass ataenius larvae typically attack and cause damage to the roots of annual bluegrass, creeping bentgrass, and Kentucky bluegrass on golf courses. They also feed on decaying organic matter, and the adults feed on manure and decaying organic matter. Because black turfgrass ataenius grubs feed on the roots of turfgrasses, the first symptoms appear as patches of thin or wilted turf that resembles drought stress, however, the turf does not recover with the application of irrigation or rainfall. As damage and subsequent root loss increases, the turf typically dies in irregular patches that eventually coalesce into larger dead areas. Heavily infested areas can be pulled or rolled up similar to loose carpet. Upon close inspection of the turf, large numbers of larvae, pupae and adults can be observed in the soil under the turf. Black turfgrass ataenius seems to prefer, and are most common in, areas of turf that are close-cut, with a moist, compacted layer of thatch. Additionally, golf course fairways that have a high proportion of annual bluegrass composition are especially susceptible. Because black turfgrass ataenius grubs are relatively small, they typically are found in higher densities than most other white grub species, with populations of 215–325 m^{-2} not uncommon. Accenting the damage associated with black turfgrass ataenius grubs, vertebrate predators frequently forage for grubs, resulting in additional turf damage.

Depending on geographic location, black turfgrass ataenius has one to two generations per year. There is typically only one generation per year in the Great Lakes states, New York, northern New England, Ontario, and other parts of its range. Adults reportedly overwinter along the edges of wooded areas along the perimeter of golf courses.

The adult beetles seek refuge in leaves, pine needles, grass clippings, and other debris in the upper 2.5–5 mm of the soil. Most of the overwintering black turfgrass ataenius adults have mated. Subsequently, in the early spring, from late March to early April, the adults become active and can be observed in swarms flying over golf course putting greens and fairways on warm afternoons as well as around lights at night. Soon thereafter, black turfgrass ataenius adults begin laying eggs in early May continuing until mid-June. Black turfgrass ataenius eggs are laid in clusters of approximately 11–12 eggs within cavities formed by the female near the soil-thatch interface. Eggs typically hatch within 7 days, and the larvae immediately begin feeding on fine, succulent roots and organic matter. This first generation of grubs typically is present from late May until early July, with damage commonly appearing in late June. Larvae require approximately 4 weeks to mature; thereafter, they burrow down into the soil profile to pupate and emerge as adults sometime in late June through early July. Upon emergence, these beetles mate and begin laying eggs in July through early August, producing a second generation of grubs which typically causes damage in August and early September. These grubs develop, mature, and pupate by late August or early September, producing adults that mate and emigrate to overwintering sites in the late fall. Generations appear to overlap and more than one life stage is common at a given time since the adults lay eggs over a period of several weeks. In geographic areas where there is not enough time to complete development of a second generation, these beetles mate but will not lay eggs. In areas of southern California, there is great variation from year to year in the occurrence of black turfgrass ataenius. Damaging populations of grubs do not occur until late in the summer in most years, but occasionally early summer damage may occur. Frequent insecticide applications for cutworms as well as high temperatures in the summer may reduce the likelihood of black turfgrass ataenius infestation on putting greens in the southern areas of the U.S.

European Chafer, *Rhizotrogus majalis* (Razoumowsky)

The European chafer is a native of Europe, where it is a serious turfgrass pest. In the U.S. as well, it is a turfgrass insect pest, primarily in the northeast. Where European chafer occurs, often it is considered the most damaging grub species. European chafer grubs are considerably larger than most other white grub species, especially Japanese beetle larvae. Thus, they commonly are more destructive than equal numbers of other species. In addition, they typically feed later into the fall and resume feeding earlier in the spring than other grub species.

European chafer adults are medium-sized, light-reddish beetles measuring approximately 13–15 mm long, with a slightly darker head and pronotum. The posterior edge of the dorsal side of the pronotum has a narrow band of light-yellow hairs, and the ventral side of the thorax is covered with pale yellow hairs. The terminal portion of the abdomen protrudes beyond the elytra, and they have distinct longitudinal grooves and minute punctuations. Both European chafers and May beetles resemble one another, however, European chafers are slightly smaller and they lack a tooth on the tarsal claws of the mesothoracic legs. Additionally, the European chafer has more distinct grooves on the elytra. Newly laid eggs are oval, shiny, milky white initially, but become dull gray after a few days. As they absorb water from the soil, the eggs become spherical, swelling to approximately 2.3–2.7 mm in diameter prior to hatching. European chafer larvae are typical C-shaped white grubs, with a yellowish-brown head and six distinct, jointed legs. The larvae can be differentiated easily from other white grub species by the raster pattern. It has two distinct, nearly parallel rows of small spines that diverge outward at the tip of the abdomen, similar to a slightly open zipper. The raster pattern, in combination with a Y-shaped anal slit, readily distinguishes European chafer larvae from other turfgrass-infesting white grub species in the temperate U.S. First instar European chafer grubs are initially translucent white, though the terminal portion of the abdomen becomes dark after feeding. Fully mature larvae are approximately 23 mm long. Both the prepupa and pupa resemble most other white grub species. They are approximately 16 mm long, smaller than May beetle pupae, yet larger than Japanese beetle pupae. European chafer pupae shed the larval exoskeleton, whereas Japanese beetle and Oriental beetle pupae lie within the shed larval skin.

European chafer larvae feed on the roots of all cool-season turfgrasses, as well as numerous grassy and broadleaf weed species in pastures and nurseries. The grubs cause thinning, wilting, and subsequent irregular patches of turf that can be readily pulled back or rolled up from the soil like a roll of carpet. Population densities of 18–28 grubs/m^2 are not uncommon in lawns and golf course turf. Damage by European chafer grubs typically appears in September, especially when the turf is already stressed by both heat and drought. Moreover, damage also can be observed in the spring when the grubs resume feeding on the previously weakened turf. Although European chafer adults occasionally will sample the margins of tree leaves, they rarely cause any measurable damage.

The European chafer has a life cycle that closely resembles those of other white grub species such as Japanese beetle and May beetle. In northern portions of Michigan and New York, adult European chafers begin emerging in mid-June and are most abundant from late June until mid-July, and terminate by late July. In areas further south, such as New Jersey, Ohio and Pennsylvania, adult activity typically occurs about 2 weeks earlier. Adults are most active on warm, clear nights when the temperature is above 19°C, and on favorable nights large numbers of adults begin emerging from the turf canopy near sunset. The adults fly to nearby trees, swarming about by the thousands. After a courtship period of approximately one hour, mating pairs begin to make their way to the turf canopy, ultimately returning into the soil before sunrise. Female European chafer adults continue to return to trees several times to re-mate during their 1- to 2-week lifetime. Each female lays 20–40 eggs in her life. Eggs are typically laid singly at 5–10 cm depth in the moist soil. Eggs hatch in approximately 2 weeks, and most hatch by late July. There are three instars of European chafer grubs; first instars are predominant until mid-August, second instars are present in early September, and third instars continue to feed and develop into November. Similar to other white grubs species, European chafers move down into the soil profile just below the frost line to overwinter. In the spring, when soil temperatures become conducive, the grubs return to the upper 2.5–5 cm near the soil-thatch interface to vigorously feed until late May. In early June the European chafer larvae begin moving down into the soil profile, to a 5–25 cm depth, to form earthen cells to pupate. The prepupal life stage requires approximately 2–4 days, while the pupal stages typically takes about 2 weeks. Thereafter, adults begin emerging in mid-June.

Green June Beetle, *Cotinus nitida* L

The green June beetle is a native of the eastern U.S., and is widely distributed east of the Mississippi river, north to St. Louis, Missouri, and south to Texas. They are most common in the southernmost edge of the temperate region where cool-season turfgrasses are grown. Because of their relatively large size, both the green June beetle adults and grubs regularly attract attention where they are abundant. Adult green June beetles are rather prolific fliers that are mistaken often for wasps as they swarm in a “buzzing” manner over the turf in mid-summer. Green June beetle grubs are relatively large compared to other turfgrass-infesting white grub species.

Adult green June beetles are considerably larger than Japanese beetles. They are approximately 19–25 mm long and 12.5 mm wide. They vary in color on the dorsal side of the body and elytra from dull brown with longitudinal stripes of green, to uniform, velvety forest green. The outer margins of the elytra range in color from tan to orange-yellow. The ventral side of the body is shiny metallic green or gold. Newly laid eggs are dull white, approximately 1.5 mm in diameter. As the eggs absorb water from the soil, they become larger, 3 mm in diameter, and more spherical in shape. First instar grubs are approximately 6–7 mm long, second instars are 15–17 mm long, and fully mature larvae are relatively large (45–48 mm long), robust, and more parallel-sided compared to other white grub species. Green June beetle grubs have short, stubby legs and mouthparts in relation to their overall body size. Upon maturation, the green June beetle forms a cocoon-like cell composed of soil particles held together by a sticky secretion, within which pupation occurs. Green June beetle pupae are large, approximately 25 mm long and 12.5 mm wide. The pupae are initially whitish, but gradually darken over time and eventually exhibit tints of the adult coloration before the adults emerge. They can be identified readily by their distinct locomotion; essentially, they scurry along on their backs, upside-down.

Green June beetle grubs primarily feed on decomposing organic matter, including compost, thatch, and grass clippings. There are indications that poorly managed turfgrass with excessive thatch may be at greater risk, and that the use of organic fertilizers just prior to the adult flights may make a turfgrass area more attractive for egg-laying. Green June beetle grubs do not feed on the roots like many other scarabs, however, they do cause considerable damage by their burrowing and tunneling behavior. The grubs make distinct, open vertical burrows with a surface hole approximately the size of a human's thumb. The burrowing and tunneling action of green June beetle larvae causes loose soil to be excavated out at the mouth of the burrow at night, forming a small mound approximately 50–75 mm across. The aforementioned mounds are frequently mistaken for ant mounds except that the soil particles are considerably coarser. This action disrupts the roots system, dislodging the turfgrass, and loosens the surface topsoil, permitting the turf to desiccate. As a result, the turf typically wilts and thins, allowing the invasion of broadleaf and grassy weeds. Adult green June beetles occasionally damage tree leaves, though they mostly feed on ripening fruits, tree sap and other sugary food sources. Similar to the grubs, the adults create little piles of soil as they burrow into and out of the turf canopy for egg-laying and resting.

Like many other scarabs, the green June beetle has a 1-year life cycle. Adults typically emerge in late June with peak activity occurring over a 2–3 week period, usually in mid-July in Kentucky; this event may be 2–3 weeks earlier in the south and 1–2 weeks later in areas further north. Green June beetle adults are active during the daytime, and rest on vegetation as well as under the thatch during the night. After mating, green June beetle female adults seek out turf areas with moist soils containing high levels of organic matter. The females burrow down into the turf approximately 5–13 cm, excavating a small cavity where she lays a cluster of 10–30 eggs. The cluster of eggs is enclosed in a small-sized sphere of soil held together by a sticky secretion. Each green June beetle female makes numerous egg chambers, laying as many as 60–75 eggs over a 2-week period of time. Eggs hatch in approximately 2 weeks. Subsequently, the young larvae begin feeding at the soil/thatch interface by early August. After continuing to feed and grow for several weeks, green June beetle larvae attain the third instar in late October or early November in the northern regions of their distribution. Third instars can be seen as early as the end of August in some Mid-Atlantic states, but also will remain active until November. As the soil temperatures continue to decline, the grubs will continue to burrow deeper into the soil profile, ultimately overwintering approximately 20–76 cm below the turf surface in a semi-dormant, non-feeding state. In some of the southern states, where soil temperatures do not drop significantly, green June beetle grubs can remain active throughout the winter on warm nights. Sometime in mid- to late April, the grubs will move slowly back up to the soil/thatch interface to feed until late May. Thereafter, mature grubs will begin preparing earthen cells or cavities, 20–40 cm below the turf surface, where they will pupate. Pupation occurs mainly in early June, and typically lasts for approximately 10–20 days. After about 3 weeks, adult green June beetles burrow upward and emerge from the soil to feed, mate, and lay eggs in susceptible areas of turf.

Japanese Beetle, *Popillia japonica* Newman

The Japanese beetle is a native to the main islands of Japan, where it is not considered a pest. However, in the eastern U.S. it is considered by many to be the worst insect pest of turfgrasses and ornamental landscapes. As a result, countless dollars and resources are aimed at controlling Japanese beetle adults and larvae. Japanese beetle larvae are white grubs that cause typical root-feeding damage. As for the adults, unlike most scarab adults, Japanese beetles attack and cause serious damage to over 300 ornamental plant species.

Japanese beetle adults are attractive, broadly oval insects that are approximately 8–11 mm long and 5–7 mm wide. The head, thorax, and abdomen are shiny, metallic green. With the exception of the head, much of the dorsal side of the body is covered with hard, coppery-brown elytra that do not fully extend to the tip of the abdomen. Another distinguishing character is the presence of five patches of white hairs that are located on each side of the abdomen, as well as another pair of white tufts on the dorsal side of the terminal abdominal segment posterior to the elytra. These tufts of hairs differentiate Japanese beetles from all other beetles that they closely resemble. Like many other insect species, the females are typically slightly larger than their male counterparts. Newly laid eggs are pearly white and oblong, approximately 1.5 mm long. Upon absorption of water from soil moisture, the eggs become spherical, almost doubling in size within a few days. The larvae are typical white grubs with three pairs of distinct, jointed legs, and a yellowish-brown head capsule; they too assume the C-shaped position in the soil and when handled. Newly hatched grubs are translucent white, becoming darker once they have fed. Like all white grub species, there are three larval instars. First instars are approximately 1.5 mm long, and fully mature third instars are 25–30 mm long. When compared to European chafers, masked chafers, and May beetles, they are considerably smaller. Japanese beetle larvae can be identified easily by their distinctive raster pattern that exhibits two rows of short spines that are arranged in the shape of a truncated V pattern. Pupae are typically scarab-like, and are cream colored initially, but gradually become tan to light brown. They measure about 14 mm long and 7 mm wide. Within a few days of adult emergence, the pupa appears metallic green.

Japanese beetle adults feed on over 300 species of herbaceous and woody ornamental plant species, including numerous popular shade trees. Initial feeding damage usually occurs in the upper canopy of preferred trees, on the upper leaf surface, leaving only a lace-like skeleton of the leaf veins. The grubs feed on the roots of equally as many plants, including all cool-season turfgrasses, weed species and ornamental plants. Damage to turfgrass by grubs results in thinning, wilting, and subsequent irregular patches of turf that can be readily pulled back or rolled up from the soil like a roll of carpet. Feeding damage by larvae to ornamental plant material frequently results in poor plant health and in some cases eventual death of the plant material.

Much like many other scarab species, the Japanese beetle has a 1-year life cycle throughout most of its range in the U.S. Depending on geographic location, adult emergence is most common in mid- to late June with peak activity occurring in early July. Emergence may occur about 2 weeks earlier in the Carolinas and 2–3 weeks later in the more northern states. Within days of emergence, mating and egg-laying occurs. Virgin female adults call males with a chemical sex attractant (pheromone). As many as 20–100 males may aggregate around a single female attempting to mate with her. After mating, the female will seek out suitable turfgrass sites in which to lay eggs. Such sites include areas with moist, loamy soil covered with well-maintained, lush, closely cut turf. Throughout this mating and egg-laying process, both male and female adults continue to feed gregariously on ornamental plants, usually beginning in the upper canopy of the tree. Females remate after each egg-laying episode, laying eggs in clutches of 1–4 eggs in the upper 7.5 cm of soil. This process is repeated every few days during the normal lifespan of a female, 30–45 days, during which she may lay as many as 40–60 eggs. After about a 2-week incubation period, the first instar grubs begin feeding on fine, succulent roots and organic matter, usually sometime in late July or early August. In approximately 2–3 weeks, the grubs will molt, becoming second instars, and eventually reaching mature grubs (third instars) after another 3–4 weeks. Throughout this time, as periods of dry soil moisture or drought exist, the grubs may burrow deeper in the soil profile. As cooler temperatures prevail in the late fall, and the first measurable frost occurs, the grubs will begin to burrow deeper into the soil to depths of about 5–20 cm below the soil surface where they will overwinter in a semi-dormant, non-feeding state. As soil temperatures warm to above 10°C in the spring (late March or early April), the grubs will begin to move back up into the root zone to resume vigorously feeding for approximately 4–6 weeks before going back down into the soil profile to form an earthen cell in which to pupate, normally in late May or early June. Pupation typically requires approximately 2–3 weeks; thereafter, adult Japanese beetles emerge. At a latitude of Kentucky, Virginia and Maryland, adults and eggs will be present in July, first and second instars present by mid-August, and third instars from late September, and overwintering until May. Prepupae and pupae are seen at this latitude in May and early June. Timing of these developmental stages will be 2–3 weeks later in northern regions and about 1–2 weeks earlier in southern regions.

May Beetles, *Phyllophaga* spp.

There are approximately 25 species of May beetles that may infest and feed on the roots of turfgrasses in North America. They are rather destructive as a result of their large size, and because they destroy the roots relatively close to the soil surface. Compared to most other white grub species, May beetles typically occur at considerably lower densities than other turf-infesting grub species.

May beetle adults are brownish, reddish-brown to almost black, medium- to large-sized, heavy-bodied beetles ranging in size from 11 to 24 cm long. Depending on species, body pubescence varies greatly; some species are almost hairless, while other are quite fuzzy. It is very difficulty to differentiate among the various species. Egg are pearly white and oval when first laid, but become more spherical after absorbing water from the soil. When fully mature and hydrated, eggs are nearly 2.5–3 mm wide. In most species, fully mature or third instar grubs are approximately 25–38 mm long. May beetle grubs have a V- or Y-shaped anal slit with the stem of the Y shorter than the arms. The most distinguishing characteristic is the raster pattern that exhibits two parallel rows of short spines, and resembles a zipper. The pupa is about 7–10 mm long, and appears white initially but turns tan as it matures. The pupa is initially enclosed in the final larval instar skin, which soon splits and is pushed back over the terminal portion of the abdomen. Thus, it lies exposed in an earthen cell created by the larva. This characteristic is common with the Asiatic garden beetle and European chafer.

May beetle grubs attack the roots of nearly all common turfgrasses. They cause extensive damage to turfgrass much like many of the other turf-infesting scarab species. The adults feed on tree leaves, chewing on the tissue between the veins, similar to Japanese beetles. Preferred hosts include birch, elm, hickory, oak, persimmon, poplar and walnut. In extreme situations, whole trees are sometimes defoliated in the spring.

Depending on the species, May beetles have 1- to 4-year life cycles. Nearly all the May beetle species that occur in the temperate U.S. have a 3-year life cycle, however, certain species have a 2-year life cycle in the transition zone and father south where warm-season turfgrasses are grown. There are a select few species that have only 1-year cycles. All *Phyllophaga* species have a life cycle that includes the developmental stages of an egg, three larval instars, a pupa, and an adult. The adults of most species are active from April to June depending on geographic location. In some southern regions, though, flight activity may be seen during any month of the year. May beetle adults emerge and are active just after sunset, when they fly to the tops of trees to feed and mate before returning to the turf before sunrise. Subsequently, they are highly attracted to lights, and often are observed bouncing off screen doors. After mating, females fly to the turf to burrow down approximately 8–10 cm to lay eggs singly in moist soil. An individual female typically lays approximately 20–50 eggs in her lifespan. After an incubation period of about 3–4 weeks, the eggs hatch and first instar grubs begin feeding on the succulent roots of turfgrass and organic matter. The larvae then quickly develop, growing and molting into fully developed second instars by early fall (September). Thereafter, they continue feeding into the late fall before the first measurable frost occurs, when they migrate downward to lower depths for overwintering. In the early spring, the following April, the second instars migrate upward to resume feeding on the roots of turfgrass, eventually molting into third instars by mid-June. The third instars continue to feed and grow, causing most of their damage in July and August. For May beetle species with a 2-year life cycle, they will reach their full size and pupate by the end of the second summer. Most of these 2-year species reach full maturity as adults by late fall of the second year, but remain in the soil throughout the winter, emerging the following spring. For species with a 3-year life cycle, as cooler temperatures prevail during the fall of the second year, the nearly fully mature larvae slowly migrate downward again in late September and early October to overwinter. Finally, in the third year of the life cycle, in the early spring during late March and early April, the third instars again migrate upward to feed throughout April and May before they complete their larval development. In June, the larvae migrate slightly downward to a depth of approximately 15–25 cm where they form an earthen cell in which to pupate. By late June, the third instars become prepupae, transform into pupae in July and August, becoming adults sometime in late August or early September. The young adults remain in the aforementioned earthen cell until the following spring, when they emerge in May or June. Regardless of whether the species has a 2- or 3-year life cycle, most of the damage is occurs during the second year.

Northern and Southern Masked Chafers, *Cyclocephala borealis* (Arrow) and *Cyclocephala lurida* (Bland)

Both northern and southern masked chafers are native to North America, and are widely distributed from the Atlantic seaboard westward to the Rocky Mountains and into the southwestern U.S., and from southern New York to as far south as South Carolina. Northern and southern masked chafers are among the most destructive insect pests of turfgrass in the Midwest and Central U.S., causing typical white grub damage. In addition, there is often significant indirect injury due to the feeding of vertebrate predators on these grubs. Distribution of both species overlaps throughout much of the Midwest. However, southern masked chafers are more common in the southern extent of their range.

Northern and southern masked chafers are quite similar in appearance and size in all life stages. Northern masked chafer adults are dull yellow-brown beetles, approximately 11–12 mm long and 6–7 mm wide. The only distinction from the southern masked chafer is that southern masked chafer is more shiny, and reddish-brown. Males and females of both species have distinguishable darker, chocolate brown color across the head and eyes that enables one to differentiate them from most other scarab species that are similar in size and color. Other important morphological characteristics that help to identify northern masked chafer beetles are the dense hair on the ventral side of the thorax, and the scattered arrangement of erect hairs on the wing covers. The adults of southern masked chafer lack such hairs. Newly laid eggs of both the northern and southern masked chafers are pearly white, oval, approximately 1.3–1.7 long, that like other white grub species, become considerably larger and more spherical after absorbing water from the soil. The larvae of northern and southern masked chafers are typical white grubs with a C-shaped body and six jointed legs. It is practically impossible to differentiate the two species. Newly hatched grubs are translucent white, becoming grayish after feeding, and they are about 4–5 mm long. Fully mature northern and southern masked chafer grubs are considerably larger and more robust than Japanese beetle larvae, ranging in size from 23 to 25 mm in length. They also have a reddish-brown head capsule compared to a more yellowish-brown head capsule in Japanese beetles. Their raster pattern exhibits an evenly spaced, non-uniform arrangement of approximately 20–30 stout hairs. Pupae are approximately 17 mm long and are creamy initially, later becoming reddish-brown as they mature.

Although northern and southern masked chafer grubs eat the roots of all turfgrasses, including endophytic cool-season species, they also feed on decaying organic matter and frequently are found in mulched plant beds, heavier organic soils and compost heaps. When damage does occur to turf, typical white grub feeding damage is common. The adults do not feed or cause damage to turf or other plant material.

The northern and southern masked chafers both have a 1-year life cycle like many other scarab species. The adults are active in June and July, with peak activity occurring in late June through early July in areas such as southern Ohio. They may be observed up to a month earlier in more southern locations. There is a distinct difference in adult behavior between northern and southern masked chafers. Southern masked chafer is predominantly active from just after sunset until around 11:00 p.m., whereas northern masked chafer is mostly active after midnight. Otherwise, their behavior is quite similar in that they swarm over the turf surface on warm, humid nights, especially after a heavy rain, in search of mates. As soon as mating occurs, the female will burrow into the turf canopy to lay her eggs in the soil. The eggs are laid singly or in small clusters in the upper 2.5–5 cm of the soil. The incubation period is approximately 14–18 days depending on temperature, and most eggs hatch by late July to mid-August. When soil moisture is adequate, the larvae will grow and develop relatively quickly, molting into second instars in approximately 3 weeks. By early September, the grubs develop into third instars, continuing to feed and grow until about mid- to late October when cooler soil temperatures force them to go deeper into the soil profile to overwinter. Similar to other white grub species, they overwinter in a earthen cell just below the frost line. In the spring, when temperatures become conducive, they migrate back up into the root zone to resume feeding until fully mature in mid- to late May. Thereafter, the fully mature larvae begin moving down into the soil profile to form earthen cells to pupate. The prepupal life stage proceeds, requiring approximately 4–6 days, while the pupal stage typically takes about 14–20 days to complete. Thereafter, adult beetles begin emerging in mid- to late June.

Oriental Beetle, *Exomala orientalis* (Waterhouse)

The Oriental beetle is native to the Philippines, but was accidentally introduced into the U.S. in Connecticut sometime before 1920. It was initially called the "Asiatic beetle" when it was first discovered in the U.S. The Oriental beetle is primarily a pest of regional importance in the northeastern temperate U.S. However, in recent years it has caused extensive damage to turfgrass (both warm- and cool-season turfgrass) as far south as northern Georgia. It is present throughout the Appalachian mountains and even the foothills in North Carolina. Like most turf-infesting scarabs, it causes typical grub damage.

Adult Oriental beetles are broadly rounded beetles approximately 9–10 mm long with relatively spiny legs. The adult beetles range in color from predominantly straw-colored to nearly entirely brownish-black. Their head is typically solid dark brown and the elytra have distinct longitudinal grooves. The eggs are somewhat milky-white, oblong, approximately 1.5 mm long, becoming slightly larger and more spherical after absorption of water. Oriental beetle larvae closely resemble Japanese beetle grubs. Both species have a transverse anal slit, though they can be differentiated easily by their raster patterns. Oriental beetle grubs have two parallel rows of 10–16 short, stout inward-pointing spines. Fully mature (third instar) Oriental beetle grubs are approximately 20–25 cm long. The prepupa resembles that of the Japanese beetle. Pupae are approximately 10 cm long, cream colored at first, but eventually become light brown as they age. The pupa also has as distinct thick fringe of hairs at the terminal segment of the abdomen.

Oriental larvae feed and destroy the roots of all cool-season turfgrasses as well as nursery stock and strawberry. The resulting damage is typical of most turf-infesting white grub species. The adults cause very little damage to plant material.

Like most scarab species that infest turf, the Oriental beetle has a 1-year life cycle. Its life cycle is similar to that of the Asiatic garden beetle and the Japanese beetle, with adults emerging in late June to early July. In many areas, the adults emerge a week or two earlier than the Japanese beetles. Because they are relatively weak fliers as compared to the Japanese beetle, they often are found crawling around, especially on flowers. Adult females lay their eggs singly 2.5–23 cm deep in moist soils. Each female lays about 25 eggs in her lifetime, throughout July and into early August. The eggs typically hatch after an incubation period of about 3 weeks. The larvae immediately begin feeding on the succulent roots of turfgrass, growing and developing into second instars by early September, and third instars by early October. Grub damage is most apparent in early September, especially when the turf is experiencing heat and drought stress. As cooler soil temperatures prevail, the nearly mature grubs burrow down into the soil to hibernate in earthen cells. In the spring, when soil temperatures are conducive in April and early May, they migrate back to the root zone to feed until early June. Thereafter, the grubs again burrow down slightly into the soil profile to pupate in earthen cells. The prepupal and pupal periods last for approximately 1–2 weeks, respectively. Nearly all of the grubs pupate by mid- to late June, and the adult beetles subsequently begin emerging in late June. Timing of these developmental changes may be approximately 1–2 week earlier in the southern region of its distribution (North Carolina) than in the more northern states.

Mole Crickets (*Scapteriscus* spp.) (Orthoptera: Gryllotalpidae)

Mole crickets are undeniably some of the most destructive insect pests of turfgrass in the southeastern United States. Four species of mole crickets can be found in the U.S., although only two of the four cause considerable damage to golf courses, lawns and sod farms. The tawny mole cricket, *Scapteriscus vicinus* Scudder, and the southern mole cricket, *Scapteriscus borellii* Giglio-Tos (formerly *S. acletus* Rehn and Hebard) are believed to have been introduced through ports in the early 1900s from South America, and are the two most prominent pest species. Both tawny and southern mole crickets can be found in the coastal region of the Southeast, from the southern portion of North Carolina over to eastern Texas. Two other species of mole crickets, the short-winged mole cricket

(*S. abbreviatus* Scudder) and the northern mole cricket (*Neocurtilla hexadactyla* Perty) can be found in the U.S. as well. The northern mole cricket is a native species that rarely, if ever, reaches pest status. It can be found from southern New England south to Florida and west to the Central Plains. The short-winged mole cricket is incapable of dispersing through flight due to its shortened wings, and thus, is typically found in coastal areas near ports of entry. When present in abundant numbers, the short-winged mole cricket can cause significant damage to turfgrass. At this time, its distribution is limited to Georgia, Florida, and some areas of the Caribbean, including Haiti, Nassau, Puerto Rico, Cuba and the Virgin Islands.

Tawny mole crickets are a more significant pest than southern mole crickets due to the fact that their diet consists mostly of plant material, including both the above-ground and below-ground parts of the turfgrass, while the southern mole crickets are primarily predaceous. The tunneling nature of both species makes them very damaging to turfgrass. As the crickets tunnel in their underground burrows, mechanical damage of the root system occurs, resulting in desiccation and susceptibility to other types of damage from foot traffic or golf carts.

Mole crickets are difficult to mistake for other turfgrass pests due to their unique appearance. Adults are relatively large, ranging from 3.2 to 3.5 cm long, and have characteristic shovel-like front legs. The pronotum of mole crickets is heavily sclerotized and their bodies are covered with a dense coat of fine hairs. The nymphs resemble the adults, but are smaller in size, and lack fully grown wings. At maturation, the front wings of the southern mole crickets and tawny mole crickets are folded back and almost reach the tip of the abdomen. To differentiate between the two species, one can look at the coloration or the tibial dactyls. Tawny mole crickets are typically golden brown with a mottled coloration on the pronotum and more robust, while southern mole crickets are grayish with four pale-colored dots on the pronotum. The most reliable distinguishing characteristic between the two pest species is the arrangement of the tibial dactyls. Both species have two dactyls, with the separation between the two for the tawny mole crickets being V-shaped and narrower than the width of one dactyl, while the southern mole crickets have a larger U-shaped space that is about the size of the width of one dactyl.

There are three distinct developmental stages of mole crickets: eggs, nymphs and adults. Both species produce one generation in most areas of their distribution, although southern mole crickets may have two generations per year in south Florida. Adults of both species have significant dispersal flights in the spring and minor flights in the fall. Tawny mole crickets typically fly from February to May in Florida, while southern mole crickets fly from March to June, and it is not uncommon to have flights of both species occurring on the same night. Flights for both species generally occur up to a month later in their northern range in the Carolinas. Tawny mole crickets will complete most flight activity before oviposition, while southern mole crickets will fly between clutches. The tendency of southern mole crickets to fly between egg-layings may have contributed to their quick spread after introduction into the U.S. Flights begin soon after sunset and continue for approximately 60–90 min in response to the calls of the males. Although the majority of flying mole crickets appear to be females, it is not uncommon for males to comprise a percentage of the flying crickets. Some of the flights are performed in an attempt to find a suitable mate, but many of the females that fly have already mated and use the intensity of the males' calls to indicate good oviposition sites. The moisture levels present in the soil influence the intensity of the calls, and because desiccation is a major factor in egg mortality, it is necessary for the females to find adequate soil moisture for successful oviposition.

Once the female finds a suitable site, she will spend about 2 weeks feeding and tunneling before laying a clutch of 25–60 eggs. Once the eggs have been laid, the female seals the tunnel and leaves the eggs to develop and hatch in 3–4 weeks, depending on the temperature. Females of both species can lay as many as 10 clutches of eggs. Oviposition begins as early as March for tawny mole crickets in northern Florida, and may continue well into April and June. Some southern mole crickets begin laying eggs as early as April in northern Florida, with peak egg-laying occurring in May and June. Timing for egg-laying and hatch is usually delayed by a month in the northern regions. Typically all tawny eggs have been laid by the beginning of July, while it is not unusual to see newly hatched southern mole cricket nymphs into September. After hatching, new nymphs will tunnel closer to the surface and begin feeding. As the nymphs continue to grow and go through 7–10 instars, damage will become more evident. By December, approximately 85% of tawny mole crickets have molted to adults, while only 25% of the slower-developing southern mole crickets reach maturity before winter. Those nymphs that do not reach adulthood by winter will complete development in the spring. Even though there are adults of both species present by fall, no mating or egg-laying appears to occur after fall flights. Crickets of both species overwinter as large nymphs or adults and do not become active again until the spring when temperatures rise. Mole cricket activity is most significant at night following heavy rains or irrigation when the crickets come to the surface to forage for food.

Effective management of mole crickets involves scouting, mapping, sampling and treatment. In the spring when adults are present, mating and flying, considerable damage may appear. Due to the large size of the crickets, unpredictable weather and large dispersal flights, it is difficult to effectively control crickets in the spring. At this time, spot treatment is advised for sensitive or critical areas. It is also very important to map those areas that appear to have significant adult activity for treatment of nymphs later. The time period after egg hatch when nymphs are small and nearer the surface is the best time to treat, usually in mid-June or early July. It is best to concentrate on those areas where adult activity was seen in the spring. Soapy water flushes can be used to confirm the presence of small nymphs in areas where adult activity was seen earlier in the year. An important aspect of control is to get the insecticide treatment to come into contact with the crickets. Therefore, areas of mole cricket activity should be allowed to dry for several days and then pre-irrigated the night before treatment, thus bringing the nymphs closer to the surface and making control easier. As crickets continue to grow and increase in feeding, damage may reappear in the fall, but effective control of small nymphs is the best way to minimize their impact.

Ground Pearls (*Margarodes* spp.) (Hemiptera: Coccidae)

Ground pearls are a common name for several species of unique scale insects that spend most of their life in the soil and feed on the roots of various species of warm-season turfgrass. The two most common species in turf are *Margarodes meridionalis* Morrill and *Eumargarodes laingi* Jakubski. These pests are present almost everywhere in the U.S. that warm season turfgrass is most common, from North Carolina across to California.

Ground pearls are subterranean, and the female spends most of its life in the soil. The pinkish-white eggs are laid in clusters in the soil and covered with a white waxy substance. The first instar nymphs that hatch are only 0.2 mm long and this crawler stage attaches itself to a root. Once attached it covers itself with a waxy substance and begins formation of the “pearl.” As the pearl grows it may appear to have a purple to yellowish globular covering. The pearls range in size from 0.5 mm to 2 mm in size. Adult females may appear in the late spring and throughout the summer. They are pinkish sac-like creatures with well-developed forelegs and are about 1.6 mm in length. The male is rarely seen and has a gnat-like appearance.

Ground pearls attack a range of warm-season turfgrasses, but appear to be most common on bermudagrass, centipede, zoysiagrass, and St. Augustinegrass. Centipede often appears to be the most severely damaged. The distribution is sporadic, but where infestation does occur, the damage can be quite serious. The nymphs (pearls) feed on the roots by extracting plant juices (and possibly injecting toxic substances), which results in an initial appearance of unhealthy, yellow turfgrass. This appearance usually worsens during hot, dry summers and the plant often will turn brown and then die. This rapid death would indicate toxin may be involved. The damaged areas vary from a few centimeters to several meters in diameter. The turfgrass usually does not regrow in these areas even the next summer. Weeds often grow in these irregular, but somewhat circular areas. Through time, the damaged areas may eventually coalesce and a significant portion of the turf may die.

The life history of this pest is not well understood across its range, but one generation per year probably occurs throughout its range. Under unfavorable conditions, the ground pearls may take longer than a year to complete their life cycle. The nymphs overwinter in the soil, and some nymphs will mature in the spring and summer, emerge from the cyst and move toward the soil surface as adults. The adults may be seen moving on the soil surface in late spring and all summer. After moving for a short period of time, they reenter the soil and move down only about 5–8 mm to secrete the waxy coat in which the eggs will be laid a few days later. The females lay eggs without mating, as they reproduce parthenogenically. They lay about 100 eggs over a 2-week period and the eggs hatch in about 10 days to 2 weeks. The new crawlers move to the roots, attach and begin to encyst once feeding is initiated. Ground pearls have been found as deep as 25–30 cm in the soil. A fungal disease of ground pearls has been reported, and ants probably play a significant role as predators.

Red Imported Fire Ant (*Solenopsis invicta* Buren) (Hymenoptera: Formicidae)

The red imported fire ant has become a pest of great significance throughout the warm season turfgrass areas of the South, particularly the Southeast west to Texas. This introduced species of ant was accidentally introduced from South America into the Mobile, Alabama, area around 1930. This ant has spread rapidly throughout the South in all areas with mild winters and adequate moisture. States as far north as Virginia and Tennessee now battle this problem.

The mounds from fire ants are typically conical in shape and vary considerably in size, but large mounds are usually 25–40 cm in diameter and may be 20–30 cm in height. The mounds may penetrate more than a meter into the soil. In very sandy soils the mounds may be less well developed. They usually are found in open sunny areas and often appear following a disturbance of the soil (e.g., construction). Mounds commonly appear at the base of trees, structures, near rotting logs and stumps, power boxes, and along curbing and sidewalks. A mound contains three forms of adult ants as well as the brood (immature ants). Adult ants can be black reproductive males, queens or worker ants. The large egg-laying queens have no wings while the unmated queens and males are winged. The worker ants (which are the ants most commonly seen foraging near the mound) are wingless, sterile females and they vary in size from 1.5 to 4 mm in length. These workers have a shiny black abdomen and reddish-brown head and thorax.

Red imported fire ants forage and feed on a variety of materials, often on insects and related organisms, seeds, carrion and discarded food items. These ants can both sting and bite, but the venom from their sting is the biggest problem. They can sting repeatedly and are quite aggressive against anything that disturbs their mound. A relatively small percentage of people are hypersensitive to the venom in the imported fire ant sting and can become quite ill from even one sting. Fire ants also cause problems by creating unsightly mounds that may smother the turfgrass, create an uneven surface, and damage mowing equipment. They do not feed directly on the turfgrass, but they can be found infesting any turfgrass species that grows in a climate appropriate for fire ant survival.

Mating flights can occur any time of year, but are most common in the spring and early summer. Mating flights often occur after a rainy period. Reproductive males and unmated females (both winged) fly in the spring and after completion of the mating flight, the newly mated queen lays eggs in a small chamber in the soil. The males die soon after the flight, while the queen sheds her wings and begin the task of starting a new colony. Approximately 10–15 eggs are laid and once they hatch in a little over a week, the queen takes care of them until they are adults in about 3 weeks. These adults then begin taking care of the queen and egg production increases up to 200 eggs per day. These new fire ants mounds are inconspicuous, and often are not noticed until fall. During the summer, the colony increases in size and by late in the year, the above-ground portion of the mound may be quite prominent. Mature colonies may contain anywhere from 100,000 to more than 500,000 ants. The workers typically live 2 months, but a queen can survive for 5 years. Some colonies may contain more than one queen. Colonies with single queens are more territorial and areas with such colonies usually will have 40–150 mounds per acre. Multiple queen colonies are less protective and workers roam freely from one mound to another. There may be more than 200 mounds per acre in these situations.

Management of Turfgrass Insect Pests

Effective and environmentally responsible insect pest management begins with a planned, well-designed control strategy that considers a multitude of tactics including but not limited to biological, chemical, cultural, and plant resistance. This pest management strategy is referred to frequently as Integrated Pest Management (IPM). IPM relies on a combination of preventative and curative (i.e., corrective) measures to keep pest densities below levels that would cause unacceptable damage. The goal of IPM is to manage pests effectively, economically, and with nominal risk to people, animals and the environment. IPM is not a rigid pest management program that precludes the use of pesticides, nor is it a biological or organic pest control program. IPM is merely a decision making process that considers all control tactics that will provide acceptable control of a respective pest. When successful, IPM typically reduces dependence on pesticides.

The process of IPM involves the following seven principal steps:

Sampling and Monitoring

Regularly inspecting areas of turf throughout the growing season enables a turfgrass manager to detect pests early, before they reach damaging levels. Monitoring can aid in assessing the need for action, provide an evaluation of the success of previously implemented control tactic(s), and develop site history information that will provide invaluable insight for potential future problems.

Pest Identification

Accurate identification is essential. The biology of a pest cannot be understood if the pest is not correctly identified.

Decision-Making

Management decisions are guided by action thresholds (density of pests that will cause unacceptable damage). As decisions are made, factors such as likelihood of success, treatment cost and environmental consequences are considered.

Appropriate Intervention

All appropriate management tactics, including biological, chemical, cultural control and plant resistance, must be considered. Turfgrass managers first must attempt to determine the cause of the pest outbreak, and make the necessary cultural management practice adjustments to reduce the risk of future problems. Occasionally, insecticide treatments may be warranted, however, always consider less toxic products when practical.

Follow-up

Through consistent and disciplined sampling and monitoring, turfgrass managers can effectively evaluate the success of a control tactic as well as determine the need for further action.

Record-Keeping

Accurate and detailed record-keeping enables a turfgrass manager to recall when and where specific pest problems have occurred and to plan to deal with them in the future. Such information can help managers to evaluate previous management practices and may provide insight in developing and/or modifying future pest management programs. Record-keeping also provides managers with a document that may circumvent potential litigation.

Employee and Client Information

Another crucial component of a successful IPM program is communication. This involves educating employees, clients and the public. Education of employees can be accomplished by developing ongoing training programs that focus on pest recognition, and biology and agronomic factors that affect pest management decisions. Other educational opportunities, such as field days, workshops and short-courses, also provide valuable training that helps induce employees to work more safely and effectively as well as helping to increase professionalism and environmental stewardship. As for effective client communication, information vehicles such as newsletters, fact sheets, bulletins, fliers, personal communication, electronic mailings, etc., all provide excellent opportunities to convey valuable information. Finally, communication to the public sector can be accomplished through newspaper articles, bulletins, open houses, town meetings, television promotions, etc.

IPM considers all appropriate management options, including biological, chemical, cultural and plant resistance.

Biological Control

Biological control is the use of predators, parasitoids, and disease-causing microbes or pathogens to suppress pest populations (Table 17). Compared to chemical control research, to date there has been very little research on the impact and use of predators and parasitoids in the turfgrass system. Most biological control research efforts have been directed at microbial control (i.e., bacterial, fungal, viral, and entomopathogenic nematodes). Moreover, of this work, much has focused on entomopathogenic nematodes (i.e., insect parasitic nematodes). Entomopathogenic nematodes are microscopic roundworms that attack and kill insect larvae, and reproduce within the dead host. They are beneficial organisms that naturally occur in most soils, and they are practically harmless to humans, plants and animals. There are numerous species of insect parasitic nematodes; different species and strains of nematodes vary in their activity against different species of insects. As with many biological control agents, specific environmental conditions must be met in order for nematodes to be effective: they are sensitive to direct sunlight and high temperatures, and they require thin films of water that enable them to move over soil particles.

Despite the potential that biological control agents possess, only a limited number of companies currently market biological control agents. As a result, product availability and cost often discourage turfgrass managers from integrating them into their integrated pest management program. To further confound the reluctance of the use of biological control agents, they are frequently directly compared to conventional insecticides, and because they do not consistently perform at the same level, they are often discounted or not considered as a viable control option. Nonetheless, more consideration should be given to biological control agents.

Chemical Control

When used judiciously, selectively and responsibly, insecticides are tremendously important tools in an overall IPM program. To date, chemical control continues to be the most common control strategy. This is likely due to numerous factors such as convenience, economics, effectiveness, familiarity and/or confidence of turfgrass managers with this strategy. Nonetheless, chemical control should not be the primary line of defense in managing turfgrass insect pests. When effective, alternative control strategies are available, always consider tactic(s) that have the least risk to people and the environment. Conversely, in some instances alternative, non-chemical control strategies may not be available. Thus, insecticide treatments may be the only control option. Subsequently, when selecting an insecticide, always consider products that are least hazardous to people and

Turfgrass Insects of the United States: Biology and Management, Table 17 Beneficial invertebrates: predators and parasitoids

Organism	Taxonomy	Type	Host(s)
Ant	Hymenoptera: Formicidae	Predator	Eggs and larvae of numerous insects
Big-eyed bug	Hemiptera: Geocoridae	Predator	Chinch bug, greenbug, mites, eggs and larvae of small arthropods
Entomopathogenic nematodes	Secernentea: Rhabditida	Predator/Pathogen	Numerous insect larvae
Green lacewings	Neuroptera: Chrysopidae	Predator	Aphids, mealybugs, and other soft-bodied arthropods
Ground beetles	Coleoptera: Carabidae	Predator	Eggs and larvae of numerous arthropods
Tiger beetles	Coleoptera: Carabidae	Predator	Eggs and larvae of numerous arthropods
Lady beetles	Coleoptera: Coccinellidae	Predator	Aphids and mealybugs
Rove beetles	Coleoptera: Staphylinidae	Predator	Eggs and larvae of arthropods
Scoliid wasps	Hymenoptera: Scoliidae	Parasitoid	Green June beetle larvae and other white grubs
Spiders	Arachnida: Araneida	Predator	Most insects
Tiphiid wasps	Hymenoptera: Tiphiidae	Parasitoid	Most white grub species

the environment, and that will provide the most effective control in an economical manner.

As previously mentioned, turfgrass insects can be categorized into three primary groups (i) leaf and stem, (ii) thatch, and (iii) root zone/soil. Subsequently, chemical control of insect pests in respective groups require specific considerations and application procedures.

Leaf and Stem Insect Pests

The turf area should be mowed and the clippings removed prior to the insecticide application to enhance the insecticide penetration into the turf canopy. A thorough irrigation before an insecticide application will help move insects out of the turf canopy (i.e., thatch and soil) and bring them to the surface. For night feeding insects such as black cutworm or sod webworm larvae, insecticide applications should be made in the late afternoon or early evening to maximize potential for exposure to the target pest and minimize the likelihood of photodegradation (i.e., sunlight decomposition) and volatilization of the insecticide, as well as reduce pesticide exposure to humans and animals. When liquid (i.e., sprayable) insecticides are used, avoid irrigation for at least 12 h to maximize contact and subsequent control. Regardless of insecticide formulation, avoid mowing turf after application for at least 24 h. When granular products are used, a moderate application (i.e., one-quarter inch or 6 mm) of irrigation is recommended to help dissolve and activate insecticide granules. Liquid and granular applications have their respective advantages and disadvantages. Liquids typically provide greater mortality from initial contact and they frequently leave a residue that results in some residual control. In contrast, granules have little initial contact activity, and because they have a tendency to bounce off the foliage, they are not effective against foliage dwelling insects such as mites and greenbugs. However, they provide somewhat longer residual control of thatch dwelling insect pests.

Thatch Inhabiting Insect Pests

Turfgrass insects that inhabit thatch can be difficult pests to control depending on the quantity of thatch accumulation, as well as the active ingredient and formulation of the insecticide. When thatch accumulation is one-half inch (12 mm) or greater, the effectiveness of insecticide applications is greatly impeded. Consequently, reducing the thatch layer by de-thatching or aerification prior to an insecticide application will increase insecticide efficacy. Another important tactic for effective management of thatch inhabiting insect pests is to apply a moderate (i.e., one-quarter inch or 6 mm) amount of irrigation prior to the insecticide application to maximize the likelihood of the treatment reaching the target pest. Overall, granular insecticides tend to perform better than liquid formulations, however, the active ingredient of the product is the overriding factor that influences the effectiveness.

Root Zone/Soil Inhabiting Insect Pests

Soil dwelling or root feeding insect pests are often the most difficult to control. Pests such as white grubs and mole crickets can be controlled with either liquid or granular insecticides. The two primary strategies for controlling soil inhabiting or root feeding insects are (i) preventative and (ii) curative (i.e., corrective) control.

Preventative control is a strategy in which an insecticide is applied before a possible insect problem and subsequent damage develops. This approach can be compared to an insurance policy; potential damage is avoided or minimized. This approach to insect pest management can be quite attractive to turfgrass managers since it is relatively easy to implement and it requires dramatically less time and effort in monitoring, sampling and decision-making. Preventative control requires the use of insecticides that have a relatively long residual activity (i.e., more than 100 days). Nonetheless, turfgrass managers must still understand the biology of the pest in order to accurately time the treatment to ensure maximum control of the target pest.

Curative control is the complete opposite of preventative control; this approach is essentially a reactionary or corrective strategy. This approach heavily relies on monitoring and sampling of turf areas. When populations of a turfgrass insect pest are determined to be above an unacceptable level (i.e., threshold), an insecticide application is made to control the pest. Curative control applications typically are applied after damage is evident, though ideally before severe damage results. Regardless of the formulation or active ingredient of the insecticide, the application must be watered in thoroughly with a minimum of one-half to three-quarters of an inch (12–18 mm) of post treatment (i.e., after the application) irrigation to move the residue through the thatch to the target zone where the pest is located. If an irrigation system is not available, simply rely on anticipated rainfall. Another effective strategy for optimal control of soil inhabiting and root feeding insects is the application of pretreatment irrigation. The application of one-half inch (12 mm) of water 24–48 h before insecticide treatment will encourage the target insects to move closer to the surface and to decrease the absorbency of the thatch. This approach is especially important if conditions have been hot and dry and insects are deeper in the soil.

When using any chemical control agent or product, always read and follow the label directions. Be conscientious of the potential impact on humans, animals and the environment. Consider using products that are the least toxic and hazardous. Ultimately, remember that there are no "silver bullets" that will eliminate all pests.

Cultural Control

Cultural control is described as suppressing pest populations or reducing their damage by normal or slightly modified management practices. These measures must be implemented before the insect reaches pest status or damage occurs. Essentially, cultural control is a proactive approach to pest management. Such management practices include, but are not limited to, (i) mowing, (ii) irrigation and drainage, (iii) fertility, and (iv) thatch management. Ultimately, healthy turfgrass is more tolerant to potentially damaging insect populations.

Mowing

Generally, proper mowing practices such as sharp mower blades and removing no more that one-third of the grass blade at each mowing will make the turf healthier and subsequently more tolerant to insect damage. Excessively close mowing and/or scalping greatly reduces plant vigor, thus decreasing tolerance to environmental stresses. As a result, close-cut turf tends to have greater susceptibility to damage from certain turfgrass insect pests. Close and consistent mowing may remove the eggs of some insect pests such as the black cutworm.

Irrigation and Drainage

Irrigation and drainage can have both a positive and negative impact on the potential for insect damage. Certain insect pests prefer hot and dry conditions while other prefer irrigated turf where soils have adequate moisture. For example, Japanese beetle adults will seek out moist areas of turf to lay their eggs. This is likely due to the fact that moist soils are required for egg and young larval survival. Thus, withholding irrigation during adult egg-laying may reduce the potential for survival of eggs and subsequent grub damage. Unfortunately, this cultural management strategy is not practical for a golf course manager since adult activity occurs in late June through August. Conversely, turfgrass insect pests such as chinch bugs prefer hot and dry conditions for survival and optimal reproduction. Therefore, irrigating or watering when chinch bugs are present will help to minimize damage and subsequent survival and reproduction. Overall, sound irrigation contributes to healthy, vigorous turf, thus, the turf is able to withstand higher pest populations and recover more rapidly from insect damage.

Fertility

Similar to the effects of irrigation and drainage, fertility also can have both a positive and negative impact on the potential for insect damage. For example, high levels of nitrogen fertility often result in rapid, succulent growth, subsequently increasing the likelihood of insect damage. Excessive nitrogen fertilization coupled with improper irrigation and mowing also can result in a thatch accumulation which provides a hospitable environment for insects such as billbugs, cutworms, chinch bugs, and sod webworms. Additionally, heavy fertilization of cool-season turfgrasses in the spring stimulates rapid shoot growth at the expense of a deep, healthy root system. These weak, shallow-rooted turfgrass plants are less likely to recover from insect damage. A proper, well balanced fertility program can result in health, vigorous turf that has a greater potential to recover from insect damage. Moreover, in some instances, fertilization coupled with appropriate irrigation can aid in the ability of turf to recuperate from insect injury such as white grub damage. For specific fertility and irrigation recommendations, consult your local cooperative extension agent or state specialist.

Thatch Management

Thatch is described as a tightly intermingled layer of living and dead roots, crowns, rhizomes, stolons and organic debris that accumulates between the zone of green vegetation and the soil surface. Certain levels of thatch (i.e., less than one-half inch or 12 mm) accumulation are beneficial, however, this layer in the turf canopy also provides a prime habitat for insect pests. In addition, thatch also acts as a barrier to the penetration of soil insecticides targeted at soil dwelling and root feeding insects. As a result, turfgrass managers frequently spend valuable time and resources attempting to reduce thatch to an acceptable level. Thatch accumulation can be managed effectively through proper irrigation, fertility, aerification and verticutting (i.e., vertical mowing or de-thatching).

Plant Resistance

Establishing insect-resistant turfgrasses is another valuable IPM tool. Resistance to insects has been discovered in numerous plants, though the degree of resistance may vary considerably from one plant species to another. Even within a species, one cultivar or variety can have varying levels of resistance to particular insect pests. When it comes to plant genetics, there are often trade-offs associated with plant resistance. While a plant may be developed for a characteristic such as color, other beneficial traits may be sacrificed or lost to attain this trait (e.g., insect resistance). Unfortunately, plant resistance to insects is a relatively low priority of both managers and plant breeders. There is higher priority or value in developing a plant material that exhibits improved color, texture, growth, cold-hardiness, disease resistance, etc. Subsequently, only a few insect resistant turfgrasses exist. Nonetheless, of the insect resistant turfgrasses that are available, most are quite effective in managing pests. One mechanism by which plant resistance is expressed is via endophyte-infected turfgrasses. Endophytes are fungi that live within healthy grass plants, but have no adverse effect on the turfgrass plants. To date, they are known to occur only in perennial ryegrass, and tall and fine-leaf fescues. Endophytes produce alkaloids that are toxins that do not harm the plant, but are either deterrents or toxicants to the insects that feed on the above-ground plant parts, including stems, leaf sheaths and leaves. Only nominal levels of the alkaloids are present in root tissues, thus, endophyte-infected turfgrasses do not provide meaningful control of root feeding insects. In addition to the insect resistance attributes that endophytes have, they also may improve stress tolerance and enhance resistance of turfgrass to some diseases. Unfortunately, there are no endophytic cultivars of Kentucky bluegrass or creeping bentgrass, nor do they occur in warm-season turfgrasses.

References

Brandenburg RL, Villani MG (1995) Handbook of turfgrass insect pests. Entomological Society of America, Lanham, MD

Niemczyk HD, Shetlar DJ (2000) Destructive turf insects. H.D.N. Books, Wooster, OH

Potter DA (1998) Destructive turfgrass insects. Ann Arbor, Chelsea, MI

Vittum PJ, Villani MG, Tashiro H (1999) Turfgrass insects of the United States and Canada. Cornell University Press, Ithaca, NY

Watschke TL, Dernoeden PH, Shetlar DJ (1995) Managing turfgrass pests. Lewis, Ann Arbor, MI, 361 pp

Turnip Aphid, *Lipaphis erysimi* (Kaltenbach) (Hemiptera: Aphididae)

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Turnip aphid is found in both tropical and temperate areas throughout the world. It is often confused with cabbage aphid, however, so distributional records and economic impact of both species are sometimes incorrectly reported.

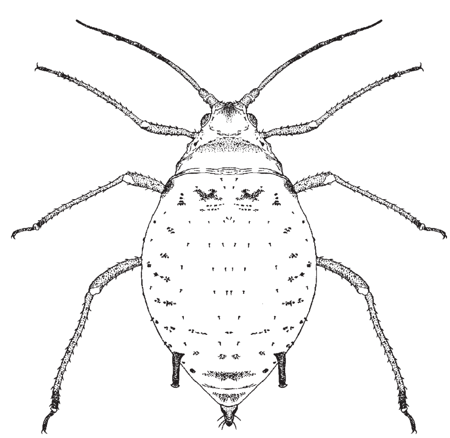
Life History

The turnip aphid is very prolific. Under temperate conditions, 11–25 generations are reported annually. Under the warmer conditions, up to 35 generations have been observed annually. Aphid longevity is usually 20–40 days, and reproduction begins about 6 days after aphids reach maturity. Wingless parthenogenetic females typically produce 80–100 young, often at a rate of 4–6 per day. Winged parthenogenetic females produce fewer offspring.

An egg-producing (oviparous) female form is known. Egg deposition rarely occurs, however, with nymph-producing (viviparous) forms occurring on crops and weeds throughout the year, even in cold climates. Oviparous females have been observed on several continents, however. Therefore eggs, although rarely observed, may occur on crops.

There are four instars. Nymphs are pale greenish yellow in color, and average about 0.6, 0.9, 1.0, and 3.3 mm in length during the four instars, respectively.

The wingless (apterous) adult females are whitish green or green in color, and measure about 1.4–2.4 mm in length. The dorsal surface of the thorax and abdomen of wingless adult females is marked with two rows of dark bands, which coalesce into a single band on the distal abdominal segments. The legs are pale with dusky joints. The antennae are dark and the cornicles pale with dusky tips. The entire body is lightly covered with a white secretion (Fig. 116).



Turnip Aphid, *Lipaphis erysimi* (Kaltenbach) (Hemiptera: Aphididae), Figure 116 **Wingless adult female of turnip aphid, *Lipaphis erysimi* (Kaltenbach).**

The winged (alate) adult females are pale green in color, with a black head and thorax. The last three abdominal segments are marked dorsally by narrow black bands. The sides of the abdomen also bear black patches. The legs are brownish to blackish, and the antennae black. The cornicles are dusky yellowish, with a small black area around the base. The wings are transparent, but marked with conspicuous black veins. Winged females measure about 1.4–2.2 mm in length.

Males have also been observed occasionally, but are too infrequent for their biology to be known. The wingless male is quite small, measuring 1.2–1.3 mm in length. It is olive-green to brown in color.

Turnip aphid generally can be differentiated from cabbage aphid by the very sparse occurrence of waxy exudate on the body, and by the slightly longer cornicles, 0.23 mm, of the former. In humid climates, however, there tends to be greater accumulation of waxy secretions on the aphid body. Therefore, it is probably better to use the shape of the cauda, a structure found at the tip of the abdomen, to differentiate these two species. When viewed from above, the cauda of cabbage aphid is triangular, about as wide as long. In contrast, the cauda of turnip aphid is slender, about twice as long as wide.

This aphid has been found associated with all *Brassica* crops, including such vegetables as broccoli, Brussels sprouts, cabbage, cauliflower, collards, kale, kohlrabi, mustard, radish, rape, turnip, and watercress. Cruciferous weeds also are known to be suitable hosts.

Turnip aphid is host to many parasitoids and predators. *Diaeretiella rapae* (MacIntosh) (Hymenoptera: Braconidae) is frequently reported to be an important biological suppressant, but in rapidly maturing crops such as radish apparently there is insufficient time for the parasitoids to attain high levels of abundance. Various ladybird beetles (Coleoptera: Coccinellidae), flower flies (Diptera: Syrphidae), lacewings (Neuroptera: Chrysopidae), and the fly *Aphidoletes aphidimyza* Rondani (Diptera: Cecidomyiidae) prey on the aphids. Fungus epizootics sometimes occur when aphid population densities are high, especially during the autumn months.

Damage

Turnip aphids feed principally on the undersides of leaves, but under high aphid densities or during the winter months the aphids may move to the center of the plant and feed on both the upper and lower surfaces of tender young foliage. They also feed readily on the stem tissue of the flowers. Heavy infestations will kill plants, and even light infestations will cause the leaves to cup, with yellowing of the foliage occurring where aphids are concentrated. Stunting of the plants is common, but contamination of foliage with aphid bodies, cast skins, and honeydew is the principal type of direct damage.

Turnip aphid may also serve as a vector of stylet-borne plant viruses. At least 10 viruses are transmitted, including cabbage black ring spot, cauliflower mosaic, radish mosaic, and turnip mosaic virus.

Management

Aphid water pan or sticky traps capture winged turnip aphids, but trap catches do not correlate well with overall aphid populations on plants. However, these techniques are useful to detect when winged aphids enter fields. This information is critical for the prevention of population establishment and the transmission of viruses.

Although sanitation is perhaps the most important factor in turnip aphid management, insecticides are used extensively. Systemic and nonsystemic insecticides are commonly applied in liquid or granular formulations, often at short intervals.

References

Capinera JL (2001) Handbook of vegetable pests. Academic, San Diego, 729 pp
Cottier W (1953) Aphids of New Zealand. New Zealand Department of Scientific and Industrial Research Bulletin 106, 382 pp
Davis JJ, Satterthwait AF (1916) The false cabbage aphid (*Aphis pseudobrassicae* Davis). Purdue University Agricultural Experiment Station Bulletin 185:915–939
Paddock FB (1915) The turnip louse. Texas Agricultural Experiment Station Bulletin 180, 77 pp

Turnip Root Maggot, *Delia floralis* (Fallen) (Diptera: Anthomyiidae)

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Turnip root maggot is found in northern regions of Asia, Europe, and North America. Turnip root maggot greatly resembles seedcorn maggot, *Delia platura* (Meigen), and many records probably represent mixed populations.

Life History

Throughout its range, there is but one generation per year. Turnip root maggots overwinter as pupae, and flies from the overwintering population emerge throughout the summer months. Late July and early August are peak emergence times.

Eggs of turnip root maggot are white, elongate, and one side is concave while the opposite side is convex. Eggs are marked with longitudinal ridges, and measure about 1.1–1.2 mm long and 0.28–0.38 mm wide. Eggs are laid in July and August, and are usually deposited in clumps in the soil around the base of plants. Females normally deposit about 200 eggs during their adult life of about 40 days. Eggs hatch 8–9 days after being deposited.

Larvae also are whitish in color, undergo three instars, and attain a length of 9–10 mm before pupating. Duration of the larval stage is 5–8 weeks. The anterior larval spiracles have 14–16 lobes, a character that is useful for distinguishing this maggot from most related species. Larvae are found feeding on the host plant from August to October. At maturity they move in the soil a short distance from the feeding site and pupate.

The puparium is oval, and bluntly rounded at each end, and brown in color. The average length is about 6.5–7.5 mm. Pupae are the overwintering stage, and therefore are present from August until the following spring, a period of 8–10 months.

Flies generally resemble cabbage maggot adults, but are slightly larger, measuring 7–9 mm long. They also lack the tuft of bristles at the base of the hind femora that is distinctive in cabbage flies, and their color tends to be a lighter gray. Adults live 1–2 months, and usually begin to deposit eggs when they are about 9–10 days old.

The host range of turnip root maggot is quite similar to that of cabbage maggot, *Delia radicum* (Linneaus), but turnip maggot is more abundant in northern latitudes and where soils are light. Turnip maggot is known principally for its damage to rutabaga and turnip, which explains the common name. However, it damages most crucifers, including weed species. It is generally considered to be a truly phytophagous insect, like cabbage maggot, rather than being attracted to stressed or plant disease-infected plants, like seedcorn maggot.

Biology of this insect is not well known, and the natural enemies are particularly poorly studied. It appears that predators and fungi that are associated with other *Delia* spp. also affect turnip root maggot. Studies in Norway showed that over 40% of turnip root maggot eggs were consumed by predators in only 2–3 days. Plots with greater numbers of carabids and staphylinids (both Coleoptera) had greater egg mortality, and insecticides interfered with predation.

Damage

Turnip root maggot can be quite damaging. In Canada's Prairie Provinces, up to 40% of commercial turnips and 80–90% of rutabagas have been made unsuitable for consumption due to feeding damage by this insect. Larvae generally confine their feeding to roots, but sometimes work their way up into petioles of the lower leaves. They normally scarify the surface of the root, rarely penetrating very deeply. For crops where the root is not harvested, such as cauliflower, the damage is much less, due to both the indirect nature of the injury and the fact that larvae tend to occur so late in the season that the plants are fairly mature.

Management

Yellow sticky traps can be used to monitor abundance of adults. Flies are more likely to land on horizontal surfaces than vertical surfaces, however, so water pan traps might be more suitable. Allyl isothiocyanate is an important element in host acceptance, functions as an oviposition stimulant, and may be useful in monitoring. Management of turnip root maggot often depends on use of insecticides, usually applied as a granular formulation at planting, to protect against larval injury.

In general, fast maturing varieties seem especially prone to damage. Chinese cabbage, mustard, and some cauliflower cultivars were especially susceptible to injury, whereas kale and radish were quite resistant, and broccoli was intermediate. In an evaluation of 22 cauliflower selections, significant differences in susceptibility to injury were identified. There was a positive correlation between plant damage and number of eggs deposited by flies.

Weather and soil conditions affect damage potential. As is the case with seedcorn maggot, damage is worse in cool, wet years. Also, in the Prairie Provinces of Canada, damage by turnip root maggot occurs principally on farms that are irrigated. In Norway, turnip root maggot is the principal crucifer pest on light soils, whereas cabbage maggot is the major pest on heavy soils.

► Vegetable Pests and their Management

References

Brooks AR (1951) Identification of the root maggots (Diptera: Anthomyiidae) attacking cruciferous garden crops in Canada, with notes on biology and control. Can Entomol 83:109–120

Capinera JL (2001) Handbook of vegetable pests. Academic, San Diego, 729 pp

Finch S (1989) Ecological considerations in the management of *Delia* pest species in vegetable crops. Annu Rev Entomol 34:117–137

Miles M (1952) Studies of British anthomyiid flies. III. Immature stages of *Delia cilicrura* (Rond.), *D. trichodactyla* (Rond.), *Erioischia brassicae* (Bch.), *E. floralis* (Fall.) and *Pegohylemyia fugax* (Mg.). Bull Entomol Res43:83–90

Miles M (1955) Studies of British anthomyiid flies. VI. The annual cycle of generations in some anthomyiid root flies. Bull Entomol Res 46:11–19

Turtle Beetles

Members of the family Chelonariidae (order Coleoptera).

► Beetles

Tussock Moths (Lepidoptera: Lymantriidae)

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Tussock moths, family Lymantriidae, total 2,490 species worldwide; actual fauna likely exceeds 3,000 species. Most of the fauna is Old World

Tussock Moths (Lepidoptera: Lymantriidae), Figure 117 Example of tussock moths (Lymantriidae), *Lymantria dispar* (Linnaeus) from Germany.

tropical (ca. 2,090 sp.). Two subfamilies are used, Orgyiinae and Lymantriinae, but this classification is uncertain. The family is in the superfamily Noctuoidea, in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults small to very large (16–135 mm wingspan); some with brachypterous females (some are apterous). Maculation mostly somber browns and grays, but some mostly yellow or white, or more colorful; a few species even with hyaline wings. Adults mostly nocturnal but some are diurnal or crepuscular. Larvae are leaf feeders, sometimes gregariously. Host plants include many different plant families. Many species are serious defoliators of forest trees (Fig. 117).

References

Bryk F (1934) Lymantriidae. Lepidopterorum catalogus 62:1–441. W. Junk, The Hague

Bryner R (2000) Lymantriidae – Trägspinner. In: Schmetterlinge und ihre Lebens räume: Arten – Gefährdung – Schutz. Schweiz und angrenzenden Gebiete, 3: 529–580, pl. 24–25. Pro Natura-Schweizerische Bund fuer Naturschutz, Basel

Ferguson DC (1978) Noctuoidea. Lymantriidae. In: Dominick RB et al (eds) The moths of America north of Mexico including Greenland. Fasc. 22.2. E. W. Classey, London, 110 pp, 9 pl

Griveaud P (1977) Insectes Lépidoptéres. Lymantriidae. Faune Madagascar 43:1–588

Holloway JD (1999) Family Lymantriidae. In: The moths of Borneo, 5: 1–188, 63 + 12 pl. Malayan Nature Society: Kuala Lumpur (Malayan Nat J 53)

Seitz A (ed) (1910–34) Familie: Lymantriidae. Die Gross-Schmetterlinge der Erde, 2: 109–141, pl. 19–22 (1910); 2(suppl.): 95–106, 283–284, pl. 8 (1932–34); 6: 535–564, pl. 72–74 (1927); 10: 291–387, pl. 38–47 (1915–25); 14: 127–205, pl. 20–28 (1926). A. Kernen, Stuttgart

Twig Borer

An insect that enters the shoot tip of a growing woody plant, causing the twig to wilt and die.

Twirler Moths (Lepidoptera: Gelechiidae)

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Twirler moths, family Gelechiidae, are a very large family, with over 4,830 species described, however, possibly with a fauna exceeding 10,000 species worldwide. Subfamily arrangements have varied but now include four subfamilies, plus many tribes: Physoptilinae, Gelechiinae, Pexicopiinae, and Dichomeridinae. The family is part of the superfamily Gelechioidea in the section Tineina, subsection Tineina, of the division Ditrysia. Adults small (4–35 mm wingspan), with head smooth-scaled and labial palpi recurved; haustellum scaled; maxillary palpi 4-segmented. Hindwings usually with distinctive falcate apical point and with long fringes (Fig. 118). Maculation varied, but mostly somber colors, but some can be colorful and with metallic-iridescent markings. Adults mostly nocturnal but some are diurnal or crepuscular. Many adults tend to twirl in circles on leaves when disturbed. Larvae have a range of feeding habits but most are leaf skeletonizers, using a

Twirler Moths (Lepidoptera: Gelechiidae), Figure 118 **Example of twirler moths (Gelechiidae), *Filatima albilorella* (Zeller) from Florida, USA.**

leaf fold or leaf tie as protection. A large variety of plants are used as hosts. Some species are economically important.

References

Clarke JFG (1969) Gelechiidae. In Clarke JFG, Catalogue of the type specimens of Microlepidoptera in the British Museum (Natural History) described by Edward Meyrick, 6:219–537; 7:1–531. British Museum (Natural History), London

Elsner G, Huemer P, Tokár Z (1999) Die Palpenmotten (Lepidoptera, Gelechiidae) Mitteleuropas: Bestimmung – Verbreitung – Flugstandort – Lebensweise der Raupen. F. Slamka, Bratislava. 208 pp (85 + 28 pl.)

Gaede M (1937) Gelechiidae. Lepidopterorum Catalogus, 79:1–630. W. Junk, The Hague

Hodges RW (1986) Gelechioidea. Gelechiidae (part). In: The moths of America north of Mexico including Greenland. Fasc. 7.1: 1–195, 4 pl. (1986); 7.6: 1–339, 5 pl. (1999). Wedge Entomological Foundation, Washington

Huemer P, Karsholt O (1999) Microlepidoptera of Europe, vol 3. Gelechiidae I (Gelechiinae: Teleiodini, Gelechiini. Apollo Books, Stenstrup, 356 pp, 14 pl

Janse AJT (1949–54) Gelechiadae [sic]. In: Janse AJT, The moths of South Africa, 5: 1–464, 202 pl. Pretoria

Li H-H (2002) The Gelechiidae of China (I) (Lepidoptera: Gelechioidea). Nankai University Press: Tianjin, 538 pp (32 pl.)

Piskunov VI (1981) Gelechiidae. In: Identification keys to the insects of European Russia. 4. (Lepidoptera), 2: 659–748. Academie Nauk, St Petersburg (in Russian)

Twisted-Wing Parasites

Members of the order Strepsiptera.

► Stylopids

Twospotted Spider Mite, *Tetranychus urticae* Koch (Acari: Tetranychidae)

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The most widespread and important of the spider mites is twospotted spider mite, *Tetranychus urticae* Koch, which is found throughout the world in temperate and subtropical locations. Though most damaging in warmer regions, twospotted spider mite survives temperate climates better than most other species of spider mites. Also, this species can become very troublesome in greenhouses everywhere.

Life History

With a life cycle of only 8–12 days at 30°C and about 17 days at 20°C, over 20 generations may develop annually, though conditions rarely allow this rate of population cycling. Overwintering may occur on many hosts in warm-winter climates, and in cold winter areas forage legumes and greenhouses often shelter these pests, but adult twospotted spider mite females also pass the winter under leaves or other organic debris in a state of diapause. The development time of the immature stages is 4–5 days at 30–32°C, but is extended to about 16–17 days when the temperature is 15°C at night and 28°C during the day.

The eggs are whitish and spherical. They measure about 0.10–0.15 mm in diameter. Eggs are often deposited singly on the lower surface of foliage, but sometimes on the upper surface, usually under dense strands of silk. Females oviposit at a rate of 5–6 eggs per day, for a total of 60–120 eggs. Duration of the egg stage is about 3 days at 30°C and 6–7 days at 20°C.

The first instar is called the larva, and is colorless initially but yellowish or pinkish in color after feeding. The body is nearly spherical in shape, and bears three pairs of legs. The terminal portion of the larval stage is a nonfeeding period called the nymphochrysalis or protochrysalis. Duration of the first instar is 1–2 days at 30°C and 2–3 days at 20°C.

There are two nymphal instars, the protonymph and the deutonymph. These stages are easily separated from the larva because they bear four pairs of legs. They tend to be green or red in color.

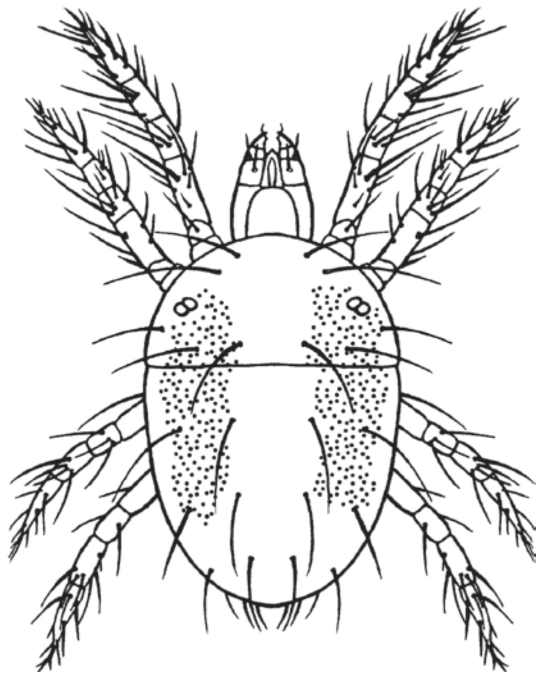
As in the larval stage, the terminal portion of each nymphal period is a nonfeeding period called the deutochrysalis and teliochrysalis, respectively. Duration of each instar is 1–2 days at 30°C and about 3 days at 20°C.

Adults are 0.4–0.5 mm long. Males are slightly smaller than females, and are usually less abundant than females. Like the nymphs, adults bear four pairs of relatively long legs. They also have numerous long hairs on their legs, and long but sparse hairs on their body. Females tend to be oval in body shape, males elongate-oval or diamond-shaped. The actively feeding female is usually greenish, with dorsolateral dark spots. Overwintering females of twospotted spider mite become orangeish red. Color is not a very reliable character with tetranychid mites; accurate determination depends on examination of tarsal characteristics and genitalia of males.

Males are attracted to immature females by a sex pheromone, perform extensive mating rituals and may mate repeatedly. The preoviposition period of females is 1–2 days. Fertilized females produce both male and female offspring; unfertilized females produce only males. Duration of the adult stage is normally about 30 days except when overwintering. The preoviposition period of adults is less than a day at 30°C, and 1–2 days at 20°C. Adults disperse by crawling and by wind-borne dispersal (Fig. 119).

These mites affect a large number of vegetable crops, though tomato, bean, and cucurbit crops are affected most often. They also damage cotton, soybean, strawberry, tree fruit crops and many ornamental plants.

The natural enemies of spider mites are numerous and diverse. Among the most important are predatory mites, particularly *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae); ladybird beetles, particularly *Stethorus* spp. (Coleoptera: Coccinellidae); dusty-wings (Neuroptera: Coniopterygidae); pirate bugs, particularly *Orius* spp. (Hemiptera: Anthocoridae); some plant bugs (Hemiptera: Miridae); and thrips, particularly *Scolothrips sexmaculatus* (Pergande) (Thysanoptera: Thripidae). Also, fungi sometimes cause epizootics.



Twospotted Spider Mite, *Tetranychus urticae* Koch (Acari: Tetranychidae), Figure 119 **Adult female twospotted spider mite, *Tetranychus urticae* Koch.**

Damage

Twospotted spider mites generally feed on the lower leaf surface. They pierce individual cells with their stylets, withdrawing the cell contents. Twospotted spider mite can feed on 18–22 cells/min, resulting in many dead cells, and often a speckled appearance. Leaf transpiration is accelerated, and affected leaves may dry and drop from the plant. Yellowing and speckling are the most common early plant responses to feeding, though reddening may also occur. Injection of plant growth regulators or interference with growth regulators during feeding is also reported. Wilting, tissue death, and leaf deformity and abcission are characteristics of prolonged and high density infestations. Disruption of photosynthesis results in stunting of plant growth and reduced fruit yields. Mite products such as webbing, eggs, cast skins, and fecal material also detract from the cosmetic quality of plants.

Prior to the 1940s spider mites were infrequently considered to be serious pests, but since then they have assumed major pest status in some crops. Apparently mite problems are induced by crop management practices, particularly the use of broad-spectrum insecticides. Also, the suitability of crops for mites is greatly enhanced when mites develop on plants that receive excessive nitrogen fertilization, grow in a dusty environment, or are stressed by inadequate moisture and high temperatures. These environmental factors can convert plants that might be only poor hosts into very good hosts, resulting in mite population increase and crop damage.

Management

Visual examination of foliage for leaf stippling on the upper surface, and mites and webbing on the lower surface, is the usual method of sampling. Older, or lower, leaves are usually examined. Infestations tend to be clumped initially, with clumping decreasing as the crop matures and females disperse to younger foliage.

Chemical insecticides (acaricides) are commonly used in greenhouses to prevent injury by mites, though natural enemies usually are capable of maintaining spider mite densities at low levels on crops grown under field conditions. In the field, insecticides directed at other pests can induce mortality among natural enemies of mites, causing spider mite population increases. Therefore, considerable effort is now directed at managing pests without disrupting natural control of mites, often by use of selective insecticides. Avoidance of early-season applications of insecticides is also recommended. Certain classes of insecticides, particularly pyrethroids, are especially disruptive. If chemicals must be applied for mite suppression, thorough coverage of the plants is essential. Frequent application of insecticides has led to many cases of resistance among spider mites. Resistance has not developed to oils, but oils are effective mostly against eggs, and frequent application leads to phytotoxicity among vegetable crops. Insecticidal soaps are similarly useful, though eggs are not entirely susceptible. Neither oil nor soap should be used at temperatures above 32°C. Sulfur is applied to some crops, but not to cucurbits, and not if temperatures exceed 32°C.

Cultural practices can have considerable influence on mite damage. Water stress disrupts the physiology of the host plant, making it more suitable for mite survival and population increase. Dry, dusty conditions also favor mite survival because blowing dust interferes with the predators of mites more than it does the mites; the latter are partially protected beneath their silk webbing. Thus, overhead sprinkler irrigation may alleviate mite problems. Excessive nitrogen fertilization of crops also favors mite population increase. Weeds and senescent crops can be important sources of mites, as can winter legume forage crops. Plant cultivars vary considerably in resistance to mites, and in some crops this offers excellent opportunity to manage mites whereas in others there seems to be little inherent resistance.

Biological suppression of mites through supplemental release of predators has been well developed for greenhouse crops. This approach is not often implemented for annual crops grown outdoors, though the successful use of the predatory mite *Phytoseilus persimilis* Athia-Henriot (Acari: Phytoseiidae) for twospotted spider mite suppression in strawberry fields shows that the approach is applicable if allowed by crop economics. This predatory mite is commonly used to suppress twospotted spider mite in greenhouses. Effective use of *P. persimilis* involves maintenance of a low level of pest mites so that the predators do not starve, and the distribution of pests (prey) uniformly in the greenhouse so that the predatory mites also will become widely distributed. Supplemental release of predatory mites may be needed to maintain a favorable ratio of predators to prey, often between 1:6 and 1:25. The maintenance of stable predator–prey–host plant relations is not a simple task, and even seemingly benign environmental changes such as variation in light intensity within the greenhouse affect stability.

► Citrus Pests and their Management
► Small Fruit Pests and their Management
► Potato Pests and their Management

References

Capinera JL (2001) Handbook of vegetable pests. Academic, San Diego, 729 pp

Carey JR, Bradley JW (1982) Developmental rates, vital schedules, sex ratios, and life tables for *Tetranychus urticae*, *T. turkestani* and *T. pacificus* (Acarina: Tetranychidae) on cotton. Acarologia 23:333–345

Huffaker CB, van de Vrie M, McMurtry JA (1969) The ecology of tetranychid mites and their natural control. Annu Rev Entomol 14:125–174

van de Vrie M, McMurtry JA, Huffaker CB (1972) Biology, ecology, and pest status, and host-plant relations of tetranychids. Hilgardia 41:343–432

Twostriped Grasshopper, *Melanoplus bivittatus* (Say), (Orthoptera: Acrididae)

This grasshopper is widely distributed in northern North America. In the United States it extends from the Atlantic to the Pacific Ocean, and is absent only from the Gulf Coast region. In southern Canada it occurs from Nova Scotia to British Columbia.

Life History

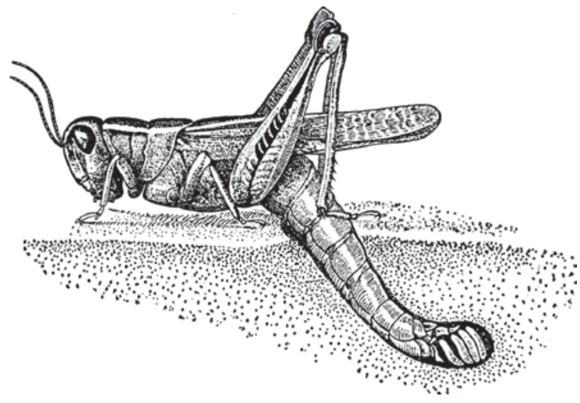
Over most of its range, twostriped grasshopper displays one generation annually, with the egg stage overwintering. In Colorado, eggs begin to hatch in June, though hatching can occur over a 4–6 week period. Nymphs may be present until September, but adults appear beginning in July. Oviposition commences in August and continues until adults are killed by cold weather. At higher elevations in British Columbia, a 2-year life cycle is reported.

The egg is elongate-cylindrical, with the ends tapering to blunt points. The eggs are olive in color and measure about 5.0 mm in length and 1.2 mm in diameter. The reported values of number of eggs per pod and total fecundity vary considerably among studies. One study reported 69.7 eggs per pod and a mean total of 129 eggs per female, whereas another reported 43.3 eggs per pod and a total of 355 eggs. The number of pods produced per female ranges from 4 to 15, with a mean interval between oviposition of 4 days, but this assumes good weather. Eggs are arranged in columns of four within a frothy secretion; the egg structure is called an egg pod. The pods are curved, measure 30–38 mm in length and 6–7 mm in diameter. They are inserted into the soil at a depth of 2–5 cm, and topped with a frothy plug. Favorite oviposition sites are along fence rows, ditch banks, and pastures with compact, undisturbed soil. Pods are often inserted among the roots of plants, and a soil moisture content of 10–20% is preferred. The act of oviposition requires about 2 h. The egg is the overwintering stage, and typically persists in the soil for 7–8 months. Embryonic development begins in the summer and autumn after oviposition, and is 60–80% complete before embryos enter diapause for the winter. However, they can be induced to hatch if exposed to about 5°C for 90 days.

Nymphal development normally requires 30–50 days. Most nymphs display 5–6 instars, but 7 instars occurs occasionally. Nymphal development time when fed lettuce or alfalfa and cultured at 21°C is about 10, 8.5, 10, 11, and 14 days, respectively for, instars 1–5. The young nymphs initially are dark brown or greenish, but gain a distinct dark stripe along the pronotum behind each eye at the third instar. The wing development is poor until instar 3, and the developing wings point downward. At instar 4, the wing orientation is reversed, with the wings oriented upward, but also pointing posteriorly. In the fifth instar, the wings are quite evident and extend out to at least the second abdominal segment. The number of antennal segments is 12–13, 17–18, 19–22, 23–25, and 24–26 for instars 1–5, respectively. Corresponding body lengths are 5–6.6, 7.4–10.4, 9–14, 15–21, and 20–17 mm. Nymphs are on the soil and seeking food each morning, but may ascend plants to escape the heat of the soil by noon. Like the adult stage, nymphs will perch on elevated roosts at night, and will sun themselves in the morning and in cool weather to attain optimal body temperature.

This is a fairly large and robust species. Males measure 23–29 mm in length, females 29–40 mm. The general body coloration is olive or brownish green dorsally and yellowish or yellowish green ventrally. The head and pronotum tend to be darker, usually olive green. A narrow but distinct yellow stripe passes from behind each eye along the pronotum and forewings, extending nearly to the wing tips. The stripes are often bordered below with black, especially on the anterior portions of the body. The stripes come together posteriorly in the forewings, forming a "V." It is this pair of yellow stripes that is the basis for the common name of this grasshopper. The forewings are usually uniform in color except for the stripes, and the hind wings colorless. The hind femora are yellow with a dark stripe along the outer face. The hind tibiae are variable, usually reddish but also greenish, yellowish, and purplish, and equipped with black spines. The male cerci are short, broad, and boot-shaped.

Adults seek crop borders and roadsides for reproduction. Mated females have a 7- to 14-day preoviposition period, after which they oviposit within the roots of grasses and weeds. Duration of oviposition is about 30 days (range 15–55 days) (Fig. 120).



Twostriped Grasshopper, *Melanoplus bivittatus* (Say), (Orthoptera: Acrididae), Figure 120 Adult female twostriped grasshopper, *Melanoplus bivittatus* (Say), depositing eggs in the soil.

Damage

This species is adaptable, and is found in a variety of habitats. However, it is most abundant in moist meadows, dense vegetation along water courses, and in disturbed, weedy areas. In the Great Plains region it is abundant in moist tallgrass regions, but uncommon in the drier shortgrass prairie. Twostriped grasshopper feeds on both grasses and broadleaf plants, but prefers the latter and fares poorly in habitats lacking broadleaf plants. Plants in the families Compositae and Cruciferae seem to be preferred. Among the uncultivated vegetation consumed is arrowleaved colt's foot, *Petasites sagittatus*; burdock, *Arctium lappa*; dandelion, *Taraxacum officinale*; dog mustard, *Eruscastrum gallicum*; flixweed, *Descurainia sophia*; needleleaf sedge, *Carex eleocharis*; leadplant, *Amorpha canescens*; oxeye daisy, *Chrysanthemum leucanthemum*; pepperweed, *Lepidium densiflorum*; plantain, *Plantago major*; redtop, *Agrostis alba*; sand dropseed, *Sporobolus cryptandrus*; Canada thistle, *Cirsium arvense*; sunflower, *Helianthus* spp.; wavyleaf thistle, *Cirsium undulatum*; mustard, *Brassica* spp.; and others. In North Dakota alfalfa fields, the plants most often consumed, after alfalfa, were kochia, *Kochia scoparia*; wild oat, *Avena fatua*; awnless bromegrass, *Bromus inermis*; tansymustard, *Descurainia sophia*; marsh elder, *Iva xanthifolia*; and quackgrass, *Agropyron repens*. On prairie, however, the plants most often consumed were Kentucky bluegrass, *Poa pratensis*; leadplant, A*morpha canescens*; and western ragweed, *Ambrosia psilostachya*. Survival rates and body weights are higher, and development times shorter, on mixed diets than on single hosts.

Twostriped grasshopper commonly infests vegetable and field crops, though most injury is limited to field margins. Among vegetable crops injured are beet, cabbage, chicory, corn, lettuce, onion, potato and likely others. Field crops such as alfalfa, birdsfoot trefoil, clover, young barley and oat, timothy, vetch and the immature seedheads of wheat also are fed upon. Flowers and ornamental plants are not immune to attack.

The natural enemies of the crop-feeding *Melanoplus* spp. are quite similar. For information on natural enemies of twostriped grasshopper, see the section on natural enemies of migratory grasshopper, *Melanoplus sanguinipes* (Fabricius).

Survival and population increase in grasshoppers are favored by hot weather. High numbers tend to occur after a period of years with abnormally hot and dry weather during the spring and summer months. This is especially true in northern areas, where it tends to be cooler. Enough precipitation is required to provide adequate food for grasshoppers, of course, but protracted periods of rainfall during egg hatch, especially if accompanied by cool weather, disrupt feeding by young grasshoppers and induce high mortality. The late onset of winter can favor grasshopper population increase because it allows adults additional time to produce eggs.

Twostriped grasshopper consumes the leaves of numerous plants. Damage is greatest in areas adjacent to weeds, and along fence rows, irrigation ditches, roadsides, and fallow fields. Damage is exacerbated by drought, which apparently increases nymphal survival rates and decreases the amount of weed vegetation available to the grasshoppers. Although the grasshoppers will feed at night if it is sufficiently warm, where nights are cool these grasshoppers tend to perch on elevated objects at night. This behavior allows them to be warmed by the light from the setting and rising sun, maximizing their period of activity. This also results in nibbling on the resting substrate by the grasshoppers; these grasshoppers will feed on the bark of bushes and young trees, and even damage shingles on buildings and eat holes in vinyl window screens while perching. The nymphs and adults are fairly dispersive, walking tens or even hundreds of meters in the search for food. At high densities they show propensity to swarm, which is expressed by band formation in the nymphal stage and flight by adults. The temperature threshold for flight is 30–32°C. Ascending to heights of 200–500 m, and flying with the wind, swarming adults can disperse long distances.

Management

Grasshopper populations are usually assessed by visual observation. A sweepnet is a useful tool to aid in collection, and its use a prerequisite to identification of the species complex. It is important to determine if grasshoppers collected from noncrop areas are crop-feeding species because there are many nonpest grasshoppers that restrict their feeding to grasses or weeds. It is advisable to monitor nearby uncultivated land, particularly weedy areas, in addition to crop plants, due to the tendency of the pest species to invade crops later in the season.

Liquid formulations of insecticides are commonly applied to foliage to protect against damage. Because grasshoppers rarely develop in crops, but instead invade from weedy areas, it is often the edges of crop fields that are most injured. Therefore, application of insecticide to the borders of crop fields is often adequate to protect an entire field. It is even better to apply insecticides to the developing grasshopper populations in weedy areas before they move to crops. This not only minimizes damage to crop plants, but often results in younger grasshoppers being targeted for elimination. Younger grasshoppers are more susceptible to insecticides, with large nymphs and adults sometimes difficult to kill.

Application of insecticide-treated bait is an effective alternative to foliar treatments for *Melanoplus* spp. because these grasshoppers spend considerable time on the soil where they come into contact with baits. Bait formulations are bulky and more difficult to apply than liquid products, so they are less often used, but have the advantage of limiting exposure of crops to insecticide residue and of minimizing mortality of beneficial insects such as predators and parasitoids due to insecticide exposure. Also, the total amount of insecticide active ingredient necessary to obtain control is usually considerably less when applied by bait because the grasshoppers actively seek out and ingest the toxin. Finally, for relatively expensive products that must be ingested to be effective, such as microbial insecticides, baits are the most effective delivery system.

The attractant used most commonly for grasshopper bait is flaky wheat bran, though other products such as rolled oats are sometimes suggested. No additives, other than insecticide (usually 5% active ingredient), are necessary because the wheat bran is quite attractive to *Melanoplus* grasshoppers. Other additives such as sawdust, water, vegetable or mineral oil, molasses, amyl acetate, salt, or sugar have been suggested, but provide little or no additional benefit over dry bran. The bait should be broadcast widely to maximize the likelihood of grasshopper contact, and should be applied while grasshoppers are in the late instars because adults ingest less bait.

Elimination of weeds within, and adjacent to, crops is the most important cultural practice, and can have material benefit in preventing damage to crop borders. However, during periods of weather when grasshoppers become numerous they may move long distances and invade crops.

Tillage is an effective practice for destruction of eggs. Deep tillage and burial are required, shallow tillage having little effect. All the crop-feeding *Melanoplus* species deposit some eggs in crop fields, especially during periods of abundance, but it is fence row, irrigation ditch, field edge, and roadside areas that tend to be the favorite oviposition sites, so tillage is not entirely satisfactory unless other steps are taken to eliminate grasshopper egg pods from these areas that cannot be tilled. Though providing suppressive effects, deep tillage is not consistent with the soil and water management practices in many areas, so may not be a good option.

Row covers, netting, and similar physical barriers can provide protection against grasshoppers. This approach obviously is limited to small plantings, and can interfere with pollination. Also, grasshoppers are capable of chewing through all except metal screening, so this approach does not guarantee complete protection.

The opportunities for biological control are limited. Historically, poultry were found to consume large numbers of grasshoppers and could provide considerable relief if the grasshopper-infested garden was small or moderate in size and the birds were plentiful. This remains a viable option for some people, and turkeys are usually considered most suitable among poultry. The birds may also inflict some direct damage to plants, however, so introduction of poultry is probably most viable when grasshoppers are plentiful and threatening.

The microsporidian pathogen *Nosema locustae* is well studied as a microbial control agent of *Melanoplus* spp. and is available commercially. It is fairly stable, and easily disseminated to grasshoppers on bait. However, its usefulness is severely limited by the long period of time that is required to induce mortality and reduction in feeding and fecundity. Also, the level of mortality induced by consumption of *Nosema* is quite low, often imperceptible. It is best used over very large areas, not just on individual farms, and should be applied at least one year in advance of the development of potentially damaging populations.

Fungi have also been investigated for grasshopper suppression. A grasshopper strain of

Beauveria bassiana has been effective in some trials, and *Metarhizium anisopliae* var. *acridum* has worked well for grasshopper and locust suppression in Africa and Australia, so it may prove useful for *Melanoplus* spp. Behavioral thermoregulation by grasshoppers, wherein they bask in the sun and raise their body temperatures, is potentially a limiting factor for use of fungi. Basking grasshoppers easily attain temperatures in excess of 35°C; such high temperatures decrease or even prevent disease development in infected grasshoppers. Inconsistent quality control in production of fungi also limits use of these organisms for grasshopper control.

► Grasshopper Pests in North America
► Grasshoppers and Locusts as Agricultural Pests
► Grasshoppers, Katydids and Crickets (Orthoptera)

References

Capinera JL, Scott RD, Walker TJ (2004) Field guide to the grasshoppers, katydids, and crickets of the United States. Cornell University Press, Ithaca, NY, 249 pp

Church NS, Salt RW (1952) Some effects of temperature on development and diapause in eggs of *Malanoplus bivittatus* (Say) (Orthoptera: Acrididae). Can J Zool 30:173–184

Parker JR (1939) Grasshoppers and their control. USDA Farmers' Bulletin 1828. 37 pp

Pfadt RE (2002) Field guide to common western grasshoppers. Wyoming Agricultural Experiment Station Bulletin 912. 288 pp

Smith DS (1966) Fecundity and oviposition in the grasshoppers *Melanoplus sanguinipes* (F.) and *Melanoplus bivittatus* (Say). Can Entomol 98:617–621

Two-Spotted Stink Bug, *Perillus bioculatus* (Fabricius) (Hemiptera: Pentatomidae, Asopinae)

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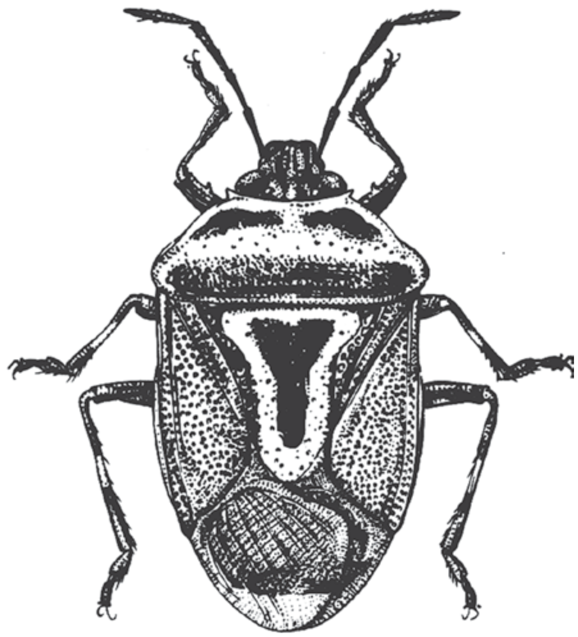
The two-spotted stink bug or double-eyed soldier bug, *Perillus bioculatus*, is a predatory bug belonging to the pentatomid subfamily Asopinae. It is believed to have originated somewhere from the southeastern Rocky Mountains to the Plains region and to have followed the eastward migration of the Colorado potato beetle, which appears to be its primary prey, at least in agricultural settings. The insect is presently found from Mexico into Canada.

Like those of other asopines, adults of *Perillus bioculatus* are broadly oval and more or less shield-shaped. Adult males are 8.5–10 mm long and the females are 10.5–11.5 mm long. Basically, there are three color forms: in the white form, the background is white with black and brown markings; in the yellow form, there are less pale areas, which are yellow rather than white, and all markings are black; in the red form, the background is red, and markings are black. The adults (Fig. 121) may gradually change from white or yellow to red, but not vice versa. The adults live for 1–2 months and are capable of laying 100–300 eggs. The bug has two to three generations per year and overwinters as an adult from September to October to April to May; adults usually hibernate in litter, but have also been found to enter buildings.

The eggs are blackish and barrel-shaped to somewhat elongate; the operculum is encircled by a row of about 15 micropylar processes, which are much smaller than in the spined soldier bug, *Podisus maculiventris*. The egg is on average 1.2 mm long and is 0.9 mm at its widest diameter. The eggs are laid in clutches consisting of 10–25 eggs, often arranged in a double row. There is no embryonic development below 15°C. At temperatures between 20°C and 25°C, eggs hatch within 5–8 days.

The nymphs are round to oval in shape. There are five nymphal instars. The body length of the five instars averages 1.5, 3, 4–5, 6–7, and 7–9 mm, respectively. First and second instars have a black head and thorax and a tomato red abdomen with dark patches. In third and fourth instars, the red background color may vary from tomato red to orange red or reddish yellow; the black color of the thorax often shows a greenish luster. In the fifth instar, there are two distinct forms; the dark



Two-Spotted Stink Bug, *Perillus bioculatus* (Fabricius) (Hemiptera: Pentatomidae, Asopinae), Figure 121 Adult of two-spotted stink bug, *Perillus bioculatus*.

form is greenish black and red, whereas in the pale form, the thorax and abdomen are mainly white to yellowish with dark markings. In the fifth instar, distinct wing pads are developed. During the last three instars, the red color may gradually change to yellow and white; on the other hand, nymphs with a yellowish background color may also become red. The carotinoid pigment responsible for the red coloration in the nymphs and the adults is believed to originate from their food. At high temperatures, the red pigment of the nymphs is quickly oxidized, yielding paler individuals.

The first instars hardly move about and form close groups. The gregariousness of the nymphs is more pronounced than in *Podisus maculiventris*, and even in later instars, the nymphs tend to form clusters, especially when they are preparing for the next molt and when temperatures are low. The first instars usually do not feed on prey and only require moisture, mainly in the form of plant juices. The nymphs start to attack prey from the second instar on. The nymphs and adults have a thickened rostrum or beak which they use to kill their prey and to suck up the liquefied prey tissues. Smaller nymphs in particular are often observed to attack prey collectively; on the other hand, gregariousness can also enhance the development of smaller nymphs by their opportunistic feeding on prey killed by larger, conspecific nymphs. Like other asopines, all predatory stages regularly feed on plant sap. Development of the nymphal stage requires about 3 weeks at 20–25°C, partly depending on food availability and quality.

Perillus bioculatus appears to be more of a specialist pentatomid predator compared to the spined soldier bug, *Podisus maculiventris*. In the field, the predator is usually found in association with the eggs and larvae of coleopterans, mainly from the Chrysomelidae family. It has been reported to feed on other insects, including the larvae of several lepidopterans. The bug appears to be, however, a rather timid predator with a dislike for highly mobile or aggressive prey. The two-spotted stink bug is best known for its predation on the Colorado potato beetle, *Leptinotarsa decemlineata*. The predator attacks all life stages of the beetle, but some scientists found that it has a preference for the eggs. Interestingly, the bugs usually suck out every egg in a mass, unlike some of the pest's predators with chewing mouthparts. It has been estimated that *Perillus bioculatus* can consume over 300 eggs during its nymphal period. This suggests a great potential for eliminating Colorado potato beetle populations provided that the pentatomid is present early enough in the season. Because natural populations of the predator in potato fields are usually too low early in the season, augmentative releases of laboratory-reared individuals may help in suppressing outbreaks of the pest in early spring. However, some workers have questioned the predator's dispersal and predation capacities, particularly under cool climates. Nonetheless, in small scale field plots, significant reductions of high density populations of Colorado potato beetle larvae have been achieved by releasing one to three second- or third-instars per plant. Like the spined soldier bug, *Perillus bioculatus* has been introduced in different parts of Europe for biological control of the Colorado potato beetle, but none of these introductions were successful. However, there are reports of established populations in the European part of Turkey since 2003, probably as a result of an accidental introduction.

High numbers of predators needed for augmentative field releases necessitate an economically viable mass production. The two-spotted stink bug can be reared on larvae of several noctuids (including *Trichoplusia* and *Spodoptera* spp.), a method that is cheaper than rearing it on the Colorado potato beetle, because the noctuids are easily mass-reared on artificial diets. The availability of an artificial diet for the predator itself may further reduce costs of mass propagation. Artificial diets have been developed that can support consecutive generations of the predator, but development and survival rates are reduced and fecundity is only one tenth of that raised on live prey.

► Stink Bugs (Hemiptera: Pentatomidae) Emphasizing Economic Importance
► Predatory Stink Bugs (Hemiptera: Pentatomidae, Asopinae)
► Bugs (Hemiptera)

References

De Clercq P (2000) Predaceous stinkbugs (Pentatomidae: Asopinae). In: Schaefer CW, Panizzi AR (eds) Heteroptera of economic importance. CRC, Boca Raton, 737–789 pp

Hough-Goldstein JA (1998) Use of predatory pentatomids in integrated management of the Colorado potato beetle (Coleoptera: Chrysomelidae). In: Coll M, Ruberson JR (eds) Predatory Heteroptera: their ecology and use in biological control. Proceedings, Thomas Say Publications in Entomology. Entomological Society of America, Lanham, 209–223 pp

Knight HH (1923) Studies on the life history and biology of *Perillus bioculatus* Fabricius, including observations on the nature of the color pattern. In: 19th Report, State Entomologist of Minnesota: 50–96

Rojas MG, Morales-Ramos JA, King EG (2000) Two meridic diets for *Perillus bioculatus* (Heteroptera: Pentatomidae), a predator of *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae). Biol Control 17:92–99

Tamaki G, Butt BA (1978) Impact of *Perillus bioculatus* on the Colorado potato beetle and plant damage. USDA Technical Bulletin 1581

Tympanum

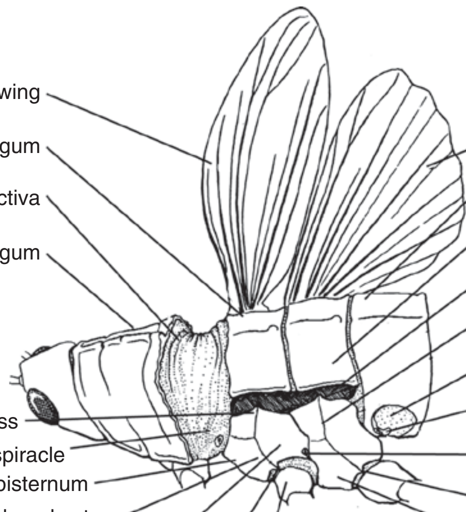
A membrane-covered cavity on the thorax, abdomen, leg or other part of the body that functions like an ear to perceive sound. These chordotonal organs are optimized to perceive high frequency sound (Fig. 122).

Typhus

There are several types of typhus, all of which are associated with arthropods. The most common are epidemic and endemic typhus. Epidemic typhus (also known as Brill disease) is associated with poor hygiene, and often is associated with cold temperatures. It is spread by lice. Historically, it is associated with periods of warfare and human disaster. Endemic typhus (also known as murine typhus) is associated with rat fleas and rat feces. It is most common during the warm weather when rats and fleas are most abundant. These forms of typhus are caused by rickettsia, either *Rickettsia prowazekii* (epidemic tphus) or *Rickettsia typhi* (endemic typhus).

Symptoms include high fever, severe headache, nausea and vomiting, abdominal pain and a transient rash. It is a severe illness, and may result in death if it is not treated, particularly in the case of epidemic typhus. Symptoms occur within 14 days of exposure, and the disease is treated with antibiotics. Sanitation and avoidance of flea-infested rats and rat feces is recommended.

Other forms of typhus include tick typhus and scrub typhus. Tick typhus, transmitted by ticks, is a form of spotted fever and is found in Africa and the Indian subcontinent. Scrub typhus is transmitted by mites, and is found in Southeast Asia and the Pacific islands. Avoidance of wild



Tympanum, Figure 122 **Head and thorax of a grasshopper (Orthoptera).**

animals and animal habitats is recommended for avoidance of these diseases.

► Mites
► Ticks
► History and Insects
► Lice
► Fleas

Type Specimen

The original specimen ("type") from which a new species description is created. The holotype.

U

Uenoidae

A family of caddisflies (order Trichoptera).

► Caddisflies

Uhler, Philip Reese

Philip Uhler was born at Baltimore, Maryland, USA, on June 3, 1835. He is known as America's greatest hemipterist. Uhler was born into a prominent merchant family but was not interested in his father's business, preferring natural history. In 1864 he was placed in charge of the insects at the Museum of Comparative Zoology at Harvard University, and the library at Cambridge, Massachusetts. He resigned in 1867 to return to Baltimore where he became assistant librarian at the Peabody Institute. In his spare time he studied entomology, economic entomology at first but then on Hemiptera. A book-buying trip to Europe in 1888 allowed him to examine many of Europe's insect collections, and he soon became a leading authority in this field. However, failing eyesight caused him to give up these pursuits in 1890. Uhler named many of Hemiptera collected on the early explorations of western North America. Notable publications include "List of Hemiptera of the region west of the Mississippi River, including those collected during the Hayden explorations of 1873," and "Hemiptera, Standard Natural History, Vol. 2." Uhler died at Baltimore, Maryland, on October 21, 1913.

References

Essig EO (1931) A history of entomology. Macmillan, New York, 1029 pp

Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Ulidiidae

A family of flies (order Diptera).

► Flies

Ultra Low Volume (ULV)

Delivery of a liquid formulation of undiluted pesticide in very small droplets.

Ultrastructure of Insect Sensilla

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The cuticle of insects is largely responsible for the success of these terrestrial arthropods. It is rigid and hard in areas requiring support and protection and flexible in regions associated with locomotion and the detection of mechanical stimuli. It is highly impermeable and restricts water loss from the body surface. Cuticle does not expand, thereby limiting growth, making it necessary for growing insects to periodically shed the existing cuticle (a process called molting) and to replace it with another, larger one. The insensitivity of insect integument also limits the reception of stimuli. This insensitivity is remedied by the presence of transcuticular sensory mechanisms, each specifically designed to detect one of a wide range of stimulus types.

Sensory perception for taste, smell, touch, sound, vision, proprioception, and geo-, thermo-, and hygroreception involves a three-stage process consisting of coupling, transduction, and encoding. Coupling connects the stimulus to the sensory neuron. Transduction converts the stimulus energy to electrical energy (receptor current). Encoding is the process that generates action potentials from the receptor current.

All type I sensilla (see below, Classification of sensilla), with the exception of certain scolopidial sensilla, consist of a specialized sensory cuticle innervated by the dendrites of one or more sensory neurons and usually three or four accessory cells that enwrap the neurons and associated sinuses. The exoskeleton and small size of insects impose certain restrictions on the nervous system, which are reflected in their behavior. Small size and short transmission fibers reduce the distance for impulse conduction and decrease reaction time. This allows them to respond very rapidly to stimuli. Size limitation also implies a decrease in neuronal number and a consequent reduction in informational capacity. The insect nervous system is organized in such a way that stimulation of a single sense cell may trigger a series of responses. Insects possess primary sense cells, which not only receive the stimulus, but initiate and transmit information by means of a direct connection with the central nervous system.

Cuticular Parts

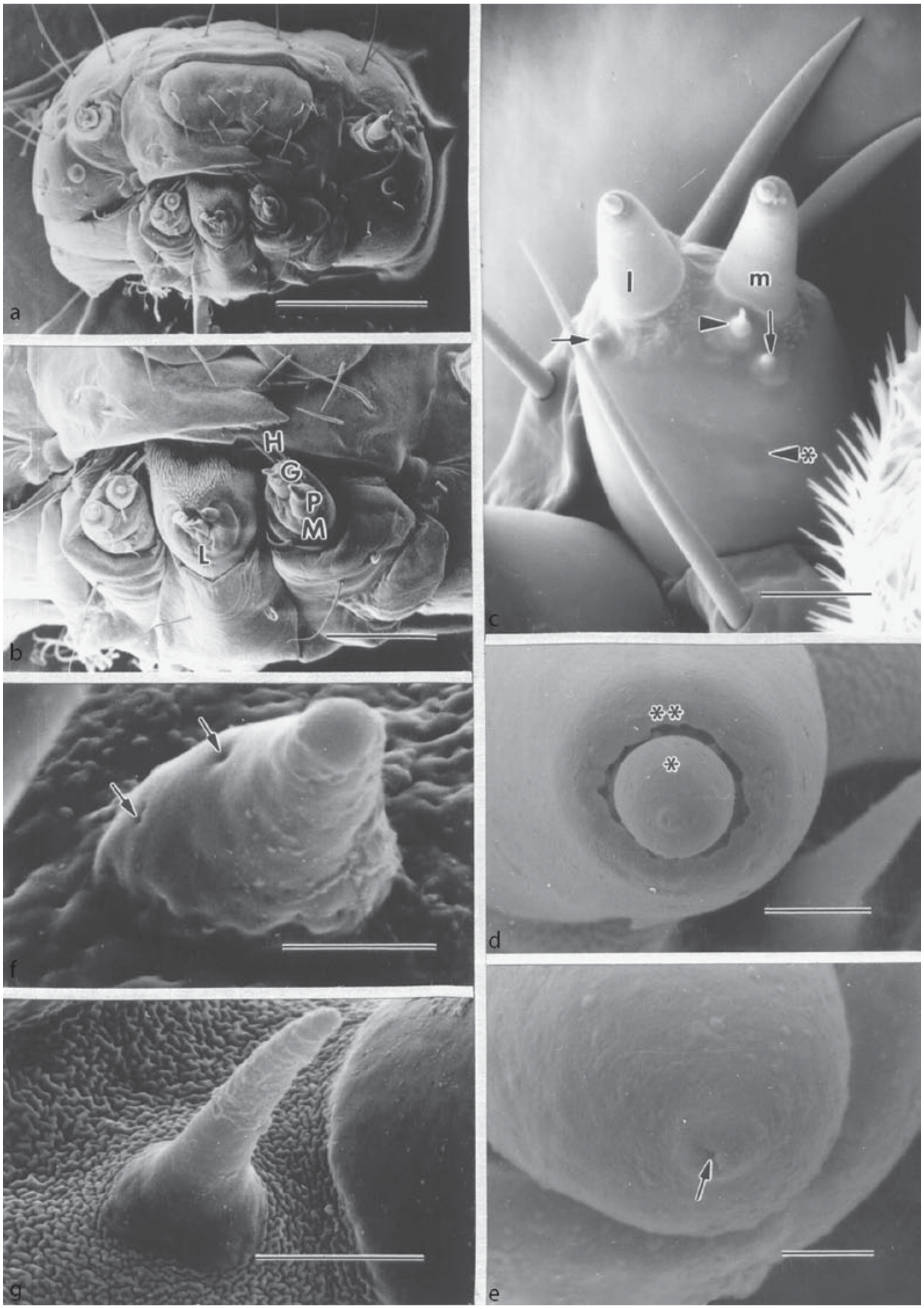
The components of an insect sensillum, that are considered to be cuticular, are those that are shed with the exuvium at a molt. These include the sensory cuticle and intracuticular structures (pore canals and pore tubules or filaments), the socket or insertion in the surrounding insensitive cuticle, and the sleeves or sheaths that extend inward around the distal part of the dendrite (Figs. 1–6).

Lipoidal pore canals are found in the body cuticle, as well as in the walls of the sensory cuticle, but are modified to varying extents. The canals usually contain pore filaments or tubules possessing an osmiophilic, lipoidal wall and a non-osmiophilic, non-lipoidal core. In most sensilla, pore canals open into the sensillar sinus liquor of the lumen within the sensory cuticle and in some sensilla, pore canals extend the length of the cuticular wall and open into the liquor of the sensillar sinus, under the sensory cuticle.

The dendritic sheath is cuticular in origin and is shed at a molt. Examination by transmission electron microscopy (TEM) reveals that the dendritic sheath is an invagination of the surface layer of epicuticle and resembles the superficial cuticulin layer in composition and density. The dendritic sheath is thought to possibly play a significant role in the stimulus transfer mechanism between the outer sensory cuticle and the enclosed dendrite in sensilla that are mechanosensitive (see below, Mechanosensilla).

Classification of Sensilla

The sensory neurons of insect sensilla are classified into two types: type I and type II. Type I neurons are bipolar, contain a ciliary structure in the distal dendrite, and innervate the sensory cuticle. The distal dendrite can be simple, branched, or lamellated in different types of sense organs. These neurons originate de novo within the epidermis. The neuronal perikaryon (cell body) remains peripheral in location, while the axon grows inward toward the central nervous system (CNS). A Type I sensillum is derived from an epidermal



Ultrastructure of Insect Sensilla, Figure 1 **SEM micrographs. (a, b) *Spodoptera frugiperda*. (c–e) *Mamestra configurata*. (f, g) *Choristoneura fumiferana*. (a) Frontal view of whole head. Scale bar = 1 mm. (b) Frontal view of ventral mouthparts. G, galea; H, dorsal guard hair on the galea; L, labium; M, maxilla; P, maxillary palp. Scale bar = 400 μm. (c) Fronto-ventral view of a right galea showing lateral (l) and medial (m) uniporous styloconic sensilla and three aporous basiconic sensilla: spire-shaped (arrowhead),** mother cell, which divides to form the nerve and sheath cells.

Type II neurons are bipolar or multipolar, lack a ciliary structure, and are never associated with cuticular processes. These neurons innervate the body wall, alimentary canal, muscles, epidermis, connective tissues, and sheath cells. They may have originated within the central nervous system and then migrated outwards to innervate mesodermal and epidermal tissues.

A type I sensillum can be defined as a sense organ that has one or more Type I bipolar neurons whose dendrites are enveloped by at least two sheath cells. All type I insect sensilla presumably evolved from an epidermal hair (seta) and all their component parts are believed to be homologous.

Traditionally, sensillar types have been classified on the basis of the morphology of their cuticular parts and their position on, within, or under the cuticle.

Sensilla Trichodea

These are hairs innervated by one to several neurons. They can vary greatly in length and are freely moveable on a basal membrane. They can be solely mechanosensitive, dually mechano- and contact chemosensitive, olfactory, or thermosensitive.

Sensilla Chaetica

These are bristles or spines innervated by one or more neurons. They are similar to the sensilla trichodea, but have thicker walls. They are typically set in a socket and can be mechano- or contact chemosensitive.

Sensilla Basiconica

These are pegs, cones, or papillae innervated by one to several neurons. They are similar in function to trichoid sensilla, as well as being hygrosensitive.

Sensilla Coeloconica

These are basiconic pegs or cones set in shallow pits innervated by two to several neurons. They are most often chemo-, thermo-, or hygrosensitive.

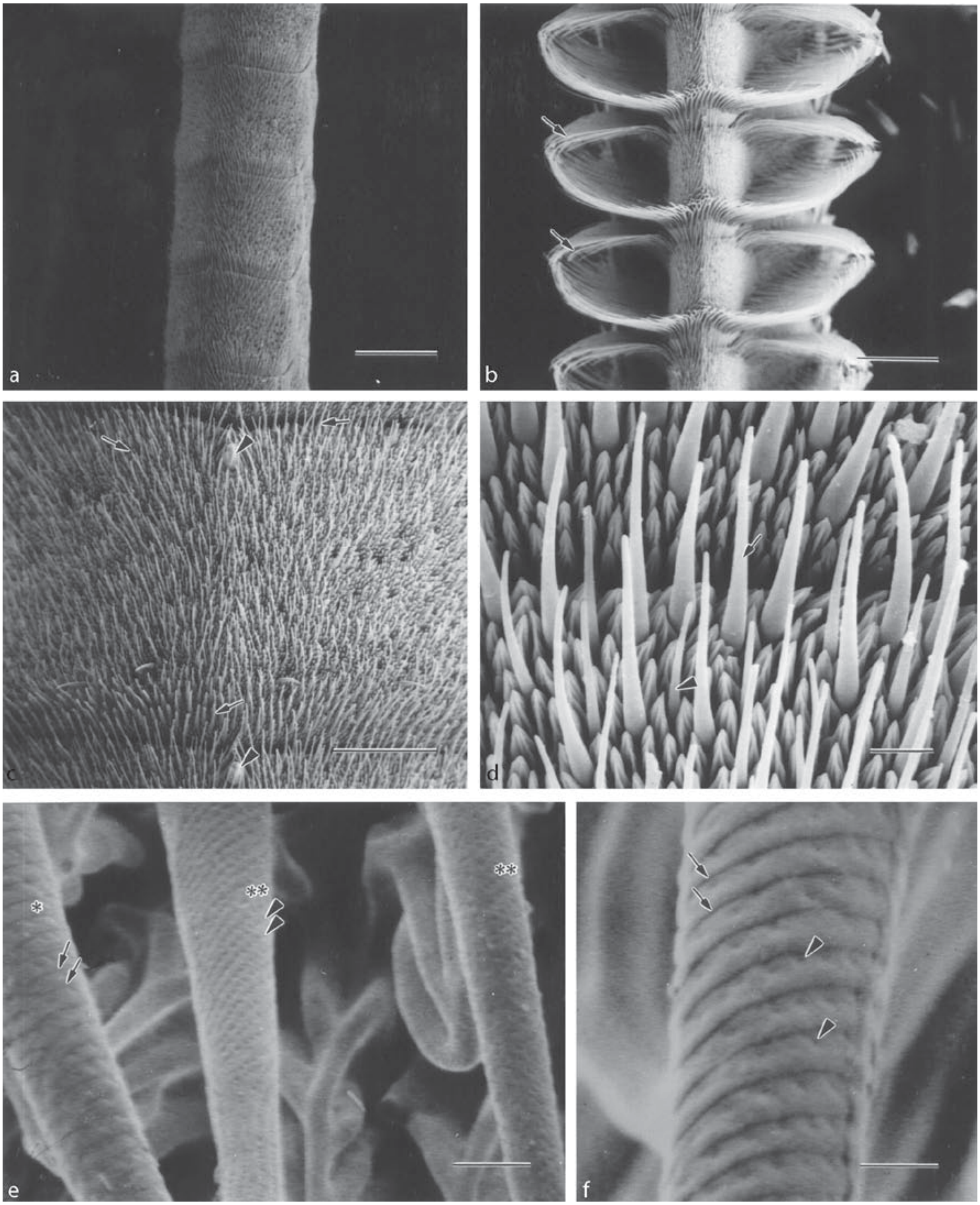
Sensilla Ampullacea

These are basiconic pegs set in deep pits innervated by two to several neurons. The surface opening is often much narrower (flask-shaped) than that of coeloconic sensilla. They have sensory characteristics similar to the sensilla coeloconica.

Sensilla Squamiformia

These are sensory scales innervated by one or more neurons and may be mechano- or chemosensitive. They have not been identified in immature insects.

lateral (horizontal arrow) and medial (vertical arrow). An aporous campaniform sensillum (arrowhead with asterisk) is located approximately midventrally on the galeal wall. Scale bar = 25 µm. (d) Higher magnification of the tip of a styloconic sensillum. Each sensillum consists of a small terminal cone or peg (asterisk) inserted into a socket (double asterisk) on a large style. Scale bar = 4 µm. (e) Apical view of the cone of a styloconic sensillum with a terminal pore (arrow). Scale bar = 1 µm. (f) Aporous basiconic sensillum. Beneath the pores (arrows), are longitudinal pore canals filled with pore tubules that extend to the surface of the cuticle. Scale bar = 2 µm. (g) Aporous spire-shaped basiconic sensillum. Scale bar = 5 µm. Both types of sensilla in (f, g) are inserted into inflexible sockets.



Ultrastructure of Insect Sensilla, Figure 2 SEM micrographs. (e, f) FESEM micrographs. (a–f) *Manduca sexta*. (a) Adult female antennal flagellum showing numerous hair-like trichoid sensilla. Scale bar = 250 μm. (b) Adult male antennal flagellum showing long multiporous pheromonal trichoid sensilla (arrows). Scale bar = 250 μm. (c) Higher magnification of an annulus from (a) showing many long, multiporous trichoid sensilla (arrows). The majority of these sensilla have ultrastructural characteristics typical of olfactory sensilla. Each arrowhead indicates an aporous styliform complex sensillum. Scale bar = 100 μm. (d) Higher magnification of a region from (c), showing long multiporous trichoid (arrow) and shorter

Sensilla Campaniformia

These are dome, bell, or cupola-shaped structures positioned at or below the surface of the cuticle. They are characteristically innervated by one neuron and are solely mechanosensitive.

Sensilla Placodea

These are plate-like sensilla innervated by several to many neurons. They are positioned level with, slightly raised above, or depressed below the surface cuticle, and are olfactory.

Sensilla Scolopophora

Also called chordotonal organs, these are subcuticular and are not associated with an external modification of the cuticle, though they maintain an attachment to it. Each sensilla unit is innervated by one to three neurons. There are two types of scolopidial sensilla: amphinematic and mononematic. Amphinematic scolopidia are drawn into a distal thread or tube and may be either integumental (direct attachment with the cuticle) or subintegumental. Mononematic scolopidia lack such a thread or tube and are subintegumental (without any direct attachment to the cuticle). Some chordotonal sensilla are propriceptive in function and respond to stretch during movements of body parts, while others respond to air-borne vibration.

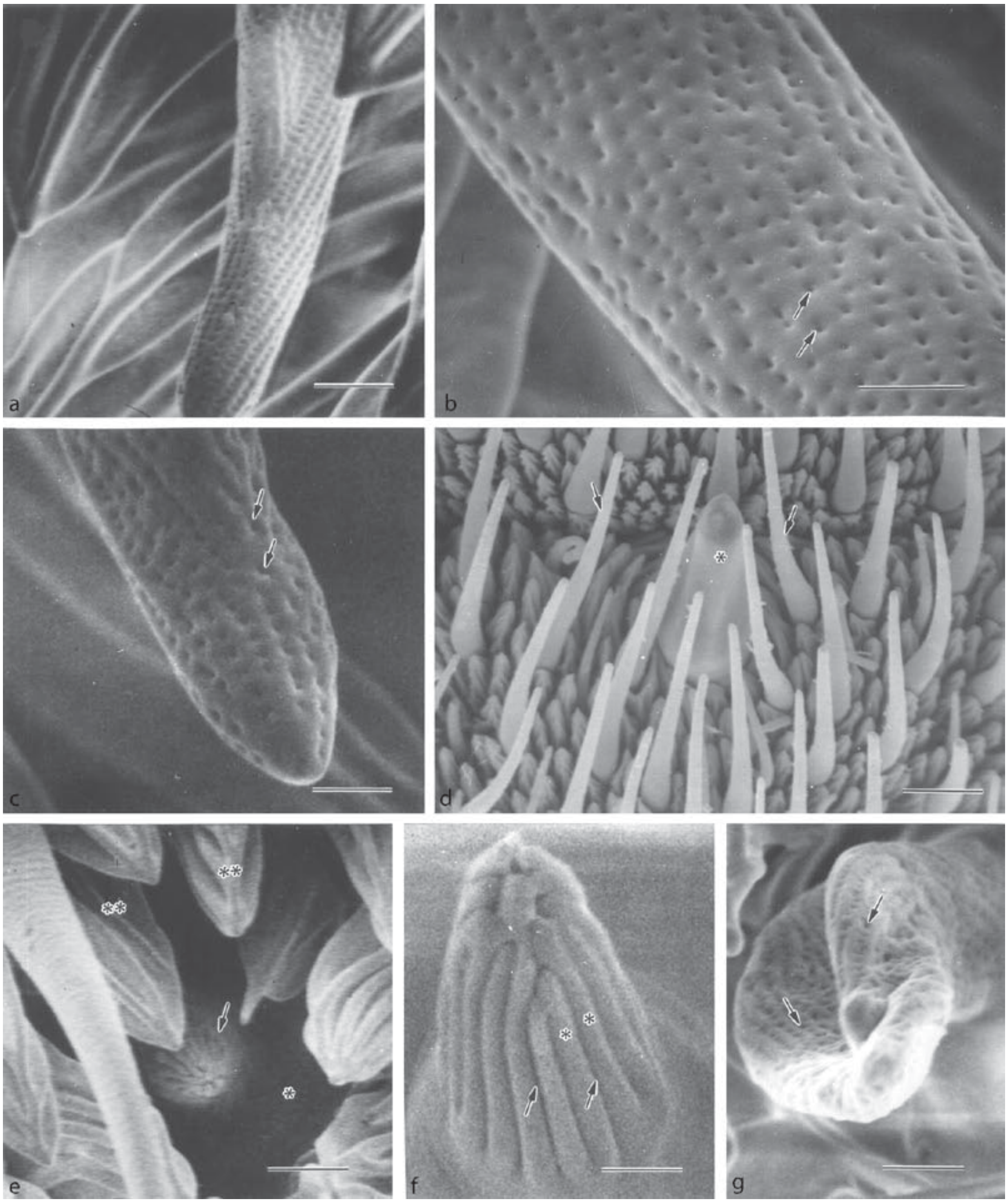
Sensilla Styloconica

These are cones, pegs, or squat hairs, inserted at the tip of a conical or cylindrical projection (style) of insensitive cuticle. They are innervated by one or a few neurons and are mechano- and/or chemosensitive.

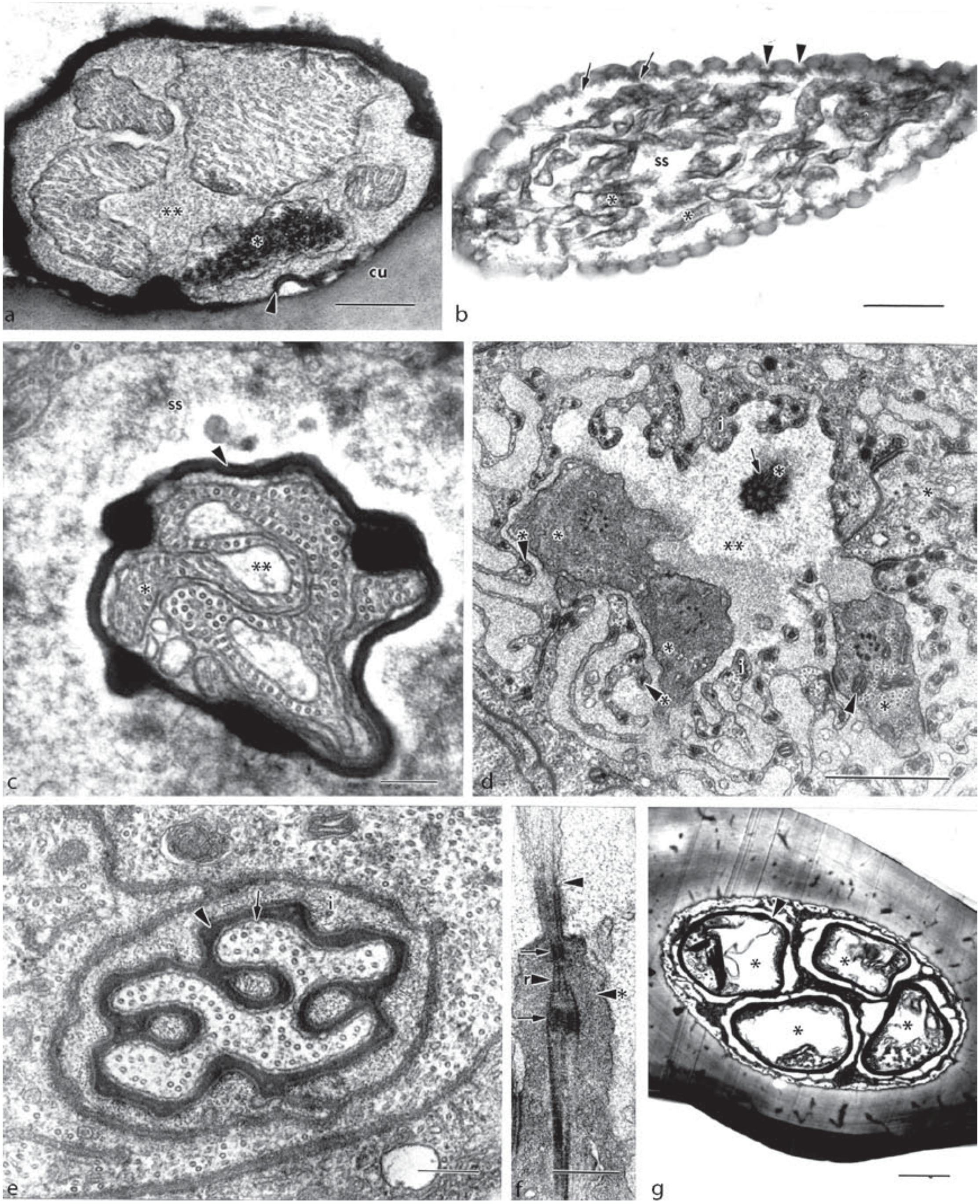
Other uniquely-shaped sensory structures have been described in insects as large conical sensory appendices, domes, knobs, partitioned plates, knobbed rods, flower-shaped domes, ear-like sensilla auricularis, clubbed hairs, and coniform or styliform complexes.

There are three main sensillar categories: AP (aporous) or NP (no-pore) sensilla, which are either mechanosensitive or hygro- and thermosensitive; UP (uniporous) or TP (terminal-pore) sensilla, containing gustatory neurons alone, or in combination with a mechanosensitive cell, and MP (multiporous) or WP (wall pore) sensilla, occurring as two main types: single-walled (SW) sensilla, with pore tubules, and double-walled (DW) sensilla, with spoke canals and the sensillar liquor as stimulus conducting systems. SW sensilla contain olfactory neurons, whereas DW sensilla contain olfactory and/or thermohygrosensitive neurons.

basiconic (arrowhead) olfactory sensilla. Scale bar = 10 μm. (e) Higher magnification of a multiporous trichoid (asterisk) and two multiporous basiconic sensilla (double asterisks) sensilla. The shaft of the trichoid sensillum bears circumferential cuticular ridges (arrows), more apparent at a higher magnification in (f). The cuticular shafts of both trichoid and basiconic sensilla bear numerous pores, more apparent at a higher magnification in (f) and (a–c). The pores of the basiconic sensillum are distributed in oblique linear rows (arrowheads) along the long axis of the sensillum. Scale bar = 1 μm. (f) Higher magnification of the middle portion of the cuticular shaft of a trichoid multiporous sensillum showing that the shaft of the sensillum bears circumferential cuticular ridges (arrows). These ridges form a helical pattern over the basal quarter of the length of the sensillum and a more circular pattern over the remaining length. The cuticular shaft is also perforated by pores (arrowheads) in cuticular depressions that are arranged in a single row along the midline of the ridges. Scale bar = 1 μm.



Ultrastructure of Insect Sensilla, Figure 3 **FESEM micrographs. (d) SEM micrograph. All figures are of *Manduca sexta* sensilla. (a) Multiporous basiconic sensillum. Scale bar = 1 µm. (b) Higher magnification of a cuticular shaft taken from the middle of a multiporous basiconic sensillum. Note the pores (arrows). Scale bar = 1 µm. (c) Higher magnification of the distal end, near the tip, of a multiporous sensillum. The pores (arrows) extend along the entire length of the sensillum. Scale bar = 0.5 µm. (d) Aporous styliform complex sensillum (asterisk) surrounded by multiporous trichoid sensilla (arrows). Scale bar = 10 µm. (e) Aporous coeloconic sensillum (arrow) lying in a deep pit (asterisk) and surrounded by microtrichia (double asterisks). Scale bar = 1.5 µm. (f) Higher magnification of coeloconic sensillum displaying numerous longitudinal ridges (asterisks). There are grooves (arrows) between the ridges. Scale bar = 0.5 µm. (g) Multiporous auriculate (spoon-shaped) sensillum endowed with numerous pores (arrows). The upper surface is deeply concavely indented. Scale bar = 1 µm.**



Ultrastructure of Insect Sensilla, Figure 4 **TEM micrographs. (a, c–f)** ***Mamestra configurata.*** **(b, g)** ***Manduca sexta*****. (a) Cross section near the base of the peg of a uniporous styloconic sensillum showing four chemosensory distal dendrites and the tubular body of the mechanosensory dendrite (asterisk). These dendrites all contain longitudinally oriented microtubules. The tubular body of the mechanosensory dendrite is composed of an accumulation of microtubules lying parallel to one another within an electron-dense matrix. The mechanosensory dendrite is closely apposed to the cuticular wall (cu) of the cone. At this level, the dendritic sheath (arrowhead) is thin on the side adjacent to the cone cuticle, prior to**

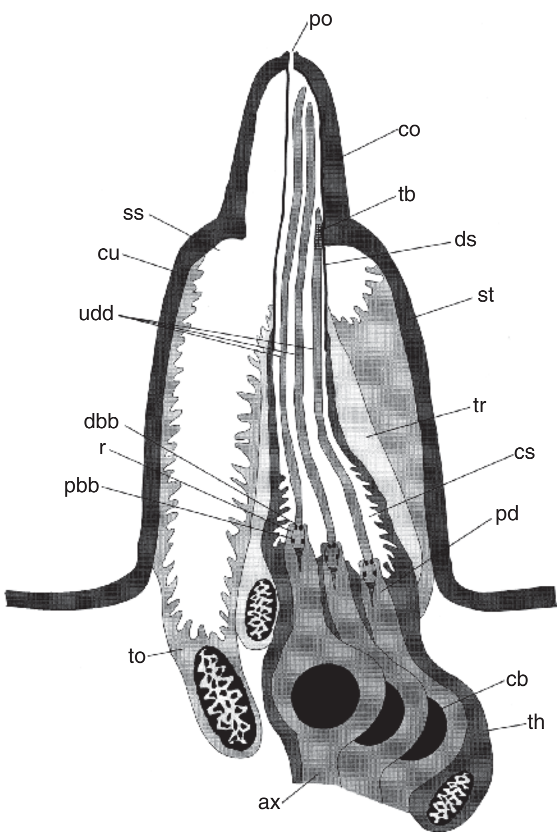
Aporous (AP) Sensilla

Mechanosensilla

AP sensilla lack a permeable pore in their sensory cuticle, but may have a typical cuticular pore canal system with pore tubules extending to the surface cuticle. During a molt, the exuvial dendritic sheath is pulled through the new cuticle at its point of cuticular insertion. When the exuvium is cast, this sheath is broken off, often resulting in a molting scar or pore. This pore can easily be misinterpreted as one that is permeable and belonging to UP sensilla.

AP sensilla are mainly mechanosensitive and are innervated by a single, unbranched neuron that is enclosed by a relatively thick dendritic sheath. The characteristic feature of these mechanosensilla is an accumulation of microtubules, called a "tubular body," usually located in the distal region of the distal dendrite. The tubular body generally consists of 50–100 tubules lying parallel to one another in an electron-dense material, although considerable variation in complexity and structure has been noted in numerous insect species. It is thought to be the site of sensory transduction.

becoming thicker, proximally. The dendrites are surrounded by the dendritic channel (double asterisk). Scale bar = 0.1 μm. (b) Multiporous auriculate sensillum. Note the numerous distal dendritic branches (asterisks) and extremely thin cuticular wall bearing numerous pores (arrowheads) and underlying pore tubules (arrows). The pore tubules, associated with each pore, extend from the base of a small circular pore kettle toward the dendrites through the surrounding sensillar sinus (ss). Some of the pore tubules appear to contact a few of the dendritic branches. Scale bar = 0.4 μm. (c) Cross section cut near the base of an aporous spire-shaped sensillum. At this level, two distal dendrites, one of which is lamellated (asterisk), are enclosed by a thick dendritic sheath (arrowhead) and surrounded by the dendritic channel (double asterisks). ss, sensillar sinus. Scale bar = 0.2 μm. (d) Cross section showing five proximal dendrites (asterisks) from a uniporous styloconic sensillum. One of the dendrites (arrow) is cut at the apex of the distal basal body of the proximal dendrite. The basal body bears a 9 × 3 + 0 microtubular configuration and nine radiating alar spokes of electron-dense material. One alar spoke arises from each of the nine triplet microtubules. At this level, the inner sheath cell (i) projects longitudinal folds with discrete complexes of microfibrils and microtubules (arrowheads with asterisks) around the proximal dendrites and encloses a ciliary sinus (double asterisks). The cytoskeletal elements are located along the inner border of the highly infolded inner sheath cell and adjacent to the ciliary sinus. Arrowhead, mitochondrion. Scale bar = 0.1 μm. (e) Cross section of a distal dendrite enclosed by a highly convoluted dendritic sheath (arrowhead) from an aporous basiconic sensillum. The microtubules within the dendrite are arranged in a single row along the periphery of the dendritic membrane (arrow). This membrane is in close apposition to the dendritic sheath. The inner sheath cell (i) enwraps the sensory neuron from its origin, near the proximal end of the dendritic sheath, to the level of the neuronal cell bodies. Scale bar = 0.2 μm. (f) Longitudinal section showing a distal dendritic segment (arrowhead) inserting into a proximal dendritic segment (arrowhead with asterisk) from a uniporous sensillum. Distal (upper arrow) and proximal (lower arrow) basal bodies are located in the distal end of the proximal dendrite. From the distal basal body, nine ciliary rootlets (r with arrowhead) extend proximally in a ring around the proximal basal body to which they attach. Scale bar = 0.5 μm. (g) Cross section showing four similar contiguous sensilla (asterisks) housed in an aporous styliform complex sensillum. Each sensillum unit is innervated by three bipolar sensory cells. Two of the distal dendrites are cylindrical and one is lamellate in shape. At this level, each of the distal dendritic bundles is individually ency a thick dendritic sheath (arrowhead). Scale bar = 1 μm.



Ultrastructure of Insect Sensilla, Figure 5
Diagrammatic reconstruction of a uniporous sensillum. This sensillum has a single pore positioned at the apex of the cone. Only three sensory cells are shown. ax, axon; cb, cell body; co, cone; cs, ciliary sinus; cu, cuticle; dbb, distal basal body; ds, dendritic sheath; pbb, proximal basal body; pd, proximal dendrite; po, pore; r, rootlets; ss, sensillar sinus; st, style; th, thecogen cell; to, tormogen cell; tb, tubular body of mechanosensitive neuron; tr, trichogen cell; udd, unbranched distal dendrites.

Thermo-Hygro Sensilla

AP sensilla may also serve a thermo-hygrosensitive function. Essential features regarded as adaptations to hygro- and thermoreception are the lack of pores; an inflexible socket; the occurrence of dendritic outer segments which fill the lumen of the peg (type 1, moist/dry receptors), or the occurrence of one or two dendritic outer segments which terminate below the peg (type 2, cold receptors or type 3, with unknown function). Typically, AP thermo-hygrosensilla are innervated by three bipolar neurons referred to as a "triad," consisting of two type-1 and one type-2 neurons.

Uniporous (UP) Sensilla

UP chemosensilla are usually termed contact chemosensitive, gustatory, or taste sensilla. Their chemosensitivity is generally predicated on contact with chemicals in solution. They are typically innervated by three to five or six unbranched distal dendrites and have one permeable apical or subapical pore, through which chemical communication between the dendrites and the external environment occurs. This pore also serves as the molting pore remaining open after the exuvial dendritic sheath is shed.

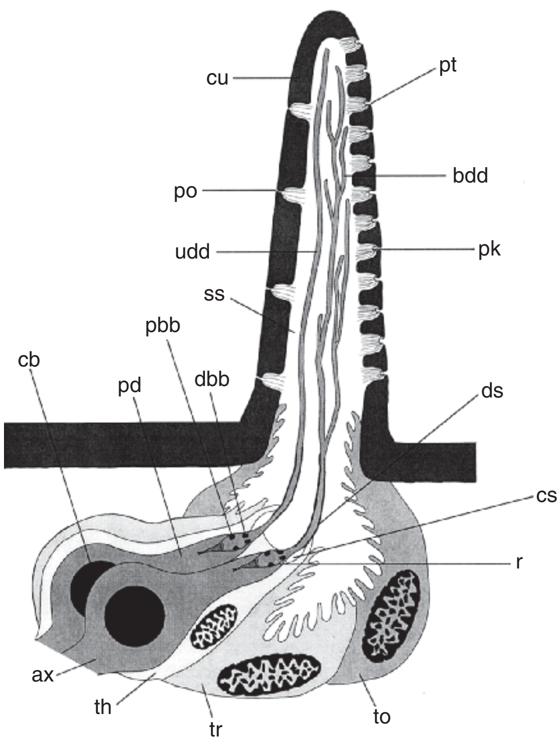
Pores of UP sensilla may have either a simple pit pore (UPP) or a sculptured porous point (UPS). The latter may vary from simple grooves leading to the pore to finger-like cuticular projections surrounding the opening. Pores vary in shape and size, ranging in diameter from 10 to 200 nm. They may contain a viscous mucoid extrusion from the dendritic channel that can cover the external opening. It is thought that this extrusion continuously fills the pore and may serve to conduct chemical stimulants within the dendritic channel to the dendrites below. Pores contain pore tubules or plugs of fenestrated fibrils of cuticular or other origin, in addition to the dendritic channel liquor. Such plugs may function by conferring selectivity to the conduction mechanism and a specificity of response to the sensillum.

Differences in the permeability of the galeal lateral and medial styloconic pegs (cones) to heavy metal ions, such as cobalt, mercury, and lead, have been shown to occur in several larval lepidopteran species, including *Mamestra configurata*, *Trichoplusia ni*, *Spodoptera frugiperda*, *Choristoneura fumiferana*, *Lymantria dispar*, and *Malacosoma lutescens*. The differences in permeability to these ion markers are of significance in interpreting the varying electrophysiological response to certain stimulants or deterrents applied to the terminal pore.

Some or all of the dendrites from UP sensory neurons extend through the dendritic channel towards the tip. Many UP sensilla contain a mechanosensitive neuron, whose dendrite terminates in a tubular body at the base of the sensory cuticle. Such sensilla are dually contact chemo- and mechanosensitive.

The dendritic sheath in UP sensilla is fused to the inner wall of sensory cuticle at the base of the pore and the liquor in the terminal dendritic channel is continuous with the liquor in the ciliary sinus. The dendritic sheath physically separates the dendritic chamber or channel from the sensillar sinus. The sheath is thought to be permeable to some small ions, but impervious to larger molecules. A permeable dendritic sheath would enable the sensillar sinus to act as a reservoir for ions, required by dendrites in producing the receptor potential and maintaining a resting potential. The dendritic channel is often appressed to the sensory cuticle along one side of the sensillum along much of its length.

In UP sensilla, pore tubules, comprising the cuticular sidewall lipoidal pore canal system, extend from the sensillar sinus through the sensory cuticle to the surface of the sensillum and selectively transport materials. The sidewall pore canal system around the terminal pore and distal portion of the dendritic sheath has been shown to be permeable to cobalt and mercury ions in some lepidopterous larvae, but not in others. The functional significance of the permeability of the sidewall pore canal system into the sensillar sinus is not known.



Ultrastructure of Insect Sensilla, Figure 6

Diagrammatic reconstruction of a multiporous sensillum showing the features of both a thick- and thin-walled sensillum in the same drawing for comparative purposes. Only two sensory cells are shown. The unbranched distal dendrite, thick cuticular wall, and pores with underlying pore tubules (left half of drawing) show features typically found in a thick-walled trichoid sensillum. The branched distal dendrite (bdd), thin cuticular wall, pore kettles, and pores with underlying pore tubules (right half of drawing) show features typically found in a thin-walled basiconic sensillum. Basiconic sensilla are typically shorter in height, have a cuticular wall that is generally thinner and pierced by a higher density of pores, have a greater number of pore tubules associated with each pore; and have many dendritic branches that fill the lumen of the sensillum, in comparison to trichoid sensilla. ax, axon; bdd, branched distal dendrite; cb, cell body; cs, ciliary sinus; cu, cuticle; dbb, distal basal body; ds, dendritic sheath; pbb, proximal basal body; pd, proximal dendrite; po, pore; pk, pore kettle; pt, pore tubule; r, rootlets; ss, sensillar sinus; th, thecogen cell; to, tormogen cell; tr, trichogen cell; udd, unbranched distal dendrite (modified from Shields and Hidebrand 1999a with permission from publisher).

Multiporous (MP) Sensilla

MP sensilla all possess an abundance of pores in their sensory cuticle. A mechanosensitive dendrite is not typically associated with these sensilla. There are two basic types of MP chemosensilla: single-walled sensilla with pore tubules and double-walled sensilla with spoke canals. MP sensilla are commonly referred to in the literature as MPP and MPG, since examination by scanning electron microscopy and TEM revealed a pitted and grooved surface, respectively.

Multiporous Pitted (MPP) Sensilla

MPP sensilla can be subdivided into two types based on thickness of the sensory cuticle and the conduction mechanism beneath the effective pore. Typically, thin- and thick-walled MPP sensilla have cuticles ~100–300 nm and 200–1000 nm, respectively. Pore density and diameter varies in thin and thick-walled sensilla, from 15–60/μm^2 to 2–20/μm^2, and 20–25 nm to 6–15 nm, respectively. The pores in both thin- and thick-walled types are funnel-shaped and flare outward from a narrowed opening just below the cuticular surface. In thin-walled MPP, each pore usually opens into a small circular chamber (pore kettle), 100–200 μm^2 in diameter, which abuts the sensillar sinus. Generally, more than 15 (sometimes as high as 50–60) pore tubules (averaging 15 nm in diameter) per pore kettle extend from its base toward the dendrites through the sensillar sinus.

Pore tubules are considered to be component parts of the sensory cuticle. The sensory pore tubule system of sensory cuticle is likely homologous with that of the pore canal and pore tubule system of the body integument. It is thought that sensory pore tubules are maintained either through the sensillar sinus or via the dendritic terminations. The cuticular pore canal system may function to transport lipoidal material from the epidermis to the surface for cuticular maintenance, in addition to the formation of a superficial lipoidal layer. This layer may act as a barrier against moisture loss through the cuticular pores and may contain proteinaceous components. It may also trap specific stimulant molecules that diffuse to the nearest pore along the pore tubules directly to a dendrite or, indirectly through the sensillar liquor.

In MPP sensilla, the dendrites emerge from the open end of the dendritic sheath, which terminates at or near the base of the sensory cuticle, into the sensillar channel. This channel is continuous with the sensillar sinus. A molting scar may be visible on the cuticular surface near the point of dendritic sheath termination.

Thin-walled MPP sensilla are typically innervated by two or three dendrites. The dendrites emerge beyond the open, distal end of the dendritic sheath and branch (about 7–150 branches). Generally, 10–12 pore tubules extend from the base of large pore kettles, which lie in close proximity to the sensillar sinus. These sensilla have a wider range of chemosensitivity than thick-walled MPP sensilla and are referred to as "generalist" sensilla.

In thick-walled MPP, the pore-kettles are reduced and cylindrical pockets often extend from the sensillar sinus toward the pore. Generally, three to eight pore tubules extend from the base of the pore funnel into the sinus either through the cuticular wall or pocket, where present. Thick-walled MPP sensilla are typically innervated by two to five unbranched neurons. These sensilla generally have a more selective range of chemosensitivity than thin-walled MPP sensilla and are referred to as "specialist" sensilla.

MPP sensilla are considered to be primarily olfactory. The transduction process is thought to involve six "steps": (i) adsorption of the molecule into a superficial lipoidal and/or proteinaceous layer at the outer surface of the sensillar wall to the nearest pore; (ii) diffusion along the pore tubules directly to the dendritic membrane or into the sensillar fluid; (iii) binding to a receptor molecule on the dendritic membrane; (iv) possible configurational change of the receptor protein; (v) resulting increase in conductance generating a receptor potential, and (vi) rapid inactivation of the odorant molecule.

Multiporous Grooved (MPG) Sensilla

MPG sensilla possess double concentric walls; the inner wall is smooth and surrounds the distal dendrites, and the outer wall is scalloped or fluted with longitudinal groves. The inner wall extends from the tip of the sensillum to near its base. The two walls are connected by cuticular spokes. Each spoke contains a radial spoke channel that is continuous with the sensillar sinus liquor. These channels, usually 20–30 nm in diameter, extend inward towards the distal dendrites. The sensillar sinus liquor bathes the dendrites. Small pores (10–20 nm in diameter) are found at the bottom of each longitudinal groove and are connected with the inside of the sensillum via the spoke channels. Material from the sensillar sinus appears to flow along the spoke channels over the grooved surface of the sensillum, presumably representing the trapping and conduction mechanism for chemical stimulant molecules.

MPG sensilla are typically innervated by two to five neurons with branched distal dendrites. In some species, the dendritic sheath may extend from near the base of the sensillum and fuse radially with the cuticle. In others, it may continue to near the ciliary region of the dendrites. The dendritic sheath is molted through an apical pore and pore tubules are absent. Wall thickness in MPG sensilla ranges from 300 to 400 nm and pore density is estimated at just over 200/μm^2. These sensilla are considered to be primarily olfactory.

Sensory Neurons

Insect sensory neurons are typically bipolar, with an enlarged perikaryon that is usually located in or below the epidermis. The dendrite extends distally from the distal pole of the cell body toward the dendritic sheath and sensory cuticle. The axon extends proximally from the perikaryon towards the central nervous system. The dendrite is abruptly constricted about midway along its length at the ciliary region (see also, below). This point demarcates the thin, distal dendritic segment from the thicker, proximal dendritic segment. The distal segment is also referred to as the ciliary segment or cilium. Typically, there is only one ciliary process per neuron.

Distal dendritic segments contain evenly dispersed longitudinal microtubules as the sole organelle. Vesicular inclusions and multivesicular bodies may also be present between the microtubules or just above the ciliary region. The distal dendritic segments are enclosed in a dendritic sheath from near their base to a variable point distally. Invaginations of the dendritic sheath produce longitudinal folds that partially or completely separate the dendrites along a portion of their length. In UP sensilla, the tip of the mechanosensitive dendrite often becomes completely separated from the other dendrites. Tight or gap junctions may also occur between the dendrites within the dendritic sheath.

The ciliary region is usually short and may be distinctly funnel-shaped, assuming a $9 \times 2 + 0$ microtubular arrangement near its point of origin. This microtubular arrangement is maintained distally in most scolopophorous and some aporous thermohygrosensilla. The ciliary region dilates into the distal dendritic segment, at its point of entry into the dendritic sheath, and the doublet microtubules separate and increase in number. Vesicular inclusions and multivesicular bodies may be present within the ciliary region.

The narrow distal dendritic segment inserts centrally into the wider tip of the thicker proximal segment. The distal and proximal, centriole-like basal bodies lie directly below the ciliary segment and are arranged in tandem. Each basal body has a $9 \times 3 + 0$ microtubular configuration. The distal basal body is located at the apex of the proximal dendritic segment, whereas the proximal basal body lies in tandem and slightly below it. The nine tubule doublets extend distally into the ciliary segment, presumably originating from the distal basal body. A circle of doublet tubules is embedded in a thin, dense "collar" or "necklace" of electron-dense material, just above the distal basal body. Rootlets with periodic cross-striations extend proximally from within the distal basal body. They pass around and attach to the proximal basal body and proceed toward the perikaryon. In scolopophorous sensilla, the rootlets are well developed and usually fuse to form a solid striated rod or ciliary root that extends toward the perikaryon. Vesicles, multivesicular bodies, and mitochondria typically surround the distal and proximal basal bodies. The vesicular contents are presumably used in the development and maintenance of the sensillar cuticular components. The cytoplasm of the proximal dendrite and perikaryon contains an abundance of rough and smooth endoplasmic reticulum, longitudinal microtubules, vesicles, Golgi bodies, free ribosomes, and mitochondria. The nuclei of the neuronal cells bodies are typically large, rounded, centrally located, and contain finely dispersed chromatin, indicative of high metabolic activity.

Axons from the sensory cells project to the CNS. The axons merge along common tracts to form nerves. Typical organelles found in the axon are mitochondria and evenly distributed longitudinal microtubules. Several wraps of glial cells individually enwrap the basal portions of each of the neuronal cell bodies and axons, typically inserting under the wrap of the inner sheath cell. In larger nerves, collections of axons are enclosed by a perineurial cell layer, which is further enclosed by a basement membrane in the hemocoel.

Sheath Cells

Accessory or sheath cells are specialized epidermal cells that envelop the neurons of insect chemosensilla. Typically, there are four sheath cells: a thecogen (inner), trichogen (intermediate), tormogen (outer), and a basal or glial cell. The inner, intermediate, and outer sheath cells enwrap the dendrites and the distal part of the nerve cell body. A basal glial cell enwraps the basal part of the cell bodies and axons. The number of sheath cells varies from 2 to 4 depending on the sensillar type. Each sheath cell forms at least one complete wrap around the neuron along most of its length and often overlaps.

The inner sheath cell typically wraps once around the sensory neuron(s), from the base of the dendritic sheath to some part of the cell body. The proximal dendrite and perikaryon of each sensory neuron are each individually wrapped by the inner sheath cell. This sheath cell usually terminates to one side of the neuronal perikaryon in an expansion containing its nucleus. The dendritic sheath is secreted by the inner sheath cell. The inner sheath cell may also be involved in the formation of the sensory cuticle if only two sheath cells are present in the sensillum.

In the ciliary region, the inner sheath cell encloses a small, ciliary sinus and also extends small microvilli into it. Microvillation indicates a possible secretory activity. The dendritic sheath and inner sheath cell form a continuous tube enclosing the contents of the ciliary sinus. A sinus liquor (fluid secreted into the ciliary sinus by the inner sheath cell) bathes the proximal and distal ends of the distal and proximal dendritic segments, respectively. This liquor is usually finely granular and electron-lucent. It is thought to contain nutrients secreted by the inner sheath cell.

The inner sheath cell also forms well-developed longitudinal desmosomal junctions with the distal termination of the proximal dendritic segments. Bundles of longitudinally-oriented microtubules and microfibrils, located along the inner border of the inner sheath cell, are associated with these junctions. The microfibrils are about 6 nm in diameter and resemble actin fibers. The microtubule and actin cytoskeletal elements may provide cellular rigidity and serve as mechanically stabilizing elements, respectively. The dendrites presumably grow through the inner sheath cell during development.

Both intermediate and outer sheath cells are very similar to each other in structure and function. The intermediate sheath cell enwraps the inner sheath cell along most of its length. The intermediate sheath cell also lines part of the sensillar sinus and extends microvilli, from its outer surface, into this sinus. This cell may secrete the sensory cuticle. The outer sheath cell envelops the intermediate sheath cell, from near the neuronal cell body to the sensory cuticle. This cell is thought to secrete the base or socket of the seta. The outer sheath cell encloses the sensillar sinus and similarly, extends microvilli from its outer surface into this sinus. Both intermediate and outer sheath cells presumably sequester nutrients from the underlying hemolymph and actively transport and secrete them into the sensillar sinus.

Since the dendritic sheath is thought to be selectively permeable to ions, the sensillar sinus, located adjacent to the dendritic channel, may function as an ion reservoir to replenish ions lost during dendritic activity. The intermediate and outer sheath cells are also thought to maintain a chemical environment appropriate for the stimulus conduction and transduction processes of the dendrites. These cells may be involved in cuticular maintenance and the provision of nutrients for the inner sheath cell. The sensillar sinus is usually larger than the ciliary sinus, however, its size is variable depending upon the type of sensillum. Similar to the inner sheath cell, the intermediate and outer sheath cells successively draw to one side near the level of the neuronal cell bodies and each terminates in an expansion containing the nucleus. The proximal extremities of the intermediate and outer sheath cells usually terminate in close proximity to the hemocoel, from which they are separated by a basement membrane. The inner, intermediate, and outer sheath cells are all rich in mitochondria, vesicles, multivesicular bodies, rough endoplasmic reticulum, free ribosomes, longitudinal microtubules, and Golgi bodies.

The glial sheath cell individually enwraps the basal portions of each of the neuronal cell bodies, always inserting under the wrap of the inner sheath cell. The glial cell also individually enwraps the axons. The cell body of the glial cell is small, as is its nucleus. Within its nucleus, the chromatin is condensed into large granules. The cytoplasm contains abundant rough endoplasmic reticulum and few mitochondria. A cytoplasmic layer of either the inner or glial sheath cell, proximally, separates all parts of every neuron from one another, from the base of the cilium. The axons within the nerve are individually enwrapped by the glial cells. The axon presumably grows through the glial cell in development.

► Taste and Contact Chemoreception

References

Altner H (1977) Insect sensillum specificity and structure: an approach to a new typology. In: Magnen J, MacLeod P (eds) Olfaction and taste IV (Paris). Information Retrieval, London, UK, pp. 295–303

Altner H, Prillinger L (1980) Ultrastructure of invertebrate chemo-, thermo-, and hygroreceptors and its functional significance. Int Rev Cytol 67:69–139

McIver SB (1985) Mechanoreception. In: Kerkut GA, Gilbert LI (eds) Comprehensive insect physiology, biochemistry and pharmacology, vol 6. Pergamon, Oxford, UK, pp 71–132

Schneider D (1964) Insect antennae. Annu Rev Entomol 9:103–122

Shields VDC (1994) Ultrastructure of the uniporous sensilla on the galea of larval *Mamestra configurata* (Walker) (Lepidoptera: Noctuidae). Can J Zool 72:2016–2031

Shields VDC (1994) Ultrastructure of the aporous sensilla on the galea of larval *Mamestra configurata* (Walker) (Lepidoptera: Noctuidae). Can J Zool 72:2032–2054

Shields VDC (1996) Comparative external ultrastructure and diffusion pathways in styloconic sensilla on the maxillary galea of larval *Mamestra configurata* (Walker) (Lepidoptera: Noctuidae) and five other species. J Morphol 228:89–105

Shields VDC, Hildebrand JG (1999) Fine structure of antennal sensilla of the female sphinx moth *Manduca sexta* (Lepidoptera: Sphingidae). I. Trichoid and basiconic sensilla. Can J Zool 77:290–301

Shields VDC, Hildebrand JG (1999) Fine structure of antennal sensilla of the female sphinx moth *Manduca sexta* (Lepidoptera: Sphingidae). II. Auriculate, coeloconic, and styliform complex sensilla. Can J Zool 77:302–313

Slifer EH (1970) The structure of arthropod chemoreceptors. Annu Rev Entomol 15:121–142

Zacharuk RY (1985) Antennae and sensilla. In: Kerkut GA, Gilbert LI (eds) Comprehensive insect physiology, biochemistry and pharmacology, vol 6. Pergamon, Oxford, UK, pp 1–69

Zacharuk RY, Shields VD (1991) Sensilla of immature insects. Annu Rev Entomol 36:331–354

Unapparent Resources

Food resources (either insect or plant) that are "hard to locate" or unapparent to potential predators or herbivores. Unapparent resources often are protected against consumption by generalist predators or herbivores by possessing a toxin that deters consumption (contrast with apparent resources).

Underwing Moths – The Genus *Catocala* (Lepidoptera: Noctuidae)

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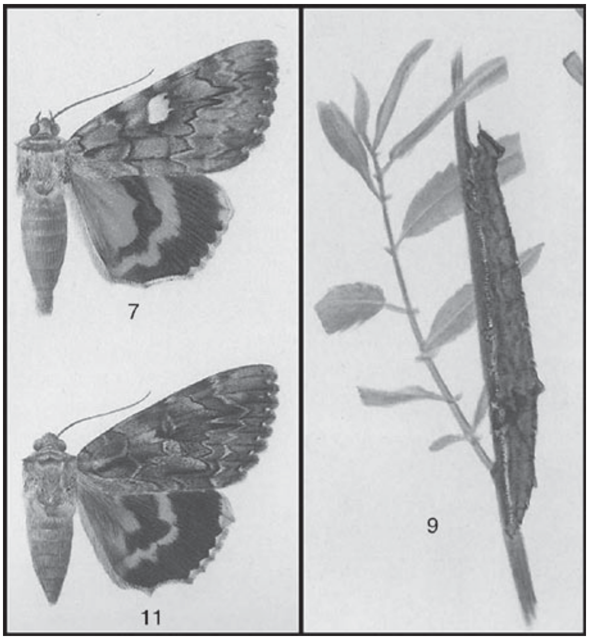
The genus *Catocala* Schrank (Fig. 7) is a speciose group of colorful and large moths in the family Noctuidae. The adults range from 4 to nearly 14 cm in wingspan. *Catocala* are commonly known as "underwings," in reference to the contrast between their drab, bark-colored forewings and their racily patterned hindwings, which are usually jet black with prominent yellow, orange, or red bands, and white fringes.



Underwing Moths – The Genus *Catocala* (Lepidoptera: Noctuidae), Figure 7 Details of adult and larval Catocala species, from Plates VI and XIII, in the monograph of North American species in the genus published by Barnes & McDunnough (1918).

Distribution

On a worldwide basis, *Catocala* is the second most speciose genus in the Noctuidae, exceeded in number of species only by cutworm moths in the genus *Euxoa* Hübner. *Catocala* occur throughout the northern hemisphere, though most frequently in deciduous forests, and the slightly more than 200 described species are split nearly evenly between the Nearctic and Palearctic regions. The *Catocala* faunas of the eastern and southern United States are among the most diverse, with 40–50 species occurring sympatrically in many areas. Interestingly, in contrast to most other Holarctic noctuid genera, there is no single species of *Catocala* whose geographic range includes both the Nearctic and Palearctic.

Phylogeny

Catocala contains several monophyletic species groups, comprising species with similar larval foodplant use. However, the relationships among these groups and of *Catocala* to other catocaline noctuids remain unclear, mirroring the incomplete understanding of phyletic relationships within the expansive subfamily as a whole. The species-level taxonomy of the Nearctic taxa has been examined in detail, but the corresponding Palearctic literature is less comprehensive, and no monographic treatment of the world fauna has been published. Most *Catocala* species were described during the nineteenth century, and the early workers in the genus, who were male, followed a tradition of coining specific epithets reflecting themes of romance, sorrow, and/or notable women. Thus, for example, *Catocala amatrix* Hübner (sweetheart), *C. lacrymosa* Guenee (tearful), *C. insolabilis* Guenée (inconsolable), *C. titania* Dodge and *C. cordelia* Hy. Edwards (from Shakespeare).

Biology

All species of *Catocala* whose life histories are known are single brooded. The adults are nocturnal and on the wing in mid to late summer in most localities. When at rest during the daytime on tree trunks and branches, adult *Catocala* conceal their brightly colored hindwings under the forewings, and are highly cryptic. However, adult *Catocala* are also wary when at rest, and will fly off suddenly and rapidly if disturbed. They usually settle again instantly upon reaching another perch, often vanishing from plain view. *Catocala* species have characteristic escape flights and resting habits: for example, some species circle the trunk and land again on the same tree, whereas others invariably fly to another tree. In studies with avian predators, the hindwings of *Catocala* have been shown to serve both as an initial startle mechanism and as a subsequent deflective device that focuses attacks away from the body. Many patterns of lepidopteran wing damage have been categorized quantitatively using *Catocala* as test subjects, and particular damage patterns have been correlated with behavioral responses on the part of predators. Field-collected *Catocala* regularly bear such wing damage patterns that can be traced to attacks by birds, bats and lizards.

Winter diapause in *Catocala* takes place in the egg stage. The eggs are laid singly or in rows or clumps on the larval foodplants. The eggs of most species are strongly dorsolaterally flattened, and the female moths have elongate, modified ovipositors which they use to secrete the eggs under exfoliating bark, or in crevices on branches and tree trunks. The larvae of most species hatch in spring and commence feeding on young foliage in April and May. Considering the genus as a whole, hatching from individual egg clutches varies from synchronous (2–3 days) to staggered (7–8 weeks), but each *Catocala* species exhibits a characteristic spread in its egg hatch that mirrors the foliating schedule of its larval foodplants.

Catocala larvae are active, semi-loopers that feed nocturnally. Most have cryptic bark-like coloration and morphologies, especially in the later instars. Mature larvae often have variously developed projections on the dorsal surface of the fifth abdominal segment that closely match leaf scars, buds, or broken branch tips; as well as a dense row of fine, sublateral filaments that are pressed against the substrate. Both of these characteristics break up the outline of the resting larva and enhance its crypsis. The young larvae rest preferentially on the midribs of leaves and on petioles, and shift to resting on branches and tree trunks as they mature. Most *Catocala* species pass through five larval instars, with some species having six or seven instars. Larval development is usually completed within 5–7 weeks of egg hatch. Pupation occurs in a loose silken cocoon of leaf litter and debris, with adults hatching in 3–4 weeks.

Unlike most other noctuid genera, the high species diversity in *Catocala* is coupled to a quite limited larval foodplant diet. In total, the genus is known to use only nine dicotyledonous families as larval hosts. However, even that liberally estimates foodplant breadth, because the overwhelming majority of *Catocala* species feed on plants in the families Fagacaeae, Salicaceae, Rosaceae, and Juglandaceae. No *Catocala* species is known to feed on plants from more than one of these plant families, and the foodplants of a given *Catocala* species are normally limited to one or more closely related plant genera. *Catocala* that use Fagacaeae, Salicaceae, and Rosaceae are found throughout the northern hemisphere, but Juglandaceae-feeding is essentially limited to North America, to a complex of two dozen closely related species apparently representing a single phyletic radiation. Although the larvae of many *Catocala* species can be collected commonly, the genus is not known to cause significant economic effect (at least in North America; possible exceptions include *C. maestosa Hulst* and *C. agrippina* Strecker, which sometimes occur in high density on pecan trees).

Collection

Because of their size and beauty, *Catocala* moths have been favorites with collectors for centuries. The adults are readily captured at both mercury vapor and ultraviolet light traps, and many species can be attracted to artificial bait sources. The term "sugaring" for moths refers to collecting using sweetened artificial bait, and *Catocala* have always figured prominently in the sugaring lore (the technique also goes by many other synonyms, such as "wine roping"). A functional artificial bait mixture requires a source of sugar as well as alcohol, but the lepidopterological literature is richly punctuated with collectors' idiosyncratic additions to lure *Catocala* and other prizes, like treacle, pureed banana, and expensive Barbados rum. Sugaring is a notoriously fickle and as yet poorly quantified collecting technique, producing divergent results in certain geographic regions, at some seasons, and under particular climatic conditions; sultry and unsettled weather immediately preceding electrical storms generally seems to be the most productive. Another time-honored, and sporting, collecting method that focuses specifically on *Catocala* is "tree tapping," in which one attempts to locate and creep up on adults without startling them as they rest during the day on tree trunks and branches.

References

Barnes W, McDunnough J (1918) Illustrations of the North American species of the genus *Catocala*. Mem Am Mus Nat Hist 3:1–47

Gall LF (1991) Evolutionary ecology of sympatric *Catocala* moths (Lepidoptera: Noctuidae). I. Experiments on larval foodplant specificity. J Res Lepidoptera 29:173–194

Gall LF, Hawks DC (2002) Systematics of moths in the genus *Catocala* (Noctuidae). III. The types of William H Edwards, Augustus R Grote, and Achille Guenée. J Lepidopterists' Soc 56:234–264

Grote AR (1872) On the North American species of *Catocala*. Trans Am Entomol Soc 4:1–20

Mitter C, Silverfine E (1988) On the systematic position of *Catocala* Schrank (Lepidoptera: Noctuidae). Syst Entomol 13:67–84

Sargent TD (1976) Legion of night: the underwing moths. University of Massachusetts Press, Amherst, MA, 222 pp

Ungulate Lice

Members of the family Haematopinidae (order Phthiraptera).

► Chewing and Sucking Lice

Unique-Headed Bugs

Members of the family Enicocephalidae (order Hemiptera).

► Bugs

Unit of Habitat Sampling

An absolute sampling technique wherein the sampling unit is the habitat inhabited by the insect (e.g., apple fruit for apple maggot, ear of corn for corn earworm).

Univoltine

Having a single generation (life cycle) per year.

Uraniidae

A family of moths (order Lepidoptera). They commonly are known as swallowtail moths.

► Swallowtail Moths
► Butterflies and Moths

Urban Entomology

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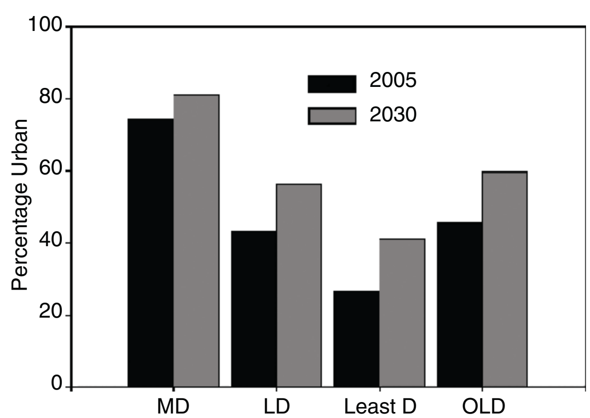
Insects and related arthropods of importance in the urban environment are broadly covered under the auspices of urban entomology. Most arthropods in human environments go unnoticed. However, some species pose significant problems because they directly affect the health of humans or their domesticated animals, attack human structures, foods, goods, materials, or plants that adorn urban settings.

A relatively small number of insect species have been intentionally introduced into the urban environment. Examples include the gypsy moth, *Lymantria dispar*, that was intentionally introduced into Massachusetts in 1868. It is highly probable also that the Asian lady beetle, *Harmonia axyridis*, was intentionally introduced in the 1980s. Many pest species have been accidentally introduced with human commerce and travel. Some invasive species have adapted themselves to disturbed human habitats and have rapidly spread worldwide via commerce and human travel. The German cockroach, *Blattella germanica*, is an excellent example of such a species. It is rarely found outdoors, preferring heated and controlled environments typically associated with human food preparation. Probably native to eastern Asia, it spread throughout the eastern Mediterranean region by Greek or Phoenician vessels. It remained in southern Russia until after the Thirty Years War (1618–1648) spreading into Europe and finally becoming established in England in the mid 1800s. It is now cosmopolitan. Interestingly, it is even becoming established in restaurants and other food handling establishments in the rapid modernization of China.

With the increasing rate of global urbanization, problems associated with arthropod pests in urban centers will continue to grow. In 1950, about 731 million people (29.0%) lived in urban areas. At the turn of the twenty-first century, this had increased to greater than 2.8 billion people (46.7%). By the year 2030, it is estimated that there will be greater than 4.9 billion people (59.9%) living in urban areas. The most dramatic increases in urbanization and challenges will occur in developing countries (Fig. 8). As these countries attain greater development, the complex of urban invasive species will likely spread to these urban centers, or attain the problem status now associated with more developed countries. Many of these countries and developing urban centers exist in areas endemic to arthropod vector borne diseases such as malaria, dengue, encephalitis, yellow fever, and plague. The importance of urban and medical entomology in tropical urban centers will increase in the future.

The urban environment can be separated into those plant and animal communities that surround dwellings and buildings and reside within the domestic environment of structures. Plant communities of urban settings can be categorized



Urban Entomology, Figure 8 **Anticipated changes in urbanization from 2005 to 2030 in various countries throughout the world: MD – more developed countries include Europe, Northern America, Australia/New Zealand and Japan; LD – less developed countries include all regions of Africa, Asia, Latin America and the Caribbean, Melanesia, Micronesia and Polynesia; Least D – least developed are defined by 34 countries in Africa, 10 in Asia, 1 in Latin America; OLD – other less developed countries (http://esa.un.org/unup).**

as areas with remnant native plants, disturbed lands populated by volunteer plants, and actively cultivated landscapes. For example, it is estimated that there are some 300 million trees in the United States. In addition, the ornamental and nursery industry continues to grow; in the United States, the estimated value of the nursery and ornamental industry was $13.4 billion in 2001. Consequently, urbanization can result in more species-diverse landscapes, however, it is typically at the expense of native plants. This may be especially true along the urban-rural interfaces, and certainly increases the likelihood of problems with invasive insect pests.

In urban animal communities, the percentage of urban specialists such as the German cockroach or house fly dramatically increases as the overall species diversity decreases. Within human dwellings, the degree to which structures are sealed and indoor environments are maintained greatly affects the diversity of insects and arthropods. Highly regulated indoor environments favor species such as the German cockroach, Indian meal moth, cat flea, flour beetles, dermestid beetles, and Pharaoh ant. Because modified indoor habitats are similar in urban centers throughout the world, these pests are readily establish in developing urban centers. The list of indoor pests in Singapore, Tokyo, Los Angeles, New York City, London, Paris, and New Delhi are remarkably similar.

Insects, arthropods, and plants can be categorized into three broad groups in regard to urbanization (see Table 1). First, "Urban Avoiders" are species that are sensitive to human disturbances, including those species adapted to old growth forests, wetlands, and grasslands. These species are displaced in the course of urbanization. Second, the "Urban Adapters" are those species that are able to survive in human disturbed environments, as well as native environments. For example, many of the wood-destroying pests such as termites are native to the region and exploit both naturally occurring wood sources and human structures. Many of the species found in urban settings belong to this group, especially the native herbivorous species found along the urban-rural interface. Finally, the "Urban Exploiters" are commensal species that are dependent on human activities. Many of the grasses, weeds, and ornamentals in urban environments are, in fact, considered to be Urban Exploiters. Consequently, the turfgrass pests such as sod webworms and chinch bugs, or ornamental plant pests such as Japanese beetle, are also considered to be exploiters. This distinction may change in different geographical regions. For example, the American cockroach, *Periplaneta americana*, lives outdoors around structures in subtropical areas such as Florida and Hawaii and is clearly an Urban Adapter. However, in more desert, semi-arid areas of Arizona and California, it is an Urban Exploiter, being restricted to sewers, greenhouses, and animal rearing facilities. Similarly, the German yellowjacket in the western United States exploits urban dwellings, however, it is widely adapted to rural habitats in Chile. Other species, such as the German cockroach, brownbanded cockroach, and cat flea, are only found inside structures throughout most of their current range.

In the process of urbanization, the diversity of native plants and animals can be dramatically altered. In core urban areas, 80% of the land may be covered with pavement or buildings. Studies of rural-to-urban gradients suggest that the species richness of butterflies, herbivorous insects, ants, and other native species decreases towards the urban centers. The number of Urban Exploiters typically increases towards the center. The urban climate and increased temperatures can result in increased floral diversity. The species richness and diversity of butterflies may even peak at moderately disturbed sites. Some species such as aphids, leafminers, cockroaches, and flies can successfully colonize even in urban centers. However, urbanization can lead to a loss of specialists such as parasitoids, leaving certain herbivorous species in abundance.

The impact of many of the urban adapters and exploiters necessitates their control in urban settings. An increased awareness of the urban community over the last 10 years of the potential harm of insecticides and herbicides has resulted in

Urban Entomology, Table 1 List of some of the most important species that are Urban Adapters and Urban Exploiters of the urban environment. The list excludes those arthropods of medical and veterinary importance

	Order	Family	Common names[a] (genus species)
Urban adapters[b]			
	Araneae	Sicariidae	Brown recluse spider (*Loxosceles reclusa*)
		Theridiidae	Black widow spider (*Latrodectus mactans*)
	Blattaria	Blattidae	Oriental cockroach (*Blatta orientalis*), Turkestan cockroach (*B. lateralis*), American cockroach (*Periplaneta americana*), smokybrown cockroach (*P. fuliginosa)*
	Isoptera	Rhinotermitidae	*Reticulitermes* spp., *Coptotermes* spp., *Heterotermes* spp.
		Kalotermitidae	*Incisitermes* spp.
	Orthoptera	Gryllotalpidae	Mole crickets (*Scapteriscus* spp.)
	Dermaptera	Forficulidae	European earwig (*Forficula auricularia*)
		Labiduridae	Striped earwig (*Labidura riparia*)
	Diptera	Culicidae	Yellowfever mosquito (*Aedes aegypt*), *Culex tarsalis,* northern house mosquito (*Culex pipens*), southern house mosquito (*C. quinquefasciatus*)
		Muscidae	House fly (*Musca domestica*), little house fly (*Fannia canicularis*)
	Hemiptera	Aphididae	Spruce aphid *(Elatobium abietinum)*, green peach aphid *(Myzus persicae)*, greenbug *(Schizaphis graminum)*
		Lygaeidae	Chinch bugs (*Blissus* spp.)
		Tingidae	Sycamore lace bug (*Corythucha ciliate*)
	Coleoptera	Anobiidae	*Hemicoelus carinatus, Hemicoelus gibbicollis*
		Bostrichidae	*Socobicia declivis, Xlyobiops basilariu, Polycaon stoutii*
		Cerambycidae	Eucalyptus longhorned borer (*Phoracantha semi-punctata*), *Altica quercetorum, Agelastica alni,* emerald ash borer (*Agrilus planipennis*), Asian long-horned beetle (*Anoplophora glabripennis*), *Pyrrhalta viburni*
		Dermestidae	Furniture carpet (*Anthrenus flavipes*), varied carpet beetle (*Anthrenus verbasci*), black carpet beetle *(Attagenus unicolor*)
		Lyctidae	Southern lyctus beetle (*Lyctus planicollis*)
	Hymenoptera	Formicidae	*Camponotus* spp., red imported fire ant (*Solenopsis invicta*), crazy ant (*Paratrechina longicornis*), *Myr-mica rubra*
		Vespidae	German yellowjacket *(Vespula germanica)*, *Polistes* spp.
	Lepidoptera	Lymantriidae	*Orgyia* spp., gypsy moth (*Lymantria dispar*), brown-tail moth (*Euproctis chrysorrhoea*)

Urban Entomology, Table 1 List of some of the most important species that are Urban Adapters and Urban Exploiters of the urban environment. The list excludes those arthropods of medical and veterinary importance (Continued)

	Order	Family	Common names[a] (genus species)
		Gracillariidae	*Cameraria ohridella*
		Geometridae	winter moth (*Operophtera brumata*)
		Tortricidae	*Tortrix viridana*
Urban exploiters[c]			
	Blattaria	Blatellidae	German cockroach (*Blattella germanica*), brown-banded cockroach (*Supella longipalpa*)
	Diptera	Culicidae	Yellowfever mosquito (*Aedes aegypti*)
	Thysanura	Lepismatidae	Silverfish (*Lepisma saccharina*), firebrat (*Thermobia domestica*)
	Hemiptera	Pseudococcidae	*Maconellicoccus hirsutus*
	Isoptera	Kalotermitidae	*Cryptotermes brevis*
	Coleoptera	Anobiidae	Furniture beetle (*Anobium punctatum*), *Xestobium rufovillosum*, cigarette beetle (*Lasioderma serricorne*), drugstore beetle (*Stegobium paniceum*)
		Cerambycidae	Old house borer (*Hylotrupes bajulus*)
		Chrysomelidae	Elm leaf beetle (*Xanthogaleruca luteola*), viburnum leaf beetle (*Pyrrhalta viburni*)
		Dermestidae	*Trogoderma* spp.
		Scarabaeidae	Japanese beetle (*Popillia japonica*), Asiatic garden beetle (*Maladera castanea*), European chafer (*Rhizotrogus majalis*), oriental beetle (*Exomala orientalis*)
	Hymenoptera	Formicidae	Pharaoh ant (*Monomorium pharaonis*), Argentine ant (*Linepithema humile*)
		Vespidae	German yellowjacket (*Vespula germanica*)
	Lepidoptera	Pyralidae	Sod webworms, indianmeal moth (*Plodia interpunctella*)
		Tineidae	Casemaking clothes moth (*Tinea pellionella*), webbing clothes moth (*Tineola bisselliella*)
		Lymantriidae	Gypsy moth (*Lymantria dispar*)

[a]Common names adopted from the Entomological Society of America "Common names of insects & related organisms"
[b]Urban adapters are species that occur in broad human land uses found in suburban landscapes. Many so-called edge species, which are adapted to the forest edge and open areas, live here. These species exploit both foods derived from human activity as well as naturally occurring foods
[c]Urban exploiters or synanthropes are dependent on human activity. Urban cities often have more in common with other urban centers than the surrounding environment. Consequently, these are often invasive and exotic species

a growing effort to incorporate Integrated Pest Management (IPM) in urban environments. For these efforts to be successful, education and outreach programs within the urban community are essential. Unlike the agricultural community, the urban community has not been actively involved in IPM processes. Baits have been extremely successful in controlling cockroaches, subterranean termites and certain species of ants. Biological control efforts have been successful in controlling a variety of ornamental pests, such as the ash whitefly, the winter moth *Operophtera brumata*, acacia psyllid, and eucalyptus borer.

► School IPM
► Cockroaches
► Ants
► Human Lice
► Bed Bugs

References

Blair RB, Launer AE (1997) Butterfly diversity and human land use: species assemblages along an urban gradient. Biol Conserv 80:113–125

Denys C, Schmidt H (1998) Insect communities on experimental mugwort (*Artemisia vulgaris* L.) plots along an urban gradient. Oecologia 113:269–277

Dreistadt SH, Dahlsten DL, Frankie GW (1990) Urban forests and insect ecology. Bioscience 40:192–198

Ebeling W (1975) Urban entomology. University of California Press, Berkeley, CA, 695 pp

Fitzgerald F (2003) Plant and animal communities in urban green spaces. Design Center for American Urban Landscape, Design Brief 5, 13 pp

McIntyre NE (2000) Ecology of urban arthropods: a review and a call to action. Ann Entomol Soc Am 93:825–835

McKinney ML (2002) Urbanization, biodiversity, and conservation. BioScience 52:883–890

Robinson WH (1996) Urban entomology: insects and mite pests in the urban environment. Chapman & Hall, London, UK, 448 pp

Uric Acid

The principal form of waste product elimination by insects. Uric acid, a purine, is synthesized by fat bodies from protein nitrogen and nucleic acid nitrogen. It is excreted from the Malpighian tubules. Though uric acid is energetically costly to produce, it is very conservative of water, and so aids greatly in water conservation.

Urodidae

A family of moths (order Lepidoptera). They commonly are known as false burnet moths.

► False Burnet Moths
► Butterflies and Moths

Urogenital Myiasis

Invasion of the urinary tract or bladder by fly larvae, resulting in bleeding, pain, and frequent urination. The insects associated with this ailment include latrine fly, *Fannia scalaris* (Fabricius) (Fanniidae); false stable fly, *Muscina stabulans* (Fallen) (Muscidae); house fly, *Musca domestica* L. (Muscidae); and lesser house fly, *Fannia canicularis* (L.) (Fanniidae).

► Myiasis

Urogomphus (pl., urogomphi)

Paired processes located dorsally on the ninth abdominal segment.

Urostylidae

A family of bugs (order Hemiptera, suborder Pentamorpha).

► Bugs

Urticaria

Itchy, and often elevated or discolored spots on the skin; wheals or hives.

Urticating Hairs

Hairs that cause a stinging or burning sensation in humans or other animals upon contact because they contain poison glands, or simply because the barbed hairs are irritating.

Usinger, Robert Leslie

Robert Usinger was born at Ft. Bragg, California, USA, on October 24, 1912. He attended the University of California-Berkeley where he received both his B.S. in 1935 and his Ph.D. in 1939. At that time he accepted a faculty position at University of California-Davis, where he worked until World War II. Following military service, he transferred to Berkeley, where he taught and conducted research. Usinger was a systematist, with expertise in Hemiptera. He traveled the world in pursuit of insects. He published several important books and monographs on systematics and Hemiptera, including "Methods and principles of systematic zoology" (with Mayr and Linsley, 1953), "Aquatic insects of California" (1956), "General zoology" (with Storer, 1965), and "Monograph of the Cimicidae" (1966). He was an active member of the International Commission on Zoological Nomenclature, and the Entomological Society of America, including service as president of the latter organization. Usinger died prematurely on October 1, 1968, in San Francisco.

Reference

Linsley EG, Smith RF (1969) Robert Leslie Usinger 1912–1968. Ann Entomol Soc Am 62:1218–1219

Uvarov, (SIR) Boris Petrovich

Boris Uvarov was born on November 5, 1888, in Ural'sk Province, Russia. He was interested in insects from an early age, and attended Petersburg (Leningrad) University from 1906 to 1910. He studied Orthoptera, and was already publishing on the importance of habitats as early as 1910 (though this was not his first paper, having already published three botanical papers). After graduating, Uvarov immediately obtained an appointment as an entomologist in southern Russia in a cotton-growing district, where he had the opportunity to work on biology and control of migratory locust and Moroccan locust. In 1915 he transferred to another office that had responsibility for Georgia and Armenia. He also lectured at Tbilisi University, and published numerous papers on local grasshoppers/locusts. This was an important period in Uvarov's formation of phase theory, in that he gained an appreciation of the importance of local conditions in insect biology. With the collapse of the Russian Empire, Uvarov relocated to London, where he worked for the Imperial Bureau of Entomology. Here he published "Locusts and grasshoppers" in English (1928), as well as taxonomic work and important reviews on nutrition and climate. Here he also began to publish profound insight into locust phases and polymorphism, and the importance of solitary versus gregarious mode of life. This was an entirely unprecedented insight into insect biology, a variation that is matched only by sociality in terms of behavior, and equivalent to climate and parasitism in terms of importance in population regulation. In England, Uvarov implemented data collection that produced important information on several locusts, including range of several species and the important concept of locust management by preventing the locusts from reaching the gregarious stage. Starting in 1945 Uvarov and a small team of acridologists received official designation as the "Anti-locust Research Centre" and conducted important studies on African and Asian locusts until his official retirement in 1959. This did not stop his entomological contributions, however, and he then published "Grasshoppers and locusts" Volume 1 in 1966, and Volume II in

1977. Uvarov's contributions totaled over 400 publications; about half were taxonomic and about half were population biology and suppression. His insight into phase biology serves as a unique and long-lasting tribute to his creativity and analytical abilities. His influence has been profound, perhaps unprecedented among grasshopper and locust workers, and for this reason he has been called the "father of acridology." He was knighted in 1961. He died in London on March 18, 1970.

References

Bey-Biyenko GY (1970) Sir Boris Uvarov (1888–1970) and his contribution to science and practice. Entomol Rev 49:559–562

Waloff N, Popov GB (1990) Sir Boris Uvarov (1888–1970): the father of acridology. Annu Rev Entomol 35:1–24

Uzelothripidae

A family of thrips (order Thysanoptera).

► Thrips

V

Vagina

The genital chamber in females; a tubular extension of the oviduct (Fig. 1).

► Reproduction

Valdivian Archaic Moths (Lepidoptera: Heterobathmiidae)

JOHN B. HEPPNER
Florida State Collection of Arthropods,
Gainesville, FL, USA

Valdivian archaic moths, family Heterobathmiidae, include about nine species, with three named thus far. The family is the single member of the superfamily Heterobathmioidea and the sole member of the suborder Heterobathmiina. Adults small (10–11 mm wingspan), with head rough-scaled, with small mandibles; labial palpi are 3-segmented and short; maxillary palpi are 5-segented and folded. Maculation is usually iridescent purple with fine spots. All are diurnally active as adults, feeding at Nothofagus (Fagaceae) flowers. Larvae are leafminers of Nothofagus trees in southern South America.

References

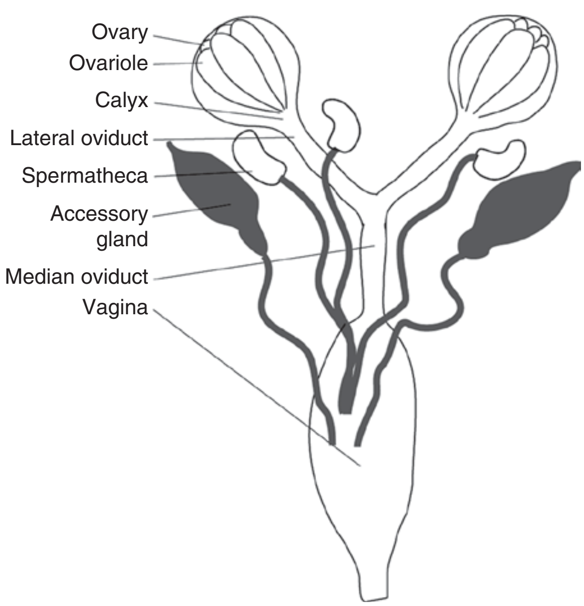
Kristensen NP, Nielsen ES (1983) The Heterobathmia life history elucidated: immature stages contradict assignment to suborder Zeugloptera (Insecta, Lepidoptera). Zeitschrift fur Zoologie, Systematik und Evolution 21:101–124

Kristensen NP, Nielsen ES (1998) *Heterobathmia valvifer* n. sp.: a moth with long apparent "ovipositor valves" (Lepidoptera: Heterobathmiidae). Steenstrupia 24:141–156

Valdivian Forest Moths (Lepidoptera: Andesianidae)

JOHN B. HEPPNER
Florida State Collection of Arthropods,
Gainesville, FL, USA

Valdivian forest moths, family Andesianidae, total only 3 known species from southern Andean forest



Vagina, Figure 1 Diagram of the female reproductive system, as found in *Rhagoletis* (Diptera) (adapted from Chapman, The insects: structure and function).

zones of Argentina and Chile. The family is the most primitive of the Monotrysian moths, in its own monobasic superfamily Andesianoidea, and in the section Nepticulina. Adults are robust and of medium size (27 to 61mm wingspan), with head scaling roughened; haustellum very short (with vestigial mandibles present); labial palpi elongated (with elongated 2nd segment); maxillary palpi 5-segmented (unfolded); and antennae bipectinate in males (filiform in females). Wing maculation is lustrous gray with numerous darker vertical striations, plus some dark spotting. Wing venation is heteroneurous but somewhat primitive with added veins. Adults apparently are nocturnal (possibly crepuscular), mainly in *Nothofagus* forests. Biologies are unknown, but larvae are likely to be stem borers.

References

Davos DR (2003) Andesianidae, a new family of monotrysian moths (Lepidoptera: Andesianoidea) from austral South America. Invertebrate Systematics 17:15–26

Gentili P (1989) Revision sistematica de los Cossidae (Lep) de la Patagonia Andina. Revista de la Sociedad Entomologica Argentina 45:3–76

Van Den Bosch, Robert

Robert van den Bosch was born on March 31, 1922, in Martinez, California, USA. He was educated at the University of California, Berkeley, where he received a degree in physical education before shifting his emphasis to entomology. He received his Ph.D. in 1950. He worked at the University of Hawaii from 1949 to 1951, the University of California-Riverside from 1951–1963, and the University of California-Berkeley from 1963 to 1978. van den Bosch had great influence in the fields of integrated pest management and biological control. Along with colleagues V.M Stern, R.F. Smith and others at the University of California, van den Bosch espoused an integrated approach to pest management that used chemical insecticides as only one element of pest suppression, relying on biological and cultural control for much mortality among pest populations. More specifically, chemical pesticides were viewed as a necessary but undesirable tactic that would be used only when absolutely necessary. The deleterious effects of pesticides including pesticide resistance among the target pests, inadvertent mortality to nontarget organisms such as beneficial insects and wildlife, and hazards to pesticide applicators were noted as reasons to avoid pesticide use. Though many have now come to accept this view, this was a radical viewpoint in the 1950s and 1960s when insecticides seemed to many to be miracle products. van den Bosch published more than 150 technical articles and several landmark books including "Biological control" (with P.S. Messenger, 1973), "Introduction to integrated pest management" (with M.L. Flint, 1981), and "The pesticide conspiracy" (1978). The latter was particularly provocative and served to sensitize both the research community and public to the lack of sound policy with regard to pesticide use in the United States. van den Bosch also served as chair of the Division of Biological Control at the University of California-Berkeley, from 1969 until his premature death at age 56, on November 19, 1978.

Reference

Hoy MA (1993) Biological control in U.S. agriculture: back to the future. Am Entomol 39:140–150

Van Duzee, Edward Payson

Edward Van Duzee was born at New York, New York, USA, on April 6, 1861. The son of a scientist, Edward was encouraged to work in the sciences, and he did so quite successfully, eventually becoming known as the greatest hemipterist in the United States. He became assistant librarian of the Grosvenor Library, a research library, in Buffalo, New York, in 1885, and then head librarian 10 years later. This environment allowed him to devote his attentions to the Hemiptera, and the bibliography of Hemiptera. Van Duzee collected throughout the United States. About 1900 he began a great monograph of the Hemiptera, a project that took 10 years to complete. It proved to be an outstanding compilation and serves as a model of completeness. Van Duzee left the Grosvenor Library after 27 years of employment, and before the catalogue was completed, due to ill health. He accepted employment as an instructor at the University of California, Berkeley, and the catalogue "Hemiptera of America north of Mexico, excepting the Aphididae, Coccidae, and Aleyrodidae" was printed by the University. Van Duzee did not enjoy teaching, and in 1916 accepted a position as assistant librarian and curator of entomology at the California Academy of Sciences. He spent the next 24 years building the insect collection, and also served as editor of the journal "The Pan-Pacific Entomologist" for the first 14 years of its existence. In all, Van Duzee published more than 250 articles over the course of his career. He died on June 2, 1940.

References

Essig EO, Usinger RL (1940) The life and works of Edward Payson Van Duzee. Pan-Pac Entomol 16:144–177
Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

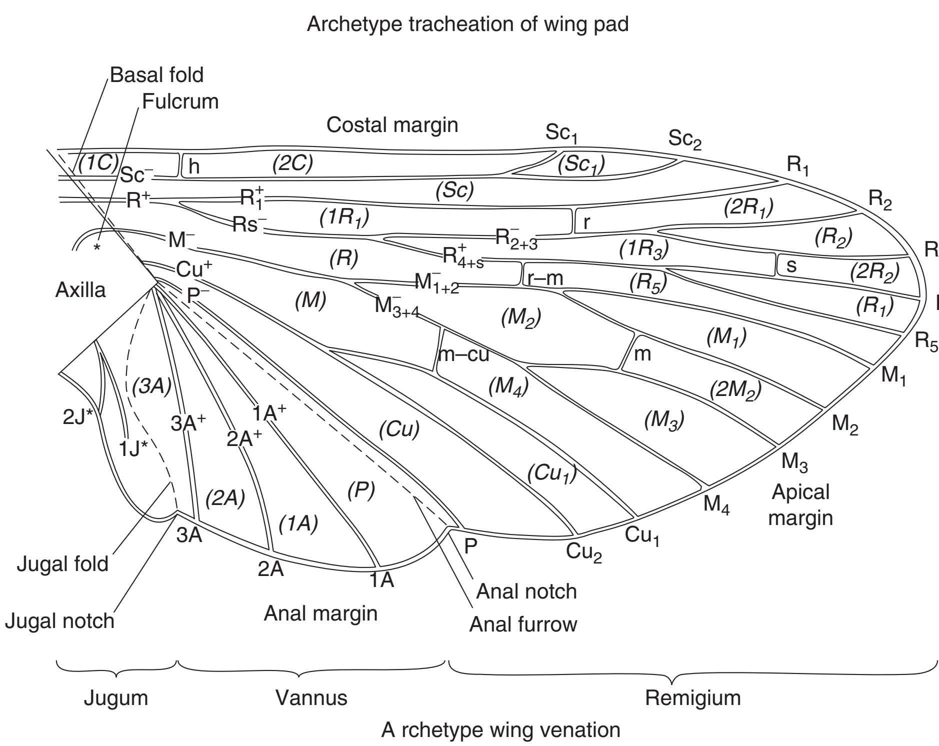
Vanhorniidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees, and Sawflies

Vannus

A region of the wing marked by a large fan-like (Fig. 2) expansion of the posterior region; the vannal region.



Vannus, Figure 2 **Hypothetical ancestral pattern of wing venation.**

Variable Intensity Sampling Plan

A sampling plan that shares the characteristics of fixed-sample size and sequential sampling plans in which prior sampling information is used to evaluate the number and allocation of subsequent sample units, but ensures that sample units are collected throughout the sample universe.

► Sampling Arthropods

Variegated

Describes structures that are varied in color or have an irregular pattern.

Variegated Cutworm, *Peridroma saucia* (Hübner) (Lepidoptera: Noctuidae)

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Variegated cutworm is found in many areas of the world. It occurs in North and South America, the Hawaiian Islands, and also portions of Europe, Asia, and North Africa. The origin of this insect is uncertain, but is thought to be Europe, where it was described in 1790. First observed in North America in 1841, it is now abundant in southern Canada and the northern United States, where it is often considered to be the most damaging cutworm pest of vegetables.

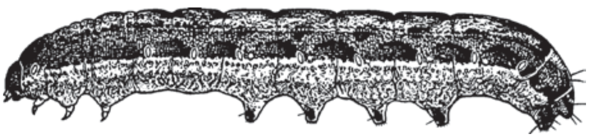
Life History

There are 2–4 generations annually, with two generations common in colder regions such as Canada, and 3–4 in warmer areas. Flights of moths are protracted, and generations are difficult to discern based on adult populations. Overwintering may occur in the pupal stage, or perhaps the larval stage, but there also is evidence that moths migrate into cooler areas from warmer latitudes each spring, and return to warmer regions in the autumn. For example, in a study conducted in Iowa, USA, 3–9% of moths collected during the spring flight were considered to have emerged from overwintering pupae, with the balance migrating from southern latitudes. The April-May spring flight in Iowa tends to be followed by generations and adult flights in June-July, August-September, and October-November. Total duration of the life stages is usually 35–70 days. Overwintering in colder areas such as Canada is unlikely except in relatively warm areas such as along the seacoast.

The egg of variegated cutworm is hemispherical in shape; the egg is flattened at the point of attachment to a leaf or plant stem. The surface of the egg is marked with ridges, about 42 in number, radiating from the center. The egg is 0.55–0.58 mm in diameter and 0.40–0.45 mm in height. Initially, eggs are white in color, but soon turn brownish. The developmental threshold for the egg stage is estimated at 3.0–6.0°C. Duration of the egg stage is 4–6 days in warm weather (20–30°C), but 10 days when held at 15°C. Eggs are deposited in clusters, often numbering several hundred per egg mass. Females may deposit 1200–1400 eggs during their life span.

There normally are six instars. The developmental threshold for the larval stage is estimated at 2.6–6.7°C. Duration of the instars is reported to be 6.5, 4.6, 4.8, 4.7, 6.7, and 16.8 days for instars 1–6, respectively, at 15°C. When reared at 25°C, instar durations are reduced to 3.1, 1.9, 2.2, 2.2, 2.9, and 8.4 days, respectively. Head capsule widths are 0.30–0.35, 0.46–0.62, 0.80–1.00, 1.20–1.65, 1.9–2.6, and about 3.0–3.2 mm, respectively. Body lengths are estimated at 2.0–3.0, 3.6–6.5, 5.3–9.0, 12–16, 25–28, and 35–46 mm for instars 1–6, respectively. Body color is (Fig. 3, Fig. 4) brownish gray to grayish black. The most distinctive character is a dorsal yellow or whitish spot, present on each of the first 4 abdominal segments, often the first six segments, although this character may be absent in early instars. Less distinctive is the black W-shaped mark on the eighth abdominal segment of the last

Variegated Cutworm, *Peridroma saucia* (Hübner) (Lepidoptera: Noctuidae), Figure 3 **Adult of variegated cutworm, *Peridroma saucia* (Hübner).**



Variegated Cutworm, *Peridroma saucia* (Hübner) (Lepidoptera: Noctuidae), Figure 4 **Larva of variegated cutworm, *Peridroma saucia* (Hübner).**

instar, and light brown or tan on the posterior end of the body. An inconspicuous black line is often present laterally above the spiracles. An orange-brown line may connect the spiracles, and below the spiracles there usually is some irregular yellowish or orange coloration. The head is orange-brown and marked with darker spots.

The larva forms a cell in the soil and pupates near the soil surface. The pupa is mahogany brown, and measures 15–23 mm long and 5–6 mm wide. The developmental threshold of the pupal stage is estimated at 4.3–8.5°C by various authors. Duration of the pupal stage is about 33 and 13 days at 15 and 25°C, respectively.

The adult is fairly large in size, the wing span measuring 43–50 mm. The front wings normally are grayish brown, tinged with reddish and shaded centrally and distally with darker brown. The background color varies, however, from dark brown to yellowish brown. A bean-shaped spot and a smaller round spot are usually evident centrally. The hind wings are iridescent or pearly white with brown veins and brown shading marginally. The head and thorax are dark brown, whereas the abdomen is lighter brown. Females produce a sex pheromone to attract males. Oviposition commences 7–14 days after emergence of the adults.

This cutworm has an extremely wide host range. Unlike some cutworms that expand their dietary range only when confronted with overpopulation and starvation, variegated cutworm feeds readily on numerous plants. Based on frequency of reports, variegated cutworm is likely to be found damaging beet, cabbage, lettuce, potato, and tomato, but nearly all vegetable crops are attacked. Variegated cutworm also is known to damage fruit trees, including apple, apricot, avocado, cherry, currant, gooseberry, grape, lemon, mulberry, orange, plum, raspberry, and strawberry. Other crops injured include alfalfa, barley, clover, corn, cotton, flax, hops, mint, sunflower, sugarbeet, sweet clover, tobacco, wheat, and many flower crops. Weeds are occasionally consumed, but seem not to be preferred. Some of the weeds eaten are jimsonweed, *Datura* sp.; dock, *Rumex* sp.; dogfennel, *Eupatorium capillifolium*; plantain, *Plantago* sp.; ragweed, *Ambrosia* sp.; and shepherdspurse, *Capsella bursa-pastoris*.

Numerous natural enemies are known from variegated cutworm; 20–75% mortality is not uncommon, with wasp and fly parasitoids accounting for most of the deaths among larvae. In a study of variegated cutworms in Oklahoma, USA, six species of Braconidae, three species of Ichneumonidae, and one species of Eulophidae were associated with this cutworm, but among the Hymenoptera only *Ophion* sp. (Ichneumonidae) accounted for more than 5% mortality. In the same study, 12 species of Tachinidae were observed, but among the Diptera only *Archytas apicifer* (Walker) and *Peleteria texensis* Curran (both Tachinidae) accounted for more that 5% mortality. In Oregon, USA, eight species of Hymenoptera were round attacking variegated cutworm larvae. The parasitoid *Meteorus communis* (Cresson) (Braconidae) was recovered from about 35% of the intermediate age larvae. Not only did the parasitism affect abundance of cutworm in subsequent generations, but caused a 93% reduction in foliage consumption by parasitized larvae. A study of variegated cutworm in Hawaii demonstrated 33–80% parasitism, with most of the parasitism due to *Hyposoter exiguae* (Viereck) (Ichneumonidae), *Cotesia marginiventris* (Cresson) and *Meteorus laphygmae* Viereck (both Braconidae) (all Hymenoptera).

Other Hymenoptera known to parasitize variegated cutworm include *Apanteles xylinus* (Say), *Chelonus insularis* Cresson, *C. militaris* (Walsh), *Meteorus autographae* Muesebeck, *M. leviventris* (Wesmael), *Microplitis feltiae* Muesebeck, *Rogas perplexus* Gahan, and *R. rufocoxalis* Gahan (all Braconidae); *Campoletis sonorensis* (Cameron), *Enicospilus merdarius* (Gravenhorst), *Nepiera fuscifemora* Graf, and *Ophion flavidus* Brulle (all Ichneumonidae); and *Dibrachys canus* (Walker) (Pteromalidae). Other Diptera parasitizing this cutworm are *Archytas aterrimus* (Robineau-Desvoidy), *A. cirphis* Curran, *Bonnetia comta* (Fallen), *Carcelia* spp., *Chaetogaedia monticola* (Bigot), *Clausicela opaca* (Coquillett), *Eucelatoria armigera* (Coquillett), *Euphorocera claripennis* (Macquart), *E. omissa* (Reinhard), *Gonia longipulvilli* Tothill, *G. porca* Williston, *G. sequax* Williston, *Lespesia archippivora* (Riley), *Madremyia saundersii* (Williston), *Peleteria texensis* (Curran), *Periscepsia helymus* (Walker), *P. laevigata* (Wulp), *Voria ruralis* (Fallen), *Winthemia leucanae* (Kirkpatrick), *W. quadripustulata* (Fabricius), and *W. rufopicta* (Bigot) (all Tachinidae). It is likely that many other wasps and flies attack this insect.

The fungus *Metarhizium anisopliae* and viruses can inflict mortality, but incidence is often low. Both a granulosis and a nuclear polyhedrosis virus are known to affect this cutworm.

Damage

Larvae cause considerable mortality to seedlings by cutting off the plant at the soil surface. Larvae also are defoliators, and although they commonly frequent low-growing herbage, they readily climb trees to feed on buds and foliage. Young larvae may remain on the foliage during the daylight hours, but feed principally during the evening hours. Large larvae often hide in the soil or other sheltered locations during the daytime hours, moving to exposed areas of foliage in the evening to feed. Larvae may burrow into tomato fruit and the heads of cabbage and cauliflower. At high densities, larvae may assume a gregarious, dispersive "armyworm" habit, but this is uncommon. This species also invades greenhouses frequently.

Larvae consume about 125 sq cm of sugarbeet or 160 sq cm of potato foliage during their larval development. Potato and many other plants can tolerate some defoliation without significant yield decrease. Late in the season, after tuber formation is nearly complete, potato can withstand up to 75% leaf loss without yield decrease. At this time up to 40 variegated cutworms per plant can be tolerated. However, at an earlier period in the season such as at full bloom, plants may be able to tolerate only three cutworms per plant.

Management

Adult populations can be monitored with blacklight traps and pheromone traps. Captures by the two types of traps are correlated, but pheromone traps capture larger numbers from the spring generation whereas blacklight traps capture larger numbers at other times of the year. Pheromone traps, although not completely species specific, provide considerable selectivity relative to blacklight traps, thereby reducing labor requirements associated with population monitoring.

Larval populations are difficult to sample. Young larvae may be found clustered on foliage, but older larvae tend to hide in sheltered locations or burrow beneath the soil surface during the daylight hours. If plants are severed at the soil surface, or have disappeared, it is important to rake the soil surface and search for cutworm larvae.

Insecticides are commonly recommended to protect young plants from cutting damage, and older plants from defoliation and fruit injury. Insecticide applications are directed at the foliage or soil, the latter because the larvae often seek shelter there. Insecticides differ greatly in their effectiveness, and larger larvae are considerably more difficult to kill. Insecticide-treated bran baits are effective against variegated cutworm. *Bacillus thuringiensis* is not recommended.

Cutworm problems often develop in weedy fields or portions of fields infested with weeds. It is advisable to till, or otherwise destroy weeds, 10–14 days in advance of planting, as this should cause small larvae to starve. If seedlings are to be transplanted into a field or garden, larger plants are preferred because they are less likely to be irreparably damaged by cutworms. Transplanted plants derive considerable protection if surrounded by a barrier such as a can or waxed paper container with the bottom removed. Aluminum foil wrapped around the base of the seedling also deters cutting by larvae.

Variegated cutworm is susceptible to infection by entomopathogenic nematodes (Nematoda: Steinernematidae and Heterorhabditidae) but demonstration of practical use under field conditions is lacking.

► Turfgrass Insects and Their Management
►Vegetable Pests and their Management
►Potato Pests and their Management

References

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, CA, 729 pp
Crumb SE (1929) Tobacco cutworms. USDA Techical Bulletin 88, 179 pp
Shields EJ (1983) Development rate of variegated cutworm (Lepidoptera: Noctuidae). Ann Entomol Soc Am 76:171–172
Shields EJ, Rouse DI, Wyman JA (1985) Variegated cutworm (Lepidoptera: Noctuidae): leaf-area consumption, feeding site preference, and economic injury level calculation for potatoes. J Econ Entomol 78:1095–1099
Walkden HH (1950) Cutworms, armyworms, and related species attacking cereal and forage crops in the central Great Plains. USDA Circular 849, 52 pp

Variegated Mud-Loving Beetles

Members of the family Heteroceridae (order Coleoptera).

► Beetles

Varley, George C

George Varley was born in 1910 and educated at Cambridge University, Cambridge, England. As a student, he became interested in mathematical models relating to population dynamics, a subject that would fascinate him for his entire career. He completed his Ph.D. in 1935 and then held a series of positions at University of California at Riverside, Cambridge University, King's College at Newcastle, and finally he was appointed Hope Professor at Oxford. He served in this latter capacity for 30 years, retiring in 1978. At Oxford, Varley worked on winter moth for 20 years, producing an unusually complete understanding of its biology, and developing key factor analysis as a method of analyzing life tables. It was a technique that would become a basic ecological method for analyzing animal populations. Varley's work proved to be very influential in population ecology. He died in 1983.

Reference

Hassell MP (1983) George C Varley, 1910–1983. Antenna 7:121–122

Varroa Mite, *Varroa destructor* Anderson and Trueman (Acari: Varroidae)

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The varroa mite, *Varroa destructor* Anderson and Trueman, is the world's most devastating pest of western honey bees (*Apis mellifera*, Hymenoptera: Apidae). Although the varroa complex includes multiple species, *V. destructor* is the species responsible for the vast majority of the damage attributed to mites from this genus. Until 2000, it was believed that *Varroa jacobsoni* Oudemans was the mite responsible for widespread honey bee colony losses. However, taxonomic work published in 2000 indicated that a previously unidentified species of varroa (*V. destructor*) was responsible for the damage; *V. jacobsoni* was shown to be only moderately harmful to western honey bees. This discussion is limited to *Varroa destructor*.

Varroa mites are ectoparasites that feed on the hemolymph of immature and adult honey bees. *Apis mellifera* is not the mite's natural host. In fact, the mite is native to Asia where it parasitizes another cavity-dwelling honey bee, *Apis cerana* (the eastern or Asian honey bee). *Apis cerana* is believed to have some natural defenses against the mite and consequently rarely is affected negatively by the mite. Only when the mite shifted hosts did people begin to realize how devastating it could be, and this occurred when colonies of *Apis mellifera* were moved to and propagated in Asia. Varroa's host shift did not occur instantly; evidence suggests that it may have taken 50–100 years. Since that time, the mite has spread around the world and has become nearly cosmopolitan in distribution (Fig. 5). Those countries not hosting varroa mites maintain strict quarantine procedures to lessen the chance of an accidental importation of the mite.

Varroa Mite Biology

Although the varroa mite is a natural parasite of *A. cerana*, most of its biology has been determined using *A. mellifera* due to the mite's importance as an economic pest on this honey bee species. With that in mind, most of the following discussion will relate to varroa's presence on *A. mellifera* rather than on *A. cerana*.

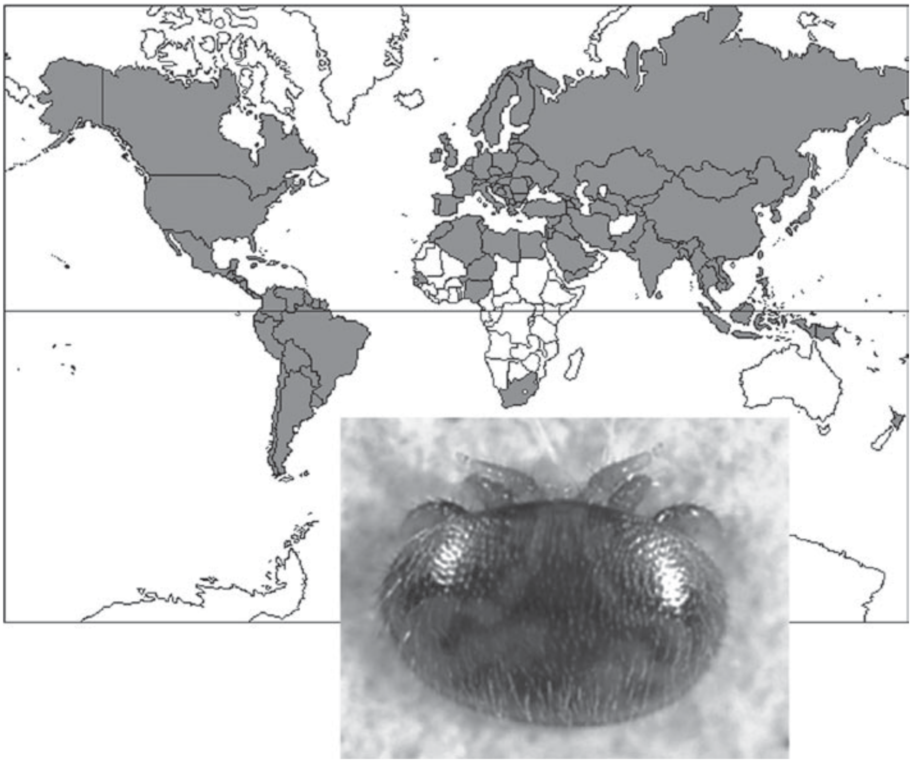
Adult female varroa mites (about 1.1 mm long and 1.6 mm wide) can be found either on adult or immature honey bees. They must, however, reproduce on honey bee brood. Immature varroa can be found only on capped brood and male varroa (about 0.8 mm long and 0.7 mm wide) will never leave these brood cells.

The adult females are brownish-red in color and oval in shape (Fig. 5) while the males are soft bodied and white. Although small according to human standards, a varroa female is one of the largest ectoparasites known when considered in relation to its host. Because varroa-associated damage is always caused by female mites, the rest of this discussion will proceed from the female varroa mite's perspective.

Adult females undergo two phases in their life cycle, the phoretic and reproductive phases. During the phoretic phase, female varroa feed on adult bees and are passed from bee to bee as bees walk past one another in the colony. During phoresy, the female varroa live on adult bees and usually can be found between the abdominal segments of the bee. Varroa puncture the soft tissue between the segments and feed on the bee's hemolymph through the puncture.

Anatomically, female varroa mites are well-adapted bee parasites. Their flattened shape allows them to fit between the abdominal segments. Furthermore, they have claws that allow them to grasp the bee and ventral setae that allow them to remain attached to the bee. The mite's cuticle has a chemical pattern similar to that of the bee's, possibly allowing it to escape notice while on the bee. Additionally, the cuticle is highly sclerotized, thus occasionally protecting it from bee aggression.

Phoretic varroa mites also can be passed between colonies of bees when infested bees drift into another colony. This happens frequently in managed honey bee situations where individual bee colonies are located within meters of one another. It is common for bees in this situation to return (drift) to the wrong colony. Interestingly, it has been shown that bees from colonies heavily infested with varroa drift more than bees from uninfested colonies. Varroa passing within a colony from bee-to-bee and between colonies by



Varroa Mite, *Varroa destructor* Anderson and Trueman (Acari: Varroidae), Figure 5 **An adult female *Varroa destructor* (photo by Michael O'Malley, University of Florida), and the worldwide distribution of *Varroa destructor* (from Ellis and Munn. 2005. Bee World 86:88–101).**

drifting demonstrate that the mites can be transmitted naturally both horizontally and vertically.

Varroa mites also may pass between colonies other ways. First, beekeepers often aid weak colonies by adding bees or brood from a healthier colony; this practice spreads the mite. Second, beekeepers may transport colonies from one area to another, facilitating the spread of varroa regionally. Third, individual colonies may swarm, moving to a new location and spreading varroa simultaneously. Finally, mites may spread between colonies as bees from the colonies rob (or steal honey from) each other. It is common for strong colonies to rob weaker colonies in periods of nectar dearth. Mites pass easily from bee to bee in these instances. All of these methods have contributed to varroa's global distribution as a honey bee pest.

The phoretic period of the mite appears to contribute to the mite's reproductive ability. Although mites artificially transferred to brood cells immediately after they mature are able to reproduce, their reproductive rate is lower than that of mites undergoing a phoretic period. The phoretic period may last 4.5–11 days when brood is present in the hive or as long as 5–6 months during the winter when no brood is present in the hive. Consequently, female mites living when brood is present in the colony have an average life expectancy of 27 days, yet in the absence of brood, they may live for many months.

In order to reproduce, phoretic mites must enter bee brood cells. Honey bees construct a waxy matrix in which they form hexagonal compartments or cells. Queen bees oviposit in these cells, and three days later, a bee larva emerges from the egg and begins to develop. Once the larva reaches a certain age, worker bees in the colony construct a waxy capping over the entrance to the cell. The larva develops into a prepupa and then a pupa under the capping. Twenty-one, twenty-four, or sixteen days after an egg is oviposited, an adult worker, drone (male), or queen bee emerges from the cell (aged respectively).

Varroa mite females must enter a brood cell before the bees seal it. In *Apis mellifera*, they may enter either a worker or drone cell, but the mites are more attracted to drone brood. A mite that is ready to reproduce will leave the adult bee on which it is feeding and crawl down the wall of the cell to the honey bee larva at the bottom of the cell. At this point, the female mite is referred to as a foundress mite. Only larvae of a certain age are attractive to the mite, that age being larvae just about to be capped or in the process of being capped. After crawling under the larva, the female mite will submerge itself in the brood food under the larva where it will remain until the cell is capped by other worker bees. While submerged, the mite erects its peretrimes which serve as breathing tubes, allowing the mite to breathe while it is submerged.

Once other worker bees have capped the cell, the larva consumes the remaining brood food, thus freeing the mite. The freed mite climbs onto the larva and begins feeding. The mite defecates on the upper part of the cell wall while feeding on the bee. Shortly thereafter, the mite lays its first egg on the surface of the cell wall. The egg is unfertilized and will develop into a male mite. Subsequent fertilized eggs are oviposited by the female mite toward the back of the cell approximately every 25–30 h. These hatch into female mites.

The newly emerged protonymphs join their mother on the ventral side of the developing bee pupa around the bee's fifth abdominal segment. Here, the mother and offspring alternate between periods of feeding on the bee and defecation on the base of the cell. The developing protonymphs molt into deutonymphs and then into adult mites. The entire process from egg to adult mite takes 6–7 days for both sexes of the mite.

Unless more than one foundress enters the cell prior to capping, mite offspring are forced to mate with their siblings. When male varroa undergo their final molt, their piercing mouthparts change into hollow tubes. The male mite uses this structure to transfer packets of sperm to openings in the female, at the base of her third pair of legs. Although the adult female varroa can infest and reproduce in more than one cell, it mates only in the cell in which it was born. Shortly after mating, the sperm transport system of the female varroa degenerates, thus prohibiting future matings.

Considering mortality in brood cells and improper matings, the average foundress mite produces about 1 offspring per worker cell she enters and about 2 offspring per drone cell (drones take longer to develop so more mites are produced in drone cells). Therefore, in the average temperate climate, mite populations can increase 12-fold in colonies having brood half of the year and 800-fold in colonies having brood year-round. This makes the mite very difficult to control, especially in warmer climates where colonies maintain brood year-round.

Effects of Varroa Mite

The varroa mite has affected the apiculture industry negatively in every country into which it has been introduced. In fact, in some areas varroa mite has all but domesticated the western honey bee. Individuals reporting the effects of varroa mite after they arrived in the USA stated that honey bee colonies could not survive unless beekeepers intervened with a chemical treatment.

Accurate estimates of the effect of varroa mite on the apiculture industry are hard to find, but it is safe to assume that the mites have killed hundreds of thousands of colonies worldwide, resulting in billions of dollars of economic loss. Varroa mites have caused beekeeper production costs to rise, thus lowering the profit margin in beekeeping.

Varroa mites also have affected the feral (wild) population of bees in many areas. Since feral colonies were not managed for varroa mites and the colonies were left unprotected, the loss of feral colonies quickly resulted as varroa continued to spread. On the other hand, feral colonies that survived varroa mites have slowly developed resistance mechanisms that have allowed them to persist in the presence of the mite. This did not happen with managed colonies because beekeepers started treating chemically for varroa mites almost instantly, thus keeping alive susceptible populations of bees. This practice is changing.

Varroa mites weaken and ultimately kill colonies by out-reproducing their host. Typically, bee populations peak in late spring to mid-summer with a steady decline in population occurring in mid- to late summer. Varroa mite population increase is similar to that of the bees but is offset by a number of weeks. Therefore, varroa mite populations are just beginning to peak when bee colony populations typically begin to decline. This is usually the start of significant varroa mite problems.

Varroa mites rarely kill adult bees, but they do shorten bee lifespan and may even alter bee behavior. Varroa mites can kill immature bees, and their ability to do so is correlated with the number of varroa mite foundresses that enter a brood cell prior to it being capped. The more mite foundresses in a cell, the less likely the immature bee will develop successfully and emerge as an adult.

Other effects of varroa mites on bees are just beginning to be understood. For some time, scientists have known that honey bees host a number of viruses. There is evidence that some of these viruses are associated with varroa mite presence and levels in a colony. It now is believed that varroa mites can transmit multiple viruses to their hosts and that these viruses, not the varroa mites themselves, may cause the majority of the damage that bees experience while hosting the mites.

To illustrate this point, one of the most telling signs of a varroa presence in a colony is the occurrence of newly emerged adult bees with misshapen (Fig. 6) wings. A virus, named deformed wing virus and present in immature bees, is responsible for this symptom. Bees with this virus are unable to use their wings; therefore, the bees will never be able to contribute to the colony's foraging efforts since they never will be able to fly. Deformed wing virus can be so prevalent in maturing bees that they can emerge without any wings at all. Researchers suspect that other viruses play an important role in the varroa mite/honey bee relationship, but the roles of these viruses are not well understood.

Varroa Mite, *Varroa destructor* Anderson and Trueman (Acari: Varroidae), Figure 6 A newly emerged worker bee with misshapen wings. A virus, transmitted to the developing bee by varroa, is responsible for this symptom (photo by Sean McCann, University of Florida).

Detection and Treatment of Varroa Mite

The detection and treatment of varroa mites is an ever-changing science. Since varroa mite's spread around the world, methods to accomplish both have been investigated and refined. Because detection and treatment are dynamic topics, this treatise will focus only on general methods rather than specific techniques.

Although small, varroa mites can be seen on adult bees with the naked eye. They often are found feeding between segments on the bees' abdomens or crawling quickly elsewhere on the bees' bodies. Varroa mites look very similar to another bee commensal, the bee louse (*Braula coeca*, Diptera: Braulidae), and this has led to mistaken identifications. Despite this, the identification can be made simple when one remembers that the bee louse is a wingless fly with six legs while the varroa is a mite with eight legs.

A much better way to look for varroa in a colony is to examine bee brood. It is easier to find mites on drone brood (although finding them on worker brood is possible) because (i) varroa mites are attracted to drone brood more strongly than they are to worker brood, and (ii) drone brood is easier to remove from the cells. Immature bee brood is white, making it very easy to see the reddish-brown varroa mite.

Even though varroa mites can be detected visually on adult and immature bees, the number of mites on each only gives one an index rather than an accurate measurement of varroa mite populations in the hive. Measurements have become more accurate with the advent of sampling tools, the most popular of which are varroa sticky screens and ether rolls.

Varroa sticky screens are pieces of cardboard coated in a sticky substance. The cardboard is then covered with a wire mesh that prohibits bees from touching the sticky substance but allows varroa to fall through the mesh. These screens can be inserted under the honey bee nest and used to trap falling varroa. Varroa, both live and dead, regularly fall off their host bees. This may be facilitated by the grooming activity of the bees, but it probably occurs naturally as well. When a sticky cardboard insert and screen are present underneath the nest, the falling varroa will pass through the screen and get trapped on the sticky surface of the cardboard. Researchers have been able to correlate varroa mite fall in 24-, 48-, and 72-hour periods with actual varroa mite populations in the colony. Sticky boards are useful because they sample the entire colony for the presence of varroa mites, rather than any subset of bees within the colony.

Ether rolls yield quicker results than sticky traps but can be less accurate because only a subset of the entire colony is sampled. In an ether roll, about 300 adult bees are collected in a glass jar, after which they are sprayed with ether. After the ether is added to the jar, the jar is lightly shaken for 30 s, during which time varroa mites present on the adult bees will adhere to the inside walls of the jar, facilitating their quantification. A newer version of this sampling protocol has been developed using powdered sugar rather than ether. Once the dusted bees are shaken, the bees can be released (they are alive) and the sugar can be dumped into water. After contacting the water, the sugar dissolves, thus facilitating varroa quantification.

Traditionally, these sampling methods were not used very often because treatment for varroa mites was recommended twice yearly, regardless of the number of mites in a colony. Recently, investigators around the world have tried to employ an integrated pest management (IPM) approach to varroa mite control. Sampling devices are paramount in this management scheme where treatment is recommended after varroa populations in a colony reach an economic threshold. A sampling device is needed in order to determine when an economic threshold is reached.

Many studies have been conducted in an effort to determine the economic threshold for varroa in a colony but results have varied. Factors affecting the economic threshold include temperature, colony strength, geographic location, the presence of other pests/pathogens, level of colony resistance to varroa, etc. As such, an economic threshold for varroa probably will not be universal and will have to be determined regionally. In the USA, independent studies have suggested that the economic threshold for varroa mite is around 3,000 mites/colony. Again, this number will vary depending on a number of factors, including those listed above. With the establishment of economic thresholds and sampling devices, varroa mite management has become easier, although IPM is not as widely practiced by beekeepers as one would hope.

Traditionally, varroa mites have been controlled chemically. In fact, chemical-based, in-hive treatments have followed varroa everywhere the mite has been introduced. Pyrethroids, organophosphates, essential oils, and organic acids have been used by many countries to control varroa. Initially, the pyrethroid fluvalinate showed high levels of efficacy (>90%) against varroa mites. However, varroa mites have a demonstrated ability to become quickly resistant to this and other synthetic acaricides. This has made many acaricides useless in areas where varroa resistance to chemicals has developed. Further exacerbating this is the issue that many of the synthetic chemicals used inside bee colonies to control varroa double as insecticides in other pest-management schemes. So, varroa mites have made it necessary for beekeepers to put insecticides into insect colonies, the results of which are only just beginning to be understood. The effects of chemical varroa treatments on honey bees include reduced longevity of queen bees, reduced sperm loads in and longevity of drones, brood death, and reduced queen laying patterns. Many more effects are believed to exist.

Because of the reduced efficacy of chemicals used to control varroa mites, attention has turned to the application of non-chemical methods for limiting varroa populations. For example, varroa are attracted disproportionately to drone brood. This has led some beekeepers to practice selective removal of drone brood from bee colonies after it has been capped. This practice eliminates a cohort of varroa mites from colonies. Also popular is the use of screened bottom boards to lower varroa mite populations. Although its level of efficacy is debated, replacing solid bottom boards of a bee colony with screen mesh can reduce varroa populations as much as 14%.

A number of other non-chemical methods purported to lower varroa mite populations are used by beekeepers, with varying degrees of success. These include placing colonies in full sunlight, dusting the adult bees in the colony (often with powdered sugar), fogging mineral oil and other liquids into the colony, using small-cell comb, etc. It is important to note that although concrete data supporting the efficacy of these methods is lacking, future research may establish a benefit from these and similar practices.

Without question, the most significant advancement toward controlling varroa non-chemically has come in the realm of bee breeding. A number of bee defensive responses to varroa have been identified and selected for in natural and artificial breeding programs; the most notable of these are hygienic behavior and grooming behavior. Bees that exhibit grooming behavior use their legs to comb themselves. They do this both to themselves and to other bees in the colony. This behavior can increase the number of varroa that fall off the bees, thus lowering the number of varroa in a colony.

Hygienic behavior is the most studied of all the natural defenses against varroa. Although it is not a behavior specifically targeted toward varroa mite, its manifestation can lower varroa mite populations within a colony. Bees that are hygienic can detect many problems that affect brood (American foulbrood, varroa, chalkbrood, etc.), even if it is capped, and remove the affected brood. Because varroa mites go into cells immediately prior to the cell being capped, hygienic bees are given little time to "find" varroa mites before the cell is capped. As a result, hygienic bees have a refined ability to detect varroa mites in capped cells, remove the capping, and abort the brood. Often, this behavior can lead to the death of the mite, thus lowering varroa populations. It is interesting to note that a heightened form of hygienic behavior called "varroa sensitive hygiene" (VSH) has been found in some bees. VSH bees are able to detect varroa in capped cells and remove only those varroa that are reproducing.

Effort also has been concentrated in finding races of bees that are generally resistant to varroa mites. This includes bees that do not have a single defensive behavior targeting varroa mite yet maintain a very low varroa mite population in the colony. The most successful of these programs includes the Russian honey bee program headed by the United States Department of Agriculture honey bee genetics lab in Baton Rouge, Louisiana, USA. Russian bees are a European subspecies of bee introduced into eastern Russia 100 + years ago. Because varroa mites are native to the area, Russian bees have developed a general resistance or tolerance to the mite. Russian bee queens were introduced into the US in 1997 and are gaining popularity among beekeepers.

Many feel that varroa control is maturing holistically even though this approach is slow to be adopted by beekeepers. Ample research has shown that an IPM-based approach to varroa mite control is more economical than the conventional methods heavily relying on chemical pesticides. For example, using any combination of the non-chemical varroa controls mentioned above can lower varroa populations in a colony >40%. Despite this, holistic varroa mite control will continue to mature and can be improved.

In conclusion, varroa remain a vexing problem for bees, beekeepers, and bee scientists alike. It generally is believed that finding a "cure" for varroa will prove one of the most significant advancements in modern-day apiculture. Varroa mite's presence in bee colonies already has led to substantial research funds being invested in studies investigating honey bee biology, ecology, and pathology. Until a cure for varroa mites is found, this parasitic mite will remain a key player in the loss of honey bee colonies globally.

► Apiculture (Beekeeping)
► Honey Bee
► *Apis mellifera* (Hymenoptera: Apidae)
► Bee Louse
► *Braula coeca* (Diptera: Braulidae)
► Tracheal Mite
► *Acarapsis woodi* (Acarina: Tarsenomatidae)

References

Anderson DL, Trueman JWH (2000) *Varroa jacobsoni* (Acari: Varroidae) is more than one species. Exp Appl Acarol 24:165–189

Webster TC, Delaplane KS (eds) (2001) Mites of the honey bee. Dadant and Sons, Inc., Hamilton, IL, 280 pp

Vas Efferens

A tube connecting the testicular follicle with the vas deferens. Some insects lack the vas efferens.

Vascular System

The system of plant tissues that conducts water, minerals, and products of photosynthesis within the plant.

Vascular Wilts

► Transmission of Plant Diseases by Insects

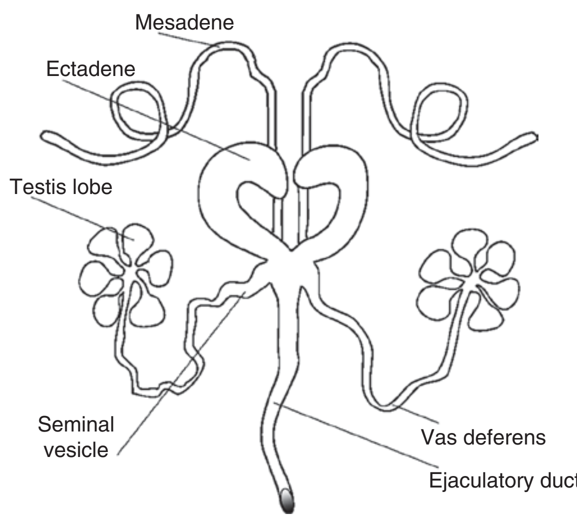
Vas Deferens (pl. Vasa Deferentia)

A tube that collects the sperm from the testicular follicles and (Fig. 7) transfers them to the seminal vesicle for storage and ejaculation.

► Reproduction

Vector

An agent, normally an animal, carrying a microorganism pathogenic for members of another species. The vector may or may not be essential for the



Vas Deferens (pl. Vasa Deferentia), Figure 7 Diagram of a male reproductive system as found in *Tenebrio* (Coleoptera) (adapted from Chapman, The insects: structure and function).

completion of the life cycle of the pathogenic microorganism.

Vector Capability of Blood-Sucking Arthropods: A Forecasting Matrix

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The ability to predict the potential for hematophagous arthropods to become vectors of pathogens is important in assessing their potential hazard to human or livestock health. The question of why one or another pathogen can be transmitted by a particular blood-feeding arthropod (hematophage), but not vectored by others, was first posed by Russian scientist Evgeny Pavlovsky, who formulated a theory of natural focality of infections and parasitic diseases.

Vladimir Beklemishev, a specialist in invertebrate evolution, comparative anatomy and systematic, was apparently the first who attempted to answer this question. He proposed a matrix based on the taxonomy of the vectors and the pathogens. According to this matrix, the ability to transmit a certain pathogen is limited to certain taxa. For example, this matrix forecasted that *Ixodes* ticks can transmit spirochetes, rickettsiae, and rickettsia-like microorganisms. However, the forecasting methodology was disregarded by the scientific community so Berlemishev's paper was never translated into English. As a result, the discovery of the vectors of Lyme disease and ehrlichiosis agents was made as late as the 1980s. Had the matrix received greater attention, the search for vectors might have progressed more rapidly.

A new, updated, prognostic matrix is presented (see Forecasting Matrix, Table 1) that takes into account food consumption of vectors. Most of the vector groups are insects, and more than half are Diptera.

According to the type of pre-adult feeding, all hematophagous arthropods can be divided into two large groups. In one group (Forecasting Matrix, Nos. 9–15), only blood (or lymph, as in bush mites) serves as a source of food, or at least part of food components must contain blood (as in flea larvae). Preimaginal (pre-adult) stages using many different sources of food, but not blood, compose the second group (Forecasting Matrix, Nos. 1–8). Only representatives of the first group (blood consumers on all stages) appear to serve as relevant or potential vectors of rickettsiae or rickettsia-like (*Ehrlichia*, *Cowdria*) microorganisms, with a single exception. The exception is triatomid bugs known as vectors of only one pathogen, *Trypanosoma cruzi*, which is the Chagas disease agent in South and Central America. This representative of the insect order Heteroptera shows a very specific type of quasi-peritrophic, chitin-like membrane in its midgut, allowing for no other parasites but pure-blood-consumers to develop. The infective form of *T. cruzi* is excreted with bug feces. These vectors might be called specific contaminators if the pathogen would not develop in the bug gut to achieve the infectious stage.

Rickettsiae develop either in digestive tract epithelium of lice and fleas (Forecasting Matrix – *dte*) or both there and in other cells, including salivary glands and ovarial cells in infected ticks and mites. This peculiar capability of rickettsiae for development and "conservation" in the gut epithelium of hematophagous arthropods allows them to survive during the vector' s molting periods (Forecasting Matrix, Nos. 9–10; 11–14) and thus to be transferred to the next stage of arthropod development, and even into the next generation. The phenomenon of transstadial transmission leads to understand how tsutsugamushi (or river, or bush) fever agent survives inside the free-living predaceous (entomophagous) nymphs and adults of trombiculid mites. Why rickettsiae are able to develop only in the vectors whose larval stage is hematophagous is not yet clear. Worm-like flea larvae are mainly detrivorous and only get the necessary components of blood from the

Vector Capability of Blood-Sucking Arthropods: A Forecasting Matrix, Table 1 Potential vector capacity forecasting matrix. Variants of transmission ability: ⊕ = proved for man; + = proved for animal; – = absent; P = potential

Hematophagous arthropod				Food sources, type of consumption				Pathogens and ability to be transmitted							
				Pre-adult stages		Adult		Viruses	Bacteriae			Protozoa			Helminths
No. of group	Taxon		Common name	Type of feeding	Source of food	Source of food	Speed of digestion	Arboviruses	Rickettsiae & rickettsia-like	Spirochetae (Borrelia)	Bacillae (Yersenia)	Pyroplasmids	Trypanosomatids	Haemosporids	Filarioidea
1	Glossinidae	Insects	Tsetse flies	adenotrophia	"mother milk"	Bl	hours	–	–	–	–	–	⊕ dtl	–	–
2	Hyppoboscidae		Bloodsucking flies	adenotrophia	"mother milk"	Bl	days	–	–	–	–	–	+dtl	–	–
3	Muscidae			detritophagia	D, M	Bl, Su	days	P	–	–	–	–	+dtl	–	–
4	Tabanidae		Horse flies	detritophagia, predatoriness	D, F, M, Flo	Bl, Su	days	P	–	–	–	–	+dtl	+bcs	⊕ bc
5	Culicidae		Mosquitoes	detritophagia, planktonophagia	D, M Zpl, Phpl	Bl, Su	days	⊕ bcs	–	–	–	–	+dtl	⊕bcs	⊕bc
6	Ceratopogonidae		Gnats	detritophagia	D, F, M	Bl, Su	Days	+bcs	–	–	–	–	+dtl	bcs	+bc
7	Phlebotomidae		Sand flies	detritophagia	D, F, M	Bl, Su	Days	⊕ bcs	–	–	–	–	⊕dtl	+bcs	P
8	Simuliidae		Black flies	Planktonophagia	M, Zpl, Phpl	Bl,	Days	P	–	–	–	–	+dtl	–	⊕ bc
9	Siphonaptera		Fleas	detritophagia, hematophagia	D, F, M, Bl (adult's excreta)	Bl	Days	–	⊕ dte	–	⊕dtl	–	+dtl	P	+bc
10	Anoplura		Lice	hematophagia	Bl	Bl	hours	–	⊕ dte	⊕dtl	–	–	–	–	–
11	Triatomidae		Kissing bugs	hematophagia	Bl	Bl	Days	–	–	–	–	–	⊕dtl	–	–
12	Ixodidae	Ticks and mites	Hard ticks	hematophagia	Bl	Bl	weeks, months	⊕ bcs	⊕ bcs	⊕ dtl,	bcs P	⊕ bcs	+dtl	–	+bc
13	Argasidae		Soft ticks	hematophagia	Bl	Bl	months	⊕ bcs	+bc	⊕ dtl,	bcs P	⊕ bcs	P	–	+bc
14	Gamasina		Mites	hematophagia	Bl	Bl	days	+bcs	+bc	+	–	–	+dtl	–	–
15	Trombiculidae		Bush mites	lymphophagia	L	Hl	days	–	⊕ bcs	–	–	–	–	–	–

Part of arthropod organism where pathogen develops (multiplies): *bc* = body cavity; *bcs* = body cavity and salivary glands; *dtl* = digestive tract lumen; *dte* = digestive tract epithelium
Sources of food: *Bl* = blood; *D* = detritus; *F* = fungi; *Flo* = free living organisms; *Hl* = haemolymph of insects; *L* = lymph of vertebrate hosts; *M* = microorganisms; *Phpl* = phytoplankton; *Su* = sugar; *Zpl* = zooplankton

blood-containing excreta of adults. Nonetheless, clearly this kind of diet is necessary to make the adult flea gut epithelium an available medium for pathogenic rickettsial penetration and proliferation.

Arboviruses are represented by numerous families with very different core and envelope structures. Arboviruses can reproduce only intracellularly. The ability of an arthropod to serve as a virus vector seems to be based less on a potential vector's properties and more on arbovirus specificity. Ticks and gamasid mites, however, are known not only as vectors of many arboviruses but also reservoirs, being capable of transmitting them both transstadially and transovarially.

The majority of true, or potential, vectors are polyphagous, polyxenous ectoparasites, which are able to obtain blood from various vertebrate species. There is only one exception that confirms the rule, i.e., the louse *Pediculus humanus corporis* (Anoplura), an obligate hematophage at all stages and, according to the matrix, a monoxenous human parasite that can be a vector of rickettsiae. Indeed, these lice provide a very good environment for the accumulation and multiplication of the specific human typhus agent, *Rickettsia provazeki*. Being obligate hematophages, lice serve as a very good reservoir for still another specific human pathogen belonging to the spirochete (*Borrelia*) group. Both these pathogens are specific human disease agents and are transmitted from man to man. Rickettsiae in lice only develop in the gut epithelium and the pathogen's transmission by lice as well as fleas is a result of an infectious insect being crushed and rickettsia-infected feces penetrating into skin scratches. Yet *Borrelia*, the above obligate blood-consuming pathogen, is only capable of development in the arthropods whose ontogenetic stages are strictly hematophagous, i.e., lice, ticks, and gamasid mites. Trombiculid mites as lymph consumers must be excluded from this group as well as fleas, whose larvae feed not only on blood containing "parental excreta" but also detritus.

Borreliae develop in the gut content of lice, ticks and mites. In lice, however, they are capable of neither invading the louse body cavity nor being transmitted specifically through the bite of an infected insect. In contrast, borreliae in infected ticks are able to migrate through the body cavity into salivary glands. Infected ticks transmit this pathogen specifically (e.g., Lyme disease pathogen by nymphs or adults of *Ixodes* ticks attached to the host skin). The peculiarities of *Borrelia* biology suggest that other blood-sucking insects are unable to transmit these pathogens.

Bacilli, e.g., the plague agent *Yersenia pestis* as a natural focal disease of man, develop successfully in the flea gut and are transmitted through flea regurgitation during attempts to suck blood from their host. This pathogen can develop and even be transmitted by ticks as well, but these acari fail to play any part in plague transmission. All other arthropods must be excluded as potential vectors of bacilli.

Protozoan agents have a much wider range of potential and real vectors. Only pyroplasmids from the genera *Theileria* and *Babesia* that show a specific mode of sporogonia in the salivary gland cells of ticks are vectored by hard and soft ticks. As no other blood-sucking arthropod has the necessary type of cells in their salivary glands, this means that it is useless to search for vectors of these specific pathogens other than ticks.

Trypanosomatids are capable of development in all blood-sucking arthropods, irrespective of preimaginal food consumption, exclusive of lymphophagous trombiculid mites and obligate human ectoparasites like body lice. Only insects, not ticks or mites, can serve as hemosporid vectors. Most of them transmit these pathogens to birds. Of special note are the *Anopheles* (Culicidae) mosquitoes, vectors of human malaria agents (i.e., *Plasmodium falciparum*, *Plasmodium vivax*, *Plasmodium malariae*, and *Plasmodium ovale*). Interestingly, inclusion of the *Pseudomonas* group of microorganisms in the larval diet is essential for the successful development of these haemosporids in the potential vector organism.

Helminths, predominantly Filarioidea nematodes, are transmitted by a very wide range of vectors, mainly insects. Among these helminths, some are very dangerous parasites (e.g., loaosis by Tabanid flies and *Onchocerca* species by black flies) which cause blindness in humans. Mosquitoes also are vectors of dangerous filarial diseases such as brugiosis and elephantiasis.

The forecasting matrix (Table 1), though gaining little attention in the past, contains important patterns that help predict likely disease-vector relationships. For example, new species of rickettsial, spirochetal and pyroplasmid pathogens might be discovered among ticks and gamasid mites. New arboviruses might be revealed among tabanids and black flies, but not likely from lice or kissing bugs. This matrix virtually precludes a successful search for hemosporid protozoans among lice and other purely hematophagous arthropods at all ontogenetic stages.

References

Alekseev AN (1985) The theory of connections of feeding types and digestion of blood-sucking arthropods with their ability to be specific vectors of transmissive diseases agents. Parazitologiya 19:3–7 (In Russian)

Beklemishev VN (1948) Interface between taxonomical position of pathogens and vectors of transmissive diseases of animals and man. Meditsinkaya parazitologiya i parazitarnye bolezni 17:385–400 (In Russian)

Goddard J (2000) Infectious diseases and arthropods. Humana Press, Totowa, NJ, 231 pp

Jadin J, Vincke IH, Dunjic A, Delville JP, Wery M, Bafort J, Scheepers-Biva M (1966) Rôle des *Pseudomonas* dans la sporogonie de l' hématozoaire du paludisme chez le moustique. Bulletin de la Société de Pathologie Exotique 59:514–525

Pavlovsky YN (ed) (1963) Human diseases with natural foci. Foreign Languages Publishing House, Moscow, Russia, 346 pp

Vector Competence

The ability of a potential vector to actually vector a disease. Many arthropods are capable of vectoring disease in an ideal (e.g., laboratory) environment, but fail to be effective vectors in the field. Some factors influencing vector competence include age of the vector and host, synchrony of vector and host, availability of alternate hosts, behavior/host preference of the vector, ability of the disease organism to maintain or increase titer in the vector, environmental conditions, prior exposure and host resistance.

Vectors of Phytoplasmas

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Phytoplasmas are phytopathogenic Mollicutes. These minute wall-less bacteria are found exclusively in phloem and primarily on sieve elements and cannot be cultured artificially. They were first associated with "yellows" diseases in 1926, although at the time they were thought to be viruses. Since then, phytoplasmas have been found in hundreds of plant species. Over 300 plant diseases are known worldwide, including economically important flowers, vegetables and orchards.

Phytoplasmas are vectored from plant to plant by a select group of Hemipterans feeding in the phloem. Of these insects, the leafhoppers and planthoppers have been shown to vector phytoplasmas, and more recently, a psylla (*Bactericera trigonica*) has been shown to vector phytoplasmas in carrots.

Once an insect has fed in the phloem of a phytoplasma-infected plant, a number of events must take place for it to be a successful vector. There are a number of anatomical and physiological barriers that the phytoplasma must overcome: it must successfully survive salivary and digestive enzymes; penetrate and replicate in the midgut cells; penetrate out of the midgut cells into the hemolymph; survive any phagocytes or encapsulation by hemocytes while in the hemolymph; travel to, penetrate and replicate in the salivary glands; and finally be released into the phloem of a plant as the insect feeds. The period of time from when the insect first acquires the phytoplasma until the time it can vector it to a new plant is the latent period. While a minimum amount of time is required for the physiological processes, it is also affected by temperature. Furthermore, vectors can acquire more than one type of phytoplasma.

There are a number of techniques available to detect and identify specific phytoplasmas in insects; however, all molecular (i.e., DNA probes, PCR/RFLP, and chromosome sequencing) and immunological (i.e., ELISA, dot hybridization and southern hybridization) tests cannot distinguish a vector species from an insect that has simply fed on an infected plant and thus has phytoplasma in its alimentary canal. To determine if an insect is a vector, it must be allowed to feed and transmit the pathogen. A relatively new technique combines molecular techniques with insect feeding. The potential vector, contained in a small tube, is allowed to feed through Parafilm on a sucrose solution. If the insect is an infective vector, PCR analysis of the sucrose will yield positive results. This technique allows rapid determination of the type of phytoplasma and the percent of infective vectors in any population.

To date, there are no efficient methods to control the spread of phytoplasma diseases, only to reduce its impact. Efforts to develop such control measures focus either on the plant or the insect vector. Phytoplasmas are not seed-transmitted but can be transmitted by grafting. Planting resistant varieties of plants or grafting to resistant rootstock is the best option to reduce spread of the disease, but resistant rootstock varieties do not exist for all plants. Tetracycline solutions have been variously applied to control infections in orchards. Such methods are usually effective only for the duration of the treatment; once stopped, symptoms return. However, currently there is research on genetically engineering plants to express antibodies, which may be a solution in the future. In cases where there are no resistant source plants, clean plants must be protected from insects with physical (nets or screening) or chemical (insecticides) means. Thorough knowledge of the biology of the vector and epidemiology of the disease will eliminate unnecessary insecticide treatments when the vector is either not present or is in a non-infective phase. If the vector is monophagous, using clean source plants and eliminating wild reservoir plants can achieve control of the disease. If the vector is polyphagous, border rows of a plant more "desirable" to the insect could be planted and heavily treated to protect the crop.

Phytoplasmas offer a great challenge to the researcher because they cannot be cultured and because there is no effective control. New molecular biological techniques are aiding in the quest for more understanding about the pathogen, pathogen-vector interaction, and pathogen-plant interaction.

References

Abad P, Font I, Dally EL, Espino AI, Jorda C, Davis RE (2000) Phytoplasmas associated with carrot yellows in two Spanish regions. J Plant Path 82(1). Available at, www.agr.unipi.it/sipav/jpp/journals/abs0300.htm

Chen YD, Chen TA (1998) Expression of engineered antibodies in plants: a possible tool for spiroplasma and phytoplasma disease control. Phytopathology 88:1367–1371

Kunkel LO (1926) Studies on aster yellows. Am J Bot 23:646–705

Lee IM, Davis RE, Gundersen-Rindal DE (2000) Phytoplasma: phytopathogenic mollicutes. Annu Rev Microbiol 54:221–255

Zhang J, Miller S, Hoy C, Zhou X, Nault L (1998) A rapid method for detection and differentiation of aster yellows phytoplasma-infected and -inoculative leafhoppers. Available at, http://esa.cos.com/cgi-bin/itinerary/index/author/zhang:::jiangua/

Vegetable Leafminer, *Liriomyza sativae* Blanchard (Diptera: Agromyzidae)

Vegetable leafminer is found commonly in southern North America, and in most of Central and South America. Occasionally it is reported in more northern areas because it is transported with plant material. It cannot survive cold areas except in greenhouses.

Host Plants

Vegetable leafminer attacks a large number of plants, but seems to favor those in the plant families Cucurbitaceae, Leguminosae, and Solanaceae. Nearly 40 hosts from 10 plant families are known in Florida. Among the numerous weeds infested, the nightshade, *Solanum americanum*; and Spanishneedles, *Bidens alba*; are especially suitable hosts in Florida. Vegetable crops known as hosts include bean, celery, eggplant, onions, pepper, potato, squash, tomato, watermelon, cucumber, beet, pea, lettuce and many other composites. Vegetable leafminer was formerly considered to be the most important agromyzid pest in North America, but this distinction is now held by American leafminer, *L. trifolii*.

Natural Enemies

Vegetable leafminer is attacked by a number of parasitoids, with the relative importance of species varying geographically and temporally. In Hawaii, *Chrysonotomyia punctiventris* (Crawford) (Hymenoptera: Eulophidae), *Halicoptera circulis* (Walker) (Hymenoptera: Pteromalidae), and *Ganaspidium hunteri* (Crawford) (Hymenoptera: Eucoilidae) are considered important in watermelon. In California and Florida, the same genera or species were found attacking vegetable leafminer on tomato or bean, but *Opius dimidiatus* (Ashmead) (Hymenoptera: Braconidae) also occurred commonly in Florida. Levels of parasitism are often reported to be proportional to leafminer density, but parasitoid effectiveness can be disrupted when insecticides are applied. Steinernematid nematodes can infect *L. trifolii* larvae when the nematodes are applied in aqueous suspension and the plants are held under high humidity conditions.

Life Cycle and Description

The developmental thresholds for eggs, larvae, and pupae are estimated at 9° to 12°C. The combined development time required by the egg and larval stages is about 7–9 days at warm temperatures (25° to 30°C). Another 7–9 days is required for pupal development at these temperatures. Both egg-larval and pupal development times lengthen to about 25 days at 15°C. At optimal temperatures (30°C), vegetable leaf miner completes development from the egg to adult stage in about 15 days.

Egg

The white, elliptical eggs measure about 0.23 mm in length and 0.13 mm in width. Eggs are inserted into plant tissue just beneath the leaf surface and hatch in about three days. Flies feed on the plant secretions caused by oviposition, and also on natural exudates. Females often make feeding punctures, particularly along the margins or tips of leaves, without depositing eggs. Females can produce 600–700 eggs over their life span, although some estimates of egg production suggest that 200–300 is more typical. Initially, females may deposit eggs at a rate of 30–40 per day, but egg deposition decreases as flies grow older.

Larva

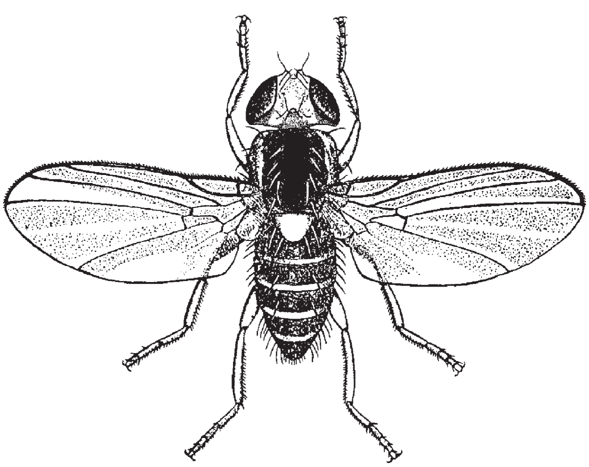
There are three active instars, and larvae attain a length of about 2.25mm. Initially the larvae are nearly colorless, becoming greenish and then yellowish as they mature. Black mouthparts are apparent in all instars, and can be used to differentiate the larvae. The average length and range of the mouthparts (cephalopharyngeal skeleton) in the three larval feeding instars is 0.09 (0.6–0.11), 0.15 (0.12– 0.17), and 0.23 (0.19–0.25) mm, respectively. The mature larva cuts a semicircular slit in the mined leaf just prior to formation of the puparium. The larva usually emerges from the mine, drops from the leaf, and burrows into the soil to a depth of only a few cm to form a puparium. A fourth larval instar occurs between puparium formation and pupation, but this is generally ignored by authors.

Pupa

The reddish brown puparium measures about 1.5 mm in length and 0.75 mm in width. After about nine days the adult emerges from the puparium. Mating initially occurs the day following adult emergence.

Adult

The adults (Fig. 8) are principally yellow and black in color. The shiny black mesonotum of *L. sativae* is used to distinguish this fly from the closely related American serpentine leafminer, *Liriomyza trifolii* which has a grayish black mesonotum. Females are larger and more robust than males, and have an elongated abdomen. The wing length of this species is 1.25–1.7 mm, with the males averaging about 1.3 mm and the females about 1.5 mm. The small size of these flies serves to distinguish them from pea leafminer, *Liriomyza huidobrensis* (Blanchard), which has a wing length of 1.7–2.25 mm. The yellow femora of vegetable leafminer also help to distinguish these species, as the femora of pea leafminer are dark. Flies normally live only about a month. Flies are uncommon during the cool months of the year, but often attain high, damaging levels by mid-summer. In warm climates they may breed continuously, with many overlapping generations per year.



Vegetable Leafminer, *Liriomyza sativae* Blanchard (Diptera: Agromyzidae), Figure 8 Vegetable leafminer adult, *Liriomyza sativae*.

Damage

Foliage punctures caused by females during the acts of oviposition or feeding may cause a stippled appearance on foliage, but this damage is slight compared to the leaf mining activity of larvae. The irregular mine increases in width from about 0.25 mm to about 1.5 mm as the larva matures, and is virtually identical in appearance and impact with the mines of *L. trifolii*. Larvae are often easily visible within the mine where they remove the mesophyll between the surfaces of the leaf. Their fecal deposits are also evident in the mines. Researchers have found that 30–60% yield increases are possible when effective insecticides were applied.

Management

Sampling

Several methods for population assessment have been studied, and collecting puparia in trays placed beneath plants and placement of yellow sticky traps to capture adults are most popular. Yellow sticky traps, however, have the advantage of being able to quickly detect invasion of a field by adults from surrounding areas.

Insecticides

Foliar application of insecticides is often frequent in susceptible crops. Insecticide susceptibility varies greatly both spatially and temporally. Many organophosphate and carbamate insecticides are no longer effective. Insecticides are disruptive to naturally occurring biological control agents, and leafminer outbreaks are sometimes reported to follow chemical insecticide treatment for other insects.

Cultural Practices

Some crops vary in susceptibility to leaf mining. This has been noted, for example, in cultivars of tomato, cucumber, cantaloupe, and beans. However, the differences tend to be moderate, and not adequate for reliable protection. Placement of row covers over cantaloupe has been reported to prevent damage by leafminer. Sometimes crops are invaded when adjacent crops are especially suitable. Weeds are a source of flies, but also a source of parasitoids.

► Vegetable Pests and their Management

References

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, CA, 729 pp

Johnson MW (1987) Parasitization of *Liriomyza* spp. (Diptera: Agromyzidae) infesting commercial watermelon plantings in Hawaii. J Econ Entomol 80:56–61

Palumbo JC (1995) Developmental rate of *Liriomyza sativae* (Diptera: Agromyzidae) on lettuce as a function of temperature. Southwest Entomol 20:461–465

Parrella MP (1987) Biology of *Liriomyza*. Annu Rev Entomol 32:201–224

Petitt FL, Wietlisbach DO (1994) Laboratory rearing and life history of *Liriomyza sativae* (Diptera: Agromyzidae) on lima bean. Environ Entomol 23:1416–1421

Schuster DJ, Gilreath JP, Wharton RA, Seymour PR (1991) Agromyzidae (Diptera) leafminers and their parasitoids in weeds associated with tomato in Florida. Environ Entomol 20:720

Vegetable Pests and their Management

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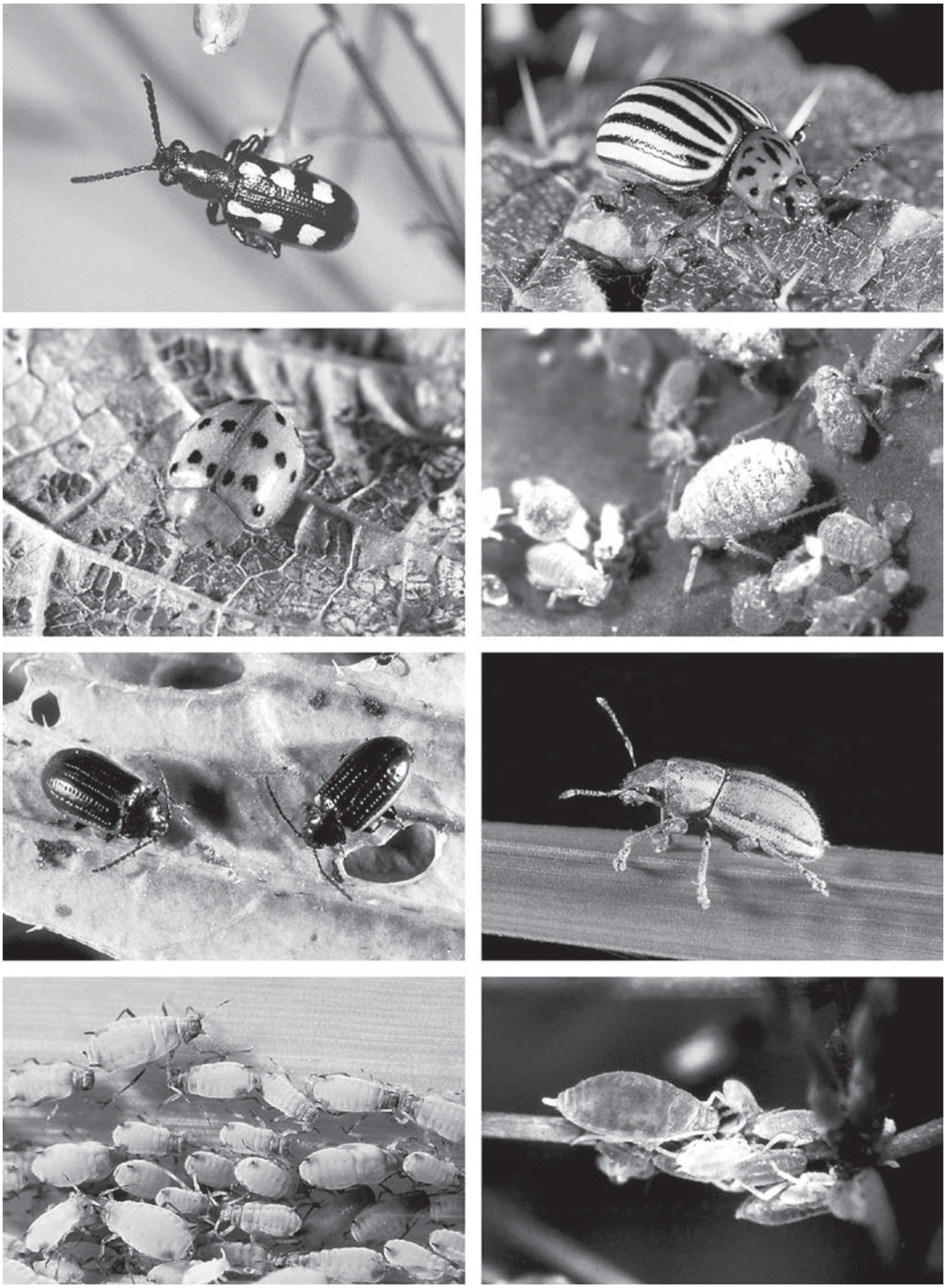
Throughout the world, vegetables are an important element of the human diet, providing a vital source of carbohydrates, vitamins, and minerals. Some vegetables remain unique to specific cultures, whereas others have gained wide acceptance and have been transported to several continents where they are grown extensively. In many cases, insect pests have been transported to new continents as well (Figs. 9 and 10). In some cases, the insects apparently were transported along with the initial plant material. In other cases, the insects were introduced as “hitch-hikers” on other products, but once gaining entrance to their new home found it quite suitable because their host plants had preceded them. Another important source of pests is host adaptation or host switching, wherein insects adapted to feeding on a particular plant (often a weed or other non-crop plant) begin feeding on introduced crops. Such insects usually adapt to crop plants in the same plant family as their original host, or inherently have a broad host range.

The major groups of vegetable crops and some key pests follow. A more complete list of pests, their hosts and geographic ranges, and the plant tissues damaged are listed in Table 2.

Artichoke (Family Compositae)

Artichoke, more correctly known as globe artichoke, is a thistle-like plant grown for the edible blossom bud. It is a perennial, with new growth arising annually from the roots. Like some other perennials, it can be grown with some success as an annual crop by planting roots, but this is not a common practice. Although artichoke can be grown over a broad geographic area, it is not cold-hardy. Commercial production is generally limited to Mediterranean climates, where the cool, moist environment favors its growth. It is not a popular vegetable, and is considered by many to be a “luxury” vegetable. The origin of artichoke appears to be the western Mediterranean region of Europe. A similar plant grown for the leaf stalks is cardoon, but this plant is not grown extensively. The key pest of artichoke is the artichoke plume moth, *Platyptilia carduidactyla* (Riley) (Lepidoptera: Pterophoridae), though such aphids as the artichoke aphid, *Capitophorus elaeagni* (del Guercio), and the bean aphid, *Aphis fabae* Scopoli (both Hemiptera: Aphididae), can be quite damaging at times.



Vegetable Pests and their Management, Figure 9 **Some vegetable pests of international significance. All have crossed national boundaries and most have spread to new continents. *Top row left*, asparagus beetle, *Crioceris asparagi*; *top row right*, Colorado potato beetle, *Leptinotarsa decemlineata*; *second row left*, Mexican bean beetle, *Epilachna varivestris; second row right*, whitefringed beetle, *Naupactus* sp.; *third row left*, yellowmargined leaf beetle, *Microtheca ochroloma*; *third row right*, cabbage aphid, *Brevicoryne brassicae*; *bottom row left*, corn leaf aphid, *Rhopalosiphum maidis*; *bottom row right*, asparagus aphid, *Brachycorynella asparagi*.**

Vegetable Pests and their Management, Figure 10 **Additional vegetable pests of international significance.** ***Top row left*****, harlequin bug, *****Murgantia histrionica*****; *****top row right*****, southern green stink bug, *****Nezara viridula*****;** ***second row left*****, diamondback moth, *****Plutella xylostella*****;** ***second row right*****, European corn borer, *****Ostrinia nubilalis*****;** ***third row left*****, imported cabbageworm, *****Pieris rapae*****;** ***third row right*****, corn earworm, *****Helicoverpa zea*****;** ***bottom row left*****, pickleworm, *****Diaphania nitidalis*****;** ***bottom row right*****, beet armyworm, *****Spodoptera exigua*****.**

Vegetable Pests and their Management, Table 2 Some important vegetable crop pests, the continents where they are found, and the crops and parts of the crop plants affected by these pests

Taxa and name	Continents affected[a]	Crops damaged[b]	Parts of crops damaged
Coleoptera: Chrysomelidae			
Acalymma vittatus (Fabricius), striped cucumber beetle	NA, SA	cucurbits, legumes	blossom, fruit, foliage, root
Aulacophora abdominalis (F.), pumpkin beetle	AU, AS	cucurbits	foliage
Ceratoma ruficornis (Oliver), redhorned leaf beetle	NA, SA	legumes	foliage
Crioceris asparagi (L.), asparagus beetle	EU, NA	asparagus	foliage, stem
Diabrotica balteata LeConte; banded cucumber beetle	NA, SA	numerous crops, but especially crucifers, cucurbits, and solanaceous crops	foliage, flower, fruit, root
Diabrotica undecimpunctata Mannerheim, spotted cucumber beetle	NA	numerous but primarily legume, solanaceous and cucurbit crops	blossom, fruit, foliage, root
Diabrotica virgifera LeConte, western corn rootworm	NA	cucurbits, sweet corn	blossom, fruit, foliage, root
Epitrix cucumeris (Harris), potato flea beetle	NA	solanaceous crops	foliage, root
Epitrix tuberis Gentner, tuber flea beetle	NA	solanaceous crops	foliage, root
Leptinotarsa decemlineata (Say), Colorado potato beetle	EU, NA	solanaceous crops	foliage
Phyllotreta cruciferae (Goeze), crucifer flea beetle	AF, EU, NA	crucifers	foliage, root
Raphidopalpa foveicollis Lucas, red pumpkin beetle	AF, AS	cucurbits	blossoms, foliage
Coleoptera: Bruchidae			
Acanthoscelides obtectus (Say), bean weevil	AF, EU, NA, SA	legumes	fruit
Coleoptera: Curculionidae			
Anthonomus eugenii Cano, pepper weevil	NA	pepper	blossom, fruit
Apion spp., weevils	AF, AS, AU, SA	numerous crops	blossom, fruit, foliage, stem
Ceutorhynchus assimilis Paykull, cabbage seedpod weevil	EU, NA	crucifers	fruit
Cylas formicarius (Fabricius), sweetpotato weevil	AF, AS, AU, NA, SA	sweet potato	root, tuber
Cylas puncticolis Boh., African sweetpotato weevil	AF	sweet potato	foliage, stem, tuber

Vegetable Pests and their Management, Table 2 Some important vegetable crop pests, the continents where they are found, and the crops and parts of the crop plants affected by these pests (Continued)

Taxa and name	Continents affected[a]	Crops damaged[b]	Parts of crops damaged
Listronotus oregonensis (LeConte), carrot weevil	NA	carrot	root, stem
Naupactus spp., whitefringed beetles	AF, AU, NA, SA	numerous crops	foliage, root, tuber
Sitona lineatus (L.), pea leaf weevil	AS, EU, NA	legumes	foliage, root
Coleoptera: Coccinellidae			
Epilachna chrysomelina (F.), 12-spotted melon beetle	AF, EU	cucurbits	foliage
Epilachna varivestris Mulsant, Mexican bean beetle	NA	bean	foliage
Coleoptera: Scarabaeidae			
Popillia japonica Newman, Japanese beetle	AS, NA	numerous crops	foliage, fruit
Diptera: Agromyzidae			
Liriomyza bryoniae (Kaltenbach), tomato leaf miner	AF, AS, EU	numerous crops	foliage
Liriomyza huidobrensis (Blanchard), pea leafminer	AS, NA, SA	numerous crops	foliage
Liriomyza sativae Blanchard, vegetable leafminer	EU, NA	numerous crops	foliage
Liriomyza trifolii (Burgess), American serpentine leafminer	EU, NA, SA	numerous crops	foliage
Melanagromyza sojae (Zehn.), bean fly	AF, AS	legumes	stem
Melanagromyza obtusa Mall., bean pod fly	AS	legumes	seed
Ophiomyia phaseoli (Tyron), bean fly	AF, AS, AU	legumes	stem
Phytomyza horticola Goureau, pea leaf miner	AF, AS, EU	numerous crops	foliage
Diptera: Anthomyiidae			
Delia antiqua (Meigen), onion maggot	AS, EU, NA	onion and related crops	root, stem
Delia platura (Meigen), seedcorn maggot	AS, AF, AU, EU, NA	numerous crops	roots, stem
Delia radicum (L.), cabbage maggot	AS, EU, NA	crucifers	root, stem
Pegomya betae Curtis, beet leafminer	AF, AS, EU, NA	chenopods	foliage

Vegetable Pests and their Management, Table 2 Some important vegetable crop pests, the continents where they are found, and the crops and parts of the crop plants affected by these pests (Continued)

Taxa and name	Continents affected[a]	Crops damaged[b]	Parts of crops damaged
Pegomya hyoscyami (Panzer), spinach leafminer	AF, AS, EU, NA	chenopods	foliage
Diptera: Cecidomyiidae			
Contarinia pisi (Winnertz), pea midge	EU	legumes	blossom
Diptera: Psilidae			
Psila rosae (Fabricius), carrot rust fly	AS, EU, NA	carrot	root
Diptera: Tephritidae			
Bactrocera cucumis (French), cucumber fly	AU	cucurbits and tomato	fruit
Bactrocera cucurbitae (Coquillett), melon fly	AF, AS	cucurbit, legume, and solanaceous crops	blossom, fruit, vine
Bactrocera dorsalis (Hendel), oriental fruit fly	AF, AS	cucurbit and solanaceous crops	fruit
Daucus ciliatus Loew, lesser pumpkin fly	AF, AS	cucurbits	fruit
Daucus frontalis Becker, African melon fly	AF	cucurbits	fruit
Eulia heraclei (L.), celery fly	EU	umbellifers	foliage
Myopardalinis pardalina Bigot, cantaloupe fruit fly	AS	cucurbits	fruit
Diptera: Tipulidae			
Tipula paludosa Meigen, European crane fly	AS, EU, NA	numerous crop	root
Hemiptera: Coreidae			
Anasa tristis (De Geer), squash bug	NA	cucurbits	foliage, fruit
Leptoglossus spp., leaffooted bugs	AF, AS, AU, NA	numerous crops	foliage, fruit
Hemiptera: Miridae			
Lygus lineolaris (Palisot de Beauvois), tarnished plant bug	NA	numerous crops	blossom, fruit, stem, foliage
Hemiptera: Pentatomidae			
Nezara viridula (L.), southern green stink bug	AF, AS, AU, EU, NA, SA	numerous crops but principally legume, crucifer, and solanceous crops	blossom, fruit
Hemiptera: Pyrrhocoridae			
Dysdercus spp., cotton stainers	AF, AS, AU, NA, SA	okra	fruit

Vegetable Pests and their Management, Table 2 Some important vegetable crop pests, the continents where they are found, and the crops and parts of the crop plants affected by these pests (Continued)

Taxa and name	Continents affected[a]	Crops damaged[b]	Parts of crops damaged
Hemiptera: Aleyrodidae			
Aleyrodes proletella (L.), cabbage whitefly	AU, EU	crucifers	foliage
Bemisia argentifolii Bellows and Perring, silverleaf whitefly	E, NA	numerous crops but especially solanaceous and cucurbit crops	foliage
Bemesia tabaci (Gennadius), cotton whitefly	AF, AS	numerous crops	foliage
Trialeurodes vaporariorum (Westwood), greenhouse whitefly	E, NA	numerous crops but especially solanaceous and cucurbit crops	foliage
Hemiptera: Aphididae			
Acyrthosiphon pisum (Harris), pea aphid	AF, AS, AU, EU, NA, SA	legumes	foliage, stem
Aphis fabae Scopoli, bean aphid	AF, AS, EU, NA, SA	chenopods, legumes	foliage, stem
Aphis gossypii Glover, melon aphid	AF, AS, AU, EU, NA, SA	numerous crops	foliage, stem
Brachycorynella asparagi (Mordvilko), asparagus aphid	AS, EU, NA	asparagus	foliage
Brevicoryne brassicae (L.), cabbage aphid	AF, AS, AU, EU, NA, SA	crucifers	foliage
Cavariella aegopodii Scopoli, willow-carrot aphid	EU, NA	umbellifers	foliage
Lipaphis erysimi (Kaltenbach), turnip aphid	AF, AS, AU, EU, NA, SA	crucifers	foliage
Macrosiphum euphorbiae (Thomas), potato aphid	AF, AS, AU, EU, NA, SA	numerous crops	foliage, stem
Myzus persicae (Sulzer), green peach aphid	AF, AS, AU, EU, NA, SA	numerous crops	foliage, stem
Nasonovia ribisnigri (Mosley), lettuce aphid	EU, NA, SA	lettuce and related crops	foliage
Pemphigus bursarius (L.), lettuce root aphid	AF, AS, AU, EU, NA	lettuce and related crops	root
Hemiptera: Cicadellidae			
Circulifer tenellus (Baker), beet leafhopper	AF, EU, NA	chenopod, cucurbit, and solanaceous crops	foliage
Circulifer opacipennis (Leth.), beet leafhopper	AF, EU, AS	chenopod, cucurbit and solanaceous crops	foliage
Dalbulus maidis (DeLong and Wolcott)	NA, SA	sweet corn	

Vegetable Pests and their Management, Table 2 Some important vegetable crop pests, the continents where they are found, and the crops and parts of the crop plants affected by these pests (Continued)

Taxa and name	Continents affected[a]	Crops damaged[b]	Parts of crops damaged
Empoasca fabae (Harris), potato leafhopper	NA	numerous crops	foliage
Macrosteles quadrilineatus Forbes, aster leafhopper	NA	several crops, especially lettuce	foliage
Hemiptera: Delphacidae			
Peregrinus maidis (Ashmead), corn delphacid	NA, SA	sweet corn	foliage
Lepidoptera: Gelechiidae			
Keiferia lycopersicella (Walsingham), tomato pinworm	NA, SA	solanaceous crops	foliage
Phthorimaea operculella (Zeller), potato tuberworm	AF, AS, AU, EU, NA, SA	solanaceous crops	foliage, tuber
Lepidoptera: Noctuidae			
Agrotis ipsilon (Hufnagel), black cutworm	AF, AS, AU, EU, NA, SA	numerous crops	foliage, fruit, stem
Agrotis segetum (Denis & Schiffermuller), turnip moth	AF, AS, EU	numerous crops	stem, root
Autographa gama (L.), silver Y moth	AF, AS, EU	numerous crops	foliage
Helicoverpa armigera (Hübner), old world bollworm	AF, AS, AU, EU	numerous crops	foliage, fruit
Helicoverpa zea (Boddie), corn earworm	NA, SA	numerous crops	foliage, fruit
Hydraecia micacea (Esper), potato stem borer	AS, EU, NA	numerous	stem
Mamestra brassicae (L.), cabbage moth	AS, EU	crucifers	foliage
Noctua pronuba (L.), large yellow underwing	AF, AS, EU	numerous	foliage, root, stem, tuber
Peridroma saucia (Hübner), variegated cutworm	AF, AS, EU, NA, SA	numerous crops	foliage, fruit, stem
Spodoptera eridania (Cramer), southern armyworm	NA, SA	numerous crops but especially cucurbit and solanaceous crops	foliage, fruit
Spodoptera exigua (Hübner), beet armyworm	AS, NA	numerous crops	foliage
Spodoptera frugiperda (J.E. Smith), fall armyworm	NA, SA	numerous crops but especially sweet corn	foliage
Spodoptera littoralis (Boisduval), African cotton worm	AF, EU	artichoke, crucifers, and solanaceous crops	foliage

Vegetable Pests and their Management, Table 2 **Some important vegetable crop pests, the continents where they are found, and the crops and parts of the crop plants affected by these pests (Continued)**

Taxa and name	Continents affected[a]	Crops damaged[b]	Parts of crops damaged
Spodoptera litura (Fabricius), rice cutworm	AU, AS	legumes, sweetpotato, and solanaceous crops	foliage
Trichoplusia ni (Hübner), cabbage looper	AF, AS, EU, NA, SA	numerous crops	foliage
Xestia spp. (L.), spotted cutworm	AF, AS, EU, NA	numerous crops	foliage, stem
Lepidoptera: Nymphalidae			
Acraea acerata Hew.	AF	sweet potato	foliage
Lepidoptera: Pieridae			
Pieris brassicae (L.), large cabbage white butterfly	AF, AS, EU	crucifers	foliage
Pieris canidia (L.), small white butterfly	AS	crucifers	foliage
Pieris rapae (L.), imported cabbageworm	AF, AS, AU, EU, NA	crucifers	foliage
Lepidoptera: Pterophoridae			
Platyptilia carduidactyla (Riley), artichoke plume moth	NA	artichoke	stem
Lepidoptera: Pyralidae			
Diaphania hyalinata L., melonworm	NA, SA	cucurbits	foliage
Diaphania indica (Saunders) pumpkin caterpillar	AF, AS, AU, NA, SA	cucurbits	foliage
Diaphania nitidalis (Stoll), pickleworm	NA, SA	cucurbits	blossom, fruit
Etiella zinckenella (Treitschke), limabean pod borer	AF, AS, AU, EU, NA, SA	legumes	fruit
Evergestis forficalis (L.), garden pebble moth	AS, EU	crucifers	foliage
Hedylepta indicata (Fabricius), bean webworm	AF, AS, SA	legumes	foliage
Leucinodes orbonalis Guenée, eggplant fruit borer	AF, AS	numerous crops	foliage, fruit
Maruca testulalis (Geyer), bean pod borer	AF, AS, AU, NA, SA	legumes	fruit
Ostrinia nubilalis (Hübner), European corn borer	AF, AS, EU, NA	sweet corn and solanaceous crops	fruit, stem
Omphisa anastomosalis Guenée, sweetpotato vine borer	AS	sweet potato	stem

Vegetable Pests and their Management, Table 2 Some important vegetable crop pests, the continents where they are found, and the crops and parts of the crop plants affected by these pests (Continued)

Taxa and name	Continents affected[a]	Crops damaged[b]	Parts of crops damaged
Plutella xylostella (L.), diamond-back moth	AF, AU, AS, EU, NA, SA	crucifers	foliage
Lepidoptera: Sesiidae			
Melittia cucurbitae (Harris), squash vine borer	NA, SA	cucurbits	stem
Lepidoptera: Sphingidae			
Agrius convulvuli (L.), sweet-potato hornworm	AF, AS, AU, EU	sweetpotato, legumes	foliage
Lepidoptera: Tortricidae			
Cydia nigricana (Fabricius), pea moth	EU, NA	legumes	fruit
Lepidoptera: Yponomeutidae			
Acrolepiopsis assectella (Zeller), leek moth	AS, EU	onion and related plants	foliage
Hymenoptera: Tenthredinidae			
Athalia spp., cabbage sawfly	AS, AF, EU	crucifers	foliage
Thysanoptera			
Frankliniella occidentalis (Pergande), western flower thrips	AS, EU, NA, SA,	primarily cucurbit and solanaceous crops	blossom
Frankliniella schulzei (Trybom)	AF	legumes, sweet potato, and solanaceous crops	foliage
Thrips palmi Karny, melon thrips	AU, AS, NA, SA	cucurbit and solaceous crops	blossom, fruit, foliage
Thrips tabaci Lindeman, onion thrips	AF, AU, AS, EU, NA, SA	onion and related crops	foliage, fruit
Acari			
Aculops lycopersici (Massee), tomato russet mite	AF, AS, AU, EU, NA, SA	solanaceous crops	foliage, stem
Polyphagotarsonemus latus (Banks), broad mite	AF, AS, AU, EU, NA, SA	numerous cops	foliage
Tetranychus urticae Koch, twospotted spider mite	AF, AU, AS, EU, NA, SA	numerous but principally cucurbit, legume, and solanaceous crops	foliage

[a]Regions are AF, Africa; AU, Australia/New Zealand; AS, Asia; EU, Europe; NA, North America; SA, South America
[b]Crops are artichoke, family Compositae; asparagus, family Liliaceae; chenopods, family Chenopodiaceae; crucifers, family Cruciferae; cucurbits, family Cucurbitaceae; legumes, family Leguminosae; lettuce, family Compositae; okra, family Malvaceae; onion, family Amaryllidaceae; pepper, family Solanaceae; solanaceous, family Solanaceae; sweet corn, family Graminae; sweet potato, family Convolvulaceae; umbellifers, family Umbelliferae

Asparagus (Family Liliaceae)

Asparagus is a hardy perennial plant, and once established, remains productive for 15 to 20 years. It is grown in many temperate climates, and is winter-hardy in most climates. It is usually grown from crowns (roots), but seeds may be used. Seeds are spread freely by birds, and it is common to find asparagus growing wild along roadsides, fences and irrigation ditches. Asparagus is popular in home gardens grown in northern areas, probably because it is one of the first crops available for harvest in the spring. It has been a popular vegetable since ancient times, and originated in the Mediterranean region. The spears or stems are harvested as they first push up from the soil; once they begin to branch, they become tough and inedible. The most serious pests are the asparagus aphid, *Brachycorynella asparagi* (Mordvilko) (Hemiptera: Aphididae), and the asparagus beetles, *Crioceris* spp. (Coleoptera: Chrysomelidae).

Bean and Related Crops (Family Leguminosae) (Bush Bean, Chickpea, Cowpea, Dry Bean, English Pea, Faba Bean, Lentil, Lima Bean, Mung Bean, Pigeon Pea, Snap Bean, etc.)

Legumes are known for their ability to harbor nitrifying bacteria; nitrogen enhances soil productivity. The cultivated legume vegetable crops are not particularly efficient as a source of nitrogen for plant growth, however, so fertilization is still required. They are, however, a relatively good source of vegetable protein, so they are an important dietary component in areas where animal protein is limited. Most of the leguminous vegetable crops are warm-weather crops and are killed by light frosts. English pea is a notable exception, thriving under early season and cool weather conditions, but killed by heavy frost. The legume vegetables are annual crops. The *Phaseolus* bean crops, such as snap bean and lima bean, are native to Central America. English pea and cowpea likely originated in Asia. The legumes are cultivated for their seeds or seed pods, and are eaten fresh or dried.

There are many important pests of legumes, and they vary among crops and geographically. The seed-attacking maggots, *Delia* spp. (Diptera: Anthomyiidae), can be important pests under cool weather conditions. The Mexican bean beetle, *Epilachna varivestris* Mulsant (Coleoptera: Coccinellidae) is important in North America. The Old World bollworm, *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae), affects pigeon pea crops in Africa and Asia. English pea is quite susceptible to infestation by the pea aphid, *Acyrthosiphon pisum* Shinji (Hemiptera: Aphididae), the pea leaf weevil, *Sitona lineatus* (L.) (Coleoptera: Curculionidae), and the pea midge, *Contarinia pisi* (Winnertz) (Diptera: Cecidomyiidae); they are most damaging in northern areas. Cowpea is plagued by cowpea weevils, *Callosobruchus* spp. (Coleoptera: Bruchidae). Locally, a number of other pests can be important, particularly thrips, leaf miners, leafhoppers, and flea beetles.

Beet and Related Crops (Family Chenopodiaceae) (Beet, Chard, Spinach, Swiss Chard)

Beet apparently originated in the Mediterranean region, and spinach originated in Iran. The beet and its relatives are biennial crops, requiring more than one year, but less than two, to complete their natural life cycle. They are grown as annuals when cultivated as vegetables. Though originally grown entirely for its foliage, cultivars of beets with edible below-ground portions (the edible "root" is mostly thickened stem material) became popular in Europe beginning about 1800. Beet and chard are not important crops except in cool-weather climates. Spinach is more popular as a commercial crop relative to other chenopods, but is relatively unpopular compared to many warm-weather vegetables. In home gardens, these crops thrive nearly everywhere. The principal pests are the green peach aphid, *Myzus persicae* (Sulzer) (Hemiptera: Aphididae), and the beet and spinach leafminer, *Pegomya* spp. (Diptera: Anthomyiidae). In western North America and in Europe, the beet leafhoppers, *Circulifer tenellus* (Baker) and *C. opacipenis* (Leth.) (both Hemiptera: Cicadellidae), can be very damaging.

Cabbage and Related Crops (Family Cruciferae) (Broccoli, Brussels Sprouts, Cabbage, Cauliflower, Chinese Cabbage, Collards, Kale, Kohlrabi, Mustard, Radish, Rutabaga, Turnip, Etc.)

Cruciferous vegetables, often called "cole" crops, are grown for their leaves. These are cool-season crops, and tolerate light freezes and even brief heavy freezes, but prolonged deep freezes are fatal. Though naturally biennials, they are grown as annuals. Cabbage and its many forms originated along the shores of Europe; mustard and radish are from Asia. Some are popular foods throughout the world, others are of regional significance. Perhaps the most interesting vegetable in this group is broccoli, which has become popular only since the 1950s. Cauliflower is a moderately important crop. Cabbage and turnip have declined in importance, though cabbage remains a significant crop. Rutabaga is an important dietary element in northern climates, and collards are important in southern areas. The principal pests of cabbage and its closest relatives include the root maggots, *Delia* spp. (Diptera Anthomyiidae); the cabbage aphid, *Brevicoryne brassicae* (Linnaeus), and the turnip aphid, *Lipaphis erysimi* (Kaltenbach) (both Hemiptera: Aphididae); the diamondback moth, *Plutella xylostella* (Linnaeus) (Lepidoptera: Pyralidae); the cabbage looper, *Trichoplusia ni* (Hübner) and the cabbage moth, *Mamestra brassicae* (L.) (both Lepidoptera: Noctuidae); and the imported cabbageworm, *Pieris rapae* (Linnaeus) (Lepidoptera: Pieridae). Mustard and radish tend to be plagued more by the green peach aphid, *Myzus persicae* (Sulzer) (Hemiptera: Apididae).

Carrot and Related Crops (Family Umbelliferae) (Carrot, Celery, Celeriac, Chervil, Coriander, Fennel, Parsley, Parsnip)

The umbelliferous vegetables are biennial, but are grown as annuals. They require cool weather to develop properly. Most survive heavy frost, but are killed by prolonged freezing weather. The major crops of this group, carrot and celery, originated in the Mediterranean region. Carrot and parsnip are grown for their roots; celery, celeriac and fennel for the swollen stem bases; and parsley and coriander (cilantro) for their foliage. Carrot and celery, and to a lesser degree parsley and coriander, are popular vegetables. Parsnip is an important crop in northern climates because it stores well during the winter months, and can even be left in the soil during freezing weather. Fennel is growing in popularity, but as yet, is a minor crop awaiting discovery by some cultures. Chervil is grown in Europe, and different types are grown for their roots and foliage. In some areas, the carrot weevil, *Listronotus oregonensis* (LeConte) (Coleoptera: Curculionidae), the willow-carrot aphid, *Cavariella aegopodii* (Scopoli) (Hemiptera: Aphididae), and the carrot rust fly, *Psila rosae* (Fabricius) (Diptera: Psilidae), are important pests. Leafhoppers (Hemiptera: Cicadellidae) sometimes transmit aster yellows disease. The American serpentine leafminer, *Liriomyza trifolii* (Burgess), and the serpentine leaf miner, *L. sativae* Blanchard (both Diptera: Agromyzidae), are often a serious threat to commercially grown celery.

Lettuce and Related Crops (Family Compositae) (Celtuce, Chicory, Endive, Escarole, Lettuce, Radicchio)

Lettuce is a popular salad vegetable. Lettuce apparently originated in Europe or Asia, and has been grown for over 2,000 years. Lettuce and most related crops are grown for their leaves, though, in the case of celtuce, the stem is eaten. Lettuce and related crops are cool-season annuals. Although killed by heavy frost, these crops are also susceptible to disruption by excessive heat. Hot weather causes lettuce to flower and become bitter tasting. Several insects are important pests of lettuce. The aster leafhopper, *Macrosteles quadrilineatus* Forbes, (Hemiptera: Cicadellidae), is an important vector of aster yellows in some production areas. Several species of aphids (Hemiptera: Aphididae), including the lettuce aphid, *Nasonovia ribisnigri* (Mosley), and the lettuce root aphid, *Pemphigus bursarius* (L.), may be damaging, though the green peach aphid, *Myzus persicae* (Sulzer), generally is the most important pest. Numerous caterpillars such as the corn earworm, *Helicoverpa zea* (Boddie), and the cabbage looper, *Trichoplusia ni* (Hübner) (both Lepidoptera: Noctuidae), also threaten lettuce crops.

Okra (Family Malvaceae)

Okra is thought to be native to Africa and is an important crop in tropical countries. It is an annual plant and is killed by light frost. Okra is grown for the seed pods which, like snap beans, are harvested before they mature. Okra is unusually tall for a vegetable crop, often attaining a height of 2 m. The pods are subject to attack by several pests. Some of the most damaging are: the red imported fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae); the cotton aphid, *Aphis gossypii* Glover (Hemiptera: Aphididae); the Old World bollworm, *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctudae); the southern green stink bug, *Nezara viridula* (Linnaeus) (Hemiptera: Pentatomidae); cotton stainers, *Dysdercus* spp. (Hemiptera: Pyrrhocoridae); and leaffooted bugs, *Leptoglossus* spp. (Hemiptera: Coreidae).

Onion and Related Plants (Family Alliaceae) (Chive, Garlic, Leek, Onion, Shallot)

The onion and its relatives are biennial or perennial plants, but cultivated as annuals. These have long been important crops, with the use of onions documented for nearly 5,000 years. Their origin is thought to be Asia. Onion is grown principally for the below-ground leaf bases, which form a bulb, but the tops are also edible. They are tolerant of cool weather, but also thrive under hot conditions. Onion and garlic are cultivated widely. The key pests of onion are onion thrips, *Thrips tabaci* Lindeman (Thysanoptera: Thripidae), and the onion maggot, *Delia antiqua* (Meigen) (Diptera: Anthomyiidae).

Rhubarb (Family Polygonaceae)

Rhubarb is cultivated as a perennial. Its origin is northern Asia, and its use can be traced back about 5,000 years. Rhubarb thrives where summers are cool. The stalks, or leaf petioles, are used as food, though this vegetable is infrequently consumed. Most commercial production occurs in northern regions, but it remains principally a home garden crop. There are few important pests of rhubarb, with the bean aphid, *Aphis fabae* Scopoli (Hemiptera; Aphididae), and the rhubarb curculio, *Lixus concavus* Say (Coleoptera: Curculionidae), perhaps the most serious.

Squash and Related Crops (Family Cucurbitaceae) (Cucumber, Melons, Pumpkin, Squash, Watermelon, Etc.)

The cucurbit crops are important vegetables, though they vary in economic importance. They are annual plants, and are warmth-loving crops. Light frost will kill cucurbits, and even cool weather will permanently disrupt growth. All are cultivated for their fruit. Squash and pumpkin originated in Central and South America; cucumber, melons and watermelon are from Africa, or perhaps Asia. Cucurbit crops have some serious insect pests, including the squash vine borer, *Melittia cucurbitae* (Harris) (Lepidoptera: Sesiidae); the squash bug, *Anasa tristis* (De Geer) (Hemiptera:

Coreidae); the melonworm, *Diaphania hyalinata* (L.), the pumpkin caterpillar, *Diaphania indica* (Saunders), and the pickleworm, *Diaphania nitidalis* (Stoll) (all Lepidoptera: Pyralidae); the red pumpkin beetle, *Aulacophora* spp., and cucumber beetles, *Acalymma* sp. (all Coleoptera: Chrysomelidae). Whiteflies (Hemiptera: Aleyrodidae) and aphids (Hemiptera: Aphididae) are plant virus vectors.

Sweet Corn (Family Graminae)

Corn, which is usually known as maize outside of North America, apparently was domesticated in Mexico, and perhaps is descended from a similar grain, teosinte. Corn originally was cultured because it was productive, a good source of carbohydrates and other nutrients, and the grain stored well. Sweet corn is a recent innovation that was first developed in the mid 1700s, and lacks the storage characteristics of the older types, or grain corn. Corn is grown for the seeds, which are clustered in a structure called the "ear." Sweet corn is a popular vegetable, and the development of fresh corn that does not quickly lose its sweetness (supersweet cultivars) has increased demand for whole-ear corn. Many pests feed on corn, including the corn earworm, *Helicoverpa zea* (Boddie), the fall armyworm, *Spodoptera frugiperda* (J.E. Smith), and several cutworms (all Lepidoptera: Noctuidae); the *Diabrotica* rootworms (Coleoptera: Chrysomelidae); the European corn borer, *Ostrinia nubilalis* (Hübner) (Lepidoptera: Pyralidae); the Japanese beetle, *Popillia japonica* Newman (Coleoptera: Scarabaeidae); and the corn leaf aphid, *Rhopalosiphum maidis* (Fitch) (Hemiptera: Aphididae).

Sweet Potato (Family Convolvulaceae)

Sweet potato is an immensely important crop in some parts of the world, principally in tropical areas. The sweet potato probably originated in Mexico and is well adapted to tropical growing conditions. Some moist-fleshed sweet potatoes are called yams, but yams are a separate species normally found in Polynesia. A perennial crop, sweet potato is normally grown as an annual. It is cultivated for its tuber. The sweet potato cannot tolerate prolonged cool weather and perishes if exposed to light frost. The sweetpotato weevil, *Cylas formicarius* (Fabricius) (Coleoptera: Curculionidae), is the most damaging pest of this crop, but the sweetpotato vine borer, *Omphisa anastomasalis* (Guenée) (Lepidoptera: Pyralidae), wireworms (Coleoptera: Elateridae), whiteflies (Hemiptera: Alyrodidae), and the flea beetle and the cucumber beetle larvae (both Coleoptera: Chrysomelidae) are economically threatening.

Tomato and Related Plants (Family Solanaceae) (Eggplant, Pepper, Potato, Tomatillo, Tomato)

The solanaceous crops are among the most important vegetable crops. Both the crops and the pests are quite diverse. Potato ranks as the most valuable, but tomato and pepper also rank among the most highly valued crops. The potato is grown for its tuber, and the other crops for their fruit. The origins of the solanaceous crops are diverse; eggplant originated in India, potato and tomato in Peru, and tomatillo and pepper in Mexico or Guatemala. Tomato, tomatillo, pepper and eggplant are warm-season perennials that are cultivated as annuals. The potato is a cool-season perennial cultured as an annual. Potato crops are at risk from the Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae), but several aphids (Hemiptera: Aphididae) also are commonly damaging, particularly the green peach aphid, *Myzus persicae* (Sulzer) and the potato aphid, *Macrosiphum euphorbiae* (Thomas) (both Hemiptera: Aphididae). Beet leafhoppers *Circulifer tenellus* (Baker) and *Circulifer opacipennis* (Leth.) (Hemiptera: Cicadellidae), can be damaging to potatoes and tomatoes. Tomato is affected by the silverleaf whitefly, *Bemisia argentifolii* Bellows and Perring (Hemiptera: Aleyrodidae); the corn earworm, *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae), and many other pests. The pepper weevil, *Anthonomus eugenii* Cano (Coleoptera: Curculionidae), is the key pest of pepper in warm-weather areas of North America.

The Characteristics of Pests

Pests vary from place to place, and from time to time. In some cases, pests are consistently abundant or damaging (so-called key pests), but in other cases, many years may pass before a particular species attains pest status. Most vegetable producers plan for the regular, or key, pests (many of them are mentioned above or are listed in the table) and take preventative actions to keep the pests from inflicting injury. It also is wise to monitor crops and to be alert for the less regular pests that come along periodically and may also require some corrective action.

The Pest Complex

Irrespective of the crop, there usually is a diversity of pests attacking, often including one or more aphids, flea beetles, leaf beetles, weevils, and cutworms or leaf-feeding caterpillars. The pest complex is often quite similar within related crops (members of the same plant family), and so it is not surprising to see the potato aphid (Hemiptera: Aphididae) on tomato, or the Colorado potato beetle (Coleoptera: Chrysomelidae) on tomato and eggplant, because they are all members of the family Solanceae and have similar plant chemistry. Some pest species distinguish among related plants, however, and so specialists, such as the pepper weevil (Coleoptera: Curculionidae), are limited to a single host, in this case, pepper.

In contrast, the pest complex often is quite different among crops from different plant families. Thus, the squash bug (Hemiptera: Coreidae) and the pickleworm (Lepidoptera: Pyralidae), are limited to Cucurbitaceae; the tuber flea beetle and the Colorado potato beetle (both Coleoptera: Chrysomelidae), are limited to Solanaceae; and the asparagus beetle (Coleoptera: Chrysomelidae), and the asparagus aphid (Hemiptera: Aphididae), are limited to asparagus.

Polyphagous species, insects with a very wide host range, display different behavior. Insects, such as the melon aphid, the green peach aphid (both Hemiptera: Aphididae), the silverleaf whitefly (Hemiptera: Aleyrodidae), and the Japanese beetle (Coleoptera: Scarabaeidae), seem to feed on almost everything. This is not true, of course, as they have preferred, or more suitable, hosts, but their host range includes hundreds of species. Thus, they can be expected to appear on, and perhaps be damaging to, many crops.

Crops are not the only factor determining the presence of pests. Weather and climate are quite important because some pests are adapted for warm climates and others for cool climates. Thus, their tolerance of weather and climate determines the extent of their geographic range as surely as an ocean or a mountain range. For instance, silverleaf whitefly (Hemiptera: Aleyrodidae), melon thrips (Thysanoptera), or broad mite (Acarina) are not seen in cool climates; nor are pea leaf weevil (Coloptera: Curculionidae), Japanese beetle (Coleoptera: Scarabaeidae), or European crane fly (Diptera: Tipulidae) found in subtropical and tropical environments. They are adapted to certain environments and cannot live outside their preadapted geographic range. Over time, they may evolve a broader tolerance and expand their geographic range, but this is a slow process. Interestingly, plants tend to be more tolerant of weather conditions than do their insect parasites. Therefore, the extremes of the host plant's geographic range often lack the "normal" complement of insect herbivores.

Weather also influences the dispersal of vegetable insects. Some species overwinter only in warm climates, dispersing northward annually.

Their ability to disperse varies from year to year depending on weather patterns, though, in many areas, it is not a question of whether or not they will disperse, but only when the dispersal will occur. Examples of annual long-range dispersal are common in North America, where species such as the black cutworm, the fall armyworm (both Lepidoptera: Noctuidae), the pickleworm (Lepidoptera: Pyralidae), the aster leafhopper, and the beet leafhopper (both Hemiptera: Cicadelidae) disperse northward annually.

Types of Damage

Insects usually affect vegetable crops by feeding directly on the harvested part of the plant (called direct pests), or on a part of the plant that is important to its productivity, such as the roots or the leaves. This latter group is known as indirect pests because they cause damage indirectly, by weakening the plant. Thus, caterpillars act as direct pests when they feed on the actual tomato fruit, but as indirect pests when they consume the tomato plant's foliage. Typically, species that function as direct pests are more damaging. Leaf feeding can be direct injury, however, when the foliage is harvested, as in lettuce or spinach. Foliage and fruit can be damaged above-ground, or plant tissues (roots, tubers, basal stem tissue) may be damaged below-ground. Damage can be manifested in leaf rolling or webbing, speckling, or growth deformities in addition to tissue removal.

A third important type of damage is plant disease transmission. Plant disease, particularly plant viruses, can be transmitted through the activities of insects. Some insects, such as aphids, may transmit diseases even to plants they do not normally feed upon. Disease transmission can occur while an aphid is sampling its environment, flying from plant to plant seeking an appropriate host. Even if the aphid alights on a plant that is unsuitable for its growth and reproduction, a short probe by the aphid with its mouthparts while it is testing the plant for suitability can be enough to transmit some viruses. Some insects also cause disease-like injury while feeding, even if they do not transmit a pathogen. This occurs when a component of the insect's saliva is toxic. Such insects are said to be toxicogenic and produce ailments such as hopperburn and psyllid yellows.

Approaches to Pest Management

Vegetable crops, like fruit crops, have high cosmetic standards. Thus, there is considerable economic pressure on vegetable producers to maintain their crops free of pests and pest-related injury. Vegetable crops, especially when marketed as fresh crops, also command a high price. The high cosmetic standards and prices cause producers to spare no effort to protect their crops from pest damage. This usually results in frequent insecticide applications. Even with the rapidly escalating costs of pesticides, insecticide costs usually are a minor component of the total costs of crop production. Thus, many growers do not hesitate to apply insecticides. It is not always necessary to apply insecticides, however, because there are times and places when insects are not sufficiently abundant to cause injury, or there are other alternative actions that can be taken to limit injury. There is adequate justification for careful monitoring of vegetable crops, and application of the economic injury level concept, which would eliminate unnecessary insecticide application.

Cultural practices, such as modifying the location or time of planting, tillage, weed control, level and type of irrigation and fertilization, and physical barriers, such as floating row covers, are techniques that can be used to reduce the ability of insects to infest and reproduce within crops. Such practices ideally will maximize environmental resistance, and eliminate the threat of pest damage. Sometimes these practices are completely adequate, and other times they are an important component of pest management that requires additional, complimentary intervention. In southern regions of the United States, for example, early-planted cucurbit crops usually escape infestation by the pickleworm (Lepidoptera: Pyralidae). Late-planted or autumn crops are routinely infested by this pest, necessitating the application of insecticides to prevent crop injury.

Host plant resistance involves the use of vegetable plant cultivars that inherently are less supportive of insect growth and development, or that are less injured by insect feeding. For example, the glossy varieties of crucifers that lack the waxy bloom and are, therefore, green rather than the normal grayish green color, are somewhat resistant to the diamondback moth (Lepidoptera: Pyralidae). Unfortunately, the genetic diversity in horticulturally acceptable vegetables (growth, shipping, appearance and taste characteristics affect "acceptability") is often quite limited, and cultivars with insect resistance often are unavailable. Also, plant breeders have not concentrated on producing pest-resistant vegetable crops to the degree that they have worked on field and forage crops. This lack of attention is due to the ready availability of insecticides and the high value of vegetables, which allows economic use of insecticides.

Biological control involves the use of biotic agents to suppress pest populations. In the case of invading pest species, this can be done by introducing natural enemies that have been "left behind" in the native land of the pest. Assuming successful introduction and establishment of an effective natural enemy, this approach sometimes results in adequate and continuous suppression, allowing cultivation of the crop without additional release of the natural enemy, and without insecticidal intervention. On the other hand, some pest problems require regular intervention. For example, many crops infested with caterpillars are treated several times during each cropping cycle with the bacterium *Bacillus thuringiensis*.

The most commonly used approach to pest suppression in vegetable crops is the use of chemical insecticides. Insecticides are used because there is almost always an effective product available; this is not true for cultural practices, host plant resistance, and biological control. Insecticides can be applied to the soil to prevent seed, seedling and young plant injury; to the foliage and fruit to protect against direct and indirect pests; and to baits or traps to reduce the number of pests available to injure crops. Insecticides can be very selective, or have a wide range of activity, depending on the need. Insecticides can be formulated to be systemic in action, to function as fumigants, and to have short or long residual activity. Thus, despite concern about the adverse effects of insecticides (primarily threats to humans and wildlife), they remain a commonly used tool for vegetable production.

References

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, CA

Hill DS (1983) Agricultural insect pests of the tropics and their control, 2nd edn. Cambridge University Press, Cambridge, UK

Hill DS (1987) Agricultural insect pests of temperate regions and their control. Cambridge University Press, Cambridge, UK

Howard RJ, Garland JA, Seaman WL (eds) (1994) Diseases and pests of vegetable crops in Canada. The Canadian Phytopathological Society and the Entomological Society of Canada, Ottawa, Ontario, Canada.

McKinlay RG (ed) (1992)Vegetable crop pests. CRC Press, Inc., Boca Raton, FL

Vein

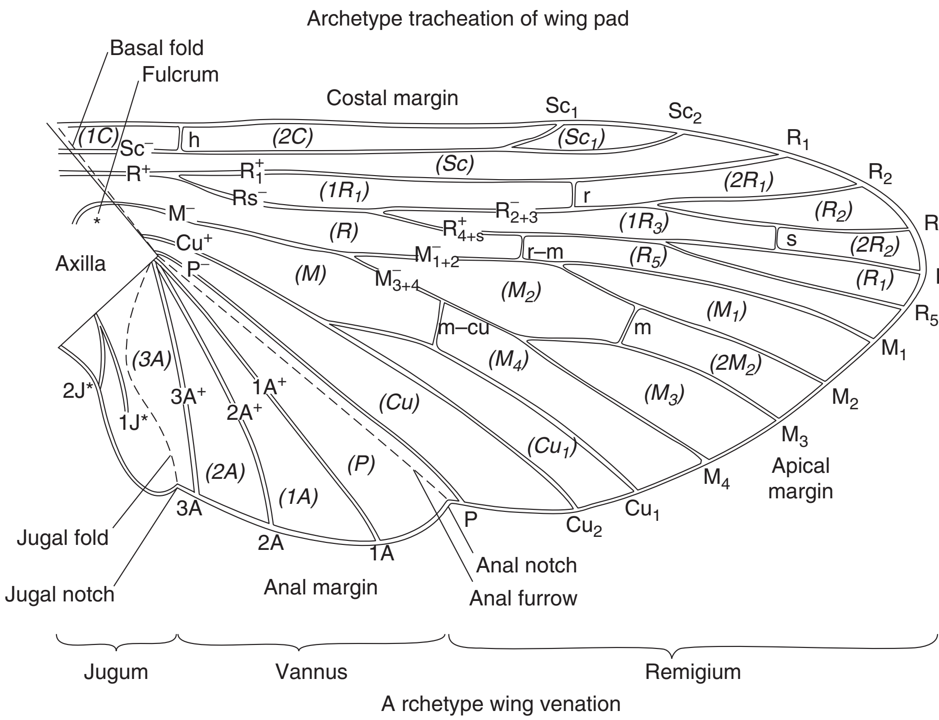
A tube running through the wings of insect, through which blood (hemolymph) is pumped (Fig. 11).

► Wings of Insects, Hemolymph

Veliidae

A family of bugs (order Hemiptera). They sometimes are called broad-shouldered water striders.

► Bugs



Vein, Figure 11 **Hypothetical ancestral pattern of wing venation.**

Velocipedidae

A family of bugs (order Hemiptera). They sometimes are called fast-footed bugs.

► Bugs

Velvet Ants (Hymenoptera: Mutillidae)

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Because of their generally bright colors and conspicuous appearance, velvet ants have long been favorite targets of insect collectors. Thus, it is with some degree of surprise that so little is known about them and their biology. Female mutillids, which are much more frequently observed than males, generally look very much like ants. They are wingless and can be seen scurrying about on the ground. They are, however, actually wasps. Their ant-like appearance, coupled with the fact that they are covered by a dense pubescence (hairs), has led to the common name of velvet ants.

Linnaeus included eight species of mutillids in his tenth edition of *Systema Naturae* in 1758. By the latter part of the nineteenth century, an estimated 3,500 to 4,000 species had been described, nearly all of which were included in the genus *Mutilla* Linnaeus. It was not until near the beginning of the twentieth century that many new genera were established.

The family Mutillidae is found worldwide but is predominantly tropical. As of 1975, there were approximately 8,000 described species. Brothers (1975) investigated the phylogeny of Mutillidae and recognized seven monophyletic subfamilies. That phylogeny is generally accepted. The family is now known worldwide from approximately 230 genera and subgenera, included in those seven subfamilies.

The higher-level classification is as follows:

Order: Hymenoptera
Superfamily: Vespoidea
  Subfamily: Myrmosinae
  Subfamily: Pseudophotopsidinae

Subfamily: Ticoplinae
Subfamily: Rhopalomutillinae
Subfamily: Sphaeropthalminae
Subfamily: Myrmillinae
Subfamily: Mutillinae

General Characteristics

Velvet ants can be divided into nocturnal and diurnal. The nocturnal mutillids are known almost exclusively from the males. They tend to be more wasp-like in appearance, brown or reddish-brown in color, and from 1 to 2 cm in length. Males almost always have two pairs of membranous wings.

Females of the diurnal velvet ants tend to be more ant-like in appearance. So far as known, all are wingless. Body color is most often black, brown, or reddish-brown. However, the body color is often not visible due to the dense pubescence. The hairs (more properly known as setae) are often brightly colored (red, orange, or yellow), or they may be a combination of one of the bright colors and black. Occasionally, the hairs may be entirely black or entirely white. The pattern of pubescence is usually species-specific. Males of even the diurnal velvet ants tend to be more wasp-like in appearance. Body color is most often black. Although some males may be brightly colored like the females, they are more frequently covered with black hairs over most of their body.

Sexual Dimorphism

As noted above, the males and females of velvet ants can look quite different (Figs. 12 and 13). Males generally have wings; females are wingless. Males tend to be more wasp-like in appearance; females tend to be more ant-like in appearance. Color of the hairs may be similar or quite different. Size may be the same or quite different. In some groups, males carry the females in flight during mating. Where this occurs, males are much larger. In other groups, females are generally much larger.

Taxonomy

The extreme sexual dimorphism in velvet ants has led to problems in taxonomy. Some genera are known from males only; others are known from females only. The same is frequently true for species within a genus. The genus *Dasymutilla* Ashmead is one of the most common genera in North America and includes all of the large, fuzzy velvet ants that most people readily recognize. The genus includes approximately 150 described species. Of those, approximately one third are known from males only, about one third from females only, and about one third are known from both sexes. In many cases, those species that exhibit a lesser degree of sexual dimorphism are known from both sexes, such as the large, red *Dasymutilla occidentalis* Linnaeus of the eastern United States commonly referred to as a “cowkiller”. In that species, males and females look almost identical except for the presence of wings in the males.

Biology

Relatively little is known about mutillid biology. It is known that mutillids are parasites (more correctly parasitoids) of other insects. Worldwide, the hosts are probably known for less than 10% of all described species. Of those that are known, most seem to be other ground-nesting bees and wasps, although there are some exceptions. A few species have been reported to parasitize tsetse flies in Africa.

Adults are generally active for only a few months out of the year, although specimens have been collected in every month of the year. Most observations have been of females, which are more limited in their mobility. Only a few observations have been recorded of mating behavior in this group. These have been almost entirely of diurnal species, as might be expected. There has been some consistency in those observations that have been made. Males usually fly a few centimeters above the ground into a slight breeze or wind, suggesting

Velvet Ants (Hymenoptera: Mutillidae), Figure 12 **A velvet ant female, *Dasymutilla occidentalis* (photo, L.J. Buss).**

Velvet Ants (Hymenoptera: Mutillidae), Figure 13 **A velvet ant male, *Dasymutilla* sp. (photo, L.J. Buss).**

that a pheromone (or sexual attractant) is involved. Courtship and mating are usually very brief with the entire process not lasting more than a couple of minutes.

Female mutillids apparently attack the larval stage of their host after the latter has spun its cocoon. Females enter the nests by digging through the soil or by breaking the walls of mud nests. Once they have gained entry, they chew a hole in the cocoon, turn around, and insert a single egg. They then plug the hole using salivary fluids and particles of soil or mud. After oviposition, about three days are required for the egg to hatch. The mutillid larva then proceeds to eat the host larva until the latter has been entirely consumed. This usually takes only a few days. The full-grown larva then spins a cocoon in the chamber prepared for the host, and pupates. Pupation is thought to take about twenty days.

In tropical and subtropical regions, there may be two to several generations a year. In the United States, mutillids apparently have only one generation a year. In colder regions, overwintering occurs in the pupal stage for most species. However, at least one species is known to overwinter in the adult stage.

Defense

One of the most interesting things about velvet ants is their vast array of defense mechanisms. First and foremost, they are wasps, and females are able to deliver a very painful sting. Interestingly, although males are not capable of stinging, they, too, have a very elaborate "stinging behavior." They do a very good acting job that will very frequently lead a potential predator to believe that they are being stung, thus affecting release of the male mutillid. Coupled with the sting, the often bright warning coloration will discourage many potential predators from attacking. Other defense mechanisms include a very tough exoskeleton, stridulation (the production of a squeaking sound that is used in mating as well as defense), quick zigzagging movements by females as they run on the ground, flight by males, and a good set of mandibles. It has been said that "an animal that discovers that the mutillid is hard-bodied and a powerful stinger is likely to remember its brilliant and unusual color pattern and to avoid it in the future" (Evans and Eberhard 1970:221).

► Wasps, Ants, Bees and Sawflies

References

Brothers DJ (1975) Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutillidae. Univ Kansas Sci Bull 50:483–648

Brothers DJ (1993) Family Mutillidae. In: Goulet H, Huber JT (eds) Hymenoptera of the world: an identification guide to the families. Centre for Land and Biological Resources Research, Ottawa, Ontario, Canada, pp 188–203
Evans HE, West Eberhard MJ (1970) The wasps. University of Michigan Press, Ann Arbor, MI
Manley DG (2000) Defense adaptations in velvet ants (Hymenoptera: Mutillidae) and their possible selective pressures. In: Austin AD, Dowton M (eds) Hymenoptera: evolution, biodiversity and biological control. CSIRO Publishing, Collingwood VIC, Australia, pp 285–289
Mickel CE (1928) Biological and taxonomic investigations of the Mutillid wasps. US Natl Mus Bull 143:1–351

Velvet Water Bugs

Members of the family Hebridae (order Hemiptera).

► Bugs

Velvety Shore Bugs

Members of the family Ochteridae (order Hemiptera).

► Bugs

Venezuelan Equine Encephalitis

Venezuelan equine encephalitis (VEE), or Venezuelan encephalitis, is principally a disease of rodents and horses, but does occur in humans. In South America, tens of thousands of human cases have been recorded, and hundreds of thousands of horse infections have been documented. It may pass undetected for decades and then erupts into significant epizootics, perhaps because it mutates easily. Strains of the virus differ considerably in their ability to infect mosquitoes and animal hosts. This viral disease is caused by an alpha virus of the Tongaviridae, and is transmitted by numerous mosquitoes, including *Aedes, Culex, Psorophora, Mansonia*, and *Deinocerites* spp. It is found in South and Central America, but occasionally occurs in southern areas of North America. In humans, it is characterized by fever, chills, headache, nausea, vomiting, and muscle and back pain. Generally, humans recover within a few weeks, with most of the time after the first few days consisting simply of lethargy or loss of energy. In severe cases, however, it progresses to encephalitis. The fatality rate in adults is less than 1%, but in children it may be 20%, and in horses it may be up to 10%.

► Mosquitoes
► Mosquitoes as Vectors of Viral Pathogens

Venoms and Toxins in Insects

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When we think of insects, images of stings, venoms, toxins and bites often flash into mind. Perhaps this is a natural outcome of interactions among people and the insect world. Insects have been selected to avoid becoming dietary fare of humans and large predators; and our own evolutionary history has imbued us with an aversion to pain or damage. Insect venoms and toxins represent potential harm to us and fall into the category of nasty things to be avoided. Biologically, venoms and toxins are contrastingly different. Venoms are physically injected into us while toxins are applied or sprayed onto our bodies, or are active upon ingestion. Toxins are poisons. Venoms are liquid blends of biologically active substances, usually including toxins, that are injected into the body via a stinger, fang, hollow spine or other mechanical delivery system. A sting is a highly specialized device whose function is the delivery of venom. Bites are associated with feeding and their defensive roles are secondary or incidental to the primary role of obtaining a meal. For example, the strong mandibles of carpenter ants are primarily used for chewing wood, capturing prey, and feeding; but in times of danger, they are useful for delivering effective bites to whatever is perceived to be threatening.

Distribution in the Insect World

Venoms and toxins are widely distributed throughout the Insecta. Beetles (Coleoptera), moths and butterflies (Lepidoptera), and grasshoppers (Orthoptera) are especially good chemists at synthesizing or sequestering a dazzling array of toxins, with cockroaches (Blattodea), bugs (Hemiptera), lacewings and relatives (Neuroptera), and sawflies and ants (Hymenoptera), also having toxic species. Classical allomones, chemical defensive compounds that are primarily effective in repelling attackers, will not be covered here because toxic roles of allomones are usually secondary. Some exceptions do exist. Nasute termites laden with terpenes and formicine ants containing enormous quantities of formic acid are known to induce toxic effects when eaten in large quantities by some predators. The nature of toxic compounds virtually runs the gamut of imagination: from hydrogen cyanide in some chrysomelid beetles to steroids in dytiscid beetles, cantharidin (active ingredient of Spanish fly) in meloid beetles, leptinotarsin and Bushman arrow poisons in chrysomelid beetles, pyrrolizidine alkaloids in the cinnabar moth (Arctiidae), and heart-toxic cardenolides in monarch butterflies, lygaeid bugs, and a variety of other insects.

Insect venoms are more limited in taxonomic distribution than toxins; nevertheless, they are widespread. The hallmark groups of venomous insects are the wasps, ants and bees in the Hymenoptera. These groups possess a highly developed specialized sting apparatus called the aculeus that evolved into an exceptionally effective stinging device. Hymenoptera are the only order that possesses a true stinger; other taxa envenomate their targets either by biting mouthparts or venom-containing setae or hollow spines. Powerful venoms are injected into prey and sometimes defensively into predators by a variety of insects including Hemiptera-Heteroptera: belostomatids, naucorids, nepids, notonectids, hydrometrids, reduviids, nabids and enicocephalids; Neuroptera: osmylids, myrmeleontids, and ascalaphids; Diptera: asilids, sciomyzids, tabanids, mycetophilids, therevids, cecidoymiids and rhagionids; and Coleoptera: lampyrids, dytiscids, gyrinids, carabids, cicindelids, hydrophilids, and silphids. Weaker venoms are known from among a variety of other families within the same four orders.

Venomous spines can be an unpleasant signature of lepidopterous caterpillars. Caterpillars in five superfamilies, the Bombycoidea, Lasiocampoidea, Noctuoidea, Papilionoidea, and Zygaenoidea are known to possess venomous setae. Some of these can produce serious dermal and systemic medical reactions. Among the most notable of the urticating caterpillars are the gypsy and brown tail moths (Lymantriidae: *Lymantria* and *Euproctis*), the puss moths (Megalopygidae: *Megalopyge*), the slug moths, including the saddleback caterpillar in the Limacodidae, the processionary moths (Notodontidae: *Thaumetopoea*), *Premolis*, a caterpillar in the Arctiidae, that causes a chronically debilitating condition in rubber plantation workers, and the buck (*Hemileuca*), io (*Automeris*) and *Lonomia* moths in the Saturniidae. A few adult moths produce venomous barbed scales called flechettes that readily detach from the body and drift through the air. Episodes of especially serious reactions to this "airborne venom" coincide with outbreaks of hemileucid or processionary adult moths.

Sting and Venoms in the Hymenoptera

The hymenopteran sting apparatus is a marvel of biological engineering. It is Nature's miniature syringe, one that preceded medical syringes, and is finer and superior in precision and function to anything developed by physicians. This biological syringe has the same function as man-made syringes – to inject powerful biologically active fluids into the bodies of other organisms. A major difference between the two, however, is that man-made syringes are for injecting beneficial substances to help the organism, whereas hymenopteran "syringes" are for injecting substances that benefit the hymenopteran.

The stinger, like a medical syringe, consists of two major parts: a needle for piercing tissue, and a reservoir for holding the fluid to be delivered (Fig. 14). In the stinger, once the sting shaft (aculeus) penetrates the target, the venom is delivered by a combination of forces from muscles surrounding the reservoir (venom sac) and/or hemostatic pressure exerted on the reservoir, sometimes aided by a system of valves. Some sting systems, such as that of the honey bee, even possess an associated set of muscles (Fig. 14) and nerves to coordinate the sliding barbed lancets on the sting shaft to enable the stinger to pierce ever deeper completely independent of the rest of the insect. The process in which the sting apparatus is torn from the body of the hymenopteran is called sting autotomy and is limited to a few species of ants and social bees and wasps. All autotomous species live in large, populous colonies and autotomy is limited to the essentially sterile worker caste.

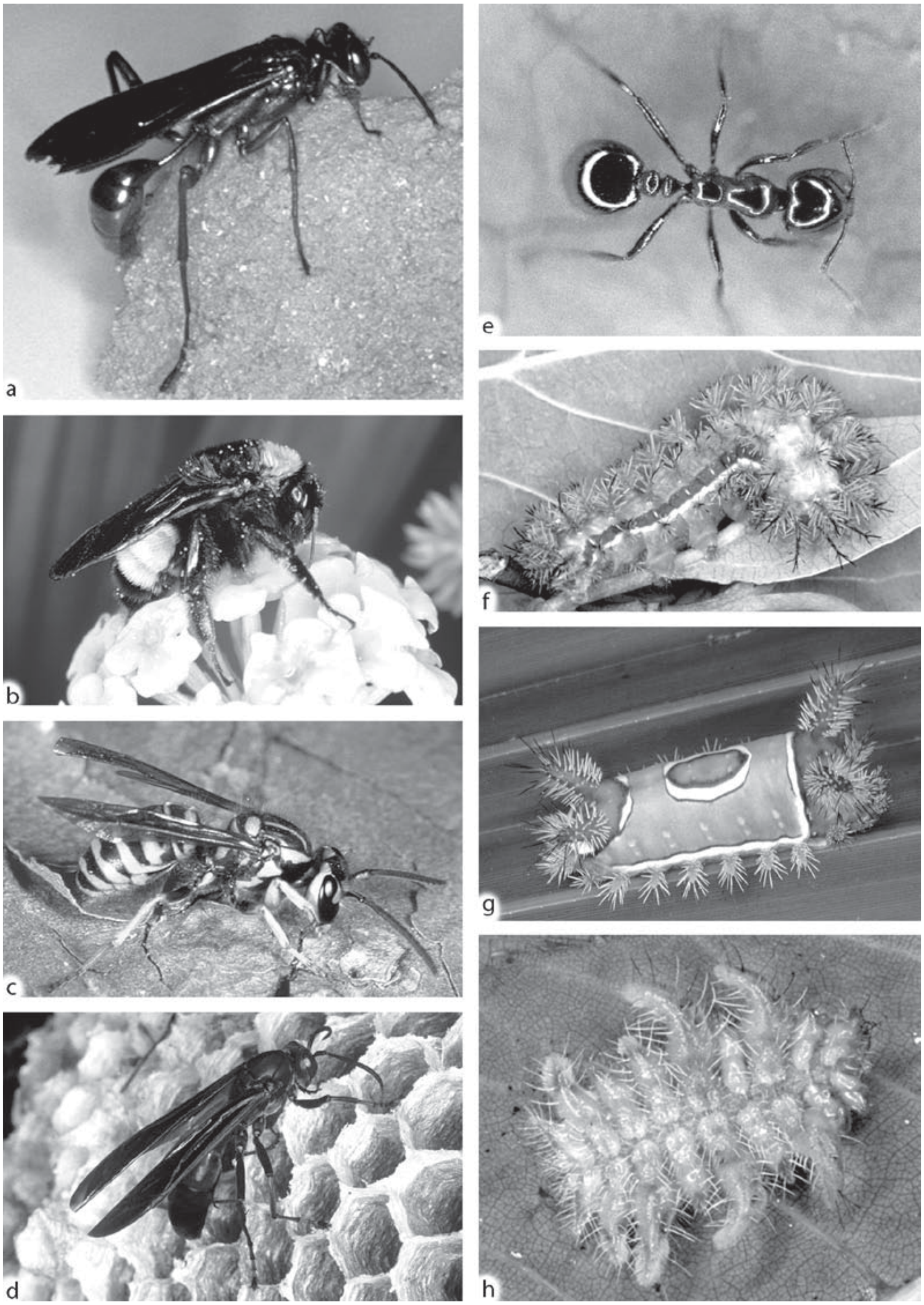
Venoms and Toxins in Insects, Figure 14 Honey bee autotomizing its sting apparatus. Note the glistening venom reservoir at the top of the sting base (photo by J.O. Schmidt).

Biological Function

Insect venom roles fundamentally relate to nutrition, either to help the venom producer in obtaining food or to help the venom producer from becoming food for something else (Fig. 15). In Hymenoptera, the ancestral use of venom is to paralyze prey as a food source for the hymenopteran's larvae. Parasitic wasps continue to use venom this way and their venoms will not be addressed further here. The more basal (Fig. 15a) lineages and the sphecid and many solitary vespid wasps of the aculeate wasps also maintain this primary use of their venoms. A major shift to defensive use of venom occurred in the bees, ants, and others in the Vespoidea. Bees shifted from the predatory lifestyle of their sphecid wasp ancestors to a vegetarian diet of pollen and nectar. No longer being needed for prey capture purposes, the venoms of bees were liberated from that constraint and evolved toward defensive uses. As a result, all bees use their stings only for personal defense or defense of their nest mates. Within the Vespoidea, sting and venom function exhibits a progression from use in prey capture to pure defense. Many groups, most notably the pompilid spider wasps and some ants, effectively use their venoms to paralyze or kill prey while concurrently being able to deliver painful stings to potential predators or adversaries, including humans. Velvet ants (Mutillidae), like the bees, evolved a lifestyle in which venom was no longer relevant to prey handling, and their venoms are strictly and effectively used for defense.

How Venoms Act Defensively: Pain

An immediate goal of an attacked hymenopteran is to stop the attack before serious damage occurs. A collateral goal is to prevent potentially harmful future attacks. The delivery of an instantaneously painful sting is an exceptionally effective means of achieving both goals. Pain (Table 3) is a organism's warning system that bodily damage is occurring, has occurred, or is about to occur. Thus, pain is ideal



Venoms and Toxins in Insects, Figure 15 **Some venom-producing insects: (a) mud dauber wasp, *Sceliphron* sp.; (b) bumble bee, *Bombus pennsylvanicus* (c) yellow jacket wasp, *Vespula squamosa;* (d) paper wasp, *Polistes metricus*; (e) red imported fire ant, *Solenopsis invicta*; (f) io moth caterpillar, *Automeris io*; (g) saddleback caterpillar, *Sabine stimulae*; (h) hag moth caterpillar, *Phobetron pithecium* (photos by James Castner, University of Florida).**

Venoms and Toxins in Insects, Table 3 **Pain levels produced by stings of representative Hymenoptera (scale 0 = lowest, 4 = highest pain)**

Taxon	Species (common name)	Acute sting pain	Duration of pain	Comments
Social Bees				
Apidae	*Apis mellifera* (honey bee)	2	4–10 min	
	Bombus sonorus (bumble bee)	2	2–5 min	
Social Wasps				
Vespidae	*Vespula* spp. (yellowjackets)	2	4–10 min	
	Dolichovespula maculata (baldfaced hornet)	2	3–4 min	
	Polistes spp. (paper wasps)	2	4–10 min	e.g., *P. fuscatus, P. exclamans, P. aurifer, dominulus*, etc.
	Polistes spp. (paper wasps)	3	5–15 min	e.g., *P. erythrocephalus, P. annularis, P. canadensis, P. infuscatus*, etc.
	Polybia occidentalis (common polybia wasp)	1	1–3 min	
	P. rejecta (a polybia wasp)	2	3–4 min	
	P. simillima (a polybia wasp)	3	5–15 min	initially 2, but burning pain of 3
	Belonogaster juncea colonialis (African fire tail wasp)	2	4–10 min	
	Agelaia myrmecophila (fire wasp)	2–3	5–15 min	
	Parachartergus fraternus (fierce wasp)	2	3–4 min	also can spray venom into eyes
	Brachygastra mellifica (honey wasp)	2	2–5 min	
	Ropalidia sp.	1	2–4 min	
	Synoeca septentrionalis (warrior wasp)	4	2 hr	initially 3, burn at 4 from 5 min to 2 hr
Ants				
Formicidae	*Myrmecia simillima, M. nigripes, M. gulosa* (bull ants)	1–2	2–5 min	sharp pain, no burning
	Odontomachus spp. (trap-jaw ants)	2	4–10 min	sharp pain, no burning
	Ectatomma spp.	2	1–4 min	*E. ruidum, E. quadridens, E. tuberculatum*
	Platythyrea lamellosa	1–2	4–10 min	itchy, burning, nettle-like, residual 20 min

Venoms and Toxins in Insects, Table 3 **Pain levels produced by stings of representative Hymenoptera (scale 0 = lowest, 4 = highest pain) (Continued)**

Taxon	Species (common name)	Acute sting pain	Duration of pain	Comments
	Streblognathus aethiopicus	2	5–10 min	burning pain, not sharp
	Pachycondyla villosa	2	4–10 min	sharp pain, not burning, same for *P. apicalis*
	Opthalmopone berthoudi	1	1–3 min	
	Megaponera foetens (Matabele ant)	1–2	2–3 min	sharp, but mild pain
	Paltothyreus tarsatus (giant African stink ant)	1–2	2–3 min	smell is worse than sting
	Termitopone crassinoda	2	4–10 min	sharp pain, not burning
	Dinoponera gigantea (giant ant)	2	4–10 min	sharp pain, not burning
	Paraponera clavata (bullet ant)	4	12–24 hr	excruciating waves of burning pain, undiminished for 12 hr; agile ants
	Eciton burchelli (army ant)	1	2–5 min	major worker
	Pseudomyrmex mexicanus	1	2–5 min	
	P. triplarinus (bull horn acacia ant)	2	4–6 min	amazingly intense for small ant
	Tetraponera sp.	1	2–4 min	
	Solenopsis invicta (red fire ant)	1	2–5 min	sharp, small ants, sting en masse
	Myrmica rubra (northern fire ant)	1	2–5 min	nettle-like, minor achy pain, lingers 20 min
	Pogonomyrmex (*Ephebomyrmex*) *cunicularius*	3	1–8 hr	slow, but intense, aching deep pain
	Pogonomyrmex (most of 20 spp.) (harvester ants)	3	1–8 hr	slow, but intense, piercing waves of aching deep pain, localized sweating, piloerection
Solitary Bees and Wasps				
Apidae	*Xylocopa* spp. (carpenter bees)	2	4–6 min	large genus, some variation in pain
	large bees in general	1	short	sharp, but minor, pain
Other bees	small bees in general	0–1	short	mostly trivial stings
Sphecidae	large *Sphex* sp.	1	short	slight pain
	Sphecius grandis (cicada killer)	1.5	2–5 min	sharp, immediate, not burning
	Chlorion aerarium	1	2–4 min	sharp, nettle-like

Venoms and Toxins in Insects, Table 3 Pain levels produced by stings of representative Hymenoptera (scale 0 = lowest, 4 = highest pain) (Continued)

Taxon	Species (common name)	Acute sting pain	Duration of pain	Comments
	Sceliphron caementarium (mud dauber wasp)	1	1–3 min	very minor
	sphecid wasps in general	0–1	short	trivial if they can penetrate skin
Scoliidae	various large species	0–1	short	sometimes residual hard spot in skin later
Mutillidae	*Dasymutilla klugii* (cow killer)	3	5–30 min	intense burning, variable reactions
	small-medium sized mutillids	1–2	2–10 min	more work needed on group
Pompilidae	*Pepsis grandis* (tarantula hawk)	4	3 min	debilitatingly intense, immediate, excruciating pain; usually vanishes 3 min
	smaller spider wasps	2–3	short	very sharp, immediate pain
Vespidae	Eumenid wasps	0–1.5	short	most minor; more work needed on group

for stopping an ongoing attack. Damage or impairment is a greater risk to a predator's survival and well being than the simple loss of a meal. An automatic reaction of predators receiving a painful sting is to abort the attack, usually by mouth gaping. Meanwhile, the future meal escapes. If the predator is a mammal, bird, lizard, or other long-lived intelligent animal, the painful experience and the insect responsible for that experience are likely to be remembered and avoided in the future. Is it any surprise that virtually all defensive venoms induce pain?

The painfulness of stings from various venomous species is not a constant. Not all stings hurt the same, and not all stings are equally effective in deterring predatory attack. Reason suggests that an extremely painful sting would be more effective in deterring attack than a mildly painful sting. But how can we scientifically distinguish between various degrees of algogenicity (the ability to produce pain) and the effectiveness of pain as a defense? Unlike action potentials in nervous networks that control muscles, electrical signals in sensory networks that transmit pain signals to the brain are not easy to measure. Modern medicine accesses pain by surveys completed by patients and clinical evaluations of facial and body expressions and signals. These are translated into numbers on a pain scale, typically a scale from 0 to 10. But pain levels produced in potential predators by an insect sting are not as easy to measure, nor as constant from one event to another. A solution to the problem is an insect sting pain scale having levels from 0 to 4. The number of levels (counting level 0) is 5 because of the inherent variability among stung people, differences in pain experienced based on body location stung, number of stings received, amount of venom delivered, etc. In the insect sting pain scale developed by the author and colleagues with the help of numerous friends and bystanders, a value for an "average" sting is determined. The sting pain of the common honey bee serves as the anchor point for the scale and is defined as pain level 2. Once anchored, a pain level of 1 represents pain clearly less than that produced by a honey bee; a pain level of 3 is more than that produced by a honey bee; and a pain level of 2 is roughly equivalent, maybe a little more, maybe a little less, than that of a honey bee. In my experience, differences between the levels are clearly evident to most people and leave little doubt. The extreme levels on the scale are 0, which represents an inability of the stinging insect to penetrate human skin or to produce pain, and 4, which represents immediate, excruciating and totally debilitating pain that completely shuts down one's ability to function normally – one simply does not walk away and act as if nothing happened after receiving a level 4 sting from an insect!

The average levels of pain induced by stings from representative stinging ants, wasps, and bees are listed in Table 3. Most ant and social bee and wasp stings are rated in the pain level range of 1–3, ample to gain the attention of a great majority of potential predators. For example, the most common insect stings, those from honey bees, yellowjacket wasps, baldfaced hornets, and paper wasps from the world's temperate regions, produce a pain level of 2. Stinging ants (ants that only bite do not qualify) are less frequently encountered in temperate climates, and those that are encountered usually produce less severe pain than their flying cousins. The one exception is the New World harvester ants in the genus *Pogonomyrmex* that live as far north as British Columbia and as far south as southern Argentina and Chile. Stings of these ants are famous for their piercing, throbbing deep pain that lasts for hours and has been described as feeling like the ripping of muscles and tendons. These stinging ants were also used in manhood rites by indigenous peoples in California because their painful and toxic stings facilitated life-guiding visions.

Solitary bee and wasp stings induce a wide range of pain intensities. The numbers in Table 3 somewhat belie the true biological situation wherein the vast majority of the more than 60,000 species are either incapable of penetrating human skin or produce a pain level, at most, of 1. Those species that command our attention are the exceptions: the spider wasps, velvet ants (Mutillidae), and the large carpenter bees. These insects are either colorful, or their striking black color contrasts with the environment surrounding them, thereby aposematically signaling predators to avoid them.

No treatment of insect sting pain would be complete without mention of the two most painfully stinging insects. The two, the bullet ant (*Paraponera clavata*) and the tarantula hawks (*Pepsis* spp.), though both producing the greatest human pain, do so in strikingly different ways. A tarantula hawk sting feels like a strike from a high voltage electric source that immediately takes over one's senses with an almost unimaginably excruciating and debilitating pain. The victim can do very little beyond releasing the wasp, then lying down and screaming. Fortunately, the pain usually abruptly subsides in 2–3 min, leaving the victim emotionally and physically exhausted, but no worse the wear in terms of long-term damage or impairment. The bullet ant impacts its victim with an immediate burning, throbbing pain that also blocks further effective functioning other than to release the ant. Even releasing the ant can be problematic, as the ant often tenaciously clings to its victim. Unlike the ephemeral pain from a tarantula hawk sting, the pain of a bullet ant sting only seems to increase over time coming in waves of intense pain followed by intervening periods of somewhat less pain. Uncontrolled trembling of the afflicted body part frequently occurs. The waves of pain continue unabated for at least 8 h, generally lasting more than 12 h, and sometimes continuing for a full day. No other insect species can meaningfully compete with the bullet ant for the title of being the most painfully stinging insect.

How Venoms Act Defensively: Damage

As effective as pain can be as a defense, it is not without its weaknesses. Pain is only a signal warning about damage, it is not damage itself. In a sense, pain alone is cheating, a form of Batesian mimicry. Unless some mechanical or physiological damage to the victim is produced by the sting, the sting is harmless. Natural selection pressure does not favor the loss of a meal because of a harmless signal; to the contrary, strong pressure would be exerted for learning to avoid or to ignore the signal and devour the cheating signaler. Intelligent and long-lived animals should adapt to stinging insects and readily exploit such, albeit spicy, morsels. In reinforcement of the effect of pain is another major activity of insect defensive stings – the ability to cause bodily damage. Damage is the "truth in advertising" of the insect sting; serious detrimental consequences can follow if stings are ignored. Consequences can include physical damage to a body part such that the part does not function well for a period of time, temporary to longer term sickness, or, though rarely, the attacker's death. Any of these effects will reduce an organism's ability to obtain food, avoid its own predators, seek a mate, or maximize reproduction. This translates into reduced fitness and exerts pressure on individuals and their genes to avoid future stings.

How is the damage potential of insect venoms measured? Unlike pain measurement, a variety of quantitative measures are available to determine damage (Table 4). The most robust and least equivocal measurement is lethality. Death is the ultimate defense, and dead predators do not attack again or produce descendants to attack the same insect or its own descendants. For insect venoms, the mouse was chosen as the model test organism because most defensive insect venoms are primarily directed against large vertebrate predators, and the mouse is a well characterized model for science and medicine. The lethalities to mice of representative insect venoms are listed in Table 4. Unlike many familiar measurements in which larger numbers indicate greater activity, lethality (LD_{50}) becomes greater as the quantity of venom needed to kill decreases; hence, the smaller the number, the more powerful the venom. Most social bees and wasps produce venoms having lethalities in the range of 2–6 mg venom/kg body weight. As a reference, rattlesnake venoms have average values around 4 mg/kg. By lethality measure, rattlesnakes and social bees and wasps produce about equally powerful venoms. The lethality values for ant venoms range widely from less than 0.1 mg/kg to somewhere over 100 mg/kg, and solitary bee and wasp venoms have low to nearly trivial lethalities.

Lethality is a strong, but indirect, measure of venom toxicity. Lethality measures the potency of the venom, but not its quantity, or the overall killing power of a sting. Lethal capacity (LC), or killing power, depends upon the potency of the venom and the amount of venom delivered. It is calculated by dividing the weight of venom per individual insect by the LD_{50} of its venom and is expressed as weight in grams of mouse that would receive a median lethal dose of venom from the sting of one average insect.

Virtually all social bee and wasp venoms pose grave potential threats of lethality to smaller vertebrate predators. With LC values from over 5 to 270 g, only one or a small number of stings from social bees and wasps are sufficient to kill a small attacking insectivore, and dozens to hundreds of stings can pose serious risks to large predators or humans. These venoms are truthful in the respect to both their advertising pain and their potential lethality.

Venomous ants present a more complex picture than social bees and wasps. LC values for the ants in Table 4 range from less than 1 g to over 1,000 g. Given that ants and social bees and wasps are highly social, with many individuals living in close-knit colonies, why the differences in their ranges of lethal capacity? Several factors might contribute to this difference. Many ants are much smaller than social wasps or bees and might not be worthy of much effort on the part of potential vertebrate predators. Also, most ant colonies are underground, or interspersed with inedible material, and are hard to consume as a unit, unlike social wasps and bees. Further, most ants produce noxious allomonal defensive chemicals and can bite viciously, qualities that social wasps and bees generally lack. These, plus the wide diversity of life styles exhibited by ants translates into great differences in selection pressures by large predators on various ant species.

Venoms and Toxins in Insects, Table 4 **Toxicity of stings of representative Hymenoptera measured by venom lethality and the lethal capacity of single stings**

Taxon	Species	LD_{50} (mg/kg)	venom per insect (µg)	Lethal capacity	Comments
Social Bees					
Apidae	*Apis mellifera* (honey bee)	2.8	160	57	
	Bombus sonorus (bumble bee)	12	760	63	
	Bombus impatiens (bumble bee)	11.5	290	25	
Social Wasps					
Vespidae	*Vespula germanica* (yellowjacket)	2.8	63	22	
	Dolichovespula maculata (baldfaced hornet)	6.1	140	23	
	Vespa mandarinia (giant hornet)	4.1	1,100	270	
	Polistes arizonensis (paper wasp)	2.0	170	85	
	P. erythrocephalus (paper wasp)	1.5	300	200	
	Polybia occidentalis (common polybia wasp)	5	28	5.6	
	P. simillima (a polybia wasp)	4.1	72	18	
	Belonogaster juncea colonialis (African fire tail wasp)	3.0	150*	50	*estimate
	Agelaia myrmecophila (fire wasp)	5.6	37	6.6	
	Parachartergus fraternus (fierce wasp)	5.3	200	38	
	Brachygastra mellifica (honey wasp)	1.5	70	47	
	Ropalidia flavobrunnea	5.9	40	6.8	
	Synoeca septentrionalis (warrior wasp)	3	270	90	
Ants					
Formicidae	*Myrmecia* spp. (bull ants)	.18–.35	300–510	860–2,830	5 species
	Odontomachus spp. (trap-jaw ants)	23–37	48–77	1.3–3.3	4 species

Venoms and Toxins in Insects, Table 4 **Toxicity of stings of representative Hymenoptera measured by venom lethality and the lethal capacity of single stings (Continued)**

Taxon	Species	LD_{50} (mg/kg)	venom per insect (µg)	Lethal capacity	Comments
	Ectatomma tuberculatum	.3	270	900	
	Ectatomma spp.	15–17	45–400	2.6–27	3 species
	Platythyrea lamellosa	11	130	12	
	Streblognathus aethiopicus	8	400	50	
	Pachycondyla villosa	7.5	130	17	
	Opthalmopone berthoudi	>32	59	~1.8	
	Megaponera foetens (Matabele ant)	>128	115	~.9	
	Paltothyreus tarsatus (giant African stink ant)	~50	420	~8	
	Termitopone crassinoda	2.8	450	160	
	Dinoponera gigantea (giant ant)	14	830	59	
	Paraponera clavata (bullet ant)	1.4	250	180	
	Pseudomyrmex mexicanus	8	16	2.0	
	P. nigrocinctus (bull horn acacia ant)	1.9	4.2	2.2	
	Tetraponera sp.	.35	45	128	
	Pogonomyrmex spp. (harvester ants)	.125–.7	~20	28–160	15 species
	P. (Ephebomyrmex) cunicularius	.09	14	155	
Solitary Bees and Wasps					
Apidae	*Xylocopa* spp. (carpenter bees)	11–30	~300	10–27	5 species
Halictidae	*Nomia heteropoda*	25	22	.88	
Sphecidae	*Sphecius grandis* (cicada killer)	46	220	4.8	
Scoliidae	*Crioscolia flammicoma*	>63	29	<.46	
Mutillidae	*Dasymutilla klugii* (cow killer)	71	420	5.9	
Pompilidae	*Pepsis* spp. (tarantula hawks)	~60–150	1,400–2,500	10–40	3 species

Some of the extreme LC values among the ants can be explained by their individual situations. Bull ants (*Myrmecia*) and harvester ants (*Pogonomyrmex*) are conspicuous diurnally active ants whose lethal venoms are probably results of intense predatory pressure from lizards, birds, and perhaps amphibians. The intensely powerful venoms of these species suggest that the ants have mostly won the arms race with vertebrate predators. The bull horn acacia ants as represented by *Pseudomyrmex nigrocinctus* use their venoms effectively to repel both small and potentially large herbivores from their symbiotic host plants. Bullet ants (*Paraponera*) are large conspicuous ants that forage amongst a hotbed of insectivorous birds, lizards, amphibians, and monkeys in the canopy tops of tropical rainforests. *Paraponera* apparently also has won the arms race against their potential predators for they have no known vertebrate predators. Ants of low venom toxicity, including *Megaponera foetens, Paltothyreus tarsatus*, and *Opthalmopone berthoudi*, probably have little need for lethal venom. *Megaponera and Paltothyreus* both have powerful mandibles and, when disturbed, release some of the most noisome stenches known in the animal world. *Opthalmopone* has enormous eyes and is the swiftest and most agile of the ponerine ants. It can simply detect and evade most large predators. The reasons for the extreme lethality of venoms of *Ectatomma tuberculatum* and *Tetraponera* sp. are not known. Both species are behaviorally timid and neither acts aggressively when attacked.

Solitary bees and wasps all appear to possess venoms of low lethality. Those that have been analyzed are among the largest and most apparent or aposematic of the group, yet even these have venoms of low damage potential. Why? For the scoliid, pompilid and sphecid wasps, toxic or lethal venoms would work against the requirement of maintaining live, fresh prey as food for their young. This explanation would not apply for mutillid wasps and all bees because they do not sting prey. Perhaps for these groups of solitary Hymenoptera that have no large nests or colonies to defend, there simply is little need for toxic venom. In solitary Hymenoptera, any defensive need is fulfilled by the pain component, which provides the necessary one time escape opportunity. Overall venom lethality correlates with colony size and social complexity within the Hymenoptera.

Insect Venoms and Ecological Factors and Opportunities

Life is a juggling act balancing nutritional needs and opportunities on the one hand, and minimizing predation risks associated with foraging on the other. Predation risk limits times and places that organisms are able to feed, molds their physical characteristics, abilities and appearances, and even affects their life spans. Imagine how organisms could change their natural history and expand their ecological niches if released from predatory pressure. Insect venoms have achieved, in part, just that. By providing a powerful defense against many predators, the venomous sting relaxed constraints on the activities of sting bearers, enabling the evolution of secondary defenses including aposematic warning colors, sounds, odors, and behaviors. Common examples of aposematic colors are the brightly contrasting yellow and black, or black and white, patterns sported by wasps and bees, the red, yellow, orange, or white and black patterns abundantly observed on mutillid wasps, the iridescent blues or blue-blacks on many spider wasps, and the jet black colors, sometimes highlighted with red, of some bees and social wasps. Aposematic sounds are common in stridulating ants and mutillid wasps, many wasps and bees that increase their buzzing pitch when threatened, and mandible clicking in hornets. Aposematic odors are more common than generally recognized and abundant in mandibular gland secretions of a wide variety of ants, mutillid wasps, spider wasps, and other wasps and bees. A classic example of aposematic behavior is the wing flicking performed during foraging by many spider wasps. These aposemata alone, or in combination, serve as powerful signals to dissuade potential predators from attack.

With aposematism backed by a painful sting came further opportunities to enhance defense via evolution of Batesian and Müllerian mimicry. Müllerian mimicry among stinging bees and wasps is a textbook example illustrating the value of convergence in aposematic models to educate predators to avoid the whole mimetic guild after sampling only one member. Batesian mimicry occurs between powerfully stinging models and a variety of the more weakly stinging wasps, bees, and many flies and other insects. Sexual mimicry between female stinging models and their stingless conspecific males is another type of mimicry that helps protect potential mates and offspring. All of these defenses are possible because of venoms.

An effective sting liberates its bearer from constraints on other insects and opens otherwise unavailable ecological opportunities. Defended hunting and predatory wasps can openly forage during the day in visible locations, something more risky for parasitic wasps and flies. Bees can forage during the day on colorful flowers in conspicuous open areas. Ants can forage virtually any time of day or year within the physical restraints of their local environments. These sting-facilitated niche expansions enabled larger populations within individual species and speciation as previously unavailable niches are occupied.

The most profound evolutionary change associated with the sting was the evolution of sociality. To become highly social (eusocial) and live in massive colonies, a species must overcome the problem that their large numbers and mass presents a nutritional bonanza for large predators. Biting, scratching, kicking and other mechanical defenses are of little effect against predators hundreds to a million times larger than the individual insect. The sting functions as an "insect gun," a weapon that essentially neutralizes the size and strength differences between adversaries. It provides the one means of defense that is exquisitely effective against huge predators: by penetrating the predator's skin, the sting bypasses the external defensive barriers and delivers painful and toxic materials directly to the pain receptors and vulnerable systems within the body. Venoms and stings might not be the ultimate genetic forces that drove the evolution of sociality, but they certainly provided the proximal means enabling higher sociality. Of all the most complex and highly social groups of insects, only the termites evolved sociality in the absence of a sting mechanism. Two factors appear to have played crucial roles in allowing this. First, termites lived in wood or soil matrices that are hard and provide excellent defensive barriers to large predators. Second, they evolved sociality before the existence of ants and the majority of the other predaceous insects that could seriously threaten them. Thus, excluding the exceptional circumstances of termites, all highly social insects possessed a sting. The importance of venom in the evolution of sociality is further illustrated by other insect groups in early stages of social evolution including some aphids that have evolved individuals with sting-like mouthparts.

The biological significance of social insects can hardly be underestimated. Ants are omnipresent and dominant insect members in virtually all of the world's terrestrial ecosystems. Social wasps are major predatory driving forces in much of the warmer parts of the world. Social bees including bumble bees, stingless bees, and the honey bees (sometimes ecologically called "pollen pigs" for their ubiquity and effectiveness in exploiting flora resources), dominate the floral resources of many flowering plant communities. Without the evolution of the hymenopteran sting and sociality, the world would look dramatically different today.

Medical Aspects of Insect Venoms

When venomous insects are mentioned, the first thing that comes to mind in most insect aficionados and non-aficionados alike, is sting allergy. What professional entomologist is not familiar with hearing in informal settings, "I might die if I am stung again?" Such statements reveal two aspects of insect venoms – they have caught people's attention, and they can be a medical threat. The attention gaining part is a testament to how stinging insects have mostly won the game of educating our species to stay clear of them. The medical aspect is more complicated. About 40 people die per year in the US as a consequence of allergic reactions to insect stings, but more telling is the statistic that 4 million US individuals are at risk of experiencing a life threatening reaction upon the next sting. This 100,000-fold difference between the two figures indicates that insect stings are not nearly as dangerous as generally perceived – one might argue that they are medically trivial – and that, once again, insects are winning the game of intimidating us, a potential predator by their assessment.

Allergy to insect venoms can be a serious problem in a small minority of individuals. At the very least, an allergic reaction is a frightening and intimidating experience. More serious is the problem that allergic people might have to restrict their lifestyles, limiting outdoor exposure, and always being wary and ready to take emergency action if stung. A very few people, less than half the number that die from lightning strikes, and less than one third the number that die in off-road vehicle accidents, do actually succumb to insect stings. Fortunately, most medical problems associated with insect stings can be prevented or alleviated with immunotherapy using a series of tiny injections of insect venom and by carrying sting kits containing epinephrine to stop reactions. Given the available technology, no one should live in fear of stinging insects. The only excitement stinging insects should engender is an admiration for their beauty, amazing lives, and importance in the environment and enrichment of our lives.

References

Beckage NE, Gelman DB (2004) Wasp parasitoid disruption of host development: implications for new biologically based strategies for insect control. Annu Rev Entomol 49:299–330

Bettini S (1978) Arthropod Venoms. Handbook of experimental pharmacology, vol 48. Springer-Verlag, Berlin, Germany

Blum MS (1981) Chemical defenses of arthropods. Academic Press, New York, NY

Schmidt JO (1982) Biochemistry of insect venoms. Annu Rev Entomol 27:339–368

Schmidt JO (1990) Hymenoptera venoms: striving toward the ultimate defense against vertebrates. In: Evans DL, Schmidt JO (eds) Insect defenses: adaptive mechanisms and strategies of prey and predators. SUNY Press, Albany, NY, pp 387–419

Schmidt JO (1992) Allergy to venomous insects. In Graham J (ed) The hive and the honey bee. Dadant and Sons, Hamilton, IL, pp 1209–1269

Wirtz RA (1984) Allergic and toxic reactions to non-stinging arthropods. Annu Rev Entomology 29:47–69

Venoms of Ectoparasitic Wasps

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The complex interactions that occur between ectoparasitic wasps and their hosts ultimately lead to altered host development, physiology, and behavior. Precisely how these host changes come about is poorly understood, but in most cases involving ectoparasitic wasps, a venom is injected into the host. Venoms of ectoparasitic non-aculeate Hymenoptera ("Parasitica") fall into two categories based on the impact on the host: those that evoke paralysis and those that are non-paralytic. The vast majority of ectoparasitic species studied produce paralyzing venoms. Such species are considered idiobionts and the venom confers an adaptive advantage in the relationship with the host: a mobile host can be permanently or temporarily paralyzed during egg laying by the female wasp. A still-mobile host is also a potential threat to developing parasitoids, consequently these venoms are more often permanent paralyzing agents. Paralyzing venoms are typically produced by the adult female wasp, however, for some ectoparasitic species (e.g., Chalcidoids), the wasp larvae produce salivary venoms/secretions that apparently can halt host development in a manner consistent with paralysis.

In contrast, non-paralyzing venoms do not render the host immobile. In fact, several species utilize non-mobile stages of the host (e.g., prepupae and pupae). These venoms seem to function by altering host physiology for the benefit of the developing parasites. In most cases, venom-induced host changes center around nutritional considerations of the immatures; female wasps must ensure that their progeny maximally use the host since for idiobiont species, the host does not feed following parasitism, and is thus a finite pool of nutrients. Venoms from ectoparasitic species belonging to the Pteromalidae and Eulophidae also are known to inhibit host molting, suppress immune responses, elevate lipid metabolism, slow or completely inhibit respiratory physiology, and alter protein expression in a variety of host tissues. Such host effects are consistent with parasitoids referred to as koinobionts, a condition more typical of endoparasitic species that depend on polydnaviruses.

Active venom proteins from ectoparasitoids, whether paralyzing agents or non-paralytic toxins, are much larger in molecular mass than those of the aculeate Hymenoptera, and perhaps this is related to the different usage of venoms among hymenopterans: aculeates use venom primarily in defense whereas venom is associated with reproductive strategies of non-aculeates. For example, low molecular weight proteins and peptides are typical of the venoms of social Hymenoptera (ants, bees, and wasps). The venoms of bees and social wasps are also abundant in neutral and basic amino acids. Comparatively few studies have examined the composition of ectoparasitic wasp venoms, but for those examined, the venom proteins are considerably larger than the aculeates. *Habrobracon hebetor* (Braconidae) produces a potent venom with at least two highly paralytic protein toxins (Brh-I and Brh-V, estimated molecular masses 71–73 kDa) and one smaller, less insectidical toxin (about 20–40 kDa). All three toxins appear to be glycosylated, a feature characteristic of mid- to high-molecular weight venom proteins of hymenopterans, but not of low molecular mass toxins. A 66-kDa venom protein has been isolated from *Euplectrus comstockii* (Eulophidae) that does not induce paralysis but does arrest host development by inhibiting larval-larval ecdysis. This arrestment protein is thought to be comprised of at least two subunits, suggesting that the native protein is possibly a dimer composed of two 33 kDa proteins. *Nasonia vitripennis* (Pteromalidae) produces a complex venom with over 9 major venom proteins visualized by denaturing electrophoresis (SDS-PAGE). A 69-kDa venom protein has been isolated from crude venom that retards host development and appears ultimately responsible for triggering death of the host.

The constituents of the venom are synthesized by venom glands, which are sometimes referred to as poison glands or acid glands. The venom glands of ectoparasitic wasps may connect to a large reservoir, or may attach directly to the distal portion of the vagina or common oviduct. Both the venom gland and reservoir are of ectodermal origin and are lined with chitin. The chitinous lining is derived from squamous epithelial cells and is an apparent necessity since many species store the venom in an active form as opposed to a precursor. Secretory cells are found throughout the venom apparatus (gland and reservoir), but localization of specific venom protein synthesis in any parasitic species has yet to occur. In at least *N. vitripennis*, the bulk of the venom is synthesized in the columnar epithelial cells lining the acid gland and is discharged directly into the lumen of the venom reservoir apparently packaged into small vesicles.

The precise tissues targeted by ectoparasitic wasp venoms have not been clearly identified, nor have the pathways activated/suppressed by these venoms been deciphered. Neuromuscular junctions most likely are targeted by paralytic venoms. For example, venom from *H. hebetor* is thought to evoke paralysis by binding to a receptor associated with the excitatory glutamatergic system on pre-synaptic membranes. Venom causes an accumulation of pre-synaptic neurotransmitter vesicles, thus blocking neurotransmitter release by inhibiting vesicle fusion with post-synaptic membranes. No other paralytic venoms from non-aculeate hymenopterans have been sufficiently studied for comparison with *H. hebetor* to determine if this is the norm or the exception among the parasitic Hymenoptera. Paralysis is, however, the norm for venoms of parasitic aculeate hymenopterans, but the mode of action of these venoms does differ from *H. hebetor*. The aculeate venoms trigger paralysis by blocking cation channels in pre- and post-synaptic membranes of host nervous and muscle tissues.

Non-paralytic venoms from ectoparasitic wasps seem to target a variety of tissues, most likely in a receptor-mediated fashion. Inhibition of larval and pupal ecdysis by *E. comstockii*, *E. plathypenae*, and *N. vitripennis*, respectively, suggests that these venoms disrupt tissue responsiveness to ecdysteroids, a condition that is not corrected by application of exogenous 20-hydroxyecdysone. This effect implies that some aspect of the receptor-hormone complex is disrupted or that the complex is not able to bind to and/or activate response elements within the cell nucleus. Venom from *N. vitripennis* also elevates *de novo* synthesis of host lipids in fat body and hemolymph, implicating an involvement of adipokinetic hormone activation and/or synthesis in response to envenomation. N. vitripennis venom also induces fly hosts to enter a developmental arrest that is characterized by a suppression of respiratory metabolism and altered protein expression, both of which show tremendous similarity to the diapause physiology of the host. The latter observation has led to speculation that the venom targets the host brain to redirect the cell-cycle control system. Consistent with this prediction is the observation that heat shock protein synthesis (hsp 23 and hsp 70) in host brains are highly upregulated following venom injection. The host response differs from a typical stress response in that all hsps are not uniformly upregulated due to envenomation by N. vitripennis, and the response persists for an extended duration.

Venom from at least two species, *Eulophus pennicornis* (Eulophidae) and *N. vitripennis*, alter hemocyte behavior in the host. In the case of *E. pennicornis*, venom is not thought to be directly associated with alterations in the numbers of circulating hemocytes, changes in phagocytic abilities, or loss of hemocyte membrane integrity, although it seems that the altered host immune response is only evident when both venom injection and oviposition occur. In contrast, venom from *N. vitripennis* specifically targets plasmatocytes and granulocytes independent of oviposition. Host plasmatocytes are destroyed within one hour of envenomation by a mechanism consistent with apoptosis. Granulocytes remain viable throughout parasitism, but lose the capacity to adhere to foreign objects and spread when cultured *in vitro*.

All ectoparasitic wasp venoms have the ability to ultimately kill the host. The most thoroughly investigated pathway eliciting host death involves the venom from *N. vitripennis*. Oncosis is the primary mechanism of host cell death. The venom apparently binds to a G-protein-sensitive receptor, activating one or more signal transduction pathways. The currently accepted mode of action for the venom involves the activation of phospholipase C, thereby elevating cAMP levels and eventually triggering release of free intracellular calcium from either mitochondria or smooth endoplasmic reticulum. Elevated intracellular calcium levels are thought to have a multiplicity of effects on target cells, including activation of cytosolic proteases that break down cytoskeletal proteins, and stimulation of endonuclease activity resulting in degradation of genomic DNA. Any of these effects can destroy the cell from within and contribute to the ultimate fate of the host, death. This mode of operation parallels the action of at least one toxin (mastoparan) isolated from several social wasps.

References

Beard RL (1963) Insect toxins and venoms. Annu Rev Entomol 8:1–18

Piek T (1986) Venoms of the Hymenoptera. Academic Press, London, UK, 570 pp

Quicke DLJ (1997) Parasitic wasps. Chapman and Hall, London, UK, 470 pp
Rivers DB, Ruggerio L, Yoder JA (1999) Venom from *Nasonia vitripennis*: a model for understanding the roles of venom during parasitism by ectoparasitoids. Trends Entomol 2:1–17
Schmidt JO (1982) Biochemistry of insect venoms. Annu Rev Entomol 27:339–368

Venoms of Endoparasitic Wasps

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During oviposition by endoparasitic wasps, secretions of maternal origin are injected into the host insect along with the egg(s). For many of these endoparasitoids in the families Ichneumonidae and Braconidae, the secretions contain endosymbiotic viruses (e.g., polydnavirus, entomopoxvirus), virus-like particles (VLPs) or ovarian proteins that aid in the manipulation or alteration of the host. Host regulation includes behavioral, biochemical and physiological changes, such as immunosuppression, altered hormone titers, and/or changes in protein expression, which functionally aid in the development of the parasitoid's larvae. In most cases, the adult female also produces a proteinaceous venom that works synergistically or additively with the viral products. Some species also rely on embryonic factors such as teratocytes that may also contribute to host regulation and immune suppression by endoparasitoids. Typically, one or more of these maternally or egg-derived factors are necessary to ensure successful development of the feeding offspring. For example, venom or ovarian components may modulate expression and replication of viruses associated with the endoparasitoids, or may function to interfere with humoral and cellular immune components. Some species, however, rely exclusively on the action of venom to subdue the insect host. In fact, there is no evidence that these latter species contain any of the other factors (e.g., viruses, VLPs, teratocytes) commonly associated with endoparasitic wasps.

Venoms from endoparasitic wasps provide a rich and diverse array of bioactive components of both peptide and non-peptide origin. Endoparasitoid venoms are largely involved in regulation of host physiology and immune defense responses rather than paralysis/prey capture, which is more typical of ectoparasitic species. This is mainly related to the parasitism strategy in which the immature parasitoid larva develops internally while the host continues to grow. Venom is produced in a pair of specialized glands (= acid glands) and stored in a sac-like reservoir that is connected to the ovipositor through a duct. The opening of the reservoir to the duct contains a muscle-like sphincter that permits control over venom release. Striated muscles surround and attach to several points along the reservoir to facilitate rapid delivery of the venom fluid into the host. The amount of venom delivered to the host during envenomation is not known but likely varies depending on species of wasp and host, and whether the host has been previously parasitized.

Very little is known about the composition and biochemical properties of venom from endoparasitic wasps. From the few species that have been studied in detail, the composition of venom appears to be a complex mixture of proteins and peptides. This complexity might provide a means for a broader host range, although in nature endoparasitic species generally display narrow host specificity, or reflect various levels of interference with host physiology and immunity. It is also plausible that some of the venom constituents synergize or alter the function of other venom proteins inside the venom gland or reservoir (e.g., inhibit enzymatic activity) or inside the host. What is known about endoparasitic wasp venoms is that an array of small to high molecular weight proteins has been identified in most venoms studied. For example, the mass of venom proteins ranges from small peptides of less than 5 kilodaltons (kDa) to proteins of over 200 kDa. Earlier studies using electrophoretic (SDS-PAGE) protein profiles of venoms isolated from species belonging to the families Ichneumonidae and Braconidae revealed that most of the proteins were high molecular weight, and that nearly all proteins were glycosylated. However, recent analyses using more sensitive approaches such as two dimensional gel electrophoresis, reverse phase high performance liquid chromatography (rpHPLC) and mass spectrometry have demonstrated that smaller peptides are also present in venom, and that many lack a carbohydrate moiety. In addition, venom proteins from endoparasitoids are mostly acidic with pH ranging from 5.0–6.5, consistent with the venoms of ectoparasitic species.

Several constituents in the venom have been tentatively identified or a functional role for the proteins/peptides has been potentially uncovered. For example, based on analyses of primary structure of venom proteins, several are predicted to be signal peptides. Many of the proteins and peptides in the venoms show high homology to several known enzymes. These include trehalase, laccase, phenoloxidase, angiotensin-converting enzyme, serine protease and metalloprotease (reprolysin) in venom from *Pimpla hypochondriaca*, phenoloxidase and phospholipases B and A2 from *P. turionellae*, a putative chitinase from *Chelonus* sp. near *curvimaculatus*, and aspartylglucosaminidase-like from *Asobara tabida*. Additional studies have suggested the presence of various heat-sensitive hydrolases in the venom from *P. hypochondriaca*, more specifically acid phosphatase, β-glucosidase, esterase, β-galactodidase, esterase lipase and lipase.

Endoparasitoid venoms also appear to contain a number of putative enzyme inhibitors. These might be directly involved in host-parasitoid interactions (e.g., inhibition of phenoloxidase activation) or in stabilization and modification of venom proteins stored in the reservoir. The latter appears to be particularly critical to *P. hypochondriaca* since it is believed to produce a constitutively active phenoloxidase in the venom gland. In addition to enzymes and inhibitors, some species also contain several catecholamines (e.g., noradrenaline), apamine and mellitin, all of which are more commonly associated with the venoms of social Hymenoptera.

The mode of action of these venom proteins remains unclear. Obviously, putative enzyme inhibitors would be predicted to interact directly with the active site of targeted venom enzymes. However, with all other venom proteins, the precise mode of action has not been determined. In many species, venom proteins interact directly with polydnaviruses (PDVs), generating either complementary or synergistic effects. The mechanisms involved are unknown but it is generally believed that the venom proteins facilitate entry and stability of PDVs into host tissues. In other wasps, expression of viral genes does not occur in the absence of venom, clearly arguing for a regulatory role of venom proteins/peptides. Some venom proteins evoke a temporary paralysis or developmental arrest, the latter of which appears to be associated with disruption of endocrine tissue. In nearly all cases, venom triggers cell death, but the mechanism of death (i.e., oncosis vs. apoptosis) seems to be dependent on the host tissues involved. Whether the pathways leading to temporary paralysis and/or host arrestment are linked to cell death remains to be determined.

References

Beard RL (1963) Insect toxins and venoms. Annu Rev Entomol 8: 1–18

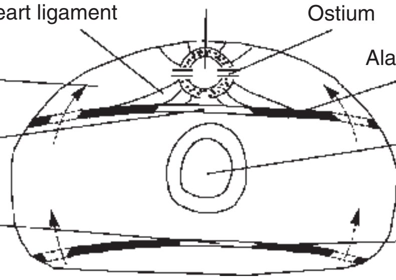
Moreau SJ, Guillot S (2005) Advances and prospects on biosynthesis, structures and functions of venom proteins from parasitic wasps. Insect Biochem Mol Biol 35(11):1209–1223

Piek T (1986) Venoms of the Hymenoptera. Academic Press, London, UK, 570 pp

Quicke DLJ (1997) Parasitic wasps. Chapman and Hall, London, UK, 470 pp

Ventral Diaphragm

A ventral layer of thin cells and muscle (Fig. 16) that assists in circulation of hemolymph around the nerve cord.



Ventral Diaphragm, Figure 16 **Cross section of an insect abdomen, showing components of the insect circulatory system and direction of hemolymph flow (adapted from Evans, Insect biology).**

Ventral Nerve Cord

The series of interconnected ganglia lying along the ventral surface of the insect, and providing nervous coordination.

Ventral

The lower surface.

Ventricle

A chamber of the insect heart (dorsal vessel).
► Dorsal Vessel: Heart and Aorta

Ventriculus

The true stomach of the insect; the midgut of the alimentary system.
► Alimentary Canal and Digestion

Vermiform

A body form that is worm-like, lacks a distinct head, and is legless. This term often is used to describe fly (Diptera) larvae, but also applies to newly hatched grasshoppers. Such newly hatched grasshoppers, called vermiform larvae, are enclosed in a membrane, so the legs are not functional. Vermiform larvae wiggle from the below-ground egg pod to the soil surface, where they free themselves from the membrane and possess functional appendages. Only after escaping from the membrane is the young hopper considered to be a first instar.

Vermileonidae

A family of flies (order Diptera). They commonly are known as worm lions.
► Flies

Vermileonidae

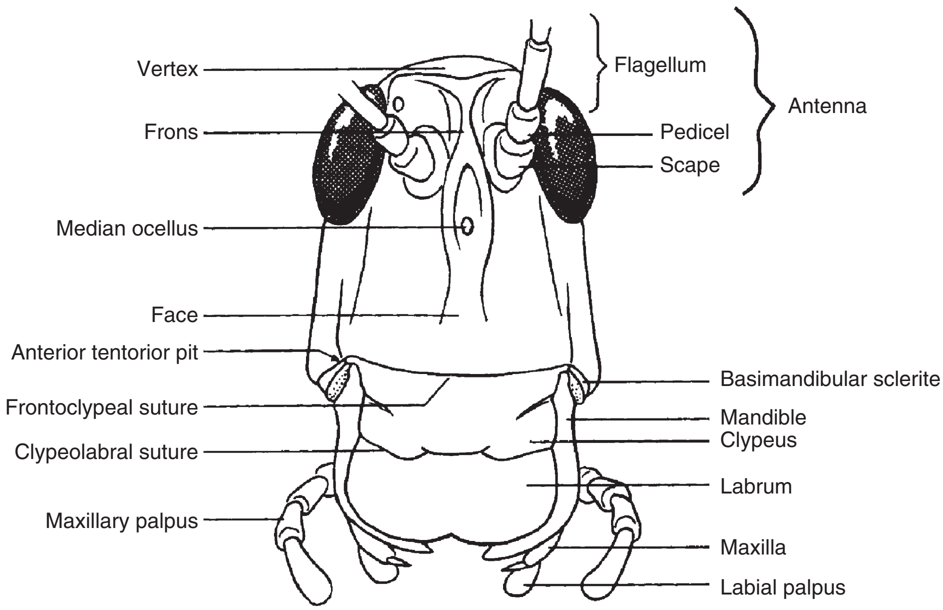
A family of flies (order Diptera).
► Flies

Vermipsyllidae

A family of fleas (order Siphonaptera). They sometimes are known as carnivore fleas.
► Fleas

Vertex

The top of the head between the compound eyes (Fig. 17).
► Head of Hexapods



Vertex, Figure 17 **Front view of the head of an adult grasshopper, showing some major elements.**

Vertical Transmission

Transmission of a pathogen between members of an arthropod species by movement from parent to progeny (transovarial or transovum transmission) or between instars within a generation (trans-stadial transmission). It is usually contrasted with horizontal transmission, in which a pathogen is passed among members of a species within the same generation, or within the same season.

Verticillium lecanii

This insect pathogen, which has long been known to be especially heterogeneous, has been reassigned to the genus *Lecanicillium* and divided into several species. Different strains and species of this group affect scale insects, whiteflies and aphids.

► *Lecanicillium*

Vesicating Species

Insect species that cause production of blisters on an animal that contacts the insect. This condition is sometimes caused vesicular dermatitis, and is most often induced by blister beetles containing cantharidin.

► Cantharidin

Vespidae

A family of wasps (order Hymenoptera). They commonly are known as paper wasps, yellow jackets, hornets, mason wasps and potter wasps.

► Wasps, Ants, Bees, and Sawflies

Vestigial

The remnants of a formerly functional organ, usually reduced in size.

Veterinary Pests and their Management

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Pests of veterinary importance are unique in their associations with animals hosts. Unlike the many pests that utilize plants or plant materials for their survival, pests of veterinary importance feed on hosts that can for the most part move from place to place. Thus, the hosts can live in a variety of habitats, move from one habitat to another during a daily cycle, and persist through a variety of climatic conditions during an annual cycle. The host range can be relatively small and associated with a central nest or burrow, or it can be practically endless in the case of herds of range cattle or migratory antelope. Likewise, the range of the pest can be limited geographically to certain locations, climates, or altitudes. Conversely, the pest can be cosmopolitan and affect similar hosts on almost every continent of the planet. Specifically, highly specialized pests can be limited to one or two host species, such as the sheep ked, *Melophagus ovinus*, a widely distributed parasite of sheep and goats.

Host Response

Pests of veterinary importance (Fig. 18) confront a host that has the ability to resist their presence through their blood chemistry and they must resist the host's attempts to wall them off and otherwise limit their feeding activities. Pests of veterinary importance also confront a host that has the ability to physically resist their presence, and most pests face the possibility of bodily injury or death each time they visit a host to feed. A number of recognized host responses may be elicited by the presence of a pest. These include muscle twitching, scratching, chewing, rolling on the ground, tail swishing, head tossing, bunching, foot stomping, and running away. The hematophagous pests are particularly vulnerable because they have no choice. There is no alternative food source. Without taking a blood meal, most cannot live or reproduce.

Economic Losses – Physical

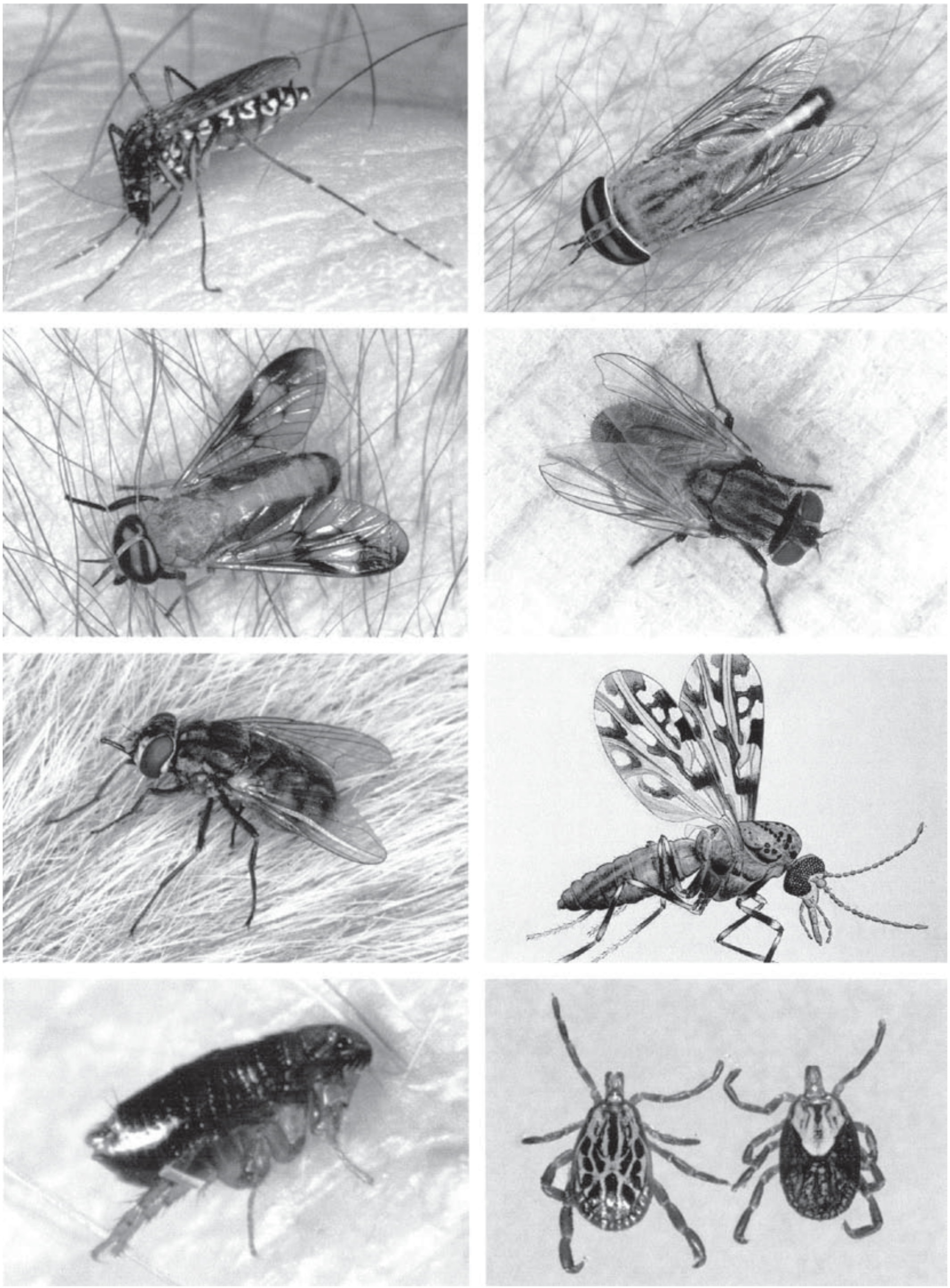
Besides the direct effects of the pest's feeding on hosts, the host response can add to, or be solely responsible for, economic loses from direct or indirect contact with the pest (Table 5). The feeding activities of some pests (e.g., lice and mites) cause itching, and host animals scratch or rub themselves incessantly, causing additional damage to affected areas as they try to gain relief. Fly worry can distract animals from eating or resting adequately, thus causing decreases in weight gains.

Economic Losses – Disease

Pests can also transmit diseases to the host, resulting in sickness or death (Table 6). Pests such as mosquitoes, phlebotomine sand flies and tsetse flies are the cause of incalculable amounts of suffering by humans and animals alike because of the disease organisms they transmit in so many parts of the world. Ticks constitute a major threat to livestock industries in many countries in the western hemisphere and in Australia and Africa. New threats arise constantly as little known diseases suddenly increase to epidemic levels (e.g., Lyme disease) and diseases prevalent in one part of the globe appear unexpectedly in another (e.g., West Nile Fever). Vector species reside in locations where associated disease organisms do not exist and the threat of infestation of the vector by the disease organism is always a possibility. Chances for dispersal of diseases and vectors have been increased greatly by international air travel.

Economic Losses – Mechanical

Host species can be killed by suffocation when certain insects, notably mosquitoes, black flies, and chironomid midges, enclose in large numbers. If insect numbers are not large enough to cause hosts to suffocate, the hematophagous pests such as mosquitoes and black flies can debilitate or kill hosts by exsanguination and/or by the amount of toxic saliva that is injected



Veterinary Pests and their Management, Figure 18 **Some arthropods of veterinary importance: *top left*, saltmarsh mosquito; *top right*, horse fly; *second row left*, deer fly; *second row right*, house fly; *third row left*, stable fly; *third row right*; biting midge; *bottom left,* flea, *bottom right*, tick (photos by J.L. Castner; biting midge by Dick Axtell).**

Veterinary Pests and their Management, Table 5 Physical loss factors caused by selected pests to livestock and poultry

Physical loss factors	Pests	Affected animals
Fly worry	Flies: *Musca domestica, Stomoxys calcitrans, Haemeatobia irritans, Hippelates* sp., *Musca autumnalis*	Cattle, horses, other livestock
Exsanguination	Flies: *Stomoxys calcitrans, Haematobia irritans,* Tabanidae, Simuliidae.	Cattle, horses, other livestock
	Mosquitoes: various species	
	Ticks: *Boophilous* spp., various species	
Suffocation	Flies: Simuliidae, Chironomidae, Mosquitoes: various species	Cattle, horses, other livestock
Disfiguration	Ticks: *Boophilous* spp., various species	Cattle, horses, other livestock
Itching/Skin Destruction	Mites: *Sarcoptes scabiei, Demodex* spp., *Psoroptes* spp., *Chorioptes* spp., *Ornithonyssus syilviarum*	Cattle, horses, poultry, other livestock
	Lice: *Haematopinus* spp., *Bovicola* spp., *Menacanthus stramineus, Menapon gallinae*	Cattle, horses, poultry, other livestock
	Flies: *Melophagous ovinus*	Sheep and goats
Gadding	Flies: *Hypoderma* spp.	Cattle

during feeding attempts. Ticks in large numbers can cause economic losses through disfiguration, blindness, and death, in addition to the possibility of transmitting diseases. Millions of dollars are spent for tick eradication programs in the US and other countries to protect the livestock industries.

Relationship Between Pest and Host

The relationship between the pest and the host can vary. Some pests remain closely associated with the host and rarely if ever leave the host. The horn fly, *Haematobia irritans*, is termed a continuous pest because after finding a host, it remains almost always on the host. The relationship with *H. irritans* is so close that adults will die if separated from the host for just a few hours. Other pests associate with the host only when feeding. The stable fly, *Stomoxys calcitrans*, is termed an intermittent pest because it takes a blood meal from the host then leaves the host until another blood meal is required. Stable fly mates, oviposits and performs daily activities other than feeding without any association with a host.

The face fly, *Musca autumnalis*, and the horn fly are so closely related with their host animal (i.e., cattle) that the immature stages of these flies can develop only in cattle manure. Horn flies are sometimes observed residing and feeding on hosts other than cattle, namely horses. However, these flies cannot lay eggs in horse manure and will therefore not produce more horn flies unless cattle are nearby.

Feeding Sites

Most pests of veterinary importance have preferred feeding sites on a host. With this approach, pests effectively divide a host and minimize feeding interference. On cattle, ticks such as *Amblyoma americanum* localize in the ears and around

Veterinary Pests and their Management, Table 6 Diseases transmitted by selected vectors and the hosts that are affected

Diseases	Vectors	Hosts
West Nile Fever	Mosquito: *Culex* spp., other species	Birds, Poultry, Horses, Humans
St. Louis Encephalitis	Mosquito: *Culex* spp.,	Birds, Humans
Equine Encephalitis	Mosquito: *Culiseta melanura, Aedes* spp., *Culex* spp.	Birds, Horses
Heartworm Disease (Dirofilariasis)	Mosquito: numerous culicine and anopheline species	Dogs, Cats
Bluetongue	Biting midges: *Culicoides variipennis, C. pallidipennis*	Sheep, Cattle
Sand Fly Fever (Leishmaniasis)	Sand fly: *Phlebotomus* spp. and *Lutzomyia* spp.	Dogs, Humans
Mastitis	Flies: *Haematobia irritans*	Cattle
Keratoconjunctivitis	Flies: *Musca autumnalis, M. domestica, Hippelates* spp.	Cattle
Nagana (Trypanosomiasis)	Tsetse fly: *Glossina morsitans* group	Domestic animals other than poultry
Plague	Flea: *Xenopsylla cheopis*, various other flea genera	Rodents, e.g., *Rattus rattus*, dogs, cats, humans
Babesiosis	Ticks: *Boophilus* spp., *Haemaphysalis punctata*, *Rhipicephalus* spp.	Cattle, Sheep, Goats
	Demacentor spp., *Anocentor nitens*	Horses
Anaplasmosis	Ticks: *Boophilus* spp., *Rhipicephalus* spp. *Ixodes* spp, *Demacentor* spp., Tabanidae (mechanical transmission by several species)	Cattle
Heartwater Fever	Ticks: *Amblyomma lepidum*	Sheep, Goats, Camels
Sarcoptic Mange	Mites: *Sarcoptes scabiei*	Humans
	S. scabiei varieties	Swine, Horses, Mules, Dogs, Sheep
Demodectic Mange	Mites: *Demodex folliculorum, D. brevis*	Humans
	Demodex spp.	Dogs, Cattle, Swine, Goats, Horses

the escutcheon beneath the tail. Horn flies feed mainly on the back or the undersides of the body. Stable flies feed mainly on the lower legs. Face flies, *Musca autumnalis*, feed around the head and eyes. Mosquitoes feed on the sides of the body. Lice are found on the neck and tail. Cattle grubs are found beneath the skin on the back.

Method of Attack

The method of attack or infestation can be unique, as is the corresponding host response. Some pests, like ticks, are able to crawl undetected up the legs and body of an animal and attach themselves in the ears. Other pests, like the adult cattle grub, are unable to cause the host direct bodily harm, yet their presence as they attempt to oviposit on the host may send the host galloping away in a panic. Mosquitoes inject an anesthetic as they probe the host. Painful effects of their feeding are thus reduced, but the subsequent allergic reaction at the bite site may persist for days. Stable flies inject no anesthetic when feeding and their bites are extremely painful. However, the pain usually ceases immediately when the fly stops feeding. Pests like the horse flies (family Tabanidae) inject not only an anesthetic, but also ample amounts of anticoagulant to keep the blood flowing. This often results in a host with dripping wounds long after the horse flies have finished feeding.

Myiasis

The infestation of living or dead tissues by fly larvae is called myiasis, and this type of development is found not only in the bots and grubs, but in other flies as well. The primary screwworm fly, *Cochliomyia hominivorax*, oviposits exclusively in open wounds on living animals. Larvae emerge to feed on the living tissues and cause debilitating to life-threatening effects on the host. By contrast, the secondary screwworm fly, *Cochliomyia macellaria*, generally oviposits on hosts that are dead. Some flies oviposit on necrotic tissues in living hosts and feed only on the dead tissues. These flies secrete an antibiotic, allantoin, and were used to clean battlefield wounds before the advent of pharmaceutical antibiotics in the 1940s.

Although most pests of veterinary importance are considered to be external parasites, several fall into the category of internal parasites. These include the bot flies of the genus *Gasterophilus*. Larvae are ingested orally or nasally and migrate to the intestinal tract, where they spend most of their lives. The larvae of cattle grubs, *Hypoderma* spp., migrate through the tissues of cattle and eventually lodge in the skin of the back with the posterior spiracles exposed to the air. Besides being painful to the host, this pest ruins the value of the hide. The human bot fly, *Dermatobia hominis*, actually captures hematophagous flies on their way to feed on a host, oviposits on them, and they in turn passively and inadvertently infest the host with *Dermatobia* larvae.

Management of Pests of Veterinary Importance

Management of the number and variety of pests has at times been difficult and it is still practically impossible to keep many of the economic pests at tolerable thresholds. During the latter part of the twentieth century, the most common form of management involved the use of pesticides. In the late 1940s and into the 1950s, DDT was relied upon for control of veterinary pests. DDT was followed by a succession of other pesticides in various pesticide groups as pests became resistant to one chemical after another. Chemical pesticides are still the basis of control for many pests (for example, ticks on cattle), but this approach becomes more difficult as resistance continues to intensify. The development of new pesticides has been stifled by the high cost of registration and the potential for a short effective period in the field because of resistance and cross resistance. The most common methods and devices for application of pesticides include sprays, dusts, dips, pesticide-impregnated cattle ear tags, back rubbers, wipe-ons, pour-ons, and baits.

Biological control, particularly for flies, has been investigated by many scientists and used most successfully in confinement poultry and swine operations. Many studies have been done with confined cattle, but results are difficult to evaluate because of the extreme variations in field conditions. The agents most commonly used are small parasitic wasps, such as *Muscidifurax raptor* and *Spalangia endius*, on poultry, dairy, and confined beef operations, and the facultative predator, *Hydrotaea aenescens*, on poultry and swine farms. The bacteria *Bacillus thuringiensis* var *israelensis* (Bti) and *B. sphaericus* have been used

Veterinary Pests and their Management, Table 7 Management of pests of veterinary importance

Management technique	Targeted pests	Situation
Pesticide		
space sprays	Flies	barns
surface applications	flies, mites	animal housing
animal applications		
sprays	flies, ticks, lice, cattle grubs, sheep keds, poultry mites, other mites	cattle, horses, pastured cattle, sheep, goats, caged laying hens, cattle, sheep
pour-ons	lice, flies, cattle grubs	cattle
wipe-ons	mosquitoes	horses
back rubbers	*Haematobia irritans*	pastured cattle
dusts	*H. irritans*	pastured cattle
ear tags	*H. irritans*	pastured cattle
larvicide	*Musca domestica*, other nuisance Diptera	caged layer houses, confined poultry
dips	ticks	pastured cattle
baits	*M. domestica*	animal housing
Biological control		
Parasitic wasps		
Muscidifurax raptor	*M. domestica*	caged laying hens, indoor confinement dairy
Spalangia endius	*M. domestica*	caged laying hens
Spalangia spp.	*M. domestica, Stomoxys calcitrans*	caged laying hens, cattle feedlots
Predaceous flies		
Hydrotaea (Ophyra) aenescens	*M. domestica*, other nuisance Diptera	caged laying hens, confined poultry
Predaceous beetles		
Carcinops pumilio	*M. domestica*	caged laying hens
Predaceous mites		
Macrocheles muscadomesticae	*M. domestica*	caged laying hens
Bacteria		
Bacillus sphaericus	Mosquitoes	larval habitats
B. thurigiensis israelensis	Mosquitoes	larval habitats
Fungi		
Beauveria bassiana	*M. domestica*	larval habitats

Veterinary Pests and their Management, Table 7 Management of pests of veterinary importance (Continued)

Management technique	Targeted pests	Situation
Entomophthora muscae	*M. domestica*	animal housing
Mechanical control		
trapping	*M. domestica; S. calcitrans*	confined livestock and poultry
	H. irritans	dairy farms
sanitation	*M. domestica*	dairy, poultry and swine farms
	S. calcitrans	dairy farms and cattle feedlots
manure management	*M. domestica*	dairy, poultry and swine farms, and cattle feedlots
habitat management	ticks	range cattle

successfully for mosquito management and the fungi *Entomophthora muscae* and *Beauveria bassiana* have been tested against house flies and a variety of pests, respectively, with varying degrees of success.

Growth regulators have also gained wide acceptance and are classified as biological control by some workers in the field. Growth regulators are used mainly for control of mosquitoes and flies in the immature stages, and their activity is based on interference with the chemicals involved with the molting process. Methoprene is widely used for mosquito control, and cyromazine is added to the feed of poultry and used successfully for controlling house flies and other nuisance Diptera. Diflubenzuron has also been tested for a number of uses in fly control.

Mechanical control, consisting mostly of sanitation and trapping, has been used, particularly for flies. Source reduction (i.e., removal of hay, manures, and other breeding sites) can be very successful for fly control on farms. Trapping programs have been advocated, but have not been widely accepted because of related costs.

Integrated pest management (IPM) has been discussed and used for many years and successful programs have been developed. Because of the variety in farm design, many IPM programs must be custom designed for each farm. The exceptions may be confined swine and poultry where the farms are quite similar because of standardized housing designs. IPM is usually based on mechanical and biological control methods, and the focused use of selected pesticides as needed.

Management (Table 7) can be very difficult because of the wide-spread movement of pests, such as flies. Also, the use by ticks, for example, of alternate hosts such as deer and other feral animals complicates management. Thus, the success of pest management on individual farms is not easy to assess. Area-wide treatment of animals has been tried with limited success because the ability of the pests to disperse has been under-estimated. However, this may be the method of the future if wide-spread pest outbreaks are to be contained.

► Myiasis
► Bluetongue Disease
► African Horse Sickness
► Cat Flea
► Mites
► Ticks
► Dirofilariasis
► Mosquitoes
► Tick Paralysis
► Tsetse Flies
► Horse Flies
► Deer Flies
► Sleeping Sickness or African Trypanosomiasis

References

Farkas R, Hogsette JA (2000) Control possibilities of filth-breeding flies in livestock and poultry production. In: Papp L, Darvas B (eds) Manual of palearctic Diptera, vol 1: General and applied dipterology. Science Herald, Budapest, Hungary, pp 889–904

Greenberg B (1971) Flies and disease, vol 1. Princeton University Press, Princeton, NJ

Greenberg, B (1973) Flies and disease, vol 2. Princeton University Press, Princeton, NJ

Harwood RF, James MT (1979) Entomology in human and animal health, 7th edn. Macmillan Publishing Co., Inc., New York, NY

Hogsette JA, Farkas R (2000) Secretophagous and haematophagous higher Diptera. In: Papp L, Darvas B (eds) Manual of palearctic Diptera, vol 1: General and applied dipterology. Science Herald, Budapest, Hungary, pp 769–792

Kettle DS (1995) Medical and veterinary entomology, 2nd edn. CAB International, Wallingford, UK

Wall R, Shearer D (1997) Veterinary entomology. Chapman and Hall, London, UK

Vibrational Communication

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Insects are small life forms in large macrocosms, and therefore require specific methods of communication to overcome the relatively large distances separating individuals from mates, food resources and optimal habitats. This small size poses the inherent problem of separation of the sexes by relatively huge distances. A voluminous literature exists on how various groups have evolved tactics and systems, largely acoustical, chemical or visual, to insure effective mate finding. The large diversity of insects suggests that other exciting and dynamic systems of communication may await discovery.

Intersexual communication using low-frequency, substrate-borne vibrations (Table 8) is a mode of communication that has long been recognized, but little explored in arthropods such as scorpions, spiders and insects. Only in the past few decades has there been much effort to differentiate this mode from air-borne sound communication, determine how widespread it is in insects and to explore its quantitative aspects and evolution in particular groups. Termites, ants and several families of land bugs use vibrations to signal alarm; hornet workers use them to stimulate oviposition by the queen; most of the other groups use vibrational signals for locating mates or in conjunction with copulation. Some bush and tree crickets and land bugs use a combination of vibrational signals and stridulation-produced acoustical songs for intersexual communication.

Substrate-borne vibrations are produced by insects in various ways including percussion (drumming, tokking), tremulation (body pushups or jerking), tymbal clicking, stridulation or combinations of these methods. Percussion involves striking some part of the body, usually the abdomen, directly against the substrate; this has traditionally been termed drumming or tokking (Afrikaans word meaning "to knock"). The contact may be quick, producing a single, low-frequency vibration wave in the substrate, or prolonged as a scrape or rub, producing a series of waves whose frequency and time intervals depend on the texture of the body part and substrate making contact. Such a rub is actually a body-substrate stridulation. Tremulation consists of some form of body movement (jerking, pushups or wagging) not involving direct contact with the substrate. Movement energy is transferred through the planted tarsi and converted to low-frequency, transverse waves in the substrate. Some genera of longhorned grasshoppers, katydids, crickets, stoneflies, female planthoppers, alderflies, and chloropid flies utilize tremulation in intersexual communication. An advantage of this over percussion is that it does not produce associated sounds in resonant substrates that might be audible and attractive to potential predators. Vibrations produced by stridulation and tymbal activity in some Hemiptera are of great importance for intersexual signaling, and their use by singing Orthoptera (crickets, grasshoppers, katydids) is widespread.

Vibrational Communication, Table 8 Insect orders known to use vibrational communication

Order	Primary method(s) of vibration production	Major function(s)
Orthoptera; Longhorned Grasshoppers, Katydids, Crickets	Percussion, Stridulation	mate finding
Blattodea; Cockroaches	Percussion, Stridulation	mate finding, mating inducement
Isoptera; termites	Percussion	colony alarm
Plecoptera; Stoneflies (representatives of all nine Arctoperlarian families)	Percussion, Stridulation, Tremulation	mate finding
Psocoptera; Booklice	Percussion	mate finding
Hemiptera/Heteroptera; True Bugs (representatives of 16 families)	Stridulation, Tremulation Tymbal Clicking	mate finding
Hemiptera; Leafhoppers, Planthoppers (representatives of 3 families)	Tymbal Clicking	mate finding
Neuroptera; Green Lacewings, Alderflies, Spongillaflies (representatives of 3 families)	Tremulation	mate finding, mating inducement
Coleoptera; Death Watch Beetles, Darkling Beetles	Percussion	mate finding
Diptera; Chloropid Flies	Tremulation	mate finding
Trichoptera; Caddisflies (representatives of 7 families)	Percussion, Tremulation	mate finding
Hymenoptera; Ants, Wasps	Percussion	colony alarm, queen Stimulation

A more detailed analysis of taxa, sexes or castes producing signals, signal functions and key references for each order were presented by Stewart (1997)

Vibrational communication is a viable, alternative evolutionary strategy for small insects that are limited in body size to house elaborate song-producing structures and the frequencies that can be effectively air-transmitted by them. The biophysical aspects of vibrations in solid substrates are complex, but the vibrations offer a good directional communication medium enabling location of a signal emitter by a receiver, and for recognition of various parameters of the emitters signal. In ways little researched and understood, one individual may be able to measure the vibrational output of another through some selectively arrived-at neuronal capacity encoded to respond only to a potential conspecific mate or sibling. Scorpions, and presumably insects, can determine direction of a signal emitter by integrating time delays as small as 0.2 ms received by sense organs of the different legs. The planted tarsi represent positions like points on a compass, and the source of a directional vibrational signal is read from the time delays of the signal in differentially reaching these positions. Distance to an emitter may be determined by intensity of wave signals received above some threshold.

A disadvantage for insects that have adopted vibrational communication is the complication of wave transmission in the heterogeneous substrates present in their habitats. The variety of waveforms produced (longitudinal, transverse, bending, surface) are distorted and dampened by natural substrates, restricting the range of communication, but this apparently has been overcome because transmission through plants, dead plant items and connected leaf mats has been demonstrated for distances up to 8 ms, that may translate to 800–1,000 times the length of the insects' bodies. Such substrates are, therefore, effective transmission mediums for vibrational signals.

Little is known of the energy cost of vibrational signaling, as an important component of reproductive effort, but in general it is considered less than for producing high-frequency airborne sounds. The cost of percussion-assisted mate-finding in some beetles is 10% or less than that of random searching over the communicable area. Such cost-saving must represent an advantage for vibrational communication and probably plays a major role in the early stages of behavioral evolution. The vibrational signals of most insects consist of simple volleys of evenly spaced signals. Out-group comparisons have indicated that these types of signals produced by percussion are ancestral, and that derived signaling to achieve species-specificity, and to possibly enable some degree of sexual selection for fitness, has involved evolution toward increased signal complexity. Complex signals have been arrived at through: (i) more sophisticated signaling methods, (ii) changes in the rhythm of signaling, or (iii) possibly increased selection of the type of natural substrates used for signal transmission. Modern species have either retained the relatively simple ancestral pattern, with slight time interval modification for species specificity, or have developed various complex systems using combinations of these three derived behaviors. The high degree of species-specificity of vibrational signals in insects make them valuable behavioral lines of evidence for delineating morphologically similar species and resolving phylogenetic relationships.

► Drumming Communication of Stoneflies
► Acoustic Communication in Insects
► Acoustic Communication (Clicking) by Caterpillars

References

Gogala M (1985) Vibrational communication in insects (biophysical and behavioral aspects). In: Kalmring K, Elsner N (eds) Acoustical and vibrational communication in insects. Proceedings, XVII International Congress of Entomology. Verlag Paul Parey, Berlin, Germany, pp 117–126

Heady SE, Nault LR, Shambaugh GF, Fairchild L (1986) Acoustic and mating behavior of *Dalbulus* leafhoppers (Homoptera: Cicadelidae). Ann Entomol Soc Am 79:727–736

Henry CS (1980) The importance of low-frequency, substrate-borne sounds in lacewing communication (Neuroptera: Chrysopidae). Ann Entomol Soc Am 73:617–621

Lighton JRB (1987) Cost of tokking: the energetics of substrate communications in the toktok beetle, *Psammododes striatus*. J Comp Physiol B 157:11–20

Maketon M, Stewart KW (1988) Patterns and evolution of drumming behavior in the stonefly families Perlidae and Peltoperlidae. Aquat Insects 10:77–98

Stewart KW, Maketon M (1991) Structures used by Nearctic stoneflies (Plecoptera) for drumming and their relationship to behavioral pattern diversity. Aquat Insects 13:33–53

Stewart KW (l997) Vibrational communication in insects, epitome in the language of stoneflies? Am Entomol 43:81–91

Viburnum Leaf Beetle, *Pyrrhalta viburni* (Paykull) (Coleoptera: Chrysomelidae)

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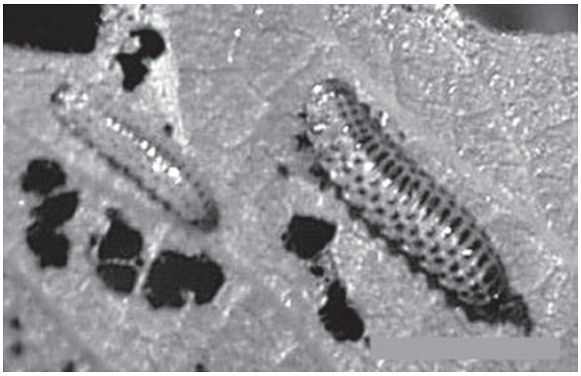
Pyrrhalta viburni (Paykull), commonly known as the viburnum leaf beetle, is a landscape pest of Eurasian origin that is quickly spreading through the northeastern United States. Breeding populations actually became established in North America (near Ottawa, Ontario, Canada) in the late 1970s, but did not reach the U.S. until

1994, when it was discovered in Maine. The pest was found in New York State in 1966, apparently the result of a separate immigration event, because the two founding locations are very widely separated. As of 2001, the beetle could be found throughout the southern half of Maine, in many of the northern and western counties of New York, as well as the northwestern tip of Pennsylvania and the northwestern corner of Vermont. Given its distribution across continental Europe, it seems likely that this pest will become commonplace throughout much of the range of *Viburnum*.

The only known hosts for *P. viburni* are in the plant genus *Viburnum*. Within the genus, however, species differ greatly in susceptibility. Some species, most notably arrowwood (*V. recognitum*) and cranberrybush (*V. trilobum* and *V. opulus*) viburnums, are devoured by the pest and are killed after only a few years of repeated infestation, while others, especially leatherleaf (*V. rhytidiophylloides*) and Koreanspice (*V. carlesii*) viburnums and their relatives, are virtually immune. Arrowwood is particularly important in the spread of *P. viburni* because it is widely distributed in native habitats, especially along large bodies of fresh water. The spread of the pest has been most rapid in such habitats. Spread of the pest may also be hastened by transport of infested nursery stock since *P. viburni* is not subject to quarantine restrictions.

The insect is univoltine, and overwinters in the egg stage. Eggs hatch in early May in upstate New York, around the time of bud break of the host plant. Larvae crawl to the tips of shoots, and begin feeding on the underside of newly expanding leaves. The larvae (Fig. 19), which are at first pale yellow, go through three instars, changing to solid black between instars. As the second and third instars grow, the black sclerites form spots and stripes as the intersegmental membranes expand. The larvae complete their development in 4–5 weeks, then crawl to the soil and burrow down several centimeters to pupate. Adults emerge several weeks later.

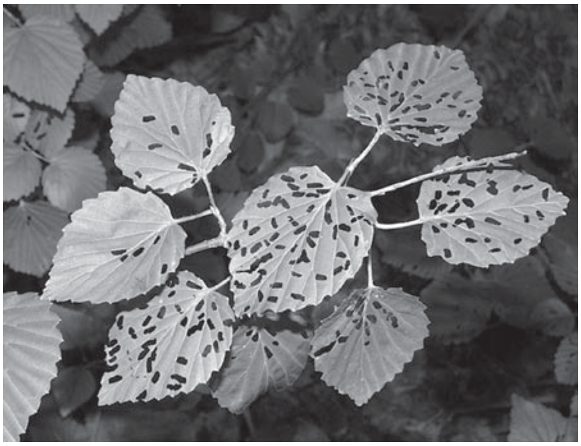


Viburnum Leaf Beetle, *Pyrrhalta viburni* (Paykull) (Coleoptera: Chrysomelidae), Figure 19 Larvae of *Pyrrhalta virburni*. Second instar is shown on left, third instar on right. (Photo by Paul A. Weston.)

Adults (Fig. 20), which resemble smaller, more drab versions of elm leaf beetle, feed on the leaves of the same host species as the larvae. Feeding damage by adults (Fig. 21) is distinctly different from that of larvae, however. Whereas larvae feed on leaf tissue between veins, leaving skeletonized leaves when populations are heavy, adults create oblong cutouts in the leaf, measuring about 2 mm wide by several mm long. Adults are active until late September or early October, all the while feeding and laying eggs on host plants. Oviposition sites of the beetle are quite distinctive; eggs are laid in masses on the underside of young shoots, generally in a linear array of several egg clusters per shoot. The female first chews a small hole into the pith of the stem, and then deposits about half a dozen eggs in the hole. She then caps the eggs with a mixture of feces and chewed foliage or bark. The caps protrude noticeably from the surface of the twig, and probably help to retain moisture and protect the eggs from natural enemies. The eggs remain dormant until the following spring.

Several species of parasitoids are known to use *P. viburni* as a host in Europe, but none of these natural enemies occurs in the U.S. Generalist predators, such as lady beetles and lacewing

Viburnum Leaf Beetle, *Pyrrhalta Viburni* (Paykull) (Coleoptera: Chrysomelidae), Figure 20 **Adult of *Pyrrhalta virburni* on twig. The adults range in size from 4.5 mm (male) to 6.5 mm (female), and are medium brown in color. (Photo by Paul A. Weston.)**



Viburnum Leaf Beetle, *Pyrrhalta Viburni* (Paykull) (Coleoptera: Chrysomelidae), Figure 21 **Feeding damage by adult *Pyrrhalta virburni*. Note that feeding occurs in discrete cutouts with rounded ends, randomly distributed across the leaf surface. (Photo by Paul A. Weston.)**

larvae, also feed on larvae, and at least one species of nematode (*Heterorhabditis bacteriophora*) effectively utilizes *P. viburni* as a host.

References

Balachowsky AS (1963) Entomologie appliquée à l'agriculture. Traité. Tome I, Coléoptères, 2nd vol. Masson, Paris, France, 1,391 pp

Becker EC (1979) *Pyrrhalta viburni* (Coleoptera: Chrysomelidae), a Eurasian pest of viburnum recently established in Canada. Can Entomol 111:417–419

Weston PA, Eshenaur BC, McNiel RE (2000) Viburnum resistance. Am Nurseryman 192:51–53

Viereck, Henry Lorenz

Henry Viereck was born at Philadelphia, Pennsylvania, USA, on March 28, 1881. In 1900 he began studying Hymenoptera at the Academy of Natural Sciences in Philadelphia. After a brief attempt at studying medicine he returned to entomology and worked at the Connecticut Agricultural Experiment Station, the Pennsylvania Department of Agriculture, Bureau of Entomology, the California State Horticultural Commission, United States Department of Agriculture Biological Survey, and the Canada Department of Agriculture. He published 92 papers on Hymenoptera, principally on Ichneumonidae and Andrenidae. He died on October 8, 1931, when he was struck by a hit-and-run motorist while collecting along a road near Loudenville, Ohio.

Reference

Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Vinegar Flies

Members of the family Drosophilidae (order Diptera).

► Flies

Vine Mealybug, *Planococcus ficus* Signoret (Hemiptera: Pseudococcidae)

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Vine mealybug, *Planococcus ficus* Signoret, is a recently introduced pest in California vineyards. Vine mealybug was first recorded from the Crimea region in the 1890s; currently, it is found in the Middle East, North African and Mediterranean countries, Pakistan, Argentina and California in the United States. While vine mealybug infestations are most damaging in vineyards, the mealybug is also an occasional pest of apple, avocado, banana, date palm, fig, mango and citrus. In the laboratory, vine mealybug can be reared on a number of hosts, including butter-nut squash (*Cucurbita moschata*) and potatoes (*Solanum tuberosum*). The vine mealybug is one of several mealybugs species that attack vineyards, e.g., *Pseudococcus maritimus* Erhorn (grape mealybug), *P. viburni* (Signoret) (obscure mealybug), *P. longispinus* (Targioni-Tozzeti) (long-tailed mealybug), and occasionally by *Planococcus citri* Risso (citrus mealybug) and *Maconellicoccus hirsutus* Green (pink hibiscus mealybug). Of these mealybugs, the vine mealybug is most closely related to the citrus mealybug. While they look very similar and can coexist in the same regions, citrus and vine mealybug populations can be separated by their sex pheromones.

Mealybugs are related to aphids and whiteflies and feed in a similar manner with long piercing-and-sucking mouthparts to remove plant juice. The vine mealybug can feed on the vine roots, trunk, canes, leaves and fruit. An adult female vine mealybug is 3–4 mm long, wingless, oval-shaped body, and covered by white wax. The secreted wax forms long filaments protruding along the body margin, which can be used to identify some mealybug species. The adult female lays from 300 to 500 eggs in a cotton-like (formed by secreted wax) ovisac. Under a controlled environment at 28°C, eggs hatch in 7–9 days. The emerging crawlers are bright-orange to yellow-orange colored. These crawlers, or first instars, are very mobile and move around the vine until they find a suitable feeding site. Once the crawler settles and begins feeding, the bright-orange body is covered by the waxy secretions and the mealybug takes on a more subdued pale white color. Females have four instars and, in the field, they can be distinguished only by their relative sizes. Each stage lasts 4–7 days, depending on temperature. Adult male mealybugs are very different in appearance. Males are about 2 mm long and have a pair of functional wings, and long caudal filaments. Males look similar to females in the egg and crawler stages, whereas the second and third instars are bit more narrow and oblong than females. Males pupate after the third instar, whereas females become reproductive in the apparent fourth instar. In California's San Joaquin Valley, there are six generations of vine - mealybugs per year.

Within-Vine Distribution

Vine mealybugs are found on all parts of the vine, including the roots. In spring, as soon as the leaf buds form and break, vine mealybug crawlers start to move up towards crown and the canes. By mid-summer, all stages of the vine mealybug can be found throughout the vine including the leaves. Starting in mid-summer and continuing through the harvest time, mealybugs begin to infest the grape bunches. (Infestation of the grape bunch begins earlier in the season as you move further south and into the desert agricultural regions in the Coachella Valley.) In heavy infestations, i.e., when the mealybug density is high, the pest can foul the grape bunches with honeydew, ovisacs, and live and dead bugs, making the fruits unmarketable. Excessive honeydew secretion also promotes the growth of sooty mold, further reducing marketability. After harvest and leaf drop, the mealybugs are found either on the trunk, typically deep under the bark or in feeding holes made by moth or beetle wood borers, or on the roots; there they remain at low densities until the following spring when the cycle is repeated.

Biological Controls

There are many species of ladybird beetles that feed on mealybugs, the most well-know is the mealybug destroyer, *Cryptolaemus montrouzieri* Mulsant (Coleoptera: Coccinellidae). Both larvae and adults of the mealybug destroyer can feed on all stages of the vine mealybug; however, the adult beetle prefers to feed on eggs in the mealybug ovisac to increase reproduction and egg deposition. The mealybug destroyer was first introduced into California from Australia in 1892. The beetles larvae also produce waxy filaments that cover the body and disguise the beetle as a mealybug destroyer (that can help the beetle evade ants which protect the mealybugs). The beetle larva can be distinguished by its distinct body segments and non-uniform length waxy filaments. Because the beetle prefers cool and relatively humid conditions, its numbers never increase to high levels in the interior parts of California where there is dry and warm climate. Lacewings also feed on mealybugs. There are brown and green lacewings resident in California vineyards. The green lacewings (*Chrysoperla* and *Chrysopa* species) are most common. Like the beetles, the lacewings are more effective when they attack the smaller mealybug stages. Both the mealybug destroyer and some green lacewing species can be purchased from commercial insectaries and released to suppress mealybugs.

Worldwide, there are several species of small (less than 2 mm) parasitic wasps (Hymenoptera: Encyrtidae) that have been found attacking the vine mealybug. These include *Anagyrus pseudococci* (Girault), *Allotropa* sp., *Leptomastidea abnormis* (Girault), *Leptomastix flavus* Mercet, *L. dactylopii* Howard, and *Coccidoxenoides peregrinus* (Timberlake). In the mid 1990's *A. pseudococci* and *L. abnormis* were released in California's Coachella Valley to suppress vine mealybug population growth and spread. *A. pseudococci* and *L. abnormis* have been recovered; however, parasitism levels rarely exceed 25%. Further north, in the San Joaquin Valley, we found that, by late-summer, resident *A. pseudococci* parasitized 80–95% of mealybugs that were exposed on leaves, bunches, canes, and trunk sections – although we have not seen any parasitized mealybugs on the roots or under refugia deep under the bark. *Allotropa* sp. contributed 1% to the total parasitism levels. *Anagyrus pseudococci* is a small wasp about 1.5 mm long. The female is brown in color and has white antennae with black at the base; the male is black, 0.7–0.9 mm long, and has hirsute, black antennae. *Anagrus pseudococci* can oviposit in second instar to adult stage mealybugs; with male offspring typically emerging from the smaller mealybugs (second to third instar) and female parasitoids emerging from the larger mealybugs. Parasitoid development time is about 18 days during the summer. *Leptomastidea abnormis* as another biological control is under investigation. It completes its life cycle in 20–22 days under laboratory conditions. *Leptomastidea abnormis* is about half the size of *A. pseudococci*, with two black bands on clear wings.

Both *A. pseudococci* and *L. abnormis* are commercially available. Researchers from University of California Berkeley and Riverside are currently investigating augmentation programs in the Coachella Valley and San Joaquin Valley. Augmentation may be needed because, although the percentage vine mealybug parasitism from naturally occurring parasitoids can be high, the parasitoids appear in the field, late in the season to effectively control the mealybug before the population moves up the vine and infests the grape bunches. Research is currently underway to investigate area-wide release programs early in the season (spring) and targeting the overwintered mealybug population.

Insecticide Controls

To control vine mealybugs, delayed-dormant insecticides (e.g., chloropyrifos [Lorsban®]) can be used to kill over-wintered mealybugs; however, control is incomplete as some over-wintered mealybugs may remain in protected regions of the vine. During the season, a number of foliar materials are available (e.g., methomyl [Lannate], imidacloprid [Provado®]) but control is still dependent on complete coverage. For this reason, one of the best insecticidal controls is a systemic application of imidacloprid [Admire®]. Effectiveness of this systemic material is dependent on good delivery to the entire root zone, which can be influenced by the irrigation system used or soil type and condition.

Cultural Controls

Sanitation is also a tool to prevent spread of the mealybugs. Weed control during the winter and early spring time may help prevent a build up of the mealybug population. Vineyard equipment, such as a grape harvester, used in an infested field should be washed thoroughly with water and bleach before moving into another field. Similarly, it is good idea for field crews to clean and change their clothing and shoes after visiting an infested field to remove any mealybugs that may cling onto their skin or clothes.

Sampling Methods

It is easy to detect the vine mealybugs during harvest in a heavily infested vineyard; the presence of shiny, honeydew and dark sooty mold on the vine and the leaves close to the trunk is an indicator of the presence of vine mealybugs on that vine in that year. For quick monitoring purposes, it is advisable to look for the sooty mold on the leaves just before the leaf fall and rain (October–November), and make plans for treatments accordingly. Currently, researchers are developing a vine mealybug sex pheromone that may greatly improve sampling for low-density mealybug populations. This is critically important because chemical treatment is recommended if only a few vines are infested in order to catch new infestations.

Other Mealybug Pest Species

The other mealybugs that are commonly found in the vineyards are grape mealybug (*Pseudococcus maritimus*), long-tailed mealybug (*P. longispinus*) and obscure mealybug (*P. viburni*). Long-tailed and obscure mealybugs are found only in the coastal grape growing regions of California. The grape mealybug is commonly found both inland and the Pacific coast of California as well as other grape growing regions like New York, Oregon and Washington states. Pears and apples are other host plants of grape mealybugs. These species can be distinguished by their two caudal filaments that are longer than the rest of the filaments and form a V-shaped tail. The grape and obscure mealybugs look very similar; however, they can be differentiated by the color of the ostiolar fluids, which are secretions from lateral ostiolar pores. The long-tailed mealybugs, as their name suggest, they have longer caudal filaments as compared with the other mealybug species.

The grape and obscure mealybugs generally have two to three generations per year, depending on temperature. The eggs and crawlers from second summer generation (August/September) overwinter. None of these mealybug species produce as much honeydew (or economic damage) as the vine mealybugs. Both obscure and long-tailed mealybugs produce very little honeydew compared to both vine and grape mealybugs.

References

Cox J (1989) The mealybug genus *Planococcus* (Homoptera: Pseudococcidae). Bull Br Mus Nat Hist 58:1–78

Malakar-Kuenen R, Daane K, Bentley W, Yokota G, Martin L, Godfrey K, Ball J (2001) Population dynamics of vine mealybug and its natural enemies in the Coachella and San Joaquin Valleys. Univ Calif Plant Prot Q 11:1–4. Available at, http://www.uckac.edu/ppq/PDF/01April.pdf, accessed 13 March 2008

McKenzie HL (1967) Mealybugs of California. University of California Press, Berkeley and Los Angeles, CA

Viral Flacherie

An infectious flacherie of silkworm larvae caused by a small nonoccluded virus.

► Flacherie

Virginopara

In aphids, the viviparous female occurring during the summer months (after the fundatrix generation).

► Aphids

Viremia

The presence of virus in the hemolymph or blood.

Virion

The mature virus, the ultimate phase of viral development. The virion is either a naked or an enveloped nucleocapsid. The term "virus" embraces all phases of the viral development, and it includes the virion.

Virulence

The quality or property of being virulent, or the ability of a pathogen to infect a host and cause disease; the quality of being poisonous; the disease-producing power of a microorganism.

Visual Attractants and Repellents in IPM

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In essence, Integrated Pest Management (IPM) is a decision-based process involving the coordinated use of multiple tactics for optimizing the control of all classes of pests in an ecologically and economically sound manner. Tactics available for use in the management of pest insects include insecticidal control and behavioral control. For insecticidal control, monitoring population levels of pest insects and their natural enemies is a key component in deciding whether or not insecticidal treatment is necessary. Visual traps that are attractive to pests or beneficial insects can be useful monitoring tools. For behavioral control, visually attractive traps, or visual repellents may be used in direct suppression of insect pests.

Development and effective deployment of visual attractants and repellents in IPM call for an understanding of several variables that influence attractancy and repellency. These include properties of insect vision, visual properties of resources sought by insects and the role of visual stimuli in the resource selection process.

Compound eyes contain the principal photoreceptors of insects. Photoreceptors of many insects are capable of perceiving a bandwidth of energy extending (in human terms) from ultraviolet (approximately 300–400 nm) through blue (400–500 nm), green (500–560 nm), yellow (560–590 nm) and orange (590–630 nm). Few kinds of insects are able to perceive red (630 nm and above). Insects with large compound eyes may possess a greater degree of visual acuity (and, therefore, are more capable of perceiving the visual properties of hosts against the background) than insects with small compound eyes. For most insects, visual acuity is highest under high intensity natural light (for example, full sunlight at midday) and lowest under low light intensity (for example, at dusk, nighttime and dawn).

There are three properties of resource items for insects that may serve as visual cues to foragers: spectral quality, pattern and dimensions. Resource items may absorb, transmit or reflect incoming light. It is the reflected light that provides the most useful information to foragers. The color of reflected light includes elements of brightness (intensity), hue (dominant wavelength) and saturation (spectral purity). The foliage of most plants reflects light at comparatively low intensity, with maximum reflectance at 550 nm and nearly no ultraviolet reflection. Some flowers may reflect moderate or high levels of ultraviolet light.

Insects may use a variety of stimuli as cues for finding resources. These include olfactory, visual and auditory stimuli. The distance at which each type of stimulus is perceived varies widely among different kinds of insects. Generally, however, olfactory and auditory stimuli are perceived at greater distances than visual stimuli, with the latter often being the principal close-range cue used by the forager. Thus, visual attractants and repellents in IPM usually are not operative at distances exceeding a meter or so (in exceptional cases, a few meters). The greater the degree of hue or intensity contrast between a visual stimulus and the background, the greater the distance at which the insect may be able to detect the stimulus.

Visually attractive traps developed to monitor pest or beneficial insects in IPM usually incorporate characteristics that mimic the color or pattern (shape) of the visual cues used in finding resources. Pests including aphids, whiteflies, leafhoppers, anthomyiid flies and some beetles, as well as beneficials including coccinellids and hymenopterous parasitoids, often are monitored by yellow traps that are believed to mimic the plant foliage used by these insects as a resource cue. Yellow may constitute a "super-normal" foliage type stimulus, because yellow emits peak energy at about the same bandwidth of the insect-visible spectrum as green foliage emits peak energy, but at a greater intensity.

Several kinds of pest thrips and some kinds of pest sawflies are monitored by white or blue traps whose reflectance mimics the color of the flowers from which the adults obtain nectar or pollen. Similarly, several kinds of biting flies are monitored by white or blue traps that appear to mimic the reflectance properties of either resting sites or host animals. In most cases, the absence of ultraviolet reflectance from white or blue traps enhances the capture of pest insects, but the converse is true in the case of some anthomyiid flies and biting flies.

The shape of a trap can be an important attribute in the monitoring of certain pests. For example, several kinds of scolytid beetles are monitored using vertical, black, cylindrical traps that mimic the trunks of coniferous (Fig. 22) host trees.

Visual Attractants and Repellents in IPM, Figure 22 **Black cylindrical funnel traps mimic the silhouette of pine trees and are used, in conjunction with odor baits, to capture bark beetles (photograph by J. Foltz).**

Similarly, some kinds of frugivorous tephritid flies are monitored using fruit-sized spheres that mimic the shape of the host fruit.

When baited with attractive odor, visually attractive traps can be used to achieve direct behavioral control of certain pest insects. The tsetse fly (*Glossina pallidipes*), for example, can be effectively suppressed in parts of southern Africa by deploying odor-baited, insecticide-impregnated targets of blue cloth at densities of 3–5 targets per km^2. Several species of tabanid flies can be suppressed by deploying large, odor-baited, dark-colored spheres, or other objects that roughly resemble the color and shape of potential hosts. The apple maggot fly, *Rhagoletis pomonella*, can be controlled effectively by ringing apple orchards with red spheres that are odor-baited and are either sticky or are treated with insecticide.

Visual stimuli have proven very effective in repelling aphids, whiteflies and thrips that vector viral pathogens of row plants. Rows of young plants are protected from viral inseminations when they are underlain (Fig. 23) with ultraviolet-reflecting mulch, such as aluminum foil, or materials sprayed with aluminum paint. Reflected ultraviolet light resembles sunlight and signals immigrating adults to keep on flying rather than settle on foliage. The use of ultraviolet-reflective mulch in protecting row crops against viral infection is expected to increase substantially when effective, biodegradable mulches replace the current non-degradable types.

► Traps for Capturing Insects

Visual Attractants and Repellents in IPM, Figure 23 **Aluminum-coated plastic mulch underneath young tomato seedlings repels alighting aphids and whiteflies (photograph by D.J. Schuster).**

References

Allan SA, Day JF, Edman JD (1987) Visual ecology of biting flies. Annu Rev Entomol 32:297–316

Kring JB, Schuster DJ (1992) Management of insects on pepper and tomato with UV-reflective mulches. Fla Entomol 75:119–129

Lindgren BS (1983) A multiple funnel trap for scolytid beetles. Can Entomol 115:299–302

Muzari MO (1999) Odour-baited targets as invasion barriers for tsetse flies: a field trial in Zimbabwe. Bull Entomol Res 89:73–77

Prokopy RJ, Owens ED (1983) Visual detection of plants by herbivorous insects. Annu Rev Entomol 28:337–364

Prokopy RJ, Wright SC, Black JL, Hu XP, McGuire MR (2000) Attracticidal spheres for controlling apple maggot flies: commercial-orchard trials. Entomologia Experimentalis et Applicata 97:293–299

Visual Mating Signals

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Evolution has sculpted and colored the surfaces of the arthropod body. Natural selection favored appearances that mislead predators through disguise and camouflage, i.e., "cryptic coloration," and those that warn enemies to stay away through bright advertisements of distastefulness or dangerous weapons, i.e., "aposematic coloration."' In addition, body surfaces may help modify the effects of the physical environment, e.g., to absorb or reflect heat. Certain colors, shapes and movements also influence the behavior of the conspecifics in contexts including social interactions, e.g., honeybee dances. Other signals evolved in the context of mating.

Visual Mating Signals, Figure 24 **There are dangers as a well as opportunities inherent in visual signals. The eye(s) of this spider may have first been caught by the firefly's bioluminescent sexual display (photo by Steven Wing).**

Sexual Selection and the Evolution of Displays

These sex-related signals, or "displays," are directed either toward rivals (usually males attempting to repel other males) or potential sexual partners (usually males attempting to attract mate-choosing females). Display surfaces, and the behaviors associated with their exhibition, have evolved through sexual selection, the process in which genes are favored because they give greater access to the opposite sex. Competition among members of one sex for access to the other results in "intrasexual selection," and mate choice and the displays directed to the choosing sex evolve through "intersexual selection."

Sexually selected displays presumably resolve competitions and/or facilitate mate choices because receivers evaluate and act on information contained in the display's colors, size and motions. The experimental evidence that arthropods perceive visual displays and then (Fig. 24) modify their reproductive activities is phylogenetically widespread. Some examples include the sexual response of fireflies (Lampyridae) to patterned electric lights, and female wolf spider's (Lycosidae) reactions to videotapes of the stylized foreleg movements the males perform during courtship.

The Basis of Sexually Selected Signals

Ultimately, both inter– and intrasexual selection occur because of differences in "parental investment" between the sexes. Parental investment is anything, material or behavioral, that a parent invests in an offspring that increases the offspring's chance of surviving at the cost of the parent being able to invest in other offspring. There is a fundamental sexual dimorphism in parental investment due to the female's initial investment in large, resource rich eggs, and the male's in small, inexpensive sperm. All other things being equal, a female's capacity to reproduce is limited by the resources she can obtain and use to produce her eggs. Multiple mates do not necessarily result in more offspring, although she may be able to choose a mate whose genetic or other qualities, sometimes illuminated through displays, result in her bearing more, or more fit, offspring. On the other hand, ejaculates are cheap and males invest little in the insemination of a female. The more females a male copulates with, the more offspring he will father. As a result, selection favors males that successfully compete with one another for access to mates, often through displays directed both to females and to other males.

There are exceptions to this "grand generality." For example, males of some species of katydids (Tettigonidae) and balloon flies (Empididae) provide females with nutritious "nuptial gifts," such as huge protein-rich ejaculates and insect cadavers. As a result, a female's reproduction is influenced by her ability to gain access to gift-bearing males. In these instances there may be sex-role reversals and males choose mates from among competing, displaying females.

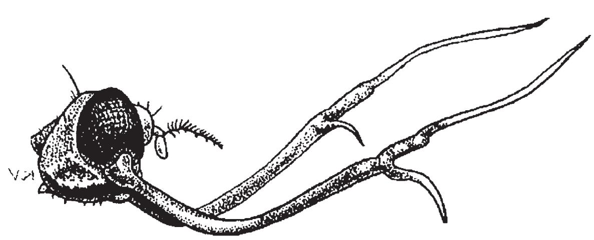
Sexual Dimorphism and Sexually Selected Displays

In some species, members of one sex differ in appearance from members of the opposite sex. Sexual dimorphism in color is suggestive of a display in one of the sexes. Charles Darwin, for example, was struck by the brilliancy of male butterfly coloration and the relative drabness of females. He, and subsequently others, proposed that sexual selection had generated colors of greater saturation and more precise demarcation in males because they were used in sexual communications while females maintained the ancestral, more cryptic, coloration. Some exceptions to the "rule" that females bear the more ancestral coloration tend to support the idea that sexual selection has been more important in the evolution of male than female coloration. There are instances in butterflies (Papilionidae), e.g., the African swallowtail, *Papilio dardanus*, where relatively palatable females are "Batesian mimics" of one or more aposematic-unpalatable species, but males maintain a pattern more typical of closely related species. It seems likely that male-signalers have conserved a coloration that is important in a visual display, and that females, either because they are the display-receiving sex or because they are not involved in intrasexual competitions, were free to abandon their ancestral coloration for one that offered more protection from predators.

However, not all sexual dimorphisms in color are the direct result of sexual selection. For example, male and female stick insects (Phasmatodea), such as *Diapheromera covilleae*, sometimes bear special resemblance to different types of foliage on their host plants, and while the two sexes look quite dissimilar, there is little in their mating behavior to suggest a visual display is the cause of the difference. On the other hand, surfaces and colors that are not sexually dimorphic may be used in displays. Movements of strikingly patterned (Fig. 25) wings are typical of sexual encounters in fruit flies (Tephritidae), but sexual dimorphism in wing coloration and marking is rare.

The Advantages and Disadvantages of Light in Communications

In comparison to chemicals and sounds, reflected light perceived as color and pattern has both advantages and disadvantages as a means of communication in insects. Among its advantages are its capacity to carry large amounts of reliable information. A signal is able to transmit a message through modulation, predictable and specific variations, e.g., Morse code, or a particular color pattern



Visual Mating Signals, Figure 25 **The head of a male antlered fruit fly *(Phytalmia cervicornis)* from New Guinea. The deer-like antlers projecting from the cheeks are as much visual propaganda as weapons (drawing by Kevina Vulinec from Sivinski 1997).**

on the surface of a wing. Visual cues may be more reliable in this sense than chemicals whose combinations and densities can be blended and obscured by even slight motions of the air. It is difficult to imagine a message consisting of patterned puffs of odor making sense to a distant receiver on a breezy day.

Some modes of communication work better than others in a given habitat and context. Among the potential disadvantages of visual displays are that they can be blocked by opaque objects that chemicals or sounds could go around, and are unlikely to reach as far as pheromones and acoustic signals. Visual signals also lack persistence in the absence of the signaler, e.g., ant recruitment trails. They can even be dangerous to the signaler, as they may be more easily tracked by predators than pheromones or sounds, and even provide an unusual opportunity for predators to lure mate-seekers. For example, fireflies (Lampyridae) can be tricked by "aggressive mimics" that produce the luminous sexual display-response that attracts males of other firefly species to their final rendezvous.

Arthropod visual signals are potentially detailed and informative, but only at short distances. The effective range of visual signals is generally limited because only a small body-surface area is available for a display and because of the poor resolution of the insect compound eye. Insect eyes can resolve details of little objects such as other insects, but only at extremely close range ("[compound eyes] & would give a picture about as good as if executed in rather coarse wool-work and viewed at a distance of a foot" [Henry Mallock]). One possible exception to the generally short range of arthropod visual signals is bioluminescence, e.g., the flashes of fireflies. An extreme example is the mass display of male *Pteroptyx* fireflies, which gather by the thousands in certain trees and flash synchronously.

Idiosyncratic details of a particular arthropod's vision also influence the forms of its visual displays. For example, jumping spiders (Salticidae) see colors and are able to detect motion while moving, but wolf spiders (Lycosidae) are color-blind and must be still to perceive movement. Jumping spiders use bright colors and "dances" in their displays, while wolf spider courtships consist largely of raising and waving darkly pigmented or hairy legs.

UV Markings

Human and arthropod vision differ in the range of light wavelengths perceived. Insects are generally insensitive to red, but can see ultraviolet light (UV). Insects that appear drab to us may, in fact, be brightly reflective in the ultraviolet range and able to communicate among themselves in color patterns that are invisible to us and perhaps invisible to some of their vertebrate predators (although diurnal birds typically see UV, as do some mammals). For example, males of certain butterflies (e.g., *Colias* spp. [Pieridae]) bear brilliant UV markings, but the extensive sexual dimorphism in these species was only discovered through specialized photography. As a result, use caution in interpreting a particular arthropod's colors until the entire spectrum is described.

The Content of Intrasexual Displays

As Charles Darwin noted, "The season of love is that of battle…," and conflicts among sexual competitors, usually males, are sometimes resolved by threats communicated through visual displays. The intensity of aggression ("agonistic behaviors"), and the investment in the colors, structures and behaviors that convey the sender's ability to fight, follows a pattern. The greater the control a male can exercise over females or the resources females require, such as oviposition or feeding sites, the more profitable it is for males to invest in weapons and advertisements of prowess. Typically, controllable resources are relatively small and rare and, thus, easily defended. As resources become common, large and spread out, they become less and less defendable and less and less likely to be associated with aggressive displays.

Antlered flies (Diptera) are classic examples of displaying males guarding a discrete resource. Projections from the head, either eye-stalks or horns sprouting from the cheeks, occur in species from nine families of flies. Perhaps the most elaborate are found in the large New Guinean fruit flies (Tephritidae) of the genus *Phytalmia*, one species of which the great nineteenth century naturalist Alfred Wallace described in the following manner: "The horns of (*P. megalotis*) are about one third the length of the insect, broad, flat, and of an elongated triangular form. They are of a beautiful pink color, edged with black, and with a pale central stripe. The front of the head is also pink, and the eyes violet pink, with a green stripe across them, giving the insect a very elegant and singular appearance."

Female *Phytalmia* oviposit in pinhole sized punctures in certain species of freshly fallen trees. These very small and rare resources attract females and are easily defended, and the owner's initial defense is accomplished through visual display. Resident (defending) and intruder males of *P. mouldsi* clash by rising up on their legs and pushing hard against each other's remarkable heads, although the antlers themselves do not play a major role in the battle. However, males whose horns are experimentally lengthened or shortened are respectively more and less likely to win fights. In addition, those whose antlers are removed altogether are treated by their rivals as females. Thus, antler-weapons serve to a great degree as displays whose size opponents appear to correlate with fighting ability.

Rival males pay attention to each other's visual displays when deciding how they will go about the all-important activities of holding resources and inseminating females. The reason is either the display is an accurate indicator of another's ability to defend its resource, or the opponent accepts that it is. "Honest advertisement" is an important principle in both intra- and intersexual signals. Over evolutionary time, a signal that exaggerates the capabilities of its sender will eventually be ignored by increasingly discriminating receivers. However, a signal that is expensive to build and display, or risky to use, is likely to honestly reflect the capacity of the sender for violence. Paradoxically, displays that "handicap" the emitter are the most useful in deciding whether it would be prudent to escalate a conflict or withdraw.

Stalk-eyes in flies are a case of what may have been a dishonest display evolving into a handicap and an honest advertisement. Smaller flies typically retreat from face-to-face confrontations with larger opponents and fights are normally between similar sized individuals. Suppose that the size of a rival is assessed by the breadth of the head, as gauged by the degree of (Fig. 26) overlap between the two sets of eyes. If so, males can appear large and conquer psychologically simply by broadening their faces. As deceitfully widened heads become more common, even further exaggeration is required, and the resulting "arms race" pulls the eyes farther and farther apart until they are at the ends of extraordinary stalks (in one 8 mm long species from Borneo, the combined length of the stalks is 20 mm). In the process, the stalks have become honest advertisements, genuine burdens that only the most robust males can produce and maneuver. Not only do males use stalk eyes to decide which opponents can be expelled and whether to fight or flee, but females also consider their size when choosing a mate.

Visual Mating Signals, Figure 26 The eyes of this male fly (*Achias* sp.) are at the ends of stalks whose combined width exceeds the length of its body. This condition, although usually less extreme, is found in a number of fly families and may be the result of trying to appear as large as possible in the opposing eyes of sexual rivals (drawing by Kevina Vulinec in Sivinski 1997).

The Content of Intersexual Displays

Location Cues: Long-Distance Signals

Because males usually benefit more from multiple matings than do females, they typically spend more energy and take greater risks than females to locate mates. When females are scattered through the environment, this often means males travel considerable distances searching for cues to find females. Because it is also in the female's interest to be found by one or more males and proceed with oviposition more quickly than other females, she may emit a relatively inexpensive signal that improves her chances of being located. Sexual pheromones are common female location cues that are typically produced in small, economical amounts and sent out with little risk as few predators or parasitoids specialize in tracking down the emitters of these chemically dilute and sporadic signals.

Modifications of female form or coloration that serve as signals to orient searching males may be less common than pheromones because the distance at which a visual cue can be perceived will generally be less than that of volatile chemicals. In addition, natural enemies without any special sensory adaptations might recognize visual signals as well as, or even better than, conspecific males. However, female location cues do seem to occur. For instance, in certain luminescent beetles like the phengodid *Phengodes nigromaculata*, larviform (Fig. 27) adult females retain the elaborate system of larval light organs that probably served as an aposematic advertisement of unpalatability. But the adult's lights are much brighter than the larva's and could act as a beacon to searching males whose large, complex male antennae suggest a female pheromone is produced as a longer distance signal as well. An alternative explanation for the brighter lights of adult females may be that chemical signaling requires more time spent exposed on the surface of the ground, and because of their greater vulnerability, females invest more in their aposematic display.

Competition among females to attract males from a distance typically will be less intense than competition among males to attract females. When males produce long-distance signals, whether chemical, acoustic, or visual, it is assumed that the signals are now more expensive than the travels females must undergo to reach the signaler, that the sender may be in greater danger from predators and parasitoids, and that females will be more likely to judge males on the basis of their signals than vice versa and respond selectively to the signals they deem most attractive.

Visual Mating Signals, Figure 27 A larviform female phengodid beetle (*Phengodes nigromaculata*) (a), and the same insect photographed by its own bioluminescence (b). The relatively bright lights of adult glow-worms may be beacons that help attract mate searching males (photos by J. Sivinski).

While there are many familiar male long-distance chemical and acoustic signals (e.g., Mediterranean fruit fly, *Ceratitis capitata*, and crickets [Gryllidae]), there seem to be fewer obvious visual examples. Part of the reason may again be the relatively limited range of vision in insects which is better suited to close-up examinations. Even so, there are a number of interesting male visual-location cues. The lights of perched male fireflies (Lampyridae) are visual equivalents of a katydid's (Tettigoniidae) song, and diurnal "beacons" that appear to advertise male positions occur in certain long-legged flies (Dolichopodidea). Male *Chrysotus pallipes* have much enlarged and shiny labial palps that emit silver flashes as they signal from the surface of leaves, and the reflected light from the tiny insect is surprisingly bright.

Courtship Displays

Courtship implies that the sender of a signal is attempting to overcome resistance in the receiver, and that the display will somehow influence (or manipulate) the receiver to copulate. This element of "seduction" can occur in long-distance signals as well, particularly those produced by males, and this blurs the distinction between long-distance beacons and courtship performances. However, greater amounts of detailed information, particularly visual information, would be available to insects in close proximity that are aware of each other's presence. Certain sexual behaviors will be unique to such close-up situations and so deserve separate consideration.

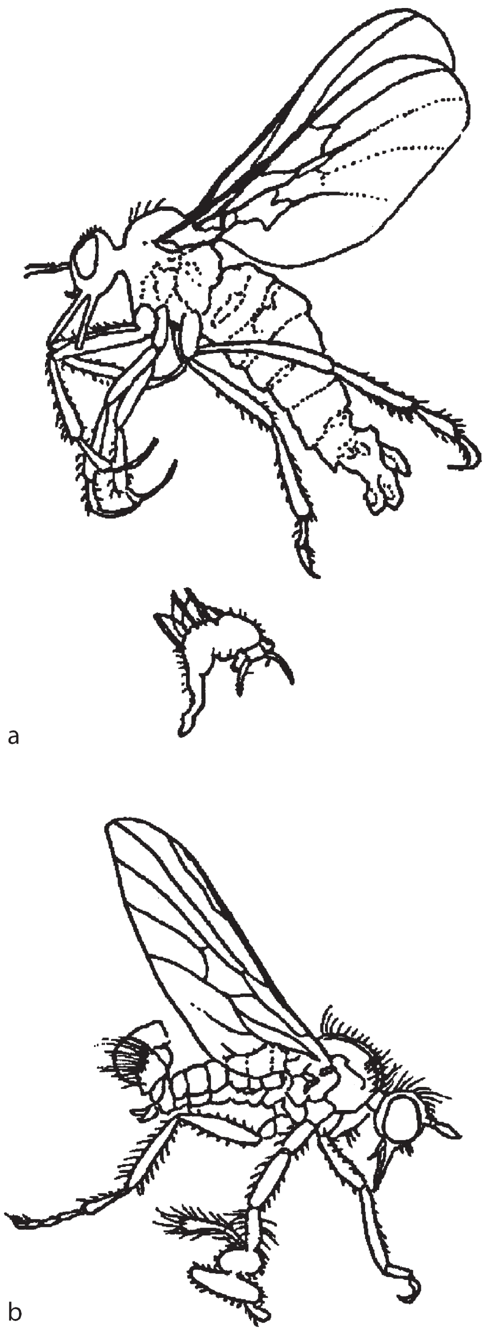
The meaning of communications with the opposite sex often is ambiguous, and there are several competing theories that attempt to explain the evolution of courtship displays. These hypotheses can be divided into the following categories: (i) displays promise a material benefit to the receiver, such as a nuptial gift of food or high female fecundity, (ii) displays advertise the genetic qualities of the performer through self imposed handicaps, and (iii) displays provide neither direct material nor genetic information, but are due to either genetic feed-back ("Fisherian run away selection") or manipulation of the receiver's perceptions ("sensory bias"). It may be that all of these are involved in the evolution of different displays.

Material Benefits

The exchange of "goods" from males to females, i.e., nuptial gifts, have been well documented in several insect groups. Examples include scorpionfly (Mecoptera) males that are required by females to produce captured prey of sufficient size, or else successful sperm transfer is not allowed. Some male Lepidoptera provide large, nutritious spermatophores during mating. The same is true of certain orthopteran males, while other orthopteran and coleopteran males provide nutritious secretions from the mouth or glands.

Such nuptial feeding invites deceit through false appearance. Things can be promised and then withheld to tempt another mate, or be promised but be completely absent. On the other hand, a female attempting to acquire a male's investment might exaggerate her fecundity, and appear to be a bigger mother and better recipient than she really is. When either sex has materials the other requires, be it protein or access to eggs, advertisements, including visual advertisements, they are likely to be elaborated through exaggeration. As in stalk-eyes, the expense of elaboration may eventually become a handicap and forge an honest display.

Empidid or dance flies (Diptera) provide examples of both male and female visual displays evolving in the context of sexual "commerce."' Predaceous male dance flies often provide mates with a (Fig. 28) prey item, but sometimes this is wrapped in a silk balloon that might have originally magnified the appearance of the gift and which, in some cases, may no longer hold anything and is perhaps only an empty promise. Even more peculiar are the odd outgrowths of the midlegs of male *Rhamphomyia scurissima*. This mass of swellings suggests the male has a small dead insect in its grasp,



Visual Mating Signals, Figure 28 **Males of many empidid species provide potential mates with an insect cadaver to eat (a). The peculiar outgrowths on the midlegs of the dance fly *Rhamphomyia scaurissima* (b) originally may have mimicked such a nuptial gift and attracted females through dishonest advertisement (drawing by Kevina Vulinec in Sivinski 1997).**

and, with this deception, he may be able to lure a gift-seeking female into a sexual encounter.

On the other side of sexual bartering are females whose apparent fecundity influences whether or not they are offered nuptial gifts. In some species, there are sex-role reversals where females swarm and males carrying insect prey choose the largest females to both feed and inseminate. Females may call attention to their abdomens, and the numbers of eggs they contain, with garish, bright silver markings. In several empidid genera, females inflate their abdomens with air until they are nearly spherical, and so may falsely appear to carry extraordinary numbers of eggs.

Genetic Benefits

Drosophila (Diptera) females that are free to pick their own mates produce more mature offspring over their lifetimes than do females that are provided with randomly chosen males. The implication is that certain males are better sires, and that females are able to recognize their genetic qualities. But what sort of qualities are they choosing and how are they recognized? It may be that phenotypes that have survived to old age or acquired the resources to attain unusually great size are reflections of an underlying genetic capacity to survive and forage effectively. For example, in certain tephritid fruit flies females prefer larger males, although the role of vision in judging size is unknown.

In general, the problem with signals that advertise such characteristics is that they can be exaggerated. Increasingly discriminating females will demand honest advertisements from prospective mates, and signals that are expensive, or dangerous, or otherwise impossible to counterfeit should become preferred. For example, it is hard for a male to appear to be more symmetrical than it actually is. The complexity of embryonic development often results in less than perfect bilateral symmetry, and the greater the number of deleterious recessive alleles in the genotype the more unlikely it becomes. As a result, "fluctuating asymmetries" in males are windows through which the value of their genes can be perceived and judged. Male *Calopteryx splendens* (Odonata: Calopterygidae) with more homogeneous wing spots perform more displays and obtain more mates, and male cerambycid beetles with more symmetrical antennae are more sexually successful. However, it is not always clear that female insects can visually discriminate fine degrees of asymmetry, and it is possible that they are attracted to male characteristics that co-vary with symmetry. For instance, a male that is more symmetrical may also have the physical capacity to signal for longer periods of time, and it is the signaling duration and not the symmetry that females find attractive.

Expense also insures honesty. A display that requires substantial material to produce, considerable energy to perform, and that places the emitter in danger is likely to be the production of a genuinely fit individual, one that had access to resources and was able to escape predators. Thus, displays are expected to be handicaps that are a burden to the insect outside of its sexual life.

Concentration on sexual matters can make males more vulnerable to predators, and it may be that the riveted attention that males focus on potential mates during courtship is in itself a handicap whose message is that "I possess such strength and agility that I can afford to give you my undivided attention and survive." Other physical trials might reveal genetic quality, e.g., females of the wolf spider *Hygrolycosa rubrofasciata* choose males on the basis of their leg-drumming rates which, in turn, are predictors of their viability.

In addition to risky, arduous or complicated behavior, physical structures may prove both costly to the signaler and attractive to the opposite sex. There are certainly any number of peculiar sexual dimorphisms in insects that could be both displays and handicaps. Many courting insects energetically use their wings, which are also important organs of predator-escape, in displays that might jeopardize their safety. For instance, potentially compromising wing motions are ubiquitous in the courtships of the tephritoid Diptera; e.g., *Callopistromyia annulipes* (Ulidiidae) males "strut" with wings upraised like a peacock's tail, and rapid wing movements are nearly universal in the sexual interactions of other large taxa like the parasitic Hymenoptera (such motions may also waft pheromones and/or produce acoustic signals).

Colors can attract both the opposite sex and the attention of predators, and in addition, some colors may be difficult or even dangerous to produce. In birds for instance, red pigments are derived from carotenoids that the animal cannot manufacture and must be obtained from food sources. Further, carotenoids are important components of the immune system and their removal from a vital health-function in order to be "painted" on the body surface may send a powerful message about both the foraging capacities and disease resistance of the signaler. Males often suffer more injuries and greater mortality than females, and this may be due to either more conspicuous colors or more risky mate-searching behaviors that expose them to predators. An illuminating case of dangerous bright coloration, as opposed to dangerous behavior, occurs in *Ischnura* damselflies (Coenagrionidae). Females may be either drably colored or brightly colored like the males ("andromorphs"). Brightly colored females are less likely to be recognized as potential mates and so avoid pestering by males. Because of their male-like appearance, they are able to lay their eggs more efficiently, but, unfortunately, they are also more likely to attract the attention of predators and, in some populations, they have only one-third the life expectancy of their plainer sisters.

Finally, color may indicate the ability of the signaler to avoid or survive debilitating diseases and larger parasites. Females may prefer such males either because they are likely to sire healthy offspring or because healthy males are less likely to transmit a disease during copulation. It has been suggested that the colors and forms of certain dung-feeding male scarab beetles might highlight the mite population they carry and allow females to choose males with lower mite loads.

Fisherian Run Away Selection

If the genes for the expression of a male trait (e.g., an element of a courtship display) and the female preference for the trait are linked, then females that choose the most extraordinary examples of the male characteristic will tend to have daughters with a still more extraordinary "taste" for the display. The extravagance of the display and the female demand for the extravagant will continue to increase hand-in-hand ("run away" in the sense of positive feedback) until the spiraling expense and danger of the signal are so great that natural selection puts an end to further elaboration. In this process, the display has no "meaning," females gain no insights into male genetic or material qualities from the display and choose mates only for their capacity to produce a more or less arbitrarily attractive set of colors, structures and behaviors.

Recently, the popularity of this theory of the origin of displays has suffered somewhat for two reasons. First, phylogenetic studies reveal that male displays have been lost in a number of lineages, much more frequently than previously had been imagined, and this loss is inconsistent with linked traits running away with one another. Second, displays increasingly are found to be reliable indicators of male quality and not simply matters of haphazard fashion. Particularly telling cases of informative signals occur when the same displays that males use to persuade females are also employed in competitive interactions with other males. A sexual rival has no reason to be intimidated by a structure or behavior that is only fashionable and not an advertisement of the ability to acquire a resource or to defend associated females. For example, in the stalk-eyed fly (Diopsidae), *Cyrtodiopsis whitei*, female harems "roost" in the company of individual males, and females prefer associations with long-stalked males because stalk-eye length is correlated to offspring quality. Eye stalks are also used in antagonistic interactions.

Sensory Bias

"Sensory bias" theories of the origin of displays suppose that male sexual displays take advantage of preferences that have evolved in females for other reasons, and so manipulate females into responding. This is another type of male signal that tells females nothing useful about male genetic or material qualities, at least in the early stages of its evolution. For example, females of the water mite *Neumania papillator* (Acari: Parasitengona) use vibrations to locate their copepod prey, and males make similar vibrations with their forelegs. Females move toward and clutch vibrating males, and are more likely to do so when they are hungry. It seems that males have exploited the female's feeding behaviors to increase their rate of sexual contact.

Manipulative visual displays occur in the wolf spider (Lycosidae) genus *Schizocosa*. Males perform leg-waving courtships, but the various species have different degrees of foreleg ornamentation. Female spiders will orient toward video tapes of male courtships, and prefer the images of males with tufts of hair on their legs, regardless of whether or not their conspecific males have such hair-tufts. Thus, females in both tufted and untufted species appear to have a pre-existing preference for hairy legs that males of some species take advantage of and that males of other species do not.

This taste for leg-tufts might be a byproduct of hunting behaviors where female spiders must orient toward and approach small moving objects in their environment. Because such a response is necessary for the display-receiver to obtain food, it is difficult for her to completely ignore the signaler, but females might become more discriminating over time and sensory bias signals could evolve to carry information about male quality. For example, female *Schizocosa* spp. are more responsive to males with symmetrical forelegs, and such symmetry may be the result of developmental stability or a successful fighting career. Foreleg displays that now are showcases for symmetry may be elaborations of what began as lures.

Copulatory and Postcopulatory Displays

A female insect may choose the sire of her offspring at several points prior to oviposition. Her responses to precopulatory courtships determine whether or not she will mate. But even while coupled, she may choose to direct sperm to different portions of her reproductive tract where they will either be used for fertilizations, or be shunted away into places where they will languish or perish. Following mating she may simply eject sperm from a particular male, or copulate again with a more suitable male whose new ejaculate will block the old sperm from reaching the ova.

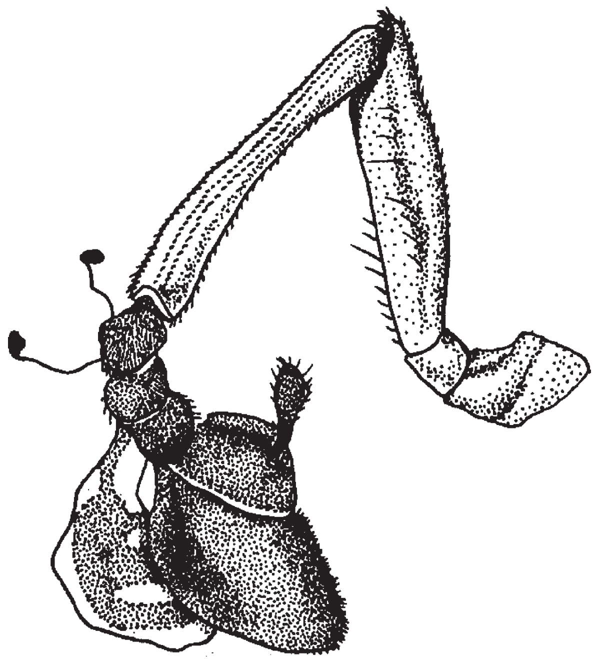
Because of these opportunities for "cryptic female choice," males may guard mates or continue courting mates with displays during and even after insemination. There are a number of male copulatory behaviors that might qualify as visual appeals to females making cryptic choices. *Sabathes cyaneus* is an unusually brightly colored mosquito whose mid legs end in a feathery "paddle" of elongate iridescent blue and gold scales. Males fly toward resting (Fig. 29) females with their paddles extended, land nearby, suspend themselves by their forelegs, and then swing and wave their ornaments. "Waggling," during which the midlegs continue to rise and fall, continues through the copulation. Mounted males of the long-legged fly *Scapius platypterus* (Dolichopodidae) insure their visual signals will be observed by resting their front legs over the female's head while the midlegs are held to the side near her eyes and waved back and forth. Males of the micropezid fly *Cardiacephala myrmex* close the gap between their foreleg motions and their mates by alternatively scratching and regurgitating on her eyes. Not only flies apply their ornaments to female

Visual Mating Signals, Figure 29 **Mosquitoes are rarely ornamented. An exception are males of the genus *Sabathes* whose midlegs are decorated with iridescent "feathers." This feather is waved before females both prior to and during mating (drawing by Kevina Vulinec in Sivinski 1997).**

eyes during copulation. Male wasps in the genus *Crabo* (Hymenoptera: Sphecidae) have the front tarsi dilated into horny plates punctured by membranous dots giving them a sieve-like appearance. During mating, these are placed over the female eyes, perhaps resulting in a specialized visual signal similar to what would be obtained by shining a light through an antique computer "punch card."

Mating Systems and Visual Displays

Arthropods seek mates in a number of ways and in a variety of places, some suited to the production of visual displays and others not. Swarms, where multiple males (or rarely females) fly in place, sometimes by the thousands, over a spot or "marker" are both common and seemingly poor places to advertise to potential mates. With numerous insects swooping about each other, signals, particularly pheromones, would be difficult to track back to their emitter. And, if the emitter cannot be identified, then cheaters who do not invest in a signal but fly about in another's "perfume-cloud," have an energetic advantage that would eventually lead to their increase and then to the collapse of the entire display system. Visual displays are somewhat more likely, but still suffer from a poor capacity for individual recognition. For example, swarming mosquitoes are typically drab, but non-swarming species are often colorful. However, if flight is slow enough and swarmers separate enough, then visual signals can and do evolve. Small species of Mayflies (Ephemeroptera) sometimes have glassy wings and their swarms resemble falling snowflakes in the sunshine. Some of the most remarkable insect ornaments occur in certain swarming, flat-footed flies (Platypezidae). Species of the North American genus *Calotarsa* have enlarged hindlegs that bear a curious collection of projections and glittering aluminum-colored flags. They fly in a slow and dignified manner while allowing their "hind feet to hang heavily downward and look as if they were carrying some heavy burden" (Fig. 30).



Visual Mating Signals, Figure 30 **Swarming insects are seldom in a position to emit visual signals. The intertwining flights of numerous insects are simply too confusing. However, there are exceptions and the hindlegs of the swarming flatfooted fly *Calotarsa insignis* are a spectacular example of insect ornamentation (drawing by Kevina Vulinec in Sivinski 1997).**

Aerial displays by non-swarming insects are easier to evolve and maintain because the complications of confusing neighbors are diminished. The brighter colors, and occasionally unique markings, of male butterflies are displayed in intrasexual encounters and some of these occur during aerial conflicts. In many species of *Photinus* fireflies (Lampyridae), males make nocturnal flights, advertising their availability with flash patterns. These patterns of flashes elicit response flashes from perched females, and through flash dialogues males locate females, land near them, and mating occurs. Some species of *Photuris*, another genus of fireflies, are aerial predators of signaling *Photinus* males. The flashing signal is more difficult for the predator to track in flight than a continuous glow. Flashing may have evolved from an ancestral continuous glow in response to this predation pressure.

Once courtship occurs on the ground or leaf surfaces or some other platform, there is finally a stable stage on which males can easily perform elaborate behaviors with complexly patterned ornaments and be relatively easily recognized as individuals with their own particular messages to send. Ground-based mating systems can consist of single males searching or occupying a signaling site (often a resource) or groups of males either aggregated at a resource or gathering in non-resource based "leks." Visual displays occur in these different mating systems. Many of the highly decorated male dolichopodid flies appear to be solitary, or at least not tightly aggregated. Striking sexual dimorphisms are also encountered in lekking species in other families. An unusual example of the latter is the scuttle fly, *Megaselia aurea* (Phoridae). Like most phorids, males are nondescript flies, cream and grey in color, but females are yellowish orange with an iridescent orange patch on their dorsal surface. In addition to their unusual coloration, females have the peculiar habit (for their sex) of gathering on leaf surfaces in groups of up to a dozen or so. Males visit these sex-role reversed leks, pair with a female, and fly off to copulate on nearby vegetation. The bright orange of the lekking females suggests a visual display directed either to female lek-mates or male visitors.

The Locations of Ornaments and Colors

The structures and colors used in visual displays occur all along the arthropod body, but there are certain points of concentration. Some display locations emphasize a particular body part. Female dance flies that call attention to, or exaggerate, the size of their ovaries enlarge and color their abdomens, and ornaments used in male-male interactions are often on the head, perhaps because the head is used in the pushing style of combat typical of Diptera. Elaborations such as eyes elongated into cow-like horns (*Zygotricha dispar* [Drosophilidae]) and antlers and eye-stalks may be embellishments of actual weapons that now also advertise sexual competitiveness.

Movement can be an important component of a signal either because receivers are likely to notice the motion and so be more likely to see the ornament, or because the motion itself is the message and the movement is made more obvious by the ornament. In either case, ornaments or motions could serve as "amplifiers" that attract the attentions of the opposite sex to the display. It has been argued that a simple preference for the first male a receptive female might see could select for such amplifiers, and that competitions among amplified males to be the first noticed might act as "mate-filters." On average, females would be most likely to couple with active, easily seen males whose apparency is a correlate of a good genetic constitution.

This premium on movement has served to concentrate signaling onto moveable body parts such as legs, wings, labial palps, antennae, and even the external genitalia. In dolichopodid flies, the male genital region is sometimes much enlarged (the hypopygium) and this may be raised and lowered during the male's courtship advance (e.g., *Dolichopus omnivagus*). In one unidentified species, males rise up on their long legs, beat their wings, lower the hypopygium until it hangs perpendicular to the body, and then slowly twirl their genitals. Dipteran legs are adorned with signaling devices that range from simple flags of enlarged setae to bizarre banners of hairy projections and strange devices. In yet another dolichopodid, *Campsicnemus magius*, the front legs are so swollen, pendanted and hairy that critics suggested the original specimens were deformed by fungi. Likewise, the fore tibia of the flower fly (Syrphidae), *Tityusia regulas*, are "enormously thickened, grooved, twisted and distorted" with an "extremely long, extremely matted" dark pile of fringe, and tarsi are extravagantly flattened with the lateral edges of the second, third, and fourth segments prolonged into narrow, down-curving lobes. Other examples occur outside of the Diptera, e.g., some male leaf-footed bugs (Coreidae) may use colorful expansions of both hind leg and antennae in defense of territories such as flower heads.

As noted earlier, while color can appeal to the opposite sex or deter rivals, it may also attract predators, and displays that can be produced only when the appropriate receiver is in a position to appreciate the signal may be safer than those that are on all the time. Ornaments on some moveable structures have the advantage of concealing and then revealing a signal in all its splendor. Consider any number of butterflies (e.g., the white M hairstreak, *Parrhasius m-album* [Lycaenidae] or the Florida purplewing, *Eunica tatila* [Nymphalidae]) whose outer wing coloration is dull and cryptic, but whose inner surface is dazzlingly bright. Such an insect at rest is difficult to detect, but with its wings opened while on its perch or in flight, it is an iridescent beacon (although one must consider the habitat, as periodic flashes of iridescence in the dappled light of a forest may be misleading or disguising).

The Phyletic Distribution of Visual Sexual Displays

Different arthropods have different capacities and opportunities for the production of visual sexual displays. Diurnal butterflies have a greater chance to employ visual signals than do nocturnal moths. As noted earlier, jumping spider (Salticidae) vision lends itself to the reception of color and complex movement, while the eyes of the related wolf spiders (Lycosidae) do not. The frenetic mass flights of small swarming flies are incompatible with visual signals, while the largely surface-bound foraging habits of dolichopodid flies may give them a ready stage on which to perform elaborate displays and so be the reason they are among the most ornamented Diptera.

As a result of these and other differences, there appears to be a clumped distribution of visual displays. There is hardly enough research to quantify this distribution, but it seems that the more derived flies (Brachycera) have a disproportionate number of apparent visual displays. Butterflies, luminous beetles and Odonata are other obvious hotspots of visual communication.

Conclusion

The diversity of arthropod visual signals is immense, owing to the evolutionary plasticity of the arthropod body and the behaviors used in combination with visual signals to modify and enhance their effects. Visual signals are adapted to a wide variety of habitats and contexts. As noted above, not all arthropod signaling evolved by sexual selection, as not all colorful arthropods are signaling to sexual partners or rivals. In fact, given the limitations of insect eyes, colors and patterns more often than not may be directed to visually acute predators such as birds and serve to startle, warn of unpalatability, or to mislead.

► Sexual selection

References

Choe JC, Crespi B (1997) The evolution of mating systems in insects and arachnids. Cambridge University Press, Cambridge, UK

Espmark Y, Amundsen T, Rosenqvist G (2000) Animal signals. Tapir Academic Press, Trondheim, Norway

Hauser MD, Kinishi M (2000) The design of animal communication. MIT Press, Cambridge, MA

Sivinski J (1997) Ornaments in the Diptera. Fla Entomol 80:142–164

Thornhill R, Alcock J (1983) The evolution of insect mating systems. Harvard University Press, Cambridge, MA, 547 pp

Vain-Wright RI, Ackery PR (1984) The biology of butterflies. Academic Press, London, UK

Vitamins

Vitamins are nutrients needed for normal growth of insects. Those required are thiamine, riboflavin, pyridoxine, niacinamide, pathothenic acid, biotin, folic acid and choline. Some insects also require carnitine, ascorbic acid, carotene, vitamin B-12, vitamin E, and others.

► Nutrition in Insects

Vitelline Membrane

A membrane surrounding the egg, which in turn is surrounded and protected by the chorion.

Vitellogenesis

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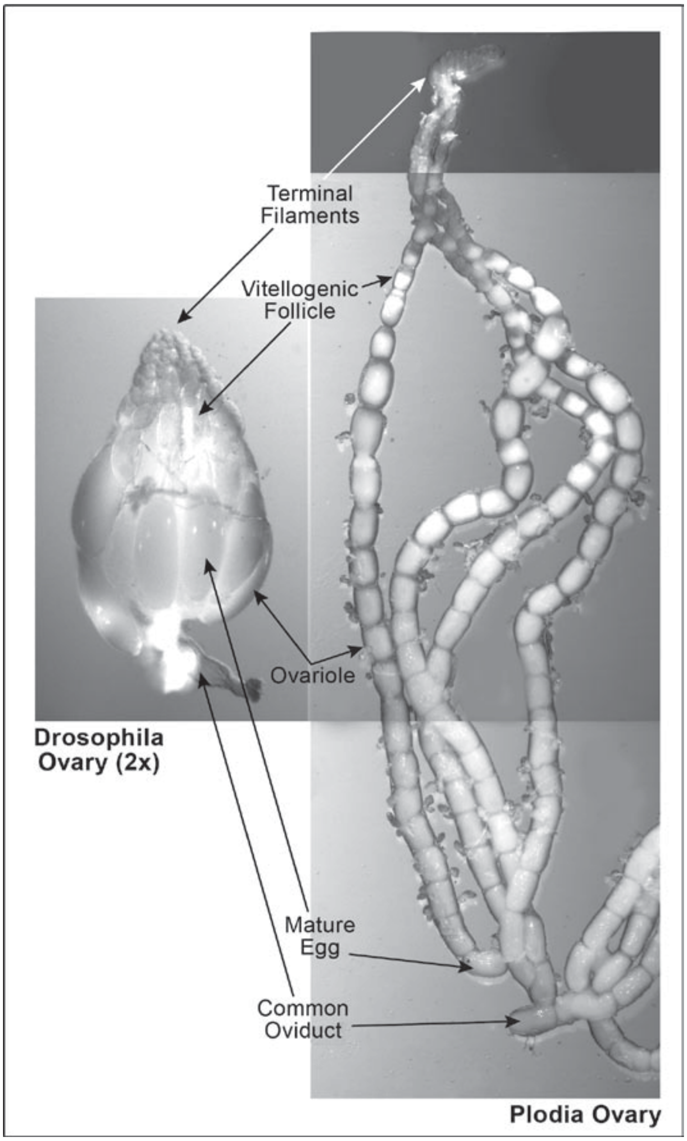
Vitellogenesis is the process of production and accumulation of yolk in a developing oocyte. Female insects seek out a nutritionally suitable environment that will potentially provide more than adequate food resources for her larvae. This behavior assures the propagation of the species. However, before the larva hatches onto its nourishing meal, each egg must come complete with all the developmental instructions (localized determinants), cytological machinery (e.g., ribosomes, mitochondria, and RNAs) and nutrients (yolk) necessary to complete embryogenesis and support the maturation of the embryo through larval hatching and into the first larval instar. The process of vitellogenesis or the production and packaging of nutrients, primarily vitellin or yolk proteins, into the developing oocyte within the ovary is critical to providing the egg with the nutrient resources to complete embryogenesis.

As described under oogenesis, the polytrophic ovary is comprised of ovarioles that contain an array of follicles in varying stages of development (Fig. 31). Each follicle within a polytrophic ovary contains an oocyte (germ cell) that is interconnected via a series of ring canals to a complement of sister nurse cells. This germ cell complex is surrounded by follicular epithelium cells that are somatically derived. After differentiation of the oocyte and nurse cells from a single blastocyst cell, the follicle goes through four stages before it completes the formation of an egg that is ready for fertilization. The previtellogenic stage provides a period of production of cytoplasmic organelles by the nurse cells and oocyte that will be required by the developing embryo. The vitellogenic stage begins with the initiation of patency, the opening of spaces between the follicle cells that permits the diffusion of materials from the hemolymph to the oocyte surface for uptake. The vitellogenic stage ends with the closure of the inter-follicular cell spaces, which is followed by the production of the vitellin membrane and the initiation of choriogenesis, the production of the eggshell or chorion. During the vitellogenic stage, the size of the oocytes increases tremendously due to the uptake of vitellogenin, nurse cell cytoplasm and water.

Vitellin, the Stored Protein of Yolk

Vitellogenesis in most insects involves the production of vitellogenin, the precursor protein of vitellin, by the fat body. Vitellogenin is secreted into the hemolymph to circulate through the body and eventually to the ovary where the protein is actively taken up by a vitellogenic oocyte via receptor mediated endocytosis and packaged in yolk spheres as vitellin.

Insect vitellogenins are phosoglycolipoproteins (proteins that have organic phosphate, sugar, and lipid moieties attached). Vitellogenins are found in other animals that deposit eggs, such as nematodes, shrimp, birds and amphibians, and the proteins all belong to a superfamily of lipoproteins that share a common evolutionary origin. Vitellogenin genes are relatively large and produce transcripts that code for polypeptides in the size range from 1,748 amino acids in the Gypsy moth, *Lymantria dispar*, to 2,139 amino acids in the *Aedes* mosquito. The vitellogenin gene is expressed in the fat body and contains a signal sequence that targets the polypeptide for processing in the endoplasmic reticulum, packaging



Vitellogenesis, Figure 31 **Vitellogenic polytrophic ovaries from the fruitfly, *Drosophila melanogaster*, and the Indian meal moth, *Plodia interpunctella*. The ovary of *Drosophila* (*left*) was dissected from a 5-day old adult. The ovary of the *Plodia* moth (*right*) was dissected from a newly eclosed adult.**

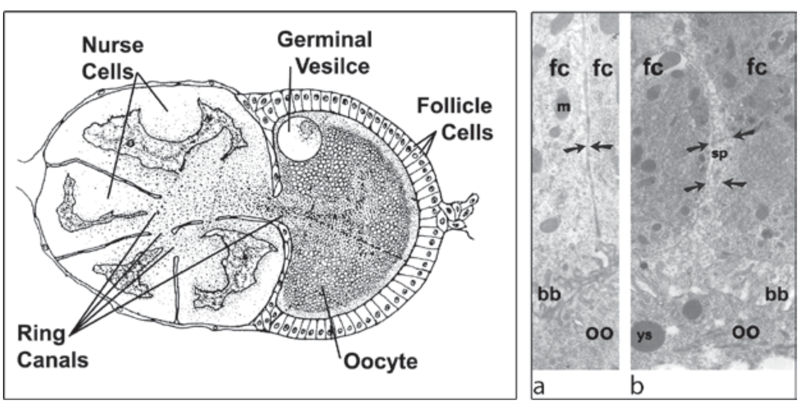
into secretory vesicles by the Golgi apparatus and secretion into the hemolymph. For most insects, the primary vitellogenin polypeptides are cleaved into a large subunit of approximately 150,000 Daltons and a small subunit of approximately 65,000 Daltons. These two subunits associate within the secretory vesicles and are secreted together into the hemolymph where they circulate to the ovaries.

The paradigm of vitellogenin production and uptake applies to most of the insect orders examined. However, the higher flies, cyclorrhaphan Diptera, utilize other proteins that are unrelated to vitellogenins as their primary source of yolk protein. While the eggs of mosquitoes contain vitellin, the eggs of the cyclorrhaphan flies contain from one to three small polypeptides that range from 40,000 Daltons to 50,000 Daltons that are produced by the follicular epithelial cells which surround the oocyte and/or by the fat body. The yolk protein genes are correspondingly small and are structurally related to genes for lipases. Thus in the cyclorrhaphans, it appears that the vitellogenin gene has been lost during evolution and the functional role of select lipases has been diverted to that of a yolk protein which replaces vitellin. This substitution of proteins appears to have been possible because lipase related proteins, such as egg specific protein (ESP) in the silkworm *Bombyx mori*, or the follicle cell yolk protein (FEYP) in the Indian meal moth, *Plodia interpunctella*, are normally secreted by the follicle cells taken up by receptor mediated endocytosis during vitellogenesis and contribute up to 50% of the proteinacious yolk in moths.

Vitellogenesis, the Period of Yolk Uptake

The follicles are arranged in the ovarioles in a linear manner and each follicle enters the vitellogenic period independently from the other follicles within the ovariole. In the previtellogenic stage, the follicular epithelium (Fig. 32) cells that surround the oocyte form tight junctions between the cells which does not allow for the entry of materials to the surface of the oocyte. As the vitellogenic stage begins, the follicle becomes patent for vitellogenesis, that is the follicular epithelium cells loosen the tight junctions which opens gaps between the follicle cells, thus allowing proteins and other nutrients within the hemolymph to penetrate to the surface of the oocyte for uptake. The vitellogenic stage lasts until the oocyte has been supplied with sufficient nutrients and determinants and the follicle cells begin the production of the vitellin membrane and the chorion.

Vitellogenin is taken up into the oocytes by receptor mediated endocytosis. The receptors for vitellogenins are large membrane-bound proteins that range from 180,000 to 214,000 Daltons. The vitellogenin receptors occur as homodimers that are localized in the clathrin pits on the oocyte plasma membrane. Once bound to the receptor, vitellogenin is carried into the endocytotic vesicles that coalesce to form yolk spheres. The vitellogenin



Vitellogenesis, Figure 32 **Vitellogenic follicles: (*left*) The generalized structure of a vitellogenic follicle from a polytrophic ovary. The germ cells, oocyte and nurse cells are connected via ring canals and surrounded by follicular epithelial cells. The germinal vesicle of the oocyte is the haploid nucleus of the germ cell. The nurse cells have polyploid nuclei. (*right*) Patency of the vitellogenic follicle. At the beginning of the vitellogenic period, the tight junctions (*part a*) between the follicular epithelial cells disappear and the intercellular spaces open (*part b*) to permit the penetration of diffusible hemolymph borne materials to the brush border of the oocyte. Opposing arrows show the plasma membranes of the follicular epithelial cells with tight junctions (a) and with open intercellular spaces during patency (b). Abbreviations: *bb* = brush border; *fc* = follicular epithelial cell; *m* = mitochondrion; *oo* = oocyte; *sp* = intercellular space; *ys* = yolk sphere.**

receptors have varying levels of specificity depending on the species of insect. In the tobacco hornworm, *Manduca sexta*, vitellogenin and lipophorin are endocytosed by two different receptors. However, in the silkmoth *Hyalophora cecropia*, the vitellogenin receptor also binds with lipophorin, and in the mosquito *Aedes aegypti*, the receptor can bind multiple ligands. Thus, the vitellogenin receptor may have a broad binding capacity in order to provide a broad spectrum carrier for the specific localization of proteins in the yolk spheres.

Endocrine Control of Vitellogenesis

The production and uptake of vitellogenin is endocrinologically regulated in various manners according to the feeding style and longevity of the adult. We can consider four different models of regulation: insects with long-lived adults that feed continuously, insects with long lived adults that feed intermittently, insects with short lived adults that feed, and insects with short lived adults that do not feed.

In the fruit fly *Drosophila melanogaster*, that has adults that are long-lived and feed often, the onset of yolk protein production is regulated by an increase in the level of juvenile hormone (JH) occurring just after adult eclosion. JH stimulates the progression of follicular development past the previtellogenic stage, stimulates yolk protein production from the follicle cells and stimulates ovarian synthesis of ecdysteroids. The ecdysteroids produced by the ovaries stimulate the fat body to produce large quantities of yolk proteins that provide the resources for the rapid growth of vitellogenic follicles. Once initiated, yolk protein production in the fat body is continuous throughout the adult stage and is dependent on a balanced maintenance of both JH and ecdysteroids and a continuous supply of food.

Alternatively, in the grasshopper *Locusta migratoria*, which has a long-lived adult, vitellogenesis is cyclic. Vitellogenesis and egg maturation are initiated by an increase in juvenile hormone after adult eclosion. As the follicles mature, they exert a feedback inhibition on juvenile hormone production which shuts off vitellogenesis. This results in a cycling of egg production throughout the adult life of this grasshopper.

In the anautogenous mosquito *Aedes aegypti*, which have long-lived adults that feed intermittently, egg production is dependent upon the acquisition of a blood meal. A complex hormonal cascade involving the gut, brain and ovaries is initiated when the mosquito has a blood meal, which results in a single cycle of egg production. Following the ingestion of blood, vitellogenesis consists of two phases. First there is an initiation phase where the arrested developing follicles become activated and the follicular epithelium cells resume mitosis and separate from the oocyte. This requires the release of egg development neurosecretory hormone (EDNH) from the brain that acts on the ovary to produce ecdysteroids. The ecdysteroids stimulate the fat body to initiate the second tropic phase that begins 5–6 hr after a blood meal and additionally on the adjacent secondary follicles to complete previtellogenesis in preparation for the next round of egg production. Under the influence of ecdysteroids, the fat body produces large amounts of vitellogenin that is taken up by the vitellogenic follicles. However, as the blood is digested, vitellogenesis declines due to hormonal feed back on the brain. A new cycle of egg production cannot be initiated until another blood meal has been taken by the female.

In the tobacco budworm, *Heliothis virescens*, which has short-lived adults that feed, the newly eclosed females must have a meal before vitellogenesis can be initiated. The meal triggers the production of JH which stimulates the fat body production of vitellogenin as well as the maturation of the follicles. Once begun, vitellogenin production by the fat body is continuous throughout the adult stage. Alternatively, the fall army worm, *Spodoptera frugiperda*, requires JH during the adult stage to stimulate follicle development and vitellogenin uptake as well as ecdysteroid production by the ovary.

Subsequently, the regulation of fat body vitellogenin production requires the ovarian ecdysteroids.

Finally, for insects that have short-lived adults that do not feed, such as the silkworm *Bombyx mori* or the Indian meal moth, *Plodia interpunctella*, vitellogenesis and oocyte maturation takes place during pharate adult development. Vitellogenin production by the fat body begins after the fall of the ecdysteroid peak that leads to adult development and is maintained continuously through the adult stage. For many of the follicles, vitellogenesis is completed during pharate adult development, and the adult female ecloses with most of her eggs completely developed and ready to be fertilized.

► Oogenesis
► Endocrine Regulation of Reproduction
► Reproduction
► Storage Proteins

References

Bownes M (1986) Expression of the genes-coding for vitellogenin (yolk protein). Annu Rev Entomol 31:507–531

Chen JS, Sappington TW, Raikhel AS (1997) Extensive sequence conservation among insect, nematode, and vertebrate vitellogenins reveals ancient common ancestry. J Mol Evol 44:440–451

Hagedorn HH, Maddison DR, Tu ZJ (1998) The evolution of vitellogenins, cyclorrhaphan yolk proteins and related molecules. Adv Insect Physiol 7:335–384

Raikhel AS, Dhadialla TS (1992) Accumulation of yolk proteins in insect oocytes. Annu Rev Entomol 37:217–251

Sappington TW, Raikhel AS (1998) Molecular characteristics of insect vitellogenins and vitellogenin receptors. Insect Biochem Mol Biol 28:277–300

Swevers L, Raikhel AS, Sappington TW, Shirk PD, Iatrou K (2005) Vitellogenesis and post-vitellogenic maturation of the insect ovarian follicle. In: Gilbert LI, Iatrou K, Gill SS (eds) Comprehensive molecular insect science. Elsevier, London, UK, pp 87–155

Telfer WH, Huebner E, Smith DS (1982) The cell biology of vitellogenic follicles in *Hyalophora* and *Rhodnius*. In: King RC, Akai H (eds) Insect ultrastructure, vol 1. Plenum Press, New York, NY, pp 118–149

Wahli W (1988) Evolution and expression of vitellogenin genes. Trends Genet 4:227–232

Vitellogenin

The major yolk proteins are called vitellogenins while being transported to the hemolymph, and consist of large glycolipoproteins which are produced by the fat body and secreted for uptake by maturing oocytes. Not all yolk proteins are vitellogenins, however, and in higher Diptera the yolk proteins are small polypeptides.

► Endocrine Regulation of Reproduction
► Vitellogenesis
► Oogenesis

Viviparous

Organisms that bear living young, as opposed to eggs.

Volant

Capable of flight.

Volatility

Ability of a substance to evaporate or vaporize.

Volunteer Plants

The unexpected and undesired emergence of plants, usually self-seeded by the previous plants.

Vulva

The opening of the vagina.

W

Waggle Dance

A dance performed by honey bees in which workers communicate with other workers the location of new food and nest sites.

► Honey Bees

Walker, Francis

Francis Walker was born at Southgate, England, on July 31, 1809. He is known principally for his collecting and writing skills. His entomological publishing commenced in 1832 when he contributed a chapter on chalcids to the "Entomological Magazine." Shortly thereafter, he undertook the editorial management of the magazine, though he remained in this capacity for much more than a year. He collected a great amount of material for the British Museum, produced several catalogues such as "List of the specimens of the dipterous insects in the collection of the British Museum," and described numerous species from both Europe and North America. Between 1851 and 1856 he published "Insecta Saundersiana" in four parts. He prepared over 20,000 descriptions in several orders, though many have been found to be faulty. Indeed, his faulty descriptions caused something of a scandal at the British Museum. He is not identified with a particular group, having described neuropterans, orthopterans, termites, hemipterans, flies, wasps, moths and beetles, but he likely had more effect on the study of Coleoptera than any other group. Walker died at Wanstead, England, on October 5, 1874.

References

Essig EO (1931) A history of entomology. The Macmillan Company, New York, 1029 pp

Papavero N (1971, 1973) Essays on the history of neotropical dipterology with special reference to collectors (1750–1905). Museu de Zoologia, Universidade de São Paulo

Walkingstick Defensive Behavior and Regeneration of Appendages

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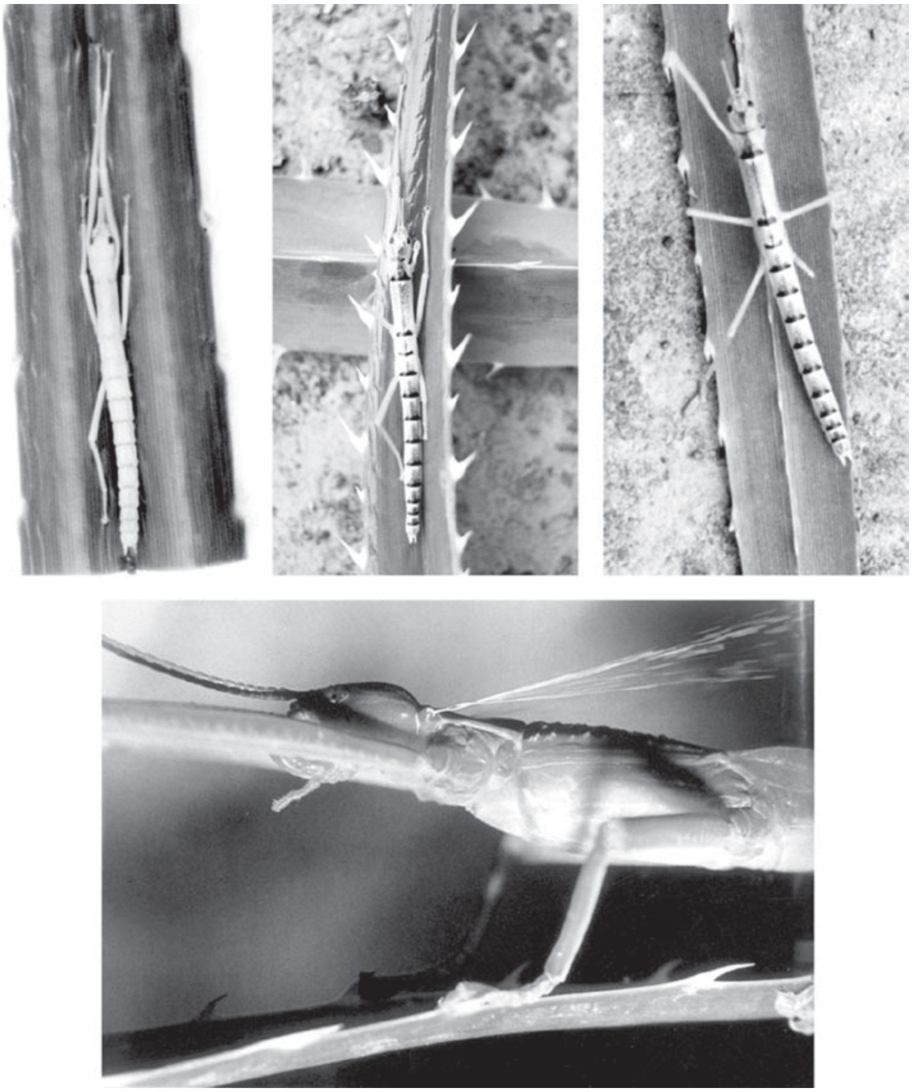
Some 2,500 species, mostly from warmer parts of the world, comprise the order Phasmatodea, the so-called stick insects. Often up to 8 cm long and frequently apterous (wingless), stick insects are slow and clumsy and, for that reason alone, are vulnerable. Many, however, are cryptically colored, armed with spines, or protected by their resemblance to twigs and tree leaves. Others that comprise only a few known species, are protected by defensive glands. In Taiwan, the walking stick insect *Megacrania tsudai* Shiraki, causes considerable damage to screw pine along the southern coast. It has three distinctive characterizations. First it can secrete a monoterpene alkaloid actinidine as a defensive chemical. Secondly, it can regenerate lost appendages, and lastly, it can reproduce individuals parthenogenetically for long periods of time (Fig. 1).



Walkingstick Defensive Behavior and Regeneration of Appendages, Figure 1 **Regeneration of appendages (*top row*) in the larva of stick insect *Megacrania tsudai* Shiraki. (*Left*) First instar of the insect in which the right metathoracic leg was amputated. (*Right*) After ecdysis, the right metathoracic leg of the second instar appeared as a miniature leg. Meanwhile, the right prothoracic leg was amputated. (*Center*) The third instar 3 days after ecdysis. The right metathoracic leg looked like its normal left leg, but is short in length. Note that the regenerated right prothoracic leg was regenerated as a miniature leg. Female *Megacrania tsudai* Shiraki showing white discharge being sprayed (below) when the insect was tapped on the abdomen.**

Chemicals such as irrdodials, nepetalactone, benzaldehyde, benzothiazole, limonene and quinoline have been reported as defensive chemicals produced by other phasmid insects from different parts of the world.

Megacrania tsudai has two large bilateral thoracic glands and, when molested, it will spray a white discharge toward the disturbance. But unlike the other stick insects, the main chemical secreted was identified as a nitrogen containing alkaloid actinidine, with other related minor compounds such as boschniakine and two stereoisomers of 1-acetyl-3-methylcyclopentane. Gas chromatography-mass spectrometry was used in these identifications.

Another feature of the insect is its ability to regenerate an amputated leg as an immature. An appendage can be regenerated during subsequent instars, indicating that at least some of the cells surrounding an appendage are sufficiently undifferentiated to retain the ability to reform that appendage. Since regeneration of a leg requires a molt, it might be related to the combination of molting hormone, juvenile hormone and signal transduction (Fig. 1).

Megacrania tsudai can produce offspring by parthenogenesis. In an enduring study, female insects have been cultivated in a laboratory for more than 10 years, with no males present in the laboratory culture or in the field.

References

Bouchard P, Hsiung CC, Yaylayan VA (1997) Chemical analysis of defense secretions of *Sipyloidea sipylus* and their potential use as repellents against rats. J Chem Ecol 23:2049–2057

Brockes JP (1997) Amphibian limb regeneration: rebuilding a complex structure. Science 276:81–87

Chow YS, Lin YM (1986) Actinidine, a defensive secretion of stick insect, *Megacrania alpheus* Westwood (Orthoptera: Phasmatidae). J Entomol Sci 21:97–101

Eisner T, Morgan RC, Attygalle AB, Smedley SR, Herath KB, Meinwald J (1997) Defensive production of quinoline by a phasmid insect *Oreophoetes peruana*. J Exp Biol 200:2493–2500

Gu SH, Chow YS, Yin CM (1997) Involvement of juvenile hormone in regulation of prothoracicotropic hormone transduction during the early last larval instar of *Bombyx mori*. Mol Cell Endocrinol 127:109–116

Ho HY, Chow YS (1993) Chemical identification of defensive secretion of stick insect, *Megacrania tsudai* Shiraki. J Chem Ecol 19:39–46

Walkingsticks

Members of an order of insects (order Phasmatodea).

► Stick and Leaf Insects

Waloff, Nadejda

"Nadia" Waloff was born at St. Petersburg, Russia, on September 2, 1909. Her family fled the Bolsheviks in 1919 and became refugees in Britain. In 1926 her mother died, and afterwards her father and oldest brother emigrated to Romania. Nadia and three siblings were taken in by Sir Boris Uvarov, director of the Anti-Locust Research Center in London. It is likely that this experience encouraged Nadia and her sister Zena to pursue careers in entomology. Waloff received a bachelor's degree from Imperial College and taught school for several years. In 1946 she began work on insect pests at Imperial College and the Pest Infestation Laboratory in Slough. Thus she embarked on a distinguished career at Imperial College and also attained a Ph.D. and Sc.D. before retiring in 1978. Both before and after her retirement, Waloff was known as an outstanding instructor. However, she conducted some very thorough and landmark research, alone and in collaboration, on flour moth diapause, population dynamics of grasshoppers, yellow meadow ant, and broom-infesting insects. She died on June 5, 2001.

Reference

Jones T, Southwood R (2002) Dr. Nadejda Waloff FRES (Hon) (1909–2001). Antenna 26:6–9

Walsh, Benjamin Dann

Benjamin Walsh was born at Frome, Somerset, England, on September 21, 1808 (Fig. 2). He graduated from Cambridge University, Cambridge. His parents wished him to enter the ministry, but he disavowed the hypocrisies of the church. He emigrated to the United States in 1838 and settled into a farming life near Cambridge, Illinois, for about 12 years. In 1850 he moved to Rock Island, Illinois, and opened a lumber yard. He retired from this in 1858 and entered the real estate business and, to a lesser degree, politics. It is

Walsh, Benjamin Dann, Figure 2 **Benjamin Walsh.**

at this time in his life that Benjamin Walsh became interested in insects, and by 1860 he was reported to have given an extemporaneous 2-h lecture to the Illinois State Horticultural Society. Soon he began publishing in farm newspapers and scientific journals. He did such a fine job at publicizing the dangers from insects that the Illinois State Legislature appointed him state entomologist. Walsh and C.V. Riley started the "American Entomologist" from 1868 to 1880. It consisted of three volumes and was considered to be an outstanding popular periodical on insects. In November 1869 Walsh was absentmindedly walking along the railroad tracks when he was struck by a train, and perished a few days later, on November 18, 1969.

Reference

Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, New Jersey, 549 pp

Walsingham, (Lord) Thomas De Gray

Thomas Walsingham was born at London, England, on July 29, 1843. He was educated at Cambridge University and served as a member of the British House of Commons. He succeeded to the title and estates of his father in 1870, and was appointed a trustee of the British Museum in 1876. His wealth allowed him to travel and to purchase specimens at will, and he developed considerable expertise in the Microlepidoptera. His collecting trips included most of southern Europe, northern Africa, and the western United States. Walsingham served as president of the Entomological Society of London, and was a member of numerous other scientific societies. Among his noteworthy publications are "Illustrations of the Lepidoptera Heterocera in the British Museum" (1879), and "North American Tortricidae" (1884). He died in London on December 3, 1919.

Reference

Essig EO (1931) A history of entomology. The Macmillan Company, New York, 1029 pp

Warble Flies

Members of the family Oestridae (order Diptera).

► Flies

Wasmann, Erich

Erich Wasmann was born on May 29, 1859, at Meran, Austria. He studied for the priesthood and entered the Jesuit order in 1875. From 1890 to 1892 he studied zoology at the University of Prague. Wasmann suffered from a lung disorder and was advised to spend as much time as possible out-of-doors. This, perhaps, led to his interest in ants, and he eventually became an authority on myrmecophiles and termitophiles. He also wrote on instinct and intelligence of ants, and the relationship of ants to other animals. He authored 433 publications with over 280 on myrmecophiles and termitophiles. Noteworthy publications included "Kritisches Verzeichniss der myrmecophilen und termitophilen Arthropoden" (1894), "Die moderne Biologie und die Entwicklungstheorie" (1910), and "The Berlin discussion of the problem of Evolution" (1909). The University of Freiburg in Germany awarded him an honorary doctoral degree in 1921, and the Jesuits established a biological journal honoring him, the "Wasman Journal of Biology." He died on February 27, 1931, in Valkenburg, Holland.

References

Anonymous (1931) Obituary, Father Erich Wasmann SJ Entomological News 42:240

Herman LH (2001) Wasmann, Erich. Bulletin of the American Museum of Natural History 265:154–155

Wasmannian Mimicry

The mimicry of ants by staphylinid beetles that live within the nests of ants.

► Mimicry

Wasp Moths

Some members of the family Arctiidae (order Lepidoptera) also known as tiger moths.

► Tiger Moths
► Butterflies and Moths

Wasps

Certain members of an order of insects (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Wasps, Ants, Bees and Sawflies (Hymenoptera)

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The order Hymenoptera includes insects commonly known as ants, bees and wasps. Most authors believe that the name has been derived from the Greek *hymen*, meaning "membrane" and referring to the parchment-like transparent wings, without any scales or hair, and which often may be clouded. However, it also has been suggested that the name is derived from *hymeno* = god of marriage (referring to the union of fore and hind wings) + *ptera* = wings.

The Hymenoptera is one of the largest orders of insects. It is estimated that about 300,000 species occur in the world, of which not more than 30% have been described. Most hymenopterans are useful and beneficial to mankind. The honey bees give us honey. They, along with other bees, are important pollinators of flowering plants that include commercial crops, particularly the fruit trees. There has been a process of co-evolution between the flowers and the hymenopterans, resulting in better pollination and fertilization, and the development of colorful and intricate flowers. Many hymenopterans are predators of insect pests, and a group of hymenopterans, commonly referred to as "parasitic Hymenoptera" are utilized in biological control projects for the control of insect pests. This method is environmentally friendly and minimizes the use of insecticides. On the other hand, phytophagous hymenopterans, such as the sawflies, have resulted in the destruction of many coniferous forests in North America. Some wasps and ants are dreaded because of their venomous stings, which cause serious reactions in some people, even resulting in death.

The order Hymenoptera is also biologically rather important. Members of the order exhibit great diversity in their way of life and behavior, and include the highly evolved social insects. The social organization of bees and wasps has been a subject of many books and comparisons with the social life of mammals, including man, and represents a peak of evolutionary behavior.

The Hymenoptera alone exhibit the haploid-diploid mechanism of sex determination. The males are haploid, having an unpaired set of chromosomes. The females are diploid, possessing a set of paired chromosomes. The females have a normal gametogenesis so that the eggs are haploid, while in the males the first meiotic division generally is abortive so that haploid sperms are produced. Normally, the unfertilized eggs develop into males, while the fertilized eggs develop into females.

The social Hymenoptera exhibit polymorphism, and sexual dimorphism is evident. They also exhibit a "caste system" where the majority of the individuals are "workers" which are undeveloped females lacking the capacity to reproduce. They are responsible for all the chores of the colony, including food gathering, maintenance of the colony, defense, etc. The "queen" is the normal female which is capable of reproducing and, depending upon the type of social organization, one to many queens may be in one colony. The haploid male is only responsible for the fertilization of the queen, and may develop and be tolerated in the colony for this function alone. The social hymenopterans also have developed the capacity to store food for the progeny in the colony. This behavior of the bees has been exploited to harvest honey from the bee colonies.

The solitary bees also provision their nests with food for their progeny. The progressive evolution of social behavior in Hymenoptera, and the mechanisms of communication amongst the members of a colony, have been studied by many entomologists.

Morphological Characters

Members of the order Hymenoptera have mouthparts adapted for biting and chewing, biting and lapping, or biting and sucking. The antennae usually are long, with ten or more segments (some exceptions), and often geniculate. There are two pairs of membranous wings; the hind wings are smaller than the fore wing and both wings are interlocked by means of hooklets called hamuli. The bases of fore wings are covered by a crescent-shaped sclerite called the tegula. The fore wing usually has a sclerotized thickened area midway along its anterior margin, called the stigma. The wings may be reduced or absent. Apterous forms occur in several families. Ants exhibit dimorphism with winged forms occurring during the swarming phase of their life cycle. The wing venation is greatly modified as many veins take a transverse course. There is often a fusion of principal veins, and in higher forms the venation is reduced. The leg is five segmented. In several families (commonly grouped as "parasitica") the base of the femur is cut off, giving the impression that there are two trochanters. This structure is called trochantellus but in most taxonomic publications the trochanters are said to be 1 or 2-segmented. The tarsus is typically 5-segmented, but in some chalcid wasps the number may be reduced. The basitarsus is modified into a pollen basket in bees. The abdomen is basally constricted, and either broadly or narrowly attached to the thorax.

One characteristic feature of the hymenopterans is that the first abdominal segment is fused with the metathorax to form the propodeum. This is quite evident in higher Hymenoptera. There is a flexible joint between the first and the second apparent abdominal segments. In the Symphyta (sawflies, etc.) the abdomen is broadly attached to the propodeum, while in Apocrita (ants, bees, wasps, etc.) the abdomen is narrowly attached to the propodeum by a short or long petiole.

The females have an ovipositor which is built on a lepismatid form from the ancestral appendages of abdominal segments 8 and 9. It is modified in different groups for sawing, boring, piercing, stinging, or it may be reduced.

There are two main types of larvae. The Symphyta larvae are caterpillar-like, with three pairs of thoracic legs and at least five pairs of prolegs on the second to sixth abdominal segments; these prolegs are devoid of crochets (found in lepidopterous larvae). They are seen crawling and feeding on foliage. The Apocrita larvae are legless, grub-like, living in nests, or in or on the body of other insects and spiders. The metamorphosis is complete (holometabolous). Pupation occurs in cocoons.

Classification

The classification adopted in *Hymenoptera of the world: an identification guide to families*, edited by Goulet and Huber (1993) is given below. They group many aculeate superfamilies and recognize only three: Apoidea, Chrysidoidea and Vespoidea. Also, they do not recognize the two convenient but informal groupings Aculeata and Parasitica. A beginner and a general reader is perhaps better served by recognizing the traditional classification of Hymenoptera into many superfamilies. The classification given in Borror, Triplehorn and Johnson (1989) is still a good general summary of the classification of the Hymenoptera.

An Outline of the Classification of the Hymenoptera

Suborder SYMPHYTA (= CHALASTOGASTRA) – sawflies, horntails
- Superfamily: CEPHOIDEA
  - Family: Cephidae – stem sawflies
- Superfamily: MEGALODONTOIDEA
  - Family: Megalodontidae
  - Family: Pamphiliidae – leaf-rolling and web-spinning sawflies
- Superfamily: ORUSSOIDEA
  - Family: Orussidae – parasitic wood wasps
- Superfamily: SIRICOIDEA
  - Family: Siricidae – horntails (Fig. 3)
- Superfamily: TENTHREDINOIDEA
  - Family: Argidae
  - Family: Blasticotomidae
  - Family: Cimbicidae
  - Family: Diprionidae
  - Family: Pergidae
  - Family: Tenthredinidae – common sawflies
- Superfamily: XYELOIDEA
  - Family: Xyelidae
- Unplaced
  - Family: Anaxyelidae
  - Family: Xiphydriidae
- Suborder: APOCRITA

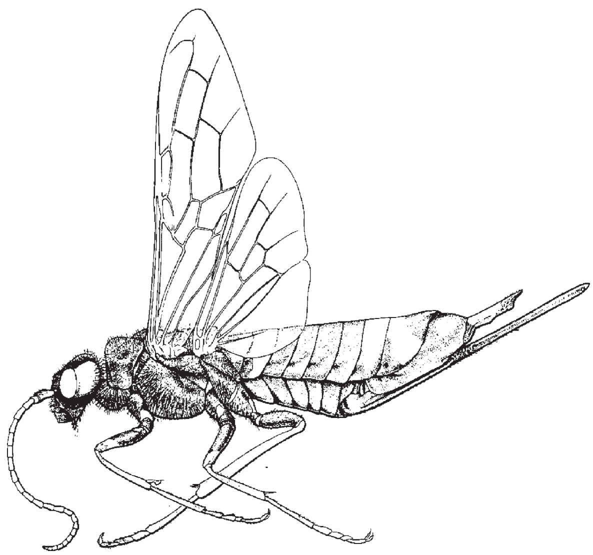
Group PARASITICA (not recognized in Goulet and Huber)
- Superfamily: CERAPHRONOIDEA
  - Family: Ceraphronidae
  - Family: Megaspilidae
- Superfamily: CHALCIDOIDEA
  - Family: Agaonidae
  - Family: Aphelinidae
  - Family: Chalcididae – chalcid wasps
  - Family: Elasmidae
  - Family: Encyrtidae
  - Family: Eucharitidae
  - Family: Eulophidae
  - Family: Eupelmidae
  - Family: Eurytomidae
  - Family: Leucospidae
  - Family: Mymaridae – fairy flies
  - Family: Ormyridae
  - Family: Perilampidae
  - Family: Pteromalidae
  - Family: Rotoitidae
  - Family: Signiphoridae
  - Family: Tanaostigmatidae
  - Family: Tetracampidae
  - Family: Torymidae
  - Family: Trichogrammatidae
- Superfamily: CYNIPOIDEA
  - Family: Charipidae
  - Family: Cynipidae – gall wasps
  - Family: Eucoilidae
  - Family: Figitidae
  - Family: Ibaliidae
  - Family: Liopteridae
- Superfamily EVANIOIDEA
  - Family: Aulacidae
  - Family: Evaniidae – ensign wasps
  - Family: Gasteruptiidae

Superfamily: ICHNEUMONOIDEA
Family: Braconidae – braconid wasps
Family: Ichneumonidae – ichneumon wasps
Superfamily: MEGALYROIDEA
Family: Megalyridae
Superfamily: MYMAROMMATOIDEA
Family: Mymarommatidae
Superfamily: PLATYGASTROIDEA
Family: Platygastridae
Family: Scelionidae
Superfamily: PROCTOTRUPOIDEA
Family: Austroniidae
Family: Diapriidae
Family: Heloridae
Family: Monomachidae
Family: Pelicinidae
Family: Peradeniidae
Family: Proctotrupidae
Family: Roproniidae
Family: Vanhorniidae
Superfamily: STEPHANOIDEA
Family: Stephanidae
Superfamily: TRIGONALYOIDEA
Family: Trigonalyidae
Suborder APOCRITA (= CLISTOGASTRA)
Group ACULEATA (not recognized in Goulet and Huber)
Superfamily APOIDEA – bees
Series: APIFORMES (formerly APOIDEA)
Family: Andrenidae – andrenid bees
Family: Anthophoridae – digger bees, cuckoo bees, carpenter bees
Family: Apidae – honey bees, bumble bees
Family: Colletidae – yellow faced bees; plaster bees
Family: Ctenoplectidae
Family: Fideliidae
Family: Halictidae – halictid bees
Family: Megachilidae – leaf-cutting bees
Family: Melittidae – melittid bees
Family: Oxaeidae
Family: Stenostritidae
Series SPECIFORMES (formerly SPHECOIDEA)
Family: Ampulicidae – ampulicid wasps
Family: Astatidae
Family: Crabronidae
Family: Heterogynaidae
Family: Mellinidae
Family: Nyssonidae
Family: Pemphredonidae
Family: Philanthidae
Family: Sphecidae – mud daubers, digger wasps
Superfamily CHRYSIDOIDEA (= Bethyloidea)
Family: Bethylidae – bethylid wasps
Family: Chrysididae – cuckoo wasps
Family: Dryinidae – dryinid wasps
Family: Embolemidae
Family: Plumaridae
Family: Sclerogibbidae
Family: Scolebythidae
Superfamily: VESPOIDEA
Family: Bradynobaenidae
Family: Formicidae – ants (formerly Formicoidea)
Family: Mutillidae – velvet ants, mutillids
Family: Pompilidae – spider wasps (formerly Pompiloidea)
Family: Rhopalosomatidae – rhopalosomatid wasps
Family: Sapygidae
Family: Scoliidae – scoliid wasps (formerly Scolioidea)
Family: Sierolomorphidae
Family: Tiphiidae – tiphiid wasps
Family: Vespidae – wasps, yellow jackets, hornets, etc.

Key to the Superfamilies

This is a simplified key to the superfamilies ignoring taxa showing exceptions to the general character states. Also, the traditional superfamilies are retained. It is based on the winged adults.

1. Abdomen joined broadly to the thorax (no waist or petiole). Hind wing with three or four closed cells (cells not open to wing margin). Fore wing with one or more distinct anal veins. Trochanters 2-segmented. Sawflies, horntails. SUBORDER SYMPHYTA.......2



Wasps, Ants, Bees and Sawflies (Hymenoptera), Figure 3 **Drawing of horntail in the family Siricidae (Source: Hymenoptera of the world: an identification guide to the families. Agriculture and Agri-Food Canada, 1993. Reproduced with the permission of the minister of Public Works and Government Services, 2003).**

Abdomen joined narrowly to thorax (a narrow waist or petiole present, abdomen flexible). Hind wing with 0–2 cells at base. Fore wing without anal veins except rarely. SUBORDER APOCRITA 5

2. Fore tibia with two apical spurs. Ovipositor blade-like and usually short 3
   Fore tibia with one apical spur. Ovipositor usually long and thin 4
3. Hind tibia with one preapical spur or none. Pronotum in dorsal view with posterior margin strongly concave (narrowed medially behind) TENTHREDINOIDEA
   Hind tibia with 2–3 preapical spurs. Pronotum in dorsal view with posterior margin weakly concave (not strongly narrowed medially behind) MEGALODONTOIDEA
4. Last tergum of female and last sternum of male each with apical, median, cylindrical projection with concave tip. Pronotum somewhat rectangular with its hind margin concave. Costal cell present and distinct SIRICOIDEA
   Last tergum and last sternum of both sexes apically thin and without cylindrical projection. Pronotum somewhat triangular with its hind margin weakly concave. Costal cell absent or narrow CEPHOIDEA
5. Legs, at least the hind leg, with two trochanters (trochanter + trochantellus) 6
   Legs with one trochanter (Proctotrupoidea runs through either half of the couplet) 14
6. Antenna usually with more than 16 segments, not elbowed. Hind wing with usually two closed cells 7
   Antenna with 15 or fewer segments, often elbowed. Hind wing with one closed cell or none. [One family of Cynipoidea – Sclerogibbidae with 17–40 segments, then costal vein absent.] 9
7. Costal cell of fore wing absent; costal and subcostal veins touching each other ICHNEUMONOIDEA
   Costal cell present, may be narrowed in some rare families 8
8. Head with a crown of tubercles around median ocellus. Ovipositor long. Abdomen elongate. Costal cell narrow STEPHANOIDEA
   Head without tubercles. Costal cell broad. Ovipositor short. Stouter insects TRIGONALYOIDEA
9. Abdominal petiole with one or two scale-like or node-like projections. Females with a sting FORMICOIDEA
   Abdominal petiole without scales. Females with a sting or an ovipositor 10
10. Abdomen inserted high on propodeum much above the level of hind coxae EVANIOIDEA
    Abdomen attached normally, near hind coxae 11
11. Hind corner of pronotum not reaching tegula, separated from tegula by an extra sclerite, "prepectus." Middle tibia with one or zero spur. Antennae usually elbowed. Coloration often metallic greenish CHALCIDOIDEA
    Hind corner of pronotum reaching tegula, prepectus absent. Middle tibia often with two spurs. Antennae elbowed or not. Coloration never metallic greenish 12
12. Costal vein absent. Radial cell large and deep, surrounded by strong veins except often the

costal margin. Abdomen compressed laterally, often covered by a single large tergite CYNIPOIDEA

Costal vein present. Radial cell present or absent; if present, not as above 13

13. Fore tibia with one apical spur. Antennae inserted on face usually above clypeus. Abdomen rounded or margined laterally PROCTOTRUPOIDEA

Fore tibia with two apical spurs. Antennae inserted on face next to clypeus and abdomen rounded laterally CERAPHRONOIDEA

14. Hind wing with 1 closed cell or none.................15

Hind wing with two closed cells. Aculeata 17

15. Hind margin of hind wing nearly always with a sharp notch near base cutting off a basal lobe (anal lobe) CHRYSIDOIDEA

Hind margin of hind wing without a sharp notch, not cutting off an anal lobe 16

16. First hind tarsal segment 0.25 as long as second. Segments 2–4 of female abdomen separate, each very long. Male abdomen club-shaped PROCTOTRUPOIDEA: PELECINIDAE

First hind tarsal segment longer than second. Abdominal tergites 2–4 fused together PROCTOTRUPOIDEA

17. Hind corner of pronotum reaching tegula, the hind edge of pronotum without a semicircular projecting lobe just below the level of tegula 18

Hind corner of pronotum not reaching tegula, the hind edge of pronotum with a projecting lobe just below the base of tegula 23

18. Tergite 1 with one or two erect scales or nodes. Second recurrent vein absent. Hind wing without an anal lobe. ANTSFORMICOIDEA [Now included under VESPOIDEA]

Tergite 1 without scales or nodes. Second recurrent vein usually present. Hind wing usually with an anal lobe 19

19. First discoidal cell (1M or discal cell) of fore wing very long, much longer than submedian cell (1M + Cu1). Fore wing usually folded lengthwise. Wasps [except Masarinae] VESPOIDEA

First discoidal cell (1M) of fore wing shorter than submedian cell (1M + Cu1). Fore wing not folded lengthwise 20

20. Mesopleuron with a straight horizontal groove across its mid-height POMPILOIDEA [Now under VESPOIDEA]

Mesopleuron without a straight horizontal groove across its mid-height 21

21. Apex of antennal segments 3–8 or more with a pair of stout bristles on upper and inner sides. Tarsal segments 2–4 of female expanded VESPOIDEA: RHOPALOSOMATIDAE

Apex of antennal segments 3–8 without a pair of stout bristles. Tarsal segments 2–4 of female not expanded 22

22. Mesosternum and metasternum together forming a plate divided by a transverse suture, and overlapping bases of middle and hind coxae. Apical half of wing membrane with fine longitudinal wrinkles (imbrications) SCOLIOIDEA [Now under VESPOIDEA]

Mesosternum and metasternum not forming such a plate. Mesosternum with two lobe-like extensions projecting between and partly covering middle coxae. Hind wing with a jugal lobe, not imbricated VESPOIDEA: TIPHIIDAE

23. First segment of hind tarsus enlarged and more or less flattened. Head and body with branched or plumose hairs. Labium usually produced as a long tongue. Bees APOIDEA

First segment of hind tarsus not noticeably enlarged. Head and body with simple hairs (hairs unbranched or plumose). Labium usually not produced as a long tongue SPHECOIDEA

Suborder: Symphyta (Chalastogastra)

The abdomen is broadly attached to the thorax. There is no constriction between them. The first abdominal segment is only partly incorporated in the thorax. The venation is more complete with numerous cross-veins, forming many wing cells. The fore wing has at least one closed anal cell and most species have a closed anal cell in the hind wing. The metanotum has a pair of raised structures known as cenchri that engage with a scaly area on the underside of the fore wings and keep them in place. These are absent, however, in the superfamily Cephoidea. The ovipositor is adapted for sawing and boring. The syphytans are phytophagous except members of the family Orussidae. Members of this suborder commonly are called sawflies, horntails, etc.

Suborder: Apocrita (Clistogastra)

The abdomen is narrowly attached to the thorax by a short or a long petiole. The first abdominal segment (usually the tergite) is intimately fused with the metathorax to form the propodeum and the basal portion of the second morphological abdomen is constricted to form a short or a long petiole by which it joins the thorax (propodeum). The thorax thus has four segments and the first apparent abdominal segment is morphologically the second segment. Because of this confusion in counting the abdominal segments, many authors refer to the three hymenopteran body parts as prosoma (head), mesosoma (thorax) and metasoma or gaster (abdomen). The wing venation and wing cells are reduced. Sometimes there are no veins and cells.

Among the Apocrita two different groups may be distinguished. Because of exceptions, these groups, called Parasitica and Aculeata, have not been accorded formal status, but still they are useful groupings.

The Parasitica includes hymenopterans the larvae of which are parasitic in or on the immature states of other insects and arachnids and develop at the expense of their hosts. The adults are free living. These insects are referred to commonly as parasitoids. They have an ovipositor to lay eggs, usually have a trochanter and trochantellus (commonly referred to, though incorrectly, as having a 2-segmented trochanter), have long filiform antennae, and have reduced venation when compared to the Symphyta. They exert natural control of unwanted insects in forests and fields and often are used for the biological control of insect pests.

The Aculeata, on the other hand, usually are either social or solitary hymenopterans, construct hives or nests, provision their nests with food for the developing larvae, have a sting (modified ovipositor), and usually have a fixed number of antennal segments and lack a trochantellus. The venation is more complete when compared with the Parasitica. There are exceptions, however, as among the superfamily Chrysidoidea, some members are parasitoids but show characteristics of the aculeate hymenopterans. Aculeata includes ants, bees and wasps exhibiting social life, polymorphism, etc.

Treatment of Representative Superfamilies and Familiess

Suborder: Symphyta

Superfamily: Cephoidea

Family Cephidae – Stem Sawflies
The Cephidae is a small family occurring in the Holarctic Region, Old World tropics and Madagascar. The larvae are stem-borers and damage the growing tip of the stem. Several species attack cereal crops.

Superfamily: Megalodontoidea

Members of this superfamily are characterized by having a very large, almost prognathous head that is widest near the clypeus. Two families are recognized, the Megalodontidae and Pamphilidae. The Megalodontinae occurs in the temperate regions of Eurasia. Their antennae are either saw-like or comb-like, and tergites 2–5 are not folded above spiracles. The larvae feed on herbaceous plants. Members of the family Pamphilidae are characterized by having thread-like or filiform antennae and tergites 2–5 having a longitudinal fold above spiracles. They are Holarctic in distribution. The larvae roll leaves or spin silk to form webs in which they feed. The larvae are gregarious and attack conifers and fruit trees.

Superfamily: Orussoidea

Family Orussidae – Parasitic Wood Wasps

Members of this group are quite different from other sawflies. They are parasitic in habits. The adults are cylindrical in cross-section and have several spines around the median ocellus. The antennae are inserted below the ventral margin of the eye. The venation is reduced. The ovipositor is very long and thin, and coiled within the abdomen when the insect is resting. The Orussidae is a very small, relict, and widely distributed family. The members are seen with an ant-like gait over tree trunks. They are parasitoids of wood boring Coleoptera and Hymenoptera larvae.

Superfamily: Siricoidea

Family Siricidae – Horntails, Wood Wasps

This group contains large wood boring sawflies occurring in the Northern Hemisphere. They have been introduced accidentally into Australia and New Zealand and are serious pests of conifers. The tip of the abdomen is produced into a long horn-like projection, giving the name horntails to these insects. The adults are large (up to 50 mm long), brightly colored, and they also are referred to as wood wasps. The pronotum is transversely folded and is collar shaped. They have a strong, drill-like ovipositor by which they drill holes in hard wood or conifer trees and insert their eggs into dead or decaying trees. They also deposit spores of a symbiotic fungus along with the eggs (Figs. 3).

Superfamily: Tenthredinoidea

Members of the superfamily Tenthredinoidea are distinguished from other Symphyta by having a short pronotum that is concave posteriorly, the fore tibia having two apical spurs, and hind tibia with one preapical spur. The antennae are thread-like, usually with nine segments (varying from 9 to 15 in some cases). The scutellum has a transverse furrow cutting off triangular post-tergite posteriorly. The ovipositor generally hardly projecting beyond the apex of abdomen. This is the largest superfamily of Symphyta, and they are distributed worldwide.

Family: Tenthredinidae

Common sawflies. The adults are brightly colored, wasp-like insects, common during spring and early summer but some species occur also during late summer and early fall. The larvae feed gregariously on foliage orienting themselves in a characteristic manner. Some species are serious pests of coniferous trees and cause heavy defoliation of forests. A few species are gall makers and leaf miners. Many species exhibit sexual dimorphism.

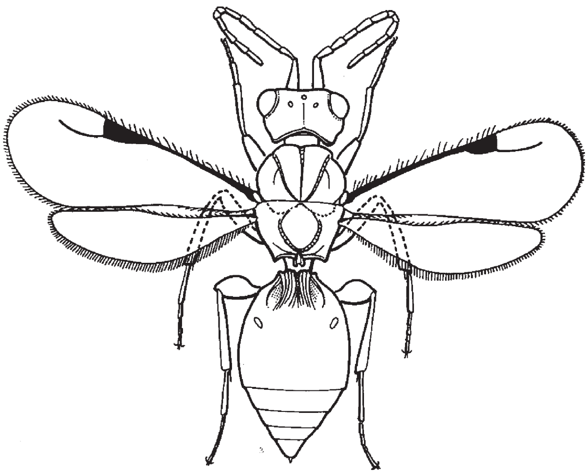
Suborder: Apocrita

Group: Parasitica

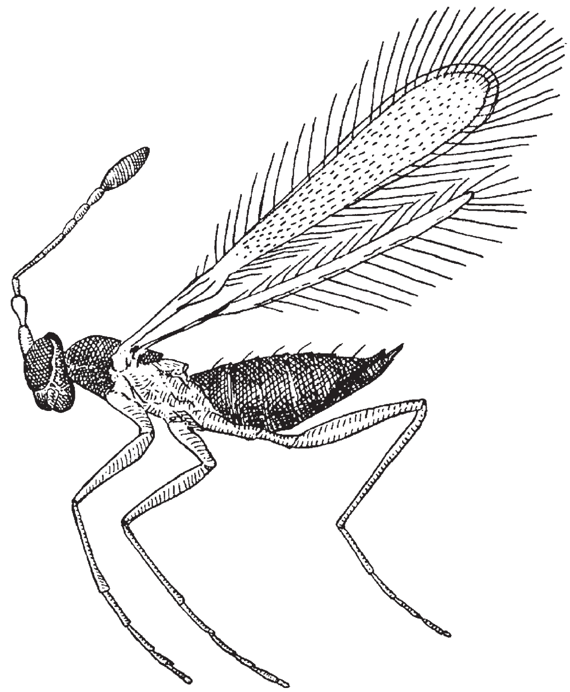
Superfamily: Chalcidoidea

The superfamily Chalcidoidea is probably the largest in the order, with about 2,500 known genera and 20,000 known species. It also contains the smallest known insects. The majority of the species are parasitoids or hyperparasitoids of other insects and of great significance in biological control. Non-parasitic, plant feeding chalcidoids are found in the families Agaonidae, Torymidae, Perilampidae and Eurytomidae. Some infest seeds and some produce galls. In the families Chalcididae and Leucospidae the hind femora are enlarged. In Mymaridae the wings have elongate fringe of hairs and these insects often are called "fairy flies."

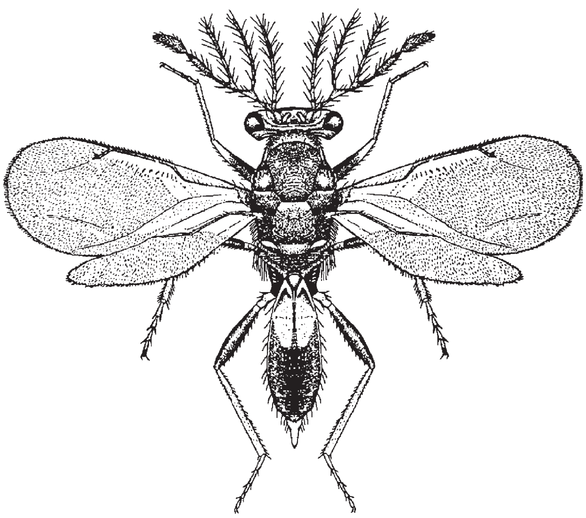
The Chalcidoidea may be recognized by having an elongate antennal scape, so that the antennae appear elbowed. The flagellum usually is differentiated into a proximal funicle and an apical club. The pronotum does not extend back to the tegula and a triangular sclerite, prepectus, is present between the hind margin of pronotum and the tegula. The wing venation is highly reduced so that generally only one vein is present in the fore wing (Figs. 4–8).



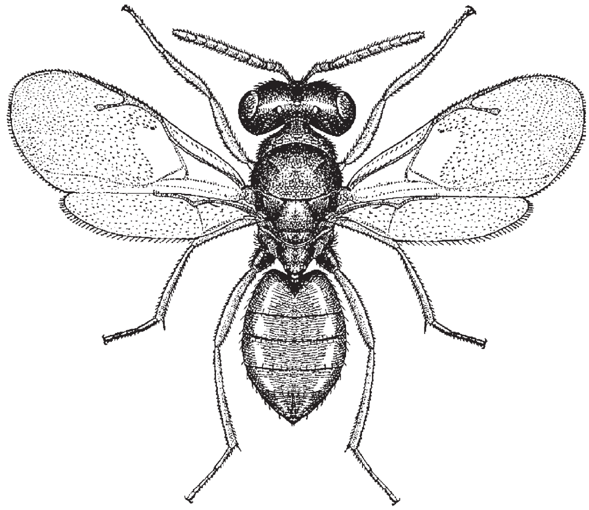
Wasps, Ants, Bees and Sawflies (Hymenoptera), Figure 4 Drawing of wasp in the family Megaspilidae (Source: Hymenoptera of the world: an identification guide to the families. Agriculture and Agri-Food Canada, 1993. Reproduced with the permission of the minister of Public Works and Government Services, 2003).



Wasps, Ants, Bees and Sawflies (Hymenoptera), Figure 6 Drawing of wasp in the family Mymaridae (U.S. Department of Agriculture).



Wasps, Ants, Bees and Sawflies (Hymenoptera), Figure 5 Drawing of wasp in the family Eulophidae (U.S. Department of Agriculture).



Wasps, Ants, Bees and Sawflies (Hymenoptera), Figure 7 Drawing of wasp in the family Pteromalidae (U.S. Department of Agriculture).

Superfamily: Cynipoidea

The cynipoids are generally small insects (except *Ibalia*), brown or black in color. The antennae are filiform, the pronotum extends back to the tegula, wing venation is reduced, with the radial cell triangular and pterostigma absent except in some rare families. The abdomen in laterally compressed (Fig. 6).

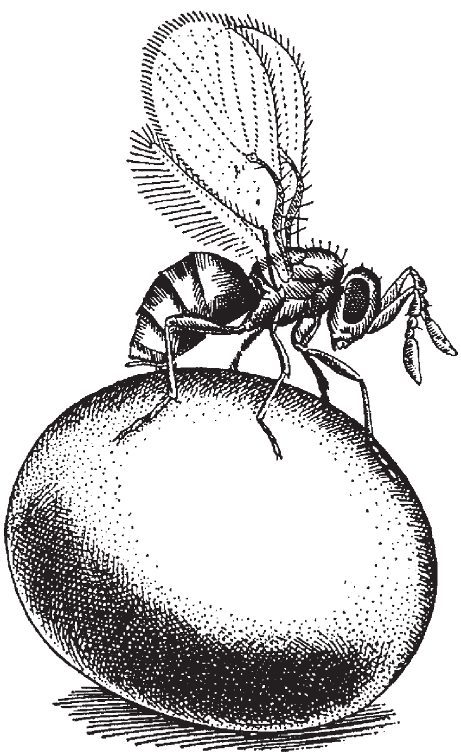
The majority of cynipoids are primary endoparasitoids developing in the larvae of holometabolous insects, or in the nymphs of Psylloidea. Most species of the family Cynipidae are gall producers and are called gall wasps. These galls commonly are seen on oak and other trees. In the family Ibalidae, the radial cell is very long and thin and the abdomen is strongly compressed and knife-like. Species of *Ibalia* may be up to 30 mm long (Fig. 7).

Superfamily: Evanioidea

In Evanioidea the abdomen is attached to the thorax high above the hind coxae, antennae are with 13–14 segments, fore wing is with a costal cell and the wing venation is fairly complete. Members of the family Evaniidae are called ensign wasps. These are black or black and red insects with the abdomen small and oval, carried like a flag high above the hind coxae. They are parasitoids of cockroach oothecae. Members of the family Aulacidae have a long, well exserted ovipositor and are endoparasitoids of wood boring coleopterous and hymenopterous larvae. In Gasteruptiidae the hind tibia is clavate, abdomen long, clavate, and ovipositor well exserted. They are ectoparasitoids of larvae of Sphecidae, Vespidae and Apidae.

Superfamily: Ichneumonoidea

This superfamily includes two families, the Ichneumonidae and Braconidae. These are small to very large insects, mostly usually fully winged, with antennae more than 13 segments, not geniculate or apically clavate. The pronotum extends back to the tegula. Wing venation is well developed and characteristic (Fig. 9).



Wasps, Ants, Bees and Sawflies (Hymenoptera), Figure 8 **Drawing of wasp in the family Trichogrammatidae (U.S. Department of Agriculture).**

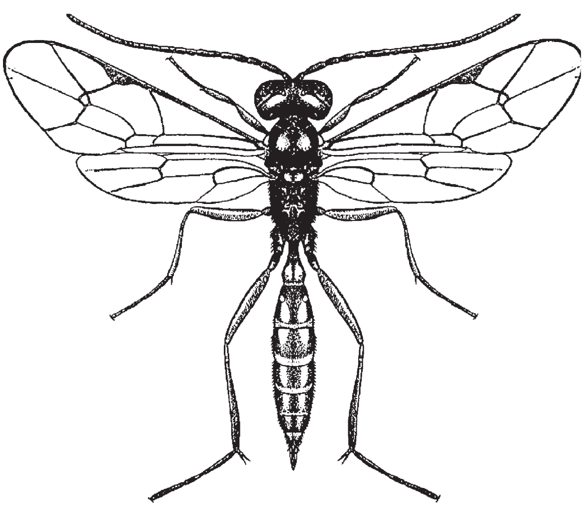
Wasps, Ants, Bees and Sawflies (Hymenoptera), Figure 9 **Drawing of wasp in the family Ichneumonidae (Source: Hymenoptera of the world: an identification guide to the families. Agriculture and Agri-Food Canada, 1993. Reproduced with the permission of the minister of Public Works and Government Services, 2003).**

The Ichneumonidae is perhaps the largest family of insects, with over 60,000 known species. Most species are ecto- or endoparasitoids of the larvae and pupae of holometabolous insects, particularly of Lepidoptera and Symphyta. Some others parasitize spider egg masses or attack bee larvae in hives. They are distinguished from the family Braconidae by the presence of second recurrent vein (2m-cu) and by the absence of the cubitus vein (1/Rs + M) in the fore wing. Abdominal tergites 2 and 3 are not fused. It includes Agriotypidae and Paxylommatidae, often considered as separate families (Fig. 10).

The family Braconidae appears to be the second largest family of insects with over 40,000 known species. It differs from the Ichneumonidae in the absence of the second recurrent vein (2m-cu) (except in Apozyginae), and by the presence of the cubitus vein (1/Rs + M) in the fore wing. Tergites 2 and 3 are fused (weakly so in Aphidiinae). It includes Aphidiidae, which are aphid parasitoids.

Superfamily: Proctotrupoidea

Members of this superfamily are parasitoids in the immature stages of other insects. They are small-sized insects with much reduced venation, but may be distinguished from the chalcids by the nature of the thorax and the abdomen. The pronotum in proctotrupids appears triangular in shape in lateral view and extends back to the tegula. The ovipositor issues from the tip of the abdomen.



Wasps, Ants, Bees and Sawflies (Hymenoptera), Figure 10 Drawing of wasp in the family Ichneumonidae (U.S. Department of Agriculture).

One member of the family Pelicinidae, the North American *Pelicinus polytrurator* (Drury) is a large (the female about 50–60 mm long), shiny black insect. The abdomen is very long and thin. The males are rare and only about 25 mm long, with the tip of abdomen swollen. They are parasitic in the larvae of June beetles, and the adults emerge in summer. Members of the family Proctotrupidae are small, about 3–10 mm long insects, with a large pterostigma and a very narrow marginal cell. They are solitary or gregarious parasites in the larvae of Coleoptera and Diptera.

Superfamily: Platygasteroidea

These are small to minute, usually black and shiny insects, and usually are classified under Proctotrupoidea. Two families, Diapridae and Platygasteridae, are placed under it. Species of Diapridae have a shelf-like protuberance on the face. They are parasitoids of the immature stages of Diptera. Members of the Scelionidae attack eggs of spiders and several groups of insects. They have highly reduced wing venation and a flattened abdomen.

Superfamily: Stephanoidea

Only one family, Stephanidae, is included here, which was classified earlier under Ichneumonoidea. The head is spherical and with a crown of about five teeth around the median ocellus. There is a slender long neck. The hind coxae are elongate and the hind femora are swollen and toothed ventrally. They are common in tropics and are parasitoids of wood boring coleopterous larvae.

Suborder: Apocrita

Group: Aculeata

Superfamily: Apoidea

The superfamily Apoidea includes insects commonly referred to as the bees. They exhibit sexual dimorphism in the number of antennal segments – 13 in male and 12 in female. Tergite VII of the female is deeply cleft medially or separated into two lateral lobes. The female gonocoxite IX is constricted but not divided into articulating proximal and distal plates. The pronotum is not extending back to tegula, usually forming a lobe covering the mesothoracic spiracle. The body hairs are branched, plumose, and the hind tarsi are usually widened. They are anthophilous, solitary or social insects (Fig. 11). Two main groups of bees are recognized: the long tongued bees and the short tongued bees.

Family: Apidae

Long tongued bees: the honey bees and the bumble bees. The first two segments of the labial palp are elongate and flattened, glossa is long and slender, and the maxillary palp is vestigial. In addition, the hind leg is modified to have a "pollen basket" composed of the enlarged tibia and the first tarsal segment, and the hind tibia has an apical margin of short, stiff setae. The jugal lobe in hind wing is shorter, and there are three submarginal cells.

The bees are important pollinators of fruit and other important crops. Their role as pollinators far exceeds their importance as providers of honey and bees wax. There are three main subfamilies. The subfamily Apinae includes the honey bees. Three species are known in the world: *Apis mellifera*, the European honey bee, widely domesticated worldwide; *A. dorsata*, the wild honey bee that is ferocious and makes a single large hive high on trees, buildings, etc., in the tropics; and a gentle, timid honey bee, *Apis florea* that makes a single hive in bushes in the tropics. The subfamily Bombinae includes the bumble bees. They are large, robust, black with yellow hairs on thorax and abdomen. They nest in hollows in the ground, have annual colonies and are important pollinators of certain kinds of clover. Members of the subfamily Euglossinae are called "orchid bees." They are brightly colored metallic bees distributed in the tropical parts of the world.

Family: Anthophoridae

These insects are also long-tongued bees that are robust and hairy, about 10–20 mm long, and usually brownish in color. The hind tibiae have

Wasps, Ants, Bees and Sawflies (Hymenoptera), Figure 11 **Photographs of some Apidae: left, bumblebee, *Bombus* sp.; right, honeybee, *Apis* sp. (photos: JL Castner).**

apical spurs, genae are short and narrow, and the maxillary palps are well developed. They nest in the ground.

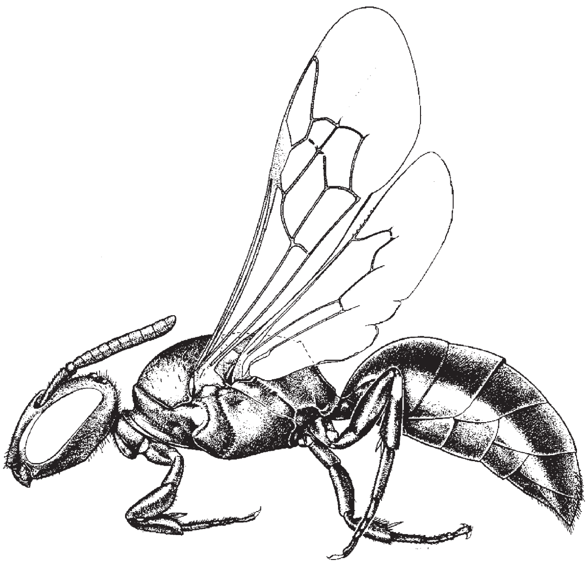
The family Anthophoridae is divided into several subfamilies. Members of the subfamily Nomadinae are called "cuckoo bees." They are parasitic in the nests of other bees, are wasp-like in appearance, and have fewer hairs on the body. Members of the common genus, *Nomada*, are reddish in color and are small to medium in size. The subfamily Anthophorinae contain bees known as "digger bees." They are robust and hairy. Most of them are solitary but some species nests in burrows in the ground, and the cells are lined with a thin wax-like substance. The subfamily Xylocopinae includes "carpenter bees." These bees nest in wood or stems of plants. The common genera are *Xylocopa* and *Ceratina*. *Xylocopa* species are large, black, shiny, resembling the bumble bees but without tufts of hair on the abdomen. The *Ceratina* species are small, about 6mm long, dark bluish-green in color.

Family: Megachilidae

These commonly are called the "leaf cutting bees." They are medium-sized, moderately robust bees, differing from other bees in having two submarginal cells in the fore wing that are about equal in size. The pollen carrying species have a tuft of hairs on the ventral side of the abdomen and not on the legs. They usually make nests in natural cavities in wood or ground and line their cells with neatly cut pieces of leaves. Most species are solitary. A few species are parasitic.

Family: Colletidae

They are "short-tongued bees." Segments 1 and 2 of the labial palp are short and not flat, similar to segments 3 and 4, the mesopleurum usually is without epistomal groove, and the volsella of the male genitalia is usually well developed. This family includes the yellow-faced bees (Hylaeinae) and the plaster bees (Colletinae). The glossa is bilobed or truncate. They nest in the ground or in various natural cavities (Fig. 12).



Wasps, Ants, Bees and Sawflies (Hymenoptera), Figure 12 Drawing of bee in the family Colletidae (Source: Hymenoptera of the world: an identification guide to the families. Agriculture and Agri-Food Canada, 1993. Reproduced with the permission of the minister of Public Works and Government Services, 2003).

Family: Andrenidae

These are also short-tongued bees. The glossa is pointed and there are two subantennal sutures below each antennal socket. They also nest in burrows in the ground, often in colonies and usually in areas with sparse vegetation.

Family: Halictidae

Members of this family resemble other short-tongued bees but have only one subantennal suture below each antennal socket. The basal vein is rather strongly arched. They also nest in the ground and some species, the "sweat bees," are attracted to perspiration.

Superfamily Sphecoidea – Sphecoid Wasps

Members of this superfamily resemble Apoidea in having sexual dimorphism in the number of antennal segments and in the nature of the genitalia. However, they have simple body hairs that are not branched, the pronotum is short and collar-like, and hind tarsi are not widened. They are solitary in habits, mostly fossorial, but some construct mud nests. They are predacious and provision their nests with lepidopterous larvae, Hemiptera, Orthoptera, Arachnida, etc. The prey is stung and the eggs laid upon them in the cell. The adults visit flowers. They commonly are known as digger wasps and mud daubers. The classification of the superfamily differs considerably: some classify it into several families, while others accord subfamily status to most families.

Family: Sphecidae

Mud daubers; digger wasps. The posterior margin of the pronotum, in dorsal view, is straight. It appears like a collar. The hind margin of pronotum, in lateral view, ends in a rounded lobe that does not reach the tegula. The episternal sulcus on the mesopleurum is more vertical than horizontal. The inner margin of the eyes is not notched in most species.

Members of the Sphecidae are solitary wasps, although some species tend to nest in a small area. A small number of species in the tropics show a eusocial behavior. Most species nest in hollows in the ground and in plant stems, wood cavities, etc. Some construct mud nests. The females hunt for other insects and spiders that serve as food for the developing larvae. The prey is stung and paralyzed before placing it in the nest, and the eggs are laid upon them. The subfamily Sphecinae includes genera like *Sceliphron* and *Chalybion* that commonly are called mud daubers. They construct nests of mud and provide them with spiders. They have a very long and slender petiole. Another common species is *Sphex ichneumoneus* (L.), which is reddish brown in color with the abdominal tip black. *Trypoxylon* belongs to the subfamily Larrinae, and commonly is referred to as organ-pipe mud daubers because they construct long tubes, attaining the length of 25 mm or more. The Crabroninae contains small to medium sized species that have black and yellow markings.

Members of the family Nyssonidae includes the cicada killer, *Sphecius speciosus* (Drury). It is a large wasp, about 40 mm long, black or rusty brown with yellow abdominal bands. It provisions the nest with cicadas.

Superfamily: Chrysidoidea

In the superfamily Chrysidoidea, the number of antennal segments is the same in the male and the female, usually 10 or 11 (more than 19 in Sclerogibbidae); tergite VII of female is complete, not cleft medially; female gonocoxite IX consists of proximal and distal portions which articulate at their point of contact; the hind wing has an anal lobe, or if the anal lobe is unclear, then the body is metallic; the hind wing is usually without closed cells; the pronotum extends back to tegula except in some Chrysididae, and the hind femur is without a trochantellus. Some species are metallic in coloration. The cuckoo wasps (Chrysididae) are external parasitoids of full grown wasp or bee larvae. Others are parasitoids of larvae of Lepidoptera and Coleoptera (Bethylidae), or parasitoids of auchenorrhynchous Hemiptera (Dryinidae).

Family: Chrysididae

The insects belonging to the family Chrysididae commonly are called the cuckoo wasps. They are small, about 8–12 mm in length, metallic blue or green in color, and the body bears coarse punctures. The adults fly in bright sunlight, visiting flowers in search for nectar. They females are seen flying in search of holes and crevices in search of their hymenopterous host eggs and larvae (usually aculeate Hymenoptera) upon which they lay their eggs. Upon hatching, the chrysidid larva feeds on the host eggs or the larvae, as well as the stored food for the host's offspring. This phenomenon is called cleptoparasitism.

Family: Bethylidae

Members of the family Bethylidae are small to medium sized, usually black in color. The females of many species are apterous and ant-like but in other species both males and females are fully winged. These wasps are parasitoids of the larvae of Lepidoptera and Coleoptera.

Family: Dryinidae

The dryinids usually have 10-segmented antennae and large heads, and broad toothed mandibles. They are parasitoids of auchenorrynchous Hemiptera. They exhibit sexual dimorphism: the males are always winged but the females may be winged to apterous. The fore tarsi of females are developed into pincer-like chelae used to grasp and hold the planthoppers as hosts. Their life history is complex and interesting.

Superfamily: Vespoidea – Wasps and Ants

The antennae bear 12 segments in the female and 13 in the male. The pronotum extends back to the tegula, its posterodorsal margin shallowly to rather deeply concave, without any lobe covering the spiracle. The metapostnotum is short and transverse, fused with the propodeum. The legs are without trochantellus (second trochanter). The fore wing has 9–10 closed cells. The hind wing has two closed cells (sometimes fewer), and has a jugal (anal) lobe. Sternites 1 and 2 are separated by a constriction. The ovipositor is modified into a short sting, issuing from the tip of the abdomen and concealed at rest. The body is devoid of plumose hairs.

The current view is that the Vespoidea includes the ants, mutillids, vespids, pompilids, scoliids and the tiphiids, all which were earlier assigned their own superfamilies. The important families are treated below.

Family: Vespidae

Yellow jackets, hornets, paper wasps, potter wasps. The fore wing has a long discal (1M) cell, much longer than the submedian (1M + Cu) cell, usually about half as long as wing, and with three submarginal cells. Wings usually folded lengthwise at rest. Posterior margin of pronotum U-shaped.

This is a relatively large group including the well-known wasps. Most species are black and yellow colored. Some species are eusocial, living in colonies. The females and the workers have a well developed sting. The social species construct a nest made out of papery material consisting of chewed up wood and plant material. Some make nests of mud (Fig. 14).

The subfamily Vespinae includes the social wasps known as the yellow jackets and hornets belonging to the genera *Vespa*, *Vespula* and *Dolichovespula*. They construct papery nests consisting of many tiers of hexagonal cells, all enclosed in a paper envelope. These can become very large. They may be constructed in open branches, hollows in the ground or tree trunks, or at any other hollow space or projecting surface around houses. The subfamily Eumeninae includes solitary wasps that construct mud nests resembling pots (potter wasps, mason wasps), commonly seen attached to houses. Most species have an elongate petiole. The subfamily Polistinae are called the paper wasps. The nests consist of a single, horizontal comb of paper cells, hanging by a slender stalk. The common genus is *Polistes*.

Family: Formicidae

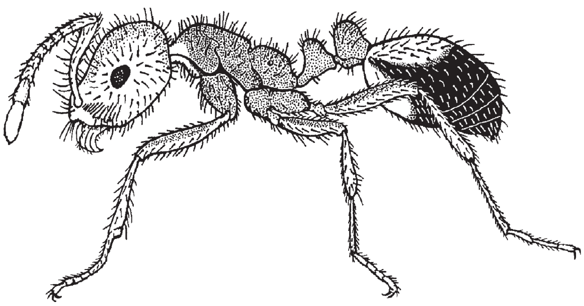
Ants. One of the most distinctive features of ants is the presence of one or two node-like protuberances on the petiole. The antennae usually are elbowed, with a long first segment, and the males may have filiform antennae. The ants are eusocial insects, living in colonies, where there are three distinctive castes: the queen, males and the workers. Winged forms, consisting of males and females, develop during the swarming season and after mating the females start a colony. The female sheds the wings, locates a nesting site, makes an excavation, and produces her first brood, which consists of workers. The workers are sterile females (Fig. 13).

Fire ants are notorious for their burning sting. Two species, *Solenopsis invicta* Buren and *S. richerti* Forel, are common in the southeastern United

States. These ants are rather aggressive and are quick to attack people and animals when disturbed. In some persons they may cause serious allergic reactions and may even lead to the death of the individual.

Family: Pompilidae

Spider wasps. The pompilids are slender wasps with spiny legs. They have a transverse suture across the mesopleurum. They prey on spiders, sting to paralyze them, and store them in their under-ground cells as food for the developing larvae.



Wasps, Ants, Bees and Sawflies (Hymenoptera), Figure 13 Drawing of an ant (family Formicidae) (U.S. Department of Agriculture).

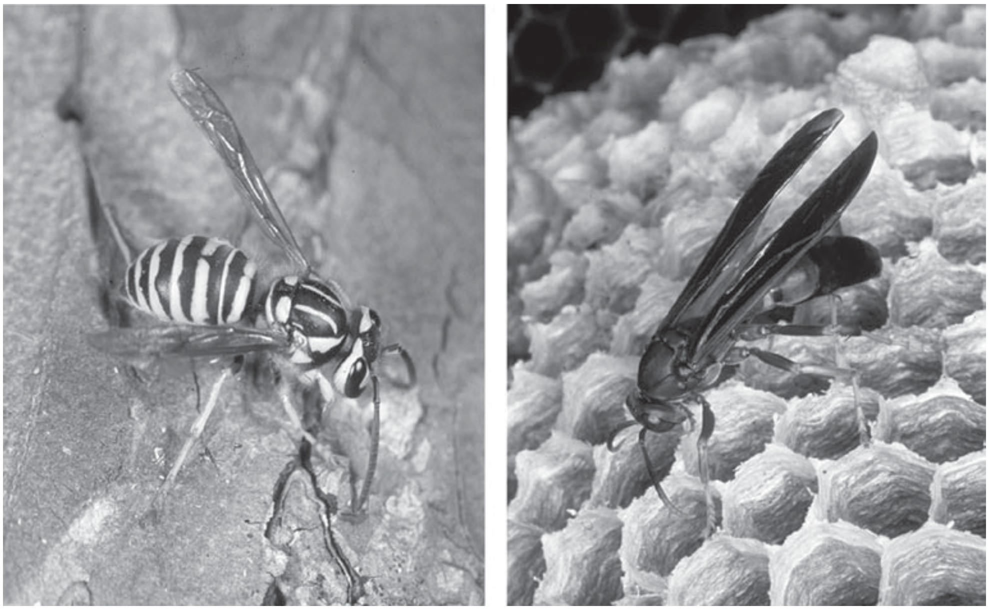
Family: Mutillidae

Velvet ants. The females are wingless, ant-like, and are covered with dense hairs. The males are winged, usually larger than the females, and also have dense hairs. A usual distinguishing feature is a structure called the "felt-like" along the side of the second abdominal segment. Most mutillids are external parasitoids of the larvae and pupae of wasps and bees.

► Ants
► Bees
► Fairy Flies
► Harvester Ants
► Honey Bee
► Sawflies
► Parasitica
► Velvet Ants
► Tiphiid Wasps

References

Arnett RH Jr (1993)American insects. A handbook of the insects of America north of Mexico. The Sandhill Crane Press, Inc., Gainesville, Florida, 850 pp



Wasps, Ants, Bees and Sawflies (Hymenoptera), Figure 14 Photographs of some Vespidae: left, paper wasp, *Polistes* sp. (photo: JL Castner); right, yellow jacket, *Vespula* sp. (photo: L Buss).

Borror DJ, Triplehorn CA, Johnson NF (1989) An introduction to the study of insects. Saunders College Publishing, Philadelphia, Pennsylvania, 872 pp
Gauld I, Bolton B (eds) (1988) The hymenoptera. British Museum (Natural History) and Oxford University Press, Oxford, UK, 332 pp
Goulet H, Huber JT (eds) (1993) Hymenoptera of the world: an identification guide to families. Agriculture Canada, Canada Communication Group Publishing, Ottawa, Canada, 668 pp
Richards OW, Davies RG (1957) A general textbook of entomology. Methuen & Co. Ltd., London, UK, 886 pp

Water Balance

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The small size of insects carries a risk of dehydration in terrestrial environments due to the limited storage capacity for water in an insect's body and the relatively large surface area for losing it. However, small size also permits escape to microclimates in which the temperature and relative humidity are more favorable. The overall flux of water through insects (and other animals) is partitioned into different avenues of water loss and gain. These are discussed below, with examples which demonstrate that they vary greatly in both absolute and relative terms. The water conservation abilities of insects in arid environments have been well studied, and many show extremely low water turnover, but liquid diets and flight in large insects can lead to high water turnover.

Water Loss

Cuticle

The wax layer in the thin outer epicuticle of insects has been critically important in their colonization of dry terrestrial environments. Insect physiologists have long known that there is a correlation between cuticular water loss and aridity of the habitat, and between cuticular water loss and the quantity of lipids in the epicuticle. The lipids responsible for waterproofing are a diverse collection of non-polar, hydrophobic molecules, dominated by long-chain saturated hydrocarbons. Their composition has been found to vary between individuals, populations and species, and as a result of thermal acclimation. Melting points of the cuticle lipids also increase during acclimation to high temperatures, and this lowers the permeability. Cuticle lipids are seen to an extreme in some insects with "wax blooms."

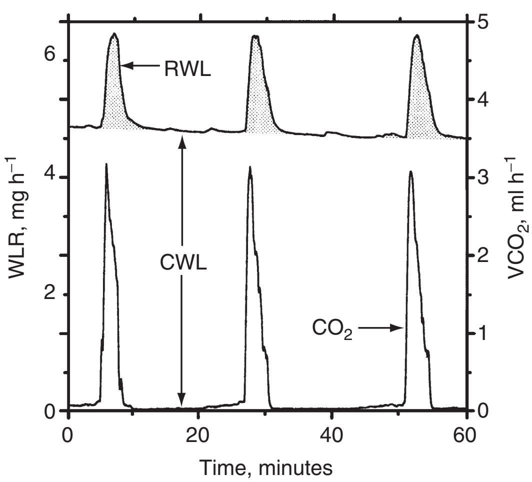
Respiration

Evaporation from insects also occurs via respiration. For some species, researchers can take advantage of the fact that periods of spiracle closure during discontinuous gas exchange allow cuticular water loss to be subtracted from total evaporative losses (Table 1). Because of spiracular control, which occurs to some degree in all insects, respiratory losses in resting insects are typically only 5–10% of total water loss. However, reduction of cuticular permeability in arid-adapted insects means that respiratory water loss assumes greater relative importance. Discontinuous gas exchange, although not universal in insects, has attracted much interest and was originally thought to function in water conservation in diapausing pupae and adult insects; however, its significance is still being debated (Fig. 15).

Respiratory water loss increases in active insects and especially during flight, when the volume of air ventilated through the tracheal system rises dramatically. Fortunately, the increased respiratory water loss is balanced to a greater or lesser extent by increased gains from metabolic water. For example, by flying at the appropriate altitude, migrating desert locusts are able to balance respiratory losses and metabolic water production during hours of sustained flight. For many insects, periods of flight are brief compared to periods of inactivity and the extra water loss due to flight will be minimal.

Water Balance, Table 1 The effects of temperature on water loss (mg per h) from the cuticle and respiratory system of the grasshoppers *Romalea guttata (microptera)* and *Taeniopoda eques* (adapted from Quinlan and Hadley. 1993. Physiol Zool 66:628–642). Note how increased temperature enhances water loss, that cuticular water loss is the principal source of water loss, and that water loss rates are significantly different even between related species. *Romalea guttata* inhabits moist climates and *T. eques* arid environments, so rates are consistent with need to maintain water balance in their normal habitat

Species and temperature (°C)	Cuticular loss	Respiratory loss	Total loss
Romalea			
15	4.62	0.11	4.72
25	8.62	0.27	8.89
30	13.28	0.52	13.80
Taeniopoda			
15	2.88	0.09	2.96
25	5.00	0.25	5.25
30	5.89	0.33	6.22



Water Balance, Figure 15 The pattern of carbon dioxide (CO_2) release (large spikes, lower portion of graph) characteristic of insects displaying intermittent or "discontinuous" ventilation, with a superimposed pattern of water loss (*smaller spikes, upper portion of graph*). The stippled areas represent respiratory water loss (RWL), which occurs when the spiracles are opened. The balance of the water loss is presumed to be cuticular water loss, and is the predominant form of loss in the grasshopper *Taeniopoda*, and most other insects (adapted from Quinlan and Hadley, 1993. Physiol Zool 66:628–642).

Excretion

The two-part excretory system of insects, consisting of Malpighian tubules and hindgut, plays a major role in water balance. The tubules secrete a fluid that is isosmotic to the hemolymph, but its volume and composition are modified during passage through the hindgut according to the water requirements of the insect. The functioning of both Malpighian tubules and hindgut is controlled by peptide hormones, but this is much better understood in Malpighian tubules. Hormonal stimulation of fluid secretion was first discovered in the blood-sucking bug *Rhodnius prolixus*, which jettisons excess water and salts in a rapid diuresis following a large blood meal. We now know that diuretic hormones are present in all insects, even when their function is not so clear, as in desert beetles. Currently the Malpighian tubules of *Drosophila melanogaster* are serving as a model system for researchers who can use the combination of physiology and genetics.

Fluid secreted by the Malpighian tubules passes into the hindgut; first through the ileum, where bulk reabsorption can occur, and then through the rectum, which is specialized for water recovery and is also responsible for ionic regulation. In most insects, rectal pads or papillae are involved in water reabsorption. Another structure with a similar function is the rectal complex, found in many Coleoptera, which produce very dry feces, and in larval Lepidoptera, where water recycling is less obvious, although the fecal water loss of caterpillars is closely regulated.

Water Gain

Food

There is huge variation in the water content of insect diets, from 2% in dry seeds to 99.9% in xylem sap. The water content of leaves varies from 50 to 90%, and phytophagous insects adjust their consumption to maintain a constant intake of dry matter. In caterpillars, preformed water in the food and fecal water loss are the two main components of the water budget – water fluxes through the gut of caterpillars are enormous – and evaporation and metabolism are therefore relatively insignificant.

Drinking

This aspect of water balance physiology has received little attention, but a surprising number of insects have been recorded drinking free water, at least under laboratory conditions. The control of drinking has been investigated in locusts and flies.

Metabolism

Metabolic water production occurs in all insects, but its importance varies with life stage and lifestyle. While the larval and adult stages of holometabolous insects usually have access to free water and preformed water in food, metabolic water is the only source of water for eggs and pupae. A beetle living in stored grain consumes dry food and has no access to free water, so metabolism becomes an important avenue of water gain. Large flying bees produce water by metabolism faster than they can lose it by evaporation, and must excrete the excess in order to avoid serious water loading.

Vapor Absorption

The ability to extract water vapor from unsaturated air is unique to certain arthropods. Different mechanisms show that this ability has evolved independently in different taxa. The rectal complex of tenebrionid beetles functions to dry the feces efficiently and its use in water vapor uptake is probably secondary. In ticks, the route of uptake is oral and involves salivary secretions. While the ability to absorb atmospheric water vapor was once thought to be confined to insects in arid conditions, soil collembolans have recently been shown to do it by accumulating organic solutes to high concentrations in their hemolymph.

Desiccation Resistance

The standard method of measuring desiccation resistance in the laboratory is to record the change in body mass of insects maintained in dry air. In addition to water loss, mass loss includes dry matter metabolized as CO_2, but in these conditions the insects are inactive and respiratory water loss is assumed to be negligible. Many studies have demonstrated higher desiccation resistance in species from arid environments. Coping with prolonged dehydration is a problem for diapausing or overwintering insects, and some show remarkable resistance to desiccation.

Behavioral Avoidance of Desiccation

Microclimates in soil and vegetation are especially important to insects with low desiccation resistance, as well as conferring thermal benefits. In general, the use of microclimates helps to reduce the costs of water regulation. Many insect herbivores living permanently on their food plants benefit from the microclimate around leaves: transpiration means that the lower leaf surface in particular develops a boundary layer of cool, humid air. Gall-forming and leaf-mining insects go further and create microenvironments within plant tissues. Aggregations of conspecific insects create their own microclimates, with evaporative and excretory water losses increasing the surrounding vapor pressure. Advantages for water balance are seen in the lower and more stable hemolymph osmolalities of group-living caterpillars, compared to isolated individuals. The benefits of manufacturing a microclimate and living in groups are taken to an extreme in social insects, whose complex nest design leads to precise control of both temperature and humidity.

Mechanisms of Desiccation Resistance in Fruit Flies

At the organismal level, desiccation resistance in insects depends on three traits: increased body water content, reduced rates of water loss, or tolerance of greater water loss. Variation in these traits has been studied in some detail in laboratory populations of *Drosophila melanogaster*, in which desiccation is a powerful selective force. Desiccation-resistant populations of flies are larger than control flies and contain more water (largely stored in the hemolymph). They lose water more slowly, mainly because of reduced respiratory losses (but not cuticular or excretory). However, the desiccation-resistant flies do not show increased tolerance of water loss. This laboratory selection has been compared with natural selection in cactus-dwelling desert *Drosophila* species, and there are some differences. In particular, wild flies do not store additional water, probably because the extra weight would hinder flight.

References

Chown SL, Nicolson SW (2004) Insect physiological ecology: mechanisms and patterns. Oxford University Press, Oxford, UK, 243 pp

Edney EB (1977) Water balance in land arthropods. Springer, Berlin, Germany, 282 pp

Gibbs AG (2002) Water balance in desert *Drosophila*: lessons from non-charismatic microfauna. Comp Biochem Physiol A 133:781–789

Hadley NF (1994) Water relations of terrestrial arthropods. Academic Press, San Diego, California, 356 pp

Willmer PG (1982) Microclimate and the environmental physiology of insects. Adv Insect Physiol 16:1–57

Water Bugs

Members of the family Corixidae (order Hemiptera).

► Bugs

Water Measurers

Members of the family Hydrometridae (order Hemiptera).

► Bugs

Water Penny Beetles (Coleoptera: Psephenidae)

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Anyone who picks up rocks out of streams or from lakeshores is probably familiar with water pennies, the tiny beetles that are found on the undersides of rocks in the water. The common water penny, larva of *Psephenus*, may be difficult to see because it resembles the surface of a rock and can cling tightly to the substrate. During daylight hours, water pennies are normally on the underside of stones, but at night they creep to the upper surface to dine upon the algae that thrive there in the sunlight. Over-wintering occurs during the larval stage. When mature, the larva crawls out of the water and settles upon a protected solid substrate such as the side or the underside of a rock near the water. Here, the larva becomes attached to the substrate all around the ciliated perimeter. The pupa then develops beneath the protective carapace of the larval skin. After 10–12 days, the adult water penny beetle emerges from the pupal skin. A median dorsal longitudinal crack in the tent-like larval carapace enables the adult to escape. Weather permitting, it flies to a rock projecting above the surface of the stream in a nearby riffle. If it is male, it joins the other male water pennies hurrying around in search of females. The females do not seek mates. They wait for the eager males to find them. After mating, the female water penny crawls down into the water and spends the rest of its life (a few days at most) seeking suitable oviposition sites and laying eggs on the underside of rocks in the riffles. The eggs, usually yellow, form a layer one egg deep. Clusters on small rocks may contain only a few dozen eggs, but clusters on large rocks usually contain hundreds of eggs, and may be deposited by several females.

After 10–15 days, tiny, almost invisible water pennies hatch. As they grow larger, they must shed their outgrown skins about six times before they leave the water to pupate. Their entire life span is about 21–24 months in Ohio and Michigan, but probably less in warmer regions. All significant feeding is done during the larval stage. Only one species of *Psephenus*, *P. herricki*, occurs in eastern and Midwestern United States and Canada, but several other species occur in western states, Mexico, and some Central and South American countries. In Neotropical regions and Asia, there are also other genera of Psephenidae with larvae like those of *Psephenus*.

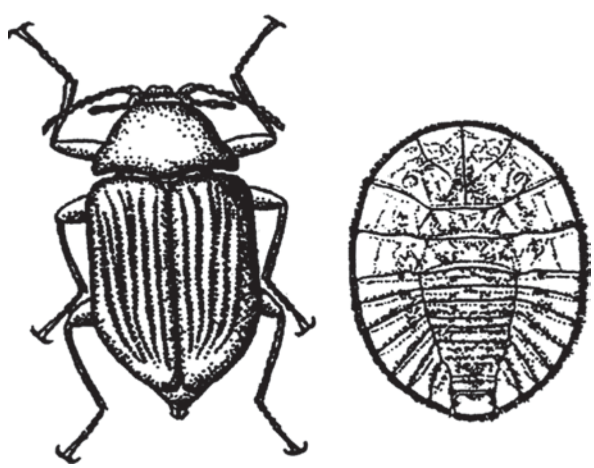
The larvae of members of the subfamily Eubrianacinae are enough like those of *Psephenus* to share the common name, "water pennies." In both subfamilies, the larvae have paired, feather-like, tracheal gills on the ventral surfaces of four or more abdominal segments. *Eubrianax* occurs in all zoogeographic realms but Australia. Members of the subfamily *Eubriinae* (or to many coleopterists, the separate Family Eubriidae) are called "false water pennies." Larvae of some Eubriine genera (e.g., *Dicranopselaphus*) look so different that no one would be likely to call them "water pennies" of any sort, and they are too uncommon to be given a common name. Seen from above, the larvae of *Afroeubria* (residents of Africa) greatly resemble the larvae of *Psephenus*, but the underside of all Eubriine larvae gives them away. Instead of paired feathery gills on several abdomimal segments, as in *Psephenus* and *Eubrianax* larvae, Eubriines have a single, retractable, tripartite gill located medially on the underside of the last (ninth) abdominal segment (Figs. 16–18). Adult Eubriines are less conspicuously associated with water than are adult Psephenines.

None of the water penny beetles are of known economic importance to man, but they are of interest to most people who are familiar with them.

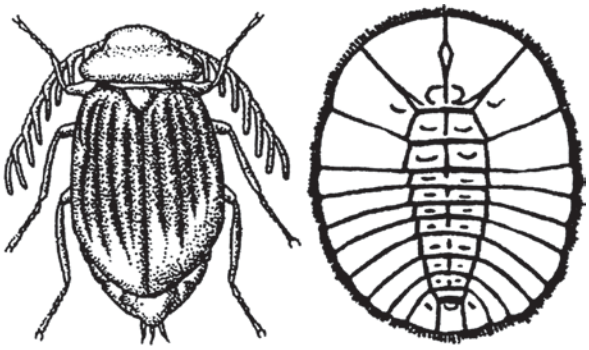
► Beetles

References

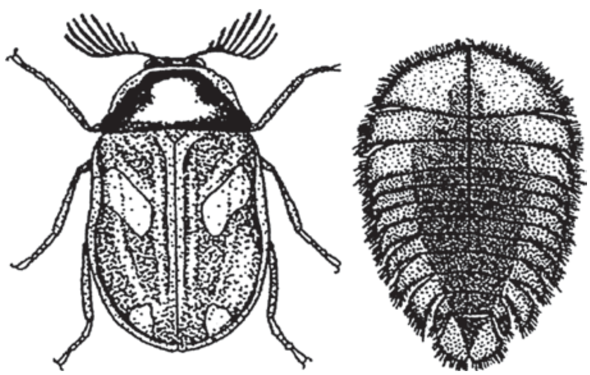
Brown HP (1983) A catalog of the Coleoptera of America north of Mexico, family: psephenidae. U.S. Department



Water Penny Beetles (Coleoptera: Psephenidae), Figure 16 ***Psephenus texanus*** **(Subfamily Psepheninae)** ***left,*** **adult male, 4–5.5 mm long, brown to black; found chiefly on rocks projecting above the water in stream riffles in southwestern Texas and north central Mexico, flying readily from rock to rock;** ***right*****, larva, common water penny, usually found clinging tightly to the undersides or sides of relatively smooth stones under water, in riffles.**



Water Penny Beetles (Coleoptera: Psephenidae), Figure 17 ***Eubrianax edwardsii*** **(Subfamily Eubrianacinae)** ***left*****, adult male, 3–4.5 mm long, yellowish to black; along rocky streams in California and Oregon;** ***right*****, larva, another type of water penny, usually found clinging to submerged stones in stream riffles.**



Water Penny Beetles (Coleoptera: Psephenidae), Figure 18 ***Acneus quadrimaculatus*** **(Subfamily** ***Eubriinae*** **or Family Eubriidae)** ***left*****, adult male, 3.5–4.5 mm long, dark brown or black with yellow or orange spots on elytra; found along small, rapid, low-elevation shady streams in California and Oregon, usually near small waterfalls;** ***right*****, larva, false water penny, found in such streams or in spray zone of falls.**

of Agriculture, Agriculture Handbook Number 529–541, prepared by Agricultural Research, 8 pp

Brown HP (1987) Biology of riffle beetles. Annu Rev Entomol 32:253–273

Brown HP, Murvosh CM (1974) A revision of the genus *Psephenus* (water penny beetles) of the United States and Canada (Coleoptera, Dryopoidea, Psephenidae). Trans Am Entomol Soc 100:289–340

McCafferty WP (1981) Aquatic entomology (subtitled The fishermen's and ecologists' illustrated guide to insects and their relatives). Science Books International, Boston, Massachusetts, 488 pp

Murvosh CM (1971) Ecology of the water penny beetle *Psephenus herricki* De Kay. Ecol Monogr 41:79–96

Water Pollution and Insects

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The impact of human activities on water resources became clear with the advent of the Industrial Revolution. Prior to this, it was mainly a localized phenomenon. For example, in the eighteenth century, the River Thames, which flows through London, England, produced such a terrible stench from raw sewage that sheets soaked in vinegar were hung in the Parliament to offset the nauseating smell. However, the English government only started to control the sewage pollution that produced these odors in the face of typhoid fever and cholera epidemics. The protection of human health and the management of ecosystems to provide essential ecological services (e.g., drinking water, waste elimination, forestry products) remain the current basis of pollution control regulation and technology in the developed world.

Pollution has been defined in various ways, but essentially it is the wrong substance in the wrong concentration, at the wrong place, at the wrong time. Water pollution can have many sources, but the most common inputs are human sewage and outputs from industrial and agricultural practices. Typically, pollution is defined as the result of anthropogenic (or human-induced) activities.

Pollution can cause changes in the structure (e.g., biodiversity) and function (e.g., primary and secondary productivity) of ecosystems. Insects are one of the major, if not the major group of organisms, that has been studied in terms of pollution. Because they are at or near the bottom of food webs, changes in insect populations will affect the remainder of the food web. In addition, insects can mark the entry point of noxious chemicals into the food web, and the economic consequences can be profound. For example, the destruction or diminishment of insect populations in fresh waters will affect the vertebrate predators such as fish and waterfowl that feed on them.

The effects of pollution on insects have to be studied at a variety of spatial and temporal scales. Effects can occur at the molecular level in fractions of seconds (biochemical effects), at the ecosystem level over several decades, and at various scales in between these extremes.

Because some insect species are sensitive to various forms of pollution while others are tolerant of these pollutants, the responses of insects have been used to detect, measure, and judge environmental disturbance. Insects are useful in biomonitoring because they are ubiquitous and have many pertinent, readily measurable biological characteristics. Food is the principal source of many pollutants for terrestrial insects, whereas aquatic insects acquire residues from both food and the abiotic environment. In this entry, we will consider both the effects of water pollution on insects and the use of insects in the biological monitoring of water quality.

Detection of Pollution Effects in Insects

A pollutant may cause deleterious effects if it influences the physiology or behavior of an organism, alters its capacity for growth, reproduction, or mortality, or changes its capacity for dispersal. Successful identification of pollution effects in insects depends on a number of conditions surrounding most studies. First is the need for adequate baseline information. Long-term monitoring of undisturbed populations is a prerequisite for detection of disturbance because natural successional changes, catastrophes, and population fluctuations may be mistakenly interpreted as pollution-caused trends in short-term studies. Historical data or paleoenvironmental approaches may provide the needed information in the absence of active, long-term, field-monitoring programs.

Second, causation can only be proven using an experimental approach. Experiments can also pinpoint early stage responses to pollution through an understanding of initial changes at different spatial and temporal scales. There is a need to link laboratory results and field surveys through field experimentation, but the experimental design must be suitable to the questions being asked to provide unequivocal answers.

Third, the species is the basic biological unit, so it should be the level at which responses to pollution are measured. There are many examples of species in the same genus responding differently to the same pollutant and dose; the lumping of taxa is a disservice in studying pollutant effects. Better autoecological knowledge of species is a prerequisite to understanding of pollution effects. Having expressed the ideal situation, practical realities such as taxonomic problems and cost often mean that higher taxonomic levels are used in biomonitoring programs.

Many abiotic and biotic factors directly or indirectly affect an organism's response to a pollutant, so it is difficult to predict the effects of pollutants and their different doses in nature. Some of the abiotic factors include: type of pollutant, concentration, duration and degree of exposure (chronic acute, lethal versus sublethal), time of year (temperature), quality of the water and sediment in which the organism lives, and interactions with other pollutants. Some of the biotic factors include: life-cycle stage (instar, age, rate of growth and development), health of the organism (parasitized or not), genetic composition (resistance), behavior with regard to exposure (cryptic or directly exposed), interactions with other species, and host alterations (important for phytophagous insects). Some of these factors are discussed more fully below.

Acute toxicity may have locally or temporarily significant effects on mortality, but sublethal effects may be more important in terms frequency of occurrence and length of exposure. Sublethal effects include disturbed enzyme functions, reduced reproduction, and altered behavior, all of which act to reduce an organism's fitness and affect its survival.

Indirect effects of pollutants on ecosystems, as mediated by insects, are often more profound than direct effects. Pollutants can influence the functioning of ecosystems by reducing species diversity, modifying food chains, and changing patterns of energy flow and nutrient cycling. For example, numbers of insects in groups naturally suppressed by fish predation tend to increase if fish are reduced by pollution such as acidification. Increased numbers of insect predators can then consume substantial amounts of small crustacean zooplankton, changing the natural relationships among trophic levels and, perhaps, affecting secondary productivity.

Life-cycle stages vary in their sensitivity to pollutants. For example, eggs are generally resistant stages, except when the pollutant is heat. Early instars seem to be more susceptible than later instars, perhaps because early instars have higher surface to volume ratios, they are more active, and they have thinner cuticles. Diapausing and pupal insects are also usually resistant stages.

It is difficult to generalize about the effects of pollution for all but the best-studied insect taxa. Most typically, some species within an insect taxon will respond positively, some will respond negatively, and some will be unaffected by a pollutant. In aquatic habitats, midges (Chironomidae), especially members of the subfamily Orthocladinae, seem to be tolerant of metal pollution. Some species of midges thrive in habitats heavily contaminated by organic matter (sewage, nutrients). Some species of mayflies (Ephemeroptera), stoneflies (Plecoptera), and caddisflies (Trichoptera) are sensitive to a number of pollutants, and have been used as indicator taxa in biomonitoring activities. In addition, most pollutant-induced changes in predators are negative, whereas changes in herbivores are often positive and are mediated through the host plant.

Relationships among exposure, dose, and effects on individual organisms (the effects of pollutants on insect populations are mediated through individuals) are complex. Different species, sexes, and life stages may react in different ways to the same exposure for both genetic and environmental reasons. Biotic interactions between individuals in a population and species within a community are also complicating factors. Therefore, generalizations for most insect groups will only be possible with the acquisition of much more taxon-specific data.

Responses of Aquatic Insect Groups to Pollution

Aquatic insects comprise all or part of 11 orders of the class Insecta and characteristically show different responses to pollution inputs, both among orders and within orders. A study done in the 1970s even demonstrated that when water quality tolerances were available for more than a single species within the same genus, the majority of genera had species listed as tolerant, facultative, or intolerant to pollution!

Typically, at the order level, three groups are considered as particularly intolerant to pollution effects: the Ephemeroptera, the Plecoptera, and the Trichoptera. The "EPT" orders (initials taken from the first letter of each order name) are also among the best known taxonomically; consequently, differential responses have been the best studied. For example, mayflies are known to be sensitive to acidification, and show reduced densities and/or richness at low-pH sites, which often result from acid deposition through precipitation (i.e., acid rain). Stoneflies are intolerant of oxygen loss (and they tend to be only found in highly oxygenated, cool-water habitats). Caddisflies are sensitive to both organic and inorganic contaminants.

However, not all EPT species are sensitive to all pollutants. Some mayflies are among the most tolerant of all aquatic insects to acidification and metal pollution. Some caddisflies occur in heavily polluted sections of European rivers. If the EPT orders are considered the most sensitive of the insects to pollution, the Diptera represent the other end of the spectrum. Increases in the percentage composition of the insect community (or even the benthic macroinvertebrate community, which includes insects, mollusks, Crustacea and other invertebrates) typically occur below releases of poorly functioning sewage treatment plants, industrial plants, and other anthropogenic inputs. Typically, these increases are in individuals of the family Chironomidae, the bloodworms (based on the hemoglobin pigment that gives a bright red color to some of the larvae). However, as mentioned for EPT, there is a broad range of tolerances not only among the species in this order, but even in the family Chironomidae.

Among the other aquatic insect orders, pollution effects have been noted as well. Species of Odonata (dragonflies and damselflies) have had their distributional range reduced because of increased eutrophication caused by the discharge of nutrients from agriculture and sewage. Hemiptera (bugs) have surface-dwelling species that are adversely affected by inputs of soap and other surfactants, and many of the water-column dwelling taxa are known to be sensitive to pesticide applications (either direct or as runoff).

Although it is evident that pollution response is best explained at the species level, tolerance values for water pollution have been developed for the different families of aquatic insects.

Tolerance values for aquatic insects. Average values for all taxa of aquatic insects reflect water quality, with 0–3.7 Excellent; 3.8–4.2 Very good; 4.3–5.0 Good; 5.1–5.7 Fair; 5.8–6.5 Fairly poor; 6.6–7.2 Poor; 7.3–10.0 Very poor.

Odonata
- Aeshnidae 3
- Calopterygidae 5
- Coenagrionidae 9
- Cordulegastridae 3
- Corduliidae 5
- Gomphidae 1
- Lestidae 9
- Libellulidae 9
- Macromiidae 3

Ephemeroptera
- Baetidae 4
- Baetiscidae 3
- Caenidae 7
- Ephemerellidae 1
- Ephemeridae 4
- Heptageniidae 4
- Leptophlebiidae 2
- Metretopodidae 2
- Oligoneuridae 2
- Polymitarcyidae 2
- Potomanthidae 4
- Siphlonuridae 7
- Trichorythidae 4

Plecoptera
- Capniidae 1
- Chloroperlidae 1
- Leuctridae 0
- Nemouridae 2
- Perlidae 1
- Perlodidae 2
- Pteronarcyidae 0
- Taeniopterygidae 2

Trichoptera
- Brachycentridae 1
- Calamoceratidae 3
- Glossosomatidae 0
- Helicopsychidae 4
- Hydropsychidae 4
- Hydroptilidae 4
- Lepidostomatidae 1
- Leptoceridae 4
- Limnephilidae 4
- Molannidae 6
- Odontoceridae 0
- Philpotamidae 3
- Phryganeidae 4
- Polycentropodidae 6
- Psychomyiidae 2
- Rhyacophilidae 0
- Sericostomatidae 3
- Uenoidae 3

- Megaloptera
  - Corydalidae 0
  - Sialidae 4
- Lepidoptera
  - Pyralidae 5
- Coleoptera
  - Dryopidae 5
  - Elmidae 4
  - Psephenidae 4
- Diptera
  - Athericidae 2
  - Blephariceridae 0
  - Ceratopogonidae 6
  - Blood-red
    - Chironomidae 8
  - Other Chironomidae 6
  - Dolichopodidae 4
    - Empididae 6
    - Ephydridae 6
    - Psychodidae 10
    - Simuliidae 6
    - Muscidae 6
    - Syrphidae 10
    - Tabanidae 6
  - Tipulidae 3

Responses of Aquatic Insects to Pollution

The continued presence of aquatic insects in a given habitat depends on their ability to survive the water quality and habitat conditions of the aquatic environment present there. Contaminants in the water can range from deficiencies (e.g., oxygen) to excess (e.g., copper) of certain components, to contamination with substances that are increasingly deleterious as concentrations increase (e.g., pesticides). However, while most species of aquatic insects react negatively to most contaminants (e.g., oil, sedimentation) there are some species that thrive. As a result, the characteristic response to contamination is that intolerant species decline, species tolerant to that specific type of contamination will appear over time or if present in low numbers increase over time, and the evenness of the community (or the distribution of individuals among the taxa present) and the composition change.

It is important to remember that, in addition to water quality, the continued presence of aquatic insects depends on habitat conditions as well. For example, if water quality conditions are not changed (i.e., no contaminants are added) but habitat declines (e.g., the riparian vegetation is removed), aquatic insect composition will change just as if water quality impairment occurred. Of course, habitat and water quality are related; for example, a change in bank stability will result in increased siltation, and consequent water quality changes caused by suspended sediments.

Below, we describe various pollution inputs that affect aquatic insects. The list is not all-inclusive and the individual effects where contaminants are co-occurring may not just be additive but may be synergistic. In each case described below, the response of insects depends on the severity of the contamination (which can vary depending on past history at a site), habitat conditions, and a variety of other factors. It is important to remember that in all these examples the response is similar: species that are intolerant of that contaminant will be eliminated, those that are tolerant will survive, those that are tolerant but not represented in the habitat before contamination may appear if they are present in the local species pool, and the composition of the aquatic insects will change.

The disposal of domestic and industrial wastes has been a major challenge of civilization. Anthropogenic inputs can be divided into three types: organic, which includes domestic sewage, industrial wastes from food processing plants, and fertilizers; chemical, which includes industrial byproducts and agricultural chemicals such as insecticides; and physical, which includes habitat disruption and its consequences (e.g., erosion and siltation). Each input differs in its effects on aquatic insects, depending on concentration, duration of exposure, and various other factors.

Organic Wastes

With inputs of organic material, the general effect is a decrease in dissolved oxygen. This effect has led to the development of the classic pollution-recovery pattern in streams that has been well known for over 100 years. In this pattern, dissolved oxygen concentrations, water conditions, and the fish, insect, and algae assemblages are described over zones that represent areas above the pollution source, within the source, below the source, and far below the source. In the upstream-most area, oxygen concentration is high, the water is clear, and fish populations are characterized by a mixture of predaceous, algivorous, and detritivorous fish; insect groups are dominated by species of Ephemeroptera, Plecoptera, and Trichoptera, and the periphyton includes *Navicula* diatoms and *Oedegonium* and *Dinobryon* algae. Where pollution inputs enter, oxygen decreases, the water becomes darker and turbid, and only tolerant fish occur – carp, buffalo, gar, and catfish. The insect assemblage becomes dominated by chironomid midge larvae and simuliid (black fly) larvae. *Paramecium*, *Beggiatoa* and *Stentor* dominate planktonic assemblages. As pollution worsens, oxygen drops to extremely low levels, the water is septic with noxious odors and floating sludge. No fish occur and only mosquito larvae (e.g., *Culex*), very tolerant dipterans such as *Eristalis*, the rat-tailed maggot, and oligochaetes such as *Tubifex* thrive. Pollution-tolerant plankton such as sewage fungus (the colonial bacteria *Sphaerotilus*), the blue-green algae *Oscillatoria* and the diatom *Melosira* predominate.

Of course, the solution to pollution has always been dilution. Recovery occurs downstream as oxygen concentration increases. If no new organic pollution sources are added, stream water quality returns through the second and then to the first pollution-recovery zone.

Probably the most widespread anthropogenic change to aquatic environments worldwide is the input of organic matter and nutrients such as nitrogen and phosphorus. Usually referred to as eutrophication, the typical causes of this type of pollution are sewage inputs containing human or animal wastes, agricultural fertilizers, or even industrial detergents. In North America and Western Europe, direct inputs of untreated sewage have been greatly reduced but inputs of mineral nutrients, which result in increases in algae, remain. Although algae produce oxygen by photosynthesis, their respiration requires oxygen and night-time reductions in oxygen concentrations are the result of eutrophication.

Chemical Wastes

In contrast to organic wastes, chemical inputs usually affect aquatic organisms through their direct toxic action, although indirect effects such as changes in pH or osmotic pressure may affect aquatic insects. Our understanding of the effects of chemical wastes on aquatic insects largely comes from toxicity tests conducted with single or multiple species of insects for either short or long durations. Toxicity testing is also a tool used in biomonitoring, and is described later.

Not unexpectedly, given that insects are their target organisms, most insecticides used to control agricultural pests exhibit toxicity to at least the aquatic insects that are related to the target pests. Even the widely used *Bti* biological insecticide (*Bacillus thuringiensis israelensis*) used to control black flies and mosquitoes shows some toxic effects on other, closely related Diptera.

A type of pollution that has caused major effects on aquatic insects is acidification. The main cause of this type of pollution is considered to be fossil fuel combustion and the long-distance transport of SO_2 and NO_x pollutants with their eventual deposition during precipitation. Acidification affects aquatic insects through changes in physiology, increases in trace metal concentrations that are toxic to some organisms, and indirectly through changing food availability by altering either photosynthetic or decomposition pathways.

Mayflies are the best studied of all invertebrates in terms of acid stress, and responses to low pH range from increases in drift rates (i.e., in which mayflies leave the substrate and “drift” downstream), reduced growth, higher respiration rates, and avoiding oviposition in acidic streams. While most Ephemeroptera species decline as pH is lowered, other more tolerant species may increase but, in general, there is an overall decrease in insect richness and productivity.

The differential responses of aquatic insects to changes in oxygen concentration and pH are evident from the results of numerous studies. Only Diptera predominate in the reduced oxygen areas of streams (the poly- and meosaprobic zones) and many mayflies are limited in their distribution to waters with pH > 5.0. Number of species in the different orders of aquatic insects showing different tolerance to organic pollution and acidification. “Poly” refers to the polysaprobic zone, which is a zone grossly polluted by organic matter; “α-meso” and “β-meso” refer to zones of increasing oxygen, and “oligo” refers to a zone of high oxygen content (from Rosenberg and Resh 1993) (Table 2).

Physical Wastes

The third category of pollution, physical wastes, generally affects aquatic insects by being abrasive or injurious to their gills, interfering with respiration, reducing food supply by reducing light penetration, or filling the interstitial spaces of substrates in which aquatic insects dwell. Habitat alterations that increase erosion are the major sources of these inputs.

Pollution sources range from municipal wastes and other consequences of urbanization, to livestock and other agricultural activities, to industrial inputs of toxic metals. To some, the changes induced by damming streams fall into the area of pollution, as does the issue of introduced species and their impact on native fauna. The literature on pollution is vast, and the individual pollutants are almost infinite in number. While specifics vary, the same pattern emerges: intolerant species are eliminated, tolerant species thrive, and the composition of aquatic insect communities under the stress is altered.

Use of Insects in Biomonitoring

Biological monitoring is the systematic use of living organisms, or their responses, to determine the quality of the environment. Biological monitoring has been a major component of water quality assessments for the past two decades. Although prior to this, assessments primarily involved chemical and physical measurements, the inclusion of a biological component has greatly improved the process. First, because water pollution is essentially a biological problem, it only makes sense to evaluate it by biological means. Second, and perhaps best explained by

Water Pollution and Insects, Table 2 Number of species in the different orders of aquatic insects showing different tolerance to organic pollution and acidifications. ‘Poly’ refers to the polysaprobic zone, which is a zone grossly polluted by organic matter; ‘α-meso’ and ‘β-meso’ refer to zones of increasing oxygen, and ‘oligo’ refers to a zone of high oxygen content (from Rosenberg and Resh 1993).

Order	Poly	α-meso	β-meso	Oligo	pH > 5.5	5.5 < 5.0	5.0 < 4.7	<4.7
Odonata	0	2	17	5	0	0	5	2
Ephemeroptera	0	6	20	23	21	20	9	13
Plecoptera	0	0	4	24	0	8	0	14
Hemiptera	0	4	2	0	0	0	2	0
Trichoptera	0	4	18	31	1	10	7	33
Megaloptera	0	2	3	2	0	0	1	2
Diptera	4	44	36	62	9	3	35	41
Coleoptera	0	8	19	18	0	0	1	0

analogy, water quality monitoring that only involves chemical and physical measurements is akin to a photograph, an instantaneous documentation of conditions at the time a sample was taken. In contrast, biomonitoring is akin to a videotape; organisms are present through the range of environmental conditions present, so they add a temporal component of past conditions to the monitoring program.

Of all groups that have been recommended for use in water quality assessments (such as fish, algae, and protozoans), macroinvertebrates are the group most frequently used and recommended. Why is this so? First, they are ubiquitous in occurrence and consequently are affected by perturbations in many different kinds of aquatic habitats. Second, there is a large number of species (perhaps 25,000 species of aquatic insects in the US and Canada alone) that exhibit a range of responses to environmental stress. Third, their sedimentary nature (or the sudden departure from it) tends to illustrate the spatial extent of a problem. Finally, they have relatively long life cycles, relative to many other groups of organisms, which allow the examination over time of features such as age structure and abundance. To be fair, the use of macroinvertebrates in biomonitoring also has disadvantages, but most of these can be accounted for in the design of biomonitoring programs.

The tradition of biological monitoring is over a century old and initially was based on the idea of indicator organisms, in which the presence of certain types of organisms in themselves were indicative of pollution status. In part, this approach was an outgrowth of the lake classification system developed by German limnologists (especially August Thienemann) that described lake categories in terms of the dominant species of Chironomidae present. Today we think of the indicator concept as rather simplistic; the assemblage of organisms present is now viewed as the best measure indicating pollution.

In the past 30 years that aquatic insects have been used in biomonitoring, there has been a shift in the type of study that has been conducted in North America. In the 1970s, emphasis was on qualitative assessments with relative (rather than absolute, i.e., number of individuals/area) samples being compared from control and test areas. However, by the next decade emphasis had switched to studies involving replicated absolute (fixed-area) samples and using inferential statistical tests. By the 1990s, emphasis was again on non-quantitative sampling and analysis involving comparisons among sites in terms of specific measures (usually referred to as metrics) or multivariate statistics in which each taxon is a variable in the analysis. Part of the key to this shift was the development and use in the 1990s of Rapid Biomonitoring Protocols, an approach encouraged by the US Environmental Protection Agency, described in detail below.

The "reference-condition approach" (RCA) has provided a powerful approach for large-scale biomonitoring programs. The "reference condition" represents a group of minimally disturbed sites organized by selected physical, chemical, and biological characteristics. The RCA is an alternative to more traditional comparisons of control vs. impacted sites in bioassessment. Sites suspected of being impacted are compared to suitable reference sites using multivariate statistics. The underlying models produce output that shows the degree of impairment of impacted sites compared to reference sites. The RCA is currently being used in national biomonitoring programs using macroinvertebrates in countries like the United Kingdom and Australia. A slightly different RCA, using "multimetrics," has been developed for water quality monitoring in the U.S.A.

The Practice of Biomonitoring

Biomonitoring approaches are available that cover hierarchical scales ranging from processes that occur at the molecular level to those that occur at the ecosystem level. In practice, however, most biomonitoring with aquatic insects is conducted at the species assemblage and community levels, and these levels are what we will describe in detail. Biomonitoring approaches used at different spatial scales. EPT = Ephemeroptera, Plecoptera, and Trichoptera (Table 3).

Water Pollution and Insects, Table 3 Biomonitoring approaches used at different spatial scales. EPT = Ephemeroptera, Plectoptera, and Trichoptera.

Hierarchical level	Examples	Advantages/disadvantages
Molecular	Changes in enzyme activity of respiratory metabolism	Subcellular levels should be sensitive, early warning indicators of stress; limited by a basic knowledge of biochemical and physiological processes in most aquatic insects
Individual	Morphological deformities; deviation from normal behavioral patterns; survival, growth, and reproduction success	Methods well developed, but indicators of stress are often qualitative
Population	Numbers of individuals; size spectra of population	Taxonomic difficulty; separation of natural variability from that caused by perturbation
Species Assemblages	Proportion of individuals in perceived pollution-intolerant groups (e.g., EPT)	Most groups viewed as intolerant are actually a mixture of intolerant and moderately tolerant taxa
Community	Taxa richness; diversity and similarity indices; biotic indices	Taxonomic difficulties; sampling problems to adequately represent proportional occurrences
Ecosystem	Structure of food webs; chemical cycling; primary and secondary production	Provides holistic view of problem; time consuming and costly

Species assemblages and community level biomonitoring involves studies that include replicated sampling and statistical analysis. The distinction between qualitative and quantitative methods is often blurred in that many rapid bioassessment programs also involve replicate sampling.

Species Richness

No matter which approach is used, similar measures (or metrics) are commonly used to distinguish between impaired and unimpaired aquatic insect assemblages and communities. The most commonly used measure is that of species richness (i.e., the number of species present), whether used for the whole community or perceived intolerant groups such as the EPT taxa. The use of species richness is based on the premise that the number of taxa decreases as water quality decreases because of the elimination of the taxa that are intolerant of a certain type of pollution. An older idea was that the number of individuals of these taxa also decreased but current evidence indicates that elimination occurs. A difficulty with using species richness is that identification, or at least the ability to distinguish taxa to count them, is required.

Abundance

Enumerations of numbers of individuals (either of the whole communities or of insect assemblages such as EPT) are often used but, in practice, are often difficult to interpret because of the high natural variability in aquatic systems. Spatial variation in substrate, flow conditions, and a myriad of other factors produce high- and low-density patches of organisms.

A classic pattern in pollution response is the elimination of certain intolerant taxa and drastic increases in tolerant taxa. This response commonly occurs with certain species of Oligochaeta and even some chironomid midge larvae in response to severe pollution conditions, especially where high amounts of organic matter result in drastic decreases in oxygen concentrations. However, this type of pollution is not the only one that induces density increases. The chironomid midge larva, *Cricotopus bicinctus*, which tends to commonly occur in low densities, often increases by orders of magnitude when the habitats it occurs in are exposed to contaminants ranging from oil to chromium.

Evenness and Diversity

Shifts in abundance of insect populations are the basis for evaluating the evenness or diversity (as opposed to richness). Evenness refers to the distribution of individuals among the taxa present. For example, two communities of stream insects may each contain 10 species and 100 individuals; however, their evenness will differ if the first community has ten individuals of each species and the second has one species with 91 individuals and the rest with one individual each.

Evenness is often calculated along with diversity indices, an approach that was widely used in the 1970s but is considered as a less reliable tool for biomonitoring by many researchers today. Depending on the formula used for calculating the diversity of a community (or species assemblage), the index value can be weighted more towards the richness or evenness component.

Biotic Indices

Biotic indices are the evaluation tool that is both widespread in use and unique to water quality monitoring programs using aquatic insects. In calculating a biotic index score, organisms collected are assigned values according to their tolerance or intolerance (ideally) to the pollutant being evaluated, but in actuality most values are based on responses of the insect to organic pollution. Examples of tolerance values are often used at the family level for many rapid bioassessment procedures in North America but in the rest of the world they are usually used at genus or species level, an approach that is more commonsensical given that there is high variability in pollution tolerance and intolerance within aquatic insect families. The actual calculation of a biotic index score involves multiplying the number of individuals of each taxon by their tolerance values, summing them, and dividing this sum by the number of individuals collected.

Functional Feeding Groups

A recent addition to biomonitoring procedures has been the incorporation of functional feeding group (FFG) measures into programs. FFG measures differ from those described above in that the former emphasizes characterization of the structural aspects of the community, while FFGs emphasize the functional aspects. The use of FFGs in biomonitoring is based on the premise that organisms evolved certain morphological-behavioral food-gathering mechanisms and can be placed in particular groups. Consequently, each of these groups is expected to occur in proportionally higher abundance in accumulations of particular food sources (or habitat types). Most biomonitoring programs characterize the species encountered as belonging to one of several functional groups: scrapers (consume attached algae); shredders (consume decomposing vascular plant tissue); collectors (consume decomposing fine particulate organic matter); and predators (consume living animal tissue). Leaf packs, for example, should have a high proportion of shredders; algae-covered rocks should have more scrapers. Departures from expected proportions could indicate contamination or disturbance (e.g., a decrease in shredder abundance could indicate deleterious changes in the riparian zone that provides the food staples for the shredders to use).

A characteristic of community based approaches used in rapid bioassessment procedures involves calculation of combination indices of many of the measures described above. While this spreads the risk of incorrect assessments using single measures, it is also perceived as giving a balance to the various measures used. The inclusion of combination indices of the various measures has given rise to the name "multimetric approaches," which (incorrectly) has been considered as the same as rapid bioassessment procedures.

Other Techniques

Two other approaches must be mentioned in the use of aquatic insects in biomonitoring: toxicity studies and paleolimnological reconstruction. Toxicity testing has the longest history of any technique in biomonitoring, and is supposedly traceable to Aristotle placing a freshwater fish in seawater to observe its reaction! Today, toxicity tests form a continuum of complexity from single-species, laboratory-based, short-term exposures, to long-term single- and multiple-species tests, to field-based toxicity testing in outdoor experimental systems. Many species of aquatic insects are used in this testing, and results of studies are used to regulate discharges, compare toxicants, and predict environmental effects of their use.

Paleolimnological approaches to biomonitoring involve using sediment cores to reconstruct the history of aquatic systems that have been exposed to impacts such as eutrophication, acidification, or climate changes. This approach is confined to lakes and large rivers, and is not widely used by regulatory agencies.

Conclusion

Water pollution is a biological problem. Consequently, the effects of pollution on insects, the most speciose group usually present in fresh waters, is expected to be a significant outcome of anthropogenic impacts. Likewise, because they show varied responses to pollution, insects are the logical basis for monitoring effects. This fact has been recognized by the existence of thousands of government- sponsored and volunteer programs all over the world that use aquatic insects to monitor water quality.

References

Fjellheim A, Raddum GG (1990) Acid precipitation: biological monitoring of streams and lakes. Sci Total Environ 96:57–66

Hall RJ, Ide FP (1987) Evidence of acidification effects on stream insect communities in central Ontario between 1937 and 1985. Can J Fish Aquat Sci 44:1652–1657

Heliövaara K, Väisänen R (1993) Insects and pollution. CRC Press, Boca Raton, Florida, USA

Hellawell JM (1986) Biological indicators of freshwater pollution and environmental management. Elsevier Applied Science Publishers, London, UK

Hilsenhoff WL (1988) Rapid field assessment of organic pollution with a family-level biotic index. J North Am Benthol Soc 7:65–68

Kerr M, Ely E, Lee V, Desbonnet A (1994) National directory of volunteer environmental monitoring programs, 4th edn. EPA 841-B-94-001. US Environmental Protection Agency and Rhode Island Sea Grant, University of Rhode Island, Narragansett, Rhode Island

Lenat DR, Resh VH (2001) Taxonomy and stream ecology – the benefits of genus- and species-level identifications. J North Am Benthol Soc 20:287–298

Resh VH, Myers MJ, Hannaford MJ (1996) Macroinvertebrates as biotic indicators of environmental quality. In: Hauer FR, Lamberti GA (eds) Methods in stream ecology. Academic Press, San Diego, California, pp. 647–667

Reynoldson TB, Norris RH, Resh VH, Day KE, Rosenberg DM (1997) The reference condition: a comparison of multimetric and multivariate approaches to assess water-quality impairment using benthic macroinvertebrates. J North Am Benthol Soc 16:833–852

Rosenberg DM, Resh VH (eds) (1993) Freshwater biomonitoring and benthic macroinvertebrates. Chapman and Hall, New York, NY

Saether OA (1979) Chironomid communities as water quality indicators. Holarctic Ecol 2:65–74

Water Scavenger Beetles

Members of the family Hydrophilidae (order Coleoptera).

► Beetles

Waterscorpions

Members of the family Nepidae (order Hemiptera).

► Bugs

Water Springtails

A family of springtails (Poduridae) in the order Collembola.

► Springtails

Water Striders

Members of the family Geridae (order Hemiptera).

► Bugs

Water Treaders

Members of the family Mesoveliidae (order Hemiptera).

► Bugs

Wax

A substance secreted by insects from glands located on various parts of the body (Fig. 19). Wax serves a protective function for most insects, but bees use wax to build cells in their hives. The term "wax," as generally applied to the lipids on an insect's cuticle, is a complex mixture of lipids, most of which do not fit the chemical definition of "wax."

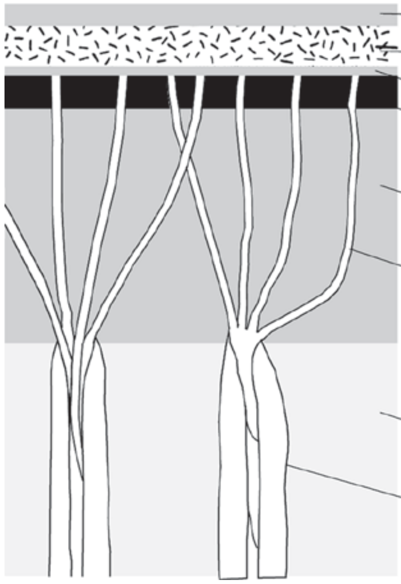
Wax Channels

Narrow-diameter channels in the epicuticular layer of the insect integument. They deliver lipids to the surface.

Wax Scales

Some members of the family Coccidae, superfamily Coccoidae (order Hemiptera).

► Bugs



Wax, Figure 19 **Cross section of the insect epicuticle (adapted from Chapman, The insects: structure and function).**

Web-Lovers

Members of the family Plokiophilidae (order Hemiptera).

► Bugs

Webspinners (Embiidina)

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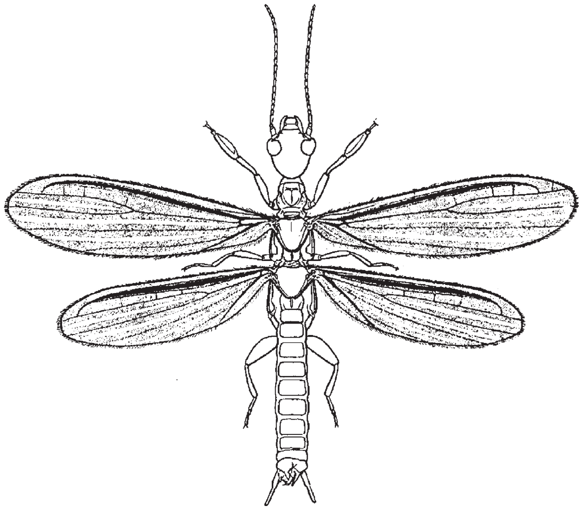
Embiidina is the oldest name for a peculiar order of semi-social, largely tropical insects later named Embiodea, Embioptera, or Embiaria. They also are known as foot-spinners and embiids. With less than 500 named species, it is regarded as a small order, but worldwide collecting indicates that it is moderately large, potentially with about 2,000 species. Because embiids tend to remain in their self-produced silk galleries, they rarely are collected by usual methods except for males attracted to lights (Fig. 20). One must search for



Webspinners (Embiidina), Figure 20 Typical alate male embiid, *Oligotoma saundersii* (Westwood) (Oligotomidae), body length 10 mm.

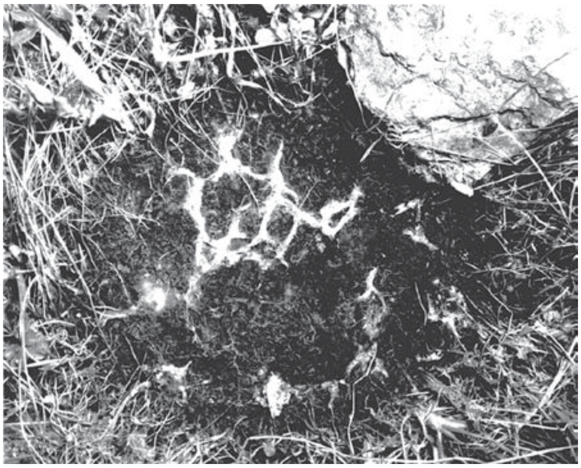
the often-obscure colonies and rear series, especially males, in laboratory cultures.

Characteristics

These are small insects, generally measuring 4–10 mm in length, though a few attain nearly one centimeter. Webspinners are soft-bodied and elongate, and pale to dark in color. They bear compound eyes, but lack ocelli. The antennae are filiform, and consist of 15–32 segments. They have chewing mouthparts. The prothorax is narrower than the head. The fore legs and hind legs are stouter than the middle legs. The tarsi have three segments, and the basal segment is markedly swollen on the forelegs. Female webspinners are wingless. Males are winged or wingless, and if winged they bear two pairs of smoky-colored membranous wings, with both pairs about equal in size and shape. The abdomen bears ten segments, and a pair of 2-segmented cerci is present at the apex. The immatures undergo four nymphal instars, and in the case of winged males, the last two bear wing pads. Webspinners display incomplete metamorphosis. All life-stages of all species have the basal segment of the fore tarsi greatly enlarged by scores of tightly-appressed, globular, multicellular silk glands. By means of a thread-like duct, the secretion of each gland is conveyed to one of a multitude of hollow, dermal, seta-like ejectors scattered on the ventral surface of the tarsus. With rapid, criss-cross strokes in many directions, even dorsally, the foretarsi produce dense-walled silk galleries ramifying in or on the food supply, usually the outer bark of trees, leaf-litter, and lichens on rocks. In arid regions, galleries are shielded beneath stones and extend down soil cracks (Fig. 21).

The galleries are just narrow enough to insure constant body hair contact with the walls and are increased in diameter as the embiids grow. Most of the order's peculiarities augment predation-escape by rapid reverse movement. These include a slender supple body with short legs, a forward-projected head, enlarged depressor muscles of hind tibiae to power reverse movement, highly sensitive cerci to guide such movement, and adaptations reducing friction of protruding structures, such as wings and ovipositor, against gallery walls.

Because females must live long enough to produce eggs and guard young, they gained maximum speed in reverse movement by becoming universally apterous by neotenic retardation of development of



Webspinners (Embiidina), Figure 21 Characteristic silk galleries under stone in a semi-arid environment, California.

adult structures (Fig. 22). In arid, open environments where flight would expose them to adverse conditions, especially predators, males of many species likewise are apterous, or subapterous, through degrees of neoteny. Fortunately, in all but one species, the male's genitalia fully develop and serve as the most useful characters in classification. Females are difficult to identify without associated adult males.

Evolution

Neotenic apterism appears to be a relatively recent adaptation. Undoubtedly, during early evolution of the order, perhaps in the Permian period, both sexes must have possessed wings. The first stage of reducing the "barb effect" of wings during reverse movement was evolution of flexibility, a weakening of most longitudinal veins. This enabled the wings to fold forward, even crumple, over the back and thereby reduce friction. However, because stiff-winged flight must have remained useful, wings evolved an ability to temporarily stiffen when extended in flight. The means was blood pressure in the full length of certain veins, particularly in the anterior radius (RA), which became a terminally closed sinus, termed radial blood sinus (RBS). Such a conspicuous vein characterizes the wings of all wing-bearing males of the order. Presence or absence of wings in males occurs throughout the order by random convergence, usually associated with climate.

Webspinners (Embiidina), Figure 22 Typical adult female, *Pararhagadochir trachelia* (Navás), body length 12 mm, from Argentina. Shows neotenic apterism of all females of the order.

Embiids primarily occur in subtropical and tropical environments from sea level to almost 4,000 meters. A few species range into temperate regions, but many suitable regions haven't been occupied due to female apterism and hazards of movement outside of galleries. Lack of dispersal of females by flight restricts the order to continental lands and explains the absence of the order on oceanic islands except for a few species, particularly of the genus *Oligotoma*, which have been widely spread in ancient and modern human commerce.

Although the order probably had an early origin, the fossil record is weak. The only possible pretertiary fossil, *Burmitembia venosa*, was found in Burmese amber (questionably Cretaceous). All Tertiary fossils, mostly in amber, are modern types.

Classification

There are various taxonomic arrangements possible, but the following eight families seem to represent a consensus currently:

- Class: Insecta
  - Order: Embiidina
    - Family: Clothodidae
    - Family: Embiidae
    - Family: Notoligotomidae
    - Family: Embonychidae
    - Family: Anisembiidae
    - Family: Australembiidae
    - Family: Teratembiidae
    - Family: Oligotomidae

Because so many taxa await description, it isn't possible to develop an adequate classification at this time. Species of Clothodidae, confined to South America, are the most plesiomorphic. The large family Embiidae is highly diverse and requires division into subfamilies and, perhaps, families. The large family Anisembiidae is confined to the Americas. Tropical Asia has a number of families, particularly Oligotomidae, and some very distinct families, such as Embonychidae. Australia also has many oligotomids, a few Notoligotomidae and an abundance of Australembiidae, a family confined to eastern Australia. The large family Teratembiidae is best represented in the Americas and Africa, with only a few Asian species. A number of additional families await description. Strangely, Madagascar doesn't appear to have endemic embiids. Apparently there are no Southern Hemisphere origins. No species is of economic importance.

References

Ross ES (1984) A synopsis of the Embiidina of the United States. Proceedings of the Entomological Society of Washington 86:82–93

Ross ES (2000a) EMBIA contributions to the biosystematics of the insect order Embiidina. Part 1, Origin relationships and integumental anatomy of the insect order Embiidina. Occasional Papers of the California Academy of Sciences 149:1–53

Ross ES (2000b) EMBIA contributions to the biosystematics of the insect order Embiidina. Part 2, A review of the biology of Embiidina. Occasional Papers of the California Academy of Sciences 149:1–36

Web-Spinning Sawflies

Some members of the family Pamphiliidae (order Hymenoptera, suborder Symphyta).

► Wasps, Ants, Bees and Sawflies

Webworms (Lepidoptera: Pyralidae)

Webworms are the larvae of Pyralidae (Crambidae) that web together vegetation, usually feeding within the rolled, folded or loosely webbed foliage. Sometimes they only rest within the silk, venturing forth to feed at night. Different species attack both grasses and forbs. Most, but certainly not all, of these larvae seem to be poorly defended chemically or physically, and perhaps derive some protection from predation and parasitism by living within the web. Certainly they are less visible to vertebrate hunters such as birds, but parasitoids often manage to locate and parasitize them.

Wedge-Shaped Beetles

Members of the family Rhipiphoridae (order Coleoptera).

► Beetles

Weeds in Crop Systems for Pest Suppression

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Weeds are generally considered to be deleterious in crop systems because of their competition with crop plants for limited water, nutrients, light, and space, and occasionally because of allelopathy. Weeds are also known to be important reservoirs for some crop pests, including bacterial, fungal, and viral pathogens, nematodes, and arthropods. In addition, weeds can obstruct harvest operations. However, weeds support beneficial arthropod populations and vegetative diversity is associated with faunal diversity. Species diversity has been related to ecosystem stability and a lower frequency of pest outbreaks, although some pests [e.g., tsetse (*Glossina* spp.) and rhinoceros beetles, (*Oryctes* spp.)], maintain low, relatively stable densities that are still economically injurious.

Vegetational diversification in polycultures to suppress pest arthropods has at times produced positive results. For example, corn/bean (*Zea* *mays* L./*Phaseolus vulgaris* L.) dicultures sustained less injury by banded cucumber beetles, *Diabrotica balteata* LeConte; fall armyworm, *Spodoptera frugiperda* Smith; and leafhoppers, *Empoasca kraemeri* Ross., than corn monocultures. Maize/legume/squash (*Cucurbita* spp.) polycultures in tropical Mexico produced higher yields and harbored 38% fewer melonworms, *Diaphania hyalinata* (L.), larvae than squash monocultures. Cover crops, such as beans, *Phaseolus* sp., in apple, *Malus* sp., orchards, have been associated with reduced codling moth, *Cydia pomonella* L.; rosy apple aphid, *Anuraphis roseus* Baker; and leafhopper infestations. Modifications of the polycultural concept include [strip cropping] to accumulate natural enemy populations or to attract pest populations into concentrated areas where they can be sprayed with insecticides. Crop rotation is another mode of vegetational diversification, conducted on a temporal rather than on a concurrent basis. A modification of crop rotation was demonstrated when canola, *Brassica napus* L., and wheat, *Triticum aestivum* L., in the winter "relayed" aphid predators to sorghum in the spring, and from sorghum to cotton in the summer. Theories that attempt to explain the lower pest infestations in many vegetatively diversified crops include: (i) spatial dilution of the pest's primary food or shelter resource, (ii) chemical or structural interference with host location and use by herbivores, and (iii) enhanced natural enemy populations resulting from increased herbivore prey abundance and diversity.

Native weed species and communities have been linked with the suppression of insect pests in cropping systems, including fall armyworm in corn; imported cabbageworm, *Pieris rapae* L., cabbage aphid, *Brevicoryne brassicae* L., and cabbage whitefly, *Aleyrodes brassicae* (Wlk.) in Brussels sprouts, *Brassica oleracea* L. cv. "Brussels sprouts." Weed growth was associated with reduced infestations of the potato leafhopper, *Empoasca fabae* (Harris), in alfalfa, *Medicago sativa* L.; velvetbean caterpillar, *Anticarsia gemmatalis* Hübner, green stink bug, *Nezara viridula* L., and corn earworm, *Heliothis zea* Boddie, in soybeans, *Glycine max* (L.) E. Merrill; and green stink bug in macadamia, *Macadamia* sp., orchards. Two cropping systems, Louisiana sugarcane, *Saccharum officinarum* L., and south Texas cotton, *Gossypium hirsutum* L., are presented as case studies because they have been more extensively examined regarding weed interactions with arthropod populations than other cropping systems, and because they demonstrate different outcomes and principles.

Louisiana Sugarcane

The intrusion of weeds, especially the perennial johnsongrass, *Sorghum halepense* (L.) C. Persoon, can cause sugarcane yield losses of up to 84%. Most weeds in sugarcane are less competitive annuals that decline after crop canopy closure blocks sunlight, but even annual weed infestations, particularly hairy crabgrass, *Digitaria sanguinalis* (L.) J. Scopali, can reduce sugarcane density, biomass, and commercial sugar yield by 24, 19, and 15%, respectively.

The importance of natural enemies in sugarcane in Louisiana was emphasized when applications of non-selective and persistent insecticides were associated with increased populations of the sugarcane borer, *Diatraea saccharalis* (F.), the key pest. Sugarcane fields in Louisiana that were infested with monocot, dicot, or monocot/dicot mixtures were found to be significantly more diverse in terms of soil surface- and foliage-associated arthropods, including predators, than weed-free sugarcane habitats. Herbivorous prey arthropods, which support populations of natural enemies, were significantly more numerous on the ground, sugarcane stalks, and sugarcane leaves in weedy habitats, and the abundance of arthropod prey was significantly greater on weed foliage than on the soil surface, or sugarcane in weedy habitats (Fig. 23).

The red imported fire ant, *Solenopsis invicta* Buren, has been identified as the most important predator of the sugarcane borer, and was found to establish significantly more colonies per unit area

Weeds in Crop Systems for Pest Suppression, Figure 23 **Weedy fields such as this sugarcane field in southern Louisiana produce greater yields than weed-free crops because weeds harbor populations of beneficial insects that suppress key pests.**

(up to 85%) in weedy than in weed-free sugarcane habitats. Imported fire ant workers were significantly more abundant on the soil surface, sugarcane stalks, and weed foliage in weedy habitats. A study using a rare earth element (samarium) as a stable-activable tracer ingested by selected colonies in weedy sugarcane had 28% smaller foraging area (because of significantly greater prey availability) than weed-free sugarcane. The reduction in territorial area and the 25% increase in foraging activity per unit area permitted more dense colonization by fire ant in weedy habitats.

At least 18 other formicid species have been identified as being natural enemies of the sugarcane borer in Louisiana, and it has been suggested that a multiple predatory ant complex is more effective than one dominated by fire ant. One study determined that fire ant foraging activity among weedy and weed-free sugarcane habitats was negatively correlated ($r = -0.069$, $P \leq 0.05$) with the abundance of the formicids *Paratrechina vividula* Nylander, but failed to influence *Pheidole moerens* Wheeler. The fire ant has displaced other indigenous formicid species from many habitats throughout its distribution in the United States.

Spiders (Araneae) are the chief egg predators of the sugarcane borer, and second only to the fire ant among overall natural enemies of the sugarcane borer. Louisiana sugarcane fields are known to support at least 84 spider species in 18 families. Vegetational complexity involving weeds is associated with increased spider diversity and abundance on the soil surface and on sugarcane foliage. Predators of the sugarcane borer such as carabids, elaterid larvae, staphylinids, dermapterans, and neuropterans are found in Louisiana sugarcane, but weed cover has not been associated with increased populations of these insect groups.

Although grass species, including *Paspalum* spp., and johnsongrass can serve as hosts to the sugarcane borer, increased numbers of predatory arthropods in weedy sugarcane appears to have overridden any deleterious influence of weeds as secondary hosts of the pest. Sugarcane borer injury (numbers of bored internodes) was reduced by 28–42% in weedy sugarcane. Economic analysis and sugarcane biomass yields in weedy versus weed-free habitats were not consistently different in plots where the sugarcane borer was controlled with fenvalerate, a pyrethroid insecticide.

Also, soil incorporated aldicarb, used for nematode control, in weedy habitats resulted in low predator populations, particularly fire ants, that were similar to levels encountered in weed-free sugarcane habitats. Sugarcane borer injury was 19–32% greater in aldicarb treated weedy areas. Therefore, the hypothesis that plant chemical or structural complexity in weedy systems interferes with host location by herbivores does not adequately explain sugarcane borer infestations trends. Predation appears to be more important.

A study in southern Louisiana revealed that weedy sugarcane field plots, without chemical control of the sugarcane borer, can yield about 12% ($P \leq 0.05$) less commercial sugar per hectare than weed-free plots mainly because of weed-induced sugarcane stand reduction. Net return (US$dollar;/ha), however, was at least 14.6% higher than in the weed-free habitats. The same study suggested that research is needed to study the effect of limited areas of natural weed growth in sugarcane fields for enhancing natural enemy populations. Similarly, in sugarcane grown in Hawaii, the association of the dipteran sugarcane borer parasite *Lixophaga sphenopheri* (Villen.) with weeds resulted in reduction of New Guinea sugarcane weevil, *Rhabdoscelus obscurus* Boisd. It was suggested that weeds be permitted to grow in limited areas or "islands" within sugarcane fields to reduce pest populations.

The greenbug, *Schizaphus graminum* (Rondani), which can obtain sugarcane mosaic virus (SCMV) from infected weeds and transmit the disease to sugarcane, was more abundant in the weedy sugarcane habitats in Louisiana, and, possibly as a result, SCMV infection of sugarcane was 14% higher than in weed-free habitats. Weeds have also been reported to be associated with higher populations of the phytophagous nematodes *Criconemella* spp., *Meloidogyne* spp., and *Tylenchorhynchus* sp. collected from sugarcane rhizospheres in southern Louisiana. In the case of *T. annulatus*, populations appeared to be influenced by SCMV infection of the host sugarcane plant.

South Texas Cotton

In south Texas, the key pest of cotton production is the boll weevil, *Anthonomus grandis grandis* Boheman, which can commonly cause greater than 50% yield losses if populations are unchecked. In nature, boll weevils have been shown to reproduce on seven *Gossypium* spp., (including *G. hirsutum* and *G. barbadense* L.), three *Cienfugosia* spp., two *Hampea* spp., and *Thespesia populnea* (L.) D. Solander *ex* J. I. Corrêa da Serra in Texas, 486 boll weevils were examined and found to have ingested 8,900 pollen grains from 58 plant families of which the majority were in the families Salicaceae (28%), Fabaceae (13%), and Poac eae (8%).

Weedy cotton field plots in the Lower Rio Grande Valley were associated with significantly higher populations of nine of eleven prey arthropod groups counted, including cicadellids, herbivorous hemipterans, lepidopteran larvae, and dipterans; and nine of the thirteen natural enemy arthropod groups counted, including *Georcoris* spp., *Orius* spp., *Nabis* spp., and neuropterans. For the most part, differences among arthropod populations in weedy and weed-free cotton plots became more substantial as the season progressed and weed biomass increased as compared to biomass early in the season. Diversity among the arthropod groups that were counted did not differ for ground associated arthropods, but was significantly higher for samples collected from cotton plant canopies in weedy habitats than on cotton plant canopies in weed-free habitats. Numbers of ant colonies in the weedy and weed-free cotton habitats were low and did not differ, and were mainly comprised of leafcutter ants, *Atta* spp., and tropical fire ants, *Solenposis geminata* (F.). The most effective predator of boll weevils in Texas cotton is the fire ant. It is reported to cause an average of 84% boll weevil mortality as compared to 0.14, 6.9, and 7% caused by parasitism, desiccation, and egg infertility, respectively, and some researchers claim that the fire ant, originally from South America, prefers boll weevils to other food sources in the cotton agroecosystem. In weedy and weed-free cotton habitats in the Lower Rio Grande Valley, fire ants were not found in any samples. Examination of fallen boll weevil infested squares revealed that, in weedy and weed-free habitats, 50% of the boll weevils were killed by heat and desiccation as compared to eight and 2% killed by ants and disease, respectively (40% survived and emerged).

Silverleaf whitefly, *Bemisia argentifolii* Bellows and Perring, numbers were significantly higher on weed-free cotton plant foliage than on weedy cotton foliage and weed foliage in the later part of the growing season. This probably reflects the whitefly's preference for cotton plants over weeds. It is possible that dense weed growth might impede or deter some whiteflies from settling on cotton plants in weedy areas. It is also possible that parasitism of silverleaf whiteflies, reported to be higher on weeds (especially hirsute species) than on cotton, contributed to the lower whitefly populations on the weeds. Higher cotton aphid, *Aphis gossypii* Glover, densities in weedy cotton habitats might have resulted from the same conditions as for whiteflies. Ants and coccinellid beetles, both of which consume aphids, were more abundant in the weedy cotton habitats. Whether more abundant in weedy or weed-free habitats, heightened prey availability was associated with twelve of the fourteen predator groups counted.

Despite a general trend for higher populations of natural enemies in the weedy habitats, boll weevil oviposition injury to squares was unaffected. As a possible explanation, predatory arthropod populations built to significantly greater levels in weedy habitats during late May and June when weed biomass was highest and when most squares had become bolls that are less vulnerable to boll weevil oviposition. Also, most natural enemies indigenous to the United States are not considered to be major causes of mortality to boll weevils. The numbers of squares counted on cotton plants in the study were not significantly different between the weedy and weed-free treatments because boll weevil damage was unaffected by the treatments and because weed growth was too light in the early season to have caused a weed related decline in square production. The significantly fewer bolls counted in the weedy habitats later in the season resulted from reduced cotton plant densities caused by weed competition and lower plant heights that were likely induced by thigmomorphogenesis (shortening of internodes resulting from physical contact with objects or wind) and shading caused by taller weeds. The significantly lower (≥50%) cotton yields reflected the lower numbers of bolls.

The results found in the weed-diversified field cotton in the Lower Rio Grande Valley of Texas agree with polyculture research in Asia where cotton yields were either unaffected or reduced when interplanted with groundnuts, *Arachis hypogaea* L.; soybeans, *Glycine max* (L.) E. Merrill; greengram, *Phaseolus aureus* W. Roxburgh; and blackgram, *P. mungo* (L.) Hepper. Further, a study in Central America found that there were fewer lacewing (Chrysopidae) eggs on cotton plants intercropped with corn and weeds than in cotton monocultures. A study in Africa showed that yields of intercropped cotton and groundnuts grown on alternating ridges did not improve in low rainfall areas, but yields were better from intercropped plants in wetter areas.

Although boll weevil injury to cotton was not suppressed in the Lower Rio Grande Valley of Texas, other insect pests of cotton might be more vulnerable to natural enemies. The differences in weed biomass and the cost to lint production suggest that the quantity of natural weed growth needed to build significantly larger numbers of natural enemy populations in weedy habitats is detrimentally competitive with the cotton crop. Although the fire ant is a key predator of boll weevils elsewhere, the hot, dry habitat in the Lower Rio Grande Valley cotton fields appears to have limited fire ant colonization to the extent that it is not a factor in boll weevil mortality.

Weed communities in cropping systems can affect arthropod populations in a number of ways, as illustrated by the cases of sugarcane in Louisiana and cotton in the Lower Rio Grande Valley of Texas. Both cases, however, illustrate that uncontrolled weed growth is deleterious to crop yield, but in the case of sugarcane, this loss can be offset by the advantage conferred primarily by the substantially higher populations of the fire ant and associated reduction in sugarcane borer injury, and lower field maintenance dollar inputs in weedy habitats. In some situations, vegetative complexity might be associated with ecological stability. In others, various parameters have interceded, such as the introduction of an exotic pest without effective natural enemies in its new habitat, to render void the benefits of ecosystem richness. For weeds to become widely integrated into IPM strategies, development of techniques for maintaining appropriate densities and diversities of innocuous weed populations in or around cropping systems will likely be a key concern.

References

Altieri MA, Whitcomb WH (1979) The potential use of weeds in the manipulation of beneficial insects. Hortsci 14:12–18

Altieri MA, Whitcomb WH (1980) Weed manipulation for insect pest management in corn. Environ Entomol 4:483–489

Jones GD, Coppedge JR (1999) Foraging resources of boll weevils (Coleoptera: Curculionidae). J Econom Entomol 92:860–869

Showler AT, Greenberg SM (2003) Effects of weeds on selected arthropod herbivores and natural enemy populations, and cotton, *Gossypium hirsutum* L., growth and yield. Environ Entomol 32:39–50

Showler AT, Reagan TE (1991) Effects of sugarcane borer, weed, and nematode control strategies in Louisiana sugarcane. Environ Entomol 20:359–370

Showler AT, Reagan TE, Knaus RM (1990) Sugarcane weed community interactions with arthropods and pathogens. Insect Sci Appl 11:1–11

Zandstra BH, Motooka PS (1978) Beneficial effects of weeds in pest management – a review. Pest Articles News Summaries 24:333–338

Weed Biological Control in Australia

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Australia has a long history in weed biological control, beginning in 1903 with the program to manage the prickly pear cactus, *Opuntia stricta* and other related cacti. Following the overwhelming success of this program, there have been over 180 insect biocontrol agents released against more than 50 species of weedy plants in Australia. Approximately 69% of these agents have established and are contributing to the management of the target weed; others have not established or are still under evaluation. These programs have targeted agricultural, pastoral, rangeland, aquatic and environmental weeds in tropical and temperate regions across Australia. Over the last one hundred years, Australia has had almost as many weed biocontrol programs as the USA and remains a world leader in the theory and practice of this discipline.

History

The potential risk of biological control agents to non-target plants was recognized from the start of biological control programs in Australia. The prickly pear biological control program was the first in the world to undertake proper host-testing trials, where the potential agents were confined to crop plants to determine if any feeding occurred. These tests are fully described in Alan Dodd's 1940 publication. No native Australian plants were tested, presumably because they were not perceived to have economic value. As there are no native Cactaceae in Australia, attack on additional cactus species was considered beneficial because these cacti were also actual or potential weeds.

Host specificity testing on plants of economic value using "no-choice" or starvation trials (where the feeding stage of the insect is confined in a cage until they die) continued to be used in all Australian weed biocontrol programs until the 1970s. Approval for the release of agents was granted by the Federal Plant Quarantine Authority and host-specificity testing protocols were gradually developed. Starting in the mid-1970s, test plant lists increasingly focused on plants related taxonomically and, later, phylogenetically, to the target weed. Since 1985, the federal conservation/environment authority also has to grant approval for release, and native plants are now included in the tests. Choice testing was increasingly used, where the potential agent is given a choice with the test plant and the target weed together in the cage. Since the 1990s, a mixture of choice and no-choice tests has become standard, and applications to release agents are made available on the internet for public comment prior to approval.

There have been very few instances of direct and significant non-target impacts recorded in Australia. One of the most notable is that of *Aconophora compressa* Walker (Hemiptera: Membracidae) from Mexico. In the 1990s this agent was released against *Lantana camara* L. (Verbenaceae), a major weed in Australia. Shortly after establishment it began feeding on certain ornamental (non-native) plants in

Brisbane, Queensland. This example highlights the necessity to conduct more research into non-target impacts and the refinement of host-specificity testing. In Australia, such work is currently underway under the auspices of the Cooperative Research Centre for Australian Weed Management.

Australia was also the first country to release a plant pathogen as a weed biocontrol agent. In 1970, the rust disease, *Puccinia chondrillina* Bubak and Syd., from Europe was released against skeleton weed, *Chondrilla juncea* L. (Asteraceae), a major weed of wheat crops. The release resulted in very successful control of the weed and has been followed by increased use of pathogens as agents, although not all have been as successful.

Conflicts of interest over the release of biological control agents to control the pasture weed Paterson's curse, *Echium plantagineum* L. (Boraginaceae), led to the introduction of the *Biological Control Act* in 1984. This Act is the first of its kind worldwide that specifically addresses the need to balance the interests of those who receive benefits from the weed and those who want the weed population reduced. The Act has since been used to resolve conflicts over the release of biological control agents for blackberry and also rabbits. However, most potential conflicts are minor and are resolved without resort to the Act.

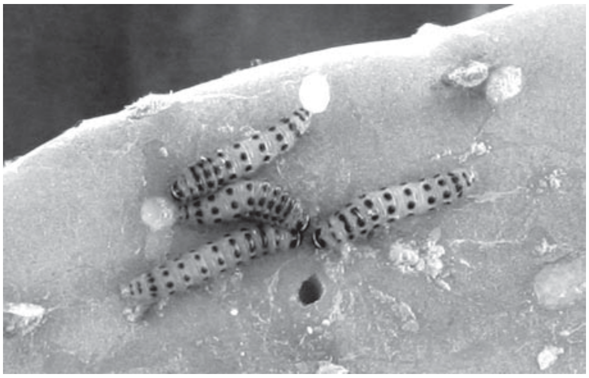
Programs Undertaken

The following examples of Australian weed biological control programs highlight the variety of invasive plants that have been targeted, the agents used and some of the issues related to weed biological control that have arisen:

Prickly Pear, *Opuntia* spp. (Cactaceae)

The first and iconic program was the biological control of prickly pear cacti, *Opuntia* spp. Prickly pear cacti were introduced into Australia in the 1800s as ornamental plants, as hedges and as the basis of a cochineal industry. There were several species introduced, including *O. stricta, O aurantiaca*, and *O. monacantha*. These plants have naturalized in Australia in semi-arid savannas, warm temperate, subtropical and tropical regions and in shaded and exposed areas. *Opuntia stricta* was first noted in rangeland areas in NSW in 1839 and by 1900 covered four million hectares. By 1926, it had expanded to cover 24 million hectares, rendering the land unusable for either grazing or cultivation.

The Commonwealth Prickly Pear Cactus Board was established in 1920 to address the cactus problem; although exploration for biological control agents began as early as 1903. As many as 150 potential agents were discovered, of which fifty were imported into Australia for host-testing. Of those released, twelve agents established. Within six years following the 1925 release of the moth *Cactoblastis cactorum* (Bergroth) (Lepidoptera: Pyralidae) (Fig. 24) more than 90% of prickly pear had been destroyed (Fig. 25). In areas where *C. cactorum* was not as effective, other agents have been effective at reducing vigor and stands of *Opuntia* spp. While there are still areas in Australia infested by prickly pear cacti, the impact of these plants is now minor and the patches are soon



Weed Biological Control in Australia, Figure 24 ***Cactoblastis cactorum*** **(Lepidoptera: Pyralidae) larvae on *Opuntia* cactus. This species is responsible for one of the most effective weed biological control programs in the history of biological control (photograph by Lorraine Edmunds).**

Weed Biological Control in Australia, Figure 25 **Prickly pear cactus pads collapsed following feeding by *Cactoblastis* larvae (photograph by Lorraine Edmunds).**

Weed Biological Control in Australia, Figure 26 ***Cyrtobagous salviniae* (Coleoptera: Curculionidae) effectively suppressed salvinia in Australia (photograph by Scott Bauer).**

identified by the biological control agents. It has been estimated that the investment of Au$19 million (2005 values) in the years between 1911 and 1930 resulted in a return of Au$3.1 billion in increased production, which equates to an astonishing cost-benefit ratio of 312:1.

Salvinia, *Salvinia molesta* D.S. Mitch (Salviniaceae)

Salvinia is a free-floating aquatic fern native to South America that was imported to Australia as an ornamental plant for ponds and aquaria. It was widely distributed and rapidly escaped into dams and waterways where it disrupted water flow, nutrient cycling and recreational use, and favored populations of disease-vectoring mosquitoes. The biomass in some areas was estimated to be 400 t/ha, and the plant is arguably the world's worst weed. During the 1960s and 1970s, unsuccessful attempts were made to control the weed in Africa using insects from northern South America. In 1977, the weed was correctly identified as *Salvinia molesta* from southern Brazil, and searches for agents were subsequently made in that area. The weevil *Cyrtobagous salviniae* Calder and Sands (Coleoptera: Curculionidae) (Fig. 26) was discovered, introduced into Australia in 1980, and very quickly established and controlled the weed. This success has since been repeated throughout the tropics where salvinia is a problem.

Lantana, *Lantana camara* L. (Verbenaceae)

This is a thicket-forming shrub native to tropical Central America. It was introduced into Australia as an ornamental plant in the 1800s and is now a highly invasive weed along the eastern coast of Australia. This plant severely reduces pasture productivity and is also toxic to livestock. Annual losses are estimated to be Au$104.3 million with an additional Au$10 million spent in control. In addition, lantana invades forest plantations and natural systems where it threatens plants and animals of conservational significance. It became the first weed in the world targeted for biological control in 1902, when agents were sought for infestations in Hawaii. Since then, lantana has been a target of biological control in several areas around the world. In Australia, the lantana biocontrol program began in 1914 and now 30 biocontrol agents have been released, 29 insects and 1 rust fungus, at an estimated cost of Au$13.6 million. Seventeen of the agents are considered established, but only four are believed to have any significant impact on the plant. The biocontrol program on lantana has contributed to an increase in pasture productivity and reduced the threat to natural environments, but the overall effect is minor, estimated at less than 10%. A related species, *Lantana montevidensis* (Spreng.) Briq., was also targeted for biocontrol, but only two species of agents were released and neither established.

Lantana is a particularly difficult weed to control because it is an artificially produced hybrid of two or more species from Central America. The hybrids were developed by gardeners in Europe in the 1700s and then planted around the world, and it has proved impossible to locate the parent plants in their native habitat. Modern genetic techniques are now being used to identify different lantana varieties and their parent plants, in the hope that this may lead to improved success.

Paterson's Curse, *Echium plantagineum* L. (Boraginaceae)

Paterson's curse is a winter annual weed in southern Australian pastures and can also be found along roadsides and bushland reserves. It was introduced to Australia as an ornamental plant in the 1800s and is currently found as a weed across large grazing areas, sometimes becoming the dominant plant. This highly competitive plant can be grazed in small quantities by sheep but is toxic to other stock. The search for biological control agents began in 1972 and the first of seven agents, the leaf-mining moth, *Dialectica scalariella* (Zeller) (Lepidoptera: Gracillariidae), was released in 1980. It failed to establish and was reintroduced in 1989 after which it did establish but has not contributed significantly to control. A crown feeding weevil, *Mogulones larvatus* Schultze (Coleoptera: Curculionidae), successfully established from releases in 1992 and is contributing to reductions in the weed. In 1993, the tap root-feeding species *Mogulones geographicus* (Goeze) (Fig. 27) was released and established and is also contributing to control. At the same time, four other insect species were introduced. Three have established, but only one of these, *Longitarsus echii* (Coleoptera: Chrysomelidae), appears to be exerting any significant pressure on Paterson's curse.

Weed Biological Control in Australia, Figure 27 (*top*) *Zygina* sp. leafhopper (Hemiptera: Cicadellidae) was released for suppression of bridal creeper in Australia (photograph by Rick Roush); (*bottom*) *Mogulones geographicus* (Coleoptera: Curculionidae) attacks the roots of Paterson's curse (photographer unknown).

Bridal Creeper, *Asparagus asparagoides* Druce (Asparagaceae)

Bridal creeper was introduced to Australia from South Africa in the 1800s as an ornamental plant and was used in bridal floral arrangements. Now a major weed across southern Australia, this creeper forms dense tuberous mats just below the soil surface and the foliage climbs over and smothers native vegetation. This plant can invade undisturbed native bushland, has become a significant problem in national parks and other conservation areas throughout southern Australia, and is thought to be responsible for the extinction of two native orchid species. It is also a problem in citrus orchards and pine plantations.

The first of three biological control agents was released in 1999. *Zygina* sp. (Fig. 27) (Hemiptera: Cicadellidae) nymphs and adults feed on the mesophyll cells of the cladodes and at high numbers can cause defoliation. The leafhopper is well-established and has had some impact on the plant. However, populations of *Zygina* have been reduced by a native parasitoid, an undescribed fairyfly, *Stethynium* sp. (Hymenoptera: Mymaridae), which lays its eggs in the leafhopper eggs. Nothing is known of the parasitoid's native hosts or of the impact of *Zygina* on the population dynamics of the wasp, and thus of its native hosts.

The second biological control agent, the rust fungus *Puccinia myrsiphylli* (Thuem.), was released in 2000 and is now having a significant impact on bridal creeper in most areas across southern Australia. A leaf beetle, *Crioceris* sp. (Coleoptera: Chrysomelidae) was released in 2002 and although establishment has been confirmed at a few release sites, it is too early to fully evaluate its impact on bridal creeper.

It is already evident that bridal creeper populations are beginning to be reduced; however, it appears that this plant has modified the communities in which it invades in such a way that additional effort to restore the native plant communities, following bridal creeper invasion and retreat, will be necessary. Replacement of bridal creeper by other plants of South African origin is already apparent.

Weedy Trees

Several woody trees have become weedy in Australia, and four have become targets of biological control programs: mimosa, *Mimosa pigra* L. (Fabaceae), parkinsonia, *Parkinsonia aculeata* L. (Fabaceae), prickly acacia, *Acacia nilotica* subsp. *indica* (Benth.) Brenan (Fabaceae) and mesquite, *Prosopis* spp. (Fabaceae). Mimosa first naturalized in the Darwin botanical gardens in 1891 and thereafter around Darwin as an inconspicuous tree. Parkinsonia, prickly acacia and mesquite were deliberately planted as shade trees in northern Australia around homesteads and watering points on cattle stations and have since become widespread in the Northern Territory, Western Australia and Queensland. Mimosa has been successfully contained to the Northern Territory and one small infestation in north Queensland. However, if unmanaged it will rapidly invade wetland areas throughout the north. These plants produce large numbers of seeds that are viable for decades. All three trees have large thorns and form dense impenetrable thickets that reduce pasture productivity, interfere with the mustering of stock and restrict access of stock to water. Mimosa is also a significant problem in conservation areas, and prickly acacia is a threat to native Mitchell grass plains.

The first releases of biological control agents against mimosa began in 1983. A total of 13 agents have been released at a cost of approximately Au$21.6 million (2005 values). Nine of these agents have established of which two, *Neurostrota gunniella* (Busck) (Lepidoptera: Gracillariidae), a tip-boring moth, and *Carmenta mimosa* Eichlin & Passoa (Lepidoptera: Sesiidae), a stem-boring moth, are already reducing the mimosa stands and restricting spread of infestations. Before *N. gunniella* was released it was noted that the moth was likely to attack non-target native plants in the genus *Neptunia* (Fabaceae). However, the cost of the potential non-target impact was weighed against the current and future impact of unchecked mimosa populations, and the release was approved. A recent study evaluating non-target impact on *Neptunia* revealed that only plants close to mimosa infestations are attacked by *N. gunniella*, and at a lower rate of attack than that on mimosa. Other studies have shown that mimosa is best managed through an Integrated Weed Management approach combining fire, herbicides and mechanical removal with the impacts of the biological control agents.

The parkinsonia biological control program has resulted in the release of three insect species but only one, the seed-feeding beetle *Penthobruchus* *germaini* Pic (Coleoptera: Chrysomelidae) has established. Unfortunately, the eggs of this beetle are heavily attacked by native parasitoids and as a result, impact on the weed is minimal.

The prickly acacia biological control program has resulted in the release of seed-feeding beetles that established but are ineffective. Other agents released in the 1990s failed to establish. A leaf-feeding moth, *Chiasmia assimilis* (Warren) (Lepidoptera: Geometridae), originating from South Africa has established and is causing severe damage to trees near the coast and is now spreading inland into more arid areas.

The mesquite biological control program began in 1992. Several insects have been released but only one, a leaf-tying moth, *Evippe* sp. (Lepidoptera: Gelechiidae), (Fig. 28) is having any impact. The moth causes defoliation of the plant and weakens it, making it more manageable by herbicides. Seed-feeding beetles released in the 1980s are also established but ineffective. As with mimosa and parkinsonia, Integrated Weed Management using several techniques is an essential approach for the control of mesquite. These plants cover large rangeland areas, where the costs of herbicides and mechanical control as the sole means of management are prohibitive.

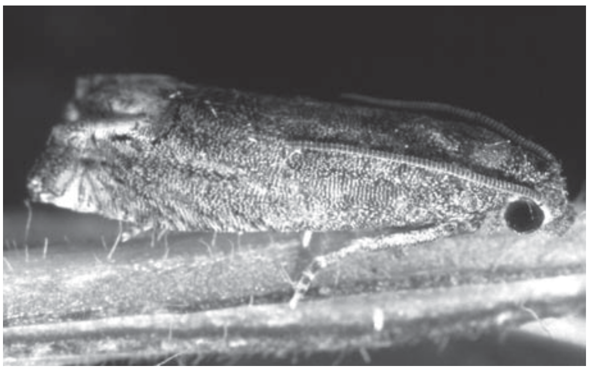
Weed Biological Control in Australia, Figure 28 Leaf damage to mesquite caused by the leaf-tying moth *Evippe* sp. (Lepidoptera: Gelichiidae) (photograph by Rieks Van Klinken).

Parthenium Weed, *Parthenium hysterophorus* L. (Asteraceae)

Parthenium is a short-lived annual herb native to Mexico. It was accidentally introduced into central Queensland in 1958 in pasture seed from the USA. It spread very rapidly until 1978 when a containment program was developed, which has slowed but not prevented further spread. Parthenium weed now infests most of the higher rainfall and semi-arid grazing and crop lands of central and north Queensland, with smaller areas in southern Queensland, which equates to a total area of at least 170,000 km^2. Parthenium is not eaten by stock and out-competes native and sown grasslands, reducing pasture productivity by 40–80%. The pollen is highly allergenic, and up to 20% of the people living in parthenium-affected areas will develop severe allergies ranging from hay fever to allergic asthma or skin conditions. Parthenium is also a serious weed of crops, but can be controlled with herbicides in grain crops, although not in sunflower. Herbicide control is not economic in pasture situations. Lost beef production from parthenium infestation was estimated in 1999 to be worth Au$17 million per year (2001 values).

Parthenium weed is a highly opportunistic annual plant with a very large persistent seed bank. Germination occurs after rain at any time of the year, and plants grow rapidly, flowering in six weeks during the summer. In winter, plants can persist as dormant rosettes to grow in spring. In the highly variable rainfall of central and north Queensland, there may be no living plants for nine months of the year. Storm rains can then lead to widespread germination, with flowering plants present in six weeks time. This presents significant challenges for biocontrol, as host-specific agents have to persist in a dormant state while the plant is absent, and emerge from dormancy at the same time as the young plants are present. For this reason, several different agents with different life cycles and dormancy strategies were introduced, in the hope that at least one would be effective regardless of the seasonal conditions.

The biological control campaign for parthenium started in 1977 and ran for 25 years, during which nine insect species and two rust diseases were imported from Mexico and from South America. All except one insect established, and all are contributing to control in some areas and seasons. The greatest benefit comes from four species: a tip-galling moth, *Epiblema strenuana* Walker (Lepidoptera: Tortricidae) (Fig. 29); a leaf-feeding beetle, *Zygogramma bicolorata* Pallister (Coleoptera: Chrysomelidae) (Fig. 30); a stem and root feeding weevil, *Listronotus setosipennis* (Hustache) (Coleoptera: Curculionidae); and a rust disease, *Puccinia melampodii* (Dictel & Holway). All four species are widespread and damaging, though their populations fluctuate with seasonal conditions. Two more species are also widespread though less damaging: a leaf-mining moth, *Bucculatrix parthenica* Bradley (Lepidoptera: Bucculatricidae), and a seed-feeding weevil, *Smicronyx lutulentus* Dietz (Coleoptera: Curculionidae). The second rust species, *Puccinia abrupta* Dictel & Holway *var partheniicola* (Jackson), and the other insects, a stem-feeding moth, *Carmenta* sp. nr. *ithacae* (Lepidoptera: Sesiidae), and a tip-galling weevil, *Conotrachelus* sp. (Coleoptera: Curculionidae), are still only present in small populations and so have minimal impact on the weed.



Weed Biological Control in Australia, Figure 29 **Moth of *Epiblema strenuana* (Lepidoptera: Tortricidae), a tip-galling caterpillar that affects parthenium weed (photograph by Rachel McFadyen).**

Weed Biological Control in Australia, Figure 30 **This leaf-feeding beetle, *Zygogramma bicolorata* (Coleoptera: Chrysomelidae) is one of the more effective biological control agents of parthenium weed in Australia (photograph by Rachel McFadyen).**

As a result of the combined effect of these agents, the impact of parthenium weed has been greatly reduced. The weed is now much easier to manage in both pastures and cropping situations, and spread has decreased significantly. Weed seed banks have reduced six-fold, from >37,000 germinable seeds/m^2 to <6,000 and they are still falling. By 1999, biocontrol had increased pasture production in affected areas by 4% and in 2006 net benefits were calculated to be worth Au$38.6 million. The impact of biocontrol continues to increase every year.

Looking Forward

The case studies presented above represent a small selection of some of the weed biological control programs in Australia. Undoubtedly, biological control can be and has been enormously successful, and has returned huge savings to the Australian economy as well as reducing the harm caused by invasive weeds and the chemical and mechanical methods used to manage them. There is a recognized need to improve the protocols and practice at each step along the path of a biological control program, from agent selection to release and post release monitoring. Australian practitioners and scientists are actively researching ways to improve selection, host-specificity assessment, establishment and evaluation of weed biological control agents. It is acknowledged that, as with other weed control tactics, there are potential risks. Every effort is made to minimize the risk and to improve the reliability of risk assessment, while concurrently aiming to improve the effectiveness of this technique. There is also a continuing effort to integrate biological control more fully into weed management plans in order to contribute to the overall health of Australian production and native systems.

References

Briese D (2000) Classical biological control. In: Sindel B (ed) Australian weed management systems. RG and FJ Richardson, Melbourne, Victoria, Australia, pp. 161–192

Briese D (2004) Weed biological control: applying science to solve seemingly intractable problems. Aust J Entomol 43:304–317

Dodd AP (1940) The biological control campaign against prickly pear. A.H. Tucker Government Printer, Brisbane, Queensland, Australia. 117 pp

Page AR, Lacey KL (2006) Economic impact assessment of Australian weed biological control. CRC for Australian Weed Management Technical Series #10. University of Adelaide, Glen Osmond, South Australia, Australia

Raghu S, van Klinken RD (2006) Refining the ecological basis for agent selection in weed biological control. Special Issue of the Aust J Entomol 45:(4)251–252

Spafford Jacob H, Briese DT (2003) Improving the selection, testing and evaluation of weed biological control agents. CRC for Australian Weed Management Technical Series #7. University of Adelaide, Glen Osmond, South Australia, Australia

Walton C (2005) Reclaiming lost provinces: a century of weed biological control in Queensland. Department of Natural Resources and Mines, Brisbane, Queensland, Australia, 104 pp

Weevils, Billbugs, Bark Beetles, and Others (Coleoptera: Curculionoidea)

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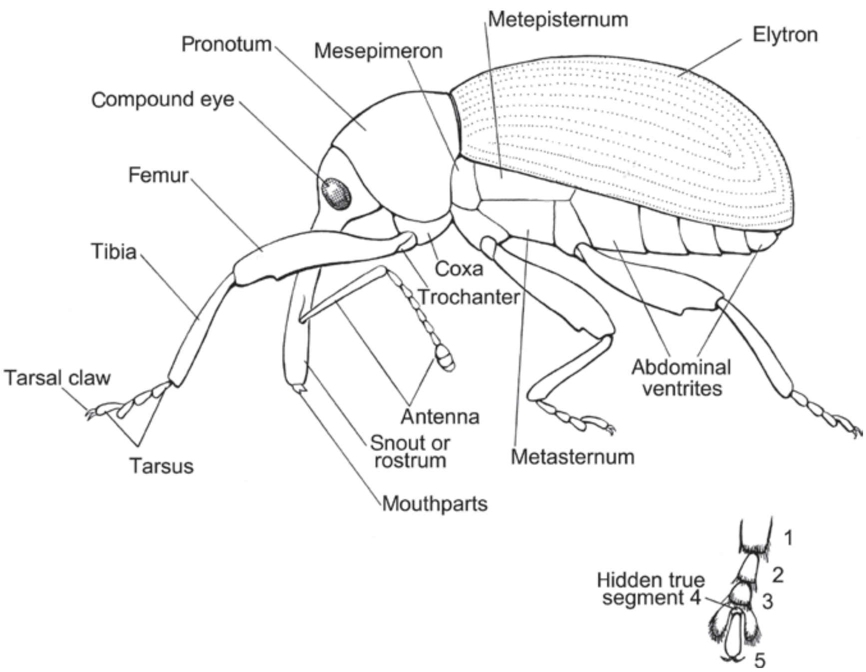
The superfamily Curculionoidea of the order Coleoptera is comprised of a number of related groups of beetles that, depending on the classification scheme adopted, number anywhere from 7 to 18 families. These classification issues generally focus on the ranks at which many groups are placed but placements of some groups are also disputed. The following classification represents a compromise but one must recognize that, as more evidence from immature stages and molecular methods is incorporated into analyses of relationships, this system is subject to change and refinement (Figs. 31–35).

- Order: Coleoptera
  - Superfamily: Curculionoidea
    - Family: Nemonychidae
      - Subfamily: Nemonychinae
      - Subfamily: Cimberidinae
      - Subfamily: Rhinorhynchinae
    - Family: Anthribidae
      - Subfamily: Anthribinae
      - Subfamily: Choraginae
      - Subfamily: Urodontinae
    - Family: Belidae
      - Subfamily: Belinae
      - Subfamily: Oxycoryninae
    - Family: Attelabidae
      - Subfamily: Attelabinae
      - Subfamily: Rhynchitinae
    - Family: Caridae
    - Family: Brentidae
      - Subfamily: Microcerinae
      - Subfamily: Brentinae (includes Cyladini)
      - Subfamily: Ithycerinae
      - Subfamily: Nanophyinae
      - Subfamily: Eurhynchinae
      - Subfamily: Apioninae (includes Antliarhinini)
    - Family: Curculionidae
      - Subfamily: Dryophthorinae
      - Subfamily: Brachycerinae (includes Ocladiini, Cryptolaryngini, Erirhinini, Raymondionymini)
      - Subfamily: Bagoinae
      - Subfamily: Cyclominae

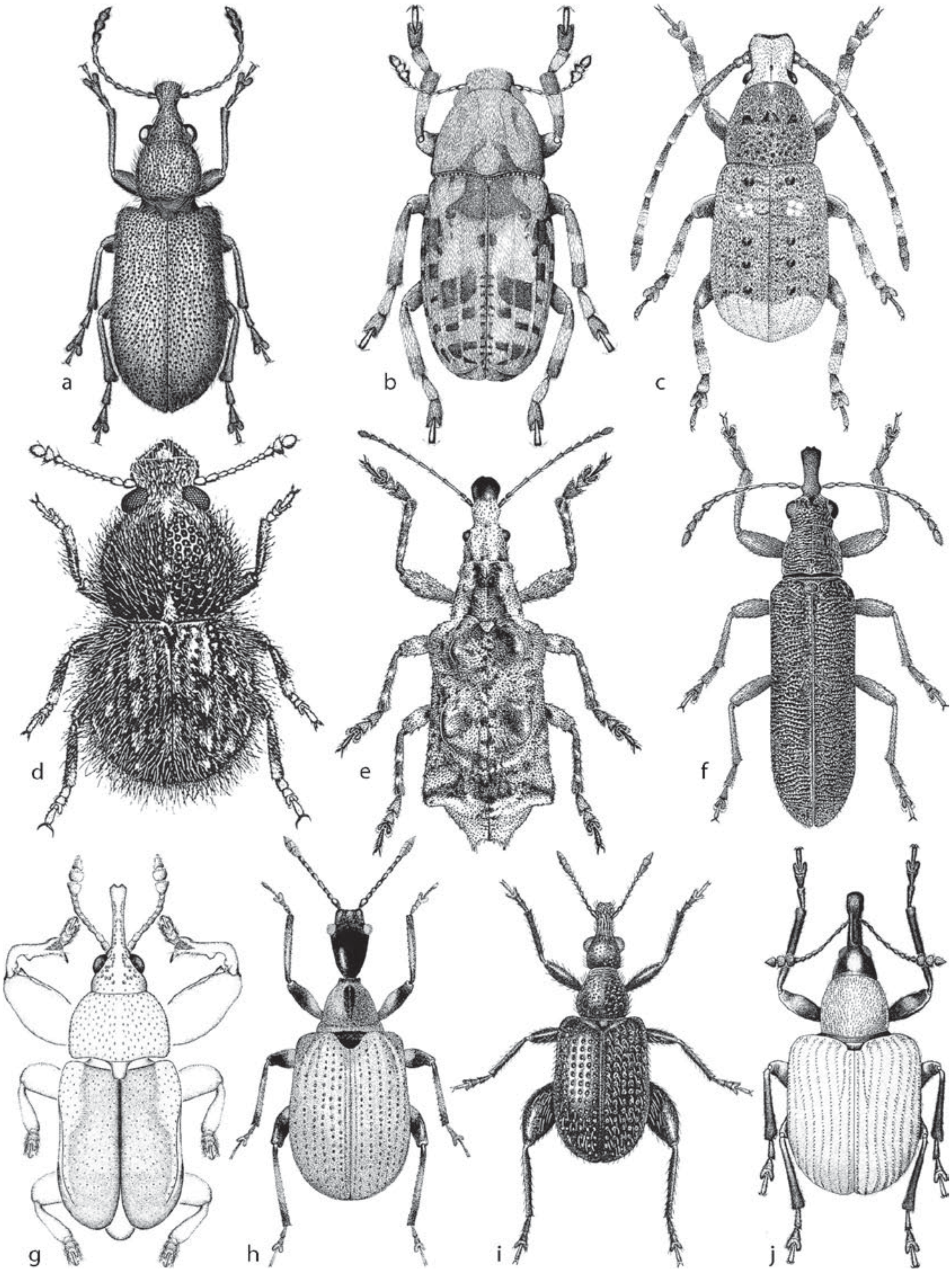


Weevils, Billbugs, Bark Beetles, and Others (Coleoptera: Curculionoidea), Figure 31 Important elements in the morphology of Curculionoidea.

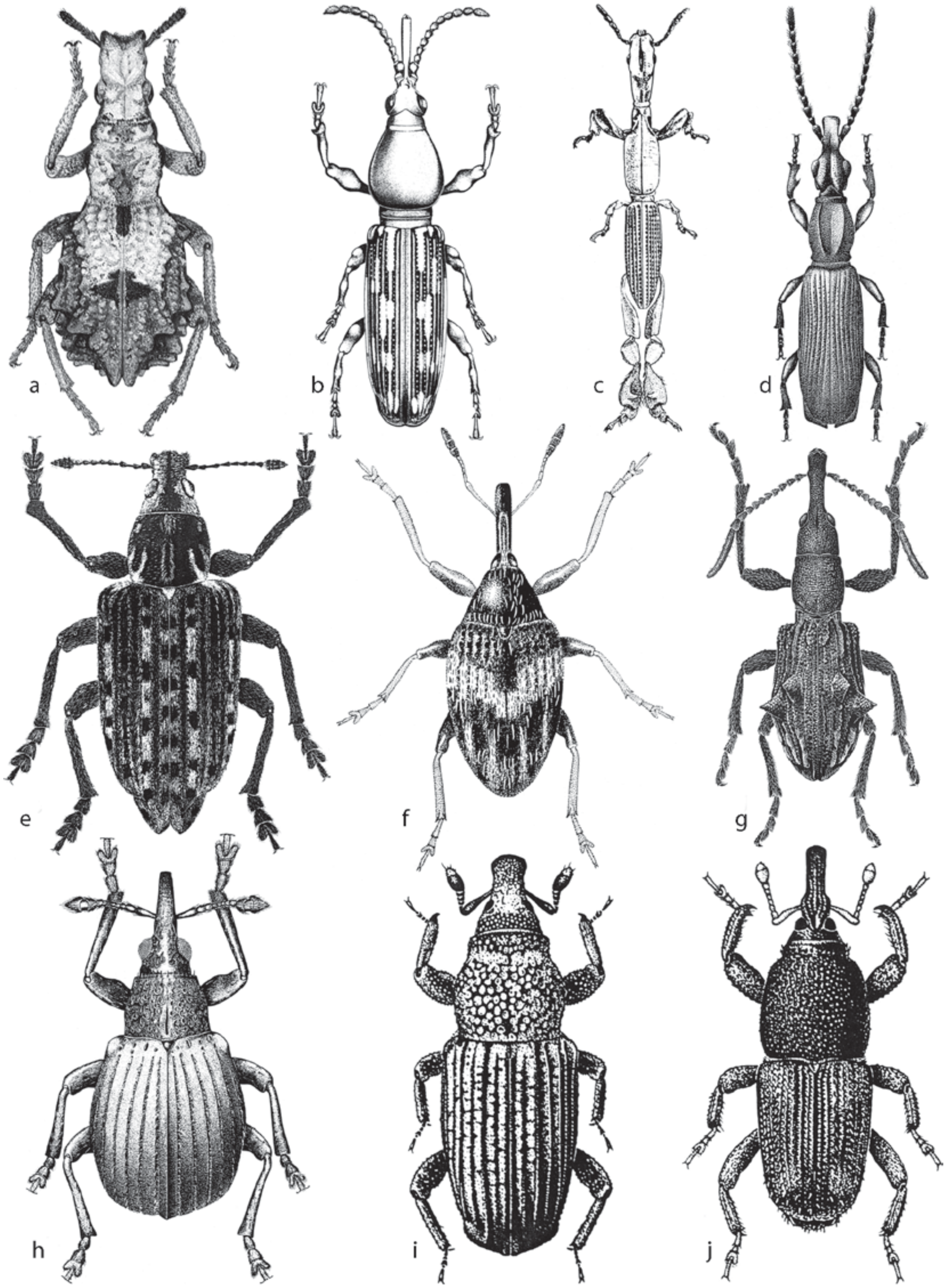
Subfamily: Entiminae
Subfamily: Hyperinae
Subfamily: Curculioninae
Subfamily: Ceutorhynchinae
Subfamily: Baridinae
Subfamily: Conoderinae
Subfamily: Lixinae
Subfamily: Molytinae (includes Mesoptiliini)
Subfamily: Cryptorhynchinae
Subfamily: Cossoninae
Subfamily: Scolytinae
Subfamily: Platypodinae

The weevils are one of the most diverse groups of organisms. Over 50,000 species have been described worldwide in the family Curculionidae, and their diversity among beetles is challenged perhaps only by Staphylinidae. Weevils are associated with virtually all kinds of plants and plant parts. Most feed on living plants, but some are saprophagous. Weevils are immediately recognizable by their elongate rostrum (or snout), with mouthparts situated at the apex, geniculate (elbowed) antennae (straight in the families of primitive weevils), a compact antennal club and have 5-segmented tarsi, although the fourth segment is usually very small and nestled between the lobes of the third making them appear 4-segmented. In the blind, soil-dwelling weevils of the tribe Raymondionymini of the Brachycerinae the tarsi are truly 4-segmented. The Curculionoidea are often called snout beetles but in some the head is scarcely prolonged and this name is less appropriate (e.g., Platypodinae and Scolytinae of the Curculionidae). The Curculionoidea were historically placed in a distinct subdivision of the Coleoptera called the Rhynchophora.

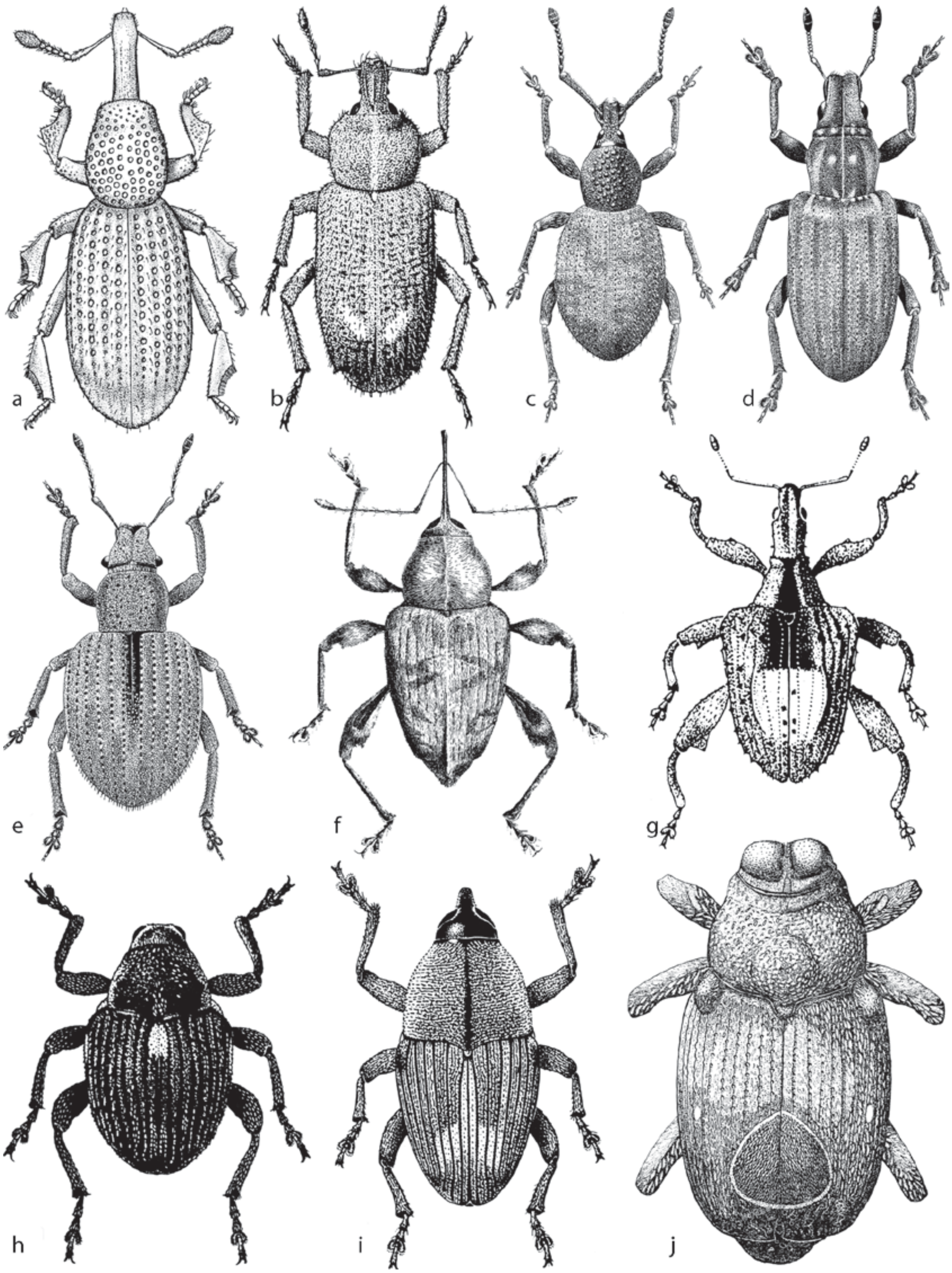
Certain other characters besides the development of a snout, form of the antennae, and tarsi distinguish the Curculionoidea from other beetles. The gular sutures are nearly always confluent, or lacking, with no gula developed (they are short but widely separated in the Nemonychidae). Notosternal sutures short and indistinct or deflected laterally, and in most groups the palps are rigid or not visible



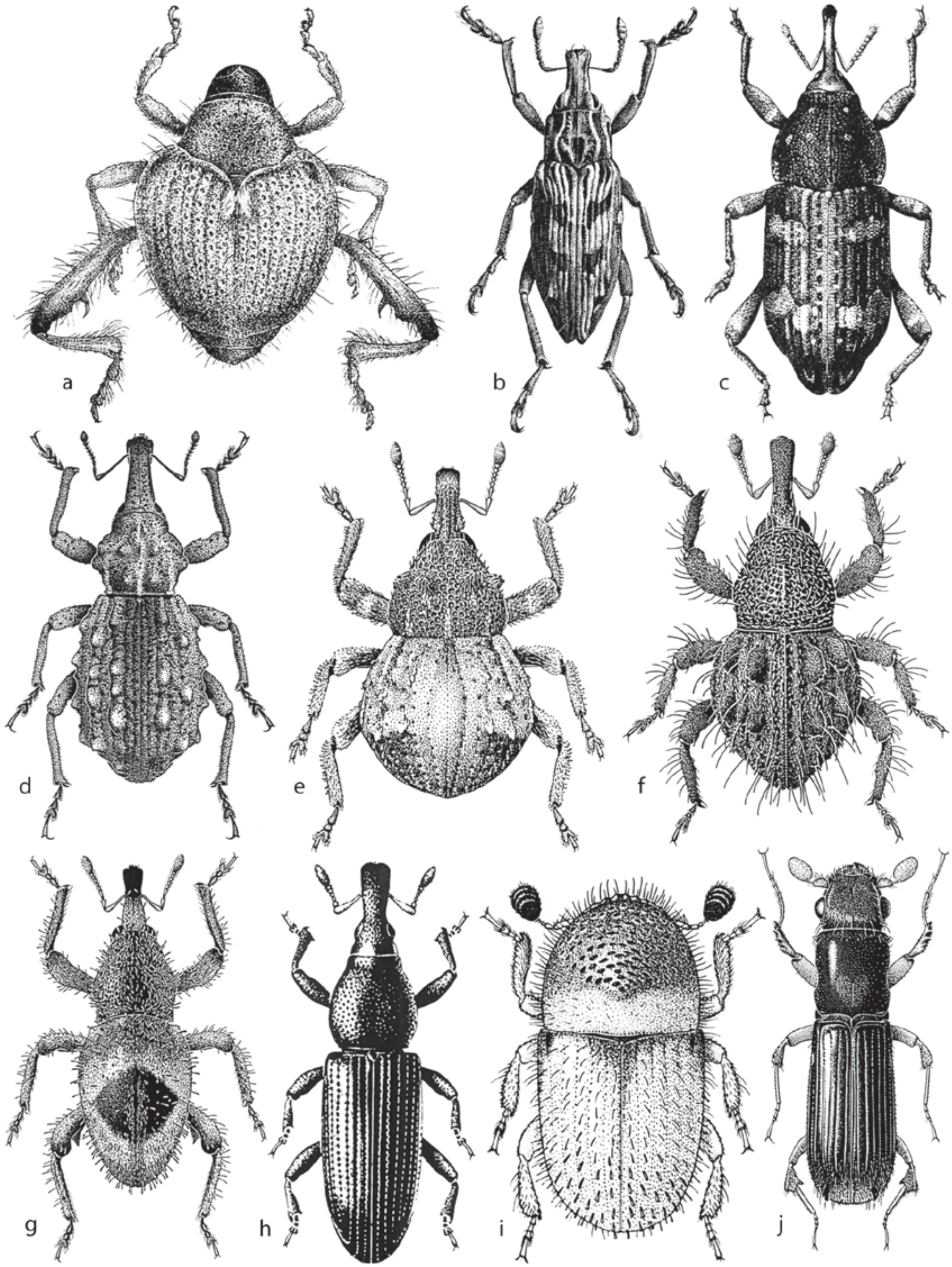
Weevils, Billbugs, Bark Beetles, and Others (Coleoptera: Curculionoidea), Figure 32 **Representative Curculionoidea – subfamilies and species: (a) Nemonychidae, *Cimberis compta;* (b) Anthribidae, *Euparius marmoreus;* (c) Anthribidae, *Platystomos albinus;* (d) Anthribidae, *Xenanthribus hirsutus;* (e) Belidae, *Agathinus tridens;* (f) Belidae, *Rhicnobelus metallicus*; (g) Belidae, *Rhopalotria slossonae*; (h) Attelanidae, *Apoderus coryli;* (i) Rhynchitinae, *Deporaus betulae*; (j) Rhynchitinae, *Merhynchites bicolor*.**



Weevils, Billbugs, Bark Beetles, and Others (Coleoptera: Curculionoidea), Figure 33 **Representative Curculionoidea – subfamilies and species: (a) Microcerinae, *Microcerus bicolor*; (b) Brentinae, *Arrhenodes minutus*; (c) Brentinae, *Cormopus distinctus*;(d) Brentinae, *Pseudanchisteus neglectus*; (e) Ithycerinae, *Ithycerus noveboracensis*; (f) Nanophyinae, *Nanophyes marmoratus*; (g) Eurhynchinae, *Eurhynchus acanthopterus*; (h) Apioninae, *Apion centrale*; (i) Dryophthorinae, *Dryophthorus* sp.; (j) Dryophthorinae, *Sitophilus oryzae*.**



Weevils, Billbugs, Bark Beetles, and Others (Coleoptera: Curculionoidea), Figure 34 **Representative Curculionoidea – subfamilies and species: (a) Brachycerinae, *Pararaymondionymus lusitanicus*; (b) Cyclominae, *Listroderes difficilis*; (c) Entiminae, *Otiorhynchus singularis*; (d) Entiminae, *Sitona lepida*; (e) Entiminae, *Strophosoma melanogramma*; (f) Curculioninae, *Curculio iowensis*; (g) Eugnominae, *Stephanorhynchus crassus*; (h) Ceutorhynchinae, *Rhinoncus australis*; (i) Baridinae, *Linogeraeus urbanus*; (j) Conoderinae, *Copturomimus lunatus*.**



Weevils, Billbugs, Bark Beetles, and Others (Coleoptera: Curculionoidea), Figure 35 **Representative Curculionoidea – subfamilies and species: (a) Conoderinae, *Tachygonus almeidai*; (b) Lixinae, *Coniocleonus nigrosuturalis*; (c) Molytinae, *Pissodes strobi*; (d) Molytinae, *Hadramphus stilbocarpae*; (e) Cryptorhynchinae, *Crooktacalles certus*; (f) Cryptorhynchinae, *Metacalles aspersus*; (g) Cryptorhynchinae, *Scelodolichus celsus*; (h) Cossoninae, *Macroscytalus remotus*; (i) Scolytinae, *Crypahlus wapleri*; (j) Platypodinae, *Platypus apicalis*.**

and the labrum is absent (except in Nemonychidae and Anthribidae). The mouthparts are small and more or less hidden in most of these beetles. The mandibles, located at the tip of the snout, are usually the only mouthparts easily visible without dissection.

This is a large and important group of beetles. Practically all feed on plant materials, and most of the larvae are burrowing in habit, infesting, twigs, flowers, fruits and seeds. Plant associations within the superfamily appear to parallel the phylogenetic position of the weevil families. For example, many members of primitive groups such as Nemonychidae, Belidae and Caridae occur on gymnosperms such as conifers, and the hyperdiversification of the Curculionidae may have paralleled the evolution of the angiosperms. The larvae are whitish, usually C-shaped, more or less cylindrical, with legs present in the primitive weevil families but reduced or lost in the more derived groups. A great many weevil species are of considerable economic importance as pests of field or garden crops, of forest, shade and fruit trees, or of stored products. Recently, many species have been introduced worldwide for the biological control of various noxious alien or pest weeds.

Family Nemonychidae, Pine-Flower Snout Beetles

This is a small group, with about 70 species worldwide placed in 21 genera in three subfamilies. These beetles are 3.0–6.0 mm in length, the antennae are straight with a loose club, and the snout is usually about as long as the prothorax and apically somewhat flattened and narrowed at the base. They differ from nearly all other families of Curculionoidea (except Anthribidae) in having the labrum distinct and the palps flexible. Adults possess the unique feature of tergite 9 being desclerotized to a narrow, well-pigmented, sharply defined band arching over sternite 9. Larvae are recognized by the frons being produced forward into a pseudoclypeus, mandibles having a diagonal masticatory ridge, and the frontoclypeal suture being effaced (also in some Anthribidae). Larvae of these beetles develop in the male cones of various conifers (Araucariaceae, Phyllocladaceae, Podocarpaceae, and Pinaceae). Adults are also usually found on conifers, but may occasionally be found on flowers of other plants. European species in the genus *Nemonyx* develop on Ranunculaceae and South American species of the genus *Rhynchitomacer* are on *Nothofagus* (Nothofagaceae). Nemonychids are found primarily in Europe, North, Central and South America, Australia (including New Caledonia and Papua New Guinea), and New Zealand. They are most diverse in the northern and southern temperate regions with few species known from the tropics. Numerous fossils have been described from the Jurassic of Kazakhstan and several Lower Cretaceous deposits (Eobelinae), but the family is absent from the Cenozoic fossil record.

Family Anthribidae, Fungus Weevils

The anthribids are elongate-oval, 0.5–20.0 (usually less than 10.0) mm in length, with the snout short, broad and flattened, and the antennae not elbowed. A distinct labrum is present as in Nemonychidae. Some species have slender antennae that may be longer than the body (hence they look like some Cerambycidae), and others have short antennae with a three-segmented club. The elytra always cover the base of the pygidium, which is always partly exposed in lateral view but is usually not visible from above. Adults are unique in that their notosternal suture is represented by a weak and transverse line extended vertically to the notum. Larvae possessing more than five setae on the frons (also in Nemonychidae). There are just over 3,000 species worldwide placed in 374 genera in three subfamilies. They are widely distributed and often very common in tropical regions. Though some adults feed on pollen, most browse on fungi and lichens. Urodontinae are found in southern Europe, Asia and Africa where they are associated with various plants, the larvae developing in stems or seed capsules. Members of the Choraginae are associated with seeds whereas the Anthribinae occur in association with rotten wood, on dead twigs or beneath loose bark affected by fungi. The larvae vary in habits. Some develop in woody fungi, some are in the fungi of certain crops (for example, corn smut), some feed in seeds, and a few bore in dead wood. The widely introduced coffee bean weevil, *Araecerus coffeae* (F.) is an important pest of seeds, berries, and dried fruits. Some species of *Anthribus* are predators on eggs of coccid scale insects. Anthribidae are known in the fossil record from the late Lower Cretaceous and more commonly from the Cenozoic in Europe and the United States.

Family Belidae

This is an odd and small group of primitive weevils found in North, Central and South America, the West Indies, Australia (including Papua New Guinea, New Caledonia and adjacent islands), New Zealand, Canary Islands, Northern Africa, South Africa, Southeast Asia, and the Pacific Islands. The family contains about 375 species placed in 39 genera in two subfamilies. Adults vary in length from 2.0 to 20.0 (most 8.0–15.0) mm and quite markedly in form as well. Some are very long, slender and cylindrical (Australian Belinae; *Araiobelus, Leptobelus*) whereas others are oval and flattened, with large front legs in the males and the elytra short, exposing the last few tergites (Allocorynina). All are characterized by straight antennae, often basally situated on the long cylindrical snout, the foretibia with a broad, apical groove or impression covered in fine vestiture on the inner face, and the spermatheca sometimes atrophied or absent. Larvae have the head deeply and permanently retracted and attached to the prothoracic shield by heavy musculature. Plant associations in the group are particularly varied and interesting. The Oxycoryninae are associated with Arecaceae (*Metrioxena*; Southeast Asia), Zamiaceae (*Afrocorynus*; Africa), Vitaceae (*Hispodes*; Africa), Araucariaceae (*Oxycraspedus*, South America), Zamiaceae (Allocorynina, North and Central America, West Indies), and the root parasitic Balanophoraceae and Hydnoraceae (Oxycorynina, Central and South America). Larvae of Aglycyderini mostly feed under bark of dead or dying twigs and branches of a variety of plants but some *Proterhinus* larvae mine in living leaves. In the Belinae of Australia, plant associations include cones and branches of Araucariaceae, twigs or branches of *Acacia* (Fabaceae), some Proteaceae, and wood of *Eucalyptus*. South American Belinae appear to be associated with ferns. Adults of the tropical American *Rhopalotria* and *Parallocorynus* (Allocorynina) are intimately involved in pollination of cycads. No authentic fossils of Belidae have been recorded from the Mesozoic era, but Oxycoryninae are known from the Cenozoic.

Family Attelabidae, Leaf-Rolling and Tooth-Nosed Weevils

This family combines two subfamilies, the Attelabinae and Rhynchitinae. Despite their different structure and biology the two are grouped together based on unique features of the larvae (epicranium with hyaline posterior extension) and adults (males with the 8th sternite fused or articulated to the 9th sternite on each side beyond the arms). Both groups also share straight antennae and a unique feature of a nervous system with the abdominal ganglia fused into one conglomerate. There are about 2,500 species placed in 150 genera, almost equally divided between the two subfamilies. They are found almost worldwide (with the exception of New Zealand and the Pacific Islands other than New Caledonia) and are most diverse in the tropics. The family is almost exclusively associated with dicot angiosperms but a few Rhynchitinae are associated with the conifer families Pinaceae and Cupressaceae.

Attelabinae, the leaf-rolling weevils, are short and robust, mostly 3.0–12.0 mm in length. Many of them are black, reddish, or black with red markings. The most interesting characteristic of this group is their method of laying eggs, from which their common name is derived. When a female is ready to oviposit, she cuts two slits near the base of the leaf, from each edge to the midrib, and rolls the part of the leaf beyond these cuts into a neat and solid ball. A single egg is laid near the tip of the leaf, usually on the underside, before the leaf is rolled up. She then gnaws the midrib of the leaf (at the end of the basal cuts) partly in two, and the leaf roll usually eventually drops to the ground. The larva feeds on the inner portion of this leaf roll and pupates either in the roll or in the ground. Generally, young or freshly emerged leaves are preferred as food. Some tropical attelabids have a mutualistic relationship with fungi which grow in the leaf rolls. The Latin term "nidus" (nest), is used for such leaf-rolls.

American attelabine "thief" weevils of the genus *Pterocolus* are brood parasites of their relatives, the leaf-rolling weevils in the Attelabinae. Adults of these small metallic blue weevils enter leaf rolls of various attelabines, destroy the eggs, and lay their own eggs. The larvae then feed in the leaf rolls that were prepared by the host attelabines.

Attelabinae can be recognized by a number of unique features: prementum broad and heavily sclerotized with apical dentiform projections; tibiae without spurs but with a large uncus; tarsal claws connate; and thoracic spiracle of the larva situated on the mesothorax or the intersegmental fold in front.

Rhynchitinae, the tooth-nosed weevils, are so named because of the teeth on the outer edges of the mandibles. They are generally 2.0–8.0 mm in length and usually occur on low vegetation. This subfamily has a couple of unique features which allow for its recognition; thin and exodontous (toothed on the outer face) mandibles, and free appendiculate tarsal claws.

As with the Attelabinae, Rhynchitinae prepare a nidus for the development of their larvae. Most oviposit in buds or shoots that are made to wilt by gnawing a basal cut disrupting the sap flow of the plant. Such a damaged terminal shoot may fall off the plant immediately or after a period of time, or may remain on the plant. Larvae develop in the terminal shoot. Larvae of *Lasiorhynchites* tunnel inside the wood of the branches of their host plants. Some species of the tribe Rhynchitini use fruits or flower buds for oviposition and can be severe orchard pests. Some other tropical species are reported to develop in seeds. Species of the Eugnamptini are leaf-miners on fresh or fallen leaves.

Attelabidae appear to have adopted a series of behaviors allowing their larvae to feed "internally" on leaves without being subject to the constraints on body form and size placed on other leaf mining insects.

A few tentative fossils of Attelabidae are known from the early Upper Cretaceous of Botswana and the United States, but the family is well represented in the Cenozoic fossil record in Europe and the United States.

Family Caridae

This is a very small and only recently recognized family of problematic position. Only four (plus one that is not yet named) genera and about 20 species are known. They are found in Australia (including New Guinea, Tasmania), Chile and Argentina. Adults are less than 5.0 mm in body length, have straight antennae, have only five pairs of abdominal spiracles and also a club-like spermathecal gland. Larvae have legs with claws, a feature not found in any other curculionoids except *Nemonyx* (Nemonychidae). All appear associated with various Cupressaceae. A number of carid fossils have been found in Lower Cretaceous deposits in Russia and the United States but several others classified as such have been misinterpreted.

Family Brentidae, Straight-Snouted and Pear-Shaped Weevils

Despite their remarkably different sizes and appearances (compare representatives of Brentinae and Apioninae), this family combines six traditionally distinct groups, some of which are of very restricted geographic distribution and diversity. Collectively the group is recognized by straight antennae (geniculate in Nanophyinae), and especially by the features of an aedeagal tegmen which is almost or completely interrupted halfway up the sides, ventrites 1 and 2 of the abdomen more convex and protruding that ventrites 3–5, the labial palps reduced to only two segments or to one in Brentinae, with only four Malpighian tubules on the hindgut (six in most other weevils) and tergite 8 of the male (pygydium) capsule-like with an inflected, tongue-like posterior margin. Members of this group exhibit a wide range of plant associations and natural history features.

Brentinae are narrow, elongate, cylindrical beetles, 5.0–42.0 mm in length, usually reddish or brownish and shining, with the snout projecting straight forward. Sexual dimorphism is often marked with the snout generally longer and more slender in the female than in the male and the head, pronotum or other structures often of a very different shape or form. In some species the elytra of males have long caudal extensions. Males of a number of species may fight or joust with other males over the attentions of a female. This group is distributed worldwide and principally tropical with only a very few species extending into temperate regions. Most adults occur under the loose bark of dead or dying trees. The larvae are wood-boring and will sometimes attack living trees. Brentinae can be divided into three main groupings based on their biology; the true wood borers (eggs laid in bark or sapwood and larvae boring into the wood), those whose larvae bore tunnels in wood from eggs laid inside the tunnels of other wood boring insects (often scolytine and platypodine weevils, or Cerambycidae), and lastly, those species that are associated with ants (myrmecophiles). Few details on the nature of their associations with ants are known, but some species have bizarre structures, particularly of the hind legs and the apex of the elytra. Most Brentinae are active at night. In the fossil record, they are know only from Pleistocene African copal.

The predominantly African Cyladini, or sweet potato weevils, are here included in Brentinae. They are antlike, slender, elongate, and 5.0–6.0 mm in length. They are easily recognized by the straight antennae and basally pedunculate pronotum. The group comprises a single genus, *Cylas*, with 24 species. These weevils are not well known even though *Cylas formicarius* (F.) is a widely introduced tropical species that is a serious pest of sweet potatoes anywhere they are grown. Its larvae tunnel in the tubers and may continue to do so after they are harvested, and adults may emerge after the sweet potatoes are in storage or on the market. Other species also bore into sweet potato tubers, while the more globose species develop in the seed capsules of other *Ipomea* species (Convolvulaceae).

Apioninae are small (3.0–7.0 mm in length or less), somewhat pear-shaped, usually blackish in color. Most of the almost 2,000 species belong to the traditional genus "*Apion*" (based on features of internal morphology, now subdivided into 20 or more genera), nearly all of which occur on dicot angiosperms (notably Fabaceae and Asteraceae). Exceptions are a few localized species living on Pinaceae (*Podapion*; North America) and Cupressaceae (*Strobilobius*; New Zealand). Larvae bore into the seeds, stems, and other parts of the plant. Adults can easily be recognized by their black, small pear-shaped form, straight antennae and an elongate trochanter (also in Nanophyinae). Some species have been introduced for biological control of pest weeds. For example, in North America, two species of *Exapion* have been introduced for biological control of gorse, *Ulex europaeus* L. and scotch broom, *Cytisus scoparius* (L.) (both Fabaceae), and one species of *Omphalapion* for control of scentless chamomile, *Matricaria perforata* Mérat. A few other species are adventive (introduced accidentally by humans into areas where they are not native). The earliest fossils date to Upper Eocene deposits in the United States and Europe.

Apioninae here include Antliarhinini, a small group of exclusively African species comprising only two genera and seven species. Some species exhibit extreme sexual dimorphism of the rostrum with the male snout short and stout but that of the female almost ridiculously long and slender (especially in *Antliarhinus zamiae* [Thunberg]) and used for drilling deep oviposition holes into cycad cones. Unique morphological features appear to be associated with life in the tight spaces in cycad cones. Species are associated only with cycads of the genus *Encephalartos*, an association that appears to be little changed since perhaps the Late Cretaceous. Their larvae develop in female cones boring in the sporophylls (scales) and central axis and sometimes the seeds. No confirmed fossils are known; one species described as such, *Antliarhinites gracilis* Heer, is a hemipteran.

Microcerinae are a distinct group of sub-Saharan African weevils comprising only three genera and 67 species. They are most diverse in the arid regions of South Africa. They are recognized by the unique features of the ovipositor, featuring flat to slightly scooped, pointed hemisternites with a lateral, non-setose stylus and also their mostly dense covering of scales and a short, stout rostrum. Some other characters suggested as unique to the group, for example, labial palps set in pits or grooves, are shared with other Brentidae. They are flightless and their elytra are fused, and they are very cryptic on the stony or sandy substrates of their habitats. Little is known about biology but larvae, as known, feed on roots in the soil. Once considered to be related to Brachycerinae and basal groups of the Curculionidae, larval characters now suggest a placement within Brentidae. No fossils are known.

The Ithycerinae includes a single species, the New York weevil, *Ithycerus noveboracensis* (Forster), which occurs in eastern North America. This beetle is shiny black, clothed with patches of gray and brown pubescence, and a yellowish scutellum. It is quite large at 12.0–18.0 mm in length. The adults occur principally on the limbs and foliage of hickory (Juglandacae), oak (Fagaceae), and beech (Betulaceae) trees. The larvae feed on the roots of these same trees. This species is often placed in its own family. Despite its rather different appearance, its genitalia and several other features indicate a relationship with Brentidaeas has been suspected for many years.

Most often confused with true Curculionidae because of their small size (3.0–6.0 mm) and geniculate antennae, Nanophyinae number about 300 species in 30 genera. They are found almost worldwide except for Central and South America. They are closely related to Apioninae and share the unique feature of an elongated trochanter. Little is know about their natural history, but most Palearctic species are associated with plants of the family Lythraceae, especially the genus *Lythrum*. Other host plants are Cupressaceae, Crassulaceae Dipterocarpaceae, Tamaricaceae and Ericaceae. Australian species live on aquatic plants and some African species develop in *Acacia* seeds. Larvae are associated with the fruits, leaves and stems and many appear to cause galls. Species have been introduced into North America for biological control of purple loosestrife, *Lythrum salicaria* L. A single fossil has been described from the Oligocene in Europe but needs reassessment.

Eurhynchinae are a small group of rare brentid weevils found exclusively in Australia and New Guinea. Only three genera and 30 species are known, although the New Guinean fauna has been very poorly explored. Within Brentidae, the Eurhynchinae possess a large number of primitive features but are characterized by the unique features of an emarginate protibial apex, submedially inserted labial palps, and a pair of bar-like sclerite in the membrane of the ovipositor. Very little is known of their natural history, but adults on leaves and larvae tunnel in the stems of plants in the families Proteaceae and Lauraceae and perhaps also Myrtaceae. Two fossil taxa are described from Southern Africa and possibly South America.

Family Curculionidae, Snout Beetles Including Bark and Ambrosia Beetles

The members of this family are by far the most commonly encountered Curculionoidea. They may be found almost everywhere, and although more than 50,000 species in more than 4,600 genera are known, this is probably only a small portion of the true diversity of the group. Weevils occur in all climates and all world regions from the extreme High Arctic of Canada to the far southern Subantarctic Islands. The subfamilial classification is outdated and needs a comprehensive phylogenetic revision. Herein, 16 subfamilies are recognized.

Members of this family are plant feeders in both living and dead plants, and many are serious pests. Almost every part of a plant may be attacked, from the roots upward. The larvae usually feed inside the tissues of the plant (including leaves) but some (Hyperinae, Ceutorhynchinae, Cionini, Gonipterini) feed externally on plant foliage. Adults may feed on leaves or parts of developing reproductive structures. Most species are host plant specific to some degree, often at the plant generic level. Both terrestrial and aquatic plants are used as hosts. Monocot plants are rarely fed upon by other Curculionoidea but numerous taxa of Curculionidae count them as hosts. Many weevil species have been introduced globally as biological control agents of weeds. A very few species appear to be associated with ants (some Cossoninae; Acamptini: and Cryptorhynchinae; *Crematogasterobius* in tropical America, *Myrmecolixus* in southern Africa). Larvae of the Australian genus *Tentegia* (Cryptorhynchinae) develop in dung, the adults rolling the fecal pellets of marsupials with adaptations (such as long hind legs) similar to those of the dung rolling scarab beetles. Only one known weevil, the South American *Ludovix fasciatus* (Gyllenhal), is a predator of grasshopper egg cases deposited into stems of the water hyacinth *Eichhornia crassipes*.

Most weevils, when disturbed, will draw in their legs and antennae, fall to the ground, and remain motionless. Many are cryptic and colored like bits of bark or dirt, and when they remain motionless they are very difficult to see. Many species (especially Conoderinae) are involved in mimicry complexes with other insects. A great variety of weevils are able to stridulate by rubbing the dorsum of the terminal abdominal segments against file-like ridges on the underside of the elytra. These sounds are often extremely weak and usually can be heard only by holding the insect close to one's ear.

Weevils show considerable variation in size, shape, and the form of the snout ranging from as long as the body (e.g., Curculioninae: *Curculio*) to absent (e.g., Scolytinae, Platypodinae and some Cossoninae). Diversity in other features of morphology is immense. Geniculate antennae, a tightly compact antennal club, spermatheca with gland and duct distinctly separate and the structure of the metendosternite characterize adult weevils. Larvae have frontal sutures that do not meet the mandibular membrane and the antennae are not completely enclosed by the frontal plate, legs are absent (expanded pedal lobes are present in some species), there are three or four dorsal abdominal folds, postoccipital condyles of the head are present and conspicuous, antennae are 1-segmented on a basal membranous cushion, and the mandibular mola is generally undeveloped.

The diversification of Curculionidae may be best attributed to their parallel evolution with angiosperms as well as the coaptation of the snout for use as an ovipositor facilitating the circumvention of evolutionary barriers to a plant-feeding way of life (i.e., host plant structural defenses, desiccation in the immature stages, and initiation and maintenance of attachment to host). The oldest known fossil curculionids are recorded from the Upper Cretaceous of Botswana and Kazakhstan (yet undescribed); older forms from the Late Lower Cretaceous of Russia assigned to Curculionidae are probably misinterpreted.

There are numerous differences of opinion regarding the limits of the family Curculionidae. Some classifications recognize Brachycerinae, Dryophthorinae and Erirhininae as separate families based on the primitive structure of their male genitalia. The Scolytinae and Pladypodinae, traditionally recognized as distinct families, are now considered to be best classified within Curculionidae. Relationships between most remaining Curculionidae are very poorly known and the classification used herein is traditional and without a strong modern phylogenetic basis.

Subfamily Dryophthorinae – Billbugs, Palm and Grain Weevils

These beetles are stout-bodied and cylindrical, usually red and/or black, and range in size from 3.0 to 30.0 mm or more. There are about 1,200 species in some 150 genera. Some of the largest weevils known belong to this group. The group is primarily tropical with some species (mainly of the genus Sphenophorus) extending into temperate zones. The antennae arise close to the eyes, and the apex of the scape reaches posterior to the eye, the basal two-thirds or more of the antennal club are smooth and shining and the prementum is deeply sunk into the oral cavity. Specialized internal features are the concealment of the 8th tergite under the seventh, the eighth sternite lacking an apodeme, the ninth sternite being reduced in size and form or absent, the tegmen with strong vertical ring and lacking parameres, and the aedeagus basally with a lateral line below the insertion point of the apodemes. The male genitalia are of a primitive type with the ventral pedon and dorsal tectum mostly still discernible (though not as distinctly as in Brachycerinae and all primitive Curculionoidea), not fused into a cylindrical tube as in other Curculionidae. There are few doubts as regards their monophyly but this latter feature of primitive genital structure has led some authors to remove Dryophthorinae from Curculionidae and to give them familial status, thus preserving a more likely monophyletic Curculionidae (as defined by their advanced genital structure).

Nearly all species are associated with monocot angiosperms, especially palms (Arecaceae) and grasses (Poaceae) and sedges (Cyperaceae) and their relatives. Orchids, bromeliads and pandans are also attacked. Larvae generally mine the fleshy stems or roots but some species occur in decayed wood or dried stored products. One of the largest species is *Rhynchophorus palmarum* (Linnaeus), which may be over 30 mm in length and occurs on palms. The diverse genus *Sphenophorus* includes the corn billbugs, which occur on various grasses including timothy and corn. The adults feed on the foliage and the larvae bore into the stalks. Among the most important pests in this group are the granary weevil, *Sitophilus granarius* (L.), and the rice weevil, *S. oryzae* (L.). These are small brownish beetles, 3.0–4.0 mm in length, that attack stored grain (wheat, maize, corn, rice, and so forth). Both adults and larvae feed on the grain, and the larvae develop inside the grains. Other dryopthorine species are pests of bananas, palms, sugarcane, bromeliads and orchids.

Subfamily Brachycerinae

This is a small group of weevils of an interesting and important phylogenetic position. Traditionally it has included only the African and circum-Mediterranean genus *Brachycerus* (and a few close relatives) but its concept here incorporates the Ocladiini, Cryptolaryngini, Erirhinini and the blind, soil-dwelling Raymondionymini. All share the primitive tactopedal form of male genitalia with a separate pedon and tectum. As with Dryophthorinae, some authors separate them as a distinct family or families.

Brachycerini have generally been related to the Microcerinae (here and now generally treated as Brentidae) but based upon the derived features of larvae lacking legs and having 3–4 abdominal folds, they are here considered as Curculionidae. The completely flat larval antennal sensorium characterizes the tribe as monophyletic (although the feature is shared with Byrsopina). As in Entiminae, adult Brachycerini possess deciduous mandibular processes used by newly emerged adults to escape the earthen pupal cells. It is unclear whether these character agreements are phylogenetically significant or convergent in these two groups. Where known, Brachycerini are associated with succulent Liliaceae and related monocots, the larvae feeding in the underground bulbs or stems of the plants. There are around 500 species in 13 genera.

The African and Asian Ocladiini are also placed near the Brachycerini. Evidence for a close relationship between Brachycerini and Ocladiini is in the form of the male genitalia and structure of the larvae. *Ocladius* occurs mainly in arid regions of Africa and the Mediterranean, its larvae, where known, developing in grasses, whereas the larva of *Desmidophorus* tunnels in stems of *Hibiscus* (Malvaceae) in southeast Asia. Another small aberrant group are the Cryptolaryngini of southern Africa (*Cryptolarynx*) and central Asia (*Perieges*), but their relationships to each other and to other brachycermes remains to be elucidated.

Adults of the Erirhinini are usually found near or in water, as the larvae of most species develop in various aquatic plants including horsetails and mosses. They are recognized by their primitive genital structure but otherwise are externally very similar to other Curculionidae and are difficult to characterize. Derived features are that the tectum of the aedeagus is represented by only a narrow strip or membrane, and a rostrum which is strongly deflexed ventrally from the base (shared with some Dryophthorinae). In recent years, many species of the Tanysphyrina have been widely introduced for the biological control of aquatic weeds (e.g., salvinia, water lettuce, and water hyacinth). Many species are good swimmers and they represent the most successful group of aquatic weevils. As presently recognized there are around 50 genera in the tribe.

Raymondionymini are a small group of pale, eyeless weevils presently known from western North America, the circum-Mediterranean region, Europe, Central and northern South America, New Zealand and Australia. They are generally difficult to find because of their very small size and soil-dwelling habits and are likely more widespread than presently documented. Little is known about their natural history and their immature stages are not known. The tarsi of these tiny weevils have only four segments. Adults are generally collected in leaf litter or by soil washing. They are now generally considered as hypogean relatives of the Erirhinini. There are around 10 genera and 50 species known.

Subfamily Curculioninae

This subfamily is a large assemblage of taxa of unresolved relationships. It includes some 20 tribes, the better known of which are Curculionini, Anthonomini, Derelomini, Eugnomini, Mecinini, Otidocephalini, Rhamphini and Tychiini.

Within Curculionini, the acorn and nut weevils of the genus *Curculio* are usually light brown in color and have a very long and slender snout that may be as long as the body or longer. The adults bore into oak acorns (*Quercus*; Fagaceae) and other nuts with their long snouts and lay their eggs in these feeding holes. Larvae develop inside the nut. Tropical species in Africa, southeast Asia and Australia are usually associated with Moraceae (*Ficus*). There are around 11 genera and 500 species recognized.

Anthonomini occur worldwide except Africa and Australia and several are important pests of cultivated plants. The adults usually feed on fruits and lay their eggs in the feeding pits, and the larvae develop inside the fruits or reproductive structures. Some species form galls and some are associated with mistletoes. Most species occur in the Central and South American tropics. The cotton boll weevil, *A. grandis* Boheman, is a well-known and serious pest of cotton. Other species of economic importance in this group are the strawberry weevil, *A. signatus* Say; the cranberry weevil, *A. musculus* Say; the apple blossom weevil, *A. pomorum* L., and the apple curculio, *A. quadrigibbus* Say. There are some 800 species in more than 70 genera.

Derelomini are a widespread pantropical group represented by some 265 species placed in 40 genera. These are small weevils, nearly all of them associated with the flowers of palms (Arecaceae) and the Neotropical unrelated Cyclanthaceae. Some feed on fruits and seeds but some feed on other floral structures and are important pollinators of the plants. The African oil palm, *Elaeis guineensis* Jacq., is pollinated exclusively by derelomine weevils of the genus *Elaeidobius*. It has been necessary to introduce the weevils along with the palms in commercial plantations.

Flea weevils, Rhamphini, are so called because of their jumping habits. The hind femora are expanded and adults can often jump substantial distances. The larvae mine the leaves of various trees, most notably oaks (Fagaceae), willows and poplars (Salicaceae) and a number of tropical plant families. The group is widely distributed throughout North America, Europe, Africa, Asia and Australia. There are some 200 species in more than 20 genera.

The larvae of most Tychiini feed on the seeds of various legumes (Fabaceae), and the adults occur on the flowers. Species are found worldwide although some genera are probably misplaced in it. There are some 35 genera and over 800 species.

The Otidocephalini are small, black shiny weevils that have the prothorax oval and narrowed at the base and thus resemble ants in general appearance. Some species develop in galls on oak formed by cynipid wasps, but most develop in twigs and stems. This group of weevils is found only in the Americas. There are 5 genera and around 200 species.

Mecinini are a small group of weevils associated mainly with Scrophulariaceae. They occur in Europe, Asia and Africa but a few species have been introduced to various countries. They feed mainly in the seed capsules of the plants. There are 13 genera and about 300 species known.

Eugnomini show a southern hemisphere (Gondwanian) distribution with species in Australia, New Zealand, New Caledonia and South America. Many species are found on flowers but larvae develop in living and dead plant tissues. There are 23 genera and approximately 200 species.

Subfamily Bagoinae

There are eight genera and slightly fewer than 300 species found almost worldwide. Adults are found in aquatic and semi-aquatic habitats. A few species have been introduced for biological control of hydrilla, *Hydrilla verticillata* (Hydrocharitaceae). They have a varnish-like coating on the body and are very similar in appearance to the aquatic Erirhinini with which they were formerly classified.

Subfamily Baridinae

This is one of the largest subfamilies of the Curculionidae, with about 4250 species placed in more than 500 genera. They are found worldwide but are exceedingly diverse in the American tropics. These small weevils are usually black, shining and stout-bodied and can generally be recognized by the upward-extending mesepimera, which are generally visible from above between the base of the pronotum and elytra. Most species feed on various herbaceous plants; a few attack cultivated plants. The potato stalk borer, *Trichobaris trinotata* (Say), attacks potato, eggplant, and related solanaceous plants. *Trichobaris mucorea* (LeConte) feeds on tobacco. Much work needs to be done on this group of weevils.

Subfamily Ceutorhynchinae

This is a large and widely distributed group with around 100 genera and over 1,000 species. It includes some important agricultural pests, particularly of Brassicaceae (e.g., cabbage, canola). The species are small in size and rounded in form, and like Baridinae, they possess upward-extending mesepimera, which are sometimes visible from above. Adults are associated with various plants, mostly Brassicaceae but also Polygonaceae and can be found in terrestrial and freshwater aquatic or semi-aquatic habitats. Larvae are associated with plant reproductive structures or are stem or root miners. Larvae of some species feed externally on plant foliage (as do larvae of Hyperinae). The grape curculio, *Craponius inaequalis* (Say) feeds on the foliage of grape and the iris weevil, *Mononychus vulpeculus* (Fabricius), attacks iris. The genus

Ceutorhynchus is a diverse array of some hundreds of species. Species in the genera *Phrydiuchus, Microplontus, Mogulones* and *Trichosirocalus* have been deliberately introduced for the biological control of pest weeds. It has recently been suggested that Ceutorhynchinae are closely related to Baridinae and Conoderinae based on wing venation and various internal characters.

Subfamily Conoderinae

Formerly known as Zygopinae, this is a widely distributed group represented throughout the world by some 2,000 species placed in over 200 genera. They feed on various herbaceous plants, mostly composites, and trees (including a few conifers). They are easily recognized by their large, dorsally situated eyes. Many are fast and active flyers and in some species males stage contests over the attention of females. Some tropical American species are thought to be involved in mimicry complexes, particularly with ants and flies.

Subfamily Cossoninae-Broad-Nosed Bark Weevils

The Cossoninae can usually be recognized by the broad short rostrum and the long curved spine at the apex of each tibia. They are usually 2.0–7.0 mm in length, and most of them are black and shiny. They occur (often in great numbers) under the loose dead bark of trees and under logs and a few occur under driftwood and along the seacoast. Some are associated with dead, fibrous leaves or stems of palms, tree ferns and *Agave*. They are found worldwide with over 1,700 species in some more than 300 genera.

Subfamily Cryptorhynchinae

Members of this very diverse, worldwide subfamily are easy to recognize as the rostrum fits into a channel between the front legs that exten posteriorly onto the mesosternum where it ends in a cup-like structure. However, such a rostral canal occurs in other weevil groups, and even within Cryptorhynchinae it is differently formed in the various groups. Together with other differences, this indicates the subfamily is an artificial group of several unrelated taxa. When these weevils are at rest, the snout is usually drawn back into this groove. Many have the elytra rough and tuberculate and look like small pieces of fungi, bark or wood. Adults and larvae are usually associated with dead wood although some are found in living plants and some in seeds. Some species are found in aquatic habitats. The Psepholacini has genera with a short and broad rostrum that dig into wood with the entire body, as do bark and ambrosia beetles, and some cossonines. Many small flightless species are found in leaf litter and at least two genera (*Crematogasterobius, Liometophilus*) are associated with ants. There are about 6,000 species in about 600 genera.

Subfamily Cyclominae

This subfamily is a composite of questionably related weevils and as such is difficult to characterize. It includes the African Cyclomini, Hipporhinini and Gronopini, the Australian Aterpini and Amycterini and the more widespread Rhythirrinini and Listroderini, together numbering more than 1,000 species placed in some 175 genera. Most of the weevils found in the high Andes Mountains are Cyclominae. A few, such as members of the South American genus *Listroderes*, are pests of vegetables and have been introduced to other parts of the world. Some members of this group breed in aquatic or subaquatic plants, and the adults are found near water.

Subfamily Entiminae-Broad-Nosed or Root Weevils

The members of this subfamily (which includes upwards of 50 tribes in some classifications) are commonly called the broad-nosed weevils, because the snout is generally short and broad, not elongate and cylindrical as in most other weevils. They are also sometimes called the root weevils because the larvae of nearly all of them feed underground in or on the roots of various plants. Pupation takes place in an underground cell constructed of soil and held together by larval secretions. Adults generally feed on plant foliage or flowers. Most of them are flightless with the elytra fused together along the suture and the hind wings are vestigial. This is a large, worldwide group containing some 12,000 species placed in over 1,000 genera. Unlike most other weevils, which exhibit a relatively high degree of host plant specificity, many Entiminae feed on a variety of host plants from many different plant families and as such are important agricultural or garden pests. Some important species in this group are the white-fringed weevils of the genus *Naupactus*, and the strawberry root and black vine weevils of the genus *Otiorhynchus*. Many Entiminae are parthenogenetic with males known only from some populations or not at all.

Entiminae are among the most diverse and common weevils in arid habitats. The fused elytra may help to present desiccation and some have developed adaptations for sand-dwelling dwelling that include dense long hairs over the body and broad legs adapted for digging. This group includes the weevils most often found at higher elevations and is one of the few groups of weevils inhabiting the subantarctic islands. Many species, particularly of the genus *Otiorhynchus*, are among the most common weevil species to have been accidentally introduced worldwide. Their often-parthenogenetic nature and their broad range of acceptable host plants would appear to facilitate establishment following such introductions.

Aside from the form of the snout, entimines are easily recognized by the presence of an elongate cusp on the mandibles of the adults that appear to be used by the adults to escape from the earthen pupal cells. These cusps are very rarely seen in adults as they are deciduous and break off very early in the adult life, generally before the adult emerges from the soil. They do, however, leave a flat scar indicating their point of attachment that is quite obvious at the ends of the mandibles.

Subfamily Hyperinae-Clover Weevils

Most members of this small group of some 400 species placed in slightly more than 30 genera feed on various clovers and are important clover pests. They are found throughout the world but are most diverse in Europe and Asia. Larvae of most species feed externally on the foliage of host plants and pupate in loosely woven silken cocoons attached to the surface of the leaves. The alfalfa weevil, *Hypera postica* (Gyllenhal), and the clover leaf weevil, *H. punctata* (Fabricius), feed on the growing tips of the plant and skeletonize the leaves; *H. meles* (Fabricius) feeds in the clover heads.

Subfamily Lixinae

These generally large (10–20 mm in body length) weevils are represented by some 1,500 species placed in about 100 genera. The most common beetles in this group are those in the genus *Lixus*, which are elongate and cylindrical, with the curved rostrum nearly as long as the prothorax. In temperate regions, many occur on weeds near water but tropical species occur in various habitats. Members of the tribe Cleonini are generally found in arid regions and are particularly diverse in Africa and central Asia. Many Lixinae feed on Asteraceae and species in a number of genera have been introduced for biological control of some pest weed species.

Subfamily Molytinae

As with the Curculioninae, this group brings together a number of questionably related taxa previously placed in other subfamilies (e.g., Hylobiini, Prionomerini, Cholini, Lepyrini, Lymantini and Pissodini). Most notable is the reclassification of a number of weevils from the Cryptorhynchinae (Ithyporini) as Molytinae. The group is also difficult to differentiate from Cossoninae and Lixinae. Some 35 tribes have been recognized by some authors and its concept as a subfamily is obscure. This subfamily includes the large American genus *Conotrachelus* and its relatives, and also the Mesoptiliini, recognized by some as a distinct subfamily.

Most members of the Molytinae are dark-colored and of moderate size (8.0–12.0 mm in body length). They are found worldwide and there are around 2,500 species placed in about 250 genera. Most are associated with woody plants and have an elongate spur at the inner apex of the tibia that appears to be used to hold onto the host plant. Many have a prosternal channel to receive the rostrum but generally this does not extend onto the mesosternum and is only evident on the prosternum between the front legs. Larvae generally tunnel in woody plants but a number are associated with seeds and fruits. Many species are found in leaf litter and some are eyeless and depigmented. Some species of *Hylobius, Pissodes* and *Magdalis* are pests of pine and other conifers and some, for example in the genus *Conotrachelus*, are pests of fruit. Members of the Neotropical Cholini are associated with various monocots including palms, heliconias and their relatives.

Subfamily Platypodinae-Pin-Hole Borers

The status and position of these weevils is still disputed by various authors. Some consider them as a distinct family related to primitive Curculionoidea, others consider them as basal within Curculionidae and related to Dryophthorinae, and some regard them as a subfamily of Curculionidae but related to the Scolytinae with which they have traditionally been linked. They were originally classified with the Bostrychidae, a totally unrelated family of beetles. They number almost 1,500 species placed in some 30 or more genera.

Platypodinae are elongate, slender, and cylindrical with the head lacking a snout and being slightly wider than the pronotum. They are brownish in color and between 2.0 and 8.0 mm in length. The tarsi (which each have five distinct segments) are very slender, with the first segment longer than the remaining segments combined. The antennae are short and geniculate and have a large unsegmented club. Internally, platypodines are characterized by numerous reductions, especially in the female reproductive structures and the male genitalia, which are reduced in size and complexity.

Platypodinae are wood-boring in living trees, but seldom attack a healthy tree. They appear to attack only dicot angiosperms. The larvae feed on ambrosia fungi that are cultivated in their galleries and which represents the sole food of the larvae and adults.

Subfamily Scolytinae-Bark Beetles or Engravers, and Ambrosia Beetles

The scolytines are small cylindrical beetles, rarely more than 6.0–8.0 mm in length, and usually brownish or black in color. The antennae are short and geniculate and have a large, flat, usually annulated club. There are about 6,000 species placed in some 225 genera. The subfamily contains two groups in terms of their biology: the bark beetles, which feed on the inner bark of trees, and the ambrosia beetles, which bore into the wood of trees and feed on ambrosia fungus, which they cultivate in their galleries. Bark beetles differ from ambrosia beetles in having a large spine or projection at the apex of the front tibiae.

Bark beetles usually live within the bark of trees, generally right at the surface of the wood, and feed on the succulent phloem tissue. Some species, especially *Ips* and *Scolytus*, deeply score the sapwood and are often called engravers. Bark beetles live in many different types of plants and some even mine other plant parts, such as the petiole of large leaves. Most of the economically important temperate scolytines belong to three genera: *Dendroctonus, Ips,* and *Scolytus*, although *Xyleborus* and others are more important pests in tropical regions. The death of an infested tree is brought about by the fungi introduced by the adult beetles and spread by the larvae. As adults and larvae interrupt the flow of nutrients by feeding in the phloem, the fungus spreads inward and clogs the water transport vessels in the sapwood, suppressing the flow of lethal pitch into the beetle galleries. The destructive bark beetles exhibit a remarkable coordination of their flying population in a tightly synchronized mass attack, overwhelming the tree's defenses by sheer numbers. Both males and females respond to a combination of odors from the resin of the host tree and chemical signals (aggregation pheromones) from the first colonists. As a result, thousands of beetles may infest the same tree simultaneously.

Bark beetles can be monogamous or polygamous in their breeding habits. In monogamous species such as *Dendroctonus pseudotsugae* Hopkins, the Douglas fir beetle, the female bores the gallery, releases pheromone, and accepts one male as her mate. In polygamous species such as *Ips pini* (Say), the pine engraver, the male does the initial boring but constructs only a nuptial chamber in which to mate with the several females he accepts into his harem. Each female bores her own egg gallery out from the nuptial chamber.

As a female bark beetle constructs her egg gallery, the male cooperates with her by following along behind her, removing boring dust and shoving it out the entry hole. The female lays her eggs in little notches at intervals along the sides of the gallery. When the eggs hatch, the tiny, C-shaped, legless larvae begin eating their way through the phloem at right angles to the egg gallery. As the larvae grow and molt, moving farther away from the adult gallery, the frass-filled larval mines become larger, forming characteristic patterns. When the larvae complete their growth, they pupate at the ends of their mines. The adults emerge through round holes they bore through the bark. After a brood emerges, the surface of an infested tree appears peppered with shot holes.

Bark beetles have a greater impact economically on the timber-producing forests of North America than any other group of insects, being credited with the death of more than 4 billion board feet of sawtimber annually, over 90% of the total insect-caused mortality. Most of the tree mortality caused by bark beetles is caused by five species of *Dendroctonus*.

Each species of bark beetle has a characteristic pattern of adult and larval galleries and a rigid preference for a particular tree species. Dutch elm disease, transmitted by elm bark beetles, is caused by a fungus introduced from Europe with the smaller European elm bark beetle, *Scolytus multistriatus* (Marsham). These beetles have spread the disease across the United States completely eliminating American elms in many urban areas. One agriculturally important species of bark beetle is the clover root borer, *Hylastinus obscurus* (Marsham), which often causes serious damage to clover. The larvae tunnel in the roots of clover and kill them.

Ambrosia beetles bore into the wood of trees, forming galleries in which both adults and larvae live. Only living or freshly killed trees, with a high moisture content, are infested. Although these beetles do not eat wood, the fungi that they cultivate stain the wood, reducing its value. The presence of these beetles can cause entire shiploads of timber or lumber to be refused at a foreign port. The larvae of ambrosia beetles develop in small cells adjoining the main galleries, and in most species the larvae are fed by the adults. Each species usually feeds on one particular type of fungus. When the females emerge and fly to another tree, they carry conidia of the fungus from the natal tree to the new host and introduce the fungus into the gallery they excavate. After the eggs hatch, the females care for the larvae until they are full grown and pupate, keeping the larval niches supplied with fresh fungus or "ambrosia," and preventing the niche from being choked with frass or excess growth of fungus.

References

Alonso-Zarazaga MA, Lyal CHC (1999) A World Catalogue of Families and Genera of Curculionoidea (Insecta: Coleoptera) (Excepting Scolytidae and Platypodidae). Entomopraxis, Barcelona, Spain, 315 pp

Anderson RS (2002) Curculionidae. In: Arnett RH Jr, Thomas MC, Skelley P (eds) American beetles, Vol 2. CRC Press, Boca Raton, Florida, pp 722–815

Anderson RS, Lyal CHC (eds) (1995) Biology and phylogeny of Curculionoidea. Proceedings of a symposium convened at the XVIII International Congress of Entomology, Vancouver, Canada, July 3–9, 1988. Memoirs Entomol Soc Washington 14:103–114

Farrell BD (1998) "Inordinate Fondness" explained: why are there so many beetles? Science 281:555–559

Kirkendall LR (1983) The evolution of mating systems in bark and ambrosia beetles (Coleoptera: Scolytidae and Platypodidae). Zool J Linnaean Soc 77:293–352

Kissinger DG (1968) Curculionidae subfamily Apioninae of North and Central America with reviews of the world genera of Apioninae and world subgenera of *Apion* Herbst (Coleoptera). Taxonomic Publications, South Lancaster, Massachusetts

Kuschel G, Leschen RAB, Zimmerman EC (2000) Platypodidae under scrutinty. Invertebr Taxonomy 14:771–805

Lawrence JL (1982) Coleoptera. In: Parker SP (ed) Synopsis and classification of living organisms, Vol 2. McGraw Hill, New York, NY, pp 482–553

Marvaldi AE (1997) Higher level phylogeny of Curculionidae (Coleoptera: Curculionoidea) based mainly on larval characters, with special reference to broad-nosed weevils. Cladistics 13:285–312

Marvaldi AE, Morrone JJ (2000) Phylogenetic systematics of weevils (Coleoptera: Curculionoidea): a reappraisal based on larval and adult morphology. Insect Syst Evol 31:43–58

Marvaldi AE, Sequiera AS, O'Brien CW, Farrell BD (2002) Molecular and morphological phylogenetics of weevils (Coleoptera, Curculionoidea): do niche shifts accompany diversification? Syst Biol 51:761–785

May BM (1993) Fauna of New Zealand. Number 28. Larvae of Curculionoidea (Insecta: Coleoptera): Systematic overview. Manaaki Whenua Press, Lincoln, New Zealand, 226 pp

Oberprieler RG, Marvaldi AE, Anderson RS (2007) Weevils, weevils, weevils everywhere. pp 491–520. In: Zhang Z-Q, Shear WA (eds) Linnaeus Tercentenary: Progress in Invertebrate Taxonomy. Zootaxa 1668: 1–766

Sforzi A, Bartolozzi L (eds) (2004) Brentidae of the world (Coleoptera: Curculionoidea). Monografie Museo Regionale di Scienze Naturali Torino 39, Torino, Italy, 976 pp

Thompson RT (1992) Observations on the morphology and classification of weevils (Coleoptera, Curculionoidea) with a key to major groups. J Nat Hist 26:835–891

Zimmerman EC (1992–1994) Australian weevils (Coleoptera: Curculionoidea). Volumes I–III, V–VI. CSIRO Press, Melbourne, Australia

Wesmael, Constantin

Professor Wesmael was born at Brussels, Belgium, in 1798. He was a noted hymenopterist, concentrating principally on the parasitic forms. However, he also studied the Neuroptera, Coleoptera, and other groups. He died at Josse-ten-Noode, Belgium, on October 25, 1872.

Reference

Anonymous (1872) Obituary, Prof. Wesmael. Entomol Mon Mag 9:167

Western Balsam Bark Beetle, *Dryocoetes confusus* Swain (Coleoptera: Curculionidae, Scolytinae)

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The western balsam bark beetle is distributed throughout the range of its host, subalpine fir, *Abies lasiocarpa*, in western North America from British Columbia and Alberta to New Mexico and Arizona. Apparently, it is the only species of the genus that is capable of causing tree mortality of healthy trees. Populations may increase after windstorms provide suitable downed host material for the insects to exploit or during prolonged periods of drought. To a lesser extent it also attacks other species of *Abies* and Engelmann spruce, *Picea engelmanni*. Akin to other tree-killing bark beetles, this insect causes tree mortality by feeding and developing in the phloem of the tree. Utilization of the phloem for habitat and nourishment results in girdling of the tree so that translocation of nutrients is impeded. In addition, upon invading its host, the insect inoculates the tree with a pathogenic fungus, *Ceratocystis dryocoetidis*. It is most likely the combined action of the insect and the fungus that cause the tree to succumb. Extensive mortality of subalpine fir, which is typically not a long-lived species, has occurred throughout its range over the last five decades to a number of disturbance agents including the western balsam bark beetle and its associated fungus.

Initial symptoms of attack include; an accumulation of a mixture of light brown boring dust and frass at the base of the tree and resin flow from the bole of the tree. Copious resin flow may also indicate that the insects have been prevented from successful entry into the tree, commonly referred to as a pitch out. Western balsam bark beetles do not produce the characteristic pitch tubes, an accumulation of resin and frass at the point of entry into the tree, that many bark beetles produce. Attacks are often seen above 2 m on the bole. Identification of successfully attack trees is often difficult. As the tree dies, the foliage changes in color to a light yellow and then a brick colored red before falling off the tree. In some areas, foliage fading can take 2–3 years to become noticeable.

Adult beetles are reddish brown to black and 3–4 mm in length. The females have a prominent, erect, dense, circular brush of red-brown to yellow setae in the frons. In British Columbia, and most likely throughout most of its range, the insect has a 2-year life cycle. However, under certain climatic conditions a 1-year life cycle may occur. The primary dispersal flight occurs during the end of June and July. A second, smaller peak in flight activity also occurs in the fall. Males initiate tree attack, excavate a nuptial chamber, and mate with several females. Invasion and infestation of a new tree involves the use of pheromones and host chemicals. Each female then constructs an egg gallery; with females radiating from the nuptial chamber commonly producing 4–9 galleries. Soon after initiation of gallery construction the females begin ovipositing on the sides of the gallery. This process continues into the fall. Eggs begin hatching in the summer and this brood spends the first winter as a young larvae. The following year the larvae resume development, pupate by late summer, and become adults by the fall but remain in the tree until the following spring. After the first year of attack, egg-laying mated females overwinter in the galleries and continue egg gallery extension and egg laying well into the second year. These females may re-emerge from the tree and attack a new tree or the same tree to deposit a third compliment of eggs.

In a British Columbia study, the average diameter of subalpine fir killed by the western balsam bark beetle ranged from 31 to 60 cm; and mortality was concentrated around the largest trees in the stands. In a Wyoming study from the Bighorn Mountains, average subalpine fir diameter of infested areas was 20 cm; but mortality did not appear to be concentrated around the largest trees. The Wyoming study also indicated that increased mortality levels were observed in dense stands with a higher host type component.

References

Bright DE Jr (1963) Bark beetles of the Genus *Dryocoetes* (Coleoptera: Scoloytidae) in North America. Ann Entomol Soc Am 56:103–115

Garbutt R (1992) Western balsam bark beetle. Forest Pest Leaflet 64. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia, Canada

Mathers WG (1931) The biology of Canadian barkbeetles. The seasonal history of *Dryocoetes confusus* Sw. Can Entomol 63:247–248

McMillin JD, Allen KK, Long DF, Harris JL, Negron JF (2003) Effects of western balsam bark beetle on spruce-fir forests of North-central Wyoming. West J Appl Forest 18:259–266

Molnar AC (1965) Pathogenic fungi associated with a bark beetle on alpine fir. Can J Bot 43:563–570

tock AJ (1991) The western balsam bark beetle, *Dryocoetes confusus* Swaine: impact and semiochemical-based management. Ph.D. Thesis. Simon Fraser University, Burnaby, British Columbia, Canada

Western Blots

Proteins are separated electrophoretically and a specific protein is identified with a radioactively labeled antibody raised against the protein in question.

Western Corn Rootworm, *Diabrotica virgifera virgifera* Leconte (Coleoptera: Chrysomelidae)

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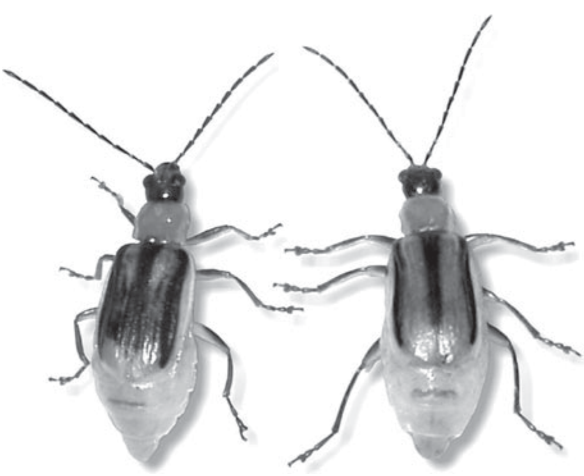
The western corn rootworm, *Diabrotica virgifera virgifera* LeConte is one of the most economically important pests of corn in the U.S. Corn Belt and southern Canada. Larvae can cause substantial injury by feeding on corn roots. Larval tunneling interrupts the integrity of root systems and may destroy individual roots or root nodes. Root feeding by larvae can adversely affect plant growth and development and reduce plant stability and grain yield. If extensive root injury coincides with heavy rains and strong winds, plants may lodge (lean over), reducing light interception by plants and resulting in mechanical harvest losses. Adults are less likely to cause economic loss in field corn, but if high beetle densities are present when silks emerge, excessive silk feeding (i.e., silk clipping) can occur which may lead to reduced pollination.

D. v. virgifera is widely distributed from northwest Mexico into the southwest U.S., across much of the north central to northeastern U.S., and is present in southern Canada. This chrysomelid beetle also has become established as an invasive species in central Europe. A subspecies, the Mexican corn rootworm, *Diabrotica virgifera zeae* Krysan and Smith occurs from Central America to Oklahoma in the U.S. The subspecies are closely related; they are morphologically very similar with no pheromonal or structural barriers to mating, and there is no ecological or temporal isolation between them. However, when male *D. v. virgifera* from a South Dakota (U.S.) population have been mated with female *D. virgifera zeae* from Texas or central Mexico many eggs are laid but most do not hatch. The reciprocal cross always produces fertile eggs. A *Wolbachia* bacteria strain that is present in most U.S. populations of *D. v. virgifera* is the cause of the unidirectional reproductive incompatibility between subspecies. *Wolbachia* could be functioning as an isolating mechanism between the subspecies in hybrid zones.

The western corn rootworm is a univoltine insect species. In the north central U.S., eggs are laid in soil (up to 30 cm deep) from late July to mid-September. Eggs are white to light yellow (size: 0.3 × 0.5 mm), remain in diapause over the winter, and hatch over approximately a 5 week period beginning in late May to early June. Newly hatched larvae are about 3 mm long and move short distances through air filled pores in the soil to locate and establish on suitable plant roots. Larval development progresses through three instars. Larvae move off of roots for brief periods to molt between instars. Third instar larvae (approximately 12 mm long) are cream colored, with a sclerotized head capsule and anal plate. When larval development is complete, larvae pupate in earthen cells. White exarate pupae remain in earthen cells for 6–13 days before adults emerge. Rate of development of immature stages is temperature and density dependent. Adults can be present from late June to September. Adults have an elongate body



Western Corn Rootworm, *Diabrotica virgifera virgifera* (Coleoptera: Chrysomelidae), Figure 36
Western corn rootworm females; examples of the variability in the black elytral pattern that can occur in a population. (Photo by L. Campbell and J. Kalisch.)

shape and range from 4.2 to 6.8 mm long. The elytra are typically straw to yellow with black markings. The black elytral pattern can be reduced to distinct vittae on the inner (sutural) and outer (humeral) margins or cover most of the elytra except for the outer edge and a patch at the apex.

The western corn rootworm has a narrow larval host range that is restricted to certain grass species but appears to be ecologically monophagous on corn. This is primarily because the western corn rootworm exhibits a strong affinity for corn fields as feeding and ovipositional sites. The generally accepted hypothesis is that the western corn rootworm evolved with corn and corn relatives in Mexico and/or Central America and only moved into the U.S. after corn was introduced. Adults are highly mobile, with dispersal occurring on two scales. Adults exhibit local or trivial movement within and among adjacent fields during the entire time adults are present. A small portion of most populations also exhibits migratory behavior which leads to dispersal over longer distances. Migrating females often are mated, but have not yet developed mature eggs. Many migration events occur during or just after peak emergence, but long-range movement has been observed throughout the adult activity period. The mobility of adults enables rootworm populations to quickly colonize first-year cornfields that do not have a resident rootworm population. A recent dramatic eastern range expansion of this species occurred from western Kansas and Nebraska (eastern range limit in 1940s) to the U.S. eastern seaboard in less than 50 years. Corn had been grown in the eastern U.S. for many years prior to the range extension by *D. v. virgifera*.

Many factors can interact to determine adult *D. v. virgifera* population densities in a cornfield at different times during the season. The number of beetles emerging within a cornfield is often a primary contributor to the total population level in the field. Planting date significantly affects when beetle emergence begins. In late planted fields, as compared to early planted fields, initial emergence is often delayed and total emergence reduced. The relative attractiveness of food sources can greatly affect immigration and emigration rates. Adult *D. v. virgifera* feed preferentially on succulent reproductive tissues of corn (i.e., pollen, silks, kernels) but will feed on corn leaves and other pollen sources when preferred corn tissues are unavailable, or present in a less preferred phenological stage. Pollinating corn fields are highly attractive to adult *D. v. virgifera*. If corn in a field pollinates later than corn in surrounding fields, beetles often move into the pollinating field from the fields that have finished pollination. Contrasts in plant phenology within and among fields can significantly affect *D. v. virgifera* distribution patterns.

The female preovipositional period is at least 10–14 days when optimal food is available (e.g., corn silks, pollen). Maximum egg production per female under optimal conditions ranges from 800 to 1,000 eggs. In most of its range, the western corn rootworm will oviposit in cornfields. In the eastern Corn Belt (i.e., area centered around east central Illinois, northwest Indiana) a population of western corn rootworm has adapted to the long-term practice of rotating corn and soybean (larval host to non-host plant) by annually depositing a significant number of eggs outside of corn. Beetles in this area also exhibit much movement back and forth between corn and soybean which is not seen in other geographic areas where *D. v. virgifera* occurs.

Biotic and abiotic factors can influence immature and adult corn rootworm survival. Although various vertebrate and arthropod predators, parasitoids, and pathogens have been reported as natural enemies of *Diabrotica* species, none appear to regulate population densities in commercial cornfields. Weather patterns can greatly influence *D. v. virgifera* survival. In the northern parts of the *D. v. virgifera* range, prolonged cold temperatures during winter can kill a high percentage of eggs. Very wet conditions (e.g., water-logged soils) during the larval/pupal period can reduce larval establishment on plants or kill larger larvae and pupae.

Various western corn rootworm management options are available to producers. Rotating corn with a crop that is not a suitable larval host will effectively prevent larval injury in most parts of the species range (exception is in the U.S. eastern Corn Belt where crop rotation has become ineffective as a management tool, see previous discussion). If corn is planted in a field for two or more successive years (continuous corn), a corn rootworm beetle scouting program and available economic thresholds can be used to determine if a chemical control tactic is needed. When necessary, chemical control tactics can be directed toward larval or adult stages. A commonly used strategy is to apply a soil insecticide at planting or first cultivation to reduce larval feeding damage and protect the primary root structure of the corn plant. Newer technologies that also target the larval stage include insecticide-treated seed and corn rootworm protected transgenic plants (i.e., corn tissues express a toxin that is lethal to rootworm larvae). An alternative strategy targets the adult stage. Insecticide applications are used to suppress beetle populations and reduce egg-laying so that larval populations the following year will not cause economic loss. To date, natural enemies (i.e., predators, parasitoids) have not been useful as biological control agents for *D. v. virgifera*. Biological agents often have provided insufficient or inconsistent control and have been too cost prohibitive to include in commercial management programs.

References

Darnell SJ, Meinke LJ, Young LJ (2000) Influence of corn phenology on adult western corn rootworm (Coleoptera: Chrysomelidae) distribution. Environ Entomol 29:587–595

Giordano R, Jackson JJ, Robertson HM (1997) The role of *Wolbachia* bacteria in reproductive incompatibilities and hybrid zones of *Diabrotica* beetles and *Gryllus* crickets. Proc Natl Acad Sci USA 94:11439–11444

Krysan JL (1999) Selected topics in the biology of *Diabrotica*. In: Cox ML (ed) Advances in Chrysomelid biology. Backhuys Publishers, Leiden, The Netherlands, pp 479–513

Krysan JL, Smith RF (1987) Systematics of the *virgifera* species group of *Diabrotica* (Coleoptera: Chrysomelidae: Galerucinae). Entomography 5:375–484

Levine E, Spencer JL, Isard SA, Onstad DW, Gray ME (2002) Adaptation of the western corn rootworm to crop rotation: evolution of a new strain in response to a management practice. Am Entomol 48:94–107

Meinke LJ (1995) Adult corn rootworm management. University of Nebraska Agricultural Research Division Miscellaneous Publication 63-C

Western Grapeleaf Skeletonizer *Harrisina brillians* Barnes and McDunnough (Lepidoptera: Zygaenidae)

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The western grapeleaf skeletonizer is one of only several species in the genus *Harrisina* in North America. Western grapeleaf skeletonizer is native to the southwestern United States and northern Mexico. Its original distribution is believed to include regions of Arizona, New Mexico, Colorado, Nevada and the Mexican states of Sonora, Chihuahua, Coahuila and San Luis Potos.

The other common species, *Harrisina americana* (Guérin), occurs over the eastern half of North America and is an occasional vineyard pest. Its biology is very similar to the western grapeleaf skeletonizer. In fact, it is attracted to the (R)-(-) enantiomer form of the primary sex pheromone component attractive to the western grapeleaf skeletonizer.

Grape production in California was first impacted by the western grapeleaf skeletonizer soon after its introduction into southern California in 1941. Although severe damage in San Diego County vineyards was reported for several years, western grapeleaf skeletonizer densities decreased by the mid-1950s because of several biological control agents.

In 1961, the western grapeleaf skeletonizer infestation extended into the San Joaquin Valley of central California. Despite attempts at eradicating this pest, first in the 1940s in southern California and later in the San Joaquin Valley, the western grapeleaf skeletonizer became firmly established in both locations.

Both in southern and central California, western grapeleaf skeletonizer populations expanded slowly from their initial points of introduction. The slow increase in their range is mainly attributed to the tendency of moths to remain near where they developed as immatures if adequate vegetation is present. The inability to eradicate this pest in the San Joaquin Valley may be due in part to several features of its biology; for example, a small percentage of the population enters diapause during early seasonal generations, and some pupae may remain in diapause for over 18 months.

Western Grapeleaf Skeletonizer *Harrisina brillians* Barnes and McDunnough (Lepidoptera: Zygaenidae), Figure 37 Western grapeleaf skeletonizer female moth adjacent to recently laid egg cluster.

Life Stages

Western grapeleaf skeletonizer eggs are laid in clusters commonly containing 50–150 eggs. Eggs are cream to light yellow in color and shaped like capsules. They are laid on their sides and do not touch one another. Moths oviposit almost exclusively on the bottom surface of leaves located most commonly at the basal portion of each shoot in the spring, and on new, fully expanded leaves as the season progresses. Healthy females lay nearly 300 eggs during their lifetime (Fig. 37).

Although there are typically five larval instars, a few individuals have only four instars. The first instar has a cream-colored head capsule and pronotal shield that is difficult to see with the unaided eye. Their body is light cream and no color pattern is present (Fig. 38). Second instar head capsules are dark, and the body lacks dark pigmentation until larvae are close to molting, at which time a faint brown mottling is visible. Furthermore, second instar larvae have pronounced body hairs. Third instars are identified by their distinctive medium brown bands that become more pronounced through the course of this life stage. Bands become blue as third instars develop. Head

Western Grapeleaf Skeletonizer *Harrisina brillians* Barnes and McDunnough (Lepidoptera: Zygaenidae), Figure 38 Grape leaf with early instar larvae.

capsules in third and later instars are retractile and relatively difficult to see, but the pronotal shield is dark and prominent. Fourth and fifth instars have distinct black and blue bands upon a bright yellow background (Fig. 39).

Although early instars have body hair, later instars (third to fifth) have urticating hairs that are

Western Grapeleaf Skeletonizer *Harrisina brillians* Barnes and McDunnough (Lepidoptera: Zygaenidae), Figure 39 Late stage larvae demonstrating atypical feeding pattern signifying a viral infection.

highly irritating to human skin, and of particular importance to farm workers when harvesting grapes. Urticating hairs are characteristic of the family Zygaenidae. The irritating factor is believed to be hydrogen cyanide, resulting from the breakdown of cyanoglucosides.

Fifth instar western grapeleaf skeletonizer larvae pupate under the bark of grapevine trunks or at the base of trunks in dried leaf litter or most anything that provides cover. The process of moving from a feeding site to a pupation site and initiation of spinning a cocoon occurs within 36 h. The cocoons are a cream color and have an anterior flap-like portion used as an exit by emerging moths. This "flap" can be teased open with forceps for removing pupae that can be relatively easily sexed.

Adult western grapeleaf skeletonizer moths are bluish-black in color. Males have a slender abdomen terminating in a v-shape as a result of soft spines. The female abdomen is considerably broader throughout with a distinctively square shaped terminus. Although both male and female moths have antennae with lateral bristles, male bristles are longer and have fine lateral hairs.

Life Cycle

The western grapeleaf skeletonizer has a very restricted host plant range. It seldom infests plant species other than several in the family Vitaceae, including commercial and wild grape (*Vitis* spp.), Virginia creeper (*Parthenocissus quinquefolia* (L.)) and Boston ivy (*P. tricuspidata* (Plauchon)).

In Arizona, western grapeleaf skeletonizer has three generations each year. Moths first occur in May, and the first brood of larvae is present during June and early July.

In Fresno County, California, moth emergence corresponding to the first seasonal flight is initiated approximately 71% of the time from mid-March to early April. Moth emergence then increases gradually and continues into early May. The second flight of moths in California's Central Valley commonly begins in early June. A 1-to-2-week period occurs between the end of the first and beginning of the second moth flights, during which time virtually no moths are caught in traps. The third moth flight period commonly begins during the last week in July. There is a small degree of overlap between second and third moth flights. Pheromone trap data suggest that a small fourth generation occurs during some years.

In San Diego County coastal areas and cooler highland areas, western grapeleaf skeletonizer spring moth flights occur approximately 1 month later than in the Central Valley. As a result, only 2–3 generations occur each year in the cooler regions.

Western grapeleaf skeletonizer egg, larval and pupal development share similar, lower and upper temperature thresholds (combined life stage estimate: 9.0 and 28.2°C, respectively). Moth longevity is about 7 days. Although longevity has been noted to vary in relation to mean daily temperature, longevity and oviposition schedules are only loosely linked to daily temperatures under climatic conditions in California's San Joaquin Valley. Male flight activity occurs almost exclusively from sunrise to late morning, whereas female flight activity gradually increases from late morning to early afternoon. It has been suggested that daytime flight behavior and black coloration enables this species to thermoregulate, thereby having a similar level of activity over a broad range of moderate to high temperatures under clear skies. This is likely to differ in coastal climates subject to frequent cloudiness. Western grapeleaf skeletonizer larvae feed extensively, if not exclusively, during daytime hours.

Pheromone Systems

The primary component of the western grapeleaf skeletonizer sex pheromone is [sec-butyl-1-(z)-7-tetradecenoate (racemic)].The pheromone is very stable when contained in a rubber septum or sheet-like polymer laminate, and effective for 4 weeks during high ambient temperatures.

Wing, delta and bucket traps (unitrap) work well for catching western grapeleaf skeletonizer moths. The bucket trap is very convenient and is capable of catching far more moths. Traps are particularly reliable in identifying when early season moth emergence first occurs, and work well when located upwind, several rows into a vineyard and approximately five vines down the row.

Biological Control

In southern California, two parasitoids have played an important role in western grapeleaf skeletonizer biological control. A braconid wasp, *Glyptapanteles harrisinae* (Muesebeck), and a tachinid fly, *Ametadoria misella* (Wulp) [= *Sturmia harrisinae* (Coquillett)], were introduced in the early 1950s. The wasp was collected in southeast Arizona, while the fly was obtained from Arizona and Mexico. *Ametadoria misella* established rapidly in the San Diego area, and parasitism of 30–70% was common within a year of release. *Glyptapanteles harrisinae* also established rapidly, however, parasitism levels dropped several years following initial establishment.

Parasitoids were first released in the San Joaquin Valley in the mid-1970s, with an intensive release effort occurring in the late 1970s. Parasitism occurred at low levels (less than 1.0%) during the first several years following initial releases. By the early 1990s, parasitism levels of 30% by *A. misella* were common.

A granulosis virus of western grapeleaf skeletonizer (HbGV) has played a key role in controlling western grapeleaf skeletonizer in the southern and interior valley regions of California. It was introduced inadvertently as a contaminant associated with parasitoids imported from Arizona and Mexico. Viral disease symptoms are very evident in most life stages of infected individuals. During oviposition, infected females frequently lay eggs in unorganized groups, with the eggs clumped into small groups several layers high. In addition, infected young larvae feed as unorganized groups, within which dead individuals are common. The appearance of the leaf area fed upon by young and old infected western grapeleaf skeletonizer larvae is considerably different from that resulting from feeding by healthy larvae. Feeding by young infected larvae on grape leaves occurs in small, more or less individual patches that do not result in well formed feeding "windows" (translucent areas consisting of leaf epidermis) typical of early feeding by healthy uninfected larvae. Fourth and fifth instar feeding by infected individuals is also patchy. This contrasts greatly with feeding by healthy larvae of similar age, in which all leaf tissues are consumed except primary and secondary leaf veins.

Within Field Distribution of Western Grapeleaf Skeletonizer

Larvae are commonly observed in greatest abundance along vineyard perimeters. This is particularly apparent where light infestations result in damage that is almost exclusively on the edge of vineyards. In contrast to the well defined edge effect in cases of low to moderate abundance, populations are readily observed throughout the vineyard when population densities are high.

For research purposes, western grapeleaf skeletonizer pupae can be monitored easily using corrugated cardboard with cell diameters equal to the diameter of fifth instars (approximately 5 mm). The corrugated cardboard can be cut into 4–8 cm wide strips and placed as bands around canes or trunks. When seeking a pupation site, the larvae will readily (if not preferentially) enter the cell-like entrance holes along the edge of a band and pupate inside.

Pheromone Traps as Monitoring Tools

Pheromone traps can be used for several purposes, including the determination of first emergence of western grapeleaf skeletonizer moths in spring, identifying the duration of primary activity during a flight period, and providing a rough approximation of relative population density. For these data to be of greatest value, they should be compared to previous years of data from the same site. To successfully identify the first date of emergence, traps should be placed in the field by mid-February in central California. Early trap placement and checking traps twice each week are necessary to accurately determine first moth emergence. For most uses, checking traps at 6 or 7 day intervals and estimating emergence as having occurred midway between intervals is adequate.

Simulation Phenology Model

A computer simulation model was developed for predicting western grapeleaf skeletonizer seasonal phenology. The model incorporates a logistic spring emergence function, a non-varying estimate of moth longevity (i.e., 7 days), and a schedule of percent daily oviposition by an average moth over a 7 day life span. In addition, egg, larval and pupal development is based on degree-day sums required to complete each life stage (145, 385, 278 degree-days, respectively). Degree-days per day are calculated from minimum/maximum temperatures utilizing a lower threshold of 9.0°C and a high temperature, horizontal threshold of 28.2°C.

The western grapeleaf skeletonizer model is initialized with the date of the first pheromone trap catch (i.e., the BIOFIX point) signifying initiation of the first annual moth flight.

References

Carr WC, Roltsch WJ, Mayse MA (1992) Diurnal and generational flight activity of the western grapeleaf skeletonizer (Lepidoptera: Zygaenidae): comparison of monitoring methods. Environ Entomol 21:112–116

Curtis CE, Landolt PJ, Heath RR, Murphy R (1989) Attraction of western grapeleaf skeletonizer males (Lepidoptera: Zygaenidae) to S-(+)-2-Butyl-(Z)-7-Tetradecenoate. J Eco Entomol 82:454–457

Roltsch WJ, Mayse MA (1993) Simulation phenology model for the western grapeleaf skeletonizer (Lepidoptera: Zygaenidae): development and adult population validation. Environ Entomol 22:577–586

Stark DM, Purcell AH, Mills NJ (1999) Natural occurrence of *Ametadoria misella* (Diptera: Tachinidae) and the granulovirus of *Harrisina brillians* (Lepidoptera: Zygaenidae) in California. Environ Entomol 28:868–875

Stern VM, Federici BA (1990) Biological control of western grapeleaf skeletonizer, *Harrisina brillians* Barnes and McDunnough (Lepidoptera: Zygaenidae), with a granulosis virus in California. In: Bostanian NJ, Wilson LT, Dennehy TJ (eds) Monitoring and integrated management of arthropod pests of small fruit crops. Intercept Limited, Andover, UK, pp 167–176

Western Harvester Ant, *Pogonomyrmex occidentalis* (Cresson) (Hymenoptera: Formicidae)

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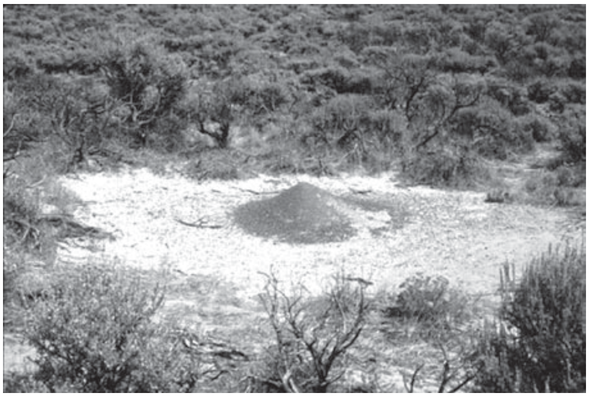
The western harvester ant is common in semi-arid shrublands and grasslands throughout much of the western interior of North America. This species, like others in the genus *Pogonomyrmex*, is called a harvester ant because the workers collect seeds for food. The western harvester ant also removes plants near nests by clipping leaves and stems. Nests of the western harvester ant are large, conical soil and gravel mounds, surrounded by a circular area cleared of vegetation. In some western rangelands where soils are favorable, the population densities of this harvester ant may exceed 50 colonies per ha and the denuded area due to nest clearings may affect 10% of the total ground surface area. Ants may also harvest a considerable portion of the seeds produced by plants. The western harvester ant is therefore both ecologically and economically important, and is sometimes considered a rangeland pest because of the reduction in the plant forage available for grazing by livestock. These ants can also inflict a painful sting when their nest is disturbed.

The significance of the mound-building and plant-clearing habits of the western harvester ant has been the subject of considerable speculation, but is likely related to temperature regulation within their nests. The conical nest mound is noticeably flattened on the side with the nest entrance, which usually faces southeast to maximize exposure to the morning sun. Removal of surrounding plants also reduces shading of the nest, especially when the sun is at a low angle. The adult workers move larvae up or down within the nest mound daily in a manner that reflects a optimal range of temperature for brood development (Fig. 40).

The foraging activity of the workers is also influenced by the soil temperature. Most seed harvesting by ants occurs when the surface temperature is between 30 and 40°C, but some foraging may be observed over a more extreme range of temperatures (20–50°C). When soil temperatures are high (40–50°C), ants frequently collect arthropods that apparently die of heat stress on the surface. Thus, although the western harvester ant is primarily seed eating, it also scavenges considerable amounts of arthropod forage, plant litter and feces.



Western Harvester Ant, *Pogonomyrmex occidentalis* (Cresson) (Hymenoptera: Formicidae), Figure 40 Nest mound and clearing of the western harvester ant, *Pogonomyrmex occidentalis* (Cresson), in the sagebrush steppe of southwestern Wyoming.

Ants harvest a wide variety of seeds available in their foraging areas, but workers consistently prefer, or avoid, the seeds of some plant species. This selective seed harvesting, along with soil modification of the nest site, often results in a different admixture of plant species near ant nests compared to surrounding areas. Ants attract nestmates to dense patches of preferred seeds by laying a recruitment pheromone along the soil surface. Workers are recruited to seeds by detecting differences in the concentration of the pheromone with their antennae as they move sinuously along the chemical trail.

The reproductive behavior, life cycle and colony longevity of the western harvester ant are similar to those in most other *Pogonomyrmex* species. During the summer, ant colonies produce numerous winged males and females ("alates") that are reproductively viable and morphologically distinct from the sterile workers. In contrast to the iron-red color of the workers, male alates are black and have disproportionately smaller heads. Female alates resemble workers in color and proportion, but are 2–3 times larger in size. In most areas, alates leave the nest between late July and early August for their nuptial flights. Alate flight activity is synchronous among colonies, usually occurring in the late morning on 2 or 3 days following a significant rainfall.

The alates aggregate on hills or cliffs, and in the uppermost portions of shrubs, trees, or structures such as fenceposts, windmills, or buildings. Males "lek" together in groups (form mating aggregations) of 5–20 individuals, and females are attracted to male aggregations by a sex pheromone. Females typically mate with several males, a behavior that later results in genetically variable workers after the queen begins reproducing in colony establishment.

After locating a suitable site, the foundress queen sheds her wings and digs a simple, vertical tunnel 10–15 cm deep. During the first few weeks, the queen must rear the first brood as well as forage for food. Most foundress queens die before the first offspring develop into adult workers. Colony mortality continues to be high during the first year when there are few workers, especially if a young colony is in close proximity to older, larger ones with well-established territories. Over time, this selective mortality near existing colonies tends to produce a regular spacing pattern between neighboring ant colonies, although territories often overlap and foraging trails may interdigitate. If a colony survives for 2 years, then it generally has a low mortality and may persist for 10–50 years. A thriving colony typically has 2,000–3,000 workers, but larger ones may harbor 10,000 workers. Colonies are monogynous (one queen) and a single queen (except for the foundress queen) lives for the entire lifespan of the colony.

Because colonies may occupy a site for several years, the digging activity of ants gradually alters the chemical and physical characteristics of soils. Levels of nutrients essential for plant growth are usually higher in nest soils than in surrounding areas. The numerous tunnels and chambers in nests also increase water infiltration from the surface, and higher levels of organic matter facilitate the retention of soil water and nutrients. As a result, the size and species of plants adjacent to nest clearings or on abandoned nest sites may differ from surrounding areas. Ants, therefore, have beneficial effects on soil productivity and plant species diversity.

The western harvester ant is usually found in deep, well-drained soils with a sandy or gravelly texture because ants excavate some nest tunnels and chambers 2–3 m deep in soil. Colony densities are highest where these soils occur, usually on upland plains or sloping terraces. In contrast, ants are often absent from shallow soils, or fine-textured clays where workers are precluded from digging deep nest tunnels, or where soil expansion and contraction makes the tunnels unstable. Repeated soil disturbance, such as heavy erosion or trampling by livestock, is also unfavorable to ants because workers spend more effort on nest reconstruction and maintenance at the expense of food collection. Under these conditions, ants are present in low densities due to high rates of colony mortality or nest abandonment. From the standpoints of soil productivity and integrity, therefore, high densities of the western harvester ant indicate a healthy range condition rather than a degraded one.

The effects of harvester ants on total plant production are usually insufficient to justify broad-scale chemical controls of ants on western rangelands. Control measures using chemically treated baits are economically feasible only on intensively managed ranches, or in rural settlements where humans commonly encounter ant colonies. Given its potential roles in soil productivity, plant species diversity, and as an indicator of soil disturbance, the absence of the western harvester ant actually might be less desirable than its presence on western rangelands.

References

Cole BJ (1994) Nest architecture in the western harvester ant, *Pogonomyrmex occidentalis* (Cresson). Insectes Soc 41:401–410

Crist TO, MacMahon JA (1991) Foraging patterns of *Pogonomyrmex occidentalis* in a shrub-steppe ecosystem: the roles of temperature, trunk trails, and seed resources. Environ Entomol 20:265–275

MacMahon JA, Mull JF, Crist TO (2000) Harvester ants (*Pogonomyrmex* spp.): their community and ecosystem influences. Ann Rev Ecol Syst 31:265–291

Rogers LE (1987) Ecology and management of harvester ants in the shortgrass plains. In: Capinera JL (ed) Integrated pest management on rangeland. Westview Press, Boulder, Colorado, pp 261–270

Wiernasz DC, Cole BJ (1995) Spatial distribution of *Pogonomyrmex occidentalis*: recruitment, mortality, and overdispersion. J Anim Ecol 64:519–527

Western Thatching Ant, *Formica obscuripes* (Forel) (Hymenoptera: Formicidae)

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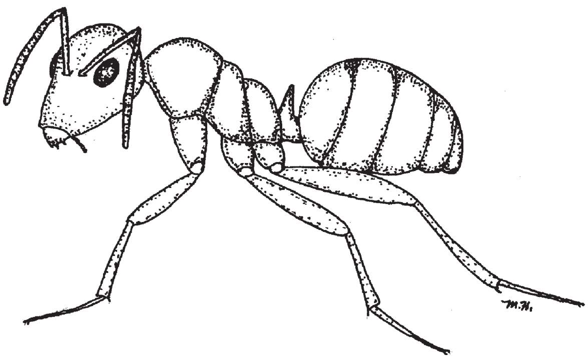
The western thatching ant, *Formica obscuripes*, is a relatively large mound-building ant. Its distribution reportedly extends from northern Indiana and Michigan westward across the northern United States and southern Canada to Oregon and British Columbia. This ant also is found in an area extending southward including Utah, Colorado, northern New Mexico and California. The host range of the western thatching ant includes various vegetation types, such as forested areas, grasslands, and sagebrush. The dome-shaped nests may vary considerably depending on age of the colony and the habitat; however, they are typically 0.5 m in height and 1.0–1.5 m in diameter. The main brood chambers typically extend to a depth of 1 m or more below the soil surface, and the thatch to a depth of one-third of a meter or less. The thatch nests are constructed from dry plant materials found in the area, such as pine needles and twigs in a pine forest or sagebrush twigs and grass in a semi-arid region. The thatch may frequently be surrounded by a sandy or bare soil ring. Another characteristic of the ant is that it constructs slightly excavated, and even partially covered, trails on the ground leading in nearly straight lines from the nest to feeding sites in trees or other plants. The ants feed upon honeydew collected from homopterous insects such as aphids, and also consume other arthropods. Ants are one of the groups of social insects that practice a division of labor, each working for the good of the whole.

The life cycle of the ant is one of complete metamorphosis, with egg, larva, pupa, and adult stages (Fig. 41). The eggs are about 0.6 mm in length and 0.3 mm in diameter. Larvae are about 6 mm in length at maturity. Worker pupae range from 3.5 to 7 mm in length, and sexual male and female pupae about 9mm. The larvae are small legless white worms. The adult ant workers appear to have at least two, and maybe three, different morphological forms. The major (maxima) workers are larger than the media workers, which in turn are larger than the minor workers (minima). The major workers are approximately 6 mm or more in length and have an orange-red head and thorax, and a black abdomen. The smaller media and minor workers (tenders) typically collect honeydew from homopterous insects (such as aphids, treehoppers, and scales on trees and low growing vegetation) and also carry brood in the nest. It has been suggested that the small black minor workers are largely restricted to working in the primary nests. They have been observed, however, along with media workers, to transport honeydew from homopterous insects on plants to small secondary ant nests in soil surrounding the basal area of plants. These secondary nests may then be utilized as transit sites for subsequent honeydew transport to larger primary nests. The small minor workers may also perform other duties in the primary nest, especially as nurse-maids for the brood and queens. The major orange-red and black workers are known to then collect honeydew



Western Thatching Ant, *Formica obscuripes* (Forel) (Hymenoptera: Formicidae), Figure 41 Western thatching ant, *Formica obscuripes* (Forel).

from smaller workers and transport it along ant trails leading to primary nests. These workers have larger crops (stomachs) and can therefore accommodate transporting larger amounts of honeydew. They also collect other arthropods (mostly insects) to use as food for the colony, and are extensively involved in nest repair. It is thought all three morphological forms can perform the same duties when necessary. During cold months of the year adult ants hibernate in the nest below ground (Fig. 42).

It has been estimated that the number of adult workers per colony may reach as high as 35,000–40,000. There is apparently a minimum spacing requirement between colonies that will be tolerated by the ants. If that space is violated, colonies tend to disperse. When disturbed, this ant species can release a stream of formic acid from the distal end of the abdomen. This appears to be a defensive mechanism, but could also serve some other function as well. It has been noted these ants will chew off the bark from the base of some plants, especially when in close proximity to the nest, and then eject formic acid directly onto the cambium layer. This seems to facilitate eventual death of the plant. As the plant dries, branches and stems break off, which may subsequently be used to further enlarge the thatch on the nest. In addition to workers, other members of the ant colony include queens and males. The number of queens per colony may vary; however, it is thought there are typically two or more in each colony. Alate (winged) sexual forms appear on top of the mounds at specific times of year. This may vary from May to August depending on the region and climatic conditions. Once the fertilized alate queen returns to earth from her nuptial flight, she breaks off her wings and then commences to seek an appropriate place to establish a new colony. This is a natural process of propagating new colonies within given species. It has been noted, however, that nuptial flights of *Formica obscuripes* may not occur in all regions of its range. The queens may live for a number of years; however, once they die, the colony will generally die within a few months. The male ants die shortly after the mating flights have been completed. Eggs that have been fertilized develop into female ants and unfertilized ones into males. The type of nutrition larvae receive is thought to have some effect on whether fertilized eggs become queens or workers. Pheromones are used very effectively as means of communication between members within the colony.

Western Thatching Ant, *Formica obscuripes* (Forel) (Hymenoptera: Formicidae), Figure 42 Mound of western thatching ant, *Formica obscuripes* (Forel) (approximately 0.6 m high and 1.5 m in diameter at base).

The western thatching ant should be considered a beneficial insect. It tunnels into the soil at its nesting site, thereby facilitating mixing and aerating of the soil. These ants feed upon a number of other insect species, including some pest species such as the western spruce budworm. It has been noted that nectaries of North American black cherry are most active during several weeks following budbreak. The western thatching ant is attracted to the nectar as a food source. Young eastern tent caterpillars, which may also be present at that time, may be captured and fed upon by these ants. In addition to feeding on other insects, including some pest species, these ants provide a measure of protection for the nectar-secreting homopterous insects they tend. This relationship may be viewed as a mutualistic one between the host plant, the aphids (for example), and the ants. Some defoliating insect pests are fed upon by the ants, thereby benefiting the ants and the plant. The ants protect aphids from their natural enemies and receive honeydew in return;

and finally, the plant provides food for the aphids and thatch material for the ant nest.

References

Bradley GA, Hinks JD (1968) Ants, aphids, and jack pine in Manitoba. Can Entomol 100:40–50

Cole AC (1932) The thatching ant, *Formica obscuripes* (Forel). Psyche 39:30–33

Headings ME (1971) The tree foraging activity of *Formica obscuripes* (Forel) and its influence on arthropoda of jack pine. M.S. Thesis. Michigan State University, East Lansing, Michigan, 117 pp (unpublished)

Holldobler B, Wilson E (1990) The ants. The Belknap Press of Harvard University Press, Cambridge, Massachusetts, 732 pp

Weber NA (1935) The biology of the thatching ant, *Formica rufa obscuripes* (Forel) in North Dakota. Ecol Monogr 5:165–206

Wilson EO (1971) The insect societies. The Belknap Press of Harvard University Press, Cambridge, Massachusetts, 548 pp

West Indian Sweetpotato Weevil, *Eusceps postfasciatus* (Fairmaire) (Coleoptera: Curculionidae)

In tropical areas, this species can be quite damaging to sweetpotato.

► Sweetpotato Weevils and Their Eradication in Japan

West Nile Fever

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West Nile Fever is an arthropod-borne human illness characterized by fever, headache, rash, muscle pains, swollen lymph nodes, and rarely, meningoencephalitis. The disease is caused by the West Nile virus. This was one of the earliest arboviral infections to be documented, the virus being isolated from the blood of an infected woman in the West Nile province of Uganda – hence the name of both the virus and the disease.

West Nile virus belongs to a group of viruses commonly known as arboviruses because they are carried (transmitted) by arthropods (jointed-legged invertebrates such as insects, ticks, etc.). It is scientifically classified under the *Flavivirus* genus within the family Flaviviridae. It is related to other encephalitis-causing viruses like Japanese encephalitis virus, Murray Valley Encephalitis virus, Saint Louis encephalitis virus and eight other viruses that form the West Nile subgroup (complex) of viruses.

West Nile virus has been isolated from vertebrates and/or arthropods in some 25 countries within the Ethiopian, Palearctic and Oriental regions of the world, extending from Portugal in the west, to South Africa to the south, and Russia and India to the east. Very recently, in 1999, it spread to North America. Apart from humans, infected vertebrate animals include cattle, sheep, horses, goats, dogs, rabbits, hares, rodents, game animals, chickens, pigeons, sparrows, and wild birds (especially wetland and migratory birds). The generally accepted view of virus transmission is that it cycles between mosquitoes and birds. Most birds are unaffected by the virus, but can amplify the virus in their blood and thus pass it on when mosquitoes bite. Periodic transmission occurs to other vertebrates and humans when mosquitoes bite them accidentally or as a result of changing their feeding behavior.

Most of the virus detections from arthropods have been in mosquitoes and ticks. Mosquitoes are recognized as the major vectors of the virus. *Culex univittatus* has been implicated as the major mosquito vector with *Culex pipiens* and *Culex neavei* as secondary vectors in the Ethiopian zoogeographical region. *Culex modestus* and *Culex pipiens* have been implicated as vectors in the Palearctic region, and *Culex tritaeniorhynchus* and *Culex quinquefasciatus* as vectors in the Oriental region. Many other species of *Culex*, *Aedes* and *Anopheles* mosquitoes are experimentally capable of transmitting West Nile virus to mammal or bird hosts, but their importance in natural transmission is unknown. West Nile virus also has been isolated from wild caught ixodid and argasid ticks in the Palearctic region, but the role of ticks in natural transmission has not been clearly defined.

The prevalence of West Nile virus infections in humans varies with geographical region, but generally ranges from 20 to 80% in endemic countries. Infection is most often without symptoms, but sporadic cases, or clusters of cases or outbreaks of West Nile fever do occur. When disease occurs, the incubation period is 1–6 days. The onset of illness is abrupt, with fever, headache, and swollen lymph nodes being the most common symptoms. Muscle, eye and abdominal pains, sore throat and vomiting may occur. A rash appears on the trunk and upper extremities of the body during or toward the end of the period of fever. Recovery usually occurs after about 5–6 days. The clinical course of the disease can be more severe or even fatal in the elderly. Meningoencephalitis is a well known complication of West Nile fever. This is associated with neck stiffness, vomiting, confusion, abnormal reflexes, disturbed consciousness, tremor of extremities, convulsions and coma.

There has been a recent upsurge of a more severe form of West Nile fever in Europe. An outbreak in 1996/1997 in Bucharest, Romania, involved more than 500 cases and a case fatality rate of almost 10%. There are reports of an outbreak in Israel involving more than 150 cases and 12 deaths in September 2000. The virus has now crossed the Atlantic ocean: an outbreak of West Nile fever occurred for the first time ever in New York City, USA, in September 1999, involving 56 cases and 7 deaths. Dozens of crows in the area also died (crows are especially sensitive to the virus), and West Nile virus was isolated from several birds, including crows and exotic birds from a local zoo. To date, some 18 species of birds including crows, robins, blue jays, and bald eagles have been infected throughout the eastern United States. Clearly, the virus is there to stay. This underscores an important current issue in public health – the rapid and frequent spread of microorganisms into new areas as a result of modern air travel and international trade. The danger is that microbes invading new territory often find hosts with no immunity, with catastrophic consequences to the hosts. West Nile fever is a relatively mild disease but its recent spread is a warning of trouble to come when more dangerous pathogens find their way into new areas.

References

Howe LM (1999) Kunjin West Nile fever update. Available at http://www.earthfiles.com/earth092.htm

Hubalek Z, Halouzka J (1999) West Nile fever – a reemerging mosquito-borne viral disease in Europe. Emerg Infect Dis (serial online) 1999 5:(15 screens). Available at http://www.cdc.gov/ncidod/EID/eid.htm

Hurlburt HS (1956) West Nile infection in arthropods. Am J Trop Med Hyg 5:76–85

Karabatsos N (ed) (1985) International catalog of arboviruses, including certain other viruses of vertebrates (3rd edition and supplements 1986–1998). Am Soc Trop Med Hyg, San Antonio, Texas

Peiris JSM, Amerasinghe FP (1994) West Nile fever. In: Beran GW, Steele JH (eds) Handbook of zoonoses. Section B: Viral, 2nd edn. CRC Press, Inc., Boca Raton, Florida, pp 139–148

West Nile Fever in the United States (update on St. Louis encephalitis). Available at http://www.who.int/disease-outbreak-news/n1999/oct/o6oct1000.html

Weta (Orthoptera: Anostostomatidae, Rhaphidophoridae)

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Weta are flightless New Zealand ensiferan Orthoptera in the families Anostostomatidae and Rhaphidophoridae. The common name is derived from the Maori word wetapunga, “God of ugly things,” that referred to the anostostomatid, *Deinacrida heteracantha*, one of the giant weta. The most familiar weta are very large insects including a number of species of long-legged cave weta (Rhaphidophoridae). Anostostomatids are the true weta and are known for gigantism and sexual dimorphism, the latter owing mainly to elaborate cephalic weapons in males. All species are omnivores, eating leaves, fruits, seeds and insect prey. When disturbed, many species stridulate and exude foul-smelling feces. Life cycles are lengthy with development from egg to adult (7–10 instars) taking at least 2 years. Adults live for a year or more, particularly alpine species which can live several years as adults, and are freeze-tolerant.

The subfamily Deinacridinae, in particular, is known for gigantism, with some *Deinacrida* female giant weta weighing in over 30 g. Four particularly large arboreal and ground-dwelling *Deinacrida* are virtually extinct on mainland New Zealand due to predation by introduced vertebrates such as rats: *D. rugosa, D. heteracantha* and *D. fallai* survive on certain islands largely due to conservation efforts including translocation of weta and eradication of alien mammalian predators; *D. mahoenui* survives in a very restricted area of dense gorse bushes on the mainland of the North Island. The other seven *Deinacrida* species are on the South Island and survive using diurnal retreats in crevices, burrows or under rocks.

Other large deinacridine anostostomatids also dig burrows or live under rocks and are known for cephalic weaponry exhibited by males. This includes the elephantine tusks of a large tusked weta *Motuweta isolata*, found only on two of the Mercury islands, and two closely related smaller species on the mainland, *M. riparia* and *Anisoura nicobarica*. Tree weta males in the genus *Hemideina* sport very long sexually selected mandibles (Fig. 43). This genus is closely related to *Deinacrida* and several *Hemideina* species are common on the mainland, often in areas of human habitation, as indicated by the common names Auckland and Wellington tree weta. Most tree weta modify beetle holes in trees into galleries, and so are common in firewood. One alpine species lives under rocks. Mating habits of deinacridines vary greatly. *Hemideina* males use their lengthy mandibles to defend harems of females in galleries from rival males; hind femur-on-abdomen stridulation may also be involved in male–male competition. Copulation occurs in association with the gallery and a small spermatophore is transferred. Both *Hemideina* and *Deinacrida* males appear to move frequently in search of mates; *Hemideina* males search for new galleries and *Deinacrida* for individual roaming females, probably detecting their mates using chemical cues. *Deinacrida* pairs remain together throughout the day and the male transfers a dozen or more spermatophores to the female in repeated copulations. For both genera eggs are laid in soil.

Weta (Orthoptera: Anostostomatidae, Rhaphidophoridae), Figure 43 **Male of a Wellington tree weta, *Hemideina crassidens*, showing the lengthy mandibles.**

Also common in New Zealand are ground weta, about 30 species of a small (about 1.5 cm) anostostomatid genus *Hemiandrus*. There are seven described species, so most are undescribed. These members of the subfamily Anostostomatinae differ from deinacridines in lacking tibial tympana and in aspects of reproduction. Pair formation follows vibrational communication between the sexes (abdominal drumming on leaves). During copulation, a spermatophylax gift that the female eats is deposited (in some species) on the female's abdomen following male attachment to secondary genitalia on the female's mid-abdomen. In these species, the ovipositor is reduced and the female lays and cares for eggs (and nymphs) in burrows over several months. Other *Hemiandrus* species have long ovipositors and oviposit in soil.

Anostostomatids share several characters including structure of the proventriculus and certain molecular characters. Phylogenetic analysis supports the family as a natural (monophyletic) group. The current geographic distribution, mainly anostostomatine species, is congruent with Gondwanaland origins for the family. They are typically known as king crickets outside of New Zealand

and are found in Australia (mainly rainforest on the east coast), southern Africa, South America, Madagascar and New Caledonia. Australian species tend to be scavengers of food on the forest floor. A number of species show gigantism and sexual dimorphism similar to New Zealand deinacridines. This includes the extended mandibles in *Henicus, Libanasa* (Africa), and *Anostostoma* (Australia), reaching 2.2 cm in length in the 8 cm-long *Anostostoma australasiae*. Long mandibles are also found in male *Libanasidus* (Africa), including the 6 cm long "Parktown prawn," *L. vittatus*, often common in the suburbs of Capetown. Most species lay eggs in soil, although an undescribed Australian species with a short ovipositor lays eggs in chambers similar to New Zealand ground weta. Some species have tibial tympana and an elaborate spermatophylax-bearing spermatophore.

References

Field LH (ed) (2001) The biology of wetas, king crickets and their allies. CABI International, Wallingford, UK, 560 pp

Gibbs G (1998) New Zealand weta. Reed Publishing. Auckland, New Zealand, 71 pp

Westwood, John Obadiah

John Obadiah Westwood was born at Sheffield, England, on December 22, 1805. He studied law, was admitted to the bar, and became a partner in a law firm. However, his principal interests were archaeology and entomology. Westwood was a noted dipterist, working on such groups as Mydidae, Bombyliidae, and Acroceridae, but possessing immense and broad knowledge on many aspects of Diptera. His artistic ability was a particular strength, and his illustrations were noted for accuracy. Of particular note is his publication "An introduction to the modern classification of insects" (1840), in which he proposed a systematic arrangement of the British insect genera. Other noteworthy publications include "Arcana entomologica," "Oriental entomology," and "Exotic insects." In 1858, a wealthy patron of Westwood's (Hope, see above) established a professorship in invertebrate zoology at the University of Oxford. Westwood was named to the professorship, where he continued his taxonomic work for 35 years. He died at Oxford on January 2, 1893 (Fig. 44).

Westwood, John Obadiah, Figure 44 **John L. Westwood.**

References

Anonymous (1893) The late professor Westwood. Can Entomol 25:261–262

Papavero N (1971, 1973) Essays on the history of Neotropical Dipterology with special reference to collectors (1750–1905). Museu de Zoologia, Universidade de São Paulo, Brazil

Wetas and King Crickets

A family of crickets (Anostostomatidae) in the order Orthoptera.

► Grasshoppers, Katydids and Crickets

Wettable Powder

Finely divided, dry pesticide material that forms a stable suspension when mixed with water.

► Insecticides
► Insecticide Formulation

Wheat Bulb Fly, *Delia coarctata* (Fallon)

This insect tunnels in the stems of grains

► Wheat Pests and Their Management

Wheat Curl Mite, *Aceria tosichella* (Kiefer) (Acari: Eriophyiae)

This is an important vector of plant virus in wheat.

► Wheat Pests and Their Management

Wheat Ground Beetle, *Zabrus tenebrioides* (Goeze) (Coleoptera: Carabidae)

This is a seedling pest in Europe.

► Wheat Pests and their Management

Wheat Head Armyworm, *Faronia diffusa* (Walker) (Lepidoptera: Noctuidae)

An occasional pest, the larvae feed on seed heads.

► Wheat Pests and Their Management

Wheat Jointworm, *Tetramesa tritici* (Fitch) (Hymenoptera: Eurytomidae)

This species is no longer considered to be much of a pest.

► Wheat Pests and Their Management

Wheat Pests and Their Management

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Bread wheat, *Triticum aestivum* L., is one of the major cereal crops, along with rice and corn. One of the first domesticated crops, it is widely grown in temperate climates, and accounts for approximately one-fifth of the acreage devoted to cereal production. Wheat is often referred to as the "staff of life," and accounts for about 20% of the calories in the human diet.

There are several other types of wheat, e.g., durum wheat and club wheat, and there are several other cereal crops with similar growth habits and production practices. Arthropod pests of wheat commonly attack these related crops as well. Barley, *Hordeum vulgare* L., is a widely adapted temperate cereal. It is used primarily for feed and in the production of malt. Oat, *Avena sativa* L., is similar to barley in adaptation, and is used primarily as a feed grain. Rye, *Secale cereale* L., is notable for its adaptation to harsh environments. However, its production is declining due to concerns about grain quality, weediness, and poor agronomic traits. Triticale, *X Triticosecale* Wittmack, is a new crop derived by crossing wheat and rye in an attempt to combine the grain quality of wheat with the hardiness of rye. It has become a useful feed and forage crop in certain areas.

Wheat may be sown either in the fall (winter wheat) or spring (spring wheat). Winter wheats are preferred over spring wheats because of greater yield potential, with the latter predominating where climatic conditions preclude the use of winter types. Seeding rates are quite flexible relative to other crops, because of the wheat plant's ability to compensate for changes in competition from its neighbors. Wheat generally responds to nitrogen fertilization, while phosphorus and potassium requirements vary with local soils. While wheat has few equals as a dryland crop, irrigated production systems are important in some regions. Most systems are designed to optimize grain production; however, wheat is also a high quality forage and is sometimes grown in dual purpose systems intended to optimize both animal and grain production.

Growth and development of wheat and related crops begins with germination and emergence of the seedling. After the appearance of several leaves, the plant enters the tillering phase, in which additional stems (tillers, culms) are formed. The spike (head, ear) starts to form near the end of the tillering phase. A rapid stem elongation phase follows. The end of stem elongation is marked by the appearance of the flag leaf (highest leaf on the stem) and the emergence of the spike. The final phase before maturity and harvest is kernel (seed) growth.

Yield of these crops is determined by the relative magnitude of three components. The priority of pest management should be to protect these components to the point that is economically feasible.

1. Spikes per unit area is determined by the number of plants established during emergence and by the number of stems formed during the tillering phase. Pests that might affect this process include wheat bulb fly, *Delia coarctata*, and wireworms.
2. Number of kernels per spike is determined during stem elongation. Pests that might affect this process include Hessian fly, *Mayetiola destructor*, and Russian wheat aphid, *Diuraphis noxia*.
3. Kernel size is determined during the period from spike emergence to plant maturity. Pests that attack the flag leaf or that feed on the developing kernels, e.g., Sunn pest, can reduce kernel size.

Various pests are important to the production of wheat and related cereal crops because of their ability to affect one or more of these yield components. Table 4 lists some of the more important wheat pests. Some are currently major pests and other have been in the past or have the potential to cause important yield reductions. Some are shown in Figures 45–47.

Wheat production systems vary greatly in the amounts of external inputs, e.g., fertilizers and pesticides, used as well as in the degree of mechanization. Limited resource growers in the Middle East, for example, produce wheat with few inputs or mechanization. Production in western North America is highly mechanized because of the large acreages involved, but other inputs are limited because of low production potential. European production is very input intensive because land is scarce and production potential is high. These differences will determine, in large part, the best pest management approaches to employ in a given production system.

Pest management strategies can be categorized as either preventive, or reactive (therapeutic). Low input wheat production systems tend to achieve pest management objectives through low cost, preventive strategies such as plant resistance, biological control or modified cultural practices. More input-intensive systems tend to emphasize the judicious use of chemical controls.

Plant resistance can be defined as the management of crop pests through the use of cultivars that are relatively resistant to a given pest. This is a relatively inexpensive but effective method employed to prevent losses to such key pests as Hessian fly and Russian wheat aphid. Limitations to this approach include the lack of resistance genes to a given pest, as well as the time required to develop an agronomically acceptable resistant cultivar. Recent advances in molecular biology may help overcome some of these obstacles.

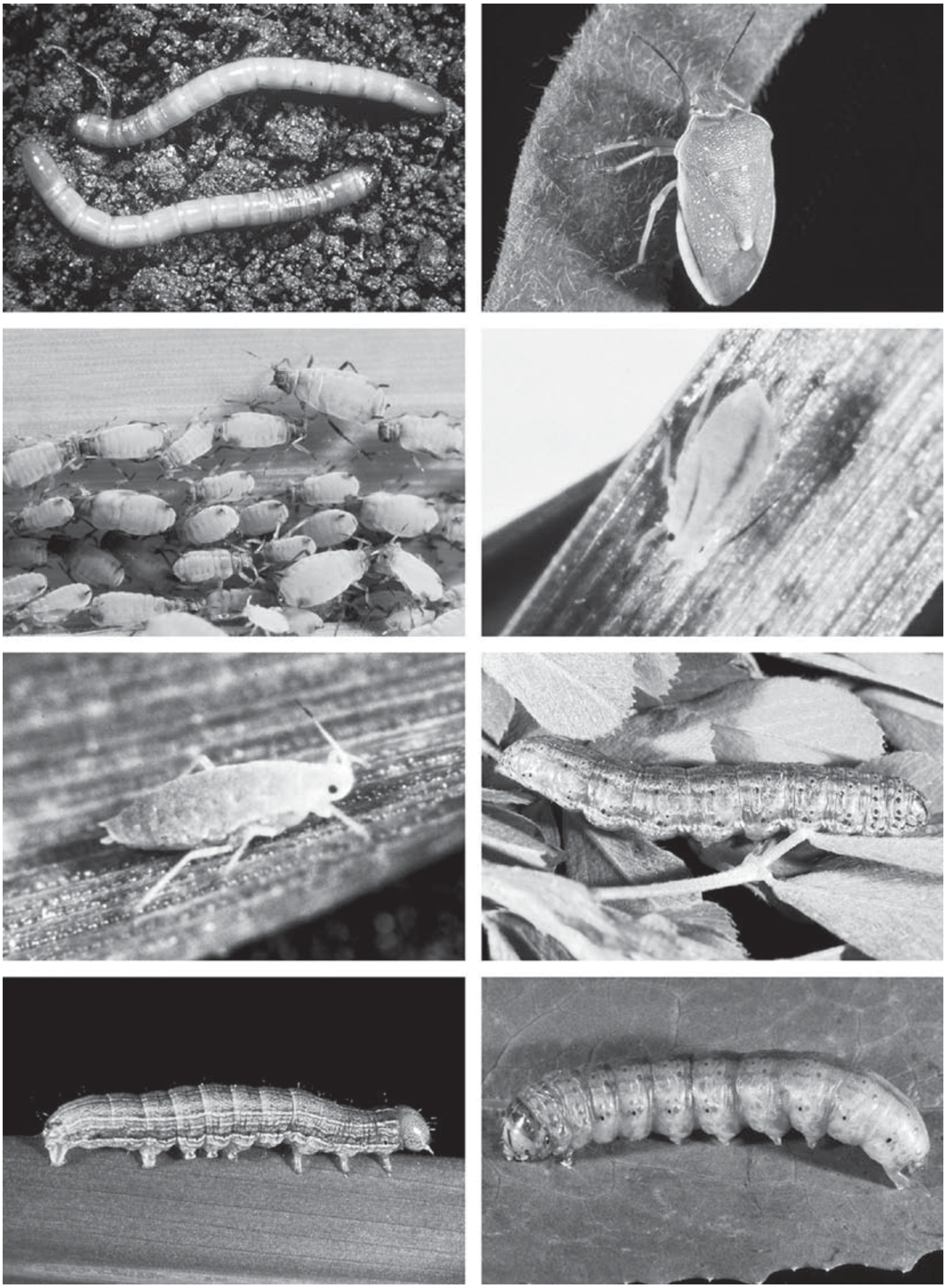
Biological control can be defined as the use of one organism to control another. In the case of crop pests, the controlling organism typically is another arthropod or a pathogen such as a bacterium, fungus or virus. The most common strategy in wheat and similar crops is to conserve naturally occurring biological control agents. Less common are releases of biological control agents into a pest's environment. Releases may be inoculative (i.e., sufficient agents to establish a population), augmentative (i.e., sufficient agents to raise an existing population to an effective level), or inundative (i.e., sufficient agents to control the pest infestation). Releases into wheat tend to be inoculative or augmentative in nature.

Modified cultural practices can be defined as changes in normal crop production operations that are intended to either make the crop environment less conducive to a given pest or more favorable for biological control agents. Examples in wheat production systems might include delayed sowing dates to avoid pest infestation, or increased crop diversification to provide additional food and shelter for biological control agents.

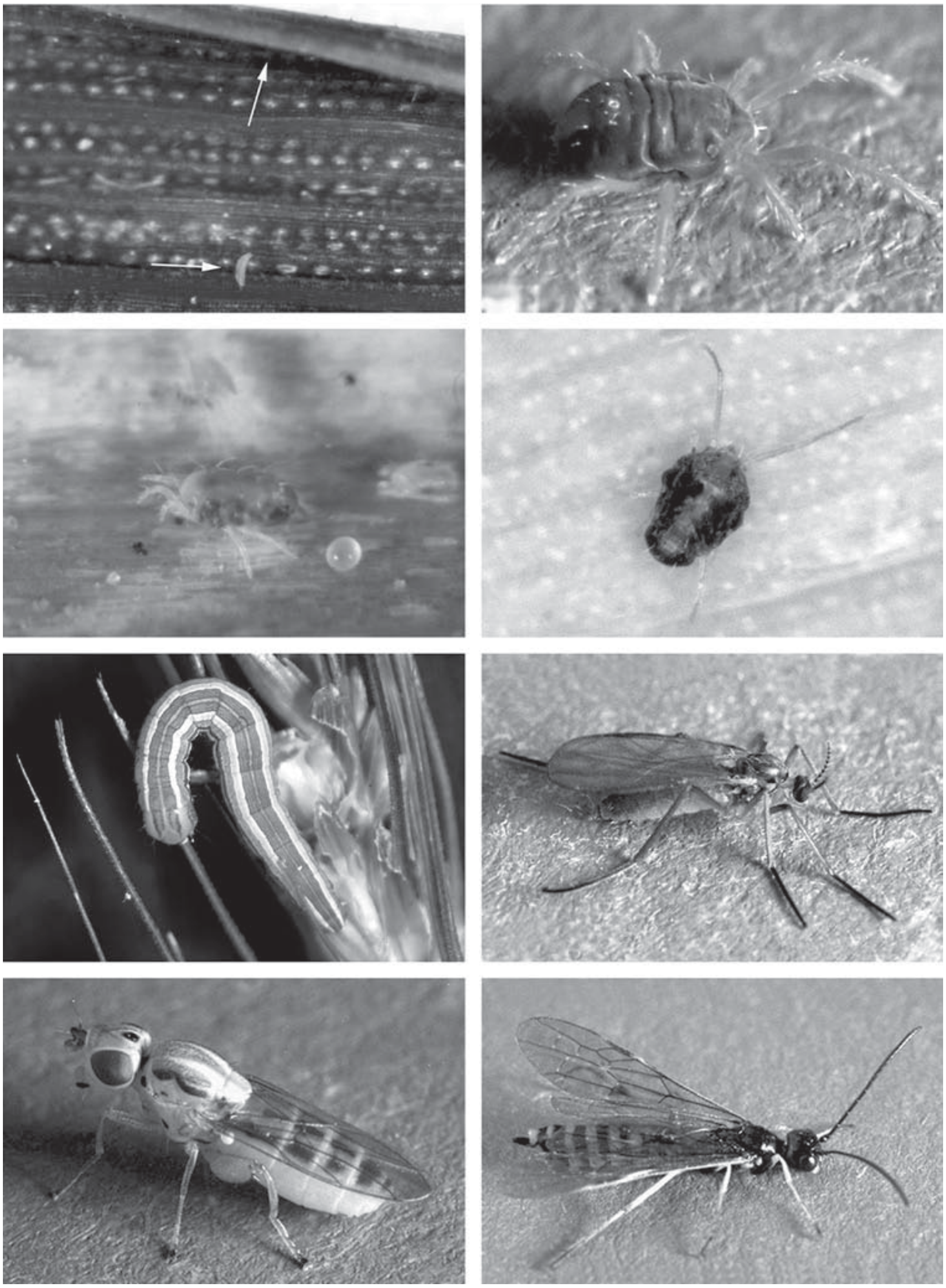
Wheat Pests and Their Management, Table 4 **Insect and Mite Pests of Wheat and Related Crops**

Common name[a]	Scientific name	Order	Family
Wheat curl mite	*Aceria tosichella* (Keifer)	Acari	Eriophyidae
Winter grain mite	*Penthaleus major* (Dugès)	Acari	Eupodidae
Banks grass mite	*Oligonychus pratensis* (Banks)	Acari	Tetranychidae
Brown wheat mite	*Petrobia latens* (Müller)	Acari	Tetranychidae
Grasshoppers	*Melanoplus* spp. (usually)	Orthoptera	Acrididae
Grain thrips	*Limothrips cerealium* (Haliday)	Thysanoptera	Thripidae
Say stink bug	*Chlorochroa sayi* (Stål)	Hemiptera	Pentatomidae
Sunn pest (and other common names)	*Eurygaster integriceps* (Puton), other *Eurygaster* and *Aelia* spp.	Hemiptera	Scutelleridae
Bird cherry-oat aphid	*Rhopalosiphum padi* (L.)	Hemiptera	Aphididae
Corn leaf aphid	*Rhopalosiphum maidis* (Fitch)	Hemiptera	Aphididae
English grain aphid	*Sitobion avenae Fabricius*	Hemiptera	Aphididae
Greenbug	*Schizaphis graminum* (Rondani)	Hemiptera	Aphididae
Rose-grain aphid	*Metopolophium dihrodum* (Walker)	Hemiptera	Aphididae
Russian wheat aphid	*Diuraphis noxia* (Mordvilko)	Hemiptera	Aphididae
Western wheat aphid	*Holcaphis tritici* (Gillette)	Hemiptera	Aphididae
Army cutworm	*Euxoa auxiliaris* (Grote)	Lepidoptera	Noctuidae
Armyworm	*Pseudaletia unipuncta* (Haworth)	Lepidoptera	Noctuidae
Pale western cutworm	*Agrotis orthogonia* (Morrison)	Lepidoptera	Noctuidae
Wheat head armyworm	*Faronta diffusa* (Walker)	Lepidoptera	Noctuidae
Wheat ground beetle	*Zabrus tenebroides* (Goeze)	Coleoptera	Carabidae
Cereal leaf beetle	*Oulema melanopus* (L.)	Coleoptera	Chrysomelidae
Wheat wireworm	*Agriotes mancus* (Say)	Coleoptera	Elateridae
Plains false wireworm	*Eleodes opacus* (Say)	Coleoptera	Tenebrionidae
Wheat bulb fly	*Delia coarctata* (Fallén)	Diptera	Anthomyiidae
Hessian fly	*Mayetiola destructor* (Say)	Diptera	Cecidomyiidae
Lemon wheat midge	*Contarinia tritici* (Kirby)	Diptera	Cecidomyiidae
Wheat midge	*Sitodiplosis mosellana* (Géhin)	Diptera	Cecidomyiidae
Frit fly	*Oscinella frit* (L.)	Diptera	Chloropidae
Wheat stem maggot	*Meromyza americana* (Fitch)	Diptera	Chloropidae
Black grain stem sawfly	*Trechelus tabidus*	Hymenoptera	Cephidae
European wheat stem sawfly	*Cephus pygmaeus* (L.)	Hymenoptera	Cephidae
Wheat stem sawfly	*Cephus cinctus* (Norton)	Hymenoptera	Cephidae
Wheat jointworm	*Tetramesa tritici* (Fitch)	Hymenoptera	Eurytomidae
Wheat strawworm	*Tetramesa grandis* (Riley)	Hymenoptera	Eurytomidae

[a]Common names approved by the Entomological Society of America are used where possible



Wheat Pests and Their Management, Figure 45 **Some wheat insects: *top left*, wireworms; *top right*, Say stink bug, *Chlorochoa sayi*; *second row left*, corn leaf aphid, *Rhopalosiphum maidus*; *second row right*, greenbug, *Schizaphis graminum*; *third row left*, Russian wheat aphid, *Diuraphis noxia*; *third row right*, army cutworm, *Euxoa auxiliaris*; *bottom left*, armyworm, *Pseudaletia unipuncta*; *bottom right*, pale western cutworm, *Agrotis orthogonia*.**



Wheat Pests and Their Management, Figure 46 **Additional wheat pests: *top left*, wheat curl mite, *Aceria tosichella*. Note curling of leaf above. Mites usually found in interveinal spaces; *top right*, winter grain mite, *Penthaleus major* (Ken Gray Image Collection, Oregon State University, modified); *second row left*, Banks grass mite, *Oligonychus pratensis*, egg and adult female; *second row right*, brown wheat mite, *Petrobia latens*, adult female; *third row left*, wheat head armyworm, *Faronta diffusa*; *third row right*, Hessian fly adult, *Mayetiola destructor* (Ken Gray Image Collection, Oregon State University, modified); *bottom left*, wheat stem maggot adult, *Meromyza americana* (Ken Gray Image Collection, Oregon State University, modified); *bottom right*, wheat stem sawfly adult, *Cephus cinctus* (Ken Gray Image Collection, Oregon State University, modified).**

Wheat Pests and Their Management, Figure 47 **Wheat jointworm adult, *Tetramesa tritici* (*left*), and wheat strawworm, *Tetramesa grandis* summer generation adult (*center*) and spring adult (*right*) (modified from Webster, F. M. 1903. USDA Entomology Bulletin 42.)**

Most reactive or therapeutic measures for pest management in wheat involve chemical control, the application of insecticides or miticides to control existing pest infestations. Chemical controls are unique in that they are capable of eliminating existing infestations over large areas in a relatively short time span. However, insecticides and miticides are poisons, and their use has associated health and environmental risks. Also, chemical controls are expensive, and are cost effective only if they are applied when the economic return from the treatment is expected to be greater than the treatment cost.

There are many examples of pests adapting to a given type of control, particularly resistant cultivars and insecticides, rendering them ineffective. In addition, many preventive controls are not sufficiently effective to completely control pest infestations. For these and other reasons, a combination of controls is generally recommended for the management of wheat pests. This multi-tactic approach is often referred to as integrated pest management or IPM.

Wheat Curl Mite

The wheat curl mite, *Aceria tosichella* (Kiefer), is found throughout Europe and North America. It is most important as a vector of Wheat Streak Mosaic virus disease. However, it can damage wheat directly by curling leaves. Leaf curling is a tight roll of the leaf margin in contrast to the looser roll of the entire leaf caused by Russian wheat aphid. The emerging spike may become trapped in the flag leaf if the latter is tightly curled.

Wheat curl mite is member of a group of microscopic, wormlike plant-feeding mites known as eriophyids. They have two pairs of legs and a few setae. Eriophyid mites are very difficult to identify because of their size and simplified external morphology, and there are many unresolved questions regarding the identities of the eriophyids associated with a given plant species.

Eggs, immature stages, and adult wheat curl mites are found in the winter on wheat and other nearby perennial grasses. As temperatures rise in the spring, mite populations develop under leaf sheaths, inside newly emerged leaves, and eventually within the wheat head glumes. Eggs are placed in rows along leaf veins. An average complete generation requires 10 days. Most mites are found on the terminal leaves and move to each new leaf as it emerges.

As the wheat plant dries down, the wheat curl mites congregate on the upper parts of the plants where they are picked up by wind currents and are carried to their oversummering grass hosts. As summer hosts start to dry down, the reverse process occurs and mites are carried by winds to newly emerged winter wheat.

The wheat curl mite attacks a wide variety of grasses, mostly in the *Agropyron*, *Elymus*, *Hilaria*, *Hordeum*, *Lolium*, *Muhlenbergia*, *Triticum*, and *Zea* genera. Corn, volunteer wheat and wheat grasses are potential important oversummering hosts. This species is also associated with garlic, onions, and other bulb crops.

Destruction of volunteer wheat and the maintenance of a volunteer-free period prior to planting winter wheat in the fall is the most effective management practice for this mite and the diseases that it vectors. Some effective varietal resistance (due to resistance to the mite) is available. Chemical control of wheat curl mites has not been shown to be an effective or economical practice.

Winter Grain Mite

The winter grain mite (also known as blue oat mite or pea mite), *Penthaleus major* (Dugès), is found in temperate areas throughout the world. It has higher moisture requirements than other mite pests of winter wheat and thus is found in more humid production regions. Crops heavily infested with winter grain mite take on a grayish or silvery cast. Plants may be stunted. Leaf tips appear scorched and entire leaves or plants can be killed.

Winter grain mite is a large dark brown to black mite, with reddish legs. A tan or orange spot is often visible on the back. This mite has two generations per year. In North America, the first begins in the fall as the oversummering eggs hatch after rains provide adequate moisture. Feeding peaks in December or January. Second generation feeding peaks in March or April. Populations decrease and oversummering eggs are produced as temperatures become unfavorably warm.

Newly-hatched mites feed on leaf sheaths and tender shoots near the ground. Older immatures and adults feed higher up on the plants at night and on cloudy or cool days. They move to the soil surface and into the soil to seek moisture and to avoid warm temperatures. Winter grain mite activity is greatest between 5 and 21°C. On hot, dry days it may be necessary to dig 10–12 cm into the soil to find the mites. The mites are not harmed by high humidity, rainfall, short periods of sleet or ice cover, or by ground frozen to a depth of several inches.

Favored hosts include small grains and grasses. Winter grain mite also has been reported to damage legumes, vegetables, ornamental flowers, cotton, peanut, and various weeds.

Little is known about winter grain mite management. Crop rotation is recommended. Infestations probably should exceed several mites per plant before chemical treatment is considered.

Banks Grass Mite

The Banks grass mite, *Oligonychus pratensis* (Banks), is a spider mite that feeds on grasses in many parts of the Americas and Africa. It attacks a wide variety of grasses, and is considered to be a serious pest of corn and an occasional pest of grass hay, sorghum, turf and wheat in irrigated crops grown in semi-arid regions.

Damaged wheat leaves are chlorotic and small plants may be killed. Damaged areas on larger plants may have a bright yellow appearance. Infested plants in the fall are often near drying corn. The undersides of infested leaves may be covered with noticeable amounts of webbing.

In North America, fertilized female Banks grass mites move into winter wheat in the fall as their summer hosts, primarily field corn, begin to dry down. Overwintering mites are bright orange. With the onset of winter conditions the mites move to the crowns of wheat plants where they feed until spring. Small pearly white eggs then are laid that mature into pale to bright green male and female adults. Mites then breed continuously on wheat and summer hosts until their return to winter wheat in the following fall. Banks grass mites produce heavy webbing to protect colonies consisting of eggs, immatures and adults. Colonies usually are found on the undersides of leaves. The time required to complete a generation varies with temperature and is usually 10–20 days.

Damaged leaves first become yellow, then brown and necrotic. Heavy populations can kill small plants and reduce kernel size in larger plants.

Crop rotation patterns that place corn adjacent to wheat should be avoided. Biological control is quite useful when Banks grass mite is on its summer host. Chemical control is commonly used against it in higher value crops, e.g., irrigated field corn.

Brown Wheat Mite

The brown wheat mite, *Petrobia latens* (Müller), is a pest of wheat and similar crops in most small grain-producing areas of the world. The economic importance of this species has been difficult to determine because it is closely associated with drought conditions. Brown wheat mite has also been reported from many other cultivated plants, including turf grasses, sorghum, onions, fruit trees, carrots, cotton, lettuce, iris, alfalfa, and clover.

Wheat leaves damaged by brown wheat mite have a finely mottled appearance, and may have chlorotic tips. Heavily infested crops appear drought stressed, and often have an overall yellowish to bronzed discoloration.

In North America, brown wheat mite spends the summer in the soil as a white egg resistant to hot, dry conditions. In the fall, as cooler, wetter conditions return, these eggs start to develop and hatch after a 10-day incubation. Adult brown wheat mites can be distinguished from other mites found on wheat by their extremely long front legs. Female mites mature after feeding on wheat for about 2 weeks and then lay round, red eggs which give rise to further fall (one or two) and spring (two or three) generations. Males have not been observed in this species. As summer conditions return, white oversummering eggs again are produced. Both red and white eggs are placed on soil particles adjacent to wheat plants.

Brown wheat mites feed on plant sap during the day and spend the night in the soil or under surface debris. Their activity peaks at about mid-afternoon on warm, calm days. This mite is not affected by cold temperatures, but populations are quickly reduced by driving rains of about 1cm or more.

Management of volunteer wheat is an important preventive measure for brown wheat mite, as it is with many winter wheat pests. Any management practices that serve to minimize drought stress also are important. Once an outbreak occurs, however, chemical control is the only effective management practice. It is often difficult to justify a chemical treatment because brown wheat mite infestations are associated with drought stress. Also, if white eggs are present and red eggs are mostly hatched, the population is in natural decline and treatment is not economically justifiable.

Thrips

Several thrips attack wheat and other small grains throughout the world, including the barley thrips, *Limothrips denticornis* (Haliday), grain thrips, *Limothrips cerealium* (Haliday) and wheat thrips, *Haplothrips tritici* (Kurdjumov). Thrips feeding results in discolored or distorted leaf tissue. More importantly these thrips feed on developing grains, resulting in sterility or poorly formed or discolored kernels.

These thrips overwinter as adults. Females are light brown to black in color, elongate, and have fringed wings. Males are smaller, and, in the case of *Limothrips*, wingless. Fertilized females move to cereals and other grasses in the spring and begin to feed on the youngest leaves. They insert their eggs in leaf tissue in sheaths or axils, and in the spike when it becomes available. Wheat thrips oviposition tends to be near or on the spike. The pale yellow (*Limothrips*) or red (*Haplothrips*) nymphs are similar in shape to the adults, and feed in leaf sheaths or in the spike. Pupation occurs in the soil. Females mate and then disperse to overwintering sites after the cereal host matures. There are one to two generations per year.

The only available management strategy for these thrips is the use of well-timed insecticide applications. Treatments must be made before flowering, and should be based on scouting and an economic threshold, if available.

Say Stink Bug

The Say stink bug, *Chlorochroa sayi* (Stål), is likely a complex of species which also includes *C. granulosus* and *C. uhleri*. Much of the research on this pest group was conducted before recent taxonomic studies revealed that three species were involved. The name Say stink bug will be used for all members of this group. It is found in the western United States and Canada, and attacks several crops including wheat, barley, alfalfa, and cotton. Russian thistle appears to be an important non-cultivated source of food and shelter throughout the year.

Damage to wheat and barley is caused by feeding on developing seeds. This results in reduced numbers of grains and shrunken, discolored and shriveled grain, and therefore reduced yield and quality. The type and amount of damage is closely related to the stage of plant and grain development, with greatest vulnerability between spike emergence and the grain "dough" stage.

Stink bugs are so called because they release a foul-smelling fluid when disturbed. The Say stink bug is large, reaching about 20 mm in length as adults. They are shield-shaped and bright green in color, and they are marked on the back with raised white dots on back as well as three white or orange spots. Say stink bug eggs are barrel-shaped and marked with white circles, when viewed from above. The eggs are usually attached to the leaf in two-row clusters.

Adult Say stink bugs overwinter in sheltered areas such as underneath tree bark or at the base of native grasses. They become active in the spring and move to various host plants, including Russian thistle, where they feed, mate and lay eggs. As their original hosts are depleted or mature, they move to cultivated crops, particularly small grains. Large groups of adults may move from field to field, remaining only as long as grains are in an acceptable developmental stage. There may be several generations during the summer before the adults move to overwintering sites in the fall.

Because of the sporadic and transitory nature of Say stink bug infestations in small grains, management strategies are generally limited to chemical control. Treatment thresholds are not well defined, but they are quite low because of the great damage potential per individual stink bug.

Sunn Pest

The Sunn pest, *Eurygaster integriceps* Puton, is the most important member of a group of shield bugs that are major pests of small grains in eastern Europe and the Near and Middle East. The information given here applies to *E. integriceps*, but the other species in the complex are quite similar in appearance and biology. These insects feed on all aboveground parts of wheat and other cereals, but the most important damage is due to direct feeding on developing grains. This results in loss of kernels and shriveled or discolored kernels. Damaged kernels have very poor baking quality, and can affect the baking quality of undamaged kernels when milled together.

Sunn pests are large insects, about 1.5 times longer than they are wide. They get their family name (shield bugs) from the fact that the scutellum (part of the thorax) extends back to cover most of the abdomen. Sunn pests are quite variable in color, ranging from yellow-brown to black.

Sunn pest has one generation per year. Eggs are laid in small clusters on leaves of cereals and many other grass hosts. Nymphs feed on leaf tissues until maturation, which usually coincides with kernel development. After 2 weeks or so of feeding, the adults fly to higher elevations to spend the summer and following winter. In more northern latitudes this period is spent in deciduous forests. In the fall they tend to move to protected overwintering sites, where large numbers can be found clustered in relatively small areas. In the spring, adults return to cereal fields and other host locations to mate and reproduce.

Chemical control is the predominant management strategy. Biological control with egg parasitoids and cultural controls, primarily the use of short season cultivars and modified harvest practices, have also been recommended.

Bird Cherry-Oat Aphid

The bird cherry-oat aphis, *Rhopalosiphum padi* (L.), is an important pest of cereals in most production areas of the world. It is important for the damage that it causes as well as for vectoring Barley Yellow Dwarf virus (BYDV). Yield loss relationships are complex, being affected by crop type, crop growth stage, crop condition, presence of other aphid species, and presence of BYDV. Grain yield losses as high as 50% have been observed in winter wheat infested at the two leaf stage.

The wingless form of the bird cherry-oat aphid is broadly oval in shape, is yellowish-green to dark green in color often with a reddish patch at the rear, and long, black-tipped cornicles. The life cycle is complex where severe winter conditions and suitable primary hosts are present. Reproduction occurs on the primary host, several species of *Prunus* trees, in the fall, and the winter is passed in the egg stage. Colonies are formed on new growth in the spring, which give rise to winged females that disperse to grasses for the summer. Their progeny are wingless, parthenogenetic females, and this form predominates on various grass hosts throughout the spring and summer. Winged males and winged, parthenogenetic females are produced in the fall for the return flight to the primary host. If winter conditions are sufficiently mild and *Prunus* plants are absent, then a simplified life cycle of parthenogenesis on grass hosts is followed throughout the year.

Management strategies include modified cultural practices such as delayed planting to avoid virus transmission and promotion of biological controls. In more intensive production systems, chemical controls based on economic thresholds are often used.

Corn Leaf Aphid

The corn leaf aphid, *Rhopalosiphum maidis* (Fitch), is an important pest of cereals in many production areas of the world, particularly in warmer climates. It is more important as a vector of viruses such as Barley Yellow Dwarf virus (BYDV) than for the plant damage it causes. Corn leaf aphids prefer to feed on the young leaves of many types of grasses, including small grains and maize. Yield losses in wheat or other cereals have not been well documented.

The wingless form of the corn leaf aphid is elongate and varies in color from yellowish green to bluish green with black legs, antennae and cornicles. The antennae and cornicles are relatively short. The cornicles are long and black in color. A simplified life cycle of parthenogenesis on grass hosts is followed in most parts of the world, although males are observed occasionally.

Management strategies include cultural practices such as modified planting dates to avoid virus transmission. Biological controls are often effective. Chemical controls are rarely recommended because of this aphid's limited damage potential.

English Grain Aphid

The English grain aphid, *Sitobion avenae* (Fabricius), is an important pest of cereals in many production areas of the world. It is important for the damage that it causes to the plant, as well as for vectoring of Barley Yellow Dwarf virus (BYDV). English grain aphids prefer to feed on upper leaves and the spikes, once they have emerged. Late season infestations can reduce grain yield and quality. Yield loss relationships are complex, being affected by crop type, crop growth stage, crop condition, presence of other aphid species, and presence of BYDV. Grain yield losses greater than 30% have been observed in wheat.

The wingless form of the English grain aphid is moderate in size and spindle-shaped. It is generally green to brown in color. The cornicles are long and black in color. The life cycle occurs entirely on grasses. Sexual reproduction and overwintering eggs occur where severe winter conditions are present. If winter conditions are sufficiently mild then a simplified life cycle of parthenogenesis on grass hosts may be followed throughout the year.

Management strategies include cultural practices such as modified planting dates. Biological controls can be effective in some situations. Plant resistance has been identified but not used commercially. In more intensive production systems, chemical controls based on economic thresholds are used.

Greenbug

The greenbug, *Schizaphis graminum* (Rondani), is an important pest of cereals in many production areas of the world. It is most important for the damage that it causes to the plant, but is also a vector of Barley Yellow Dwarf virus (BYDV). Leaf tissue affected by greenbug is often discolored yellow or red due to the phytotoxic nature of its saliva. Yield loss relationships are complex, being affected by crop type, crop growth stage, crop condition, presence of other aphid species, and presence of BYDV. Grain yield losses greater than 50% have been observed in several crops.

The wingless form of the greenbug is relatively small and more elongate than oval in shape. It is generally light green in color, with a darker green dorsal stripe. The cornicles are mostly colorless with darker tips. The life cycle occurs entirely on grasses. Sexual reproduction and overwintering eggs occur where severe winter conditions are present. If winter conditions are sufficiently mild then a simplified life cycle of parthenogenesis on grass hosts may be followed throughout the year.

Management strategies include modified cultural practices such as delayed planting to avoid virus transmission and reduced tillage. Biological controls can be effective in some situations. Greenbug resistant varieties have been used widely in sorghum, but the development of biotypes has limited the sustainability of this approach. In more intensive production systems, chemical controls based on economic thresholds are often used; however, greenbug resistance to carbamate and organophosphate insecticides has been documented.

Rose-Grain Aphid

The rose-grain aphid, *Metopolophium dirhodum* (Walker), is an important pest of cereals in many non-tropical areas of the world. It is important as a direct plant pest as well as a vector of Barley Yellow Dwarf virus (BYDV). Rose-grain aphids prefer to feed on the upper leaves of wheat and other grasses, but rarely on the spike. Yield loss relationships are complex, being affected by crop type, crop growth stage, crop condition, presence of other aphid species, and presence of BYDV. Grain yield losses of 10–20% have been observed in wheat.

The wingless form of the rose-grain aphid is spindle shaped, and is yellowish green to green with a dorsal stripe on the abdomen. The antennae, legs and cornicles are generally pale. The life cycle is usually complex, although a simpler life cycle of parthenogenesis on grasses is common in western Europe. Reproduction occurs on the primary host, several species of *Rosa*, in the fall, and the winter is passed in the egg stage. Colonies are formed on new growth in the spring, which give rise to winged females that disperse to grasses for the summer. Their progeny are wingless, parthenogenetic females, and this form predominates on various grass hosts throughout the spring and summer. Winged males and winged, parthenogenetic females are produced in the fall for the return flight to the primary host.

Management strategies include modified cultural practices such as delayed planting to avoid virus transmission and promotion of biological controls. In more intensive production systems, chemical controls based on economic thresholds are often used.

Russian Wheat Aphid

The Russian wheat aphid, *Diuraphis noxia* (Mordvilko), is an important pest of wheat and barley in western North America and South Africa. It also damages these crops sporadically in North Africa, southern Europe, the Middle East, Central Asia, Chile and Argentina. It is important for the direct damage that it causes to its hosts, but is not considered an important vector of plant viruses. Damage symptoms include tightly rolled leaves, white or purple leaf streaking and stunted plants. Yield loss relationships are complex, being affected by crop type, crop growth stage, crop condition, and the presence of other aphid species. Grain yield losses as high as 80% have been observed in malt barley.

The wingless form of the Russian wheat aphid spindle-shaped, light green in color, and may have a somewhat waxy appearance. The antennae are short and the cornicles are greatly reduced. The supracaudal process is unique among the cereal aphids. In the New World and South Africa a life cycle of parthenogenesis on a variety of cool season grass hosts is followed. Sexual reproduction and an overwintering egg stage are commonly observed in Old World populations. The closely related western wheat aphid, *Diuraphis tritici* (Gillette), is found in western North America, has a similar life cycle and causes similar damage.

Management strategies include modified cultural practices and promotion of biological controls. Resistant varieties have been developed in wheat and are grown widely in areas with consistent Russian wheat aphid infestations. In more intensive production systems, chemical controls based on economic thresholds may be used.

Army Cutworm

The army cutworm, *Euxoa auxiliaris* (Grote), occurs in the cereal production areas of much of western North America. This is a climbing cutworm found feeding at night and on cloudy days on the aerial portions of small grains and many other plants. Yield loss relationships are poorly understood, with the degree of loss being particularly influenced by crop growth stage, plant population and drought stress. Losses in winter wheat in excess of 30% have been observed. More losses observed when there is relatively little foliage, which increases the likelihood of damage to the crown.

Army cutworm larvae are nearly 5 cm long when fully grown, generally colored light gray with lighter markings and a pale stripe running down the back. Adults are small moths, with a wingspan of about 3–4 cm. They are nuisance invaders of homes and other structures during their spring migration to higher elevations.

The army cutworm has one generation per year. Eggs hatch in the fall following a rainfall. The winter is passed as partially grown caterpillars, which feed on warmer days. They feed more frequently in the spring and develop more rapidly. As daytime temperatures rise, the army cutworm is found under soil clods and other debris during the day. This is a climbing cutworm that always feeds above ground during the night and on cloudy days. Pupation occurs in a small chamber constructed several inches below the soil surface. Moths emerge in May and June and migrate to higher elevations to escape high summertime temperatures. In late summer and early fall, the moths return to the plains to lay their eggs in wheat fields and other cultivated areas.

Because of the sporadic nature of outbreaks, management strategies are mostly limited to insecticide treatments based on economic thresholds. Pyrethroid insecticides, as a group, have been quite effective.

Armyworm

The armyworm, *Pseudaletia unipuncta* (Haworth), is a pest of small grains and other grass crops in North America east of the Rocky Mountains. Armyworm outbreaks occur only occasionally, more commonly during cool, wet springs, because natural population regulation usually prevents the development of economically significant infestations. The common name comes from this species' habit of moving in mass once they deplete local food sources. Damage commonly occurs when armyworm larvae defoliate the lower portions of various crops, although complete defoliation may occur during severe infestations. Defoliation is often complete, with only the leaf midribs left uneaten. Armyworm feeding in small grains near crop maturation is even more serious because it can result in spikes being clipped off and lost when larvae chew through the last remaining green tissue just below.

Mature larvae are about 4 cm in length, smooth-bodied, and dark grey to greenish-black. They have five stripes, three on the back and two on the sides, running the length of the body. While the stripes on the back are variable in color, the stripes on the sides are pale orange with a white outline. The head capsule is remarkable for its "honeycomb" of black markings.

Armyworms pass the winter as partially grown larvae in the southern part of their range. Armyworm moths migrate to the northern part of their range in early summer. The moths have grayish-brown forewings, each with a white spot near the center, and grayish-white hind wings. The wingspan is approximately 4 cm. Armyworm moths lay their eggs in rows or clusters on the lower leaves of various grass crops. They prefer dense, lush vegetation for egglaying. Newly hatched larvae move with a looping (inchworm) action. Larvae feed at night and on cloudy days, and hide under crop debris during sunny periods. One or more generations may occur per year.

Pale Western Cutworm

The pale western cutworm, *Agrotis orthogonia* Morrison, occurs in North America from the western High Plains to the Pacific and from Canada to New Mexico. It is a more consistent problem in the northern plains states and southern Canada. It is potentially one of the most devastating insect pests of wheat in the region. Pale western cutworm is a subterranean cutworm, and feeds on stems below ground just above the moisture line. In drier soils larvae tend to feed further down on the stem and consume little tissue before moving to the next stem. This results in many severed stems and entire fields may be lost in a matter of days. In moister soils larvae feed further up on the stem and consume most of a single stem, which results in less overall damage to the crop.

Pale western cutworm larvae have greyish white, unmarked abdomens. They are distinguished from other similarly unmarked cutworms by the presence of two distinct vertical brown bars on the front of the head capsule. Eggs are deposited in loose soil. Some eggs may hatch within a few weeks, but most wait until the following spring when air temperatures at the soil surface reach 21°C. Hatch may be delayed for up to several months if moisture and temperature conditions are unfavorable. Larvae prefer loose, sandy or dusty soil and are found most easily in the driest parts of the field, such as hilltops. Pupation occurs in chambers constructed several inches below the soil surface. Emergence of the gray to brownish white adult moths occurs in late summer and fall. They have an approximately 3–4 cm wingspan and are distinguished from other cutworm moths by the white undersurface of the wings.

Outbreaks are associated with dry conditions in the previous spring, because rainfall events of more than 6–7 mm tend to drive the cutworms to the soil surface and expose them to increased predation and parasitism. If the preceding May and June had fewer than 10 days with 6–7 mm or more inches of rainfall, then pale western cutworm population densities can be expected to increase. If the preceding May and June had more than 15 such days then pale western cutworm abundance will be greatly reduced.

Because of the sporadic nature of outbreaks, management strategies are mostly limited to insecticide treatments based on economic thresholds. Pyrethroid insecticides, as a group, have been quite effective.

Wheat Head Armyworm

The wheat head armyworm, *Faronta diffusa* (Walker), is found in most cereal production areas of North America north of Mexico and east of

Arizona. Wheat head armyworm feeds on various grasses and small grains crops, with the first observed outbreaks occurring on timothy. While wheat head armyworm is considered to be a minor pest, its habit of feeding on developing spikes and grains gives it significant damage potential. Damaged kernels have the attachment end gouged out, as if they had been damaged in storage by *Sitophilus* spp. weevils.

Little is known about the life history of this insect. It spends the winter as a pupa in the soil. The small brown moths emerge to lay eggs in rows within leaf sheaths in the spring, and larvae can be found in wheat in June. First generation larvae feed on the heads of wheat at night and hide near the base of the plant during the day. Fully grown larvae are variable in color, ranging from light green to brown. They are tapered towards the rear, and have several stripes that vary in width and color.

No chemical control data or economic threshold studies are available for this insect. Infestations often are limited to field margins. If an outbreak occurs, any registered contact insecticide should be effective against this insect.

Wheat Ground Beetle

The wheat ground beetle, *Zabrus tenebroides* (Goeze), is an important pest of seedling winter wheat in many parts of Europe. Larvae feed on the leaves of young plants, causing a frayed or skeletonized appearance, or tunnel in the crown. Loss of plant stand often results. Adults feed on developing grains, but this damage is not considered to be as important as that caused by the larvae. Yield loss relationships can be significant under conditions unfavorable for compensatory plant growth.

The adults are small (about 1 cm) reddish brown ground beetles. Eggs are laid in soil when moisture content is adequate, usually from July through September. The larval stage is found from late September through the following spring, when the adults appear. The larvae, up to 3 cm in length, have a whitish body and brown head, thorax and legs. They overwinter in chambers in the soil, and feed actively on host plants during periods of active crop growth.

Management strategies emphasize cultural practices including adequate fertilization to encourage crop compensation in thinned stands, and crop rotation. Insecticide treatments targeting the larvae also are recommended.

Cereal Leaf Beetle

The cereal leaf beetle, *Oulema melanopus* (L.), has been known in Europe as an occasional pest of small grains for more than a century. It was introduced into North America in 1962, and has spread to most cereal production in the northern half of the United States. Adults and larvae defoliate small grains, especially those sown in the spring. Losses as high as 75% in barley and oats have been reported. Reduction in malt barley quality is of special concern.

Adult cereal leaf beetles prefer to feed on young, actively growing leaves. They chew completely through the leaf, between the veins, resulting in linear streaking of the leaf. This damage is easily confused with that of flea beetles. Larvae feed only on the upper surface of the leaves. They feed down to the leaf cuticle, staying between the veins, resulting in distinctive linear "window-pane" damage. Larval feeding differs from adult damage in that it is wider and limited to the upper surface of the leaf. Tips of damaged leaves may turn white, and heavily infested fields may have a frosted appearance.

Adult cereal leaf beetles are about 5–7 mm long, with a metallic blue head and wing covers, a red pronotum (neck) and orange-yellow legs. The eggs are less than 2 mm long, yellow when first laid, but darkening to yellow-brown when about to hatch. Larvae appear dark and slug-like. Their skin is yellowish brown, and is covered by a mass of slimy, dark fecal material.

Cereal leaf beetles spend the winter in protected sites like grass crowns, grain stubble, wooded areas, or under house siding. They become active when air temperatures are above 10°C. They feed on wild grasses and move to small grains when available. Females mate in the spring, and begin to lay eggs about 2 weeks later. A single female may lay up to 300 eggs over a 6 week period. The eggs hatch in 4–23 days, depending on temperature. Larvae feed for 10–21 days, depending on temperature, before crawling down the plant to pupate in the upper two inches of soil. The larval feeding period can last up to 2 months, due to continuous overwintering adult emergence and egg laying. The pupation period lasts 2–3 weeks.

Newly emerged adult beetles feed for 2–3 weeks on the new succulent growth of a wide variety of grasses, after which they disperse to overwintering sites where they enter dormancy. Winter mortality, due extreme temperatures and natural enemies, ranges to from 40 to 70%. There is one generation of cereal leaf beetle per year.

Effective biological controls are available, and are used preventively and successfully. The larval parasite *Tetrastichus julis* (Walker) has been an effective biological control agent in the western United States. The egg parasite *Anaphes flavipes* (Forester) has worked well in combination with larval parasites in the eastern United States. Insecticide treatments are used to control existing infestations based on the potential for economic losses greater than the cost of treatment.

Wireworms and False Wireworms

Wireworms and false wireworms attack wheat in most production regions of the world. Important North American wireworm species include the wheat wireworm, *Agriotes mancus* (Say), the prairie grain wireworm, *Ctenicera aeripennis destructor* (Brown), and the Great Basin wireworm, *C. pruinina* (Horn). Important false wireworms include several *Eleodes* species, such as the prairie false wireworm, *E. opacus* (Say), are found in drier production regions of North America. Wireworms and false wireworms damage wheat by feeding on seeds, seedlings and young plants, resulting in lost stand. Yield losses occur if plant population losses are large enough to overcome the compensatory ability of the crop.

Adult wireworms are known as click beetles, which get their name from the sound they make as they jump. They are elongate brown or grey beetles, with parallel sides and rounded at the head and rear. The damaging larval stage is cylindrical, slender, hard-bodied, usually a shiny brown or pale yellow in color. The flightless adult false wireworms are known as darkling beetles. These are large black or reddish brown beetles, which can be recognized by the odd angle that the body is held at when they run. The larvae are similar in appearance to wireworm larvae.

Wireworm adults lay their eggs in soil and most of the life cycle is spent in the larval stage. Larvae will be found at varying depths in the soil, depending on temperature and moisture. Life cycles are variable, lasting from 1 to 9 years. The false wireworms have a similar life cycle, although most are completed within 3 years.

Management strategies emphasize cultural practices that promote rapid germination and seedling growth to shorten the period that the plant is most vulnerable to attack. Insecticidal seed treatments also are commonly used.

Wheat Bulb Fly

The wheat bulb fly, *Delia coarctata* (Fallén), is an important European pest of wheat and other small grains. It is also found in North America, but generally is not considered to be an important pest there. Larvae tunnel in the base of the main stem or tillers, resulting in the loss of plants or spikes.

The adults are small, slender gray flies with relatively large wings and a bristly appearance. They lay their eggs in the soil in mid summer. The elongate white eggs hatch during the winter and the larvae move to grass hosts and bore into the base (bulb) of the main stem or one of the tillers. After several weeks, when about 3/4 grown, the maggots move to another stem, either on the same plant or a new plant. Pupation occurs in late spring, and within a few weeks adults emerge from the soil to mate and lay the eggs of the next generation.

Management strategies include early planting of winter crops to obtain larger more tolerant plants at the time of larval hatch, and delayed planting of spring crops to avoid the hatch and infestation period. Chemical controls include treatment of the seed, seedbed and plants. Expert systems and other decision support tools are available to help improve the efficacy and cost effectiveness of insecticide treatments.

Hessian Fly

The Hessian fly, *Mayetiola destructor* (Say), has spread from its original home in the Caucasus region of Eurasia to most major wheat producing regions of the world. It has been a pest of wheat in the United States since the eighteenth century, and is considered to be one of the most serious pests of wheat in the world. Damage to the plant is caused by the larval stage, which sucks juices from the plant. Feeding results in stunted and dead tillers and plants, and broken stems resulting in unharvestable grains. Hessian fly prefers wheat but also attacks barley and rye.

The adult is a small grey or black midge. The eggs are cylindrical and glossy red in color. The wormlike larvae vary in color, but are greenish white when fully grown. Pupation occurs within a glossy brown protective case (puparium) referred as a "flaxseed."

In the fall, adults emerge from stubble and volunteer winter wheat to lay several hundred eggs on the leaves of young plants. The adults die within a few days of emergence. At about the same time the eggs hatch and the larvae move to the crown of the plant to feed. The larvae usually finish their development before the onset of cold weather. Winter is passed in the "flaxseed" stage. Pupation and a second flight of adults occurs in the spring at about the time of jointing. Larvae of the spring generation feed in leaf sheaths and then form the puparia in which they spend the summer.

The use of resistant varieties is the most effective method of managing Hessian fly in areas where it is a key pest. However, Hessian fly biotypes often develop in response to the deployment of resistant varieties. Delaying planting to avoid the short egg-laying period is also an effective management practice. The "fly-free" date is a term for the time after which wheat can be planted to avoid Hessian fly infestations. Destruction of volunteer wheat also helps to reduce Hessian fly infestations.

Wheat Midge

The wheat midge, *Sitodiplosis mosellana* (Géhin), is found in most wheat production areas in the Northern Hemisphere, and can be a key pest of wheat under favorable conditions. The lemon wheat blossom midge is a related species, *Contarinia tritici* (Kirby), that is similar in appearance, life cycle and damage. However, its distribution is limited to Europe and Asia. Wheat midge larvae feed on developing kernels of wheat and other grasses, causing them to shrivel, crack and become deformed. These losses in yield and quality can be great enough and the midge difficult enough to control in certain areas that ceasing wheat production is the only economic solution.

The adult wheat midge is a small, fragile orange fly with prominent black eyes, long legs, and oval fringed wings. They emerge from the soil in late June or early July. Females are active during the evening hours, laying eggs on freshly emerged spikes. The orange maggots hatch within 1 week and move to the interior of the spike to feed on the surface of a developing kernel. After 2–3 weeks, fully grown larvae drop to the soil to overwinter. However, under dry conditions they may enter a resting stage that may last even to the time of harvest. Overwintering larvae remain in the soil for one to several winters, usually in the top several inches, until conditions are favorable for pupation.

Larvae then become active and move to the soil surface to pupate.

Management of wheat midge has relied on insecticide treatments to control adults and prevent egg laying, and to kill larvae before they enter the spikes. The most effective treatments are applied between 70% spike emergence and flowering. Larval surveys may be used to assess wheat midge risk and the advisability of sowing an alternate crop. Some sources of resistance in wheat to wheat midge have been identified.

Frit Fly

The frit fly, *Oscinella frit* (L.), is found in cereal production areas throughout the Northern Hemisphere, but is considered to be an important pest only in Europe. The nature of the damage caused by frit fly depends on the growth stage of the crop. Infestation of small plants results in dead plants or stems, while damage to the spike by later generations results sterility.

The adult is a small, robust black fly. Elongate, white eggs are deposited on cereals and other grass hosts. The pale yellow larvae mine leaves when newly hatched and later bore in stems or feed on undeveloped florets. Pupation occurs on the plant. There typically are three generations per year, with adults active in April–May, June–July and August–September.

Management recommendations include control of volunteer plants and other alternate hosts, as well as early sowing of spring grains to promote larger, more tolerant plants at the time of first generation infestation. In Europe, insecticides may be used to protect seedlings.

Wheat Stem Maggot

The wheat stem maggot, *Meromyza americana* Fitch, is found throughout North American cereal production areas. Damage to small plants results in dead tillers or plants, and damage to larger plants results in white, sterile spikes. Yield losses of 10–15% have been observed in heavily infested fields.

Wheat stem maggot passes the winter in the larval stage, in the lower parts of the stems of wheat and other hosts. They pupate in the spring and the greenish yellow, striped adults emerge in June. The white, cylindrical eggs are laid on the leaves and stems of wheat and other hosts. The newly hatched pale green maggots of this generation enter the leaf sheaths and tunnel into the tender tissues of the stem. Tunnels in wheat are usually 5–8 cm in length, and result in white, sterile spikes. Another generation of flies emerges in midsummer to lay eggs on volunteer cereal plants and other grasses. The fall generation emerges in late August to early September and lays eggs in the new winter wheat crop.

The use of delayed planting, following the dates recommended to escape Hessian fly infestations, is an effective management practice. Destruction of volunteer plants is also recommended. The effectiveness of chemical control is unknown, and currently not recommended.

Sawflies

Three sawflies attack cereals in the Northern Hemisphere: The black grain stem sawfly, *Trachalus tabidus* (Fabricius); the European wheat stem sawfly, *Cephus pygmaeus* (L.); and the wheat stem sawfly, *Cephus cinctus* Norton. The wheat stem sawfly is prevalent in western North America, particularly in the northern Great Plains, while the other two species are found in eastern North America and Europe. All three have similar field biology and cause similar damage. The following information is specific to wheat stem sawfly but should apply in general to the other species as well.

When they are mature, wheat stem sawfly larvae move to the base of the stem and gnaw a ring around the inside of the stem. The weakened stems break easily, making grain unavailable for harvest. Complete crop losses have been observed.

The wheat stem sawfly overwinters in the larval stage within wheat stems in a ground-level tunnel. Pupation occurs in May and the slender black and yellow adult sawflies are present from mid June to mid July. Females place single white, crescent-shaped eggs within stems of cereals and other host grasses. These hatch into pale yellow, legless worms similar in appearance to a caterpillar. The sawfly larvae tunnel up and down the stem. Mature larvae move to the base of the stem to form their overwintering chamber. The inside of the stem is chewed away, and the stem usually breaks at the point of this damage. The larvae then plug the area just below the break, forming the chambers in which they will pass the winter and pupate the following spring.

The use of solid stem wheat varieties is the most common management recommendation for wheat stem sawfly. Solid stems are, however, associated within lower yield potential. Several cultural controls also have been suggested, including destruction of stubble in the late fall or early spring. This is effective in reducing sawfly overwintering, but may conflict with soil and water conservation goals. Delayed planting of spring wheat and the use of trap crops are additional recommended cultural practices. Biological controls are considered to be of limited effectiveness. There are no effective chemical controls.

Wheat Jointworm

The wheat jointworm, *Tetramesa tritici* (Fitch), is most common in eastern North America and the Pacific Northwest. Once considered one of the major wheat pests, on a par with Hessian fly, it is now thought to be of only minor importance. Larval feeding causes the formation of small stem galls, resulting in malformed tillers prone to breakage.

The wheat jointworm overwinters in the pupal stage within stem galls in wheat stubble. The small black adult wasps gnaw their way out of the pupal chambers in April and May and spend the following month in wheat laying their eggs in wheat stems just above one of the nodes. The small white larvae form cells in the stem wall where they feed on plant sap. The swelling formed by the presence of the cell is referred to as a stem gall. Larvae cease feeding at about the time of wheat ripening.

The only available management recommendations are late fall or early spring stubble destruction and growing the current year's crop at some distance from the previous year's crop. Effective insecticide treatments are not available.

Wheat Strawworm

The wheat strawworm, *Tetramesa grandis* (Riley), is found in most North American wheat production areas. Once considered one of the major wheat pests, on a par with Hessian fly, it is now thought to be of only minor importance. Spring generation larvae feed on and destroy the developing spike. Summer generation larvae feed within the stem, just above one of the nodes, reducing yield and quality to an undetermined degree.

The wheat strawworm overwinters in the pupal stage within a feeding cell in the wheat stem, usually located near a node. In the spring, the small, black wingless spring adults emerge and lay the small, white, bulb-like eggs near the growing point of a tiller. The robust, pale yellow larvae hatch and destroy the growing point and form a feeding cell at the base of the tiller. Pupation occurs within the cell, and within 2 weeks the larger, winged summer adults (females only) emerge. The summer adults lay their eggs near one of the upper joints where the larvae feed and mature within the stem. Summer-form larvae are longer and more slender than those formed in the spring generation. A cell is formed near one of the joints where the larvae pass the summer and fall until pupation.

Recommended cultural controls include late fall or early spring stubble destruction, growing the current year's crop at some distance from the previous year's crop, and control of volunteer wheat plants. The use of early maturing varieties allows escape from the summer generation. No chemicals controls are known to be effective.

References

Blackman RL, Eastop VF (2001) Aphids on the world's crops: an identification and information guide, 2nd edn. Wiley, New York, NY

Burton RL, Starks KJ, Peters DC (1980) The army cutworm. Oklahoma State University Agricultural Experiment Station Bulletin B-749. Stillwater, Oklahoma

Caffrey DJ, Barber GW (1919) The grain bug. USDA Bulletin 779, Washington

Cook RJ, Veseth RJ (1991) Wheat health management. APS Press, St. Paul, Minnesota

Critchley BR (1998) Literature review of sunn pest *Eurygaster integriceps* Put. (Hemiptera, Scutelleridae). Crop Prot 17:271–287

Foster JE, Taylor PL, Araya JE (1986) The Hessian fly. Purdue Agricultural Experiment Station Bulletin 502. Purdue University, West Lafayette, Indiana

Hatchett JH, Starks KJ, Webster JA (1987) Insect and mites pests of wheat. In: Heyne EG (ed) Wheat and wheat improvement, 2nd edn. Agronomy Monograph 13. American Society of Agronomy, Madison, Wisconsin, pp 625–675

Haynes DL, Gage SH (1981) The cereal leaf beetle in North America. Ann Rev Entomol 26:259–287

Hein GL, Campbell JB, Danielson SD, Kalisch JA (1993) Management of the army cutworm and pale western cutworm. University of Nebraska NebGuide C-35, Lincoln, Nebraska

Jeppson LR, Keifer HH, Baker EW (1975) Mites injurious to economic plants. University of California Press, Berkeley, California

Jones TH, Young JEB, Norton GA, Mumford JD (1990) An expert system for management of *Delia coarctata* (Diptera: Anthomyiidae) in the United Kingdom. J Eco Entomol 83:2065–2072

Kryazheva LP, Ovsyannikova Y, Pisarenko VN, Sorokina MV, Shokh GV, Dubrovin NN (1990) Main features of the damage caused by the grain beetle *Zabrus tenebrioides* Gz (Coleoptera, Carabidae) in the southern USSR. Entomol Rev 69:157–167

Lewis T (1997) Thrips as crop pests. CAB International, Wallingford, Oxon, UK

McPherson JE, McPherson RM (2000) Stink bugs of economic importance in America north of Mexico. CRC Press, Boca Raton, Florida

Painter RH, Bryson HR, Wilbur DA (1954) Insects and mites that attack wheat in Kansas. Kansas Agricultural Experiment Station Bulletin 367. Manhattan, Kansas

Peairs FB (1986) Management of spider mites in corn. Colorado State University Cooperative Extension Service in Action 5.555. Ft. Collins, Colorado, 4 pp

Peairs FB (1996) Armyworms. Colorado State University Cooperative Extension Fact Sheet 5.503. (http://www.ext.colostate.edu/pubs/insect/05503.html. Fort Collins, Colorado

Peairs FB (1999) Mites in wheat. Colorado State University Cooperative Extension Service in Action 5.578. Ft. Collins, Colorado. 4 pp, online only (http://www.ext.colostate.edu/pubs/insect/05578.pdf

Peairs FB, Archer TL (1999) Spider mites. In: Steffey KL, Rice ME, All J, Andow DA, Gray ME, Van Duyn JW (eds) Handbook of corn insects. Entomological Society of America, Lanham, Maryland, pp 104–106

Phillips WJ, Poos FW (1940) The wheat jointworm and its control. USDA Farmers Bulletin 1006. U.S. Government Printing Office, Washington, DC

Phillips WJ, Poos FW (1953) The wheat strawworm and its control. USDA Farmers Bulletin 1323. U.S. Government Printing Office, Washington, DC

Quisenberry SS, Peairs FB (eds) (1998) A response model for an introduced pest – the Russian wheat aphid. Thomas Say Publications in Entomology, Entomological Society of America, Lanham, Maryland

Webster RL (1911) The wheat-head army-worm as a timothy pest. Iowa State College Agricultural Experiment Station Bulletin 122. Ames, Iowa

Weiss MJ, Morrill WL (1992) Wheat stem sawfly revisited. Am Entomol 38:241–245

Wheat Stem Maggot, *Meromyza americana* Fitch (Diptera: Chloropidae)

Cultural management techniques are used to manage this stem-damaging insect.

► Wheat Pests and their Management

► Flies

Wheat Stem Sawflies: *Cephus cinctus* Norton, *Cephus pygmaeus* (L.) and *Trachelus tabidus* (F.) (Hymenoptera: Cephidae)

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Several species of sawfly (Hymenoptera: Cephidae) are pests of wheat and other cereal crops worldwide. The Cephini, the tribe to which these agriculturally important species belong, includes 50–60 grass-feeding species. This tribe evolved in the Old World, and only four species are found in

North America: *Calameuta clavata* (Norton), a non-pest species, *Cephus cinctus* Norton, the wheat stem sawfly, *C. pygmaeus* (L.), the European wheat stem sawfly, and *Trachelus tabidus* (F.), the black grain stem sawfly.

Cephus cinctus is widely distributed across North America, from California to the Mississippi River and British Columbia to Manitoba. Many authorities consider it a native North American insect which adapted to wheat as European settlers began large-scale cultivation of cereal crops. Alternatively, there is some evidence that *C. cinctus* may have been inadvertently introduced into North America from northeastern Asia. A sawfly species from eastern Siberia, *C. hyalinatus* Konow, has recently been synonymized with *C. cinctus* using morphological features in preserved specimens. This has greatly expanded the distribution of *C. cinctus* to include northeastern Asia. Several other species, including *C. camtschatcalis* Enslin and *C. zahaikevitschi* Ermolenko, may also be conspecific with *C. cinctus*. The co-occurrence of *C. cinctus* in Asia and North America, and preponderance of *Cephus* species in Asia, suggests the possibility that *C. cinctus* may have been introduced from Asia to North America (Fig. 48).

Cephus pygmaeus and *Trachelus tabidus* are found in Europe, Asia and North Africa. *Cephus pygmaeus* has a wider distribution than *T. tabidus*, but the latter species appears to be more common in the Mediterranean region. Both species were introduced into North America in the late 1800s, and became pests of small grain crops. In North America, *C. pygmaeus* has been found from northern Virginia to Ontario, but not west of Pennsylvania. *Trachelus tabidus* spread east and south from a probable point of entry somewhere between New York City and Richmond, Virginia, and is now found in Ohio, Pennsylvania, Maryland, Delaware, Virginia and North Carolina, but apparently not in Canada. Following a successful biological control effort against *C. pygmaeus* and *T. tabidus* in the 1930s, these two species were reduced to non-economic status.

Wheat Stem Sawflies: *Cephus cinctus* Norton, *Cephus pygmaeus* (L.) and *Trachelus tabidus* (F.) (Hymenoptera: Cephidae), Figure 48 **A female wheat stem sawfly (*Cephus cinctus*) ovipositing into a wheat stem.**

Host Plants

Wheat, barley, and rye are the main cereal crops attacked by sawflies, though infestation in other small grains such as triticale, spelt, and others have been observed. Cultivated oats do not support sawflies. Until recently, in western North America, *C. cinctus* attacked primarily spring wheat, while winter wheat suffered less damage because of its earlier sowing date and more advanced growth stage when sawflies emerge. Winter wheat now sustains extensive damage in the northern Great Plains. The choice of host plant appears to be related as much to stem diameter and phenological growth stage as to particular grass species. *Cephus cinctus* feeds on a number of grasses including species of Agropyron, *Bromus*, *Elymus*, and *Elytrigia*, in addition to cereal crops. The known host range for *Cephus pygmaeus* is wider than reported for *C. cinctus* and includes *Agropyrum*, *Avena*, *Bromus*, *Hordeum*, *Phleum*, *Secale*, and *Triticum*. The range of non-cultivated host plants for *T. tabidus* is unknown.

Biology

The biology of the agriculturally important sawflies is very similar and, at least for the three pest species found in North America, has been well studied. Females deposit eggs into the elongating stems of host plants in early summer and the developing larvae feed by moving up and down the length of the stem. Though several eggs may be laid within a stem, only a single larva survives to maturity. As the plant matures, and usually prior to harvest, the larva moves down to the base of the stem and chews a V-shaped notch around the inside of the stem. The stem lumen is plugged with frass and sawdust below the notch, forming a chamber or hibernaculum. The notch weakens the stem, which usually breaks, producing a "stub" that remains anchored in the ground. The sawfly larva undergoes an obligatory diapause within this chamber during the winter or the dry season. The stub is often covered with debris or soil, and is therefore well protected from excessive cold or dry conditions. The diapausing larva is contained within a thin membranous cocoon. Diapause is broken as temperatures, moisture levels and/or photoperiods increase in the spring. Post-diapause development includes prepupal and pupal stages lasting approximately 2–30 days depending on ambient temperatures. Adults emerge from the cocoon and use their mandibles to exit the stub through the plug. The agriculturally important species have a single generation per year, with a short-lived (7–10 days) and apparently non-feeding adult stage.

Damage and Yield Loss

Feeding by sawfly larvae reduces vascular efficiency resulting in fewer kernels per head and lower kernel weight, and can also reduce the protein content of the grain. Additional grain loss is the result of lodging after the inside of the stem is girdled. *Cephus cinctus* was first reported as a pest in Canada's Prairie Provinces in the late 1890s, and continues to be a key constraint to cereal production in the northern Great Plains. Damage is greatest in Montana, North Dakota, Alberta, Saskatchewan, and Manitoba. Infestation levels of more than 70% have been recorded with the weight of grain per head reduced by more than 20%. Losses of approximately 80% have been reported from central Montana. Annual losses to wheat, barley, rye, triticale and other cereal crops may exceed US $100 million in the region.

Prior to the successful biological control campaign against *C. pygmaeus* and *T. tabidus*, infestation levels as high as 45% for *C. pygmaeus* and 65% for *T. tabidus* were reported in eastern North America. *Trachelus tabidus* may have caused greater damage to wheat than *C. pygmaeus*, though the latter species is more widely distributed. Neither species is currently considered a serious pest of wheat in North America. Pest surveys from the 1980s detected less than 5% infestation in wheat from *C. pygmaeus*.

Cephus pygmaeus is also a pest in Europe and the North Africa/Mediterranean region, with reported infestation levels of up to 40% in Morocco, and reductions of 6–17% in kernel weight and 30–45% in kernel number. Damage and grain weight reductions of more than 45% have been reported from Switzerland, France, Germany, Belgium, Poland and Romania.

Several other sawfly species are pests of small grains in other parts of the world. Wheat yield losses in China of 6% have been reported for *C. fumipennis*, with some cultivar losses exceeding 30%. The lack of published literature on many of these other species may result from being less well studied or may be due to incorrect field identification.

Natural Enemies

The most important sawfly natural enemies are parasitic Hymenoptera, though 5–10% of overwintering sawfly larvae may be killed by pathogenic fungi. There are also unpublished reports of at least one predator attacking sawflies but predators and pathogens have relatively little impact on sawfly population dynamics compared to parasitoids. The list of parasitoids attacking cephids appears extensive, though little is known about most species. Many species attack other hosts found in grasses or are obligate or facultative hyperparasitoids. Primary parasitoids of gramivorous Cephidae are found in the following families: Braconidae, Eulophidae, Ichneumonidae, and Pteromalidae. The most important, and the most well-studied are the braconids and ichneumonids. Most natural enemy complexes include one or more members of each family. The exception is the natural enemy complex attacking *C. cinctus*. Thus far, no ichneumonids have been recovered from *C. cinctus*. This is interesting because ichneumonids dominate the natural enemy complexes of other *Cephus* species. In terms of biology, the braconids are larval ectoparasitoids, while the other species are larval or egg-larval endoparasitoids.

Management

Management of wheat stem sawfly has focused on the development of resistant wheat cultivars, various tillage operations to destroy larvae and/or pupae in the stubble, and biological control using exotic parasitoids. Pesticides are generally too costly, given the relatively low value of wheat, and are ineffective because the larvae are concealed within the stem. Efforts to develop resistant wheat cultivars with solid-stems began in the 1930s following earlier reports that this trait provided resistance to *C. pygmaeus* in Europe. The first solid stemmed cultivar ("Rescue") was released in 1946, and this has been followed by a number of other solid stemmed cultivars. The performance of these cultivars has been variable. Sawfly larvae apparently suffer higher mortality and/or cause less damage in solid stemmed versus hollow stemmed cultivars, though resistant cultivars generally have lower yield and protein content than alternative hollow stemmed cultivars. Recent studies suggest that there may be a negative association between protein content and stem solidness but that yield per se should not be affected by the solid stemmed character. In addition, the degree of stem solidness in a given cultivar may be reduced by light, temperature, moisture supply, and plant spacing. The variable field performance resulting from interactions among environmental variables and resistant cultivars has reduced farmers' confidence in these cultivars.

Tillage, either in the spring or fall, has also produced equivocal results with significant limitations. Several reports indicate that tillage can reduce populations of wheat stem sawfly. A number of tillage implements have been evaluated, but the critical factor seems to be separating soil from the base of the wheat stem. Soil attached to the base of the stem insulates sawfly larvae from low temperatures and low humidity. Unfortunately, though tillage operations may be somewhat effective in controlling wheat stem sawfly, there are several important disadvantages associated with this strategy. Tillage requires an additional field operation, increasing wheat production costs and reducing profitability. Second, tillage operations also increase soil erosion rates, and run counter to no-till recommendations.

Biological control efforts have been directed against the three agriculturally important sawfly species in North America: *Cephus cinctus*, *C. pygmaeus*, and *T. tabidus*. Exotic parasitoids were established against the latter two species, and continue to maintain host populations below economic levels. Some authors have questioned whether the introduced natural enemies are the key regulating factor, or whether other factors may be involved, but without further study this question cannot be answered. All attempts, including three different projects covering more than 15 years, to find and establish exotic natural enemies against *C. cinctus* have ended in failure. There has been a renewed interest in North America to manage wheat stem sawfly using exotic natural enemies, particularly from eastern Asia.

► Wasps, Ants, Bees and Sawflies
► Wheat Pests and their Management

References

Holmes ND (1977) The effect of wheat stem sawfly, *Cephus cinctus* (Hymenoptera: Cephidae), on the yield and quality of wheat. Can Entomol 109:1591–1598

Ivie MA (2001) On the geographic origin of the wheat stem sawfly (Hymenoptera: Cephidae): a new hypothesis

of 47:84–97introduction from northeastern Asia. Am Entomol
Morrill WL, Kushnak GD, Bruckner PL, Gabor JW (1994) Wheat stem sawfly (Hymenoptera: Cephidae) damage, rates of parasitism, and overwinter survival in resistant wheat lines. J Eco Entomol 87:1373–1376
Shanower TG, Hoelmer KA (2004) Biological control of wheat stem sawflies: past and future. J Agric Urban Entomol 21:197–221
Wallace LE, McNeal FH (1966) Stem sawflies of economic importance in grain crops in the United States. U.S. Department of Agriculture Technical Bulletin 1350. 50 pp
Weiss MJ, Morrill WL (1992) Wheat stem sawfly (Hymenoptera: Cephidae) revisited. Am Entomol 38:241–245

Wheat Thrips, (Thysanoptera)

Several species of thrips damage wheat crops.

► Wheat Pests and Their Management
► Thrips

Wheeler, William Morton

William Morton Wheeler was born on March 19, 1865, at Milwaukee, Wisconsin, USA. He had a diverse career, but established himself as one of the foremost authorities on ants and other social insects. Wheeler's early schooling in Milwaukee was marked by behavioral problems, so his father enrolled him in a strict German school with a reputation for extreme severity of discipline. He stayed on to attend the German-American College, which led to a position in 1884 at Ward's Natural Science Establishment in New York, a vendor of natural history supplies to schools and museums. Wheeler returned to Milwaukee in 1885, taught high school for 2 years and became custodian of the new Milwaukee Public Museum. There he developed proficiency in morphology, embryology and cytology. He left in 1890 to accept a fellowship at Clark University. He began to publish on insects and received his Ph.D. from Clark in 1892. He followed his professor, C.O. Whitman, to the University of Chicago, where he became an instructor. Following a study trip to Europe, Wheeler was made an assistant professor of embryology, though his entomological interested began to expand to include more than embryology. In 1899 he was made professor of zoology at the University of Texas. In 1903 he became curator of invertebrate zoology at the American Museum of Natural History, which allowed him to devote most of his time to ants. In 1908 Wheeler returned to teaching, and became professor of economic entomology at Harvard University, and where he became dean of the Bussey Institution. Wheeler traveled over much of the world, and published prodigiously, authoring almost 500 publications. Among his noteworthy publications are "Ants: their structure, development and behavior" (1910), "Social life among the insects" (1923), and "A study of insect behavior" (1930). Wheeler died On April 19, 1937, at Cambridge, Massachusetts.

References

Essig EO (1931) A history of entomology. The Macmillan Company, New York, 1029 pp
Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, New Jersey, 549 pp

Whiplash Dermatitis

A term used in Australia for dermatitis linearis.

► Dermatitis Linearis

Whirligig Beetles

Members of the family Gyrinidae (order Coleoptera).

► Beetles

Whiteflies (Hemiptera: Aleyrodidae)

This group consists of only about 1,200 species, though it occurs mostly in the tropics and is not well studied, so this is likely an underestimate of its actual size. There are 126 genera described, but only seven have more than 50 species, and many genera contain only a single species. Because adults are so similar, classification is based on the structure of the fourth instar, the "pupal case." Though there are advantages to this system, one of the serious disadvantages is that the form of the pupal case is affected by the form of the host plant cuticle, resulting in variable appearance. The classification is as follows:

Order: Hemiptera
- Suborder: Sternorrhyncha
  - Superfamily: Aleyrodioidea
- Family: Aleyrodidae
  - Subfamily: Udamoselinae?
  - Subfamily: Aleurodicinae
  - Subfamily: Aleyrodinae

The Udamoselinae is based on a single specimen (which has subsequently disappeared), and has never again been collected; thus, its existence is questionable. The Aleurodicinae are found principally in South America, are relatively large for whiteflies, and are considered to be primitive. The wing venation is not as reduced as in Aleyrodinae, and the pupal cases are more complex.

Appearance and Biology

Whiteflies typically are only 1–3 mm in length. The wings are transparent, or clouded. Wing venation is always reduced. The adult is often covered with a powdery white wax, the basis for the family name. However, not all species are white, and some are black (e.g., citrus blackfly, *Aleurocanthus woglumi*). Adults have two pairs of wings. The antennae usually are 7-segmented. The tarsi bear two tarsomeres, with the apical tarsomere bearing two claws and possessing an empodium between the claws. The immatures resemble scale insects; they are flattened, oval, and secrete a waxy material. A conspicuous fringe is sometimes present. The anal opening (vasiform orifice) of the immature opens dorsally on the last abdominal segment, and has diagnostic value.

Parthenogenesis occurs in some species. Females deposit their small, oval or elongate eggs on a short stalk that is inserted into the leaf tissue of the host. Sometimes the female deposits waxy material near the eggs, or deposits the eggs in a circle on the surface of a plant leaf. The first instars are very small, but have long legs and antennae, and crawl actively. They are transparent to translucent. Thereafter the appendages are reduced and the two nymphal stages are sessile. This is followed by the so-called pupal stage, during which some feeding occurs. Pupae often have large dorsal setae, though a few are present in nymphs. The adult typically emerges from a T-shaped slit on the dorsal surface of the pupal case. The mouthparts of the piercing-sucking type; both sexes feed.

Damage

Whiteflies can be very destructive pests, particularly in the tropics and subtropics. They injure plants directly through their feeding (removal of plant sap) and indirectly through transmission of plant viruses. To a much lesser degree, the production of honeydew by these insects (and subsequent growth of sooty mold) also affects the value of crops because it coats the foliage and other plant parts.

Whiteflies are the tropical equivalent of the aphids found in more temperate regions. They are vagile and opportunistic, building to high densities when weather and host plant condition are suitable. They feed almost entirely on angiosperms, avoiding gymnosperms. Among angiosperms they feed mostly on dicotyledonous plants, though the Graminae, Palmae and Smilacaceae among the monocots support whiteflies. The whiteflies do not display a great degree of host specificity.

Some of the more common, and important species, are treated below:

Greenhouse Whitefly, *Trialeurodes vaporariorum* (Westwood)

Greenhouse whitefly is found widely around the world, including most of the temperate and subtropical regions North America, South America, Europe, Central Asia and India, northern and eastern Africa, New Zealand and southern Australia. It does not thrive in most tropical locations, and occurs in colder regions only by virtue of its ability to survive winter in greenhouses. In colder areas, it overwinters only in such protected locations, but in mild-winter it survives outdoors throughout the year. The origin of this species is not certain, but is thought to be Mexico or the southwestern United States.

Host Plants

This species has a very wide host range, with over 300 species recorded as hosts. However, some hosts are more suitable. Vegetable plants often serving as good hosts are bean, cantaloupe, cucumber, lettuce, squash, tomato, eggplant, and occasionally cabbage, sweet potato, pepper, and potato. Among greenhouse-grown vegetables, the most common hosts are tomato, eggplant, and cucumber. When adults land on a favored host plants such as eggplant, they almost always remain to feed and oviposit; on a less preferred host such as pepper they usually take flight after tasting the plant. Many ornamental plants serve as good hosts, including ageratum, aster, chrysanthemum, coleus, gardenia, gerbera, lantana, poinsettia, salvia, verbena, zinnia and many others.

Natural Enemies

Natural enemies of greenhouse whitefly are numerous, but few are consistently effective, especially under greenhouse conditions. Greenhouse whitefly is attacked by the common predators of small insects, including minute pirate bugs (Hemiptera: Anthocoridae), some plant bugs (Hemiptera: Miridae), green lacewings (Neuroptera: Chrysopidae), brown lacewings (Neuroptera: Hemerobiidae), and ladybirds (Coleoptera: Coccinellidae). Parasitic wasps attacking greenhouse whitefly are largely confined to the family Aphelinidae, but many species are involved and they vary regionally. Those known from North America, including Hawaii, are *Encarsia formosa* Gahan, *Aleurodophilus pergandiella* (Howard), *Eretmocerus haldemani* Howard, *Prospaltella transvena* Timberlake, and *Aphidencyrtus aphidivorus* (Mayr). Although these agents exercise considerable control on whitefly populations in weedy areas or on crops where insecticide use is minimal or absent, they do not survive well in the presence of most insecticides. *Encarsia formosa* has been used successfully under greenhouse conditions, and to a lesser extent field conditions, to affect biological suppression; for more information, see the section on biological control.

The pathogens of greenhouse whitefly are principally fungi, particularly *Aschersonia aleyrodis*, *Paecilomyces fumosoroseus*, and *Verticillium lecanii*. All occur naturally and can cause epizootics in greenhouses and fields, and also have been promoted for use in greenhouses as bioinsecticides. *Aschersonia* is specific to whiteflies, *Verticillium* has a moderately wide host range, and *Paecilomyces* has a broad host range. For optimal development of disease, high humidity is required. *Aschersonia* is spread principally by rainfall, so often fares poorly in greenhouse environments.

Life Cycle and Description

The development period from egg to adult requires about 25–30 days at 21°C. Thus, because the preoviposition period of adults also is short, less than 2 days above 20°C, a complete life cycle is possible within a month. Greenhouse whitefly can live for months, and oviposition time can exceed the development time of immatures; this results in overlapping generations. Optimal relative humidity is 75–80%. The developmental threshold for all stages is about 8.5°C.

Eggs are oval in shape, and suspended from the leaf by a short, narrow stalk. The eggs initially are green in color and dusted with white powdery wax, but turn brown or black as they mature. The eggs measure about 0.24 mm in length and 0.07 mm in width. Eggs are deposited on the youngest plant tissue, usually on the underside of leaves in an incomplete circular pattern. Up to 15 eggs may be deposited in a circle which measures about 1.5 mm in diameter. This pattern results from the female moving in a circle while she remains with her mouthparts inserted into the plant. This pattern is less likely on plants with a high density of trichomes because plant hairs interfere with the oviposition behavior. Duration of the eggs stage is often 10–12 days, but eggs may persist for over 100 days under cool conditions. When cultured at 18, 22.5, and 27°C, egg development requires an average of 15, 9.8, and 7.6 days, respectively. Maximum fecundity varies according to temperature; optimal temperature is 20–25°C regardless of host plant. When feeding on eggplant, greenhouse whitefly produces over 500 eggs, on cucumber and tomato about 175–200 eggs (Drost et al. 1998).

The newly hatched whitefly nymph is flattened, oval in outline, and bears functional legs and antennae. The perimeter is equipped with waxy filaments. The first instar measures about 0.3 mm in length. It is translucent, usually appearing to be pale green in color but with red eyes. After crawling one cm or so from the egg it settles to feed and molt. Development if the first instar requires 6.5, 4.2, and 2.9 days, respectively, when cultured at 18, 22.5, and 27°C. The second and third nymphal stages are similar in form and larger in size, though the legs and antennae become reduced and nonfunctional. They measure about 0.38 and 0.52 mm in length, respectively. Duration of the second instar requires about 4.3, 3.2, and 1.9 days whereas third instars require 4.5, 3.2, and 2.5 days, respectively when cultured at 18, 22.5, and 27°C. The fourth nymphal stage, which is usually called the "pupa," differs in appearance from the preceding stages. The fourth instar measures about 0.75mm in length, is thicker and more opaque in appearance, and is equipped with long waxy filaments. The pupal stage actually consists of the fourth nymphal instar period, which is a period of feeding, plus the period of pupation, which is a time of transformation to the adult stage. Thus, pupation occurs within the cuticle of the fourth instar. Duration of the fourth instar period and pupal period are 8.7 and 5.9, 5.9 and 4.0, and 4.5 and 2.8 days, respectively, at 18, 22.5, and 27°C.

Individuals of greenhouse whitefly which develop on lightly or moderately pubescent leaves tend to be relatively large and to have four pairs of well developed dorsal waxy filaments. In contrast, whiteflies developing on densely pubescent leaves tend to be smaller, and to bear more that four pairs of dorsal filaments. These morphological variations are not entirely consistent, and have led to considerable taxonomic confusion.

Adults are small, measuring 1.0–2.0 mm in length. They are white in color, with the color derived from the presence of white waxy or mealy material, and have reddish eyes. They bear four wings, with the hind wings nearly as long as the forewings. The antennae are evident. In general form, viewed from above, this insect is triangular in shape because the distal portions of the wings are wider than the basal sections. The wings are held horizontally when at rest; this characteristic is useful for distinguishing this species from the similar-appearing silverleaf whitefly and sweetpotato whitefly, which hold their wings angled or roof-like when at rest. Mating may occur repeatedly, though females can also produce eggs without mating.

Damage

Adult and nymphal whiteflies use their piercing-sucking mouthparts to feed on the phloem of host plants. This results in direct damage, resulting in localized spotting, yellowing, or leaf drop. Under heavy feeding pressure wilting and severe growth reduction may occur. Whiteflies also secrete large amounts of sugary honeydew, which coats the plants with sticky material, and must be removed from fruit before it is marketed. The honeydew also provides a substrate for growth of sooty mold, a black fungus that interferes with the photosynthesis and transpiration of plants.

Greenhouse whitefly is, as the common name suggests, primarily a pest in greenhouses, and is a serious limitation to the production of plants grown in such structures. However, it can also be a field pest, often in warmer climates but also in cool climates when seedlings contaminated with whiteflies are transplanted into the field. For example, in Hawaii field-grown tomatoes suffered a 5% reduction in fruit weight with as few as 0.7 whiteflies per square cm of leaf tissue, and a 5% reduction in grade-A fruit due to contamination with honeydew at densities of about 8.3 whiteflies per square cm of leaf.

Greenhouse whitefly is capable of transmitting viruses to plants, but is not considered to be a serious vector, particularly relative to the *Bemisia* spp. However, greenhouse whitefly transmits beet pseudo-yellow virus to cucumber in greenhouse culture.

Management

Although whitefly nymphs and adults can be detected readily by visual examination of foliage, most monitoring systems take advantage of the attraction of adults to yellow, and use yellow sticky traps to capture flying insects. Sticky cards or ribbons are suspended at about the height of the crop for optimal monitoring. Traps must be placed close to plants or close to the ground or population densities will be underestimated.

Applications of insecticides are often made to minimize the effects of whitefly feeding on crops in greenhouses. Greenhouse whitefly feeds on the lower surface of foliage and is sessile throughout most of its life, habits that minimize contact with insecticides, and resulting in frequent applications and effectiveness mostly against the adult stage. In greenhouse culture, application intervals of only 4–5 days are common, and sytemic insecticides are often used to increase the likelihood of insect contact with toxins. Thus, whitefly resistance to nearly all classes of insecticides is known, and rotation of insecticide classes is encouraged. Mixtures of insecticides are often used, which is indicative of high levels of resistance among whiteflies to insecticides. Field populations of greenhouse whitefly invariably are derived from greenhouse populations, and possess similar resistance to many insecticides. Applications of petroleum oils and biological control agents help to avoid difficulties with insecticide resistance.

Few cultural practices are available, but disruption of the whitefly population with host-free periods is important. Continuous culture of plants allows whiteflies to move from older to younger plants. Similarly, weeds may allow whiteflies to bridge crop-free periods, and should be eliminated.

Seasonal inoculative release of the parasitoid *Encarsia formosa* Gahan into crops infested with greenhouse whitefly has been used extensively for suppression of whiteflies on greenhouse-grown vegetable crops. Excellent suppression of whiteflies is attainable, but on host plants such as cucumber and eggplant, which are very favorable for whitefly reproduction and have hairy leaves that interfere with parasitoid searching, frequent releases must be made. Alternatively, cucumber varieties with reduced trichome density have been developed which favor parasitism. Another critical factor is temperature, because low greenhouse temperatures are more suitable for whitefly activity than parasitoid activity. Daytime temperatures of about 24°C seem to be optimal; temperatures of 18°C or less suppress parasitoid searching. A cold-tolerant *Encarsia* strain that is active at 13–17°C has also been used to overcome this temperature problem. Interference from pesticides can markedly affect parasitoid survival, so other pests such as mites must be managed biologically also. Lastly, release rates are important because if too many parasitoids are released the host whiteflies are driven nearly to extinction, leading to disappearance of the parasitoids; this is most likely to occur in small greenhouses. Alternatively, parasitoid releases can be made throughout the season, irrespective of whitefly presence. Although the protocols and technologies for whitefly management using *E. formosa* have been perfected for use in greenhouses, management under outdoor conditions awaits further research.

Silverleaf Whitefly, *Bemisia argentifolii* Bellows and Perring and Sweetpotato (or Cotton) Whitefly, *Bemisia tabaci* (Gennadius)

Silverleaf whitefly and sweetpotato whitefly are closely related whitefly species which cannot be distinguished easily by appearance, although there are some biological differences. Much literature from tropical environments around the world referring to sweetpotato whitefly probably pertains to silverleaf whitefly and other closely related species. Until the identities of these species are accurately determined, their distribution will remain unknown and some aspects of their biologies will remain confused. Cooler climates do not experience major problems with silverleaf whitefly except when overwintering in greenhouses occurs or vegetable transplants originate from whitefly-infested areas.

Host Plants

Silverleaf whitefly has a very wide host range. There may be 500 worldwide. Sweet potato, cucumber, cantaloupe, watermelon, squash, eggplant, pepper, tomato, lettuce, broccoli and many other crops are hosts, but suitability varies. For example, sweet potato, cucumber, and squash are much more favorable for whitefly than are broccoli and carrot. Various weeds and field crops may favor survival of whiteflies during vegetable-free periods. Wild lettuce, *Lactuca serriola*, and sowthistle, *Sonchus* spp., are examples of suitable weed hosts. Cotton, soybean, and to a lesser degree alfalfa and peanut are field crop hosts. Sweetpotato whitefly has a narrower host range than silverleaf whitefly.

Weather

Silverleaf whitefly thrives under hot, dry conditions. Rainfall seems to decrease populations, although the mechanism is not known. Silverleaf whitefly is not a strong flier, normally moving only short distances in search of young tissue. However, under the proper weather conditions dramatic, long-distance flights involving millions or billions of insects are observed. Such flights normally occur in the morning as the sun heats the ground, and the insects invariably move downwind.

Natural Enemies

Numerous predators, parasitoids, and fungal diseases of silverleaf whitefly are known. General such as minute pirate bugs (Hemiptera: Anthocoridae), green lacewings (Neuroptera: Chrysopidae), and ladybirds (Coleoptera: Coccinellidae) are important, as are many parasitic wasps, particularly in the genera *Encarsia* and *Eretmoceris* (both Hymenoptera: Aphelinidae). While these agents exercise considerable control on whitefly populations in weedy areas or on crops where insecticide use is minimal or absent, they do not survive well in the presence of most insecticides.

Life Cycle and Description

Silverleaf whitefly can complete a generation in about 20–30 days under favorable weather conditions. In tropical countries up to 15 generations per year have been reported, but in the United States there are considerably fewer.

The egg is about 0.2 mm long, elongate, and tapers distally; it is attached to the plant by a short stalk. The whitish eggs turn brown before hatching, which occurs in 4–7 days. The female deposits 90–95% of her eggs on the lower surfaces of young leaves.

All instars are greenish, and somewhat shiny. The flattened first instar is mobile, and is commonly called the "crawler" stage. It measures about 0.27 mm long and 0.15 mm wide. Movement is usually limited to the first few hours after hatch, and to a distance of 1–2 mm. Duration of the first instar is usually 2–4 days. The feeding site is normally the lower surface of a leaf, but sometimes greater than 50% of the nymphs are found on the upper surface, and feeding location seems not to affect survival. The second and third instars are similarly flattened, but their leg segmentation is reduced and they do not move. Duration of these instars is about 2–3 days for each. Body length and width are 0.36 and 0.22 mm, and 0.49 and 0.29 mm, for the second and third instar, respectively. The sessile fourth instar is usually called the "pupa" although this is not technically correct because some feeding occurs during this instar. The appearance of the fourth instar is variable, depending on the food plant; this stage tends to be spiny when developing on a hairy leaf but has fewer filaments or spines when feeding on smooth leaves. The fourth instar measures about 0.7 mm in length and 0.4 mm in width. Duration of the fourth instar is about 4–7 days. Total pre-adult development time averages 15–18 days in the temperature range of 25–32°C, but increases markedly at lower temperatures. The lower and upper developmental thresholds are considered to be about 10 and 32°C.

The adult is white in color and measures 1.0–1.3 mm in length. The antennae are pronounced and the eyes red. Oviposition begins 2–5 days after emergence of the adult, often at a rate of about five eggs per day. Adults typically live 10–20 days and may produce 50–150 eggs, although there are records of over 300 eggs per female. Females may reproduce without fertilization but males are common, sometimes outnumbering females, so most females are probably fertilized.

Damage

Adult and nymphal whiteflies use their piercing-sucking mouthparts to feed on the phloem of host plants. This results in direct damage, which is manifested in localized spotting, yellowing, or leaf drop. Under heavy feeding pressure wilting and severe growth reduction may occur. Systemic effects also are common, with uninfested leaves and other tissue being severely damaged as long as feeding whiteflies are present on the plant. A translocated toxicogenic secretion by nymphs, but not by adults, is implicated. Usually it is the young, developing tissue that is damaged by whiteflies feeding on older tissue. Once the whiteflies are removed, new plant growth is normal if a disease has not been transmitted. Damaged foliar tissue, however, does not recover once injured. Among leafy vegetables and crucifers, white streaking or discoloration, especially of veins, is common. Studies in Texas and Arizona demonstrated similar losses, and indicated that yields could be optimized if plants were treated with insecticide at whitefly densities of 3 adults per leaf or 0.5 large nymphs per 7.6 cm^2 of leaf area.

A disorder called irregular ripening affects tomato fruit when whiteflies feed on tomato foliage. Although the tomato foliage is not damaged, the internal portions of the fruit do not ripen properly and the surface is blotched or streaked with yellow.

Squash silverleaf, a disorder responsible for the common name of *B. argentifolli*, has been known from Israel since 1983. Silverleaf symptomology includes blanching of the veins and petioles, and eventually the interveinal areas of the leaf. The fruit of both yellow and green fruited varieties also may be blanched.

In addition to direct damage, silverleaf whitefly also causes damage indirectly by transmitting plant viruses. Over 60 plant viruses, most belonging to a group called geminiviruses, are known to be transmitted to crops by silverleaf whitefly. Some viruses, such as tomato yellow leaf curl virus, cause more damage than the insect feeding alone, so the effects are devastating. Unfortunately, unlike the case with the phytoxemia caused by the whitefly salivary secretions, once viruses are inoculated into the plant there is no recovery by the host even if the whiteflies are eliminated.

Lastly, whiteflies cause injury by excreting excess water and sugar in the form of honeydew. This sticky substance accumulates on the upper surface of leaves and fruit, and provides a substrate for growth of a fungus called sooty mold. The dark mold inhibits photosynthetic activity of the foliage, and may also render the fruit unmarketable unless it can be washed thoroughly and the residues removed.

Management

Eggs tend to be concentrated on young foliage and mature larvae on older foliage. Large nymphs are a good stage for population assessment because they do not move and are large enough to see without magnification. Adults tend to be concentrated close to the soil. Such distributions must be considered in population assessment prior to initiating management practices. Visual observation of the lower leaf surface and vacuum sampling are less time consuming, and in some cases more precise, than yellow sticky traps.

In southern states, where silverleaf whitefly can be the most important insect problem on some vegetable crops, frequent applications of insecticides are often made to minimize the direct and indirect effects of whitefly feeding. Whitefly resistance to nearly all classes of insecticides is known, and rotation of insecticide classes is encouraged. Mixtures of insecticides are often used, which is indicative of high levels of resistance. Most agriculturalists suggest that whitefly numbers be maintained at low levels because once they become abundant they are difficult to suppress; this, of course, exacerbates development of insecticide resistance. The phytotoxemia and disease transmission potential of this insect exaggerates its damage potential, further justifying frequent application of insecticides.

Silverleaf whitefly feeds on the lower surface of foliage and is sessile throughout most of its life – habits that minimize contact with insecticides. Frequent insecticide application also disrupts naturally occurring biological control agents. In an attempt to minimize the cost and disruptive effects of insecticides, and to reduce the evolution of insecticide resistance, soaps and oils have been extensively studied for whitefly control. The mechanism of control by surfactants such as soaps and oils is not clearly understood, but disruption of the insect cuticle, physical damage, and repellency are postulated. In any event, mineral and vegetable oils alone, or in combination with soaps and detergents, can provide some suppression of whiteflies. Combination of insecticide and oil often enhances whitefly control.

Although a great number of predators, parasitoids, and fungal diseases are known to attack silverleaf and sweetpotato whitefly, no biotic agents are known to provide adequate suppression alone. Under greenhouse conditions, parasitoids can be released at high enough densities to provide some suppression, especially when insecticidal soap and other management techniques are also used. Under natural field conditions, parasitism does not usually build to high levels until late in the growing season. Insecticides often interfere with parasitoids, of course, and effective use of biological control agents will probably be limited to cropping systems where insecticide use is minimized and other management techniques are used which favor action of predators, parasitoids, and disease agents. *Verticillium*, *Paecilomyces*, and other fungi similarly show some promise under greenhouse conditions, but are limited by low humidity under field conditions.

Cultural controls can be vitally important in managing silverleaf whitefly. Incorrect crop management, in particular, can create or exacerbate whitefly problems. Whiteflies can move from crop to crop, and area-wide crop-free periods help diminish populations. Thus, prompt tillage of land and destruction of crop residues after crop maturity is recommended. Similarly, weeds can harbor whiteflies, whitefly-transmitted diseases, and whitefly parasitoids, so weed management is a consideration. Trap crops such as cucumbers can be used to provide temporary protection to less preferred crops such as corn.

Row covers and other physical barriers can reduce infestation of crops, and infection with disease. Screen hole sizes of about 0.19 square mm or smaller are required to successfully exclude silverleaf whitefly. Colored and aluminum mulches provide only temporary reduction in whitefly abundance and disease transmission.

Disease Transmission

Growers generally rely on whitefly suppression to manage disease incidence. This is not entirely satisfactory, however, and removal of virus-infected plants is often suggested to minimize within-field spread of viruses. Since whiteflies may transmit disease from one crop to another, or from weeds to crops, vegetation management is important. As noted above, reflective mulches have not produced economic benefits consistently. Mineral and vegetable oils inhibit virus transmission. Row covers or other physical barriers can substantially prevent disease transmission, but are often not practical.

► Whitefly Bioecology and Management
► Greenhouse Whitefly
► Sweetpotato and Silverleaf Whitefly

References

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, 729 pp

Cock WJW (1993) *Bemisia tabaci* – an update 1986–1992 on the cotton whitefly with an annotated bibliography. CAB International, United Kingdom, 78 pp

Gerling D (1990) Whiteflies: their bionomics, pest status and management, 348 pp

Mound LA, Halsey SH (1978) Whitefly of the world. British Museum, Chichester, UK, 340 pp

van Lenteren JC, van Roermund HJW, Sutterlin S (1996) Biological control of greenhouse whitefly (*Trialeurodes varorariorum*) with the parasitoid *Encarsa formosa*: how does it work? Biol Control 6:1–10

Whitefly Bioecology and Management in Latin America

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Though some 1,200 whitefly (Hemiptera: Aleyrodidae) species have been described to date, only a few species are economically important agricultural pests. In Latin America (which for the purposes of this article includes Mexico, Central America, the Caribbean region and South America), less than a dozen whitefly species have historically caused economically-important damage to crops. The important species include *Aleurocanthus woglumi* (on citrus), *Aleurocybotus occiduus* (rice and sorghum), *Aleurodicus dispersus* (bananas), *Aleurodicus talamancensis* (bananas), *Aleurothrixus floccosus* (citrus, guava and other fruit trees), *Aleurotrachelus socialis* (cassava), *Bemisia tabaci* (many crops), *Bemisia tuberculata* (cassava), *Trialeurodes vaporariorum* (many crops), and *Trialeurodes variabilis* (cassava and papaya).

The most damaging and widespread whitefly species worldwide, and in Latin America, are *B. tabaci* and *T. vaporariorum*. The former species is by far the most important pest and vector of many plant viruses, particularly in the lowlands and mid-altitude (up to 1,200 m) valleys of the tropics. *Trialeurodes vaporariorum* is also a major pest of many crops in the tropical highlands (above 1,000 m of altitude) and temperate regions of the world, and is known to transmit several economically important plant viruses.

Damage and Economic Importance

All *B. tabaci* and *T. vaporariorum* life stages (eggs, nymphs and adults) are normally found on the underside of leaves. Crawlers emerging from eggs barely move from the point of hatching, after which they settle for the remainder of their lives, until the adult stage emerges.

Both nymphs and adults use their long mouthparts (stylets) to reach the phloem of the leaves and remove sap (rich in sugars and amino acids) that is continuously excreted. The sweet substance ("honeydew") covers the plant parts where the whiteflies are feeding, providing a suitable substrate for some superficial fungi known as "sooty molds." These fungi cover the leaves and other photosynthetic tissues of the affected plants, blocking sunlight. The sooty molds also reduce the quality of the produce, particularly in the case of cotton lint, which cannot be processed when covered by the honeydew and mycelium of the fungus.

In recent years, a new biotype ("B") of the whitefly *B. tabaci* appeared in Latin America. It is known to inject toxicogenic substances present in nymph's saliva that can induce physiological disorders such as uneven ripening of tomato, squash silverleaf, pumpkin white stem, white streaking in cole crops, as well as pod and stem blanching of snap beans and lettuce, respectively. Some authors have proposed that the new biotype is actually an entirely new species (*Bemisia argentifolii*), but this has not gained wide acceptance among entomologists (Fig. 49).

However, the main damage caused by *B. tabaci* is associated with its notable capacity to transmit over 200 different plant viruses, belonging for the most part to the genus *Begomovirus*, family *Geminiviridae*. *B. tabaci* also transmits viruses in other genera, namely, *Carlavirus*, *Crinivirus*, *Ipomovirus* and *Potyvirus*. These viruses affect many food and industrial crops, particularly in the tropical and sub-tropical regions of the world. *T. vaporariorum* has also gained some notoriety as a vector of some important plant viruses, particularly in sub-tropical and high-altitude tropical environments, but the number of these viruses is still low when compared to the number of viruses transmitted by *B. tabaci*. *T. vaporariorum* is the main vector of criniviruses (*Closteroviridae*).

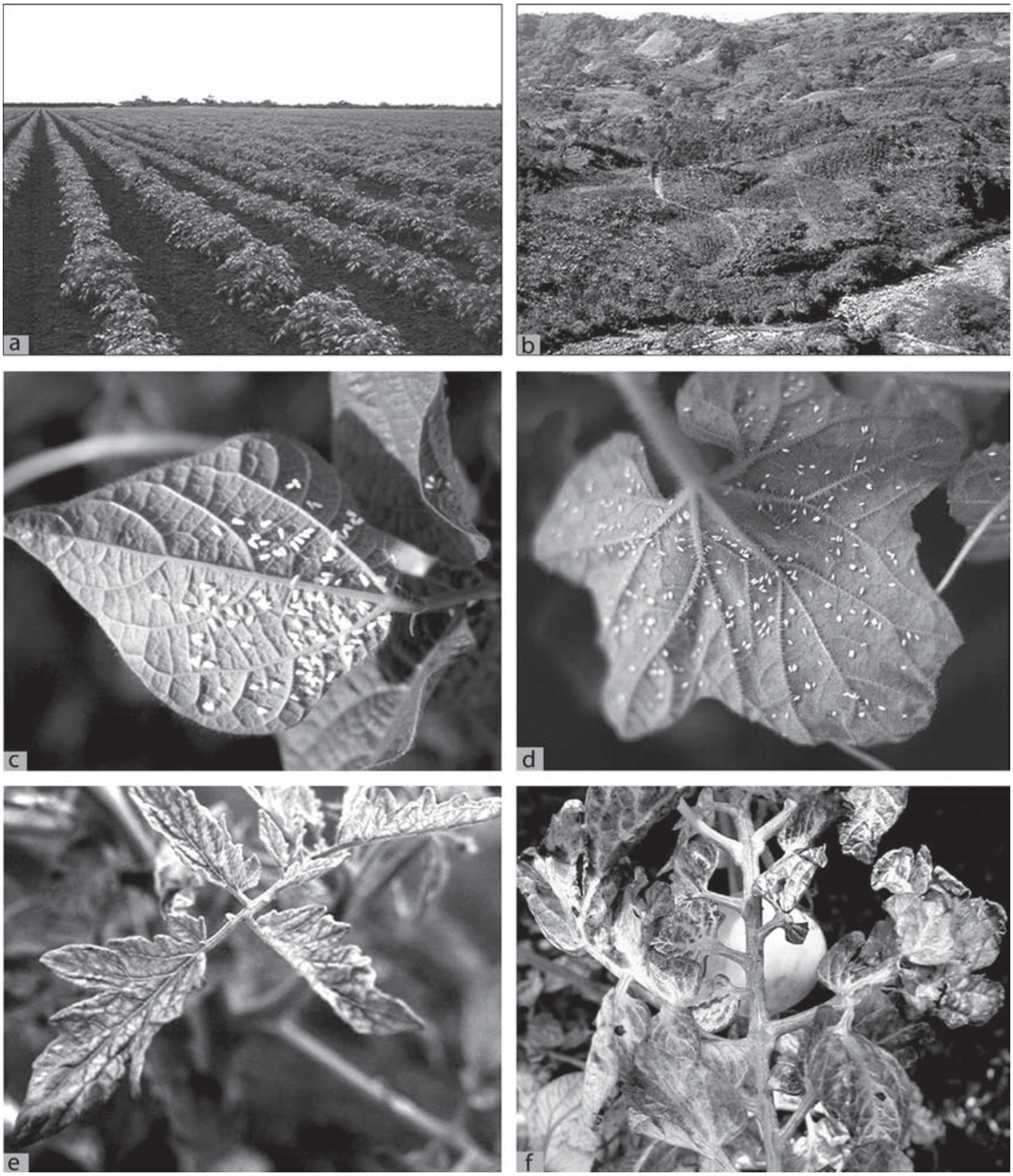
So far in Latin America, 35 crops (23 of them fully confirmed) have been reported as feeding and/or reproductive hosts of *B. tabaci*, including mainly annual but also perennial crops (see Table 5) in 14 plant families: Apocynaceae, Asteraceae, Caricaceae, Convolvulaceae, Cruciferae, Cucurbitaceae, Euphorbiaceae, Fabaceae, Malvaceae, Myrtaceae, Passifloraceae, Pedaliaceae, Solanaceae and Vitaceae. The principal hosts, considering their socioeconomic importance, area covered and damage levels, are tomato, common bean, melon, watermelon, cotton, bell pepper and hot peppers. *Trialeurodes vaporariorum* feeds on more than 250 plant species. The crops most affected by *T. vaporariorum* are dry and snap beans, tomato, peppers, cucumber, squash, eggplant, potato, pea (*Pisum sativum*), broad bean (*Vicia faba*), and cotton.

The feeding and/or reproductive performance of *B. tabaci* on a given host also depends on the particular biotype involved. For instance, in some Latin American countries where the "A" biotype still predominates, it does not colonize tomato to a significant extent, whereas huge numbers of eggs and nymphs are frequently observed on bell pepper. This situation is completely reversed in the case of the "B" biotype, which colonizes tomato, but does not lay eggs in most pepper cultivars.

Bemisia tabaci and *T. vaporariorum* also feed and/or breed on hundreds of wild plant species. Worldwide, *B. tabaci* has been observed on at least 500 plant species belonging to 74 families, but its full host range remains unknown both in Latin America and worldwide, and will certainly keep increasing due to the ability with which the "B" biotype adapts to new host plants. Despite its well-documented polyphagous nature, *B. tabaci* shows a distinct preference for members of certain families, such as Fabaceae, Asteraceae, Malvaceae, Solanaceae, Euphorbiaceae and Cucurbitaceae. *Trialeurodes vaporariorum* is mostly found on plant species in the Solanaceae, Fabaceae, and Cucurbitaceae.

Bioecological Characteristics

There are several biological and ecological characteristics of *B. tabaci* that can be important for its management in terms of assessing the risk of damage and the potential for successfully controlling it. Three key characteristics are discussed here: genetic plasticity reproductive potential and virus transmission.



Whitefly Bioecology and Management in Latin America, Figure 49 ***Top row***, **contrasts between current cropping systems in Latin America: a large tomato monoculture in Bahía, Brazil (a), and a "mosaic" of beans and vegetables interspersed between coffee and sugarcane plantations in Turrialba, Costa Rica (b) (Photos by Luko Hilje). Middle row, large whitefly populations: *T. vaporariorum* on common beans in Colombia (c), and *B. tabaci* on melons in Guanacaste, Costa Rica (d) (Photos by Luko Hilje and CIAT, respectively). Bottom row, plants affected by whitefly-borne viruses: tomato yellow mosaic virus (ToYMoV), transmitted by *B. tabaci* to tomatoes in Grecia, Costa Rica (e), and an undetermined crinivirus vectored by *T. vaporariorum* to tomatoes in Colombia (f) (Photos by Luko Hilje and CIAT, respectively).**

Whitefly Bioecology and Management in Latin America, Table 5 Host crops of *Bemisia tabaci* reported to date in Latin America[a]

Scientific name	Family	Common name
Abelmoschus (= Hibiscus) esculentus	Malvaceae	Okra
Capsicum annuum	Solanaceae	Bell pepper
Capsicum frutescens	Solanaceae	Hot pepper
Carica papaya	Caricaceae	Papaya
Citrullus lanatus	Cucurbitaceae	Watermelon
Cucumis melo	Cucurbitaceae	Melon
Cucumis sativus	Cucurbitaceae	Cucumber
Cucurbita argyrosperma	Cucurbitaceae	Pipián
Cucurbita maxima	Cucurbitaceae	Squash
Cucurbita moschata	Cucurbitaceae	Ayote
Cucurbita pepo	Cucurbitaceae	Squash
Fernaldia pandurata	Apocynaceae	Loroco
Glycine max	Fabaceae	Soybean
Gossypium hirsutum	Malvaceae	Cotton
Lycopersicon esculentum	Solanaceae	Tomato
Manihot esculenta	Euphorbiaceae	Cassava
Medicago sativa	Fabaceae	Alfalfa
Nicotiana tabacum	Solanaceae	Tobacco
Passiflora edulis f. flavicarpa	Passifloraceae	Passion fruit
Phaseolus acutifolius	Fabaceae	Tepary bean
Phaseolus vulgaris	Fabaceae	Common bean
Solanum melongena	Solanaceae	Eggplant
Vitis vinifera	Vitaceae	Grape
To be confirmed		
Arachis hypogaea	Fabaceae	Peanuts
Brassica oleracea var. capitata	Cruciferae	Cabbage
Brassica oleracea var. italica	Cruciferae	Broccoli
Brassica oleracea var. botrytis	Cruciferae	Cauliflower
Helianthus annuus	Asteraceae	Sunflower
Ipomoea batatas	Convolvulaceae	Sweet potato
Lactuca sativa	Asteraceae	Lettuce
Phaseolus lunatus	Fabaceae	Lima bean
Psidium guajava	Myrtaceae	Guava
Raphanus sativus	Cruciferae	Radish
Sesamum indicum	Pedaliaceae	Sesame
Solanum tuberosum	Solanaceae	Potato

[a]Based upon Anderson and Morales (2005) and Hilje (2003), but including only those crops recorded by either whitefly taxonomists or specialists working with molecular techniques. Crops to be confirmed include those which have been reported as hosts elsewhere and on which whiteflies closely resembling *B. tabaci* have been collected, but still requiring full confirmation.

Genetic Plasticity

The remarkable plasticity of *B. tabaci* makes its management extremely difficult. For instance, *B. tabaci* can rapidly develop resistance to insecticides, including novel ones, as has occurred in recent years with some neonicotinoids and insect growth regulators. Also, it has expanded its geographic range by adapting to higher altitudes and latitudes. *Bemisia tabaci* can be found at altitudes over 2,000 m in Costa Rica, which is unusual for this species. The altitudinal dissemination of *B. tabaci* is often aided by the movement of propagative material from the lowlands to the highlands.

Bemisia tabaci can also give rise to a series of races or biotypes that vary in their host-plant relationships, as well as in their ability to induce physiological disorders. The efficiency of transmission of plant viruses by *B. tabaci* also differs among biotypes, though the original biotypes were usually more efficient vectors. So far, some 23 biotypes have been detected worldwide by means of molecular and biochemical methods. The most widely distributed in Latin America is the new "B" biotype, followed by the original "A" biotype, as well as an undetermined number of regional biotypes (Table 6).

So far, the "A", "B" and "Q" are the only biotypes that have received some degree of attention in terms of understanding their life cycles, physiology, behavior, and host-plant relationships. Such studies are crucial, not just because of their academic value, but also due to their practical consequences. For instance, in contrast to the "A" biotype, the "B" biotype can feed or breed on cole crops (cabbage, cauliflower and broccoli), lettuce, citrus and papaya, and can successfully develop on tomato; its nymphs can induce the aforementioned syndromes on tomato, squash, cole crops and lettuce. The "B" biotype also has a higher (two-fold) fecundity, and is more cold-tolerant. Interestingly, some biotypes can coexist on the same plant species and even on the same plant, as it has been noticed in Guanacaste, Costa Rica, where individuals of the "A" and "B" biotypes have been collected along with other undescribed biotype on the same jalapeño pepper plants.

Trialeurodes vaporariorum is also capable of developing genetic resistance to insecticides, but it does not seem to exhibit the high genetic variability of *B. tabaci*. However, in highly disturbed and chemically contaminated agro-ecosystems, *T. vaporariorum* can attack an unusually large number of cultivated and wild plant species.

Reproductive Potential

This characteristic depends on the insect's fecundity, generation time, sex ratio, and longevity, but these parameters can vary depending on the biotype, temperature and relative humidity, as well as the quality and age of the host plant species or cultivar.

For *B. tabaci* raised under controlled conditions (25°C and 65% relative humidity) in Venezuela, average fecundity (number of eggs/female) was 194 (possibly corresponding to the "B" biotype); generation time (interval elapsing between two successive generations) was 42 days; sex ratio (females: males in the offspring) varied from 3:1 to 1:1, but females can show arrhenotokic parthenogenesis (unmated females can give rise to a 100% male offspring); and adult longevity typically ranges from 11 to 20 days. For *T. vaporariorum* raised at 23°C and 80% relative humidity in Brazil, average fecundity was 186 eggs; generation time was 23 days; sex ratio also varied; and adult longevity was about 24 days.

Tropical regions offer a unique agroecological environment for *B. tabaci* to fully express its reproductive potential. Temperature, rainfall and air humidity are normally much higher than in temperate areas, and photoperiod varies only slightly throughout the year. Since temperature is fairly constant but quite high, and insects are poikilothermic, *B. tabaci* can breed continuously, giving rise to very high densities and overlapping generations.

Optimal temperatures for *B. tabaci* development range between 30 and 33°C. At these temperatures,

Whitefly Bioecology and Management in Latin America, Table 6 **Distribution of *Bemisia tabaci* biotypes in Latin America to date**

Country	Region	Biotypes
Mexico	North	A, B
Guatemala	Central	A, B and others
Belice	Central	B
El Salvador	Central	A, B
Honduras	Central	A, B and others
Nicaragua	Central	B and others
Costa Rica	Central	A, B and others
Panama	Central	A, B
Cuba	Caribbean	B
Dominican Republic	Caribbean	A, B
Haiti	Caribbean	B
Puerto Rico	Caribbean	B
Jamaica	Caribbean	B
Colombia	South	A, B
Venezuela	South	A, B
Ecuador	South	A, B
Peru	South	A, B
Brazil	South	B
Bolivia	South	B
Chile	South	B (?)
Uruguay	South	?
Paraguay	South	?
Argentina	South	A, B and others

fecundity increases and generation time shortens, leading to very rapid population growth. Such temperature values are easily reached during the dry season, when thermal accumulation ("physiological time") is high. This is particularly true in irrigated, hot and dry areas devoted to export crops such as melons, watermelon and vegetables, where furrow or drip irrigation provides enough moisture for nymphs to complete their development. On the contrary, sprinkler irrigation, which mimics rainfall, has adverse effects on whitefly populations, due to dislodgment of adults from plants. There also are possible negative effects of increased relative humidity on the immature stages, or increased incidence of entomopathogenic fungi, associated with sprinkler irrigation.

Populations of *B. tabaci* are normally lower during the rainy season. Nevertheless, it is not unusual to observe tomato and bean fields 100% affected by whitefly-borne viruses, even during the rainy season. This typically occurs when farmers plant soon after the dry season and when whitefly populations are still high, or whenever the rainfall levels are lower than normal.

Trialeurodes vaporariorum is adapted to much cooler environments than *B. tabaci*, and is more characteristic of sub-tropical and temperate agro-ecosystems than true tropical environments.

However, this whitefly species causes total yield losses in several crops grown in the tropics at altitudes higher than 1,000 m, where the temperature is cool or cold and humidity can range from very dry to very humid within the year. *Trialeurodes vaporariorum* populations also increase rapidly during dry periods of the year.

Virus Transmission

In contrast to the majority of whitefly species, *B. tabaci* has the ability to acquire and transmit over 200 different viruses, mainly begomoviruses, which cause significant yield losses in important crops such as tomato, bell and hot peppers, beans, and various cucurbits including melon and squash. *Bemisia tabaci* can rapidly disseminate viruses in the field even when populations are not appreciable, and cause severe crop damage in susceptible plantings. Hence, economic thresholds are not recommended for whitefly vectors of plant viruses.

As expected due to the high levels of biodiversity inherent to the neotropics, there are many endemic whitefly-borne viruses yet to be discovered and named. In fact, any one of these crops may be affected by several types of viruses either in different countries or different areas within a given country, as it occurs with tomato, which is affected by at least 17 types of begomoviruses in America. Moreover, sometimes they appear in mixed infections, giving rise to complex synergistic interactions.

However, some of these native viruses could eventually be displaced by more competitive exotic viruses, as has already occurred in several countries with *Tomato yellow leaf curl virus* (TYLCV), an Old World virus that was accidentally introduced in the Caribbean Basin. TYLCV was first detected in the Dominican Republic, and then moved rapidly into Haiti and other Caribbean islands (Puerto Rico, Cuba, Bahamas, Jamaica and Guadeloupe). This virus then emerged in Florida, USA and in Yucatan, Mexico. So far, TYLCV has been managed through the use of virus-resistant tomato cultivars and novel insecticides. Curiously, TYLCV has not adapted well in Yucatan, Mexico. Nevertheless, TYLCV has caused millions of dollars worth of direct damage to tomato plantations in the Dominican Republic and Haiti, and considerable damage to the tomato paste industry of that island during the initial epidemics suffered in the early 1990s.

The higher degree of pathogenicity and virulence shown by exotic Old World viruses such as TYLCV may be related to their long-term association with mixed cropping systems and aggressive vectors, such as biotype "B" of *B. tabaci* in the Old World. The significant damage caused by TYLCV in the Dominican Republic may be also associated to the coincidental introduction of TYLCV and the "B" biotype in a country that was beginning to promote both traditional and non-traditional export crops, including common bean, tomato, melons, eggplant, peppers, and other susceptible crops. On the other hand, the arrival of TYLCV in other Caribbean islands and in Yucatan, has not caused a rapid displacement of the existing neotropical begomoviruses of tomato, probably because of the more traditional cropping systems in these latter locations.

It is important to note that these pathosystems often involve at least four components: *B. tabaci* biotypes, begomoviruses, crops, and whitefly and virus hosts. Each element is an important biological variable that, when combined, could give rise to unmanageable, severe outbreaks of highly damaging virus problems.

Northern Mexico, Guatemala and Brazil are examples of countries where the diversification of cropping systems, with a view to producing export crops, resulted in major pandemics of begomoviruses. Several crops were affected, and significant crop losses caused by the whitefly-transmitted viruses brought the diversification effort to a halt. For instance, the 1990s witnessed severe attacks of different begomoviruses in several crops grown for export in northern Mexico, including common bean, tomato, cucurbits, and peppers. In 2001, over 1,000 ha of melon were severely damaged in Zacapa, Guatemala, with unexpected high losses. Common bean, tomato and peppers were also severely attacked in the lowlands and mid-altitude valleys of southeastern Guatemala. In Brazil, a major campaign to promote high value horticultural crops for export in the mid-1990s met with a similar disastrous fate, resulting in loss of hundreds of thousands of hectares to whitefly-transmitted viruses.

Trialeurodes vaporariorum has gained notoriety as a vector of plant viruses only in the last two decades, particularly in temperate regions. However, this whitefly species has now been shown to transmit criniviruses in the tropical highlands of South America, affecting important crops such as potato and tomato.

Management Alternatives

Historically, insecticides have been the first line of defense against *B. tabaci* and *T. vaporariorum* in both their roles as direct pests and virus vectors. This pattern is seen not only in Latin America, but in most agricultural regions of the world. Unfortunately, the first insecticides used to control whiteflies were conventional, broad-spectrum products applied singly or, more often, in mixtures of organophosphates and pyrethroids, known as "cocktails." These products soon failed to control these whitefly pests due to the outstanding genetic capacity that whiteflies have to develop resistance to insecticides of different nature. Farmers soon reacted to this situation by spraying three times a week, and even daily against these pests. Obviously, these insecticide applications were not a cost-effective approach, and increased production costs by at least 30%. For instance, in Guatemalan cotton fields, *B. tabaci* had developed resistance to 16 different insecticides by 1987, reaching resistance levels as high as 980X for biphenthrin and cyhalothrin, and over 2000X for quinalphos and deltamethrin.

In view of this situation, new chemistries such as neonicotinoids (e.g., imidacloprid, acetamiprid, thiamethoxam, nitenpyram and thiacloprid) and insect growth regulators (e.g., buprofezin and pyriproxyfen), were developed and widely used despite their higher prices. Unfortunately, insecticide abuse (excessive number of applications) and misuse (active ingredient diluted with other products) still occurs in several Latin American countries, which along with the lack of complementary IPM programs (like the ones so far implemented in Israel, southwestern USA and elsewhere) pose a high risk for the emergence of new whitefly populations possessing resistance to the new compounds.

Despite the presence of many native natural enemies (parasitoids, predators and entomopathogenic fungi) of *B. tabaci* and *T. vaporariorum* in Latin America, including at least ten different species of the parasitoid *Eretmocerus*, and two species of *Encarsia*, biological control agents have not been widely used or observed to be effective control agents in whitefly-affected agricultural regions. The explanation for this observation is the slow action of biological control agents, as compared to insecticides. In general terms, biological control can only be effective in areas where neither insecticide abuse nor viruses vectored by whiteflies occur.

Alternative whitefly control strategies are available and can be highly effective when used properly. Some of these IPM practices include:

Phytosanitary Campaigns

In past years, successful whitefly control measures were implemented in the Dominican Republic, Mexico and Cuba, supported by legal measures that required the strong participation of the affected farmers. These campaigns were mostly based on the implementation of a susceptible or host crop-free period.

In the early 1990s, the processing tomato industry in the Azua Valley and other production areas of the Dominican Republic were critically affected by production drops due to the introduction of TYLCV. The cultivated area in the Azua Valley dropped from 8,805 ha in 1989 to 3,729 has in 1993, whereas yield decreased from 21.6 to 11.3 MT/ha within the same period. This situation forced the nascent tomato paste industry in the Dominican Republic to import tomato paste from Chile. The enforcement of legal measures that banned cultivation of *B. tabaci* reproductive hosts up to 90 days before the main tomato growing season, along with crop rotations with non-whitefly hosts, such as sorghum, significantly diminished begomovirus incidence in Azua. These legal measures were complemented by planting of TYLCV-tolerant hybrids and a judicious insecticide use scheme, which allowed the tomato industry in the Dominican Republic not only to subsist, but also to increase the area planted to 8,940 ha and yields to 30.4 t/ha.

Host Plant Resistance

In the 1980s, a major crop improvement project was launched by the PROFRIJOL network to incorporate genetic resistance to whitefly-transmitted viruses affecting common bean in Latin America. This was conducted under the coordination of the International Centre for Tropical Agriculture (CIAT), in Colombia. Despite the termination of this successful project due to the economic crises that have affected national and international agricultural research institutions in Latin America, some international projects (such as CRSP-USAID) continue to generate begomovirus-resistant common bean varieties in Central America from its main pilot site at the Pan-American Agricultural School (Zamorano) in Honduras.

REDCAHOR was another network created in the early 1990s to improve horticultural crops in Central America, but it was short lived. In past years, only some semi-commercial initiatives in Guatemala (University of San Carlos and University of Wisconsin), and the Tropical Whitefly IPM Project coordinated by CIAT, are developing tomato hybrids and varieties possessing resistance to whitefly-borne begomoviruses. The most advanced tomato breeding project in Latin America is now conducted by the Horticultural Research Institute "Liliana Dimitrova" in Havana, Cuba.

Physical Exclusion

Because young plants are more susceptible to damage by whiteflies and whitefly-transmitted viruses, seedlings must be protected in seedbeds before transplanting in the field (e.g., tomato and pepper seedlings). Seedlings are usually protected in insect-proof screenhouses or glasshouses, or at least with insect-proof fleece placed over the seedbeds. This practice has been increasingly accepted over the years, thanks to a few entrepreneurs who produce virus-free seedlings for sale. Also, some farmers use micro-tunnels to produce their own seedlings.

Among the many mesh sizes commercially available, it has been shown that a 50-mesh screen effectively stops *B. tabaci* adult entrance into protected structures, while allowing adequate airflow through the screening to favor seedling development. However, structures constructed with screens or plastics treated with an absorbing additive that blocks a portion of the ultraviolet light spectrum, and which hinders the ability of *B. tabaci* to locate plants, are still uncommon due to the high cost of this novel technology. In Israel and elsewhere, it has been shown that greenhouses protected with these ultraviolet-blocking materials have lower whitefly populations and less virus incidence, in comparison to similar materials that transmit more ultraviolet light.

Another approach that has gained acceptance, especially in Mexico and Guatemala, is the use of "floating" row covers to reduce the spread of whitefly-transmitted viruses. With this technology, field-sown or transplanted seedlings can be protected in their early stages of development by temporarily covering them with lightweight materials, such as spun-bonded polyester, and there is no need for any supporting structure.

The cover remains over the plants until it is necessary to remove it to allow bee pollination and other cultural practices.

Mulching

Mulches are used for certain crops in order to control weeds or to avoid contact of delicate fruits with the soil. However, some mulches have been shown to reduce the number of whiteflies, and incidence of whitefly-transmitted viruses in certain crops. Aluminum, silver or metallic mulches have proven to be most effective in reducing *B. tabaci* adults on plants. The most important factor is not the color of the mulch, but the intensity with which the light is reflected off the mulched soil. The main constraints to the adoption of this method of whitefly control include the high cost and the environmental impact of discarded plastics.

An environmentally-friendly and cost-effective alternative to mulching is the use of ground covers, which have been successfully tested in commercial tomato fields in Costa Rica. Instead of repelling whiteflies, they mask the young tomato plants from viruliferous whiteflies. Among several promising candidate plant species, coriander (*Coriandrum sativum*, Apiaceae) stood out, as farmers can harvest it 35 days after planting, after the critical period of tomato plant susceptibility is over. This technique warrants more attention, as it is particularly well suited for small farms.

Chemical Repellents

Any compound capable of keeping whiteflies away from susceptible plants reduces the possibility of virus inoculation and subsequent disease expression. Protection can be achieved either by feeding deterrent (acting after contact) or repellent (acting at a distance, as vapors) substances.

It has been shown that in proper doses, both cooking and mineral oils can deter *B. tabaci* without causing phytotoxicity, but these are not widely used by farmers. Moreover, in Costa Rica, after testing approximately 70 hydroalcoholic extracts from plants, deterrence of whiteflies was detected in the following ten species: worm-seed (*Chenopodium ambrosiodes*, Chenopodiaceae), sword bean (*Canavalia ensiformis*, Fabaceae), "chile muelo" (*Drymis granatensis*, Winteraceae), bitterwood (*Quassia amara*, Simaroubaceae), mother of cocoa (*Gliricidia sepium*, Fabaceae), neem (*Azadirachta indica*, Meliaceae), wild "tacaco" (*Sechium pittieri*, Cucurbitaceae), "sorosí" (*Momordica charantia*, Cucurbitaceae), fish bean (*Tephrosia vogelii*, Fabaceae), and wild sunflower (*Tithonia diversifolia*, Asteraceae). Some of them are currently receiving additional research.

Volatile substances of botanical origin, mainly alcohols and aldehydes, can repel whiteflies. Repellency has been shown to exist for cinnamaldehyde, perialdehyde, 1-hexanal and Z-3-hexen-1-ol. These compounds have been further tested by enclosing them in controlled-release dispensers to avoid phytotoxicity and increase their life span both in field crops and commercial greenhouses.

Concluding Remarks

Whereas the knowledge on whitefly-related crop production problems has significantly increased in the past two decades, *B. tabaci* and *T. vaporariorum* are still major pests and vectors of plant viruses that affect many industrial and food crops in Latin America. The main reason for the apparent difficulty in controlling these pests has been the economic crises that drastically reduced crop production-oriented research and crop improvement projects in Latin America. Technical assistance or, rather, the lack of it, is also another major cause of the continuous emergence of insecticide-resistant populations of *B. tabaci* and *T. vaporariorum* in Latin America. In the absence of resistant varieties and technical assistance, farmers do not have alternatives different from chemical control. Insecticide abuse soon leads to the elimination of the natural enemies of whiteflies, and emergence of insecticide-resistant whiteflies.

Also, a major factor that have contributed to the existing escalation in the number of whitefly biotypes and whitefly-borne viruses has been the diversification of the traditional cropping systems in Latin America. Promotion of mixed cropping systems that include both traditional and non-traditional export crops provides continuous food for whitefly pests year round. In addition to the continuous availability of plants suitable for whitefly survival, the plasticity of begomoviruses, and the ease with which they form genetic recombinants, are also notable factors driving the epidemics of old and new begomoviruses in many commercial crops grown for local consumption or export in Latin America. Consequently, technology generation and transfer efforts should be reconsidered and strengthened in Latin America, particularly in view of the challenge presented by the unavoidable integration of Latin American agricultural markets into a highly competitive globalized world.

► Greenhouse Whitefly
► Sweetpotato and Silverleaf Whiteflies
► Whiteflies
► Plant Viruses and Insects
► Transmission of Plant Diseases by Insects

References

Anderson PK, Morales FJ (eds) (2005) Whitefly and whitefly-borne viruses in the tropics: building a knowledge base for global action. Publication 341. CIAT, Colombia, 351 pp

Brown JK (1994) Current status of *Bemisia tabaci* as a plant pest and virus vector in agroecosystems worldwide. FAO Plant Prot Bull 42: (12) 332

Brown JK, Bird J (1992) Whitefly-transmitted geminiviruses in the Americas and the Caribbean Basin: past and present. Plant Dis 76:220–225

Caballero R (1993) Moscas blancas neotropicales (Homoptera: Aleyrodidae): hospedantes, distribución, enemigos naturales e importancia económica. In: Hilje L, Arboleda O (eds) Las moscas blancas (Homoptera: Aleyrodidae) en América Central y el Caribe. Serie Técnica. Informe Técnico No. 205. CATIE, pp 10–15

Gerling D (ed) (1990) Whiteflies: their bionomics, pest status and management. Athenaeum Press, New Castle, UK, 348 pp

Gerling D, Mayer RT (eds) (1996) *Bemisia* 1995: taxonomy, biology, damage, control and management. Intercept, UK, 702 pp

Hilje L (1995) Aspectos bioecológicos de *Bemisia tabaci* en Mesoamérica. Manejo Integrado de Plagas (Costa Rica) 35:46–54

Hilje L (2003) Estatus del manejo de *Bemisia tabaci* en América Latina y el Caribe: ocho preguntas pertinentes. Manejo Integrado de Plagas y Agroecología (Costa Rica) 70:88–99

Morales FJ (2006) History and current distribution of begomoviruses in Latin America. In: Thresh JM (ed) Advances in virus research. Academic Press, London, UK, pp Elsevier, 127–162

Morales FJ, Jones PG (2004) The ecology and epidemiology of whitefly-transmitted viruses in Latin America. Virus Res 100:57–65

Naranjo SE, Ellsworth PC (2001) Challenges and opportunities for pest management of *Bemisia* in the New Century. Special issue. Crop Prot 20(9):707–869

White Grubs, *Phyllophaga*, and Others (Coleoptera: Scarabaeidae)

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The whitish, soil-dwelling larvae of scarab beetle species are called white grubs. Traditionally, white grubs were considered to be members of the genus *Phyllophaga*, but increasingly the larvae of other members of the family Scarabaeidae such as *Anomala*, *Aphodius, Ataenius*, *Cyclocephala*, *Exomala*, *Polyphylla*, *Popilla*, *Rhizotrogus*, and other are included in this general term because they have a very similar appearance and biology.

Life History

The life cycle of the various species ranges from 1 to 4 years, although in the *Phyllophaga* species it is 2–4 years, with the 3-year life cycle most frequent. Duration of the life cycle is often related to latitude.

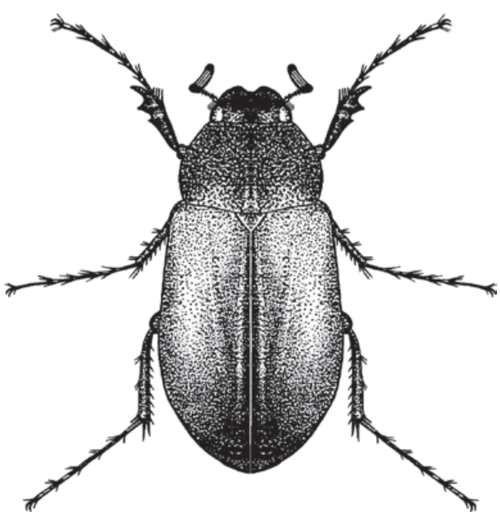
In southern areas, 2-year life cycles are common, whereas in the north three to 4 year cycles occur.

The general, 3-year life cycle starts with oviposition in the spring or early summer, followed by feeding and growth until autumn when cold weather induces a period of inactivity, and overwintering by second instar larvae. During the second year, feeding is resumed in the spring, the third instar is attained, and feeding continues until cold weather when another period of inactivity occurs. In the spring of the third year larval growth is completed, and pupation occurs during the summer. The adult remains in the soil until the following spring. Thus, the 3-year life cycle occurs during a 4-year calendar period (Fig. 50).

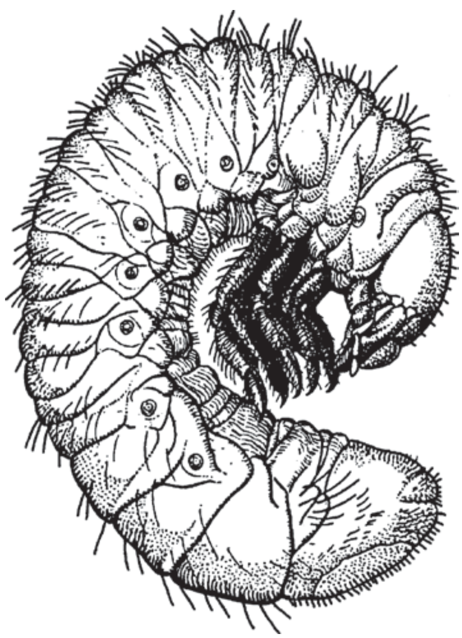
In the typical 2-year life cycle, oviposition occurs in the summer, eggs hatch in late summer, and young larvae commence feeding, quickly attaining the third larval instar, and then overwinter. They feed again throughout the second summer and overwinter as mature third instars. The following spring they feed briefly, pupate, and adults emerge, mate, and oviposit. Thus, in the 2-year cycle larvae develop more quickly, and the adult does not undergo a period of arrested development, as occurs in the 3-year cycle. The 2-year period of development occurs over three calendar years (Fig. 51).

Following is a description of common June beetle, *P. anxia*, perhaps the most abundant and damaging *Phyllophaga* in North America. It serves well to illustrate the biology of white grubs and June beetles. In Quebec, Canada, common June beetle displays the typical 3-year life cycle. Adults begin to fly in May and oviposit in June. First instar grubs are abundant in July and molt into second instars in August. The second instars overwinter, molting into third instars during June of the second year. Third instars overwinter at the end of the second year, developing into prepupae during June of the third year, and pupating in July. Adults are fully formed by September but remain in the soil until the following spring. As noted previously, the 3-year life cycle is spread over four calendar years.

About 10 days after mating, the female deposits its pearly white elongate-oval eggs about 2.4 mm long and 1.5 mm wide. The eggs absorb water, becoming enlarged in size, and eventually measure about 3 mm in length and 2 mm in width. Mean fecundity is about 55 eggs per female. Eggs hatch after about 20–30 days.



White Grubs, *Phyllophaga*, and Others (Coleoptera: Scarabaeidae), Figure 50 **Adult of *Phyllophaga* sp.**



White Grubs, *Phyllophaga*, and Others (Coleoptera: Scarabaeidae), Figure 51 **Larva of *Phyllophaga* sp., a common white grub.**

Young grubs often feed on decaying vegetation before turning to root feeding, but are not associated with manure. The grubs are pearly white, with a dark head and legs. They bear a thin covering of stout hairs, and when dug from the soil they assume a curved body posture or C-shape. Although the grubs feed at a depth of perhaps 5–15 cm during the summer months, they descend to about 30–100 cm during the winter months. Depth of burrowing is markedly affected by soil and moisture conditions and age of the grub. Survival of grubs is higher in light soils and with moderate moisture conditions; heavy rain is detrimental both to oviposition and survival of young grubs. Grubs pass through three instars over about a 24 month period that is spread over part of three calendar years. Larvae prepare a cell in the soil for pupation. This cell also serves as the overwintering site for the adult, which does not emerge from the soil until the following spring.

The body of adult *P. anxia* is oblong ovate in shape, dark brown in color, and measures 17–21 mm in length. The elytra are marked with numerous fine, shallow punctures. The underside of the thorax bears a dense coat of long hairs. The antennae are 10-segmented and elbowed and expanded at the tip. The basal segments of the legs are generally stout, the tibiae broadened and armed with teeth or stout spurs, but the tarsal segments are elongate and narrow.

Many predators, parasitoids, and pathogens of white grubs are documented. Larvae of robber flies (Diptera: Asilidae) and beeflies (Diptera: Bombyliidae) are frequently found in association with grubs. Among the parasitoids are such tachinids as *Cryptomeigenia theutis* (Walker), *Eutrixa exilis* (Coquillett), *Eutrixoides jonesii* Walton, and *Microphthalma* spp. (all Diptera: Tachinidae); the light flies, *Pyrgota* spp. (Diptera: Pyrgotidae); and the wasps *Pelecinus polyturator* (Drury) (Hymenoptera: Pelecinidae); and *Tiphia* spp. (Hymenoptera: Tiphiidae). Of the parasitoids, only *Tiphia* spp. are documented to be of considerable importance, sometimes accounting for up to 50% mortality among grubs. Mites (Acari: several families) are commonly associated with grubs and beetles; eggs and pupae generally are free of mites. However, few of these mite associates are thought to be parasitic or detrimental to white grubs. All the common groups of insect pathogens have been found associated with white grubs, especially *Metarhizium anisopliae* and *Beauveria bassiana* fungi. There is no evidence that these pathogens, and many of the other associates of white grubs, have significant impact on grub density.

Damage

Both larvae and adults can be damaging, but they usually have markedly different feeding preferences. Larvae are found in the soil, and normally feed on the roots of grasses. Adults, however, usually feed on the leaves and flowers of deciduous trees and shrubs, particularly ash, elm, hackberry, hickory, locust, oak, poplar, walnut, and willow, and sometimes pine. Root crops such as beet, potato, and turnip are among the crops most susceptible to injury by larvae, but corn and strawberry are sometimes damaged, and the seedlings of virtually all vegetables are susceptible if grub density is high. Crops other than grasses are not preferred oviposition sites, so damage usually occurs only when crops are planted into land that recently has been grass sod, pasture, or sometimes grass crops such as timothy, small grains, or sorghum. Tree seedlings, especially conifers, are damaged when planted into grass sod or pasture. Alfalfa and clover seem to be avoided even though both crops often contain some grass. Adults disperse widely, and trees adjacent to grassland, especially when few in number, are sometimes injured by defoliation.

White grubs have limited mobility; their distribution is largely a function of oviposition preference by females. Thus, although the roots and tubers of crops may be consumed, this is often due to conversion of grassland bearing partially grown grubs to crop production areas, and a decrease in the availability of their preferred host plants, grasses. Typically, larvae clip the roots of plants with fibrous roots systems, especially during the second year of larval life, resulting in the wilting and death of young plants. However, they may chew holes into larger roots and tubers, damage that may not be apparent until harvest.

Damage to trees by adults also occurs, particularly in more temperate areas. In such areas, the transition from cold, wet weather to warm, dry weather is abrupt, causing mass emergence of adults and defoliation of nearby trees. In contrast, in warmer areas, the gradual increase in temperatures causes a protracted emergence by adults and the defoliation of trees is less apparent. Adults prefer young foliage, feeding from the edge toward the center of the leaves. They feed at night and hide during the day, so the cause of damage is often overlooked.

Management

Estimates of grub density are often made by digging and examining 0.3 m^3 sections of sod and soil. Due to the highly aggregated distribution of grubs and eggs, however, extensive sampling is required to obtain a high degree of precision, often 50–100 samples. Light traps are used to monitor populations of June beetles because they are nocturnal; such traps collect mostly males. Flights normally occur between sunset and midnight, and then again at sunrise, and are initiated by a combination of temperature and photoperiod stimuli.

White grubs and June beetles are controlled with insecticides by application to soil or tree foliage, respectively. Soil applications predominate except perhaps for protection of foliage in fruit crops. Persistent insecticides are used in soil environments, applied preplanting or at planting. Insecticide resistance has developed in some regions.

Because of the attraction of June beetles to grasses, particularly short or mowed grass, there is considerable risk when crops are planted into land that supported grass during the previous year, or when crops are grown adjacent to grass pastures or sod. If clover is planted immediately following grass, the risk to subsequent crops is reduced, partly because grubs rarely injure clover, but also because June beetles prefer not to oviposit in clover fields. It is also important that crops be free of grass and other weeds during the flight of June beetles, or considerable oviposition may occur. However, if grubs are already in the soil, the presence of grass weeds can be advantageous because grubs will feed preferentially on the grass.

Plowing and disking are sometimes recommended for destruction of grubs because the soft bodies of larvae are easily damaged by tillage. Also, tillage exposes grubs to birds, which can often be seen following tractors and consuming large numbers of exposed insects.

There have been few attempts to implement biological suppression of white grubs, other than the use of domestic animals such as poultry and swine to consume larvae. The spore-forming bacteria *Bacillus popillae* and *Bacillus lentimorbus* will infect and kill white grubs, but this expensive treatment is usually reserved for use on turf, where the bacteria can recycle through generation after generation of grubs. Entomopathogenic nematodes (Nematoda: Steinernematidae and Heterorhabditidae) have been evaluated for white grub suppression. Grubs are susceptible to infection, and high levels of suppression have been attained by both injection and surface application, but the results have not been consistent.

Larvae of scarab beetles.

► Turfgrass Insects and their Management

References

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, 729 pp

Forschler BT, Gardner WA (1990) A review of the scientific literature on the biology and distribution of the genus *Phyllophaga* (Coleoptera: Scarabaeidae) in the southeastern United States. J Entomol Sci 25:628–651

Luginbill Sr P, Painter HR (1953) May beetles of the United States and Canada. USDA Tech Bull 1060:102 pp

Ritcher PO (1966) White grubs and their allies, a study of North American scarabaeoid larvae. Oregon State University Press. Corvallis, Oregon, 219 pp

White Muscardine

A mycosis of various larval, pupal, and adult insects, caused by the fungus *Beauveria bassiana*.

► Muscardine

Whites

Some members of the family Pieridae (order Lepidoptera).

► Yellow-White Butterflies

► Butterflies and Moths

Whorl

The arrangement of leaves in a circle around the stem.

Wiedemann, Christian Rudolph Wilhelm

Christian Wiedemann was born in Braunschweig, Germany, in 1770. He obtained a medical degree in Jena, Germany, in 1792, and beginning in 1805 obtained a series of positions at the University of Kiel. His medical publications included books on anatomy, resuscitation of asphyxiated and drowned persons, and midwifery. In addition to his medical work, Wiedemann became very interested in Diptera. From 1800 to 1806 he edited the "Archiv für Zoologie und Zootomie," and from 1817 to 1825 the "Zoologisches Magazin." About this time he began a thorough study of exotic Diptera in several collections, including a redescription of Fabricius' flies, which was published in both Latin and German. Wiedemann also published an "Analecta Entomologica," with new descriptions, and then the "Aussereuropäische zweiflügelige Inseckten." He had access to rich collections from throughout South America and the West Indies, and named many new species. He died in 1849 at Kiel, Germany.

Reference

Papavero N (1971, 1973) Essays on the history of Neotropical Dipterology with special reference to collectors (1750–1905). Museu de Zoologia, Universidade de São Paulo

Wigglesworth, (SIR) Vincent Brian

Vincent Wigglesworth was born at Kirkham, England, and educated at Cambridge University. He was employed by the London School of Hygiene and Tropical Medicine, the University of London, and Cambridge University. He also directed the unit of Insect Physiology at Cambridge from 1943–1967 and was named Quick professor of biology. He was knighted for his profound contributions to insect physiology. Wigglesworth was one of the foremost insect physiologists of the 20th century, and is best known for his work with Rhodnius prolixus, a blood-sucking bug. His research included work on the hormonal basis for growth and molting, the role of brain secretions in regulating growth, function of sense organs, respiration in eggs, the role of the cuticle in preventing water loss, diel periodicity, and others. Probably his most important contribution, however, was the early work documenting the presence and importance of hormones regulating insect growth and development. His most important publications were "The physiology of insect metamorphosis" (1954), "The control of growth and form" (1959), and "The principles of insect physiology" (6 editions, 1939 to 1965). Wigglesworth's insect physiology was the standard insect physiology text for decades. He died in 1994.

Reference

Locke M (1994) Professor Sir Vincent B Wigglesworth C:B:E M:D:F:R:S (1899–1994). Journal of Insect Physiology 40: 823–826

Williams, Carroll Milton

Carroll Williams was born on December 2, 1916, in Richmond, Virginia, USA. He received a bachelor's degree from the University of Richmond in 1937, and a Ph.D. from Harvard University in 1941. He also earned a M.D. from Harvard. Appointed to the faculty of biology at Harvard in 1946, he was named Bussey Professor of Biology in 1965. Williams chaired the Biology Department from 1959 to 1962 and the Cellular and Developmental Biology Department from 1972 to 1973. Williams was a pioneer in insect endocrinology. He was the first to extract and characterize juvenile hormone. He also discovered brain hormone, and with the collaboration of others, partially characterized ecdysone. Williams also popularized the idea of 'third generation pesticides,' using synthetic hormones or hormone analogs as a means of specifically regulating insect populations without harming other forms of life. Although 'third generation' pesticides have not supplanted the second, there have been significant inroads made toward the use of insect hormones for pest management. Williams received numerous awards and honors over the course of his career, including the George Leslie Award, the Boylston medal, the AAAS-Newcomb Cleveland prize, the Howard Taylor Ricketts Award, and the Entomological Society of America's Founders Memorial Award. He also was a member of the prestigious National Academy of Sciences. Williams died on October 1, 1991.

Reference

Branton D, Dafatos FC, Wilson EO (1996) Memorial minutes on Carroll Williams (FAS) and Aaron Gissen (HMS) and Louis Zetzel. The Harvard University Gazette. Seen at www.news.Harvard.edu/gazette/1996/03.21/MemorialMinutes.htm (August 2002)

Williston, Samuel Wendell

Samuel Williston was born at Boston, Massachusetts, USA, on July 10, 1852. He is known as an authority on Diptera and paleontology. He was raised in Kansas, however, and attended Kansas State University and left before completing his degree to seek his fortune. After contracting malaria, he returned to collect and complete his degree in 1872. He then commenced the study of medicine, and became interested in fossils, attaining an M.S. degree from University of Kansas in 1875. He became an assistant paleontologist at Yale University, and then received his M.D. in 1880 and his Ph.D. in 1885. At Yale University, he specialized in anatomy, and remained there until 1890. Williston then moved back to the University of Kansas, where he held the rank of professor and dean of the Medical School. In 1902 he moved to the University of Chicago, where he remained until his death. Although Williston's career did not include entomology, it was his recreational pastime – not an uncommon situation with "entomologists" of the era. And even as a part-time entomologist he attained recognition as a dipterist, and a renowned authority of Syrphidae. In fact, he turned down an offer from C.V. Riley to become a professional entomologist. He was a prolific writer, authoring 283 publications, most in paleontology but 97 in entomology. Among his important publications were "Synopsis of North American Syrphidae" (1886), and "Manual of the families and genera of North American Diptera" (1896). Williston died at Chicago on August 30, 1918.

Reference

Essig EO (1931) A history of entomology. The Macmillan Company, New York, 1029 pp

Wilt Disease

Infection of lepidopteran larvae by many nuclear polyhedrosis viruses; the expression of infection is a drooping or wilting of larvae, followed by death.

Window Flies

Members of the family Scenopinidae (order Diptera).

► Flies

Wing

The paired membranous structures used for flight in insects. One pair (called the primaries) is normally attached to the mesothorax, the other pair (called the secondaries) to the metathorax. Either or both pairs may be absent. Some wings are modified for purposes other than flight.

► Wings of Insects

Wing Coupling

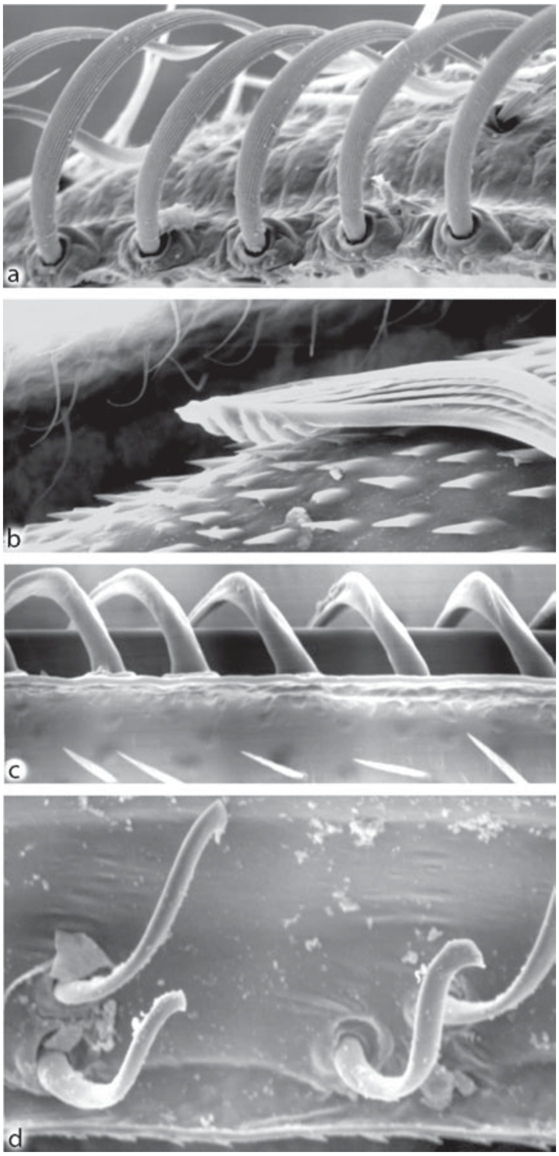
IAN STOCKS
Clemson University, Clemson, SC, USA

Although fossil remains suggest that early insects possessed lobes on the prothoracic segment suitable for gliding, we can infer that the first insects to use powered flight did so by using the mesothoracic (FW) and metathoracic wings (HW). Flight is energetically expensive, and many groups evolved mechanisms that enhanced flight efficiency and aerodynamic control. One solution is to ensure that relative FW and HW motion does not cause interference, thereby reducing flight efficiency and diminishing flight stability.

Many neopterous insects (those able to fold their wings posteriorly over their dorsum) have specialized structures that join the paired wings into a single aerofoil, thereby becoming functionally dipterous. In some neopterous groups, including Coleoptera, Neuroptera, Mecoptera, and some hemimetabolous orders, the paired wings operate principally by a phase shift in their motion. Some insects have solved the aerodynamic interference problem by modifying one pair so that it no longer has a role in generating lift (e.g., HW in Diptera, FW in Strepsiptera and Coleoptera) and does not function as a wing.

Insects with wings that are joined by specialized morphological adaptations occur in the "hemipteroid assemblage" (Psocoptera, Thysanoptera, Heteroptera, Coleorrhyncha, Hemiptera: "Auchenorrhynca," and Hemiptera: Sternorrhyncha), Hymenoptera, Lepidoptera, and Trichoptera. With the exception of Hymenoptera, and possibly some members of the "hemipteroid assemblage," wing-coupling is probably a derived (apomorphic) condition within each group. For example, in both Lepidoptera and Trichoptera, each of which has evolved a diversity of morphological adaptations for wing coupling, basal taxa in the order do not couple the wings (Fig. 52).

The terminology used to discuss wing coupling is used rather loosely in the literature, and typically connotes a greater concern for functional considerations than phylogenetic concerns, such as homology (Fig. 53). The term "hamulus" (pl. hamuli, literally "little hooks"), used primarily for the structures in Hymenoptera, is also used for similar structures in Trichoptera and Aphididae, even though they are substantially different in developmental origin and overall morphology. Similarly, "jugum" and its approximate cognate "fibula" are often used to designate the lobe-like expanded anal area at the basal-posterior margin of the wing. Such lobes occur in many mecopterans, lepidopterans, and trichopterans, and, depending on groups under consideration, may or may not be homologous structures. The term "frenulum-retinaculum" (Fig. 54) is used only in the Lepidoptera, referencing the frenular spine(s) and retinacular clasp on the HW and FW, respectively. However, as will be discussed below, even within this system there is considerable morphological variation. The terms "frenulum" and "frenular" have also been used rather loosely in the literature, but Braun argued to restrict the term "frenulum" to spines arising from the costal sclerite itself, with the term "costal spines" reserved for



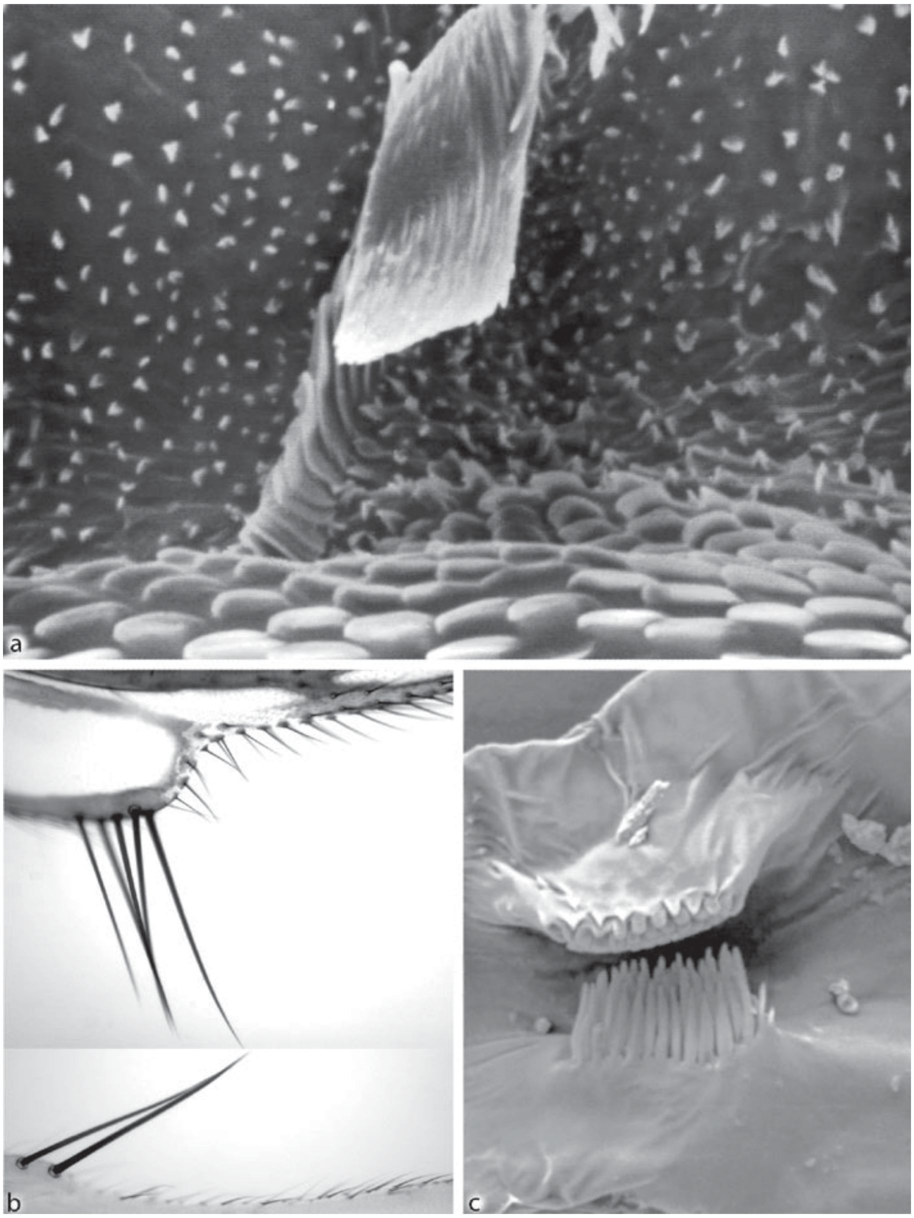
Wing Coupling, Figure 52 **Wing coupling mechanisms: (a) *Mystacides sepulchralis* hind wing hamuli (Leptoceridae: Trichoptera); (b) *Molanna ulmerina* hind wing hamulus engaged with FW posterior vein (Molannidae: Trichoptera); (c) *Vespula* sp. hind wing hamuli (Vespidae: Hymenoptera); (d) *Macrophya* sp. hind wing hamuli (Tenthredinidae: Hymenoptera).**

spines arising generally from the costal vein, both of which types may be used in wing coupling. Coupling due to an "amplexiform" arrangement of the wings, by which an expanded region of one wing overlaps part of the other wing, is most notable in certain Lepidoptera, but is also the means by which mayflies keep their wings together during the down stroke; subtle variations in the contour of the FW and HW, engendering an "amplexiform" overlap, might also enhance coupling in some trichopterans and possibly some psocopterans.

Little empirical evidence, such as videography, exists to support the conclusion that wing coupling is actually achieved by structural wing modifications. Indeed, high speed videography eventually demonstrated that micropterygid moths and rhyacophilid caddisflies *do not* couple their wings during flight. Conversely, high speed cinematography elucidated some of the flight mechanics of *Thrips physapus* (Thysanoptera) and *Piezodorus lituratus* (Heteroptera: Pentatomidae), including HW-FW coupling. In most instances where direct observation has not validated that wings are coupled, claims are based on the inference of a form-function relationship. Also, wing-coupling in many trichopterans and some hymenopterans might be used to enhance swimming through the water column in the search for submerged oviposition sites. Similarly, in some cases the wing modifications inferred to be wing-coupling devices might simply serve to change the position of the wings, such as by bringing the HW out of its resting position, or by securing one or both wings against the body wall.

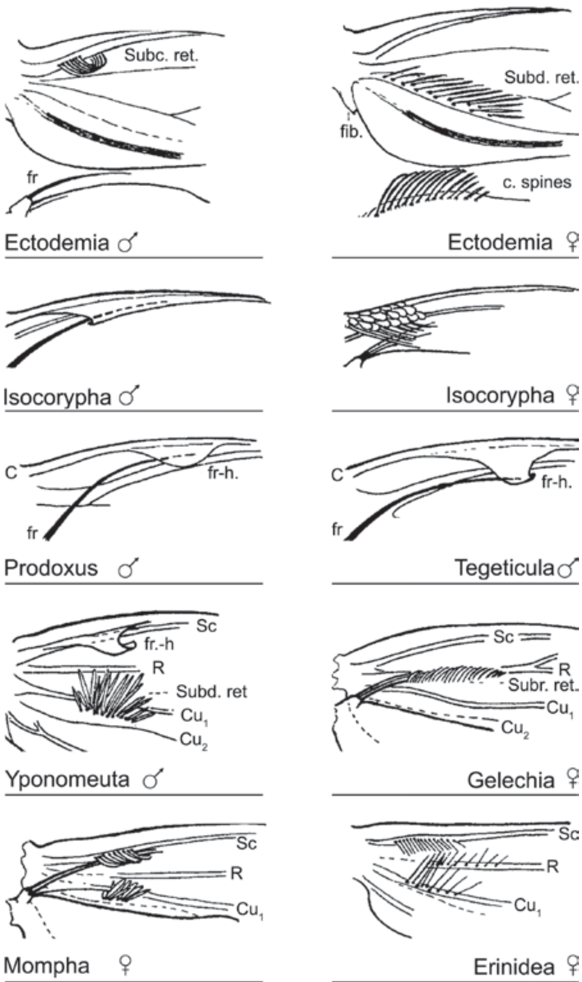
The "Hemipteroid Assemblage"

Discussion of wing-coupling structures in a group as extensive as the "hemipteroids" is problematic, but a great deal has been learned about the functional morphology of the various mechanisms and of the systemic value of these structures in less inclusive groups. Wing-coupling structures in certain psocopterans appear similar to those of some "homopterans," but this has not



Wing Coupling, Figure 53 **Additional wing coupling mechanisms: (a) *Cerastipsocus* sp. front wing (Psocidae: Psocomorpha); (b) *Panorp*a sp. front and hind wings (Panorpidae: Mecoptera); (c) *Sinea* sp. front wing (Reduviidae: Heteroptera).**

been studied in sufficient detail and could be a convergence. Those of thysanopterans appear to be unlike those of any other "hemipteroids," but this observation also could be due to insufficient taxon coverage. Within "Homoptera" (Hemiptera: "Auchenorrhyncha" and Sternorrhyncha) and Heteroptera, the wing coupling structures are phylogenetically useful at the family level. The placement of Coleorrhyncha is still unclear, but examination of the wing-coupling structure suggests a closer relationship to the Heteroptera than to any "homopteran" group.



Wing Coupling, Figure 54 The frenulum and its retinaculum in the Lepidoptera (modified from Braun, A. 1924. Annals of the Entomological Society of America 17: 234–257).

Psocoptera

Recent phylogenetic analyses do not treat Psocoptera as monophyletic, but the groups Psocomorpha and Trogiomorpha, which contain most of the common species of "psocopterans," do appear to be monophyletic. Almost no published information is available about wing coupling in psocopterans, but many taxa do have coupling mechanisms that bear an overall resemblance to a generalized homopteran-type of coupling. Two structures on the forewing, the "nodus" and "nodulus," are involved with FW-HW interaction, but only the nodulus engages the wings as a coupling mechanism. Two basic types of nodulus can be discerned, but a hook-shaped nodulus comprised of truncated spines that are basally fused appears to be an autapomorphy of Psocomorpha. In *Cerastipsocus* sp. (Psocomorpha, Psocidae), the coupling system is simply a clasp, or hook, comprised of a "tuft" of sclerotized, curved projections that arise from the terminus of the anal vein and posterior cubitus (first anal, 1A; CuP) on the posterior margin of the forewing. With wings mounted *in vitro*, the costal margin of the hind wing engages the groove formed by the clasp, and the margins of the wings assume a somewhat amplexiform configuration wherein the contours of the opposed FW-HW margins "overlap." Whether this position is assumed in flight is unknown.

Hemiptera: Auchenorrhyncha

Wing coupling structures have been documented in detail by scanning electron microscopy (SEM) in taxa from Fulgoromorpha (e.g., Cixiidae, Flatidae, Delphacidae), Cicadomorpha (Cicadidae), and "Jassidomorpha" (e.g., Cercopidae, Membracidae, and Cicadellidae). Sufficient morphological differences exist in the coupling mechanisms that three general types can be recognized, corresponding roughly with the above-mentioned groups. The basic wing-coupling apparatus (WCA) principally involves a "wing-coupling fold" along the posterior margin of the FW and a corresponding "wing-coupling lobe" on the anterior margin of the HW. Both structures are generally more strongly sclerotized and are often armed with a highly imbricated surface bearing serrations, denticles, or spatulate flanges sculpted onto the cuticle. In at least some "Jassidomorpha" and Fulgoromorpha, the HW costal margin is armed with a few stout "sensillae" which are articulated, innervated, peg-like "setae." They are presumed to function as coupling-hooks ("hamuli"), coupling-proprioceptive sensillae, or both.

Hemiptera: Sternorrhyncha

Species in the families Aphididae and Psyllidae possess HW structures that function as hamuli. Electron micrographs of the HW-coupling system of aphids reveal a single tight cluster of small spiral-shaped chitinous projections (of variable number, depending on species) from the membrane at the edge of the HW, which fit into a groove on the FW formed by a reflexed and more heavily sclerotized wing membrane. Although the "socket" from which the hamuli originate is apparently different from that of a typical socketed seta, they might be true setae and not highly modified and sculptured cuticular projections.

Psyllids, as represented by the blackberry psyllid, *Trioza tripunctata* (Fitch), have short but stout socketed spines that begin as a cluster on the humeral sclerite and the base of the costa, and several more that form a linear group on the costal margin after a short intervening space. A single, strongly curved hamulus occurs roughly at the halfway point on the margin. As with aphids, these hamuli engage with the FW in a groove formed by the posterior margin.

Heteroptera + Coleorrhyncha

Wing-coupling is widespread in Heteroptera and the mechanics of coupling are well understood, with significant detail provided by SEM imaging. A ventral "clip" (also referred to as "clasp") on the posterior margin of the FW engages a recurved and highly sclerotized costal margin (dorsal ridge). The clasp is a bipartite structure composed of pad and spinaculum, separated by a groove. Both the clasp and dorsal ridge may be ornamented with elaborate projections, flanges, serrations, or teeth that help secure the wing union.

The wing-coupling apparatus of *Peloridium hammoniorum* Breddin, a representative of the enigmatic Coleorrhyncha, bears closer affinity to those of heteropterans than those of "homopterans," but is distinctively different. In *P. hammoniorum*, the HW costal margin assumes a complex "S-shape" and is ornamented with coarse microsculpting. The profile formed by this shape presents an inner and outer groove, with the inner groove contacting the coupling apparatus of the forewing. The ventral surface of the forewing presents a bipartite clasp, with one part composed of about 20 sclerotized, spine-like projections that form a closely packed crown, and the second part composed of a sclerotized but flattened and round-tipped cluster of about four projections, which also are grouped closely.

Thysanoptera

Specialized fringes of setae ("cilia") on the wings of many thysanopterans (e.g., *Thrips physapus* L., Thripidae: Terebrantia) appear to be intimately involved with flight mechanics, and effectively double the wing surface area. Wing coupling is accomplished primarily by hooked setae on the HW that secure two long setae on the proximate, posterior region of the FW, but coupling could possibly be enhanced by other setae originating on the HW. Thysanoptera wings are in general lanceolate and possess fringes of long setae, but many taxa also have corrugated surfaces with wart-like swellings and rows of stout and curved macrotrichia. Thus, wing coupling might be more widespread than currently documented.

Endopterygota

Mecoptera

No species of mecopteran is known to be functionally dipterous, but structures of their wings suggest the possibility that wing coupling in at least Lepidoptera and some Trichoptera is derived from a mecopteran condition. In Panorpidae, for example, the posterior angle of the FW is enlarged into a lobe that bears a linear cluster of stout socketed setae (i.e., those derived from trichogen and tormogen cells, and often containing dendrites) known as frenular spines. The basal anterior region of the HW is also armed with such spines, and the FW spines and HW spines appear to interact during the wing beat. Such an interaction probably alters wing-beat frequency and/or blade angle, and possibly provides neurosensory feedback on relative wing position. Also, the wing margins are densely armed with short but stout socketed setae, and could be morphological precursors of the socketed setae, known as hamuli, in many Trichoptera and all Hymenoptera.

Hymenoptera

Hymenopterans from both suborders "Symphyta" (sawflies) and Apocrita (wasps and allies) couple their wings via hamuli, and the coupling mechanisms in many apocritan groups are so highly developed that each FW-HW pair assumes the profile and contour of a single, but flexible, wing blade. Even within Hymenoptera, the microstructure and number of the hamuli can vary significantly, but in all known cases the hamuli engage the posterior margin of the FW by hooking over a sclerotized "ridge" that forms a trough-like region. The sclerotized ridge is usually armed with microsculpted spurs that appear to provide further grip to the hamuli and prevent excessive sliding while the wing is in motion.

A comparative morphological analysis within a phylogenetic context revealed that there were three basic types of hamuli within the order: basal hamuli, which are found only in the symphytans Xyelidae, Pamphiliidae, and Xiphydriidae; secondary hamuli, which are either openly spaced or clustered, depending on group; and distal hamuli, which occur in all winged Hymenoptera. Several small studies have examined whether there is a relationship between certain flight parameters and the number and structure of the hamuli, but there is little conclusive evidence suggestive of a substantial pattern.

Trichoptera

Discussion of the biology and phylogeny of the Trichoptera invariably impinges on that of the Lepidoptera, which together form the higher taxon Amphiesmenoptera (lit. "dressed-up wings"). Indeed, Micropterygidae, the basal most taxon in Lepidoptera, was originally treated as a terrestrial branch of the Trichoptera. Current phylogenies are still unclear on the number of suborders within Trichoptera (or their topology), but typically the three suborders "Spicipalpia," Annulipalpia, and Integripalpia are discussed. Regardless of the eventual phylogenetic resolution, wing coupling in Trichoptera is a derived condition within each major group, with the basal taxa in each "suborder" functionally tetrapterous.

Several morphologically distinct coupling systems have evolved, but they all rely on modified socketed setae of one wing engaging with the partner wing in some manner. The most questionable type of coupling, which could be only an elaborated "frenular bristle"-based FW-HW interaction mode, is common in many Annulipalpia (e.g., Philopotamoidea), Integripalpia (e.g., Limnephiloidea), and "Spicipalpia" (e.g., Rhyacophilidae). In these groups, a cluster of stout setae at the proximate, anterior region of the HW interacts with a lobe on the proximate, posterior region of the FW, and this type of system co-occurs, depending on group, with coupling that is more properly of the hamular type.

The term "hamulus" is used broadly and denotes a functional role, and hamuli of striking overall structural similarity to those found in hymenopterans occur in members of several families of Trichoptera, many of which are believed to be accomplished fliers. In many of the integripalpian taxa, such as Leptoceroidea and Sericostomatoidea, hamuli are dispersed over part or most of the HW costal vein and couple with the wing vein that defines the posterior margin (posterior vein, circumferential vein) of the FW. Variations of this system, derived independently of those in integripalpian families, occur in the Hydropsychidae: Macronematinae (Annulipalpia). Hydropsychidae: Hydropsychinae have evolved a "reverse hamular-clip" system, wherein the costal vein of the HW "clips" into a structure on the ventral surface of the FW. A series of recurved spines originating on the FW anal vein oppose a patch of dense, acuminate, spine-like microacanthae (i.e., cuticular spines) located on the wing membrane between the anal vein and the posterior vein. Distally directed recumbent spines along the HW costal vein are "pinched" between the FW apparatus, and secure the wing. A similar system evolved in the Calamoceratidae (Integripalpia), which are also accomplished fliers, but in this case the "reverse-clip" is formed by two patches of socketed, denticulate setae, with one patch arising from the posterior vein and the other from a patch of wing membrane above the anal vein.

Lepidoptera

Wing venation and coupling mechanisms in Lepidoptera were used by some of the first lepidopteran systematists to subdivide the order. The shifting position of Micropterygidae between Lepidoptera and Trichoptera notwithstanding, the suborders Jugatae or Frenatae were created by Comstock to reflect the distinction between lepidopterans that used either a modified jugal lobe to "join" the wings (Hepialidae and "Micropterygidae," which in earlier classifications included taxa now placed in Agathaphagidae and Heterobathmiidae), or specialized frenular bristles on the HW that engaged a specialized retinacular clasp on the FW. As noted previously, micropterygids do not couple their wings, but hepialids *may* couple via a modified, thumb-like, jugum that hooks over the HW costal margin.

The true frenulum is sexually dimorphic; in males, several closely spaced spines become fused distally into a single spine, and recent phylogenies treat the presence of the single male frenular spine as a synapomorphy of the grade Heteroneura. The retinaculum, which serves as the FW "clasp," is also highly variable throughout the order, especially in females, and may be formed by modified spines, setae, scales, or flanges of wing membrane that protrude from the wing surface. The typical male retinaculum is a chitinous flange arising from either a vein or the interveinal membrane near the FW costa or subcosta.

Many Lepidoptera with large wing surface area, including the Papilionoidea (Butterflies), Hesperoidea (Skippers), and some bombycoids (e.g., giant silk moths), use "amplexiform" coupling, and rely on no specialized coupling structures. Instead, a greatly enlarged humeral angle (proximal anterior margin of the HW) rests below the FW posterior margin. These typically larger-bodied Lepidoptera generally have low wing-beat cycles, and use the greatly expanded wing surface area for primarily gliding flight.

A uniquely modified coupling system has evolved in the Sessiidae, a group that includes exceptionally good and typically day-active fliers. Like other moths, they have a frenular-retinacular coupling system, but they also are able to position the recurved posterior margin of the FW into an oppositely recurved groove on the anterior margin of the HW, thereby effectively sealing the margin along its entire length.

References

Basibuyuk HH, Quicke DLJ (1997) Hamuli in the Hymenoptera (Insecta) and their phylogenetic implications. J Nat Hist 31:1563–1585

Betten C (1934) The caddis flies or trichoptera of New York. NY State Museum Bull 292:1–576

Braun A (1924) The frenulum and its retinaculum in the Lepidoptera. Ann Entomol Soc Am 17:234–257

D'Urso V (2002) The wing-coupling apparatus of Hemiptera Auchenorrhyncha: structure, function, and systematic value. Denisia 4:401–410

Huxley J, Barnard PC (1988) Wing-scales of *Pseudoleptocerus chirindensis* Kimmins (Trichoptera: Leptoceridae). Zool J Linnaean Soc 92:285–312

Kristensen NP (1999) Lepidoptera, moths and butterflies, Evolution, systematics, and biogeography. Handbook of zoology; vol 2: Morphology, physiology, and development; vol IV Arthropoda: Insecta. De Gruyter, Berlin

Ni X, Johnson GD, Quisenberry SS (2002) Comparison of hindwing hamuli from five species of cereal aphids (Hemiptera: Aphididae). Ann Entomol Soc Am 95:109–114
Tillyard RJ (1918) The panorpoid complex. Part i. the wing-coupling apparatus, with special reference to the Lepidoptera. Proc Linn Soc NSW 43:286–319
Wood DM (1979) An SEM survey of wing coupling structures in selected Costa Rican and U.S. Hemiptera and Homoptera. M.Sc. Thesis. University of Wyoming, Laramie
Yoshizawa K (2005) Morphology of Psocomorpha (Psocodea: "Psocoptera"). Insecta Matsumurana 62:1–44 (new series)

Wing Covers

The forewings of adult insects when they are thicker than the hind wings and cover the hind wings when the insect is at rest.

► Wings of Insects

Winged Walkingsticks

A family of walkingsticks (Phasmatidae) in the order Phasmatodea.

► Walkingsticks and Leaf Insects

Wing Pad

The incompletely developed wings of nymphs.

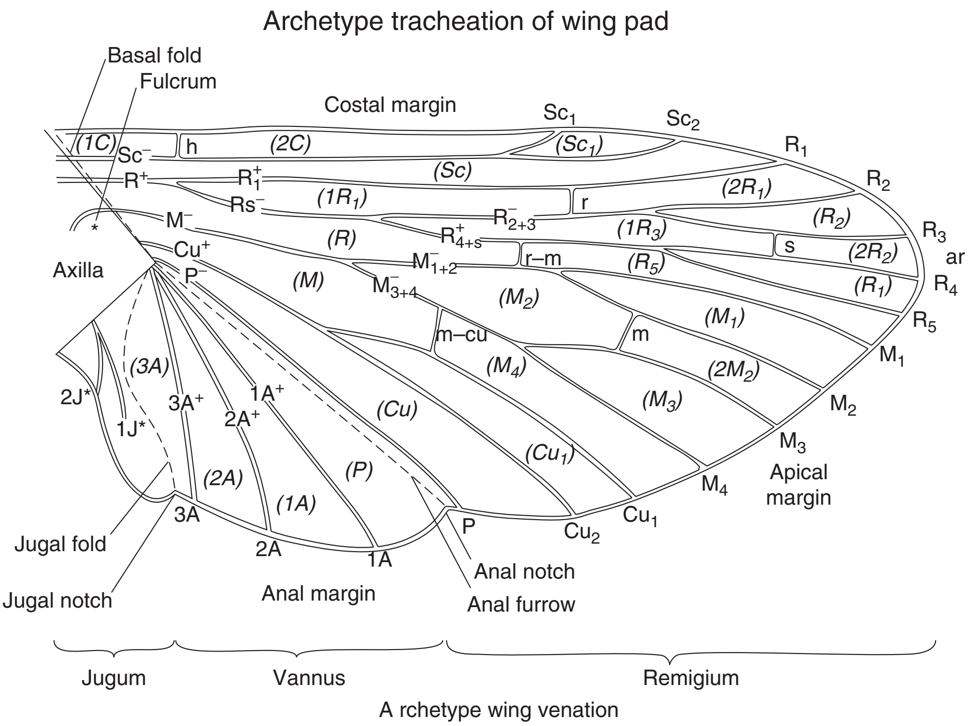
Wings of Insects

The ability to fly is one of the factors responsible for the biological and evolutionary success of insects. Typically, adult insects bear two pairs of wings that articulate with the thorax, though some have but one pair and others are wingless. Wings may be present in immature hemimetabolous insects, but they are incompletely developed (and called wing pads) until the adult stage is attained. Mayflies (Ephemeroptera) are exceptional in having a winged stage (the subimago) prior to reaching the adult stage, which also is winged.

The wings are flattened regions of the integument, arising dorsolaterally between the nota and pleura of the meso- and metathoracic segments. They receive rigidity, in part, from the veins contained within the wings. The veins are thickened regions of the integument that remain separated, allowing blood (hemolymph) to be pumped through the veins. This is critical during expansion of the wings following emergence of the adults. The veins also contain trachea and nerves. Folds also are present in the wings, and take two forms: flexion lines, where bending occurs during flight, and folding lines, where the wing folds during periods of rest. The wings are normally transparent and membranous, though they may be iridescent, pigmented, or even thickened and opaque. A thickened, pigmented spot is found on the anterior edge of some insect wings, and is called the pterostigma or stigma. This region of greater mass reduces wing flutter during gliding, and enhances control of wing movement during wing beats. When at rest, the wings are held over the back, and in many insects involves folding. Longitudinal folding is most common, but transverse folding also occurs. The wings of Coleoptera and Dermaptera fold transversely so they can fit beneath the elytra.

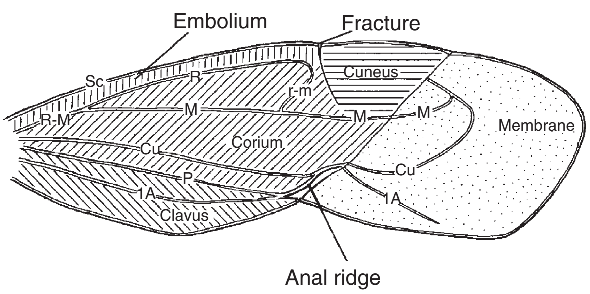
Areas of the Wing

Most of the wing veins are concentrated in the anterior region of the wings; this gives maximum efficiency and support during flight. The anterior edge is called the costal margin. The posterior region often bears separate lobes. The posterior region at the base of the front wing in Lepidoptera and Trichoptera is called the jugal lobe or jugum. Flies (Diptera) often have three separate lobes, the thoracic squama, alar squama, and the alula. The posterior wing edge is called the anal margin; the distal edge is the apical margin. The angle between the costal and apical margins is called the apical angle. The angle at the base of the anterior portion of the wing is the humeral angle. The anal area of the wing os the posterior region including



Wings of Insects, Figure 55 **Generalized wing venation showing wing regions and major veins.**

the anal veins. The costal area is the anterior region of the wing immediately behind the anterior edge. A fold in the wing often occurs in the cubito-anal area, and is called the anal furrow. A notch may also be present along the posterior edge, canned the anal notch (Figs. 55 and 56).

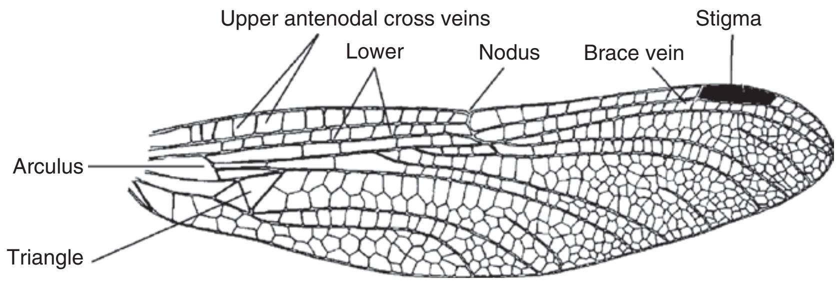


Wings of Insects, Figure 56 **A typical hemelytron, showing the thickened basal portion and the membranous distal (apical) portion of the front wing of a bug (Hemiptera).**

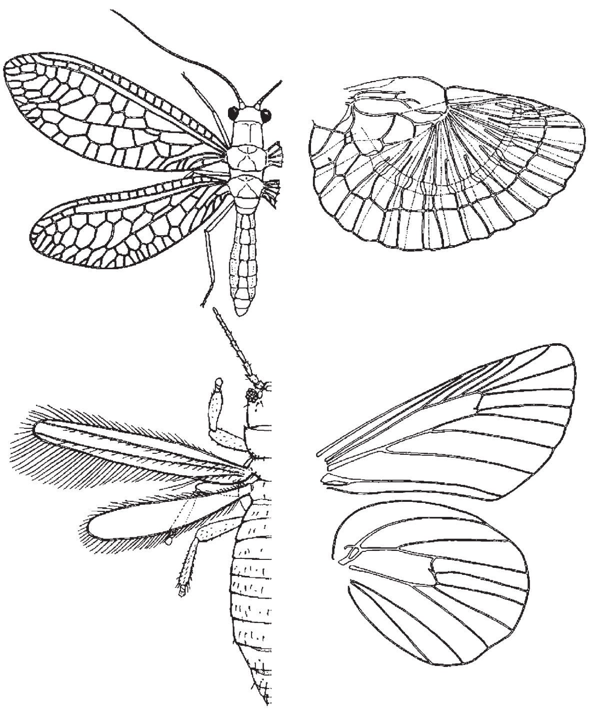
Wing Form

Wing form varies among the orders of insects. The front wings and hind wings are very similar in shape in the Odonata, Isoptera, Embiidina, and Mecoptera. In contrast, the hind wing is wider in Plecoptera, Mantodea, Blattodea, and Orthoptera. In some orders the hind wings are considerably smaller than the front wings, such as in Ephemeroptera and Hymenoptera. In Diptera, the hind wings (called halteres) are so reduced as to not aid directly in flight; in male Strepsiptera it is the front wings that are reduced to haltere-like structures. Wings also may be branched, a common condition in some Lepidoptera, or fringed, as in Thysanoptera, some Lepidoptera (e.g., Tinaeoidea), and some Hymenoptera (e.g., Mymaridae) (Fig. 57).

Wings may be shortened; when both pairs are reduced they are said to be brachypterous or micropterous. Wingless insects are called apterous. The size or occurrence of wings may



Wings of Insects, Figure 57 **The front wing of a dragonfly, showing net-winged venation and other characters found in Odonata.**



Wings of Insects, Figure 58 **Comparative wing structure showing diversity among insect wings: top left, lacewing wings (Neuroptera); top right, hind wing of an earwig (Dermaptera); bottom left, thrips wings (Thysanoptera); bottom right, skipper butterfly wings (Lepidoptera).**

vary seasonally or geographically within the same species; such polymorphism is common in Hemiptera, and to a lesser degree in Orthoptera (Fig. 58).

The front wings may be modified in form, and often are more sclerotized than the hind wings. The front wings of Coleoptera and Dermaptera are heavily sclerotized and called elytra; the wing venation is lost in these structures. In some beetles, particularly the Curculionidae, the front wings are fused together and cannot open. In Orthoptera, Mantodea, and Blattodea the front wings are thickened, but veins are evident; they are called tegmina. In the Hemiptera/Heteroptera, the basal portion of the front wings are thickened, but the apical region is membranous; these are called hemelytra.

Wing Coupling

The front and hind wings of insects are affected primarily by the distortions of the thorax, and do not move independently. Although not physically linked in Odonata and Orthoptera, many orders have anatomical coupling mechanisms that assist in synchronization of wing beat. Apparently the two-winged condition is more efficient than the four-winged condition, so they move together. The coupling takes the form of a jugal lobe at the base of the front wings, the humeral lobe at the base of the hind wings, and setae called frenular bristles. There are many variations among the different insect groups.

Wing Venation

In some primitive insects the pattern of insect veins is irregular. In most insects, however, the pattern of venation is dominated by a few longitudinal veins that radiate from the wing base to the broader wing tip. The principal longitudinal veins (and their standard abbreviation), ordered from leading to trailing edge, are: the costa (C), subcosta (Sc), radius (R), media (M) but often divided into anterior media (MA) and posterior media (MP), cubitus (similarly divided into CuA and CuB or Cu1 and Cu2), and anal veins (numbered 1A, 2A, 3A, etc.). These major veins may branch, with the given numerical subscripts. Cross veins connect the major veins transversely, and normally are named after the longitudinal veins they connect. The area enclosed by veins is called a cell, and wing cells are named after the anterior vein.

► Locomotion
► Wing Coupling

References

Chapman RF (1982) The insects, structure and function, 3rd edn. Harvard University Press, Cambridge, Massachusetts
Comstock JH (1918) The wings of insects. Comstock Publishing Company, New York
Dudley R (2000) The biomechanics of insect flight. Princeton University Press, Princeton, New Jersey
Snodgrass RE (1935) Principles of insect morphology. McGraw-Hill, New York
Wootton RJ (1979) Function, homology, and terminology in insect wings. Systematic Entomology 4:81–93

Wing Venation

The pattern of tubular vessels (veins) lying between the upper and lower surfaces of the wing in adult winged insects.

► Wings of Insects

Winter Crane Flies

Members of the family Trichoceridae (order Diptera).

► Flies

Winter Grain Mite, *Penthaleus major* (Duges) (Acari: Penthaleidae)

This pest damages wheat in high-moisture areas.

► Wheat Pests and their Management

Winter Moth, *Operophtera brumata* (L) (Lepidoptera: Geometridae) and Its Biological Control

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University of Florida, Gainesville, FL, USA

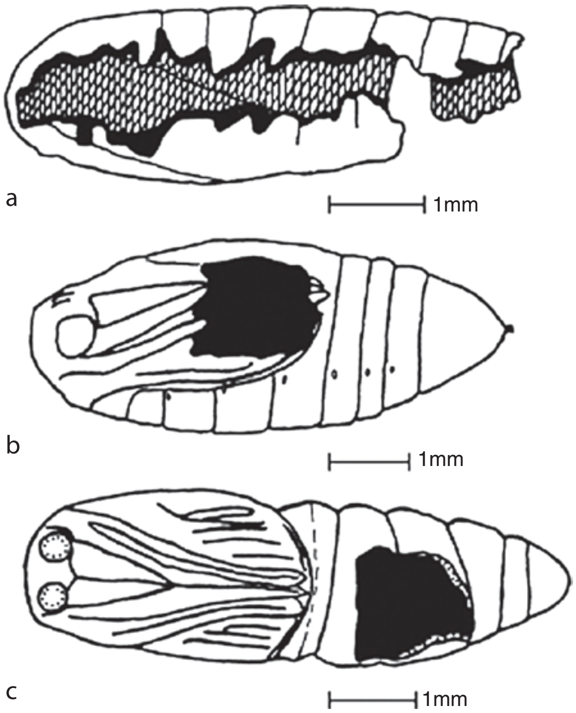
This insect, native to the Palearctic Region, was at one time placed in a family called Hydriomenidae. Wingless adult females, emerging in November from pupae in the soil, climb the trunks of deciduous trees. During their ascent, they mate with winged males. Eggs spend the winter in the treetops. Larvae, hatching from eggs in early spring when temperatures average about 13°C, feed on the first flush of leaves, whose tannin content is low. Timing of hatch is critical because larvae that hatch too soon face starvation. Larvae that hatch too late encounter increasing levels of tannins in the leaves, making digestion difficult. Fully grown larvae descend to the soil on silken threads in May, burrow into the soil, spin a cocoon, and pupate therein. The insect thus spends 6 months in the summer and autumn as a pupa in the soil.

Male moths have a wingspan of 28–33 mm with alternating pale buff and darker brown bands on the forewings and a similar but paler pattern on the hindwings (Fig. 59). They are active at night, fly well, and are attracted to artificial light and to pheromone of female winter moths. Wings of females are so reduced that they cannot fly. The adult stage is reached during early winter. Females lay an average of 150 eggs, which are deposited in crevices in bark of trees. The larvae are loopers, green with pale lines on the sides and a darker line dorsally.

Winter Moth, *Operophtera brumata* (L) (Lepidoptera: Geometridae) and its Biologicalcontrol, Figure 59 **Winter moth male (*left*) and female (*right*) lent by Dr L. Humble Lyle Buss.**

Trees attacked by the larvae include especially oaks (*Quercus* spp.), but also on several other genera of hardwoods, and a few conifers. Populations fluctuate from year to year, but seldom are important pests in their native range, in large part because of population regulation by natural enemies. Damage is reflected in varying annual increment of timber production.

At a study site near Oxford, England, it was determined that the principal biotic factor limiting population size of winter moth at low population levels was predation on the pupae. Predation by generalist predators of the genera *Philonthus* (Coleoptera: Staphylinidae) and *Abax* and *Pterostichus* (Carabidae) and the typical damage they caused to winter moth pupae (Fig. 60) was characterized visually in the laboratory in the mid-1960s. In the field, predation was quantified using serological methods, and later by burying pupae and then unearthing them for visual inspection. Both methods had defects. The serological method allowed specific identification of beetle predators, but was complicated by need to measure predator population sizes, to measure rates of digestion of prey proteins, and to assume that detection of prey protein in one individual predator indicated its killing of only one pupa. The burial method made specific identification of predators very difficult and, because of the unnatural burial of pupae, perhaps did not allow staphylinid beetles to follow tunnels made by prepupal hosts to their pupation sites. Also, burying pupae in disturbed soil may have made it easier for carabids to dig and find these prey. Therefore, the burial method may have over-emphasized the importance of Carabidae. Nevertheless, results from use of the two methods broadly agreed. Remarkably, the proportion of winter moth pupae killed by *Philonthus decorus* (Gravenhorst), assessed earlier by a serological method and later by a burial method, was identical at 42%; the major point of contention between the two studies was in the assessment of predation by shrews (*Sorex*) relative to that by Carabidae.



Winter Moth, *Operophtera brumata* (L) (Lepidoptera: Geometridae) and its Biologicalcontrol, Figure 60 **Winter moth pupae attacked by (a) *Pterostichus cupreus* (L.) (Carabidae), (b) *Philonthus decorus* (Staphylinidae), and (c) larva of *Athous haemorrhoidalis* (F.) (Elateridae). From Frank (1967) J Anim Ecol, vol 36, by permission of Blackwell Publishing.**

Long-term studies of winter moth at this site (Wytham Woods), beginning in 1949, contributed to methods for construction and analysis of insect life tables. In these methods, population density at the various stages during development is measured. Mortality occurring between two successive stages, reported as a k-value, is the difference between the logarithmic values of population density of the two successive stages. When two mortality factors, for example two parasitoids, act on one developmental stage, the separate mortalities caused by each can be treated as successive even when in reality they are simultaneous. When k-values for all stages have been calculated, total generational mortality (K) is their sum. For winter moth life tables using the data collected at Wytham Woods, k5 was the value assigned to predation on the pupae. It was the only one of the k-values shown to be positively density dependent. In this same study, k2 was the value assigned to mortality caused to the larvae by the parasitoid *Cyzenis albicans* (Fallén) (Diptera: Tachinidae); it was shown to be trivial and not density dependent, indicating that this parasitoid had no substantial effect.

Unusual defoliation of hardwoods was recognized in Nova Scotia, Canada, by 1935. By 1949, the culprit had been determined as winter moth, now damaging apple orchards, too. It had evidently arrived as an invasive species from Europe, and had become a very important pest. The Canadian Forest Service investigated and arranged for importation from continental Europe of parasitoids belonging to six species. Released in Nova Scotia, two of them became established: *Agrypon flaveolatum* (Gravenhorst) (Hymenoptera: Ichneumonidae) and *Cyzenis albicans*. In the main study area, adult densities dropped from >1,000 adults per tree in 1954 to <1 in 1963. This was a huge success for classical biological control.

In 1976, a native species, *Operophtera bruceata* (Hulst), seemed to be causing unusual problems near the city of Victoria, on Vancouver Island. In 1978 it was learned that outbreaking populations were mixed, including *Operophtera brumata*. Consequently, *Cyzenis albicans* and *Agrypon flaveolatum* were imported from eastern Canada and released in 1979–1980. Once again these biological control agents seemed to have suppressed winter moth populations.

Study of the declining winter moth population in British Columbia showed that k5, pupal predation, had become an important mortality factor. Moth pupae, buried and later unearthed, showed damage just as had been observed under laboratory conditions in England. The obvious conclusion was that the two parasitoids (*A. flaveolatum* and *C. albicans*) were effective control agents at high densities of the moth, but in fact the parasitoids were supplanted in importance by native generalist beetles at low densities. Data from Nova Scotia likewise showed the importance of pupal predation (k5).

The importance of the parasitoids was not demonstrated in England, where population densities were always low. In England, *C. albicans* was attacked by a hyperparasitoid; also, few of the eggs it deposited on leaves were ingested by winter moth larvae because of low host population density. Conditions were far more favorable for it in Canada, where it was released in dense host populations without the hyperparasitoid.

A possible explanation of the increased value of pupal predation following introduction of the biological control agents into eastern and then western Canada is interaction. Thus, dead winter moth pupae containing living pupae of *Cyzenis albicans* for 10 months may have provided an abundant food source for generalist beetle predators for 10 months, rather than the 6 months for which the food source represented by the healthy host pupae was available. This additional food source might have maintained predatory beetle populations at higher levels than in the absence of such prey. Alternatively, predatory beetles may prefer the food source offered by healthy prey pupae rather than the food source presented by parasitized pupae, thus concentrating attack on healthy pupae. The specific identity (nor even the generic identity) of the beetle predators has not yet been determined in either eastern or western Canada. There still are unanswered questions, and now winter moth has invaded the Pacific Northwest and New England of the USA.

► Life Tables

References

Feeny P (1970) Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology 51:565–581

Frank JH (1967) The insect predators of the pupal stage of the winter moth, *Operophtera brumata* (L.) (Lepidoptera: Hydriomenidae). J Anim Ecol 36:375–389

Frank JH (1967) The effect of pupal predators on a population of winter moth, *Operophtera brumata* (L.) (Lepidoptera: Hydriomenidae). J Anim Ecol 36:611–621

Frank JH (1968) Notes on the biology of *Philonthus decorus* (Gr.) (Col., Staphylinidae). Entomol Mon Mag 103:273–277

Hassell MP (1969) The behavioural response of a tachinid fly (*Cyzenis albicans* (Fall.)) to its host, the winter moth (*Operophtera brumata* (L.)). J Anim Ecol 37:627–639

Roland J (1988) Decline in winter moth population in North America: direct versus indirect effect of introduced parasites. J Anim Ecol 57:523–531

Roland J, Embree DG (1995) Biological control of the winter moth. Annu Rev Entomol 40:475–492

Varley GC (1970) The effects of natural predators and parasites on winter moth populations in England. Proc Tall Timbers Conf Ecol Anim Control Habitat Manage 2(1970):103–116

Winter Stoneflies

Members of the stonefly family Taeniopterygidae (order Plecoptera).

► Stoneflies

Wireworm

The larva of click beetles (order Coleoptera, family Elateridae).

Wireworms, Several Genera and Species (Coleoptera: Elateridae)

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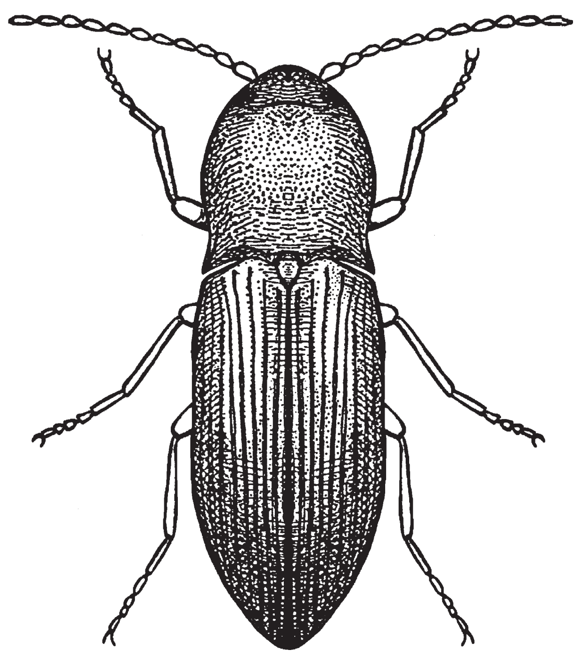
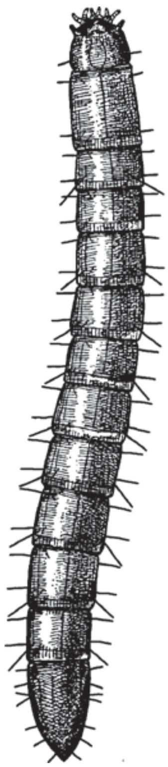
Wireworms are the larvae of click beetles (Figs. 61 and 62). Several genera contain species that cause damage to crop plants including:

- *Aeolus mellillus* (Say), flat wireworm
- *Agriotes mancus* (Say), wheat wireworm
- *Agriotes lineatus* (Linneaus), lined click beetle
- *Agriotes sputator* (Linnaeus), common click beetle
- *Athous haemorrhoidalis* (Fabricius), garden wireworm
- *Conoderus falli* Lane, southern potato wireworm
- *Conoderus vespertinus* (Fabricius), tobacco wireworm
- *Conoderus amplicollis* (Gyllenhal), Gulf wireworm
- *Ctenicera pruinina* (Horn), Great Basin wireworm
- *Ctenicera aeripennis aeripennis* (Kirby), Puget Sound wireworm



Wireworms, Several Genera and Species (Coleoptera: Elateridae), Figure 61 Click beetle, the adult form of wheat wireworm, *Agriotes mancus* (Say).



Wireworms, Several Genera and Species (Coleoptera: Elateridae), Figure 62 Larva of wheat wireworm, *Agriotes mancus* (Say).

- *Ctenicera aeripennis destructor* (Brown), prairie grain wireworm
- *Ctenicera glauca* (Germar), dryland wireworm
- *Limonius californicus* (Mannerheim), sugarbeet wireworm
- *Limonius agonus* Say, eastern field wireworm
- *Limonius canus* LeConte, Pacific Coast wireworm
- *Melanotus communis* (Gyllenhal), corn wireworm
- *Melanotus longulus oregonensis* (LeConte), Oregon wireworm

Life History

As might be expected with different species occurring in many areas of the world, the biology is quite variable. The life cycle often requires 3 years, but sometimes takes only 1 year in warm climates, whereas it may extend up to 10 years in cold areas. In the case of *Melanotus communis*, egg deposition occurs in June, eggs hatch in July, and larvae require four additional summers to complete their development. A strong association of larvae with cool, moist soil is evident, although warmer soil will be tolerated if it is moist. The larval morphology is fairly typical of wireworms. They are yellow to yellow brown in color, shiny, and elongate. The head, thoracic plate, and anal plate are darker in color. Pupation occurs in the autumn, and then adults overwinter in the soil in pupal cells.

Most flight activity occurs in May and June. Adults fly throughout the evening hours. Females display a fairly high fecundity, some species producing 1,500 eggs. Adults are reddish brown to black, uniform or variable in color, elongate and flattened. Some species are small, less than 10 mm long, but commonly attain 15 mm in length. There often are numerous instars (ten or more), particularly among the species with long development times. Adults tend to be short-lived, usually perishing within a month of emergence from the soil.

The natural enemies of wireworms are not well known, and generally seem to be unimportant. In Florida, for example, *M. communis* is parasitized by the wasp *Pristocera armifera* (Say) (Hymenoptera: Bethylidae), but only about 4% of wireworm larvae are affected. Birds are often observed to follow tractors as soil is tilled, and to consume wireworms. However, they likely glean only a small proportion of larvae.

Damage

Wireworms feed belowground on seeds, roots, and other plant tissue. Nearly all crops can be damaged by wireworms, but corn, small grains, and tuber producing crops are especially damaged. Crops with harvested roots or tubers, such as carrots and potatoes, are most easily injured, as even surface scarring can result in loss. Grass sod and grass crops such as sorghum are highly attractive to click beetles, so crops planted immediately after grasses are most susceptible to injury. Most species prefer high moisture, and it is the heavier, wet portions of fields that are most likely to experience damage. Larvae tend to move toward the soil surface in the spring as the soil warms, where they feed until the soil warms; they then move deeper in the soil where it is cooler. Larvae again return to the upper layer of the soil in the autumn when the soil surface cools, and feed until it becomes cold, when they return to a position deep in the soil until the soil warms in the spring.

Management

Considerable effort has been made to develop baits for wireworm sampling. Growers are advised to assess the population densities of wireworm larvae prior to planting in the spring by baiting wireworms. Baiting is accomplished by burying whole wheat, corn, sorghum or other attractive food sources in the soil at a depth of 10–15 cm, and by counting the number of wireworm larvae attracted. Soaking the bait for 1 day increases its attractiveness. Baiting does not work well if the soil is less than 8°C, so a sheet of transparent plastic is sometimes placed over the section of soil containing bait; this warms the soil and increases the mobility of wireworm larvae, allowing a more accurate assessment. Larvae can also be separated from the soil by sifting; a screen with 6–7 meshes per cm is desirable. Soil sampling followed by screening is an accurate, but labor intensive, means to predict wireworm problems prior to planting. Spatial distribution of larvae is variable, but sometimes aggregated, requiring extensive sampling.

Adult populations can also be sampled. Pitfall traps and sticky traps are useful for sampling adult populations on the soil surface and in flight, respectively. Click beetle catches on sticky traps and in light traps are not completely equivalent, so both types of trap should be used in population studies. Pheromone traps are beginning to come into use for these insects.

Insecticide is often applied to prevent susceptible crops from being injured by wireworms. The most common approach to wireworm suppression is to apply persistent liquid or granular formulations at planting, and to incorporate the insecticide into the soil near the seeds or seedlings. Preplant applications generally, but not always, are more effective than postplant treatments. Sometimes insecticides are applied broadcast over the entire field, but more commonly they are applied in bands over or along the rows. For long-duration crops, the planting time application may be followed by a mid-season application. Insecticide also may be incorporated into the irrigation water. Effectiveness varies considerably among insecticides, and some insecticide resistance has been reported. Soils with high organic matter content sometimes interfere with insecticide efficacy.

Grasses are particularly attractive to many wireworms. A strong relationship between wireworms and previous growth of sod is usually apparent. Grass cover crops such as sorghum-sudan can be highly attractive, and it is important to have the fields free of such grasses during peak flights. Where crops can be flooded, 6 weeks of flooding or two 4-week periods of flooding separated by 2 weeks of drying can eliminate wireworms.

References

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, 729 pp

Glen R, King KM, Arnason AP (1943) The identification of wireworms of economic importance in Canada. Can J Res (D) 21:358–387

Parker WE, Howard JJ (2001) The biology and management of wireworms (*Agriotes* spp.) on potato with particular reference to the U.K. Agric For Entomol 3:85–98

Thomas CA (1940) The biology and control of wireworms. Pennsylvania Agric Exp Station Bull 392, 90 pp

Wireworms of Potato

Several species of wireworms injure potato.

► Potato Pests and Their Management

Wireworms of Wheat

Wheat is sometimes damaged by wireworm feeding.

► Wheat Pests and Their Management

Wirth, Willis Wagner

Willis Wirth was born on October 17, 1916, near Dunbar, Nebraska. He studied biology at Peru (Nebraska) State Teachers College and received a B.S. degree from Iowa Sate University in 1940, a M.S. degree from Louisiana State University in 1947, and a Ph.D. from the University of California at Berkeley in 1950. He served as an officer in the U.S. Public Health Service during World War II, working on malaria control and quarantine. From 1949 to 1983, Wirth was a research entomologist with USDA, ARS at the National Museum of Natural History, Smithsonian Institution, in Washington, DC. He served on many special assignments over the years, working in Australia, Florida, Texas, New York, Panama, and several locations in Europe. Wirth became a renowned authority on biting midges, studying the taxonomy and public health implications of Ephydridae, Chironomidae, Canaceidae, Dolichopodidae, and Ceratopogonidae. Wirth provided committee service for the Entomological Society of America, and was an adjunct professor at the University of Maryland and the University of Florida. After retiring in 1984, Wirth moved to Gainesville, Florida, to take an active role in the Florida State Collection of Arthropods. He published over 400 papers, mostly on biting midges, and particularly on Ceratopogonidae. He died September 3, 1994, in Gainesville, Florida.

Reference

Mount GA, Kline DL, Hagan DV, Grogan W (1995) Willis Wagner Wirth. Am Entomol 41:63–64

Witches Broom

An abnormal growth form in plants characterized by dense clustering of branches and often caused by the feeding secretions of piercing-sucking insects.

Wolcott, George N

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University of Florida, Gainesville, FL, USA

George Norton Wolcott (Fig. 63) was born in Utica, New York on July 12, 1889, to David Clinton Wolcott and his wife Marion Delia Benedict. He attended Utica Free Academy in Utica, New York, and upon graduation in 1905, attended New York State College of Agriculture (now Cornell University). He received the B.S. in either 1907 or 1909, and the M.S. in Agriculture in 1915. In 1925 Wolcott was awarded the Ph.D. in Entomology from Cornell University. He married Magdalen Hall in 1919 and the couple had three children: Ann, David, and Oliver. Although he initially (in 1910) worked as a

Wolcott, George N, Figure 63 George Wolcott.

Federal Agent in the Bureau of Entomology of the Department of Agriculture in Texas, his most significant contributions to agricultural entomology were made in Puerto Rico. There, he worked with the Sugar Producers Association from 1910 to 1912 and as Director of Entomology of the Insular Experiment Station, Rio Piedras, from 1914 to 1916 and again from 1932 to 1956, when he retired and returned to the mainland. Between 1919 and 1929 he held various positions as Entomologist, initially in Puerto Rico, then in the Dominican Republic, Haiti and Peru, returning each time to Puerto Rico, the place he seemed to love. One of his most notable undertakings was to control the lesser sugarcane borer, *Diatraea saccharalis* (F.) (Lepidoptera: Pyralidae) in Puerto Rico. He initiated the release of the egg parasitoid *Trichogramma minutum* Riley (Hymenoptera: Trichogrammatidae) for *D. saccharalis* egg population reduction and eliminated the burning of sugarcane fields to prevent the destruction of parasitoid populations. He was equally successful in control of *D. saccharalis* in Haiti. Dr. Wolcott also conducted extensive studies on several coleopteran pests of sugarcane, including the sugarcane rhinoceros beetle, *Strategus barbigerus* Chapin, the white grubs *Lachnosterna* sp. and *Phyllophaga* sp. (Coleoptera: Scarabaeidae), and the sugarcane root weevil (= sugarcane rootstock borer), *Diaprepes abbreviatus* L. (Coleoptera: Curculionidae). Wolcott promoted the use of beneficials, including parasitoids, in pest control programs and to that end, traveled extensively through the Caribbean and Latin America, collecting various parasitoids such as *Cryptomeigenia aurifacies* Walton and *Eutrixoides jonesii* Walton (Diptera: Tachinidae) and *Tiphia parallela* Smith (Hymenoptera: Scoliidae) for white grub control. One of Dr. Wolcott's contributions to entomology in Puerto Rico has also had a significant and longlasting beneficial impact on biocontrol in the southeastern United States. He introduced the wasp *Larra americana* Saussure (later identified as *L. bicolor* F.) (Hymenoptera: Sphecidae) into Puerto Rico from Brazil for the control of the mole cricket *Scapteriscus didactylus* (Latreille) (Orthoptera: Gryllotalpidae) ("La changa"), a pervasive agricultural pest in Puerto Rico. This single classical biological control effort by Dr. Wolcott laid the foundation for current biological control successes against mole cricket pests of turfgrass throughout the southeastern United States. More than 200 of Dr. Wolcott's publications and manuscripts continue to serve as important references for scientists who study pest problems in the Caribbean region. In particular, his "Insectae Borinquenses," a revised annotated check-list of Puerto Rican insects, is a classic. At one time some of his books had been adopted as texts by several agricultural colleges and institutes in the Caribbean. Dr. George N. Wolcott was not only a prolific writer and meticulous researcher, but he trained many in entomological techniques. He also revived the once defunct Entomological Society of Puerto Rico, founded by Dr. Van Dine, to further promote the exchange of ideas among entomologists and other agricultural scientists throughout the Caribbean Basin.

References

Lawrence PO (2000) The pioneering work of George N. Wolcott: implications for U.S.– Caribbean entomology in the 21st century. Fla Entomol 83:388–399

Wolcott GN (1936) Insectae Borinquenses. A revised annotated check-list of the insects of Puerto Rico. J Agric Univ Puerto Rico 20:1–600

Wolcott GN (1941) The establishment in Puerto Rico of *Larra americana* Saussure. J Eco Entomol 34:53–56

Wollaston, Thomas Vernon

Thomas Wollaston was born at Scotter, Lincolnshire, England, on March 9, 1822. He obtained a B.A. and M.A. from Jesus College, Cambridge. Suffering from ill health, he wintered at Madeira for several years and visited Cape Verde and St. Helena, setting the stage for his studies of island fauna. Among his important publications were:

"Insecta Maderiensia" (1854), a treatise on the variation in species (1856), a museum bulletin of the Coleoptera of the Canary Islands (1864), "Coleoptera Atlantidum" (1865), "Coleoptera Hesperidum" (1867), and "Coleoptera Sanctae-Helenae" (1877). On these islands he elucidated the endemic fauna, discovering numerous new species of beetles. He died January 4, 1878, at Teignmouth, England.

References

Anonymous (1878a) Obituary, Thomas Vernon Wollaston. Entomol Mon Mag 14:213–215

Anonymous (1878b) Obituaries, Mr. T.V. Wollaston, M.A., F.L.S. Can Entomol 10:34–35

Wood-Attacking Insects

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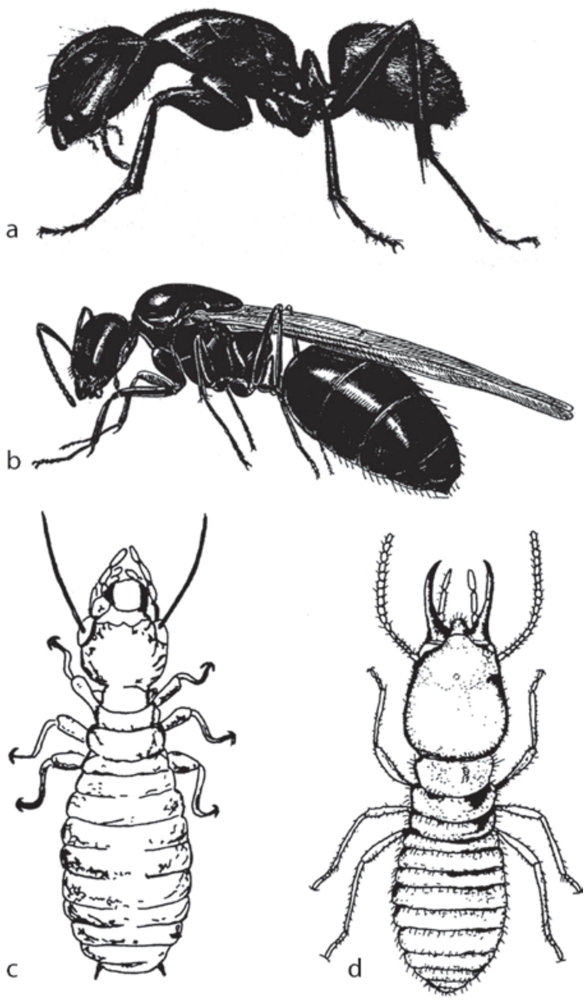
The relentless advance of western civilization has involved, among other things, deforestation concomitant with construction of centrally heated homes, businesses, and other facilities in place of the once-extensive woodlands. The termites, carpenter ants, beetles, and other insects that formerly dwelled within woodlands, of course, proceeded to invade the structural lumber used in today's construction. This lumber is obtained both from increasingly expensive hardwoods such as oak, hickory, ash, and maple, and from less desirable softwoods such as pine, hemlock, fir, redwood, and other evergreen trees. Both have a central, dark-colored, non-living heartwood and an outer light-colored, living sapwood, and both are susceptible to attack by wood-destroying insects, except for the heartwood of black locust, cypress, cedar, redwood, and certain other trees which is relatively resistant to attack.

Carpenter ants, termites, powderpost beetles, and the old house borer are among the many insects with destructive habits found in and around wooden buildings. They share little phylogenetic relationship other than joint inclusion in the overall class Insecta and a predilection to burrow in and chew wood. Carpenter ants, unlike termites, are true ants. Termites are insects whose ant-like appearance is responsible for the common name "white ant" often applied to them. Reproductive forms of ants and termites have membranous wings, lacking in non-reproductive forms, and both exhibit a highly developed social behavior. This is as opposed to powderpost beetles and the old house borer which are true beetles and not in the least ant-like in appearance. These beetles have thick forewings (elytra) covering membranous hindwings and can be distinguished from one another by, among other attributes, their antennae, which are relatively short in the powderpost beetles and relatively long in the borer.

Carpenter Ants

Among the commonly encountered carpenter ants are the black carpenter ant, *Camponotus p. pennsylvanicus* (De Geer), and the reddish brown carpenter ant, *C. ferrugineus* (F.), of the eastern United States; the red carpenter ant, *C. novaboracensis* (Fitch), of the northern states; *C. herculeanus* (L.) and the west coast carpenter ant, *C. modoc* (Wheeler), of the western states; the Florida carpenter ant, *C. abdominalis floridanus* (Buckley); and the Hawaiian carpenter ant, *C. variegatus* (F. Smith) (Fig. 64).

In their natural woodland habitat, carpenter ants play an important role as predators of defoliating caterpillars, aphids, and other insects. They also break down vulnerable, dying trees and logs and stumps resulting therefrom. Unfortunately, they have turned to colonization of structural wood as mankind has increasingly replaced woodland with heated buildings. Carpenter ants require wood with a relatively high moisture content, for which reason the "Minimum Property Standards and Building Codes" of HUD (U.S. Department of Housing and



Wood-Attacking Insects, Figure 64 **Wood-feeding insects: (a) a carpenter ant worker, (b) a carpenter ant queen, (c) a termite worker, (d) a termite soldier, specifically *Prorhinotermes simplex* (Hagen) (a is after USDA, b is after U.S. Bureau of Entomology, c is modified and redrawn from Duncan & Pickwell, d is modified and redrawn from U.S. National Museum).**

Urban Development) specify that only wood with a moisture content of less than 20% is appropriate for construction. One can predict with some certainty that a carpenter ant infestation in or around a specific structure stems from a preexisting or current moisture problem at that site.

Carpenter ants have an evenly rounded thorax separated from the apparent abdomen by a pedicel, or "waist" -like constriction that is lacking in termites. The pedicel in carpenter ants bears a single peg-like node. This node, together with the elbowed antennae, the circle of "hair" at the abdominal apex, and the large front and the small hind pair of strongly veined wings, helps identify them.

As the name carpenter suggests, these insects chew and tunnel within wood, but they do not actually eat it. At the outset they tunnel within moist, weathered wood, and then they may extend their activities into adjacent sound wood. They make nests in which to rear their young, whether in an infested house or in a nearby tree, post, or utility pole. They capture caterpillars, aphids, and other insects to feed their larvae which, like helpless fledglings, await the arrival of food.

Carpenter ant colonies consist of three kinds of individuals: numerous wingless, sterile female workers, a few winged reproductive males called drones, and usually only a single winged reproductive female called the queen. Workers resemble reproductive individuals except for their lack of wings. They either make chambers in wood in which to tend the eggs and larvae of the next generation, or they forage outside the nest. They may travel over 90 m in search of prey insects, animal remains, plant juices, and honeydew from aphids or scale insects to feed the queen and young back in the nest. They are prone to invade homes in early spring in absence of insect prey, foraging for sugars, meats, fats, and other food scraps found on kitchen counters, within dishwashers, in other food preparation and storage areas, and even search potted indoor plants for any infesting aphids or scale insects. These invaders may become so troublesome that they prompt a rash of calls to local pest control operators for help in eradicating them.

The relatively longer hours of daylight and the spring rains that follow are cues for adult carpenter ants to emerge from overwintering pupae. The winged reproductive female and male ants, like many other insects, are attracted to artificial light. They fly into brightened areas from tree stumps, logs, or other infested areas and gain access to the structural wood of buildings through the eaves, attic, sliding doors, or windows. Once established at these points, which are usually moist due to exposure to direct rainfall or condensation, they then may colonize adjacent areas of sound wood. They may also gain entry through sturdy tree roots penetrating a basement or garage wall, through tree branches in contact with the roof, or through firewood carelessly stacked against outside walls.

Numbers of winged swarmers appear and take flight in late spring, again causing alarm on the part of homeowners who fear that these troublesome insects are termites rather than ants. This triggers a second rash of calls to professional pest control operators. The winged ants in question consist of drones and of females destined to become queens. They mate, and the drones die soon afterward. Each inseminated queen breaks off her wings, burrows into wood with a favorable moisture content (usually 20% or more), settles within a hollow destined to become the new nest, and rears her first young. New workers emerge some weeks later from the initially laid eggs and soon take over all nest building, tending of young, and foraging, leaving the new queen to devote herself exclusively to egg laying. It takes more than 3–4 years to establish a productive colony, a single one of which may eventually have as many as 3,000 individual members.

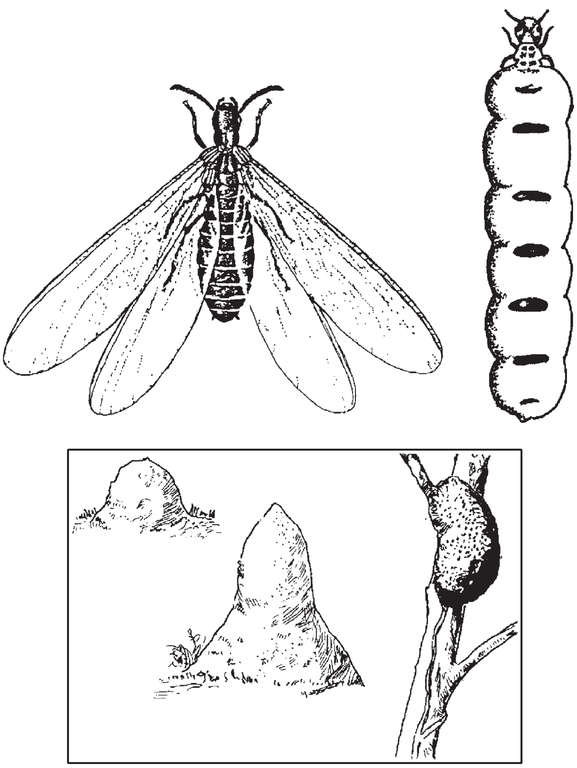
Carpenter ants overwinter in the pupal stage either in the nest, in soil, or at times under flower pots and other places of concealment. Their total life cycle takes about 50–70 days for completion.

As noted, carpenter ants do not eat wood, but they may severely damage it through their chewing. Workers make slit-like openings in the surface of the infested wood. They use these holes to eject loosened debris, leaving the chambers within with a clean, almost "sandpapered" appearance. This is opposed to the "dirty" appearance of termite tunnels. The ejected wood may be in the form of shavings or a fine sawdust depending on the nature and condition of the wood. Occasional cone-shaped mounds of sawdust piled up to 30 cm high on the floor beneath infested wood are evidence of carpenter ant activity. The ants damage windows, doors, flooring, attic joists, sill plates, fascia boards, eaves, beams, baseboards, decks, indoor swimming-pool boardwalks, wooden columns supporting porches, entrances, roofs, and fences. They also bite with their powerful mandibles, though this behavior is of negligible concern.

- Suggested remedial methods for use against carpenter ants include:
- Prevention of condensation on the building's wood components
- Keeping the roof intact and leakproof, especially at the chimney flashing, around vents, and where roof levels change
- Checking gutters and down spouts to see that they properly collect roof runoff and spill it onto ground-level splash blocks directed away from the house
- Installing window wells that slope away from the house and, if necessary, covering them with a plastic bubble
- Checking for leaks in plumbing, heating pipes, hot water heater, and clothes washer
- Ventilating and/or de-humidifying if dampness is a problem
- Using yellow exterior light installations where practical
- Trimming off tree branches touching the building
- Eliminating nearby tree stumps or logs with potential for carpenter ant activity
- Finally, locating the likely site of an infesting colony and its foraging runways and applying registered, EPA-approved insecticide formulations at that site after reading and carefully following the product label directions. Assuming the preceding is beyond the resources of the householder, as it often is, the control effort should be entrusted to a state-licensed, certified pest control operator.

Termites

Termites are small, reclusive, true wood-eaters belonging to insect order Isoptera. They lack the "wasp waist" of ants, from which they are further distinguished by their straight, bead-like rather than elbowed antennae and their usually colorless, dirty white appearance. Termites convert dead and decaying wood and plant derivatives into useful humus in nature, reducing and recycling the debris. Moreover, they serve as a much sought-after, wild food delicacy in some countries. They are of greatest concern, however, because of the extensive damage they cause to crops, trees, and buildings. They are a far more serious problem than are either carpenter ants or powderpost beetles (Fig. 65).



Wood-Attacking Insects, Figure 65 Wood-feeding insects: (a) a termite queen before having shed her wings, (b) a tropical termite queen visibly swollen with eggs, her abdominal tergites appearing as dark, segmentally repeated suffusions, (c) the above-ground termitaria or nests of three different species of tropical termite, with the far-right tree nest showing a pencil-like, Y-shaped tunnel leading to the ground (a is modified and redrawn from Elzinga, b is modified and redrawn from Skaife, c is modified and redrawn from Snodgrass).

Termites occur worldwide. About 2,200 species are known, mostly from tropical or subtropical regions, where some construct massive nests called termitaria, some up to 6 m high, composed of earth, saliva, and fecal materials. There are about 45 species in the United States, primarily in warmer regions. They are not nearly as well established in the colder, boreal parts of the country, but the advent of centrally heated buildings has provided an opportunity for them to occupy some of those areas too. Most of our local species either live in galleries within moist decaying logs or build nests in the ground.

Subterranean termites including *Reticulitermes* spp., damp wood termites including *Zootermopsis* spp., dry wood termites such as *Incisitermes* spp. and *Cryptotermes* spp., and the desert dry wood termite, *Marginitermes hubbardi* (Banks), are among the 30 native species known for their damage to plants and buildings. Notable for their destructiveness are *Reticulitermes flavipes* (Kollar) of the eastern, midwestern, and southern states, *Reticulitermes hesperus* Banks of the western states, and the Formosan subterranean termite, *Coptotermes formosanus* Shiraki, that has spread from the Orient into Honolulu and from there into many southern states.

Termites have three distinct castes: reproductives, workers, and soldiers. The juveniles or nymphs have the potential of developing, as needed, into functional reproductives, workers, or soldiers. Caste determination is determined not at the time of hatching, but is mediated through a pheromone exchange dependent on the specific requirements of the colony at a given time. This trophallaxis or mutual grooming, like that of ants, is the means by which wood particles and pheromonal secretions are spread throughout the colony, and the process is ultimately responsible for the colony's social organization. The fully winged original founders of the colony, the king and queen, are the primary reproductives. However, short-winged or wingless supplementary reproductives may be produced if the king or queen dies or if groups of termites become isolated from the parental colony. These supplementary reproductives may then take over colony formation.

A mature colony of termites produces large numbers of winged kings and queens, called swarmers or alates, in spring with the onset of rain showers, usually in May–June but in heated buildings as early as March–April. Incidentally, this timing coincides with that of the winged carpenter ants in and around homes. The alate termites fly about weakly before landing and shedding their wings. The female emits a pheromone which attracts the male, and they pair. Together they excavate a chamber within the soil beneath a rotting log or wood, and they remain underground in this "nuptial chamber" for life. The king mates with the queen, she lays eggs, and the royal pair then takes initial care of the hatched young, feeding them predigested nutrients. Later, when able to feed on wood, the nymphs and new workers assume all nest responsibilities except reproduction. The king and queen continue mating from time to time, and the queen's abdomen may become visibly distended with eggs. The delicate-bodied, colorless, wingless, blind, moisture- and darkness-requiring workers carry out all foraging, feeding, nest building, and other non-reproductive duties. They excavate passageways through the soil and reach structural wood directly if it is in contact with the soil, or they gain access to it indirectly through cracks in concrete slabs and foundations or by constructing earthen shelter tubes over concrete and masonry not in contact with soil. These tubes, which are reliable indicators of termite infestation, offer protection from desiccation and help the termites reach structural wood over foundations and other obstructions. They are constructed of a grayish, plaster-like sealant of saliva, excrement, soil particles, and bits of wood. They include: (i) narrow, branching, fragile exploratory tubes which are abandoned after contact with the above-surface wood or other cellulose material, (ii) lighter colored drop tubes suspended from floor joists or crawl spaces from wood to ground and composed exclusively of wood particles, and (iii) more substantially built working tubes used to facilitate the workers' movements from soil to wood.

Though termites eat wood, a dietetic feat that few other animals can perform, they lack the digestive enzymes required to break down and assimilate the nutrients of this cellulose-laden substance. How do they eat a food they cannot digest? The answer involves minute single-celled microorganisms housed within the termites' specialized alimentary canal that provide the required enzymes. The relationship between the two organisms is a mutualistic one in which the protozoans receive a dark, moist sheltering home and an abundance of masticated food both for their use and for that of the host termite that provides the food. Neither can live without the other. Newly hatched termites lack these intestinal protozoans and die if unable to become infected. Newly molted termites not only shed their skin but also cast the entire lining of the hind gut, including the protozoans lodged within. However, like the newly hatched termites, they quickly infect themselves through oral and anal food exchanges with their nest mates and become functional wood eaters themselves.

Termite foragers are delicate-bodied, colorless, wingless workers that require darkness and moisture. They construct pencil-like runways to bridge any masonry, sub floors, support piers, or metal supportive joists that they must traverse from their nest in the ground, where they find needed moisture, to the house above, whose wood they eat. These tunnels, like their above-ground galleries, are lined with a grayish, plaster-like sealant of saliva, excrement, and soil and so are reliable indicators of infestation except, of course, when concealed (as they sometimes are) within the foundation's hollow cinder blocks. Thus, one cannot rely upon discovery of a warning sawdust trail such as that left behind by carpenter ants or powderpost beetles. Damage may be far advanced, and the wood close to structural failure, before discovery of termite infestation.

Termite soldiers are characterized by an enlarged yellowish-brown, hard head with powerful jaws. The function of this wingless, blind caste is to defend the colony from enemies, particularly ants. Termite soldiers, kings, queens, and young nymphs are unable to feed themselves, so they must be fed, mouth-to-mouth, by other nymphs and workers.

Mark-release-recapture methods indicate that often it is not a single colony that is active in a given area, as previously thought, but sometimes several decentralized entities interconnected by a network of underground tunnels with different nesting and foraging sites. The foraging populations of six *Reticulitermes flavipes* entities have been estimated as ranging from 200,000 to 5 million termites. Once foragers initially locate food, they secrete a pheromone resulting in an increase both in numbers of individuals and in increased activity. The foraging territory may encompass up to one-third acre, and the foraging distance may exceed 70 m.

How can one determine whether an infestation is a carpenter ant or a termite one? Termite tunnels are obvious indicators of infestation. In absence of them, however, large numbers of accumulated, similar-sized, delicately veined wings in and around lighted places are indicative of termites. If, on the other hand, one finds dead ants with attached, strongly veined, dissimilar-sized wings, this is indicative of carpenter ant infestation.

Termites have been called hidden invaders because they can eat away the wood of a door or window without leaving the slightest hint of their presence. They leave a thin papery covering of wood over such wooden elements as they infest, which consequently may crumble under slight pressure. Usually 3–8 years of untreated termite infestation is sufficient to cause extensive damage to a house. The annual cost of termite treatment in the United States is estimated at about two billion dollars.

Periodical inspection is indicated if one is to avoid the consequences of extensive termite infestation. This inspection should include general areas such as entrance doors and frames, walls, ceilings, sagging or buckling floors, slightly raised wallpaper, baseboards, closets, areas around showers, tubs, and window frames. In basements, foundation walls, sill plates, window sills, wooden stairwell bases, and plumbing should be inspected, along with floor joists and plumbing running through the floor; in attics, areas around chimneys, vent pipes, and roof rafters should be examined; and at the exterior of the house, firewood, form boards, or wood debris stacked against the house, planters, railroad ties, landscape timbers, fence posts, trellises, crawl space access doors, and windows and openings near pipes should be inspected. One should also tap the wood elements of the house with the handle of a screwdriver. A hollow sound indicates a hidden problem. HUD's "Minimum Property Standards and Building Codes" approves use only of pressure-treated, dry (moisture content less than 20%) lumber for construction. The above procedures and standards notwithstanding, no wood is ever entirely safe from the ravages of termites. These insidious creatures gain entry into buildings whenever they find favorable conditions.

Remedial methods for termites involve correction of moisture problems as soon as detected and scrupulously avoiding the soil-wood contact of which termites avail themselves to enter a building. Specifically:

- Grading the building lot so as to drain water away from the foundation
- Maintaining the gutters, keeping them free of leaks, clear of debris, and with the down spouts discharging away from the foundation
- Embedding deck, fence, and other posts in cement
- Assuring proper attic ventilation
- Covering three-quarters of the crawl space by polyethylene sheet (leaving one-fourth open) and providing proper crawl space ventilation
- Applying immediate control treatment if termites are seen indoors or immediately outside the building
- Establishing an effective termite barrier between buildings (including garages) and the surrounding lot. This step may involve employment of termite-certified, licensed pest control operators who apply registered, EPA-approved termiticides per the label directions.

Real estate agencies in some states are required by law to have buildings inspected by licensed pest control operators for the incidence of termites and other wood-destroying organisms. A formal report of corrective measures, if indicated, is required before finalization of the real estate transaction. In some states, builders are required by law to treat lots against termite infestation before undertaking construction, and they must provide appropriate warranties to that effect.

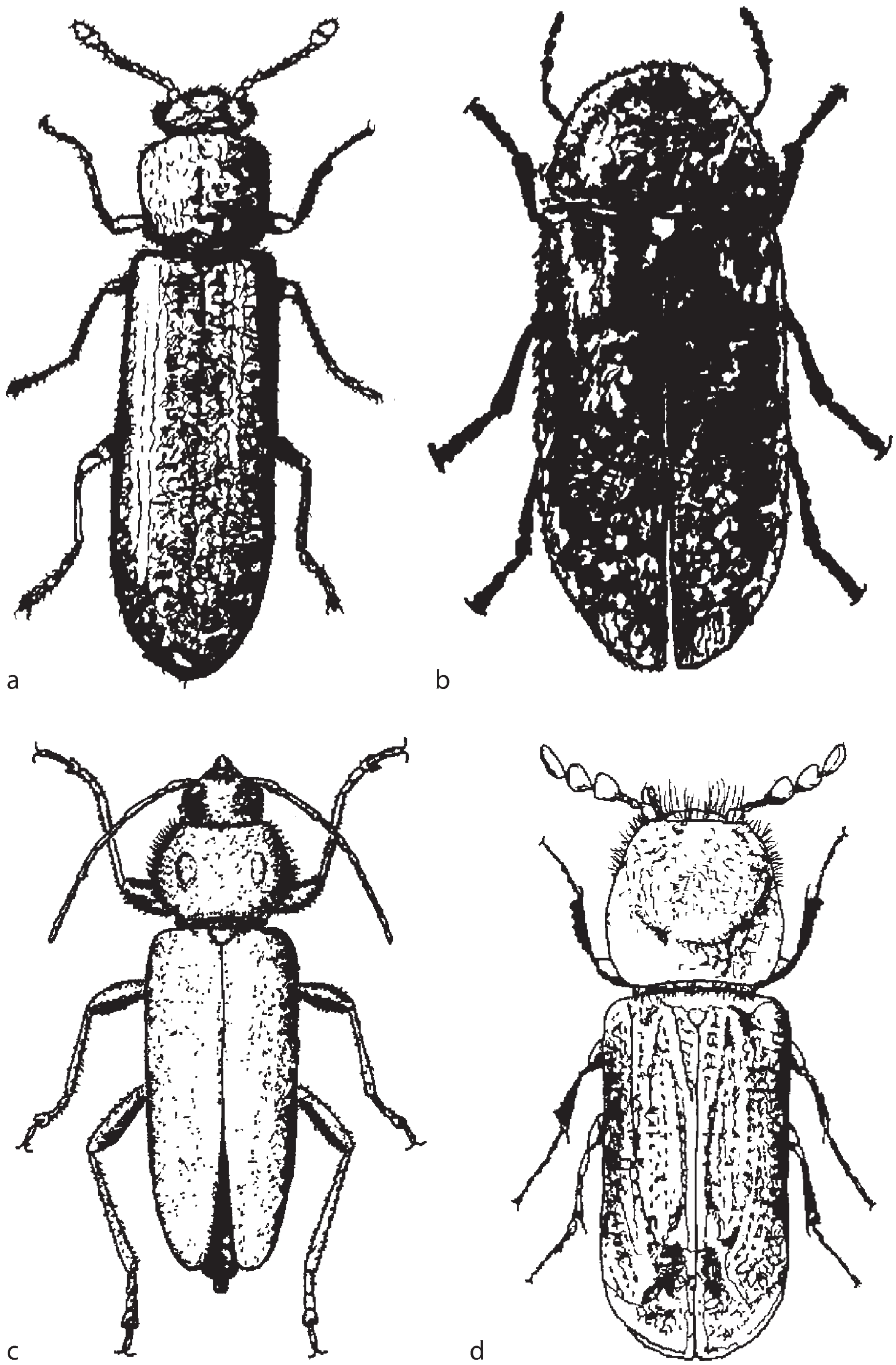
Powderpost Beetles

The related taxa of Coleoptera, the Anobiidae and Bostrichidae (some consider Lyctinae to be a separate family also), include species collectively termed powderpost beetles. All of them damage timber, reducing its inner tissues to powder and perforating it with "pinholes" or "shot holes," hence the common name. However, the nature of their frass (which is a mixture of sawdust and excrement) and the "shot holes" that they produce vary with the species. Powderpost beetles rank next to termites with respect to the overall damage done to buildings and to the dry seasoned timber that they infest and re-infest.

Ten of the 66 known species of Lyctinae, or "true powderpost beetles," occur in the United States, of which the *brown lyctus beetle Lyctus brunneus* Stephens and the European lyctus beetle *L. linearis Goeze* are ones of major concern. They infest seasoned hardwood with at least a 3% starch content. They attack the seasoned sapwood of such trees as ash, hickory, oak, elm, pecan, maple, poplar, cherry, sycamore, and walnut, as well as lumber, wood paneling, window and door frames, hardwood floors, furniture, tool handles, pallets, imported hardwood products, and even bamboo. They rarely infest lumber older than 5 years, and they never attack painted or varnished wood. They produce a powdery frass that, unlike that of the other powderpost beetles, is so fine as to resemble talcum powder. Development from egg to adult takes from 2–4 years, except in the south of the U. S. where two generations per year may occur. As the adult lyctines emerge from their holes they eject their powdery frass which often trickles out like raindrops. The adult is a small (usually under 5–6 mm long), flattened, reddish-brown or black beetle with a prominent head constricted behind the eyes. Each antenna has a long basal segment and a 2-segmented club (Fig. 66).

Bostrichids other than Lyctinae, or "false powderpost beetles," are of less consequence than powderpost beetles because the hardwoods that they infest are not commonly used for interior floors, woodwork, and trims, and they do not re-infest seasoned wood. Most false powderpost beetles are larger (some up to 52 mm long) than other powderpost beetles. They are usually black, elongate, and subcylindrical, with the head usually deflexed and covered by the hood-like thorax. Each antenna has a 3–4 segmented club. Their frass is coarse, meal-like, and tightly packed. Among important bostrichids are the black polycaon, *Polycaon stouti* (LeConte), cylindrical beetles up to 25 mm long whose prominent head, unlike that of the other bostrichids, is visible from above, not being concealed beneath the thorax, and the lead cable borer, *Scobicia declivis* LeConte, a reddish-brown beetle, 5–6 mm long, that normally bores in oak, maple, and other trees but may bore through the lead covering of aerial telephone cables.

There are nearly 260 species of anobiids in the United States, of which the furniture beetle, *Anobium punctatum* (DeGeer), and the deathwatch beetles *Xestobium rufovillosum* (De Geer), *Hemicoelus* spp., and the commonly encountered *Euvrilletta peltata* (Harris) are the most important. The furniture beetle is a reddish-brown cylindrical beetle 4–6 mm long. It lays its eggs either on the wood surface or inside emergence holes in finished wood. The eggs hatch in 6–10 days, and the larvae tunnel into wood. The larval stage typically lasts 2–5 years in processed wood, but in nature in dead tree branches the



Wood-Attacking Insects, Figure 66 **Wood-feeding insects: (a) a lyctine powderpost beetle, (b) an anobiid powderpost beetle, specifically the death-watch beetle *Xestobium rufovillosum* (De Geer), (c) the old house borer *Hylotrupes bajulus* (L.), (d) a bostrichid powderpost beetle, specifically the lead-cable borer *Scobicia declivis* Le Conte (a is modified and redrawn from USDA, b is modified and redrawn from Ohio Biological Survey, c is modified and redrawn from Bennett, Owens, & Corrigan, d is modified and redrawn from Mallis).**

life cycle is sometimes completed within a single year, probably because fungal and/or bacterial attack on the tree branch may make more nutrients available. The deathwatch beetle *Xestobium rufovillosum* is an insect that derives its name from its habit of tapping the head or jaws against wood. This ticking sound, actually a mating signal, becomes audible during periods of prolonged quiet, as during a wake or in the night, hence the common name. The emerging adults are slender, 6 mm long, dark beetles with lengthened, but not clubbed, antennae. They attack building timbers in poorly ventilated areas often previously damaged by moisture or fungi. *Euvrilletta peltata* is a reddish or brownish powderpost beetle covered by yellow hairs. It attacks both seasoned and unseasoned wood and is a serious pest of crawl space timbers in southeastern U.S.

Old House Borer

Over 1,200 species of the long-horned beetle family Cerambycidae are known from the United States, yet of that total only the old house borer, *Hylotrupes bajulus* (L.), of the Atlantic seaboard states causes significant damage to structural wood. Other long-horned species occasionally found in structural lumber emerge from the timbers and infest outside trees, but the old house borer attacks both seasoned and unseasoned lumber and re-infests previously attacked wood. This unfortunate habit may be responsible for its "old house" appellation, though it infests new homes too, particularly when infested lumber is used in construction. Its creamy white, peg-shaped larvae hollow out extensive galleries in the seasoned softwoods of the sills, floor joists, studs, door jams, flooring, siding, and rafters of old buildings. It attacks conifers, pines, spruce, fir, and hemlock but not hardwoods. The adult is a slightly flattened, dark, gray-black to brown-black beetle up to 25 mm long with yellowish gray hair on its body. Two raised, black glossy knobs on the prothorax help to distinguish it.

- Remedial measures suitable both for wood-damaging powderpost beetles and for the old house borer include:
- Selecting quality, kiln-dried, pressure-treated wood for construction
- Making periodic inspections for infestation
- Applying varnishes or paints to lumber

Notwithstanding these precautions, these insects may gain entry into the household and then usually can be eradicated only by fumigation carried out by trained professional help.

Other Wood-Damaging Insects

Some other wood-destroying insects, though economically insignificant compared to carpenter ants, termites, powderpost beetles, and the old house borer, deserve mention. Among the wood-damaging Coleoptera of minor importance are the golden buprestid, *Buprestis aurulenta* L., which attacks fire, lightning, or disease-damaged wood in the western states; the wharf borer, *Nacerdes melanura* (L.), whose larvae bore into the heartwood and sapwood of the seasoned softwoods used in fresh-water and marine wharf pilings; the parthenogenetic and paedogenetic telephone pole beetle, *Micromalthus debilis* LeConte, whose larvae attack oak and chestnut logs, wooden panels, as well as telephone poles; the curculionid *Hexarthrum ulkei* (Horn) whose larvae occasionally infest wooden buildings in eastern U.S., excavating small, irregular tunnels filled with a fine frass composed of distinct ovoid fragments; the spider beetle *Sphaericus gibboides* Boieldieu, which damages stored animal and vegetable products and tunnels in the wood of kitchen cabinets made of Douglas fir to pupate; the ambrosia beetle *Gnathotrichus sulcatus* (Le Conte) that bores complex tunnels into freshly cut wood and feeds on a fungus growing on the tunnel walls; and the wide-headed beetle *Platypus wilsoni* Swaine that infests fire, lightning, and disease-damaged hardwood and coniferous trees. Among the wood-damaging Hymenoptera of minor concern are the large carpenter bee *Xylocopa v. virginica* (L.), known for its characteristic round entry holes of about one-half inch in diameter in doors, porches, window sills, wooden beams, and fences from which pour a fine stream of sawdust; the horntail *Tremex columba* (L.), sometimes accidentally transported in firewood and poor grades of lumber used for construction; and the leaf-cutting bee *Megachile relativa* Cresson, which does not directly damage the sidings of homes but attracts woodpeckers that, in the act of predation on the bees, themselves cause serious destruction.

► Termites
► Ants
► Powderpost Beetles

References

Christensen C (1983) Technician's handbook to the identification and control of insect pests. Franzak & Foster Co., Cleveland, Ohio, 208 pp

Garry BW, Owens JM, Corrigan RM (1982) Pest control operations, 4th edn. Purdue University/Edgell Communications Project, Randolph, New Jersey, 495 pp

Hickin NE, Edwards R (1975) The insect factor in wood decay. St. Martin's Press, New York, New York, 383 pp

Mallis A (1997) Handbook of pest control – the behavior, life history, and control of household pests. Mallis Handbook & Technical Training Co., Cleveland, Ohio, 1456 pp

Moore HB (1979) An introduction to wood-destroying insects (their identification, biology, prevention, and control). Book redistributed by Pest Control Magazine, Cleveland, Ohio, 133 pp

Wood Gnats

Members of the family Anisopodidae (order Diptera).

► Flies

Wood Nymphs

Some members of the family Nymphalidae, subfamily Satyrinae (order Lepidoptera).

► Bush-Footed Butterflies
► Butterflies and Moths

Wood Rot

Insects are sometimes implicated in wood rot.

► Transmission of Plant Diseases by Insects

Woody Vegetation

Plants with rigid, woody, stems that do not die back annually. (contrast with herbaceous vegetation).

Wood Wasps

Members of the family Xiphydriidae (order Hymenoptera: suborder Symphyta).

► Wasps, Ants, Bees and Sawflies

Wood-Stain Diseases

Some insects, particularly bark beetles, transmit wood-stain fungi to trees.

► Transmission of Plant Diseases by Insects

Woolly Aphids

Members of the family Eriosomatidae (order Hemiptera).

► Aphids
► Bugs

Woolly Whitefly

► Citrus Pests and Their Management
► Whiteflies

Worker

A member of the nonreproductive caste in social insects that contributes to the welfare of the colony through nest building, foraging for food, and brood and queen maintenance. Workers often are armed with stings.

► Ants
► Bees
► Wasps, Ants, Bees and Sawflies

Worm Lions

Members of the family Vermileonidae (order Diptera).

► Flies

Wrinkled Bark Beetles

Members of the family Rhysodidae (order Coleoptera).

► Beetles

X

X-Chromosome

A sex chromosome that usually is present in two copies in females (XX) and in one copy (unpaired) in males (XO or XY).

Xenasteiidae

A family of flies (order Diptera).

► Flies

Xenic Culture

Culture of insects when an unknown number of species (usually of microorganisms) are present.

Xerophytic

Living in dry places.

Xiphocentonidae

A family of caddisflies (order Trichoptera).

► Caddisflies

Xiphydriidae

A family of wasps (order Hymenoptera, suborder Symphyta). They commonly are known as wood wasps.

► Wasps, Ants, Bees and Sawflies

Xyelidae

A family of sawflies (order Hymenoptera, suborder Symphyta).

► Wasps, Ants, Bees and Sawflies

Xylomyid Flies

Members of the family Xylomyidae (order Diptera).

► Flies

Xylomyidae

A family of flies (order Diptera). They commonly are known as xylomyid flies.

► Flies

Xylophagid Flies

Members of the family Xylophagidae (order Diptera).

► Flies

Xylophagidae

A family of flies (order Diptera). They commonly are known as xylophagid flies.

► Flies

Xylophagous

Feeding on or in woody plant tissue.

Xyphiopsyllidae

A family of fleas (order Siphonaptera).

► Fleas

Y

Y-Chromosome

A sex chromosome that is characteristic of males in species in which the male typically has two dissimilar sex chromosomes (XY).

Yellow Dog Tick, *Haemaphysalis leachi* (Audouin) (Acari: Ixodidae)

This is a common pest of dogs in Africa and Asia.
► Ticks

Yellow-Faced Bees

Members of the family Colletidae (order Hymenoptera, superfamily Apoidae).
► Bees
► Wasps, Ants, Bees, and Sawflies

Yellow Fever

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The mosquito borne yellow fever virus causes severe disease in humans. Yellow fever was first described as a disease in the early part of the seventeenth century. The disease was one of the most devastating and important diseases in Africa and the Americas during the next 300 years. There were yellow fever outbreaks in many port cities in the Americas that involved thousands of human cases. The specter of yellow fever was much feared throughout Africa and the Americas due to the havoc caused by the disease and the accompanying economic disruption. The last major yellow fever epidemic in the United States occurred in New Orleans in 1905. There were about 4,000 human cases of yellow fever and nearly 500 people died from yellow fever during this epidemic.

The history of yellow fever epidemics provides numerous examples why this disease inspired dread and fear in Africa, the U.S., Central America, the Caribbean and South America. Examples of the numbers of deaths during outbreaks are startling: 6,000 dead in Barbados in 1647; 3,500 deaths in Philadelphia; 1,500 in New York City in 1798; 29,000 deaths in Haiti in 1802; 20,000 deaths in over 100 American towns in 1878. Yellow fever has re-emerged with an upsurge of human cases in the latter half of the twentieth century. There were 100,000 cases and 30,000 deaths in Ethiopia in 1960–1962; 17,500 cases with 1,700 deaths in Upper Volta in 1983; Cameroon 20,000 cases with 1,000 deaths in 1990. The World Health Organization officially reported 18,735 yellow fever cases with 4,522 deaths for the period 1987–1991.

Insect Vectors

Several different mosquito species can be involved with the transmission of yellow fever depending on the geographic region and habitat. The most important mosquito species involved worldwide in the transmission of yellow fever to humans is *Aedes aegypti*, also known as "the yellow fever mosquito." The association between yellow fever transmission to humans by *Aedes aegypti* was a major breakthrough in understanding this dread disease. Major Walter Reed, U.S. Army, was the leader of the scientists who were able to show the role of *Aedes aegypti* in their work while stationed in Cuba in 1901. The subspecies *Aedes aegypti aegypti* is widely distributed throughout the tropics and subtropics of the world. This form is able to breed in a variety of artificial containers, i.e., flower pots, tires, water jars, many commonly found around human habitats. *Aedes aegypti aegypti* also has a distinct preference for humans as a source of blood that makes this species particularly efficient in circulating a pathogen from infected humans to uninfected humans. As a result, this highly urbanized mosquito species has the capability of sustaining the urban epidemics of yellow fever that have occurred during the last 300 years. The control of *Aedes aegypti aegypti* populations is considered of primary importance in reducing the risk of urban areas to yellow fever.

There are other mosquitoes that can be involved in yellow fever virus transmission. In tropical regions of the Western Hemisphere, mosquitoes in the genus Hemagogus transmit yellow fever virus to monkeys in the forest canopy. This is called the jungle yellow fever cycle in the Americas. The danger occurs when these canopy mosquitoes infect humans when trees are felled for clearing, and the infected human returns to an urban environment where *Aedes aegypti aegypti* can become infected, resulting in an urban epidemic. In tropical Africa, the mosquito *Aedes africanus* transmits yellow fever virus between forest dwelling canopy monkeys; *Aedes bromeliae*, *Aedes vittatus* and *Aedes furcifer-taylori* transmit the virus to monkeys in the savanna and gallery forest regions of Central Africa. The epidemic danger to humans is when infected humans bring the virus to urban centers inhabited by *Aedes aegypti*.

The Virus

Yellow fever virus is a member of the group of viruses called Flavivirus. The virus has been found in the tropical regions of the Americas and Africa, and there have been historical yellow fever incursions for brief outbreaks in parts of Europe. The yellow fever virus has never been demonstrated in Asia, Australia or the Pacific despite the presence of *Aedes aegypti* in these regions. The reason for this is unknown and the subject of much speculation. Although Walter Reed showed *Aedes aegypti* transmits the agent of yellow fever in 1901, and that the agent was smaller than bacteria, it was not until 1927 that yellow fever was shown to be a virus.

The Disease

Yellow fever symptoms may range from clinically inapparent to fatal. Studies have shown that in some regions of Latin America as much as 90% of the population have been infected with yellow fever virus and have no clinical symptoms of disease. Once an infected mosquito bites a human, the incubation period is generally 3–6 days. Mild cases appear similar to many other common illnesses that produce a fever. However, when clinical disease occurs, the onset of the disease is very sudden. There is high fever (102°–104°F), headache, malaise, back pain, chills, prostration, nausea, slow pulse and vomiting. Yellow fever virus can be found in the blood of the patient for about 4 days after infection, and as a result the patient is capable of infecting mosquitoes during this time. Some individuals show a rapid recovery at this point and the symptoms stop. This phase can last from 3 to 4 days. More severe cases also have their symptoms subside for a brief remission but symptoms return in a day or so with fever, vomiting, abdominal pain, prostration, dehydration, jaundice due to liver involvement, internal bleeding, bleeding of the nose, mouth, gums or in their urine, kidney or liver failure. The internal bleeding results in blood in the vomit, called "black vomit" due to the color, and dark stools. No virus is in the blood at this point so the patient is not infectious to mosquitoes. There is no cure; treatment is supportive to try to reduce the severity of these symptoms. This is the diphasic part of yellow fever. Twenty to fifty percent of people who enter the second phase die from yellow fever. Death usually occurs between the 7th and 10th day of the illness. Some very severe atypical cases of yellow fever may die as early as 3 days after the onset of symptoms. Mortality from yellow fever is about 10% of clinical cases but has reached as high as 50% of those people developing symptoms.

Dr. Max Theiler developed a vaccine against yellow fever, called the 17D vaccine, in the 1930s. In 1951, Dr. Theiler received a Nobel Prize for his work. This vaccine is still widely used and provides excellent protection against yellow fever for 10 years post-vaccination. There are studies showing that protection may be as long lived as 30–35 years after being vaccinated in some people.

Monkeys also can be infected with yellow fever virus. In most tropical regions of the world monkeys serve as the wild host, maintaining the virus in the absence of human involvement. Many monkey species experience yellow fever disease and suffer deaths. One of the early signs of yellow fever in a region may be the discovery of dead monkeys.

Impact and Problems

Yellow fever remains a serious and dread disease in many parts of the world despite advances in understanding mosquito transmission, advances in mosquito control, advances in understanding human risk and the development of a very effective and safe vaccine. The continued appearance of yellow fever epidemics in Africa, and the appearance of yellow fever cases in the Americas are all cause for concern that this dread disease remains very dangerous. In addition, the historical absence of yellow fever in Asia despite the presence of *Aedes aegypti* is also cause for concern since Asian populations would be extremely susceptible due to lack of any native immunity to the yellow fever virus. Asian populations may be extremely vulnerable to yellow fever with potentially catastrophic consequences.

The ability to interrupt a yellow fever outbreak will depend on being able to bring to bear a diverse array of tools including an efficient and effective mosquito control program and a massive vaccination program. Both are extremely difficult to accomplish in many regions of the world where the risk of a yellow fever outbreak may be greatest. Successful mosquito control against *Aedes aegypti* has reduced the number of yellow fever cases in many cities. However, mosquito control resources may be non-existent and delivery of vaccine insufficient. In the 1990s, the worldwide annual production of yellow fever vaccine was about 15 million doses with demands on vaccine extremely unpredictable. A vaccination program that is geared to regions in advance of an expected epidemic is cost effective, but it is unlikely to be successful because of the time delay in identifying the epidemic and because it takes 5–7 days for the vaccine to provide any protection after inoculation. On the other hand, a campaign to vaccinate the entire population in the absence of yellow fever would be extremely costly and require a long-term commitment to vaccinate anyone entering the population through birth or immigration. The challenges of yellow fever remain formidable.

► Mosquitoes
► History and Insects

References

Monath TP (1989) Yellow fever. In: Monath TP (ed), The arboviruses: epidemiology and ecology. CRC Press, Boca Raton, FL, pp 139–231

Strode GK (ed) (1951) Yellow fever. McGraw-Hill, New York, NY, 710 pp

Tabachnick WJ (1991) Evolutionary genetics and insect borne disease. The yellow fever mosquito, *Aedes aegypti*. Am Entomol 37:14–24

Yellow Flies

Some members of the family Tabanidae (order Diptera).

► Flies

► Horse Flies and Deer Flies (Diptera: Tabanidae)

Yellow Jackets

Members of the family Vespidae (order Hymenoptera).

► Wasps, Ants, Bees, and Sawflies

Yellow Mealworms

► Stored Grain and Flour Insects

Yellows

Some members of the family Pieridae (order Lepidoptera).

► Yellow-White Butterflies

► Butterflies and Moths

Yellowstriped Armyworm, *Spodoptera ornithogalli* (Guenée) (Lepidoptera: Noctuidae)

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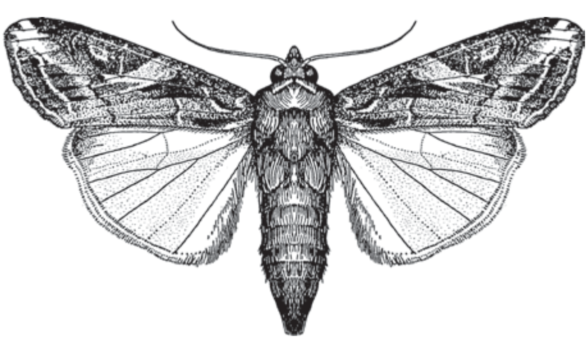
The distribution of this insect includes most of North America, Central and South America, and many Caribbean islands. As a pest, however, its occurrence is limited principally to the southeastern USA. A very similar species called western yellowstriped armyworm, *Spodoptera praefica* (Grote), largely replaces *S. ornithogalli* in the western USA.

Life History

Generally there are three or four generations annually, with broods of adults present in March-May, May-June, July-August, and August-November. Some of the latter brood overwinter as pupae rather than emerging as adults. Although eggs, larvae and adults of yellowstriped armyworm may be present in autumn or early winter, they cannot withstand cold weather, and perish. Development time, from egg to adult, is about 40 days.

The eggs are greenish to pinkish brown in color and bear 45–58 small ridges. In shape, the egg is a slightly flattened sphere, measuring 0.46–0.52 mm in diameter and 0.38–0.40 mm in height. Females typically deposit clusters of 200–500 eggs, usually on the underside of leaves. Total fecundity was determined to be over 3,000 eggs under laboratory conditions. The eggs are covered with scales from the body of the adults. Duration of the egg stage is 3–5 days at warm temperatures (Fig. 1).

Larvae initially are gregarious in behavior, but as they mature they disperse, sometimes spinning strands of silk upon which they are blown by the wind. There usually are 6 instars, although 7 instars have been reported. Head capsule widths are about 0.28, 0.45, 0.8–1.0, 1.4–1.6, 2.0–2.2, and 2.8–3.0 mm, respectively, for instars 1–6. The larva grows from about 2.0 to 35 mm in



Yellowstriped Armyworm, *Spodoptera ornithogalli* (Guenée) (Lepidoptera: Noctuidae), Figure 1 **Adult yellowstriped armyworm, *Spodoptera ornithogalli* (Guenée).**

length over the course of development. Duration of the larval stage is 14–20 days, with the first three instars requiring about 2 days each and the last three instars requiring about 3 days each. Coloration is variable, but mature larvae tend to bear a broad brownish band dorsally, with a faint white line at the center. More pronounced are black triangular markings along each side, with a distinct yellow or white line below. A dark line runs laterally through the area of the spiracles, and below this is a pink or orange band. Dark subdorsal spots are found on the mesothorax of yellowstriped armyworm, and the triangular shape of these spots aids in distinguishing this insect from sweetpotato armyworm, *Spodoptera dolichos*, and velvet armyworm, *S. latifascia*, in southeastern USA. The head is brown but has extensive blackish markings (Fig. 2).

Larvae pupate in the soil within a cell containing a thin lining of silk. The reddish brown pupa measures about 18 mm in length. Duration of the pupal stage is 9–22 days, normally averaging 12–18 days.

The moths measure 34–41 mm in wing span. The forewings are brownish gray with a complicated pattern of light and dark markings. Irregular whitish bands normally occur diagonally near the center of the wings, with additional white coloration distally near the margin. The hind wings of yellowstriped armyworm are opalescent white, with a narrow brown margin; the sexes are dimorphic. Under laboratory conditions average longevity of adults is 17 days, with most egg production completed by the tenth day.

These species are very general feeders, reportedly damaging many crops, including alfalfa, blackberry, cotton, clover, grape, lentil, peach, rape, raspberry, sorghum, soybean, sugarbeet, sweetclover, sunflower, tobacco, wheat, and several vegetable and flower crops. Some of the weed species known to be suitable hosts are castorbean, *Ricinus communis*; dock, *Rumex* sp.; gumweed, *Grindelia* sp.; horse nettle, *Solanum carolinense*; horseweed, *Erigeron canadensis*; jimsonweed, *Datura* sp.; lambsquarters, *Chenopodium album*;

Yellowstriped Armyworm, *Spodoptera ornithogalli* (Guenée) (Lepidoptera: Noctuidae), Figure 2
Mature larva of yellowstriped armyworm, *Spodoptera ornithogalli* (Guenée).

morningglory, *Ipomoea* sp.; plantain, *Plantago lanceolata*; prickly lettuce, *Lactuca scariola*; and redroot pigweed, *Amaranthus retroflexus*.

Several wasp parasitoids affect *S. ornithogalli* including *Rogas laphygmae* Viereck, *R. terminalis* (Cresson), *Zele mellea* (Cresson), *Chelonus insularis* Cresson and *Apanteles griffini* Viereck (all Hymenoptera: Braconidae). Also, *Euplectrus plathypenae* Howard (Hymenoptera: Eulophidae) attacks larvae and causes a cessation of feeding within 2 days. Thus, this parasitoid is particularly valuable at minimizing damage. Numerous flies have been found to parasitize these armyworms including *Archytas* spp., *Choeteprosopa hedemanni* Brauer and Bergenstamm, *Euphorocera omissa* (Reinhard), *E. tachinomoides* Townsend, *Lespesia aletiae* (Riley), *L. archippivora* (Riley), *Omotoma fumiferanae* (Tothill), *Winthemia quadripustulata* (Fabricius), and *W. rufopicta* (Bigot) (all Diptera: Tachinidae). A nuclear polyhedrosis virus is highly pathogenic to larvae, and survivors that do not succumb exhibit reduced fecundity. Undoubtedly predators are important, but their effect has not been quantified.

Damage

Larvae damage plants principally by consumption of foliage. The small, gregarious larvae tend to skeletonize foliage but as the larvae grow and disperse they consume irregular patches of foliage or entire leaves. However, they will also feed on the fruits of tomato, cotton, and other plants. Larval consumption of soybean was estimated to total 115 sq cm; this is an intermediate value relative to some other lepidopterous defoliators.

Management

Insecticides are applied to foliage to prevent injury by larvae. The microbial insecticide *Bacillus thuringiensis* can be applied to kill armyworms, but should be applied when the larvae are young as they become difficult to control as they mature. Larvae will consume bran bait containing insecticide.

Proximity of crops to rangeland containing weed hosts, or to alfalfa, may be important factors predisposing other crops to injury. At high densities, especially if alfalfa hay is mowed, larvae will sometime disperse simultaneously and invade nearby fields. Physical barriers such as trenches can be used to deter such dispersal.

References

Adler PH, Willey MB, Bowen MR (1991) Temporal oviposition patterns of *Heliothis zea* and *Spodoptera ornithogalli*. Entomologia Experimentalis et Applicata 58:159–164

Capinera JL (2001) Handbook of vegetable pests. Academic Press, San Diego, 729 pp

Crumb SE (1929) Tobacco cutworms. USDA Tech Bull 88, 179 pp

Crumb SE (1956) The larvae of the Phalaenidae. USDA Tech Bull 1135, 356 pp

Yellow-White Butterflies (Lepidoptera: Pieridae)

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Yellow-white butterflies, family Pieridae (including jezebels, orangetips, sulphurs, whites, and alfalfa and cabbage butterflies), total about 1,275 species worldwide, most being Indo-Australian (ca. 515 sp.). Four subfamilies are recognized: Pseudopontiinae (a single African species), Dismorphiinae, Pierinae, and Coliadinae. The family is in the superfamily Papilionoidea (series Papilioniformes), in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults small to large (23–100 mm wingspan); antennae often with weak clubs. Wings mostly triangular or rounded; hindwings usually small and rounded, but sometimes larger than forewings and somewhat pointed (Dismorphiinae); body usually slender but sometimes robust. Maculation usually variously yellow or white, with darker spots or patches of various shape (rarely without markings); rarely hyaline; sometimes very colorful, and many with special UV coloration ve different from what is evident under white light. Pierinae are mostly white species and Coliadinae have more of the colorful and yellow species; many pierid colorations are from pterin or flavone deposits. Adults diurnal. Larvae leaf feeding (one species feeds gregariously in Mexico). Various plants are utilized, including Capparidaceae, Leguminosae, Loranthaceae, and Santalaceae, among others, but

Yellow-White Butterflies (Lepidoptera: Pieridae), Figure 3 **Example of yellow-white butterflies (Pieridae), Anthocharis sara Lucas from California, USA.**

especially Cruciferae. Some economic species are known, particularly on cabbages and other crucifers (Fig. 3).

References

Courtney SP (1986) The ecology of pierid butterflies: dynamics and interactions. Adv Ecol Res 15:51–131

Eitschberger U (1984) Systematische Untersuchungen am *Pieris napi-bryoniae*-Komplex (s.l.) (Lepidoptera, Pieridae). In: *Herbipoliana. Marktleuthen*. 2 volumes (1104 pp., 101 pl.)

Feltwell J (1982) Large white butterfly. The biology, biochemistry and physiology of *Pieris brassicae* (Linnaeus). W Junk, The Hague. 538 pp (In Series Entomologica, 18)

Krzywicki M (1962) Pieridae. In: Klucze do Oznaczania Owadów Polski. 27. Motyle – Lepidoptera, 65: 1–45, 1 pl. [part]. Polskie Towardzystwo Entomologiczne [in Polish], Warsaw

Pleisch E, Sonderegger P (eds) (1987) Pieridae – Weisslinge. In: Schmetterl inge und ihre Lebensräume: Arten – Gefährdung – Schutz. Schweiz und angrenzenden Gebiete, 1: 136–162, pl. 2–4. Pro Natura-Schweizerische Bund fuer Naturschutz, Basel

Seitz A (ed) (1906–31) Familie: Pieridae. In: Die Gross-Schmetterlinge der Erde, 1: 39–74, pl. 17–27 (1906–07); 1(suppl.): 93–125, 332–335, pl. 7 (1930–31); 5:53–111, 1014–1026, pl. 18–30 (1908–24); 9: 119–190, pl. 50–73 (1909–10); 13:29–69, pl. 10–22 (1910). A Kernen, Stuttgart

Talbot G (1932–1935) Pieridae. In: Lepidopterorum Catalogus, 53, 60: 1–697. W Junk, Berlin

Yolk

The nutritive matter of the egg, from which the developing embryo derives sustenance.

► Embryogenesis
► Endocrine Regulation of Insect Reproduction
► Oogenesis

Yponomeutidae

A family of moths (order Lepidoptera). They commonly are known as ermine moths.

► Ermine Moths
► Butterflies and Moths

Young, Jr., David A

David Young was born May 26, 1915, at Wilkinsburg, Pennsylvania, USA. He obtained a B.A. degree from the University of Louisville in 1939 and then taught science in the public school system from 1939 to 1941. In 1942 he was awarded a M.S. from Cornell University. Serving in the military during World War II, he returned to serve as an instructor at the University of Louisville from 1946 to 1948. He also studied at the University of Kansas, and was awarded a Ph.D. in 1950. Young then joined the United States National Museum and was employed by the Insect Identification and Foreign Parasite Introduction Section of USDA from 1950 to 1957. Young joined the faculty of North Carolina State University in 1957, where he retired in 1980 but continued his writing until 1986. Young was an internationally acclaimed leafhopper specialist. He described 807 new species, 207 new genera, and a new tribe. Among other publications, he authored the monumental "Taxonomic study of the Cicadellinae (Hemiptera: Cicadellidae)," which was published in three parts and treated 292 genera from throughout the world. He died on June 8, 1991.

Reference

Deitz LL (1991) David A. Young, Jr. Am Entomol 37:251

Yucca Moths (Lepidoptera: Prodoxidae)

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Yucca moths, family Prodoxidae, total 65 species, mostly western Nearctic, but now also including some genera (Lamproniinae) from other regions that previously were placed in Incurvariidae. The family is in the superfamily Incurvarioidea, in the section Incurvariina, of division Monotrysia, infraorder Heteroneura. There are two subfamilies: Prodoxinae and Lamproniinae. Adults small (5–33 mm wingspan), with rough head scaling; haustellum reduced, scaled; labial palpi porrect; maxillary palpi folded, five-segmented (rarely four-segmented). Maculation often is white with various darker markings, or more colorful and iridescent. Adults are diurnal. Larvae are seed, flower stalk, or stem borers; rarely gall makers. Host plants are various yucca plants (Agavaceae) for the well-known yucca pollinators of North America, while other species (Lamproniinae) are on hardwood trees and bushes.

References

Davis DR (1967) A revision of the moths of the subfamily Prodoxinae (Lepidoptera: Incurvariidae). Bull U S Natl Mus 255:1–170

Nielsen ES, Davis DR (1985) First Southern Hemisphere prodoxid and the phylogeny of the Incurvarioidea (Lepidoptera). Syst Entomol 10:307–322

Pellmyr O (1999) Systematic revision of the yucca moths in the *Tegeticula yuccasella* complex (Lepidoptera: Prodoxidae) north of Mexico. Syst Entomol 24:243–271

Powell JA, Mackie RA (1966) Biological interrelationships of moths and *Yucca whipplei* (Lepidoptera: Gelechiidae, Blastobasidae, Prodoxidae). Univ Calif Publ Entomol 42:1–59

Z

Zachvatkin (Jasykov), Aleksei Alekseevich

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A.A. Jasykov (Yazykov in the modern English transcription) was born on December 1, 1905, in Ekaterinburg. He spent his childhood with his parents in Montreux, Switzerland. His father came from an old noble family. According to the traditions of the Russian nobility, he received a home education with tutors in sciences and culture. Just before the beginning of World War I, the family returned to Moscow where his private home education was continued. His early interest in natural history brought him in 1920 to the State University of Moscow where he worked first in the university herbarium and then in the Zoological Museum of the university. There he specialized in entomology, particularly in the taxonomy of Cicadinae (Hemiptera: Cicadidae). After the October revolution of 1917, he could no longer officially enter the university because he was from a noble family. However, the university professors allowed him to attend some courses. His only formal education was at a painting studio in Moscow. From 1926 through 1931 he worked as a technical assistant in the Central Asian Institute of Plant Protection. Participating in numerous expeditions, he showed his great and numerous talents in research. He published several papers concerning the systematics of the Cicadinae and the parasites of the Acridinae (Orthoptera: Acrididae). He also discovered specific features of hypermetamorphosis in the Meloidae and Bombyliidae. Restoring his lost documents, he took the surname of his stepfather. The last work by Jasykov was published in 1931, and from 1932 all his papers were signed as Zachvatkin. For a short time he worked in the All-Union Institute of Plant Protection in Leningrad, and in 1933 he was invited to the Entomological Laboratory of the Research Institute of Zoology of the State University of Moscow. Soon he began to study the Tyroglyphidae (Acarina), an important group of stored products pests, and to develop measures for damage prevention. In 1935 he received a Ph.D. degree, and in 1939 a Doctor of Biological Sciences degree. In 1941 he was appointed a professor of the Department of Entomology of the university. In addition to his applied research, he conducted fundamental research in acarology. The discovery of primitive segmented mites (Endeostigmata) and the differences in tagmosis and in the development of the fourth legs of mites from various groups allowed him to distinguish three independent groups of Acarina: Acariformes, Parasitiformes and Opilioacarina. This concept was strongly supported by V.N. Beklemishev, the leading specialist in comparative anatomy and morphology of invertebrates. Being a noted authority in general embryology and in the embryology of arthropods, he developed a theory of the origin of multicellular organisms and of the evolution of ontogenesis in lower invertebrates. He also created a new concept of the origin of Holometabola and Hemimetabola.

Many of his ideas were later confirmed in the works of his followers. He was twice awarded the Stalin Prize. In 1948, when Soviet biology was suppressed by Lysenkoism, he was forced to accept the position of the Deputy Dean of the Faculty of Biology and Pedology of the university. He became very depressed by his constant battles with Lysenko's henchmen and he passed away in Moscow on December 14, 1950. His main publications include "Tyroglyphoid mites (Tyroglyphoidea)" (1941) and "Comparative embryology of lower invertebrates" (1949). Many manuscripts and lectures were included in his posthumous book "Collected scientific works" prepared by his pupils and friends and published in 1953.

Reference

Zachvatkin (Jasykov) YA (1995) Aleksei Alekseevitch Zachvatkin (Jasykov). Arthropoda Selecta 4:(1)93–97 (in Russian with English summary)

Zeller, Philipp Christoph

Philipp Zeller was born at Steinheim-on-the-Mur, Würtemberg, Germany, on April 8, 1808. He began collecting insects as a boy, and though he received a degree from the University of Berlin, he obtained no formal instruction in entomology. He began working at the gymnasium at Frankfort on the Oder in 1830, and devoted his leisure time to study of insects, especially the Lepidoptera, eventually becoming known as an authority on Microlepidoptera, including Pyralidae and Tineidae. He began publishing in 1833, and was named Professor by the King of Prussia in 1852. Among his important publications were "North American Micro-Lepidoptera" (1872, 1873, 1875) and "Natural history of the Tineina" (with H.T. Stainton) (1855). He named many of the economically important Microlepidoptera from around the world. Zeller died at Grunhof, Germany, on March 27, 1883.

References

Anonymous (1883) Obituary notices, Prof. P.C. Zeller. Can Entom 15:176–177

Essig EO (1931) A history of entomology. The Macmillan Company, New York, 1029 pp

Stainton HT (1883) Philipp Christoph Zeller. Entomol Monthly Mag 20:1–8

Zetterstedt, Johann Wilhelm

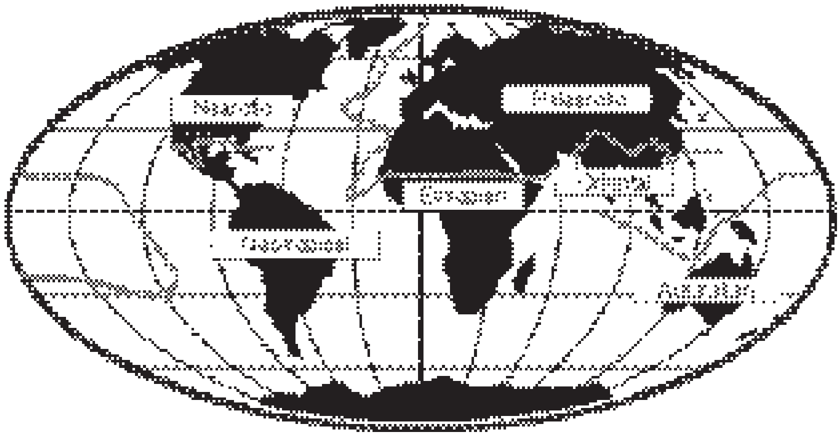
Johann Zetterstedt was born on May 20, 1785, near Mjölby, Sweden. Interested in biology from his youngest days, Zetterstedt entered Lund University in 1805, and received a doctoral degree in 1808. He was named docent in botany in 1812, but there was no salary attached to this position, so he supported himself with private lessons. In 1822, he was awarded a position at the University, and worked there until his retirement in 1853. In 1869 he received an honorary degree. Zetterstedt's list of publications is not very long, but includes some important works, including "Fauna insectorum Lapponica" (1828), "Insecta Lapponica descripta" (six issues between 1838 and 1840), and the monumental "Diptera Scandinaviae disposita et descripta" (14 volumes between 1842 and 1860). He died December 23, 1874, at Lund, Sweden.

Reference

Herman LH (2001) Zetterstedt, Johann Wilhelm. Bull Am Mus Nat His 265:157–158

Zoogeographic Realms

Dissimilar distributions of existing animals (normally illustrated by vertebrates), usually isolated geographically and defined by continents (Fig. 1), but sometimes separated by mountain ranges or other physiographic features. The principal realms are:



Zoogeographic Realms, Figure 1 **The traditional zoogeographic realms.**

Australian Realm

Australia and nearby islands, with a preponderance of marsupials, large flightless birds, and parrots, as well as an absence of mammals. This is sometimes called the Austalasian realm.

Oriental Realm

India and southeast Asia south through Indonesia, with tree shrews, orangutan, and gibbon.

Ethiopian Realm

Africa, though northernmost Africa is more similar to Europe (Palearctic realm), with antelopes, giraffes, elephants, rhinoceros, gorillas, dogs, and cats. This is sometimes called the African or Afrotropical realm.

Neotropical Realm

South and Central America including the Caribbean Islands, with sloths, armadillos, anteaters, tapirs, toucans, and hummingbirds.

Holarctic Realm

(Nearctic and Palearctic realms) – the Holarctic realm includes most of the northern hemisphere, but is often subdivided into the Nearctic realm (North America south to central Mexico) and the Palearctic realm (Europe and Asia except for southeast Asia). The faunas of the Nearctic and Palearctic are really quite similar, with such animals as vireos, wood warblers, deer, bison and wolves.

Some authors, however, subdivide the realms further, treating separately the African island of Madagascar (Malagasy realm) and the contact area of the Australian and Oriental realms, particularly the Indonesia-Papua New Guinea area (Indo-Australian realm). The zoogeographic realms are sometimes called the biogeographic realms but this is not particularly desirable because plant distribution does not entirely conform to the regions formed by animal distribution.

► Floristic Kingdoms

Zoogeography

The distribution of animal groups in space.

► Zoogeographical Realms

Zoonosis (pl. zoonoses)

Diseases of animals that may be transmitted to humans, often by arthropods.

Zoophagous

Feeding on animals or animal products.

Zopheridae

A family of beetles (order Coleoptera). They commonly are known as ironclad beetles.

► Beetles

Zoraptera

An order of insects. They commonly are known as angel insects or zorapterans.

► Angel Insects

Zorapterans

Members of the insect order Zoraptera.

► Angel Insects

Zorotypidae

A family of angel insects (order Zoraptera).

► Angel Insects

Zygaenidae

A family of moths (order Lepidoptera). They commonly are known as smoky moths and burnet moths.

► Burnet Moths

► Butterflies and Moths

Zygote

A fertilized egg formed as the result of the union of the male and female gametes.

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